Zootaxa 3857 (4): 501–526
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

http://dx.doi.org/10.11646/zootaxa.3857.4.3
http://zoobank.org/urn:lsid:zoobank.org:pub:76021E0C-7542-455B-82F4-C670A3DC8806

Phylogenetic re-evaluation of fossil and extant micro-echinoids with revision of *Tridium*, *Cyamidia,* and *Lenicyamidia* (Echinoidea: Clypeasteroida)

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Abstract

Tridium kieri Tandon & Srivastava, 1980, a clypeasteroid micro-echinoid from the Middle Eocene of Kachchh, India, has an apical system with just 3 gonopores. This condition is otherwise almost unknown among clypeasteroids, yet the morphology of *Tridium* is very similar to that of extant *Fibularia*, including members of another relatively poorly known genus from the Indian subcontinent and Western Australia, *Cyamidia* Lambert & Thiéry, 1914. Re-examination of the type and additional material of *T. kieri* and *Cyamidia paucipora* Brunnschweiler, 1962, along with specimens identified as *C. nummulitica nummulitica* (Duncan & Sladen, 1884), allows for redescription of these forms. For the first time, maps of coronal plate architecture of *Tridium* and *Cyamidia* are developed, and SEM images of test surface details of the former are provided. Such new sources of data aid determination of their phylogenetic position among a subset of laganiform clypeasteroid taxa. During these analyses, new data were uncovered for two additional enigmatic, fibulariid taxa, *Leniechinus herricki* Kier, 1968 (Middle Eocene, North America), and *Lenicyamidia compta* Brunnschweiler, 1962 (Eocene, Western Australia). Both species were added to the overall analysis. These observations lead to the conclusion that *Tridium* falls within the genus *Fibularia* Lamarck, 1816, prompting reassignment of *T. kieri* to *Fibularia* along with refinement of the diagnosis of the Fibulariidae Gray, 1855. The Western Australian representative of *Cyamidia*, *C. paucipora*, was found to represent juveniles of *Lenicyamidia compta*; it is here synonymized with the latter. The genus *Cyamidia* thus appears to be restricted to the Indian Subcontinent.

Key words: Fibulariidae, Indian Subcontinent, Western Australia, phylogeny, Eocene, Recent

Introduction

The Clypeasteroida (sand dollars and their allies) includes forms such as sea biscuits and sea pancakes that can attain the size of dinner plates as well as extremely miniaturized taxa of about the same dimensions as apple seeds. Many of the latter are referred to as "micro-echinoids", and are usually assigned to the family Fibulariidae Gray, 1855. Indeed, the type genus of the family, *Fibularia* Lamarck, 1816, includes the very smallest of all extant echinoids. Some previous workers concerning themselves with the origins of the sand dollars (e.g., Durham 1955, 1966; Kier 1974; Wang 1984) assumed that micro-echinoids such as fibulariids represent the most "primitive" clypeasteroids. However, Clark (1914) and Telford *et al.* (1983) suggested that fibulariids actually were highly specialized forms and not at all representative of the common ancestor of the Clypeasteroida, suggestions that the analyses by Mooi (1990) and Kroh & Smith (2010) have substantiated in a phylogenetic context. The implication is that the fibulariids and perhaps all clypeasteroid micro-echinoids are highly reduced, paedomorphic forms. In such taxa, substantial terminal portions of the ontogeny observed in larger-tested, more basal sister taxa are lost, along with attendant phylogenetic data that could be crucial to the understanding of their placement, and ultimately, of the evolutionary processes leading to their miniaturization.

For these reasons, the systematics of micro-echinoids is particularly problematic because the absolute number of phylogenetically informative morphological characters that can be applied to both fossil and extant forms is

Accepted by M. Eleaume: 21 Jul. 2014; published: 1 Sept. 2014

small. If unusually distinctive characters do become apparent, they are seized upon as indicative of new higher taxa through the typological naming conventions often inherent in the recognition of significant disparity, but not necessarily of phylogenetic position.

Examples of this can be found among members of the Fibulariidae, in which unusual features of fossil taxa such as a primary subject of this paper, *Tridium kieri* Tandon & Srivastava, 1980, were used to justify the establishment of new higher taxa to contain them. The genus *Tridium* was described by Tandon & Srivastava (1980) largely on the basis of the existence of only three gonopores in the madreporic plate of the apical system. The only known species in the genus, *T. kieri*, is an extremely small (usually less than 5 mm in length) Middle Eocene fibulariid with an almost spherical test, reduced petaloids, and an oral periproct placed relatively close to the mouth (Fig. 1). Apart from the loss of the gonopore in interambulacrum 2 (Fig. 2A), *T. kieri* also displays a series of unique attributes of tuberculation (Fig. 2B), and the peristomial region (Fig. 2C) that will be discussed below. *Tridium kieri* is indeed an unusual fibulariid, but its generic attribution needs to be explored in the context of the most thorough phylogenetic analyses possible, even in recognition of the problems involved in finding phylogenetic characters cited above.

Among fibulariids there are several other taxa that seem to share some of the peculiar features of *Tridium*, particularly ring-shaped flanges in the peristomial area. One of these is *Cyamidia nummulitica nummulitica* (Duncan & Sladen, 1884), the type species of *Cyamidia* Lambert & Thiéry, 1914. There are no published plate maps for this poorly known micro-echinoid, and very little other data that could be assessed for phylogenetic placement. Four varieties (*C. nummulitica nummulitica*, *C. n. obesa*, *C. n. oviformis*, and *C. n. plana*) and a second species of *Cyamidia* (*C. rotunda*) were described by Duncan & Sladen (1884), but these are difficult to distinguish based on the original descriptions. Although we were unable to borrow the material originally used by Duncan & Sladen (1884), a lot from the Natural History Museum in London contains specimens labelled as, and most closely resembling, the type species *C. nummulitica nummulitica*. We were able to extend our knowledge of this species sufficiently to include it in our phylogenetic analyses detailed below. Other material in the same lot was also examined, but these specimens differed in overall test shape, lateral profile, and degree of petaloid development. In the absence of verifiable types, we were unable to determine if these were conspecific, representative of any of the other *Cyamidia* taxa described by Duncan & Sladen (1884), or some other taxon entirely.

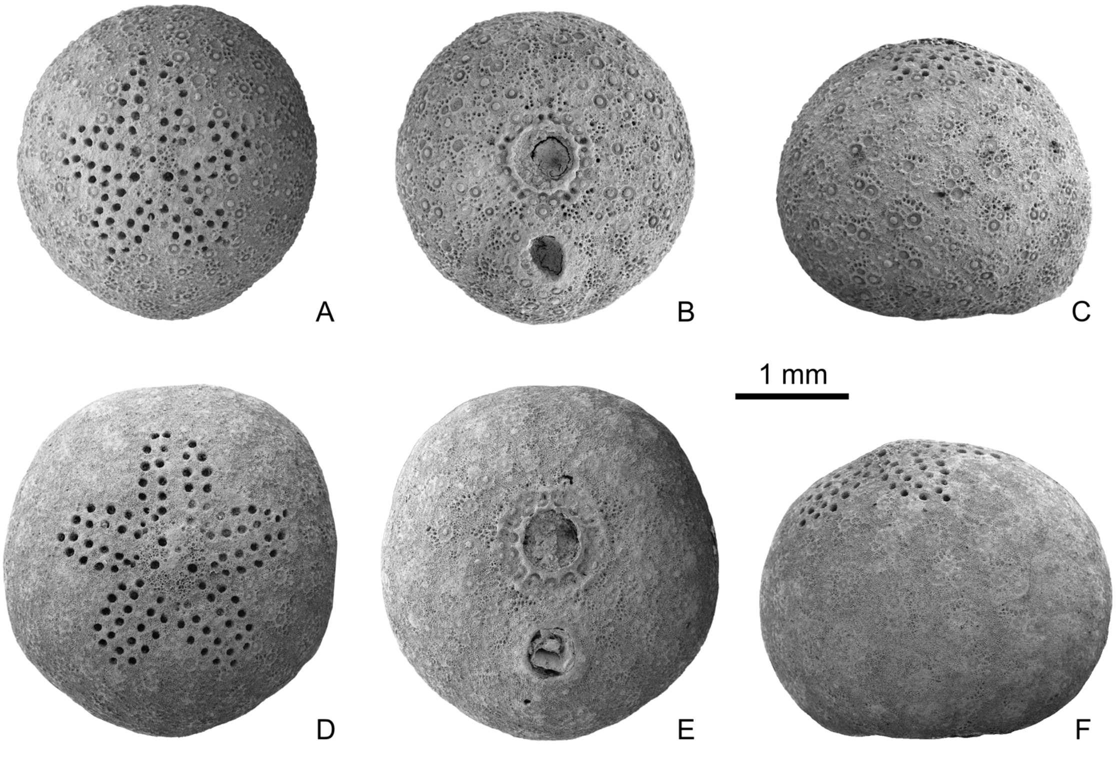

FIGURE 1. SEM images of the test of two specimens of *Tridium* (= *Fibularia*) *kieri*. A. NHMW 2011/0420/0001, aboral view. B. NHMW 2011/0420/0001, oral view. C. NHMW 2011/0420/0001, left lateral view. D. NHMW 2011/0420/0002, aboral view. E. NHMW 2011/0420/0002, oral view. F. NHMW 2011/0420/0002, right lateral view.

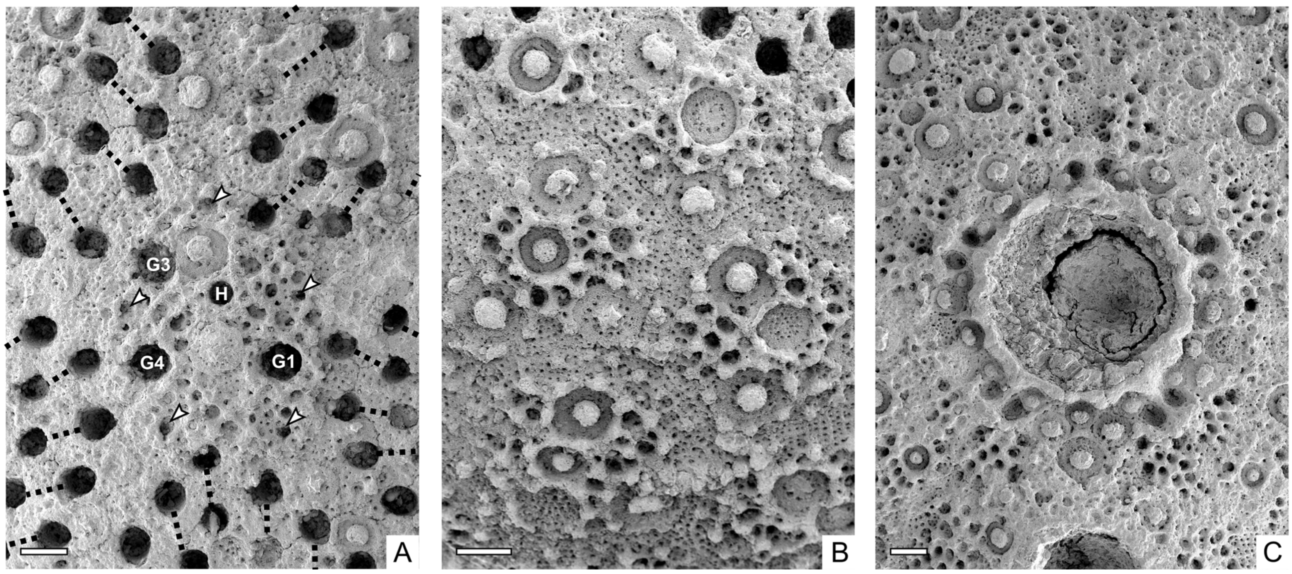

FIGURE 2. SEM images showing details on test surface of *Tridium* (= *Fibularia*) *kieri,* NHMW 2011/0420/0001. A. Apical region, pores of each respiratory tube foot linked by dotted lines, other apertures labelled: H = hydropore; G1, G3, G4 = gonopores of interambulacra 1, 3, and 4 respectively; ocular pores indicated by arrows. B. Surface features of test just above ambitus in interambulacrum 2. C. Peristomial region showing circumoral ring, buccal pores, and proximal part of periproct (bottom of image). All scale bars 100 µm long.

Finally, we were able to include data for the three remaining genera previously assigned to the fibulariids. *Leniechinus* Kier, 1968, represented only by its type species, *L. herricki* Kier, 1968, is known exclusively from type material at the National Museum of Natural History, Washington DC. We re-examined specimens of *L. herricki* in order to evaluate its features for comparison with *Tridium* and the other fibulariids. *Lenicyamidia* Brunnschweiler, 1962 is yet another poorly understood genus from the Eocene of Australia represented by a single species, *Lenicyamidia compta* Brunnschweiler, 1962. Brunnschweiler's (1962) description of *Lenicyamidia* left certain aspects of its apical morphology open to question, but Philip (1966) was able to clarify that the apical system was monobasal with four gonopores. Based on the type material, generously loaned by Geoscience Australia, we were able to evaluate all necessary characteristics for inclusion in both the species- and genus-level analyses detailed below. Likewise, we reassessed a second species proposed by Brunnschweiler (1962), *Cyamidia paucipora*, the only representative of that genus recorded from outside of the type region on the Indian Subcontinent.

