

# Lower Tithonian mono- and dicyrtid Nassellaria (Radiolaria) from the Solnhofen area (southern Germany)

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## ABSTRACT

A highly diverse association of monocyrtyd and dicyrtid nassellarians is described from the lower Tithonian Mühlheim Member of the Solnhofen area. Nine genera and 52 species are described as new, and a new family is defined. Spicular nassellarians are first reported from the Jurassic, bridging the pre-existing long stratigraphic gap between the Middle Triassic and the Paleogene. The first occurrence of Sethoperidae Haeckel, 1881 is dated back from the Eocene to the Pliensbachian and the range of the Cuniculiformidae De Wever, 1982 is extended up to the Cenomanian by the inclusion in it of the genus *Cassideus* Pessagno, 1969, the definition of which is emended. The range of the family Foremanellinidae Dumitrica, 1982 is also extended up to the lower Tithonian where it is represented by the genus *Sanniopileus* n. gen. Among the new genera described herein it is interesting to mention *Poculinapora* n. gen., very close to *Napora* Pessagno, 1977 but bearing an apical tube. Beside the lower Tithonian species, one species is described from the Bajocian of Japan.

## KEY WORDS

Radiolaria,  
Nassellaria,  
Upper Jurassic,  
lower Tithonian,  
southern Germany,  
Solnhofen area,  
new family,  
new genera,  
new species.

## RÉSUMÉ

*Radiolaires nassellaires mono- et dicyrtides du Tithonien inférieur de la région de Solnhofen (Allemagne méridionale).*

Une association très diverse de nassellaires monocyrtes et dicyrtides du Tithonien inférieur (Membre de Mühlheim) de la région de Solnhofen est décrite. Neuf genres, 52 espèces et une famille sont nouvellement définis. Des nassellaires spiculaires, trouvés pour la première fois dans le Jurassique, permettent de combler une lacune d'information entre le Trias et le Paléogène. L'apparition des Sethoperidae Haeckel, 1881 survient au Pliensbachien. L'extension des Cuniculiformidae De Wever, 1982 est prolongée jusqu'au Cénomaniens suite à l'inclusion dans cette famille du genre *Cassideus* Pessagno, 1969 dont la définition est émondée. L'extension des Foremannellinidae Dumitrica, 1982 est prolongée jusqu'au Tithonien inférieur où elle est représentée par le nouveau genre *Sanniopileus* n. gen. Parmi les nouveaux genres décrits, il est intéressant de mentionner *Poculinapora* n. gen., très proche de *Napora* Pessagno, 1977 dont il se distingue par la présence d'une corne apicale tubulaire. À côté des espèces du Tithonien inférieur d'Allemagne, une espèce de Sethoperidae du Bajocien du Japon est décrite.

## MOTS CLÉS

Radiolaria,  
Nassellaria,  
Jurassique supérieur,  
Tithonien inférieur,  
Allemagne méridionale,  
région de Solnhofen,  
nouvelle famille,  
nouveaux genres,  
nouvelles espèces.

## INTRODUCTION

Late Jurassic radiolarian associations of southern Germany were mainly reported from the Northern Calcareous Alps (Steiger & Steiger 1993, 1994). Apart from single specimens figured by Geyer (1961), Stürmer (1963), and Schairer (1971: figs 23, 24), the first radiolarian faunas from the Swabian/Franconian Alb were recently described by Kiessling (1997) from the Oxfordian of the southern Franconian Alb. Late Kimmeridgian radiolarian faunas from the Swabian Alb were published by Zügel *et al.* (1998). Following a rather accidental finding of radiolarians in the lower Tithonian Mühlheim Member of the Mörnsheim Formation (*Hybonoticerias hybonotum* Zone) from the Solnhofen area (Zeiss 1977), further sampling revealed radiolarian faunas throughout different sections of this member (Zügel 1997). This paper continues a first short publication of a monocyrtid nassellarian type with double-shelled cephalis (Dumitrica & Zügel 1998). This time we describe all monocyrtid and dicyrtid nassellarians with widely open apertures found in the Mühlheim

Member of the Mörnsheim Formation in order to make known this interesting fauna.

Late Jurassic monocyrtid and dicyrtid nassellarians with widely open aperture were so far restricted to only four genera: *Saitoum* Pessagno, 1977, *Napora* Pessagno, 1977, *Pseudopoulpus* Takemura, 1986, and *Cornutella* Ehrenberg, 1838. The first two genera are fairly diverse and widespread (Baumgartner *et al.* 1995), whereas the others were so far restricted to very few samples from the Tithonian of the Antarctic Peninsula (Kiessling 1999). Mono- and dicyrtid nassellarians from a highly diverse and well preserved radiolarian fauna were described by Takemura (1986) from the Middle Jurassic of Japan. Some genera of that fauna (*Pseudopoulpus*; *Reticulotubulus* Takemura, 1986; *Takoum* Takemura, 1986) have a short reappearance in the lower Tithonian of the Solnhofen area, proving that their ranges are much longer than previously considered. Other taxa (genera and families) presented in this paper were only known from Lower Jurassic (De Wever 1982), Middle Triassic (Kozur & Mostler 1981; Dumitrica 1991), Middle Cretaceous (Pessagno

1969), or even only from the Cenozoic. Spicular nassellarians occurring in the lower Tithonian show also close affinities with some forms described by Dumitrica (1982a) from the Middle Triassic.

Together with the monocyrtid nassellarian with a double-shelled cephalis previously described (Dumitrica & Zügel 1998), the mono- and dicyrtid nassellarians herein described offer a complete spectrum of this group in the Solnhofen area during the lower Tithonian. Thus, this fauna proves how incomplete our knowledge on the range and diversity of fossil radiolarians is.

#### LOCALITIES, SECTIONS AND MATERIAL

Samples are derived from two composite sections in the vicinity of Mühlheim, a small village about 4 km south of the town of Solnhofen. One section is located about 1 km NNE of Mühlheim, around the slope of the “Solnhofer Berg”. It is figured as Horstberg quarry in Meyer & Schmidt-Kaler (1994: figs 45, 46) and shortly described by Keupp (1977: 95, 96, fig. 13).

In the Horstberg section, the lower part of the Mühlheim Member is only accessible in the southern quarry (Hob 1-31; Fig. 1). It starts on top of the Solnhofen Formation (Zeiss 1977) characterized by an undulatory surface due to some syndepositionary folded limestone beds (slump horizon, “Krumme Lage” beds, Barthel *et al.* 1990). Platy limestones are predominant in the lower part, replaced by mainly laminated limestone beds to the top. Undulatory cherts are mainly found in the centre of the limestone beds. As most conspicuous bed, a chert layer of 20-30 cm thickness is intercalated about 1.5 m below the top of the southern quarry (Fig. 2).

Beds at the base of the northern quarry cannot be correlated with those at the top of the southern quarry. However, by comparison of the inaccessible part of the northern quarry with the section in the southern quarry a lithostratigraphic gap of about 1 m only is supposed. The section in the northern quarry (Hob 32-57; Fig. 1) is composed

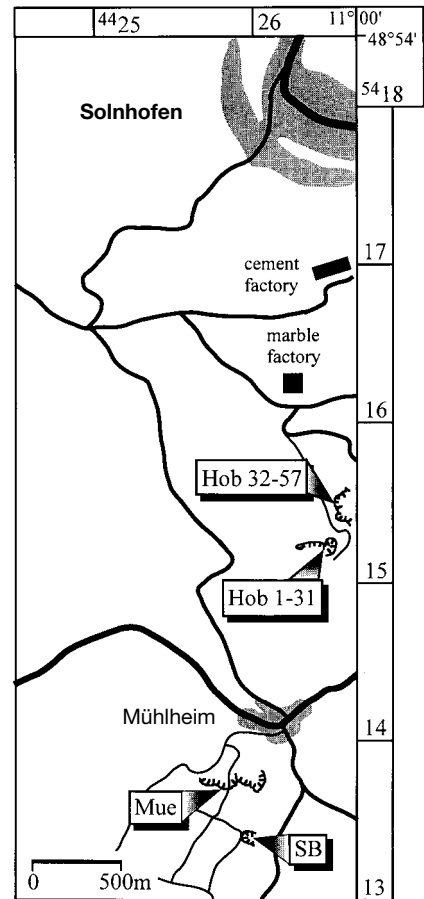
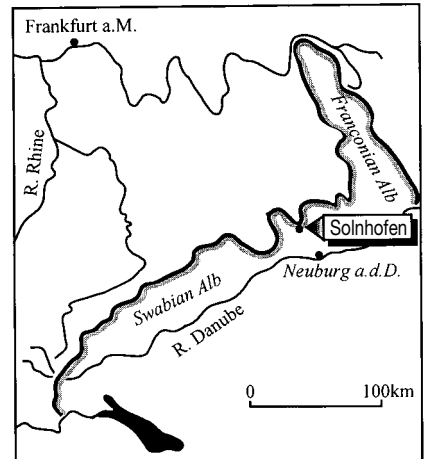


FIG. 1. — Locality map with sections Mühlheim, Schaudiberg old quarry (Mue), Mühlheim, Schaudiberg new quarry (SB), Horstberg, southern quarry (Hob 1-31), and Horstberg, northern quarry (Hob 32-57).

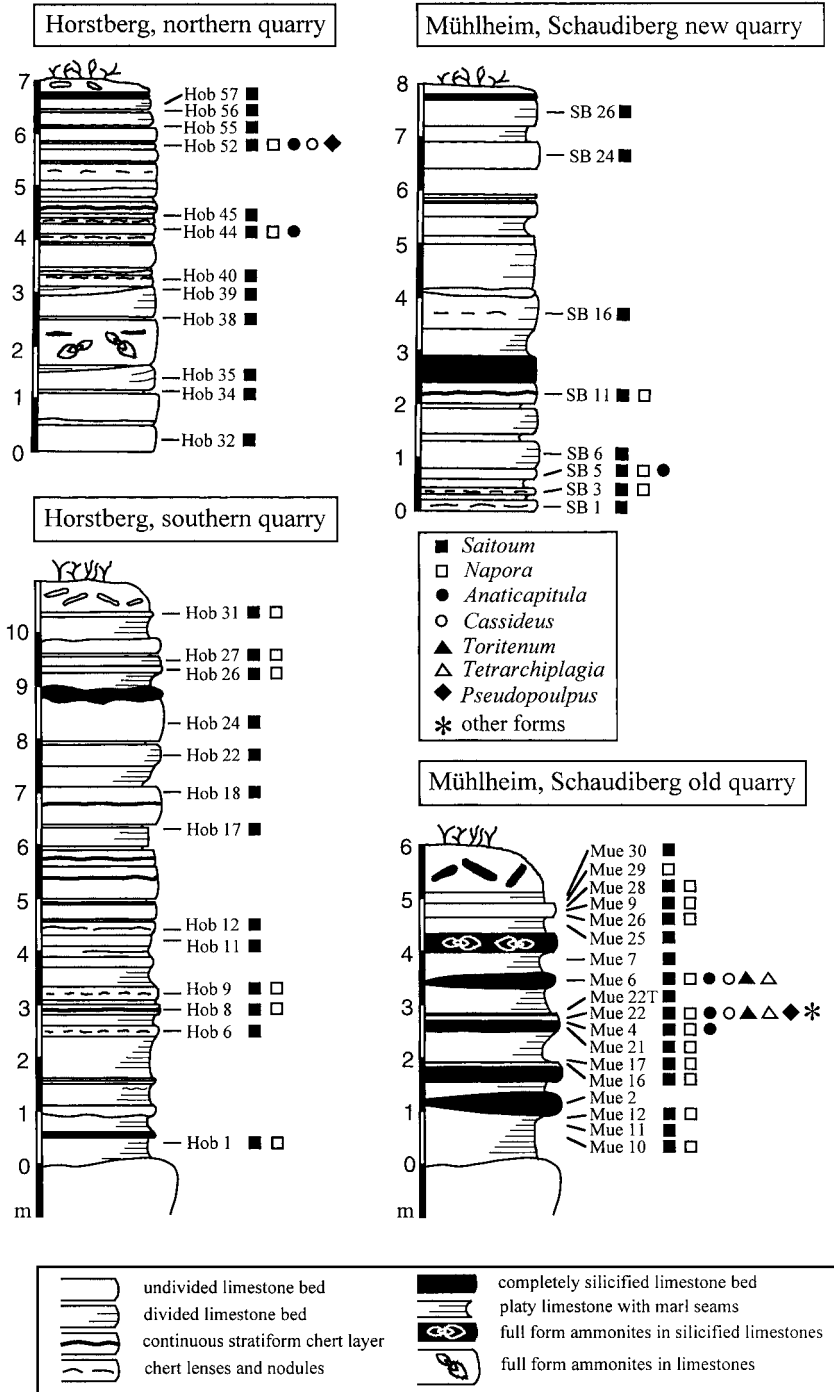


FIG. 2. — Distribution of monocyrtid and dicyrtid nassellarian genera in sections. Note the contrast between the wide distribution of low diverse associations with *Saitoum* Pessagno, 1977 and *Napora* Pessagno, 1977 compared to the high diversity in sample Mue 22.

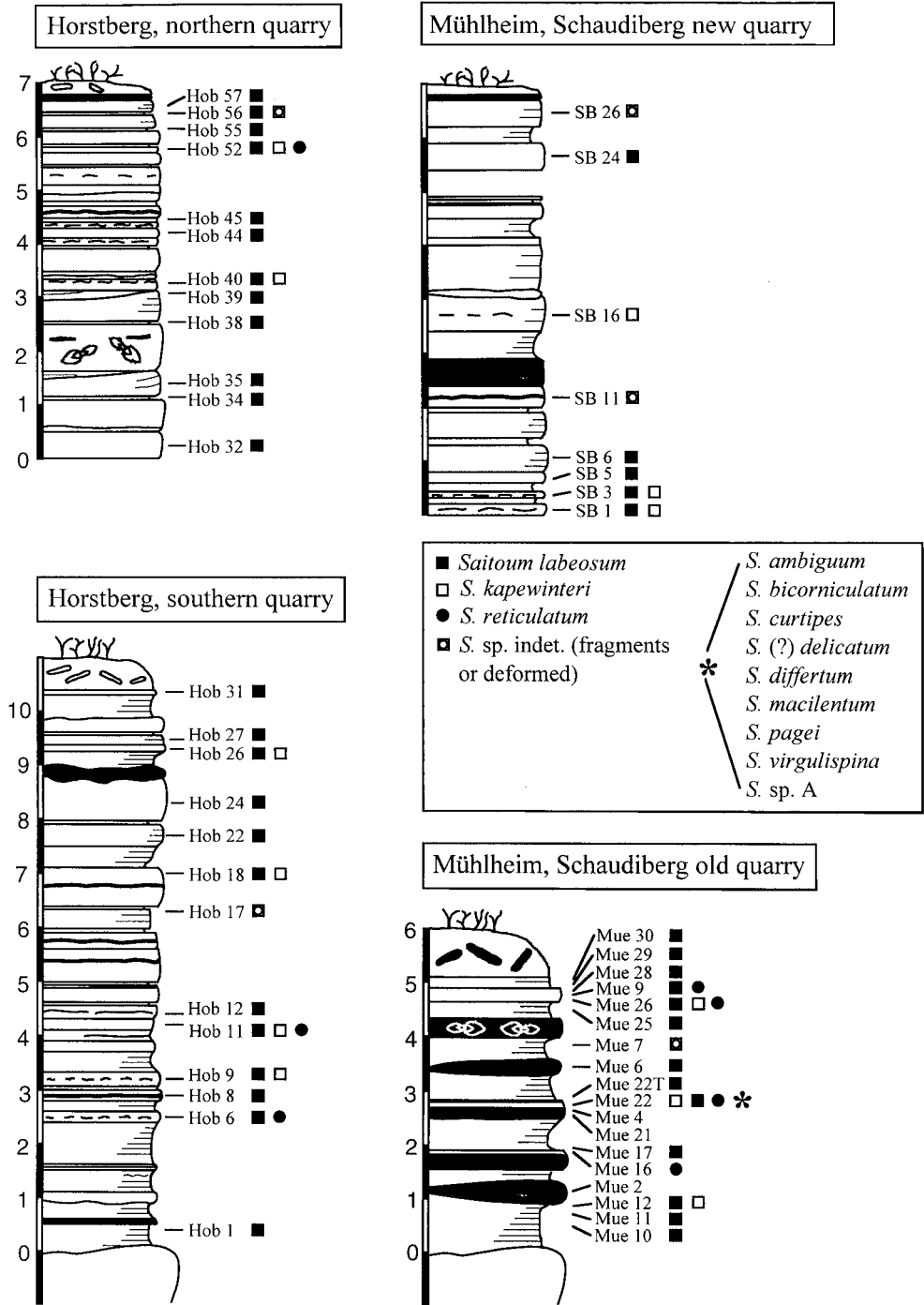


FIG. 3. — Distribution of different species of *Saitoum* Pessagno, 1977 in sections. Note the ubiquitous occurrence of the very robust species *Saitoum labeosum* n. sp. and the high diversity in sample Mue 22. For legend, refer to Fig. 2.

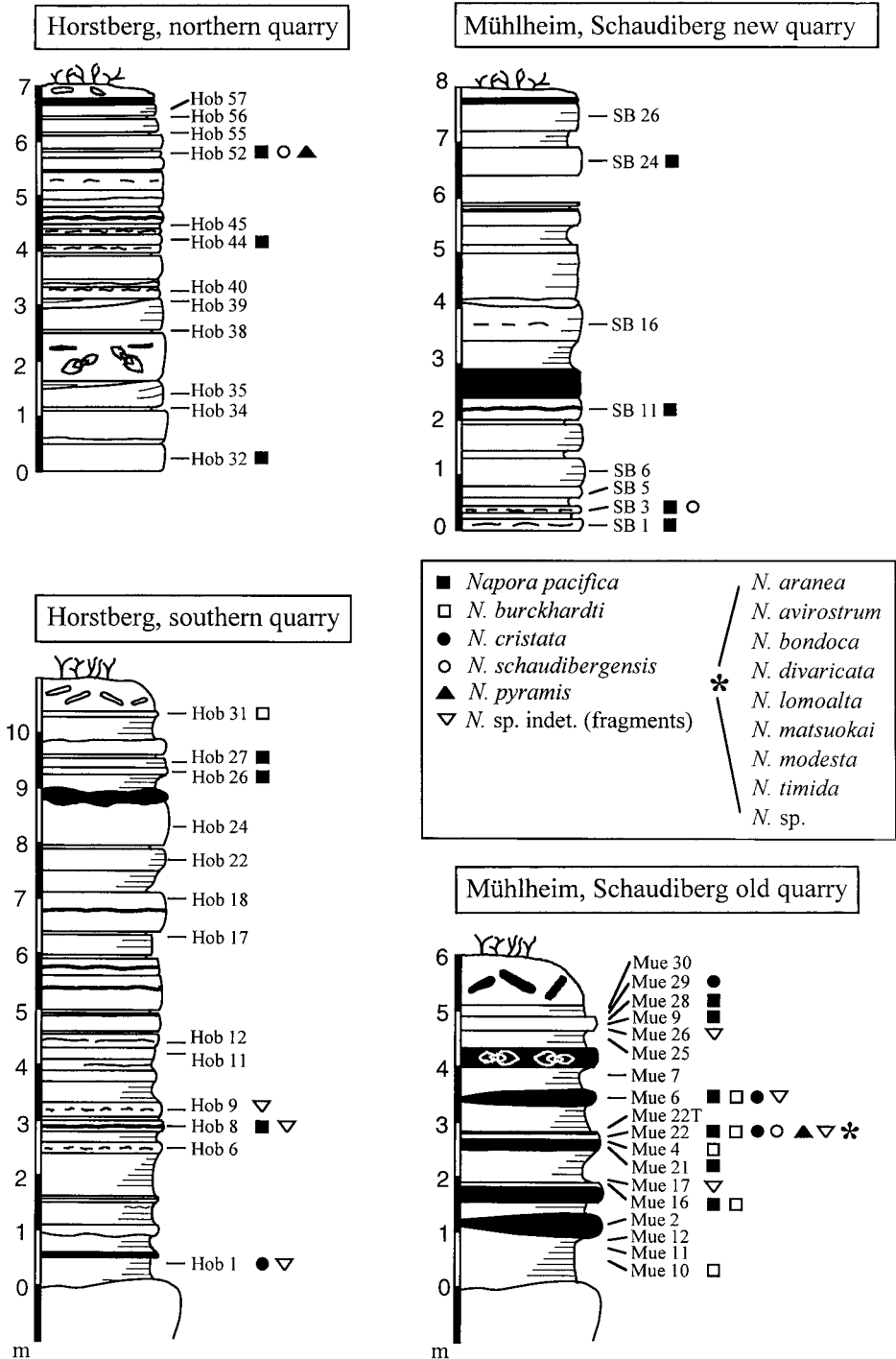


FIG. 4. — Distribution of different species of *Napora* Pessagno, 1977 in sections. Note the common occurrence of the robust *Napora pacifica* Kiessling, 1999 and the high diversity in Mue 22. For legend, refer to Fig. 2.

of limestone beds with only minor intercalations of platy limestones. Chert horizons are concentrated in the middle part of the section. The most conspicuous bed is a thick limestone bed without any lamination. It is the only bed where ammonites are well preserved (Fig. 2).

The second composite section is located 0.5 to 1 km south of Mühlheim, with the lower part of the section exposed in the old Schaudiberg quarry (Meyer & Schmidt-Kaler 1994: cover picture). Samples are derived from a small accessible part of the section, located on the left hand of the southern entrance (Mue; Fig. 1). Almost completely silicified limestone beds are intercalated in platy limestones. Apart from one bed where ammonites and bivalves are well preserved, all beds are laminated (Fig. 2).

As in the Horstberg section, the base of the upper part of the section in the new Schaudiberg quarry (Fig. 2) cannot be correlated with the topmost beds of the old quarry. Taking into account the minor dip of the strata, and considering that there is no tectonic complications, an outcrop gap of a very few meters is supposed. The section (SB; Fig. 1) is dominated by thick limestone beds, often internally divided into thick plates. Chert layers are mainly restricted to the lower half of the section, with one thick bed completely silicified.

A very great number of species, including the greatest majority of holotypes, is derived from the sample Mue 22 extracted from the old Schaudiberg quarry (Fig. 2). It is taken from the topmost 5 cm of a partly silicified limestone bed of about 30 cm thickness, about 2 m above the base of the Mühlheim Member.

Only *Saitoum* and *Napora* are widely distributed throughout the sections (Fig. 2). Other genera of monocyrtid and dicyrtid nassellarians are mainly restricted to the sample Mue 22, apart from some rare occurrences in the samples Mue 6 and Hob 52. In all sections *Saitoum labeosum* n. sp. and *Napora pacifica* Kiessling, 1999 are much more frequent than all the other species (Figs 3; 4). Considering the robust structure of both species compared to other species of these genera, their high frequencies may be related to preservational

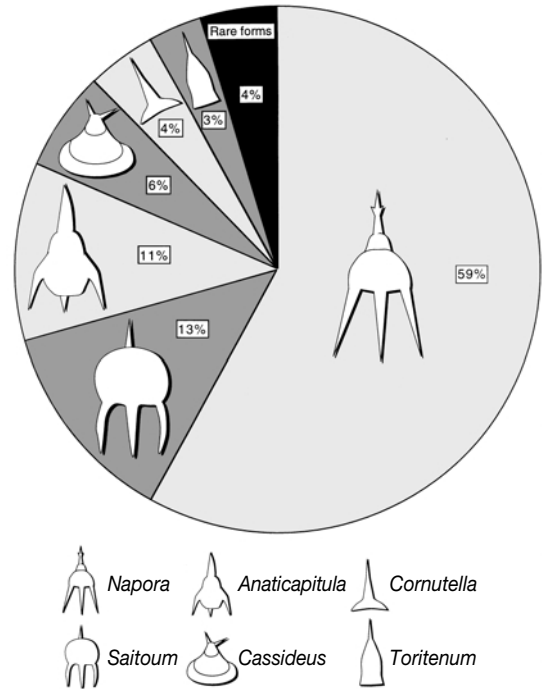


Fig. 5. — Quantitative distribution of monocyrtid and dicyrtid radiolarian genera in sample Mue 22, based on 300 specimens.

factors. *Saitoum labeosum* n. sp., for instance, is preserved even when radiolarian tests are badly preserved, and is still determinable by the characteristic protruding pore rims on the cephalic wall. As already stated for the general diversity of monocyrtid and dicyrtid nassellarians, the diversity of *Napora* and *Saitoum* is much higher in sample Mue 22 (Figs 3; 4). Frequency of *Saitoum* varies between 1 and 7% of the radiolarian association, whereas *Napora* reaches up to 4%. Other genera never reach even 1% of the radiolarian faunas.

Among the monocyrtid and dicyrtid nassellarian fauna in sample Mue 22 (Fig. 5) *Napora* makes up almost 60%, with a dominant occurrence of *Napora pacifica* Kiessling, 1999. Second and third ranks in frequencies are occupied by *Saitoum* and *Anaticapitula* n. gen., both with over 10%. Only three more genera are over 1%, such as *Cassideus* Pessagno, 1969, *Cornutella*, and *Toritenum* n. gen. Despite the

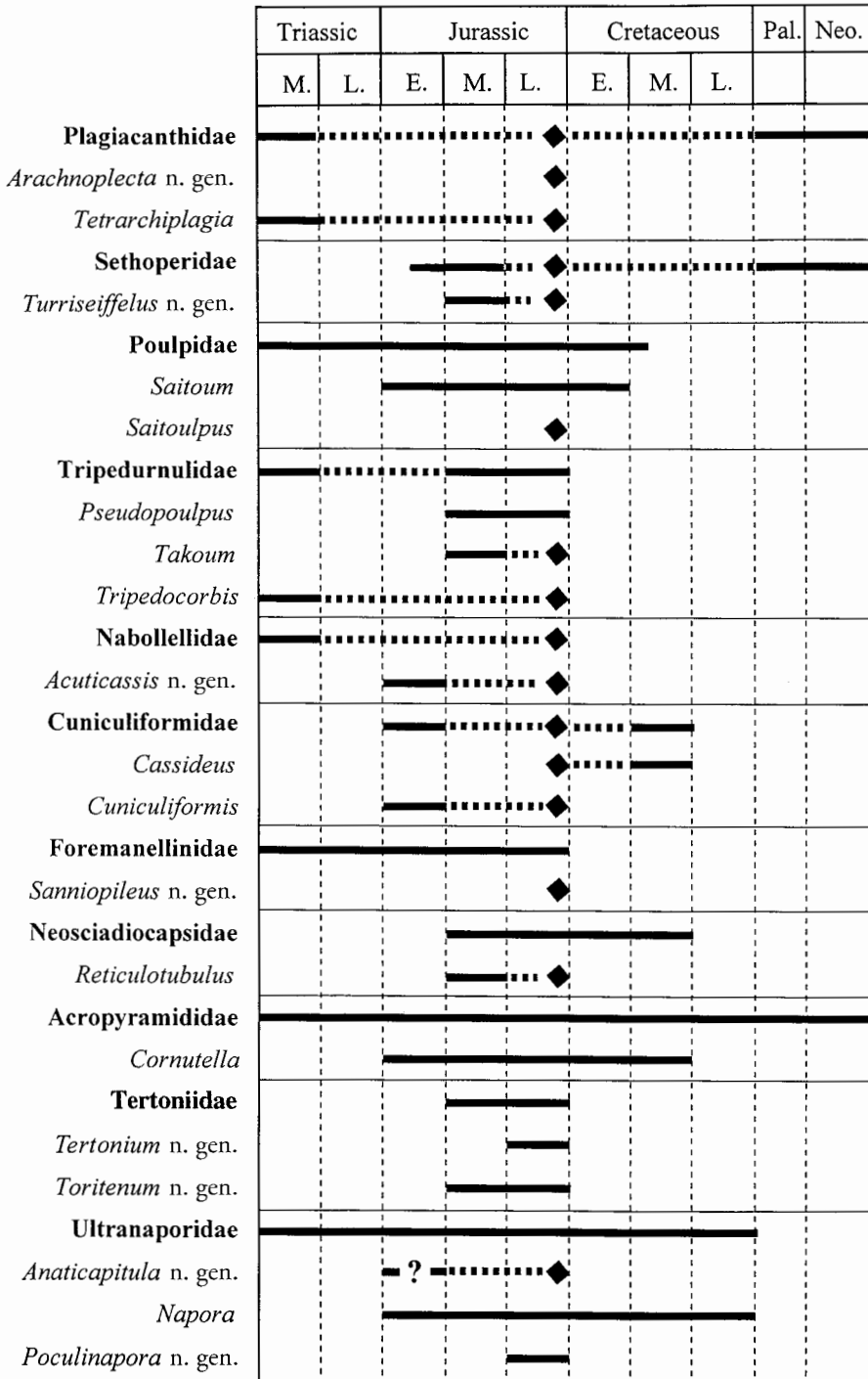


FIG. 6. — Stratigraphic range of monocyrtid and dicyrtid radiolarian families and genera described in the present paper. Stratigraphic intervals without evidence in dotted lines, early Tithonian occurrences from the Solnhofen area indicated by squares.



rarity of *Tetrarchiplagia* Dumitrica, 1982, *Turriseiffelus* n. gen., *Saitulpus* n. gen., *Reticulotubulus*, *Tertonium* n. gen., and *Poculinapora* n. gen., extensive examination, far beyond the quantitative investigation, of sample Mue 22 resulted in at most five to 20 specimens for each species. Only two specimens of the monospecific *Arachnoplecta* n. gen. were found among millions of radiolarians in Mue 22.

## STRATIGRAPHY

The biostratigraphic age of the Mörnshheim Formation, with the Mühlheim Member at its lower part, is the early Tithonian Hybonotum Zone, defined by ammonites (Zeiss 1977; Zeiss & Schweigert 1999). According to the radiolarian zonation by Baumgartner *et al.* (1995), the Mühlheim Member radiolarian association (Zügel 1997) accords with a stratigraphic position at the base of the Unitary Association Zone 12 (early Tithonian), corresponding well to the ammonite stratigraphy. Some previously described monocyrtid and dicyrtid species, such as *Saitoum pagei* Pessagno, 1977 and *Napora pacifica* accord well to this stratigraphic position. The first species reaches up to the early Tithonian, the second is reported from the upper part of the early Tithonian (Subzone 4b, Hull 1997).

Numerous appearances of representatives from families so far known from the Triassic, the Liassic, or the Middle Jurassic point out the singularity of sample Mue 22 (Fig. 6) and the imperfection of our knowledge of the range of most radiolarian taxa. Thus, the stratigraphic range of Squinabollellidae Kozur & Mostler, 1979 and Cuniculiformidae can be expanded to the Late Jurassic. The same is true on generic level for the Triassic *Tetrarchiplagia*, the Liassic *Cuniculiformis* De Wever, 1982, and the Middle Jurassic *Reticulotubulus* and *Takoum*. An extremely long lasting stratigraphic gap from the Middle Triassic to the Paleogene in the record of the family Plagiacanthidae

Hertwog, 1879 is bridged by the discovery of *Tetrarchiplagia* and *Arachnoplecta* n. gen. *Cassideus* is dated back from the Middle Cretaceous to the lower Tithonian, and the family Sethoperidae even from the Paleogene to the lower Pliensbachian. The uncommonly complete preservation of monocyrtid and dicyrtid nassellarians offers an exceptional view on the diversity and evolution of this group in the Late Jurassic.

## SYSTEMATICS

### REMARKS

In each family the genera and species are described in alphabetical order. Unless otherwise indicated, holotypes are derived from the type locality at the old Schaudiberg quarry, south of the village of Mühlheim (section Mue; Fig. 1). Type horizon is the topmost, partly silicified horizon in a partly silicified limestone bed, about 2 m above the base of the Mühlheim Member (sample Mue 22; Figs 2-4). Furthermore the known range is early Tithonian (Hybonotum Zone) for all genera and species restricted so far to the Solnhofen area. Thus, only wider ranges and occurrences are given in the following systematic descriptions.

All holotypes and paratypes mounted on stubs for examination in electron microscopy will be deposited in the collection of Musée de Géologie, Lausanne, when the whole radiolarian fauna will be described. A few holotypes and paratypes, all mounted in hyrax on glass slides, are deposited in the collection of Bâtiment de Géologie, Muséum national d'Histoire naturelle, Paris.

### ABBREVIATIONS

A	apical spine;
Ax	axial spine;
D	dorsal spine;
L	primary lateral spine;
l	secondary lateral spine;
MB	median bar;
MNHN	Muséum national d'Histoire naturelle, Paris;
V	ventral spine.

