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Early Tithonian Saturnalidae (Radiolaria) from the Solnhofen area (Southern Franconian Alb, southern Germany)

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with 15 figures

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Abstract: In order to complete the study of the very rich early Tithonian (*Hybonoticeras hybonotum* Zone) radiolarian fauna from the Mühlheim Member of the Mörnsheim Formation outcropping in the Solnhofen area, the taxa of the family Saturnalidae are described. Although rather rare, the Saturnalidae of this member contain 14 species, ten of which are new. These species belong to four genera, one of which is new (*Moebicircus* n. gen.), and two subfamilies (Hexasaturnalinae and Saturnalinae). The taxonomy at generic level of these late Jurassic radiolarians is founded on the basis of the position of the blades along the ring and number and morphology of the spines. Type of spines (simple or forked) has either species level value or none, depending on species. Special attention was given to anomalies, which sometimes are rather frequent, since they can give information of paleobiological and paleoecological orders. Among them frequent cases of open ring and additional spines with *Dicerosaturnalis* and Siamese twins skeletons with *Spongosaturninus* and *Dicerosaturnalis* are to be noted. The authors hope that this new taxonomy will give a better image of the evolution and radiation of the Saturnalidae during the Tithonian.

Keywords: Radiolaria • Saturnalidae • Taxonomy • Tithonian • Solnhofen • Southern Germany

Kurzfassung: Die Radiolarien-Taxa der Familie Saturnalidae aus dem Unteren Tithon des Mühlheim-Members (Mörnsheim-Formation) aus der Umgebung von Solnhofen werden beschrieben. Sie vervollständigen damit die Studie über die sehr reiche Radiolarien-Fauna der *Hybonoticeras hybonotum*-Zone. Obwohl die Saturnalidae innerhalb des Mühlheim-Members recht selten sind, können 14 Arten (davon 10 neue) dieser Familie zugeteilt werden. Diese 14 Arten wiederum gehören zu vier Gattungen (darunter *Moebicircus* n. gen.) und zu zwei Unterfamilien (Hexasaturnalinae und Saturnalinae). Die taxonomische Einordnung dieser spätjurassischen Radiolarien auf der Gattungsebene basiert auf der Position der Leisten auf dem Ring und der Anzahl und Morphologie der Stacheln. Die Form der Stacheln (einfach oder gegabelt) ist, je nach Art, von kleinerer oder größerer Bedeutung. Besondere Aufmerksamkeit gehört den ziemlich häufig vorkommenden Anomalien. Sie liefern Informationen über die paläobiologische und die paläoökologische Zuordnung. Häufig sind Fälle mit offenen Ringen und zusätzlichen Stacheln (*Dicerosaturnalis*) und siamesische Zwillingsskelette von *Spongosaturninus* und *Dicerosaturnalis*. Die Autoren hoffen, mit dieser neuen taxonomischen Einteilung zu einem besseren Bild über die Evolution und die Verbreitung der Saturnalidae während des Tithoniums beitragen zu können.

Schlüsselwörter: Radiolaria • Saturnalidae • Taxonomie • Tithonium • Solnhofen • Süddeutschland

Introduction

Following the discovery of the highly diverse and well-preserved radiolarian fauna from the early Tithonian Mühlheim Member of the Mörnsheim Formation in the Solnhofen area (ZÜGEL 1997), the present authors started its taxonomic study in 1998. In three previous papers (DUMITRICA & ZÜGEL 1998, 2002, 2003) we described all mono- and dicyrtid nassellarians with widely open aperture and an interesting genus with hagiastrid medullary shell and spherical cortical shell. In the present paper we describe all saturnalid radiolarian species occurring in this fauna that contains more than 550 species and is the richest and best-preserved early Tithonian ra-

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diolarian fauna so far known. Its very high diversity contradicts the data so far published (BAUMGARTNER et al. 1995; DANELIAN & JOHNSON 2001) that show a decline of radiolarian diversity during the Kimmeridgian and early Tithonian and a spectacular increase of the number of first appearances in the late Tithonian close to the Jurassic-Cretaceous boundary. It proves doubtlessly the incompleteness of the fossil record and its dependence on the preservation factor as well as our erroneous conclusions regarding the rates of evolution and extinction of radiolarian species during the Tithonian.

As many other groups of radiolarians the Saturnalidae of the Tithonian are only partly known. The greatest part of our knowledge about them come from the works of some authors among whom are to be mentioned SQUINABOL (1914), DONOFRIO & MOSTLER (1978), YANG (1993), JUD (1994), BAUMGARTNER et al. (1995), HULL (1997), KIESSLING (1999), to cite only some of the most important contributions. Their taxonomy especially is insufficiently founded, resulting in the assignation of almost all species to a single genus – *Acanthocircus* SQUINABOL. The problem with almost all these contributions is that they took into account in taxonomy especially the shape of the ring and number of spines but not the structure of the ring. Fossil record suggests that the ring structure (bladed or not and number and position of blades) and number of spines are among the most important taxonomic elements. Based on these elements, in this paper we found it necessary to split the long-ranged genus *Acanthocircus* into several genera. The result is another image on the evolutionary trends and radiation of the Saturnalidae during the latest Jurassic.

Geological setting

In southern Germany, the late Jurassic deposits crop out as a wide arch on the northern rim of the Suabian and Franconian Alb. They are covered by the Tertiary Molasse to the southeast and bordered by the Bohemian Massif in the northeast. The Tithonian deposits form the top of this Jurassic series and are generally represented by massive sponge-algal limestones interfingering with bedded limestones (MEYER & SCHMIDT-KALER 1989; BARTHEL et al. 1990). Paleogeographic reconstruction of this area (MEYER & SCHMIDT-KALER 1989) shows continental areas to the northwest ("Rheinisches Land" or "Mitteldeutsche Schwelle") and to the east (Bohemian Massif), and shallow marine basins to the southwest. These basins were separated from each other and from the Helvetian Basin of the northern Tethyan Realm by sponge-algal mounds, coral reefs, and carbonate shoals.

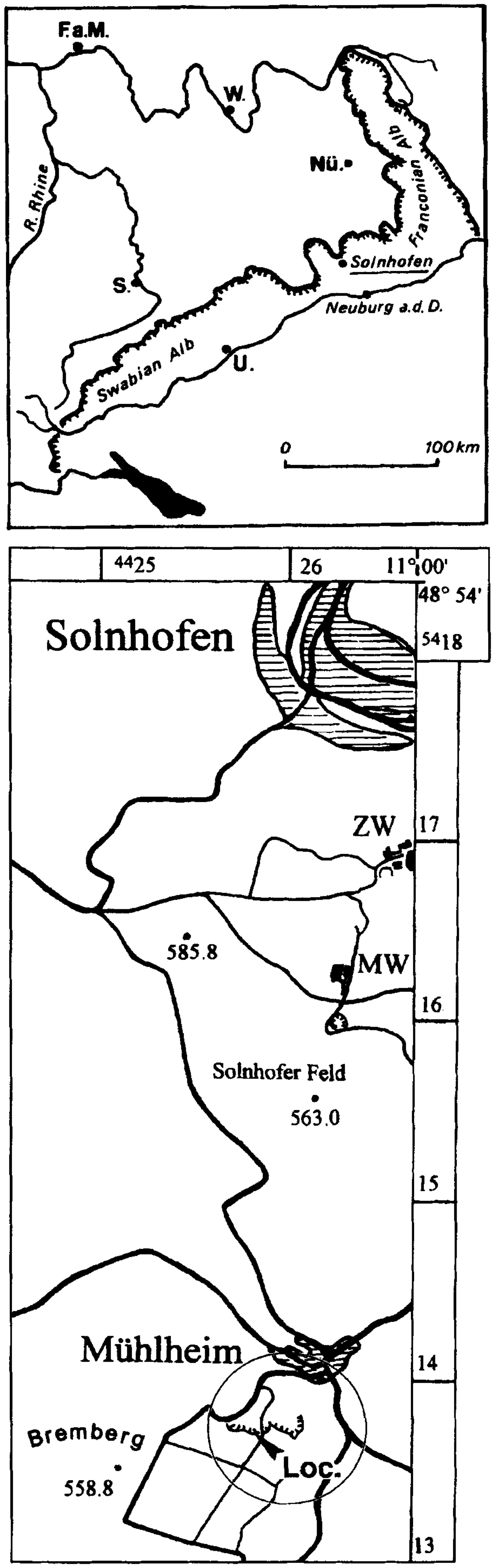

Fig. 1. Locality map: Mühlheim "Schaudiberg" (Loc. with arrow). – Abbreviations: F.a.M = Frankfurt am Main, W. = Würzburg, Nü. = Nürnberg, S. = Stuttgart, U. = Ulm, ZW = Zementwerk (cement factory), MW = Marmorwerk (marble factory).

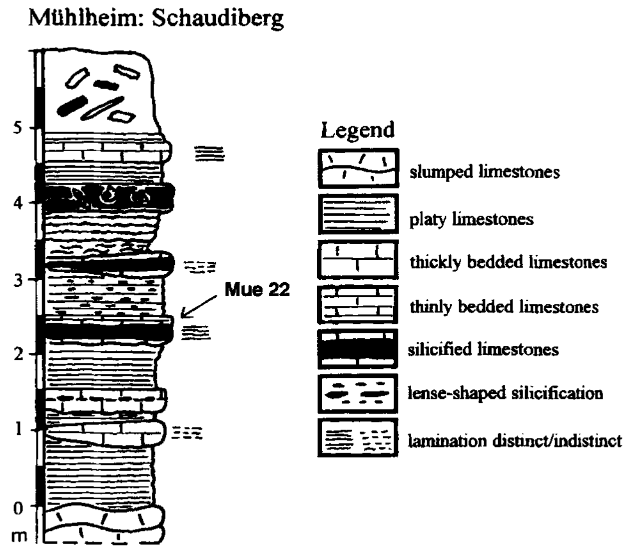

Fig. 2. Section Mühlheim, Schaudiberg old quarry, with position of sample Mu 22 in the Mühlheim Member of the Mörnsheim Formation. Solnhofen Formation is below 0 level (after DUMITRICA & ZÜGEL 2003).

In the Southern Franconian Alb, from which the present fauna comes, the early Tithonian sedimentation was controlled by the culmination of the sponge-algal-coral barrier in the south, that led to restricted back-reef overturn ("holomixis") and planktonic (mainly nannoplankton) immigration from the Tethys. Stable marine conditions established with the transgression that took place at the base of the Mörnsheim Formation (KEUPP 1977).

Although two composite sections have been investigated for radiolarians by the junior co-author (DUMITRICA & ZÜGEL 2003) we present here only the saturnalid fauna coming from one section, in fact from a single sample (Mue 22). This sample, which is the richest and contains the best-preserved radiolarians, was collected from the lower member (Mühlheim Member) of the Mörnsheim Formation cropping out in Schaudiberg old quarry (Fig. 1). The section is located 0.5 to 1 km south of Mühlheim. Stratigraphically, it starts on top of the Solnhofen Formation (ZEISS 1977), a formation characterized by a series of synsedimentary folded limestone beds (slump horizons), and consists of an alternate bedding of platy limestone, limestone beds and silicified limestone beds characteristic of the Mühlheim Member. The sample Mu 22 was collected from the topmost 5 cm of a partly silicified limestone bed of about 30 cm thick, at about 2 m above the base of this member (Fig. 2).

From biostratigraphical point of view the Mühlheim Member of the Mörnsheim Formation belongs to the early Tithonian *Hybonotum* Zone defined by ammonites (ZEISS 1977; ZEISS & SCHWEIGERT 1999), which is the lowermost zone of the stage. In term of radiolarian biostratigraphy it belongs to the base of the radiolarian Unitary Association Zone 12 (early Tithonian) (ZÜGEL 1997) as defined by BAUMGARTNER et al. (1995).

Morphology of Saturnalidae

The Saturnalidae are radiolarians characterized by a peripheral ring and a small, two- to many-layered spongy or latticed central shell that usually is dissolved during fossilization and that is mainly connected to the ring by two polar rays or spines (**P**), which are the only primary rays of the test (Fig. 3). As already shown (DUMITRICA 1985) (Fig. 4) the initial skeleton of all saturnalids, or at least of all Jurassic, Cretaceous and Cenozoic species for which this skeleton could be studied until present, is a heteropolar, sack-like shell improperly called microsphere, having a characteristic primary skeleton at the apical end. This skeleton starts from a median bar (**MB**) from the ends of which diverge two pairs of basal rays (**B**) interconnected distally by arches forming a primary ring (**PR**) that includes four pores or gates separated by **MB** and **B**, namely two longitudinal gates (**LG**) aligned on the direction of the polar rays and two transversal gates (**TG**) aligned on the direction of **MB**. The two polar rays characteristic of the Saturnalidae arise always from the primary ring on perpendicular direction to **MB**. They should be better called primary or lateral rather than polar because they are not at all polar relative to the initial skeleton, but we prefer to preserve this name that

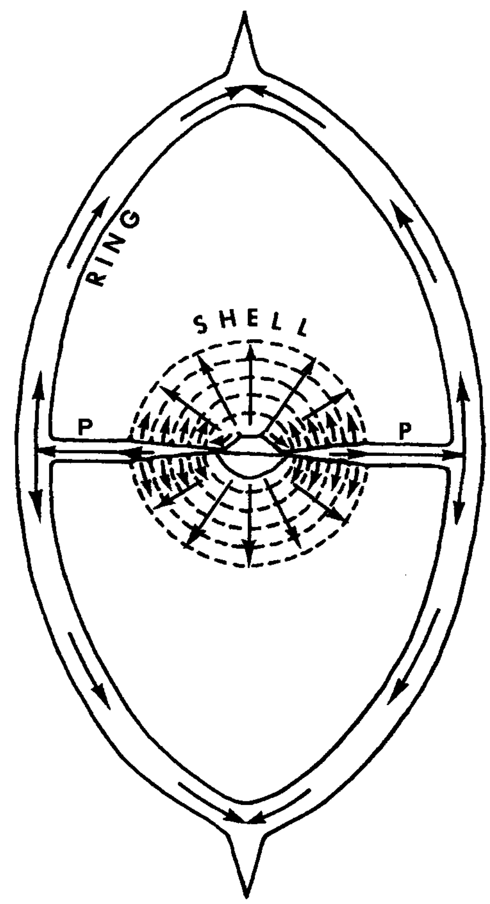

Fig. 3. Schematic structure of the skeleton of the family Saturnalidae with its directions of growth (arrows) starting from the microsphere: P – polar ray.

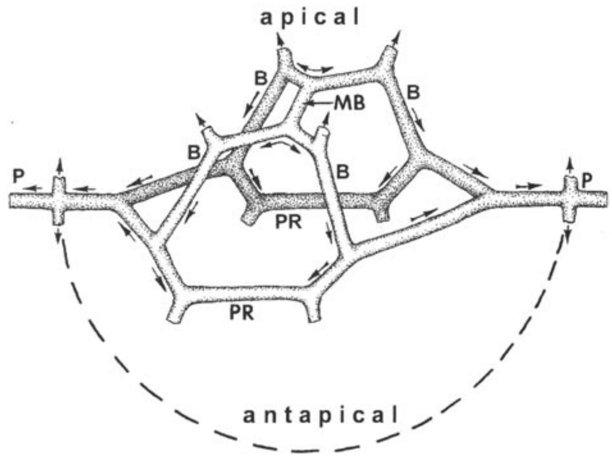

Fig. 4. Diagram illustrating the primary skeletal structure of the family Saturnalidae with the directions of growth starting from the median bar: MB – median bar, B – basal rays, PR – primary ring, P – polar rays.

is already in use taking into account that they are polar relative to the whole skeleton. The antapical part of the "microsphere" arises from the first descending branch of the polar rays and from the primary ring, and is a more or less complex sack-like shell. This initial shell, first described on the basis of some Cretaceous and Tertiary species (DUMITRICA 1985), is also very well exhibited on some early Tithonian specimens with partly broken test (see plates).

