Corals from the Early Cretaceous (Barremian - Early Albian) of Puebla (Mexico) - Introduction and Family Stylinidae

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ABSTRACT

The present contribution is the first instalment of a systematic revision of the Early Cretaceous (Barremian to Early Albian) corals of Puebla, Mexico. The coral fauna preserved in the Tehuacán region represents one of the most species rich associations of its kind from the Early Cretaceous of the New World. This article provides a brief overview of the research history, geology, lithostratigraphy and biostratigraphy, and reports the presence of corals of the family Stylinidae (suborder Stylinina). The family is represented by the genera Acanthocoenia (one species), Enallhelia (two species), Stylangia (one species) and Stylina (six species).

Key words: corals, taxonomy, Cretaceous, Puebla, Mexico.

RESUMEN

El presente estudio es el primero en una serie de revisiones sistemáticas de los corales del Cretácico Inferior (Barremiano - Albiano Temprano) de Puebla, México. La fauna coralina preservada en la región de Tehuacán representa una de las asociaciones más diversas de su tipo para el Cretácico Temprano del Nuevo Mundo. Este artículo proporciona una breve revisión histórica de las investigaciones, geología, litoestratigrafía y estratigrafía local, y reporta la presencia de corales de la familia Stylinidae (suborden Stylinina). La familia se encuentra representada por los géneros Acanthocoenia (una especie), Enallhelia (dos especies), Stylangia (una especie) y Stylina (seis especies).

Palabras clave: corales, taxonomía, Cretácico, Puebla, México.
INTRODUCTION

The outcrop area in the south-eastern part of the Mexican state Puebla (southwest of the Tehuacán Valley) has been known for a long time as an extremely fossiliferous area, containing abundant shallow marine invertebrate fossil remains (e.g., Feldmann et al., 1995; Gómez-Espinoza et al., 2010). Corals represent some of the most abundant body fossils, second only to molluscs (bivalves, gastropods).

Research on the diverse coral association began more than a century ago. Felix (1891) published a coral fauna from San Antonio Salinas (now San Antonio Texcalal; Aguilera (1906) published, based on his collections around San Juan Raya, a fossil list with numerous coral taxa, but unfortunately did not include descriptions and illustrations of the material. A small part of the Aguilera collection was systematically revised by Reyeros-Navarro (1963). The corals described by Felix (1891) were revised by Löser (2006). Some samples from the Aguilera collection were mentioned or figured (Löser, 2008a, 2009; Löser et al., 2009).

Despite previous efforts, much of the coral fauna from the San Juan Raya area remains rather poorly understood. In this study, the corals from the Aguilera collection are combined with recently collected material in order to provide a much better account of one of the largest coral faunas in the New World. Due to the large amounts of material and numerous species that compose this new collection, in addition to the time-consuming process necessary to produce thin sections, the detailed taxonomic revision will be published in subsequent instalments.

STUDY AREA

The study area is located in the Zapotitlán Basin (Martínez-Amador et al., 2001). The area is limited on the east by Cenozoic deposits of the Tehuacán Valley, by the Pozo Hondo fault on the west (Mendoza-Rosales et al., 2010), by the basement high consisting of the Cozahuicite granite and Acatlán and Oaxaca metamorphic complexes on the South (Elías-Herrera and Ortega-Gutiérrez, 2002); and by the Albion and Cenomanian platform deposits on the north (Calderón-García, 1956). The depositional environment of the Zapotitlán Basin consists of a mixed marine sedimentary system, with synsedimentary faults in an extensive regime (Mendoza-Rosales, 2010).

Lithostratigraphy

Most of the Tehuacán Valley has been interpreted as a low energy environment with shallow platform waters (Barceló-Duarte, 1978). The Early Cretaceous of the Zapotitlán Basin (South-eastern Puebla and partly Northern Oaxaca) encompasses a succession reaching from the Barremian to the Early Albian, consisting of the following formations: Zapotitlán Fm. (Barremian), San Juan Raya Fm. (Aptian) and Cipiapa Fm. (Albian; cf. Aguilera, 1906).

The oldest rocks belong to the Zapotitlán Fm. This formation represents the basal unit deposited at the beginning of the Early Cretaceous transgression. The deposits are composed of carbonaceous mudstones, shales and wackes with intercalations of calcareous breccias. These are arranged in coarsening-up successions of one to two meters thickness, showing upward a gradual increase in the percentage of arenites and a simultaneous decrease in carbonaceous material; its sedimentary facies represents at the top a deposit in a shallow marine environment (Barceló-Duarte, 1978).

Sandstone layers occur in thin to medium tabular beds, with flute cast, tool mark and channel fillings; they also include cross and parallel stratification as well as convoluted lamination, with slumps and some growth faults. The calcareous shale layers are finely laminated, with some occasional sandstone lenses; the former are interspersed with lenticular medium to thick layers of conglomerates and breccias of limestone and sandstone, containing corals, gastropods, bivalves, ammonites and sponges. The limestones occur in thin to medium beds ranging from laminated mudstone to wackestone. The Zapotitlán Fm. accumulated on a slope as turbidite deposits associated with a fault. The total thickness of the Zapotitlán Fm. has been estimated at up to 1300 m (Calderón-García, 1956; Barceló-Duarte, 1978). Laterally, the formation shows variation in its sedimentology (Barceló-Duarte, 1978). Calderón-García (1956) initially divided the Zapotitlán Fm. into the lower Agua del Cordero Member and upper Agua del Burro Member. Barceló-Duarte (1978), however, reinterpreted this view and proposed a new stratigraphic model that subdivided the Zapotitlán Fm. in three smaller ones: the fine-clastic Zapotitlán Fm., the coarse-clastic Agua del Cordero Fm. and the carbonate-rich Agua del Burro Fm. These formations, however, remain informal because the work by Barceló-Duarte (1978) has not been officially published. The contact between the Zapotitlán Fm. and the San Juan Raya Fm. is marked by a massive limestone bed that belongs to the Agua del Burro Member (sensu Calderón-García, 1956).

