

Taxonomic significance of test morphology in the echinoid genera *Diadema* Gray, 1825 and *Echinothrix* Peters, 1853 (Echinodermata)

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ABSTRACT

Test morphologies were examined for both living and denuded specimens of all established species of *Diadema* Gray, 1825 and *Echinothrix* Peters, 1853, including two colour morphs of *Echinothrix calamaris* (Pallas, 1774). Twenty-eight morphological characters were measured and analysed using ordination by multi-dimensional scaling (MDS) and cluster analysis. Specific test features were found which differentiated the species. Of these the apical systems, markings on the genital plates, features of the median areas of the interambulacra and distribution of iridophores were particularly useful forms of taxa distinction. Well defined associations in test morphologies were found between *Diadema antillarum* Philippi, 1845, *D. ascensionis* Mortensen, 1909, *D. mexicanum* A. Agassiz, 1863, *D. savignyi* Michelin, 1845 and *D. paucispinum* A. Agassiz, 1863. *Diadema setosum* (Leske, 1778) and particularly *D. palmeri* Baker, 1967 appeared to be outlying species within the genus; *D. palmeri* being the only species within the genus *Diadema* to have a monocyclic apical system. Test morphologies of *Echinothrix diadema* (Linnaeus, 1758) and *E. calamaris* were distinctly different, with marked differences in test size and shape, plate arrangements, features of the apical system and structures of the median areas of the interambulacra. The different colour morphs of *E. calamaris* demonstrated similar test features; however, differences were found which suggest that the brown colour morph may be a separate species or subspecies.

KEY WORDS

Echinodermata,
sea urchin,
morphology,
Diadema,
Echinothrix.

RÉSUMÉ

Signification taxonomique de la morphologie du test chez les genres d'échinides Diadema Gray, 1825 et Echinothrix Peters, 1853 (Echinodermata).

La morphologie du test a été examinée pour des spécimens vivants et dénudés de toutes les espèces établies de *Diadema* Gray, 1825 et d'*Echinothrix* Peters, 1853, y compris deux morphes de couleur d'*Echinothrix calamaris* (Pallas, 1774). Vingt-huit caractères morphologiques ont été mesurés et analysés en utilisant la classification par la graduation multi-dimensionnelle (MDS) et l'analyse par segments. Nous avons trouvé des dispositifs spécifiques du test qui différencient les espèces. Parmi ceux-ci, les systèmes apicaux, les inscriptions des plaques génitales, les dispositifs des secteurs médians de l'interambulacra et la distribution des iridophores sont des formes particulièrement utiles pour la distinction des taxons. Cependant, beaucoup de similitudes ont été également trouvées. Des associations distinctes dans la morphologie du test ont été trouvées entre *Diadema antillarum* Philippi, 1845, *D. ascensionis* Mortensen, 1909, *D. mexicanum* A. Agassiz, 1863, *D. savignyi* Michelin, 1845 et *D. paucispinum* A. Agassiz, 1863. *Diadema setosum* (Leske, 1778) et *D. palmeri* Baker, 1967 semblent être des espèces périphériques dans le genre; *D. palmeri* est la seule espèce de *Diadema* à avoir un système apical monocyclique. Les morphologies du test d'*Echinothrix diadema* (Linnaeus, 1758) et d'*E. calamaris* étaient distinctement différentes, avec des différences marquées pour la taille et la forme du test, l'arrangements des plaques, les dispositifs du système apical et les structures des secteurs médians de l'interambulacra. Les différents morphes de couleur d'*E. calamaris* ont démontré des dispositifs semblables du test; cependant, on a trouvé des différences distinctes qui suggèrent qu'elles puissent être des espèces ou des sous-espèces distinctes.

MOTS CLÉS

Echinodermata,
oursin,
morphologie,
Diadema,
Echinothrix.

INTRODUCTION

Recent research has indicated that echinoids play an important role in the ecology of coral reefs (Hughes 1994; Lirman 2001; Williams & Polunin 2001). One group of sea urchins, the Diadematidae Peters, 1855, has been shown to have a very important role as reef grazers, particularly due to their size and numbers (Hughes *et al.* 1987). Species of the genus *Diadema* Gray, 1825 have been reported to be the most widespread and ecologically important shallow water genera of tropical sea urchins (Lawrence & Sammarco 1982; Lessios 1988; Birkeland 1989; Carpenter 1997). Distinctions in their distributions and ecology have not been easy to elucidate because of difficulties in making

reliable identifications (Clark & Owen 1965; Pearse 1970, 1998).

Lessios *et al.* (2001) examined the mitochondrial DNA of 482 individuals of *Diadema*, with a reasonable geographic coverage including the originally proposed component species. Lessios *et al.* (2001) reiterated H. L. Clark's (1925) view that morphological differences between species are sometimes so slight that specimens can usually not be identified without knowing where they were collected, thus addressing the need for clear diagnostic structures to be established.

Members of the family Diadematidae have tests that are approximately spherical, but depressed apically. The family name is derived from the naked test shape and structure, resembling that of a

crown or diadem (Gray 1825). This is particularly apparent in the genera *Diadema* and *Echinothrix* Peters, 1853 whose test morphologies were closely examined in this study.

This investigation seeks to answer the question: do test structures of species within the genera *Diadema* and *Echinothrix* contain diagnostic species-specific characters that can be used to identify and differentiate these closely related species? This information was then used to compare morphological relationships between species. The intention of this investigation is not to describe the generic test features of *Diadema* and *Echinothrix*, extensively done by Mortensen (1940), and by Baker (1967) for *Diadema palmeri*, but to point out differences in our findings where they occur.

MATERIALS AND METHODS

Preserved specimens of *Diadema* and *Echinothrix* were examined at the Zoological Museum, Copenhagen, the Smithsonian Museum of Natural History, Washington, the Natural History Museum, London, the New Zealand National Institute of Water and Atmospheric Research, Wellington, and the Museum of New Zealand, Wellington. Both denuded tests and complete specimens were examined and compared. Correct identifications of preserved specimens were made using spine (Coppard & Campbell 2004) and tridentate pedicellariae morphology (Coppard & Campbell in press) and the geographical collection data of each specimen was carefully noted. Living specimens were also observed in their natural habitats and collected from Mexico, Jamaica, Hawaii, Fiji, Panama, Cook Islands, Tahiti, New Caledonia and New Zealand, preserved in 70% ethanol and stored in clearly labelled glass jars. Specimens were measured (horizontal diameter, vertical diameter, diameter of apical system, periproct and peristome) and examined using a binocular light microscope. Particular attention was paid to the apical systems, of which the genital plates and the periproct were of particular importance. The plate arrangements of the ambulacra and interambulacra

were carefully studied. This was aided by adding small quantities of 70% ethanol to the naked test, which as it evaporated helped define the edges and features of the individual plates. Photographs were taken to provide a visual record of the test structures typical to the species, allowing for a direct comparison between species to be made. A minimum number of 20 specimens were examined for each species. This was particularly significant for *D. palmeri*, where only very limited numbers of specimens exist in collections. The collection of this species was also greatly restricted due to their limited distribution and protected habitat. A maximum of 200 specimens were examined for the more widely distributed species *D. savignyi*, *D. setosum*, *E. calamaris* (white and brown colour morphs) and *E. diadema*.

