

SATURNALIACEA DEFLANDRE AND SOME OTHER STRATIGRAPHICALLY IMPORTANT RADIOLARIA FROM THE HETTANGIAN OF LENGGRIS/ISAR (BAVARIA, NORTHERN CALCAREOUS ALPS)

Heinz Kozur & Helfried Mostler

With 17 plates and 2 tables

Abstract: In the Kirchstein Limestone of the type locality 6.5 km WSW of Lenggris/Isar (Bavaria) rich radiolarian and sponge spicule associations have been discovered about 1 m above the Rhaetian Dachstein Limestone. The radiolarians indicate Hettangian age.

All discovered species of the Saturnaliacea DEFLANDRE, 1953 have been described. Additionally, the stratigraphically important species of other radiolarian families have been described. 2 families, 7 genera and 63 species have been newly established.

Zusammenfassung: Im Kirchsteinkalk der Typuslokalität 6,5 km WSW von Lenggris/Isar (Bayern) wurden ca. 1 m über dem rhätischen Dachsteinkalk reiche Radiolarien und Schwammspicula-Faunen entdeckt. Die Radiolarien zeigen Hettangian-Alter an.

Alle nachgewiesenen Arten der Saturnaliacea DEFLANDRE, 1953 werden beschrieben. Überdies werden auch die stratigraphisch wichtigen Arten anderer Radiolarienfamilien beschrieben. 2 Familien, 7 Gattungen und 63 Arten wurden neu aufgestellt.

1. Introduction

The microfossil content of the Kirchstein Limestone (siliceous limestones) from the type locality has been investigated by the present authors. Some of the excellently preserved sponge spicules have been already described by MOSTLER (1989 a, b). In the present paper the first radiolarians (Parasaturnalidae, Acanthocircidae and some other stratigraphically important forms) are described. Further papers with descriptions of the other radiolarian groups are in press.

2. Age of the investigated beds

Our samples were taken from the Kirchstein Limestone of the type locality Kirchstein 6.5 km WSW of Lenggris/Isar in Bavaria (see TOLLMANN, 1976). The best preserved radiolarians were found in sample L 1 about 1 m above the Rhaetian Dachstein Limestone. All described radiolarians derived from this sample.

The type locality of the Kirchstein Limestone lies in the northern marginal zone of the Lechtal Nappe. According to TOLLMANN (1976) the thickness of the Kirchstein Limestone is some tens to more than 100 meters. The lower horizon is about 30 m thick. This lower part of the Kirchstein Limestone has yielded *Schlotheimia angulata* (SCHLOTHEIM) of Upper Hettangian age. The higher Kirchstein Limestone belongs to the Sinemurian.

The radiolarian fauna indicates Hettangian age for sample 1. This is in good agreement with the geological position of sample L 1 and with the above mentioned data by TOLLMANN (1976) on the Hettangian ammonite fauna from the lower part of the Kirchstein Limestone. *Ellipsoxiphus suessi* (DUNIKOWSKI, 1882), closely related or even identical with *Pantanellium kluense* PESSAGNO & BLOME (1980), *E. browni* (PESSAGNO & BLOME, 1980) and *E. tanuensis* (PESSAGNO & BLOME, 1980) indicate Hettangian age. According to PESSAGNO & BLOME (1980) *E. tanuensis* is restricted to the Lower Hettangian, *E. browni*, in turn, to the Upper Hettangian.

Gorgansium alpinum n. sp. occurs in Japan from the topmost conodont proven Rhaetian up to the basal *Parahsuum simplum* zone and therefore has its main occurrence in the Hettangian. *G. blomi* n. sp. occurs in the Hettangian of British Columbia.

Earliest Liassic age is also indicated by the occurrence of *Betraccium bavaricum* n. sp., *B. hettanicum* n.sp., *B. inaequiporatum* n. sp. and *B. verticispinosum* n. sp. The genus *Betraccium* PESSAGNO & BLOME, 1980 was until now regarded as Norian and Rhaetian genus disappearing at the Rhaetian/Liassic boundary (PESSAGNO et al., 1987). Neither in western North America nor in Japan this genus was found above the Rhaetian. Our 4 *Betraccium* species are therefore the youngest representa-

tives of this genus. This indicates a position of our radiolarian fauna near the Triassic/Jurassic boundary. Resedimentation from Rhaetian beds can be excluded in our fauna, because the underlying shallow subtidal to supratidal Rhaetian Dachstein Limestone does not contain any radiolarians.

The same stratigraphic importance as the last *Betraccium* species has *Xenorom jurassicum* n.sp., because also the genus *Xenorom* BLOME, 1984 was until now unknown above the Triassic.

The formerly assumed very sharp break in the radiolarian faunas between the Rhaetian and Hettangian cannot be confirmed. Many Triassic genera have in the Hettangian their last occurrence or their last frequent occurrence and many typical Hettangian or Liassic genera began already in the Rhaetian or even in the Norian. For instance, the genus *Relanus* PESSAGNO & WHALEN, very frequent in the Hettangian and absent in the Sinemurian, began with the primitive *Relanus browni* (BLOME, 1984) already in the Norian, but remains extremely rare up to the Lower Rhaetian. However, in the Upper Rhaetian this genus is already rather frequent. The genera *Droltus* PESSAGNO & WHALEN 1982, and *Paracanoptum* YEH, 1987, so far regarded as typical Liassic genera, are already present in the Rhaetian. Also the important Lower Liassic genus *Parahsuum* YAO, 1982 is present in Rhaetian beds. Even the Rhaetian zonal index species, *Canoptum rhaeticum* KOZUR & MOSTLER, 1981 (= *C. triassicum* YAO, 1982) is still rarely present in the Hettangian (also in our fauna).

The Upper Rhaetian and Hettangian radiolarian fauna is so similar, that Hettangian radiolarian faunas have been often placed into the Rhaetian (e.g. uppermost conodont-free part of the *Canoptum triassicum* Zone of Japan, see YAO, 1982) or Rhaetian radiolarian faunas have been placed into the Hettangian, like the lower part of the *Canoptum merum* Zone of western North America (see below).

The differences between the Rhaetian and Hettangian radiolarian faunas concern mostly the species level, but also several new genera appeared at or somewhat above the base of the Hettangian, especially among the Nassellaria. The characteristic and common *Relanus hettangicus* n. sp. is not yet present in the Rhaetian. The Hettangian Parasaturnalidae are mostly represented by other species than in the Rhaetian. Most characteristic are elongated forms with the long axis perpendicular to the polar spines and forms with quadratic or rectangular ring, still rare and untypical in the Norian and Rhaetian. Many species of *Pseudoheliodiscus* KOZUR & MOSTLER, 1983, *Liassosaturnalis* n. gen. and *Pseudacanthocircus* n. gen. appeared

in the Hettangian. The latter 2 genera have not yet been reported from the Triassic, but the first appearance of *Pseudacanthocircus* in the Rhaetian cannot be excluded, because this genus is very common and differentiated in the Hettangian. *Parahsuum* YAO, 1982 and *Praecanutus* n. gen. are common in the Hettangian and here represented by several species, unknown from the Rhaetian.

The separation between the Hettangian and Sinemurian radiolarian faunas is likewise easy. Many species of the Canoptidae and Bagotidae appeared at the base of the Sinemurian or within this stage. The forerunners of these forms can be found in the Hettangian, therefore several phylomorphogenetic lines can be recognized that are useful for separation of Hettangian and Sinemurian nassellarian faunas (e.g. *Canutus* in the Sinemurian and its forerunner in the Hettangian, KOZUR & MOSTLER, in press).

Also the Spumellaria faunas from the Hettangian and Sinemurian can be easily distinguished. At the base of the Sinemurian appeared the first true Hagiastrids (PESSAGNO et al., 1987). Both in the Hettangian and in the Sinemurian the Parasaturnalidae are common, they have identical generic, but rather different species composition. *Palaeosaturnalis* DONOFRIO & MOSTLER, 1978, still common in the Hettangian and there represented by several species, is very rare in the Sinemurian and Pliensbachian and only represented by one species in each stage, before it disappeared in the Toarcian. Near the Hettangian/Sinemurian boundary several Triassic holdovers disappeared, e.g. *Betraccium* PESSAGNO & BLOME, 1980, still common in the Hettangian (4 species).

According to PESSAGNO et al. (1987) *Crucella* PESSAGNO, 1971 s.str. and *Katroma* PESSAGNO & POISSON, 1981 appeared at the base of the Sinemurian, but both genera are already present in the Hettangian, *Crucella* is here even common. The oldest typical *Crucella* species with tapering tips of the rays, *Crucella longispinosa* (KOZUR & MOSTLER, 1978) is already present in the Carnian, where the genus *Triassocrucella* KOZUR, 1984 with bulbous ends of the rays is still dominant. *Crucella prisca* n. sp. is also known from the topmost conodont-proven Rhaetian of Japan. The appearance of *Crucella* and *Katroma* can be therefore not used for separating the Hettangian and Sinemurian radiolarian faunas.

The investigated Hettangian radiolarian fauna, the first rich Hettangian radiolarian assemblage of the world, is here discriminated as *Relanus hettangicus* Zone, defined by the range of the index species and a characteristic radiolarian assemblage. The *Relanus hettangicus* Zone contains the following characteristic and stratigraphically important species: *Canoptum rhaeticum* KOZUR & MOSTLER 1981, (rare), *Paracanoptum primitivum* n. sp.

(common), *Relanus hettangicus* n. sp. (very common), *Relanus longus* n. sp. (rare), *Relanus multiperforatus* n. sp. (rare), *Relanus striatus* n. sp. (common), *Droltus eurasiaticus* n. sp. (common), *Droltus carinaspinosus* n. sp. (rare), *Droltus robustospinosus* n. sp. (rare), primitive *Parahsuum simplum* YAO (rare), *Parahsuum primitivum* n. sp. (rare), *Syringocapsa coliforme* HORI, 1988 (rare), *Katroma* spp. (rare), *Betraccium bavaricum* n. sp. (rare), *Betraccium hettangicum* n. sp. (common), *Betraccium inaequiporatum* n. sp. (rare), *Betraccium verticispinosum* n. sp. (common), *Crucella carteri* n. sp. (common), *Crucella hettangica* n. sp. (rare), *Crucella prisca* n. sp. (common), *Ellipsoxiphus suessi* (DUNIKOWSKI, 1882) (common), *Ellipsoxiphus browni* (PESSAGNO & BLOME) (common), *Ellipsoxiphus tanuense* (PESSAGNO & BLOME, 1980) (common), *Gorgansium alpinum* n. sp. (rare), *Gorgansium blomei* n. sp. (rare), *Xenorum jurassicum* n. sp. (rare). Very characteristic and common for the *Relanus hettangicus* zone are different species of Parasaturnaliidae described in the present paper (see taxonomic part). Moreover, additionally more than 100 species of Nassellaria, Spumellaria and some Entactinaria are present in our material from the *Relanus hettangicus* Zone that will be described in separate papers by the present authors.

Age: Hettangian.

Distribution: Alps, Hungary, British Columbia and Oregon, Japan.

Remarks: The correlation with the higher part of the Zone 05 (*Canoptum merum* Concurrent Range Zone) of British Columbia and Oregon is indicated by the rich occurrence of the genus *Relanus* PESSAGNO & WHALEN, 1982, which is in North America nearly restricted to this zone. Moreover, also *Ellipsoxiphus browni*, *E. tanuense* and *Gorgansium blomei* are restricted to this zone. The index species, *C. merum* PESSAGNO & WHALEN, 1982 is not present in our material, but it occurs together with *C. praeannulatum* PESSAGNO & WHALEN, 1982 and *Relanus reefensis* PESSAGNO & WHALEN, 1982 in the higher Rhaetian of the Alps. All these 3 species are restricted to the *C. merum* Zone of the western North America. For this reason a large part of the *C. merum* Zone seems to be Rhaetian and not Hettangian in age.

Further but not time-related differences are the common presence of the genus *Betraccium* in our material that disappeared at the top of the Norian in western North America and the common occurrence of the genus *Crucella* s. str. that begins in western North America only in the basal Sinemurian.

More similarities exist between the *Relanus hettangicus* Zone and the topmost *Canoptum "triassicum"* Zone (*Canoptum triassicum* YAO, 1982 is a younger synonym of *C. rhaeticum* KOZUR & MOSTLER, 1981) and the lowermost *Parahsuum simplum* Zone of Japan. *Canoptum rhaeticum* KOZUR & MOSTLER, 1981 (= *C. triassicum* YAO, 1981), *Droltus eurasiaticus* n. sp. (= *Parahsuum* ? sp. A YAO, 1982), primitive *Parahsuum simplum* YAO, *Syringocapsa coliforme* HORI, 1988, *Crucella prisca* n. sp. (= *Staurodoras* ? sp. sensu IGO & NISHIMURA, 1984) and *Gorgansium alpinum* n. sp. (= *Gorgansium* sp. A sensu IGO & NISHIMURA, 1984) occur both in this interval of the Japanese sections and in the *Relanus hettangicus* Zone of the Alps.

Most of the common species between these Japanese radiolarian associations and the *Relanus hettangicus* Zone begin in Japan (and partly also in Europe: *C. rhaeticum*) already in conodont proven Rhaetian. Moreover, the highest conodont proven Rhaetian of Japan contains exclusively *Misikella posthernsteini* KOZUR & MOCK. In Europe still 2 Rhaetian conodont zones follow above the *Misikella posthernsteini* faunas, the *M. ultima* Zone and the *Neohindeodella detrei* Zone (KOZUR & MOCK, in press). Therefore the Rhaetian/Hettangian boundary as drawn by the Japanese radiolarian specialists at the base of the *Parahsuum simplum* Zone may be correct or it may be situated only a little deeper, but still somewhat above the conodont extinction datum.

3. Taxonomic part

Beside the Saturnaliacea DEFLANDRE, 1953 also some stratigraphically important species of other radiolarian genera are described to demonstrate the age of our radiolarian fauna. The remaining more than 100 new species will be described in other papers (KOZUR & MOSTLER, in press).

Locus typicus for all new species is the type locality of the Kirchstein Limestone at the Mt. Kirchstein 6.5 km WSW of Lenggries/Isar (Bavaria) as described by TOLLMANN (1976). The stratum typicum lies about 1 m above the Rhaetian Dachstein Limestone. The age of the stratum typicum is Hettangian. All figured Hettangian specimens are from sample L 1 (from the stratum typicum) that has yielded the best preserved faunas. The data of the locus typicus and stratum typicum for these Hettangian species will not be repeated in the descriptive part (see above and chapter 2.)

All material is stored in the Geological Institute of the Innsbruck University under the repository numbers KoMo 1990 I/1–42.

Subclass **Radiolaria** MÜLLER, 1858
Order **Polycystina** EHRENBERG, 1838
Suborder **Spumellaria** EHRENBERG, 1875
Superfamily **Saturnalicaea** DEFLANDRE, 1953

Diagnosis: Shell primary spongy, consisting of many concentric layers. A tiny microsphere with large pores is always present. In stratigraphically younger forms a second, larger medullary shell evolved within the spongy meshwork. Later this second medullary shell was transformed by enlargement into a latticed cortical shell or a cortical shell evolved outside the second medullary shell. In the beginning, this cortical shell is still covered by a thicker spongy layer (*Spongosaturninus* CAMPBELL & CLARK, 1944). Finally, this spongy layer on the latticed cortical shell is absent or it became very thin and delicate, preserved only in some specimens of a species (as in *Saturnalis circularis* HAECKEL).

Two round polar or peripolar spines (first order spines), rarely 3, 4 or more first order spines are present. Smaller auxiliary spines are in stratigraphically older taxa often, in stratigraphically younger taxa rarely present. The polar spines are terminally mostly differentiated, in the Oertlispongidae KOZUR & MOSTLER, 1980 often in form of halfringlike, mostly flattened structures, often with secondary outer spines.

In the saturnalid forms the halfrings join to a saturnalid ring. In stratigraphically older and few stratigraphically younger forms this ring is roundish, flat, often broad, undifferentiated and at the outer margin always spined; its outline is roundish. In stratigraphically younger forms it is mostly differentiated by ridges. Its outer margin is often without spines or few outer spines are concentrated around the ring poles, perpendicularly to the polar/peripolar spines. In these forms the ring is mostly elliptical or rectangular with the long axis perpendicularly to the polar spines (transversally elliptical or transversally rectangular).

Distribution: Middle Triassic to Recent, very common from the Middle Triassic to Pliensbachian, after the Cretaceous very rare.

Assigned families: Saturnalidae DEFLANDRE, 1953 emend

Synonym: Vitorfidae PESSAGNO, 1977

Parasaturnalidae KOZUR & MOSTLER, 1972 emend.
KOZUR & MOSTLER, 1983

Synonym: Acanthocircidae PESSAGNO, 1977

Oertlispongidae KOZUR & MOSTLER, 1980

Pseudacanthocircidae n. fam.

Saturnalideidae n. fam.

Remarks: The basic subdivision of the Mesozoic saturnalids was established by KOZUR & MOSTLER (1972).

Later PESSAGNO (in PESSAGNO et al., 1979), DONOFRIO & MOSTLER (1978) revised some genera of the Parasaturnalidae and KOZUR & MOSTLER (1981) revised the saturnalid genera and introduced new genera and suprageneric taxa.

KOZUR & MOSTLER (1983) and De WEVER (1984) presented independently each other 2 classifications of the saturnalid radiolarians and DUMITRICĂ (1985) discussed the systematic position of this group.

Different evaluations of the morphologic characters of the saturnalids lead to different classifications. According to KOZUR & MOSTLER (1983) the saturnalid radiolarians have polyphyletic origin and belong partly to the Entactinaria, partly to the Spumellaria. DUMITRICĂ (1985) questioned the polyphyletic character of the saturnalids and pointed out that the saturnalids are more related to the Entactinaria than to the Spumellaria. On the other hand, he excluded partly exactly the same groups from the saturnalid radiolarians as it was done by KOZUR & MOSTLER (1983) and he confirmed by this the polyphyletic origin for the same groups of saturnalid radiolarians that have been excluded from the saturnalids s. str. by KOZUR & MOSTLER (1983) (Hungarosaturnalinae KOZUR & MOSTLER, 1983 of Austrosaturnalidae KOZUR & MOSTLER, 1983).

The Entactinaria character of the saturnalids s. str. is not clear from the figures by DUMITRICĂ (1985). Like their forerunners (Oertlispongidae), they have a microsphere that is in some taxa asymmetric and remembers therefore somewhat to the pentactine spicular system of Entactinaria. However, the polar spines are never prolongations of basal rays as in true Entactinaria. Moreover, the Early Mesozoic Entactinaria have no microsphere, but the pentactine shell is large to very large or the Entactinaria spicular system is point- or bar-centred. Further detailed studies are necessary to clear finally the taxonomic position of the Saturnaliacea. A strong point-centred entactinarian spicular system as in the Spongo-saturnaloididae KOZUR & MOSTLER, 1983, as figured by KOZUR & MOSTLER (1983, pl. 3, fig. 1) is surely not present in the Saturnaliacea, so that the polyphyletic origin of the ringed radiolarians is beyond any doubt and it was finally also accepted by DUMITRICĂ (1985, p. 185).

KOZUR & MOSTLER (1981) recognized the supraspecific importance of the position of polar/peripolar rays in saturnalids (polar = opposite to outer spines on the ring, peripolar = opposite to interspine space or on smooth rings). De WEVER (1981) placed forms with polar and peripolar spines still in the same genus or even in the same species group. However, De WEVER (1984) regarded the differences between forms with polar or peripolar spines as

so fundamental that he subdivided his family Saturnalidae DEFLANDRE, 1953 s. l. into the Palaeosaturnalinae KOZUR & MOSTLER, 1981 and Saturnalinae DEFLANDRE, 1953 emend. on the base of this difference. However, we cannot confirm that the presence of polar or peripolar spines is more than a generic difference. From the Norian to Recent we find forms with polar and peripolar spines and many form groups in this long time interval have representatives with polar and peripolar spines. Moreover, even transitional forms are present between such "pairs" that have either one polar and one peripolar spine or the polar spines run to the margin of the base of the outer spine. In forms with 4 equivalent first order spines 2 may be in polar, 2 in peripolar position. Form "pairs" with polar/peripolar spines are *Palaeosaturnalis* (Cordevolian, Bajocian) *Mesosaturnalis* (Norian Upper Cretaceous), *Stauracanthocircus* (Norian Pliensbachian) *Stauromesosaturnalis* (Hettangian Pliensbachian), *Pseudoheliodiscus* (Cordevolian Bajocian) *Praemesosaturnalis* (Norian Upper Cretaceous).

As seen from these "form pairs" the forms with peripolar spines seemingly developed from forms with polar spines, because they began generally later within a "form pair". On the other hand the above listed "form pairs" show clearly that the development of forms with peripolar spines is interactive in several different lines. In all these lines transitional forms are present (see above). If we would use the presence of polar or peripolar spines to separate 2 big groups of suprageneric rank within the saturnalids than we would arbitrarily separate closely related forms of different lines. Therefore we cannot support the subdivision of the saturnalids proposed by De WEVER (1984).

On the other hand, in the Pseudacanthocircidae n. fam. that comprise phylogenetically near related forms, only taxa with peripolar spines are known. Therefore any generalization of the importance of a single morphologic feature for the suprageneric taxonomy should be avoided. Like in other fossil groups (e.g. ostracods) the same morphologic feature can be in one suprageneric taxon very stable and of high-rank taxonomic value, in an other suprageneric taxon, in turn, of minor taxonomic value.

The subdivision of the saturnalids into Saturnalinae DEFLANDRE, 1953 and Palaeosaturnalinae KOZUR & MOSTLER, 1981 by De WEVER (1984) cannot be accepted also for priority reasons. The Palaeosaturnalinae KOZUR & MOSTLER, 1981 sensu De WEVER (1984) (pro Palaeosaturnalini KOZUR & MOSTLER, 1981) contain also the genus *Heliosaturnalis* KOZUR & MOSTLER, 1972, the nominate genus for the Heliosaturnalinae KOZUR & MOSTLER, 1982. Therefore in any case the Palaeosaturnalinae KOZUR & MOSTLER, 1981 would

be a younger synonym of the Heliosaturnalinae KOZUR & MOSTLER, 1972.

Also "form pairs" of genera with and without auxiliary spines can be observed, e.g. *Palaeosaturnalis* (Cordevolian Bajocian) *Pseudoheliodiscus* (Cordevolian Bajocian), *Mesosaturnalis* (Norian Upper Cretaceous) *Praemesosaturnalis* (Norian Upper Cretaceous), *Hexasaturnalis* (Toarcian Upper Cretaceous) *Yaosaturnalis* (Dogger Upper Cretaceous), *Praeacanthocircus* (Cordevolian Pliensbachian) *Pseudacanthocircus* (Rhaetian Upper Cretaceous), *Parasaturnalis* (Bajocian Lower Cretaceous) *Japonisaturnalis* (Pliensbachian Bajocian).

So far all authors have accepted that the presence or absence of auxiliary spines is a generic difference. PES-SAGNO (in PESSAGNO et al., 1979) separated even the Parasaturnalinae KOZUR & MOSTLER 1972 (without auxiliary spines) from the Heliosaturnalinae KOZUR & MOSTLER, 1972 (with auxiliary spines) on the base of this difference. However, the "form pairs" with and without auxiliary spines have the same or similar stratigraphic ranges. Except of the above mentioned "pairs", in the following genera forms with and without auxiliary spines are known, partly even within one species: *Spongosaturninus* CAMPBELL & CLARK (within one species: *S. ellipticus* CAMPBELL & CLARK), *Eospongosaturninus* n. gen. (within one species: *E. protoformis* (YAO)), *Praehexasaturnalis* KOZUR & MOSTLER, 1983, *Liasosaturnalis* n. gen. (within one species: *L. parvus* n. sp., *L. undulatus* n. sp.).

However, also this feature cannot be evaluated in the same manner in different taxa. The Cordevolian *Pseudoheliodiscus* KOZUR & MOSTLER, 1972 and *Palaeosaturnalis* DONOFRIO & MOSTLER, 1978 are clearly different, in spite of the fact that the type species of both genera came from the same layer and both genera have the same stratigraphic range. No transitional forms between the Carnian *Pseudoheliodiscus* and *Palaeosaturnalis* species can be found. Either only 2 polar spines are present (*Palaeosaturnalis*) or beside of the 2 polar spines numerous auxiliary spines are present (*Pseudoheliodiscus*).

Distinct taxa are also those forms, in which the number of the auxiliary spines is reduced to 24 (5). Often in these forms the former small auxiliary spines have the same size as the polar or peripolar spines so that 4–6 (7) first order spines are present, cross-like or slightly diagonally arranged. These forms (*Stauracanthocircus* KOZUR & MOSTLER, 1983) can be easily distinguished both from forms without auxiliary spines and from forms with numerous small auxiliary spines.

Quite different is the situation, if in one sample (or in one population) in a morphologically uniform group both

specimens occur that have 2 polar or peripolar spines without auxiliary spines and such specimens occur that have 1, 2, 3 and more auxiliary spines. If these morphotypes with and without auxiliary spines have the same stratigraphic range, than they belong surely to the same species, if all other taxonomic features are the same. Therefore the genera *Spongosaturninus* CABELL & CLARK, *Eospongosaturninus* n. gen. and *Liassosaturnalis* n. gen. have surely representatives with and without auxiliary spines within one species.

Somewhat different is the situation in *Praehexasaturnalis* KOZUR & MOSTLER, 1983. In this genus 2 Norian species are present, in which no auxiliary spines can be observed, the Middle Norian to Upper Norian *P. elegans* (KOZUR & MOSTLER, 1972) and the Upper Norian *P. tenuispinosus* (DONOFRIO & MOSTLER, 1978). During the Rhaetian the general morphological character of the latter species remained unchanged, but 2 tiny auxiliary spines evolved (cross-like arranged with the polar spines). This form, *P. tetradialatus* n. sp. continued into the Hettangian, where the auxiliary spines became somewhat more pronounced. In the Hettangian a further species occurred, morphologically identical with *P. tenuispinosus* and *P. tetradialatus*, but with 5-10 auxiliary spines (*P. kirchsteinensis* n. sp.). No specimens without auxiliary spines were found in the Hettangian.

In this case the absence, presence, number and arrangement of the auxiliary spines can be used for separating 3 species (*P. tenuispinosus*, *P. tetradialatus*, *P. kirchsteinensis*) that are otherwise morphologically identical. However, also in this case the presence and absence of auxiliary spines cannot be used for separating 2 genera, because *P. kirchsteinensis* is an end form without successor. On the other hand, it cannot be placed into *Pseudoheliodiscus*, because it did not derive from Triassic representatives of *Pseudoheliodiscus* (with numerous, specifically constant or nearly constant numbers of auxiliary spines), but it has derived from Norian species of *Praehexasaturnalis* without auxiliary spines, nearly related to *Palaeosaturnalis*.

The main problem in the taxonomy of the saturnalids (as in many other radiolarian groups) is the independent and iterative development of the same features in different lines. On the other hand, these trends can be of considerable stratigraphic value, if the development in different lines is known, because some trends were realized in different lines to different times.

Moreover, single morphologic changes that define in their combination a higher evolved taxon, can be realized also in other groups without combination with other morphological changes. By this, for instance, the outline of

the saturnalid ring can be very similar in clearly separated groups (even in forms, not related to true saturnalids), whereas within one low rank taxonomic unit (genus or exceptionally even species) different ring outlines can be observed. In other lines, in turn, the ring outline remained constant from the Cordevolian up to the Upper Cretaceous and even in the recent successors.

For these reasons, the geometric Haeckelian system united into one group phylomorphogenetically related forms, into other groups phylomorphogenetically quite different, but morphologically homoeomorph forms. For the first description of new taxa the morphological classification is necessary also in our time, but if we know more material and phylomorphogenetic lines, a phylomorphogenetically based taxonomy should be elaborated.

The following trends can be observed in the development of the Meso-Cenozoic saturnalids:

- Development of a second latticed medullary shell around the microsphere and finally development of a latticed cortical shell. This latter trend can be first observed in the Upper Cretaceous. It leads to the development of the Saturnalidae from the Pseudoacanthocircidae, but it can be also observed in recent descendants of the Parasaturnalidae (*Saturnalium* HAECKEL, 1887). The same trend can be observed in different lines within the Trematodiscacea. This development has within a phylomorphogenetic line suprageneric importance (family rank), but it does not indicate direct relations between the newly evolved taxa with latticed cortical shell, because they evolved from different forerunners.

- Development of a narrow differentiated ring (with ridges). Also this trend can be observed in 2 different lines, but with constant and different mode of development within the 2 lines. Moreover, the development of ridges on the ring began to different times within the 2 lines. From the Parasaturnalidae (*Pseudoheliodiscus*) evolved in the Middle Norian *Octosaturnalis* n. gen., a taxon with tricarinate outer spines. From the ridges on the outer spines connecting ridges to adjacent spines run along the outer margin of the ring, both on its upper and lower surfaces. By this, the ring is highest on its outer margin and lowest on its inner margin. Moreover, a distinct furrow developed on the outer side of the ring between the upper and lower ridge on the ring. This furrow is connected with the furrows between the ridges on the outer spines of the ring. By reduction of the outer spine number to (7) 6-4 and still stronger development of the ridges on the ring the genus *Hexasaturnalis* KOZUR & MOSTLER, 1983 evolved during the Liassic from *Octosaturnalis* n. gen. *Hexasaturnalis*, in turn, is the forerunner of *Acanthocircus* SQUINABOL, 1903 s. str. (basal Middle Jurassic to Lower Cretaceous). In

Acanthocircus the ring is in general higher than broad and the outer furrow is deep, but also in this genus the inner side of the ring is lower than the outer one.

Within the Pseudacanthocircidae n. fam. the development of the ridges on the ring began only during the basal Middle Jurassic. On the contrary to the Acanthocircinae (Parasaturnalidae), the ridges evolved on the upper and lower surface of the **inner side** of the ring. By this the ring displays a triangular cross section with its wide base inside. This type of ring can be observed for the first time in the genus *Eospongosaturninus* n. gen. and in primitive *Spongosaturnalis* CAMPBELL & CLARK, 1944, both from the basal Middle Jurassic. This ring type remained unchanged within the Pseudacanthocircidae n. fam. until the end of the Cretaceous and also the Saturnalidae DEFLANDRE, 1953 s. str. (Upper Cretaceous-Recent) that evolved from the Pseudacanthocircidae n. fam., have the same type of ring differentiation.

- Development of a narrow, transversally oval to rectangular ring (long axis perpendicular to the polar/peripolar spines). This ring form is invariably present in the Pseudacanthocircidae n. fam. (Cordevolian-Upper Cretaceous). It remained unchanged also in the Upper Cretaceous-Recent Saturnalidae DEFLANDRE, 1953 s. str.

In contrary to this invariable general ring outline of the Pseudacanthocircidae/Saturnalidae (transversally oval, very rarely transversally rectangular), the Parasaturnalidae display big variations in the general ring outline. The Carnian Parasaturnalidae have always roundish rings. During the Norian and Rhaetian, but especially during the Liassic forms with transversally oval/rectangular rings appeared in several lines that are homoeomorphic to the Pseudacanthocircidae and Saturnalidae. However, in the Parasaturnalidae this trend is not fixed to the whole family. Even within many Hettangian species the ring outline varies from round to clearly transversally oval or even from vertically oval (long axis parallel to the polar/peripolar spines) to transversally oval or from vertically rectangular to transversally rectangular. After the strong incision in the diversity and frequency of Parasaturnalidae during the basal Toarcian only the persistent group with roundish or subroundish ring outline survived until the end of the Cretaceous. Also the recent Saturnalidae n. fam. that evolved from the Parasaturnalidae have a roundish ring outline.

Within the genus *Palaeosaturnalis* DONOFRIO & MOSTLER, 1978 the first transversally oval or transversally rectangular forms appeared during the Norian, but still in the Liassic the ring outline remained mostly intraspecifically variable. Only in some Hettangian species the distinct transversally oval outline is specifically fixed, but

all these forms disappeared already in the Sinemurian. Only very few *Palaeosaturnalis* species with round or slightly vertically oval ring outline occur from the Sinemurian to the Bajocian before this genus finally disappeared.

In the genus *Stauracanthocircus* KOZUR & MOSTLER, 1983 rectangular ring outlines are dominant, but in the most species the ring outline is very variable (from transversally rectangular to quadratic vertically rectangular or from transversally oval to roundish vertically oval).

In *Liassosaturnalis* n. gen. forms with vertically oval ring outline dominate, but the variability is likewise high (vertically oval to roundish or transversally oval).

The primitive Acanthocircinae PESSAGNO, 1977 began with forms with octagonal ring outline. During the Liassic evolved by reduction of the number of the strong outer spines forms with heptagonal, hexagonal and rounded tetragonal ring outline (7, 6 and 4 outer spines). In the Middle Jurassic the rounded tetragonal ring outline was transformed into transversally oval ring outline that is typical for the higher evolved Acanthocircinae. This transversally oval ring outline became still more prominent by the arrangement of 1-2 spines in the polar region of the long axis.

- Reduction of the number of auxiliary spines. This trend can be observed within several lines of the saturnalids. It is accompanied by enlargement of the auxiliary spines that became finally as large as the polar spines. In the Pseudacanthocircidae n. fam. already the most primitive form, *Praeacanthocircus carnicus* KOZUR & MOSTLER from the Cordevolian, has only 6 inner spines of nearly the same size. In the Palaeosaturnalidae this stage of development is only reached during the Liassic (genus *Stauracanthocircus* KOZUR & MOSTLER).

- Appearance and disappearance of auxiliary spines. Highly evolved Oertlispongidae with large shell (reaching near to the inner side of the half rings branching from the terminal part of the polar spines) have numerous, but mostly indistinct auxiliary spines on the inner side of the half rings. If the shell is relatively small and does not reach near to the inner side of the half ring, no auxiliary spines are present. Therefore the presence or absence of auxiliary spines in the earliest saturnalids (that evolved from Oertlispongidae) is a primary feature. The frequent occurrence of forms with auxiliary spines in the Cordevolian to Pliensbachian interval and its rare occurrence in Middle Jurassic or younger beds does not indicate that forms without auxiliary spines developed in several lines from forms with auxiliary spines, but this change reflects rather the disappearance of most of the Parasaturnalinae KOZUR & MOSTLER (with many taxa that have auxiliary spines).

In spite of the fact that the number of auxiliary spines is reduced in several lines, we do not know any line, in which the forms without auxiliary spines have evolved from forms with auxiliary spines. On the contrary, in some lines the development of forms with auxiliary spines from forms without auxiliary spines can be observed, e.g. *Praehexasaturnalis tenuispinosus* (without auxiliary spines, Upper Norian), *P. tetraradiatus* (with 2 auxiliary spines in cross-like arrangement with the polar spines, Rhaetian-Hettangian) *P. kirchsteinensis* (5-9 auxiliary spines, Hettangian). In the Bajocian *Eospongosaturninus* n. gen. forms with and without auxiliary spines occur within one species. It has evolved from *Pseudacanthocircus* n. gen., in which auxiliary spines are unknown.

- Changes in the denticulation or spinosity of the outer ring margin. Here different trends can be observed in different lines. The Parasaturnalidae have primary strongly spined rings. In the Norian began in some lines a reduction of the spine number. One trend lead to the development of forms with fewer, but very strong and partly carinate spines. This trend of reduction is accompanied by a change of the ring outline from roundish to octagonal, heptagonal, hexagonal and finally rounded tetragonal (development of earliest *Acanthocircinae*). In an other line the spines (with exception of the spines opposite to the polar spines) became rarer, smaller and finally they disappeared (*Liassosaturnalis* n. gen.).

In the *Pseudacanthocircidae* n. fam., in turn, the oldest representatives have a smooth ring. In younger forms the ring remained either smooth or denticles evolved at the polar regions of the long axis, rarely of the short axis. Finally these spines may cover the whole outer ring.