Our analysis considered two questions. The first was whether or not *Tridium*, *Cyamidia*, and *Leniechinus* could be placed reliably within the Fibulariidae. This necessitated a genus-level analysis. With these determinations evaluated, we then considered the question of the placement of *Tridium* itself among the known species of *Fibularia*.

Abbreviations:

BT—Bootstrap support
BR—Bremer support
CASG—California Academy of Sciences, Geology collections, San Francisco
CPC—Commonwealth Palaeontological Collection, Canberra (see Geoscience Australia)
DGUL—Department of Geology, University of Lucknow, Lucknow
GA—Geoscience Australia, Canberra
MPTs—most parsimonious trees
NHM—Natural History Museum, London
NMNH—National Museum of Natural History (Smithsonian Institution), Washington DC
NHMW—Naturhistorisches Museum Wien, Austria
TL—test length

Phylogenetic analysis of fibulariid genera

In order to resolve the position of the enigmatic genera *Cyamidia* and *Tridium* within the Clypeasteroida, we carried out a phylogenetic analysis using the matrix of Kroh & Smith (2010), augmented with data for *Tridium kieri*, *Cyamidia n. nummulitica*, *Leniechinus herricki*, and *Lenicyamidia compta* (matrix for taxa not included in Kroh & Smith 2010 is provided in Table 1). As the general position of these taxa as members of the Clypeasteroida is undisputed, we restricted the analysis to the clypeasteroids and their immediate sister-taxa (oligopygids, *Conoclypus*, and *Cassidulus*). With the help of partial dissection, detailed preparation to reveal new aspects of test morphology, and SEM imaging, we were able to score most of the characters used by Kroh & Smith (2010). Through the use of these techniques, we could add these taxa to the pre-existing dataset with missing data values of less than 15%, and even then, the missing data pertained largely to external appendages such as spines or pedicellariae, which are usually unknown among most fossil echinoids.

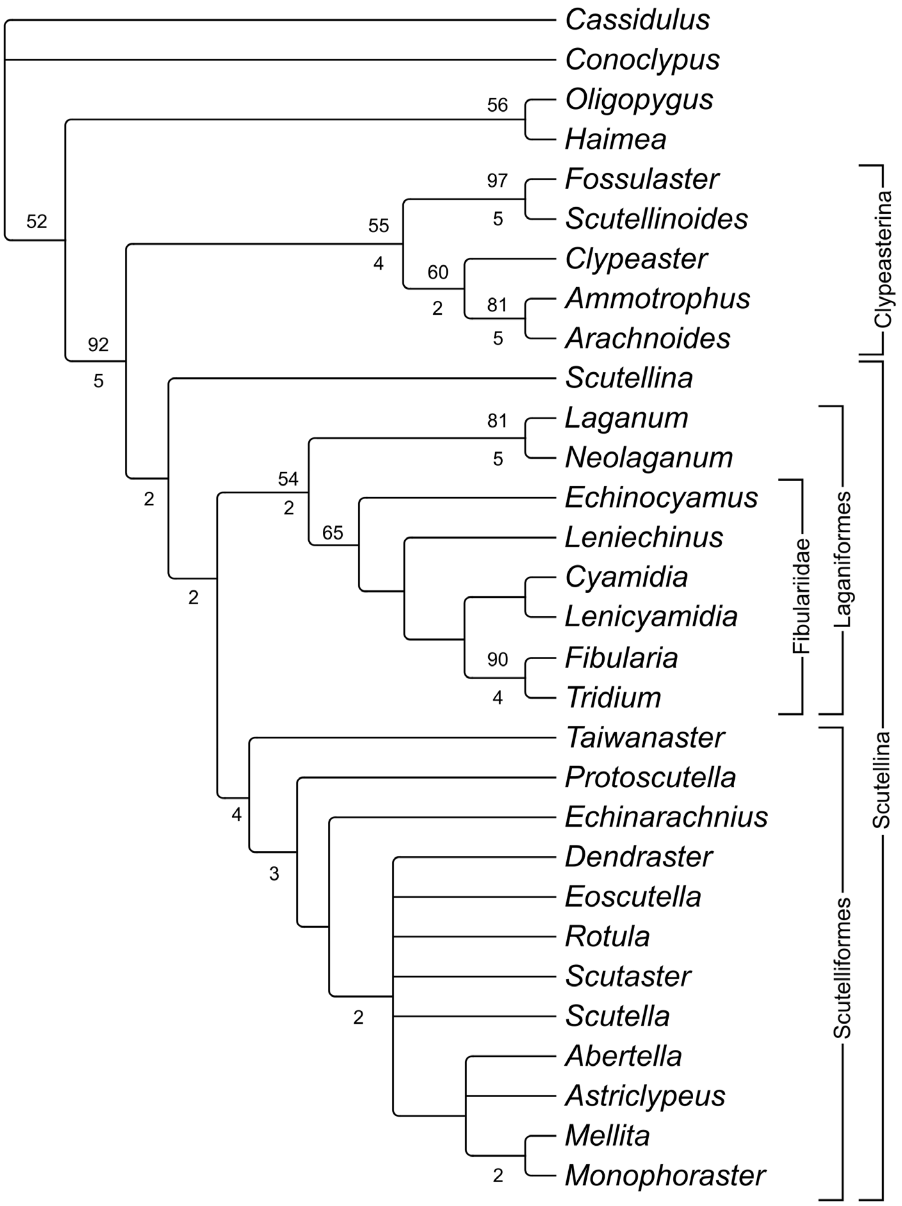

FIGURE 3. Phylogenetic relationships among clypeasteroid genera and relevant outgroups showing positions of *Tridium* (=*Fibularia*), *Cyamidia*, *Lenicyamidia*, and *Leniechinus* when these taxa are added to and coded for the matrix of Kroh & Smith (2010). Strict consensus tree of two MPTs. Numbers above branches indicate bootstrap values above 50%, those below indicate Bremer indices above 1 (all other nodes collapse one step away from the shortest tree).

Heuristic analysis using PAUP* version 4.0b1 (Swofford 1998) employing 10,000 random repetition cycles and treating all characters as unordered and of equal weight resulted in ten most parsimonious trees of 350 steps length, a consistency index (without phylogenetically uninformative characters) of 0.50, a homoplasy index of 0.50, and a retention index of 0.65. Two different tree topologies are included with the most parsimonious trees, fundamentally differing in the placement of *Rotula* within the Scutelline clade. Laganiform relationship, in contrast, is fully resolved. *Tridium* is unambiguously placed as sister-taxon to *Fibularia*, within the laganiform clade (Fig. 3). Bootstrap and Bremer support for this sister-group relationship is relatively strong (BT = 90, BR = 4), since there are several characters that fix *Tridium* within a clade that includes known fibulariids. *Tridium* is never found outside this group in any aspect of the analysis. Support for the pairing of the family Laganidae Desor, 1858 with the Neolaganidae Durham, 1954 and taxa traditionally assigned to fibulariids is also unambiguous, but nodes within the latter clade are poorly resolved. Nevertheless, it is clear that *Cyamidia* and *Leniechinus* are unequivocally members of the Fibulariidae, which also includes *Echinocyamus*. The rest of the tree topology is consistent with the original results of Kroh & Smith (2010). Due to the high intraspecific variability of paired interambulacral basicoronal plate-to-plate contacts, characters D26 and D27 of Kroh & Smith (2010) were excluded from the analysis. Analysis including these characters added considerable noise and caused failure to resolve laganiform relationships, mainly due to variable rooting of the *Laganum*+*Neolaganum* clade with respect to other laganiforms. All trees, however, find a sister-group relationship of *Fibularia* and *Tridium*, a close association of *Cyamidia* and *Lenicyamidia* and a relatively basal position (within laganiforms) of *Echinocyamus* and *Leniechinus*.

Based on these morphological and cladistic analyses, the position of *Tridium*, *Cyamidia,* and *Leniechinus* within the laganiform clade can be confirmed and the genera are here maintained in the family Fibulariidae (*sensu* Kroh & Smith, 2010). The suggestion by Tandon & Srivastava (1980), largely on the basis of gonopore number, that a new (unnamed) family be established to receive *Tridium* can therefore be rejected.

Phylogenetic analysis of fibulariid micro-echinoid species

We further evaluated the position of *Tridium* and *Cyamidia* within the Fibulariidae to determine if there was phylogenetic justification for placing these taxa in separate genera, or if they fell into other known genera. Our analysis included all known extant *Fibularia*: the type species, *F. ovulum* Lamarck, 1816, *F. cribellum* de Meijere, 1903, *F. japonica* Shigei, 1982, *F. nutriens* H.L. Clark, 1909, and *F. plateia* H.L. Clark, 1928. *Fibularia volva* L. Agassiz & Desor, 1846 was omitted because it possesses characteristics suggesting placement in *Fibulariella*, a genus that is more closely related to rotulids than fibulariids (Mooi *et al.* 2001). To test the monophyly of the group further, we included as many of the best-known fossil species as could be coded for the relevant features: *F. damensis* Kier, 1972, *F. dubarensis* Kier, 1957, and *F. gregata* Tate, 1885. We were also able to include information for most other fibulariid genera including *Lenicyamidia* (based on the type material) and *Leniechinus* (of which we observed specimens, NMNH 462808).

To test for monophyly of *Fibularia* to the exclusion of other fibulariid taxa such as *Tridium*, several other taxa had to be assessed. These included two forms presently considered laganids, *Laganum laganum* (Leske, 1778) and *Sismondia occitana* (Defrance, 1827) as well as the relatively well-known extant fibulariid type species of *Echinocyamus*, *E. pusillus* (O.F. Müller, 1776), and *Mortonia*, *M. australis* (Des Moulins, 1837).

TABLE 1. Matrix of characters and taxa used in genus-level analysis. See Kroh & Smith (2010) for description of characters.

	A1	A2	A3	A4	A5	A6	A7	A8	A9	A10	A11	A12	A13	A14	A15	A16	A17	A18	A19	A20	A21	A22	A23	A24	A25
Tridium	1	0	0	1	0	0	0	0	0	0	0	0	0	-	0	0	2	1	0	0	0	0	0	0	-
Cymidia	1	1	0	1	0	0	0	0	0	0	0	0	0	-	0	0	2	1	0	0	0	0	0	0	-
Lenicyamus	1	1	0	1	0	0	0	0	0	0	0	0	0	-	0	0	2	1	0	0	0	0	0	0	-
Leniechinus	1	1	0	1	0	0	0	0	0	0	0	0	0	-	0	0	2	1	0	0	0	0	0	0	-
	A26	A27	A28	A29	A30	A31	A32	A33	A34	A35	A36	B1	B2	B3	B4	B5	B6	B7	B8	B9	B10	B11	B12	B13	B14
Tridium	0	0	0	0	0	0	0	0	0	?	?	0	2	1	0	-	-	-	-	-	-	0	-	0	-
Cymidia	0	?	?	0	0	0	0	0	0	?	?	0	2	1	0	-	-	-	-	-	-	0	-	0	-
Lenicyamus	0	0	1	0	0	0	0	0	0	?	?	0	2	1	0	-	-	-	-	-	-	0	-	0	-
Leniechinus	0	1	1	0	1	0	0	0	0	?	?	0	2	1	0	-	-	-	-	-	-	0	-	0	-
	B15	B16	B17	B18	B19	B20	B21	B22	B23	B24	B25	B26	B27	B28	B29	B30	B31	B32	B33	B34	B35	B36	B37	B38	B39
Tridium	0	0	-	1	0	0	1	2	3	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	(0&1)
Cymidia	0	0	-	0	0	0	1	2	4	0	0	1	0	0	0	?	0	0	0	0	0	0	0	0	(0&1)
Lenicyamus	0	0	-	0	0	0	1	2	4	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	(0&1)
Leniechinus	0	0	-	1	0	0	1	2	4	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	(0&1)
	B40	B41	B42	B43	B44	B45	B46	B47	C1	C2	C3	C4	C5	C6	C7	C8	C9	C10	C11	C12	C13	C14	C15	C16	C17
Tridium	1	?	?	?	4	2	?	2	1	0	0	-	0	-	-	0	0	-	0	0	0	0	0	1	0
Cymidia	1	?	?	?	4	2	?	2	1	0	0	-	0	-	-	0	0	-	0	0	0	0	0	3	0
Lenicyamus	1	?	?	?	?	?	?	3	1	0	0	-	0	-	-	0	0	-	0	0	0	0	0	3	0
Leniechinus	1	?	?	?	4	2	?	2	1	0	0	-	0	-	-	0	0	-	0	0	0	0	0	3	0
	C18	C19	C20	C21	C22	C23	C24	C25	C26	C27	C28	C29	C30	C31	C32	C33	C34	C35	C36	C37	C38	C39	C40	C41	C42
Tridium	0	0	0	0	0	1	0	1	0	-	-	-	-	0	0	0	1	1	1	1	1	0	0	0	0
Cymidia	0	0	0	0	0	1	0	1	0	-	-	-	-	0	0	0	1	1	1	1	?	0	0	0	0
Lenicyamus	0	0	0	0	0	1	0	1	0	-	-	-	-	0	0	0	1	1	1	1	1	0	0	0	0
Leniechinus	0	0	0	0	0	1	0	1	0	-	-	-	-	0	0	0	1	1	1	1	?	0	0	0	0
	C43	C44	C45	C46	C47	C48	C49	C50	C51	C52	C53	C54	C55	C56	C57	C58	C59	C60	C61	C62	C63	C64	C65	C66	C67
Tridium	0	1	0	-	?	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	-	-	-	-	-
Cymidia	0	1	0	-	?	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	-	-	-	-	-
Lenicyamus	0	1	0	-	?	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	-	-	-	-	-
Leniechinus	0	1	0	-	?	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	-	-	-	-	-
	C68	C69	C70	C71	D1	D2	D3	D4	D5	D6	D7	D8	D9	D10	D11	D12	D13	D14	D15	D16	D17	D18	D19	D20	D21
Tridium	-	-	-	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0	2
Cymidia	-	-	-	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0	2
Lenicyamus	-	-	-	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0	2
Leniechinus	-	-	-	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0	2

