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Blechschmidtia n. gen. and *Tjerkium* n. gen., a case of phyletic gradualism of the Triassic saturnalid Radiolaria

by

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Abstract.–DUMITRICA P. and HUNGERBÜHLER A., 2007. *Blechschmidtia* n. gen. and *Tjerkium* n. gen, a case of phyletic gradualism of the Triassic saturnalid Radiolaria. *Bull. Soc. vaud. Sc. nat. 90.4:* 217-243.
The paper describes two new Late Triassic saturnalid radiolarian genera (*Blechschmidtia* n. gen. and *Tjerkium* n. gen.) and several new species of these genera from Oman and Sicily. They seem to represent a lateral lineage of the family Saturnalidae developed from the same oertlispongid stock as all the saturnalids. These genera constitute a rather homogenous group that differs from the other Triassic saturnalid radiolarians by having usually a ring with 4 main spines and outer margin of ring turned up and down. The evolution of the genus *Blechschmidtia* from its first appearance from the oertlispongid genus *Steigerispongus* KOZUR & MOSTLER up to its extinction is followed and described in detail.

Keywords: Radiolaria, evolution, Trias, *Blechschmidtia*, *Tjerkium*, *Steigerispongus*, Saturnalidae, oertlispohnids, Oman, Sicily.

Résumé.–DUMITRICA P. et HUNGERBÜHLER A., 2007. *Blechschmidtia* n. gen. and *Tjerkium* n. gen., un cas de gradualisme phylétique des Radiolaires Saturnalides du Trias. *Bull. Soc. vaud. Sc. nat. 90.4:* 217-243.
Deux nouveaux genres de radiolaires Saturnalides (*Blechschmidtia* n. gen. et *Tjerkium* n. gen.) ainsi que plusieurs nouvelles espèces provenant d'Oman et de Sicile sont décrits dans le présent article. Ces formes semblent représenter une lignée latérale de la famille des Saturnalidae qui s'est développée à partir de la même souche d'oertlispongidés que les autres Saturnalides. Les genres décrits constituent un groupe relativement homogène qui diffère des autres Saturnalides triassiques par leur anneau possédant communément 4 épines principales et une bordure recourbée. L'évolution du genre *Blechschmidtia*

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depuis sa première apparition à partir du genre *Steigerispongus* Kozur & Mostler jusqu'à sa disparition est retracée et décrite en détail.

Mots clés: Radiolaires, évolution, Trias, *Blechschmidtia*, *Tjerkium*, *Steigerispongus*, Saturnalidae, oertlispongidés, Oman, Sicile.

Introduction

At present, it is generally admitted that the radiolarian family Saturnalidae DEFLANDRE appeared for the first time in the early Carnian from some evolved members of the family Ortlispongidae KOZUR & MOSTLER by the appearance of a second foliaceous spine similar with and opposite to the main foliaceous spine characteristic of this latter family, and that the genus *Angulosaturnalis* LAHM 1984 is intermediary between the Oertlispongidae and the Saturnalidae (Kozur and Mostler 1983, 1990). Although the two authors attached this genus to the Oertlispongidae it should be considered as the oldest member of the Saturnalidae as it had been originally done (Lahm 1984) because, unlike the Oertlispongidae, it has two opposite foliaceous spines, which is the main evolutionary jump towards building the saturnalid-type skeleton. The only difference from the Saturnalidae is that the lateral extremities of the two wing-shaped foliaceous spines of *Angulocircus* are not fused to form a ring. However, this is a secondary process, which is easier to be accomplished evolutionarily once the wing extremities are sufficiently long.

In the present paper we want to show that the same saturnalid ring could be built along a short lateral lineage from the same oertlispongid stock. In this lineage we recognize two new genera, *Blechschmidtia* n. gen. and *Tjerkium* n. gen. They represent a rather homogenous group that differs from the other Triassic saturnalids by commonly having a ring with usually 2 equatorial spines and 2 sinistrally twisted polar spines along with turned borders of the ring.

Material studied

Besides the literature, most of our data comes from 3 sections in Oman (Wadi Bani Khalid, Hamadiyin I and II) and from the Pizzo Mondello section, Sicily. A few samples from other sections have also been used.

1. *Wadi Bani Khalid* section (UTM 706511/2496352).

The section is described in Blechschmidt *et al.* (2004, Figure 4). It is located in the Oman Mountains and from geological point of view belongs to the Hamrat Duru Group of the Hawasina Complex. The section offers one of the best outcrops of the Radiolarian Chert Member of the Triassic Zulla Formation. This member has a thickness of about 55 m in this section and

consists of thin-bedded, red and green radiolarian ribbon chert with interbedded siliceous shale. Its lower boundary is gradual, and its top is marked by a level with *Halobia beyrichi* (MOJSISOVICS). The member spans the interval Late Anisian (Illyrian)–Early Norian. All radiolarians are preserved in chert and have been extracted with diluted HF according to the method developed by DUMITRICA (1970).

2. *Hamadiyin I* section (UTM 582811/2521071)

Both Hamadiyin I and Hamadiyin II sections are located northwest of the Hamadiyin and Haliw localities, a few hundred meters north of the road Izki-Sinew, and expose, from bottom to top, the two formations of the Umar Group of the Hawasina Complex: the Sinni Formation, and the Haliw or Aqil Formation. The Sinni Formation is composed mainly of volcanic rocks. The Haliw Formation (GLENNIE *et al.* 1974) or Aqil Formation (BECHENNEC *et al.*, 1992) is composed of Triassic-Cretaceous predominantly siliceous pelagic deposits and calcirudite and/or megabreccia with reworked shallow-marine carbonates. We prefer to use here the name of Haliw instead of Aqil Formation for this unit because it has priority. Bechennec *et al.* (1992) only precised its content, boundaries and age.

The Humadiyin I section exposes the lower part of the Haliw Formation overlying the ophiolites of the Sinni Formation, which consists, in this section, of only the first two members: a lower member of about 13 m of cherty limestone, and an upper member of about 15 m of filamentous red chert with rare levels of filamentous limestone. Three samples from the latter member, which is late Carnian to early Norian in age, contained a rather diverse and relatively well-preserved radiolarian assemblage interesting for this paper: HA4 at 13 m above the base of the section, HA10 at 26.5 m above the base, and HA11 at 28.5 m above the base. The last sample represents also the top of this section.

3. *Hamadiyin II* section (UTM 5747471/2247306)

The section is located west of the previous section and is much more complete and very well exposed. It corresponds to Figure 15 of BECHENNEC *et al.* (1992) representing the type section of their Aqil Formation. The rocks outcropping along this section belong to 5 members of which the first 4 span the Carnian-Pliensbachian interval. The first two members are similar to those of the Hamadiyin I section. The lower chert member has 18 m. A single sample from this section at about 14 m above the base of the chert member (HU9), late Carnian in age, is interesting for the present paper.

4. *Batain Plain*

From this area only 2 samples are interesting for this paper. Both are coming from the Sal Formation (HAUSER *et al.* 2001) and were collected by Dr. Marc Hauser in the Batain Group, north-eastern coast of Oman: H 851 and H929. Sample H851 (UTM 783523/2475166) contains a poor radiolarian assemblage

(PETERS *et al.,* 2001, p. 76) and the conodont *Paragondolella carpathica* (MOCK) (determination by H. Kozur) that situates the sample in the middle late Carnian, middle Tuvalian *Paragondolella carpathica* Zone. Sample H929 contains an earliest Norian assemblage.

5. *Pizzo Mondello* section

The section is very well known due to its wonderful exposure of the Carnian-Norian rocks (MUTTONI *et al.* 2001, 2004; KRYSTIN *et al.* 2002). The section is very well exposed on the southern flank of the Pizzo Mondello Mountain (Sicani Mountains, Sicily). From this section 3 samples are interesting for this paper: A38 at 33 m, A9a at 95 m and A10a at 99 m above the base of the section which is the contact with the underlying Mufara Formation. In the late Carnian – early Norian portion, which is of special interest for this paper, radiolarians have been considerably corroded during diagenensis, especially due to the contact with calcareous nannofossils that left deep imprints on the siliceous skeletons.

