A new coral family and three new genera (Scleractinia) from the Lower Cretaceous of Puebla and Sonora, Mexico

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RESUMEN

Corales solitarios actualmente asignados al género Plesiosmilia son comunes en faunas de corales del Jurásico Tardío y Cretácico Temprano. El género está mal definido y su posición sistemática es dudosa. Además, el examen de material tipo ha mostrado que el género incluye corales de diferentes morfologías. Aquí, un grupo común de corales es separado en un nuevo género de coral solitario y dos géneros nuevos de corales faceloïdes. Los tres géneros nuevos pertenecen a una familia nueva. El material descrito viene del Valangiano-Lower Hauterivian of San Juan Raya (Puebla) and the Lower Albian of Rayón (Sonora, ambos México).

Palabras clave: corales; Cretácico; Scleractinia; México; Puebla; Sonora.

INTRODUCTION

Since Alloiteau (1952, 1957), the classification of the Mesozoic corals is mainly based on the microstructure of the septal blade, a principal morphologic part of the skeleton of Scleractinian corals. Alloiteau was followed by later authors (Morycowa, 1964, 1971; Roniewicz and Morycowa, 1993; Roniewicz, 1996, among many others). Septal microstructure refers principally to the size of the trabeculae, calcification centres that make up the septa. Whereas in earlier studies the absolute size of trabeculae was taken into account (Roniewicz, 1996), Löser (2016) proposed to relate the size of the trabeculae to the thickness of septa. Moreover, it was shown that the microstructure may vary within the same coral (Löser, 2016: fig. 3.3.1.4) depending on its position in the septal blade. In addition to the septal microstructure, the presence of perforations in the septa, and the presence or absence of synapticulae, and other peculiar characteristics such as penneulae or auriculae, are considered crucial for the definition of the families and higher taxonomic ranks such as superfamilies or suborders. The way in which to classify Mesozoic corals – based on the fine structure of the skeleton, as proposed by Alloiteau and refined by later authors – works properly when these skeletal structures are preserved. The skeleton of Scleractinian corals is made of aragonite, a mineralogical variation of calcite that is usually post-mortem diagenetically transformed into calcite. During this process, skeletal microstructures can become altered or completely lost. A second diagenesis may replace the calcite by silica, resulting in even more alteration. Hence, the preservation of microstructures is an exception, not the rule. Of course, it is possible to compare material that has no microstructures at all to a genus that is based on a proper study of the septal microstructure. But it is not possible to form a diagnosis for a new genus on material without showing septal microstructures, because the systematic position cannot be proven without its knowledge.

In the 19th century, post-palaeozoic corals were principally classified into families. This concept was improved by Americans Vaughan and Wells (1943) who introduced suborders. Their French counterpart, James Alloiteau and later authors followed them and applied suborders within the order Scleractinia for the distinction of larger groups. Nevertheless, only some suborders are well limited or clearly based on type material (Löser, 2016), whereas others are poorly defined and/or used in a very broad sense. Because the order group is not covered by the code of the International Commission of Zoological Nomenclature (ICZN) it makes this taxonomic level highly conceptual. In order to avoid conceptual and non-type-based classification on the one hand, and to present a more consistent concept for the taxonomic level above the family on the other, Löser (2016) introduced the superfamily as a principal taxonomic level to group Mesozoic Scleractinian corals, distinguishing 27 superfamilies and 56 families.

Some superfamilies and families had an informal character because no formally established names were available. One of these groups is that of the genus *Plesiosmilia* Milaschewitsch, 1876, and related or synonymous genera first introduced in Löser (2013a). *Plesiosmilia* itself cannot serve as type for a new family because the type of the type species *Plesiosmilia turbinata* Milaschewitsch, 1876 is silicified. The types of the type species of possible junior synonyms (*Elasmosmilia* Beauvais, 1961, *Lophosmilia* Milne Edwards and Haime, 1848a, *Peplosmilia* Milne Edwards and Haime, 1851, among others, see below) are equally
poorly preserved. There exists the family Axosmiliidae Geyer, 1955 based on Axosmilia Milne Edwards and Haime, 1848a, but the type specimen of Caryophyllia extinctorium Michelin, 1841 (type species of Axosmilia) is equally extremely poorly preserved. The same applies to the family Ellipsosmiliidae Alloiteau, 1957 where the type specimen of Montlivaltia cornucopia Milne Edwards and Haime, 1848b, type species of Ellipsosmilia d’Orbigny, 1849, is not available and, moreover, from a locality where all corals are silicified.