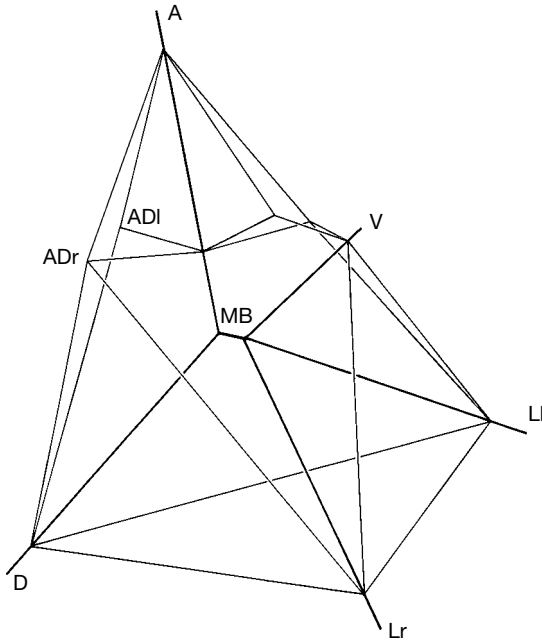


FIG. 7. — Structure of the skeleton of *Arachnoplecta architectonica* n. gen., n. sp. Abbreviations: **A**, apical spine; **ADI**, left junction area among one planiform structure of the apical spine, one of the dorsal spine, and one of the left primary spine; **ADr**, right junction area among one planiform structure of the apical spine, one of the dorsal spine, and one of the right primary lateral spine; **D**, dorsal spine; **Lr**, right primary lateral spine; **Li**, left primary lateral spine; **MB**, median bar; **V**, ventral spine.

Subclass **RADIOLARIA** Müller, 1858  
 Superorder **POLYCYSTINA** Ehrenberg, 1838,  
 emend. Riedel 1967  
 Order **NASSELLARIA** Ehrenberg, 1875  
 Family **PLAGIACANTHIDAE** Hertwig, 1879

TYPE GENUS. — *Plagiacantha* Claparède, 1856.

Genus *Arachnoplecta* n. gen.

TYPE SPECIES. — *Arachnoplecta architectonica* n. gen., n. sp.

ETYMOLOGY. — From the Greek *arachne*: spider; and *plecta*: hunting net. Feminine gender.

DIAGNOSIS. — Plagiacanthidae with initial spicule consisting of long and equally developed apical, dorsal, and primary lateral spines, and a shorter ventral spine, all of them originating in a short median bar. Apical, dorsal

and primary lateral spines non-bladed but with four net-like structures radiating in two perpendicular planes. Each plane net-like structure supported at its base by a bar closely aligned to the spine representing one blade in a four-bladed spine. Ventral spine simple, with straight branches diverging also in four perpendicular directions.

REMARKS

*Arachnoplecta* n. gen. differs from all other plagiacanthids described so far by having four net-like structures around each spine in two perpendicular planes.

*Arachnoplecta architectonica* n. sp.  
 (Figs 7; 8)

HOLOTYPE. — Photo No. 54908, 54909, 54912, 54915; stub Mue 22/17; Musée de Géologie, Lausanne, No. 74375 (Figs 7; 8).

PARATYPE. — MNHN, bât. de Géologie, No. Gg 2001/2090.

ETYMOLOGY. — From the Latin *architectonicus*: architectonic, according to its architectural design.

MATERIAL EXAMINED. — Two specimens of which only the holotype is complete, both from the type horizon (sample Mue 22).

DIMENSIONS (IN µM). — Length of spines 270-280, thickness of spines 5, maximum thickness of spines including blade-forming bars 17, span 490.

DESCRIPTION

Tetrahedral skeleton as with genus, formed by the apical, dorsal, and primary lateral spines, and by a system of net-like planes. Apical, dorsal, and primary lateral spines equal in length. Apical spine straight, and dorsal and primary lateral spines slightly curved downwards. In the central part of skeleton all spines simple, cylindrical and slender. In the proximal part, at about the same distance from the median bar, apical, dorsal, and both primary lateral spines give rise to four bars aligned to the spines. These bars diverge slightly over a short distance to run strictly parallel in the median part of the spines. Finally they converge to form a pseudo four-bladed structure in the distal part. Each of the four blade-forming bars connected to spines by short bars arising slightly obliquely at subequal distances from the main

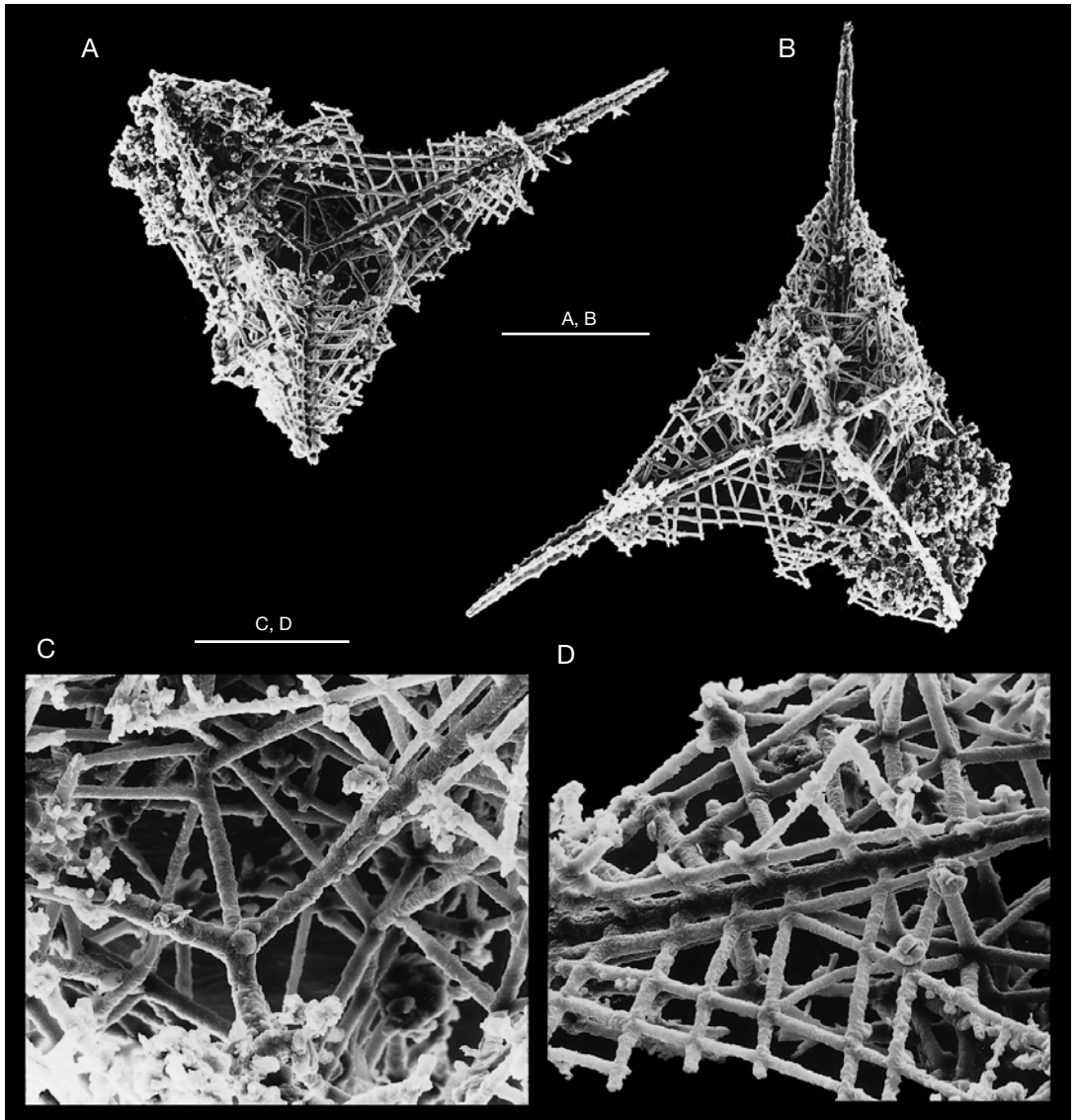


FIG. 8. — *Arachnoplecta architectonica* n. gen., n. sp., holotype; **A**, basal view (dorsal spine is directed towards the base of the figure and ventral spine towards the upper part); **B**, dorsal view (apical spine is directed towards the upper part of the figure); **C**, detail of **A** showing the median bar, the two primary lateral spines, and the ventral spine; **D**, detail of the left primary lateral spine with bars aligned to the central rod. Scale bars: A, B, 100 µm; C, D, 30 µm.

spines. This results in longitudinal rows of tetrahedral meshes proximally and medially, and small circular to elliptical pores distally. On the middle portion of main spines these short bars radiate slightly obliquely from the central axis and continue beyond the blade-forming bars to

form part of the net-like planes. From the nodes of the blade-forming bars arises also bars parallel with the edges of the tetrahedron extending between spines in the plane of the radiating bars. Both types of bars intersect forming rhomboidal to tetrahedral meshes in each plane of the four

blades. Spatial position of net-like planes in the skeletal architecture depends on the type of spine; on A it is different from that on D, and the two L. On the apical spine two net-like blades are in the latero-dorsal part forming an angle of 45° with the dorsal part of the sagittal plane. These blades join one blade of spine D and one blade of each primary lateral spine in two symmetrical places, noted here ADr and ADl, forming a triple junction. The other two blades of the apical spine form angles of 45° with the sagittal plane, but in the ventral part. Proximally they are supported by two proximal branches of the apical spine, and meet branches of the ventral spine directed latero-apically. Dorsal spine and the two primary lateral spines develop two of their four-bladed structures in three planes corresponding to the three lateral faces of the pyramid these spines outline. These structures leave in the basal part of the skeleton a wide pyramidal space. In the apical direction the other two blades of the dorsal spine and one blade of each primary lateral spine join two blades of the apical spine in ADr and ADl, whereas the other blade of the two primary lateral spines join the ventral spine. Ventral spine simple, without blade-forming bars but with straight branches radiating approximately in four perpendicular directions.

#### REMARKS

The planiform net-like structures of this species resemble those of the Tertiary or Quaternary species *Plectaniscus cortiniscus* Haeckel, 1887, but the planiform structures of the latter are simpler, forming six diagonal planes at 120° between each pair of spines.

#### Genus *Tetrarchiplagia* Dumitrica, 1982

TYPE SPECIES. — *Tetrarchiplagia arborescens* Dumitrica, 1982; original designation.

#### *Tetrarchiplagia ramosa* n. sp. (Fig. 9A-I)

HOLOTYPE. — Photo No. 58432; stub Mue 22/21; Musée de Géologie, Lausanne, No. 74376 (Fig. 9A).

ETYMOLOGY. — From the Latin *ramosus*: branched.

MATERIAL EXAMINED. — 16 specimens from the type horizon (sample Mue 22).

DIMENSIONS (IN  $\mu\text{M}$ ). — Length of apical spine 140-235 (av. 195), of dorsal spine 190-245 (av. 225), of primary lateral spines 160-245 (av. 210), of ventral spine 20-75 (av. 50), of median bar 4-6; distance of first verticil from MB on D and L 30-50 (av. 40), on A 55-80 (av. 65).

#### DESCRIPTION

Spicule with apical, dorsal, ventral, and both primary lateral spines originating in a very short median bar. A, D, and L stout, long, subequal, with a number of verticils oriented at about right angles to the spines, and generally decreasing in length to the distal part of the spines. Ventral spine small, thin, directed obliquely upward, distally slightly curved downwards when longer. Apical spine straight with three verticils of which the first has generally five branches, the second three, rarely more, and the third two or three. Branches of first and second verticils with one or two verticils of spinules. Dorsal and primary lateral spines equal, longer than A, and curved downward. They bear four verticils of which the first has generally three branches, the second two or three, and the third and fourth two branches. Branches of first verticil, rarely of the second, bear spinules. Except V all spines increase slowly in diameter to the last verticil, then taper distally.

#### REMARKS

*Tetrarchiplagia ramosa* n. sp. resembles somehow the Triassic species *T. verticillata* Dumitrica, 1982 and *T. abietinoides* Dumitrica, 1982 by having verticils of three or four branches, but differs from both by the number of verticils, size of branches, presence of spinules on some branches, etc. Together with the following species, this is the first Jurassic species of the family Plagiacanthidae so far described bridging the pre-existing long gap between the Middle Triassic and the Paleogene. It is noteworthy, however, that they are not the only species of the family occurring in the Jurassic. Work in progress of the senior author proves that, although much sparser than in the Middle Triassic, at least three more species occur in the Lower and Middle Jurassic.

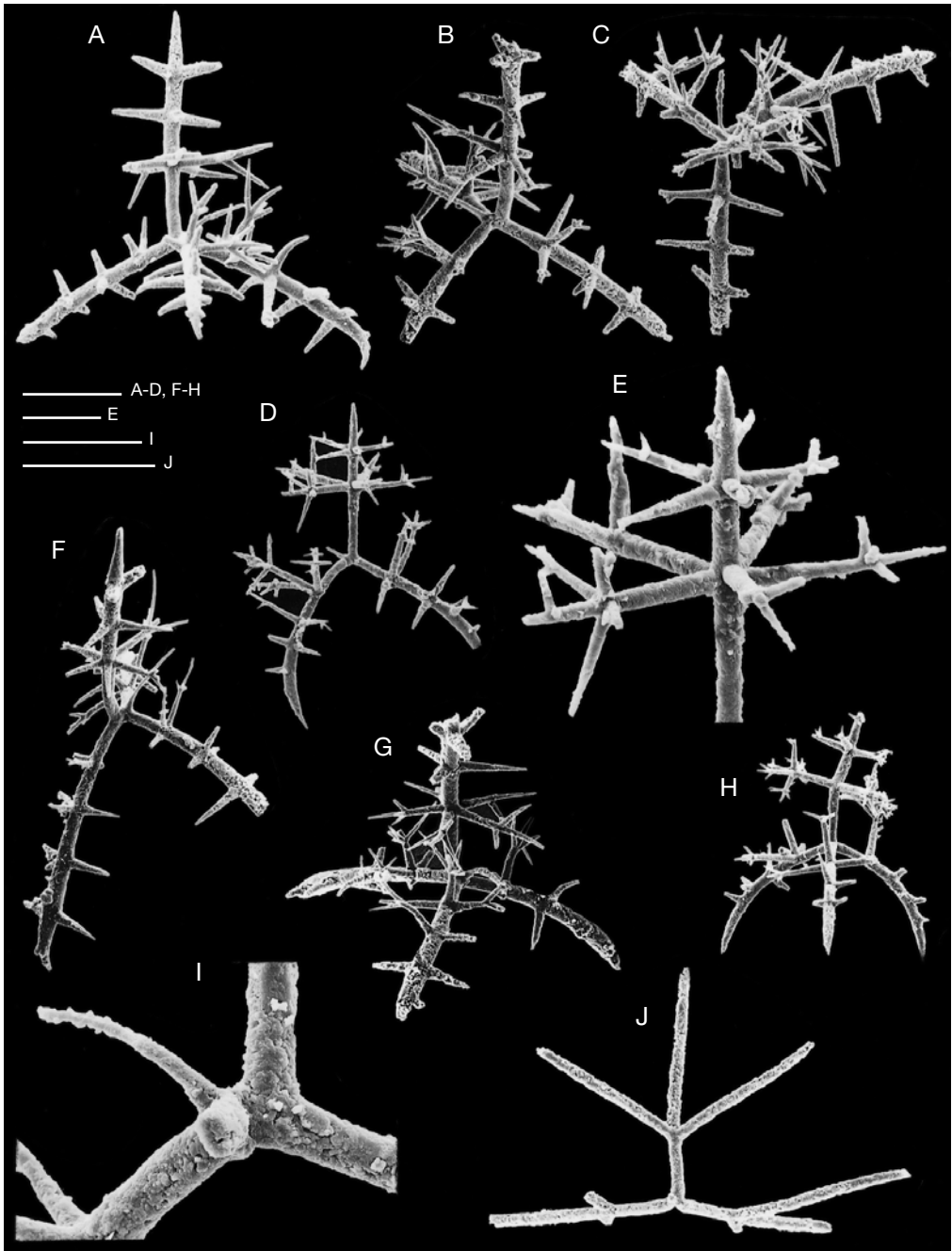


FIG. 9. — **A-I**, *Tetrarchiplagia ramosa* n. sp.; **A**, holotype, right lateral view; **B-I**, paratypes; **B, C**, left lateral and apical views of the same specimen; **D, E**, left lateral view and detail of apical spine of the same specimen showing a smaller angle between **D** and **L**; **G**, oblique ventral view; **H**, dorsal view of a small specimen with strongly curved **D** and **L**; **I**, left lateral view, detail of the central part showing the slender ventral spine and **LI** broken off; **J**, *Tetrarchiplagia tithoniana* n. sp., paratype, apical view. Abbreviations: **D**, dorsal spine; **L**, primary lateral spine; **LI**, left primary lateral spine. Scale bars: **A-D**, **F-H**, **J**, 100  $\mu$ m; **E**, **I**, 30  $\mu$ m.

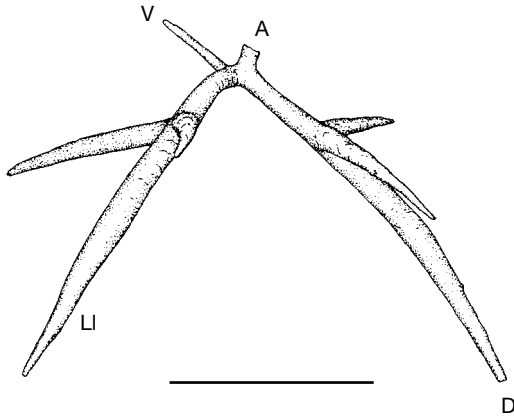


FIG. 10. — *Tetrarchiplagia tithoniana* n. sp., holotype, left lateral view; note that spines A and Lr are broken off. Abbreviations: A, apical spine; D, dorsal spine; Ll, left primary lateral spine; Lr, right primary lateral spine; V, ventral spine. Scale bar: 0.1 mm.

*Tetrarchiplagia tithoniana* n. sp.  
(Figs 9J; 10)

HOLOTYPE. — MNHN, bât. de Géologie, No. Gg 2001/2089 (Fig. 10).

ETYMOLOGY. — From its occurrence in the Tithonian.

MATERIAL EXAMINED. — Two specimens from the type horizon (sample Mue 22).

DIMENSIONS (IN  $\mu\text{M}$ ). — Length of D and L 190-200, of spinules 90-100, of V 40.

DESCRIPTION

Spicule with a thin, relatively short ventral spine and with A, D and L massive, arranged according to the diagonals of a tetrahedron. Apical spine broken off in both specimens available but, by comparison with other species having D and L with the same type of branching, it might be straight and have a verticil of three spinules. Median bar very short. Spines D and L equal, slightly curved downward, gently tapered distally, and provided with two long spinules in a V-shaped position. Secondary lateral spines missing.

REMARKS

Although the species is only represented by two incomplete specimens, it is well distinguished

from the other Mesozoic species of *Tetrarchiplagia* so far described (Dumitrica 1982a).

Family SETHOPERIDAE Haeckel, 1881,  
emend. Petrushevskaya 1971

TYPE GENUS. — *Sethopera* Haeckel, 1881.

KNOWN RANGE. — Lower Jurassic (Pliensbachian) to Recent.

Genus *Turriseiffelus* n. gen.

TYPE SPECIES. — *Turriseiffelus invalidus* n. gen., n. sp.

ETYMOLOGY. — From its resemblance with the Eiffel Tower in Paris.

KNOWN RANGE. — Bajocian to early Tithonian.

DIAGNOSIS. — Mono- and dicyrtid nassellarians with a hemispherical cephalis including an initial skeleton consisting of median bar, apical, dorsal, ventral, and primary lateral spines, and the arches AL, AD, LD and LV (or LL), the last two forming four collar pores. Ventral spine short. Dorsal spine short in most cases. Primary lateral spines, exceptionally dorsal spine, extended outside cephalis into three-bladed feet. Apical spine extended into a three-bladed horn. Blades of both apical horn and feet perforated, bearing one or more longitudinal rows of rounded rectangular meshes. Cephalic and thoracic wall, when present, reticulate, formed of crossing bars.

REMARKS

*Turriseiffelus* n. gen. differs from other sethoperid genera by having commonly only two feet. Most other characters, such as the initial spicule lacking secondary lateral spines, the systems of arches, the branched spines, and the cephalic wall, built by crossing bars forming triangular or quadrangular pores, are common with most members of the family. Perforated blades more or less similar to those of *Turriseiffelus* n. gen. or spines with branches in the planes of the three blades are found in all or only in some spines of many sethoperids, as for example in the apical horn of *Clathrocanium* Ehrenberg, 1860, in all spines of *Pteropilium reticulatum* (Popofsky, 1913) (Petrushevskaya 1971), etc. Moreover, *Callimitra*(?) sp. of Abelmann (1992) has a rather similar morphology to *Turriseiffelus* n. gen.

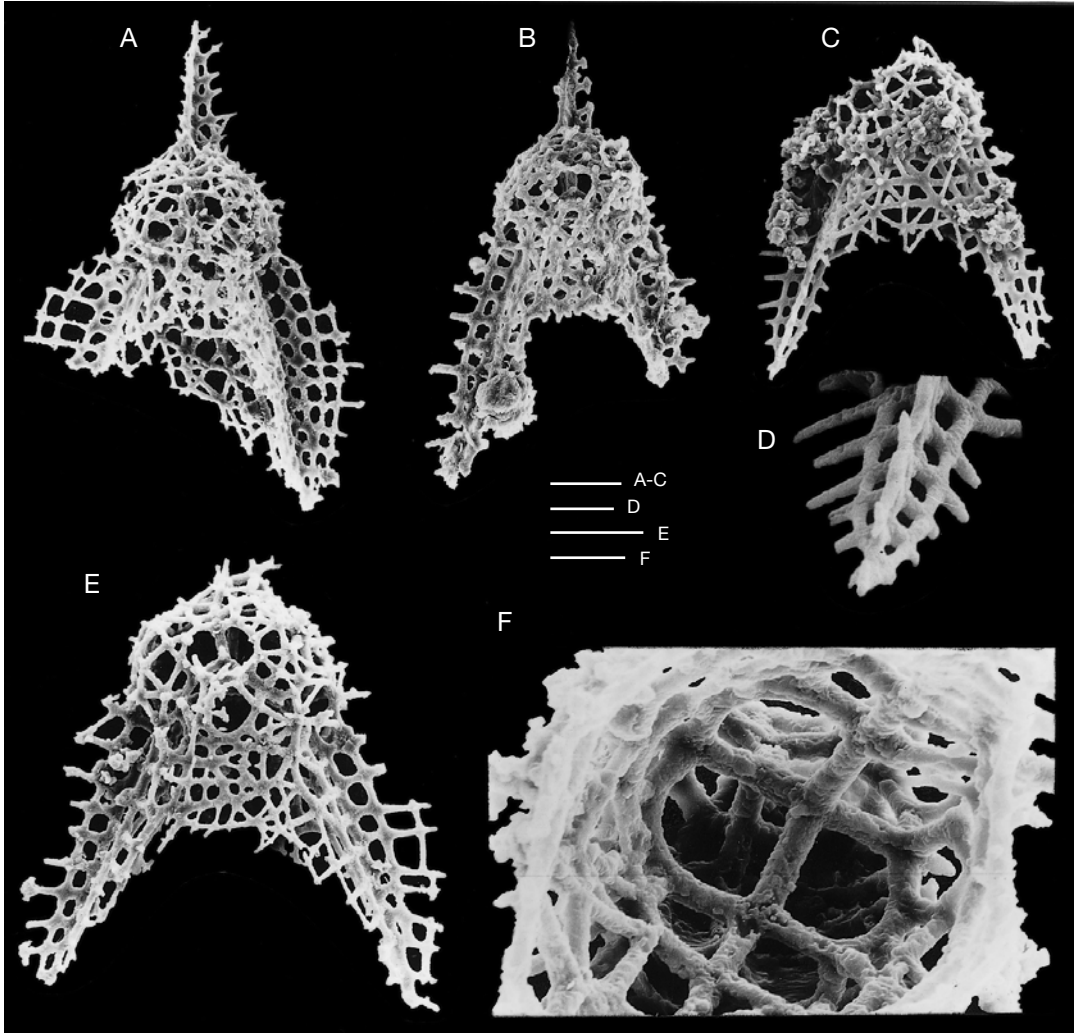


FIG. 11. — *Turriseiffelus invalidissimus* n. gen., n. sp.; **A**, holotype showing the well preserved apical horn; **B-F**, paratypes; **B**, specimen with partly preserved apical horn; **C**, specimen with apical horn corroded; **D**, same, detail of one foot; **E**, specimen with apical horn corroded; **F**, basal view of the initial spicule and arches. Scale bars: A-C, E, 30  $\mu\text{m}$ ; D, F, 10  $\mu\text{m}$ .

*Turriseiffelus invalidissimus* n. sp.  
(Fig. 11)

HOLOTYPE. — Photo No. 58105; stub Mue 22/20; Musée de Géologie, Lausanne, No. 74377 (Fig. 11A).

ETYMOLOGY. — From the Latin *invalidissimus*: the most invalid, the most infirm, since by comparison to *Turriseiffelus invalidus* n. gen., n. sp. it is lacking the fragile apical horn in most specimens.

MATERIAL EXAMINED. — 11 specimens from the type horizon (sample Mue 22).

DIMENSIONS (IN  $\mu\text{m}$ ). — Length without apical horn 120-175 (av. 155), of cephalis 50-70 (av. 60), of feet 80-120 (av. 105), of apical horn 27-60 (av. 42), total width 110-170 (av. 140), width of cephalis 70-85 (av. 75).

DESCRIPTION

Test composed of a hemispherical cephalis and two feet. Initial skeleton with arches AL, AD, DL, and LV. Apical spine prolonged externally into a three-bladed horn with one, exceptionally two,

rows of tetragonal meshes. Ventral spine, at least in one specimen, with a verticil of four branches at the level of the cephalic wall of which two form the arches LV and two tend to connect the arches AL. Cephalis with large meshes closed by small bars arranged in rosettes. Central rod of the feet straight, accompanied by three slightly curved bars. Bars and central rod connected by lateral branches of the rods, partly continuous beyond the bars to form a pectinate structure. Distally the bars around the central rod of each foot tend to come closer to the rod and finally join it forming size-decreasing meshes. Thoracic skirt composed of a coarse net-like or rosette-like meshwork.

#### REMARKS

The species is compared to *T. invalidus* n. gen., n. sp., see under the latter species.

#### *Turriseiffelus invalidus* n. sp. (Fig. 12A, B, D)

HOLOTYPE. — Photo No. 57101; stub Mue 22/19; Musée de Géologie, Lausanne, No. 74378 (Fig. 12A).

ETYMOLOGY. — From the Latin *invalidus*: invalid, infirm, since by comparison to Eiffel Tower this species has only two feet.

MATERIAL EXAMINED. — Two specimens from the type horizon (sample Mue 22).

DIMENSIONS (IN  $\mu\text{M}$ ). — Total length 520-535, length of apical horn 210-230 (av. 220), of cephalis 65-95 (av. 85), of feet 240-320 (av. 275), total width 230-345, width of cephalis 85-117 (av. 100).

#### DESCRIPTION

Test composed of a bell-shaped cephalis, an apical horn, and two feet diverging at about 60°. Proximal part of the feet connected by a skirt forming a conical thorax. Initial skeleton as described for the genus but with an arch between the primary lateral spines instead of arches between the ventral spine and the primary lateral spines. In basal view this arch forms a trapezoidal outline with the primary lateral spines. Arch not connected to the ventral spine which has an upper position and which bears some branches before

merging in the cephalic wall. Apical horn and feet three-bladed. Blades formed by three bars regularly aligned and connected to a central rod which represents extension of the apical and primary lateral spines respectively, leaving regular rectangular pores. Two blades of the apical horn connected to the outer blades of the feet and to the arches AL. The inner blades of the feet are connected to the slightly curved thoracic skirt. Usually well preserved blades of apical horn and external blades of feet with two ranges of thorns. Apart from the connection zone to feet, thoracic skirt formed by a dense meshwork of small bars, mostly resulting in rosette-like structures. Part of cephalic and thoracic wall usually double-layered, both layers with rosette-like structures. Distalmost parts of feet splitted off to thorn-like projections, as the three bars aligned to the central rod diverge.

#### REMARKS

*Turriseiffelus invalidus* n. gen., n. sp. differs from *Turriseiffelus invalidissimus* n. gen., n. sp. mainly by the presence of only one row of pores along apical horn and feet. It differs from both *T. invalidissimus* n. gen., n. sp. and *T. yaoi* n. gen., n. sp. by the practical absence of arches VL, presence of an arch LL, and by a bunch of spines at the distal end of feet. Minor differences concern the presence of a dense, thin-layered cephalic wall in *T. invalidus* n. gen., n. sp.

#### *Turriseiffelus yaoi* n. sp. (Fig. 13)

HOLOTYPE. — MNHN, bât. de Géologie, No. Gg 2001/2091 (Fig. 13).

ETYMOLOGY. — The species is dedicated to Prof. Akira Yao (Osaka City University, Japan) who provided a residue from his famous IN 7 sample in which the species was found.

TYPE LOCALITY. — Right side of the Kiso river, east of Unuma, Kagamihara City, Gifu Prefecture, inner zone of Southwest Japan (35°24'1''N, 136°57'41''E) (Ichikawa & Yao 1976).

TYPE HORIZON. — Sample IN 7, manganese-carbonate nodule embedded in red siliceous mudstone which grades upsection into grey siliceous mudstone.



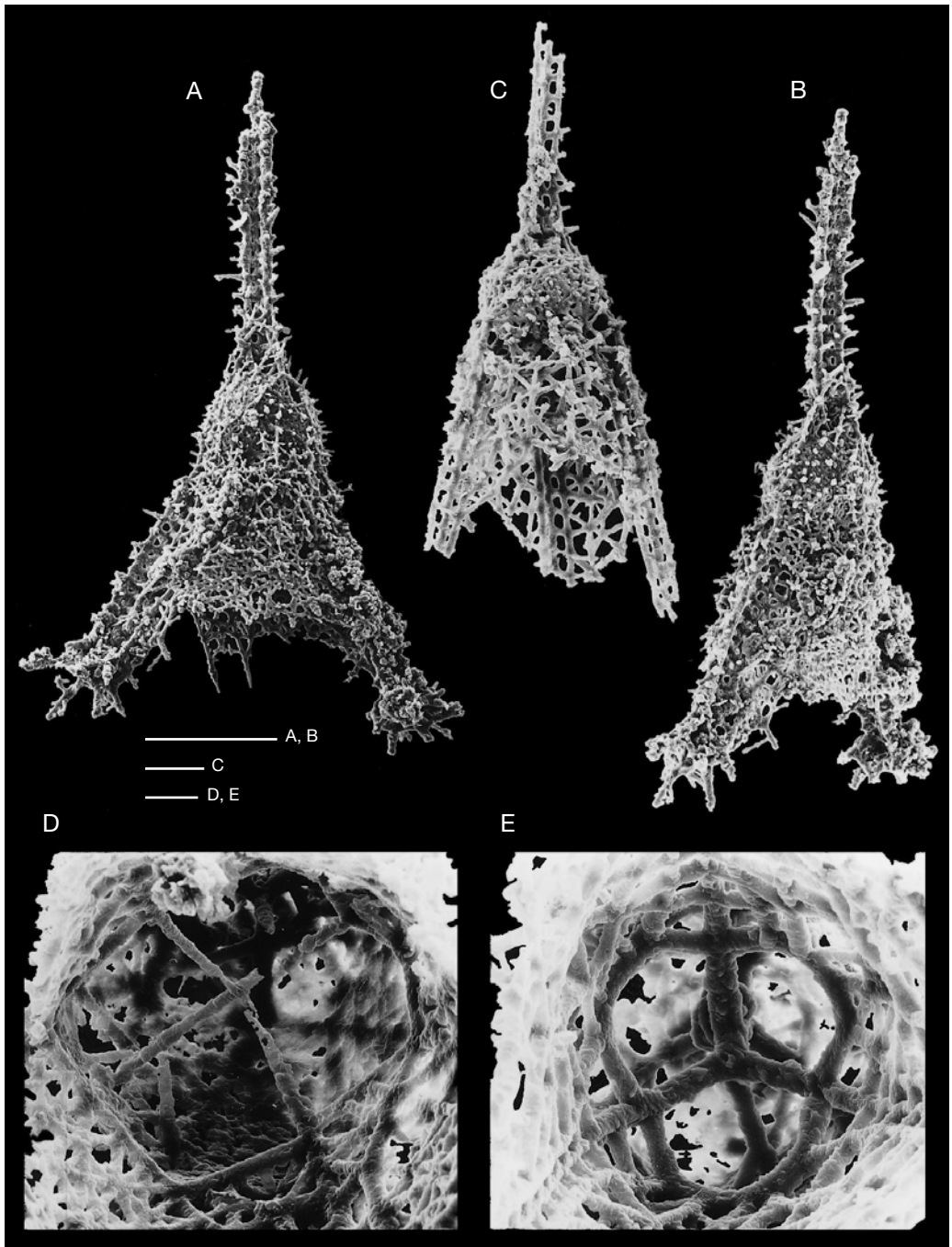


FIG. 12. — **A, B, D**, *Turriseiffelus invalidus* n. gen., n. sp.; **A**, holotype; **B, D**, paratypes; **D**, basal view of initial spicule and arches; **C, E**, *Turriseiffelus* sp.; **C**, right lateral view; **E**, basal view showing details of the initial spicule and arches. Scale bars: **A, B**, 100 µm; **C**, 30 µm; **D, E**, 10 µm.

