

# Morphology, taxonomy and distribution of the Early Cretaceous coral genus *Holocoenia* (Scleractinia) and its first record in the Caribbean

**Hannes Löser**

*Estación Regional del Noroeste, Instituto de Geología, Universidad Nacional Autónoma de México,  
Blvd. Luis Donaldo Colosio S/N y Madrid, 83250 Hermosillo, Sonora, Mexico.  
loeser@paleotax.de*

## ABSTRACT

*Although ten species are currently assigned to the Early Cretaceous coral genus *Holocoenia*, its characteristics are poorly known. Using material from the type locality of the type species *Astrea micrantha* along with described and undescribed material from France, Mexico, Poland and Spain, the genus is revised. It has a cerioid form with small calices, compact septa, a styliform columella, and an incomplete septothecal to synapticulothecal wall. Provisionally, it is assigned to the family *Thamnasteriidae*, being closely related to *Mesomorpha* and *Thamnasteria*. The genera *Stereocaenia* and *Paretallonia* are considered junior synonyms of *Holocoenia*. According to the present revision the genus contains only two species, which range from the Valanginian to the Aptian. *Holocoenia micrantha* is restricted to the central Tethys whereas *Holocoenia jaccardi* extends geographically from South America (Aptian of Argentina) and southern North America (Aptian of Puebla, Mexico) to the eastern Tethys (Hauterivian of Georgia). The indication of the genus in the San Juan Raya area in Puebla is the first indication in Central America. While the genus has been indicated in only eleven outcrop areas, making it rather rare, in many of these localities samples of *Holocoenia* are common.*

*Key words: corals, Scleractinia, Holocoenia, Early Cretaceous.*

## RESUMEN

*Aunque actualmente existen diez especies asignadas al género de coral *Holocoenia*, poco sabemos sobre sus características. En este trabajo se revisa este género usando muestras de la localidad tipo de la especie *Astrea micrantha*, así como material nuevo de Francia, Polonia y España. Este género es cerioide con cálices pequeños, septos compactos, una columna estiliforme y una pared incompleta de septotecal a sinapticulotecal. De manera provisional, el género está asignado a la familia *Thamnasteriidae*, muy cercano a *Mesomorpha* y *Thamnasteria*. Los géneros *Stereocaenia* y *Paretallonia* se consideran como sinónimos de *Holocoenia*. Según la revisión presente, el género tiene solamente dos especies, que tienen un rango desde el Valanginiano hasta el Aptiano. *Holocoenia micrantha* está restringido al mar de Tethys central, mientras que *Holocoenia jaccardi* muestra una distribución más amplia desde Sudamérica (Aptiano de Argentina) y América central (Aptiano de Puebla) hasta el mar de Tethys oriental (Hauteriviano de Georgia). Las evidencias del género en el área de San Juan Raya en Puebla, representan los primeros registros para América central. Aunque el género ha sido registrado solamente en once localidades y por tanto se considera raro, en muchas de estas localidades las muestras de *Holocoenia* son abundantes.*

*Palabras clave: corales, Scleractinia, Holocoenia, Cretácico Temprano.*

## INTRODUCTION

The early Cretaceous coral genus *Holocoenia* is poorly known and interpreted by various authors in different ways. Even though the genus is rare, its species are distributed over a wide area and are punctually abundant. Because the genus was never properly revised, the species are distributed among three synonymous genera. The systematic study of multiple coral collections and the sampling of various outcrops have brought together a considerable amount of material allowing the present revision at the generic and species level.

The genus *Holocoenia* was first established by Milne-Edwards and Haime (1851: 99) on the basis of the species *Astrea micrantha* Roemer, 1841. The type species was designated by Milne-Edwards and Haime (1851) and the genus was monospecific when created. *Astrea micrantha* derives from the Hils conglomerates, a shallow marine, siliciclastic transgression sediment which cropped out in Lower Saxon (Germany). These sediments were formed during the transgression of the very Late Valanginian to very Early Hauterivian (late Paucinodum / early Amblygonium zone; Michael 1974). The type locality of *Astrea micrantha* is Berklingen, a small village a few kilometers southeast of Braunschweig. The outcrop, probably a sand or clay pit, does not exist anymore. The description of the new genus by Milne-Edwards and Haime (1851) is brief and more a differentiating diagnosis: in comparison to *Thamnasteria* the genus *Holocoenia* is characterised by having a prominent styliform columella and septa with “entire edges” (a smooth distal margin).

D’Orbigny (1850a) established about 300 new species, all with very brief descriptions and lacking illustrations. Among many others, he created a species *Centrastrea collinaria* with the type locality Fontenoy in the Yonne department (France). The small village Fontenoy is practically surrounded by fields where the Calcaire à Spatangus, brownish-yellow oolitic marls, crops out. These sediments are extremely rich in fossils and contain a very diverse coral fauna (Löser, 2001). They belong to the basal Hauterivian (zone of *Acanthodiscus radiatus*) and represent remains of the same transgressions that formed the Hils conglomerates. The holotype of *Centrastrea collinaria* (MNHN, Coll. d’Orbigny B14279, old number 5292) could not be found (but recorded in the online catalogue of the MNHN).

The first illustration of *Centrastrea collinaria* was provided by de Fromentel (1857). He assigned the species to *Holocoenia* and discussed also the synonymy of the three species (*C. collinaria*, *C. excavata*, *C. microphyllia*) established by d’Orbigny (1850a). De Fromentel (1857) also mentioned *Holocoenia micrantha* providing a quoted description. Both species, *H. collinaria* and *H. micrantha* have the same calicular dimensions and the same number of septa, but de Fromentel (1857) did not discuss the synonymy of these species, probably because of the absence of correct data on *H. micrantha*.

Bölsche (1866) revised the corals from the Hils conglomerates and gave a detailed description, but no illustration of *Holocoenia micrantha*. He did, however, mention that *Centrastrea collinaria* and *Holocoenia micrantha* are the same species.

De Fromentel (1883) described and illustrated both species again, but he gave no calicular diameter for *Centrastrea collinaria* (but did for *H. micrantha*). In the following years, *Centrastrea collinaria* was quoted with *Centrastrea* or *Holocoenia* as the genus name, whereas *Holocoenia micrantha* always retained the same genus name. Both species were mentioned occasionally in the literature, but they were almost always from the Late Valanginian / Early Hauterivian of Lower Saxon or from the Early Hauterivian of the Paris basin.

Through the years, various species were attributed to *Holocoenia*, such as *Holocoenia indica* Stoliczka, 1873, *Holocoenia ramosa* Stoliczka, 1873, *Holocoenia jaccardi* Koby, 1897, *Holocoenia chelussii* Prever, 1909, *Holocoenia formai* Prever, 1909, and *Holocoenia polymorpha* Prever, 1909.

Alloiteau (1952: 629) mentioned that *Holocoenia* (*sic*) is a genus with a poorly known structure, differing from *Thamnasteria* by the compactness of septa, which are always in a low number. Practically *en passant* Alloiteau (1952) established the genus *Stereocaenia*. As the type species, Alloiteau designated *Holocoenia collinaria* de Fromentel. However, de Fromentel never established such a species and therefore Alloiteau will say, that de Fromentel had misidentified his material: it did not belong to *Centrastrea collinaria* d’Orbigny, 1850 *sensu stricto* but to another species for which Alloiteau (1952) created a new genus. According to the ICZN (1999, article 11.10) *Stereocaenia collinaria* therefore becomes available as the type species with Alloiteau (1952) as its author. The type is represented by the sample depicted by de Fromentel (1857), kept at the MNHN under the number M03564. The description of the new genus is short: “differs from the previous [= *Holocoenia*] by the lateral fusion of rudimentary septa with the numerous septa of the first and second cycle and the presence of numerous scattered calcification centres”. The illustration (Alloiteau 1952, fig. 112) is poor. The “fusion of rudimentary septa” are interpreted herein as the septa of the second generation which are connected by synapticulae to the septa of the first generation. The microstructural interpretation is suspect because in material from the Hauterivian of the Paris basin, microstructures are rarely preserved. As can easily be counted in this illustration, the total number of septa is eighteen, with little difference from *Holocoenia micrantha*, and there is no trace of septa connected to each other.

