Δελτίο Ελληνικής Γεωλογικής Εταιρίας τομ. XXX/2, 513-520, 1994
Πρακτικά 7ου Επιστημονικού Συνεδρίου, Θεσσαλονίκη, Μάιος 1994

Bulletin of the Geological Society of Greece vol. XXX/2, 513-520, 1994
Proceedings of the 7th Congress, Thessaloniki, May 1994

THE IMPORTANCE OF MORPHOFUNCTIONAL ANALYSIS FOR THE IRREGULAR ECHINOIDS ' MODE OF LIFE RECONSTRUCTION

J. Mitrovic-Petrovic* and A. Maran**

ABSTRACT

This paper points out the importance of some morphological characteristics for the reconstruction of the living conditions and the mode of life on the example of several Mesozoic Irregular echinoids. For this purpose we examined Jurassic genus *Clypeus* as well as Cretaceous genera *Micraster* and *Stigmatopygus*.

INTRODUCTION

For the reconstruction of the living conditions and the mode of life of certain groups of marine fossilous organisms different methods are used: actualistic, empiric, biogeochemic, morphofunctional analysis, ecological adaptation and others.

Besides these methods, also the associated fauna and characteristics of sediments where fossls are found provide precious data.

MATERIAL AND METHODS

In our opinion, however, method of morphofunctional analysis is the most suitable and the most reliable, especially in the cases when organisms have no relatives in today's seas.

The purpose of this paper is to show on the example of several Mesozoic genera of Irregular echinoids the importance of some morphological characteristics for the reconstruction of the living conditions and the mode of life.

In this light the Jurassic genus *Clypeus* and Cretaceous genera *Micraster* as well as *Stigmatopygus* are examined.

GENUS CLYPEUS LESKE, 1778

Clypeus is one of the oldest representatives of Irregularia. It first appeared and thrived in the Middle Jurassic period and just a few species lived on into the Upper Jurassic. For this reason it can be taken for a Middle Jurassic genus.

Our research is based on the material collected in East Serbia. Among several dozens of samples five species were identified: *Clypeus boblayei* Michelin, *Cl. mulleri* Wright, *Cl. davosianus* Cotteau, *Cl. sinantus* Leske and *Cl. ploti* (Klein) (J. Mitrovic-Petrovic, 1972, 1988). The genus is known in many European and African countries.

Shape. Its large size, circular or subcircular margin, flat oral side and

* Faculty of Mining and Geology, Institute of Regional Geology and Paleontology, Kamenicka 6, BEOGRAD, Yugoslavia.
** Museum of Natural History, Njegoseva 51, BEOGRAD, Yugoslavia.

very low profile provided the genus with great stability (Pl. I, fig. 1, 1a). It can be supposed that the genus resisted the powerful water movements very successfully. Because of these characteristics, it was very difficult to extricate it from the bottom and overturn. Some other echinoid representatives possess similar shape and very low profile (discoidal forms) (e. g. genera *Scutella* and *Amphiope*) for which it is positively known, that they live in the littoral zone. Also they are exposed to the influence of powerful water movements. Also some other groups of Invertebrata (e.g. recent gastropod genus *Patella*) possess the circular margin and the low profile as adaptable features to powerful action of waves.

On the other hand, this shape and the low profile may be adaptable features for burrowing in the loose soil.

Round margin leads one to suppose that *Clypeus*, like Regular echinoids moved in more than one direction.

Petals. The presence of elongated transversal crack-like pores in petals on the aboral side, indicates that there existed specialized tubefeet for gas exchange (respiratory function). Such tubefeet helped to maintain high metabolism which is a characteristic of warm water species. It is well known that inhabitants of cold water had slower metabolism (Pl. I, fig. 1).

