Geol. Paläont. Mitt. Innsbruck	ISSN 0378-6870	Bd. 13	1	S. 1-47	Ibk., Dez. 1983

THE POLYPHYLETIC ORIGIN AND THE CLASSIFICATION OF THE MESOZOIC SATURNALIDS (RADIOLARIA)

by H. Kozur and H. Mostler*)

with 5 textfigs., 1 table and 7 plates

Summary

The Mesozoic saturnalids are a polyphyletic group and belong partly to the Spumellaria EHRENBERG, 1875, partly to the Entactinaria KOZUR & MOSTLER, 1982. The spumellarian saturnalids derived from the Oertlispongidae KOZUR & MOSTLER, 1980. All hitherto known genera of Mesozoic saturnalids (with exception of the Saturnalidae DEFLANDRE, 1953, which begin in the Upper Cretaceous, but are mostly post-Mesozoic) are revised and a suprageneric classification is proposed.

2 new families, 3 new subfamilies, 6 new genera, and 12 new species are established.

Zusammenfassung

Die mesozoischen Radiolarien mit saturnalidem Ring sind eine polyphyletische Gruppe und gehören teils zu den Spumellaria EHRENBERG, 1875, teils zu den Entactinaria KOZUR & MOSTLER, 1982. Die Spumellaria unter den Radiolarien mit saturnalidem Ring stammen von den Oertlispongidae KOZUR & MOSTLER, 1980. Alle bisher bekannten mesozoischen Radiolariengattungen mit saturnalidem Ring (mit Ausnahme der Saturnalidae DEFLANDRE, 1953, die erst in der Oberkreide spärlich einsetzen, aber hauptsächlich post-mesozoisch sind) werden revidiert und eine supragenerische Klassifikation dieser Gruppe wird vorgestellt.

2 neue Familien, 3 neue Unterfamilien, 6 neue Gattungen und 12 neue Arten werden aufgestellt.

*) authors' addresses: Dr. sc. Heinz Kozur, Hungarian Geological Institute, Népstadion út 14, H-1143 Budapest, Hungary; Univ.-Prof. Dr. Helfried Mostler, Institut für Geologie und Paläontologie der Universität Innsbruck, Universitätsstraße 4, A-6020 Innsbruck, Austria.

Introduction

From the Upper Ladinian (Longobardian) until the top of the Mesozoic the saturnalids [1] are a remarkable group of many radiolarian faunas. The largest diversity of the saturnalids can be observed in the Upper Triassic, where several short-living guide forms occur. This Upper Triassic maximum has its definitive end in the topmost Pliensbachian or lowermost Toarcian. After this time the Acanthocircinae PESSAGNO, 1977, and the Hexasaturnalinae n.subfam. flourished whereas the diversity and frequency of the Heliosaturnalinae KOZUR & MOSTLER, 1972 (highly diverse in the Upper Triassic, moderately diverse in the Liassic) strongly decreased. Entactinarian saturnalids, highly diverse in the Triassic, were until now not discovered in post-Triassic sediments.

The phylomorphogenetic relationships of the Mesozoic saturnalids can be only understood, if we regard their oldest - Triassic - representatives. Before 1972 Triassic saturnalids were quite unknown. KOZUR & MOSTLER, 1972, described for the first time a highly diverse saturnalid fauna from the Upper Triassic of Austria. Such highly diverse and rich faunas were not reported in any later publication.

The following genera were distinguished among the Triassic saturnalids by KOZUR & MOSTLER, 1972:
Austrisaturnalis KOZUR & MOSTLER, 1972
Heliosaturnalis KOZUR & MOSTLER, 1972
Parasaturnalis (*Japonisaturnalis*) KOZUR & MOSTLER, 1972
Praeheliostaurus KOZUR & MOSTLER, 1972
Pseudoheliodiscus KOZUR & MOSTLER, 1972
Spongosaturnalis CAMPBELL & CLARK, 1944
Spongosaturnaloides KOZUR & MOSTLER, 1972

Two new suprageneric taxa were introduced for these genera: Heliosaturnalinae KOZUR & MOSTLER, 1972, and *Carinacyclia* KOZUR & MOSTLER, 1972, the family Veghicycliidae KOZUR & MOSTLER, 1972, was introduced. This family is related to the Heliosaturnalinae KOZUR & MOSTLER, 1972, but on the other hand it is the oldest family with latticed disk and the basis group of the Lithocycliacea EHRENBERG, 1854 emend. KOZUR & MOSTLER, 1972 (younger synonym: Coccodiscacea HAECKEL, 1862).

De WEVER, 1979 (in De WEVER et al., 1979) has adopted the generic classification of KOZUR & MOSTLER, 1972, but in the suprageneric classification he was even a little more conservative and he put all genera into the subfamily Saturnalinae DEFLANDRE, 1953, whereas two years later (adopting now the classification proposed by PESSAGNO, 1979) even sharply rejected the assignment of the Triassic genera to the family Saturnalidae DEFLANDRE, 1953, as "Haeckelian systematics".

TICHOMIROVA, 1975, introduced four species with flat simple spiny ring and 5-8 first order spines at the inner side of the ring the genus *Saturnosphaera* TICHOMIROVA, 1975.

---

[1] footnote: The term saturnalid is used here for all Radiolaria with saturnalid ring, independent of their phylogenetic relationship.

PESSAGNO, 1977, introduced the family Acanthocircidae PESSAGNO, 1977.

DONOFRIO & MOSTLER, 1978, presented a monographic revision of the saturnalids. For Mesozoic saturnalids with flat spined ring, two polar spines, with or without auxiliary spines on the inner margin of the ring they introduced the new genus *Palaeosaturnalis* DONOFRIO & MOSTLER, 1978. They regarded the Acanthocircidae PESSAGNO, 1977, as younger synonym of the Saturnalidae DEFLANDRE, 1953.

KOZUR, 1979, introduced the genus *Pessagnosaturnalis* KOZUR, 1979, for the same species as for *Palaeosaturnalis* DONOFRIO & MOSTLER, 1978, but the type species of *Palaeosaturnalis* DONOFRIO & MOSTLER, 1978, *Spongosaturnalis triassica* KOZUR & MOSTLER, 1972, has only two polar spines, whereas the type species of *Pessagnosaturnalis* KOZUR, 1979, *Spongosaturnalis heisseli* KOZUR & MOSTLER, 1972, has two polar spines and auxiliary spines. Therefore *Palaeosaturnalis* DONOFRIO & MOSTLER, 1978, and *Pessagnosaturnalis* KOZUR, 1979, are not synonymous each other, in spite of the fact that they were introduced for the same species group.

PESSAGNO in PESSAGNO, FINCH & ABOTT, 1979 (in the following shortly quoted as PESSAGNO, 1979), quite revised the saturnalids. He elevated the Parasaturnalinae KOZUR & MOSTLER, 1972, to a family and removed it so from the Saturnalidae DEFLANDRE, 1953. He placed his Acanthocircidae PESSAGNO, 1977, as younger synonym to the Parasaturnalidae KOZUR & MOSTLER, 1972 (and to the Parasaturnalinae KOZUR & MOSTLER, 1972), and the Heliosaturnalinae KOZUR & MOSTLER, 1972, and Veghicyclidae KOZUR & MOSTLER, 1972, as subfamilies into the Parasaturnalidae KOZUR & MOSTLER, 1972.

Only some small fragments of *Veghicyclia* sp. were present in PESSAGNO's collection. They only show the outermost part of the latticed disk of an undeterminable species. it is impossible to get any conclusions about the generic relations of such fragments. This perhaps explains, why PESSAGNO, 1979, placed the Veghicyclidae KOZUR & MOSTLER, 1979, in the Parasaturnalidae KOZUR & MOSTLER, 1972. The figured fragment looks like a ring fragment, but in reality it is a disk fragment (if it belongs to *Veghicyclia* KOZUR & MOSTLER, 1972). PESSAGNO, 1979, regarded the classification by KOZUR & MOSTLER, 1979, as highly artificially similar to the Haeckelian one.

Whereas De WEVER, 1979, still has used the classification proposed by KOZUR & MOSTLER, 1972, placing even in a little more conservative sense all Triassic saturnalids in the subfamily Saturnalinae DEFLANDRE, 1953, De WEVER, 1981, in turn adopted the classification by PESSAGNO, 1979, without changes. Even the remarks that KOZUR & MOSTLER's classification of the saturnalids (placing all Triassic saturnalids in the family Saturnalidae DEFLANDRE, 1953, using only two new subfamilies) is a "Haeckelian systematics" was adopted - in spite of the fact that De WEVER, 1979, himself, placed all Triassic saturnalids even in a single subfamily Saturnalinae DEFLANDRE, 1953. The only change in comparison with PESSAGNO's classification was to place *Parasaturnalis* KOZUR & MOSTLER, 1972 (type species: *Spongosaturnalis ? diplocyclis* YAO, 1972), in the synonymy of *Japonisaturnalis* KOZUR & MOSTLER, 1972. But according to the IRCN this is impossible, because the genus *Japonisaturnalis* KOZUR & MOSTLER, 1972, was originally established as a subgenus of *Parasaturnalis* KOZUR & MOSTLER, 1972.

As shown by KOZUR & MOSTLER, 1981, the emendation of the Parasaturnalinae KOZUR & MOSTLER, 1972, by PESSAGNO, 1979, adopted by De WEVER, 1981, has replaced one artificial group (the Saturnalidae DEFLANDRE, 1953 s.l.) by another even more artificial one. Whereas the Parasaturnalinae KOZUR & MOSTLER, 1972, are a closely related group, the emendation of this taxon has

created a highly artificial group with representatives of several quite distinct families and even of two suborders. We do not want to term such artificial subdivisions as "Haeckelian systematics" because of our respect to E. HAECKEL, who has contributed more to the knowledge of the Radiolaria than all we present day radiolarian specialists - and this without modern optic microscopes and without scanning electrone microscope. But we cannot agree that a classification that separates radiolarians with spongy and latticed shell in a high taxonomic level is a natural one and a classification that does not regard this feature as the most decisive one is an artificial classification. Only the real phylomorphogenetic relations recognized by transitional forms indicate natural and not only morphological relations.

All attempts of radiolarian classifications made in recent time are still far from a real natural classification. New data will bring revolutionary changes in the present day classification. This is demonstrated in the present paper for some Triassic saturnalids, whereas from the most post-Triassic saturnalids the central structure is still unknown so that still further drastica changes seem to be possible.

Like of other fossil groups, also the radiolarian classifications will remain artificially, if we regard some special morphological and structural characters to be important, other ones to be unimportant. By this method we will only replace one artificial classification by another one in dependence on the "most important character" that we will subjectively choose. In different phylomorphogenetic lines different characters can be most important. What is very important in one line may be quite unimportant in another line and vice versa. We know a lot of such examples in the ostracod classification where a lot of phylomorphogenetic lines are already well studied.

Sampling points for the figured specimens

Sample MD 1:

Recoaro (Vicentinian Alps), outcrop 4,5 km W of the village of Recoaro (Passo della Gabiola). Nodular limestone. Lower Ladinian.

Sample TT 13:

Tretto (Vicentinian Alps), outcrop NW of the village of San Ulderico (road to Palle). Nodular limestone. Lower Ladinian.

Sample X 12:

Köveskál (Balaton Highland), outcrop NE of the village near the cemetery. Top of the nodular limestone, bed with *Protrachyceras rubrum*, *Daonella lommeli* and a lot of conodonts (above all *Gondolella trammeri*). Lower Longobardian.

Sample Köveskál 6:

The same section as for sample X 12. Limestone with *Posidonia wengensis*, 15 cm above the highest thicker (70-80) tuffitic layer, about 4 m above the sample X 12. Longobardian.

Sample Y-6:

Göstling (Austria), section at the street from Göstling to Lunz. Upper Cordevolian.

Samples AS 7, AS 7/13, AS 8, AS 22:

Göstling (Austria). Upper Cordevolian. Exact sampling points see MOSTLER & SCHEURING, 1974.

Sample Zul'óv γ:

Manin Unit (Western Carpathians). Gondolella navicula subzone of the Metapolygnathus spatulatus A.Z. (Lower Norian). Pebble from Middle Cenomanian conglomerates.

Proposal for a new classification of the Mesozoic saturnalids

Our classification regards the outer morphology (outline, cross section, width and outer sculpture of the ring, shape of the shells and their attachment to the ring by polar and partly also auxiliary spines), the central structure (presence or absence of a spicular system) and the structure of the shells.

Subclass Radiolaria MÜLLER, 1858

Order Polycystina EHRENBERG, 1838

Suborder Entactinaria KOZUR & MOSTLER, 1982

Family Austrisaturnalidae n.fam.

Diagnosis: Ring always flat, moderate to very broad. Its outer margin is smooth or spined. There are always 4 two- or four-bladed in cross position that join in the centre in a spicular system. Auxiliary spines on the inner margin of the ring may be present.

Cortical shell in taxa with auxiliary spines large, spherical, directly connected with the inner margin of the ring, always with very large pores that may be partly closed by an inner fragile layer with small pores. In taxa without auxiliary spines the cortical shell is small, subquadratic, widely separated from the ring, with small pores, mostly covered by a layer of microgranular silica and with nodes on the vertices.

Spicular system with median bar that bears three spines on each end.

Occurrence: Longobardian and Cordevolian of Austria, Hungary and Italy, Longobardian of Japan; ? Tuvalian of Sicily.

Included genera: *Austrisaturnalis* KOZUR & MOSTLER, 1972
Praeheliostaurus KOZUR & MOSTLER, 1972
Hungarosaturnalis n.gen.

Remarks: The Spongosaturnaloididae n.fam. have a point centred spicular system with mostly very robust spicules. The ring is always narrow with outer spines, often two or three rings are present, the shell has an irregular shape, is flat-discoidal and consists of irregularly joined bars that branch off from the 3-5 polar spines that are never situated in cross position.

Subfamily Austrisaturnalinae n.subfam.

Diagnosis: Ring moderate to very broad, flat, always connected with the relatively small cortical shell by 4 at least two-bladed polar spines in cross position. Outer ring margin mostly smooth, sometimes with short, blunt triangular spines. Inner margin always without auxiliary spines.

Cortical shell subquadratic, latticed, but mostly covered by a layer of microgranular silica. Medullary shell, if present, latticed.

Spicular system with median bar and three spines at both of its ends.

Occurrence: Longobardian and Cordevolian of Hungary and Austria.

Included genus: *Austrisaturnalis* KOZUR & MOSTLER, 1972.

Remarks: The Hungarosaturnalinae n.subfam. have a spherical large cortical shell with very large pores, often partly closed by an inner fragile layer with small pores. Auxiliary spines are always present.

Genus *Austrisaturnalis* KOZUR & MOSTLER, 1972

Type species: *Austrisaturnalis quadriradiatus* KOZUR & MOSTLER, 1972

Austrisaturnalis spinosus n.sp.

(Pl. 3, fig. 2)

Derivatio nominis: According to the spines on the outer margin of the ring.

Holotype: The specimen on pl. 3, fig. 2; rep. no. T 5826.

Locus typicus: Göstling (Austria).

Stratum typicum: Sample AS 7/13, Upper Cordevolian (see MOSTLER & SCHEURING, 1974).

Diagnosis: Ring very broad, outer margin with 13-16 short triangular spines. 4 two-bladed polar spines in cross position join the rather small subquadratic cortical shell with the ring.

Cortical shell latticed, with small pores, that are partly or totally closed by a layer of microgranular silica. Small nodes at the vertices. Medullary shell not always visible, latticed.

Spicular system with median bar and spines at each end.

Measurements: Diameter of whole test: 157-169 µm. Diameter of cortical shell: 50-55 µm. Width of ring: 30-33 µm. Length of spines: 7-12 µm.

Occurrences: Upper Cordevolian of Göstling, Austria.

Remarks: *Austrisaturnalis quadriradiatus* KOZUR & MOSTLER, 1972, which has the same structure of the spicular system and of the shells, has no spines at the outer margin of the ring.

Subfamily Hungarosaturnalinae n.subfam.

Diagnosis: Ring flat, broad to very broad. Outer marign with 4 spines in cross position or with numerous spines. Inner margin always with 4 four-bladed polar spines in cross position and numerous auxiliary spines.

Cortical shell always large, spherical, more or less closely connected with the inner margin of the ring. The very large pores are often partly closed by an inner fragile layer with small pores. Medullary shell also rather large, spherical and with large pores. It is connected by numerous spines with the cortical shell.

Spicular system not definitely observed, probably with median bar and 3 spines at both ends of the median bar.

Occurrence: Longobardian-Cordevolian, ? Tuvalian. Japan, European Tethys.

