

A new species and comparative morphology of Philippine sea biscuits (Echinoidea: *Clypeaster*)

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Abstract

A new species of clypeasterid sea biscuit, *Clypeaster brigittae* **n. sp.**, is described from material collected in the Philippines at depths between 100 and 200 m. The new taxon increases the number of *Clypeaster* species recorded from the Philippines to nine, representing nearly a quarter of the world's diversity of the genus. Other Philippine species include: *C. annandalei* Koehler, 1922; *C. fervens* Koehler, 1922; *C. humilis* (Leske, 1778); *C. japonicus* Döderlein, 1885; *C. latissimus* (Lamarck, 1816); *C. pateriformis* Mortensen, 1948; *C. reticulatus* (Linnaeus, 1758); and *C. virescens* Döderlein, 1885. Using type material where available, each of these species is compared and contrasted with *C. brigittae* **n. sp.** in tables consisting of new data derived from general test shape and size, petal structure, food grooves, plate architecture, internal structure, and morphology of spines, pedicellariae, and tube feet.

Keywords: Echinoidea, Clypeasteroidea, Clypeasteridae, *Clypeaster*, sea biscuits, new species, Philippine fauna, comparative morphology, identification tables

Introduction

The irregular echinoids known colloquially as sea biscuits and sea pancakes are members of the family Clypeasteridae L. Agassiz, 1835, in the order Clypeasteroidea A. Agassiz, 1872. Recent molecular analyses indicate that the “true” sand dollars, once placed in the Clypeasteroidea, should now occupy a different clade, the Scutelloidea Monniardino Koch *et al.*, 2018, leaving the Clypeasteridae as the only extant family in the order. This family presently contains three extant lineages, the Clypeasterinae L. Agassiz, 1835, Arachnoidinae Duncan, 1889, and Ammotrophiae Durham, 1955. Of these, the Clypeasterinae consists of a single extant genus, *Clypeaster* Lamarck, 1801. Within this taxon, the high-tested forms are referred to in the vernacular as “sea biscuits” (the more flattened forms as “sea pancakes”), but “sea biscuit” is also commonly used to refer to the genus as a whole when colloquial names are invoked. There have been unsuccessful attempts to split the genus into multiple genera, or to subdivide the genus itself into subgenera (summarized in Mortensen 1948b). The most recent morphological phylogeny failed to find consistent support for these subgroupings (Mihaljević *et al.* 2011). It should be pointed out that even with 41 extant species presently recognized, the diversity of extant *Clypeaster* does not make its recognition as a single genus particularly unusual in comparison with other megadiverse forms (such as some genera of insects or mollusks).

However, Mortensen (1948b) also estimated that there were in excess of 350 nominal fossil *Clypeaster* found in strata from the Eocene to the Recent, which does return the diversity to an unwieldy level likely to cause considerable challenges for a complete revision of the group. Some attempts to deal with what appears to be rampant splitting among fossil *Clypeaster* taxa have been made on a local level (e.g. Kroh 2005), but a full assault on the mountain of paleontological nomenclature on a global scale has yet to be made. With that in mind, and in an ongoing effort to describe the diversity of taxa in modern oceans, most neontologists have generally ignored the seemingly endless job of dealing with the fossil forms when describing new extant species discovered since Mortensen's

(1948b) monograph of the group (e.g. Brito 1959; Serafy 1970, 1971; Pawson & Phelan 1979). We will follow suit in the hope that the framework established here for collecting appropriate data will aid in future assessments of the diversity of *Clypeaster* throughout its stratigraphic range.

Members of *Clypeaster* are known from the tropical to subtropical margins of all the continents, except Antarctica. Of the known extant species, six are found in the Eastern Pacific, 14 in the Atlantic, and 21 in the Indo-Pacific region including Hawaii and westward to the Philippines, Australia, and the Indian Ocean including the east coast of Africa. Members of the genus can be found just subtidally to the deep sea, though none seems classifiable as habitually abyssal forms except perhaps for *C. lamprus* H.L. Clark, 1914, an Atlantic species that has so far been found at depths as great as 2670 m.

The *Clypeaster* fauna of the Philippines was partially reviewed by van Noordenburg (2008), who provided thorough descriptions and illustrations of five known species, plus the new species, which was described and illustrated, but not named. Schultz (2005, 2009) included data on all nine of the species treated herein, without singling them out as part of a special Philippine echinoid fauna or developing data towards identification of the Philippine forms in particular. However, Schultz (2005, 2009) provided excellent images and summary descriptions for all of these, including a new species cited as the one described in van Noordenburg (2008), which remained unnamed. Mooi & Munguia (2014) provided the first complete faunal compendium of echinoids from the Philippines, listing seven species of *Clypeaster*, omitting *C. japonicus* Döderlein, 1885, and the new species. We include *C. japonicus* herein because some licensed Philippine dealers of marine curios listed specimens under that name. These are not distinguishable from *C. japonicus* as described and figured from Japan, where it was once thought to be endemic. We expect that further research will uncover additional specimens of *C. japonicus* from the Philippines, because other echinoid species suggested to be endemic to Japan have subsequently been found to occur in the Philippine archipelago, such as *Fibularia japonica* Shigei, 1982 (Schultz 2009; Mooi unpublished data).

This study was initiated in order to determine the affinities of the distinctive, unnamed species alluded to above. Ascribed to the genus *Clypeaster*, specimens such as the ones illustrated by van Noordenburg (2008) sometimes appear for purchase online from licensed dealers with permits to export from the Philippines. Acquisition of this material prompted full comparison with other *Clypeaster*, including a detailed examination of the comparative morphology of all members of the genus occurring in the Philippines. Much of the data we gathered to facilitate this comparison are novel for this group of echinoids, and revealed that the new material represented a new species, *Clypeaster brigitteae* n. sp., described herein.

Clypeaster species are difficult to distinguish for those not trained in the systematics of the genus, because they do not always possess readily identifiable distinguishing features. Most of the species differ one from another more by degree of expression of certain features, such as slight changes of test and petal shape, than by possession of unique characteristics. For this reason, the data gathered here are formulated and presented so that identifications might be easier than from lengthy, sometimes ambiguous dichotomous keys such as those in Mortensen (1948b). Because the first step in assessing biodiversity occurs so often in the field, and by workers who might not have ready access to sophisticated laboratory resources, images of special test and external appendage features are presented as light micrographs, as one might observe them under a field microscope.

There is only one published phylogenetic analysis targeting *Clypeaster* (Mihaljević *et al.* 2011), but this included only about a third of the known taxa and provided codings for six of the nine species now known to occur in the Philippines. These data were not presented in such a way as to aid in identification of individual *Clypeaster* taxa, which is part of the reason that the tables and discussions of comparative morphology in the present work were felt to be necessary. There is a possibility that these data could foster similar analyses in broader phylogenetic studies, particularly those integrating fossils with extant taxa, as mentioned above.

Material and Methods

Specimens studied in order to perform the comparative analysis among Philippine species of *Clypeaster* were obtained from collections at the institutions indicated in Table 1. Studied material of the new species was collected from three localities in the Philippines (Fig. 1, Table 2), and purchased by the authors from Filipino purveyors of marine curios with export permits issued by the Bureau of Fisheries and Aquatic Resources under the Philippine Department of Agriculture.

TABLE 1. Material of Philippine *Clypeaster* studied. Institutional abbreviations listed in text (Material and Methods). Not necessarily all figured herein, but used for data collection, assessment of variation.

Species	Institution	Catalogue #	Locality	Comments
<i>annandalei</i> Koehler, 1922	MNHN	IE-2013-10656	Gulf of Aden	7 syntypes
	MNHN	IE-2013-10621	Gulf of Aden	5 syntypes
<i>fervens</i> Koehler, 1922	MNHN	IE-2016-766	Red Sea	non-type
	MNHN	IE-2016-700	Gulf of Suez	non-type
<i>humilis</i> (Leske, 1778)	CASIZ	187161	Philippines	non-type
	CASIZ	187162	Philippines	non-type
	CASIZ	196858	Philippines	non-type
	CASIZ	215178	Philippines	non-type
	CASIZ	215217	Philippines	non-type
	MNHN	IE-2016-762	Red Sea	non-type
<i>japonicus</i> Döderlein, 1885	MNHN	IE-2016-705	Gulf of Suez	non-type
	CASIZ	087636	Japan	non-type
<i>latissimus</i> (Lamarck, 1816)	MNHN	IE-2016-771	Japan	non-type
	CASIZ	087636	Japan	non-type
	MNHN	IE-2016-771	Japan	non-type
	CASIZ	087636	Japan	non-type
<i>pateriformis</i> Mortensen, 1948a	CASIZ	087636	Japan	non-type
	MNHN	IE-2016-771	Japan	non-type
	CASIZ	087636	Japan	non-type
	MNHN	IE-2016-771	Japan	non-type
<i>reticulatus</i> (Linnaeus, 1758)	CASIZ	187321	Philippines	holotype
	CASIZ	186322	Philippines	non-type
	CASIZ	196856	Philippines	non-type
	CASIZ	203668	Philippines	non-type
	CASIZ	203671	Philippines	non-type
	CASIZ	215165	Philippines	non-type
	MNHN	IE-2016-830	Gulf of Suez	non-type
	MNHN	IE-2016-633	Red Sea?	non-type
<i>virescens</i> Döderlein, 1885	CASIZ	233415	Philippines	non-type
	CASIZ	190417	Philippines	non-type
	CASIZ	192163	Philippines	non-type
	CASIZ	191646	Taiwan	non-type
	MNHN	IE-2016-650	Tonga	non-type

A subset of the newly collected material of the new species, as well as of selected specimens from other species used in the comparative analysis, was prepared and cleaned by brushing and/or immersion in 5% sodium hypochlorite solution (household bleach). Specimens were photographed under a variety of light conditions to reveal test surface detail and plate patterns, or drawn with a camera lucida. Visibility of suture lines was enhanced for photography, observation of plate architecture, and for the production of plate maps, by light application with a paint brush of a 50% solution of glycerine in 95% ethanol. After painting, specimens were allowed to dry until glycerine was primarily deposited in suture lines, which became darkened in contrast to the surrounding stereom.

Spines, pedicellariae, and tube feet were removed from the test with fine, needle-nosed forceps and placed in bleach until soft tissues were removed by maceration. Photos and measurements were taken, or drawings made using a compound microscope. An assessment of variation in the number of longitudinal ribs on aboral and oral primary spines was made by removing five spines from each of three specimens of the new species, plus from one to three specimens of each of the other Philippine species according to availability. These were then broken at the midpoint of the shaft so that a cross-section could be viewed and the ribs counted.

As indicated in Figure 2, ambulacra and interambulacra are labelled using Lovén's system (Lovén 1874), and taxonomic nomenclature follows Kroh & Mooi (2020).

TABLE 2. Data for all studied specimens of *Clypeaster brigitteae* n. sp., listed in order of increasing TL. For abbreviations, see text. — = missing data.

CASIZ Catalog Number	Locality	Depth (m)	Condition	TL	TW	TH	PerisL	PerisPos	InfundD
187450 Paratype	Balut Island, Mindanao	150	entire, cleaned but unbleached	62.7	55.2	17.0	4.6	29.3	8.2
187411 Paratype	Balut Island, Mindanao	100–200	entire, with spines	64.5	57.7	19.0	4.9	30.1	8.4
234820 Paratype	Balicasag Island, Bohol	100–200	entire, cleaned but unbleached	66.6	60.2	21.0	3.9	32.4	8.6
234819 Paratype	Balicasag Island, Bohol	100–200	entire, with spines	69.2	60.9	19.0	4.3	33.3	7.1
234826 Paratype	Mactan Island, Cebu	180	dissected to show internal structure, with some spines	70.1	62.7	—	4.2	34.2	9.7
187409 Paratype	Balut Island, Mindanao	100–200	entire, some spines	70.3	63.1	21.2	5.1	33.7	8.2
234827 Paratype	Mactan Island, Cebu	180	fragments, partially reassembled, bleached to show internal structure and plate patterns	73.0	66.2	18.8	—	—	—
234822 Paratype	Mactan Island, Cebu	180	entire, with full spination	75.0	67.8	19.5	—	35.7	9.9
234825 Paratype	Balicasag Island, Bohol	100–200	dissected to show internal structure, partially bleached, no spines	84.2	77.4	—	4.2	—	—
234821 Paratype	Balicasag Island, Bohol	100–200	entire, partially cleaned but unbleached, some spines	88.7	82.7	20.6	4.4	43.4	8.2
234824 Holotype	Mactan Island, Cebu	180	entire, with full spination	93.8	85.1	25.2	6.2	45.1	11.6
234823 Paratype	Mactan Island, Cebu	180	entire but with some damage around peristome, bleached	94.6	88.5	25.9	4.0	45.4	13.5

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TABLE 2.(Continued)

CASIZ Catalog Number	PeripL	PeripPos	ApexPos	PetIIIL	PetIIW	PetIIInt	PetIIopen	PetIIapore#
187450 Paratype	2.7	57.0	31.6	18.2	10.3	6.7	5.4	36
187411 Paratype	3.1	60.2	32.6	20.3	10.8	7.0	5.5	30
234820 Paratype	2.3	62.7	35.7	23.4	12.2	7.1	6.8	35
234819 Paratype	2.4	64.8	34.9	20.5	13.4	8.5	7.2	33
234826 Paratype	2.7	66.2	—	—	12.4	6.7	—	—
187409 Paratype	3.1	64.8	38.1	20.7	12.4	7.8	6.1	34
234827 Paratype	2.3	68.2	37.8	21.1	11.5	7.5	7.6	39
234822 Paratype	2.9	69.8	37.4	26.1	13.2	7.6	6.7	—
234825 Paratype	3.2	78.6	—	28.8	13.5	8.5	9.7	41
234821 Paratype	2.7	83.5	44.9	29.2	14.8	9.2	10.8	41
234824 Holotype	5.1	86.3	46.8	27.8	17.0	11.1	10.3	39
234823 Paratype	2.9	89.6	47.8	31.9	15.8	9.5	10.8	41

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TABLE 2.(Continued)

CASIZ Catalog Number	AmbIVL	PetIVL	PetIVW	PetIVInt	PetVopen	PetVapore#	AmbVL	PetVL	PetVW	PetVInt	PetVopen	PetVapore#
187450 Paratype	29.5	16.4	10.7	6.4	4.8	32	33.7	18.3	10.6	6.9	6.0	33
187411 Paratype	30.8	17.5	10.5	5.9	5.5	29	36.4	20.0	10.9	7.0	6.4	31
234820 Paratype	34.1	21.7	11.5	5.8	5.6	35	36.8	22.8	12.7	7.0	7.3	38
234819 Paratype	33.7	20.0	13.1	8.1	7.6	35	36.8	20.8	14.4	9.2	9.7	37
234826 Paratype	—	—	12.5	7.3	—	—	—	—	11.8	6.9	—	—
187409 Paratype	35.1	21.3	11.5	6.7	5.4	35	37.7	21.2	12.8	8.1	7.2	35
234827 Paratype	35.3	21.9	11.4	6.9	6.8	40	37.7	23.3	12.1	8.3	8.7	40
234822 Paratype	35.8	24.2	12.7	7.5	7.1	—	39.7	23.8	13.8	8.5	8.5	—
234825 Paratype	—	28.1	13.6	7.5	8.3	44	—	30.9	14.9	9.5	10.3	44
234821 Paratype	43.2	28.6	15.5	9.2	9.7	43	47.3	31.1	16.2	9.7	10.8	45
234824 Holotype	45.2	29.3	15.3	10.5	10.5	41	50.8	30.5	17.9	11.3	13.3	42
234823 Paratype	48.0	32.5	15.4	8.6	9.4	44	51.6	33.7	15.8	9.0	10.5	45

