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Cretaceous corals from the Huetamo region, Michoacán and Guerrero, southwestern Mexico

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ABSTRACT

The Cretaceous corals (Anthozoa, Scleractinia) of the Huetamo region of southwestern Mexico, an area in the tectonically problematic Guerrero terrane, are investigated for the first time. This study provides a detailed, modern taxonomic foundation for future work on Mexican Cretaceous corals. Thirty-nine species are described and illustrated: 20 from the lower Aptian Cumburindio Formation, one from lower Aptian strata of the San Lucas Formation, and 18 from the upper Albian-lower Cenomanian upper member of the Mal Paso Formation. At the species level, the coral faunas from these formations are entirely different from each other. Of the 21 species from the lower Aptian, three are described as new: *Saltocyathus cumburindioensis* n. sp., *Actinaraea michoacanensis* n. sp, and *Thamnarea hornosensis* n. sp. About 50 percent of the lower Aptian coral species have been reported previously from pre-Albian strata in the European region. This faunal similarity is the strongest geographic affinity recognized in this study. Of the 18 coral species from the upper Albian-lower Cenomanian, 11 are described as new, whereas another one of these species recently has been described and designated as the type species of a newly recognized dendrophylliid genus, *Blastozopsammia guerreroterion* Filkorn and Pantoja-Alor, 2004. The 11 coral species from the upper Albian-lower Cenomanian herein described as new are: *Actinastrea chumbitaroensis* n. sp., *Preverastraea coatlicuae* n. sp., *Preverastraea tocae* n. sp., *Latiphyllia mexicana* n. sp., *Thecosmilia guerreroensis* n. sp., *Mycetophyllopsis azteca* n. sp., *Orbignygyra? incognita* n. sp., *Thalamocaeniopsis mexicanensis* n. sp., *Thamnasteria tonantzinae* n. sp., *Paracycloseris effrenatus* n. sp., and *Ovalastrea malpaso* n. sp. Analogies with extant corals indicate that most of the coral species from the Cretaceous formations of southwestern Mexico were zooxanthellate, hermatypic, reef-building species.

Associations of scleractinian corals and rudist bivalves were observed at three localities, two in the Cumburindio Formation and one in the Mal Paso Formation. The two occurrences in the Cumburindio Formation are: an association of a large species of ramose, microsolenid coral, *Thamnarea hornosensis* n. sp., preserved in situ along with valves of the rudists *Praecaprina* and *Caprina* at the exposures in the Arroyo Los Hornos, near Turitzio; and a diverse assemblage of reef corals that conformably overlies a bed primarily composed of valves of the rudist *Amphitriscoelus* near the top of the stratigraphic section at the Loma de San Juan, Turitzio, Michoacán. The coral and rudist association in the Mal Paso Formation involves a diverse assemblage of reef corals and the rudists *Radiolites* and *Mexicaprina* within an interval near the top of the stratigraphic section that is exposed at a locality in the state of Guerrero, just north of Chumbítaro, Michoacán. None of these specific kinds of coral and rudist associations has been recognized previously at any other localities.

Key words: Corals, Lower Cretaceous, southwestern Mexico.

RESUMEN

Se investiga por vez primera los corales cretácicos de la región de Huetamo en el sureste de México, provenientes del terreno Guerrero, un área problemática desde el punto de vista tectónico. Este estudio aporta bases para futuras investigaciones sobre corales cretácicos de México. Se describen e ilustran 39 especies: 20 de ellas pertenecen a la Formación Cumburindio del Aptiano inferior, una proviene de estratos del Aptiano inferior de la Formación San Lucas y 18 son del Albiano superior-Cenomaniano inferior del miembro superior de la Formación Mal Paso. Al nivel específico, las faunas de corales de estas formaciones son completamente diferentes entre sí; de las 21 especies del Aptiano inferior, tres son descritas como nuevas: *Saltocyathus cumburindioensis* n. sp., *Actinaraea michoacanensis* n. sp y *Thamnarea hornosensis* n. sp. Cerca del 50% de las especies de corales del Aptiano inferior han sido reportadas de estratos pre-albianos en la región europea. Esta similitud faunística es la más fuerte afinidad geográfica reconocida en este estudio. De las 18 especies de corales del Albiano superior-Cenomaniano inferior, 11 son descritas como nuevas, mientras que otra de esas especies ha sido recientemente descrita y designada como la especie tipo de un nuevo género: *Blastozopsammia guerreroterion* Filkorn and Pantoja-Alor, 2004. Las 11 especies de corales del Albiano superior-Cenomaniano inferior aquí descritas como nuevas son: *Actinastrea chumbitaroensis* n. sp., *Preverastraea coatlicuae* n. sp., *Preverastraea tocae* n. sp., *Latiphyllia mexicana* n. sp., *Thecosmilia guerreroensis* n. sp., *Mycetophyllopsis azteca* n. sp., *Orbignygyra? incognita* n. sp., *Thalamocaeniopsis mexicanensis* n. sp., *Thamnasteria tonantzinae* n. sp., *Paracycloseris effrenatus* n. sp. y *Ovalastrea malpaso* n. sp. Las analogías con corales existentes indican que la mayoría de las especies de corales de formaciones del Cretácico del suroeste de México, eran especies hermatípicas, constructoras de arrecifes y asociadas a zooxantelas.

Las asociaciones entre corales escleractinios y bivalvos rudistas fueron observadas en tres localidades, dos en la Formación Cumburindio y una en la Formación Mal Paso. Las dos asociaciones en la Formación Cumburindio son una especie grande del coral microsolérido ramoso *Thamnarea hornosensis* n. sp., preservado in situ junto con valvas de los rudistas *Praecaprina* y *Caprina,* en afloramientos del Arroyo Los Hornos, cerca de Turitzio, y una diversa composición de corales arrecifales que sobreyacen concordantemente a una capa compuesta principalmente por valvas del rudista *Amphitriscoelus*, cerca de la cima de la sección estratigráfica de la Loma de San Juan, Turitzio, Michoacán. La asociación de corales y rudistas en la Formación Mal Paso involucra una composición diversa de corales arrecifales y los rudistas *Radiolites* y *Mexicaprina*, dentro de un intervalo cerca de la cima de la sección estratigráfica expuesta en una localidad del estado de Guerrero, al norte de Chumbítaro, Michoacán. Ninguna de estas asociaciones a nivel específico entre corales y rudistas ha sido reconocida previamente en alguna localidad.

Palabras clave: Corales, Cretácico Inferior, México suroccidental.

INTRODUCTION

Cretaceous corals were discovered in southwestern Mexico more than a century ago. However, the taxonomy and stratigraphic distribution of the corals from this region have never been studied. Furthermore, despite the numerous studies of many other Cretaceous invertebrate groups from Mexico over the past hundred years, the corals of the entire Mexican Cretaceous System were rarely studied and they remain largely unknown. Therefore, one of the ultimate underlying purposes of this study is to provide a detailed taxonomic base that will serve as a modern foundation for future work on the Cretaceous corals of Mexico.

The study area is within the Huetamo region and is located in a rugged and remote part of the states of Michoacán and Guerrero (Figures 1, 2). It also lies within the Guerrero terrane, a tectonically problematic region that has been interpreted as an allochthonous terrane that is thought to have accreted to the western margin of Mexico sometime during the Cretaceous or early Tertiary (Campa and Coney, 1983) (Figure 3). The study area presently lies between the Cretaceous Caribbean biogeographic province and the Pacific biogeographic province. Therefore, the determination of the faunal affinities between the newly discovered coral faunas of the Huetamo region and the coral faunas known from other parts of Mexico, the Gulf Coast of Texas, the Caribbean, and the Pacific eventually should help in refining interpretations of the paleogeographic position of the Guerrero terrane during the Early Cretaceous.

This study is the first major investigation of the Cretaceous corals of the Huetamo region of southwestern Mexico. The corals described in this study are from outcrops of the Cumburindio Formation (lower Aptian) south of Huetamo, near Turitzio, Michoacán; from the San Lucas Formation (lower Aptian) at a hill about 8 km south-southeast of Huetamo, Michoacán; and from the Mal Paso Formation (upper Albian-lower Cenomanian) northeast of Ciudad Altamirano and in the state of Guerrero, just north of Chumbítaro, Michoacán. Corals are abundant and diverse in both the Cumburindio and Mal Paso formations and, although the corals frequently occur with other marine invertebrates (bivalves, gastropods, echinoids, and sponges), at some horizons they are by far the most abundant component of the fauna. Altogether, 39 different coral species are recognized: 20 from the Cumburindio Formation, one from the San Lucas Formation, and 18 from the Mal Paso Formation. Based on analogies with extant coral species, it is inferred that the majority of these fossil coral species were zooxanthellate or hermatypic forms that were capable of contributing to the development of reefs.

A paleontological reconnaissance of the Huetamo region was made by the authors in January 1994. At that time, numerous outcrops in the area were visited and a few small collections of corals were made. Geologic investigations made during subsequent visits to the area in January and November 1995, January to February 1996, and January to February 1997, concentrated on fossiliferous outcrops of the lower Aptian Cumburindio Formation near Turitzio, Michoacán, and the upper Albian-lower Cenomanian upper member of the Mal Paso Formation in the state of Guerrero, just north of Chumbítaro, Michoacán.

The diverse Cretaceous coral faunas from the Huetamo region have remained mostly unknown until the present study. The earliest mention of Cretaceous corals in Michoacán was from the western district of Coalcomán, about 60 km west of the present study area, and two species were identified, *Trochoseris sinuosa* Fromentel, 1857, and *Thamnastraea pedunculata* Fromentel, 1857 (Urquiza, 1883, p. 41-42, figs. 20-23). However, later comments indicate that the identifications were likely incorrect (Heilprin, 1891, p. 459-460) and the species have not been reported again from this area. In the adjacent state of Guerrero, the Morelos Formation yielded specimens that John Wells identified as *Epistreptophyllum* sp. cf. *E. budaensis* Wells (Fries, 1960, p. 55), but evidently the species was never described. Prior to the present investigation, only three species of coral had been reported from the Mal Paso Formation outcrops in the study area: *Actinastrea guadalupe* [sic], *Pollyphilloceris* [sic] *convexa* and *Thammnastheria* [sic] sp. (García Barrera, 1993, p. 45). Subsequently, the majority of the published information on the corals of the Huetamo region has been derived from the recent investigations by the present authors (Filkorn and Pantoja-Alor, 1994, 1995a, 1995b; Pantoja-Alor and Filkorn, 1995; Filkorn, 2002a, 2002b, 2002c), including description of a new genus and species of coral from the Mal Paso Formation, *Blastozopsammia guerrero-*

terion Filkorn and Pantoja-Alor, 2004. In addition, literature searches for the present investigation have resulted in the compilation of extensive, detailed reviews of the published articles which pertain to the occurrences and previous work on Mexican Cretaceous corals and this information has been presented in two earlier publications (see Filkorn, 2003, 2006). This analysis of the literature has revealed that the previous studies most relevant to the present investigation are those from other regions of Mexico, particularly the detailed studies of the Cretaceous coral faunas from: Tehuacán and vicinity, Puebla (Felix, 1891; Löser, 2006), about 350 km east of the Huetamo region; San Juan Raya and vicinity, Puebla (Reyeros-Navarro, 1963), and northwestern Oaxaca (Reyeros, 1983), about 300 km east of the Huetamo region; the vicinity of Lampazos, Sonora (Scott and González León, 1991; Baron Szabo and González León, 1999, 2003), about 1,500 km northwest of the Huetamo region; and Cerro de Cristo Rey, Chihuahua and New Mexico (Turnšek et al., 2003), about 1,600 km north-northwest of the present study area. Refer to the published articles on the previous studies of Mexican Cretaceous corals (Filkorn, 2003, 2006) for further discussion of the coral occurrences mentioned above and a thorough review of other reported occurrences of Cretaceous corals in Mexico.

This study contributes new taxonomic information and occurrence records for Early Cretaceous corals, data that are necessary for interpreting the paleobiogeographic histories of the corals and the global distribution and evolution of coral reefs. Furthermore, this study elucidates the interpretations of the Early Cretaceous paleogeography of southwestern Mexico. The Cretaceous corals of southwestern Mexico are important with regard to global paleoceanographic and paleobiogeographic interpretations because southern continental Mexico was centrally positioned in the path of western Tethyan surface currents through the tropics during the Early and middle Cretaceous. Therefore, when utilized as a proxy for surface currents, the biogeographic distributions of the Cretaceous coral species from the Huetamo region are key indicators of Tethyan surface current flow patterns between the European eastern realm and the equatorial Caribbean western realm during the Early and middle Cretaceous. Regional and global comparisons of the coral species identified from the Huetamo region also help facilitate reconstructions of their paleobiogeographic histories and evolution. These topics are discussed in the section on paleobiogeography.

The objectives of this investigation are to describe the Cretaceous coral species of the Huetamo region and thus establish a modern taxonomic base that will serve as a foundation for future studies; to report the observed stratigraphic distributions of the coral species within the study area; and to examine their global paleobiogeographic distributions.

LOCATION

The study area is located in the Huetamo region of southwestern Mexico, about 200 km southwest of Mexico City and 140 km northeast of the city of Zihuatanejo on the Pacific Coast (Figure 1). The study area encompasses part of the border between the states of Michoacán and Guerrero and is both inland and northeast of the western part of the Sierra Madre del Sur. The study area is also within the part of Mexico commonly known as Tierra Caliente and it is along the fringe of significant urban development in this part of Mexico. Two of the largest cities within the area are Huetamo and Ciudad Altamirano and the only major paved road is Mexican highway 51 (Figure 2). The geology of this region

Figure 1. The location of the study area in southwestern Mexico is indicated by the rectangle with the arrow. The boundaries of the Guerrero terrane and its three subterranes in southwestern Mexico are outlined. The Zihuatanejo subterrane, which includes the town of the same name and Puerto Vallarta, lies along the southwestern coast of Mexico; the Huetamo subterrane is the region that includes the study area; and the Teloloapan subterrane, the easternmost of the three, is the region that includes the town of the same name. Cenozoic rocks, mostly volcanics, cover the area between the Zihuatanejo and Huetamo subterranes, as well as much of the southern half of the Guerrero Terrane inland and north of the three subterranes. The boundary of the Guerrero terrane is from Freydier et al. (1997, p. 485) and the boundaries of the subterranes are from Centeno-García (1994, p. 127). An enlarged sketch map of the study area is shown in Figure 2.

and adjacent areas has been explored and discussed earlier by several travelers and geologists including J. Burkart (1832, 1836), Virlet d'Aoust (1866), M. Bárcena (1874, 1875, 1877, 1885), M. Urquiza (1883), J. G. Aguilera (1897a, 1897b, 1907), C. E. Hall (1903), T. Barrera and D. Segura (1927), M. Santillán (1929), C. Burckhardt (1930), Y. S. Bonillas (1937), V. R. Garfias and T. C. Chapin (1949), and others, but detailed geologic investigations in the Huetamo area did not commence until the 1950s (de Cserna and Pantoja-Alor, 1955; Pantoja-Alor, 1959).

Figure 2. Sketch map of the study area, the Huetamo region of the Huetamo subterrane, with positions of the localities where Cretaceous corals were collected. Localities 1-4 are in the Cumburindio Formation, lower Aptian, at: 1, the western flank of Loma Teremitio, latitude 18 degrees 32.39 minutes north, longitude 100 degrees 57.13 minutes west; 2, the Arroyo Los Hornos and adjacent slopes to the south, latitude 18 degrees 32.10 minutes north, longitude 100 degrees 56.74 minutes west; 3, the crest of Loma de San Juan, latitude 18 degrees 31.28 minutes north, longitude 100 degrees 56.65 minutes west; and 4, near the village of Las Eras, southwest of Turitzio, latitude 18 degrees 30.60 minutes north, longitude 100 degrees 59.0 minutes west. Locality 5, Upper part of the lower member of the San Lucas Formation, lower Aptian, at the eastern flank of Loma La Cuchilla, latitude 18 degrees 33.81 minutes north, longitude 100 degrees 52.04 minutes west. Locality 6, upper member of the Mal Paso Formation, upper Albian-lower Cenomanian, about 0.75 km north of the rural village of Chumbítaro, State of Michoacán, latitude 18 degrees 29.3 minutes north, longitude 100 degrees 42.5 minutes west. Map redrawn from Mexican 1:50,000 scale topographic sheets Huetamo (E14A64) and Coyuca de Catalán (E14A74).

The corals examined in this study were collected primarily from two general areas that are about 25 km apart: one in the western part of the study area in the vicinity of the village of Turitzio and the other in the eastern part of the study area in the vicinity of the small rural village of Chumbítaro (Figure 2). The coral-bearing Cretaceous strata that crop out in the western part of the Huetamo area near Turitzio belong to the lower Aptian Cumburindio Formation and those that crop out in the eastern part of the Huetamo area near Chumbítaro belong to the upper Albian-lower Cenomanian upper member of the Mal Paso Formation. Despite the relatively short map distance between these two areas, the Cretaceous stratigraphic sequences and sedimentary facies of each area are different, in part due to differences in tectonic setting (see Filkorn, 2002a), and thus each area has its own set of stratigraphic terminology. Furthermore, extensive sampling of corals during this study revealed that the species composition of the Cretaceous coral faunas from these two areas is entirely different as well.

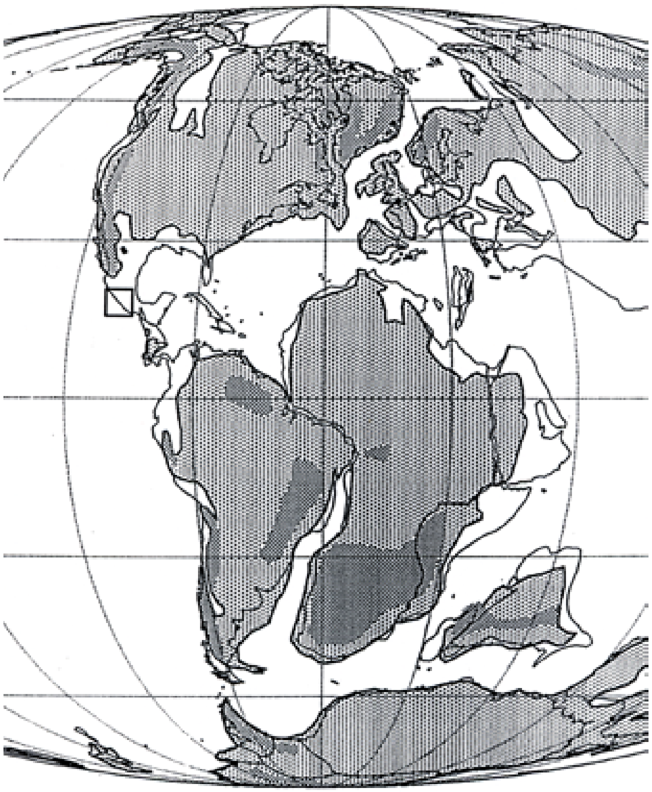


Figure 3. Early Aptian plate reconstruction and paleocoastline map. The approximate position of the study area in the southern part of the Guerrero terrane is indicated by the square. Aptian (120 Ma) paleocoastline base map modified from Smith et al. (1994, p. 40).

STRATIGRAPHY

INTRODUCTION

The Cretaceous stratigraphy of the Huetamo region was originally described by Jerjes Pantoja-Alor in 1959 and it has been reviewed and discussed in several later studies (de Cserna, 1978; de Cserna et al., 1978a, 1978b; Pantoja-Alor, 1993a, 1993b, 1993c; Pantoja-Alor et al., 1994). The latest version of the stratigraphic terminology is utilized in this study. The Cretaceous strata of Huetamo region are subdivided into East and West areas based on differences in depositional sequences and therefore each of these two areas has its own set of stratigraphic nomenclature. The Cretaceous System of the West Huetamo area, in order of deposition, comprises the Cumburindio, Turitzio, and Huetamo Formations (Figure 4). The San Lucas, El Cajón, Mal Paso, and Cutzamala formations compose the correlative Cretaceous stratigraphic section in the East Huetamo area (Figure 4). Only two of these Cretaceous formations, the Cumburindio Formation of the West Huetamo area and the Mal Paso Formation of the East Huetamo area, have thus far yielded abundant and diverse coral faunas (Filkorn and Pantoja-Alor, 1994, 1995a, 1995b; Pantoja-Alor and Filkorn, 1995). Although corals frequently occur with other macrofauna, including bivalves, gastropods, echinoids, and sponges, at some horizons corals are by far the most abundant component of the fauna. The geologic ages of the coral-bearing formations have been determined by using biostratigraphy and their relative stratigraphic positions within each of their respective Cretaceous sequences. The limestone terminology used in this study is from the classifications of Dunham (1962) and Embry and Klovan (1971).

WEST HUETAMO AREA

In the West Huetamo area, the lowermost Cretaceous strata are interbedded volcaniclastics and limestones of the Cumburindio Formation. The Aptian age of the Cumburindio Formation is based on the occurrence of several different age-diagnostic invertebrate taxa, including foraminifera, rudist bivalves, and ammonites (Pantoja-Alor, 1998). The orbitolinid foraminiferan *Palorbitolina lenticularis* (Blumenbach) from the Cumburindio Formation at the Arroyo Los Hornos, just north of the village of Turitzio, Michoacán, indicates an early Aptian age for the unit (Schroeder and Cherchi, 1993; Pantoja-Alor et al., 1994). This age determination is supported by the occurrence of another characteristic Aptian species, the rudist *Amphitriscoelus waringi* Harris and Hodson, 1922 (Alencáster and Pantoja-Alor, 1992, 1996a; Pantoja-Alor et al., 1994), and the occurrence of the ammonite *Pseudohaploceras liptoviense* (Zeuschner), a species that ranges from Barremian to early Aptian (González-Arreola et al., 1996). The rudist fauna from the Cumburindio Formation also includes species of *Praecaprina, Caprina* (Alencáster and Pantoja-Alor, 1993; Pantoja-Alor, 1993c, 1996; Pantoja-Alor and Alencáster, 1994), *Pantojaloria, Huetamia,* and *Douvillelia* (Alencáster and Pantoja-Alor, 1995, 1996b, 1998).

Fossil corals have been collected from three localities with exposed sections of the Cumburindio Formation in the vicinity of Turitzio, Michoacán (Figure 2). In addition, one coral specimen has been collected from the lower part of the Cumburindio Formation in the vicinity of the small rural village of Las Eras, about 4.5 km southwest of Turitzio. Of the other three localities near Turitzio, only one coral species has been identified from the material collected at the northernmost locality situated on the southwestern slope of the southern end of Loma Teremitio, an elongate hill about 1.5 km north of Turitzio. The strata at Loma Teremitio are poorly exposed compared to the other sampled localities. Corals are particularly abundant in the other two of the three localities, the Arroyo Los Hornos and adjacent slopes about 1 km north of Turitzio and a small hill at the southern edge of Turitzio that is locally known as Loma de San Juan. The locations of these three stratigraphic sections are roughly aligned in a north-south orientation and spaced about 1 km apart. The lithologies and sequence of sedimentary facies of each of the three sections are different from one locality to the next, despite the relatively short map distances between them. Lateral lithofacies relationships along this linear belt of outcrops indicate abrupt changes in the depositional environment over the same distance. Lithologies range from primarily biogenic limestones in the north at Loma Teremitio to mostly volcaniclastics in the south at Loma de San Juan. The section at the Arroyo Los Hornos is geographically positioned between the two aforementioned localities and composed of both carbonate and volcaniclastic strata. Accordingly, depositional environments range from shallow marine to

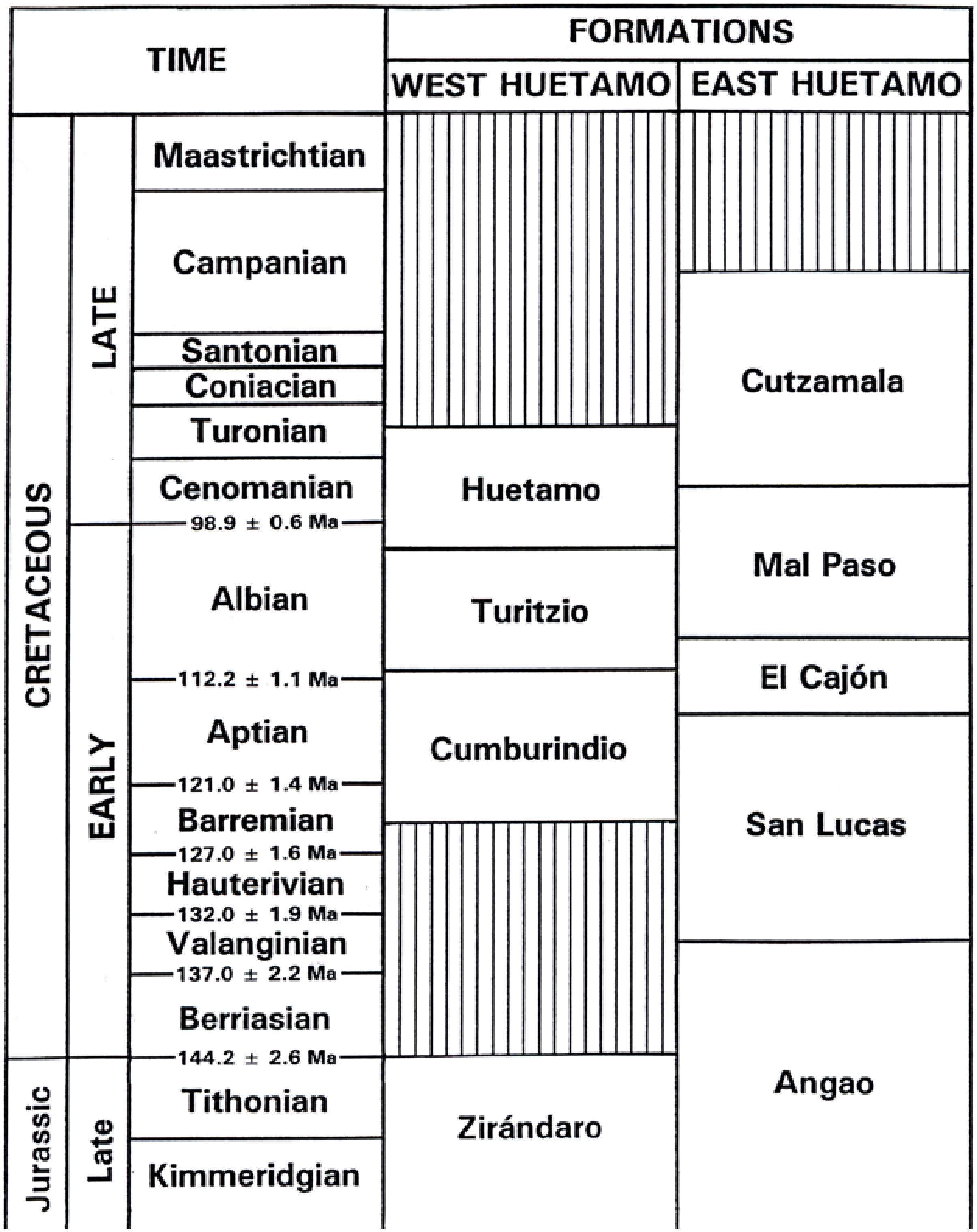


Figure 4. Stratigraphic correlation chart of the Late Jurassic and Cretaceous formations in the Huetamo region of southwestern Mexico. The fossil corals described in this study are from lower Aptian strata of the Cumburindio Formation in the West Huetamo area and from lower Aptian strata of the San Lucas Formation and upper Albian-lower Cenomanian strata of the Mal Paso Formation in the East Huetamo area. The ages of the upper part of Zirándaro Formation and the lower part of the Cumburindio Formation are approximate. The boundary dates for the Early Cretaceous ages are from Gradstein et al. (1995). Figure modified from Pantoja-Alor (1993c, p. 15).

carbonate platform to deeper marine, possibly restricted or lagoonal, and proximal to a source of volcaniclastics. These same facies relationships in vertical succession are a record of the Early Cretaceous geographic evolution of that region.

The Cumburindio Formation strata on the southern side of the Arroyo Los Hornos, just below the northwest fence line of Turitzio cemetery, are interbedded fine-grained volcaniclastics and calcareous mudstones that dip toward the east. Small massive cerioid coralla and fairly large phaceloid coralla occur in living position at some horizons in this section. The bioclastics in the limestone beds exposed within the Arroyo Los Hornos itself are nearly exclusively composed of rudist bivalves, mostly *Praecaprina* sp. and *Caprina* sp. Only one coral species has been discovered in the rudist biostromes, the large, ramose microsolenid *Thamnarea hornosensis* n. sp. The occurrence of this species is discussed below in the sections on systematic paleontology and paleoecology.

The section of the Cumburindio Formation exposed at the western side of the Loma de San Juan, just south of Turitzio, is laterally equivalent to the section at Arroyo Los Hornos, but at Loma de San Juan there is a greater thickness of volcaniclastics and much less limestone. The stratigraphic section measured at this locality is about 73 m thick (Figure 5). The bedding in the section is parallel and dips about 18 degrees east-northeast. Coral colonies were collected in situ from two main fossiliferous horizons, one in the lower part of the section at the base of the hill and the other in the upper part of the section at the top of the hill. Most of the strata between these fossiliferous horizons are composed of gray, medium-bedded, moderately well sorted, medium- and coarse-grained volcaniclastics. However, numerous small (< 20 cm diameter), isolated, massive coralla were found loose on the slope of this intervening volcaniclastic portion of the stratigraphic section. Based on external morphological similarities, most of these coral species appear to be the same as those that are present in the strata adjacent to the Arroyo Los Hornos, but the majority of the specimens from the latter locality are very poorly preserved and taxonomically indeterminable. Altogether, the beds at these two localities have yielded several identified coral species, including the majority of the massive cerioid, meandroid, and thamnasteroid growth forms known from the Cumburindio Formation.

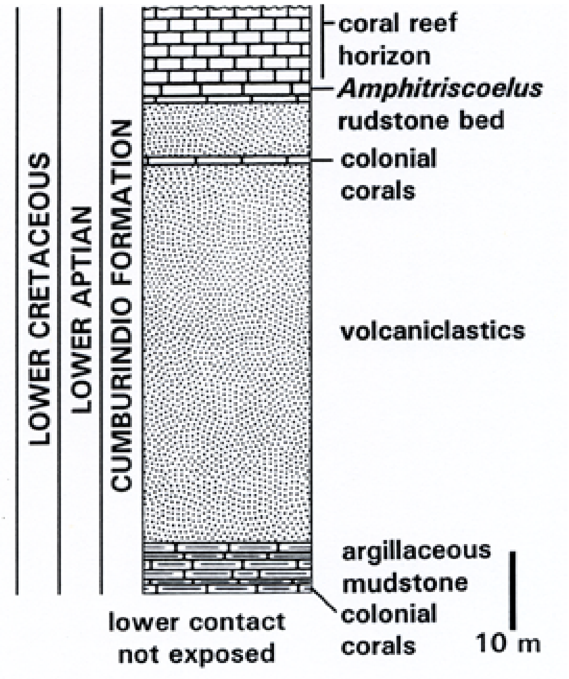


Figure 5. Stratigraphic section of the Cumburindio Formation, lower Aptian, at a small hill locally known as Loma de San Juan, just south of Turitzio, State of Michoacán. Coordinates for this locality are latitude 18 degrees 31.28 minutes north, longitude 100 degrees 56.65 minutes west. Labeled horizons include the *Amphitriscoelus* rudstone bed with overlying coral reef horizon at the top of the section and two other horizons where colonial corals were found in place, one in the upper part of the section and the other at the base of the section. The top of the section is truncated by the present surface of erosion and the lower part of the formation is not exposed at this locality. Refer to the text for further explanation of the section. Vertical scale bar = 10 m.

In the upper part of the section of the Cumburindio Formation at the Loma de San Juan, a 0.8 m thick packstone-rudstone bed of nerineid gastropods and small colonial corals is overlain by a 1.5 m thick rudstone bed primarily composed of the rudist *Amphitriscoelus*. The *Amphitriscoelus* bed is tabular and laterally continuous and the upper surface lacks any appreciable relief. This *Amphitriscoelus* bed is conformably overlain by an approximately 9 m thick boundstone bed composed of a taxonomically diverse assemblage of colonial scleractinian corals. The thickness of this coral reef bed is a conservative minimum because the section is truncated within this horizon by the present surface of erosion. Thus, the ultimate depositional fate of the coral reef is unknown. However, strata at the base of the dip slope on the eastern side of the same hill are composed of volcaniclastics that are lithologically similar to those lower in the section. Therefore it seems probable that reef growth was terminated when the reef was buried by an influx of volcaniclastics.

The coral reef horizon exposed at the southern crest and upper dip slope of the Loma de San Juan contains the highest species diversity of corals known from the Cumburindio Formation. Furthermore, the majority of the coral species known from the formation are from this locality. The coral fauna from this section is discussed in more detail in the paleoecology section of this study. Overall, at the generic level, the coral fauna is characteristic of the coral faunas known from the Barremian and Aptian, a time that is typically referred to as the Urgonian interval of reef development.

EAST HUETAMO AREA

The lowermost unequivocal Cretaceous strata in the East Huetamo area are conglomerates, sandstones, and shales of the lower member of the San Lucas Formation. In a stratigraphic section at Las Paredes, about 6 km northwest of the town of San Lucas, ammonites from near the base of the San Lucas Formation are late Valanginian in age, whereas those stratigraphically higher in the formation are characteristic of the Barremian (Gómez-Luna et al., 1993). Here, the San Lucas Formation conformably(?) overlies the Angao Formation of purported pre-Valanginian and possibly Late Jurassic (as old as Kimmeridgian) age. However, lithologic and sedimentologic similarities between these two formations suggest that they were deposited as turbidites in closely related settings, proximal in the Angao Formation and more distal in the San Lucas Formation (Gómez-Luna et al., 1993). Barremian ammonites also have been collected from the same member of the San Lucas Formation at another stratigraphic section, in Tiringueo, about 6 km southeast of San Lucas (González-Arreola et al., 1996). The gastropod species from the San Lucas Formation indicate an Aptian age (Buitrón-Sánchez, 1993).

One coral species, *Cladophyllia stewartae* Wells, 1944, has been collected from the lower Aptian San Lucas Formation strata that crop out on the northeast flank of Loma La Cuchilla, a hill just to the north of the village of Los Cuachalalates, Michoacán, and about 8 km south-southeast of Huetamo (Figure 2). The name of the hill as it appears on the Mexican 1:50,000 scale Huetamo (E14A64) topographic map is Loma La Cuchilla, but it is locally known as Loma Cuachalalate (according to J. Pantoja-Alor) or Sierrita del Cuachalalate (Pantoja-Alor, 1993b, 1993c). The coral species was found in a block of dendroid coral packstone collected from loose debris on the northeast flank of the hill. Because of the early Aptian age of the horizon, the species is described in the same part of the section on systematic paleontology as the species from the lower Aptian Cumburindio Formation.

The second, younger coral fauna examined in this study was collected from an outcrop of the upper Albian-lower Cenomanian upper member of the Mal Paso Formation in the state of Guerrero, about 0.75 km north of Chumbítaro, Michoacán (Figure 2). The exposed stratigraphic section is about 200 m thick and mostly composed of limestone beds of lagoonal and reefal origin, primarily wackestone, but it also contains beds of packstone, floatstone, rudstone,

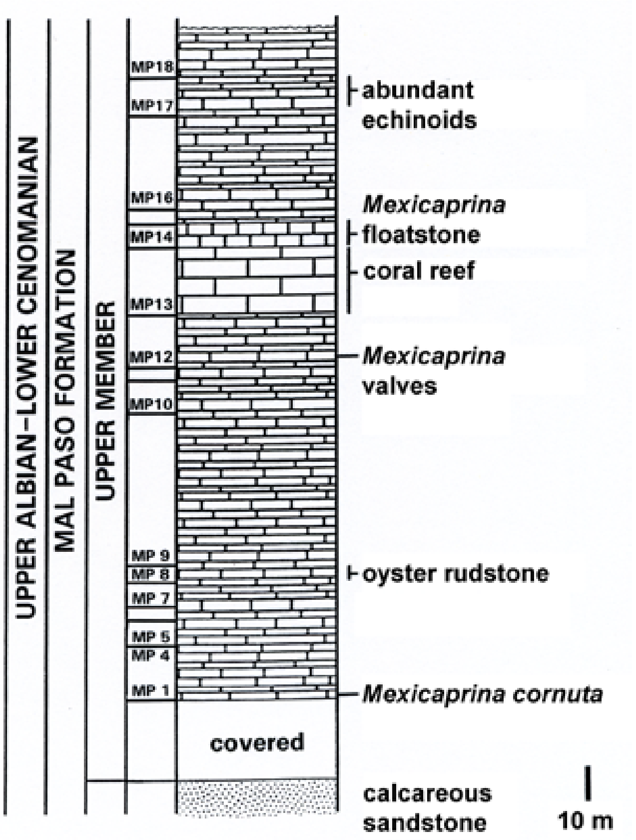


Figure 6. Stratigraphic section of the upper member of the Mal Paso Formation, upper Albian-lower Cenomanian, at the studied outcrop in the State of Guerrero, just north of the border with the adjacent State of Michoacán and about 0.75 km north of the rural village of Chumbítaro, State of Michoacán. Coordinates of the locality are latitude 18 degrees 29.3 minutes north, longitude 100 degrees 42.5 minutes west. The stratigraphic section is subdivided into numbered lithologic intervals for reference. The coral reef horizon (MP13) and overlying bed of *Mexicaprina* (MP14) are labeled, as well as the horizon which yielded *M. cornuta* (MP 1). Calcareous sandstone at the base of the section is part of the lower member of the Mal Paso Formation. Refer to the text for further explanation of the section. Vertical scale bar = 10 m.

and framestone (Figure 6). Overall, the lithologic, sedimentologic, and paleontologic evidence suggests that the upper member of the Mal Paso Formation at this locality represents a transgressive marine sequence. The measured section is stratigraphically continuous upward from the clastic beds of the lower member of the Mal Paso Formation and it is truncated at the top by the present surface of erosion. The measured section is subdivided into stratigraphic zones based on lithologic and paleontologic characteristics and these informal units are numbered from the base upward, MP 1 through MP18. The use of these informal unit numbers made it possible to refer to certain horizons and their relative positions within the stratigraphic section. The upper part of this section is exposed subparallel to the bedding planes and on a dip-slope that here dips east-northeast 22-25 degrees toward the axis of the northward plunging Mal Paso syncline. The underlying El Cajón Formation is exposed as a resistant, high ridge to the east of this fossiliferous locality where it defines the structurally equivalent eastern limb of the Mal Paso syncline and western limb of the adjacent Characo anticline.

The environments of deposition, analyses of the associated invertebrate fauna, and determination of the geologic age of the upper member of the Mal Paso Formation have been discussed in detail in two earlier publications that are derived from the present study (Filkorn, 2002a; Filkorn and Pantoja-Alor, 2004), therefore only a synopsis is given here. Additional comments on the stratigraphic distribution of corals and other related invertebrate species are presented in the paleoecology section of this study. The stratigraphy of the section indicates a transition of depositional environments from the base upward through lagoonal, back reef, coral reef, fore reef, and deeper marine settings. The beds have yielded a diverse invertebrate fauna composed of echinoids, gastropods, sponges, rudists, and other bivalves, and many of these taxa have been used previously by other authors to propose an Albian or late Albian age (refer to the discussion in Filkorn, 2002a). The most significant age-diagnostic taxa from these strata are species of the rudist *Mexicaprina*, including *M. cornuta* Coogan, 1973, and *M. alata* Filkorn, 2002a, and the pectinid bivalve *Pecten roemeri* Hill, 1889. Also notable is the occurrence of the rudist *Radiolites* cf. *R. costata* Scott, 1990, in erect, suprastratal clusters stratigraphically below the coral reef horizon (MP 13) and as isolated specimens attached to corals within the coral reef. The occurrence of these species constrains the age of the coral-bearing beds of the upper member of the Mal Paso Formation to the interval of late Albian-early Cenomanian (see Filkorn, 2002a).

Although the majority of the coral diversity and specimen abundance occurs in the coral reef (MP 13), corals also were observed at several other horizons within the studied stratigraphic section, particularly in units MP 5, MP 7, MP 9, MP10, MP17, and MP18. An oyster-rich rudstone bed (MP 8) marks a transition in the stratigraphic thicknesses of beds from thin- and medium-bedded limestones to medium- and thick-bedded limestones. Furthermore, the abundance and diversity of mollusks and corals increase above this bed and the small spines of echinoids become one of the most prevalent features of the bioclastic material in the rock. Above the oyster-rich rudstone bed (MP 8), in one of the thicker beds in the section (MP 9), the rudist *Radiolites* cf. *R. costata* Scott, 1990, occurs in small, erect clusters along with the large pectinid bivalve *Pecten roemeri* Hill, 1889, nerineid gastropods, and isolated colonies of massive corals. Farther up section, scattered valves of *Mexicaprina alata* Filkorn, 2002a, and other mollusks occur at a horizon in unit MP12, about 10 m stratigraphically below the coral reef (MP 13), but this unit did not yield any corals. The base of the coral reef (MP 13) appears to have been formed through the successive colonizations of these underlying molluscan bioclastics.

The coral reef (MP 13) is about 19 m thick and primarily composed of medium- to large-sized massive corals and sparsely distributed, medium- to large-sized phaceloid and ramose corals. Non-coral taxa found within this bed include abundant *Pecten roemeri* Hill, 1889, *Radiolites* cf. *R. costata* Scott, 1990, large nerineids, *Mexicaprina alata* Filkorn, 2002a, and massive colonies of the stromatoporoid *Actinostromaria* sp. With the exception of the small, solitary *Epistreptophyllum* sp., all of the coral specimens collected from the coral reef horizon are colonial species. Furthermore, the vast majority of these coralla are preserved in situ. Many of the corals and stromatoporoids in the coral reef have been bored by endolithic bivalves and much of the molluscan shell material from this interval exhibits evidence of boring sponges. Intra-reef rock matrix between the larger fossils in the coral reef is mostly an echinoid spine wackestone-floatstone with occasional packstone. The corals from this horizon are discussed further in the paleoecology section of this study.

The coral reef is overlain by a 6.5 m thick *Mexicaprina* floatstone (MP14) which has not yielded any corals. The top of this bed marks the last observed occurrence of *Mexicaprina* species in the measured section. The stratigraphic thickness of the bedding above the *Mexicaprina* floatstone bed becomes thinner, from thin- to medium-bedded, while the compositional proportion and thickness of argillaceous mudstone or wackestone intercalated in the section increases as the overall abundance of fossils decreases. However, the bioclastics that are present in this upper part of the section are fine- to very fine-grained and well-sorted, in contrast to those in the lower part of the section.

A 1.2 m thick wackestone (MP17) in the upper part of the measured section yielded relatively few specimens of six colonial coral species. One of the species belongs to the genus *Actinastrea*, a genus that also is represented in the fauna of the main coral reef (MP 13) and considered as an important pioneer in the colonization of substrates for reefs (Scott, 1981). Although the coral fauna from unit MP 17 indicates incipient reef development, a reef was not formed at this horizon. Furthermore, these coral specimens represent the highest stratigraphic occurrence of reef corals in the measured section. The corals from this horizon are discussed further in the paleoecology section of this study. One of the more argillaceous beds within this stratigraphic interval contains abundant whole tests of echinoids. Although the majority of the tests are preserved whole, their spines are neither attached nor are they common in the surrounding rock. This occurrence of only the echinoid tests in the upper part of unit MP 17 is the converse of the type of echinoid preservation observed in the intra-reef wackestone-packstone of the main coral reef (MP 13) where spines are ubiquitous, but the tests are not present. Based on these two kinds of complimentary styles of echinoid preservation within the same section, it seems likely that the spines had been removed from the tests while they were in the shallower ecologic setting and that weak currents subsequently transported the whole hollow tests into a deeper water depositional setting. Only two species of corals occurred stratigraphically above the zone of abundant echinoids. One of these coral species, the colonial dendrophylliid *Blastozopsammia guerreroterion* Filkorn and Pantoja-Alor, 2004, is a thin-branched, ramose coral that is preserved in the form of fragmented branches in a coral packstone. The majority of the extant dendrophylliid species are azooxanthellate and many live in deeper water marine environments that are atypical of modern coral reef depositional settings (Wells, 1956; Cairns, 2001). The other coral species found above the zone of abundant echinoids is the solitary cunnolitid *Paracycloseris effrenatus* n. sp. which occurs in abundance in a 1 m thick bed (MP 18) of fine-grained wackestone. The relatively small (about 20 mm in diameter), solitary, cupolate corallum of this species indicates that it was not a reef-building coral. The measured stratigraphic section at this locality is truncated within the MP 18 horizon by the present surface of erosion.

TECTONIC SETTING AND PALEOBIOGEOGRAPHIC IMPLICATIONS OF THE CRETACEOUS CORAL FAUNAS

The study area in the Huetamo region of southwestern Mexico lies within the Guerrero terrane, one of the largest tectonic terranes of the continental margin of western Mexico (Figure 1). The tectonic setting of the Huetamo region has been discussed in an earlier report from this study (Filkorn, 2002a), therefore only a summary is given here along with information on the paleobiogeographic significance of the coral faunas from this region. The Guerrero terrane is Late Jurassic to Late Cretaceous in age and mostly composed of rocks with a magmatic arc affinity (Centeno-García et al., 1993). This terrane is believed to have become part of continental North America by the early Tertiary (Campa and Coney, 1983), but the actual time of accretion is poorly constrained (Johnson et al., 1991, p. 122) in part due to the lack of knowledge about its paleogeographic position during the Early Cretaceous (Centeno-García, 1994, p. 190). The part of the Guerrero terrane in southwestern Mexico is composed of several smaller terranes including the Zihuatanejo, Huetamo, and Teloloapan subterranes (Figure 1; Campa and Coney, 1983, p. 1046; Centeno-García et al., 1993). Each of these three subterranes possesses a distinct set of distinguishing features, including a different stratigraphic sequence, metamorphic grade, and type of structural deformation (Coney and Campa, 1987). The fossil coral localities examined in this study lie within the Huetamo subterrane (Figures 1, 2).

Of the 21 coral species from the lower Aptian strata of the Huetamo region, only eight (about 38 percent) are conspecific with those reported earlier from the Lower Cretaceous of the Tehuacán region in the state of Puebla, Mexico (Felix, 1891; Reyeros-Navarro, 1963), a locality about 350 km to the east of the study area. However, of the same 21 coral species, nearly an equal number (nine species, or about 43 percent) also have been reported from the European Cretaceous. Interestingly, the majority of the species common to these other two areas are neither the same nor cosmopolitan species: only two of the species have been reported from both regions. Therefore, the degree of similarity between the lower Aptian coral fauna from the Huetamo region and that from the Tehuacán region does not appear to be significant with regard to tectonic interpretations of the position of the Guerrero terrane during the Early Cretaceous. Even less similarity occurs between the coral species from the late Albian-early Cenomanian fauna of the Mal Paso Formation and those from the Tehuacán region. Of the 18 coral species collected from the Mal Paso Formation, only one has been reported previously from the Tehuacán region. However, 13 (or about 72 percent) of the 18 coral species recognized in the Mal Paso Formation were not known previously from any other localities. Overall, the coral species from the lower Aptian are better known and more widely distributed: only three (or about 14 percent) of the 21 species reported from the lower Aptian in this study are described as new. Other similarities among the coral faunas known from other regions of the globe are discussed in the section on paleobiogeography.

The rather weak similarities among the Cretaceous coral faunas of the adjacent regions of Mexico may be due to several unrelated factors. One of the main reasons is that the coral faunas from both the Huetamo and Tehuacán regions are from different ages. The coral fauna from the lower Aptian of the Huetamo region is similar to that from the Neocomian of the Tehuacán region, but the age of the latter is not precisely known and may range from early Barremian to late Aptian. The importance of the age difference with regard to faunal similarity is demonstrated by this study: although all of the studied coral localities in the Huetamo region are within a distance of 25 km, the coral species known from the lower Aptian Cumburindio Formation are entirely different from those known from the upper Albian-lower Cenomanian upper member of the Mal Paso Formation. This indicates that a total turnover in coral species occurred over a period of at most 22 million years (the time interval from the Barremian-Aptian boundary to the Albian-Cenomanian boundary based on the time scale of Gradstein and others [1995]) and possibly as brief as an interval of 16 million years, i.e., within the narrowest possible limits of the time interval from latest early Aptian to earliest late Albian (based on ages from Gradstein and others [1995]). Furthermore, the corals of the Tehuacán region still are not well known. The numerous reports of corals from the Tehuacán region indicate that a significant portion of the coral fauna remains unknown (see Aguilera, 1906; Filkorn, 2003). As for the late Albian-early Cenomanian coral fauna from the Huetamo region, no coral fauna of similar age has been described from the Tehuacán region. Another reason for the faunal difference could be due to differences in depositional environments. For example, the lower Aptian corals from the Huetamo region were deposited in a mixed carbonate-volcaniclastic depositional environment, whereas those from the Tehuacán region were deposited in a more siliciclastic depositional environment.

The strongest paleontologic evidence for an earlier rather than later accretion time of the southern part of the Guerrero terrane comes from the occurrences of two rudist bivalve genera in the Huetamo region: *Amphitriscoelus* Harris and Hodson, 1922, in the lower Aptian of the Cumburindio Formation (Pantoja-Alor et al., 1994; Alencáster and Pantoja-Alor, 1996a; and this study), and *Mexicaprina* Coogan, 1973, in the upper Albian-lower Cenomanian upper member of the Mal Paso Formation (Filkorn, 2002a; and this study). The relatively limited geographic and stratigraphic distributions of these taxa in the Early and middle Cretaceous of the Caribbean province indicate that the Huetamo region was part of the same paleobiogeographic domain. The implications of the occurrence of *Amphitriscoelus* in the lower Aptian of the Cumburindio Formation have been discussed previously (Pantoja-Alor et al., 1994; Alencáster and Pantoja-Alor, 1996a) and the tectonic significance of the species of *Mexicaprina* in the upper Albian-lower Cenomanian upper member of the Mal Paso Formation of the Huetamo region has been examined in an earlier report from this study (Filkorn, 2002a).

MATERIAL AND METHODS

The Cretaceous corals from two areas within the Huetamo region are investigated in this study. Coral specimens have been collected from outcrops of the lower Aptian Cumburindio Formation in the vicinity of Turitzio, Michoacán, and from outcrops of the upper member of the upper Albian-lower Cenomanian Mal Paso Formation in the state of Guerrero, just north of the rural village of Chumbítaro, Michoacán. Two of the stratigraphic sections that contained corals were described and measured by using the Brunton pocket transit and eye-height method and, for some beds, a tape measure. Field work started in January, 1994, and further field studies and coral collections were made during January and November, 1995, January-February 1996, and January-February, 1997.

All of the Cretaceous coral specimens described previously from Mexico and deposited in the Colección Nacional de Paleontología at the Instituto de Geología, Universidad Nacional Autónoma de México, in Mexico City were re-examined and photographed in January, 1994, as part of the preliminary investigations for the taxonomic work encompassed by this study. Furthermore, a detailed review of the literature on Cretaceous corals and other reef fauna from Mexico and the rest of the globe also has been made (see Filkorn, 2001, 2003, 2006).

Although the majority of the newly collected coralla seemed to be well-preserved based on their external appearance, almost all of them are thoroughly recrystallized internally and thus the original skeletal architecture and microstructure are totally obliterated and indiscernible. Due to the frequently encountered extensive recrystallization, it was difficult or impossible to prepare properly oriented thin sections from some of the specimens. Thus, the material used for thin sections of some of the species was not as well-preserved as would have been desired, but it was the best of the examined material.

Corals from the lower Aptian Cumburindio Formation typically are completely recrystallized to calcite. No original skeletal aragonite has been detected in any of the samples analyzed by x-ray diffraction. The internal regions commonly are dark gray to black crystalline calcite and they lack any observable trace of the original skeletal architecture. An external, silicified rind is present on some of the coralla that were interbedded with volcaniclastics, but this layer proved to be less taxonomically significant that initially anticipated because the silica replacement did not accurately replicate the original skeletal structures. Corals from the coral reef zone of the Cumburindio Formation generally lacked the external rind of silica. Due to the recrystallization, diagenetic alteration, and weathering, the morphological characteristics required for confident taxonomic classification are not preserved on many of the coralla from the Cumburindio Formation. After making numerous serial slices through these recrystallized coralla, sometimes rare, small zones or pockets were discovered which contained preserved vestiges of the skeletal architecture. The descriptions of the skeletal structures of many of the coral species from the Cumburindio Formation are based on studies of these vestiges of relatively well-preserved material.

Corals from the upper Albian-lower Cenomanian Mal Paso Formation appear to be fairly well-preserved externally, but internally the majority of the skeletal material is either recrystallized or not preserved at all because of dissolution. Analyses of samples of skeletal material indicate that all of the coralla are recrystallized to calcite. Some of the larger, massive coralla exhibit evidence of internal dissolution and two distinct stages of subsequent diagenetic mineralization. Vugs formed by dissolution within the cores of these coralla were later lined first by a layer of dark brown sparry or dog tooth calcite and secondly filled by coarsely crystalline celestite. Identifications of the recrystallized skeletal mineralogy and diagenetic minerals have been confirmed by x-ray diffraction.

Oriented thin sections were prepared for each identified coral species, if a sufficient amount of material was available, in order to facilitate the taxonomic descriptions and species identifications. These oriented thin sections include at least one transverse section and one longitudinal section for the majority of the species. Whenever possible, the thin sections for each species were made from the same corallum that was photographed on the external surface. However, in some cases the corallum with the best preserved external detail was entirely recrystallized internally and therefore the oriented thin sections had to be made from a conspecific specimen. Billets or chips were cut from the most well-preserved portions of the coralla by using a tile saw with a diamond blade. Thin sections of these billets were made using standard thin section techniques.

Scanning electron microscopy was performed with an International Scientific Instruments SX-40A scanning electron microscope (SEM). Elemental analyses of some of the coral mineral phases were made with a Princeton Gamma-Tech energy dispersive x-ray system attached to the same SEM. A Bio-rad SEM coating system was used to coat the SEM samples prior to photography or elemental analysis. A gold (Au) coating was applied to samples that were to be photographed by the SEM and a carbon (C) coating was applied to samples that were to be analyzed for elemental composition by the energy dispersive x-ray system.

Determination of the mineralogical compositions of samples of scleractinian coralla and diagenetic phases was made by x-ray diffraction analysis. Samples were powdered and analyzed with a Rigaku Geigerflex x-ray diffractometer. No original skeletal aragonite was detected in any of the analyzed samples.

The photographs shown in the figures of the coral species were made using five different methods. Most photographs of external surfaces of coralla were taken with a Polaroid MP-4 Land Camera and Kodak Technical Pan 4 x 5 inch black and white film. Corallum surfaces were whitened with ammonium chloride if enough surface relief was present, otherwise the natural color contrast of the surface was photographed. Finer, low-relief features on a few corallum surfaces were photographed with the SEM, as discussed above. Field photographs were used to illustrate the largest corallum discovered in the Cumburindio Formation as it appeared in the outcrop. This specimen obviously was too large to collect in its entirety, but some of its branches were sampled and studied in detail and these are illustrated in the same figure as the field photographs. Photographs of the thin sections were made using two methods. For relatively low magnification photographs, the thin sections were projected onto Kodak Technical Pan film with a Simmon Omega variable condenser enlarger. For higher magnifications, a petrographic microscope was used. These photomicrographs were taken with a Wild Photoautomat MPS 45/51S, with a 35 mm magazine, fitted to a Leitz Laborlux 12 Pol petrographic microscope. Transmitted polarized light was used to make the photomicrographs. Photographs from all of the negatives made from thin sections thus show the positive image of the thin sections.

The morphological terminology used in the descriptions of the coral species essentially is that used by J. W. Wells (1956) in the “Treatise on Invertebrate Paleontology, Part F, Coelenterata”. The sequence of morphological features in the species descriptions is modeled from a hierarchically structured list of scleractinian characteristics by M. Bertling (1995). Although there have been substantial increases in knowledge on the taxonomic diversity of corals since the Treatise volume was published in 1956, much of the essential morphological terminology has changed little over the last 175 years. However, the systematic classification presented in the Treatise is more than 50 years old and considered by most modern paleontologists and coral taxonomists to be badly outdated. The systematic classification scheme utilized in this study is adapted from more recent works, specifically those of J. E. N. Veron (1995) and D. Turnšek (1997). This classification scheme is reviewed at the beginning of the section on systematic paleontology.

The limestone terminology used in this study is from the classification scheme of Dunham (1962), with additional terms from a subsequent modification by Embry and Klovan (1971). The combined sets of terms provide a more precise and more useful means of conveying the physical characteristics of the limestones while simultaneously providing information on the environment of deposition.

Systematic Paleontology

Introduction

The systematic paleontology section is divided into two parts because the coral species that are described are from two different geologic ages and there are no species in common. Coral species from the lower Aptian Cumburindio Formation are described in the first part and those from the upper Albian-lower Cenomanian upper member of the Mal Paso Formation are described in the second part. The first part also includes one species from lower Aptian strata of the San Lucas Formation.

All of the coral specimens described in this study are deposited in the Colección Nacional de Paleontología at the Instituto de Geología (IGM), Universidad Nacional Autónoma de México, México D. F., Mexico.

Scleractinian classification

The higher level taxonomic groups (suborders and families) used in the systematic paleontology section are adapted from the classification schemes outlined by Veron (1995) and Turnšek (1997). The sequence of suborders within the classification scheme is modeled primarily after the possible phylogenetic relationships outlined by Turnšek (1997, p. 36) with addition of two suborders, as indicated by an asterisk (*), from the scleractinian family tree presented by Veron (1995, p. 110). The placements of these latter two suborders within the classification scheme are tentative. Other modifications to the classification scheme are noted in the text. Turnšek's (1997) classification scheme of the scleractinian suborders and their possible phylogenetic groupings is used as a template for the list of coral species presented at the beginning of each of the two systematic paleontology subsections.

The coral descriptions presented herein are based upon specimens collected during this study. In several cases newly collected specimens are described and assigned to species that originally were described and named in an earlier work. In these latter situations, the descriptions of the Mexican specimens are given in order to document their morphological characteristics and to support the taxonomic determinations.

The sequence of the morphological features presented within each of the species descriptions is modeled after a hierarchically structured list of scleractinian characteristics (see Bertling, 1995). The morphological terminology essentially follows that of Wells (1956), with minor additions as necessary.

Abbreviations

The following abbreviations are used in the systematic paleontology section.

Coral morphology:
CD : calicular diameter;
LCD: lesser calicular diameter;
GCD : greater calicular diameter;
H: height;
S_x: septa of x cycle, where x = 1, 2, 3, 4, and so on;
$S_x>S_y$: size relationship of septa: septa of x cycle larger than septa of y cycle;
C_x: costae of x cycle, where x = 1, 2, 3, 4, and so on;
$C_x>C_y$: size relationship of costae: costae of x cycle larger than costae of y cycle.

Other abbreviations:
IGM: Colección Nacional de Paleontología, Instituto de Geología, Universidad Nacional Autónoma de México, Mexico City;
M : prefix on labels of thin sections of coral specimens from the upper member of the Mal Paso Formation in the state of Guerrero, just north of Chumbítaro, Michoacán, Mexico;
MP : prefix on an informal numbering of lithologic units of the upper member of the Mal Paso Formation at the same locality mentioned above;
TZ: label on thin sections of coral specimens from the Cumburindio Formation in the vicinity of Turitzio, Michoacán, Mexico.

Fossil localities

The Cretaceous corals examined in this study have been collected from the following localities. The location, stratigraphic horizon, age, and latitude-longitude coordinates are given for each locality. The coordinates are based on the Mexican 1:50,000 scale topographic sheets Huetamo (E14A64) and Coyuca de Catalán (E14A74). The positions of these localities are shown in Figure 2.

1. Western flank of Loma Teremitio, about 1.5 km north-northwest of the town of Turitzio, Michoacán. Cumburindio Formation, lower Aptian. Latitude 18 degrees 32.39 minutes north, longitude 100 degrees 57.13 minutes west.
2. The Arroyo Los Hornos and adjacent slopes to the south, about 1 km north of Turitzio, Michoacán. Cumburindio Formation, lower Aptian. Latitude 18 degrees 32.10 minutes north, longitude 100 degrees 56.74 minutes west.
3. The crest of a small hill locally known as Loma de San Juan, just south of Turitzio, Michoacán. Cumburindio Formation, lower Aptian. Latitude 18 degrees 31.28 minutes north, longitude 100 degrees 56.65 minutes west.
4. Near the village of Las Eras, just southwest of Turitzio. Cumburindio Formation, lower Aptian. Latitude 18 degrees 30.60 minutes north, longitude 100 degrees 59.0 minutes west.
5. The eastern flank of Loma La Cuchilla, locally called Loma de Los Cuachalalates, a hill about 7 km south-southeast of Huetamo, Michoacán. Upper part of the lower member of the San Lucas Formation, lower Aptian. Latitude 18 degrees 33.81 minutes north, longitude 100 degrees 52.04 minutes west.
6. In the state of Guerrero, about 0.75 km north of the rural village of Chumbítaro, Michoacán, and just north of the state border. Upper member of the Mal Paso Formation, upper Albian-lower Cenomanian. Latitude 18 degrees 29.3 minutes north, longitude 100 degrees 42.5 minutes west.

PART 1: LOWER APTIAN CORAL SPECIES

The 20 coral species identified from the lower Aptian strata of the Cumburindio Formation are listed below. One species, *Stylina regularis* Fromentel, 1862, from lower Aptian strata of the San Lucas Formation also is listed below and described in this section. Suborders primarily are from Turnšek (1997, p. 36) with two additions, indicated by an asterisk (*), from Veron (1995, p. 110). The possible phylogenetic relationships of the suborders are indicated by their arrangement into four main groups (from Turnšek, 1997, p. 36). The placements of the two suborders from Veron (1995) within the four main groups are tentative.

Group 1

Suborder Pachythecaliina Eliášová, 1976 (Triassic)
Suborder Stylophyllina Beauvais, 1981a (Triassic)
Suborder Amphiastreina Alloiteau, 1952
  Family Amphiastraeidae Ogilvie, 1897
    Genus *Amphiastrea* Étallon, 1859
      Amphiastrea aethiopica Dietrich, 1926
  Family Heterocoeniidae Oppenheim, 1930
    Genus *Latusastrea* d'Orbigny, 1849
      Latusastrea alveolaris (Goldfuss, 1829)

Group 2

Suborder Archaeocoeniina Alloiteau, 1952
  Family Actinastraeidae Alloiteau, 1952
    Genus *Actinastrea* d'Orbigny, 1849
      Actinastrea pseudominima (Koby, 1897)
  Suborder Stylinina Alloiteau, 1952
  Family Cladophylliidae Morycowa and Roniewicz, 1990
    Genus *Cladophyllia* Milne Edwards and Haime, 1851
      Cladophyllia stewartae Wells, 1944
  Family Cyathophoridae Vaughan and Wells, 1943
    Genus *Cyathophora* Michelin, 1843
      Cyathophora haysensis Wells, 1932
      Cyathophora micrommatos (Felix, 1891)
  Family Stylinidae d'Orbigny, 1851
    Genus *Stylina* Lamarck, 1816
      Stylina regularis Fromentel, 1862

Group 3

Suborder Distichophylliina Beauvais, 1981a (Triassic)
Suborder Rhipidogyrina Roniewicz, 1976
  Family Rhipidogyridae Koby, 1905
    Genus *Saltocyathus* Morycowa and Masse, 1998
      Saltocyathus cumburindioensis n. sp.
  Family Trochoidomeandridae Turnšek, 1981
    Genus *Rhipidomeandra* Morycowa and Masse, 1998
      Rhipidomeandra bugrovae Morycowa and Masse, 1998

Suborder Faviina Vaughan and Wells, 1943
Family Isastraeidae Alloiteau, 1952
Genus *Isastrea* Milne Edwards and Haime, 1851
Isastrea whitneyi Wells, 1932
Suborder Astreoina Alloiteau, 1952 *
Family Faviidae Gregory, 1900
Genus *Eohydnophora* Yabe and Eguchi, 1936
Eohydnophora ovalis Masse and Morycowa, 1994
Genus *Eugyra* Fromentel, 1857
Eugyra lanckoronensis (Morycowa, 1964)
Suborder Meandriina Alloiteau, 1952
Suborder Caryophylliina Vaughan and Wells, 1943
Suborder Dendrophylliina Vaughan and Wells, 1943 *

Group 4

Suborder Archaeofungiina Alloiteau, 1952 (Triassic)
Suborder Fungiina Verrill, 1865
Family Actinacididae Vaughan and Wells, 1943
Genus *Actinaraea* d'Orbigny, 1849
Actinaraea michoacanensis n. sp.
Genus *Thamnarea* Étallon, 1864
Thamnarea hornosensis n. sp.
Family Calamophylliidae Vaughan and Wells, 1943
Genus *Calamophyllia* Blainville, 1830
Calamophyllia sandbergeri Felix, 1891
Family Haplaraeidae Vaughan and Wells, 1943
Genus *Meandrophyllia* d'Orbigny, 1849
Meandrophyllia sauteri (Felix, 1891)
Family Siderastreidae Vaughan and Wells, 1943
Genus *Siderofungia* Reis, 1889
Siderofungia irregularis Felix, 1891
Suborder Microsolenina Morycowa and Roniewicz, 1995
Family Latomeandridae Alloiteau, 1952
Genus *Fungiastraea* Alloiteau, 1952
Fungiastraea crespoi (Felix, 1891)
Family Microsolenidae Koby, 1890
Genus *Microsolena* Lamouroux, 1821
Microsolena guttata Koby, 1897
Genus *Polyphylloseris* Fromentel, 1857
Polyphylloseris conophora (Felix, 1891)
Family Synastraeidae Alloiteau, 1952
Genus *Felixastraea* Oppenheim, 1930
Felixastraea mexicana Reyeros-Navarro, 1963

Class Anthozoa Ehrenberg, 1834
Subclass Zoantharia Blainville, 1830
Order Scleractinia Bourne, 1900
Suborder Amphiastreina Alloiteau, 1952
Family Amphiastraeidae Ogilvie, 1897
Genus *Amphiastrea* Étallon, 1859

Type species. *Amphiastrea basaltiformis* Étallon, 1859 (p. 500-502).

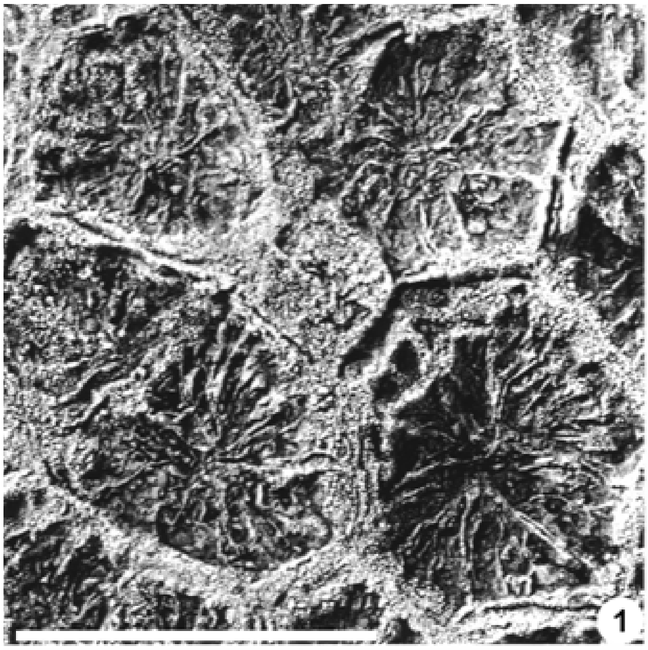
***Amphiastrea aethiopica* Dietrich, 1926**
Figure 7

Amphiastrea aethiopica Dietrich, 1926, p. 62-63, pl. 8, fig. 1; Hackemesser, 1936, p. 9; Bendukidze, 1961, p. 6-7, pl. 5, fig. 8; Turnšek and Buser, 1976, p. 51-52, 76, pl. 5, figs. 4-6; Turnšek, 1992, p. 164; Baron-Szabo and Steuber, 1996, p. 21, pl. 11, fig. 3; Turnšek, 1997, p. 13, pl. 13, figs. a-e; Baron-Szabo and González-León, 1999, p. 480, fig. 4k; Baron-Szabo and González-León, 2003, p. 192.

Description. Corallum colonial, attached, cerioid or subcerioid, weakly aphroid, massive, flattened inverted cone-shaped, noncostate, small in size; the examined specimen, a fragment, about 60 x 60 mm in width and 45 mm in height. Colony formation by intratentacular(?) budding. Corallites distinct, prismatic, closely packed, axes perpendicular to corallum surface. Calices distinct, typically monocentric; calicular margins irregularly polygonal, four, five, six or seven sided. CD variable from 2 to 8 mm, depth of calices 1-2 mm.

Septa well-developed but often vaguely defined peripherally, weakly insert, laminar, and solid. Septa typically 24 in

Figure 7. *Amphiastraea aethiopica* Dietrich, 1926, IGM-6996, Cumburindio Formation, lower Aptian, Loma de San Juan, Turitzio, State of Michoacán, Mexico. 1, Detail of weathered oral surface of corallum, scale bar = 1 cm; 2, transverse thin section, corallum recrystallized, same scale as Figure 7.1; 3, longitudinal thin section, same scale as in Figure 7.1; 4, transverse thin section, detail of septa, dissepiments and wall of one corallite, scale bar = 1 mm; 5, longitudinal thin section, detail of dissepiments and corallite walls, same scale as Figure 7.4; 6, same section, detail of vesicular dissepiments, same scale as Figure 7.4.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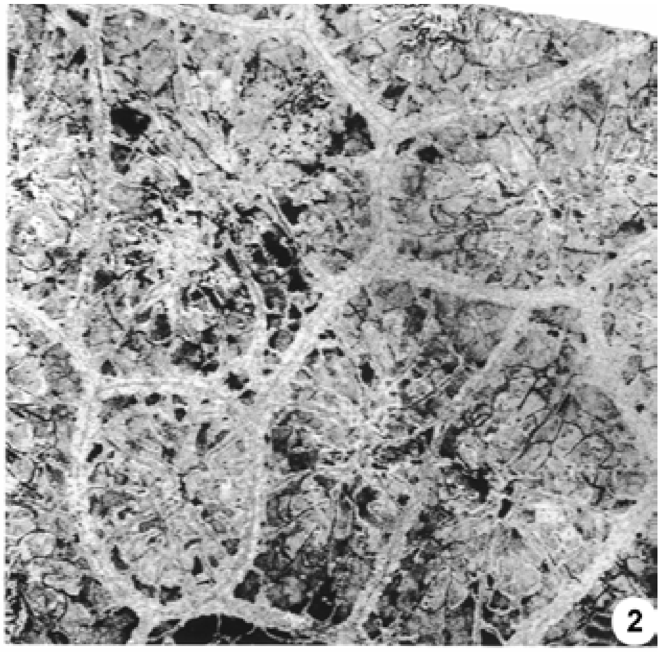
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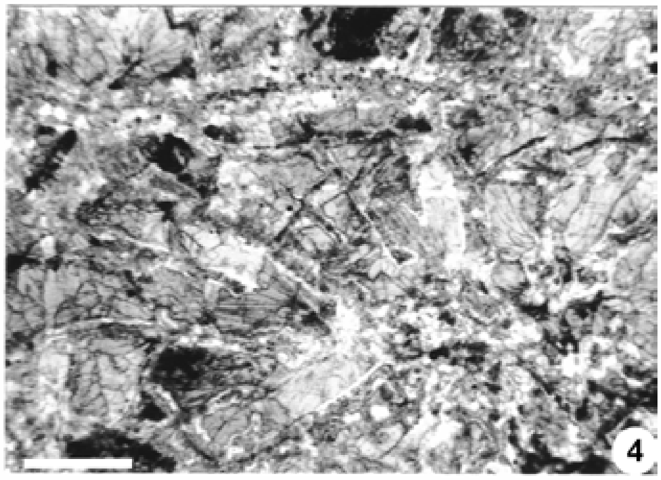
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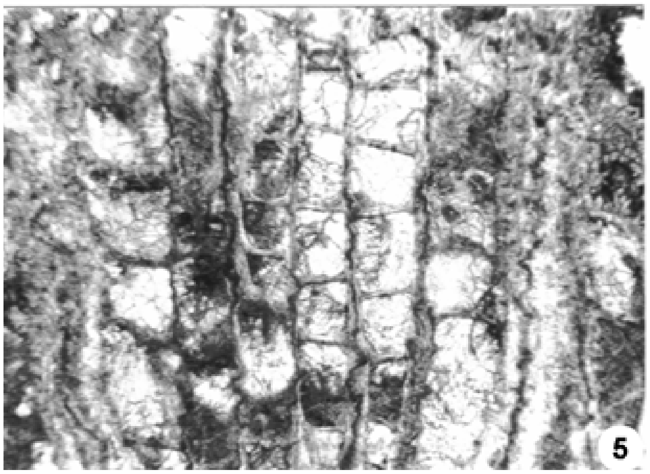
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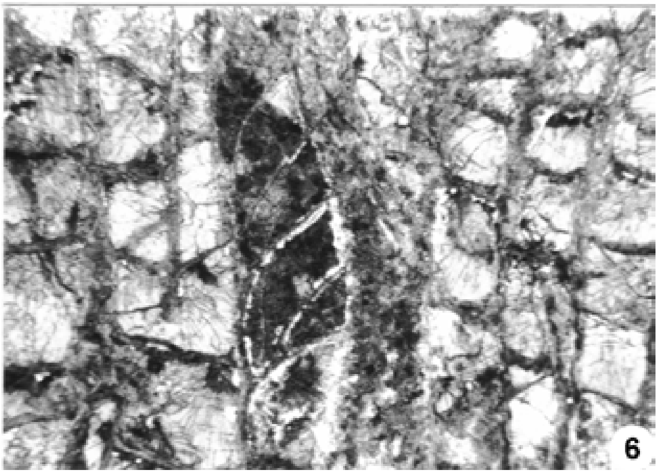
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number, radially arrayed with a generally hexameral symmetry and in three septal cycles; size relationship of septa: $S_1>S_2>S_3$. S_1 thin, straight or broadly curved in cross-section, typically extended from outer wall nearly to corallite axis. S_2 similar to S_1 in shape, but slightly smaller and often separated from wall by a narrow zone of vesicular endothecal dissepiments. S_2 commonly extended to near corallite axis also. S_3 developed but reduced, length much shorter than that of S_2, and also frequently separated from outer wall by the zone of dissepiments, but even more so than the S_2. Lateral surfaces of septa smooth; septal margins smooth. Inner margins of S_1 and S_2 often thickened axially and fused aborally. Pali and columella absent.

Wall epithecal, about 0.5 mm thick, those of adjacent corallites often fused together and up to 1 mm thick at calicular margin. Upper, distal edges of walls terminated by linear, raised, parallel, twin ridges. Endothecal dissepiments numerous, thin, discontinuous, primarily in two zones: a tabular central region and a vesicular outer region. Dissepiments spaced about 1 mm apart. Exterior lateral surface of corallum ornamented with fine, horizontal growth lines.

Material examined. One small fragment of a colony, IGM-6996, with three thin sections (TZ-36 through TZ-38).

Occurrence. Cumburindio Formation, lower Aptian; the coral reef horizon at the crest of a small hill known as Loma de San Juan, just south of Turitzio, Michoacán, Mexico. The coordinates of this locality are: 18° 31.28' N, 100° 56.65' W.

The only other known Mexican occurrence of this species has been reported from the upper Barremian-lower Aptian and upper Aptian-middle Albian strata of the Cerro de Oro Formation in the northern part of the state of Sonora (Baron-Szabo and González-León, 1999, p. 480).

This species also has been reported from the Urgonian (Barremian-Aptian) of Tanzania, East Africa (the type locality), and western Slovenia, the Barremian-Aptian of Yugoslavia, the Aptian of Greece, the Lower Cretaceous (Hauterivian-Barremian) of Crimea, and the Cenomanian(?) of Greece. The East African Cretaceous strata were previously thought to be older, within the Neocomian (Schuchert, 1918).

Discussion. The morphological characteristics of the Mexican corallum described above are the same as those typically attributed to *Amphiastrea aethiopica*, therefore the specimen is assigned to that species.

Only one other morphologically similar species of *Amphiastrea* has been reported from the American Cretaceous: *Connectastrea infundibuliformis* Wells, 1932 (p. 236-237, pl. 33, figs. 6, 7). The latter genus, *Connectastrea* Koby, 1904 (p. 67), subsequently has been considered a junior synonym of *Amphiastrea* by some authors (see Vaughan and Wells, 1943, p. 231; Wells, 1956, p. F397). Wells (1932) noted that *Connectastrea* was previously known only from the Upper Jurassic and that *C. infundibuliformis* was morphologically similar to the type species, *A. piriformis* Gregory, 1900 (p. 71-72, pl. 14, fig. 14, pl. 15, figs. 1, 2), from the Upper Jurassic of India and Portugal, except the latter species possesses corallites that are smaller, from 3 to 5 mm in CD. The single corallum of *A. infundibuliformis* described by Wells was the only coral specimen collected from the uppermost Glen Rose Formation in Comal County, Texas, and it is the only known occurrence of that species. The type specimen possesses polygonal calices with shared single walls and an average CD of 8 mm, and septa that are relatively thick, weakly exsert, and 12 to 18 in number.

Several other species of *Amphiastrea* are known from the Cretaceous of Europe, including *Amphiastrea gracilis* var. *caespitosa* de Angelis, 1905c, and *A. waltheri* de Angelis, 1905c, both from the Urgonian of Capri, and *A. paronai* Prever, 1909, *A. guiscardii* Prever, 1909, *A. delorenzoi* Prever, 1909, and *A. minima* Prever, 1909, from the Cenomanian of Monti d'Ocre, Italy (Felix, 1914a, p. 13, 1914b, p. 87). Three species of *Amphiastrea* recently have been reported from the Aptian of Greece: *A. aethiopica* Dietrich, 1926, *A.* cf. *A. aethiopica* Dietrich, 1926, and *A. minima* Prever, 1909 (Baron-Szabo and Steuber, 1996, p. 21).

Members of this genus also have been reported from the Cretaceous deposits of Japan (Eguchi, 1951) and several species have been described, including *Amphiastrea hiraigaensis* (p. 15-16, pl. 2, figs. 9, 10), *A. yabei* (p. 16, pl. 12, figs. 4, 5), *A.* sp. (p. 16-17, pl. 12, fig. 6), *A.* sp. (p. 17, pl. 12, figs. 1, 2, 3), and *A. kamoensis* (p. 59-60, pl. 24, figs. 10a, 10b).

Family Heterocoeniidae Oppenheim, 1930

Genus *Latusastrea* d'Orbigny, 1849

Latusastrea d'Orbigny, 1849, p. 10; d'Orbigny, 1850b, p. 387; Vaughan and Wells, 1943, p. 231; Alloiteau, 1952, p. 643; Wells, 1956, p. F397; Beauvais, 1976, p. 25-26, pl. 6, fig. 3.

Pleurocoenia d'Orbigny, 1849, p. 7.

Type species. *Explanaria alveolaris* Goldfuss, 1829 (p. 110, pl. 38, fig. 6).

Latusastrea alveolaris (Goldfuss, 1829)

Figure 8

Explanaria alveolaris Goldfuss, 1829, p. 110, pl. 38, fig. 6; Quenstedt, 1881, p. 822-824, pl. 175, figs. 27-31.

Latusastraea alveolaris (Goldfuss, 1829). Becker and Milaschewitsch, 1875, p. 166-167, pl. 40, figs. 1a, 1b; Beauvais, 1976, p. 25-26, pl. 6, fig. 3.

Latusastrea alveolaris (Goldfuss, 1829). d'Orbigny, 1850b, p. 387; Vaughan and Wells, 1943, p. 316, pl. 24, figs. 7, 7a; Geyer, 1954, p. 192-193, pl. 16, fig. 1; Wells, 1956, p. F397, fig. 293; Lauxmann, 1991, p. 145, pl. 6, figs. 6-8.

Latusastraea cf. *L. polygonalis* (Fromentel, 1862). Felix, 1891, p. 157-158, pl. 24, figs. 1, 1a, 1b; Löser, Bach, and Müller, 2002, p. 50.

Latusastrea sp. Löser, 2006, p. 24, figs. 2J-L.

Description. Corallum colonial, attached, plocoid, incrusting to foliaceous, very faintly striated or granulated, and small in size, the largest specimen about 35 x 45 mm in width and 70 mm in height. Colony formation by intratentacular budding. Corallites laterally compressed, cuneiform or subcylindrical, closely packed, partly protuberant, and aligned in parallel, vertically oriented rows. Corallite axes oriented at low angle relative to corallum surface.

Calices unevenly distributed, monocentric, extended laterally outward from corallum surface with oral surfaces oriented upward. Calicular margins elliptical to crescentic in outline. Calices shallow with small, funnel-shaped axial areas. Greater dimension of CD typically about 4 mm and oriented horizontally, parallel to corallum surface. Lesser dimension of CD about 2 mm, oriented perpendicular to colony surface, and angled outward relative to corallum surface, typically 45 degrees or steeper. Intercalice distance highly variable: typically 3-12 mm vertically along side of corallum and 1-4 mm horizontally along lateral transect across same area.

Septa unequally developed, non-exsert, laminar, and solid. Septa typically 24 in number, differentially developed in each half of corallite, markedly bilateral in symmetry, and inserted in three septal cycles. Septa unequally developed within each cycle, the expected relationship between ontogenetic sequence and septal development or size instead replaced by strongly bilateral, symmetrical development of septa within calice. Generalized size relationship among septa, $S_1>S_2>S_3$, corresponds only to septa in that half of corallite proximal to corallum surface. Septa of all three cycles present in distal half of corallite, but weakly developed and very short relative to those in opposite half. Septa blade-shaped in cross section, straight or gently curved, closely spaced, and thin. S_1 well-developed on proximal side of corallite, oriented nearly parallel to LCD and often elongated into axial region. S_1 about 0.2 mm in width, their length typically equal to or greater than half the LCD. S_2 similar to S_1 in shape, only slightly thinner and shorter. S_3 thinner and shorter than S_2, their length about half that of the S_2. Interseptal spaces nearly equal to width of adjacent septa. Lateral surfaces of septa uneven to faintly crenulated. Septal margins appear beaded. Pali and columella absent.

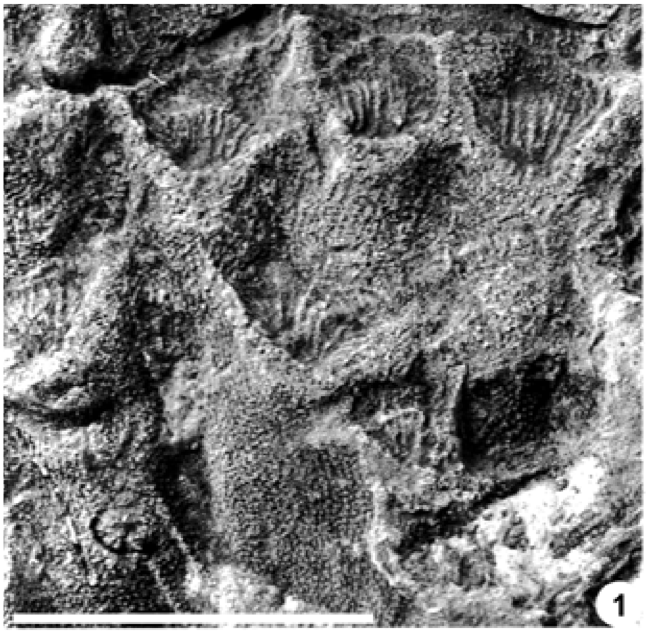
Wall primarily septothecal and thin. Endothecal dissepiments formed in two zones: tabular, thin, spaced about two per mm in near axial regions and vesicular in peripheral regions adjacent to wall. Exothecal dissepiments or coenosteum vesicular and in a narrow zone. Outer surface of corallum faintly costate or striated and granulated.

Material examined. Two specimens: IGM-6997, a small corallum or part of a corallum (figured); and a small fragment, IGM-6998, with two thin sections (TZ-22 and TZ-23).

Occurrence. Cumburindio Formation, lower Aptian; the coral reef horizon at the crest of a small hill called Loma de San Juan, just south of Turitzio, Michoacán, Mexico. The coordinates of this locality are: 18° 31.28' N, 100° 56.65' W. The only other Mexican occurrence of this species is from the Lower Cretaceous in the vicinity of Tehuacán, state of Puebla (see comments in the discussion).

The other occurrences of this species are from the Upper Jurassic of Europe.