Peristome and anus. Around the peristome there were more or less developed phyllodes. The function of phyllodes, together with an increased number of tubefeet, was to efficiently collect food from the substrate and to transport it toward the mouth. This is a clear indication that *Clypeus* was a depositovor. A rather large anus points to this mode of feeding also, because depositovores, together with the organic substance they take, bring a large quantity of sediments into their organisms. Later they excrete these sediments through the anus. Large anus indicates that the excrement was abundant and that the pieces of feces were large. This means that *Clypeus* was a nonselective depositovor and that like recent Cassiduloids, it took a great quantity of sediments. Deep posterior groove that extended on the aboral side from the apex to posterior margin, testifies to the great quantity of excrement. Anus was always situated on the bottom of this groove, at a smaller or larger distance from the apex (Pl. I, fig. 1). The functional feature of the groove seems to have lied in somewhat longer and denser spines (as evidenced by larger and denser tubercles) along its edges. One line of spines inclined towards the other thus forming a reticulate structure. This structure served to isolate the aboral respiratory area from the matter (quite abundant excrement). Spines forming an arch over the back groove also indicate that *Clypeus* lived burrowed in the sediments. To such echinoids the problem of disposing of excreta is very important, as it can not be carried away by currents. A similar groove is noted also in some other Irregular echinoids (*Galeropygus*, *Echinobrissus* etc.).

Tuberculation. There is a great difference between tuberculation on the aboral and oral side in size, as well as in density. This indicates that spines on the aboral side had different function in comparison with those on the oral side. Aboral ones are of a small, uniform size and uniform distribution. This means that aboral spines were also of uniform size and density. Such distribution and density represent adaptation to infaunistical mode of life. Thin, densely spaced spines prevented sediments from penetrating to the aboral side and thus enabled normal respiration. Larger in size, stronger and irregularly distributed tubercles on the oral side indicate that the spines on the oral side were larger. Their function was to enable burrowing into the sediment.

Morphofunctional analysis of the genus *Clypeus* indicates the conditions under which this ancient extinct genus lived.

1. *Clypeus* lived in shallow waters and on the loose soil into which, most likely, it burrowed itself (it belonged to endofauna). This mode of life is indicated by the following:

- Fine, densely set uniform spines on the aboral surface, which prevented sediment penetration to test surface, and thus protected normal respiration.
- Sparser and stronger spines on the oral surface which also served for burrowing.
- Presence of the ambulacral groove where the anus was situated.

2. Water temperature was very high. Elongated transversal crack-like pores in the petaloids on the abcral surface suggest the presence of specialized tubefeet for gas exchange. This kind of tubefeet indicates high metabolism, which proves that water was warm.

3. The relation between *Clypeus* and water movements is difficult to establish. Its large, round skeleton with a flat solid base and a very low profile, was successfull in resisting strong water movements. On the other hand, contemporary relatives (*Cassidulus*, *Apatopygus*) live burried in sheltered places, where water currents are very weak. As *Clypeus* most likely used to burry itself, it was probably not exposed to strong water movements.

4. By the mode of feeding it was a depositovor. This is indicated by the presence of phyllodes as well as by shapes, sizes and positions of the peristome and anus.

5. The round margin leads us to suppose that *Clypeus* like Regular echinoids moved in all directions.

GENUS MICRASTER AGASSIZ, 1836

Micraster is an exclusively Upper Cretaceous genus. It had a significant geographical distribution. It is known in many European countries (both northern and southern). Besides in Europe, it is known in the USA and Madagaskar.

Morphofunctional analysis of several species of this genus from the Upper Cretaceous sediments of Yugoslavia is made.

Examination and reconstruction of the mode of life of the genus *Micraster* was done by a considerable number of British authors: K. A. Kermack (1954), D. Nichols (1959 a, b), R. B. Stokes (1975) and some others. S. Maczynska (1968) payed considerable attention to this problem. Short reviews of paleoecological characteristics of *Micraster*, can be found in papers by the following authors: E. Szoreny (1955), J. Mitrovic-Petrovic (1966), J. Mitrovic-Perovic and T. Ljubotenski (1990) .

Profile. Morphological characteristics of some species of genus *Micraster* are considerably varied. The profile which may be more or less conical or flattened is the most important (Pl. I, fig. 2b, 3). In both cases profile heights vary considerably, but conical forms are generally higher than the flattened. According to most authors: K. A. Kermack (1954), D. Nichols (1959 a, b), S. Maczynska (1968), species with flattened skeletons used to live burried in soil (belonged to endofauna) while forms with conical skeleton moved slowly on the surface of the sediment (belonged to epifauna). Such opinion is based, among other things on the observation of mode the of life of recent Spatangoids.

