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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

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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*.

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