

SAND DOLLARS OF THE GENUS *DENDRASTER* (ECHINOIDEA: CLYPEASTEROIDA): PHYLOGENETIC SYSTEMATICS, HETEROCHRONY, AND DISTRIBUTION OF EXTANT SPECIES

Rich Mooi

ABSTRACT

All of the previously described extant members of the genus *Dendraster* are reviewed in light of new information on their taxonomy, phylogeny, ontogeny, and distribution. Allometric and multivariate analyses, in conjunction with qualitative comparisons of test morphology and external appendages, indicate that there are three valid living taxa: *D. excentricus* (Eschscholtz, 1831), *D. vizcainoensis* Grant and Hertlein, 1938, and *D. terminalis* (Grant and Hertlein, 1938). A neotype is designated for *D. excentricus*, and locations of type material given for the other species. None of the *Dendraster* species described by Clark (1948) are valid: *D. rugosus* and *D. mexicanus* are junior synonyms of *D. vizcainoensis*, and *D. laevis* is actually the adult form of *D. terminalis*. Until now, the latter species was known only from juvenile material, but it is a *Dendraster* in which the gonopores appear earlier than in any other large scutelline. Plate patterns, food grooves, spination, and podial spicules are figured and described for each species. A dichotomous key is also provided. Known distributions are discussed in light of new data, particularly those concerning the occurrence of fossil *Dendraster* in the Gulf of California, where living species are unknown. Quaternary expansion of the genus is attributable almost entirely to the northward movement of a single species, *D. excentricus*. Preliminary phylogenetic analysis of the living taxa suggests that *D. excentricus* and *D. vizcainoensis* are sister taxa, and that *D. terminalis* is the sister to this clade. *D. terminalis* exhibits several features that can be interpreted as paedomorphic.

Sand dollar echinoids of the genus *Dendraster* are arguably among the most common macrobenthic invertebrates of the northeastern Pacific Ocean. The most frequently encountered member of the genus, *D. excentricus*, is known to occur from southern Alaska to southern Baja California in huge numbers almost everywhere there is a suitable shallow water, sandy bottom. *Dendraster* has become a favorite of studies on the life history (Merrill and Hobson, 1970; Niesen, 1977; Highsmith, 1982; Emllet, 1986), developmental biology (Burke, 1983, 1984; Highsmith and Emllet, 1986; Boidron-Metairon, 1988), distribution (Beadle, 1991; Nakamura, 1994; Smith, 1981), feeding (Timko, 1976; O'Neill, 1978), and morphology (Chia, 1969a; 1969b; 1973; Emllet, 1982; 1983; Beadle, 1989) of sand dollars in general. The genus has also been a major part of monographs on fossil sand dollars (Kew, 1920; Grant and Hertlein, 1938; Wagner, 1974) and has been included in numerous stratigraphic treatises, especially for California (see references cited in Beadle, 1991). In spite of this, with the exception of some analyses of intraspecific variation (Raup, 1956; Stanton et al., 1979), surprisingly few studies have focused on the systematics of the living species.

Eschscholtz (1831) described "*Scutella excentrica*" from material collected during Russian circum-global expeditions. Agassiz, in Agassiz and Desor (1847), recognized *S. excentrica* as a member of a distinct genus, making *D. excentricus* the type, and only species of *Dendraster*. Lambert (1899) erected the family Dendrasteridae into which Lambert and Thiéry (1909) eventually placed *Dendraster*, *Scutellaster*, and some of what

were subsequently recognized to be protoscutellids and scutellids (Durham, 1955). As Beadle (1991) noted, a wide variety of taxa have been associated with this family over the years, and its precise taxonomic limits have still to be determined. At the moment, only *Dendraster* and *Merriamaster*, a genus of fossils, are unequivocally considered to be members of the Dendrasteridae. It is not the purpose of this paper to revise this situation, but to concentrate on assessing the taxonomic status of the known living species.

As summarized in Grant and Hertlein (1938), many fossil taxa were subsequently ascribed to *Dendraster*. In that same paper, Grant and Hertlein named a subspecies of *D. excentricus*, *D. e. elongatus*, but did not otherwise add taxa to the single known living species. However, they did describe a fossil species from the "Quaternary" of Bahía Sebastián Vizcaíno, Baja California, which they called *D. vizcainoensis*. Since 1938, only a handful of papers have tried to elaborate on what was known of the taxonomy and relationships of living *Dendraster*. Clark (1948), working from vast amounts of material collected during the Allan Hancock Pacific expeditions, cast doubt on the validity of *D. e. elongatus*, but added three new species of living *Dendraster*: *D. laevis*, *D. mexicanus*, and *D. rugosus*. Although the figures and descriptions given by Clark (1948) were excellent, he did not provide very much information on external appendages, and some of his statements on the presence of ophicephalous and triphyllous pedicellariae appear to be incorrect (see Mortensen's footnote in Clark [1948:317], and discussion below).

Mortensen (1948) accepted Clark's (1948) three new species, but was apparently hampered by a lack of material for direct study: "Though not having seen any specimens I would think these species distinct; but Clark does not point out clearly how they differ from *D. excentricus*, and the key here given to the recent species of this genus is therefore not very satisfactory" (Mortensen, 1948:381). The present work is also intended to add descriptive data that should improve on Mortensen's key.

In his section on the species of *Echinocyamus*, Mortensen (1948:202) suggested that *Echinocyamus terminalis* Grant and Hertlein, 1938, known only from Isla de Guadalupe off México, was actually a young *Dendraster* of some unknown species. Grant and Hertlein (1938) described this echinoid from what they perceived to be adults, based on the fact that some of the types have gonopores, as shown in their illustrations. Durham (1955) reiterated Mortensen's (1948) conclusion that this tiny clypeasteroid was not some aberrant fibulariid with a marginal periproct (the inspiration for the name "*terminalis*"), but a *Dendraster*. It would appear that neither Mortensen nor Durham were willing to recognize *E. terminalis* as anything more than a juvenile *Dendraster* that could not be ascribed to any known species. However, it has been informally suggested (Beadle, 1991) that it comprises a possible additional species, *Dendraster terminalis*. The status of the name "*D. terminalis*" will be explored further in this paper by comparing Grant and Hertlein's (1938) types with material of other dendrasterids, as well as with descriptions of similarly tiny taxa such as *Fibularia*, *Echinocyamus*, and *Marginoproctus*.

Mironov (1991) monographed *Marginoproctus* Budin, 1980, a poorly known genus he placed in the Fibulariidae, and included *E. terminalis* in this genus without examining Grant and Hertlein's types. Mironov did not seem disturbed by the spectacular range extension that this represented for *Marginoproctus*, but did try to correlate morphological differences among species in that genus with depth. He based these correlations on the fact that *E. terminalis* lives in shallower water than the other species in *Marginoproctus*. Mortensen's (1948) discovery that *E. terminalis* was a scutellid, and not a fibulariid seems to have been overlooked by Mironov, and it now seems that *Marginoproctus* itself should

be placed in the Scutellina, and not within the fibulariid laganines (Mooi and Chen, 1996). The relationship of *E. terminalis* to *Marginoproctus* needs to be reassessed in light of the very different plate patterns that these two taxa exhibit (Mooi and Telford, unpublished data).

The only relatively recent treatment of the genus *Dendraster* was that of Durham et al. (1980). Although no synonymies or taxonomic justifications were given, these authors apparently treated Clark's (1948) *D. mexicanus* and *D. rugosus* as junior synonyms of *D. vizcainoensis* Grant and Hertlein (1938). As mentioned above, *D. vizcainoensis* was originally described as a fossil, making Durham et al.'s (1980) account the first one to treat it as a living taxon. Mortensen (1948) did not mention *D. vizcainoensis* anywhere in his monograph, and it would seem that neither he nor Clark (1948) compared it to *D. mexicanus* or *D. rugosus*. Durham et al. (1980), as well as all works to date, consider Clark's *D. laevis* to be a valid taxon. To summarize the present situation, as stated in Beadle (1991), the genus *Dendraster* now includes three living species: *D. excentricus*, *D. vizcainoensis*, and *D. laevis*, with a possible fourth species, *D. terminalis*, informally proposed. Potentially related fossil taxa also need to be considered in any attempt to revise the extant forms. *Dendraster granti* Durham, 1950 is one of those taxa.

While working in the benthic invertebrate collections at the Scripps Institution of Oceanography (SIO), I came upon two lots labeled as *D. laevis* from Isla de Guadalupe, the type locality of *D. terminalis*. Together, these lots comprise a full size range from just a few millimeters test length up to full grown *D. laevis*. The comments of Mortensen (1948) regarding the possible relationship of *E. terminalis* to some as yet unknown juvenile *Dendraster* invited comparison with the types of *E. terminalis* housed at the California Academy of Sciences. It also became clear that formal decisions regarding the status of all of Clark's (1948) species were required. Therefore, qualitative and quantitative comparisons of many specimens throughout the known ranges of all described living taxa are developed here. The morphometric comparisons of the living *Dendraster* species will also shed some light on heterochronic events within the dendrasterid clade. Although it is premature to conduct a formal phylogenetic analysis, all of the conclusions regarding diagnoses of the taxa and tentative cladistic relationships are based on identification of potential synapomorphies for clades within the dendrasterids. It is hoped that this phylogenetically oriented revision of the living taxa and their variants can form the basis for additional works considering the myriad described fossil taxa of a biologically and paleontologically important group of sand dollars.

MATERIALS AND METHODS

SOURCES OF MATERIAL. —To aid future researchers in determining where gaps in our knowledge might still exist, precise references to the material used as sources for each type of data are given below (additional information is available from the author). Terminology is that of Mooi (1989). Recent and fossil material were obtained from the invertebrate collections of the California Academy of Sciences, San Francisco, California (CASIZ); the geology collections of the same museum (CASG); the Natural History Museum of Los Angeles County, Los Angeles, California (LACM); the National Museum of Natural History, Washington, D.C. (NMNH); the Scripps Institution of Oceanography, La Jolla, California (SIO); and from personal collections of the author (RM).

ANALYSES. —Qualitative differences in test morphology and external appendages were used to determine whether extant nominal taxa were valid. Initial observations suggested that *D.*

Table 1. Coefficients of least squares regressions against test length for each of the three recognized species of *Dendraster*. Lines for each species in a given regression are significantly different at the $P < 0.001$ level, except for peristome position in *D. excentricus* and *D. vizcainoensis*, and test width in *D. vizcainoensis* and *D. terminalis*.

Regression/Species	<i>b</i>	<i>lna</i>	r^2	<i>n</i>
PETALOID IV LENGTH				
<i>excentricus</i>	1.222	-1.897	0.986	30
<i>vizcainoensis</i>	1.152	-1.829	0.988	76
<i>terminalis</i>	1.144	-1.989	0.973	25
TEST WIDTH				
<i>excentricus</i>	1.044	-0.121	0.999	60
<i>vizcainoensis</i>	1.052	-0.192	0.998	79
<i>terminalis</i>	1.073	-0.242	0.998	41
TEST HEIGHT				
<i>excentricus</i>	0.841	-1.315	0.987	60
<i>vizcainoensis</i>	0.869	-1.338	0.956	79
<i>terminalis</i>	0.710	-1.050	0.940	41
APEX POSITION				
<i>excentricus</i>	1.109	-0.847	0.998	60
<i>vizcainoensis</i>	1.038	-0.714	0.997	79
<i>terminalis</i>	1.098	-1.015	0.997	41
PERISTOME POSITION				
<i>excentricus</i>	1.055	-0.853	0.999	60
<i>vizcainoensis</i>	1.045	-0.890	0.998	79
<i>terminalis</i>	1.059	-0.937	0.998	41
PERISTOME LENGTH				
<i>excentricus</i>	0.597	-1.185	0.979	60
<i>vizcainoensis</i>	0.501	-0.802	0.967	79
<i>terminalis</i>	0.429	-0.773	0.919	41
PERIPROCT POSITION				
<i>excentricus</i>	0.992	-0.033	0.999	60
<i>vizcainoensis</i>	1.007	-0.118	0.999	79
<i>terminalis</i>	0.985	-0.003	0.999	41

vizcainoensis, *D. mexicanus*, and *D. rugosus* were synonyms. This possibility was explored using a rotated factor principal component analysis (PCA) performed on petaloid measures using JMP for the Macintosh. This focus on petaloids stemmed from the fact that petaloid dimensions (particularly width of the poriferous zone) are most heavily relied upon to distinguish these taxa in the original descriptions. Qualitative data also indicated that *D. laevis* was synonymous with *D. terminalis*, but that *D. excentricus* was a distinct taxon. Therefore, additional PCA analyses were generated incorporating all nominal taxa. Results from the PCA analyses were supplemented by least squares regressions in order to discern ontogenetic differences for individual features among the species. Regressions on natural logarithmic transformations of morphometric data were performed using Statview for the Macintosh to generate lines of the form $\ln y = b \ln x + \ln a$. Using qualitative data and the PCA analyses as guides, it was decided that sufficient material existed to perform bivariate analyses on test measures from three taxa: *D. excentricus*, *D. vizcainoensis*, and *D. terminalis*. Using Statview for the Macintosh and the methods described in Zar (1974: 292-298), Student *t* tests for significant difference between slopes and between intercepts were calcu-

lated for the regressions listed in Table 1. The null hypothesis that the slopes (or intercepts) of two lines were equal was rejected at the $P < 0.001$ level.

TEST MORPHOMETRY. — The following measurements were made to the nearest tenth of a millimeter: test length (measured along anterior/posterior axis [APA]), test width (greatest width orthogonal to APA), test height (at highest point along APA), apex position (distance along APA from ambitus at ambulacrum III to anterior edge of madreporic plate), peristome length, peristome position (distance along APA from ambitus at ambulacrum III to anterior edge of peristome), periproct position (distance along APA from ambitus at ambulacrum III to anterior edge of periproct). Data were collected from the following species and lots (number of specimens measured and abbreviated locality given in parentheses). In some cases, measurements had to be obtained from photographs in published works. Because dendrasterid tests are almost planar, measurements from photos contain negligible error. *Dendroaster excentricus*: CASIZ 081138 (7, Bolinas Bay, Marin County, California), CASIZ 081139 (26, Monterey Bay, California), CASIZ 090430 (15, Drake's Bay, Marin County, California), CASIZ 090437 (2, Ocean Beach, San Francisco, California), CASIZ 090441 (6, Stinson Beach, Marin County, California), CASIZ 090444 (4, off San Francisco Zoo, California); *Dendroaster vizcainoensis*: Holotype measured from photo in Grant and Hertlein (1938), Paratype CASG 6947 (1, Quaternary, Bahía Sebastián Vizcaíno, Baja California, México), CASIZ 090450 (8, outside Scammon's Lagoon, Baja California, México), CASIZ 090458 (2, Bahía Santa Rosalía, Baja California, México), CASIZ 094405 (25, outside Scammon's Lagoon, Baja California, México), LACM 67-60.15 (1, Isla San Martín, Baja California, México), LACM 71-160.2 (6, Punta Rompiente, Baja California, México); *Dendroaster mexicanus*: Holotype LACM 37-11.5 (1, Bahía Rosario, Baja California, México), Paratype CASIZ 029950 (1, Bahía Rosario, Baja California, México), Paratype LACM 37-11.6 (1, Bahía Rosario, Baja California, México), LACM 59-272.1 (9, identified as *D. mexicanus* by F. Ziesenhenné, off Scammon's Lagoon, Baja California, México), LACM 59-272.2 (21, identified as *D. mexicanus* by F. Ziesenhenné, off Scammon's Lagoon, Baja California, México); *Dendroaster rugosus*: Holotype measured from photo in Clark (1948), Paratype LACM 32-19.1 (1, Bahía Sebastián Vizcaíno, Baja California, México); *Dendroaster laevis*: Holotype LACM 39-80.1 (1, Santa Barbara Island, California), Paratypes LACM 39-80.2 (13, Santa Barbara Island, California), CASIZ 087664 (1, Orange County, California), LACM Alan Hancock Foundation Number 31.1 (15, Islas Los Coronados, México), SIO E2488 (7, Isla de Guadalupe, México), SIO E2490 (4, Isla de Guadalupe, México); *Echinocyamus terminalis*: Holotype CASIZ 029939 (1, Isla de Guadalupe, México), Paratypes CASIZ 029940 (3, Isla de Guadalupe, México), CASIZ 090664 (4, Isla de Guadalupe, México).