Discussion. The diameter of the calices, the number and arrangement of the septa, and the granulated exterior surfaces of the corallum are most similar to those characteristics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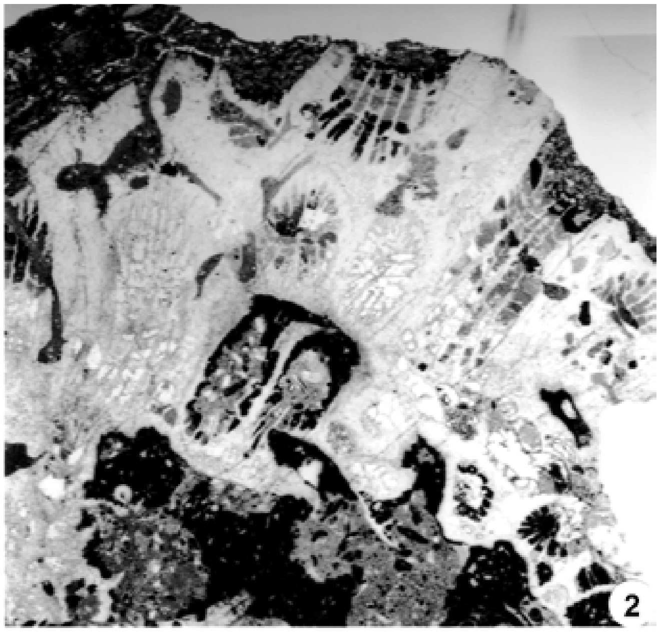
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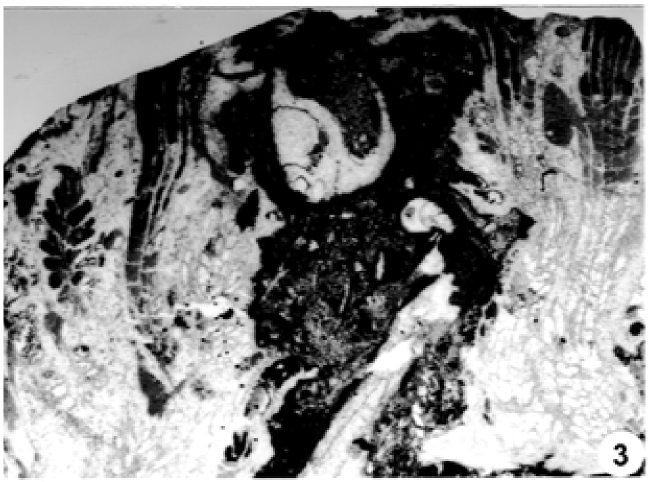
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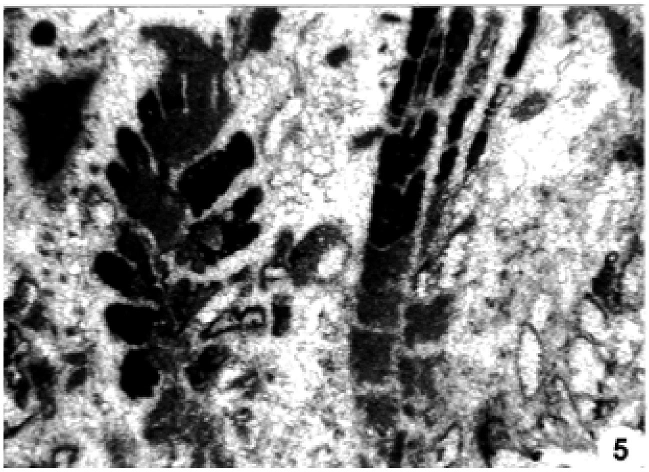
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typically attributed to *Latusastrea alveolaris*, thus the specimens examined are referred to that species. The species described by Felix (1891, p. 157-158, pl. 24, figs. 1, 1a, 1b) as *Latusastraea* cf. *L. polygonalis* (Fromentel, 1862) appears to possess these same morphological characteristics, therefore it is tentatively reassigned to *L. alveolaris*.

Suborder Archaeocoeniina Alloiteau, 1952
Family Actinastraeidae Alloiteau, 1952
Genus *Actinastrea* d'Orbigny, 1849

Type species. *Astrea geminata* Goldfuss, 1826 (p. 69-70, pl. 23, figs. 8e, f; d'Orbigny, 1849, p. 10).

Actinastrea pseudominima (Koby, 1897)

Figure 9

Astrocoenia pseudominima Koby, 1897, p. 59-60, pl. 15, figs. 4, 4a; ?Felix, 1909, p. 174; Felix, 1914a, p. 74; Felix, 1914b, p. 37; Dietrich, 1926, p. 93-94, pl. 6, fig. 9; Gregory, 1930, p. 200, pl. 18, fig. 5; Hackemesser, 1936, p. 71-72, pl. 7, fig. 14; Marković, 1951, p. 192, pl. 5, fig. 4.

*Actinastrea pseudominima (*Koby, 1897). Bendukidze, 1961, p. 8; Morycowa, 1964, p. 18, pl. 1, figs. 2-5, pl. 2, fig. 2; Morycowa, 1971, p. 33-39, pl. 1, figs. 1-3, pl. 2, fig. 1, pl. 3, fig. 1, pl. 4, fig. 1, pl. 5, fig. 3, text figs. 6a, 11-14; Sikharulidze, 1977, p. 69-71, pl. 7, fig. 1; Sikharulidze, 1979, p. 303-304; Kuzmicheva, 1980, p. 92, pl. 34, fig. 1; Morycowa, 1984, p. 78, pl. 17, fig. 2; Geyer and Rosendahl, 1985, p. 167, pl. 2, fig. 1; Kuzmicheva, 1987, p. 217-220, pl. 1, figs. 1a, b; Kuzmicheva, 1988, p. 154, pl. 1, figs. 1a, b; ?Löser, 1989, p. 98, pl. 21, fig. 3, text fig. 3; Morycowa, 1989, p. 60, pl. 18, fig. 2; Eliášová, 1992, p. 402, pl. 5, fig. 3; Turnšek, 1992, p. 164; Abdel-Gawad and Gameil, 1995, p. 8, pl. 4, figs. 3-6; Morycowa and Masse, 1998, p. 736, 738, figs. 10.1, 10.3.

Astrocoenia hexamera Fritzsche, 1923, p. 318-319, pl. 3, fig. 7.

Description. Corallum colonial, attached, cerioid, incrusting to massive to ramose, and noncostate. Size relatively large; examined specimen 20 cm in diameter and 10 cm in height. Colony formation by extratentacular budding. Corallites distinct, prismatic, usually six-sided, closely packed. Calices monocentric, margins subcircular to rounded polygonal in outline. CD variable, from 1 to 2 mm; depth of calices about 1 mm. Calices typically separated by intercalice distance of about 0.5 to 1 mm. Calicular centers typically spaced 1-2 mm apart, rarely 3 mm.

Septa well-developed, weakly exsert, laminar, and solid. Septa typically 24 in number, radially arrayed, hexamerally symmetrical, and inserted in three septal cycles. Size relationship among septa: $S_1 \geq S_2 > S_3$. S_1 and S_2 laminar to slightly blade-shaped in cross section, straight, and very thin, less than 0.1 mm. Septa of first two cycles extended from wall to columella. Full complement of S_3 (12 septa) typically present but weakly developed. S_3 slightly thinner than S_2 and about half the length of the S_2. S_2 thickened at insertion points of S_3. Lateral surfaces of septa smooth or finely granular; septal margins smooth. Inner margins of S_1 and S_2 fused to columella. Inner margins of S_3 fused to parental S_2 aborally.

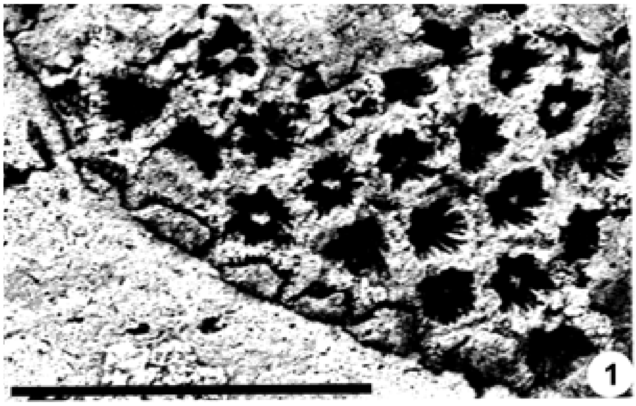
Pali-like structures developed aborally on S_2 at insertion of S_3. Columella well-developed, styliform, solid, vertically continuous, cylindrical to elliptical or asteriform in cross section. Width of columella about 0.5 mm, or about one-fourth to one-third the CD.

Wall septothecal. Endothecal dissepiments tabular, discontinuous, thin, vertically spaced about 5-6 per mm.

Material examined. One large massive to ramose corallum, IGM-6999, with three thin sections (TZ-39 through TZ-41). The corallum was collected from an in situ occurrence at the base of the Loma de San Juan (see occurrence).

Occurrence. Cumburindio Formation, lower Aptian. Coralla of this species are common in the lowermost exposed argillaceous mudstone beds at the base of the western flank

Figure 8. *Latusastraea alveolaris* (Goldfuss, 1831), Cumburindio Formation, lower Aptian, Loma de San Juan, Turitzio, State of Michoacán, Mexico. 1, IGM-6997, detail of weathered oral surface of corallum, lateral view, scale bar = 1 cm; 2, IGM-6998, thin section, corallum recrystallized, same scale as Figure 8.1; 3, same corallum, primarily longitudinal thin section, same scale as Figure 8.1; 4, oblique longitudinal section, detail of septa and dissepiments in one calice, scale bar = 1 mm; 5, longitudinal thin section, detail of two adjacent corallites with different orientations, nearly transverse on left and longitudinal on right, same scale as Figure 8.4; 6, same section, detail of dissepiments in two adjacent corallites, same scale as Figure 8.4.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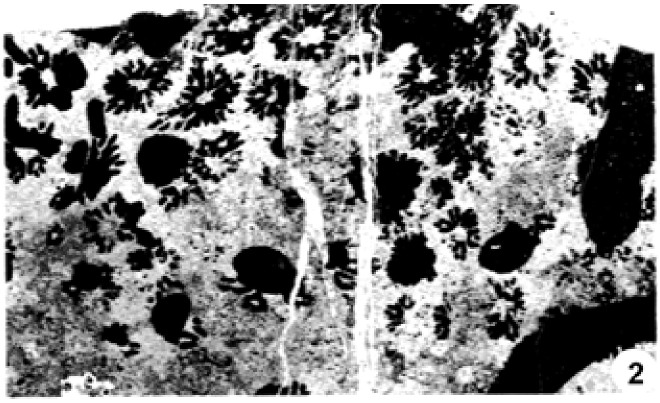
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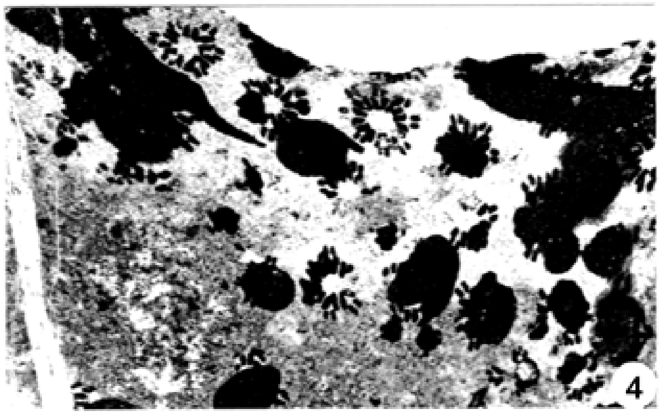
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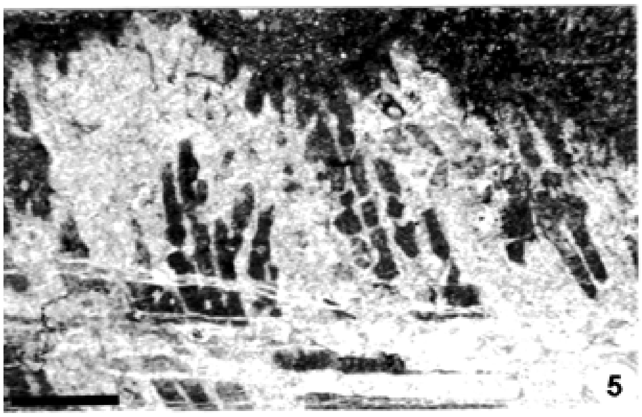
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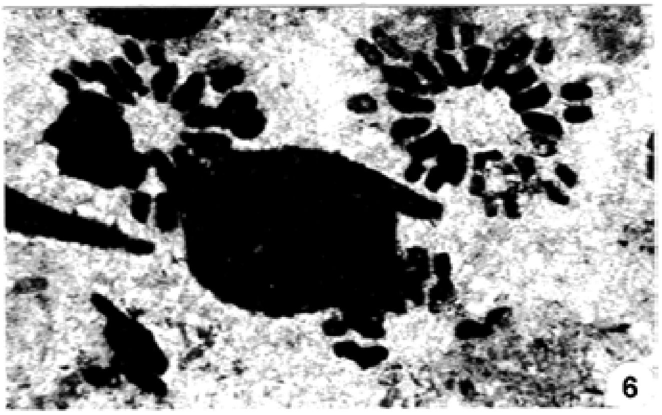
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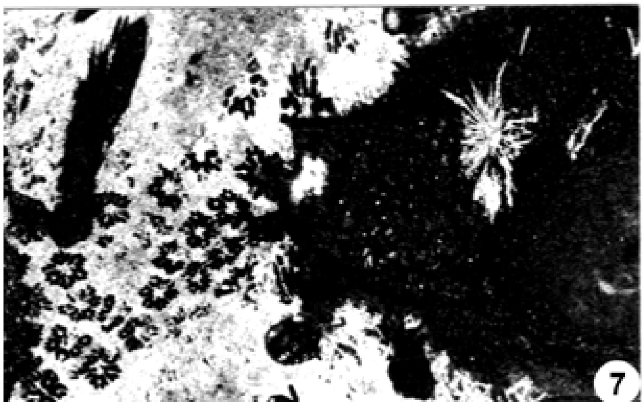
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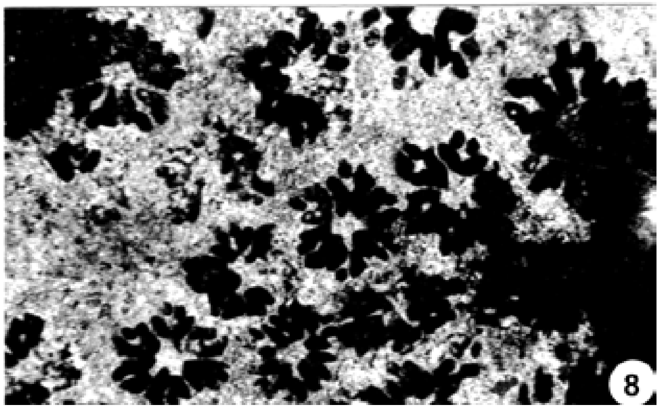
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of a small hill locally known as Loma de San Juan, just south of Turitzio, Michoacán, Mexico. This locality is just west-northwest of the position of the coral reef locality at the crest of the same hill. The coordinates of the latter locality are: 18° 31.28' N, 100° 56.65' W.

This species also has been reported from the Urgonian of Reignier, Switzerland, which is the type locality; the Urgonian north of Freretown, Kenya, East Africa; the lower Valanginian of southern Spain; the Neocomian (Hauterivian-Barremian), Barremian and Aptian of Poland; the Neocomian (Hauterivian-Barremian) of German East Africa (Tanzania); the Hauterivian of Crimea, the lower Barremian of Georgia, Turkmenistan and France; the Barremian-Aptian of the Soviet Carpathians and Yugoslavia; the lower Aptian of Romania; the Aptian of Serbia; the Albian of northern Sinai Peninsula, Egypt; the middle Cretaceous (Cenomanian) of Greece; the ?Cenomanian of Syria and Germany; and the upper Cenomanian-lower Turonian of Czechoslovakia.

Astrocoenia hexamera Fritzsche, 1923 (p. 318-319, pl. 3, fig. 7), which has been considered a junior synonym of *A. pseudominima* (Koby, 1897) (Dietrich, 1926, p. 94; Morycowa, 1964, p. 18), was originally described from the Neocomian of Molle Alto, Chile.

Discussion. The morphological characteristics of the Mexican specimen described above are the same as those typically attributed to *Actinastrea pseudominima* (Koby, 1897), therefore the material is assigned to that species.

Some of the other species of *Actinastrea*, including *A. kellumi* (Wells, 1946), *A. whitneyi*, and *A. cesaredensis*, also possess pali-like trabecular extensions from the upper margins of the septa (Wells, 1946, p. 2).

Additional data on the stratigraphic and geographic distributions of this genus are provided in the discussion sections given for *A. guadalupae* (Roemer, 1849) and *A. chumbitaroensis* n. sp. in the second part of the section on systematic paleontology.

Suborder Stylinina Alloiteau, 1952

Family Cladophylliidae Morycowa and Roniewicz, 1990

Discussion. The family was erected to accommodate three genera, *Cladophyllia*, *Apocladophyllia* and, with reservation, *Halysitastraea* Geyer, 1968.

Genus *Cladophyllia* Milne Edwards and Haime, 1851 (p. 81)

Type species. *Lithodendron dichotomum* Goldfuss, 1829 (p. 44, pl. 13, figs. 3a, b), by subsequent designation (Wells, 1933, p. 172).

Cladophyllia stewartae Wells, 1944b

Figure 10

Cladophyllia n. sp. Hedberg and Pyre, 1944, p. 7.

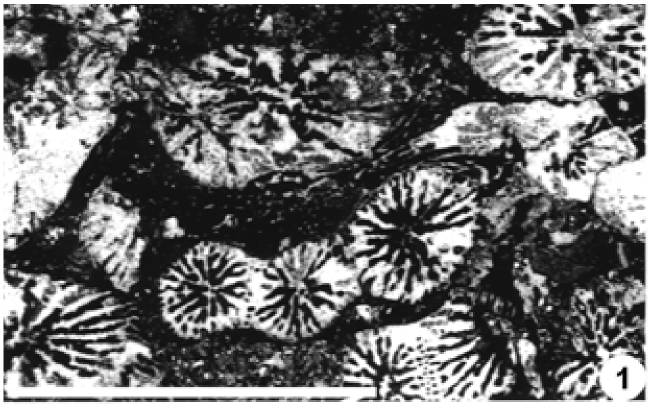
Cladophyllia stewartae Wells, 1944b, p. 442, pl. 74, figs. 2, 3; Morycowa and Roniewicz, 1990, p. 168, 170.

Description. Corallum colonial, attached, phaceloid, bushy, noncostate; size of corallum unknown. Colony formation by dichotomous intratentacular distomodaeal budding. Branches generally cylindrical, typically from 3 to 4 mm in diameter, subparallel to intertwined, frequently bifurcated, and laterally free but closely spaced (3 mm or less) or in contact and fused to each other. Each length of branch between bifurcations essentially composed of a single elongate corallite. Branch insertions spaced about 8 mm apart. Apophyses between branches absent. Corallite morphological characteristics essentially the same as those given for the branches.

Calices monocentric; calicular margins circular to subcircular in outline. CD typically from 3 to 4 mm, or slightly less than the diameter of the branch. Depth of calices about 1 mm. Axial region at center of calice about one-third the CD in diameter.

Septa well-developed, exsert(?), laminar and solid. Trabecular microstructure not preserved. Septa typically at least 24 in number, arranged hexamerally and inserted in three septal cycles: $S_1 \geq S_2 > S_3$. Some S_4 occasionally present but very weakly developed. Septa blade-shaped in cross section and straight, those of the first cycle about 0.2 mm in width. S_1 and S_2 extended from wall to columella in axial

Figure 9. *Actinastrea pseudominima* (Koby, 1897), IGM-6999, Cumburindio Formation, lower Aptian, western base of Loma de San Juan, Turitzio, State of Michoacán, Mexico. 1, Part of the oral surface, weathered, scale bar = 1 cm; 2, transverse thin section, same scale as Figure 9.1; 3, oblique longitudinal thin section, same scale as Figure 9.1; 4, transverse thin section with some of the larger, more widely spaced corallites, same scale as Figure 9.1; 5, detail of oblique longitudinal thin section, scale bar = 1 mm; 6, detail of corallites shown above, same scale as Figure 9.5; 7, transverse thin section of some of the smaller corallites, same scale as Figure 9.1; 8, same section, detail of corallites, same scale as Figure 9.5.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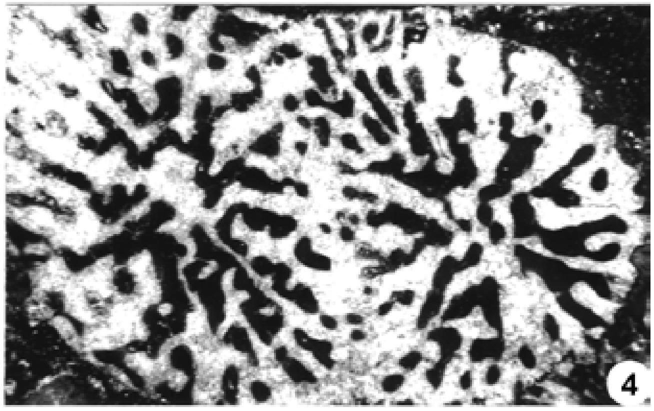
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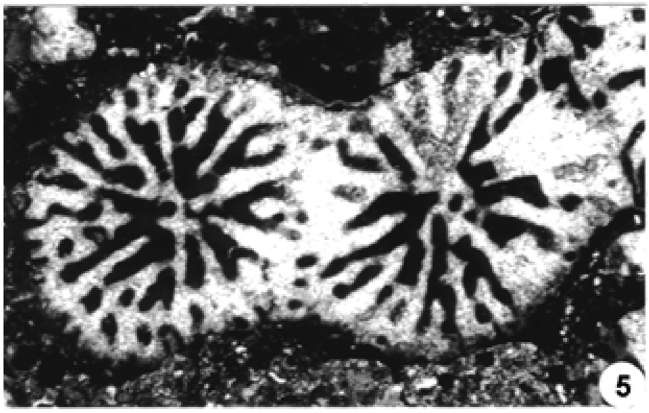
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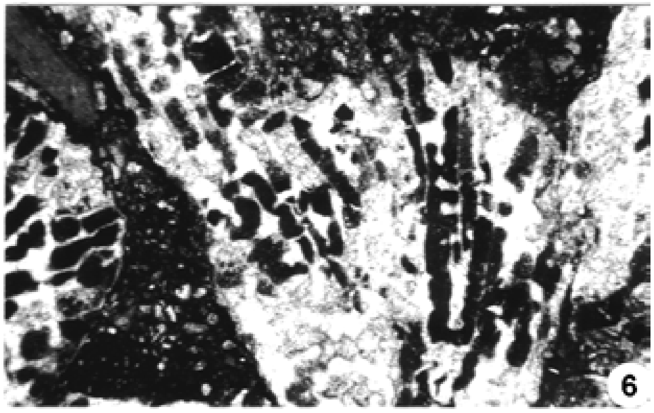
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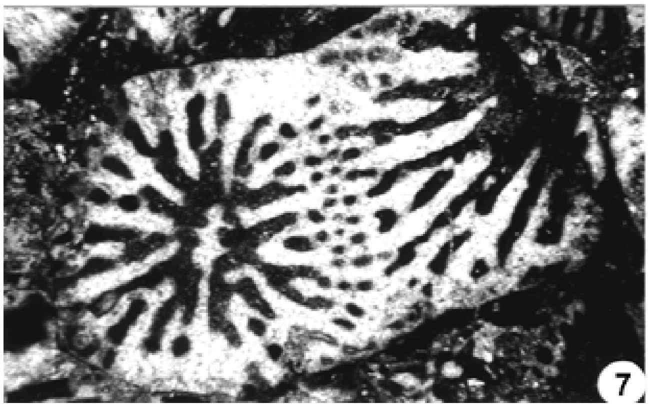
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region of corallite. S_3 about half the length of S_2 and slightly thinner. S_4, when present, about one-third the size of the S_3, or smaller. Interseptal spaces equal to or narrower than width of adjacent septa. Lateral surfaces of septa ornamented by elongate granulations or dentations approximately 0.2 mm in height and vertically spaced 0.25 mm apart, or 4 per mm. Septal margins similarly granulated. Inner margins of S_1 intermittently fused to columella by axially extended septal trabeculae.

Columella well-developed, trabecular, densely constructed, vertically continuous, and subcylindrical or irregularly shaped in cross section. Columella about 0.7 mm in diameter, or slightly less than one-third the CD. Intertwined columellar trabeculae intermittently fused to inner margins of S_1 and S_2.

Wall weakly septothecal, possibly secondarily parathecal and epithecal. Endothecal dissepiments thin, tabular, laterally discontinuous, vertically spaced 0.5-1 mm apart, and generally more common in peripheral region of corallite. External surface of corallites exhibit low, very fine, transverse ridges or lines, interpreted as growth lines.

Material examined. Specimen IGM-7000, a lithologic sample of a phaceloid coral packstone, with three thin sections (TZ-27 through TZ-29).

Occurrence. Upper part of the lower member of the San Lucas Formation, lower Aptian, from the eastern flank of Loma La Cuchilla, a hill located about 7 km south-southeast of Huetamo, Michoacán. The hill is locally known as Loma de los Cuachalalates, a name derived from the small village of Los Cuachalalates at the southwestern end of the hill. The approximate coordinates of this locality are: 18° 33.81’ N, 100° 52.04’ W.

Cladophyllia stewartae was originally described from specimens that were collected from the upper Barranquín Formation in the state of Sucre, northeastern Venezuela (Wells, 1944).

Discussion. The characteristics of the material examined herein essentially conform to the description of the species given by Wells (1944b). Most of the material is recrystallized and partially silicified, but vestiges of the original architecture are preserved in a few of the corallites. The specimens exhibit intratentacular dichotomous budding of corallites by development of a wall from two of the opposed S_1, a characteristic of the members of this genus (Morycowa and Roniewicz, 1990, p. 169). The outermost portion of the wall (epitheca) typically is not preserved in the material examined and therefore the underlying peripheral edges of the septa are exposed. Accordingly, the corallum branches often appear to be costate. This feature of the external surface, i.e. the “... (?)costosepta covered with epitheca...”, has been noted by Morycowa and Roniewicz (1990, p. 170), but alternatively it could be interpreted as a product of differential weathering. Ghosts of the wall structure observed in thin section suggest that the outer surfaces have been modified by dissolution or recrystallization, or both.

Morycowa and Roniewicz (1990) recently revised the genus and emended the generic diagnosis. The presence of lateral connections between the branches, termed apophyses, was utilized by them as the primary diagnostic characteristic of *Apocladophyllia*. The material examined herein lacks apophyses, although in some sections the branches appear to be in lateral contact and fused and their cylindrical shape deformed into polygonal prisms.

A few other species of *Cladophyllia* are known from the Cretaceous of the Americas, but they are clearly morphologically distinct from *C. stewartae* (see Wells, 1944b). The geographically and stratigraphically nearest form is *C. miroi* Felix, 1891, from the Aptian near Tehuacán, state of Puebla, Mexico, but its corallites are much narrower than those of *C. stewartae*. *Cladophyllia furcifera* Roemer, 1888, is known from the middle Albian Edwards Limestone of Texas, but its corallites are shorter and thicker than those of *C. stewartae*. The genus, and family, overall reportedly ranges from the Bajocian to the Albian (Morycowa and Roniewicz, 1990).

Figure 10. *Cladophyllia stewartae* Wells, 1944, IGM-7000, upper part of lower member of San Lucas Formation, Aptian, eastern flank of Loma La Cuchilla, a hill located about 7 km SSE of Huetamo, State of Michoacán, Mexico. 1, Thin section with several transverse and oblique sections of branches, scale bar = 1 cm; 2, thin section with longitudinal and oblique sections of branches, same scale as Figure 10.1; 3, transverse section of corallite, scale bar = 1 mm; 4, transverse thin section of branch in process of bifurcation, same scale as Figure 10.3; 5, transverse thin section of nearly completed branch bifurcation, same scale as Figure 10.3; 6, detail of longitudinal thin section, same scale as Figure 10.3; 7, transverse oblique thin section of corallites and wall region, same scale as Figure 10.3; 8, detail of longitudinal section near branch bifurcation, same scale as Figure 10.3.

Family Cyathophoridae Vaughan and Wells, 1943
Subfamily Cyathophorinae Vaughan and Wells, 1943
Genus *Cyathophora* Michelin, 1843

Type species. *Cyathophora richardi* Michelin, 1843 (p. 104, pl. 26, figs. 1a, 1b) (= *Astrea bourgueti* Defrance, 1826, p. 380) (Vaughan and Wells, 1943, p. 109; Wells, 1956, p. F375).

***Cyathophora haysensis* Wells, 1932**
Figure 11

Cyathophora haysensis Wells, 1932, p. 237, pl. 30, fig. 4, pl. 32, fig. 5; Eguchi, 1933, p. 122; Hedberg and Pyre, 1944, p. 7; Wells, 1944b, p. 433-434, pl. 69, figs. 5, 6; ?Reyeros, 1983, p. 15-16, pl. 2, fig. 3, pl. 3, fig. 2; Baron-Szabo, 1997, p. 39, pl. 3, fig. 5; Baron-Szabo and González-León, 1999, p. 478, fig. 4a.

Description. Corallum colonial, attached, plocoid, incrusting to ramose, distinctly costate, and small in size, the largest specimen about 100 x 50 mm in width and 40 mm thick. Branches lath-shaped. Colony formation by extracalicular budding. Corallites cylindrical, evenly distributed, with axes oriented perpendicular to corallum surface. Calices well-delineated and monocentric. Calicular margins generally circular in outline with a strong overprint of hexameral symmetry produced by differential development of the three septal cycles. CD typically 2.5-3.0 mm. Distance between calices ranges from 0.6 to 2.4 mm.

Septa well-developed, exsert, laminar, and structurally continuous with costae. Septa typically 24 in number and distinctly hexamerally arrayed in three septal cycles. Size relationship among septa: $S_1 >> S_2 > S_3$. S_1 robust, straight, wedge-shaped in cross section near wall, but more blade-shaped toward corallite axis. S_1 approximately 0.3 mm thick and up to 1 mm in length, or between about half to two-thirds the distance from wall to corallite axis. S_2 wedge-shaped in cross-section, about 0.2 mm in thickness, straight, very much shorter than S_1, 0.15 mm in length or about one-fifth the length of S_1, or one-tenth the distance from wall to corallite axis. S_3 typically developed, similar in appearance to S_2, but slightly smaller in thickness and length. Lateral surfaces of septa flat and unornamented. Septal margins smooth, the inner edges oriented nearly vertical.

Pali and columella absent. Corallite axial region hollow, the width of the void, as delineated by inner edges of S_1, approximately half the CD.

Wall septothecal, nonperforate, thin, and solid. Endothecal dissepiments tabular, horizontal, about 0.2 mm in thickness, vertically spaced about 0.5 mm apart, and continuous across corallite interior spaces. Coenosteum tabular to vesicular; dissepiments arched convex-upward, thinner, and more numerous, but less regular in distribution than those of the endotheca.

Costae robust, straight, smooth, radially (hexamerally) arrayed around calices, and structurally continuous with septa of the same cycle. Costae narrow, approximately 0.25 mm in width. Costae appear as steep-sided, sharp-crested, straight ridges. Costae of the three septal cycles weakly differentiated by width and height, $C_1 > C_2 > C_3$. Intercostal furrows distinct and slightly narrower in width than the widths of adjacent costae. Costae typically confluent with those of adjacent corallites, but not necessarily with those of the same septal cycle; some C_1 correspond to either C_2 or C_3. Linearity of costae typically abruptly deflected at confluences.

Material examined. Three small branches or coralla, only one with the surface details well-preserved, IGM-7001 (figured); and thin sections from two other fragments, IGM-7002 (thin section TZ-10), and IGM-7003 (thin section TZ-11). Skeletal material typically is recrystallized and the microarchitecture and trabecular microstructure are not preserved.

Occurrence. Cumburindio Formation, lower Aptian; the western flank of Loma Teremitio, a hill about 1.5 km north-northwest of the town of Turitzio, Michoacán, Mexico. The approximate coordinates of this locality are: 18° 32.39' N, 100° 57.13' W.

Cyathophora haysensis Wells, 1932, also is known from the lower Albian lower Glen Rose of Hays County, Texas (Wells, 1932, p. 237), the Aptian upper Barranquín Formation of Sucre, northeastern Venezuela (Wells, 1944b, p. 433; Hedberg and Pyre, 1944, p. 7), and the middle Albian of the Espinazo del Diablo Formation in the northern region of the state of Sonora, Mexico (Baron-Szabo and González-León, 1999, p. 478).

Discussion. Several species of the genus *Cyathophora* have been described from the Cretaceous. The diameter and spacing

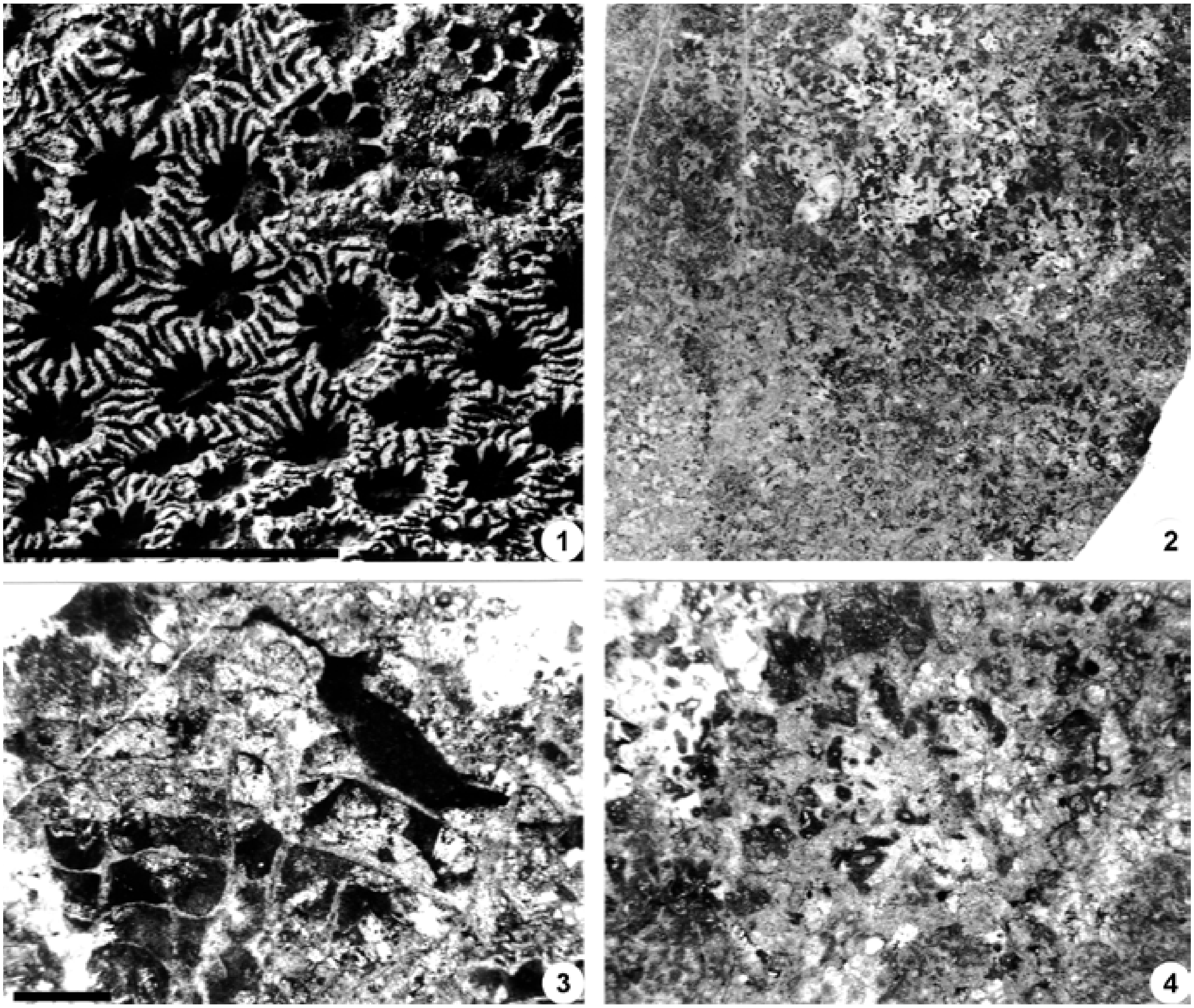


Figure 11. *Cyathophora haysensis* Wells, 1932, Cumburindio Formation, lower Aptian, west slope of Loma Teremitio, north of Turitzio, State of Michoacán, Mexico. 1, IGM-7001, detail of weathered oral surface of corallum, scale bar = 1 cm; 2, IGM-7002, transverse thin section, corallum recrystallized, same scale as Figure 11.1; 3, IGM-7003, longitudinal thin section, scale bar = 1 mm; 4, same section shown in Figure 11.2, detail of one corallite, same scale as Figure 11.3.

of the calices, the number of septa, and the symmetry of the septal arrangement, usually are fairly consistent within individual colonies and therefore they are the primary morphological characteristics used to distinguish the various species from each other. Symmetry of the septal arrangement can be characterized as either tetrameral, pentameral, or hexameral.

In the original description of *Cyathophora haysensis*, Wells (1932, p. 237) stated that the average CD was 3.0 mm, that the calices were spaced about 1.0 mm apart, that the septa were 10 to 12 in number, and that four tabular endothecal dissepiments occurred in a space of 2 mm. Later, Wells (1944b, p. 433-434) emended the species description and gave 20 to 24 as the corrected number of septa. Additionally, he noted that a specimen from Venezuela had calices with a CD of 2.5 to 3.0 mm and a spacing of 3 to 4 mm between calicular centers.

The well-preserved specimen described above, IGM-7001, has calices with a CD of 2.5 to 3.0 mm that are spaced

0.6 to 2.4 mm apart and possess 24 septa that are hexamerally arrayed in three complete cycles. These characteristics are the same as those listed above for *Cyathophora haysensis*, thus the specimens are referred to that species.

The specimens referred to *Cyathophora haysensis* by Reyeros (1983, p. 15-16, pl. 2, fig. 3, pl. 3, fig. 2) and Baron-Szabo (1997, p. 39, pl. 3, fig. 2) possibly belong to other species: the former possesses calices with only two cycles of pentamerally arrayed septa (10 septa) and the latter possesses calices with a variable number of septa, typically fewer, and extremely short S_1 (less than one-sixth the CD).

Several other species of *Cyathophora* have been described from the Cretaceous of the Americas and most of them are easily distinguished from *C. haysensis*. *Cyathophora haysensis* is morphologically similar to *C. atempa* Felix, 1891 (p. 155, pl. 25, figs. 7, 7a, 8), from Neocomian strata near Tehuacán, state of Puebla, except that the latter characteristically possesses a smaller CD (2.0-2.5 mm) and fewer septa (18-22). The specimens assigned to *C. atempa* by Reyeros-Navarro (1963, p. 9-10, pl. 4, figs. 7, 8) reportedly possess a columella and therefore they probably belong to another genus. *Cyathophora steinmanni* Fritzsche, 1923 (p. 316-317, pl. 3, fig. 8, pl. 4, fig. 3), from the Neocomian (Gerth, 1928, p. 14) of Molle Alto, Chile, has calices 1.75-2.0 mm in diameter and spaced about 2 mm apart, with up to three cycles of hexamerally arrayed septa (based on the original description). *Cyathophora hedbergi* Wells, 1944b (p. 434, pl. 69, figs. 7, 8), from the upper Barranquín Formation of Venezuela, possesses calices that are on average 2 mm in diameter and spaced 0.5-1.0 mm apart, and 12 septa hexamerally arrayed in two cycles. *Cyathophora parvula* Wells, 1948 (p. 609-610, pl. 89, fig. 1), from the Lower Cretaceous of Trinidad, possesses calices that are 1.0-1.5 mm in diameter and spaced 0.2-0.5 mm apart, and two cycles of hexamerally arrayed septa. *Cyathophora micrommatos* (Felix, 1891), from Neocomian strata near Tehuacán, state of Puebla, also is morphologically distinct from *C. haysensis* (see the following species description).

Cyathophora haysensis also is morphologically similar to some other species of *Cyathophora* described from the Lower Cretaceous of Europe, except that those from the latter region possess only two cycles of septa instead of three: *C. icaunensis* (d'Orbigny, 1850a) (Hauterivian, France), with calices 3-3.5 mm in diameter; *C. pygmaea* Volz, 1903 (p. 26-27, pl. 4, figs. 4-7) (Neocomian, Bukowina), with calices 0.5-0.7 mm in diameter; and *C. regularis* Fromentel, 1884 (Hauterivian, France, Switzerland), with calices about 2.5 mm in diameter (Wells, 1944b, p. 434). *Cyathophora miyakoensis* (Eguchi, 1936), from the Lower Cretaceous of Japan and Europe, possesses calices 0.7-1.5 mm in diameter and one to two cycles of rudimentary septa (Turnšek, 1997, p. 64).

Cyathophora micrommatos (Felix, 1891)

Figure 12

Cryptocoenia micrommatos Felix, 1891, p. 154, pl. 24, figs. 5, 5a, 5b; Löser, Bach, and Müller, 2002, p. 38.
Cyathophora micrommatos (Felix, 1891). Wells, 1933, p. 90.
Pseudocoenia micrommatos (Felix, 1891). Löser, 2006, p. 20, figs. 2B-C.

Description. Corallum colonial, attached, plocoid to subcerioid, incrusting to massive to ramose, costate, and small to large in size, up to at least 15 cm in diameter and 15 cm in height. Branches of ramose growth forms cylindrical to lath-shaped. Corallites distinct, cylindrical to prismatic, and closely packed. Colony formation by intratentacular(?) budding. Calices monocentric. Calicular margins generally subcircular in outline. CD about 1.5 to 2.0 mm. Depth of calices about 1 mm. Intercalice distance from 0.5 to 1 mm.

Septa weakly developed, weakly exsert, and laminar. Septa continuous as septocostae at calicular margin. Number of septa variable; typically eight, but as few as four or as many as 14. Septa tetramerally arranged in from one to three septal cycles, the last cycle typically incomplete: four S_1, four S_2 and up to six S_3. Size relationship among septa: $S_1>S_2>S_3$. Septa wedge-shaped in cross section, straight, and vertically continuous within calice but apparently absent beneath calicular floor. S_1 and S_2 very short, their length less than one-fourth the CD. S_3 weakly developed when present, and reduced to short, narrow ridges. Lateral surfaces of septa smooth. Septal margins smooth. Pali and columella absent. Corallite axis hollow orally.

Wall apparently septothecal(?) and very thin. Endothecal dissepiments tabular, arched slightly convex upward, thin, laterally continuous within corallite, and vertically spaced about three per mm. Exothecal dissepiments tabular to vesicular. Costae well-developed, structurally continuous with septa, but nonconfluent with those of adjacent corallites.

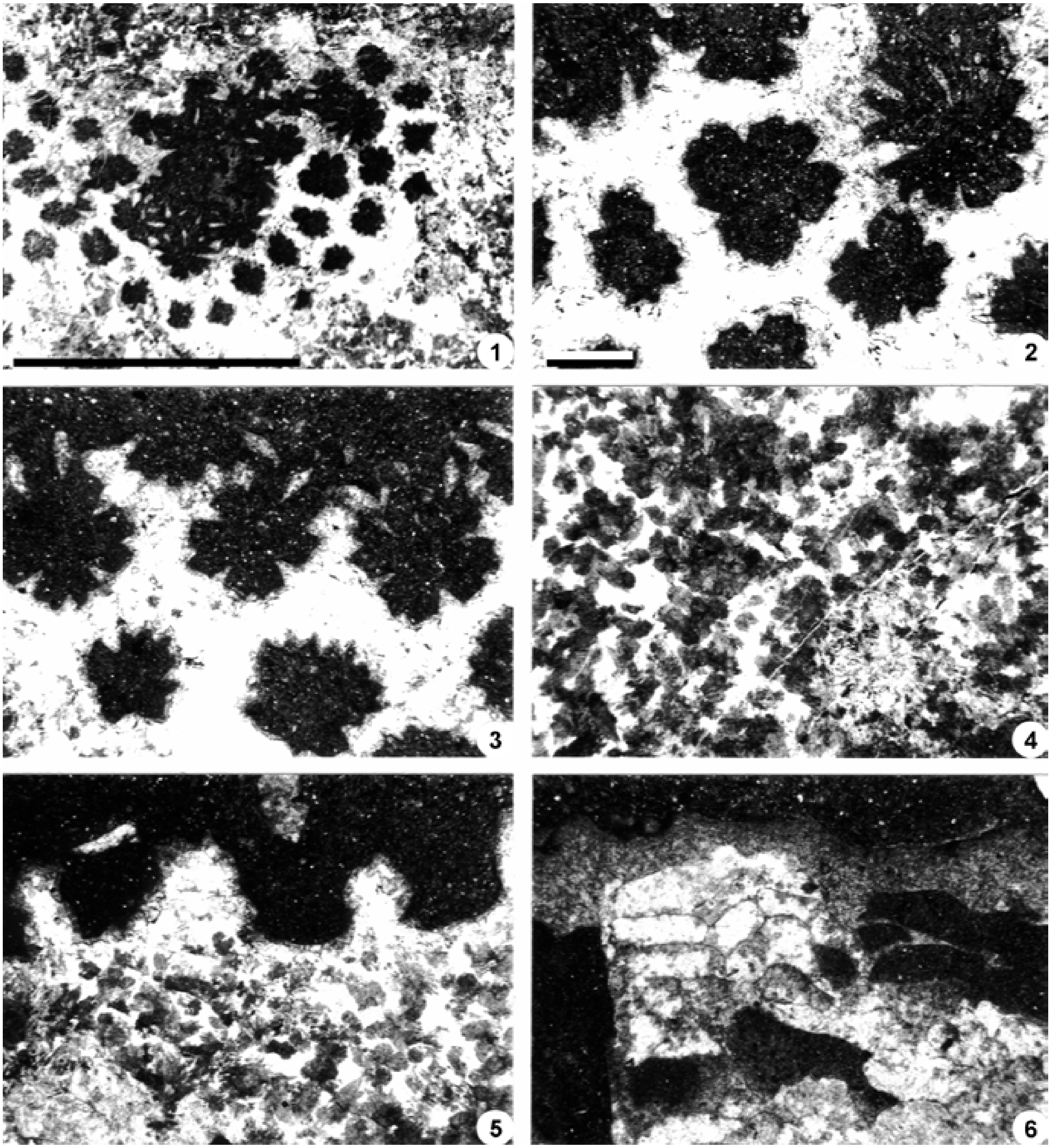


Figure 12. *Cyathophora micrommatos* (Felix, 1891), IGM-7004, Cumburindio Formation, lower Aptian, western base of Loma de San Juan, Turitzio, State of Michoacán, Mexico. 1, Transverse thin section of uneven corallum surface, scale bar = 1 cm; 2, transverse section taken near calicular margins, detail of corallites, scale bar = 1 mm; 3, transverse section, detail of corallites with tetrameral septal symmetry, same scale as Figure 12.2; 4, transverse thin section taken below level of calicular floors, same scale as Figure 12.2; 5, longitudinal thin section, detail of adjacent corallites and walls, same scale as Figure 12.2; 6, longitudinal thin section with relict dissepiments and parathecal wall zone, same scale as Figure 12.2.

Material examined. One corallum, IGM-7004, with four thin sections (TZ-30 through TZ-33). The specimen consists of branches of a large ramose corallum mostly enclosed in argillaceous mudstone. The corallum is recrystallized and skeletal microstructure was not observed.

Occurrence. Cumburindio Formation, lower Aptian. Coralla of this species are common in the lowermost exposed argillaceous mudstone beds at the base of the western flank of the Loma de San Juan, Turitzio, Michoacán, Mexico. This locality is just west-northwest of the coral reef horizon at the crest of the same hill. The coordinates of the latter position are: 18° 31.28' N, 100° 56.65' W.

This species was originally described (Felix, 1891) from material collected from the Neocomian strata near Tehuacán, state of Puebla, Mexico.

Discussion. The morphological characteristics of the material examined are nearly identical to those described for *Cyathophora micrommatos*. The only notable exception is that the calices described herein are slightly larger in diameter than the dimensions given in the original description. Refer to the discussion section given for the preceding species for additional comments on some of the other members of this genus.

Family Stylinidae d'Orbigny, 1851
Subfamily Stylininae d'Orbigny, 1851
Genus *Stylina* Lamarck, 1816

Type species. *Stylina echinulata* Lamarck, 1816 (p. 221).

Discussion. Several other genera have been considered junior synonyms of *Stylina*, including: *Fascicularia* Lamarck, 1816; *Branchastrea* Blainville, 1830; *Gemmastrea* Blainville, 1834; *Stylopora* M'Coy, 1848; ?*Adelocoenia*, *Conocoenia*, ?*Convexastrea*, *Cryptocoenia*, ?*Decacoenia*, ?*Dendrocoenia*, *Lobocoenia*, ?*Tremacoenia* d'Orbigny, 1849; *Acanthocoenia* d'Orbigny, 1850a; *Pseudocoenia* d'Orbigny, 1850c; *Platysmilia* Toula, 1889; and *Dendroseris* Gregory, 1929 (Wells, 1956, p. F376).

Stylina regularis **Fromentel, 1862**
Figure 13

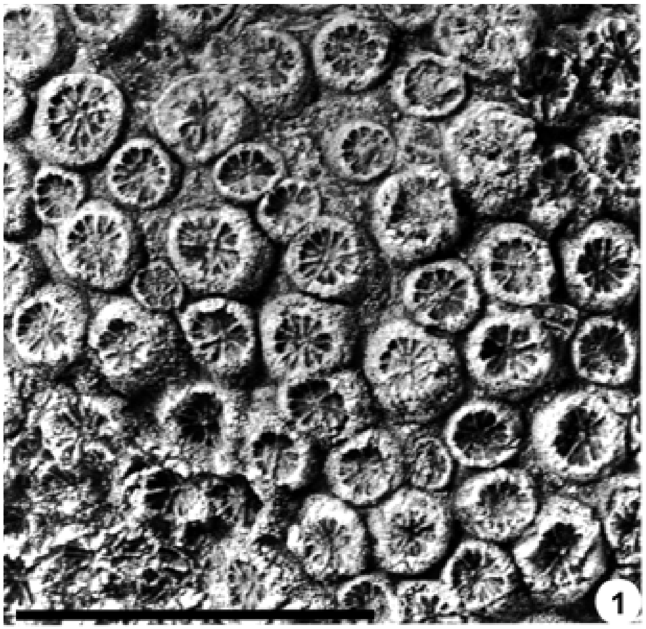
Stylina regularis Fromentel, 1862, p. 430; 1867, p. 514-515, pl. 135, figs. 2, 2a; Morycowa, 1964, p. 34-36, pl. 10, fig. 7, pl. 15, fig. 3, pl. 19, figs. 1a, 1b, 2; Morycowa, 1971, p. 47-48, pl. 5, figs. 2a, 2b, text fig. 6d; Turnšek and Buser, 1974, p. 93, 113, pl. 4, figs. 2, 3; Sikharulidze, 1977, p. 82-83, pl. 13, fig. 4; Sikharulidze, 1979, p. 303-304; Turnšek and Mihajlović, 1981, p. 15, pl. 8, figs. 4, 5; Morycowa, 1984, p. 80-81, pl. 19, figs. 4-5; Scott and Aleman, 1984, p. 1140-1141; ?Liao and Xia, 1985, p. 134, pl. 3, fig. 3; Turnšek, 1992, p. 165; ?Liao and Xia, 1994, p. 147, pl. 39, fig. 5; Baron-Szabo and Steuber, 1996, p. 6, pl. 1, figs. 3, 4; Turnšek, 1997, p. 192, pl. 192, figs. a-e.

Description. Corallum colonial, attached, plocoid, incrusting to massive, irregularly globular, noncostate, small in size, examined specimen about 65 x 40 mm in width and 65 mm in height. Colony formation by extratentacular budding. Corallites generally cylindrical but appear tympanoid orally, irregularly distributed over surface of corallum and densely to loosely packed. Upper oral portions of corallites typically weakly protuberant up to 1 mm above intercorallite coenosteal surfaces.

Calices distinct, monocentric, the margins circular in outline. CD slightly variable, from 1.5 to 2.0 mm; depth of calices typically less than 1 mm. Calices positioned in centers of protuberant oral portions of corallites. Intercalice distance variable from about 0.5 mm at points of contact of adjacent corallites to about 2 mm between widely spaced corallites.

Septa well-developed, non-exsert, laminar and solid. Trabecular architecture not preserved. Septa typically 24 in

Figure 13. *Stylina regularis* Fromentel, 1862, IGM-7005, lowest part of Cumburindio Formation, lower Aptian, near Las Eras, State of Michoacán, Mexico. 1, Detail of weathered oral surface of corallum, scale bar = 1 cm; 2, transverse thin section, corallum recrystallized, corallites with circular calices and polygonal outer margins, same scale as Figure 13.1; 3, longitudinal oblique thin section, same scale as Figure 13.1; 4, transverse thin section, detail of two corallites, scale bar = 1 mm; 5, longitudinal thin section, detail of dissepiments and wall, same scale as Figure 13.4; 6, transverse thin section, detail of septa, oblique transverse view, scale bar = 1 mm.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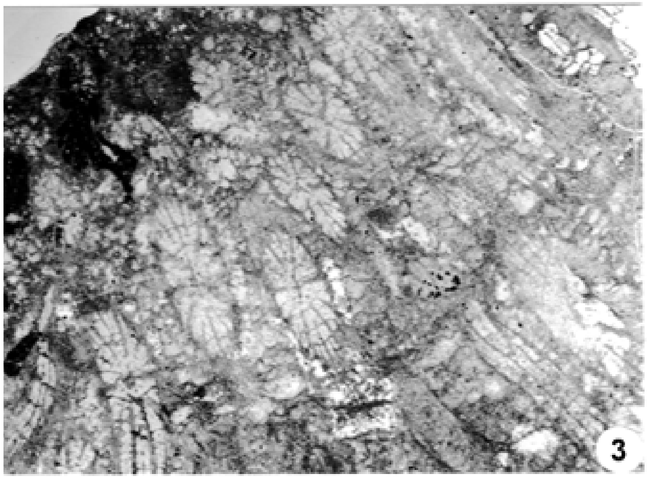
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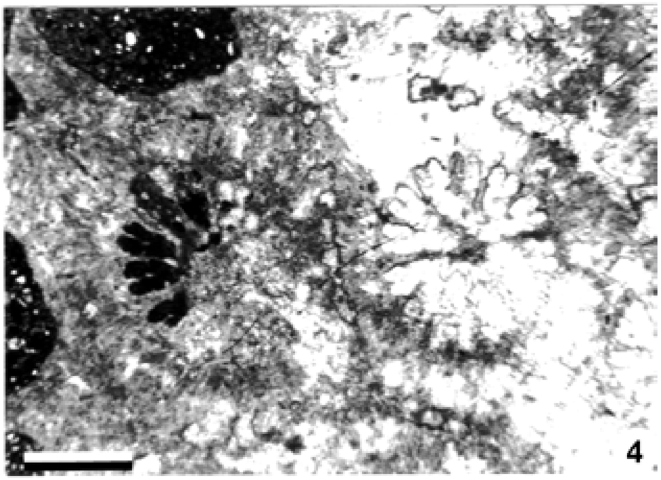
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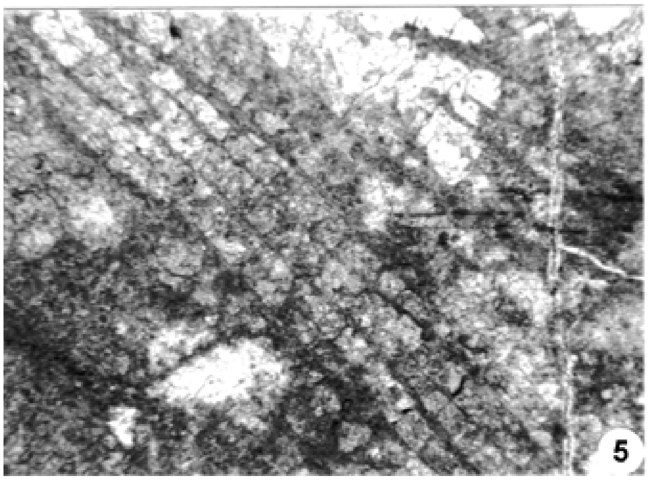
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number, radially arrayed, hexamerally symmetrical, and inserted in three complete septal cycles. Size relationship among septa: $S_1>S_2>S_3$. Septa blade-shaped in cross section, straight, and very thin. S_1 extended from wall to perimeter of corallite axis, but orally the inner edges typically thicken and remain laterally free of the columella. S_1 thickest, about 0.1 mm in width. S_2 slightly shorter and thinner than the S_1, their length equal to about one-fourth the CD. S_3 typically fully developed but much shorter and thinner than the S_2. Length of S_3 about half the length of the S_2. Width of interseptal spaces about equal to width of adjacent septa of lower two cycles. Lateral surfaces of septa uneven to coarsely granulated. Septal margins typically smooth and, at least orally, laterally free.

Columella well-developed, styliform, solid, vertically continuous, and lath-shaped. Columella about 0.1 mm in width, 0.25 mm in length, and oriented length parallel to the plane of two of the axially opposed S_1. Septa of lower cycles commonly fused to columella deep in aboral portion of corallite.

Wall well-developed, septothecal, dense and solid. Thickness of wall about 0.5 mm. Endothecal dissepiments tabular, thin, typically continuous, and vertically spaced about 1 mm apart.

Protuberant oral portions of corallites often separated by orally concave coenosteal regions. Coenosteum appears solid, the outer surfaces commonly granular in the orally concave areas between corallites and occasionally faintly striated near calices.

Material examined. The description is based on a single corallum, IGM-7005, with two thin sections (TZ-34 and TZ-35). External morphology is fairly well-preserved, but internally the skeletal microstructure is recrystallized.

Occurrence. Cumburindio Formation, lower Aptian; from near the village of Las Eras, Michoacán. The approximate coordinates of this locality are: 18° 30.60’ N, 100° 59.0’ W.

This species, which has a fairly broad geographic distribution in the Early Cretaceous (Berriasian - Aptian), also has been reported from Poland (Barremian-Aptian), Greece, France, Romania, Yugoslavia (Barremian-Aptian), Serbia, Georgia (lower Barremian), and (?)Tibet (Lower Cretaceous).

Discussion. The morphological characteristics of the corallum described above are the same as those typically attributed to *Stylina regularis*, therefore the specimen is referred to that species.

Although several other previously described species of *Stylina* are known from the Cretaceous of the American continents, none of them appear to be conspecific with the present form. *Stylina tehuacanensis* (Felix, 1891) from near Tehuacán in the state of Puebla, Mexico, originally described as a species of *Stylophora* by Felix (1891, p. 161-162, pl. 22, figs. 2, 8, 8a) and subsequently reassigned to *Stylina* by Wells (1944b, p. 435), primarily differs by the smaller calices and the number of septa (6). Furthermore, a recent re-examination of Felix’s type material indicated that *S. tehuacanensis* should be referred to the genus *Polytremacis* d’Orbigny, 1849 (Löser, 2006, p. 53). *Stylina collinsi* Gregory, 1899 (p. 460, fig. 3), from Neocomian age limestone near the town of Guadalcazar, state of San Luis Potosi, Mexico, has octamerally arrayed septa. *Stylina harrisoni* (Gregory, 1929) from Trinidad, originally described as the type species of *Dendroseris* Gregory (1929, p. 66-68, pl. 8, figs. 1, 2, 3, 4a, 4b) but later reassigned to the genus *Stylina* (Wells, 1944b, p. 435) and redescribed (Wells, 1948, p. 610-611, pl. 89, figs. 2, 3, 4), possesses hexamerally arrayed septa, but differs by the ramose growth form of the colony, the typically smaller calices, and the smaller number of septa (12). *Stylina sucrensis* Wells, 1944b (p. 435-436, pl. 70, fig. 1), from the Barranquín Formation of northeastern Venezuela and the Lower Cretaceous at San Pedro Yucunama, state of Oaxaca, Mexico (Reyeros, 1983, p. 17, pl. 4, fig. 1), primarily differs by the solid peritheca, and the number of septa (16) and their octameral or tetrameral arrangement. Wells (1944b, p. 436) also provided a review of the other species of *Stylina* which possess tetramerally or octamerally arranged septa. The generic assignment of *Stylina vaughani* Reyeros-Navarro, 1963 (p. 10-12, pl. 2, fig. 2), from near Tehuacán, state of Puebla, is doubtful based on the original description and figures. *Stylina columbaris* Scott and Aleman, 1984, from the Atocongo Formation (Hauterivian-Barremian) of Cerros Perico, Peru, primarily differs from *S. regularis* by the slightly larger corallites (GCD range of 1.83 to 2.43 mm) and the variable number and arrangement of the septa. The species described as *Cryptocoenia neocomiensis* d’Orbigny, 1850a, by Felix (1891, p. 154) was later tentatively reassigned to the genus *Stylina* by Wells (1933, p. 90), but this determination remains questionable.

A few other species attributed to *Stylina* resemble the form described herein, but the affinities between these species and *S. regularis* presently are uncertain. Included here are several species described by Eguchi (1951) from the Cretaceous of Japan. *Stylina*? *japonica* Eguchi, 1951 (p. 46-47, text figs. 2, 3, pl. 16, fig. 1), possesses calices that are about the same size as those of *S. regularis* and has hexamerally arrayed septa also, but only two cycles are developed. *Stylina nakasai* Eguchi, 1951 (p. 60, pl. 22, fig. 7), possesses three cycles of septa (24) that are hexamerally arrayed, but the calices are smaller than those of *S. regularis*. Eguchi (1951, p. 61) also briefly described, but did not illustrate, *Stylina* sp., a species that possesses calices that are about the same diameter as those of *S. regularis* and in which three cycles of hexamerally arrayed septa are developed. Finally, *S. higoensis* Eguchi, 1951 (p. 74, pl. 12, figs. 6, 7, 8, 9), possesses two cycles of hexamerally arrayed septa, although the number of costae (24) indicate the possible presence of a third cycle of septa, but the calices are much smaller than those of *S. regularis*, only 0.7-1.0 mm in diameter.

Suborder Rhipidogyrina Roniewicz, 1976
Family Rhipidogyridae Koby, 1905
Genus *Saltocyathus* Morycowa and Masse, 1998

Type species. *Saltocyathus urgonensis* Morycowa and Masse, 1998 (p. 734-735, figs. 7.1-7.5, 8).

***Saltocyathus cumburindioensis* new species**

Figure 14

Diagnosis. Corallum relatively large in size, flabellate; calicular margin elliptical. Septa numerous and relatively thick. Tabular endothecal dissepiments vertically spaced about 6 per 5 mm.

Description. Corallum solitary, attached, conical to flabellate, costate, and relatively large in size, the largest specimen about 40 x 75 mm in diameter (CD) and 75 mm in height.

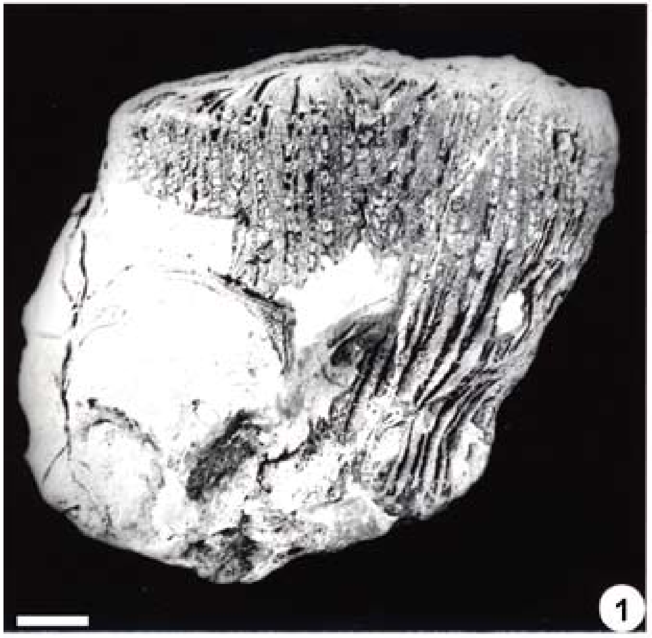
Corallite turbinate in lower portion and flabellate orally. Base of corallum expanded into peduncle. Calice monocentric and laterally elongate, possibly dicentric(?). Calicular margin elliptical in outline. Depth of calice unknown, but most likely greater than 10 mm as determined from exposed portions of highly exsert septa.

Septa well-developed, robust, numerous, typically highly exsert, laminar, solid, and commonly secondarily(?) laterally thickened. Septa estimated to be 76 to 84 in number based on counts of septa in two halves of corallites, and even more numerous in laterally continuous, flabellate calices. Septa hexamerally arrayed in five septal cycles, the first four complete, the fifth nearly fully developed. Very small, weakly developed lonsdaleoid septa also present. Size relationship among septa: $S_1 \geq S_2 > S_3 > S_4 > S_5$. Septa generally straight, wedge- or blade-shaped in cross section, widest at junction with wall and gradually smoothly tapered toward corallite axis. S_1 up to 4 mm in width orally at junction with wall and extended three-fourths distance from wall to corallite axis. Upper portions of S_1 exsert up to at least 8 mm above calicular margin. S_2 nearly the same in size as the S_1 only slightly thinner and less exsert. S_3 nearly as thick as the S_2, but much less exsert and unequal in length, generally extended about half the distance from the wall to the axis, but those nearer to the axial plane of the GCD typically longer than those nearer to the axial plane of the LCD. S_4 about 1-2 mm in width at junction with wall and about 5-11 mm in length, their lengths unequally developed with respect to position along calicular margin relative to GCD and LCD, similar to those of preceding cycle. S_5 about 1 mm in width at junction with wall and usually 1-3 mm shorter than laterally adjacent parental S_4. Interseptal spaces consistently about 1 mm in width near to calicular margin and typically wider axially due to shape and lengths of septa. Lateral surfaces of septa generally smooth. Septal margins smooth, their upper edges highly arched orally, laterally free, and gently inclined toward corallite axis. Inner portions of septal margins fused by abundant dissepiments deep in axial region of calice.

Columella absent, axial region of calice deep and hollow orally and occupied by fusion of inner septal margins and endothecal dissepiments aborally.

Wall well-developed, primarily parathecal, possibly occasionally intermittently secondarily epithecal(?). Endothecal dissepiments well-developed, tabular, abundant, thin, mostly laterally continuous, inclined toward axis of corallum axially and arched convex orally in peripheral region. Endothecal dissepiments vertically spaced 0.5-3.0 mm apart, or on average 6 per 5 mm. Outer surface of corallum generally smooth but broadly uneven or undulated.

Etymology. The species *S. cumburindioensis* n. sp. is named for the formation in which the samples were found, the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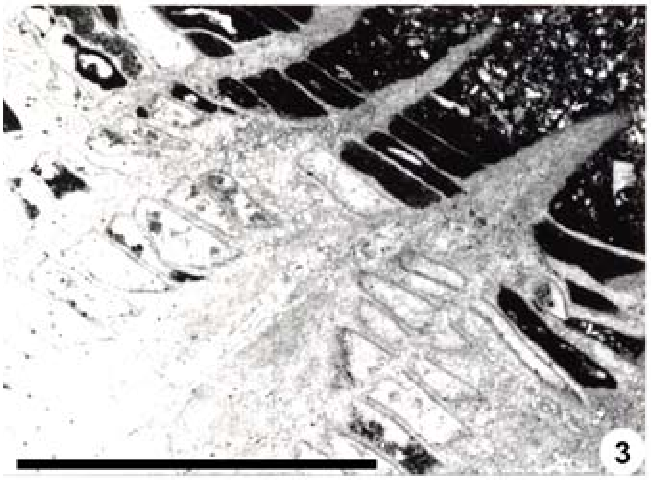
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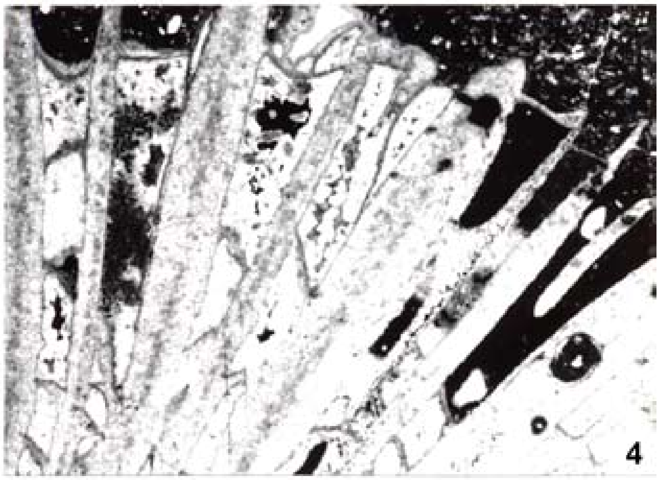
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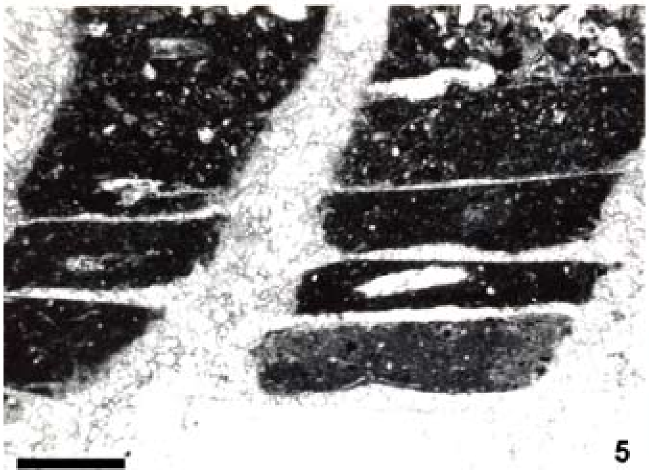
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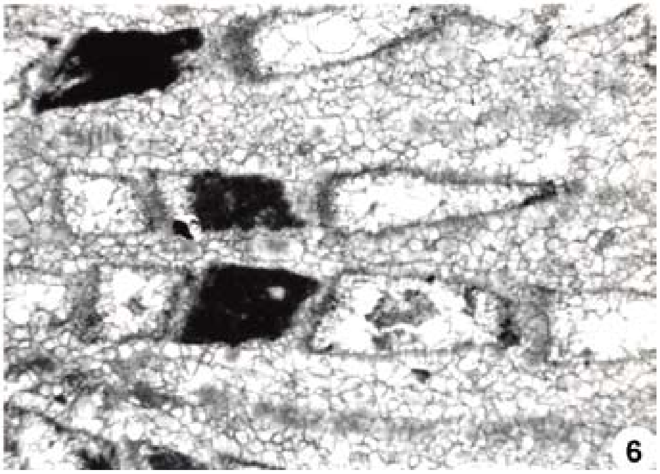
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Cumburindio Formation, which is indicated by the addition of the Latin suffix -*ensis* = place.

Types. Two specimens: one fairly well-preserved, holotype IGM-7006, but the calice is not exposed; and paratype IGM-7007, a small, weathered fragment, with two thin sections (TZ-49 and TZ-50). An indeterminate form of hydnophoroid coral epibiont is present on the lateral aboral area and calicular center of the holotype.

The type stratum is the Cumburindio Formation, lower Aptian. The type locality is the Loma de San Juan, just south of Turitzio, Michoacán, Mexico. The approximate coordinates of the type locality, as determined from the Mexican 1:50,000 scale Huetamo (E14A64) topographic map, are: 18° 31.28' N, 100° 56.65' W.

Occurrence. Known only from the type locality. The coordinates of this locality are given above. The specimens were found on the upper slopes of the Loma de San Juan. The only other reported occurrence of this genus is from the lower Aptian of France.

Discussion. The species described above primarily differs from the type species, *Saltocyathus urgonensis* Morycowa and Masse, 1998 (p. 734-735, figs. 7.1-7.5, 8), by the relatively larger size of the corallum, the laterally elongate calice, and the more numerous septa. The laterally elongate calice of the single complete corallum is interpreted as a feature of the species. Alternatively, the elongation of the calice may be due to incipient intratentacular division.

This species actually may be more abundant in the Cumburindio Formation than presently recognized: weathered lateral surfaces of the described material and the size of the specimens superficially resemble those same characteristics of some rudist species that occur in this formation.

Family Trochoidomeandridae Turnšek, 1981
Genus *Rhipidomeandra* Morycowa and Masse, 1998

Type species. *Rhipidomeandra bugrovae* Morycowa and Masse, 1998 (p. 735-736, figs. 9, 10.6-10.7, 11).

Rhipidomeandra bugrovae Morycowa and Masse, 1998
Figure 15

Rhipidomeandra bugrovae Morycowa and Masse, 1998, p. 735-736, figs. 9.1a, b, 9.2a, b, 9.3, 10.6, 10.7, 11.

Description. Corallum colonial, attached, meandroid, massive, hemispherical, noncostate, large in size, at least 24 x 26 cm in width and 13 cm in height. Colony formation by incomplete intratentacular polystomodaeal budding.

Corallites flabelliform and typically linearly arrayed within series. Series well-defined by walls, discontinuous, narrow but laterally elongate, straight, curved or sinuous, and frequently bifurcated or trifurcated by intratentacular budding. Width (LCD) of series ranges from 1 to 3 mm, slightly wider at areas of incipient budding, but most commonly about 2 mm. Length (GCD) of series ranges from a few mm to at least 10 cm. Collines well-developed, continuous, those of adjacent series directly connected to each other. Combined width of two fused collines approximately equal to width of series or slightly wider, 2 to 3 mm. Ambulacrum absent.

Calices monocentric to polycentric, opposite margins typically parallel to each other and frequently interrupted by budding of daughter corallites.

Septa well-developed, weakly exsert, laminar, solid, relatively thick. Trabecular architecture not preserved. Septa oriented perpendicular to series walls, generally bilaterally symmetrical across axial plane of series and radially arrayed at ends of series; hexameral symmetry not apparent. Different sizes of septa indicate the presence of at least two and often three cycles of septa. Size relationship among septa: $S_1 \geq S_2 > S_3$. S_1 commonly lath-, inverted wedge- or club-shaped, rarely blade-shaped, in cross section, relatively thick, about 0.2-0.4 mm in width, and frequently noticeably thickened at inner margin. S_2 usually blade- or lath-shaped in cross section and variable in size, but generally slightly thinner and shorter than the adjacent S_1. S_1 and some S_2 extended laterally from wall to perimeter of axial plane of series, but typically they do not penetrate the axial plane itself. S_3 frequently developed laterally to the S_2 only very much smaller in size, their width and length less than half

Figure 14. *Saltocyathus cumburindioensis* n. sp., Cumburindio Formation, lower Aptian, Loma de San Juan, Turitzio, State of Michoacán, Mexico. 1 and 2, IGM-7006, lateral and oral views of corallum, respectively, scale bar = 1 cm; 3, IGM-7007, oblique longitudinal thin section, edges of septa and tabular dissepiments, scale bar = 1 cm; 4, same corallum, transverse thin section, same scale as Figure 14.3; 5, oblique longitudinal thin section, detail of septa and dissepiments, scale bar = 1 mm; 6, transverse thin section, detail of recrystallized septa, dissepiments, and small lonsdaleoid(?) septa, same scale as Figure 14.5.


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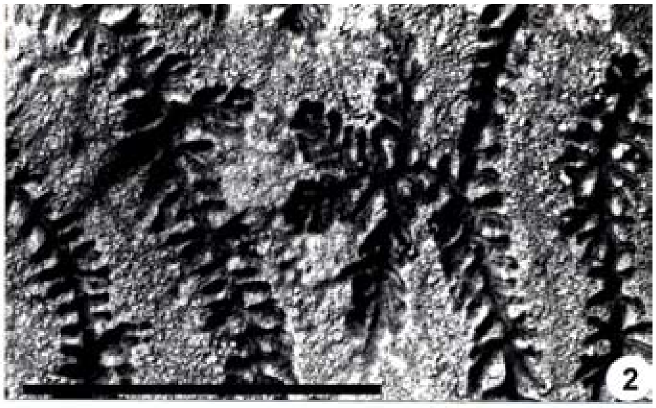
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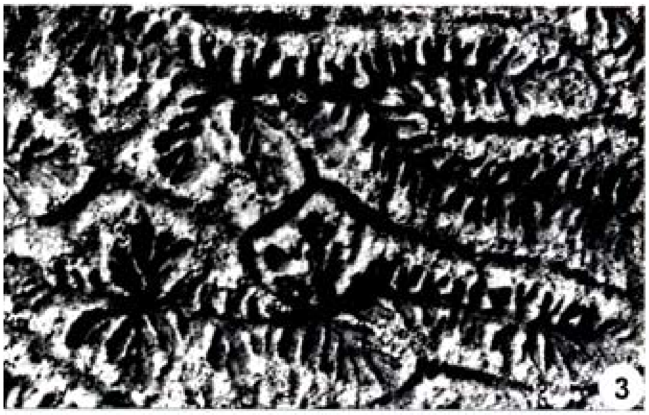
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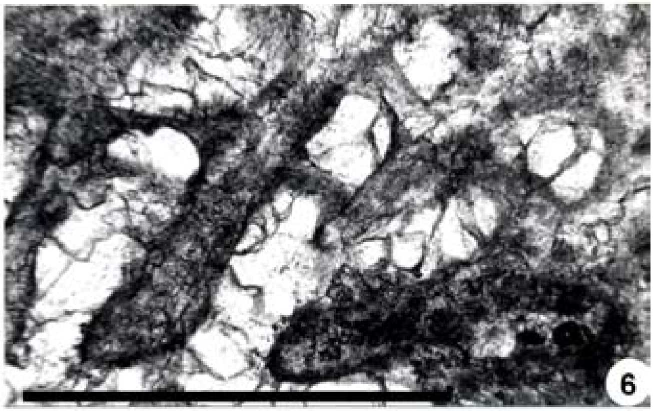
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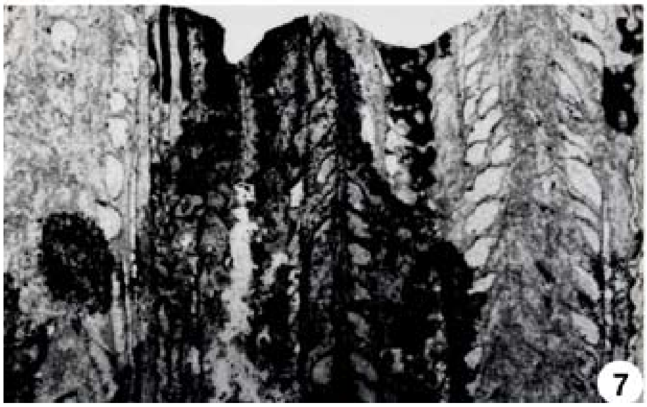
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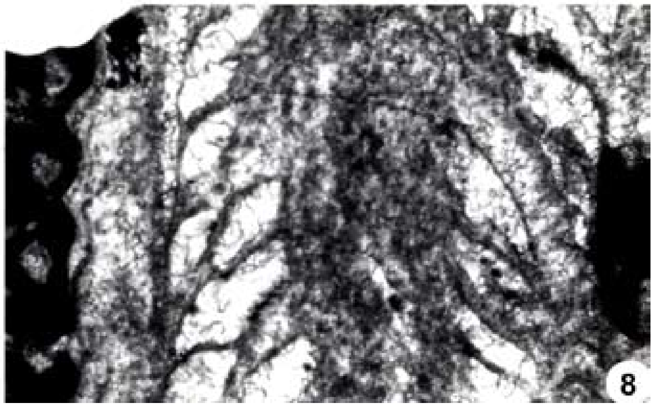
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those dimensions for the S_2. Some S_3 occasionally exhibit a peripheral lonsdaleoid appearance. Typically about 12 to 14 septa occur along 5 mm of wall. Interseptal spaces variable in width, about 0.25 mm, or approximately equal to width of primary septa. Lateral surfaces of septa of lower cycles ornamented with low ridges or carinae and appear undulated; carinae consistently vertically spaced about 1 mm apart. Septal margins typically smooth, the inner edges laterally free. Inner edges of S_1 adjacent to series axis commonly much wider than the peripheral portions of the same septum.

Columella apparently absent orally but possibly rarely present as a weakly developed, vertically and laterally discontinuous laminar structure deeper within axis of series. Axial plane of series typically occupied by a narrow, continuous, hollow void approximately 0.2 mm in width, or about one-tenth of the dimension of lesser CD.

Wall well-developed around series, formed by two distinctly different structural zones, primarily septothecal and secondarily parathecal. Innermost layer of wall septothecal and relatively thin, about 0.25 mm in width. Outermost layer of wall robustly parathecal and relatively thick, about 1-1.5 mm in width. Parathecal dissepiments vesicular, inclined toward series axis at about 45 degrees, arched convex oral-axially, and consistently vertically spaced about 1 mm apart. Combined width of two fused walls of laterally adjacent series about 3 mm. Endothecal dissepiments sometimes present but weakly developed, thin and laterally discontinuous.

Material examined. One specimen, IGM-7008, with two thin sections (TZ-01 and TZ-02). The corallum is the largest colony yet found in the coral reef horizon of the Cumburindio Formation at the Loma de San Juan, Turitzio. Most of the corallum is coarsely recrystallized calcite; skeletal morphology is preserved only in small, isolated regions sparsely scattered throughout the colony.

The oral surface of the corallum exhibits evidence of several kinds of epibionts including: the cylindrical traces of a commensal serpulid annelid entrenched along series axes; and preserved portions of other species of corals, a thamnasteroid form and an indeterminate species of *Cyathophora*.

Occurrence. Cumburindio Formation, lower Aptian; the coral reef horizon at the crest of the Loma de San Juan, just south of Turitzio, Michoacán, Mexico. The coordinates of this locality are: 18° 31.28' N, 100° 56.65' W.

The only other reported occurrences of this species are from the upper Barremian and lower Aptian of southern France and the upper Barremian of southwest Turkmenistan (Morycowa and Masse, 1998).

Discussion. The morphologic details of the Mexican specimen described above are the same as those described for *Rhipidomeandra bugrovae* Morycowa and Masse, 1998, therefore the corallum is referred to that species.

This species was originally described from the upper Barremian and lower Aptian of southern France and the upper Barremian of southwest Turkmenistan (Morycowa and Masse, 1998). The Mexican specimen described above is the only other reported occurrence of this species. This species has the largest corallum yet found in the coral reef horizon of the Cumburindio Formation at the top of the Loma de San Juan, Turitzio.

Suborder Faviina Vaughan and Wells, 1943
Family Isastraeidae Alloiteau, 1952
Genus *Isastrea* Milne Edwards and Haime, 1851

Type species. *Astrea helianthoides* Goldfuss, 1826 (p. 65, pl. 22, fig. 4a).

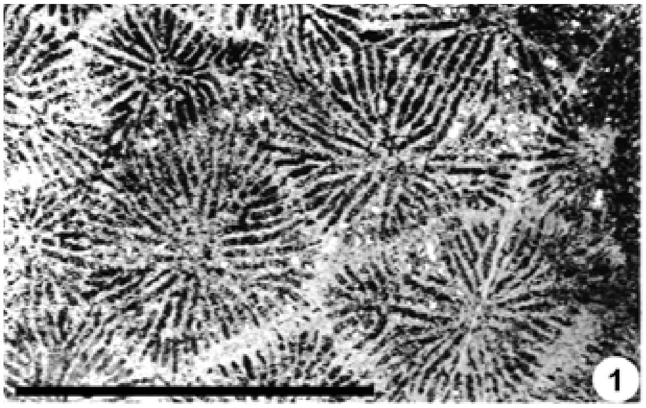
Isastrea whitneyi Wells, 1932

Figure 16

Isastrea whitneyi Wells, 1932, p. 245, pl. 39, figs. 4, 5; Eguchi, 1933, p. 122; Wells, 1946, p. 3-4, pl. 2, figs. 1-3; Allison, 1955, p. 408; von der Osten, 1957a, p. 697; 1957b, p. 573, 576, pl. 63, fig. 10; ?Scott, 1984a, p. 341-342, pl. 2, fig. 14.