SYSTEMATIC PALEONTOLOGY

The holotypes and paratypes of the new species will be stored in the collection of the Musée Géologique de Lausanne.

Class Radiolaria MÜLLER, 1858
Subclass Polycystina EHRENBERG, 1838, emend. RIEDEL, 1967
?Order Entactinaria KOZUR & MOSTLER, 1982
Superfamily Saturnaliacea DEFLANDRE, 1953
Family Saturnalidae DEFLANDRE, 1953

Genus *Blechschmidtia* n. gen.

Type species: *Blechschmidtia bertinelliae* n. sp.

Diagnosis: Late Triassic Saturnalidae with a spongy spherical skeleton and two polar and commonly two equatorial spines. Base of polar spines and outer margin of ring around spines more or less sinistrally turned. In early evolutionary stages ring not yet closed, formed of two recurved wings. Outer margin of ring or wings turned up and down according to a sinistral twist, so that in each half the right external margin is bent upward and the left external margin downward. During evolution this margin changes into a ridge and starts moving towards the inner margin of ring whereas the outer margin starts being armed with an increasing number of intercalary spines. Shell spongy, arranged in 5-6 or more concentric layers. With or without auxiliary rays.

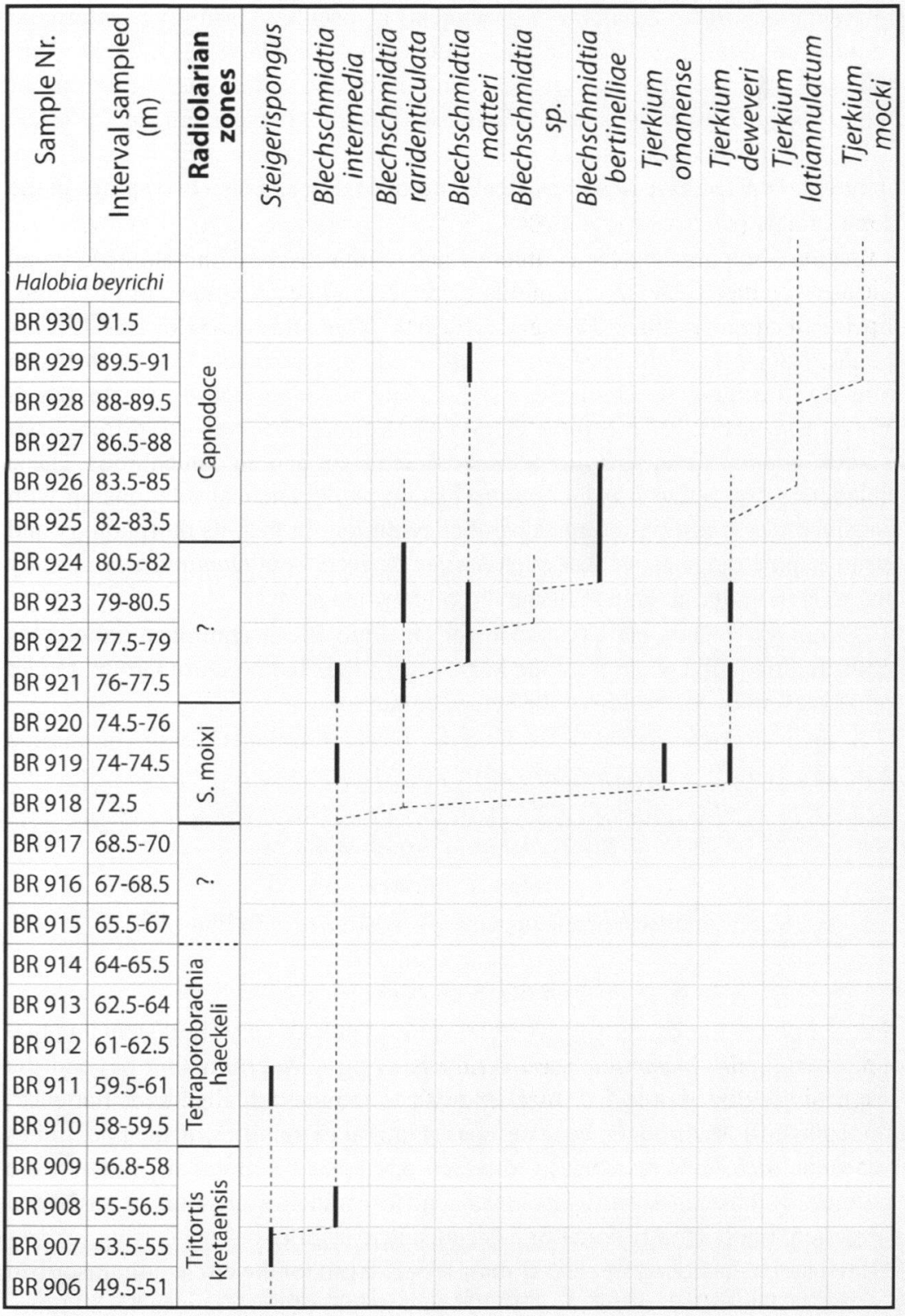

Figure 1.–Occurrence of species of genera *Blechschmidtia* n. gen. and *Tjerkium* n. gen. in the Wadi Bani Khalid reference section, Oman, and their probable phylogenetical relationships. Thick lines mark occurrences in the samples of the section, thin, interrupted lines mark record gaps and supposed phylogenetic connections.

Remarks: *Blechschmidtia* n. gen. is a peculiar primitive saturnalid radiolarian genus probably closely related to *Angulocircus* LAHM from which it differs by having twisted polar spines and turned margin of ring or wings. From *Palaeosaturnalis* DONOFRIO & MOSTLER, emend. KOZUR & MOSTLER, to which some of its species have been assigned, it also differs in having twisted base of spines, bent margin of ring and also two spines in the equatorial axis when ring is closed.

A morphologically very close genus to Blechschmidtia is represented by a new genus, *Berlahmium* TEKIN & DUMITRICA (paper in progress), having as type species *Dumitricasphaera planustyla* LAHM, 1984. This genus, from which spines of two undescribed late Ladinian species have been already illustrated by Dumitrica (1982, Plate 12, Figures 6-9) and to which *Palaeosaturnalis* (?) *incomptus* SUGIYAMA should be attached, differs from *Blechschmidtia* in only having a three-bladed stem and no conical root. These characters prove that *Blechschmidtia* has no phylogenetical relationship with *Berlahmium*. It just represents a parallel evolution. In fact, its morphology and stratigraphic range prove that *Berlahmium* derived from *Dumitricasphaera* by the reduction of one branch of the three-branched spines.

Etymology: The genus is named for Dr. Ingo Blechschmidt to honour his contribution to the geology of the Mesozoic of the Hamrat Duru Group, Oman and as a sign of friendship of the senior co-author.

Range and occurrence: Late Triassic (early Carnian to early or middle Norian), Tethys.

Blechschmidtia intermedia n. sp.
(Plate 1, Figures 1-5)
?*Acanthocircus* spp. (pars) –YOSHIDA 1986, Plate 17,
Figure 9, non 1-8.

Description: Ring laterally open. Polar spines flat with very short stem and two long recurved wings, which are gently tapering and terminating beyond the level of the centre of shell. Distal end of polar spines usually short, flattened, and sinistrally twisted. In very rare cases lateral extremities of the two spines may coalesce but centrifugally directed spines at the point of junction are commonly absent. Sometimes, distal end of branches are curved in lateral direction. Shell spongy made of 5-6 concentric layers.
Dimensions: Diameter of central shell 135-175 μm, of the circle circumscribed by the two branches of spines 210-300 μm, length of polar spines 45-80 μm.
Material: 15 illustrated specimens.
Holotype: Plate 1, Figure 4, BR919, Zulla Formation, Wadi Bani Khalid, Oman.