The peripheral ring, which is characteristic of most saturnalids, is ontogenetically built of two opposite lateral extensions of the polar rays (Fig. 4). These extensions surround the shell and merge two by two in the area of the axis perpendicular to polar rays closing the ring. The peripheral ring of the Tithonian saturnalids herein discussed is completely or partly three-bladed, with one blade on the inner margin and two on the outer margin, or vice-versa. When it is not completely three-bladed the portions that are not bladed are at the extremities of the ring. The blades may preserve their initial position on the whole ring, which is that in the area of the polar rays, or may twist, changing their position at the two extremities. The ring may be also four-bladed, with two blades on the inner margin and two on the outer margin, but in this case it seems that this character is derived from one of the two cases and especially from the type with only one blade on the outer margin.

This bladed structure is an evolutionary character of the ring of the Saturnalidae that seems to have appeared twice during their history: the first three- and four-bladed saturnalids appeared in the middle or late Norian and in the Rhaetian at both species with and without polar spines, but they seem to have completely disappeared during the Triassic-Jurassic boundary crisis since no such type is known so far in the Hettangian, Sinemurian, and Pliensbachian. Three- and four-bladed ringed saturnalids reappeared during the Toarcian only from Early Jurassic species without polar spines. They diversified within the Middle Jurassic – Late Cretaceous interval whereas the non-bladed ringed saturnalids disappeared slowly practically by the end of the late Jurassic. The Cretaceous species with non-bladed ring [*Acanthocircus angustus* DONOFRIO & MOSTLER, *A. irregularis* SQUINABOL, *A. subquadratus* (DONOFRIO & MOSTLER), *A. tympanum* O'DOGHERTY] do not seem to be phylogenetically connected to the Jurassic species

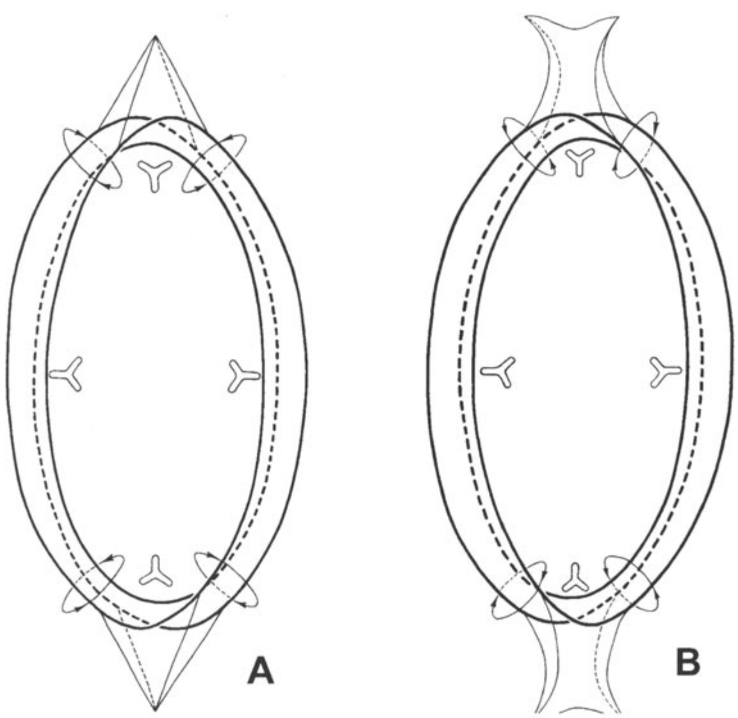

Fig. 5. Diagram illustrating the Möbius strip pattern in *Moebicircus* n. gen. A – sinistral twisting, B – dextral twisting.

but seem to have their origin in species of *Acanthocircus* with three- or four-bladed ring by the reduction of blades.

Since these characters occur at certain stratigraphic intervals and certain morphologies, we consider that the position of the blades has a generic or even subfamily level value. As a consequence, the taxonomy presented here is primarily based on the morphology and structure of the peripheral ring, the outermost part of the skeleton and, in fact, the part which is commonly preserved in fossil state and on the basis of which most species are distinguished. Disregard of the position of blades leads to errors in the generic determination of species. Examples are numerous, some of them can be found in the synonymy list of the present paper.

In this paper we have also paid a particular attention to different types of anomalies occurring in each species and of their frequency, since they can give information about the paleobiology of these radiolarians as for example the mode of growth of the skeleton and especially of the ring. The rather large number of anomalies in some species is probably due to some minor changes in salinity and temperature of the basinal environment in which the radiolarian fauna of the Mühlheim Member of the Mörnsheim Formation seems to have lived.

A difficult taxonomic problem in the present state of knowledge is the presence in the Tithonian and Berriasian of pairs of practically co-occuring species with a similar ring but with simple spines and with forked spines, as for instance: a) *Dicerosaturnalis trizonalis* (simple spines) – *D. dicranacanthos* (forked spines), b) *Moebicircus ruthae* (simple spines) – *M. furiosus* (forked spines), c) *Spongosaturninus corpulentus* (simple spines) – *S. matsuokai* (forked spines), d) *Spongosaturninus radius* (simple spines) – *S. tortuosus* (forked and tortioned spines). In the case when there are intermediary morphotypes between the two types we think that the solution is to consider them as extreme varieties of a single species. It is the case of the pair *Dicerosaturnalis trizonalis* – *D. dicranacanthos* (see below) where we consider that the latter species represents variations of the species *D. trizonalis*. For the other pairs and especially for the last one, where the spines of *S. tortuosus* are not only forked but also strongly torsioned, this solution is difficult to follow.

The Saturnalidae are relatively rare as number of specimens (less than 0.1 %) in this very rich fauna, but are interesting because they are represented by many new species and also because many specimens preserve the spongy shell and the initial skeleton. They are also interesting from biostratigraphical point of view because they contain some species that had been known to first occur later, in the late Tithonian.

Systematic descriptions

In this part we describe all saturnalid radiolarian species found in the mentioned sample of which many are new. In order not to repeat their geographical and stratigraphical locations we mention that they are as follows:

Locus typicus: Mühlheim, Schaudiberg quarry.

Stratum typicum: Topmost silicified horizon in a partly silicified limestone bed, about 2 m above the base of the Mühlheim Member.

Class Radiolaria MÜLLER, 1858
Subclass Polycystina EHRENBERG, 1838, revised RIEDEL, 1967
Order Entactinaria KOZUR & MOSTLER, 1982

Superfamily Saturnaloidea DEFLANDRE, 1953

Remarks: Based on the structure of the intial skeleton of the members of this superfamily, where an initial spicule with a median bar, 4 basal rays, 4 apical rays, and a primary ring could be recognized, DUMITRICA (1985) had mentioned that this group has more entactinarian than spumellarian affinities. In spite of these affinities DUMITRICA & DUMITRICA JUD (1995) continued to include the saturnalid radiolarians in the order Spumellaria. The consequences of these structural affinities have been taken later (DE WEVER et al. 2001), when the Saturnalidae have been assigned to the order Entactinaria. There is, however, a problem with this assignation because on that occasion the Oertlispongidae, which are considered the ancestors of the Saturnalidae (KOZUR & MOSTLER 1983, 1990), have been assigned to the order Spumellaria. Fact is that despite the affirmation by KOZUR & MOSTLER (1990: 182) we know neither the initial skeleton of the Oertlispongidae nor that of the Triassic Saturnalidae because of its dissolution, at least in the specimens we sectioned. On the other hand, it is true that the two polar rays of the Saturnalidae are not a prolongation of the basal rays of the initial spicule recognized by DUMITRICA (1985) as it happens in the true Entactinaria, a fact already remarked by DUMITRICA (1985) and used as an argument by KOZUR & MOSTLER (1990) against an entactinarian nature of the Saturnaloidea. In agreement with the last authors, "further detailed studies are necessary to clear finally the taxonomic position of the Saturnaliacea". It is quite possible that the entactinarian-like structure of the initial skeleton of the Jurassic to Recent Saturnalidae is a subsequent acquisition or reorganization of this skeleton as a consequence of the increase of the symmetry of the skeleton by the appearance of a foliaceous spine similar to and opposite to the main foliaceous spine of the Oertlispongidae during the transition to the Saturnalidae. If so, one could speak in this case of an "entactinarization" of the initial skeleton.

Family Saturnalidae DEFLANDRE, 1953

Subfamily Hexasaturnalinae KOZUR & MOSTLER, 1983, revised

1983 Hexasaturnalinae KOZUR & MOSTLER: 27.
2001 Hexasaturnalinae KOZUR & MOSTLER. – DE WEVER et al.: 208.

Type genus: *Hexasaturnalis* KOZUR & MOSTLER (1983: 28).
Included genera: *Hexasaturnalis* KOZUR & MOSTLER, 1983; *Dicerosaturnalis* DUMITRICA & JUD, 1994.
Range: Toarcian – Albian or possibly younger.

Revised diagnosis: Saturnalidae with two or more spines, a polygonal or elliptical three-bladed ring of which one blade is always on the inner margin and two on the outer margin, and a many-layered spongy perimicrospheric shell attached commonly to the ring by only the two polar rays. Without polar spines, exceptionally with auxiliary rays.

Remarks: We follow here the diagnosis established in DE WEVER et al. (2001). This diagnosis differs from the original one that did not take into account the position of the blades, the most distinctive character of the subfamily. This revised diagnosis corresponds partly to the diagnosis of the subfamily Acanthocircinae PESSAGNO as revised by KOZUR & MOSTLER (1990: 204) in the synonymy of which these authors included also the subfamily Hexasaturnalinae. Since we give a suprageneric value to the position of the three blades on the ring we consider the Hexasaturnalinae an independent suprageneric taxon and the Acanthocircinae a junior synonym of the subfamily Saturnalinae. The Late Cretaceous saturnalids described by FOREMAN (1975) with the same position of the blades as in the Hexasaturnalinae do not belong to this subfamily; they seem to have originated in some *Acanthocircus* species with blades on both margins of the ring by reduction of the inner blades. Also, we exclude from this subfamily the Norian genus *Octosaturnalis* KOZUR & MOSTLER, 1990, because it has polar spines, a character never seen with the genera of the Hexasaturnalinae. It follows that despite the structural similarity of the ring this genus cannot be the stratigraphically oldest and most primitive representative of this subfamily, as KOZUR & MOSTLER (1990) considered. As discussed above, the fossil record proves that the three- and four-bladed ring structure that appeared with some saturnalids during the Norian disappeared at the end of the Rhaetian during the Triassic-Jurassic crisis.

Genus *Dicerosaturnalis* DUMITRICA & JUD in O'DOGHERTY, 1994

* 1994 *Dicerosaturnalis* DUMITRICA & JUD in O'DOGHERTY: 248.
1997 *Dicerosaturnalis* DUMITRICA & DUMITRICA-JUD. – DUMITRICA et al.: 18.

Type species: *Saturnulus trizonalis* RÜST, 1898.

Range: Bathonian – Albian or probably younger. Although according to O'DOGHERTY (1994: 258) the last species of the genus [*D. amissus* (SQUINABOL, 1914)] disappeared at the end of the Aptian, the extension of the range of *Dicerosaturnalis* up to the Albian is based on the finding by the senior co-author of a species of this genus in the late Albian sample NSF 884 of PESSAGNO (1977b) coming from the Great Valley Sequence, California.

Remarks: The first diagnosis of the genus, with the designation of the type species, was published by O'DOGHERTY (1994) under the authorship of DUMITRICA & JUD, and the second by DUMITRICA et al. (1997). Although according to ICZN art. 51c the name is valid, PESSAGNO & HULL (2002) treated it as nomen nudum on the reason that it was not specified that it was a new genus, although no articles of the ICZN consider that this mention is one of the criteria of availability. Moreover, PESSAGNO & HULL (2002) included this genus in the synonymy of the genus *Acanthocircus* SQUINABOL, although the latter is not only a different genus but, in our opinion, it belongs also to another subfamily of the family Saturnalidae (see also DE WEVER et al. 2001).

We do not know yet the structure of the many-layered shell of the other species of *Dicerosaturnalis* because of its complete dissolution or poor preservation in most faunas but the type species shows a radial structure due to numerous continuous thin rays originated in the microsphere and the first perimicrospheric shells. This structure differs from that of the shell of all the other species described under other genera in the present paper and resembles that of the shell of the Pliensbachian saturnalid species described by DE WEVER (1981). Consequently it seems that the radial structure of the shell is a primitive structure or a structure characteristic of Early Jurassic saturnalids.

As noted by DUMITRICA & DUMITRICA-JUD (2005), *Dicerosaturnalis* arose during the Bathonian from *Hexasaturnalis nakasekoi* DUMITRICA & DUMITRICA-JUD by the reduction of the number of spines from two to one, and is the result of a trend towards elongated ring. In this idea the early-middle Bajocian specimen with a single spine at each end of the ring, illustrated by YAO (1997: fig. 215) as *Acanthocircus* sp. B, does not belong to *Dicerosaturnalis* but represents probably an anomaly of *Hexasaturnalis suboblongus* (YAO, 1972) or a true species of this genus.

***Dicerosaturnalis trizonalis* (RÜST, 1898)**
Figs. 6A–K, 7A–J, 8A–N, 9A–M, 10A–C

1898 *Saturnulus dizonius* RÜST: 8, pl. 2 fig. 3.
* 1898 *Saturnulus trizonalis* RÜST: 9, pl. 2 fig. 4.
1914 *Saturnalis novalensis* SQUINABOL: 268, 297, pl. 20 (1) fig. 1, pl. 23 (4) fig. 7.
1914 *Saturnalis dicranacanthos* SQUINABOL: 289, text-fig. 1, pl. 22 figs. 4, ?5, 6, 7, ?pl. 23 fig. 8.
1914 *Saturnalis amissus* SQUINABOL: 296, pl. 23 figs. 2–5.
1916 *Saturnulus* sp. FISCHLI: 46, fig. 55.