Alloiteau (1957) provided a detailed description of *Holocoenia* based on material from the Hauterivian of the Paris basin which Alloiteau (1957: 205) believed to belong to *Holocoenia micrantha* [“spécimens ... que nous avons déterminés d’après les descriptions et figurations originales

(celle-ci très mauvaises)”; “we have determined them after the original descriptions and illustrations (which are very poor)”. Thus it is questionable how Alloiteau managed to determine material using poor descriptions and illustrations. The original description and depiction are indeed poor, and the differentiating diagnosis given by Milne-Edwards and Haime (1851) does not provide much additional information. Only the description provided by Bölsche (1866) gives precise information. He was the only researcher who studied material from the type locality of the type species of *Holocoenia* despite of Roemer. However, Alloiteau (1957) provided a diagnosis different from that of Bölsche (1866), suggesting that Alloiteau most likely had material different from *Holocoenia micrantha* in hand, and with this material it was easy to separate *Holocoenia* from *Stereocaenia*. Bölsche (1866) had already mentioned that one could easily become confused because *Holocoenia micrantha* looks like *Actinastrea* (e.g., *Actinastrea cornueliana* d’Orbigny, 1850, has the same appearance and dimensions as *Holocoenia micrantha*), and it is likely that Alloiteau (1957) examined a species of this genus. Since he did not give an illustration of his material, it remains uncertain what Alloiteau considered *Holocoenia*.

Alloiteau (1957) gave also a detailed description of *Centrastrea collinaria* d’Orbigny, 1850, and assigned it as type species to the genus *Stereocaenia*. Since he had previously assigned (Alloiteau, 1952) *Centrastrea collinaria* d’Orbigny, 1850 sensu de Fromentel, 1857 as type species, this second designation is invalid. It is confusing that the illustrations of *Stereocaenia collinaria* in Alloiteau (1957) are all labeled as “*Stereocaenia* (*Holocoenia*) *collinaria* de From. sp.”, indicating a possible synonymy of both genera. The distinction between *Stereocaenia* and *Holocoenia* as proposed by Alloiteau (1957: 207) is not based on any type material but only on the imagination which had Alloiteau about both genera.

After Alloiteau (1957), *Holocoenia* was not generally accepted by coral taxonomists. Instead of using *Holocoenia*, the genus name *Stereocaenia* was applied. *Holocoenia* species were attributed to *Stereocaenia*, such as *Centrastrea collinaria* d’Orbigny 1850 (by Fricot *et al.*, 1995) or *Astrocoenia triboleti* Koby, 1897 (by Morycowa, 1964). To increase the confusion, Sikharulidze (1972) established the genus *Paretallonia* with the type species *P. bendukidzeae* from the Hauterivian of Georgia, which fits perfectly into the concept of *Holocoenia*. After Sikharulidze (1972), true *Holocoenia* material was assigned to *Paretallonia* (e.g., by Baron-Szabo 1997) making the confusion complete.

The diagnosis given by Baron-Szabo (2002) for *Holocoenia* is based on *Holocoenia polymorpha* Prever, 1909. She assigned the genus to the Actinastreaeidae family. It is correct that all syntypes of *Holocoenia polymorpha* belong to the genus *Actinastrea*, but *H. polymorpha* is not the type species of *Holocoenia* and can therefore not be used to provide an updated diagnosis or to redefine the systematic position of *Holocoenia*.

## MATERIAL

Unpublished material mentioned under occurrences in the systematic part comes from the following localities:

1. Berklingen (Lower Saxon, Germany). Hils conglomerates. Late Valanginian to earliest Hauterivian (late Paucinodum / early Amblygonium zone. For details see Michael (1974).
2. Fields east of the Fontenoy village (Yonne, France). Calcaire à Spatangus. Basal Hauterivian (Radiatus zone). For details see Corroy (1925).
3. San Juan Area (Puebla, Mexico). San Juan Raya Formation. Aptian. For details see Calderón-García (1956) and Reyerros-Navarro (1963). The stratigraphy is only an approximation; a (Late) Barremian to Early Aptian instead of Aptian age is also possible. Detailed investigation on the stratigraphy of the San Juan Raya Formation is under progress.

## SYSTEMATIC PALAEOONTOLOGY

The following institutional abbreviations are used: FGUB: Facultad de Geología de la Universidad de Barcelona, Spain; BSP: Bayerische Staatssammlung für Paläontologie und Geologie München, Germany; GIN: Geologicheskij Institut, Tbilisi, Georgia; IGM: Colección Nacional de Paleontología, Instituto de Geología, UNAM, Ciudad de México, Mexico; MB: Naturkundemuseum der Humboldt-Universität Berlin, Germany; MGSB: Museo Geológico del Seminario de Barcelona, Spain; MHNG: Muséum d’histoire naturelle de la Ville de Genève, Switzerland; MNHN: Muséum National d’Histoire Naturelle, Paris, France. The following abbreviations are applied in dimensions of the corals: c: calicular diameter; ccd: distance of calicular centres; cm: calices per 25 mm<sup>2</sup>; s: number of septa; sd: density of septa. The abbreviations used in the synonymy lists follow Matthews (1973): \*: earliest valid publication of the species name; ?: the assignation of this description to the species is doubtful (so marked quotations are not reflected in the stratigraphic and palaeobiogeographic distribution); non: the described material does not belong to the species concerned; p: the described material belongs only in part to the species concerned; v: the specimen was observed by the author. A year in italics indicates that the quotation is provided with neither a description nor an illustration.

### Order Scleractinia Bourne, 1900

Herein the classification system proposed by Alloiteau (1952) is applied, and not that of Vaughan and Wells (1943) because the latter is much more dedicated to Tertiary corals than to those of the Cretaceous. The family Thamnasteriidae belongs to the suborder Fungiina because of the presence of synapticalae and pores in the septal blades.

Suborder Fungiina Verrill, 1868-70  
Family Thamnasteriidae Reuss, 1864

***Holocoenia* Milne-Edwards and Haime, 1851  
emend. de Fromentel, 1857**

**Type species.** *Astrea micrantha* Roemer, 1841, original designation by Milne-Edwards and Haime (1851).

**Synonyms.** *Stereocaenia* Alloiteau, 1952; *Paretaillonia* Sihkarulidze, 1972.

**Diagnosis.** Cerioid colony with small calices. Septa compact, in radial symmetry and always two generations. Septal face with few granules. Wall incomplete, made of synapcticulae and septa. Columella styliiform. Endotheca present, made of thin dissepiments. Budding extracalicular. Septal microstructure unknown.