GNONOPORE ANALYSIS.—Presence or absence of gonopores was recorded for all of the material listed above. For comparison with non-*Dendroaster* species, test length and presence or absence of gonopores were also noted for the following species and lots. *Echinarachnius parma* (Lamarck, 1816): CASIZ 081140 (4, Alaska), CASIZ 081245 (5, Massachusetts), NMNH 9693 (3, Massachusetts), NMNH 13596 (11, Massachusetts), NMNH 16225 (3, Massachusetts), NMNH 25022 (11, Massachusetts), NMNH E30851 (3, Alaska), NMNH E30854 (2, Alaska), NMNH E30876 (27, Alaska); *Mellita tenuis* Clark, 1940: CASIZ 087842 (7, Fort Meyers, Florida), NMNH E15706 (9, Egmont Key, Florida), RM (18, Cedar Key, Florida), RM (3, Sarasota, Florida); *Echinodiscus bisperforatus* Leske, 1778: RM (25, Cape Infanta, South Africa).

TEST WEIGHT ANALYSIS. — Test length and the weight of the bleached test were recorded for the following CASIZ lots, format as above: *Dendroaster excentricus*: 081135 (25, Punta Colonet, Baja California, México); *Dendroaster vizcainoensis*: 094405 (25, outside Scammon's Lagoon, Baja California, México), 090451 (1, Bahía Santa Rosalía, Baja California, México), 090460 (1, outside Scammon's Lagoon, Baja California, México). A least squares regression was performed on these data according to the methods described above.

PETALOID MORPHOMETRY. — The following measurements were made to the nearest tenth of a millimeter: length of petaloid pore pair column in ambulacra IVa and Va, maximum width of petaloids in ambulacra IV and V, maximum width of poriferous zones of petaloids in ambulacra IV and V (calculated by subtracting the maximum width of the interporiferous zone from the maxi-

mm width of the petaloid). Data were collected from the following species and lots, format as above. *Dendraster excentricus*: CASIZ 081138 (10, Bolinas Bay, Marin County, California), CASIZ 090432 (4, San Francisco Bay, California), CASIZ 090441 (11, Stinson Beach, Marin County, California), RM (4, Ocean Beach, San Francisco, California); *Dendraster vizcainoensis*: Holotype measured from photo in Grant and Hertlein (1938), Paratype CASG 6947 (1, Quaternary, Bahía Sebastián Vizcaíno, Baja California, México), CASIZ 090450 (8, outside Scammon's Lagoon, Baja California, México), CASIZ 090451 (1, Bahía Santa Rosalía, Baja California, México), CASIZ 090452 (1, outside Scammon's Lagoon, Baja California, México), CASIZ 090458 (2, Bahía Santa Rosalía, Baja California, México), CASIZ 090460 (2, Scammon's Lagoon, Baja California, México), CASIZ 094405 (25, outside Scammon's Lagoon, Baja California, México), LACM 71-160.2 (6, Punta Rompiente, Baja California, México); *Dendraster mexicanus*: Holotype LACM 37-11.5 (1, Bahía Rosario, Baja California, México), Paratype CASIZ 029950 (1, Bahía Rosario, Baja California, México), Paratype LACM 37-11.6 (1, Bahía Rosario, Baja California, México), LACM 59-272.1 (23, identified as *D. mexicanus* by F. Ziesenhenné, off Scammon's Lagoon, Baja California, México); *Dendraster rugosus*: Holotype measured from photo in Clark (1948), Paratype LACM 32-19.1 (2, Bahía Sebastián Vizcaíno, Baja California, México); *Dendraster laevis*: Holotype LACM 39-80.1 (1, Santa Barbara Island, California), Paratypes LACM 39-80.2 (19, Santa Barbara Island, California), CASIZ 087664 (1, Orange County, California), SIO E2490 (4, Isla de Guadalupe, México); *Dendraster granti*: Paratype CASG 2431 (5, near Loreto, Baja California, México).

EXTERNAL APPENDAGES. — Using the techniques of Mooi (1990a:27), cleaned external appendages were examined and drawn from the following species and lots (test lengths and abbreviated localities are given in parentheses). *Dendraster excentricus*: CASIZ 075614 (39.9 mm, Punta Colonet, Baja California, México), CASIZ 081134 (56.2 mm, 56.4 mm, Monterey Bay, California), CASIZ 081135 (58.6 mm, Punta Colonet, Baja California, México), CASIZ 081137 (45.2 mm, Channel Islands, California), CASIZ 081141 (71.7 mm, Puget Sound, Washington), CASIZ 081144 (26.9 mm, 27.1 mm, 54.6 mm, San Diego, California), CASIZ 090410 (61.6 mm, San Francisco, California), CASIZ 090430 (12.9 mm, Drake's Bay, Marin County, California), CASIZ 090431 (3.3 mm, 8.1 mm, 14.6 mm, Monterey Bay, California), CASIZ 090453 (61.7 mm, Vancouver Island, British Columbia, Canada), CASIZ 095692 (5.3 mm, 21.5 mm, Coos Bay, Oregon), CASIZ 095707 (16.1 mm, Coos Bay, Oregon); *Dendraster vizcainoensis*: LACM 71-160.2 (57.1 mm, Punta Rompiente, Baja California, México), CASIZ 081142 (42.9 mm, off Scammon's Lagoon, Baja California, México); *Dendraster mexicanus*: Holotype LACM 37-11.5 (56.8 mm, Bahía Rosario, Baja California, México), Paratype CASIZ 029950 (1, Bahía Rosario, Baja California, México), Paratype LACM 37-11.6 (1, Bahía Rosario, Baja California, México), LACM 59-272.1 (39.7 mm, identified as *D. mexicanus* by F. Ziesenhenné, off Scammon's Lagoon, Baja California, México), LACM 59-272.2 (17.8 mm, 37.3 mm, identified as *D. mexicanus* by F. Ziesenhenné, off Scammon's Lagoon, Baja California, México); *Dendraster rugosus*: Paratype LACM 32-19.1 (39.1 mm, Bahía Sebastián Vizcaíno, Baja California, México); *Dendraster laevis*: Holotype LACM 39-80.1 (53.5 mm, Santa Barbara Island, California), Paratype LACM 39-80.2 (28.9 mm, 34.4 mm, Santa Barbara Island, California), CASIZ 090396 (32.6 mm, Isla San Martín, Baja California, México), LACM Alan Hancock Foundation Number 31.1 (36.4 mm, Islas Los Coronados, México), SIO E2490 (5.8 mm, Isla de Guadalupe, México); *Echinarachnius parma*: CASIZ 010964 (10.7 mm, Alaska), CASIZ 090680 (68.8 mm, Massachusetts), CASIZ 092545 (66.2 mm, Alaska); *Scaphechinus mirabilis*: CASIZ 081231 (59.9 mm, Japan).

BIOGEOGRAPHY, PALEONTOLOGY, PLATE AND FOOD GROOVE PATTERNS. — In addition to the biogeographic and paleontological data available from the literature and the specimens listed above, specimens from the extremes of the ranges of all species were particularly sought out. These are listed below along with material upon which general observations of test morphology, plate, and food groove patterns were examined and/or drawn (using techniques of Mooi, 1990a). *Dendraster excentricus*: CASIZ 075614 (Punta Colonet, Baja California, México), LACM 88-222.1 (mixed lot with *D. vizcainoensis*, Bahía Santa María, Baja California, México), NMNH E34290 (Channel Islands, California), NMNH E34291 (San Diego, California), NMNH E34299 (Bahía Tortugas,

Baja California, México); *Dendraster vizcainoensis*: CASG 66774.01 (Quaternary fossil, San Pedro, Deadman Is., Los Angeles County, California), CASG 66775.01 (Quaternary fossil, Las Posas Hills, Ventura County, California), CASG 66776.01 (Quaternary fossil, San Diego, California), CASG 66777.01 (Quaternary fossil, Ventura County, California), CASG 66778.01 (Quaternary fossil, San Diego, California), CASG 66779.01 (Quaternary fossil, San Diego, California), CASG 66780.01 (Quaternary fossil, San Diego, California), CASIZ 094408 (Quaternary fossil, San Diego, California), LACM 71-160.2 (Punta Rompiente, Baja California, México), LACM 88-222.1 (mixed lot with *D. excentricus*, Bahía Santa Maria, Baja California, México); *Dendraster mexicanus*: LACM 59-272.1 (identified as *D. mexicanus* by F.C. Ziesenhenné, off Scammon's Lagoon, Baja California, México); *Dendraster laevis*: Paratype LACM 39-80.2 (Santa Barbara Island, California), CASIZ 090456 (no locality data), SIO E2488 (Isla de Guadalupe, México), SIO E2490 (Isla de Guadalupe, México); *Echinocyamus terminalis*: Holotype CASIZ 029939, Paratype CASIZ 029940 (Isla de Guadalupe, México).

SYSTEMATIC ACCOUNT

GENERAL TAXONOMIC FINDINGS. — Qualitative analyses of test morphology and external appendages strongly suggest the existence of three valid extant species of *Dendraster*: *D. excentricus* (Eschscholtz, 1831), *D. vizcainoensis* Grant and Hertlein, 1938, and *D. terminalis* (Grant and Hertlein, 1938). Rather than elaborate on these comparisons here, morphological observations are discussed below for each species under the heading “*Diagnosis and Comparison with Other Species*”. Only general conclusions drawn from the analyses will be discussed here. PCA of test measures for all nominal species of extant *Dendraster* run counter to qualitative observations by showing large overlaps in the distributions of specimens in multivariate space (Fig. 1A). Abundant type material exists for *D. mexicanus*, but only the few type specimens of *D. rugosus* could be included in the PCAs. Additional specimens of *D. mexicanus* (identified as such from Clark's descriptions by F. Ziesenhenné) were included in the PCA of petaloid features. Some separation of *D. excentricus* from the rest of the taxa is evident when petaloid measures only are considered (Fig. 1B), but *D. vizcainoensis*, *D. mexicanus*, and *D. rugosus* continue to display strong overlap with each other and with *D. terminalis*.

It is only when feature by feature comparisons are made through allometric analysis that the three taxa indicated by the qualitative data become better differentiated (Table 1). Clark (1948) used relative widths of the poriferous and interporiferous zones of the petaloids to distinguish *mexicanus* from *rugosus*. The PCA on petaloid features of *D. vizcainoensis*, *D. mexicanus*, and *D. rugosus* alone shows that both type and other material continue to display considerable overlap (Fig. 2). Regression analysis of width of the poriferous zone against test length again fails to distinguish these taxa (Fig. 3). Therefore, no consistent differences could be found between *D. vizcainoensis*, *D. mexicanus*, and *D. rugosus* in either the quantitative or qualitative data. The fossil taxon, *D. granti* Durham, 1950 is also not distinct by these, or any other criteria (Fig. 3). Accordingly, these four taxa, along with other fossil material that compares favorably with them, are discussed under the senior synonym, *D. vizcainoensis* Grant and Hertlein, 1938, and the implied synonymy in Durham et al. (1980) is upheld.

The size range of the *D. laevis* material from SIO clearly shows that *Echinocyamus terminalis* previously thought to be adult are indistinguishable from juvenile *D. laevis* (Fig. 4). All the SIO specimens (in addition to all other material previously identified as *D. laevis*) should receive the name of its senior synonym, *D. terminalis* (Grant and Hertlein,

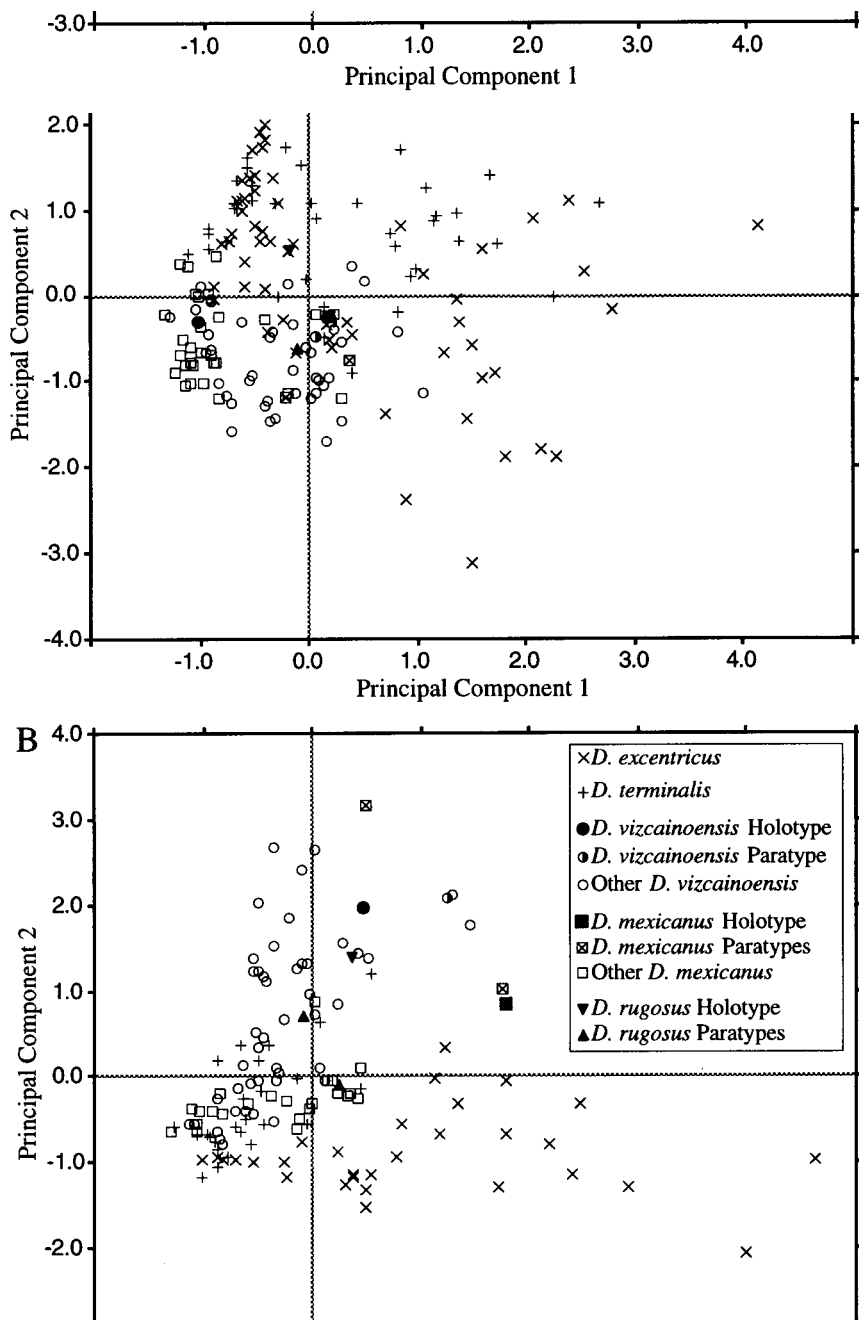


Figure 1. PCA results for nominal species of extant *Dendroaster*. (A) Plot of projection scores calculated from analysis of test measures. Factor 1 represents overall size, and the eigenvectors that load highest on factor 2 are peristome length and test height. (B) Plot of projection scores calculated from analysis of petaloid measures. Factor 1 represents overall size, and the eigenvectors that load highest on factor 2 are interperiferous zone widths of petaloids IV and V. Key to symbols in B applies to both plots.