To the west, the Zapotitlán Fm. transitions into a shallower facies, represented by the limestone of the Agua del Burro Fm. (sensu Barceló-Duarte, 1978); the latter is overlain conformably by the clastic San Juan Raya Fm. of Aptian age (Calderón-García, 1956; Barceló-Duarte, 1978; Mendoza-Rosales, 2010).

The San Juan Raya formation is generally interpreted as a shallow marine deposit; the unit consists of a siliciclastic-carbonate succession that includes alternating thick lenticular beds of sandstone and sillstone, the latter frequently bioturbated. The deposits consist mainly of multidirectional trough cross-bed sets, wavy and lenticular beds, and show flaser structures. The lithology is mainly medium
to coarse grained sandstone, but contains intercalated layers of shale and siltstone. Sedimentary structures include small-scale cross-stratification, planar, nearly horizontal laminated bedding and hummocky cross-stratification (owing to storm events). The formation also contains abundant Thalassinoides burrows and reworked fossils.

The shale beds may reach a thickness of various tenths of meters. The intercalated, more consolidated, sediment layers generally measure 3–30 cm, but can reach a thickness up to three meters. The limestone beds contain a diverse association of animal and plant fossils. The upper portion of the San Juan Raya Fm. is characterised by an increased shale bed thickness, and a coral fauna almost exclusively represented by solitary forms of the genus Plesiosmilia. In highest levels, also beds with colonial, shallow marine corals can be found. The total thickness of the San Juan Raya Fm. is estimated at up to 800 meters (Barceló-Duarte, 1978). The contact between San Juan Raya Fm. and Cipiapa Fm. is sharp and disconformable. The limestone of the Cipiapa Fm. contains a fauna of corals and molluscs (mainly rudist bivalves).

Stratigraphy

Felix and Lenk (1891) assigned a Barremian age to the Zapotitlán Fm. based on the ammonite fauna. Aguilera (1906) proposed a more limited stratigraphic range to the Late Barremian, but this was later changed again to the Barremian by Calderón-García (1956). Aguilera (1906) interpreted the San Juan Raya Fm. as a succession within the Zapotitlán Fm. and assigned an Aptian age to the former. Aguilera (1906) assigned the Cipiapa Fm. to the Cenomanian, but this was later changed to the Early Albian or Late Albmion to Cenomanian by Calderón-García (1956). Although ammonite remains are not particularly rare, at least in the Zapotitlán Fm. and San Juan Raya Fm., their biostratigraphic information has never been well-established in relation to their relative position in the measured columns; furthermore, there are no published measured stratigraphic columns of this formation. The ammonite species identified by Barceló-Duarte (1978, based on Müllerried 1933abc, 1934) indicate a Barremian age for the Zapotitlán Fm; rudist data (Felix, 1891; Burckhardt, 1930; Müllerried, 1933abc; see below), however, suggest a Hauterivian to Barremian age for this formation. Ammonite data (Barceló-Duarte, 1978; based on Müllerried, 1933abc, 1934; see also González-Arreola, 1974) indicates an Aptian age for the San Juan Raya Fm. Nerinoid gastropods indicate an Aptian age with species having a tendency to the Early Aptian (e.g., Nerinea galatea) or Late Aptian (e.g., Nerinea hicoriensis; Alencáster de Cserna, 1956). Recent data from the nerineid gastropods from the region of San Juan Raya (Buitrón-Sánchez and Barceló-Duarte, 1980) do not provide conclusive information on the age: according to Kollmann and Peza (1997), Cossmannina (Eunerinea) lutticie (Blankenhorn, 1890) actually belongs to Diptyxis sp.; this genus has many species that range from the Late Jurassic through the early Late Cretaceous. Neoptixis galatea (Coquand, 1865) has a wide geographic and stratigraphic distribution, generally ranging from the Hauterivian to the Albian, but being most abundant in the Early Aptian. Nerinea (Nerinea) sanjuanensis Buitrón-Sánchez and Barceló-Duarte, 1980 is a species endemic to the outcrop area. The Cipiapa Fm. was originally assigned to the Alban and/or Cenomanian (Aguilera, 1906; Calderón-García, 1956). Barceló-Duarte (1978) excluded the earliest Albian without providing appropriate biostratigraphic data. It is possible that the highest parts of the San Juan Raya Fm. belongs to the earliest Albian since the remarkable facies change at the top of this formation can be correlated with the transgressive cycle in the Albian Mammillatunum zone (see González-León et al., 2008).

All the formations contain abundant populations of rudist bivalves. These are represented by extensive biostromes with a remarkably low biodiversity, consisting exclusively of the caprinids Retha tulae (Felix, 1891) and Amphistricoelus primaevus Pantoja-Alor et al., 2004. The lowermost Zapotitlán Fm. (Zapotitlán Fm. sensu Barceló-Duarte, 1978) represents a notable exception, as the rudists are mainly found as solitary individuals or very small bouquets. In addition to the former caprinid taxa, the Zapotitlán Fm. (senu Barceló-Duarte, 1978) also includes some representatives of the requieniid genus Toucasia. Retha tulae is by far the most abundant rudist in all the localities, constructing massive biostromes composed of hundreds of individuals in both the Agua del Burro Member of the Zapotitlán Fm. (senu Calderón-García, 1956) and the San Juan Raya Fm. The material referable to Retha tulae found in these formations is identical to that reported by Skelton and Masse (1998), which belongs to the W. S. Adkins Collection housed in the Mesozoic Stratigraphy and Paleontology collections of the University of Texas, Austin, USA.