**Remarks.** *Holocoenia* forms small to medium large colonies, circular or with an irregular shape. In siliciclastic environments flat and laterally extended, often with pillar like elevations indicating a certain sediment stress. In carbonatic environments the colonies have a massive growth form. Colonies often with a wrinkled holotheca. The outer appearance of the colony might be cerioid or thamnasterioid. The colony is cerioid with well separated polygonal to circular calices. The calices are slightly depressed, the walls slightly elevated with costae running over the wall. The septa are compact and thick. They are almost always free and rarely connected to each other as in *Thamnasteria* or *Mesomorpha*. The Septa always appear in two size orders, one long which reach the columella and one shorter which reach about half or less of those of the first order. There exists no clear symmetry. Though it is radial, calices with eight, nine, ten or even eleven septa of the first order can be found in the same colony. Septal number in all *Holocoenia* species is always between 16 and 22, but 20 septa are most common. Septa and costae cannot be clearly distinguished; obviously septa are bisepetal blades where the external part of one septum forms a septum of another calice. The columella is styliiform, clearly visible, slightly elevated and large compared to the small diameter of the calices. Septa of the first order can be attached to it. The wall is septothecal with many synapcticulae. It is not compact as it can be seen in longitudinal sections. Synapcticulae are only found in the wall. The endotheca consists of few thin dissepiments. - The genus was originally described as *Holocaenia*, but the name was later changed by de Fromentel (1857) to *Holocoenia*, a

change of spelling which was later generally accepted and which is therefore valid.

**Comparison.** *Mesomorpha* and *Thamnasteria* are closely related genera, and both form astreoid to thamnasterioid colonies without a well-defined wall. Moreover, septa are often (*Mesomorpha*) or sometimes (*Thamnasteria*) attached to other septa. Both genera have no clear septal size orders as in *Holocoenia*. *Actinastrea* is very similar but differs by the mostly compact wall, the absence of synapcticulae, the presence of fine thorns at the lateral septal faces, and septal swellings.

**Systematic position.** The systematic position is preliminary. The genus also shares many characteristics with the suborder Archeocaeniina (*Astrocoeniina* p.p.). It is closely related to *Etallonasteria* Roniewicz, 1987, a Jurassic coral genus very similar to *Holocoenia* but without columella.

**Species.** Only two species are accepted here: *Holocoenia micrantha* (Roemer, 1841) and *Holocoenia jaccardi*, Koby, 1897. Both species are morphologically identical, and differ only in their calicular diameter. Though both species co-occur at some localities or in some regions, species can be clearly distinguished by their calicular dimensions. Other species assigned to *Holocoenia* or its synonymous genera belong to one of these two species or other genera. Species originally assigned to other genera but belonging to *Holocoenia*, are synonymous with one of the two species. In Table 1 the dimensions and some statistical values of the examined material are provided.

**Distribution range.** Valanginian to Early Aptian. Late Aptian is questionable.

***Holocoenia micrantha* (Roemer, 1841)**

Figures 1, 2a-c

- \* 1841 *Astraea micrantha* Roemer, p. 113, pl. 16: 27
- 1849 *Thamnastrea micrantha* - Milne-Edwards and Haime, p. 158
- 1850a *Centrastraea collinaria* d'Orbigny, (2), p. 93
- 1850a *Synastrea micrantha* - d'Orbigny, (2), p. 94
- 1850b *Centrastraea collinaria* - d'Orbigny, p. 177
- 1850b *Synastrea micrantha* - d'Orbigny, p. 178
- 1851 *Astrea micrantha* Roemer - Milne-Edwards and Haime, p. 99
- 1851 *Thamnastrea ? collinaria* - Milne-Edwards and Haime, p. 112
- 1851 *Thamnastrea ? micrantha* - Milne-Edwards and

Table 1. Comparison of dimensions of both *Holocoenia* species.

Sample	Dimension	Number of measurements	Minimum value (mm)	Maximum value (mm)	Average (mm)	Standard deviation (mm)
MB K2466	cl	20	1.18	1.75	1.457	0.172
	ccd	30	1.1	1.9	1.514	0.227
BSP 2003 XX 5258	cl	20	1.05	1.6	1.28	0.164
	ccd	30	0.79	1.84	1.28	0.269



- Haime, p. 111
- 1857 *Holocoenia micrantha* - de Fromentel, p. 53
- v 1857 *Holocoenia collinaria* - de Fromentel, p. 54, pl. 7: 9, 10
- 1857 *Holocoenia micrantha* - Milne-Edwards, (2), p. 250
- 1857 *Thamnastraea* ? *collinaria* - Milne-Edwards, (2), p. 583
- 1861 *Holocoenia collinaria* - de Fromentel, p. 200
- 1861 *Holocoenia micrantha* - de Fromentel, p. 200
- 1862 *Holocoenia collinaria* de Fromentel - de Fromentel, p. 410
- 1866 *Holocoenia micrantha* - Bölsche, p. 476
- 1867 *Holocoenia micrantha* Roem. sp. - Bölsche, p. 40
- 1868 *Holocoenia collinaria* (D'Orb.) E. de Fromentel - de Fromentel, p. 86, pl. 8: 3
- 1881 *Holocoenia micrantha* - Quenstedt, p. 996, pl. 182: 3
- 1883 *Holocoenia collinaria* - de Fromentel, p. 516, pl. 138: 1, pl. 139: 2
- 1883 *Holocoenia micrantha* - de Fromentel, p. 517
- ? 1887 *Centrastraea collinaria* - Mallada, p. 170, pl. 62: 4
- non v 1909 *Holocoenia micrantha* - Prever, p. 128, pl. 14: 8 [= *Stylina* sp.]
- ? 1937 *Centrastraea collinaria* d'Orbigny, 1849 - Bataller, p. 201
- 1952 *Holocoenia collinaria* de Fromentel - Alloiteau, p. 659, fig. 112
- 1956 *Holocoenia collinaria* Fromentel, 1867 - Wells, p. 372, fig. 263.2
- 1957 *Centrastraea collinaria* d'Orb. 1850 - Alloiteau, p. 206
- p 1957 *Stereocaenia collinaria* de From. sp. - Alloiteau, fig. 272-274, pl. 19: 4, non pl. 1: 10 [= *Mesomorpha* or *Thamnastraea* sp.]
- ? 1978 cf. *Holocoenia micrantha* (Roemer) - Wingfield, Evans and Deegan, p. 30
- non 1980 *Stereocaenia collinaria* (Fromentel, 1857) - Kuzmicheva, p. 100, pl. 37: 2 [= *Mesomorpha* sp.]
- non 1983 *Stereocaenia collinaria* (Fromentel, 1857) - Kuzmicheva, p. 34, pl. 3: 4 [not pl. 2: 4 as indicated] [= *Mesomorpha* or *Thamnastraea* sp.]
- non 1987 *Stereocaenia collinaria* (d'Orbigny, 1850) - Kuzmicheva, p. 246, pl. 5: 3 [= *Mesomorpha* sp.]
- non 1988 *Stereocaenia collinaria* (Fromentel, 1857) - Kuzmicheva and Aliev, p. 168, pl. 5: 3 [= *Mesomorpha* sp.]
- v 1995 *Stereocaenia* (= *Holocoenia*) *collinaria* d'Orbigny - Fricot, Colleté and Brossard, p. 32, text-fig. 35
- v 1997 *Paretallonia bendukidzeae* Sikharulidze, 1972 - Baron-Szabo, p. 76, pl. 11: 1, 3, 4
- v 2001 *Holocoenia jaccardi* Koby, 1897 - Löser, p. 45, pl. 2: 7
- 2002 *Holocoenia micrantha* (Roemer, 1841) - Löser *et al.* p. 347 [detailed synonymy here]
- 2002 *Stereocaenia collinaria* (d'Orbigny, 1850) - Löser *et al.*, p. 616 [detailed synonymy here]
- 2002 *Stereocaenia collinaria* Alloiteau 1952 - Löser *et al.*, p. 616 [detailed synonymy here]
- v p 2006 *Holocoenia jaccardi* Koby 1897 - Löser and Ferry, p. 483, fig. 5.4 [not fig. 5 = *Holocoenia jaccardi*]

**Types.** The type of *Astrea micrantha* is presumably lost. It was sought but not found in the following institutions: the Hildesheim Museum dedicated to F.A. Roemer, in the collections of the Naturkundemuseum Berlin, the collections of the Geologische Bundesanstalt (Berlin), the Geowissenschaftliche Sammlung of the University Bremen, the University collection of Göttingen, and the Staatlichen Naturhistorischen Museum Braunschweig, all in Germany. Topotypical material was sought in the same collections and only one small sample was found in the Naturkundemuseum Berlin, which is used here as a reference sample (MB K2466.1). The holotype of *Centrastraea collinaria* d'Orbigny, 1850 is probably not lost (according to written communication by E. Morycowa, Kraków), but it is not available. The holotype of *Stereocaenia collinaria* Alloiteau, 1952 (MNHN M03564) was available for study but there was no opportunity to make a polished section to clearly prove its systematic position. Thin sections made by Alloiteau were not available for study. The holotype of *Paretallonia bendukidzeae* Sikharulidze, 1972 is deposited in the Tbilisi Geological Institute (GIN) under the number 36/77, but was not available for study.