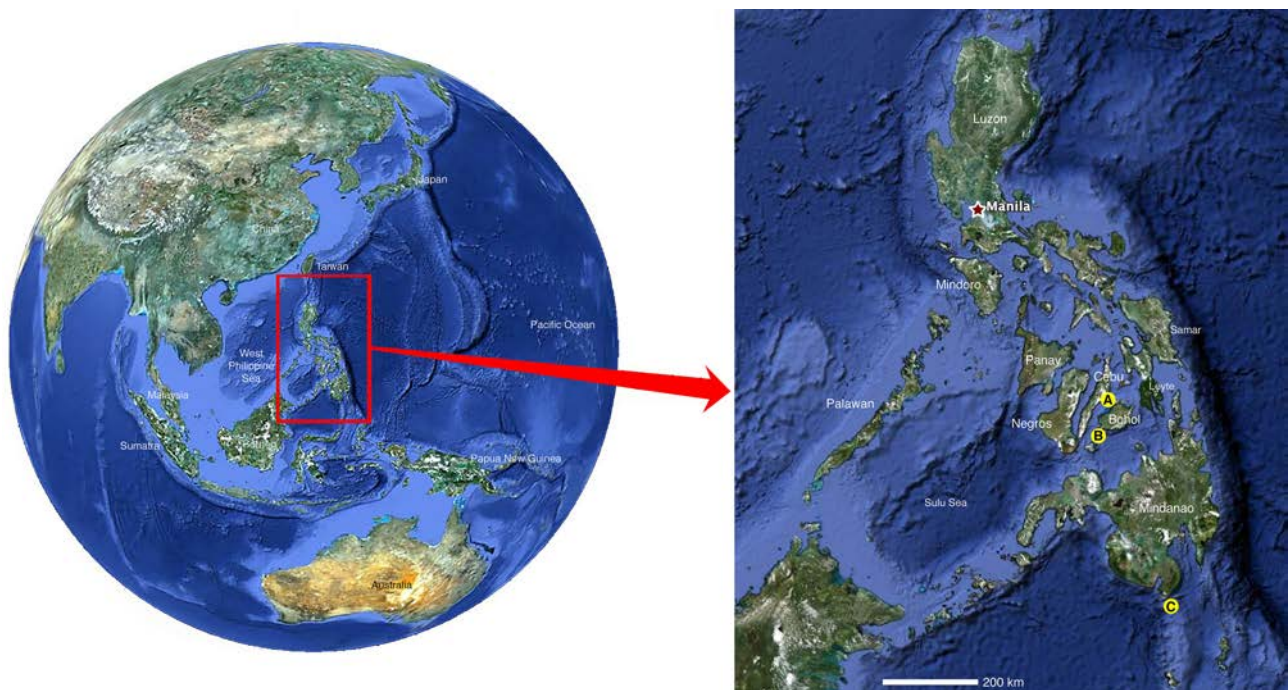


FIGURE 1. *Clypeaster brigitteae* n. sp., maps showing location of Philippines, and of three localities from which specimens were collected (adapted from googleearth.com). A: Holotype CASIZ 234824; paratypes CASIZ 234822, 234823, 234826, 234827, Mactan Island, Cebu, Philippines. B: Paratypes CASIZ 234819 to 234821, 234825, Balicasag Island, Philippines. C: Paratypes CASIZ 187409, 187411, 187450, Balut Island, Mindanao, Philippines.

Institutional Abbreviations:

CASIZ	California Academy of Sciences (Invertebrate Zoology).
MNHN	Museum National d'Histoire Naturelle, Paris, France.
USNM	United States National Museum of Natural History, Washington, District of Colombia.

Measurements and Meristics Abbreviations (see Figure 2 for measurement parameters):

AmbIVL	Length of ambulacrum IV, measured from corresponding edge of madreporic plate (ocular IV) to point at which perradial suture in ambulacrum IV intersects ambitus.
AmbVL	Length of ambulacrum V, measured from corresponding edge of madreporic plate (ocular V) to point at which perradial suture in ambulacrum V intersects ambitus.
ApexPos	Apex position, measured from anterior edge of madreporic plate (ocular III) to point at which perradial suture in ambulacrum III intersects ambitus. Also corresponds to length of ambulacrum III (see below for other ambulacral length definitions).
InfundD	Infundibulum depth, measured orthogonally from horizontal plane tangential to oral surface of test to anterior edge of peristome.
PeripL	Periproct length, measured from points at which interr radial suture intersects anterior and posterior margins of periproct.
PeripPos	Periproct position, measured from anterior edge of periproct to point at which perradial suture in ambulacrum III intersects ambitus.

PerisL	Peristome length, inner distance from point at which perradial suture in ambulacrum III reaches peristomial edge to point at which interrarial suture in interambulacrum 5 reaches peristomial edge.
PerisPos	Peristome position, measured from anterior edge of peristome to point at which perradial suture in ambulacrum III intersects ambitus.
PetIIIapore#	Number of respiratory pore pairs in “a” column of petal in ambulacrum III.
PetIIIInt	Maximum width of interporiferous zone in ambulacrum III, measured between inner pores of respiratory pore pairs in each column (approximately half-way distally along petal from corresponding ocular).
PetIIIL	Length of petal in ambulacrum III, measured from corresponding edge of madreporic plate (ocular III) to inner pore of last respiratory pore pair in ambulacrum IIIa.
PetIIIopen	Openness of distal end of petal in ambulacrum III, measured between inner pores of last respiratory pore pairs in each column.
PetIIIW	Maximum width of petal in ambulacrum III, measured from outer pores of each respiratory pore pair column (approximately half-way distally along petal from corresponding ocular).
PetIVapore#	Number of respiratory pore pairs in “a” column of petal in ambulacrum IV.
PetIVInt	Maximum width of interporiferous zone in ambulacrum IV, measured between inner pores of respiratory pore pairs in each column (approximately half-way distally along petal from corresponding ocular).
PetIVL	Length of petal in ambulacrum IV, measured from corresponding edge of madreporic plate (ocular IV) to inner pore of last respiratory pore pair in ambulacrum IVa.
PetIVopen	Openness of distal end of petal in ambulacrum IV, measured between inner pores of last respiratory pore pairs in each column.
PetIVW	Maximum width of petal in ambulacrum IV, measured from outer pores of each respiratory pore pair column (approximately half-way distally along petal from corresponding ocular).
PetVapore#	Number of respiratory pore pairs in “a” column of petal in ambulacrum V.
PetVInt	Maximum width of interporiferous zone in ambulacrum V, measured between inner pores of respiratory pore pairs in each column (approximately half-way distally along petal from corresponding ocular).
PetVL	Length of petal in ambulacrum V, measured from corresponding edge of madreporic plate (ocular V) to inner pore of last respiratory pore pair in ambulacrum Va.
PetVopen	Openness of distal end of petal in ambulacrum V, measured between inner pores of last respiratory pore pairs in each column.
PetVW	Maximum width of petal in ambulacrum V, measured from outer pores of each respiratory pore pair column (approximately half-way distally along petal from corresponding ocular).

TH	Test height, measured orthogonally from horizontal plane tangential to oral surface to centre of madreporic plate.
TL	Test length, measured from point at which perradial suture in ambulacrum III intersects ambitus to point at which interr radial suture intersects ambitus in interambulacrum 5.
TW	Test width at widest point, measured orthogonal to anterior-posterior axis, just posterior to intersection with ambitus of perradial sutures in ambulacra II and IV.

Systematic part

Class Echinoidea Leske, 1778

Irregularia Latreille, 1825

Order Clypeasteroida A. Agassiz, 1872

Family Clypeasteridae L. Agassiz, 1835

Subfamily Clypeasterinae L. Agassiz, 1835

Genus *Clypeaster* Lamarck, 1801

Clypeaster brigitteae n. sp.

Figures 3–8, tables 2–5, 11.

Diagnosis. Among all known extant taxa, very few *Clypeaster* species possess completely unique features (i.e. autapomorphies). Therefore, early workers used unique combinations of relatively conspicuous features to diagnose new species, and this is also the approach here. Nevertheless, among the *Clypeaster* species recorded from the Philippines, *Clypeaster brigitteae* n. sp. is unique with respect to certain characters, and these are marked with an asterisk in the following list of relevant characters:

Clypeaster with all petals widely open*; fewer than 9 respiratory pore pairs counted within a section 5 mm long along the length of single column in each petal; only 1 or 2 primary tubercles in poriferous zone between adjacent respiratory pore pairs*; interambulacral basicoronals separated from first pair of post-basicoronals by two plates from each adjacent ambulacrum; single occluded distal plate (very rarely two) in petal*; aboral primary tubercles not densely distributed (only about 50/cm²)*; valves of ophicephalous large (largest of trio usually about 400 µm long).

Type and other material studied. A total of 12 specimens (Table 2), consisting of a holotype (CASIZ 234824, Mactan Island, Cebu, Philippines) and 11 individually cataloged paratypes (CASIZ 187409, 187411, 187450, 234819–234823, 234825–234827, Balicasag Island, Bohol and Balut Island, Mindanao, Philippines), were available for study, obtained in a donation to the California Academy of Sciences by the second author in 2008–2009, or purchased with export permits by the first author through online dealers in the Philippines. See Table 2 for a complete list of all material of the new species studied, repository numbers, localities and depth, condition of each specimen as of this writing, and morphometrics for major features.

Etymology. The new species is named after the late spouse of the second author, Brigitte.

Description. This description relies primarily on the holotype, CASIZ 234824 (Figs. 3, 5C, 7, 8). However, in order to maintain this specimen intact with nearly complete spination, other specimens were used in dissections and other preparations to obtain additional data and imagery (as noted in Table 2 and in the figure captions). Meristics and percentage calculations are from the holotype unless otherwise noted. Measurements from all specimens are given in Table 2.

tact with third and fourth post-basicoronals (interambulacral plates 4a and 5b), aboral edge with fourth and fifth (5a and 6b) (Fig. 5B). Periproctal membrane slightly sunken, covered in small plates (slightly larger near peristomial edge) surrounding small, central anal opening, plates bearing dense cover of miliary spines, triphyllous pedicellariae, and relatively small tridentate pedicellariae, but no primary spines (Fig. 5C).

Ambulacra—Petaloid adapically, petals broad, with pore pair columns continuously diverging or parallel distally, only slightly converging in some cases (Figs. 3, 4B, C). Ambulacra widen near ambitus in oral view, approximately twice width of interambulacra at ambitus (Figs. 5A, B), most commonly with 8 to 10 plates in any given column (half-ambulacrum). Ambulacra with paired basicoronals, all in agreement with Lovén's Rule (sensu David *et al.* 1996), ambulacral plates Ib, IIb, IIIa, IVb, Va about 2/3 length of other plate in pair (Fig. 5B). All ambulacral plates with densely arranged unipores scattered between spine tubercles, each unipore supporting single accessory tube foot.

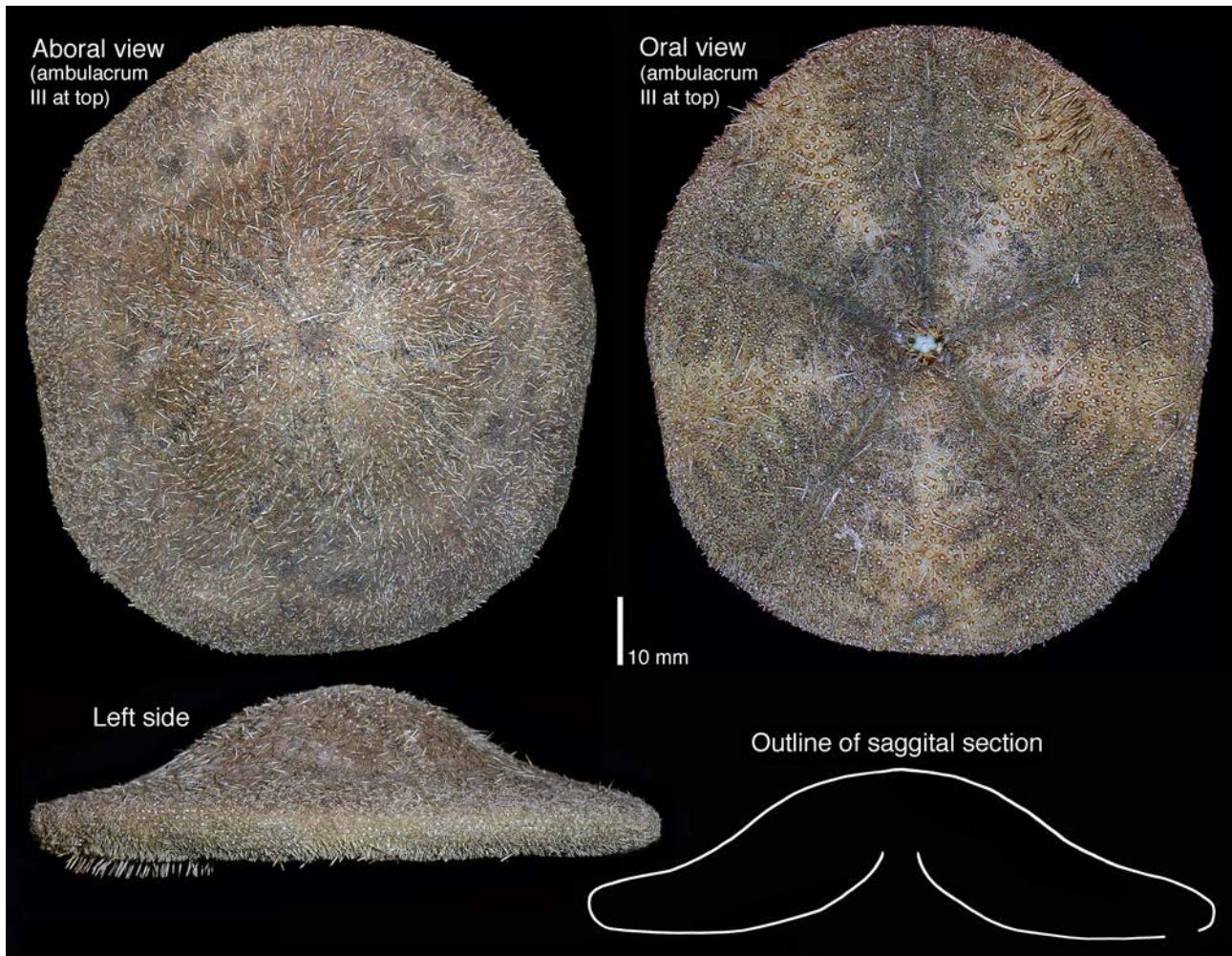


FIGURE 3. *Clypeaster brigittae* n. sp., different views of holotype CASIZ 234824, Mactan Island, Cebu, Philippines, 93.8 mm TL.

