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**MORPHOLOGICAL VARIATION IN THE CENOZOIC  
ECHINOID CLYPEASTER AND ITS ECOLOGICAL AND  
STRATIGRAPHICAL SIGNIFICANCE**

by

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**The importance of Clypeaster**

Six characteristics give *Clypeaster* particular importance among Neogene echinoid genera:

1 *Clear morphological distinction.* Even in poor fossil material, echinoids of the order Clypeasteroidea can easily be recognized by their accessory tube-foot pores and internal skeletal pillars. Clypeaster is among the most distinctive and best-known of clypeasteroids, with a fossil record that is especially well documented.

2 *High preservation potential.* Rigid interplate suturing plus support and stress distribution by its internal pillar network, make the Clypeaster test particularly robust (SEILACHER, 1979; SMITH, 1984). Preservation potential is often further enhanced by an infaunal mode of life.

3 *Wide geographic distribution.* Clypeaster is one of the most widespread clypeasteroid genera in Recent seas (GHIOLD, 1985) and appears to have been tropicopolitan throughout the Neogene. Individual species have been reported to range widely (ALI, 1983), but tend to be confined to single faunal provinces.

4 *High species diversity.* With more than 400 named species (DURHAM, 1966), Clypeaster has the highest recorded internal diversity of any echinoid genus.

5 *Characteristic Cenozoic range.* The order Clypeasteroidea is exclusively Cenozoic, originating in the Palaeocene (KIER, 1982). The earliest species of Clypeaster presently known in Middle Eocene (ROMAN, 1968). By early Oligocene times the genus was common and widespread in the Tethyan region, but did not reach its maximum geographic range or species diversity until the Miocene.

6 *Local abundance.* Ecological success and high preservation potential have ensured that Clypeaster is numerically, as well as taxonomically, among the best represented of all Neogene echinoid genera. Beds rich in Clypeaster specimens occur widely within Oligo-Miocene shallow water carbonate marine facies (BOGGILD and ROSE, 1985).

**Factors limiting biostratigraphic use**

Despite high recorded species diversity, rapid evolutionary change and common, widespread occurrence, Clypeaster has been little used in biostratigraphy. There seem to be five main reasons for this omission:

1 *Species concepts differ widely between authors.* For example, ROSE (1985) has demonstrated how differences in species concept, even between recent contemporaneous authors, lead to differences in name and number of Clypeaster species recorded from Malta, and to strikingly different faunal lists from the late Miocene of Malta compared to that of Crete. In general, species recognition and comparison from the literature are difficult.

2 *Substantial infrapopulation variation occurs in many test characters commonly regarded as species diagnostic.* In consequence, the number of species described from any region tends to be grossly exaggerated (CHALLIS, 1980; PODDUBIUK, 1985).

3 *Few structural innovations punctuate the evolutionary history of the genus.* There are still no generally accepted criteria for recognition of clades, and hence for sub-generic grouping of species.

4 *Gradual phyletic change is seldom discernable.* Most species of Clypeaster are defined on the basis of quantitative differences in a small number of shared test characters. In consequence, phyletic relationships between species are usually obscure, and serial changes that might reliably serve for correlation are not recognizable.

5 *Adaptive strategies are commonly repeated.* Similar morphologies have repeatedly evolved quite independently. For example, the major changes leading to the extant Caribbean species *C. rosaceus* were paralleled during the evolution of some other large and inflated Clypeasters, such as the Mediterranean Neogene *C. altus*. Individual species morphology may thus be of more obvious palaeoenvironmental than taxonomic or stratigraphic significance.

#### Main features of interspecific variation

In Clypeaster, interspecific (as contrasted with infraspecific) test variation occurs mainly in seven features:

1 *Test size.* Adult size in echinoids is subject to environmental modification, notably by food supply and temperature but may still be an important taxonomic character. While it is not the best indicator of overall size because of shape variation, test length is the measure traditionally used in taxonomy. Within the genus it varies from around 20 mm up to nearly 250 mm.

2 *Ambital outline.* Two characteristics almost invariably covered during description of a Clypeaster specimen are pentagonality and elongation of the test outline in the ambital plane. Degree of pentagonality is very striking in individual specimens, but shows such great infraspecific variation that it is rarely of taxonomic significance. In contrast, degree of elongation is infraspecifically stable, and has both taxonomic and autoecological significance. Width/length ratios in the genus range from 70% to 105%, but in individual species they normally vary by less than 15%. Ratios under 85% are typically associated with an active deep burrowing mode of life; 85–95% with superficial burrowers and also with epibenthic forms; over 95% with low superficial burrowers and ploughers.