The morphological data were statistically analysed using PRIMER (Plymouth Routines In Multivariate Ecological Research; see Clarke & Warwick 1994). Cluster analysis and ordination by multi-dimensional scaling (MDS) were applied to the data to establish levels of similarity between species. Euclidean distances of taxonomic similarity between species were measured, this being the most widely used measure of distance in numerical taxonomy (Bridge 1993). Group average linkage was used for clustering, as it is the preferred method in numerical taxonomy (Sneath & Sokal 1973), lacking some of the extremes that may occur with other clustering (Bridge 1993).

RESULTS

Test measurements, proportions and features for each species of *Diadema* and *Echinothrix* are shown in the Appendix. Drawings of the apical systems showing species-specific characters, particularly on the genital plates and on the periproct are shown in Figure 1. Photographs of the median areas of the interambulacra showing the variation in characters that occur between species are shown in Figure 2. A key to the species of the genera *Diadema* and *Echinothrix* using test morphology is presented below.

KEY TO THE SPECIES OF THE GENERA *DIADEMA* GRAY, 1825 AND *ECHINOTHRIX* PETERS, 1853
 BASED ON TEST MORPHOLOGY

1. Apical system monocyclic 2
 — Apical system hemicyclic 5
2. Swollen periproctal cone with white platelets present in the membrane. Large naked median areas present down the mid-lines of the interambulacra 3
 — Small periproctal cone with no white platelets present in the membrane. Many tubercles on genital plates *E. diadema*
3. Triangular-shaped naked median areas on the interambulacra. Arch-shaped depressions on genital plates. Black anal ring present *D. palmeri*
 — No triangular-shaped naked median on the interambulacra, no arch-shaped depressions on genital plates. No black anal ring. Green bands of iridophores present down the mid-lines of the interambulacra 4
4. Ambulacra prominently raised aborally. Genital plates significantly longer than wide
 *E. calamaris* (brown colour morph)
 — Ambulacra only slightly raised aborally. Genital plates not significantly longer than wide
 *E. calamaris* (white colour morph)
5. Orange anal ring. Blue/green “spot” markings on genital plates *D. setosum*
 — No distinct orange anal ring. No “spot” markings on genital plates 6
6. Distinct arch-shaped depressions on the genital plates of adults (spines not banded) 7
 — No arch-shaped depressions on the genital plates of adults (spines not banded) 8
7. Test distinctly rounded pentagonal when viewed aborally. Test (in living echinoids) black with a brown tinge and only a faint pattern of blue iridophores down the mid-lines of the interambulacra *D. mexicanum*
 — Test distinctly circular not rounded pentagonal when viewed aborally. Test (in living echinoids) distinctly black, with a bold pattern of iridophores down the mid-lines of the interambulacra *D. savignyi*
8. Interambulacral plates number 12-14, corresponding to fewer spines ... *D. paucispinum*
 — Interambulacral plates number 15-16 9
9. Six series of primary tubercles on the interambulacra *D. antillarum*
 — Four or five series of primary tubercles on the interambulacra *D. ascensioins*

Diadema antillarum Philippi, 1845

Specimens of *D. antillarum* examined in this study were collected from Barbados, Gulf of Mexico, Jamaica, North Panama, Puerto Rico and the Virgin Islands. A maximum horizontal test diameter (h.d.) of 105 mm was observed in this species, with a corresponding vertical diameter (v.d.) of 50 mm. A mean horizontal test diameter of 85 mm and a mean vertical diameter of 45 mm were found

from 50 specimens measured. Standard deviations (SD ±) in adult test size corresponded to 5.1 mm (h.d.) and 3.7 mm (v.d.).

Test colour in living specimens was typically black, with continuous blue lines of iridophores present down the mid-line of the interambulacra and around the apical system. Such markings were not as bold as in *D. savignyi*. White spots on the naked median areas of the interambulacra were clearly visible at night. During the day these marks

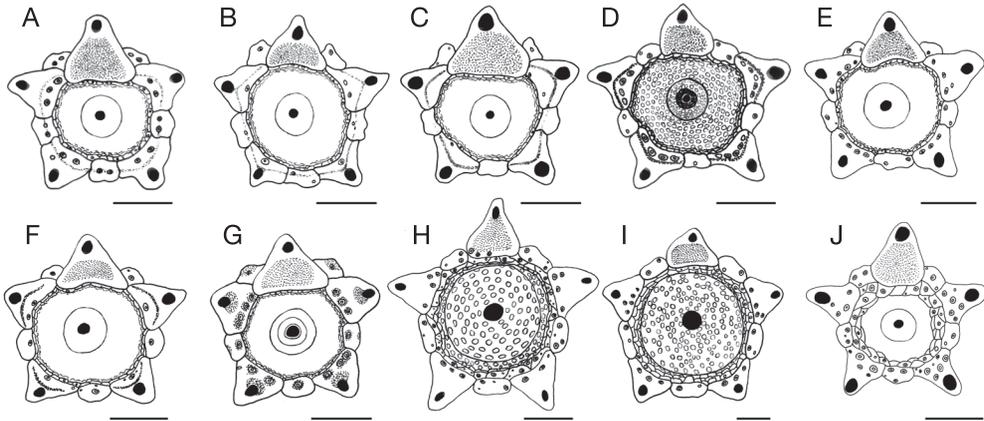


FIG. 1. — Drawings of the apical systems, showing species specific characters of the periproct and genital plates: **A**, *Diadema antillarum*; **B**, *D. ascensionis*; **C**, *D. mexicanum*; **D**, *D. palmeri*; **E**, *D. paucispinum*; **F**, *D. savignyi*; **G**, *D. setosum*; **H**, *Echinothrix calamaris* (brown colour morph); **I**, *E. calamaris* (white colour morph); **J**, *E. diadema*. Scale bars: 5 mm.

became smaller and less distinct, to the extent that specimens appeared to be completely black.

The ambulacra measured 25-33% of the width of the interambulacra measured at the ambitus. No differences were found from Mortensen's (1940) detailed description of the plate arrangements and features of the pore zones.

The apical system was distinctly depressed and hemicyclic (Fig. 1A), measuring 18-22% of the test's horizontal diameter (h.d.) in adults, a somewhat larger percentage in juveniles. The periproct measured 10-14% (h.d.) and had a small black anal cone with no anal ring or other distinct markings.

The genital plates (Fig. 1A) typically had between two and four small tubercles along their inner edge. When viewed on the naked test, distinct arch-shaped depressions were present on the genital plates of juvenile specimens. This feature appeared to fade with age. These markings corresponded to the corners of the pentamerous apical ring of iridophores, seen in living specimens.

A clear groove occurred down the mid-line of each interambulacrum. This bisected as it approached the naked median area (Fig. 2A). In living specimens this groove contained iridophores, forming clear blue lines, which bisected around the naked white spots, visible at night.

The peristome was black in colour and ranged in size from 45-50% (h.d.).

Diadema ascensionis Mortensen, 1909

Specimens of *D. ascensionis* examined in this investigation were collected from the South Atlantic islands of Ascension and St. Helena. Adult specimens had a mean horizontal test diameter of 70 mm (SD \pm 5.2 mm) and a vertical diameter of 40 mm (SD \pm 3.4 mm). Maximum test diameters of 84 mm (h.d.) and 46 mm (v.d.) were found from 28 specimens examined.