Petals—Posterior paired petals (I and V) slightly longer than anterior paired petals (II and IV). Posterior paired petals longest relative to TL, petal V 60.0% length of corresponding test radius in planar view, but 32.5% TL; anterior paired petals next longest, petal IV 64.8% length of corresponding test radius, but 31.2% TL; anterior unpaired petal shortest, petal III 59.4% length of corresponding test radius, but 29.6% TL. Petal V width at widest point 19.0% TL, interporiferous zone 12.0% TL, distance between inner pores of distalmost respiratory pore pair in petal 14.2% TL (117.7% of maximum interporiferous zone width and a measure of the “openness” of the petal at its distal end, see Materials and Methods and Fig. 2); petal IV width 16.3% TL, interporiferous zone 11.2% TL, distance between inner pores of distalmost respiratory pore pair in petal 11.2% TL (100.0% of maximum interporiferous zone width and a measure of the “openness” of the petal at its distal end, see Materials and Methods and Fig. 2); petal III width 18.1% TL, interporiferous zone 11.8% TL (92.8% of maximum interporiferous zone width and a measure of

the “openness” of the petal at its distal end, see Materials and Methods and Fig. 2). Respiratory tube foot pore pairs strongly conjugated, inner pore slightly elongate or almost circular, outer pore only slightly elongated (Figs. 4B, C, D). Column a of petal V with 42 pore pairs; of petal IV with 44; of petal III with 41. One or two (rarely three) primary tubercles situated along ridge between adjacent pore pairs. Plating within petals of typical clypeasterid architecture, with primary plate spanning entire distance from outer edge of petal to perradial suture, alternating with demiplate spanning just less than half that distance from outer edge of petal (Figs. 4B, C, D). One or two occluded plates present at tips of petals (e.g. Fig. 4D).

Interambulacra—Narrower than ambulacra and straight on oral surface, slightly widening towards ambitus, but containing paired, zig-zag plates between petals right up to madreporic plate. Typically, five, occasionally six, post-basicoronal plates in each half-interambulacrum in oral interambulacra. Single, narrow basicoronal in each interambulacrum (Fig. 5D), typically but not always reaching ends of adjacent ambulacral basicoronals. Interambulacra disjunct, separated from first pair of interambulacral post-basicoronals by two adjacent oral ambulacral post-basicoronals (Fig. 5B, 11). In some specimens, first interambulacral post-basicoronal in one column can be greatly reduced so that it is not contiguous with second post-basicoronal in corresponding column (see interambulacra 2 and 3 in Fig. 5B), but it is not known if this is typical or unique, as it was decided not to prepare additional specimens to produce plate maps for other members of type series.

Tubercles—Of two main types, primary and miliary. Aboral miliary tuberculation homogeneous, primary tubercles relatively sparse, only about 50/cm². Oral tubercles slightly larger than those on aboral surface, particularly in interambulacra. Tubercles perforate, slightly crenulate, primaries with distinct, deeply sunken areole, miliaries with shallow areole, filling spaces between primaries and greatly outnumbering them (orally by at least 10 to 1, and approximately 20 to 1 on aboral surface). Abundant miliary tubercles on apical system (Fig. 4A) and periproctal membrane (Fig. 5C), primary tubercles lacking in those areas. No tubercles on peristomial membrane.

Food grooves—Unbranched, extending from edge of peristome, following perradial suture, shallowing and narrowing gradually, fading to merge with test surface just short of ambitus (Fig. 5A). Populated by specialized food groove miliary spines (Figs. 7F, G).

Internal structure—Strongly developed, with four or five peripheral, circumferentially arranged walls (sensu Mooi 1990; Mihaljević *et al.* 2011) in ambulacra, spanning space between floor and ceiling of test (Figs. 6A, B). Some reduced walls on inner side of channel that bears gut. Complicated masses of bars in interambulacra, continuing on proximal side of gut towards and beneath lantern (Figs. 6A, B). Minute, extremely thin, attenuated needles on both floor and ceiling of test (Figs. 6D–F), most strongly expressed in ambulacra. Some needles span entire space between floor and ceiling to join together to form thin columns or pillars (Fig. 6F).

Lantern—Of typical clypeasterine morphology (Mooi 1989, 1990), not protrusible, with strongly developed outer wings separated from almost rudimentary inner wings by continuous, ring-like arrangement of supra-alveolar processes at summit of lantern (Fig. 6G). Epiphyses and rotules rudimentary, compasses absent, as typical in clypeasteroids (Mooi 1989, 1990). Wings of each pyramid, particularly outer wings, strongly convoluted with subdivided walls connecting ambulacraly situated pyramidal muscle attachment surfaces to interambulacraly positioned symphysis between demi-pyramids underlying tooth slide (Figs. 6G, H). Tooth slide almost vertical, but biting surfaces of keeled tooth strongly angled relative to longitudinal axis of tooth to meet along nearly vertical axis from mouth through top of lantern. When in life position over peristome at top of infundibulum, entire lantern slightly canted forward so that supra-alveolar processes at anterior of lantern noticeably lower than at posterior (Fig. 6C). Lantern supports (auricles) of typical clypeasterid configuration (Kier 1970; Mooi 1989, 1990), consisting of pairs of elongated, relatively thin, upright processes, one support for every pair contributed by adjacent ambulacral basicoronal (Fig. 6B).

Spines—Of two main types, primary (Figs. 7A, B) and miliary (Figs. 7C–F), corresponding to tubercle types described above, and as typical for other *Clypeaster* (Telford *et al.* 1987). Aboral primaries only about half length of oral primaries, much narrower, finer with about 75% number of longitudinal ribs (Figs. 7A, B). Core of spine sometimes hollow, sometimes with nearly solid meshwork (Fig. 7A, B). So-called “hyaline point” (Serafy 1971) present at tips of undamaged, uneroded primaries on both aboral and oral surfaces (Figs. 7A, B). Miliary spines of variable length (Figs. 7C–F), rounded, blunt, slightly swollen distally but not crown-shaped, longest in interambulacral regions of oral surface, aboral interambulacral miliaries (Fig. 7D) about 80% length of oral interambulacral miliaries (Fig. 7C), aboral ambulacral miliaries shorter still, only 50% length of oral interambulacral miliaries (Fig. 7E). Miliary spines within food grooves short, only about half length of miliaries from adjacent oral ambulacra (Fig. 7F).

TABLE 3. Range, depth, and general test features of all species of *Clypeaster* recorded to occur in the Philippines (* = feature based on images or examination of type material). *C. japonicus* is included as it has been recorded in the Philippines by collectors, and further suspected to occur there on the basis of a specimen identified as that species by the authors (CASIZ 232217).

Species of <i>Clypeaster</i>	Range	Depth (m)	Approximate Maximum TL (mm) ¹	% TH/TL ²	% TW/TL ²	Oral Surface Contour ³	Periproct Distance from Ambitus	Inflated Margin ⁴	Internal Structure ⁵	Oral Interambulacral Plate Disjunction ⁶
<i>brigitteae</i> new species	Philippines	100–200	100*	23–32*	87–93	Flat near margin, infundibulum deep, ~50%*	<own length*	no*	bars well developed; 4 or 5 walls*	2*
<i>annandalei</i> Koehler, 1922	Arabia to Philippines, Malaysia	160–550	120*	29–43*	92–97	Flat near margin, infundibulum deep, ~70%*	~own length*	no*	bars rudimentary, 2 or 3 disjunct walls	1
<i>fervens</i> Koehler, 1922	Arabia, Seychelles and east at least to Philippines	13–216	90*	24–32*	73–91	No flat areas, infundibulum deep, ~50%*	<own length*	no*	bars absent; 1 poorly developed wall	1
<i>humilis</i> (Leske, 1778)	Indo-Pacific, Red Sea and east	0–216	160	13–27	80–88	Flat but angled upwards towards peristome, infundibulum shallow, ~75%	≤own length or less	no	bars present as rows of pillars; 4 or 5 walls	1
<i>japonicus</i> Döderlein, 1885	Japan, sporadic reports in Philippines	0–75	125	24–32	80–90	No flat areas, infundibulum deep, sharply defined near peristome, ~40%	<own length	no	bars rudimentary; single wall	1 or 2
<i>latissimus</i> (Lamarck, 1816)	Malaysia, east Indo-Pacific, West Australia	25–56	250*	8–13*	76–85	Flat near margin, infundibulum shallow, ~90%*	>1.7X own length*	no*	bars extremely elaborated into dense regions of pillars; >15 walls	2

...Continued on the next page

TABLE 3. (Continued)

Species of <i>Clypeaster</i>	Range	Depth (m)	Approximate Maximum TL (mm) ¹	% TH/TL ²	% TW/TL ²	Oral Surface Contour ³	Periproct Distance from Ambitus	Inflated Margin ⁴	Internal Structure ⁵	Oral Interambulacral Plate Disjunction ⁶
<i>pateriformis</i> Mortensen, 1948a	Philippines, Malaysia	33–90	75*	10–13*	98–99*	Flat near margin, infundibulum shallow, ~85%*	>2X own length*	no*	bars extremely elaborated into dense regions of pillars; >15 walls	2*
<i>reticulatus</i> (Linnaeus, 1758)	Indo-Pacific, to Hawaii	0–125	80	17–38	72–87	No flat areas near margin, infundibulum deep but gradually sloping upwards towards peristome, ~30%	1–1.5X own length	yes	bars near periproct only; no walls	1
<i>virescens</i> Döderlein, 1885	Indo-Pacific	27–630	125	18–27	88–97	Flat near margin, infundibulum deep, ~75%	<own length	no	bars strongly developed; 5 or 6 walls	1

¹Known upper size limit, rounded up to the nearest 5 mm, based on examination of CASIZ, MNHN, and USNM specimens, and descriptions in the literature and of type series.

²Approximate, range based on examination of CASIZ, MNHN, and USNM specimens, and descriptions in the literature and of type series.

³Percentage based on approximate point at which test begins to inflect upwards towards the peristome – measured from the ambitus along oral interambulacrum 4.

⁴In *C. reticulatus*, the margin is inflated relative to the rest of the distal part of the oral surface so that the distal ends of the petals are below the altitude of the margin.

⁵Based on new observations and radiographs in Mihaljević *et al.* (2011). Structure described is only that distal to the path of the gut. Terminology adopted from Mooi (1989, 1990) and Mihaljević *et al.* (2011): bars = interambulacral, peripheral radiating buttresses (but not actually “radial” as used in Mihaljević *et al.* [2011]); walls = concentric, circumferential buttresses made of peripheral ambulacral pillars connected to form nearly solid partitions.

⁶Number of ambulacral plates in each column adjacent to interradiial suture between basicoronal and first post-basicoronal in posterior interambulacrum (interambulacrum 5). See also Figs. 5B, 11.

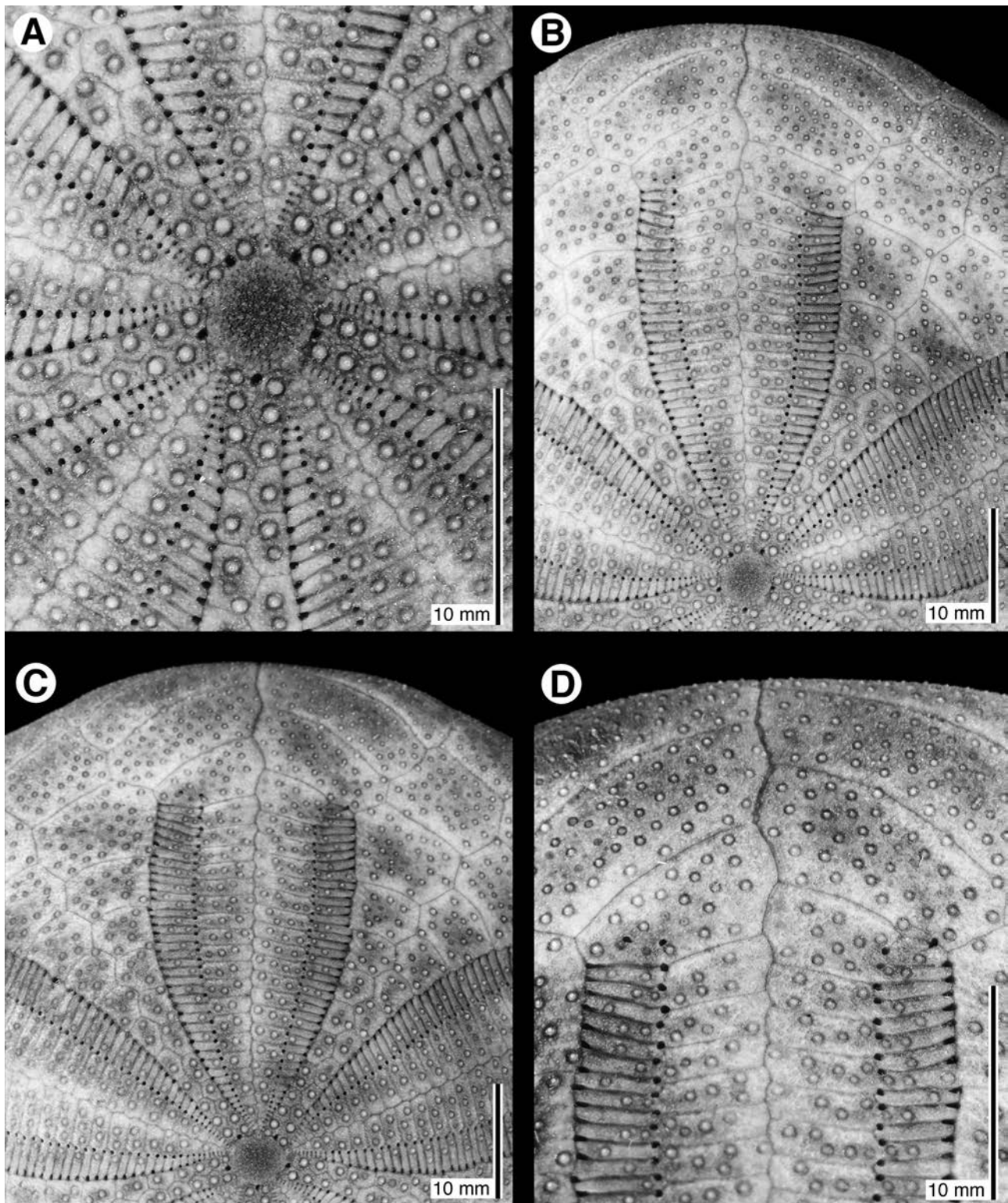


FIGURE 4. *Clypeaster brigitteae* n. sp., paratype CASIZ 234821, Balicasag Island, Bohol, Philippines, 88.7 mm TL, photographs of aboral surface morphology of cleaned but not bleached specimen, painted with 50% glycerine in 95% ethanol. A: Detail of apical system. B: Petal in ambulacrum III. C: Petal in ambulacrum IV, specimen rotated to place distal part of petal and ambitus at top. D: Detail of distal portion of petal in ambulacrum IV.

