RAPID EVOLUTION IN ECHINOIDS

by PORTER M. KIER

ABSTRACT. The evolution of the irregular echinoid and of the sand dollar occurred in a very short time. The first irregular echinoid appears abruptly in the Early Jurassic (Sinemurian); and by the Toarcian, only ten million years later, irregular echinoids possess all the features necessary to permit them to live buried in the sediment. The first clypeasteroid appears in the Paleocene. By the middle Eocene its very specialized descendants, the sand dollars, have a worldwide distribution. This rapid evolution and diversification seem to result from a sudden adaptive breakthrough. The presence of so few intermediates indicates the evolutionary steps must have been large.

TWO of the most significant events in the evolution of the echinoids are the development of the irregular echinoid and the subsequent appearance of the sand dollar. Both of these events were believed to have occurred over a long period of time (Durham 1966, p. U289) but new evidence suggests otherwise. The irregular echinoid was assumed to have evolved during the Triassic and perhaps during the latter part of the Paleozoic. However, study of the Triassic faunas indicates that no irregulars were present then and that the great changes from the regular to the irregular echinoid occurred during the early part of the Early Jurassic. Likewise, it was believed (Durham 1966, p. U290) that the clypeasteroids arose during the Late Cretaceous and Paleocene. New evidence suggests that the first clypeasteroid actually appeared in the Paleocene, and that the great evolution to the sand dollar occurred during the early Eocene.
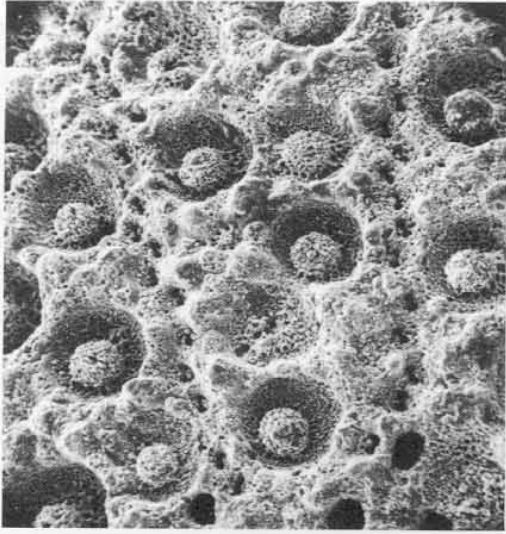
EVOLUTION OF THE IRREGULAR ECHINOID

The first irregular echinoid, *Plesiechinus hawkinsi* Jesionek-Szymańska (text-fig. 1B), occurs in the Early Jurassic (Sinemurian). This echinoid, a pygasterid, differs from all other echinoids of the same age or older in having an asymmetrical test with small tuberculation, short and numerous spines, differentiated pores with the adapical pores larger than the adoral ones, posteriorly eccentric periproct, and presumably keeled teeth (although the lantern was not found with any specimens of this species, Melville (1961) found keeled teeth in a *Pygaster*).

One might assume that the great changes necessary to derive this irregular echinoid from a regular form would have taken a very long time. Many workers believe that these changes occurred during the Triassic or possibly in the Paleozoic. They attributed the lack of intermediates found during the Triassic to the poor fossil record of that period. However, that does not appear to be the case. Although it is true that few echinoids are known from the Triassic, particularly from the Early and Middle Triassic, a prolific echinoid fauna occurs in the Late Triassic St. Cassian beds of Italy. These beds (Kier 1977b) have been painstakingly searched by Rinaldo Zardini who has found many complete tests and thousands of fragments. I have searched through all this material and have failed to find any keeled teeth or any test fragments with the fine tuberculation of an irregular echinoid. As shown by Kier (1977a), irregular echinoids are much more likely to be preserved than regular echinoids. Had they been living during St. Cassian time, they should have been preserved as fossils. Furthermore, no irregular echinoids or any form resembling them have been found in the lowermost Jurassic (Hettangian).