1938). Therefore, none of Clark's (1948) new species are found to be valid. The synonymies given below are abbreviated and include all the different names applied to a taxon, plus names used in major monographs.

Order CLYPEASTEROIDA L. Agassiz 1935
 Suborder Scutellina Gray, 1825
 Family Dendrasteridae Lambert, 1899
Dendraster L. Agassiz in L. Agassiz and Desor, 1847

Dendraster excentricus (Eschscholtz, 1831)
 Figures 1; 5A; 6A, B; 7A, B; 8C-F, K-N; 9; 10; 11; 13

Scutella excentrica — Eschscholtz, 1831, p. 19; pl. 20, figs. 2a-c (type species of the genus).

Echinarachnius excentricus — Valenciennes, 1846, pl. 10.

Dendraster excentricus — L. Agassiz and Desor, 1847, p. 135.

Scutella striatula — Conrad, 1857, pl. 9, figs. 1a, b (not mentioned in text, reported as fossil).

Echinarachnius excentricus — A. Agassiz, 1872-1874, p. 107, 524; pl. 13a, figs. 1-4.

Dendraster excentricus — Clark, 1914, p. 70; pl. 125, figs. 4, 5.

Dendraster excentricus — Kew, 1920, p. 121; pl. 31, figs. 1a-c; pl. 32, figs. 1, 2.

Echinarachnius (Dendraster) excentricus — Mortensen, 1921, p. 99; pl. 14, figs. 5, 6.

Dendraster excentricus var. *elongatus* — Clark, 1935, p. 122.

Dendraster excentricus elongatus — Grant and Hertlein, 1938, p. 87; figs 16, 17.

Dendraster excentricus — Clark, 1948, p. 310; pl. 49, fig. 32.

Dendraster excentricus — Mortensen, 1948, p. 382; pl. 60, figs. 1-5; pl. 61, figs. 1; 6, pl. 63, fig. 3.

Dendraster excentricus — Durham, 1955, p. 158; figs. 4c, 5b, 11, 21a, b.

Dendraster excentricus — Durham et al., 1980, p. 166; figs. 11.7a-d.

DESCRIPTION. — *Dendraster excentricus* has been well-described in Agassiz (1874), Clark (1948), Mortensen (1948), and Durham et al. (1980), so only a brief overview is required here. The species is extremely variable in size, with some individuals (especially in the Puget sound area) regularly exceeding 100 mm in test length. There is also considerable variation in the camber of the test, with both flat and high-domed forms co-occurring, sometimes in the same bay (Fig. 6A, B).

D. excentricus is typical of the genus in having a circular, slightly elongate, or even sub-pentagonal test (Fig. 5A). Most members of the species have a relatively heavy test made of thick plates. There is a conspicuous peripheral buttress and pillar system, well illustrated by Mortensen (1948: pl. 63, fig. 3). The buttresses lend the test sufficient strength that it often survives the postmortem journey from subtidal sand dollar bed to the beach without breaking. This is in part responsible for the echinoid's familiarity to anyone who has spent any time on northwestern beaches. The mouth is almost central on the oral surface, displaying to a much lesser degree the eccentricity shown by the apical system (Fig. 5A). The periproct is submarginal, typically piercing the test at the distal edges of the second pair of post-basicoronal plates (Fig. 5A). In juveniles, the interambulacra are continuous, but in adults, all interambulacra are widely discontinuous (Fig. 5A). The degree of discontinuity increases with age (see description of *D. terminalis*, below). As in most scutellines, there are four gonopores.

The food grooves bifurcate just at the end of the ambulacral basicoronals (Fig. 5A), and branch again on either the second or third post-basicoronals. These main branches con-

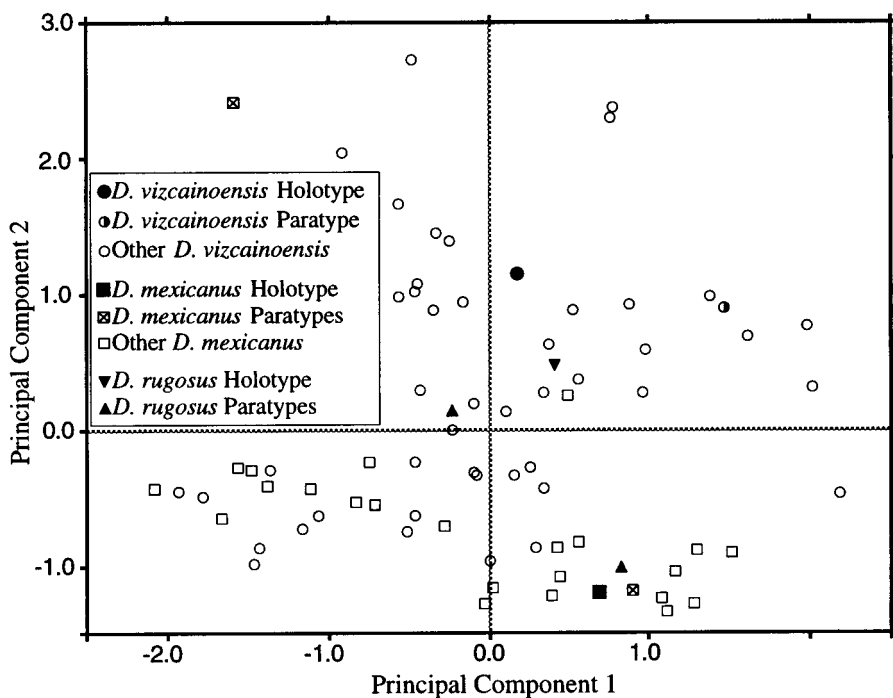


Figure 2. PCA results for petaloid measures from *Dendroaster vizcainoensis* and taxa here considered to be synonymous with it. Factor 1 represents overall size, and the eigenvectors that load highest on factor 2 are interporiferous zone widths of petaloids IV and V.

tinue onto adjacent interambulacral columns. In older animals, there is additional, more distal branching, and many short tributaries can also come off the major elements of the food groove system (Mooi, 1989: fig. 25g). Posteriorly, the main branches continue onto the aboral surface (Fig. 5A), occasionally entering the interporiferous zone of the posterior paired petaloids and traveling more than half the length of the petaloid towards the apical system. Branches of anterior food grooves (those in columns IIb, IIIa, IIIb, and IVa of Lovén's system) are usually somewhat reduced, with very few, if any, of the branches reaching the aboral surface (Fig. 5A). Those in ambulacrum III usually do not even reach the ambitus.

The eccentricity of the apical system is related to inequality of petaloid lengths. The petaloid in ambulacrum III tends to be the longest, with those in ambulacra I and V being much shorter. The latter have a "compressed" look caused by distortion of the posterior ambulacral columns in conjunction with the posterior displacement of the apical system (Fig. 5A). The poriferous zones are relatively wide. The zone in any given ambulacral column is approximately as wide as the interporiferous zone. There are three to four "trailing podia" at the end of each column of pore pairs.

Spines of dendroasterids occur in fewer varieties than in lunulate scutellines. There are two major types: primary and miliary, with some recognizable sub-categories, especially in primaries (Mooi, 1989; 1990a). In *D. excentricus*, primary spines on the oral surface

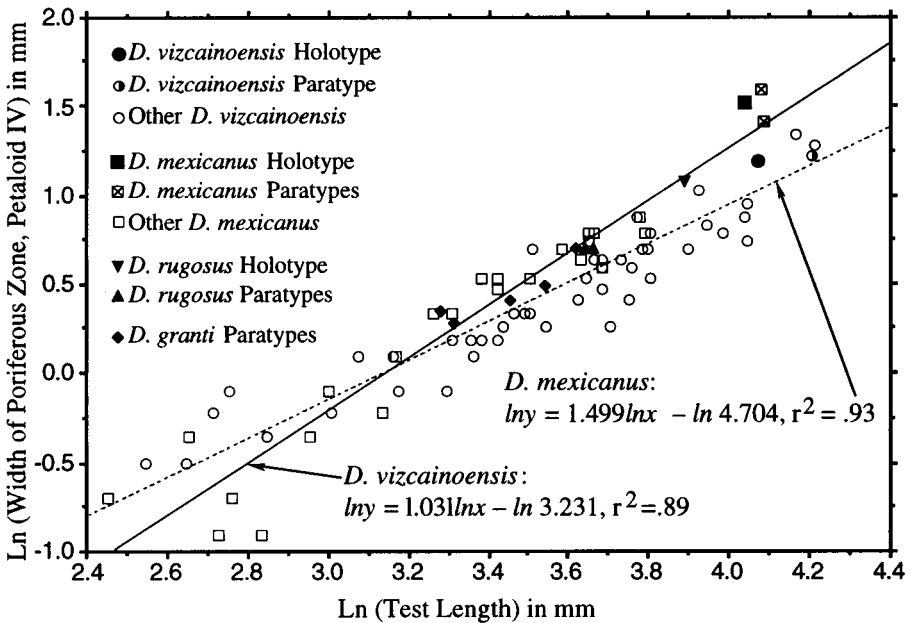
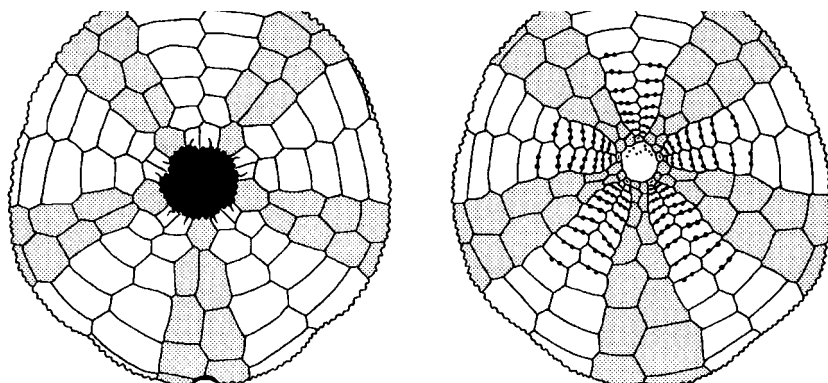


Figure 3. Width of the poriferous zone in petaloid IV as a function of test length in *Dendroaster vizcainoensis* and taxa here considered to be synonymous with it. Regressions for *D. vizcainoensis* and *D. mexicanus* are not significantly different.

have a conspicuous, expanded, club-shaped end (see SEM in Mooi, 1990a: fig. 7C). In some populations, the club is conspicuously flattened (Fig. 7A), forming an almost impenetrable pavement, or spine canopy. The spine becomes increasingly club-shaped with the age of the sand dollar, and juveniles often have only a slight bend in the distal part of the spine shaft, without tip expansion (Fig. 7B). Over the majority the oral surface, primaries occur in long and short varieties. The longest spines occur over most of the oral surface, particularly in the interambulacra. These are the locomotory spines. A shorter variety of primaries can be found in narrow bands 5 to 10 spines wide, and running parallel to the food grooves. Because of a conspicuous bend about half way up the shaft, these are known as geniculate spines (Mooi, 1989: fig. 29a). Additional primary spine types can be recognized from around the periproct and peristome, but these grade continuously into the oral, locomotory primaries. The same is true for the spines at the ambitus, which form a robust fringe that marks a transition zone from the aboral club-shaped primaries to the oral locomotories. Military spines tend to be longer on the oral surface than aborally. Each military supports a fluid- and fiber-filled sac common to most other members of the *Scutellina* (Mooi, 1986b).

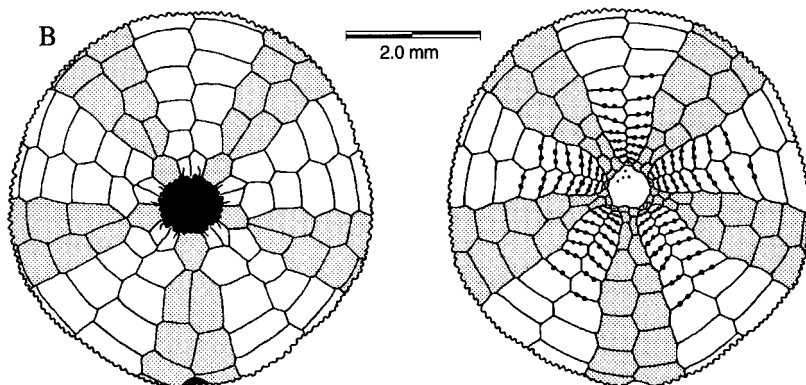
Pedicellariae are of two varieties: biphylloous and bidentate. Each of the two valves of biphylloous pedicellariae (Fig. 8M) are approximately 50 μm long, and equipped with fine teeth. Together, the two valves articulate to form a jaw attached by a flexible, muscular neck about 100 μm long to a stem element approximately 120 μm long. Bidentate pedicellariae are of similar construction, but are much larger. Valves exceed 150 μm in length, and are equipped with two or three elongated, dagger-like distal teeth (Fig. 8K).

CASIZ 29940, Paratype: *Echinocyamus terminalis* Grant & Hertlein, 1938



SIO E2490: "*Dendraster laevis* H.L. Clark, 1948"

B



CASIZ 29939, Holotype: *Echinocyamus terminalis* Grant & Hertlein, 1938

C

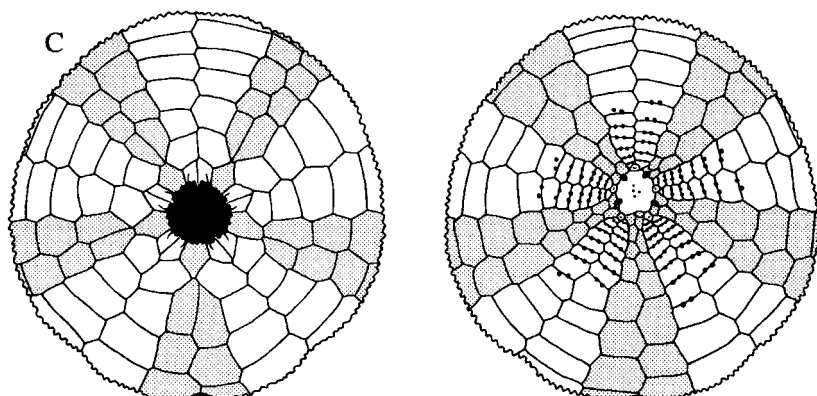


Figure 4. Plate patterns of juvenile *Dendraster*, oral surface on the left, aboral on the right, all from Isla de Guadalupe, México. (A) Specimen identified as *Dendraster laevis*; (B) Holotype of *Echinocyamus terminalis*, without gonopores; (C) Paratype of *Echinocyamus terminalis*, with gonopores. Interambulacral plates shaded, mouth and periproct in solid black. All figures to scale.