The Cipiapa Fm. contains individuals that are comparable to the genus Caprinuloidea, which has a stratigraphic range from the Late Aptian to the Early Cenomanian, although most species are found from the middle to Late Albmian (Steuber, 2002). Rudist data alone do not allow a precise age assignment of the various lithostratigraphical units.

Outcrop areas and localities

The coral samples come from four outcrop areas close to the road from Tehuacán to Santiago Chazumba (Figure 1).

(1) San Antonio Texcala

The river bed north of San Antonio Texcala sediments of the Zapotitlán Fm. (Barremian) are exposed. Supposedly the material described by Felix (1891) is from here (see Löser 2006 for more explanations). There is some material
recently collected (sample point SA1), which is not identical with the Felix locality.

(2) San Lucas Teteletitlán

Outcrop area located to the north of San Lucas Teteletitlán, containing sediments of the San Juan Raya Fm. (here probably latest Aptian to basal Albian) and the Cipiapa Fm. (early Albian). The material was recently collected.

(3) San Juan Raya

A large area with several riverbeds with well exposed sections and rich fossil material. All belong to the San Juan Raya Fm. (Aptian). The sample material comes mainly from the historic Aguilera collection (see below) without exact sample location, but there are also more recent collections.

(4) Atecoxco

East of Atecoxco the La Compañía section (Mendoza-Rosales, 2010) yielded rich coral material in several beds. The section is preliminarily assigned to the Zapotitlán Fm. and ranges from the Late Barremian (sample point CIA 26) to the Early Aptian (sample points AC 89, CIA45, CIA 48, CIA 56, CIA 58).

Coral occurrence

Corals occur in all formations. In the Zapotitlán Fm, they occur mainly in small bioherms or in solid limestone beds. Corals weather out rarely. The corals reported by Felix (1891) are exceptionally weathered out, but because the exact sample locality is unknown, even its assignment to the Zapotitlán Fm. cannot be confirmed. Corals are very abundant in the limestone beds within the San Juan Raya Fm. They have small (less than 10 cm in diameter) to large (up to 30 cm in its largest dimension) colony sizes. The composition of the coral associations differs from bed to bed.

Typical associations are the following: Actinastreopsis/Cryptocoenia (with small gastropods). Cryptocoenia/Ellipsocoenia/Eugyra (with oysters, pectinids and small gastropods). Cryptocoenia/Eugyra (with oysters; Figure 2a). Cryptocoenia/Plesiosmilia (with oysters; Figure 2b). Ellipsocoenia only (with oysters; Figure 2c). Ellipsocoenia/Hexasmilia/Polyphyllosomia. Ellipsocoenia/Plesiosmilia (with nerineids; Figure 2d). Eugyra (with dominating oysters; Figure 2e). Some beds contain only small isolated patches with corals (Figure 2f).

The coral associations are generally poor in species diversity; however, considering the several limestone beds with differing coral associations, the total number of species reaches a considerable value. The corals weather out easily from the limestone banks and therefore can be found amassed in river beds cutting the San Juan Raya Fm. Reviewing the whole San Juan Raya Fm, the total generic and specific diversity is very high. The state of preservation varies, but in general, corals are not well preserved. Corals from the Cipiapa Fm. weather not out from the compact limestone but limestone boulders containing corals can be easily collected from the talus debris. The coral fauna of the Cipiapa Fm. is diverse and well preserved.

The three formations form the most species rich Barremian to Early Albian coral fauna of the whole American continent, and represent one of the oldest New World Cretaceous coral faunas. Coral faunas from the Early Cretaceous of the Western Atlantic are poor in species with a few exceptions: the Hauterivian of Jamaica (Benbow Inlier; Löser et al., 2009; 18 species), the Barremian to Early Aptian of Venezuela (Wells, 1944; 23 species), and the Late Barremian to Early Albian of Northern Mexico (Sonora; Baron-Szabo and González-León, 1999, 2003; Löser and Minor, 2007; Löser, 2011; ca. 150 species). There exist numerous outcrops with small coral faunas in Texas (USA), but most are younger than Aptian (Löser and Minor, 2007; 33 species).

MATERIAL

Coll. Aguilera

The material from the Aguilera coral collection, collected about 100 years ago, was obtained from several sample points within the large outcrop area. Sample locations of material from the Aguilera collection are entirely unknown. The lithology and state of preservation of the fossils vary greatly between specimens. The reasons for
Figure 2. Facies types with corals. a: Cryptocoenia/Eugyra (with oysters); b: Cryptocoenia/Plesiosmilia (with oysters); c: Ellipsocoenia only (with oysters); d: Ellipsocoenia/Plesiosmilia (with nerineids); e: Eugyra (with dominating oysters); f: small coral patch. Scale bar 20 mm, with exception for f (length of hammer about 30 cm).
that are explained above. It is assumed that all corals from the collection are derived from the San Juan Raya Fm. The Aguilera collection forms part of the National Mexican Palaeontological Collection, housed at the Instituto de Geología, Universidad Nacional Autónoma de México (UNAM), Mexico City.

Coll. Felix

Although the corals from the Felix collection were recently revised (Löser, 2006), new information on the geological and stratigraphic context shed a new light on the relationships between the faunas. The Felix material was collected from a ravine located to the north of San Antonio Texcala. The exact location is currently unknown (Löser, 2006). The Felix collection is housed at the Leipzig University (Germany).