Description. Corallum colonial, attached, cerioid, incrusting to massive, septocostate, and small to medium in size, the

Figure 15. *Rhipidomeandra bugrovae* Masse and Morycowa, 1988, IGM-7008, Cumburindio Formation, lower Aptian, Loma de San Juan, Turitzio, State of Michoacán, Mexico. 1, Portion of the oral surface, scale bar = 1 cm; 2, detail of oral surface, scale bar = 1 cm; 3, oral surface with deeply weathered walls, same scale as Figure 15.2; 4, transverse thin section, same scale as Figure 15.2; 5, transverse thin section, detail of series with a few lonsdaleoid septa, scale bar = 1 mm; 6, same section, detail of septa and dissepiments, scale bar = 1 mm; 7, longitudinal thin section, same scale as Figure 15.5; 8, same section, detail of dissepiments and wall of two adjacent series, same scale as Figure 15.6.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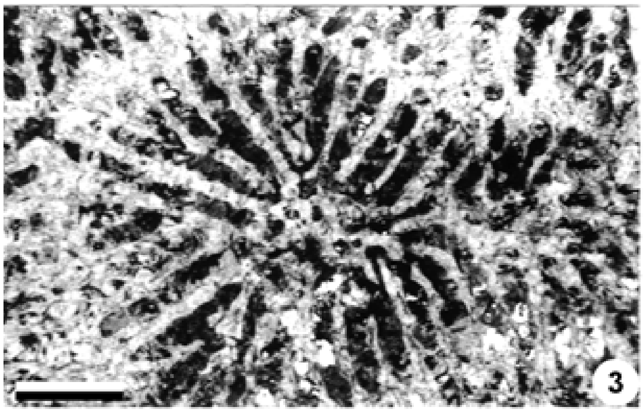
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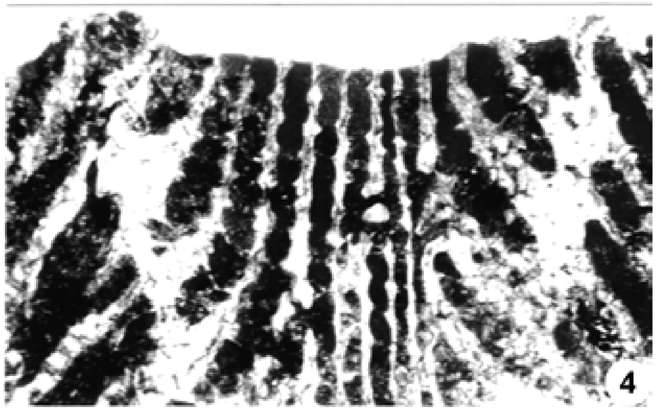
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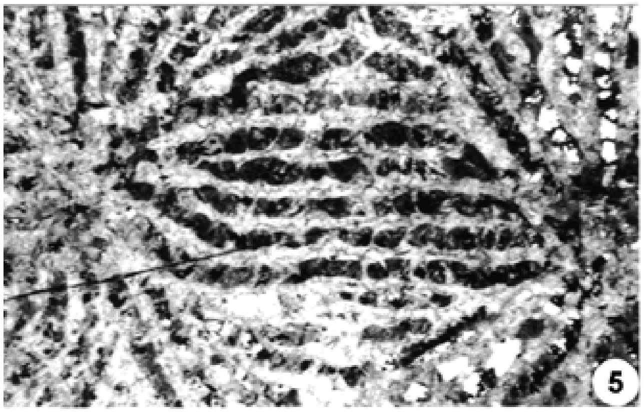
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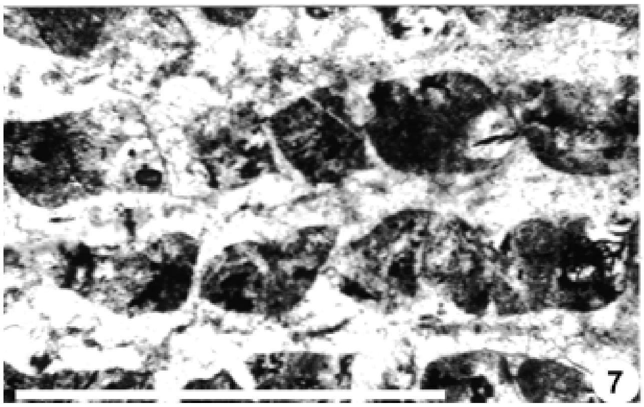
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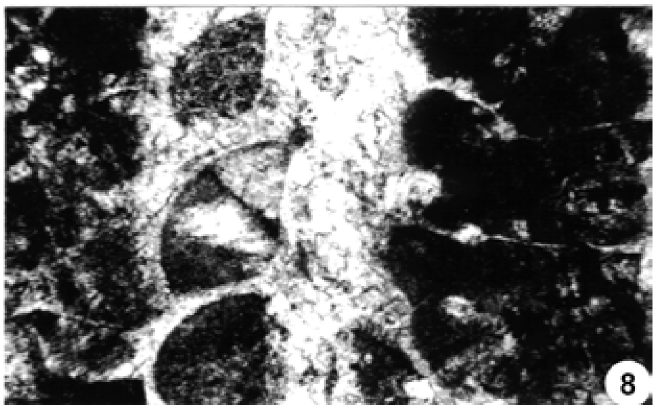
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examined specimen about 80 mm in diameter and 50 mm in height. Colony formation by intratentacular distomodaeal budding with temporary lamellar linkages. Corallites prismatic, closely packed, axes oriented perpendicular to corallum surface. Calices distinct, permanent condition monocentric. Calicular margins polygonal in outline, usually five or six sided. CD typically ranges from 3 to 6 mm; depth of calice 1-2 mm. Calicular centers spaced 5-6 mm apart.

Septa well-developed, weakly insert, laminar, with sparsely distributed perforations. Septa structurally continuous as weakly exsert septocostae at calicular margin. Septa from 42 to 68 in number, radially arrayed with a generally hexameral symmetry, in at least four complete cycles with a number of S_5 usually present also. Size relationship of septa: $S_1 \geq S_2 > S_3 > S_4 > S_5$. Septa blade-shaped in cross-section and straight or curved. Septa thin, the S_1 about 0.25 mm thick, those of each successively higher cycle only slightly narrower than those of the previous cycle. Lengths of S_1 and S_2 often nearly the same and equal to about four-fifths distance from wall to corallite axis. First two cycles of septa extended into and fused with columella. Lengths of S_3 variable from only slightly shorter than S_2 to about one-half length of S_2; a few longer S_3 also extended into and fused with columella. Lengths of S_4 about one-fourth length of S_1. S_5 very short, about half length of S_4. Lateral surfaces of septa ornamented with coarse, scattered granulations, some developed into somewhat continuous carinae. Septal margins appear beaded or dentate, a result of distal terminations of septal trabeculae. Small paliform-like structures present adjacent to columella.

Columella trabecular, spongiose, vertically continuous, orally papillose, width about one-fifth of CD; structurally contributed to by lateral trabecular extensions from inner margins of S_1, S_2 and some of S_3.

Wall septothecal, secondarily parathecal, typically well-developed but sometimes weakly developed or absent. Endothecal dissepiments thin, tabular, discontinuous, most abundant near corallite wall, and vertically spaced 5-6 per mm.

Costae distinct, ridge-like, with sharp upper edges. Costae structurally continuous with septa, but slightly thicker, and laterally spaced 3-4 per mm. Costae confluent or nonconfluent with those of adjacent corallites.

Material examined. One corallum, IGM-7009, with four thin sections (TZ-06 through TZ-09). The specimen is mostly recrystallized and silicified; only a few regions within the corallum exhibit preserved relics of the skeletal architecture.

Occurrence. Cumburindio Formation, lower Aptian. Specimens are from the western slope of the Loma de San Juan, just south of Turitzio, and the western slopes adjacent to the Arroyo Los Hornos, just west of the Turitzio cemetery, Michoacán, Mexico. The approximate coordinates for these two localities are: 18° 31.28' N, 100° 56.65' W; and 18° 32.10' N, 100° 56.74' W, respectively.

This species was originally described from the lower Albian lower Glen Rose of Comal, Blanco and Hays counties, Texas. A single specimen which may be referable to this species has been reported from the Lower Cretaceous Knowles Limestone in the subsurface of Texas (Scott, 1984a). The Knowles Limestone was originally described as a Jurassic unit (Mann and Thomas, 1964), but the age was later determined to be Lower Cretaceous (Cregg and Ahr, 1984; Finneran et al., 1984), specifically upper Berriasian-Valanginian (Scott, 1984a). Other reported occurrences of this species in Mexico are from: the Aptian lower Cuchillo Formation of the Sierra de Acatita, and the (?)lower Albian upper Cuchillo Formation in the outlier of the Sierra del Venado, state of Coahuila, Mexico; and the Aptian-middle Albian Alisitos Formation at Punta China, northwestern Baja California, Mexico. This species also has been reported from the Barremian Taguarumo Member of the Barranquín Formation in eastern Venezuela.

Figure 16. *Isastrea whitneyi* Wells, 1932, IGM-7009, Cumburindio Formation, lower Aptian, western slope of the Loma de San Juan, Turitzio, State of Michoacán, Mexico. 1, Transverse thin section, material mostly recrystallized and silicified, intratentacular buds developed on some of the corallites, scale bar = 1 cm; 2, oblique longitudinal thin section, same scale as Figure 16.1; 3, transverse thin section, detail of corallite with small intratentacular bud, scale bar = 1 mm; 4, oblique longitudinal thin section of upper part of corallite, same scale as Figure 16.3; 5, transverse thin section of two corallites, wall zone weakly developed, septocostae confluent between calicular centers, same scale as Figure 16.3; 6, longitudinal thin section of two corallites, wall structure partially preserved, same scale as Figure 16.3; 7, transverse thin section, detail of septocostae, scale bar = 1 mm; 8, longitudinal thin section, detail of wall structure, central septothecal zone and adjacent parathecal zones, the latter well-preserved on one side of the septotheca and faintly discernible on the other, same scale as Figure 16.7.

Discussion. The morphological characteristics of the corallum described above are the same as those typically attributed to *Isastrea whitneyi*, therefore the specimen is referred to that species. Another member of this genus, *I. neocomiensis* Fromentel, 1857, recently has been reported from the Lower Cretaceous (upper Barremian-lower Aptian) Cerro de Oro Formation in the state of Sonora, Mexico (Baron-Szabo and González-León, 1999, p. 476, fig. 3c), but that species possesses corallites which appear to be larger in diameter than those of the species described above.

Suborder Astreoina Alloiteau, 1952
Family Faviidae Gregory, 1900

Discussion. The family Faviidae Gregory, 1900, formerly placed within the suborder Faviina Vaughan and Wells, 1943 (Turnšek, 1997, p. 34), most recently has been considered to belong to the suborder Astreoina Alloiteau, 1952 (Morycowa, 1997).

Genus *Eohydnophora* Yabe and Eguchi, 1936

Type species. *Eohydnophora tosaensis* Yabe and Eguchi, 1936 (p. 142-143, figs. 1-3).

Eohydnophora ovalis **Masse and Morycowa, 1994**
Figure 17

Eohydnophora ovalis Masse and Morycowa, 1994, p. 440, 442, pl. 2, figs. 1a-c, 2a-c, text figs. 4a-d; Baron-Szabo, 1997, p. 38, pl. 3, figs. 1, 3

Description. Corallum colonial, attached, hydnophoroid, massive to ramose, and variable in size: fragments of ramose coralla up to 30 x 65 mm in width and 75 mm in height (IGM-7012), fragments of massive coralla as large as 80 x 90 mm in width and 60 mm in height (IGM-7013). Corallites interconnected, valleys confluent, narrow and laterally elongate; walls discontinuous.

Series (calices) continuous, confluent, narrow and deep, about 0.5 mm in width and 1.5-2.0 mm in depth, with nearly vertical to steeply inclined sides. Collines discontinuous, protuberant; shape variable from rounded conical or nearly cylindrical to irregularly asteriform or laterally elongate and ridge-like. Collines typically about 2.0-2.5 mm in width, occasionally up to 6 mm in length, and 1.5-2.0 mm in height. Collines generally broadly conical to slightly flattened, and ornamented with septocostae. Colony formation by circummural polystomodaeal intratentacular (hydnophoroid) budding. Calices confluent, polycentric, the dimensions the same as those given for the series.

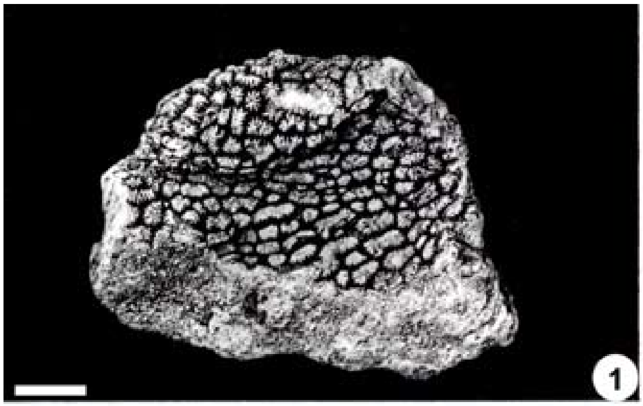
Septa well-developed, weakly exsert peripherally onto collines as septocostae, laminar and solid. Septa arrayed perpendicular to series and radially from collines, symmetry within series not apparent. Septa numerous, typically ontogenetically dimorphic or in two cycles, and arranged in an alternating pattern on the sides of collines. S_3 uncommon, usually absent, but occasionally weakly developed and very deep in calice, in pairs, one on each side of one of the S_2. Size relationship of septa: $S_1>S_2>S_3$. Septa blade-shaped in cross section, straight, and laterally spaced about 3-4 per 2 mm. S_1 thickened toward axial plane of series, about 0.3 mm in width, and very short, typically less than 0.5 mm in length, and spaced about 0.5 mm apart. S_2 tapered toward axial plane and about half the size of the S_1. S_3, when present, about half the size of the S_2. Lateral surfaces of septa smooth. Septal margins smooth, the inner edges nearly vertical. Pali absent.

Columella entirely absent or (?)poorly developed, lamellar, solid, thin, deep in calice and laterally discontinuous.

Wall primarily septothecal, thin, about 0.15-0.4 mm in width, and both laterally and vertically continuous around collines. Endothecal dissepiments tabular to vesicular, thin and irregularly spaced, 3-4 per mm. Exothecal dissepiments within collines vesicular, arched orally, and similarly spaced.

Costae well-developed, distinct, arrayed radially from collines and structurally continuous with septa. Costae

Figure 17. *Eohydnophora ovalis* Masse and Morycowa, 1994, Cumburindio Formation, lower Aptian, Loma de San Juan, Turitzio, State of Michoacán, Mexico. 1, IGM-7010, lateral view of small fragment of ramose corallum, scale bar = 1 cm; 2, detail of oral surface of same specimen, scale bar = 1 cm; 3, IGM-7011, a small massive corallum, transverse thin section, mostly recrystallized and silicified, same scale as Figure 17.2; 4, longitudinal thin section, mostly recrystallized and silicified, same scale as Figure 17.2; 5, transverse thin section, detail of one colline with nine septa, scale bar = 1 mm; 6, longitudinal thin section, detail of tabular and vesicular dissepiments, same scale as Figure 17.5; 7, transverse thin section, detail of septum and adjacent wall, scale bar = 1 mm; 8, longitudinal thin section, detail of tabular dissepiments, same scale as Figure 17.7.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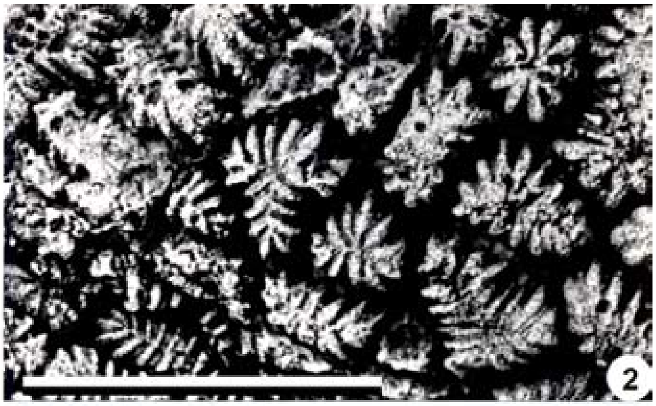
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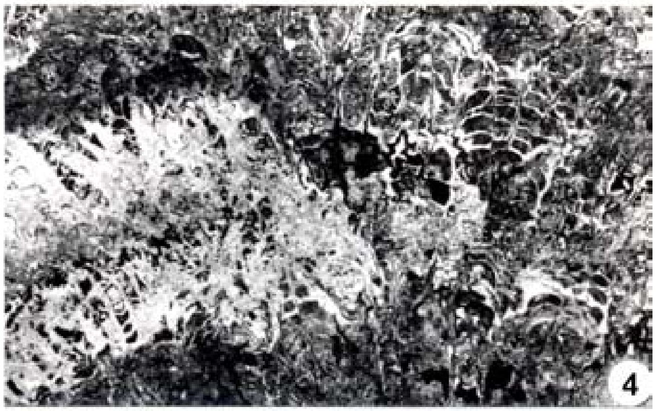
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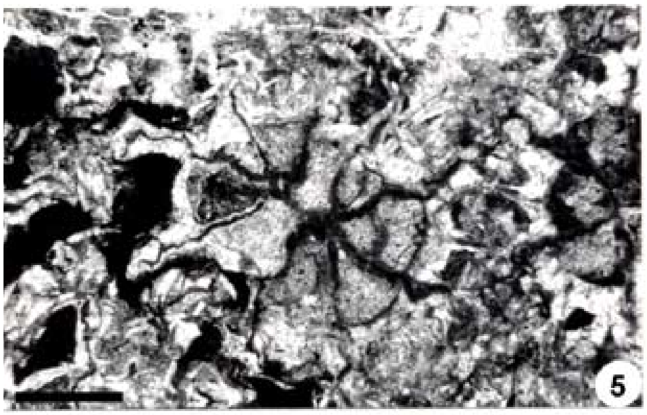
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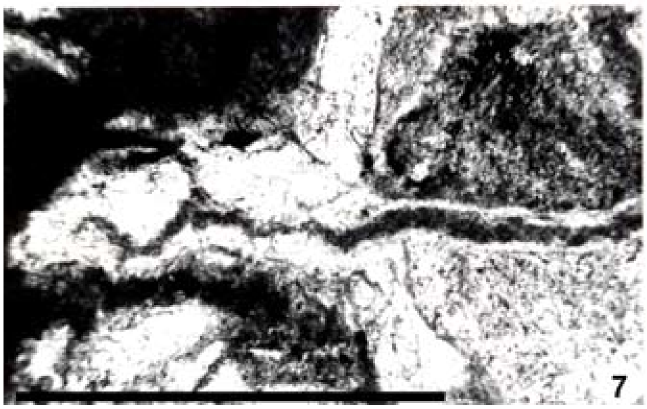
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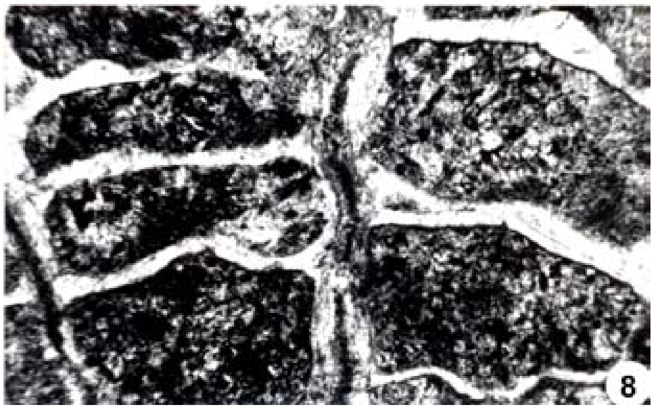
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approximately equal to septa in thickness, but tapered distally toward colline centers. Size relationship of costae: $C_1>C_2$. Intercostal furrows widest along upper and outer perimeter of collines and gradually tapered toward center of colline. Costae of adjacent corallites generally not confluent.

Material examined. Four specimens from the Loma de San Juan, Turitzio: IGM-7010, a small fragment of a ramose or foliaceous corallum (figured); IGM-7011, a small massive corallum with three thin sections (TZ-19 through TZ-21); IGM-7012, a larger fragment of a ramose corallum; and IGM-7013, a fragment of a massive corallum.

Occurrence. Cumburindio Formation, lower Aptian; the coral reef horizon at the crest of the Loma de San Juan, just south of Turitzio, Michoacán, Mexico. The coordinates of this locality are: 18° 31.28' N, 100° 56.65' W.

This species was originally described from the lower Aptian of Monts de Vaucluse (Rustrel) and the chaînon (secondary range) of La Fare, France. The species recently has been reported from the lower Aptian of the eastern Alps.

Discussion. The morphological details of the specimens described above are the same as those described for *Eohydnophora ovalis*, therefore the Mexican material is referred to that species.

The only other similar species previously reported from North America is *Hydnophora* (?) *blancoensis* Wells, 1932 (p. 243, pl. 35, fig. 7), from the lower Glen Rose outcrops along the Blanco River in Hays County, Texas. The external morphological features of *H. blancoensis* appear to be about the same as those of the Mexican specimens described above; however, the single type specimen is badly weathered and architecture of the skeletal structure is unknown.

Several other species described from the Lower Cretaceous of Europe also are similar to the Mexican material. *Hydnophora ackermanni* Zlatarski, 1972, from the Aptian of Bulgaria, appears to be externally similar to the Mexican specimens, but the Mexican coralla possess larger collines. *Eohydnophora incerta* (Morycowa, 1971), from the Aptian of Romania (Turnšek, 1997, p. 85), has collines which are relatively more compact and narrower than those of the Mexican specimens. *Eohydnophora picteti* (Koby, 1897), primarily known from the Lower Cretaceous of Europe and Japan, possesses relatively wider series and longer collines (Turnšek, 1997. p. 86). *Eohydnophora crassa* (Fromentel, 1862), from the Barremian-Aptian of Europe, also primarily differs from the Mexican specimens by the relatively longer and more widely spaced collines (Masse and Morycowa, 1994).

Genus *Eugyra* Fromentel, 1857

Type species. *Eugyra cotteaui* Fromentel, 1857 (p. 30-31, pl. 3, figs. 4-5).

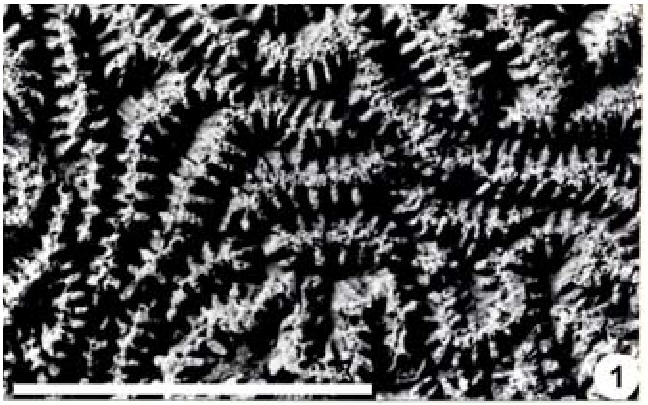
Discussion. On the basis of trabecular architecture and septal ornamentation, Morycowa (1997) transferred the genus *Eugyra* Fromentel, 1857, from the family Stylinidae d'Orbigny, 1851 (suborder Stylinina Alloiteau, 1952) to the family Faviidae Gregory, 1900 (suborder Astreoina Alloiteau, 1952).

The genus *Eugyra* Fromentel, 1857, is macroscopically homeomorphic with *Myriophyllia* d'Orbigny, 1849, and *Pseudomyriophyllia* Morycowa, 1971. In fact, *Eugyra* previously was considered to be a junior synonym of *Myriophyllia* d'Orbigny, 1849, by some authors (Vaughan and Wells, 1943, p. 112; Wells, 1956, p. F376, and others). The presence of a rudimentary columella in the type specimen of *E. cotteaui* recently was recognized during redescription of the type species (Morycowa, 1997), but previously the genus typically was at least in part diagnosed by the lack of a columella. Recent examination (Morycowa, 1997) of some of the essential diagnostic features of these three genera suggests that the precise taxonomic affinities of many of the species which have been assigned to this group need to be re-evaluated.

Eugyra lanckoronensis (Morycowa, 1964)

Figure 18

Figure 18. *Eugyra lanckoronensis* (Morycowa, 1964), Cumburindio Formation, lower Aptian, Loma de San Juan, Turitzio, State of Michoacán, Mexico. 1, IGM-7015, detail of weathered upper surface of corallum, scale bar = 1 cm; 2, IGM-7014, transverse thin section, same scale as Figure 18.1; 3, same corallum, primarily longitudinal thin section, but slightly oblique along right margin, same scale as Figure 18.1; 4, detail of transverse thin section, scale bar = 1 mm; 5, detail of longitudinal thin section, same scale as Figure 18.4; 6, same corallum, oblique longitudinal section, same scale as Figure 18.4; 7, longitudinal thin section, detail of dissepiments, scale bar = 1 mm; 8, transverse thin section of septa, same scale as Figure 18.7.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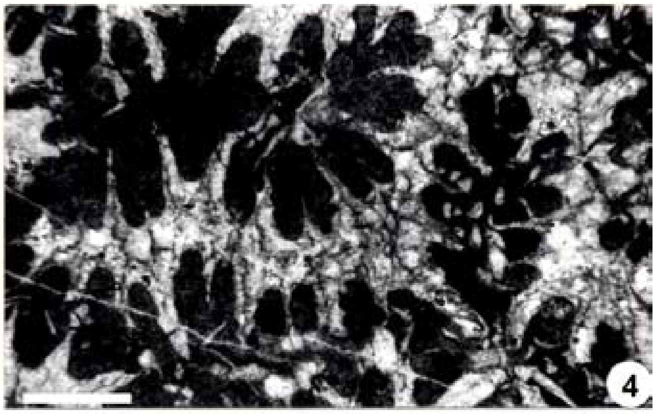
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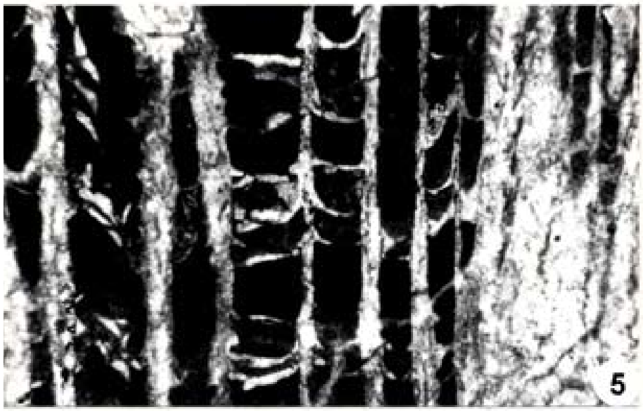
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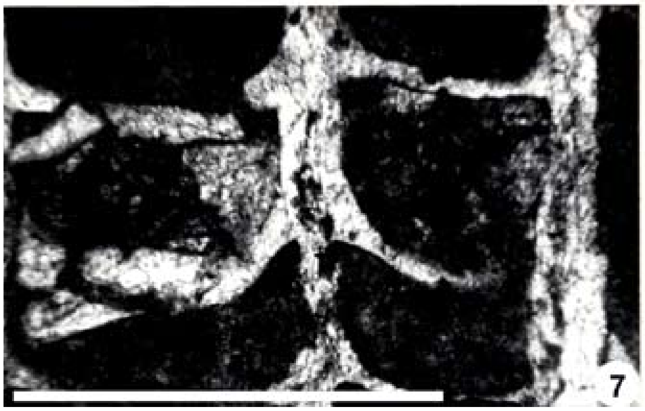
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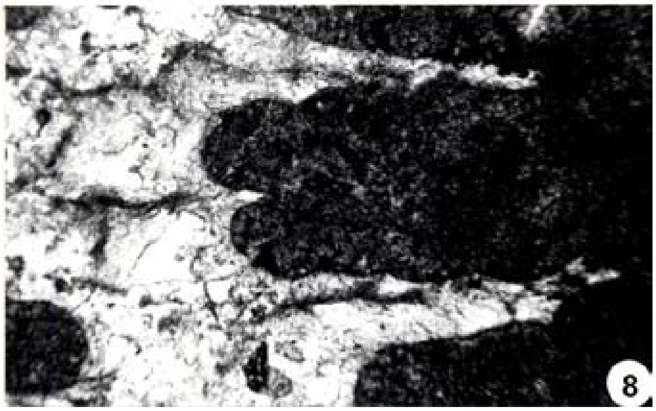
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Myriophyllia lanckoronensis Morycowa, 1964, p. 50-51, pl. 9, figs. 3a-b, pl. 10, figs. 2, 3, text fig. 6; Morycowa and Lefeld, 1966, p. 525-526, pl. 32, figs. 1, 2.

Eugyra lanckoronensis (Morycowa, 1964). Morycowa, 1971, p. 58-60, pl. 9, fig. 1, text figs. 16, 17a; Turnšek and Buser, 1976, p. 49, 75, pl. 3, figs. 1-4; Kuzmicheva, 1980, p. 94-95, pl. 35, figs. 1a, b; Turnšek and Mihajlović, 1981, p. 18, pl. 12, figs. 1-3; Morycowa, 1984, p. 82, pl. 21, fig. 4; Kuzmicheva, 1987, p. 224-225, pl. 1, fig. 5a, b; Kuzmicheva, 1988, p. 157-158, pl. 2, figs. 1a, b; Morycowa, 1989, p. 63, pl. 22, fig. 4; ?He and Xiao, 1990, p. 150, pl. 17, fig. 13; Turnšek, 1992, p. 164; Baron-Szabo and Steuber, 1996, p. 9, pl. 3, figs. 1, 2; Baron-Szabo, 1997, p. 50, pl. 4, fig. 5; Baron-Szabo and Fernández-Mendiola, 1997, p. 45, figs. 4c, e; Turnšek, 1997, p. 91, pl. 91, figs. a-f; Morycowa and Masse, 1998, p. 755, fig. 18.3

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Description. Corallum colonial, attached, meandroid, incrusting to massive, hemispherical, and weakly costate. Colony formation by polystomodaeal intratentacular budding.

Corallites confluent and closely packed. Series continuous, narrow, the lesser CD typically from 1.0 to 1.6 mm, most commonly about 1.5 mm, and up to 2.4 mm in some partially monocentric calices. Series up to at least 15 mm in length and about 1 mm in depth. Calices typically polycentric within series, their margins commonly elongate and parallel or subparallel to each other. Collines typically laterally discontinuous, bifurcated, occasionally conical but more typically elongate and narrow or ridge-like with steep sides and sharp crests, and gently curved to sinuous in oral view. Collines range from 1 to at least 15 mm in length and about 0.5 mm in width. Each colline composed of the laterally expanded distal edges of septa from mutually adjacent series. Ambulacrum absent.

Septa well-developed, weakly exsert peripherally, laminar and solid. Septa numerous, generally oriented perpendicular to both wall and axial plane of series and arranged offset or alternate to those of the adjacent series. Septa somewhat bilaterally symmetrical within series; hexameral symmetry not apparent. Cycles of septa poorly defined, but different sizes of septa indicate the presence of two cycles, and perhaps occasionally part of a third cycle: $S_1 \geq S_2 >> ?S_3$. Septa 12-15 in number along 5 mm of colline summit. S_1 wedge- to blade-shaped in cross section, usually straight, about 0.25 mm in width and from two-thirds to slightly greater than the distance from the wall to the series axial plane in length. Four to five S_1 per 2 mm along collines. S_2 sometimes present between the S_1 and highly variable in size, typically nearly the size of the S_1 but sometimes very short, less than one-fourth the size of the S_1. Alternatively, some of the smaller septa may be a portion of the S_3. Lateral surfaces of septa smooth or occasionally slightly uneven or granulated. Septal margins appear smooth. Interseptal spaces about equal to width of septa. Pali absent. Columella uncommon, weakly developed, lamellar, or entirely absent; hollow axial regions often penetrated by inner edges of primary septa.

Wall well-developed, septothecate, about 0.5 mm thick, and composed of combined fusion of alternating septa from two laterally adjacent series into a single shared thecal structure. Endothecal dissepiments tabular, laterally continuous, thin, vertically spaced about 0.5 mm apart or about 4-5 per 2 per mm. Dissepiments appear nearly flat to concave upward between septa but slightly arched convex upward within individual series between collines. Surface of corallum uneven due to different heights of adjacent series and collines. Upper surfaces of collines occasionally weakly ornamented by faint septocostae.

Material examined. Two specimens: IGM-7014, 80 x 90 mm in width and 75 mm in height, with two thin sections (TZ-12 and TZ-13); and IGM-7015, 80 x 70 mm in width and 55 mm in height. Small commensal serpulids are attached to the oral surfaces of one corallum (IGM-7014) and the other corallum is in places encrusted by an indeterminate species of *Cyathophora*.

Occurrence. Cumburindio Formation, lower Aptian; the coral reef horizon at the crest of the Loma de San Juan, just south of Turitzio, Michoacán, Mexico. The coordinates of this locality are: 18° 31.28' N, 100° 56.65' W.

This species also has been reported from the lower Barremian of France, the lower Aptian of Romania, Greece and Germany, and the Barremian-lower Aptian of Poland, eastern Serbia, Slovenia, the Soviet Carpathians, and Azerbaidzhan, and the Albian of northern Spain and (?)Tibet.

Discussion. The morphology of the specimens described above is the same as that described for *Eugyra lanckoronensis*

(Morycowa, 1964), therefore the Mexican coralla are referred to that species.

Several species of *Eugyra*, and those of the other morphologically similar genera *Myriophyllia* d'Orbigny, 1849, and *Dendrogyra* Ehrenberg, 1834, have been reported from Lower Cretaceous rocks of Mexico and adjacent areas. The specimens described herein are morphologically distinct from any of those previously reported from this region. The species of *Eugyra* and those of other morphologically similar genera reported from Mexico and the Caribbean region are discussed below.

Three species from Early Cretaceous (Barremian-Aptian) strata in the state of Puebla, Mexico, were described by Felix (1891, p. 159-161): *Eugyra cotteaui* Fromentel, 1857; *E. neocomiensis* Fromentel, 1857; and *Dendrogyra mariscali* Felix, 1891. The first two species initially were described from the European Cretaceous (Fromentel, 1857), whereas the third is known only from reported Mexican occurrences. All three of these species subsequently were considered to belong to the genus *Myriophyllia* d'Orbigny, 1849 (Wells, 1944b, p. 436), and one of them, *M. neocomiensis* (Fromentel, 1857), later was reported from the state of Oaxaca, in the same region of Mexico (Reyeros, 1983, p. 18-19).

Eugyra cotteaui Fromentel, 1857 (p. 30-31, pl. 3, figs. 4, 5), which is the type species of *Eugyra*, possesses meandroid series typically 1.5 to 2.0 mm in width, if parallel, but non-parallel series range from 3.0 to 3.5 mm. Sizes of septa indicate that two, or sometimes three, cycles of septa are present. The number of septa along 2 mm of colline length is usually 7, 3 to 5 of which are S_1 (Morycowa, 1997, p. 290). According to these figures, along 5 mm of colline length the number of septa would be about 17 or 18. In addition, a feeble, rudimentary columella sometimes is present (Wells, 1944b; Morycowa, 1997). The Mexican specimens of *E. cotteaui* described by Felix (1891, p. 159-161) possess series 2-4 mm in width with septa often alternating in size and 10-14 in number, including 5-7 larger septa, along 5 mm of colline length. The columella presumably is absent (Wells, 1944b, p. 436). A recent re-examination of Felix's material indicated that some of his specimens of *Eugyra cotteaui* should be referred to *Pseudomyriophyllia* cf. *P. carpathica* Morycowa, 1971 (Löser, 2006, p. 29, 56).

Eugyra neocomiensis Fromentel, 1857 (pl. 3, figs. 6, 7; 1877, p. 442, pl. 103, fig. 1), typically possesses series 1.5-2.0 mm in width, sometimes as much as 2.5 mm, septa in two cycles, with 6-9 septa in 2 mm or 15-23 in 5 mm, and a discontinuous lamellar columella (Morycowa and Masse, 1998, p. 754). The Mexican specimens assigned to *E. neocomiensis* Fromentel, 1857, by Felix (1891, p. 159) possess series 1-2 mm in width and septa alternating in size and 7-9 in number along 2 mm of colline length, or about 17-23 in number along 5 mm of colline length. The presence or absence of the columella was not noted by Felix. However, based on the apparent absence of a columella in the topotypes of *E. neocomiensis* Fromentel, 1857, the Mexican specimens presumably lack a columella (Wells, 1944b, p. 436). A recent re-examination of Felix's material indicated that some of his specimens of *Eugyra neocomiensis* should be referred to *Eugyra affinis* Prever, 1909 (Löser, 2006, p. 28, 56). The specimens referred to *Myriophyllia neocomiensis* (Fromentel, 1857) by Reyeros (1983, p. 18-19, pl. 5, fig. 2, pl. 6, fig. 1) reportedly possess series 1-1.5 mm in width and lack a columella. The figures of the hypotype corallum (IGM-2718) presented by Reyeros show that the series typically range from 1.5 to 2 mm in width and that the number of septa along 5 mm of colline length ranges from about 10-12.

Dendrogyra mariscali Felix, 1891 (p. 161, pl. 24, figs. 4, 4a), possesses series 2-4 mm in width with septa alternating in size and 14-16 in number, including 7-8 larger septa, along 5 mm of colline length, and a laterally discontinuous lamellar columella (see Felix, 1891, pl. 24., figs. 4, 4a; and Wells, 1944, p. 436). Felix's holotype of *Dendrogyra mariscali* recently has been re-assigned to the genus *Meandroria* Alloiteau, 1952, but this generic determination also had been considered to be problematic (Löser, 2006, p. 36, 56).

Eugyra cuyleri Wells, 1932 (p. 237-238, pl. 35, fig. 4), from the lower Glen Rose (lower Albian) of Texas and Lower Cretaceous of Trinidad, possesses series that average 2 mm in width with septa equal in size and 3-4 in number along 2 mm of colline length (Wells, 1932), or about 7-10 septa per 5 mm (Wells, 1944b, p. 436; 1948, p. 612); the columella is absent (Wells, 1932).

Dendrogyra dumblei Wells, 1933 (p. 149, pl. 5, fig. 10), from the Edwards Limestone, Comal County, Texas, subsequently was reassigned (Wells, 1944b) to the genus *Myriophyllia*. The corallum of this species has series 1.5-2 mm in width with septa equal in size and 10-12 in number along 5 mm of colline length; a well-developed lamellar columella is present.

Myriophyllia borrachensis Wells, 1944b (p. 436-437, pl. 70, figs. 2, 3), from the Chimana and upper Barranquín formations, northeastern Venezuela, has series that average 2.5 mm in width and septa weakly alternate in size and 7-9 in number along 5 mm of colline length; typically a lamellar columella is present deep in the series, but the structure also may be weak or absent.

Myriophyllia trinitatis Wells, 1948 (p. 612, pl. 89, fig. 7, pl. 90, fig. 3a), from the Lower Cretaceous of Trinidad, has relatively short, narrow series that range from 1 to 1.75 mm in width and septa alternate in size and 15-20 in number along 5 mm of colline length; the columella is absent.

Another species, *E. felixi*, was reported from the U-bar Formation in southwestern New Mexico (Campbell, 1988, p. 83), but the species was not described or figured.

The Mexican specimens described above also are morphologically similar to some of the other species that are known from the European Cretaceous. However, based on characters of the width of series, relative sizes and spacing of septa, and presence or absence of a columella, the Mexican specimens referred to *Eugyra lanckoronensis* appear to be taxonomically distinct. Some of these species, and the characteristics listed above, if known, are given here.

Eugyra interrupta Fromentel, 1862 (p. 410, 429), has series 2.5-3 mm in width and 10 longer septa in 5 mm.

Eugyra continua (Blanckenhorn, 1890, p. 10, pl. 1, fig. 8), has series 1.2-2.5 mm in width, 12-15 septa in 5 mm, and lacks a columella (Felix, 1909, p. 173, pl. 7, fig. 8, 8a, 1913, p. 98; Wells, 1948, p. 612).

Eugyra digitata Koby, 1896 (p. 21-22, pl. 8, figs. 4-7), has series 2-3 mm in width and typically 12 septa in 5 mm (Wells, 1948, p. 612).

Eugyra pusilla Koby, 1896 (p. 22, pl. 8, figs. 8-9), has series only 1 mm in width and numerous, closely spaced septa, 12 in 2 mm, or about 30 in a distance of 5 mm (Wells, 1948, p. 612). The variety *E. pusilla pauciseptata* de Angelis, 1905 (1905a, 1905b, p. 217, pl. 14, fig. 13), has series 0.75-1.5 mm in width and 5-6 septa in 2 mm (de Angelis, 1905c, p. 36-37), or about 12-15 septa in 5 mm. The coralla referred to this variety by Alloiteau (in Hupe and Alloiteau, 1947, p. 199-200, pl. 2, fig. 10) have been redescribed as *Hydnophora alloiteaui* Reig, 1991 (p. 25-26, pl. 7, figs. 4, 5). The subspecies *E. pusilla rariseptata* Morycowa, 1964 (p. 45-46, pl. 9, fig. 1a-b, pl. 10, fig. 1) has series with variable width, from 0.7 to 1.2 mm, and fewer septa, from 15 to 22 in 5 mm.

Eugyra pontica Karakasch, 1907 (p. 254, pl. 22, fig. 5), and the subspecies *E. pontica hydnophoroides* Bendukidze, 1961 (p. 12-13, pl. 4, fig. 8), have series 1.5-2 mm in width and 9-12 septa in 5 mm (Sikharulidze, 1985, p. 22).

Eugyra bernardi (Prever, 1909, p. 81-82, pl. 3, figs. 18, 18a), has series 1-2 mm in width, 13-16 septa in 5 mm, and no columella (Hackemesser, 1936, p. 10, pl. 1, figs. 1, 2; Wells, 1948, p. 612).

Eugyra robusta Hackemesser, 1936 (p. 11, pl. 1, figs. 3, 4), has series 2-3.5 mm in width and only 4 septa in 5 mm.

Eugyra arasensis Alloiteau, 1947 (in Hupe and Alloiteau, p. 197-199, pl. 2, fig. 4, text fig. 2), has series 3-5 mm in width, 12-14 septa in 5 mm, and no columella (Reig, 1994, p. 35, fig. 1a).

Eugyra crassisepta Reig, 1989 (p. 25, pl. 6, fig. 5), has series 2.5-3.2 mm in width, 7-8 septa in 5 mm, and no columella. Three other species of *Eugyra* recently have been described by that same author: *Eugyra vivesi* Reig, 1994 (p. 33, figs. 1c, 2c), has series 2.5-4.5 mm in width, 7-8 septa in 5 mm, and no columella; *E. calzadai* Reig, 1994 (p. 33-34, figs. 1e, 2b), has series 5-6 mm in width, about 10 septa in 5 mm, and no columella; and *E. casanovai* Reig, 1994 (p. 34-35, figs. 1b, 2a), has series 2-3.5 mm in width, 14-16 septa in 5 mm, and no columella.

Species of *Eugyra* also have been described from Africa (Gregory, 1930, p. 200-201, pl. 18, fig. 6), Asia (He and Xiao, 1990) and Japan (Eguchi, 1951, p. 12-14, 45, 54-55).

Suborder Fungiina Verrill, 1865
Family Actinacididae Vaughan and Wells, 1943
Genus *Actinaraea* d'Orbigny, 1849

Type species. *Agaricia granulata* Münster, in Goldfuss, 1829 (p. 109, pl. 38, figs. 4a, b; d'Orbigny, 1849, p. 11).

Actinaraea michoacanensis **new species**
Figure 19

Actinaraea sp. cf. *A. arborescens* (Felix, 1891). Hedberg and Pyre, 1944, p. 7.

Actinaraea arborescens (Felix, 1891). Wells, 1944b, p. 440, pl. 72, figs. 1-5, pl. 74, fig. 1; von der Osten, 1957b, p. 572; Baron-Szabo, 1997, p. 88.

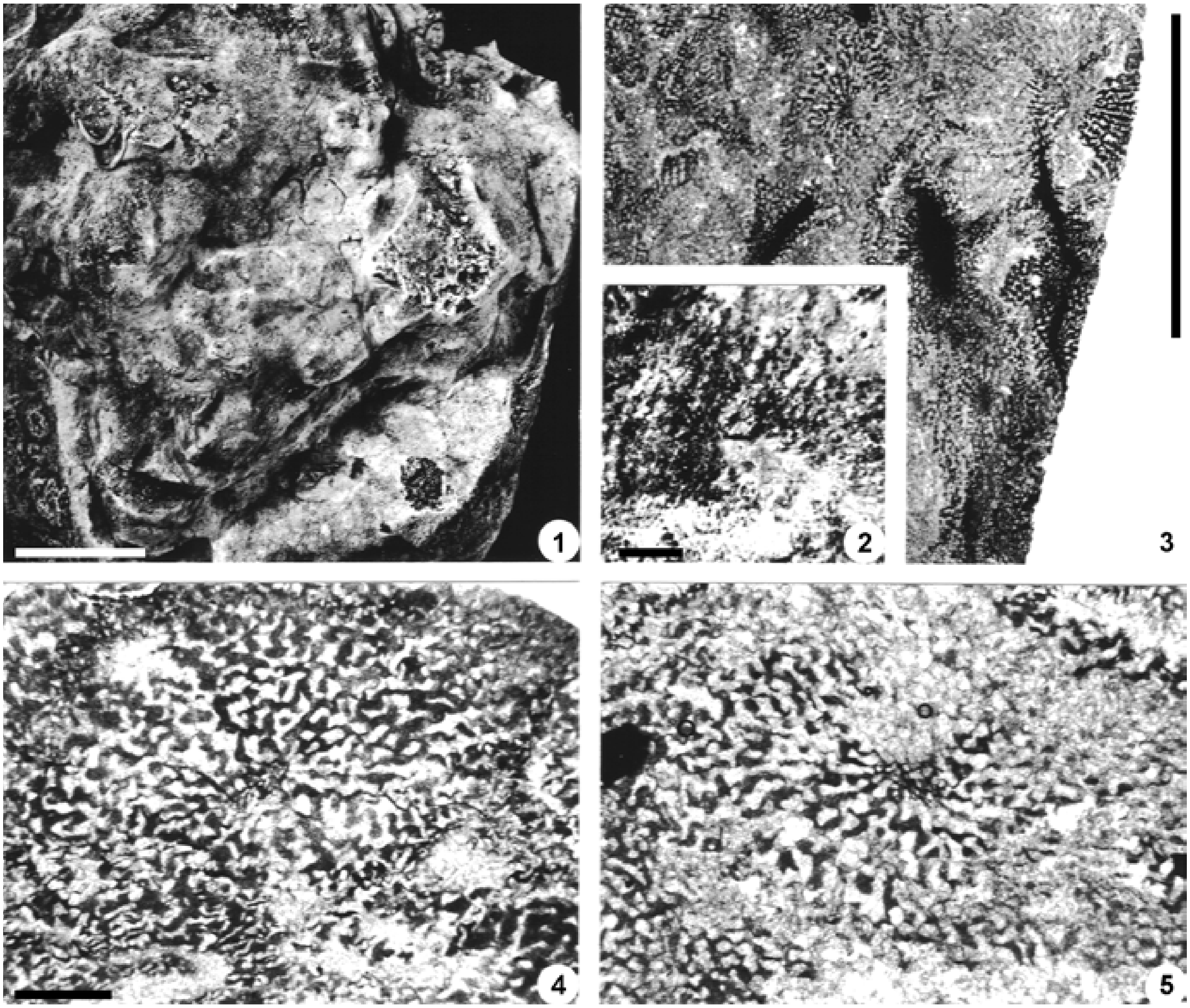

Figure 19. *Actinaraea michoacanensis* n. sp., holotype IGM-7016, Cumburindio Formation, lower Aptian, Loma de San Juan, Turitzio, State of Michoacán, Mexico. 1, Portion of the lateral surface of the corallum, scale bar = 1 cm; 2, detail of scleractinian epibiont on side of corallum, scale bar = 1 mm; 3, transverse thin section, scale bar = 1 cm; 4 and 5, transverse thin section, detail of corallites, scale bar = 1 mm.

Diagnosis. Corallum massive to ramose. Calices 2-5 mm in diameter; calicular centers spaced 3.5-7 mm apart. Septa numerous, up to four complete cycles developed in larger corallites.

Description. Corallum colonial, attached, plocoid, superficially thamnasteroid in appearance, massive to ramose, faintly costate or striated. Size of examined specimen about 45 x 50 mm in width and 75 mm in height. Colony formation by extratentacular budding from coenosteal region. Branches columnar, short, irregular in shape, often subcylindrical, elliptical in cross section, and about 10-30 mm in diameter. Branches typically with abundant, smaller branch offshoots of 5-10 mm in diameter, irregularly spaced, protuberant nodular or short cylindrical in shape, and oriented upward and outward from sides of colony.

Corallites weakly delineated by walls, generally cylindrical, orally protuberant or flush, up to about 5 mm in outside diameter, and unevenly distributed over surface of corallum. Calices exclusively monocentric, either superficial or orally concave and shallow, and typically less than 1 mm in depth. Calicular margins circular or subcircular in outline. CD variable from 2 to 5 mm. Calicular centers spaced 3.5-7 mm apart.

Septa well-developed, non-exsert, laminar and highly fenestrate. Septa occasionally continuous beyond calicular margin as weak septocostae, but typically the extracalicular extensions of septocostal structures become intermeshed with the coenosteum and indiscernible. Number of septa variable and directly related to calice diameter as in these examples: CD 2 mm, 20 septa; CD 2.5 mm, 30 septa; CD 4 mm, 38 septa; and CD 5 mm, about 50 septa. Number of septa indicates the presence of from three to four complete septal cycles, and occasionally a portion of the fifth cycle on larger corallites. Septa typically radially arrayed around calicular axis and usually without any apparent hexameral symmetry. General size relationship among septa: $S_1=S_2\geq S_3>S_4(>S_5)$. Septa usually straight, laminar and fenestrate in cross section, and nearly equal in width, about 0.1 mm. Typically S_1, S_2 and some of S_3, or 12 to 18 septa, extend from wall to corallite axis. S_4 usually about half as long as S_3. S_5 usually peripheral when present, inserted near to calicular margin and very short. Interseptal spaces approximately equal to, or slightly less than, width of septa. Synapticulae abundant, simple trabecular in structure, oriented subhorizontally between septa and spaced about 0.2 mm apart, or about 5-6 per mm. Lateral surfaces of septa generally uneven and undulated due to fenestrate structure of septa. Septal margins beaded in appearance.

Columella trabecular, spongiose, orally papillose, usually vertically continuous, and about 0.5 mm in diameter. Columella composed of closely intermeshed trabecular rods and frequently laterally intermittently fused to inner margins of S_1, S_2 and some of S_3.

Wall typically moderately well-developed, synapticulothecal, and usually about 1 mm in width. Wall composed of a concentric, vertically continuous zone of very closely spaced, horizontally oriented, synapticular rods.

Coenosteal surfaces of corallum faintly costate or striated near calices and usually spinose or granular in appearance over other intercorallite areas farther from calices. Coenosteal striae, or distal portions of septocostae, spaced about 4-5 per mm. Coenosteum between corallites composed of an intermeshed continuation of septa-synapticulae trabecular elements, only the architectural structure lacks well-defined organization.

Etymology. The species *A. michoacanensis* n. sp. is named for where the samples were found, the Mexican state of Michoacán, which is indicated by the addition of the Latin suffix -*ensis* = place.

Types. One fragment of a corallum, holotype IGM-7016, with one thin section (TZ-48). Most of the specimen is internally recrystallized and partly silicified. The original skeletal architecture is apparent only in a thin rind along portions of the exterior surface.

The type stratum is the Cumburindio Formation, lower Aptian. The type locality is in the coral reef horizon at the top of the Loma de San Juan, just south of Turitzio, Michoacán, Mexico. The approximate coordinates of the type locality, as determined from the Mexican 1:50,000 scale Huetamo (E14A64) topographic map, are: 18° 31.28’ N, 100° 56.65’ W.

Occurrence. Known from the type locality and Venezuela. The coordinates of the type locality are given above. The specimens described by Wells (1944b) are from the Lower Cretaceous upper Barranquín Formation of northeastern Venezuela.

Discussion. The morphological characteristics of the described specimen, with minor exceptions, generally encompass those given by Wells (1944b, p. 440, pl. 72, figs. 1-5, pl. 74, fig. 1) in his description of *Actinaraea arborescens* (Felix, 1891) from the Barranquín Formation of northeastern Venezuela. The corallites of the Mexican specimen exhibit a broader range of diameters (2-5 mm) than those of the Venezuelan specimens (3-3.5 mm), and they possess a larger number of septa. However, calices of about equal diameter on both of these specimens possess about the same number of septa. Other similarities include the growth form of the corallum, development of the columella, the number of septa which reach the columella (at least 12 on comparable sized corallites), and the lateral spacing of the coenosteal striae or septocostae (4-5 per mm, or about 9-10 in 2 mm). Therefore, the species described herein and the *A. arborescens* of Wells (1944b) are considered to be conspecific. Unfortunately, the coralla that Wells (1944b) described as *A. arborescens* (Felix, 1891), later were considered not to be conspecific with *Thamnoseris arborescens* Felix, 1891 (p. 152, pl. 25, figs. 11, 11a, 15). However, Wells’s assignment of the specimens to the genus *Actinaraea* evidently was correct (Baron-Szabo, 1997, p. 88-89; Löser, 2006, p. 52) and the morphology of the Mexican specimen described above supports this taxonomic determination. Therefore, this species is described as new.

The morphological characteristics of the new species differ from those of the other previously described species attributed to this genus. The type species, *A. granulata* from the Upper Jurassic of Europe, possesses corallites that are much smaller in diameter, only 1.6-2.0 mm (Turnšek, 1997, p. 6). Another species from the Upper Jurassic of Europe, *A. minuta* Roniewicz, 1966 (p. 250, pl. 25, fig. 1), also differs by the smaller size of the corallites, which are only about 1.5 mm in diameter (Roniewicz, 1976, p. 91). *Actinaraea tenuis* Morycowa, 1971 (p. 128-130, pl. 35, figs. 1a-d, pl. 36, figs. 1a-c, text fig. 37), from the lower Aptian of Romania and other Lower Cretaceous localities in Europe (Turnšek, 1997, p. 7) and Texas (Scott, 1984a, p. 344), has smaller calices, relatively fewer septa, and a less dense skeletal architecture. A species described from the Campanian of Spain, *A. morycowai* Reig, 1995 (p. 34-35, pl. 5, figs. 1-4), has a massive corallum with larger corallites and widely spaced calicular centers.

A single, small (0.6 mm diameter) scleractinian epibiont is attached to the side of the examined corallum (see Figure 19.2, center). Wells (1944b, pl. 72, fig. 4) also noted a small, solitary corallite, *Stylosmilia gregorii*, associated with his specimen of *A. arborescens*. The two occurrences are strikingly similar: both seem to involve the same host and epibiont species. Additionally, some 1 mm diameter annelid tubes were observed attached to the oral surface of the corallum.

Genus *Thamnarea* Étallon, 1864

Type species. *Thamnarea digitalis* Étallon, in Thurmann and Étallon, 1864 (p. 412, pl. 58, figs. 6a-c), by subsequent designation (Gregory, 1900, p. 193).

***Thamnarea hornosensis* new species**

Figure 20

Diagnosis. Corallum typically large, greater than 1 m in both diameter and height, and exclusively ramose; branches elongate, from 8 to 20 mm in diameter, but most commonly about 15 mm. Distance between calicular centers from 4 to 5 mm. Number of septa variable, usually 10-12 axially, but as many as 40-56 peripherally. Septocostae laterally spaced 4 per mm.

Description. Corallum colonial, attached, thamnasteroid, ramose, faintly costate, typically large in size, diameter and height up to at least 1 m, and overall fan-shaped. Branches robust, generally cylindrical to subcylindrical, highly elongate, usually vertically continuous, slightly tapered along length, frequently bifurcated, diameter from 8 mm to 20 mm, but most often about 15 mm. Branches oriented parallel to subparallel to each other and very closely spaced or in lateral contact with each other, the interbranch spaces from 0 to about 5 mm. Branches arrayed candelabrum-style, radially outward but primarily upward from basal portion of colony. Surfaces of branches nearly smooth, but overall uneven and broadly undulated by low, bulbous, lateral growths approximately 10 mm in diameter. Colony formation by polystomodaeal intratentacular marginal budding with lamellar linkages.

Corallites peripherally confluent with adjacent corallites and oriented with axes nearly perpendicular to branch surfaces. Calices distinct, superficial, monocentric, margins generally circular in outline. Calice diameters poorly defined due to lack of theca, but discontinuities in peripheral continuations of confluent linear septocostae indicate a variable CD from 3 mm to a maximum of about 7 mm, but most typically 5 mm. Calicular centers small, shallow, pit-like or funnel-shaped depressions in surface of corallum; centers spaced about 4-5 mm apart.

Septa well-developed, barely exsert, fenestrate, and structurally continuous as septocostae. Number of septa variable, only 10-12 axially, but up to about 40 to 56 in peripheral corallite regions. Septa typically hexamerally symmetrical and radially arrayed in four complete cycles with portions of the fifth cycle sometimes present also. Size relationship among septa: $S_1 \geq S_2 > S_3 > S_4 > S_5$. Septa somewhat blade-shaped in cross section, straight to curved, and very thin, width about 0.1 mm. S_1 and most S_2 extended into corallite axis. Septa of higher cycles typically similar in width to those of lower cycles but proportionately shorter in length. Synapticulae well-developed, numerous, and irregularly distributed. Synapticulae vertically spaced about five per mm. Lateral surfaces of septa uneven or undulated due to fenestrate trabecular structure. Upper septal margins nearly smooth; inner margins of S_1 and S_2 often axially fused, those of higher cycles commonly fused to septa of previous cycle.


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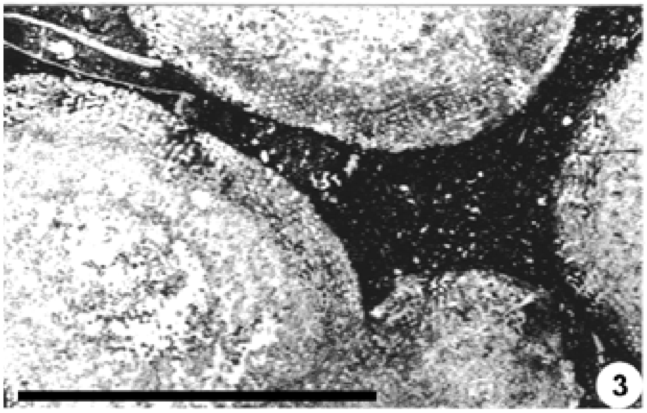
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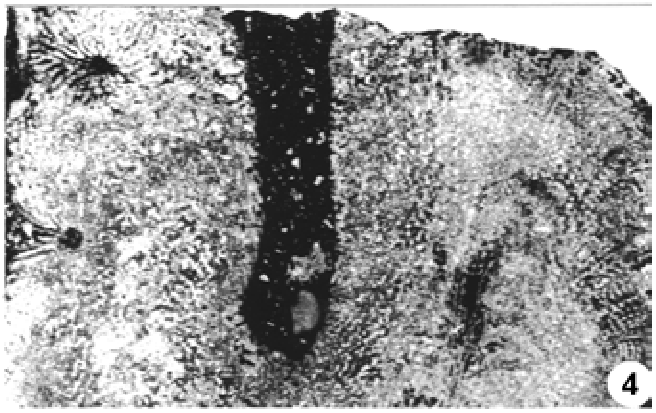
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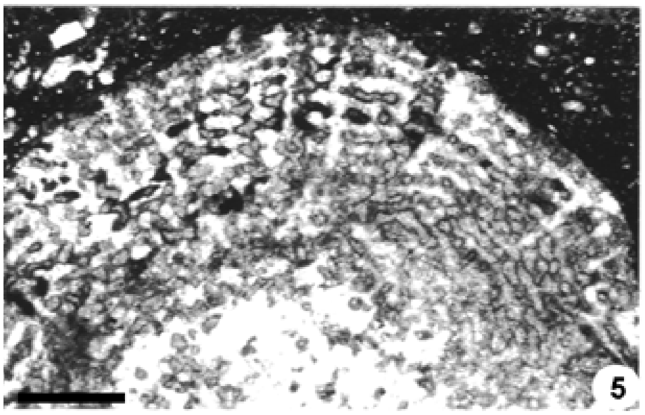
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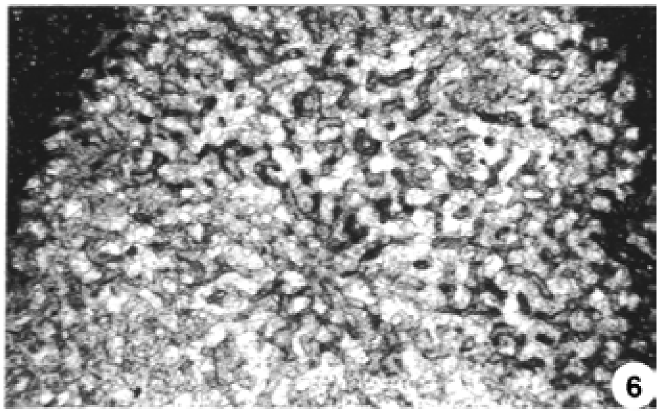
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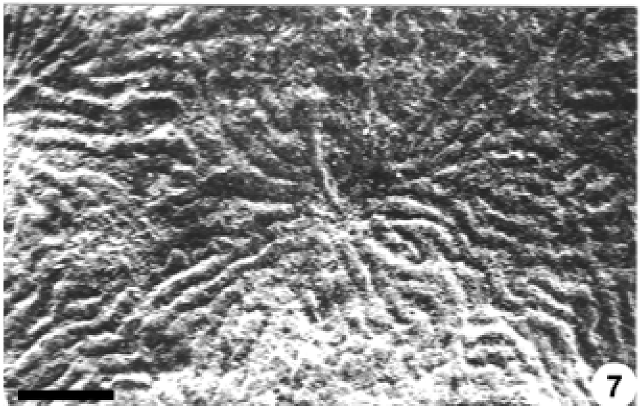
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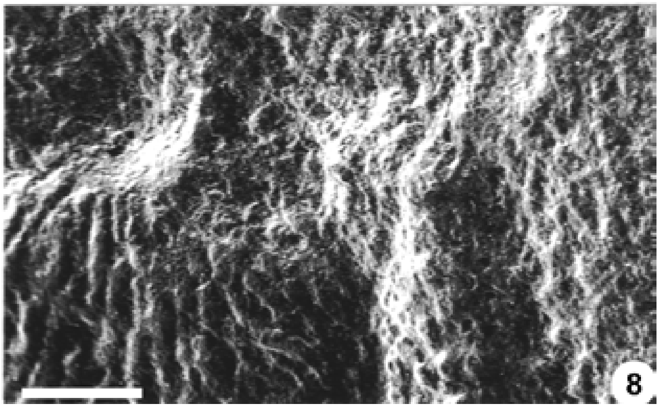
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Interseptal spaces typically slightly narrower than width of septa. Pali absent. Columella weakly developed, trabecular, vertically discontinuous, very thin, and orally papillose.

Wall generally absent, but the peripheral margins of corallites somewhat delineated by a highly fenestrate boundary of synapticulae which indicates the possible presence of a very weakly developed synapticulotheca. Endotheca and exotheca not observed.

Costae well-developed but very faintly expressed, structurally continuous with septa as septocostae, frequently confluent between septa of adjacent corallites, and laterally spaced 4 per mm. Intercostal furrows narrow, approximately equal to the interseptal spaces in width. Upper edges of costae nearly smooth, similar to ornamentation of upper margins of septa.

Etymology. The species is named for its type locality, the Arroyo Los Hornos, which is indicated by the addition of the Latin suffix -*ensis* = place.

Types. Several dozen branches collected from the outcrop of a single large colony, holotype corallum IGM-7017, with nine thin sections (TZ-62 through TZ-70).

The type stratum is the Cumburindio Formation, lower Aptian. The type locality is in the Arroyo Los Hornos, about 1 km north of Turitzio, Michoacán, Mexico. The approximate coordinates of the type locality, as determined from the Mexican 1:50,000 scale Huetamo (E14A64) topographic map, are: 18° 32.10’ N, 100° 56.74’ W.

The shape of the corallum as it appears in the outcrop probably has been modified by lateral compression during burial and compaction, and by subsequent exhumation and weathering. The skeletal structure of most of the examined branches is not preserved internally due to extensive recrystallization and partial silicification. The corallum of *T. hornosensis* is the largest of any of the coral species known from the Cumburindio Formation.

The type specimen was found at the top of a bed of rudist bioclastics which probably served as the initial attachment point of the colony. Corallum branches are often encrusted by epibionts including small serpulid annelids, a species of sponge, and a species of thin, linear, creeping bryozoan (see Figure 20.8; distal end at right of center).

Occurrence. Known only from the type locality. The coordinates of this locality are given above. The description is based on samples from a single colony that was discovered cropping out at a knickpoint in the thalweg of the Arroyo Los Hornos. This same species also was observed in the weathered surface of the next higher resistant limestone ledge, which is slightly further upstream and stratigraphically up section from the type horizon. The species has the largest corallum yet discovered in the Cumburindio Formation. Field photographs of the corallum are shown in Figure 20.1 and 20.2.

Discussion. *Thamnarea hornosensis* n. sp. is morphologically similar to several other previously described species, but the large size and growth form of the corallum, diameter of the branches (8-20 mm, typically 15 mm), distance between calicular centers (4-5 mm), variable number of septa (10-12 axially, 40-56 peripherally), and relative spacing of the septocostae (4 per mm) serve to distinguish it from other species, including two from nearby deposits in the Lower Cretaceous of Mexico and South America. *Thamnaraea holmoides* Felix, 1891 (p. 143, pl. 22, figs. 1, 1a), from Neocomian strata near Tehuacán, state of Puebla, Mexico, has a small, columniform corallum with thicker branches (18-24 mm), calicular centers that are typically more widely spaced (6 mm), and overall fewer septa (12-14 axially, but only 20-24 peripherally). However, the holotype of *T. holmoides* is

Figure 20. *Thamnarea hornosensis* n. sp., holotype corallum IGM-7017, Cumburindio Formation, lower Aptian, from the Arroyo Los Hornos, just north of Turitzio cemetery and about 1 km north of Turitzio, State of Michoacán, Mexico. 1, View of upper surface of outcrop at knickpoint in the Arroyo Los Hornos, corallum in lateral view with distal ends of branches toward the left and basal region toward the right, height of hammer for scale = 28 cm; 2, view of weathered cross section perpendicular to bedding plane, corallum in lateral view with distal ends toward right, note underlying accumulation of rudist valves shown in lower half of figure, height of hammer for scale = 28 cm; 3, transverse thin section through portions of four branches, structure mostly recrystallized axially, scale bar = 1 cm; 4, longitudinal thin section taken just above branch bifurcation, the portion of the section on the left more tangential to the outer surface of the branch, same scale as Figure 20.3; 5, detail of transverse thin section of branch, scale bar = 1 mm; 6, detail of transverse thin section of corallite (tangential longitudinal thin section of branch), same scale as Figure 20.5; 7, scanning electron micrograph of weathered surface of branch, scale bar = 1 mm; 8, scanning electron micrograph of weathered surface of branch, one calicular center shown in upper left and distal end of bryozoan epibiont shown near lower right, scale bar = 1 mm.

poorly preserved and it has tentatively been reassigned to the genus *Kobyastraea* Roniewicz, 1970 (Löser, 2006, p. 37, 57). *Dendraraea anzoateguensis* Wells, 1944b (p. 440-441, pl. 73, figs. 1-3), from the Chimana Formation (Lower Cretaceous) of La Borracha Island, northeastern Venezuela, has a small, nodular corallum, smaller corallites, and calicular centers that are more closely spaced (2-3 mm).

A few other species of *Thamnarea* are known from the Lower Cretaceous. *Thamnarea cancellata* Koby, 1898 (p. 86-87, pl. 20, figs. 7-10a), from the Urgonian of Switzerland, possesses a small, massive or nodular corallum and calicular centers that are more closely spaced (1.5-2.0 mm). *Thamnarea mammelonata* Turnšek, 1981 (in Turnšek and Mihajlović, 1981, p. 38-39, pl. 46, figs. 2-6, pl. 47, figs. 1-4), from the Barremian- ower Aptian of Serbia and Lower Cretaceous of Hungary (Császár and Turnšek, 1996), has a cylindrical corallum with calices situated on prominent mammelons, calicular centers that are more closely spaced (2-4 mm), and septa that are fewer in number (16-22).

Two species from the upper Oxfordian of Europe also appear to be similar to, yet morphologically distinct from, *T. hornosensis* n. sp.: *T. digitalis* Étallon, 1864, the type species, and *T. arborescens* Étallon, 1864 (in Thurmann and Étallon, 1864, p. 412, pl. 58, figs. 6 and 5, respectively). The type species possesses a similar corallum growth form and branch morphology, but the branches are thicker (20-40 mm in diameter), the calicular centers are more widely spaced (5-7 mm), and the septa are fewer in number (18-24) (Koby, 1888, p. 412, pl. 110, fig. 7). The other species, *T. arborescens*, possesses branches that typically are thinner (6-15 mm in diameter) and septa that are fewer in number (12-20) (Koby, 1888, p. 411, pl. 110, figs. 2-6). One other European Jurassic species, *T. pulchella* Ogilvie, 1897 (p. 154, pl. 10, fig. 14, 14a), also has a ramose growth form, but the branches are thinner (8-10 mm) and calicular centers more closely spaced (about 2 mm). Other species from the Jurassic of Europe, including *T. granulosa* and *T. bacillaris* Koby, 1888, and the Jurassic of India, including *T. amorpha* and *T. tuberosa* Gregory, 1900, possess coralla with massive hemispherical or globular growth forms.

Family Calamophylliidae Vaughan and Wells, 1943
Genus *Calamophyllia* Blainville, 1830

Type species. *Calamophyllia striata* Blainville, 1830 (p. 312), by subsequent designation (Milne Edwards and Haime, 1850, p. xxxiii) (Wells, 1956, p. F380).

Calamophyllia sandbergeri Felix, 1891
Figure 21

Calamophyllia sandbergeri Felix, 1891, p. 153, pl. 22, fig. 9; Felix, 1914a, p. 40; Wells, 1944b, p. 438, pl. 71, figs. 2, 3, pl. 74, figs. 1, 5; Wells, 1948, p. 612-613, pl. 89, fig. 3a, pl. 90, figs. 1, 2; von der Osten, 1957b, p. 572; Scott and Brenckle, 1977, p. 185; Scott, 1981, p. 467; Reyeros, 1983, p. 19-20, pl. 6, fig. 2; Scott, 1990, p. 31, 40, 82; Fagerstrom, 1987, p. 427-429.

Diplarea venezuelensis Gregory, 1927, p. 441, pl. 13, figs. 1a, 1b.

Calamophyllia sp. cf. *C. venezuelensis* (Gregory, 1927). Hedberg and Pyre, 1944, p. 7.

Calamophylliopsis sandbergeri (Felix, 1891). Löser, Bach, and Müller, 2002, p. 34.

Thecosmilia sandbergeri (Felix, 1891). Löser, 2006, p. 35, fig. 3E.

Description. Corallum colonial, attached, phaceloid, robust, typically large in size, height up to at least 30 cm. Branches essentially cylindrical, 4-6 mm in diameter, elongate, bifurcated frequently, parallel to subparallel, very closely spaced and occasionally in contact with each other. Branches of corallum arrayed radially upward and outward from origin point of colony. Corallum faintly costate. Colony formation by distomodaeal intratentacular budding with temporary lamellar linkages.

Figure 21. *Calamophyllia sandbergeri* Felix, 1891, Cumburindio Formation, lower Aptian, western slope adjacent to Turitzio cemetery, north of Turitzio, State of Michoacán, Mexico. 1, IGM-7018, detail of weathered surfaces of branches in limestone, branch bifurcation in lower center of figure, scale bar = 1 cm; 2, transverse thin section, branches mostly recrystallized, scale bar = 1 cm; 3, longitudinal thin section, recrystallized, same scale as Figure 21.2; 4, detail of transverse thin section shown above in Figure 21.2, scale bar = 1 mm; 5, detail of longitudinal thin section shown above in Figure 21.3, same scale as Figure 20.4; 6, detail of transverse section of laterally compressed corallite possibly in the process of bifurcation, same scale as Figure 20.4; 7, IGM-7019, specimen from Loma de San Juan, Turitzio, State of Michoacán; transverse thin section, same scale as Figure 20.2; 8, detail of corallite shown in upper left of previous figure, same scale as Figure 20.4.


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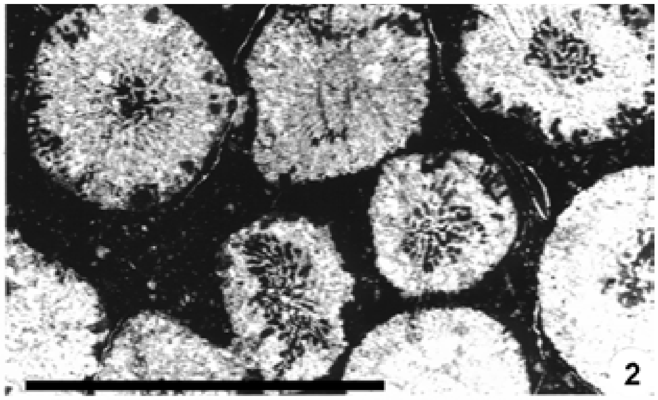
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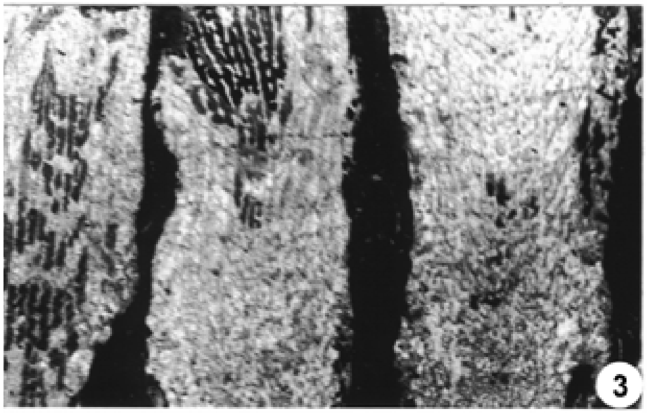
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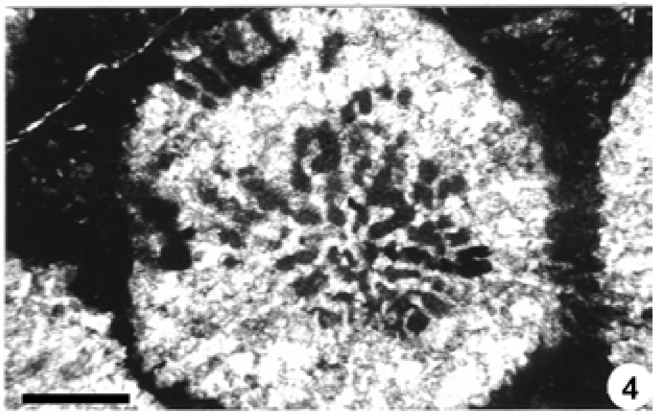
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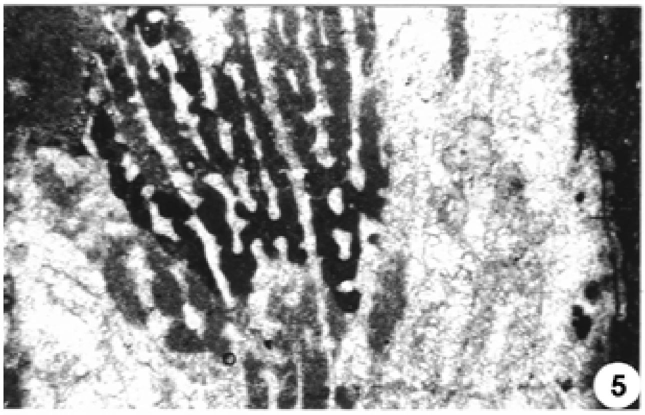
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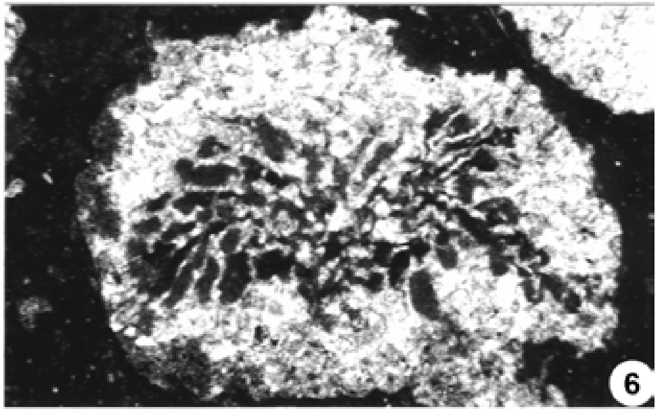
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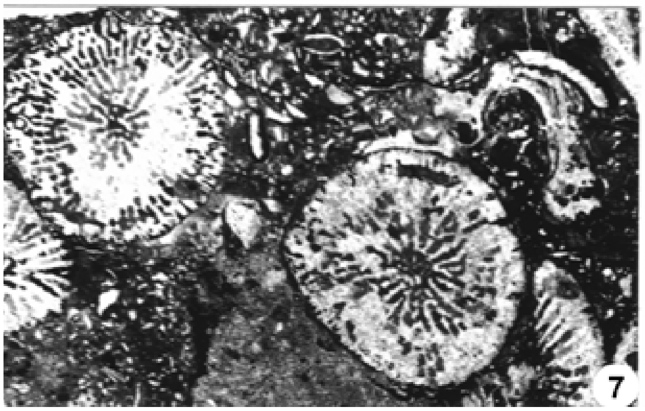
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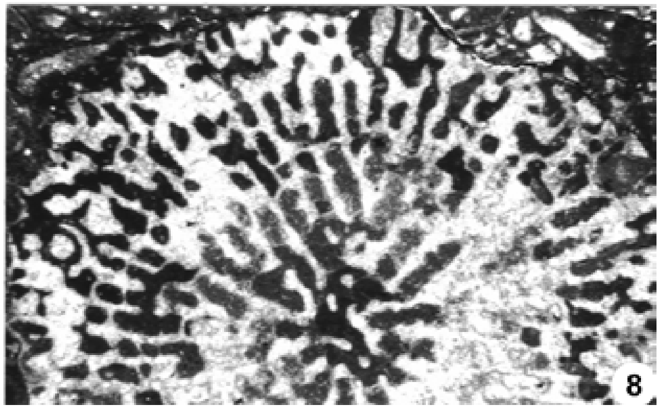
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Corallites cylindrical, vertically continuous, laterally free, parallel, closely-spaced or in contact, each one a branch segment of the corallum. Corallites typically 4-6 mm in diameter, slightly thicker below branch bifurcations, and up to at least 10 cm in length.

Calices distinct, monocentric, margins usually circular to subcircular in outline or slightly distorted by infringement of adjacent corallites. CD slightly smaller than branch diameter, 4-6 mm.

Septa well-developed, generally laminar, and fenestrate. Trabecular architecture not preserved. Septa structurally continuous with costae. Septa radially arrayed, typically 46 to at least 72 in number, hexamerally symmetrical and inserted in from four to nearly five complete septal cycles. Size relationship among septa: $S_1 \geq S_2 > S_3 > S_4 >> S_5$. Septa generally laminar to slightly blade-shaped in cross section and fairly straight. S_1 approximately 0.1 mm in width and two-fifths the CD in length. S_2 about equal to the S_1 in size; S_3 only slightly shorter than the primary S_1 and S_2. S_1, S_2 and some of the S_3 extended from wall toward corallite axis and into perimeter of columella. S_4 about half the length of S_3. Some of the S_5 typically present but weakly developed, their length about half that of the S_4. Width of interseptal spaces about two times the width of the adjacent septa. Synapticulae common especially near wall, spaced two or three per mm, and flattened or lath-shaped in cross section. Lateral surfaces of septa smooth to slightly crenulated. Upper septal margins beaded.

Pali or paliform lobe-like structures present adjacent to and intermeshed with outer margin of columella. Columella fairly well-developed, vertically continuous, trabecular, spongiose, orally papillose, width about one-third of the CD; an open, low density structure of intermeshed trabeculae contributed to by axial extensions from inner margins of S_1, S_2 and some S_3.

Wall primarily synapticulothecal and developed in a narrow zone around outer perimeter of corallite. Wall secondarily reinforced by additional synapticulae or sparsely distributed endothecal dissepiments, and possibly also by paratheca.

Costae absent or weakly developed and faint, confluent and structurally continuous through wall with septa. Costae very low, wedge-shaped in cross section, sharp-crested, ridge-like, and approximately equal in width.

Material examined. A sample of one of the coralla from the in situ occurrences near Turitzio cemetery, IGM-7018, with two thin sections (TZ-16 and TZ-17), and IGM-7019, with one thin section (TZ-18), a small fragment from the reef horizon at Loma de San Juan, Turitzio. The skeletal architecture is only occasionally preserved; most of the skeletal material examined is coarsely recrystallized or partially silicified.

Occurrence. Cumburindio Formation, lower Aptian. The material examined is from the western slope below Turitzio cemetery, just north of Turitzio and just south of the Arroyo Los Hornos, and from the Loma de San Juan, just south of Turitzio, Michoacán, Mexico. The coordinates of these localities are: 18° 32.10’ N, 100° 56.74’ W; and 18° 31.28’ N, 100° 56.65’ W, respectively. A number of large, especially well-developed colonies occur in situ in the uppermost ledge forming unit which crops out a few meters down slope and west of the cemetery fence.

This species also has been reported from the Aptian strata near Tehuacán, state of Puebla (Felix, 1891), near Tepelmeme, state of Oaxaca (Reyeros, 1983), the Barranquín Formation of northeastern Venezuela (Wells, 1944b), and the Lower Cretaceous of Trinidad (Wells, 1948). In the north, the species reportedly occurs in the Lower Cretaceous (lower Albian) of Arizona (Scott, 1981, p. 467; see also Grocock, 1975, p. 22).

Discussion. The morphological characteristics of the described specimens are the same as those given by Wells (1944b, p. 438) in his description of *Calamophyllia sandbergeri* Felix, 1891, from Venezuela, therefore the coralla are referred to that species. However, a recent re-examination of the type specimens of *C. sandbergeri* revealed that most of the material is poorly preserved and that the only specimen that could be determined, the lectotype (Löser, 2006, p. 35, 56), seemed to possess some characteristics which apparently were different from those that had previously been considered as typical for this species. As a consequence, this species was reassigned to another genus (*Thecosmilia*) and the majority of the occurrences listed in the synonymy given above were then considered not to be synonymous (see Löser, 2006, p. 35). Because of the potential influence of the style of preservation on the appearance of preserved morphological characteristics, all of this material needs to be compared in more detail by the study of oriented cross sections. Until this kind of re-examination is made, the generic assignment and species synonymy given above are retained in their earlier form.

Wells (1948, p. 613) also noted that *Calamophyllia sandbergeri* appeared to be most similar to, yet still distinct from, a few other species of *Calamophyllia* from the Cretaceous of Europe, including *C. compressa* d'Orbigny, 1850a (Urgonian, France), *C.*? *corymbosa* Koby, 1897 (Urgonian, Morteau), *C. stutzi* Koby, 1897 (Urgonian, Switzerland), *C. zumoffeni* (Felix, 1909), and *C. baali* (Felix, 1909) (Cenomanian, Syria).

Family Haplaraeidae Vaughan and Wells, 1943
Genus *Meandrophyllia* d'Orbigny, 1849

Type species. *Meandrina lotharinga* Michelin, 1843 (p. 100, pl. 22, fig. 2).

***Meandrophyllia sauteri* (Felix, 1891)**
Figure 22

Latimaeandra sauteri Felix, 1891, p. 148, pl. 23, fig. 2; Reyeros, 1983, p. 23.
Latimaeandraraea sauteri (Felix, 1891). Felix, 1914a, p. 60; Löser, Bach, and Müller, 2002, p. 50.
Meandraraea sauteri (Felix, 1891). Wells, 1932, p. 251; Löser, 2006, p. 39, figs. 4B-C.
Meandrarea ? *sauteri* (Felix, 1891). Wells, 1933, p. 90.
Meandrophyllia sauteri (Felix, 1891). Wells, 1944b, p. 439.

Description. Corallum colonial, attached, cerioid to meandroid, massive, hemispherical, costate, and medium to relatively large in size, the figured specimen 14 cm in diameter and 5 cm in height. Colony formation by di- or tristomodaeal intratentacular budding with indirect trabecular linkages. Corallites typically well-defined, prismatic to flabellate in shape, often linearly arrayed within series walls. Series discontinuous, narrow, subprismatic or subcylindrical, and often laterally elongate and irregularly shaped. Width of series (LCD) variable, 5-7 mm, and up to as much as 20 mm in length (GCD). Series centers typically laterally spaced 4-6 mm apart. Collines continuous, curved to sinuous, low, broad and ridge-like with sharp crests defined by septocostal ornamentation. Height of collines 1-2 mm, width of collines vaguely delineated due to confluence of septocostae with septa. Ambulacrum absent.

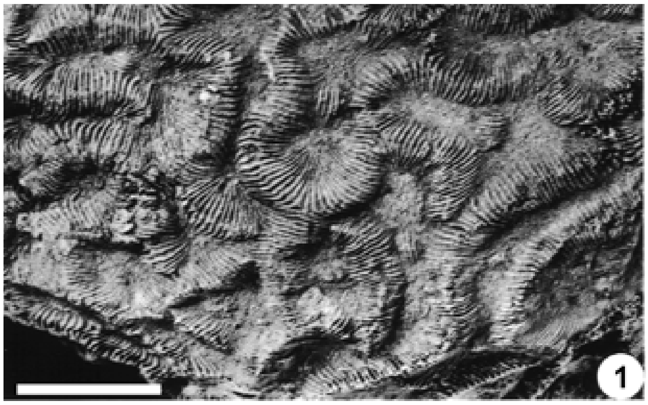
Calices well-defined, monocentric to polycentric within the series; calices essentially equal to series. Calicular margins subpolygonal to subcircular to highly elliptical or laterally elongate. Depth of calices 1-2 mm.