Frontal ambulacrum. Other important characteristics are width and depth of the groove where the frontal ambulacrum is set. This narrow and deep groove is an indicator of burrowing. Functional significance of thes groove lies in the fact that spines on both groove sides inclined toward the either side of the narrow groove, forming some sort of a reticulate structure for isolation of alien material from the bottom, thus enabling their normal respiratory function. This groove is rather large at *M. cortestudinarium* (Goldfuss) and *M. rostratus* (Montell) from Santonian age and very narrow at *M. brogniarti* Hebert from Campanian age (Pl. I, fig. 2).

Fasciole. The presence of subanal fasciole is also characteristic of burrowing forms. Subanal fascioles are clearly observable in *M. coranguinum* (Agassiz), *M. coranguinum rostratus* (Montell), *M. glyphus* Schluter and *M. brogniarti* Hebert. Functional significance of subanal fasciole lies in the fact that clavules concentrated under anus could rapidly remove the material through the anus. That is very important for burrowing forms, as they were more or less immobile. They also had an important role in forming a subanal tunel.

Peristome. Distance between the peristome and the anterior margin can serve as a criterion for burrowing. Burrowing forms have peristome very close to the anterior margin. Functional importance of this peristome position lies in the fact that food was partly transported through the groove of frontal ambulacrum on the oral side. The shorter the groove, the faster and more effective the transport of food. In *Micraster cortestudinarium* (Goldfuss), *M. coranguinum* Agassiz and *M. normaniae* Bucaille, peristome is a little farther from the anterior margin. In *M. brogniarti* Hebert, *M. nobilis* (Stoliczka) and *M. glyphus* Schluter, peristome is situated close to the anterior margin (Pl. I, fig. 2a).

D. Nichols (1959 b) observed that the depth of *Micraster* burrowing had changed through geological time. According to this author, older forms were burrowed shallower in relation to the younger. His conclusion was based on the fact that in younger forms the characteristics of the burrowing species are more pronounced. This opinion is confirmed by S. Maczynska (1968) on the basis of the material from Poland. We share this opinion on the basis of our material. *Micraster cortestudnarium* (Goldfuss) e.g. from the Coniacian-Santonian age is the oldest species in our collection. It has a relatively large and shallow groove while peristome is set a little farther from the anterior margin. In *M. glyphus* Schluter and *M. brogniarti* Hebert from Campanian age, the anterior groove is deeper and peristome is very close to the anterior margin. This fact shows that forms from the youngest horizons possess a more succesfull type of adaptability to burrowing in relation to older ones.

R. A. Stokes (1975) points out that the depth of burrowing depends also on the nature of the sedment. Living on a coarse-grained sediment it is very easy for Spatangoids to maintain the respiratory canal and to throw out utilized water into the surrounding sediments. This process is more difficult in the case when animal is burried in the fine homogenous mud. All of the examined examples originate from limestone, sandy and marly limestone which belonged to the fine and homogenous sediment before diagenesis.

Tuberculation. Very fine tuberculation is also a characteristic of burrowing forms. Tuberculation is not well preserved in examined examples, but it is known that *M. cortestudinarium* (Goldfuss), *M. coranguinum* Agassiz and all other species from the examined association had a fine tuberculation.

On the basis of analyzed morphological features, living conditions and the mode of life of Micraster can be characterized as following:

1. Genus lived in the water of small depth (probably sublittoral) on the loose bottom. Species with flattened aboral side were probably burrowed in the sediment. Forms with conical skeletons moved slowly on the surface of the

sediment.

2. On the basis of morphofunctional characteristics it was not possible to conclude about the water temperature, because petals of forms from the north and south regions are very similar.

It was Zoke (1951) who, according to Smith (1984), was the first to notice that the development of tubefeet, specialized for gas exchange, could be a very reliable indicator of water temperature. According to him, all Cretaceous species of the genus *Hemiaster* (Spatangoids) can be classified into two groups: the representatives from the Circum-Mediterranean region, which have long petals with numerous ambulacral pores, and those from Northern Europe which have short petals, especially the posterior pair, and a comparatively small number of pores. Since metabolism in echinoids generally increases with a rise in temperature, echinoids living in warmer water require larger volumes of oxygen than those living in colder waters. This explains the fact why the *Hemiaster* species that lived near the Cretaceous Paleoequator had long petals with numerous tubefeet, while those in regions with more temperate climates had short petals with a comparatively small number of tubefeet.