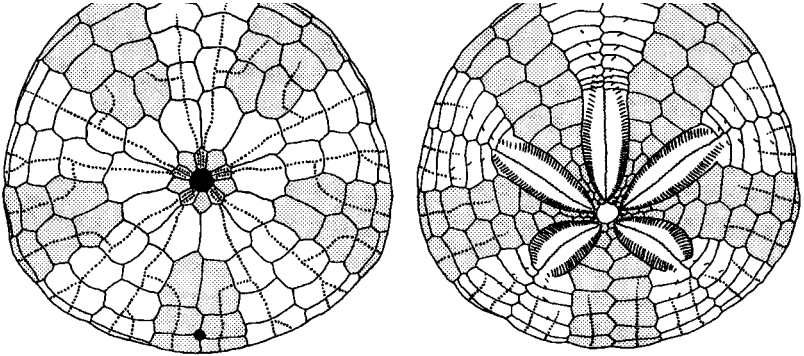
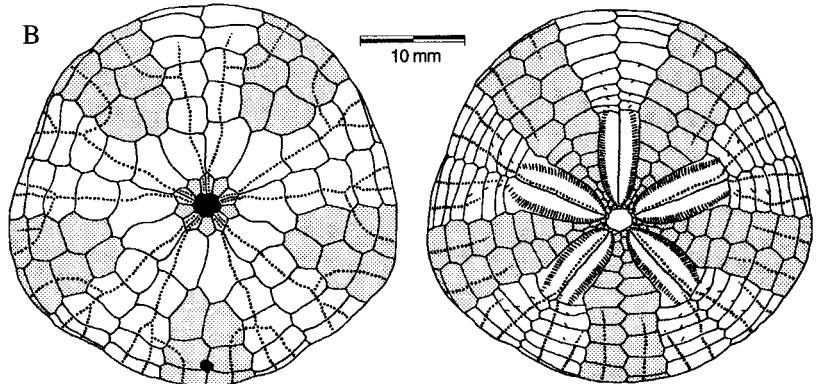
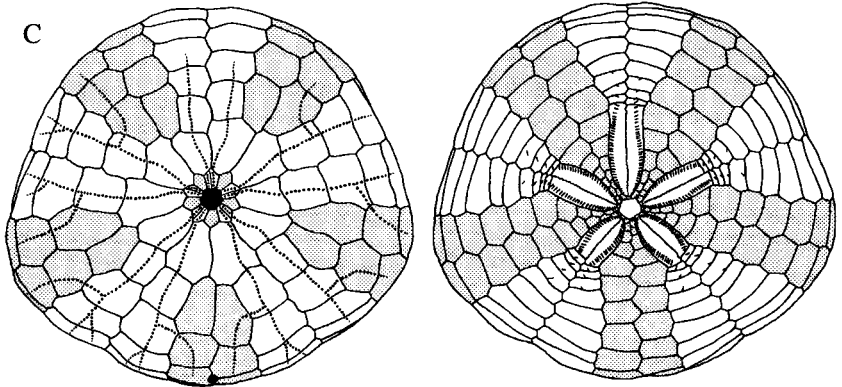
[=*Dendraster laevis* H.L. Clark, 1948]*Dendraster excentricus* (Eschscholtz, 1831)*Dendraster vizcainoensis* Grant & Hertlein, 1938*Dendraster terminalis* (Grant & Hertlein, 1938)

Figure 5. Plate and food groove patterns of adults of the three recognized species of *Dendraster*, oral surface on the left, aboral on the right. (A) CASIZ 075614, Punta Colonet, Baja California, México; (B) LACM 59-272.1, entrance to Scammon's Lagoon, Baja California, México; (C) LACM 39-80.2, paratype, north of Santa Barbara Island, California. Interambulacral plates shaded, details of petaloid plating omitted, mouth and periproct in solid black, food grooves represented by dotted lines. All figures to scale.

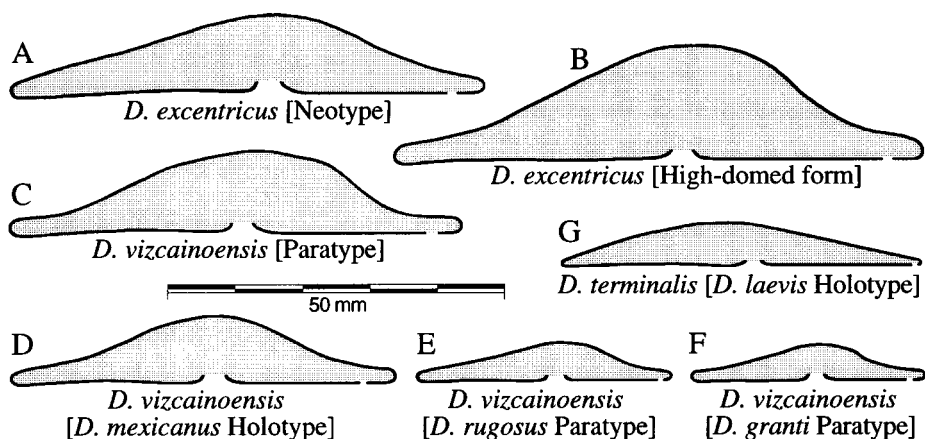


Figure 6. Profiles of the three recognized species of *Dendraster*. (A) CASIZ 081372, Ocean Beach, San Francisco, California; (B) CASIZ 090445, Puget Sound, Washington; (C) CASG 6947, Bahía Sebastián Vizcaíno, Baja California, México; (D) LACM 37-11.5, Bahía Rosario, Baja California, México; (E) LACM 32-19.1, Bahía Sebastián Vizcaíno, México; (F) CASG 7849, north of Loreto, Baja California, México; (G) LACM 39-80.1, Channel Islands, California. All views from the left side so that the peristome is represented by leftmost opening in oral surface, periproct by the rightmost. All figures to scale.

The neck is usually somewhat longer than the valves, and the stem is approximately 150 μm in length (Fig. 8L).

The paired spicules from the tips of the accessory podia are considerably more variable than usually depicted for other clypeasteroids (Mooi, 1986a). This is a previously unrecognized source of variation in sand dollars. The spicules can be of relatively simple 3-point structure (in deer-hunters' parlance)(Fig. 8C, F), or they can be extremely elaborate, with as many as 7 or 8 points (Fig. 8D). They can be variable within a given population or even in a single individual (Fig. 8C and D, or F).

As noted by Durham et al. (1980), *D. excentricus* is variable in color from pale gray through browns of varying shades to almost black. Although there are many exceptions, the southern populations tend to be lighter in color than those in the northern parts of its range. The jet-black coloration of the specimens from Puget Sound is seldom, if ever, found in Mexican *D. excentricus*.

TYPES AND TYPE LOCALITY. —*D. excentricus* is the type species of the genus. Johann Friedrich Eschscholtz collected and described material from two Russian circum-global expeditions, one from 1815 to 1818, and the other from 1823 to 1826. It is unclear from which of the two expeditions that the types of *D. excentricus* came. The expeditions' material was, at least in part, housed in Tartu, Estonia, probably at the Dorpat University Zoological Museum (Dorpat was the old German name for Tartu). Eschscholtz died in the same year that the description of *D. excentricus* was published, and his widow apparently sold his collections to the Zoological Museum of Moscow University (I am grateful to A. Miljutin, Mammal Curator of the Zoological Museum at Tartu University for much of the above information). The Zoological Museum in Moscow has only a single specimen of *Dendraster* with the label "*Echinarachnius excentricus*, San Diego, Cali-

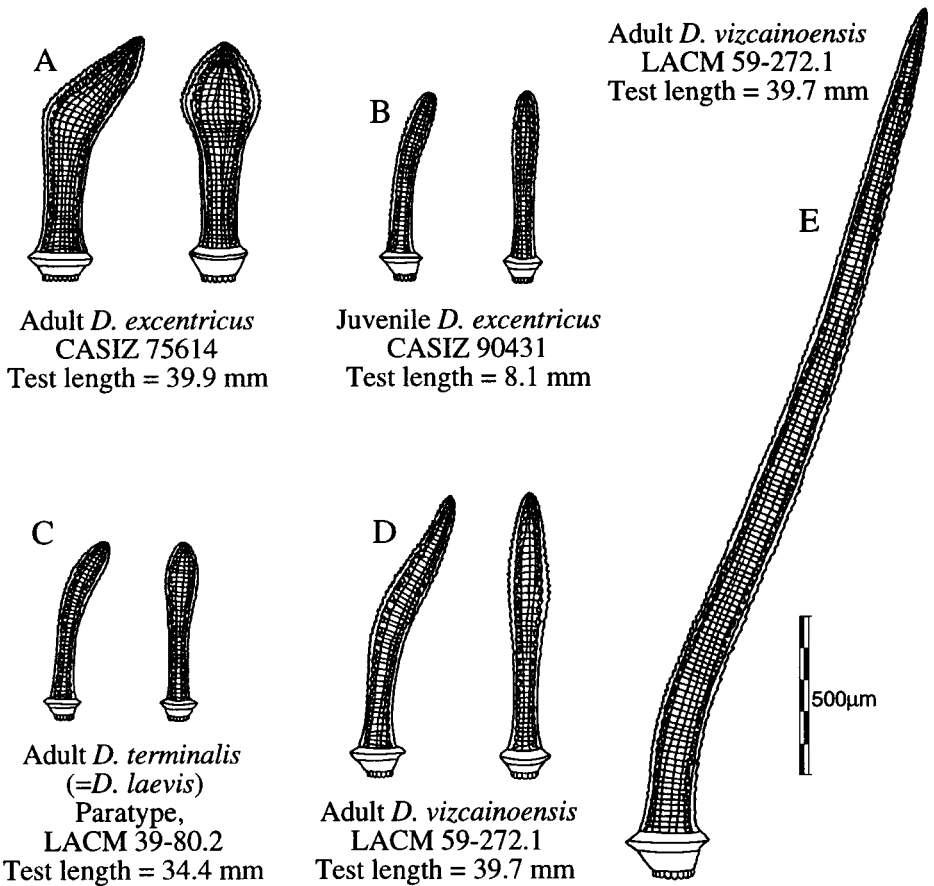


Figure 7. Aboral club-shaped spines of the three recognized species of *Dendraster*. (A) to (D), spines from interambulacrum 2, shown from the “side” (that is, the “downslope” direction towards the ambitus of the sand dollar is to the right) and from the “front” (as if viewed from the apex of the sand dollar); (E) spine from adjacent to food groove, shown only in side view. All figures to scale.

fornia, NB-141” (A. Mironov, pers. comm.). Accordingly, the types are here considered to be lost.

Eschscholtz (1831) recorded the species “An der Küste der Insel Unalashka, am kamschatischen Meere.” As Mortensen (1948) noted, there are no post-1831 records of this species from anywhere near Kamchatka. Unalaska is at least a plausible locality, in spite of the fact that the most northerly verifiable locality is Juneau, Alaska. Rathbun (1886) was therefore correct in challenging the validity of the type locality.

With the uncertainty surrounding the actual collecting site of Eschscholtz’s material, it is impossible to designate a neotype from the type locality. Eschscholtz (1831) described two specimens, one 76.2 mm long and 80.4 mm wide, the other 80.4 mm long and 88.9 mm wide. It seems prudent to choose a neotype that not only closely matches Eschscholtz’s original description, but also undeniably lies within the known range of *D. excentricus*. A neotype, CASIZ 081372, collected by P. Carlstroem at Ocean Beach, San Francisco, California is here designated (Fig. 9). This locality is close to the center of the range of *D.*

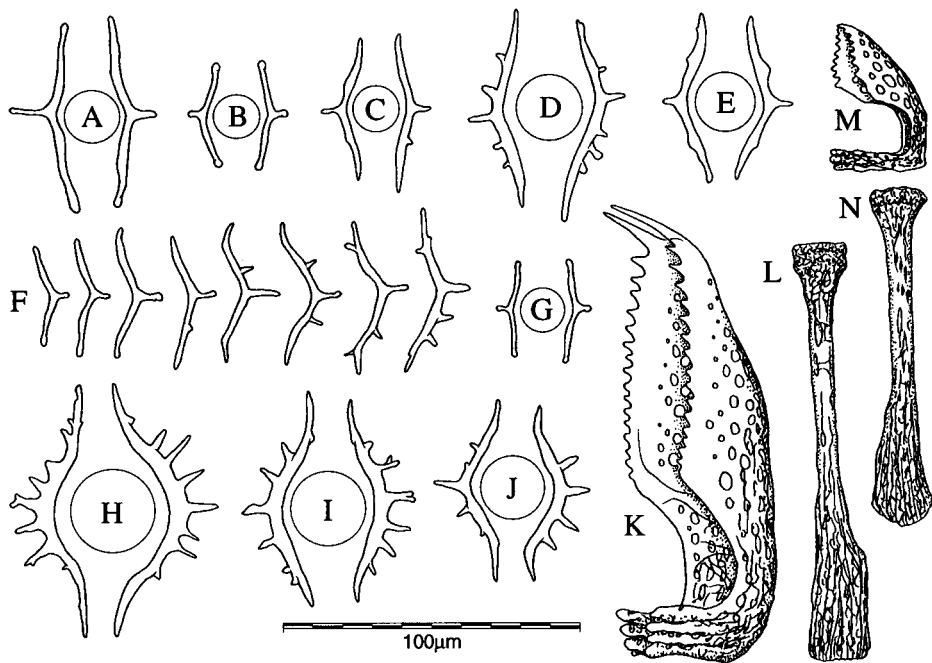


Figure 8. Podial (A-J) and pedicellarial (K-N) skeletal elements from the oral surfaces of living species of *Dendraster*, *Echinarachnius*, and *Scaphechinus*: (A) *Echinarachnius parma*, Alaska, 68.8 mm test length, CASIZ 092545; (B) *Scaphechinus mirabilis*, Japan, 59.9 mm test length, CASIZ 081231; (C) *Dendraster excentricus*, Monterey Bay, California, 3.3 mm test length, CASIZ 090431; (D) Same specimen as in (C); (E) *D. excentricus*, Puget Sound, 71.7 mm test length, CASIZ 081141; (F) *D. excentricus*, San Diego, California, 27.1 mm test length, CASIZ 081144, variety of isolated spicules from eight different podia on the same specimen; (G) *D. laevis* Holotype, Channel Islands, California, 53.5 mm test length, LACM 39-80.1; (H) *D. mexicanus* Holotype, Bahía Rosario, México, 58.6 mm test length, LACM 37-11.5; (I) *D. vizcainoensis*, Punta Rompiente, México, 57.1 mm test length, LACM 71-160.2; (J) *D. rugosus* Paratype, 39.1 mm test length, Bahía Sebastián Vizcaíno, México, LACM 32-19.1; (K) Isolated valve of bidentate pedicellaria from *D. excentricus*, Punta Colonet, México, 58.6 mm test length, CASIZ 081135; (L) Stem of bidentate pedicellaria from same specimen as in (K); (M) Isolated valve of biphyllous pedicellaria from *D. excentricus*, Puget Sound, Washington, 71.7 mm test length, CASIZ 081141; (N) Stem of biphyllous pedicellaria from same specimen as in (M). A-E, G-J show pairs of spicules in natural arrangement on either side of connective tissue sheath, represented by circle. All figures to scale.

excentricus, and the specimen has a near-perfect coat of spines. Characteristics of the neotype are as described for the species. The following measurements were taken in the same manner as for the allometric analyses described above: test length 71.1 mm, test width 74.7 mm, test height 10.8 mm, apex position 44.9 mm, peristome length 3.6 mm, peristome position 36.0 mm, periproct position 64.5 mm, petaloid V length 17.6 mm, petaloid V width 9.6 mm, petaloid IV length 24.1 mm, petaloid IV width 10.5 mm, petaloid III length 27.3 mm, petaloid III width 10.2 mm.