Included genera: *Hungarosaturnalis* n.gen.
Praeheliostaurus KOZUR & MOSTLER, 1972

Remarks: The Austrisaturnalinae n.subfam. have a smaller subquadratic cortical shell with small pores, mostly closed by a layer of microgranular silica. This shell is always considerably separated from the ring. No auxiliary spines are present.

Genus *Hungarosaturnalis* n.gen.

Derivatio nominis: According to the rich occurrence in the Cordevolian of Hungary.

Type species: *Hungarosaturnalis multispinosa*n.gen.n.sp.

Diagnosis: Ring flat, broad to very broad with 8-12 broad, terminally rounded, sometimes blunt or even expanded spines. There are never 4 pointed prominent spines in cross position considerably larger than the other ones. Inner side of ring always with 4 prominent four-bladed polar spines in cross position and numerous auxiliary spines.

Coarsely latticed cortical shell large, spherical, closely connected with the inner margin of the ring. Large and high outer pore frame often partly closed by an inner fragile layer with small pores. Medullary shell relatively large, coarsely latticed, connected by numerous spines with the cortical shell.

Spicular system probably with median bar which bears 3 spines at each of its ends.

Occurrence: Longobardian of Japan, Hungary and Southern Alps.

Included species: *Hungarosaturnalis multispinosa* n.gen.n.sp.
Saturnosphaera pileata NAKASEKO & NISHIMURA, 1979
Saturnosphaera triassica NAKASEKO & NISHIMURA, 1979
Hungarosaturnalis longobardica n.sp.

Remarks: *Praeheliostaurus* KOZUR & MOSTLER, 1972, from the Cordevolian, has always in continuation of the 4 polar spines on the outer side of the ring 4 prominent, sharply pointed spines which are considerably larger than the other ones or the only spines at the outer margin of the ring.

Hungarosaturnalis multispinosa n.gen.n.sp.

(Pl. 4, fig. 1; pl. 5, fig. 5; pl. 6, fig. 1; pl. 7, figs. 2, 3)

Derivatio nominis: According to the numerous spines on the outer margin of the ring.

Holotype: The specimen on pl. 4, fig. 1, and pl. 5, fig. 5; rep. no. T 5828

Locus typicus: Köveskál, Balaton Highland.

Stratum typicum: Sample Köveskál 6 (Longobardian).

Diagnosis: With the character of the genus. Outer margin of ring always with 12 moderately long, broad, terminally rounded or blunt spines.

Measurements: Diameter of whole test: 253-292 µm. Diameter of cortical shell: 153-164 µm. Diameter of medullary shell: 41-43 µm: Diameter of pores: 12-15 µm. Width of ring: 20-36 µm. Length of spines: 27-40 µm.

Occurrence: Frequent in the Longobardian of Hungary.

Remarks: *Hungarosaturnalis pileata* (NAKASEKO & ISHIMURA, 1979), *H. triassica* (NAKASEKO & NISHIMURA, 1979) and *H. longobardica* n.sp. have only 8 spines.

Hungarosaturnalis longobardica n.sp.

(Pl. 4, fig. 3; pl. 5, fig. 4)

Derivatio nominis: According to the occurrence in the Longobardian.

Holotypus: The specimen on pl. 5, fig. 4; rep. no. T 5834.

Locus typicus: Köveskál (Balaton Highland).

Stratum typicum: Sample Köveskál 6 (Longobardian).

Diagnosis: With the character of the genus. Outer margin of ring with 8 broad, terminally broadly rounded spines. The spines in prolongation of the 4 polar spines are a little longer than the others, but otherwise quite similar.

Measurements: Diameter of whole test: 292-345 µm. Diameter of cortical shell: 145-162 µm. Width of ring: 38-50 µm. Length of spines: 23-50 µm.

Occurrence: Longobardian of Hungary.

Remarks: *Hungarosaturnalis multispinosa* n.gen.n.sp. has always 12 spines.

Hungarosaturnalis pileata (NAKASEKO & NISHIMURA, 1979) from the Longobardian of Japan has larger, considerably more slender and terminally knob-like broadened spines.

Hungarosaturnalis triassica (NAKASEKO & NISHIMURA, 1979) from the Longobardian of Japan and Hungary has distal tapering, terminally only a little rounded spines.

Hungarosaturnalis longobardica n.sp. shows a little transitional character to *Praeheliostaurus* KOZUR & MOSTLER, 1972. But in this genus either no other spines are present than those in prolongation of the 4 polar spines, or the other spines are considerably smaller. Moreover, both the spines in prolongation of the polar spines and (if present) the smaller spines are terminally sharply pointed in *Praeheliostaurus* KOZUR & MOSTLER, 1972.

Family Saturnaloididae n.fam.

Diagnosis: Spicular system of 4-6 spines robust, point centred, connected with 3-5 strong, equal in size rays that run until the ring structure. The inner spicular system is surrounded by a loose network of short bars and large pores which may be covered by a layer of microgranular silica. This irregular network forms a discoidal shell. The ring structure may be simple or multiple (2-3 rings), its outer margin bears numerous spines. Inner margin with or without auxiliary spines. Ring(s) always narrow, with oval cross section.

Occurrence: Upper Triassic of Tethyan realm.

Included genera: *Spongosaturnaloides* KOZUR & MOSTLER, 1972
Ploechingerella n.gen.

Remarks: The stout inner spicular system has some similarity to a pentactine. Because of this stout spicular system the inner connection of the rays is mostly preserved, quite contrary to the contemporaneous spumellarian saturnalids.

The presence of an entactinarian inner spicular system distinguishes this family and the Austrisaturnalidae n.fam. from all other Mesozoic saturnalids which have a coarsely latticed microsphere and numerous spongy cortical shells.

The Austrisaturnalidae n.fam. always have 4 polar spines which connect the regular spherical to subquadratic latticed cortical shell which the ring which is often very broad and entirely flat. Their spicular system has a long median bar with 3 spines at both of its ends. Latticed medullary shell present.

Genus *Ploechingerella* n.gen.

Derivatio nominis: In honour of Dr. B. PLÖCHINGER, Vienna.

Type species: *Parasaturnalis* (*Japonisaturnalis*) *multiperforatus* KOZUR & MOSTLER, 1972.

Diagnosis: With the character of the family. Ring double- or three-fold with large pores between the rings. Small, often indistinct auxiliary spines present.

Occurrence: Upper Triassic of the Tethyan realm.

Included species: *Parasaturnalis* (*Japonisaturnalis*) *multiperforatus* KOZUR & MOSTLER, 1972.

Remarks: *Japonisaturnalis* KOZUR & MOSTLER, 1972, shows homeomorphy in the ring structure, but the shell - so far known - is quite different. It is spherical and consists of several closely spaced spongy layers, connected by a lot of radial bars. In the centre a coarsely latticed small microsphere is present. But in the typical Bajocian *Japonisaturnalis* species the shells are never preserved. The multiple cortical shell can be concluded only from the sculpture of the polar spines. Only in Liassic taxa, very similar to *Japonisaturnalis* KOZUR & MOSTLER, 1972, the cortical shells are present.

The double ring of *Ploechingerella* n.gen. developed from cross bars between the outer spines of the single ring of *Spongosaturnaloides* KOZUR & MOSTLER, 1972. The third ring developed in the same manner from the outer spines of the second ring. The structures inside the ring are the same as in *Spongosaturnaloides* KOZUR & MOSTLER, 1972, with exception of the presence of small auxiliary spines and the large extent of the irregular very flat shell.

Ploechingerella multiperforata (KOZUR & MOSTLER, 1972)

1972 *Parasaturnalis* (*Japonisaturnalis*) *multiperforatus* n.subgen.n.sp. - KOZUR & MOSTLER, p. 44, pl. 4, figs. 18, 20
1972 *Parasaturnalis* (*Japonisaturnalis*) cf. *japonicus* (YAO, 1972) - KOZUR & MOSTLER, p. 44, pl. 3, fig. 19

Remarks: In this species representatives with two and three rings are known. All transitionsbetween these two morphotypes can be observed.

Genus *Spongosaturnaloides* KOZUR & MOSTLER, 1972

Type species: *Spongosaturnalis* (*Spongosaturnaloides*) *quinquespinosa* KOZUR & MOSTLER, 1972

Remarks: In the inner part always 5 spines are present which run in direction of the inner margin of the ring. But not in all species all spines reach the ring. Often they end near the outer margin of the irregular discoidal shell. In this case only 3 or 4 spines are connected with the ring.

Spongosaturnaloides trispinosus n.sp.

(Text-fig. 2; pl. 2, fig. 1)

Derivatio nominis: Because only 3 spines are connected with the ring.

Holotype: The specimen on text-fig. 5 and pl. 2, fig. 1; rep. no. T 5822.

Locus typicus: Göstling (Austria).

Stratum typicum: Sample AS 8, Upper Cordevolian (see MOSTLER & SCHEURING, 1974).

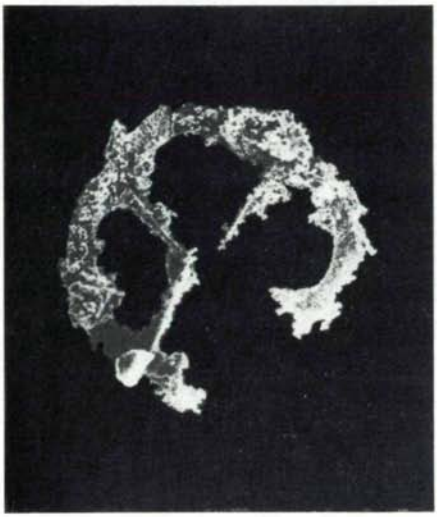
Diagnosis: Very robust spicular system point centred. 3 spines of the spicular system are connected with 3 robust spines that run to the ring. A fourth spine of the spicular system is perpendicular to the other three and connected with the irregularly discoidal shell. The irregularly large pores of the shell are mostly covered by a layer of microgranular silica and nodes or short blunt spines are present on the shell surface.

The ring is narrow and bears numerous (mostly 18) large outer spines. Some of these spines may be connected by transverse bars. By this a large pore is included between the ring, the bar and the two adjacent spines.

Measurements: Diameter of whole test: 395-422 µm. Width of ring: 17-22 µm. Length of spines: 56-78 µm.

Occurrence: Upper Cordevolian of Austria.

Remarks: *Spongosaturnaloides quinquespinosa* (KOZUR & MOSTLER, 1972) has 5, rarely 4 spines, running from the ring to the point centred spicular system. Moreover, there are fewer (13-16) and a little shorter outer spines in this species.



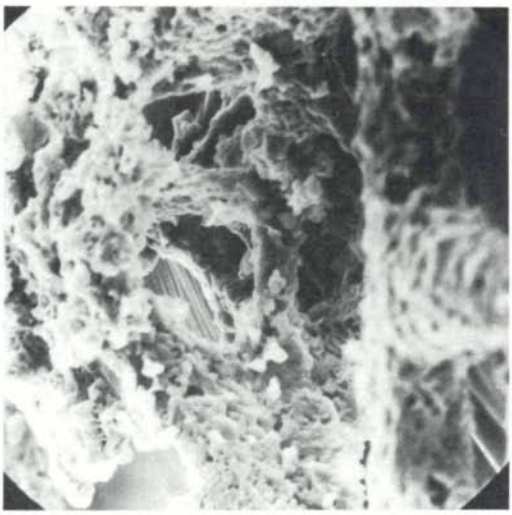


Fig. 1: *Austrisaturnalis* sp., sample Köveskál 6, Longobardian with *Daonella lommeli*, the same specimen as on pl. 7, fig. 1, where the detail of the spicular system is shown in a stereoscan photo, x 240.

Fig. 2: *Spongosaturnaloides trispinosus* n.sp., sample AS 8, detail of the holotype, figured on pl. 2, fig. 1. Nearly equatorial view, x 1000.

Spongosaturnaloides multidentatus n.sp.

(Pl. 3, fig. 1)

Derivatio nominis: According to the numerous outer spines of the ring.

Holotype: The specimen on pl. 3, fig. 1; rep. no. T 5823.

Locus typicus: Göstling (Austria).

Stratum typicum: Sample AS 8, Upper Cordevolian (see MOSTLER & SCHEURING, 1974).

Diagnosis: Spicular system very robust, point centred or with very short indistinct median bar. 4, sometimes 5, very robust spines are connected with 4, sometimes 5, strong equal in size rays which run to the ring. A further robust spine runs almost perpendicularly to the other spines towards the irregularly discoidal shell which is composed of irregularly connected robust bars which enclose large irregular pores of different size. At the junction point of the bars (vertices) irregular, short, blunt spines or long nodes are present. Outer margin of the ring with more than 20 short spines.

Measurements: Diameter of whole test: 235-250 µm. Width of the ring: 15-20 µm. Length of spines: 15-27 µm.

Occurrence: Cordevolian of Austria.

Remarks: *Spongosaturnaloides quinquespinosus* (KOZUR & MOSTLER, 1972) has a similar inner structure and 5, rarely 4, rays but considerably fewer (13-16) outer spines of the ring.

Sporgosaturnaloides trispinosus n.sp. has considerably larger and a little fewer outer spines and mostly only 3 rays.

? Family Triarcellidae KOZUR & MOCK, 1981

Diagnosis: See KOZUR & MOSTLER, 1981, p. 26.

Occurrence: Lower Norian of the Tethyan realm.

Remarks: The genus *Triarcella* KOZUR & MOCK, 1981 (in KOZUR & MOSTLER, 1981) derived most probably from *Kahlerosphaera* KOZUR & MOSTLER, 1979, in a way that two of the terminal side spines of adjacent main spines grow together to form a ring like the saturnalid ring. Also in *Dumitricasphaera* KOZUR & MOSTLER, 1979, the terminal side spines of the (in this genus two) polar spines may grow together to an incomplete ring.

Neither in *Kahlerosphaera* KOZUR & MOSTLER, 1979, nor in *Triarcella* KOZUR & MOCK, 1981, the central structure is well known. Therefore it is unknown, whether a spicular system is present or not. In the first case the Triarcellidae KOZUR & MOCK, 1981, are closely related to three-spined Entactinaria, in the latter case to three-spined Spumellaria. In both cases they are homeomorphic to the saturnalids s.str. which have never bladed polar spines and derived from the Oertlispongidae KOZUR & MOSTLER, 1980.

Suborder Spumellaria EHRENBERG, 1875

Superfamily Lithocycliacea EHRENBERG, 1854 emend. KOZUR & MOSTLER, 1972

= Coccodiscacea HAECKEL, 1862 sensu KOZUR & MOSTLER, 1972

Family Saturnalidae DEFLANDRE, 1953

Diagnosis: Ring circular, subcircular or subquadratic, very narrow, with oval to round cross section, often bladed or with swellings and furrows. Outer margin of ring smooth or entirely spiny.

Cortical and medullary shells widely separated from the ring. Two polar spines. No auxiliary spines.

Occurrence: Upper Cretaceous-recent.

Remarks: Among the Parasaturnalidae KOZUR & MOSTLER, 1972 emend., there is a group (highly evolved taxa from the Hexasaturnalinae n.subfam.) which , with exception of the spongy cortical shells, is quite identical with the Saturnalidae DEFLANDRE, 1953. At least some of these taxa have a rather large outer medullary shell. The Saturnalidae DEFLANDRE, 1953, may derive from this group by loss of the spongy cortical shells.

Family Parasaturnalidae KOZUR & MOSTLER, 1972 emend.

Diagnosis: Cortical shells globular, spongy, medullary shell(s) latticed. An equatorial ring is always present. Only in the most primitive taxa two half-rings, still not connected with each other, are present. Outline of ring circular, subcircular, subquadratic, hexagonal, polygonal or strongly elongated with the long axis perpendicular to the polar spines.

Ring primarily flat, undifferentiated and rather broad. In higher evolved taxa the ring is narrow, oval to round in cross section or highly differentiated (bladed or with swellings and furrows). Outer margin of ring mostly spined, rarely smooth.

Primarily 2 polar spines (first order spines) and often auxiliary spines (second order spines) are present. The auxiliary spines may be tranformed into additional first oder spines.

Occurrence: Cordevolian (Lower Carnian, Upper Triassic) - Upper Cretaceous.

Remarks: The Parasaturnalidae KOZUR & MOSTLER, 1972 emend. were introduced by KOZUR & MOSTLER, 1972, as a subfamily. Here this subfamily is preserved in the primary scope, but together with other subfamilies it is regarded as part of the Parasaturnalidae KOZUR & MOSTLER, 1972 in a broader sense.