Test colour was black, commonly with a red tinge. This was more noticeable in juvenile specimens. The same pattern of iridophores occurred in this species as in *D. antillarum* and *D. savignyi*, with lines of iridophores down the mid-lines of the interambulacra and a ring around the apical system. This feature was not as obvious as in the afore-mentioned species. White dots were present on the naked median areas of the interambulacra, being more obvious at night, not always visible during the day.

The shape of the test was very similar to that of *D. antillarum*. The ambulacra measured 25-30% of the width of the interambulacra measured at

the ambitus and as reported by Mortensen (1940) showed no variation to that of *D. antillarum*.

The apical system (Fig. 1B) was distinctly depressed, hemicyclic and measured 20-26% (h.d.) in adults, a slightly larger percentage of the test's horizontal diameter in juveniles. The periproct measured 12-18% (h.d.), with a small black anal cone with no distinguishing features. Both the apical system and the corresponding periproct tended to be larger in this species than in *D. antillarum*. The genital plates (Fig. 1B) had fewer tubercles (between zero and two) than *D. antillarum*, with distinct arched depressions seen on the denuded tests of juveniles. These markings tended to fade with age.

The mid-lines of the interambulacra on the naked test had no obvious markings. On living specimens, thin lines of iridophores were found in these areas. These lines bisected the naked median "spot" areas of the interambulacra.

The peristome was black with a purple tinge and measured 40-50% (h.d.).

Diadema mexicanum A. Agassiz, 1863

Specimens of *D. mexicanum* studied in this investigation were collected from the Galapagos Islands, and from Acapulco, Mazatlan and Pochutla in Mexico. Adult specimens had a mean horizontal test diameter of 75 mm (SD \pm 6.1 mm) and a mean vertical diameter of 40 mm (SD \pm 4.2 mm). Maximum test diameters of 92 mm (h.d.) and 46 mm (v.d.) were recorded from 48 specimens examined.

As reported by H. L. Clark (1948), the test was black with a brown tinge. The patterns of iridophores were similar to those seen in *D. antillarum* and *D. ascensionis*. However, like *D. ascensionis*, the blue colour was not bold or distinct. Mortensen (1940) correctly reported the presence of faint blue lines that proceeded from each side of the genital pore down to the ambitus where they bisected the naked median areas. These faint parallel lines were not always continuous, with the presence of small side branches between secondary spines. Mortensen (1940) also reported that there were no white spots

in the adapical naked interambulacral area. Obvious white spots were not typically seen on specimens during the day. However, at night distinct white spots with faint white lines were seen leading from the naked median areas to the genital pores. These features were visible on the denuded test of some specimens (Fig. 2B, faint white marking surrounded by area of darker pigment), but were not visible on all specimens.

The shape of the test was distinctly rounded pentagonal rather than horizontally circular and more flattened in appearance than *D. antillarum*. The ambulacra measured 25-30% of the interambulacra measured at the ambitus.

The apical system (Fig. 1C) was slightly depressed, hemicyclic and measured 20-25% of the test's horizontal diameter. The periproct measured 12-16% (h.d.) and was black with a small anal cone. The genital plates (Fig. 1C) were similar in shape to those of *D. antillarum*. However, they had fewer tubercles (between zero and two) while the genital pores were typically larger. Similar to *D. savignyi*, a distinct arch-shaped depression was present on the genital plates in both juveniles and adults, forming the corners of the pentamerous apical ring.

The peristome was deep brown in colour and measured 45-50% (h.d.).

Diadema palmeri Baker, 1967

Specimens were collected from the Poor Knights Island and from Hen and Chickens Island, New Zealand. Mean test diameters measured 65 mm (h.d.) (SD \pm 4.8 mm) by 35 mm (v.d.) (SD \pm 2.6 mm) in adult specimens. Maximum test diameters of 78 mm (h.d.) by 44 mm (v.d.) were recorded from 20 specimens examined.

As first reported by Baker (1967), the test was spectacularly red with a striking pattern of iridophores (Fig. 2J). These occurred as brilliant blue or lilac lines radiating down each side of the naked median areas of the interambulacra, as spots on each interambulacral plate on the adradial edge of each column, and as ring around the periproct.

The ambulacra typically measured 20-25% of the interambulacra at the ambitus. Large naked areas

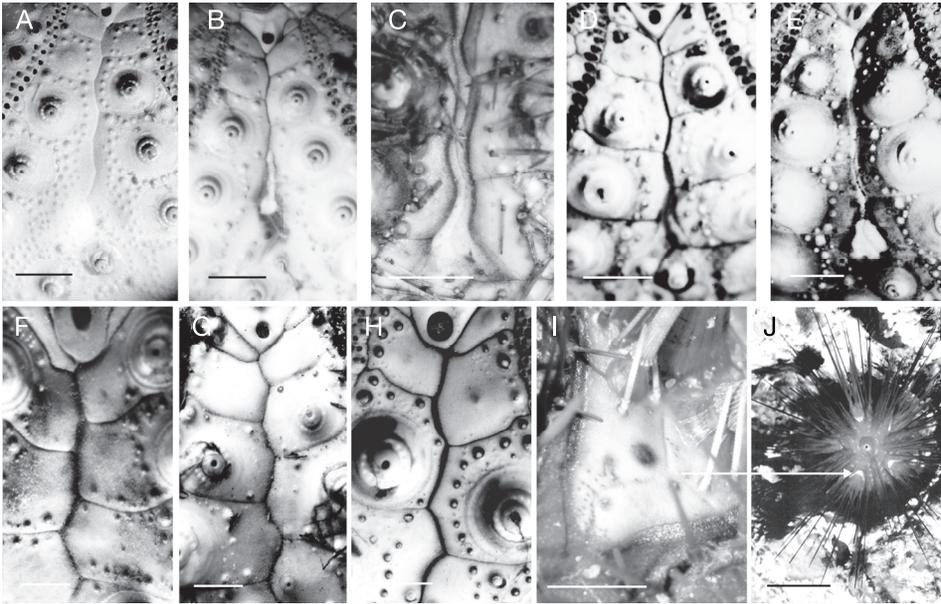


FIG. 2. — A-I, photographs of the median areas of the interambulacra, showing the variation in characters that occur: A, *Diadema antillarum*; B, *D. mexicanum*; C, D, *D. savignyi*; E, *D. setosum*; F, *Echinothrix calamaris* (brown colour morph); G, *E. calamaris* (white colour morph); H, *E. diadema*; I, *D. palmeri*; J, *D. palmeri* (whole specimen). Scale bars: A-I, 5 mm; J, 50 mm.

occurred on the median areas of the interambulacra (Fig. 2I). These were triangular and cream in colour, with a thin line of iridophores either side. A single, large, red spot accompanied by two to four smaller spots were typically seen in the centre of the naked median areas.

The apical system (Fig. 1D) measured 29-32% of the test's horizontal diameter, was monocyclic, with all ocular plates insert. The genital plates (Fig. 1D) had between two and six tubercles on their inner edge, with corresponding spines found on living specimens. Strong arch-shaped depressions were found on the naked genital plates. These formed the corners of the pentamerous apical ring. The genital pores were relatively small in relation to other species of the genus.

The periproct measured 16-18% (h.d.) and had a small anal cone that was slightly lighter in colour than the test, with white platelets present in the skin. A black anal ring was present around the opening, unique among species of *Diadema*.