DIAGNOSIS AND COMPARISON WITH OTHER SPECIES. — When large samples of *D. excentricus* are available for allometric analysis, the features listed in Table 1 can be used to distinguish the three *Dendraster* species. *D. excentricus* is separable from the other living taxa on the basis of what appear to be plesiomorphic features for the genus (Mooi, 1987). In

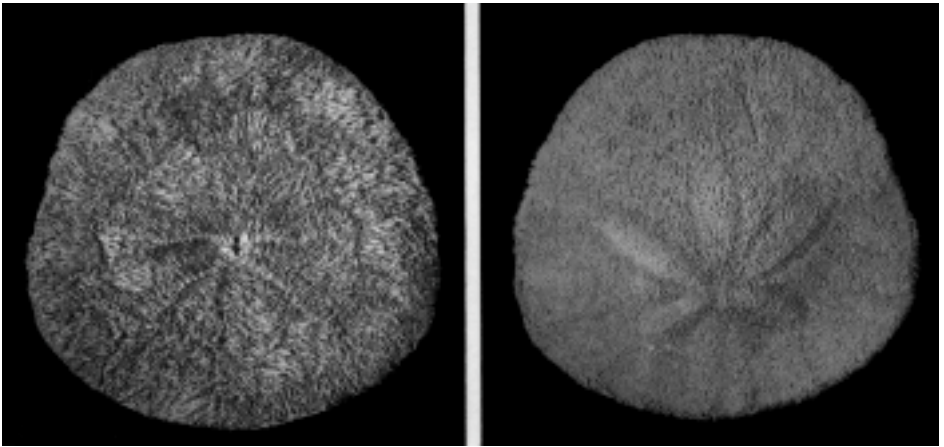


Figure 9. Neotype of *Dendraster excentricus*, CASIZ 081372, Ocean Beach, San Francisco, California. Oral surface on the left, aboral on the right, test length 71.1 mm.

other words, there are no identifiable autapomorphies for *D. excentricus* (see below for further discussion of dendrasterid phylogeny). *D. excentricus* is of much heavier construction than either *D. vizcainoensis* or *D. terminalis* (Fig. 10). *D. excentricus* also tends to be more eccentric, with concomitant exaggerated distortion of the posterior petaloids. Petaloid characters feature prominently in systematic treatments of both fossil and extant taxa, but the variability in eccentricity and therefore in degree of modification of the posterior paired petaloids makes these features unreliable. Perhaps most important is the fact that the aboral primary spines of adult *D. excentricus* (Fig. 7A), although much coarser and longer than in *D. terminalis* (Fig. 7C), never attain the extraordinary heterogeneity in length seen in *D. vizcainoensis* (Fig. 7D, E). The podial spicules are also of some use in distinguishing *D. excentricus* from other *Dendraster* species. Although extremely variable in the amount of branching from the main part of each spicule (Fig. 8C-F), it is generally true that the spicules have fewer points than those of *D. vizcainoensis* (Fig. 8H-J) but more than the extremely simple, small spicules of *D. terminalis* (Fig. 8G). Part of the variation within *D. excentricus* is caused by increasing complexity with size (and presumably ontogeny) of the spicule itself. However, this does not apply equally to all scutelline taxa, as the spicules of *E. parma* (Fig. 8A) can be very large without adding points. Therefore, it is better to examine as many spicules as possible from a number of specimens in assessing this character.

DISTRIBUTION. — *D. excentricus* is known only from the west coast of North America, where it prefers fine siliceous sands from the low intertidal to a depth of approximately 90 m (Durham et al., 1980). With the exception of some fossil *D. vizcainoensis* from the east side of Baja California, the range of *D. excentricus* contains within it the distributions of all known species of *Dendraster*. Like Rathbun (1886) and Mortensen (1948), Wagner (1974) cast doubt on the occurrence of *D. excentricus* north and west of Juneau, Alaska. This is here considered the known northern limit of the species. The southern limit is also imperfectly known. Merrill and Hobson (1970) indicate that the southern limit is “Bahía Almejas”, without citing the source of their information. Clark (1948)

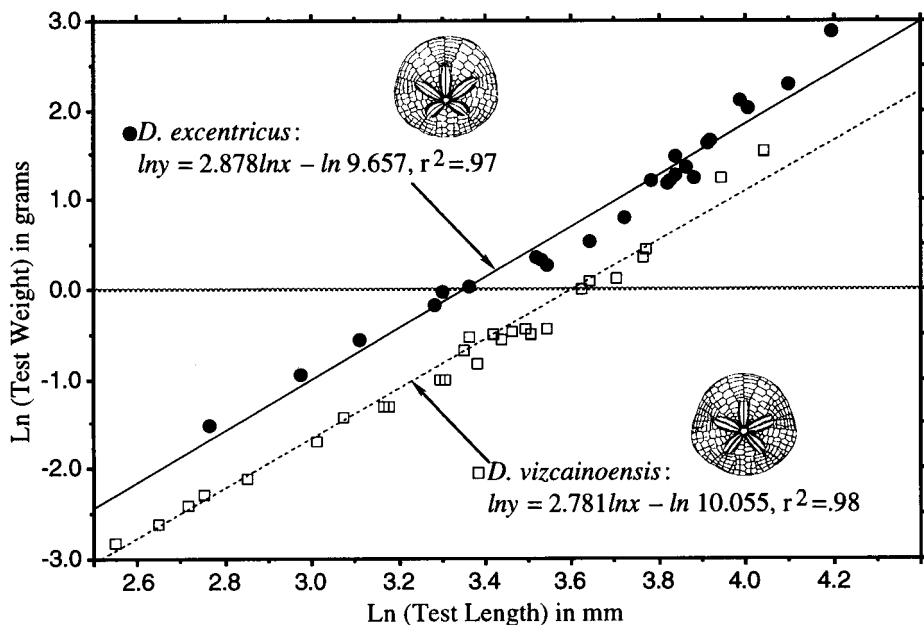


Figure 10. Weight of the test as a function of test length for *Dendraster vizcainoensis* and *D. excentricus*. Slopes and intercepts of regression lines are significantly different at the $P < 0.001$ level.

states that the R/V *VELERO* took *D. excentricus* "near the tip of Lower California." No more precise information exists, in spite of extensive searches through collections and the literature (particularly with respect to the Allan Hancock Pacific Expeditions). Caso (1980) plotted several localities for *D. excentricus* within the Gulf of California on her distribution maps. She does not support her map data beyond providing a list showing material from "Bahía Muleje" and "Islas Coronado, Méx." The latter locality refers to material from the Allan Hancock collection donated to the Museum of Comparative Zoology, Harvard. I was unable to find the locality of Bahía Muleje, but Caso seems to have confused the Coronados Islands (in Spanish, Islas Los Coronados, from which the Allan Hancock expeditions took many *D. excentricus*), which are just south of San Diego, with Isla Coronados, which is in the Gulf south of Bahía Concepción. In her discussion of the distribution she states that there "existen opiniones muy diversas y hasta cierto punto contradictorias," but apart from her maps, does not make special mention of *D. excentricus* in the Gulf. Therefore, in spite of frequent collecting within the Gulf, there are no reliable records of living *Dendraster* from there. It is extremely doubtful that this species occurs south or east of Cabo San Lucas, and might not occur south of Bahía Almejas (Fig. 11).

D. excentricus is recorded as a Pliocene fossil from rocks near San Diego, Los Angeles, and San Francisco (Grant and Hertlein, 1938). It is also found in Pleistocene strata from southern California and from Baja California (Kew, 1920; Grant and Hertlein, 1938). The diagnostic features discussed above do not always unambiguously distinguish *D. excentricus* from fossil *Dendraster* known by other names. Many of these taxa will un-

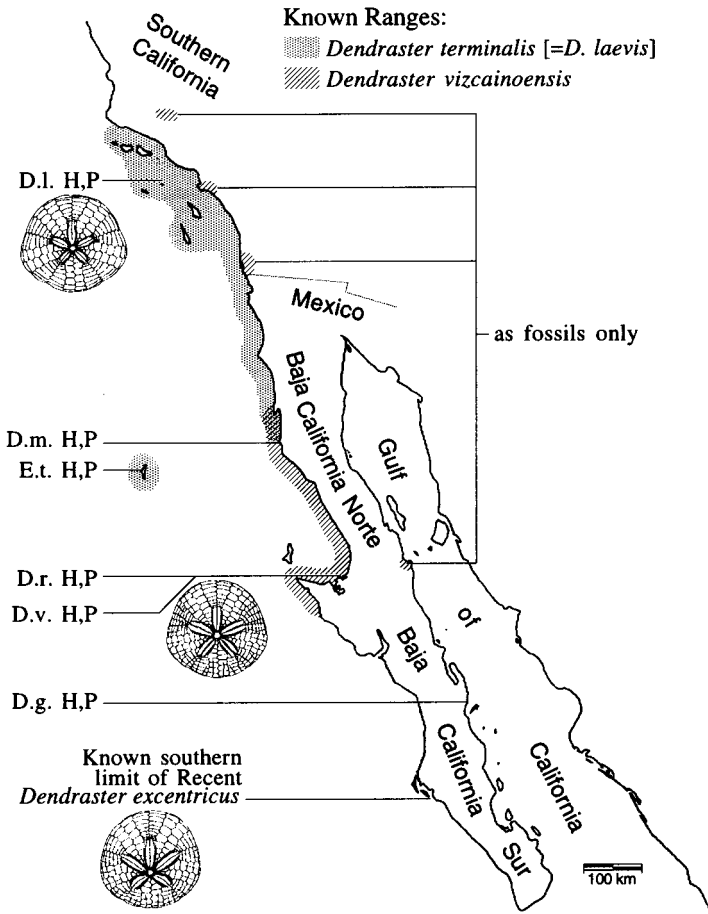


Figure 11. Geographic distribution of *Dendraster terminalis* and *D. vizcainoensis* showing type localities of valid and synonymized taxa. Shading represents data from the literature as well as from collections examined in this study. Although *D. terminalis* is represented in collections only by insular populations, the literature implies that it also occurs off the mainland. H = holotype, P = paratype, D.v. = *D. vizcainoensis* Grant and Hertlein, 1938 (synonyms: D.g. = *D. granti* Durham, 1950, D.m. = *D. mexicanus* Clark, 1948, D.r. = *D. rugosus* Clark, 1948), E.t. = *Echinocyamus terminalis* Grant and Hertlein, 1938 (synonym: D.l. = *D. laevis* Clark, 1948).

doubtedly prove to be conspecific with the type species of the genus, but much more work will be necessary to demonstrate this.

REMARKS.—*D. excentricus* is the only clypeasteroid described to feed in an upright posture, with the anterior end of the test embedded in the sand. Merrill and Hobson (1970) suggest that *D. terminalis* (= *D. laevis*) might also exhibit upright posture, but full descriptions of this have yet to be published. Usually buried at low tide, some populations of *D. excentricus* slowly emerge as the tide returns, tilting the posterior edge upwards into the water column. Although this species can undoubtedly feed when lying flat on the bottom as described for other sand dollars (Telford et al., 1985), the majority of work on the feeding mechanism of *D. excentricus* has been done on the way in which

aggregations of the echinoid can enhance the hydrodynamic efficiency of suspension feeding while in the upright posture (Timko, 1976; O'Neill, 1978). The marked eccentricity of the apical system in *D. excentricus* appears to be an adaptation to keep the gonopores and most of the petaloids above the level of the sand while upright. There seem to be no published reports of the other two species adopting this posture, but the eccentricity of *D. vizcainoensis* suggests that it might do so. As noted by Booloottian (1964), *D. excentricus* can be host to the acorn barnacle *Paraconcovus pacificus* (Pilsbry, 1916) (= *Balanus concavus pacificus*). Examination of material used for this study, plus about 70 additional beachwash specimens collected at Ocean Beach, San Francisco, supports Booloottian's finding that *Paraconcovus* tends to settle on the posterior half of the living sand dollar. This is probably related to the upright position adopted by *D. excentricus* when feeding.

Clark's (1935) *D. excentricus elongatus* was not considered by Mortensen (1948) or any subsequent worker to be a valid taxon, and I see no reason to dispute this conclusion. It is not consistent to name a subspecies based on slight changes in length to width ratio without also naming new taxa on the basis of the many other features that can vary as much, if not more than test width.

Variations in test camber and eccentricity of *D. excentricus* (Raup, 1956; Stanton, et al., 1979; Nakamura, 1994) have been the subject of work attempting to correlate body form with environmental factors. Extreme variants can lead to taxonomic confusion unless material from all parts of the known range is taken into account. No characters have so far been discovered that can consistently be used to identify phylogenetically distinct populations within what is now called *D. excentricus*. However, other sources of evidence might show otherwise. Because of its enormous geographic range and morphological diversity, the species is ripe for inclusion in further morphometric studies and molecular analyses that explore patterns of gene flow in planktotrophic marine invertebrates.

Dendraster vizcainoensis Grant and Hertlein, 1938
 Figures 1; 2; 3; 5B; 6C-F; 7D, E; 8H-J; 10; 11; 13

Dendraster vizcainoensis — Grant and Hertlein, 1938, p. 90; pl. 8, figs. 1, 2, 3.

Dendraster vizcainoensis similis — Grant and Hertlein, 1938, p. 90; pl. 27, figs. 1, 2; pl. 28, fig. 8.

Dendraster mexicanus — Clark, 1948, p. 313; pl. 51, figs. 37-39.

Dendraster rugosus — Clark, 1948, p. 318; pl. 52, figs. 40, 41.

Dendraster mexicanus — Mortensen, 1948, p. 385.

Dendraster rugosus — Mortensen, 1948, p. 385.

Dendraster granti — Durham, 1950, p.41; pl. 47, figs 3-12.

Dendraster vizcainoensis — Durham et al., 1980, p. 168; figs. 11.8a-c.