......*continued on the next page*

TABLE 1. (Continued)

	D22	D23	D24	D25	D26	D27	D28	D29	D30	D31	D32	D33	D34	D35	D36	D37	D38	D39	D40	D41	D42	D43	D44	D45	D46
Tridium	2	1	0	0	(0&1)	0	0	3	0	2	0	0	0	1	0	1	1	0	0	0	0	0	0	-	1
Cymidia	2	1	0	0	(0&1)	(0&1)	0	3	1	2	0	0	0	1	0	1	1	0	0	0	0	0	0	-	1
Lenicyamus	2	1	0	0	(0&1)	(0&1)	0	3	1	1	0	1	0	1	2	1	1	0	0	0	0	0	0	-	1
Leniechinus	2	1	0	0	1	0	1	3	1	2	0	1	0	1	2	1	1	1	0	0	0	0	0	-	1
	D47	D48	D49	D50	D51	D52	D53	D54	D55	D56	D57	D58	D59	D60	D61	D62	D63	D64	D65	D66	D67	E1	E2	E3	E4
Tridium	0	2	2	1	-	0	0	0	1	0	-	-	0	0	0	0	2	0	0	0	0	0	0	0	0
Cymidia	0	2	2	1	-	0	0	0	0	0	-	-	0	0	0	0	2	0	0	0	0	1	1	0	0
Lenicyamus	0	2	2	1	-	0	0	0	0	0	-	-	0	0	0	0	2	0	0	0	0	1	1	0	0
Leniechinus	0	2	2	1	-	0	0	0	0	0	-	-	0	0	0	0	2	0	1	0	0	1	?	0	0
	E5	E6	E7	E8	E9	E10	E11	E12	E13	E14	E15	E16	E17	E18	E19	E20	E21	E22	E23	E24	F1	F2	F3	F4	F5
Tridium	0	0	0	0	-	0	0	-	0	0	?	0	0	-	1	0	0	0	0	0	1	1	?	?	?
Cymidia	0	0	0	0	-	0	0	-	0	0	?	0	0	-	1	0	0	0	0	0	1	1	?	?	?
Lenicyamus	0	0	0	0	-	0	0	-	0	0	?	0	0	-	1	0	0	0	0	0	1	1	?	?	?
Leniechinus	0	0	0	0	-	0	0	-	0	0	?	0	0	-	1	0	0	0	0	0	1	1	?	?	?
	F6	F7	F8	F9	F10	F11	F12	F13	F14	F15	F16	G1	G2	G3	G4	G5	G6	G7	G8	G9	G10	G11	G12	G13	G14
Tridium	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	0	?	?	?	?	0
Cymidia	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	0	?	?	?	?	0
Lenicyamus	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	0	?	?	?	?	0
Leniechinus	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	0	?	?	?	?	0
	G15	G16	G17	G18	G19	G20	G21	G22	G23	G24	G25	G26	G27	G28	G29	G30	G31	G32	G33	G34	G35	G36	G37	G38	G39
Tridium	0	?	?	0	1	2	0	0	1	-	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0
Cymidia	0	?	?	1	1	2	0	0	1	-	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0
Lenicyamus	0	?	?	1	1	2	0	0	1	-	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0
Leniechinus	0	?	?	1	1	2	0	0	1	-	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0
	G40	G41	G42	G43	G44	G45																			
Tridium	0	0	-	-	-	-																			
Cymidia	0	0	-	-	-	-																			
Lenicyamus	0	0	-	-	-	-																			
Leniechinus	0	0	-	-	-	-																			

TABLE 2. Matrix of characters and taxa used in species-level analysis. See text for description of characters.

Taxa	Characters																		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Laganum laganum	0	0	1	0	0	1	0	2	0	0	0	0	0	0	0	0	1	0	0
Sismondia occitana	0	0	0	0	0	0	0	2	0	0	0	0	1	1	0	0	0	?	?
Mortonia australis	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	1	0	0	0
Leniechinus herricki	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	?	?
Echinocyamus pusillus	0	0	0	0	0	0	0	0	1	1	0	1	1	1	0	1	0	1	1
Lenicyamidia compta	0	2	1&2	0	0	0	0	0	1	1	0	1	1	0	0	0	1	?	?
Cyamidia nummulitica	0	2	2	0	0	0	0	0	1	1	0	1	1	0	0	0	1	?	?
Tridium kieri	1	2	2	1	1	2	0	0	1	1	0	1	1	0	1	1	0	?	?
Fibularia gregata	1	2	2	1	1	0	0	1	1	1	0	1	1	?	0	1	0	?	?
Fibularia ovulum	1	2	2	1	1	0	0	1	2	1	0	1	1	0	0	1	0	1	1
Fibularia dubarensis	1	2	?	1	1	0	0	1	2	1	0	1	1	0	0	1	0	1	?
Fibularia damensis	0	2	2	1	1	0	0	1	1	1	0	1	1	0	0	1	0	?	?
Fibularia plateia	0	2	2	1	1	0	1	0	1	2	0	1	1	0	0	1	0	1	1
Fibularia nutriens	0	2	2	1	1	0	1	0	1	2	0	1	1	0	0	1	0	1	1
Fibularia cribellum	0	2	2	1	1	0	1	1	2	2	1	1	1	0	0	1	0	1	1
Fibularia japonica	0	2	2	1	1	0	1	1	2	2	1	1	1	0	0	1	0	1	1

The matrix of scores for the species-level analysis is shown in Table 2. The following is a description of the characters used in that analysis:

1. Test shape: flattened, test height typically less than 50% of test length (0); globular, test height greater than 60% of test length (1).
2. Internal buttresses: present (0); absent except in interambulacrum 5 (1); completely absent (2).
3. Contact between plate I.a.2/ V.b.2 and basicoronal plate 5: broad (0); narrow, i.e. just touching (1); occluded (2).
4. Ambulacral plate height at the ambitus: low (0); high, almost equant (1).
5. Relative width of interambulacrum 5 compared to ambulacrum V in oral view: less than 50% (0); more than 70% (1).
6. Gonopore number: four (0); five (1); three (2).
7. Sexual dimorphism expressed as gonopores size in females greater than that in males: absent (0); present (1).
8. Hydropore groove: absent (0); short (1); long and often complex (2).
9. Hydropore number: many (0); one (1); two (2).
10. Total petaloid pore pair number (in adult specimens): many hundreds (0); reduced, usually between 60 and 120 pore pairs (1); highly reduced, typically below 30 pore pairs in total (2).
11. Petaloid pore size: small, individual pores less than 3% of test length in diameter (0); large, more than 3% (1).
12. Interporiferous zone width (in ambulacrum III): broad, wider than single poriferous zone (0); narrow, as wide as or narrower than single poriferous zone (1).
13. Food grooves: present (0); absent (1).
14. Ambital accessory pores arranged in clear lines along sutures: no (0); yes (1).
15. Circumoral ring: absent (0); present (1). In *Tridium* a raised stereom ridge frames the peristome adoral to the buccal pores. This ridge is possibly associated with the insertion of the peristomial membrane.
16. First post-basicoronal of interambulacrum 5: Clearly elongated (0); short, usually shorter than wide (1).
17. Periproct shape: equant or transverse (0); anterior-posteriorly elongate (1).
18. Periproctal plates: many small plates (0); five plates (1).
19. Periproctal spines: present (0); absent (1).

In some of the previous literature (e.g., Brunnschweiler 1962; Kier 1968), a potential character involving the prominence of what superficially looks like a ring or flange just distal to the buccal pores has been advanced as a feature separating forms such as *Cyamidia*, *Leniechinus*, possibly *Lenicyamidia*, and particularly *Tridium*. The ring-like flange is actually expressed as a series of circumferential bars overlying the sphaeridial chamber. When the bars extend slightly into the adjacent interambulacral basicoronal regions (as can be observed in forms such as *Tridium*) then the impression of a more or less complete ring is enhanced. In *Fibularia* and *Tridium* the test is very thin, and the bar provides additional thickness to the test in the area over the sphaeridium (Fig. 4). In addition, the bars are present in other laganiform and scutelliform taxa to some degree. In larger forms such as *Laganum*, the distinctiveness of the bars (and therefore the appearance of a flange) is reduced by adjacent surface ornamentation in the form of spine tubercles and sometimes the expression of large glassy tubercles. The relative prominence of test surface texture adjacent to the bars also varies among micro-echinoids, which further exaggerates the apparent distinctiveness of the flange. Therefore, this feature is not regarded as holding any phylogenetic signal relevant to the analysis.

This flange, which lies distal to the buccal pores, should not be confused with the more proximal circumoral ring expressed in *Tridium* (Fig. 4). The visibility of this ring, which appears to mark the insertion of the peristomial membrane onto the edge of the peristome, is autapomorphic for *Tridium* (see below), and likely signifies a unique downward turning of the infundibular region around the peristome in this clypeasteroid.

Another feature that can be used to distinguish among certain micro-echinoids such as *Leniechinus* and *Lenicyamidia* is the presence of enlarged primary spine tubercles lateral to a less densely spined central region on the oral surface. The phylogenetic signal of this feature is undermined by the fact that it has independently evolved among subgroups of cassiduloids, and most importantly, among non-laganiform clypeasteroids completely unrelated to *Leniechinus* and *Lenicyamidia*. For example, in *Lenita* Desor, in Agassiz & Desor, 1847, these tubercles are extremely similar, but it has been shown that *Lenita* is a basal scutelliform with no close relationship to any fibulariid laganiforms (Mooi 1990: 41).

Periproct position, as simply scored by its placement along the midline of interambulacrum 5, lacked the certainty required to capture phylogenetic signal better recorded by architectural position in terms of plate configuration. In all the taxa considered for this part of our analysis, the periproct consistently had its anterior edge in contact with the first pair of post-basicoronals in interambulacrum 5. It was clear from a survey of the plate maps of a variety of micro-echinoid taxa that the position of the periproct was directly correlated with the degree of elongation of basicoronal 5 itself, and it was this that formed the basis of our scoring (character 16).

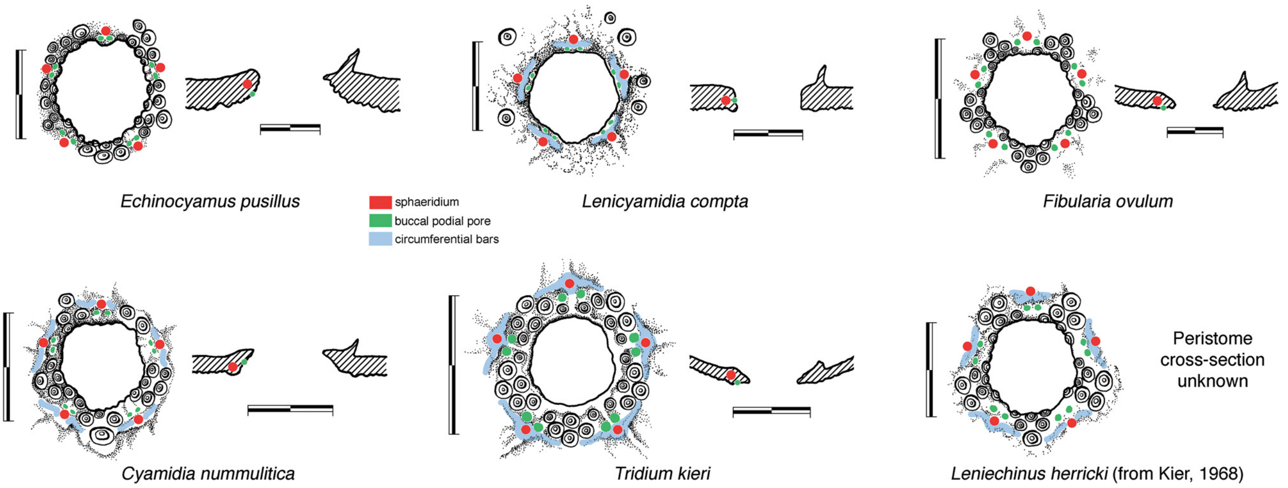

FIGURE 4. Morphology of the peristomial region in six species of fibulariids, including *Cyamidia*, *Tridium* (= *Fibularia*), *Lenicyamidia*, and *Leniechinus*. On the left for each species is the oral view depicting tuberculation, sculpturing, and positions of buccal pores and sphaeridial chambers, with accompanying scale bar. On the right for each species is a sagittal section through the test (hatched) around the peristome, anterior to the left, with accompanying scale bar. In all cases, scale bar is 1.0 mm long.