An interesting mode of development of a slightly spined to nearly smooth narrow ring from a heavily spined broad ring with big triangular spines have been observed in a new Norian *Mesosaturnalis* species (pl. 12, fig. 5) described in an other paper. In this species the broad ring is internally subdivided into a stable inner ring and a stable outer ring, the latter with big spines. During corrosion processes a zone of material weakness between the 2 partial rings is removed nearly totally and both partial rings became separated. The inner ring with the peripolar spines has a small spine in most of the spaces between the big spines on the outer ring, including opposite to the peripolar spines. These small spines connect both partial rings, if they are not yet totally separated. If the 2 partial rings became totally separated, a narrow ring (former inner partial ring) with small outer spines evolved. By this process a form with small polar spines developed from a form with peripolar spines. This mode of ring change could perhaps explain the occurrence of *Saturnalium* HAECKEL with

narrow spined ring and polar spines in recent material in spite of the disappearance of the last genera with polar spines (*Palaeosaturnalis* DONOFRIO & MOSTLER, *Pseudoheliodiscus* KOZUR & MOSTLER) during the Lower Dogger.

- Development of double rings. This feature developed several times in independent, only partly near related lines from Parasaturnalinae with single ring. For the first time a double ring developed already during the Cordevolian (*Heliosaturnalis* KOZUR & MOSTLER, 1972). As already shown by KOZUR & MOSTLER (1972, 1983) *Heliosaturnalis* evolved from parasaturnalids with single ring and numerous long outer spines by development of connecting bars about in the midlength of the outer spines (*Pseudoheliodiscus Heliosaturnalis*). During the Liassic a still undescribed new genus evolved by the same "*Heliosaturnalis* mode" from *Praemesosaturnalis* KOZUR & MOSTLER, 1981.

Japonisaturnalis KOZUR & MOSTLER, 1972 evolved from *Stauromesosaturnalis* n. gen. partly by the above described "*Heliosaturnalis* mode", partly by dichotomous branching of the outer spines of the single ring and connecting of the branches to a second ring ("*Parasaturnalis* mode"). In this case the spines on the outer ring are not situated in prolongation of the spines on the inner ring, but opposite to the pores between the rings. The Jurassic *Parasaturnalis* KOZUR & MOSTLER, 1972 evolved exclusively by this latter mode from *Mesosaturnalis* species with terminally forked spines, present in the highest Triassic.

In parasaturnalids with multiple rings (Upper Cretaceous *Pseudosaturnalis* KOZUR & MOSTLER, 1972), the further rings evolved either by the "*Heliosaturnalis* mode" or by the "*Parasaturnalis* mode" from the outer spines of the second ring.

Because double or multiple rings developed within the Parasaturnalidae several times from different genera (*Pseudosaturnalis*, *Heliosaturnalis*, *Meosaturnalis*, *Parasaturnalis*, *Stauromesosaturnalis*, *Japonisaturnalis*, *Praemesosaturnalis* undescribed new genus), the suprageneric taxa based on this feature are here abandoned.

The Cordevolian forms with 2-3 rings and with 5 long first order spines on the inner side of the inner ring (*Ploechingerella* KOZUR & MOSTLER, 1983) display a strong entactinarian spicular system like *Spongosaturnaloides* KOZUR & MOSTLER, 1972. Therefore they do not belong to the true saturnalid radiolarians (Parasaturnalidae KOZUR & MOSTLER, 1972), but to the family Spongosaturnaloididae KOZUR & MOSTLER, 1983 nom. corr. of the Entactinaria. By a printing mistake, the Spongosaturnaloididae were written as Saturnaloididae in KOZUR & MOSTLER (1983, p. 9, under the diagnosis),

but correctly written by KOZUR & MOSTLER (1983, p. 5).

The below following subdivision of the Saturnaliacea DEFLANDRE, 1953 is based on complex evaluation of all available morphological and structural data and on the evaluation of phylomorphogenetic lines. Similarities in ring outline, sculpture, outer denticulation, presence or absence of auxiliary spines, polar versus peripolar spines and shell structure alone are not regarded as decisive for suprageneric classification. Only the combination of the different features under consideration of the real phylogenetic connection (so far these connections could be already found) are regarded as the base for a more natural classification of the saturnalid radiolarians. This is the only way to distinguish between real relations and morphological homoeomorphies of not closer related forms. Because some phylomorphogenetic lines are not yet known and the shell structure of many Cretaceous forms is unknown, uncertainties remain that will be discussed.

Family **Oertlispongidae** KOZUR & MOSTLER, 1980

Diagnosis (KOZUR & MOSTLER, 1981 for Oertlisponginae): Spherical to subspherical spongy shell consisting of 10 or more, sometimes 5-10 concentric layers that surround a tiny microsphere. Primary spines with round cross sections, mostly 2 polar spines, rarely 3 spines in one plane. The primary spines are distally mostly bifurcated, broadly flattened or otherwise differentiated. Often the spines are strongly arched, sometimes more than a half-arch. Auxiliary spines often present.

Distribution: Illyrian to Sevastian, very frequent in the Middle Triassic, especially in the Ladinian.

Assigned genera:

Oertlispongia DUMITRICĂ, KOZUR & MOSTLER, 1980

Synonym: *Falcispongia* DUMITRICĂ, 1982

? *Vinassaspongia* KOZUR & MOSTLER, 1979

? *Zhamoidasphaera* KOZUR & MOSTLER, 1979

Neopaurinella KOZUR & MOSTLER, 1981

Paroertlispongia KOZUR & MOSTLER, 1981

Baumgartneria DUMITRICĂ, 1982

Pterospongia DUMITRICĂ, 1982

Spongoserrula DUMITRICĂ, 1982

Angulocircus LAHM, 1984

Remarks: The Oertlispongidae KOZUR & MOSTLER, 1980 are here reduced to the Oertlisponginae sensu KOZUR & MOSTLER, 1981. *Acaeniospongia* KOZUR & MOSTLER, 1981 and *Kulacella* KOZUR & MOSTLER, 1981, only tentatively assigned to the Oertlispongidae by KOZUR & MOSTLER (1981) do not belong to the Oertlispongidae.

The Oertlispongidae are the basis groups of the Saturnaliacea as already pointed out by KOZUR & MOSTLER (1983). All transitional forms between highly evolved Oertlispongidae and Parasaturnalidae are present.

Genus *Angulocircus* LAHM, 1984

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

Distribution: Cordevolian-Julian

Assigned species:

Spongosaturnalis bipartitus KOZUR & MOSTLER, 1972

Synonym: ? *Pseudoheliodiscus ? interruptus* KOZUR & MOSTLER, 1983

Angulocircus laterospinosus LAHM, 1984

Angulocircus multispinosus LAHM, 1984

Pseudoheliodiscus donofrioi KOZUR & MOSTLER, 1983

Synonym: *Angulocircus longispinosus* LAHM, 1984

Remarks: Until now, this genus was placed into saturnalid genera (*Spongosaturnalis* CAMPBELL & CLARK, 1944) *Pseudoheliodiscus* KOZUR & MOSTLER, 1972 *Angulocircus* LAHM, 1984). However, it belongs to highly evolved Oertlispongidae KOZUR & MOSTLER, 1980, because the half-rings are not yet fused to a saturnalid ring. Moreover, even the position of the half-rings is within the 2 known species not yet fixed within one plane. Any angle between the 2 half-rings is possible; they may be situated even perpendicularly to each other.

Pterospongia DUMITRICĂ, 1982 is distinguished by the absence of auxiliary spines on the inner margin of the half-rings. Only in *Pterospongia incisus* DUMITRICĂ, 1982 tiny indistinct auxiliary spines are present in some specimens.

Angulocircus LAHM, 1984 is a transitional form between the Oertlispongidae and the Parasaturnalidae (*Pseudoheliodiscus* KOZUR & MOSTLER, 1972). The distance between the ends of both half-rings is very short. According to this feature alone, *Angulodiscus* could be either regarded as representative of highly evolved Oertlispongidae or of primitive Parasaturnalidae. However, the distinct differences in the denticulation of the 2 half-rings (long spine opposite to the polar spine of one half-ring against shorter triangular spine opposite to the polar spine of the other half-ring) and the variable angle of the half-rings against each other are additional characters of the Oertlispongidae. Polar differences in ring denticulation can be also observed in some species of the Parasaturnalidae, but open rings and inclination of some parts of the ring against the equator plane occur in the saturnalids only in pathologic forms.

Family **Parasaturnalidae** KOZUR & MOSTLER, 1972

Synonym: Acanthocircidae PESSAGNO, 1977

Diagnosis: Shell globular, spongy, with numerous concentric layers and with tiny microsphere displaying large pores. Complete equatorial ring always present. Ring in stratigraphically older forms and in persistent conservative taxa among stratigraphically younger forms always flat, mostly broad. Ring outline mostly roundish, in higher evolved forms also subquadratic, rectangular or elliptical with long axis parallel to the polar/peripolar spines or perpendicularly to them. Ring surface in the most forms undifferentiated, in higher evolved forms partly with ridges on the lower and upper side of the outer ring margin that connect ridges on the outer spines. In higher evolved Acanthocircinae these ridges on the ring cover the whole narrow ring which is in these forms higher than broad or as high as broad as displaying a lateral furrow on the outer margin.

Outer margin of ring always with spines, mostly along the whole ring, but in higher evolved forms often only at the polar regions of the long axis or opposite to the polar spines.

Ring primarily with 2 polar spines (first order spines) on the inner side of the ring. Later peripolar spines (likewise first order spines, but situated between 2 outer spines and not opposite of an outer spine as in polar spines) are increasingly frequent. auxiliary spines (second order spines) in Late Triassic and Liassic representatives often present, since the Middle Jurassic only very rare. In Norian and Liassic forms often 4, 6 or more, rarely 3, 5 first order spines are present (2 polar/peripolar spines and additional spines of the same or nearly the same size that evolved from auxiliary spines).

Distribution: Cordevolian Upper Cretaceous.

Assigned genera: See under the subfamilies.

Remarks: The Upper Cretaceous to Recent Saturnalidae DEFLANDRE, 1953 have a latticed cortical shell, by some forms still covered by a thin spongy layer. The ring exhibits always a transversally oval outline and a triangular cross section with broad base inside.

The Tertiary to Recent Saturnalideidae n. fam. displays the same roundish ring outline as the most Parasaturnalidae, but also in this family a latticed cortical shell is present. The Saturnalideidae n. fam. evolved by development of a latticed cortical shell from the Parasaturnalidae KOZUR & MOSTLER. *Saturnalium* HAECKEL, 1887 is therefore the last and only living representative of the parasaturnalid stock.

The Pseudacanthocircidae n. fam. have invariably a transversally elongated ring. By this feature the early Pseudacanthocircidae n. fam. and the early Parasaturnalidae KOZUR & MOSTLER (always with roundish ring out-

line) are clearly distinguished each other. Later transversally elongated rings evolved also in some Parasaturnalidae (especially in the Acanthocircinae). These forms display strong homoeomorphy to the Pseudacanthocircidae n. fam., but have never a triangular ring cross-section with broad base inside.

Highly evolved Oertlispongidae KOZUR & MOSTLER, 1980 are connected by all transitions with the Parasaturnalidae KOZUR & MOSTLER. All forms, in which the ring is complete or where the half rings are at least at one side connected, are placed into the Parasaturnalidae KOZUR & MOSTLER. All forms, in which the ends of the half-rings are close to each other, but still on both sides separated, are placed into the Oertlispongidae KOZUR & MOSTLER. Atavistic forms, in which the saturnalid ring is on one side widely open, occur still in the Jurassic.

Subfamily **Parasaturnalinae** KOZUR & MOSTLER, 1972

Diagnosis: Shell globular, spongy, with numerous concentric layers and with tiny microsphere. In higher evolved forms also a larger, latticed second medullary shell may be present. Equatorial ring always present, but in most primitive forms on one side not yet closed. Ring always flat, mostly broad, circular, in higher evolved forms (especially in the Liassic) also subquadratic, rectangular, rarely hexagonal or oval with long axis in prolongation of polar/peripolar spines or perpendicularly to them.

Outer margin of ring always with spines, but in Hettangian forms their number may be strongly reduced, sometimes to 2 spines opposite to the polar spines. The spines are flat or oval in cross section. Only in the transitional field to early Acanthocircinae the marginal spines are differentiated (torsion, secondary spines). Only in these transitional forms indistinct ridges connect the spines across the outer ring margin. In all other Parasaturnalinae the ring is quite undifferentiated.

2 polar spines (opposite to outer spines), later increasingly peripolar spines (likewise first order spines, but situated opposite to the interspine spaces) at the inner margin of ring connect the shell with the ring. Auxiliary spines (second order spines) often present. In higher evolved forms the auxiliary spines may be transformed into additional first order spines. By this, forms evolved that have 4 first order spines in cross-like arrangement or 6 (7) first order spines, 2 of them vertically arranged, the other 4 (5) diagonally arranged. Other forms have numerous first order spines opposite to the spaces between the outer spines of the ring. Rarely 3 first order spines can be observed.

Distribution: Very frequent from the Cordevolian up to the Pliensbachian with the maximum diversity from the

Norian to Hettangian. Rare from the Toarcian to Upper Cretaceous, with a second smaller maximum in the Upper Cretaceous. Above the Bajocian only taxa with peripolar spines have been observed.

Assigned genera:

Parasaturnalis KOZUR & MOSTLER, 1972

Japonisaturnalis KOZUR & MOSTLER, 1972

? *Pseudosaturnalis* KOZUR & MOSTLER, 1972

Heliosaturnalis KOZUR & MOSTLER, 1972

Pseudoheliodiscus KOZUR & MOSTLER, 1972 emend.

PESSAGNO, 1979

Synonym: *Pessagnosaturnalis* KOZUR, 1979

Saturnosphaera TICHOMIROVA, 1975

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

Mesosaturnalis KOZUR & MOSTLER, 1981

Praemesosaturnalis KOZUR & MOSTLER, 1981

Praehexasaturnalis KOZUR & MOSTLER, 1983

Stauracanthocircus KOZUR & MOSTLER, 1983

Remarks: All transitions between highly evolved Oertlispongidae KOZUR & MOSTLER, 1980 and Parasaturnalinae KOZUR & MOSTLER, 1972 are known (see under Parasaturnalidae KOZUR & MOSTLER, 1972).

The Acanthocircinae PESSAGNO, 1977 have directly evolved from the Parasaturnalinae KOZUR & MOSTLER, 1972. In transitional forms of the Parasaturnalinae the first indistinct marginal ridges on the ring, connecting the outer spines, can be observed. The most primitive representative of the Acanthocircinae, *Octosaturnalis* n. gen., is still similar to the Parasaturnalinae, but has already very robust, broad, tricarinate spines and a distinct ridge on the upper and lower side of the outer marginal parts of the ring. These ridges connect the ridges on neighbouring spines and are therefore interrupted at the base of the spines.

The higher evolved Acanthocircinae are distinguished by elongated oval, narrow rings that are in cross section higher than broad and display a distinct furrow on the lateral outer margin. The spines of these forms are concentrated to the polar region of the long axis (1-2 spines each pole). These forms are clearly distinct from the Parasaturnalinae. Only some extreme Liassic Parasaturnalinae have an elongated oval ring that is, however, always flat, undifferentiated, on the whole margin spined and displays polar spines.

The Saturnalideidae n. fam. have developed from Upper Cretaceous Parasaturnalinae (persistent group with roundish ring). This family, represented only by one recent genus, is clearly distinguished by a latticed cortical shell. Already in the Liassic some taxa of the Parasaturnalinae have a rather big, latticed second medullary shell. There-

fore it is possible that the Upper Cretaceous species of the genera *Pseudosaturnalis* KOZUR & MOSTLER, 1972, *Mesosaturnalis* KOZUR & MOSTLER, 1981, *Praemesosaturnalis* KOZUR & MOSTLER, 1981 and *Praehexasaturnalis* KOZUR & MOSTLER, 1983 have already a latticed cortical shell, covered by a spongy layer. In this case, they would belong to the Saturnalideidae n. fam. and with exception of *Pseudosaturnalis* (type species from the Upper Cretaceous), they would all belong to new genera, because the type species of *Mesosaturnalis*, *Praemesosaturnalis* and *Praehexasaturnalis* from the Late Triassic have only a latticed microsphere. Unfortunately, the inner shell structures of the Upper Cretaceous representatives of the above mentioned genera are unknown.

P. catadelos (FOREMAN, 1968) has according to FOREMAN (1968) possibly a latticed cortical shell covered by spongy material, but the small thorns on the peripolar spines indicate rather a spongy structure of the whole outer shell without latticed cortical shell. For this reason, the genus *Pseudosaturnalis* is for the moment furthermore placed into the Parasaturnalinae.

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

Synonym: *Pessagnosaturnalis* KOZUR, 1979

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

Pseudoheliodiscus alpinus n. sp.

(Pl. 5, figs. 1, 3, 5-9, 11, 12)

Derivatio nominis: According to the occurrence in the Alps.

Holotype: The specimen on pl. 5, fig. 1; rep.-no KoMo 1990 I-31

Material: More than 100 specimens.

Diagnosis: Spongy shell large, only a little smaller than the inner margin of the ring, partly reaching until the inner margin of the ring. Shell surface with numerous short, needle-shaped spines. Shell consisting of several concentric layers. Microsphere latticed.

Ring circular, moderately broad, flat, undifferentiated, with 11-13, mostly 12 very large spines that tapers continuously toward their distal ends; some of it may be bifurcated. Beside the 2 strong polar spines, there are still 4-7 large auxiliary spines, mostly opposite to interspine spaces, but 1 or 2 of them may be situated opposite to spines.

Measurements:

Diameter of shell = 108-135 µm

Diameter of ring = 175-200 µm

Width of ring = 16-20 µm

Length of spines = 60-100 µm

Distribution: Hettangian of Alps and of the Várhegy Cherty Limestone Formation of Csövár (Hungary). Very frequent.

Remarks: *Pseudoheliodiscus riedeli* KOZUR & MOSTLER, 1972 displays shorter and numerous (about 20) auxiliary spines and its shell grow a little over the inner margin of the ring.

Pseudoheliodiscus alpinus n. sp. contains morphological transition forms to the genus *Stauracanthocircus* KOZUR & MOSTLER, 1983 emend. Forms with 4 large auxiliary spines in diagonal arrangement against the polar spines are not rare. They correspond otherwise perfectly with the specimen that display 5-7 large auxiliary spines. The large shell, never present in *Stauracanthocircus* KOZUR & MOSTLER, 1983, indicates that these specimens with 4 auxiliary spines belong to *P. alpinus* n. sp. The 4 auxiliary spines in diagonal arrangement against the polar spine indicate only intraspecific variability in the number of auxiliary spines (4-7). They do not indicate real phylomorphogenetic transitions to the genus *Stauracanthocircus*, but only homoeomorphy.

Pseudoheliodiscus robustospinosus n. sp.

(Pl. 2, figs. 3, 8; pl. 4, figs. 8-11; pl. 5, fig. 10)

1978 ? *Spongosaturnalis* sp., pars FEARY & HILLS, p. 366, only the specimen on fig. 9

Derivatio nominis: According to the broad, robust spines.

Holotype: The specimen on pl. 3, fig. 8; rep.-no. KoMo 1990 I-32

Material: More than 50 specimens.

Diagnosis: Shell spongy, consisting of several concentric layers. Latticed microsphere tiny. Few needle-like short spines may be present on the shell surface.

Ring subspherical to subquadratic, moderately broad to broad, flat, undifferentiated, with 8-11 moderately long, broad, robust, triangular spines, rarely with terminal bifurcation. One axial spine has the same form and length as the circum-axial spines, the other one is more slender and generally longer. Beside the 2 polar spines additionally 4-7, mostly large, robust auxiliary spines are present, situated mostly opposite to interspine spaces, but partly also opposite to outer spines.

Measurements:

Diameter of shell = 80–105 μm

Diameter of ring = 157–205 μm

Width of ring = 15–25 μm

Length of spines = 20–60 μm

Distribution: Hettangian of the Alps and of Csövár (Northern Hungary, Várhegy Cherty Limestone Formation), ? Jurassic of New Zealand.

Remarks: *Pseudoheliodiscus alpinus* n. sp. has more and considerably longer spines and a larger shell.

Pseudoheliodiscus massivus n. sp.

(Pl. 4, fig. 5)

Derivatio nominis: According to the massive polar spines.

Holotype: The specimen on pl. 4, fig. 5; rep.-no. KoMo 1990 I-36

Material: 5 incomplete specimens.

Diagnosis: Shell relatively small, spongy, with several concentric layers and tiny latticed microsphere. Polar spines very robust. 5-6 large, robust auxiliary spines. Ring circular, moderately broad, with triangular spines opposite to the polar spines (one may be more slender and longer) and only 4-6 triangular, relatively short circumaxial spines.

Measurements:

Diameter of shell = 80–90 μm

Diameter of ring = 180–190 μm

Width of ring = 18–21 μm

Length of spines = 20–30 μm

Distribution: Hettangian of the type locality.

Remarks: *Pseudoheliodiscus ? inaequispinosus* n. sp. has also small and few spines. However, the ring is elliptical with the long axis parallel to the polar spines. At one polar area of the long axis the ring is concave.

Pseudoheliodiscus ? inaequispinosus n. sp.

(Pl. 4, fig. 4)

Derivatio nominis: According to the irregularly spaced spines

Holotype: The specimen on pl.4, fig.4; rep.no. KoMo 1990 I-37

Material: 4 specimens.

Diagnosis: Shell relatively small, spongy, consisting of several concentric layers. Microsphere latticed. Polar spines robust, partly one polar spine and one peripolar spine is present. 1-4, mostly small auxiliary spines. Ring narrow to moderately wide, oval, with long axis parallel to the polar spines. The ring is irregularly covered by short, triangular spines. A spiny and an almost smooth half of the ring may be present.

Measurements:

Diameter of shell = 80–89 μm

Diameter of ring (long axis) = 192–200 μm

Diameter of ring (short axis) = 176–180 μm

Width of ring = 18–20 μm

Length of spines = 9–16 μm

Distribution: Hettangian of the type locality.

Remarks: See under *Pseudoheliodiscus massivus* n. sp.

Pseudoheliodiscus ? inaequispinosus n. sp. is perhaps a transitional form to *Liassosaturnalis* n. gen. that has no or only one circumaxial spine and 2 spines opposite to the polar spines.

***Pseudoheliodiscus nevirianii* n. sp.**

(Pl. 4, figs. 1, 2)

Derivatio nominis: In honour of A. NEVIANI, one of the pioneers of Mesozoic radiolarian research

Holotype: The specimen on pl. 4, fig. 1; rep.-no. KoMo 1990 I-4

Material: 9 specimens.

Diagnosis: Unit large, shell globular to slightly ellipsoidal, spongy, consisting of several concentric layers. Tiny latticed microsphere. Ring narrow, flat, undifferentiated, elliptical with long axis perpendicularly to the polar spines. 11-12 triangular to rounded triangular peripheral spines (including the axial spines), at one pole of the long axis longer than at the other pole. Axial spines not longer than adjacent spines, with typical rounded triangular shape. 2 robust polar spines and 5-6 very long, strong auxiliary spines are present.

Measurements:

Diameter of shell = 133–160 μm

Diameter of ring (long axis) = 353–367 μm

Diameter of ring (short axis) = 247–273 μm

Width of ring = 20–27 μm

Length of denticles = 27–60 μm , occasionally some spines are shorter than 10 μm

Distribution: Hettangian of the type locality.

Remarks: *Pseudoheliodiscus nevirianii* n. sp. is a transitional form to the genus *Stauracanthocircus* KOZUR & MOSTLER, 1983 emend. By reduction of the number of auxiliary spines to 4 evolved *Stauracanthocircus asymmetricus* n. sp. that has a similar denticulation (larger denticles at one pole of the long axis than at the opposite pole).

***Pseudoheliodiscus* n. sp. A**

(Pl. 2, fig. 6)

Remarks: This distinct species has numerous slender, relatively short spines and 8 strong, long auxiliary spines, partly nearly as strong as the polar spines. Only one damaged specimen is present from the Hettangian part of the Kirchstein Limestone.

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

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

***Palaeosaturnalis blomei* n. sp.**

(Pl. 9, fig. 9)

Derivatio nominis: In honour of Dr. Ch. D. BLOME, Menlo Park, California

Holotype: The specimen on pl. 9, fig. 9; rep.-no. KoMo 1990 I-41

Material: 7 damaged specimens.

Diagnosis: Shell spherical, spongy, consisting of several concentric layers. Microsphere latticed. Polar spines very robust. Ring narrow, flat, undifferentiated, slightly transversally elliptical. Axial spines triangular, short. Circumaxial spines triangular, short, but adjacent to the polar axis distinctly larger than axial spines.

Measurements:

Diameter of shell = 68–73 μm

Diameter of ring (long axis) = 179–185 μm

Diameter of ring (short axis) = 146–154 μm

Length of axial spines = 10–12 μm

Length of circumaxial spines = 13–23 μm

Distribution: Hettangian of the type locality.

Remarks: This species can be easily distinguished from other *Palaeosaturnalis* species by the short axial spines, distinctly shorter (about half of size) than the adjacent circumaxial spines.

***Palaeosaturnalis haeckeli* n. sp.**

(Pl. 9, figs. 6, 8)

Derivatio nominis: In honour of the great pioneer of radiolarian research, E. HAECKEL

Holotype: The specimen on pl. 9, fig. 6; rep.-no. KoMo 1990 I-40

Material: 17 specimens.

Diagnosis: Shell subspherical to subellipsoidal, spongy, consisting of several concentric layers. Microsphere latticed. Ring subelliptical to roundish subrectangular, sometimes subcircular, narrow, flat, undifferentiated. Long axis mostly perpendicularly to the polar axis, in some specimens parallel to it. Polar spines very robust. One axial spine has about the same size and form as the adjacent spines on both sides, the other axial spine is very long and needle-shaped. Adjacent to the axial spines 1-2 long, widely spaced circumaxial spines are situated, followed by 2-3 (mostly 3) closely spaced smaller spines.

Measurements:

Diameter of shell = 85–90 μm

Diameter of ring (in the polar spine axis) = 210–220 μm

Diameter of ring (perpendicularly to the polar spine axis) = 205–250 μm

Width of the ring = 15–23 μm

Length of the circumaxial spines adjacent to the axial spines = 50–60 μm

Length of the spines around the pole perpendicularly to the polar axis = 25–40 μm

Length of the long axial spine = 90–104 μm

Distribution: Hettangian part of the Kirchstein Limestone at the type locality.

Remarks: The circumaxial spines in *Palaeosaturnalis subovalis* n. sp. are not regularly differentiated in their length.

In *Palaeosaturnalis blomei* n. sp. both axial spines are smaller than the adjacent circumaxial spines.

***Palaeosaturnalis lenggriesensis* n. sp.**

(Pl. 1, fig. 8; pl. 13, figs. 10, 11)

Derivatio nominis: According to the occurrence in the Hettangian of Lenggries (Bavaria)

Holotype: The specimen on pl. 13, fig. 11; rep.-no. KoMo 1990 I-43

Material: 31 specimens.

Diagnosis: Shell spherical, spongy, consisting of several concentric layers. Microsphere latticed. Ring broad, flat, undifferentiated, slightly elliptical or rounded subrectangular, with long axis mostly perpendicularly to the polar spines. 10–12 triangular, relatively short spines. Axial spines in typical forms as broad and long as the circumaxial spines. Polar spines very robust.

Measurements:

Diameter of shell = 84–90 μm

Diameter of ring (long axis) = 168–240 μm

Diameter of ring (short axis) = 160–210 μm

Width of ring = 16–25 μm

Length of spines = 16–45 μm

Distribution: Hettangian of the Alps and Csövár (Várhegy Cherty Limestone Formation), Northern Hungary.

Remarks: *Palaeosaturnalis rectangularis* n. sp. has a rectangular ring outline and one axial spine is distinctly larger than the other one. Some specimens, determined as *Palaeosaturnalis* cf. *leggriesensis* n. sp. display a rounded subrectangular to subelliptical outline. They can be regarded as transitional forms between *P. lenggriesensis* n. sp. and *P. rectangularis* n. sp. From typical representatives of *P. lenggriesensis* n. sp. they are especially distinguished by axial spines of different length.

Pseudoheliodiscus robustospinosus n. sp. has the same outline and type of spines, but the axial spines have different length and auxiliary spines are present.

***Palaeosaturnalis liassicus* n. sp.**

(Pl. 1, figs. 2, 3; pl. 12, figs. 1, 3, 4, 6, 8–10; pl. 13, figs. 1, 2, 6, 7)

1982 *Palaeosaturnalis* sp. D YAO, pl. 4, fig. 2

Derivatio nominis: According to the mass occurrence in the Hettangian (Liassic)

Holotype: The specimen on pl. 12, fig. 9; rep.-no. KoMo 1990 I-38

Material: Several 100 specimens.

Diagnosis: Shell spongy, consisting of several concentric layers. Microsphere latticed. Shell surface with numerous short, needle-like spines. Ring narrow, flat, undifferentiated. Ring outline variable, mostly slightly transversally elliptical to subrectangular, but few specimens are transversally elliptical to subrectangular, few others rounded subquadratic, subcircular or slightly subelliptical with the long axis parallel to the polar spines. 11–13, mostly 12 very long, needle-shaped spines, exceptionally single spines are terminally broadened or bifurcated.

Measurements:

Diameter of shell = 95–110 μm

Diameter of ring (vertical axis) = 150–205 μm

Diameter of ring (transversal axis) = 180–230 μm

Width of ring = 14–19 μm

Length of spines = 55–110 μm

Distribution: Hettangian of the Alps, Csövár (Northern Hungary, Várhegy Cherty Limestone Formation), Japan.

Remarks: *Palaeosaturnalis dotti* (BLOME, 1984) (= *Acanthocircus harrisonensis* BLOME, 1984, *A. latus* BLOME, 1984, *A. supleensis* BLOME, 1984, *A. sp. B* BLOME, 1984) displays likewise very variable ring outline, but the ring and the spines are broader. Only in one of our specimens the spines are similarly broad (*P. cf. liassicus* n. sp., pl. 12, fig. 4). The 2 polar spines in *P. dotti* (BLOME, 1984) are more delicate.

Most similar is *Palaeosaturnalis fluegeli* (KOZUR & MOSTLER, 1972) with circular to slightly transversally elliptical ring. Also in this form, like in all Triassic *Palaeosaturnalis* species, the polar spines are more delicate than in *P. liassicus* n. sp.

***Palaeosaturnalis parvispinosus* n. sp.**

(Pl. 1, fig. 5; pl. 13, figs. 3, 5, 8; pl. 14, fig. 1)

Derivatio nominis: According to the very small circumaxial spines

Holotype: The specimen on pl. 13, fig. 3; rep.-no. KoMo 1990 I-46

Material: 46 specimens.

Diagnosis: Shell slightly ellipsoidal, spongy, consisting of several concentric layers. Microsphere latticed. Ring very narrow, flat, undifferentiated, of variable outline (roundish, rounded subquadratic, elliptical with long axis parallel to the polar spines or perpendicularly to them). 5–9 mostly very short circumaxial spines widely spaced. 2 axial spines larger than circumaxial spines. Polar spines long and very robust.

Measurements:

Diameter of shell (long axis) = 80–90 μm
Diameter of shell (short axis) = 64–75 μm
Diameter of ring (long axis) = 192–255 μm
Diameter of ring (short axis) = 154–225 μm
Width of ring = 9–16 μm

Length of circumaxial spines = 4–24 μm

Length of axial spines = 16–50 μm

Distribution: Hettangian of the Alps and Northern Hungary (Csövár, Várhegy Cherty Limestone Formation).

Remarks: *Palaeosaturnalis parvispinosus* n. sp. may be a transitional form to *Liassosaturnalis* n. gen. that has only well developed axial spines, whereas the circumaxial spines are missing or only one is present. Rudiments of peripheral spines are in this genus indicated by partly angular undulations of the outer ring margin.

***Palaeosaturnalis rectangularis* n. sp.**

(Pl. 1, figs. 9, 10)

Derivatio nominis: According to the rectangular outline of the ring

Holotype: The specimen on pl. 1, fig. 10; rep.-no. KoMo 1990 I-44

Material: 29 specimens.

Diagnosis: Shell spherical, spongy, consisting of several concentric layers. Microsphere latticed. Ring flat, narrow to moderately broad, undifferentiated, rectangular with long axis parallel or perpendicular to the polar axis. 12–15 relatively short peripheral spines of variable shape, mostly broadly triangular and slender needle-shaped spines occur in the same specimen. One axial spine is as long as the circumaxial spines, the other one is larger and needle-shaped or slender triangular. Polar spines very robust.

Measurements:

Diameter of shell = 80–90 μm
Diameter of ring (long axis) = 187–215 μm
Diameter of ring (short axis) = 160–200 μm
Width of ring = 15–23 μm

Length of circumaxial spines = 16–35 μm

Length of the large axial spine = 43–60 μm

Distribution: Hettangian of the Alps and of Csövár (Northern Hungary, Várhegy Cherty Limestone Formation).

Remarks: *Palaeosaturnalis lenggriesensis* n. sp. has a rounded subrectangular outline and the polar spines have the same length and shape as the circumaxial spines.

Palaeosaturnalis cf. *lenggriesensis* n. sp. is seemingly a transitional form to *P. rectangularis* n. sp., from which it is distinguished by its roundish subelliptical to roundish subrectangular ring outline.

***Palaeosaturnalis schaaft* n. sp.**

(Pl. 11, figs. 9–13; pl. 12, figs. 2, 7, 11)

Derivatio nominis: In honour of Dr. A. SCHAAF, Strasbourg

Holotype: The specimen on pl. 11, fig. 11; rep.-no. KoMo 1990 I-42

Material: More than 50 specimens.

Diagnosis: Shell subellipsoidal to spherical, spongy, consisting of several concentric layers. Microsphere latticed. Ring narrow, flat, undifferentiated. Its outline is variable, circular, subcircular, elliptical with long axis parallel to the polar axis or perpendicular to it. Spines moderately long, varying in length, especially by intercalation of one or few short spines that have a shorter distance to each other than the longer spines. One of the axial spines is longer than the circumaxial spines. Strong polar spines.

Measurements:

Diameter of shell = 85–100 μm

Diameter of ring (long axis) = 190–260 μm

Diameter of ring (short axis) = 185–240 μm

Width of ring (short axis) = 12–20 μm

Length of circumaxial spines = 35–50 μm , intercalated small spines 15–30 μm

Length of the long axial spine = 50–70 μm

Distribution: Hettangian of the Alps and of Northern Hungary (Csövár, Várhegy Cherty Limestone Formations).

Remarks: Specimens with circular ring are similar to *Palaeosaturnalis zapfei* (KOZUR & MOSTLER, 1972). However, *P. zapfei* has always a circular ring and all spines, including the axial spines, have the same length.

***Palaeosaturnalis subovalis* n. sp.**

(Pl. 1, fig. 7; pl. 13, figs. 4, 9)

Derivatio nominis: According to the suboval ring outline

Holotype: The specimen on pl. 13, fig. 4; rep.-no. KoMo 1990 I-39

Material: More than 50 specimens.

Diagnosis: Shell slightly ellipsoidal, spongy, consisting of several concentric layers. Microsphere latticed. Ring suboval to oval, narrow, flat, undifferentiated, with 9–11 slender, relatively short spines. One axial spine as long as the circumaxial spines, the other one is considerably longer and somewhat more slender. A larger smooth segment is present to both sides of the axial spines. Polar spines very robust.

Measurements:

Diameter of shell (parallel to polar axis) = 76–90 μm

Diameter of shell (perpendicular to polar axis) = 60–77 μm

Diameter of ring (parallel to polar axis) = 192–215 µm
Diameter of ring (perpendicularly to polar axis) = 190–240 µm

Width of ring = 13–20 µm

Length of circumaxial spines = 26–37 µm

Length of long axial spine = 56–64 µm

Distribution: Hettangian of the Alps and Northern Hungary (Csövár, Várhegy Cherty Limestone Formation)

Remarks: In *Palaeosaturnalis haeckeli* n. sp. the circumaxial spines are more variable in their length. On both sides of the axial spines 1-2 large, widely spaced spines are present. The remaining circumaxial spines are smaller and closely spaced.

"*Palaeosaturnalis*" fragilis n. sp.

(Pl. 14, fig. 2, 3)

Derivatio nominis: According to the very fragile ring
Holotype: The specimen on pl. 14, fig. 3; rep.-no. KoMo 1990 I-48

Material: 11 damaged specimens.

Diagnosis: Unit very big, but fragile. Shell not preserved, but according to the remnants on the polar spines it is spongy and consists of several concentric layers. Ring very narrow, fragile, flat, undifferentiated, with elongated elliptical outline (long axis perpendicularly to the polar axis). The about 20 needle-like spines vary strongly in length even in one specimen. Axial spine longer than circumaxial spines, a little robust, but also needle-shaped. Polar spines very long, robust.