1973 *Acanthocircus dizonius* (RÜST) (?). – FOREMAN: 260, pl. 4 figs. 4–5.
1973 *Acanthocircus trizonalis* (RÜST) (?). – FOREMAN: 261, pl. 4 figs. 6–8.
1973 *Spongosaturnalis dicranacanthos* (SQUINABOL). – MOORE: 824, pl. 3 figs. 1, 3.
1973 *Spongosaturnalis amissus* (SQUINABOL). – MOORE: 824, pl. 3 fig. 2.
1977a *Acanthocircus dicranocanthos* (SQUINABOL). – PESSAGNO: 73, pl. 3 fig. 5.
1977b *Acanthocircus dicranocanthos* (SQUINABOL). – PESSAGNO: 31, pl. 2 fig. 6.
1978 *Acanthocircus trizonalis* (RÜST) (?) emend. – FOREMAN: 744, pl. 1 fig. 7.
1978 *Acanthocircus dicranacanthos* (SQUINABOL). – DONOFRIO & MOSTLER: 28, pl. 2 fig. 3, pl. 4 figs. 4, 7–9, pl. 5 figs. 10, 11.
1978 *Acanthocircus amissus* (SQUINABOL). – DONOFRIO & MOSTLER: 23, text-fig. 7, pl. 1 figs. 1, 10, pl. 5 figs. 4, 6, 9, non figs. 1–3, pl. 6 figs. 4, 6, non figs. 8, 11.
1979 *Acanthocircus dicranocanthos* (SQUINABOL). – NAKASEKO et al.: 21, pl. 2 fig. 7.
1980 *Acanthocircus dicranacanthos* (SQUINABOL). – BAUMGARTNER et al.: 49, pl. 1 fig. 11.
1980 ?*Acanthocircus dicranacanthos* (SQUINABOL). – HOLZER: 156, pl. 1 figs. 1–12, pl. 2 figs.7–9.
1981 *Acanthocircus dicranacanthos* (SQUINABOL). – NAKASEKO & NISHIMURA: 141, pl. 1 fig. 6.
1981 *Acanthocircus dicranacanthos* (SQUINABOL). – KOCHER: 51, pl. 12 fig. 3.
1981 *Acanthocircus dicranacanthos* (SQUINABOL). – SCHAAF: 431, pl. 7 fig. 1, pl. 16 fig. 3.
1981 *Acanthocircus trizonalis* (RÜST). – SCHAAF: 431, pl. 16 fig. 1.
1981 *Acanthocircus trizonalis* (RÜST). – DE WEVER & THIÉBAULT: 584, pl. 2 fig. 16.
1982 *Acanthocircus dicranocanthos* (SQUINABOL). – AOKI: pl. 1 fig. 3.
1983 *Acanthocircus dicranacanthos* (SQUINABOL). – ORIGLIA-DEVOS: 58, pl. 4 figs. 2, 4.
1983 *Acanthocircus trizonalis* (RÜST). – ORIGLIA-DEVOS: 61, pl. 4 figs. 6–7.
1983 *Acanthocircus* sp. A gr. – ORIGLIA-DEVOS: 63, pl. 4 fig. 8, non figs. 9–10 = *Dicerosaturnalis angustus* (BAUMGARTNER), pl. 5 fig. 1, non figs. 2–3 = *Dicerosaturnalis angustus* (BAUMGARTNER).
1984 *Acanthocircus dicranacanthos* (SQUINABOL). – SCHAAF: 106–107.
1984 *Acanthocircus trizonalis* (RÜST). – SCHAAF: 155–156, fig. 5.
1984 *Acanthocircus dicranacanthos* (SQUINABOL). – SANFILIPPO & RIEDEL: 591, figs. 5.2a–c.
1984 *Acanthocircus trizonalis* (RÜST). – SANFILIPPO & RIEDEL: 592, figs. 5.1a–d.
1984 *Acanthocircus dicranacanthos* (SQUINABOL) part. – OZVOLDOVA & SYKORA: pl. 1 fig. 6, non fig. 7.
1986 *Acanthocircus dicranacanthos* (SQUINABOL). – AITA & OKADA: pl. 1 fig. 5.
1986 *Acanthocircus dicranacanthos* (SQUINABOL). – DE WEVER et al.: pl. 6, figs. 3, 4.
1987 *Acanthocircus dicranacanthos* (SQUINABOL). – OZVOLDOVA & PETERCAKOVA: 118, pl. 31 fig. 2.
1987 *Acanthocircus dicranacanthos* (SQUINABOL). – PAVSIC & GORICAN: 22, pl. 2 fig. 2.
1987 *Acanthocircus trizonalis* (RÜST). – PAVSIC & GORICAN: 22, pl. 2 fig. 3.
1988 *Acanthocircus dicranacanthos* (SQUINABOL). – OZVOLDOVA: pl. 3 fig. 7.
1988 ?*Acanthocircus amissus* (SQUINABOL). – OZVOLDOVA: pl. 3 fig. 8.
1988 *Acanthocircus trizonalis* (RÜST). – THUROW: 396, pl. 10 fig. 2.
1988 *Acanthocircus* sp. – THUROW: 396, pl. 10 fig. 1.
1989 *Acanthocircus dicranacanthos* (SQUINABOL). – DANELIAN: 130, pl. 1 figs. 9–11.
1989 *Acanthocircus trizonalis* (RÜST). – DANELIAN: 133, pl. 1 figs. 14–17.
1989 *Acanthocircus dicranacanthos* (SQUINABOL). – KITO: 152, pl. 16 fig. 8.
1989 *Acanthocircus amissus* (SQUINABOL, 1914). – OZVOLDOVA: 139, pl. 5 fig. 2.
1989 ?*Acanthocircus dicranacanthos* (SQUINABOL). – TUMANDA: pl. 2 fig. 12.
1992 *Acanthocircus dicranacanthos* (SQUINABOL). – STEIGER: 34, pl. 5 figs. 3–6.
1992 *Acanthocircus amissus* (SQUINABOL). – STEIGER: 34, pl. 5 fig. 7.
1992 *Acanthocircus variabilis* (SQUINABOL). – STEIGER: 35, pl. 5 fig. 9.
1992 ?*Acanthocircus dicranacanthos* (SQUINABOL). – OZVOLDOVA & PETERCAKOVA: pl. 1 figs. 1–2, 11.
1992 ?*Acanthocircus* sp. B. – OZVOLDOVA & PETERCAKOVA: pl. 1 fig. 3.
1992 ?*Acanthocircus* sp. A. – OZVOLDOVA & PETERCAKOVA: pl. 1 fig. 4.
1993 *Acanthocircus dicranocanthos* (SQUINABOL). – YANG: 80, pl. 13 figs. 3, 5, non figs. 7, 19 [= *Dicerosaturnalis angustus* (BAUMGARTNER)].
1993 *Acanthocircus trizonalis* (RÜST)(?). – YANG: 84, pl. 13 figs. 4, 6, non fig. 16 [= *Dicerosaturnalis angustus* (BAUMGARTNER)].
1994 *Acanthocircus trizonalis* (RÜST) gr., part. – GORICAN: 60, pl. 3 fig. 1, non fig. 2 = *Dicerosaturnalis angustus* (BAUMGARTNER).
1994 ?*Acanthocircus trizonalis* (RÜST). – JUD: 60, pl. 2 figs. 9–11.
1994 *Dicerosaturnalis amissus* (SQUINABOL). – O'DOGHERTY: 248, pl. 43 figs. 1–3.
1994 *Acanthocircus dicranacanthos* (SQUINABOL). – CHIARI: pl. 1 fig. 1.
1995 ?*Acanthocircus trizonalis dicranacanthos* (SQUINABOL), emend. FOREMAN. – BAUMGARTNER et al.: 72, pl. 3087 figs. 1–5, 7–8, non fig. 6 = *Dicerosaturnalis major* (SQUINABOL).
1995 *Acanthocircus trizonalis trizonalis* (RÜST). – BAUMGARTNER et al.: 74, pl. 3083.
1997 *Acanthocircus dicranacanthos* (SQUINABOL). – HULL: 29, pl. 9 fig. 3, non fig. 4 = *Moebicircus furiosus* (JUD).
1997 *Dicerosaturnalis dicranacanthos* (SQUINABOL). – DUMITRICA et al.: 18, pl. 1 fig. 15.
1997 *Acanthocircus dicranacanthos* (SQUINABOL). – YANG & MATSUOKA: pl. 1 fig. 6.
1998 *Acanthocircus trizonalis* (RUEST). – MATSUOKA: fig. 177.

1999 *Acanthocircus dicranacanthos* (SQUINABOL). – MEKIK et al.: 732, figs. 7A, B.
2001 *Dicerosaturnalis trizonalis* (RÜST). – YEH & CHENG: pl. 5 fig. 9.
2002 *Acanthocircus dicranacanthos* (SQUINABOL). – VISHNEVSKAYA & MURCHEY: pl. 6 fig. 3.
2004 *Dicerosaturnalis trizonalis* (RÜST). – GORICAN & SMUC: pl. 1 fig. 2.

Dimensions (in µm, based on 22 specimens): Diameter of microsphere 22–26 (average 24), of spongy shell 142–269 (average 202), length of ring 478–689 (average 601), breadth of ring at middle 259–333 (average 301), maximum breadth 278–372 (average 341), length of spines 52–143 (average 96).

Description: Ring commonly elongate elliptical with round or slightly acute ends; more or less frequently ring tends to be rhombic or subrhombic. Irrespective of its shape the middle part of ring is slightly constricted. Ring three-bladed, blades thick, one on the inner margin and two on the outer margin. Each end of elliptical ring bears one spine and, on each face, one triangular callus of variable thickness at the base of spine and on the external blade. Spines variable in shape; they may be simple, short and pointed, longer and spatulate or more or less forked. Usually spines are slightly twisted dextrally, never sinistrally. On the lateral side of the spines, between the calluses of the two faces, a deep circular depression is developed. Shell spongy, many-layered, number of layers about 10; layers interconnected by numerous thin rays which continue across the shell and extend beyond it giving the surface of shell a hispid aspect. Structure of apical part of microsphere difficult to disentangle because of the presence of additional bars that screen the true initial skeleton.

Remarks: The holotype comes from probably upper Tithonian or Berriasian portion of the Maiolica Formation of Cittiglio, Southern Alps, North Italy. Although it shows an additional arch perpendicular to the ring, the species cannot be invalid and considered a nomen dubium as O'DOGHERTY (1994) suggested. This arch is probably a fragment of a radiolarian stuck to the test (O'DOGHERTY 1994) and represents no impediment in the recognition of the species. Of course, RÜST's drawing does not show the three-bladed structure of the ring, but the trilobate shape of the two calluses is well marked.

Dicerosaturnalis trizonalis arose from *D. angustus* (BAUMGARTNER) by the extension of the calluses along the external blades and, as a consequence, the change of their shape from simple, elongate to trilobate. The transition between the two species seems to have taken place during the Kimmeridgian and to have been gradual and relatively slow, as very rare early Tithonian specimens with still intermediate characters suggest (Figs. 8J, 9K). Recently DUMITRICA & DUMITRICA-JUD (2005) considered that *D. angustus* gave rise to *D. dicranacanthus*. There is no contradiction between this statement and what we said above about the origin of *D. trizonalis* because, as the synonymy list shows, most specimens determined as *D. dicranacanthos* in the literature belong to *D. trizonalis*.

We consider *D. dicranacanthos* (lectotype SQUINABOL 1914, pl. 23 fig. 7, subsequent designation by PESSAGNO 1977a: 74), a synonym of *D. trizonalis*. The almost constant co-occurrences of the specimens with simple spines, assignable to the latter species, with those with forked spines, assignable to the former species, in most Tithonian and early Cretaceous assemblages, the constant transitions between them, and the weak development of the two teeth of the spines is the best argument that both belong to a single species. A taxonomic problem still difficult to solve for the moment refers to the specimens with a robust ring, rounded ends, thick trilobate calluses, and the two teeth of the spines flat, with rounded ends and very divergent, comparable with what SQUINABOL (1914: pl. 22 fig. 5, pl. 23 fig. 8) illustrated as *D. dicranacanthos*. Such morphotypes are common in the Valanginian and especially Hauterivian (see BAUMGARTNER et al. 1995: 73, pl. 3087) and may have a systematic and stratigraphic value. According to PESSAGNO (1977a) they should be assigned to other species.

Variability: As variability we shall discuss only the shape of the spines and of the ring and the degree of development of the calluses, three of the most visible characters and most commonly used in the discrimination of the species of this genus. This variability is very wide not only in this population but, as it seems, with the whole species (see also DONOFRIO & MOSTLER 1978: text-fig. 7).

The shape of the ring is commonly elliptical with rounded ends and slight constrictions at the connection with polar rays. Many specimens have, however, a ring with rather acute ends, and rather rarely the ring is rhombic (Figs. 7B, D, 8A). Since between these extreme morphologies all kind of intermediary forms occur we consider that the shape of the ring has no taxonomic value in this species.

As concerns the shape of the spines we found that about 75 % of the specimens in sample Mu 22 have simple, unforked spines. The exact percentage is impossible to establish because there are specimens that have a simple spine at one end and a forked spine at the other end. The simple spines are usually flattened distally and slightly spatulate. Sometimes they are more or less twisted dextrally (Figs. 6A, 7B, E), never sinistrally. Their distal end may be pointed, rounded, or broad and

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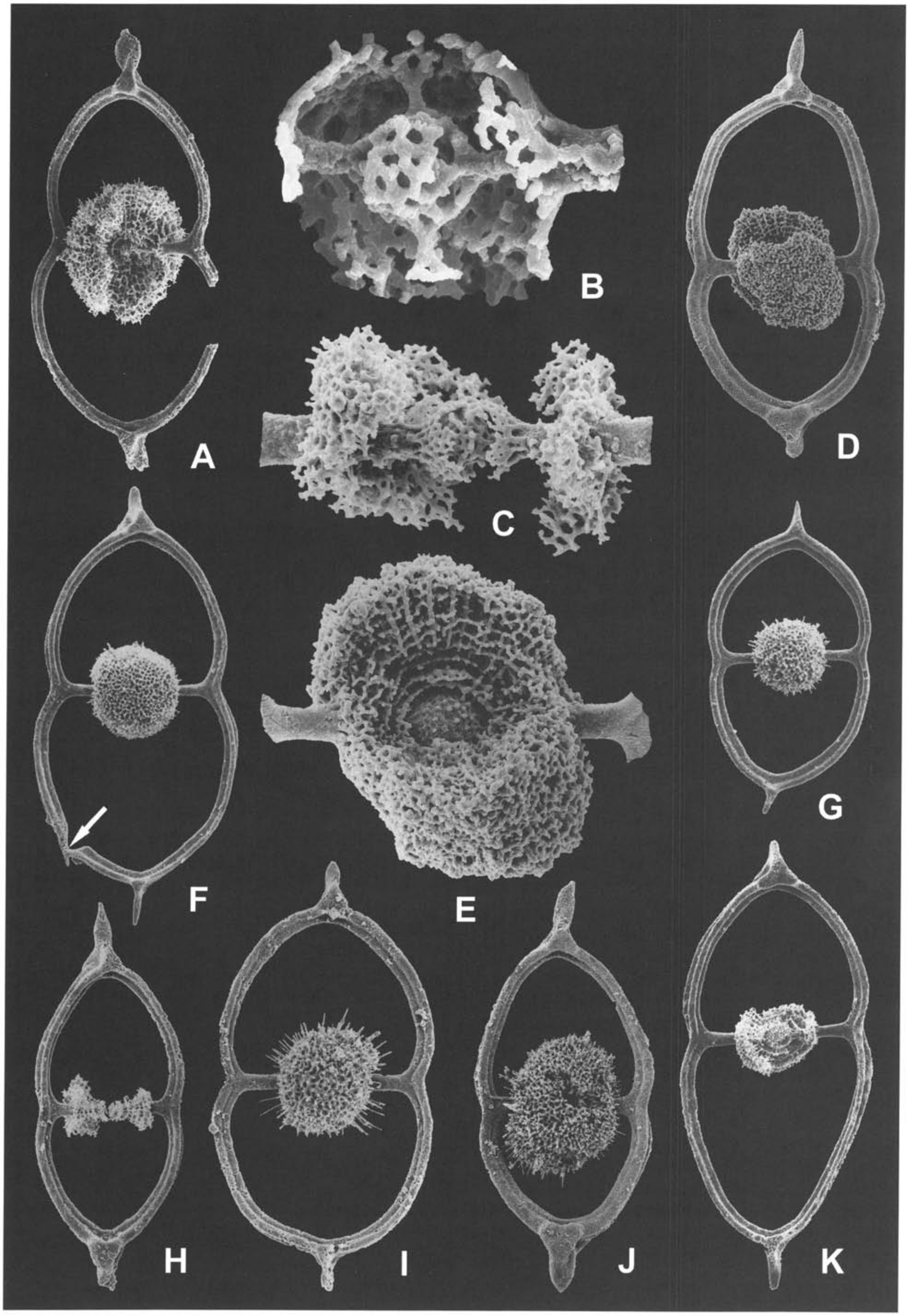
Fig. 6. A–K: *Dicerosaturnalis trizonalis* (RÜST). Normal skeletons with simple spines. B. microsphere of fig. 6A in antapical view; C. details of innermost shells; E. detail of shell of fig. 6D showing the radial structure of the many-layered shell; F. the arrow points to a portion of the ring broken and slightly repaired during the life of the specimen. – A, D, F–K x100; B x1000; C x350; E x250.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blunt. The last type makes the morphological passage to the forked spines by the appearance of an incision between the two margins of the spines. When the two margins diverge the result is the appearance of a swallowtail structure. Spine forking is the result of the fact that the borders of the flat spines are slightly thicker than the blade between them. The two branches of the forked spines may lie in the plane of the ring, but most commonly the right branch lies at a higher level than the left branch because of the dextral twisting of the spines. A single specimen was found with a simple spine at one end and a three-forked spine at the other (Figs. 8K, Ka).

The callus is not always triangular or three-rayed and thick as in the holotype. Sometimes it is very slightly marked (Figs. 6G, 7B, D, etc.), or even when it is well marked it is not triangular but elongated on the lower and upper margins of the spines and not on the external blades (Figs. 8J, 9K). This morphotype resembles rather well *Dicerosaturnalis angustus* (BAUMGARTNER). There is, however, a slight difference between the spines of the two species in the case of such calluses. It concerns the length of the spines; *D. angustus* has the spines very short, sometimes with a tiny spike, whereas *D. trizonalis* has spikes longer and replaced usually by small spatulas. It is interesting to note that *D. angustus*, which is still present in the upper Tithonian of the Taman Formation, east-central Mexico (YANG 1993), is missing in the sample Mu 22.

In conclusion, the separation of the species into subspecies on the basis of the shape of ring and spines is not possible, at least at the level of the Tithonian, because of the great number of transitional individuals and of the fact that all these morphotypes occur in the same sample, that is practically in the same fossil population.