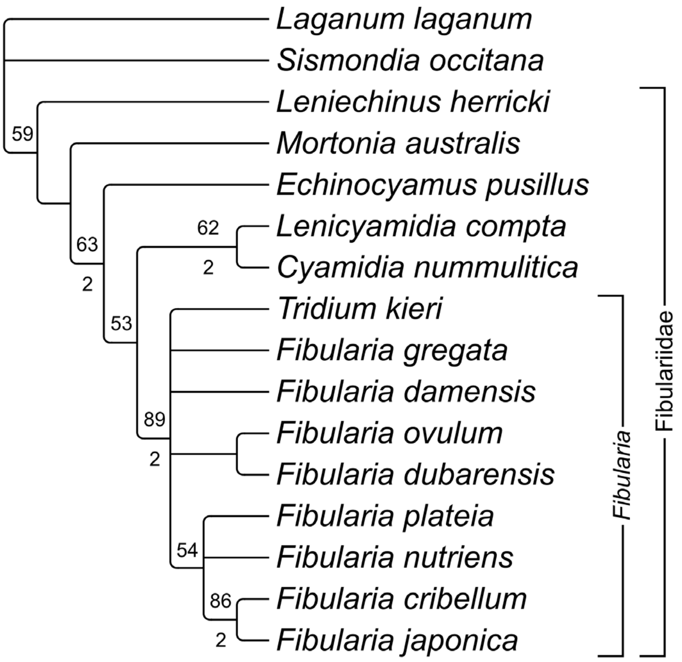

FIGURE 5. Phylogenetic relationships among fibulariid species and relevant laganiforms showing positions of *Tridium* (= *Fibularia*), *Cyamidia*, *Lenicyamidia*, and *Leniechinus*. Numbers above branches indicate bootstrap values above 50%, those below indicate Bremer indices above 1 (all other nodes collapse one step away from the shortest tree).

The analysis consistently found a monophyletic *Fibularia* clade, which included *Tridium*. The node supporting the inclusion of *Tridium* in *Fibularia* received moderate bootstrap but not particularly strong Bremer support (Fig.

5). Heuristic analysis using PAUP* version 4.0b1 (Swofford 1998) employing 1,000 random repetition cycles resulted in fifteen most parsimonious trees of 33 steps length, a consistency index (without phylogenetically uninformative characters) of 0.76, a homoplasy index of 0.24, and a retention index of 0.85. The trees mainly differ from each other in the exact placement of *Tridium kieri* and *Fibularia damensis* within the *Fibularia* clade, which variably fall within either the clade of *F. ovulum*, *F. gregata*, and *F. dubarensis* or a second clade containing *F. cribellum*, *F. japonica*, *F. nutriens*, and *F. plateia*. *Cyamidia* and *Lenicyamidia* are weakly supported as sister taxa forming an immediate outgroup to *Fibularia* + *Tridium*. Other fibulariid echinoids (*Echinocyamus*, *Leniechinus*, *Mortonia*, and *Sismondia*) form successive outgroups, but branching order is poorly supported.

Systematic paleontology

Class Echinoidea Leske, 1778

Subclass Euechinoidea Bronn, 1860

Infraclass Acroechinoidea Smith, 1981

Irregularia Latreille, 1825

Microstomata Smith, 1984

Neognathostomata Smith, 1981

Order Clypeasteroida L. Agassiz, 1835

Infraorder Laganiformes Desor, 1857

Family Fibulariidae Gray, 1855

Emended diagnosis. Laganiform echinoids with internal buttresses reduced either to simple radiating partitions in all, or a subset of the interambulacra, or entirely lacking.

Genus *Cyamidia* Lambert & Thiéry, 1914

Type species. *Echinocyamus nummuliticus nummuliticus* Duncan & Sladen, 1884, p. 132, by original designation (Lambert & Thiéry 1914: 288).

Emended diagnosis. Small fibulariids with an antero-posteriorly elongated periproct, and an apparent ring-like flange around the peristome made of slightly exaggerated bars just distal to the buccal pores.

Remarks. This genus differs from the type genus *Fibularia* in having low ambulacral plates at the ambitus, an elongate periproct, and the interambulacra much narrower than the ambulacra, notably at the ambitus. *Cyamidia nummulitica nummulitica* tends also to have a lower overall test height to test length, but the applicability of this feature to all members of the genus *Cyamidia* will require full assessment of all the taxa ascribed to it by Duncan & Sladen (1884).

Cyamidia nummulitica nummulitica (Duncan & Sladen, 1884)

Figures 4, 6.

1884 *Echinocyamus nummuliticus* Duncan & Sladen: 132–134, pl. 25: figs 14–20.
1914 *C.*[*Cyamidia*] *nummulitica* Duncan et Sladen (*Echinocyamus*)—Lambert & Thiéry: 288.

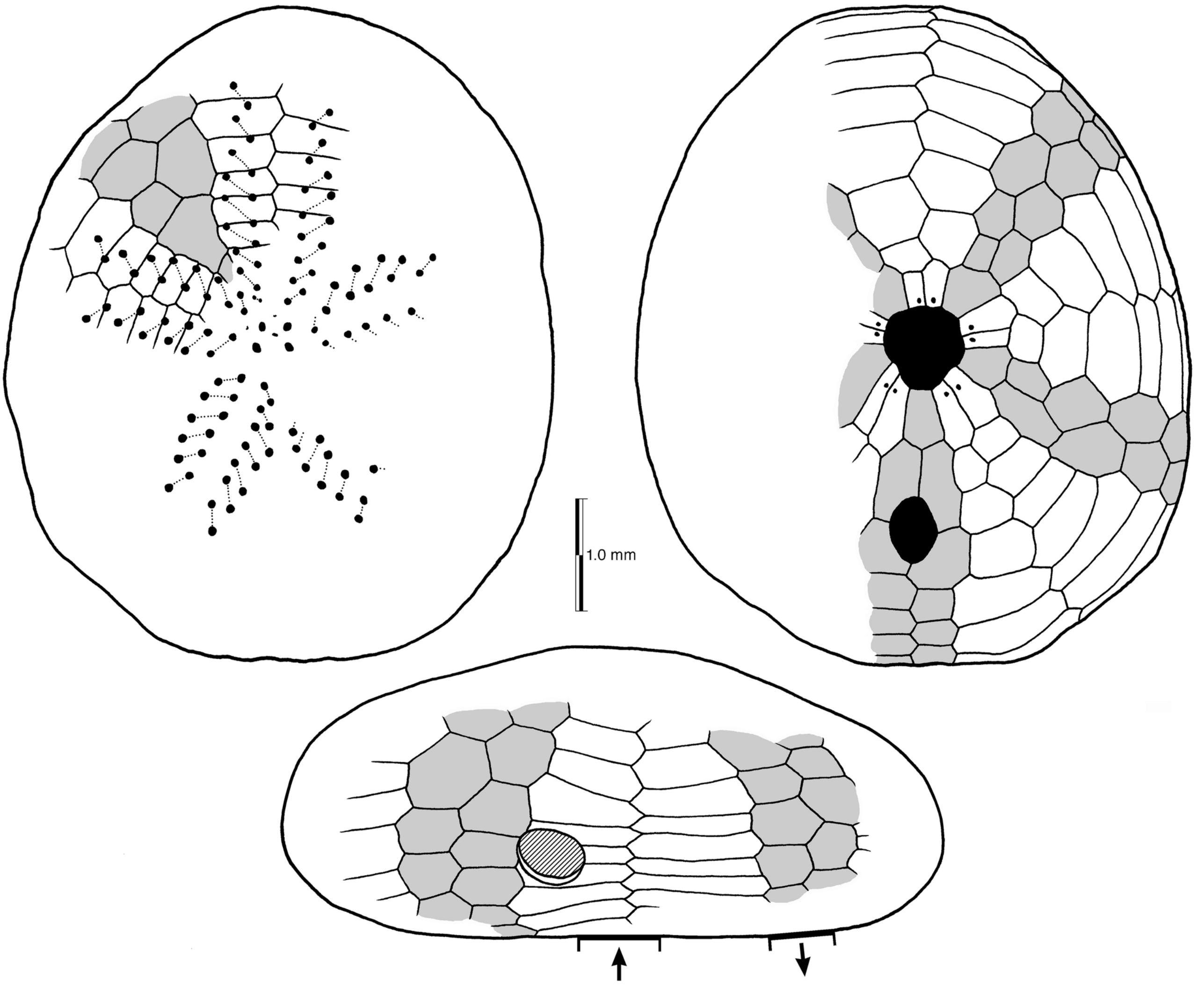

FIGURE 6. Partial plate architecture of *Cyamidia nummulitica nummulitica*, NHM E692. In aboral view, pores of each respiratory tube foot linked by finely dotted lines. In oral view, peristome and periproct in solid black, buccal pores indicated by small dots adjacent to peristome. Interambulacra shaded. For side view, upward arrow indicates peristome, downward arrow indicates periproct. The hole at the ambitus seen in lateral view is a likely predatory borehole (ichnogenus *Oichnus* sp.).

Type material. Syntypes in the collection of the Geological Survey of India, Kolkata [not seen].

Material studied. NHM E692, from Sind, Pakistan.

Type locality. Several localities were listed by Duncan & Sladen (1884), but because none of the known specimens were selected as the name-bearing type, a type locality is likewise unknown.

Type stratum. Kirthar Formation, Middle to Late Eocene (Jafa & Rai 1994; Rai 2007).

ZooBank LSID. urn:lsid:zoobank.org:act:6A8F5B2A-5FE2-400B-AD93-D7785BBD18E5

Description. *Size and shape*—Corona small, approximately 6 mm in TL; shape ovoid when viewed aborally; slightly flattened in profile, maximum height less than 50% of TL.

Internal buttressing—Absent.

Apical system—Situated centrally, at the apex of the corona; monobasal, with four gonopores and a single central hydropore, not situated in a pit or groove; ocular pores are small and indistinct, lying well outside the area enclosed by the gonopores, almost directly between most proximal pores in each petal.

Ambulacra—Ambulacral plating simple; ambulacra expanding distal to peristome to form fan-shaped array at least twice the width of interambulacra at ambitus; petals short, with 10 to 17 faintly conjugate respiratory pore pairs in each ambulacrum; pore pairs lying strongly oblique, crossing the ambulacral plates; distal pore pairs becoming even more strongly oblique with distance between pores in each pair slightly decreasing; width of interporiferous zones remaining largely constant along each paired petal, but increasing slightly at the distal end of the anterior, unpaired petal; petaloid region large, extending about 70% of TL; food grooves absent; buccal pores large, facing obliquely towards the peristome; accessory pores situated in oblique patches in centres of plates, axis of patches angled towards perradial suture proceeding distally, apparently not along sutures; ambitus initiating at approximately seventh pair of ambulacral postbasicoronal plates.

Interambulacra—Adapically, two unpaired plates lie in tandem adjacent to apical system; four or five post-basicoronal interambulacrals in each column visible in oral view; posterior unpaired interambulacrum expanding slightly in region accommodating periproct; a few scattered accessory pores visible near centres of some interambulacrals, particularly on the ambitus and oral surface.

Tuberculation—Primary tubercles crenulate, perforate; approximately same diameter on oral and aboral surfaces, evenly distributed in ambulacra and interambulacra without differentiation into locomotory regions; miliary tubercles distributed among primaries.

Peristome—Larger than periproct, about 13% TL; infundibulum extremely shallow; peristomial opening facing directly downwards almost at midpoint of oral surface; framed by basicoronal circlet in which ambulacral plates are approximately same length as adjacent interambulacrals, although basicoronals are slightly longer around posterior half of peristome; 4 to 6 enlarged primary tubercles, areoles abutting, in each interambulacral area adjacent to peristome; in each ambulacrum, slightly elevated ridge or bar of stereom just distal to buccal pores, each bar extending slightly laterally from perradial bulge containing sphaeridium.

Periproct—Small, approximately 10% TL; facing downwards approximately halfway between posterior edge of peristome and posterior edge of the corona in oral view; distinctly elongated along anterior-posterior axis; bounded by first (5.a.2, 5.b.2) and second (5.a.3, 5.b.3) pairs of post-basicoronal plates.

Perignathic girdle—Consisting of five small processes (auricles), one on internal surface of each interambulacral basicoronal.

Sphaeridia—One per ambulacrum; fully enclosed; situated beneath distinct transverse bar just distal to buccal pores.

Spines, pedicellariae, lantern—Unknown.

Remarks. Duncan & Sladen (1884) distinguished three varieties (to be treated as subspecific taxa according to The Code) of *Echinocyamus* (= *Cyamidia*) *nummulitica* in addition to the form *n. nummultica* upon which we are basing our descriptions: *C. n. obesa*, *C. n. oviformis* and *C. n. plana*. These differ mainly in overall shape of the corona, particularly in terms of test height and degree of petaloid development. They might well represent valid species or subspecies, but this can only be clarified by re-examination of types, and analysis of intraspecific variation based on a large number of specimens.

A fourth form described by Duncan & Sladen (1884), *Echinocyamus rotundus*, later placed in *Cyamidia* by Lambert & Thiéry (1914), may or may not represent a second species in the genus. It is based on a unique, worn specimen that, judging from the poor figures, does not show the typical peribuccal stereom bars observed in *Cyamidia nummulitica*. It does, however, appear to have the elongate periproct that seems to separate this genus from most other fibulariids.

Cyamidia paucipora Brunnschweiler, 1962

Figures 7A–C, 8–9, 10D, 11.

1962 *Cyamidia paucipora* Brunnschweiler: 162–164; fig. 1A–D.

Type material. GA CPC 2825 (holotype; Figs 7A–C, 10D).

Material studied. In addition to the holotype, 7 "topotypes" (GA CPC 2826, 41767–41772) of Brunnschweiler (1962).