Measurements:

Diameter of ring (long axis) = 427–452 µm

Diameter of ring (short axis) = 287–300 µm

Width of ring = 12–17 µm

Length of circumaxial spines (maximum variation in one specimen) = 7–3 µm

Length of axial spines = More than 90 µm (not fully preserved)

Distribution: Hettangian Kirchstein Limestone of the type locality.

Remarks: This species belongs surely not to *Palaeosaturnalis* DONOFRIO & MOSTLER, 1978. It has perhaps evolved by total reduction of the auxiliary spines from large representatives of *Stauracanthocircus* KOZUR & MOSTLER, 1983.

A new genus for this species will be only established, if more material (with preserved shell) will be found. Because of the very large, but very fragile ring only broken specimens could be found. However, this species can be recognized even among strongly damaged specimens.

Genus *Praehexasaturnalis* KOZUR & MOSTLER, 1983 emend.

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

Emended diagnosis: Spongy shell globular, consisting of several concentric layers. Microsphere latticed.

Ring mostly narrow, rarely moderately broad, in most primitive forms with 8 spines and with rounded octagonal outline to rounded hexagonal outline, later invariably with rounded hexagonal to hexagonal outline and 6 spines, occasionally with 1-2 further, mostly distinctly smaller spines.

Most primitive forms only with polar spines, higher evolved forms additionally with 2-12 auxiliary spines.

Distribution: Norian - Hettangian,? Upper Cretaceous. World-wide.

Assigned species:

Palaeosaturnalis tenuispinosus DONOFRIO & MOSTLER, 1978

Synonym: *Acanthocircus vigrassi* BLOME, 1984

Spongosaturnalis elegans KOZUR & MOSTLER, 1972

Acanthocircus burnensis BLOME, 1984

Synonyma: *Acanthocircus lupheri* BLOME, 1984

Acanthocircus macoyensis BLOME, 1984

Acanthocircus ochocoensis BLOME, 1984

Acanthocircus prinevillensis BLOME, 1984

Acanthocircus silverensis BLOME, 1984

Praehexasaturnalis germanicus n. sp.

Praehexasaturnalis kirchsteinensis n. sp.

Praehexasaturnalis tetradialatus n. sp.

? *Praehexasaturnalis* n. sp. A (= *Spongosaturnalis* ? sp. FOREMAN, 1971, pl. 1, fig. 6)

Remarks: KOZUR & MOSTLER (1983) assumed that *Praehexasaturnalis* KOZUR & MOSTLER, 1983 represents the forerunner of *Hexasaturnalis* KOZUR & MOSTLER, 1983, because the striking hexagonal ring outline is in both genera the same and *Hexasaturnalis* began later than *Praehexasaturnalis*.

As already pointed out under the remarks to the Saturniacea DEFLANDRE, 1953 and Parasaturnalidae KOZUR & MOSTLER, 1972, *Praehexasaturnalis* is a dead-ending sidebranch of the Parasaturnalidae, in which the same hexagonal ring outline as in primitive Acanthocircinae PESSAGNO, 1977 emend. (*Hexasaturnalis* KOZUR & MOSTLER, 1983, *Yaosaturnalis* KOZUR & MOSTLER, 1983) evolved, but the other characteristics of the Acanthocircinae (peripolar spines, ridges on the outer margin of the ring) never evolved.

Within the genus *Praehexasaturnalis* for the first time the development of taxa with auxiliary spines from taxa without auxiliary spines have been observed. Both

morphologically and phylogenetically near related forms, connected by transitional forms, are here united into *Praehexasaturnalis* that is therefore here used in a broader sense as by KOZUR & MOSTLER (1983). The forms with auxiliary spines continued seemingly until the Upper Cretaceous without larger morphological changes. These Upper Cretaceous forms have the highest number of auxiliary spines (about 12). However, the inner structure of the shell of these Upper Cretaceous forms is unknown. Therefore they can be only tentatively assigned to *Praehexasaturnalis*.

***Praehexasaturnalis germanicus* n. sp.**

(Pl. 6, figs. 1, 2)

Derivatio nominis: According to its occurrence in Bavaria (Germany)

Holotype: The specimen on pl. 6, fig. 2; rep.-no. KoMo 1990 I-51

Material: 22 specimens.

Diagnosis: Shell globular, spongy, consisting of several concentric layers. Microsphere latticed. Ring narrow, flat or with shallow elliptical cross-section, undifferentiated, outline rounded heptagonal to rounded subquadratical. 7 very long, slender, needle-like spines. Polar spine robust, auxiliary spines (mostly 5-6) always present.

Measurements:

Diameter of shell = 105–125 μm

Diameter of ring (in polar axis) = 165–175 μm

Diameter of ring (perpendicular to polar axis) = 170–175 μm

Width of ring = 12–25 μm

Length of spines = 35–110 μm

Distribution: Hettangian of Alps and Northern Hungary (Várhegy Cherty Limestone Formation of Csövár)

Remarks: *Praehexasaturnalis kirchsteinensis* n. sp. has only 6 spines and always a hexagonal ring outline.

***Praehexasaturnalis kirchsteinensis* n. sp.**

(Pl. 6, figs. 4, 5, 7)

Derivatio nominis: According to the type locality

Holotype: The specimen on pl. 6, fig. 5; rep.-no. KoMo 1990 I-50

Material: Several 100 specimens.

Diagnosis: Spongy shell globular, big, comprising largest part of the ring cavity. It consists of several concentric layers. Microsphere latticed. The shell surface is covered by numerous delicate, short, needle-like spines. Ring flat or with shallow oval cross-section, narrow, undifferentiated, outline hexagonal, with 6 very long, slender spines in the 6 corners of the ring. 2 polar spines very strong, nearly totally overgrown by the shell. 5-10 auxiliary spines of different size always present.

Measurements:

Diameter of shell = 96–120 μm

Diameter of ring (in polar axis) = 156–170 μm

Diameter of ring (perpendicular to the polar axis) = 160–170 μm

Width of ring = 15–20 μm

Length of spines = 70–95 μm

Distribution: Frequent in the Hettangian of the Alps and of Northern Hungary (Csövár, Várhegy Cherty Limestone Formation).

Remarks: See under *P. tetraradiatus* n. sp.

***Praehexasaturnalis tetraradiatus* n. sp.**

(Pl. 6, figs. 8, 9, 11, 12)

Derivatio nominis: According to the 4 rays at the inner margin of the ring (2 polar spines, 2 auxiliary spines)

Holotype: The specimen on pl. 6, fig. 11; rep.-no. KoMo 1990 I-49

Material: More than 50 specimens.

Diagnosis: Shell large, globular, spongy, consisting of several concentric layers. Microsphere latticed. Shell surface with delicate, short, needle-like spines. Ring narrow, flat, undifferentiated, outline hexagonal. 6 very large, slender spines in the 6 corners of the ring. Axial spines a little larger and robuster than the 4 circumaxial spines. Polar spines robust. 2 auxiliary spines cross-like arranged with the polar spines, mostly short, elongated triangular.

Measurements:

Diameter of shell = 110–120 μm

Diameter of ring (in polar axis) = 144–170 μm

Diameter of ring (perpendicular to polar axis) = 144–170 μm

Width of ring = 13–21 μm

Length of spines = 90–125 μm

Distribution: Rhaetian and Hettangian, Alps, Northern Hungary (Csövár, Csövár Limestone Formation and Várhegy Cherty Limestone Formation), Japan, Philippines.

Remarks: The phylomorphogenetic development within the genus *Praehexasaturnalis* KOZUR & MOSTLER, 1983 emend. is now well known. The oldest forms (Lower to Middle Norian) have 8 needle-like spines, all of about the same length (the axial spines may be somewhat larger than the circumaxial spines, like in the stratigraphically younger forms). The main stock (with narrow ring) of these oldest *Praehexasaturnalis* is represented by *Praehexasaturnalis burnensis* (BLOME, 1984), synonyma see under the genus. The outline of this species is still variable (roundish octagonal, roundish suboval, subquadratic).

The next younger form is *Praehexasaturnalis elegans* (KOZUR & MOSTLER, 1972) from the Middle and Upper Norian. In this species the 2 spines perpendicularly to the polar spines are already distinctly shorter than the remaining spines, the outline of the ring is rounded hexagonal to rounded subquadratic.

In the Upper Norian (? to Rhaetian) *Praehexasaturnalis tenuispinosus* (DONOFRIO & MOSTLER, 1978) occur, in which the 2 spines perpendicularly to the polar spines are not more present. The ring outline is hexagonal.

In the (highest Upper Norian ?) Rhaetian and Hettangian *Praehexasaturnalis tetraradiatus* n. sp. occur, that coincides morphologically with *P. tenuispinosus*, but has 2 auxiliary spines additional to the polar spines. These 4 inner spines are cross-like arranged.

In the Hettangian *P. kirchsteinensis* evolved that remained morphologically unchanged, but displays 5-10 auxiliary spines.

Maybe that Upper Cretaceous forms with the same morphological character, but with peripolar spines, are the last representatives of this line that yields important guide forms for the Norian to Hettangian time-interval. 5 distinct zones can be discriminated within this interval by evaluation of the phylomorphogenetic development within the genus *Praehexasaturnalis*: *P. burnensis* without *P. elegans* (Lower Norian) *P. elegans* without *P. tenuispinosus* (Middle Norian) *P. tenuispinosus* without *P. tetraradiatus* (Upper Norian, higher Upper Norian radiolarian faunas not yet well investigated) *P. tetraradiatus* without *P. kirchsteinensis* (? uppermost Norian, Rhaetian) *P. tetraradiatus* and *P. kirchsteinensis* (Hettangian).

Taxonomically this development is interesting, because taxa with auxiliary spines evolved from taxa without auxiliary spines. Moreover, in *P. tetraradiatus* the 2 polar spines and the 2 auxiliary spines are cross-like arranged, like in the genus *Stauracanthocircus* KOZUR & MOSTLER, 1983 emend. This is surely a homoeomorphy (see under this genus).

Genus *Stauracanthocircus* KOZUR & MOSTLER, 1983 emend.

Type species: *Pseudoheliodiscus concordis* De WEVER, 1981

Emended diagnosis: Typical forms large. Shell spongy, globular or with rhombic or polygonal equatorial outline and subhemiglobular or somewhat flattened lower and upper side. Around the latticed microsphere several concentric or subconcentric layers of spongy meshwork are present.

Ring narrow to very narrow, flat or with shallow elliptical cross-section, undifferentiated. Outline variable, mostly rectangular, quadratic, sometimes subelliptical,

rarely roundish. Outer margin with many spines of different length. 2 long polar spines and 2-4 long auxiliary spines are present. If there are 2 auxiliary spines, than they are always arranged in cross-like position with the polar spines. If there are 4 auxiliary spines, they are diagonally arranged against the polar spines, but the midline of the 2 pairs of auxiliary spines lies again in a cross-like position with the polar spines. The auxiliary spines become often as strong as the polar spines. In this case 4 or 6 first order spines of the above mentioned arrangements are present.

Distribution: Very rare in the Norian and Rhaetian, frequent in the Hettangian and Pliensbachian. Typical forms were until now only found in the Liassic.

Assigned species:

Pseudoheliodiscus concordis De WEVER, 1981

? *Quadrisaturnalis dickinsoni* YEH, 1989

Stauracanthocircus asymmetricus n. sp.

Stauracanthocircus circularis n. sp.

? *Stauracanthocircus ? hettangicus* n. sp.

Stauracanthocircus quadratus n. sp.

? *Stauracanthocircus poetschensis* n. sp.

Stauracanthocircus pessagnoii n. sp.

Stauracanthocircus ruesti n. sp.

Stauracanthocircus transitus n. sp.

Stauracanthocircus triangulospinosus n. sp.

Remarks: Originally only forms with 4 long inner rays (first order spines) in cross-like position were placed into *Stauracanthocircus*. However, all transitional forms are present to forms with 6 first order spines or with 2 polar spines and 4 a little smaller auxiliary spines. 2 pairs of auxiliary spines are in these forms diagonally arranged to the polar spines. By fusion of the 2 pairs of diagonally arranged spines 2 auxiliary spines in cross-like position to the polar spines evolved. Often such forms are present, in which on one side still a pair of diagonally arranged auxiliary spines occur, whereas on the other side the other pair of auxiliary spines is already fused to one auxiliary spine perpendicularly arranged to the polar spines. Therefore also forms with 4 auxiliary spines diagonally arranged to the polar spines or with 6 first order spines of the same arrangement (the 4 auxiliary spines have in these forms the same size as the polar spines) are here placed into *Stauracanthocircus* KOZUR & MOSTLER, 1983 emend.

The development of 4 cross-like arranged inner rays occurred iteratively in the Parasaturnalidae KOZUR & MOSTLER, 1972, but also in not related forms with saturnalid ring and coarsely latticed cortical shell. It represents a function-morphologically stable construction and has originally no larger taxonomic meaning. Only in combination with other taxonomic features it can be used for separation of genera.

The first time this construction can be found in the Austrosaturnalidae KOZUR & MOSTLER, 1983 from the Longobardian and Carnian. These forms with saturnalid ring have a primary latticed shell with big pores and they do not belong to the Saturnaliacea DEFLANDRE, 1953 with primary spongy shells.

Few forms with 4 cross-like arranged spines of nearly the same size or with only slightly larger polar spines appeared during the Norian, e.g. "*Spongosaturnalis*" *quadriradiatus* KOZUR & MOSTLER, 1972. These forms have always a circular ring outline and long spines of almost invariable size, typical for many Triassic *Pseudoheliodiscus* and *Palaeosaturnalis* species. Seemingly these forms are homoeomorphic to *Stauracanthocircus* and nearer related to *Pseudoheliodiscus*. They are surely not directly related to the typical large Liassic *Stauracanthocircus* species. Polar spines and auxiliary spines are rather fragile in these forms.

A second Norian group with 2 polar spines and 2 auxiliary spines in cross-like arrangement is represented by *Stauracanthocircus* ? *poetschensis* n. sp. These forms have a rectangular to quadratic very broad ring with relatively small ring cavity. Also the (Lower) Norian "*Quadrisaturnalis*" *dickinsoni* YEH, 1989 belongs to this group. *Quadrisaturnalis* YEH, 1989 was established for forms, mostly identical with *Praeheliostaurus* KOZUR & MOSTLER, 1972 and the type species of *Quadrisaturnalis* YEH, 1979 (*Quadrosaturnalis grandis* YEH, 1979) belongs to this genus. The latticed cortical shell with big pores is typical for this genus. However, neither in "*Quadrisaturnalis*" *dickinsoni* YEH nor in *Stauracanthocircus* ? *poetschensis* n. sp. a shell was found. The shell remnants at the polar spine indicate rather a spongy shell consisting of several concentric layers. Therefore these forms are probably true parasaturnalids. On the other hand, they are surely not the forerunner of the typical Liassic *Stauracanthocircus* species, but may belong to an other species group of this genus. The Hettangian *Stauracanthocircus* ? *ruesti* n. sp. belongs probably also to this group, distinguished from typical Liassic *Stauracanthocircus* species by the very strong peripheral spines and at the Norian forms also by the broader ring. So long the shell of the Norian forms and their relation to the Liassic *S. ruesti* n. sp. (with preserved shell) are not yet known, it cannot be decided, whether these forms belong to *Stauracanthocircus* or not. They are here tentatively assigned to this genus.

Taxa with 2 or 4 auxiliary spines in the above described "*Stauracanthocircus* arrangement" developed also from taxa without auxiliary spines. This was observed in the genus *Praehexasaturnalis* KOZUR & MOSTLER, 1983 (see under this genus). *Praehexasaturnalis tetrara-*

diatus n. sp. with 2 auxiliary spines in cross-like arrangement to the polar spines is the transitional form between the Upper Norian *P. tenuispinosus* (DONOFRIO & MOSTLER, 1978) (without auxiliary spines) and the Hettangian *Praehexasaturnalis kirchsteinensis* n. sp. (with 5-10 auxiliary spines). In spite of the cross-like arrangement of the polar spines and 2 auxiliary spines, *P. tetraradiatus* n. sp. is not related to *Stauracanthocircus*.

The "*Stauracanthocircus* arrangement" of the auxiliary spines/polar spines can be also found in the 2 known species of *Liassosaturnalis* n. gen., which is likewise not nearer related to *Stauracanthocircus*. In these species forms without auxiliary spines and with 1-6 auxiliary spines are present in one population (one sample) of otherwise morphologically identical forms. Specimens with 2 and 4 auxiliary spines have the typical "*Stauracanthocircus* arrangement" of the auxiliary and polar spines. Whereas in *Praehexasaturnalis tetraradiatus* n. sp. the "*Stauracanthocircus* arrangement" of the auxiliary spines/polar spines is within the species fixed, in *Liassosaturnalis* the "*Stauracanthocircus* arrangement" is even only part of the intraspecific variability within species that contain also forms without "*Stauracanthocircus* arrangement" of the auxiliary spines/polar spines (specimens without auxiliary spines or with 1, 3, 5, 6 auxiliary spines).

Stauracanthocircus ? *hettangicus* n. sp., in turn, corresponds in the ring outline and denticulation to *Palaeosaturnalis subovalis* n. sp. However, we have found only forms with 2 auxiliary spines in cross-like arrangement with the 2 polar spines or forms, in which on one side 2 closely spaced auxiliary spines are present, whereas at the opposite side only one auxiliary spine, perpendicular to the polar spines, is present. This arrangement corresponds to the transitional forms between *Stauracanthocircus* species with 2 and with 4 auxiliary spines. Transitional forms to *Palaeosaturnalis subovalis* n. sp. (with one auxiliary spine) have not been found. Therefore *Stauracanthocircus* ? *hettangicus* n. sp. cannot be united with this species. It is here tentatively assigned to *Stauracanthocircus*, in spite of the fact that it is surely not nearer related to typical representatives of this genus.

***Stauracanthocircus asymmetricus* n. sp.**

(Pl. 2, fig. 9; pl. 8, figs. 7-10; pl. 9, figs. 1-5,7,10,12)

Derivatio nominis: According to the asymmetric size distribution of the spines

Holotype: The specimen on pl. 2, fig. 9; rep.-no. KoMo 1990 I-52

Material: Several 100 specimens.

Diagnosis: Unit large. Spongy shell mostly roundish polygonal, rarely subspherical, mostly with hexagonal equa-

torial outline. It consists of several layers of spongy meshwork around a latticed microsphere. Ring mostly narrow, in extreme forms moderately broad, always flat, undifferentiated. Ring outline variable, mostly elliptical to subelliptical with long axis perpendicularly to the polar axis, partly rounded subrectangular to subquadratic. The 14-22 peripheral spines are at one polar region of the long axis long, cylindrical to needle-shaped. On the opposite pole the spines are slender triangular to broadly triangular and considerably shorter. Polar spines long, but mostly rather slender. 6 auxiliary spines long, mostly as strong as the polar spines or only a little narrower, rarely distinctly narrower.

Measurements:

Diameter of shell = 105–150 μm

Diameter of ring (in polar axis) = 200–270 μm

Diameter of ring (perpendicularly to the polar axis) = 235–340 μm

Width of ring = 11–25 μm

Length of spines (in the half with long spines) = 30–70 μm

Length of spines (in the half with short spines) = 7–30 μm

Distribution: Common in the Hettangian of the Alps and Northern Hungary (Csövár, Várhegy Cherty Limestone Formation).

Remarks: By the different length and shape of the spines in the 2 halves of the ring along the long axis this species is easily to recognize. The other typical *Stauracanthocircus* species of the Hettangian display, moreover, different ring outlines. *S. pessagnoii* n. sp., *S. quadratus* n. sp., *S. transitus* n. sp., and *S. triangulospinosus* n. sp. have rectangular to quadratic ring outline, *S. circularis* n. sp. displays circular ring outline. *S. pessagnoii* n. sp., *S. quadratus* n. sp. and *S. triangulospinosus* n. sp. have, moreover, only 2 auxiliary spines in cross-like arrangement with the polar spines.

Specimens of *S. asymmetricus* n. sp. with concave incision of the ring around the polar spines are in the ring outline similar to *Stauracanthocircus concordis* De WEVER, 1981. However, this species displays 2 auxiliary spines in cross-like arrangement with the polar spines. Moreover, in most specimens of *S. asymmetricus* n. sp. the concave incision of the ring around the polar spines is not present.

Pseudoheliodiscus nevanii n. sp. has the same differences in the size and shape of the spines in the 2 halves of the ring along the long axis. However, this species has 5-6 auxiliary spines and only 11-12 peripheral spines. *Pseudoheliodiscus nevanii* n. sp. is seemingly near related to the forerunner of typical representatives of *Stauracanthocircus* KOZUR & MOSTLER, 1983 emend. *Stauracanthocircus asymmetricus* n. sp., in turn, is the most primitive representative of typical *Stauracanthocircus* species.

***Stauracanthocircus circularis* n. sp.**

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

Derivatio nominis: According to the circular ring outline, exceptional for the genus *Stauracanthocircus*

Holotype: The specimen on pl. 2, fig. 5; rep.-no. KoMo 1990 I-57

Material: 41 specimens.

Diagnosis: Spongy shell globular, consisting of several concentric layers. Microsphere latticed. Ring very narrow to narrow, flat, undifferentiated, outline circular to subcircular. The 9-11 peripheral spines are small, triangular and widely spaced. The axial spines are mostly distinctly bigger than the circumaxial spines, but also not large. Polar spines robust, distinctly broader than the 4, diagonally arranged auxiliary spines.

Measurements:

Diameter of shell = 100–135 μm

Diameter of ring = 250–305 μm

Width of ring = 10–24 μm

Length of circumaxial spines = 7–20 μm

Length of axial spines = 11–35 μm

Distribution: Hettangian Alps and Northern Hungary (Csövár, Várhegy Cherty Limestone Formation).

Remarks: *Stauracanthocircus circularis* n. sp. is by its circular/subcircular ring outline and its small, widely spaced spines well distinguished from all other *Stauracanthocircus* species.

***Stauracanthocircus hettangicus* n. sp.**

(Pl. 7, figs. 2, 7)

Derivatio nominis: According to the occurrence in the Hettangian

Holotype: The specimen on pl. 7, fig. 2; rep.-no. KoMo 1990 I-60

Material: 12 specimens.

Diagnosis: Spongy shell ellipsoidal, consisting of several layers and a latticed microsphere. Ring narrow, flat to shallow elliptical in cross-section, undifferentiated, outline subelliptical with long axis parallel to the polar axis. 7-8 slender triangular to needle-shaped, moderately long circumaxial spines and 2 long axial spines. One of the axial spines is larger than the other one and displays cylindrical shape. A larger unspined part of the ring is present to both sides of the axial spines, but partly also in this sector 1-2 spines are present. Polar spines very robust, broad. 2-4 auxiliary spines in typical "*Stauracanthocircus* arrangement". The auxiliary spines are considerably thinner than the polar spines.

Measurements:

Diameter of shell (long axis parallel to polar spines) = 95–104 μm

Diameter of shell (short axis) = 85–90 μm
Diameter of ring (parallel to polar spines) = 180–195 μm
Diameter of ring (perpendicularly to polar spines) = 145–180 μm

Width of ring = 12–20 μm

Length of circumaxial spines = 25–50 μm

Length of axial spines = 50–74 μm

Distribution: Hettangian part of Kirchstein Limestone at the type locality.

Remarks: *Stauracanthocircus* ? *hettangicus* n. sp. is in its size, shape and spinosity very similar to *Palaeosaturnalis subovalis* n. sp. However, transitional forms to this species (with one auxiliary spine) have not been found. On the other hand, also *Stauracanthocircus* sp. B is very similar, but with more subrectangular ring outline and shorter, more triangular spines. Number and arrangement of circumaxial spines, the different length and shape of the axial spines and the very robust polar spines are identical with *S.* ? *hettangicus* n. sp. *Stauracanthocircus* sp. B, in turn, is nearly related to the typical *Stauracanthocircus* species *S. pessagnoii* n. sp. (see under this species). For the moment, *S.* ? *hettangicus* n. sp. is tentatively placed into the genus *Stauracanthocircus* KOZUR & MOSTLER, 1983 emend., but we cannot exclude near relations to *Palaeosaturnalis subovalis* n. sp.

***Stauracanthocircus quadratus* n. sp.**

(Pl. 3, figs. 1, 6; pl. 8, figs. 2, 3, 5)

Derivatio nominis: According to the mostly quadratic ring outline

Holotype: The specimen on pl. 8, fig. 3; rep.-no. KoMo 1990 I-56

Material: 37 specimens.

Diagnosis: Spongy shell consisting of several concentric layers and a latticed microsphere. Equatorial shell outline quadratic to subquadratic. Ring narrow to very narrow, flat, undifferentiated, outline quadratic to rectangular, polar sides slightly concave. In general 6 spines are present, one circumaxial spine at each corner and 2 axial spines. All spines are needle-like, mostly long. The axial spines are in general somewhat longer than the circumaxial spines. Rarely 1-2 small additional spines are present on one of the polar sides of the ring. Polar spines distinctly stronger than the 2 auxiliary spines. Inner spines always cross-like arranged.

Measurements:

Diameter of shell = 95–120 μm

Diameter of ring (parallel to polar spines) = 190–240 μm

Diameter of ring (perpendicularly to polar spines) = 230–260 μm

Width of ring = 10–15 μm

Length of spines = 30–80 μm

Distribution: Hettangian of Alps and Northern Hungary (Csövár, Várhegy Cherty Limestone Formation).

Remarks: *Stauracanthocircus pessagnoii* n. sp. has more spines and rounded corners.

***Stauracanthocircus pessagnoii* n. sp.**

(Pl. 3, fig. 7)

Derivatio nominis: In honour of Prof. Dr. A. A. PESSAGNO, Dallas

Holotype: The specimen on pl. 3, fig. 7; rep.-no. KoMo 1990 I-55

Material: 12 specimens.

Diagnosis: Shell spongy, consisting of several layers of spongy meshwork around a latticed microsphere. Equatorial outline of shell quadratic to rhombic. Ring very narrow, flat, undifferentiated, outline subquadratic with rounded corners. 10 needle-shaped spines (2 axial spines and 8 circumaxial spines, situated in each corner and near to the corners on the sides parallel to the polar spines). 2 polar spines and 2 auxiliary spines in cross-like arrangement. Polar spines distinctly broader than auxiliary spines.

Measurements:

Diameter of shell (parallel to the polar spines) = 90–100 μm

Diameter of shell (diagonally to the polar spines) = 80–86 μm

Diameter of ring (parallel to polar spines) = 221–239 μm

Diameter of shell (perpendicularly to polar spines) = 205–218 μm

Width of ring = 10–17 μm

Length of spines = 20–33 μm

Distribution: Hettangian part of Kirchstein Limestone at the type locality.

Remarks: *Stauracanthocircus quadratus* n. sp. displays a quadratic to rectangular outline and only 6-7 peripheral spines.

Stauracanthocircus sp. B (pl. 3, fig. 5) displays similar outline and arrangement of the peripheral spines, but the shell is subspherical with rounded subquadratic equatorial outline, the ring is broader, the peripheral spines are more triangular and the polar spines are very robust.

***Stauracanthocircus* ? *poetschensis* n. sp.**

(Pl. 7, fig. 8; pl. 8, figs. 1, 4)

Derivatio nominis: According to the occurrence in the Pötschen Limestone

Holotype: The specimen on pl. 8, fig. 1; rep.-no. KoMo 1990 I-59

Locus typicus: Pötschenwand (Austria, Hallstatt Nappe)

Stratum typicum: Sample POM 6/7, siliceous limestone of higher Middle Norian age

Material: 41 specimens.

Diagnosis: Shell not preserved, but remnants at the polar spines indicate a spongy shell consisting of several layers. Ring broad, flat, undifferentiated, outline hexagonal, subhexagonal with long axis perpendicularly to the polar spines or subquadratic. 11-13 slender triangular to needle-like very large spines alternate with somewhat to considerably smaller spines. 2 polar and 2 auxiliary spines in cross-like arrangement. Polar spines slender triangular, bigger than the auxiliary spines or of nearly the same size.

Measurements:

Diameter of ring (parallel to polar spines) = 158–200 μm

Diameter of ring (perpendicular to polar spines) = 170–225 μm

Width of ring = 20–40 μm

Length of spines = 15–110 μm

Distribution: Middle Norian of the Alps.

Remarks: "*Quadrisaturnalis*" *dickinsoni* YEH, 1989 (= "*Quadrisaturnalis*" *quadratus* YEH, 1989) from the Norian of Oregon has 8 spines, most of them very broad and at least in their proximal part with parallel sides.

Differences to *Stauracanthocircus ruesti* n. sp. see under this species.

***Stauracanthocircus ruesti* n. sp.**

(Pl. 6, fig. 10; pl. 7, figs. 1, 3)

Derivatio nominis: In honour of one of the pioneers of fossil radiolarian studies, D. RÜST

Holotype: The specimen on pl. 7, fig. 1; rep.-no. KoMo 1990 I-58

Material: 19 specimens.

Diagnosis: Spongy shell, consisting of several concentric layers. Microsphere latticed. Ring narrow to moderately broad, flat, undifferentiated. Ring outline rectangular to subrectangular (with long axis parallel to the polar spines), partly also quadratic. 12-14 very long, needle-like spines. Polar spines robust. 3-4, very rarely 5 auxiliary spines delicate, shorter than the polar spines, in typical "*Stauracanthocircus* arrangement".

Measurements:

Diameter of shell = 80–100 μm

Diameter of ring (parallel to polar spines) = 104–180 μm

Diameter of ring (perpendicularly to polar spines) = 152–165 μm

Width of ring = 12–25 μm

Length of spines = 55–115 μm

Distribution: Hettangian part of the Kirchstein Limestone from the type locality.

Remarks: By its very long spines *Stauracanthocircus ruesti* n. sp. is quite different from all other Hettangian *Stauracanthocircus* species. The only similar species is

the Middle Norian *Stauracanthocircus ? poetschensis* n. sp. This species has a similar ring outline and similar large spines. However, it has always 2 polar spines in cross-like arrangement with the 2 polar spines. Moreover, the long axis of the ring lies perpendicularly to the polar spines, the ring is broader and the polar spines are shorter.

***Stauracanthocircus transitus* n. sp.**

(Pl. 3, figs. 2, 9; pl. 7, figs. 6, 9)

Derivatio nominis: According to the transitional position from species with 4 diagonally arranged auxiliary spines to species with 2 auxiliary spines arranged in cross-like position with the polar spines

Holotype: The specimen on pl. 3, fig. 9; rep.-no. KoMo 1990 I-53

Material: 27 specimens.

Diagnosis: Unit large. Shell spongy, consisting of several layers of spongy network around a latticed microsphere. Equatorial outline of shell quadratic to rhombic. Ring subrectangular to subquadratic with rounded corners, very narrow, flat, undifferentiated. 19-26 needle-shaped peripheral spines of variable length. Within this species all transitions are present between forms with 4 auxiliary spines, diagonally arranged to the polar spines, to forms with 2 auxiliary spines, cross-like arranged with the 2 polar spines. In specimens with 4 auxiliary spines the distance between 2 adjacent auxiliary spines is not large. Therefore the diagonally arrangement of these auxiliary spines is not far from a cross-like arrangement with the polar spines. Often on one side one pair of auxiliary spines is already fused to one auxiliary spines situated perpendicularly to the polar spines, whereas on the other side the 2 auxiliary spines are still separated and diagonally arranged. Moreover, one auxiliary spine on both sides (or on one side) may be arranged already perpendicularly to the polar spines (cross-like arrangement), whereas the other spine of the pair diverges only a little (diagonal arrangement). Auxiliary spines and polar spines mostly of the same size (all are first order spines).

Measurements:

Diameter of shell (along the first order spines) = 130–150 μm

Diameter of shell (diagonally to the first order spines) = 110–130 μm

Diameter of ring (parallel to the polar spines) = 275–294 μm

Diameter of ring (perpendicularly to the polar spines) = 270–286 μm

Width of ring = 10–15 μm

Length of spines = 10–55 μm

Distribution: Hettangian of the Alps and Northern Hungary (Csövár, Várhegy Cherty Limestone Formation).

Remarks: *Stauracanthocircus triangulospinosus* n. sp. displays always 4 first order spines in cross-like arrangement. The peripheral spines are slender triangular.

Stauracanthocircus asymmetricus n. sp. has always 4 auxiliary spines, diagonally arranged to the polar spines. The peripheral spines on one half of the ring along the long axis are long and needle-shaped to cylindrical, like in *S. transitus* n. sp., on the opposite half of ring considerably shorter and triangular.

In the Pliensbachian *Stauracanthocircus concordis* (De WEVER, 1981) the ring is concave around the polar spines and distinctly convex perpendicularly to the polar spines. In few specimens of *S. transitus* n. sp. (pl. 3, fig. 2) the ring is slightly to distinctly convex perpendicularly to the polar spines, but not yet concave around the polar spines. These forms (*S. cf. transitus* n. sp.) are transitional forms to *S. concordis* (De WEVER), but still nearer related to *S. transitus* n. sp.

Stauracanthocircus triangulospinosus n. sp.

(Pl. 3, figs. 8, 10; pl. 7, fig. 5)

Derivatio nominis: According to the slender triangular peripheral spines

Holotype: The specimen on pl. 3, fig. 10; rep.-no. KoMo 1990 I-54

Material: 45 specimens.

Diagnosis: Spongy shell with quadratic to rhombic equatorial outline. It consists of several concentric layers of spongy meshwork and displays a latticed microsphere. Ring very narrow, flat, undifferentiated, outline subrectangular to subquadratic with slightly rounded corners. The 22-24 peripheral spines are short and slender triangular. Among the 4 first order spines in cross-like arrangement no differentiation into polar and auxiliary spines is possible.

Measurements:

Diameter of shell (along the first order spines) = 100–125 μm

Diameter of shell (diagonally to the first order spines) = 100–105 μm

Diameter of ring (long axis) = 232–255 μm

Diameter of ring (short axis) = 195–208 μm

Width of ring = 8–11 μm

Length of spines = 10–25 μm

Distribution: Hettangian of Alps and Northern Hungary (Csövár, Várhegy Cherty Limestone Formation).

Remarks: *Stauracanthocircus transitus* n. sp. has a similar ring outline, but it is larger, the spines are needle-shaped and often 3 or 4 auxiliary spines are present.

Stauracanthocircus sp. A.

(Pl. 8, fig. 6)

Remarks: This form (only one broken specimen) is similar to *Stauracanthocircus transitus* n. sp., but has very fragile and mostly short peripheral spines. It is seemingly a pathologic form, in which parts of the ring turned out of the equatorial plane. Most probably it belongs to *S. transitus* n. sp.

Distribution: Hettangian part of the Kirchstein Limestone at Mt. Kirchstein.

Stauracanthocircus sp. B

(Pl. 3, fig. 5)

Remarks: The outline of the ring, number and arrangement of the peripheral spines are similar as in *Stauracanthocircus pessagnoii* n. sp. However, the ring is broader, the peripheral spines are mostly triangular, the polar spines are very robust and the shell is subglobular.

There are also similarities to *Stauracanthocircus ? hettangicus* n. sp., but this species has a subelliptical ring outline and larger spines.

Distribution: Hettangian part of the Kirchstein Limestone at Mt. Kirchstein.

Stauracanthocircus sp. C

(Pl. 2, fig. 1)

Remarks: Only one damaged specimen of a distinct *Stauracanthocircus* species with circular ring outline, cylindrical circumaxial spines and broadly cylindrical, terminal rounded triangular axial spines is present. Probably it has the same asymmetric spinosity as *Stauracanthocircus asymmetricus* n. sp. or *Pseudoheliodiscus nebianii* n. sp. However, only a part of the second half of the ring is preserved. Therefore no exact description of this probably new species is possible. The near related *Stauracanthocircus asymmetricus* n. sp. is distinguished by its ring outline.

Genus *Stauromesosaturnalis* n. gen.

Derivatio nominis: According to the peripolar spines (as in *Mesosaturnalis* KOZUR & MOSTLER, 1983), cross-like arranged with 2 auxiliary spines

Type species: *Stauromesosaturnalis schizospinosus* n. gen. n. sp.

Diagnosis: Shell spherical or subspherical with rounded subquadratic equatorial outline, spongy, consisting of several concentric layers and a tiny latticed microsphere.