Pedicellariae— Of three main types: triphyllous (Fig. 8F), tridentate (Figs. 8C–E), and ophicephalous (Figs. 8A, B). Following observations pertain to all specimens with well preserved complement of external appendages. Triphyllous widely distributed over entire test, extremely small and numerous, with long, flexible neck connect-

ing three rounded valves to thin but robust stem, flexible neck about same length as stem, valves of usual shape for *Clypeaster*, with extremely short teeth on distal edges (Fig. 8F). Tridentates principally of two sizes, with three valves, those of smaller form (Fig. 8C) only slightly shorter than those of larger form (Fig. 8E). Smaller version scattered widely over oral surface, densely distributed (as many as 5/mm²), particularly in infundibulum, much rarer aborally, nearly absent in aboral regions where ophicephalous pedicellariae most densely distributed. Larger tridentates tending to be more common near peristome and periproct. Only small version found on periproctal membrane. Valves of small form meet distally for about one third length of valve when pedicellaria closes, versus about one quarter in large form. Valves of both types with small proximal teeth along edges where valves meet, but with one, or more typically two longer distal teeth (Figs. 8C–E). Entire tridentate jaw connected to robust stem (Fig. 8D) by flexible neck about half as long as stem. Ophicephalous pedicellariae apparently absent on oral surface, but on aboral surface, extremely densely distributed (as many as 4/mm²) all around peripheral portion of test inward from ambitus to point at which test slopes steeply upward towards apical system. Ophicephalous rare in this inner region, particularly proximal to apical system. Ophicephalous of typical *Clypeaster* morphology (Figs. 8A, B), with 3-valved jaw directly attached to top of vase-like stem (Fig. 8B), each valve connected to stereom meshwork in inner region of distal cup at top of stem by collagenous straps weaving between handles, inserting proximal to hinge of each valve. Handles always of three different lengths in single jaw, smallest nesting within medium-sized, then medium-sized within longest (Fig. 8A). Distal part of each valve with rounded, helmet-shaped head, inner surface of head with unbroken, oval ring of >30 prominent, sharp teeth, usually 4–6 additional teeth between head and top of hinge (Fig. 8A).

Tube feet—Of respiratory and accessory types, as typical for *Clypeaster* (Mooi 1986). Respiratory tube feet leaf-like, straddling conjugated respiratory tube foot pores in petals as described above, lacking spicules. Accessory tube feet varying in size and shape, distributed as typical for other *Clypeaster* (Mooi 1986; Telford *et al.* 1987), tube feet extending from unipores distributed on all ambulacral plates, occasionally on interambulacra in areas bordering the ambulacra as well, although not on interambulacral basicoronals (Fig. 5D). Smaller accessory tube feet in food grooves, small number of somewhat larger food groove tube feet just distal to slightly enlarged buccal tube feet as described for other species (Mooi 1986). Spicules in tips of accessories (not known for buccals) like those of other *Clypeaster*, but elaborate, with two to three concentric rings of fenestrae, and peripheral projections pointing both proximally and distally (Fig. 7I).

Sphaeridia—Two per ambulacrum, one in each ambulacral basicoronal, located at outer edges of food groove near peristome just distal to buccal tube feet (Fig. 5D), consisting of solid sphere of imperforate stereom inside chamber entirely enclosed within surrounding ambulacral plate.

Colour. Unknown in living specimens. Aboral surface of dried specimens brown to purplish or grayish brown, oral surface slightly paler, approaching beige in interambulacra of some specimens, centres of some plates slightly darker, particularly aborally, so that major sutures and tube foot fields stand out in contrast (Fig. 3).

Occurrence. Holotype collected by tangle net off Mactan Island, Cebu, Philippines, four paratypes from Mactan Island, four from Balicasag Island, Bohol, and three from Balut Island, Mindanao (Fig. 1, Table 1), at depths from 100 to 200 m.

Biology. *C. brigittae* n. sp. has not been observed in its habitat, but gut and food groove contents suggest that it lives on soft bottoms with low particle size ranges. Food preferences are only partially known, because the gut contents are significantly broken up or pulverized, presumably by chewing action of the lantern (Telford *et al.* 1987). Materials remaining in the food grooves suggest that the animal is a detritivore, with some preference for foraminiferans. However, as the specimens were primarily collected by tangle net, material normally gathered by the animals before capture could have been lost, and no quantitative assessments were possible. Low gonopore size suggests that the species possesses planktotrophic larvae (F. Armstrong and R. Mooi unpublished data concerning gonopore size in the genus).

Remarks. *Clypeaster brigittae* n. sp. appears to fit some of the features listed by Mortensen (1948b) for the section (or subgenus) *Stolonoclypus* A. Agassiz, 1863, given the well-developed bars and walls of the internal skeleton. However, even Mortensen (1948b: 88) was concerned that the “numerous species here enclosed in this section evidently do not form a natural group”. Mihaljević *et al.* (2011) were also unable to recover these so-called subgenera as monophyletic taxa, and this nomenclature is therefore abandoned, as indicated in Kroh & Mooi (2020).

C. brigittae n. sp. is most easily distinguished from all other *Clypeaster* through the combination of several conspicuous features, such as low density of respiratory tube feet in the petals, all of which are also widely open,

and low density of aboral primary spines (or tubercles on cleaned individuals). Of all known Atlantic species, only *C. cyclopilus* H.L. Clark, 1941, *C. euclastus* H.L. Clark, 1941, and *C. ravenelii* (A. Agassiz, 1869) have all petals even slightly similar to those of *C. brigitteae* n. sp. in terms of continuously diverging pore pair columns. However, these species all differ from *C. brigitteae* n. sp. in several other respects, including that the petals are very small in *C. cyclopilus*, the test is extremely flat in *C. euclastus*, and strongly pentangular with an inflated margin in *C. ravenelii*. Among Indo-Pacific forms, *C. tumidus* (Tenison-Woods, 1878) has continuously diverging petals, but is found only in Australia, and has an extremely high, domed test.

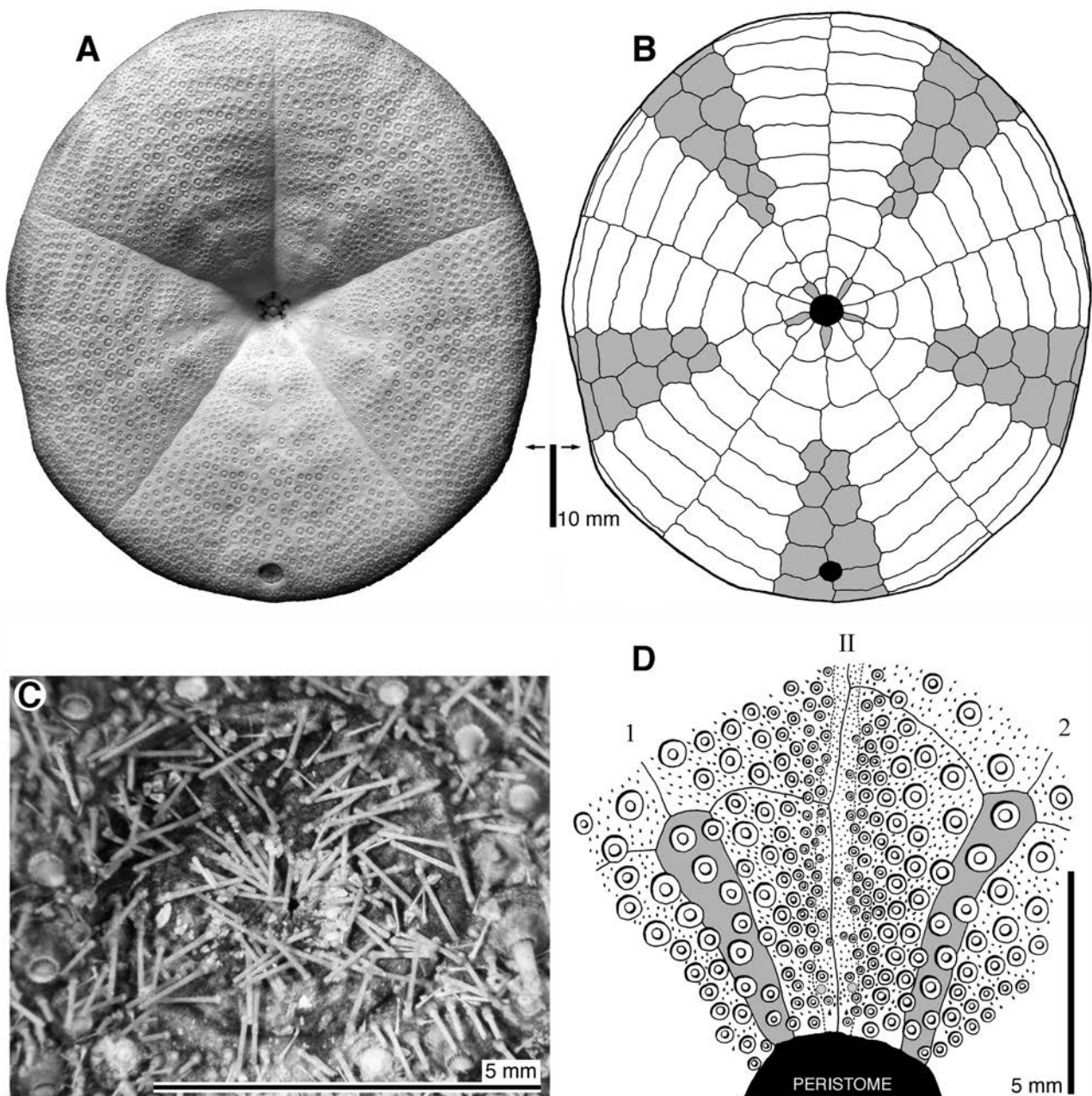


FIGURE 5. *Clypeaster brigitteae* n. sp. A: paratype CASIZ 234827, Mactan Island, Cebu, Philippines, 73.0 mm TL, oral view of bleached test, ambulacrum III at top. B: Drawing of oral view of same specimen as in A, showing plate architecture (interambulacral plates shaded, peristome and periproct in solid black). C: Holotype CASIZ 234824, Mactan Island, Cebu, Philippines, 93.8 mm TL, detail of periproct. D: Paratype CASIZ 234823, Mactan Island, Cebu, Philippines, 94.6 mm TL, drawing of detail of peristomial region centred on ambulacrum II, with interambulacral basicoronals 1 and 2 (shaded), showing plate pattern (solid lines), position of food groove (fine, broken lines on either side of perradial suture), primary tuberculation (paired concentric circles, miliary tubercles omitted), accessory tube foot pores (small dots), buccal tube foot pores (larger, teardrop-shaped dots in ambulacrum near peristome), and positions of sphaeridia (shaded, dotted circles in ambulacrum near peristome).

Some characters used in previous descriptions of new taxa in the genus have proven unreliable in the distinction of *C. brigitteae* n. sp., and for this reason, they have not been emphasized in the present tabular comparisons of Philippine *Clypeaster*. For example, the hyaline point on primary spines used by Serafy (1971), needs to be reassessed for all taxa, because the primary spines of all the species examined herein have a hyaline point to some degree, except for oral spines of *C. virescens* and *C. latissimus*, in which spines are distally spatulate (Table 5). This suggests that the degree to which this point is expressed is dependent on the condition of the spines, which are often worn or broken in museum material.

The presence or absence of stereom meshwork in the axial cavity of spines, a character also used in some keys (Serafy 1971), is similarly not reliable because it is variably expressed within a given taxon. In several Philippine species, including *C. brigitteae* n. sp., even spines from a single specimen can have either a dense meshwork or a narrow, hollow axial cavity.

TABLE 4. Petal and food groove characteristics of all species of *Clypeaster* recorded to occur in the Philippines (* = feature based on images or examination of type material). *C. japonicus* is included as it has been recorded in the Philippines by collectors, and further suspected to occur there on the basis of a specimen identified as that species by the authors (CASIZ 232217).

Species of <i>Clypeaster</i>	Petal Shape	Petal Size ¹	Petal Pore Pair Density ²	# Primary Tubercles Between Respiratory Pore Pairs ³	# Occluded Plates in Petal IVa ⁴	# Occluded Plates in Petal IIIb ⁴	Food grooves ⁵
<i>brigitteae</i> new species	All open, distal 1/2 of columns parallel*	~.6*	5–8*	1–2*	2*	1*	well-defined, ending short of ambitus
<i>annandalei</i> Koehler, 1922	Anterior open, posterior paired petals with columns converging distally*	~.6*	6–8*	3–4*	5–6*	4–5*	well-defined, ending at ambitus
<i>fervens</i> Koehler, 1922	Columns of all converging distally*, but variable	~.6*	9–12*	3–4*	4–5*	4*	well-defined, ending short of ambitus
<i>humilis</i> (Leske, 1778)	Columns of all converging distally	.5–.6	10–13	5–13	8–10	8	well-defined, ending short of ambitus
<i>japonicus</i> Döderlein, 1885	Anterior open, posterior paired petals with columns converging distally*	>.7	6–7	4–7	6–8	3–4	well-defined, short, ending about 1/3 length from ambitus
<i>latissimus</i> (Lamarck, 1816)	Columns of all converging distally*	.5–.6*	7*–8	15–20* (10–12 in Philippine specimens)	6*	6*	well-defined, ending short of ambitus

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TABLE 4. (Continued)

Species of <i>Clypeaster</i>	Petal Shape	Petal Size ¹	Petal Pore Pair Density ²	# Primary Tubercles Between Respiratory Pore Pairs ³	# Occluded Plates in Petal IVa ⁴	# Occluded Plates in Petal IIIb ⁴	Food grooves ⁵
<i>pateriformis</i> Mortensen, 1948a	Columns of all converging distally*	<.5*	11	4–7	4?*	4?*	
<i>reticulatus</i> (Linnaeus, 1758)	Columns of all strongly converging distally	~.6	7–11	3–4	4–7	3–5	poorly defined, ending about 1/3 length from ambitus
<i>virescens</i> Döderlein, 1885	Anterior open, posterior paired petals with columns converging distally	.5–.6	7–9	3–4	6–7	2–3	well- defined, ending short of ambitus

¹Based on ratio of PetIVL to AmbIVL, but in planar measurements from photos so that images of type specimens could be used.

²Number of respiratory pore pairs in 5 mm of column length in petal IVa, near midpoint of petal range based on examination of CASIZ, MNHN, and USNM specimens, and descriptions in the literature and of type series.

³Number of tubercles in poriferous zone between adjacent pore pairs near midpoint of petal IVa, where poriferous zone is generally widest.

⁴Approximate number, from specimens close to upper size range for the species, range based on examination of CASIZ, MNHN, and USNM specimens, and descriptions in the literature and of type series.

⁵A food groove is well-defined if it forms a shallow ditch, exhibits reduced spination and absence of primary spines, and is, for at least part of its length, in a cleft or valley along the perradial suture. Poorly defined grooves, such as those in *C. reticulatus*, are nearly flush with the test surface, although they still exhibit reduced spination.

Comparative morphology of Philippine *Clypeaster*

C. brigitteae n. sp. is immediately distinguishable from all other *Clypeaster* on the basis of petal and spination features discussed above, but differs from the other Philippine taxa (and these taxa from each other) in several other ways. Because a sizable proportion of the global complement of *Clypeaster* occur in the Philippines, an examination and summary of the features that have been shown here to help understand this fauna can guide future work on the genus as a whole, and on the fossil taxa not considered here.