Not only is there Plesiosmilia in this group, there are also more solitary (Actinosmilia d’Orbigny, 1849, Carantoseris Alloiteau 1952, Cenomanosmilia Alloiteau 1949, Ceratosmilia Alloiteau, 1957, Dautlusmilia Kuzmicheva, 2002, Plesiollites Löser, Steuber and Löser, 2018, Trochophyllia Alloiteau, 1952) and yet unnamed phaceloid corals. All these genera cannot be assigned with certainty to this informal group because it is poorly defined. The Plesiosmilia Group is widely distributed in space and time ranging from the Jurassic into the Late Cretaceous. The present contribution therefore introduces a new formal genus and family name in order to replace the Plesiosmilia Group by a more proper unit. Moreover, another two related genera are established.

**Study area**

The material described herein comes from two localities in Mexico (Figure 1). A part of the material comes from the famous outcrop area of San Ruan Raya in Puebla (Figure 2a, 2b). Coral occurrence, localities and stratigraphy were discussed by Löser et al. (2013). For a long period of time this area was considered to be Aptian in age, until the study of nano-fossils that revealed an Upper Valanginian to Lower Hauterivian age (González León et al., 2015), which is supported by the composition of the coral fauna (Löser, 2021). The studied material comes from the historic Aguilar collection, which is kept in the fossil collection of the Institute of Geology at the UNAM (National Autonomous University of Mexico) in Mexico City. The exact locality of the material is unknown. The other part of the material comes from central Sonora (Figure 2c, 2d). Around the village of Cerro de Oro, shallow marine strata of the Cerro de Oro Fm (Bisbee Group) yields fossils with an Upper Barremian to Lower Aptian age (González León and Lucas, 1995; Baron-Szabo and González León, 1999; Löser, 2011; Velázquez-Heras et al., 2021). The studied material is kept at the Northwest Regional Station (ERNO) in Hermosillo, Sonora. Because the studied material comes from collections, no exact sample positions can be given.

**MATERIAL AND METHODS**

For the present study, approximately 300 coral specimens that are similar to Plesiosmilia ranging from the Upper Jurassic to the Upper Cretaceous were examined, and 75 of them are type specimens. Around 125 thin sections were available for the study. Thin sections were scanned by passing light through them using a flatbed scanner with an optical resolution of 6,400 dpi. Scanned images were then transferred to greyscale bit maps. Their quality was amended using histogram contrast manipulation (contrast stretching) where possible. Corallite dimensions of each specimen were systematically measured. In the phaceloid corals, 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 corallites, in relation to the size of the thin sections. Septa were counted for numerous corallites. For the corallite diameter and septal counts in one thin section of the colonial corals, the following values were obtained:

- n, number of measurements or counts
- min–max, lowest and highest measured or counted values (mm for measurements)
- µ, arithmetic mean (average)
- s, standard deviation
- v, coefficient of variation according to K. Pearson
- µ±s, first interval
- c, corallite diameter
- cmin, small corallite diameter
- cmax, Large corallite diameter
- s, septa.

**Figure 1. Study area, general view.**
Thin sections were measured and values were calculated using the Palaeontological Database System PaleoTax, module PaleoTax/Measure (https://www.paleotax.de/measure). Morphometric data of the corals were compared against those of specimens in worldwide fossil coral collections, and an associated image database located in the ERNO. Data storage and processing were carried out using the PaleoTax database programme (Löser, 2004). Collection acronyms as follows: ERNO, Northwest Regional Station at the UNAM (Hermosillo, Sonora, Mexico); IGM, Institute of Geology at the UNAM, Mexico City, Mexico; MGB, Geological Museum of the City of Barcelona (Catalonia, Spain).

**SYSTEMATIC DESCRIPTION**

Order Scleractinia Bourne, 1900  
Superfamily Misistelloidea Eliášová, 1976  

**Diagnosis.** Solitary and colonial (astreoid, phaceloid, plocoid) corals. Septa compact, in varying thickness, in a subregular radial symmetry. Septal outline enlarged rhombic. Septa not connected to each other (Rayasmiliidae) or only in the centre of the corallite (Misistellidae). Lateral faces with fine granulae or smooth, upper margin smooth.


**Families**

Misistellidae Eliášová, 1976 and Rayasmiliidae n. fam. (formerly Plesismilia group).