**Synonyms.** *Centrastraea collinaria* d'Orbigny, 1850; *Stereocaenia collinaria* Alloiteau, 1952.

**Dimensions.** c: (1.0) 1.4–1.5 (1.7) mm, ccd: (1.2) 1.5–1.6 (2.0) mm, cm: 10–11, s: 18–20, sd: 4–5 / 1 mm.

**Remarks.** *Holocoenia collinaria* d'Orbigny, 1850 was uni-

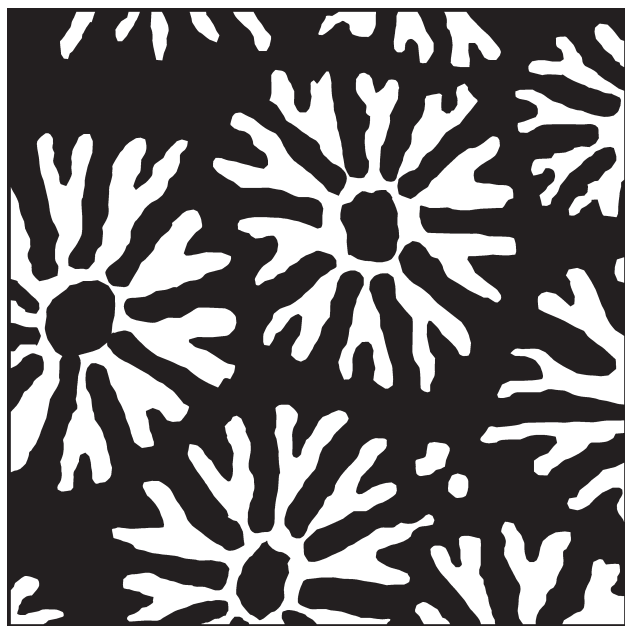


Figure 1. *Holocoenia micrantha* (Roemer, 1841). Drawing after thin section MB K2466.1. Latest Valanginian to Earliest Hauterivian of Berklingen near Braunschweig (Lower Saxon, Germany). Illustration width about 3 mm.

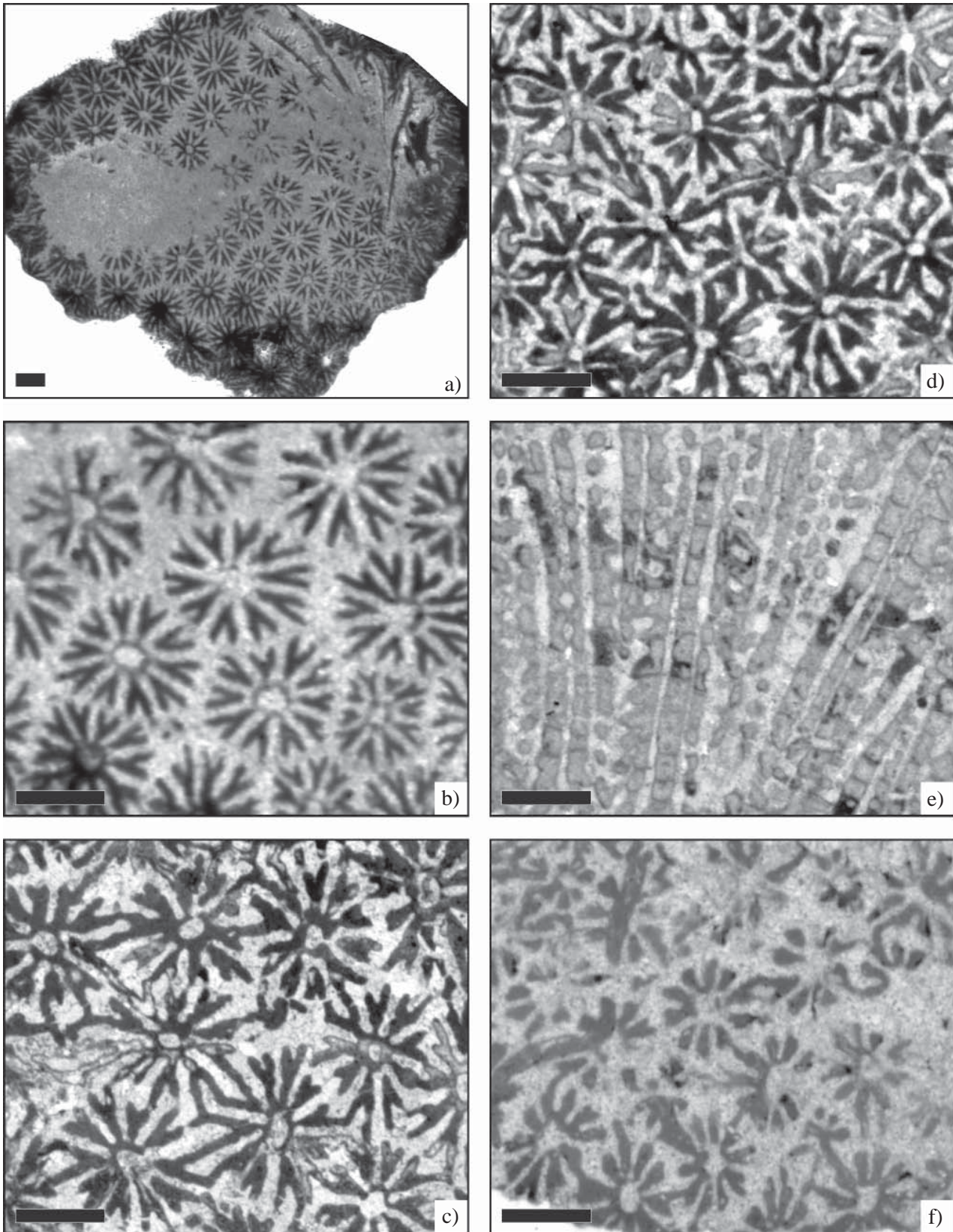


Figure 2. a-c: *Holocoenia micrantha* (Roemer, 1841). a-b: Transversal thin section MB K2466.1. Latest Valanginian to Earliest Hauterivian of Berklingen near Braunschweig (Niedersachsen, Germany); c: Transversal thin section BSP 2003 XX 5260. Late Barremian of Pont de Laval near St.Remèze (Ardèche, France). d-f: *Holocoenia jaccardi* Koby, 1897. d-e: Transversal and longitudinal thin section BSP 2003 XX 5258. Late Barremian of Pont de Laval near St.Remèze (Ardèche, France). f: Transversal thin section IGM 9255. Aptian (? Late Barremian) of the Barranca Agua del Burro section, San Juan Raya (Puebla, Mexico). Scale bar in all figures 1 mm.



