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SPECIAL ISSUE
Taxonomic Studies of Upper Jurassic (Tithonian) Radiolaria from the Taman Formation,
east-central Mexico

Yang Qun

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TAXONOMIC STUDIES OF UPPER JURASSIC (TITHONIAN) RADIOLARIA FROM THE TAMAN FORMATION, EAST-CENTRAL MEXICO

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ABSTRACT

The upper Tithonian Radiolaria (Upper Jurassic; Zone 4) of the Taman Formation represent a highly abundant and diversified fauna of outer neritic to bathyal environment. Thirteen families (one new), forty-four genera (seven new), and one hundred and seventy-two species level taxa (forty-nine new) are documented herein. Biostratigraphically important taxa present in this assemblage include Acanthocircus dicranocanthos, Vallupus hopsoni, Bivallupus, Parvicingula excelsa, and Perispyridium. The distinctive Jurassic "marker" Perispyridium rapidly decreases in abundance towards the top of Subzone 4 beta and does not occur in Subzone 4 alpha. Curiously, the Taman radiolarian fauna is poor in Mirifusus and completely lacks Ristola altissima, R. procera, Eucyrtidieium ptyctum, and Sethocapsa (?) celia, which are common, distinctive upper Tithonian elements elsewhere. This radiolarian fauna is associated with ammonites, calpionellids, and pectenaceans. It includes the Kossmatia-Durangites assemblage and the lower part of Substeueroceras-Prionoceras assemblage of Imlay (1980). Furthermore, the base of Zone 4 corresponds closely to the first occurrence of hyaline calpionellids. The radiolarian assemblage is correlated with radiolarian faunas in other areas, such as the Cape Verde Basin (East Atlantic) and Oman. Additionally, a new genus (Loopus, Family Pseudodictyomitridae), described herein from the Taman, bridges the correlation of Tithonian between North America and Japan.

Subfamilies Tetradiotriniacae Baumgartner and Higumastrinae Baumgartner are treated herein as synonyms on the basis of their internal test structure. Two new genera (Neoparanaella and Pseudohigumastra) of the Family Hagiastriadeia and one new genus (Tetrastrum) of Spumellarina family incertae sedis are erected herein.

The Acaeniotylidae, n. fam., is established herein to include a unique group of Radiolaria represented by the well-known genus Acaeniotype Foreman. The new family is characterized by having a tubercular cortical shell, a latticed medullary shell and a number (varying among genera) of secondary spines on the test surface. Three new genera (Acastea, Acusten and Praeconosphaera) of this family are erected herein, and Genus Acaeniotype Foreman is emended.

The following genera are common in the Taman (Zone 4): Acaeniotylidae, n. fam., Hagiastriadeia, Patulibrachchiidae, Hsuidae, Parvivaccidae, Parasaturnalidae (Acanthocircus), Epittingidae (Perispyridium), Archaeodictyomitridae, Pseudodictyomitridae, Syringocapsidae, Xiphostiidae, and Ultranaporidae (Napora).

Paleobiogeographically, the upper Tithonian Taman faunas described herein belong to the Northern Tethyan Province of Pessagno et al. (1987a), because of the common occurrence of both Pantanellidae and Parvicingula and the lack of Ristola.

Keywords Radiolaria, Upper Jurassic, east-central Mexico, Taman Formation
PART 1. INTRODUCTION

During the last twenty years, radiolarian studies have been undergoing a period of great intensification among research groups throughout the world. The results of these studies show that Radiolaria are not only an excellent biostratigraphic tool in Cenozoic (Riedel and Sanfilippo 1977; Sanfilippo et al. 1983), Mesozoic (Baumgartner 1984; Yao 1990; Pessagno et al. 1987b), and Paleozoic (Nodine-Zeller, Holdsworth and Jones 1980a, b), but also useful in paleogeographical reconstruction (Pessagno et al. 1984, 1986, 1987a; Yang 1991). Radiolaria are especially helpful in understanding the complexity of many eugeoclinal terranes such as the California Coast Ranges (Pessagno 1976, 1977a, b) and the eastern Asian continental margin (Mizutani and Kojima 1992; Yang and Mizutani 1991). These terranes are notorious for their lack of biostratigraphic controls; therefore, without the help of Radiolaria, their tectonic complexity often becomes a puzzle to geological investigations.

The purpose of this study was to describe, in detail, the upper Tithonian (Upper Jurassic) radiolarian faunas of the Taman Formation near Tamazuchale, east-central Mexico (Text-figures 1, 2), so as to reveal as many characteristics as possible of the upper Tithonian (Zone 4 sensu Pessagno et al. 1987b; Text-figure 4 herein) radiolarian fauna and, therefore, to provide the means for global biostratigraphic correlation of this zone.

This study is a continuation of the studies recently initiated by Pessagno and Longoria (Pessagno et al. 1984, 1986, 1987a, b, 1989; Yang and Pessagno 1989; Longoria 1984, 1985) on the Taman Formation. Abundant and diversified radiolarian faunas, ranging from Superzone 1 (upper part) to Subzone 4 alpha (sensu Pessagno et al. 1987b; Callovian to upper Tithonian), have since been discovered from the Taman. This report, however, focuses on the Zone 4 Radiolaria of the Taman Formation (upper Tithonian).

According to Pessagno et al. (1987a), the Radiolaria of the Taman Formation represent a Northern Tethyan assemblage, which contains many elements in common with those in the Boreal strata and with those in the Central Tethyan strata (sensu Pessagno et al. 1986, 1987a). This implies that there is great potential for the Taman radiolarian fauna to be used in biostratigraphic correlations among wide geographic areas.

This report consists of six parts and two appendices. Parts 2–6 are each devoted to a family or a group of families of Radiolaria from the upper Tithonian strata of the Taman Formation. The current section (Pt. 1) presents the general characteristics in lithostratigraphy and biostratigraphy of the radiolarian faunas under study. Following sections are arranged in this order: Pt. 2, Pantanellidae; Pt. 3, Hagiastridae and Patuliibrachiidae; Pt. 4, Xiphostylidae, Paravaccidaceae and Parasaturnalidae; Pt. 5, Acaniostylidae; and Pt. 6, Nassellariina.

Measurements under the systematic paleontology in the following chapters were made with an eyepiece micrometer mounted in a stereoscopic reflected light microscope. Standard deviation (SD) used throughout the systematic descriptions was calculated by

\[
SD^2 = \frac{[(X_1 - X_m)^2 + (X_2 - X_m)^2 + \ldots + (X_n - X_m)^2]}{n},
\]

where "X_m" stands for the mean and "n" for the number of specimens measured.

Zonal designations and faunal realms/provinces used throughout this report refer to those used by Pessagno et al. (1984, 1986, 1987a, b).
TEXT-Figure 1. Regional index map of study areas (modified from Pessagno et al. 1987a). Refer to Text-figure 2 for details.
Stratigraphic Summary

Middle (upper Bathonian or lower Callovian) and Upper Jurassic (Oxfordian to Tithonian) strata in east-central Mexico are part of a transgressive sequence that occurs above Middle Jurassic continental strata (Cahuasas Formation; Carrillo Bravo 1965) and below Cretaceous limestone platform strata (Ahuclatian Formation; Aptian to Cenomanian; Bondelos 1956; Longoria 1984; Suter 1987, fig 2-e). According to Longoria (1984), the transgressive cycle extended into the Early Cretaceous (Valanginian to Barremian). This sequence begins with Tepeix Calcarenite (upper Bathonian / lowermost Callovian; Erben 1956; Westermann 1984), followed by the "Sangtiago Formation" (Callovian to Oxfordian; Cantu Chapa 1969, 1971; Imlay 1980; see Longoria 1984 and Pessagno et al. 1987a for nomenclatural problems of this unit), the Taman Formation (Kimmeridgian to Tithonian), the Pimienta Formation (Berriasian; Heim 1926, 1940; Pessagno et al. 1987a), and the Chapulhuacan Formation (Berriasian to Aptian; Bondelos 1956; Longoria 1984). The whole sequence typically consists of black, clayey limestone, shale, and nodular limestone.