Coll. Mendoza-Rosales

Part of the newly collected material comes from a measured section close to Atecoxco (Mendoza-Rosales, 2010). Published material forms part of the National Mexican Palaeontological Collection, housed at the Instituto de Geología, Universidad Nacional Autónoma de México (UNAM), Mexico City.

Coll. Löser

Most of the new material comes from measured sections within the San Juan Raya Fm. This material forms now part of the palaeontological collection of the Estación Regional del Noroeste, Instituto de Geología, UNAM, in the city of Hermosillo, Sonora state, Mexico.

METHODS

From the 31 samples 29 oriented thin sections in transverse and longitudinal directions were obtained. Thin sections were examined using a Zeiss STEMI 2000-C stereo microscope. Microphotographs for illustration purposes were obtained using a transparency scanner Epson Perfection V750-M Pro with an optical resolution of 6,400 dots per inch. Scanned images were transferred to grey scale bit maps. Their quality was amended by histogram contrast manipulation (contrast stretching) where possible.

To gain more insight into the intraspecific variation of fossil corals and to obtain a better strategy for comparing species, calicular dimensions in thin sections obtained from one to three different samples of each species were systematically measured. To achieve statistical significance, the largest number of possible measurements was taken. This number was mainly determined by the size and quality of the thin section and the size of the single calices in relation to the size of the thin sections. Thin sections were measured and values were calculated using the program PaleoTax/Measure (http://www.paleotax.de/measure).

For each type of measurement (calicular diameter and distance, width and distance of calicular rows) in one thin section the following values were obtained and presented for each species in this study:

- \( n \) number of measurements;
- \( \text{min-max} \) lowest and highest measured value (mm);
- \( \mu \) arithmetic mean (average; mm);
- \( s \) standard deviation (mm);
- \( \text{cv} \) coefficient of variation according to K. Pearson (Weber, 1986; percent);
- \( \mu \pm s \) first interval (mm).

Details on the mathematical background is presented in Löser (2012). The numerical characters obtained from the fossils were compared against those on specimens in worldwide fossil coral collections. Data storage and processing were carried out using a Hdb2Win/PaleoTax database (Löser, 2004) on post-Paleozoic corals and an associated sample and image database (18,700 specimens, 13,500 images), located in the Estación Regional de Noroeste (ERNO), Sonora, Mexico. Range charts of species and correlation dendrograms were calculated using programs of the Hdb2Win/Interpreter. Graphic images of the results were obtained using PaleoTax/Graph.

Collection abbreviations are as follows:
- BSPG Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany;
- CAMSM The Sedgwick Museum of Earth Sciences, Cambridge, UK;
- ERNO Estación Regional del Noroeste, Instituto de Geología, UNAM, Hermosillo, Mexico;
- GPS Geologische und Paläontologische Sammlung der Universität Leipzig, Germany;
- GZG Geowissenschaftliches Zentrum Göttingen, Germany;
- IBP Universität Bonn, Geologisch-Paläontologisches Institut;
- IGM Instituto de Geología, UNAM, Mexico City, Mexico;
- MB Museum für Naturkunde der Humboldt-Universität, Berlin, Germany;
- MNHN Muséum National d’Histoire Naturelle, Paris, France;
- NMB Naturhistorisches Museum Basel, Switzerland;
- NMBE Naturhistorisches Museum Bern, Switzerland;
- SAZU Paleontoloski institut Ivana Rakoveca, Ljubljana, Slovenia;
- SMNS Staatliches Museum für Naturkunde, Stuttgart, Germany;
The suborder Stylinina is uncertain. The stylinids sensu stricto shows a strong relationship to the Rhipidogyrids: They share the existence of a strong columella, auriculae, unproportionally thicker septa of the first cycle and very small trabeculae with this group.

Family Stylinidae d’Orbigny, 1851

Discussion. According to the literature, the family counts with about 50 genera. Many of them belong to other families, are unknown because the type of their type species is not available, or are synonyms.

Acanthocoenia d’Orbigny, 1850

Type species. Acanthocoenia rathieri d’Orbigny, 1850 by monotypy.

Discussion. The genus Acanthocoenia was briefly and clearly defined by d’Orbigny (1850) as being a Styлина with a pentameral septal symmetry. No such material was found during fieldwork in the Paris Basin or among collection material. Nevertheless, Acanthocoenia is not a phantom taxon. Material was described and illustrated by Volz (1903) and is here reported in detail.

Acanthocoenia neocomiensis Volz, 1903

Figures 3a-e

* Acanthocoenia neocomiensis Volz, 1903, p. 21, pl. 3, fig. 21-23.

v Styлина tehuanacensis (Felix, 1891). Reyeros de Castillo, 1983, p. 17, pl. 4, fig. 2, pl. 5, fig. 1.

Dimensions. See table 1.

Description. Plocoid colony. Calicular outline circular. Septa compact. Microstructure of medium size trabeculae. Septa in cross section externally thick, then equal in thickness, first cycle unproportionally thicker than other cycles. Symmetry of septa radial and regularly pentameral. Cycles of septa subregular. Septal cycles differ in length and thickness. First septal cycle reaches 40% of the calicular diameter, further cycles are shorter. Septa free, but often connected to the columella. Septal upper border unknown, lateral face occasionally with granules, inner margin with auriculae, which have more a rhopaloid form. Pali or paliform lobes absent. Costae present, non-confluent, surface granulated. Synapticulae absent. Columella styliform, large. Endotheca consists of thin tabulae. Wall present, compact, probably parathecal. Coenosteum broad, consisting of costae and exothecal dissepiments. Budding extracalicial.

Material. ERNO L-7104, L-7105, L-7106, L-7107, L-7109, L-7111, L-7112, L-7242, 6 thin sections.

Occurrence. Early Aptian of Atecoxcó, La Compañía. Aptian of San Juan Raya.