Many identifications are attempted post mortem, often from dried or preserved material. It is our experience that although some echinoids are strikingly distinctive in absolute colour, or alternatively by colour pattern even as preserved specimens, only a few *Clypeaster* taxa exhibit useful differences. The usual caveats regarding faded or chemically altered pigments in preservatives are relevant. Therefore, not only is colour inconsistent among living specimens of a given species, it is especially variable in dried or preserved material. Specimens that have not been in preservative, but dried immediately or soon after being collected live (often the case for examples sold online to collectors), or that have experienced long exposure to sunlight or formalin, fade readily to a dull beige or light brown (Figs. 9, 10). Certain pigments, perhaps especially reds, are disproportionately affected by age or exposure to light and preservatives. However, certain colours and colour patterns are worth noting in the comparisons below, as they might help with identification in the field, or with recently collected, well-preserved material. The colour of the test itself, especially when bleached, is nearly always white or slightly grayish in all species.

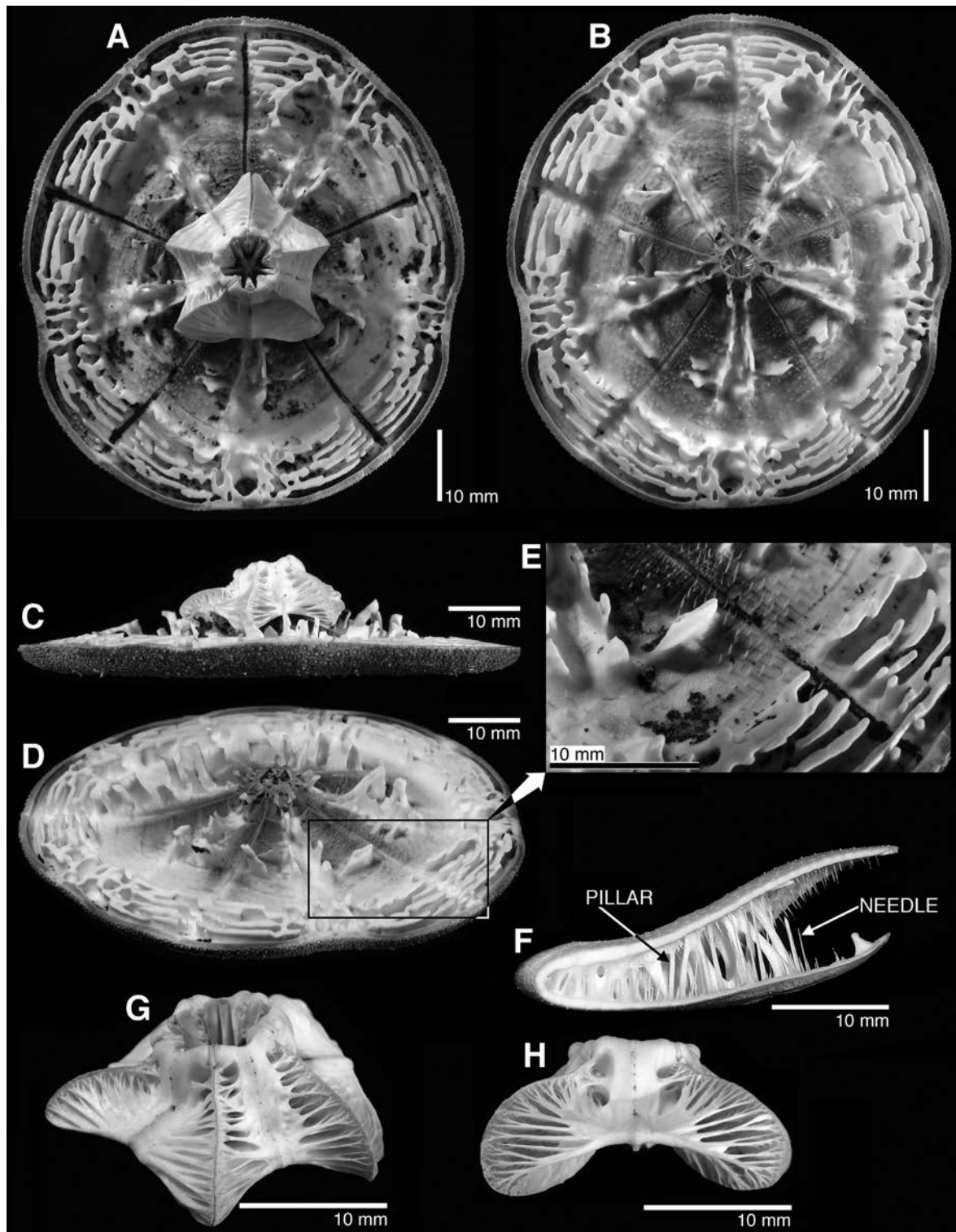


FIGURE 6. *Clypeaster brigitteae* n. sp., photographs of internal structure and Aristotle's lantern. A–E, G, and H show preparations from cleaned but not bleached specimen from paratype CASIZ 234826, Mactan Island, Cebu, Philippines, 70.1 mm TL, F shows bleached preparation from paratype CASIZ 234827, Mactan Island, Cebu, Philippines, 73.0 mm TL. A: Aboral view of specimen in which aboral surface was cut away, Aristotle's lantern still in place. B: Aboral view of preparation in A, Aristotle's lantern removed. C: Direct view of left side of preparation in A. D: Slightly oblique, left side view of preparation in B. Box indicates area shown in E. E: Magnified, oblique, left side view of inner surface of portion of interambulacrum 4 and ambulacrum V showing bars, walls, pillars and needles. F: Section through test along perradius showing pillars and needles. G: Slightly oblique, left side view of Aristotle's lantern from preparation shown in A and C. H: Direct posterior view of Aristotle's lantern shown in G.

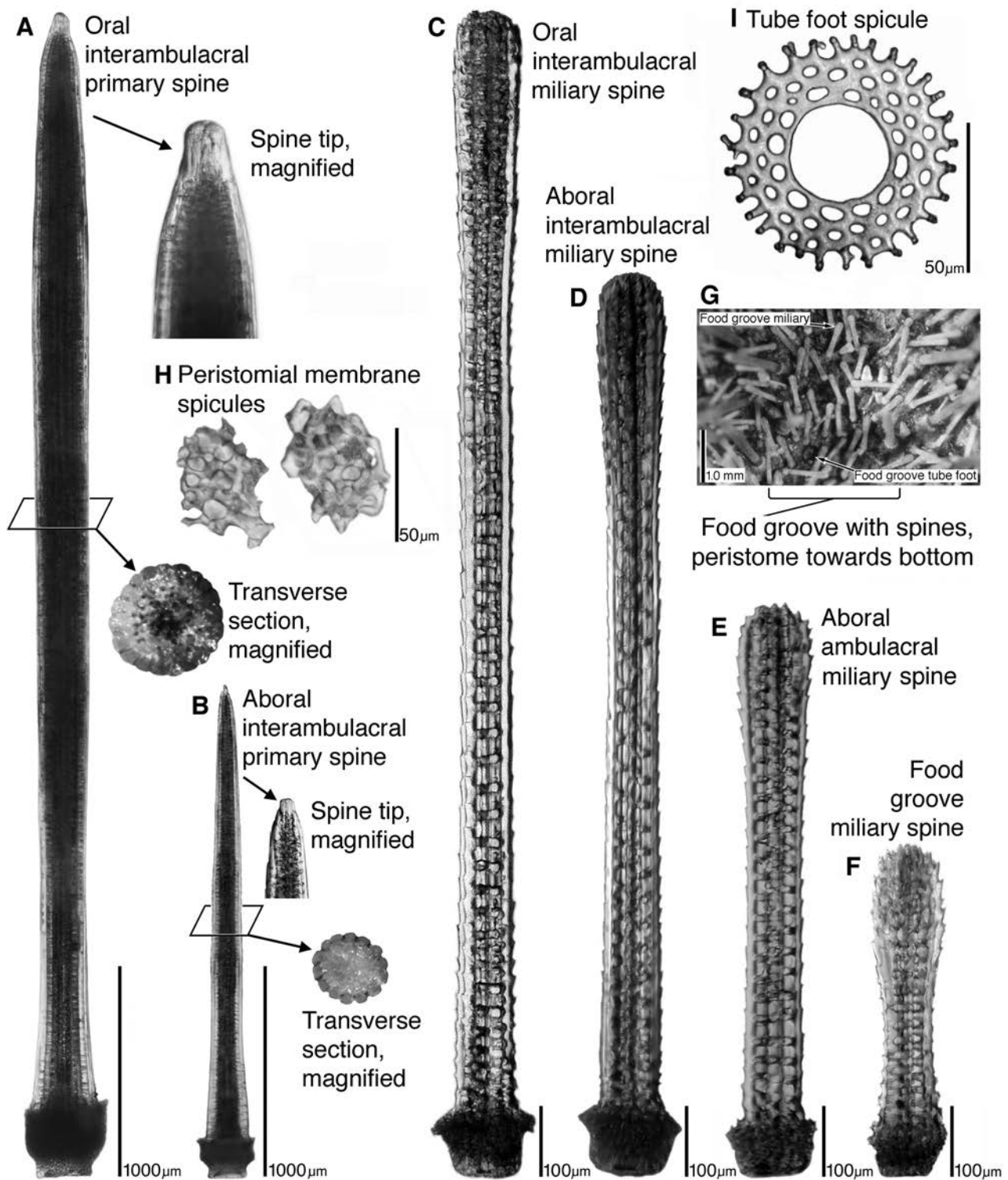


FIGURE 7. *Clypeaster brigitteae* n. sp., spines and spicules, all from holotype CASIZ 234824, Mactan Island, Cebu, Philippines, 93.8 mm TL unless indicated otherwise. A: Bleached oral interambulacral primary spine with magnified tip and transverse section. B: Bleached aboral oral interambulacral primary spine with magnified tip and transverse section. C: Bleached oral interambulacral miliary spine. D: Bleached aboral interambulacral miliary spine. E: Bleached aboral ambulacral miliary spine. F: Bleached food groove miliary spine. G: Food groove in ambulacrum II just distal to peristome showing spination and tube feet. H: Bleached spicules from peristomial membrane of paratype CASIZ 234823, Mactan Island, Cebu, Philippines, 94.6 mm TL. I: Bleached spicule from tip of tube foot on oral surface.

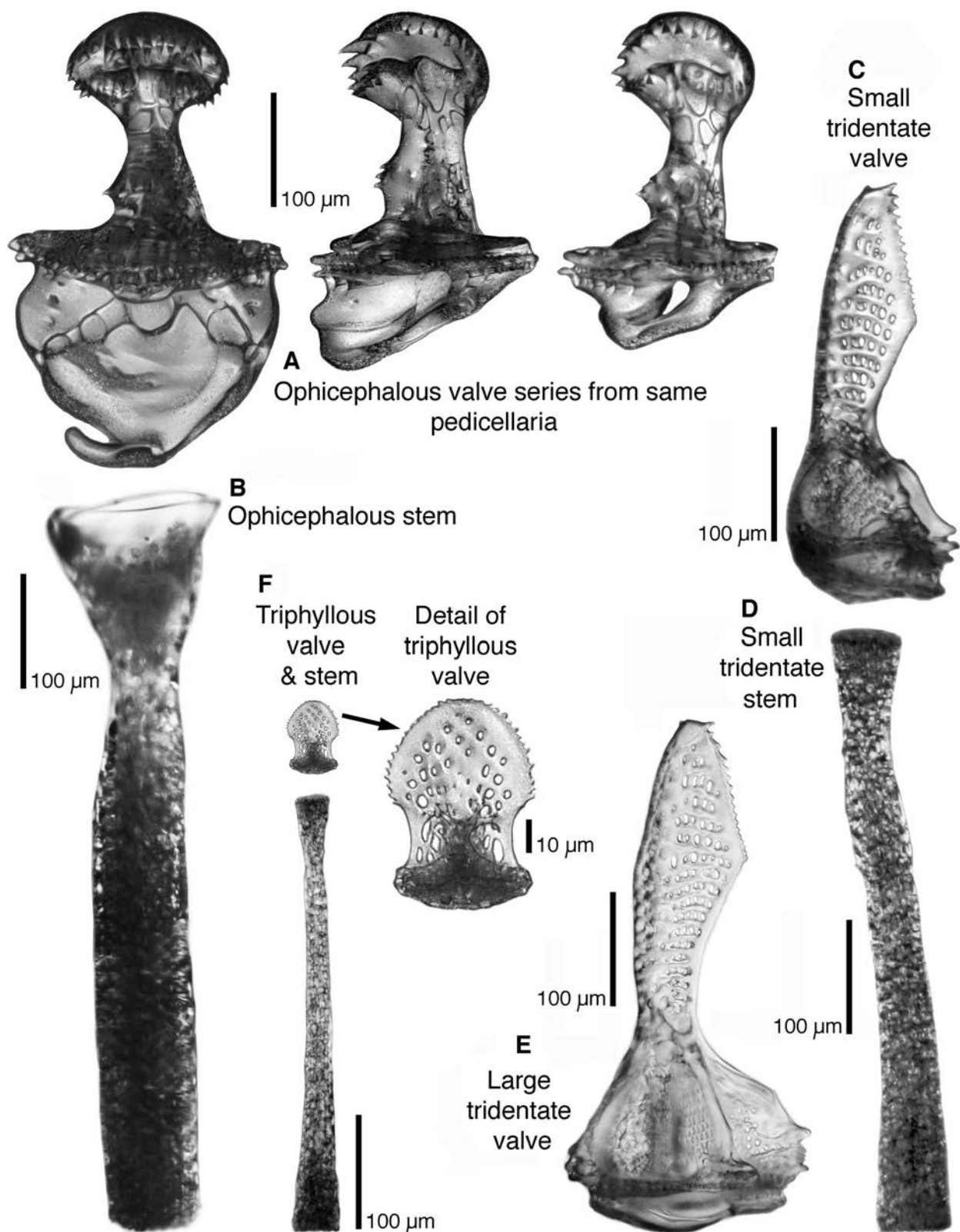


FIGURE 8. *Clypeaster brigitteae* n. sp., bleached pedicellariae valves and stems from holotype CASIZ 234824, Mactan Island, Cebu, Philippines, 93.8 mm TL. A: Series of valves from same ophicephalous pedicellaria on aboral surface. B: Stem of ophicephalous pedicellaria on aboral surface. C: Valve of small tridentate pedicellaria from oral surface. D: Stem of small tridentate pedicellaria from oral surface. E: Valve of large tridentate pedicellaria from oral surface. F: Valve, magnified view of valve, and stem of triphyllous pedicellaria from oral surface.

TABLE 5. Tuberculation and external appendage characteristics of all species of *Clypeaster* recorded to occur in the Philippines (* = feature based on images or examination of type material). *C. japonicus* is included as it has been recorded in the Philippines by collectors, and further suspected to occur there on the basis of a specimen identified as that species by the authors (CASIZ 232217).