fied by de Fromental (1857) with *Centrastrea microphyllia* d'Orbigny, 1850 and *Centrastrea excavata* d'Orbigny, 1850. *Centrastrea microphyllia* remains an unknown species. Its type is not available. The illustration provided by de Fromental (1887) is poor and the description is incomplete since it starts on the very last page of the 16<sup>th</sup> (and last) instalment of the revision of the Cretaceous corals within the Paléontologie française, which is also the last page of the whole publication that was not completed. *Centrastrea excavata* d'Orbigny, 1850 is considered a species different from *Holocoenia* and was in recent literature assigned to *Mesomorpha*. The species is not revised: its type (MNHN 5291) is a small unsectioned sample that may belong to *Mesomorpha* or *Thamnasteria*. The material mentioned by Bataller (1937; probably only in reference to Mallada 1887) was sought in the MGSB (Barcelona), but not found. It is not registered in the files and according to Sebastian Calzada (Barcelona, pers. comm. June 2007) this is a sure indication that the material is not held in the collection. The age of the La Avellà outcrop is also questionable. It was originally published as Hauterivian (Götz *et al.*, 2005), but new material kindly provided by S. Tomás (Barcelona) included a *Felixigyra* species, a genus which is absent in the Hauterivian elsewhere.

**Occurrence.** *Astrea micrantha* Roemer, 1841: Early Valanginian of Arzier, La Violette quarries (Vaud, Switzerland); Latest Valanginian to Earliest Hauterivian (late Paucinodum / early Amblygonium zone) of Apelnstedt and Berklingen near Braunschweig (Lower Saxon, Germany); Early Hauterivian (Radiatus zone) of the various outcrops near the villages Fontenoy, Gy-l'Evêque, and Les Saints (Yonne, France) and near Vallières and Marolles (Aube, France); Hauterivian (?Barremian) of the La Avellà section near Catí (Valencia, Castellón, Spain; FGUB AV-C-6); Late Barremian of Pont de Laval near St.Remèze (Ardèche, France); Latest Barremian to Early Aptian (Weissi zone) of the outcrops Mahdtal, Mitteleck, Obere Gottesackerwände, Seealpe in the Allgäu Mountain range (Bavaria, Germany). - Additional occurrences indicated for *Centrastrea collinaria* d'Orbigny, 1850: Early Hauterivian (Radiatus zone) of Morancourt and Saint Dizier (Haute-Marne, France) and outcrops near the villages Chenay, Leugny, Saint-Sauveur and Venoy (Yonne, France).

**Range.** Valanginian to Early Aptian (Weissi zone).

### *Holocoenia jaccardi* Koby, 1897

Figures 2d-f

v p 1850a *Astrocoenia Cornueliana* d'Orbigny, p. 92  
 \*1897 *Holocoenia Jaccardi* Koby, p. 35, pl. 4: 4, 5  
 v 1897 *Astrocoenia Triboleti* Koby, p. 62, pl. 14: 6-8  
 1928 *Astrocoenia* cf. *Triboleti* Koby - Gerth, p. 7  
 v p 1935 *Astrocoenia Cornueliana* d'Orb. - Cottreau, pl. 74: 7 [non fig. 6]  
 v non 1936 *Holocoenia* ex. aff. *jaccardi* Koby, 1898 - Hackemesser, p. 21

? 1959 *Holocoenia* [sic] *Jaccardi* Koby - Bonev, p. 478, pl. 2: 1  
 v 1964 *Stereocaenia triboleti* (Koby, 1896) - Morycowa, p. 77, pl. 23: 1-3  
 v 1970 *Stereocaenia triboleti* (Koby) - Czerminski, p. 129  
 1972 *Paretallonia bendukidzeae* Sikharulidze, p. 643, text-fig. 1, 2  
 1985 *Paretallonia Bendukidzeae* Sikh., 1972 - Sikharulidze, p. 62, pl. 28: 2  
 v 1989 *Stereocaenia triboleti* (Koby, 1896) - Morycowa, p. 65, pl. 27: 1, 2  
 non 1996 *Paretallonia bendukidzeae* Sikharulidze, 1972 - Császár and Turnšek, p. 434, fig. 4 [= *Cryptoconia* sp.]  
 v non 1996 *Paretallonia bendukidzeae* Sikharulidze - Wilmsen, p. 360, pl. 3: 3 a, b, 4 [= *Actinastrea* sp.]  
 v non 1997 *Paretallonia* cf. *bendukidzeae* Sikharulidze - Wilmsen, pl. 32: 3, 4 [= *Actinastrea* sp.]  
 2002 *Holocoenia micrantha* (Roemer, 1841) - Löser *et al.* p. 347 [detailed synonymy here]  
 2002 *Paretallonia bendukidzeae* Sikharulidze, 1972 - Löser *et al.*, p. 498 [detailed synonymy here]  
 2002 *Stereocaenia triboleti* (Koby, 1896) - Löser *et al.*, p. 617 [detailed synonymy here]  
 v 2005 *Holocoenia jaccardi* Koby, 1897 - Götz, Löser and Schmid, p. 876, fig. 8C  
 v p 2006 *Holocoenia jaccardi* Koby, 1897 - Löser and Ferry, p. 483, fig. 5.5 [not fig. 4 = *Holocoenia micrantha*]

**Holotype.** The holotype of *Holocoenia jaccardi* is officially not available. The specimen of the collection of the Muséum d'Histoire naturelle de Neuchâtel (No. 26735) is suspected to be the holotype, even though it is not marked as such and its identity with the sample figured by Koby cannot be assured. Syntypes of *Astrocoenia Triboleti* are available at the Muséum d'Histoire naturelle de la Ville de Genève (MHNG 4852), but they are poorly preserved.

**Synonyms.** *Astrocoenia triboleti* Koby, 1897; *Paretallonia bendukidzeae* Sikharulidze, 1972.

**Dimensions.** c: (0.8) 0.9–1.2 (1.3) mm, ccd: (0.9) 1.0–1.4 (2.0) mm, cm: 12–14, s: (16) 18–20, sd: 5–6 / 1 mm.

**Remarks.** *Holocoenia jaccardi* and *Holocoenia triboleti* were described by the same author in the same year. Priority is given to the first species not only because of page precedence but because it has been assigned by Koby to *Holocoenia*, whereas the other species to *Astrocoenia*. Moreover, the (? type) material available of *Holocoenia jaccardi* is much better preserved than those of *Holocoenia triboleti*. The material described by d'Orbigny as *Astrocoenia Cornueliana* consists of various syntypes of which one (MNHN R09357 = Coll. d'Orbigny 5284A) belongs to *Holocoenia*. Specimen MNHN A24821 was selected as lectotype of *Astrocoenia Cornueliana* according to the collection database of the MNHN without giving a reference, which makes this designation according to the ICZN (1999; Art. 72.4.7) invalid. The material described by Gerth is kept at the Nationaal Natuurhistorisch Museum (Leiden, The

Netherlands; RGM.143057). With the kind help of Jacob Leloux (Leiden) photographs of the sample and thin sections were made available to the author.

**Occurrence.** Early Hauterivian (Radiatus zone) of the outcrops near the village Gy-l'Evêque (Yonne, France); Hauterivian of Shkmeri (Racha, Georgia), Kvemo-Chalovani and Sachkhere (Imereti, Georgia), Wieliczka, Buków (Malopolskie, Wieliczka, Poland). Hauterivian (?Barremian) of the La Avellà section near Catí (Valencia, Castellón, Spain); Barremian of Morteau (Doubs, France); Early Barremian of the section NW Archiane in the Vercors Mountain range (Drôme, France); Late Barremian of outcrops at Pont de Laval, Belvédère du Serre-de-Tourne and Belvédère du Gaud near St.Remèze (Ardèche, France), Trzemesna near Tarnów (Malopolskie, Tarnów, Poland); Early Aptian of Jastrzebia near Lanckorona (Malopolskie, Wadowice, Poland); Aptian (? Late Barremian) of the San Juan Raya area (Puebla, Mexico; IGM 9253); Aptian of Sierra Vaca Muerta (Neuquén, Argentina).