Other Occurrence. Barremian to Early Aptian of Romania (Suceava) Pojorîta area, Cimpulung-Moldovenesc, Valea
Figure 3. a-e: Acanthocoenia neocomiensis Volz, 1903. a-d: ERNO L-7111, a: transverse thin section; b-c: transverse thin section, detail; c: longitudinal thin section. d: ERNO L-7112, transverse thin section. f-g: Enallhelia anomalos (Felix, 1891), IGM 9264; f: transverse thin section; g: transverse thin section, detail. h-i: Stylina bullosa Blanckenhorn, 1890, IGM 9266. h: transverse thin section; i: transverse thin section, detail. Scale bar 1 mm.
Seaca, Valea Mesteacan. Early Albian of Mexico (Oaxaca) Tepelmeme, El Rodeo Ranch.

Discussion. The type material of this species presumably was lost during World War II. Comparison is based on the data in the primary literature.

Enallhelia Milne Edwards and Haime, 1849

Type species. Lithodendron compressum Goldfuss, 1829 by subsequent designation in Milne Edwards and Haime (1851).

Enallhelia anomalos (Felix, 1891)
Figures 3f-g

*v Prohelia anomalos Felix, 1891, p. 162, pl. 23, figs. 4, 4a-c.


v Prohelia anomalos Felix. Carreño et al., 1989, p. 99, fig. 34b.

v Enallhelia anomalos (Felix, 1891). Löser, 2006, p. 21, fig. 2G, H.

Dimensions. See table 2.

Material. ERNO L-7120, IGM 9259; 4 thin sections.

Occurrence. Early Aptian of Atecoxco, La Compañía. Late Aptian of San Lucas Teteletitlán.

Other Occurrence. Tithonian of Japan (various localities).

Stylangia de Fromentel, 1857

Type species. Stylangia neocomiensis de Fromentel, 1857 by monotypy.

Diagnosis. Plocoid colony. Calicular outline circular. Calices very small, very slightly elevated over the colony surface. Septa compact. Microstructure of small trabeculae, septa marked with a median dark line. Septa in cross section close to the wall thick, thinner towards the calicular centre, first cycle disproportionately thicker than other cycles. Symmetry of septa radial and regularly hexameral. Three cycles. Septal cycles differ in length and thickness. First septal cycle reaches 40% of the calicular diameter, further cycles are shorter. Septa free. Septal upper margin unknown, lateral face occasionally with large thorns, inner margin with auriculae. Pali or paliform lobes absent. Most septa of the first cycle are attached to the columella. Costae present, non-confluent, surface unknown. Synapticulae absent. Columella styliform. Endotheca unknown. Wall present, compact, probably parathecal. Coenosteum broad (ca. 100% of the calicular diameter), consisting of costae and small isolated trabecules, granulated at its surface. Budding extracalicinal.

Discussion. De Fromentel (1861: 178) later changed the name Stylangia to Prohelia because it does not belong to the Astrangiidae and the suffix -angia should not confuse.
Figure 4. a-c: Enallhelia nipponica Eguchi, 1942, IGM 9259. a: thin section of a colony; b: transverse thin section, detail; c: longitudinal thin section.
d-f: Stylangia neocomiensis de Fromentel, 1857, ERNO L-7113. d: transverse thin section; e: transverse thin section, detail; f: longitudinal thin section.
g-i: Styлина inwaldensis (Ogilvie, 1897), ERNO L-7110. g: transverse thin section; h, transverse thin section, detail; i: longitudinal thin section. Scale bar 1 mm.
genera have different type species and are not objectively synonymous. The type of the type species of Prohelia is not available. Stylangia is very closely related to Stylophelia and differs only by its encrusting, partly thick branching growth mode.

**Species.** The genus is monospecific. Stylangia laddi Wells, 1944 belongs to Stylomisilia.

**Range and distribution.** Early Cretaceous, Central Tethys and Western Atlantic.

**Stylangia neocomiensis** de Fromentel, 1857

Figures 4d-f

*V* Stylangia neocomiensis de Fromentel, 1857, p. 38, pl. 5, fig. 3-5.

Prohelia neocomiensis. de Fromentel, 1861, p. 178; de Fromentel, 1879, p. 491, pl. 121, fig. 1; Koby, 1896, p. 11, pl. 2, fig. 8.

Stylangia cf. neocomiensis de From. Alloiteau and Dercourt, 1966, p. 318, pl. 3, fig. 5.

**Dimensions.** See Table 4.

**Description.** As for the genus.

**Material.** ERNO L-7113; 2 thin sections.

**Occurrence.** Late Aptian of San Lucas Teteletitlán.

**Other Occurrence.** Early Cretaceous of Switzerland (Neuchâtel) Travers, Les Grands-Champs; Greece (Argolida) Nafplion, Pronia. Early Hauterivian (Radiatus zone) of France (Aube and Yonne), various localities (Argolída) Nafplion, Pronia. Early Hauterivian (Radiatus zone) of France (Aube and Yonne), various localities.

**Stylina de Lamarck, 1816**

**Type species.** Stylina echinulata de Lamarck, 1816 by monotypy. - *Stylina echinulata* was originally described as an extant coral species. Milne Edwards and Haimé (1848: 289) realised that the type material is from the Late Jurassic of France. The designation of *Stylinia granulosa* de Fromentel, 1863 as type species by Dacque (1933) is not valid, because this species was not one of the originally included species. Also the designation of *Stylina echinulata* from the Early Cretaceous of Puebla (Mexico) by Milne Edwards and Haimé (1947: 191) is invalid.

**Type of the type species.** The type material is supposedly lost. The samples examined by Milne Edwards and Haimé (MNHN nn), from which Alloiteau obtained thin sections, still exist. They have no type status. The diagnosis given here is based on these thin sections.