DESCRIPTION. — The description of the types given by Grant and Hertlein (1938) was based on fossil material. Therefore, some additional information is warranted here to supplement the descriptions of *D. vizcainoensis* given by Durham et al. (1980), and of *D. mexicanus* and *D. rugosus* given by Clark (1948). *D. vizcainoensis* is today found subtidally down to about 30 m (Durham et al., 1980) and tends to be relatively small (seldom exceeding 60 mm test length), although individuals over 90 mm in test length are not uncommon at some fossil localities. The eccentricity of *D. vizcainoensis* is relatively low, and never attains the values seen in more eccentric populations of *D. excentricus*. The

test of *D. vizcainoensis* also tends to be somewhat more elongate than in *D. excentricus*, but this is by no means diagnostic (Fig. 5B). The camber of the test is not highly variable in populations of living specimens, but was apparently extremely variable in extinct populations from the east side of Baja California (Fig. 6C-F). Some of these specimens were remarkably high-domed, whereas others were extremely flat. This is not unlike the situation found for *D. excentricus* in some parts of its range. The test is relatively lightly built (Fig. 10), with very thin plates especially in the center of the oral surface. Oral interambulacral disjunctions, peristome and periproct positions are as in *D. excentricus* (Fig. 5B). Food grooves, although not more elaborately branched than in *D. excentricus*, continue much farther onto the aboral surface, and are more developed in ambulacrum III. At least one branch in each paired ambulacrum extends up the center of the petaloid all the way to the apical system, a condition not seen in any other scutelline (Fig. 5B). The petaloids themselves have relatively narrow poriferous zones, but this feature is also variable. There are four gonopores.

The aboral primary spines are club-shaped in the centers of the interambulacra, but tend to have attenuated tips distal to the swollen part of the shaft (Fig. 7D). Aboral primaries adjacent to the food grooves are remarkably elongated and pointed (Fig. 7E). Although described by Clark (1948), these spines have not been illustrated before. Relative to test size, the primary spines of the oral surface are also very long, and when seen with the spines intact, the echinoid is more bristly and "hirsute" than any other extant sand dollar. When denuded, the test shows distinct tracts of greatly enlarged tubercles running up the centers of the petaloids and adjacent to each aboral extension of the food grooves, both ambulacral and interambulacral. Podial spicules can have in excess of 15 points (Fig. 8H-J). Pedicellariae are like those of *D. excentricus*, but the valves are usually smaller.

D. vizcainoensis is not darkly colored, varying between greenish gray, purplish, or light beige. The long spines are almost always whitish, lending an even paler aspect to the living echinoid.

TYPES AND TYPE LOCALITIES. — *D. vizcainoensis* Grant and Hertlein, 1938: HOLOTYPE, San Diego Natural History Museum Loc. 395 (Quaternary fossil, Punta Santa Rosalía, Bahía Sebastián Vizcaíno, Baja California, México); PARATYPES, CASG 6947 (Quaternary fossil, Puerto de Santo Domingo, Bahía Sebastián Vizcaíno, Baja California, México), University of California at Los Angeles 6086 (Quaternary fossil, Puerto de Santo Domingo, Bahía Sebastián Vizcaíno, Baja California, México). See Figure 11.

D. mexicanus Clark, 1948: HOLOTYPE, LACM 37-11.5 (Recent, Bahía Rosario, Baja California, México); PARATYPES, LACM 37-11.6 (Recent, holotype locality), CASIZ 029950 (Recent, holotype locality). See Figure 11.

D. rugosus Clark, 1948: HOLOTYPE, LACM Alan Hancock Foundation no. 50 (Recent, Bahía Sebastián Vizcaíno, Baja California, México); PARATYPES, LACM 37-11.6 (Recent, holotype locality). See Figure 11.

D. granti Durham, 1950: HOLOTYPE, CASG 14985 (Plio-Pleistocene [?] fossil, locality A3559, north of Loreto, Baja California, México); PARATYPES, Museum of Paleontology, University of California, Berkeley 14986-9, 14991-2, 15382, 15385 (Fossil, holotype locality), CASG 7848-50 (Fossil, holotype locality). See Figure 11.

DIAGNOSIS AND COMPARISON WITH OTHER SPECIES. —The test of *D. vizcainoensis* is usually less eccentric than in *D. excentricus*, but more so than in *D. terminalis*. However, some *D. excentricus* can have eccentricities as low as that for *D. vizcainoensis*, so this

character is not always diagnostic. *D. vizcainoensis* is very lightly built. *D. excentricus* of the same test length are considerably heavier (Fig. 10). In *D. vizcainoensis*, food grooves are more strongly developed in the anterior part of the test than in *D. excentricus*, and travel much further up the petaloids towards the ambitus than in any other *Dendraster* (Fig. 5B). In *D. terminalis*, the food grooves do not extend onto the aboral surface at all. The poriferous zones of *D. vizcainoensis* are narrower than those in similarly sized *D. excentricus*, but not more so than in *D. terminalis*. The most diagnostic feature of *D. vizcainoensis* is the nature of the aboral spines. The aboral primaries are much more elongate than in either *D. excentricus* or *D. terminalis*, and the club-shaped distal portion is attenuated to a fine point, even in the shortest aboral primaries (Fig. 7D). Those adjacent to the aboral extensions of the food grooves can be extremely long, with no sign of the club-shaped end (Fig. 7E). The long aboral primaries are mounted on greatly enlarged tubercles, which can be 2 or 3 times the diameter of those supporting the shorter aboral primaries. For this reason, it is relatively easy to determine the nature of the spination in denuded beachwashed tests, or even on well-preserved fossils. The podial spicules can also be diagnostic. They are the most complex in the Scutellina, with many well-developed points that can themselves branch (Fig. 8H-J). Although the podial spicules of *D. excentricus* can have many points, they never approach the complexity of some of the larger spicules in *D. vizcainoensis*.

DISTRIBUTION. — The known range of *D. vizcainoensis* is shown in Figure 11 along with the type localities for the junior synonyms *D. mexicanus*, *D. rugosus*, and *D. granti*. It would appear that *D. vizcainoensis* is similar to *D. excentricus* in inhabiting onshore, siliceous, sandy, subtidal areas to depths of about 30 m (Durham et al., 1980). *D. vizcainoensis* seems to have contracted its range since the Plio-Pleistocene. It is known as Pliocene or Pleistocene fossils from at least two localities within the Gulf of California, including the type locality of *D. granti*. In addition, Emerson and Hertlein (1964) list Pliocene "*Dendraster* cf. *D. granti*" just inside the Gulf at Isla San José. The CASIZ collections include Quaternary *D. vizcainoensis* from the San Diego and Los Angeles areas, much further north than the present range. Although Durham et al. (1980) suggest that it might occur "as far north as San Diego and [be] mistaken for *D. excentricus*", I have not been able to find records of Recent material from any further north than Bahía San Quintín. The southern limit of extant *D. vizcainoensis* seems to be in the region of Bahía Tortugas, south of Punta Eugenia, Baja California. It is very common in the Bahía Sebastián Vizcaíno region.

REMARKS. — Durham et al., (1980) were the first to recognize that Clark's (1948) *D. mexicanus* and *D. rugosus* were identical with Grant and Hertlein's (1938) fossil *D. vizcainoensis*. Clark (1948) used the relative width of the poriferous and interporiferous zones to separate *D. mexicanus* from *D. rugosus*, but this criterion is unreliable and cannot be used to distinguish between any of the species here considered synonymous with *D. vizcainoensis* (Figs. 2, 3). Durham (1950) distinguished *D. granti* from *D. vizcainoensis* by the larger tubercles on the oral surface and by its smaller size. However, spine tubercles of juvenile specimens are larger relative to test size, and specimens of *D. vizcainoensis* that are the same size as *D. granti* type material are indistinguishable from it. Clark (1948:317) said of his *D. mexicanus*: "Pedicellariae very numerous, chiefly minute ophicephalous or triphyllous, crowded among the spines." Mortensen, in a footnote to Clark's (1948: 317) statement, and in Mortensen (1948), indicates his surprise at the suggested presence of both ophicephalous and three-valved pedicellariae in a

Dendraster. As Mortensen (1948:385) indicates, there are neither three-valved nor ophicephalous pedicellariae on any *Dendraster* species, and my own unsuccessful search for these types of pedicellariae suggests that Clark (1948) was in error. Mortensen (1948:383) also comments on Clark's (1914) drawings of aboral primary spines: "The figures given by Clark, 1914, Pl. 125. 4, 5, are rather fantastic, or at least, I have never seen anything like." However, Clark's (1914) figures are not so "fantastic" if the spines had come from a *D. vizcainoensis*. They are a good match for some of the shorter aboral primaries of this species. The locality given for the *Albatross* material described by Clark (1914) is within the southern part of the range of *D. vizcainoensis*, so it is not impossible that Clark was, in fact, working with *D. vizcainoensis* and not *D. excentricus*. Caso's (1986) *D. rugosus* was from well outside the range of *D. vizcainoensis*, and her figures indicate that her specimen was actually a juvenile *Clypeaster*, possibly *C. europacificus*.

Dendraster terminalis (Grant and Hertlein, 1938)

Figures 1; 4; 5C; 6G; 7C; 8G; 11; 12; 13

Echinocyamus terminalis — Grant and Hertlein, 1938, p. 48; figs. 5, 6A, B.

Dendraster laevis — Clark, 1948, p. 312; pl. 50, figs. 34-36.

Dendraster laevis — Mortensen, 1948, p. 385.

Dendraster juvenile — Durham, 1955, p. 134.

Dendraster laevis — Durham, 1955, p. 159; fig. 21d.

Dendraster laevis — Durham et al., 1980, p. 168; figs. 11.9a-d.

DESCRIPTION. — With the recognition that *D. terminalis* and *D. laevis* are conspecific, it is possible to expand upon the descriptions given by Clark (1948) and Durham et al. (1980). Although this species is generally the smallest of the three extant taxa, it can attain test lengths in excess of 60 mm. Lightly built and delicate, the test is also low-domed (Fig. 6G), as reflected by the combination of relatively low intercept and slope values in the regression of height versus length (Table 1). The basicoronal system is small, but the interambulacra are widely disjunct in the adults (Fig. 5C, 12C). As in other dendrasterids, the degree of disjunction increases with age (Fig. 12). Comparison of specimens of different ages also shows an increase in width to length ratio in some specimens (Fig. 12), but this is not always well expressed. The apical system is almost central, and the petaloids relatively narrow and short (Fig 5C). However, they still follow the typical dendrasterid pattern: shortest petaloids posteriorly, longest anteriorly. The food grooves do not continue onto the aboral surface (Fig. 5C). They are shallow and sometimes indistinct, particularly in smaller specimens. The peristome is relatively small (Table 1), and the periproct is just submarginal. In some specimens, gonopores appear very early in ontogeny, when the test attains a length of approximately 5 mm (Fig. 13).

The spination of *D. terminalis* is very fine. The aboral primaries lack well-developed club-shaped tips (Fig. 7C), and resemble those of juvenile *D. excentricus* (Fig. 7B). There is no heterogeneity of aboral primary spine length. The oral primaries are longer, but not markedly so. Pedicellariae are of the two sorts known in other *Dendraster*. Podial spicules are very small and simple (Fig. 8G).

In live and in well-preserved specimens, *D. terminalis* is usually a light brownish-yellow aborally, but somewhat darker on the oral surface.

TYPES AND TYPE LOCALITIES. — *D. terminalis* Grant and Hertlein, 1938: HOLOTYPE, CASIZ 029939 (Recent, Isla de Guadalupe, México); PARATYPES, CASIZ 029940 (Recent, holotype locality), University of California, Los Angeles 7713a, b (Recent, holotype locality). See Figure 11.

D. laevis Clark, 1948: HOLOTYPE, LACM 39-80.1 (Recent, north of Santa Barbara Island, California); PARATYPES, 39-80.2 (Recent, holotype locality). See Figure 11.

DIAGNOSIS AND COMPARISON WITH OTHER SPECIES. — The very flat, thin-edged, delicate test, relatively small petaloids and peristome are diagnostic of this species. In life or in well-preserved material, the light brown color and fine spination are also useful in identification. The lack of a prominent attenuation or well-developed club-shaped tip on the aboral primaries distinguish it from *D. vizcainoensis* and *D. excentricus* respectively. *D. terminalis* is the only *Dendraster* in which the food grooves are restricted to the oral surface. This is a good feature for identification of adult specimens, but in juveniles of the other two species, food grooves can be likewise absent from the aboral surface. The podial spicules of *D. terminalis* always lack the secondary branching or additional points so characteristic of those in *D. excentricus* and *D. vizcainoensis*. The very early appearance of the gonopores in *D. terminalis* is also diagnostic.

DISTRIBUTION. — Clark (1948) knew *D. terminalis* (as *D. laevis*) from the Channel Islands south to the Islas Los Coronados off northwestern México. The SIO material indicates that it also occurs at Isla de Guadalupe, México (Fig. 11). Durham et al. (1980) suggest that *D. terminalis* ranges “possibly as far south as Bahía de Tortuga [presumably Bahía Tortugas]” on Baja California, but I have not been able to verify this. I have seen material from Isla San Martín, near Bahía San Quintín (Fig. 11). Outside of Isla de Guadalupe, this is the southernmost record of which I am aware. The majority of *D. terminalis* collections come from offshore islands. It therefore seems to be a more insular species, and is not found in waters as shallow as those in which *D. excentricus* and *D. vizcainoensis* are capable of living. Caso (1980) plotted *D. terminalis* within the Gulf on her map, but just as for *D. excentricus* (see above), she seems to have confused Clark’s (1948) “Coronados Islands, México” which are near San Diego, with the Isla Coronados found in the Gulf of California. Therefore, *D. terminalis* is not known to occur in the Gulf of California.

No fossils of this species are known.

REMARKS. — Very early appearance of gonopores in some specimens of *D. terminalis* was partly responsible for the inability of several echinologists to recognize that the very tiny, but supposedly “mature” *Echinocyamus terminalis* (Grant and Hertlein, 1938) was the same as Clark’s (1948) *D. laevis*. Interestingly, Grant and Hertlein’s (1938) holotype completely lacks gonopores (Fig. 4B), although several of the paratypes have them (Fig. 4C). Juvenile “*D. laevis*” from the type locality (Fig. 4A) are indistinguishable from the holotype of *E. terminalis* (Fig. 4B). Therefore, the *E. terminalis* types are in fact juveniles of a species with early-appearing gonopores that “grow up into” *D. laevis*. This in turn means that Mironov’s (1991) conclusions regarding *E. terminalis* must be modified to exclude it from *Marginoproctus* Budin, 1980. It also means that *Echinocyamus* can no longer be considered as occurring off the California coast.