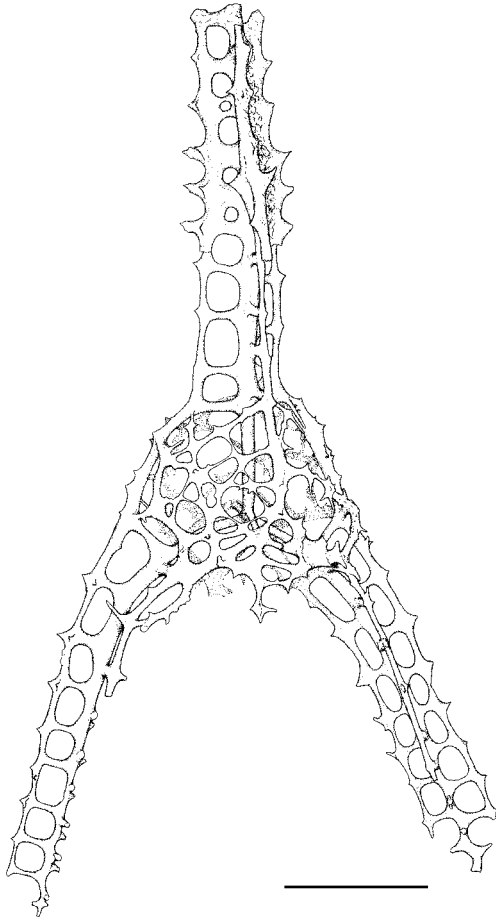


FIG. 13. — *Turriseiffelus yaoi* n. gen., n. sp., holotype, dorsal view. Scale bar: 50  $\mu$ m.

OCCURRENCE. — *Unuma echinatus* Assemblage-zone (Yao *et al.* 1980), Unitary Association Zone 3 dated as early-middle Bajocian (Yao & Baumgartner 1995).

MATERIAL EXAMINED. — One specimen from the type horizon.

DIMENSIONS (IN  $\mu$ M). — Total length of skeleton 320, length of apical horn 135, of cephalis 60, of feet 125-135.

DESCRIPTION

Test composed of a bell-shaped cephalis, a long apical horn and two feet. Initial skeleton with MB, a long, thick apical spine and primary lateral spines, short dorsal and ventral spines, and arches AL, AD, LD, and LV. Cephalic wall thin, reticu-

late, consisting of intercrossing bars forming triangular or quadrangular meshes of variable size. Apical spine extended into a long horn, and primary lateral spines into long feet, all of them three-bladed. Blades with a longitudinal row of rounded quadrangular pores. One blade of apical horn aligned with arch AD, the other two with arches AL and the external blade of the feet. One of the lateral blades of feet aligned with arch LD, the other with arch LV. Feet straight, diverging from one another at an angle of about 40°. Thorax incomplete, short, similar to the cephalis in structure, and represented by only its proximal part formed by a short downward prolongation of the wall of the cephalis and extended between the latter and the lateral blades of the feet.

REMARKS

*Turriseiffelus yaoi* n. gen., n. sp. resembles *T. invalidus* n. gen., n. sp. from which it differs by the presence of arches LV instead of arches LL, and by missing the distal bunch of spines of the feet.

*Turriseiffelus* sp.  
(Fig. 12C, E)

MATERIAL EXAMINED. — A single specimen from sample Mue 22.

REMARKS

This specimen resembles *T. invalidus* n. gen., n. sp. and *T. yaoi* n. gen., n. sp. in skeletal morphology, but differs from both by having three feet.

Family POULPIDAE De Wever, 1981

TYPE GENUS. — *Poulpus* De Wever *in* De Wever, Sanfilippo, Riedel & Gruber, 1979.

Genus *Saitoum* Pessagno, 1977

TYPE SPECIES. — *Saitoum pagei* Pessagno, 1977; original designation.

KNOWN RANGE. — Jurassic-Cretaceous.

## REMARKS

For many monocyrtid lower Tithonian species from the material we studied in the present paper it is difficult to establish whether they belong to the genus *Poulpus* or to the genus *Saitoum*. Some of them have the arches Al rather well marked on the surface and sometimes the arch AV is weakly sketched. In other species of comparable morphology, especially when the cephalic wall is thick, these arches are not visible. As De Wever (*in De Wever et al.* 1979) remarked, the members of the genus *Poulpus* are superficially similar to *Saitoum pagei*, the type species of the genus *Saitoum*, the only difference is that the genus *Poulpus* has the three arches Al and AV marked as depressions on the surface of the cephalis, whereas *Saitoum* has no arches.

In order to better understand the differences between the two genera we also examined some specimens of *S. pagei* from our material and found that this species has also the three arches Al and AV. They are very weak on some segments as compared to those of *Poulpus* and are marked externally by three longitudinal constrictions so that the cephalis of *S. pagei* is three-lobate in apical view. Takemura (1986) showed also a well marked arch AV in *Saitoum levium* De Wever, 1981. Therefore *Poulpus* could be considered a junior synonym of *Saitoum*. In order to preserve it we think that a better distinction between the two genera could be the presence or absence of the apical horn: the genus *Poulpus* could be characterized by the absence of the apical horn and *Saitoum* by its presence. In all the three Triassic species initially assigned to *Poulpus*, the type species included, the apical horn is absent. Other Triassic species assigned to this genus are also characterized by the absence of the apical horn, or when it is present it looks like a very short thorn. *Saitoum*, on the contrary, has always a rather well developed apical horn. A character common to both genera is also the absence of verticils of spines on feet.

*Saitoum* was described without a distal velum. Our well preserved material proves that a velum is almost always present, its absence being due to poor preservation.

*Saitoum ambiguum* n. sp.

(Fig. 14A-D)

HOLOTYPE. — Photo No. 58130, 58131; stub Mue 22/20; Musée de Géologie, Lausanne, No. 74379 (Fig. 14A, B).

ETYMOLOGY. — From the Latin *ambiguus*: ambiguous.

MATERIAL EXAMINED. — Three specimens from the type horizon (sample Mue 22).

DIMENSIONS (IN  $\mu\text{M}$ ). — Length of cephalis 45-65 (av. 55), of feet 35-50 (av. 45), of apical horn 35, of ventral or secondary lateral spines 12-14, width of cephalis 55-75 (av. 65).

## DESCRIPTION

Cephalis very small, globular. Initial skeleton with well marked arches AV and AL. Apical horn long, three-bladed. Wall of cephalis thin, rather smooth, with rounded pores of very variable size. Ventral spine and secondary lateral spines of the initial spicule prolonged outside cephalic wall into short, three-bladed spines. Axobate short but present. Feet curved, three-bladed, strongly diverging. Due to the arches of the initial skeleton the spines V and I have one blade upward directed, and the feet one blade downward directed.

## REMARKS

The systematic position of this species is uncertain. Morphologically it resembles the species of *Saitoum* but has the secondary lateral spines extended outside which is a character of the genus *Takoum*. However, *Takoum* has no arch AV.

*Saitoum bicorniculatum* n. sp.

(Fig. 14E-G)

HOLOTYPE. — Photo No. 13741, 13742; Musée de Géologie, Lausanne, No. 74378 (Fig. 14E, F).

ETYMOLOGY. — From the Latin *bi*: two; and *corniculatum*: having small horns.

MATERIAL EXAMINED. — Two specimens from the type horizon (sample Mue 22).

DIMENSIONS (IN  $\mu\text{M}$ ). — Length of cephalis 55-58, of feet 95-105, of apical horn 30-37, of ventral spine 20-30, width of cephalis 70.

## DESCRIPTION

Cephalis very small, low, trapezoidal in lateral view, with long apical horn and ventral spine, and three long curved feet. Apical horn straight, three-bladed, strongly eccentric and inclined dorsally. Ventral spine well developed but shorter than the apical. Cephalic wall with small pores of variable size and irregular arrangement; usually size of pores decreases apically. Feet long, strongly divergent and curved inwardly. Lower border of cephalis simple.

## REMARKS

Morphologically, this new species is very close to *S. pagei* from which it differs by having a well developed ventral spine, a low cephalis, and pores without protruding rims.

*Saitoum curtipes* n. sp.

(Fig. 14H-J)

HOLOTYPE. — Photo No. 58491; stub Mue 22/21; Musée de Géologie, Lausanne, No. 74381 (Fig. 14H).

ETYMOLOGY. — From the Latin *curtus*: short; and *pes*: foot.

MATERIAL EXAMINED. — Five specimens from the type horizon (sample Mue 22).

DIMENSIONS (IN  $\mu\text{M}$ ). — Length of cephalis 70-78 (av. 73), of feet 30-45 (av. 35), of apical horn 31-37 (av. 35), width of cephalis 75-95 (av. 80).

## DESCRIPTION

Cephalis very small, subspherical, with very slender apical horn and feet. Cephalic wall with sparse circular or elliptical pores, each pore with a protruding rim. Ditrems present. Apical horn, slender, needle-like, three-bladed proximally, half as long as diameter of cephalis. Feet slender, strongly divergent and curved downwards. They are practically bladeless but some specimens show very low blades or a triangular cross section proximally. Lower border of cephalis with a thin rim. Axobate short.

## REMARKS

*S. curtipes* n. sp. resembles *S. labeosum* n. sp. in having a subglobular cephalis with the same sys-

tem of pores with protruding rims, but differs from this species by being less robust, by having apical horn and feet slender and the latter strongly divergent and curved. It is morphologically closed to *S. reticulatum* n. sp. from which it differs by having shorter and slender feet and rims of pores not connected to form a reticulum.

*Saitoum(?) delicatum* n. sp.

(Fig. 14K-M)

HOLOTYPE. — Photo No. 58450; stub Mue 22/21; Musée de Géologie, Lausanne, No. 74382 (Fig. 14K).

ETYMOLOGY. — From the Latin *delicatus*: fine.

MATERIAL EXAMINED. — Five specimens from the type horizon (sample Mue 22).

DIMENSIONS (IN  $\mu\text{M}$ ). — Length of cephalis 40-50 (av. 45), of feet 35-45 (av. 40), of apical horn 34-41 (av. 53), width of cephalis 45-60 (av. 55).

## DESCRIPTION

Cephalis very small, globular with slender, cylindrical apical horn and feet. Initial skeleton with arch AV well marked by a constriction. Arches Al less marked. Cephalic wall thick with rounded pores of various size. Thin-walled specimens with larger pores, thick-walled specimens with small pores due to a superimposed deposition of silica. Apical horn straight, long, gently tapering. Feet straight, long, strongly divergent. Ventral spine very short, three-bladed, pyramidal. Thick-walled specimens with remains of a very delicate velum.

## REMARKS

The species is questionably assigned to *Saitoum* because of the constriction along the arch AV. Although it has cylindrical apical horn and feet *S.(?) delicatum* n. sp. does not seem to be closely related to *S. curtipes* n. sp., *S. elegans* De Wever, 1981, or *S. labeosum* n. sp.

*Saitoum differtum* n. sp.

(Fig. 15A-C)

HOLOTYPE. — Photo No. 58465, 58466; stub Mue 22/21; Musée de Géologie, Lausanne, No. 74382 (Fig. 15A, B).

ETYMOLOGY. — From the Latin *differtus*: full.

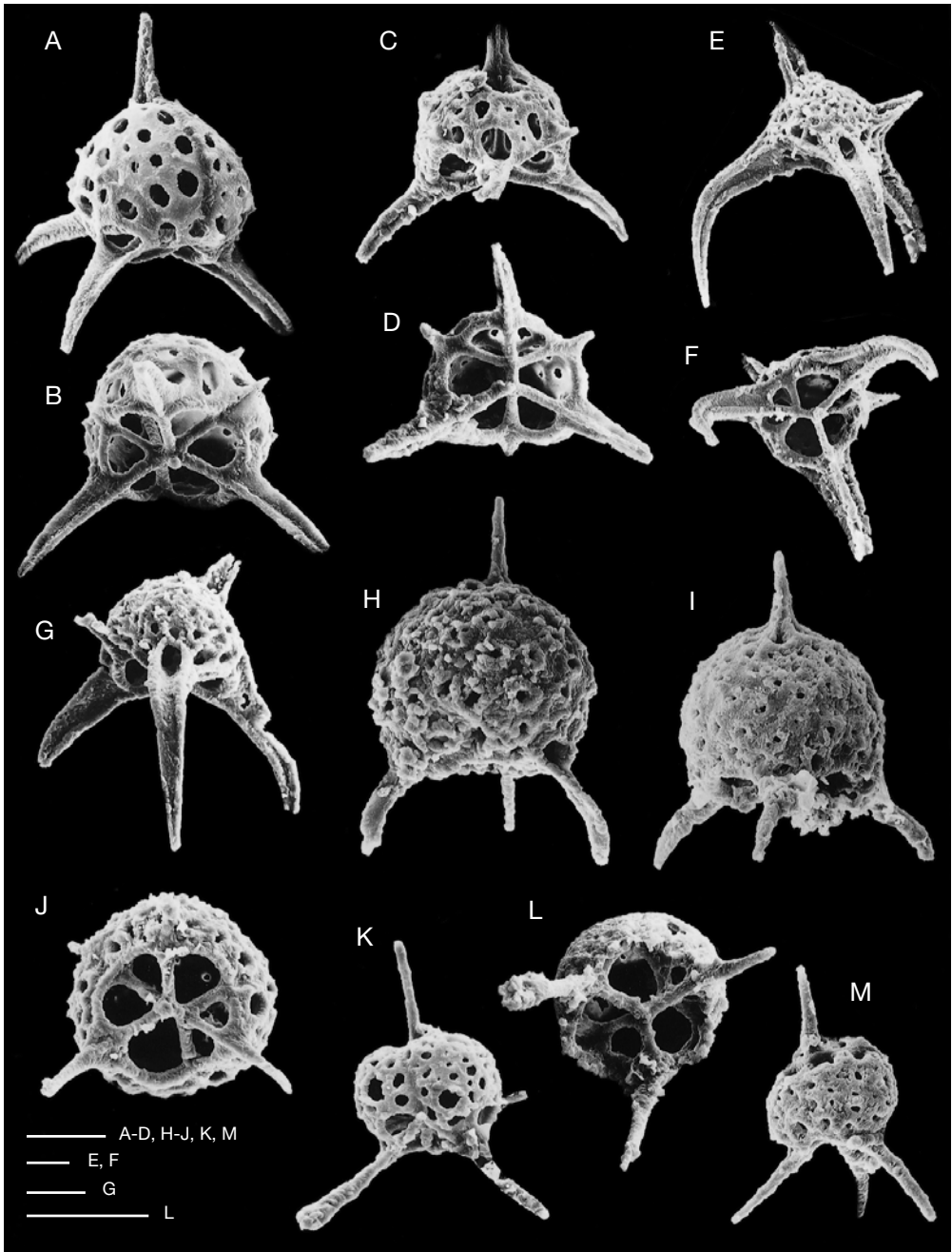


FIG. 14. — **A-D**, *Saitoum ambiguum* n. sp.; **A, B**, holotype, latero-ventral and basal views respectively; **C, D**, paratype, dorsal and basal views showing the two secondary lateral spines extended outside wall; **E-G**, *Saitoum bicorniculatum* n. sp.; **E, F**, holotype, right lateral and basal views showing the long ventral spine and the dorsally displaced apical horn; **G**, paratype, left lateral view; **H-J**, *Saitoum curtipes* n. sp.; **H**, holotype, ventral view; **I, J**, paratypes; **I**, specimen with remnants of velum; **J**, basal view; **K-M**, *Saitoum(?) delicatum* n. sp.; **K**, holotype, ventral view showing a constriction along arch AV; **L, M**, paratypes; **L**, basal view showing remnants of velum; **M**, right lateral view showing a constriction along arch Al. Abbreviations: **A**, apical spine; **I**, secondary lateral spine; **V**, ventral spine. Scale bars: 30  $\mu\text{m}$ .

MATERIAL EXAMINED. — Two illustrated specimens from the type horizon (sample Mue 22).

DIMENSIONS (IN MM). — Length of cephalis 50-60, of feet 30-35, of horn 25-30, width of cephalis 60-65.

#### DESCRIPTION

Cephalis globular, thick-walled with very small pores and surface covered by a pustulate layer. Apical horn stout, about as long as half the width of the cephalis, three-bladed, pointed, with thick blades. Ventral spine extremely short. Arch AV probably present, not visible from outside. Feet strongly divergent, stout, pointed, slightly curved. They are approximately as long as the apical horn, three-bladed, with thick blades and narrow grooves. Velum short, only partly preserved.

#### REMARKS

*Saitoum differtus* n. sp. differs from the other species of the genus by short, stout, and strongly divergent feet, and the cephalic wall covered by a pustulate layer.

#### *Saitoum kapewinteri* n. sp. (Fig. 15D, E, N)

HOLOTYPE. — Photo No. 38490, 38491; stub Hob 32; Musée de Géologie, Lausanne, No. 74384 (Fig. 15D, N).

ETYMOLOGY. — The species is named for Dr. Klaus-Peter Winter, Geological and Palaeontological Institute, Frankfurt am Main, Germany.

TYPE LOCALITY. — Horstberg, northern quarry, about 1 km NNE of Mühlheim, 2.5 km S of Solnhofen.

TYPE HORIZON. — Sample Hob 32, 40 cm limestone bed, about 1.5 m below limestones with well preserved ammonites.

MATERIAL EXAMINED. — Of the 15 photographed specimens a single specimen comes from the rich material of sample Mue 22, where the species is extremely rare. All the other specimens were found in the samples Mue 9, SB 3, Hob 32, and Hob 52.

DIMENSIONS (IN  $\mu\text{M}$ ). — Length of cephalis 67-78 (av. 73), of feet 55-72 (av. 63), of apical horn 40-60 (av. 50), width of cephalis 74-80 (av. 76).

#### DESCRIPTION

Cephalis globular, robust, thick-walled, generally poreless except for a few very small pores scat-

tered here and there, three pores at the base of the apical horn, one above each foot, and the pores of the ditreme. Ditreme around the ventral and secondary lateral spines, the former with a much more protruding rim than the latter. Surface densely pustulate. Apical horn long, conical, sometimes with thickened base. Feet slightly longer than apical horn, oval or elliptical in cross section, slightly curved and weakly divergent. Their distal ends pointed, usually with a weak keel on the external side. Distal part of cephalis slightly constricted, bearing a very thick, expanded but short lobe between feet. Elements of initial spicule very robust, flattened laterally. Velum very thin and very rarely preserved.

#### REMARKS

Morphologically *Saitoum kapewinteri* n. sp. is very close to *S. elegans* from which it differs in having commonly small lobes between feet, a shorter cephalis, sensibly shorter, thicker, and less divergent feet. Moreover, a ditreme may exist around the secondary lateral spines. Given all these characters, and the fact that our specimens are older than all the specimens of *S. elegans* so far illustrated, with a single exception (Baumgartner *et al.* 1995: pl. 3022, fig. 3) all Berriasian in age, it is possible that this new species represents the ancestor of *S. elegans* and is transitional between the latter and *S. levium* or *S. corniculum* De Wever, 1981.

#### *Saitoum labeosum* n. sp. (Fig. 15F-I, L)

*Saitoum* sp. A – Kiessling 1995: pl. 61, fig. 17.

*Saitoum* sp. aff. *S. dercourti* Widz & De Wever, 1993 – Zügel *et al.* 1998: 12, pl. 1, fig. 10.

HOLOTYPE. — Photo No. 23086; stub Mue 9; Musée de Géologie, Lausanne, No. 74385 (Fig. 15F).

ETYMOLOGY. — From the Latin *labeosus*: thick-lipped.

TYPE LOCALITY. — From the same section as Mue 22.

TYPE HORIZON. — Sample Mue 9, from the central part of a 20 cm thick limestone bed, non-silicified apart from small silicified lenses, 50 cm above a conspicuous silicified limestone bed with well preserved ammonites.

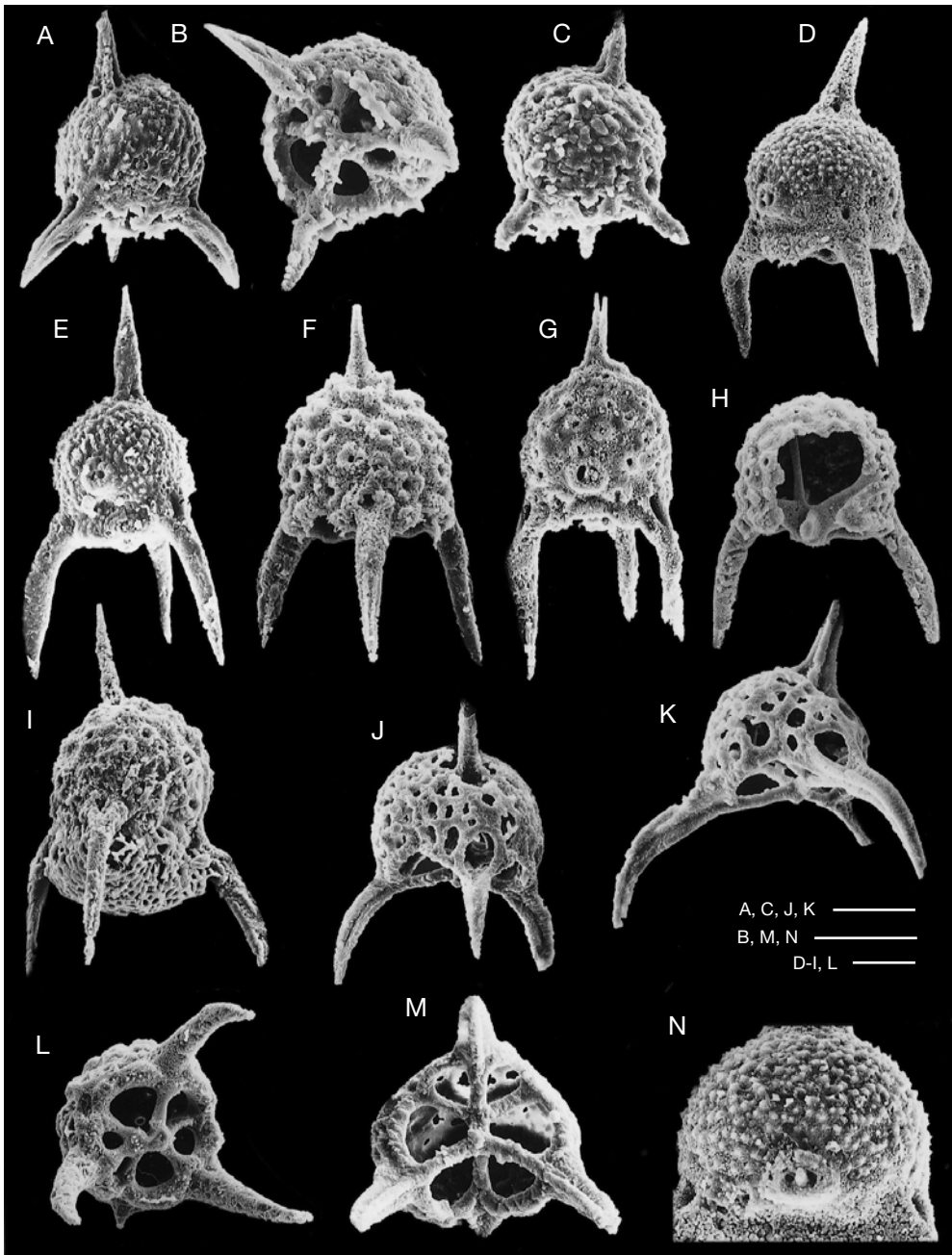


FIG. 15. — **A-C**, *Saitoum differtum* n. sp.; **A, B**, holotype, right lateral and basal views; **C**, paratype, left lateral view; **D, E, N**, *Saitoum kapewinteri* n. sp.; **D, N**, holotype; **D**, view from the left primary lateral spine; **N**, detail, ventral view; **E**, paratype, ventral view; **F-I, L**, *Saitoum labeosum* n. sp.; **F**, holotype, dorsal view; **G-I, L**, paratypes; **G**, ventral view showing the ditreme; **H**, broken specimen, right lateral view showing the thin apical spine and thick median bar; **I**, specimen with distally closed velum; **L**, basal view showing the left secondary lateral spine prolonged outside (anomaly?); **J, K, M**, *Saitoum macilentum* n. sp.; **J, M**, holotype, dorsal and basal views; **K**, paratype, left lateral view showing a strong arch Al. Abbreviations: **A**, apical spine; **I**, secondary lateral spine. Scale bars: 30  $\mu$ m.

MATERIAL EXAMINED. — 16 specimens of which six from sample Mue 9, two from Mue 6, three from Mue 22, one from sample SB 3, one from sample Hob 11, and three from sample Hob 32.

DIMENSIONS (IN  $\mu\text{M}$ ). — Length of cephalis 75-95 (av. 80), of feet 65-85 (av. 75), of apical horn 30-60 (av. 40), width of cephalis 80-95 (av. 85).

#### DESCRIPTION

Cephalis globular, thick-walled, with pores surrounded by thick protruding rims. Collar border between dorsal and primary lateral feet thick, protruding. Initial spicule robust with MB strongly swollen basally, but with A thin inside the cephalic cavity. Apical horn long, generally thin, three-bladed, with thick blades and very narrow grooves. Distal end of ventral spine surrounded by a wide ditrema with protruding rim placed above the thickened cephalic border. Feet usually as long as the diameter of cephalis or shorter, downward directed or slightly divergent and slightly curved. They are massive or rounded triangular in cross section proximally and medially, and sensibly three-bladed distally, with one external and two internal blades. When well preserved, cephalis continues distally in a very delicate velum. In very few specimens where the velum is well preserved it is closed distally.

#### REMARKS

By the shape of cephalis and length and curvature of feet *Saitoum labeosum* n. sp. may be compared with *S. dercourtii* Widz & De Wever, 1993 from which it differs by having pores with thick protruding rims, a different collar border, and massive feet.

#### *Saitoum macilentum* n. sp. (Fig. 15J, K, M)

HOLOTYPE. — Photo No. 60023, 60024; stub Mue 22/23; Musée de Géologie, Lausanne, No. 74386 (Fig. 15J, M).

ETYMOLOGY. — From the Latin *macilentus*: thin.

OCCURRENCE. — Early Tithonian, Hybonotum Zone.

MATERIAL EXAMINED. — Nine illustrated specimens, all from the type horizon (sample Mue 22).

DIMENSIONS (IN  $\mu\text{M}$ ). — Length of cephalis 40-60 (av. 50), of feet 40-65 (av. 55), of apical horn 34-42 (av. 36), width of cephalis 45-70 (av. 60).

#### DESCRIPTION

Cephalis globular to hemispherical, smooth-surfaced, with pores of variable size and arrangement. Apical horn long, three-bladed, blades thin, gently pointed distally. Arches AI and AV well marked. Ventral spine very short, three-bladed. Feet long, three-bladed, strongly diverging and curved, tapering distally. No velum or remains of a velum visible in the specimens available.

#### REMARKS

*Saitoum macilentum* n. sp. may be compared to the Middle Jurassic *Poulpus* sp. of Takemura (1986) in having rather large pores and diverging, curved feet. Among the specimens assigned to this species some are different in the degree of divergence of feet or the thickness of cephalic wall.

#### *Saitoum pagei* Pessagno, 1977 (Fig. 16A, B)

*Saitoum pagei* Pessagno, 1977a: 98, pl. 12, figs 11-14. — Köcher 1981: 89, pl. 16, figs 2, 3. — De Wever & Caby 1981: pl. 2, fig. H. — Baumgartner 1984: 783, pl. 8, fig. 12. — Baumgartner *et al.* 1995: 486, pl. 3020, figs 1-4. — Kiessling 1995: pl. 61, fig. 15, non fig. 16. — Yao 1997: pl. 8, fig. 353.

*Saitoum* aff. *pagei* – Gorican 1987: 186, pl. 2, fig. 2.

MATERIAL EXAMINED. — Five specimens from sample Mue 22.

OCCURRENCE. — Late Bajocian to early Tithonian according to Baumgartner *et al.* (1995). Worldwide.

#### REMARKS

The specimens from sample Mue 22 are complete, preserving the apical horn and a velum-like structure descending from the distal rim of the cephalis.

#### *Saitoum reticulatum* n. sp. (Fig. 16C, D)

*Saitoum pagei* – Matsuoka 1998: pl. 10, fig. 157.

*Saitoum* sp. – Mekik *et al.* 1999: 728, fig. 7K.



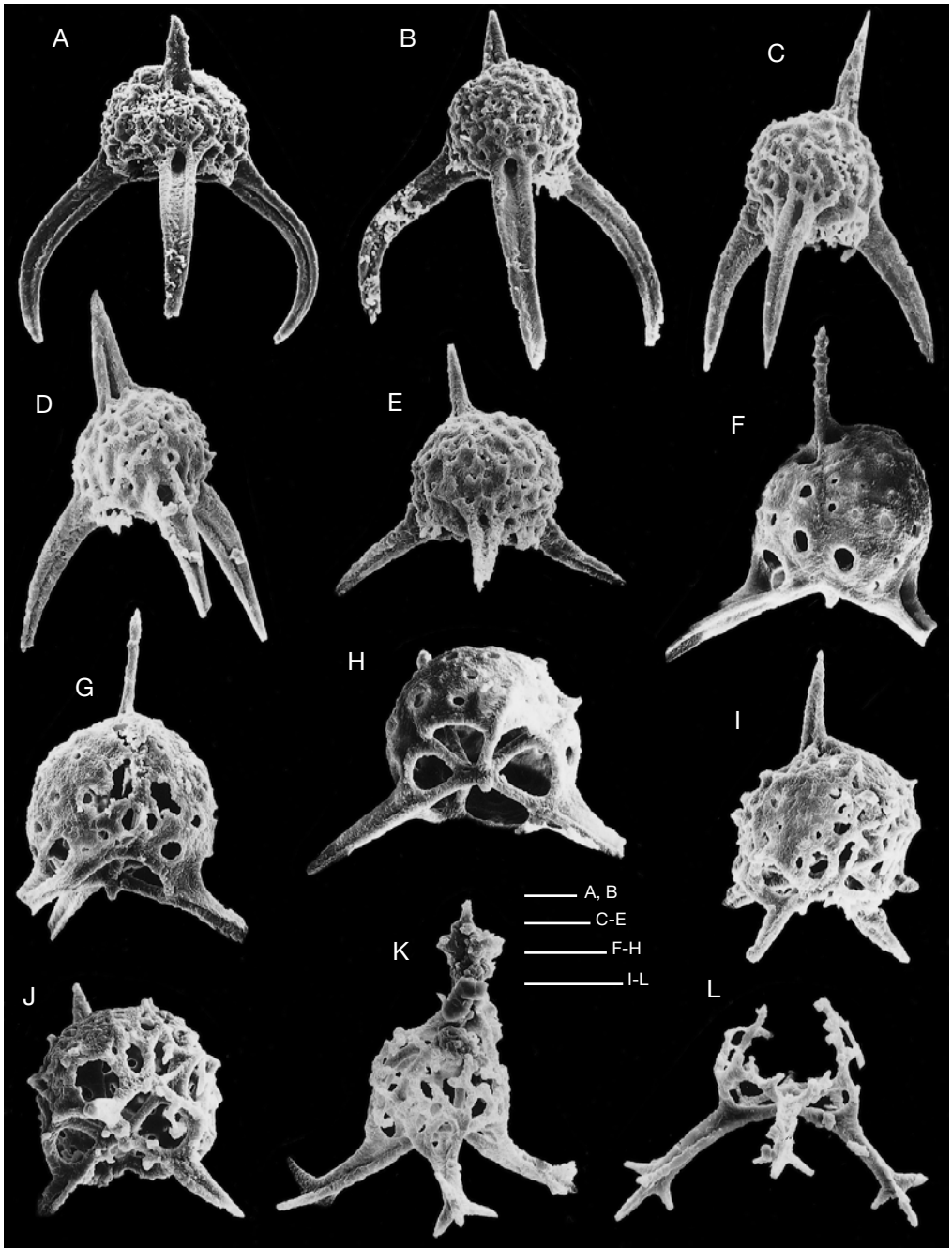


FIG. 16. — **A, B**, *Saitoum pagei* Pessagno, 1977; **A**, dorsal view showing slight constrictions along arches AI; **B**, right lateral view showing remnants of velum; **C, D**, *Saitoum reticulatum* n. sp.; **C**, holotype, left lateral view showing remnants of velum; **D**, paratype, right lateral view; **E**, *Saitoum* sp. aff. *S. reticulatum* n. sp., right lateral view; **F-H**, *Saitoum virgulispina* n. sp., holotype, right lateral, ventral, and basal views respectively; **I, J**, *Saitoum* sp. A, right lateral and basal views; **K, L**, *Saitulpus neojurassicus* n. gen., n. sp.; **K**, holotype, left lateral view; **L**, paratype, dorsal view. Abbreviations: **A**, apical spine; **I**, secondary lateral spine. Scale bars: 30  $\mu$ m.