3 *Test profile.* The most important aspects of longitudinal test profile are: height relative to length, ambital tumidity and its variation, shape of the ambital plane in cross-section, size and distinctness of the apical mound, nature of any adoral convexity and characteristics of its adambital margins. Test height varies from <15% to >65% of test length, but wide infraspecific variation is normal, so it is important as a taxonomic character only at the extreme ends of its range. Marginal tumidity, the thickness of the strongly curved edge zone of the test relative to total test height, may show considerable variation round the test perimeter. It is normally greatest at the anterior end, decreasing to a minimum at a posterior trailing edge. Its maximum value is often of considerable taxonomic use, being generally stable within individual species but varying from 5% to 100% within the genus as a whole. High marginal tumidities and large posterior decrease in tumidity are typical of deep burrowing and ploughing

species. Ambital elevation, relative to marginal tumidity or to test height, can also be stable within species and of use in species differentiation and palaeoecological interpretation. In burrowing forms it is always about 50% of margin thickness, and typically 20–50% of test height, while in epibenthic forms it is frequently less than 40% of margin thickness and may be less than 5% of test height. Ambital plane curvature is a much less widely recognised and understood morphological characteristic in *Clypeaster*. Normally it is negligible but in a few species (e.g. *C. cotteaui*) a distinctive anterior-posterior upward concavity is developed, producing a highly distinctive arching of the lower surface of the test by over 5% of test height. Adoral concavity in *Clypeaster* ranges from negligible to about 50% of test height. It may occupy only the central part of the oral surface and form a distinct buccal cavity around the peristome or extend more or less uniformly almost to the ambitus, although wide infraspecific variation is common. The adambital margins may be well rounded or severely flattened adorally, the former typical of relatively deep burrowers and ploughers, the latter of epifaunal and superficially burrowing forms where the spines borne on these marginal zones are almost entirely responsible for locomotion.

**4 Test construction.** Whether they act as skeletalized tethers (SEILACHER, 1979) or compressive struts (TELFORD, 1985), the distribution of internal pillars within a clypeasteroid test is generally related to test morphology. In low sharp-edged species pillars are normally small, numerous, and distributed evenly from mouth to ambitus. Forms with higher tests and a less distinct margin have fewer pillars, concentrated mid-radially. Some large epibenthic *Clypeaster*s have a double rather than single test wall. This can increase test thickness to more than 7 mm (6% of test length) in Recent *C. rosaceus*.

**5 Petal character.** Traditionally the most significant characters in *Clypeaster* species differentiation have been associated with their petal systems, functionally very important as gas exchange organs. The five petals often differ considerably and should be analysed individually. Intraspecifically the most stable and important elements of petal morphology are length relative to the perradial distance from ocular to ambitus, maximum width relative to length, position of this width maximum, degree of closure relative to it, width of poriferous zones and details of the respiratory pores, most obviously their number. Petal length ranges from <40% to >85% of perradial length. Although subject to some allometric growth and ecological controls its infraspecific variation for any particular petal rarely exceeds 10%. Maximum petal width and its distance from the ocular are both infraspecifically stable but respectively range within the genus from 35–65% and 40–100% of the petal's length. The width of the petal at its distal end is also important taxonomically and ranges from 0 to 100% of maximum petal width. Width of poriferous zones is a measure of respiratory tube-foot width, a direct control on the area of the gas exchange surface. Within the genus it ranges from <15% to >25% of maximum petal width. Number of respiratory pores per petal normally increases throughout life but once adulthood has been reached the addition rate is low. In sexually mature specimens of any one species it rarely varies by more than 10 but within the genus as a whole it ranges from under 20 to over 60. Degree of petal inflation, although highly distinctive in individual specimens, is subject to very considerable infraspecific variation and is of little taxonomic or morphotypic value.

**6 Periproct position.** With few exceptions, periproct morphology and size seem to be of little taxonomic importance in *Clypeaster*. This is not true of periproct position, which ranges from inframarginal to submarginal, the separation of the rear of

the periproct from the posterior margin of the test varying from less than 1% to over 8% of test length. For use in species discrimination, the distance is stablest when described in terms of periproct lengths, ranging from 20–400% on this scale.

7 *Tuberculation*. Clypeasteroid tubercles are partially or completely sunken beneath the test surface and often very well preserved. It is normally possible to deduce from them absolute measures and patterns of spine size, packing density, articulation angle and power stroke direction as well as direct tubercle characteristics such as packing style and area utilization efficiency. Patterns tend to be stable within a species, but may vary significantly between species with differing modes of life.