Type locality. Sample M24 from point 221 on airphoto No. 5170 on Run 2, Moogooloo Hill (hill crest located at 23° 36′ 12″ S, 114° 44′ 14″ E; exact coordinates of sampling locality unknown); about 8 miles SSE of the Pleiades Hills, Northwest Division, Western Australia.

Type stratum. Merlinleigh Sandstone, Late Eocene (see Darragh & Kendrick 2010: pp. 24–25)

ZooBank LSID. urn:lsid:zoobank.org:act:AC48DF0B-22B0-4ED3-AB19-1B1EBAFB1799

Description. *Size and shape*—Corona very small, up to 3.5 mm in TL in material originally attributed to this species; outline distinctly oval (antero-posteriorly elongated) in aboral view; slightly flattened in profile, maximum height decreasing with size, being up to 70% of TL in smallest and approximately 56% TL in largest specimens.

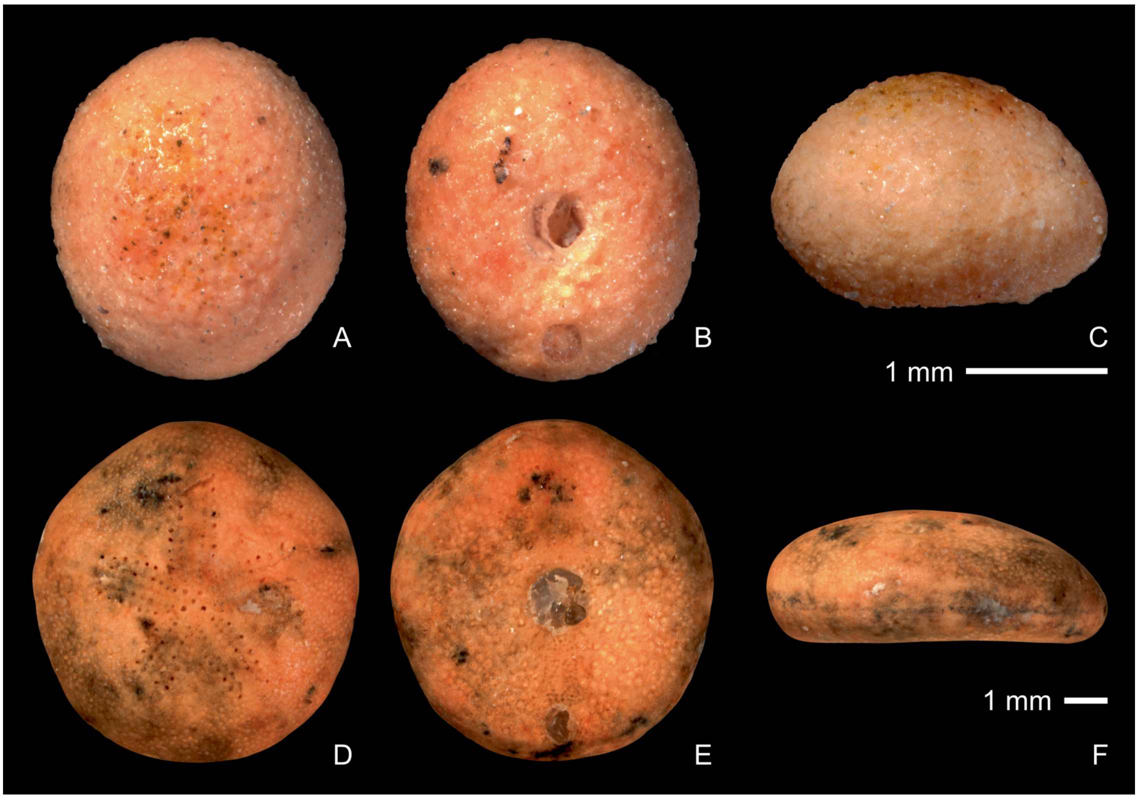

FIGURE 7. Brunnschweiler's (1962) holotypes: A–C. *Cyamidia paucipora* (= juvenile *Lenicyamidia compta*), GA CPC 2825; D–F. *Lenicyamidia compta*, GA CPC 2827. Aboral (A, D), oral (B, E) and left lateral views (C, F).

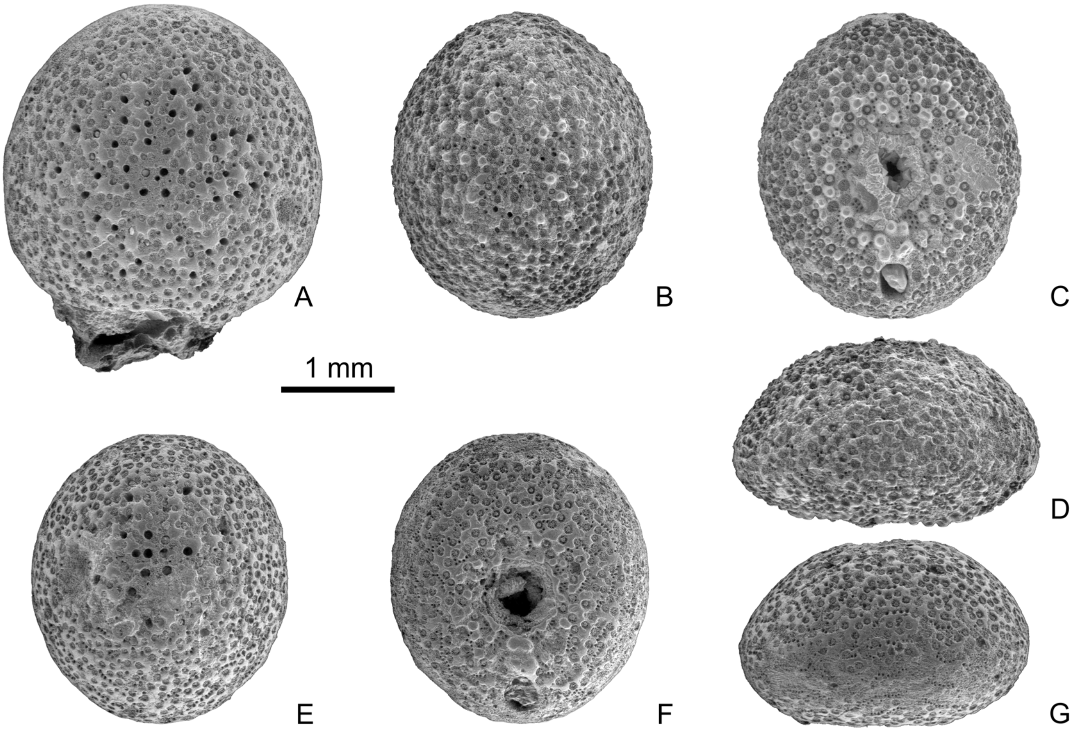

FIGURE 8. SEM images of the test of three specimens of *Cyamidia paucipora* (= juvenile *Lenicyamidia compta*). A. GA CPC 41767, aboral view. B–D: GA CPC 41768, aboral (B), oral (C) and left lateral view (D); E–G: GA CPC 41769, aboral (E), oral (F) and left lateral view (G).

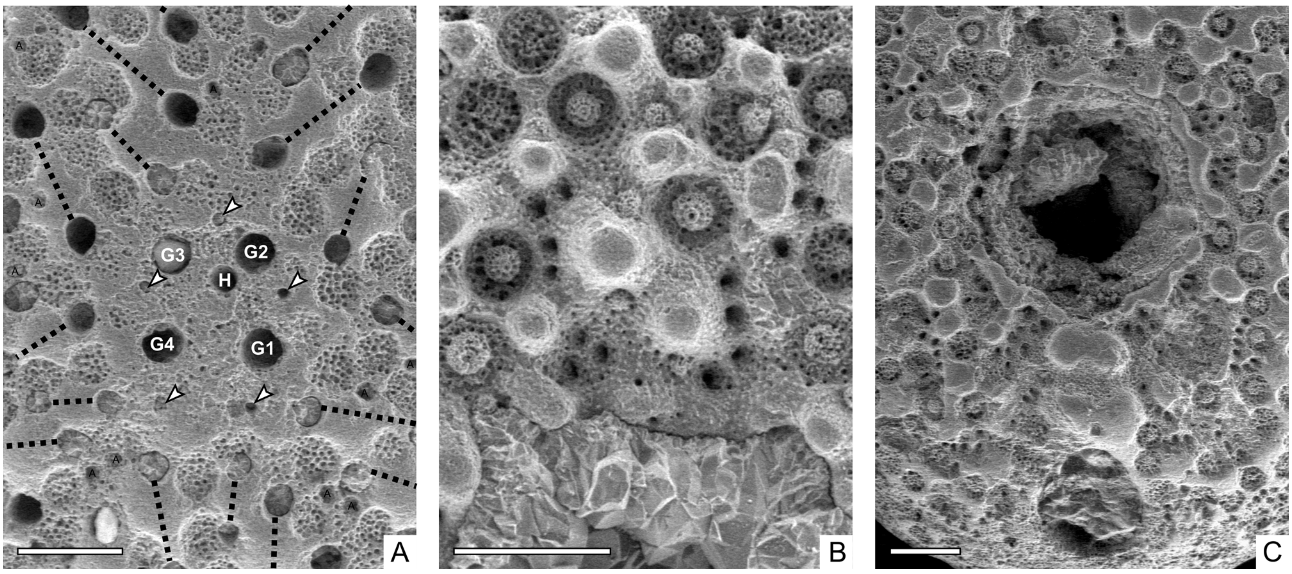

FIGURE 9. SEM images showing details on test surface of *Cyamidia paucipora* (= juvenile *Lenicyamidia compta*). A. Apical region of specimen GA CPC 41767, pores of each respiratory tube foot linked by dotted lines, other apertures labelled: H = hydropore; G1, G2, G3, G4 = gonopores of interambulacra 1, 2, 3, and 4, respectively; ocular pores indicated by arrows. B. Ornamentation of test just anterior of the peristome in specimen GA CPC 41768. C. Peristomial region of specimen GA CPC 41769 showing peristomial region and periproct (bottom of image). All scale bars 200 µm long.

Internal buttressing—Absent.

Apical disc—Situated centrally, at apex of corona; monobasal, with four gonopores and single hydropore which lies close to genital pore 2 and not situated in pit or groove; ocular pores small and located outside area enclosed by gonopores (Fig. 9A); gonopores open in specimens as small as 2.55 mm, but may still be completely closed in slightly larger specimens (2.69 mm TL).

Ambulacra—Plating not easily discernable, but ambulacra appear to expand towards ambitus; petals short, with up to five non-conjugate respiratory pore pairs in each ambulacrum; pore pairs strongly oblique, with obliqueness increasing distally; in small specimens with well-preserved surface detail, interporal areas raised, with glossy surface reminiscent of glassy tubercles, in slightly larger specimens this area is less raised but still appears to be composed of massive, unperforated stereom; interporiferous zones narrow and of constant width along petal; petaloid region large, extending about 60% of TL; food grooves absent; buccal pores not visible in oral view, apparently lying close to peristome and facing horizontally into it; accessory pores crowded in small oblique clusters in centre of each plate; widespread isolated accessory pores present between these clusters, including in interporiferous zones; ambitus initiating at approximately fourth pair of ambulacral postbasicoronal plates.

Interambulacra—Adapically, two unpaired plates lie in tandem adjacent to apical system (Fig. 10D); basicoronal plates stout and quadrangular; ambital plating not discernable; a few scattered accessory pores present both in aboral and oral interambulacral plates.

Tuberculation—Primary tubercles crenulate, perforate; homogeneously distributed on aboral surface; on oral surface, towards the peristome, tubercles up to 1.5 times larger and more widely scattered, separated by ridges bearing glassy tubercles and granules (Fig. 9B); tubercles entirely missing on basicoronal plate of interambulacrum 5 and most of plate surface of plates 5.a.2 and 5.b.2; here large glassy tubercles are found instead (Fig. 9C).

Peristome—Relatively large, about 25% TL; facing directly downwards; infundibulum shallow, but with down-turned, almost vertical lip; incomplete ring of slightly elevated ambulacral stereom bars framing peristome; distinct perradial bulge containing the sphaeridium in centre of each bar; in oral view, buccal pores are hidden by these bars.

Periproct—Smaller than peristome, approximately 12% TL; positioned inframarginally and facing obliquely down-/backwards in oral view; distinctly elongated along anterior-posterior axis; anterior end bounded by first pair of post-basicoronal plates (5.a.2, 5.b.2), other sutures not discernable.

Perignathic girdle—Consisting of five small processes (auricles), one on each interambulacral basicoronal plate.