I am convinced that this change from a regular echinoid to *Plesiechinus hawkinsi* must have occurred extremely quickly during the latter part of the Hettangian or early Sinemurian. Evolution then continued at a rapid rate, because by the Toarcian, still within the Early Jurassic, the cassiduloid *Galeropygus dumortieri* (Paris) (text-fig. 1C) has appeared with all the features of an irregular
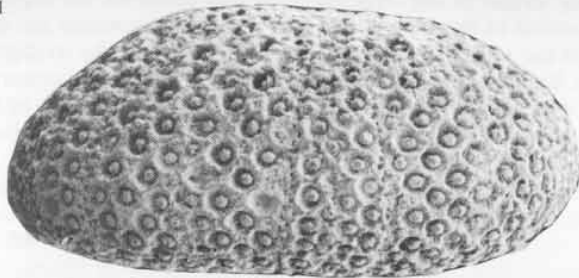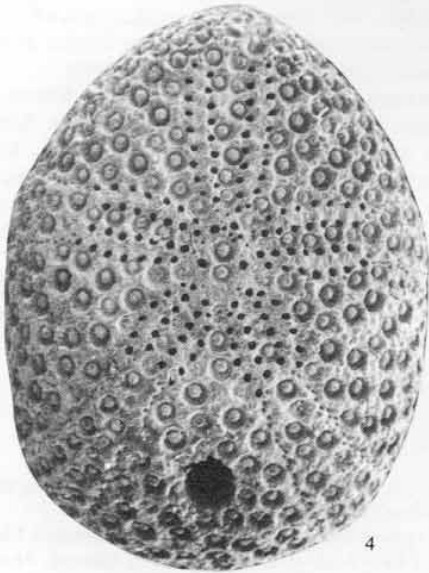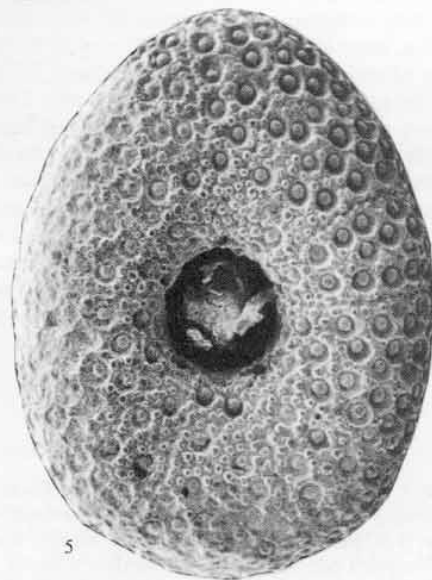
echinoid. It is more advanced than *P. hawkinsi* in having a more flattened and elongate test, a more eccentric periproct, larger adapical pores forming incipient petals, and smaller, more numerous, tubercles and spines. Its peristome is smaller, elongate, and eccentric anteriorly. There are no gills. The most profound differences are the lack of a lantern and lantern supports and the presence of well-developed phyllodes.

Presumably, one of the reasons for this rapid evolution was that these changes enabled echinoids to occupy a habitat not available to them before. They were now able to burrow (Smith 1978) into the sediment and extract the organic material contained within. Simpson (1944, 1953), and later Stanley (1979), proposed that a higher taxon arises rapidly through the occurrence of a sudden adaptive breakthrough. During the Triassic all echinoids apparently lived on the surface of the sea floor and could not burrow into the sediment. They all had jaws and grooved teeth which were used (presumably like modern regular echinoids) to tear off and chew organic material which was then passed into the gut. The small amount of faecal discharge could be easily carried away by water currents. Most modern irregular echinoids lacking teeth feed differently. They burrow (text-fig. 1)

TEXT-FIG. 1. Evolution of the irregular echinoid showing the changes that enabled the echinoid to live buried in the substrate. A, an Hettangian regular echinoid such as *Diademopsis*; B, the earliest known irregular, *Plesiechinus hawkinsi* Jesionek-Szymańska; C, a cassiduloid, *Galeropygus*.

EXPLANATION OF PLATE 1

Figs. 1–5. *Togocyamus seefriedi* (Oppenheim). Paleocene, Ekekoro Formation, Ekekoro quarry, 55 km north-west of Lagos, Nigeria. 1, accessory pore on dorsal side of USNM 312503 just beyond petal I. The large pores on the lower right side are at the end of petal I, × 74. 2, enlarged view of accessory pore in USNM 312504 showing large neural pore, × 500. 3, side view of USNM 312505, × 19. 4, top view of USNM 312503, × 13. 5, bottom view of USNM 312504, × 15.

PLATE 1

KIER, *Togocyamus*

into the sediment, collect large amounts of sediment with their tube-feet, and pass it through the gut while extracting the organic material. The sediment is then expelled through the anus (periproct). Most of the differences between an irregular and regular echinoid relate to these differences in mode of feeding.