The peristome measured 35-45% (h.d.) and was predominantly red in large adult specimens, paler in juveniles.

Diadema paucispinum A. Agassiz, 1863

Specimens were collected from Puako Bay, Hau-nomu Bay, and Kahe Point on the main Hawaiian island of Oahu, as well as from Kahului, in Maui. Specimens were also collected from the islands of Viti Levu and Taveuni in Fiji. Adult specimens had mean test diameters of 70 mm (h.d.) (SD \pm 4.4 mm) by 40 mm (v.d.) (SD \pm 3.1 mm). Maximum test diameters of 82 mm (h.d.) by 48 mm (v.d.) were recorded from 62 specimens.

Tests were black with a distinct red tinge in young specimens. This colouration was lost with age, becoming jet-black, exhibiting a bluish hue in adults. The ambulacra measured 22-26% of the interambulacra at the ambitus and were not as prominent as reported by Agassiz (1863).

The numbers of iridophores were noticeably reduced in this species. No apical ring was observed, while the pattern of iridophores down the mid-lines of the interambulacra were not constant. Typically, iridophores were found among the base of the tubercles on the interambulacra above the ambitus. Mortensen (1940) reported that no white spots were present on the naked median areas of the interambulacra. This was true of specimens during the day. However, at night, light red/brown patches were found in these areas.

The test was reported by Mortensen (1940) to be somewhat more flattened than in the other species of the genus. This did not prove to be a consistent or reliable feature.

The interambulacra were as Mortensen (1940) described, with fewer interambulacral plates (12-14) than in specimens of the same size in *D. savignyi* or *D. setosum* (15-16 plates). This corresponds to the fewer spines found in this species (*D. paucispinum*).

The apical system (Fig. 1E) measured 20-28% of the test's horizontal diameter, was hemicyclic with no iridophores present. The periproct measured 11-15% (h.d.), was uniformly black with a small anal cone and no markings. The genital plates had from two to six small tubercles on their inner edge, but no arch-shaped depressions. This feature was not even found on juveniles in this study. No other distinct markings on the genital plates were found.

The peristome was black and measured 40-45% (h.d.).

Diadema savignyi Michelin, 1845

Specimens of *D. savignyi* were collected from the Amirante Is. (Seychelles), Eniwetok Atoll (Marshall Islands), Ryuka Island (Japan), Nouméa (New Caledonia), Suva (Fiji), Rarotonga (Cook Islands) and Apia (Samoa). Adult specimens had mean test diameters of 70 mm (h.d.) (SD \pm 4.2 mm) by 40 mm (v.d.) (SD \pm 2.1 mm). Maximum test diameters of 88 mm (h.d.) by 44 mm (v.d.) were recorded from 200 specimens examined.

The tests of living specimens were typically black and horizontally circular, while the apical system was conspicuously depressed. The ambulacra typically

measured 28-30% of the interambulacra measured at the ambitus with pore zones that were only slightly widened towards the peristome.

White lines radiated out from the genital plates down the mid-lines of the interambulacra. In some specimens such lines terminated in white spot markings on the naked, unbleached test (Fig. 2C). This was not a consistent feature, with no such marking observed on the naked, unbleached test of specimens examined from Japan (Fig. 2D). The naked median areas had small red/brown spot markings during the day, these varied in size between specimens. At night these spot markings increased in size as the chromatophores retracted, revealing the white/cream test.

A bold pattern of iridophores was found on the aboral surface. This took the form of lines rather than spots as found in *D. setosum*. Lines of iridophores occurred down the mid-lines of the interambulacra. These bisected the naked median continuing to just below the ambitus. Rings of iridophores occurred around the tubercles on the ambulacra. However, this feature was not found on all specimens. A pentamerous ring of iridophores also occurred around the apical system.

The apical system (Fig. 1F) was hemicyclic and measured 22-28% of the test's horizontal diameter. The periproct measured 13-18% (h.d.) and had a small anal cone, with no ring or platelets present. The genital plates (Fig. 1F) had clear arch-shaped depressions both in adults and juveniles. Tubercles varied in number from one to three and were typically present on the inner edge of the genital plates. These usually consisted of one larger and two smaller spines.

The peristome was black with a burgundy tinge and measured between 42-50% (h.d.).

Diadema setosum (Leske, 1778)

Specimens of *D. setosum* were collected from Port Louis (Mauritius), Sulawesi Is. (Indonesia), Nouméa (New Caledonia), Luzon (Philippines), Lizard Is. (Australia) and Suva (Fiji). Adult specimens were found to have mean test diameters of 70 mm (h.d.) (SD \pm 3.7 mm) by 40 mm (v.d.) (SD \pm 2.9 mm).

Maximum test diameters of 84 mm (h.d.) by 48 mm (v.d.) were recorded from 200 specimens examined.

Tests were black with a green tinge occasionally seen on large adult specimens. This was particularly apparent on specimens from Fiji. The typical shape of the test was horizontally circular, with the apical system conspicuously depressed. The ambulacra typically measured 24–30% of the interambulacra measured at the ambitus.

The naked median areas had white spots seen both day and night. These white spots were also visible on the naked test (Fig. 2E) in conjunction with white lines continuing from the spot marking along the mid-lines of the interambulacra to the genital plates. A bold pattern of blue iridophores occurred in this species. These have been described as “spots” by many authors (Sarasin & Sarasin 1887; Agassiz & Clark 1908; Clark 1921; Mortensen 1940). The pattern of iridophores occurred as a series of “spots” down the mid-lines of the interambulacra. These bisected the naked median areas continuing down just below the ambitus. Lines of blue “spots” also occurred as two series down the ambulacra in some specimens. A single blue “spot” was also present on each genital plate, including above the madreporite.

The apical system (Fig. 1G) was hemicyclic and measured 22–28% of the test’s horizontal diameter. The periproct measured 12–20% (h.d.) and had a small black anal cone with a distinct orange anal ring, unique to the species. No platelets were present in the membrane. The genital plates had from three to five tubercles present along their inner edge, with green/blue spot markings when viewed on the denuded test (Fig. 1G). These represented the location of the blue iridophores observed in living specimens.

The peristome was grey in colour and measured 40–50% (h.d.).

Echinothrix calamaris (Pallas, 1774)

Specimens were collected from Ryuka Is. (Japan), Red Sea (Egypt), Mariana Is. (Guam), Ignoitijala (Maldives), Luzon (Philippines), Dravuni Is.,

Taveuni Is., Yanuca Is., Suva (Fiji), and Nouméa (New Caledonia).

This species is reported to have the broadest range of colour morphs of any species in the family Diadematae (H. L. Clark 1925). The most commonly found colour morphs throughout the Indo-Pacific were the white (interambulacral spines) and brown (test and ambulacral spines) and the completely brown colour morph. These were commonly found together throughout the Pacific, and were therefore closely studied in this investigation.