For the first time, PESSAGNO, 1979, elevated the Parasaturnalinae KOZUR & MOSTLER, 1972, to a family. But the emendation by PESSAGNO, 1979, adopted by De WEVER, 1981 is rejected here, because it had created a highly artificial group, which comprises besides Mesozoic spumellarian saturnalids with spongy cortical shells also two families of the Entactinaria with internal spicular system (with the genera *Austrisaturnalis* KOZUR & MOSTLER, 1971, *Praeheliostaurus* KOZUR & MOSTLER, 1972, and *Spongosaturnaloides* KOZUR & MOSTLER, 1972, included in the Parasaturnalidae by PESSAGNO, 1979, and De WEVER, 1981) as well as the family Veghicyclidae KOZUR & MOSTLER, 1972, the oldest known Lithocycliacea EHRENBERG, 1854, with latticed disk. Therefore the Parasaturnalidae PESSAGNO, 1979, and De WEVER, 1981, include taxa of two suborders and four quite different families.

Moreover, this classification was already inconsistent by its definiton and genus assignment. In spite of the fact that the Parasaturnalidae sensu PESSAGNO, 1979, and De WEVER, 1981, were defined to have spongy cortical shells (contrary to the Saturnalidae DEFLANDRE, 1953, with latticed cortical shell), both authors also placed *Pseudoheliostarurus* KOZUR & MOSTLER, 1972, with coarsely latticed cortical shell (defined in the genus diagnosis by KOZUR & MOSTLER, 1972 and visible in the SEM photos of the included species) in this family.

The Saturnalidae DEFLANDRE, 1953, are distinguished by latticed cortical and medullary shells.

The Veghicyclidae KOZUR & MOSTLER, 1972, have a latticed disk, open only in its central part. This latticed disk - with exception of its distal part - is overgrown by lenticular to globular spongy cortical shells. Therefore the outer morphology seems to be a little similar to that of the Parasaturnalidae with double or multiple rings, but the inner structure of the Parasaturnalidae with double or multiple ring and of the Veghicyclidae is quite different. The shell of the Parasaturnalidae ends on the inner margin of the single, double or multiple ring and no latticed disk, overgrown by cortical shell, is present.

The Triarcellidae KOZUR & MOSTLER, 1981, the Austrosaturnalidae n.fam. and the Spongosaturnaloididae n.fam. are homeomorph taxa with

saturnalid ring, but are distinguished by their internal spicular system, now well known in the two latter families and supposed in the first one.

Subfamily Parasaturnalinae KOZUR & MOSTLER, 1972

Diagnosis: Double or multiple ring always with circular outline. Individual ring very narrow, with oval to roundish cross section. Between the rings more or less large pores are present. Spines on the outer margin always opposite to the pores, never opposite to the bars between the pores. Cortical shell spongy. Two polar spines. Auxiliary spines may be present.

Occurrence: ? Liassic, Bajocian to Upper Cretaceous.

Included genera: *Parasaturnalis* KOZUR & MOSTLER, 1972
Japonisaturnalis KOZUR & MOSTLER, 1972
Pseudosaturnalis KOZUR & MOSTLER, 1972

Remarks: Here this subfamily is used in the same sense as by KOZUR & MOSTLER, 1972, but the Triassic *Japonisaturnalis* species is excluded as a homeomorphic form with quite different central structure (*Ploechingerella* n.gen., see Spongosaturnaloididae n.fam., Entactinaria).

In the Parasaturnalinae KOZUR & MOSTLER, 1972, we include genera with or without auxiliary spines. Here the presence or absence of auxiliary (second order) spines is regarded as a generic feature, but not as a suprageneric one like in PESSAGNO's and De WEVER's classification. The presence or absence of auxiliary spines depends on the size of the outer cortical shell. If it reaches or nearly reaches the inner margin of the ring, auxiliary spines are present, if not, only first order spines (polar spines and sometimes other spines of the same size) are present.

The subfamily Parasaturnalinae KOZUR & MOSTLER, 1972, was redefined by PESSAGNO, 1979, to include only taxa without auxiliary spines, but also *Japonisaturnalis* KOZUR & MOSTLER, 1972, with auxiliary spines was included in this subfamily by PESSAGNO, 1979. This is justified and we have been doing it this way since we have introduced the Parasaturnalinae KOZUR & MOSTLER, 1972 (see above), but in this case, of course, the emendation of the Parasaturnalinae KOZUR & MOSTLER, 1972, by PESSAGNO, 1979, adopted by De WEVER, 1981, was incorrect.

De WEVER, 1981, still has even complicated the *Parasaturnalis/Japonisaturnalis* problem a little more. He placed the type species of *Parasaturnalis* KOZUR & MOSTLER, 1972, *Spongosaturnalis? diplocyclis* YAO, 1972, in *Japonisaturnalis* KOZUR & MOSTLER, 1972. But according to the IRCN this is impossible, because *Japonisaturnalis* KOZUR & MOSTLER, 1972, was established as a subgenus of *Parasaturnalis* KOZUR & MOSTLER, 1972. Moreover, the specimens figured as *Japonisaturnalis diplocyclis* (YAO, 1972) by De WEVER, 1981, have auxiliary spines, quite absent in *Parasaturnalis* KOZUR & MOSTLER, 1972, and even in the Parasaturnalinae sensu PESSAGNO, 1979 (a classification which was declared to be a natural classification by De WEVER, 1981, and adopted without changes).

Japonisaturnalis diplocyclis (YAO, 1972) sensu De WEVER, 1981, is neither a *Parasaturnalis* (auxiliary spines present!) nor a representative of the Parasaturnalinae (neither in our classification nor in the classification by PESSAGNO, 1979, if we regard PESSAGNO's emended diagnosis). The outer

spines of the ring are in prolongation of the radial bars between the inter-ring pores. Here these specimens are regarded as highly evolved representatives of the Heliosaturnalinae KOZUR & MOSTLER, 1972.

The Liassic *Japonisaturnalis japonicus* (YAO, 1972) sensu De WEVER, 1981, is also quite different from this species described by YAO, 1972, from the Bajocian Unuma echinatus Zone. The fragmentary specimen figured by De WEVER, 1981, has 4 first order polar spines in cross position and opposite to all ring pores there are always two tiny spines. On the contrary *Japonisaturnalis japonicus* (YAO, 1972) has always one large spine opposite to the ring pores, two polar spines and two or three mostly large auxiliary spines.

"*Japonisaturnalis japonicus*" sensu De WEVER, 1981, seems to be the oldest hitherto known representative of the Parasaturnalinae KOZUR & MOSTLER, 1972.

Like the Parasaturnalidae KOZUR & MOSTLER, 1972 sensu PESSAGNO, 1979, and De WEVER, 1981, also the Parasaturnalinae sensu these authors, are a highly artifical group. According to PESSAGNO, 1979, the Parasaturnalinae do not only include the 3 genera which were included by KOZUR & MOSTLER, 1972, in the present paper (see above), but also the genera *Acanthocircus* SQUINABOL, 1903 (sensu PESSAGNO, 1979, and De WEVER, 1981, including the quite different genus *Palaeosaturnalis* DONOFRIO & MOSTLER, 1978), *Austrisaturnalis* KOZUR & MOSTLER, 1972, and *Spongosaturnaloides* KOZUR & MOSTLER, 1972. Therefore also the Parasaturnalinae sensu PESSAGNO and De WEVER include taxa of different families and subfamilies of the Spumellaria (Heliosaturnalinae KOZUR & MOSTLER, 1972, Acanthocircinae PESSSAGNO, 1977), and Entactinaria (Austrisaturnalidae n.fam.).

The Heliosaturnalianae KOZUR & MOSTLER, 1972, separated from the Parasaturnalinae KOZUR & MOSTLER, 1972, also in the classification by PESSAGNO, 1979, are superficially very similar to the Parasaturnalinae s.str. But all Parasaturnalinae from the (?) Liassic, Bajocian-Upper Cretaceous have the outer spines always above the pores, but never above the radial bars separating the pores. This can be observed in genera with and woithout auxiliary spines, in genera with two rings like in taxa with more than two rings. There is a fundamental difference in the growing mechanism to the Heliodiscinae. In the latter subfamily at first this completely flat, often broad inner ring with long spines is built up. Later connecting bars developed in some distance above the base of the spines creating a second (outer) ring. By this all outer spines always continue to the inner ring. Because both subfamilies show the same differences in all taxa and both subfamilies are restricted to different time intervals (double ring Heliodiscinae: Upper Triassic to Liassic; Parasaturnalinae: ? Liassic, Bajocian-Upper Cretaceous) they can be well separated and they do not seem to be directly related wo each other.

The Acanthocircinae PESSAGNO, 1976, always have a strong elongation of the ring (+ spines) with the long axis perpendicular to the polar spines. The ring is never double or multiple.

Also the Hexasaturnalinae n.subfam. have a hexagonal or polygonal outline. Taxa with secondarily roundish ring outline from the Upper Cretaceous are quite different from the contemporaneous Parasaturnalinae s.str. which, at this time, always have a multiple ring.

Subfamily Heliosaturnalinae KOZUR & MOSTLER, 1972 emend.

Diagnosis: Ring always circular or subcircular and very flat, mostly broad, sometimes very broad. If the ring is narrow (very rare) then it is also quite flat. Outer margin with large, often highly differentiated spines. Ring mostly single. A second ring may be present, but its outer spines always run to the inner ring.

Cortical shells always closely spaced, spongy. The outer one is either loosely connected with the inner margin of the ring or quite separated from it. Medullary shell latticed.

Primarily two polar spines are present, but also second order auxiliary spines are often present. In higher evolved taxa sometimes 4 or more large first order spines are present.

Occurrence: Cordevolian to Upper Cretaceous, very frequent in the Upper Triassic, frequent in the Liassic until the Pliensbachian, later mostly very rare.

Remarks: In the Cordevolian there are 3 species, where the ring is not closed, but consists of two half-rings in one place or in different planes. From specimens, where the two half-rings are still widely separated, all transitions may be observed, e.g. in the holotype of *Pseudoheliodiscus bipartitus* (KOZUR & MOSTLER, 1972) or generally in *Pseudoheliodiscus interruptus* n.sp., two specimens where the two half-rings are almost connected with each other (e.g. the specimen figured on pl. 1, fig. 4). The species with two half-rings which only occur near the lowermost occurrence of the Heliosaturnalinae indicate that the saturnalid ring has evolved from two half-rings. This indicates that the forerunners of the Heliosaturnalinae should be found within highly evolved Oertlispongidae KOZUR & MOSTLER, 1980.

The tendency to build up half-rings or similar structures is common in the Oertlispongidae KOZUR & MOSTLER, 1980, within several evolutionary lines. Already in the most primitive genus *Oertlispongus* DUMITRICĂ, KOZUR & MOSTLER, 1980, we can observe this tendency during the Lower Ladinian (*Oertlispongus longirecurvatus* n.sp., *O. annulatus* n.sp.). Beginning in the higher part of the Lower Ladinian Oertlispongidae with very broad, flattened spines appeared. In the Upper Ladinian within the Oertlispongidae species appeared, which have flattened, broad recurvated spines with long spines on the outer side (*Spongoserrula rarauana* DUMITRICĂ, 1982, see text-fig. 3). At the same time, partly a little later within the Longobardian, species with bilateral symmetrical, flattened broad spines with smooth or spiny outer margin appeared (e.g. *Pterospongus patrulii* DUMITRICĂ, 1982, see text-fig. 4). The polar spine of this species already has almost the form of a half-ring. If such species have two so highly differentiated spines in polar position then already the evolutionary stage of *Pseudoheliodiscus bipartitus* (KOZUR & MOSTLER, 1972) and the other two primitive *Pseudoheliodiscus* species with half-rings are present.

But also almost full rings, attached only to one side, have evolved within the Oertlispongidae during the Longobardian (*Baumgartneria curvispina* DUMITRICĂ, 1982, see text-fig. 5).

The derivation of the Heliosaturnalidae KOZUR & MOSTLER, 1972 emend. from the Oertlispongidae KOZUR & MOSTLER, 1980, is also indicated by the fact that in both families the shell structure is identical. Therefore the Oertlispongidae KOZUR & MOSTLER, 1980, are a very important basis group of the Spumellaria EHRENBERG, 1875, from which both the Sponguracea HAECKEL, 1862 emend. KOZUR & MOSTLER, 1981, and the Lithocycliacea EHRENBERG, 1854 emend. KOZUR & MOSTLER, 1972, 1981 derived. Here the boundary of

these two superfamilies is defined in the way that all taxa with closed or nearly closed equatorial structures (ring, latticed disk) are placed in the Lithocycliacea EHRENBERG, 1854 emend. KOZUR & MOSTLER, 1972 (= Coccodiscacea HAECKEL, 1862 sensu KOZUR & MOSTLER, 1972).

The differences between the Heliosaturnalinae KOZUR & MOSTLER, 1972 emend. and the Parasaturnalinae KOZUR & MOSTLER, 1972, were discussed under the latter subfamily.

The Acanthocircinae PESSAGNO, 1977, are clearly distinguished by the narrow, mostly highly differentiated ring, the absence of auxiliary spines in all taxa and by the strong elongation of the ring (+ spines) with the long axis perpendicular to the polar spines. The Acanthocircinae PESSAGNO, 1977, have apparently evolved from the Cordevolian *Praeacanthocircus* n.gen. with a smooth, strongly elongated ring (with the long axis perpendicular to the polar spines).

The Hexasaturnalinae n.subfam. have a highly differentiated narrow ring (mostly bladed or with swellings) and a predominantly subquadratic, hexagonal or polygonal outline. Primitive Triassic taxa from the Norian still have a flat, but also narrow ring. They are distinguished from the Heliosaturnalinae KOZUR & MOSTLER, 1972 emend. by their hexagonal or octogonal ring outline. Hexasaturnalinae n.subfam. with secondarily circular or subcircular ring outline have a differentiated (mostly bladed) narrow ring or the cross section of the ring is at least roundish and not flat.

Tribus Heliosaturnalini KOZUR & MOSTLER, 1972

Diagnosis: With the character of the subfamily. Ring always double. Spines of the outer ring run to the inner ring. Pores between the two rings large. Auxiliary spines always present. Outer cortical shell always reaches to the inner margin of the ring.

Occurrence: Cordevolian of the Tethyan realm.

Included genus: *Heliosaturnalis* KOZUR & MOSTLER, 1972.

Remarks: The Palaeosaturnalini KOZUR & MOSTLER, 1981, always have a single ring. The outer cortical shell is often quite detached from the inner margin of the ring. The auxiliary spines are often absent.

The Veghicyclidae KOZUR & MOSTLER, 1972, have a latticed disk instead of a double ring. To a large part this one-layer disk is overgrown by a spongy lenticular to globular shell or by a single layer of spongy meshwork. Only the innermost part of the latticed disk is open, but it never has a well defined inner margin. In this open central part there are always 4 short polar spines in cross position which run to a tiny microsphere, in very short distances surrounded by spongy globular shells.

Perhaps the latticed disk has evolved by inward-growing of a primary double ring in the same manner as the outer ring of *Heliosaturnalis* KOZUR & MOSTLER, 1972, evolved from the single ring of *Pseudoheliodiscus* KOZUR & MOSTLER, 1972 emend. By this connecting bars would have grown between the auxiliary spines, As the auxiliary spines are more irregular than the outer spines, in the inner part of the disk no clear ring structure could evolve. Therefore the latticed disk of the Veghicyclidae KOZUR & MOSTLER, 1972, has more or less concentrically arranges pores, but no clear ring structures can be recognized.

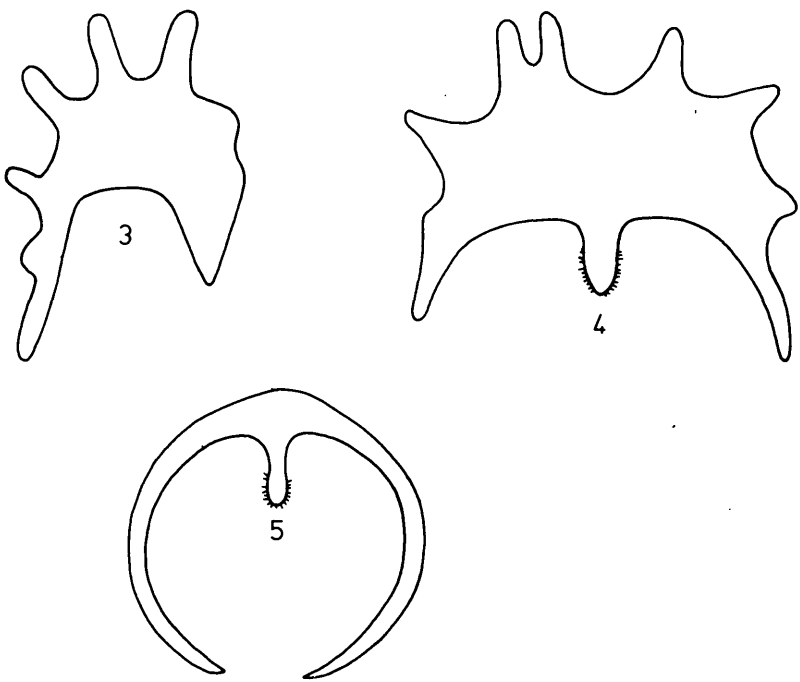


Fig. 3: *Spongoserrula rarauana* DUMITRICĂ, 1982
Fig. 4: *Pterospongus patrulii* DUMITRICĂ, 1982
Fig. 5: *Baumgartneria currispina* DUMITRICĂ, 1981

All species from DUMITRICĂ, 1982

By the presence of a latticed disk instead of a double ring the Veghicyclidae KOZUR & MOSTLER, 1972 are the first typical Lithocycliacea EHRENBERG, 1854 emend. KOZUR & MOSTLER, 1972, 1981. On the other hand in spite of all the differences the first spumellarian saturnalids (Heliosaturnalinae KOZUR & MOSTLER, 1972 emend.) are closely enough related to the Veghicyclidae KOZUR & MOSTLER, 1972, so that they also should be placed in the Lithocycliacea EHRENBERG, 1854, with the decisive common feature of equatorial structures.