The posterior migration of the periproct made it possible for the irregular echinoid to leave this large volume of discharged sediment in its trail rather than over its dorsal surface. At the same time that the periproct migrated, most irregular echinoids increased the oxygen-gathering capability of their dorsal tube-feet by greatly broadening them. The result was the formation of the 'petals' so typical of most irregulars. Specialized tube-feet were also produced around the mouth. They were larger, more numerous, and were used to collect sediment that was then passed to the mouth.

EVOLUTION OF THE CLYPEASTEROID ECHINOID

The first clypeasteroid echinoid, *Togocyamus* (Pl. 1, figs. 1-5), appears in Paleocene strata. By the middle Eocene the highly specialized sand dollar had evolved. Until now it was believed that these developments required a long time from the Cretaceous through the Eocene. New evidence indicates that the change was much more rapid. In fact the change from a cassiduloid ancestor to a clypeasteroid probably occurred within the Paleocene; and the change from a primitive clypeasteroid to a sand dollar occurred during the early Eocene.

The earlier 'Cretaceous' origin of the clypeasteroids was based on the supposed occurrences of three species of clypeasteroids in the Late Cretaceous. These occurrences are probably erroneous. One of the three species is too poorly preserved to be identified, and the stratigraphic data with the other two are inadequate. Extensive collecting has been done in the Late Cretaceous beds where these two species supposedly were found and neither Meijer (1965) nor Ernst (1972) have found any clypeasteroids. Ernst, in the course of his study, examined over 15000 echinoids from the Late Cretaceous.

The chronologically later origin of the clypeasteroids is supported by their absence from the Paleocene of the Western Hemisphere. An exhaustive search by Kier through washings of the Paleocene Vincentown, Aquia, and Clayton Formations (from which eighteen echinoid species are known) revealed no fragments that could be identified as clypeasteroid, although echinoid fragments are very common. It is noteworthy that the small fibularids, like those found in the Paleocene of Africa, were absent but normally would be expected in this material. They usually live buried in this type of sediment and are small enough to have their tests preserved intact in these sands.

The earliest confirmed clypeasteroid, *Togocyamus*, occurs in the Paleocene of West Africa. It differs so markedly from all previous echinoids that there is disagreement as to its origin. Some workers consider the clypeasteroids to be derived from a holectypoid, but Phelan (1977, p. 419) makes a strong case for their derivation from a juvenile stage of a cassiduloid. Its evolution must have been extremely rapid and probably occurred within the Paleocene. The Late Cretaceous echinoid record is not only extensive but very well studied (Ernst 1972) and no intermediates have been found there. Current information indicates that the subsequent diversification and radiation of the clypeasteroids from a fibularid to a sand dollar occurred very abruptly (text-fig. 2) in the early part of the middle Eocene. Only two species, both fibularids, are known in the Paleocene: *Togocyamus*


EXPLANATION OF PLATE 2

Figs. 1-3. *Sismondia logotheti* Fraas. Early Eocene, from Siout (=Assiout), Egypt.   1, 2, 3, top, bottom, side views of topotype B22908, Muséum National d'Histoire Naturelle, Paris, × 5.