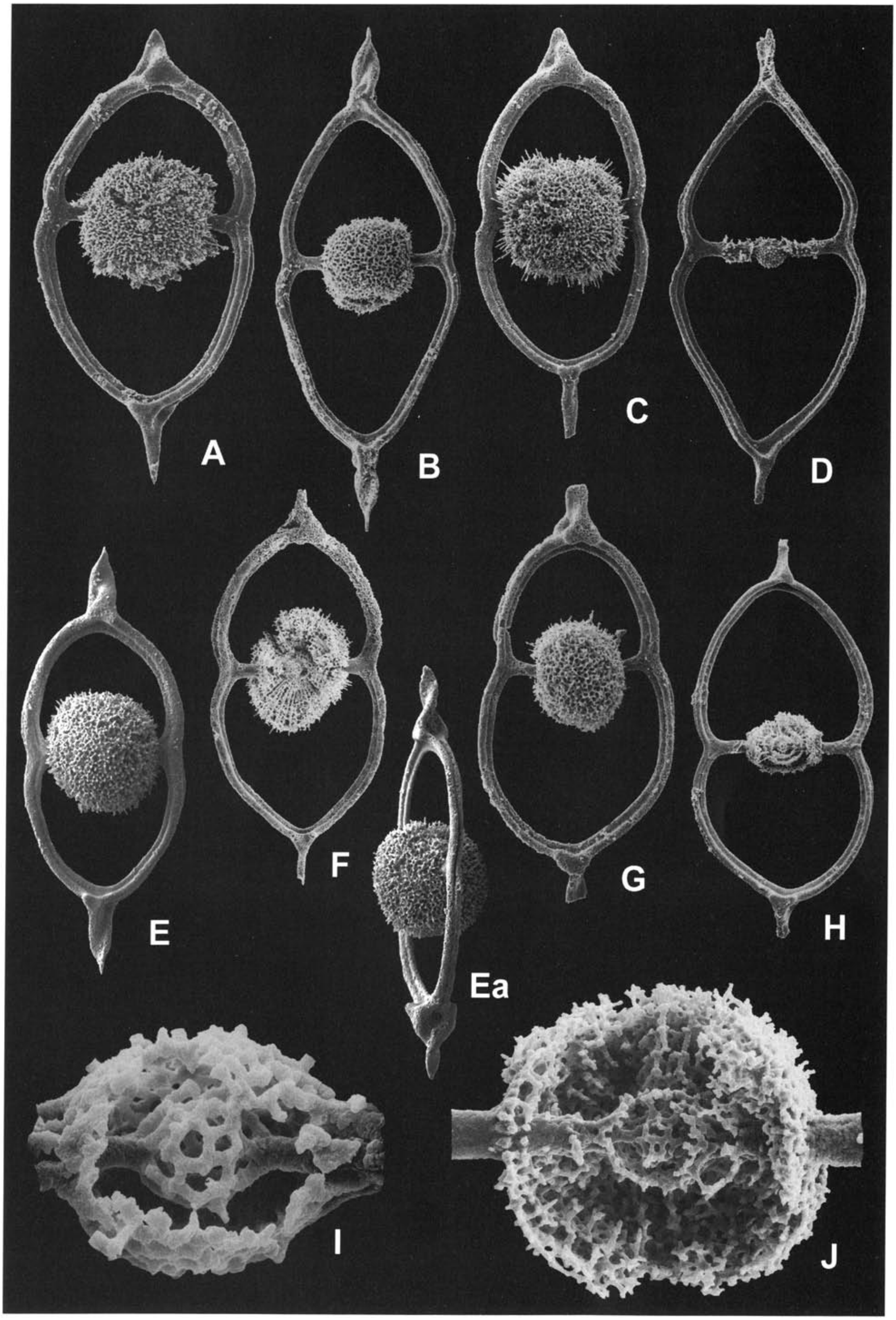
Anomalies: It seems that the anomalies are frequent in this species, although the great number of abnormal forms could result from the fact that *D. trizonalis* is the most frequent saturnalid species in this fauna and, accordingly, the possibility to find abnormal individuals is greater than in the case of rare species. The following types of anomalies are the most common:

1. Additional spines at one end (Figs. 8N, 9A–F). These anomalies have a single spine at an end and 2 or even 3 at the other end. The additional spines may be close to each other, in which case the shape of the ring is not modified, or rather spaced, in which case the half of the ring where the additional spines are located is much larger. Enlargement of one half of the ring determines the deviation of the polar rays; they do not lie any more along the polar axis as in normal specimens but make an angle the size of which depends on the breadth of the larger half of the ring: the greater the breadth the greater the angle in that half. This is the result of the fact that the polar rays are always practically perpendicular on the bars of the ring. The specimen illustrated in Fig. 9E is also interesting in having not only two spines at one end but also having these spines forked in plane perpendicular to the plane of the ring. Such cases are extremely rare in the Saturnalidae.
2. Opened ring: Since the growth direction of the ring is from the polar rays to the ends of the ellipse the ring may be opened at these ends, where the two arms of the ring originated in the polar rays should meet. Usually it is open at a single end (Figs. 9B, H–M) and only in a single case we found a specimen with both ends open (Fig. 9G). In the case of a single open end the anomaly seems to have resulted from the fact that the two portions of the ring were not in the same plane so they could not meet to merge. Arriving at this area they bent, as programmed by the genetic code, lost the three-bladed structure, started thinning to end up at a certain level between the distal end of the ring and the shell, or they could even touch the shell (Fig. 9H). At the bending area one or both branches of the ring or none could build a spine. Sometimes one of the arms of the ring, after bending at the distal pole of the ring, could merge with the other arm at a certain level (Figs. 9I, 10A) or even at the distal end of the polar ray (Fig. 9J). In a single case, the two branches of the ring ended suddenly after building a spine (Fig. 9K).
3. Siamese twins: We found only two cases of this type of anomaly (Figs. 10B, C). The twins are very irregular and have in common the shell, one polar ray or none, and a portion of the ring. Such anomalies, although very rare, have been already described in other groups of radiolarians (DE WEVER 1985; DUMITRICA & ZÜGEL 2002) and have been also found by the senior co-author, but not yet published, in one middle Anisian spumellarian and one early Ladinian nassellarian Radiolaria.

There are also other anomalies more difficult to systematize as for example: asymmetric ring, irregular or undeveloped callus (Fig. 7B). One specimen (Fig. 6F, arrow) seems to show a partly repaired damaged ring, another specimen (Fig. 8M) a deformed and partly broken ring during the skeletogenesis, when the skeleton was still soft, and, another one, an anomalous specimen without one half of ring (Fig. 8L).

Range and occurrence: Late Kimmeridgian to probably late Aptian, cosmopolitan.

Fig. 7. A–J: *Dicerosaturnalis trizonalis* (RÜST). Normal specimens with simple spines. Note the variability of the shape of the ring and dextrally twisted spines with some specimens. Ea. specimen from E in side view showing the narrow groove between the external blades and the deep lateral depression at the base of spines; I. microsphere and first extramicrospheric shell of fig. H; J. shell of a non-illustrated specimen, showing inside the microsphere in lateral view and the first perimicrospheric shell. – A–H x100; I x1000; J x400.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Subfamily Saturnalinae DEFLANDRE, 1953

* 1953 Saturnalinae DEFLANDRE: 419.
1977a Acanthocircidae PESSAGNO, part.: 73.
2001 Saturnalinae DEFLANDRE. – DE WEVER et al.: 208.

Type genus: *Saturnalis* HAECKEL, 1887.
Genera included: *Saturnalis* HAECKEL, *Acanthocircus* SQUINABOL, *Spongosaturninus* CAMPBELL & CLARK, *Vitorfus* PESSAGNO, *Aurisaturnalis* DUMITRICA & DUMITRICA-JUD, *Moebicircus* n. gen.
Range: Early Jurassic (?) to Recent.

Remarks: The family Acanthocircidae was erected by PESSAGNO (1977a) for the Saturnalidae with test consisting of latticed medullary shell(s) and spongy cortical shell. Since the ring of both Tertiary and most Cretaceous saturnalids has the same three-bladed structure with one blade on the outer margin and two on the inner margin the Acanthocircidae are here considered a junior synonym of the Saturnalinae DEFLANDRE. In fact, since the ring is the most important distinctive and evolutionary element of the Saturnalidae the latticed or spongy structure of central test seems to be less important at family or subfamily level. If we compare the structure of the test of *Vitorfus* PESSAGNO (microsphere and two latticed shells, *Spongosaturnalis* CAMPBELL & CLARK (microsphere and many-layered spongy shell, but no lattice shell), *Spongosaturninus* CAMPBELL & CLARK (microsphere plus two latticed shells and possibly a peripheral spongy shell), *Saturnalis* HAECKEL (microsphere plus a cortical latticed shell and possibly a spongy fabric between the two) as illustrated by DUMITRICA (1985) one can suppose that this structure is of systematic value especially at generic level. For this reason we follow here the definition of the subfamily established in DE WEVER et al. (2001).

Genus *Spongosaturninus* CAMPBELL & CLARK, 1944, revised herein

* 1944 *Spongosaturninus*, n. gen. CAMPBELL & CLARK: 7.

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

Revised diagnosis: Saturnalids with perimicrospheric shell spongy, many-layered and an elliptical ring with two opposite distal spines. When the ring has two or more spines at each end the additional ones are shorter and in lateral position. Ring usually three-bladed with one blade on the external margin and two on the internal margin, sometimes four-bladed or without blades. Microsphere as for the subfamily.

Remarks: The genus was initially described as having three concentric shells, outer shell spongy and inner a double lattice shell. Based on the type species and on the other species initially included in this genus we consider more important the elliptical ring and the presence of one main spine at either end than the number of shells. The genus seems to have appeared in the Toarcian with species with weakly developed blades, and disappeared at the end of the Cretaceous. Unlike the closely related genus *Moebicircus* n. gen., the blades of the ring of *Spongosaturninus* are not twisted at the two distal ends and do not change their position. The shape of the ring and the presence of the two end spines are also characters in common with *Dicerosaturnalis* DUMITRICA & DUMITRICA-JUD, but this genus has a blade on the internal margin and two on the external margin, and another structure of the spongy shell.

In the lower Tithonian sample Mu 22 the species of this genus can be assigned to two well-defined groups:

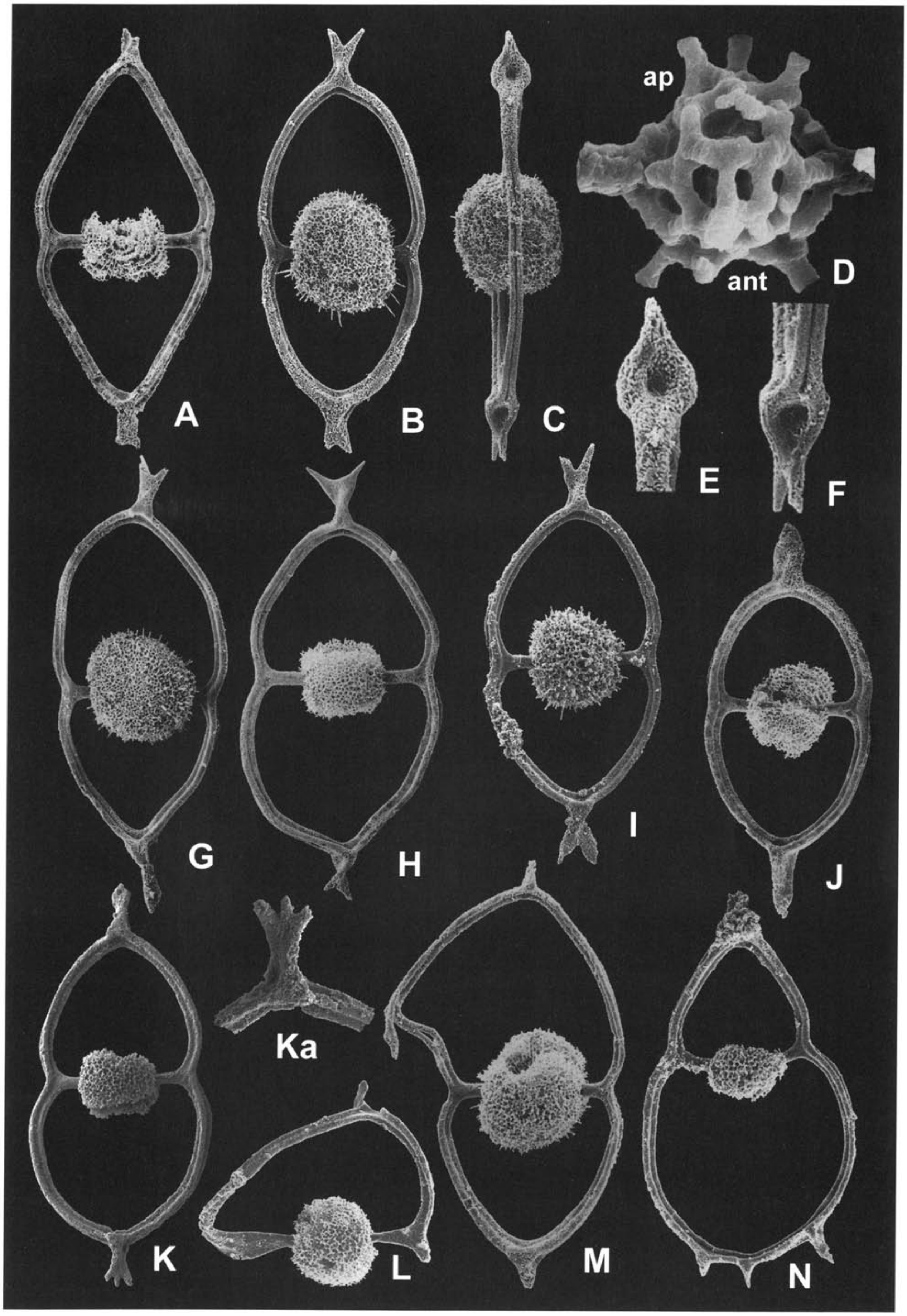
A) a group of species with broad ring and flat spines (*S. corpulentus* n. sp. and *S. matsuokai* n. sp.) and

B) a group of species with naviculoid ring, four-bladed spines of which two blades are a prolongation of the outer blade of the ring and two are perpendicular to them and connected with the inner blades of the ring (*S. kiesslingi* n. sp., *S. medioangustus* n. sp., *S. radius* n. sp., and *S. tortuosus* n. sp.). The latter group has all structural characters of the type species whereas the former would represent a lateral branch. It is also to note the presence of Siamese twins skeletons in the latter group.

In the same genus one can include also species with or without a callus described by previous authors such as: *Saturnalis ellipticus* SQUINABOL, 1903, *Spongosaturnalis nematodes* FOREMAN, 1968, *S. campbelli* FOREMAN, 1968, *S. bispinus* YAO, 1972, *Acanthocircus meyerhofforum* HULL, 1997, *A. dumitricai* KIESSLING, 1999, *A. vaigaloensis* PESSAGNO & HULL, 2002, the species illustrated by DUMITRICA et al. (1997: 19, pl. 1 fig. 6) as *Acanthocircus* (?) n. sp. 2 and by MATSUOKA (1998: fig. 179) as *Acanthocircus* sp. aff. *A. dicranacanthos* (RÜST), which is frequent in the Berriasian – Valanginian of the Tethys, and also the species described by CAMPBELL & CLARK (1944) as *Spongosaturninus parvulus*, *S. parvulus lateralispinosus*, and *S. latuformis*.

Range: Toarcian to Maastrichtian.

Fig. 8. A–N: *Dicerosaturnalis trizonalis* (RÜST), specimens with normal and abnormal ring, with forked and simple spines. C. same specimen as B in lateral view showing the deep narrow groove between the two blades of external margin and the deep depression at the base of spines; E, F. details of fig. C; D. microsphere of shell illustrated in Fig. 7J: ap – apical part, ant – antapical part; note that the apical initial structure is complicated by appearance of some additional bars; Ka. detail of the trifurcate spine of fig. K. – A–C, G–K, L–N x100; D x1500, E, F, Ka x200.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Group A

Spongosaturninus corpulentus n. sp.
Figs. 10D–F, ?H

Derivatio nominis: From the Latin *corpulentus* – thick.
Holotype: Fig. 10D, coll. Musée de Géologie Lausanne, No. 74395.
Material: Three specimens in sample Mu 22 and one specimen illustrated by Matsuoka from the Berriasian of Mariana Trench but not yet published.
Dimensions (in µm, based on 3 specimens): Diameter of shell 95–118 (average 104), breadth of ring along polar rays 268–278 (average 271), maximum breadth 273–289 (average 278), length of ring 400–418 (average 407), of spines 36–62 (average 50).