HOLOTYPE. — Photo No. 13753; Musée de Géologie, Lausanne, No. 74387 (Fig. 16C).

ETYMOLOGY. — From the Latin *reticulatus*: reticulate.

OCCURRENCE. — Early Tithonian, Hybonotum Zone to basal Berriasian (Matsuoka 1998).

MATERIAL EXAMINED. — 11 specimens from the type horizon (sample Mue 22), one specimen from sample Mue 6, three specimens from sample Mue 9.

DIMENSIONS (IN  $\mu\text{M}$ ). — Length of cephalis 60-70 (av. 65), of feet 75-90 (av. 80), of apical horn 40-60 (av. 50), width of cephalis 70-80 (av. 75).

DESCRIPTION

Cephalis globular, short, with small pores surrounded by thin protruding rims. Most rims interconnected by ridges forming a reticulum on the surface of cephalis. Base of cephalis without thick border. Apical horn long, tapered, three-bladed, with blades thin, separated by deep grooves. Feet divergent, curved, gently tapered distally, and three-bladed, the odd blade internal. External blades separated by large, rounded grooves as prolongations of a wide cephalic pore. Remains of a very thin velum preserved in some specimens.

REMARKS

*Saitoum reticulatum* n. sp. resembles *S. pagei* in general shape of cephalis and superficial ornamentation, but differs essentially from it in having much shorter and less curved feet.

*Saitoum* sp. aff. *S. reticulatum* n. sp.  
(Fig. 16E)

MATERIAL EXAMINED. — One specimen from sample Mue 22.

OCCURRENCE. — Early Tithonian, Hybonotum Zone.

REMARKS

This specimen has the surface of the cephalis similar to that of *S. reticulatum* n. sp., but its feet are shorter, rather straight, and strongly diverging.

*Saitoum virgulispina* n. sp.  
(Fig. 16F-H)

HOLOTYPE. — Photo No. 60015-60017; stub Mue 22/23; Musée de Géologie, Lausanne, No. 74388 (Fig. 16F-H).

ETYMOLOGY. — From the Latin *virgula*: thin rod; and *spina*: spine.

MATERIAL EXAMINED. — One specimen from the type horizon (sample Mue 22).

DIMENSIONS (IN  $\mu\text{M}$ ). — Length of cephalis 65, of apical horn 40, width of cephalis 70.

DESCRIPTION

Cephalis globular, thin-walled, smooth-surfaced, with circular or subcircular pores of various size; some pores rather wide, others very small. All pores with slightly protruding rim. Apical horn long, slender, needle-like with circular cross section. Axobate present, short. Arches Al and AV rather well marked. Ditreme present on both sides of ventral and secondary lateral spines. Feet moderately long, straight, strongly divergent, three-bladed, and pointed.

REMARKS

Although we have only a single specimen of this species it is very different from the other species so far described to be considered a new species. Its cephalis with rather wide pores with protruding rims and straight divergent feet makes it close to *Poulpus oculatus* De Wever, 1982, but this species has a long three-bladed apical horn.

*Saitoum* sp. A  
(Fig. 16I, J)

MATERIAL EXAMINED. — One specimen from sample Mue 22.

REMARKS

This species has short, three-bladed, strongly pointed apical horn and feet. Cephalic wall with small spines and irregular surface. Feet are very divergent, slightly recurved distally.

Genus *Saitulpus* n. gen.

TYPE SPECIES. — *Saitulpus retrospina* n. gen., n. sp.

ETYMOLOGY. — The name is formed from part of *Saitoum* and part of *Poulpus*, because this new genus combines characters of the two genera.

DIAGNOSIS. — Test monocyrtid with a globular cephalis, a well developed apical horn and feet, all bearing usually one or more verticils of spines. Initial

cephalic skeleton with arches AV and AI forming longitudinal constrictions, and arches VL, LI, and ID forming the base of cephalis. Without well marked ditreme.

#### REMARKS

*Saitulpus* n. gen. is herein erected to include species with a long apical horn, usually bearing a verticil of spines, arches AI and AV, and feet with one or more verticils of spines. From *Poulpus* it differs in having long apical horn and feet with verticils of spines. From *Saitoum* it differs in having rather visible arches and verticils of spines on feet and apical horn; all species of these two genera have simple apical horn and feet. The general shape of *Saitulpus* n. gen. resembles generally that of the Triassic species of *Baratuna* Kozur & Mostler, 1981 described by Dumitrica (1991), but *Baratuna* has no arch AV.

#### *Saitulpus neojurassicus* n. sp. (Fig. 16K, L)

HOLOTYPE. — Photo No. 60056; stub Mue 22/23; Musée de Géologie, Lausanne, No. 74389 (Fig. 16K).

ETYMOLOGY. — From its occurrence in the Upper Jurassic.

MATERIAL EXAMINED. — Two specimens from the type horizon (sample Mue 22).

DIMENSIONS (IN  $\mu\text{M}$ ). — Length of cephalis 45, of feet 45-50, of apical horn 50, of spines on feet 8-14, width of cephalis 40-60.

#### DESCRIPTION

Cephalis highly globular, raised dorsally toward the apical horn. Apical horn long, three-bladed, with a distal verticil of three short spines, and an axial pointed spine. Arch AV probably present. Ventral spine very short, three-bladed, pyramidal. Pores polygonal, irregular in size and arrangement, separated by narrow intervening bars. Feet strongly divergent, three-bladed, slightly torsioned in clockwise direction and bearing a distal verticil of short spines directed obliquely. Beyond the verticil feet terminate in a pointed axial spine which is slightly three-bladed.

#### REMARKS

The morphology of this species is rather similar to that of some Middle Triassic species of the genus *Baratuna* (Dumitrica 1991).

#### *Saitulpus retrospina* n. sp. (Fig. 17A-D)

HOLOTYPE. — Photo No. 60092; stub Mue 22/23; Musée de Géologie, Lausanne, No. 74390 (Fig. 17A).

ETYMOLOGY. — From the Latin *retro*: back; and *spina*: spine.

MATERIAL EXAMINED. — Seven specimens from the type horizon (sample Mue 22).

DIMENSIONS (IN  $\mu\text{M}$ ). — Length of cephalis 36-41 (av. 38), of feet 30-55 (av. 40), of apical horn 32-46 (av. 36), of spines on feet 16-32 (av. 21), width of cephalis 46-51 (av. 48).

#### DESCRIPTION

Cephalis very small, globular, thin-walled, with pores of various size, arrangement, and shape, most of them rounded polygonal. Apical horn and feet three-bladed, usually slightly torsioned, with a verticil of three secondary spines. Spines long, recurved, with denticles or very small thorns on the external, convex side. Beyond the verticil distal ends of apical horn and feet pointed, shorter than the proximal portion between cephalis and verticil. Arches AI marked by a weak constriction. Ventral spine very short outside cephalic wall, inclined about  $45^\circ$  above the horizontal plane of shell. Arch AV not well marked.

#### REMARKS

The species is very well distinguished from the other species of the genus by the long, recurved spines on feet and apical horn.

#### *Saitulpus* sp. aff. *S. retrospina* n. sp. (Fig. 17E)

MATERIAL EXAMINED. — One specimen from sample Mue 22.

DIMENSIONS (IN  $\mu\text{M}$ ). — Length of cephalis 45, of feet 40, of apical horn 25, width of cephalis 60.

#### REMARKS

The species, from which we have only one specimen, differs from *S. retrospina* n. gen., n. sp. by the lack of recurved spines on feet and apical horn. One foot may have one or two spines beyond the verticil. Unfortunately, the specimen is coarsely recrystallized so that the details of the spines are not perfectly preserved.

#### *Saitulpus spinipes* n. sp. (Fig. 17F, G)

HOLOTYPE. — Photo No. 58454, 58455; stub Mue 22/21; Musée de Géologie, Lausanne, No. 74391 (Fig. 17F, G).

ETYMOLOGY. — From the Latin *spina*: spine; and *pes*: foot.

MATERIAL EXAMINED. — One specimen from the type horizon (sample Mue 22).

DIMENSIONS (IN  $\mu\text{M}$ ). — Length of cephalis 40, of feet 65, of apical horn 50, width of cephalis 60.

#### DESCRIPTION

Cephalis hemispheric with wide, rounded polygonal (triangular, quadrangular, pentagonal) pores. Arches Al well marked forming constrictions along cephalis. Apical horn about as long as cephalis, three-bladed, with a verticil of three spines toward the distal end. Distal end of horn beyond the verticil short, three-bladed, pointed. Ventral and secondary lateral spines not prolonged outside wall. Feet long, three-bladed; lateral blades with two pairs of spines, inner blade without spines.

#### REMARKS

Although the description of the species is only based on holotype, because of its rarity, the species is very well individualised. It differs from *S. neojurassicus* n. gen., n. sp. and *S. retrospina* n. gen., n. sp. especially by having feet with two pairs of spines.

Family TRIPEDURNULIDAE Dumitrica, 1991

TYPE GENUS. — *Tripedurnula* Dumitrica, 1991.

#### Genus *Pseudopoulpus* Takemura, 1986

TYPE SPECIES. — *Pseudopoulpus yamatoensis* Takemura, 1986; original designation.

#### REMARKS

As noted by Dumitrica (1991), by its morphology, the Jurassic genus *Pseudopoulpus* seems to be a junior synonym of the Middle Triassic genus *Baratuna*.

#### *Pseudopoulpus crassispinosus* n. sp. (Fig. 18A-D, I)

HOLOTYPE. — Photo No. 33758, 33760; stub Mue 22/8; Musée de Géologie, Lausanne, No. 74392 (Fig. 18A, B).

ETYMOLOGY. — From the Latin *crassus*: thick; and *spinosus*: spiny.

MATERIAL EXAMINED. — 10 specimens from the type horizon (sample Mue 22).

DIMENSIONS (IN  $\mu\text{M}$ ). — Total length 135-240 (av. 190), length of apical horn 35-90 (av. 60), of cephalis 75-120 (av. 95), of feet 55-90 (av. 75), of secondary horns 35-60 (av. 45); total width 120-200 (av. 155), width of cephalis 85-115 (av. 100).

#### DESCRIPTION

Cephalis globular with a distinctly visible dorsal lobe and with the ventral part inflate. Apical part of the cephalis with a stout apical horn and two or three stout secondary horns which are directed obliquely, shorter than the apical horn. Secondary horns generally aligned with primary lateral spines and, when three, also with the ventral spine. Feet short, straight or slightly curved outward, rapidly tapering. All feet and horns three-bladed, with additional long grooves on the blades. Ventral spine short, needle-shaped or pyramidal, well above the cephalic base. MB, D, V, and L with small spongy appendages, MB sometimes even completely wrapped up in a spongy tissue. Cephalic base slightly constricted, bordered by the collar ring formed of the arches DI, LI, and VI, exceptionally completely closed by a spongy tissue. Pores of cephalis pentagonally

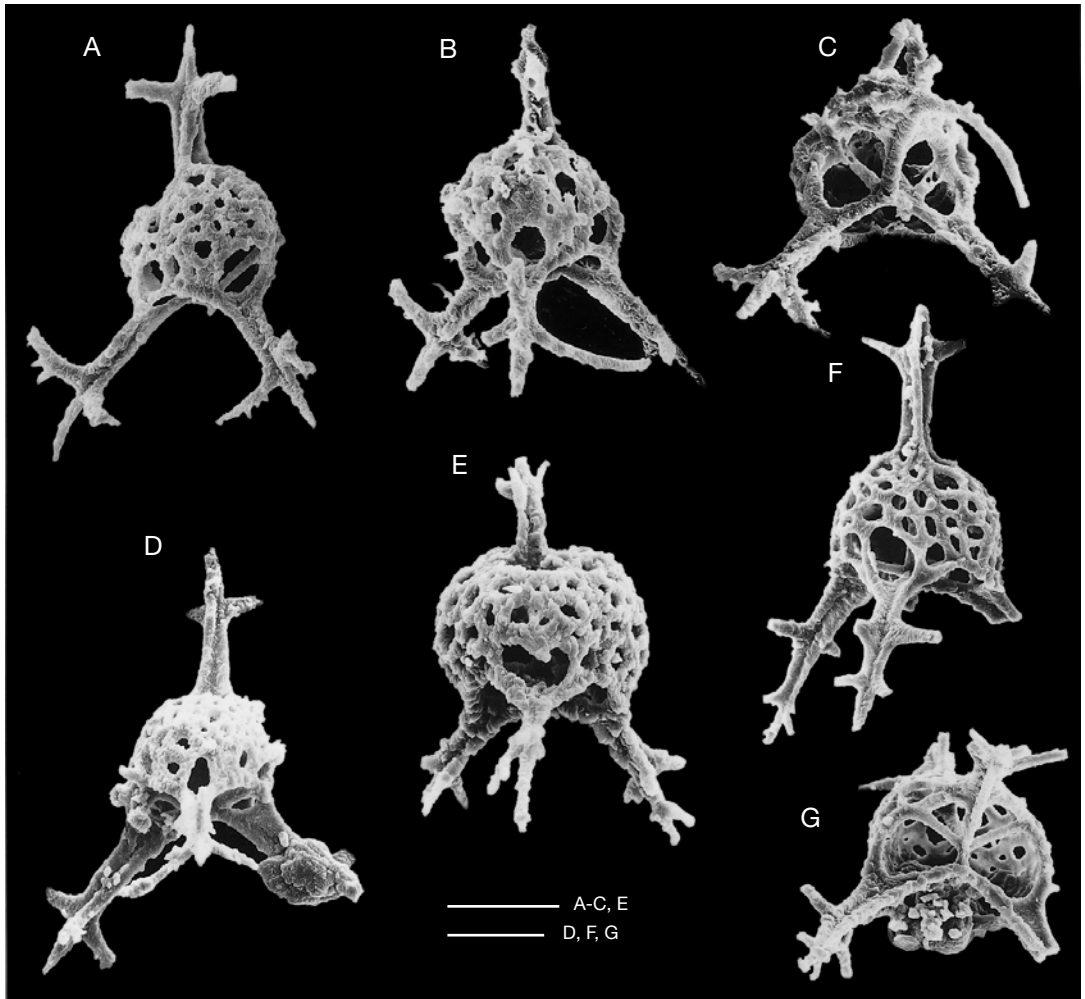


FIG. 17. — **A-D**, *Saitulpus retrospina* n. gen., n. sp.; **A**, holotype, with foot of the left primary lateral spine broken off, right lateral view; **B-D**, paratypes; **B, C**, left lateral and basal views; **D**, left lateral view; **E**, *Saitulpus* sp. aff. *S. retrospina* n. gen., n. sp., dorsal view; **F, G**, *Saitulpus spinipes* n. gen., n. sp., holotype, dorsal and basal views. Scale bars: 30  $\mu$ m.

or hexagonally framed, with nodes at vertices giving the surface a knobby aspect.

#### REMARKS

The main differences between *Pseudopoulpus crassispinosus* n. sp. and the species described by Takemura (1986) are the same as for *P. tenuibirsutus* n. sp. *P. crassispinosus* n. sp. differs from *P. tenuibirsutus* n. sp. mainly by having three completely three-bladed horns on the apical part and robust feet with additional grooves developed on blades.

#### *Pseudopoulpus spinosus* Kiessling, 1999 (Fig. 18F)

*Pseudopoulpus spinosus* Kiessling, 1999: 64, pl. 14, figs 15, 16, 18.

**MATERIAL EXAMINED.** — One specimen from sample Mue 22.

**OCCURRENCE.** — The species was described from the early Tithonian, Zone 4, subzone 4 beta of Pessagno *et al.* (1987, 1993) and Pessagno & Hull (1996) of Antarctic Peninsula (Kiessling 1999). In the early Tithonian at Mühlheim (sample Mue 22) the species is extremely rare but perfectly similar to the Antarctic type specimens.

*Pseudopoulpus tenuihirsutus* n. sp.  
(Fig. 18E, G, H, J)

HOLOTYPE. — Photo No. 31417; stub Mue 22/4; Musée de Géologie, Lausanne, No. 74424 (Fig. 18G).

ETYMOLOGY. — From the Latin *tenuis*: thin; and *hirsutus*: bristly.

MATERIAL EXAMINED. — Six specimens from the type horizon (sample Mue 22).

DIMENSIONS (IN  $\mu\text{M}$ ). — Total length 280-320 (av. 295), length of apical horn 25-105 (av. 60), of feet 95-165 (av. 135), of secondary horns 35-85 (av. 55), of cephalis 110-135 (av. 125); total width 235-285 (av. 255), width of cephalis 125-150 (av. 140).

DESCRIPTION

Well rounded globular cephalis with three straight diverging feet and three or more secondary horns on the apical part. Apical horn and secondary horns long and thin, three-bladed at the base, rounded in cross-section, and curved in the median and distal parts. Ventral spine short, thin, and close to the base of cephalis. Cephalic base constricted, strengthened by an ovate basal ring formed of the arches VL, Ll, and Dl. Arches Al strongly pronounced on the inner side, connecting A and l below the apical part of the cephalis. Externally they are marked by a slight constriction and by a row of pores at the boundary with the slightly protruding dorsal lobe. Inside cephalic cavity D, V, and especially L bear small branched, spongy appendages which sometimes are so robust that they curve the bars. Feet slightly constricted at their bases, with maximum width in the median part. Grooves of feet narrow and deep; at the most proximal part additional shallow grooves may develop. Cephalic wall with irregularly arranged pores. Pores hexagonally or pentagonally framed, with small nodes at vertices which very rarely give rise to small thorns. Smaller pores especially in the centre of the dorsal lobe.

REMARKS

*Pseudopoulpus tenuihirsutus* n. sp. differs from the two species described by Takemura (1986) by having secondary horns on the apical part of the cephalis and a less inflated ventral part. From

*P. crassispinosus* n. sp. it differs by the morphology of feet, apical horn and secondary spines. Whereas *P. tenuihirsutus* n. sp. gives a rather fragile impression, *P. crassispinosus* n. sp. is much more compact. Moreover, the dorsal lobe is more pronounced in the latter species.

Genus *Takoum* Takemura, 1986

TYPE SPECIES. — *Takoum hexagonum* Takemura, 1986; original designation.

*Takoum takemurai* n. sp.  
(Fig. 19A-F)

HOLOTYPE. — Photo No. 58132-58134; stub Mue 22/20; Musée de Géologie, Lausanne, No. 74393 (Fig. 19A-C).

ETYMOLOGY. — The species is named for Dr. Atsushi Takemura, to honour his contribution to the knowledge of the initial structures of many Jurassic nassellarians.

MATERIAL EXAMINED. — 15 specimens from the type horizon (sample Mue 22).

DIMENSIONS (IN  $\mu\text{M}$ ). — Length of cephalis 42-51 (av. 48), of apical horn 26-32 (av. 29), of dorsal spine 33-60, of primary lateral spines 35-95 (av. 60), of secondary lateral spines 35-47 (av. 39), width of cephalis 52-65 (av. 59).

DESCRIPTION

Cephalis small, hemispherical, low, with rounded pores of various arrangement and size, decreasing generally in size apically. Surface of cephalis rough due to some small thorns. Apical horn, dorsal spine, primary and secondary lateral spines long, straight, three-bladed proximally, circular in cross section medially and distally. Sometimes they are covered by very tiny thorns. Dorsal, secondary and primary lateral spines extended laterally. Ventral spine very short, hardly extended outside shell wall, directed obliquely upward. Arches Al, Dl, Ll and LV well marked, whereas arch AV seems to be missing.

REMARKS

*Takoum takemurai* n. sp. has the initial cephalic structure of *T. hexagonum* type but differs from

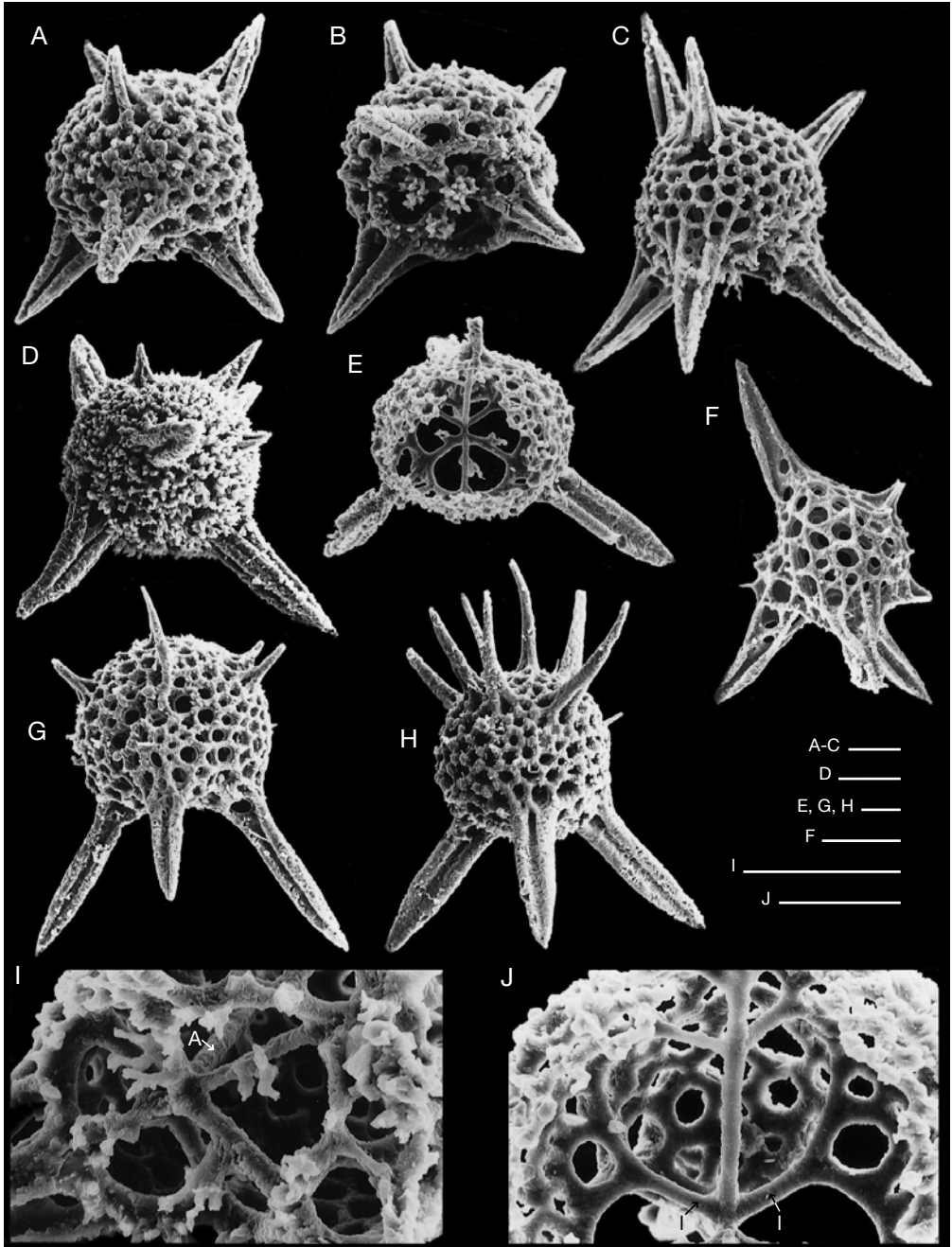


FIG. 18. — **A-D, I**, *Pseudopoulpus crassispinosus* n. sp.; **A, B**, holotype, left lateral and basal views showing a thick spongy tissue around median bar, ventral spine, and primary lateral spines; **C, D, I**, paratypes; **C**, right lateral view; **I**, same, basal view showing details of initial spicule and arches; **D**, basal view showing an exaggerate overgrowth of spongy tissue covering completely the collar aperture; **E, G, H, J**, *Pseudopoulpus tenuihirsutus* n. sp.; **E, J**, paratype, partly broken specimen, ventro-apical view, and detail of the dorsal lobe with arches **A**; **G**, holotype, dorsal view showing the slightly pronounced dorsal lobe; **H**, paratype with a large number of additional horns, left lateral view; **F**, *Pseudopoulpus spinosus* Kiessling, 1999, right lateral view showing a pronounced dorsal lobe. Abbreviations: **A**, apical spine; **I**, secondary lateral spine. Scale bars: 30  $\mu$ m.

this species in having a very short cephalis. The cephalis of *T. hexagonum* is very high, wider apically than basally, and the ventral spine is as long as the other spines.

Genus *Tripedocorbis* Dumitrica, 1991

TYPE SPECIES. — *Tripedocorbis ramulispinus* Dumitrica, 1991; original designation.

RANGE. — Middle Anisian-lower Tithonian, although no species was described within the long interval between these two extremes.

REMARKS

The genus *Tripedocorbis* was known so far only in the middle Anisian. The new lower Tithonian species (*T. tardus* n. sp.) described below, with all characters of the genus, suggests that its range is much longer than initially known.

*Tripedocorbis tardus* n. sp.  
(Fig. 19G-J)

HOLOTYPE. — Photo No. 60084, 60086; stub Mue 22/23; Musée de Géologie, Lausanne, No. 74394 (Fig. 19G, H).

ETYMOLOGY. — From the Latin *tardus*: late.

MATERIAL EXAMINED. — Two specimens from the type horizon (sample Mue 22).

DIMENSIONS (IN  $\mu\text{M}$ ). — Height of cephalis without feet 68-85, maximum diametre 57-58, length of feet 50-58.

DESCRIPTION

Cephalis inverted conical, open apically, with pores variable in size, shape and arrangement, most of them triangular to tetragonal by intersection of bars of various thickness and directions. Initial spicule with spines A, V, D, L, l, and a small Ax, united by the arches Al, Dl, Ll, and LV. D and L prolonged into thin massive, straight strongly divergent feet armed with small spinules radiating obliquely. Apical spine prolonged along the dorsal part of the cephalic wall up to its apex and shortly beyond it. Ventral spine extended outside cephalic wall. Secondary lateral spines short, not prolonged beyond cephalis.

REMARKS

*Tripedocorbis tardus* n. sp. may be compared to the middle Anisian species *T.(?) gratiosus* Dumitrica, 1991 by its general shape and by having an apically open cephalis, but differs from it by a shorter ventral spine, longer feet armed with spinules, and by the lack of transverse ribs.

Family NABOLLELLIDAE Dumitrica  
in De Wever *et al.*, 2001

TYPE GENUS. — *Nabolella* Petrushevskaya, 1981 (replacement name for *Squinabolella* Kozur & Mostler, 1979, homonym of *Squinabolella* Pessagno, 1969).

REMARKS

The family-group name Squinabollellidae Kozur & Mostler, 1979 has been replaced, as its type genus is a junior homonym and thus invalid (ICZN 1999: Article 39).

Genus *Acuticassis* n. gen.

TYPE SPECIES. — *Acuticassis gotica* n. gen., n. sp.

ETYMOLOGY. — From the Latin *acutus*: pointed, acute; and *cassis*: helmet. Feminine gender.

DIAGNOSIS. — Test monocyrtid with a large rounded conical cephalis bearing an apical horn and three feet. Initial spicule formed of MB and spines A, D, V, two L and two l. Spines free inside cephalic cavity and connected by the arches AV, Al, lD, Ll and LV in the cephalic wall. Spine A extended into an apical horn, spines D and the two L extended into basal feet. Cephalic wall reticulate with arches of various diametre and length.

REMARKS

Although the family is only known in the Middle and Upper Triassic (Kozur & Mostler 1979, 1981), the system of arches of this new genus resembles that of *Nabolella* Petrushevskaya, 1981 and *Fuelopicyrtis* Kozur & Mostler, 1981. From the former genus, *Acuticassis* n. gen. differs by the lack of a thoracic skirt, from the latter by having only three feet and no secondary spines.



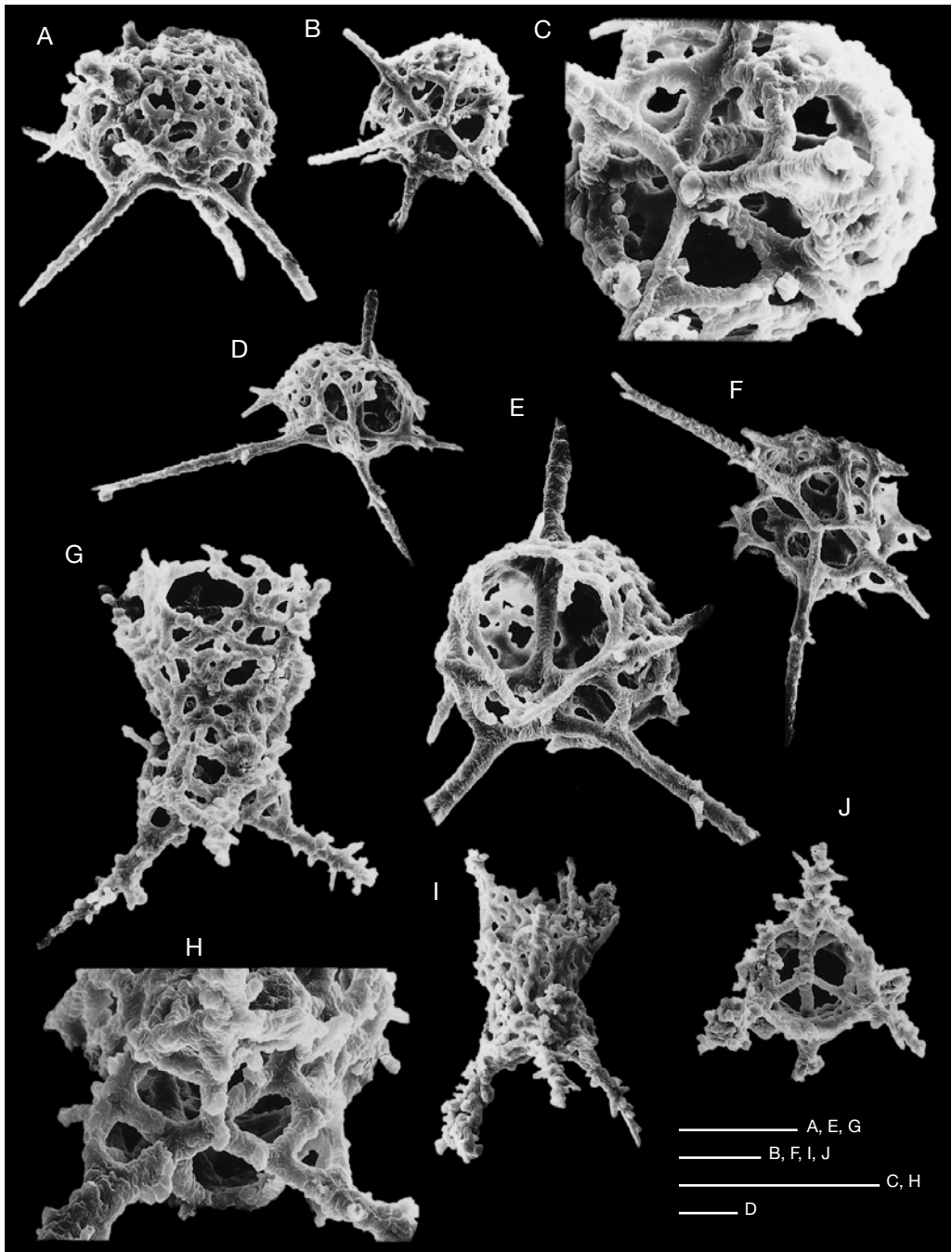


FIG. 19. — **A-F**, *Takoum takemurai* n. sp.; **A-C**, holotype, right lateral and basal views, and details of the initial spicule and arches; **D-F**, paratype, partly broken but with some spines completely preserved, left lateral, dorsal and basal views; **G-J**, *Tripedocorbis tardus* n. sp.; **G, H**, holotype, left lateral and basal views respectively with details of the initial spicule and arches; **I, J**, paratype, dorsal and basal views. Scale bars: 30  $\mu$ m.