It has been suggested that the late Middle Jurassic (Callovian) to Early Cretaceous (Berriasian-Barremian) transgressive cycle in this part of the Sierra Madre Oriental represented a period of seafloor spreading that led to the opening of the Gulf of Mexico (Buffler et al. 1980; Longoria 1984, 1985).
TEXT-Figure 3. Composite stratigraphic column of the Taman Formation and approximate positions of the samples collected for this study. (1) Strata and samples above this line are located near Huauchinango (see Text-figure 1); those below this line represent the Taman-Tamazunchale area (Text-figure 2). (2) Samples collected along unpaved road above Barrio de Guadalupe (Text-figure 2). (3) Samples collected on the river of Moctezuma near Barrio de Guadalupe. "?" = samples collected at isolated localities; L.T. = lower massively bedded member of the Taman Formation. See Appendix 1 for details.
Lithostratigraphy

The Taman Formation (Heim 1926, 1940; Cantu Chapa 1969, 1971; Text-figure 3 herein) consists of interbedded dark gray shale and micritic limestone. Dark gray micritic limestone nodules, 7.6 cm (3 in.) to 90 cm (3 ft) in diameter, commonly occur in the upper half of the lower member and throughout the upper member. Both the bedded micritic limestone and the limestone nodules contain abundant Radiolaria.

At the type locality near the village of Taman (Text-figure 2), Pessagno et al. (1987a) divided the Taman Formation into two informal members: the lower massively bedded limestone member intercalated with a minor amount of shale and the upper thin member with thick intervals of shale (Text-figure 3).

The lower member of the Taman Formation is characterized by medium- to thick-bedded, dark gray to black micritic limestone, interbedded with thin layers of black shale; while the upper member is distinguished by thin-bedded, black, micritic limestone, interbedded with thick layers of black shale and siltstone. In addition, the upper member occasionally contains olistostromal masses, indicating deposition on a steep slope. The two component members of the Taman Formation are recognizable from the type area to as far south as the state of Puebla (Text-figure 1).

It has been estimated that the thickness of the Taman Formation ranges from 200 m (656 ft) to 500 m (1,640 ft; Erben 1956). However, as pointed out by Pessagno et al. (1987a), because some workers (e.g., Cantu Chapa 1971) included the upper member of the Taman Formation sensu Pessagno et al. (ibid.) in the Pimienta Formation, the actual thickness of the Taman Formation may be considerably greater. At the type locality, it is estimated that the upper thin-bedded member of the Taman alone is at least 150 m (480 ft) thick.

In the type area (Taman-Tamazunchale area, Text-figure 2), the Taman Formation conformably overlies the "Santiago Formation", which is characterized by black, often phyllitic shale with a minor amount of black, micritic, carbonaceous limestone beds and nodules. The Taman Formation is conformably overlain by the Pimienta Formation (sensu Pessagno et al. 1987a), which consists of thin-bedded, gray (weathering maroon), micritic limestone interbedded with black shale, chert, and occasional green vitric tuff.

Nomenclatural problems pertaining to the Taman Formation and underlying and overlying units are discussed by Longoria (1984) and Pessagno et al. (1987a).

This study focuses on the uppermost portion of the lower member (from 6 meters below the contact with the upper member) and the upper member of the Taman Formation (upper Tithonian sensu Pessagno et al. 1984, p. 7).

Biostratigraphy

Ammonites occur in the lower Kimmeridgian to upper Tithonian strata of the Taman Formation as well as in the Oxfordian strata of the underlying "Santiago Formation" and in the Berriasian strata of the overlying Pimienta Formation (Burckhardt 1930; Erben 1956; Cantu Chapa 1969, 1971, 1976; Imlay 1939, 1980; Pessagno et al. 1987a). Radiolaria are the most abundant microfossils in the Taman Formation. Calcipellids and nannoconodds are common at some horizons (Pessagno et al. 1984).
<table>
<thead>
<tr>
<th>Chrono-stratigr.</th>
<th>Bio-strat.</th>
<th>Primary marker taxa</th>
<th>Supplementary marker taxa</th>
</tr>
</thead>
<tbody>
<tr>
<td>L.K. Berri. Z.5</td>
<td>Subzone 4 α Sz. 5A</td>
<td>Obesacapsa rotunda</td>
<td>(see Pessagno, 1977b)</td>
</tr>
</tbody>
</table>

**TEXT-FIGURE 4.** Primary and supplementary marker taxa of Zone 4, Subzones 4 α and 4 β of Pessagno et al. (1987b).

In the Taman-Tamazunchale area, the lower massively bedded member of the Taman Formation is assignable to the Ataxioceras (lower Kimmeridgian), Idoceras (uppermost lower Kimmeridgian), Glochiceras gp. fialar (upper Kimmeridgian), and Virgatosphinxites mexicanus-Aulacomyella neogaea (lower to upper Tithonian) zones of Cantu Chapa (1971). Furthermore, Longoria (in Pessagno et al. 1984) discovered the calpionellid Crassicollaria intermedia in the uppermost 6 m (19.7 ft) of the lower member; these strata also contain Subzone 4 β Radiolaria (Pessagno et al. 1987b).

Pessagno et al. (1984, p. 7) used the first occurrence of hyaline calpionellids (such as Crassicollaria Lorenz) to mark the base of the upper Tithonian. Therefore, the upper 6 m of the lower massively bedded member of the Taman Formation are assignable to upper Tithonian as so defined.

In the type area, the upper thin-bedded member of the Taman Formation contains Mazapilites Burckhardt and Aulacomyella neogaea Imlay in the lower 30 m (96.8 ft). From 62 m (204 ft) above the contact between the lower and upper members to near the contact between the Taman and Pimienta Formations, Salinites grassiumatum (Imlay) is commonly present. Pessagno et al. (1987a) correlated the upper 6 m interval of the lower member and the lower 61 m of the upper member with
Imlay's *Substeueroceras-Proniceras* Assemblage. Radiolaria are very abundant and diversified in the upper member of the Taman Formation as well as in the lower member. They are present in both the limestone nodules and the micritic limestone beds. Unfortunately, many samples contain Radiolaria that are calcified and difficult to extract from the matrix. Some samples, however, contain silicified or pyritized Radiolaria, which are often well-preserved and diversified.

On the basis of co-occurring ammonites and calpionellids, the radiolarian assemblage from the uppermost 6 m portion of the lower Taman and all of the upper Taman in Taman-Tamazunchale area is assignable to Subzone 4 beta (Pessagno et al. 1984, 1987a, b; see Text-figure 4 herein). Subzone 4 alpha Radiolaria are found in the upper thin-bedded member of the Taman Formation at a locality near Huauchinango, Puebla (Text-figure 1; also refer to Appendix I).

**Faunal Characteristics**

**ABUNDANT AND DIVERSIFIED PANTANELLIIDAE:** Pessagno et al. (1987a) used the abundance and diversity of the Pantanellidae as one of the criteria to distinguish the Tethyan Faunal Realm from the Boreal Faunal Realm. They (ibid., p. 6) pointed out that the diversity of the Pantanellidae is three to four times greater in the Northern Tethyan samples than it is in the Southern Boreal samples. According to this study, the upper Tithonian radiolarian fauna (Northern Tethyan sensu Pessagno et al., ibid.) extracted from the Taman Formation contains at least thirty-three species level taxa which belong to the family of Pantanellidae. Characteristically, this fauna contains abundant and diversified pantanellid subfamily Vallupinae (Pessagno and MacLeod 1987; Yang and Pessagno 1989) as well Subfamily Pantanelliniaceae (Pessagno 1977b; Pessagno and Blome 1980).

**POOR IN MIRIFUSUS:** *Mirifusus* Pessagno is a common, distinctive genus in Upper Jurassic and lowermost Cretaceous strata of both the Tethyan and Boreal Realms (Pessagno et al. 1984, 1987b). However, only fragments of *Mirifusus* have been found in the Taman Formation. At present, it is unclear why such is the case. However, factors such as water depth and/or other oceanographic attributes may have contributed to the peculiarity of this radiolarian fauna; further studies in paleoecology and/or sedimentary environment of the Taman are necessary.