Description: Ring wide, elliptical with a blade on the external margin and two on the internal margin and a flat triangular spine at each end. Middle of ring slightly constricted. Ends of ring rounded to slightly acute. External blade may have thickened border. Spines flat, short, triangular resulted from the extension of the external margin and with base slightly twisted sinistrally. Central shell spherical and small. Polar rays long, cylindrical.

Remarks: The photo of a specimen from the Berriasian of the Mariana Trench provided by A. Matsuoka shows very short, almost indistinct spines. *S. corpulentus* is very close to *S. matsuokai* n. sp. from which it differs in only having triangular instead of forked spines. This species differs from species with similar morphology in having the base of spines sinistrally twisted. The ancestor of the species is unknown.

Anomalies: A single anomaly was recorded (Fig. 10H). This specimen, that is questionably assigned to this species, has no spine at an end of the ring whereas at the other end the ring seems to be of the *Moebicircus* type, the blade of the right internal margin crossing obliquely the ring to form one margin of the spine.

Range and occurrence: Tithonian – Berriasian: lower Tithonian, Mörsheim Formation, Solnhofen area, southern Germany; Berriasian, Mariana Trench, western Pacific.

Spongosaturninus matsuokai n. sp.
Figs. 10E, G, I–L

Derivatio nominis: The species is named for Dr. Atsushi Matsuoka, Niigata University, Japan, for his contribution to the knowledge of Mesozoic radiolarians.
Holotype: Fig. 10I, coll. Musée de Géologie Lausanne, No. 74396.
Material: Five specimens in sample Mu 22, of which only the holotype is complete, and one specimen illustrated by Matsuoka from the Berriasian of Mariana Trench but not yet published.
Dimensions (in µm, based on 5 specimens): Diameter of shell 98–111 (average 104), breadth of ring along polar rays 269–277 (average 273), maximum breadth of ring 272–283 (average 277), length of ring without spines 420–427 (average 423), length of spines 61–66 (average 63).

Description: Ring wide, elliptical with a blade on the external margin, two on the internal margin and a forked spine on each end. At the ends of ring the internal blades make a wide angle and the ring may be more or less twisted sinistrally. Spines flat, broad, forked, resulted by the elongation of the external blade, which is bent up on a short distance, on the right side, and down, on the left side, at the boundary between the ring and the spines according to a sinistral twisting. Ring usually slightly constricted medially. Shell spherical, spongy, small relative to the size of the ring and connected to the latter by long, cylindrical polar rays.

Remarks: The species was compared with *S. corpulentus* n. sp. under the latter species. Despite the difference in age and geographical area the photographed specimen from the Beriasian of the Mariana Trench, western Pacific, sent to senior co-author by A. Matsuoka is perfectly similar to the holotype.

Anomalies: No anomaly was recorded.

Range and occurrence: Tithonian – Berriasian: lower Tithonian, Mörsheim Formation, Solnhofen area, southern Germany; Berriasian, Mariana Trench, western Pacific.

Group B

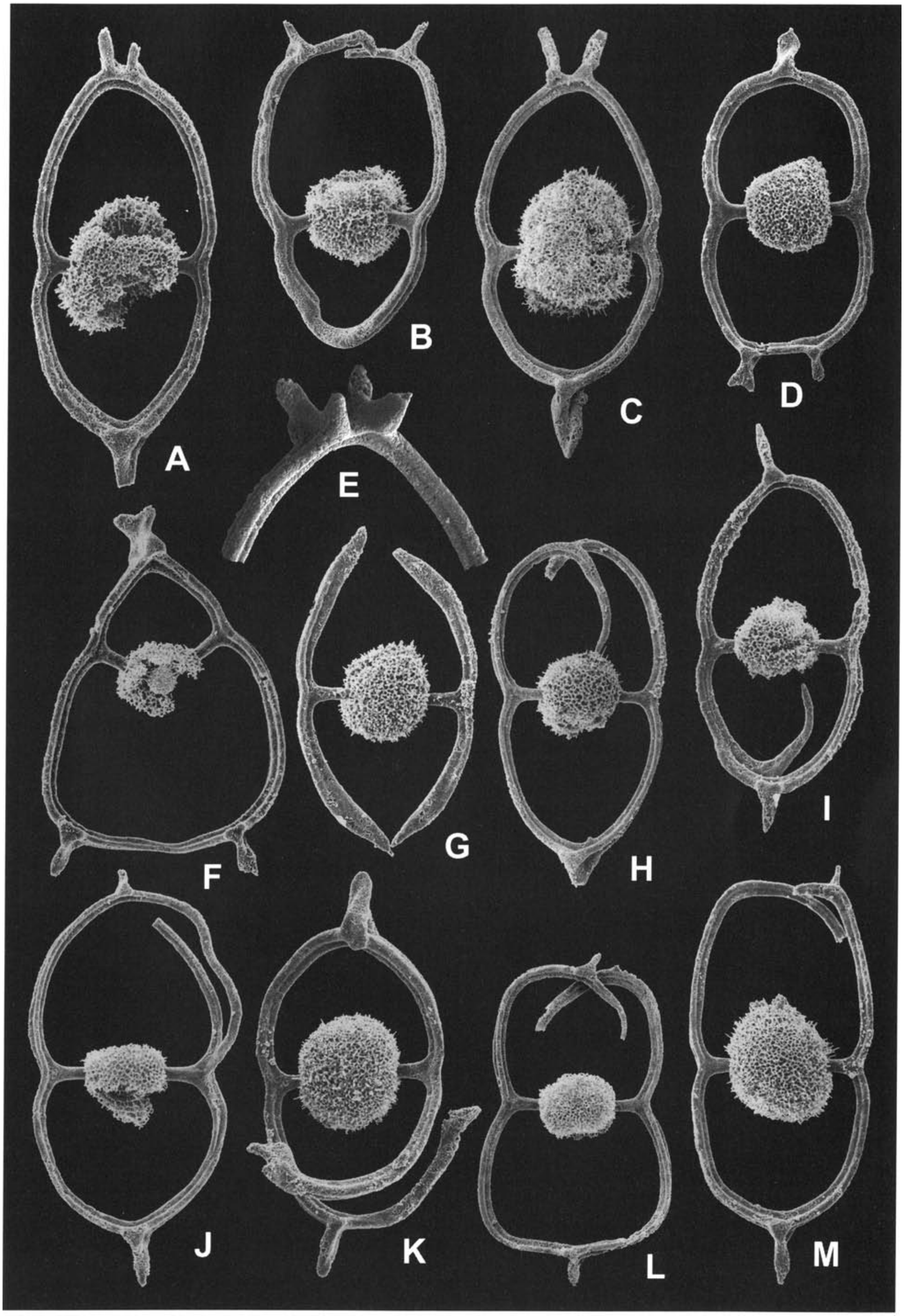
Spongosaturninus kiesslingi n. sp.
Figs. 12A–E, G

1914 *Saturnalis minimus* SQUINABOL: 287, pl. 22 fig. 1, non pl. 23 figs. 6, 6a designated as lectotype of *Vitorfus minimus* (SQUINABOL) by O'DOGHERTY (1994).

Derivatio nominis: The species is named for Wolfgang Kiessling (Institut für Paläontologie, Berlin) for his valuable contribution to the knowledge of Mesozoic Radiolaria.
Holotype: Fig. 12A, coll. Musée de Géologie Lausanne, No. 74397.
Material: Ten specimens in sample Mu 22.
Dimensions (in µm, based on 7 specimens): Diameter of shell 78–100 (average 86), length of ring without spines 244–267 (average 251), with spines 287–385 (average 324), maximum breadth of ring 125–134 (average 131).

Description: Ring elongate elliptical with acute ends armed with a relatively short triangular spine. Sides of ring convex with a very weak constriction or none at the connection with polar rays. External blade broad, simple, not divided longitudinally into two secondary blades by a secondary groove. Internal blades also high, perpendicular to the equatorial plane of the ring. At the distal ends they fuse under an acute angle and give rise to a blade that extends up to the distal end of the spine.

Fig. 9. A–M: *Dicerosaturnalis trizonalis* (RÜST); abnormal specimens with or without additional spines, with closed or open ring. – All figures except E x100; E x200.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Commonly in face view this blade does not run in the middle of the spine but is slightly deviated to the right or to the left due to a slight sinistral twisting of the blades. Inside the angle made by the two inner blades there is always a small characteristic triangle formed by a blade lying in the plane of the external blade of the ring (Fig. 12C). Perimicrospheric shell spongy, without radial structure, with a diameter slightly smaller than or almost equal with the distance between the two sides of the ring along the polar rays. Usually some thin spines of this test are longer and are connected distally to the ring in the peripolar area.

Remarks: This new species is close to *N. radius* n. sp. from which it differs in having a broader ring, broad, simple external blade and diameter of spongy shell slightly smaller than the internal breadth of the ring. The presence of the small triangular area on the inner side of two ends of the ring is also a distinguishing character. As concerns *Saturnalis minimus* SQUINABOL, 1914 the situation is much more clear after the paper by O'DOGHERTY (1994) who designated the middle Cretaceous specimen of SQUINABOL, 1914, pl. 23 fig. 6 as the lectotype of *Vitorfus minimus* (SQUINABOL). In this situation the specimen of SQUINABOL, 1914, pl. 22, fig. 1 coming from late Tithonian or Berriasian of Cittiglio has no status and can be assigned to other species of this age. We consider it a synonym of *S. kiesslingi* based on the shape of the ring, although it could be also assigned to other species occurring in the Tithonian – Berriasian interval.

Anomalies: A single anomaly was recorded among the 8 specimens so far known (Fig. 12G). It is of Siamese twins type having in common the spongy shell and half the ring.

Range and occurrence: Tithonian – ?Berriasian: lower Tithonian, Mörnsheim Formation, Solnhofen area, southern Germany; Tithonian or Berriasian, Cittiglio, Southern Alps.

Spongosaturninus medioangustus n. sp.
Figs. 12F, I–M

1999 *Acanthocircus minimus* (SQUINABOL). – KIESSLING: 36–37, pl. 7 fig. 9.

Derivatio nominis: From the Latin *medium* – middle and *angustus* – narrow, because of the constricted middle part.
Holotype: Fig. 12L, coll. Musée de Géologie Lausanne, No. 74398.
Material: Five illustrated specimens in sample Mu 22.
Dimensions (in µm, based on 5 specimens): Diameter of central shell 74–87 (average 80), length of ring without spines 235–252 (average 245), with spines 346–383 (average 365), breadth of ring along polar rays 104–112 (average 108), maximum breadth of ring 106–124 (average 113), length of spines 50–78 (average 62).

Description: Ring long and usually narrow with the middle part slightly constricted. Outer blade thickened in the middle portion of ring and divided into two secondary blades by a longitudinal groove. Spines relatively long, pointed, four-bladed, sometimes slightly dextrally twisted so that the blades perpendicular on the ring are slightly displaced to the right on the distal end of the spines.

Remarks: *Spongosaturninus medioangustus* n. sp. differs from *S. kiesslingi* n. sp. in having the spines longer, the ring narrower, more constricted, and the outer blade divided into two blades by a groove in the middle part of the ring. From *S. radius* n. sp. it differs in having a constricted ring at the middle part, the external groove not extended up to the base of spines, the median blade of spines less high and, in some specimens, the spongy shell smaller than the inner distance between the two sides of the ring in the middle part. A specimen with rather similar ring but without the blade perpendicular to the plane of the ring along the spines was illustrated by HULL (1997: pl. 9 fig. 1) from the upper Tithonian of Stanley Mt., California. Also, PESSAGNO (1976: pl. 11 fig. 15) illustrated under the name of *Spongosaturninus ellipticus* CAMPBELL & CLARK an upper Campanian specimen that resembles very much this new species, the only differences being the absence of the constriction at the middle part and also of the visible shoulders at the distal part of the ring. Although this specimen does not belong to *S. ellipticus*, which is a Maastrichtian species with very long spines and shorter ring, this resemblance is worth mentioning because no similar species was until now reported between the Tithonian and Campanian.

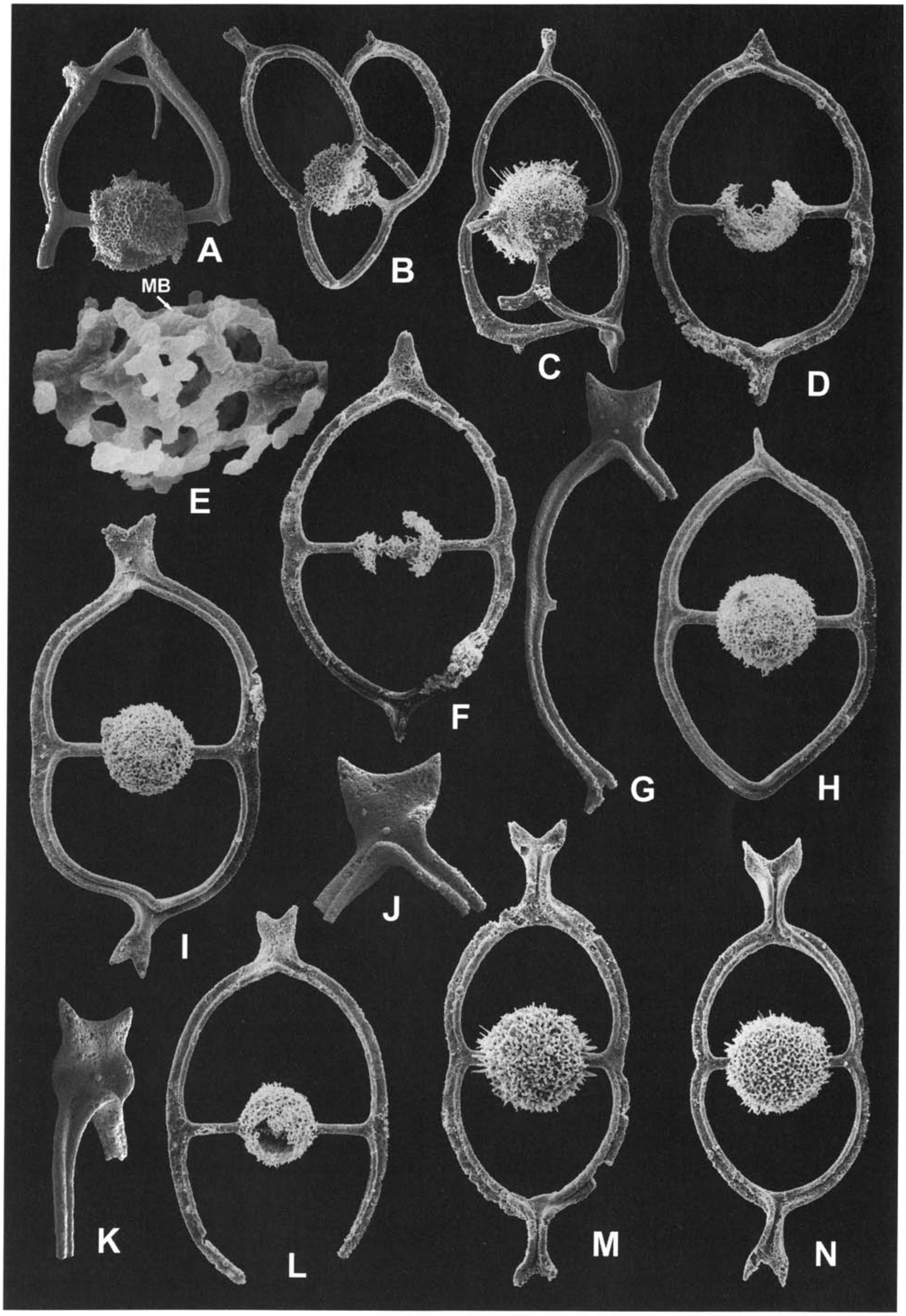
Anomalies: A single anomaly of Siamese twins type was recorded (Fig. 12I). The two rings have in common the spongy shell and one polar ray.