*Acuticassis gotica* n. sp.  
(Fig. 20)

HOLOTYPE. — Photo No. 58426-58428; stub Mue 22/21; Musée de Géologie, Lausanne, No. 74395 (Fig. 20A, B, H).

ETYMOLOGY. — From the Latin *goticus*: Gothic, for the Gothic outline of the test.

MATERIAL EXAMINED. — Nine specimens from the type horizon (sample Mue 22).

DIMENSIONS (IN  $\mu\text{M}$ ). — Total length 230-300 (av. 265), length of cephalis 135-175 (av. 160), of apical horn 60-80 (av. 70), of feet 35-110 (av. 60), width of cephalis 140-165 (av. 150).

DESCRIPTION

Cephalis rounded conical with the wall supported by the primary arches forming well marked ridges interconnected by secondary ridges of various directions and lengths. Pores polygonal, commonly triangular and quadrangular, resulting from connecting bars between ridges. Initial spicule thin, with a long median bar. Apical horn long, straight, with three wide blades at its base directed and connected to the arches AV and AL. Blades perforated by polygonal pores similar to those of the cephalic wall. Feet straight, three-bladed, aligned to D and L, and diverging at an angle of about  $45^\circ$  to the axis of shell. V and I marked outside by very short vertices. Base of cephalis with a broad, slightly expanded rim connected to the blades of the feet. Inner part of rim slightly constricted, with remains of a probably thin and short postcephalic velum.

REMARKS

See under the genus.

Superfamily FOREMANELLINACEA  
Dumitrica, 1982

Family CUNICULIFORMIIDAE De Wever, 1982

TYPE GENUS. — *Cuniculiformis* De Wever, 1982.

RANGE. — Middle Triassic (lower Ladinian) to Upper Cretaceous (Cenomanian).

EMENDED DIAGNOSIS. — Dicyrtid nassellarians whose initial spicule has no dorsal spine and whose apical and

ventral spines are usually extended outside test wall into long horns. Cephalis small. Thorax much larger than cephalis, bell-shaped, conical or cylindrical, simple or with one or more external circumferential ridges, with or without thoracic skirt (Dumitrica *in De Wever et al.* 2001).

REMARKS

Originally the family was described as comprising monocyrtid nassellarians with cephalic wall prolonged into a velum. This velum is, however, a true thorax similar to the thorax of the family Neosciadiocapsidae Pessagno, 1969. The family should therefore be considered as comprising dicyrtid rather than monocyrtid nassellarians. Until present the family was reduced to the genus *Cuniculiformis* De Wever, 1982. In this paper we also include the genus *Cassideus* Pessagno, 1969 in this family for the reasons presented below.

Genus *Cassideus* Pessagno, 1969

TYPE SPECIES. — *Cassideus riedeli* Pessagno, 1969; original designation.

EMENDED DIAGNOSIS. — Dicyrtid, conical, helmet-shaped Cuniculiformiidae with two long, three-bladed cephalic horns representing prolongations of apical and ventral spines of the initial spicule. Initial spicule without dorsal spine. Cephalis small, perforate. Thorax conical proximally, flaring distally to form broad thoracic skirt. Boundary between conical thorax and flaring skirt marked at the inner side by an imperforate circumferential ridge. Thoracic wall coarsely perforate, pores alternate, arranged in circumferential rows. Thorax with or without one or more external circumferential ridges. Without thoracic velum.

RANGE. — Tithonian or older to Cenomanian.

REMARKS

The genus *Cassideus* was erected for two lower Cenomanian species characterised by a dicyrtid, helmet-shaped test with two long primary horns (apical and ventral) and a conical, distally flaring thorax forming broad thoracic skirt. It was originally included within the family Neosciadiocapsidae Pessagno, 1969 but, according to the original remarks, it differed from all other Neosciadiocapsidae genera by possessing two primary horns and by lacking a cephalopyle

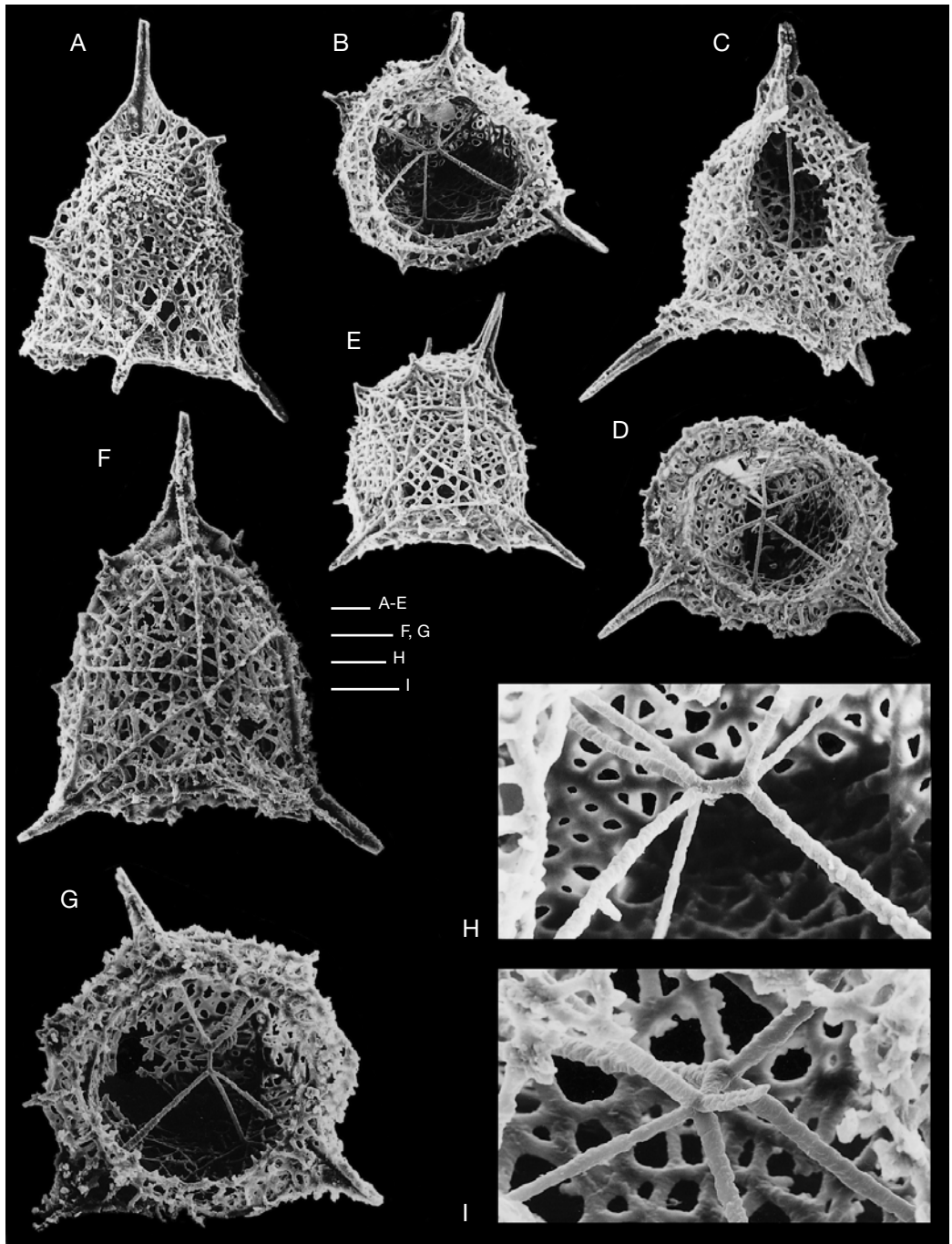


FIG. 20. — *Acuticassis gotica* n. gen., n. sp.; **A, B, H**, holotype, right lateral and basal views showing details of initial spicule respectively; **C-G, I**, paratypes; **C, D, I**, partly broken specimen, dorsal and basal views showing details of the initial spicule in dorsal view respectively; **E**, left lateral view; **F, G**, dorsal and basal views of same specimen. Scale bars: A-G, 30 µm; H, I, 10 µm.

and a thoracic velum. The absence of the velum was supposed to be due to preservation.

Based on a basal view of a paratype of the type species (Pessagno 1969: pl. 27, fig. 1), the genus was considered as possessing the dorsal spine. The presence of this spine in *Cassideus* created initially problems in the assignation of our three new species to this genus because, although their morphology was of *Cassideus* type, none of them has the D spine. In this situation we were tempted to assign them to the genus *Cuniculiformis* De Wever, 1982, but this genus has no thoracic skirt. The best solution would have been to erect a new genus for our species, a genus that would have combined the morphology of the genus *Cassideus* with the initial cephalic structure of the genus *Cuniculiformis*, or to make our own investigation of cephalic structure on the two species of the genus *Cassideus* (*C. riedeli* and *C. yoloensis*). Our attempt to find in the lower Cenomanian type sample (NSF 350 of Pessagno 1969) the two species failed, but we succeeded in finding two specimens of *Cassideus yoloensis* in the upper Albian sample NSF 884 of Pessagno (1977b). Their investigation has shown that none of these specimens has the D spine. How then could be interpreted the presence of this spine in *C. riedeli*, the type species of the genus? Several answers were possible: 1) this species certainly has the D spine; if so, its morphology did not correlate with what we knew from the other species assigned herein to this genus and from the other species of the genus *Cuniculiformis*, that is especially the presence of the two long cephalic horns; 2) normally *C. riedeli* has no D spine, its presence in the specimen illustrated is an anomaly; 3) *Cassideus riedeli* and *C. yoloensis* are not congeneric; this possibility would have been strange because all the other characters answer perfectly the definition of the genus; and 4) the paratype that shows the D spine and that is illustrated as *C. riedeli* does not belong to this species and genus.

It is this last possibility that we consider the solution of the problem. The specimen illustrated by Pessagno (1969: pl. 27, fig. 1) in a basal view and which shows a dorsal spine does not represent *Cassideus riedeli* but *Petasiforma glaskockensis* Pessagno, 1969. This is the only neosciadiocapsid

species occurring in the type sample and possessing several circumferential ridges similar to those of *Cassideus riedeli*. In our attempt to solve this problem we found a well preserved specimen of *P. glaskockensis* in the type sample (NSF 350) and studied it thoroughly. In basal view the cephalic structure is perfectly the one illustrated by Pessagno in what he considered *C. riedeli*: a well developed dorsal spine and a rather long axobate. There is another argument in favour of our idea. The specimen illustrated by Pessagno shows the apical part of the cephalis broken off. *C. riedeli*, with its robust apical and ventral horns and ribs on cephalis could not break like that specimen. Only *P. glaskockensis*, with its thin, fragile cephalic wall, could show such a break.

Thus, the genus *Cassideus* has no dorsal spine and must be transferred from the Neosciadiocapsidae to the family Cuniculiformiidae. Its definition is herein emended accordingly. It derived probably from the genus *Cuniculiformis* by acquiring a thoracic skirt and an internal circumferential ridge separating the two segments.

### *Cassideus biannulatus* n. sp.

(Fig. 21A-D, L)

HOLOTYPE. — Photo No. 45646, 45649; stub Mue 22/16; Musée de Géologie, Lausanne, No. 74396 (Fig. 21A, B).

ETYMOLOGY. — From the Latin prefix *bi*: two; and *annulatus*: having rings.

MATERIAL EXAMINED. — 12 illustrated specimens and tens of not illustrated specimens from the type horizon (sample Mue 22).

DIMENSIONS (IN  $\mu\text{M}$ ). — Total length 155-180 (av. 170), total width 160-225 (av. 195), length of cephalis 25-55 (av. 40), of apical horn 25-45 (av. 35), of ventral horn 30-85 (av. 55), diameter of collar ridge 50-70 (av. 60), of proximal thoracic circumferential ridge 80-100 (av. 90), of thorax at the boundary with thoracic skirt 85-130 (av. 110), distance between collar ridge and proximal thoracic ridge 15-25 (av. 20), and between the latter and the boundary with thoracic skirt 45-70 (av. 55).

### DESCRIPTION

Conical to hat-shaped test. Cephalis small, hemispherical at the top, increasing rapidly in

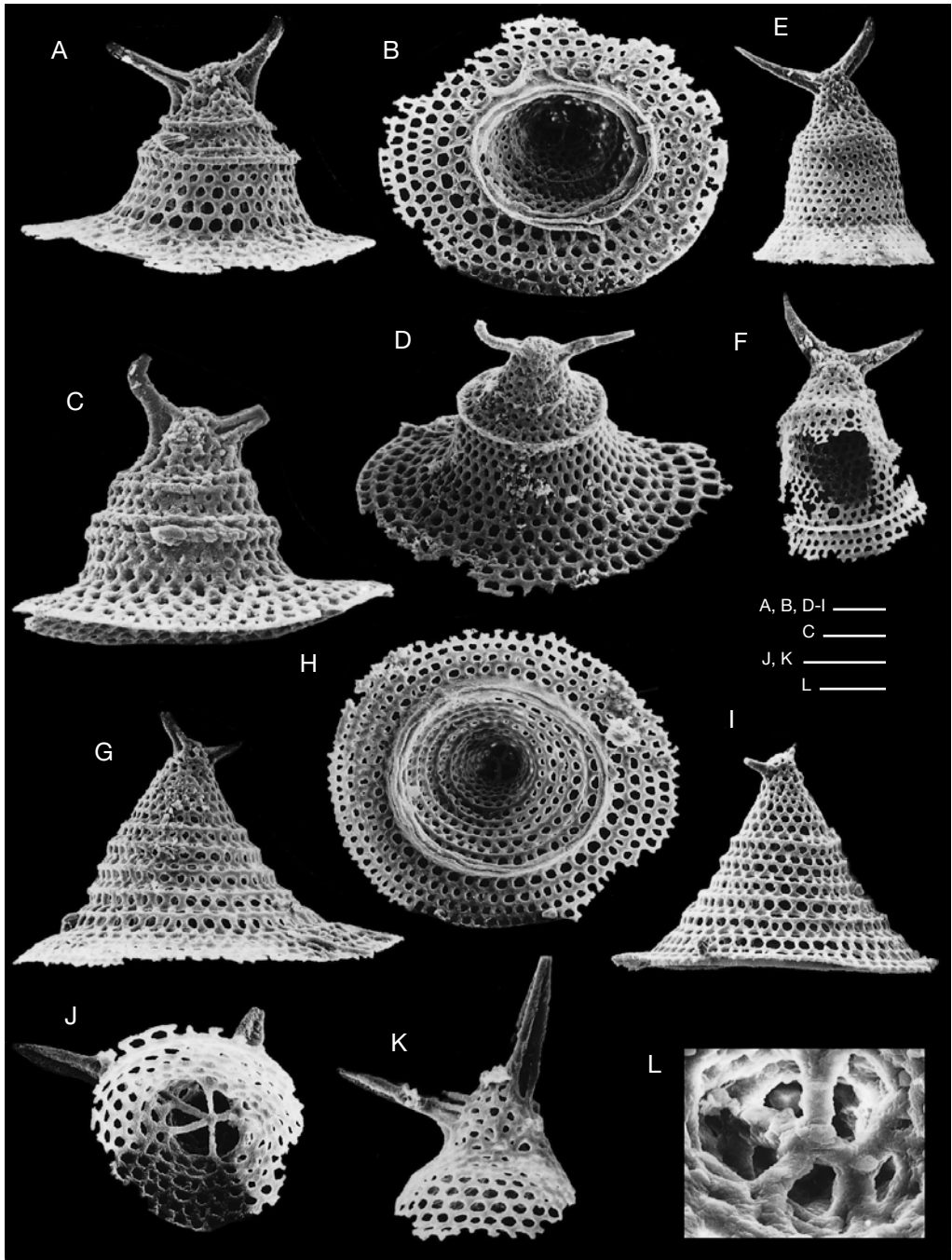


FIG. 21. — **A-D, L**, *Cassideus biannulatus* n. sp.; **A, B**, holotype, left lateral and basal views; **C, D, L**, paratypes; **C**, right lateral view; **D**, latero-apical view; **L**, basal view of initial spicule showing the absence of dorsal spine; **E, F**, *Cassideus deweveri* n. sp.; **E**, holotype, left lateral view; **F**, paratype, right lateral view; **G-I**, *Cassideus scalariconus* n. sp.; **G, H**, holotype, right lateral and basal views; **I**, paratype, left lateral view; **J, K**, *Cuniculiformis* sp., fragment, basal and left lateral views. Scale bars: A-K, 30 µm; L, 10 µm.

diametre towards the boundary with the thorax. Horns three-bladed proximally, non-bladed distally. Apical horn often distinctly curved in ventral direction in the non-bladed portion. Ventral horn straight or slightly curved upwards, variable in length but generally longer than apical horn. Boundary between cephalis and thorax not marked externally. It is above the former of the two circumferential ridges. This ridge may be rather distinct or weakly marked, partly reduced to a circumferential row of knobs. Main part of thorax high conical, commonly with a well pronounced ridge at the proximal part, separated from the former ridge by a concave belt with three to four transverse rows of alternate pores. Rarely, this ridge reduced to a circumferential shoulder. Distal part of thorax strongly flaring, forming a thoracic skirt which lies in the horizontal plane or may be undulate. Internally the boundary between high conical part and skirt marked by a thick circular rim which can be interpreted as a lumbar septal partition. Usually thorax circular in transversal section throughout, but in some specimens it may be slightly compressed laterally. Cephalic wall with small, irregularly arranged pores on the apical part and more or less regularly arranged in circumferential rows on the distal part. Thoracic pores rounded to longitudinally ovate, arranged in alternate transversal rows. On the thoracic skirt circular bars separating the transversal rows of pores often thicker than the bars separating the pores in each row. Velum absent.

#### REMARKS

*Cassideus biannulatus* n. sp. resembles very much *C. riedeli* and *C. yoloensis*. From both it differs especially by having two circumferential ridges on the thorax.

#### *Cassideus deweveri* n. sp. (Figs 21E, F; 22)

HOLOTYPE. — Photo No. 58119; stub Mue 22/20; Musée de Géologie, Lausanne, No. 74397 (Fig. 21E).

PARATYPES. — MNHN, bât. de Géologie, No. Gg 2001/2100-2101.

ETYMOLOGY. — The species is named for Prof. Patrick De Wever (MNHN) to honour his valuable contribution to the knowledge of Mesozoic and Paleozoic radiolarians.

MATERIAL EXAMINED. — Four specimens from the type horizon (sample Mue 22).

DIMENSIONS (IN  $\mu\text{M}$ ). — Height of test without horns 118-125, of proximal part 47-50, of middle and distal part of thorax 55-65, of skirt 20-30, diametre of thorax at the boundary between proximal and middle part 65-75, at the boundary with skirt 90-92, maximum diametre of skirt 118-130, length of apical and ventral horns 60-65.

#### DESCRIPTION

Test high, conical, with apical and ventral horns robust. Apical horn curved, obliquely upward directed, ventral horn straight or very weakly curved, inclined about  $30^\circ$  above the horizontal plane. Both bladed proximally and massive medially and distally. Cephalis with small pores, externally undistinguished from the proximal part of thorax with which it forms a low cone. Middle and distal part of thorax high conical to subcylindrical, straight or weakly constricted medially, well separated from the proximal part and thoracic skirt by the change in outline, and having nine to 10 transverse rows of alternate pores. Thoracic skirt expanded at an angle of about  $50^\circ$  below the horizontal plane and bearing four to six transverse rows of alternate pores.

#### REMARKS

*Cassideus deweveri* n. sp. resembles *C. biannulatus* n. sp. by having a rather similar shape and two robust horns but differs from it by being slightly higher, by the lack of two circumferential thoracic ridges, and by the less expanded thoracic skirt.

#### *Cassideus scalariconus* n. sp. (Fig. 21G-I)

HOLOTYPE. — Photo No. 57120, 57121; stub Mue 22/19; Musée de Géologie, Lausanne, No. 74398 (Fig. 21G, H).

ETYMOLOGY. — From the Latin *scalae*: scale; and *conus*: cone.

MATERIAL EXAMINED. — 12 illustrated specimens from the type horizon (sample Mue 22) and others not illustrated.

**DIMENSIONS (IN  $\mu\text{M}$ ).** — Total length 150, length of apical horn 25, length of ventral horn 25-30, total width 195-215 (av. 205), width of cephalis 25-35 (av. 30), of the thorax above the thoracic skirt 130-135 (av. 132).

#### DESCRIPTION

Conical to hat-shaped test. Cephalis small, perforate, undistinguished externally from thorax. Apical horn directed obliquely upward, curved in ventral direction. Ventral horn straight, directed obliquely upward. Both horns three-bladed proximally, rapidly tapering to a circular cross-section. Apical horn slightly longer than ventral horn. Thorax wide-conical, its proximal part with four to six pore rows, without circumferential ridges. Main part of thorax scalariform, usually with five circumferential ridges separated by concave areas with two rows of alternate pores. Circumferential depressional bars separating the two transverse rows of pores in each concave area are circumferential ridges on the interior surface, resulting in a zigzag outline. Pores wide, rounded hexagonal, alternate, separated by thin intervening bars. Thoracic skirt horizontal or slightly subhorizontal with four to five transverse rows of pores. Pores alternate or partly in square pattern, decreasing in size distally. Internally the boundary between the conical part of thorax and the skirt marked by a thick composite circular rim which can be interpreted as a lumbar septal partition.

#### REMARKS

This new species differs from *C. biannulatus* n. sp. by having a conical thorax, shorter horns, and by the high number and distribution of circumferential ridges. Its thorax is morphologically closer to *C. riedeli* in having a great number of transverse ridges but differs in that the ridges are very uniformly distributed.

#### Genus *Cuniculiformis* De Wever, 1982

**TYPE SPECIES.** — *Cuniculiformis plinius* De Wever, 1982; original designation.

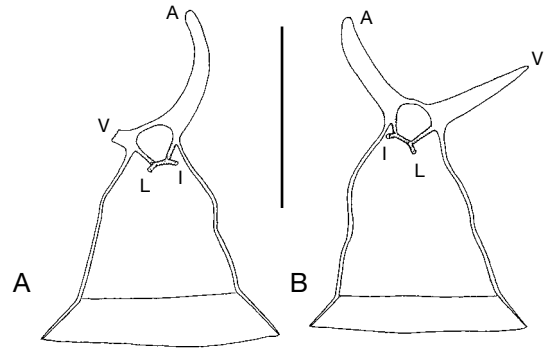


FIG. 22. — *Cassideus deweveri* n. sp., paratypes MNHN, bât. de Géologie, No. Gg 2001/2100 and MNHN Gg 2001/2101, in left lateral and right lateral views respectively, shape of shell and place of the initial spicule. Abbreviations: **A**, apical horn; **L**, primary lateral spine; **I**, secondary lateral spine; **V**, ventral spine. Scale bar: 0.1 mm.

#### *Cuniculiformis* sp.

(Fig. 21J, K)

**MATERIAL EXAMINED.** — One specimen from sample Mue 22.

#### REMARKS

This species, of which we have only a fragment, resembles somehow *Cuniculiformis aristotelis* De Wever, 1982 in having straight, robust apical and ventral corns and a similar outline but differs from it in having wider pores and a completely reduced median bar.

#### Family FOREMANELLINIDAE Dumitrica, 1982

**TYPE GENUS.** — *Foremanellina* Dumitrica, 1982.

#### Genus *Sanniopileus* n. gen.

**TYPE SPECIES.** — *Sanniopileus stultus* n. gen., n. sp.

**ETYMOLOGY.** — From the Latin *sannio*: fool; and *pileus*: cap, pointing out the resemblance to a fool's cap. Masculine gender.

**DIAGNOSIS.** — Test dicyrtid with cephalis having all spines of the initial spicule (A, V, Lr, Ll, lr, ll) extended externally into long three-bladed spines. D absent. The two L steeply inclined, attached to the thoracic wall. Thorax conical, widely open distally, with surface covered by transverse ridges.

## REMARKS

*Sanniopileus* n. gen. differs from *Foremanellina* Dumitrica, 1982 in that the two L spines are steeper inclined downward forming longitudinal ribs along the thorax. *Recoaroella* Dumitrica, 1982, *Riedelius* De Wever, 1982, and *Hilarisirex* Takemura & Nakaseko, 1982 differ from *Sanniopileus* n. gen. by having at least a part of all four lateral spines lying in the thoracic wall. *Sanniopileus* n. gen. is the youngest member of the family Foremanellinidae, but by its morphology it cannot be derived from the Middle Jurassic genera *Hilarisirex* or *Diceratigalea* Takemura & Nakaseko, 1982, which are the youngest representatives of the family known so far. The morphology of its thorax, with transverse ridges and triangular or quadrangular pores, is closer to the Lower Jurassic genus *Riedelius* De Wever, 1982.

*Sanniopileus stultisissimus* n. sp.  
(Fig. 23E-I)

HOLOTYPE. — Photo No. 44785, 44788; stub Mue 22/14; Musée de Géologie, Lausanne, No. 74399 (Fig. 23E, F).

ETYMOLOGY. — From the Latin *stultisissimus*: most mad.

MATERIAL EXAMINED. — Three illustrated specimens from the type horizon (sample Mue 22).

DIMENSIONS (IN  $\mu\text{M}$ ). — Total length with spines 95-115 (av. 105), length of cephalothorax 80-140 (av. 105), of cephalis 35, of thorax 30-60 (av. 45), of apical horn 18-26, of ventral and secondary lateral spines 25-45 (av. 35), of primary lateral spines 35-65 (av. 50), of secondary lateral spines 50; total width with spines 80-140 (av. 105), width of cephalis 50, of thorax 60-75 (av. 65).

## DESCRIPTION

Test short, conical, spiny. Apical, ventral and secondary lateral spines of the initial spicule extended outside test wall into horns directed obliquely upward and laterally. Horns bladed, pointed. The two primary lateral spines directed obliquely downward, bladed and pointed but connected to the thoracic wall on most part of their length. A varying number of accessory

spines (four to eight), similar in morphology to the other spines, arise from the thorax at different levels and are directed laterally downward. Cephalis and proximal part of thorax with polygonal (triangular or quadrangular) pores separated by bars. Most part of thorax with rather irregular transverse ridges. One or two rows of triangular or quadrangular pores between ridges. Distal part of thorax wide open.

## REMARKS

This species differs from *Sanniopileus stultus* n. gen., n. sp. by having a number of secondary spines arising from about two or more levels of the thorax with angles equal to the primary lateral spines. Secondary spines arising from a proximal level resemble the primary lateral spines in length and angles, those arising from a distal level are shorter.

*Sanniopileus stultus* n. sp.  
(Fig. 23A-D, J)

HOLOTYPE. — Photo No. 42183, 42184; stub Mue 22/10; Musée de Géologie, Lausanne, No. 74400 (Fig. 23A, B).

ETYMOLOGY. — From the Latin *stultus*: foolish, mad.

MATERIAL EXAMINED. — 15 illustrated specimens and many others not illustrated from the type horizon (sample Mue 22).

DIMENSIONS (IN  $\mu\text{M}$ ). — Total length 165-270 (av. 195), length of cephalothorax 125-140 (av. 130), of cephalis 30-45 (av. 35), of thorax 85-100 (av. 90), of apical horn 35-55 (av. 40), of ventral and secondary lateral spines 35-75 (av. 45), of primary lateral spines 90-195 (av. 125), total width 170-180 (av. 175), width of cephalis 43-52 (av. 48), of thorax 80-95 (av. 85).

## DESCRIPTION

Cephalis hemispherical, well rounded, with small pores irregularly distributed. All spines three-bladed. Apical horn subaxial, straight but slightly curved at the base. Base of horn V a little above bases of horns I<sub>r</sub> and II. Ventral and secondary lateral horns strongly curved at the base to achieve a subhorizontal direction, forming right angles with the axis of test. Collar boundary marked by the arches LI forming a small ridge on the surface of test. Ridge runs below the arches VL to connect, on the ventral part, the bases of horns L<sub>r</sub>



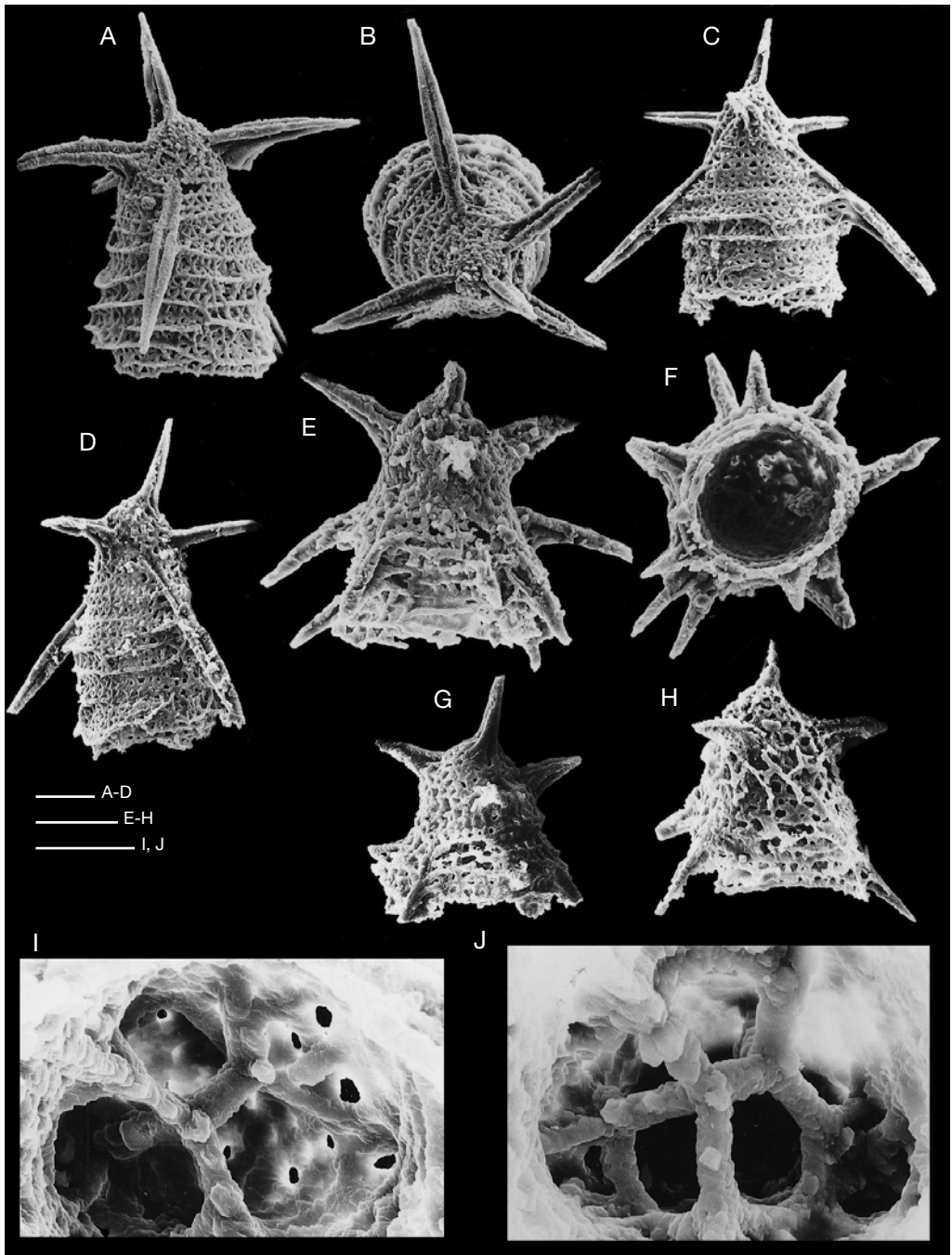


FIG. 23. — **A-D, J**, *Sanniopileus stultus* n. gen., n. sp.; **A, B**, holotype, right lateral and apical views showing the absence of dorsal spine; **C, D, J**, paratypes; **C, D**, ventral and left lateral views; **J**, basal view of initial spicule showing the absence of dorsal spine; **E-I**, *Sanniopileus stultissimus* n. gen., n. sp.; **E, F**, holotype, left lateral and basal views; **G-I**, paratypes; **G, I**, left lateral and basal views with details of the initial spicule; **H**, ventral view. Scale bars: A-H, 30  $\mu$ m; I, J, 10  $\mu$ m.

and Ll. Thorax short, conical with irregular circumferential ridges. Most ridges not continuous, either fading out or being attached to the previous ridge. Several ridges on the proximal part of the thorax slightly garland-shaped, fixed between the insertions of the primary lateral spines. On the inner side of thorax only very few ridges are visible. Circumferential band between ridges concave in outline, usually with one, rarely two circumferential bars parallel with ridges. These bars and ridges interconnected by a system of bars in a zigzag pattern forming triangularly-framed pores. Usually these zigzagged bars arranged to form a system of rosettes centred on the circumferential bars. This regular pattern commonly disturbed in the zones where the ridges disappear. Spines Lr and Ll protruding the test wall at the collar boundary. They are three-bladed with an inner blade directed towards the centre of test, and two outer blades. Proximal parts of these spines connected to the test wall through the inner blade, distal parts free, slowly tapering. Spines Lr and Ll of variable length, either ending above the thoracic aperture or reaching far beyond it. Distal part of thorax wide open.