Septa well-developed, exsert as septocostae, laminar and solid peripherally but irregularly sparsely perforate or fenestrate oral-axially and especially near to columella. Septal perforations about 0.3 mm in diameter. Septa structurally continuous as septocostae. Septa radially arrayed around corallite axis, from 30 to 38 in number, more numerous on elongate corallites, hexameral symmetry weakly developed or absent, and often bilaterally symmetrical within laterally elongate series. Septa apparently in at least three complete cycles with a portion of the fourth cycle usually present also. Size relationship among septa: $S_1 \geq S_2 > S_3 > S_4$. Septa blade-shaped in cross section, straight or slightly curved, and approximately 0.1 mm in width. S_1 and S_2 typically extended from wall to columella. S_3 similar to those of the earlier cycles, only slightly shorter. S_4 about half the length of the S_3, the cycle characteristically incomplete. Width of interseptal spaces from one to two times width of adjacent septa. Lateral surfaces of septa generally smooth but frequently interrupted by granulations or carinae, both of which may be the result of the formation of endothecal dissepiments. Septal margins commonly beaded or dentate, the oral-axial portions often lacerate in appearance. Inner margins of S_1 and S_2 loosely intermeshed with columella.

Columella well-developed, trabecular, orally papillose and vertically continuous. Columella composed of several loosely intermeshed axial trabeculae contributed to by axial trabecular extensions from the inner margins of the S_1 and S_2, the entire structure about 1 mm in width, or one-fifth the dimension of the LCD. Columella laterally elongate and continuous between the calicular centers of polycentric calices.

Wall weakly developed, primarily synapticulothecal orally and secondarily parathecal aborally. Synapticulae of wall vertically spaced about 2 rods per mm. Wall commonly developed only between series and not between polycentric calices within series. Endothecal dissepiments well-developed, discontinuous and abundant; tabular near axial regions of corallites and vesicular (paratheca) in peripheral regions near wall. Dissepiments spaced 0.5-0.8 mm apart.

Costae well-developed, subequal in size or occasionally dimorphic, in the latter case arrayed in alternating fashion. Costae structurally similar to and continuous with septa, only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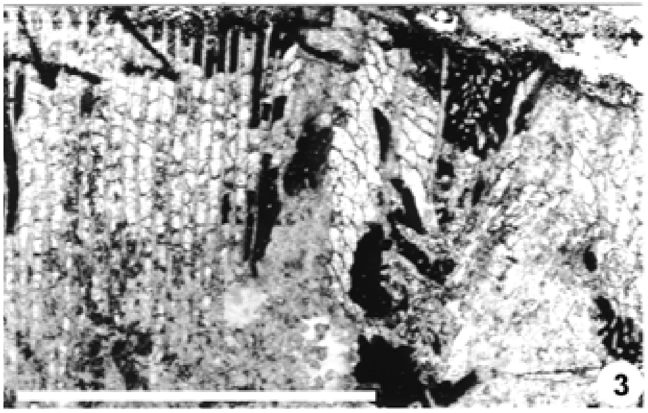
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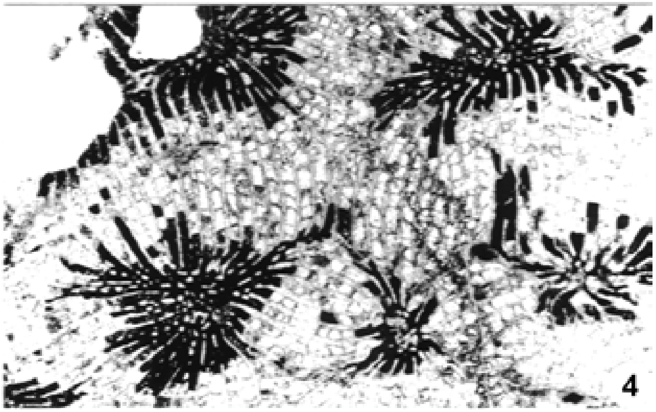
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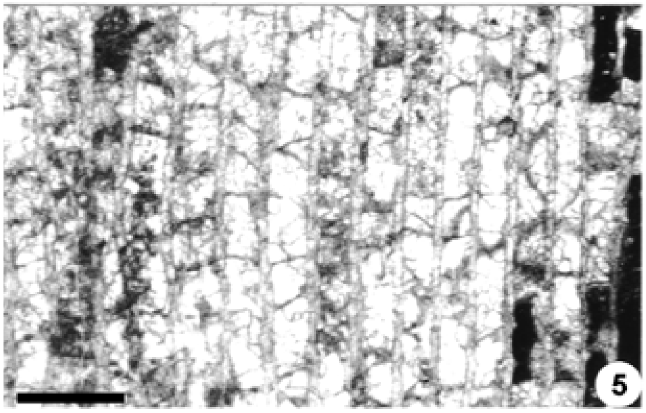
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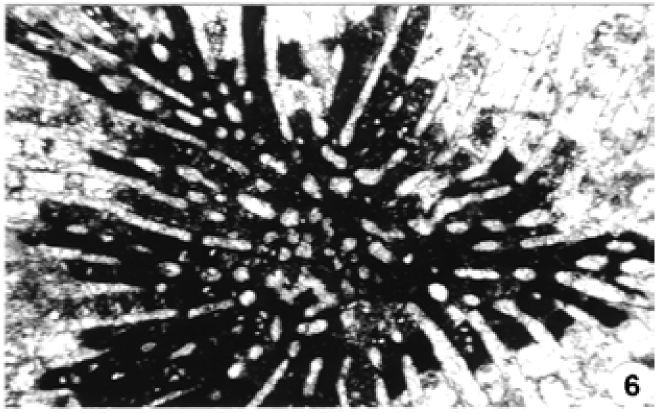
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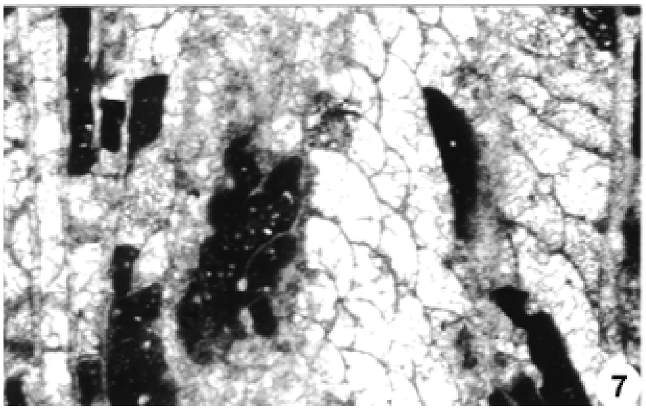
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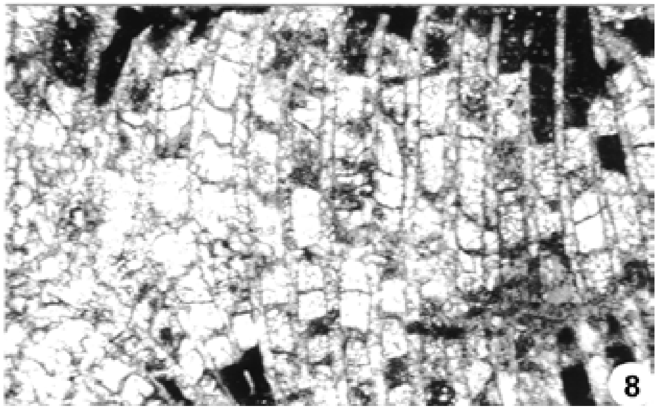
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slightly thicker in width. Costae blade-like, upper edges sharp and beaded, lateral surfaces vertical. Intercostal furrows narrow and deep, the crests of costae laterally spaced about 0.5 mm apart, or 10-12 costae per 4 mm. Costae typically confluent between adjacent series.

Material examined. The description is based on two coralla: IGM-7020, with three thin sections (TZ-51, TZ-55, and TZ-57), a specimen with a well-preserved exterior surface; and IGM-7021, with two thin sections (TZ-58 and TZ-59), a specimen with some relics of skeletal architecture preserved in a few small patches.

Occurrence. Cumburindio Formation, lower Aptian; the coral reef horizon at the crest of the Loma de San Juan, and in loose debris on the western slope of the same hill, just south of Turitzio, Michoacán, Mexico. The coordinates of this locality are: 18° 31.28' N, 100° 56.65' W.

This species was originally described from the Lower Cretaceous strata in the vicinity of Tehuacán, state of Puebla, Mexico. No other occurrences are known.

Discussion. The morphological characteristics of the coralla described above are the same as those described for *Meandrophyllia sauteri* (Felix, 1891), therefore the coralla are referred to that species. Although this species has been mentioned several times in the discussions of other related forms (see synonymy), the material examined herein is the only other occurrence recorded in the literature.

Family Siderastreidae Vaughan and Wells, 1943

Genus *Siderofungia* Reis, 1889

Type species. *Columnastraea bella* Reuss, 1869 (p. 243, pl. 21, figs. 5a, 5b) by original designation (Reis, 1889, p. 110-111, pl. 4, figs. 19a, b).

***Siderofungia irregularis* Felix, 1891**

Figure 23

Siderofungia irregularis Felix, 1891, p. 151-152, pl. 22, figs. 12, 12a; Felix, 1914a, p. 45; Wells, 1932, p. 250, pl. 35, fig. 3, pl. 39, fig. 2; Eguchi, 1933, p. 123; Bendukidze, 1961, p. 31, pl. 3, fig. 5; Turnšek, 1992, p. 165; Baron-Szabo and Steuber, 1996, p. 27, pl. 16, fig. 5; Császár and Turnšek, 1996, p. 434, fig. 8.14.

Synastrea irregularis (Felix, 1891). Hedberg and Pyre, 1944, p. 7.

Periseris irregularis (Felix, 1891). Wells, 1944b, p. 439, pl. 71, fig. 4; Wells, 1956, p. F380; von der Osten, 1957a, p. 697; 1957b, p. 572, 573, 576, pl. 63, figs. 11, 14; Reyeros, 1983, p. 21-22, pl. 8, fig. 2, pl. 9, fig. 1.

Siderastraea (*Siderofungia*) *irregularis* (Felix, 1891). Turnšek and Mihajlović, 1981, p. 34, pl. 39, figs. 3-4.

Siderastrea irregularis (Felix, 1891). Löser, Bach, and Müller, 2002, p. 62.

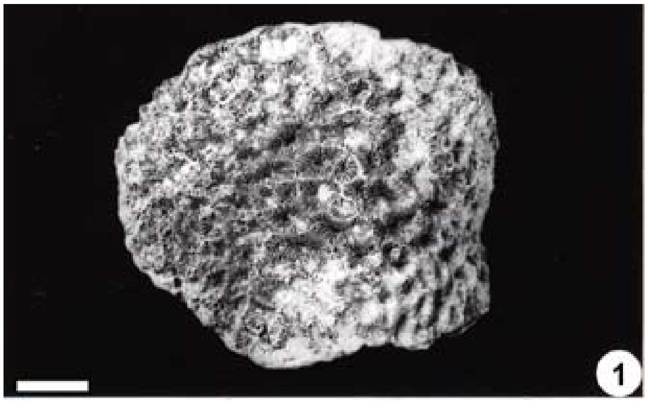
Thamnoseris irregularis (Felix, 1891). Löser, 2006, p. 50.

Description. Corallum colonial, attached, cerioid, massive, hemispherical, septocostate, small to medium in size: figured specimen 55 x 80 mm in diameter and 40 mm in height. Colony formation by distomodaeal intratentacular budding with lamellar linkages.

Corallites prismatic and arranged directly adjacent to each other, ambulacrum absent. Calices well-defined by walls, typically monocentric, and orally concave or funnel-shaped. Calicular margin usually polygonal, four to six sided, or irregularly polygonal or subpolygonal in outline. Calicular margin laterally elongate if in the process of intratentacular budding. CD of monocentric calices variable from 3-7 mm, but typically 5-6 mm on well-developed, mature corallites. GCD of calices in process of budding laterally elongate up to about 10 mm. Depth of calices 1-3 mm. Calicular centers typically slightly less than 1 mm in diameter, those of adjacent corallites spaced about 3-4 mm apart.

Septa well-developed, generally non-exsert, laminar and primarily solid but occasionally irregularly perforate

Figure 22. *Meandrophyllia sauteri* (Felix, 1891), IGM-7020, Cumburindio Formation, lower Aptian, Loma de San Juan, Turitzio, State of Michoacán, Mexico. 1, Portion of the oral surface along the margin of the corallum, scale bar = 1 cm; 2, detail of oral surface, centers of calices partly filled by limestone matrix, scale bar = 1 cm; 3, longitudinal thin section, oral ends of septocostae along top margin of figure, scale bar = 1 cm; 4, transverse thin section, same scale as Figure 22.3; 5, longitudinal thin section, detail of septa, scale bar = 1 mm; 6, transverse thin section, detail of columella and axial portions of septa, same scale as Figure 22.5; 7, longitudinal thin section, detail of vesicular paratheca in vicinity of wall region, same scale as Figure 22.5; 8, transverse thin section, detail of septocostae and wall zone, same scale as Figure 22.5.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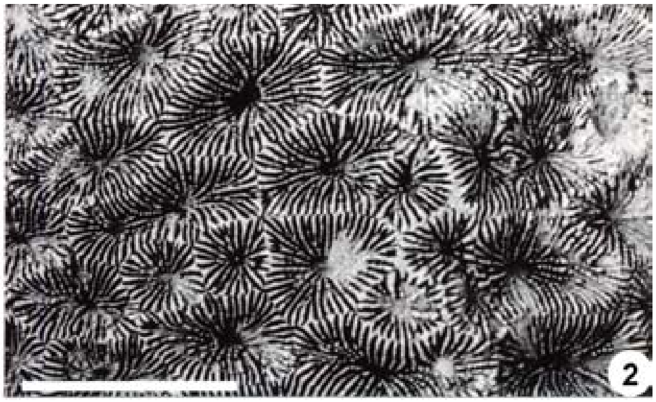
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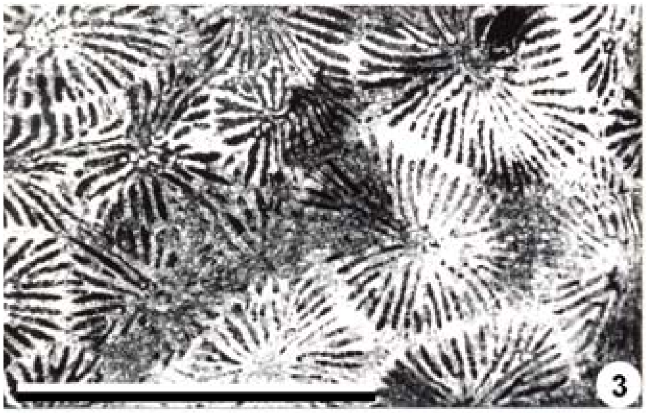
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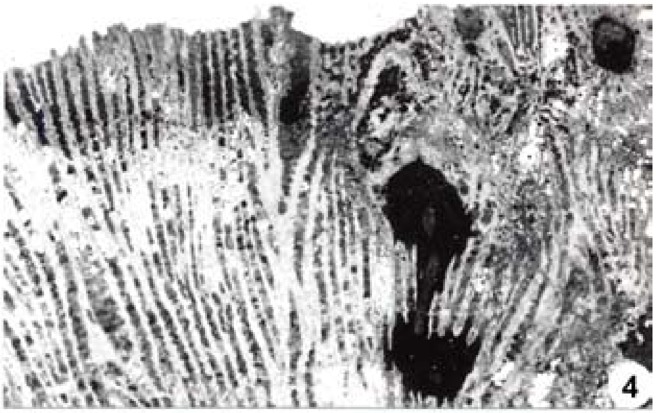
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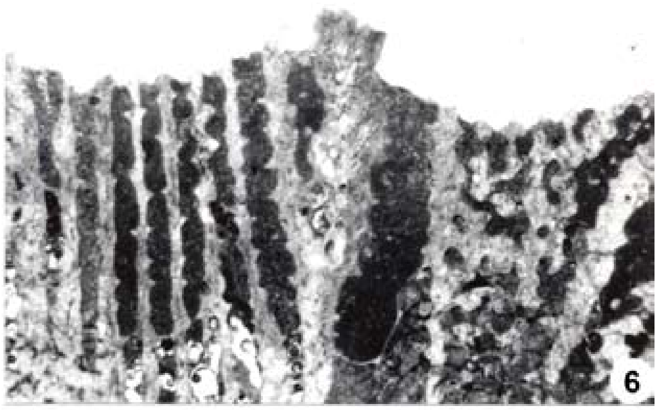
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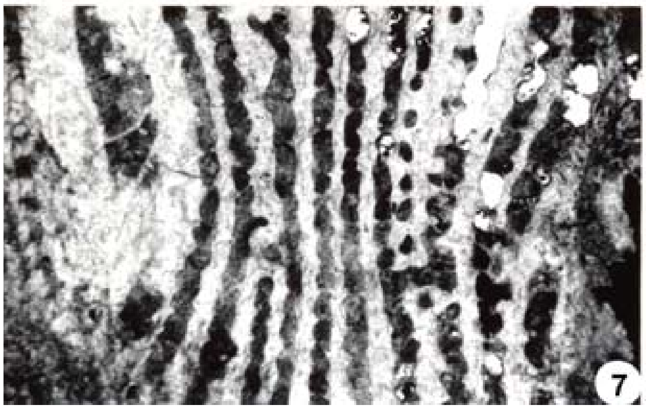
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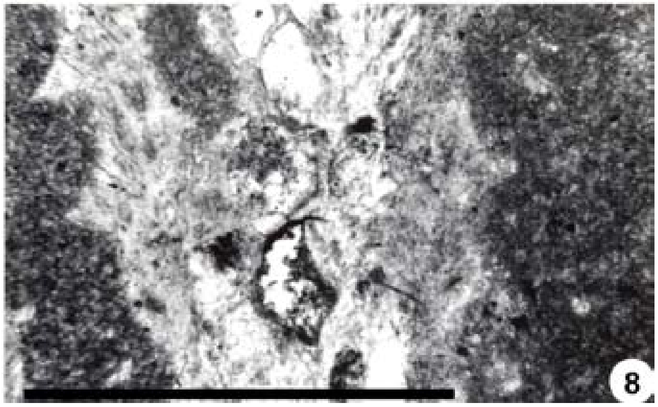
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orally and axially in vicinity of columella. Septal trabeculae inclined toward axis of corallite, their angle of divergence from the wall about 30-40 degrees. Septa structurally continuous onto edge of calicular margin as low septocostae. Number of septa variable, typically 40 to 50 on mature, monocentric calices, but more numerous on laterally elongate calices in the process of budding. Septa weakly hexamerally symmetrical due to unequal development of septal cycles, either ontogenetically advanced or retarded within different parts of the same corallite. Septa typically arrayed in at least four cycles, the first three cycles usually complete, the fourth cycle nearly fully developed. Some septa of fifth cycle occasionally present, but very rarely. Size relationship among septa: $S_1 \geq S_2 > S_3 > S_4 > S_5$. Septa generally blade-shaped in cross section, straight or gently curved, and thin, the S_1 and S_2 only about 0.1-0.2 mm in width, that of higher cycles only slightly thinner. S_1 and S_2 typically extended from wall to perimeter of axial region at calicular center. S_3 typically about two-thirds the length of the S_2, laterally free orally and fused to the parental S_2 aborally. Length of S_4 about half that of the S_3. S_5 weakly developed when present, their length usually only about half that of the adjacent parental S_4. Interseptal spaces 0.2-0.3 mm in width, or approximately equal to, or slightly greater than, the width of the adjacent septa. Lateral surfaces of septa ornamented with a dense array of coarse, conical granulations with pointed terminations. Upper portions of septal margins granulated or beaded, a result of septal trabeculae extended orally from the edges of septa; beads spaced about 4 per mm along septal margins. Short, laterally free, pali-like trabecular rods extended orally from upper, axial inner margins of S_1 and S_2. Inner margins of septa of lower cycles sometimes thickened axially in aboral region of corallite and often intermittently fused to each other with laterally extended trabeculae and to columella with axially extended trabeculae. Septa of laterally adjacent corallites commonly arrayed in alternate fashion at their mutual junction and fusion with wall.

Columella well-developed, trabecular, orally papillose, fairly dense, vertically continuous, and about 1 mm in diameter. Columella often with a single, nearly axially positioned, styliform trabecular rod surrounded by about 8-12 additional trabecular papillae of septal(?) origin. Columella contributed to by axial trabecular extensions from inner margins of S_1 and S_2.

Wall usually well-developed, weakly synapticulothecal, secondarily parathecal, and variable in thickness, about 0.2-0.4 mm. Wall commonly composed of the intermeshed, peripheral edges of septa of two adjacent corallites in an alternate fashion and often appears as a zig-zag structure in transverse cross section due to incorporation and lateral fusion of halves of nonconfluent septa of adjacent corallites into a fused, shared structure. Wall secondarily parathecal. Endothecal dissepiments well-developed, abundant, thin, often laterally continuous, generally gently inclined away from corallite axis, and mostly highly vesicular axially and tabular abaxially. Vesicular dissepiments convex orally and vertically spaced about 4-5 per mm. Tabular dissepiments vertically spaced about 3 per mm.

Septa structurally continuous into wall as septocostae. Septocostae usually slightly wider than septa, fairly low, their margins with a beaded ornamentation the same as that of the septal margins. Septocostae of adjacent corallites occasionally confluent, but most typically nonconfluent. Septocostae often bifurcated at junction with wall, each of the septal halves structurally combined with a septal half from the adjacent corallite and intermeshed to form a fused, shared, wall structure. Septocostae spaced about 3 per mm along oral edge of wall. Width of intercostal furrows equal to width of interseptal spaces.

Material examined. One corallum, IGM-7022, with three thin sections (TZ-46, TZ-47, and TZ-47a). The specimen is mostly recrystallized and silicified. In addition, corallum IGM-7023 is questionably referred to this species.

Occurrence. Cumburindio Formation, lower Aptian; the coral reef horizon at the crest the Loma de San Juan, and in loose debris on the western slope of the same hill, just

Figure 23. *Siderofungia irregularis* Felix, 1891, IGM-7022, Cumburindio Formation, lower Aptian, Loma de San Juan, Turitzio, State of Michoacán, Mexico. 1, Portion of the oral surface, scale bar = 1 cm; 2, detail of oral surface, scale bar = 1 cm; 3, transverse thin section, mostly recrystallized and silicified, scale bar = 1 cm; 4, longitudinal thin section, same scale as Figure 23.3; 5, transverse thin section, detail of wall region and portions of two adjacent corallites, scale bar = 1 mm; 6, longitudinal thin section, wall zone at center, same scale as Figure 23.5; 7, longitudinal thin section of one corallite, synapticulae between septa shown at right center of figure, weakly preserved wall zone along left margin, same scale as Figure 23.5; 8, longitudinal thin section, detail of parathecal wall zone of vesicular dissepiments, scale bar = 1 mm.

south of Turitzio, Michoacán, Mexico. The coordinates of this locality are: 18° 31.28' N, 100° 56.65' W.

This species was originally described from the Lower Cretaceous (Aptian) strata near Tehuacán, state of Puebla, Mexico. Other reported occurrences of this species in the Americas are from: the Lower Cretaceous strata near San Pedro Yucunama, Río Mixteco, and El Rodeo Tamazulapan, state of Oaxaca, Mexico; the lower Albian lower Glen Rose along the Blanco River, Hays County, and the basal Glen Rose along the Guadalupe River, Comal County, Texas; the upper Aptian-lower Albian upper Barranquín Formation, state of Sucre, eastern Venezuela.

This species also has been reported from: the Hauterivian of Crimea; the Hauterivian-Aptian of the Mecsek Mountains, Hungary; the Barremian-lower Aptian of eastern Serbia; and the lower Aptian of Greece.

Discussion. The morphological characteristics of the specimen described above are the same as those typically attributed to *Siderofungia irregularis*, therefore the specimen is referred to that species. The holotype reportedly had been located within the Felix collection at Leipzig, but subsequently it was misplaced before it could be photographed and studied in detail (Löser, 2006, p. 51). Therefore, the generic assignment and species synonymy given above reflect those that have been presented in earlier studies of this taxon.

Suborder Microsolenina Morycowa and Roniewicz, 1995
Family Latomeandridae Alloiteau, 1952
Genus *Fungiastraea* Alloiteau, 1952

Type species. *Astrea laganum* Blainville, 1834, non Michelin, 1841 (p. 19, pl. 4, figs. 9a, 9b) (Löser, 1994)

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Fungiastraea crespoi (Felix, 1891)
Figure 24

Thamnastraea crespoi Felix, 1891, p. 146, pl. 22, fig. 5; Felix, 1914a, p. 51; ?Ackermann, 1932, p. 10-11.

Thamnasteria crespoi (Felix, 1891). Wells, 1933, p. 90; Reyeros-Navarro, 1963, p. 4-5, pl. 1, figs. 1, 4; Reyeros, 1983, p. 15, pl. 2, figs. 1, 2.

Synastrea sp. cf. *S. crespoi* (Felix, 1891). Wells, 1948, p. 615, pl. 90, fig. 12.

Synastrea crespoi (Felix, 1891). Wells, cited in Barr, 1962, p. 394.

Fungiastraea crespoi (Felix, 1891). Löser, 1994, p. 66-68, text figs. 52, 53, 54, pl. 9, fig. 4, pl. 11, fig. 8, 9; Baron-Szabo and Steuber, 1996, p. 27, pl. 16, figs. 2, 3; Sanders and Baron-Szabo, 1997, p. 74, pl. 21, fig. 8; Baron-Szabo, 1997, p. 87-88, pl. 16, fig. 3; Baron-Szabo and González-León, 1999, p. 490, figs. 5a, 6i.

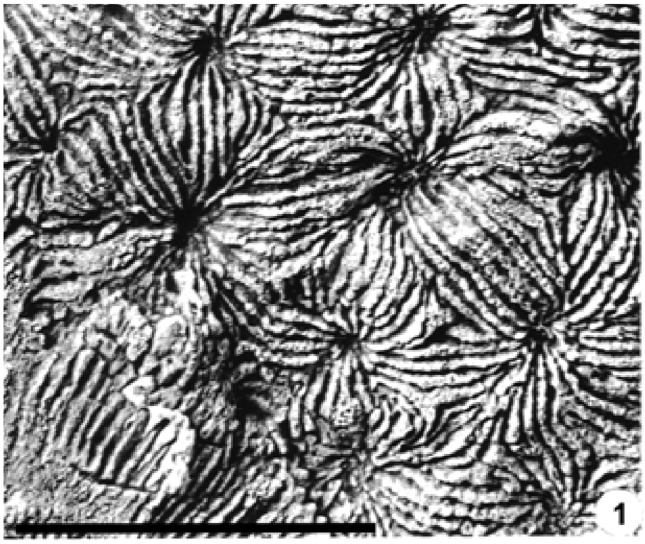
Astraeofungia crespoi (Felix, 1891). Löser, 2006, p. 48.

Description. Corallum colonial, attached, thamnasteroid, massive, hemispherical, costate, and relatively small in size: largest of two specimens 90 x 70 mm in width and 55 mm in height. Colony formation by polystomodaeal intratentacular budding with lamellar linkages. Corallites typically laterally confluent with each other, walls generally absent.

Calices distinct, monocentric, margins generally subcircular to rounded polygonal in outline. CD variable from 5 to 8 mm, but generally poorly delineated due to overall paucity of wall structures. Depth of calices about 1.5 mm. Calicular centers concave, often pit-like, about 1 mm in diameter, and typically spaced 4-8 mm apart.

Septa well-developed, exsert, laminar, perforate peripherally to highly fenestrate axially, structurally continuous as septocostae. Trabecular architecture not preserved. Septa radially arrayed around corallite axis, 16 to 38 in number, weakly hexamerally symmetrical. Septa typically not differentiated into distinct cycles, although their number indicates the presence of from just more than two (16 septa) to nearly four (38 septa) complete cycles. Size relationship among septa: $S_1=S_2\geq S_3>S_4$. Septa blade-shaped in cross section, straight or curved, about 0.2 to 0.5 mm in width, the widest portion most distal to the corallite axis.

Figure 24. *Fungiastraea crespoi* (Felix, 1891), Cumburindio Formation, lower Aptian, reef horizon at the top of Loma de San Juan, Turitzio, State of Michoacán, Mexico. 1, IGM-7025, oral surface of corallum, scale bar = 1 cm; 2, IGM-7024, longitudinal thin section, same scale as Figure 24.1; 3, detail of same thin section, scale bar = 1 mm; 4, same corallum, transverse thin section taken just below oral surface, same scale as Figure 24.1; 5, same thin section, detail of septocostae of two adjacent corallites, same scale as Figure 24.3; 6, same corallum, transverse thin section taken just below oral surface, near edge of upper surface of corallum, same scale as Figure 24.1; 7, same thin section, detail of septa and columella at corallite center, same scale as Figure 24.3.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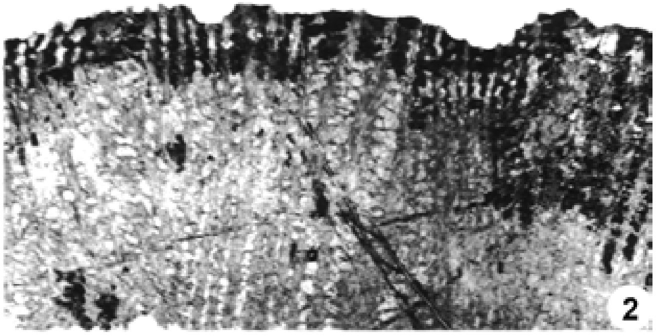
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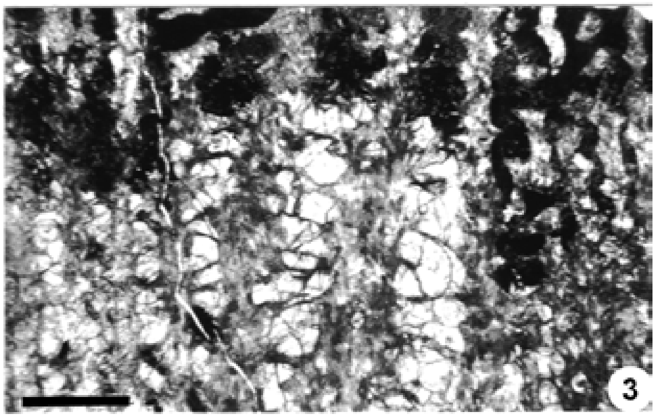
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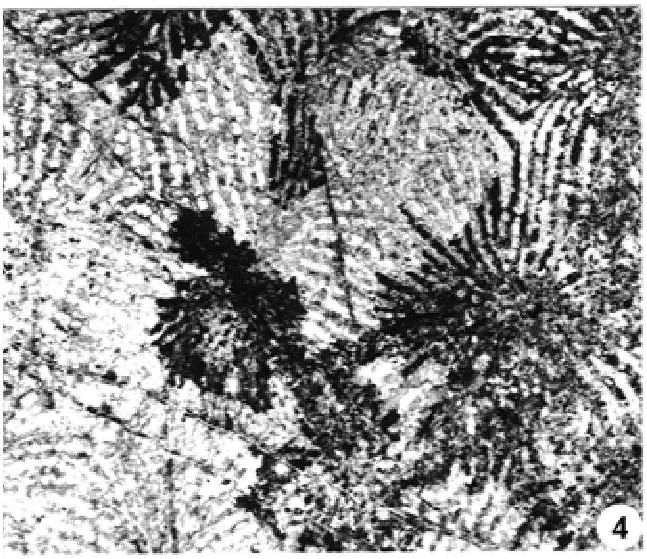
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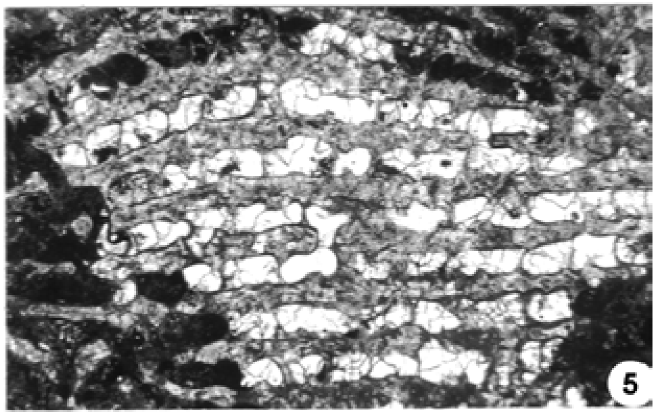
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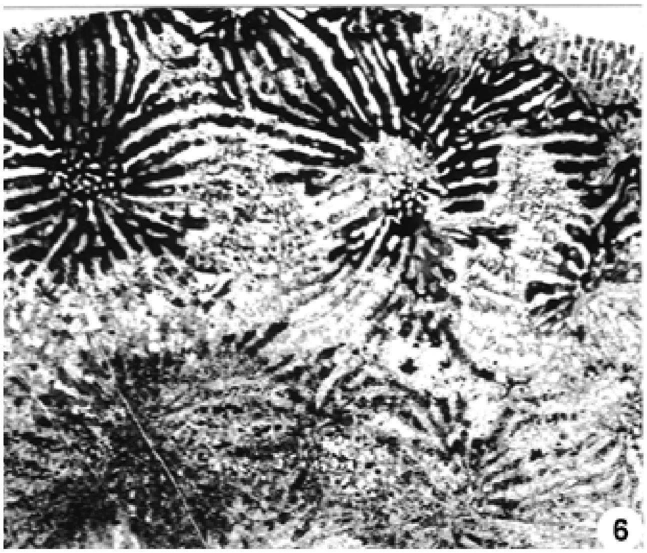
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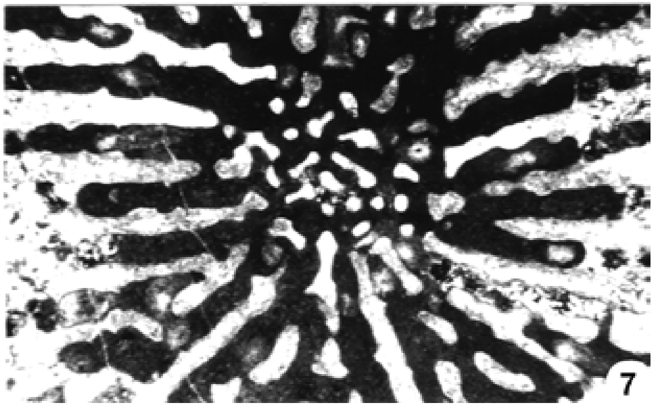
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Most of the septa of the first two and part of the third cycles typically extended into the axial region of the corallite where they frequently become intermittently fused or intermeshed with the columella. Septa of higher cycles usually only developed in peripheral regions and much shorter than those of earlier cycles. Interseptal spaces about 0.3 mm in width, or about equal to width of septa. Synapticulae sparsely distributed axially but frequently formed between septa and commonly more abundant in peripheral regions of corallites. Lateral surfaces of septa uneven, granulated or ornamented by continuous, undulated ridges or carinae formed by septal trabeculae. Septal carinae inclined toward corallite axis and spaced about 5 per mm along length of septum. Septal margins beaded along upper edges.

Pali-like structures or septal spines extended orally from the highly fenestrate inner margins of septa in axial regions of corallites directly adjacent to columella. Columella appears trabecular and orally papillose, formed by an intermeshed network of the septal extensions mentioned above, and about 1 mm in diameter. However, the columella alternatively may be described as a weakly developed single, discontinuous, narrow, cylindrical style about 0.2 mm in diameter that is intermittently contributed to by, or fused with, lateral trabecular extensions of the inner margins of septa.

Wall absent or very weakly developed and synapticulothecal. Endothecal dissepiments usually well-developed, vesicular, laterally discontinuous, very thin, especially common in peripheral zone of corallite, and vertically spaced about 0.2 mm apart, or 4-5 per mm.

Costae well-developed, robust, structurally continuous with septa as septocostae, and confluent with those of adjacent corallites in groups of about six or eight. Lateral surfaces of costae and costal margins ornamented the same as those features of the septa. Intercostal spaces about 0.3 mm in width, or approximately equal to width of adjacent costae.

Material examined. The description is based on two specimens: corallum IGM-7024, with three thin sections (TZ-03 through TZ-05); and figured specimen IGM-7025.

Occurrence. Cumburindio Formation, lower Aptian; the coral reef horizon at the crest of the Loma de San Juan, and in loose debris on the western slope of the same hill, just south of Turitzio, Michoacán, Mexico. The coordinates of this locality are: 18° 31.28' N, 100° 56.65' W.

This species also has been reported from the Aptian of the state of Puebla, the middle Albian of the state of Sonora, the Lower Cretaceous of the state of Oaxaca, and the Lower Cretaceous of Trinidad. The reported European occurrences of this species are from the lower Aptian and upper Turonian-lower Coniacian of Austria, the Aptian of Greece, and the lower Aptian and lower Cenomanian of Germany.

Discussion. The morphological characteristics of the examined specimens are the same as those described for *Fungiastraea crespoi*, therefore the coralla are referred to that species. This species was originally described from the state of Puebla, Mexico. The type specimen reportedly is lost (Löser, 2006, p. 48).

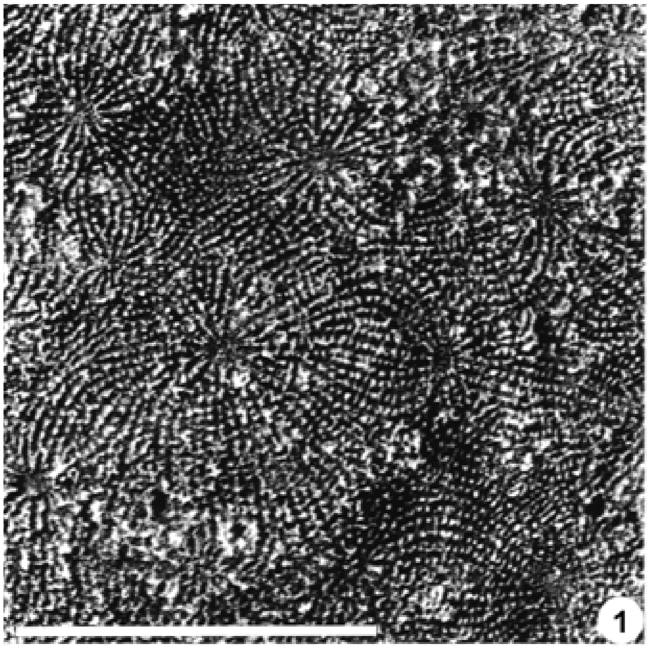
Family Microsolenidae Koby, 1890
Genus *Microsolena* Lamouroux, 1821

Type species. *Microsolena porosa* Lamouroux, 1821 (p. 65, pl. 74, figs. 24-26).

***Microsolena guttata* Koby, 1897**
Figure 25

Microsolena guttata Koby, 1897, p. 83-84, pl. 21, figs. 1, 1a, 2, 2a, 2b; Wells, 1932, p. 252; Wells, 1948, p. 615; Bendukidze, 1961, p. 31-32, pl. 3, figs. 6a, 6b; Turnšek and Buser, 1974, p. 101, 117, pl. 11, fig. 1; Sikharulidze, 1979, p. 303; Turnšek and Mihajlović, 1981, p. 35, pl. 41, figs. 1-5; ?Scott, 1984a, p. 342, 344, pl. 2, fig. 11; Sikharulidze, 1985, p. 47-48, pl. 22, fig. 2; Kuzmicheva, 1988, p. 172, pl. 7, figs. 1a, b; Turnšek, 1992, p. 164; Császár and Turnšek, 1996, p. 434, fig. 7.2; Turnšek, 1997, p. 129, pl. 129, figs. a, b, c.

Figure 25. *Microsolena guttata* Koby, 1897, IGM-7026, Cumburindio Formation, lower Aptian, Loma de San Juan, Turitzio, State of Michoacán, Mexico. 1, Oral view of a portion of the weathered upper surface, scale bar = 1 cm; 2, transverse thin section, same scale as Figure 25.1; 3, longitudinal thin section, same scale as Figure 25.1; 4, transverse thin section, detail of corallite, scale bar = 1 mm; 5, longitudinal thin section, detail of fenestrate septocostal structure, same scale as Figure 25.4; 6, transverse thin section, detail of small, newly budded corallite, same scale as Figure 25.4.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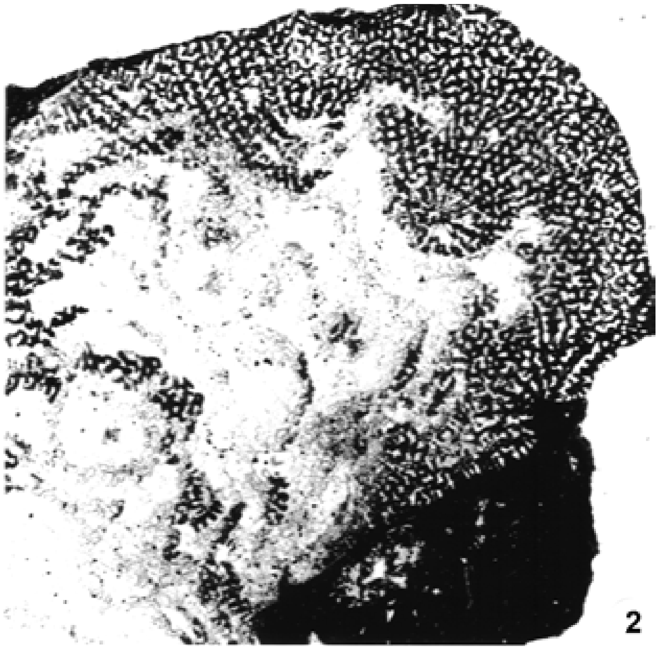
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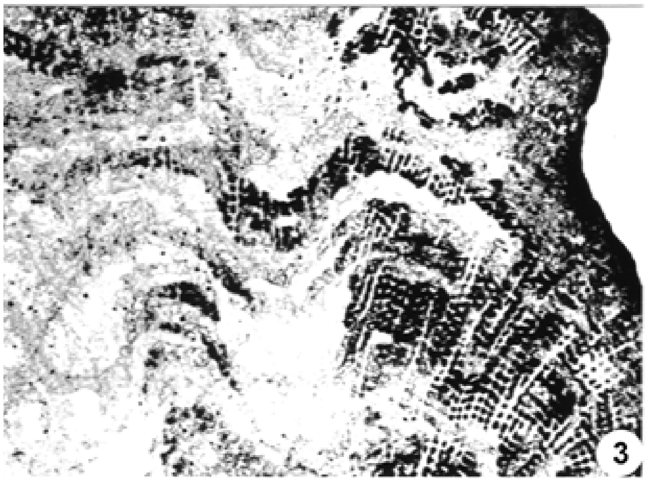
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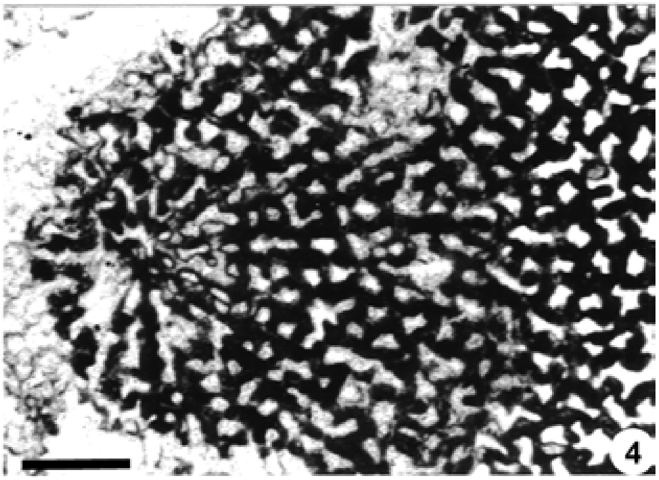
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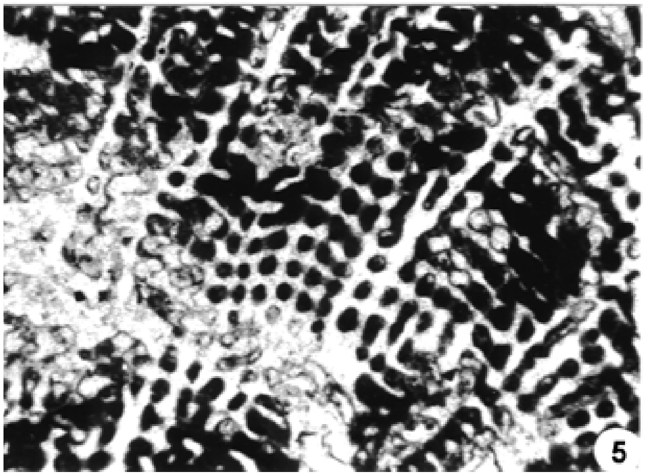
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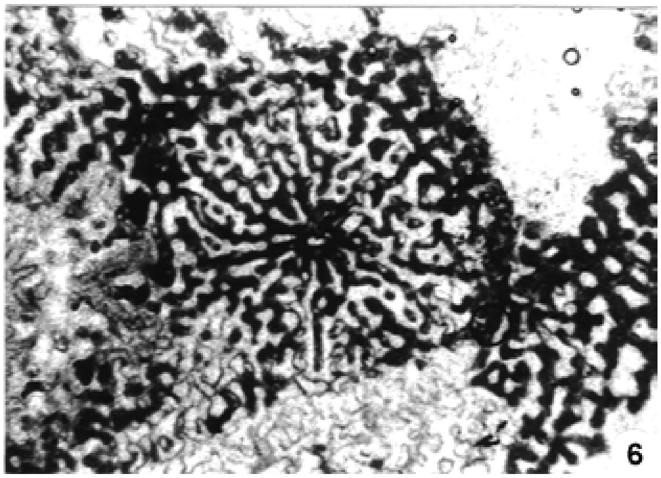
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Description. Corallum colonial, attached, thamnasteroid, massive, septocostate, and relatively small in size. Colony formation by intratentacular marginal budding.

Corallites generally subcylindrical to subprismatic in shape and laterally confluent with each other. Calices superficial, monocentric, centers well-defined, margins subcircular to subpolygonal in outline and only weakly delineated. CD ranges from 3.5 to nearly 7 mm, but most commonly about 5 mm. Calicular centers approximately 1 mm in diameter, concave orally, and spaced 3.5 to 6.5 mm apart.

Septa well-developed, weakly exsert and highly fenestrate. Septa typically continuous beyond calicular margin as confluent septocostae. Septa radially arrayed from calicular center, typically 30 to 38 in number, weakly hexamerally symmetrical, and apparently in three complete cycles with a portion of the fourth cycle typically present also. Size relationship among septa: $S_1 \geq S_2 > S_3 > S_4$. Septa subequal in width, about 0.2 mm, or the width of the septal trabecular rods, and proximally blade-shaped in cross section. S_1 typically extended into corallite axis, the inner margins commonly loosely fused to each other. Length of S_2 usually equal to or only slightly shorter than that of the S_1. S_3 inserted close to corallite axis, but noticeably shorter in length than the S_2. Some S_4 commonly present, but the cycle is typically incomplete. S_4 much shorter than the S_3, inserted nearer to calicular margin than to calicular center. Width of interseptal spaces approximately equal to width of septa. Synapticulae abundant, rod-shaped, structurally similar to septal trabeculae, often laterally continuous, and consistently evenly distributed between septa at about 4 per mm both vertically and laterally. Diameter of synapticulae equal to that of septal trabeculae, about 0.2 mm. Lateral surfaces of septa uneven, undulated by fenestrate trabecular structure of septa, and frequently interrupted by laterally extended synapticular trabeculae. Septal margins robustly beaded orally due to distal extension of septal trabeculae. Diameter of septal beads approximately 0.2 mm, the same as the septal trabeculae, and spaced about 4 per mm along septal margins. Inner margins of S_1 commonly intermittently fused to each other in axis of corallite. Inner margins of S_2 typically laterally free; those of the S_3 and S_4 laterally free orally but commonly fused to the parent septum in the aboral region of the corallite.

Columella weakly developed, trabecular, discontinuous, and apparently formed by loosely fused inner margins of S_1. Width of axial structure about 0.8-1.0 mm in diameter. Some calices exhibit a small, single, cylindrical trabecular rod or lath in the corallite axis.

Wall either absent or weakly developed and formed from synapticular rings in vicinity of calicular margin. Endotheca and exotheca not observed.

Surface of corallum septocostate. Septocostae structurally the same as the septa, typically laterally confluent with those of adjacent corallites, and closely spaced at about 3-4 per mm laterally. Septocostal margins robustly beaded, the arrangement and size of the ornamentations identical to those characteristics as given above for the septa.

Material examined. Two small coralla: the figured specimen, IGM-7026, about 50 x 50 mm in width and 35 mm in height, with four thin sections (TZ-42 through TZ-45); and IGM-7027, about 60 x 75 mm in width and 35 mm in height, with one thin section (TZ-56).

Occurrence. Cumburindio Formation, lower Aptian; the coral reef horizon at the crest of the Loma de San Juan, and in loose debris on the western slope of the same hill, just south of Turitzio, Michoacán, Mexico. The coordinates of this locality are: 18° 31.28' N, 100° 56.65' W.

This species also has been reported from the Urgonian of Switzerland (Morteau, the type locality), the Barremian of Georgia and Azerbaidzhan, the Barremian-Aptian of Slovenia and Crimea, and the Lower Cretaceous of Hungary. A specimen from the Lower Cretaceous (upper Berriasian-Valanginian) Knowles Limestone of Texas (Scott, 1984a) is very similar to this species, but the diameter of the calices is slightly smaller.

Discussion. The morphological characteristics of the specimens are the same as those typically attributed to *Microsolena guttata*, therefore the coralla are referred to that species. The Mexican specimens described above possess corallites from 3.5 to about 7 mm in diameter with calicular centers spaced 3.5-6.5 mm apart and 6-7 septocostae in 2 mm. These characteristics are most similar to those recently described (Turnšek, 1997, p. 129) for *M. guttata*.

Several other species of this genus have been reported from the Cretaceous of Mexico and adjacent regions, but none of them appears to be conspecific with the Mexican specimens described above. *Microsolena texana* Wells, 1932 (p. 252-253, pl. 37, fig. 5, pl. 35, fig. 2), a species from the lower Glen Rose (lower Albian) of Texas, has corallite centers spaced more widely (average of 7.5 mm), a larger number of septa (40-50), and relatively fewer septocostae (6 per 5 mm). Another species from Texas, *M. williamsonensis* Wells, 1944a (p. 100, pl. 20, figs. 1-4) from the Buda Limestone (Cenomanian), possesses relatively smaller features: corallites are more closely spaced, their centers from 2 to 3 mm apart, and septocostae are more abundant, 30 in 5 mm (or 12 in 2 mm).

Two species of this genus have been described from the Lower Cretaceous of Trinidad: *M. kugleri* Wells, 1948 (p. 615, pl. 91, figs. 3-5) and *M. delicatula* Wells, 1948 (p. 615, pl. 91, figs. 6, 7). Both species possess smaller corallites with centers that are more closely spaced (3-5 mm and 2-5 mm, respectively) and relatively more abundant septocostae (10 per 2 mm and 8-10 per 2 mm, respectively). The only previously observed morphological distinction between *M. kugleri* and *M. guttata* concerned the distance between calicular centers, a dimension which had been considered to be consistently greater in the latter species (5-6 mm) (Wells, 1948). However, the distance between calicular centers of *M. guttata* given in one of the most recent descriptions (Turnšek, 1997, p. 129) is 4-6 mm, which indicates that some overlap in this dimension exists with *M. kugleri*. Therefore, there is even less morphological difference than initially recognized and the distinction between these two species is less certain. The latter species also has been reported from Albian strata in the northern part of the state of Sonora, Mexico (McKee and Anderson, 1998, p. 1522).

Other occurrences of species of this genus that have been reported from the Lower Cretaceous of North America include *M. distefanoi* (Prever, 1909) from the Knowles Limestone in the subsurface of Texas (Scott, 1984a), and *M. distefanoi* and *M. kobyi* Prever, 1909, from the state of Sonora, Mexico (Baron-Szabo and González-León, 1999). The *Latimaeandra* sp. described by Felix (1891, p. 149) also may belong to this genus. *Microsolena* sp. Hamilton, 1956 (p. 59-60, pl. 6, fig. 4), a species dredged from Hess Guyot, also appears to be similar, except the calicular centers are more widely spaced.

Genus *Polyphylloseris* Fromentel, 1857

Polyphylloseris Fromentel, 1857, p. 67-68; Wells, 1956, p. F392; 1986, p.52.

Mastophyllia Felix, 1891, p. 146; Oppenheim, 1930, p. 215.

Type species. *Polyphyllastrea convexa* d'Orbigny, 1849, by subsequent designation (Wells, 1936, p. 126).

***Polyphylloseris conophora* (Felix, 1891)**

Figure 26

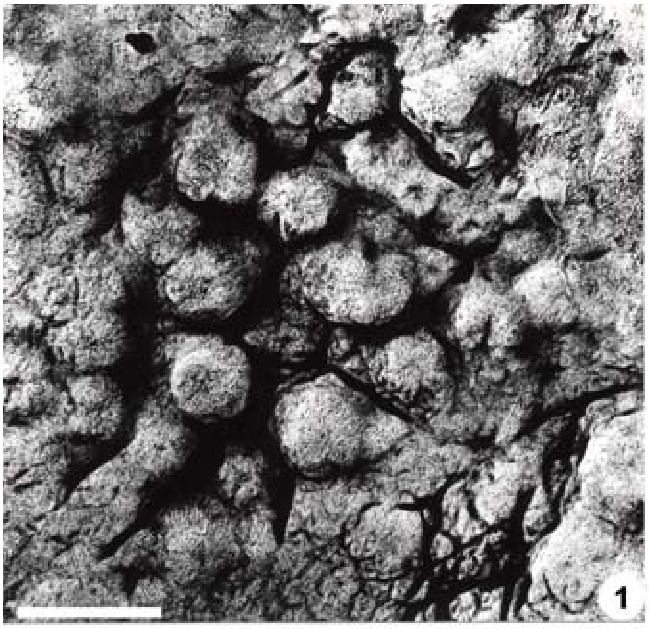
Mastophyllia conophora Felix, 1891, p. 146-147, pl. 23, figs. 9, 9a; Oppenheim, 1930, p. 218; Wells, 1932, p. 251; Wells, 1986, p. 38.

Polyphylloseris conophora (Felix, 1891). ?Reyeros-Navarro, 1963, p. 15-16, pl. 4, figs. 1-6; Löser, Bach, and Müller, 2002, p. 60; Löser, 2006, p. 44, figs. 4H-I.

Description. Corallum colonial, attached, thamnasteroid, pedunculate, foliaceous, disk-shaped, and large in size, the examined specimen a fragment about 20 cm in length, 20 cm in width, and 8 cm in height. Colony formation by polystomodaeal intratentacular marginal budding. Corallites confluent, generally cylindrical, commonly protuberant, closely spaced and fairly evenly distributed on upper surface of corallum. Corallite walls weakly defined by synapticulae.

Mature calices set in centers of protuberant cylindrical or dome-shaped bosses or bourrelets, circular in outline, 3-5 mm in diameter and 1-3 mm in height. Arrangement of calices causes upper surface of corallum to appear somewhat plocoid. CD vaguely delineated, range about 3 to 5 mm. Calicular surface convex, slightly flattened, and commonly with centrally located calicular pit about 1 mm in depth. Calicular centers spaced 5-9 mm apart. Calicular bosses spaced 1-3 mm apart.

Septa well-developed, weakly exsert, highly fenestrate, each one formed by a single fan system of trabeculae. Septa continuous beyond calicular margins as septocostae. Septa variable in number, 20 to 24 axially but 50 to about 60 peripherally on larger corallites, radially arranged around corallite axis, weakly hexameral, and apparently inserted in three or four complete septal cycles with a portion of the S_5 sometimes present also. Size relationship among septa: $S_1 \geq S_2 > S_3 > S_4 (> S_5)$. Septa blade-shaped in cross section and generally straight. Septa of first and second cycles nearly equally developed, about 0.2 mm in width, and extended from wall into corallite axis. S_3 usually slightly shorter than septa of earlier cycles, but commonly some of them reach the perimeter of the corallite axis. S_4, and S_5 when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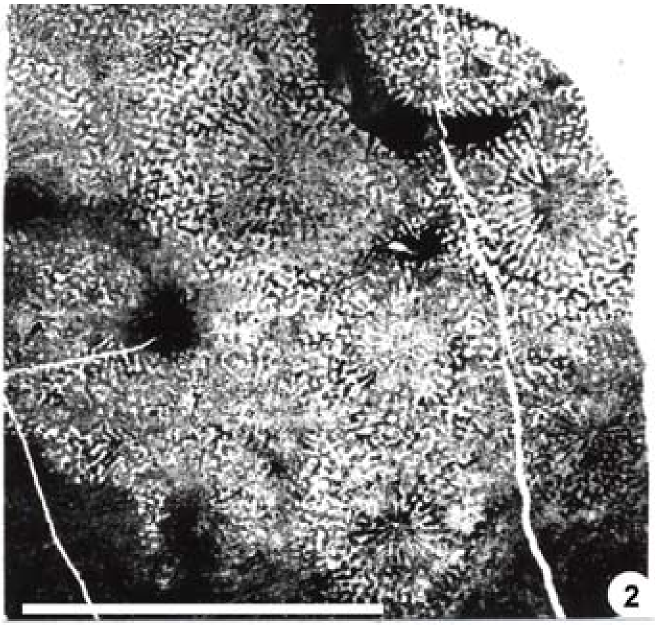
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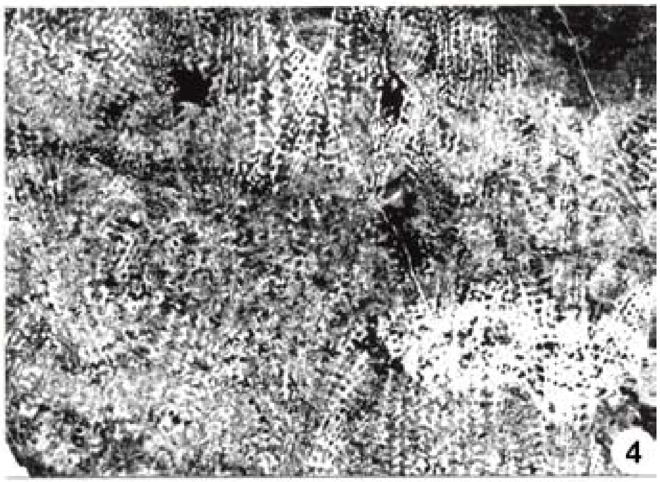
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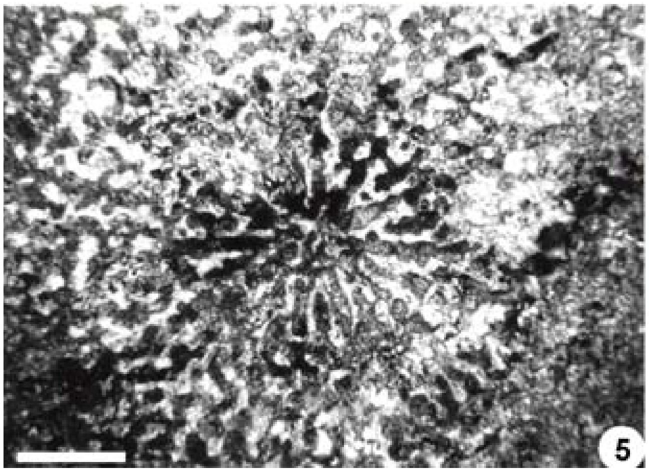
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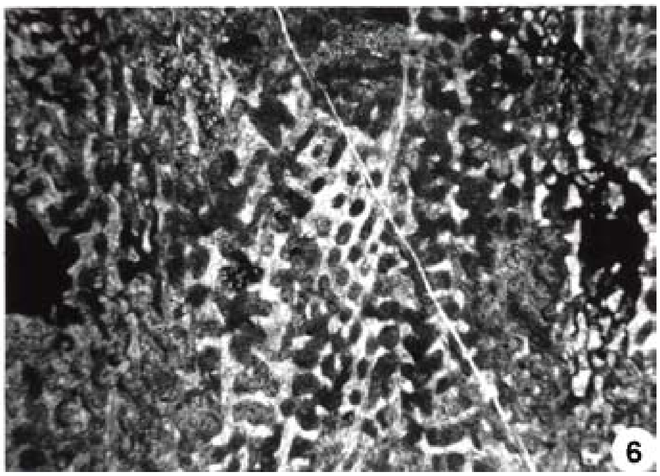
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present, developed peripherally and typically incomplete. Interseptal spaces narrower than width of the adjacent septa. Synapticulae commonly well-developed between septa and closely spaced. Lateral surfaces of septa uneven. Upper septal margins beaded. Inner edges of septa, particularly the S_1 and S_2, typically interconnected by trabecular extensions across corallite axis.

Columella weakly to moderately well-developed, trabecular, vertically continuous and deep in calicular centers. Width of columella approximately equal to or less than one-fifth of CD.

Wall primarily synapticulothecal, secondarily reinforced aborally and axially by endothecal dissepiments. Wall highly fenestrate, developed peripherally in a narrow zone around corallite about 0.5 mm in thickness. Endothecal dissepiments tabular to vesicular and often present in circumcolumellar axial regions deep in corallite.

Coenosteal regions sparsely distributed between some corallites, highly porous, composed of structural continuations of septa and trabecular components, probably synapticulae, extended from the adjacent corallites. Coenosteal surfaces finely costate or granulated and spinose. Surfaces of corallum finely costate both orally and aborally. Costae typically appear as low, thin striae or ridges, spaced about four per mm. Costae on oral upper surface of corallum confluent between corallites and structurally continuous with septa. Costae on aboral lower surface or underside of corallum linear, parallel and continuous, oriented parallel to direction of growth. Aboral underside of corallum exhibits low amplitude sinusoidal growth ridges oriented with long axes perpendicular to direction of growth. Growth ridges cause underside of corallum to appear corrugated. Distance between crests of growth ridges about 10 mm.

Material examined. One large fragment of a corallum, IGM-7028, with three thin sections (TZ-24 through TZ-26). The upper surface of the corallum is deeply weathered, but the excellent preservation of the fine striae on the lower surface clearly indicates that this portion of the colony was suspended above the substrate during growth. The corallum is recrystallized and the majority of the original structure within the specimen is not preserved

Occurrence. Cumburindio Formation, lower Aptian; the coral reef horizon at the crest of the Loma de San Juan, and in loose debris on the western slope of the same hill, just south of Turitzio, Michoacán, Mexico. The coordinates of this locality are: 18° 31.28' N, 100° 56.65' W.

Polyphylloseris conophora (Felix, 1891) was initially described from the Neocomian strata near Tehuacán, state of Puebla, Mexico. This species also has been reported from the Lower Cretaceous San Juan Raya Formation in the state of Puebla, but the specimens probably are not conspecific (see discussion given below).

Discussion. The morphological characteristics of the corallites on the Mexican specimen described above are the same as those described for *Polyphylloseris conophora* (Felix, 1891), therefore the corallum is assigned to that species. This species and *P. polymorpha* Felix, 1891 (p. 143-144, pl. 22, figs. 4, 6, 6a) were first described from Neocomian strata near Tehuacán, state of Puebla, Mexico. The latter species differs by the columnar growth form of the corallum, the more numerous septa, and the closer spaced septocostae. *Polyphylloseris conophora* also has been described from the Lower Cretaceous San Juan Raya Formation of Puebla (Reyeros-Navarro, 1963, p. 15-16, pl. 4, figs. 1-6). However, that occurrence is questioned in the species synonymy given above because most of those specimens have a columnar growth form and larger corallites with more numerous septa. These characteristics are more similar to those of *P. polymorpha* than those of *P. conophora*.

Another Lower Cretaceous species, *P. simondsi* (Wells, 1932) (p. 250-251, pl. 36, figs. 4, 5, pl. 39, fig. 6) from the lower Glen Rose of Texas, possesses a corallite morphology and corallum growth form which are similar to those of the species described above, but primarily differs by the smaller number of septa, the weakly developed columella, and the widely spaced septocostae (5 per 2 mm).

Figure 26. *Polyphylloseris conophora* (Felix, 1891), IGM-7028, Cumburindio Formation, lower Aptian, Loma de San Juan, Turitzio, State of Michoacán, Mexico. 1, Weathered upper or oral surface of corallum, scale bar = 1 cm; 2, transverse thin section taken just below upper surface of corallum, scale bar = 1 cm; 3, base of corallum, detail of longitudinal striae or costae, same scale as Figure 26.2; 4, longitudinal thin section, same scale as Figure 26.2; 5, transverse thin section, detail of one corallite, scale bar = 1 mm; 6, longitudinal thin section, detail of fenestrate skeletal structure, same scale as Figure 26.5.

Family Synastraeidae Alloiteau, 1952
Genus *Felixastraea* Oppenheim, 1930

Type species. *Cyathoseris zitteli* Felix, 1903a (p. 227-228, pl. 22, figs. 2, 2a), by original designation (Oppenheim, 1930, p. 243-245, pl. 38, figs. 9, 9a, pl. 43, fig. 10).

***Felixastraea mexicana* Reyeros-Navarro, 1963**

Figure 27

Felixastraea mexicana Reyeros-Navarro, 1963, p. 13-15, pl.5, figs. 3, 4.

Description. Corallum colonial, attached, generally meandroid, massive, costate, medium to large in size. Colony formation by polystomodaeal intramural intratentacular budding with lamellar linkages between centers. Corallites flabellate and confluent or thamnasteroid within series. Series closely-packed, size variable, typically expanded laterally up to several cm in length and frequently bifurcated, but narrow in width, only 2 to 5 mm. Each series consists of one or more confluent corallites. Collines continuous, uniform in size, protuberant, highly contorted or sinuous in oral view, those of adjacent series joined together by narrow zone of ambulacrum about 0.6 to 1 mm in width. Combined width of ambulacrum and adjacent collines about 2.5-4.0 mm. Collines and ambulacrum ornamented with costae. Calices well-defined by collines, mono- to polycentric, laterally elongate and contorted, frequently bifurcated, CD 2-5 mm, depth 2-4 mm.

Septa well-developed, weakly exsert peripherally, laminar, highly fenestrate or perforate, and formed from compound trabeculae. Septa structurally continuous as costae across adjacent collines and ambulacrum. Septa numerous, nearly equally developed, arrayed radially from calice centers or bilaterally across narrow, elongate calices. Number of septal cycles indeterminable, but apparently three to five cycles developed based on the number of septa. Septa blade-shaped in cross section, straight or curved toward corallite axis, and very thin, 0.2 mm or less in width. Most septa extended from wall into axial region. Interseptal spaces equal to or less than width of the adjacent septa. Synapticulae common and especially abundant along wall, vertically spaced about 0.5 mm apart. Lateral surfaces of septa dentate. Septal margins highly dentate. Pali absent.

Columella weakly developed, trabecular, composed of only a few small rods or laths, the width of the entire structure less than one-third the CD.

Wall primarily synapticulothecal, secondarily reinforced and thickened basally. Walls of adjacent series connected by narrow ambulacrum. Endothecal dissepiments developed near wall.

Costae well-developed, structurally continuous with septa but consistently thicker, about 0.2 mm in width, nearly equal in size and blade-shaped in cross section with vertical sides and sharp crests. Costae confluent between adjacent series. Intercostal spaces deep and slightly narrower than costae. Costal margins dentate.

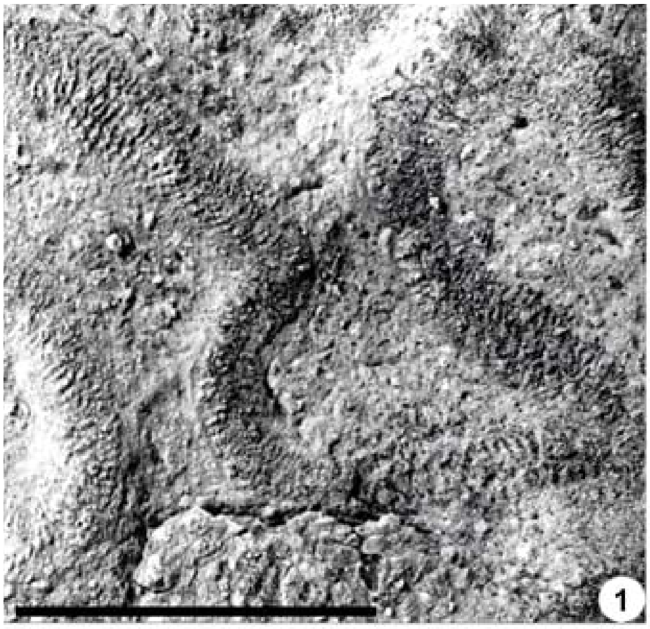
Material examined. One specimen, IGM-7029, with two thin sections (TZ-14 and TZ-15). The colony is in fragments, mostly recrystallized internally, and partly silicified in a thin layer along the exterior surface. A few small, 0.4 mm diameter tubes, probably commensal serpulids, are preserved on the outer surface of the corallum.

Occurrence. Cumburindio Formation, lower Aptian; the coral reef horizon at the crest of the Loma de San Juan, and in loose debris on the western slope of the same hill, just south of Turitzio, Michoacán, Mexico. The coordinates of this locality are: 18° 31.28’ N, 100° 56.65’ W.

This species was originally described from the Lower Cretaceous San Juan Raya Formation in the state of Puebla, Mexico, which is its only other reported occurrence.

Discussion. Oppenheim (1930, p. 242) established the genus *Felixastraea* and designated *Cyathoseris zitteli* Felix, 1903a (p. 227-228, pl. 22, fig. 2, 2a), as the type species. The genus remained monospecific until Reyeros-Navarro (1963, p.

Figure 27. *Felixastraea mexicana* Reyeros, 1963, IGM-7029, Cumburindio Formation, lower Aptian, Loma de San Juan, Turitzio, State of Michoacán, Mexico. 1, Detail of weathered oral surface of corallum, sinuous colline exposed, calices filled by limestone, scale bar = 1 cm; 2, transverse thin section taken just below upper surface of corallum, same scale as Figure 27.1; 3, oral view of corallum fragment, scale bar = 1 cm; 4, transverse thin section, detail of calicular center, septa and wall, scale bar = 1 mm; 5, same section, detail of colline and adjacent septa, same scale as Figure 27.4; 6, same section, detail of septa, calicular center toward the left, scale bar = 1 mm.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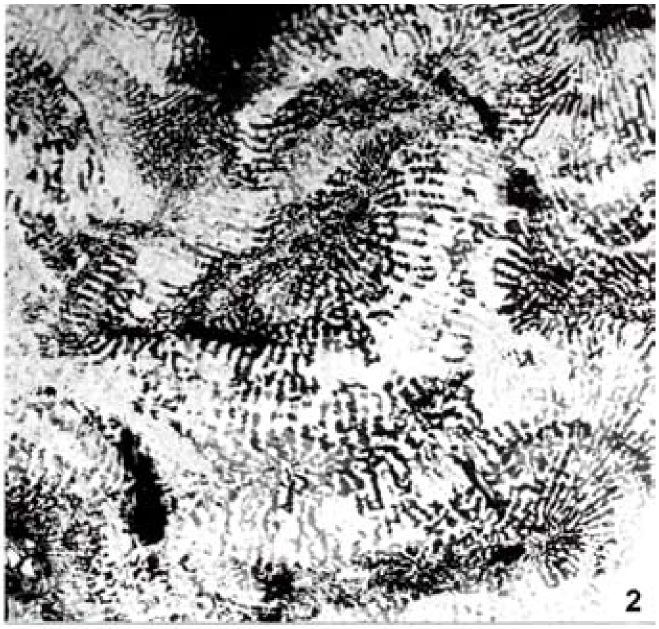
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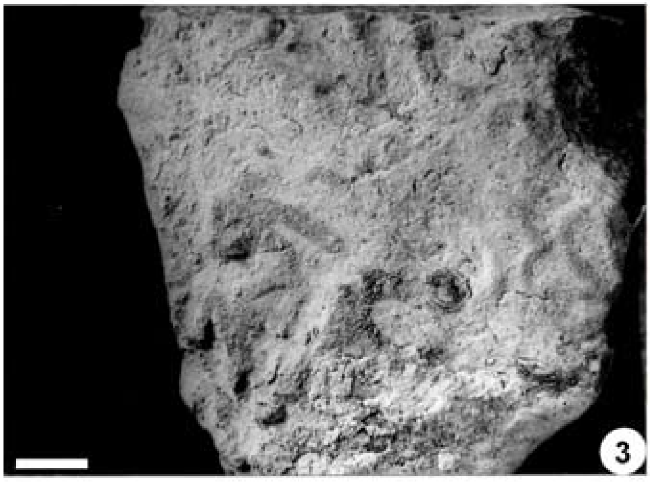
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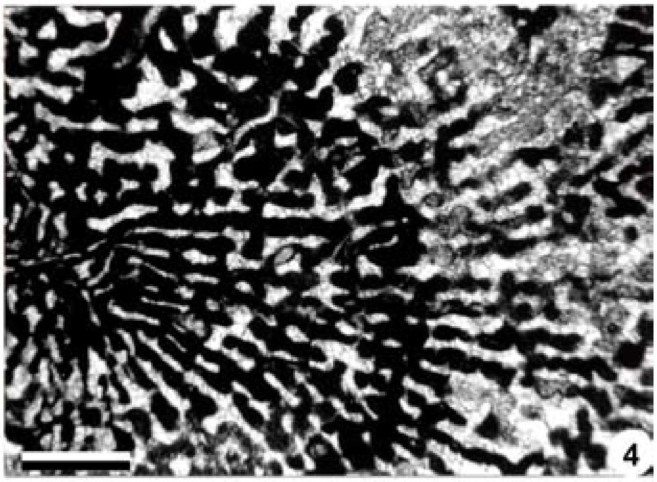
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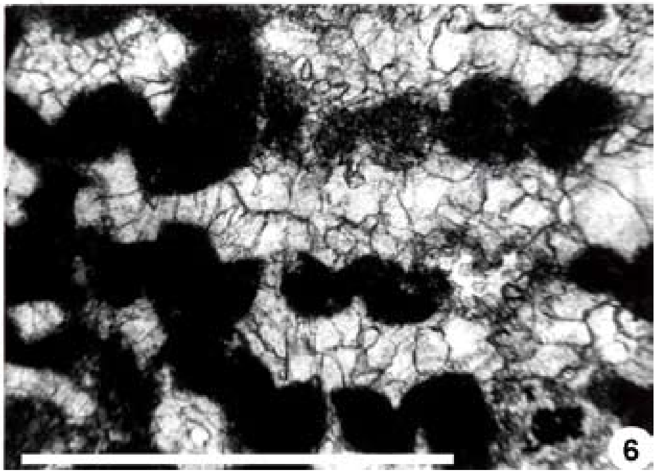
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13-15) described *Felixastraea mexicana* as new. She distinguished *F. mexicana* from *F. zitteli* by the variable heights of the calices, the shape of the oral surface of the corallum, the general shape and height of the corallum, and the presence of fewer septa. The type specimen of *F. mexicana* is about the same in size as that of *F. zitteli* based on comparison of the plates given by Reyeros-Navarro (1963, pl. 5, figs. 3, 4) and Oppenheim (1930, pl. 38, figs. 9, 9a, pl. 43, fig. 10), respectively. The greater length of the oral surface of the two type specimens is about 50 mm on *F. mexicana* and 58 mm on *F. zitteli*, the difference between the two only 8 mm. The corallum described herein is fragmented, but the dimensions of the oral surface of the largest fragment are larger than both of the aforementioned type specimens, about 70 mm by 70 mm; if the corallum is reconstructed from the associated fragments, the oral surface is nearly twice as large, about 120 mm across. The other areas of supposed differences between the two species are, on closer examination, actually very difficult to confirm. In general, the corallum size and the other characteristics which Reyeros-Navarro utilized to distinguish between the two species are potentially highly variable at the species level, especially within such a growth form as that of the members of *Felixastraea*. The two species may be the same, but examination of additional specimens of both of them would be necessary to confirm a synonymy. The type species of the genus is from the Gosauschichten at Nefgraben (Oppenheim, 1930, p. 243).

PART 2: UPPER ALBIAN-LOWER CENOMANIAN CORAL SPECIES

The 18 coral species identified from the upper member of the Mal Paso Formation are listed below. Suborders are from Turnšek (1997, p. 36) with two additions, indicated by an asterisk (*), from Veron (1995, p. 110). The possible phylogenetic relationships of the suborders are indicated by their arrangement into four main groups (from Turnšek, 1997, p. 36). The placements of the two suborders from Veron (1995) within the four main groups are tentative.

GROUP 1

Suborder Pachythecaliina Eliášová, 1976 (Triassic)
Suborder Stylophyllina Beauvais, 1981a (Triassic)
Suborder Amphiastreina Alloiteau, 1952

GROUP 2

Suborder Archaeocoeniina Alloiteau, 1952
    Family Actinastraeidae Alloiteau, 1952
        Genus *Actinastrea* d'Orbigny, 1849
            Actinastrea guadalupae (Roemer, 1849)
            Actinastrea chumbitaroensis n. sp.
Suborder Stylinina Alloiteau, 1952

GROUP 3

Suborder Distichophylliina Beauvais, 1981a (Triassic)
Suborder Rhipidogyrina Roniewicz, 1976
    Family Rhipidogyridae Koby, 1905
        Genus *Preverastraea* Beauvais, 1976
            Preverastraea coatlicuae n. sp.
            Preverastraea tocae n. sp.
Suborder Faviina Vaughan and Wells, 1943
    Family Montlivaltiidae Dietrich, 1926
        Genus *Latiphyllia* Fromentel, 1861
            Latiphyllia mexicana n. sp.
        Genus *Thecosmilia* Milne Edwards and Haime, 1848
            Thecosmilia guerreroensis n. sp.
        Genus *Elasmophyllia* d'Achiardi, 1876
            Elasmophyllia tolmachoffana (Wells, 1932)
        Genus *Mycetophyllopsis* Oppenheim, 1930
            Mycetophyllopsis azteca n. sp.
Suborder Astreoina Alloiteau, 1952 *
    Family Faviidae Gregory, 1900
        Genus *Eohydnophora* Yabe and Eguchi, 1936
            Eohydnophora picteti (Koby, 1897)
    Family Placocoeniidae Alloiteau, 1952
        Genus *Columnocoenia* Alloiteau, 1952
            Columnocoenia ksiazkiewiczi Morycowa, 1964
Suborder Meandriina Alloiteau, 1952
    Family Dendrogyridae Alloiteau, 1952
        Genus *Orbignygyra* Alloiteau, 1952
            Orbignygyra? *incognita* n. sp.
Suborder Caryophylliina Vaughan and Wells, 1943
Suborder Dendrophylliina Vaughan and Wells, 1943 *
    Family Dendrophylliidae Gray, 1847
        Genus *Blastozopsammia* Filkorn and Pantoja-Alor, 2004
            Blastozopsammia guerreroterion Filkorn and Pantoja-Alor, 2004

Group 4

Suborder Archaeofungiina Alloiteau, 1952 (Triassic)
Suborder Fungiina Verrill, 1865
  Family Dermosmiliidae Koby, 1889
    Genus *Epistreptophyllum* Milaschewitsch, 1876
      Epistreptophyllum sp.
  Family Thamnasteriidae Vaughan and Wells, 1943
    Genus *Thalamocaeniopsis* Alloiteau, 1953
      Thalamocaeniopsis mexicanensis n. sp.
    Genus *Thamnasteria* Lesauvage, 1823
      Thamnasteria tonantzinae n. sp.
Suborder Microsolenina Morycowa and Roniewicz, 1995
  Family Cunnolitidae Alloiteau, 1952
    Genus *Paracycloseris* Wells, 1934
      Paracycloseris effrenatus n. sp.
  Family Latomeandridae Alloiteau, 1952
    Genus *Ovalastrea* d'Orbigny, 1849
      Ovalastrea malpaso n. sp.
  Family Microsolenidae Koby, 1890
    Genus *Dimorpharaea* Fromentel, 1861
      Dimorpharaea barcenai (Felix, 1891)

Class Anthozoa Ehrenberg, 1834
Subclass Zoantharia Blainville, 1830
Order Scleractinia Bourne, 1900
Suborder Archaeocoeniina Alloiteau, 1952
Family Actinastraeidae Alloiteau, 1952

Genus *Actinastrea* d'Orbigny, 1849

Type species. *Astrea geminata* Goldfuss, 1826 (p. 69-70, pl. 23, figs. 8e, f; d'Orbigny, 1849, p. 10).

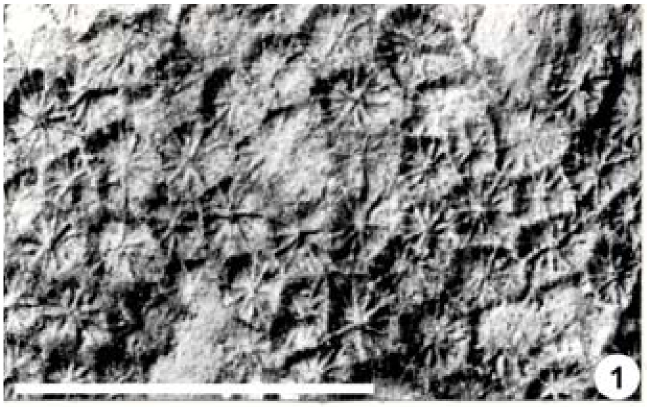
Discussion. The genus *Actinastrea* d'Orbigny, 1849 (p. 10), and several other genera previously had been considered to be junior synonyms of *Astrocoenia* Milne Edwards and Haime, 1848b (p. 469) (Vaughan and Wells, 1943, p. 103). *Actinastrea* was later considered to be a taxonomically distinct genus and several nominal genera that formerly were considered to be junior synonyms of *Astrocoenia* were listed as junior synonyms of *Actinastrea* (Wells, 1956, p. F370). One of the junior synonyms of *Actinastrea* listed by Wells (1956, p. F370), *Enallocoenia* d'Orbigny, 1849 (p. 7), subsequently has been considered to be a taxonomically distinct genus. The taxonomy of *Actinastrea* and other morphologically similar nominal genera remains in a state of flux. Beauvais (1964, p. 108-112) reviewed the morphology of the genera *Enallocoenia* d'Orbigny, 1849, *Allocoenia* Étallon, 1859 (p. 477-478), and *Stephanastrea* Étallon, 1862 (p. 226, 258; Thurmann and Étallon, 1864, p. 401-402, pl. 57, fig. 2), and considered them to be distinct taxa. Roniewicz (1976, p. 34) made a brief comparison of the morphological characteristics of these same three genera, *Actinastrea* d'Orbigny, 1849, and *Coenastrea* Étallon, 1862 (p. 226, 258; Thurmann and Étallon, 1864, p. 402-403, pl. 57, figs. 3-4). Stanley and Beauvais (1990, p. 358) noted problems with the taxonomy of the members of *Actinastrea* and referred *Astrocoenia hyatti* Wells, 1942b, to the genus *Coenastrea* Étallon, 1862; however, the latter genus previously had been considered to be unrecognizable (Wells, 1956, p. F437). It is evident that further work is needed to clarify the taxonomy of *Actinastrea* and the other morphologically similar genera.

Actinastrea guadalupae (Roemer, 1849)

Figure 28

Astrocoenia guadalupae Roemer, 1849, p. 391-392; Roemer, 1852, p. 87, pl. 10, figs. 8a, b; Hill, 1887, p. 302; Hill, 1889b, p. 7; Hill, 1889c, p. 1, 25; Boyle, 1893, p. 54; Vaughan, 1903, p. 39; Felix, 1914c, p. 235; Wells, 1933, p. 156-158, pl. 18, figs. 11, 12, 13; Wells, 1941b, p. 306; Hamilton, 1956, p. 57; Prinz, 1991, p. 194.
Astrocoenia sanctisabae Roemer, 1852, p. 100; non Wells, 1933, p. 151-152, 158.
Astrocoenia guadaloupae [sic] Roemer, 1849. Meek, 1864, p. 2.
non *Astrocoenia sanctasabae* Roemer, 1852. White, 1879, p. 268, 269.
Astrocoenia texana [sic] Adkins, 1928, p. 77.
Actinastrea guadalupae (Roemer, 1849). Wells, 1956, p. F370, fig. 262,6d.
Actinastrea guadalupe (Roemer, 1849). García-Barrera, 1993, p. 45.