Test diameters varied significantly between colour morphs. Adult specimens of the white colour morph had a mean horizontal test diameter of 108 mm (SD \pm 8.2 mm) and a mean vertical diameter of 45 mm (SD \pm 5.4 mm). Adults of the brown colour morph typically grew to a significantly larger size, with mean test diameters of 120 mm (h.d.) (SD \pm 8.7 mm) and 60 mm (v.d.) (SD \pm 5.5 mm). Mortensen (1940) reported that the largest recorded specimen of *E. calamaris* measured 130 mm (h.d.) from the old collection of the “Royal Museum”, Copenhagen. The largest specimen recorded in this study, from 200 specimens of each colour morph measured 143 mm (h.d.) by 68 mm (v.d.) and was of the brown colour variety. In comparison, the largest white colour morph only measured 119 mm (h.d.) by 52 mm (v.d.).

The ambulacra in both colour morphs measured 24–28% of the interambulacra measured at the ambitus and widened distinctly towards the periproct, narrowing beneath the ambitus then widening towards the peristome. Many authors including Clark & Rowe (1971) have differentiated this species from *Echinothrix diadema* by the ambulacra which are distinctly raised aborally in *E. calamaris*. This feature was, however, not constant, and as Mortensen (1940) reported, “considerable variation occurs in the elevation aborally of the ambulacra”. Such variation was most apparent between colour morphs. The test of the white colour morphs was typically more flattened aborally, while the ambulacra were less distinctly raised and the interambulacra less correspondingly sunken. The brown colour morph had clearly raised ambulacra and interambulacra that were sunken aborally. This differentiation appeared to increase with age.

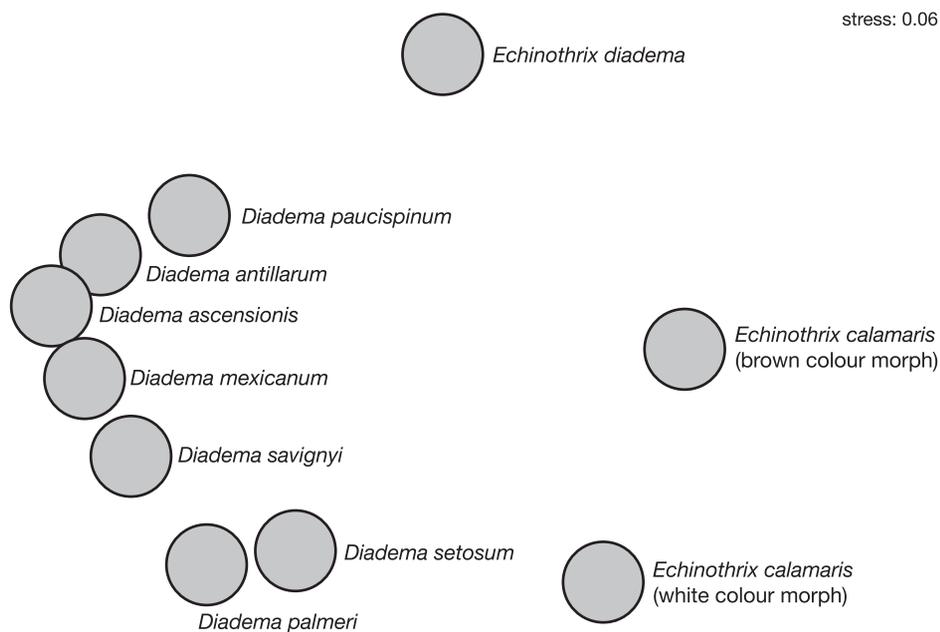


FIG. 3. — MDS plots of taxonomic similarity based on 28 test characters.

Large, naked median areas occurred down the mid-line of the interambulacra (Fig. 2F, G) as green or blue bands in living specimens. Green bands could also be seen on the denuded test of the white colour morph. This feature was, however, less noticeable on the naked test of the brown colour morph. The interambulacra was green on the naked test, in contrast to the white ambulacra. This was more apparent on the white colour morph.

The apical systems measured 23-28% of the test's horizontal diameter in the brown colour morph (Fig. 1H) and 25-30% in the white colour morph (Fig. 1I). Both were monocyclic and conspicuously depressed. The periproct measured 14-20% (h.d.) in the brown colour morph and 16-20% in the white colour morph. In living specimens both colour morphs had a large, swollen anal cone with small white platelets present in the membrane. Mortensen (1940) reported that one particular specimen from Hawaii had spines on the periproct; this feature was never seen in this study.

The genital plates (Fig. 1H, I) had tubercles present along their inner edge. When viewed on the

naked test, the genital plates typically had a green tinge, particularly in the white colour morph. The gonopores were relatively small (smaller than in *E. diadema*) with no other distinguishing features. The brown colour morph typically had a slightly smaller apical system than the white colour morph, with more elongated genital plates.

The peristome was large and typically measured 42-50% (h.d.) in the brown colour morph and 40-48% in the white colour morph. Mortensen (1940) reported that spines may be present on the buccal plates. However, these were never seen in this investigation, even in very large specimens.

Echinothrix diadema (Linnaeus, 1758)

Specimens were collected from Malmahera (Indonesia), Haunomu Bay, Kahe Point (Hawaii), Bougainville Is. (Papua New Guinea), Mariana Is. (Guam), Ignoitijala (Maldives), Luzon (Philippines), Dravuni Is., Taveuni Is., Yanuca Is., Suva (Fiji), and Nouméa (New Caledonia).

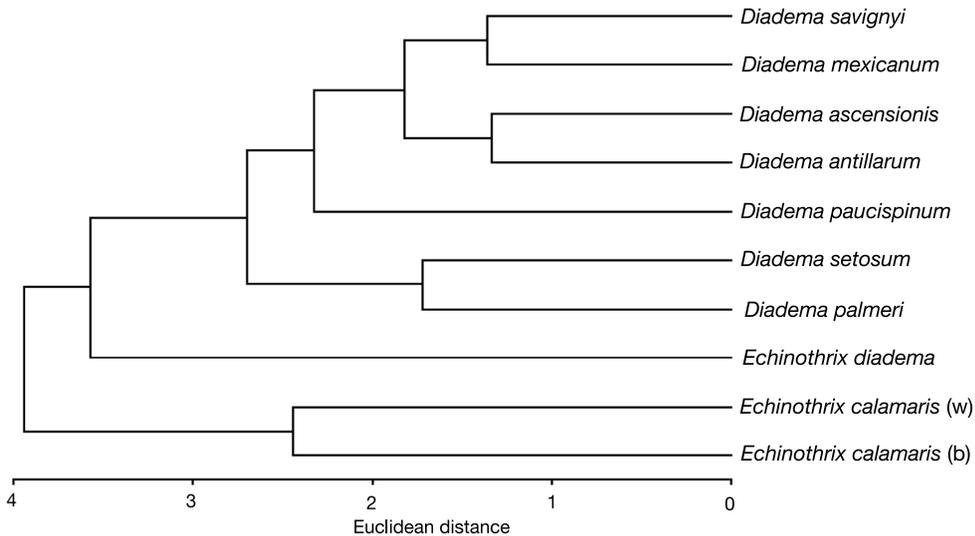


FIG. 4. — Cluster analysis based on 28 test characters (zero Euclidean distance = greatest similarity). Abbreviations: **b**, brown colour morph; **w**, white colour morph.

The tests were black with a blue-green sheen in young specimens. This feature was lost with age. Juveniles had very different colouration to the adults. However, this was mainly associated with the spines as the test remained black.