#### REMARKS

By its morphology this species differs significantly from all the Foremanellinidae so far described.

Family NEOSCIADIOCAPSIDAE Pessagno, 1969

TYPE GENUS. — *Neosciadiocapsa* Pessagno, 1969.

Genus *Reticulotubulus* Takemura, 1986

TYPE SPECIES. — *Reticulotubulus foremanae* Takemura, 1986; original designation.

#### REMARKS

*Reticulotubulus* is herein provisionally assigned to the family Neosciadiocapsidae due to its ventral tube and the helmet-conical to hat-shaped test. It differs from other neosciadiocapsids by missing a velum.

### *Reticulotubulus tintinnabulum* n. sp.

(Fig. 24A-C, I, J)

HOLOTYPE. — Photo No. 58111-58114; stub Mue 22/20; Musée de Géologie, Lausanne, No. 74401 (Fig. 24A, B, I, J).

ETYMOLOGY. — From the Latin *tintinnabulum*: small bell.

MATERIAL EXAMINED. — Seven illustrated specimens and many others not illustrated from the type horizon (sample Mue 22).

DIMENSIONS (IN  $\mu\text{M}$ ). — Total length 160-225 (av. 180), length of apical horn 30-40 (av. 35), of cephalis 25-40 (av. 35), of thorax 105-160 (av. 130), width of cephalis 35-55 (av. 50), of median part of thorax 95-120 (av. 105), of distal part 150-190 (av. 170).

#### DESCRIPTION

Test bell-shaped composed of two segments. Cephalis small, hemispherical, with a slender tri-radiate apical horn. Ventral spine connected to the two primary lateral spines by strong arches VL, not attached distally to test wall but continued into a ventral tube. Ventral tube long, latticed, cylindrical. Primary lateral spines and dorsal spine run shortly along the proximal interior wall of thorax. Collar stricture absent, the cephalis passing gradually into thorax, which is bell-shaped, having an expanded proximal part and a wide conical distal part, both separated by a wide concave portion. Distalmost part of thorax not preserved, but it seems to be ragged. Test fragile with very small pores on the cephalis and rounded hexagonal pores, increasing in size distally and alternately disposed in longitudinal rows, on the thorax.

#### REMARKS

*Reticulotubulus tintinnabulum* n. sp. resembles sensibly *R. foremanae* from which it differs by missing a collar stricture.

Family ACROPYRAMIDIDAE Haeckel, 1881

TYPE GENUS. — *Acropyramis* Haeckel, 1881.

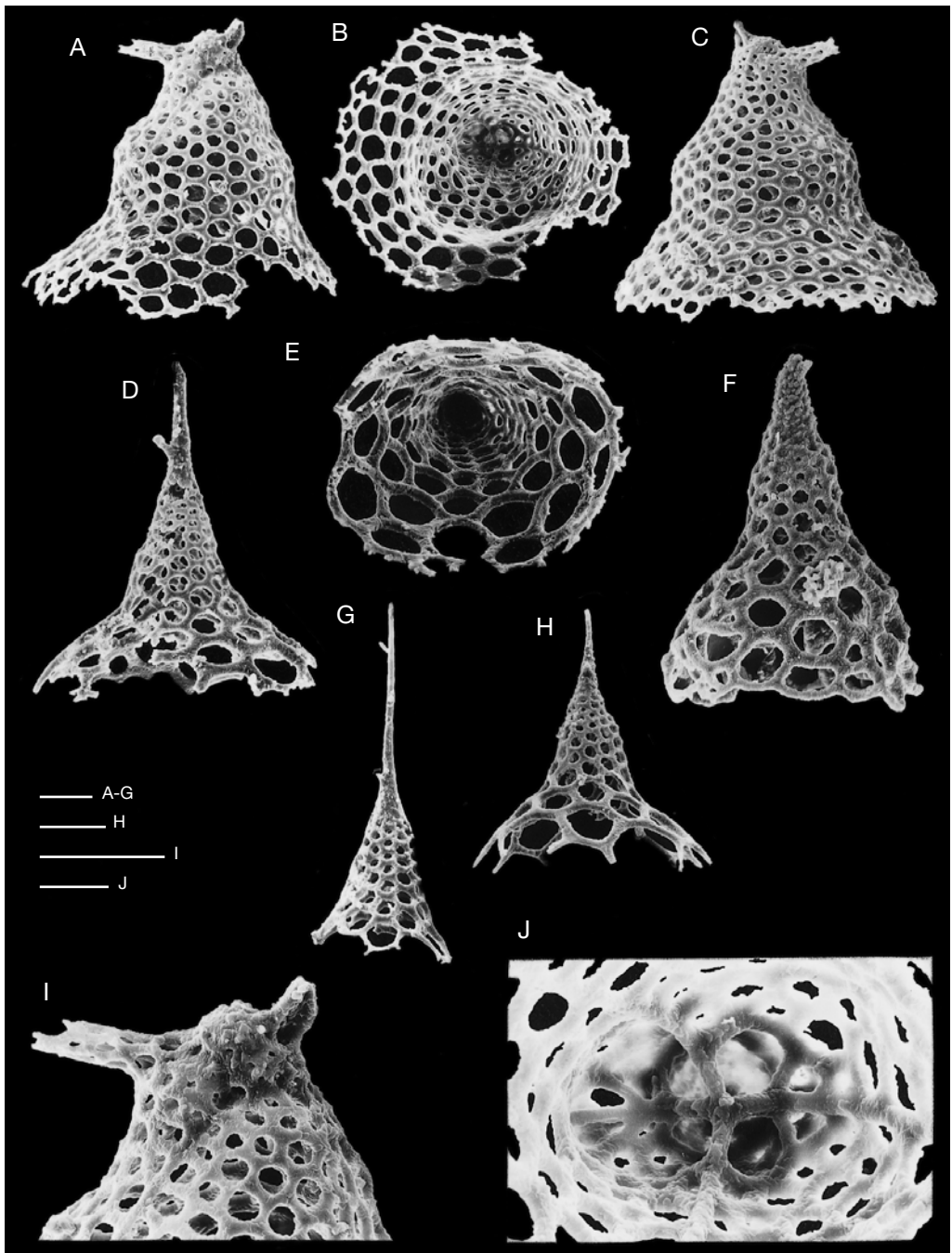


FIG. 24. — **A-C, I, J**, *Reticulotubulus tintinnabulum* n. sp.; **A, B, I, J**, holotype, left lateral and basal views with details of the proximal part of shell and of the initial spicule, note prolongation of ventral spine along the tube; **C**, paratype, right lateral view; **D-H**, *Cornutella tella* n. sp.; **D**, holotype; **E-H**, paratypes; **E**, basal view; **F**, apically broken specimen with garland-shaped distal end; **G**, young specimen; **H**, specimen with large terminal pores. Scale bars: A-I, 30 µm; J, 10 µm.

Genus *Cornutella* Ehrenberg, 1838

TYPE SPECIES. — *Cornutella clathrata* Ehrenberg, 1838; by monotypy.

*Cornutella tella* n. sp.  
(Fig. 24D-H)

HOLOTYPE. — Photo No. 45641; stub Mue 22/16; Musée de Géologie, Lausanne, No. 74402 (Fig. 24D).

ETYMOLOGY. — Arbitrary combination of letters.

MATERIAL EXAMINED. — 12 illustrated specimens and many other specimens not illustrated from the type horizon (sample Mue 22).

DIMENSIONS (IN  $\mu\text{M}$ ). — Total length 180-235 (av. 210), length of apical horn and cephalis 50-130 (av. 85), of conical part of thorax 50-75 (av. 60), of inflated part 45-90 (av. 70); maximum width of cephalis at collar boundary 15-30 (av. 20), of conical part of thorax 45-65 (av. 60), of distal part 130-180 (av. 150).

## DESCRIPTION

Test high conical with a widely inflated distal part. Cephalis very small, imperforate with a straight apical horn and a short ventral spine, both massive, circular in cross section. Collar boundary not marked outside. Thorax slowly increasing in diameter up to the distal part which is widely inflated, convex in outline as if moulding a spherical calotte. Most proximal part of thorax with infilled pores. Main part of thorax net-like with hexagonally framed pores arranged alternately in commonly 12 longitudinal rows. Size of pores gradually increasing distally. Distal part of test usually not completely developed, without rim, irregular, with thinner bars as if individuals died before completion. Only one specimen of about 20 shows a complete, garland-shaped terminal rim. In this specimen, however, the regular hexagonal pore pattern is strongly disturbed in the terminal pores.

## REMARKS

*Cornutella tella* n. sp. differs from all species of *Cornutella* so far described by its expanded distal part resembling a spherical calotte.

## Family TERTONIIDAE n. fam.

TYPE GENUS. — *Tertonium* n. gen.

RANGE. — Lower Pliensbachian-Tithonian.

DIAGNOSIS. — Dicyrtid nassellarians with small cephalis and large conical thorax. Thorax with an indefinite number of circumferential ridges separated by two or more rows of alternate pores. Initial spicule with MB, A, V, two L, two l, and D. L and l sometimes prolonged outside test wall.

## REMARKS

This family is erected to define a group of Jurassic species resembling somehow the Parvicingulidae Pessagno, 1977 by the presence of circumferential ridges separated by rows of transverse pores, but differing from them in that these ridges do not correspond to internal planiform partitions which are missing. The large postcephalic segment is therefore interpreted herein as representing a single chamber – the thorax.

This group of species seems to predominantly occur in the Kimmeridgian-Tithonian. Hull (1997: 174, pl. 51, figs 1, 2, 20) illustrated two undetermined and undescribed species from this interval in California, and Kiessling (pers. comm.) found a species in the lower Tithonian of the Antarctic Peninsula. A species assignable to this family was also illustrated by Takemura (1986), Hattori (1989), and Yao (1997) as *Parvicingula(?) obesa* Takemura, 1986 from probably Bajocian manganese concretions (*Unuma echinatus* Zone) of Japan, and a specimen assignable to *Toritenum* n. gen. was found by us in the very rich material from the lower Pliensbachian of Turkey partly studied by De Wever (1982).

Genus *Tertonium* n. gen.

TYPE SPECIES. — *Tertonium rectum* n. gen., n. sp.

ETYMOLOGY. — Name formed by an arbitrary combination of letters. Neuter gender.

RANGE. — Early Kimmeridgian to late Tithonian.

DIAGNOSIS. — Broadly conical to four-sided tent-shaped test with D, L and V prolonged downward along thorax and extended into spines.

## REMARKS

*Tertonium* n. gen. differs from *Toritenum* n. gen. in having D, L and V prolonged along thorax.

*Tertonium curvicornum* n. sp.

(Fig. 25A-C, I, J)

?Nassellaria gen. et sp. indet. 4 – Hull 1997: 174, pl. 51, fig. 2.

HOLOTYPE. — Photo No. 58406; stub Mue 22/20; Musée de Géologie, Lausanne, No. 74403 (Fig. 25A).

ETYMOLOGY. — From the Latin *curvus*: curved; and *cornum*: horn.

OCCURRENCE. — Upper lower Kimmeridgian? (Subzone 2 alpha 2, Hull 1997) to early Tithonian, Hybonotum Zone.

MATERIAL EXAMINED. — Eight illustrated specimens and many others not illustrated from the type horizon (sample Mue 22).

DIMENSIONS (IN  $\mu\text{M}$ ). — Total length 505-655 (av. 575), length of apical horn 140-200 (av. 165), of thorax 320-455 (av. 385), of upper thorax 105-175 (av. 130), of lower thorax 205-300 (av. 255), total width 370-515 (av. 400), width of upper thorax without spines 235-275 (av. 255), of lower thorax 240-315 (av. 275).

## DESCRIPTION

Test large, composed of a conical proximal part including cephalis and upper thorax, and a cylindrical distal part. Cephalis and upper thorax with a double-layered wall. Apical horn thick, three-bladed, with two blades on the dorsal part and one on the ventral part. Blades with broadened rim, separated by deep grooves. Horn with the proximal part straight, vertical, and the distal part pointed, strongly curved in dorsal direction at about its middle part. At this point the ventral blade gives rise to a ventrally directed thorn. Cephalis conical externally, perforated by small pores irregularly distributed within the meshes of the outer layer. Collar boundary marked by the onset of spinal prolongations on the outer surface (V, D, the two L). Upper thorax widely conical, rounded in cross section. Spinal prolongations are first integrated in the thoracic wall, with only the outer blade appearing at the surface. This blade is still connected to the neighbouring pore

frames of the spongy outer layer of the wall. Lateral blades of the spinal prolongations are covered by the spongy layer, and appear late, usually at the level of a strong circumferential ridge. Beyond this ridge the spines are free, three-bladed, straight, and directed obliquely downward at an angle of about 45°. Lower part of thorax generally cylindrical with wavy outline due to some circumferential ridges and/or constrictions. Outer layer of the wall still present on the upper part of this segment. Pores small, alternately disposed in circumferential rows, two, three or more in each interval between ridges. Distal part of thorax always corroded in our specimens.

## REMARKS

*Tertonium curvicornum* n. gen., n. sp. differs from *T. rectum* n. gen., n. sp. by having a curved apical horn, shorter and straight spines diverging from the upper part of thorax, and by a cylindrical, spineless lower thorax. The specimen illustrated by Hull (1997) from the upper lower Kimmeridgian of the Taman Formation, east-central Mexico, might be related to this species, but it differs from the latter by seemingly having only two or three spines on thorax, and in having a segmented thorax with deep segmental constrictions. Since the apical horn of the Mexican specimen is broken, it is impossible to know whether it was originally curved or straight.

*Tertonium rectum* n. sp.

(Fig. 25D-H)

Nassellaria gen. et sp. indet. 1 – Hull 1997: 174, pl. 51, figs 1, 20.

HOLOTYPE. — Photo No. 45630, 45633; stub Mue 22/16; Musée de Géologie, Lausanne, No. 74404 (Fig. 25D, E).

ETYMOLOGY. — From the Latin *rectus*: straight.

OCCURRENCE. — Early Tithonian, Hybonotum Zone to upper Tithonian, subzone 4 beta.

MATERIAL EXAMINED. — Nine illustrated specimens and many others not illustrated from the type horizon (sample Mue 22).

DIMENSIONS (IN  $\mu\text{M}$ ). — Total length 645-710, total width 565-780 (av. 655), length of upper thorax

without spines 110-215 (av. 170), of lower thorax 145-215 (av. 185), maximum width of upper thorax 235-345 (av. 285), of lower thorax 240-290 (av. 270), length of apical horn 190-325 (av. 240), of spines of upper thorax 170-345 (av. 270), of spines of lower thorax 210.

#### DESCRIPTION

Test composed of a small cephalis and a two-partite thorax. Cephalis short-conical externally, porous, partly covered by the broad base of a long three-bladed apical horn. Pores of cephalis small, open within irregular areas formed by a network of transversal and longitudinal ridges. The latter ridges coalesce apically to form the three blades of the apical horn. Boundary between cephalis and thorax marked at the inner side by weak arches, and on the outer surface by the onset of the four spines – D, V, and two L at the top of the thorax. Upper part of thorax rapidly increasing in width, rectangular in cross section, forming a well marked pyramid whose edges are represented by the downward prolongations of the ventral, dorsal, and primary lateral spines. At the base of this upper part these prolongations emerge from the test wall forming four long three-bladed spines. Spines recurved and distally pointed. Lower part of thorax slowly increasing in diameter, rectangular in cross section with edges formed by four secondary spines arising from the thoracic wall and extended distally into three-bladed spines. Compared to the primary spines, these spines are straight and less divergent. Wall of thorax thin, supported by continuous circumferential ridges. Ridges follow each other at irregular intervals and correspond internally to grooves. Wall between ridges convex externally with variable number (two to six) of transverse rows of alternate pores. Especially on the upper part of thorax ridges bear small thorns, probably remains of an external spongy layer.

#### REMARKS

*Tertonium rectum* n. gen., n. sp. differs from *T. curvicornum* n. gen., n. sp. especially by having four spines on the lower thorax. Although its distal part is missing, the specimen illustrated by Hull (1997) from the upper Tithonian of the

California Coast Ranges is rather similar to the specimens from the sample Mue 22. The preserved part of that specimen only differs from our specimens in having straight primary spines extended from the upper thorax.

#### Genus *Toritenum* n. gen.

TYPE SPECIES. — *Toritenum hirsutum* n. gen., n. sp.

ETYMOLOGY. — The name is an anagram of the genus *Tertonium* n. gen. Neuter gender.

KNOWN RANGE. — Lower Pliensbachian to lower Tithonian.

DIAGNOSIS. — Test conical with or without a well developed apical horn, with the spines of the initial spicule not protruding. Thorax with a variable number of circumferential ridges separated by depressionary intervals bearing transverse rows of pores. Distal part of thorax widely open.

#### REMARKS

This new genus resembles *Tertonium* n. gen. from which it only differs by not having the spines D, V, and the two L of the initial spicule extended outside. The genus is rather well represented in the lower Tithonian assemblage of sample Mue 22. A species assignable to this genus was illustrated by Takemura (1986), Hattori (1989), and Yao (1997) as *Parvicingula(?) obesa* Takemura, 1986 from probably Bajocian manganese concretions (*Unuma echinatus* Zone) of Japan. Another species was illustrated by Kiessling (1999: pl. 15, figs 1, 2) as *Eucyrtidium(?)* sp. from the lower Tithonian of Antarctic Peninsula, and the oldest but not yet described was found by us in the lower Pliensbachian fauna of Turkey partly studied by De Wever (1982).

#### *Toritenum corpulentum* n. sp. (Fig. 26D-G)

HOLOTYPE. — Photo No. 54980; stub Mue 22/17; Musée de Géologie, Lausanne, No. 74405 (Fig. 26D).

ETYMOLOGY. — From the Latin *corpulentus*: corpulent, fat, stout.

MATERIAL EXAMINED. — Six illustrated specimens and about 20 not illustrated specimens from the type horizon (sample Mue 22).

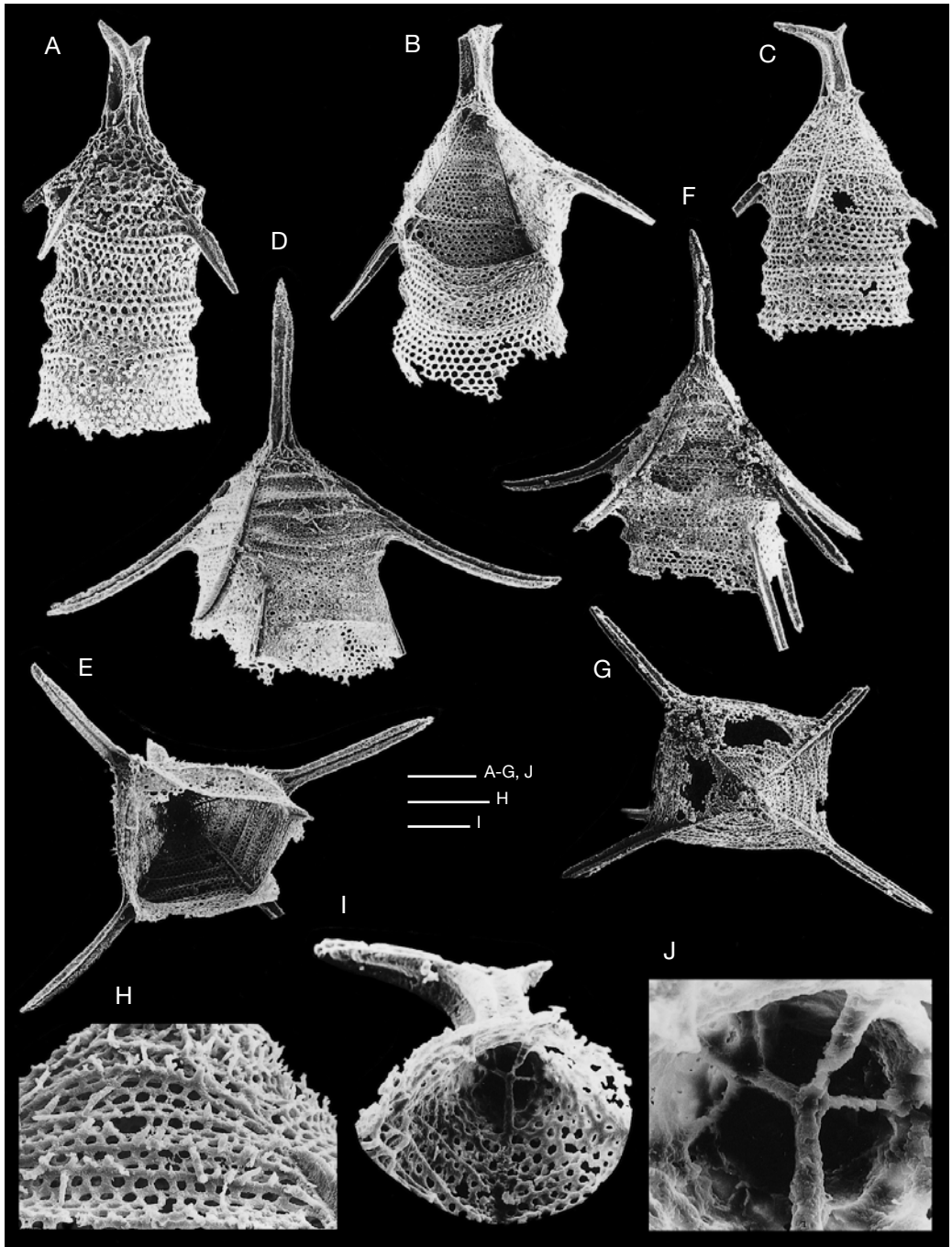


FIG. 25. — **A-C, I, J**, *Tertonium curvicornum* n. gen., n. sp.; **A**, holotype, right latero-dorsal view; **B, C, I, J**, paratypes; **B, C**, right lateral views; **I, J**, basal view showing details of initial spicule; **D-H**, *Tertonium rectum* n. gen., n. sp.; **D, E**, holotype, dorsal and basal views; **F-H**, paratypes; **F, G**, right lateral and apical views; **H**, detail of surface of proximal part of thorax. Scale bars: A-G, 100  $\mu$ m; H, I, 30  $\mu$ m; J, 10  $\mu$ m.

DIMENSIONS (IN  $\mu\text{M}$ ). — Length without apical horn 305-440 (av. 375), length of apical horn 20-130 (av. 65), of cephalis 45-47 (av. 55), of thorax 250-380 (av. 315), maximum width of cephalis 75-115 (av. 90), of thorax 240-280 (av. 265).

#### DESCRIPTION

Test large, conical proximally, cylindrical medially with a slightly widening distal end. Cephalis hemispherical with a moderately long, slender apical horn. Pores of cephalis very small, irregularly disposed. Collar boundary above the first circumferential ridge of the thorax and well marked by a sudden change in outline from subcylindrical to wide-conical. Thorax large, increasing rapidly in diameter up to one third of its length, then cylindrical medially, and increasing again distally. Wall thin with six to 12 rather closely spaced circumferential ridges separated by commonly two to five transverse rows of alternate pores. Ridges of proximal part, especially, with fine thorns.

#### REMARKS

Morphologically *Toritenum corpulentum* n. gen., n. sp. is very close to *T. hirsutum* n. gen., n. sp. from which it only differs by being thicker, by having a thin and short apical horn, a well marked cephalis, closer ridges, and a wider distal end.

#### *Toritenum hirsutum* n. sp. (Fig. 26A-C, H)

*Parvicingula* sp. aff. *P.(?) obesa* – Hattori 1989: 89, pl. 44, fig. F.

HOLOTYPE. — Photo No. 45636; stub Mue 22/16; Musée de Géologie, Lausanne, No. 74406 (Fig. 26A).

ETYMOLOGY. — From the Latin *hirsutus*: hirsute, hairy.

OCCURENCE. — Early Middle Jurassic of Japan (Hattori 1989), early Tithonian (Hybonotum Zone).

MATERIAL EXAMINED. — 15 illustrated specimens and many others not illustrated from the type horizon (sample Mue 22).

DIMENSIONS (IN  $\mu\text{M}$ ). — Total length 465-560 (av. 505), length of apical horn 90-120 (av. 105), width of cephalis measured on the first circumferential ridge 75-120 (av. 95), maximum width of test 200-265 (av. 225).

#### DESCRIPTION

Test highly conical composed of a short conical cephalis and a very long conical to cylindrical thorax. Cephalis with small pores distributed irregularly and a long, robust three-bladed apical horn in axial position. Transition between cephalis and apical horn gradual in both outline and superficial ornamentation, longitudinal ridges on the cephalis coalescing gradually on the blades of the horn. Collar boundary marked by a circumferential ridge. V, D, and the two L shortly prolonged on the inner surface of thorax but not visible on the outer surface. Proximal part of thorax rapidly increasing in diameter, middle and distal parts commonly cylindrical or even slightly tapering distally. Thorax usually with seven to 10 or more circumferential ridges separated by concave bands. Ridges on proximal part usually rather close to each other, with two to four transverse rows of alternate pores between two ridges. Median and distal parts with larger intervals between ridges, which may have seven to 10 transverse rows of alternate pores. Pores small and rounded. Cephalis and proximal part of thorax, especially, covered by numerous small thorns, size and frequency of thorns decreasing distally.

#### REMARKS

*Toritenum hirsutum* n. gen., n. sp. is the most frequent species of this family in the sample Mue 22, outnumbering by 10 times the total number of specimens of the other species. The specimen illustrated by Hattori (1989) is quite probably the oldest representative of this species. It only differs from our specimens in not having small thorns on cephalis and proximal part of thorax. The species illustrated by Kiessling (1999) as *Eucyrtidium(?)* sp. differs from *T. hirsutum* n. gen., n. sp. in being higher-conical.

#### Family ULTRANAPORIDAE Pessagno, 1977

TYPE GENUS. — *Ultranapora* Pessagno, 1977.

#### Genus *Anaticapitula* n. gen.

TYPE SPECIES. — *Anaticapitula clauda* n. gen., n. sp.



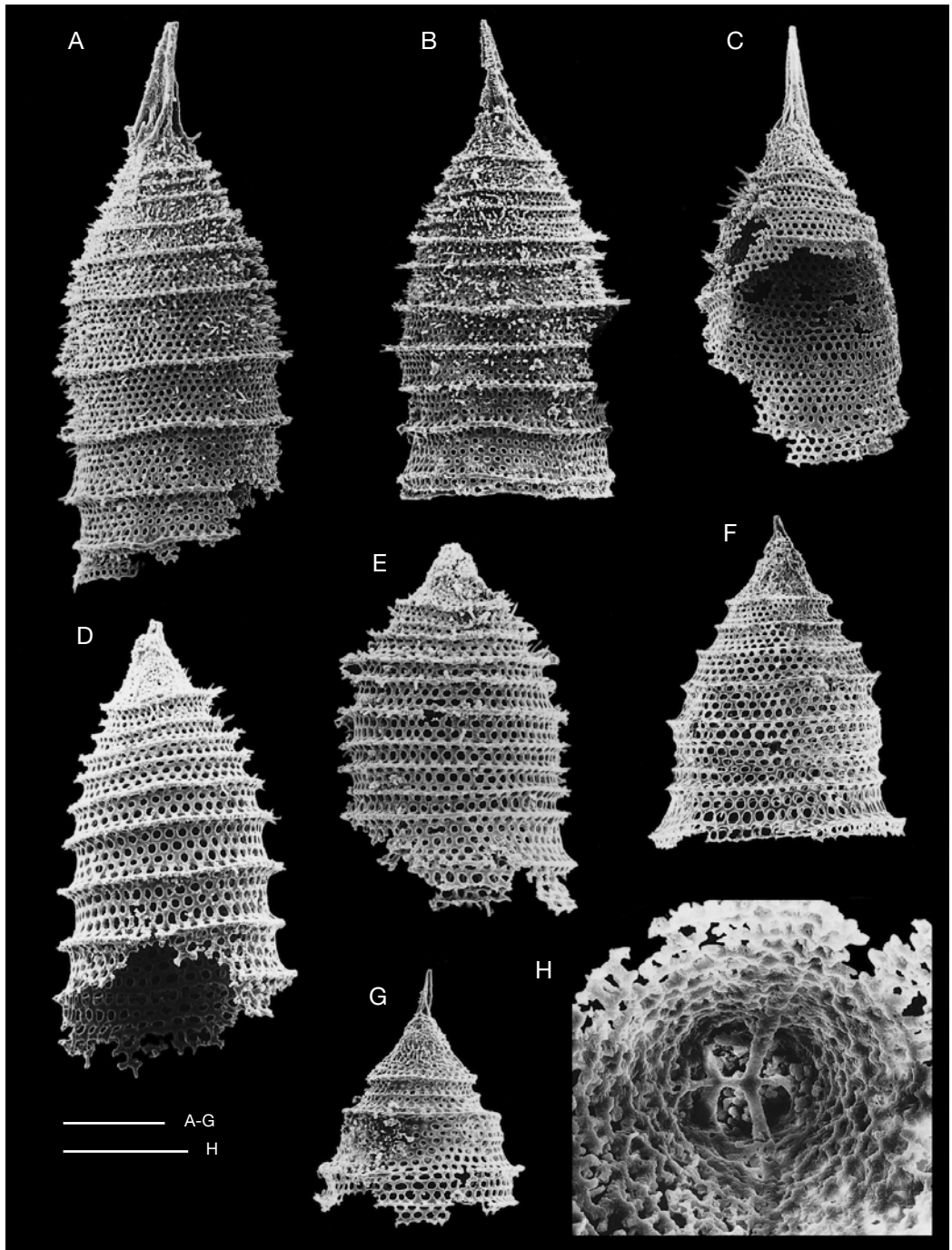


FIG. 26. — **A-C, H**, *Toritenum hirsutum* n. gen., n. sp.; **A**, holotype; **B, C, H**, paratypes; **C**, broken specimen showing non-segmented internal surface; **H**, broken specimen, basal view showing details of initial spicule; **D-G**, *Toritenum corpulentum* n. gen., n. sp.; **D**, holotype; **E-G**, paratypes. Scale bars: A-G, 100 µm; H, 30 µm.

ETYMOLOGY. — From the Latin *anas*: duck; and *capitulus*: small head. Feminine gender.

KNOWN RANGE. — Lower Jurassic to Lower Cretaceous.

DIAGNOSIS. — Highly ovate dicyrtid test with bladed apical horn and thorax prolonged into a thin-walled terminal tube. Cephalis and thorax continuous externally, without collar stricture. Initial spicule with A, V, D, two L, two I, and a long Ax. Cephalis and thorax with a superimposed network of strong ridges. With or without feet representing external extensions of L and D. Feet, when present, with an outer blade and two lateral blades.

#### REMARKS

By its general shape and the tubular prolongation of the thorax this genus shows characters in common with the genus *Rhopalosyringium* Campbell & Clark, 1944. A comparable axobate was illustrated by De Wever (1982) in the Lower Jurassic species *Ovum pertusum* De Wever, 1982. *Jacus(?) anatiformis* De Wever, 1982, described from the lower Pliensbachian of Turkey, is also almost identical to *A. pennata* n. gen., n. sp. and, although De Wever (1982) did not mention the presence of Ax in his species, a small light-grey spot opposite to the ventral spine, representing probably a small Ax, is visible in a broken specimen figured by him (De Wever 1982: pl. 11, fig. 13). *Jacus(?) italicus* Jud, 1994 described from the Lower Cretaceous (Jud 1994) has a morphology similar to *J.(?) anatiformis* and should also be assigned to the genus *Anaticapitula* n. gen. From *Napora*, *Anaticapitula* n. gen. differs by having a well developed Ax in the initial spicule, thorax continuous with the velum, no crown of spines on the apical horn, and a much larger cephalis.

#### *Anaticapitula clauda* n. sp. (Fig. 27A, B, K)

*Artostrobium(?)* sp. A – Matsuoka 1998: 171, fig. 150.

HOLOTYPE. — Photo No. 28320; stub Mue 22/1; Musée de Géologie, Lausanne, No. 74407 (Fig. 27A).

ETYMOLOGY. — From the Latin *claudus*: lame, without feet.

MATERIAL EXAMINED. — 16 illustrated specimens from the type horizon (sample Mue 22) and from other samples.