Remarks: The species closely resembles *Palaeosaturnalis* (?) *incomptus*

SUGIYAMA, 1997 (Plate 1, Figures 9, 10) in having the outer margin bent according to the sinistrally twisted flat polar spines, but differs essentially from it in not having a bladed stem and in having a conical root with 5-6 levels of accessory spines as remnants of the dissolved layers of shell. *P.* (?) *incomptus* has a three-bladed stem, with one blade reduced, and no conical root, as a proof of its origin in a species with two three-branched polar spines and a latticed central shell. These differences prove that in spite of morphological resemblance the two species belong to different genera and even families. In fact, *P.* (?) *incomptus* is not a saturnalid but is closely related to the species *Dumitricasphaera planustyla* LAHM, 1984.
Etymology: From the Latin *intermedius*, *-ia*, *-ium* = intermediary.
Range and occurrence: Early Carnian to early Norian, Japan, Oman, and Sicily.

Blechschmidtia raridenticulata (KOZUR & MOCK, 1981)
(Plate 1, Figures 6-8)

Palaeosaturnalis raridenticulatus KOZUR & MOCK – KOZUR & MOSTLER, 1981, p. 56, Plate 61, Figure 5; ?TEKIN 1999, p. 111, Plate 17, Figures 4, 5.

?*Acanthocircus* spp. YOSHIDA 1986, Plate 7, Figure 7, non 1-6, 8, 9.

Description: Shell spongy, spherical, its diameter a little smaller than the inner diameter of the ring. Ring slightly elongated perpendicularly to polar axis, flat and relatively narrow, with two polar spines and two equatorial spines. Stem of polar rays very short, almost indistinct due to the large diameter of the shell. When the spongy shell is dissolved polar rays are usually triangular, being represented especially by the roots. Polar spines relatively long, flat and sinistrally twisted up to 90° at their base. Equatorial spines needle-shaped, practically equal in length with polar spines. External margin of ring smooth and, in each quarter, bent up or down according to the sinistral twist of the polar spines. This margin is the continuation of the margin of the twisted polar spines and the turning decreases from the polar spines to the equatorial spines.
Dimensions: Diameter of central shell 95-170 μm, of ring 175-240 μm, breadth of ring blade 20-28 μm, length of spines more than 100 μm.

Remarks: Although the original description does not mention the up and down turn of the border of the ring because of the very poor preservation of the holotype, this character is visible on the lower left side of the ring. Similarly, the specimens illustrated by TEKIN (1999) don't show this turn, reason for which we questionably include these specimens into this species. On the contrary, this character is very well expressed on all our specimens. According to its morphology and FAD, this species should have evolved from *Blechschmidtia intermedia* by the fusion of the distal ends of the lateral wings of the spines.

A rather similar species was described by BLOME (1984) as *Acanthocircus rotundus* BLOME from the late Carnian? – early to middle Norian of east-central Oregon and by YEH (1989) as *Acanthocircus* sp. aff. *A. rotundus* BLOME from the same area. The shape of the ring of this species resembles that of *B. raridenticulata*, but its ring shows no turn of the outer margin, the polar spines have no twist, and the stem and root of the polar rays are longer. Although a phylogenetical connection between the two species is not excluded, in which case *A. rotundus* would have evolved from *B. raridenticulata* by the loss of the bent border, it is also possible that Blome's species belongs to another lineage.

A taxonomic problem raises also the early Norian specimen illustrated by BRAGIN and KRYLOV (1999) and BRAGIN (2007) from Cyprus as *Liassosaturnalis parvus* KOZUR & MOSTLER. This specimen, that is not at all *L. parvus*, differs from *B. raridenticulata* by the absence of equatorial spines, in having no turned margin and longer polar rays.

Range and occurrence: Late Carnian of Oman (*M. polygnathiformis* conodont Zone and *Spongotortilispinus moixi* radiolarian Zone), Zulla Formation, Wadi Bani Khalid section (samples BR921, BR923); late Carnian / ?earliest Norian of Sicily, Pizzo Mondello section, (sample A9a); early Norian of Western Carpathians and probably Turkey.

Blechschmidtia matteri n. sp.
(Plate 2, Figures 1-4)

Description: Ring circular, narrow, commonly with 12 equidistant spines of which two are polar, two equatorial and two are intercalary in each quarter of the ring. Spines short and thin, the polar and equatorial ones being slightly longer than the others. Ring narrow, with a ridge positioned upside in the first and third quarters and downside in the second and fourth. Usually the intercalary spines in each quarter are not coplanar; they originate either in the turned margin or in the turning place of the margin, which corresponds to the plane of the ring. Stem and root taken together are shorter and broader than the portion of the polar spine outside the ring.
Dimensions: Diameter of central shell 120 μ, external diameter of ring 208-232 μm, length of polar and equatorial spines 50-72 μm, of intercalary spines 20-30 μm.
Material: Holotype, which is the only entire specimen, plus several paratypes, all represented by fragments of different sizes.
Holotype: Plate 2, Figure 2, BR923, Zulla Formation, Wadi Bani Khalid section, Oman.

Remarks: The species is rather rare but very characteristic by its number of spines on the periphery of the ring. The specimen (a fragment) illustrated

by CHIARI *et al.* (1996) as *Acanthocircus* sp., from the Carnian of Albania, differs from our specimens in having 3 intercalary spines in one quarter, the only one complete. It belongs probably to a new species intermediary between *B. matteri* and *B. bertinelliae* because no specimen recorded in our samples show 3 intercalary spines. The specimen illustrated by PESSAGNO *et al.* (1979) considered as coming from the middle-upper Norian (*Pantanellium silberlingi* Zone) or the lower Norian (*Capnodoce* Zone) of PESSAGNO *et al.* (1979) has the same number of spines. This specimen differs from *Blechschmidtia matteri* by having a slightly broader and flat ring and by missing bent margins.

Etymology: The species is named for Prof. Albert Matter, Institute of Geology, University of Berne for his contribution to the geology of Oman.

Range and occurrence: Late Carnian to earliest Norian of Oman: late Carnian of Zulla Formation (Wadi Bani Khalid section, sample BR922 and BR923), earliest Norian of Haliw Formation (sample HA10) and Sal Formation (sample H929).

Blechschmidtia bertinelliae n. sp.
(Plate 2, Figures 5-10)

Description: Ring circular with 2 polar spines, 2 equatorial spines and 6-7 teeth or small spines in each quarter. Space between polar spines and first adjacent tooth in each quarter is deeper and wider than between teeth. Ring blade relatively narrow with a ridge positioned upside in the first and third quarters and downside in the second and fourth quarters. Ridges start from the polar spines, on the external border, and then they traverse obliquely the ring to disappear on the inner or near the inner margin in the equatorial area. Central shell spherical, its diameter varying between half the inner diameter of ring to a little smaller than this diameter. Stem and root together short, broad.
Dimensions: Diameter of central shell 100-120 μm, external diameter of ring without teeth 230-280 μm, internal diameter 180-230 μm, length of polar and equatorial spines 40-110 μ.
Material: About 20 specimens of which 10 are entire, the others are fragments of various sizes.
Holotype: Plate 2, Figure 6, Pizzo Mondello, sample A10a, early Norian, Pizzo Mondello, Sicily.

Remarks: *Blechschmidtia bertinelliae* n. sp. is the most evolved species of the evolutionary lineage of this genus. Unlike the other species it doesn't have the margin of the ring bent successively up and down but a ridge in the same alternate position. This ridge is situated near the external border of the ring in the vicinity of the polar spines and migrates, arriving near the internal margin in the vicinity of the equatorial spines. The intercalary spines or teeth originate in a crest developed in the plane of the ring in the zone where the

margin of the ring started bending in the more primitive species of the genus. This trend towards forming a crest in the plane of the ring is already sketched in *Blechschmidtia matteri*, the forerunner of *B. bertinelliae*.

Etymology: The species is named for Dr. Angela Bertinelli, Università degli Studi di Perugia, for her contribution to the study of Mesozoic radiolarians.