**Range.** Hauterivian to Aptian (range into the Late Aptian is questionable).

## OTHER SPECIES

Species originally or currently assigned to *Holocoenia*, but not being synonymous with one of the above described species and which do not belong to *Holocoenia* (all Cretaceous material was available to the author):

*Holocoenia chelussii* Prever, 1909 - both syntypes belong to *Columnocoenia*.

*Holocoenia indica* Stoliczka, 1873 - the species belongs very probably to *Astreopora*.

*Holocoenia polymorpha* Prever, 1909 - all five syntypes belong to *Actinastrea*.

*Holocoenia ramosa* Stoliczka, 1873 - both syntypes belong the same *Columnocoenia* species.

It is very probably that the genus does not occur in the Jurassic. The three species established by de Fromentel (1856) without illustration do not fit well into the concept of the genus. *Holocoenia cesaredensis* Koby, 1904 was assigned by Geyer (1955) to the genus *Convexastrea*. *Thamnastrea scita* Milne-Edwards and Haime, 1851 was assigned by Beauvais (1966) to *Stereocaenia*. *Thamnastrea scita* belongs to *Thamnasteria* (for instance see Pandey and Fürsich 2003). The material described by Beauvais (1966) does not belong to *Thamnasteria scita*, but to *Thamnasteria mettensis* (according to Lathuilière 2000).

## Stratigraphic and palaeobiogeographic distribution

Though both species are restricted to a few outcrops, they are not rare in those outcrops. *Holocoenia micrantha* is common in the Early Hauterivian of the Paris basin. It is abundant in the recently investigated faunas of Ardèche and

Drôme (Barremian, France) and Catí (Hauterivian, probably Barremian; Spain). *Holocoenia jaccardi* is abundant in the San Juan Raya area.

The genus was up to now only indicated in the Boreal (France and Germany) and the central (southern France, southern Germany, Poland, Spain, Switzerland) to eastern Tethys (Georgia); the indication of *Holocoenia jaccardi* in the Aptian (probably Late Barremian to Early Aptian) of Puebla (Mexico) is the first indication of the genus *Holocoenia* in the Caribbean realm at all (Figure 3). Both species differ in their distribution. Whereas *Holocoenia micrantha* shows a very limited geographical distribution occurring only in the Boreal and central Tethys, *Holocoenia jaccardi* shows a wider distribution and was found between South and southern North America and the eastern Tethys.

The genus occurs in outcrops with a siliciclastic facies (such as in the Boreal in northern France and northern Germany, in the northern Tethys in France and Poland, in the Caribbean in Mexico) and in carbonate ramps or platforms (such as in northern margin of the central Tethys in southern France, southern Germany, and Switzerland). It has not been indicated in the coral rich sediments of the central Tethys (such as the Early Aptian of Greece, the Hauterivian to Aptian of Spain).

Both species almost co-occur in time (Figure 4) with the exception that *H. micrantha* was already indicated in the Valanginian, whereas *H. jaccardi* might reach into the Late Aptian. But this is not certain as the whole outcrop area around San Juan Raya (Puebla, Mexico) needs revision of its stratigraphy and the outcrops in Argentina are imprecisely dated. Both species are most widely distributed in the Hauterivian, but also appear with a considerable distribution during the Late Barremian to Early Aptian.

## CONCLUSIONS

The long story of this genus clearly demonstrates the importance of proper description and illustration to prevent confusion and the assignment of the same species to multiple genera. Above all, clear illustration is essential, since although the concepts of interpreting certain morphological elements may change through time, the fossil itself, and hence illustration, remains the same. After *Holocoenia* was established, it was twice created under different names (*Stereocaenia*, *Paretallonia*) due to insufficient knowledge of type material or misunderstandings of the literature. Unfortunately, this type of situation is not an exception and is very common in the study of Cretaceous corals.

## ACKNOWLEDGEMENTS

It is a pleasure to thank Jacques Ayer and Jean-Paul Haenni (Neuchâtel), Sebastian Calzada (Barcelona),



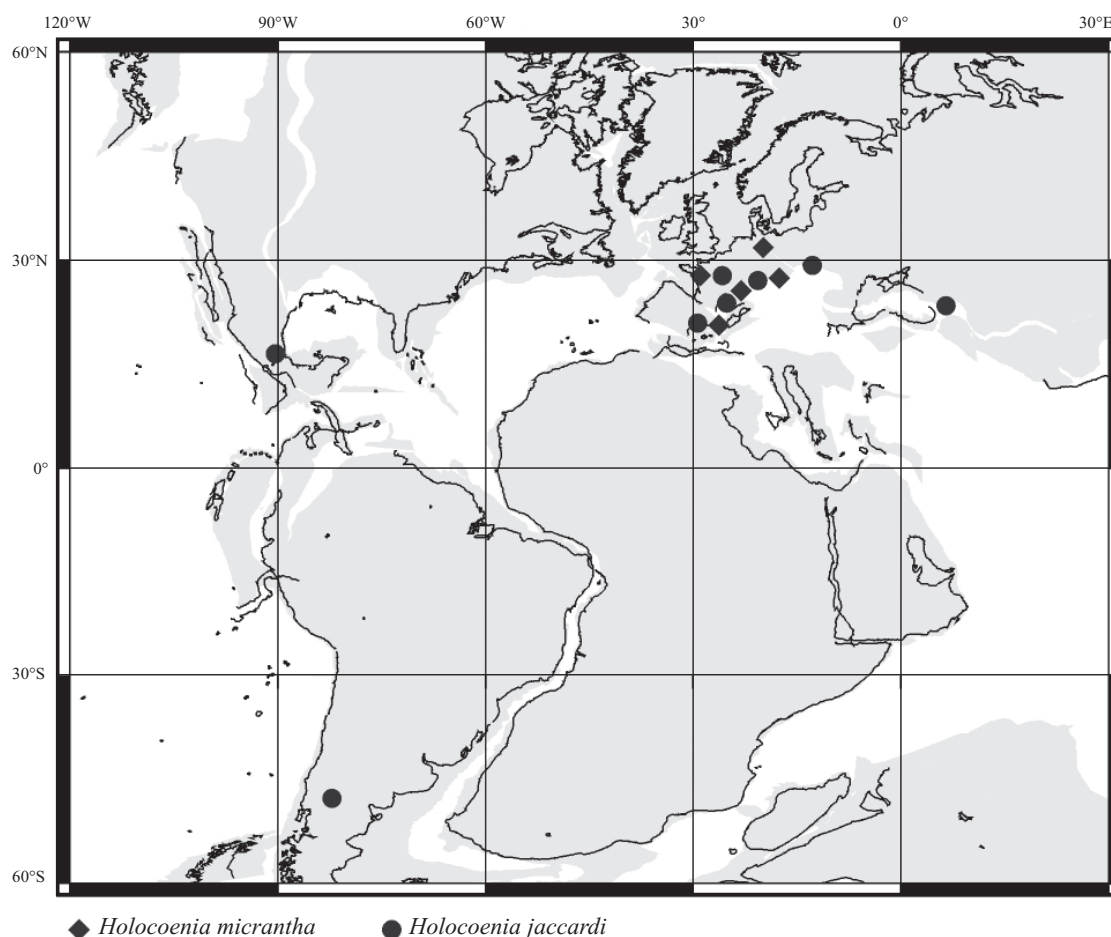


Figure 3. Palaeobiogeographic distribution of the various species of *Holocoenia*. Plate tectonic reconstruction (125 Ma) with plates moved relative to the magnetic reference frame (created using the Advanced Plate Tectonic Reconstruction Service, Ocean Drilling Stratigraphic Network, <http://www.odsn.de>); present day shorelines in black, plate fragments in grey.