Range and occurrence: Upper Kimmeridgian – lower Tithonian: Lower Tithonian, Mörsheim Formation, southern Germany; upper Kimmeridgian to lower Tithonian, Antarctic Peninsula.

Spongosaturninus radius n. sp.
Figs. 12N–R, 13A

Derivatio nominis: From the Latin *radius* – shuttle.
Holotype: Fig. 12O, P, coll. Musée de Géologie Lausanne, No. 74399.
Material: Nine illustrated specimens in sample Mu 22.
Dimensions (in µm, based on 7 specimens): Diameter of microsphere 27, of spongy test 97–127 (average 109), length of ring without spines 196–249 (average 219), of spines 47–96 (average 72), breadth of ring at middle 74–104 (average 89), maximum breadth 87–113 (average 95).

Fig. 10. A–C: *Dicerosaturnalis trizonalis* (RÜST); A. abnormal specimen with partly closed ring; B, C. Siamese twins anomalies. – **D, F, H**: *Spongosaturnalis corpulentus* n. sp.; D. holotype. – **E, G, I–L**: *Spongosaturnalis matsuokai* n. sp.; E. microsphere of fig. L, MB, median bar; I. holotype; J, K. face and oblique views of the spine of fig. G. – **M, N**: *Moebicircus furiosus* (JUD). – A–C x100; D, F–I, L–N x150; E x 1000; J, K x200.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Description: Ring elongate elliptical, slightly heteropolar, with two blades on the external margin separated by a deep, narrow groove, two on the internal margin, and a robust four-bladed spine at each end. Spines unequal, one being wider and triangular in face view, the other thinner with a well-marked constriction at the boundary with the ring. This constriction marks the end of the groove of the outer margin. Blades of the spines perpendicular to the equatorial plane of the ring are very high with a convex outline in lateral view. Perimicrospheric test spongy, spherical, large as compared to the ring, its diameter usually greater than the breadth of the ring, which it covers on its middle portion.

Remarks: *Spongosaturninus radius* n. sp. was compared to *S. medioangustus* n. sp. under this species.

Anomalies: Of the nine specimens illustrated from the sample Mu 22 one is an anomaly (Fig. 13A) of Siamese twins type with two complete rings perpendicular to each other having in common the spongy test and the two polar rays.

Range and occurrence: Lower Tithonian, Morhsheim Formation, Solnhofen area, southern Germany.

Spongosaturninus tortuosus n. sp.

Figs. 13B–J, L–N

Derivatio nominis: From the Latin *tortuosus* – tortuous, twisted.
Holotype: Figs. 13F, G, coll. Musée de Géologie Lausanne, No. 74400.
Material: Thirty-five specimens in the sample Mu 22, of which 14 illustrated, and one from Oman.
Dimensions (in µm, based on 12 illustrated specimens): Diameter of microsphere 26, of spongy shell 85–128 (average 112), total length of ring with spines 420–486 (average 462), length of spines 100–148 (average 121), breadth of ring at middle 94–110 (average 101), maximum breadth of ring 97–112 (average 196).

Description: Ring small, narrow, elongate elliptical with one forked spine at each end. Ends of ring twisted dextrally up to 90° or even more relative to the equatorial plane of the ring so that the plane of the spines may be practically perpendicular to the plane of the ring. Blades of the internal margin of the ring thick and low. External blade divided into two secondary blades by a deep, very narrow longitudinal groove on the portion between the two spines. Spines robust, strongly forked usually, four-bladed proximally, with three-bladed and dextrally twisted arms; blades broad, formed alternatively by the prolongation of the external blade of the ring and by the blades developed on the ring from the internal blades. Sides of ring parallel or slightly constricted medially. Perimicrospheric test spongy, spherical or subspherical, its diameter equal to that of the breadth of the ring or greater, covering the middle part of the latter and leaving only two relatively small triangular hollows between the shell and the ends of the ring.

Remarks: By the exaggerated twisting of spines this species is one of the strangest saturnalids. It is very close to *S. radius* from which it only differs in having both spines twisted and forked.

Anomalies: Of the 35 specimens in sample Mu 22 three are anomalies: two (Figs. 13M, N) are of Siamese twins type having two more or less regular rings and a single shell with two polar rays in common, similar to the Siamese twins of the species *S. radius* discussed above; the third (Figs. 13I, J) has one end normal and the other end with the two parts of the ring long, crossed and partly fused.

Range and occurrence: Lower Tithonian, Mörnshein Formation, Solnhofen area, southern Germany, and Wahrah Formation, Oman (UTM 778953/2454097).

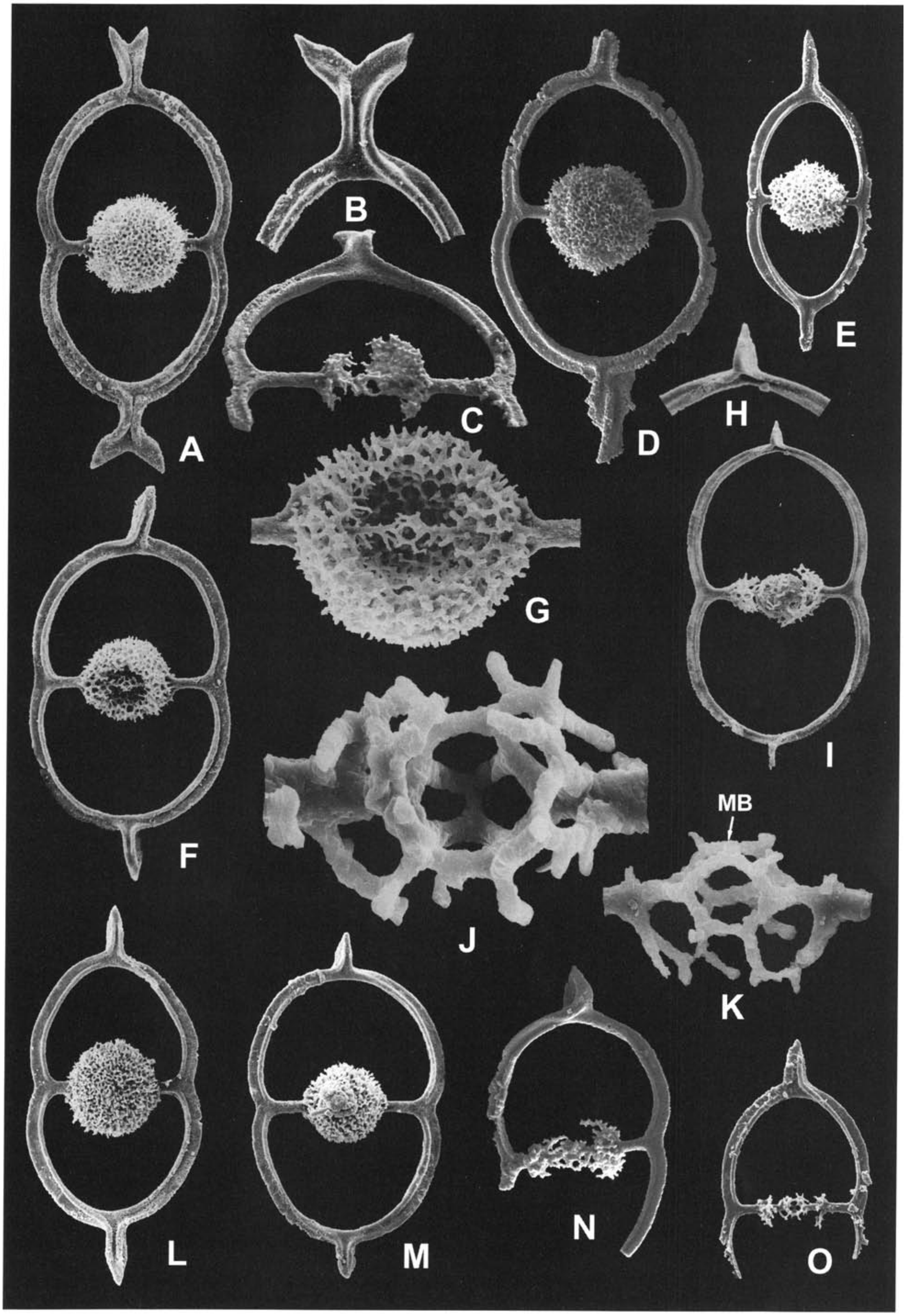
Genus *Moebicircus* n. gen.

Type species: *Acanthocircus furiosus* JUD, 1994.
Derivatio nominis: The genus is named for August Ferdinand Möbius (1790–1868), the German mathematician who "discovered" the surface (strip) that now bears his name. Masculine gender.

Diagnosis: Saturnalids with spongy central shell, polar rays, and elliptical three-bladed ring, of which two blades are on the inner margin and one on the outer margin on most part of its circumference. Ends of ring with a four-bladed spine. Blades of each spine alternately formed by the prolongation of an inner and an outer blade of the ring, which is twisted dextrally or sinistrally at the two ends of the circumference according to the Möbius strip pattern. Additional spines, when present, are in lateral position and arise from the outer margin of the ring.

Remarks: By many characters (shape of ring, position of blades, presence of a spine at each end of the ring) this new genus is closely related to *Spongosaturninus* CAMPBELL & CLARK, from which it probably derived and from which it differs in having the ring built according to the Möbius strip pattern and in having also a four-bladed distal spine the blades of which are alternately formed by the prolongation of an inner and an outer blade of the ring. As it is known the Möbius strip has only one edge and only one side and can be made by taking a narrow strip of paper, giving it a half twist, and

Fig. 11. A, B: *Moebicircus furiosus* (JUD); B. detail of a spine showing the twisting of the blades and their position along spine. – **C–G, J–M, O**: *Moebicircus ruthae* n. sp.; C. oblique view showing the twisting of ring at distal part; D. specimen with an anomalous spine; G. detail of fig. F; J. detail of the apical structure of the microsphere of fig. O in antapical view; K. detail of the microsphere of fig. G in lateral view, MB, median bar. L. holotype. – **H–I**: *Moebicircus* (?) sp. 1; H. detail of upper spine of fig. I. – **N**: *Moebicircus* (?) sp. 2. –A, E, F, L–O x150; B–D, I x200; G, H x400; J, K x1500.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joining the ends with tape to form a closed ring. The ring of the genus *Moebicircus* shows the same features (Fig. 5) by twisting the blades of the ring at the two extremities. The sense of twisting may be dextral or sinistral and, according to fossil record, seems to be constant in each species. Taking into account these features and its stratigraphic range, *Moebicircus* n. gen. seems to have derived from *Spongosaturninus* and to be the ancestor of *Vitorfus* PESSAGNO, 1977. *Vitorfus* sp. C, for instance, illustrated by PESSAGNO (1977b) from the upper Albian of California, shows a rather similar connection between the blades of the four-bladed distal spines and the blades of the three-bladed ring.

Twisting of the blades of the ring according to the Möbius strip pattern is not only characteristic of this genus. It is a trend that started in the lower Toarcian to species of the *Hexasaturnalis* type. The oldest species with such a character was illustrated by MATSUOKA et al. (1994: 54, figs. 17, 18) as *Mesosaturnalis* sp. b, but the same character appears also with the species *Eospongosaturnalis protoformis* (YAO 1972) that first appears at almost the same stratigraphic level. Both these species are members of the subfamily Hexasaturnalinae. As fossil record proves, in the subfamily Saturnalinae this trend appeared much later, in the lower Tithonian or Kimmeridgian.

The following species may belong to this genus: *Acanthocircus furiosus* JUD, *Moebicircus ruthae* n. sp., *Acanthocircus longispinosus* DONOFRIO & MOSTLER, 1978, *A. longispinosus* DONOFRIO & MOSTLER in MATSUOKA (1998: fig. 181), and *Spongosaturnalis* sp. aff. *Saturnalis lateralis* gr. CAMPBELL & CLARK in RENZ (1974).

Range: Lower Tithonian to Barremian as far as known.

Moebicircus furiosus (JUD, 1994)

Figs. 10M, N, 11A, B

* 1994 *Acanthocircus furiosus* JUD: 59, pl. 2 figs. 4–7.
1995 *Acanthocircus furiosus* JUD. – BAUMGARTNER et al.: 64, pl. 5003 figs. 1–4.
1997 *Acanthocircus* (?) *furiosus* JUD. – DUMITRICA et al.: 18, pl. 1 fig. 5.
1997 *Acanthocircus dicranacanthos* (SQUINABOL), part. – HULL: 29, pl. 9 fig. 4, non fig. 3.
1998 *Acanthocircus furiosus* JUD. – MATSUOKA: 171, pl. 12 fig. 180.

Description: Ring long, elliptical, constricted in the middle part at the connection with polar rays, widely arches at the two ends, and bearing at each end one forked, four-bladed spine. At distal ends on each side of ring blades are twisted dextrally before continuing along the spines.

Remarks: The specimens from the Mörnsheim Formation are very similar to those illustrated from younger stratigraphic levels, the only difference concerns the shape of the forked spines in some specimens. In the upper Tithonian – Hauterivian interval the two branches of the fork are generally short, pointed, and very little divergent, whereas in the sample Mu 22 in most cases the two branches of the fork are broader and only distally pointed. A single specimen of the eight we found (Fig. 11A) has at one end a spatulate spine, common in this early Tithonian population, and at the other end a spine similar to the spines of the holotype and paratypes (JUD 1994).

The shell of the species was not preserved in any of the specimens so far illustrated. The very good preservation of the radiolarian fauna from the sample Mu 22 proves that the shell is spongy, many-layered and that in its centre is the same microsphere as the one previously described by DUMITRICA (1985).

Range and occurrence: Lower Tithonian – upper Hauterivian (JUD 1994), cosmopolitan in the Tethyan Realm (Mariana Trench, Oman, Italy, California Coast Ranges). In our opinion a range extended down to late Oxfordian – early Kimmeridgian (BAUMGARTNER et al. 1995) is erroneous.

Moebicircus ruthae n. sp.

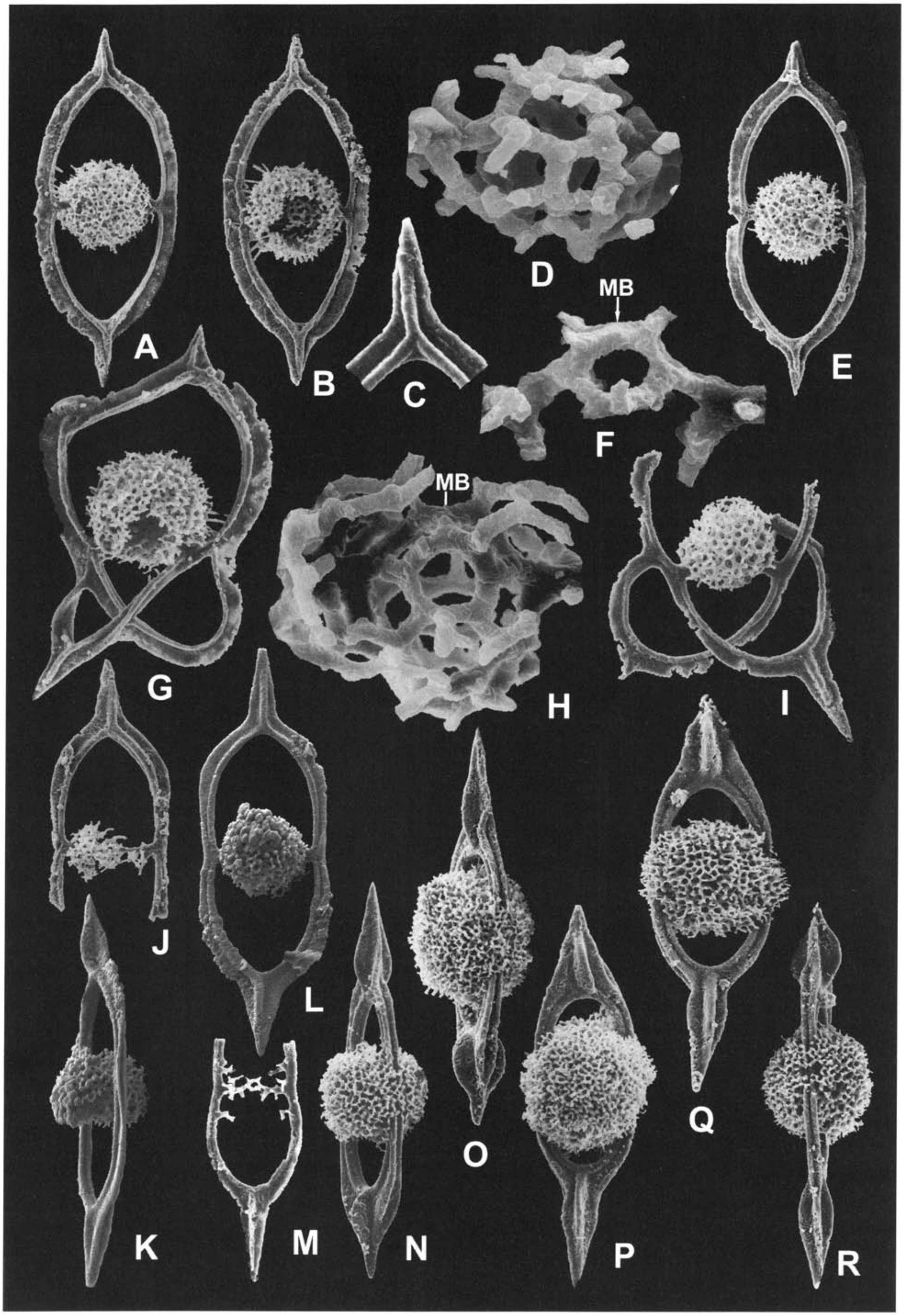
Figs. 11C–G, J–M, O

Derivatio nominis: The species is named for Ruth Dumitrica-Jud to honour her contribution to the knowledge of the Tithonian – Early Cretaceous radiolarians and her "sponsoring" the radiolarian research of the senior author.
Holotype: Fig. 11L, coll. Musée de Géologie Lausanne, No. 74401.
Material: Forty specimens in sample Mu 22 of which 18 illustrated and 5 illustrated but not published specimens in the Berriasian of the Mariana Trench.
Dimensions (in µm, based on 14 specimens): Diameter of central shell 80–121 (average 99), length of ring without spines 275–380 (average 322), breadth of ring along polar rays 147–235 (average 190), maximum breadth of ring 152–245 (average 204), length of spines 40–75 (average 56).