**LACK OF RISTOLA ALTISSIMA, R. PROCERA, AND EUCYRTIDIUM PTYCTUM:** These taxa are completely absent in the upper Tithonian strata of the Taman Formation; however, they are common in the upper Tithonian strata in other regions. *Ristola altissima* (Rüst) and *R. procera* (Pessagno) occur in both the Tethyan and Boreal Realms (Pessagno et al. 1984, 1986, 1987a, b). Their absence in the Taman Formation may also be paleoenvironmentally controlled. Likewise, the absence of *Eucyrtidiellum ptyctum* (Riedel and Sanfilippo) in the Taman fauna is equally enigmatic; this species makes its final occurrence in the upper part of upper Tithonian worldwide (Pessagno et al. 1984, 1987b; Baumgartner 1984).

It is suggested that the lack of *Mirifusus, Ristola altissima, R. procera* and *Eucyrtidiellum ptyctum* in the upper Tithonian strata of the Taman Formation could possibly be paleobathymetrically related, although the specific parameters of the depositional environment of the Taman need to be studied. In other words, these radiolarian taxa might be stenobathic, lower bathyal to abyssal organisms that were not distributed in shallower waters such as where the Taman Formation was deposited. The aforementioned radiolarian taxa have unusually thick shells which, like certain types of planktonic foraminifers, may have served as a ballast mechanism for floating at greater depths in the water column.
Correlation with Other Areas

DSDP Site 367 (Foreman 1978; Cape Verde Basin, off NW coast of Africa)

Zone 4 Radiolaria of the Taman Formation are correlative with the interval from 37-1 (80-82 cm) to 34-4 (104-108 cm; in Foreman, ibid.) of DSDP Site 367. This correlation is supported by the following lines of evidence: (1) Emulivia hopsoni Pessagno and Podocapsa amphitreptera Foreman co-occur in both the Zone 4 strata (Subzone 4 beta) and the DSDP Site 367 interval cited above. Both species are morphologically distinctive. In North America, Emulivia hopsoni does not extend above the top of Zone 4 (upper Tithonian sensu Pessagno et al. 1984), while Podocapsa amphitreptera does not range below the base of Zone 4. (2) Acanthocircus dicanocanthos (Squinabol) occurs in both the correlated intervals but not below. It has been used as a primary marker taxon for defining the base of Zone 4 (Pessagno et al. 1984, 1987a, b). (3) The DSDP 367 interval (see above) occurs immediately below the first occurrence of Obesacapsula rotunda (Hinde), a marker taxon of Zone 5 (Lower Cretaceous: Berriasian-Valanginian) of Pessagno (1977b).

It is worth noting that the form herein referred to as Podocapsa sp. cf. amphitreptera (see pl. 23, figs. 12, 16) also occurs in the DSDP interval cited above (see Foreman 1978, pl. 1, fig. 16). Data from Oman (Tippit 1981), DSDP (Foreman 1978), and east-central Mexico (this study, see below) show that this species occurs in the upper Tithonian strata only.

It is not clear, however, whether Foreman's 367-34-4 to 367-35-2 interval belongs to Subzone 4 alpha or to Subzone 4 beta (Text-figure 4), because Foreman did not document any Peripsyridium Dumitrica in that fauna.

Oman (Tippit 1981)

OM 191 (sample locality of Tippit, ibid.) of the Halfa Formation, Oman, is correlated here with the Zone 4 radiolarian fauna of the Taman Formation. The common and distinctive elements are Podocapsa sp. cf. amphitreptera (see discussion above), Acanthocircus dicanocanthos (Squinabol), Loopus sp. B (pl. 23, fig. 9 herein; Tippit 1981, p. 329, pl. 7, fig. 9), and Acaenioptyle umbilicata Foreman. The fact that Peripsyridium Dumitrica does not occur in the Halfa radiolarian fauna (Tippit 1981, p. 214), coupled with the presence of Acanthocircus dicanocanthos, Eucyrtidiellum pytctum and Ristola altissima, indicates that the biostratigraphic position of Tippit's OM 191 is equivalent to Subzone 4 alpha (sensu Pessagno et al. 1987b; Text-figure 4 herein). The Halfa radiolarian fauna of Tippit is of the Central Tethyan Province (sensu Pessagno et al. 1987a), evidenced by the presence of common Pantanelliidae and the total lack of Parvicingula Pessagno (sensu Pessagno and Whalen 1982).

It is worth noting that Loopus primitivus (Matsuoka and Yao) figured herein (Part 6) from the Taman Formation is also present in the Tithonian strata of Japan (Pseudodictyomitra primitiva Zone of Matsuoka and Yao 1986). Pessagno and Mizutani (1992) correlate this Japanese zone with the upper part of Subzone 3 alpha (sensu Pessagno et al. 1987b). Recent results indicate that upper Tithonian Radiolaria may occur in northeast Japan (Kato and Iwata 1989).

Recent development in radiolarian studies in Argentina (Pajuna 1988) indicates that the North America-based Zone 4 Radiolaria, represented by the Vallupus hopsoni assemblage, also occurs in South America (the Austral Faunal Realm; Pessagno, verbal communication).
Although studies of upper Tithonian Radiolaria on a global scale are still in their infancy, data now available indicate that Radiolaria will be quite useful for chronostratigraphic correlation among the Tethyan, Boreal and Austral Faunal Realms.

PART 2. PANTANELLIIDAE

Introduction

The family Pantanelliidae Pessagno (1977b) are not only biostratigraphically important (Blome 1984; Pessagno et al. 1987a, b), but also useful in paleolatitudinal reconstruction (Pessagno et al. 1984, 1986, 1987a). They are diversified and abundant in the Upper Triassic (Blome, ibid.), Jurassic (Pessagno et al. 1987a; Yang and Pessagno 1989), and Cretaceous (Pessagno 1977b) radiolarian faunas of the Tethyan Realm (sensu Pessagno et al., ibid.). Pessagno et al. (1987a, fig. 3) used the abundance and diversity of the Pantanelliidae as a main criterion to distinguish the Tethyan Faunal Realm from the Boreal Faunal Realm.

Pessagno et al. (1987a) presented a systematic study of the Upper Jurassic (Kimmeridgian to Tithonian) Pantanelliidae from the Taman Formation, east-central Mexico. The present study, however, focuses on the Pantanelliidae in the upper Tithonian strata (Zone 4 of Pessagno et al. 1987b) of the Taman Formation. This study is largely based on new samples collected by Dr. E. A. Pessagno, Jr., and the present author during 1985; however, samples collected by Dr. E. A. Pessagno, Jr. and Dr. J. F. Longoria (Univ. Texas, Dallas) during 1982 to 1984 were also analyzed. A closer examination of these additional upper Tithonian samples from the Taman Formation has revealed a surprisingly diversified assemblage of the Pantanelliidae, especially the subfamily Vallupinacea Pessagno and MacLeod (1987).

Data collected for this study indicate that the Vallupinacea reached its acme of development during early late Tithonian times (Subzone 4 beta of Pessagno et al. 1987b) in North America. It is anticipated that this event can be used in the future for global biostratigraphic correlation of the upper Tithonian bathyal and abyssal strata within the Tethyan, the Boreal (Southern Boreal Province), and the Austral Realms (refer to Yang and Pessagno 1989).

The subfamily Pantanelliinae uncovered from the upper Tithonian strata of the Taman Formation are described and illustrated herein. Text-figures 5 and 6 show the occurrences and ranges, respectively, for the Pantanelliinae of the upper Tithonian Taman radiolarian fauna. The Tithonian Vallupinacea from the Taman Formation were reported by Yang and Pessagno (1989); their occurrence in the Taman Formation is presented in Text-figure 8, but their detailed systematic description is omitted (refer to Yang and Pessagno 1989).

Systematic Paleontology

Class ACTINOPODA
Subclass RADIOLARIA
Order POLYCYSTIDA
Suborder SPUMELLARIINA
Superfamily LIOSPHERACEA
Subsuperfamily LIOSPHERILAE
Family PANTANELLIIDAE Pessagno 1977b; sensu Pessagno and Blome 1980

Type genus: Pantanellium Pessagno 1977a.