Range and occurrence: Upper part of the late Carnian to early Norian of Oman: Zulla Formation, Wadi Bani Khalid section (BR925, BR926), Sal Formation (H929), Haliw Formation (HA11, HU9) and Pizzo Mondello (A9a, A10a), Sicily.

Blechschmidtia sp. (Figure 2)
Acanthocircus sp. A – PESSAGNO *et al.,* 1979, p. 169, Plate 3, Figure 8.
Acanthocircus sp. – CHIARI *et al.*, 1996, Plate 1, Figure 1.

Remarks: As discussed under *Blechschmidtia matteri*, the species illustrated by CHIARI *et al.* (1996) from the upper Carnian of Albania seems to be a new species intermediary between *B. matteri* and *B. bertinelliae*. The specimen illustrated by PESSAGNO *et al.* (1979) from the early Norian (or late Carnian?) or late middle Norian of Baja California seems to be conspecific with that illustrated by CHIARI *et al.*(1996), although it shows no ridge. It is possible that the ridge disappears gradually in younger populations.

Genus *Tjerkium* n. gen.

Type species: *Tjerkium deweveri* n. sp.
Diagnosis: Triassic saturnalids with flat, very broad ring bearing usually 4 spines of which two are polar and two equatorial. Sometimes intercalary spines are also present. Rarely the equatorial spines are absent. Outer margin of ring undulated, turned up and down according to the sinistral twist of spines. Ring with or without auxiliary or subsidiary rays.

Remarks: Morphologically, this genus has all the characters of *Blechschmidtia raridenticulata* (KOZUR & MOSTLER), from which it differs in having a broad ring. In fact one can consider that it is a synonym of *Blechschmidtia* n. gen. The problem is that in the Wadi Bani Khalid reference section two of its species occur before *B. raridenticulata*, that is before the formation of the ring. To solve this problem we have only two variants: a) to consider that the FAD of *B. raridenticulata* recorded in the Wadi Bani Khalid section is not the true FAD of this species; b) that despite the morphological resemblance the two genera are not closely related, the genus *Tjerkium* belonging to another phylogenetical lineage.
Taking into account that the morphology of the ring is very special and

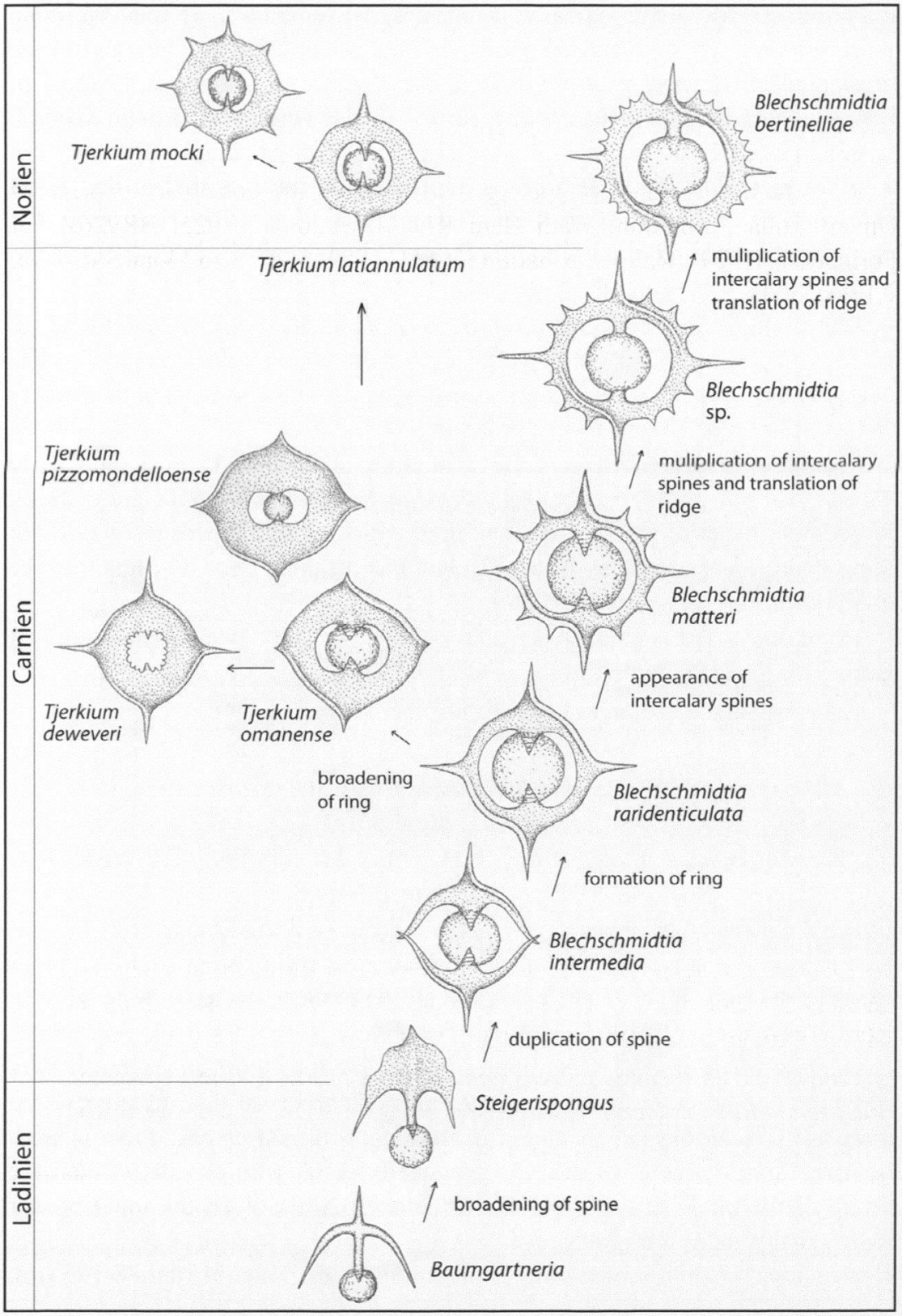

Figure 2.–Evolutionary model of the genera *Blechschmidtia* n. gen. and *Tjerkium* n. gen.

unknown in any other Triassic saturnalid, we consider: a) that *Tjerkium* is closely related to *Blechschmidtia*, b) that it represents a lateral lineage originated in *Blechschmidtia raridenticulata*, and c) that the true FAD of *B. raridenticulata* is older than that recorded in the Wadi Bani Khalid section. It should be at least as old as the stratigraphic level of sample BR919 if not a little older. The last possibility is supported by the fact that at the oldest level at which the species was recorded in this section (BR921) the ring was perfectly formed and that no intermediary specimen between this species and *B. intermedia* was found until present.

Morphologically it is also close to *Palaeosaturnalis* DONOFRIO & MOSTLER emend. KOZUR & MOSTLER from which it differs in having the outer margin of the ring undulated according to the sinistral twist of the base of spines. It has also always a very broad ring.

This new genus had a very fast radiation in the late Carnian and early Norian, but the phylogenetical relationships between its species are difficult to decipher because we do not know their exact FAD and because we do not see a evolutionary trend as in *Blechschmidtia*. In this genus it seems that the evolution followed several directions.

Etymology: The genus is named for Prof. Dr. Tjerk Peters, University of Berne, for his contribution to the geology of Oman.

Range: Upper Carnian to lower or middle Norian.

Tjerkium deweveri n. sp.
(Plate 3, Figures 1-4)
Praeheliostaurus sp. aff. *P. levis* KOZUR & MOSTLER – DE WEVER *et al.* 1979, p. 80, Plate 2, Figure 1.

Description: Spongy shell globular to lens-shaped filling completely the inner space of the ring and even enclosing the inner border of the latter. Stem absent. Root of polar spines short, triangular in face view. Ring foliaceous, very broad, circular to square shaped with rounded border and four short spines, rarely two, of which two are polar and two equatorial. All corners of the ring are twisted sinistrally so that the outer margin of the ring is turned up and down in each quarter. Inner diameter of the ring practically equal with or smaller than the width of the blade of the ring. When the shell is dissolved the inner border shows many short subsidiary rays.