Species of <i>Clypeaster</i>	Tubercle Density ¹	Oral/Aboral Primary Spine Length (ratio) ²	Oral Surface Spination ³	Aboral Primary Spine Tip Shape	Oral Primary Spine Tip Shape	Ophicephalous Valve L (µm) ⁴	Ophicephalous Stem L (µm) ⁵	# Ribs along Aboral Primary Spines ⁶
<i>brigitteae</i> new species	50*	5.5/2.5 (2.2)*	tubercles equal*	pointed*	pointed*	400*	650*	15*
<i>annandalei</i> Koehler, 1922	80*	4.5/2.5 (1.8)	tubercles equal*	pointed*	pointed, slightly curved*	350	1000	12 ⁷
<i>fervens</i> Koehler, 1922	90*	3.0/1.5 (2.0)	tubercles equal*	pointed	pointed	300	400	10
<i>humilis</i> (Leske, 1778)	250 (Red Sea) (390 in Philippine specimens)	2.5/1.0 (2.5)	tubercles equal	pointed to slightly swollen	pointed	250	400	12
<i>japonicus</i> Döderlein, 1885	100	3.0/2.0 (1.5)	tubercles equal	pointed	pointed	300	750	13
<i>latissimus</i> (Lamarek, 1816)	390* (280 in Philippine specimens)	5.5/1.5 (3.7)	tubercles equal*	slightly club-shaped	spatulate	300	750	12
<i>pateriformis</i> Mortensen, 1948a	160	3.0/1.0 (3.0)*	tubercles equal*	pointed*	pointed*	200	300	14 ⁸

...Continued on the next page

TABLE 5. (Continued)

Species of <i>Clypeaster</i>	Tubercle Density ¹	Oral/Aboral Primary Spine Length (ratio) ²	Oral Surface Spination ³	Aboral Primary Spine Tip Shape	Oral Primary Spine Tip Shape	Ophicephalous Valve L (µm) ⁴	Ophicephalous Stem L (µm) ⁵	# Ribs along Aboral Primary Spines ⁶
<i>reticulatus</i> (Linnaeus, 1758)	150	3.0/1.5 (2.0)	reduced	pointed	pointed	300	500	12
<i>virescens</i> Döderlein, 1885	80	4.5/2.0 (2.25)	tubercles equal	pointed	slightly spatulate, curved	300	850	12

¹Aboral primary tubercle number per cm², rounded to nearest ten.

²Near midpoint of interambulacrum 4, oral and aboral spine lengths to nearest .5 mm (with calculated ratio).

³In *C. reticulatus*, the region surrounding the peristome is sparsely populated by primary tubercles that also tend to be smaller than those on the rest of the oral surface (Fig. 12A).

⁴Length of longest valve, including handle proximal to hinge, from pedicellariae on aboral surface, near posterior ambitus, to nearest 50 µm.

⁵From pedicellariae on aboral surface, near posterior ambitus, to nearest 50 µm.

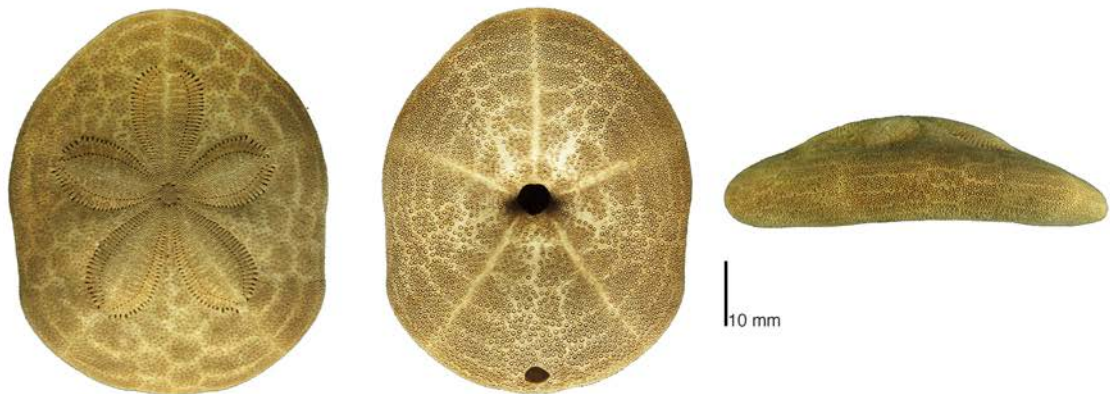
⁶Approximate number based on cross section about half way along shaft of typical primary spine from aboral interambulacrum 4 in large adult specimen (allometry is strongly negative for external appendages, so it does not vary appreciably during ontogeny).

⁷We found none with fine, numerous ribs as described and depicted by Mortensen (1948b: p. 57, fig. 42).

⁸From figure in Mortensen (1948b: p. 65, fig. 45), who did not specify the surface from with the spine was taken. It could be from an oral spine, in which rib numbers are typically higher.



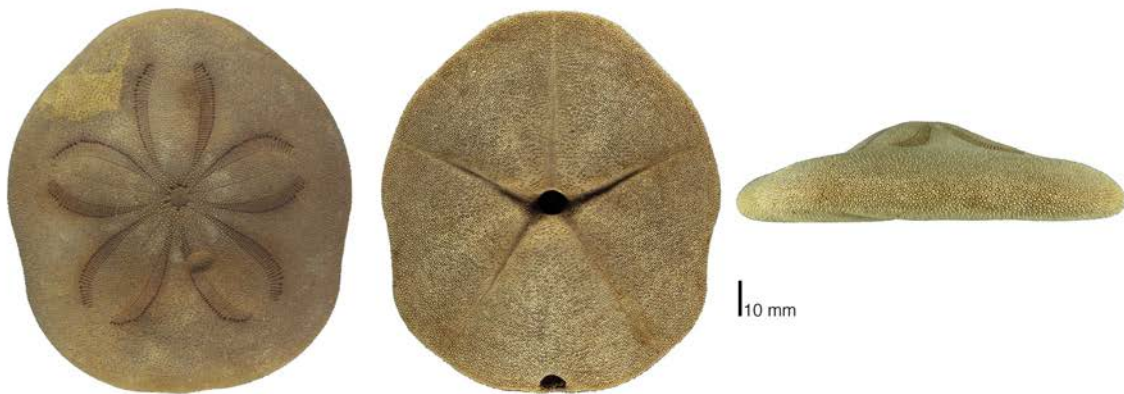
Clypeaster annandalei Koehler, 1922 [MNHN syntype IE-2013-10656, Gulf of Aden]



Clypeaster fervens Koehler, 1922 [MNHN IE-2016-766, Red Sea]



Clypeaster humilis (Leske, 1778) [MNHN IE-2016-762, Red Sea]



Clypeaster japonicus Döderlein, 1885 [MNHN IE-2016-771, Japan]

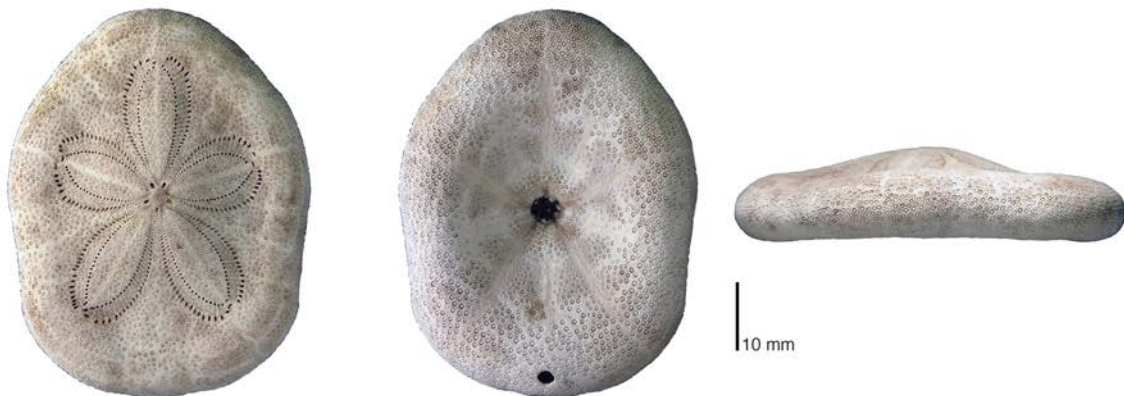
FIGURE 9. Photographs of *Clypeaster* species recorded from the Philippines (other than *C. brigitteae* n. sp.). Left to right for each: aboral, oral, and left side views.



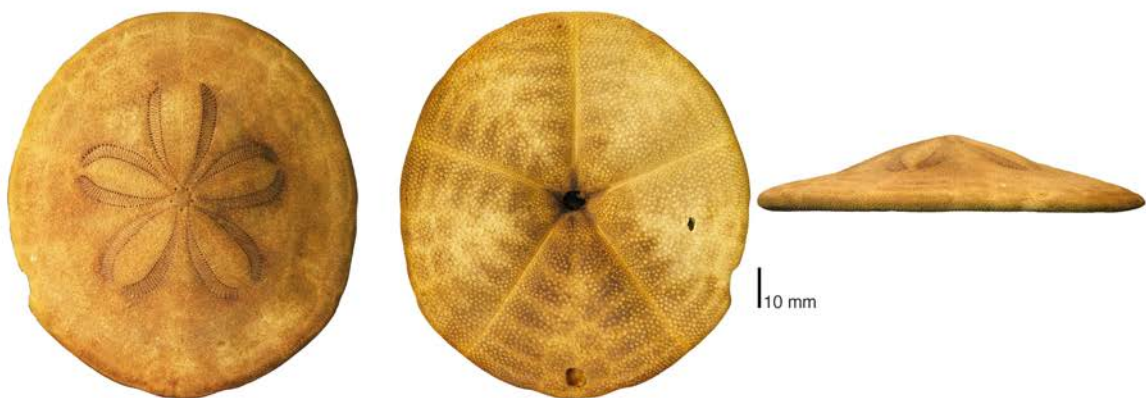
Clypeaster latissimus (Lamarck, 1816) [CASIZ 227318, Philippines]



Clypeaster pateriformis Mortensen, 1948 [MNHN IE-2016-666, Indonesia]



Clypeaster reticulatus (Linnaeus, 1758) [CASIZ 187321, Philippines] - bleached test



Clypeaster virescens Döderlein, 1885 [CASIZ 233415, Philippines]

FIGURE 10. Photographs of *Clypeaster* species recorded from the Philippines (other than *C. brigitteae* n. sp.), continued from Fig. 9. Left to right for each: aboral, oral, and left side views.

The comparative morphology of general test features (Table 3), petal and food groove morphology (Table 4), and tuberculation and external features (Table 5), indicate that all the species have suites of features that can be used to identify them unambiguously, even in the field. These data can be used to mitigate confusion in some of the literature pointed out by Mortensen (1948b), and which still exists in some cases in online identifications, marine curio dealer websites, and in the scientific literature. The data suggest four main morphotypes on the basis of overall test height, shape, and size (Figs. 9, 10), and it is helpful to use these generalized groupings to facilitate more detailed comparisons.

The first of these groups consists of relatively high-tested forms that express a domed or campanulate (bell-shaped) camber with a correspondingly well-developed infundibulum. *C. brigitteae* n. sp., *C. annandalei*, and *C. virescens* exemplify this morphotype. A second morphotype is intermediate in test height relative to test length, with a camber that rises more or less gradually from a relatively thick test margin, and includes *C. fervens* and *C. japonicus*. *C. reticulatus*, which is variable in test height, has an inflated margin so distinct among the Philippine species it is here considered a morphotype of its own. The remaining forms, *C. humilis*, *C. latissimus*, and *C. pateriformis*, are characterized by flattened tests with low TH relative to TL, and almost planar oral surfaces. Although arranged alphabetically in Tables 3–5 (largely because other characters can lead to alternative groupings), these taxa are considered below in order of these main morphotypes.

1. Relatively high, somewhat campanulate test:

C. brigitteae n. sp.—The new species differs from all Philippine species of *Clypeaster* in having the two columns of respiratory pore pairs in all of its petals continuously diverging towards the ambitus, the lowest aboral primary tubercle density, lowest number of primary tubercles in the spaces between respiratory pore pairs, and lowest number of occluded plates in the petals (Fig. 4D). Although *C. virescens* also has a relatively low number of occluded plates, it is still in the range of two or three, instead of only one in *C. brigitteae* n. sp. The latter also differs from other Philippine taxa, except *C. latissimus* and *C. pateriformis*, and some examples of *C. japonicus*, in having the interambulacral basicoronal plate separated from corresponding post-basicoronals by two plates from adjacent ambulacra (Fig. 11). *C. brigitteae* n. sp. seems to be darkly pigmented, particularly in the centres of the plates, but no distinctive patterning is otherwise discernible (Fig. 3).

C. annandalei Koehler, 1922—Among Philippine taxa, this taxon is most similar to *C. brigitteae* n. sp. in the strikingly light, thin-walled test, pronounced infundibulum, and low respiratory pore pair density, although in adults this is never as low as in *C. brigitteae* n. sp. *C. brigitteae* n. sp., has a comparatively low aboral tubercle density, and a small number of occluded plates at the ends of the petals (only two for *C. brigitteae* n. sp., and five or six in *C. annandalei*). Mihaljević *et al.* (2011: fig. 7A) used what was presumably the anterior petal of a specimen of *C. annandalei* to illustrate plate occlusion in an open petal (the others being closed in this species). By our count, there seem to be only one or at most, two occluded plates in their image, suggesting that plate occlusion in the anterior petal can approach the condition seen in petal IVa of *C. brigitteae* n. sp. However, none of the petals in the aboral view of *C. annandalei* in Mihaljević *et al.* (2011: fig. 2A) looks very much like the plate map of the petal in their figure 7A, and there is nothing to suggest that this is not drawn from the same specimen. The overall shape of all the petals of the individual in their figure 2A is different, and the pore pair count is approximately 30 in each column, but in excess of 50 in the petal in figure 7A. Our examination of Koehler's (1922) syntype series at the MNHN indicates that the specimen in figure 2A of Mihaljević *et al.* (2011) is only 60% TL of the largest MNHN specimens, yet even among these larger specimens, there are only about 40 respiratory pore pairs in each column. It would appear that a petal from *C. annandalei* is not actually depicted in figure 7A of Mihaljević *et al.* (2011). Our examination of Koehler's types of *C. annandalei* shows that the typical number of occluded plates is much higher than that suggested by Mihaljević *et al.* (2011), and that this feature remains a reliable separator between *C. annandalei* and *C. brigitteae* n. sp. As suggested above, the petals of *C. annandalei* all converge ("close") distally except for the anterior petal (Fig. 9), a feature it shares only with *C. japonicus* (Fig. 9) and *C. virescens* (Fig. 10). This is, in part, responsible for difficulties in separating these three species. *C. annandalei* differs from *C. fervens* in respiratory pore pair density and by its more flattened oral surface, particularly near the ambitus. In addition, the bars and circumferential walls of the internal structure are less developed in *C. fervens* than in *C. annandalei*. *C. virescens* shares with *C. annandalei* a very lightly built test and flattening of the oral surface distal to the infundibulum, but the former has a conspicuously lower test, and significantly more highly developed system of internal bars and walls. Relative to the aboral primary spines, *C. virescens* also has much longer oral primary spines (Fig. 12C) than in *C. annandalei*. In addition, in *C. virescens*, these are spatulate (Fig. 12C), not pointed as in *C. annandalei*. Although the

ophicephalous stems and valves of *C. virescens* and *C. annandalei* are similar in size, and among the largest known in the genus, the stems of the ophicephalous are slightly longer in the latter species. Dried and some wet-preserved specimens of *C. annandalei* have a distinctive, reddish orange or almost rose colouration that is expected to be more vibrant in living examples. However, specimens of the type series at the MNHN are dark brown (Fig. 9), suggesting darkening in the preservative (ethanol).