Figs. 4-6. *Periarchus lyelli* (Conrad). Middle Eocene, Castle Hayne Formation, from North Carolina Lime Company pit, adjacent to Tuckahoe Church, 3·8 miles (6·1 km) west of Comfort, Jones County, North Carolina.   4, 5, 6, side, top, bottom views of USNM 312506, × 1.
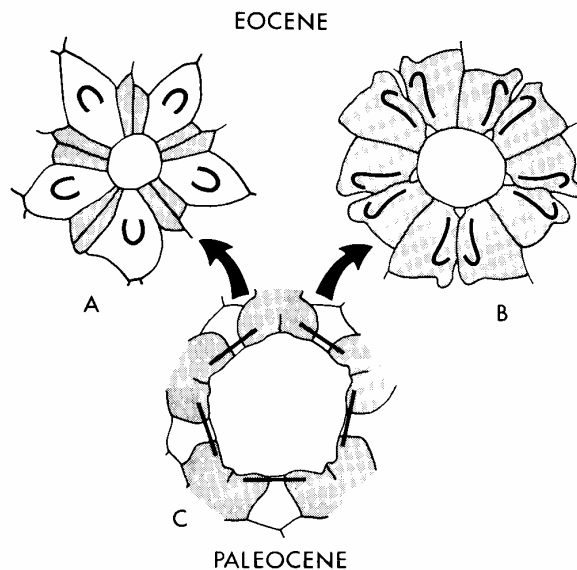
PLATE 2
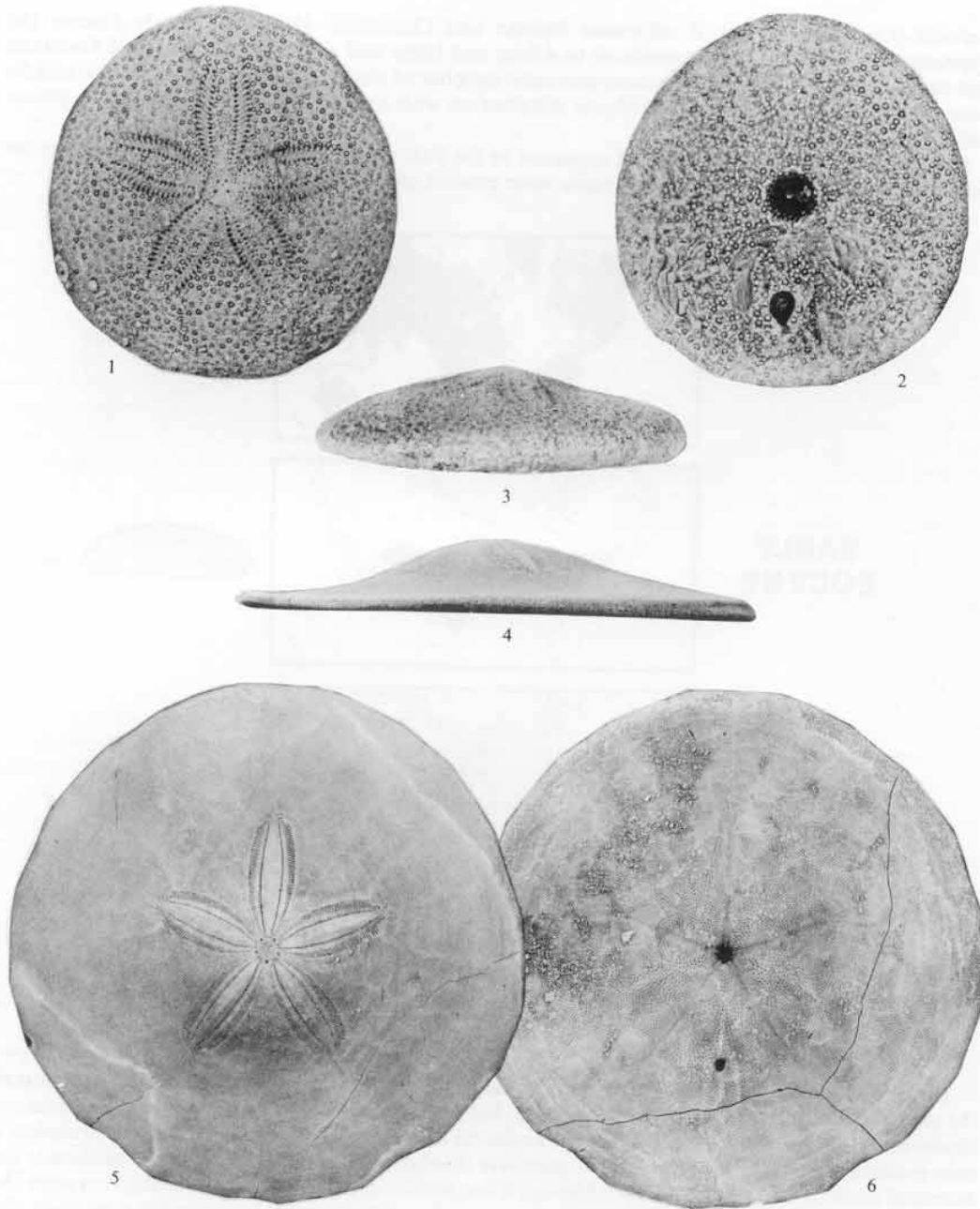
KIER, *Sismondia, Periarchus*

seefriedi (Oppenheim) and *T. alloiteaui* Roman and Gorodiski. During the early Eocene the clypeasteroids (text-fig. 2) were confined to Africa and India and consist of six species of fibularids and two species of *Sismondia*, the most primitive member of the laganids. By the end of the middle Eocene, the clypeasteroids had worldwide distribution with over 62 species representing 20 genera and 4 families.