**Family Rayasmiliidae new family**

*Type genus.* Rayasmilia n. gen.  
*Zoobank ID.* urn:lsid:zoobank.org:act:EB179F35-6BA4-4263-805E-9413199D27BE.  

**Comparison.** The new family differs in two aspects from the Misistel-
lidae. The septa in the Misistellidae shows a zigzag pattern towards the coralite centre. They are connected in the coralite centre to form a type of columella, and they are also connected to each other.

**Discussion.** In Löser (2013a) the family was introduced as the informal Plesiosmilia-group. The genus Plesiosmilia cannot serve as a type taxon, since its type and toptotypical material is silicified and fine skeletal structures are, therefore, unknown. The family belongs to the superfamily Misistelloidea that is based on the family Misistellidae. The family was originally assigned to the suborder Astrationida where it is misplaced. The suborder Astrationida Alloiteau, 1952 was originally characterised as having compact septa with a strongly ornamented upper septal border. The latter may imply that the trabeculae are large. Later, the suborder was synonymised with the suborder Faviina Vaughan and Wells, 1943 that has clearly large trabeculae (Garberoglio et al., 2021). The type of the type species of the name-giving genus Astrea Lamarck, 1801 (type species Madrepora rotulosa Ellis and Solander, 1786) was never the object of a detailed examination (the type is figured in Löser 2016). Further, the new family cannot be assigned to the suborder Meandrinina Alloiteau, 1952 that has – in comparison to the Astrationida and Faviina – smooth distal margins; however, the septal blades are made up of medium-sized trabeculae (Löser, 2016, fig. 3.3.1.3). For those coral workers who still apply suborders, the new family remains without suborder.

**Genera**

For the moment, we include here six genera (Table 1). The number of genera is surely higher but since many genera lack information about their fine skeletal structure, mainly the septal microstructure, they probably cannot be assigned to any family. Principally for the genus Rayasmilia, many similar genera exist (see below for more details). Morycowa and Marcopoulou-Diacantoni (2002) illustrate under the name Plesiofavia dubia (de Fromentel, 1857) asteroid colonies that have the microstructures as stated for the family. This material cannot be assigned to Plesiofavia because this genus belongs as a junior synonym of Ovalastrea d’Orbigny, 1849 to the family Latomeandridae de Fromentel, 1861 (see Löser, 2016).

**Distribution**

Upper Jurassic to Cretaceous, worldwide. It is possible that the family already occurs in the Middle Jurassic, but no sectioned material was to hand to confirm this. Further, the family may continue into the Palaeogene, but Cenozoic corals are usually not examined using thin sections and their microstructure is, therefore, unknown.

**Genus Rayasmilia new genus**

**Type species.** Rayasmilia salvata n. sp.

**Zoobank ID.** urn:lsid:zoobank.org:act:1A96D599-5E3E-42F7-813A-DBA8AD6725C.

**Diagnosis.** Solitary turbinate coral of circular to elliptical outline. Septa compact, made of small trabeculae, not connected to each other, in a regular radial symmetry. Wall absent. Epitheca present. Endotheca well developed. Columella lamellar.

**Description.** Solitary turbinate coral. Coralite outline circular to elliptical, diameter up to 45 mm, but generally below 30 mm, pit depressed. Septa compact. Microstructure of small-sized trabeculae, septa with a median dark line. Septa in cross section biconieiform thick close to the wall, thinner towards the centre. Septa strong with a thickness of one millimetre or more. Symmetry of septa radial and regularly in varying systems, but 12 being most common. Cycles of septa regular. Septal cycles differ in length and thickness. First septal cycle extends to the coralite centre, later cycles are subsequently shorter. Septa are not connected to each other. Septal upper margin smooth, lateral face smooth or finely granulated, inner margin smooth. Pali absent. Some septa of the first cycle may, rarely, be attached to the columella. Costae present but short, smooth on their surface. Symapticulae absent. Columella lamellar. Endotheca consists of numerous dissepiments. Wall absent. Epitheca present.

**Etymology.** After the type locality San Juan Raya. The Spanish word raya translates into line, corresponding well to the microstructural feature of the new genus. The suffix -smilia is commonly used for solitary corals.