Adult specimens had mean test diameters of 92 mm (h.d.) (SD \pm 6.3 mm) and 55 mm (v.d.) (SD \pm 4.4 mm). The maximum test diameters recorded for this species in this study were 110 mm (h.d.) by 61 mm (v.d.) from 200 specimens examined. The tests were not as flattened aborally as seen in *E. calamaris*, while the ambulacra were not conspicuously raised or the interambulacra conspicuously sunken. The tests had a greater vertical diameter to horizontal diameter ratio than *E. calamaris* and thus had a more rounded appearance. The ambulacra measured 22–26% of the interambulacra measured at the ambitus, increasing in width towards the periproct but not increasing in width towards the peristome.

The apical system was monocyclic (Fig. 1J) and measured 20–25% (h.d.). Therefore, it was smaller than in *E. calamaris*. The periproct measured 12–15% (h.d.) and had a small black anal cone (not swollen as in *E. calamaris*) lacking white platelets or other distinguishing features.

The genital plates (Fig. 1J) had four to eight tubercles present, not just along their inner edge but distributed all over the plate beneath the gonopores. The gonopores were particularly large in this species, made more noticeable by the reduced size of the apical system.

The peristome was black and measured 38–46% (h.d.), being somewhat smaller than in *E. calamaris*.

COMPARISON BETWEEN SPECIES WITHIN GENERA

Comparisons using ordination by multi-dimensional scaling (MDS), and cluster analysis using Euclidean distances of taxonomic similarity, based on 28 test features, are illustrated in Figures 3 and 4.

From the dendrogram (Fig. 4) a distinct association can be seen between the white and brown colour morphs of *E. calamaris*. Although this shows a reasonable level of similarity, it is not as high as would be expected for two colour morphs of the same species (zero Euclidean distance). This level of similarity is considerably less than for different species within the genus *Diadema*. The MDS plot

(Fig. 3) substantiates this, with a large distance between the white and the brown colour morphs of *E. calamaris*. From this information it can be surmised that based on test structures and proportions, the brown and white colour morphs of *E. calamaris* are possibly separate species.

The next group incorporates all the species of the genus *Diadema*, as well as *E. diadema*. *Echinothrix diadema* is the first divergent species, indicating only slight association with species of *Diadema*. Each of the two species in a group composed of *D. palmeri* and *D. setosum*, possessed species-specific test features. This is supported by the MDS plot which indicates their disassociation from other members of the genus. The next group comprises all other species of *Diadema*. *Diadema paucispinum* is the first divergent species from this grouping, which then subdivides into two groups composed of *D. mexicanum* and *D. savignyi*, and *D. antillarum* and *D. ascensionis*. These clusterings are illustrated on the MDS plot, with *D. antillarum* and *D. ascensionis* showing the closest association.

DISCUSSION

The findings of this study have shown that specific test structures and features can be used to identify and differentiate species of the genera *Diadema* and *Echinothrix*.

Many authors have disagreed upon the significance and even the presence of certain features used in species identification. Rowe & Richmond (1997) mistakenly described *E. diadema* as having, "prominent, raised ambulacral zones" as well as, "a conspicuous anal sac usually grey covered with fine white spots". These features are typical of the brown colour morph of *E. calamaris*, commonly mistaken for *E. diadema*. Gosliner *et al.* (1996) show a photo of the brown colour morph of *E. calamaris* representing what they believe to be *E. diadema*, stating, "*Echinothrix diadema* has a light and dark spotted anal sac". This photo clearly shows the green naked median areas down the midline of the interambulacra, as well as the swollen periproctal cone with white platelets present in the

membrane, all typical features of the brown colour morph of *E. calamaris*.

Mortensen (1940) reported that in young specimens of *D. antillarum*, a primary tubercle corresponded to each arc of three pore-pairs. In adults this association was not found, indicating that the number of tubercles and their corresponding spines disappeared with age. The findings of this investigation found this proved to be correct. Mortensen (1940) also reported that the interambulacra of *D. ascensionis* showed a distinct difference to *D. antillarum* in the size and orientation of the tubercles and their corresponding areoles, being of a slightly larger size in *D. ascensionis*. Although this was apparent in some specimens, too much variation between specimens occurred to use this as a definitive feature of the species.

Mortensen (1940) reported that the median series of tubercles of *D. ascensionis* occurred in a straight line and were very inconspicuous, with only four or five series of larger primary tubercles present in each interambulacrum, against six series in *D. antillarum*. From specimens of both species examined in this investigation, comparing specimens of a similar age and test size, these were found to be reliable features in differentiating the two species. Mortensen (1940) also used the number of tubercle series in the median areas of the interambulacra to differentiate other species of *Diadema*. He stated, "in *D. ascensionis* and *D. savignyi* there is almost constantly only an unpaired median series, in *D. antillarum* two very well developed inner series, besides, in large specimens, a median series. But then in *D. setosum* there is great variation in this regard; some specimens have only the single median series, others two distinct inner series besides the median one, and all intermediate stages occur". This investigation found that great variation does occur in the number of median series in *D. setosum*, particularly in specimens from different geographic regions when comparing equally sized specimens (specimens examined from Fiji had two inner series; specimens from the Philippines had a single inner series). Such variation was also found in *D. savignyi* and *D. paucispinum*. This feature proved to be more conservative in *D. mexicanum* and in *D. palmeri* where two distinct inner series

occurred, with only a single median series observed on the tests of *D. mexicanum*.

Agassiz & Clark (1908) reported that the number of secondary and milliary tubercles on the oral side were larger in *D. mexicanum* than in *D. antillarum*. From our observations this held to be true in larger specimens, but was not consistent. Mortensen (1940) stated that too much variation existed in this respect to differentiate the two species. Agassiz & Clark (1908) reported that the gill slits were wide and shallow in *D. mexicanum* and deep and narrow in *D. antillarum*. Mortensen (1940) found this feature to be unreliable, but did state that they appeared to be less wide in *D. antillarum*. From our observations such a feature appeared to be very unreliable in differentiating the species.

Baker (1967) reported that the peristome in *D. palmeri* measured 35% (h.d.) and was significantly smaller than seen in *D. setosum*, which he reported measuring 44% (h.d.). He based this on measurements taken from seven specimens of each species with similar horizontal diameters. Although typically the peristome of *D. palmeri* is slightly smaller than that of other members of the genus, this study found the size of the peristome to be variable (35-45% h.d.). Therefore too much emphasis should not be placed on such a feature, particularly when looking at such a small sample size. A far more interesting test feature of this species is the presence of a monocyclic apical system, where all the ocular plates are insert (Fig. 1D). Other species in the genus *Diadema* all have hemicyclic apical systems (Fig. 1A-C, E-G) with ocular plates two and three exert (Mortensen 1940). This is therefore a significant morphological feature of the species.

Mortensen (1940) reported that the naked median areas were not as clear in *D. savignyi* as in *D. setosum*, explained by the primary tubercles being slightly larger in *D. savignyi*. This investigation found this to be unreliable, the naked median area being as distinct in *D. savignyi* as in *D. setosum* when viewed on the naked test (Fig. 2C, E, respectively), while the primary tubercles were typically the same size.

Agassiz & Clark (1908) reported that in *D. setosum* the second series of tubercles on the interambulacra begins abactinally on the seventh or eighth coronal

plate, while in *D. savignyi* the second series begins on the sixth (sometimes fifth or seventh) coronal plate. From this investigation it was apparent the second series of tubercles continued to the fifth or sixth plate from above in both species, as first reported by Mortensen (1940).