For *Micraster* found in Yugoslavia it be indirectly concluded that they lived in warm water. High temperature of water during the Upper Cretaceous is confirmed by numerous reefs (in general constructed by rudists), which points to the tropical-subtropical character of water.

3. Micrasters were not exposed to strong water movements, whether they burrowed or belongd to epifauna.

4. By the mode of feeding they were depositovores. This is indicated by the presence of phyllodes as well as by the length of frontal ambulacrum on the oral side.

GENUS STIGMATOPYGUS D' ORBIGNY, 1856

The genus *Stigmatopygus* d'Orbigny is known from Upper Cretaceous sediments of Europe, India and Africa. Morphofunctional analysis is made on numerous specimens of species *Stigmatopygus elatus* (Forbes) d'Orbigny, originating from Lower Maastrichtian sediments from south India, Tamilnadu State (J. Mitrovic-Petrovic and K. Ramamoorthy 1993).

Shape. Although *Stigmatopygus* varies in shape, its ambitus outline is invariably oval. According to Kier (1974), echinoids with elongated tests were able to move more easily through the sediments than those whose test was circular in marginal outline (Pl. I, fig. 4, 4a).

Depression with the anus on the aboral side. A very important morphological and, above all, functional feature of the genus *Stigmatopygus* is an aborally situated bottle-shaped depression with the anus at its end (Pl. I, fig. 4c). It can safely be assumed, that along both edges of the groove long, closely spaced spines were arranged. One line of spines inclined towards the other, thus forming a reticulate structure. This structure protected the respiratory system on the aboral side from excrements passed from anus. We have already described the similar phenomenon in the genus *Clypeus* and pointed out the problem of the excrement disposing in burrowing echinoids.

Petals. Comparatively long ambulacra and elongated transversal crack-like pores in petals (i. e. the outer rows of poriferous zones) on the aboral side indicate that there existed specialized tubefeet for gas exchange. Such tubefeet helped to maintain high metabolism which is a characteristic of warm water species (Pl. I, fig. 4).

Phyllodes. The function of well developed phyllodes around the peristome, together with an increased numer of tubefeet within phyllodes, was to collect food from the substrate efficiently. This is a clear indication that *Stigmatopygus* was a depositovor. According to Kier (1974), Jurassic Cassiduloids were the first to develop phyllodes. During the Mesozic the number of tubefeet in phyllodes decreased. Reduction in their number was compensated by the developing of broad and more efficient tubefeet (Pl. I, fig. 4a).

Tuberculation. Fine, densely spaced tubercles of uniform size found on the aboral side indicate a former presence of thin, densely spaced spines preventing sediments from penetrating to the aboral side, and thus enabling normal respiration. Larger in size and stronger oral tubercles indicate that the spines on the oral side were larger, their function being to enable burrowing into coarse sea-floor sediment (Pl. I, fig. 4, 4a).

The morphofunctional analysis allows certain conclusions concerning the mode of life of *Stigmatopygus* and its favourite paleoenvironment.

1. *Stigmatopygus* was a shallow water genus that burrowed into coarse-grained sediments. This conclusion is based on the shape of skeleton, tuberculation on the oral side and depression with the anus on the aboral side.

2. For subsistence it required warm water. It is confirmed primarily by the appearance of petals (long petals with elongated transversal crack-like pores).

3.Considering its feeding habits, it was a depositovor (very well developed phyllodes around the peristome).

CONCLUSIONS

The morphofunctional analysis of Irregular echinoids has shown that many of morphological characteristics may be very usefull indicators of the living conditions and mode of life. Among them, we can especially underline the shape and height of the skeleton, feature of petals, shape and position of peristome and anus, presence of phyllodes, presence of fascioles and tuberculation.

In our opinion, this method is most suitable and most reliable, especially in the cases when organisms have no relatives in today's seas. Of course, it would be best to use this method in combination with others (if possible).

Characteristics of the sediments, as well as the associated fauna, are also of great importance.