**Occurrence.** Upper Jurassic to Cenomanian, worldwide.

**Comparison.** The new genus is difficult to compare to similar coral genera because most of the type material of these genera does not show microstructures. The following genera could be related to the new genus:

- **Axiphyllum** Quenstedt, 1880. – The type material of the type species is silicified. The genus is considered to be a synonym of Plesiosmilia.
- **Axosmilia.** – The type of the type species is poorly preserved and there are no thin sections available.
- **Cenomanosmilia.** – There are no thin sections available and toptotypical material could not be obtained since the type locality is no longer accessible. The types seem to be strongly recrystallised.
- **Ceratosmilia.** – The septal microstructure is unknown because the type of the type species is silicified.
- **Dautlasmilia.** – The columella is stronger and seems to be spongiosae. Elasmosmilia. – The type of the type species is completely recrystallised. Ellipsosmilia. – The type of the type species is silicified.
- **Lophosmilia.** – The type material of the type species is lost. There exists only an unjustified neotype. There are no thin sections available.
- **Peplosmilia.** – The type of the type species is only fragmentarily preserved.
- **Plesiolites.** – The genus is similar to Rayasmilia but has a cupulate form comparable to Cyclolites Lamarck, 1801.
- **Plesiosmilia.** – The septal microstructure is unknown because the type of the type species is silicified.
- **Saltocathus** Morycowa and Masse, 1998. – The type of the type species is poorly preserved, the thin sections are fragmentary and show a strongly recrystallised coral.
- **Trochophyllia.** – There are no thin sections available. The septal microstructure is unknown. The genus does not show a columella.

The genera Kobypyllia Baron-Szabo and Fernández Mendiola, 1997 and Montlivaltia Lamouroux, 1821 are, in their outer appearance, very similar to the new genus, but they differ in larger trabeculae (easily visible at the upper and outer septal margin) and – in Montlivaltia – the absence of a columella. Material described as ?Placosmilia Milne Edwards and Haime, 1848a and ?Lasmoegyra d’Orbigny, 1849 by Löser et al. (2019) is very similar but has larger trabeculae that are only visible in well preserved material. Caryophyllids have a very reduced endothea

<table>
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<th>Table 1. Genera of the Rayasmiliidae n. fam.</th>
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**Type.** Rayasmilia dubia Morycowa and Marcopoulou-Diacantoni (2002) illustrate under the name Plesiofavia dubia (de Fromentel, 1857) asteroid colonies that have the microstructures as stated for the family. This material cannot be assigned to Plesiofavia because this genus belongs as a junior synonym of Ovalastrea d’Orbigny, 1849 to the family Latomeandridae de Fromentel, 1861 (see Löser, 2016).
and a septothecal wall. The genus *Aulosmilia* Alloiteau, 1952 is comparable in its general structure, but differs by way of its septal microstructure, septal outline, the T-shaped inner septal margins, a septothecal wall, and septa of younger cycles that are attached to septa of older cycles. *Aulosmilia* has its mayor distribution in the Upper Cretaceous and Palaeogene, but also rarely occurs in the Lower Cretaceous. For instance, *Pleurosmilia fromenteli* Angelis d’Ossat, 1905 in Baron-Szabo and Steuber, 1996. Species with very thin septa (such as *Aulosmilia bella* Reig Oriol, 1991, *Axosmilia mexicana* Wells, 1946, *Pleuromisma whitneyi* Wells, 1933, or syntype MGB 20521 of *Pleosmosma casanasi* Angelis d’Ossat, 1905) are not included in *Rayasmilia*, at the present time; however, they may belong to *Bathmosmilia* Alloiteau, 1958. The same applies to similar solitary corals from the Upper Cretaceous (for instance, material assessed as *Plesiosmilia* in Löser, Steuber and Löser, 2018), whereby the microstructure consists of small trabeculae marked by a dark line that is traversed by perpendicular dark lines.


Most common is a duodecameral symmetry, but there are also species with a decameral or hexameral septal symmetry. The number of septa does not increase with the growth of the coral. The septa grow in a very early ontogenetic stage of the coral. When this stage is reached, the coral mostly increase in height, but very little in diameter. Therefore the species can be distinguished by the septal symmetry, the number of septa does not increase with the growth of the coral. The septa of the species can be distinguished by the septal symmetry, the number of septal cycles, and the diameter.

**Rayasmilia salvata new species**

![Figure 3](image-url)

v2013a *Pleiosmilia hennigi* (Dietrich, 1926) – Löser, fig. 5.10
v2013b *Pleiosmilia hennigi* (Dietrich, 1926) – Löser, fig. 3.1

**Diagnosis.** *Rayasmilia* with a duodecameral septal symmetry with three septal cycles resulting in 48 septa. Corallite diameter about 16 mm.