Dimensions: Diameter of spongy shell and inner diameter of ring 88-175 μm, outer diameter of ring measured from the base of spines 375-412 μm.

Material: More than 100 specimens from the upper Carnian portion of the Bani Khalid section, 2 from the Pizzo Mondello section, and one from Monte Cammarata, Sicily.

Holotype: Plate 3, Figure 3, sample A9a, Pizzo Mondello.

Remarks: The specimen illustrated by De Wever *et al.* (1979) from the Monte Cammarata area resembles very much the specimens from the Pizzo Mondello section, from which it only differs in having a slightly narrower ring blade. Morphologically, *Tjerkium deweveri* n. sp. is closely related to *Palaeosaturnalis latiannulatus* KOZUR & MOSTLER from which it differs in that the latter has the inner diameter larger than the width of the ring blade, and a smooth inner border of the ring. Although the photograph of the holotype of *P. latiannulatus* is not conclusive, it seems that it also shows slightly twisted corners. From *T. pizzomondelloense* n. sp. it differs in having broader ring blade, much smaller inner diameter of ring, and auxiliary rays. The population of the sample BR919, Oman, from where we have more than 100 specimens, shows a wide variability from squarish to circular, from a well undulated margin, like in Sicily, to a practically flat one. Also, some specimens have a very small inner diameter and very short spines, which are even absent in some of them.

Etymology: The species is named for Dr. Patrick De Wever who first illustrated this species.

Range and occurrence: Upper Carnian (late Tuvalian) to lowermost Norian of Oman (sample BR919, Zulla Formation, Wadi Bani Khalid section, and sample H851, Sal Formation) and Sicily (Monte Cammarata and sample A9a, Pizzo Mondello).

Tjerkium omanense n. sp.
(Plate 3, Figures 5-7)

Description: Ring broad, rounded squarish or rhombic, in the latter case with long axis transversal to polar axis. Outer margin of ring in first and third quarters turned upward, and in second and fourth quarters turned downward. Polar spines short and thin, with base sinistrally twisted. Equatorial spines short to very short, with a slightly dextrally twisted base. Inner margin of ring smooth, without auxiliary or subsidiary rays. Shell small, spherical, connected to the ring by the two polar rays and usually by small apophyses around them. In a single case (Plate 3, Figure 5) there are two auxiliary or subsidiary rays aligned with the equatorial spines.

Dimensions: Length of ring without spines 320-363µ, breadth of ring without spines 290-310, inner diameter of ring 145-172µ.

Material: Nine specimens, of which 7 in BR919, Zulla Formation, Wadi Bani Khalid section, Oman, and 2 in H851, Sal Formation, Batain Plain, Oman.

Holotype: Plate 3, Figure 7, BR919, Zulla Formation, Wadi Bani Khalid section, Oman.

Remarks: This new species resembles the early Norian species *Tjerkium latiannulatum* (KOZUR & MOSTLER) in having a smooth inner margin of

the ring and 4 spines, but differs from it in having the outer margin turned as described. From the other species of the genus it differs not only in having the inner margin of ring smooth but also in having the equatorial spines and corners dextrally twisted. This is because the entire external border in each quarter is turned in the same sense. A morphologically close species is also *Blechschmidtia raridenticulata* from which it differs in having a much broader ring and much shorter spines.

Etymology: From its occurrence in Oman.

Range and occurrence: Late Carnian, Zulla and Sal Formations, Oman.

Tjerkium pizzomondelloense n. sp.
(Plate 3, Figures 8, 9)

Description: Ring rhombic, flat and very broad, elongated in the direction of the equatorial spines. External margin of each quarter curved upward and downward giving the ring an undulate aspect. Corners of ring armed with short spines, all twisted sinistrally. Ring slightly longer along the equatorial axis. Inner margin of ring smooth or denticulate. Spongy shell smaller than the inner diameter of the ring. Stem of polar spines missing.
Dimensions: Height of ring with spines measured along polar axis 350-375 μm, width of ring measured along equatorial axis 425 μm, width of blade of ring 90-97 μm, breadth of inner diameter of ring along long axis 125-145 μm.
Material: Two specimens in the latest Carnian / ? earliest Norian, sample A9a, Pizzo Mondello, Sicily.
Holotype: Plate 3, Figure 9, A9a, Pizzo Mondello section, Sicily.

Remarks: *Tjerkium pizzomondelloense* n. sp. resembles very much *Tjerkium latiannulatum* (KOZUR & MOSTLER) in having a broad ring, four spines of which only two are polar, but differs from it in having the external margin strongly turned successively upward and downward, in being slightly elongated equatorially, and in having a short conical root. *P. latiannulatus* is, on the contrary, slightly elongated on polar directions and its polar rays are longer. *T. pizzomondelloense* is also very close to *Blechschmidtia raridenticulata* (KOZUR & MOSTLER) from which it only differs in having shorter spines and broader ring. Another species very close to this species is *T. omanense* n. sp., but this species has no undulated margin and its equatorial spines are dextrally twisted.

Etymology: From its occurrence in the Pizzo Mondello section.

Range and occurrence: latest Carnian / ? earliest Norian, sample A9a Pizzo Mondello section, Sicily.

Tjerkium latiannulatum (KOZUR & MOSTLER) (Figure 2)

Palaeosaturnalis latiannulatus KOZUR & MOSTLER, 1983, p. 20, Plate 5, Figure 1; TEKIN, 1999, p. 110, Plate 17, Figure 1, 2; BRAGIN & KRYLOV, 1999, p. 556, Figure 9D; BRAGIN, 2007, p. 993, Plate 9, Figure 6.

Remarks: The species was compared to *T. pizzomondelloense* n. sp. and *T. omanense* n. sp. under the latter species. Since both this species and *T. mocki* have the outer margin of the ring very slightly turned or twisted it is possible that this character common to almost all Carnian species of the genus disappeared during evolution.

Range and occurrence: latest Carnian-earliest Norian (*E. primitia* Conodont Zone) to early Norian (*E. abneptis* Conodont Zone) in Western Carpathians, Antalya (Turkey), and Cyprus.

Tjerkium mocki (KOZUR & MOSTLER) (Figure 2)

Palaeosaturnalis mocki KOZUR & MOSTLER, 1983, p. 21, Plate 5, Figure 2; TEKIN, 1999, p. 110, Plate 17, Figure 3; BRAGIN & KRYLOV, 1999, p. 556, Figure 9G, 9H; BRAGIN 2007, p. 994, Plate 9, Figure 7.

Remarks: This species, from which only 4 specimens have been so far illustrated in the literature, seems to be part of the *Tjerkium latiannulatum* (KOZUR & MOSTLER) group from which it only differs in having one shorter intercalary peripheral spine in the middle of each quarter of the ring. Although not mentioned in the original description, the outer margin of the ring is also slightly sinistrally twisted around spines.

Range and occurrence: Early Norian, *E. abneptis* conodont Zone and *navicula* Subzone of *spatulatus* A. Z.: Western Carpathians, Antalya (Turkey), and Cyprus.

Origin and evolution of the genera *Blechschmidtia* and *Tjerkium*

According to their morphology, central shell structure, and stratigraphic range the two new genera are undoubtedly saturnalids and seem to represent an early lateral branch of the evolutionary tree of this family. In order to find out their forerunner we should take into account: a) the morphology of the spines of the oldest species, b) the stratigraphic level of its first appearance, and c) the stratigraphic level of the species or genus we consider as its forerunner.

Blechschmidtia intermedia n. sp. is the oldest species of the new genus. In the Wadi Bani Khalid section (Blechschmidt *et al.*, 2004) it was recorded in sample BR908 at the upper part of the *Tritortis kretaensis* Zone (early Carnian).