Remarks: As originally defined by Pessagno (1977b, p. 32), this family is characterized by possessing a latticed cortical shell and a single latticed medullary shell, both with nodes developed at pore frame vertices. Secondary radial beams connect the cortical shell to the medullary shell at nodal points. Primary radial beams connect directly with primary spines on the exterior of the cortical shell.

Three subfamilies have been established within this family: (1) Pantanelliniinae Pessagno (1977b; emend. Pessagno and Blome 1980), (2) Capnodocininae Pessagno (1979; emend. Blome 1984), and (3) Vallupinae Pessagno et al. (1987a). The subfamilies Pantanelliniinae and Vallupinae are discovered from the Taman.


Subfamily PANTANELLIINAE Pessagno 1977b; sensu Pessagno and Blome 1980

Type genus: Pantanellium Pessagno 1977a.

Range and occurrence: Same as for family.

Genus Gorgansium Pessagno and Blome 1980

Type species: Gorgansium silviesense Pessagno and Blome 1980.

Remarks: Several morphological forms occur sporadically in the Taman Formation; they are figured but unnamed herein due to their rare occurrence.

Range and occurrence: Upper Triassic (Carnian) to Upper Jurassic (upper Tithonian) or higher. Central Tethyan Province to Southern Boreal Province.

Gorgansium spp.

Plate 1, figures 7, 8, 13, 17, 19, 23; plate 2, figures 8, 13, 14, 17, 23


Genus Pantanellium Pessagno 1977a; sensu Pessagno and Blome 1980

Type species: Pantanellium riedeli Pessagno 1977a.

Range and occurrence: Same as for family and subfamily.

Pantanellium cantuchapai Pessagno and MacLeod

Plate 2, figures 12, 18

Pantanellium cantuchapai PESSAGNO and MACLEOD 1987, p. 20, pl. 1, figs. 8, 9, 13-15, 22; pl. 7, fig. 2.
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<td>Pantanellium westermannii</td>
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<td>Pantanellium sp. B</td>
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■ = ABUNDANT; ■■■■ = COMMON; ■■■■■■ = RARE; □ = ABSENT.

**TEXT-Figure 5.** Occurrence and relative abundance of Pantanellinae from the upper Tithonian strata of the Taman Formation. Rare = 1–2 specimens; common = 3–6 specimens; abundant = more than 6 specimens.

**Remarks:** Pantanellium cantuchapai Pessagno and MacLeod is distinguished from Pantanellium westermannii Pessagno and MacLeod by having much longer polar spines.

**Range and occurrence:** Zone 4, Subzone 4 beta; upper Tithonian. Upper thin-bedded member of Taman Formation, east-central Mexico. Text-figures 5 and 6.
= range,  
? = uncertain first or last occurrence.  
* = range extending beyond this point.

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<tr>
<td>Pantanellium spp.</td>
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**Pantanellium deflectum**, n. sp.  
Plate 1, figures 10, 11, 15, 18, 24; plate 2, figures 7, 20

*Description*: Cortical shell subspherical, with a mixture of hexagonal and pentagonal pore frames. Well-developed and rounded nodes present at vertices of pore frames. Two polar spines unequal in length and obliquely (rather than directly) opposed to each other. Shorter spine very massive, subparallel-sided for proximal two thirds or more, then rapidly decreasing in width distally; longer spine less massive, gradually decreasing in width in distal direction, and sharply pointed. Both spines with three wide, rounded longitudinal ridges alternating with three narrow longitudinal grooves.

*Remarks*: Pantanellium deflectum, n. sp., is the only species of the genus, so far as known, which possesses two obliquely opposed massive polar spines.

*Etymology*: Deflectus-a-um (Latin, adj.) = bending or turning aside.

*Measurements* (μm): Holotype + 9 paratypes. See Text-figure 7 for system of measurements.

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*Deposition of types*: Fossil Depository of Nanjing Institute of Geology and Palaeontology.

**Pantanellium formosum, n. sp.**

Plate 1, figures 2, 21, 26; plate 2, figures 10, 25

Pantanellium sp. E PESSAGNO et al. 1987a, p. 26, pl. 2, figs. 6, 15, 21.

Description: Cortical shell subspherical, composed of a mixture of hexagonal and pentagonal pore frames. Weakly developed nodes present at vertices of each pore frame. Two polar spines very massive, unequal in length, parallel-sided on proximal two-thirds or so, and then rapidly decreasing in width distally. Shorter spine with three massive and rounded longitudinal ridges alternating with three deep and narrow longitudinal grooves; longer spine with longitudinal ridges and grooves of about similar width.

Remarks: This species differs from *Pantanellium riedeli* Pessagno (1977a, p. 78, pl. 6, figs. 5-11) in possessing more massive polar spines and a more rounded cortical shell. However, the two species share a weakly nodose, medium-sized cortical shell and two moderately massive polar spines. It is, therefore, probable that *Pantanellium formosum, n. sp.*, was derived from *P. riedeli*.

Etymology: Formosus-a-um (Latin, adj.), finely formed.

Measurements (µm): Holotype + 9 paratypes. See Text-figure 7 for system of measurements.

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<thead>
<tr>
<th></th>
<th>Holotype</th>
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Type locality: MX-85-25 (see Appendix I).

Deposition of types: Fossil Depository of Nanjing Institute of Geology and Palaeontology.
**Range and occurrence:** Zone 4, Subzone 4 beta; upper Tithonian. Taman Formation, east-central Mexico. Text-figures 5 and 6.

**Pantanellium** sp. cf. *formosum*, n. sp.
Plate 1, figure 4; plate 2, figures 5, 9, 24

**Remarks:** This form differs from *Pantanellium formosum*, n. sp., in having well-developed nodes at the vertices of the pore frames.

**Range and occurrence:** Zone 4, Subzone 4 beta; upper Tithonian. Taman Formation, east-central Mexico. Text-figure 5.

**Pantanellium heimi** Pessagno and MacLeod
Plate 1, figures 3, 16, 20

**Pantanellium heimi** PESSAGNO and MACLEOD 1987, p. 20, pl. 1, figs. 5, 6, 17–21, 24.

**Range and occurrence:** Zone 4, Subzone 4 beta; upper Tithonian. Upper thin-bedded member of Taman Formation, east-central Mexico. Text-figures 5 and 6.

**Pantanellium meraceibaense** Pessagno and MacLeod
Plate 2, figures 6, 22

**Pantanellium meraceibaense** PESSAGNO and MACLEOD 1987, p. 22, pl. 5, figs. 5, 6, 18, 19; pl. 7, fig. 4.

**Range and occurrence:** Zone 1 (uppermost part) to Zone 4, Subzone 4 beta; lower Kimmeridgian to upper Tithonian. Lower and upper members of Taman Formation, east-central Mexico. Text-figures 5 and 6.

**Pantanellium parvulum** Pessagno and MacLeod
Plate 2, figures 2, 15

**Pantanellium parvulum** PESSAGNO and MACLEOD 1987, p. 22, pl. 1, fig. 2; pl. 5, figs. 12, 17; pl. 7, fig. 8.

**Range and occurrence:** Zone 2, Subzone 2 beta to Zone 4, Subzone 4 alpha; upper Kimmeridgian to upper Tithonian. Lower and upper members of Taman Formation, east-central Mexico. Text-figures 5 and 6.

**Pantanellium quintachillaense** Pessagno and MacLeod
Plate 2, figures 4, 21

**Pantanellium quintachillaense** PESSAGNO and MACLEOD 1987, p. 23, pl. 5, figs. 7, 9, 13, 15; pl. 7, fig. 3.

**Remarks:** This species appears to be closely related with *Pantanellium tierablancaense* Pessagno and MacLeod (1987, p. 24, pl. 6, figs. 5, 7, 8, 13–18).

**Range and occurrence:** Zone 2, Subzone 2 beta to Zone 4, Subzone 4 beta; upper Kimmeridgian to upper Tithonian. Lower and upper members of Taman Formation, east-central Mexico. Text-figures 5 and 6.
**Pantaneillium ranchitoense** Pessagno and MacLeod
Plate 1, figure 6; plate 2, figure 3

**Pantaneillium ranchitoense** PESSAGNO and MACLEOD 1987, p. 23, pl. 1, figs. 1, 25; pl. 5, figs. 4, 8, 22; pl. 7, fig. 6.