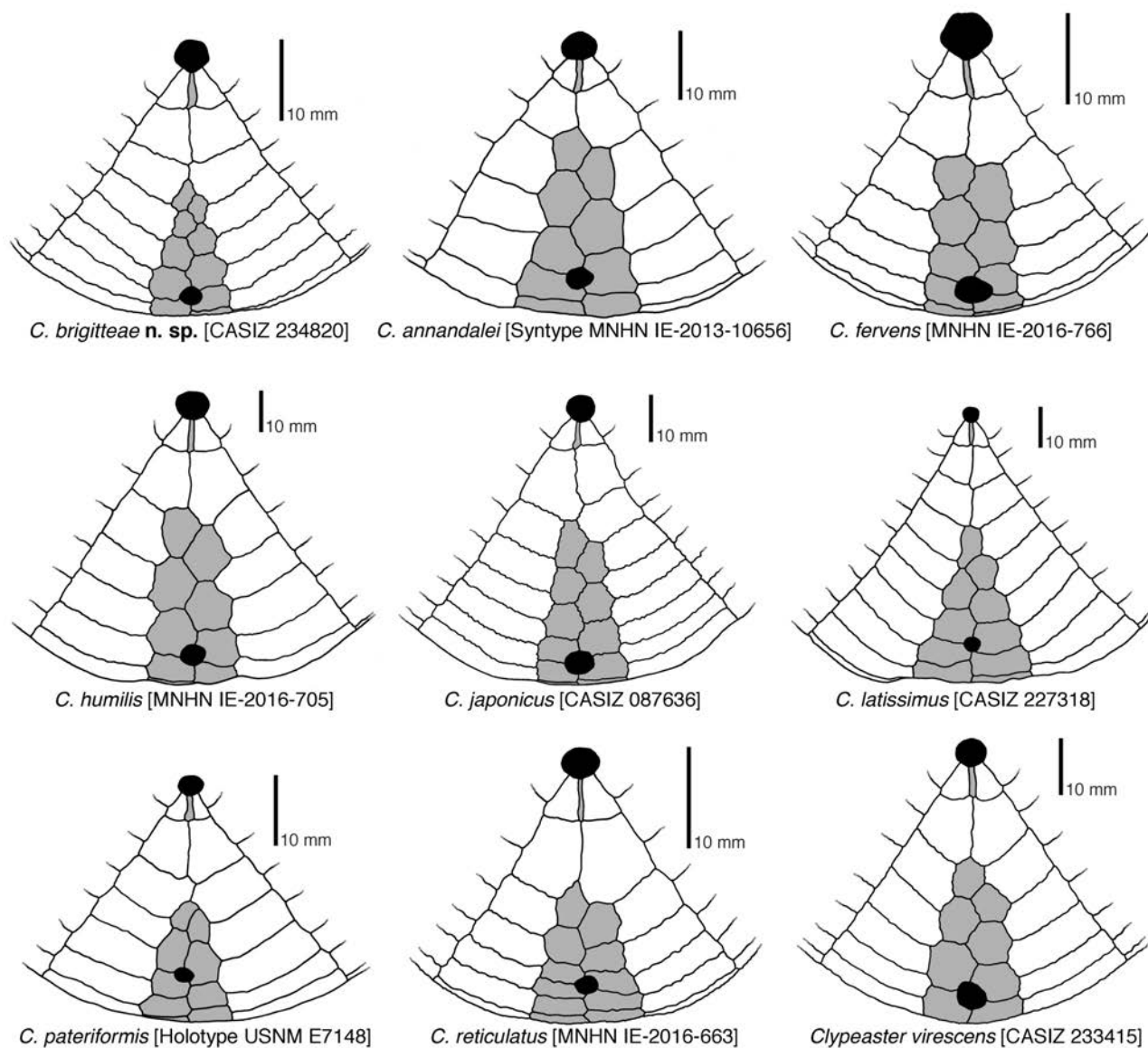


FIGURE 11. Drawings of oral surface showing plate architecture in posterior interambulacrum (interambulacrum 5) of all *Clypeaster* species recorded from the Philippines. Interambulacral plates shaded, peristome and periproct in solid black, posterior edge of test at bottom.

C. virescens Döderlein, 1885—A moderately high-tested form, this species has a very lightly built test with a flattened camber. In spite of the strongly developed system of bars and walls in the interior periphery of the test, it is much lighter than similarly sized forms with open anterior but closed paired petals, such as *C. japonicus*, due to the thinness of the test walls throughout. Except for *C. brigitteae* n. sp., *C. virescens* has the lowest number of occluded plates at the ends of the petals among the Philippine species. Well preserved examples with full spination illustrate that *C. virescens* is unusual in having elongated, curved, spatulate spines (Fig. 12C). Among the Philippine taxa, only *C. latissimus* has similar spines (Fig. 12B), but in the latter form, the ratio of oral primary spine length to aboral primary spine length is higher than in *C. virescens*. Dried specimens of *C. virescens* are greenish brown, fading to light brown or beige with increasing age, but leaving paler plate sutures that allow plate patterns to be discerned over much of the test. Often, the oral surface is somewhat darker and greener than the aboral surface, contrasting strongly

with the long, pale, whitish primary spines. True to the meaning of its species name, several of the ethanol-preserved specimens of *C. virescens* examined at the MNHN are distinctly deep greenish, notably on the oral surface. However, it should be noted that in some cases, irregular echinoids, particularly neognathostomates, exhibit the strange phenomenon of turning varying shades of green in certain preservatives (Mortensen (1948b), notably in ethanol, and it remains unknown to what extent this greenish colour is exhibited by living specimens of *C. virescens*.

2. Moderately high test with relatively thick ambitus and smoothly arched camber:

C. fervens Koehler, 1922—This species was known only from a single specimen at the time it was described, but additional material, collected since Mortensen's (1948b) monograph, has helped to distinguish this species among the Philippine forms, at least. The species is most notable for the low development of its internal bars and walls. In this respect, it is most like *C. japonicus*, which nonetheless differs from *C. fervens* because in the latter, at least in the type, all of the petals converge as they approach the margin of the test. However, as illustrated in Mortensen (1948b), this feature appears to vary in *C. fervens*, with some examples having divergent pore pair columns in the anterior petal. It is not known to what extent this might be due to misidentification of *C. japonicus* as *C. fervens* outside what is normally considered the former's previously assumed endemic distribution around Japan. In any case, adult *C. japonicus* have more deeply incised food grooves, notably as they approach the peristome (Fig. 9), than in *C. fervens*, which also tends to have a higher respiratory pore pair density. *C. fervens* tends to have fewer occluded plates at the ends of the petals than *C. japonicus*. Based on available data, it would appear that *C. fervens* does not have more than one pair of ambulacral plates forming the disjunction between the interambulacral basicoronal and the first post-basicoronal (Fig. 11), whereas *C. japonicus* has two. *C. fervens* is lightly pigmented, even as dried or ethanol-preserved specimens, which are beige or light brown, with a slightly paler oral surface and no discernible contrasting pattern.

C. japonicus Döderlein, 1885—A species reported from shallower water in Japan than its congeners, in the Philippines, the full bathymetry of *C. japonicus* has yet to be documented. As noted above, it is most easily confused with *C. fervens*, but distinguished from it primarily by the characters noted. It is unlike most other Philippine *Clypeaster* in that the food grooves tend to lose their distinctive, deeply incised character about 1/3 of the length of the corresponding perradius from the peristome (Fig. 9). Although this is similar to *C. reticulatus* (Fig. 10), *C. japonicus* should not be confused with that species because of the former's poorly demarcated food grooves, distinctively heterogeneous oral tuberculation (Fig. 12A), closure of all petals (Fig. 10), and the overall test shape. In addition, in large *C. japonicus*, the poriferous zones are characteristically slightly lower than the level of the test in surrounding interporiferous zones, leading to their sunken appearance (Fig. 9). In life, *C. japonicus* can be strikingly light purplish, lavender or reddish brown on both oral and aboral surfaces, with contrasting dark brown poriferous zones. Preserved or dried material can be much darker, fading to brown or dark beige.

3. Small, low test with inflated margin:

C. reticulatus (Linnaeus, 1758)—This relatively small form attains the lowest maximum TL of all the known Philippine taxa. The maximum size reported here is from extraordinary examples found in the Red Sea, and is seldom attained by those from the Philippines, the largest examples of which tend to be 50–60 mm TL. *C. reticulatus* is unique among all *Clypeaster* in the reduction in density of primary tubercles (and accompanying spines, which are also somewhat shorter) in a ring-shaped region surrounding the peristome (also noted by Arachchige *et al.* 2019). Although the general morphology and TH varies within its known, very broad range, this feature of the tuberculation (Fig. 12A), combined with the inflated margin (Fig. 10), allows *C. reticulatus* to be distinguished readily from all other members of the genus. In some specimens of *C. reticulatus*, the periproct can be slightly more than its own length distant from the ambitus, but this is not sufficiently consistent to be a distinguishing feature of the species. When alive, *C. reticulatus* is typically marked with dark mottling contrasting with the very light greyish or beige aboral surface (Fig. 13A), also illustrated by Mooi & Munguia (2014: fig. 2). This mottling can be very pronounced in the aboral ambulacral areas, but is often also expressed on the darker, deeper brown oral surface (Fig. 13B), and is retained in ethanol-preserved specimens. In old, dried material, notably that in the MNHN recorded from the Red Sea region, the colour can be almost uniformly light brown, likely due to fading related to aging of the specimen after drying (Figs. 13C, D).

4. Low test with sharply defined ambitus:

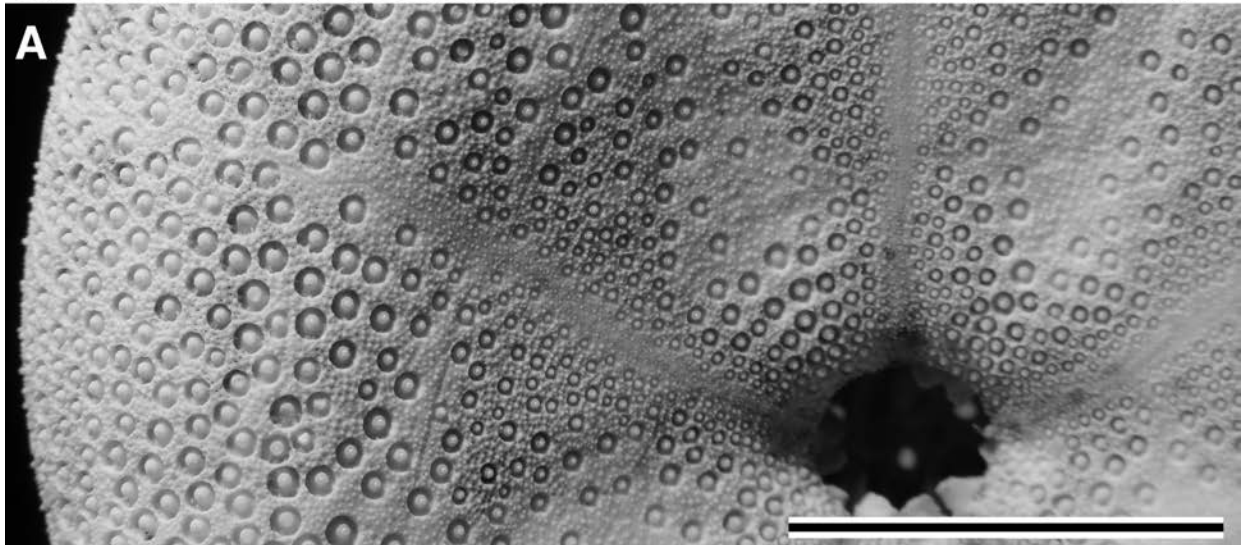
C. humilis (Leske, 1778)—Along with *C. reticulatus*, this is the most abundant of all sea biscuits found in the Philippines. Although specimens from near to what is presumed to be the type locality in the Red Sea can have a relatively high test with thickened margins in some cases, all the specimens seen by the authors from the Philippines

have a sharp ambitus and low test, particularly distal to the ends of the petals. In most specimens, the respiratory pore pair columns converge so dramatically distally that they almost touch (Fig. 9). The number of primary tubercles spanning the poriferous zone can attain the highest values among the Philippine *Clypeaster* (5–13, see Table 4), with the exception of some very large specimens of *C. latissimus*. Maximum respiratory pore pair density is also the highest of all Philippine *Clypeaster* (10–13, see Table 4). Spination is remarkably fine and even aborally. The density of aboral tubercles reaches 250/cm², a value exceeded only by *C. latissimus* (Table 5). The aboral primary spine tips in *C. humilis* are slightly swollen, but not quite club-shaped as they are in *C. latissimus*. Most living specimens of *C. humilis* collected in the Philippines by the first author have strikingly demarcated, chocolate-brown poriferous zones that contrast strongly with the light beige-grey of the surrounding areas on the aboral surface (Fig. 13E). The oral surface is only slightly darker, and lacks mottling of any kind (Fig. 13F). This colour pattern is retained in ethanol-preserved material, but is much less pronounced in dried specimens. In old, dried material, notably that in the MNHN from the Red Sea (Fig. 9), the colour can be almost uniformly light brown.

C. latissimus (Lamarck, 1816)—This is among the largest of all *Clypeaster* species, routinely attaining sizes in excess of 200 mm TL. In most individuals, particularly those from the Philippines, the test is considerably longer than wide. In the type specimen at the MNHN (Tables 1, 4), there are usually more than 15, and as many as 20 primary spine tubercles between respiratory tube foot pores. However, among specimens examined from the Philippines, this number is much lower, a phenomenon also observed to a lesser degree in *C. humilis*. *C. latissimus* is unique among Philippine taxa in possessing slightly club-shaped spines, more densely distributed over the aboral surface than in any *Clypeaster* in which this feature has been examined. The ratio of oral primary spine length to that of aboral primaries (3.7, see Table 5) is also the highest among Philippine taxa, and the long oral spines are conspicuously spatulate (Fig. 12B). *C. latissimus* also has the highest number of oral ambulacral plates in each column, notably in the paired posterior ambulacra, in which there are usually as many as ten in each column (half ambulacrum). Most other species have only seven or eight, but *C. brigitteae* n. sp. is similar to *C. latissimus* in having as many as nine. *C. latissimus* and *C. pateriformis* are the only *Clypeaster* in the archipelago to have the periproct placed more than its own length from the ambitus, with the exception of some specimens of *C. reticulatus* (which is so different from either of these species in other respects that it cannot be confused with them). In addition, the bars and circumferential walls inside the periphery of the test of *C. latissimus* reach the greatest levels of elaboration among all Philippine forms, *C. pateriformis* being the only species with any remotely similar degree of development. The ophicephalous pedicellariae can be extremely rare on *C. latissimus*. In many hours of intense searching on 5 different specimens with well-preserved spination, only 2 or 3 ophicephalous pedicellariae were found, all of them on the same individual. Colour of living or ethanol-preserved *C. latissimus* is unknown, but dried specimens are evenly dark, greenish brown aborally, and usually somewhat paler on the oral surface.