Tribus Palaeosaturnalini KOZUR & MOSTLER, 1981

Diagnosis: Ring single, always flat, with circular to subcircular outline, mostly broad to very broad, rarely narrow. Ring mostly closed, but in most primitive species still two half-rings, not fused with each other, are present. Outer margin of the ring always with stout long spines along the whole margin, often differentiated in different manner (Secondarily spined, bifurcated, twisted, expanded).

Cortical shells spongy, medullary shell latticed. Two polar spines, with or without auxiliary spines. In higher evolved taxa also 4 or more first order spines (polar spines s.l.) may be present.

Occurrence: Carnian to Upper Cretaceous. Very frequent from the Cordevolian-Pliensbachian with absolute maximum in the Norian. Mostly rare to very rare from the Middle Jurassic to the Upper Cretaceous.

Included genera: *Palaeosaturnalis* DONOFRIO & MOSTLER, 1978 emend. KOZUR & MOSTLER, 1981
Pseudoheliodiscus KOZUR & MOSTLER, 1972 emend. PESSAGNO, 1979
Synonym: *Pessagnosaturnalis* KOZUR, 1979
Saturnosphaera TICHOMIROVA, 1975
Mesosaturnalis KOZUR & MOSTLER, 1981
Praemesosaturnalis KOZUR & MOSTLER, 1981

Remarks: The Palaeosaturnalini KOZUR & MOSTLER, 1981, are directly related to highly evolved Oertlispongidae KOZUR & MOSTLER, 1980. Species, in which two half-rings are still present, have to be regarded as transitional forms of *Pterospongus* DUMITRICĂ, 1982 (Oertlispongidae KOZUR & MOSTLER, 1980).

The Heliosaturnalini KOZUR & MOSTLER, 1972, are clearly distinguished by their double ring.

Genus *Palaeosaturnalis* DONOFRIO & MOSTLER, 1978 emend. KOZUR & MOSTLER, 1981

Type species: *Spongosaturnalis triassicus* KOZUR & MOSTLER, 1972

Remarks: PESSAGNO, 1979, placed typical *Palaeosaturnalis* species in *Acanthocircus* SQUINABOL, 1903, and De WEVER, 1981, followed him and placed the type species of *Palaeosaturnalis* DONOFRIO & MOSTLER, 1978, in *Acanthocircus* SQUINABOL, 1903.

The ring in *Acanthocircus* is quite different from the ring of *Palaeosaturnalis*. In *Acanthocircus* it is always very narrow and mostly bladed or with swellings or furrows. Only in very primitive *Acanthocircus* species the ring is still undifferentiated, but even in these species the ring is very narrow and never flat, but oval to round in cross section. Moreover, there is no *Acanthocircus* species with circular ring outline. In *Acanthocircus* the ring is almost exclusively strongly elongated with the long axis perpendicular to the polar spines. In the very rare exceptions where the ring is not strongly elongated, there are long outer spines at the poles, perpendicular to the polar spines. Therefore, ring + spines, without any exception, are strongly elongated in the direction perpendicular to the polar spines.

The discovery of the Cordevolian *Praeacanthocircus carnicus* n.gen. n.sp. with strongly elongated smooth ring makes it now highly probable that *Acanthocircus* SQUINABOL, 1903, has even not directly evolved from *Palaeosaturnalis* species with narrow ring, but belongs to a blind ending side branch in the devlopment of the spumellarian saturnalids.

Mesosaturnalis KOZUR & MOSTLER, 1981, the direct successor of *Palaeosaturnalis* DONOFRIO & MOSTLER, 1978, occurs together with typical *Acanthocircus* species throughout the whole Jurassic and Cretaceous and it has never changed its flat, rather broad circular ring in an *Acanthocircus* type of ring. Therefore the *Acanthocircus* ran parallel from the Cordevolian (early Upper Triassic) until the Upper Cretaceous without any transition form in this long period.

Palaeosaturnalis latiannulatus n.sp.

(Pl. 5, fig. 1)

Derivatio nominis: According to the very broad ring.

Holotype: The specimen on pl. 5, fig. 1; rep. no. T 5842.

Locus typicus: Zul'óv γ, Manin Unit (Western Carpathians).

Stratum typicum: *Navicula* Subzone of spatulatus A.Z. (Lower Norian). Pebble in Middle Cenomanian conglomerates.

Diagnosis: Ring circular to subcircular, very broad, entirely flat and undifferentiated. Outer margin with only 4 long spines. Two spines are situated opposite to the 2 polar spines, the other two are perpendicular to these spines. At least 4 spongy cortical shells are present.

Measurements: Diameter of whole test: 413-444 µm: Outer diameter of ring: 353-373 µm. Inner diameter of ring: 152-167 µm. Width of ring: 93-100 µm.

Occurrence: Until now only known from the locus typicus.

Remarks: *Palaeosaturnalis raridenticulatus* KOZUR & MOCK, 1981, from the same beds has a considerably narrower ring and a larger inner diameter of the ring, whereas the arrangement of the spines is identical.

Palaeosaturnalis mocki n.sp.

(Pl. 5, fig. 2)

Derivatio nominis: In honour of Dr. R. MOCK, Bratislava.

Holotype: The specimen on pl. 5, fig. 2; rep. no. T 5843.

Locus typicus and stratum typicum: As for *P. latiannulatus* n.sp.

Diagnose: Ring broad, circular, entirely flat and undifferentiated. Outer margin with 8 spines. Two spines opposite to the two polar spines and two, about perpendicular to the polar spines, are a little larger than the other four spines. Always one of these smaller spines is situated between two larger ones.

Measurements: Diameter of whole test: 389–445 µm. Outer diameter of ring: 279–298 µm. Inner diameter of ring: 150–167 µm. Width of ring: 56–67 µm.

Occurrence: Until now only known from the locus typicus.

Remarks: In *Palaeosaturnalis latiannulatus* n.sp. the ring is even broader and only 4 outer spines in cross position are present.

Genus *Pseudoheliodiscus* KOZUR & MOSTLER, 1972 emend. PESSAGNO, 1979

Type species: *Pseudoheliodiscus riedeli* KOZUR & MOSTLER, 1972

Synonym: *Pessagnosaturnalis* KOZUR, 1979.

Diagnosis: Ring circular, broad, flat and undifferentiated. Outer margin always with large spines along the whole margin. Inner margin with two polar spines opposite to outer spines and with auxiliary spines.

Several spongy cortical shells. The outer one reaches the inner margin of the ring or is only a little separated from it. Sometimes the outer shell overgrows even a little the inner margin of the ring. Medullary shell latticed.

Occurrence: Cordevolian to Bajocian.

Included species: *Pseudoheliodiscus riedeli* KOZUR & MOSTLER, 1972
Spongosaturnalis bipartitus KOZUR & MOSTLER, 1972
Spongosaturnalis heisseli KOZUR & MOSTLER, 1972
Spongosaturnalis kahleri KOZUR & MOSTLER, 1972
Spongosaturnalis latus KOZUR & MOSTLER, 1972
Spongosaturnalis primitivus KOZUR & MOSTLER, 1972
Spongosaturnalis pseudosymmetricus KOZUR & MOSTLER, 1972
Pseudoheliodiscus finchi PESSAGNO, 1979
Pseudoheliodiscus viejoensis PESSAGNO, 1979
Pseudoheliodiscus yaoi PESSAGNO & POISSON, 1981
Pessagnosaturnalis KOZUR & MOCK, 1981
Pseudoheliodiscus donofrioi n.sp.
? *Pseudoheliodiscus ? interruptus* n.sp.

Remarks: In all *Pseudoheliodiscus* species two polar spines and numerous second order auxiliary spines are present. In KOZUR & MOSTLER, 1979, these species were placed in *Pseudoheliodiscus* KOZUR & MOSTLER, 1972, if the outer cortical shell is directly connected with the inner margin of the ring or even overgrows a little the inner margin of the ring. All species, in

which the cortical shell is separated a little from the inner margin of the ring, were place in *Spongosaturnalis* CAMPBELL & CLARK, 1944. PESSAGNO, 1979, also placed this latter species group in *Pseudoheliodiscus* KOZUR & MOSTLER, 1972 emend. and here we use *Pseudoheliodiscus* in this emended sense. In this broader sense *Pessagnosaturnalis* KOZUR, 1979, established for the latter speciesgroup, is a younger synonym of *Pseudoheliodiscus* KOZUR & MOSTLER, 1972.

De WEVER, 1981, placed even more species in *Pseudoheliodiscus* KOZUR & MOSTLER, 1972, species, in which one polar spine or both are situated opposite to an interspine space on the outer margin of the ring and species with several first order spines without any differentiation in polar and auxiliary spines. For the first group KOZUR & MOSTLER, 1981, have introduced the genus *Praemesosaturnalis* KOZUR & MOSTLER, 1981, for the second group the genus *Saturnosphaera* TICHOMIROVA, 1975, exists.

At first view all these differences do not seem to be very important and the genus *Pseudoheliodiscus* in this very broad sense seems to be justified. But the genera *Pseudoheliodiscus* KOZUR & MOSTLER, 1972 emend. PESSAGNO, 1979: Cordevolian-Bajocian (frequent only in the Upper Triassic), *Saturnosphaera* TICHOMIROVA, 1975: Sevatian-Pliensbachian (frequent only in the Lower Jurassic), and *Praemesosaturnalis* KOZUR & MOSTLER, 1981: Sevatian to Upper Cretaceous, have clearly different stratigraphic ranges and within the phylomorphogenetic lines the changes from *Pseudoheliodiscus* into *Saturnosphaera* are not reversible.

Pseudoheliodiscus donofrioi n.sp.

(Pl. 2, fig. 4)

Derivatio nominis: In honour of Dr. D.A. DONOFRIO, Innsbruck.

Holotype: The specimen on pl. 2, fig. 4; rep. no. T 5841.

Locus typicus: Göstling (Austria).

Stratum typicum: Sample Y 6, Upper Cordevolian.

Diagnosis: Ring separated into two half-rings in one plane which are almost connected with each other. Both half-rings moderately broad, flat, undifferentiated. The 12-14 outer spines are very long, but strongly differing in size. Cortical shells spongy, the outermost one reaches the inner margin of the ring. Two polar spines and numerous auxiliary spines are present.

Measurements: Diameter of whole test: 398-496 µm. Diameter of outermost shell: 172-189 µm. Width of ring: 17-34 µm.

Occurrence: Cordevolian of Austria.

Remarks: *Pseudoheliodiscus bipartitus* (KOZUR & MOSTLER, 1972) has the same type of half-rings, but thespines are considerably shorter and more triangular in outline.

Pseudoheliodiscus riedeli KOZUR & MOSTLER, 1972, has similar long spines, but the ring is closed.

Pseudoheliodiscus? interruptus n.sp.

(Pl. 1, figs. 1-3)

Derivatio nominis: According to the quite interrupted ring.

Holotype: The specimen on pl. 1, fig. 3; rep. no. T 5837.

Locus typicus. Göstling (Austria).

Stratum typicum: Sample Y 6, Upper Cordevolian.

Diagnosis: Cortical shell large, spongy. Two bladed polar spines and auxiliary spines are present. Each half-ring flat, broad, with large outer spines, quite separated from each other under an angle of 50-90°.

Measurements: Diameter of whole unit: 296-375 µm. Diameter of outer cortical shell: 173-185 µm. Width of ring: 20-40 µm.

Occurrence: Cordevolian of Göstling (Austria).

Remarks: Most probably this species belongs to a new genus. It is even unsure, whether it is a representative of the Palaeosaturnalini KOZUR & MOSTLER, 1981, because the inner structure is not well known. On the other hand, it is a transition form to *Dumitricasphaera* KOZUR & MOSTLER, 1979. There exists a still undescribed *Dumitricasphaera* species with two strong, long, bladed polar spines, in which only two, but very long secondary distal spines are present, which branch off under a mutual angle of 50-90°. This is the direct forerunner of *P.? interruptus* n.sp., but also from this species the inner structure is not well known.

Genus *Saturnosphaera* TICHOMIROVA, 1975 emend.

Type species: *Saturnosphaera gracilis* TICHOMIROVA, 1975

Diagnosis: Ring circular, flat, undifferentiated, moderately broad to narrow. Outer margin with long spines. Inner margin with 5-12 moderately long to long first order spines of equal size without any differentiation in polar and auxiliary spines. A part or all of these spines are situated opposite to the interspine spaces on the outer side of the ring. Outer spongy cortical shell large and it often reaches to the inner margin of the ring.

Occurrence: Sevatian-Pliensbachian.

Included species: *Saturnosphaera gracilis* TICHOMIROVA, 1975
Synonym: *Spongosaturnaloides tichomirovae* KOZUR & MOSTLER, 1972
Spongosaturnalis convertus KOZUR & MOSTLER, 1972
Saturnosphaera acifer TICHOMIROVA, 1975
Pseudoheliodiscus radiosus De WEVER, 1981

Remarks: In the classification by PESSAGNO, 1979, adopted by De WEVER, 1981, this genus belongs to *Pseudoheliodiscus* KOZUR & MOSTLER, 1972. KOZUR & MOSTLER, 1981, placed *Saturnosphaera* TICHOMIROVA, 1975, in *Spongosaturnaloides* KOZUR & MOSTLER, 1972, which has the same ring structure and also several long first order spines without any differentiation in polar and auxiliary spines. But now an internal spicular system was found

in *Spongosaturnaloides* what excludes this genus from all spumellarian saturnalids.

Spongosaturnalis gracilis KOZUR & MOSTLER, 1972, still has a little size difference between the 2 polar spines and the auxiliary ones. As the polar spines are opposite to the interspine spaces on the outer margin of the ring, this species is here placed in *Praemesosaturnalis* KOZUR & MOSTLER, 1981, where it represents a transitional form to *Saturnosphaera* TICHOMIROVA, 1975. As these two "*gracilis*" species are now not placed in one genus any more, *Saturnosphaera gracilis* TICHOMIROVA, 1975, does not have to be replaced any more because of homonymy with *Praemesosaturnalis gracilis* (KOZUR & MOSTLER, 1972) like in the classification of PESSAGNO, 1979, KOZUR & MOSTLER, 1981, and De WEVER, 1981, where these two "*gracilis*" species are in one genus. Therefore *Spongosaturnaloides tichomirovae* KOZUR & MOSTLER, 1981, which replaced *Spongosaturnaloides gracilis* (TICHOMIROVA, 1975) because of homonymy with *Spongosaturnaloides gracilis* (KOZUR & MOSTLER, 1972), is now regarded as a younger synonym of *Saturnosphaera gracilis* TICHOMIROVA, 1975. Likewise in the classification of PESSAGNO, 1979, adopted by De WEVER, 1981, *Saturnosphaera gracilis* TICHOMIROVA, 1975, had to be replaced as a homonym of *Spongosaturnalis gracilis* KOZUR & MOSTLER, 1972, because in this classification both species belong to *Pseudoheliodiscus* KOZUR & MOSTLER, 1972 emend. PESSAGNO, 1979.

The 2 species, placed in *Saturnosphaera* TICHOMIROVA, 1975, do not belong to this genus, but to *Hungarosaturnalis* n.gen. They have a coarsely latticed cortical shell, 4 bladed polar spines in cross position, and a different central structure (see Austrisaturnalidae n.fam.). The assignment to the genus *Saturnosphaera* TICHOMIROVA, 1975, was most probably preferred because of the drawings by TICHOMIROVA, 1975, in which a latticed cortical shell is shown for *Saturnosphaera* TICHOMIROVA, 1975. But no photo indicates such a shell and the only *Saturnosphaera* species from which the shells are clearly known, *Saturnosphaera radiosa* (De WEVER, 1981) shows spongy cortical shells.