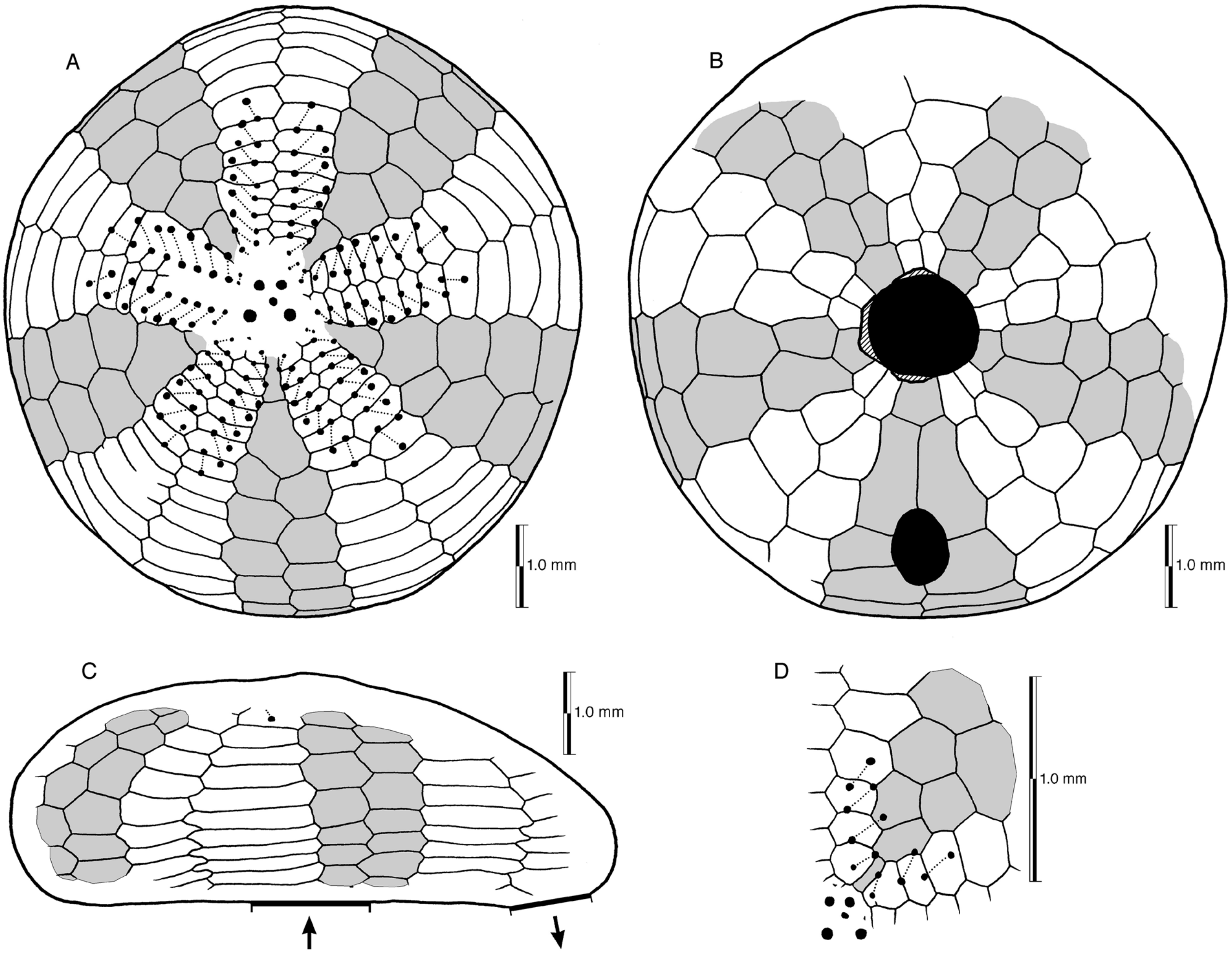

FIGURE 10. Partial plate architecture of *Lenicyamidia compta* and *Cyamidia paucipora* (= juvenile *Lenicyamidia compta*). A–C. *L. compta*: A. aboral view of GA CPC 41774; B. oral view of the holotype GA CPC 2827; C. left lateral view of GA CPC 41774; D. *C. paucipora*, holotype CPC 2825, adapical part of interambulacrum 2. Labelling conventions as in Fig. 6.

Sphaeridia—One per ambulacrum; fully enclosed; situated beneath distinct transverse bar just distal to buccal pores.

Spines, pedicellariae, lantern—Unknown.

Remarks. Brunnschweiler (1962) established a new species for the specimens described above and attributed it to the genus *Cyamidia* on the basis of its elongate periproct and lack of internal buttressing. It was differentiated from previously described species of *Cyamidia* by its larger and more marginal periproct, the smaller number of petaloid pores and the glassy tubercles between the periproct and peristome. Brunnschweiler, however, did not take allometric growth into account. In most clypeasteroids, and indeed most echinoids, the periproct and peristome are proportionally larger in smaller specimens and the petaloid pore pair number is lower. The main difference from other *Cyamidia* species is therefore the presence of glassy tubercles between the periproct and peristome and the more marginal periproct (although periproct position too tends to change during early ontogeny).

Cyamidia paucipora co-occurs with the larger species *Lenicyamidia compta* at the type locality. At first glance the two species appear very different—the former is very small, high, and ovoid in outline, while the latter is larger, more flattened and rounded. It also has a distinct oral tuberculation pattern. Upon closer examination, however, the two forms appear to be part of a single ontogenetic series, with the main differences being related to differential growth. Test height, for example, increases only slowly during growth (Fig. 11), causing the end members to look very different. When included in the same graph, specimens attributed to *C. paucipora* by Brunnschweiler (1962) fall along the same regression lines as *L. compta*. The size gap between *C. paucipora* and *L. compta* apparently led Brunnschweiler to believe that he was dealing with two different taxa. This discontinuity in the size distribution

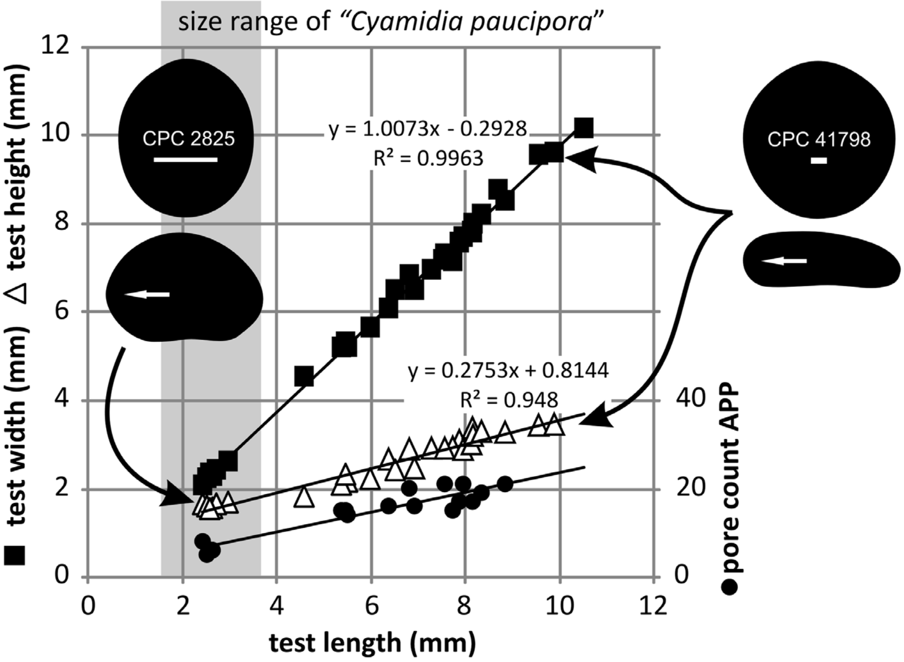

FIGURE 11. Scatter plot of test width (solid squares; n = 30), height (open triangles; n = 27) and respiratory pore number (solid circles; n = 17) vs. test length for the material attributed to *Lenicyamidia compta* and *Cyamidia paucipora* by Brunnschweiler (1962). Size range of *C. paucipora* highlighted by grey backfill. Thumbnail images show outline and profile for the smallest and largest complete specimens. Within profiles, scale bars 1.0 mm long, arrows indicate anterior end. APP = anterior paired petals (i.e. petal II or IV).

might have other reasons including, but not limited to: a) collection bias (the small specimens probably being picked from sieving residues, while the larger ones might have been hand-picked in the field); b) year-cohorts (many marine invertebrates reproduce only once annually, leading to different size cohorts within populations particularly among miniaturized, paedomorphic forms in which these size differences are exaggerated).

The only other difference between *C. paucipora* and *Lenicyamidia*, apart from shape and pore pair number, is that in tuberculation pattern. However, the oral, medial area of glassy tubercles in *Lenicyamidia* can easily be derived from the corresponding area in *Cyamidia paucipora*. The latter also largely lacks spine-bearing tubercles, and features glassy ones in the oral, medial area instead (Fig. 9C). Based on these observations, the two species are here considered synonymous and *Lenicyamida compta* is chosen as the senior synonym (Principle of the First Reviser; ICZN 1999 Art. 24.2).

Genus *Fibularia* Lamarck, 1816

Type species. *Fibularia ovulum* Lamarck, 1816 by ICZN Opinion 207 (1954: 350).

Emended diagnosis. Small, occasionally almost spherical fibulariids entirely lacking internal buttresses; interambulacra very wide at ambitus, over 70% width of ambulacra; ambulacral plates very high at ambitus, each plate almost as high as wide.

Fibularia kieri (Tandon & Srivastava, 1980) (new combination)

Figures 1–2, 4, 12

1980 *Tridium kieri* Tandon & Srivastava: 1–3, pl. 1: figs. 1–6

Type material. Department of Geology, University of Lucknow, K 651 (holotype), K 652–K 653 (paratypes).

Material studied. DGUL: 10 specimens (K 654–K 663), and numerous specimens without repository numbers; CASG: 4 specimens (72990, 72991); NHMW: 5 specimens (NHMW 2011/0420/0001–0005), all from type locality.

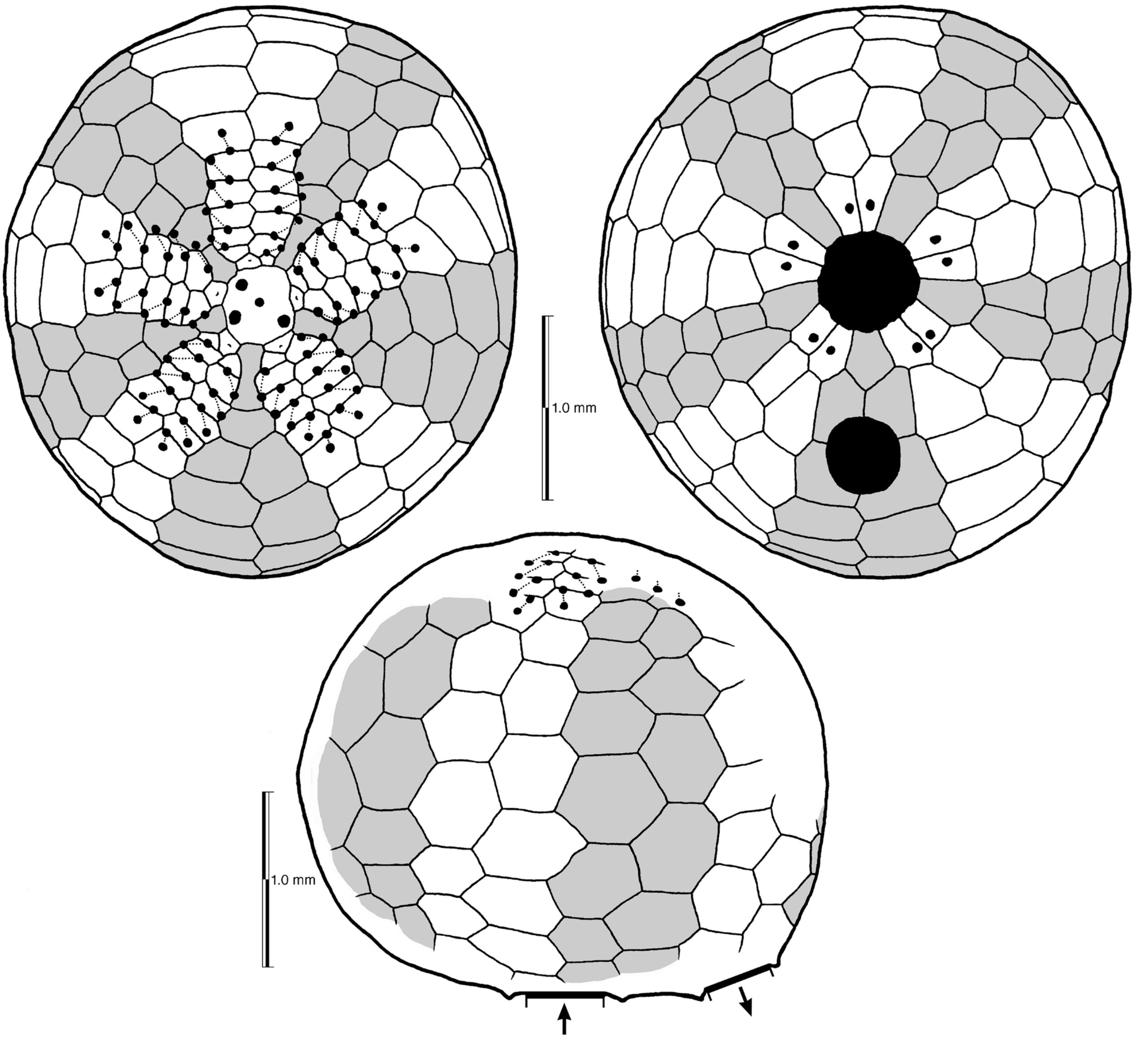

FIGURE 12. Plate architecture of *Tridium* (= *Fibularia*) *kieri*, CASG 72990. Labelling conventions in Fig. 6.

Type locality. Near village of Guvar, Kachchh, India (23°38′10″ N, 68°32′30″ E).

Type stratum. *Nummulites beaumonti* Zone of Tandon (1976), Middle Eocene.