A full size range of *D. terminalis* illustrates the usual ontogenetic features and changes characteristic of other species of *Dendraster* (Fig. 12). Disjunction of the interambulacra starts at a test length of approximately 10 mm (Fig. 12). As described above, *D. terminalis* is unique in acquiring gonopores very early in ontogeny. No other scutelline that attains

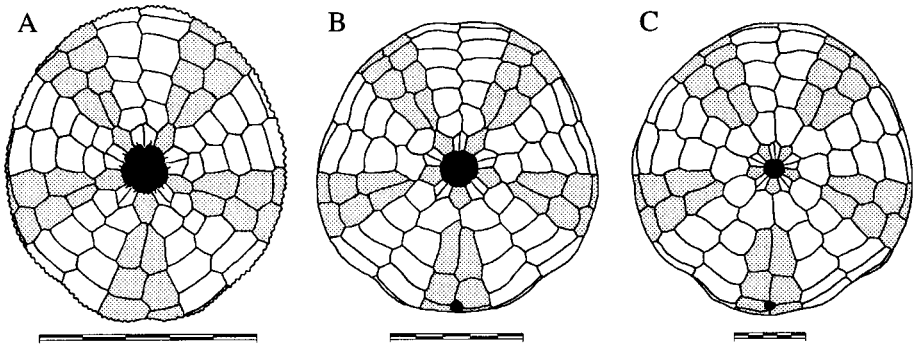


Figure 12. Oral views of *Dendraster terminalis* (Grant and Hertlein, 1938), all from Isla de Guadalupe, México: (A) Early juvenile, 7.3 mm test length, without gonopores, SIO 2488; (B) Late juvenile, 10.3 mm test length, without gonopores, SIO 2490; (C) Adult with gonopores, 20.3 mm test length, SIO 2490. Interambulacral plates shaded, mouth and periproct in solid black.

comparable adult sizes has genital openings as small as 5 mm in test length (Fig. 13). Grant and Hertlein (1938) ascribed the “lack of prominent genital pores” in some of their type material not to immaturity, but to sexual dimorphism. There does not appear to be prominent sexual dimorphism in gonopore size, or any other character, in this species.

Very little is known about the biology of *D. terminalis*. Merrill and Hobson (1970:599) indicate that it can adopt the upright feeding posture described above for *D. excentricus*, but detailed observations have still to be published. *D. terminalis* also exhibits several features that suggest retention of juvenile characteristics into adulthood (see below), but there is no obvious explanation based on habitat alone for either the early onset of gonopore formation or paedomorphosis.

KEY TO THE EXTANT SPECIES OF *DENDRASTER*

1a. Test low, with sharp ambitus (Fig. 6G); petaloids short, those in ambulacra I and V less than half the length of their corresponding ambulacra (Fig. 5C); food grooves restricted to oral surface (Fig. 5C); aboral primary spines neither conspicuously swollen to produce club-shaped tip nor distally attenuated (Fig. 7C); podial spicules simple, with only 3 points (Fig. 8G); gonopores often appearing when test approaches 5 mm in length *D. terminalis*

1b. Test variable in height (Fig. 6A-F), but almost always conspicuously domed and with thick ambitus (some aberrant populations from Washington State have a low test [P. Carlstrom, pers. comm.], but the margin is still thicker than in *D. terminalis*); petaloids long, those in ambulacra I and V reach at least halfway down their corresponding ambulacra (Fig. 5A, B); food groove extending from oral surface onto aboral surface (Fig. 5A, B); aboral primary spines conspicuously swollen to produce club-shaped tip or distally attenuated (Fig. 7A, D); podial spicules usually with more than 3 points (Fig. 8C-F, H-J) (several specimens might need to be checked for this feature, as some *D. excentricus* have relatively simple spicules, as in Fig. 8F); gonopores not appearing until test approaches 20 mm in length 2

2a. Test constructed of thick plates, not especially fragile around peristome; aboral primary spines of uniform length in a single specimen, short and strongly club-shaped (Fig. 7A) over entire aboral surface (aboral primary tubercles also of uniform size); podial spicules usually with fewer than 6 points, exceptionally with 7 (Fig. 8C-F) *D. excentricus*

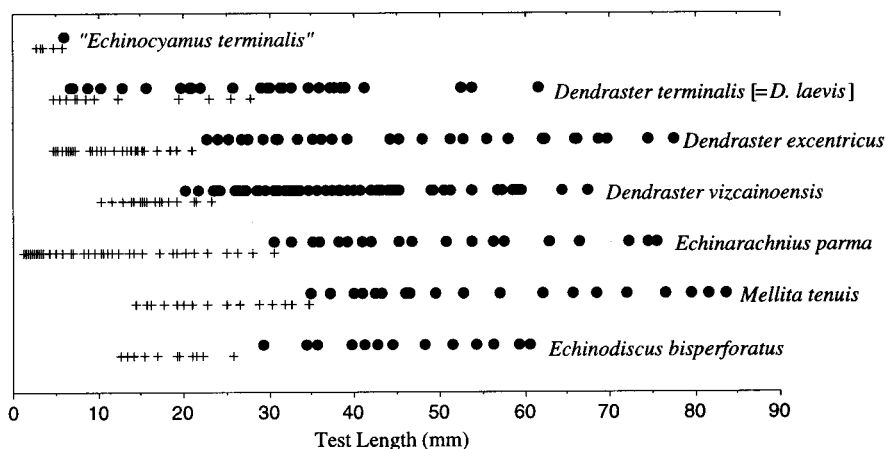


Figure 13. Presence of gonopores as a function of test length in selected scutellines. Crosses indicate specimens without gonopores, dots indicate specimens with gonopores.

2b. Test lightly built, fragile, especially around peristome; aboral primary spines of varying length in a single specimen (Fig. 7D, E), very long and pointed adjacent to food grooves and in interporiferous zone of petaloids (tubercles are much larger in these same areas); podial spicules very elaborate, usually with more than 6 occasionally branched points, exceptionally with fewer (Fig. 8H-J) *D. vizcainoensis*

DISCUSSION

PHYLOGENY. — The outgroup of the family Dendrasteridae is still a subject of some dispute. Some workers feel that similarities in spination (Mooi, 1987) and tooth morphology (Jensen, 1981) link dendrasterids and the lunulate mellitid taxa. It is possible that these features are in fact plesiomorphic for the Scutellina, and do not offer solid evidence for relationships among the scutellines. This being the case, and given the uncertainty in the relationships of non-lunulate sand dollars (see review in Beadle, 1989), it is difficult to determine the polarity of characters within the Dendrasteridae.

It would appear that the only unequivocal dendrasterids are the genera *Merriamaster* and *Dendraster*. *Merriamaster* is known only as a Neogene fossil of the western United States. It is tempting to consider it as a monophyletic outgroup to *Dendraster*, but there is absolutely no phylogenetic evidence to support this. *Merriamaster* is a somewhat aberrant, miniaturized dendrasterid with reduced food grooves and only slight eccentricity. Some of the specimens are preserved well enough to show that they had extremely long spines, and that there might be the same heterogeneity of spination as in *D. vizcainoensis*. Therefore, there is a distinct possibility that *Merriamaster* is most closely related to a subset of *Dendraster*, making the latter paraphyletic, or necessitating synonymy of *Merriamaster* with *Dendraster*. In either case, the likelihood that *Merriamaster* evolved from some taxon well within the *Dendraster* clade indicates that it cannot be used as an outgroup to *Dendraster*.

Without any readily identifiable outgroup for *Dendraster*, resolution of the relationships among the three living species must rely on character states not found in other scutellines, but that are present in *Dendraster*, or a subset thereof. Eccentricity is one such character, and it tends to support monophyly of *Dendraster* plus *Merriamaster*. Eccentricity is known in other taxa, such as *Scutellaster* and *Echinarachnius*, but these groups have characters that place them well outside the *Dendraster* clade. *Scaphechinus*, a living genus from the western Pacific, is very similar to *Dendraster* in plate and food groove pattern. Although these are plesiomorphic features, and do not establish *Scaphechinus* as the sister group to the dendrasterids, *Scaphechinus* is here viewed as a reliable extant outgroup for *Dendraster*. Apart from eccentricity, there are no other unequivocal synapomorphies for the Dendrasteridae, and no autapomorphies for *Dendraster* itself that would exclude *Merriamaster*. Because both these genera have a rich fossil record, excluding fossils from a phylogenetic analysis will cause the picture to remain incomplete. At present, and without considering any of the fossil taxa, we can say only that the three extant species of *Dendraster* form a clade, and that it is possible to resolve the relationships among these species. Future work should be able to use this as a starting point for an analysis that will consider the complete history of this important group.

There are two character states found in a subset of extant *Dendraster* that are not found in any other living scutelline: 1. Continuation of the food grooves onto the aboral surface. This characteristic is well known in fossil *Dendraster*, and is probably found in *Merriamaster* as well. Among extant *Dendraster*, it occurs in *D. excentricus* and *D. vizcainoensis* (Fig. 5A, B), but not *D. terminalis* (Fig. 5C). 2. Highly complex podial spicules. Spicules are completely unknown from fossils, but they are well documented for living scutellines (Mooi, 1986a). More detailed comparison of podial spicules in the non-lunulates *Echinarachnius* and *Scaphechinus* (Fig. 8A, B), long associated with dendrasterids in systematic treatments, show that complexity of podial spicules is a synapomorphy for *D. excentricus* and *D. vizcainoensis*.

Because of the amount of evolution represented by fossils that are omitted from the above treatment, the suggestion that *D. excentricus* and *D. vizcainoensis* are sister taxa should not be taken as an indication that they are particularly closely related. Putative stem taxa are not considered here. In addition, *D. terminalis* should not be considered as somehow representative of a "primitive" *Dendraster*. There are several autapomorphies, including early appearance of gonopores, that indicate a high degree of specialization of *D. terminalis*. As discussed below, some features such as reduced eccentricity, poorly developed clubs on aboral primaries, thin, fragile test, and even the absence of aboral food grooves could result from heterochronic processes such as paedomorphosis. Paedomorphosis is a well-known confounder of phylogenetics that can only be avoided through careful analysis, especially of features that are not affected by ontogenetic changes.

ONTOGENY AND HETEROCHRONY. — The vast majority of work on very early ontogeny of echinoids has focused on the cellular dynamics, spicule formation, and behavior of larvae. Much less is known about events in post-metamorphic ontogeny. Mooi (1988; 1990b) emphasized the significance of ontogenetic analyses in understanding the relationships among clypeasteroids, and Beadle (1989) showed how knowledge of post-metamorphic juveniles within *Dendraster* can demonstrate the sudden appearance of unusual morphologies. The latter's study of the origin of eccentricity in dendrasterids was also very important in pointing out the significance of heterochrony in the history of the dendrasterids. That the type material of *D. terminalis* represents the early juvenile of *D.*

laevis, a junior synonym, also highlights the taxonomic importance of full descriptions of the post-metamorphic ontogeny of sand dollars.

Establishing the type of heterochrony operating within a given species depends on knowing the age of specimens to be compared. Usually, absolute age data are unavailable, and allometry of many individuals is used to make inferences about a species' development. For comparative studies, it is helpful to have markers along ontogenetic trajectories that can fix events in ontogeny, and permit comparison of ontogenetic changes among species. For echinoids, one such marker is the appearance of the gonopores. Comparison of the test length at which gonopores first appear are extremely rare for the sand dollars. However, this can be very informative, as Figure 13 shows. It is clear from this analysis that *D. terminalis* develops gonopores at smaller sizes than any other large scutelline, including representatives of the Echinarachniidae, Mellitidae, and Astrictypeidae. Mortensen (1948:380) notes that in one species of *Scaphechinus*, the "pores have not yet appeared in a specimen 23 mm long," suggesting that among possible candidates for an extant outgroup to *Dendraster*, gonopores do not appear at small test sizes. As noted above, this phenomenon was at least partially responsible for the taxonomic confusion surrounding *D. terminalis*, including its placement in the wrong suborder.

Although it is too early in our knowledge of the ecology of these species to speculate on the adaptive significance of early appearance of gonopores, it is useful to point out that it is correlated with paedomorphosis of certain features in *D. terminalis*. In order to identify such features, it is necessary to first determine which were present in the ancestor of the *Dendraster* clade. This is not the easiest of tasks, given our incomplete knowledge of the relationships among fossil taxa. However, the lightly built, fragile test, small petaloids, and low level of differentiation in aboral primary spination all suggest retention of juvenile features. Relying strictly on *Scaphechinus* for outgroup comparison, it would appear that simplicity of the podial spicules and restriction of the food grooves to the oral surface are synapomorphies for *D. excentricus* and *D. vizcainoensis* (see above). However, we cannot rule out the possibility that both these features are also results of paedomorphosis. Among dendrasterids, this suite of paedomorphic features seem to be unique to *D. terminalis*, and might be related to the fact that it is the only *Dendraster* not known to occur in very shallow, subtidal habitats. So little is known of its life cycle that the paedomorphosis noted above is very difficult to relate to what little is known of the biology of species such as *Mellita grantii* and *Encope stokesi* (see Ebert and Dexter, 1975; Dexter, 1977). These taxa also exhibit paedomorphic features, but much more study will be necessary to establish any general principles at work in generating these unusual morphologies.

DISTRIBUTION. — There is now abundant evidence that at least one species of *Dendraster*, *D. vizcainoensis*, was present in the Gulf of California possibly as late as the Pleistocene. Why is *Dendraster* no longer found there? One possibility is elevation of temperatures within the Gulf since the Pliocene. *D. excentricus* ranges far north, and seems to be typical of relatively cold water. *D. vizcainoensis* seems to be more at home in warmer habitats, as its occurrence in and around Scammon's Lagoon and Bahía Sebastián Vizcaíno indicate. Neither this species nor *D. terminalis* are found further north than southern California, indicating that these taxa are restricted to somewhat warmer waters than *D. excentricus*. However, even in the southern parts of their range, the three extant *Dendraster* are most abundant in regions that show relatively depressed sea temperatures (see maps in Brusca, 1980). None of the extant *Dendraster* are found in water as warm as that now

found within the Gulf of California. Extirpation of *D. vizcainoensis* from the Gulf probably began with isolation of populations in the northern part of the Gulf during post-Pleistocene warming. At that point, single or sustained high-temperature events would be sufficient to end survival of these isolates. The same warming, especially in the southern part of the Gulf, could prevent recruitment from Pacific coast populations around the southern tip of Baja.

Further studies could still implicate other physical or biological factors in the present-day exclusion of *Dendraster* from the Gulf. Very few data on clypeasteroid temperature tolerance exist. It is possible that echinoid larvae are even more subject to environmental constraints than adults. Competition for suitable habitat is unlikely to have been involved in making the Gulf a marginal habitat for *Dendraster*. Species that could be considered in this regard include the lunulates *Encope grandis* L. Agassiz, 1841, *Encope californica* Verrill, 1870, and *Mellita grantii* Mortensen, 1948. Resource partitioning has been documented for some sand dollar species (Telford and Mooi, 1986; Telford et al., 1987), but it is unlikely that substrate preferences of *Dendraster*, *Encope*, and *Mellita* are sufficiently alike to prohibit co-existence. The upright posture of *Dendraster* would further tend to reduce overlap in habitat requirements. More work is required to determine: i) if *Dendraster* and other sand dollar species co-existed in the Gulf in the past; ii) how preference studies like those of Telford and Mooi (1986) can estimate the likelihood of competitive exclusion; iii) if rising sea surface temperatures can cause the complete extirpation of either the adults or planktonic larvae of a sand dollar; iv) the correlation in timing of events such as the warming of the Gulf, isolation of Gulf populations, and subsequent disappearance of *Dendraster*.