**Range and occurrence:** Zone 2, Subzone 2 beta to Zone 4, Subzone 4 beta; upper Kimmeridgian to upper Tithonian. Lower and upper members of Taman Formation, east-central Mexico. Text-figures 5 and 6.

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**Pantaneillium westermanni** Pessagno and MacLeod
Plate 2, figure 11

**Pantaneillium westermanni** PESSAGNO and MACLEOD 1987, p. 24, pl. 1, figs. 4, 12, 16; pl. 2, fig. 1.

**Range and occurrence:** Zone 4, Subzone 4 beta; upper Tithonian. upper Tithonian. Upper thin-bedded member of Taman Formation, east-central Mexico. Text-figures 5 and 6.

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**EXPLANATION OF PLATES**

All figures are scanning electron micrographs of upper Tithonian (Zone 4; Upper Jurassic) Radiolaria from the Taman Formation. Scale of each plate = number of microns (µm) cited for each figure.

**PLATE 1**

Pantaneillinae from the Taman Formation, east-central Mexico.

1, 9, 14, 25. **Pantaneillium whalenae** Pessagno and MacLeod.
Views of the same specimen. MX-84-8, lower Taman. Scale = 87.5, 33.0, 41.4, 33.0 µm.

2, 21, 26. **Pantaneillium formosum**, n. sp.
MX-84-8, lower Taman. Scale = 76.8, 41.7, 41.7 µm. Nontype.

3, 16, 20. **Pantaneillium heimi** Pessagno and MacLeod.
MX-85-4, upper thin-bedded member. Scale = 82.8, 38.7, 38.7 µm.

4. **Pantaneillium** sp. cf. *formosum*, n. sp.
MX-84-8, lower massively bedded member. Scale = 85.7 µm.

5, 12, 22. **Pantaneillium** sp. B.
MX-85-12, upper thin-bedded member. Scale = 70.9, 33.3, 41.4 µm.

6. **Pantaneillium ranchitoense** Pessagno and MacLeod.
MX-84-8, lower massively bedded member. Scale = 52.8 µm.

7, 17. **Gorgansium** sp.
Views of the same specimen. MX-84-13, upper Taman. Scale = 120.0, 47.8 µm.

8, 19, 23. **Gorgansium** sp.
Views of the same specimen. MX-84-8, lower massively bedded member. Scale = 75.0, 30.6, 41.4 µm.

10, 11, 15, 18. **Pantaneillium deflectum**, n. sp.
MX-84-8, lower Tamän. Figs. 10, 15, 24 = holotype; scale = 72.9, 39.8, 39.8 µm. Figs. 11, 18 = paratype; scale = 83.3, 53.6 µm.

13. **Gorgansium** sp.
MX-84-8, lower massively bedded member. Scale = 81.0 µm.
**Pantanellium whalenae** Pessagno and MacLeod
Plate 1, figures 1, 9, 14, 25

**Pantanellium whalenae** PESSAGNO and MACLEOD 1987, p. 25, pl. 2, figs. 1-3, 10-13, 18, 24.


**Pantanellium** sp. A
Plate 2, figures 1, 16, 19

Remarks: This form is characterized by having a peculiar polar spine (the longer one) which has three very wide, parallel-sided longitudinal grooves alternating with three narrow longitudinal ridges. The longitudinal grooves on the longer spine remain open throughout and the ridges are not converged at the spinal tip.

*Range and occurrence:* Zone 4, Subzone 4 beta; upper Tithonian. Upper thin-bedded member of Taman Formation, east-central Mexico. Text-figure 5.

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**PLATE 2**

Pantanellinae from the upper thin-bedded member of the Taman Formation.

1, 16, 19. **Pantanellium** sp. A.
Views of the same specimen. MX-85-25. Scale = 75.6, 48.5, 31.7 μm.

2, 15. **Pantanellium parvulum** Pessagno and MacLeod.
MX-85-23. Scale = 58.6, 39.0 μm.

3. **Pantanellium ranchitoense** Pessagno and MacLeod.

4, 21. **Pantanellium quintachilense** Pessagno and MacLeod
Views of the same specimen. MX-85-25 = 83.3, 39.0, 50.3 μm.

5, 9, 24. **Pantanellium** sp. cf. *formosum*, n. sp.
Views of the same specimen. MX-85-25 = 83.3, 39.0, 50.3 μm.

6, 22. **Pantanellium meraceibaense** Pessagno and MacLeod.
Views of the same specimen. MX-85-23. Scale = 81.1, 47.1 μm.

7, 20. **Pantanellium deflectum**, n. sp.
Views of the same specimen (nontype). MX-85-26. Scale = 88.2, 54.5 μm.

8, 17. **Gorgansium** sp.
Views of the same specimen. MX-85-23. Scale = 78.9, 48.8 μm.

10, 25. **Pantanellium formosum**, n. sp.
Holotype. MX-85-25. Scale = 59.4, 40.0 μm.

11. **Pantanellium westermanni** Pessagno and MacLeod.
MX-85-25. Scale = 50.9 μm.

12, 18. **Pantanellium cantuchapai** Pessagno and MacLeod.
Views of the same specimen. MX-85-24. Scale = 83.3, 57.7 μm.

13, 14, 23. **Gorgansium** spp.
Fig. 13 from MX-85-25; scale = 87.5 μm. Figs. 14, 23 = views of another specimen; MX-85-26; scale = 87.7, 56.0 μm.
TEXT-Figure 8. Occurrence and relative abundance of Vallupinae from the upper Tithonian strata of the Taman Formation. Rare = 1–2 specimens; common = 3–6 specimens; abundant = more than 6 specimens (after Yang and Pessagno 1989).

**Pantanellium** sp. B
Plate 1, figures 5, 12, 22

Pantanellium sp. H PESSAGNO et al. 1987a, pl. 2, figs. 9, 22.
Range and occurrence: Zone 4, Subzone 4 beta; upper Tithonian. Upper thin-beded member of Taman Formation, east-central Mexico. Text-figure 5.

Remarks: This form is characterized by having a medium-sized cortical shell with numerous small, cylindrical nodes at the pore frame vertices, and two unequal polar spines (the shorter one being extremely massive).

Subfamily VALLUPINAE Pessagno and Macleod 1987a; emend. Yang and Pessagno 1989

Type genus: Vallupus Pessagno and Blome 1984.

Remarks: The Vallupinace from the Taman Formation is described in detail by Yang and Pessagno (1989). Therefore, systematic descriptions for this subfamily is omitted here; Text-figure 8 shows their occurrence in the Taman Formation. It is noted that since the publication of Yang and Pessagno (1989), the Vallupinace have also been discovered from Upper Jurassic strata in Japan (Kato and Iwata 1989) and west Pacific Ocean (Matsuoka 1992).

PART 3. HAGIASTRIDAE AND PATULIBRACCHIIDAE

Introduction

The Hagiastridae Haeckel and Patulibrachiidae Pessagno have been meticulously analyzed by Baumgartner (1980) on the basis of internal skeletal structure as well as external morphology. The systematic classification thereby proposed by Baumgartner has been widely adopted. Baumgartner (1980) separated the Hagiastridae Riedel sensu Baumgartner (1980) from the Patulibrachiidae Pessagno sensu Baumgartner, and established that the two families belong to different superfamilies.

The Hagiastridae have a latticed cortical shell and a discrete medullary shell, the two being connected to each other by subsidiary beams (refer to Baumgartner 1980, text-fig. 3, A) and separated by the cortical spaces (loc. cit.). Therefore, the Hagiastridae belong to Superfamily Liiphaeracea Haeckel sensu Pessagno and Blome (1980) (= Actinommacea of European workers). On the other hand, the Patulibrachiidae have a test with no discrete medullary shell. Instead, the internal structure of the Patulibrachiidae is homogenous with no differentiation of hollow canals, cortical spaces, or primary beams. Thus, this family is included in Subsuperfamily Pseudoaulophacielae Riedel sensu Pessagno (1971) of Superfamily Spongodiscacea Haeckel sensu Pessagno (1971, 1973).