Other occurrences. Jhadwa (23°30′30″ N, 68°36′30″ E), Panandro (23°41′ N, 68°45′05″ E) villages and Ratchelo nala, 3.2 km south of Baranda village (23°34′20″ N, 68°43′10″ E), Kachchh, India.

Emended diagnosis. Very small, almost spherical *Fibularia* unique among laganiforms in having only 3 gonopores, lacking gonopore in interambulacrum 2 position; infundibulum completely lacking, with peristomial region everted outwards until even with surrounding oral surface; buccal pores facing directly downwards, not into peristome; distinct circumoral ring proximal to buccal pores; periproct surrounded by slight, spout-like ridge; density of spine tubercles greatly reduced, only 2 to 4 primary tubercles found in tight grouping near centre of ambital plates; sutures of ambital plates smooth, lacking external structures such as spine or pedicellaria tubercles or glassy tubercles.

ZooBank LSID. urn:lsid:zoobank.org:act:8AC353E9-96E0-4274-BC94-561CC0AA8130

Description. *Size and shape*—Corona small, largest specimens not exceeding 5 mm TL; corona globular, almost spherical, with barely subequal length, width and height; aboral outline nearly circular, very slightly acuminate posteriorly; profile of corona likewise circular, very slightly flattened adorally in peristomial region.

Internal buttressing—Absent.

Apical system—Central in aboral view; monobasal, with three gonopores, lacking gonopore in interambulacral position 2; gonopores well within madreporic plate; single, central hydropore, opening flush with plate surface, not in pit or groove; ocular pores small and indistinct, almost directly between most proximal pores in each petal.

Ambulacra—Ambulacral plating simple; petals short, consisting of 4 to 6 large, faintly conjugate respiratory pore pairs in each ambulacrum; pore pairs lying strongly oblique, crossing ambulacral plates; distal pore pairs becoming even more strongly oblique with distance between pores in each pair slightly decreasing; width of interporiferous zones remaining largely constant in adapical two thirds of each petal, but decreasing slightly towards distal end; distally, obliqueness of pore pairs increases so that most distal pore pairs are oriented almost parallel to radius; in some adapical pore pairs, outer pore pierces interambulacral plate rather than ambulacral; petaloid region large, extending almost 70% of TL in aboral view; buccal pores large, facing downwards rather than into the peristome; accessory pores small, barely larger than openings in stereom meshwork; usually crowded in patches around large tubercles in middle of plates; except for very well-preserved specimens, pores only visible close to peristome; food grooves absent.

Interambulacra—Adapically, two unpaired plates lie in tandem adjacent to apical system; four, occasionally five post-basicoronal interambulacrals in each column visible in oral view; interambulacrum 5 not expanding in region accommodating periproct, but continuously divergent in oral view; a few scattered accessory pores visible in some interambulacrals; at ambitus, interambulacra at least as wide as ambulacra; each column comprising large, hexagonal plates of equal height and width.

Tuberculation—Patchy and sparse, with 1 to 4 tubercles concentrated in small clusters separated from tubercles in adjacent plates by areas of unornamented stereom; areoles wide, approximately three times diameter of boss, slightly sunken; miliary tubercles indistinct, although small tubercles about 20% diameter of the primary tubercles likely represent miliaries, or perhaps attachment points for pedicellariae; glassy tubercles absent.

Peristome—Small, approximately 17% TL; circular; facing directly downwards almost centrally on oral surface but slightly displaced approximately 1–2% TL posteriorly; opening not sunken, lacking infundibulum; rimmed by sharp, raised ridge of relatively dense stereom forming circumoral ring; framed by basicoronal circlet in which ambulacral plates are approximately same length as adjacent interambulacrals; 4 to 6 enlarged primary tubercles, areoles abutting, in each interambulacral area adjacent to peristome; in each ambulacrum, slightly elevated ridge or bar of stereom just distal to buccal pores, extending only slightly laterally from perradial bulge containing sphaeridium.

Periproct—Small, about 13% TL; subcircular to subpentagonal in outline, sometimes slightly antero-posteriorly elongated; facing downwards halfway between peristome and posterior margin; bounded by first (5.a.2, 5.b.2) and second (5.a.3, 5.b.3) pairs of post-basicoronal plates; margin of periproct very slightly raised into slight "spout".

Perignathic girdle—Consisting of five small processes (auricles), one on the internal surface of each interambulacral basicoronal.

Sphaeridia—One per ambulacrum; fully enclosed; situated beneath low transverse bar just distal to buccal pores.

Spines, pedicellariae, lantern—Unknown.

Remarks. In the original description Tandon & Srivastava (1980: fig. 2) showed the third pair of post-basicoronal plates forming part of the periproctal margin, but this was not in agreement with their own description in the text. We were able to determine that the third pair of post-basicoronals plays no part in the construction of the periproctal margin. In addition, Tandon & Srivastava (1980: fig. 2) depicted a small plate just distal to each ambulacral basicoronal, which in turn suggested that the ambulacral basicoronals were significantly shorter than the interambulacral basicoronals, causing the ambulacral basicoronals to be isolated from the adjacent interambulacral first post-basicoronals in every case. However, these small, additional plates are not apparent from our observations. In fact, the ambulacral basicoronals are nearly equal in length to the interambulacral basicoronals. The ambulacral basicoronals are in contact with the adjacent interambulacral first post-basicoronals in nearly every radius, as in other fibulariids. The illustration in Tandon & Srivastava (1980: fig. 1) also shows the outer pores of the petals not piercing the interambulacra, but we have identified several outer pores proximal to the apical system that emerge through the interambulacrals.

Tandon & Srivastava (1980) and Smith & Kroh (2011) identified the presence of just three gonopores as the sole autapomorphy of the genus, thereby distinguishing it from *Fibularia*. We have identified several other features that are autapomorpic in *T. kieri* (see diagnosis above), but these unique, phylogeneticially uninformative features do not serve to distinguish *T. kieri* from *Fibularia* in a cladistic sense, and we here consider *Tridium* a junior synonym of *Fibularia*. Smith & Kroh (2011) additionally questioned whether three gonopores were consistent in larger populations. Genital pore 2, however, is missing in all known specimens (N > 350) and it is unlikely that this is a case of abnormal development. Except in rare cases of specimens obviously affected by sublethal predation or other growth deformations, gonopore development is usually consistent within clypeasteroid species and not prone to variation.

Curiously, Tandon & Srivastava (1980: p. 2) indicated that "no female was found". Sexual dimorphism in clypeasteroids, and even in micro-echinoids such as *Fibularia plateia*, *F. cribellum*, and *F. japonica*, is known from differences in gonopore diameter and sometimes even from the presence of brood pouches, as in *F. nutriens*. However, Tandon & Srivastava (1980) made no such measurements. It is most likely that this species exhibits no readily detectable sexual dimorphism than the rather low likelihood that there were no females represented in the over 350 specimens collected.

Re-examination of *Fibularia kieri* shows that the missing gonopore is not the sole autapomorphy of that taxon. The patchy tuberculation, with concomitant lack of ornamentation in proximity to the plate sutures, and especially features of the peristomial region are very different from what is usually observed in fibulariids or in other echinoids in general. The most adoral tubercles usually support spines that are internally directed towards the mouth in the centre of the peristomial membrane, more or less parallel or at low angles to the surface of that membrane. Likewise, the buccal podia (and the pores supporting them) are directed towards the mouth in most clypeasteroids, so that the podia can more easily reach into it (Mooi 1986).

In *F. kieri*, the situation is quite different. Here the adoral tubercles and buccal pores face downwards rather than towards the peristome. The tubercles would have supported spines that extended at right angles to the test and to the plane of the peristomial membrane. Unless they were significantly bent inwards, they would not have formed a grill across the membrane as seen in other clypeasteroids. In addition, the buccal podia would have been well situated to reach downwards at right angles to the test, but not into the mouth region. A peristomial infundibulum, observed in almost all other clypeasteroids, is lacking, giving the peristomial region a flat aspect flush with the surrounding corona. The entire organization has the appearance of having been everted, or “turned outwards” (Fig. 4).

The function of the inner circumoral ring is unclear. In comparison with taxa in which the infundibulum is not everted, the position of the ring would correspond to the line of insertion of the peristomial membrane. No similar structure has been observed in other clypeasteroids. A superficially similar ring is developed in *Leniechinus* and *Cyamidia*, but this lies more distally, aboral to the buccal pores. In these taxa, this outer ring is formed by lateral expansion of the ambulacral bars overlying the sphaeridia. In *Tridium* these are slightly expanded laterally as well, but fail to meet interradially, being separated by wide gaps across the interambulacra.

Genus *Lenicyamidia* Brunnschweiler, 1962

Type species. *Lenicyamidia compta* Brunnschweiler, 1962, p. 165, by original designation.

Emended diagnosis. Small fibulariids with an antero-posteriorly elongated periproct, and a distinct naked medial zone on the oral surface, with the tubercles bilaterally arranged left and right of it.

Remarks. Like *Cyamidia* this taxon differs from the type genus *Fibularia* in having low ambulacral plates at the ambitus and an elongate periproct. It differs from *Cyamidia* mainly by its distinctive oral tuberculation, which is similar to that seen in *Leniechinus*, *Lenita*, and some cassidulids. In contrast to the former two, however, the enlarged tubercles are not distinctly invaginated, but have only moderately sunken areoles.

Lenicyamidia compta Brunnschweiler, 1962

Figures 4, 7D–F, 10A–C, 11, 13–14.

1962 *Lenicyamidia compta* Brunnschweiler: 165–169, figs 2–3.
1966 *Lenicyamidia compta* Brunnschweiler—Philip: 116–117, fig. 1.

Type material. GA CPC 2827 (holotype, Figs 7D–F, 10B) and GA CPC 2828 (paratype).

Material studied. GA CPC 2827–2829, 41773–41799.

Type locality. Sample M24 from point 221 on airphoto No. 5170 on Run 2, Moogooloo Hill (hill crest located at 23° 36′ 12″ S, 114° 44′ 14″ E; exact coordinates of sampling locality unknown); about 8 miles SSE of the Pleiades Hills, Northwest Division, Western Australia.

Type stratum. Merlinleigh Sandstone, Late Eocene (see Darragh & Kendrick 2010: pp. 24–25)

ZooBank LSID. urn:lsid:zoobank.org:act:90041316-5191-4933-A119-6C0E598DD5D2

Description. *Size and shape*—Corona small, not exceeding 10 mm in TL among available specimens; outline in aboral view forming slightly angular circle; distinctly flattened in profile, maximum height between 30 and 40% of test length.

Internal buttressing—Absent, but ambulacral plates bear large pits internally and are about half as thick as interambulacral plates in their centre (Fig. 14C), explaining peculiarly shaped internal casts (Fig. 14C) reported by Brunnschweiler (1962: fig. 2E); pits associated with pores for accessory tube feet (Fig. 14B).

Apical system—Situated centrally, at apex of corona; monobasal, with four gonopores and single central hydropore, not situated in pit or groove; ocular pores small and indistinct, lying well outside area enclosed by gonopores.

Ambulacra—Ambulacral plating simple; ambulacra expanding only slightly towards ambitus where they are barely wider than interambulacra; petals short, with up to 21 non-conjugate respiratory pore pairs in each ambulacrum; pore pairs strongly oblique, crossing ambulacral plates; interporal ridge smooth and formed by unperforated stereom; distal pore pairs becoming even more strongly oblique with distance between pores in each pair slightly decreasing; width of interporiferous zones widest halfway along petals and becoming slightly narrower again distally; petaloid region large, extending about 70% of TL; food grooves absent; buccal pores large and located close to peristomial edge, facing horizontally into peristome, externally visible only in broken specimens (Fig. 14E) since they are hidden by transverse stereom bars in oral view; accessory pores evenly distributed all over test on aboral surface (including interporiferous zones and interambulacral plates), but forming patches obliquely crossing ambulacral plates and less common elsewhere on oral surface; ambitus initiating at approximately fourth to fifth pair of ambulacral postbasicoronal plates.

Interambulacra—Adapically, two unpaired plates lie in tandem adjacent to apical system; three or four post-basicoronal interambulacrals in each column visible in oral view; posterior unpaired interambulacrum expanding distinctly in region accommodating periproct; basicoronal plates usually extending only to first adjacent ambulacral plate, except in interambulacrum 2, where usually extending to second adjacent ambulacral plate on one or both sides; in largest specimen with plate sutures visible (CPC 41796), basicoronal plates of interambulacra 1, 3 and 4 also extend on one side to second adjacent ambulacral plate due to presence of large spine-bearing tubercles on margins of these plates (usually missing in smaller specimens) and fact that sutures are curved to make room for tubercles slightly modifies plate outline in such a way that they come into contact with second ambulacral plates; accessory pores evenly spread over aboral interambulacra, but less common, though present on oral interambulacral plates.

Tuberculation—Primary tubercles crenulate, perforate, homogeneously distributed on aboral surface; on oral surface, in contrast, there is a narrow area between the periproct and peristome (Fig. 14 D), as well as anterior of the latter (Fig. 14 A), free of primary tubercles; instead densely covered with glassy tubercles; lateral to this medial area are located primary tubercles with slightly sunken areoles, these tubercles larger than aboral tubercles.

Peristome—Larger than periproct, about 18% TL; infundibulum extremely shallow but with near-vertical walls; peristomial opening facing directly downwards almost at midpoint of oral surface; framed by basicoronal circlet in which ambulacral plates only slightly longer than adjacent interambulacrals; plates of basicoronal circlet distinctly longer in posterior half of test; only scattered single tubercles present on interambulacral basicoronals adjacent to peristome, mainly on larger specimens; peristome framed by broken circle of circumferential bars overlying sphaeridial chambers (Fig. 14E).