A rather similar type of spine is characteristic of the genus *Scutispongus* KOZUR & MOSTLER that evolved from the Fassanian-early Longobardian genus *Baumgartneria* DUMITRICA, as DUMITRICA (1982) suggested for *Scutispongus undulatus* (DUMITRICA), by the broadening of the lateral wings of the main spine, a trend common to almost all Longobardian Oertlispongidae. Under this genus KOZUR and MOSTLER (1996) illustrated a series of Longobardian species, all of them having a large, foliaceous and more or less bilaterally symmetrical main polar spine, usually needle-like lateral terminations, and sometimes a slightly sinistrally twisted apical spine. The spines of *B. intermedia* n. sp. resembles so much those of *Scutispongus*, e.g. *S. tortilispinus* KOZUR & MOSTLER, that it would have been undoubtedly assigned to this genus if they were find detached from the spongy shell. According to data by KOZUR and MOSTLER (1996) *Scutispongus* is one of the most characteristic radiolarian genera of the Tethyan Longobardian (late Ladinian), but it is still present in the early Carnian, as its last occurrence in the Wadi Bani Khalid section was recorded in BR911. Taking into account all these data, we consider that *Scutispongus* is the only possible forerunner of *Blechschmidtia*.

The transition from *Scutispongus* to *Blechschmidtia* should have followed the same pattern as that from the Oertlispongidae with foliaceous main spine (probably a species of *Scutispongus* as well) and *Angulocircus* LAHM: duplication of the main polar spine of *Scutispongus* and its positioning in face of it, in the same polar axis. By this process the skeleton gained not only more complexity but also an equatorial plane perpendicular to polar axis and a bilateral symmetry relative to it. This was a mutational process that needed no intermediary specimens. Such a transition and the appearance of the characteristic ring have been supposed by KOZUR and MOSTLER (1983) and illustrated by GUEX (1993, Figure 8).

Blechschmidtia intermedia is very rare in the early Carnian, its occurrence at this stratigraphic level is in fact based on a single specimen (Plate 1, Figure 1). As far as we know, it is also missing in the middle Carnian (*Tetraporobrachia haeckeli* Zone) both in Oman and in other faunas of this age we know. In the Wadi Bani Khalid reference section (Oman) it reappears, and is rather frequent, in sample BR919 that contains a radiolarian fauna characteristic of the *Spongotortilispinus moixi* KOZUR & MOSTLER and the conodont *Metapolygnathus polygnathiformis* proving that it is not younger than early Tuvalian 3 (L. Krystyn, pers. comm.). At almost the same level it is common in the late Carnian (middle Tuvalian) sample H851 from the Batain Plain, Oman. The species occurs also at approximately the same level in the Pizzo Mondello section (sample A38). Along this entire interval the species' morphology is very constant. The lateral extremities of the spines remain independent and only rarely partly coalesce (Plate 1, Figure 5).

Starting with sample BR921 to BR924, on an interval of 4 m of the late Tuvalian the evolution of this lineage is very fast: BR921 marks the FAD of *B. raridenticulata*, BR922 the FAD of *B. matteri* n. sp., and BR924 the FAD of *B. bertinelliae* n. sp. Along this short lineage the following events take place: closing of the ring, appearance of two equatorial spines, later of intercalary spines and their multiplication, and change of the turned outer margin into a ridge and its translation toward the inner border (Figure 2).

The sample BR921 records the first appearance of *Blechschmidtia raridenticulata*, which marks the closing of the ring by the suture of the lateral extremities of the two spines. This appearance could be correlated with that recorded in the Pizzo Mondello in sample A9a, the position of which in the section is above that of sample A38. As we discussed under the genus *Tjerkium*, it is possible that the true FAD of this species is in BR919 or earlier. This species has also 2 equatorial spines perpendicular to the polar ones originated in the place of suture of these extremities. The appearance of these equatorial spines is a logical result of the fusion of the distal ends of the two spines, which are already laterally recurved in some specimens of *B. intermedia* (Plate 1, Figures 2, 3). The species preserves the up and down turns of the outer margin of the spines according to the sinistral twist of the polar spines. This sense of twist produces upturn in the first and third quarter of the ring and downturn in the second and fourth quarter. The turned border is always smooth and decreases in height toward the equatorial spines.

In sample BR922 of the Wadi Bani Khalid section, that is 1.5 m above the previous sample, the FAD of *Blechschmidtia matteri* n. sp. was recorded. The same species was found in sample HA10 in the Hamadiyin I section that can very well be correlated with BR922. This species differs from *B. raridenticulata* not only by the appearance of two relatively short spines in each quarter of ring but also by their position and evolutionary consequences. These intermediary spines are practically coplanar and originate in the bent zone of the outer margin, foregoing the change of the turned portion of the outer margin into a ridge. This character is less marked in this species than in the following one. It is possible that some intermediary specimens between the two species, with shorter intermediary spines, existed but none was found, possibly because *B. matteri* appeared abruptly by a mutation and not by a gradual emergence of these spines. Anyway, both by its FAD and its more complex morphology, this species is logically a direct descendant of *B. raridenticulata*.

Finally, in sample BR924, 3 m above the FAD of *B. matteri*, we recorded the FAD of *Blechschmidtia bertinelliae* that seems to be the last species of this phylogenetical lineage. In both sections Hamadiyin I and II, its FAD occurs above that of *B. matteri*, in the upper part of the chert member, namely in HA 11 (1.5 m above HA10) in Hamadiyin I and about 15 m above the base of the chert member in the Humadiyin II section. In the Pizzo Mondello section

B. matteri was not recorded but the FAD of *B. bertinelliae* occurs above that of *B. raridenticulata*. It results that the succession of the appearance of species is similar in all studied sections.

In *B. bertinelliae* the number of intercalary spines is greater, 5-7 in each quarter, and the turned margin of the ring is a true ridge. This ridge does not remain near the outer margin of the ring, as in *B. matteri*, but moves diagonally along the ring in each quarter arriving up to the inner border in the zone of the equatorial spines where it usually gradually fades. Although the morphological differences between *B. bertinelliae* and *B. matteri* suggest that a gradual transition between the two species should have existed, no transitional morphotype was found so far in the studied sections. One of such transitional morphotypes could be the late Carnian fragment of ring illustrated by CHIARI *et al.* (1996, Plate 1, Figure 1) from the late Carnian of Albania as *Acanthocircus* sp., which we consider as *Blechschmidtia* sp. in the present paper. This specimen has a ring morphologically intermediary between the two species, with 3 spines in the single quarter preserved and a true ridge that arrives in the middle of the ring band near the equatorial spine. By its translated ridge this specimen is evolutionarily closer to *B. bertinelliae* than to *B. matteri*. The Norian specimen illustrated by PESSAGNO *et al.* (1979) as *Acanthocircus* sp. A from the San Hippolito Formation of Baja California has also a similar number of intermediary spines, but it has no ridge perpendicular to the ring. Given its bad preservation and younger age, it is possible that either the ridge was destroyed by fossilization or disappeared during the evolution within the species.

The evolutionary lineage *Baumgartneria – Scutispongus - Blechschmidtia intermedia – B. raridenticulata – B. matteri – Baumgartneria* sp. *– B. bertinelliae* exposed above is, in our opinion, one of the most instructive evolutionary lineages proving the phyletic gradualism in the evolution of the Triassic Saturnalidae as a materialization of a trend towards greater complexity of skeleton. This lineage could be compared with the lineage of the Early Cretaceous genus *Aurisaturnalis* (DUMITRICA and DUMITRICA JUD 1995).