Beadle (1991) documented the expansion of dendrasterids in space and time along the Pacific coast of North America. Based on the fossil record, he suggested that the dendrasterids expanded southward to Baja in the Late Miocene and Early Pliocene, and then northward during the Quaternary. It is a truism to say that the history of a supra-specific taxon's diversification is a sum of the histories of its constituent species. Presumably, as speciation occurs, each species embarks on its own, independent evolutionary trajectory, largely without being influenced by the history of its congeners. Therefore, it is somewhat misleading to discuss the expansion of a supra-specific taxon as if it were a cohesive ecological or phylogenetic unit. It is more informative to examine the individual histories of the taxa within the clade. In this context, the "dendrasterid expansion" in the Quaternary is almost entirely due to the expansion of a single, apparently opportunistic species, *D. excentricus*, and not the widened distribution of the family as a whole. If the removal of *D. vizcainoensis* from the Gulf of California is considered, there has actually been a contraction of the southern range of the genus since the Quaternary that partially offsets the northward expansion of *D. excentricus*.

Because of the ranges inhabited by its constituent species, *Dendraster* is fertile ground for the analysis of environmental parameters that govern species distributions. The distributions of other marine invertebrates (particularly mollusks) are limited by environmental factors to the point where they help describe several northwest Pacific faunal provinces (see review in Brusca, 1980). These factors apparently do not apply to *D. excentricus*, which crosses the boundaries between all of the provinces from Alaska to Bahía Magdalena. Coupled with analyses of *Dendraster*'s unusual morphology, biogeographic studies might be able to put this into a historical context.

For example, several beaches in the San Francisco area are littered with both fossil *Scutellaster* (which became extinct during the Quaternary, possibly as late as the end of the Pleistocene) and living *D. excentricus*. There seems to be little, if any, temporal overlap of these taxa in this area (Beadle, 1991), further suggesting that *Dendraster* replaced (but did not necessarily displace) *Scutellaster*. *Scutellaster* also had an apical system that was posterior to the midpoint of the test. Although never as eccentric as some *Dendraster* are known to be, the striking coincidence of this morphology with a north-western Pacific distribution needs to be explored to determine if there is any causal correlation between eccentricity and Pacific coast habitats. Perhaps this will also shed light on whether there is a connection between the extinction of *Scutellaster* and the northward expansion of *D. excentricus*.

ACKNOWLEDGMENTS

I would like to acknowledge the friendship and help of the late and dearly missed D. Chivers, to whom this paper is dedicated. I would also like to express thanks to C. Groves and G. Hendler of the LACM for their tireless efforts in tracking down Hancock types and other specimens. S. Luke provided critical material from SIO. C. Ahearn and D. Pawson provided loans from the NMNH. B. Van Syoc, L. Kools, and J. DeMouthe helped with collections and specimen data from CASIZ and CASG. A. Miljutin and A. Mironov provided valuable information regarding Eschscholtz and the disposition of his type material. B. Van Syoc, M. Telford, C. Powell, and two other reviewers provided fitting amendments to the manuscript. S. Middleton prepared the photos in Fig. 9. N. Holland extended bibulous hospitality during my stay in La Jolla. Research was supported by CAS In-House research funds.

LITERATURE CITED

- Agassiz, A. 1872-1874. Revision of the Echini. Mem. Mus. Comp. Zool. 3: 383-762.
- Agassiz, L. 1841. Échinides. Famille des clypéastroides. Des Scutelles. Monographies des Echinodermes vivans et fossiles 2: 1-151.
- _____ and P. Desor. 1847. Catalogue raisonné des espèces, des genres et des familles d'Échinides. Ann. Sci. Nat., Zool., series 3. 7:129-168; 8: 4-35, 355-380.
- Beadle, S. C. 1989. Ontogenetic regulatory mechanisms, heterochrony, and eccentricity in dendrasterid sand dollars. Paleobiology 15: 205-222.
- _____. 1991. The biogeography of origin and radiation: Dendrasterid sand dollars in the northeastern Pacific. Paleobiology 17:3 25-339.
- Boidron-Metairon, I. 1988. Morphological plasticity in laboratory-reared echinoplutei of *Dendraster excentricus* (Eschscholtz) and *Lytechinus variegatus* (Lamarck) in response to food conditions. J. Exp. Mar. Biol. Ecol. 119: 31-41.
- Booolootian, R. A. 1964. The occurrence of *Balanus concavus* on the test of *Dendraster excentricus*. Bull. S. Cal. Acad. Sci. 63: 185-191.
- Brusca, R. C. 1980. Common intertidal invertebrates of the Gulf of California. Univ. Arizona, Tucson. 513 p.
- Budin, I. N. 1980. A new genus of sand dollars of the family Fibulariidae (Echinoidea). Zoologicheskii Zhurnal 59: 305-308 (in Russian).
- Burke, R.D. 1983. Development of the larval nervous system of the sand dollar, *Dendraster excentricus*. Cell Tissue Res. 229: 145-154.
- _____. 1984. Pheromonal control of metamorphosis in marine invertebrate larvae: Stimulus and response. Can. J. Zool. 61: 1701-1719.

- Caso, M. E. 1980. Los equinoideos del Pacífico de México, parte tercera - Orden Clypeasteroidea. Centro de Cienc. del Mar y Limnol. Univ. Nal. Autón. México, Publ. Esp. 4: 1-252
- _____. 1986. Los equinodermos del Golfo de California colectados en las campañas SIPCO I-II-III a bordo del B/O "El Puma". An. Inst. Cienc. del Mar y Limnol. Univ. Nal. Autón. México 13: 91-184.
- Chia, F.-S. 1969a. Histology of the pedicellariae of the sand dollar, *Dendraster excentricus* (Echinodermata). J. Zool. London 157: 503-507.
- _____. 1969b. Some observations on the locomotion and feeding of the sand dollar *Dendraster excentricus* (Eschscholtz). J. Exp. Mar. Biol. Ecol. 3: 162-70.
- _____. 1973. Sand dollar: A weight belt for the juvenile. Science. 181: 73-74.
- Clark, H.L. 1914. Hawaiian and other Pacific Echini. The Clypeastridae, Arachnoididae, Laganidae, Fibulariidae, and Scutellidae. Mem. Mus. Comp. Zool. 46: 1-78.
- _____. 1935. Some new echinoderms from California. Annals. Mag. Nat. Hist., 10th series. 15: 120-129.
- _____. 1940. Revision of the keyhole urchins (*Mellita*). Proc. U.S. Nat. Mus. 89: 435-444.
- _____. 1948. A report on the Echini of the warmer eastern Pacific, based on the collections of the Velero III. Allan Hancock Pacific Exped. 8: 225-352.
- Conrad, T. A. 1857. Report on the palaeontology of the survey. Rep. Explorations and Surveys to Ascertain the Most Practicable and Economical Route for a Railroad from the Mississippi River to the Pacific Ocean. 7: 189-196.
- Dexter, D. M. 1977. A natural history of the sand dollar *Encope stokesi* L. Agassiz in Panama. Bull. Mar. Sci. 27: 544-551.
- Durham, J. W. 1950. 1940 E. W. Scripps Cruise to the Gulf of California. Part II, Megascopic paleontology and marine stratigraphy. Geol. Soc. Am. Mem. 43: 1-216.
- _____. 1955. Classification of clypeasteroid echinoids. Univ. Calif. Publ. Geol. Sci. 31: 73-198.
- _____, C.D. Wagner and D.P. Abbott. 1980. Echinoidea: The sea urchins. Pages 16-176 in R.H. Morris et al., eds. Intertidal Invertebrates of California. Stanford University, California. 690 p.
- Ebert, T.A. and D.M. Dexter. 1975. A natural history study of *Encope grandis* and *Mellita grantii*, two sand dollars in the northern Gulf of California, Mexico. Mar. Biol. 32: 397-407.
- Emerson, W.K. and L.G. Hertlein. 1964. Invertebrate megafossils of the Belvedere Expedition to the Gulf of California. Trans. San Diego Soc. Nat. Hist. 13: 333-368.
- Emlet, R.B. 1982. Echinoderm calcite: A mechanical analysis from larval spicules. Biol. Bull. 163:264-275.
- _____. 1983. Locomotion, drag, and the rigid skeleton of larval echinoderms. Biol. Bull. 164: 433-445.
- _____. 1986. Larval production, dispersal, and growth in a fjord: A case study on larvae of the sand dollar *Dendraster excentricus*. Mar. Ecol. Prog. Ser. 31: 245-254.
- Eschscholtz, F. 1831. Zoologischer Atlas, enthaltend Abbildungen und Beschreibungen neuer Thierarten, während des Flottcapitains von Kotzebue zweiter Reise um die Welt, auf der Russisch-Kaiserlichen Kreigeschluupp Predpriaetië in den Jahren 1823-1826. Viertes Heft. G. Reimer, Berlin. 19 p.
- Grant, U. S. IV and L. G. Hertlein. 1938. The west American Cenozoic Echinoidea. Publ. Univ. Calif. Los Angeles Math. Phys. Sci. 2: 1-225.
- Highsmith, R.C. 1982. Induced settlement and metamorphosis of the sand dollar (*Dendraster excentricus*) larvae in predator free sites: Adult sand dollar beds. Ecology 63: 329-337.
- _____. and R. B. Emllet. 1986. Delayed metamorphosis: Effect on growth and survival of juvenile sand dollars (Echinoidea: Clypeasteroidea). Bull. Mar. Sci. 39: 347-361.
- Jensen, M. 1981. Morphology and classification of Euechinoidea Bronn, 1860—A cladistic analysis. Vidensk. Medd. Dansk Nat. Foren. 143: 7-99.

- Kew, W. S. W. 1920. Cretaceous and Cenozoic Echinoidea of the Pacific coast of North America. Univ. California Publ. Bull. Dept. Geol. 12: 23-236.
- Lamarck, J. B. 1816. Histoire Naturelle des Animaux sans Vertèbres. III. Paris. 130 p.
- Lambert, J. M. 1899. Études sur quelques Échinides de l'Infra-Lias et du Lias. Bull. Soc. Sci. Hist. et Nat. de l'Yonne 53: 3-57.
- _____ and P. Thiéry. 1909-1925. Essai de nomenclature raisonnée des Échinides. Chaumont, Librairie L. Ferrière. 607 p.
- Leske, N. G. 1778. Additamenta ad Jacobi Theodori Klein naturalem dispositionem Echinodermatum et lucubratiunculam de aculeis echinorum marinarum. Lipsiae, Leipzig. 278 p.
- Merrill, R. J. and E. S. Hobson. 1970. Field observations of *Dendraster excentricus*, a sand dollar of western North America. Am. Midland Naturalist 83: 595-624.
- Mironov, A. N. 1991. Sea urchins of the genus *Marginoproctus* (Echinoidea, Fibulariidae). Zoologychesky Zhurnal 1991: 147-151 [in Russian].
- Mooi, R. 1986a. Non-respiratory podia of clypeasteroids (Echinodermata, Echinoidea): II. Diversity. Zoomorphology 106: 75-90.
- _____. 1986b. Structure and function of clypeasteroid miliary spines (Echinodermata, Echinoidea). Zoomorphology 106: 212-223.
- _____. 1987. A cladistic analysis of the sand dollars (Clypeasteroidea: Scutellina) and the interpretation of heterochronic phenomena. Ph.D. Thesis, University of Toronto, Canada. 208 p.
- _____. 1988. Tininess in clypeasteroids: The phylogenetic and functional implications of being small. Page 806 in R. D. Burke et al., eds. Echinoderm Biology, Proc. 6th Int. Echinoderms Conf. A. A. Balkema, Rotterdam. 818 p.
- _____. 1989. Living and fossil genera of the Clypeasteroidea (Echinoidea: Echinodermata): An illustrated key and annotated checklist. Smithsonian Contrib. Zool. 488: 1-51.
- _____. 1990a. Paedomorphosis, Aristotle's lantern, and the origin of the sand dollars (Echinodermata: Clypeasteroidea). Paleobiology 16: 25-48.
- _____. 1990b. Progenetic miniaturization in the sand dollar *Sinaechinocyamus*: Implications for clypeasteroid phylogeny. Pages 137-143 in C. De Ridder et al., eds. Echinoderm Research, Proc. 2nd European Conf. on Echinoderms. A. A. Balkema, Rotterdam. 343 p.
- _____ and C. P. Chen. 1995. Weight belts, diverticula, and the phylogeny of the sand dollars (Clypeasteroidea: Echinoidea). Bull. Mar. Sci. 57: 186-195.
- Mortensen, T. 1921. Studies of the development and larval forms of echinoderms. G. E. C. Gad, Copenhagen. 261 p.
- _____. 1948. A monograph of the Echinoidea. IV.2. Clypeasteroidea. C.A. Reitzel, Copenhagen. 471 p.
- Nakamura, R. 1994. Hydrodynamic limits to the bathymetric distribution of *Dendraster excentricus*. Pages 797-801 in: B. David et al., eds. Echinoderms through time (Echinoderms Dijon). Proc. 8th Int'l. Echinoderms Conf. A. A. Balkema, Rotterdam. 940 p.
- Niesen, T. M. 1977. Reproductive cycles of two populations of the Pacific sand dollar *Dendraster excentricus*. Mar. Biol. 42: 365-373.
- O'Neill, P. L. 1978. Hydrodynamic analysis of feeding in sand dollars. Oecologia 34: 157-174.
- Rathbun, R. 1886. Catalogue of the collection of recent Echini in the United States National Museum. Proc. U.S. Nat. Mus. 9: 1-282.
- Raup, D. M. 1956. *Dendraster*: A problem in echinoid taxonomy. J. Paleo. 30: 685-694.
- Smith, A. L. 1981. Comparison of macrofaunal invertebrates in sand dollar beds and in adjacent areas free of sand dollars. Mar. Biol. Berl. 65: 191-198.
- Stanton, R. J., Jr., J. R. Dodd and R. R. Alexander. 1979. Eccentricity in the clypeasteroid echinoid *Dendraster*: Environmental significance and application in Pliocene paleoecology. Lethaia 12: 75-78.
- Telford, M., R. Mooi and O. Ellers. 1985. A new model of podial deposit feeding in the sand dollar, *Mellita quinquesperforata* (Leske): The sieve hypothesis challenged. Biol. Bull. 169: 431-448.

- Telford, M. and R. Mooi. 1986. Resource partitioning by sand dollars in carbonate and siliceous sediments: Evidence from podial and particle dimensions. *Biol. Bull.* 171: 197-207.
- _____, _____ and A. S. Harold. 1987. Feeding activities of two species of *Clypeaster* (Echinoidea, Clypeasteroidea): Further evidence of clypeasteroid resource partitioning. *Biol. Bull.* 172: 324-336.
- Timko, P. L. 1976. Sand dollars as suspension feeders: A new description of feeding in *Dendraster excentricus*. *Biol. Bull.* 151: 247-259.
- Valenciennes, A. 1846. Zoophytes. In: A. A. Du Petit-Thouars, *Voyage autour du monde sur le frégate la "Venus", pendant les années 1836-1839*. Gide et cie, Paris. 34 p.
- Verrill, A. E. 1870. Descriptions of echinoderms and corals from the Gulf of California. *Amer. J. Sci.*, ser. 2. 49: 93-100.
- Wagner, C. D. 1974. Fossil and Recent sand dollar echinoids of Alaska. *J. Paleo.* 48:105-123.
- Zar, J. H. 1984. *Biostatistical analysis*. Prentice-Hall, New Jersey. 718 p.

DATE ACCEPTED: July 27, 1995

ADDRESS: *Department of Invertebrate Zoology and Geology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118-4599, E-mail: rmooi@cas.calacademy.org.*