In summary, the first clypeasteroid appeared in the Paleocene, and by the middle Eocene its far more complex and specialized descendants were present all around the world.
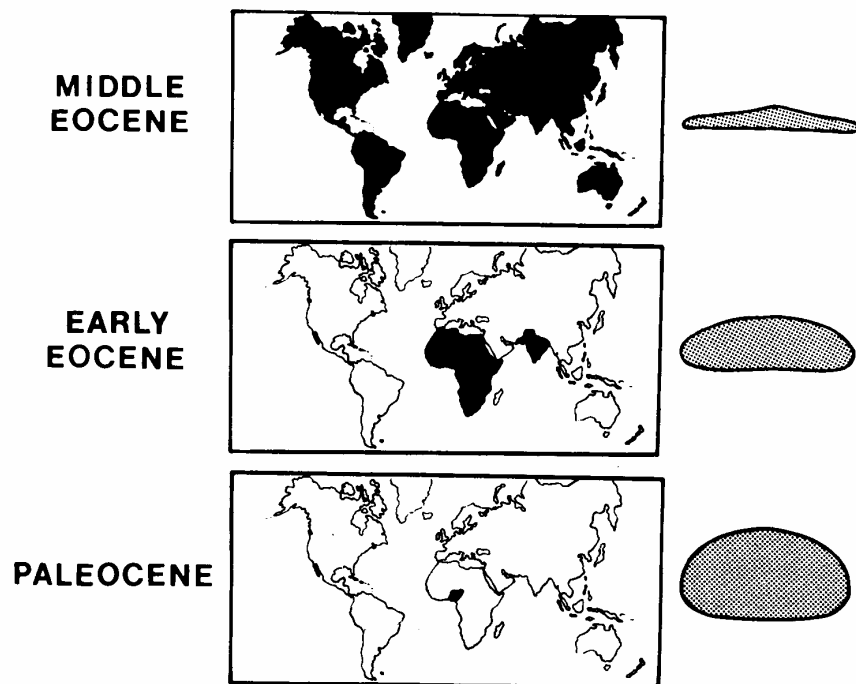
TEXT-FIG. 2. Evolution and radiation of the clypeasteroid echinoid. The Paleocene clypeasteroids are confined to West Africa and are a small, high species with incipient petals. In the early Eocene they are more flattened, have more-developed petals, and occur in Africa and India. By the middle Eocene they are fully developed sand dollars and are present all around the world.

The Cretaceous origin of the clypeasteroids was suggested by previous workers not only because of the supposed occurrence of Cretaceous species, but also because it was believed that the Palaeocene fibularids were not primitive enough to be ancestral to all later clypeasteroids. New information is now available on *Togocyamus*. It is more primitive than previously thought and could be close to the ancestral stock of all clypeasteroids. Although it has been assumed that its lantern supports were like those found in later fibularids with each support composed of a single interambulacral plate, the supports in *T. seefriedi* (Oppenheim) are both interambulacral and ambulacral in origin. Each support (text-fig. 3c) is formed by the extension of the primordinal interambulacral plate and the adjacent half-ambulacral plates. This discovery is important for it has been suggested (Philip 1965, p. 58; Kier 1970, p. 105) that the clypeasteroids could be divided into two orders on the basis of the character of the lantern supports. The suborder Clypeasterina includes all those clypeasteroids

EOCENE

PALEOCENE

TEXT-FIG. 3. The lantern supports in the clypeasteroids. C, the oldest clypeasteroid, the Paleocene *Togocyamus seefriedi* (Oppenheim) has lantern supports (indicated by a solid line) composed of ambulacral (shaded) and interambulacral plates; A, B, Eocene clypeasteroids have lantern supports composed of interambulacral plates as in the suborder Scutellina (A) or ambulacral plates as in Clypeasterina (B).

having ambulacral lantern supports (text-fig. 3B); in the suborder Scutellina the supports are interambulacral (text-fig. 3A). The presence of supports, both interambulacral and ambulacral in origin, in the oldest known and most primitive clypeasteroid adds weight to the supposition that *Togocyamus* is close to the ancestral stock of both suborders. By simply reducing the size of the ambulacral extensions and increasing the size of the interambulacral ones, supports could be produced that are typical of later species of the fibularids and the rest of the Scutellina. Conversely, the reduction in the size of the interambulacral and increase in the ambulacral extensions would produce the typical Clypeasterina supports that first appear in the late Eocene.