**Diagnosis.** Placoid colony. Calicular outline circular. Septa compact. Microstructure of septa unknown. Septa in cross section close to the wall slightly thicker, towards the coralite axis equal in thickness, first cycle disproportionately thicker than other cycles. Symmetry of septa radial. Stylina may show a differing number of septal systems (6, 8, 10) and septal cycles (2, 3, 4). Cycles of septa subregular. Septal cycles differ in length and thickness. First septal cycle reaches close to the columnella, subsequent cycles are shorter. Septa not connected to each other. Septal upper margin unknown, lateral face with occasional granules, inner margin with auriculae. Pali or paliform lobes absent. Costae present, non-confusent, surface unknown. Synapticulae absent. Columnella styliform. Endotheca consists of thin tabulae. Wall present, compact, probably parathecal. Coenosteum broad (ca. 100% of the calicular diameter), consisting of costae and exotheal dissepiments. Budding extracalicular.

**Synonyms.** The following genera are subjective synonyms and have been synonymized after having studied the type specimens of their respective type species (type species and their types are given in parentheses): Cellulastraea Blanckenhorn, 1890 (Cellulastraea crenata Blanckenhorn, 1890; SMNS 60381); Conocoenia d’Orbigny, 1849 (Astraea tumularis Michelin, 1844; MNHN M00252); Decaphyllum Frech, 1885 (Decaphyllum koeneni Frech, 1885; MB K 6048 [thin sections], GZG 772-21 [sample]); Gemmastrea Blainville, 1834 (Astraea tubulosa Goldfuss, 1829; IPB GF299); Helioystyla Lafuste, 1957 (Adelocoea corallina d’Orbigny, 1850; MNHN R09321); Hexahelioecina Roniewicz, 1966 (Helioecina stellata Roniewicz, 1966; ZPAL H III 664); Kobycoenia Beauvais, 1964 (Alloiteaucoenia claudiopolisensis, Beauvais, 1964; NMB); Octohelioecina Roniewicz, 1966 (Helioecina corallina Koby, 1881; MNHN A32667, NMB D4310-12, NMBE 5015279); Plesioystyla Alloiteau, 1958 (Plesioystyla hourcqi Alloiteau, 1958; MNHN M05152); Stylopora McCoy, 1848 (Stylopora solida McCoy, 1848; CAMSM J34968-70); Tremoecina d’Orbigny, 1849 (Tremoecina submarina d’Orbigny, 1849; MNHN R09323).

**Range and distribution.** (?) Early Jurassic to latest Early Cretaceous (Early Albanian). - The genus does not reach the Turonian. The both Late Turonian species Sarcinula quinuncialis Michelin, 1841 (later assigned to Stylina) and Stylina arambourgi Alloiteau, 1941 are doubtful: the types of both species are derived from Uchaux (France, Vaucluse) and poorly preserved. The material from the Cenomanian of the Czech Republic described by Počta (1887) probably belongs to Stelidioseris. The material from the Late Cretaceous of Mexico (Oaxaca, San Pedro

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Yucunama) described by Reyeros de Castillo (1983) as *Stylina sucrensis* Wells, 1944 belongs to *Actinastrea*. The Late Cretaceous material from Italy (Veneto, Belluno, Lago di Santa Croce, Calloneghe) described by Zuffiardi-Comerci (1927), as well as the Late Cretaceous samples from Spain (Cataluña, Lèrida, Com. Pallars Jussà, Mun. Pallars Jussà, Toralla) listed by Bataller (1937) and those from Italy (Lazio, Roma, Prenestini Mts, Rocca di Cave) by Carbone et al. (1980) are all unavailable and doubtful. The genus is most abundant in the Late Jurassic, less abundant from the Berriasian to Early Aptian and generally rare from the Late Aptian to Albamian. *Stylina* occurs worldwide, but is rare in the Western Hemisphere.

**Relationship.** *Heliocoenia* Etallon, 1859 and *Alloiteaucoaenia* Beauvais, 1964 differ from *Stylina* by having a bilateral symmetry. *Acanthocoenia* differ by a pentameral septal symmetry. *Stylangia* (? and *Prohelia*) are encrusting forms and generally have the same structure as *Stylina*, but *Stylangia* differs in the formation of its coenosteum. *Enallhelia* is thick-branching. *Stylohelia* de Fromentel, 1861 has a different coenosteum and is comparable to *Stylangia*.

**Species.** A total of 201 species of *Stylina* have been described: 146 from the Jurassic and 55 from the Cretaceous (Lathuilière, 1989; Löser 2000). At least for the Cretaceous, half of them are synonyms. The species are distinguished on the basis of their calicular dimensions and septal symmetry and number.

**Stylina bullosa** Blanckenhorn, 1890

Figures 3h-i

vp *Cryptochaena ramosa*, Toula, 1889, p. 83, pl. 5, fig. 10, 11.

*v* *Stylina bullosa* Blanckenhorn, 1890, p. 11, pl. 2, fig. 1.

? *Stylina bullosa* Blaukennhorn. Felix, 1903, p. 177, pl. 17, fig. 4.


vp *Stylina regularis* de Fromentel 1862. Morycowa, 1964, p. 34, pl. 10, fig. 7, pl. 15, fig. 3, pl. 19, fig. 1, 2.

v *Stylina giebulaensis* Liao, 1982, p. 157, pl. 4, fig. 2, 3, pl. 5, fig. 1.

v *Cryptochaena viaderi* Reig Oriol, 1991, p. 16, pl. 4, fig. 5, 6.

*Stylina sugiyamai* Eguchi. Kashiwagi et al., 2002, p. 10 fig. 5.4.