Description. Corallum colonial, attached, cerioid, massive, hemispherical or thick-branched ramose, noncostate. Size of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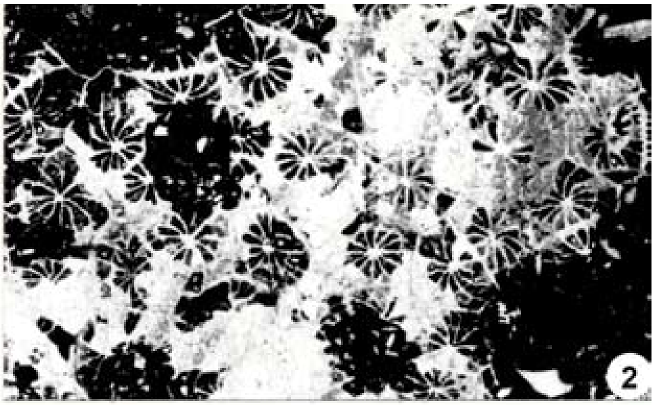
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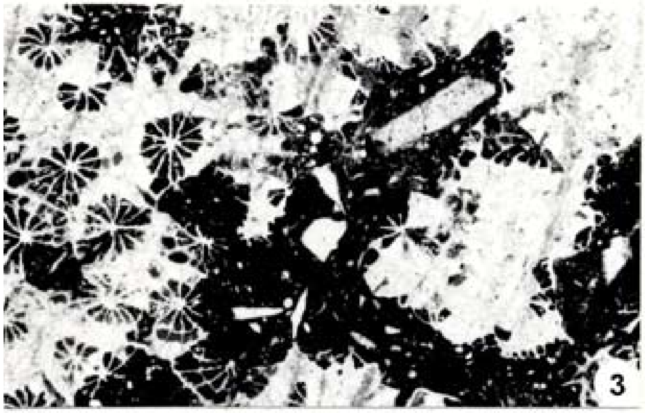
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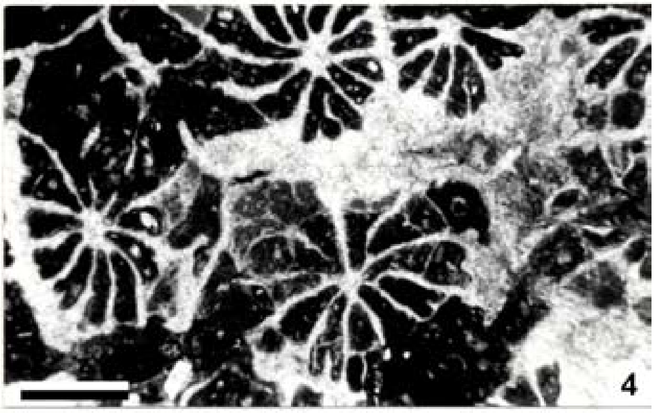
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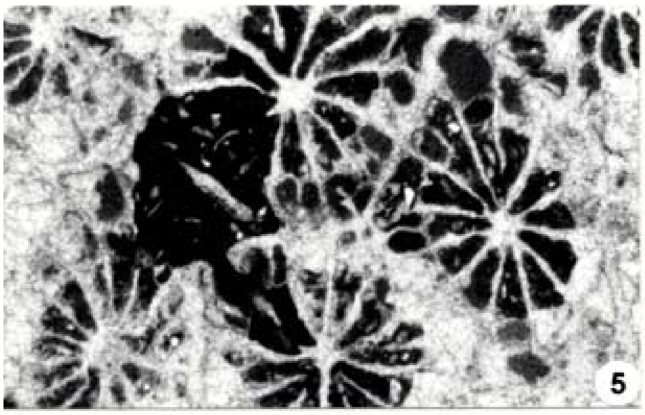
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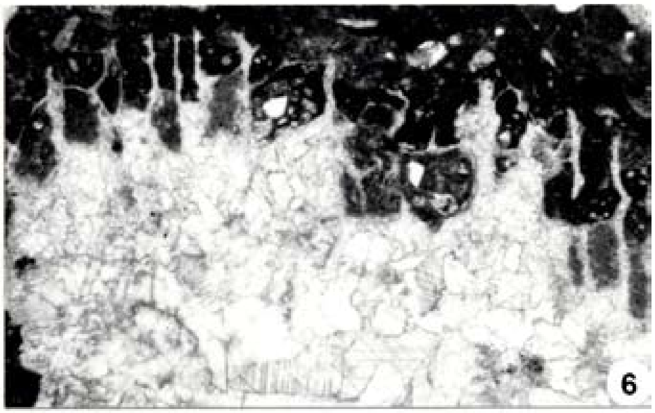
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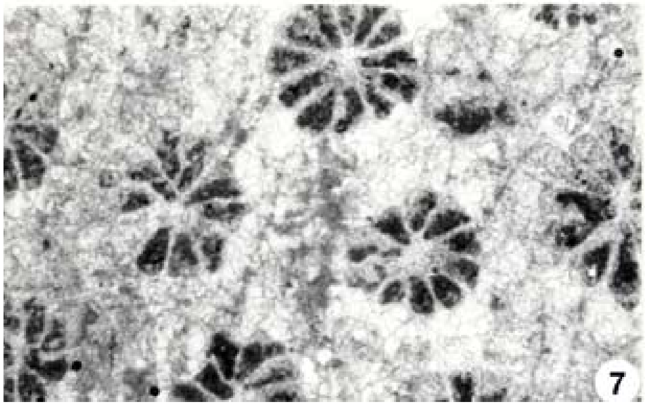
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corallum variable from about 6 cm to nearly 1 m in diameter. Colony formation primarily by extratentacular budding and, less commonly, by intratentacular budding.

Corallites well-defined, prismatic and closely packed; axes oriented perpendicular to surface of corallum. Calices distinct and monocentric. Calicular margins regularly or irregularly polygonal in outline and 4-6 sided. CD ranges from 1.8 to 2.8 mm. Depth of calices very shallow, from about 0.3 mm to nearly even with surface of corallum. Calices separated by well-defined walls approximately 0.2 mm thick.

Septa well-developed, very weakly exsert at calicular margin, laminar and solid. Trabecular architecture not preserved. Septa variable in number, characteristically at least 12 larger septa and four to eight smaller septa of the third cycle. Septa hexamerally arrayed in from two to three cycles, the last cycle typically incomplete. Size relationship among septa: $S_1 \geq S_2 > S_3$. S_1 and S_2 laminar or slightly blade-shaped in cross section, usually straight or gently curved, and about 0.1 mm in width. S_1 and usually most of the S_2 extend from wall to columella at corallite axis. S_3 blade- or wedge-shaped in cross section, about 0.1 mm in width, weakly developed and very short, normally less than one-fourth the CD. S_3 typically extend oral-axially into calice only a short distance above uppermost layer of endothecal dissepiments. Interseptal spaces typically wider than septa, often up to twice width of adjacent septa. Lateral surfaces of septa typically smooth, but occasionally carinate in appearance at fusion with endothecal dissepiments. Septal margins smooth. Inner margins of S_2 fused to axial portion of S_1 in vicinity of S_1 fusion with columella in aboral region of calice. Oral portions of inner margins of free-standing septa often slightly thickened axially.

Columella well-developed, styliform, typically cylindrical, solid and vertically continuous. Columella 0.2-0.4 mm in diameter, or about one-sixth to one-fourth the CD. Columella may possibly appear larger due to lateral fusions from inner margins of S_1 and S_2.

Wall well-developed, septothecal and solid, but very thin, only about 0.1 mm in width. Walls of adjacent corallites fused into a common mural structure about 0.2 mm in width. Recrystallization of adjacent walls and endothecal dissepiment zones may cause the wall to appear much thicker (see Figure 28.7).

Endothecal dissepiments common, usually tabular, laterally continuous, inclined toward corallite axis peripherally, inflected aborally near axis, and very thin but solid. Dissepiments vertically spaced 0.3-0.8 mm apart.

Material examined. Six coralla: IGM-7030 (figured); IGM-7031 (figured), with two thin sections (M-16 and M-17); IGM-7032; IGM-7033; IGM-7034; and IGM-7035. The first four of the specimens listed are from the coral reef horizon (unit MP13), whereas the latter two are from higher in the section, unit MP17. Coralla typically are thoroughly coarsely recrystallized internally; only occasionally is a thin portion of the outermost region preserved well enough to facilitate a taxonomically useful description.

Occurrence. The upper member of the Mal Paso Formation, upper Albian-lower Cenomanian. The fossil locality is in the state of Guerrero, just north of the border with the adjacent state of Michoacán, about 0.75 km north of the rural village of Chumbítaro, Michoacán. The coordinates of this locality are: 18° 29.3' N, 100° 42.5' W.

The species is very common in the coral reef horizon of the upper member of the Mal Paso Formation. Although many of the colonies ranged in size from 10 to 20 cm in diameter, one prolific growth observed in weathered cross section in the field evidently attained a very large size, over 1 m in diameter.

The other occurrences are from the Edwards Limestone and Devils River Limestone, middle and upper Albian, respectively, Texas (Wells, 1933, p. 157).

Figure 28. *Actinastrea guadalupae* (Roemer, 1849), upper member of the Mal Paso Formation, upper Albian-lower Cenomanian, about 0.75 km north of Chumbítaro, Michoacán, in the State of Guerrero, Mexico. 1, IGM-7030, detail of weathered oral surface of corallum, scale bar = 1 cm; 2, IGM-7031, transverse thin section, corallum partially recrystallized, same scale as Figure 28.1; 3, same specimen, transverse thin section, same scale as Figure 28.1; 4, same specimen, transverse thin section, detail of corallites, scale bar = 1 mm; 5, same specimen, transverse thin section, partially recrystallized, detail of corallites, same scale as Figure 28.4; 6, same specimen, longitudinal thin section, detail of septa and wall in vicinity of calicular margin, same scale as Figure 28.4; 7, same specimen, transverse thin section, mostly recrystallized, detail of corallites modified by recrystallization, walls thickened and calices proportionately smaller, same scale as Figure 28.4; 8, same specimen, longitudinal thin section, detail of upper edges of septa and dissepiments in vicinity of calicular margin, same scale as Figure 28.4.

Discussion. The morphological characteristics of the described coralla are the same as those described for *Actinastrea guadalupae* (Roemer, 1849) by Wells (1933), therefore the material is assigned to that species.

Some of the reported interspecific variability in wall thickness and calice diameter may in fact be due to recrystallization of adjacent walls and endothecal zones which can produce simultaneously much thickened mural structures and proportionately smaller calices.

Morphological characters typically employed to distinguish between the species of *Actinastrea* primarily include: size of corallites (CD); number and development of septa; and the symmetry of the septal arrangement.

Species of *Actinastrea* frequently were reported as *Astrocoenia* in older literature. The geographic range of the genus is cosmopolitan and its geologic range extends to at least as early as the Triassic.

The genus needs to be revised, as evident from the literature, but a thorough revision is beyond the scope of this study. For this work, emphasis is placed on comparisons with the species of *Actinastrea* reported from the Cretaceous of the Americas. Some of the species known from the Cretaceous of other parts of the globe, as well as some from the Jurassic, also are discussed.

Roemer originally described *Astrocoenia guadalupae* as new in 1849 (p. 391-392), but he did not provided illustrations to accompany this description. Three years later (1852, p. 87) he again described the same species, as indicated by his citation of the original description in the species synonymy, and he referred to two figures which he provided in plate 10 (figs. 8a, b). The captions for these two figures appeared on page 87 and also on page 100 of that same paper, but the species name given on the latter page is *Astrocoenia sanctisabae* n. sp. instead of *A. guadalupae*. This unfortunate error caused confusion in some later works. White (1879) listed *Astrocoenia sanctasabae* Roemer in two different collections of Cretaceous fossils, one from near Helotes, Bexar County, Texas (p. 268) and the other from near Salado, Bell County, Texas (p. 269). Later, in the remarks given for *Stephanocoenia*? sp., Wells (1933) commented: "The specimen to which White referred in the above paper [1879, p. 269] as "*Astrocoenia sanctisabae*", imputing the species for some unknown reason to Roemer, is identical with several large, massive specimens from the Buda Limestone along Shoal Creek in Austin". "White's name has no standing, because "*Astrocoenia sanctisabae*" has never been described or figured (Wells, 1933, p. 152)". The specimens related to both of the *A. sanctasabae* occurrences listed by White (1879, p. 268, 269) probably are not *A. guadalupae* Roemer; instead, they probably should be reassigned to the genus *Stephanocoenia*, as Wells indicated previously (see Wells, 1933, p. 158).

Only three other species of *Actinastrea* have been described previously from the Cretaceous of Mexico. Felix (1891, p. 156) described a species of *Actinastrea* from the Neocomian strata near Tehuacán, state of Puebla, and stated that the corallites of the specimens he examined possessed an average CD of 2.5 mm and 24 hexamerally arrayed septa. Felix compared the corallite morphology of his species of *Actinastrea* with that of *Actinastrea globosa* (Fromentel, 1870, p. 614, pl. 188, fig. 1) and noted that Fromentel gave 2.5-4.0 mm as the range of CD for the corallites, but that the specimen illustrated by Fromentel (1870, pl. 188, fig. 1) showed that the CD is only about 2 mm. Despite his acknowledgement of some apparent morphological discrepancies, Felix assigned the Mexican form to *Actinastrea globosa* (Fromentel, 1870). This taxonomic determination is here queried pending examination of specimens from the Tehuacán region. Unfortunately, neither Felix's specimens of *Actinastrea globosa* nor any other member of the family Actinastraeidae have been located during a recent re-examination of the coral specimens from Tehuacán (Löser, 2006, p. 55).

Imlay described *Actinastrea hispaniensis* (Imlay, 1940, p. 138, pl. 1, figs. 21, 22; Wells, 1946, p. 1) from the Berriasian-Valanginian Carbonera Formation near Las Cuevas, Durango, and indicated that the species characteristically possessed corallites with a CD of 1.5-2 mm and 16-20 septa (eight to ten principal septa, 4-5 S_1 + 4-5 S_2, with smaller septa, 8-10 S_3, in between the principal septa) in an octameral or decameral arrangement. In contrast, *A. guadalupae* possesses slightly larger corallites and more numerous septa which are arrayed hexamerally.

Reyeros (1983, p. 13-14, pl. 1, fig. 1) reported *Actinastrea* cf. *A. decaphylla madagascariensis* Alloiteau, 1958, from the Upper Cretaceous Yucunama Formation near San Pedro Yucunama, Oaxaca. However, based on her description and figure of the species, her taxonomic determination is considered doubtful even at the generic level and, when compared to the original description and figure of *A. decaphylla* var. *madagascariensis* Alloiteau, 1958 (p. 185, pl. 35, fig. 1), it seems highly unlikely that the Mexican species is conspecific (contrary to comments on the Mexican form made by Prinz, 1991, p. 194). The species described by Alloiteau, from the Campanian(?) of Madagascar, possesses corallites with a CD of 1.75-3 mm and 20 septa which are arrayed decamerally, 5 S_1+ 5 S_2 + 10 S_3 (pentamerally?), whereas the species from Mexico possesses smaller corallites (CD 1.5-2 mm) and more numerous septa (20-24) which seem hexamerally arranged. Additionally, in the Mexican species the growth form of the colony is subcerioid, calicular margins are invariably circular in outline, and none of the septa extends to the columella (except possibly aborally, deep within the calice, as previously noted by Reyeros, 1983, p. 13-14). In members of *Actinastrea*, the growth form typically is cerioid, the calicular margins are polygonal, and at least the S_1, and also usually the S_2, extend to the columella. Additional better preserved specimens are needed in order to precisely determine the taxonomic identity of the Mexican species.

One other occurrence of *Actinastrea* in the Cretaceous of Mexico is noted here: Allison (1955, p. 405, 408) reported *Astrocoenia* (probably a species of *Actinastrea*) from the Albian Alisitos Formation at Punta China, Baja California.

Several other species of *Actinastrea* are known from the Cretaceous of North America, and some of them, like *A. guadalupae*, also can be characterized by the possession of three cycles of hexamerally arrayed septa (as many as 24 in number).

Astrocoenia nidiformis Cragin (1895a, p. 50; reassigned to the genus *Actinastrea* by Scott, 1970, p. 55), from the Belvidere beds (Cragin, 1895b; Twenhofel, 1924, p. 51; Kauffman, 1984, p. 290), Kansas, and the Comanche Peak Formation and Devils River Limestone, Texas (Wells, 1933, p. 152-156), primarily differs from *A. guadalupae* by the smaller calices (CD 1.25-1.50 mm) and the fusion of the S_3 to their respective S_2. Another species from the Cretaceous of Kansas, *Astrocoenia conica* Logan, 1899 (p. 215, pl. 26, figs. 1-3), has calices with a relatively large CD (up to 8 mm) and numerous septa; the species most likely does not belong to either *Astrocoenia* or *Actinastrea*.

Actinastrea whitneyi (Wells, 1932, p. 230-231, pl. 31, fig. 6, pl. 32, figs. 1, 2, pl. 37, fig. 1), from the lower Glen Rose of the Trinity Group, Texas, but also reported from the Mural Limestone, Arizona (Grocock, 1975; Scott, 1981) and from the Barranquín Formation, Venezuela (von der Osten, 1957a, p. 697; 1957b, p. 575, pl. 63, figs. 6, 7), is similar to *A. guadalupae* except that the S_3 unite with their respective S_2 (see Wells, 1933, p. 153), only the six S_1 reach the columella, and two of these six S_1 usually are slightly larger than the other four and seem to bilaterally partition the calice longitudinally into halves. Another species from the lower Glen Rose of Texas and Mural Limestone (Scott, 1981), *A. scyphoidea* (Wells, 1932, p. 231-232, pl. 32, fig. 3, pl. 33, fig. 3), has an encrusting growth form and possesses smaller corallites (CD 1.5-1.75 mm) with only 12 septa.

Actinastrea bellensis (Wells, 1933, p. 158, pl. 19, figs. 5, 6), from the middle Albian Comanche Peak Formation near Belton, Texas, primarily differs from *A. guadalupae* by the smaller calices (CD about 1 mm) and smaller number of septa (only 12).

Actinastrea pattoni (Wells, 1933, p. 158-159, pl. 19, figs. 1, 2), from the Edwards Limestone, Texas, primarily differs from *A. guadalupae* by the much smaller calices (CD about 1 mm), and the smaller number of septa (16-20) in a characteristically octameral arrangement (Wells, 1933, p. 153).

Actinastrea budaensis (Wells, 1933, p. 160, pl. 19, fig. 3), from the Buda Limestone, Austin, Texas, is similar to *A. guadalupae* in the CD of the calices (2.0-2.5 mm), the number of septa (24), and in the number of septa which reach the columella (12). However, in the former species the S_1 and S_2 are thicker and the S_3 are often fused to their respective S_2, whereas in the later species the S_2 are usually fused to an adjacent S_1 and the inner margins of the S_3 are laterally free.

Actinastrea? *dickersoni* (Wells, 1941a, p. 287-288, pl. 43, fig. 4), from the Upper Cretaceous of Cuba, possesses three cycles (24 in number) of hexamerally arrayed septa, but in contrast to *A. guadalupae*, the corallites are slightly larger (CD 2-3 mm) and the S_2 are not as robust as the S_1.

A number of other occurrences of *Actinastrea* have been reported from the Cretaceous of North America; however, the majority of this material has not been described. *Actinastrea* evidently is one of the more commonly encountered corals in reef facies of: the Lower Cretaceous Mural Limestone in the southwestern United States and northern Mexico (Ransome, 1904; Darton, 1925, p. 142; Stoyanow, 1949; Grocock, 1975; Scott and Brenckle, 1977; Scott, 1979; Rigby and Scott, 1981; Roybal, 1981; Scott, 1981; Schreiber and Scott, 1987; Warzeski, 1987, p. 343; Hartshorne, 1989, p. 324); the

Albian Howell's Ridge Member of the U-Bar Formation of New Mexico (Campbell, 1988); and the subsurface Lower Cretaceous (Albian) of the Gulf Coast (Scott, 1990). In the Western Interior Basin, Cobban (1951, p. 2188) reported *Astrocoenia* sp. (probably referable to the genus *Actinastrea*) from the Upper Cretaceous (Turonian) Turner sandy member of the Carlile Shale at a locality about six miles north of Belle Fourche, South Dakota. The genus also has been reported from the Cretaceous of Jamaica (Coates, 1977a, p. 90, listed as *Astrocoenia*).

Members of *Actinastrea* (mostly reported as *Astrocoenia*) also have been noted in the later Mesozoic of California (*A. petrosa* Gabb, 1864, p. 208, pl. 31, figs. 274, 274a; 1869, p. 254; Durham, 1962, p. 37) and Canada (*A. irregularis* Whiteaves, 1884, p. 246; 1900, p. 304, pl. 33, fig. 1).

A number of species of *Actinastrea* occur in the Cretaceous of South America. Two species of *Actinastrea* are known from the Neocomian of Chile (Fritzsche, 1921), *A. minima* (Fromentel, 1857) (Fritzsche, 1923, p. 318, pl. 4, fig. 2) and *A. hexamera* (Fritzsche, 1923, p. 318-319, pl. 3, fig. 7). The first of these two species reportedly possesses small corallites (CD 1-1.5 mm) in which 20 septa are arrayed decamerally (10 S_1 and 10 S_2), and thus seems quite distinct from *A. guadalupae*. The second of the two, *A. hexamera*, is similar to *A. guadalupae* in that both possess three cycles (24 in number) of hexamerally arrayed septa, 12 of which reach the columella, but primarily differs from the latter by the smaller diameter of the corallites (CD 1.0-1.5 mm).

Thamnastrea harrisoni Gregory, 1927 (p. 442-443, pl. 13, figs. 2a-c), from the Urgonian El Cantil Formation at Punceres, state of Monagas, eastern Venezuela, subsequently was reassigned to *Astrocoenia* (see Gerth, 1928, p. 14, footnote; Wells, 1944b, p. 433), and here it is considered a species of *Actinastrea*. *Actinastrea harrisoni*, based on the original description and figures, possesses three cycles (24 in number) of hexamerally arrayed septa, 12 of which reach the columella, as in *A. guadalupae*, but primarily differs from the latter by the smaller corallites (CD about 2 mm) and the more robustly developed S_3.

Actinastrea peruviana (Wells, 1941b, p. 305-307, pl. 44, fig. 1), from the upper Aptian Pananga Limestone near La Brea in northwestern Peru, has corallites that are smaller (CD average about 1.5 mm) than those of *A. guadalupae*, and typically possesses a smaller number of septa (12-16).

Actinastrea barranquinensis (Wells, 1944b, p. 432, pl. 69, figs. 1, 2), from the Barranquín Formation at Las Cinco Ceibas, state of Sucre, Venezuela, primarily differs from *A. guadalupae* by the possession of larger corallites (CD 3-3.5 mm) with a larger number of septa (36).

Actinastrea barranquiniana (von der Osten, 1958; nomen novum for *Astrocoenia minima* von der Osten, 1957b, p. 574, pl. 63, fig. 13), from the Barranquín Formation of Venezuela also, primarily differs from *A. guadalupae* by the smaller size of the corallites (CD 0.8-1.0 mm), the smaller number of septa (16), and the octameral arrangement of the septa.

Prinz described (1991, p. 193-194) a species of *Actinastrea* from the Lower Cretaceous of El Way, northern Chile, and referred the specimens to *A. whitneyi* (Wells, 1932). However, based on the reported variability in the size of the corallites (CD up to 4 mm) and the figures of the species provided by Prinz (1991, p. 194, and pl. 7, fig. 3, respectively), the species appears to be more closely allied to *A. barranquinensis* (Wells, 1944b).

Several other species of *Actinastrea* also have been reported from the South American Cretaceous. Most of these species originally were described from European occurrences, and their occurrences in South America typically are only listed or the specimens very briefly described. Included here are: *A. colliculosa* (Trautschold, 1886), *A.* cf. *A. triboleti* (Koby, 1897), and *A.* aff. *A. regularis* (Fromentel, 1857) from the Aptian of the Neuquen basin, Argentina (Gerth, 1928, p. 7-8, 14; Weaver, 1931, p. 164); *A. retifera* (Stoliczka, 1873) from the Upper Cretaceous of Chile (Gerth, 1928, p. 14); and *Astrocoenia* cf. *A. ramosa* Milne Edwards and Haime, 1848a, and *Astrocoenia* sp. from the Upper Cretaceous of Curaçao (Gerth, 1928, p. 3-4).

Two species of Cretaceous (Aptian-Cenomanian) age that have been dredged from guyots in the South Pacific are of particular interest here: *Astrocoenia revellei* Hamilton, 1956 (p. 57, pl. 5, fig. 3), from Hess Guyot, and *A. dietzi* Hamilton, 1956 (p. 57-58, pl. 5, fig. 2), from Cape Johnson Guyot. The first of the two species, *A. revellei*, appears to belong to the genus *Actinastrea* and so it is here reassigned to that genus. Furthermore, the cerioid growth form of the corallum, the polygonal shape of the calicular margin, the diameter of the calice (CD about 2.1 mm), and the number, arrangement and development of the septa (24 septa hexamerally arrayed in three cycles, S_1 and S_2 fused to styliform columella, S_3

weakly developed and about one-sixth the CD in length) indicate a close affinity to *A. guadalupae* (an affinity also noted by Hamilton, 1956, p. 57). Thus, it seems possible that *A. revellei* (Hamilton, 1956) could be a junior synonym of *A. guadalupae* (Roemer, 1849). The other species mentioned above, *Astrocoenia dietzi* Hamilton, 1956, does not appear to be allied to the genus *Actinastrea* based on the original description and figure of the species. Most specifically, the reported presence of dense peritheca between the corallites (see Hamilton, 1956, p. 57) does not support an assignment of the species to *Actinastrea*.

Members of *Actinastrea* also are common in the Jurassic of North America. *Actinastrea maloniana* (Vaughan, 1905, p. 34-35, pl. 2, figs. 1-3), from the Malone beds (Tithonian); Wells, 1946, p. 2) of Texas (Albritton, 1938, p. 1761), primarily differs from *A. guadalupae* by the smaller number of septa (16-20) and their characteristically octameral (Wells, 1933, p. 153) or decameral (Wells, 1942b, p. 3) arrangement.

Actinastrea hyatti (Wells, 1942b), originally described from the Kimmeridgian upper Sundance Formation of Wyoming and subsequently reported from several localities in the Jurassic of the Western Interior (Imlay, 1952, 1956, p. 577-578, 583-584, 1964, 1965, 1967, p. 33; 1980, p. 80, 89), primarily differs from *A. guadalupae* by the characteristically ramose growth form of the colony and the dimorphic development of the first two cycles of septa ($S_1>S_2$).

Actinastrea kellumi (Wells, 1946, p. 2-3, pl. 1, fig. 1), from the La Casita Formation (Kimmeridgian-Portlandian (Tithonian)) of the state of Durango, Mexico, is similar to *A. guadalupae*, except the walls of *A. kellumi* are much thicker (0.5 mm).

Reyeros (1974) described two species of *Actinastrea* from the Upper Jurassic of the Sierra de Águila in the northern part of the state of Chihuahua, Mexico: *A. crassoramosa* (Michelin, 1843, p. 109, pl. 25, fig. 2) and *A. tenuisepta* (Koby, 1885, p. 296, pl. 87, figs. 5-5a). However, she did not compare the material with the other previously described species of *Actinastrea* known from the North American Jurassic. The first of these two species, *A. crassoramosa*, is the type species of *Enallocoenia* d'Orbigny, 1849, purportedly a taxonomically distinct genus (Beauvais, 1964, p. 111-112), whereas the latter species, *A. tenuisepta*, was tentatively reassigned to *Stephanastrea* Étallon, 1862 (Roniewicz, 1976, p. 36). Detailed comparisons of these Mexican species with the other Jurassic species should be made in order to determine more precise affinities.

Specimens of *Actinastrea* also have been reported from the Jurassic (Oxfordian) Smackover Limestone in the subsurface of the Gulf Coast (Wells, 1942a, p. 126, 128, pl. 21, fig. 5; Baria et al., 1982; Crevello and Harris, 1984, p. 73). Earlier Mesozoic occurrences in South America include: several species from the Jurassic of Chile (Prinz, 1986, 1991) and the Lower Jurassic of Peru (Tilmann, 1917; Wells, 1953, p. 3-5, fig. 1: *Actinastrea* sp. cf. *A. lissoni* [Tilmann, 1917]). The geologic range of the genus extends to at least as early as the Triassic as indicated by several reported occurrences (for example see Prinz, 1991, p. 158).

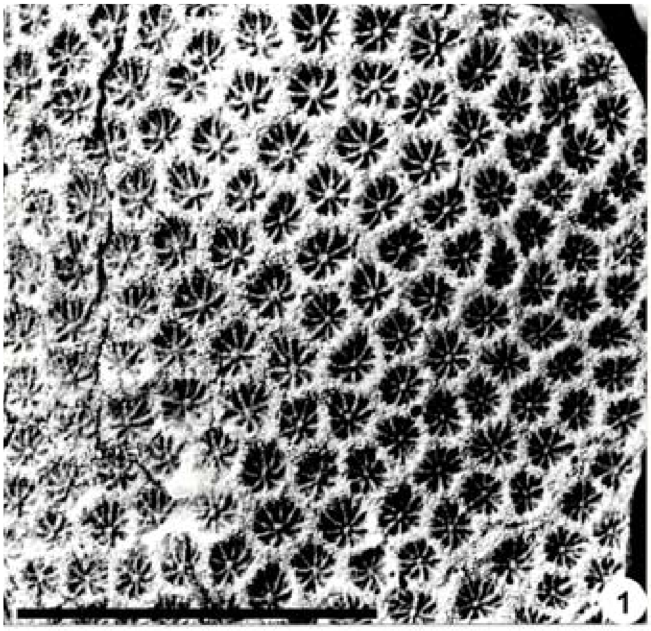
Actinastrea chumbitaroensis new species
Figure 29

Diagnosis. Corallum ramose. Calicular margin typically hexagonal. CD 1.2-1.8 mm. Distance between calicular centers about 1.5 mm. Septa 16 in number, octamerally arrayed in two cycles, and laterally free orally. Columella prominent, styliform, cylindrical.

Description. Corallum colonial, attached, cerioid, ramose, and noncostate. Branches relatively small in size and subcylindrical or lath-shaped. Colony formation by extratentacular budding and, possibly, with occasional intratentacular distomodaeal budding.

Corallites well-defined, prismatic, and closely spaced. Corallite axes oriented perpendicular to surface of corallum. Calices distinct and typically monocentric. Calicular margin characteristically hexagonal, rarely quadrilateral, sides often equal in length. CD ranges from 1.2 to 1.8 mm, but most commonly about 1.5 mm. Calices laterally spaced about 0.2 mm apart from each other; distance between calicular centers about 1.5 mm. Calicular margins of adjacent corallites typically fused together into a ridge-like mutual boundary about 0.1 mm in width orally and thickened aborally to about 0.2 mm.

Septa well-developed, non-exsert, laminar, and solid. Trabecular architecture not preserved. Septa characteristically 16 in number and arrayed octamerally in two complete cycles ($8\ S_1 + 8\ S_2$) with size relationship: $S_1>S_2$. S_1 blade-shaped in cross section, straight, about 0.3 mm in width at junction with wall, and tapered toward corallite axis. Length of S_1 about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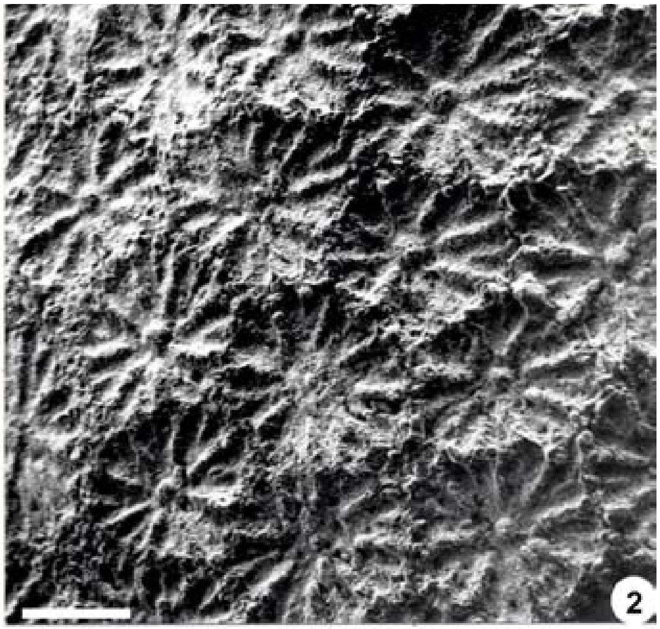
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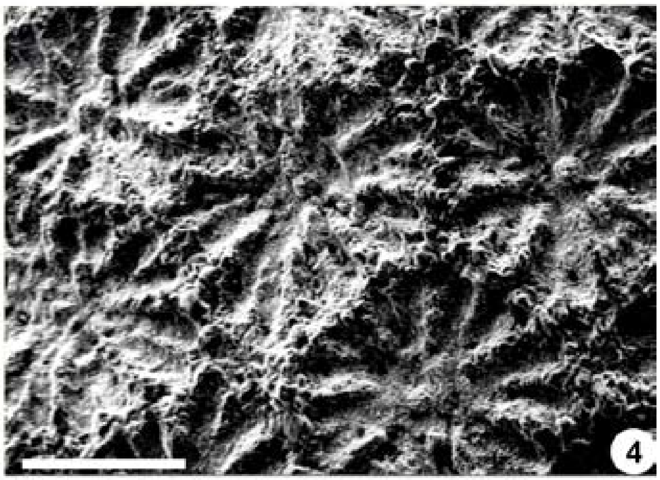
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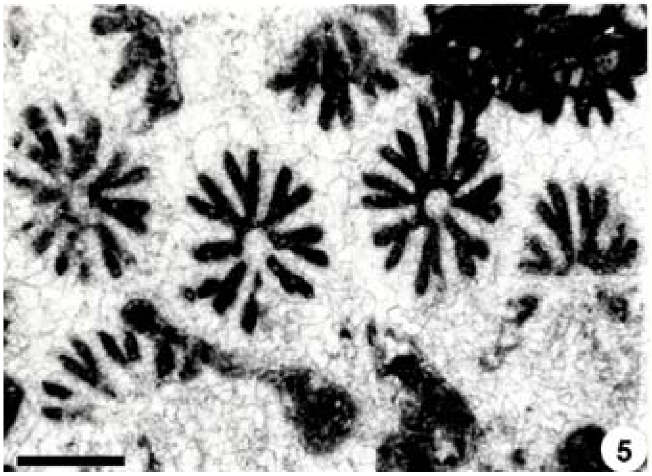
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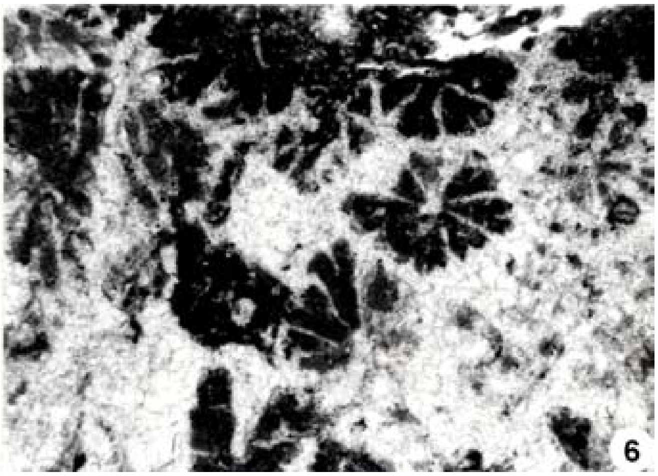
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0.6 mm, or three-fourths distance from wall to columella. Inner edges of S_1 terminated at about 0.2 mm from columella in oral portion of calice, but may be fused to columella deeply aborally in corallite. S_2 blade-shaped in cross section, slightly narrower than S_1, and about 0.4 mm in length, or half the distance from wall to columella. Interseptal spaces about 0.2 mm in width. Lateral surfaces of septa appear smooth or laterally granulated. Septal margins appear smooth, inner margins laterally free. Pali absent.

Columella well-developed, prominent, styliform, cylindrical, solid, vertically continuous, about 0.2-0.3 mm in diameter, and laterally free from septa in oral portion of corallite. Inner edges of S_1 may be fused to columella deep within aboral region of corallite.

Wall appears septothecal, solid, usually fused with wall of adjacent corallite, the resultant combined mural structure about 0.2 mm in width. Endotheca tabular, very thin, closely spaced.

Etymology. The species is named for the village of Chumbítaro, Michoacán, which is just south of the type locality of the species in the state of Guerrero, by adding the Latin suffix -*ensis* = place.

Types. Three fragments: holotype IGM-7036 (20 x 33 mm in width and 15 mm in height; Figure 29.1); paratype IGM-7037 (28 x 18 mm in width and 40 mm in height; Figure 29.2-29.6), with two thin sections (M-01 and M-02); and paratype IGM-7038 (20 x 35 mm in width and 35 mm in height). All of the specimens are recrystallized and slightly weathered.

The type stratum is the upper member of the Mal Paso Formation, upper Albian-lower Cenomanian. The type locality is in the state of Guerrero, just north of the border with the adjacent state of Michoacán, about 0.75 km north of the rural village of Chumbítaro, Michoacán. The coordinates of this locality, as determined from the Mexican 1:50,000 scale Coyuca de Catalán (E14A74) topographic map, are: 18° 29.3' N, 100° 42.5' W.

Occurrence. Known only from the type locality. The specimens were collected from loose material on the weathered exposure of unit MP17, but they may have been derived from an adjacent bed. The coordinates of this locality are given above.

Discussion. The description is based on three recrystallized corallum fragments. Externally the samples clearly exhibit morphological features which preclude their assignment to the other member of this genus that is known from the upper member of the Mal Paso Formation, *A. guadalupae* (Roemer, 1849).

Actinastrea chumbitaroensis n. sp. differs from the previously described members of *Actinastrea* that are at least in part also characterized by the possession of octamerally arrayed septa.

Actinastrea maloniana (Vaughan, 1905, p. 34-35, pl. 2, figs. 1-3), from the Malone beds of Texas, primarily differs from *A. chumbitaroensis* n. sp. by the encrusting or massive growth form of the corallum and the larger CD, from 1.5 to 2.5 mm (Wells, 1933, p. 153).

Actinastrea cf. *A. ramosa* (Milne Edwards and Haime, 1848a, p. 298) and *Actinastrea* sp., both briefly described by Gerth (1928, p. 3-4) as species of *Astrocoenia* from the Upper Cretaceous of Curaçao, also possess octamerally arrayed septa and calices of similar size (CD 1-1.5 mm and CD 1-2 mm, respectively). However, neither species was figured by Gerth (1928) and, based only on his brief descriptions, a more accurate comparison of these forms with *A. chumbitaroensis* n. sp. cannot be made.

Actinastrea cf. *A. triboleti* (Koby, 1897), described by Gerth (1928, p. 7-8) as a species of *Astrocoenia* from the Aptian of the Neuquen basin, Argentina, differs from *A. chumbitaroensis* n. sp. by the variable number of septa, 8-10 S_1 and 8-10 S_2, and the smaller diameter of the calices.

Actinastrea pattoni (Wells, 1933, p. 158-159, pl. 19, figs. 1, 2), from the Edwards Limestone, Texas, primarily differs from *A. chumbitaroensis* n. sp. by the encrusting growth form of the corallum and the much smaller diameter of the calices, the CD only about 1 mm (Wells, 1933, p. 153).

Figure 29. *Actinastrea chumbitaroensis* n. sp., upper member of the Mal Paso Formation, upper Albian-lower Cenomanian, about 0.75 km north of Chumbítaro, Michoacán, in the State of Guerrero, Mexico. 1, Holotype IGM-7036, detail of weathered surface of corallum fragment, scale bar = 1 cm; 2, paratype IGM-7037, SEM photograph of weathered oral surface, scale bar = 1 mm; 3, same specimen, thin section, mostly coarsely recrystallized, same scale as Figure 29.1; 4, same specimen, SEM photograph, detail of oral surface of several calices, scale bar = 1 mm; 5, same specimen, transverse thin section, detail of septal arrangement and columella of several corallites, scale bar = 1 mm; 6, same specimen, transverse thin section, detail of corallites in deeper, central portion of corallum, mostly recrystallized, same scale as Figure 29.5.

Actinastrea hispaniensis (Imlay, 1940, p. 138, pl. 1, figs. 21, 22; Wells, 1946, p. 1) from the Berriasian-Valanginian Carbonera Formation near Las Cuevas, Durango, primarily differs from *A. chumbitaroensis* n. sp. by the massive growth form of the corallum, the variable number of the septa (16-20, inserted as 4-5 S_1, 4-5 S_2, and 8-10 S_3), and the slightly larger diameter of the calices (CD of 1.5-2 mm).

Two Upper Cretaceous species of *Actinastrea* with octamerally arrayed septa, *A. octolamellosa* (Michelin, 1847, p. 302-303, pl. 72, fig. 2a-b) and *A. ramosa* (Sowerby, in Sedgwick and Murchison, 1832, p. 417, pl. 37, fig. 9; see Michelin, 1847, p. 303, pl. 72, fig. 4a-b), both from Europe, possess calices that differ in size from those of *A. chumbitaroensis* n. sp.: CD 1.5-2.1 mm and CD 1-1.2 mm, respectively (see Turnšek, 1997, p. 8-9).

Refer to the discussion section given for *A. guadalupae* (Roemer, 1849) for additional comments on the taxonomy and stratigraphic and geographic distributions of this genus.

Suborder Rhipidogyrina Roniewicz, 1976
Family Rhipidogyridae Koby, 1905
Genus *Preverastraea* Beauvais, 1976

Type species. *Aulastraeopora chelussii* Prever, 1909 (p. 140-141, pl. 10, fig. 36, text figs. 41, 42), by original designation (Beauvais, 1976, p. 25).

Discussion. The genus *Preverastraea* Beauvais, 1976, has been referred to the suborder Rhipidogyrina, family Rhipidogyridae, by Morycowa and Marcopoulou-Diacantoni (1994). Their classification is followed here.

***Preverastraea coatlicuae* new species**
Figure 30

Diagnosis. Corallum plocoid. Wall of corallite developed as single parathecal zone; outer corallite wall absent. CD 4-5 mm. Septa 12 in number and hexamerally arrayed in two cycles.

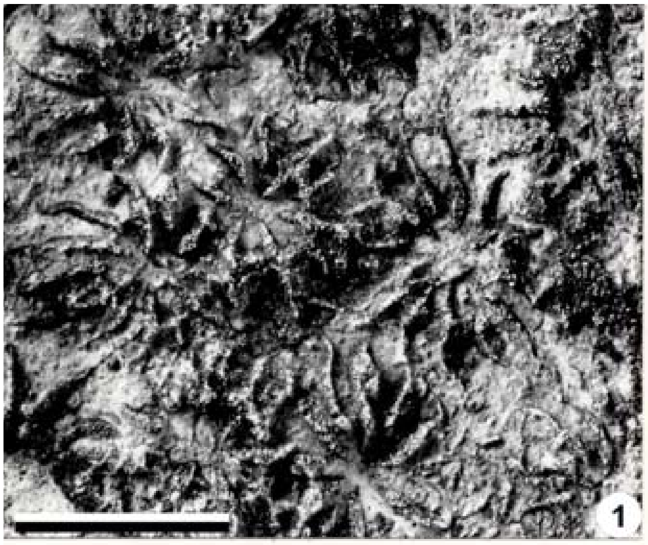
Description. Corallum colonial, attached, plocoid, massive, costate, and hemispherical or laterally elongate, low, and mound-shaped. Size of corallum variable, observed range from as small as 8 cm in diameter and 5 cm in height, to as large as about 38 cm in diameter width and 16 cm in height based on field observations. Colony formation by extratentacular budding.

Corallites well-defined, generally cylindrical, subparallel to each other, slightly protuberant, and primarily aligned upward. Corallites laterally spaced 2-7 mm apart, the distance filled by well-developed coenosteum. Calices exclusively monocentric. Calicular margin roughly circular in outline or vaguely petaliform. CD fairly consistent, 4-5 mm; depth of calice about 2 mm. Calicular centers spaced 6-15 mm apart.

Septa well-developed, relatively short, exsert, solid, and structurally continuous with robust costae. Septa typically 12 in number and arranged hexamerally in two cycles. Size relationship among septa: $S_1 >> S_2$. S_1 wedge-shaped in cross section, about 1 mm in width at junction with wall, and tapered toward corallite axis. S_1 from 1.5 to 2.0 mm in length, or about three-fourths distance from wall to corallite axis. S_2 wedge-shaped in cross section, slightly narrower than S_1, about 0.8 mm in width, but very much shorter, about 0.5-1.0 mm in length, less than half that of S_1, or about one-fourth distance from wall to axis. Interseptal spaces 0.5-0.8 mm in width, or about as wide as adjacent S_2. Lateral surfaces of septa mostly smooth with few sparsely distributed pointed, conical lateral projections or granulations about 0.2 mm in width and height (possibly in part due to fusion of septa and endothecal dissepiments). Septal margins appear smooth or minutely dentate(?); axial edges commonly laterally free, sharp, and recurved abaxially or sometimes bifurcated. Pali absent.

Columella absent, axial region hollow orally and partitioned by endothecal dissepiments aborally. Axial region

Figure 30. *Preverastraea coatlicuae* n. sp., holotype IGM-7039, upper member of the Mal Paso Formation, upper Albian-lower Cenomanian, about 0.75 km north of Chumbítaro, Michoacán, in the State of Guerrero, Mexico. 1, Detail of portion of weathered oral surface of corallum, scale bar = 1 cm; 2, oral view of part of corallum, scale bar = 1 cm; 3, transverse thin section of several corallites; note well-developed parathecal wall of corallites and complete absence of outer wall, scale bar = 1 cm; 4, transverse thin section, detail of septa and parathecal wall, scale bar = 1 mm; 5, longitudinal thin section of a corallite, slightly oblique, upper edge of calice at top center of figure, coenosteal structure in left third of figure, skeleton in lower part of figure partially coarsely recrystallized, same scale as Figure 30.3; 6, longitudinal thin section, detail of vesicular dissepiments of coenosteum, same scale as Figure 30.4; 7, longitudinal thin section, detail of paratheca (left), endotheca, and septa, same scale as Figure 30.4.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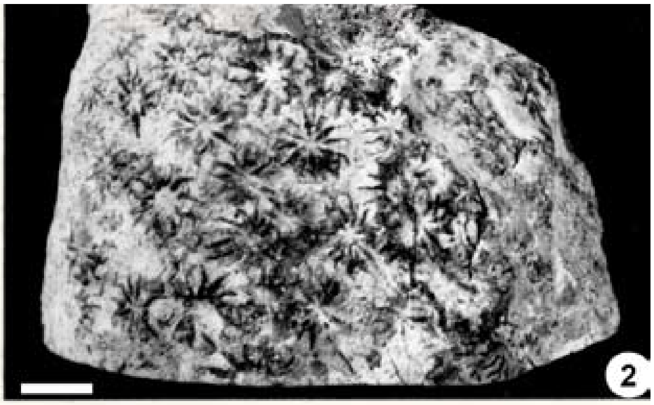
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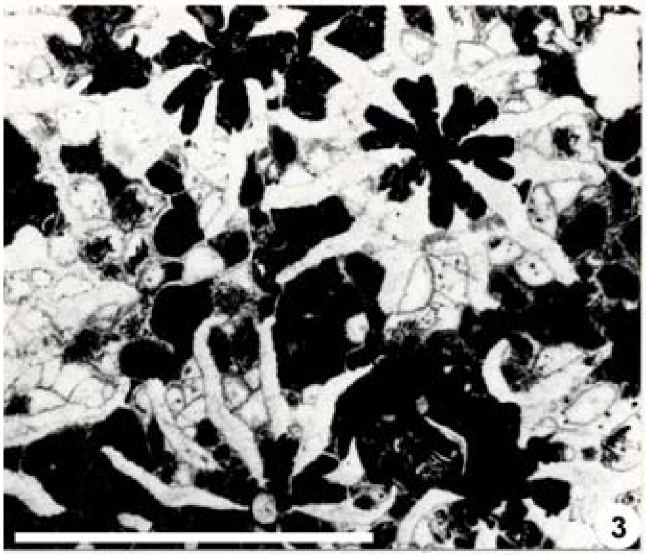
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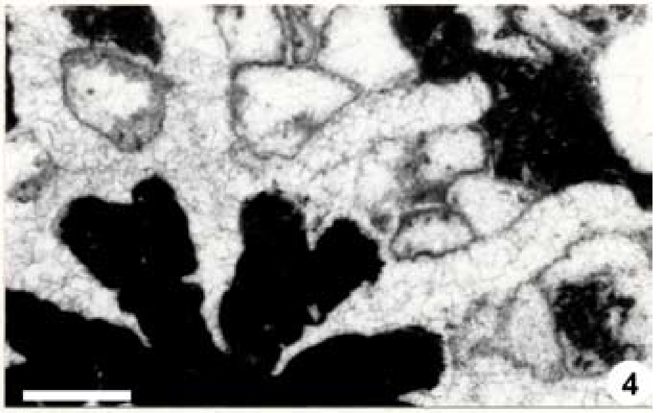
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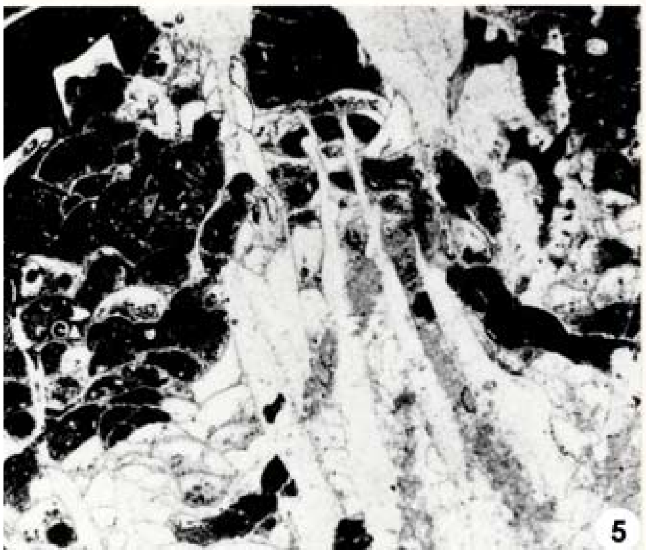
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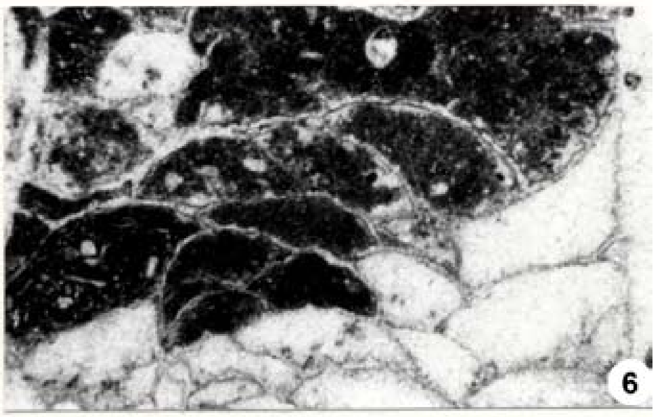
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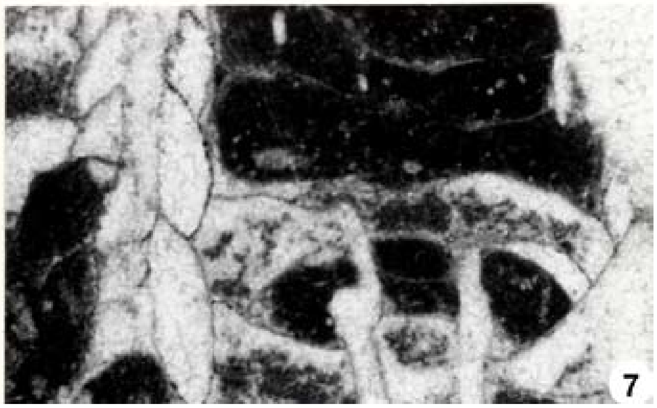
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1-1.5 mm in width, or about one-fourth to one-third the CD. Vertically aligned inner margins of S_1 encircle perimeter of axial region.

Wall well-developed, parathecal, about 0.7-2.0 mm in thickness, and composed of a zone of vesicular dissepiments. Outer or secondary corallite wall absent. Parathecal dissepiments convex orally, concave aborally, about 0.5-2.0 mm in width, and vertically spaced 0.5-2.0 mm apart. Endothecal dissepiments tabular, laterally discontinuous, commonly oriented subhorizontal, about 0.1-0.2 mm in thickness and vertically spaced about 1-2 mm apart.

Coenosteum extensively developed, composed of vesicular exothecal dissepiments, and structurally similar to, and often continuous with, those of paratheca. Coenosteal areas of corallum surface slightly concave and costate.

Costae well-developed, robust, straight, curved or slightly sinuous, wedge-shaped in cross section, and structurally continuous with septa. Costae of adjacent corallites typically nonconfluent. Width of costae equal to that of respective septa, but often slightly tapered distally. Length of costae much greater than that of respective septa, commonly several times length of septa. Typically C_1>>C_2, but heights nearly subequal. C_1 sometimes up to at least 2 mm in height, C_2 only slightly shorter. Lateral surfaces of costae smooth. Intercostal furrows about as wide as S_2 proximally and usually wider distally. Costae of younger corallites not as robust as those of older corallites. Peripheral boundary of corallite commonly somewhat weakly delineated by abrupt distal deflections or terminations of costae. Costae, mainly C_1, with internal network of tubular passageways or galleries about 0.3-0.5 mm in diameter (possibly borings?).

Etymology. The species is named for Coatlicue, an Aztec goddess of the Earth.

Types. Holotype IGM-7039, with two thin sections (M-22 and M-23); and paratype IGM-7040. The holotype corallum is about 85 x 150 mm in width and 75 mm in height. The paratype specimen, 90 x 140 mm in width and 90 mm in height, is only a portion of a much larger corallum that was about 38 cm in diameter. The skeletal structure of both specimens is preserved only in the outermost few centimeters of the corallum, internally they are coarsely recrystallized.

The type stratum is the upper member of the Mal Paso Formation, upper Albian-lower Cenomanian. The type locality is in the state of Guerrero, just north of the border with the adjacent state of Michoacán, about 0.75 km north of the rural village of Chumbítaro, Michoacán. The coordinates of this locality, as determined from the Mexican 1:50,000 scale Coyuca de Catalán (E14A74) topographic map, are: 18° 29.3' N, 100° 42.5' W.

Occurrence. Known only from the type locality. The coordinates of this locality are given above. This species is common in the coral reef horizon of the upper member of the Mal Paso Formation. It also was observed in beds stratigraphically below the reef horizon, in units MP9 and MP5. This species was one of the two primary contributors to the reef build-up at this locality. Boring bivalves were observed in some of the coralla, particularly in the corallite axes.

Discussion. The morphology of the species described above is most similar to that described for species assigned to *Preverastraea*, therefore the species is referred to that genus. However, the majority of the other species of *Preverastraea* typically possess corallites with both an internal wall and an outer wall (Morycowa and Marcopoulou-Diacantoni, 1994). The outer walls of adjacent corallites of these other species are combined into a shared structure which produces an overall appearance of a cerioid corallum. The single parathecal wall of *P. coatlicuae* n. sp. is analogous to the inner wall of these other species, but the corallites of the new species totally lack an outer wall and the corallum is thus plocoid in appearance. Two of the species referred to this genus previously, *P. felixi* (Hackemesser, 1936) and *P. diplothecata* (Hackemesser, 1936), possess corallites in which the outer wall is usually developed, but occasionally it is absent (see Hackemesser, 1936, pl. 2, figs. 2, 3, 5, 7). Therefore, the complete absence of the corallite outer wall in *P. coatlicuae* n. sp. is considered to be a taxonomically significant character at the species level and not the generic level.

Other major differences between *P. coatlicuae* n. sp. and the other members of the genus include the number of septa and their position of development within the corallites. Corallites of *P. coatlicuae* n. sp. typically have only 12 septa in two cycles, whereas corallites of the other species usually possess more than 12 septa (two cycles plus some septa of the third cycle). Furthermore, these additional septa are frequently inserted from the outer wall and they do not extend into the internal wall of the corallite.

Preverastraea tocae new species

Figure 31

Diagnosis. Corallum plocoid or subcerioid. Wall of corallite developed as single parathecal zone; outer corallite wall absent. CD 2.2-6 mm. Septa 12-24 in number and hexamerally arrayed in two to three cycles.

Description. Corallum colonial, attached, plocoid or subcerioid, massive, hemispherical, and costate. Colony formation by extratentacular budding.

Corallites generally cylindrical and closely spaced. Peripheral boundaries between adjacent corallites vaguely delineated. Corallites oriented radially with respect to shape of corallum, axes subparallel to each other. Calices well-defined and exclusively monocentric. Calicular margin circular to subcircular in outline. CD variable, most commonly about 5 mm, but as small as 2.2 mm on newly budded corallites and up to about 6 mm on largest corallites. Depth of calices about 1 mm. Calices spaced 1-2 mm apart, or about 6-10 mm between calicular centers.

Septa well-developed, exsert, laminar, solid, and structurally continuous as septocostae. Number of septa variable from 12 to 24 and directly related to diameter of calice. For examples: CD 3.5 mm, 12 septa; CD 5.0 mm, 14 septa; CD 5.5 mm, 22 septa. Septa hexamerally arrayed in at least two complete cycles with some of those of third cycle usually present also, but weakly developed. Size relationship among septa: $S_1 > S_2 >> S_3$. S_1 blade-shaped in cross section, straight, relatively thick, about 0.5 mm in width, tapered axially, and 2.0 mm in length (for CD of 5.0 mm) or about four-fifths distance from wall to corallite axis. S_2 usually wedge-shaped in cross section, their width about equal to that of S_1 at junction with wall, but their length only about half that of S_1 or about two-fifths distance from wall to corallite axis. S_3 very weakly developed, wedge- or blade-shaped in cross section, inserted peripherally along calicular margin, about 0.3 mm in width at junction with wall, and very short, usually less than 0.5 mm. Interseptal spaces between S_1 and S_2 about 0.5-0.7 mm, those between S_3 and adjacent septa slightly narrower. Synapticulae absent. Lateral surfaces of septa appear smooth except for numerous fusions with endothecal dissepiments. Septal margins smooth; inner edges laterally free orally, oriented vertically, and sometimes bifurcated at junctions with endothecal dissepiments. Pali absent.

Columella absent. Axial region delineated by vertically aligned inner edges of S_1, about 1.0 mm in diameter or approximately one-fifth CD, hollow orally, and occupied by endothecal dissepiments aborally.

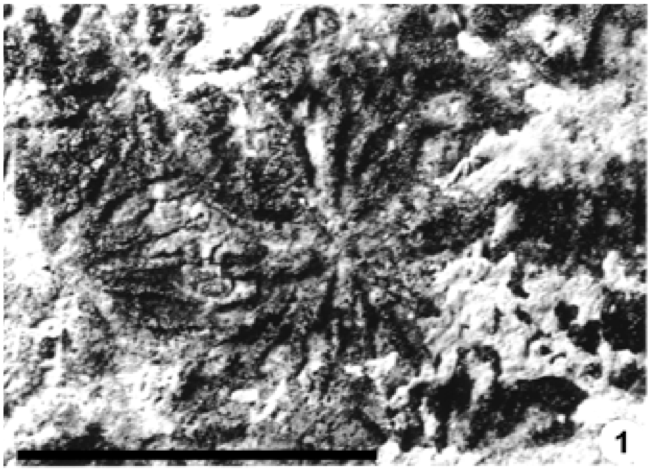
Wall weakly to moderately well-developed, parathecal, those of closely adjacent corallites laterally confluent as a common, shared mural structure about 1-2 mm in width. Parathecal dissepiments vesicular, thin, typically arched convex orally, 1-2 mm in width, and vertically spaced 0.5-1.0 mm apart. Endothecal dissepiments mostly tabular, abundant, laterally continuous, very thin, generally oriented concave orally across diameter of corallite, vertically spaced about 0.5 mm apart peripherally, and oriented subhorizontal and slightly more closely spaced axially. Exothecal dissepiments structurally similar to those of endotheca.

Costae robust, vertically continuous, and structurally continuous with septa. Width of costae equal to that of respective septa. Height of costae subequal, attenuated abaxially; C_1 up to 1 mm, those of subsequent cycles slightly lower. Width of intercostal furrows equal to that of interseptal spaces at junction with wall and widened distally toward peripheral margin of corallite. Costae of adjacent corallites typically nonconfluent or sometimes subconfluent.

Etymology. The species is named for Toci, an Aztec goddess of the Earth.

Types. Holotype IGM-7041, with two thin sections (M-18 and M-19); and paratype IGM-7042. The holotype is 70 x 120 mm in width and 90 mm in height, and the paratype is 90 x 130 mm in width and 60 mm in height. The holotype specimen is recrystallized, but internally the general morphology of the skeletal architecture is preserved well enough to permit a fairly complete description. The external morphology of the paratype corallum is badly weathered and internally the skeletal structure is thoroughly coarsely recrystallized.

The type stratum is the upper member of the Mal Paso Formation, upper Albian-lower Cenomanian. The type locality is in the state of Guerrero, just north of the border with the adjacent state of Michoacán, about 0.75 km north of the rural village of Chumbítaro, Michoacán. The coordinates of this locality, as determined from the Mexican 1:50,000 scale Coyuca de Catalán (E14A74) topographic map, are: 18° 29.3’ N, 100° 42.5’ W.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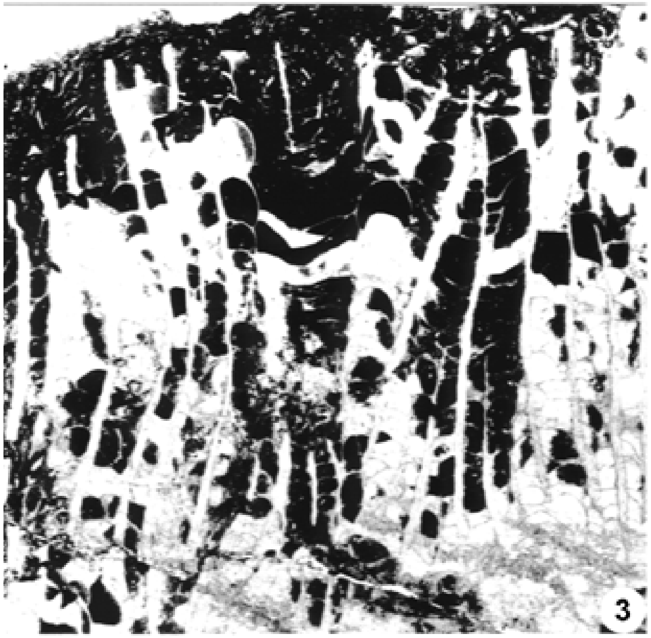
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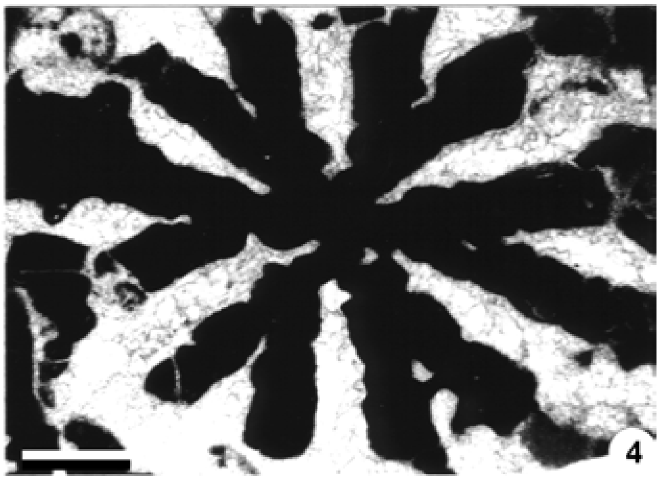
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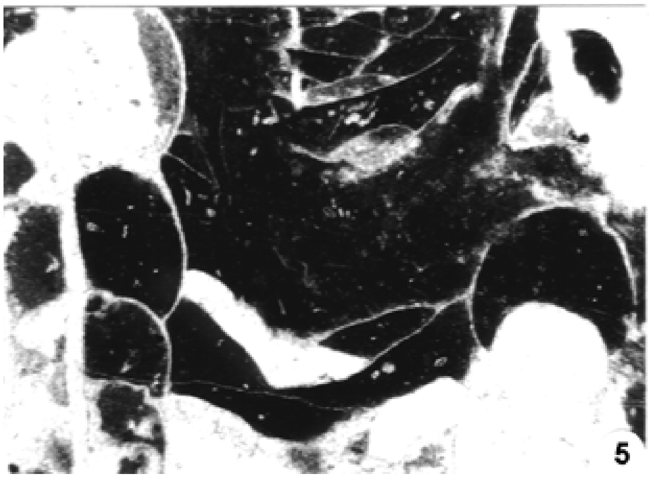
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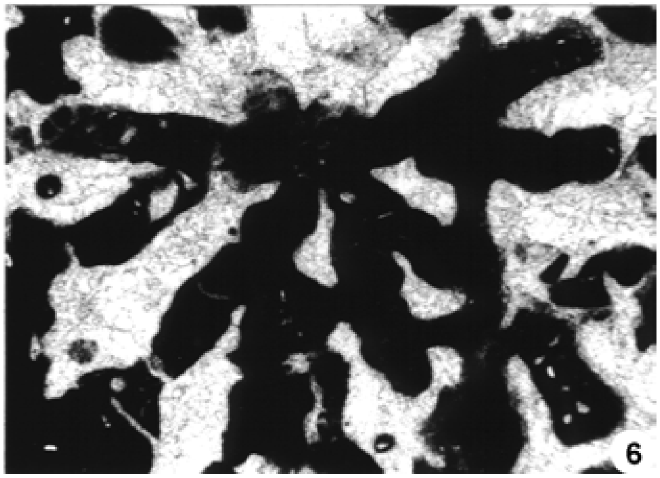
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Occurrence. Known only from the type locality. The coordinates of this locality are given above. The holotype corallum is from the coral reef horizon of the upper member of the Mal Paso Formation; the paratype corallum is from the lower portion of unit MP9, which is stratigraphically just below the reef horizon

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Discussion. This species is most similar to the species described earlier, *P. coatlicuae* n. sp. However, *P. tocae* n. sp. possesses corallites that are more closely spaced and the corallum tends to be less plocoid and more subcerioid. Additional differences include the variable and typically higher number of septa and the general lack of well-developed coenosteum. As with *P. coatlicuae* n. sp., corallites of *P. tocae* n. sp. also lack an outer wall. Refer to the discussion given for *P. coatlicuae* n. sp. for comment on wall structures of this genus.

Suborder Faviina Vaughan and Wells, 1943
Family Montlivaltiidae Dietrich, 1926
Genus *Latiphyllia* Fromentel, 1861

Latiphyllia Fromentel, 1861, p. 164; Wells, 1956, p. F399.
Glyphephyllia Fromentel, 1873, p. 463-465, pl. 96, figs. 1-1c, pl. 97, figs. 1, 1a, pl. 99, figs. 1-1b.

Type species. *Lobophyllia requienii* Michelin, 1841 (p. 18, pl. 4, fig. 6), by subsequent designation (Wells, 1936, p. 114).

***Latiphyllia mexicana* new species**
Figure 32

Diagnosis. Corallum typically phaceloid, flabellate, and relatively large in size. Calicular diameters larger than those of other members of genus: LCD typically 30-40 mm, GCD 45-125 mm. Costae laterally spaced 3-4 per 5 mm.

Description. Corallum colonial, attached, phaceloid, flabellate to meandroid, and costate. Each corallum composed of single laterally continuous flabellate series. Smaller, immature specimens solitary in appearance and conical or trochoid. Colony formation by polystomodaeal linear intratentacular budding.

Each corallite or series essentially comprises one corallum. Corallite (series) laterally compressed, cylindrical or flabellate in shape. Series laterally continuous, straight, gently curved or contorted, free-standing, and phaceloid in appearance. Calice monocentric (immature) through polycentric (mature series). Calicular margin circular (immature) to highly elliptical and contorted elliptical in outline. Depth of calice unknown.

Septa well-developed, non-exsert(?), laminar, irregularly porous, relatively thin, and structurally continuous with costae. Septa numerous, typically more than 100 in number in larger coralla, and arranged in five cycles. Size relationship among septa: $S_1=S_2\geq S_3>S_4>S_5$. Septa hexamerally arranged in smaller coralla, but bilaterally arranged in series of larger specimens due to mode of colony formation (intratentacular budding). Primary septa, those of first and second cycles, extend to axial region of corallum; septa of higher cycles shorter, extended from three-fourths to half distance form wall to axis. Septa blade-shaped in transverse cross section, generally straight or gently curved, and relatively thin, about 1 mm or less in thickness. Interseptal spaces typically wider than adjacent septa. Lateral surfaces of septa appear granulate or carinate. Synapticulae absent. Details of septal margins not observed. Pali absent. Columella absent; axis of corallum occupied by endothecal dissepiments and axial edges of larger septa.

Wall well-developed, parathecal, and relatively thick. Parathecal dissepiments vesicular, thin, convex oral-axially, laterally continuous with endothecal dissepiments, and vertically irregularly spaced about 1-2 mm apart. Endothecal dissepiments well-developed, abundant, vesicular, and similar in structure and spacing to those of paratheca.

Epitheca occasionally present, but very thin and both laterally and vertically discontinuous. Costae well-developed and comprised of distal terminations of septa.

Figure 31. *Preverastraea tocae* n. sp., holotype IGM-7041, upper member of the Mal Paso Formation, upper Albian-lower Cenomanian, about 0.75 km north of Chumbítaro, Michoacán, in the State of Guerrero, Mexico. 1, Detail of portion of weathered oral surface of corallum, scale bar = 1 cm; 2, transverse thin section of several corallites; note plocoid aspect of corallite arrangement and lack of secondary outer, same scale as Figure 31.1; 3, longitudinal thin section of upper portion of corallum; note well-developed parathecal wall of corallites and absence of outer wall, same scale as Figure 31.1; 4, transverse thin section, detail of corallite axis, septa, and parathecal wall, scale bar = 1 mm; 5, longitudinal thin section, detail of two parathecal walls and tabular to vesicular dissepiments, same scale as Figure 31.4; 6, transverse thin section, detail of bored(?) septa and parathecal wall, same scale as Figure 31.4.

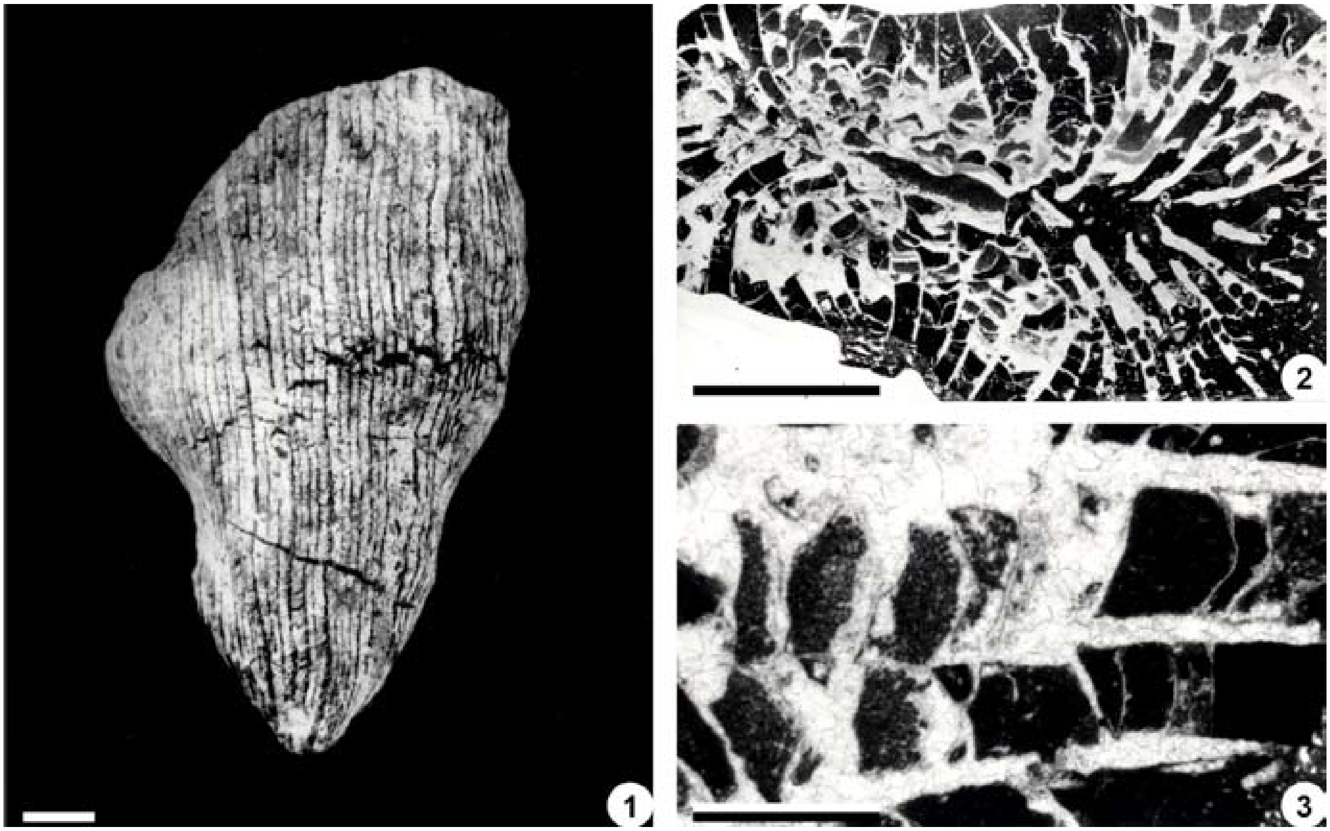

Figure 32. *Latiphyllia mexicana* n. sp., upper member of the Mal Paso Formation, upper Albian-lower Cenomanian, about 0.75 km north of Chumbítaro, Michoacán, in the State of Guerrero, Mexico. 1, Holotype IGM-7043, lateral (GCD) view of corallum, scale bar = 1 cm; 2, paratype IGM-7044, transverse thin section, scale bar = 1 cm; 3, same specimen, transverse thin section, detail of three septa and vesicular dissepiments of endotheca; axis of corallum toward left, wall of corallum toward right, scale bar = 1 mm.

Costae laterally spaced 3-4 per 5 mm. Intercostal furrows wider than costae and very shallow in depth.

Etymology. The species is named for the country of Mexico.

Types. Holotype IGM-7043; figured paratype IGM-7044, with one thin section (M-60); and 15 other paratypes, IGM-7045, IGM-7046, IGM-7047, IGM-7048, IGM-7049, IGM-7050, IGM-7051, IGM-7052, IGM-7053, IGM-7054, IGM-7055, IGM-7056, IGM-7723, IGM-7724, and IGM-7725. Measurements of the specimens are given in Table 1.

The type stratum is the upper member of the Mal Paso Formation, upper Albian-lower Cenomanian. The type locality is in the state of Guerrero, just north of the border with the adjacent state of Michoacán, about 0.75 km north of the rural village of Chumbítaro, Michoacán. The coordinates of this locality, as determined from the Mexican 1:50,000 scale Coyuca de Catalán (E14A74) topographic map, are: 18° 29.3’ N, 100° 42.5’ W.

All of the coralla are recrystallized and most of them are incomplete; the original oral surfaces and edges of calices are not preserved on the specimens. The depth of the calice or series is unknown because the actual calicular margins of the specimens are not preserved. The basal apexes of most of the coralla are also missing, but the lowermost preserved portions of a few of the specimens with missing apexes are sharply curved to one side. Borings of endolithic bivalves were observed in several of the specimens; most of these borings are nearly perpendicular to the surfaces of the host corals and they penetrate them from all sides. These latter two observations indicate that the growth position of the corals was an upright, phaceloid orientation and that the corals lived attached to some hard substrate.

Table 1. Measurements of *Latiphyllia mexicana* n. sp. coralla from the upper member of the Mal Paso Formation, state of Guerrero, Mexico. LCD = lesser calicular diameter; GCD = greater calicular diameter; H = height.

	Measurements (mm)		
Specimen	LCD	GCD	H
holotype			
IGM-7043	30	60	100
paratypes			
IGM-7044	30	50	120
IGM-7045	32	87	93
IGM-7046	32	81	115
IGM-7047	58	60	160
IGM-7048	50	107	124
IGM-7049	40	125	80
IGM-7050	30	46	61
IGM-7051	38	60	70
IGM-7052	32	100	90
IGM-7053	40	66	85
IGM-7054	38	60	60
IGM-7055	38	46	36
IGM-7056	32	55	102
IGM-7723	26	36	27
IGM-7724	38	65	75
IGM-7725	35	56	75

Occurrence. Known only from the type locality. The coordinates of this locality are given above. The majority of the specimens, including the holotype, were collected from the coral reef horizon in the upper member of the Mal Paso Formation. One of the paratypes was found stratigraphically below this horizon, in unit MP5, and another specimen was collected from a higher bed, unit MP17.

Discussion. The species described above possesses morphological characteristics that are different from those of the other Cretaceous members of the genus *Latiphyllia*. One of the most apparent distinguishing features of *L. mexicana* n. sp. is the relatively broader width or LCD of the series, typically 30-40 mm.

Latiphyllia sinuosa (Reuss, 1854), possesses series that are normally only 15 mm in width, although a maximum of 30 mm has been reported for one specimen (Hackemesser, 1936, p. 35). *Latiphyllia neocomiensis* Fromentel, 1873 (p. 461-462, pl. 111, figs. 1, 1a), possesses series that are relatively more narrow in width, 10-20 mm. The species of *Glyphephyllia* described by Fromentel (1873, p. 463-465), *G. dumortieri*, *G. flabellata*, and *G. excelsa*, possess narrow series, 6-8 mm, 10-14 mm, and 10-12 mm, respectively, whereas series of *L. mexicana* n. sp. are wider, most commonly 30-40 mm in width. *Glyphephyllia crassisepta* Hackemesser, 1936 (p. 37, pl. 5, figs. 1-2), is most morphologically similar to the Mexican species, but the series are typically more narrow, 25-35 mm in width. Some of the smaller coralla of *L. mexicana* n. sp. superficially resemble the genus *Montlivaltia* Lamouroux, 1821.

Genus *Thecosmilia* Milne Edwards and Haime, 1848b (p. 468)

Type species. *Lithodendron trichotomum* Goldfuss, 1826 (p. 45, pl. 13, fig. 6).

Thecosmilia guerreroensis new species

Figure 33

Diagnosis. Corallum relatively small for genus. Corallites monocentric, elongate, tapered aborally, and laterally free orally. CD 12-15 mm. Septa relatively few in number, typically 24, and arranged hexamerally in three cycles.

Description. Corallum colonial, attached, phaceloid and costate. Corallum of single, weathered specimen 7.5 x 5.0 cm in width, 9.0 cm in height, and comprised of portions of 17 corallites. Colony formation by extratentacular budding. Each branch of corallum composed of a single, elongate corallite. Branches arranged parallel or subparallel to each other.

Corallites conical, ceratoid, elongate, often slightly curved or scolecoid, and tapered aborally. Basal angle about 20-25 degrees. Corallites closely spaced, 0-5 mm apart, and sometimes in lateral contact, but not fused to each other. Corallites up to at least 8.5 cm in height, oral ends 12-15 mm in diameter, aboral ends as small as 4 mm. Calices exclusively monocentric. Calicular margins circular to subcircular in outline, CD 12-15 mm. Calices about 3-5 mm in depth with hollow central axial region.


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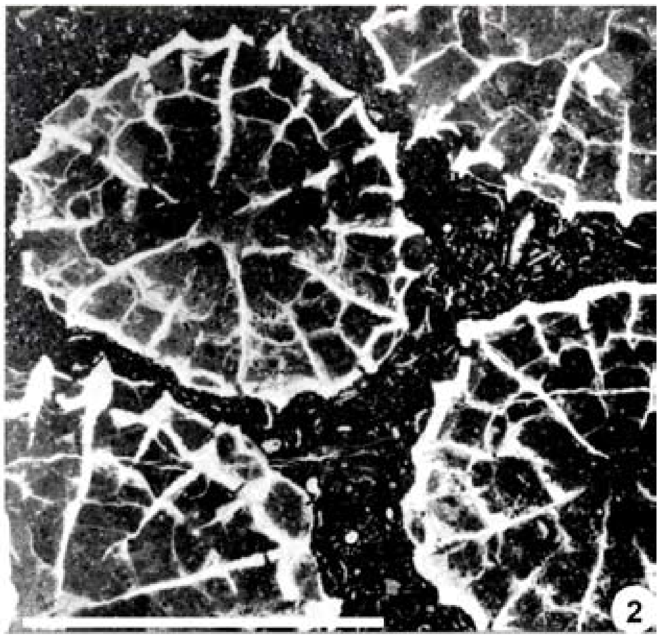
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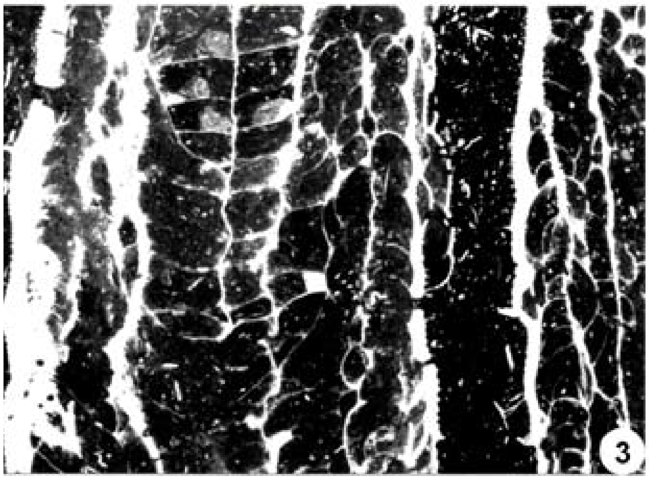
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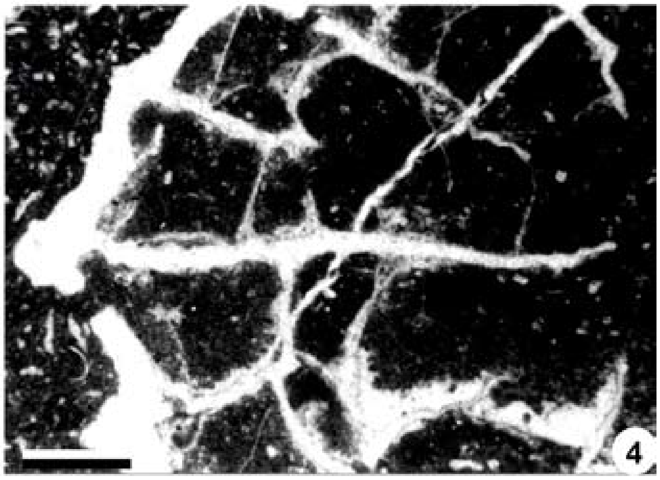
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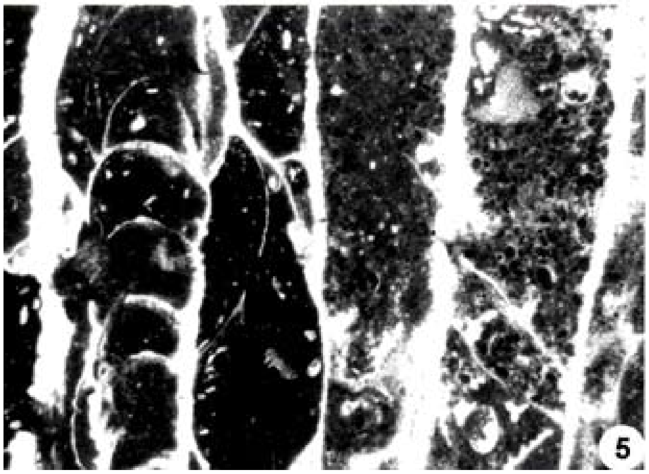
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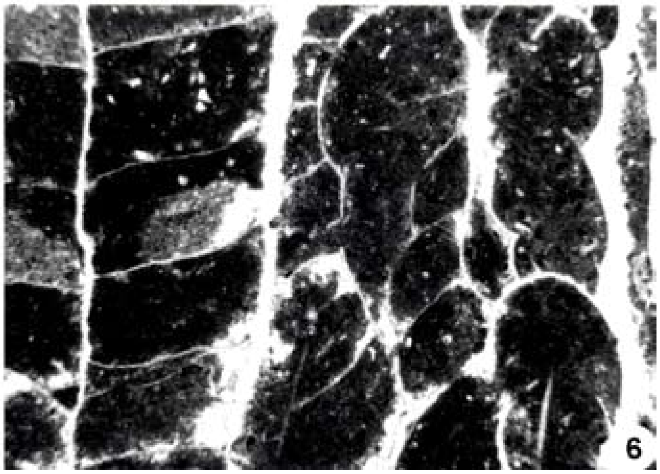
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Septa well-developed, weakly exsert, laminar, mostly solid and vertically continuous, with few sparsely distributed perforations of 0.2-0.5 mm diameter (some possibly borings?). Trabecular microstructure not preserved. About four trabeculae per mm along vertically oriented section of S_1. Septa structurally continuous with costae. Septa typically 24 in number and hexamerally arrayed in three cycles; some septa of fourth cycle occasionally present in larger calices (one with CD of 14 mm has 30 septa). Size relationship among septa: $S_1>S_2>S_3(>S_4)$. Septa blade-shaped in cross section and usually straight and laterally crenulate. S_1 about 0.2 mm in width and nearly half the CD in length. S_2 slightly thinner than S_1 and about one-fourth the CD in length, or half the distance from wall to corallite axis. S_3 slightly thinner than S_2 and about one-eighth the CD in length, or one-fourth the distance from wall to corallite axis. Interseptal spaces relatively wide, about 1 mm, or about five times width of adjacent septa. Synapticulae absent. Lateral surfaces of septa uneven, usually crenulate in appearance, possibly additionally disrupted by fusion of numerous endothecal dissepiments. Septal margins minutely granulated or dentate. Axial portions of septal margins laterally free except for connections to dissepiments.