Genus *Mesosaturnalis* KOZUR & MOSTLER, 1981

Type species: *Palaeosaturnalis levis* DONOFRIO & MOSTLER, 1978

Diagnosis: Single ring circular to subcircular, variably wide but mostly broad, always flat and undifferentiated. Whole outer margin with spines. Two polar spines, always situated opposite to interspine spaces on the outer margin of the ring. No auxiliary spines.

Cortical shells spongy, outer one always considerably smaller than the inner diameter of the ring. Medullary shell(s) latticed.

Occurrence: Sevatian (very rare) to Upper Cretaceous (frequent).

Included species: See KOZUR & MOSTLER, 1981, p. 57-58.

Remarks: The polar spines of *Palaeosaturnalis* DONOFRIO & MOSTLER, 1978, are situated opposite to spines on the outer margin of the ring.

Praemesosaturnalis KOZUR & MOSTLER, 1981, has auxiliary spines.

Spongosaturnalis CAMPBELL & CLARK, 1944, always has a very narrow ring at least with round cross section but mostly bladed, with swellings or furrows.

Praemesosaturnalis KOZUR & MOSTLER, 1981

Type species: *Spongosaturnalis bifidus* KOZUR & MOSTLER, 1972

Diagnosis: Single ring circular to subcircular, variably wide but mostly broad, always flat and undifferentiated. Whole outer margin with spines that are sometimes considerably differentiated. Two polar spines, one of these or both opposite to interspine spaces on the outer margin of the ring. Auxiliary spines always present.

Cortical shells spongy, outer one reaches to or almost to the inner margin of the ring. Medullary shell(s) latticed.

Included species: *Spongosaturnalis bifidus* KOZUR & MOSTLER, 1972
Spongosaturnalis gracilis KOZUR & MOSTLER, 1972
Spongosaturnalis latifolius KOZUR & MOSTLER, 1972
Spongosaturnalis multidentatus KOZUR & MOSTLER, 1972
Spongosaturnalis ? sp. FOREMAN, 1971
Saturnalin gen. et spec. indet. FOREMAN, 1971
? *Pseudoheliodiscus pamphyliensis* De WEVER, 1981
Pseudoheliodiscus poissoni De WEVER, 1981

Remarks: The polar spines of *Pseudoheliodiscus* KOZUR & MOSTLER, 1972, are always situated opposite to marginal spines.

Mesosaturnalis KOZUR & MOSTLER, 1981, has no auxiliary spines.

Subfamily Acanthocircinae PESSAGNO, 1977 emend.

Emended diagnosis: Ring perpendicular to the axis of polar spines, strongly elongated or at the poles perpendicular to the polar spines with long spines, or these both characters are combined. Ring always very narrow, mostly bladed, with swellings or furrows, in most primitive taxa with oval to round cross section without differentiation. Outer margin of ring sometimes smooth but mostly with spines, often restricted to the poles of the long axis, sometimes also with spines along the whole outer margin.

Cortical shells spongy, medullary shell tiny, with large pores. Almost exclusively two polar spines are present. Only in the most primitive *Praeacanthocircus* n.gen. in addition to the 2 polar spines 4 spines of almost the same size are present.

Occurrence: Carnian-Upper Cretaceous, in the Upper Triassic extremely rare. Frequent from the Bajocian to the Upper Cretaceous.

Included genera: *Acanthocircus* SQUINABOL, 1903
Synonym: *Spongosaturninus* CAMPBELL & CLARK, 1944
Praeacanthocircus n.gen.

Remarks: The Parasaturnalinae KOZUR & MOSTLER, 1972, have a double or multiple ring with circular outline.

The Heliosaturnalinae KOZUR & MOSTLER, 1972 emend., have a flat, mostly broad, circular spiny ring. Besides the 2 or rarely more polar spines, auxiliary spines are often present.

The hexasaturnalinae n.subfam. have a hexagonal, subquadratic, polygonal or subcircular outline of the ring.

Genus *Acanthocircus* SQUINABOL, 1903

Type species: *Saturnulus trizonalis* RÜST, 1898
= *Acanthocircus irregularis* SQUINABOL, 1903

Synonym: *Spongosaturninus* CAMPBELL & CLARK, 1944

Diagnosis: Unit strongly elongated perpendicularly in the direction of the axis of the polar spines by a ring which is mostly strongly elongated in this direction, by long terminal spines on the poles perpendicularly to the polar spines or by both features together. Ring very narrow, bladed or with swellings or furrows, only in the most primitive taxa not differentiated, but with round or oval cross section. Outer margin of ring rarely smooth, mostly with spines in the polar region of the long axis, sometimes with spines along its outer margin. Two polar spines. No other first order spines or auxiliary spines.

Cortical shell spongy, medullary shell tiny, latticed.

Occurrence: Liassic-Upper Cretaceous.

Remarks: *Spongosaturnalis* CAMPBELL & CLARK, 1944, always has a totally spined ring of circular to subcircular outline.

Palaeosaturnalis DONOFRIO & MOSTLER, 1978, is distinguished by a circular, always flat and undifferentiated, mostly broad to very broad spiny ring.

Additional to the 2 polar spines *Praeacanthocircus* n.gen. still has 4 spines which have almost the same size as the polar spines.

Genus *Praeacanthocircus* n.gen.

Derivatio nominis: According to the similarity to *Acanthocircus* SQUINABOL, 1903, and the occurrence before this genus.

Type species: *Praeacanthocircus carnicus* n.gen.n.sp.

Diagnosis: Very narrow ring strongly elongated, perpendicularly to the polar spines. Outer margin smooth or with tiny spines in the polar region of the long axis. Cross section of ring oval. Two polar spines at the short axis of the ring and 4 further spines of almost the same size are present.

Cortical shells spongy. Outer one rather widely separated from the inner margin of the ring.

Occurrence: Cordevolian of Göstling (Austria). Liassik of Turkey.

Included species: *Praeacanthocircus carnicus* n.gen.n.sp.
Praeacanthocircus n.sp. (= *Pseudoheliodiscus* sp. A De WEVER, 1981).

Remarks: *Acanthocircus* SQUINABOL, 1903, has only two polar spines and no additional spines. Otherwise *Praeacanthocircus* n.gen. is identical with the most primitive Liassic species of *Acanthocircus* SQUINABOL, 1903, in which the ring is still undifferentiated.

Praeacanthocircus carnicus n.gen.n.sp.

(Pl. 2, fig. 2)

Derivatio nominis: According to the occurrence in the Carnian.

Holotype: The specimen on pl. 2, fig. 2; rep. no. T 5836

Locus typicus: Göstling (Austria).

Stratum typicum: Sample AS 7, Upper Cordevolian (see MOSTLER & SCHEURING, 1974).

Diagnosis: With the character of the genus. Outer margin of ring quite smooth.

Measurements: Long axis: 250 µm. Short axis: 170 µm.

Occurrence: Only one specimen from the locus typicus is known.

Remarks: Only one slightly damaged specimen is known from the huge radiolarian material of the Cordevolian from Göstling. Because of its decisive importance for the knowledge of the early evolution of Acanthocircinae PESSAGNO, 1977, it is described here in spite of the unsufficient representation.

The outline of the smooth, very narrow ring, its oval cross section and the position of the polar spines in the short axis, is quite identical with that of *Acanthocircus* SQUINABOL, 1903, and quite different from the contamporaneous Palaeosaturnalini KOZUR & MOSTLER, 1981. Moreover, the cross section of the ring is already oval and not quite flat like in all Heliosaturnalinae KOZUR & MOSTLER, 1972 (including the Palaeosaturnalini KOZUR & MOSTLER, 1981).

Praeacanthocircus n.sp. (= *Pseudoheliodiscus* sp. A sensu De WEVER, 1981) is distinguished by the presence of tiny spines at the outer margin of the ring in the polar region of the long axis.

Subfamily Hexasaturnalinae n.subfam.

Diagnosis: Ring always narrow, outline hexagonal, subquadratic, polygonal and in the stratigraphically youngest taxa also subcircular. Ring always narrow, in transitional taxa at least with oval to round cross section, but mostly strongly bladed and with furrows. 2, very rarely 4 polar spines (in cross position) are present. The polar spine attachment segment of the ring is often depressed inwards. Auxiliary spines very rarely present.

Cortical shells spongy, mostly widely detached from the ring. Medullary shell(s) latticed, at least in some taxa relatively large.

Occurrence: Norian to Upper Cretaceous.

Included genera: *Hexasaturnalis* n.gen.
Spongosaturnalis CAMPBELL & CLARK, 1944
Praehexasaturnalis n.gen.
Stauracanthocircus n.gen.
Yaosaturnalis n.gen.

Remarks: The Heliosaturnalinae KOZUR & MOSTLER, 1972 emend. always have a flat undifferentiated, more or less broad, circular, rarely subcircular ring. In the Hexasaturnalinae n.subfam. only the transitional genus to the Heliosaturnalinae KOZUR & MOSTLER, 1972 emend., *Praehexasaturnalis* n.gen.

from the Norian, still has a flat ring, but already the typical hexagonal to octogenal outline of the narrow ring. The likewise primitive Liassic *Stauracanthocircus* n.gen. has a very narrow ring without differentiation, but already with oval cross section. In all other genera of the Hexasaturnalinae n.subfam. the narrow ring is highly differentiated (mostly strongly bladed) or has a round cross section.

As mentioned above, already the oldest transitional genus (*Praehexasaturnalis* n.gen.) of the Hexasaturnalinae n.subfam. has the typical hexagonal to octogonal outline of the ring. Highly evolved Hexasaturnalinae n.subfam. from the Upper Cretaceous often have a secondary subcircular outline of the ring (evolved from polygonal taxa), but they are clearly distinguished from the contemporaneous Heliosaturnalinae KOZUR & MOSTLER, 1972 emend., with circular, but flat and broad ring by their very narrow ring with round cross section or mostly with differentiations (bladed, swellings, furrows).

The Acanthocircinae PESSAGNO, 1977, have a similar cross section and differentiation of the ring as the Hexasaturnalinae n.fam., but the ring (+ spines) is always considerably elongated perpendicularly to the axis of the polar spines. The development of both subfamilies has been different since the Triassic.

The Parasaturnalinae KOZUR & MOSTLER, 1972, have a double or multiple ring, always with circular outline.

The subcircular Upper Cretaceous taxa of the Hexasaturnalinae n.subfam. are already very similar to the Saturnalidae DEFLANDRE, 1953, and only distinguished by the presence of spongy cortical shells. Apparently by the loss of these shells the Saturnalidae DEFLANDRE, 1953, evolved from the Hexasaturnalinae n.subfam., but a quite independent development from Spumellaria with latticed cortical shell and without rings cannot be quite excluded at the present day state of knowledge.

Genus *Hexasaturnalis* n.gen.

Derivatio nominis: According to the outline.

Type species: *Spongosaturnalis ? hexagonus* YAO, 1972

Diagnosis: Ring and outer spines strongly bladed. Outline of ring hexagonal to octogenal or subquadratically rounded. 4-8 very strong outer spines. Two massive polar spines opposite to interspine spaces on the outer margin of the ring. No auxiliary spines. Ring often a little constricted in the polar spine attachment region.

Cortical shells spongy, widely separated from the inner margin of the ring. Medullary shell latticed.

Occurrence: Bajocian to Upper Cretaceous.

Included species: *Spongosaturnalis ? hexagonus* YAO, 1972
? Saturnalis euganeus SQUINABOL, 1914
Spongosaturnalis (?) sp. FOREMAN, 1973
Spongosaturnalis ? inuyamensis YAO, 1972
Spongosaturnalis ? septispinus YAO, 1972
Spongosaturnalis ? tetraspinus YAO, 1972

Remarks: By increase of the number of marginal spines the hexagonal to octogonal outline of the ring is transformed to a polygonal to subcircular one. In this manner the genus *Spongosaturnalis* CAMPBELL & CLARK, 1944, evolved in the Cretaceous from *Hexasaturnalis* n.gen.

Praehexasaturnalis n.gen. from the Norian has the same outline of ring, but the polar spines are still situated opposite to the marginal spines and the narrow ring is still flat to shallow oval in cross section.

Yaosaturnalis n.gen. has the same outline and structure of ring as *Hexasaturnalis* n.gen., but auxiliary spines are present.

Genus *Spongosaturnalis* CAMPBELL & CLARK, 1944

Type species: *Saturnalis multidentatus* SQUINABOL, 1914[1]
(= *Spongosaturnalis spiniferus* CAMPBELL & CLARK, 1944)

Diagnosis: Ring very narrow with cross section or differentiated (bladed, with swellings or furrows). Outline of ring subcircular, more or less constricted in the attachment regions of the 2 polar spines which are always situated opposite to the interspine spaces on the outer margin of the ring. Whole outer margin of ring with numerous spines.,

Cortical shells spongy, outer one widely separated from the inner margin of the ring. Medullary shell(s) latticed.

Occurrence: Middle and Upper Cretaceous.

Remarks: In general *Acanthocircus* SQUINABOL, 1903, has quite a different outline of the ring and the spines are mostly restricted to the polar region of the long axis. Also the *Acanthocircus* species with totally spined ring are mostly quite different by an elongated outline of the ring. Only *Acanthocircus italicus* (SQUINABOL, 1914) with suboval outline is similar, but on the other hand this species is rather different from the genus *Acanthocircus* SQUINABOL, 1903, as defined by its type species.

Hexasaturnalis n.gen. is distinguished by its hexagonal to octogonal ring outline and the fewer but larger spines. By increase of the spine number the ring outline of *Hexasaturnalis* n.gen. has changed through polygonal to subcircular. By this *Spongosaturnalis* CAMPBELL & CLARK, 1944, has seemingly evolved from *Hexasaturnalis* n.gen.

Genus *Praehexasaturnalis* n.gen.

Type species: *Palaeosaturnalis tenuispinosus* DONOFRIO & MOSTLER, 1978

Derivatio nominis: According to the supposed phylogenetic line *Praehexasatur-*

[1]footnote: Holotype here defined by the specimen figured by SUINABOL, 1914, on pl. 23, fig. 11

Genus *Praehexasaturnalis* n.gen.

Type species: *Palaeosaturnalis tenuispinosus* DONOFRIO & MOSTLER, 1978

Derivatio nominis: According to the supposed phylogenetic line *Praehexasaturnalis* n.gen. -- *Hexasaturnalis* n.gen.

Diagnosis: Ring narrow but not differentiated yet. Its cross section is flat. Outline of ring hexagonal to octogonal. 8-6 very strong marginal spines. 2 polar spines opposite to marginal spines. No auxiliary spines. No auxiliary spines.

Cortical shells spongy. Medullary shells latticed.

Occurrence: Norian of the Tethyan realm.

Included species: *Palaeosaturnalis tenuispinosus* DONOFRIO & MOSTLER
Spongosaturnalis elegans KOZUR & MOSTLER, 1972

Remarks: In the ring outline this new genus is quite identical with *Hexasaturnalis* n.gen. but the ring is still flat to shallow oval in cross section and has no ridges. Moreover, the polar spines are situated opposite to the marginal spines.

Palaeosaturnalis DONOFRIO & MOSTLER, 1978, is distinguished by its circular outline. Moreover, in the most species the ring is broader.

Praehexasaturnalis n.gen. is a perfect transitional form between *Palaeosaturnalis* DONOFRIO & MOSTLER, 1978, and *Hexasaturnalis* n.gen. As for the first time in this genus the typical ring outline of the Hexasaturnalinae n.subfam. appears, it is already placed in this subfamily.

Genus *Stauracanthocircus* n.gen.

Derivatio nominis: According to the 4 polar spines in cross position.

Type species: *Pseudoheliodiscus concordis* De WEVER, 1981

Diagnosis: Ring with flat to oval cross section, very narrow, spiny, outline subquadratic to suboval, in the shorter axis always a little constricted. 4 polar spines in cross position. No auxiliary spines.

Cortical shells spongy, widely separated from the inner margin of the ring. Medullary shell latticed.

Occurrence: ? Rhaetian, Pliensbachian.

Included species: *Pseudoheliodiscus concordis* De WEVER, 1981
Stauracanthocircus n.sp. (= *Pseudoheliodiscus* sp. aff. *concordis* De WEVER, 1981)

Remarks: *Spongosaturnalis* CAMPBELL & CLARK, 1944, has only 2 polar spines and a subcircular ring outline. The ring has a round cross section or is differentiated (bladed etc.).

Stauracanthocircus n.gen. derived from a new genus within the Palaeosaturnalini KOZUR & MOSTLER, 1981, which still has the typical circular, broad, flat ring, but already 4 polar spines in cross position. *Spongosaturnalis quadriradiatus* KOZUR & MOSTLER, 1972, and n.gen.n.sp. (= *Pseudoheliodiscus* ? *quadriradiatus* KOZUR & MOSTLER, 1972 sensu De WEVER, 1981) belong to this new genus. The latter species would be a good type species, but we have no material from this species. *Spongosaturnalis quadriradiatus* KOZUR & MOSTLER, 1972, in turn, is still somewhat transitional to *Pseudoheliodiscus* KOZUR & MOSTLER, 1972 emend. PESSAGNO, 1979, and therefore not a good type species for the new genus. In this species two opposite polar spines are still clearly smaller than the perpendicular two ones. The latter are true polar spines, whereas the two smaller ones are still transitional between first order polar spines and second order auxiliary spines.