**Dimensions.** See Table 5.

**Material.** IGM 9266; 1 thin section.

**Occurrence.** Aptian of San Juan Raya.


**Stylina inwaldensis** (Ogilvie, 1897)

Figures 4g-i

*v Diplocoenia inwaldensis* Ogilvie, 1897, p. 165, pl. 18, fig. 7-8.

v *Stylina foliosa* Ogilvie, 1897, p. 170, pl. 16, fig. 15.

v *Stylina milleporacea* Ogilvie, 1897, p. 173, pl. 17, fig. 8.

v *Stylina sucrensis* Wells, 1944, p. 435, pl. 70, fig. 1.

*S. solomkoi* Karakash. Bendukidze, 1961, p. 8, pl. 1, fig. 1, 4, 3-5.

v *Stylina parvistella* Volz, 1903. Morycowa, 1971, p. 45, pl. 7, fig. 1; Turnšek and Mihajlovic, 1981, p. 14, pl. 8, fig. 1-3; Liao and Xia, 1985, p. 134, pl. 3, fig. 5; Liao and Xia, 1994, p. 147, pl. 39, fig. 6; Császár and Turnšek, 1996, p. 434, fig. 15; Götz et al., 2005, p. 874, fig. 8A

*S. elegans* Eichwald, 1865. Kuzmicheva, 2002, p. 173, pl. 25, fig. 5

**Dimensions.** See Table 6.

**Material.** ERNO L-7110; 2 thin sections.

**Occurrence.** Early Aptian of Atocoxco, La Compañía.

**Other Occurrence.** Tithonian of Czech Republic, Stramberk. Cretaceous of Serbia (East Serbia) Skuvija. Berriasian to Valanginian of China (Xizang [= Tibet] Autonomous Region) Baingoin county. Hauterivian of Spain (Valencia, Castellón) La Avelâ, Catí. Early Hauterivian (Radiatus zone) of France (Yonne) various localities (BSPG 2003 XX 5010). Early Hauterivian of Ukraine (Krymskaya Bakhchisarajskij district; Fotisala; Mangusch; Alma river, Partizany [= Sably]). Late Barremian to Early Aptian of Hungary (Baranya Megye) Mesec Mts, Jánosipuszta. Early Aptian of Serbia (East Serbia) Rajcjinica; Zljebine; Venezuela (Sucre) Cumaná, Las Cinco Ceibas. Early Aptian

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**Table 5. Dimensions of Stylina bullosa** Blanckenhorn, 1890.

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**Table 6. Dimensions of Stylina inwaldensis** (Ogilvie, 1897).

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</table>
(Lenticularis zone) of Romania (Suceava) Pojorîta area, Cîmpulung-Moldovenesc, Valea Seaca.

**Discussion.** Comparable material is generally assigned to *Stylina parvistella*, but this species has smaller dimensions (calicular diameter 0.7-0.9 mm according to its author; the type material is lost). *Stylina inwaldensis* is applied instead of *Stylina foliosa* because it is better preserved and the type material more clearly shows the characteristics of the species. *Stylina inwaldensis* is generally a common Early Cretaceous *Stylina* species.

**Stylina pachystylina** Koby, 1896

Figure 5d

*\textit{v} Stylina pachysty]la Koby, 1896 p. 26, pl. 5, fig. 6. non

**Dimensions.** See Table 7.

**Material.** IGM 9223; 1 thin section.

**Occurrence.** Aptian of San Juan Raya.

**Other Occurrence.** Barremian of France (Doubs) Morteau.

Figure 5. a-c: *Stylina rozkowskae* (Morycowa, 1964), IGM 9257. a: transverse thin section; b: transverse thin section, detail with preserved microstructures; c: longitudinal thin section. d: *Stylina pachysty]la* Koby, 1896, IGM 9223, transverse thin section. e-f: *Stylina sugiyamai* Eguchi, 1951, IGM 9245. e: transverse thin section; f: transverse thin section, detail. g-i: *Stylina urgonica* (Dietrich, 1926), IGM 9203. g: transverse thin section; h: transverse thin section, detail; i, longitudinal thin section. Scale bar 1 mm.
**Stylina rozkowskae** (Morycowa, 1964)  
Figures 5a-c

*Heliocoenia rozkowskae* Morycowa, 1964, p. 40, text-fig. 4, pl. 7, fig. 6, pl. 8, figs. 3, 4.

*Heliocoenia rozkowskae* Morycowa 1964. Turnšek and Mihajlovic, 1981, p. 12, pl. 4, fig. 4-7; Morycowa, 1989, p. 62, pl. 21, fig. 1, 2; Morycowa and Masse, 1998, p. 742, fig. 13.3.

*Stylina sugiyamai* Eguchi, 1951  
Figures 5e-f


**Dimensions.** See Table 8.

**Material.** IGM 9257; 4 thin sections.

**Occurrence.** Early Aptian of Atenco, La Compañía.

**Other Occurrence.** Cretaceous of Serbia (East Serbia) Skuvija. Early Late Barremian of France (Bouches-du-Rhône) Chainon la Fare, Saint Chamas, canal EDF. Late Barremian of Poland (Malopolskie, Tarnów) Tarnów, Trzemesna. Early Aptian of France (Vaucluse) Rissas Mts; Poland (Malopolskie, Wadowice) Lanckorona, Jastrzebia.

**Stylina sugiyamai** Eguchi, 1951  
Figures 5e-f

*vp Stylina micropora* Koby, 1896, p. 25, pl. 6, fig. 1 [non pl. 5, fig. 3, 4].

*Stylina sugiyamai* Eguchi, 1951, p. 60, pl. 22, fig. 7.