OCCURRENCE. — Early Tithonian from the Solnhofen area, southern Germany and early Berriasian from western Pacific (Mariana Trench).

DIMENSIONS (IN  $\mu\text{m}$ ). — Total length 170-210 (av. 185), length of apical horn 30-55 (av. 45), maximum width 85-105 (av. 95), width of the thoracic constriction 65-85 (av. 70), of basal rim 70-110 (av. 90).

#### DESCRIPTION

Highly ovate to ovoid main test comprising the cephalis and the thorax. Distal part of thorax tubular, slightly increasing in diameter distally. Initial spicule as for the genus, with Ax much thinner than the other spines and curved when completely preserved. Apical horn pyramidal, subaxial with three broad blades; two blades originated in the top of cephalis, the third connected to the dorsal spine and extending as a rib along the surface of test. Cephalic and thoracic wall covered by broad longitudinal and diagonal ridges that are melting distally to form a superimposed outer layer with few small pores. Terminal tube bearing very small, irregularly scattered pores.

#### REMARKS

*Anaticapitula clauda* n. gen., n. sp. differs from all other species of *Anaticapitula* n. gen. by lacking feet. The specimen illustrated by Matsuoka (1998) as *Artostrobium(?)* sp. A may be well compared to the specimens from the Solnhofen area.

#### *Anaticapitula germanica* n. sp. (Fig. 27C, D)

HOLOTYPE. — Photo No. 34989; stub Mue 22/6; Musée de Géologie, Lausanne, No. 74408 (Fig. 27C).

ETYMOLOGY. — From its German type locality.

MATERIAL EXAMINED. — 11 illustrated specimens from the type horizon (sample Mue 22).

DIMENSIONS (IN  $\mu\text{m}$ ). — Total length 180-220 (av. 200), of apical horn 45-60 (av. 50), of feet 65-95 (av. 80), of cephalis 35-40 (av. 38), of thorax with terminal tube 55-80 (av. 65), width of cephalis 60-65 (av. 62), of thorax with feet 105-130 (av. 120), of terminal tube measured at the distal rim 45-60 (av. 50).

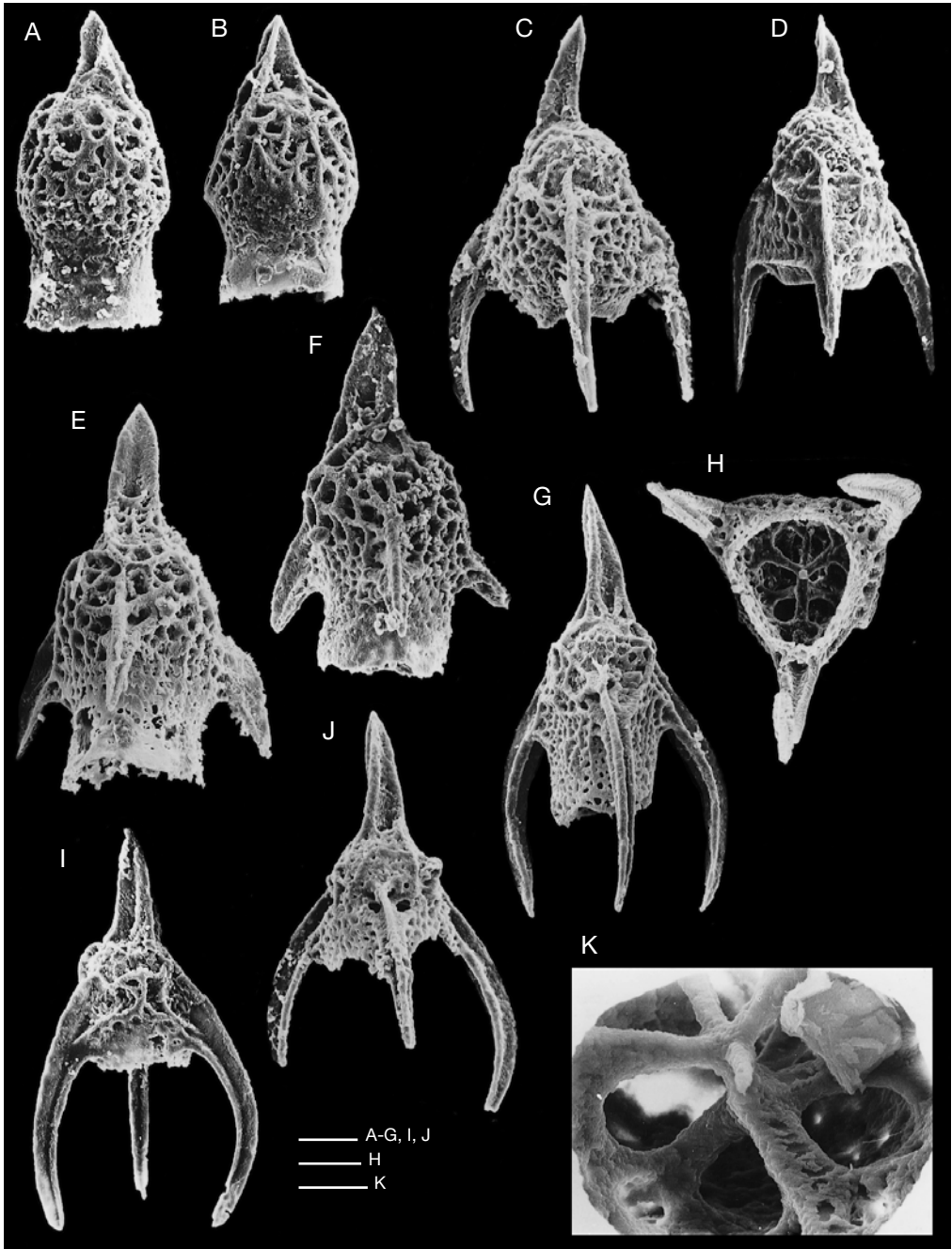


FIG. 27. — **A, B, K**, *Anaticapitula clauda* n. gen., n. sp.; **A**, holotype, left lateral view; **B, K**, paratypes; **B**, right latero-dorsal view; **K**, basal view showing initial cephalic structure, note thin Ax; **C, D**, *Anaticapitula germanica* n. gen., n. sp.; **C**, holotype, right lateral view; **D**, paratype, view from LI; **E, F**, *Anaticapitula pennata* n. gen., n. sp.; **E**, holotype, view from LI; **F**, paratype, ventral to right lateral view; **G-J**, *Anaticapitula tenera* n. gen., n. sp.; **G**, holotype, view from LI; **H-J**, paratypes; **H**, basal view, note Ax in the centre; **I**, ventral view; **J**, view from LI. Abbreviations: **Ax**, axial spine; **LI**, left primary lateral spine; **LR**, right primary lateral spine. Scale bars: A-H, I, J, 30 µm; K, 10 µm.

## DESCRIPTION

Test conical with well rounded hemispherical cephalis and inflated thorax. Cephalis with slightly curved, three-bladed apical horn. Surface of cephalis with a system of irregularly arranged ridges. On the lower part of cephalis some ridges aligned along the arches of the initial skeleton. Initial spicule with A, V, D, two L, and two l. Ax moderately long, simple. Arches Dl, Ll, and VL clearly expressed on the inner side of test. Thorax either rounded or triangular in cross section, its distal part tapering, leaving a rounded triangular aperture. Thoracic wall double-layered; inner layer thin, perforated by small pores; outer layer with a superimposed system of strong pore frames, partly fused to irregular ridges. Distal part of thoracic wall poreless forming a short terminal tube or a velum. In some specimens it is separated from thorax by a transversal ridge, and in very few specimens it is closed distally. Feet three-bladed with the external blade emerging from the collar suture, and the two lateral blades arising from the distal part of thorax.

## REMARKS

*Anaticapitula germanica* n. gen., n. sp. differs from *A. pennata* n. gen., n. sp. by a well distinct cephalis, a very short terminal tube, and much longer feet.

*Anaticapitula pennata* n. sp.

(Fig. 27E, F)

HOLOTYPE. — Photo No. 31632; stub Mue 22/4; Musée de Géologie, Lausanne, No. 74409 (Fig. 27E).

ETYMOLOGY. — From the Latin *pennatus*: winged.

MATERIAL EXAMINED. — Two illustrated specimens from the type horizon (sample Mue 22), and two specimens from sample Mue 6.

DIMENSIONS (IN  $\mu\text{M}$ ). — Total length 200-240 (av. 220), length of apical horn 60-80 (av. 70), of feet 25-50 (av. 40), of cephalis 30-40 (av. 35), of thorax without terminal tube 50-65 (av. 55), of terminal tube 50-75 (av. 60), diameter of cephalis 70-100 (av. 80), of thorax with feet 130-160 (av. 145), of terminal tube 55-90 (av. 75).

## DESCRIPTION

Test short cylindrical with a robust three-bladed apical horn and three three-bladed feet arising at

the level of the collar boundary. Initial spicule with moderately long Ax. Cephalis thick-walled, covered with a robust external layer forming polygonal (usually triangular to quadrangular) meshes, size of meshes decreasing distally. Feet with the two lateral blades connected to the test at the lower part of thorax. Feet short, divergent, slightly curved, and rapidly tapering, their distal ends above the base of the terminal tube. The latter is short, cylindrical to slightly triangular in cross section.

## REMARKS

*A. pennata* n. gen., n. sp. was compared to *A. clauda* n. gen., n. sp. under the latter species. From *Jacus(?) anatifformis* it differs in being shorter, in having a shorter terminal tube and a slightly different superficial ornamentation. Although De Wever (1982) described his species as having a large ventral pore, this pore is not visible in none of the original figures.

*Anaticapitula tenera* n. sp.

(Fig. 27G-J)

HOLOTYPE. — Photo No. 45668; stub Mue 22/16; Musée de Géologie, Lausanne, No. 74410 (Fig. 27G).

ETYMOLOGY. — From the Latin *tenerus*: young.

MATERIAL EXAMINED. — Nine specimens from the type horizon (sample Mue 22).

DIMENSIONS (IN  $\mu\text{M}$ ). — Total length 240-280 (av. 260), total width 135-155 (av. 145), length of apical horn 60-80 (av. 75), of feet 110-125 (av. 115), width of cephalis 65-85 (av. 70), of terminal tube 60-80 (av. 70).

## DESCRIPTION

Test consisting of cephalis and cylindrical thorax. Cephalis globular with a robust, three-bladed apical horn and three curved three-bladed feet. Initial spicule as described for the genus, with Lr, Ll, and D prolonged into the three feet, and V and l and ll expressed outside test wall as three pointed nodes situated approximately at the middle height of cephalis or a little above, between the feet. Arches Al, AV, Dl, Ll, and LV of the initial skeleton expressed outside test wall by

ridges. Apical horn slightly subaxial, pointed distally, with broad blades, each blade united at the surface of cephalic wall with one of the three pointed nodes marking the arches Al and AV. Feet equal, longer than apical horn, divergent proximally and strongly curved distally. They are three-bladed, one blade external and usually united with one of the pointed nodes, the other two blades lateral. At the inner side their axis makes a pair of larger pores in the proximity of the arches. Cephalic wall with more or less regular and pronounced ridges and pores very small, scattered in the depressions among ridges. Thorax velum-like, thin-walled, attached to cephalis and feet proximally, free distally and tubular with rounded triangular cross-section. Pores of this segment very small, dense and irregularly distributed.

#### REMARKS

*Anaticapitula tenera* n. gen., n. sp. is very close to *Jacus(?) anatiformis* from which it differs by having longer, curved feet. From *A. germanica* n. gen., n. sp. it differs by having curved feet and well marked arches on the surface of cephalis. By these arches it resembles the Triassic species of the genus *Eonapora* Kozur & Mostler, 1979. *Jacus(?) italicus* Jud, 1994 and *Jacus(?) sp. aff. J.?(?) italicus* of Matsuoka (1998) are also close to this species from which they differ in having shorter, sturdier feet.

#### Genus *Napora* Pessagno, 1977

*Napora* Pessagno, 1977a: 94.

*Jacus* De Wever, 1982: 204; type species: *Jacus coronatus* De Wever, 1982.

TYPE SPECIES. — *Napora bukryi* Pessagno, 1977; original designation.

RANGE. — Lower Jurassic to Upper Cretaceous.

#### REMARKS

The study of the initial spicule of the species *Napora modesta* n. sp. in transmitted light showed that the cephalic initial skeleton consists of MB, V, A, two L, two l, D, and the arches VL, Ll, lD, Al. The arch AV is absent, but an arch AD

seems to exist because one of the three blades of the apical horn has a dorsal direction.

Genus *Jacus* De Wever, 1982 is herein considered a junior synonym of *Napora*. The differences between these two genera concern only the superficial structure of thorax, a character that can be considered of specific level. The absence of the cephalocone, considered by De Wever (1982) an additional distinctive character from *Napora*, has no value because in both genera it is nothing else than the short ventral spine. Moreover, both genera have the apical horn with a verticil of three spines or spinules as extensions of the three blades; exceptions are very rare. This is also a character that differentiates *Napora* and *Jacus* from *Anaticapitula* n. gen.

Members of the genus *Napora* are among the most frequent dicyrtid nassellarians in the lower Tithonian radiolarian assemblage studied in the present article, although some species are very rare.

#### *Napora aranea* n. sp.

(Fig. 28A, B)

HOLOTYPE. — Photo No. 42556; stub Mue 22/11; Musée de Géologie, Lausanne, No. 74411 (Fig. 28A).

ETYMOLOGY. — From the Latin *aranea*: spider, spider's web.

MATERIAL EXAMINED. — Eight specimens from the type horizon (sample Mue 22).

DIMENSIONS (IN  $\mu\text{m}$ ). — Total length 400-570 (av. 480), length of apical horn with the crown of spines 120-185 (av. 160), of cephalis 30-35 (av. 32), of thorax 100-110 (av. 105), of velum 65-90 (av. 75), of feet 150-255, width of cephalis 42-50 (av. 45), of thorax 115-165 (av. 145).

#### DESCRIPTION

Cephalis small, globular to hemispherical with pustulate surface. Apical horn three-bladed with two to three verticils of three branches in the planes of blades. Branches strongly ramified usually in the planes of blades, and connected in the same planes by a system of parallel or sub-parallel bars forming a network resembling a spider's web. Ventral spine very short externally, bladed, pyramidal. Collar suture well marked

outside by a slight constriction and the absence of pustules. Thorax bell-shaped, slightly constricted distally, approximately three times the width of the cephalis. Pores small, usually irregularly arranged on the proximal part, and larger, arranged in transverse rows on the distal part. Transverse rows separated by more or less distinct transverse ridges. Surface of thorax rough, with small thorns on pore frame vertices. Feet long, three-bladed, straight or slightly curved outward or inward. Velum thin, delicate, as long as or shorter than thorax. It is triangular in cross section, usually with quadrangular pores disposed in transverse rows between transverse ridges.

## REMARKS

*Napora aranea* n. sp. differs from all the species of *Napora* so far known by its branched, spider's web-shaped apical horn. An apical horn somehow similar has the Albian-Turonian species *Napora spinifera* (Pessagno 1977b), but this species has shorter subsidiary spines on the distal part of the horn and does not develop spider's web branches.

*Napora avirostrum* n. sp.  
(Fig. 28C-E)

HOLOTYPE. — Photo No. 58511; stub Mue 22/21; Musée de Géologie, Lausanne, No. 74412 (Fig. 28C).

ETYMOLOGY. — From the Latin *avis*: bird; and *rostrum*: beak.

MATERIAL EXAMINED. — Nine illustrated specimens from the type horizon (sample Mue 22).

DIMENSIONS (IN  $\mu\text{M}$ ). — Total length 220-295 (av. 250), length of apical horn 40-50 (av. 45), of cephalis 25-45 (av. 30), of thorax 50-90 (av. 60), of velum 25-50 (av. 35), of feet 75-150 (av. 100), width of cephalis 35-60 (av. 45), of thorax 95-145 (av. 110).

## DESCRIPTION

Cephalis globular, practically imperforate with a three-bladed apical horn. Proximal half of horn thick and strongly expanded at the upper part where blades end up with a crown of very small subsidiary spines, two to three for each blade. Distal part of horn conical, pointed, approximately as long as proximal part. Ventral spine well

expressed outside, pyramidal, many-bladed. Boundary between cephalis and thorax difficult to establish outside because there is no visible stricture and the thoracic wall covers the lower part of cephalis. Thorax conical to pyramidal with about five transversal rows of wide pores. Pores alternately arranged, polygonally framed. Transversal ridge above the second basal row of pores sometimes very high. Feet broad, strongly divergent and curved, robust, external ridge forming a longitudinal ridge along thorax. Velum short slightly lobate, with very small pores.

## REMARKS

This species resembles *Napora schaudibergensis* n. sp. in general characters but differs by having a much wider thorax and feet much more divergent and much more curved inward. Some specimens have a very strong transversal rib on thorax. The apical horn is also thinner than that of *N. schaudibergensis* n. sp.

*Napora bondoca* n. sp.  
(Fig. 28F, G)

HOLOTYPE. — Photo No. 58905; stub Mue 22/21; Musée de Géologie, Lausanne, No. 74413 (Fig. 28F).

ETYMOLOGY. — From the latinized Rumanian word *bondoc*: short and stout.

MATERIAL EXAMINED. — Four specimens from the type horizon (sample Mue 22).

DIMENSIONS (IN  $\mu\text{M}$ ). — Total length 145-175 (av. 170), length of apical horn 40-50 (av. 45), of cephalo-thorax 65-80 (av. 75), of feet 45-65 (av. 60), width of apical horn 20-30 (av. 25), of cephalis 39-47 (av. 42), of thorax 70-85 (av. 80).

## DESCRIPTION

Test small, pyramidal, robust. Cephalis globular, imperforate with a very stout, short apical horn. Horn three-bladed with thick blades and deep, narrow grooves in the proximal half, and pyramidal in the distal part. Ventral spine well developed outside, pyramidal with several blades. Thorax short pyramidal, thick-walled, with generally four transverse rows of polygonally framed, rounded pores. Feet usually as long as thorax,

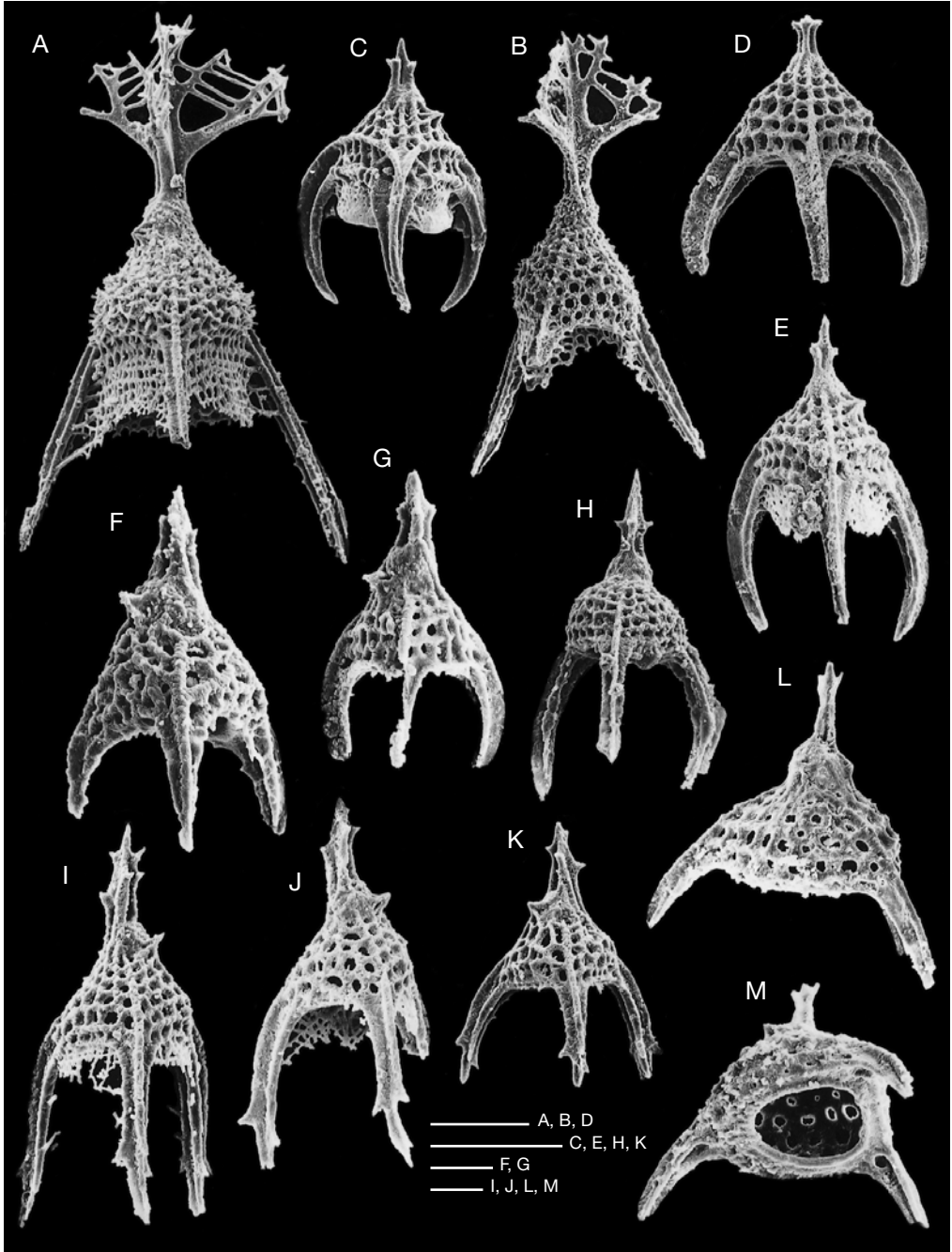


FIG. 28. — **A, B**, *Napora aranea* n. sp.; **A**, holotype, view from Ll; **B**, paratype, dorsal view; **C-E**, *Napora avirostrum* n. sp.; **C**, holotype, view from Lr; **D, E**, paratypes; **D**, dorsal view; **E**, view from Lr; **F, G**, *Napora bondoca* n. sp.; **F**, holotype, view from Ll; **G**, paratype, view from Ll; **H**, *Napora burckhardtii* Pessagno, Whalen & Yeh, 1986, dorsal view; **I-K**, *Napora cristata* n. sp.; **I**, holotype, right lateral view; **J, K**, paratypes; **J**, right lateral view; **K**, view from Ll; **L, M**, *Napora divaricata* n. sp., holotype, ventral and basal views. Abbreviations: **Ll**, left primary lateral spine; **Lr**, right primary lateral spine. Scale bars: A-E, H, K, 100  $\mu$ m; F, G, I, J, L, M, 30  $\mu$ m.

tapering distally, slightly divergent and curved. External ribs of feet prolonged from cephalis along thorax where they form the three edges of the pyramid. Velum not preserved in our specimens but its remains are visible on the proximal part of the lateral blades of feet.

#### REMARKS

This species differs from *Napora boneti* Pessagno, Whalen & Yeh, 1986 by having stouter apical horn and feet, external blade of feet much higher on the thorax, feet shorter. From *Napora cruda* Yang, 1993 it differs by the lack of subsidiary grooves on the proximal part of apical horn. All these three species are otherwise rather close morphologically.

#### *Napora burckhardti*

Pessagno, Whalen & Yeh, 1986  
(Fig. 28H)

*Napora burckhardti* Pessagno, Whalen & Yeh, 1986: 37, pl. 10, figs 2-5, 15, 16, 21-23.

*Napora* sp. 1 – Matsuoka 1998: 171, pl. 10, fig. 159.

MATERIAL EXAMINED. — Five specimens from sample Mue 22, two specimens from sample Mue 6.

OCCURRENCE. — Early Tithonian, Hybonotum Zone, Solnhofen area, Germany; early Tithonian of east-central Mexico and lower Berriasian from Mariana Trench (SW Pacific).

#### REMARKS

The specimens from the Mühlheim Member have the same type of cephalis, thorax, and feet as those of *N. burckhardti*, but the apical horn is always three-bladed distally and its middle part is swollen, with subsidiary spines. In *N. burckhardti* the distal part of the apical horn is circular in cross section and the middle part has no subsidiary spines.

#### *Napora cristata* n. sp.

(Fig. 28I-K)

*Napora* sp. E – Pessagno *et al.* 1986: 46, pl. 10, fig. 18.

HOLOTYPE. — Photo No. 54928; stub 22/17; Musée de Géologie, Lausanne, No. 74414 (Fig. 28I).

PARATYPES. — MNHN, bât. de Géologie, No. Gg 2001/2092, Gg 2001/2094-2097.

ETYMOLOGY. — From the Latin *cristatus*: crested.

OCCURRENCE. — Early Tithonian (Hybonotum Zone) to late Tithonian (Zone 4 of Pessagno *et al.* 1984).

MATERIAL EXAMINED. — 10 specimens from the type horizon (sample Mue 22), one specimen from sample Mue 9.

DIMENSIONS (IN  $\mu\text{M}$ ). — Total length 215-265 (av. 245), length of apical horn 50-65 (av. 60), of cephalis 20-30 (av. 25), of thorax 50-65 (av. 55), of velum 60-65 (av. 62), of feet 85-130 (av. 110); total width 125-155 (av. 135), width of cephalis 40-50 (av. 45), of thorax 85-95 (av. 90).

#### DESCRIPTION

Cephalis small, imperforate and smooth, well distinguished from thorax. Apical horn long and very slightly curved ventrally, three-bladed, with a crown of three small spines at the distal part of blades. Blades unequal, the dorsal blade shorter than the two blades aligned with the primary lateral spines. Consequently the three small spines from the distal part of the blades arise at two levels, the spine on the dorsal blade is nearer to the cephalis than the other two. Apical horn pointed beyond the crown of spines. Ventral spine short externally, beak-shaped. Thorax pyramidal with four to five transversal rows of large pores. Feet slightly divergent, straight or slightly curved, often with one or two teeth on the distal part of blades. Distal part gently tapering and usually slightly recurved. Length of feet equal somehow with the height of cephalothorax or longer. Velum very delicate and short, connecting the proximal half of the inner blades of the feet.

#### REMARKS

*Napora cristata* n. sp. is quite probably the forerunner of the Cretaceous species *Napora praespinifera* Pessagno, 1977. The apical horn of both species is almost identical but in *N. cristata* n. sp. it is shorter, thicker, and only some blades have two subsidiary spines. The thorax of this new species has also fewer and larger pores, and feet are usually slightly recurved distally and have at



least one small spine on each blade. The velum is much more robust and longer in *N. praespinifera* and is preserved in even poorly preserved specimens, whereas in the well preserved specimens of *N. cristata* n. sp. it is delicate and short. Possibly the differences between these two species are only of subspecies level. Anyway, *N. praespinifera*, *N. cristata* n. sp., and *Napora (Ultranapora)* sp. A and sp. B of Pessagno (1977b) represent a rather closely related group of species.

*Napora divaricata* n. sp.  
(Fig. 28L, M)

*Napora* sp. aff. *N. latissima* – Hull 1997: 118, pl. 45, figs 6, 22.

HOLOTYPE. — Photo No. 60035, 60036; stub Mue 22/23; Musée de Géologie, Lausanne, No. 74415 (Fig. 28L, M).

ETYMOLOGY. — From the Latin *divaricatus*: straddled.

MATERIAL EXAMINED. — One specimen from the type horizon (sample Mue 22).

DIMENSIONS (IN  $\mu\text{M}$ ). — Length of apical horn 40-45, of cephalis 20-45, of thorax 50-70, of feet more than 80-90; diametre of cephalis 33-40, of thorax 100-130 (dimensions based on holotype and the specimen illustrated by Hull [1997], from sample SM-48, Tithonian, Stanley Mt.).

OCCURRENCE. — Lower Tithonian, Hybonotum Zone from Solnhofen area, Germany, upper lower to upper Tithonian, Stanley Mountain, California.

DESCRIPTION

Cephalis bulbous, imperforate with a slender apical horn bearing three subsidiary spines and a short distal horn. Ventral spine short, bladed, at the base of cephalis. Thorax wide, short pyramidal with three to four transverse rows of wide alternate pores separated by transversal costae on the middle and distal parts, and small, irregularly arranged pores on the proximal part. Feet wide diverging, curved, slender, about as long as thorax.

REMARKS

The specimen from our material resembles rather perfectly the Tithonian specimen illustrated by Hull from which it only differs by having a longer apical horn.

*Napora lomoalta* Hull, 1997  
(Fig. 29A, B)

*Napora* sp. aff. *pyramidalis* – Kiessling 1995: pl. 60, figs 14, 15; 1999: 72, pl. 14, fig. 12.

*Napora lomoalta* Hull, 1997: 118, pl. 45, figs 9, 21; pl. 46, figs 1, 16, 19, 21, 23.

MATERIAL EXAMINED. — 15 specimens from sample Mue 22.

OCCURRENCE. — Lower to upper Tithonian (Zone 4, Subzones 4 beta and alpha of Pessagno *et al.* 1993) in Antarctic Peninsula, Stanley Mountain, California Coast Ranges, and lower Tithonian (Hybonotum Zone) in Solnhofen area, Germany.

REMARKS

Some specimens herein assigned to this species resemble very well the holotype, others have a more robust thorax. Very few specimens have two to three small spines on the distal end of feet. All are pyramidal as the type specimens, with a well perforate subtriangular cephalis, and a massive apical horn at base, composed of several ridges which converge distally to form a more slender triradiate horn. Nodes of subsidiary spines are very weakly developed, as in the holotype, with two to three very small thorns in each node. Unlike the topotype, most of our specimens have a rather well preserved velum; it is triangular in cross-section, thin-walled, and as long as thorax. Some specimens have also one or two small spines on the distal end of some feet.

*Napora matsukoi* n. sp.  
(Fig. 29C, D)

HOLOTYPE. — Photo No. 54934; stub 22/17; Musée de Géologie, Lausanne, No. 74416 (Fig. 29C).

PARATYPE. — MNHN, bât. de Géologie, No. Gg 2001/2093.

ETYMOLOGY. — The species is named in honour of Dr. Atsushi Matsuoka (Niigata University, Japan) for his valuable contributions to the knowledge of Mesozoic radiolarians.

MATERIAL EXAMINED. — Seven specimens from the type horizon (sample Mue 22).

DIMENSIONS (IN  $\mu\text{M}$ ). — Total length 180-225 (av. 205), length of apical horn 42-53 (av. 48), of cephalis 23-31 (av. 26), of thorax 30-45 (av. 35), of feet 75-110 (av. 90), total width 100-135 (av. 120), width of cephalis 35-45 (av. 40), of thorax 70-90 (av. 75).

## DESCRIPTION

Cephalis large, globular, imperforate, with a thick three-bladed, gently tapering apical horn. At its middle part the horn bears on each blade two or three very small subsidiary spines. Distal part of horn also three-bladed. Dorsal blade extended downward on cephalic surface, lateral blades have their base on the top of cephalis. Ventral spine well developed externally, many-bladed, pyramidal. Thorax pyramidal, well separated from cephalis externally, generally with five transverse rows of pores of which the distal ones are well marked. Feet longer than cephalothorax, slightly diverging and curved with distal end pointed. External blade of each foot forms a rib along thorax. Velum not preserved but some remains prove that it was originally present.

## REMARKS

This new species resembles especially *Napora lomoalta* but differs from it by having simple blades on apical horn, cephalis practically imperforate and well distinguished from thorax, and feet curved.

*Napora modesta* n. sp.  
(Fig. 29E-G)

HOLOTYPE. — Photo No. 58514; stub Mue 22/21; Musée de Géologie, Lausanne, No. 74417 (Fig. 29E).

PARATYPES. — MNHN, bât. de Géologie, No. Gg 2001/2098-2099.

ETYMOLOGY. — From the Latin *modestus*: modest.

MATERIAL EXAMINED. — 12 specimens from the type horizon (sample Mue 22).

DIMENSIONS (IN  $\mu\text{M}$ ). — Total length 130-185 (av. 160), length of apical horn 30-50 (av. 40), of cephalis 20-25 (av. 22), of thorax 30-45 (av. 35), of feet 50-75 (av. 60), total width 80-145 (av. 115), width of cephalis 20-35 (av. 30), of thorax 60-90 (av. 75).

## DESCRIPTION

Cephalis relatively large, hemispherical, entirely perforate, with small, usually quadrangular pores arranged in oblique rows. Apical horn slender, distinctly three-bladed, with a distinct verticil in the middle part giving rise to three well devel-

oped spines arising almost perpendicularly to the axis of the apical horn. Thorax broadly conical, widely opened, thin-walled, commonly with quadrangular, unequal pores arranged in more or less distinct transverse rows, especially in the distal part. Feet strongly diverging, slender, curved inward, shorter or longer than height of cephalis and thorax. Outer blades of feet well pronounced on the thoracic wall. All blades of feet more or less dentate.