Genus *Yaosaturnalis* n.gen.

Derivatio nominis: In honour of Prof. Dr. A. YAO, Osaka.

Type species: *Spongosaturnalis* ? *minoensis* YAO, 1972

Diagnosis: Ring and spines strongly bladed. Outline of the ring hexagonal. 6 very strong outer spines. 2 polar spines opposite to interspine spaces on the outer margin of the ring. 2-4 small auxiliary spines. Cortical shells spongy.

Occurrence: Bajocian of Japan and Hungary.

Included species: *Spongosaturnalis* ? *minoensis* YAO, 1972

Remarks: *Hexasaturnalis* n.gen. has no auxiliary spines but it is identical otherwise.

Family Veghicyclidae KOZUR & MOSTLER, 1972

Diagnosis: One-layer latticed sisk outside with large spines, inner margin indistinct. In well preserved specimens the latticed disk reaches almost to the centre. Innermost part of the latticed disk very thin and therefore often broken away. Pores in the outer part of disk distinctly to indistinctly conentrically arranged, in the inner part arranged more irregularly. In the central opening of the disk always 4 short thin spines in cross position are present which run to a tiny microsphere which is surrounded by spongy shells.

Cortical shell(s) mostly lenticular, sometimes globular, covering about the half or more of the latticed disk. Sometimes the whole latticed part of disk is covered by a spongy layer ending near the disk margin in a circular carina. In this case a lenticular shell is present only in the central part.

Occurrence: Upper Triassic, most frequent in the Carnian, rarely in the Norian.

Included genera: *Veghicyclia* KOZUR & MOSTLER, 1972
Carinacyclia KOZUR & MOSTLER, 1972

Remarks: The Veghicyclidae KOZUR & MOSTLER, 1972, are the oldest representatives of the Lithocycliacea EHRENBERG, 1854 emend. KOZUR & MOSTLER, 1972, 1981, with latticed disk. In *Carinacyclia* KOZUR & MOSTLER, 1972, even the spongy covering layer of the latticed disk is present.

No real ring structures are present between the pores. By this also specimens with fully preserved spongy shells can be easily distinguished from the Heliosaturnalini KOZUR & MOSTLER, 1972. As visible in specimens with removed spongy shells, the inner structure of the Heliosaturnalini KOZUR & MOSTLER, 1972 (and therefore also of the Parasaturnalidae KOZUR & MOSTLER, 1972 emend.) and of the Veghicyclidae KOZUR & MOSTLER, 1972, is quite different. No latticed disk is present in any parasaturnalid genus. Most probably the latticed disk has evolved by inward growing of the ring in the Heliosaturnalinae KOZUR & MOSTLER, 1972 emend., in a way that connecting bars were built up between the auxiliary spines.

Like the modern Lithocycliacea EHRENBERG, 1854, the genus *Carinacyclia* KOZUR & MOSTLER, 1972 already has a spongy covering layer on the upper and lower side of the latticed disk, still not present in *Veghicyclia* KOZUR & MOSTLER, 1972. Therefore both genera are rather different in their structures and the placing of both genera in one by PESSAGNO, 1979, is not well understandable.

In any case the Veghicyclidae KOZUR & MOSTLER, 1972, are the basic group for Lithocycliacea EHRENBERG, 1854, with latticed disk, whereas the Heliodiscinae KOZUR & MOSTLER, 1972 emend. (Parasaturnalidae KOZUR & MOSTLER, 1972 emend.) are the basic group for the spumellarian saturnalids. Because of this fact and the striking differences in the inner strucutres between the Veghicyclidae KOZUR & MOSTLER, 1972, and the Palaeosaturnalidae KOZUR & MOSTLER, 1972 emend., it is impossible to place the Veghicyclidae KOZUR & MOSTLER, 1972, as subfamily in the Parasaturnalidae KOZUR & MOSTLER, 1972, as proposed by PESSAGNO, 1979, and adopted by De WEVER, 1981.

Genus *Veghicyclia* KOZUR & MOSTLER, 1972

Type species: *Veghicyclia pulchra* KOZUR & MOSTLER, 1972

Remarks: As already pointed out in KOZUR & MOSTLER, 1978 (appendix) *Veghicyclia robusta* KOZUR & MOSTLER, 1972, is a synonym of *V. austriaca* KOZUR & MOSTLER, 1972. The differences are caused by intraspecific variations.

Veghicyclia multispinosa KOZUR & MOSTLER, 1972 is a synonym of *V. globosa* KOZUR & MOSTLER, 1972. The globular shell is partly destroyed in the material of *V. multispinosa* KOZUR & MOSTLER, 1972, therefore it seems to be shallower (more lenticular). So the differences between these two species are only preservation-controlled.

The specimen figured by KOZUR & MOSTLER, 1972, on pl. 3, fig. 2, belongs to *V. goestlingensis* KOZUR & MOSTLER, 1972, and not to *V. haeckeli* KOZUR & MOSTLER, 1972. The specimen figured by KOZUR & MOSTLER, 1972, on pl. 3, fig. 3, belongs to *V. haeckeli* KOZUR & MOSTLER, 1972, and not to *V. austriaca* KOZUR & MOSTLER, 1972.

Superfamily Sponguracea HAECKEL, 1862 emend. KOZUR & MOSTLER, 1981

Family Oertlispongidae KOZUR & MOSTLER, 1980

Genus *Oertlispongus* DUMITRICĂ, KOZUR & MOSTLER, 1980

Type species: *Oertlispongus inaequispinosus* DUMITRICĂ, KOZUR & MOSTLER, 1980

Oertlispongus annulatus n.sp.

(Pl. 1, fig. 6)

Derivatio nominis: According to the ring-like main spine.

Holotype: The specimen on pl. 1, fig. 6; rep. no. T 5839.

Locus typicus: Tretto (Vicentinian Alps).

Stratum typicum: Sample TT 13, Lower Ladinian.

Diagnosis: Spongy spherical shell consists of numerous concentric layers. Polar spine recurvated ring-like. The distal end of this stout polar spine is connected with the shell. Minor spine in polar position, straight, often absent. By-spines in a bunch in the middle part of the shell, often absent.

Measurements: Diameter of shell: 109-123 µm.

Occurrence: Lower Ladinian of the Southern Alps.

Remarks: The strongly recurvated distal end of *Oertlispongus longicurvatus* n.sp. is not connected with the shell.

Oertlispongus longirecurvatus n.sp.

(Pl. 1, fig. 5)

Derivatio nominis: According to the very long, extremely strongly recurvated polar spine.

1982 *Oertlispongus inaequispinosus* DUMITRICĂ, KOZUR & MOSTLER - DUMITRICĂ, p. 64-65, pl. 1, figs. 6, 7, 9, non! figs. 2, 4.

Holotype: The specimen on pl. 1, fig. 5; rep. no. T 5838.

Locus typicus: Recoaro (Vicentinian Alps).

Stratum typicum: Sample MD 1, Lower Ladinian.

Diagnosis: Spongy shell spherical with 5-8 concentrical layers. Main spine stout, strongly recurvated in the direction of the shell, but not connected with it. Minor spine rarely preserved (? or not present). By-spines in a bunch on the middle part of the shell, sometimes missing.

Measurements: Diameter of shell: 86-91 µm. Length of straight part of spine: 85-98 µm. Length of recurvated part of spine: 181-207 µm.

Occurrence: Lower Ladinian of the Southern Alps and of Transsylvanian Nappes.

Remarks: In *Oertlispongus inaequispinosus* DUMITRICĂ, KOZUR & MOSTLER, 1980, the main spine is never recurvated in the direction of the shell.

In *Oertlispongus annulatus* n.sp. the recurvated part is attached to the shell.

Conclusions

As shown in the example of saturnalids, all characters of the radiolarians have to be considered to get a more reliable classification of this fossil group. To regard only the shell structure and the presence or absence of auxiliary spines as suprageneric characters like in the classification of PESSAGNO, 1979, adopted by De WEVER, 1981, and regarded there as natural "non-Haeckelian" classification, does not give a classification near to the natural one.

As known since HAECKEL the morphology is one of the most important characters for the classification of the radiolarians. Because of a lot of homeomorphies, the outer morphology cannot be the only criterion of the radiolarian classification. But likewise also the shell structures show considerable homeomorphy. Spongy and latticed shell structures developed independently in several families of all radiolarian suborders.

Besides the outer morphology (including the presence or absence of bipolarity) and shell structures the central structure of the radiolarians (presence or absence of a central spicular system) is an important feature for the suprageneric systematics of radiolarians. In the special case of the saturnalids the following features should be considered: Outline, cross section and sculpture of ring, presence, distribution and form of marginal spines, number and differentiation of polar spines, presence or absence of auxiliary spines. Size and structures of cortical and medullary shells, presence or absence of an internal spicular system.

The presence and absence of auxiliary spines is a subordinate character. Both in the spumellarian and entactinarian saturnalids genera with and without auxiliary spines are present. This is only a function of the size of the outermost cortical shell. If it reaches nearly or entirely to the inner margin of the ring, auxiliary spines are present. If the outermost cortical shell is widely separated from the ring, second order auxiliary spines are absent. The presence or absence of auxiliary spines is here considered only as a generic character and not a suprageneric one like in the classification by PESSAGNO, 1979, adopted by De WEVER, 1981. Perhaps it is only a species difference.

Only the consideration of the above mentioned three main characters (outer morphology, shell structure, and central structure) and above all the changes of these characters in phylomorphogenetic lines will finally give us a more natural classification of the radiolarians.

According to the central structure the Mesozoic saturnalids belong to 2 suborders, to the Entactinaria KOZUR & MOSTLER, 1982, with internal spicular system, until now only found in Triassic saturnalids, and to the Spumellaria EHRENBERG, 1875, which represent the main stock of saturnalids.

Within the spumellarian saturnalids we can observe the following trends: There is a conservative stock (Heliosaturnalinae KOZUR & MOSTLER, 1972 emend.) with more or less broad, entirely flat and undifferentiated spiny ring.

The only more important supraspecific change within this group is the shifting of the polar spines from a position opposite to the marginal spines in a position opposite to the interspine spaces. This is a rectilinear evolution. In the Carnian all species belong to the first group (polar spines opposite to marginal spines), from the Norian to the Bajocian both groups occur with decreasing frequency of the first one, and from the Upper Jurassic to the Upper Cretceous only the latter group occurs.

A second supraspecific development in the Heliosaturnalinae is the transformation of second order auxiliary spines into first order spines, so that the polar spines and the auxiliary spines cannot be distinguished any more. This development only occurs in some taxa. By this development genera with 4 or more first order spines evolved (e.g. *Saturnosphaera* TICHOMIROVA, 1975). This is a blind ending development and cand be observed only from the Norian to the Liassic (see table 1).

The Heliosaturnalinae KOZUR & MOSTLER, 1972 emend., are the basic group for all other spumellarian saturnalids and most probably also for typical representatives of the Lithocycliacea EHRENBERG, 1854 emend. KOZUR & MOSTLER, 1972, 1981, with latticed disk. The latter may have evolved from the Heliosaturnalinae KOZUR & MOSTLER, 1972 emend., by multiplication of the ring to a latticed disk.

The other spumellarian saturnalids evolved in several lines which started in different times during the Upper Triassic. The common character of all these derived spumellarian saturnalids is that the ring got very narrow, it got an oval to round cross section and finally it got more or less undifferentiated (bladed, swellings, furrows).

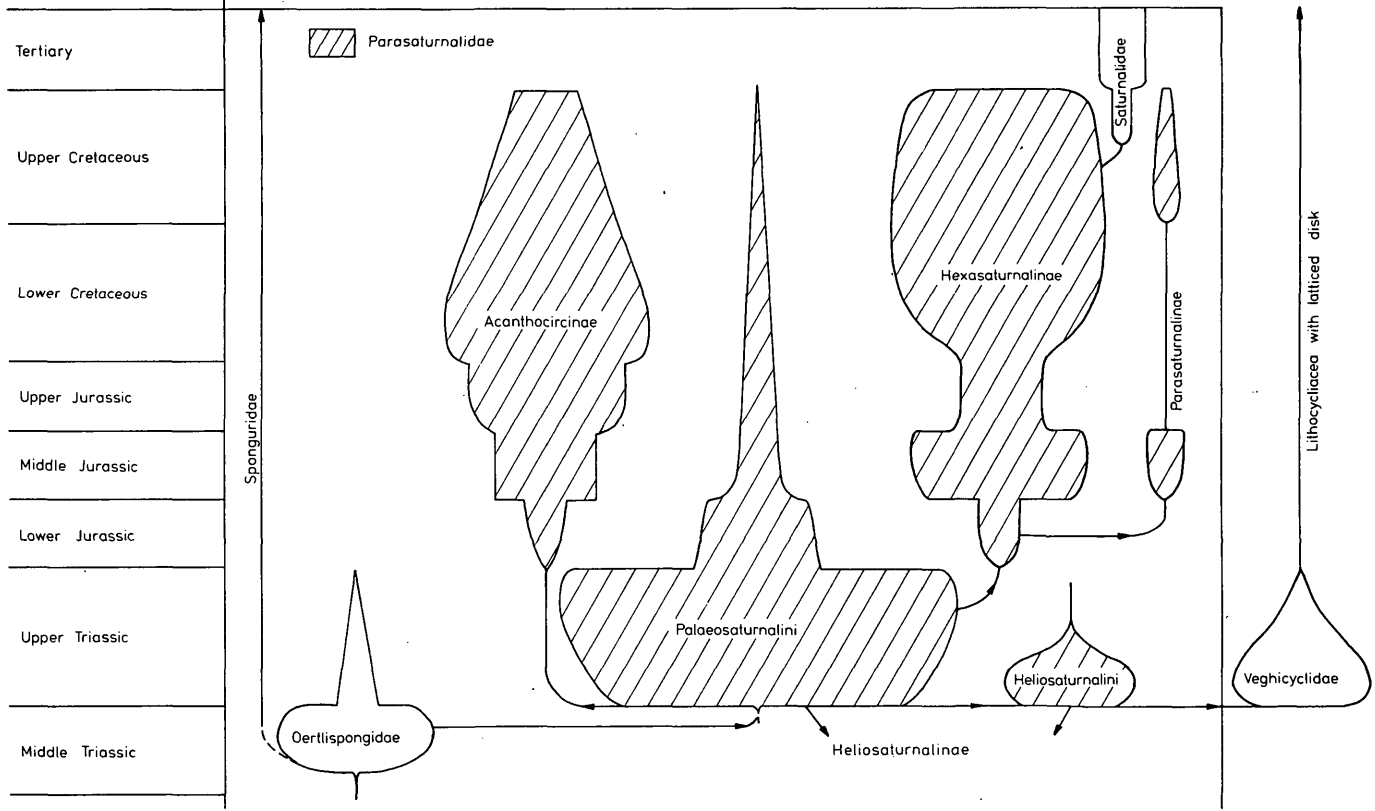
Already in the Lower Carnian (Cordevolian) the Acanthocircinae PESSAGNO, 1977 emend., and most probably both subfamilies have independently developed from the Oertlispongidae KOZUR & MOSTLER,1980. In the Acanthocircinae PESSAGNO, 1977 emend., not only the cross section of the ring changed, but also the outline of the ring. Already the ring of the most primitive Cordevolian Acanthocircinae is strongly elongated perpendicularly to the axis of the polar spines. This feature and the smooth ring in the most primitive Acanthocircinae indicate that the Heliosaturnalinae and the Acanthocircinae do not have the same forerunners within the Oertlispongidae. As in the Ortlispongidae in different lines ring structures or half-ring structures evolved and genera with smooth or spined half-rings occur, the assumption of different forerunners for the Acanthocircinae and Heliosaturnalinae within the Oertlispongidae is highly probable. Moreover, there exist taxa with round and more elongated half-rings within the Oertlispongidae.

The highly specialized Acanthocircinae were certainly not the forerunners of the Saturnalidae DEFLANDRE, 1953, because this family has no representatives with strongly elongated ring and the medullary shell of the Acanthocircinae is always a tiny latticed microsphere.

The Parasaturnalinae KOZUR & MOSTLER, 1972, surely derived directly from the Heliosaturnalinae KOZUR & MOSTLER, 1972 emend. They have preserved the circular outline of the rings and its quite spiny outer margin. The ring is double or multiple in this group, a development which iteratively occurs within the Parasaturnalidae KOZUR & MOSTLER, 1972 emend. But the growing mechanism of the double ring is quite different in the Heliosaturnalini KOZUR & MOSTLER, 1972, and in the Parasaturnalinae KOZUR & MOSTLER, 1972 (see these taxa).