#### Common morphotypes and their distribution

The main features of gross test morphology do not vary independently. Many features almost invariably occur together, thus limiting the number of commonly occurring overall test morphologies. Distinctive and recurring combinations of test characters characterize "morphotypes".

Many morphotypes were regarded as subgenera (LAMBERT and THIÉRY, 1925; MORTENSEN, 1948) until proven polyphyletic origins and the existence of intermediate forms led to their rejection (DURHAM, 1966). The character combinations they possess do, however, have considerable functional and ecological significance. Each main morphotype represents a particular adaptive strategy, rather than a monophyletic taxonomic group. That similar morphologies evolved independently many times is evidence that adaptive strategies were repeated, presumably to exploit the commonly available environmental niches.

The principle can be illustrated by six particularly widespread and distinctive morphotypes. Major features of their morphology are summarized in the accompanying table, time of first occurrence and inferred depth of burrowing in a separate figure. For convenience, each morphotype has been designated here with the name of an early, well-known and widely occurring representative species.

1 '*biarritzensis*' Named after the *C. biarritzensis* species group (which includes *C. trotteri*), widespread in the early Oligocene of S Europe, N Africa and the Middle East (ROSE, 1966; DURHAM and MOJAB, 1983). Many species once included in the subgenera *Biarritzella*, *Laginidea*, and *Guebhardanthus* are closely comparable, including Eocene *C. marbellensis*.

2 '*oxybaphon*' After *C. oxybaphon*, widespread in the mid-Cenozoic of southern USA and the Caribbean islands. Although relatively rare in *Clypeaster* itself, this morphotype is well seen in other clypeasteroids, particularly some Laganids.

3 '*cotteaui*' After the *C. cotteaui* species group (which includes *C. batheri*, sensu PODDUBIUK and ROSE, 1985; PODDUBIUK in prep.) widespread in the late Oligocene of the Caribbean islands; species closely similar in morphology and stratigraphic age also occur in the Mediterranean region (ROSE, 1966). Comparable species have been referred by MORTENSEN (1948) to the subgenera *Pavaya*, *Paleanthus*, *Laubeanthus*, and sometimes *Rhaphidoclypus*.

4 '*concaus*' After *C. concaus*, widespread in the Early/Middle Miocene of the Caribbean region (PODDUBIUK, 1985; in prep.). In the past, species with this morphotype were generally referred to *Bunactis* or *Stolonoclypus*.

5 '*margitanus*' After *C. margitanus*, well-known from the late Middle Miocene of the central Mediterranean region (CHALLIS, 1980). Similar species have generally

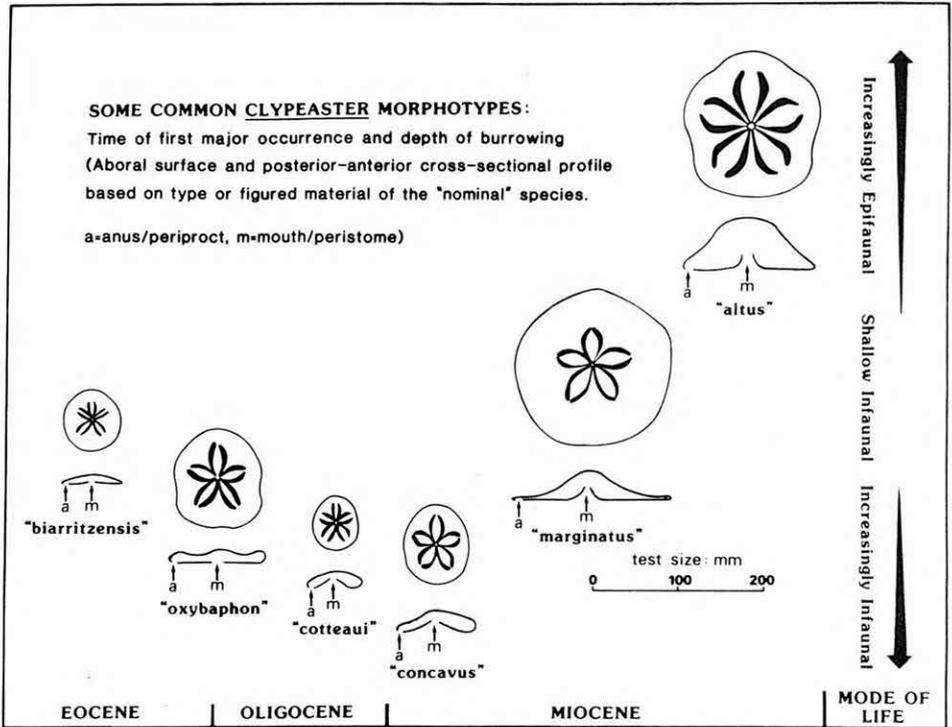


Fig. 1.

been ascribed to *Paratinanthus*, *Platyclypeina*, sometimes *Stolonoclypus*, and occasionally *Coronanthus*.