Ring narrow, flat, undifferentiated, with subelliptical to rounded quadratic outline and numerous, relatively short peripheral spines. 2 peripolar and 2 auxiliary spines (also opposite to interspine spaces) are cross-like ar-

ranged. In early forms the peripolar spines are somewhat broader than the auxiliary spines. In highly evolved forms all 4 spines have the same size. At least opposite to the peripolar spines, in higher evolved forms opposite to all 4 inner spines the ring is concavely incised.

Distribution: Hettangian to Pliensbachian.

Assigned species:

Stauromesosaturnalis schizospinosus n. gen. n. sp.

Stauromesosaturnalis deweveri n. sp.

Remarks: *Stauracanthocircus* KOZUR & MOSTLER, 1983 emend. has polar spines.

Praemesosaturnalis KOZUR & MOSTLER, 1983 has several small auxiliary spines, not cross-like arranged with the peripolar spines. This genus is probably the forerunner of *Stauromesosaturnalis* n. gen. However, also a direct derivation from *Stauracanthocircus* KOZUR & MOSTLER, 1983 emend. by transformation of the polar spines into peripolar spines cannot be excluded.

Japonisaturnalis KOZUR & MOSTLER, 1973 has evolved from *Stauromesosaturnalis* species with bifurcated peripheral spines. If the terminal branches of adjacent spines grow together, a second ring evolved, separated from the primary ring by a pore ring. The first true *Japonisaturnalis* KOZUR & MOSTLER, 1972 is known from the Pliensbachian.

***Stauromesosaturnalis schizospinosus* n. gen. n. sp.**

(Pl. 3, fig. 3)

Derivatio nominis: According to the bifurcated or otherwise branched peripheral spines

Holotype: The specimens on pl. 3, fig. 3; rep.-no. KoMo 1990 I-61

Material: 7 specimens.

Diagnosis: Shell spongy, consisting of several concentric layers and a central latticed microsphere. Equatorial shell outline rounded subquadratic. Ring very narrow, flat, undifferentiated. Ring outline subelliptical (long axis perpendicular to the peripolar spines), with distinct concave incision above the peripolar spines. 22-24 short peripheral spines, terminally bifurcated or asymmetrically branched. Peripolar spines distinctly broader than the 2 auxiliary spines. The 4 inner spines are cross-like arranged.

Measurements:

Diameter of shell = 100–110 μm

Diameter of ring (parallel to peripolar spines) = 196–209 μm

Diameter of ring (perpendicular to peripolar spines) = 241–263 μm

Width of ring = 13–17 μm

Length of spines = 19–30 μm

Distribution: Hettangian part of Kirchstein Limestone at the type locality.

Remarks: *Stauromesosaturnalis schizospinosus* n. gen. n. sp. is the forerunner of the Pliensbachian *Japonisaturnalis* n. sp. A (= *Japonisaturnalis japonicus* sensu De WEVER, 1981, pl. 1, fig. 6). By fusion of the terminal branches of adjacent peripheral spines a second ring evolved that encloses together with the primary ring and the primary peripheral spines of the pore ring.

The Pliensbachian *Stauromesosaturnalis deweveri* n. sp. displays terminally unbranched spines, the ring is concavely incised opposite to all 4 first order spines that have all the same size.

***Stauromesosaturnalis deweveri* n. sp.**

Derivatio nominis: In honour of Dr. P. De WEVER, Paris, who figured this species for the first time 1981 *Pseudoheliodiscus* ? sp. aff. *P. concordis* De WEVER, p. 142, pl. 2, fig. 4

Holotype: The specimen, figured by De WEVER (1981, pl. 2, fig. 4) as *Pseudoheliodiscus* ? sp. aff. *concordis*

Locus typicus: Gümüslü Unit (Western Taurus, eastern Domuz Dag Massif), north of Korkuteli, Sögütlü gorge, 1 km NW of Gümüslü village, Turkey

Stratum typicum: Sögütlü dere Formation, radiolarian limestone, Pliensbachian

Diagnosis: Shell globular, spongy. Ring narrow, flat, undifferentiated, outline rounded subquadratic, opposite to the 4 first order spines concavely incised. 21 short, triangular peripheral spines. 4 first order inner spines of equal size in cross-like arrangement, all opposite to interspine spaces. Peripolar and auxiliary spines cannot be separated.

Measurements (holotype):

Diameter of shell = 150 μm

Diameter of ring along the inner spines = 250 μm and 260 μm

Width of ring = 15–18 μm

Length of spines = 14–25 μm

Distribution: Pliensbachian of the type locality.

Remarks: See under *Stauromesosaturnalis schizospinosus* n. gen. n. sp.

Genus *Liassosaturnalis* n. gen.

Derivatio nominis: According to the occurrence in the Liassic

Type species: *Liassosaturnalis parvus* n. gen. n. sp.

Diagnosis: Unit small. Shell spherical to slightly ellipsoidal, spongy, consisting of several concentric layers of spongy meshwork and of a central latticed microsphere.

Ring narrow, flat, undifferentiated. Ring outline subcircular, elliptical or subelliptical. Axial spines always present. Remaining ring smooth or with one rudimentary spine. Angular undulations as rudiments of former spines

often present. 2 polar spines very robust. Without or with 1-6 long, delicate auxiliary spines.

Distribution: Hettangian of the Alps and Northern Hungary.

Assigned species:

Liassosaturnalis parvus n. gen. n. sp.

Liassosaturnalis undulatus n. sp.

Remarks: By the unspined or nearly unspined outer ring margin with distinct axial spines this genus is clearly separated both from *Pseudoheliodiscus* KOZUR & MOSTLER, 1972 and from *Palaeosaturnalis* DONOFRIO & MOSTLER, 1978, which have always many and mostly long circumaxial peripheral spines. *Palaeosaturnalis parvispinosus* n. sp. is probably closer related to the forerunner of *Liassosaturnalis* n. gen. In this species only 5-9 short, widely spaced circumaxial spines are present.

Mesosaturnalis KOZUR & MOSTLER, 1981 and *Praemesosaturnalis* KOZUR & MOSTLER, 1981 are additionally separated by their peripolar spines.

Pseudacanthocircus n. gen. has never polar spines and auxiliary spines. Unspined ring can be often found in this genus.

Liassosaturnalis parvus n. gen. sp.

(Pl. 4, figs. 3, 7, 12; pl. 6, fig. 6)

Derivatio nominis: According to the small size of the unit

Holotype: The specimen on pl. 4, fig. 12; rep.-no. KoMo 1990 I-62

Material: 39 specimens.

Diagnosis: Unit small. Shell slightly ellipsoidal, spongy, consisting of several concentric layers. Microsphere latticed. Ring narrow, flat, undifferentiated. Ring outline subcircular or elliptical, with long axis parallel or perpendicular to the polar spines. No circumaxial spines, but axial spines well developed. 2 very robust polar spines. auxiliary spines either missing or rarely 1-4 delicate auxiliary spines are present.

Measurements:

Diameter of shell (parallel to polar spines) = 75–80 μm

Diameter of shell (perpendicularly to polar spines) = 57–63 μm

Diameter of ring (parallel to polar spines) = 157–187 μm

Diameter of ring (perpendicularly to polar spines) = 140–213 μm

Width of ring = 7–16 μm

Length of axial spines = 10–27 μm

Distribution: Hettangian of Alps and Northern Hungary (Csövár, Várhegy Cherty Limestone Formation).

Remarks: *Liassosaturnalis undulatus* n. sp. is larger and has angular undulations on the outer margin of the ring as

rudiments of peripheral spines. Sometimes also a small peripheral spine is present.

Liassosaturnalis undulatus n. sp.

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

Derivatio nominis: According to the angular undulations on the outer margin of the ring

Holotype: The specimen on pl. 1, fig. 6; rep.-no. KoMo 1990 I-63

Material: 51 specimens.

Diagnosis: Shell subspherical to subellipsoidal, spongy, consisting of several concentric layers of spongy meshwork. Microsphere latticed. Ring narrow, flat, undifferentiated. Ring outline variable, subcircular, slightly subelliptical, elliptical, with long axis parallel or perpendicularly to the polar spines. Outer margin of ring with angular undulations as rudiments of former circumaxial spines. Sometimes a single circumaxial spine is still present. Polar spines very robust. auxiliary spines either missing or 1-6 fragile, long auxiliary spines are present.

Measurements:

Diameter of shell (parallel to polar spines) = 70–84 μm

Diameter of shell (perpendicularly to polar spines) = 73–76 μm

Diameter of ring (parallel to polar spines) = 175–220 μm

Diameter of ring (perpendicularly to polar spines) = 164–272 μm

Width of ring = 10–20 μm

Length of circumaxial spine (if present) = 5–16 μm

Length of axial spines = 7–40 μm

Distribution: Hettangian of Alps and Northern Hungary (Csövár, Várhegy Cherty Limestone Formation).

Remarks: *Liassosaturnalis parvus* n. gen. n. sp. is mostly smaller and has a smooth outer margin of ring.

Subfamily **Acanthocircinae** PESSAGNO, 1977 emend.

Synonym: Hexasaturnalinae KOZUR & MOSTLER, 1983

Emended diagnosis: Shell spongy, consisting of several concentric layers of spongy meshwork around a central latticed microsphere. Ring outline in primitive forms still variable: octagonal, heptagonal, rounded tetragonal or slightly elliptical with long axis perpendicularly to the polar axis. From the latter forms taxa with strongly transversally elliptical rings evolved. This ring outline is present in all highly evolved Acanthocircinae.

Most primitive forms have 8, 7, 6 or 4, very rarely 5 tricarinate spines. The carinae of the peripheral spines are connected on the outer margin of the upper and lower ring surface by distinct high ridges that enclose on the lateral outer surfaces by distinct high ridges that enclose on the

lateral outer surface of the ring a furrow that continues into the furrows on the spines. The inner part of the ring is in these primitive forms still flat. In higher evolved forms only 4, later by fusion only 2 strong peripheral spines are present that are in the beginning still tricarinate, later bicarinate with carinae perpendicularly to the ring plane. These carinae are, like in the primitive forms, connected by a ridge on the lower and upper surfaces of the ring. These ridges are very high and separated by a deep furrow on the outer lateral surface of the ring and later even additionally by a shallow furrow on the inner lateral surface of the ring. Parts of the inner ring margin, at least in its lower part, remained still wedge-like, but as a whole the ring is in these highly evolved forms higher than broad.

2 peripolar spines. Only in the most primitive forms, transitional to the Parasaturnalinae, polar spines are still present. In primitive forms auxiliary spines are sometimes present.

Distribution: Norian, Aptian, until the Liassic very rare.
Assigned genera:

Acanthocircus SQUINABOL, 1903

Hexasaturnalis KOZUR & MOSTLER, 1983

Yaosaturnalis KOZUR & MOSTLER, 1983

Octosaturnalis n. gen.

Remarks: The Acanthocircinae PESSAGNO, 1979 emend. have evolved from the Parasaturnalinae KOZUR & MOSTLER, 1972. In the Middle and Upper Norian existed a distinct group of *Pseudoheliodycus* and *Praemesosaturnalis* species within the Parasaturnalinae that have distorted peripheral spines turned out the ring plane under different angles. The 2 edges of these spines, often differentiated by secondary spines, are connected by a narrow, mostly indistinct ridge at the outer margin of the ring. This is already a characteristic feature of the Acanthocircinae, but otherwise these species are still typical Parasaturnalinae with broad, flat ring and numerous (10-12) peripheral spines. They are here regarded as transitional group to primitive Acanthocircinae within the Parasaturnalinae.

In another group within the Norian to Hettangian Parasaturnalinae the number of the peripheral spines is reduced to 6-8 and an octagonal to hexagonal ring outline evolved, characteristic for primitive Acanthocircinae. However, in these forms the marginal spines are not distorted and connecting ridges on the ring between adjacent peripheral spines are not present. This group (*Praehexasaturnalis* KOZUR & MOSTLER, 1983) evolved in the Rhaetian and Hettangian auxiliary spines and deviated by this again for the Acanthocircinae. *Praehexasaturnalis* KOZUR & MOSTLER, 1983 is now not more regarded as the forerunner of *Hexasaturnalis* KOZUR & MOSTLER, 1983, a primitive representative of the Acanthocircinae. It

was a dead-ending side branch within the Parasaturnalinae, in which some features of primitive Acanthocircinae (ring outline, reduction of number of peripheral spines) evolved, but the most characteristic feature of the Acanthocircinae, the ridges on the outer part of the ring, have never developed in this group.

Within the Norian-Liassic genus *Stauracanthocircus* KOZUR & MOSTLER, 1983 forms with rectangular rings are frequent and partly also elliptical rings are present, the ring is narrow and few representatives display even a reduction of the peripheral spine number (6). However, also in this group the ring remains undifferentiated and *Stauracanthocircus* disappeared without successors within the Toarcian.

Both *Praehexasaturnalis* KOZUR & MOSTLER, 1983 and *Stauracanthocircus* KOZUR & MOSTLER, 1983 have been placed originally into the Hexasaturnalinae KOZUR & MOSTLER, 1983. However, our new investigations have shown that both groups are blind-ending taxa within the Parasaturnalinae that developed some morphological characters of the Acanthocircinae, but not the most characteristic differentiation of the ring. Therefore they cannot be regarded as forerunners of *Hexasaturnalis* KOZUR & MOSTLER, 1983, a primitive representative of the Acanthocircinae PESSAGNO, 1977 emend. Even they cannot be united with *Hexasaturnalis* into one subfamily Hexasaturnalinae KOZUR & MOSTLER, 1983. This subfamily is here regarded as synonym of the Acanthocircinae PESSAGNO, 1977. However, in tribus rank the Hexasaturnalini KOZUR & MOSTLER, 1983 can be furthermore separated from the Acanthocircini PESSAGNO, 1977.

Within the Hettangian *Palaeosaturnalis* evolved a group with very variable ring outline, varying from circular to transversally elliptical (even intraspecifically). The latter ring outline is typical for higher evolved Acanthocircinae PESSAGNO, but also for the Pseudacanthocircidae n. fam. This outline has therefore iteratively developed in different saturnalid radiolarians. It does not indicate closer relations. Also in this species group of *Palaeosaturnalis* the ring remained flat, undifferentiated and with some exceptions rather broad. These forms disappeared without successors at the top of the Hettangian or a little later. Also this group cannot be regarded as forerunners of the Acanthocircinae PESSAGNO, 1977 emend.

The Pseudacanthocircidae n. fam. are in the ring outline homoeomorph to highly evolved Acanthocircinae (*Acanthocircus* SQUINABOL). These highly evolved Acanthocircinae and the Pseudacanthocircidae are morphologically only separated by the different mode of ring differentiation. In highly evolved Pseudacanthocircidae al-

ways the inner margin is elevated, the outer margin, in turn, wedge like (ring with triangular cross section with broad base inside). Moreover, the highly evolved Pseudacanthocircidae have mostly a strongly spined ring, whereas the highly evolved Acanthocircinae have only 2 (rarely 2-4) peripheral spines around the long axis poles.

In contrary to the highly evolved Acanthocircinae and Pseudacanthocircidae, their primitive representatives are morphologically very different: Octagonal, heptagonal, hexagonal or rounded tetragonal ring outline, 4-8 stout, tricarinate spines, strong ring differentiation by ridges near the outer margin in early Acanthocircinae and strongly transversally elongated ring outline, undifferentiated ring, primary undenticulated ring, later partly with numerous, but small spines in early Pseudacanthocircidae.

The phylomorphogenetic relations within the Acanthocircinae PESSAGNO, 1977 emend. are now well known. The most primitive Norian forms (*Octosaturnalis* n. gen.) have still 8 stout, tricarinate peripheral spines, polar spines and auxiliary spines. During the Liassic the spine number is reduced to 6 and forms with peripolar spines evolved (*Yaosaturnalis* KOZUR & MOSTLER, 1983 = *Kozurastrum* De WEVER, 1984 with auxiliary spines and *Hexasaturnalis* KOZUR & MOSTLER, 1983 without auxiliary spines). Forms with 4 stout, tricarinate spines appeared for the first time in the basal Middle Jurassic. From these forms evolved by prolongation of the ring (strongly transversally elongated elliptical outline) still in the lower part of Middle Jurassic the first, most primitive *Acanthocircus* species, *A. suboblongus* (YAO, 1972).

This species has still the same type of ring differentiation (connecting ridges between adjacent peripheral spines on the lower and upper surface of the outer part of the ring) as in the primitive Acanthocircinae (*Octosaturnalis* n. gen., *Hexasaturnalis* KOZUR & MOSTLER, 1983, *Yaosaturnalis* KOZUR & MOSTLER, 1983).

The Middle Jurassic *A. suboblongus* (YAO, 1972) is the forerunner of the Late Jurassic *A. variabilis* (SQUINABOL, 1914). In this species the outer ridges on the upper and lower surfaces of the ring are almost as broad as the whole ring and the ring is because of the high and broad ridges at least as high as wide, in all subsequent species even higher than wide.

All transitional forms are known between *A. variabilis* (SQUINABOL, 1914) with still 4 spines (2/2 along the poles of the long ring axis) and the Late Jurassic to Lower Barremian *A. dicranacanthos* (SQUINABOL, 1914). These transitional forms have been already figured by SQUINABOL (1914, p. 22, fig. 7). 2 spines at both pole fused to one spine that is distally still separated into 2 branches, the unfused remnants of the originally 2 spines.

In transitional forms at one pole the 2 spines are already fused in the above described manner, whereas at the opposite pole the 2 spines are not yet fused.

By total fusion of the spines (also the unfused terminal parts of the 2 spines have been fused). *A. trizonalis* (RÜST, 1898) (= *A. amissus* SQUINABOL, 1914) evolved from *A. dicranacanthos* (SQUINABOL, 1914). With the disappearance of *A. trizonalis* (RÜST) at the top of the Aptian the genus *Acanthocircus* SQUINABOL and with it the Acanthocircinae PESSAGNO disappeared. All reported younger "*Acanthocircus*" are representatives of the Pseudacanthocircidae n. fam. or of the Saturnalidae DEFLANDRE, 1953.

Genus *Octosaturnalis* n. gen.

Derivatio nominis: According to the 8 stout tricarinate peripheral spines and the octagonal outline of the ring

Type species: *Octosaturnalis carinatus* n. gen. n. sp.

Diagnosis: Octagonal ring broad, flat, with 8 stout, tricarinate spines. The ridges on the spines are connected by distinct, but narrow ridges on the upper and lower surfaces of the outer part of the ring. These ridges are considerably narrower than the width of the ring. They enclose a distinct furrow on the lateral outer surface of the ring.

Polar spines small, 6-8 small auxiliary spines present.

Distribution: Norian of Northern Calcareous Alps.

Assigned species: *Octosaturnalis carinatus* n. gen. n. sp.

Remarks: The stout tricarinate peripheral spines and the connecting ridges on the upper and lower surfaces (that border a furrow on the lateral outer margin of the ring) are almost identical with *Hexasaturnalis* KOZUR & MOSTLER, 1983, the immediate forerunner of *Acanthocircus* SQUINABOL, 1903. However, *Hexasaturnalis* has peripolar spines and only 4-7, mostly 6 tricarinate peripheral spines and heptagonal, hexagonal or roundish tetragonal to slightly transversally elliptical ring outlines.

The carinate spines and the connecting ridges between adjacent spines across the outer part of the ring surfaces are the most characteristic features of all Acanthocircinae PESSAGNO, 1977 emend. Therefore *Octosaturnalis* n. gen. is the stratigraphically oldest and most primitive representative of this subfamily. It has still transitional character to the Parasaturnalinae (broad, flat ring, relatively high number of spines, polar spines, not more present in younger representatives of the Acanthocircinae).

Also within the Parasaturnalinae KOZUR & MOSTLER, 1972, there is a species group with transitional character to the Acanthocircinae PESSAGNO, 1977

emend. *Pseudoheliodiscus kahleri* (KOZUR & MOSTLER, 1972) and few further, still undescribed Parasaturnalinae have distorted spines, in which the 2 edges of the spines turned out the ring plane under different angles. These edges of adjacent peripheral spines are connected on the outermost part of the ring surfaces by narrow, mostly indistinct ridges. Concerning the numerous peripheral spines (10-12) these forms are still typical Parasaturnalinae. They are not direct forerunners of the earliest Acanthocircinae PESSAGNO, 1977 with tricarinate spines, but near related to them.

***Octosaturnalis carinatus* n. gen. n. sp.**

(Pl. 10, figs. 1, 3, 4)

Derivatio nominis: According to the stout tricarinate spines

Holotype: The specimen on pl. 10, figs. 1, 3, 4; rep.-no. KoMo 1990 I-24

Locus typicus: Pötschen road, Hallstatt area (Austria)

Stratum typicum: Norian Pötschen Limestone, sample Ptx 1

Material: 7 specimens.

Diagnosis, distribution and remarks: See under the genus.

Measurements:

Diameter of ring = 128–140 μm

Width of ring = about 20 μm

Width of ridges on the ring surfaces = about 4 μm

Length of the spines = 100–110 μm

Genus *Yaosaturnalis* KOZUR & MOSTLER, 1983

Synonym: *Kozurastrum* De WEVER, 1984

Type species: *Spongosaturnalis ? minoensis* YAO, 1972

Remarks: De WEVER (1984) established for typical *Praemesosaturnalis* species the genus *Kozurastrum* De WEVER, 1984. He stated that this genus differs from *Mesosaturnalis* KOZUR & MOSTLER, 1981 by the presence of auxiliary spines. This is exactly the difference between *Mesosaturnalis* KOZUR & MOSTLER, 1981 and *Praemesosaturnalis* KOZUR & MOSTLER, 1981 as pointed out by KOZUR & MOSTLER (1981, 1983). Therefore the *Kozurastrum* species, with exception of the type species, belong to *Praemesosaturnalis* KOZUR & MOSTLER, 1981.

The type species of *Kozurastrum* De WEVER, 1984, *Spongosaturnalis ? minoensis* YAO, 1982, is, however, a typical representative of the early Acanthocircinae. It displays tricarinate peripheral spines and strong connecting ridges on the upper and lower surface of the outer part of the ring, nearly as broad as half of the ring's

width. For this species KOZUR & MOSTLER, 1983 introduced the genus *Yaosaturnalis* KOZUR & MOSTLER, 1983. Because the type species of *Yaosaturnalis* KOZUR & MOSTLER, 1983 and of *Kozurastrum* De WEVER, 1984 are identical, the latter genus is a younger synonym of *Yaosaturnalis* KOZUR & MOSTLER, 1983, in spite of the fact that almost all species of *Kozurastrum* belong to *Praemesosaturnalis* KOZUR & MOSTLER, 1981.

Family **Saturnalideidae** n. fam.

Diagnosis: Latticed cortical shell, connected with a circular, undifferentiated ring by 2 polar spines. Numerous peripheral spines.

Distribution: ? Tertiary, Recent.

Assigned genus: *Saturnalium* HAECKEL, 1887

Remarks: The Saturnalideidae n. fam. evolved from the Parasaturnalidae KOZUR & MOSTLER, 1972 by development of a latticed cortical shell.

The Saturnalidae DEFLANDRE, 1953 s. str. have likewise a latticed cortical shell, but the ring is always transversally elongated, smooth or with spines along the poles of the long axis, differentiated by a ridge on the lower and upper surface of the inner side of the ring (triangular cross section with broad base inside).

Family **Pseudacanthocircidae** n. fam.

Diagnosis: Shell globular, spongy, consisting of many concentric layers. Microsphere latticed, displaying large pores. Second latticed medullary shell may be present in advanced representatives.

Ring always transversally elliptical, smooth or with mostly very short spines either along the whole margin or concentrated around the long axis or short axis poles. In primitive forms, persisting partly up to the Cretaceous, the ring is undifferentiated, with shallow elliptical cross-section. In more advanced forms the ring is differentiated by a ridge on the inner side of the ring. By this it has a triangular cross-section with the broad base inside.

Ring and shell connected by 2 peripolar spines, only in few primitive forms with polar spines, but the taxonomic position of these latter taxa is unclear. Further 4 first order spines, arranged diagonally against the peripolar spines, may be present in primitive forms. Tiny auxiliary spines only exceptionally present around the base of the peripolar spines.

Distribution: Lower Carnian-Upper Cretaceous. In the Triassic extremely rare.

Assigned genera:

Pseudacanthocircus n. gen.

Spongosaturnalis CAMPBELL & CLARK, 1944

Spongosatruninus CAMPBELL & CLARK, 1944

Praeacanthocircus KOZUR & MOSTLER, 1983

Eospongosaturminus n. gen.

? *Spinoellipsella* n. gen.

Triacanthocircus n. gen.

Remarks: The Pseudacanthocircidae n. fam. are homoeomorphic to highly evolved Acanthocircinae PESSAGNO, 1977 that have evolved from the Parasaturnalinae KOZUR & MOSTLER, 1972. Primitive Pseudacanthocircidae n. fam. from the Triassic and Liassic are still quite different from contemporaneous early Acanthocircinae and Parasaturnalinae. The oldest representative of the Pseudacanthocircinae n. fam., *Praeacanthocircus* KOZUR & MOSTLER, 1983 has already during the Lower Carnian a narrow, smooth, transversally strongly elongated ring with peripolar spines and 4 additional, diagonally arranged first order spines. The contemporaneous Parasaturnalinae KOZUR & MOSTLER, 1972 have all a broad, flat, circular ring with numerous spines. Acanthocircinae PESSAGNO, 1977 had not yet evolved in this time.

The Norian to Liassic early Acanthocircinae PESSAGNO, 1977 have not yet transversally strongly elongated rings and the upper and lower ring surfaces have distinct ridges, connecting the ridges of the tricarinate spines. Highly evolved Acanthocircinae PESSAGNO, 1977 have both a transversally strongly elongated elliptical ring and ridges on the ring as the highly evolved contemporaneous Pseudacanthocircidae n. fam. However, in the Pseudacanthocircidae n. fam. the ridges evolved on the inner side of the ring that has in highly evolved forms therefore invariably a triangular cross section with the broad basis inside. In the Acanthocircidae the ring is broadest on its outer side, where a furrow is present on the lateral outer surface.

Primitive Pseudacanthocircidae n. fam. have similarities to some highly evolved Parasaturnalinae KOZUR & MOSTLER, 1972. Some Liassic *Palaeosaturnalis* KOZUR & MOSTLER, 1972 display a transversally elongated elliptical ring. These forms are only distinguished by their polar spines, with exception of *Spinoellipsella* n. gen. never present in the Pseudacanthocircidae n. fam. Moreover, transversally elongated elliptical ring outline is not fixed in highly evolved Parasaturnalinae. Except this ring outline also forms with roundish or vertically elongated elliptical ring may occur in the same species.

Strong homoeomorphy exists between spined Liassic Pseudacanthocircidae n. fam. and highly evolved Upper Cretaceous *Mesosaturnalis* KOZUR & MOSTLER, 1981 with transversally somewhat elongated subelliptical ring. However, even these highly evolved Upper Cretaceous *Mesosaturnalis* species have mostly a circular, broad ring. Contemporaneous latest Triassic and Lower Hettangian *Mesosaturnalis* species have almost exclu-

sively a circular ring. The few representatives of *Mesosaturnalis* with transversally slightly elongated ring from this time interval have very long spines, untypical for the Pseudacanthocircidae n. fam.

Genus *Pseudacanthocircus* n. gen.

Derivatio nominis: According the morphologic similarity with *Acanthocircus* PESSAGNO, 1903

Type species: *Pseudacanthocircus mediospinosus* n. gen. n. sp.

Diagnosis: Shell spherical, never reaching the ring, spongy, consisting of several concentric layers and a microsphere. 2 peripolar spines connect the shell with the narrow, transversally strongly elongated elliptical ring. Outer margin of the ring smooth or partly to totally denticulated. Cross section of the undifferentiated ring shallow elliptical to almost flat. Auxiliary spines never present.

Distribution: ? Rhaetian, Liassic.

Assigned species:

Pseudacanthocircus mediospinosus n. gen. n. sp.

Pseudacanthocircus baumgartneri n. sp.

Pseudacanthocircus laevis n. sp.

Pseudacanthocircus mocki n. sp.

Pseudacanthocircus praesimplex n. sp.

Pseudacanthocircus terminospinosus n. sp.

Pseudacanthocircus troegeri n. sp.

Remarks: *Praeacanthocircus* KOZUR & MOSTLER, 1983 from the Cordevolian to Pliensbachian is distinguished by the presence of 4 diagonally arranged first order spines additionally to the peripolar spines. Moreover, in this genus the ring has never outer spines. *Praeacanthocircus* KOZUR & MOSTLER, 1983 is the oldest representative of the Pseudacanthocircidae n. fam., because it is already present in the Cordevolian together with the first Parasaturnalinae KOZUR & MOSTLER, 1972. *Pseudacanthocircus* n. gen. has probably evolved from this genus by disappearance of the 4 first order spines (additionally to the 2 peripolar spines). *Triacanthocircus* n. gen. with only one additional first order spine may be transitional between *Praeacanthocircus* KOZUR & MOSTLER, 1983 and *Pseudacanthocircus* n. gen.

An independent development of *Pseudacanthocircus* n. gen. from Oertlispongidae KOZUR & MOSTLER, 1980 with smooth ring (*Oertlispongus longirecurvatus* KOZUR & MOSTLER, 1983, *O. annulatus* KOZUR & MOSTLER, 1983) cannot be excluded. However, Triassic species of *Pseudacanthocircus* are so far unknown and in the well studied Carnian and Norian radiolarian faunas probably not present.

Also a development from *Mesosaturnalis* KOZUR & MOSTLER, 1981 by development of a transversally

strongly elongated ring cannot be quite excluded. Against this derivation speaks especially that the early *Pseudacanthocircus* species have a high percentage of unspined forms and forms, where only parts of the ring are spined. Such forms are unknown in the genus *Mesosaturnalis* KOZUR & MOSTLER, 1981 that has always a totally spined ring. The short spines of *Pseudacanthocircus* n. gen. have developed secondarily on a primary smooth ring.

Spongosaturnalis CAMPBELL & CLARK, 1944 is the successor of *Pseudacanthocircus* n. gen. This genus has the same ring outline and the same type of ring denticulation (smooth to densely spinose), but it is clearly distinguished by a distinct bulge along the whole inner margin of the ring. By this, the ring has a triangular cross section with the broad basis inside.

In *Eospongosaturninus* n. gen. the spongy shell reaches the ring and overgrows it around the base of the peripolar spines. Moreover, a bulge is present along the inner margin of the long sides of the ring.

In *Spongosaturninus* CAMPBELL & CLARK, 1944, which evolved from *Eospongosaturninus* n. gen., additionally a latticed cortical shell is present.

Saturnalis HAECKEL, 1882 has a similar ring outline, but in cross-section the ring is triangular with broad basis inside (bulge on the inner margin of ring) and a latticed cortical shell is present.

***Pseudacanthocircus mediospinosus* n. gen. n. sp.**

(Pl. 10, figs. 6, 8)

Derivatio nominis: According to the unusual arrangement of the short spines in the middle part of the ring

Holotype: The specimen on pl. 10, fig. 8; rep.-no. KoMo 1990 I-27

Material: 31 specimens.

Diagnosis: Shell small, spongy, consisting of numerous concentric layers. Microsphere latticed. Ring transversally strongly elongated elliptical, flat, in large parts smooth. The short denticles occur only around the short axis pole. Polar regions of the long axis always smooth.

Measurements:

Diameter of shell = 95–110 μm

Diameter of ring (long axis) = 279–320 μm

Diameter of ring (short axis) = 192–230 μm

Width of ring = 10–16 μm

Length of spines = 2–16 μm

Distribution: Hettangian part of the Kirchstein Limestone at the type locality.

Remarks: *Pseudacanthocircus mediospinosus* n. gen. n. sp. is easily distinguished from other *Pseudacanthocircus* species, by the position of the short peripheral spines.

***Pseudacanthocircus baumgartneri* n. sp.**

(Pl. 11, fig. 6)

Derivatio nominis: In honour of Dr. P. O. BAUMGARTNER, Zürich

Holotype: The specimen on pl. 11, fig. 6; rep.-no. KoMo 1990 I-30

Material: 3 specimens.

Diagnosis: Unit small, but shell large, reaching almost until the ring. Shell spongy, but with relatively robust pattern. Ring asymmetrical, undifferentiated, transversally subelliptical, cross-section shallow elliptical. Outer margin of ring with 14–15 irregularly spaced short spines, more closely spaced at the narrower polar area of the long axis.

Measurements:

Diameter of shell = 68–70 μm

Diameter of ring (long axis) = 153–160 μm

Diameter of ring (short axis) = 110–123 μm

Width of ring = 7–10 μm

Length of spines = 4–13 μm

Distribution: Hettangian part of the Kirchstein Limestone at the type locality.

Remarks: This species is different in outline and concerning the big shell (compared with the small ring) from all other *Pseudacanthocircus* species. *Pseudacanthocircus baumgartneri* n. sp. or any near related form could be the forerunner of *Vitorfus* PESSAGNO, that is distinguished by a latticed cortical shell growing beyond the ring in the region of the peripolar spines.

***Pseudacanthocircus laevis* n. sp.**

(Pl. 2, fig. 2; pl. 11, fig. 8)

Derivatio nominis: According to the smooth ring

Holotype: The specimen on pl. 11, fig. 8; rep.-no. 1990 I-26

Material: 15 specimens.

Diagnosis: Shell spongy, consisting of several concentric layers. Ring small, transversally elliptical, without spines, in cross-section nearly flat, without differentiation, above the peripolar spines considerably broader than in the other parts of the ring.

Measurements:

Diameter of shell = 80–86 μm

Diameter of ring (long axis) = 226–238 μm

Diameter of ring (short axis) = 168–180 μm

Width of ring = 10–13 μm , above the peripolar spines 20–30 μm

Distribution: Hettangian part of the Kirchstein Limestone at the type locality.

Remarks: *Pseudacanthocircus pseudosimplex* n. sp. has a narrower ring, not broadened around the peripolar spines.

***Pseudacanthocircus mocki* n. sp.**

(Pl. 1, fig. 1; pl. 10, fig. 9)

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

Holotype: The specimen on pl. 1, fig. 1; rep.-no. KoMo 1990 I-28

Material: 11 specimens.

Diagnosis: Shell spongy, consisting of several concentric layers. Microsphere latticed. Ring transversally elliptical, undifferentiated, cross-section flat to shallow elliptical. 21–23 very short, triangular peripheral spines, regularly distributed along the whole outer margin, but not above the peripolar spines.

Measurements:

Diameter of shell = 120–131 μm

Diameter of ring (long axis) = 250–400 μm

Diameter of ring (short axis) = 205–250 μm

Width of ring = 10–16 μm

Length of spines = 4–10 μm

Distribution: Hettangian part of Kirchstein Limestone at the type locality.

Remarks: *Pseudacanthocircus troegeri* n. sp. has considerably longer spines.

***Pseudacanthocircus pseudosimplex* n. sp.**

(Pl. 11, fig. 2)

Derivatio nominis: According to the morphological similarity to *Spongosaturnalis simplex* (SQUINABOL, 1914)

1981 *Acanthocircus simplex* (SQUINABOL) De WEVER, p. 140–141, pl. 1, fig. 1

Holotype: The specimen on pl. 11, fig. 2; rep.-no. KoMo 1990 I-27

Material: 23 specimens.

Diagnosis: Shell spongy, consisting of several concentric layers. Microsphere latticed. Ring transversally strongly elongated, very narrow, cross-section nearly flat to shallow oval, without any bulge. No peripheral spines.

Measurements:

Diameter of shell = 70–75 μm

Diameter of ring (long axis) = 225–289 μm

Diameter of ring (short axis) = 150–181 μm

Width of ring = 7–11 μm

Distribution: Hettangian to Pliensbachian. Alps, Hungary, Turkey.

Remarks: The drawing of *Spongosaturnalis simplex* (squinalbol, 1914) by SQUINABOL (1914) show no bulge on the ring. However, restudies of radiolarians from the higher Upper Jurassic, from where "*Saturnalis*" *simplex* was described by SQUINABOL (1914) have shown that the ring in "*Saturnalis simplex*" is high and has distinct

bulges on the inner side of the ring (triangular cross-section with broad basis inside). It belongs therefore to *Spongosaturnalis* CAMPBELL & CLARK, 1944 emend.