Many similarities in test morphology were seen for species in the genera *Diadema* and *Echinothrix*. It was found that *D. antillarum*, *D. ascensionis*, *D. mexicanum*, and *D. savignyi* had similar test morphologies, including size and shape of test, tubercle arrangements, markings on genital plates, patterns of iridophores and features of the periproct and peristome. *Diadema paucispinum* had many features in common with these species, as well as species-specific characters, of which the reduced number of interambulacral plates and the reduced distribution of iridophores were of particular distinction.

Research by Lessios *et al.* (2001) based on mitochondrial DNA verifies that *D. setosum* is the first outlying species forming a sister clade to the other *Diadema*. They found *D. palmeri* to be the next outlying species, indicating an early evolutionary split from the *Diadema* clade. These results combine well with the morphological evidence. Lessios *et al.* (2001) reported that presence a sister clade where *D. mexicanum* is a distinct out-group and *D. antillarum*, *D. paucispinum* and *D. savignyi* form a polytomy. This relates well to the morphological evidence, with a close association in the test features between these four species.

Lessios *et al.* (2001) proposed that *D. antillarum* is composed of two clades, one from the western and central Atlantic (*D. antillarum*-a) and the other from the eastern Atlantic (*D. antillarum*-b). Within the western and central Atlantic clade was an additional site unique to specimens from the central Atlantic islands of Ascension and St Helena. Lessios *et al.* (2001) believe that this substantiated Pawson's (1978) decision to demote *D. ascensionis* to a subspecies of *D. antillarum*, rather than accept it as a separate species as advocated by Mortensen (1940). Our results demonstrate that the structures of the test of *D. ascensionis* and *D. antillarum* are very similar, the closest within the genus; however, structural differences do exist.

The two species in the genus *Echinothrix* are so distinctly different that it is surprising that so many mistakes in identification have been made. Mortensen (1940) stated that, "if there were more species grouped around *calamaris* on one side, and similarly *diadema* on the other side, I would think, they ought to form two genera". From observations in this study, the brown colour morph of *E. calamaris* should possibly be considered a separate species or subspecies, as its test morphology had distinct differences from other colour morphs. Based on this information, questions must be raised about the morphologies of the other colour morphs in this species. One possible explanation is that *E. calamaris* is a polytypic species, the different colour morphs therefore being subspecies. However, the sympatric distributions of the white and brown colour morphs in the Pacific indicates they may in fact be separate species. This clearly requires further investigation, supported by genetic analysis.

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APPENDIX

TABLE 1. — Test measurements, proportions and features for *Diadema antillarum* Philippi, 1845 and *D. ascensionis* Mortensen, 1909. Abbreviation: **SD**, standard deviation.

	<i>D. antillarum</i>	<i>D. ascensionis</i>
Origin of specimens examined	Barbados, Gulf of Mexico, Jamaica, N Panama, Puerto Rico, Virgin Islands	Ascension and St Helena islands (South Atlantic)
Test colour	black	black (red tinge)
Test shape	hemispherical	hemispherical
Test distinctions	ambulacra slightly raised aborally	ambulacra slightly raised aborally
Iridophore pattern (interambulacra)	blue lines (faint)	blue lines (faint)
Iridophore pattern (apical system)	blue ring (faint)	blue ring (faint)
Iridophore pattern (genital plate)	blue arch (faint)	blue arch (faint)
Mean horizontal test diameter (SD)	85 mm (5.1 mm)	70 mm (5.2 mm)
Mean vertical test diameter (SD)	45 mm (3.7 mm)	40 mm (3.4 mm)
Maximum horizontal test diameter observed	105 mm	84 mm
Maximum vertical test diameter observed	50 mm	46 mm
Markings on test (median area of interambulacra)	day: no marking; night: faint white spot	day: no marking; night: faint white spot
Markings on naked test (median area of interambulacra)	none	none
Markings on naked test (genital plate)	arch-shaped (fades with age)	arch-shaped (fades with age)
Number of tubercles on genital plate	2-4 small tubercles	0-2 small tubercles
Height to width (at widest point) ratio of genital plate	0.76:1	0.71:1
Diameter of gonopore (% of genital plate height)	29%	31%
Form of apical system	hemicyclic	hemicyclic
Form of periproct (distinguishing features)	small black, no ring or platelets	small black, no ring or platelets
Apical system (% of horizontal test diameter)	18-22%	20-26%
Periproct (% of horizontal test diameter)	10-14%	12-18%
Peristome (% of horizontal test diameter)	45-50%	40-50%
Ambulacra % of interambulacra (at ambitus)	25-33%	25-30%
Tubercle structure	perforate and crenulate	perforate and crenulate
Number of median series of tubercles on interambulacra	2	1
Rudimentary tube feet present on the peristome	no	no
Buccal tube feet present	5 pairs	5 pairs
Spines present on the buccal plates	no	no
Number of specimens examined	50	28

TABLE 2. — Test measurements, proportions and features for *Diadema mexicanum* A. Agassiz, 1863 and *D. paucispinum* A. Agassiz, 1863. Abbreviation: **SD**, standard deviation.

	<i>D. mexicanum</i>	<i>D. paucispinum</i>
Origin of specimens examined	Galapagos Islands, Mexico (Acapulco, Mazatlan, Pochutla)	Hawaii (Oahu, Maui), Fiji (Viti Levu, Taveuni)
Test colour	black (brown tinge)	black (red tinge in juveniles, blue tinge in adults)
Test shape	rounded pentagonal	hemispherical
Test distinctions	ambulacra slightly raised aborally	ambulacra slightly raised aborally
Iridophore pattern (interambulacra)	blue lines (faint)	faint blue lines
Iridophore pattern (apical system)	blue ring (faint)	no apical ring observed
Iridophore pattern (genital plate)	blue arch (faint)	no iridophores
Mean horizontal test diameter (SD)	75 mm (6.1 mm)	70 mm (4.4 mm)
Mean vertical test diameter (SD)	40 mm (4.2 mm)	40 mm (3.1 mm)
Maximum horizontal test diameter observed	92 mm	82 mm
Maximum vertical test diameter observed	46 mm	48 mm
Markings on test (median area of interambulacra)	day: no marking; night: faint white spot	light brown spot marking (night only)
Markings on naked test (median area of interambulacra)	white spot marking	none
Markings on naked test (genital plate)	arch-shaped	none
Number of tubercles on genital plate	0-2 small tubercles	2-6 tubercles
Height to width (at widest point) ratio of genital plate	0.69:1	0.71:1
Diameter of gonopore (% of genital plate height)	35%	30%
Form of apical system	hemicyclic	hemicyclic
Form of periproct (distinguishing features)	small black, no ring or platelets	small black, no ring or platelets
Apical system (% of horizontal test diameter)	20-25%	20-28%
Periproct (% of horizontal test diameter)	12-16%	11-15%
Peristome (% of horizontal test diameter)	45-50%	40-45%
Ambulacra % of interambulacra (at ambitus)	25-30%	22-26%
Tubercle structure	perforate and crenulate	perforate and crenulate
Number of median series of tubercles on interambulacra	1	variable (1 or 2)
Rudimentary tube feet present on the peristome	no	no
Buccal tube feet present	5 pairs	5 pairs
Spines present on the buccal plates	no	no
Number of specimens examined	48	62

TABLE 3. — Test measurements, proportions and features for *Diadema savignyi* Michelin, 1845 and *D. setosum* (Leske, 1778). Abbreviation: **SD**, standard deviation.