The evolutionary trends of the species of the genus *Tjerkium* n. gen are not perfectly understood yet. As discussed above, by its morphology, this genus should have its logical origin in *Blechschmidtia raridenticulata* by a trend towards the broadening of the ring. However, this genus has its first appearance before that of this species in the Wadi Bani Khalid reference section, and it first appears in the same sample with this species in the Pizzo Mondello section. In order to support our idea, and knowing that the first appearance of a species in a section does not implicitly mean its real FAD, we consider that the FAD of the *B. raridenticulata* should be somewhere below, in other term earlier than that of *Tjerkium* as recorded in the Wadi Bani Khalid section. Unfortunately we do not know yet at which stratigraphic level. Surely the species is not yet present

in the very well preserved radiolarian fauna of the *Hexaporobrachia haeckeli* zone (Late Julian) from Turkey (under study by TEKIN and DUMITRICA) or from the Reifling Limestone from Grossreifling or Göstling (Austria). The evolution of this genus is less interesting than that of *Blechschmidtia* and more difficult to decipher because of the sparse occurrences of its species in the studied intervals. The only thing that one can say in the present state of knowledge is that *Tjerkium mocki* should have been originated in *T. latiannulatum* by the appearance of one intercalary spine in each quarter of ring during the earliest Norian.

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PLATES 1-3

Plate 1

Figures 1-5.– *Blechschmidtia intermedia* n. gen., n. sp. 1 – BR908, early Carnian, Zulla Formation, Wadi Bani Khalid section, Oman; 2 – A38, late Carnian, Pizzo Mondello section, Sicily; 3-5 – BR919, late Carnian, Zulla Formation, Wadi Bani Khalid section, Oman; 4 – holotype.

Figures 6-8.–*Blechschmidtia raridenticulata* (KOZUR & MOSTLER). 6 – A9a, latest Carnian / ? earliest Norian, Pizzo Mondello, Sicily; 7, 8 – BR921, late Carnian, Zulla Formation, Wadi Bani Khalid section, Oman.

Figures 9, 10.–*Palaeosaturnalis* (?) *incomptus* SUGIYAMA, BR918, late Carnian, Zulla Formation, Wadi Bani Khalid section, Oman

Plate 1

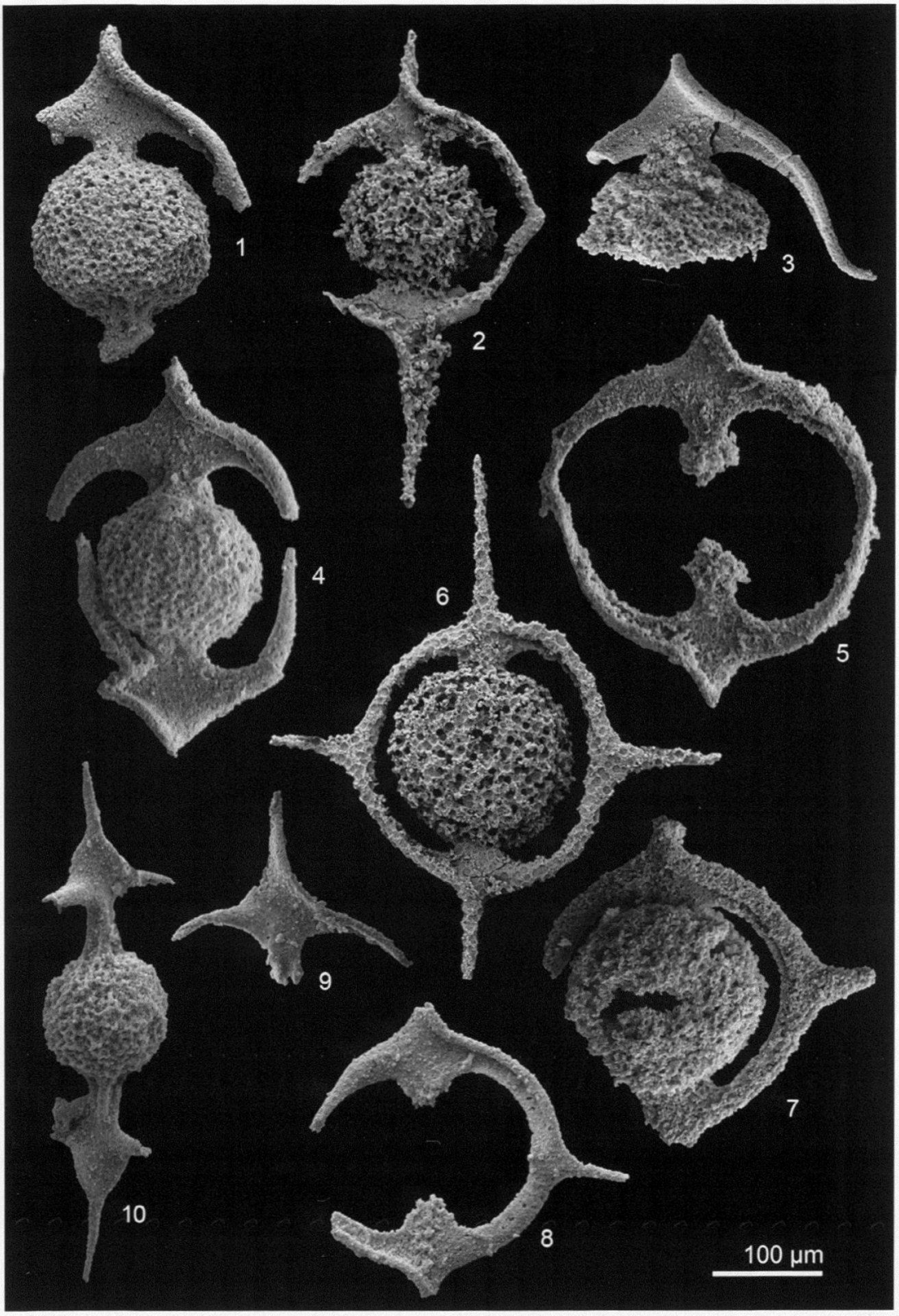


Plate II

Figures 1-4.–*Blechschmidtia matteri* n. gen., n. sp.; 1 – H929, earliest Norian, Sal Formation, Batain Plain, Oman; 2 – holotype, BR923, late Carnian, Zulla Formation, Wadi Bani Khalid, Oman; 3, 4 – HA10, earliest Norian, Haliw Formation, Humadiyin, Oman.

Figures 5-10.–*Blechschmidtia bertinelliae* n. gen., n. sp. 5 - H929, earliest Norian, Sal Formation, Batain Plain, Oman; 6, 8, 10 – A10a, early Norian, Pizzo Mondello section, Sicily; 6 – holotype; 7, 9 – BR926 and BR925, respectively, latest Carnian-earliest Norian, Zulla Formation, Wadi Bani Khalid section, Oman.