Description: Ring elliptical with rounded to slightly acute ends and a slight constriction at the connection with polar rays. Ring three-bladed with an external blade and two internal blades. Distal ends with a four-bladed, relatively short spine. Spine simple, gently tapered or blunt. Blades of ring twisted dextrally at the base of spines and extended along spines up to their tip.

Remarks: The morphology of the species is rather constant, the most visible variability concerns the ratio be-

Fig. 12. A–E, G: *Spongosaturninus kiesslingi* n. sp.; A. holotype; C. detail of spine and end of ring; D. microsphere of fig. B; G. anomaly of Siamese twins type. – **F, I–M**: *Spongosaturninus medioangustus* n. sp.; F. detail of microsphere of fig M: MB, median bar; I. anomaly of Siamese twins type; K. lateral view showing the forked external blade of ring by a secondary groove. – **H, N–R**: *Spongosaturninus radius* n. sp.; H. detail of microsphere in lateral view: MB, median bar; O, P. holotype in lateral and face view; Q, R. same specimen in face and lateral view. – A, B, E, J–R x200; C x500; D, F, H x1500; 7, 9 x250.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tween length and breadth of ring. The species is very close to *M. furiosus* from which it differs in not having forked spines. Although there is no record of the two species at older levels this resemblance suggests that *M. ruthae* gave rise to the latter species. *M. ruthae* seems to be closely related to *Acanthocircus longispinosus* DONOFRIO & MOSTLER, 1978 from which it differs in having shorter spines and longer ring.

Anomalies: No anomaly was remarked.

Range and occurrence: Lower Tithonian – Berriasian: Lower Tithonian, Mörsheim Formation, Solnhofen area, southern Germany; Berriasian, Mariana Trench, western Pacific.

Moebicircus ? sp. 1
Figs. 11H, I

Remarks: This morphotype, from which we have only one specimen, has an 8-shaped ring and a short distal spine at either end flattened in plane perpendicular to the plane of the ring. Ring is three-bladed, with two blades on the inner margin and one on the outer margin. At one end, in the neighbouring of the spine, the external blade of the ring of both sides thickens resulting in two high external blades, which fuse on either side to give rise to the spine. On the other end (lower end in pl. Fig 11I) the blades of the ring seem to be twisted sinistrally so that on the upper face the inner blade of the right side becomes perpendicular to the ring and merges in the base of the spine where it fuses with the outer blade of the left side. The shape of the ring and the upper spine resemble that of *Dicerosaturnalis angustus* (BAUMGARTNER, 1995) (*Acanthocircus trizonalis angustus* BAUMGARTNER in BAUMGARTNER et al. 1995), but the ring has two blades on the inner margin and one on the outer margin.

Range and occurrence: Lower Tithonian, Mörnsheim Formation, Solnhofen area, southern Germany.

Moebicircus ? sp. 2
Fig. 11N

Remarks: From this morphotype we have only the illustrated specimen. It does not show a twisting of the blades of the ring as in *Moebicircus* but only a displacement of the outer blade before continuing along the spine which is short and flattened in plane perpendicular to the ring. This spine resembles also that of *Dicerosaturnalis angustus* BAUMGARTNER, 1995.

Range and occurrence: Lower Tithonian, Mörnsheim Formation, Solnhofen area, southern Germany.

Genus *Acanthocircus* SQUINABOL, 1903

* 1903 *Acanthocircus* SQUINABOL: 124.
1944 *Spongosaturnalis* CAMPBELL & CLARK: 7.

Type species: *Acanthocircus irregularis* SQUINABOL, 1903 [subsequent designation by CAMPBELL (1954)].

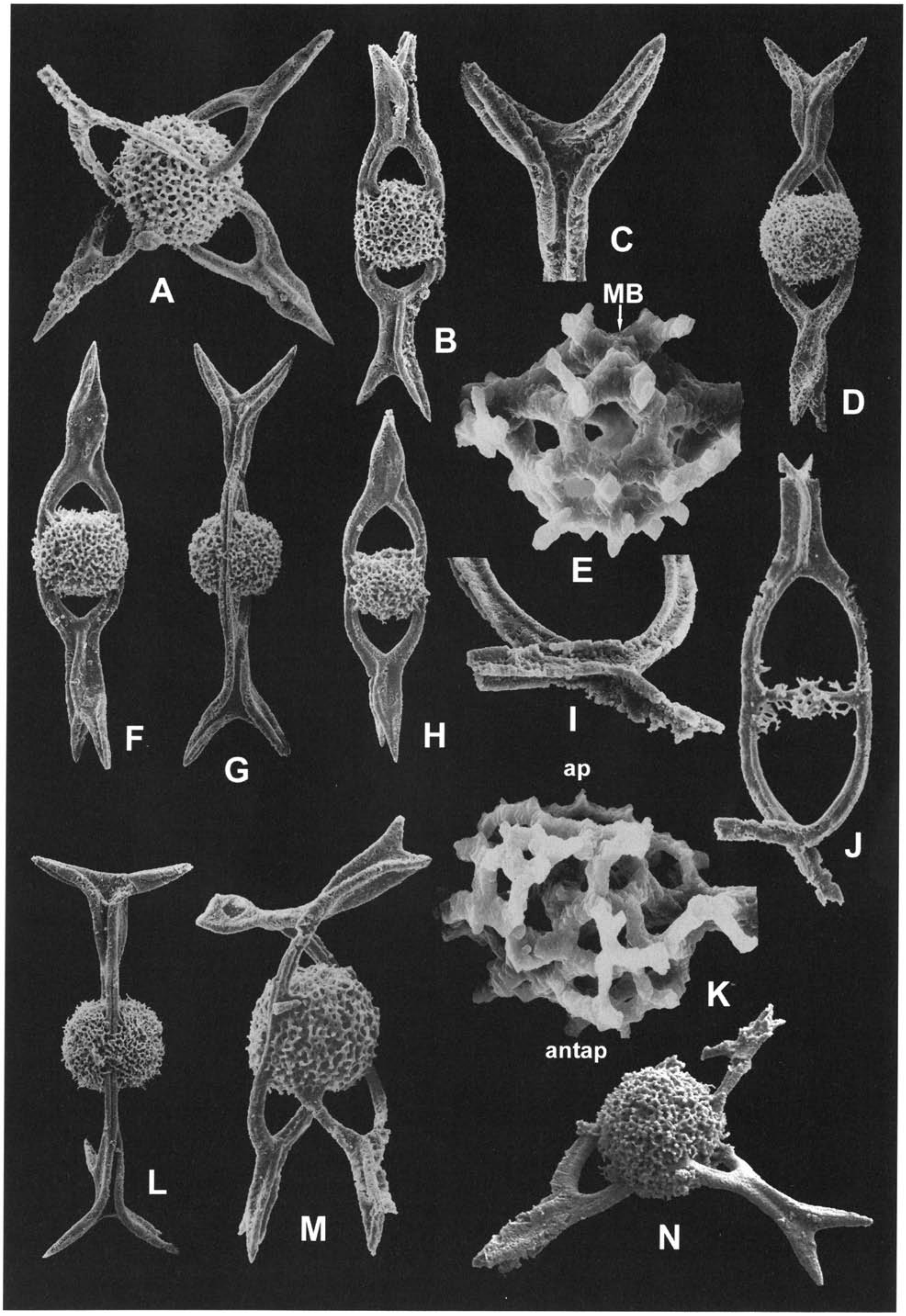
Remarks: During the last 3 decades this generic name has been applied to almost all Cretaceous and to a part of the Jurassic Saturnalidae irrespective of the number of spines or the number and position of blades, if any. Although on morphological and/or evolutionary reasons some species previously assigned to it have been transferred to other genera (*Vitorfus* PESSAGNO, *Aurisaturnalis* DUMITRICA & DUMITRICA-JUD, *Dicerosaturnalis* DUMITRICA & DUMITRICA-JUD, etc) its volume is still too large as compared to other genera. In this paper we retained from it other species, which we assigned either to *Spongosaturninus* CAMPBELL & CLARK, or to *Moebicircus* n. gen. Even so the species still assigned to this genus show a wide morphological variety, from species with subcircular to elongate ring, with or without peripheral spines, with three blades, of which two on the inner margin, with 4 blades or even, practically, without blades. The reason of this situation seems to be the peculiar morphology of *Acanthocircus irregularis* SQUINABOL, the type species of the genus. This species has usually a flattened ring without blades, but some specimens show a three-bladed structure especially in the middle part, with two blades on the inner margin and one at the outer margin (O'DOGHERTY 1994). The absence of blades on the ring or only on a part of the ring seems to be an evolutionary character. Similarly, the absence of peripheral spines is an evolutionary character. For this reason in the present paper we assign to this genus only species with or without peripheral spines but with circular, subcircular to elliptical ring without a well-developed spine at the ends of the ring. Viewed in such a way this genus has as perfect synonym the genus *Spongosaturnalis* CAMPBELL & CLARK, 1944.

Range: Middle or Upper Jurassic to Maastrichtian.

Acanthocircus calvus n. sp.
Figs. 13K, 14A–C, E

Derivatio nominis: From the Latin *calvus* – bald.
Holotype: Fig. 14C, coll. Musée de Géologie Lausanne, No. 74402.
Material: Twenty-eight specimens in sample Mu 22 of which 8 illustrated.
Dimensions (in µm, based on 8 specimens): Diameter of microsphere 19–20, of spongy shell 108–153 (average 126),

Fig. 13. A: *Spongosaturninus radius* n. sp., anomaly of Siamese twins type. – **B–J, L–N**: *Spongosaturninus tortuosus* n. sp., holotype and paratypes showing various degrees of twisting and anomalies; C. detail of a spine of holotype; E. detail of the microsphere of fig. J in lateral view: MB, median bar; F, G. holotype in face and lateral views; I. detail of lower part of fig. J showing that the two arms of ring are partly fused; J. anomaly with one end of ring partly open; M, N. anomalies showing two types of Siamese twins. – **K:** *Acanthocircus calvus* n. sp., microsphere of specimen illustrated in Fig. 14E, lateral view. – A, J, M, N x250; B, D, F–H, L x150; C x300; E, K x1500; I x400.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length of ring 338–465 (average 406), breadth of the ring along polar rays 182–265 (average 224), in distal region 230–321 (average 267).

Description: Ring smooth, roughly rectangular, commonly bilaterally symmetrical both relative to longitudinal and transversal axes, although one half is sensible larger than the other. Ring circumference made of two main parts, a median part on both sides of the polar rays made of straight, slightly divergent, three-bladed bars, and a distal part, which forms a kind of arch connecting the former. Middle part broad with an external blade in the plane of ring and two internal blades almost perpendicular to the plane of ring. Distal parts of ring thin, unbladed in the middle part, widely arched or slightly acute. Transition between the two parts of ring gradual. Shell spherical, spongy, many-layered, with a microsphere typical for the Saturnalidae. Polar rays four-bladed, each blade continuing the inner blades of the ring.

Remarks: *Acanthocircus calvus* is well distinguished from all the other species of the genus by its straight three-bladed, slightly divergent sides, smooth, arched dorsal ends, and the four-bladed polar rays. From *Spongosaturnalis protoformis* YAO, 1972, with which it resembles very much, it differs by the position of the odd blade of the ring on the middle part of ring. This blade is internal with the latter species and all blades are usually twisted before disappearing on the distal ends.

Anomalies: No anomaly found.

Range and occurrence: Lower Tithonian, Mörnsheim Formation, Solnhofen area, southern Germany.

Acanthocircus simplex (SQUINABOL, 1914)
Figs. 14D, F–H

* * 1914 *Saturnalis simplex* SQUINABOL: 286, pl. 22 (3) fig. 2.
* 1997 *Acanthocircus protoformis* (YAO). – HULL: 31, pl. 9 fig. 14.

Material: Ten specimens in sample Mu 22, of which 7 illustrated.
Dimensions (in µm, based on 7 specimens): Diameter of microsphere 19, of spongy central shell 93–109, length of ring 350–449 (average 382), breadth of ring along the axis of polar rays 238–286 (average 257), maximum breadth of ring 250–300 (average 280).

Description: Ring smooth, oval, symmetrical relative to the long axis but asymmetrical relative to the short axis, one half being wider than the other. Ring three-bladed with a broad blade on the outer margin and two on the inner margin. On the distal end of the wider half blades of the ring tend to disappear, the bar of the ring is thinning and becomes oval in cross section. The distal end of the narrower half changes neither the three-bladed structure of the ring nor the breadth of the external blade. On the middle part, in the area of connection with the polar rays, ring and external blade are constricted. This area is usually separated by the rest of the ring by a broadening of the external blade, which results in the appearance of two shoulders.

Remarks: The specimens from the sample Mu 22 resemble perfectly the holotype illustrated by SQUINABOL (1914) from the Jurassic from Fontanafredda (Colli Euganei, Italy) that shows the same shape and the same difference in thickness of the ring at the two ends. It differs essentially from *Spongosaturnalis protoformis* YAO by the external position of the odd blade of the ring. From *A. calvus* n. sp. it differs by having curved instead of straight sides, one distal end three-bladed, and by a sharp constriction of the external blade in the central part, at the contact with the polar rays. Although included in the synonymy of this species *Acanthocircus protoformis* (YAO) of HULL (1997) from the lower upper Kimmeridgian of Mexico differs from our specimens by having also two blades on the outer margin.

Anomalies: No anomaly recorded.

Range and occurrence: Upper Kimmeridgian – Tithonian: lower Tithonian, southern Germany; Tithonian?, Colli Euganei (Italy); upper Kimmeridgian, Mexico.