Columella absent. Axial region often elliptical in cross section, approximately 0.5-2.0 mm in diameter as defined by vertically aligned inner margins of the six S_1, and hollow orally, but partitioned by numerous, subhorizontal, tabular endothecal dissepiments deep within calice and aborally.

Wall well-developed, mostly solid with few holes or perforations (some possibly borings?), about 0.3 mm in thickness. Wall structure appears primarily parathecal, but possibly also partly synapticulothecal or septothecal, occasionally with thin external layer of exothecal dissepiments. Endothecal dissepiments abundant and typically developed in two distinct zones: a peripheral zone of vesicular dissepiments (possibly parathecal in origin) about 1.5-2.0 mm in thickness, and a central zone of tabular dissepiments. Vesicular dissepiments of peripheral zone about 0.5-2.0 mm in width, convex orally and concave aborally in vertical cross section view, and vertically spaced 0.5-1.5 mm apart. Distal or outermost portion of vesicular zone possibly incorporated into wall structure. Tabular dissepiments of central zone generally oriented concave oral-axially and nearly horizontal axially. Tabular dissepiments mostly laterally continuous and vertically spaced about 1 mm apart. Proximal or innermost boundary of vesicular zone with central tabular zone appears in transverse cross section as a semicontinuous ring or pseudotheca positioned concentrically 1.5-2.0 mm within true outer wall. Boundary between peripheral vesicular and central tabular endothecal zones typically coincident with, and fused to, inner septal margins of S_3. Outer zone of exothecal dissepiments, similar in structure to that of vesicular endothecal zone, sometimes present on aboral areas of corallum.

Costae typically well-developed, subequal, wedge-shaped in cross section, and structurally continuous with septa. Costae wider than septa, about 1 mm in width and 1 mm in height; crests of costae normally sharp and laterally spaced 1.5-2.0 mm apart. Intercostal furrows about 1 mm in width, 1 mm in depth, and usually concave or nearly flat, but sometimes partially filled by exothecal dissepiments and convex, or entirely covered by dissepiments. Surfaces of costae appear granulated in some cross section views, about 6-7 granules per mm vertically. Outer surface of corallum mostly smooth or finely granulated in similar manner.

Etymology. The species name is derived from the Mexican state of Guerrero, where the type specimen was found, by adding the Latin suffix *-ensis* = place.

Types. Holotype IGM-7726, with two thin sections (M-24 and M-25). The specimen is a weathered part of a corallum which exhibits portions of at least 17 corallites. The type stratum is the upper member of the Mal Paso Formation, upper Albian-lower Cenomanian. The type locality is in the state of Guerrero, just north of the border with the adjacent state of Michoacán, about

Figure 33. *Thecosmilia guerreroensis* n. sp., holotype IGM-7726, upper member of the Mal Paso Formation, upper Albian-lower Cenomanian, about 0.75 km north of Chumbítaro, Michoacán, in the State of Guerrero, Mexico. 1, Lateral view of weathered surface of corallum in limestone matrix, scale bar = 1 cm; 2, transverse thin section, scale bar = 1 cm; 3, longitudinal thin section, one corallite in left three-fourths of figure and a portion of another corallite along right margin; note outer layer of epitheca along left margin, same scale as Figure 33.2; 4, transverse thin section, detail of S_1 and two smaller adjacent S_3, scale bar = 1 mm; 5, longitudinal thin section of half of one corallite, detail of vesicular parathecal dissepiments, wall, and outer layer of epitheca on left of figure, axis of corallite toward right, same scale as Figure 33.4; 6, longitudinal thin section of half of one corallite, detail of vesicular parathecal dissepiments and wall on right of figure, tabular endothecal dissepiments in axial region of corallite on left of figure, same scale as Figure 33.4.

0.75 km north of the rural village of Chumbítaro, Michoacán. The coordinates of this locality, as determined from the Mexican 1:50,000 scale Coyuca de Catalán (E14A74) topographic map, are: 18° 29.3' N, 100° 42.5' W.

Occurrence. Known only from the type locality. The coordinates of this locality are given above. The single specimen was found in float debris on unit MP10, but it may have been derived from unit MP11; both units are a few meters stratigraphically below the coral reef horizon in the upper member of the Mal Paso Formation.

Discussion. *Thecosmilia guerreroensis* n. sp. differs from the other members of *Thecosmilia* that have been reported from the Cretaceous of Mexico, Texas, and Venezuela. Two species, *Thecosmilia tobleri* Koby, 1897 (p. 38, pl. 13, figs. 1-4) and *T. oaxaquensis* Reyeros, 1983 (p. 24, pl. 11, fig. 2, pls. 12-14), have been described from the Albian-Cenomanian age Teposcolula Limestone at Coixtlahuaca, state of Oaxaca, Mexico (Reyeros, 1983, p. 24, pls. 11-14). The Mexican specimen of *T. tobleri* (IGM-2725) primarily differs from *T. guerreroensis* n. sp. by the wider branches (corallites) that range from 14-20 mm in diameter and the more numerous septa, as many as 48, in four complete cycles. The other species from Oaxaca, *T. oaxaquensis* (IGM-2726 through IGM-2729), primarily differs from *T. guerreroensis* n. sp. by the narrower branches (corallites) that range from 6-9 mm in diameter. Another species of *Thecosmilia*, *T. bassanii* Prever, 1909 (p. 80-81, text fig. 6, pl. 3, fig. 6), from the middle Albian strata of the Espinazo del Diablo Formation in the Lampazos area of the state of Sonora, Mexico (Baron-Szabo and González-León, 1999, p. 472, fig. 2f), mainly differs from *T. guerreroensis* n. sp. by the narrower monocentric corallites that range from 7-11 mm in diameter and the more abundant septa, from 30 to 40 in number.

Thecosmilia(?) sp. Wells (1932, p. 240-241, pl. 30, fig. 3), from the upper Aptian lower Glen Rose Formation on Blanco River, Hays County, Texas, has corallites that are about the same diameter as those of *T. guerreroensis* n. sp., but at least twice as many septa, about 60, are present, half of which reach the axis of the corallite.

Two species of *Thecosmilia* have been reported from the Lower Cretaceous upper Barranquín Formation of northeastern Venezuela: *T. tobleri* Koby, 1897, discussed above, from Port Pirítú, state of Anzoátegui (Gregory, 1927, p. 440), and *T. cumanensis* Wells, 1944b (p. 441, pl. 71, fig. 2, pl. 73, figs. 4-7, pl. 74, fig. 1), from Las Cinco Ceibas, state of Sucre. The latter species primarily differs from *T. guerreroensis* n. sp. by the narrower corallites (branches) that range from 6-8 mm in diameter and the more numerous septa, from 36 to 48 in number.

Genus *Elasmophyllia* d'Achiardi, 1876

Elasmophyllia d'Achiardi, 1876, p. 149; Vaughan and Wells, 1943, p. 161; Alloiteau, 1952, p. 614; Wells, 1956, p. F400.

Type species. *Elasmophyllia gigantea* d'Achiardi, 1876 (p. 149-150, pl. 8, figs. 4a-c, pl. 9, fig. 1).

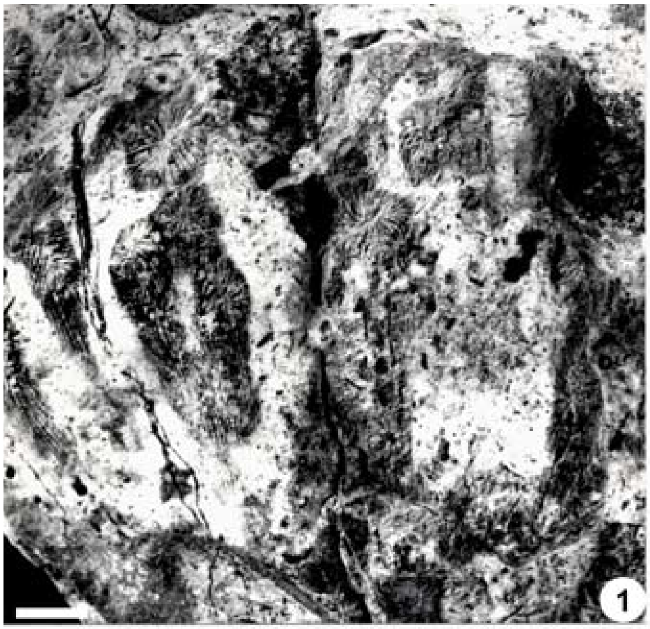
Elasmophyllia tolmachoffana (Wells, 1932)
Figure 34

Aplosmilia (?) *tolmachoffana* Wells, 1932, p. 234, pl. 30, fig. 2, pl. 31, fig. 2.

Elasmophyllia tolmachoffana (Wells, 1932). Hedberg and Pyre, 1944, p. 7; Wells, 1944b, p. 442, pl. 72, figs. 6, 7, 8; Wells, 1948, p. 616, pl. 91, figs. 1, 2; (?)Reyeros, 1983, p. 25-26, pl. 15, figs. 1, 2, 3, pl. 16, figs. 1, 2.

Description. Corallum colonial, attached, phaceloid and weakly costate. Shape of corallum mound-like and low, width generally greater than height. Dimensions of two coralla (length, width, height): 17 x 10 x 8 cm, and 14 x 9 x 12 cm. Upper surface as defined by oral ends of corallites overall generally convex. Colony formation by di- or tristomodaeal intratentacular budding with direct, lamellar linkages.

Figure 34. *Elasmophyllia tolmachoffana* (Wells, 1932), IGM-7727, upper member of the Mal Paso Formation, upper Albian-lower Cenomanian, about 0.75 km north of Chumbítaro, Michoacán, in the State of Guerrero, Mexico. 1, Lateral view of weathered surface of corallum in limestone matrix, scale bar = 1 cm; 2, transverse thin section of two adjacent corallites, scale bar = 1 cm; 3, longitudinal thin section, section through corallite on left positioned more centrally, that of corallite on right positioned more tangentially, same scale as Figure 34.2; 4, transverse thin section, detail of columella and septa in axial region of corallite, scale bar = 1 mm; 5, transverse thin section, detail of septa and dissepiments in peripheral region of corallite, same scale as Figure 34.4; 6, transverse thin section, detail of columella, septa, and dissepiments, same scale as Figure 34.4.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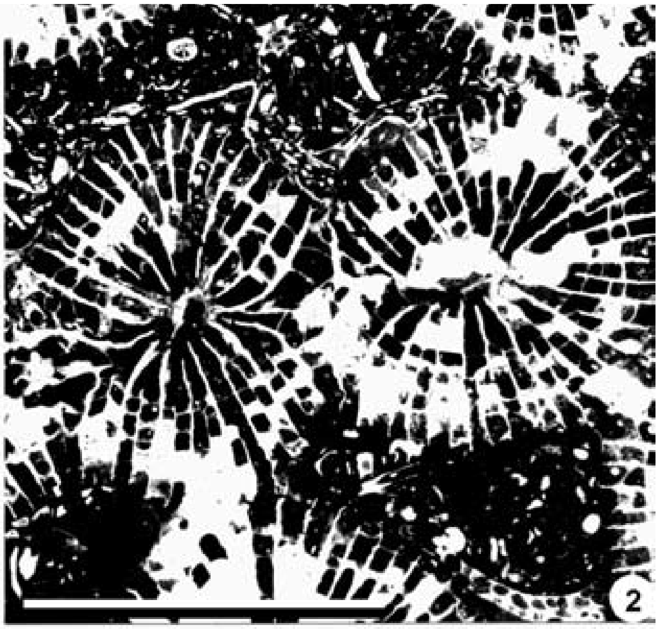
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Branches subparallel, radially arrayed, cylindrical to flabellate, and vertically elongate. Each branch length composed of a single vertically continuous corallite. Branches frequently bi- or trifurcated to form new branches. New branches formed at low angle to parent branch, about 15-25 degrees, and usually laterally connected to the parent for as much as several cm vertically. Diameter of cylindrical branches typically 8-12 mm, but as small as 6 mm on newly budded offshoots and up to at least 15 mm on mature branches. Larger diameter of laterally fused, elongate, or flabellate branches typically greater than that of cylindrical branches, up to 30 mm. Branches laterally spaced 0-10 mm apart.

Corallites generally cylindrical to flabellate, straight, laterally free or fused with parent corallite, and frequently bi- or trifurcated to form new branches. Dimensions and arrangement of corallites the same as those given for the branches. Calices mono-, di-, or tricentric. Calicular margin of monocentric calices circular, subcircular or elliptical in outline, CD 6-15 mm. GCD of di- or tricentric calices usually larger, up to 24 mm for a dicentric calice in process of budding. Calice concave orally, about 1-2 mm in depth at center.

Septa well-developed, weakly exsert, laminar, primarily solid with few, sparsely distributed, irregular perforations or discontinuities. Trabecular architecture not preserved. Number of septa variable and directly related to diameter and development of calice. For examples: monocentric calices, CD 6 mm, 30 septa; CD 7 x 8 mm, 38 septa; CD 11 mm, 50 septa; CD 12 mm, 64 septa; and a tricentric calice, CD about 12 x 12 mm, 80 septa. Septa generally hexamerally arrayed and inserted in from three to five cycles, the latter usually weakly developed and incomplete when present. Size relationship among septa: $S_1 \geq S_2 > S_3 > S_4 > S_5$. S_1 and S_2 blade-shaped in cross section, about 0.1 mm in width, tapered axially, and extend from wall to perimeter of axial region, or to about 0.5 mm from corallite axis. S_3 similar to S_1 and S_2, only slightly thinner and shorter. S_4 thinner and much shorter than S_3, their length equal to about half the distance to the axis. S_5, when present, weakly developed and peripheral, the cycle typically incomplete. Width of interseptal spaces relatively wide, from 2 to 4 times width of adjacent septa. Synapticulae absent. Lateral surfaces of septa granulated, uneven or carinate, possibly in part due to lateral fusions with abundant endothecal dissepiments. Septal margins appear smooth or uneven to finely dentate orally. Inner edges of septal margins typically laterally free, although commonly one or two of the axially opposed, parallel S_1 appear structurally continuous with the lamellar columella. Peripheral edges of septa continuous into wall zone.

Columella weakly developed, laminar, vertically discontinuous, often oriented length parallel to, and often in structural continuity with, one or two of the axially opposed S_1. Columella approximately 0.1 mm in width, or about equal to width of proximal portion of primary septa, and usually about one-fifth the CD in length. Axial region of corallite typically clearly delineated by spaces between proximal edges of septa (S_1-S_3) and columella.

Wall primarily parathecal and secondarily weakly epithecal. Parathecal wall zone 1.2-2.0 mm thick. Parathecal dissepiments vesicular, arched convex orally, and vertically spaced 1-2 per mm. Endothecal dissepiments abundant, tabular, laterally continuous, arched slightly concave orally, oriented nearly horizontal axially, and vertically spaced 1-2 per mm. Epitheca weakly developed, thin and discontinuous. Weathered surface of corallum appears striate or weakly costate.

Material examined. Three coralla: the described corallum, IGM-7727, with three thin sections (M-29 through M-31); IGM-7728; and IGM-7729, with one thin section (M-32), a colony from unit MP17.

Occurrence. The upper member of the Mal Paso Formation, upper Albian-lower Cenomanian. The locality is in the state of Guerrero, just north of the border with the adjacent state of Michoacán, about 0.75 km north of the rural village of Chumbítaro, Michoacán. The coordinates of this locality are: 18° 29.3’ N, 100° 42.5’ W. This species is common in the coral reef horizon, unit MP13. One corallum was collected from unit MP17.

This species was originally described from the lower Albian of the lower Glen Rose Formation, Texas (Wells, 1932, p. 234), and subsequently reported from the upper Barranquín Formation, Venezuela (Wells, 1944b, p. 442), the Lower Cretaceous of the Central Range, Trinidad (Wells, 1948, p. 616), and possibly the middle Cretaceous of Oaxaca (Reyeros, 1983, p. 26).

Discussion. The morphological characteristics of the examined coralla, except for the width of interseptal spaces (from 2 to 4 times width of adjacent septa), are well within the range of those described for *Elasmophyllia tolmachoffana* (Wells, 1932) and therefore the specimens are referred to that species.

The specimens described by Reyeros (1983, p. 25-26), IGM-2731 (pl. 15, fig. 1) and IGM-2730 (pl. 15, figs. 2, 3, pl. 16, figs. 1, 2), exhibit an atypical, heterogeneous morphology and thus they are doubtfully referred to this species. Specimen IGM-2731, based on the single, lateral view (pl. 15, fig. 1) of a partially exposed branch in matrix, possesses corallites with diameters that range from 2.1 to 4.7 mm, a range that is much smaller than that typically described for this species. The other specimen, IGM-2730, is one sample with several cross sections of corallites exposed; all of these corallites probably do not belong to the same species, nor even the same genus. The specimen shown in plate 15, figure 2, is a weathered longitudinal section of a branch with a diameter, if the indicated magnification of x 8 is correct, of 2.5-3.1 mm. The weathered transverse section of the corallite shown in plate 15, figure 3, has a CD of 5-5.75 mm, 46 septa, costae, and lacks a columella. The corallites shown in plate 16, figures 1 and 2, are morphologically very different from each other. Plate 16, figure 1, is a transverse section view of a corallite with a diameter of about 7.5 mm (not 6.7 mm, as calculated from the 43 mm diameter measured from the figure at a supposed magnification of x 6.4) and with about 50 septa, robust costae, few endothecal dissepiments, and no columella. Plate 16, figure 2, is a slightly oblique transverse section through two corallites with diameters of about 6.5 mm (not 5 mm, as calculated from the 32 mm diameters measured from the figure at a supposed magnification of x 6.4) and with about 38 septa, but no costae, and with some endothecal dissepiments and a well-developed trabecular columella. As indicated above, all of these morphological features cannot be attributed to *Elasmophyllia tolmachoffana* (Wells, 1932), and thus the assignment of these specimens to this species seems doubtful.

Genus *Mycetophyllopsis* Oppenheim, 1930

Mycetophyllopsis Oppenheim, 1930, p. 377-379, pl. 16, figs. 4, 4a; Vaughan and Wells, 1943, p. 160, pl. 25, fig. 10; Alloiteau, 1952, p. 612; Wells, 1956, p. F399, fig. 294,3.

Type species. *Mycetophyllia antiqua* Reuss, 1854 (p. 104-105, pl. 23, fig. 9).

Diagnosis. Corallum meandroid. Columella absent. Ambulacrum absent. Series laterally united by low, shared parathecal wall.

Mycetophyllopsis azteca new species

Figure 35

Diagnosis. Corallum meandroid, series relatively few in number. Septa relatively thin with wide interseptal spaces.

Description. Corallum colonial, attached, possibly pedunculate, meandroid, massive, inverted conical, laterally elongate, weakly costate, and comprised of relatively few series. Colony formation by polystomodaeal intratentacular budding with direct, lamellar linkages.

Corallites conical to flabellate, often in linear series and laterally elongate, and oriented upward from base of colony. Series typically discontinuous, linear, and separated from adjacent series by low colline formed by shared wall. Collines typically continuous, very weakly developed, and relatively low in height with broadly rounded, septocostate, upper surfaces. Ambulacrum absent.

Series (calices) typically polycentric, rarely di- or monocentric. Calicular margins elliptical to flabellate, but most commonly highly laterally elongate in outline. CD of series variable, from about 12 mm in width (or LCD) x 25 mm in length (or GCD) to at least as large as 30 mm x 80 mm. Calice relatively shallow, only about 1-2 mm in depth. Collines typically narrow orally, about 2-4 mm in width, and broadened aborally. Distance between centers of laterally adjacent series about 10-20 mm.

Septa well-developed, weakly exsert, laminar, primarily solid, relatively thin, and peripherally continuous as septocostae. Number of septa variable, usually abundant within series, and commonly arrayed radially around each calicular center. Symmetry of septal arrangement and actual number of septal cycles obscured by polystomodaeal intratentacular fusion within series. However, based on different sizes of septa, at least three cycles appear to be developed. Apparent size relationship among septa: $S_1 \geq S_2 > S_3$. S_1 laminar to blade-shaped in cross section, straight or gently curved, and relatively thin, only about 0.2 mm in width. Length of S_1 usually slightly less than half CD. S_2 similar to S_1 in every respect except often slightly shorter in length. S_3, or those of higher cycles, structurally similar to

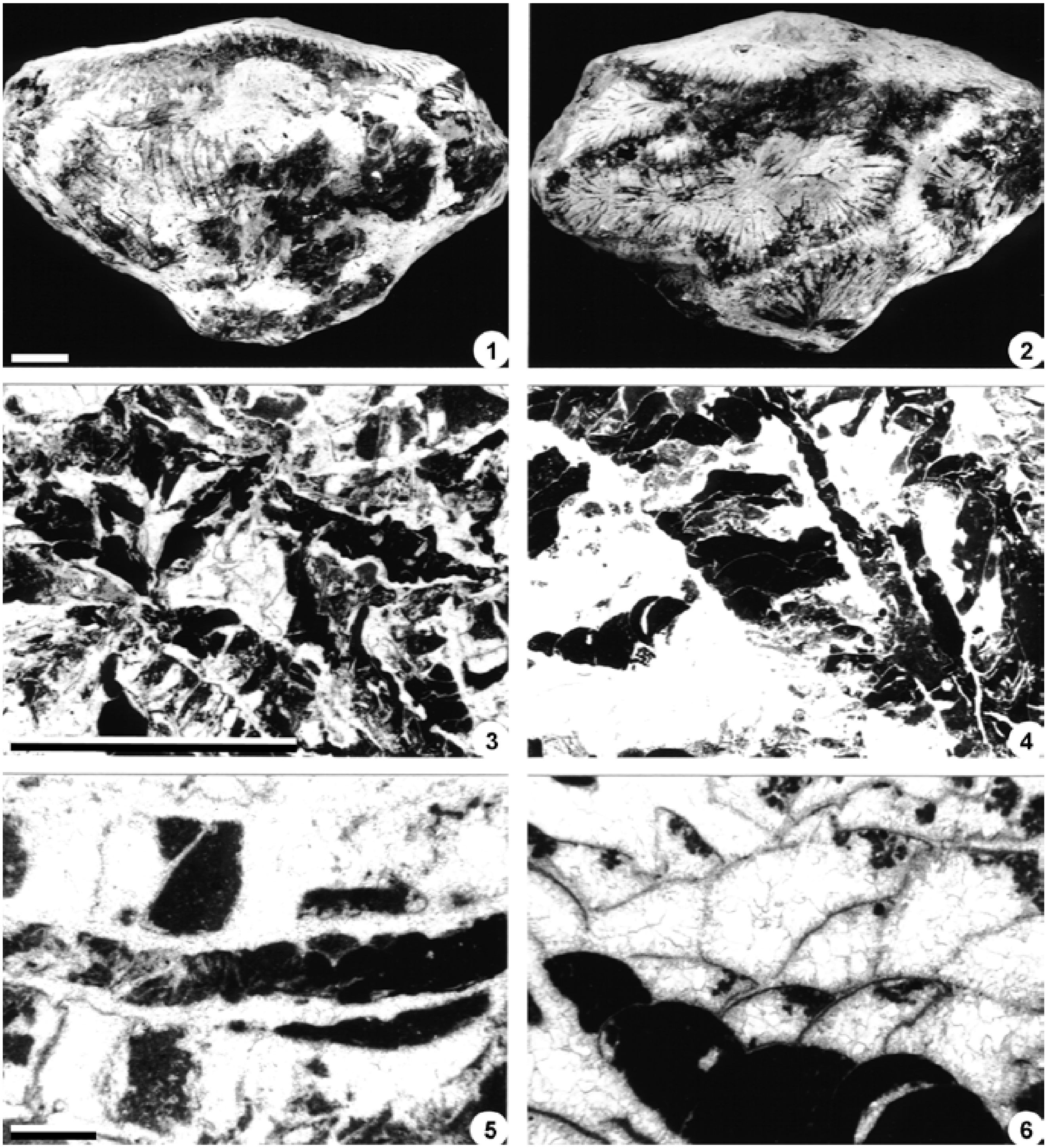


Figure 35. *Mycetophyllopsis azteca* n. sp., upper member of the Mal Paso Formation, upper Albian-lower Cenomanian, about 0.75 km north of Chumbítaro, Michoacán, in the State of Guerrero, Mexico. 1, Holotype IGM-7730, lateral view of corallum, scale bar = 1 cm; 2, same specimen, oral view of corallum, same scale as Figure 35.1; 3, paratype IGM-7731, transverse thin section, septa of parts of two calicular centers, scale bar = 1 cm; 4, same specimen, longitudinal thin section, vesicular dissepiments of endotheca and paratheca, same scale as Figure 35.3; 5, same specimen, transverse thin section, detail of septa, partially recrystallized, scale bar = 1 mm; 6, same specimen, longitudinal thin section, detail of vesicular dissepiments of paratheca, same scale as Figure 35.5.

those of previous cycles, usually weakly developed, inserted peripherally along series margin, and very much shorter than S_2. Lamellar linkages between calicular centers within series typically consist of 3-5 septa of first or second cycles aligned parallel with each other in a zone about 3-4 mm in width. Synapticulae absent. Interseptal spaces relatively broad, about 1 mm in width or about five times width of adjacent septa. Lateral surfaces of septa primarily smooth but often broadly undulated or carinate in appearance due to numerous fusions with endothecal dissepiments. Septal margins beaded orally from terminations of septal trabeculae; beads spaced about 4 per mm along upper margins. Inner edges of septa usually laterally free except for fusions with dissepiments.

Columella absent. Axial region about 2 mm in diameter, or about one-tenth LCD, hollow orally, and often occupied by endothecal dissepiments and occasionally some S_1 or S_2 aborally.

Wall parathecal and relatively thick, those of laterally adjacent series invariably fused into a common, confluent, shared mural structure about 5-7 mm in width. Parathecal dissepiments irregularly shaped, vesicular to somewhat laterally continuous and tabular in appearance, and vertically spaced about 0.5-1.0 mm apart. Endothecal dissepiments abundant and structurally similar to, and continuous with, those of parathecal wall.

Costae weakly developed, subequal, structurally continuous with septa, and laterally spaced about 1 mm apart, or about 3-5 costae per 5 mm. Costae of adjacent series usually either confluent or subconfluent. Epitheca weakly developed when present and both vertically and laterally discontinuous.

Etymology. The species is named for the ancient people of Mexico, the Aztec.

Types. Holotype IGM-7730; paratype IGM-7731, with two thin sections (M-11 and M-12); and paratype IGM-7732. Measurements of these specimens are given in Table 2.

The type stratum is the upper member of the Mal Paso Formation, upper Albian-lower Cenomanian. The type locality is in the state of Guerrero, just north of the border with the adjacent state of Michoacán, about 0.75 km north of the rural village of Chumbítaro, Michoacán. The coordinates of this locality, as determined from the Mexican 1:50,000 scale Coyuca de Catalán (E14A74) topographic map, are: 18° 29.3' N, 100° 42.5' W.

Table 2. Measurements of *Mycetophyllopsis azteca* n. sp. coralla from the upper member of the Mal Paso Formation, state of Guerrero, Mexico. The basal portion of the second paratype is not preserved.

	Measurements (mm)		
Specimen	width	length	height
holotype			
IGM-7730	53	95	56
paratypes			
IGM-7731	60	90	50
IGM-7732	57	92	38

Occurrence. Known only from the type locality. The coordinates of this locality are given above. The type specimens were collected from the coral reef horizon of the upper member of the Mal Paso Formation.

Discussion. Only two species of *Mycetophyllopsis* are known, the type species *Mycetophyllopsis antiqua* (Reuss, 1854), and the species described herein as new. *Mycetophyllopsis azteca* n. sp. primarily differs from the type species by the less robustly developed septa and the relatively wider interseptal spaces. The sizes of the coralla of these two species are remarkably similar based on comparison of the material examined herein and the measurements of the type specimen, 68 x 90 mm in width and 52 mm in height, given by Oppenheim (1930, p. 378).

Suborder Astreoina Alloiteau, 1952

Family Faviidae Gregory, 1900

Discussion. Refer to the discussion of this family given in the first part of the section on systematic paleontology.

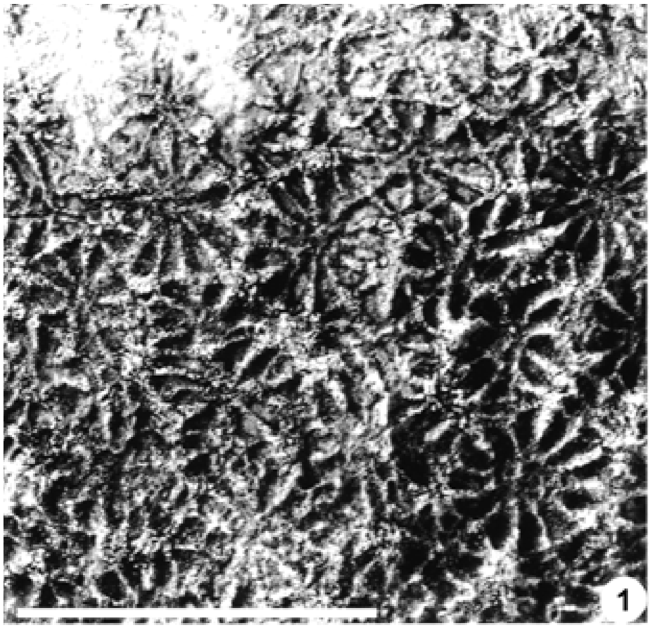
Genus *Eohydnophora* Yabe and Eguchi, 1936

Type species. *Eohydnophora tosaensis* Yabe and Eguchi, 1936 (p. 142-143, figs. 1-3).

Eohydnophora picteti **(Koby, 1897)**

Figure 36

Hydnophora picteti Koby, 1897, p. 45, pl. 8, figs. 1-2; de Angelis d'Ossat, 1905c, p. 26-27, pl. 2, figs. 1-2;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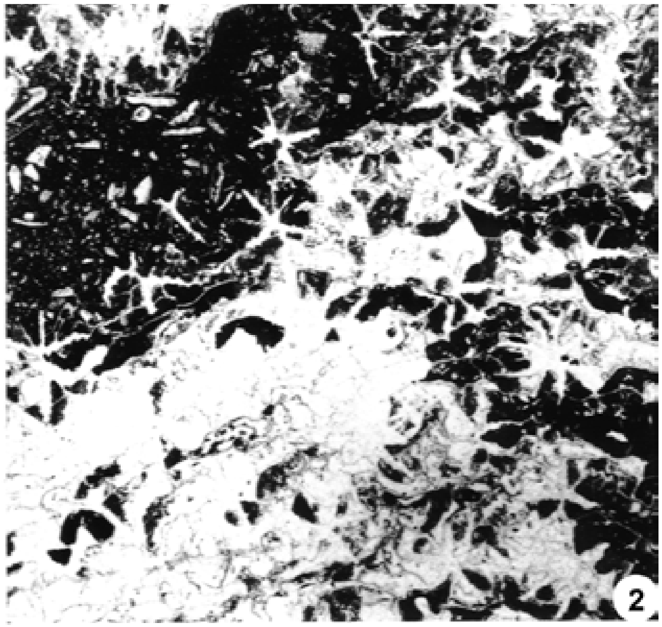
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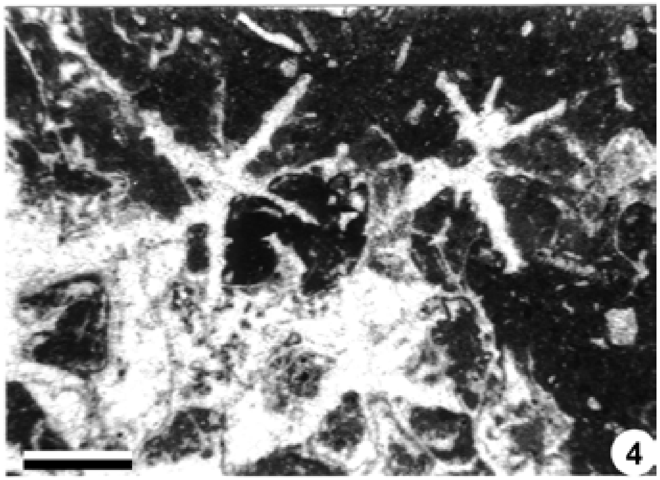
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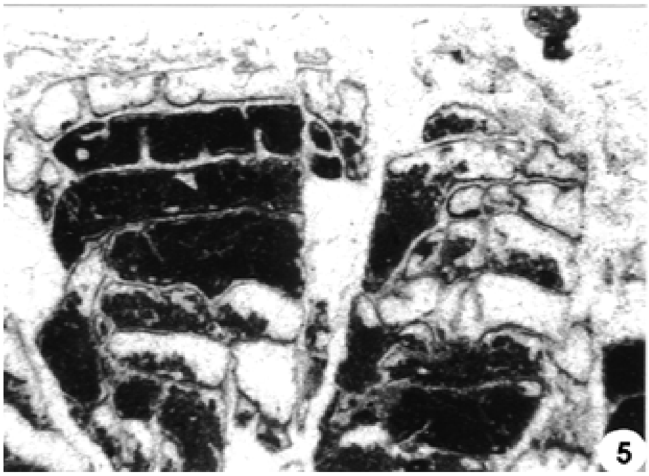
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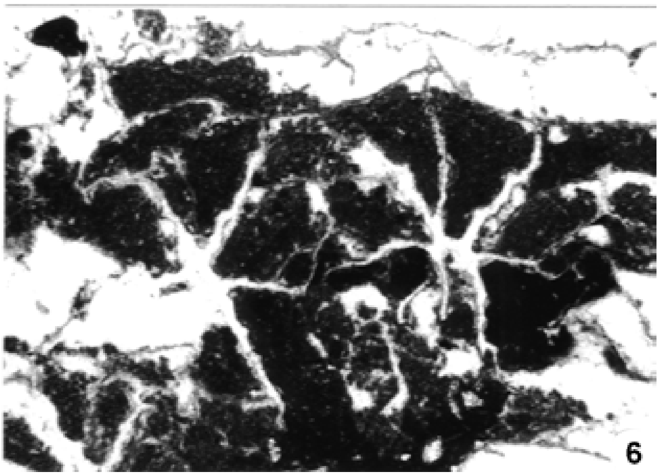
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?Prever, 1909, p. 83-84, pl. 27, fig. 3; Kochansky-Devidé, 1951, p. 107; Marković, 1951, p. 189, pl. 4, figs. 2a-b.

Felixigyra sp. ind. 1 Morycowa, 1964, p. 53-54, pl. 9, fig. 4, pl. 10, fig. 6, text fig. 8.

Felixigyra sp. Morycowa and Lefeld, 1966, p. 528-529, pl. 32, fig. 6a-b.

Felixigyra picteti (Koby, 1897). Scott, 1990, p. 13-16, 31, 40, fig. 10G.

Eohydnophora picteti (Koby, 1897). Eguchi, 1951, p. 14, pl. 2, fig. 7; Morycowa, 1971, p. 65-66, pl. 13, fig. 1; Turnšek and Buser, 1974, p. 95, 113-114, pl. 5, figs. 3-4; Turnšek and Buser, 1976, p. 50, 75, pl. 4, figs. 3-6; Turnšek and Mihajlović, 1981, p. 18, pl. 12, figs. 4-6; Morycowa, 1984, p. 83, pl. 21, figs. 1-2; Morycowa, 1989, p. 63, pl. 22, figs. 1-2; Morycowa and Decrouez, 1993, p. 206-207, pl. 1, figs. 3-4; Masse and Morycowa, 1994, p. 435-438, pl. 1, figs. 1-5, text fig. 3; Abdel-Gawad and Gameil, 1995, p. 16, pl. 13, figs. 7-9; Turnšek, 1997, p. 86, pl. 86, figs. A-G.

Description. Corallum colonial, attached, hydnophoroid, massive to ramose, non-costate, and relatively small in size. Branches cylindrical or lath-shaped. Corallites laterally weakly interconnected, valleys relatively short, shallow, and superficially confluent; walls relatively short and discontinuous.

Series (calices) superficially continuous, confluent orally, relatively shallow, about 1.2-3.0 mm in width and 1.0-1.5 mm in depth, with gently sloped sides. Collines discontinuous and slightly protuberant; shape variable from equant, acutely asteriform to laterally elongate. Collines relatively narrow, typically about 0.2-0.5 mm in width, usually very short, 0.5-1.8 mm in length, and 1.0-1.5 mm in height. Collines generally ridge-like with rounded crests. Colony formation by circummural polystomodaeal intratentacular (hydnophoroid) budding. Calices superficially confluent, polycentric, the dimensions the same as those given for the series.

Septa well-developed, non-exsert, laminar, and solid. Septa arrayed perpendicular to calicular centers and radially from collines; septal symmetry within series not apparent. Septa numerous, mostly equal, and extended nearly entire distance from colline to center of series. Distinct cycles of septa indiscernible, but a few weakly developed septa may belong to a secondary cycle. Septa laminar to slightly blade-shaped in cross section, usually straight, and laterally spaced about 3 per 2 mm of colline length. Septa slightly thicker near junction with colline, about 0.15-0.4 mm in width, and gently tapered axially. Septa commonly about 1.0-1.8 mm in length. Lateral surfaces of septa slightly uneven. Upper septal margins smooth; inner edges not observed. Pali and columella absent.

Wall septothecal, solid, laterally discontinuous, relatively thin, about 0.2-0.5 mm in width, and structurally equivalent to colline. Endothecal dissepiments primarily tabular, thin, and vertically spaced about 5 per 2 mm. Exothecal dissepiments within collines absent. Costae absent, septa structurally confluent into collines.

Material examined. Three fragments of coralla: IGM-7733, a fragment of a lath-shaped branch 50 x 20 mm in width and 60 mm in height, the surface of which is shown in Figure 36.1; IGM-7734, a fragment of a cylindrical branch 50-60 mm in diameter and 80 mm in height, with two thin sections (M-46 and M-47); and IGM-7735, a small fragment of a branch about 35 x 25 mm in width and 45 mm in height. The skeletal material is recrystallized and the microstructure is not preserved.

Occurrence. The upper member of the Mal Paso Formation, upper Albian-lower Cenomanian. The locality is in the state of Guerrero, just north of the border with the adjacent state of Michoacán, about 0.75 km north of the rural village of Chumbítaro, Michoacán. The coordinates of this locality are: 18° 29.3' N, 100° 42.5' W. The few specimens of this species were found in the coral reef horizon, thus it probably was an uncommon component of the reef biota.

Figure 36. *Eohydnophora picteti* (Koby, 1897), upper member of the Mal Paso Formation, upper Albian-lower Cenomanian, about 0.75 km north of Chumbítaro, Michoacán, in the State of Guerrero, Mexico. 1, IGM-7733, detail of weathered oral surface of corallum fragment, scale bar = 1 cm; 2, IGM-7734, transverse thin section, corallum recrystallized, same scale as Figure 36.1; 3, same specimen, longitudinal (upper half of figure) and oblique longitudinal (lower half of figure) thin section, same scale as Figure 36.1; 4, same specimen, transverse thin section, detail of collines and septa, scale bar = 1 mm; 5, same specimen, longitudinal thin section, detail of tabular dissepiments and wall, same scale as Figure 36.4; 6, same specimen, transverse thin section, detail of collines, septa, and dissepiments, same scale as Figure 36.4.

The only other reported occurrences in North America are from the Albian Stuart City Formation and the lower Albian Rodessa Limestone of Texas, and the Mural Limestone (Scott, 1990, p. 10, 14, 31). Most other occurrences of this species are from older strata in Europe.

This species also has been reported from the Urgonian (probably Barremian) of Switzerland (types), the lower Barremian of France, the Barremian and lower Aptian of Italy, Slovenia, Serbia, France, and Poland, the Aptian-Albian of Japan, the lower Aptian of Romania, the Aptian of Greece, and the Senonian (reworked) of Yugoslavia.

Discussion. The morphology of the species described above is most similar to that described for *Eohydnophora picteti*, therefore the Mexican material is referred to that species. The intraspecific variability of this species, particularly with regard to the size and spacing of the collines and the thickness of the septa, has been discussed by Masse and Morycowa (1994).

Another species of this genus also occurs in Mexico: *Eohydnophora ovalis* Masse and Morycowa, 1994, from the lower Aptian Cumburindio Formation near the village of Turitzio, state of Michoacán. Refer to the discussion given for *E. ovalis* in the first part of the systematic paleontology section for additional discussion on the occurrences of the members of *Eohydnophora*.

Family Placocoeniidae Alloiteau, 1952

Genus *Columnocoenia* Alloiteau, 1952

Type species. *Columnocoenia lamberti* Alloiteau, 1957 (p. 135-136, figs. 94, 95, pl. 7, fig. 5, pl. 19, fig. 5).

Columnocoenia ksiazkiewiczi Morycowa, 1964

Figure 37

Columnocoenia ksiazkiewiczi Morycowa, 1964, p. 67-69, pl. 17, figs. 1-4, pl. 18, fig. 1, text fig. 16; Morycowa, 1971, p. 95-96, pl. 24, fig. 1, text fig. 30A-B; Kuzmicheva, 1980, p. 97-98, pl. 36, fig. 2; Kuzmicheva, 1988, p. 162-163, pl. 3, fig. 4; Prinz, 1991, p. 196, pl. 8, figs. 7-8; Scott and González-León, 1991, p. 62, fig. 6F; Moussavian, 1992, p. 122, pl. 23, fig. 1; Baron-Szabo, 1993, p. 158, pl. 3, figs. 1a-c, text fig. 5; Baron-Szabo, 1994, p. 445; Löser, 1994, p. 19-21, pl. 5, figs. 5-6, pl. 10, figs. 1-3, pl. 12, fig. 3, text figs. 10-11; Morycowa and Marcopoulou-Diacantoni, 1994, p. 252-253, 272, pl. 4, figs. 5-6; ?Abdel-Gawad and Gameil, 1995, p. 15, pl. 12, figs. 11-12; Löser and Raeder, 1995, p. 47; Baron-Szabo and Steuber, 1996, p. 12, pl. 4, figs. 5-6; Császár and Turnšek, 1996, p. 430, 434, fig. 7.7; Baron-Szabo, 1997, p. 58, 60, pl. 4, fig. 3; Baron-Szabo and Fernández-Mendiola, 1997, p. 47, fig. 5C; Löser, 1998, p. 176; Baron-Szabo and González-León, 1999, p. 473-475, fig. 3a.

Columastrea striata (Goldfuss, 1829) Löser, 1989, p. 116-117, pl. 25, fig. 1, text fig. 22.

Description. Corallum colonial, attached, plocoid, massive, hemispherical, and costate. Size of corallum usually small, the figured specimens about 55 x 60 mm in width and 50 mm in height, but as large as 18 cm in diameter based on field observations. Colony formation by extratentacular budding.

Corallites generally cylindrical, gently tapered aborally, loosely packed, unevenly distributed, axes oriented subparallel to each other and primarily upward. Calices well-delineated, exclusively monocentric, and commonly orally protuberant about 0.5 mm. Calicular margin typically circular or subcircular in outline. CD variable, most commonly from 3.0 to 3.5 mm, but as small as 2.0 mm and a few to as large as 4.5 mm. Calices relatively deep, about 2.0 mm. Calices rarely in lateral contact, commonly spaced about 1-5 mm apart, or at a distance of about 4-8 mm between calicular centers, the latter dimension typically about 6.5 mm.

Septa well-developed, exsert, laminar, primarily solid, and structurally continuous with costae. Septa typically 24 in number in corallites with CD of 3 mm or larger, and hexamerally arrayed in three complete cycles. Size relationship among septa: $S_1>S_2>S_3$. S_1 blade-shaped to laminar in cross section, solid, usually straight, about 0.4 mm in width at junction with wall and tapered toward corallite axis. Length of S_1 about 1.2 mm, or about two-thirds distance from wall to corallite axis. S_2 similar to S_1 in shape and slightly narrower. Length of S_2 sometimes nearly equal to length of S_1, but more commonly noticeably shorter and equal to about half distance from wall to corallite axis. S_3 typically weakly developed, very thin, and usually laminar in cross section but often with structural discontinuities.

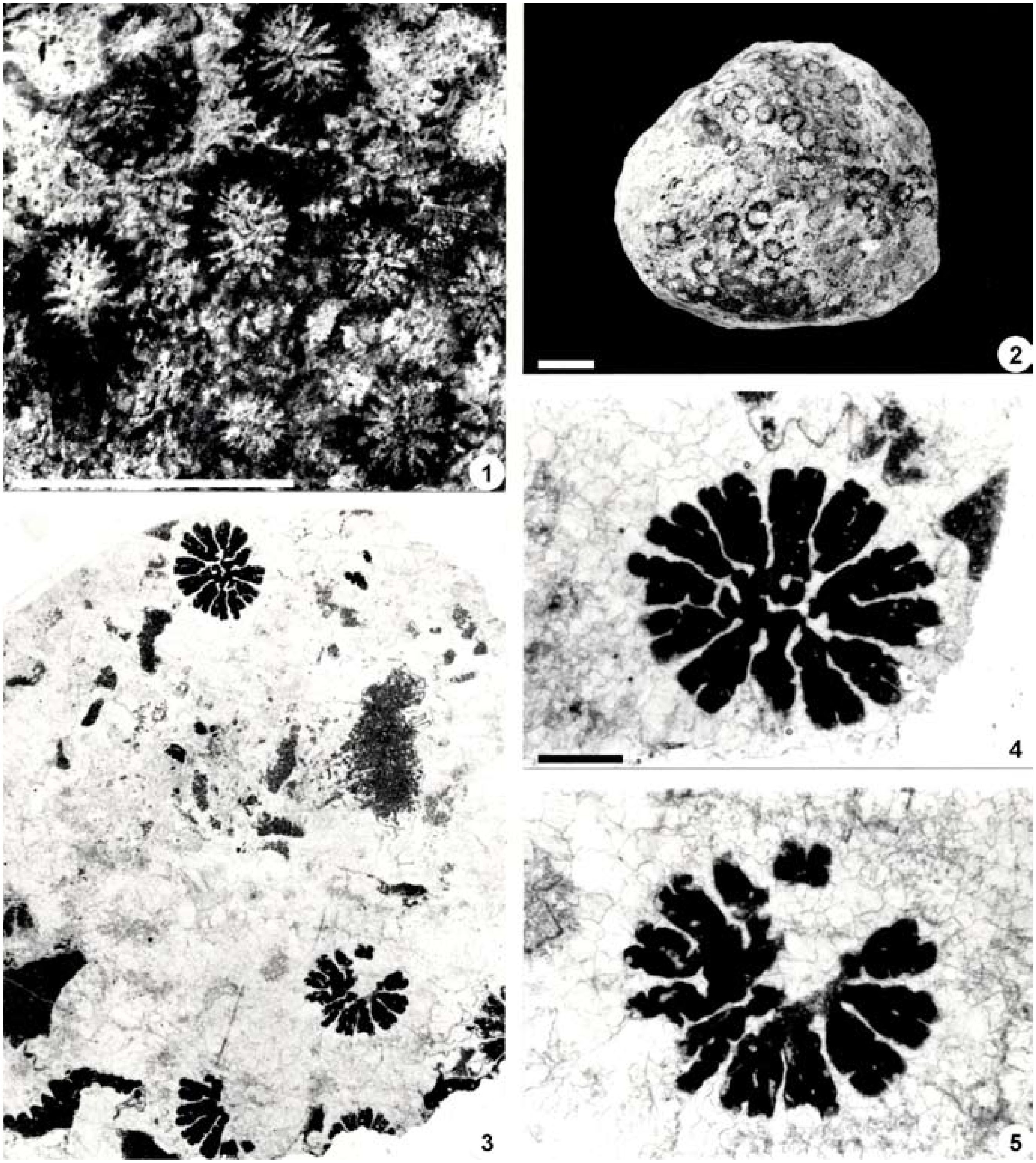

Figure 37. *Columnocoenia ksiazkiewiczi* Morycowa, 1964, upper member of the Mal Paso Formation, upper Albian-lower Cenomanian, about 0.75 km north of Chumbítaro, Michoacán, in the State of Guerrero, Mexico. 1, IGM-7736, detail of weathered lateral surface of corallum, scale bar = 1 cm; 2, same specimen, upper surface of corallum, scale bar = 1 cm; 3, IGM-7737, transverse thin section, recrystallized, same scale as Figure 37.1; 4, same specimen, transverse thin section, detail of septa and costae, scale bar = 1 mm; 5, same specimen, transverse thin section, detail of septa, same scale as Figure 37.4.

Length of S_3 about 0.5 mm, or one-fourth distance from wall to corallite axis. Interseptal spaces commonly about 0.5 mm in width. Synapticulae, or probably more precisely lateral trabecular fusions, commonly developed between inner margins of S_1, S_2 and columella within a narrow zone immediately peripheral to axial region. Synapticulae-like lateral trabecular connections rod-shaped, about 0.1-0.2 mm in diameter, and vertically spaced about 4 per mm. Lateral surfaces of septa uneven, sparsely granulated or carinate, the latter vertically spaced at about 4 per mm and possibly a result of fusions of septa and endothecal dissepiments. Septal margins poorly preserved orally, uneven, possibly dentate or beaded. Inner margins of S_1 and often some S_2 thickened and intermittently laterally connected to each other and to columella with trabecular rods. Inner margins of S_3 laterally free orally and lacerate or beaded aborally. Pali-like trabecular rods weakly developed on inner edges of S_1 and S_2 and form a single crown around axial region.

Columella weakly developed, laminar, vertically discontinuous. Width of columella about 1 mm, or nearly one-third CD. Columella intermittently laterally fused to inner margins of S_1 and S_2. Columellar trabeculae rod-shaped and about 0.2 mm in diameter.

Wall well-developed, septothecal, solid, about 0.2-0.3 mm in width. Endothecal dissepiments tabular, mostly laterally continuous, and vertically spaced about 0.5-1.0 mm apart. Exothecal dissepiments well-developed between corallites, primarily vesicular in structure, arched convex orally, about 0.5-2.0 mm in width and vertically spaced 0.5-1.0 mm apart.

Costae structurally continuous with septa, robust, vertically discontinuous into coenosteum, and subconfluent or nonconfluent with those of adjacent corallites. Costae wedge-shaped in cross section and ridge-like with sharp crests. C_1 and C_2 subequal, about 0.5 mm in height, 0.4 mm in width, or typically equal to width of septa at wall, and tapered distally. Width of C_3 usually much wider than S_3 at wall, nearly equal to width of C_2. Crests of costae laterally spaced 0.5-0.8 mm apart.

Surface of coenosteum typically concave between corallites and uneven between costae, the latter feature a surface expression of vesicular exothecal structure.

Material examined. Three specimens: IGM-7736 (figured), 58 x 62 mm in width and 55 mm in height; IGM-7737 (figured), 55 x 60 mm in width and 50 mm in height, with two thin sections (M-27 and M-28); and IGM-7738, 83 x 100 mm in width and 58 mm in height. The skeletal material is thoroughly recrystallized and most of the structure is completely obliterated.

Occurrence. The coral reef horizon of the upper member of the Mal Paso Formation, upper Albian-lower Cenomanian. The fossil locality is in the state of Guerrero, just north of the border with the adjacent state of Michoacán, about 0.75 km north of the rural village of Chumbítaro, Michoacán. The coordinates of this locality are: 18° 29.3' N, 100° 42.5' W.

This species, and *C. ksiazkiewiczi bucoviensis* Morycowa, 1971, a subspecies, have been reported from the upper Barremian-lower Aptian Cerro de Oro Formation and the middle Albian Espinazo del Diablo Formation of the state of Sonora, Mexico (Scott and González-León, 1991, p. 55, 62, fig. 6F; Baron-Szabo and González-León, 1999).

Columnocoenia ksiazkiewiczi also has been reported from the Lower Cretaceous (Hauterivian-Barremian) at El Way, just south of Antofagasta, Chile (Prinz, 1991, p. 196).

This species was originally described from the Barremian-lower Aptian Grodziszcze beds of the Polish Carpathians at Jastrzebia, Trzemesna, and Buków, Poland. Other reported occurrences are from: the Valanginian-lower Hauterivian of Hungary; the Barremian-Aptian of the Soviet Carpathians, Turkmenistan, Azerbaidzhan, and Ukraine; the lower Aptian of Germany, Romania, and Greece; the upper Aptian and Albian of northern Spain; the Albian and Cenomanian of Greece; and the lower Cenomanian of Germany.

Discussion. The morphological characteristics of the specimens from the Mal Paso Formation are most similar to those typically attributed to *C. ksiazkiewiczi* Morycowa, 1964, therefore the coralla are referred to that species. The only notable difference between these specimens and most of the other coralla referred to *C. ksiazkiewiczi* is the occasionally slightly larger distance between calices.

Suborder Meandriina Alloiteau, 1952
Family Dendrogyridae Alloiteau, 1952
Genus *Orbignygyra* Alloiteau, 1952

Type species. *Diploria neptuni* d'Orbigny, 1850c (p. 208).

***Orbignygyra*? *incognita* new species**

Figure 38

Diagnosis. Corallum meandroid and massive. Series relatively narrow, about 1-2 mm in width. Septa laterally spaced 3 per 2 mm along wall of series. Columella absent.

Description. Corallum colonial, attached, meandroid, massive, and noncostate(?). Colony formation by polystomodaeal intratentacular budding.

Series laterally continuous, straight or curved, irregularly spaced, and narrow, about 1-2 mm in width. Intratentacular budding frequent, but irregularly spaced; one to four new series budded simultaneously from parent series. Collines absent. Series separated by ambulacrum. Ambulacrum typically much wider than series and from 2-4 mm in width. Structure and surface ornamentation of ambulacrum unknown.

Calices arranged in laterally continuous series and frequently polycentric. Width of series (LCD) about 1-2 mm, length of series (GCD) ranges from about 4 to 15 mm.

Septa well-developed, non-exsert(?), laminar, solid, relatively few in number, and usually bilaterally symmetrical within series. Septa mostly subequal in size, although some smaller septa suggest presence of two septal cycles. Septa laterally spaced about 3 per 2 mm along wall of series. Septa blade-shaped or clavate in transverse cross section, often laterally expanded axially, and rounded or flattened at their axial margin. Width of septa highly variable, from relatively thin, about 0.1 mm, to fairly thick, about 0.25 mm. Axial inner edges of claviform septa sometimes thickened to as much as twice their width. Most larger septa extend to perimeter of axial region of series. Lateral surfaces of septa appear smooth. Upper margins of septa not observed; inner axial margins of septa rounded or clavate and flattened. Pali absent. Columella absent; axis of series typically hollow orally.

Wall well-developed, parathecal(?). Endotheca possibly present. Coenosteum of ambulacrum solid(?) or vesicular(?).

Etymology. The species name is derived from the Latin *incognitus* = unknown or strange, an allusion to the uncertainty of some of its morphological characteristics.

Type. Holotype IGM-7739, with two thin sections (M-61 and M-62). The single specimen is about 75 x 90 mm in width and 70 mm in height. The corallum is mostly embedded in wackestone matrix and thoroughly coarsely recrystallized to very dark brown calcite. Due to the relatively poor preservation caused by the extensive recrystallization, the morphological characteristics of the wall and ambulacrum are uncertain or unknown.

The type stratum is the upper member of the Mal Paso Formation, upper Albian-lower Cenomanian. The type locality is in the state of Guerrero, just north of the border with the adjacent state of Michoacán, about 0.75 km north of the rural village of Chumbítaro, Michoacán. The coordinates of this locality, as determined from the Mexican 1:50,000 scale Coyuca de Catalán (E14A74) topographic map, are: 18° 29.3' N, 100° 42.5' W.

Occurrence. Known only from the type locality. The coordinates of this locality are given above. The holotype corallum is from the coral reef horizon of the upper member of the Mal Paso Formation.

Discussion. This species is tentatively assigned to *Orbignygyra* because the overall gross morphology of the corallum is most similar to the described characteristics of that genus. Because some of the morphological details of the species are not confidently known, and because most, if not all, of the other species of *Orbignygyra* possess a thin, laminar columella, the generic determination is also questionable. *Orbignygyra*? *incognita* n. sp. somewhat resembles *O. daedalea* (Reuss, 1854, p. 94, pl. 14, figs. 3-4), but the latter species possesses series that are slightly wider, 2.5 mm, and it exhibits a very thin lamellar columella (Turnšek, 1994, p. 12, pl. 6, figs. 1-3; 1997, p. 143, pl. 143). *Diploria latisinuata* Felix, 1903b (p. 276, pl. 20, fig. 16), later referred to *Orbignygyra* (Reig, 1989, p. 13), has wider series, more numerous septa (9-10 septa in 5 mm), and a very thin lamellar columella. *Orbignygyra linarii* (Bataller, 1937), *O. campaniensis* Reig, 1989, and *O. ilerdensis* Reig, 1989, have septa that are more numerous and more closely spaced than those of *O. incognita* n. sp. and they also possess a thin, laminar columella (Reig, 1989, p. 12-15).

Suborder Dendrophylliina Vaughan and Wells, 1943

Family Dendrophylliidae Gray, 1847

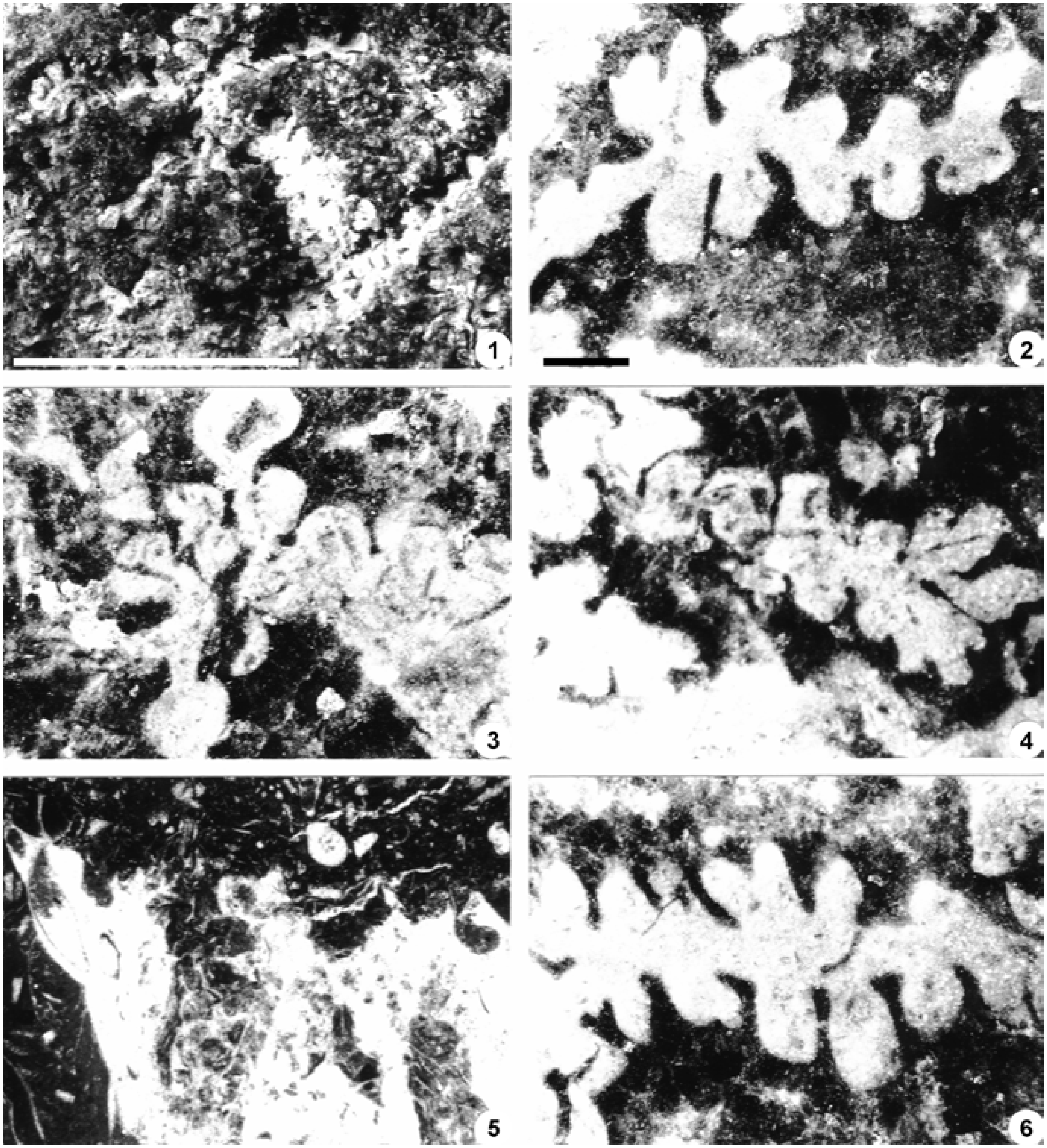

Figure 38. *Orbignygyra? incognita* n. sp., holotype IGM-7739, upper member of the Mal Paso Formation, upper Albian-lower Cenomanian, about 0.75 km north of Chumbítaro, Michoacán, in the State of Guerrero, Mexico. 1, Oral view of part of corallum, skeleton weathered and coarsely recrystallized; note intratentacular budding of series, scale bar = 1 cm; 2, transverse section, polished surface, detail of series with septa of variable thickness and relatively wide adjacent ambulacrum, scale bar = 1 mm; 3, transverse section, polished surface, series with incipient buds, same scale as Figure 38.2; 4, transverse section, zone of narrow ambulacrum between two adjacent series, same scale as Figure 38.2; 5, longitudinal thin section, detail of parathecal(?) wall structure (on left) and solid(?) or vesicular(?) coenosteal structure, same scale as Figure 38.2; 6, transverse section, detail of series with some relatively thick, axially flattened or T-shaped septa, same scale as Figure 38.2.

Discussion. The family Dendrophylliidae has been revised recently by Cairns (2001).

Genus *Blastozopsammia* Filkorn and Pantoja-Alor, 2004

Type species. *Blastozopsammia guerreroterion* Filkorn and Pantoja-Alor, 2004 (p. 506, figs. 3-4).

***Blastozopsammia guerreroterion* Filkorn and Pantoja-Alor, 2004**

Figures 39, 40

Blastozopsammia guerreroterion Filkorn and Pantoja-Alor, 2004, p. 506, figs. 3-4.

Description (summarized from the original description in Filkorn and Pantoja-Alor, 2004). Corallum colonial, ramose. Branches cylindrical, 3-6 mm in diameter, and gently tapered toward distal end. Branch bifurcations nearly dichotomous; angle of divergence 30-60 degrees. Branches composed of an axial corallite surrounded by a sheath of radial corallites and coenosteum. Colony formation by extratentacular budding. Radial corallites typically aligned with S_1 of axial corallite.

Corallites cylindrical and dimorphic: axial corallites and radial corallites. Axial corallites continuous, some at least 30 mm in length, and 1.5-2.5 mm in diameter. Radial corallites developed from sides of axial corallites, 1.0-2.5 mm in length and 1.0-1.5 mm in diameter. Axes of radial corallites oriented at high angle to axial corallite, approximately 70-85 degrees. Oral margins of radial corallites slightly protuberant or level with coenosteal surface.

Calices monocentric. Calicular margins circular. Axial corallite CD 1.25-2.0 mm and radial corallite CD 0.8-1.25 mm. Calices of radial corallites separated by coenosteal regions, evenly distributed, and regularly spaced 0.8-1.3 mm apart.

Septa well-developed, laminar, solid, and about 0.1 mm in width. Septa 24-36 in number, hexamerally arrayed, in three complete cycles and part of fourth cycle. Incipient Pourtalès plan sometimes present in axial corallites at insertion of S_4. Size relationship among septa: $S_{1-2}>S_4\geq S_3$. Septa straight, laminar. S_1 and S_2 extended to perimeter of corallite axis, about 0.8 mm in length, or 80 percent radius of calice. Length of S_3 about half that of S_2. Radial corallites also exhibit three cycles of septa, except S_3 of radial corallites weakly developed and typically present only near wall. Pairs of S_4 sometimes present and arranged in Pourtalès plan. Length of S_4 greater than or equal to that of S_3, but less than S_2. Distal edges of septa thickened at junction with wall. Interseptal synapticulae absent. Lateral surfaces of septa smooth. Axial septal margins of S_1 and S_2 thickened aborally and intermittently fused to columella and to each other with trabecular connections. In transverse cross section, these interseptal trabeculae appear as a discontinuous ring around axial region. Axial septal margins of S_3 aborally fused to adjacent parental S_2.

Pali or pali-like structures appear to occur on S_2 of radial corallites, based on observations of cross sections. However, these structures also may be due to thickened S_2 at insertion of S_3. Columella of axial corallite weakly developed, trabecular, vertically continuous, and merged with trabecular extensions from axial margins of S_{1-2}. Axial region of corallites 0.3-0.5 mm in diameter. Columella also developed in radial corallites, only structurally less porous and somewhat more styliform in appearance.

Wall well-developed, synapticulothecate. Wall of axial corallite composed of two concentric synapticular rings, about 0.3 mm in width, and derived from thickened distal edges of septa. Wall of radial corallites composed of single layer of synapticulae, 0.2-0.3 mm in width, and possibly partly formed from coenosteal trabeculae. Synapticulae within wall of radial corallites inclined toward corallite axis and slightly more closely spaced vertically than those within wall of axial corallites, about 5 per mm versus 3-4 per mm, respectively. Endo- and exothecal dissepiments absent.

Coenosteum well-developed, reticulate, and highly porous. Coenosteum layer typically 1-2 mm in thickness around axial corallite. Coenosteal surface faintly costate to striate, porous, and spinose. Calicular margin of radial corallites often costate along upper oral edge of corallite wall.

Material examined. Holotype IGM-6967, from a block of coral packstone about 95 x 110 x 50 mm, with two petrographic thin sections; paratypes IGM-6968 and IGM-6969, two blocks of coral packstone about 60 x 90 x 55 mm and 90 x 140 x 70 mm, respectively, and numerous other coral fragments (unnumbered paratypes) within the same rock samples.


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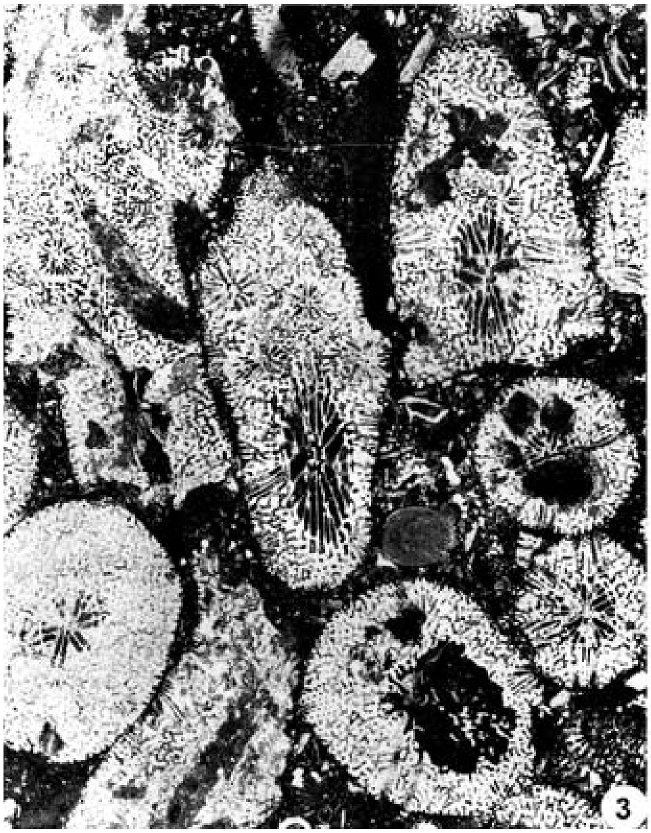
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Occurrence. Known only from the type locality in the upper part of the upper member of the Mal Paso Formation, upper Albian-lower Cenomanian. The fossil locality is in the state of Guerrero, just north of the border with the adjacent state of Michoacán, about 0.75 km north of the rural village of Chumbítaro, Michoacán. The coordinates of this locality are: 18° 29.3' N, 100° 42.5' W.

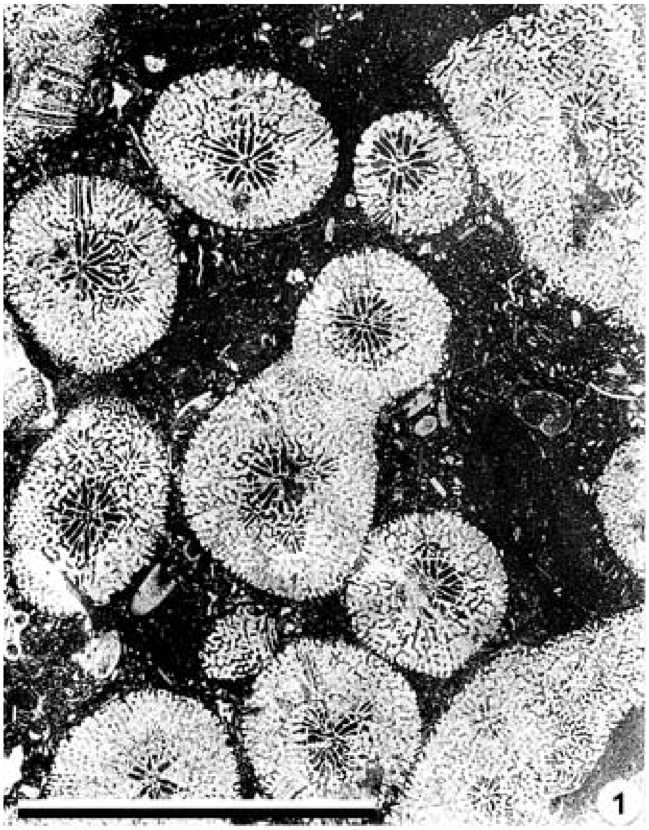
Discussion. The evolutionary significance of *Blastozopsammia guerreroterion* has been discussed in an earlier publication (see Filkorn and Pantoja-Alor, 2004). Thus, the taxonomic distribution of the continuous axial corallite, one of the most distinguishing characteristics of *Blastozopsammia*, is only briefly reviewed below. In addition, the temporal and spatial distributions of the species of *Petrophyllia* Conrad, 1855 (p. 266) (= *Archohelia* Vaughan, 1919; see Cairns, 2001, p. 39-40) are examined in more detail because they compose the record of the only other scleractinian genus that is also both characterized by a continuous axial corallite and reported from Cretaceous rocks.

A continuous axial corallite with radially budded secondary or daughter corallites is a remarkably rare feature among the many described scleractinian genera and species. The only other scleractinian genera that are partly diagnosed by the possession of this morphological characteristic are the zooxanthellate acroporid *Acropora* Oken, 1815, and the azooxanthellate oculinid *Petrophyllia* Conrad, 1855 (= *Archohelia* Vaughan, 1919). Although some species of the faviid *Cladocora* Ehrenberg, 1834, the faviid *Cyphastrea* Milne Edwards and Haime, 1848a (p. 494), and the dendrophylliid *Dendrophyllia* Blainville, 1830, possess a continuous axial corallite, the majority of the other members of these three genera lack this feature.

Petrophyllia (= *Archohelia*) is composed of species that presumably were azooxanthellate, nonreef-building taxa. This presumption is based on the sole known extant species of this genus, the azooxanthellate *Petrophyllia rediviva* (Wells and Alderslade, 1979), from the coast of Queensland, Australia. Therefore, the distribution of *Petrophyllia* also is especially significant with regard to *Blastozopsammia* because *Petrophyllia* is the only other azooxanthellate colonial scleractinian known to have formed monospecific coral build-ups in non-reef marine environments during Cretaceous time. Interestingly, the specimens of *Blastozopsammia* from the Cretaceous type locality also are from a monospecific coral deposit. Therefore, because of the similarities in mode of occurrence and paleoecology of *Blastozopsammia* and *Petrophyllia*, in addition to the morphological similarity of their coralla, the distribution of *Petrophyllia* is here examined in greater detail.

The fossil record of *Petrophyllia* is fairly extensive, but because the reported occurrences are frequently obscure, scattered throughout the literature, and both stratigraphically and geographically widely separated, the overall temporal and spatial distributions of this genus are poorly known. *Petrophyllia* has recently been investigated and some of the newly compiled occurrence data are reviewed here. The observed geologic range of *Petrophyllia* is Early(?) Cretaceous to Recent and the genus encompasses 18 described species, 17 of which are nominal taxa. Of these 18 species, one is extant (*P. rediviva*, as noted above) and the other 17 are known exclusively from fossils. Of these 17 fossil species, 15 are from the Tertiary and two are from the Cretaceous. The stratigraphic and geographic distributions of the 15 Tertiary species are as follows. One species, *P. limonensis* (Vaughan, 1919, p. 353-354, pl. 80, figs. 1-3; the type species of *Archohelia*), is known from the Pliocene to (?)Pleistocene of Costa Rica and Florida (Felix, 1929, p. 601; Schuchert, 1935, p. 601; Weisbord, 1974, p. 414; Cairns, 1999, p. 110). Six of the Tertiary species are Oligocene in age, five of which have been reported from Mississippi (Vaughan, 1900, p. 114, 116, 118, 122, 123, 1919, p. 353; Grabau and Shimer, 1909, p. 103; Cooke, 1922, p. 81, 83; Shimer and Shrock, 1944, p. 121), and the sixth from the state of Washington (Durham, 1942, p. 93-94). Only one of the species known from the Oligocene of Mississippi also has an Eocene occurrence (Patagonia; Felix, 1925, p. 228). In addition to these species, the Eocene occurrences of *Petrophyllia* consist of eight other species: one from California (Vaughan, 1927; Squires, 1999, 2001) and Washington (Durham, 1942, p. 94); three from

Figure 39. *Blastozopsammia guerreroterion* Filkorn and Pantoja-Alor, 2004, from holotype sample IGM-6967, upper member of the Mal Paso Formation, upper Albian-lower Cenomanian, about 0.75 km north of Chumbítaro, Michoacán, in the State of Guerrero, Mexico. 1, Polished surface, longitudinal cross section of branch with a vertically continuous axial corallite, the holotype specimen IGM-6967, scale bar = 1 cm; 2, thin section, branch at center in oblique section, same scale as Figure 39.1; 3, thin section, both transverse and oblique sections of branches, same scale as Figure 39.1; 4, thin section, mostly transverse sections of branches, same scale as Figure 39.1.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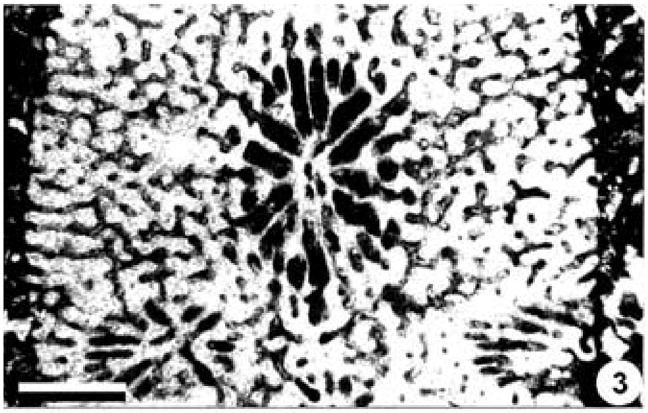
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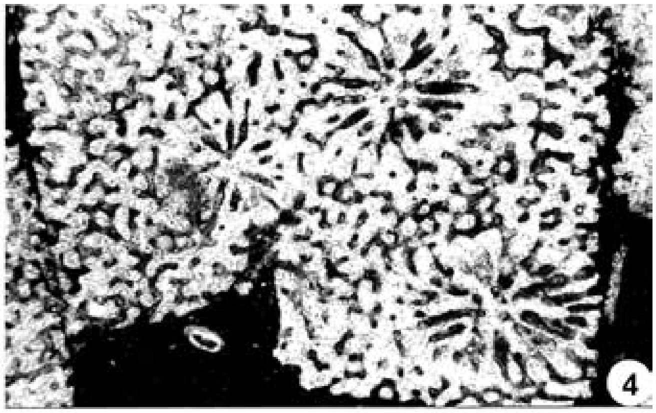
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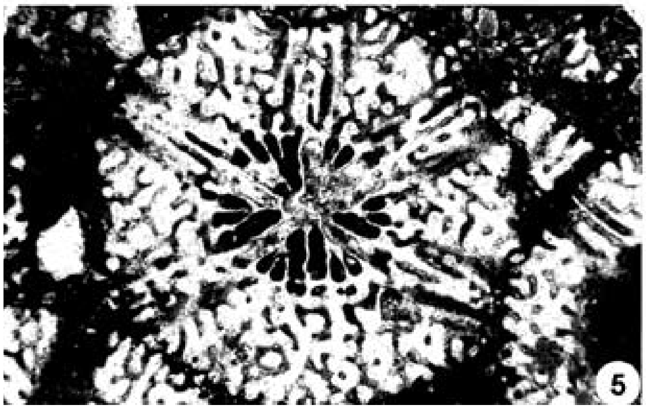
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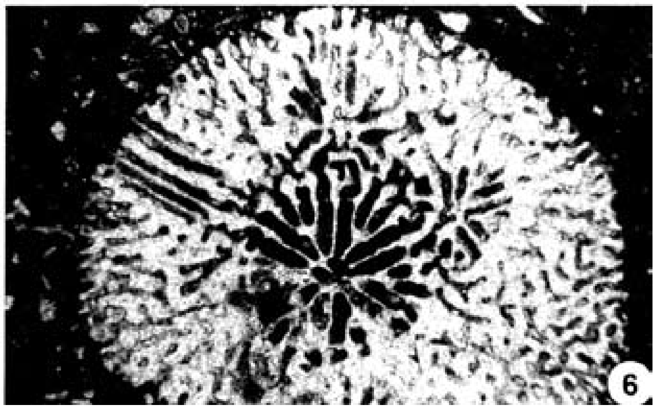
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Alabama (Vaughan, 1900, p. 121, 123, 1919, p. 353, 1941, p. 281-282), and one species each from Texas (Vaughan, 1900, p. 120, 1919, p. 353; Shimer and Shrock, 1944, p. 121), Louisiana (Vaughan, 1941, p. 282-284), Mississippi (Vaughan, 1900, p. 115, 1919, p. 353), and Barbados (Wells, 1945, p. 9-10).

Only two of the 17 species of *Petrophyllia* known from the fossil record have been reported from Cretaceous strata. The oldest known occurrence of *Petrophyllia* is *Petrophyllia* sp. (reported as *Archohelia* sp.) from the middle Albian Edwards Limestone in Kerr County, Texas (Wells, 1933, p. 162-163, pl. 21, figs. 1-2), but the generic assignment is questionable. The only other known Cretaceous species of *Petrophyllia* is *P. dartoni* (Wells, 1933, p. 223-224, pl. 25, figs. 11-12, pl. 27, figs. 31-35). The latter species was originally described from its occurrence in the Carlile zone (Turonian) of the Mancos Shale near Lamy, New Mexico, where it formed a monospecific coral deposit that has been considered to be the first and, for some time, the only cold- or deep-water azooxanthellate coral build-up known from the Cretaceous (Coates and Kauffman, 1973). The deposit of *P. dartoni* at Lamy, New Mexico, typically has been the only Cretaceous occurrence of *Petrophyllia* noted in subsequent literature (cited as *Archohelia*: see Perkins, 1951, p. 16; Kelley and Northrop, 1975, p. 61, 63; Cairns and Stanley, 1982, p. 615; Fagerstrom, 1987, p. 434-435; Stanley and Cairns, 1988, p. 237; Filkorn, 1993). However, several additional occurrences of *P. dartoni* in the Cretaceous Western Interior of North America are now known, some from anecdotal notices in published articles on other geological investigations in that region and some from cataloged museum specimens and recent field studies. These additional occurrences of *Petrophyllia dartoni* have extended its geologic range from the Turonian into the Cenomanian and broadened its geographic distribution southward into other areas of New Mexico, westward into Arizona, and northward into Wyoming. The other occurrences in New Mexico are in the upper Cenomanian of the Colorado Formation in the Big Burro Mountains, southwestern New Mexico (Cobban et al., 1989, p. 15-16); in the lower Turonian Bridge Creek Limestone Member of the Mancos Shale near Truth or Consequences, southern New Mexico (Hook and Cobban, 1981, p. 13-14; Cobban, personal communication, 1995; specimens D11019 and D11564 at the USGS in Denver); in the Mancos Shale of the Twenty-two Spring quadrangle, Valencia County (Cobban, personal communication, 1995; USGS D10534); and in the Virden section of the Canador Peak quadrangle, Hidalgo County (Cobban, personal communication, 1995; USGS D11554). Reported occurrences of *A. dartoni* in Arizona are in the Cenomanian beds of the Mancos Shale at Blue Point, Black Mesa, northeastern Arizona (Elder, 1987, p. 28; Kirkland, 1991, microfiche p. 17; Elder, 1991, p. 123); in the Cenomanian strata at Blue Point (not the same Blue Point as cited above), Black Mesa (Repenning and Page, 1956, p. 267, "an abundant coral"; USNM 085602, four branch fragments collected by O'Sullivan 17 July 1954, may be from this locality, as well as Museum of Northern Arizona (MNA) specimens P2.7701 and P2.7703); and from a locality 10 miles north of Lupton (MNA P2.1120). *Petrophyllia* is known from only one locality in Wyoming. The occurrence is based on a specimen in the Smithsonian Institution labeled USNM 123439, collected by Cobban, Reeside, etc., 1951, lot 5119, Cody Shale, middle Niobrara equivalent, Turonian. This specimen is from northeast of Shotgun Butte, along the East Fork of Sheep Creek, in Fremont County, Wyoming. The Wyoming *Petrophyllia* locality is significant because it represents the northernmost recognized occurrence of the genus in the Cretaceous Western Interior Seaway during the Late Cretaceous.

Petrophyllia reportedly also occurs in the Late Cretaceous and Tertiary of the Eastern Pacific (Durham, 1966; Heck and McCoy, 1978), but neither descriptions nor figures of these specimens have been published (Durham and Allison, 1960, p. 71; Hertlein and Grant, 1960, p. 78).

Figure 40. *Blastozopsammia guerreroterion* Filkorn and Pantoja-Alor, 2004, from holotype sample IGM-6967, upper member of the Mal Paso Formation, upper Albian-lower Cenomanian, about 0.75 km north of Chumbítaro, Michoacán, in the State of Guerrero, Mexico. 1, Transverse thin section of several branches with axial corallites and relatively thick layer of coenosteum, center branch in process of branching, scale bar = 1 cm; 2, transverse thin section of both larger and smaller diameter branches, same scale as Figure 40.1; 3, transverse thin section, slightly oblique, detail of axial corallite and coenosteum, scale bar = 1 mm; 4, longitudinal (tangential) thin section of branch, detail of radial corallites and coenosteum, same scale as Figure 40.3; 5, transverse thin section of smaller diameter branch, axial corallite and five radially arrayed secondary buds that are aligned with the primary septa of the parent corallite, same scale as Figure 40.3; 6, transverse thin section, detail of axial corallite with radial buds that have originated from the synapticulothecal wall zone of the parent corallite, same scale as Figure 40.3.

Suborder Fungiina Verrill, 1865
Family Dermosmiliidae Koby, 1889 (p. 570)
Genus *Epistreptophyllum* Milaschewitsch, 1876

Epistreptophyllum Milaschewitsch, 1876, p. 210-212, pl. 50, figs. 2-4a.
Phegmatoseris Milaschewitsch, 1876, p. 212-213, pl. 50, figs. 5, 5a.
Phragmatoseris Milaschewitsch. Duncan, 1884, p. 148.
Lithoseris Koby, 1886, p. 338-340, pl. 93, figs. 32-33a.
Protethmos Gregory, 1900, p. 162-165, pl. 18, figs. 7a-7c, 10a-13b.
Metethmos Gregory, 1900, p. 165-167, pl. 2A, fig. 5, pl. 18, figs. 4a-6b, 8a-9b, 11a-11c.
Frechia Gregory, 1900, p. 167-168, pl. 21, figs. 1a-3b.
Calamosmilia Koby, 1905, p. 81-82, pl. 26, figs. 6-10a, 12-13a.

Type species. *Epistreptophyllum commune* Milaschewitsch, 1876 (p. 210-211, pl. 50, figs. 2, 2a), by subsequent designation (Wells, 1936, p. 111).

Epistreptophyllum sp.

Figure 41

Description. Corallum solitary, attached(?), trochoid, straight or cornute, and finely costate. Base of corallum truncated by transverse fracture, an indication of possible former presence of pedicle or basal attachment. Basal angle above truncation approximately 35 degrees. Corallum small in size. Measurements of two specimens examined: height 22 mm, CD 17 mm; and height 23 mm, CD 19 mm. Both specimens about 7 mm in diameter at basal truncation. Calicular margin circular or subcircular in outline. Depth of calice about 2 mm as preserved.