***Pseudacanthocircus terminospinosus* n. sp.**

(Pl. 10, fig. 2; pl. 11, figs. 1, 4)

Derivatio nominis: According to the restriction of the spines to the polar regions of the long axis

? 1981 *Acanthocircus italicus* (SQUINABOL) De WEVER, p. 141, pl. 1, fig. 2

Holotype: The specimen on pl. 10, fig. 2; rep.-no. KoMo 1990 I-25

Material: 29 specimens.

Diagnosis: Shell spongy, consisting of several concentric layers. Microsphere latticed. Second latticed medullary shell perhaps present. Ring transversally strongly elongated elliptical, opposite to the peripolar spines a little to distinctly concave, narrow, cross-section shallow oval to almost flat, without differentiation. Largest parts of the ring smooth. In the polar region of the long axis with 1–3 short spines, often spines are only present at one pole or the number of spines is different on both poles.

Measurements:

Diameter of shell = 91–100 μm

Diameter of ring (long axis) = 217–240 μm

Diameter of ring (short axis) = 160–180 μm

Width of ring = 8–13 μm

Length of spines = 4–7 μm

Distribution: Hettangian to Pliensbachian. Alps, northern Hungary, Turkey.

Remarks: *Pseudacanthocircus pseudosimplex* n. sp. displays identical morphological features, but the whole ring is smooth.

Pseudacanthocircus mediospinosus n. sp. has only spines around the short pole.

"*Acanthocircus*" *italicus* (SQUINABOL) sensu De WEVER (1981) is larger, but otherwise identical. It is here determined as *Pseudacanthocircus* cf. *terminospinosus* n. sp. The real *Spongosaturnalis italicus* (SQUINABOL, 1914) has a bulge on the inner side of the ring, but it may be indistinct in forms with few spines. The number of the spines is more variable and as a whole greater (4–14). Forms with 4–6 spines are most similar and seemingly transitional forms to the genus *Pseudacanthocircus* n. gen. The bulge on the ring is in these forms rather indistinct and therefore the triangular cross-section of the ring is not yet pronounced, but the ring is on the inner side clearly higher than in *Pseudacanthocircus terminospinosus* n. sp. However, also these forms can be clearly distinguished, because *Pseudacanthocircus terminospinosus* n. sp. has never more than 3 spines on the ring.

***Pseudacanthocircus troegeri* n. sp.**

(Pl. 11, fig. 7)

Derivatio nominis: In honour of Dr. habil. K. A. TROEGER, Freiberg, Germany

Holotype: The specimen on pl. 11, fig. 7; rep.-no. KoMo 1990 I-29

Material: 7 specimens.

Diagnosis: Shell spongy, consisting of several concentric layers. Microsphere latticed. Ring flat, undifferentiated, transversally elliptical, with numerous (24) relatively long spines.

Measurements:

Diameter of shell = 104–116 μm

Diameter of ring (long axis) = 261–270 μm

Diameter of ring (short axis) = 202–219 μm

Width of ring = 12–15 μm

Length of spines = 11–30 μm

Distribution: Hettangian part of the Kirchstein Limestone at the type locality.

Remarks: Outline of the ring and spines corresponds to the Cretaceous *Spongosaturnalis multidentatus* (SQUINABOL, 1914). However, as in all *Spongosaturnalis* species, the ring in *S. multidentatus* (SQUINABOL, 1914) is strongly differentiated by an inner ridge. The cross section of the ring is therefore triangular with broad basis inside.

By the flat undifferentiated ring and the numerous relatively long spines, *Pseudacanthocircus troegeri* n. sp. is the only *Pseudacanthocircus* species that is similar to *Mesosaturnalis* KOZUR & MOSTLER, 1981. However, the transversally elongated ring outline is different from this genus. Moreover, the Norian to Liassic *Mesosaturnalis* species have all considerably fewer (about 10) and longer spines.

Genus *Spongosaturnalis* CAMPBELL & CLARK, 1944 emend.

Type species: *Spongosaturnalis spiniferus* CAMPBELL & CLARK, 1944

Emended diagnosis: Shell spongy, never reaching until the ring, with several concentric layers. Microsphere with big pores. Ring transversally elliptical, always with a ridge on the inner side of the narrow ring. Cross-section of the ring triangular with broad base inside. Outer margin of ring smooth or with peripheral spines that are mostly relatively short.

Distribution: ? Middle Jurassic, Upper Jurassic to Upper Cretaceous

Assigned species:

Spongosaturnalis spiniferus CAMPBELL & CLARK, 1944

Saturnalis ellipticus SQUINABOL, 1903

Saturnalis italicus SQUINABOL, 1914

Saturnalis multidentatus SQUINABOL, 1914

Saturnalis simplex SQUINABOL, 1914

Spongosaturnalis campbelli FOREMAN, 1968

Acanthocircus breviaculeatus DONOFRIO & MOSTLER, 1978

Acanthocircus squinaboli DONOFRIO & MOSTLER, 1978

? *Saturnalis subquadratus* DONOFRIO & MOSTLER, 1978

Remarks: The Liassic *Pseudacanthocircus* n. gen. is distinguished by the undifferentiated, rather flat ring. It is the forerunner of *Spongosaturnalis* CAMPBELL & CLARK, 1944.

In the Middle Jurassic *Eospongosaturninus* n. gen. the spongy shell reaches on the ring around the peripolar spines. This is also the case in the Upper Cretaceous *Spongosaturninus* CAMPBELL & CLARK, 1944 that has, moreover, a second latticed medullary shell and a third latticed medullary shell or latticed cortical shell, covered by spongy meshwork.

The Tertiary to Recent *Saturnalis* HAECKEL, 1882 has a latticed cortical shell, which is only rarely covered by a thin layer of delicate spongy meshwork.

Acanthocircus SQUINABOL, 1903 is a homoeomorph form with ridges on the outer side of the ring or on the whole ring, but also in the latter case a distinct furrow is present on the outer lateral surface of the ring. Therefore the cross-section of the ring is always different in *Acanthocircus* SQUINABOL, 1903 and *Spongosaturnalis* CAMPBELL & CLARK, 1944.

Spongosaturnalis CAMPBELL & CLARK, 1944 emend. comprises also forms with smooth and sparsely spined transversally elliptical ring. Therefore an emendation of the original diagnosis was necessary. All transitions between the totally spined typical *Spongosaturnalis* to the unspined ring of *S. simplex* are known. Sometimes the number of the spines varies considerably even within one species, e.g. in *Spongosaturnalis italicus* (SQUINABOL, 1914).

Genus *Spongosaturninus* CAMPBELL & CLARK, 1944

Type species: *Spongosaturninus ellipticus* CAMPBELL & CLARK, 1944

Diagnosis: The shell consists of a tiny latticed microsphere, a second latticed medullary shell and a rather large third latticed medullary shell (or cortical shell) covered by a thick layer of spongy meshwork that reaches along the peripolar spines on the ring or even beyond the ring.

Ring transversally strongly elongated elliptical, with distinct ridge on the inner margin of the ring. Cross-section of the ring therefore triangular with broad base inside. The ring has mostly 1-3 spines in each polar region of the long axis, but may be additionally spined around the whole outer ring margin.

Distribution: Upper Cretaceous.

Assigned species:

Spongosaturninus ellipticus CAMPBELL & CLARK, 1944

Spongosaturnalis lateralispinosus CAMPBELL & CLARK, 1944

Spongosaturninus latiformis CAMPBELL & CLARK, 1944

Spongosaturninus parvulus CAMPBELL & CLARK, 1944

Spongosaturnalis nematodes FOREMAN, 1968

Remarks: *Spongosaturninus* CAMPBELL & CLARK, 1944 is a transitional group to the Saturnalidae DEFLANDRE, 1953. The third medullary shell is so large that it can be also regarded as cortical shell (see DUMITRICĂ, 1985). However, the spongy layer on this shell is always thicker than the distance between the second and third (medullary) shells. In *Saturnalis* HAECKEL, 1882 disappeared this thick outer spongy layer. By this the outer latticed medullary shell was transformed into a latticed cortical shell.

Genus *Praeacanthocircus* KOZUR & MOSTLER, 1983

Type species: *Praeacanthocircus carnicus* KOZUR & MOSTLER, 1983

Praeacanthocircus spinosus n. sp.

Derivatio nominis: According to the presence of small peripheral spines

1981 *Pseudoheliodiscus* sp. A De WEVER, p. 144, pl. 4, figs. 5, 7

Holotype: The specimen, figured by De WEVER (1981, pl. 4, fig. 7) as *Pseudoheliodiscus* sp. A

Locus typicus: Gümüslü Unit (Western Taurus, eastern Domuz Dag Massif) north of Korkuteli, Sögütlü gorge, 1 km NW of Gümüslü village, Turkey

Stratum typicum: Sögütlü dere Formation, radiolarian limestone, Pliensbachian (bedded siliceous limestones below Upper Pliensbachian ammonoid-bearing beds)

Diagnosis: Shell spongy, relatively large, but not reaching the asymmetrical, transversally elliptical ring. Cross-section of ring shallow oval to nearly flat. Larger parts of the ring smooth, only in the polar region of the long axis small spines are present at both poles or only at one pole. Beside the peripolar spines 4 further first order spines are

present, diagonally arranged to the peripolar spines.

Measurements:

Diameter of shell = 130–135 μm

Diameter of ring (long axis) = about 250–300 μm (ring in this direction not fully preserved)

Diameter of ring (short axis) = 210–230 μm

Width of ring = 15–25 μm

Length of spines = about 5 μm

Distribution: ? Upper Sinemurian, Pliensbachian of Turkey.

Remarks: The material of this species is incomplete preserved, but very important for phylomorphogenetic considerations. It shows that in *Praeacanthocircus* KOZUR & MOSTLER, 1983 the same type of ring sculpture is present as in *Pseudacanthocircus* n. fam. (smooth, short spines around the poles, short spines around the whole outer margin of the ring) and also in the Saturnalidae DEFLANDRE, 1953 s. str. which derived from the *Pseudacanthocircidae* n. fam.

Eospongosaturninus n. gen.

Derivatio nominis: Forerunner of *Spongosaturninus* CAMPBELL & CLARK, 1944

Type species: *Spongosaturnalis protoformis* YAO, 1972

Diagnosis: Shell large, spongy, consisting of several concentric layers. Microsphere latticed. The shell reaches on the ridge around the base of the peripolar spines.

Ring transversally elongated elliptical, narrow to moderately broad, in parts of the ring undifferentiated, in other parts with ridge near the inner side of the ring. Outer margin of ring smooth or with one peripolar spine on the long axis poles. Near the base of the peripolar spines tiny auxiliary spines may be present.

Distribution: Middle Jurassic of Japan.

Assigned species:

Spongosaturnalis protoformis YAO, 1972

? *Spongosaturnalis bispinus* YAO, 1972

Remarks: *Eospongosaturninus* n. gen. is the forerunner of *Spongosaturninus* CAMPBELL & CLARK, 1944 that has more distinct ridges along the whole inner margin of the ring, a latticed second medullary shell and a rather large third medullary shell (transitional to a cortical shell) covered by a still rather thick spongy layer.

Pseudacanthocircus n. gen. has an undifferentiated ring and the shell reaches never until the ring.

Spongosaturnalis CAMPBELL & CLARK, 1944 displays more distinct ridges along the whole inner margin of the ring and the shell does not reach the ring.

Eospongosaturninus n. gen. lies in the transition field between the genera *Pseudacanthocircus* n. gen.,

Spongosaturninus CAMPBELL & CLARK, 1944 and *Spongosaturnalis* CAMPBELL & CLARK, 1944. The type species is surely the forerunner of *Spongosaturninus* CAMPBELL & CLARK, 1944. In *Eospongosaturninus* ? *bispinosus* (YAO, 1972) the overreach of the shell on the ring is not so distinct and in several specimens the inner ridge on the ring is indistinct, partly even missing (YAO, 1972, pl. 2, fig. 9). The specimen, figured by YAO (1972, pl. 2, fig. 8) as *Spongosaturnalis bispinosus* belongs to an other species and is probably the first representative of the genus *Spongosaturnalis* CAMPBELL & CLARK, 1944.

The genus *Acanthocircus* SQUINABOL, 1903 has strong outer ridges on the ring or the ridges cover the whole ring. A deep furrow on the lateral outer side of the ring is always present. This genus is only homoeomorphic to the Pseudacanthocircidae n. fam. (and in it to *Eospongosaturninus* n. gen.) and evolved from the parasaturnalinid stock.

Genus *Spinoellipsella* n. gen.

Derivatio nominis: According to the transversally elliptical spiny ring

Type species: *Spinoellipsella densispinosa* n. gen. n. sp.

Diagnosis: Unit small. Shell relatively large, reaching in fully preserved forms in the short axis until the ring. It is spongy and consists of several concentric layers around a latticed microsphere.

Ring flat, undifferentiated, moderately broad, with numerous broad, but always short, triangular spines. 2 polar spines.

Distribution: Hettangian of the Alps.

Assigned species:

Spinoellipsella densispinosa n. gen. n. sp.

Spinoellipsella latispinosa n. sp.

Remarks: *Palaeosaturnalis* DONOFRIO & MOSTLER, 1978 is distinguished by the mostly circular or sub-rectangular ring and the considerably larger spines.

Pseudacanthocircus n. gen. has the same outline of the ring, but peripolar spines.

The taxonomic position of *Spinoellipsella* n. gen. is not clear. A derivation from *Palaeosaturnalis* DONOFRIO & MOSTLER, 1978 is possible. In this case it would be a blind-ending side-branch of the Parasaturnalidae KOZUR & MOSTLER, 1972. However, the numerous broad, triangular spines are typical for several taxa within the Pseudacanthocircidae n. fam., but quite unknown within the genus *Palaeosaturnalis* DONOFRIO & MOSTLER, 1978 and within the Parasaturnalidae KOZUR & MOSTLER, 1972 at all. Therefore the placement into the Pseudacanthocircidae n. fam. that have the same ring outline, is

more probably than the placement into the Parasaturnalidae KOZUR & MOSTLER, 1972.

Spinoellipsella densispinosa n. gen. n. sp.

(Pl. 1, fig. 4; pl. 11, figs. 3, 5)

Derivatio nominis: According the numerous, closely spaced, short, broad spines

Holotype: The specimen on pl. 1, fig. 4; rep.-no. KoMo 1990 I-34

Material: 21 specimens.

Diagnosis: With the character of the genus. Ring transversally elliptical, moderately wide, one half-ring smaller than the other one. Numerous (27-29) short, triangular spines are closely spaced along the whole ring.

Measurements:

Diameter of shell = 80–90 μm

Diameter of ring (long axis) = 147–158 μm

Diameter of ring (short axis) = 117–138 μm

Width of ring = 9–19 μm

Length of spines = 3–6 μm

Distribution: Hettangian part of the Kirchstein Limestone at the type locality.

Remarks: *Spinoellipsella latispinosa* n. sp. displays fewer, widely spaced, broader spines.

Spinoellipsella latispinosa n. sp.

(Pl. 2, fig. 4)

Derivatio nominis: According to the broad spines

Holotype: The specimen on pl. 2, fig. 4; rep.-no. KoMo 1990 I-35

Material: 4 specimens.

Diagnosis: With the character of the genus. Ring moderately broad, transversally strongly elongated elliptical, asymmetrical (one half-ring larger than the other one), with 10-16, broadly triangular, short, widely spaced spines.

Measurements:

Diameter of shell = 80–83 μm

Diameter of ring (long axis) = 183–190 μm

Diameter of shell (short axis) = 123–129 μm

Width of ring = 17–20 μm

Length of spines = 7–10 μm

Distribution: Hettangian part of the Kirchstein Limestone at the type locality.

Remarks: *Spinoellipsella densispinosa* n. gen. n. sp. has considerably more, closely spaced and not so broad spines.

Genus *Triacanthocircus* n. gen.

Derivatio nominis: According to the 3 inner spines

Type species: *Triacanthocircus muelleri* n. gen. n. sp.

Diagnosis: Spongy shell subspherical, on the side of the

auxiliary spine rounded conical, opposite side hemiglobular. The shell consists of several concentric layers of spongy meshwork. Microsphere latticed.

Ring transversally elliptical, undifferentiated, in cross-section flat to shallow oval. Peripheral spines very short to moderately long. Middle sector of ring to both sides of the peripolar spines smooth. A third inner spine is situated perpendicularly to the 2 peripolar spines. It is a little narrower than the peripolar spines.

Distribution: Hettangian of the Alps.

Assigned species:

Triacanthocircus muelleri n. gen. n. sp.

Triacanthocircus squinaboli n. sp.

Remarks: *Triacanthocircus* n. gen. is morphologically transitional between *Praeacanthocircus* KOZUR & MOSTLER, 1983 with 6 first order spines (2 peripolar spines and 4 additional spines) and *Pseudacanthocircus* n. gen. that has only the 2 peripolar spines without additional first order spines.

***Triacanthocircus muelleri* n. gen. n. sp.**

(Pl. 9, fig. 11; pl. 10, figs. 5, 7, 10)

Derivatio nominis: In honour of Prof. Dr. A. H. MÜLLER, Freiberg, Germany

Holotype: The specimen on pl. 10, fig. 7; rep.-no. KoMo 1990 I-31

Material: 9 specimens.

Diagnosis: With the character of the genus. The 9–12 peripheral spines on the ring are very short.

Measurements:

Diameter of shell = 70–90 µm

Diameter of ring (long axis) = 230–240 µm

Diameter of ring (short axis) = 170–180 µm

Width of ring = 10–15 µm

Length of spines = 5–10 µm

Distribution: Hettangian part of the Kirchstein Limestone at the type locality.

Remarks: *Triacanthocircus squinaboli* n. sp. displays longer spines and a wider unspined area around the peripolar spines.

***Triacanthocircus squinaboli* n. sp.**

(Pl. 3, fig. 4)

Derivatio nominis: In honour of S. SQUINABOL, one of the pioneers of the fossil Radiolaria research

Holotype: The specimen on pl. 3, fig. 4; rep.-no. KoMo 1990 I-33

Material: 3 specimens.

Diagnosis: With the character of the genus. The 10 spines are long for the genus and concentrated in the polar area of the long axis.

Measurements:

Diameter of shell = 80–86 µm

Diameter of ring (long axis) = about 250 µm

Diameter of ring (short axis) = 184–196 µm

Width of ring = about 10 µm

Length of spines = 20–25 µm

Distribution: Hettangian part of the Kirchstein Limestone at the type locality.

Remarks: *Triacanthocircus muelleri* n. gen. n. sp. distinguished by its considerably shorter spines.

Family Saturnalidae DEFLANDRE, 1953 emend.

Emended diagnosis: Latticed microsphere and latticed cortical shell always present. Additionally a latticed second medullary shell may be present. Between the medullary shell(s) and the cortical shell a very loose, delicate spongy meshwork is present. Very rarely the cortical shell is covered by a thin layer of spongy meshwork.

Ring transversally elliptical with ridge on the inner side. Cross-section of ring trigonal with broad base inside. Outer margin of ring smooth or with spines in the polar region on the long axis. 2 peripolar spines.

Distribution: Upper Cretaceous-Recent.

Assigned genera:

Saturnalis HAECKEL, 1882

Vitorfus PESSAGNO, 1977

Remarks: The Saturnalidae evolved from the Pseudacanthocircidae n. fam. by development of a large latticed shell inside the spongy meshwork and following lost of the outer spongy layer. *Spongosaturninus* CAMPBELL & CLARK, 1944 is a transitional form between both families. In this genus the third latticed medullary shell is already as large as a cortical shell, but the surrounding spongy meshwork is still thicker than the distance between the second and third latticed medullary shells. By disappearance of the outer spongy layer the outer latticed medullary shell is transformed into a cortical shell. In atavistic (?) forms of *Saturnalis circularis* HAECKEL, 1882 the type species of *Saturnalis* HAECKEL, 1882, the latticed cortical shell is still covered by a very thin spongy layer (NAKASEKO & NISHIMURA, 1982, pl. 3, fig. 3). The very fragile, loose spongy meshwork inside the latticed cortical shell is only preserved in well preserved specimens. Both these features indicate the derivation of the Saturnalidae DEFLANDRE, 1953 s. str. from saturnalids with spongy shell.

The ridge on the inner side of the ring causes the triangular cross-section of the ring (with broad base inside, see NAKASEKO & NISHIMURA, 1982, pl. 4, fig. 3). This differentiation of the ring confirms the derivation of the Saturnalidae DEFLANDRE, 1953 s. str. from highly

evolved Pseudacanthocircidae n. fam. that have all this type of ring differentiation, quite different from the ring differentiation of the Acanthocircinae PESSAGNO, 1977 emend. (see there).

Superfamily **Actinommacea** HAECKEL, 1862 emend. KOZUR & MOSTLER, 1979

Family **Pantanellidae** PESSAGNO, 1977

Remarks: The terminology and abbreviations for the description of the Pantanellidae have been adopted from PESSAGNO & BLOME (1980).

Genus ***Ellipsoxiphus*** DUNIKOWSKI, 1882

Type species: *Xiphosphaera (Ellipsoxiphus) suessi* DUNIKOWSKI, 1882 = *Xiphosphaera (Ellipsoxiphus) parvoforaminosus* DUNIKOWSKI, 1882

Synonyma: *Druppactrylis* HAECKEL, 1887

Pantanellium PESSAGNO, 1977

Remarks: KOZUR & MOSTLER (1979) recognized that *Pantanellium* PESSAGNO, 1977 is a younger synonym of *Druppactrylis* HAECKEL, 1887. Our restudy of Lower Jurassic radiolarians described by DUNIKOWSKI (1882) has shown that *Ellipsoxiphus* DUNIKOWSKI, 1882 originally introduced as subgenus of *Xiphosphaera* HAECKEL, 1882, is identical with *Pantanellium*, too. CAMPBELL (Treatise, 1954) figured under *Ellipsoxiphus* DUNIKOWSKI, 1882 a recent species that does not belong to this genus.

Two species, *Xiphosphaera (Ellipsoxiphus) suessi* DUNIKOWSKI, 1882 and *X. (E.) parvoforaminosus* DUNIKOWSKI, 1882 were originally placed into the subgenus *Ellipsoxiphus*. The holotype of *E. suessi* is better preserved and corresponds best to the genus diagnosis. Therefore it was described first in DUNIKOWSKI's paper. Quite surprisingly, CAMPBELL (1954) has chosen the not so well preserved *X. (E.) parvoforaminalis* as type species of *Ellipsoxiphus*. In the holotype of this species, part of the second primary spine is broken away and the big pores are partly closed by recrystallisation and filling with sediment material. For this reason, by using the primitive microscopes of the last century, the partly closed big pores appeared as 1-3 small pores. Moreover, some (? pathologic) forms of *Ellipsoxiphus* show subdivision of some large pores into 2 or more smaller ones (e.g. *Pantanellium* sp. I in PESSAGNO & BLOME, 1980 pl. 3, figs. 6, 12, 19 or *Pantanellium* aff. *cumshewaense* in SASHIDA, TONISHI & IGO, 1986, fig. 5/10). This feature has no specific or even generic importance. The only real difference between the two holotypes is that the cortical shell in *X. (E.) parvoforaminosus* is a little fewer elongated than in *X. (E.) suessi*, but this difference lies within the intraspecific vari-

ability. Both species are here regarded as synonymous. The priority is given to *E. suessi* because of its better preserved holotype.

E. kluensis (PESSAGNO & BLOME, 1980) is very similar and possibly identical. The only difference is that the polar spines are stronger in *E. suessi* (DUNIKOWSKI, 1882), but their strength shows intraspecific variability. As in *E. suessi*, also in *E. kluensis* the ellipsoidal cortical shell is sometimes more, sometimes fewer elongated. In any case, *E. suessi* belongs to the *E. kluensis* group, characteristic for Lower Liassic (? and topmost Rhaetian) rocks.

Ellipsoxiphus suessi (DUNIKOWSKI, 1882)

(Pl. 14, fig. 12; pl. 15, figs. 12, 13)

1882 *Xiphosphaera (Ellipsoxiphus) suessi* nov. sp. DUNIKOWSKI, pl. 5, fig. 50

1882 *Xiphosphaera (Ellipsoxiphus) parvoforaminosus* nov. sp. DUNIKOWSKI, p. 186, pl. 5, fig. 51

Remarks: This species is figured here to present a SEM picture of the first described *Ellipsoxiphus* species. No generic differences against *Druppactrylis* HAECKEL, 1887 and *Pantanellium* PESSAGNO, 1977 can be observed.

Age: Hettangian of the Alps and northern Hungary (Csövár, Várhegy Cherty Limestone Formation).

Ellipsoxiphus browni (PESSAGNO & BLOME, 1980)

(Pl. 14, fig. 14, pl. 15, figs. 11, 14)

1980: *Pantanellium browni* PESSAGNO & BLOME, n. sp. PESSAGNO & BLOME, p. 239, pl. 4, figs. 5-7 12, 14, 16, 19, 20

Remarks: Some of our specimens are identical with this species, other are very similar and determined here as *Ellipsoxiphus* cf. *browni* (Pl. 14, fig. 14; pl. 15, fig. 11). In these forms the nodes occurring at vertices of pore frames are larger.

Distribution: Hettangian of the Alps, (Upper) Hettangian of western North America.

Ellipsoxiphus tanuensis (PESSAGNO & BLOME, 1980)

(Pl. 14, figs. 10, 11)

1980: *Pantanellium tanuense* PESSAGNO & BLOME, n. sp. PESSAGNO & BLOME, p. 247, pl. 4, figs. 3, 4, 24

Remarks: This typical form with spherical cortical shell and predominance of hexagonal pore frames is easily to determine and together with *E. suessi* (DUNIKOWSKI, 1882) the most frequent *Ellipsoxiphus* species in our material. In some specimens the nodes occurring at vertices of pore frames are a little larger. They are here determined as *Ellipsoxiphus* cf. *tanuensis*.

Distribution: Hettangian of the Alps, Lower Hettangian (? Upper Rhaetian) of western North America.

Ellipsoxiphus cf. danaensis (PESSAGNO & BLOME, 1980)

(Pl. 14, fig. 13; pl. 15, fig. 15)

1980: *Pantanellium danaense* PESSAGNO & BLOME, n. sp. PESSAGNO & BLOME, p. 241, pl. 4, figs. 9-11, 15

Remarks: The spines at the vertices of pore frames are longer than in the type material. However, the bars of pore frames, thin along Y and high along Z are strongly corroded and therefore the spines at the vertices appear higher.

Distribution: Hettangian of the Alps, and northern Hungary, (Upper) Hettangian and Sinemurian of western North America.

Genus *Betraccium* PESSAGNO, 1979

Type species: *Betraccium smithi* PESSAGNO, 1979

Betraccium bavarium n. sp.

(Pl. 14, figs. 4, 9)

Derivatio nominis: According to its occurrence in Bavaria

Holotype: The specimen on pl. 14, fig. 4; rep.-no. KoMo 1990 I-20

Material: 21 specimens.

Diagnosis: Cortical shell subspherical with large trigonal, tetragonal and pentagonal pores. Distinct nodes, partly with small, needle-like spines are situated on pore frame vertices. Bars of the pore frames narrow in Y direction and moderately high in Z direction. 4-5 pore frames visible on top and bottom surfaces along an axis in line with that of a given primary spine. Primary spines long, symmetrically arranged, equidistant and of nearly equal length. No or only very slight torsion along the largest part of the spines. Only their terminal part displays a slight torsion. Tips of the primary spines elongated into needle-like prolongations.

Measurements:

Diameter of the cortical shell = 108–120 μm

Length of the primary spines = 100–120 μm

Distribution: Hettangian part of the Kirchstein Limestone at the type locality.

Remarks: *Betraccium inaequiporatum* n. sp. has the same pore frames, but the primary spines display no torsion and the cortical shell is smaller.

Betraccium verticispinosum n. sp. displays strong torsion of the distal part of the primary spines and the nodes on the pore frame vertices display distinct spines.

Betraccium hettangicum n. sp.

(Pl. 14, fig. 5)

Derivatio nominis: According to the occurrence in the Hettangian

Holotype: The specimen on pl. 14, fig. 5; rep.-no. KoMo 1990 I-1

Material: 12 specimens.

Diagnosis: Cortical shell subspherical with large, predominantly quadratic pore frames having indistinct pyramidal cones at pore frame vertices. Bars of the pore frames narrow in Y- and low to moderately high in Z-direction. 4-5 pore frames visible on top and bottom surfaces along an axis in line with that of a given primary spine. Primary spines long, symmetrically arranged, equidistant and of equal length, with 3 wide grooves alternating with 3 ridges. Grooves and ridges displaying moderate torsion.

Measurements:

Diameter of cortical shell = 100–110 μm

Length of primary spines = 83–93 μm

Distribution: Until now only known from the Hettangian part of the Kirchstein Limestone at the type locality.

Remarks: *Betraccium hettangicum* n. sp. is a quite typical representative of the genus *Betraccium* (symmetrically arranged, equidistant spines of equal length, torsion of the spines, very large pores of the cortical shell). It is the youngest typical representative of the genus *Betraccium*. From Triassic species it is distinguished by the predominantly quadratic pore frames. The Hettangian *Betraccium inaequiporatum* is distinguished by primary spines without torsion and by different pore frames.

Betraccium inaequiporatum n. sp.

(Pl. 14, fig. 6)

Derivatio nominis: According to the different pore frame present in the same specimen

Holotype: The specimen on pl. 14, fig. 6; rep.-no KoMo 1990 I-2

Material: 5 specimens.

Diagnosis: Cortical shell spherical with large, trigonal, tetragonal and pentagonal pore frames in the same specimens. Very short pyramidal spines are situated at pore frame vertices. Bars of the pore frames narrow in Y direction and low in Z direction. 5-6 pore frames visible on top and bottom surfaces along an axis in line with that of a given primary spine. Primary spines long, symmetrically arranged, equidistant and of equal length, with 3 deep grooves alternating with 3 ridges. No torsion of the spines.

Measurements:

Diameter of cortical shell = 80–88 μm

Length of primary spines = Ca. 80 μm

Distribution: Until now only known from the Hettangian part of the Kirchstein Limestone at the type locality.
Remarks: The equidistant primary spines of equal length and all other generic characters of *B. inaequiporatum* n. sp. are typical for the genus *Betraccium*. However, the spines display no torsion. By this feature *B. inaequiporatum* n. sp. is clearly separated from the most Triassic representatives of this genus (see below), but also from the Hettangian *B. hettangicum* n. sp. and *B. verticispinosum* n. sp.. Moreover, the presence of trigonal, tetragonal and pentagonal pore frames in the same specimen is a quite unique feature for the genus *Betraccium* and can be only observed in the Hettangian species *B. inaequiporatum* n. sp. and *B. bavaricum* n. sp.

CHENG (1989) figured from the Philippines under *Betraccium* sp. A, B, C Upper Norian forms without torsion of the primary spines. However, the Upper Norian age was determined by the presence of *Betraccium* PESSAGNO & BLOME and the absence of *Capuchnosphaera* DE WEVER. Rhaetian or even Lower Hettangian age for these faunas cannot be excluded.

***Betraccium verticispinosum* n. sp.**

(Pl. 14, figs. 7, 8)

Derivatio nominis: According to the distinct spines on the pore frame vertices

Holotype: The specimen on pl. 14, fig. 8; rep.-no. KoMo 1990 I-19

Material: 15 specimens.

Diagnosis: Cortical shell spherical with large tetragonal and trigonal pores. The distinct nodes on the pore frame vertices end in needle-like spines. Bars of the pore frames very narrow in Y-direction and low to moderately high in Z-direction. 5-6 pore frames visible on top and bottom surfaces along an axis in line with that of a given primary spine. Primary spines long, symmetrically arranged, equidistant, but with slightly different length. Their ridges and grooves displaying strong torsion in the distal third. Remaining part of the primary spines almost without torsion.

Measurements:

Diameter of cortical shell = 88–110 μm

Length of primary spines = 84–110 μm

Distribution: Hettangian part of the Kirchstein Limestone at the type locality.

Remarks: *Betraccium inaequiporatum* n. sp. displays no torsion of the spines.

Betraccium hettangicum n. sp. displays a moderate torsion of the primary spines throughout their whole length.

Betraccium alpinum n. sp. displays only in the terminal part of the primary spines a slight torsion, and spines

on the pore frame vertices, if present, are not so pronounced.

Genus ***Gorgansium*** PESSAGNO & BLOME, 1980

Type species: *Gorgansium silviesense* PESSAGNO & BLOME, 1980

***Gorgansium alpinum* n. sp.**

(Pl. 16, fig. 12)

1984 *Gorgansium* sp. A, pars IGO & NISHIMURA, pl. 3, figs. 18, ? 20, ? 21, ? 23, pl. 4, fig. 8

Derivatio nominis: According to the first discovery of the genus *Gorgansium* in the Liassic of the Alps

Holotype: The specimen on pl. 16, fig. 12; rep.-no. KoMo 1990 I/3

Material: 15 specimens.

Diagnosis: Cortical shell spherical with large, predominantly pentagonal pore frames having well developed nodes at pore frame vertices. Bar of pore frames thin in Y-direction, but thickened near the pore frame vertices; high in Z direction. 6-7 pore frames visible both along AB and CD. Primary spines with 3 broad ridges having a shallow secondary furrow. Primary furrows between the ridges deep, but narrow. One spine almost twice as long as the other two spines that are situated nearer each other than to the longer spine.

Measurements:

AB = 100–110 μm

AT = 105–115 μm

CD = 95–102 μm

EF and GH = 67–70 μm

Distribution: Hettangian of the Alps and from Japan.

Remarks: *Gorgansium blomi* n. sp. has a subspherical cortical shell, the 3 primary spines have either all almost the same length or two spines are somewhat shorter than the third one, the pore frames are broader in Y and no distinct nodes at pore frame vertices are present.

***Gorgansium blomi* n. sp.**

(Pl. 16, fig. 13)

1980: *Gorgansium* sp. C PESSAGNO & BLOME, p. 236, pl. 4, fig. 8

Derivatio nominis: In honour of Prof. Dr. CH. D. BLOME, Dallas

Holotype: The specimen on pl. 16, fig. 13; rep.-no KoMo 1990 I/4

Material: 7 specimens.

Diagnosis: Cortical shell subspherical, outline almost straight between the two closely spaced spines. All 3 primary spines have either almost the same length or the two

closely spaced spines are somewhat shorter than the third primary spine. The 3 primary spines are tricarinate, with moderately broad ridges and furrows. Pore frames moderately broad in Y direction and very high in Z-direction. Pore frames predominantly hexagonal. 5 pore frames visible along AB; 6 pore frames visible along CD. No distinct nodes at pore frame vertices.

Measurements:

AB = 100–115 μm

AT = 48–50 μm

CD = 125–130 μm

EF and GH = 45–50 μm

Distribution: Hettangian of Alps and British Columbia.

Remarks: This distinct form is identical with *Gorgansium* sp. C from the Hettangian of British Columbia described by PESSAGNO & BLOME (1980).

Superfamily **Trematodiscacea** HAECKEL, 1862 emend. KOZUR & MOSTLER, 1978

Synonyma: Spongodiscacea HAECKEL, 1862 sensu BAUMGARTNER, 1980

Euchitoniidae HAECKEL 1887 sensu CAMPBELL, 1954

Remarks: CAMPBELL (1954) revised the "subsuperfamily" Euchitoniidae HAECKEL, 1887 to a rather natural group including also the Trematodiscidae HAECKEL, 1862 and the Spongodiscidae HAECKEL 1862 (mostly dated as HAECKEL, 1882 or 1881). Some forms, like *Hagiastrum* HAECKEL, 1882 with the type species *Hagiastrum plenum* RÜST, 1885 do not belong to this "subsuperfamily", but CAMPBELL (1954) used *Hagiastrum* in an other sense for forms that belong to his Euchitoniidae. The oldest family taxon which CAMPBELL (1954) placed into the Euchitoniidae HAECKEL, 1887 are the Trematodiscidae HAECKEL, 1862 that have therefore the priority also in superfamily rank.

PESSAGNO (1971) enclosed into the Spongodiscacea HAECKEL, 1881 all Spumellaria with spongy tests varying in shape, lacking sieve plates, latticed shells, or chambered rays and having pore frames symmetrically or asymmetrically arranged. In this original definition the nominate family Spongodiscidae HAECKEL, 1862 are excluded from the Spongodiscacea, because they have at least one latticed medullary shell. Later, PESSAGNO (1973) included into the Spongodiscacea also forms with spongy cortical shell and latticed medullary shell, but he excluded furthermore forms that belong to the Trematodiscidae HAECKEL, 1862 and forms with chambered arms.