6 'altus' After *C. altus*, widespread in the later Miocene of the Mediterranean region (CHALLIS, 1980). This morphotype includes *Clypeaster* (sensu stricto), *Tholeopelta*, *Oxyclypeina*, *Pliophyma*, plus some species formerly referred to *Bunactis* and *Rhaphidoclypus*.

### Conclusion

Time of first appearance and subsequent quantitative importance vary from one morphotype to another with a general pattern of increasing diversity through time. Clypeaster morphotypes, which can easily be recognized in the field, are thus significant indices of maximum stratigraphic age. The 'biarritzensis', 'cotteai', 'concaus', and 'altus' morphotypes are broadly characteristic of U. Eocene/L. Oligocene, L/M. Miocene, and U. Miocene/Pliocene strata respectively, at least in the West Tethyan/Caribbean area, although examples of all are still extant.

By analogy with Recent species and analysis of functional morphology it can be inferred that early Clypeasters belonging to the 'biarritzensis' morphotype were adapted to very shallow burrowing modes of life. Subsequent morphotype development seems to reflect an expansion of the ecological range of the genus, as it adapted

Table 1

Major features of some common *Clypeaster* morphotypes

Morphotype	Test size	Ambital outline	Marginal tumidity	Test profile	Test construction	Petal character	Periproct position	Aboral tuberculation
' <i>biarritzensis</i> '	small; typical adult length 70 mm	subpentagonal, subradial	thin; little anterior —posterior differentiation	very depressed; petaloid area little inflated; flat adorally	pillars many, evenly spaced; wall single	widely open, subradially arranged; long—short	well separated from margin	fine, sparse- dense
' <i>oxybaphon</i> '	medium; typical adult length 110 mm	subpentagonal, bilateral	thick; slight-moderate anterior— posterior differentiation	depressed; low, dished submarginally, petaloid area slightly inflated/ concave adorally	pillars few, concentrated ambitally; wall single	slightly open, bilaterally arranged; long	separated from margin	very variable
' <i>cotteau</i> '	small; typical adult length 70 mm	suboval, bilateral	thick; slight anterior —posterior differentiation	depressed; petaloid area not inflated; concave adorally	pillars few, evenly spaced; wall single	open, bilaterally arranged; mod.—long	well separated from margin	coarse, sparse
' <i>concaus</i> '	medium; typical adult length 90 mm	subpentagonal, bilateral	thick; strong anterior —posterior differentiation	mod. inflated; distinct wedged petal mound; concave adorally	pillars few, concentrated ambitally; wall single	slightly open bilaterally arranged; long	adjacent to or slightly separated from margin	fine, dense
' <i>marginatus</i> '	large; typical adult length 150 mm	subcircular, subradial	thin; very slight anterior —posterior differentiation	mod. inflated; distinct but unwedged petal mound; flat adorally	pillars many, evenly spaced; wall single	closed, subradially arranged; short	well separated from margin	fine, dense
' <i>altus</i> '	large; typical adult length 120 mm	subpentagonal to subcircular, subradial	very thick; little anterior —posterior differentiation	highly inflated; petal mound often indistinct; flat adorally	pillars v. few, distant from ambitus; wall may be double	open, sub- radially ar- ranged; long —v. long	adjacent to margin	coarse, sparse

to more varied burrowing and surface-dwelling strategies. Initially ('*cotteau*', '*concavus*'), morphotypes represent increasingly infaunal adaptations. Efficient epifaunal adaptations (e.g. '*altus*' morphotype) occur relatively late in the stratigraphic record.

Variation in the qualitative importance of morphotypes generally may in part reflect changing shallow water carbonate sedimentation patterns. Increasingly epifaunal trends in eastern Caribbean *Clypeasters* seem to correlate with the spread of seagrass communities there (PODDUBIUK, 1985). Seagrass arrival reduced the amount of ecospace available for shallow burrowers whilst providing a large new food source for epibenthos.

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