Periproct—Small, approximately 12% TL; facing down- and slightly backwards; located close to posterior margin on oral side; distinctly elongated along anterior-posterior axis; bounded by first (5.a.2, 5.b.2), second (5.a.3, 5.b.3), and one plate (5.b.4) of the third pair of post-basicoronal plates.

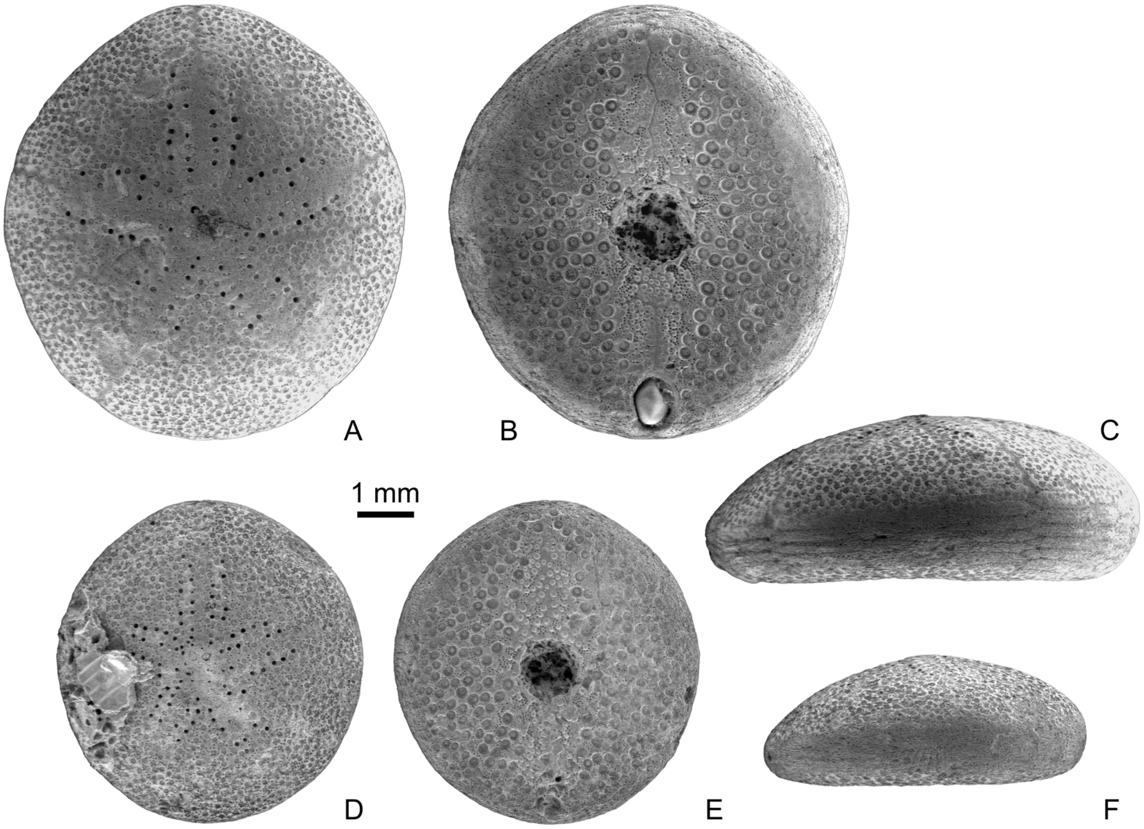

FIGURE 13. SEM images of the test of three specimens of *Lenicyamidia compta*. A–C. GA CPC 41774, aboral (A), oral (B) and right lateral view (C); D–F. GA CPC 41773, aboral (D), oral (E) and right lateral view (F).

Perignathic girdle—Consisting of five small processes (auricles) attached to the internal surface of each interambulacral basicoronal; on their adoral side a pair of minute depressions (likely muscle scars for insertion of lantern protractors) located in each interambulacrum.

Sphaeridia—One per ambulacrum; fully enclosed (Figs 4, 14E); situated beneath distinct transverse bar just distal to buccal pores.

Spines, pedicellariae, lantern—Unknown.

Remarks. Brunnschweiler (1962) illustrated the apical disc as being composed of four genital plus an additional central plate. However, Philip (1966) showed that the apical disc was of typical clypeasteroid monobasal structure. The illustration of an "internal mold" by Brunnschweiler (1962: fig. 3) in reality represents an internal view of the oral surface (and thus shows a mirror image of the outside plating pattern). This accounts for the apparent deviation from Lovén's Rule in his drawing.

The peristomial region of *L. compta* is markedly different from that of other fibulariids studied here (Fig. 4). There are no clusters of tubercles on interambulacral basicoronals, the sides of the peristomial infundibulum are very steep and the circumferential stereom bars are very close to the peristomial edge, almost overhanging it in some cases.

The oral tuberculation of *Lenicyamidia* was compared with that of *Lenita* by Brunnschweiler (1962). While both possess a medial zone free from spine-bearing tubercles, there are two obvious differences: 1) in *Lenita* the tubercles have deeply incised, asymmetrical areoles (these are shallow and near symmetrical in *Lenicyamidia*); and 2) large glassy tubercles are lacking in this zone in *Lenita*. It seems likely, therefore, that this tuberculation pattern is not homologous, but has adaptive significance causing it to have arisen independently in several neognathostome clades. In addition, *Lenita*, which is an early scutelline, differs in many other respects, including possession of biserial interambulacra at the apex, paired basicoronals, and other features not found in laganiforms. In contrast, *Lenicyamidia*, is clearly a laganiform, having two uniserial plates in the adapical interambulacra and a basicoronal circlet typical of fibulariids.

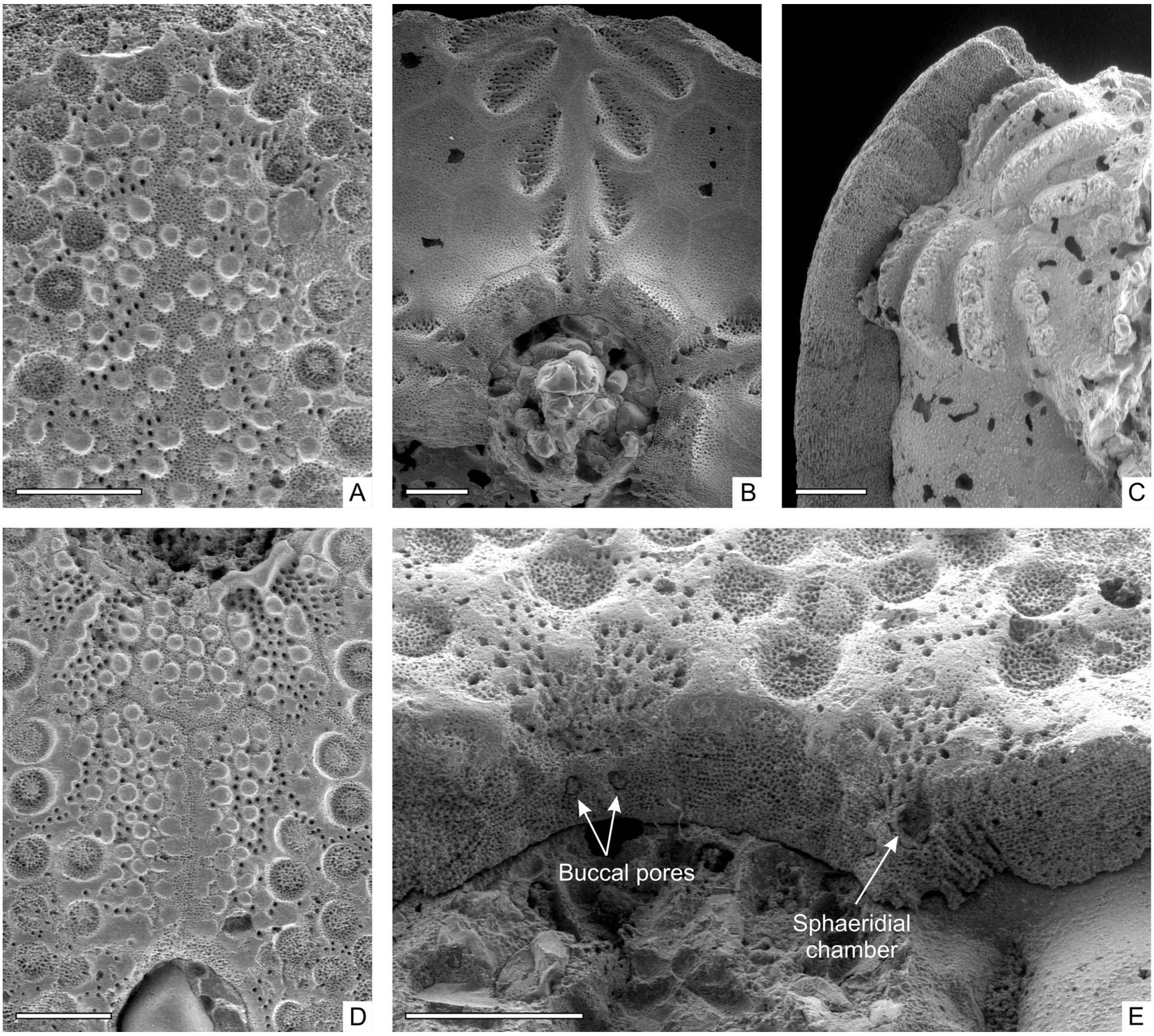

FIGURE 14. SEM images showing details on test surface of *Lenicyamidia compta*. A. Ornamentation of test just anterior of the peristome in specimen GA CPC 41773. B. Internal view of oral ambulacra and peristome (lower part of image) in specimen GA CPC 41775 showing perignatic girdle and sunken fields of accessory pores. C. Internal mould of specimen GA CPC 41776, showing sunken fields of accessory pores as elevated ridges and thickness of the test at the ambitus. D. Ornamentation of test just posterior of the peristome in specimen GA CPC 41774. E. Cross section through peristomial region of specimen GA CPC 41777 showing buccal pores and sphaeridial chamber. All scale bars 500 µm long.

Leniechinus and *Lenicyamidia*

In the genus-level analysis based on the Kroh & Smith (2010) dataset, branching order within the fibulariids is poorly resolved. When *Lenicyamidia* was excluded, *Leniechinus* was recovered as a sister group to *Fibularia* + *Tridium* in an unresolved trichotomy with *Cyamidia* (Fig. 3). However, in the species-level analysis, *Leniechinus* falls to the base of the fibulariid clade, below the nodes joining *Echinocyamus* and *Mortonia* to the more crownward fibulariids (Fig. 5). The reason for this discrepancy is based on the observation that more features could be scored for the extant taxon *Echinocyamus* than for the incompletely known fossil taxon *Leniechinus* in the genus-level analysis. Moreover, in the species-level analysis several features that turn out to be relatively plesiomorphic within the Fibulariidae overall push *Leniechinus* more basally. For example, the relatively high number of pore pairs in the petaloids, along with the width of the interporiferous zones, tend to exclude *Leniechinus* from the more crownward fibulariids, making it plesiomorphically more similar to *Mortonia*.

Kier (1968) stated that *Leniechinus* was likely more closely related to *Lenita* than to other fibulariids such as *Lenicyamidia*, based at least in part on the presence of internal buttresses (which are lacking in *Lenicyamidia*). Internal buttresses can be greatly reduced in paedomorphic scutellines so that they resemble those of fibulariids. Mooi (1990) excluded *Lenita* from his concept of the laganines. Nearly all the characters he listed as synapomorphies for the scutellines cannot be determined in *Lenita*. Nevertheless, *Lenita* is neither a laganine nor a clypeasterine, as it clearly lacks laganiform synapomorphies. In *Lenita*, the interambulacral columns plesiomorphically remain paired all the way to the apical system, the hydropores are numerous and scattered across the madreporite (seen in laganiforms only in taxa such as *Peronella*), and the periproct is strongly aboral, separated from the peristome by at least three pairs of post-basicoronal plates. *Lenita* also expresses key features in the symmetry of the oral surface plating that are also very unlike those of laganiforms. In contrast, the present analysis firmly places *Leniechinus* among the laganiforms. For these reasons, *Leniechinus* cannot be considered closely related to *Lenita*. Similarities in oral tuberculation between *Lenita* and *Leniechinus* (the supposed locomotory tubercles) appear to be convergent.

Lenicyamidia compta, on the other hand, does have affinities with fibulariids. It possesses key features that place it crownward in the fibulariid clade, even above the nodes that join *Leniechinus*, *Mortonia*, and *Echinocyamus* to the family (Fig. 5). It has reduced petaloids, narrow interporiferous zones, and completely lacks internal buttresses. Among all the fibulariids, the elongate periproct and test plate pattern places it with *Cyamidia*.

Acknowledgements

We gratefully acknowledge the loan of *Cyamidia* specimens by Timothy Ewin (NHM) and the loan of Brunnschweiler's types by John Laurie (Geoscience Australia). Thanks to Frank Holmes for advice and to Dan Topa (NHMW) for assisting in scanning electron microscopy. Additional material of taxa such as *Fibularia* and *Leniechinus* was made available by Kathy Hollis and Daniel Levin (NMNH, Smithsonian Institution). The helpful comments of two anonymous reviewers are gratefully acknowledged.

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