KOZUR & MOSTLER (1978) followed with their superfamily Trematodiscacea HAECKEL, 1862 emend.

largely CAMPBELL (1954), but named their superfamily for priority reasons not Euchitoniacea HAECKEL, 1887, but Trematodiscacea HAECKEL, 1862. Radiolarians with elliptical, cylindrical, sometimes constricted, in primitive forms rarely spherical spongy, often heteropolar test were placed into the superfamily Sponguracea HAECKEL, 1862 emend. KOZUR & MOSTLER, 1981.

BAUMGARTNER (1980) followed KOZUR & MOSTLER (1978), but he named the Trematodiscacea HAECKEL, 1862 emend. KOZUR & MOSTLER, 1978 again as Spongodiscacea HAECKEL, 1882. This would be not possible for priority reasons, but the Spongodiscidae have been also established by HAECKEL, 1862. However, by the first revising authors KOZUR & MOSTLER (1978) the Spongodiscidae HAECKEL, 1862 have been placed into the Trematodiscacea HAECKEL, 1862. Therefore the name Trematodiscacea HAECKEL, 1862 emend. KOZUR & MOSTLER 1978 has the priority against the Spongodiscacea HAECKEL, 1862 (both family taxa have been established in the same paper by HAECKEL, 1862).

PESSAGNO (1971, 1973) cannot be regarded as the first revising author, because he never placed the Trematodiscacea into the same superfamily as the Spongodiscacea. On the contrary, his diagnosis for the Spongodiscacea excluded the Trematodiscidae from the Spongodiscacea.

Also KOZUR & MOSTLER (1978) discussed the possibility that the Trematodiscacea (in a restricted sense for forms with concentric or spiral structure covered by a lower and upper spongy layer) and the Spongodiscacea (lacking the central concentric or spiralic structure) could belong to 2 different superfamilies, but they recognized several transitions between both groups. We have now studied material from Barbados to discuss once more this possibility. In this Tertiary material both Spongodiscidae HAECKEL, 1862, Orbiculiformidae PESSAGNO, 1973 and all transitional forms between both families are present. Moreover, also Trematodiscidae HAECKEL, 1862 are present, with transitional forms to the Spongodiscidae.

Both in the Orbiculiformidae and in the Spongodiscidae the spongy meshwork is often arranged into concentric rings or spirals. They are more pronounced in many Neozoic Spongodiscidae and Orbiculiformidae, than in Mesozoic Orbiculiformidae, but even in the oldest typical Orbiculiformidae from the Lower Carnian of Austria species with distinct concentric arrangements of the spongy meshwork are present.

In transitional forms between Spongodiscidae and Trematodiscidae the concentric structure is very pronounced and the forms are flat and quite plane. In true Tre-

matodiscidae the concentric or spiralic structure is not only strong, but separated from the remaining test as an inner single layer of concentric or spiralic pore frames with strong bars (both the rings or spirals and the transverse bars that separate big pores). This inner layer is covered on the lower and upper side by a layer of spongy meshwork. The transitional forms indicate that both groups belong to the same superfamily as assumed already by CAMPBELL (1954) and KOZUR & MOSTLER (1978). In both groups discoidal and armed forms can be observed.

The Trematodiscacea have in their centre a tiny microsphere, already recognizable in Triassic forms. In Neozoic forms often a somewhat larger second latticed medullary shell encloses this microsphere.

Genus *Crucella* PESSAGNO 1971

Type species: *Crucella messinae* PESSAGNO, 1971

Crucella carteri n. sp.

(Pl. 15, figs. 2, 4, 9)

Derivatio nominis: In honour of Dr. E.S. CARTER, Vancouver

Holotype: The specimen on pl. 15, fig. 4; rep.-no. KoMo 1990 I/8

Material: More than 100 specimens.

Diagnosis: 4 rays short, with very broad base. Pore frames large, parallelogram-shaped, subordinately trigonal. Mostly 4 bars originate in the vertices of pore frames. Terminal spines robust, proximally broad, tricarinate.

Measurements:

Diameter of cortical shell between the spines: 88–96 μm

Length of the rays = 40–60 μm

Maximum width of the rays = 58–63 μm

Maximum length of the spines = 70–87 μm

Distribution: Until now only known from the Hettangian part of the Kirchstein Limestone at the type locality.

Remarks: *Crucella prisca* n. sp. is most similar, but this species is distinguished by different pore frames.

Crucella hettangica n. sp.

(Pl. 15, fig. 7)

Derivatio nominis: According to its occurrence in the Hettangian part of the Kirchstein Limestone

Holotype: The specimen on pl. 15, fig. 7; rep.-no. KoMo 1990 I/7

Material: 4 specimens.

Diagnosis: 4 rays long, slender, with slightly tapering tips. Pore frames tetragonal to pentagonal. Terminal spines tricarinate, distally rounded, very long and needle-shaped.

Measurements:

Width of cortical shell between the rays: 70–75 μm

Maximum width of rays: 40–48 μm

Length of rays: 80–85 μm

Maximum length of terminal spines: 116 μm

Distribution: Hettangian part of the Kirchstein Limestone in the type locality and Várhegy Cherty Limestone Formation of Csövár (northern Hungary).

Remarks: *Crucella longispinosa* (KOZUR & MOSTLER, 1978) from the Lower Carnian of Austria has the same type of terminal spines, but the rays are shorter and broader.

Crucella angulosa CARTER; CAMERON & SMITH, 1988 from the Late Pliensbachian to Middle Toarcian of western North America is similar, but the terminal spines are basally very broad.

Crucella prisca n. sp.

(Pl. 15, figs. 1, 3, 5, 8, 10)

1984 *Staurodoras* (?) sp. IGO & NISHIMURA; pl.5, figs. 12, 13

Derivatio nominis: Oldest known Jurassic *Crucella* species

Holotype: The specimen on pl. 15, fig. 10; rep.-no. KoMo 1990 I/6

Material: More than 100 specimens.

Diagnosis: Tapering tips of the 4 short, especially proximally broad rays with long, robust tricarinate spines. Pore frames of *Alievium* type, single pores tetragonal or trigonal. Vertices of pore frames node-like. 4–6, mostly 5 bars originate from the vertices.

Measurements:

Diameter of cortical shell between the rays: 92–110 μm

Length of the rays = 56–65 μm

Maximum width of the rays = 54–60 μm

Length of the spines = More than 80 μm

Distribution: Uppermost part of the *Canoptum rhaeticum* A. Z. s.str. (conodont proven uppermost Rhaetian), *Relanus hettangicus* Zone, (Hettangian), Lower Sinemurian part of the *Parahsuum simplum* Zone. Alps, northern Hungary (Csövár), Japan.

Remarks: *Crucella squamosa* (KOZLOVA, 1971) has roundish to oval pores frames.

Crucella longispinosa (KOZUR & MOSTLER, 1978) from the Lower Carnian has similar rays (form and length), but the spines are very long and except of their proximal part needle-shaped.

Crucella angulosa CARTER; CAMERON & SMITH, 1988 has proximally slender rays of nearly the same width throughout its length. In our material only one specimen shows this latter feature, but also in this specimen the length to width ratio is smaller than in *C. angulosa*. Moreover, the pore frames are different.

Crucella hettangica n. sp. has larger and slender rays and larger and more needle-shaped terminal spines.

Crucella carteri n. sp. has larger, parallelogram-shaped pore frames.

Some of our specimens have considerably shorter terminal spines (40–50 µm), but are otherwise identical with *C. prisca* n. sp. They are here determined as *C. cf. prisca* n. sp.

Genus *Paronaella* PESSAGNO, 1971

Type species: *Paronaella solanoensis* PESSAGNO, 1971

Paronaella striata n. sp.

(Pl. 15, fig. 6)

Derivatio nominis: According to the linear pore arrangement in large parts of the rays

Holotype: The specimen on pl. 15, fig. 6; rep.-no. KoMo 1990 1/5

Material: 2 specimens.

Diagnosis: Test composed of 3 rays with circular cross section that are distally only a little broader than proximally. Pores of irregular shape and size are lineary arranged in the proximal parts of the rays. In the distal part the pore arrangement is irregular or indistinctly linear. Especially in the distal part of the rays irregular short spines are present at some vertices of pore frames in the marginal parts of the rays. Internal structure of the rays spongy.

Measurements:

Length of the rays = 132–136 µm

Minimum width of the rays = 24 µm

Maximum width of rays (without spines) = 32–35 µm

Distribution: Until now only known from the Hettangian part of the Kirchstein Limestone at the type locality.

Remarks: The outer morphology with rather distinct linear arrangement of the pore frames in the proximal parts of the rays remembers to *Homoeoparonaella* BAUMGARTNER, 1980, but the inner structure is typical for *Paronaella* PESSAGNO, 1971. True hagiastriids, present since the Lower Sinemurian, are not yet present in our Hettangian material.

Subordo **Entactinaria** KOZUR & MOSTLER, 1982

Superfamily **Hexastylacea** HAECKEL, 1882 emend. PETRUSEVSKAJA, 1979

Family **Triplosphaeridae** VINASSA DE REGNY, 1898 emend. KOZUR & MOSTLER, 1981

Genus *Xenorum* BLOME, 1984

Type species: *Xenorum largum* BLOME, 1984

Xenorum jurassicum n. sp.

(Pl. 16, fig. 15)

Derivatio nominis: According to its occurrence in the Jurassic (so far only known from the Upper Triassic)

Holotype: The specimen on pl. 16, fig. 15; rep.-no. KoMo 1990 I-21

Material: 3 specimens.

Diagnosis: Cortical shell spherical, with large tetragonal, pentagonal and smaller trigonal pore frames. Outer layer exhibiting large polygonal pore frames with large and high nodes at the pore frame vertices, often ending in short spines. 3 primary spines symmetrically arranged, of medium length, tricarinate, with broad ridges and deep furrows between the ridges, without or with slight torsion.

Measurements:

Diameter of cortical shell = 136–144 µm

Length of spines = 80–89 µm

Distribution: Hettangian part of the Kirchstein Limestone at the type locality.

Remarks: *Xenorum jurassicum* n. sp. has the typical shell structure of the genus *Xenorum* BLOME, 1984 known so far only from the Late Triassic. The 2 former described species, *X. flexum* BLOME, 1984 and *X. largum* BLOME, 1984, have spines with strong torsion, but *Xenorum* sp. A BLOME is a Late Triassic species without torsion of the spines, like *X. jurassicum* n. sp.

Suborder **Nassellaria** EHRENBERG, 1875

Family **Canoptidae** PESSAGNO, 1979

Canoptum PESSAGNO, 1979

Type species: *Canoptum poissoni* PESSAGNO, 1979

Canoptum rhaeticum KOZUR & MOSTLER, 1981

1981 *Canoptum rhaeticum* n. sp. KOZUR & MOSTLER, p. 103–104, pl. 20, figs. 1–4

1982 *Canoptum triassicum* YAO, n. sp. YAO, p. 60, pl. 3, figs. 1–4

Distribution: According to KOZUR & MOSTLER (1981) this species is rare in the Norian and widely distributed in the Rhaetian. According to YAO (1982) it occurs in the Sevatian and Rhaetian of Japan. However, seemingly this species occurs here also above the highest occurrence of Rhaetian conodonts, but below the appearance of *Parahsuum simplex* YAO that begins within the Hettangian. According to IGO & NISHIMURA (1984) *C. rhaeticum* (= *C. triassicum*) ranges upward until the lowermost sample with *Parahsuum simplum* YAO. Therefore this species has a total range from the Middle Norian up to the Hettangian but it is common only in the Rhaetian worldwide distribution.

This range is for the upper part confirmed in our Hettangian material that contains still rarely *C. rhaeticum*. The uppermost *C. "triassicum"* Zone of Japan (above the last occurrence of Rhaetian conodonts) is here excluded from the *C. rhaeticum* A.Z. and tentatively placed into the *Relanus hettangicus* Zone. This interval has a quite distinct fauna, clearly separated both from the *C. rhaeticum* A.Z. s.str. and from the *Parahsuum simplum* Zone that begins within the Hettangian.

In Japan the ranges of the radiolarians from this interval are well studied by HORI (1988) in the Kurusu section. It comprises here a short interval of the samples KU (c) 1, Ku (e) 2, Ku (b) 15 between the last occurrence of Rhaetian conodonts and the first occurrence of *Parahsuum simplum* that comprises only about 2 m of chert. In this interval *Droptus eurasiaticus* (= *Parahsuum* ? sp. A) and *Syringocapsa coliforme* HORI make their first appearances. Both species are also present in our material. The discussed interval in the Kurusu section corresponds probably to the topmost Rhaetian and (Lower) Hettangian.

Genus *Paracanoptum* YEH, 1987

Type species: *Canoptum anulatum* PESSAGNO & POISSON, 1981

Paracanoptum primitivum n. sp.

(Pl. 17, figs. 7, 9-13)

Derivatio nominis: According to the primitive stage in the *Paracanoptum* development

Holotype: The specimen on pl. 17, fig. 12; rep.-no. Ko-Mo 1990 I-22

Material: More than 50 specimens.

Diagnosis: Multicyrtid test conical. Cephalis hemispherical to rounded conical, imperforate. Thorax and following segments trapezoidal. Cephalis and thorax, sometimes also abdomen not separated on the outer surface by strictures. Surface of cephalis smooth. Thorax and abdomen covered by small nodes. Postabdominal segments well visible on the outer surface. Inner pore frames of postabdominal segments consisting of 2 rings of pores between adjacent circumferential rings. These 2 pore rings are separated by a more or less distinct ring. Pore frames linearly arranged. Pores of different size and shape, mostly oval or polygonal. Inner pore frames covered by a layer of microgranular silica. The strictures are poreless, in the proximal part with irregular nodes, in the distal part smooth. Circumferential ridges in the proximal part of test with short vertical ribs or elongated nodes, arranged as "H-linked" ridges. In the distal part of test often only nodes or elongated nodes are present on the circumferential ridges. In many specimens even the nodes become here indistinct. 2 rings of tiny pores are present on the upper and lower part of the

circumferential ridges, but these tiny pores are often closed (partly because of recrystallization).

Measurements:

Length of test = 173–190 µm

Maximum width = 80–90 µm

Distribution: Hettangian of the Alps and northern Hungary. (Várhegy Cherty Limestone Formation of Csövár).

Remarks: In *Paracanoptum anulatum* (PESSAGNO & POISSON, 1981) from the Upper Sinemurian and Pliensbachian the "H-linked" frames on the circumferential ridges are more pronounced and the pores in the outer layer are more distinct. Moreover, the test of *P. anulatum* is more slender.

Paracanoptum rugosum (PESSAGNO & POISSON, 1981) from the Upper Sinemurian and Pliensbachian has the same shape of the test as *P. primitivum* n. sp., but the circumferential ridges are more pronounced (sharper separated from the strictures) and the distances between 2 circumferential ridges are larger than in *P. primitivum*.

Genus *Relanus* PESSAGNO & WHALEN, 1982

Type species: *Relanus reefensis* PESSAGNO & WHALEN, 1982

Relanus hettangicus n. sp.

(Pl. 16, figs. 1, 4, 5, 7, 10, 11, 14; pl. 17, figs. 8, 14-16)

Derivatio nominis: According to the frequent occurrence in our Hettangian material

Holotype: The specimen on pl. 17, fig. 16; rep.-no. Ko-Mo 1990 I-9

Material: Several 100 specimens.

Diagnosis: Multicyrtid, elongated spindle-shaped. Cephalis, thorax and abdomen, sometimes also the first postabdominal segment built up an outside unsegmented cone. Postabdominal segments outside hoop-like, closely spaced, gradually increasing in width until the last 4-5 chambers, which decrease rather rapidly toward the distal end. Distal aperture relatively small.

The cephalis bears an externally situated short horn and it is imperforate like the thorax. Other segments with two rings of vertically elongated, irregularly shaped and sized pores, covered outside by a layer of microgranular silica that is mostly imperforate or pierced by tiny pores along the circumferential ridges. On the inner side the circumferential ridges are very high and narrow. In the distal narrow segments the layer of microgranular silica is thin and here the inner pores are sometimes also outside visible and only partly closed by the layer of microgranular silica. The outer layer is especially in the proximal half of the test covered by mostly indistinct rings of small nodes.

Measurements:

Length = 227–267 µm

Maximum width = 86–98 µm

Distribution: Very frequent in the Hettangian of the Alps and northern Hungary (Várhegy Cherty Limestone Formation of Csövár).

Remarks: *Relanus* PESSAGNO & WHALEN, 1982 is seemingly a very characteristic genus of Hettangian radiolarian faunas. It began sporadically and very rarely in the Middle Norian and became only in the Late Rhaetian more frequent. After its maximum in the Hettangian, *Relanus* disappeared at the top of the Hettangian.

Relanus reefensis PESSAGNO & WHALEN, 1982 is more slender and only the last segment decreases in width. Moreover, numerous small pores are visible on the outer surface above all along the circumferential rings.

Relanus hettangicus n. sp. is similar to *Canoptum rhaeticum* KOZUR & MOSTLER, 1981. This species has no apical horn and the outer segmentation begins higher.

Relanus multiperforatus n. sp. is distinguished by numerous small pores on the outer surface of microgranular layer.

***Relanus multiperforatus* n. sp.**

(Pl. 16, figs. 2, 3)

Derivatio nominis: According to the numerous small pores in the layer of microgranular silica

Holotype: The specimen on pl. 16, fig. 3; KoMo 1990 I/10

Material: 4 specimens.

Diagnosis: Test conical to elongated spindle-shaped. Cephalis hemispherical, imperforat, with distinct, asymmetrically, externally situated apical horn. Remaining chambers trapezoidal, gradually increasing in width until 6th or 7th postabdominal chamber. The distal 4-5 chambers become again narrower. Cephalis, thorax and abdomen outside united into a unsegmented cone. Postabdominal segments outside visible as low rounded rings of large, vertically elongated pores, covered on the outer side by a layer of microgranular silica pierced by numerous small pores along the circumferential ridges. In the constrictions only few pores are visible in the marginal part of the ridges.

Measurements:

Length = 252–300 µm

Maximum width = 100–123 µm

Distribution: Until now only known from the Hettangian part of the Kirchstein Limestone at the type locality.

Remarks: *Relanus reefensis* PESSAGNO & WHALEN, 1982 is very slender, the segmentation is outside more pronounced and the outside unsegmented proximal part is missing.

In the latter feature (outside unsegmented cone of cephalis, thorax and abdomen) *R. multiporatus* n. sp. corresponds to *R. hettangicus* n. sp., but this species has no or only a few tiny pores in the outer layer of microgranular silica.

***Relanus longus* n. sp.**

(Pl. 17, fig. 19)

Derivatio nominis: According to the long, slender test
Holotype: The specimen on pl. 17, fig. 19; rep.-no. KoMo 1990 I/11

Material: 23 specimens.

Diagnosis: Test long, very slender, with a large distal part of equal width. Cephalis hemispherical with asymmetrically (externally) situated horn. Segmentation until the abdomen or first postabdominal segment outside not visible. Remaining segments closely spaced, outside visible as low hoop-like rings separated by relatively narrow constrictions. Postabdominal segments increase gradually in width until the fifth or sixth postabdominal segment. The following 5-6 segments have about the same width. Inner pore frames consist of two rings of pores in the postabdominal segments and in the abdomen, covered by a layer of microgranular silica that is only in the distal segment pierced by tiny pores along the circumferential rings. In the proximal part of the test indistinct nodes are present.

Measurements:

Length = 261–279 µm

Maximum width: 75–79 µm

Distribution: Until now only known from the Hettangian part of the Kirchstein Limestone at the type locality.

Remarks: *Relanus reefensis* PESSAGNO & WHALEN, 1982 has more pronounced segments outside visible until the proximal part of the test. Numerous small pores are present in all postthoracic segments.

Relanus hettangicus n. sp. is elongated spindle-shaped with distinctly decreasing width of segments in the distal part.

***Relanus striatus* n. sp.**

(Pl. 16, figs. 8, 9; pl. 17, fig. 17, 18)

Derivatio nominis: According to the faint short vertical ribs on the circumferential ring

Holotype: The specimen on pl. 17, fig. 17; rep.-no. KoMo 1990 I/12

Material: 4 specimens.

Diagnosis: Test conical to slender conical. Cephalis asymmetrically conical with rather strong, excentrically (externally) situated apical horn and sometimes also with tiny lateral horn. Following closely spaced segments trapezoidal, increasing gradually in width and height, but the

last 4-5 segments decrease again very slowly in width. Segmentation on the outer surface well visible. Cephalis and thorax imperforate. Remaining segments with two rings of pores, on the outer surface covered by a layer of microgranular silica, pierced along the circumferential rings by two rings of small pores. Until the second to fourth post-abdominal segment mostly no pores are present. The outer rings of the postabdominal segments are covered by a ring of low, densely spaced nodes that are in the upper half of test prolonged into very short, narrow, very low ribs, partly "H-linked" frames. In the lower part of test these ribs are indistinct.

Measurements:

Length = 275–401 μm

Maximum width: 90–109 μm

Distribution: Until now only known from the type locality of the Kirchstein Limestone in its Hettangian lower part.

Remarks: By the surface sculpture this species is well distinguished from all other *Relanus* species. *Paracanoptum* YEH 1987 has no apical spine.

Family Bagotidae PESSAGNO & WHALEN, 1982

Synonym: Canutidae PESSAGNO & WHALEN, 1982

Remarks: PESSAGNO & WHALEN (1982, p. 117) recognized several differences between the Bagotidae and Canutidae that cannot be confirmed by our investigations. Only in some *Canutus* species the outer layer consists exclusively of bars that are anchored to the pillar-like nodes of the inner layer. In several other *Canutus* species some or all bars are connected with the bars of the inner pore frames. This is quite the same shell structure as in the Bagotidae. Moreover, both in the Bagotidae and in the Canutidae (*Canutus* s.l.) the outer layer is often reduced to nodes on the pore frame vertices and finally even these nodes may become indistinct. The only remaining difference between the Bagotidae and Canutidae is, that in the Canutidae the pore frames of the inner layer are linearly arranged throughout the whole test, whereas in the Bagotidae the pore frames of the inner layer are in the proximal part often irregularly arranged. However, the part with irregularly arranged pore frames has different length and may even disappear within one species, like in some *Parahsuum* species. It may be also present in some typical Canutidae (e.g. *Praecanutus* n. gen.). This difference cannot be used for separating family taxons.

As the first revising authors we give here the Bagotidae the preference against the Canutidae, both published in the same paper. The Bagotidae have the page priority and the Canutidae were based only on one genus.

Genus Parahsuum YAO, 1982

Type species: *Parahsuum simplum* YAO, 1982

Synonyma: *Drulanta* YEH, 1987

Fantus YEH, 1987

Remarks: *Parahsuum* YAO, 1982 comprises both species, where all pore frames are linearly arranged and species with irregular pore frames in the proximal third of the test. In some species, like in the type species, both types occur together in one population. *Drulanta* YEH, 1987 and *Fantus* YEH, 1987 are forms, in which all pore frames are linearly arranged, like in the holotype of *Parahsuum simplum* YAO, 1982. As already recognized by HORI & YAO (1988), *Drulanta* and *Fantus* cannot be separated from *Parahsuum*. *Lupherium* PESSAGNO & WHALEN, 1982 is similar, but has a apical horn and it is here not regarded as younger synonym of *Parahsuum* YAO, 1982 as in HORI & YAO (1988). However, we place it in the same family as *Parahsuum* (Bagotidae) and not into the Hsuidae PESSAGNO & WHALEN, 1982. We could not recognize the growing type of the Hsuidae as published by PESSAGNO & WHALEN (1982), but the growing mechanism is quite identical with that of the Bagotidae PESSAGNO & WHALEN, 1982.

Some of the *Canutus* s.l. species, but not the type species *Canutus tipperi* PESSAGNO & WHALEN, 1982, belong also to *Parahsuum* YAO, 1982. Therefore *Canutus* PESSAGNO & WHALEN, 1982 is not synonymous with *Parahsuum* YAO, 1982. *Canutus* can be distinguished from *Parahsuum* by an outer layer that covers parts or all of the inner pore frames with very large rectangular pores. Moreover, typical *Canutus* have a spindle-shaped test. More elongate subconical species of *Canutus* s.l., in which the outer layer is reduced to nodes on the pore frame vertices or directly superimposed on the inner pore frames (no bars of the outer pore frame between the bars of the inner pore frames) as *Canutus giganteus* PESSAGNO & WHALEN, 1982, *C. indomitus* PESSAGNO & WHALEN, 1982 and *C. izeensis* PESSAGNO & WHALEN, 1982 are here placed into *Parahsuum* YAO, 1982. *Canutus giganteus* PESSAGNO & WHALEN, 1982 (Pliensbachian) is seemingly even a younger synonym of *Parahsuum simplum* YAO, 1982 (Hettangian to Pliensbachian).

Parahsuum simplum YAO, 1982

(Pl. 17, fig. 2)

1982 (March) *Parahsuum simplum* YAO, n. sp. YAO, p. 61, pl. 4, figs. 1-4, 6-8, non! fig. 5

1982 (June) *Canutus giganteus* PESSAGNO & WHALEN, n. sp. PESSAGNO & WHALEN, p. 127-128, pl. 4, figs. 5, 13.

Distribution: Hettangian to Pliensbachian of Japan, Hettangian of the Alps.

Remarks: The specimen figured in YAO (1982, pl. 4, fig. 5) belongs to *Parahsuum ovale* HORI & YAO, 1988. In our material *P. simplum* YAO, 1982 is still very rare and represented by very primitive specimens. The pore frames are already rectangular as in typical *P. simplum*, but their size and the linear arrangement of the pore frames is not yet so regular as in typical representatives of this species.

In *Parahsuum primitivum* n. sp. the pore frames are irregular in size and shape and the linear arrangement of the pores is missing or indistinct in the upper third of the test.

***Parahsuum primitivum* n. sp.**

(Pl. 17, fig. 1)

Derivatio nominis: According to the primitive stage within the genus *Parahsuum* YAO, 1982

Holotype: The specimen on pl. 17, fig. 1; rep.-no KoMo I-16

Material: 6 specimens.

Diagnosis: Test conical, multicystid, with 4-5 postabdominal chambers. No strictures visible on the outer surface. Cephalis hemispherical, imperforate, distally with few small pores. Other segments trapezoidal. In the proximal third to half of the test the pores are irregularly spaced and shaped and their size differs. In the distal part of the test the pore frames are aligned in vertical rows. However, also here the pores have different size and shape. Small nodes are present on the pore frame vertices.

Measurements:

Length of test = 120–136 μm

Maximum width = 80–86 μm

Distribution: Hettangian part of the Kirchstein Limestone at the type locality and Várhegy Cherty Limestone Formation (Hettangian) of Csövár (northern Hungary).

Remarks: In *Parahsuum simplum* YAO, 1982 the pores are regularly rectangular and the pore frames are aligned in regular rows. Only in a small proximal part (thorax, abdomen, but never in postabdominal segments) the pores are irregularly arranged in some specimens.

Genus *Droltus* PESSAGNO & WHALEN, 1982

Type species: *Droltus lyellensis* PESSAGNO & WHALEN, 1982

***Droltus carinaspinosus* n. sp.**

(Pl. 17, fig. 5)

Derivatio nominis: According to the tricarinate apical horn

Holotype: The specimen on pl. 17, fig. 5; rep.-no. KoMo 1990 I-14

Material: 23 specimens.

Diagnosis: Test conical, mostly with 6 postabdominal chambers. Cephalis conical, with strong, tricarinate apical horn. Thorax and following segments trapezoidal. Cephalis and thorax covered by a layer of microgranular silica, imperforate or with few small single pores. Pores in the remaining chambers become increasingly larger toward the final chamber that is again a little narrower. Outer latticed layer of abdomen and proximal postabdominal chambers with irregularly sized and shaped polygonal pore frames. Pore frames of the last 3-4 chambers larger, more regular, predominantly tetragonal, aligned in vertical rows.

Measurements:

Length of the test = 183–207 μm

Maximum width = 85–89 μm

Distribution: Hettangian part of the Kirchstein Limestone at the type locality.

Remarks: *Droltus robustospinosus* n. sp. has a very robust tricarinate apical horn and the outer layer of the apical part of the test is arranged in coarse pore frames.

***Droltus eurasiaticus* n. sp.**

(Pl. 17, figs. 3, 4)

1982 *Parahsuum* (?) sp. A YAO, pl. 3, fig. 6

Derivatio nominis: According to its occurrence in Eurasia

Holotype: The specimen on pl. 17, fig. 3; rep.-no. KoMo 1990 I-13

Material: More than 100 specimens.

Diagnosis: Test conical, multicystid, with 6-7 postabdominal segments lacking strictures at joints. Cephalis rounded conical, imperforate, with prominent apical horn. Cephalis covered by a layer of microgranular silica. Thorax and subsequent chambers trapezoidal in cross section. Pores arranged in vertical lines. In the thorax they are closed by a layer of microgranular silica. In the remaining chambers the pores are open and become increasingly larger toward the final postabdominal chamber. Outer latticed layer indistinct to distinct, with large pore frames, arranged in vertical lines and with small to distinct nodes at the pore frame vertices.

Measurements:

Length of the test = 200–214 μm

Maximum width = 83–100 μm

Distribution: *Droltus eurasiaticus* n. sp. occurs in Japan according to the data by YAO (1982) in the uppermost *Canoptum "triassicum"* Zone (above the last occurrence of Rhaetian conodonts) up to the basal *Parahsuum simplex* zone. The range in Japan is therefore Upper Rhaetian (?), Hettangian. In our material *D. eurasiaticus* occurs in the Hettangian part of the Kirchstein Limestone and in the Hettangian Várhegy Cherty Limestone Formation of Csövár (northern Hungary).

Remarks: The other *Droltus* species of our material have tricarinate spines.

***Droltus robustospinosus* n. sp.**

(Pl. 17, fig. 6)

Derivatio nominis: According to the very strong tricarinate apical horn

Holotype: The specimen on pl. 17, fig. 6; rep.-no KoMo 1990 I-15

Material: 7 specimens.

Diagnosis: Multicyrtid. Test in the apical part conical, distally cylindrical, with 5-6 postabdominal segments. Cephalis conical, with very strong, tricarinate apical horn. Thorax, abdomen and proximal postabdominal segments trapezoidal, distal postabdominal segments cylindrical. Cephalis imperforate. Following segments with an inner layer that has 2 rings of pores of different size and shape, but mostly oval or roundish. Pore frames of the outer layer in the proximal part coarse and irregular. In the distal part of the test the pore frames of the outer (and inner) layers are aligned in irregular vertical rows of different length.

Measurements:

Length of the test = 167–193 µm

Maximum width = 80–83 µm

Distribution: Hettangian part of the Kirchstein Limestone at the type locality.

Remarks: *Droltus carinaspinosus* n. sp. displays a conical test and only the last 2 chambers are cylindrical. The outer layer has smaller pore frames in the proximal part of the test and predominantly tetragonal pores in the distal part of the test.

Family **Syringocapsidae** FOREMAN, 1973

Genus **Syringocapsa** NEVIANI, 1900

Type species: *Theosyringium robustum* VINASSA DE REGNY, 1900

***Syringocapsa coliforme* HORI, 1988**

(Pl. 16, fig. 6)

1988 *Syringocapsa coliforme* HORI, n. sp. HORI, p. 556-558, figs. 8/1-10

Distribution: According to HORI (1988) *S. coliforme* occurs in Japan from the Rhaetian up to the Sinemurian. However, it begins in the Kurusu section 22 cm above the last occurrence of Rhaetian conodonts. Therefore it may be restricted to the Hettangian and Sinemurian.

Addendum:

Table 1: Distribution of saturniid stock, without Acanthocircinae.

Table 2: saturniid stock and parasaturniid stock (only Acanthocircinae)

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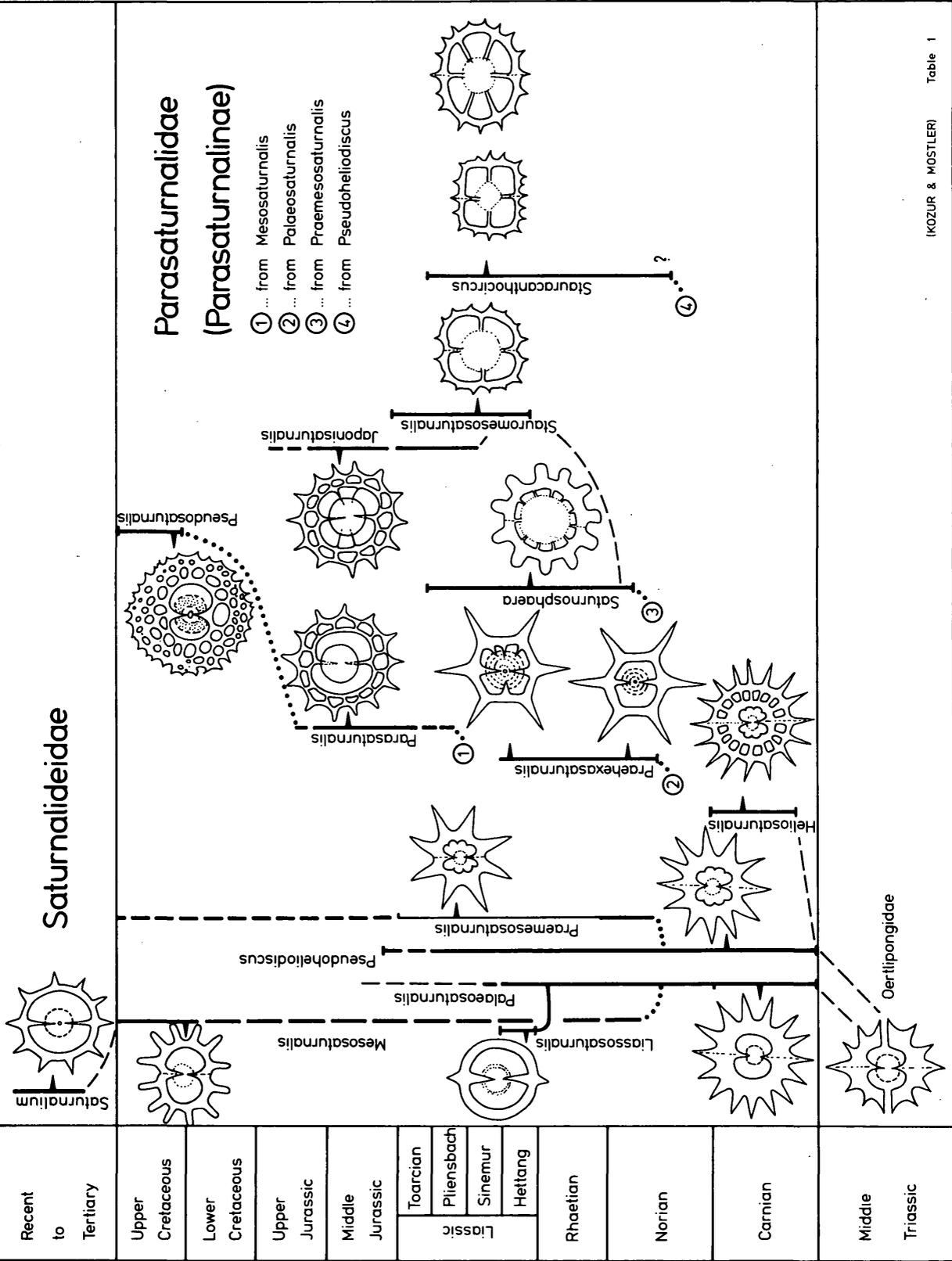
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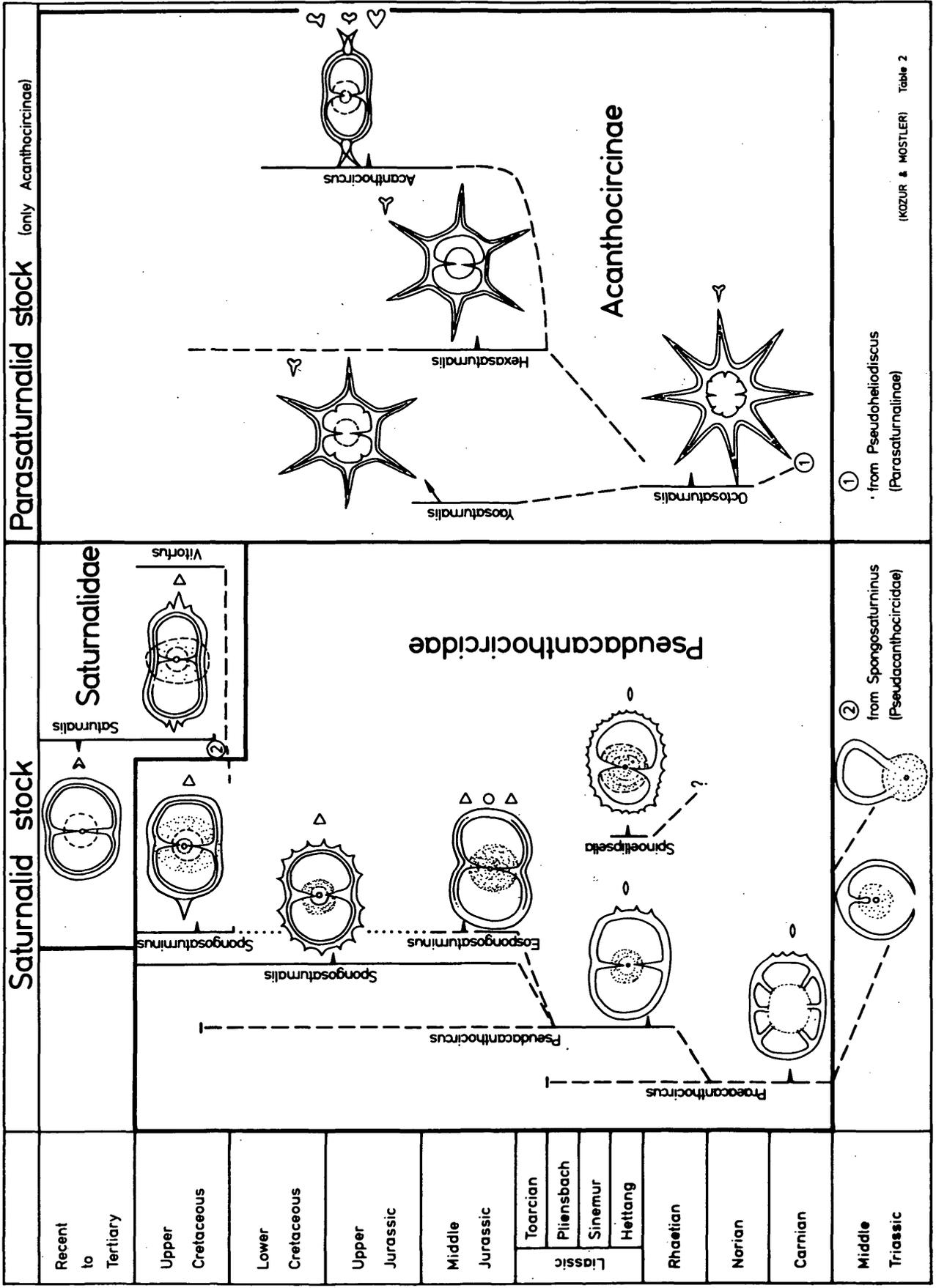
Dr. sc. Heinz KOZUR, Rézsü u. 83, H-1029 Budapest/Hungary; Univ.-Prof. Dr. Helfried Mostler, Institute for Geology and Paleontology, Innsbruck University, Innrain 52, A-6020 Innsbruck/Austria

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Distribution of the Parasaturnalid stock (without Acanthocircinae; see table 2)





Explanation of plates

If not mentioned otherwise, alle figured specimens derived from the type locality of the Kirchstein Limestone at Mt. Kirchstein, 6.5 km WSW of Lenggries/Isar (Bavaria), sample L 1, Kirchstein Limestone, about 1 m above the Rhaetian Dachstein Limestone, Hettangien.