Septa well-developed, laminar, fenestrate axially, and continuous with costae. Trabecular microstructure not preserved. Septa of earlier cycles usually appear solid, those of later cycles typically more fenestrate than those of earlier cycles. Septal trabeculae spaced 4 per mm along transverse section of septum. Septa numerous and hexamerally arrayed in five complete cycles with a portion of the sixth cycle present also. Size relationship among septa: $S_1 \geq S_2 \geq S_3 > S_4 > S_5 > S_6$. Septa typically blade-shaped in cross section, tapered axially, straight, and very thin, those of earlier cycles up to about 0.2 mm in width at junction with wall, those of later cycles slightly thinner. S_1, S_2, and most of S_3 extend to columella at axis of corallum. Length of S_4 nearly equal to that of S_3. Septa of subsequent cycles proportionately shorter than those of previous cycle. Interseptal spaces about twice width of adjacent septa. Synapticulae absent. Lateral surfaces of septa uneven, undulate or carinate, due to trabecular structure of septa. Septal margins not preserved in calicular region. Pali-like septal trabeculae arrayed around, and laterally intermeshed with, columella.

Columella developed, trabecular, cylindrical, vertically continuous, spongiose, orally papillose, about 2 mm in diameter, and laterally intermittently fused to axial edges of adjacent septa.

Wall weakly developed, primarily parathecal, possibly secondarily synapticulothecal, and weakly differentiated from endothecal dissepiments. Parathecal dissepiments vesicular. Endothecal dissepiments tabular. Epitheca absent.

Costae well-developed, structurally continuous with septa but usually slightly wider, subequal, low in height, and laterally spaced 2 per mm. Distal margins of costae beaded; beads spaced about 5 per mm. Intercostal furrows about twice width of costae.

Material examined. Two specimens: IGM-7740 (figured); and IGM-7741 (figured), with two thin sections (M-53 and M-54). The calicular margins of the specimens are not preserved and the internal skeletal structures have been mostly obliterated by recrystallization.

Occurrence. The upper member of the Mal Paso Formation, upper Albian-lower Cenomanian. The fossil locality is in the state of Guerrero, just north of the border with the adjacent state of Michoacán, about 0.75 km north of the rural village of Chumbítaro, Michoacán. The coordinates of this locality are: 18° 29.3’ N, 100° 42.5’ W.

Discussion. The species described above possesses the essential morphological characteristics of the genus *Epistreptophyllum*, therefore it is assigned to that genus. However, the taxon is not assigned to any particular nominal species for two main reasons: 1), some studies have noted a very broad range of intraspecific morphological variability in some species of *Epistreptophyllum* (for examples, see Gill, 1982; Pandey and Lathuiliere, 1997); and 2), only two specimens have been examined in this study.

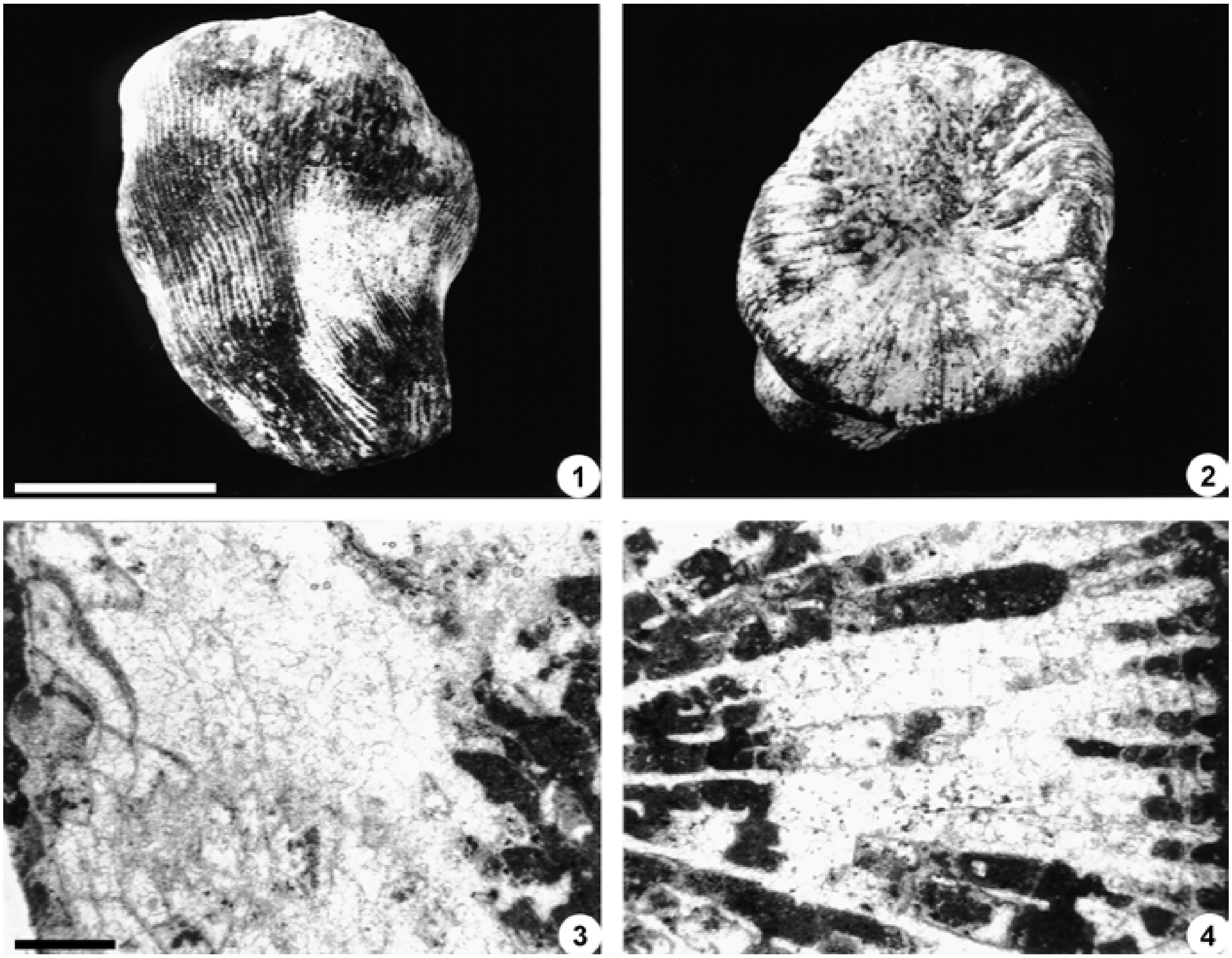

Figure 41. *Epistreptophyllum* sp., upper member of the Mal Paso Formation, upper Albian-lower Cenomanian, about 0.75 km north of Chumbítaro, Michoacán, in the State of Guerrero, Mexico. 1, IGM-7740, lateral view of corallum, scale bar = 1 cm; 2, same specimen, oral view of corallum, same scale as Figure 41.1; 3, IGM-7741, longitudinal thin section, outer edge of wall and vesicular dissepiments of paratheca on left, axis of corallum toward right, but mostly recrystallized, scale bar = 1 mm; 4, same specimen, transverse thin section, detail of septa and costae, partially coarsely recrystallized, same scale as Figure 41.3.

Members of *Epistreptophyllum* have been reported previously from the Cretaceous of Mexico. Fries (1960, p. 49, 55, 198) reported the occurrence of corals in the lower Cenomanian strata of the Morelos Formation, state of Guerrero, and listed a species that was identified by J. W. Wells, *Epistreptophyllum* sp. cf. *E. budaensis* Wells. However, a description of the latter species could not be found in the literature and therefore it seems likely that it was never described. Two small, cylindrical specimens of ?*Epistreptophyllum* sp. from the Cárdenas Formation in the state of San Luis Potosí, Mexico, have been briefly described and figured by Myers (1968, p. 80, pl. 16, figs. 1-2). In northwestern Mexico, a species referred to as *Epistreptophyllum* sp. has been reported from the Lower Cretaceous rocks of the Lampazos area, state of Sonora (González-León and Buitrón-Sánchez, 1984; González-León, 1988), but the species was neither described nor figured.

Family Thamnasteriidae Vaughan and Wells, 1943
Genus *Thalamocaeniopsis* Alloiteau, 1953

Type species. *Thalamocaeniopsis ouenzensis* Alloiteau, 1953 (p. 880-882, pl. 28, figs. 3, 6, pl. 29, fig. 5).

Discussion. The genus *Thalamocaeniopsis* Alloiteau, 1953, has been questionably considered to be a junior synonym of *Anomastraea* Marenzeller, 1901 (p. 124-126, pl. 1, figs. 3, 3a) (Wells, 1956, p. F385). However, *Thalamocaeniopsis* is known only from the Early Cretaceous, whereas *Anomastraea* is known only from Recent occurrences. Further studies of the types of these two genera are needed to clarify their taxonomic relationship.

Thalamocaeniopsis mexicanensis **new species**

Figure 42

Diagnosis. Corallum relatively large for genus and massive to ramose. CD ranges from 2.5 mm to 8 mm, commonly 5 mm. Calicular centers typically spaced 4-6 mm apart.

Description. Corallum colonial, attached, cerioid, costate, and massive and hemispherical or ramose with thick branches. Massive coralla range in size from 80 x 60 mm in width and 40 mm in height up to at least 95 mm in width and 95 mm in height; ramose coralla typically larger (based on field observations). Colony formation by intratentacular budding.

Corallites prismatic, separated by well-defined, shared wall structure, and arranged with corallite axes oriented subparallel to each other and perpendicular to surface of corallum. Calices distinct, typically monocentric, but possibly dicentric if in process of budding. Calicular margin polygonal to rounded subpolygonal in outline, usually with 5 or 6 subequal sides. CD variable from about 2.5 mm to 6 mm, commonly 5 mm, but occasionally laterally elongate to 8 mm if in process of budding. Calice slightly concave and shallow, usually less than 1 mm in depth at center. Calicular centers typically spaced 4-6 mm apart.

Septa well-developed, non-exsert, fenestrate, and continuous as costae. Each septum composed of a single fan system of trabeculae. Trabecular microstructure not preserved. Septal trabeculae about 0.1 mm in diameter and spaced 3-4 per mm along transverse cross section. Diameter of septal fenestrae usually equal to or greater than that of septal trabeculae. Number of septa variable and directly related to CD; for examples: CD 3.0 mm, 30 septa; CD 4.0 x 5.5 mm, 44 septa; CD 5.0 x 5.5 mm, 46 septa; CD 6 mm, 48 septa. Septa weakly hexamerally arranged in from three to four cycles, the latter cycle commonly incomplete. Size relationship among septa: $S_1=S_2\geq S_3>S_4$. Septa straight or gently curved and subequal in width, typically about 0.1 mm. S_1, S_2, and some S_3 (about 18 septa total) extend from wall to columella. Length of S_4 variable, usually less than half that of S_3. Interseptal spaces about 0.3 mm, or three times width of adjacent septa. Synapticulae generally developed near columella and near wall. Lateral surfaces of septa uneven, undulate, or carinate due to fenestrate trabecular structure of septa. Septal margins beaded orally; beads formed by terminations of septal trabeculae spaced 3-4 per mm along upper margin of septa. Axial edges of longer septa intermittently fused to columella and laterally to each other with synapticular rods, those of shorter septa typically fused to respective parent septa. Pali-like trabeculae on axial edges of longer septa commonly structurally integrated with columella.

Columella well-developed, trabecular, vertically continuous, orally papillose, cylindrical, and about 0.8-1.0 mm in diameter. Columella peripherally intermeshed with axial edges of S_1, S_2, and some S_3.

Wall usually developed, primarily synapticulothecal, perforate, about 0.5 mm in width, and possibly secondarily parathecal aborally. Walls of laterally adjacent corallites typically combined into a single, shared mural structure. Endothecal dissepiments abundant aborally, generally sub-tabular, thin, laterally continuous, closely spaced, and inflected convex orally across diameter of corallite. Coenosteum absent.

Upper edge of wall costate. Costae structurally similar to septa, subequal, low, continuous with respective septa but generally about twice as wide, and spaced about 3 per mm along upper edge of wall.

Figure 42. *Thalamocaeniopsis mexicanensis* n. sp., holotype IGM-7742, upper member of the Mal Paso Formation, upper Albian-lower Cenomanian, about 0.75 km north of Chumbítaro, Michoacán, in the State of Guerrero, Mexico. 1, Oral view of a portion of the weathered upper surface of the corallum; note incipient intratentacular budding of some of the calices, scale bar = 1 cm; 2, oblique transverse thin section, same scale as Figure 42.1; 3, longitudinal thin section, same scale as Figure 42.1; 4, transverse thin section of several corallites, same scale as Figure 42.1; 5, longitudinal thin section, detail of fenestrate skeletal architecture, scale bar = 1 mm; 6, transverse thin section, detail of fenestrate septa, intracalicular synapticulae, columella, and synapticulothecate wall, same scale as Figure 42.5.


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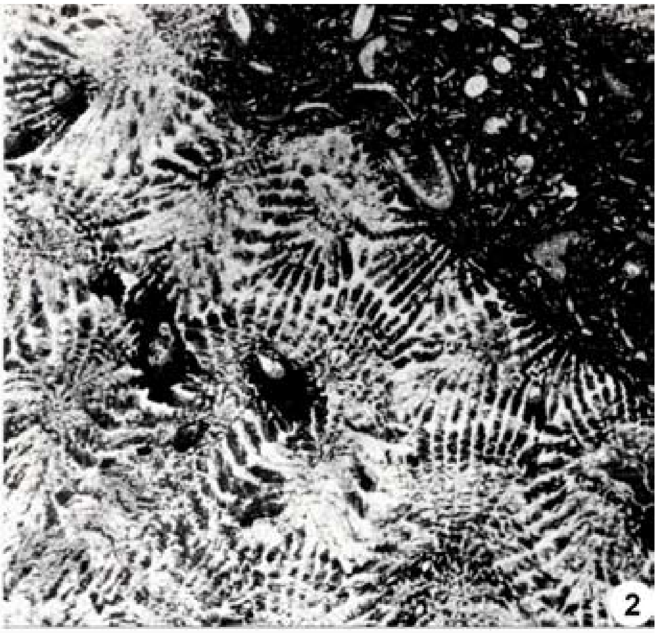
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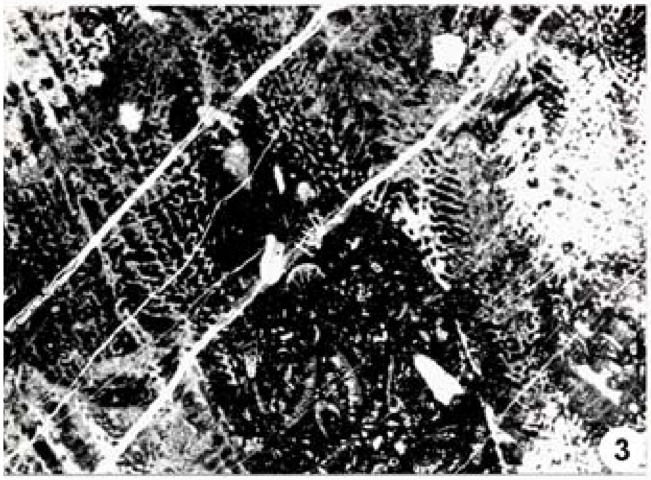
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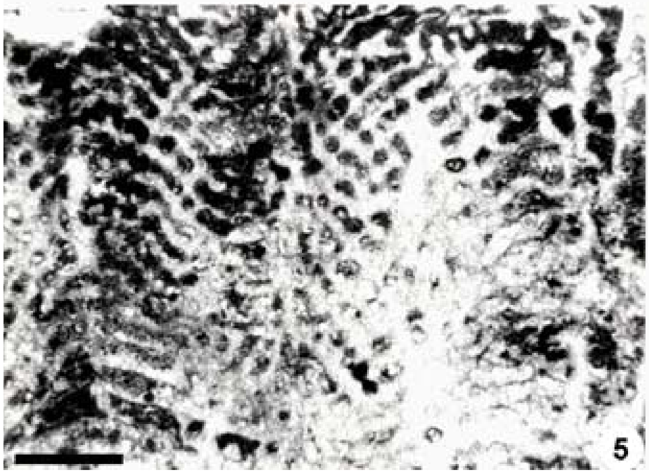
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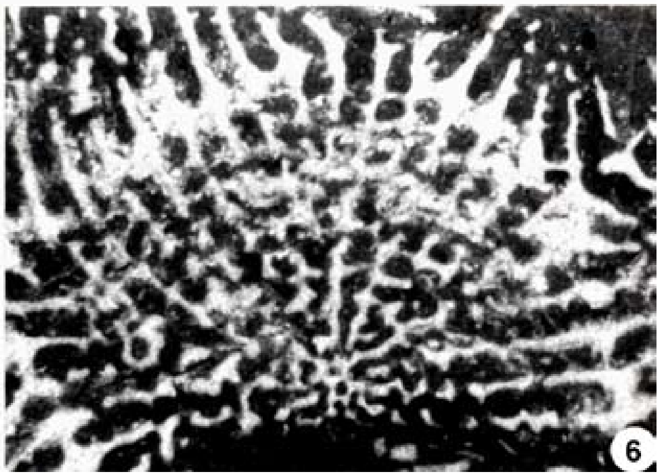
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Etymology. The species is named for the country of origin, Mexico, by adding the Latin suffix -*ensis* = place to the adjective of Mexico, Mexican.

Types. Holotype IGM-7742, with two thin sections (M-20 and M-21); and paratypes IGM-7743, IGM-7744, IGM-7745, IGM-7746, and IGM-7747. All of the specimens are from the coral reef horizon (unit MP13) except the latter corallum which is from unit MP17. The skeletal architecture described above is mainly based on the holotype, a relatively well-preserved corallum.

The type stratum is the upper member of the Mal Paso Formation, upper Albian-lower Cenomanian. The type locality is in the state of Guerrero, just north of the border with the adjacent state of Michoacán, about 0.75 km north of the rural village of Chumbítaro, Michoacán. The coordinates of this locality, as determined from the Mexican 1:50,000 scale Coyuca de Catalán (E14A74) topographic map, are: 18° 29.3' N, 100° 42.5' W.

Occurrence. Known only from the type locality. The coordinates of this locality are given above. This species is common in the coral reef horizon (unit MP13) of the upper member of the Mal Paso Formation; specimens also occur stratigraphically above the coral reef horizon in unit MP17.

The type species, *Thalamocaeniopsis ouenzensis* Alloiteau, 1953, is from the Early Cretaceous (Aptian) of Algeria, North Africa.

Discussion. The morphology of *Thalamocaeniopsis mexicanensis* n. sp. primarily differs from that described for the type species by the larger size of the corallum, the massive to ramose growth form of the corallum, the relatively larger diameter of the calices, and the wider spacing between calicular centers.

Genus *Thamnasteria* Lesauvage, 1823

Type species. Astrea dendroidea Lamouroux, 1821 (p. 85, pl. 78, fig. 6) (= Thamnasteria lamourouxii Lesauvage, 1823, p. 243-244, pl. 14, figs. 1-2).

***Thamnasteria tonantzinae* new species**

Figure 43

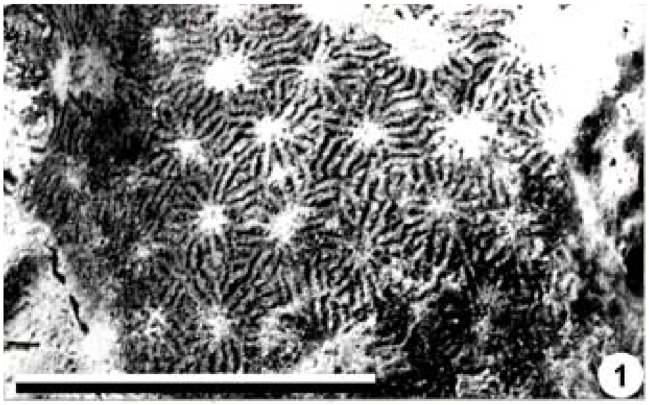
Diagnosis. Corallum massive to ramose. Calices small, CD 1.6-2.4 mm. Calicular centers closely spaced, from 1.6 to 3 mm apart. Septa variable in number: 8-10 axially, but as many as about 30 peripherally. Synapticulothecal wall sometimes weakly developed aborally

Description. Corallum colonial, attached, thamnasteroid, massive to ramose, and finely septocostate. Size of corallum at least 30 cm in width and height. Branches variable in size and shape, commonly 10-20 mm in diameter, but observed range from about 5 to at least 60 mm in diameter, generally irregularly cylindrical or lath-shaped, often broadly uneven, with nodular or bulbous projections (incipient branches?), elongate, and often gradually tapered along branch length. Branches of corallum typically oriented subparallel to each other and commonly bifurcated at irregular intervals with an angle of divergence less than 30 degrees. Colony formation by intratentacular budding with lamellar linkages.

Corallites weakly differentiated from each other, laterally confluent orally due to lack of wall, boundaries only vaguely delineated orally by convergence of septocostae, and sometimes weakly defined suborally by fenestrate synapticulothecal wall. Corallite axes oriented approximately perpendicular to surface of corallum.

Calices somewhat superficial, typically monocentric, and weakly delineated orally by slight, broadly convex protuberance of marginal region. CD about 1.6-2.4 mm.

Figure 43. *Thamnasteria tonantzinae* n. sp., holotype corallum IGM-7748, upper member of the Mal Paso Formation, upper Albian-lower Cenomanian, about 0.75 km north of Chumbítaro, Michoacán, in the State of Guerrero, Mexico. 1, Portion of weathered surface of a larger fragment of the corallum, scale bar = 1 cm; 2, another weathered surface area of the same fragment, same scale as Figure 43.1; 3, tangential thin section of a smaller branch fragment, corallites in transverse section, skeletal material partially coarsely recrystallized, same scale as Figure 43.1; 4, longitudinal thin section of a smaller branch fragment, skeleton mostly coarsely recrystallized, same scale as Figure 43.1; 5, transverse thin section, detail of septa, pali-like structures, and columella of several adjacent corallites, scale bar = 1 mm; 6, longitudinal thin section near outer surface of branch fragment, detail of septa and synapticulae, skeleton mostly coarsely recrystallized, same scale as Figure 43.5; 7, transverse thin section, detail of features of corallites deeper within branch, skeleton partially coarsely recrystallized, same scale as Figure 43.5; 8, longitudinal thin section near outer surface of branch fragment, detail of septa and synapticulae, skeleton mostly coarsely recrystallized, same scale as Figure 43.5.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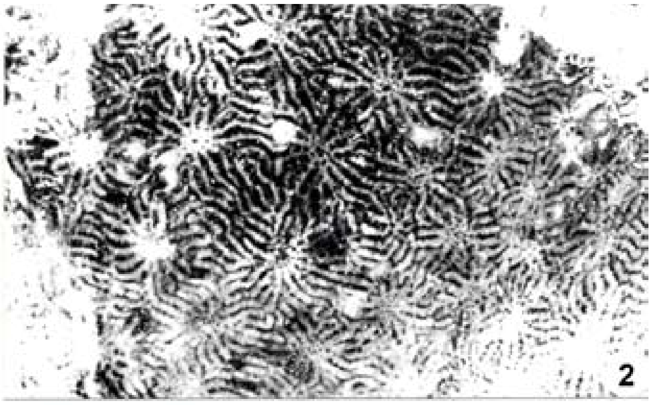
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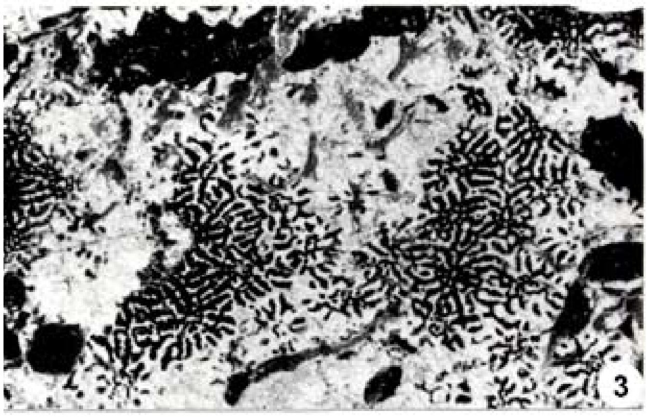
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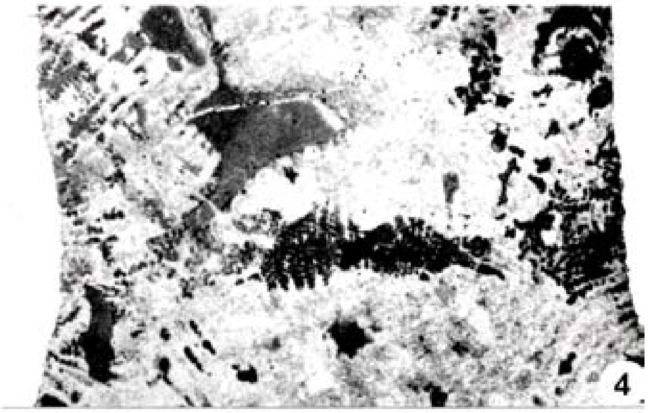
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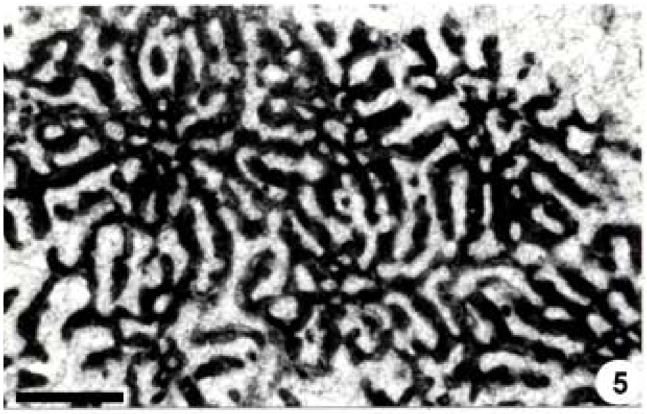
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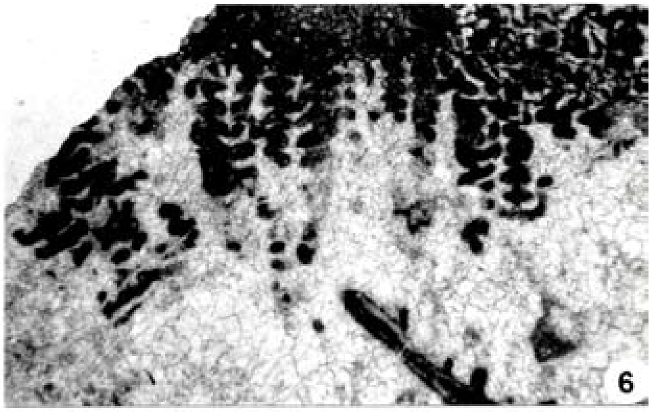
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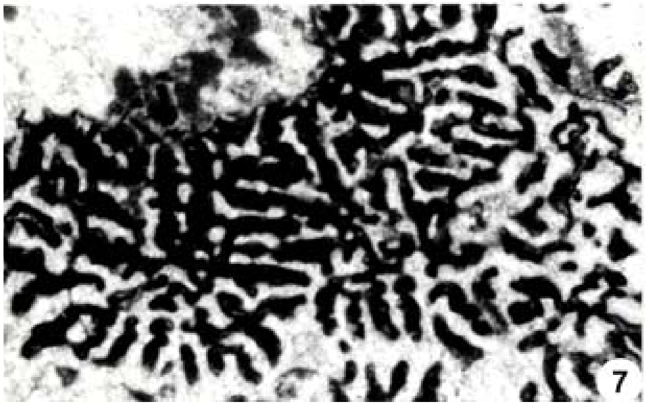
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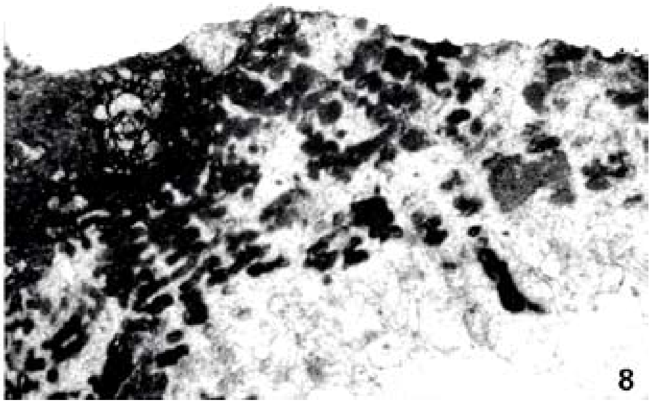
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Calicular centers well-defined, slightly concave, very shallow, and spaced 1.6-3 mm apart.

Septa well-developed, weakly exsert, laminar, and irregularly fenestrate. Each septum composed of a single fan system of trabeculae. Trabecular microstructure not preserved. Septa variable in number: usually 8-10 primary septa extend nearly to columella, some of them bifurcated distally, and as many as about 30 present peripherally. Septa radially arrayed; septal symmetry and number of septal cycles obscure. Septa laminar to blade-shaped in cross section and about 0.1-0.2 mm in width. Interseptal spaces about equal to width of septa. Synapticulae present between inner margins of primary septa, developed concentrically around columella in a cylinder about 0.7 mm in inside diameter, or at a distance of 0.1-0.2 mm abaxially from columella, and vertically spaced about 4 per mm. Trabecular fusions frequently occur between inner margins of septa and columella. Synapticulae also sometimes present between septocostae within the intercorallite region. Lateral surfaces of septa sometimes appear coarsely granulated or carinate in cross section, particularly axially, possibly due to fusion of fenestrate trabecular structure of septa and synapticulae. Septal and septocostal margins coarsely beaded orally; beads about 0.2 mm in diameter and spaced 4 per mm along margins. Inner margins sometimes flattened axially.

Pali-like structures about 0.1-0.2 mm in diameter developed on oral-axial margin of primary septa and arranged in a single crown around columella.

Columella well-developed, usually styliform and solid in appearance, roughly cylindrical, vertically continuous, often circular or elliptical in cross section, and about 0.2-0.4 mm in diameter.

Wall absent orally, but sometimes synapticulothecal and weakly developed aborally. Endotheca not observed; exotheca absent. Surface of corallum finely septocostate. Width and structure of costae similar to those features as described for the septa. Distal portions of septocostae often bifurcated and typically confluent with those of adjacent corallites. Intercostal spaces about 0.3 mm in width or nearly twice width of adjacent costae. Septocostae laterally spaced 8 per 2 mm.

Etymology. The species is named for Tonantzin, an Aztec goddess of the Earth.

Types. Holotype corallum IGM-7748, with four thin sections (M-03, M-05, M-06, and M-39).

The type stratum is the upper member of the Mal Paso Formation, upper Albian-lower Cenomanian. The type locality is in the state of Guerrero, just north of the border with the adjacent state of Michoacán, about 0.75 km north of the rural village of Chumbítaro, Michoacán. The coordinates of this locality, as determined from the Mexican 1:50,000 scale Coyuca de Catalán (E14A74) topographic map, are: 18° 29.3' N, 100° 42.5' W.

The holotype specimens are fragments of the branches of a single, large, ramose corallum from unit MP17. The material is mostly coarsely recrystallized internally and extensively bored. Some of the borings are interconnected, subspherical chambers 1-2 mm in diameter which are interpreted as sponge galleries. Small serpulid annelid tubes about 0.6 mm in diameter occur as epibionts on some of the branch surfaces.

Occurrence. Known only from the type locality. The coordinates of this locality are given above. The single massive to ramose corallum was found in situ and partially weathered out from unit MP17

Discussion. The species described above appears to be most similar to *Thamnasteria hoffmeisteri* Wells, 1933 (p. 189-190, pl. 15, fig. 21, pl. 23, figs. 18-19), from the lower Cenomanian Buda Limestone of Williamson County, Texas. However, *T. hoffmeisteri* primarily differs from *T. tonantzinae* by the massive growth form and relatively small size of the corallum (75 mm in diameter and about 40 mm in height), the more widely spaced calicular centers (average of 3 mm), and a smaller number of septa (15-20). In contrast to *T. hoffmeisteri*, *T. tonantzinae* n. sp. has a massive to ramose growth form and a larger corallum (about 30 cm in width and height), calicular centers that are more closely spaced (1.6-3.0 mm apart), and more numerous septa in the peripheral regions of the calices (as many as about 30).

Suborder Microsolenina Morycowa and Roniewicz, 1995
Family Cunnolitidae Alloiteau, 1952
Genus *Paracycloseris* Wells, 1934

Paracycloseris Wells, 1934, p. 85-86; Vaughan and Wells, 1943, p. 135; Alloiteau, 1952, p. 668; Wells, 1956, p. F387; Alloiteau, 1957, p. 338.

Type species. *Paracycloseris elizabethae* Wells, 1934 (p. 86-87, pl. 3, figs. 5-10, pl. 5, figs. 1-2).

Paracycloseris effrenatus new species

Figure 44

Diagnosis. Diameter of corallum small for genus. Septa numerous and inserted in normal hexameral pattern. Columella trabecular, well-developed, and narrow.

Description. Corallum solitary, unattached, cupolate and noncostate. Corallum typically small in size, from about 5 mm to 20 mm in diameter, but most commonly 11-14 mm. Height of corallum up to 3 mm in specimen with diameter of 16 mm, but most specimens generally much shorter, about 1.5 mm.

Calice exclusively monocentric. Calicular margin circular to subcircular in outline. CD equal to diameter of corallum. Depth of calice generally very shallow, at most only about 1 mm.

Septa well-developed, very weakly exsert (less than 0.5 mm) beyond calicular margin, those of earlier cycles primarily laminar and solid, those of later cycles laminar with few perforations. Each septum composed of a loose, single fan system of trabeculae. Septal perforations secondarily filled, especially on septa of earlier cycles. Trabecular microstructure not preserved. Number of septa variable and directly related to diameter of corallum. For examples: CD 9 mm, 48 septa; CD 10.3 mm, 68 septa; CD 11.5 mm, 72 septa; CD 12.5 mm, 82 septa; CD 14 mm, 100 septa; CD 20 mm, about 144-156 septa. Septa consistently hexamerally arrayed and inserted in from four to five complete cycles. Some S_6 usually present in coralla with a diameter greater than 13 mm. Size relationship among septa: $S_1 \geq S_2 \geq S_3 > S_4 > S_5 > S_6$. Septa of first three cycles blade-shaped in cross section, straight, and nearly equal in length. Width of S_1-S_3 about 0.2-0.4 mm, generally widest distally and aborally at junction with wall and tapered orally and axially. Usually S_1, S_2 and most S_3 extend to columella. S_4 slightly shorter than S_3 and inserted close to periphery of columella, within 0.5 mm. S_5 noticeably much shorter than S_4 and inserted at about 2.5 mm from corallite axis, or about 2.0 mm from margin of columella. S_6 usually weakly developed, short, and present only along peripheral margin of calice. Interseptal spaces approximately as wide as septa. Synapticulae developed aborally, possibly as part of wall structure. Synapticular rods about 0.2 mm in diameter and spaced 3 per mm along radius of corallum. Synapticular rods also occur aborally between S_5 and adjacent S_2. Lateral surfaces of septa coarsely granulated or carinate, the structures spaced about 5-6 per mm along distal edge of larger septa. Septal margins uneven, especially toward axis of corallum, and ornamented with beads or dentations, the latter spaced about 3-4 per mm, slightly wider toward distal end. Distal edges of margins oriented nearly vertical. Pali-like dentations occur on axial portions of septal margins of S_1-S_3 and cause columella to appear much wider and more papillose.

Columella well-developed, trabecular, spongiose, orally papillose, vertically continuous, roughly circular in cross section, and narrow. Width of columella usually less than one-sixth the CD, but even smaller in aboral region of axis. Columella contributed to by trabecular extensions from axial inner margins of septa of first three cycles.

Wall primarily synapticulothecal and secondarily filled and basally thickened by epitheca. Entire mural structure solid, without perforations, and about 1 mm thick. Endotheca absent.

Base of corallum covered by epitheca and slightly aborally convex or concave, often with broad, concentric undulations. Small, conical projection from center of base (peduncle?) of some specimens indicates that some specimens may have been attached when young. Surface of epitheca ornamented with concentric pattern of extremely fine growth lines. Costae absent.

Etymology. The species name is the Latin *effrenatus* = unrestrained, for the unattached mode of life of the corallum.

Types. Holotype, IGM-7749, with a CD of 11.6 mm and about 72 septa; figured paratype IGM-7750 (thin section M-07), with a CD of 11 mm and about 72 septa; figured paratype IGM-7751 (thin section M-08), with a CD of 12.8 mm and about 100 septa; and paratype lot IGM-7752, at least 15 specimens, most of which are still attached to the limestone matrix and only partially exposed to view.

The type stratum is the upper member of the Mal Paso Formation, upper Albian-lower Cenomanian. The type locality is in the state of Guerrero, just north of the border with the adjacent state of Michoacán, about 0.75 km north of the rural village of Chumbítaro, Michoacán. The coordinates of this locality, as determined from the Mexican 1:50,000 scale Coyuca de Catalán (E14A74) topographic map, are: 18° 29.3' N, 100° 42.5' W.

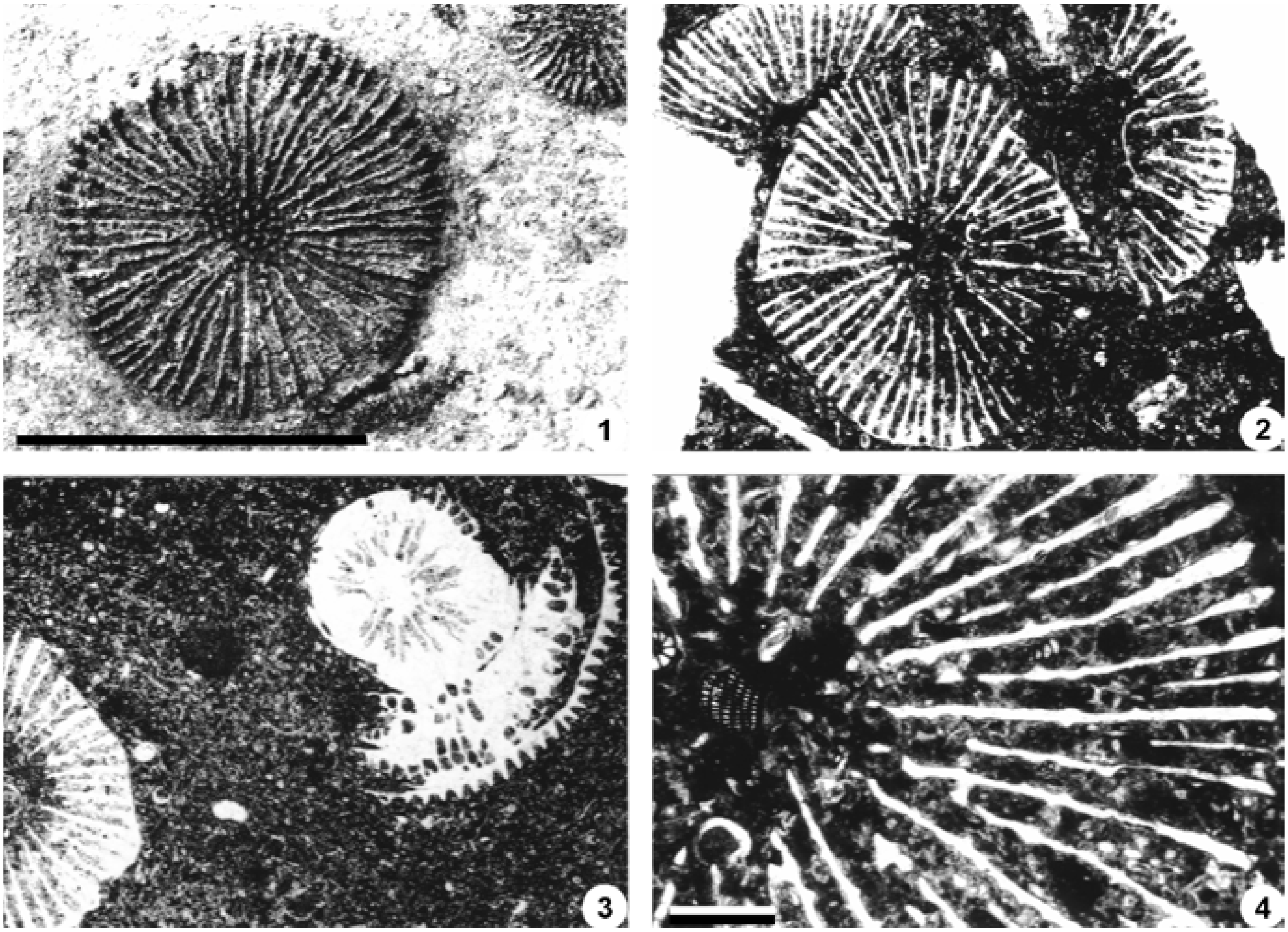

Figure 44. *Paracycloseris effrenatus* n. sp., upper member of the Mal Paso Formation, upper Albian-lower Cenomanian, about 0.75 km north of Chumbítaro, Michoacán, in the State of Guerrero, Mexico. 1, Holotype IGM-7749, detail of weathered oral surface of corallum, scale bar = 1 cm; 2, paratype sample IGM-7750, slightly oblique transverse thin section through portions of three coralla, same scale as Figure 44.1; 3, paratype sample IGM-7751, slightly oblique transverse thin section through basal portions of two coralla, same scale as Figure 44.1; 4, same specimen as shown in center of Figure 44.2, detail of septa, scale bar = 1 mm.

Occurrence. Known only from the type locality. The coordinates of this locality are given above. All of the specimens are from unit MP18 in the upper part of the upper member of the Mal Paso Formation. Numerous specimens were exposed on weathered surfaces of the bed, most of them oriented oral side up and parallel or subparallel to bedding.

The type species of *Paracycloseris*, *P. elizabethae*, is known from the Upper Cretaceous of Jamaica (Campanian), Cuba and Mexico (Vaughan and Wells, 1943, p. 135; Wells, 1956, p. F387). In addition, two unnamed species have been reported from the Albian of Egypt (Abdel-Gawad and Gameil, 1995).

Discussion. The type species, *Paracycloseris elizabethae* Wells, 1934 (p. 86-87, pl. 3, figs. 5-10, pl. 5, figs. 1, 2), was originally described from the Upper Cretaceous of Jamaica (Campanian). *Paracycloseris effrenatus* n. sp. primarily differs from *P. elizabethae* by the smaller diameter of the corallum, the normal hexameral insertion of the septa, and the narrower, much less robust columella.

Abdel-Gawad and Gameil (1995, p. 24, pl. 7, figs. 5-8) described two species of this genus from the Albian of Egypt: *Paracycloseris* sp. 1 and *Paracycloseris* sp. 2. Based on the descriptions and figures, both of these species appear to be morphologically distinct from *P. effrenatus* n. sp. *Paracycloseris* sp. 1 possesses numerous thin dissepiments, numerous simple synapticulae, and a granulated, costate, aboral surface, whereas *P. effrenatus* n. sp. lacks dissepiments, has few synapticulae distributed only near the wall, and has an undulated, noncostate aboral surface. *Paracycloseris* sp. 2 has a costate aboral surface, a septothecal wall, and S_3 that extend only two-thirds the distance from the calicular margin to the axis. In contrast, *P. effrenatus* n. sp. has a noncostate aboral surface, a synapticulothecate wall secondarily reinforced by epitheca, and S_3 that extend nearly to the axis.

Family Latomeandridae Alloiteau, 1952

Genus *Ovalastrea* d'Orbigny, 1849

Ovalastrea d'Orbigny, 1849, p. 10; Vaughan and Wells, 1943, p. 120; Wells, 1956, p. F380.
Ebrayia Ferry, 1870, p. 189-193.
Favoidioseris Wells, 1933, p. 179-180.
Favioseris Wells, 1934, p. 82.
Ambiguastraea Alloiteau, 1952, p. 673.

Type species. *Astrea caryophylloides* Goldfuss, 1827 (p. 66, pl. 22, fig. 7).

***Ovalastrea malpaso* new species**

Figure 45

Diagnosis. Corallum massive, typically hemispherical or subspherical, and frequently relatively large in size. Calices relatively large, CD 6-12 mm, and laterally spaced 2-7 mm apart. Septa fenestrate axially and numerous, usually four complete cycles and about half of fifth cycle.

Description. Corallum colonial, attached, plocoid, massive, hemispherical or subspherical, costate, and typically relatively large in size, up to at least 30 cm in diameter and 25 cm in height. Colony formation by intratentacular budding. Linkages within polystomodaeal calices indirect, trabecular.

Corallites well-delineated, generally cylindrical, but often laterally compressed or subflabellate in appearance orally. Corallites of upper region of corallum packed more closely together than those of lateral or lower regions. Corallite axes oriented perpendicular to surface of corallum. Oral portions of corallites usually slightly protuberant about 1-4 mm above intercorallite coenosteal areas.

Calices distinct, typically monocentric and less commonly dicentric or rarely tricentric, the latter two morphologies produced by incipient intratentacular budding. Calicular margin of monocentric calices generally circular, subcircular, or elliptical in outline. Calicular margin of polystomodaeal calices usually either elliptical or irregularly elliptical in outline. CD variable from about 6 to 12 mm on monocentric calices; GCD slightly larger on polystomodaeal calices. Distance between calices variable, shorter on upper areas of corallum and slightly longer on lateral and lower areas of corallum; overall range about 2-7 mm. Calices concave, about 2-4 mm in depth.

Septa well-developed, non-exsert, laminar peripherally and fenestrate axially. Each septum composed of a single fan system of trabeculae. Trabecular microstructure not preserved. Number of septa variable, usually numerous, and proportionately fewer in smaller calices and more in larger monocentric calices or di- or tricentric calices. As examples: subcircular calicular margin with CD of 8 x 9.5 mm, 66 septa; irregularly elliptical margin with CD of 8 x 13 mm, 78 septa; elliptical margin with CD of 9 x 13 mm, 79 septa. Septa typically arrayed in at least four complete cycles with a portion of the fifth cycle usually present also. Symmetry of septal arrangement not apparent; expected hexameral pattern of cyclical septal insertion obscured, possibly disrupted by mode of colony formation (intratentacular budding). Size relationship among septa: $S_1=S_2\geq S_3\geq S_4>S_5$. S_1 and S_2 laminar to slightly blade-shaped in cross section and about 0.2 mm in width. Septa of each successive cycle only slightly smaller than those of the previous cycle. Commonly S_1, S_2, S_3, and a few of the S_4 extend to columella. Septal trabeculae cylindrical, circular to subcircular in cross section, and spaced 4-6 per mm along length of septa. Interseptal spaces approximately equal to, or slightly wider than, width of widest adjacent septa. Synapticulae absent except near wall. Lateral surfaces of septa uneven and carinate or granulate in appearance due to fenestrate trabecular structure of septa. Septal margins ornamented with beads or dentations spaced about 5 per mm along upper edge of septa. Distal edges of septa generally thickened slightly at junction with wall and continuous beyond wall and into coenosteum as costae. Axial portions of septal margins of S_1-S_3 commonly intermeshed with columella.

Columella well-developed, trabecular, spongiose, highly porous, and vertically continuous. Columella primarily composed of loosely intertwined trabecular rods with additional structural contributions from axial inner margins of S_1-S_3 and some S_4. Columella typically 2-3 mm in diameter, or about one-fourth to one-third the CD.


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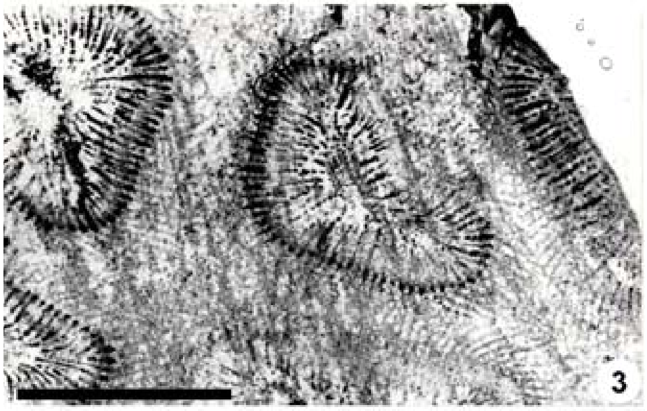
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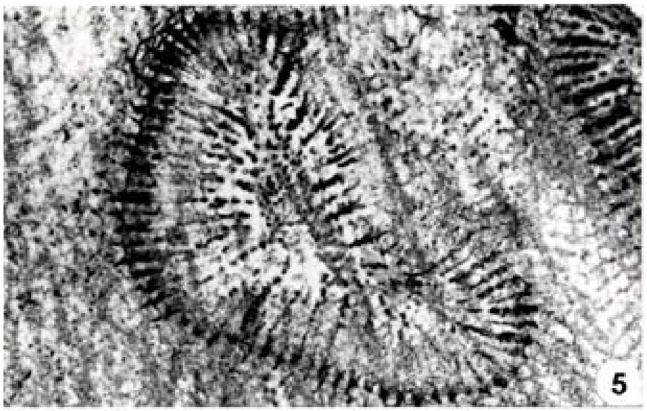
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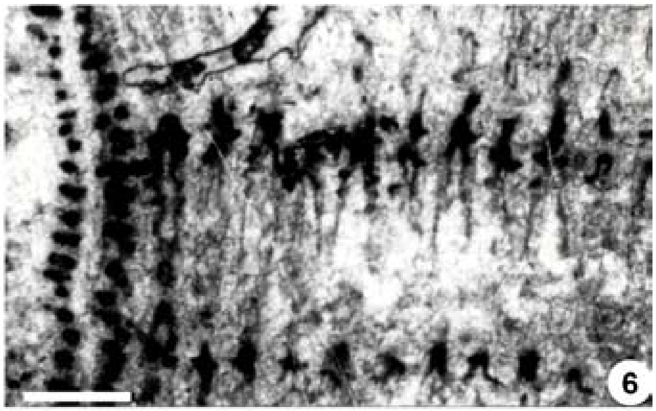
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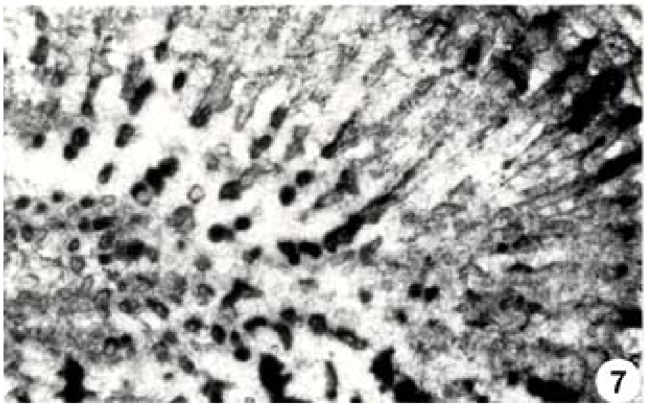
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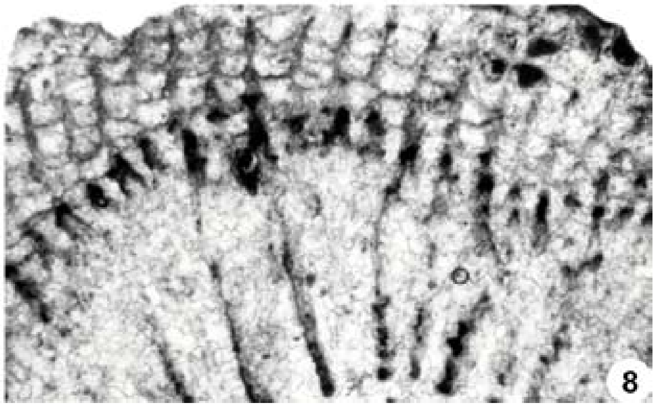
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Wall well-developed, synapticulothecal, perforate, and about 0.8-1.0 mm in thickness. Endotheca absent.

Coenosteum extensively developed between corallites and composed of layered or laminated vesicular exothecal dissepiments; thickness of individual layers ranges from 0.8 to 2.0 mm. Coenosteal surfaces generally concave, depressed areas between the protuberant calices.

Costae robust, structurally continuous with septa and nearly equal in size, those of latest cycles only slightly smaller than those of earlier cycles. Costae wedge-shaped in cross section, about 0.2 mm in height, and spaced about 3-4 per mm. Crests of costae sharp and ornamented with dentations similar to those of the septal margins. Width of intercostal furrows about equal to, or slightly wider than, width of costae.

Etymology. The species is named for the Mal Paso Formation, the type stratum.

Types. Holotype IGM-7753, about 19 x 23 cm in diameter and 20 cm in height, with three thin sections (M-13 through M-15); and paratype IGM-7754, about 12 x 13 cm in diameter and 8 cm in height. The holotype is a massive corallum from the coral reef zone (unit MP13), whereas the paratype is a portion of a massive corallum from lower in the section, unit MP5.

The type stratum is the upper member of the Mal Paso Formation, upper Albian-lower Cenomanian. The type locality is in the state of Guerrero, just north of the border with the adjacent state of Michoacán, about 0.75 km north of the rural village of Chumbítaro, Michoacán. The coordinates of this locality, as determined from the Mexican 1:50,000 scale Coyuca de Catalán (E14A74) topographic map, are: 18° 29.3’ N, 100° 42.5’ W.

Occurrence. Known only from the type locality. The coordinates of this locality are given above. This species is one of the primary contributors to coral reef development in the upper member of the Mal Paso Formation. Large, massive, hemispherical colonies of this species are common in the reef horizon (MP13), and smaller colonies occur sporadically in some of the limestone beds stratigraphically below the reef zone as well.

Discussion. The massive, plocoid growth form of the corallum and the polystomodaeal condition of some of the calices support the determination that this species is a member of the genus *Ovalastrea*. Several species of *Ovalastrea* have been described from the American Cretaceous, but none of them possesses the characteristics of *Ovalastrea malpaso* n. sp.

Wells (1933) described two species and one variety of this genus under the name *Favoidioseris* Wells, 1933, which has been considered a junior synonym of *Ovalastrea* (see Vaughan and Wells, 1943, p. 120; Wells, 1956, p. F380). Therefore, the species of *Favoidioseris* subsequently have been reassigned to *Ovalastrea* (see Cairns, 1991, p. 8). *Ovalastrea fredericksburgensis* (Wells, 1933, p. 180-182, pl. 21, figs. 15-18), from the Comanche Peak Formation and Edwards Limestone (both middle Albian) of Texas, is unlike the *O. malpaso* n. sp. in that it characteristically formed smaller coralla with smaller corallites. The variety *O. fredericksburgensis* var. *alta* (Wells, 1933, p. 182, pl. 21, fig. 19), also from the Comanche Peak Formation, Texas, formed small coralla also, but possesses corallites that are even smaller (average CD of 4 x 5 mm) and more protuberant (up to 3.5 mm) than the typical form. *Ovalastrea pecosensis* (Wells, 1933, p. 182-183, pl. 22, figs. 4, 5), from Denton age (Albian) strata in western Pecos County, Texas, is morphologically similar to the Mexican specimens with regard to arrangement of corallites, shapes of calicular margins, and range of CD, but the corallum is very much smaller than that of *O. malpaso* n. sp. Furthermore, according to Wells (1933), the specimens of *O. pecosensis* are silicified, distorted, and badly weathered, and therefore a more detailed comparison

Figure 45. *Ovalastrea malpaso* n. sp., holotype IGM-7753, upper member of the Mal Paso Formation, upper Albian-lower Cenomanian, about 0.75 km north of Chumbítaro, Michoacán, in the State of Guerrero, Mexico. 1, Portion of weathered oral surface of corallum, scale bar = 1 cm; 2, detail of same surface, scale bar = 1 cm; 3, transverse thin section of corallites from lower side of corallum, skeletal material mostly recrystallized, scale bar = 1 cm; 4, longitudinal thin section, mostly recrystallized, upper edge of calice along top of figure, coenosteal structure in upper right; note relic skeletal growth bands in lower left of figure, scale bar = 1 cm; 5, transverse thin section, detail of di- to tricentric corallite, same scale as Figure 45.4; 6, longitudinal thin section, detail of septa in center and right of figure and synapticulothecal wall along left margin of figure, scale bar = 1 mm; 7, transverse thin section, mostly recrystallized, detail of columella, lower left of figure, and septa; note septal fenestrae in vicinity of columella, same scale as Figure 45.6; 8, transverse thin section, detail of synapticulothecal wall across center of figure (left to right), septa in lower half of figure, and coenosteal dissepiments with costae, top portion of figure, same scale as Figure 45.6.

of these specimens with the Mexican species is not possible. Wells (1933, p. 183) also noted a strong morphological similarity between *O. pecosensis* and a Cenomanian species from France, *O. ambigua* (Fromentel, 1879), except that the columella is false in the latter species.

The genus *Favioseris* Wells, 1934, also is a junior synonym of *Ovalastrea* (see Vaughan and Wells, 1943, p. 120; Wells, 1956, p. F380). Therefore, the type species of *Favioseris*, *F. anomalos* Wells, 1934 (p. 82-83, pl. 4, figs. 19, 20), is provisionally transferred to *Ovalastrea*. *Ovalastrea anomalos* (Wells, 1934), known from the Upper Cretaceous of Jamaica, primarily differs from *O. malpaso* n. sp. by the smaller size of the corallum, the much smaller corallites (average CD of circular calices 3 mm), the smaller number of septa (24-45), and the absence of a columella.

Ovalastrea rutschi Wells, 1948 (p. 613, pl. 90, figs. 3, 4), from the Lower Cretaceous of the Central Range and the Toco Formation, Trinidad (Barr, 1962, p. 394), differs from the Mexican species in several respects including the smaller size of the corallum, the permanently monocentric calices, the smaller corallites (CD range 2.0-3.5 mm), and the smaller number of septa (as many as 42).

Another morphologically similar Mexican species, from the Lower Cretaceous San Juan Raya Formation, state of Puebla, was described by Reyeros (1963, p. 12-13, pl. 2, fig. 5, pl. 3, figs. 1-2) as *Baryphyllia confusa* (d'Orbigny, 1850c). However, this species primarily differs from *O. malpaso* n. sp. by the pedunculate attachment and relatively very small size of the corallum.

Family Microsolenidae Koby, 1890

Genus *Dimorpharaea* Fromentel, 1861

Type species. *Microsolena koechlini* Haime, in Milne Edwards, 1860 (p. 202), by subsequent designation (Gregory, 1900, p. 188, following Koby, 1887, p. 387).

***Dimorpharaea barcenai* (Felix, 1891)**

Figure 46

Thamnastraea barcenai Felix, 1891, p. 144-145, pl. 22, fig. 3, pl. 23, figs. 7, 7a; Felix, 1914a, p. 50.

Dimorpharaea barcenai (Felix, 1891). Gregory, 1900, p. 189; Wells, 1932, p. 253, pl. 37, fig. 4; 1933, p. 90; Sikharulidze, 1979, p. 303; 1985, p. 44-45, pl. 20, fig. 3; Császár and Turnšek, 1996, p. 431, 434, fig. 8.9; Löser, Bach, and Müller, 2002, p. 42.

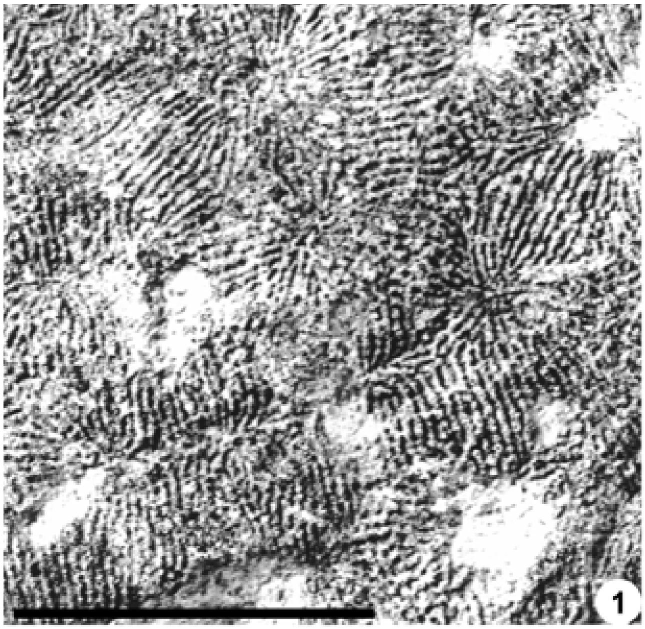
Astraeofungia barcenai (Felix, 1891). Löser, 2006, p. 48, fig. 3J.

Description. Corallum colonial, attached, thamnasteroid, massive, convex orally, tapered toward base, and finely septocostate. Size of single specimen 85 x 80 mm in width and 50 mm in height. Colony formation by circumoral polystomodaeal budding and some intramural polystomodaeal budding with temporary indirect, trabecular linkages.

Corallites generally subcylindrical or weakly subprismatic in shape, laterally confluent with each other due to lack of walls, and arranged with axes subparallel to each other and perpendicular to upper surface of corallum. Calices superficial, typically well-defined axially but vaguely delineated peripherally, and usually monocentric unless in process of intramural budding. Calicular margin weakly delineated, generally subcircular to subpolygonal, but laterally elongate in cases of incipient budding. CD slightly variable, approximately 3-6 mm. Calices concave, very shallow, less than 1 mm in depth. Calicular centers well-defined, about 1 mm in diameter, and commonly spaced about 4-6 mm from center to center. Calicular centers of corallites in process of budding laterally elongate to 4 mm.

Septa well-developed, weakly exsert, regularly fenestrate, and structurally continuous as septocostae. Each septum composed of a single fenestrate fan system of trabeculae. Trabecular microstructure not preserved. Symmetry of septal arrangement and number of septal cycles obscured by corallite budding; however, septa generally radially arrayed from calicular centers and overall number of septa indicates that up to four cycles of septa may be present. Number of

Figure 46. *Dimorpharaea barcenai* (Felix, 1891), IGM-7755, upper member of the Mal Paso Formation, upper Albian-lower Cenomanian, about 0.75 km north of Chumbítaro, Michoacán, in the State of Guerrero, Mexico. 1, Oral view of part of weathered upper surface of corallum, scale bar = 1 cm; 2, transverse thin section of central upper area of corallum, partially coarsely recrystallized, with cross sections of numerous endolithic bivalves, same scale as Figure 46.1; 3, longitudinal thin section, same scale as Figure 46.1; 4, transverse thin section, detail of calicular center, columella, septa, and septocostae, partially coarsely recrystallized, scale bar = 1 mm; 5, longitudinal thin section, detail of septa-septocostae and synapticulae, same scale as Figure 46.4; 6, transverse thin section, detail of incipient intramural budding of corallite, trabecular columella, and septa-septocostae, same scale as Figure 46.4.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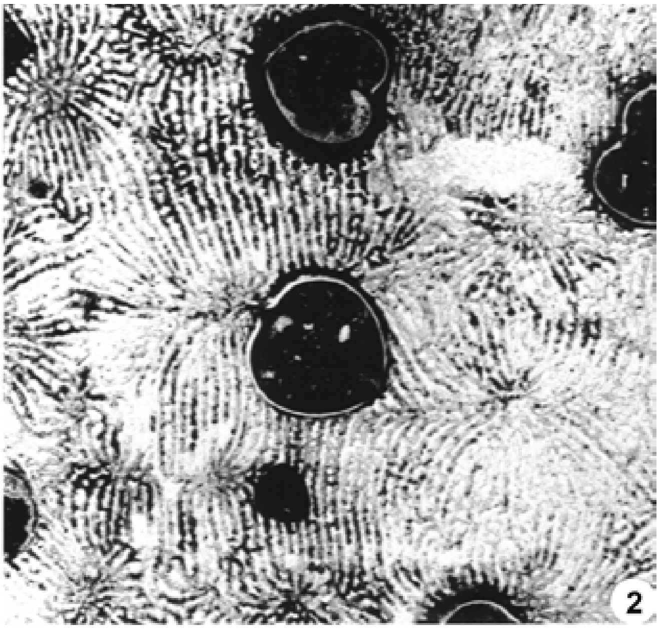
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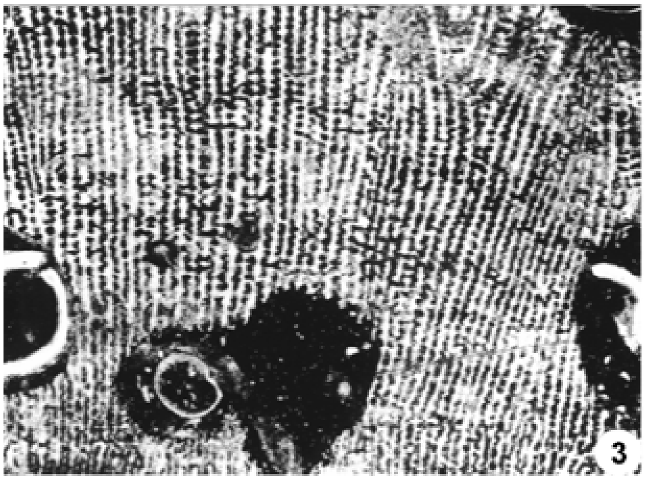
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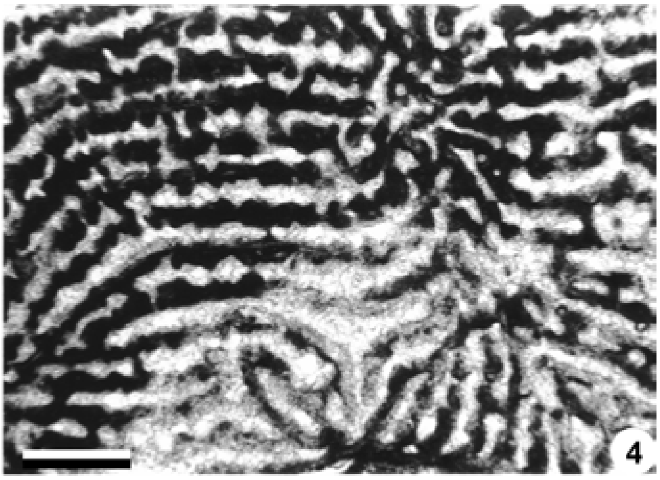
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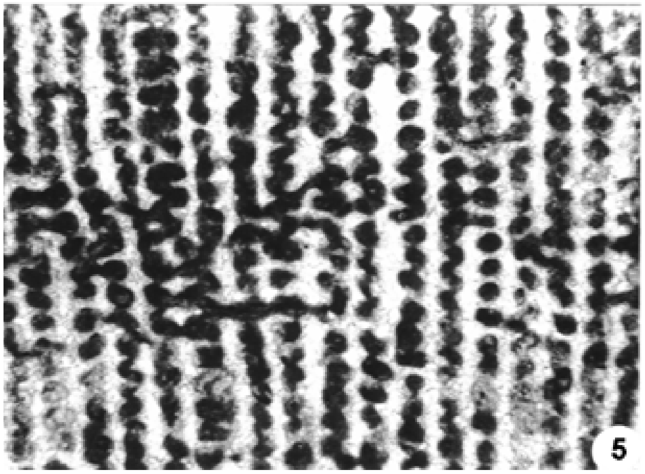
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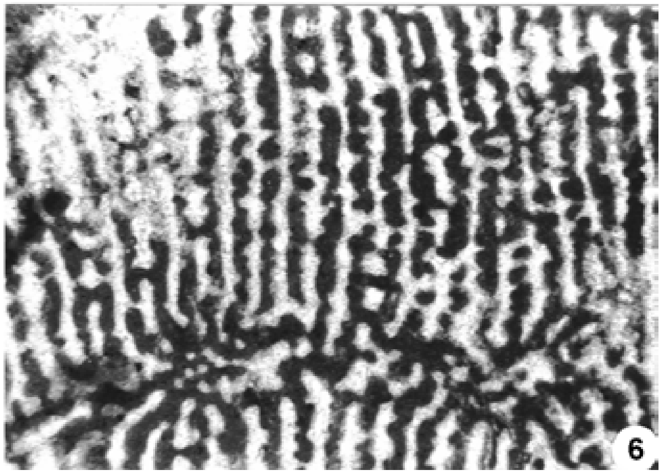
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septa variable, about 8-15 present in vicinity of corallite axis, but about 20-40 present peripherally along calicular margin. Approximate size relationship among septa: $S_1 \approx S_2 \geq S_3 > S_4$. S_1, S_2, and some S_3 commonly extend to margin of axial region. S_4, or those of higher cycles, typically inserted peripherally by bifurcation of septa of previous cycles. Septa straight or gently curved and subequal in width, about 0.2 mm. Septal fenestrae about 0.2 mm in diameter. Interseptal spaces about equal to or slightly wider than width of septa. Synapticulae abundant throughout corallum, simple, cylindrical or rod-shaped, and vertically spaced about 4-5 per mm. Lateral surfaces of septa uneven and undulate or carinate in appearance due to fenestrate structure of septa and numerous fusions with synapticulae. Septal margins beaded orally; beads spaced about 3-4 per mm along length of septocostae. Pali-like trabecular structures, or columellar papillae, often present on inner edges of septa which surround calicular axis.

Columella weakly developed, trabecular, vertically continuous, orally papillose, usually subcylindrical and about 0.5-0.8 mm in diameter, but occasionally laterally elongate as trabecular linkage between corallites in process of budding and up to about 4 mm in length. Columella composed of few, intermeshed trabecular rods about 0.2 mm in diameter arranged in an open meshwork and usually contributed to by lateral trabecular extensions from inner edges of adjacent septa.

Wall absent. Lateral transitions between corallites often indicated by convergence of or inflection in confluent septocostal-synapticular skeletal structure. Endothecal and exothecal dissepiments absent.

Costae well-developed, structurally similar to and continuous with septa, and typically confluent with those of adjacent corallites. Upper surface of corallum finely septocostate with very low relief. Septocostal areas between calicular centers orally convex, rounded and low. Septocostae laterally spaced about 6-7 per 2 mm, or about 15-18 per 5 mm.

Material examined. One corallum, IGM-7755, with four thin sections (M-41 through M-44). Numerous bivalve endobionts occur within the colony.

Occurrence. The specimen was collected from the coral reef horizon of the upper member of the Mal Paso Formation, upper Albian-lower Cenomanian. The fossil locality is in the state of Guerrero, just north of the border with the adjacent state of Michoacán, about 0.75 km north of the rural village of Chumbítaro, Michoacán. The coordinates of this locality are: 18° 29.3' N, 100° 42.5' W.

This species was originally described from the Neocomian strata near Tehuacán, state of Puebla, Mexico. The only other reported occurrence in North America is in the lower Glen Rose Formation (lower Albian) on Blanco River, Hays County, Texas. Other reported occurrences are from the Hauterivian-Aptian of Hungary and the lower Barremian of Georgia (SSR).

Discussion. The morphological characteristics of the specimen described above are essentially the same as those described previously for *Dimorpharaea barcenai* (Felix, 1891), therefore the corallum is referred to that species. The basal portion of the specimen is not as pedunculate as the specimen figured by Felix (1891, pl. 23, figs. 7, 7a), but it is tapered toward its base and the peduncle may not have been preserved. Additionally, the upper surface of the corallum is slightly convex, whereas the specimen figured by Felix (1891) has a nearly flat upper surface. Except for these minor differences in corallum shape, the characteristics of the specimens appear to be the same.

PALEOECOLOGY

INTRODUCTION

Taxonomically diverse assemblages of colonial corals and other organisms have been discovered at certain horizons in the Cumburindio and Mal Paso formations. Many of these organisms are both laterally and stratigraphically closely spaced within the rock and frequently in direct contact with or attached to each other. The growth forms of colonial corals within these high diversity intervals also span a fairly broad spectrum and include, for examples, encrusting, massive, ramose, foliaceous, and phaceloid corallum morphologies. The occurrence of these diverse growth forms and their juxtaposition within the rock indicate that the deposits were organically bound concurrently with coral growth and local sedimentation. The limestones produced by the combination of these biological and depositional factors include bafflestone, bindstone, and framestone. Evidence for the former presence of some amount of topographic relief on the depositional surfaces within these deposits was observed at some localities. Overall, the paleontologic and lithologic characteristics of these horizons are similar to those described for other Early and middle Cretaceous coral reef deposits.

Analogies with living corals indicate that the majority of the fossil corals from the Cumburindio and Mal Paso formations were reef-building species. Corals that build reefs or contribute to the development of reefs also are typically hermatypic corals (constructional zooxanthellate corals; Schuhmacher and Zibrowius, 1985), which are corals that live in symbiotic relationship with a microscopic, photosynthesizing alga, called zooxanthellae, harbored in their polyps. However, because the symbiotic algae are in the soft, living parts of the coral and not in the skeleton, direct evidence for the presence of alga is not preserved in the fossil record (Cowen, 1983, 1988). Therefore, the inference that most of the coral species were zooxanthellate is based on analogy with extant forms (Wells, 1957), specifically the preserved morphological features of the corals, and sedimentological evidence. The arrangement and size of the corallites, the relatively high levels of colony integration, the colony growth forms, and the sizes and shapes of the coralla (Coates and Oliver, 1973; Hubbard, 1973; Wells, 1973; Coates and Jackson, 1985, 1987), along with the characteristics of the enclosing lithologies (Hubbard and Pocock, 1972), support the interpretation that the majority of the fossil coral species were zooxanthellate. Furthermore, many of the associated biotic components also suggest a shallow marine habitat within the photic zone.

The symbiotic relationship between corals and photosynthetic algae effectively limits the ecologic distribution of constructional zooxanthellate corals to substrates in relatively shallow (< 100 m), well-lighted, warm, marine water. However, this ecological definition is an overly simplified generalization (see Rosen, 1977). In reality, the observed range of any one of the supposed controlling ecological parameters is affected by other conditions of the environment. Thus, the precise ecological limitations on the distribution of these corals are dependent on the interplay of a vast number of environmental factors (Huston, 1985). Of these factors, water temperature is one of the most important with regard to modern coral reefs, but whether the limitation is physiological or ecological is unclear. The optimum temperature for zooxanthellate coral growth is variable because it is related to other local environmental conditions as well, including light intensity, nutrient supply, and salinity (Goreau and Goreau, 1960; Kinsey and Davies, 1979; Tomascik and Sander, 1985; Burke, 1994; Veron, 1995). For examples, the optimum temperature for growth in Hawaiian reefs is about 26°C (Jokiel and Coles, 1977), whereas in the Floridian reefs it is between 28 and 30°C (Shinn, 1966). The coral biotas of both the Cumburindio and Mal Paso formations indicate that the marine water generally was within this temperature interval and of normal salinity.

Azooxanthellate corals, the corals that characteristically lack symbiotic algae, are known from shallow-water habitats as well (for examples see Schuhmacher, 1984; Hubbard and Wells, 1986). However, because they lack algal symbionts, they are not restricted to shallow-water habitats. Some extant azooxanthellate colonial species form coral build-ups in deeper, colder, aphotic marine environments (for examples, see Neumann et al., 1977; Reed, 1980; Mullins et al., 1981; Fricke and Hottinger, 1983; Fricke and Knauer, 1986; Newton et al., 1987; Messing et al., 1990; Hovland et al., 1998). This ecologic distinction is clarified because one of the species from the Mal Paso Formation, the colonial dendrophylliid *Blastozopsammia guerreroterion* Filkorn and Pantoja-Alor, 2004, may have been a member of this group. The paleoecologic implications of this species have been examined in an earlier publication (Filkorn and Pantoja-Alor, 2004) and further discussed in the systematic paleontology section of this study, therefore they are only briefly reviewed below.

Species diversity of modern reef corals and the overall abundance of coral reefs both decrease as mean temperature decreases, which notably also correlates with an increase in latitude (Veron, 1995). Modern coral reefs are limited by a minimum sustained temperature of 18°C, beyond which point partial or total mortality occurs depending on the duration of exposure. Few build-ups of zooxanthellate reef corals survive at temperatures below this minimum (Macintyre and Pilkey, 1969; Burns, 1985). However, the actual limiting factor with regard to latitudinal distributions of coral reefs may not be the mortality caused by the lower temperatures, but rather the decrease in coral metabolism (Clausen and Roth, 1975; Crossland, 1984) and the increase in competition from macroalgae (Johannes et al., 1983). Some coral species that survive near their lower temperature limit at localities in higher latitudes may develop unusual growth forms or exhibit other distinct morphologies from repeated events of partial mortality and subsequent regeneration (Veron, 1995; also see Hughes and Jackson, 1980). At higher temperatures, modern reef corals generally are limited to a maximum sustained temperature of about 30 to 34°C (Veron, 1995), although some occurrences just above this upper limit have been noted (Kinsman, 1964). The higher values of the maximum occur in the tropics, whereas the lower values occur in temperate zones (Coles and Jokiel, 1977). These higher temperatures cause heat stress and disruption of the coral-zooxanthellae symbiotic relationship, a process known as bleaching. Many of the modern large-scale bleaching events have been correlated to temperature increases caused by El Niño-Southern Oscillation climatic fluctuations, but localized tide-induced heat stress bleachings are common in the tropics (Veron, 1995). Bleaching, either directly or indirectly, can cause mortality of coral reefs at both local and regional scales.

Another major factor in the distribution of modern zooxanthellate reef corals is the amount of light in the ambient marine environment. Light is essential to these corals because their algal symbionts require it for photosynthesis (Goreau and Goreau, 1960; Veron, 1995). In general, the intensity of solar light is highest near the surface of the water and it decreases with increasing depth. This decrease in light intensity with increasing water depth has a marked influence on the depth distribution of reef corals (Huston, 1985). Thus, the deepest habitats of reef corals are at least in part delineated by the minimum amount of light required for photosynthesis to occur in their algal symbionts. Although the specific light requirement of the algal symbionts is a limiting factor, the lower depth limit of photosynthesis is variable because it is in turn affected by the local environmental conditions of the overlying water column, such as turbidity caused by suspended sediment and plankton. Several taxonomically distinct species of algal symbionts have been identified in extant corals, but typically only one kind is present in any single coral species (Rowan and Powers, 1991). Thus, the maximum depth for a particular coral species is partly determined by the light requirement of the specific kind of zooxanthellae that it contains. However, the differences in minimum light requirements alone may not be significant enough to cause a marked decrease in diversity with depth. Dense assemblages of taxonomically diverse and relatively large zooxanthellate coral colonies similar to those in shallow-water reef habitats have been reported from depths of as much as 70 m (Goreau and Wells, 1967; Kühlmann, 1983; Fricke and Meischner, 1985).

Although intense light is available at and near the surface of the water, coral species diversity in very shallow reef habitats frequently is relatively low. Generally reef coral taxonomic diversity increases from 0 to 15 m depth, attains a maximum at depths of about 15 to 30 m, and starts to decrease at approximately 25 to 40 m (Huston, 1985). Based on these observations, species diversity in shallower habitats is controlled by factors other than light intensity. Among these other factors are several kinds of ecological and biological disturbances that affect the ecology of the reef and introduce a higher degree of variability to the environment. These shallow-water disturbances include: periods of subaerial exposure during unusually low extremes in low tides; periods or events with potentially destructive wave energy; pulses of sedimentation (also important in deeper habitats); high rates of algal growth (or algal blooms); and changes in intensity of grazing by herbivores and corallivores (Moyer et al., 1982; Huston, 1985; Karlson and Hurd, 1993; Aronson and Precht, 1997). Thus, taxonomic diversity and species distribution within shallow-water reef habitats can be greatly affected by the actual chronology and sequence of disturbance events that occurred throughout the history of the reef (Potts, 1984; Hughes, 1989; Jackson, 1991).

The influence of differences in light intensity, hydrological energy, and type of substrate, or any combinations thereof, with concurrent changes in depth of substrate can cause different growth patterns among colonies of the same coral species as well as differences in growth rate (Wood Jones, 1907; Vaughan, 1910, 1911, 1912, 1913a, 1913b, 1914a, 1914b, 1914c, 1915, 1919b; Mayor, 1924; Edmondson, 1929; Yonge, 1931, 1935; Shinn, 1966; Graus and Macintyre, 1976; Graus et al., 1977; Oliver et al., 1983; Höfling, 1989; and others). However, just because a particular coral species has a fast rate of growth does not necessarily imply that it also has ecologic dominance over other coral species that grow more slowly: interspecific aggression also is an important consideration (Lang, 1973). At a local scale, even the effects of gradients in hydrological or other environmental conditions with depth can result in different distributions for different species and induce an ecological-biological zonation (for examples see Goreau, 1959; Maragos, 1974; Stearn, 1982).

Intraspecific, environmentally induced morphological variability is frequently observed in extant reef corals (Budd, 1993; Hoeksema, 1993), but it is often difficult to determine whether the morphological variation among fossil coralla was caused by differences in paleoenvironmental factors or genetic variation (Barnabás, 1954; Pfister, 1977; Foster, 1979, 1985). However, the observation that a high degree of intraspecific morphological variability can occur within the same habitat (Van Veghel and Bak, 1993; Budd et al., 1994; Weil and Knowlton, 1994) implies that it may have occurred in fossil coral species as well. Furthermore, the potential effects of both paleoenvironmental and genetic variations within a single lineage over relatively long intervals of time (millions of years) may result in a phylogeny without any apparent long-term morphological trends (see Budd and Coates, 1992).

Rudist bivalves also are common in the Cumburindio and Mal Paso formations and frequently they occur adjacent to corals within the same stratigraphic horizons. The paleoecological significance of the rudists, an extinct group, is based primarily on paleontological studies. The members of this group exhibit a fairly broad range of growth orientation and valve morphology, each combination of which was better adapted to a particular ecological setting (for examples see Yonge, 1967; Skelton, 1976, 1978, 1979, 1982, 1985; Kauffman and Sohl, 1979; Scott, 1979, 1981; Kauffman and Johnson, 1988; Ross and Skelton, 1993). Whether rudists harbored photosynthesizing algae in a symbiotic relationship similar to that of zooxanthellate corals is still uncertain and debatable (see Vogel, 1975; Kauffman and Johnson, 1988; Lewy, 1995). The fact that rudists and corals frequently do not occur together may indicate that for the most part their ecological niches, including specific requirements and limitations, were distinctly different (see Scott, 1979, 1981, 1984b, 1988; Scott et al., 1990). Rudists may have been able to tolerate and thrive in habitats that were unfavorable for corals, such as those with relatively higher levels of hydrologic energy or turbidity or with broader ranges of salinity and temperature (Lewy, 1995). Furthermore, many rudist species of the Early Cretaceous probably were gregarious soft-sediment dwellers on carbonate platforms rather than reef-builders (Gili et al., 1995). The occurrences of rudists encountered during this study and their ecologic and stratigraphic relationships with the corals are discussed below.

The paleoecologic interpretations for the occurrences of the fossil corals described in this study are based on the information outlined above. Because the majority of the corals presumably were zooxanthellate and thus restricted to substrates within the marine photic zone, most of the coral habitats must have been at depths of less than 100 m. However, the relatively diverse coral assemblages and growth forms at some horizons indicate much shallower habitats, probably from about 10 to 30 m. The general lack of well-sorted packstones and grainstones, lithologic evidence for high-energy sedimentary facies, and the ubiquitous presence of carbonate mudstone as the matrix in most of the limestones indicate that most of the coral habitats were near to or below normal wave base. The temperature of the water in these habitats presumably was within the limits observed for extant zooxanthellate reef coral growth, about 20 to 30°C.

Cumburindio Formation

Corals have been collected from the Cumburindio Formation at four localities in the general vicinity of Turitzio, Michoacán (Figure 2). Two of these four localities yielded only one identifiable coral species each. A locality in the lower part of the Cumburindio Formation near the village of Las Eras, about 4.5 km southwest of Turitzio, yielded only one coral specimen, a corallum of the plocoid stylinid *Stylina regularis*

Fromentel, 1862. The northernmost Turitzio locality, situated on the southwestern slope of the southern end of Loma Teremitio, an elongate hill about 1.5 km north of Turitzio, yielded specimens of the plocoid cyathophorid *Cyathophora haysensis* Wells, 1932. The remaining two localities in the Cumburindio Formation contained numerous corals: the Arroyo Los Hornos about 1 km north of Turitzio, and Loma de San Juan, a small hill just south of Turitzio. The positions of the latter three localities, Loma Teremitio, Arroyo Los Hornos, and Loma de San Juan, are aligned north to south and only about 1 km apart from each other, but the lithologies and sequence of sedimentary facies at each of these localities are different. Thus, the vertical succession and lateral facies relationships of the beds at these three localities are a record of the changes in the paleoecologic and paleogeographic settings in this region. The northernmost section of Loma Teremitio is primarily composed of biogenic limestones that laterally become interbedded with volcaniclastics to the south at the Arroyo Los Hornos. Conversely, the southernmost section at the Loma de San Juan is mostly volcaniclastics that laterally become interbedded with limestone beds in the section at Arroyo Los Hornos to the north. Accordingly, the paleoecologic settings of these rocks is mostly shallow marine in the north, grading to carbonate platform in the central area, and becoming more proximal to a source of volcaniclastics in the south at Loma de San Juan while spanning a deep to shallow marine transition. The only coral reef horizon discovered in the Cumburindio Formation is at the top of the southernmost outcrop at the Loma de San Juan.