The upper Tithonian strata of the Taman Formation, east-central Mexico, contain abundant and diversified hagiastrids and patulibrachiids, including four subfamilies, thirteen genera (three new), and thirty-seven species (ten new). Text-figures 9 and 10 show occurrence and relative abundance of the Hagiastridae and Patulibrachiidae discovered from the Taman (Zone 4), figured herein (pls. 3-7). Stratigraphic ranges of selected hagiastrid and patulibrachiid taxa are shown in Text-figure 11. See Appendix I for descriptions of all sample localities cited below (prefixed with MX-).
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- **ABUNDANT**:
- **COMMON**:
- **RARE**:
- **ABSENT**:

TEXT-Figure 9. Occurrence and relative abundance of Hagiastridae in the upper Tithonian strata of the Taman Formation. Rare = 1–2 specimens; common = 3–6 specimens; abundant = more than 6 specimens.
## Lithostratigraphic Units

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**TEXT-Figure 10.** Occurrence and relative abundance of Patulibrachiidae in the upper Tithonian strata of the Taman Formation. Rare = 1–2 specimens; common = 3–6 specimens; abundant = more than 6 specimens.

- **ABUNDANT:**
- **COMMON:**
- **RARE:**
- **ABSENT:**
Relationship between Tetradytryminae and Higumastrinae

Baumgartner (1980) divided the Hagiastridae into four subfamilies on the basis of symmetry displayed by the cross-section of the rays. Likewise, the Patulibracchiidae are divided into two subfamilies according to the cross-section of their rays (Baumgartner 1980, text-fig. 8). While most of the subfamilies, as defined by Baumgartner, can be followed and are used here, this study indicates that the establishment of Subfamily Tetradytryminae Baumgartner (1980), including one genus (Tetradytryma Baumgartner), is unnecessary. The genus Tetradytryma Baumgartner is, instead, included here within Subfamily Higumastrinae Baumgartner (1980), and the name Tetradytryminae Baumgartner is treated as a subjective synonym of Higumastrinae Baumgartner.

According to Baumgartner (1980), Tetradytryma differs from Pseudocrucella Baumgartner (Subfamily Higumastrinae) in that the former genus has a single median external beam and two lateral external beams on the ray, while Pseudocrucella possesses multiple median external beams; consequently, the internal skeletal structures are also different. However, two related morphotypes (Pseudocrucella sp. and Tetradytryma(?) sp.; see below) extracted from the Taman suggest that Tetradytryma and Pseudocrucella are more closely related than implied by Baumgartner's (1980) classificatory scheme.

| = range. |
| ? = uncertain first or last occurrence. |
| * = range extending beyond this point. |

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<td>Santonaella obesa, n. sp.</td>
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in which the two genera are placed under different subfamilies. The two transitional forms possess characteristics of both genera cited above. *Pseudocrucella* sp. (pl. 4, figs. 8, 19) possesses one ray with a single, massive median external beam on the top and bottom surfaces, and other three rays having two to three tenuous median external beams, while *Tetraditryma* (?) sp. (pl. 7, figs. 9, 17, 20) possesses four rays with one median external beam on the distal part of each ray but two to three tenuous median beams on the proximal part. This indicates a morphological transition from *Pseudocrucella* to *Tetraditryma* through the change from multiple tenuous median external beams to one massive median external beam and related internal modifications. Therefore, the subfamilial characteristics described by Baumgartner (1980) for Tetraditryminae Baumgartner are considered here as only of generic importance.

**Spongy versus Latticed Shell**

The relationship between spongy and latticed shell structures among Hagiastridae and Patulibrachiidae is essential to understanding the phylogenetic relationship between the two families. As pointed out by Baumgartner (1980), Kozur and Mostler (1979) questioned the supra-generic importance of latticed *versus* spongy pore frames among the ray-forming spumellarians. Kozur and Mostler (ibid.) found that some Paleozoic and Mesozoic genera contain both forms with latticed shells and forms with spongy shells. In this study, it is found that both linear and geometric pore frames and spongy (i.e., triangular) pore frames may be present in one species, even in one individual (e.g., pl. 4, fig. 8), and that some species may be considered as having a transitional shell between spongy and latticed. It is also apparent that external geometric and linearly arranged pore frames do not always correspond to the existence of an internal discrete medullary shell; likewise, external irregularly shaped and arranged pore frames are not always indicative of an internal spongy structure.

A typical spongy shell, however, is usually characterized externally by dominant triangular pore frames with tenuous bars, quintuple (five-way) and sextuple (six-way) junctures (instead of triple and cross junctures), and pronounced nodes at the junctures (e.g., *Crucella angulata*, n. sp., pl. 4, figs. 3, 4, 20, 24). A latticed shell, on the other hand, may possess some tenuous triangular pore frames with nodes developed at vertices, but is always dominated by larger quadrangular, pentagonal or hexagonal pore frames (e.g., *Pseudocrucella haekeli*, n. sp., pl. 3, figs. 2, 12, 14-16, 18, 20). It is curious to note that *Crucella angulata*, n. sp., which is a spongy species, may develop some larger rectangular pore frames at distal part of each ray (pl. 4, fig. 4; pl. 5, fig. 2), resembling *Pseudocrucella haekeli*. As pointed out above, *Pseudocrucella haekeli*, n. sp., also possesses some sponge-like pore frames on its test surface. It is, therefore, inferred that these two species, one with a spongy shell and the other with a latticed shell, are phylogenetically related: *Pseudocrucella haekeli* may have been derived from a *Crucella angulata*-like ancestor. If this postulation is correct, one may assume that at least part of the Hagiastridae have evolved from the Patulibrachiidae.

It is likely that Hagiastridae may have multiple origins, such as an *Emiluvia*-like ancestor, a hypothesis first suggested by Baumgartner (1980, p. 284) and also supported by evidence found in this study (see *Pseudohigumastra* sp. cf. *minuta* below).

Criteria for subdivisions within Hagiastridae and Patulibrachiidae are summarized in Text-figure 12. Terminology used in this report follows Baumgartner (1980).
Subfamily HAGIASTRINAE Riedel 1971; emend. Baumgartner 1980

**Type genus:** Hagiastrium Haeckel 1881.

**Remarks:** This subfamily is characterized by possessing rays circular to subcircular in cross-section, with three or more radial-symmetrically arranged primary canals. Genera included are Hagiastrium Haeckel sensu Baumgartner (1980), Archaeohagiastrum Baumgartner (1984), Homoeoparonaella Baumgartner (1980), Neoparonaella, n. gen., and Didactylum Baumgartner (1980).

**Range and occurrence:** Lower Jurassic (lower Sinemurian or lower) to Lower Cretaceous. Worldwide.

Genus *Archaeohagiastrum* Baumgartner 1984

**Type species:** *Archaeohagiastrum minitum* Baumgartner 1984.

**Remarks:** This genus is distinguished by possessing four rays which are arranged at right angles to each other in one plane, each with six external beams enclosing one internal beam. It differs from *Tetratrabs* Baumgartner in its simpler internal structures.

**Range and occurrence:** According to Baumgartner (1984), this genus ranges from Sinemurian or lower to Callovian in Europe and west Atlantic basin (Blake Bahama Basin, DSDP Leg 76). In this
study, new species are found in the Taman Formation, east-central Mexico, thus extending the generic range to the Tithonian.

*Archaeohagiastrum exile*, n. sp.
Plate 5, figures 6, 16, 19; plate 7, figures 1, 13, 23

*Description*: Four rays equal or subequal in length. Very narrow and slender, parallel-sided. Each ray with a massive, long and triradiate spine at distal end. Six external beams massive and straight, each connected to adjacent beams by short bars, forming large, regular rectangular pore frames. Medium-sized nodes present at vertices of pore frames. Fourteen to twenty pore frames present along axis of each ray. Central area very small, composed of several irregular pore frames.

*Remarks*: This species is distinguished by possessing exceptionally narrow, slender, and parallel-sided rays, each with a massive spine at the end. It is noted that a form documented by Baumgartner (1984, p. 767, pl. 4, figs. 8, 9) as Hagiastrid sp. A has the same type of ray (i.e., very narrow and long with six straight external beams). Baumgartner (ibid.) related his Hagiastrid sp. A with a single-ray genus; however, it is probable that his species is closely affiliated with *Archaeohagiastrum exile*, n. sp., because of their similar ray structure.
Etymology: *Exilis, -e* (Latin adj.) = slender, thin.