Plate 1

- Fig. 1: *Pseudacanthocircus mocki* n.sp., holotype, x200.
Figs 2, 3: *Palaeosaturnalis liassicus* n.sp., x200, fig. 3: pathologic form with open ring.
Fig. 4: *Spinoellipsella densispinosa* n.gen.n.sp., holotype, x300.
Fig. 5: *Palaeosaturnalis parvispinosus* n.sp., pathologic form with branching of the ring, x300.
Fig. 6: *Liassosaturnalis undulatus* n.gen.n.sp., holotype, x200.
Fig. 7: *Palaeosaturnalis subovalis* n.sp., x200.
Fig. 8: *Palaeosaturnalis* cf. *lenggriesensis* n.sp., x200.
Figs 9, 10: *Palaeosaturnalis rectangularis* n.sp., fig. 9: x200, fig. 10: holotype, x300.

Plate 2

- Fig. 1: *Stauracanthocircus* sp.C, x200.
Fig. 2: *Pseudacanthocircus* ? *laevis* n.sp., x300.
Figs 3, 8: *Pseudoheliodiscus robustospinosus* n.sp., fig. 3: x200, fig. 8: holotype, x300.
Fig. 4: *Spinoellipsella latispinosa* n.gen.n.sp., holotype, x300.
Figs 5, 7: *Stauracanthocircus circularis* n.sp., x200, fig. 5: holotype.
Fig. 6: *Pseudoheliodiscus* n.sp.A, x200.
Fig. 9: *Stauracanthocircus asymmetricus* n.sp., holotype, x200.

Plate 3

- Figs 1, 6: *Stauracanthocircus quadratus* n.sp., x200, fig. 1: pathologic form with open ring.
Fig. 2: *Stauracanthocircus* cf. *transitus* n.sp., x200.
Fig. 3: *Stauromesosaturnalis schizospinosus* n.sp., holotype, x200.
Fig. 4: *Triacanthocircus squinaboli* n.sp., holotype, x200.
Fig. 5: *Stauracanthocircus* sp.B, x300.
Fig. 7: *Stauracanthocircus pessagnoii* n.sp., holotype, x300.
Figs 8, 10: *Stauracanthocircus triangulospinosus* n.sp., x200, fig. 10: holotype.
Fig. 9: *Stauracanthocircus transitus* n.sp., holotype, x200.

Plate 4

- Fig. 1: *Pseudoheliodiscus neviranii* n.sp., holotype (slightly tilted), x150.
Fig. 2: *Pseudoheliodiscus neviranii* n.sp., x150.
Fig. 3: *Liassosaturnalis parvus* n.gen.n.sp., x300.
Fig. 4: *Pseudoheliodiscus inaequispinosus* n.sp., holotype, x250.
Fig. 5: *Pseudoheliodiscus massivus* n.sp., holotype, x300.
Fig. 6: *Liassosaturnalis undulatus* n.gen.n.sp., x250.
Fig. 7: *Liassosaturnalis parvus* n.gen.n.sp., x300.
Fig. 8: *Pseudoheliodiscus robustospinosus* n.sp., x250.
Fig. 9: *Pseudoheliodiscus robustospinosus* n.sp., x300.
Fig. 10: *Pseudoheliodiscus* cf. *robustospinosus*, x200.
Fig. 11: *Pseudoheliodiscus robustospinosus* n.sp., x250.
Fig. 12: *Liassosaturnalis parvus* n.gen.n.sp., holotype, x300.

Plate 5

- Fig. 1: *Pseudoheliodiscus alpinus* n.sp., holotyp), x250.
Fig. 2: *Liassosaturnalis undulatus* n.gen.n.sp., x250.
Fig. 3: *Pseudoheliodiscus alpinus* n.gen.n.sp., x200 (specimen with four large auxiliary spines, diagonally arranged against the polar spine, homoeomorph form with *Stauracanthocircus* KOZUR & MOSTLER, 1983 emend., but clearly distinguished by the big shell).
Fig. 4: *Liassosaturnalis undulatus* n.gen.n.sp. (pathologic form), x200.
Fig. 5: *Pseudoheliodiscus alpinus* n.sp. (with four large auxiliary spines), x200.
Fig. 6–9: *Pseudoheliodiscus alpinus* n.sp., x200.
Fig. 10: *Pseudoheliodiscus robustospinosus*, x200.
Fig. 11, 12: *Pseudoheliodiscus alpinus* n.sp, x200.

Plate 6

- Fig. 1: *Praehexasaturnalis germanicus* n.sp., x200.
Fig. 2: *Praehexasaturnalis germanicus* n.sp., holotype, x200.
Fig. 3: *Liassosaturnalis undulatus* n.gen.n.sp., x300.
Fig. 4: *Praehexasaturnalis kirchsteinensis* n.sp., x200.
Fig. 5: *Praehexasaturnalis kirchsteinensis* n.gen.n.sp., holotype, x250.
Fig. 6: *Liassosaturnalis parvus* n.sp., x300.
Fig. 7: *Praehexasaturnalis kirchsteinensis* n.sp., x200.
Fig. 8, 9: *Praehexasaturnalis tetraradiatus* n.sp., x200.
Fig. 10: *Stauracanthocircus ruesti* n.sp., x200.
Fig. 11: *Praehexasaturnalis tetraradiatus* n.sp., holotype, x200.
Fig. 12: *Praehexasaturnalis tetraradiatus* n.sp., x250.

Plate 7

- Fig. 1: *Stauracanthocircus ruesti* n.sp., holotype, x200.
Fig. 2: *Stauracanthocircus ? hettangicus* n.sp., holotype, x200.
Fig. 3: *Stauracanthocircus* cf. *ruesti*, x250.
Fig. 4: *Stauracanthocircus circularis* n.sp., x200.
Fig. 5: *Stauracanthocircus triangulospinosus* n.sp., x250.
Fig. 6: *Stauracanthocircus transitus* n.sp., x200.
Fig. 7: *Stauracanthocircus ? hettangicus* n.sp., x200.
Fig. 8: *Stauracanthocircus poetschensis* n.sp. (POM 6/7), x300.
Fig. 9: *Stauracanthocircus transitus* n.sp., x200.

Plate 8

- Fig. 1: *Stauracanthocircus ? poetschensis* n.sp., holotype (POM 6/7, Pötschenwand), x200.
Fig. 2: *Stauracanthocircus quadratus* n.sp., x200.
Fig. 3: *Stauracanthocircus quadratus* n.sp., holotype, x200.
Fig. 4: *Stauracanthocircus ? poetschensis* n.sp. (POM 6/7, Pötschenwand), x250.
Fig. 5: *Stauracanthocircus quadratus* n.sp., x200.
Fig. 6: *Stauracanthocircus* sp.A, x200.
Fig. 7–9: *Stauracanthocircus asymmetricus* n.sp., x200.
Fig. 10: Deformed *Stauracanthocircus asymmetricus* n.sp., x200.

Plate 9

- Fig. 1–4,
7, 10, 12: *Stauracanthocircus asymmetricus* n.sp., x200.
Fig. 5: *Stauracanthocircus* cf. *asymmetricus* n.sp., x200.
Fig. 6: *Palaeosaturnalis haeckeli* n.sp., holotype, x200.
Fig. 8: *Palaeosaturnalis haeckeli* n.sp., holotype, x200.
Fig. 9: *Palaeosaturnalis blomei* n.sp., x300.
Fig. 11: *Triacanthocircus muelleri* n.gen.n.sp., x200.

Plate 10

- Fig. 1: *Octosaturnalis carinatus* n.gen.n.sp., holotype (Ptx1), x150.
Fig. 2: *Pseudacanthocircus terminospinosus* n.gen.n.sp., holotype, x200.
Fig. 3, 4: *Octosaturnalis carinatus* n.gen.n.sp., holotype (Ptx1, Pötschen road), x400.
Fig. 5: *Triacanthocircus muelleri* n.gen.n.sp., x200.
Fig. 6: *Pseudacanthocircus mediospinosus* n.gen.n.sp., x200.
Fig. 7: *Triacanthocircus muelleri* n.gen.n.sp., holotype, x200.
Fig. 8: *Pseudacanthocircus mediospinosus* n.gen.n.sp., holotype, x200.
Fig. 9: *Pseudacanthocircus mocki* n.gen.n.sp., x200.
Fig. 10: *Triacanthocircus muelleri* n.gen.n.sp., x200.

Plate 11

- Fig. 1: *Pseudacanthocircus terminospinosus* n.gen.n.sp., x250.
Fig. 2: *Pseudacanthocircus pseudosimplex* n.gen.n.sp., holotype, x200.
Fig. 3: *Spinoellipsella densispinosa* n.gen.n.sp., x300.
Fig. 4: *Pseudacanthocircus terminospinosus* n.sp., x300.
Fig. 5: *Spinoellipsella densispinosa* n.sp., x300.
Fig. 6: *Pseudacanthocircus baumgartneri* n.gen. sp., holotype, x300.
Fig. 7: *Pseudacanthocircus troegeri* n.gen.n.sp., holotype, x200.
Fig. 8: *Pseudacanthocircus laevis* n.gen.n.sp., holotype, x300.
Fig. 9: Pathologic *Pseudosaturnalis schaaafi* n.sp., x200.
Fig. 10: *Palaeosaturnalis* cf. *schaaafi* n.sp., x200.
Fig. 11: *Palaeosaturnalis schaaafi* n.sp., holotype, x200.
Fig. 12: *Palaeosaturnalis schaaafi* n.sp., x200.
Fig. 13: *Palaeosaturnalis* cf. *schaaafi*, x200.

Plate 12

- Fig. 1, 3, 6, 8–10: *Palaeosaturnalis liassicus* n.sp., x200, fig. 9: holotype.
Fig. 2: Pathologic *Palaeosaturnalis schaaafi* n.sp., with obtuse angle between the two polar spines, x200.
Fig. 4: *Palaeosaturnalis* cf. *liassicus*, x200.
Fig. 5: *Mesosaturnalis* n.sp. (sample POM 6/7 from Pötschenwand, Middle Norian), development of an unspined or very slightly spined narrow ring with axial spine, opposite to an inner polar spine from a form with broad, heavily spined ring and peripolar spine (for explanation see discussion of Saturnaliacea DEFLANDRE, 1953), x300
Fig. 7: *Palaeosaturnalis schaaafi* n.sp., x200.
Fig. 11: *Palaeosaturnalis* cf. *schaaafi*, x200.

Plate 13

- Fig. 1, 2: *Palaeosaturnalis liassicus* n.sp., x200.
Fig. 3: *Palaeosaturnalis parvispinosus* n.sp., holotype, x250.
Fig. 4: *Palaeosaturnalis subovalis* n.sp., holotype, x250.
Fig. 5: *Palaeosaturnalis parvispinosus* n.sp., x250.
Fig. 6: Pathologic *Palaeosaturnalis liassicus* n.sp. with obtuse angle between the polar spines and ring deformation, x200.
Fig. 7: Pathologic *Palaeosaturnalis liassicus* n.sp. with obtuse angle between the polar spines and ring deformation. Additionally two fragile auxiliary spines evolved for stabilization of the asymmetric polar ring system, x180.
Fig. 8: *Palaeosaturnalis parvispinosus* n.sp., x200.
Fig. 9: Pathologic form of *Palaeosaturnalis subovalis*, x300.
Fig. 10: *Palaeosaturnalis lenggriesensis* n.sp., x200.
Fig. 11: *Palaeosaturnalis lenggriesensis* (holotype), x250.

Plate 14

- Fig. 1: *Palaeosaturnalis parvispinosus* n.sp., x200.
Fig. 2: "*Palaeosaturnalis fragilis*" n.sp., x200.
Fig. 3: "*Palaeosaturnalis fragilis*" n.sp., holotype, x150.
Fig. 4: *Betraccium bavaricum* n.sp., holotype, x250.
Fig. 5: *Betraccium hettangicum* n.sp., holotype, x300.
Fig. 6: *Betraccium inaequiporatum*, holotype, x250.
Fig. 7: *Betraccium verticispinosum* n.sp., x300.
Fig. 8: *Betraccium verticispinosum*, holotype, x250.
Fig. 9: *Betraccium bavaricum* n.sp., x250.
Fig. 10: *Ellipsoxiphus tanuensis* (PESSAGNO & BLOME, 1980), x350.
Fig. 11: *Ellipsoxiphus cf. tanuensis* (PESSAGNO & BLOME, 1980), x350.
Fig. 12: *Ellipsoxiphus suessi* (DUNIKOWSKI, 1882), x300.
Fig. 13: *Ellipsoxiphus cf. danaensis* (PESSAGNO & BLOME, 1980), x300.
Fig. 14: *Ellipsoxiphus cf. browni* (PESSAGNO & BLOME, 1980), x350.

Plate 15

- Fig. 1: *Crucella prisca* n.sp., x250.
Fig. 2: *Crucella carteri* n.sp., x250.
Fig. 3: *Crucella prisca* n.sp., x200.
Fig. 4: *Crucella carteri* n.sp., holotype, x300.
Fig. 5: *Crucella prisca* n.sp., x200.
Fig. 6: *Paronaella striata* n.sp., holotype, x250.
Fig. 7: *Crucella hettangica* n.sp., holotype, x250.
Fig. 8: *Crucella cf. prisca* n.sp., x250.
Fig. 9: *Crucella cf. carteri* n.sp., x200.
Fig. 10: *Crucella prisca* n.sp. (holotype), x250.
Fig. 11: *Ellipsoxiphus cf. browni* (PESSAGNO & BLOME, 1980), x300.
Fig. 12, 13: *Ellipsoxiphus suessi* (DUNIKOWSKI, 1882), fig. 12: x350, fig. 13: x300.
Fig. 14: *Ellipsoxiphus browni* (PESSAGNO & BLOME, 1980), x300.
Fig. 15: *Ellipsoxiphus cf. danaensis* (PESSAGNO & BLOME, 1980), x300.

Plate 16

- Fig. 1, 4, 7, 10: *Relanus hettangicus* n.sp., x300.
Fig. 2: *Relanus multiperforatus* n.sp. (apical horn on the backside of the specimen and therefore not well visible), x250.
Fig. 3: *Relanus multiperforatus* n.sp., holotype, x250.
Fig. 5: *Relanus hettangicus* n.sp. (photo from the direction of excentric apical horn), x300.
Fig. 6: *Syringocapsa coliforme* HORI, 1988, x300.
Fig. 8: *Relanus striatus* n.sp., x300.
Fig. 9: *Relanus striatus* n.sp. (recrystallized specimen), x300.
Fig. 11: *Relanus hettangicus* n.sp., x200.
Fig. 12: *Gorgansium alpinum* n.sp., holotype, x300.
Fig. 13: *Gorgansium blomei* n.sp., holotype, x400.
Fig. 14: *Relanus hettangicus* n.sp., x500.
Fig. 15: *Xenorum jurassicum* n.sp., holotype, x250.

Plate 17

- Fig. 1: *Parahsuum primitivum* n.sp., holotype, x350.
Fig. 2: *Parahsuum simplum* YAO 1982, x300.
Fig. 3: *Droltus eurasiaticus* n.sp., holotype, x300.
Fig. 4: *Droltus eurasiaticus* n.sp., x300.
Fig. 5: *Droltus carinaspinosus* n.sp., holotype, x300.
Fig. 6: *Droltus robustospinosus* n.sp., holotype, x300.
Fig. 7, 9, 10: *Paracanoptum primitivum* n.sp., x300.
Fig. 8: *Relanus hettangicus* n.sp., x300. (Photo from the opposite direction of apical horn, that is not visible)
Fig. 11: *Paracanoptum* cf. *primitivum* n.sp., x350.
Fig. 12: *Paracanoptum primitivum* n.sp., holotype, x300.
Fig. 13: *Paracanoptum primitivum* n.sp., x350.
Fig. 14: *Relanus hettangicus* n.sp., x250.
- Fig. 15: *Relanus hettangicus* n.sp., x200.
Fig. 16: *Relanus hettangicus*, holotype, x300.
Fig. 17: *Relanus striatus* n.sp., holotype, x200.
Fig. 18: *Relanus striatus* n.sp. (holotype), x300.
Fig. 19: *Relanus longus* n.sp. (holotype), x300.