**Description.** As for the genus.

**Etymology.** Feminine form of the Latin participle *salvatus*, to save. It refers to the intention to save or to assure the informal concept in the form of a better defined taxon.

**Type.** Holotype IGM 9193. Mexico, Puebla, San Juan Raya area. Cretaceous, San Juan Raya Formation, Upper Valanginian to Lower Hauterivian.

**Measurements.**

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**Occurrence.** Valanginian to Santonian, worldwide.

**Genus Rayaphyllia new genus**

**Type species.** *Rayaphyllia atheca* n. sp.

**Zoobank ID.** urn:lsid:zoobank.org:act:AF03F810-D1FE-496F-8775-EA32A4330593.

**Diagnosis.** Phaceloid coral. Septa compact, made of small trabeculae, not connected to each other, in a subregural radial symmetry. Wall absent. Epitheca present. Endotheca well developed. Columella absent.

**Description.** Phaceloid colony. Corallite outline circular or elliptical, diameter up to 16 mm but generally below 10 mm. Septa compact. Microstructure of small-sized trabeculae, septa with a median dark line. Septa in cross-section, bicuneiform close to the wall, thinner towards the centre. Septal maximum thickness around 500 µm for the first cycle. Septa of subregural septal cycles differ in length and thickness. First septal cycle extends to the calicular centre, later cycles are subsequently shorter. Septa occasionally connected, only by means of dissepiments. Septal distal margin unknown, lateral face and inner margin smooth. Pali absent. Costae hardly present, surface unknown. Synapticular absent. Columella absent. Endotheca consists of dissepiments, in two regular rings in the type species. Wall absent. Epitheca present. Coenosteum absent. Budding intracalcinal.

**Etymology.** After the type locality San Juan Raya. The suffix *-phyllia* (Greek for leaf) is commonly used for phaceloid corals.

**Occurrence.** Aptian to Santonian, 1990, but the type material of the type species is poorly preserved and insufficiently described.

**Species.** The type species, *Thecosmilia distefanoi* Prever, 1909a, and with certain reservation *Montlivaltoides ngariensis* He and Xiao, 1990.

**Rayaphyllia atheca new species**

![Figure 4](image-url)

v1889 *Lophosmilia (?)* spec. – Toula, p. 84, pl. 6, fig. 3
v2019 *Montlivaltoides typicus* He & Xiao, 1990 – Löser et al., p. 215, fig. 337
**Zoobank ID.** urn:lsid:zoobank.org:act:5BE5E6F-F2E8-4F37-9395-02D9999A72ED.

**Diagnosis.** *Rayaphyllia* with a corallite diameter of six to eight millimetres, and between 48 and 48 septa.

**Description.** As for the genus.

**Etymology.** The Latin word *theca* (box, capsule, cover, container) refers in extant corals to the lateral boundary of the corallite. In Mesozoic corals, the term wall is more common. *Atheca* refers to the absence of a wall.

**Type.** Holotype IGM 9204. Mexico, Puebla, San Juan Raya area. Cretaceous, San Juan Raya Formation, Upper Valanginian to Lower Hauterivian.

**Measurements.**
A new coral family and three new genera (Scleractinia) from the Lower Cretaceous, Mexico


**Etymology.** Named after its origin, the Mexican state Sonora. The suffix -phyllia (Greek for leaf) is commonly used for phaceloid corals.

**Occurrence.** Tithonian to Middle Albian (?Cenomanian), worldwide.

**Discussion.** The only comparable genus is *Montlivaltoides* He and Xiao, 1990, but the type material of the type species is poorly preserved and insufficiently described.

**Figure 3.** *Rayasmilia salvata* n. sp., n. gen. Holotype IGM 9193. 1, transversal thin section; 2, transversal thin section, detail of the corallite centre; 3, transversal thin section, detail of the microstructure; 4, transversal thin section, detail of the epitheca; 5, oral view; 6, longitudinal thin section. Scale bars = 1 mm.

**Genus** *Sonoraphyllia* new genus

**Type species.** *Sonoraphyllia aurea* n. sp.


**Diagnosis.** Phaceloid coral. Septa compact, made of small trabeculae, not connected to each other, in a regular radial symmetry. Wall absent. Epitheca present. Endotheca well developed. Columella lamellar.

