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The test architecture of *Clypeaster* (Echinoidea, Clypeasteroida) and its phylogenetic significance

MORANA MIHALJEVIĆ[1], IWAN JERJEN[2] & ANDREW B. SMITH[3]

[1]*Paläontologisches Institut und Museum, Universität Zürich, Karl Schmid-Strasse 4, 8006 Zürich, Switzerland. E-mail: morana.miha@gmail.com*

[2]*Empa - Swiss Federal Laboratories for Materials Testing and Research, Überlandstrasse 129, 8600 Dübendorf, Switzerland. E-mail: Iwan.Jerjen@empa.ch*

[3]*Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW75BD, UK. E-mail: a.smith@nhm.ac.uk*

Abstract

Clypeaster is a speciose echinoid genus with almost 50 extant and approximately 350 extinct species, encompassing a great heterogeneity of form. While some attempts to subdivide this genus have been made, none has gained widespread support, and all recent taxonomic treatments have left the genus intact. Here we report new data on internal buttress arrangement, determined from X-Ray tomography, and plate architecture, and use this to establish relationships amongst 19 extant species encompassing 8 of the 10 nominal subgenera that have been proposed. A cladistic analysis of these characters allows us to test the validity of previously suggested subgenera of *Clypeaster.* Our analysis confirms that *Clypeaster* is monophyletic with the clypeasteroid family Arachnoididae (as represented by *Arachnoides* and *Ammotrophus*) as its immediate sister-group. It also identifies *Orthanthus* as the most primitive subgenus in the family *Clypeaster.* However, none of the previously proposed subdivisions of *Clypeaster* were recovered as clades and test architecture proves too homoplasous to allow a confident basis on which to subdivide the genus.

Key words: Echinoidea, *Clypeaster*, test structure, buttressing, phylogeny

Introduction

Clypeaster is the type genus of the Clypeasteroida, an order of irregular echinoids that includes the sand dollars and sea biscuits. It is a common shallow-water echinoid that is to be found in all of the world's tropical and subtropical seas and lives in or on soft sediments from the littoral zone down to ca. 500 m, although most species are confined to the shallow continental shelf (Mortensen 1948b). There are some 49 currently available species names for living *Clypeaster*, making it the most speciose extant genus of echinoid. The fossil record of *Clypeaster*, extending back to the Middle Eocene, encompasses yet another 350 nominal species (Durham 1955; Mortensen 1948b; Poddubiuk & Rose 1984; Rose & Poddubiuk 1987; Smith 2005; Kier & Lawson 1978; Kroh 2010). Due to its rather sturdy test it is one of the commonest fossil echinoids in the Tertiary (Michelin 1855). Yet subdividing *Clypeaster* taxonomically has proved to be difficult, largely because its various species show extensive gradation in test shape (Figs. 1–3). Gradation of features can be observed in traits such as test size, ambital outline, test profile, petal shape, periproct position and tuberculation (Hopkins 1988; Rose & Poddubiuk 1987). A difficult situation has been made much worse by palaeontologists establishing new fossil species based on minor shape differences in poorly preserved specimens and without reference to taxa described in other regions, which has undoubtedly led to the inflation of the number of nominal species (Poddubiuk 1985).

There have been several attempts to divide this diverse genus, starting with Agassiz (1863) and culminating in Mortensen (1948b), who reviewed and summarized all previous subdivision attempts (Pomel 1887; Lambert 1912; Lambert & Thiéry 1909–1925). Mortensen accepted 10 subgenera of *Clypeaster* (Table 1) based on a range of test characters including test shape, thickness of the test's edge, petal form and internal structure, but his definitions and diagnoses were rather vague and there is inconsistency in how individual traits are reported (Table 1). Probably as

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