Plate 1

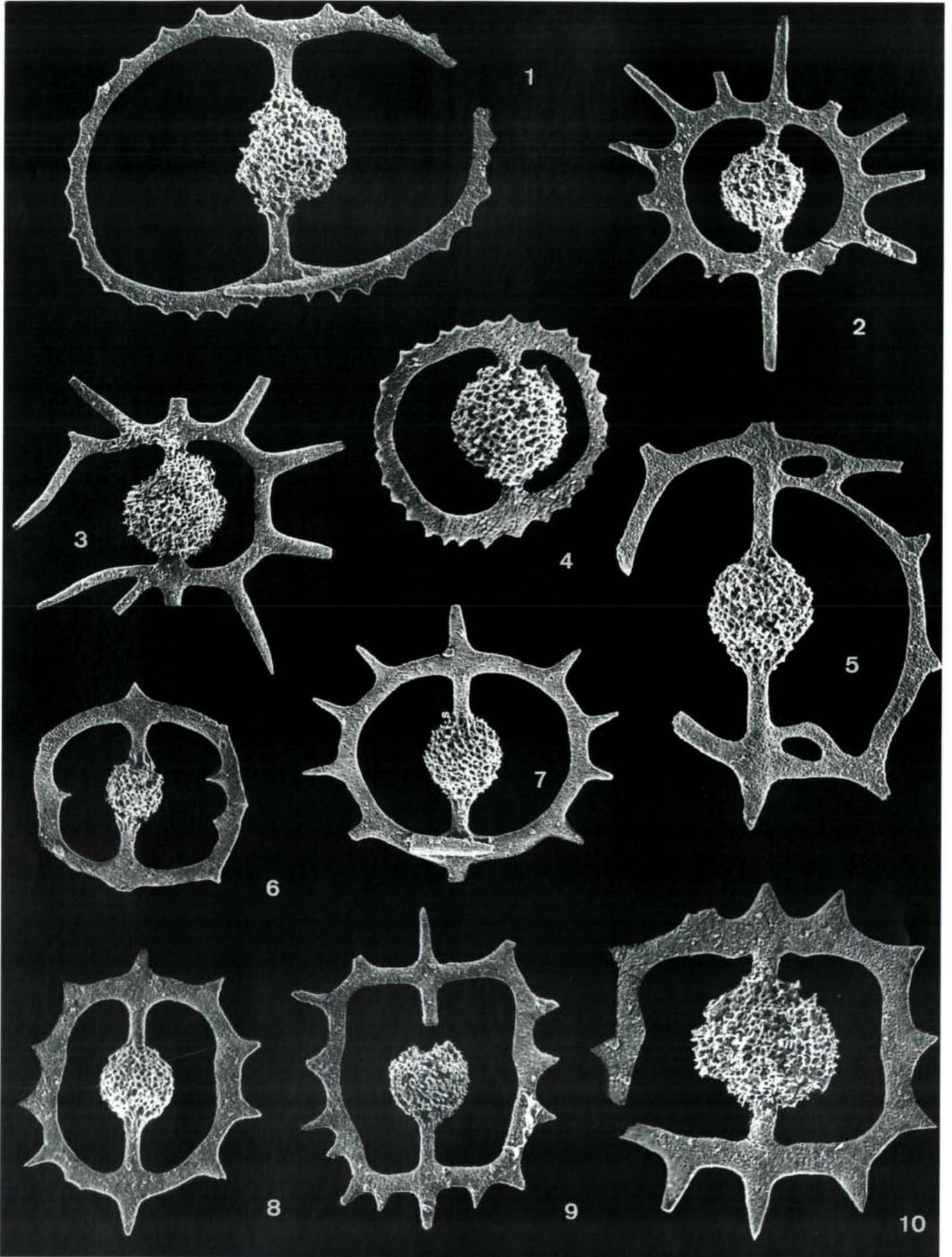


Plate 2

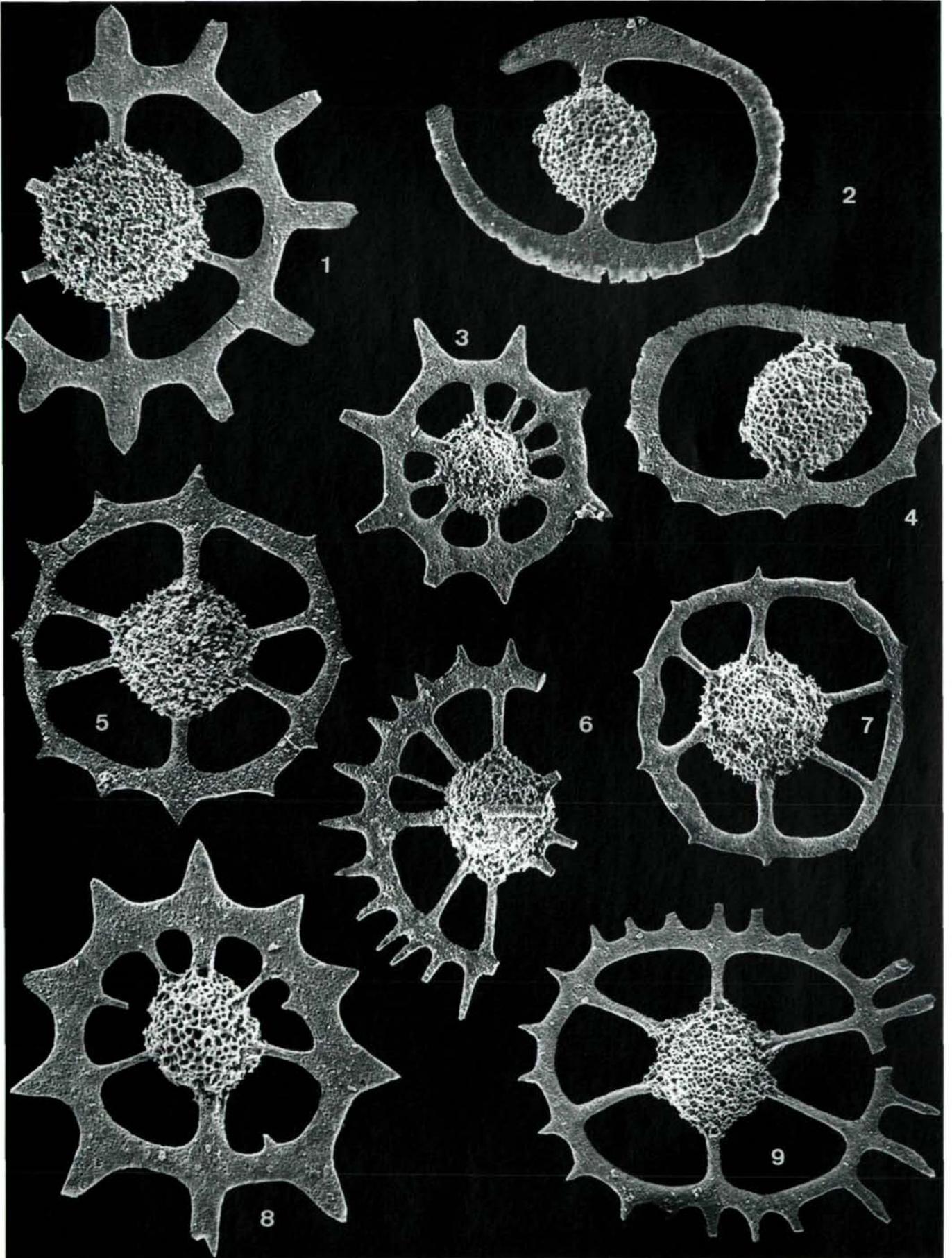


Plate 3

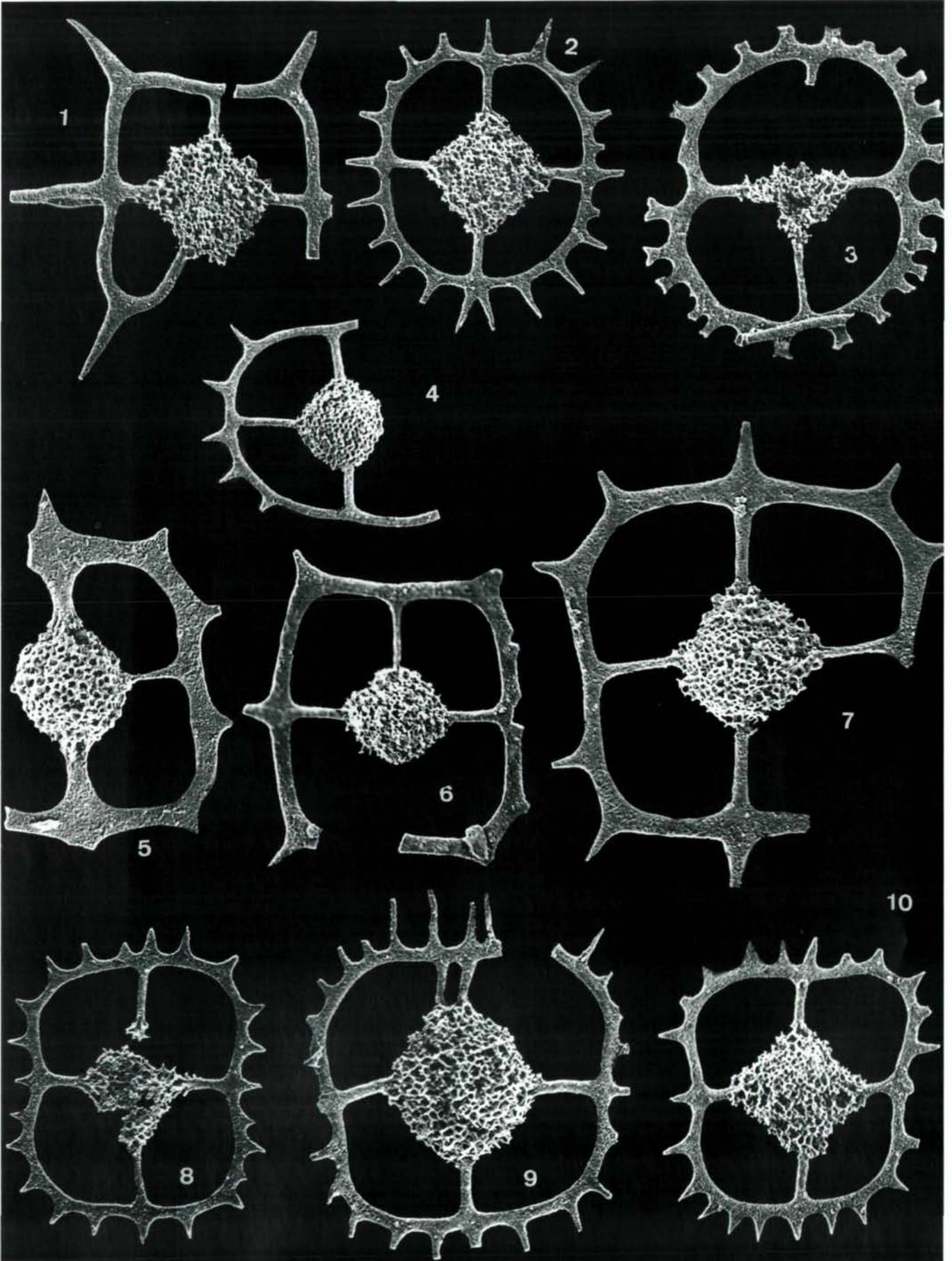


Plate 4

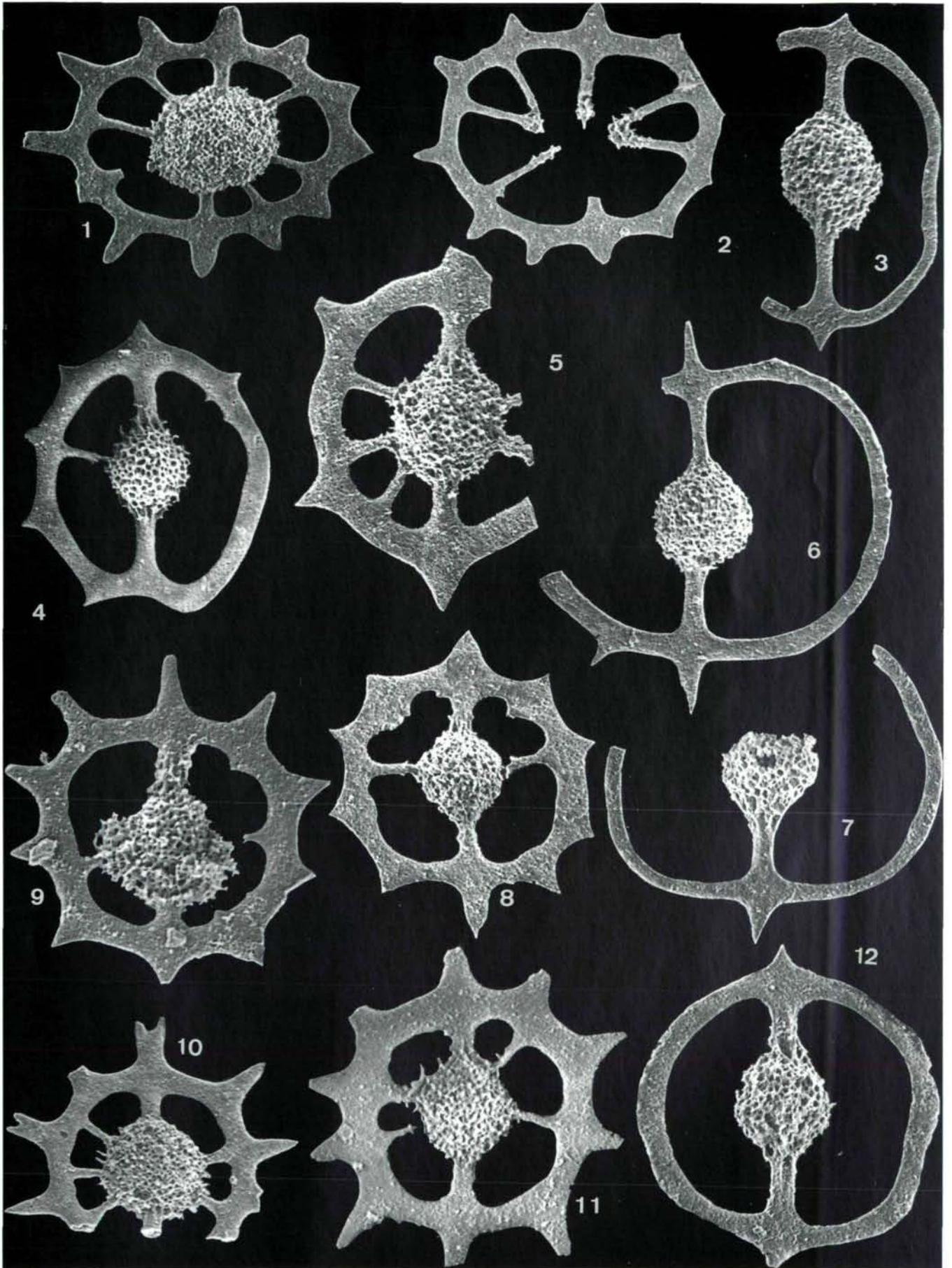


Plate 5

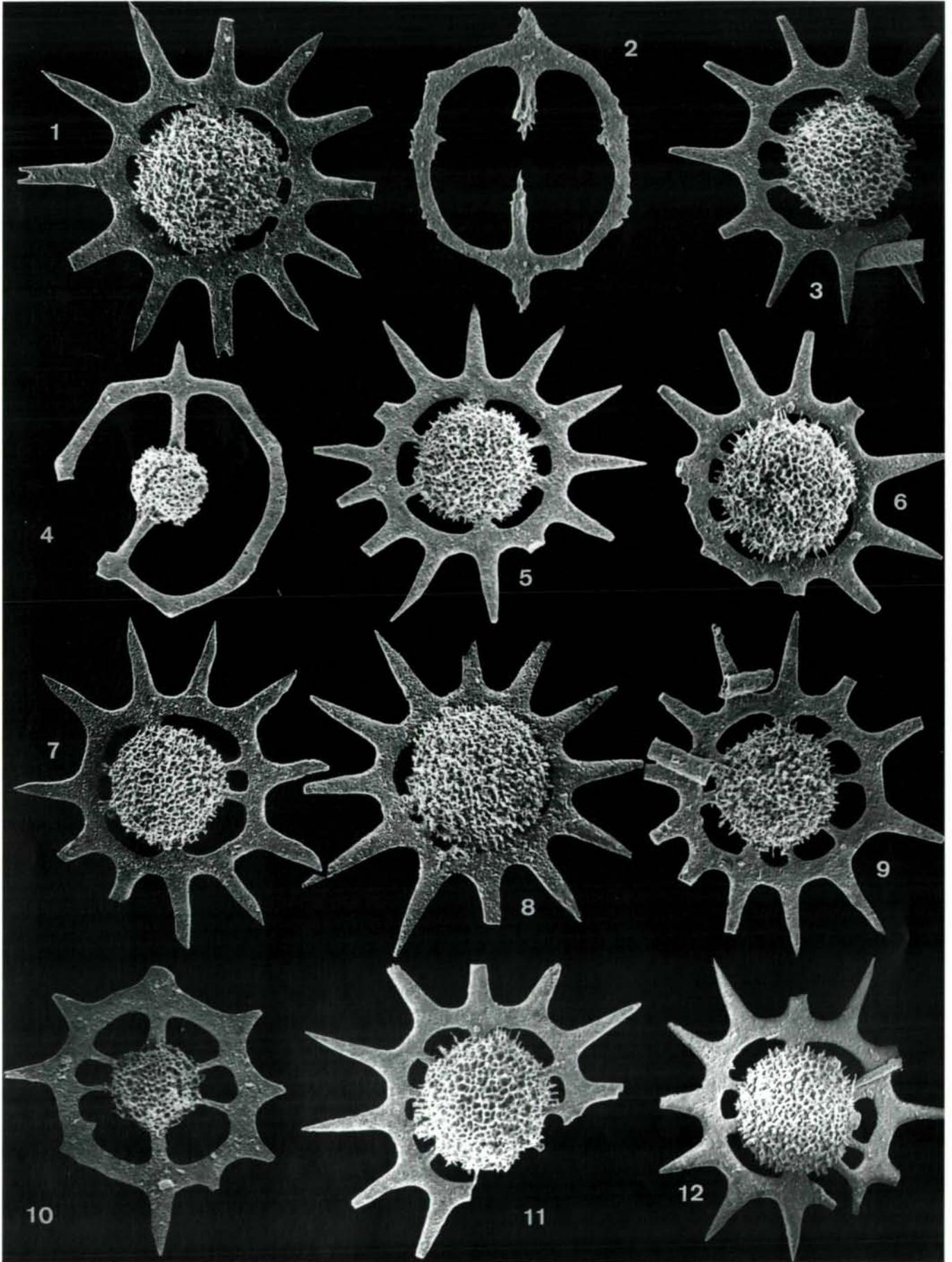


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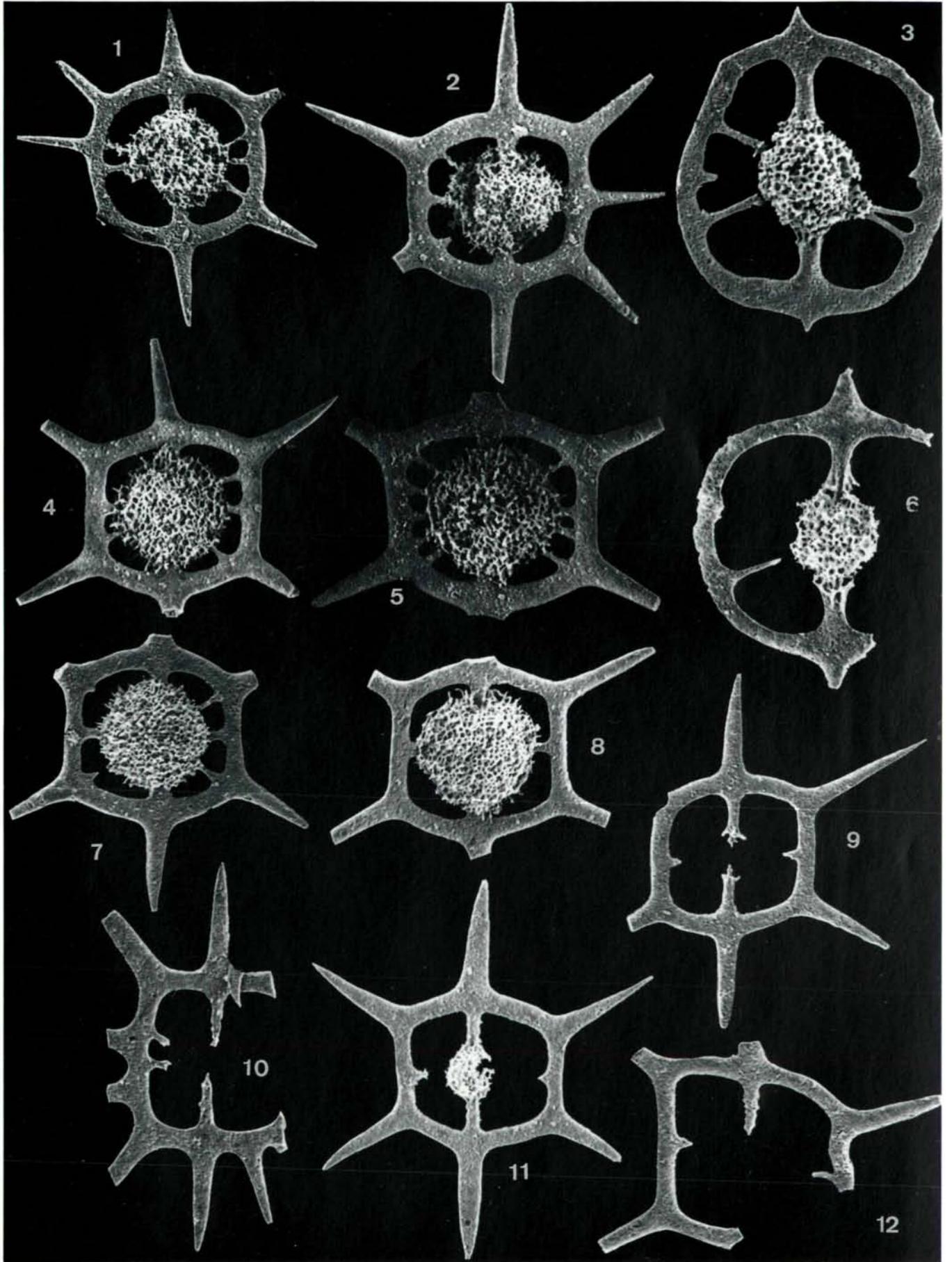


Plate 7

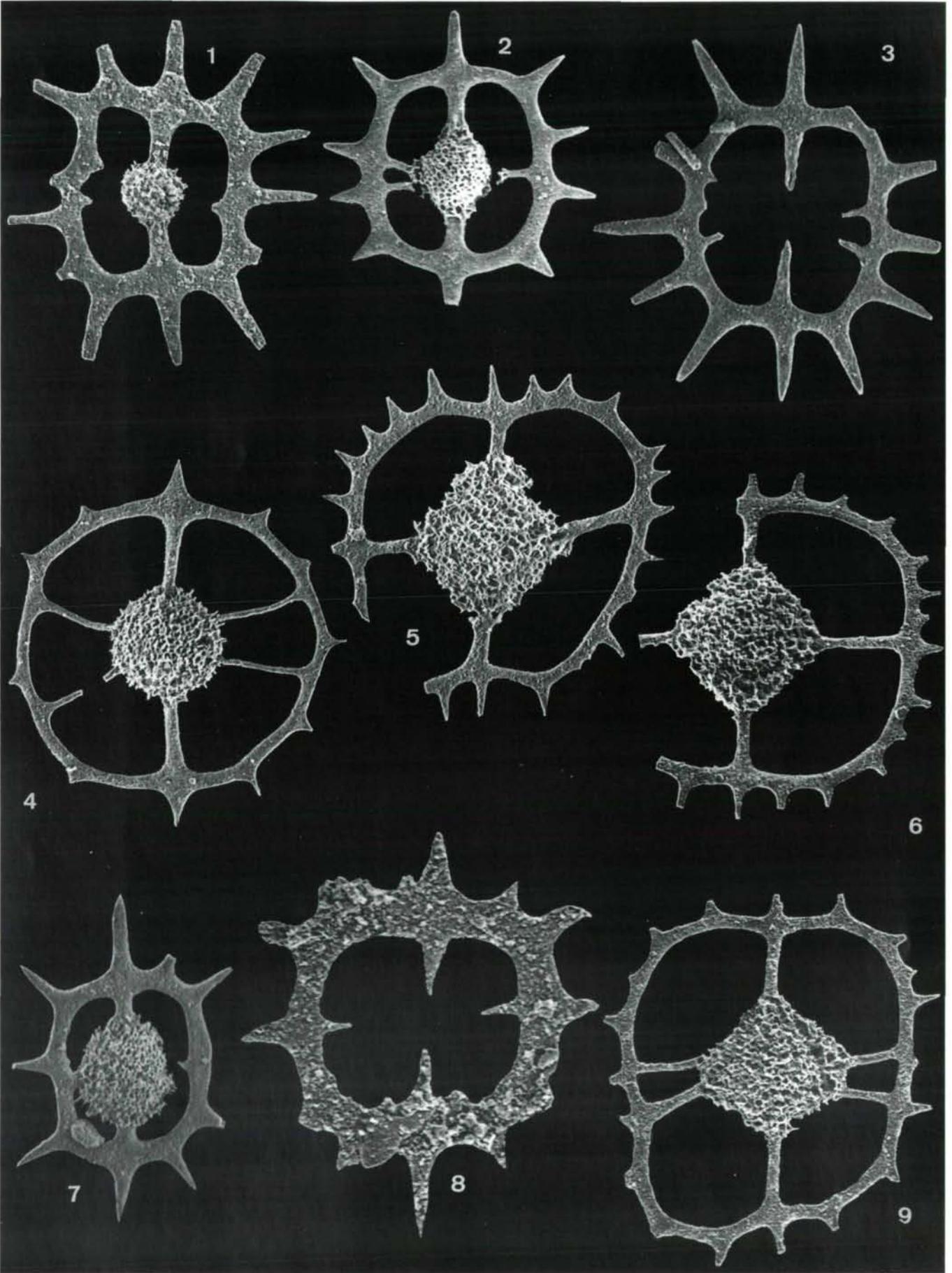


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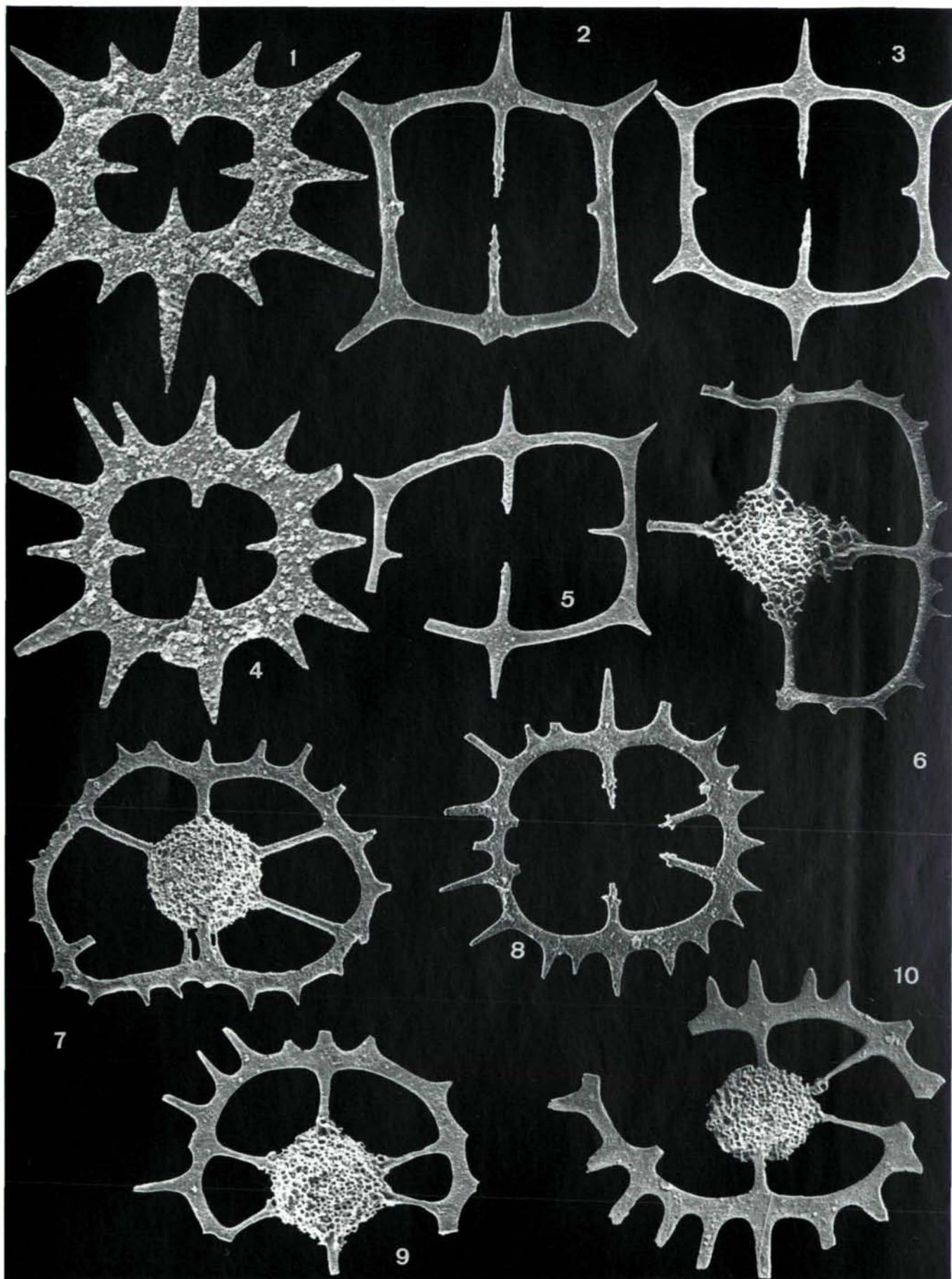


Plate 9

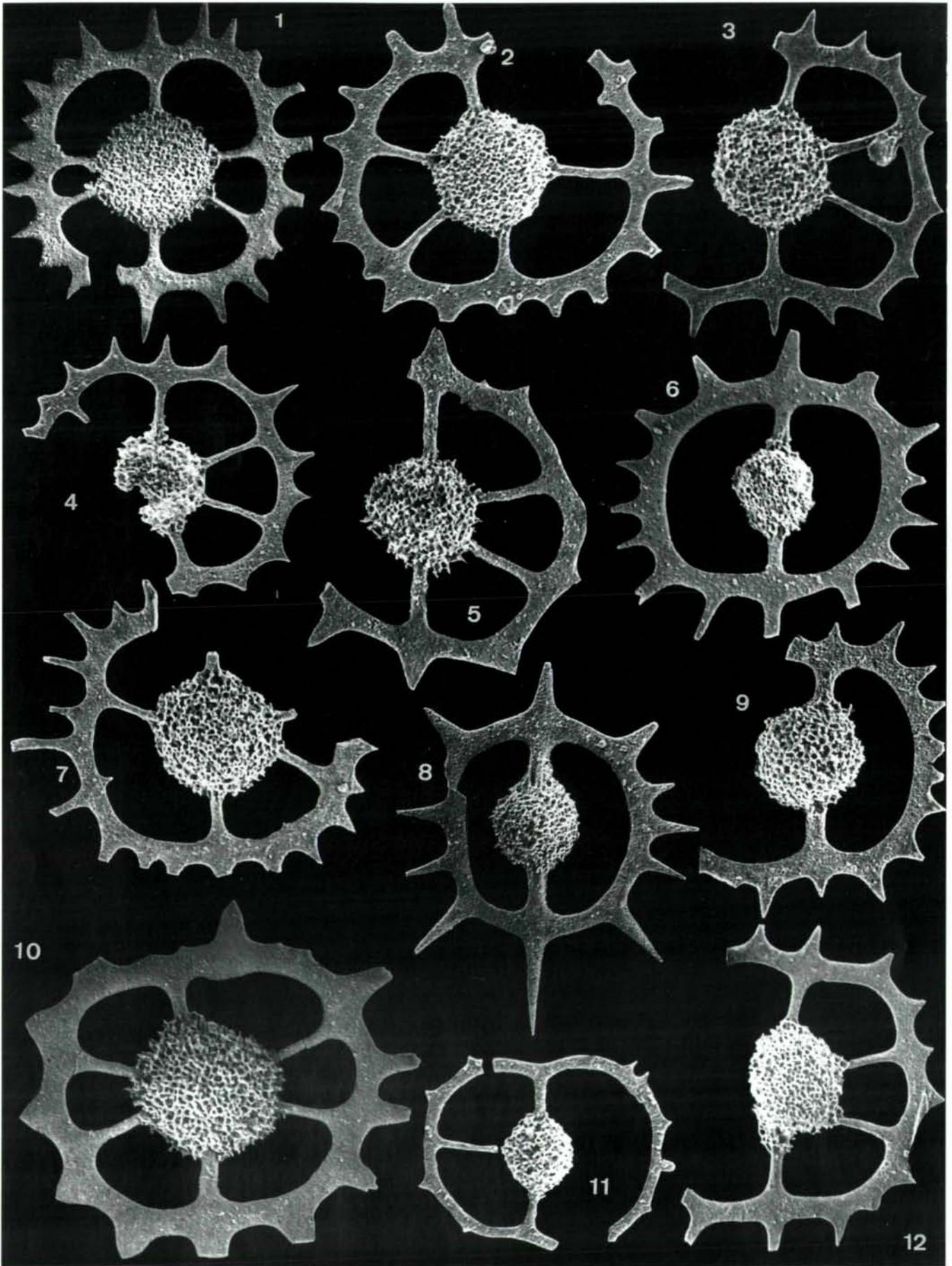


Plate 10

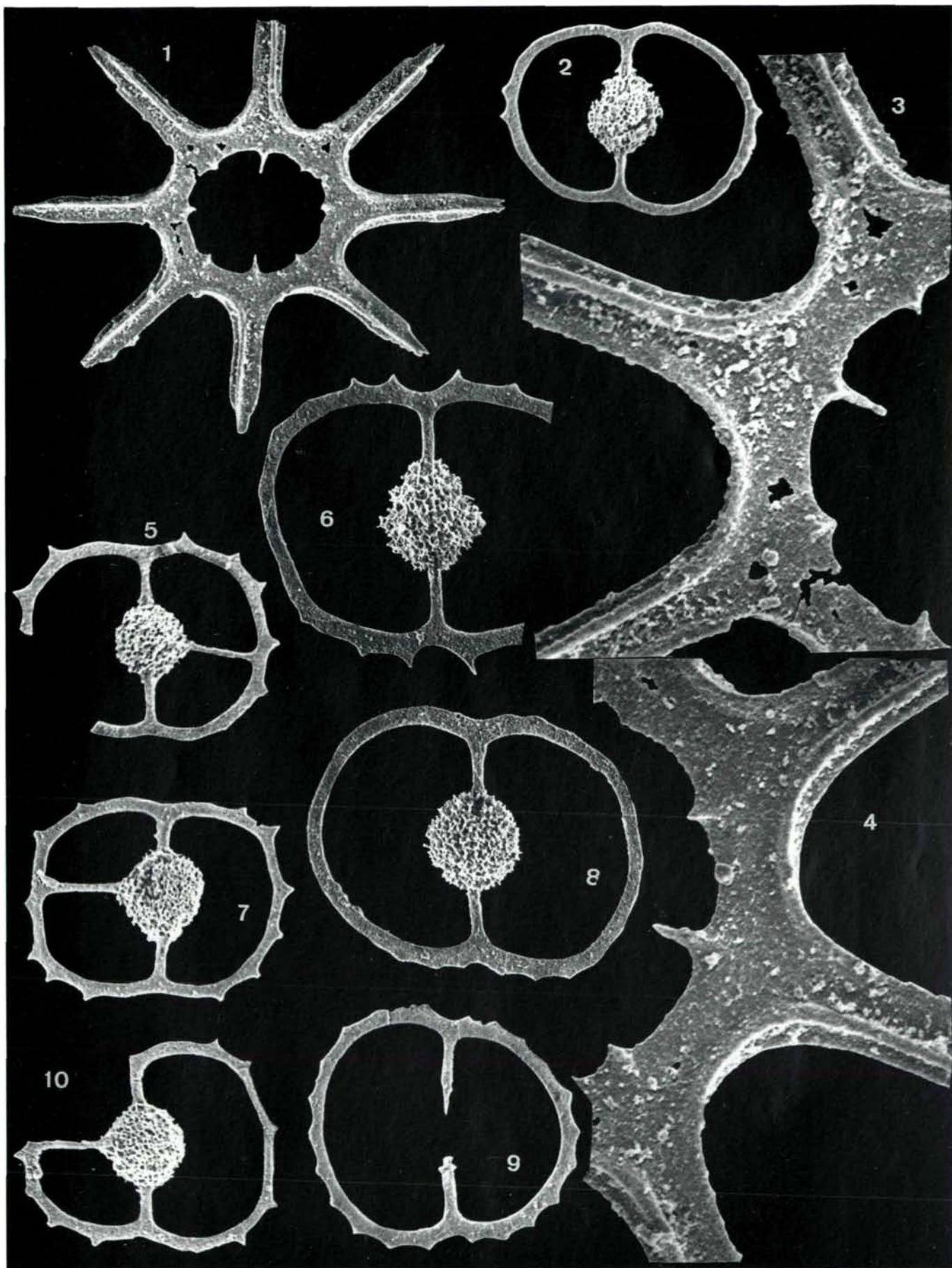


Plate 11

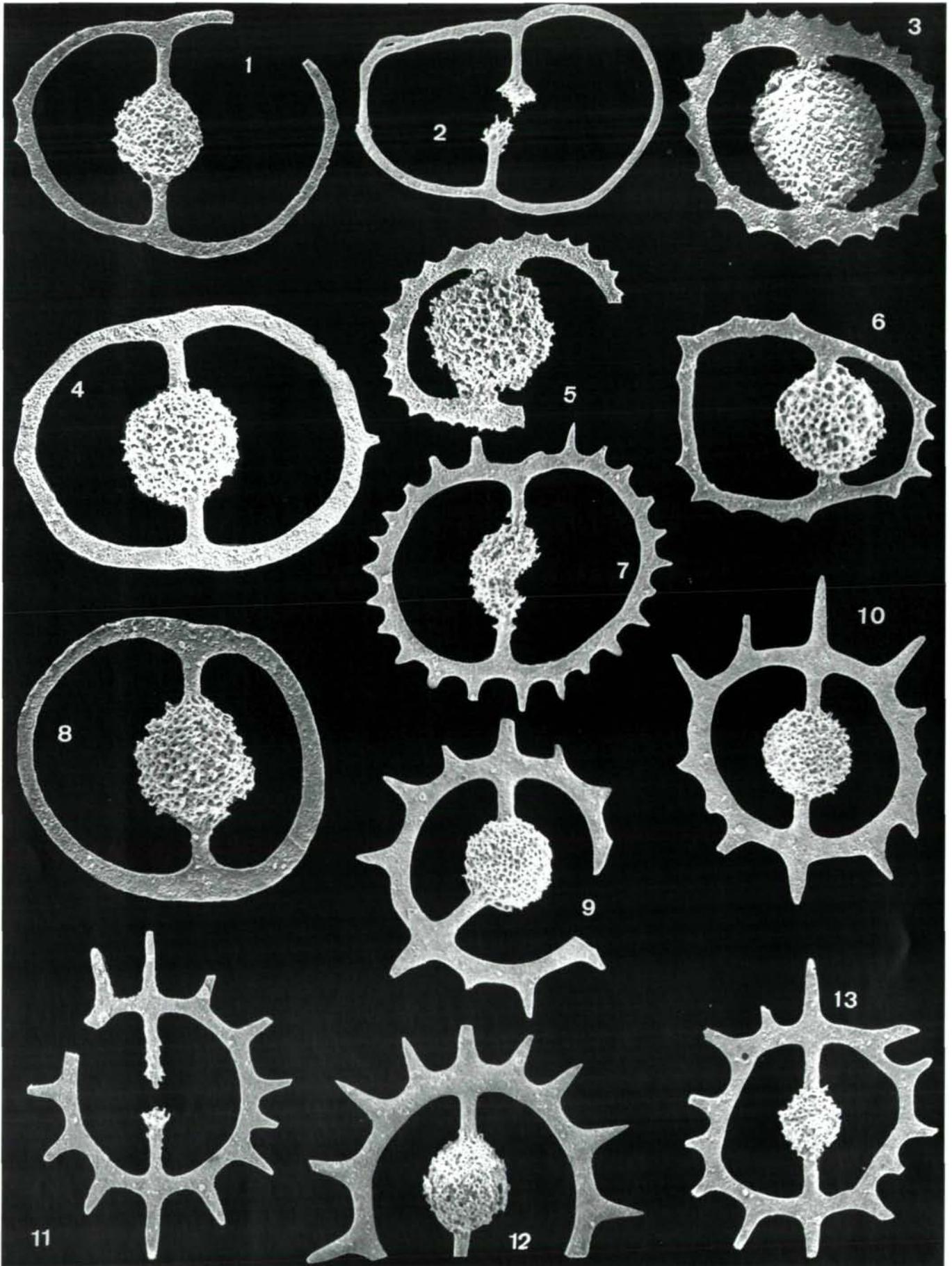


Plate 12

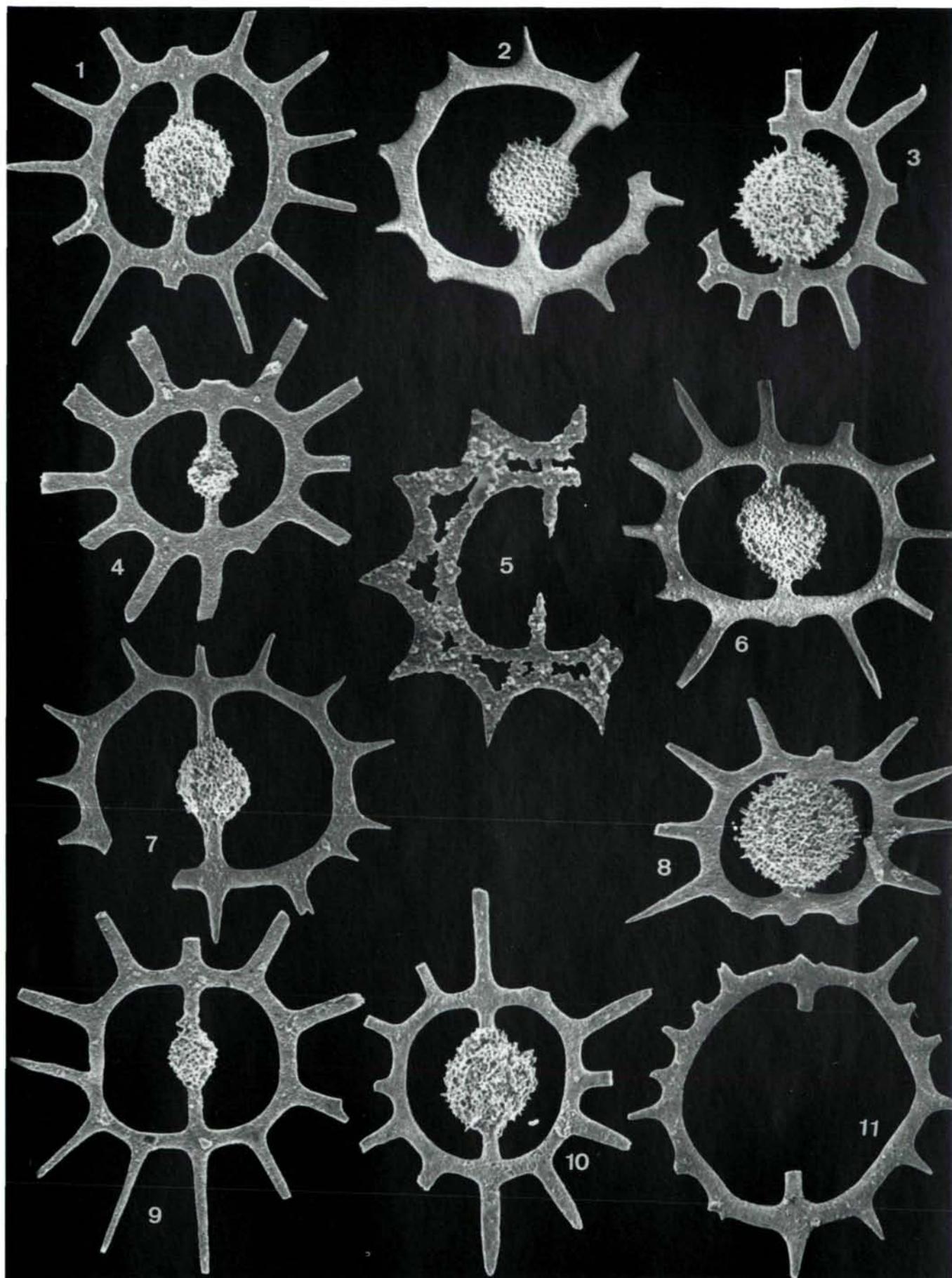


Plate 13

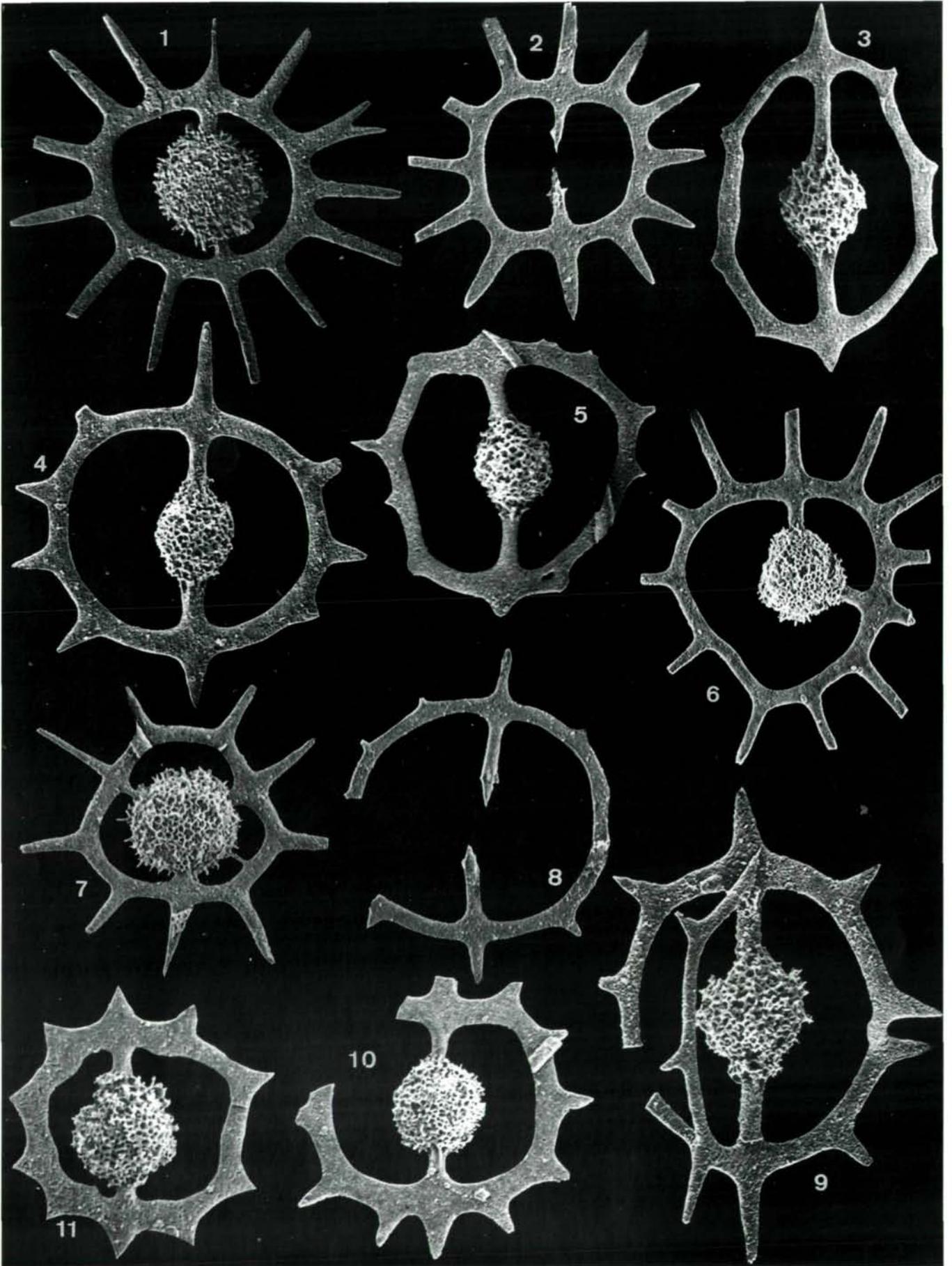


Plate 14

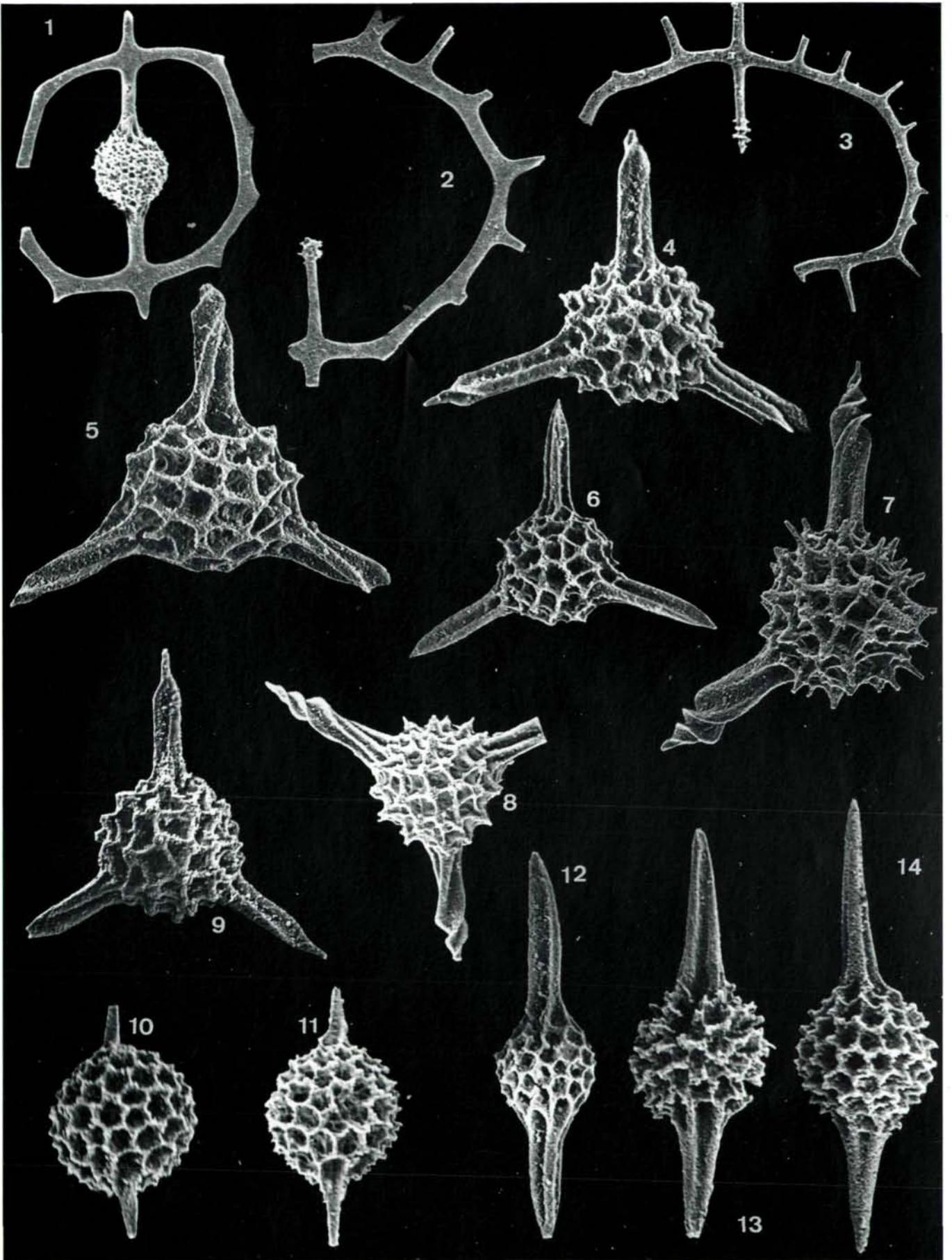


Plate 15