All but one of the coral species from the Cumburindio Formation are colonial forms with large phaceloid, dendroid or ramose coralla, or small to medium-sized massive plocoid, cerioid, meandroid, thamnasteroid, or hydnophoroid coralla. The growth forms and high level of corallite integration of these coralla indicate that they were zooxanthellate, reef-building coral species. Although many of these corals occurred as isolated individual colonies in the studied stratigraphic sections, one extensive horizon in the upper part of the section at Loma de San Juan contained a highly diverse, autochthonous accumulation of corals that is interpreted as a coral reef

The Cumburindio Formation strata exposed on the southern side of the Arroyo Los Hornos, just below the northwest fence line of Turitzio cemetery, are interbedded fine-grained volcaniclastics and calcareous mudstones that contain isolated, small, massive cerioid coralla and large phaceloid coralla preserved in living position. Unfortunately, almost all of the massive coralla from these beds are completely recrystallized internally and therefore it was impossible to use this material to make taxonomic determinations. One of the species is the same as one that had been identified from a specimen found at the northern locality, the plocoid cyathophorid *Cyathophora haysensis* Wells, 1932. However, based on superficial morphological similarities, some of the same massive species also occur in the middle part of the Cumburindio Formation section at the Loma de San Juan. One of the most abundant corals in the beds adjacent to the Arroyo Los Hornos is the phaceloid calamophylliid *Calamophyllia sandbergeri* Felix, 1891. Coralla of this species range up to at least 30 cm in height and width and many of them are exposed, weathered out in relief, on a ledge of one of the more resistant limestone beds. Although the coralla of this species are abundant at this particular horizon, none was observed to be coalesced or intergrown with other adjacent colonies and thus any potential establishment of a coral reef had not yet attained the thicket stage of development before the horizon was buried by sediment. Smaller coralla of this species also were found to the south in the coral reef zone at the Loma de San Juan.

The thickest, most resistant carbonate strata in the Cumburindio Formation are well-developed rudist biostromes that are exposed both as ledges at knickpoints in the Arroyo Los Hornos and as low-relief ridges and crests on the adjacent slopes. Furthermore, the majority of the carbonate build-ups in the Cumburindio Formation are composed mostly of rudist skeletal material. Only one horizon with a coral-dominated reef facies has been discovered in this unit and that bed is located at the top of the section at the Loma de San Juan, just south of Turitzio. The limestone beds exposed within the Arroyo Los Hornos itself are nearly exclusively composed of rudist bivalves. However, in one part of the section exposed along the thalweg of the Arroyo Los Hornos, a single large, ramose, colony of the microsolenid coral *Thamnarea hornosensis* n. sp. is preserved with abundant valves of the rudists *Praecaprina* sp. and *Caprina* sp. This microsolenid colony appears to have coexisted with the rudists and contributed to the development of a rudist-dominated, rudist-coral biostrome. The preserved portion of this colony is fairly large, about 1.6 m in length and 1.4 m in width, and it exhibits a broad, fan-like shape (see Figure

20). The corallum is composed of numerous subparallel, closely packed, elongate, narrow branches that range from 1 to 2 cm in diameter. An indeterminate species of linear, creeping bryozoan is attached to some of the coral branches (see Figure 20.8). The coral specimen is preserved lying on its side and it appears to have been laterally flattened by compaction, indicating that it was toppled prior to burial. The substrate underlying the coral colony is composed almost entirely of rudist valves. This evidence indicates that the coral specimen colonized the rudist valve substrate and then grew more than a meter vertically while very little if any rudist bioclastic material accumulated around the base of the corallum. The fact that the corallum was originally upright during growth is supported by weathered transverse sections of the same coral species in the next highest limestone bed in the arroyo, where the branches are oriented with long axes vertical, perpendicular to the substrate. No other occurrences of this type of microsolenid coral-rudist association are known from Mexico.

The coral fauna from the Cumburindio Formation section exposed at the Loma de San Juan, just south of Turitzio, is the most diverse Aptian coral fauna discovered in southern Mexico. Although this section is laterally equivalent to the section at Arroyo Los Hornos, the majority of the beds are composed of volcaniclastics and limestone is present only at the base and top of the section. The majority of the corals from this section occurred in situ in these two limestone intervals. Two coral species occurred in living position in the mudstone beds at the base of the section: *Actinastrea pseudominima* (Koby, 1897), and *Cyathophora micrommatos* (Felix, 1891). The coralla of both of these species are similar in shape and size, and both possess a massive to ramose growth form. The same bed also yielded a large species of the ostreid bivalve *Arctostrea* Pervinquière, 1910 (see Pervinquière, 1910a, 1910b). Because the substrate probably was soft, unstable, and otherwise barren except for the corals, it is possible that this bivalve had lived as an epibiont, attached to the corals (see Carter, 1968, p. 461).

Most of the strata above the basal fossiliferous mudstone horizon are composed of gray, medium-bedded, moderately well sorted, medium- and coarse-grained volcaniclastics. Some small massive coralla found scattered on the weathered slopes of the volcaniclastics may have been derived from these beds. These coral species appear to be the same as those that were found to the north in the beds adjacent to the Arroyo Los Hornos. Included in this group of species are: the cerioid isastraeid *Isastrea whitneyi* Wells, 1932; the meandroid haplaraeid *Meandrophyllia sauteri* (Felix, 1891); the cerioid siderastreid *Siderofungia irregularis* Felix, 1891; and the thamnasteroid latomeandrid *Fungiastraea crespoi* (Felix, 1891). Although these coral species evidently lived on soft substrates in environments with relatively high rates of sedimentation, they represent the most abundant massive cerioid, meandroid, and thamnasteroid growth forms collected from the Cumburindio Formation.

The most fossiliferous limestone beds at the Loma de San Juan occur at the top of the hill, in the upper part of the section, and they appear to conformably overlie the bedded volcaniclastics. The entire fossiliferous interval is about 11.3 m thick and composed of three distinct zones. The lowermost unit of these fossiliferous beds is a 0.8 m thick packstone-rudstone bed composed of nerineid gastropods and small colonial corals. This bed is overlain by a tabular 1.5 m thick rudstone bed with abundant valves of the rudist *Amphitriscoelus*. Some of the rudists are preserved with both valves joined together, which suggests that the organisms were not transported prior to burial and that they actually had lived at this site. As preserved, the geometric characteristics of the rudist bed indicate that the rudists did not protrude very far above the surface of the substrate and thus the rudist growth during vertical accumulation of the deposit was constratal and not suprastratal (see Gili et al., 1993, 1995). An extensive, coral-rich boundstone bed conformably overlies the bed of *Amphitriscoelus*. This coral boundstone is at least 9 m thick and it contains the most diverse assemblage of corals found in the Cumburindio Formation. The diversity, growth forms, distribution, and sizes of the colonial corals in this unit indicate that the bed is a coral reef. Therefore, the observation that the base of the coral reef bed conformably overlies the *Amphitriscoelus* rudist bed supports the interpretation that some later Cretaceous coral to rudist assemblage successions may have been environmentally induced and not the result of competition for the same ecologic niche (see Gili et al., 1995; Filkorn, 2002b). The strata at this locality are significant because they contain the first recognized occurrence of a rudist- to coral-dominated assemblage succession from the Lower Cretaceous strata of southwestern Mexico. Although the faunal succession at the base of the unit is preserved, the upper bounding surface of the coral reef and its contact with any overlying unit are not exposed at this locality because the section is truncated by the present surface of erosion. Therefore the actual original thickness of the coral reef bed and the cause for the termination of reef growth are unknown. However, beds of volcaniclastics exposed near the base of the dip slope on the eastern side of the Loma de San Juan suggest that the coral reef may have been buried during a resurgence of local volcanic activity.

The most diverse coral fauna and the majority of coral species known from the Cumburindio Formation are from the coral reef horizon in the upper part of the section at the Loma de San Juan. The coral fauna is dominated by colonial species with massive, ramose, or foliaceous growth forms that typically are closely spaced or directly adjacent to each other. The largest corallum collected from this coral reef zone is a massive colony of the trochoidomeandrid *Rhipidomeandra bugrovae* Morycowa and Masse, 1998, that is about 24 - 26 cm in diameter and 13 cm in height. The most abundant coralla are massive and foliaceous species, most commonly members of the Faviidae, including the hydnophoroid *Eohydnophora ovalis* Masse and Morycowa, 1994, and the meandroid *Eugyra lanckoronensis* (Morycowa, 1964). Other commonly encountered species are microsolenids, including large, pedunculate, plate-like coralla of *Polyphylloseris conophora* (Felix, 1891) and smaller, massive colonies of *Microsolena guttata* Koby, 1897. Small coralla of the massive actinacidid *Actinaraea michoacanensis* n. sp. and the ramose calamophylliid *Calamophyllia sandbergeri* Felix, 1891, also are common in the coral reef. Three other species from this coral reef are considered to be rare because each is represented by only one collected specimen: the massive, cerioid amphiastraeid *Amphiastrea aethiopica* Dietrich, 1926; the foliaceous heterocoeniid *Latusastrea alveolaris* (Goldfuss, 1829); and the massive, meandroid synastraeid *Felixastraea mexicana* Reyeros, 1963. The only solitary corals discovered in the Cumburindio Formation are relatively large specimens that are described as a new species of rhipidogyrid, *Saltocyathus cumburindioensis* n. sp. Although it is a solitary coral, this rhipidogyrid species could have been zooxanthellate and it is large enough to have contributed to the development of the coral reef.

The coral species that occur in the argillaceous mudstone at the base of the section at Loma de San Juan are different from those found higher in the section and in the coral reef horizon. This faunal difference is attributed to environmental differences, as evident from the differences in the enclosing lithologies. The coral species discovered in the volcaniclastic lower part of the section at Loma de San Juan, some of which appear to be the same as those found in the strata adjacent to the Arroyo Los Hornos to the north, are relatively minor components of the coral reef horizon. The lithological evidence indicates that the observed vertical faunal succession was not the result of a biologically induced vertical faunal zonation. Evidence of any lateral or vertical faunal zonation within the coral reef horizon was not discernible at this locality.

The most abundant coral specimens from the Cumburindio Formation outcrops adjacent to the Arroyo Los Hornos and the western flank of the Loma de San Juan are small- to medium-sized, encrusting or massive forms which occur as independent coralla scattered throughout the section at different calcareous volcaniclastic horizons. These coralla often have an inverted conical shape with a smoothly convex upper surface in lateral view, and a circular outline in oral view. This shape indicates that the normal upward and outward radiating growth pattern of the colony was able to continue without being affected by high sedimentation rates or impinging adjacent colonies. However, numerous examples of attachment and encrustation by organisms also occur and these indicate that competition for hard calcareous substrates was probably intensified by the relatively small amount of area available for colonization. Coral and mollusk epibiont associations include coral species commonly encrusted on bivalves and gastropods, as well as other coral species, and at least two other different species of bivalves commensal with corals, one typically found attached to the surfaces of coral colonies and the other, possibly a species of mytilid, found exclusively bored into coral skeletal material (for examples of boring commensal mytilids, see Yonge, 1955; Goreau et al., 1969, 1970, 1972, 1976; Warme, 1977; Kleemann, 1980, 1994a, 1994b; Savazzi, 1982). Serpulid tubes also occur on some of the coral surfaces. Despite the large number of epibiont occurrences and the great abundance of corals and other carbonate-generating species, the combination of relatively deeper water, a primarily soft substrate, and excessive sedimentation rates ultimately prevented the formation of a well-developed coral reef facies in most strata of the Cumburindio Formation.

The single coral species collected from the lower Aptian San Lucas Formation on the northeast flank of Loma La Cuchilla, a hill just to the north of the village of Los

Cuachalalates, Michoacán, is only preserved as fragments in a block of dendroid coral packstone. Most of the larger bioclasts within the rock are fragmented branches of the cladophylliid *Cladophyllia stewartae* Wells, 1944. This is the only occurrence of *C. stewartae* known from the Huetamo area. However, because the sample was not in place, it was impossible to determine how this interesting bed was related to the surrounding stratigraphy.

Mal Paso Formation

The coral fauna from the upper Albian-lower Cenomanian upper member of the Mal Paso Formation at the studied outcrop in the state of Guerrero, about 0.75 km north of Chumbítaro, Michoacán (see Figure 2), is mostly composed of colonial species with reefal affinities. Only two of the 18 identified coral species are solitary, *Epistreptophyllum* sp. and *Paracycloseris effrenatus* n. sp., and only one of the colonial species, *Blastozopsammia guerreroterion* Filkorn and Pantoja-Alor, 2004, may have been an azooxanthellate, nonreef- building form. The other 15 coral species from the Mal Paso Formation most likely were constructional zooxanthellate taxa, or reef-building coral species.

The strata of the upper member of the Mal Paso Formation are primarily composed of marine limestones of lagoonal and reefal origin, mostly wackestone, with some horizons of packstone, floatstone, rudstone, and framestone. The stratigraphic section is subdivided on the basis of lithologic and paleontologic characteristics and these informal units are numbered from the base upward, MP 1 through MP18. The sequence of beds in the upper member of the Mal Paso Formation in general record successive changes from shallow lagoonal and back-reef environments to a coral reef environment to a relatively deeper marine environment of deposition. Interpretations of lateral facies relationships are based on the observed vertical sequence of the facies. Bioclastics in the lower and middle portion of the section typically are bioeroded, sparsely distributed, unoriented, and unsorted fragments of mollusks, dendroid corals, and echinoid spines. The abundance and size of bioclasts generally increase upward through the lower part of the section. Small, massive colonies of *Ovalastrea malpaso* n. sp. and *Preverastraea* sp. occur sporadically in horizons MP 5 and MP 9 and abundant, recrystallized, fragmented branches of dendroid coralla are common in unit MP 7. Above these units, a resistant 4.4 m thick oyster-rich rudstone horizon, MP 8, delineates a change from thin- and medium-bedded limestones to medium- and thick-bedded limestones. An increase in the abundance and diversity of mollusks and corals also occurs above this horizon and echinoid spines are ubiquitous in the carbonate matrix. Scattered massive coral colonies occur in the next higher bed in the section, unit MP 9, along with small, upright clusters of the rudist *Radiolites* cf. *R. costata* Scott, 1990, large specimens of the pectinid bivalve *Pecten roemeri* Hill, 1889, and nerineid gastropods. The only known specimen of the phaceloid montlivaltid *Thecosmilia guerreroensis* n. sp. was collected from loose debris on the surface of unit MP10, but the corallum may have been derived from the overlying beds, perhaps unit MP11. Above these beds, in unit MP12, valves of *Mexicaprina alata* Filkorn, 2002a, occur with other mollusks about 10 m below the coral reef horizon (MP13), but corals were not found in the same bed.

The coral reef of the Mal Paso Formation, unit MP13, has yielded the most diverse Albian-Cenomanian coral fauna from the Huetamo region, a total of 16 species. The majority of the corals in this coral reef are colonial species: the only solitary form recognized is *Epistreptophyllum* sp. Medium- to large-sized massive coralla are common in this bed, but medium to large-sized phaceloid and ramose growth forms also occur. The majority of the corals appear to have been preserved in living position, with convex oral surfaces oriented toward the top of the bed. Initiation of reef development in the lowermost part of the coral reef horizon primarily was achieved by colonization of molluscan substrates.

The most abundant, prolific, and conspicuous constituents of the coral fauna are large, massive, plocoid colonies of the latomeandrid *Ovalastrea malpaso* n. sp. and the rhipidogyrids *Preverastraea coatlicuae* n. sp. and *P. tocae* n. sp. The coralla of the latter genus are the largest massive colonies found in the Mal Paso Formation. Colonies of the massive to ramose, cerioid actinastraeid *Actinastrea guadalupae* (Roemer, 1849), some as large as 1 m in diameter (in weathered transverse section), also are common in the coral reef horizon. However, most of the *A. guadalupae* coralla observed in the Mal Paso Formation typically are small- to medium-sized. Members of the genus *Actinastrea* were important in the development of the reef community because they were among the first organisms to colonize new substrates and initiate reef growth (Scott, 1981, 1990). Thus, they helped to stabilize the substrate and provided a base for subsequent colonizations of other reef-building coral species. The phaceloid montlivaltids *Latiphyllia mexicana* n. sp. and *Elasmophyllia tolmachoffana* (Wells, 1932) also are common in the coral reef horizon, as well as coralla of the massive to ramose thamnasteriid *Thalamocaeniopsis mexicanensis* n. sp. Based on field observations, the massive to ramose hydnophoroid faviid *Eohydnophora picteti* (Koby, 1897) and the massive plocoid placocoeniid *Columnocoenia ksiazkiewiczi* Morycowa, 1964, also are fairly common. Most of the other coral species collected from the coral reef horizon evidently are uncommon because they are represented by relatively few specimens. These include the meandroid, pedunculate montlivaltid *Mycetophyllopsis azteca* n. sp., the massive meandroid dendrogyrid *Orbignygyra*? *incognita* n. sp., and the massive thamnasteroid microsolenid *Dimorpharaea barcenai* (Felix, 1891). In addition to the diverse and abundant corals, the fauna of the coral reef also includes *Pecten roemeri* Hill, 1889, large nerineids, abundant *Radiolites* cf. *R. costata* Scott, 1990, some *Mexicaprina alata* Filkorn, 2002a, and, in the upper part of the coral reef horizon, massive colonies of the stromatoporoid *Actinostromaria* sp. *Pecten roemeri* is most abundant both in and just below the coral reef zone, the same stratigraphic interval that includes the lowest occurrence of *Mexicaprina alata*.

The entire coral reef horizon (MP13) at this locality is 19 m thick. Based on the lateral extent of bedding surfaces within the coral reef and the weathered exposures of some of the massive and ramose coral colonies, the reef may have had a meter or more of relief on its surface during its deposition. The rock between the corals and other macrofossils in the coral reef horizon is an echinoid spine wackestone-floatstone with patchy packstone. This echinoid spine wackestone intra-reef rock indicates that the depositional environment was fairly well circulated, yet overall wave energy was moderately low. Despite the astonishing abundance of echinoid spines in the coral reef horizon, echinoid tests were not found here. Mollusks from just below and within the coral reef horizon typically exhibit the borings of sponges (see Buitrón-Sánchez and Pantoja-Alor, 1994) and upper surfaces of corals and stromatoporoids frequently have borings of endolithic bivalves.

A lateral pattern of coral species distribution, or biozonation, is evident within the vertical succession of this coral-rich horizon and is inferred to have been induced by localized variations in wave energy, water depth, and stage of colonization. The initial stage of reef facies development was substrate colonization by an actinastraeid species identified as *Actinastrea guadalupae* (Roemer, 1849). Reef development was further advanced by additional colonizations of other coral species and continued upward growth of massive to ramose actinastraeids. The reef-core facies consists of a taxonomically and morphologically diverse coral fauna. Growth forms commonly include both massive and ramose coralla. The dominant reef-building species are massive, plocoid colonies of the latomeandrid *Ovalastrea malpaso* n. sp. and the rhipidogyrids *Preverastraea coatlicuae* n. sp. and *P. tocae* n. sp. The phaceloid montlivaltids *Latiphyllia mexicana* n. sp. and *Elasmophyllia tolmachoffana* (Wells, 1932), and colonies of the massive to ramose thamnasteriid *Thalamocaeniopsis mexicanensis* n. sp. also contributed to reef development. Massive stromatoporoids, *Actinostromaria* sp., are present near the top of the coral reef unit and therefore they probably occupied the seaward margin or fore-reef areas of the coral reef. A generally similar pattern of coral biozonation has been described from the early Albian strata of the Mural Limestone in Arizona (Scott, 1981). Although the coral reef facies of the Mal Paso Formation is well-developed, it may not have had a broad lateral extent because its outcrop can only be traced out for a short distance and laterally equivalent facies toward the west and south are of deeper water origin, whereas those from north are shallow lagoonal in origin.

Coralla from the upper member of the Mal Paso Formation typically are recrystallized to coarse-grained calcite and quite often the details of corallite morphology and original skeletal microstructure are entirely obliterated. Generally the outermost regions of the coralla are the best preserved portions and the degree of skeletal recrystallization increases toward their centers. Large, massive coralla often contain dissolution cavities or vugs which exhibit evidence of one major interval of dissolution and two subsequent phases of diagenetic mineral precipitation, the first one composed of dogtooth calcite and the second composed of coarse celestite. Collapse structures on the tops of some of these massive coralla indicate that the dissolution occurred after burial, but prior to compaction and lithification.

A 6.5 m thick *Mexicaprina*-rich floatstone bed (MP14) directly overlies the coral reef horizon; no corals were found in this unit and specimens of *Mexicaprina* were not found above this horizon. Above the *Mexicaprina*-rich horizon, the strata are thin- to medium-bedded and the relative amount and thickness of intercalated argillaceous mudstone and wackestone increase markedly while fossil content sharply decreases. In additional contrast to the lower part of the section, the bioclasts in the upper portion of the section are fine- to very fine-grained and well-sorted. Farther up in the section, just below a zone with abundant echinoids, a 1.2 m thick wackestone bed, MP17, yielded relatively few specimens of six colonial coral species. Four of the six species, *Thalamocaeniopsis mexicanensis* n. sp., *Latiphyllia mexicana* n. sp., *Elasmophyllia tolmachoffana* (Wells, 1932), and *Actinastrea guadalupae* (Roemer, 1849), also occurred in the coral reef horizon, whereas the other two have not been identified in the material collected from lower units. One of the other two species, the thamnasteriid *Thamnasteria tonantzinae* n. sp., is represented by a single, large (> 30 cm), thin-branched, ramose corallum found in situ, whereas the other species, the ramose, cerioid actinastraeid *Actinastrea chumbitaroensis* n. sp., is represented by a few loose branch fragments. Because species of *Actinastrea* are considered to have been members of a group of organisms which pioneer or initiate colonization of substrates (Scott, 1981), sometimes in deeper water (Scott, 1990, p. 19), this horizon likely represents a short-lived pulse of incipient substrate colonization that probably failed because environmental conditions were unfavorable. Nonetheless, unit MP17 contained the highest stratigraphic occurrence of reef corals observed at this locality.

In addition to the species of *Radiolites* and *Mexicaprina*, two other rudist taxa, *Texicaprina* sp. and *Immanitas* sp., also have been reported from the outcrops of the upper member of the Mal Paso Formation just north of Chumbítaro (Pantoja-Alor, 1993c, p. 26-27). Although the precise stratigraphic horizon of these species was not specifically noted, some weathered specimens of *Texicaprina*? sp. were observed weathered out on the surface of the beds that are stratigraphically above the coral reef horizon.

The zone of abundant echinoids is in one of the more argillaceous mudstone horizons in the upper part of unit MP17. Echinoid tests from this zone typically are preserved whole, but the spines are neither attached to the tests nor preserved in abundance within the same bed. This is in marked contrast to the intra-reef wackestone-packstone of the main coral reef horizon (MP 13) where echinoid spines are ubiquitous. This observation indicates that the spines were most likely separated from the tests in a different, probably shallow-water, environment and that the de-spined, whole tests subsequently were transported by weak currents to their final depositional site in deeper water. Fragments of *Blastozopsammia guerreroterion*, Filkorn and Pantoja-Alor, 2004, a thin-branched, ramose, dendrophylliid coral, also occurred in the upper part of the section. Extant members of the Dendrophylliidae typically are azooxanthellate and they commonly occur in deeper, non-reef, marine environments (Wells, 1956; Cairns, 2001). The only other corals found above the zone of abundant echinoids are abundant specimens of the cunnolitid *Paracycloseris effrenatus* n. sp. in unit MP18, a 1 m thick bed of fine-grained wackestone. This species has a thin, solitary, cupolate corallum typically less than 20 mm in diameter, thus it is not a reef-building coral. The only likely azooxanthellate and ahermatypic coral species, *Blastozopsammia guerreroterion* and *Paracycloseris effrenatus* n. sp., respectively, are from the stratigraphically highest units in the section. Thus, the overall lithologic, sedimentologic, and paleontologic evidence suggests that the strata of the upper member of the Mal Paso Formation at this locality represent a transgressive marine sequence.

The fact that the coral reef in the upper member of the Mal Paso Formation appears to have been drowned ultimately may help with regional and global chronostratigraphic correlation. The local event may correlate with the global sea level rise and widespread drowning of carbonate platforms and guyots that occurred during the latest Albian (Röhl and Ogg, 1996, 1998; Winterer, 1998), a drowning known as the late Albian *Rotalipora appenninica*-event (Grötsch and Flügel, 1992; Grötsch et al., 1993). Further study is needed to determine if such a correlation exists.

SKELETAL GROWTH BANDS

Skeletal growth bands or density bands, a cyclic growth feature commonly observed in many modern reef coral species, are preserved in some of the fossil coralla from the Mal Paso Formation. Modern coral growth bands are mostly annual in origin and similar in appearance to those found in tree rings, thus the study of skeletal banding in corals has been termed sclerochronology (Hudson et al., 1976). The skeletal banding of corals typically is studied by the x-radiography of thin, longitudinal slices of coralla, but differential weathering of fossil material also can reveal skeletal bands (Weber and White, 1977). Each annual cycle of skeletal growth is comprised of a layer of relatively lower density material followed by a layer of higher density material (Hudson et al., 1976). The layers of maximum skeletal density, which frequently are also the thinner bands, have been correlated to periods of above average water temperature (Weber et al., 1975; Hudson et al., 1976; Fairbanks and Dodge, 1979). Thus, regardless of the reef locality, the higher density bands are formed during the times of seasonal high temperatures (Fairbanks and Dodge, 1979). However, no annual density bands have been recognized in Caribbean specimens of the massive, zooxanthellate reef corals Montastrea cavernosa and M. annularis that were collected from below 18 m depth, even though coralla of these same species from shallower habitats exhibited well-developed annual bands (Weber and White, 1977). This observation indicates that development of skeletal density banding may be at least partly moderated by a factor influenced by depth, perhaps photosynthesis. Some azooxanthellate, deep-water corals reportedly have very thin (< 10 microns), weakly-developed growth bands, but the cause of the supposed banding and the time represented by each band are unknown (Lazier et al., 1999); they may be the result of differential growth and thus not entirely analogous to the density bands of shallow-water reef corals. In general, the growth bands of coral skeletons contain a record of many environmental parameters that can be utilized to study both local and regional paleoclimatic conditions and both short- and long-term climatic variability (for examples see Fairbanks and Dodge, 1978, 1979; Emiliani et al., 1978; Carriquiry et al., 1994; Swart et al., 1996; Tudhope et al., 1996; Adkins et al., 1998). Growth bands also have been identified in Mesozoic fossil scleractinians, including both branched and massive species from the Jurassic of Europe (Ali, 1984; Geister, 1995; Insalco, 1995).

Growth bands have been recognized in parts of some coralla of the reef-building species *Ovalastrea malpaso* n. sp. These growth bands, as studied in longitudinal thin section, are composed of a relatively thick, optically lighter layer about 1.6-3.5 mm in thickness and a relatively thin, optically darker layer about 0.2-0.4 mm in thickness (see Figure 45.4, 45.6). Thus, if the growth bands are annual in origin, then the rate of growth for this particular corallum ranged from about 1.8 to 3.9 mm per year. The top and upper lateral surfaces of the corallum had the relatively higher rates of growth, whereas the lower lateral surfaces had the relatively lower rates. Thus, the maximum annual growth rate for this middle Cretaceous coral was about the same as that of other extant Caribbean coral species with massive growth forms (for example see Weber and White, 1977). Based on this initial analysis, future studies of additional specimens from the Cretaceous of Mexico are warranted.

PALEOBIOGEOGRAPHY

INTRODUCTION

Coral biogeography has been an interesting topic of investigation and discussion for more than a century. The observations of coral reef species, some seemingly identical, at localities frequently separated by broad expanses of open ocean have provided essential evidence for the formulation of modern biogeographical theories. Furthermore, reef corals are excellent subjects for paleobiogeographic investigations because they only thrive within a relatively limited range of ecological conditions and because most species typically are colonial, attached, shallow-water, benthonic organisms with a high probability of preservation in the fossil record (see Grigg and Hey, 1992). These intrinsic characteristics therefore indicate that fossil reef corals typically are found where they lived (except for tectonic displacement) and that the proper environment must have obtained at that particular site for at least as long as the duration of their growth. In addition, models of preservational biases suggest that the overall fossil record of scleractinian corals is likely an accurate representation of their evolution (Lasker, 1978).

Several biogeographic theories or methods have been proposed to account for the observed distributions of organisms. Most of these biogeographic ideas have been derived from or at one time applied to distributions of benthonic shallow marine organisms such as reef corals. The most notable of these concepts with regard to coral biogeography and paleobiogeography are: Darwin's centers-of-origin biogeography; panbiogeography; vicariance biogeography; dispersion biogeography; and ecological biogeography (Veron, 1995).

Darwin's centers-of-origin biogeographic theory (the center-of-diversity of Stehli and Wells, 1971; Briggs, 1987) is no longer considered a valid explanation for coral biogeography because it is not consistent with plate tectonics and modern data on the distributions of coral species in the Indo-Pacific (Pandolfi, 1992; Veron, 1995). In principle, centers-of-origin species originations are by sympatric speciation and dispersion occurs after the speciation event. Although centers-of-origin investigations have not explained coral biogeographic distributions, the analyses have yielded important observations related to modern centers-of-diversity that nonetheless remain valid. For example, areas of high coral diversity in the Indo-Pacific, the Caribbean, and the western Indian Ocean (the latter only weakly delineated; see Ortmann, 1892; Boshoff, 1981; Carbone et al., 1994; Veron, 1995; Riegl, 1996) are located in the tropical western regions of ocean basins. Among the general trends in diversity that have been recognized are: latitudinal and longitudinal decreases in diversity away from centers-of-diversity; latitudinal diversity decrease correlates with decrease in ocean surface temperature; and regions with the highest generic diversity (centers-of-diversity) also exhibit young generic ages (Stehli and Wells, 1971; Veron, 1995). Currently these modern centers-of-diversity are best explained by the Vortex model of coral biogeography (Jokiel and Martinelli, 1992). In this scenario, species are transported by dispersal on surface currents into the regions of high diversity from surrounding, isolated peripheral areas. This model allows for the possibilities of both sympatric and allopatric speciations and the subsequent dispersal of species from centers of high diversity. A modified version of this model can be used to explain the observed distributions of Cretaceous zooxanthellate coral species. This idea, termed the Dynamic Conveyor model, is outlined in the summary part of this section.

Panbiogeography, as conceptualized and promoted by L. Croizat (1982) and discussed by others (Craw, 1982; Craw and Weston, 1984; Seberg, 1986; Page, 1987, 1988), has been considered to be more relevant to the biota of terrestrial environments than to the biota of the marine realm (Veron, 1995). The method involves plotting lines between the map locations of disjunct populations of certain organisms, thus connecting the two geographic areas with so-called "tracks". An overlap or coincident path of several of these types of tracks from different species produces what has been termed a "generalized track". Upon further plotting and analysis of the biologic relations between other regions, these generalized tracks may eventually cross with other generalized tracks, the intersections of which are called "nodes". These nodes are the supposed points of origin for the analyzed taxa. Application of this method of biogeographic analysis to corals and other marine species is hindered by factors such as a good fossil record, dispersal over long distances, changes in ocean currents, and changes in sea level (Veron, 1995).

Vicariance biogeography as a theory (Croizat et al., 1974; Sober, 1988; Wiley, 1988a, 1988b) necessitates that part of the geographic range of an ancestral species is later inhabited by a descendant species following reproductive isolation from the ancestral population by the formation of a barrier. No dispersion occurs either before or during vicariant speciations. In effect, the barrier eliminates genetic transfer between the two populations and allows for the possibility of allopatric speciation in one or both areas of the ancestral population. Changes in ocean surface currents can result in the separation of populations of the same coral species and lead to vicariant speciation events. Thus, vicariant biogeography is directly applicable to coral biogeography. However, the importance of vicariance in coral biogeography is far outweighed by the process of dispersion (Veron, 1995). Nonetheless, periods of species origination are distinct from periods of species dispersal. In coral biogeography, as a contrast to vicariance, sites of species origin cannot be correlated with or restricted to sites of occurrence (Veron, 1995).

Dispersion biogeography is similar to vicariance biogeography in that a barrier separates two populations and thus any resulting origination is by allopatric speciation. However, the principles that primarily distinguish dispersion biogeography from vicariance biogeography are that dispersion must occur across a pre-existing barrier in the former scenario, whereas it must not occur in the latter (Cracraft, 1984). Several types of potential barriers have been recognized in the marine realm and each has an effect on the degree of reproductive isolation of a dispersed (or founder) population (Palumbi, 1994). However, because most corals possess the ability to disperse over long distances, intergradations of dispersion and vicariance may occur. As noted above, the process of dispersion is extremely important in scleractinian corals (Veron, 1995). Furthermore, based both on paleontologic (Fleming, 1967) and modern biologic investigations (Grigg et al., 1981; Grigg, 1981; Pandolfi, 1992), marine dispersion seems to have been a significant means of establishing new invertebrate populations in relatively distant and previously isolated regions in the geologic past as well as in modern habitats.

Ecological biogeography, the study of the geographic distribution of habitats, represents an attempt to explain the biogeographic distributions of organisms by examining the physical conditions and biological relationships within the environments that they inhabit. Thus, the explanation for the observed distribution essentially is based on ecological factors. This concept arose from the idea that some characteristics of large-scale or regional environments may enhance or limit biogeographic distributions. For example, zooxanthellate reef corals themselves are a group of organisms that is defined by eco-physiological criteria. This concept, that biogeography can be correlated to an ecosystem, has much significance with regard to Cretaceous benthonic marine faunas of the Tethys Sea (Masse, 1992). Thus, the classical Tethys also can be defined and identified by the geographic extent of its biological components. For the Early Cretaceous Tethyan tropical infralittoral environments (carbonate platforms and reefs), the characteristic taxa primarily are rudist bivalves, dictyoconid foraminifera, and dasycladacean calcareous algae (Masse, 1992). Other fossil groups, including orbitolinids and other larger foraminifera, scleractinian corals, and stromatoporoids, also are important ecological markers, but they can range into surrounding circalittoral environments. Other commonly encountered Cretaceous fossils such as ammonites, other benthonic foraminifera, brachiopods, other bivalves, gastropods, echinoids, and ostracodes also occur, but the ecologic ranges of these groups extend beyond the limits of warm, shallow, tropical marine environments (Masse, 1992).

The planktonic larval stage is the most commonly cited method of coral species dispersal (Rosen, 1988; Grigg and Hey, 1992; Veron, 1995, p. 87; Veron, 2000). Most (about 75 percent) extant zooxanthellate corals are hermaphroditic. In addition, most (also about 75 percent) extant zooxanthellate corals sexually reproduce by spawning large numbers of eggs and sperm for external fertilization. Alternatively, internal fertilization also may occur in some corals and the resulting planulae brooded for some time before being released into the ocean. Both of these modes of reproduction also can occur within the same species at different times or in separate geographic locations (Veron, 2000). The different modes of reproduction may have had some effect on survivorship during regional environmental perturbations and extirpations, but among coral genera both types exhibit about the same geographic ranges (Edinger and Risk, 1995). Regardless of the actual mode of sexual reproduction, some planulae, which are also zooxanthellate, can exist adrift in surface currents for months before they finally settle and attach to the substrate (Veron, 2000). Although the planktonic larval stage occurs in most coral species, over long distances this type of dispersal may have been coupled with other feasible permutations including island-hopping (or stepping-stones; Mac Arthur and Wilson, 1967; Wilson and Kaufmann, 1987; Grigg and Hey, 1992) and rafting (Feilden, 1893; Jokiel, 1990; Veron, 1995; and references therein).

Rafting, the process of transportation of coral or other biota along with a floating object, may be more common than previously thought (Jokiel, 1990; and references therein). Recent studies have shown that some colonial coral species can colonize oceanic flotsam such as logs and pumice fragments and thus extend their geographic ranges beyond the viable limit of their larval stages. Rafted corals deposited alive in other reef habitats can colonize the newly reached areas and establish local populations. In addition, if the environment remains favorable, rafted corals can survive afloat for extended intervals of time (several years), grow to maturity, and eventually reproduce. In the latter case, the rafted coral colony itself can become a source of planktonic larvae that also can disperse and colonize new areas (Jokiel, 1990). Furthermore, this type of one-way intermittent connection between widely separated reef habitats undoubtedly resulted in the establishment of geographically peripheral, down-current populations of certain coral species. If the initial colonization of the distal population was due to some unusual or uncommon circumstance (climatic or oceanographic perturbation; volcanic eruption) and the newer population remains genetically isolated from the ancestral, up-current population, then the possibility exists for subsequent allopatric speciation.

The common theme to all of these biogeographic concepts and modes of dispersal with regard to zooxanthellate corals is that they require an oceanic surface current to serve as the means of transport between suitable shallow-water habitats. Without this surface current connection, colonization and development of new coral reefs cannot occur. Thus, the ultimate control on coral species distribution is oceanic surface circulation (see Veron, 1995, 2000).

PALEOBIOGEOGRAPHY OF THE CRETACEOUS CORALS OF THE HUETAMO REGION

The entire known geologic and geographic ranges of each coral species described in this study are utilized in the following paleobiogeographic analysis (Figure 47). The species distributions have been compiled from the occurrence sections given for each of the species described in the section on systematic paleontology. Thus, the complete known paleobiogeographic history of each coral species, including both first and last occurrences, has been considered in the analysis. Pre-existing, pre-Cretaceous biogeographic distributions are not a major factor in the paleobiogeographic distributions of these coral species because only one of the species has been reported from pre-Cretaceous rocks (one Late Jurassic occurrence).

The plate reconstructions that are used for the base maps in this section (from Smith et al., 1994) have been selected because they are fairly recent compilations and because they show the paleocoastlines clearly. The relative positions of the major continental landmasses shown on these maps, particularly for the regions of Mexico and Europe, are approximately the same as those depicted on most of the other reconstructions that were reviewed, including those by Barron et al. (1981), Scotese et al. (1988), Funnell (1990), Wilson et al. (1991; western North America), and Hay et al. (1999). Admittedly, the geologic histories of geographic regions have an influence on the biogeographic distributions of organisms (see Rosen, 1985). However, the changes in the relative positions of the main geographic regions in relation to the position of Mexico during the time interval of primary interest, Aptian through Albian (about 22 million years), are considered to be less of a factor in determining coral species distributions than that of the influence of changes in surface current circulation patterns during that same time interval.

The Cretaceous corals of southwestern Mexico are important with regard to global and regional paleoceanographic and paleobiogeographic interpretations because southern continental Mexico was centrally positioned in the tropical western Tethyan region during the Early and middle Cretaceous. Therefore, when utilized as a proxy for surface currents, the biogeographic distributions of the Cretaceous coral species from the Huetamo region are key indicators of Tethyan surface current flow patterns (Filkorn, 2002c) between the European eastern realm and the tropical Caribbean western realm during the Early Cretaceous (Fig. 48). Furthermore, changes in the geographic ranges of some coral species over certain time intervals serve as indicators of changes in surface current circulation patterns within the tropical western Tethys Sea (Figures 49, 50). These aspects of Mexican Cretaceous coral paleobiogeography are discussed in detail below. Regional and global comparisons of the

Cretaceous coral species identified from the Huetamo region also facilitate reconstructions of the paleobiogeographic histories and evolution of the corals.

LOWER APTIAN CORALS FROM THE HUETAMO REGION

Nineteen (or about 90 percent) of the 21 coral species from the lower Aptian strata of the Huetamo region have been reported previously from other regions of the globe. The temporal and spatial distributions of the coral species identified from the Huetamo region are charted in Figure 47. This chart includes the 21 species from the lower Aptian as well as the 18 species from the upper Albian-lower Cenomanian. Only two (or about 10 percent) of the 21 species from the lower Aptian are known only from the Huetamo region: *Saltocyathus cumburindioensis* n. sp. and *Thamnarea hornosensis* n. sp. The only other occurrence of a species of *Saltocyathus* is in the lower Aptian of France (*S. urgonensis* Morycowa and Masse, 1998; further discussed below), whereas *Thamnarea hornosensis* n. sp. has affinities with *T. holmoides* Felix, 1891, a species from the Neocomian of the Tehuacán region, state of Puebla.

Eight (or about 38 percent) of the 21 coral species from the lower Aptian of the Huetamo region also are known from southeastern Mexico, including the Barremian or Aptian of the Tehuacán region, a locality about 360 km to the east in the state of Puebla. Furthermore, four (or 50 percent) of the eight species common to both of these regions are not known from any other localities. Thus, these four species, *Cyathophora micrommatos* (Felix, 1891), *Meandrophyllia sauteri* (Felix, 1891), *Polyphylloseris conophora* (Felix, 1891), and *Felixastraea mexicana* Reyeros, 1963, are considered to be endemic to southern Mexico. The remaining four species that are common to both regions are, in varying degrees, more broadly distributed. One of these four species, *Latusastrea alveolaris* (Goldfuss, 1829), is otherwise known only from the Upper Jurassic of Europe. Thus, the reports of this species from southern Mexico are its only known Early Cretaceous occurrences and the only known occurrences in the New World. The later, western occurrences of this species in the Cretaceous of Mexico indicate that it continued to exist in the western Tethyan realm, possibly in a coral reef refugium, after it had been extirpated in the eastern Tethyan realm. Of the remaining three species, both *Calamophyllia sandbergeri*

Figure 47. Chart of spatial and temporal distributions (paleobiogeographic distributions) of the coral species from the Huetamo region described in this study. Ages of occurrences in each geographic region are represented by a system of letters and numbers as noted in the following key.

Ages of occurrences:
Cretaceous (note: Maastrichtian, Campanian, and Santonian are not used in the chart)
8 = Coniacian
7 = Turonian
6 = Cenomanian
5 = Albian
4 = Aptian
3 = Barremian
2 = Hauterivian
1 = Valanginian
0 = Berriasian
Jurassic
J= Jurassic
Supplementary information on ages and occurrences:
U = prefix on age to indicate upper
M = prefix on age to indicate middle
L = prefix on age to indicate lower
? = if before age, the occurrence is questionable;
if after the age, the age itself is questionable
* = occurrence of same genus, but different species
- = age of occurrence spans the given time intervals;
for example, 4-5 means Aptian through Albian
/ = age of occurrence is either one age or the other;
for example, 3/4 means Barremian or Aptian

Species from Huetamo region	Geographic distribution of species and ages of occurrences											
	Huetamo region, Turitzio area, Michoacán	Huetamo region, Chumbitaro, Guerrero	Southeastern Mexico (Puebla, Oaxaca)	Northwestern Mexico (Sonora, Baja) and southwestern US	Texas and northeastern Mexico	Northern South America (Venezuela, Trinidad)	Western South America (Chile)	Europe (west of Ural Mts. and Caspian Sea)	North Africa	Western Asia (east of Ural Mts. and Caspian Sea)	East Africa	Eastern Asia (Tibet, Japan)
Actinastrea guadalupae (Roemer, 1849)		U5/L6			M5-U5							
Actinastrea chumbitaroensis n. sp.		U5/L6										
Preverastraea coatlicuae n. sp.		U5/L6										
Preverastraea tocae n. sp.		U5/L6										
Latiphyllia mexicana n. sp.		U5/L6										
Thecosmilia guerreroensis n. sp.		U5/L6										
Elasmophyllia tolmachoffana (Wells, 1932)		U5/L6										
Mycetophyllopsis azteca n. sp.		U5/L6	?		L5	U4/L5						
Eohydnophora picteti (Koby, 1897)		U5/L6		5	L5-5			L3-4				4/5
Columnocoenia ksiazkiewiczi Morycowa, 1964		U5/L6		U3/L4, M5			2/3	1-6		3/4		
Orbignygyra? *incognita* n. sp.		U5/L6										
Blastozopsammia guerreroterion		U5/L6										
Epistreptophyllum sp.		U5/L6										
Thalamocaeniopsis mexicanensis n. sp.		U5/L6							4*			
Thamnasteria tonantzinae n. sp.		U5/L6										
Paracycloseris effrenatus n. sp.		U5/L6										
Ovalastrea malpaso n. sp.		U5/L6										
Dimorpharaea barcenai (Felix, 1891)		U5/L6	L3/U4		L5			2-4				
Amphiastraea aethiopica Dietrich, 1926	L4			U3/L4, U4/M5				2-4, 6			3/4	
Latusastrea alveolaris (Goldfuss, 1829)	L4		L3/U4					UJ				
Actinastrea pseudominima (Koby, 1897)	L4						0/3	1-4, 6-L7	5, 6?	L3	2-3/4	
Cladophyllia stewartae Wells, 1944	L4					4						
Cyathophora haysensis Wells, 1932	L4			M5	L5	4						
Cyathophora micrommatos (Felix, 1891)	L4		L3/U4									
Stylina regularis Fromentel, 1862	L4							L3-4				?
Saltocyathus cumburindioensis n. sp.	L4							L4*				
Rhipidomeandra bugrovae Morycowa and Masse, 1998	L4							U3-L4		U3		
Isastrea whitneyi Wells, 1932	L4			4/M5	U4-L5	3						
Eohydnophora ovalis Masse and Morycowa, 1994	L4							L4				
Eugyra lanckoronensis (Morycowa, 1964)	L4							L3-5				?5
Actinaraea michoacanensis n. sp.	L4					4						
Thamnarea hornosensis n. sp.	L4											
Calamophyllia sandbergeri Felix, 1891	L4		L3/U4	L5		4						
Meandrophyllia sauteri (Felix, 1891)	L4		L3/U4									
Siderofungia irregularis Felix, 1891	L4		L3/U4		U4-L5	U4-L5		2-4				
Fungiastraea crespoi (Felix, 1891)	L4		L3/U4	M5		4		L4-4, L6, U7-L8				
Microsolena guttata Koby, 1897	L4							3-4				
Polyphylloseris conophora (Felix, 1891)	L4		L3/U4									
Felixastraea mexicana Reyeros Navarro, 1963	L4		4									

Felix, 1891, and *Fungiastraea crespoi* (Felix, 1891) have been reported from the Aptian of northern South America (Trinidad; and Venezuela for the former species) and the Albian of the northwestern Mexico-southwestern US region. The latter species also is known from the Lower Cretaceous (Aptian) and Upper Cretaceous (Cenomanian-Coniacian) of Europe. The remaining species, *Siderofungia irregularis* Felix, 1891, is known from the upper Aptian or lower Albian of Venezuela, the upper Aptian to lower Albian of Texas, and the Hauterivian to Aptian of Europe. Based on these distributions, *Calamophyllia sandbergeri* Felix, 1891, is endemic to the western Tethyan region and both *Fungiastraea crespoi* (Felix, 1891) and *Siderofungia irregularis* Felix, 1891, originated in Europe and subsequently dispersed to the Americas.

Seven (or about 33 percent) of the 21 coral species from the lower Aptian of the Huetamo region also are known from localities along the northern margin of South America, specifically in Venezuela and Trinidad. Included in these seven species are the three discussed immediately above. Of the other four of the seven species, two are known only from the Huetamo region and the Aptian of northeastern Venezuela: *Cladophyllia stewartae* Wells, 1944, and *Actinaraea michoacanensis* n. sp. The remaining two species, *Cyathophora haysensis* Wells, 1932, and *Isastrea whitneyi* Wells, 1932, exhibit a somewhat parallel distribution both temporally and spatially: earlier occurrences are in the southern part of their geographic ranges, whereas later occurrences are in the northern part of their ranges. For example, in addition to Aptian occurrences in Venezuela and the state of Michoacán, *C. haysensis* has been reported from the lower Albian of Texas and the middle Albian of the state of Sonora. Similarly, *I. whitneyi* occurs earlier in the south, the Barremian of Venezuela and the lower Aptian of the Huetamo region, whereas the northern occurrences in the Aptian and lower Albian of the state of Coahuila, the lower Albian of Texas, and the Albian of Baja California, are mostly relatively later. The distributions of *Calamophyllia sandbergeri* Felix, 1891, *Fungiastraea crespoi* (Felix, 1891), and *Siderofungia irregularis* Felix, 1891, the other three species common to both the Huetamo region and the northern part of South America, also display the same basic trend, at least for the occurrences in the Western Hemisphere. Both *Calamophyllia sandbergeri* and *Fungiastraea crespoi* have earlier occurrences in the Aptian of southern Mexico and northern South America (Trinidad; and Venezuela for the former species) and later occurrences in the Albian of the northwestern Mexico-southwestern US region. The spatial distribution of *Siderofungia irregularis* also is similar, but the temporal trend is not as distinct because the ages of the occurrences reported from these regions are not all precisely known. Nonetheless, *S. irregularis* has been reported from the upper Aptian or lower Albian of Venezuela and the upper Aptian to lower Albian of Texas (in addition to its occurrences in the Hauterivian to Aptian of Europe). Thus, the paleobiogeographic distributions of these five species in the Western Hemisphere reveal a general trend: the earlier occurrences are more to the south and east, whereas the later occurrences are relatively more to the north and west.

Five (or about 24 percent) of the 21 coral species from the lower Aptian of the Huetamo region also have been reported from the northwestern Mexico-southwestern US region. These five species include four whose distributions are discussed above: *Cyathophora haysensis* Wells, 1932, *Isastrea whitneyi* Wells, 1932, *Calamophyllia sandbergeri* Felix, 1891, and *Fungiastraea crespoi* (Felix, 1891). The fifth species common to both of these regions, *Amphiastrea aethiopica* Dietrich, 1926, has a fairly broad temporal and spatial distribution. In Mexico, this species occurs in the lower Aptian of the Huetamo region and the upper Barremian or lower Aptian and the upper Aptian or middle Albian of the state of Sonora. However, both the earliest and latest occurrences of this species are from Europe where it ranges from the Hauterivian to Aptian; it also has been reported from the Cenomanian. The only other known occurrence of this species is from the Barremian or Aptian at its type locality in East Africa. Overall, the distribution of *A. aethiopica* suggests that it originated in Europe during the Hauterivian and subsequently dispersed to the New World by the Aptian. However, its temporal and spatial distribution in Mexico is somewhat similar to that outlined in the preceding paragraph.

Three (or about 14 percent) of the 21 coral species from the lower Aptian of the Huetamo region also occur in the northeastern Mexico-Texas region. The distributions of these three species, *Cyathophora haysensis* Wells, 1932, *Isastrea whitneyi* Wells, 1932, and *Siderofungia irregularis* Felix, 1891, are discussed above.

Ten (or about 48 percent) of the 21 coral species from the lower Aptian of the Huetamo region also have been reported from Europe. This is the highest degree of faunal similarity recognized in this study. Four of the ten species with both Mexican and European occurrences are discussed above: *Amphiastrea aethiopica* Dietrich, 1926; *Latusastrea alveolaris* (Goldfuss, 1829); *Siderofungia irregularis* Felix, 1891; and *Fungiastraea crespoi* (Felix, 1891). The other six species are: *Actinastrea pseudominima* (Koby, 1897); *Stylina regularis* Fromentel, 1862; *Rhipidomeandra bugrovae* Morycowa and Masse, 1998; *Eohydnophora ovalis* Masse and Morycowa, 1994; *Eugyra lanckoronensis* (Morycowa, 1964); and *Microsolena guttata* Koby, 1897. Of these six species, *Actinastrea pseudominima* (Koby, 1897), has the broadest distribution, but only one other occurrence has been reported from the Western Hemisphere (Chile). Most of the other reported occurrences of this species, including the earliest (Valanginian) and latest (Turonian), are from Europe. This species also has been reported from other localities in the Eastern Hemisphere, including Africa and Asia. Based on the fact that the earliest known occurrence is in Europe, this species most likely originated there and subsequently dispersed to the Mexican region by the Aptian. The remaining five species show a remarkably similar trend in both relatively narrow temporal and restricted spatial distributions. The earliest occurrences of all but one of these species are reported from Europe and the Mexican occurrences reported in this study are only slightly younger. The only exception to this distribution trend, *Eohydnophora ovalis* Masse and Morycowa, 1994, is known only from the lower Aptian of Europe and the lower Aptian of the Huetamo region; any possible age difference between the occurrences in these two regions cannot be discerned. *Stylina regularis* Fromentel, 1862, occurs in the lower Barremian to Aptian of Europe and the lower Aptian of the Huetamo region, Mexico. *Rhipidomeandra bugrovae* Morycowa and Masse, 1998, occurs in the upper Barremian and lower Aptian of Europe (France), the upper Barremian of Western Asia (Turkmenistan), and the lower Aptian of the Huetamo region. *Eugyra lanckoronensis* (Morycowa, 1964) has been reported from the lower Barremian to Albian of Europe, the lower Aptian of the Huetamo region, and(?) the Albian of Tibet. *Microsolena guttata* Koby, 1897, is known from the Barremian to Aptian of Europe and the lower Aptian of the Huetamo region. Furthermore, at the generic level, *Saltocyathus cumburindioensis* n. sp. from the lower Aptian of the Huetamo region is most similar to *S. urgonensis* Morycowa and Masse, 1998, from the lower Aptian of France; these two species are the only known members of that genus.

The fact that ten (or nearly 50 percent) of the 21 coral species from the lower Aptian of the Huetamo region also occur in Europe indicates a strong paleobiogeographic affinity between these two regions. Furthermore, the temporal aspect of this affinity is additionally strengthened by the fact that the earliest reported occurrences of each of the ten species are from Europe. Thus, based on these spatial and temporal relationships, the ten species dispersed from Europe to the New World by the Aptian.

In summary, the strongest paleobiogeographic affinity of the lower Aptian coral fauna from the Huetamo region of Mexico is with the pre-Albian coral faunas of Europe. This is supported by the common occurrences of 10 species, or about 50 percent of the coral fauna. Other geographic affinities of the 21 coral species from the lower Aptian of the Huetamo region include, in decreasing level of similarity, the southeastern Mexico region (eight species, or about 38 percent of the fauna), the northern South America region (seven species, or about 33 percent of the fauna), the northwestern Mexico-southwestern US region (five species, or about 24 percent of the fauna), and the northeastern Mexico-Texas region (three species, or about 14 percent of the fauna).

Seven of the 21 species have relatively limited geographic distributions and therefore they are considered to be endemic to the areas of their observed geographic ranges. Four of these species, *Cyathophora micrommatos* (Felix, 1891), *Meandrophyllia sauteri* (Felix, 1891), *Polyphylloseris conophora* (Felix, 1891), and *Felixastraea mexicana* Reyeros, 1963, are endemic to southern Mexico during the Barremian(?) and Aptian. Two other species, *Cladophyllia stewartae* Wells, 1944, and *Actinaraea michoacanensis* n. sp., are endemic to the Huetamo region and northeastern Venezuela during the Aptian. One other species, *Calamophyllia sandbergeri* Felix, 1891, is endemic to the western Tethyan region, including the southern Mexico and northern South America regions during the Aptian and the northwestern Mexico-southwestern US region during the Albian.

The Western Hemisphere paleobiogeographic distributions of five of the species, *Cyathophora haysensis* Wells, 1932, *Isastrea whitneyi* Wells, 1932, *Calamophyllia sandbergeri* Felix, 1891, *Fungiastraea crespoi* (Felix, 1891), and *Siderofungia irregularis* Felix, 1891, indicate the same general temporal and spatial trend: the earlier occurrences are more to the south and east, whereas the later occurrences are relatively more to the north and west.

The relatively high degree of faunal similarity between the corals of the lower Aptian of the Huetamo region and the Barremian-Aptian corals of Europe indicates the existence of a dispersal pathway between these two regions. Therefore, regardless of the actual mode of planktonic dispersal, the coral distributions indicate that a relatively strong Tethyan surface paleocurrent flowed from Europe to the New World through the western part of the Tethys Sea during the earliest Aptian (Figure 48). This inferred westward direction of paleocurrent flow is corroborated by several model simulations of Cretaceous ocean circulation and other biogeographic evidence (for examples see Luyendyk et al., 1972; Gordon, 1973; Berggren and Hollister, 1974; but see Barron and Peterson, 1989, for an alternative view). However, the exact course that this current followed cannot be confidently determined from the available data. Of the seven coral species that are common to the Huetamo region and the northern South America region, two (*Siderofungia irregularis* Felix, 1891, and *Fungiastraea crespoi* (Felix, 1891)) also are known from Europe, which is a weak indication that the current may have followed a more southerly course. Evidence for a direct pathway through the western Tethys, or a northern course along the eastern coast of North America, is entirely absent. Thus, only the weak faunal affinity between the northern South America region and Europe supports the interpretation of a southern surface flow route. In the absence of other supporting evidence for the latter interpretation, a direct course between the regions of southwestern Mexico and Europe is an equally plausible alternative. The distribution of Cretaceous reef deposits in the western Tethys is reviewed below in the discussion section.

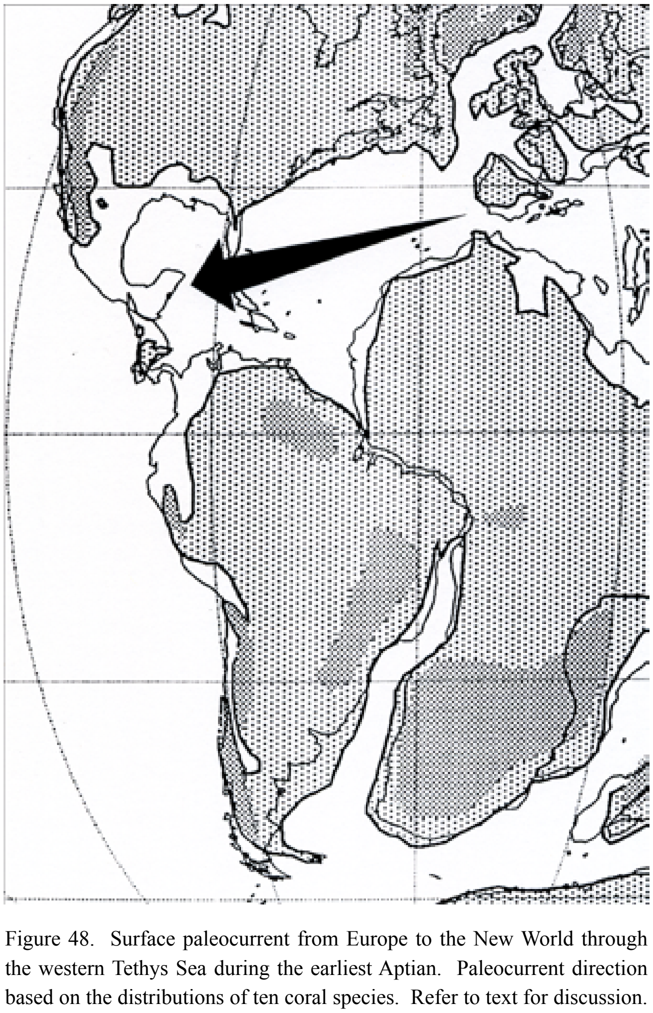

Figure 48. Surface paleocurrent from Europe to the New World through the western Tethys Sea during the earliest Aptian. Paleocurrent direction based on the distributions of ten coral species. Refer to text for discussion. Aptian (120 Ma) paleocoastline base map modified from Smith et al. (1994, p. 40).

The path that this Europe-to-Mexico surface current followed after it had reached southern Mexico cannot be determined from the distribution data discussed above except to note that it did not turn sharply northward during the early Aptian. However, either later in the Aptian or in the early Albian a north- or northwest-flowing current was developed in the Mexican region as evident from the paleobiogeographic shifts in the ranges of several coral species. As discussed above, five of the species (*Cyathophora haysensis* Wells, 1932; *Isastrea whitneyi* Wells, 1932; *Calamophyllia sandbergeri* Felix, 1891; *Fungiastraea crespoi* (Felix, 1891); and *Siderofungia irregularis* Felix, 1891) have older occurrences (Barremian or Aptian) in the southern and eastern areas of their geographic ranges and younger occurrences (upper Aptian or lower to middle Albian) that are farther north and west. This northward shift in geographic distributions may have been facilitated by the development of a north- or northwest-flowing surface current in Mexico (Figure 49).

UPPER ALBIAN-LOWER CENOMANIAN CORALS FROM THE HUETAMO REGION

Most of the 18 coral species from the upper Albian-lower Cenomanian of the Huetamo region are known only from the specimens described in this study (Figure 47). Only five (or about 28 percent) of the 18 species are known from other

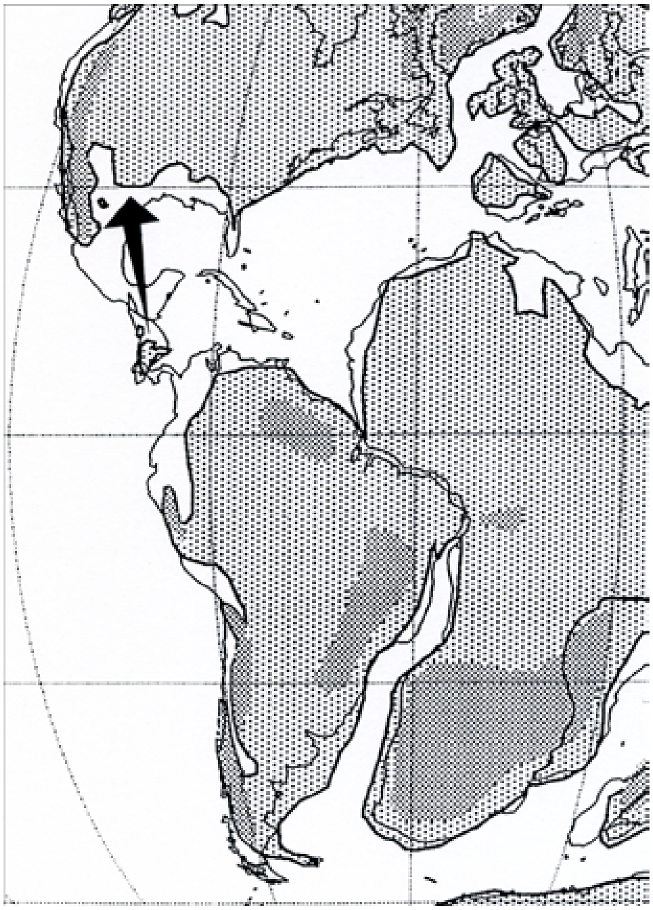

Figure 49. Surface paleocurrent from southern Mexico, flowing north or northwest, into northern Mexico during the later Aptian to early Albian. Paleocurrent based on the distributions of five coral species with older occurrences (Barremian or Aptian) in the southern and eastern areas of their geographic ranges and younger occurrences (upper Aptian or lower to middle Albian) that are farther north and west. Refer to text for discussion. Aptian (120 Ma) paleocoastline base map modified from Smith et al. (1994, p. 40).

occurrences. Of these five species, only two (or about 11 percent of the fauna), *Dimorpharaea barcenai* (Felix, 1891) and, questionably, *Elasmophyllia tolmachoffana* (Wells, 1932), also occur in the southeastern Mexico region (states of Puebla and Oaxaca). The latter species is the only element of the coral fauna that also occurs in the northern South America region (upper Aptian of Venezuela and Trinidad).

Two (or about 11 percent) of the 18 coral species also occur in the northwestern Mexico-southwestern US region: *Eohydnophora picteti* (Koby, 1897) (Albian of Arizona) and *Columnocoenia ksiazkiewiczi* Morycowa, 1964 (upper Barremian or lower Aptian, and middle Albian of the state of Sonora). However, both of these species have earliest known occurrences in Europe (lower Barremian and Valanginian, respectively) and both have been reported from other regions (discussed below).

Four (or about 22 percent) of the 18 coral species from the upper Albian-lower Cenomanian of the Huetamo region also occur in the northeastern Mexico-Texas region. However, based on the reported ages of these species in the latter region, all of the northern occurrences are older than those in the Huetamo region of Mexico. This is in contrast to the temporal and spatial distribution trend discussed earlier for some of the lower Aptian to lower Albian corals of the same regions. One of the four species, *Actinastrea guadalupae* (Roemer, 1849), primarily is known from the middle and upper Albian of Texas. With the exception of the material described in this study, no other occurrences of this species are known. The remaining three species common to both regions have occurrences in the lower Albian of Texas: *Elasmophyllia tolmachoffana* (Wells, 1932), *Eohydnophora picteti* (Koby, 1897), and *Dimorpharaea barcenai* (Felix, 1891). As noted earlier, *Elasmophyllia tolmachoffana* is the only species of the upper Albian-lower Cenomanian coral fauna that also occurs in the northern South America region (upper Aptian of Venezuela and Trinidad). Other occurrences of *Eohydnophora picteti* include the Albian of Arizona (mentioned above), the lower Barremian to Aptian of Europe, and the Aptian or Albian of Japan. In addition to the occurrences in Mexico and Texas noted above, *Dimorpharaea barcenai* also occurs in the Hauterivian to Aptian of Europe. However, at least in the Western Hemisphere, the temporal and spatial distributions of these four species record a southward shift from the lower to middle Albian of Texas to the upper Albian-lower Cenomanian of the Huetamo region of Mexico. Thus, in order for these species to have dispersed in this manner, a southward flowing surface current from the northeastern Mexico-Texas region to the southwestern Mexico Huetamo region during the middle to late Albian is implied (Figure 50). This southward flowing current may have been caused or deflected by a current flowing southward through the flooded Western Interior Seaway of North America (see Beauvais and Beauvais, 1974; Ericksen and Slingerland, 1990). The North American spatial and temporal distributions of *Columnocoenia ksiazkiewiczi* Morycowa, 1964, a species known from the upper Barremian or lower Aptian and the middle Albian of the state of Sonora and the upper Albian-lower Cenomanian of the Huetamo region

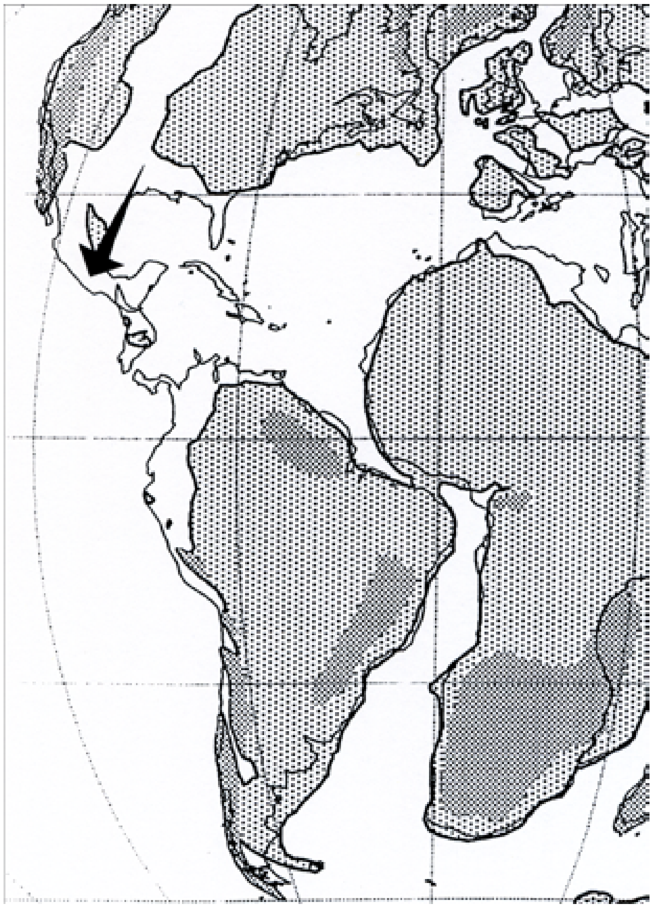

Figure 50. Surface paleocurrent flowing from the northeastern Mexico-Texas region to the southwestern Mexico Huetamo region during the middle to late Albian. Paleocurrent based on the Western Hemisphere distributions of four coral species with relatively older occurrences in the lower to middle Albian of Texas and relatively younger occurrences in the upper Albian-lower Cenomanian of the Huetamo region of Mexico. Refer to text for discussion. Albian (105 Ma) paleocoastline base map modified from Smith et al. (1994, p. 39).

(discussed above), also support this interpretation. However, this species also has been reported from the Hauterivian or Barremian of the western South America region (Chile), the Valanginian to Cenomanian of Europe, and the Barremian or Aptian of Turkmenistan.

In contrast to the earlier coral fauna from the Huetamo region, the upper Albian-lower Cenomanian coral fauna exhibits a relatively much weaker affinity with the corals of Europe. Only three (or about 17 percent) of the 18 coral species from the mid-Cretaceous of the Huetamo region also have been reported from the Cretaceous of Europe. The distributions of these three species, *Eohydnophora picteti* (Koby, 1897), *Columnocoenia ksiazkiewiczi* Morycowa, 1964, and *Dimorpharaea barcenai* (Felix, 1891), are discussed above. However, it is important to note that the earliest European occurrences of these three species predate the known occurrences in North America. The relatively weaker affinity of the two coral faunas suggests that the surface paleocurrent connections between these two regions also were relatively weakened during the middle to late Albian.

Discussion

Many previous studies on the paleobiogeography of Cretaceous corals consist of generalized compilations of the geographic distributions of reef and non-reef coral species during various Cretaceous ages (for examples, see Beauvais, 1981b, 1981c, 1986, 1992), but most of these works lack detailed documentation of taxonomic information. Furthermore, the use of unreliable or inconsistent coral taxonomy and weakly constrained geologic ages of faunas also can affect the outcome of paleobiogeographic analyses (Rosen and Turnšek, 1989). The results of this study are based on thoroughly taxonomically reviewed coral species and precise geologic ages, therefore the paleobiogeographic distributions of the species and the changes in their geographic ranges through time are considered to be accurate.

The relatively strong similarity between the coral faunas of Mexico and Europe during the Aptian may in part be due to the fact that the faunas of Europe are known fairly well because they have been the subject of numerous investigations over the past century. However, the same reasoning does not account for the lack of similarity of the later, Albian coral faunas. Therefore, the species distribution data indicate that changes in the relative strength and direction of surface paleocurrents are likely explanations for the observed changes in faunal affinity.

An earlier comparison of the Aptian coral faunas of Europe and Mexico reported that nine percent of the species known from Mexico were common to Europe, whereas 91 percent of the species known from Mexico were endemic (Beauvais, 1992). However, the Mexican Aptian coral fauna evaluated in that analysis (reportedly from Wells, 1946) consisted of only 13 species. A comparison of the Albian coral faunas from these two regions (Beauvais, 1992) also is misleading. In that comparison, 50 percent of the Mexican Albian coral species were common to Europe and the other 50 percent were considered endemic to Mexico. However, the Mexican Albian coral fauna used in that analysis consisted of only two species. Sampling bias obviously was a major factor in these faunal comparisons (see Belasky, 1992). Further investigations of Mexican Aptian and Albian coral occurrences may lead to additional contributions to the number of species present in this region and the degree of faunal similarity may then need to be re-evaluated.

The fairly high degree of similarity between the early Aptian coral fauna of the Huetamo region and the pre-middle Aptian fauna of Europe, ten species or about 50 percent of the early Aptian Mexican coral fauna, is interesting because of the extensive distance between the two regions. Therefore, in order for these species to have been dispersed from Europe to the southern Mexico region a dispersal corridor or pathway must have been established along some route between the two regions. However, there are no known occurrences of these species at localities situated between Europe and the southern part of Mexico. As noted above, seven of the lower Aptian coral species from the Huetamo region also have been reported from the northern South America region, but of those same seven species only two, *Siderofungia irregularis* and *Fungiastraea crespoi*, also occur in Europe. This weak faunal similarity is the only potential evidence for a surface current flow from Europe to Mexico along a southern route through the western Tethys Sea. Most of the additional supporting argument for this supposed flow configuration is based on the lack of evidence for the viable alternatives. However, at the genus level a few faunal similarities may help to establish a dispersal pathway along the more southern route. These similarities include the occurrence of *Thalamocaeniopsis* Alloiteau, 1953, in the Aptian of Algeria, a genus represented by *Thalamocaeniopsis* n. sp. in the late Albian-early Cenomanian of the Huetamo region. Another similarity is the occurrence of *Paracycloseris* Wells, 1934, in the Albian of Egypt and in the late Albian-early Cenomanian of the Huetamo region; the genus also occurs in the Upper Cretaceous of Jamaica, Cuba, and Mexico (Vaughan and Wells, 1943; Wells, 1956). Other possible intermediate biogeographic connecting points may exist in the Caribbean region, but for the most part the coral species have not been described or identified even though many occurrences of reef faunas have been reported. Direct, long distance, westward dispersal is a possibility, perhaps even a more likely option with the assistance of rafting or island-hopping, but currently the only supporting evidence for this scenario is that the other possibilities are weak alternatives. The reports of Cretaceous corals and reef deposits from many areas within the Caribbean region (Cuba, Jamaica, Puerto Rico, Guatemala, Belize, Honduras, Venezuela, Trinidad, Brazil) as well as those from more distant places (the Atlantic margin of North America, North Africa, the Middle East, and all points west of Mexico including those in and along the ancestral Pacific Ocean and Indian Ocean) need to be re-evaluated in order to understand the significance of their roles in the overall pattern of coral biogeography (Filkorn, 2001).

Although the species of each of the two coral faunas from the Huetamo region are entirely different from each other, some similarities occur at the generic level. A total of 34 genera are represented by the 39 species (refer to Figure 47). The 21 species from lower Aptian strata are arrayed among 20 genera, whereas the 18 species from upper Albian-lower Cenomanian strata are distributed among 16 genera. The only two of the 21 species from the lower Aptian that belong to the same genus are *Cyathophora haysensis* Wells, 1932, and *C. micrommatos* (Felix, 1891), but this genus is not represented in the later fauna. Of the 16 genera in the upper Albian-lower Cenomanian fauna, all are represented by one species each except for two, *Actinastrea* d'Orbigny, 1849, and *Preverastraea* Beauvais, 1976, each of which encompasses two of the 18 species. Altogether only two of the 34 identified coral genera are represented in both faunas: *Actinastrea* d'Orbigny, 1849, and *Eohydnophora* Yabe and Eguchi, 1936. The genus *Actinastrea* is represented in the lower Aptian by *A. pseudominima* (Koby, 1897), and in the upper Albian-lower Cenomanian by *A. guadalupae* (Roemer, 1849) and *A. chumbitaroensis* n. sp. The genus *Eohydnophora* is represented in the lower Aptian fauna by *E. ovalis* Masse and Morycowa, 1994, whereas in the later fauna it is represented by *E. picteti* (Koby, 1897).

The total difference in the species composition of the two faunas indicates that a complete turnover in coral species occurred over a period of at most 22 million years, the time interval from the Barremian-Aptian boundary to the Albian-Cenomanian boundary (Gradstein et al., 1995), and possibly as few as 16 million years, the interval within the narrowest possible limits from latest early Aptian to earliest late Albian (based on ages from Gradstein et al., 1995). Future studies of Mexican coral faunas that span the interval of early Aptian to early Cenomanian are necessary to determine the tempo of this faunal changeover.

SUMMARY

The highest faunal similarity among the early Aptian coral species described in this study, about 48 percent of the Aptian fauna, is with the coral fauna of the European region. The temporal relationships of the occurrences of these species in Europe and in Mexico indicate that the species were dispersed to North America from localities in the European region. Thus, a westward flowing surface current from Europe to North America is inferred to explain the spatial-temporal distributions of these species. Faunal affinities among the early Aptian coral species of the Huetamo region and adjacent, neighboring regions within the Western Hemisphere also have been recognized, but generally the relationships are weaker. The percentage of the 21 early Aptian coral species common to neighboring regions generally decreases from the south to the north, from northern South America (33 percent) and southeastern Mexico (38 percent) to northwestern Mexico-southwestern US (24 percent) and northeastern Mexico-Texas (14 percent). This distribution trend may be due to latitudinal attenuation of species diversity or it may be the product of taxonomic or sampling biases, but the observation is interesting nonetheless.

The geographic ranges of several (five, or about 24 percent) of the coral species from the early Aptian of the Huetamo region shift northward through time. The northward shift in the distributions of these species is attributed to the development of a north- to northwest flowing surface current during the late Aptian to early Albian.

The majority (13, or about 72 percent) of the late Albian-early Cenomanian coral species from the Huetamo region are known only from that area, thus they are considered to be endemic taxa. Furthermore, faunal affinities with other regions are relatively weak, including those of Europe as well as the adjacent areas. However, the geographic ranges of several (four, or about 22 percent) of the coral species from the late Albian- early Cenomanian of the Huetamo region shift southward through time. The earlier occurrences are located in the early to middle Albian of Texas, whereas the later occurrences are from the late Albian-early Cenomanian of the Huetamo region. Thus, the temporal-spatial distributions of these species indicate the development of a south- to southwest flowing surface current from Texas to southern Mexico during the middle to late Albian. This inferred current may help to explain why most of the other late Albian-early Cenomanian coral species are endemic. Furthermore, the flow direction of this same inferred surface current also may help explain why most of the rudist species from contemporaneous localities in southwestern Mexico (for examples, those described by Palmer, 1928) are endemic as well.

The number of coral species that are endemic to the Mexican study area and adjacent regions is relatively lower during the early Aptian and much higher during the late Albian-early Cenomanian. Of the 21 early Aptian species, four are endemic to southern Mexico, two are endemic to southern Mexico and northern South America, and one is endemic to the western Tethyan region. However, as noted above, 13 (or about 72 percent) of the 18 late Albian-early Cenomanian coral species from the Huetamo region are endemic to that region. The results of this study corroborate the observations of some of the earlier analyses of Cretaceous coral paleobiogeography. In particular, the general similarity of coral faunas of the Caribbean and Europe during the Berriasian to Aptian, the lack of endemic genera in the Caribbean region during the same interval of time, and the subsequent initiation of Caribbean coral endemism in the Albian (Coates, 1973, 1977b, 1985) are temporally paralleled by the paleobiogeographic distributions of the Mexican coral faunas presented in this study.

As noted earlier in the paleobiogeography section, modern centers-of-diversity are best explained by the Vortex model of coral biogeography (Jokiel and Martinelli, 1992). In this model, the surface circulation pattern of the Pacific Ocean ultimately causes coral species from isolated peripheral areas to be transported into and concentrated in the tropical western regions of modern ocean basins. This process ultimately results in an accumulation of coral species in these areas and eventually leads to development of a center-of-diversity. The process is current-induced and the transportation of species is by dispersal on surface currents. The model was originally developed from and applied to modern distributions of coral species. It is proposed here that a modified version of this model can be used to explain the observed distributions of Cretaceous zooxanthellate reef coral species. The Cretaceous version of the modified Vortex model is termed the Dynamic Conveyor model of coral biogeography and it is briefly described here. The primary distinction between the two models is that in the Cretaceous Dynamic Conveyor model the surface current circulation was probably a nearly continuous circum-global flow that traversed and interconnected most tropical and subtropical marine areas. Another distinction is that the modern Vortex model was based on a nearly steady-state of surface currents, whereas in the Cretaceous Dynamic Conveyor model the current pattern is not constant but rather incorporates significant changes in flow patterns caused by gradual tectonic changes in the positions of land masses. In other words, both time and tectonics are considered to be significant factors. In this sense, the Cretaceous centers of high diversity or areas of species accumulation are neither temporally nor spatially fixed locations. In addition, high diversity areas may later themselves become isolated peripheral habitats that may mainly disperse species to other newly established areas of accumulation (centers-of-origin biogeography revisited). Furthermore, the Early Cretaceous configuration of ocean basins was entirely different from that of modern times and circulation patterns also were different. The Cretaceous sea essentially was one continuous water mass primarily within the ancestral Pacific and Indian Ocean basins (the Panthalassa Ocean). This ocean was latitudinally restricted in the ancestral Mediterranean-proto-Atlantic-Caribbean realm (the Tethys Sea), the main east-west connection between the western Indian Ocean and the eastern Pacific Ocean. The exact locations of Cretaceous high diversity centers remain to be determined, but it is predicted that potential areas of accumulation logically include regions where surface currents were deflected or restricted by coastal regions with suitable environmental conditions. Thus, eustatic sea level changes are also accommodated in this model. The currents in these types of situations would serve a dual function as an intermittent conveyor, both bringing new taxa into a new area as well as transporting established taxa out to other down-current habitats. In effect, both processes may occur simultaneously, but a perfect balance is unlikely and either one probably could dominate given a particular configuration of currents and interconnected coastal regions. In the Cretaceous Dynamic Conveyor model, the configuration of currents and interconnected coastal habitats is ephemeral even though the basic, large-scale circum-equatorial flow regime is maintained throughout the period. Predictions of Cretaceous biogeographic distributions based on the Dynamic Conveyor model include: centers-of-diversity would be located where warm or tropical surface currents were deflected or restricted by coastal regions with suitable ecological habitats; positions of centers-of-diversity would change through time; and actual locations of species originations would be outside of the centers-of-diversity. Detailed investigations of the geographic and stratigraphic distributions of Cretaceous coral species are needed to be able to recognize if any of these patterns exist.

Summary and conclusion

This study is the first detailed investigation of the Lower and middle Cretaceous coral faunas from the Huetamo region of southwestern Mexico, a part of the tectonically problematic Guerrero terrane. An extensive, detailed review of the previous works on the Cretaceous corals of Mexico was compiled as part of the research for this investigation and it has been presented in an earlier publication (Filkorn, 2003).

Abundant and taxonomically diverse assemblages of scleractinian corals have been discovered in two of the Cretaceous stratigraphic units of the Huetamo region, the Cumburindio and Mal Paso formations. In addition, one coral species has been discovered in the San Lucas Formation. A total of 39 coral species arrayed among 34 genera are described and illustrated in this study. The corals are from the lower Aptian strata of the Cumburindio (20 species) and San Lucas (one species) formations and the upper Albian-lower Cenomanian upper member of the Mal Paso Formation (18 species). These formations have no coral species in common. Three of the 21 species from lower Aptian strata are described as new: *Saltocyathus cumburindioensis* n. sp., *Actinaraea michoacanensis* n. sp., and *Thamnarea hornosensis* n. sp. Eleven of the 18 coral species from the upper Albian-lower Cenomanian upper member of the Mal Paso Formation also are described as new: *Actinastrea chumbitaroensis* n. sp.; *Preverastraea coatlicuae* n. sp.; *Preverastraea tocae* n. sp.; *Latiphyllia mexicana* n. sp.; *Thecosmilia guerreroensis* n. sp.; *Mycetophyllopsis azteca* n. sp.; *Orbignygyra*? *incognita* n. sp.; *Thalamocaeniopsis mexicanensis* n. sp.; *Thamnasteria tonantzinae* n. sp.; *Paracycloseris effrenatus* n. sp.; and *Ovalastrea malpaso* n. sp. In addition, one genus and species discovered during the investigation of the coral fauna of the Mal Paso Formation has been described as new in an earlier publication: *Blastozopsammia guerreroterion* Filkorn and Pantoja-Alor, 2004.

Analogies with living corals indicate that the majority of the fossil corals from the Cumburindio and Mal Paso formations most likely were reef-building species, also known as hermatypic corals or constructional zooxanthellate corals, that presumably lived in symbiotic relationship with a microscopic, photosynthesizing alga (zooxanthellae) harbored in their polyps. This symbiotic relationship between the corals and the photosynthetic algae effectively limited their ecologic distribution to substrates in relatively shallow, well-lighted, warm, marine water.

Associations of scleractinian corals and rudist bivalves have been observed at three localities, two in the lower Aptian Cumburindio Formation of the state of Michoacán and one in the upper Albian-lower Cenomanian Mal Paso Formation of the state of Guerrero. The two occurrences in the Cumburindio Formation are: an association of a large species of ramose, microsolenid coral, *Thamnarea hornosensis* n. sp., preserved in situ along with valves of the rudists *Praecaprina* sp. and *Caprina* sp. at the exposures in the Arroyo Los Hornos; and a diverse assemblage of reef corals that conformably overlies a bed primarily composed of valves of the rudist *Amphitriscoelus* sp. near the top of the stratigraphic section at the Loma de San Juan, Turitzio. The coral-rudist association in the upper member of the Mal Paso Formation concerns a diverse assemblage of reef corals and the rudists *Mexicaprina* sp. and *Radiolites* sp. None of these kinds of coral-rudist associations has been reported previously from Mexico or any other site.

The paleobiogeographic histories of the coral species described in this study reveal geographic affinities with several regions, mainly Europe, and the adjacent areas of southeastern Mexico, northern South America, northwestern Mexico-southwestern US, and northern Mexico-Texas. About half of the lower Aptian coral species from the Huetamo region have been reported previously from the pre-Albian of the European region. This faunal similarity is the strongest geographic affinity recognized in this study.

The temporal and spatial distributions of these coral species can be utilized as a proxy for the surface current circulation patterns that existed during different intervals of Cretaceous time. These distributions indicate that a surface current flowed from Europe to southwestern Mexico during the early Aptian. Subsequent changes in the spatial distributions of some of the coral species indicate that a surface current with a major component of north- and northwestern-flow from southwestern Mexico to the northeastern Mexico-Texas region and the northwestern Mexico-southwestern US region was flowing during the late Aptian and early Albian. Other changes in spatial distributions suggest that the surface current flow direction later was to the south, in direct contrast to the previous trend, from the northeastern Mexico-Texas region to the southwestern Mexico Huetamo region during the middle to late Albian. This inferred reversal of flow direction may help explain why some of the late Albian faunal elements of southwestern Mexico, including many of the corals described herein and many of the rudist species described previously (see Palmer, 1928) are endemic to that region.

Overall, there appears to be a temporal trend in colony size; that is, the earlier fauna from the early Aptian is mainly composed of species with mostly small corallites and small-sized coralla, whereas the later fauna from the late Albian-early Cenomanian is dominated by species with relatively larger corallites and large-sized coralla. This general trend is very similar to a trend observed in the Neogene to recent coral faunas of the Caribbean region (Johnson et al., 1995) and indicates that, with regard to corallite size, corallum size and growth form, the long-term evolution of scleractinian corals may be cyclic.

Some of the scleractinian coral species from the Huetamo region appear to have the potential to be utilized in biostratigraphic correlations of the Mexican Cretaceous. However, further investigations of the stratigraphic distributions of these coral species in Mexico are required in order to refine their use in biostratigraphy.

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