Table 1

Distribution of the spumellarian saturnalids
(Sponguridae and Lithocycliacea with latticed disk without frequency scale)



The Hexasaturnalinae n.subfam. have directly evolved from the Heliosaturnalinae KOZUR & MOSTLER, 1972 emend., beginning in the Norian. At first only the outline of the ring has changed from circular to hexagonal or octogonal. All other characters of the Heliosaturnalinae remained unchanged in the beginning. Only later the ring got highly differentiated and finally some highly evolved taxa got again a subcircular outline of the ring, whereas the cross section of the ring remained round or the differentiation of the ring remained unchanged. These Hexasaturnalinae with secondarily subcircular ring may be the forerunners of the Saturnalidae DEFLANDRE, 1953, which are only distinguished by a latticed cortical shell instead of spongy ones.

References

De WEVER (1981): Parasaturnalidae, Pantanellidae et Sponguridae (Radiolaires polycystines) du Lias de Turquie. - Rev. Micropaléont. 24 (3), p. 138-156, 3 figs., 5 pls., Paris.

De WEVER, P.; SANFILIPPO, A. et al. (1979): Triassic radiolarians from Greece, Sicily and Turkey. - Micropaleontology, 25 (1), p. 75-110, 5 figs., 1 tab., 7 pls., New York.

DONOFRIO, D.A. & H. MOSTLER (1978): Zur Verbreitung der Saturnalidae (Radiolaria) im Mesozoikum der Nördlichen Kalkalpen und Südalpen. - Geol. Paläont. Mitt. Innsbruck, 7 (5), p. 1-55, 8 figs., 5 tabs., 7 pls., Innsbruck.

DUMITRICĂ, P. (1982): Triassic Oertlisponginae (Radiolaria) from Eastern Carpathians and Southern Alps. - D.S. Inst. Geol. Geofiz., 67 (3), p. 57-76, 12 pls., Bucureşti.

DUMITRICĂ, P.; KOZUR, H., & H. MOSTLER (1980): Contribution to the radiolarian fauna of the Middle Triassic of the Southern Alps. - Geol. Paläont. Mitt. Innsbruck, 10 (1), p. 1-46, 1 fig., 15 pls., Innsbruck.

FOREMAN, H.P. (1971): Cretaceous Radiolaria, Leg 7, DSDP. - In: WINTERER, E.L. et al.: Initial reports of the Deep Sea Drilling Project, 7 (2), p. 1673-1693, 5 pls., Washington.

FOREMAN, H.P. (1973): Radiolaria from DSDP Leg 20. - In: HEEZEN, B.C.; MacGREGOR, I.D., et al.: Initial reports of the Deep Sea Drilling Project, 20, p. 249-305, 1 fig., 4 tabs., 16 pls., Washington.

HAECKEL, E. (1882): Entwurf eines Radiolarien-Systems auf Grund von Studien der Challenger-Radiolarien. - Jena. Zeitschr. Naturwiss., 15 (n.F. 8), p. 418-472, Jena.

KOZUR, H. (1979): *Pessagnosaturnalis* n.gen., eine neue Gattung der Saturnalidae DEFLANDRE, 1953 (Radiolaria). - Z. geol. Wiss., 7 (5), p. 669-672, Berlin.

KOZUR, H. & H. MOSTLER (1972): Beiträge zur Erforschung der mesozoischen Radiolarien. Teil I: Revision der Oberfamilie Coccodiscacea HAECKEL 1862 emend. und Beschreibung ihrer triassischen Vertreter. - Geol. Paläont. Mitt. Innsbruck, 2 (8/9), p. 1-60, 4 pl., Innsbruck.

KOZUR, H. & H. MOSTLER (1978): Beiträge zur Erforschung der mesozoischen Radiolarien. Teil II: Oberfamilie Trematodiscacea HAECKEL 1862 emend. und Beschreibung ihrer triassischen Vertreter. - Geol. Paläont. Mitt. Innsbruck, 8 (Festschr. W. HEISSEL), p. 123-182, 5 pls., Innsbruck.

KOZUR, H. & H. MOSTLER (1981): Beiträge zur Erforschung der mesozoischen Radiolarien. Teil IV: Thalassosphaeracea HAECKEL 1862, Hexastylacea HAECKEL, 1882 emend. PETRUSEVSKAJA, 1979, Sponguracea HAECKEL, 1862 emend., und weitere triassische Lithocycliacea, Trematodiscacea, Actinommacea und Nassellaria. - Geol. Paläont. Mitt. Innsbruck, Sonderband, p. 1-208, 69 pls., Innsbruck.

MOSTLER, H. & B.W. SCHEURING (1974): Mikrofloren aus dem Langobard und Cordevol der Nördlichen Kalkalpen und das Problem des Beginns der Keupersedimentation im Germanischen Raum. - Geol. Paläont. Mitt. Innsbruck, 4 (4), p. 1-35, 2 figs., 2 tabs., 2 pls., Innsbruck.

NAKASEKO, K. & A. NISHIMURA (1979): Upper Triassic Radiolaria from southwest Japan. - Sci. rep., col. educ. Osaka Univ., 28 (2), p. 61-109, 1 fig., 1 tab., 12 pls., Osaka.

PESSAGNO, E.A. (1977): Upper Jurassic Radiolaria and radiolarian biostratigraphy of the California Coast Ranges. - Micropaleont., 23 (1), p. 56-113, 4 figs., 12 pls., New York.

PESSAGNO, E.A. & A. POISSON (1981): Lower Jurassic Radiolaria from the Gümüşlü allochthon of southwestern Turkey (Taurides occidentales). - Bull. Res. Expl. Inst. Turkey, 92, p. 47-69, 2 figs., 15 pls., Ankara.

TICHOMIROVA, L.B. (1975): Novyj rod Saturnpsphaera (radioljarii) iz kremnistych tolšč Sichote-Alinja. In: ŽAMOJDA, A.I.: Sistematičeskoe i stratigrafičeskoe značenie radioljarij; p. 52-58, 1 fig., 1 pl., Leningrad.

YAO, A. (1972): Radiolarian fauna from the Mino belt in the northern part of the Inoyama area, central Japan. Part I. Spongosaturnalids. - J. Geosci. Osaka City Univ., 15, p. 21-64.

Explanation of plates

PLATE 1

Figs. 1-3: *Pseudoheliodiscus ? interruptus* n.sp., sample Y 6. Fig. 1, 2: x 200; fig. 1: rep. no. T 5845, fig. 2: rep. no. T 5846. Fig. 3: holotype, x 260, rep. no. T 5837.

Fig. 4: *Pseudoheliodiscus bipartitus* (KOZUR & MOSTLER, 1972), somewhat deformed specimen, sample Y 6. x 160, rep. no. T 5838.

Fig. 5: *Oertlispongus longirecurvatus* n.sp., holotype, sample MD 1, x 320, rep. no. T 5839.

Fig. 6: *Oertlispongus annulatus* n.sp., holotype, sample MD 1, x 300, rep. no. T 5840.

PLATE 2

Fig. 1: *Spongosaturnaloides trispinosus* n.sp., holotype, sample AS 8, x 180, rep. no. T 5822.

Fig. 2: *Praeacanthocircus carnicus* n.gen.n.sp., holotype, sample AS 7, x 360, rep. no. T 5836.

Fig. 3: *Spongosaturnaloides quinquespinosus* (KOZUR & MOSTLER, 1972), sample AS 7, x 260, rep. no. T 5284.

Fig. 4: *Pseudoheliodiscus donofrioi* n.sp., holotype, sample Y 6, x 180, rep. no. T 5841.

PLATE 3

Fig. 1: *Spongosaturnaloides multidentatus* n.sp., holotype, sample AS 8, rep. no. T 5823, a) whole test, x 260; b) almost equatorial view, spicular system well visible, x 660; c) oblique equatorial view, spicular system well visible, x 1000.

Fig. 2: *Austrisaturnalis spinosus* n.sp., holotype, sample AS 7/13, x 400, rep. no. T 5826.

PLATE 4

Figs. 1, 2: *Hungarosaturnalis multispinosus* n.sp., sample X 12, fig. 1: holotype, x 260, rep. no. T 5828, a) plane view; b) oblique view; fig. 2: x 240, rep. no. T 5830.

Fig. 3: *Hungarosaturnalis longobardicus* n.sp., sample Köveskál 6, x 260, rep. no. T 5835.

PLATE 5

Fig. 1: *Palaeosaturnalis latiannulatus* n.sp., holotype, sample Zul'óv γ, x 150, rep. no. T 5842.

Fig. 2: *Palaeosaturnalis mocki* n.sp., holotype, sample Zul'óv γ, x 180, rep. no. T 5843.

Fig. 3: *Pseudoheliodiscus viejoensis* PESSAGNO, 1979, sample Zul'óv γ, x 280, rep. no. T 8544.

Fig. 4: *Hungarosaturnalis longobardicus* n.sp., holotype, sample Köveskál 6, x 220, rep. no. T 5834.

Fig. 5: *Hungarosaturnalis multispinosus* n.sp., the same specimen as on pl. 4, fig. 1, holotype, view in the plane of equatorial ring, sample X 12, x 260, rep. no. T 5828.

PLATE 6

Fig. 1: *Hungarosaturnalis multispinosus* n.sp., sample Köveskál 6, rep. no. T 5829, a) whole specimen, coarsely latticed medullary shell well visible, x 260, b) detail, interior part of medullary shell with spicular system, x 1300.

Fig. 2: *Palaeosaturnalis triassicus* (KOZUR & MOSTLER, 1972), sample AS 22, rep. no. T 5847, a) whole specimen, x 220, b) detail from the central part, x 1200.

PLATE 7

Fig. 1: *Austrisaturnalis* sp., steroscan photo, detail of innermost part, where 2 of the 4 first order polar spines are still connected. the other 2 are broken away in the central part and now only connected with the outer ring. Inside of the fragmentary medullary shell with large pores a bar-centred spicular system is clearly visible. 3 spines branch off from each end of the bar. Typical Entactinaria spicular system. Sample Köveskál 6, x 1300, rep. no. T 5833.

Figs. 2, 3: *Hungarosaturnalis multispinosus* n.sp., sample Köveskál 6, fig. 2: outer shell preserved, x 200, rep. no. T 5831, fig. 3: outer and inner shell destroyed, first order polar spines and auxiliary spines well visible, x 260, rep. no. T 5832.

Fig. 4: *Veghicyclia globosa* KOZUR & MOSTLER, 1972, sample AS 22, x 130, rep. no. T 5844.

Repository site: The material is deposited in the collection of the Hungarian Geological Institute, Budapest.