Morphological features are particularly reliable indicators of the depth of the sea floor, temperature of the water, degree of the water movements, but also of the mode of movement or burrowing of the animal, its mode of feeding etc.

The examination of genera indicates the following:

Clypeus livedi in shallow waters and on the loose soil into which most likely, it burrowed. The water temperature was very high of a tropical - subtropical character. Its morphological features indicate that it was successful in resisting strong water movements, still its contemporary relatives live buried in sheltered places where the currents are very weak. By the mode of feeding it was depositovor. Probably, like Regular echinoids, they were able

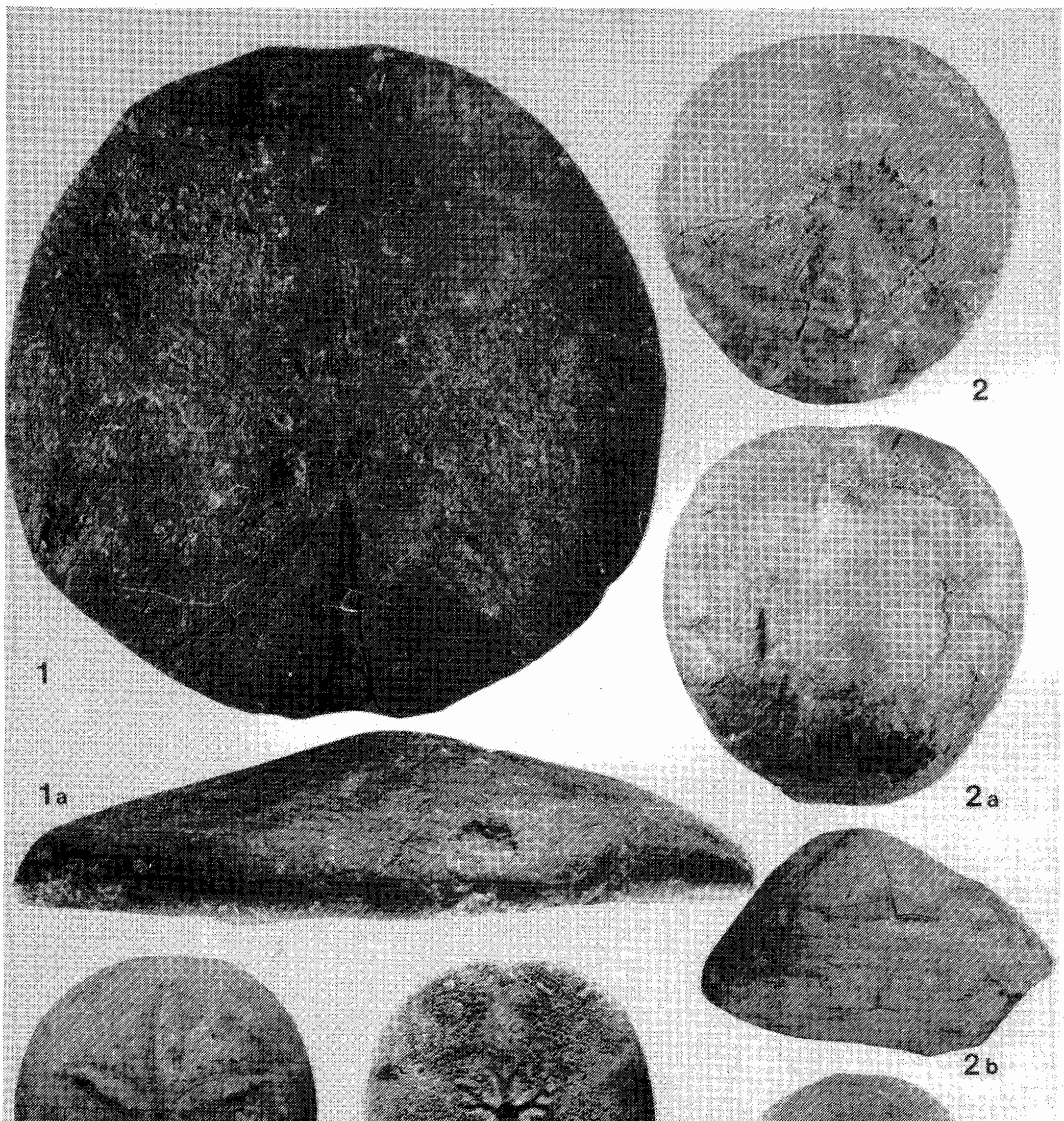
PLATE I

Fig. 1: *Clypeus boblayei* Mich.: aboral side (x1) a): lateral view (x1)