Danielle Decrouez (Genève), G. Haldar (Calcutta), Peter Jung and René Panchaud (Bâle), Dieter Korn (Berlin), Jacob Leloux (Leiden), Christine Perrin (Paris), Elzbieta Morycowa (Kraków), Daniele Ormezzano (Torino), Carmen Perrilliat (Mexico City), Sara Tomás (Barcelona), and Winfried Werner (München) who allowed me to study material of their respective museum or institute collections, which made this study possible. Juliane Fenner (Hannover), Fritz Krüger (Braunschweig), Mike Reich (Göttingen), and

Jürgen Vespermann (Hildesheim) searched their collections for type or topotypical material of *Astrea micrantha* for which I am grateful. The quality of the paper was enhanced by reviews by Jacob Leloux (Leiden) and an anonymous reviewer. For grammatical correction I would like to thank Kimberly Franklin (Tucson, Arizona).

Field work in France and preparation of thin sections was covered by DFG project FL 42/73. Examination of the Mexican material was realised within the framework of

Stratigraphy \ Species	Valanginian		Hauterivian		Barremian		Aptian	
	Early	Late	Early	Late	Early	Late	Early	Late
<i>micrantha</i>	—	—	—	—	—	—	—	—
<i>jaccardi</i>	—	—	—	—	—	—	—	—

Figure 4. Stratigraphic distribution and commonness of *Holocoenia* species. The thickness of the bars indicates the number of regions (not localities) in which the species concerned was found.

CONACyT project 52442-Q. The ability to use the Jurassic Coral Database compiled by Bernard Lathuilière (Nancy) is greatly appreciated.

## REFERENCES

- Alloiteau, J., 1952, Embranchement des coelentérés, *in* Piveteau, J. (ed.), *Traité de Paléontologie* (1): Paris, Masson, 376-684.
- Alloiteau, J., 1957, Contribution à la systématique des Madréporaires fossiles: Paris, Centre National de la Recherche Scientifique, 462 p.
- Baron-Szabo, R.C., 1997, Die Korallenfazies der ostalpinen Kreide (Helvetikum: Allgäuer Schrättenkalk; Nördliche Kalkalpen: Brandenberger Gosau), *Taxonomie, Palökologie: Zitteliana*, 21, 3-97.
- Baron-Szabo, R.C., 2002, *Scleractinian corals of the Cretaceous*: Knoxville, Tenn., privately published, 538 p.
- Bataller, J., 1937, La fauna coral·lina del Cretàcic de Catalunya i regions limítrofes: *Arxius de l'escola superior d'agricultura, (N.S.)* 3(1), 1-299.
- Beauvais, L., 1966, Révision des madréporaires du Dogger de la collection Koby: *Eclogae Geologicae Helvetiae*, 59(2), 989-1024.
- Bölsche, W., 1866, Die Korallen des norddeutschen Jura- und Kreidegebirges: *Zeitschrift der Deutschen Geologischen Gesellschaft*, 18, 439-486.
- Bölsche, W., 1867, Die Korallen des norddeutschen Jura- und Kreidegebirges: Berlin, J.F. Starcke, 50 p.
- Bonev, E.S., 1959, [Aptian fauna from the Predshansk anticline in the region of east Stara Planina.]: *Nauchni trudove Vissh selskostopanski institut*, 6, 463-504.
- Bourne, G.C., 1900, The Anthozoa, *in* Lankester, R. (ed.), *Treatise on Zoology*, 2. Porifera and Coelenterata: London, A. & C. Black, 59-79.
- Calderón-García, A., 1956, Bosquejo geológico del a región de San Juan Raya. Guía de campo, *in* Maldonado-Koerdell, M. *et al.* (eds.) *Estratigrafía del Mesozoico y Tectónica del sur del Estado de Puebla; Presa de Valsequillo, Sifón de Huexotitlanapa y problemas hidrológicos de Puebla: Congreso Geológico International, Excursion A-11*, 7-91.
- Corroy, G., 1925, Le Néocomien de la bordure orientale du Bassin de Paris: *Bulletin de la Société des Sciences Naturelles de Nancy*, 2(4), 171-506.
- Cottreau, J., 1935, Types du prodrome de paléontologie stratigraphique universelle (11): *Annales de Paléontologie*, 24, 37-52.
- Császár, G., Turnšek, D., 1996, Vestiges of atoll-like formations in the Lower Cretaceous of the Mecsek Mountains, Hungary: *Cretaceous Research*, 17, 419-442.
- Czerminski, J.E., 1970, Geology of Poland, 2. Catalogue of fossils, 2. Mesozoic: Warszawa, Wydawnictwa Geologiczne, 1-254.
- d'Orbigny, A., 1850a, Prodrôme de Paléontologie stratigraphique universelle des animaux mollusques et rayonnés (v. 1-2): Paris, Masson, 1-394, 1-428.
- d'Orbigny, A., 1850b, Catalogue des espèces fossiles de mollusques, bryozoaires, de polypiers et d'amorphozoaires de l'étage néocomien: *Revue et Magasin de Zoologie, Pure et Appliquées, sér. 2*, 2, 170-181.
- Fricot, C., Colleté, C., Brossard, C., 1995, L'Hauterivien, *in* Colleté, C. Fricot, C., Matron, M., Toucasson, R., Treffot, G. (eds.), *La géologie du département de l'Aube: Troyes, Association Géologique auboise*, 31-38.
- Fromentel, E. de, 1856, Note sur les polypiers fossiles de l'étage portlandien de la Haute-Saône: *Bulletin de la Société Géologique de France, sér. 2*, 13, 851-865.
- Fromentel, E. de, 1857, Description des polypiers fossiles de l'étage Néocomien: *Bulletin de la Société des Sciences Historiques et Naturelles de l'Yonne*, 1-78.
- Fromentel, E. de, 1861, Introduction à l'étude des polypiers fossiles: *Mémoires de la Société d'émulation du Doubs, 3e ser.*, 5, 1-357.
- Fromentel, E. de, 1862, Polypiers, *in* Gras, S. (ed.), *Description géologique du département de Vaucluse*: Paris, F. Savy, 429-431.
- Fromentel, E. de, 1868, Polypiers, *in* Lorient, P. de (ed.), *Monographie des couches de l'étage Valangien des carrières d'Arzier (canton de Vaud)*: Genève, H. Georg, *Matériaux pour la paléontologie suisse ou recueil des monographies sur les fossiles du Jura et des Alpes*, 4 (2), 85-88.
- Fromentel, E. de, 1883, Zoophytes, terrain crétacé (12): *Paléontologie française*, 8, 513-528.
- Fromentel, E. de, 1887, Zoophytes, terrain crétacé (16): *Paléontologie Française*, 8, 609-624.
- Gerth, H., 1928, Beiträge zur Kenntniss der mesozoischen Korallenfaunen von Südamerika: *Leidse Geologische Mededelingen*, 3(1), 1-5.
- Geyer, O.F., 1955, Korallen-Faunen aus dem Oberen Jura von Portugal: *Senckenbergiana Lethaea*, 35 (5-6), 317-356.
- Götz, S., Löser, H., Schmid, D.U., 2005, Reef development on a deepening platform: two Early Cretaceous corallgal patch reefs (Catí, Llàcova Formation, eastern Spain) compared: *Cretaceous Research*, 26, 864-881.
- Hackemesser, M., 1936, Eine kretazische Korallenfauna aus Mittel-Griechenland und ihre paläobiologischen Beziehungen: *Palaeontographica, Abteilung A*, 84, 1-97.
- International Commission on Zoological Nomenclature (ICZN), 1999, *International Code of Zoological Nomenclature: The International Trust for Zoological Nomenclature*, <<http://www.iczn.org/iczn/index.jsp>>
- Koby, F., 1897, Monographie des polypiers crétacés de la Suisse, 2ème partie: *Abhandlungen der Schweizerischen Paläontologischen Gesellschaft*, 23, 29-62.
- Koby, F., 1904, Description de la faune jurassique du Portugal, polypiers du Jurassique supérieur: *Communicacoes da Commissao do Servico Geológico de Portugal*, 1-167.
- Kuzmicheva, E.I., 1980, [Corals], *in* Chernov, V.G. *et al.* (eds.), [Urgonian sediments of the Soviet Carpathes.]: Moskva, Nauka, 90-108.
- Kuzmicheva, E.I., 1983, [Phylum Coelenterata], *in* Aliev, M.M. (ed.), [The Valangian of Mangyshlak.]: Moskva, Nauka, 28-34.
- Kuzmicheva, E.I., 1987, [Corals from Lower Barremian organogenous buildups in the Malyy Balkhan and Tuarkeyr], *in* Amanniyazov, K.N. (ed.), *Geologicheskoe stroenie Turkmenistana: Aschabad, Ylum*, 217-262.
- Kuzmicheva, E.I., Aliev, O.B., 1988, Corals, *in* Ali-Zade, A.A., Aliev, G.A., Aliev, M.M. (eds.), *Cretaceous fauna of Azerbaijan: Baku, Elm*, 153-184.
- Lathuilière, B., 2000, Coraux constructeurs du Bajocien inférieur de France. 2ème partie: *Geobios*, 33 (2), 153-181.
- Löser, H., 2001, Le site de Vallières (département de l'Aube, France) : résultats préliminaires sur des coraux de l'Hauterivien inférieur (Crétacé): *Bulletin Annuel de l'Association Géologique de l'Aube*, 22: 39-53.
- Löser, H. and 25 co-authors, 2002, *Catalogue of Cretaceous Corals*, 2. List of Citations: Desden, CPress, 784 p.
- Löser, H., Ferry, S., 2006, Coraux du Barrémien du Sud de la France (Ardèche et Drôme): *Geobios*, 39(4), 469-489.
- Mallada, L., 1887, Sinopsis de las especies fósiles que se han encontrado en España. Sistema Cretáceo inferior: *Boletín de la Comisión del Mapa geológico de España*, 14, 1-172.
- Matthews, S.C., 1973, Notes on open nomenclature and on synonymy lists: *Palaeontology*, 16 (4), 713-719.
- Michael, E., 1974, Zur Paläoökologie und Faunenführung im westlichen Bereich des norddeutschen Unterkreide-Meeres: *Geologisches Jahrbuch, (A: Allgemeine und regionale Geologie)*, 19, 1-67.
- Milne-Edwards, H., 1857, Histoire naturelle des coralliaires ou polypes proprement dits (v. 1+2): Paris, Librairie encyclopédique de Roret, 1-326, 1-633.
- Milne-Edwards, H., Haime, J., 1849, Recherches sur les polypiers, 4. Monographie des Astreides, 2. Astréens, 4-5. Appendice: *Annales de Sciences naturelles, sér. 3*, 12, 95-197.