*vp Stylina regularis* de Fromentel 1862. Morycowa, 1964, p. 34, pl. 10, fig. 7, pl. 15, fig. 3, pl. 19, fig. 1, 2; Morycowa, 1971, p. 47, text-fig. 6 d, pl. 5, fig. 2; Löser, 2010, p. 601, fig. 4.4.

*Heliocoenia rarauensis* Morycowa, 1971, p. 47, fig. 1.

*Stylina sugiyamai* Eguchi, Löser and Mori, p. 85 fig. 2.4

**Dimensions.** See Table 9.

**Material.** IGM 9203; 3 thin sections.

**Occurrence.** Aptian of San Juan Raya.

**Other Occurrence.** Tithonian of Japan (Kochi-ken) Takaoka-gun, Sakawa-cho, Nishiyamagumi. Barremian to Early Aptian of Romania (Suceava) Pojorîta area, Cimpulung-Moldovenesc, Rarau Mt. Barremian (Moutoniceras - Giraudi zone) of France (Drôme) Serre de Bleyton. Late Barremian of France (Bouches-du-Rhône) Orgon (UP 32); Poland (Malopolskie, Tarnów) Tarnów, Trzemesna. Late Barremian to Early Aptian (Sartousi - Weisi zone) of Switzerland (Schwyz) Drusberg, Käsernalp. Early Aptian of Greece (Viotti) Arachova (BSPG 2003 XX 5536); Poland (Malopolskie, Wadowice) Lanckorona, Jastrzebia (ERNO L-5429); Slovenia (West Slovenia) Banska Planota, Osojnica (SAZU P-505). Early Aptian (Lenticularis zone) of Greece (Viotti) Levadia, roadcut near Perachorion NW Levadia (BSPG 2003 XX 5735); Romania (Suceava) Pojorîta area, Cimpulung-Moldovenesc, Valea Izvorul Alb.

**Stylina urgonica** (Dietrich, 1926)  
Figures 5g-i

*Agathelia urgonica* Dietrich, 1926, p. 75, pl. 5, fig. 1, pl. 8, fig. 2.

*Stylina urgonica* (Dietrich, 1926). Löser, 2008b, p. 44, pl. 2, fig. 3.

**Dimensions.** See Table 10.

**Material.** IGM 9203; 3 thin sections.

**Occurrence.** Aptian of San Juan Raya.

**Other Occurrence.** Early Aptian (Weissi - Furcata zone) of Tanzania (Tanganyika, Mtwara) Kiturika Mts, Naiwanga, Ndakasha Mt.

**DISCUSSION**

**Taxonomic composition**

The family Stylinidae in the Tehuacán region is represented by a high diversity assemblage, particularly in the
Corals from the Early Cretaceous of Puebla (Mexico)

Aptian, which contains ten distinct species; the diversity in Barremian strata is somewhat more modest, with two species. However, with a total of four genera, the area presents a great supra-specific diversity. An interesting aspect is the relative abundance of the genus *Acanthocoenia* in the study area. The genus is very rare in the Aptian of the Central Tethys, and the present material is the first that has allowed the identification of this genus in thin sections. Further occurrences are doubtful because of the unavailability of the material (d’Orbigny, 1850; Volz, 1903) or the poor state of preservation (Löser and Raeder, 1995). The occurrence of *Stylangia* in the Early Albian represents the first well-constrained occurrence of this genus for the Early Cretaceous outside from its type area in the Paris Basin.

**Distribution**

The corals of the Family Stylinidae in the Tehuacán Valley show a stratigraphic or facies zonation (Figure 6).

Except for *Enallhelia anomalos*, all species of the family are restricted to the Aptian. The stratigraphic range of the stylinids found in the Early Cretaceous of Puebla lies clearly in the Latest Jurassic to the Early Aptian (Figure 7). Stylinid species have long stratigraphic ranges, and thus the gaps in the Berriasian and Valanginian record are likely due to the regression of the sea level during these time periods. In all likelihood, stylinids are not preserved in these strata due to erosion of the shallow marine sediments during emersion or transgression of the Late Valanginian to Early Hauterivian. Decreasing carbonate sedimentation in the Tethys due to OAE1 and the Western Pacific due to changed ocean currents (Iba and Sano, 2007) has limited the diversity of coral communities in a large scale, resulting also in the extinction of the family during the Albian (Löser, 2013).

**Palaeobiogeography**

Members of the Family Stylinidae are either common or poorly documented in the Western Atlantic. Apart from some reports from Venezuela (Wells, 1944) and Jamaica (Löser et al., 2009), the genus occurs only in Puebla in the New World. Stylinids are completely unknown from the Aptian to Cenomanian of the Texas platform, as well as from the Late Barremian to Albian of the Bisbee Basin. Former reports on putative stylinids from these areas (e.g., Löser and Minor, 2007) turned out to belong the genus *Stelidioseris*, or other genera of the family Columastraeidae. The absence of stylinids in these areas cannot be explained by lower water temperatures because the high latitude epicontinental sediments of the Hauterivian of the Paris Basin are relatively rich.
in stylinids. The fauna from Puebla is the most species-rich association in the Western Hemisphere known to date. The stylinid populations from Puebla allow considerable insight into the palaeobiogeographic relationships with Tethyan and Western Pacific faunas (Figure 8). It must be emphasized that the number of species in the Puebla fauna, as well as those in the correlating faunas, are too low to draw clear conclusions on the precise palaeobiogeographical distribution of the corals, as the three different stratigraphic levels do not correlate much with each other. The Barremian stylinids show closer relationships to the Latest Jurassic to Early Cretaceous faunas, whereas the Aptian stylinids correlate only with Barremian to Aptian faunas. The Late Aptian stylinids are isolated.

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