Fig. 2: - *Micraster cortestudinarium* Gold.: aboral side (x1) a) : oral side (x1) b): lateral view (x1)

Fig. 3: - *Micraster coranguinum* Ag.: lateral view (x1) a) : oral side (x1)

Fig. 4: - *Stigmatopygus elatus* (Forb.) d'Orb.: aboral (x1) a): oral side (x1), b): lateral view (x1), c): posterior view (x1)


1
1a
2
2a
2b
3
3a
4
4a
4b
4c

the move in all directions.

Micraster lived in the shallow water, of small depth (sublittoral) on the loose bottom. Species with flattened aboral sides were probably burrowed in the sediment. Forms with conical skeletons moved slowly on the surface of the sediment. They weren't exposed to strong water movements. On basis of their morphological characteristics it wasn't possible to conclude about the water temperature.

Stigmatopygus was a shallow water genus that burrowed into coarse - grained sediments. For subsistence it required warm water. Considering feeding habits, it was a depositovor.

REFERENCES

KERMACK, L. (1954). A biometrical study of Micraster coranguinum and M. (Isomicraster) senoniensis. - *Philos. Trans. Royal Soc. London set B 649*, Vol. 237, 375-428.

KIER, P. (1974). Evolutionary Trends and Theire Functional significance in the Post-paleozoic Echinoids. *Jour. Paleont. 48, supp. to No 3. The Paleont. Soc. Mem.* 5, 1-95. Washington.

MACZYNSKA, S. (1968). Echinoid of the genus Micraster L. Agassiz from the upper Cretaceous of the Cracow-Michow area. *Prace Mus. Ziemi 12, Prace Paleozoologiczne*, 87-168, Warszawa

MITROVIC - PETROVIC, J. (1966). Les echinides du cretace et du miocene de la Serbie. *Ann. Geol. Penis. Balk.* 87-163, Beograd.

MITROVIC - PETROVIC, J. (1972). Importance du genre d'echinide Clypeus Leske pour le discernement et la division du jurassique moyen de la Serbie de l'Est. *Comp. rendus Soc. Serbe Geol. pour les annes 1968, 1969 et 1970*, 261-265, Beograd.

MITROVIC - PETROVIC, J. (1988). Morphofunctional analysis of the echinoid genus Clypeus Klein. *Ann. Geol. Penis. Balk.* 287-298, Beograd.

MITROVIC - PETROVIC, J. and LJUBOTENSKI, T. (1990). Biostratigraphical and Paleoecological importance of Spatangoida (Echinoidea) from Kuru Dere locality near £tip. *XII Congr. Geol. Yugosl.* Tom I, 380-390, Ohrid.

MITROVIC - PETROVIC, J. and RAMMAMORTHY, K. (1993). Functional morphology of Stigmatopygus elatus (Echinoidea; Cassiduloida) from the lower Maestrichtian of South India. *Ann. Geol. Penis. Balk. 5/1,* 123-138, Beograd.

NICHOLS, D. (1959 a). Changes in the Chalk Heart Urchin Micraster interpreted in relation to living forms. *Philos. Trans. Royal Soc. London.* Ser. B 693, Vol. 242, 347-437, London.

NICHOLS, D. (1959 b). Mode of life and Taxonomy in Irregular Sea-urchins. *Spec. publ. System. Assoc. Publ.* 3, 61-80, London.

SMITH, A. (1984). Echinoid Paleobiology. 1-193, London.

STOKES, R. B. (1975). Royames et provinces faunique du Cretace etablis sur la base d'une etude systematique du genre Micraster. *Mem. du Mus. Nation. d' Hist. Natur.* Ser. nouv. XXXI, 1-94, Paris.

SZORENY, E. (1955). Bakony kreta Echinodeak. *Geol. Hungar. Ser. Paleont.* 26, 1-286, Budapest.