- Milne-Edwards, H., Haime, J., 1851, A monograph of the British fossil corals, 2. Corals from the oolitic formations: Palaeontographical Society Monographs, 5, 74-146.
- Morycowa, E., 1964, Hexacoralla des couches de Grodziszczce (Néocomien Carpathes): Acta Palaeontologica Polonica, 9(1), 1-114.
- Morycowa, E., 1989, Class Anthozoa Ehrenberg, 1834, in Malinowski, L. (ed.), Geology of Poland, 3. Atlas of guide and characteristic fossils, 2c. Mesozoic, Cretaceous: Warszawa, Wydawnictwa Geologiczne, 58-67.
- Pandey, D.K., Fürsich, F.T., 2003, Jurassic corals of east-central Iran: Beringeria, 32, 3-138.
- Prever, P.L., 1909, Anthozoa, in Parona, C.F. (ed.), La fauna coralligena del Cretaceo dei Monti d'Ocre nell' Abruzzo Aquilano: Memorie descrittive della carta geologica d'Italia, 5(1), 51-147.
- Quenstedt, F.A., 1881, Petrefactenkunde Deutschlands, 6. Röhren- und Sternkorallen: Leipzig, Fues Verlag, 1-1094.
- Reuss, A.E., 1864, Die fossilen Foraminiferen, Anthozoen und Bryozoen von Oberburg in Steiermark: Denkschriften der Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Klasse, 23, 1-38.
- Reyeros-Navarro, M.M., 1963, Corales del Cretácico inferior de San Juan Raya, Estado de Puebla: Paleontología Mexicana, 17, 1-21.
- Roemer, F.A., 1841, Die Versteinerungen des norddeutschen Kreidegebirges: Hannover, Hahn'schen Hofbuchhandlung, 145 p.
- Roniewicz, E., 1987, Correction of homonymy of the generic name Etallonia Roniewicz, 1966 into Etallonasteria nom.n.: Acta Palaeontologica Polonica, 32, 152.
- Sikharulidze, G.Ya., 1972, [The new genus Paretallonia (Hexacorallia) from Lower Cretaceous sediments in western Georgia]: Soobshcheniya Akademii Nauk Gruzinskoj SSR, 68(3), 641-644.
- Sikharulidze, G.Ya., 1985, [Hexacorals from the Urgonian facies of the Dzirul Massif and its northern frame]: Trudy Akademija Nauk Gruzinskoj SSR, Geoliceskij Institut, 59, 1-110.
- Stoliczka, F., 1873, The corals or Anthozoa from the Cretaceous rocks of South India: Memoirs of the Geological Survey of India, Palaeontologia Indica, 8(4/5), 130-202.
- Vaughan, T.W., Wells, J.W., 1943, Revision of the suborders, families and genera of scleractinia: Geological Society of America, Special Paper 44, 1-363.
- Verrill, A.E., 1868-70, Notes on the Radiata in the museum of Yale College, with descriptions of new genera and species. No. 6. Review of the corals and polyps of the West Coast of America: Transactions of the Connecticut Academy of Arts and Sciences, 1(2), 377-567.
- Wells, J.W., 1956, Scleractinia, in Moore, R.C. (ed.), Treatise on Invertebrate Paleontology: University Press of Kansas, F, 328-444.
- Wilmsen, M., 1996, Flecken-Riffe in den Kalken der "Formación Altamira" (Cenoman, Cobreces/Toñanes-Gebiet, Prov. Kantabrien, Nord-Spanien): Stratigraphische Position, fazielle Rahmenbedingungen und Sequenzstratigraphie: Berliner geowissenschaftliche Abhandlungen (E), 18, 353-373.
- Wilmsen, M., 1997, Das Oberalb und Cenoman im Nordkantabrischen Becken (Provinz Kantabrien, Nordspanien): Faziesentwicklung, Bio- und Sequenzstratigraphie: Berliner geowissenschaftliche Abhandlungen (E), 23, 1-167.
- Wingfield, R.T.W., Evans, C.D.R., Deegan, S.E., 1978, Geological and geophysical survey of the Wash: Report of the Institute of Geological Science, 78(18), 1-32.

Manuscript received: April 14, 2008

Corrected manuscript received: September 17, 2008

Manuscript accepted: September 19, 2008