*Measurements (μm):* Holotype + 9 paratypes. See *Text-figure 13(B)* for system of measurements.

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*Cotype localities:* MX-84-13 and MX-85-22 (see Appendix I).

*Deposition of types:* Fossil Depository of Nanjing Institute of Geology and Palaeontology.

*Range and occurrence:* Zone 4, Subzone 4 beta; upper Tithonian. Upper thin-bedded member of Taman Formation, east-central Mexico. Text-figures 9 and 11.

**Archaeohagiastrum sp. cf. minutum** Baumgartner
Plate 5, figures 4, 13, 22

*Remarks:* This form differs from *Archaeohagiastrum minutum* Baumgartner (1984, p. 759, pl. 2, figs. 9-13) in possessing much less massive rays.

*Range and occurrence:* Zone 4, Subzone 4 beta; upper Tithonian. Upper thin-bedded member of the Taman Formation, east-central Mexico. Text-figure 9.

Genus *Homoeoparaonaella* Baumgartner 1980

*Type species:* *Paronaella elegans* Pessagno 1977.

*Remarks:* This genus is characterized by possessing three equally or subequally arranged, rounded rays with numerous (>6) external beams and by possessing radially arranged internal beams and canals.

*Range and occurrence:* Jurassic (Callovian or lower) to Cretaceous (Aptian). Worldwide.

**Homoeoparaonaella elegans** (Pessagno)
Plate 5, figure 9

*Paronaella elegans* PESSAGNO 1977a, p. 70, pl. 1, figs. 10, 11.
*Homoeoparaonaella elegans* (Pessagno). - BAUMGARTNER 1980, p. 289, pl. 1, fig. 15; pl. 2, figs. 2-6; pl. 11, fig. 6.

*Range and occurrence:* Zone 2, Subzone 2 beta to Zone 4, Subzone 4 beta; upper Kimmeridgian to upper Tithonian. Worldwide. Text-figures 9 and 11.

Genus *Neoparaonaella*, n. gen.

*Type species:* *Neoparaonaella delicata*, n. sp.

*Description:* Test composed of three latticed rays arranged equally or subequally in one plane. Each
ray fusiform in cross-section (Text-figure 14) with eight external beams and two lateral auxiliary beams; two lateral auxiliary beams not directly connected to internal primary beam, but to adjacent external beams by transverse bars on surface. Each ray enclosing four primary canals separated by four equally arranged primary lamellae, and four secondary canals, as illustrated in Text-figure 14.

Remarks: This genus is distinguished from all other three-rayed hagiastrids by possessing two fringe-like lateral auxiliary beams on each ray; as a result, the cross-sections of the rays are fusiform in shape (see pl. 3, figs. 9, 17; Text-figure 14). Internally, each ray contains four primary canals (plus four secondary canals) surrounded by eight linear external beams and two lateral auxiliary beams.

Samples collected by Pessagno et al. (unpublished) show that Neoparonaella, n. gen., also occurs in Zones 2 and 3 (sensu Pessagno et al. 1987b) in the Taman Formation.

Etymology: Neo-, Greek prefix, new, + Paronaella Pessagno (1971).
Range and occurrence: Zone 2 to Zone 4, Subzone 4 alpha; Kimmeridgian, or lower, to Tithonian or higher. Lower and upper members of the Taman Formation, east-central Mexico. See Text-figures 9 and 11.

**Neoparonaella delicata**, n. sp.
Plate 3, figures 1, 5, 6, 9, 10, 17, 22; plate 7, figure 12

Description: Test small, with three moderately broad and short rays which are equally arranged and slightly expanding distally. Each ray with a short spine at tip. Lateral auxiliary beams on each ray fringe-like, sometimes broken on proximal part of ray. Eight external beams straight. Pore frames on surface of rays rectangular and medium in size. Central area small with irregular pore frames.

Remarks: This species is distinguished by its small size, rays slightly expanding distally and its delicate rectangular pore frames on each ray.

**Neoparonaella delicata**, n. sp., is quite common in the upper Tithonian part of the Taman Formation.

Etymology: *Delicatus*-a-*um* (Latin, adj.) = delightful, charming.

Measurements (µm): Holotype + 9 paratypes. See Text-figure 13(A) for system of measurements.

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Type Locality: MX-84-8 (see Appendix I).

Deposition of types: Fossil Depository of Nanjing Institute of Geology and Palaeontology.

Range and occurrence: Zone 4, Subzones 4 alpha and 4 beta; upper Tithonian, insofar as known. Lower and upper members of the Taman Formation, east-central Mexico. Text-figures 9 and 11.

**Neoparonaella** sp. cf. *delicata*, n. sp.
Plate 7, figures 11, 24

Remarks: This form differs from *Neoparonaella delicata*, n. sp., in possessing massive nodules on test surface.

Range and occurrence: Zone 4, Subzone 4 beta; upper Tithonian. Upper thin-bedded member of the Taman Formation, east-central Mexico. Text-figure 9.

**Neoparonaella** sp.
Plate 7, figures 14, 19, 22

Remarks: This form is distinguished by possessing a bulbous spongy tip on each ray.

Range and occurrence: Zone 4, Subzone 4 beta; upper Tithonian. Upper thin-bedded member of the Taman Formation, east-central Mexico. Text-figure 9.
Subfamily HIGUMASTRINAE Baumgartner 1980; emend. herein

Tetraditryminae BAUMGARTNER 1980, p. 296 = subjective synonym.

Type genus: Higumastra Baumgartner 1980.

Emended definition: Hagiastrids with rays characterized by bilateral symmetry in cross-section.

Remarks: The emended definition given here essentially follows Baumgartner (1980) for Higumastrinae, but Subfamily Higumastrininae Baumgartner is used here to include both Higumastrinae Baumgartner (1980) and Tetraditryminae Baumgartner (1980), the latter being treated here as a subjective synonym. As described by Baumgartner (1980, p. 296), the subfamilial characteristics for Tetraditryminae are considered here as only of generic importance; they are, in effect, compatible with the descriptions for Higumastrinae Baumgartner (1980, p. 290). Evidence resulting from this study also suggests close relationship between Tetraditryma Baumgartner, which was the only generic taxon placed under Tetraditryminae, and Pseudocrucella Baumgartner, which is a member of the Higumastrinae (further discussion under Relationship Between Higumastrinae and Tetraditryminae above).

As emended herein, this subfamily now includes the following genera: Higumastra Baumgartner, Pseudocrucella Baumgartner, Tetraditryma Baumgartner, Pseudohigumastra, n. gen. Only four-rayed forms have been described in this subfamily so far.

Range and occurrence: Lower Jurassic (Lower Sinemurian) to Lower Cretaceous (Albian or higher). Worldwide.

Genus Higumastra Baumgartner 1980

Type species: Higumastra inflata Baumgartner 1980.

Remarks: This genus is characterized by possessing four rounded rays arranged at right angles to each other in one plane and with large, linearly arranged pore frames; internally, each ray has a vertical median septum and two very large lateral canals.

Range and occurrence: Lower Jurassic (Sinemurian) to Lower Cretaceous (Albian or higher). Worldwide.

Higumastra sp. cf. inflata Baumgartner

Plate 3, figures 7, 8; plate 7, figure 8

Remarks: This form differs from Higumastra inflata Baumgartner (1980, p. 290, pl. 3, figs. 1, 2, 5-9, 11) in possessing four rays that, instead of being medially inflated, gradually decrease in width in a distal direction.

Range and occurrence: Zone 4, Subzone 4 beta; upper Tithonian. Upper thin-bedded member of Taman Formation, east-central Mexico. Text-figure 9.

Genus Pseudocrucella Baumgartner 1980

Type species: Crucella sanfilippoae Pessagno 1977.
Remarks: This genus is distinguished from other four-rayed hagiastrids by possessing rectangular rays with less regularly arranged pore rows on the top and bottom surfaces. It differs from Crucella Pessagno (1971, emend. Baumgartner 1980) in having a medullary shell differentiated from the cortical shell.