	<i>D. savignyi</i>	<i>D. setosum</i>
Origin of specimens examined	Seychelles, Japan, New Caledonia, Cook Islands, Samoa, Fiji	Mauritius, Indonesia, Australia, New Caledonia, Fiji, Philippines
Test colour	black	black
Test shape	hemispherical	hemispherical
Test distinctions	ambulacra slightly raised aborally	ambulacra slightly raised aborally
Iridophore pattern (interambulacra)	blue lines (bold)	lines of blue spots
Iridophore pattern (apical system)	blue ring (bold)	no apical ring
Iridophore pattern (genital plate)	blue arch (bold)	blue spot of iridophores
Mean horizontal test diameter (SD)	68 mm (4.2 mm)	76 mm (3.7 mm)
Mean vertical test diameter (SD)	38 mm (2.1 mm)	40 mm (2.9 mm)
Maximum horizontal test diameter observed	78 mm	84 mm
Maximum vertical test diameter observed	44 mm	48 mm
Markings on test (median area of interambulacra)	white spot marking (typically night only)	white spot marking (day and night)
Markings on naked test (median area of interambulacra)	geographic variation, white spot/ no spot	white line and spot markings
Markings on naked test (genital plate)	distinct arched depression	green/blue spot marking (typically)
Number of tubercles on genital plate	1-3 tubercles	3-5 tubercles
Height to width (at widest point) ratio of genital plate	0.69:1	0.72:1
Diameter of gonopore (% of genital plate height)	28%	25%
Form of apical system	hemicyclic	hemicyclic
Form of periproct (distinguishing features)	small black, no ring or platelets	small black, orange ring, no platelets
Apical system (% of horizontal test diameter)	22-28%	22-28%
Periproct (% of horizontal test diameter)	13-18%	12-20%
Peristome (% of horizontal test diameter)	42-50%	40-50%
Ambulacra % of interambulacra (at ambitus)	28-30%	25-30%
Tubercle structure	perforate and crenulate	perforate and crenulate
Number of median series of tubercles on interambulacra	variable (1 or 2)	variable (1 or 2)
Rudimentary tube feet present on the peristome	no	no
Buccal tube feet present	5 pairs	5 pairs
Spines present on the buccal plates	no	no
Number of specimens examined	200	200

TABLE 4. — Test measurements, proportions and features *Diadema palmeri* Baker, 1967 and *Echinothrix diadema* (Linnaeus, 1758). Abbreviations: **na**, not applicable; **SD**, standard deviation.

	<i>D. palmeri</i>	<i>E. diadema</i>
Origin of specimens examined	Poor Knights Island, Hen and Chickens Island, New Zealand	Hawaii, Papua New Guinea, Maldives, Fiji (Dravuni, Yanuca, Taveuni islands)
Test colour	red (scarlet)	black (blue/green tinge in young adults)
Test shape	hemispherical	hemispherical, more rounded than <i>E. calamaris</i>
Test distinctions	ambulacra slightly raised aborally	ambulacra very slightly raised aborally
Iridophore pattern (interambulacra)	blue/turquoise lines	none
Iridophore pattern (apical system)	blue/turquoise ring	none
Iridophore pattern (genital plate)	blue/turquoise arch (bold)	none
Mean horizontal test diameter (SD)	65 mm (4.8 mm)	92 mm (6.3 mm)
Mean vertical test diameter (SD)	35 mm (2.6 mm)	55 mm (4.4 mm)
Maximum horizontal test diameter observed	78 mm	110 mm
Maximum vertical test diameter observed	44 mm	61 mm
Markings on test (median area of interambulacra)	naked triangular area, cream in colour	no markings, only small naked median area
Markings on naked test (median area of interambulacra)	large naked triangular area,	no markings or pigmentation
Markings on naked test (genital plate)	distinct arched depression	no markings
Number of tubercles on genital plate	2-6 tubercles	4-8 tubercles
Height to width (at widest point) ratio of genital plate	0.54:1	0.85:1
Diameter of gonopore (% of genital plate height)	20%	36%
Form of apical system	monocyclic	monocyclic
Form of periproct (distinguishing features)	small red cone, white platelets, black ring	small black anal cone, no ring or platelets
Apical system (% of horizontal test diameter)	29-32%	20-25%
Periproct (% of horizontal test diameter)	16-18%	12-15%
Peristome (% of horizontal test diameter)	35-45%	38-46%
Ambulacra % of interambulacra (at ambitus)	20-25%	22-26%
Tubercle structure	perforate and crenulate	perforate and crenulate
Number of median series of tubercles on interambulacra	2	na
Rudimentary tube feet present on the peristome	no	no
Buccal tube feet present	5 pairs	5 pairs
Spines present on the buccal plates	no	no
Number of specimens examined	20	200

TABLE 5. — Test measurements, proportions and features for *Echinothrix calamaris* (Pallas, 1774). Abbreviations: **na**, not applicable; **SD**, standard deviation.

	<i>E. calamaris</i> (brown)	<i>E. calamaris</i> (white)
Origin of specimens examined	Egypt, Guam, Fiji (Dravuni, Yanuca, Taveuni Is., Viti levu)	Japan, Guam, Philippines, Fiji (Dravuni, Yanuca, Taveuni Is., Viti levu)
Test colour	brown	burgundy/brown
Test shape	hemispherical, rounded orally, flattened aborally	hemispherical, flattened orally and aborally
Test distinctions	ambulacra conspicuously raised aborally	ambulacra raised aborally
Iridophore pattern (interambulacra)	green bands	green bands
Iridophore pattern (apical system)	none	none
Iridophore pattern (genital plate)	none	none
Mean horizontal test diameter (SD)	120 mm (8.7 mm)	108 mm (8.2 mm)
Mean vertical test diameter (SD)	60 mm (5.5 mm)	45 mm (5.4 mm)
Maximum horizontal test diameter observed	143 mm	119 mm
Maximum vertical test diameter observed	68 mm	52 mm
Markings on test (median area of interambulacra)	green band of iridophores	green band of iridophores
Markings on naked test (median area of interambulacra)	no markings or pigmentation	green pigment present
Markings on naked test (genital plate)	typically no marking present	green patch marking
Number of tubercles on genital plate	1-5 tubercles	1-5 tubercles
Height to width (at widest point) ratio of genital plate	1.1:1	0.73:1
Diameter of gonopore (% of genital plate height)	20%	22%
Form of apical system	monocyclic	monocyclic
Form of periproct (distinguishing features)	large, brown, white platelets present	large, brown, white platelets present
Apical system (% of horizontal test diameter)	23-28%	25-30%
Periproct (% of horizontal test diameter)	14-18%	16-20%
Peristome (% of horizontal test diameter)	42-50%	40-48%
Ambulacra % of interambulacra (at ambitus)	24-28%	24-28%
Tubercle structure	perforate and crenulate	perforate and crenulate
Number of median series of tubercles on interambulacra	na	na
Rudimentary tube feet present on the peristome	no	no
Buccal tube feet present	5 pairs	5 pairs
Spines present on the buccal plates	no	no
Number of specimens examined	200	200