Plate 2

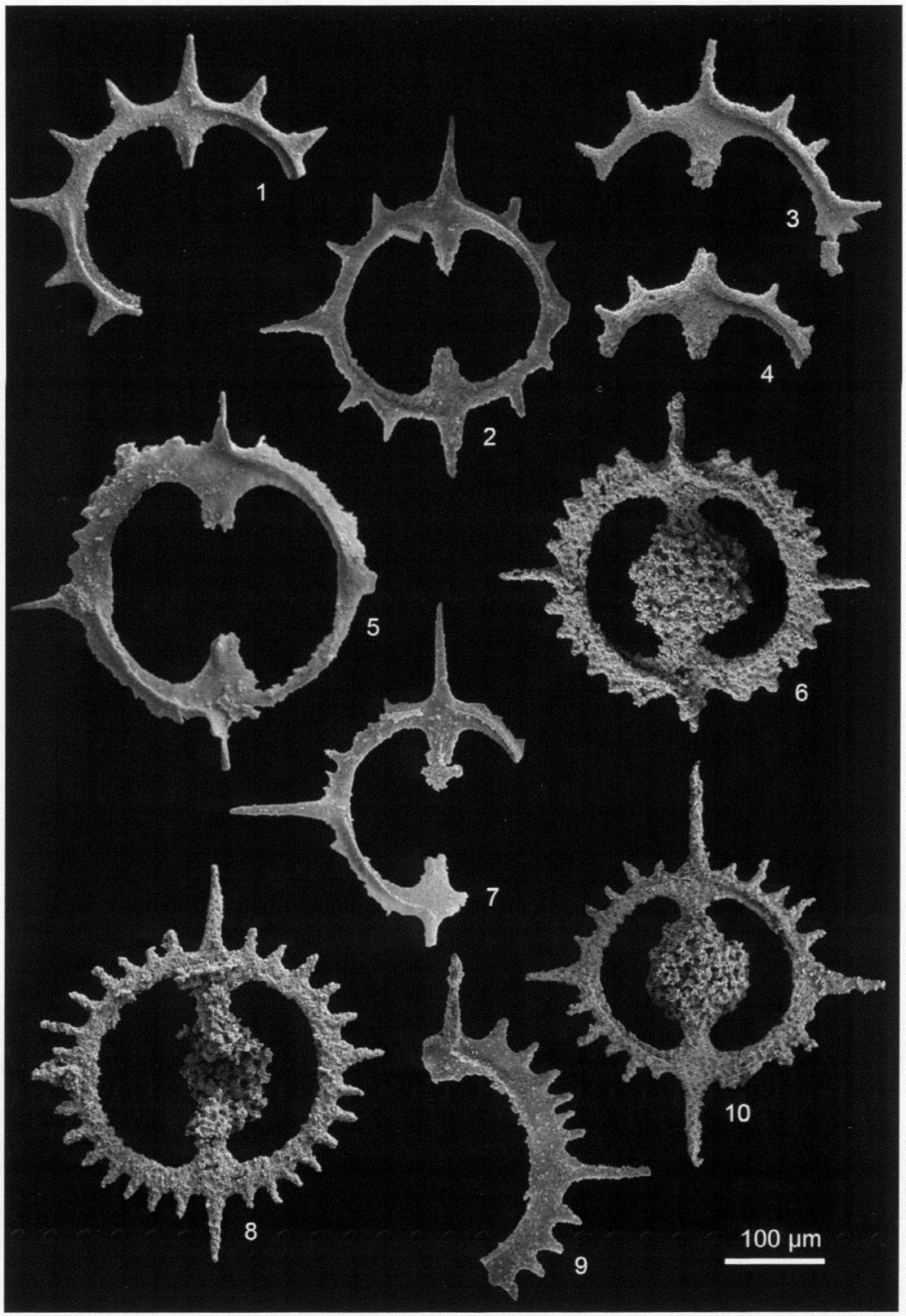


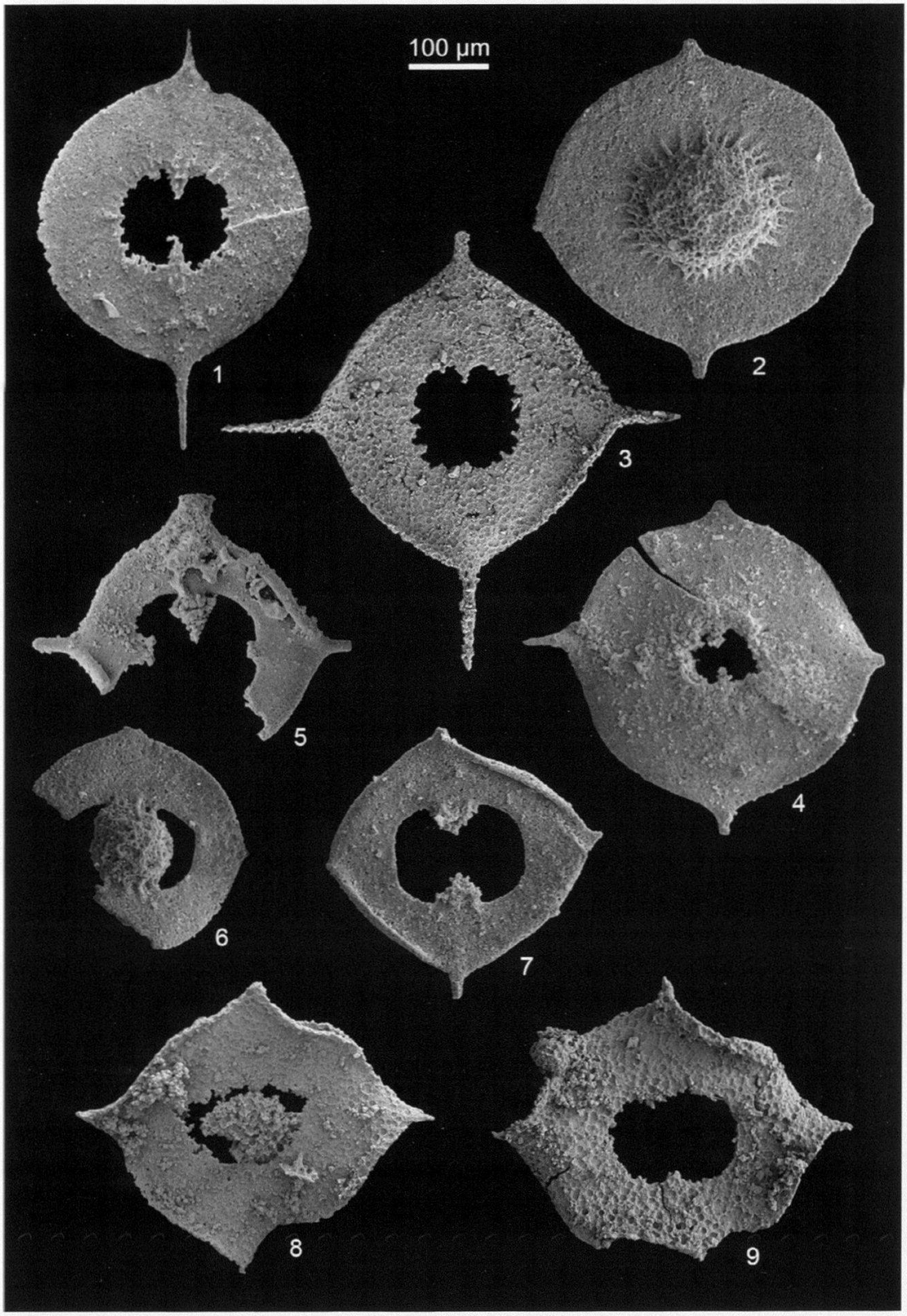
Plate 3

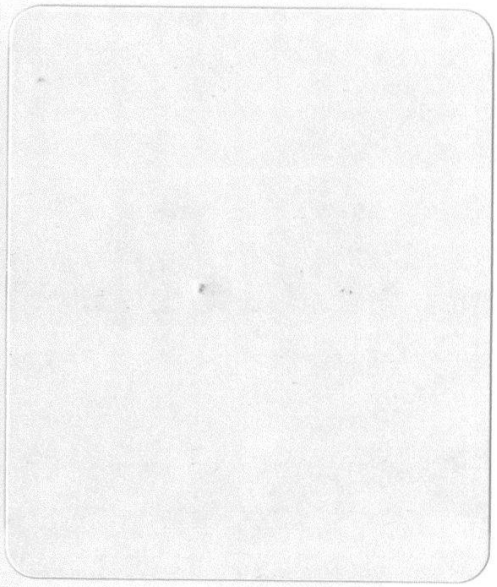
Figures 1-4.–*Tjerkium deweveri* n. gen., n. sp. 1, 2, 4 - BR919, late Carnian, Zulla Formation, Wadi Bani Khalid section, Oman, showing the variability of the species; 3 - holotype, A9a, latest Carnian / ? earliest Norian, Pizzo Mondello section, Sicily.

Figures 5-7.–*Tjerkium omanense* n. gen., n. sp., late Carnian, Oman. 5 - anomalous specimen, H851, Sal Formation, Batain Plain, showing the presence of 2 auxiliary rays aligned with the equatorial spines; 6, 7 - BR919, late Carnian, Zulla Formation, Wadi Bani Khalid section; 7, holotype.

Figures 8, 9.–*Tjerkium pizzomondelloense* n. gen., n. sp., A9a, latest Carnian / ? earliest Norian, Pizzo Mondello section, Sicily; 9, holotype.

Plate 3





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