A second discovery in *Togocyamus* is that its accessory pores are few in number and are restricted to the border of the ambulacra (Pl. 1, fig. 1). As pointed out by Durham (1966, p. U451), accessory pores are an exclusive feature of the clypeasteroids, occurring in all species. The fact that they are less well developed in this species than in any other is further evidence of the primitiveness of this form.

In the light of the primitive features of *Togocyamus*, we can now postulate the evolutionary history of the earliest clypeasteroids:

1. The Paleocene *Togocyamus* (Pl. 1, figs. 3-5) has a small, high test with its periproct in a primitive dorsal position, slightly developed petals with simple nonconjugate pores, a very erect lantern with supports of interambulacral and ambulacral origin. Its few accessory pores are confined to the borders of the ambulacra. It has no food grooves and has a large peristome.

2. By the early Eocene, *Sismondia* (Pl. 2, figs. 1-3) has a larger, more flattened test, a lower lantern, interambulacral lantern supports, and a ventral periproct. The petals are better developed with conjugate pores; the accessory pores are far more numerous.

3. The middle Eocene *Protoscutella* and *Periarchus* (Pl. 2, figs. 4–6) are typical sand dollars having a large, very flattened test, food grooves, very wide and low lantern, and a very small peristome. Accessory pores are spread all over the ambulacra, and the test is strongly reinforced by calcareous supports that are pierced by many canals for the water vascular system serving these pores. The adoral plate arrangement is now distinctive; there are far fewer and larger plates than in earlier clypeasteroids. As pointed out by Durham (1966, p. U450), these changes in the adoral plates result from the flattening of the test. In flattened species the number of plates on the adoral surface is determined at an early ontogenetic stage and thereafter growth is only by enlargement of the plates.

The morphological changes that produced the sand dollar are specializations that enabled the echinoid to live more efficiently in sand (Seilacher 1979). The flattened test made it easier for the echinoid to burrow. The accessory tube-feet were used to pass sand over the top of the test and to convey food to the food grooves. The better-developed petals increased the respiratory capability of the petaloid tube-feet by increasing their area. The internal supports strengthened the test, enabling the sand dollar to live in environments of higher energy. The change from the erect lantern and large peristome in the primitive fibularid to the low lantern with horizontal teeth and small peristome in the sand dollar reflects a change in eating habits. According to Märkel (1974, 1978; Märkel, Gorny, and Abraham 1977) and Nichols (1959), the fibularid uses its lantern to scrape organic material from sand grains. This feeding method puts little stress on the teeth. The sand dollar, however, uses the teeth for grinding and chewing. The great stress can be withstood because the teeth are horizontal, and the stress is transmitted to the long axis of the teeth. The larger peristome in the fibularid permits the teeth to extend further out of the test to grasp food; in the sand dollar the sand is passed to the teeth within the test.

If it is true, as suggested herein, that the clypeasteroids originated in the Paleocene then all these changes necessary to derive a sand dollar from a cassiduloid ancestor occurred within 20 million years. Certainly there can be little question that the evolution from a fibularid to a typical sand dollar occurred between the beginning of the early Eocene and the latter part of the middle Eocene, a period of less than 10 million years.

CONCLUSIONS

The sudden appearance of the first irregular and the first clypeasteroid echinoids and their rapid diversification indicate a rate of evolution much faster than previously supposed. The mechanisms producing these great changes are uncertain, but the evolutionary steps must have been large. If each speciation event produced only small morphological change, than a multitude of transitional species would have resulted. The fossil record of the irregular echinoids is excellent (Kier 1977a). Even if this rapid evolution occurred in peripherally isolated populations, somewhere in the world we should have found more of these transitional species. I believe the absence of a large number of transitional species is explained not because they have not been preserved as fossils, but because they never existed. This conclusion supports Stanley's (1979, p. 212) statement that 'rates of evolution are highest early in adaptive radiation, when degree of divergence per speciation event is high . . .'.

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PORTER M. KIER

Department of Paleobiology
Smithsonian Institution
Washington D.C. 20560
U.S.A.