Plate 1

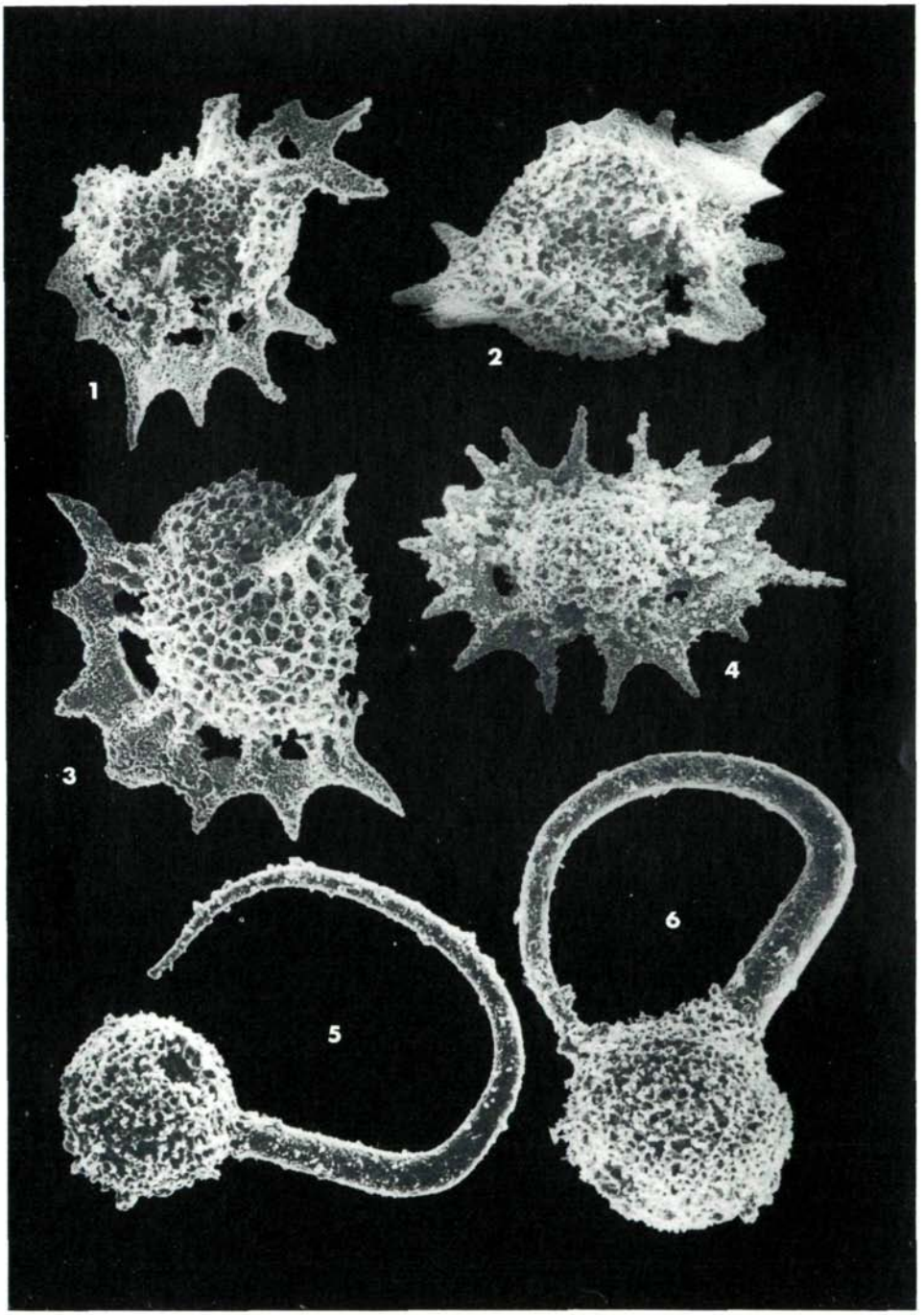


Plate 2

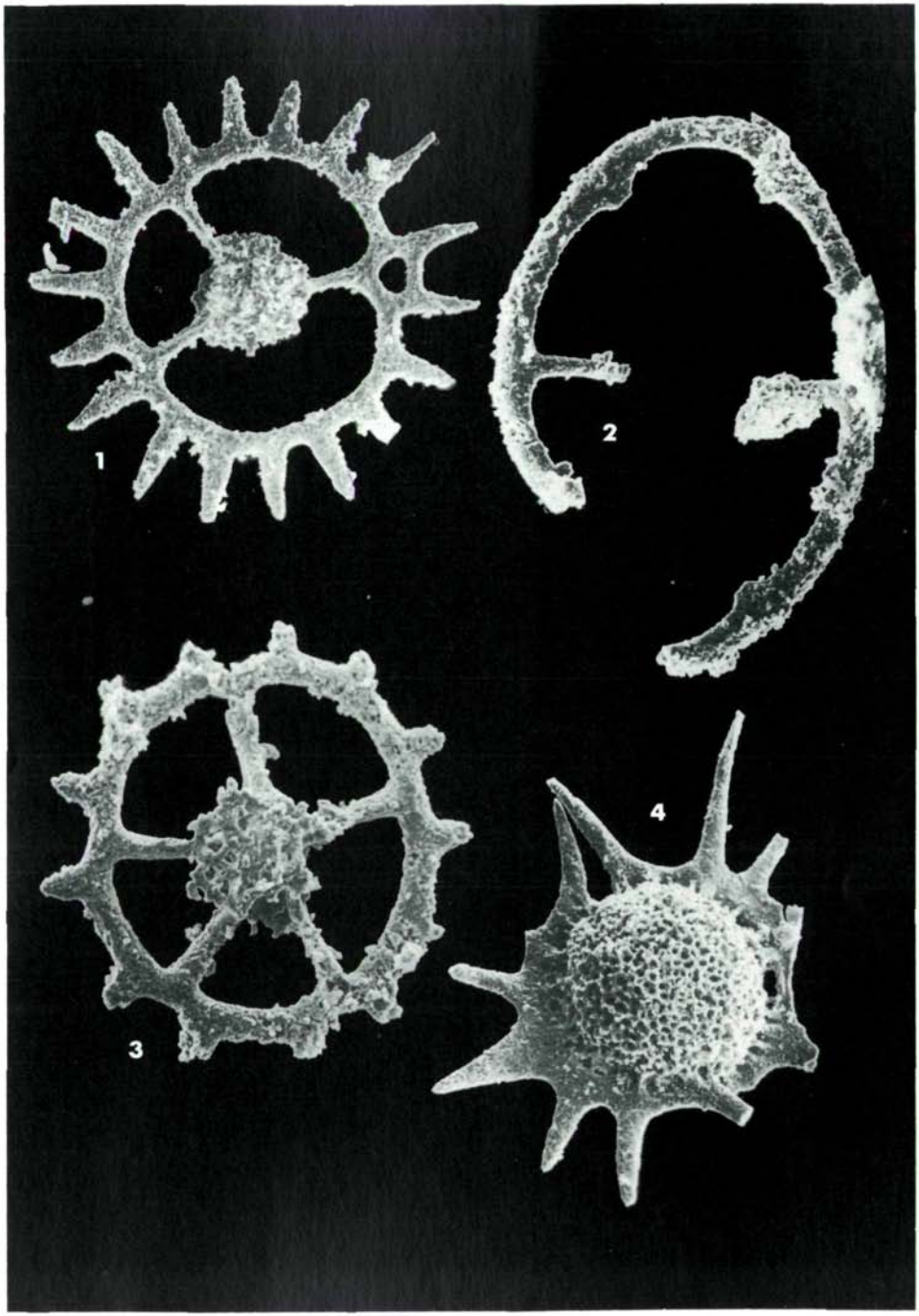


Plate 3

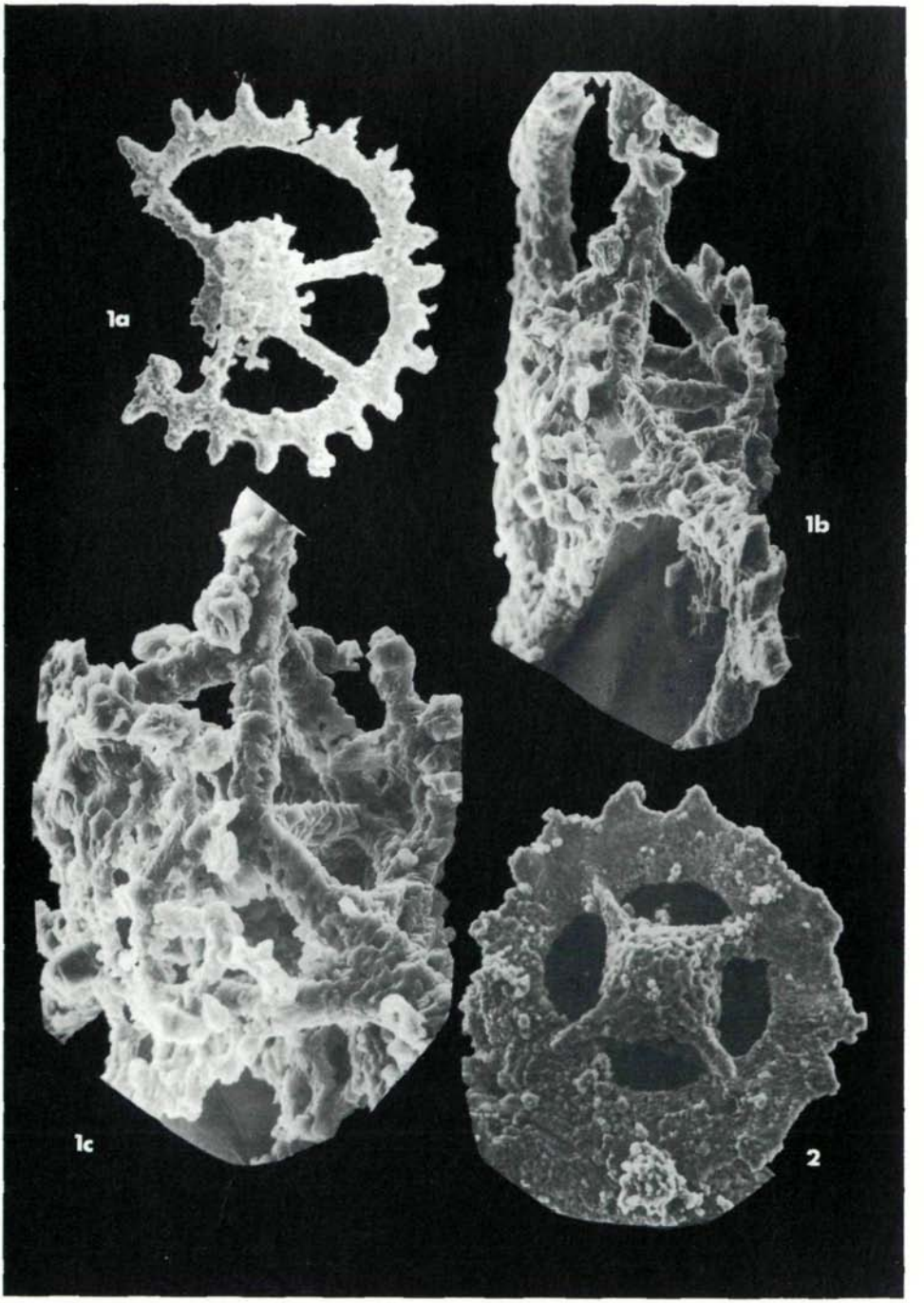


Plate 4

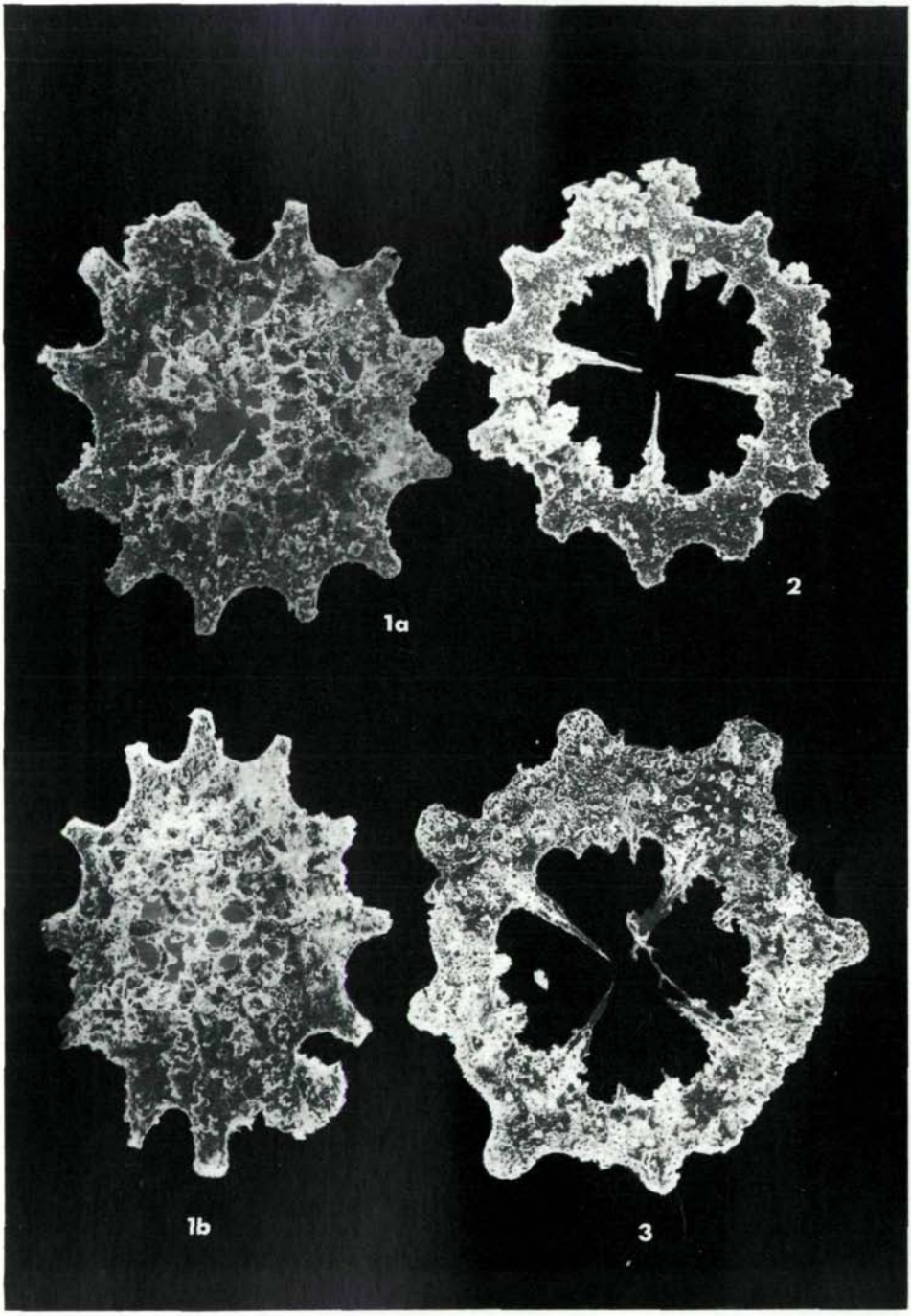


Plate 5

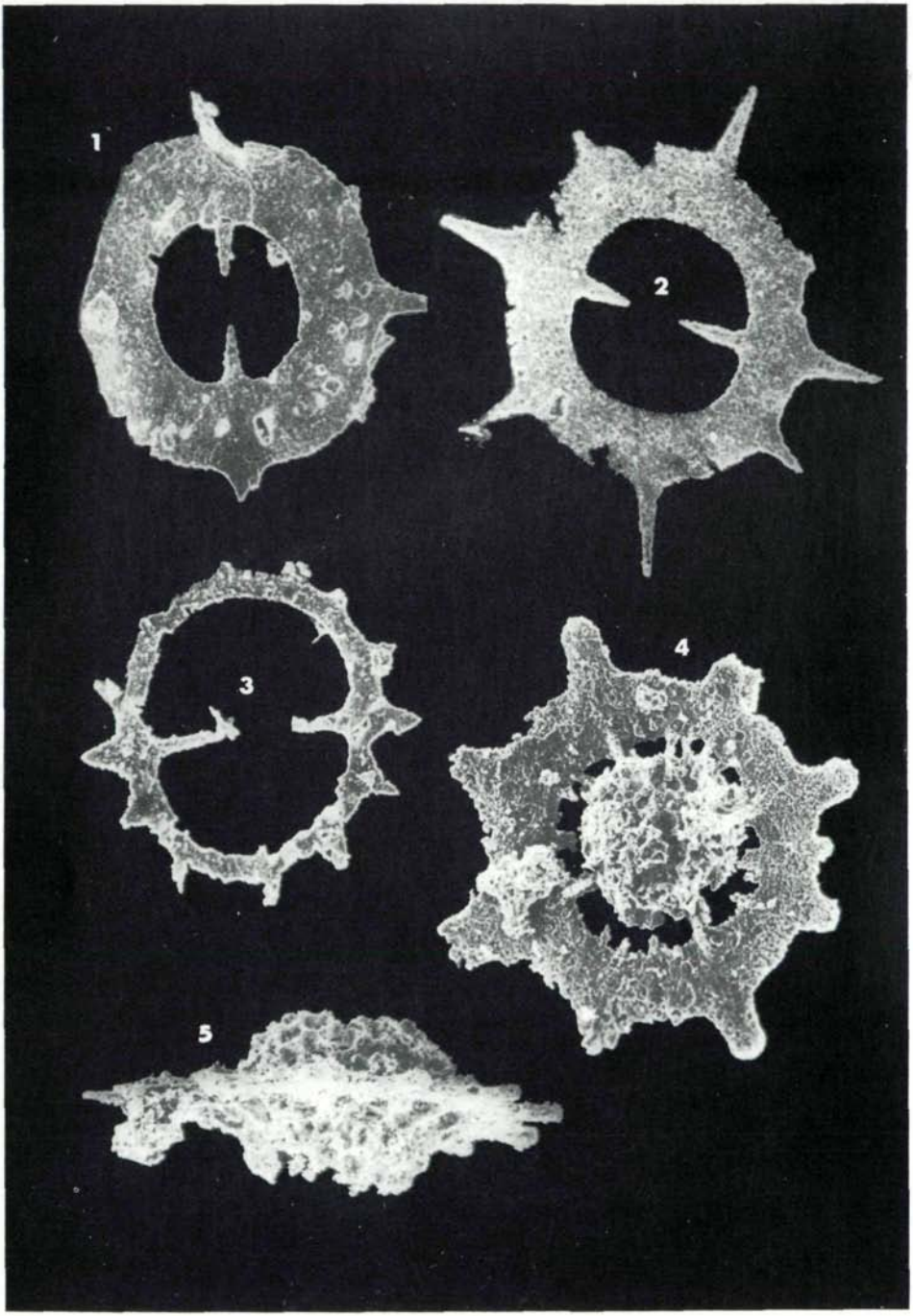


Plate 6

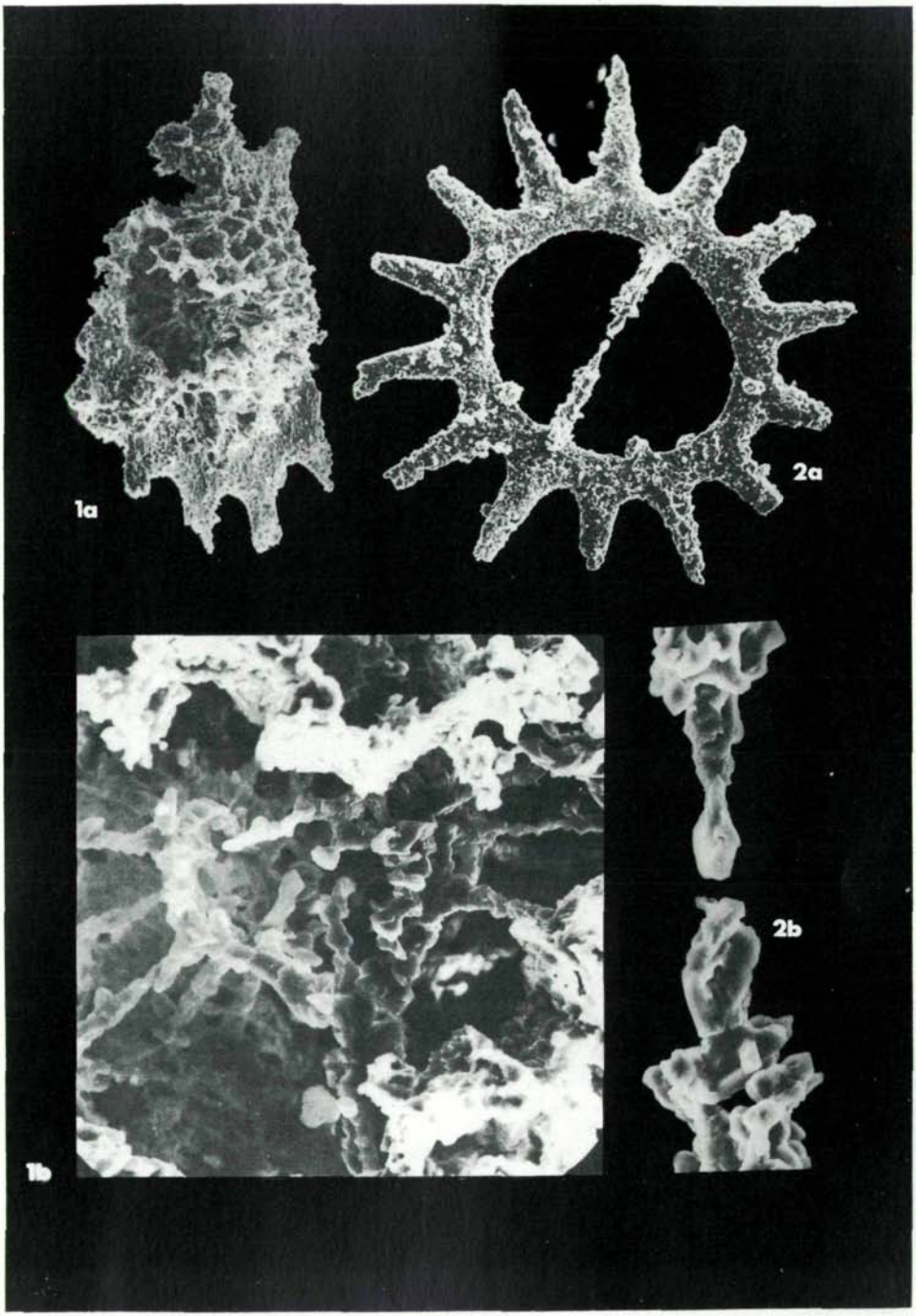


Plate 7