C. pateriformis Mortensen, 1948a—Among the most poorly known of all extant *Clypeaster*, the type, housed at the USNM, was collected east of the island of Luzon in 1908, but remains the only specimen so far recorded from the Philippines. The data presented here were collected from this specimen, as well as from an individual examined at the MNHN, collected off Indonesia in 1980 (Fig. 10). Among Philippine *Clypeaster*, *C. pateriformis* is unique in being almost circular (TL almost equal to TW). Mortensen (1948b: 68) suggested that *C. pateriformis*, *C. latissimus* and *C. telurus* H.L. Clark, 1914 (the latter found in Australia and New Caledonia, not recorded from the Philippines) “form a group of their own, characterized mainly by the great distance of the periproct from the edge of the test”. All three of these species also have extreme development of the internal peripheral bars and walls (see above), which seems to be a feature of all the greatly flattened, almost sand dollar-like forms of *Clypeaster* (sensu Seilacher 1979). *C. pateriformis* lacks the club-shaped aboral spines of either *C. latissimus* or *C. telurus*, making it unique among these flattened taxa with more proximally placed periprocts. In addition, *C. pateriformis* has among the smallest petals of all the Philippine *Clypeaster*, each petal being distinctly less than half the length of the corresponding perradius (Fig. 10). Like *C. brigitteae* n. sp., *C. japonicus*, and *C. latissimus*, with which it cannot otherwise be confused, *C. pateriformis* has two pairs of ambulacral plates forming the disjunction between the interambulacral basicoronal and the first post-basicoronal (Fig. 11), but additional material will be needed to determine if this is a reliable characteristic for the species. Colour in life is unknown, but the holotype of *C. pateriformis* at the USNM is pale brown, and the dried specimen at the MNHN is an even, dark greenish brown, somewhat paler on the oral surface (Fig. 10).

Clypeaster reticulatus, reduced oral tuberculation in ambulacra II & III [CASIZ 187321]



Clypeaster latissimus, spatulate primary spines in oral interambulacrum 3 [CASIZ 206955]



Clypeaster virescens, primary spines in oral interambulacrum 4 [MNHN IE-2016-650]

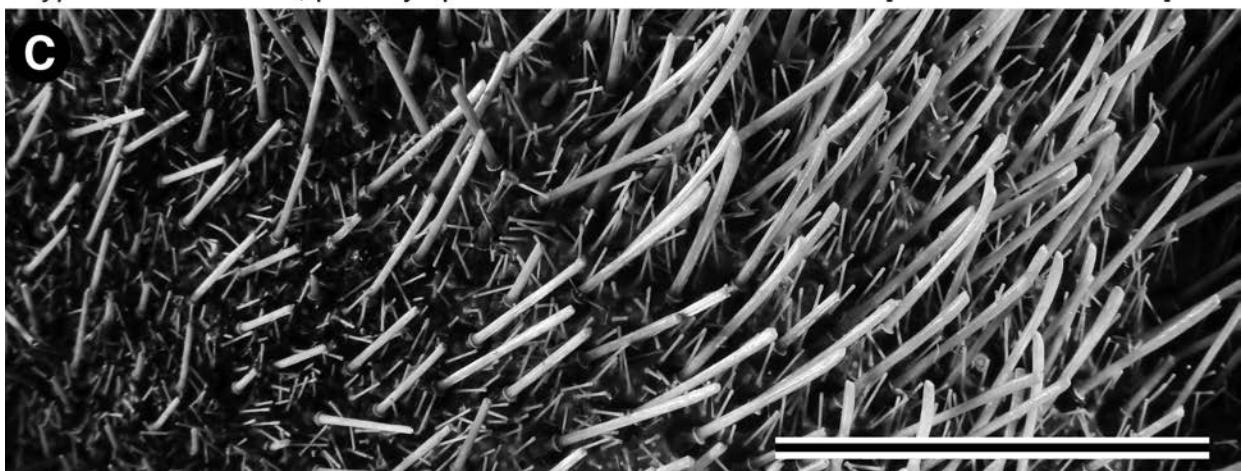


FIGURE 12. Tuberculation and spination on oral surface of selected species of *Clypeaster* recorded from the Philippines.

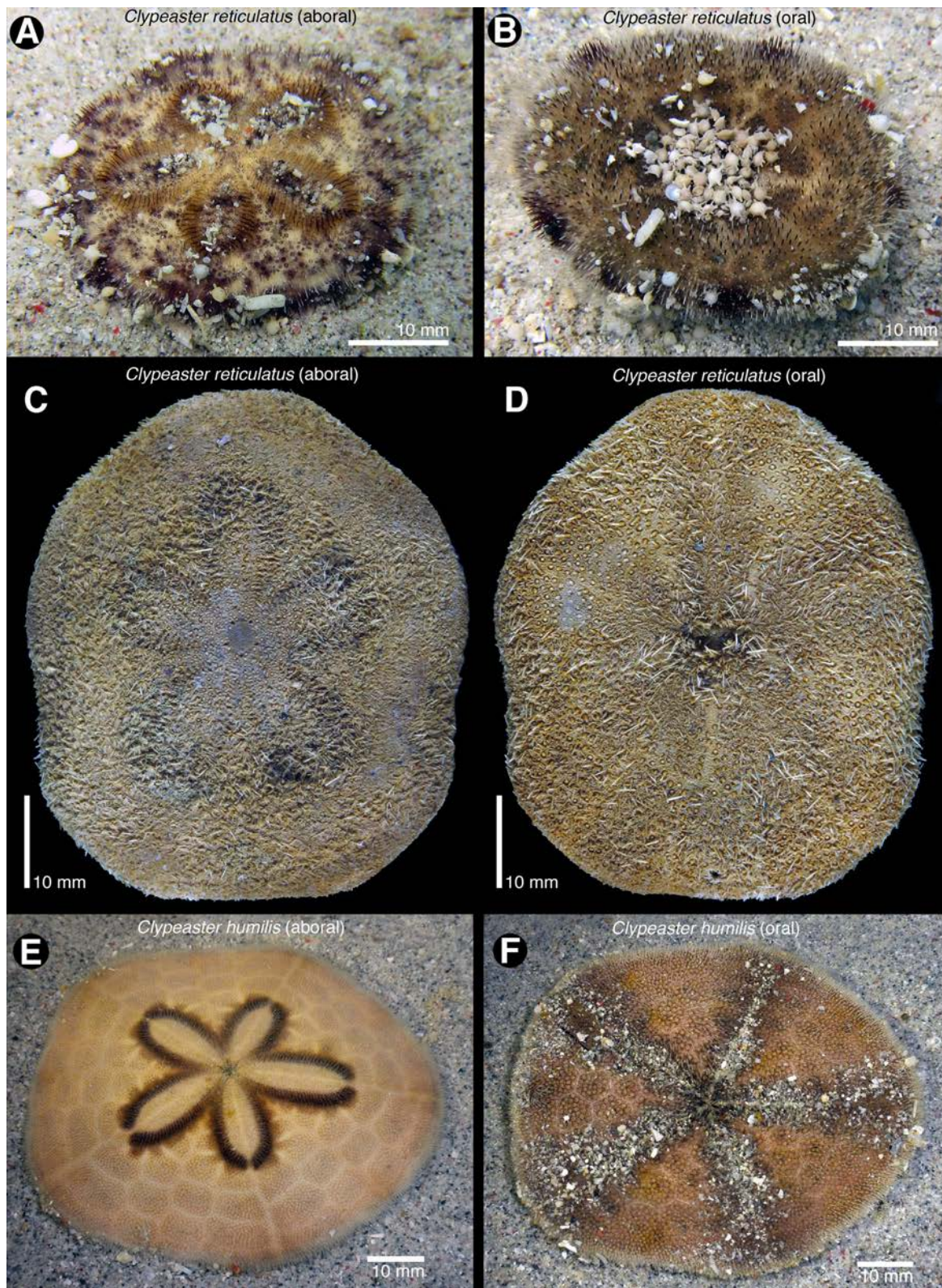


FIGURE 13. Colouration in Philippine *Clypeaster*. A: *Clypeaster reticulatus*, aboral surface, photographed alive, in the field, Verde Island Passage, Philippines, 2011. B: *Clypeaster reticulatus*, oral surface, inverted and photographed alive, in the field, Verde Island Passage, Philippines, 2011 (note collected foraminiferans used for food). C: *Clypeaster reticulatus*, aboral surface, preserved museum specimen in the Cotteau Collection, MNHN-IE-2016-830, Gulf of Suez. D: *Clypeaster reticulatus*, oral surface, preserved museum specimen in the Cotteau Collection, MNHN-IE-2016-830, Gulf of Suez. E: *Clypeaster humilis*, aboral surface, photographed alive in the field, Verde Island Passage, Philippines, 2011. F: *Clypeaster humilis*, oral surface, inverted and photographed alive in the field, Verde Island Passage, Philippines, 2011.

Discussion

The fact that *C. brigitteae* **n. sp.** is relatively easily distinguished from other *Clypeaster*, yet has not been described until now, is indicative of our low level of knowledge not only of the genus itself, but of the fauna of the Philippines. Specimens turned up in trawls among the islands of the Philippines south of Luzon, but the species remained unnamed pending a full comparison of all *Clypeaster*, with a focus on those taxa from the Philippines, as well as the acquisition of additional material that could fill out the known range and scope of variation. Reviews of the literature on echinoids from the region (Mooi & Munguia 2014) also highlighted the fact that undiscovered diversity existed in the Philippines. Mooi & Munguia (2014) did not make a full analysis of the diversity of *Clypeaster* occurring there, although they provided a framework within which to develop more information concerning members of the genus from the archipelago. The present paper is intended to remove much of the ambiguity that remains concerning the identification of these species. The use of tabular data focussing on specific types of morphology can avoid the constraints and information voids left by a dichotomous key.

The new species increases to nine the number of *Clypeaster* known to occur in the Philippines. No other archipelago or country of comparable size has more extant species of the genus. In fact, only the United States records more species of *Clypeaster*, because it spans so much of the Indo-Pacific, tropical distribution of the genus by including taxa occurring off of Hawai'i, some of which are apparently endemic to those islands. That large, relatively easily collected specimens of sea biscuits such as *C. brigitteae* **n. sp.** are still being described from the Philippines, and that 22% of the world's biodiversity of the group occurs there, underscores the need to better understand all the factors that make the apex of the Coral Triangle in the Indo-Pacific such a critical centre of biodiversity, notably for echinoids (Mooi & Munguia 2014).

The issues discussed above in comparisons of occluded plate configurations at the end of the petals between *C. brigitteae* **n. sp.** and *C. annandalei* centre on the lack of complete data for all species. The images representing plate architecture of petals in Mihaljević *et al.* (2011) lack many suture lines even in the areas of interest in assessing plate occlusions. Although it might be expected to be more fully examined in such a taxonomic work, the lack of suture lines is not mentioned in the text, making it difficult to assess the reliability of such figures. Characteristics such as plate occlusion were regarded by Mihaljević *et al.* (2011) as critical in morphological phylogenetic analysis, and for this, accurate plate maps are necessary.

Some features are remarkable in the lack of influence on their expression patterns by size variation, at least in individuals considered mature (those in which gonopores have appeared). These features include spine and pedicellular sizes, as well as the number of ribs on the aboral primary spines (Table 5). In addition, within a given species, values varied little from individual to individual in spite of differences in test size, indicating that the relative lack of influence of allometry might lead them to be useful in systematics across the genus as a whole. For example, food groove miliary spines are seldom mentioned in any treatment of *Clypeaster* morphology. The present survey suggests that in *C. brigitteae* **n. sp.**, *C. annandalei*, *C. fervens*, *C. humilis*, *C. latissimus*, and *C. pateriformis*, these miliaries are short (one half or less than the length of the miliaries in adjacent ambulacral areas), as previously indicated for *C. rosaceus* (Linnaeus, 1758) and *C. subdepressus* (Gray, 1825) (Telford *et al.* 1987). However, in *C. japonicus*, they can be relatively long (well over half the length of the adjacent miliaries). In *C. reticulatus* they are, like the food grooves themselves, not well-differentiated. The number of ribs along primary spines is also surprisingly stable among spines in an individual, and even within a given species. However, the values tend to overlap considerably among species, making this feature much less useful among clypeasterines than some studies might suggest (e.g. Mortensen 1948b).

Unless extremes of expression in petal size are considered (e.g. very small petals of *C. pateriformis*, or very large ones in *C. japonicus*), petaloid area or petal lengths are not reliable distinguishing features when gauged as a percentage of the length of the corresponding ambulacrum. It is possible that an illusion of petal size differences can be caused, at least in part, by changes in the width of the test. This tends to lengthen the perradial sutures of the paired ambulacra and therefore the apparent sizes of the accompanying petal. This study finds that relative petal sizes, used extensively by some authors (Mortensen 1948b; Schultz 2005, 2009) are not as reliable in taxonomy as assessments of the number of primary tubercles between respiratory tube feet, density of the respiratory pore pairs along the petal, number of occluded plates, or degree to which the petals close distally.

The interesting, yet under-utilized, nature of the tube foot spicules in accessory tube feet shows promise in systematics of the genus, just as they have in demonstrating overall differences among major clades in the Clypeast-

eroida and Scutelloida. As surveyed by Durham (1955) and Mooi (1986), the Clypeasteroida differ from the Scutelloida in having a ring-like spicular structure in the tips of the accessory tube feet, with some Clypeasteridae expressing the most elaborate form: a completely closed, fenestrated ring adorned with peripheral knobs and points, suggesting a sophisticated watchmaker's gear (Fig. 7I). Variation in this gear-like morphology has not been fully explored, but seems to differ both among species and among tube foot types in a given species (Mooi 1986). Preliminary data collected by the first author on tube foot spicule morphology from about 10 other species, several of them from the Indo-Pacific, suggest promise for further work. This is also expected to be the case with pedicellarial types and distributions on the test, which vary among species in ways indicating new directions not only for phylogenetic analyses, but for studies of echinoid functional morphology.

Likewise, the unusual tipping forward of the lantern in life position described herein (Fig. 6C) does not seem to have been recorded for any clypeasteroid or scutelloid. It is unknown if there is a functional reason for this orientation, or how widespread this feature is, even among *Clypeaster* species.

New phylogenetic studies strongly support non-monophyly of the Clypeasteroida sensu lato (Mongiardino Koch *et al.* 2018). This leads to the suggestion that strikingly similar morphologies between Clypeasteroida and Scutelloida have been derived independently. In turn, it means that enhanced knowledge of morphology and diversity in both groups, such as that presented here, will be important in reconciling this non-homology with past studies supporting derivation from the same structures in a common ancestor of both lineages (Mooi 1990).

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