## REMARKS

This new species is well distinguished from all the other species of *Napora* so far described by its denticulate feet, thin-walled thorax, and the presence of one verticil of long spines on the apical horn.

*Napora pacifica* Kiessling, 1999  
(Fig. 29H, I)

*Napora* sp. E – Pessagno *et al.* 1986: 46, pl. 10, fig. 18.

*Napora* sp. F – Pessagno *et al.* 1986: 46, pl. 10, fig. 9.

“*Napora pacifica*” – Kiessling 1995: pl. 61, figs 2, 5 (*nomen nudum*).

*Napora pacifica* Kiessling, 1999: 70, pl. 14, figs 1, 6.

*Napora pacifica* – Hull 1997: 120, pl. 46, figs 5, 6, 17.

MATERIAL EXAMINED. — More than 100 specimens from sample Mue 22, and from other samples.

OCCURRENCE. — Lower to upper Tithonian of Antarctica, California, east-central Mexico, Solnhofen area (Germany).

## REMARKS

This species is the most frequent ultranaporid in the sample Mue 22. It was also found in sample Mue 6, but represents a rare faunal element in several other samples from different sections of the Mühlheim Member. Our well preserved material shows a well developed velum, which is the only difference from the type material. Remnants of such a velum were also illustrated by Hull (1997). Some specimens bear also two subsidiary spines on each blade of the apical horn.

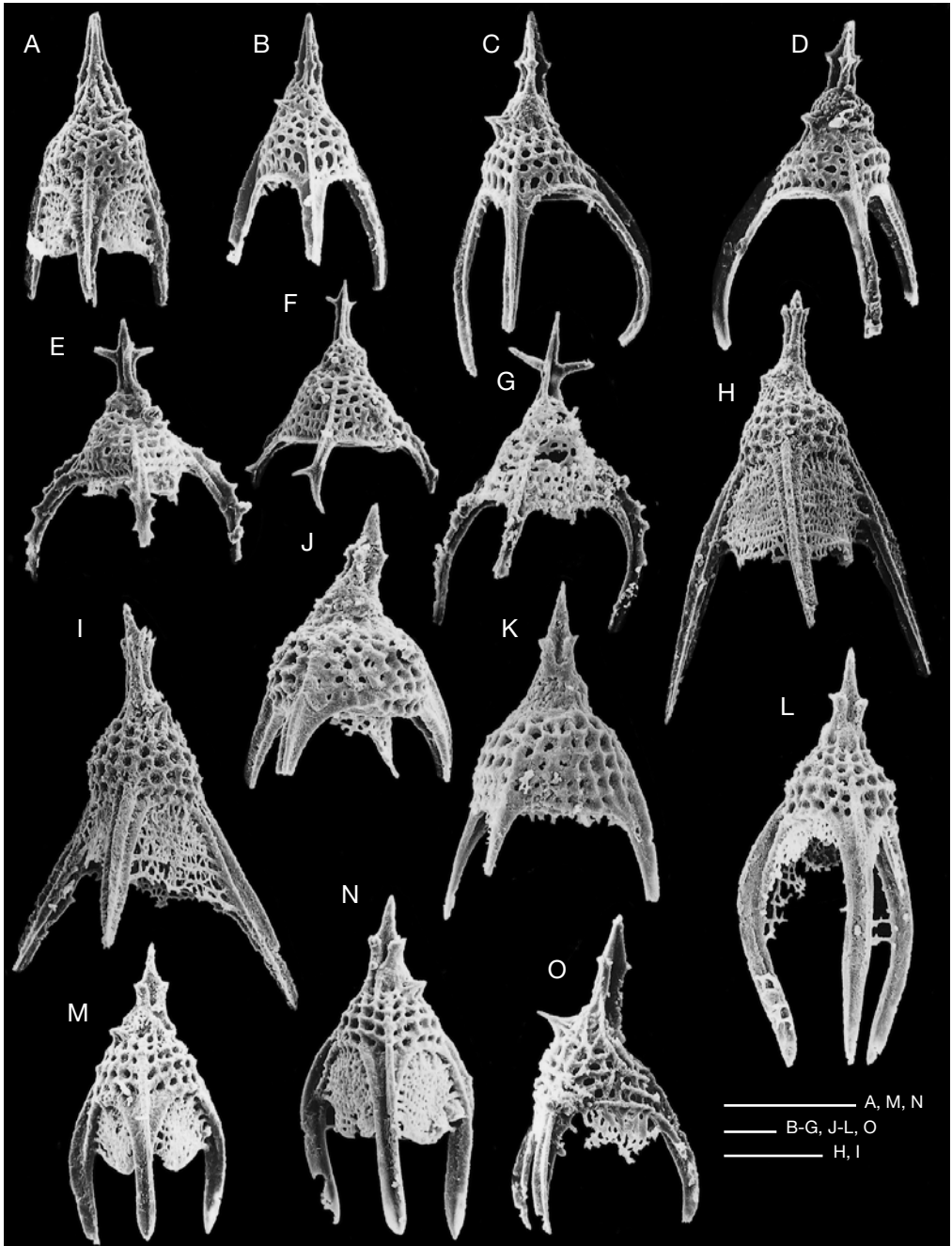


FIG. 29. — **A, B**, *Napora lomoalta* Hull, 1997; **A**, right lateral view; **B**, view from Ll; **C, D**, *Napora matsukoi* n. sp.; **C**, holotype, left lateral view; **D**, paratype, left lateral view; **E-G**, *Napora modesta* n. sp.; **E**, holotype, dorsal view; **F, G**, paratypes; **F**, dorsal view; **G**, view from Lr; **H, I**, *Napora pacifica* Kiessling, 1999; **H**, view from Ll; **I**, view from Lr; **J, K**, *Napora pyramis* n. sp.; **J**, holotype; **K**, paratype; **L-N**, *Napora schaudibergensis* n. sp.; **L, M**, paratypes; **L**, dorsal view; **M**, view from Ll; **N**, holotype, view from Lr; **O**, *Napora* sp., left lateral view. Abbreviations: Ll, left primary lateral spine; Lr, right primary lateral spine. Scale bars: A, H, I, M, N, 100  $\mu$ m; B-G, J-L, O, 30  $\mu$ m.

*Napora pyramis* n. sp.  
(Fig. 29J, K)

HOLOTYPE. — Photo No. 13759; Musée de Géologie, Lausanne, No. 74418 (Fig. 29J).

ETYMOLOGY. — From the Latin *pyramis*: pyramid.

MATERIAL EXAMINED. — Four illustrated specimens of which two from the type horizon (sample Mue 22), one specimen from sample Mue 9, and another one from sample Hob 32.

DIMENSIONS (IN  $\mu\text{M}$ ). — Total length 175-195 (av. 185), length of apical horn 43-49 (av. 47), of cephalis 23-37 (av. 30), of thorax 45-60 (av. 55), of feet 53-61 (av. 58), total width 105-120 (av. 115), width of cephalis 38-45 (av. 41), of thorax 90-100 (av. 95).

DESCRIPTION

Test subpyramidal with a robust, apical horn. Proximal part of apical horn three-bladed; blades thick externally, broader terminally, each one with two very short thorns or only with a transversal blade; distal part conical, generally longer than the proximal part. Cephalis globular, smooth, poreless. Ventral spine very weakly marked externally. Thorax well distinguished from cephalis, subpyramidal, with four or six transverse rows of circular pores. Pores usually in square pattern distally, decreasing in size proximally and infilled toward the collar stricture. Feet usually shorter than thorax, very slightly curved, their external blade forming edges on the distal part of thorax. Velum very short when present.

REMARKS

This species is very close to *Napora burckhardti* from which it differs by short and rather straight feet and a pyramidal thorax. From *N. pyramidalis* Baumgartner, 1984 it differs in having a distinct smooth cephalis and a pronounced collar stricture because of the sudden inflation of the thorax.

*Napora schaudibergensis* n. sp.  
(Fig. 29L-N)

HOLOTYPE. — Photo No. 27809; stub Mue 22/1; Musée de Géologie, Lausanne, No. 74419 (Fig. 29N).

ETYMOLOGY. — From the Schaudiberg quarry, type locality of the species.

MATERIAL EXAMINED. — 14 illustrated specimens from the type horizon (sample Mue 22) and one illustrated specimen from sample Hob 32.

DIMENSIONS (IN  $\mu\text{M}$ ). — Total length 205-285 (av. 245), length of apical horn 36-56 (av. 45), of cephalothorax 65-100 (av. 75), of feet 100-145 (av. 120), total width 113-162 (av. 132), width of thorax 70-120 (av. 88).

DESCRIPTION

Cephalis small, weakly marked, practically imperforate. Apical horn very robust, short, three-bladed proximally with wide, externally expanded, rounded ridges and deep, narrow grooves. Distally it terminates into a conical or pyramidal axial spine which is as long as or longer than proximal, bladed part. At the boundary between the two parts the blades may develop a crown of very short subsidiary spines, usually two or three for each blade, or a transversal blade. Ventral spine well developed externally, bladed, pyramidal, arising from the collar stricture. Thorax robust, hemispherical to conical with five transverse rows of pores. Pores quadrangularly to hexagonally framed, intervening bars thick with nodes at vertices. Feet long, slightly diverging and inwardly curved, commonly twice as long as to three times longer than thorax. Velum usually preserved, well differentiated from thorax by its delicate wall with transverse rows of pores. Distal part of velum well marked by a rim, three-lobate.

REMARKS

*Napora schaudibergensis* n. sp. is morphologically very close to *Napora parva* Takemura, 1986 and *N. triangularis* Takemura, 1986 from which it differs by having a shorter and more robust apical horn with thickened blades and deep, narrow grooves, cephalis better marked, thorax more robust. From *N. timida* n. sp. it differs by a less robust and more conical thorax, a more robust apical horn with longer distal spine, and a better marked cephalis. A species very close to this species is *N. avirostrum* n. sp. from which it differs by less divergent feet, much more robust proximal portion of apical horn, and slightly longer distal portion.

*Napora timida* n. sp.  
(Fig. 30A, B)

HOLOTYPE. — Photo No. 54922; stub Mue 22/17; Musée de Géologie, Lausanne, No. 74420 (Fig. 30A).

ETYMOLOGY. — From the Latin *timidus*: shy, because of its hidden cephalis.

MATERIAL EXAMINED. — Five specimens from the type horizon (sample Mue 22).

DIMENSIONS (IN  $\mu\text{M}$ ). — Total length 350-395 (av. 370), length of apical horn 35-50 (av. 40), of cephalothorax 135-140 (av. 138), of velum 65-100, of feet 175-195 (av. 185), total width 230-260 (av. 250), width of thorax 165-175 (av. 170).

DESCRIPTION

Test bell-shaped with cephalis hidden in the thoracic wall and cavity. Due to this position of the cephalis the slightly pyramidal ventral spine seems to originate in the upper part of thorax. Apical horn short, thin by comparison to the shell, three-bladed, with truncated, expanding blades distally and a central thorn, together forming a crown-like structure. Thorax thick-walled, robust, large hexagonal and pentagonal pore frames with vertices strengthened by small nodes. Pores alternately arranged in five to six transversal rows. Feet robust, diverging proximally and curving inward distally. Outer blades of feet broader than lateral blades. Thoracic velum finely porous, thin-walled, connected to thoracic aperture and to the proximal part of the feet by numerous fine bars. Aperture of the velum wide open, triangular.

REMARKS

The specimens from Mue 22 are morphologically very close to *N. collieri* Hull, 1997 by having the blades of the apical horn extended on the surface of cephalis up to the proximal end of thorax, a comparable apical horn and curved feet, but differ by the external blade being broader, thorax less rounded, apical horn thinner, and cephalis hidden in the thorax. By their broad external blade the feet of our specimens resemble those of *N. latissima* Takemura, 1986 and *N. triangularis*.

*Napora* sp.  
(Fig. 29O)

MATERIAL EXAMINED. — One specimen from sample Mue 22.

REMARKS

This species, from which we have only one specimen, is well distinguished from all the others occurring in the lower Tithonian fauna studied by having the surface of the cephalothorax with costae oriented in different directions. These costae represent high frames of pores.

Genus *Poculinapora* n. gen.

TYPE SPECIES. — *Poculinapora poculigera* n. gen., n. sp.

ETYMOLOGY. — From the Latin *poculum*: cup; and *Napora*.

RANGE. — Tithonian so far as known.

DIAGNOSIS. — Dicyrtid nassellarians with a small cephalis and a large subglobular thorax. Cephalis with a well developed hollow apical horn. Apical tube subaxial between the two blades aligned with the primary lateral spines of the initial skeleton. Thorax with a large circular or triangular aperture and three three-bladed feet, one blade external, two blades lateral. Thoracic velum usually present.

REMARKS

Except for the hollow apical horn, the morphology and structure of the cephalis, thorax and feet of this new genus are similar to those of the genus *Napora*. In fact, this genus could be defined as *Napora* with hollow apical horn. Four new species (*P. marsupiala* n. gen., n. sp., *P. poculigera* n. gen., n. sp., *P. spathulipes* n. gen., n. sp., and *P. tripartita* n. gen., n. sp.), all of them from the very rich sample Mue 22, are assigned to this genus. A fifth species, *Napora espinosa* Hull, 1997, also Tithonian in age, shows very clearly the same character along the ventral groove (Hull 1997: pl. 45, fig. 19) (Fig. 32A) and should be assigned to this new genus. All these five species have a rather similar globular thorax and a well distinct cephalis. Before discussing the hollow structure of the apical horn one should mention that the three blades

and grooves of the apical horn of *Napora* are generally aligned approximately with the three feet. Accordingly, there are two blades, herein called lateral, aligned with the two feet representing prolongations of the primary lateral spines of the initial spicule, one blade, herein called dorsal, aligned with the dorsal spine and foot, one ventral groove opposite to the dorsal foot, on the direction of the ventral spine, and two latero-dorsal grooves between the dorsal and lateral blades.

In four species (*Poculinapora espinosa* n. comb., *P. marsupiala* n. gen., n. sp., *P. poculigera* n. gen., n. sp., and *P. spathulipes* n. gen., n. sp.) (Fig. 32A, C-F) the tube of the apical horn is certainly situated along the ventral groove which is closed in the ventral part. It represents the prolongation of the cephalic pore open in this area in front of the apical horn. In *P. tripartita* n. gen., n. sp. the tube would seem to be axial, at least on the distal portion. Because this position is difficult to explain it seems that in this case the axis of the horn (prolongation of the apical spine) is strongly displaced dorsally.

The tube is a simple hollow in *P. marsupiala* n. gen., n. sp., *P. spathulipes* n. gen., n. sp., and *P. espinosa* n. comb. In *P. tripartita* n. gen., n. sp. and some specimens of *P. poculigera* n. gen., n. sp. the tube, or at least its distal end, seems to be subdivided by some septa or bars radiating from the axis.

The genus *Poculinapora* n. gen. undoubtedly derived from a species of *Napora* by developing a tube along the ventral groove. A species susceptible to be such an ancestor could be *Napora pacifica* that is the most frequent species of *Napora* at this stratigraphic level and that has the thorax and feet rather similar to those of *Poculinapora* n. gen., and an apical horn with a rather variable distal part.

*Poculinapora marsupiala* n. sp.  
(Figs 30D, E; 32F)

HOLOTYPE. — Photo No. 58165; stub Mue 22/20; Musée de Géologie, Lausanne, No. 74421 (Fig. 30D).

PARATYPES. — MNHN, bât. de Géologie, No. Gg 2001/2115-2116.

ETYMOLOGY. — From the Latin *marsupialis*: marsupial.

MATERIAL EXAMINED. — Six specimens from the type horizon (sample Mue 22).

DIMENSIONS (IN  $\mu\text{M}$ ). — Total length of test 290-345 (av. 320), length of apical horn 80-100 (av. 90), of cephalis 25-40 (av. 35), of thorax 55-61 (av. 59), of feet 130-160 (av. 145), total width 140-195 (av. 165), width of cephalis 37-40 (av. 39), of thorax 90-100 (av. 95).

DESCRIPTION

Cephalis small, globular, practically imperforate and slightly pustulate. Apical horn long, slightly curved dorsally. Dorsal blade of horn well marked, separated from the other two blades by two deep grooves. These blades are free in the distal half and connected in the proximal half around the groove forming a tube. Distal part of the tube obliquely cut. Thorax hemispherical, thick-walled, well separated from cephalis, with three or four transverse rows of pores on the inflate part. Pores arranged especially in square pattern and decreasing in size apically. Thoracic velum thin-walled, short, partly preserved, uniting laterally the feet in their proximal part. Feet long, slightly curved and slightly divergent. Lateral blades of feet with subparallel borders or even slightly broader distally. External blade tapering distally.

REMARKS

*Poculinapora marsupiala* n. gen., n. sp. is well distinguished by its dorsally curved and obliquely cut apical horn.

*Poculinapora poculigera* n. sp.  
(Figs 30F-I; 32D)

HOLOTYPE. — Photo No. 58169, 58170; stub Mue 22/20; Musée de Géologie, Lausanne, No. 74422 (Fig. 30F, I).

PARATYPES. — MNHN, bât. de Géologie, No. Gg 2001/2117-2118.

ETYMOLOGY. — From the Latin *poculum*: cup; and *gero*: to bear, to have.

MATERIAL EXAMINED. — Four specimens from the type horizon (sample Mue 22).

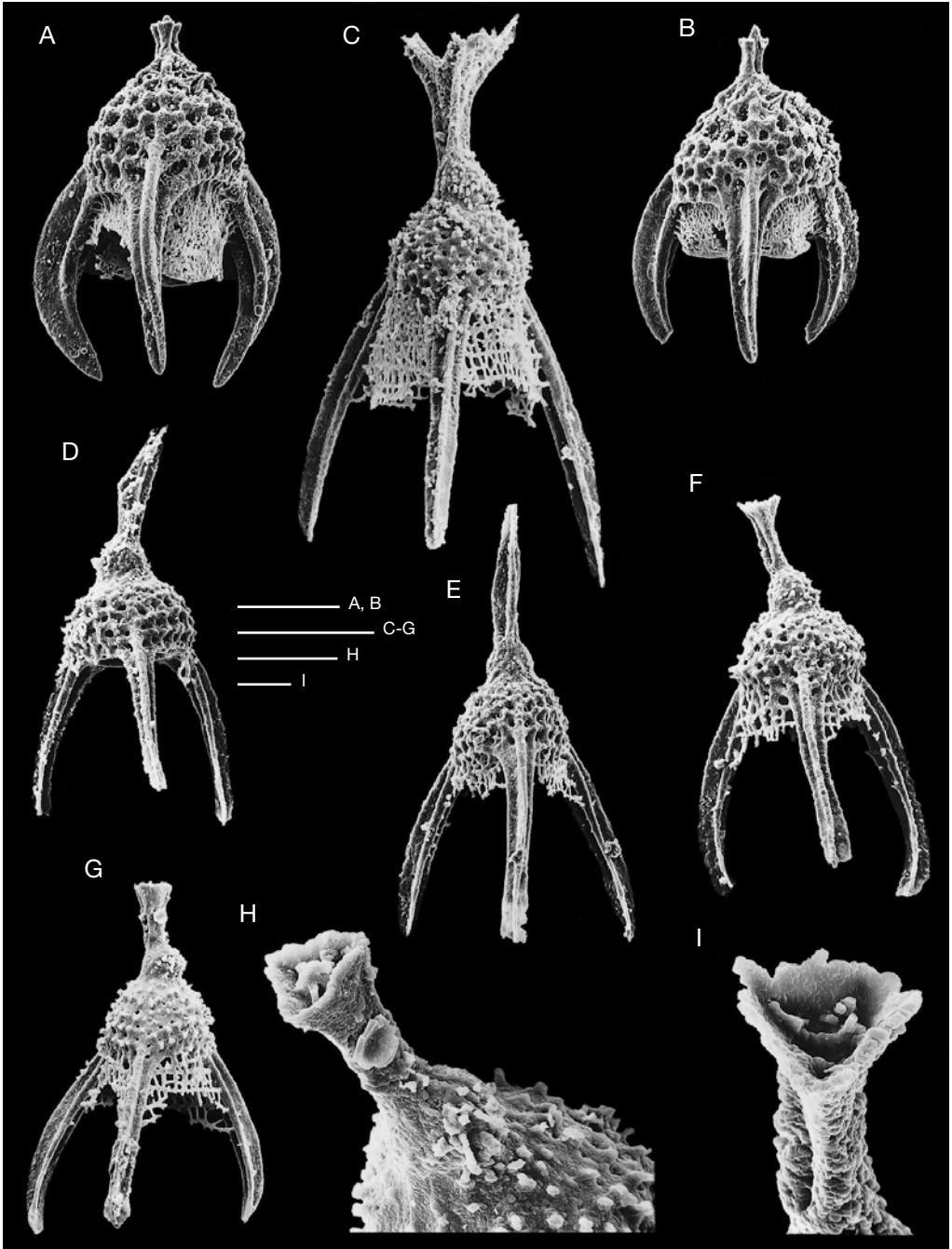


FIG. 30. — **A, B**, *Napora timida* n. sp.; **A**, holotype, view from Lr; **B**, paratype, view from Lr; **C**, *Poculinapora tripartita* n. gen., n. sp., holotype, view from Lr; **D, E**, *Poculinapora marsupialia* n. gen., n. sp.; **D**, holotype, view from Ll; **E**, paratype, dorsal view; **F-I**, *Poculinapora poculigera* n. gen., n. sp.; **F, I**, holotype, view from Lr and detail of apical horn; **G, H**, paratype, view from Lr and detail of apical horn in subapical view. Abbreviations: **Ll**, left primary lateral spine; **Lr**, right primary lateral spine. Scale bars: A-G, 100 µm; H, 30 µm; I, 10 µm.

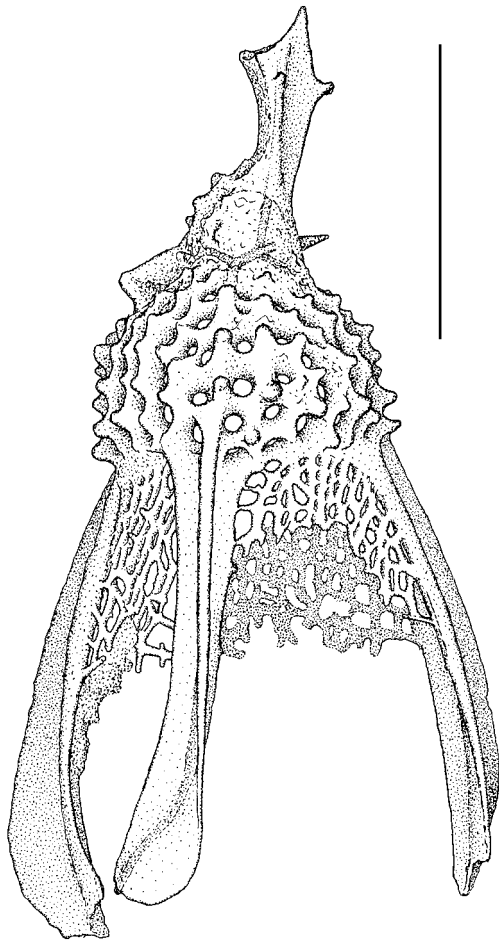


FIG. 31. — *Poculinapora spathulipes* n. gen., n. sp., holotype, left lateral view. Scale bar: 0.1 mm.

**DIMENSIONS (IN  $\mu\text{M}$ ).** — Total length of shell 275-320 (av. 305), length of apical horn 57-64 (av. 59), of cephalis 37-40 (av. 38), of thorax 59-64 (av. 60), of feet 140-155 (av. 150); total width 175-220 (av. 205), width of cephalis 38-44 (av. 41), of thorax 105-115 (av. 110).

#### DESCRIPTION

Cephalis small, globular, imperforate, smooth or slightly pustulate, separated from thorax by a shallow constriction. Apical horn straight or slightly curved, inverted pyramidal, having a wide cavity with triangular transverse section. Border of this cavity (distal end of horn) straight, thin, without spines but frayed due to corrosion. Inner space of this cavity simple or divided by a

longitudinal septa. Thorax hemispherical with pustulose surface and pores arranged in four to six transverse rows; in distal rows they are arranged in a square pattern, in proximal rows alternate. Size of pores decreases apically. Feet long, divergent, and curved. Lateral blades of feet expanded distally, external blade tapered distally. Feet connected proximally by a thin post-thoracic velum with quadrangular meshes.

#### REMARKS

This new species differs from *P. marsupialis* n. sp. and *P. tripartita* n. gen., n. sp. by having no terminal spine on the apical horn and by the funnel-shaped distal part of the apical horn.

#### *Poculinapora spathulipes* n. sp. (Figs 31; 32C, E)

**HOLOTYPE.** — MNHN, bât. de Géologie, No. Gg 2001/2119 (Figs 31; 32C).

**PARATYPE.** — MNHN, bât. de Géologie, No. Gg 2001/2120 (Fig. 32E).

**ETYMOLOGY.** — From the Latin *spathula*: spatula; and *pes*: foot.

**MATERIAL EXAMINED.** — Two specimens from the type horizon (sample Mue 22).

**DIMENSIONS (IN  $\mu\text{M}$ ).** — Total length of shell with horn and feet 300-330, of apical horn 60, of cephalis 35, of thorax 70-75, of feet 130-150; width of cephalis 40-60, of thorax 95-130.

#### DESCRIPTION

Cephalis small, globular, imperforate with a weakly pustulate surface. Apical horn triradiate with very short subsidiary spines and a short distal spine. Dorsal blade with a pair of subsidiary spines arising a little lower than on the two lateral blades. Tube along ventral groove funnel-like with oblique border, lower ventrally and higher dorsally. Ventral spine thick externally, below the collar stricture or almost not marked. Thorax thick-walled, hemispherical, with five to seven transverse rows of circular pores. Pore frames thick with strong nodes at vertices. Nodes free or interconnected by a spongy network covering the



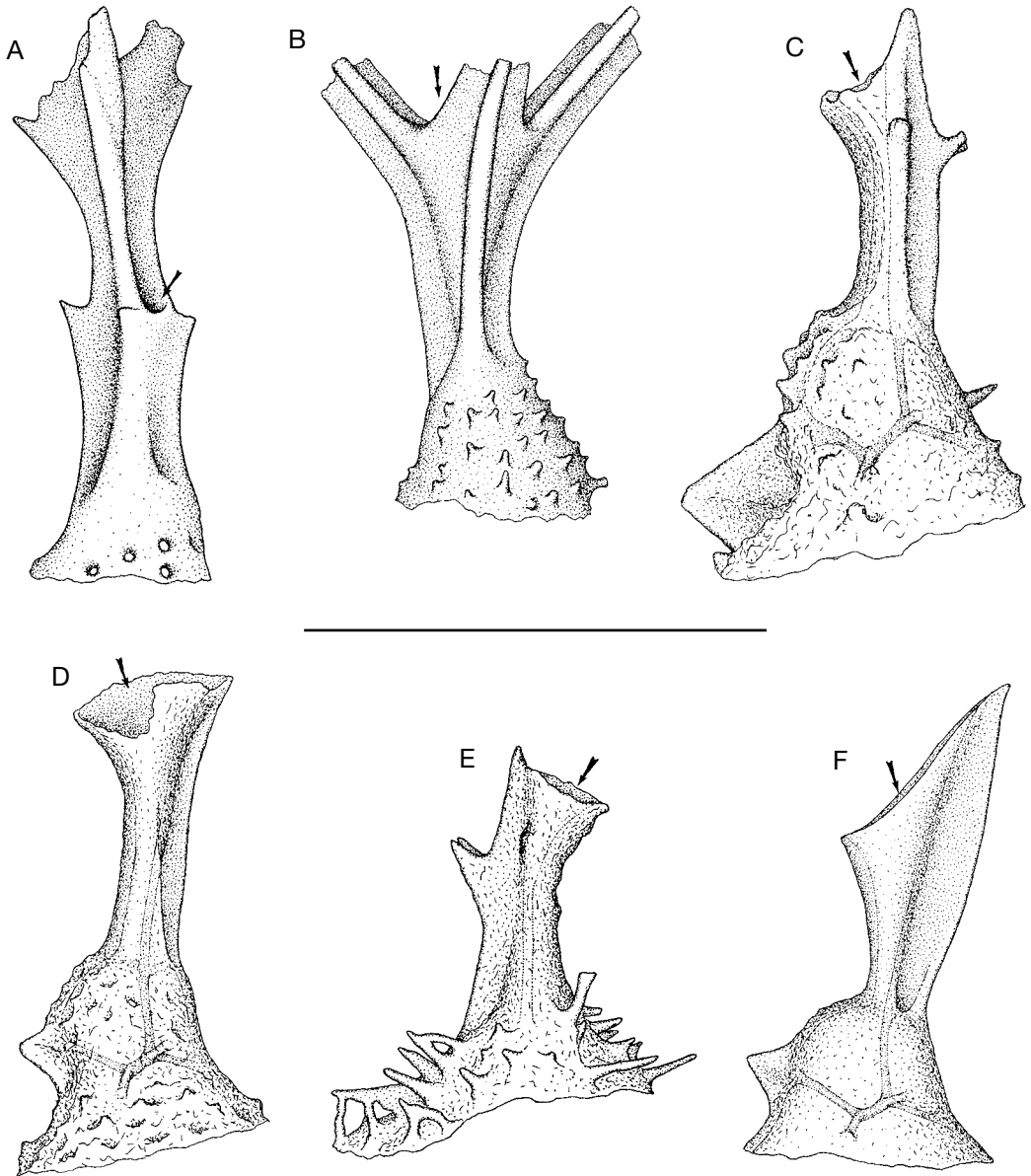


FIG. 32. — Apical horns of *Poculinapora* n. gen.; **A**, *P. espinosa* n. comb., right lateral view; **B**, *P. tripartita* n. gen., n. sp., holotype, right lateral view; **C**, **E**, *P. spathulipes* n. gen., n. sp., holotype and paratype in left lateral and right lateral views respectively; **D**, *P. poculigera* n. gen., n. sp., paratype, left lateral view; **F**, *P. marsupiala* n. gen., n. sp., paratype, left lateral view. All arrows point to the opening of the tube along the apical horn. Scale bar: 0.1 mm.

thorax and cephalis. Feet long, three-bladed, slightly diverging and slightly curved with distal ends rounded, spatulate. Velum well developed between feet.

#### REMARKS

Morphologically *Poculinapora spathulipes* n. gen., n. sp. is close to *P. poculigera* n. gen., n. sp. from which it differs by having a short ventral horn

and subsidiary spines on blades. Feet of both species are rather similar but the spatula of the feet of this new species is wider. By the morphology of the apical horn, that still preserves the crown of subsidiary spines of *Napora*, this species and *P. espinosa* n. comb. seem to be the most primitive of the genus *Poculinapora* n. gen. The species is based on the holotype and paratype; the former is longer and narrower, the latter is shorter, thicker, and has the cephalis and thorax covered with a layer of spongy fabric.

*Poculinapora tripartita* n. sp.  
(Figs 30C; 32B)

HOLOTYPE. — Photo No. 30851; stub Mue 22/3; Musée de Géologie, Lausanne, No. 74423 (Figs 30C; 32B).

ETYMOLOGY. — From the Latin *tripartitus*: having three parts, divided into three.

MATERIAL EXAMINED. — One specimen from the type horizon (sample Mue 22).

DIMENSIONS (IN  $\mu\text{M}$ ). — Total length 437, length of apical horn from base to the verticils of spines 72, of cephalis 37, of thorax 75, of velum 95, of feet 200-230, diametre of cephalis 50, of thorax 110, of velum 130.

DESCRIPTION

Cephalis small, globular with a pustulate surface. Apical horn long, three-bladed, increasing in width distally, and divided into three straight, long, strongly divergent, three-bladed spines lying in the planes of the blades of the horn. One blade of these distal spines continues one of the blades of the apical horn, the other two connect two blades of the other two spines forming an inverted pyramidal or conical cavity. This cavity seems to be divided, at least distally, into three compartments by three longitudinal septa or radial bars radiating from the axis of the horn toward the interradial zones. Ventral spine very short externally. Collar suture well marked externally by a constriction and the absence of pustules. Thorax globular, subhemispherical, with the distal part slightly constricted, and with very small, circular pores. Surface of thorax rough, pustulate or spiny. Feet long, three-bladed, slightly divergent, and slightly curved inward.

Velum very delicate, about as long as thorax, and connected on almost its whole length to the lateral blades of the feet. It has quadrangular or triangular meshes aligned usually in transverse rows.

REMARKS

This new species, from which we have only one specimen, resembles *Napora aranea* n. sp. and *N. pacifica* in having a similar cephalis and thorax, but differs from them in having the feet slightly curved inward and especially in having the apical horn with the structure as described above.

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