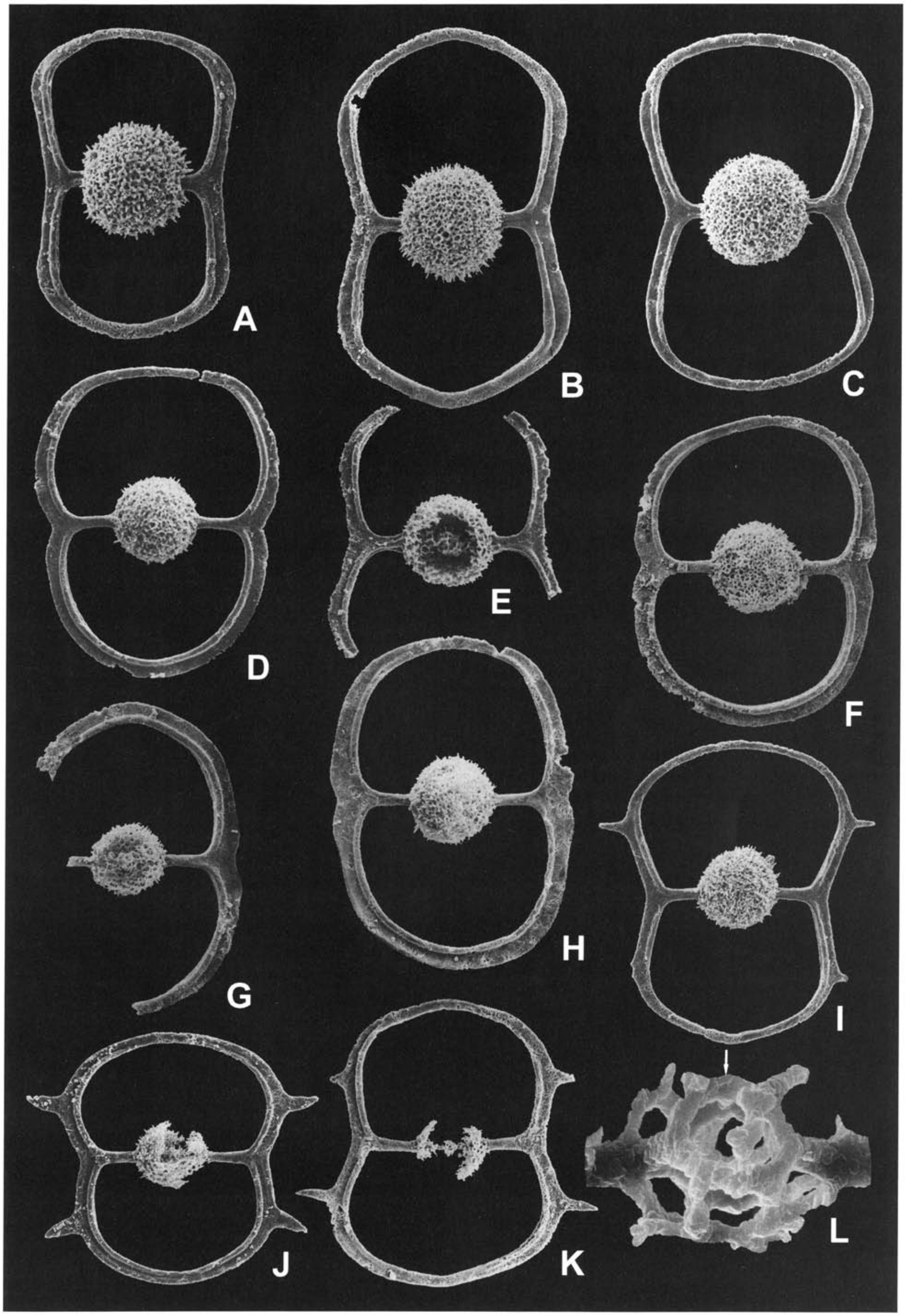
Acanthocircus spelae n. sp.
Figs. 14I–L, 15A, B

1993 *Acanthocircus* sp. YANG: 88, pl. 13 figs. 8, 9.

Derivatio nominis: The species is named for Spela Gorican to honour her contribution to the knowledge of Mesozoic radiolarians.
Holotype: Fig. 14J, coll. Musée de Géologie Lausanne, No. 74403.
Material: Nineteen specimens in the sample Mu 22, of which 12 illustrated, and 2 from the Tithonian of the Taman Formation (east-central Mexico).
Dimensions (in µm, based on 12 specimens): Diameter of microsphere 18–19, of spongy central shell 95–118 (average 104), length of ring 380–444 (average 405), breadth of ring along polar rays 211–313 (average 272), maximum breadth at the base of spines 258–375 (average 331).

Description: Ring 8-shaped, three-bladed, with two blades on the internal margin and one on the external margin, and 4 spines, one on each side. The two halves of ring equal or unequal, one being sometimes slightly wider. External blade broader on the two sides of the ring, narrowing towards the distal ends, which may preserve the three-bladed structure or may be circular or oval in cross section when the ring is very thin. Ends of ring widely arched. External blade of the ring sometimes thickened either on the middle part of the ring or at its

Fig. 14. A–C, E: *Acanthocircus calvus* n. sp.; C. holotype. – **D, F–H**: *Acanthocircus simplex* (SQUINABOL). – **I–L**: *Acanthocircus spelae* n. sp.; J. holotype; L. detail of the microsphere of fig. K. – A–H x150; I–K x120; L x1500.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ends. Spines flat, triangular or spatulate, straight or slightly bent towards the ends of the ring. They generally arise from the external blade at the middle distance between polar rays and distal end of the ring.

Remarks: By its general shape and ring structure *Acanthocircus spelae* n. sp. is close to *A. calvus* n. sp., from which it differs in bearing the four peripolar spines and a shorter ring. Although the specimens illustrated by YANG (1993) from the upper Tithonian of Mexico are structurally similar to those from the lower Tithonian of the Solnhofen area, they differ by being longer and by having the distal ends much more arched.

Anomalies: No anomaly recorded.

Range and occurrence: Tithonian: lower Tithonian, Mörnsheim Formation, Solnhofen area, southern Germany; upper Tithonian, east-central Mexico.

Acanthocircus breviaculeatus DONOFRIO & MOSTLER, 1978

Figs. 15D–G

* 1978 *Acanthocircus breviaculeatus* DONOFRIO & MOSTLER: 26, pl. 1 fig. 9, pl. 3 figs. 12, 14.
1987 *Acanthocircus breviaculeatus* DONOFRIO & MOSTLER. – PAVSIC & GORICAN: 22, pl. 2 fig. 1.
1992 *Acanthocircus breviaculeatus* DONOFRIO & MOSTLER. – STEIGER: 35, pl. 6 figs. 5–7.
1997 *Acanthocircus breviaculeatus* DONOFRIO & MOSTLER. – DUMITRICA et al.: 18, pl. 1 figs. 13, 14.
non 1981 *Acanthocircus breviaculeatus* DONOFRIO & MOSTLER. – DE WEVER: 141, pl. 1 figs. 3, 4.

Material: Seven specimens, all from sample Mu 22.
Dimensions (in µm, based on 6 specimens): Diameter of spongy test 73–90 (average 85), breadth of ring at middle 207–238 (average 220), maximum breadth 235-262 (average 253), length of ring 280–327 (average 295).

Description: Peripheral ring 8-shaped, slightly constricted in the middle part and bearing 8–12, commonly 10 peripheral spines. Ring three-bladed, with two blades on the inner margin, but tending to become four-bladed by the thickening of the outer margin on the whole circumference or only on some portions, resulting in formation of a narrow groove on both surfaces. Ring widely arched at both ends, which tend to become slightly flattened. Breadth of outer blade commonly slightly larger on the middle portion and narrower at the two ends. Peripheral spines relatively short, triangular, flattened or slightly four-bladed, their number is commonly five in number in each half but may vary from 4 to 6, rarely 7. Length of spines usually decreases toward the two ends. The two peripolar spines rather far from one another, and the bars of ring between these spines and peripolar rays straight. Perimicrospheric test spongy, many-layered, without radial structure.

Remarks: Most specimens from the Mörsheim Formation assigned to *Acanthocircus breviaculeatus* differs from the holotype of this species in being shorter, in having the two peripolar spines farther off from the polar rays, and in having the ring shape slightly squarish. By these characters they may be well comparable with one of the two paratypes of the species (DONOFRIO & MOSTLER 1978, pl. 3 fig. 12). On the other way, by the longer distance between the peripolar spines this species seems to be close to *Acanthocircus spelae* n. sp.

Anomalies: No anomalies of the ring or spines have been recorded.

Range and occurrence: Tithonian – Berriasian: lower Tithonian, Mörnsheim Formation, Solnhofen area, southern Germany; common in upper Tithonian to Berriassian from central and western Tethys.

Acanthocircus echinocircus n. sp.

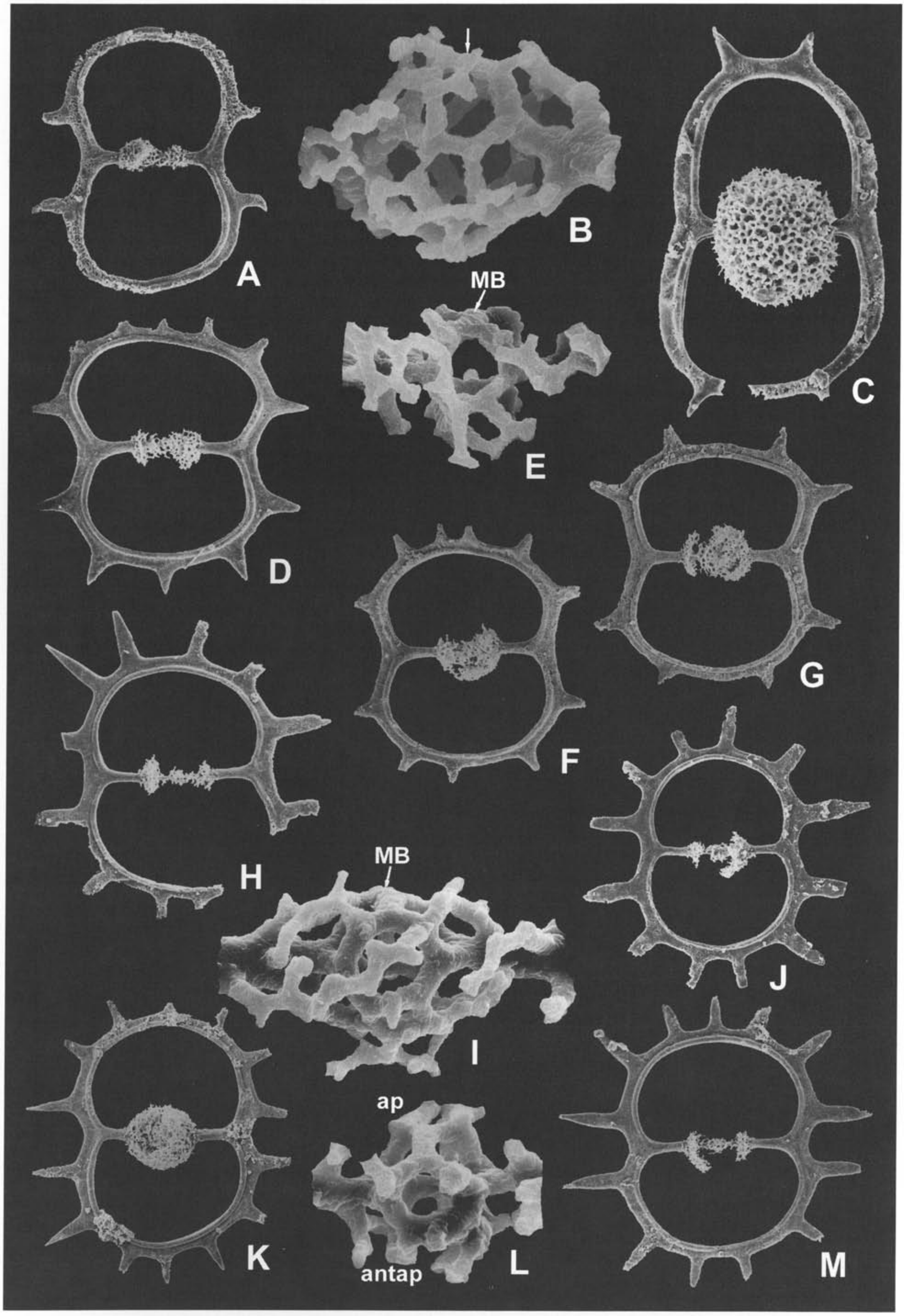
Figs. 15H–M

1973 ?*Spongosaturnalis* (?) *aculeatus* (RÜST) (?). – FOREMAN: 261, pl. 4 fig. 2.
1973 ?*Spongosaturnalis* (?) sp. aff. *S.* (?) *aculeatus* (RÜST). – FOREMAN: 261, pl. 4 figs. 1, 3.
1978 *Palaeosaturnalis hueyi* (PESSAGNO) part. – DONOFRIO & MOSTLER: 35, pl. 1 fig. 5, non figs. 2, 3, 6.
1993 *Acanthocircus* sp. cf. *yaoi* YANG: 88, pl. 14 figs. 8, 11, 15.

Derivatio nominis: From the Latin *echinus* – urchin and *circus* – circle.
Holotype: Fig. 15J, coll. Musée de Géologie Lausanne Nr. 74404.
Material: Fourteen specimens from the sample Mu 22 and 3 from the Taman Formation, east-central Mexico.
Dimensions (in µm, based on 11 specimens): Diameter of microsphere 18–23 (average 21), of spongy shell 94–105 (average 100), breadth of ring at middle 242–282 (average 273), maximum breadth of ring 277–316 (average 304), length of ring 355–368 (average 370).

Description: Ring 8-shaped, three-bladed with two blades on the inner margin and one on the outer margin, and with 12–14, commonly 12 spines originated in the outer blade. Ring slightly constricted in the middle part and rounded at the two ends. Spines long, flat, pointed, but commonly with parallel to subparallel sides on the proximal portion and commonly decreasing sensibly in length on the distal ends of ring. The two peripolar spines close to one another, parallel or subparallel. Peri-

Fig. 15. A, B: *Acanthocircus spelae* n. sp.; B. detail of microsphere of fig. A, arrow points to MB. – **C**: *Acanthocircus* sp. – **D–G**: *Acanthocircus breviaculeatus* DONOFRIO & MOSTLER; E. detail of microsphere of fig. D: MB, median bar. – **H–M**: *Acanthocircus echinocircus* n. sp.; I. detail of microsphere of fig. M: MB, median bar; L. detail of microsphere of fig. H: ap, apical part, antap, antapical part; M. holotype. – A, D, F–H, J, K, M x125; B, E, I, L x1500; C x200.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microspheric test subspherical to slightly ellipsoidal, spongy, many-layered, without radial structure.

Remarks: *Acanthocircus echinocircus* is very close to *Acanthocircus breviaculeatus* DONOFRIO & MOSTLER, 1978 from which it differs by the greater number of spines, by longer spines and essentially by having the two peripolar spines much closer to one another and the ends of ring rounded, never flattened. The specimens of *A.* sp. cf. *yaoi* illustrated by YANG (1993) from the upper Tithonian Taman Formation of east-central Mexico are perfectly similar to those from the Solnhofen area. *A. echinocircus* differs from *A. yaoi* YANG, 1993 by having shorter and flattened spines rather than four-bladed. One of the 4 specimens illustrated by DONOFRIO & MOSTLER (1978) as *Palaeosaturnalis hueyi* (PESSAGNO) from the lower Cretaceous of the Southern Alps seems to be also conspecific with this new species. Unfortunately we have no precise information on the locality and stratigraphic level of this specimen. The specimens illustrated by FOREMAN (1973: pl. 4 figs. 1–3) differ from this new species either in having the spines conical or in not having parallel peripolar spines.

Anomalies: No anomalies of the ring or spines have been recorded.

Range and occurrence: Tithonian; lower Tithonian, Mörnsheim Formation, Solnhofen area, southern Germany; upper Tithonian, Southern Alps and Taman Formation, east-central Mexico.

Acanthocircus sp.

Fig. 15C

Remarks: This species, from which we have only the illustrated specimen, resembles partly *A. calvus* n. sp. and *A. simplex*, but differs in having two spines at each end. The two halves are also dissimilar, one being larger and having a thinner bar at the distal end. Both distal ends are flattened, without ridges. Spines are also different, at the wider distal end they are thinner than at the narrower end. As far as we know no similar form has been so far published.

Dimensions (in μm): Diameter of spongy shell 124, length of ring without spines 312, breadth of ring along polar rays 184, maximum breadth 208.

Range and occurrence: Lower Tithonian, Mörnsheim Formation, Solnhofen area, southern Germany.

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