**Description.** Phaceloid colony. Calicular outline circular to elliptical, diameter 8-10 mm. Septa compact. Microstructure of small-sized trabeculae, septa with a median dark line. Septa in cross-section, bicuneiform close to the wall, thinner towards the centre. Septal maximum thickness 500 µm. Symmetry of septa irregularly radial with subregular cycles. Septal cycles differ in length and thickness.


**Etymology.** Named after its origin, the Mexican state Sonora. The suffix -phyllia (Greek for leaf) is commonly used for phaceloid corals.

**Occurrence.** Tithonian to Middle Albian (?Cenomanian), worldwide.

**Discussion.** The only comparable genus is *Montlivaltoides* He and Xiao, 1990, but the type material of the type species is poorly preserved and insufficiently described.
Figure 4. *Rayaphyllia atheca* n. sp., n. gen. Holotype IGM 9204. 1, transversal thin section; 2-3, transversal thin section, detail; 4, longitudinal thin section. Scale bars = 1 mm.


**Sonoraphyllia aurea** new species

Figure 5

v1999 *Placophyllia bandeli* Baron-Szabo, 1998 – Baron-Szabo and González-León, p. 475, fig. 3e, f

**Zoobank ID.** urn:lsid:zoobank.org:act:FCBCD8F0-390A-45DF-A71D-3A3717E23BB0

**Diagnosis.** *Sonoraphyllia* with a corallite diameter of 8 to 10 mm, and 37 to 48 septa.

**Description.** As for the genus.

**Etymology.** Latin *aurea* for gold after the type locality, Cerro de Oro (Gold Hill).

**Type.** Holotype ERNO 2161 Mexico, Sonora, Cerro de Oro. Cretaceous, Cerro de Oro Formation, Upper Barremian to Lower Aptian.

**Measurements.**

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<td>cmax</td>
<td>9.1-10.5 mm</td>
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<td>septa</td>
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**Occurrence.** Upper Barremian to Middle Albian, worldwide.
DISCUSSION

Taxonomy

Before the fundamental works of Alloiteau became published, already more than 100 families within the order Scleractinia were established. Many of them are based on genera where the type material of the corresponding type species is now lost, poorly preserved or from localities where all corals are silicified (such as the Kimmeridgian Nattheim in southern Germany or the Cenomanian Isle de Aix area in western France). Numerous families are now considered to be synonymous. To date, more than 200 families (for less than 2,000 genera from the Triassic to recent) are formally established. This high number is due to a change in the classification concept that was first introduced by Alloiteau. The application of thin sections and the study of microscopic characteristics of the septal morphology created a more stable and clear concept. Many genera are still without a proper family and many families are still applied in a traditional concept based on macromorphological characteristics.

Palaeoecology

Whereas members of the phaceloid genera Sonoraphyllia and Rayaphyllia are rare, or not yet fully recognised in the fossil record, the genus Rayasmilia is rather common. Among all of the approximately 400 coral genera that occur in the Cretaceous, the genus Rayasmilia belongs to the occasional genera having nearly 60, out of 2,000 localities. Rayasmilia is more common during the Aptian and Albian. It occurs together with hermatypic colonial corals and, therefore, lived in shallow marine environments. Among the solitary corals that occur in the time period Hauterivian to Albian, Rayasmilia is the most common of all solitary corals. From the Cenomanian on, with increasing diversity of ahermatypic corals, the ahermatypic corals Microbacia Milne Edwards and Haime, 1849 and Parasmina Milne Edwards and Haime, 1848 are
the most common solitary corals, that are not sharing the area with shallow marine colonial corals (*Aulosmilia* and *Cyclolites* being the most abundant solitary coral genera living together with hermatypic corals from the Cenomanian on). In Berriasian to Valanginian strata, the most common solitary coral is *Montlivaltia* (for abundance calculation see Löser 1989: 113). This replacement process was gradual (Figure 6) with the greater *Rayasmilia* (51). No data from the Early Turonian due to a global coral gap.

**ACKNOWLEDGMENTS**

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Figure 6. Proportion of the three genera *Montlivaltia*, *Rayasmilia*, and *Aulosmilia* through the Cretaceous, based on positively identified specimens. Specimens from localities with a range in time of more than 13.3 ma (duration of the longest stage, the Albian) are excluded. Number of included localities: *Montlivaltia* (42), *Rayasmilia* (45), and *Aulosmilia* (51). No data from the Early Turonian due to a global coral gap.