Range and occurrence: Middle Jurassic (Bajocian) to Lower Cretaceous (Barremian). Worldwide.

_Pseudocrucella haeckeli_, n. sp.
Plate 3, figures 3, 4, 11, 13, 19, 21, 23

_Pseudocrucella_ sp. A BAUMGARTNER 1980, pt., pl. 8, figs. 3, 7 only.
_Pseudocrucella_ sp. AITA 1987, pl. 13, fig. 17.

Description: Four rays slender, subparallel-sided proximally and gradually decreasing in width distally. Each ray with one relatively massive and quite long spine at distal end. Sides of rays concave and side-view of each ray wedge-shaped, thickness decreasing towards tip of ray (pl. 3, fig. 21). Two lateral external beams on surface of each ray relatively massive with two to three tenuous median external beams in between; median external beams sometimes merging or branching. Transverse bars together with external beams forming irregularly quadrangular pore frames on surface. Pore frames in central area non-geometrical. Well-developed nodes present on surface.

Remarks: This species differs from _Pseudocrucella adriani_ Baumgartner (1980, p. 291, pl. 8, figs. 4, 8, 12, 15, 16) in being more nodose and in lacking the peculiar pattern of oblique bars between external beams. It differs from _P. procera_ Osvoldova (Osvoldova and Sykora 1984, p. 270, pl. 12, fig. 2, pl. 15, figs. 6, 7, pl. 16, fig. 5) in having less prominent median external beams, relatively smaller, more numerous and less geometric pore frames, and a much shorter spine at tip of each ray.

This species superficially resembles _Crucella angulata_, n. sp., but differs from the latter not only in the internal structures, but also in possessing relatively larger and predominantly quadrangular (rather than small, triangular) pore frames on the test surface. In addition, _Crucella angulata_, n. sp., has larger and more densely spaced nodes, while _Pseudocrucella haeckeli_, n. sp., has pore frames with pronounced linear arrangement on sides of each ray (pl. 3, fig. 21).

A specimen figured by Rüst (1898, p. 29, pl. 9, fig. 9) appears to be similar to this species. However, it is not clear as to the nature of cross-section of the rays and the surface ornamentation of that Rüst's species.

Etymology: This species is named after Ernst Haeckel in honor of his pioneering work on Radiolaria.

Measurements (μm): Holotype + 9 paratypes. See Text-figure 13(B) for explanation of system of measurements.

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Type locality: MX-84-8 (see Appendix I).

Deposition of types: Fossil Depository of Nanjing Institute of Geology and Palaeontology.

Pseudocrucella sp.
Plate 4, figures 8, 19

Remarks: This form superficially resembles Tetraditryma pseudopleana Baumgartner (1980, p. 297, pl. 7, figs. 1-11), but differs from the latter species in possessing one to three mostly slender (rather than one massive) median external beams on the top and bottom surfaces of each ray. In addition, this species has a prominently nodose surface.

Curiously, one of the four rays in this form (pl. 4, fig. 8) has a single, massive median external beam, which is characteristic of Genus Tetraditryma Baumgartner (1980). Another form, illustrated herein as Tetraditryma (?) sp. (pl. 7, figs. 9, 17, 20), has a median external beam which branches into 2-3 tenuous beams on the proximal part of each ray. Thus, it appears that Pseudocrucella, which is characterized externally by possessing several median external beams on the surface of each ray, is closely related to Tetraditryma through transitional forms such as those described above. It is, therefore, suggested here that the two genera be classified under one subfamily-Higumastriinae Baumgartner, unified by bilaterally symmetrical structures of the rays. The subfamilial characteristics for Tetraditrymae Baumgartner are, in my opinion, only of generic importance and the name Tetraditrymae Baumgartner (1980) is herein treated as a subjective synonym of Higumastriinae Baumgartner.

Range and occurrence: Zone 4, Subzone 4 beta; upper Tithonian. Lower massively bedded member of Taman Formation, east-central Mexico. Text-figure 9.

Genus Pseudohigumastra, n. gen.

Type species: Pseudohigumastra minuta, n. sp.

Description: Test composed of four rays arranged in one plane. Each ray with four external beams and transverse bars between two beams on top and bottom surfaces. Internally, only one primary beam present, connected to each of the four external beams via subsidiary beams (see Text-figure 15). Lacking skeletal covering on sides of each ray.

Remarks: Pseudohigumastra, n. gen., is distinguished from all other genera in the family Hagiastridae by possessing four co-planar and equally arranged rays, each of which has a single row of pores on the surface, lacks covering on the sides, and has only one internal beam (Text-figure 15).

Pseudohigumastra apparently has a bilaterally symmetrical internal structure within each ray, which is anatomically comparable to that of Higumastra Baumgartner (Text-figure 15 herein). Moreover, the single row of pores on the top and bottom surfaces of each ray in this genus is comparable with the prominent "median pore row" in Higumastra Baumgartner (1980, p. 290). It is, therefore, apparent that the two genera are closely related.

Etymology: Pseudo-, Greek prefix, superficially resembling, + Higumastra Baumgartner (1980).

Range and occurrence: Zone 3 to Zone 4, Subzone 4 beta; lower to upper Tithonian, insofar as known. Taman Formation, east-central Mexico.
**Pseudohigumastra minuta**, n. sp.
Plate 7, figures 2-4, 15, 16, 19, 21

*Description:* Test small, relatively thick, with four narrow and equally disposed rays. Each ray gradually decreasing in width in distal direction with a massive and moderately long spine at tip. A single row of pore frames present on top and bottom surfaces of each ray; pore frames rectangular, with moderately well-developed nodes at vertices. Pore frames in central area less geometrical and irregularly arranged.

*Remarks:* It is noted that individuals occurring at lower stratigraphic levels are larger and, sometimes, possess a bifurcating spine at the tip of a ray.

*TEXT-Figure 15.* Comparison of ray cross-sections between *Higumastra* Baumgartner and *Pseudohigumastra*, n. gen.
Etymology: *Minutus-a-um* (Latin, adj.) = small, little.

Measurements (µm): Holotype + 9 paratypes. See Text-figure 13(B) for system of measurements.

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Type locality: MX-84-26 (see Appendix I).

Deposition of types: Fossil Depository of Nanjing Institute of Geology and Palaeontology.

Range and occurrence: Same as for genus. Text-figures 9 and 11.

**Pseudohigmastra** sp. cf. *minuta*, n. sp.
Plate 5, figures 3, 14, 15

Remarks: This form differs from *Pseudohigmastra minuta*, n. sp., by possessing four much shorter latticed rays, each with a very long and quite massive tetraradate spine at the tip. Interestingly, this form is very similar to *Emiluvia* Foreman. If, as Baumgartner (1980) suggested, an *Emiluvia*-ancestor for the Hagiastriidae is valid, the present form is likely one of the primitive hagiastries derived from a species of *Emiluvia* simply by extending pore frames onto the four spines.

Range and occurrence: Zone 4, Subzone 4 beta; upper Tithonian. Upper thin-bedded member of Taman Formation, east-central Mexico. Text-figure 9.

Genus *Tetraditryma* Baumgartner 1980

Type species: *Tetraditryma pseudoplena* Baumgartner 1980.

Remarks: This genus is characterized by four rectangular rays equally or subequally arranged in one plane, each with three prominent external beams on the top and bottom surfaces. Baumgartner (1980) originally classified this genus under Subfamily Higumastrinae Baumgartner (1980) which is considered here as a subjective synonym of Subfamily Higumastrinae Baumgartner (1980). See further discussion under Relationship Between Higumastrinae and Tetraditryminae (above).

Range and occurrence: Middle Jurassic (Bajociam) to Lower Cretaceous (Berriasian). Worldwide.

**Tetraditryma pseudoplena** Baumgartner
Plate 5, figures 7, 23

Hagiastrum *plenum* Haeckel. – PESSAGNO 1977a, p. 72, pl. 2, fig. 14.
**Tetraditryma pseudoplena** BAUMGARTNER 1980, p. 297, pl. 1, fig. 9; pl. 7, figs. 1-11; 1984, p. 788, pl. 9, figs. 12, 14.