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

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**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 *Thammasteria*. 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 ceriode 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 Thammasteriidae, muy cercano a *Mesomorpha* y *Thammasteria*. 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 transgressional sediment which cropped out in Lower Saxony (Germany). These sediments were formed during the transgression of the very Late Valanginian to very 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 *Holocoenia* is Berklingen, a small village a few kilometers southeast of Braunsweg. 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 columnella 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 oolithic 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 Saxony 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 *Stereoecaenia*. 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) *Stereoecaenia 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* ("spècimens ... que nous avons déterminés d’après les descriptions et figurations originales...")
(cette-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 Böltsche (1866) gives precise information. He was the only researcher who studied material from the type locality of the species of *Holocoenia* despite of Roemer. However, Alloiteau (1957) provided a diagnosis different from that of Böltsche (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*. Böltsche (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 tribolleti* 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 Actinastreidae 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).


3. San Juan Area (Puebla, Mexico). San Juan Raya Formation. Aptian. For details see Calderón-García (1956) and Reyeros-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 PALAEONTOLOGY**

The following institutional abbreviations are used: FGUB: Facultad de Geologia de la Universidad de Barcelona, Spain; BSP: Bayerische Staatsammlung 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: Musée 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 mm²; *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 synapticulae 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; Paretallonia Sikharulidze, 1972.


**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 circular calices. The calices are slightly depressed, the 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 *Astrea micrantha* Roemer, p. 113, pl. 16: 27
1849 *Thamnastrea micrantha* - Milne-Edwards and Haime, p. 158
1850a *Centrastraella collinaria* d’Orbigny, (2), p. 93
1850a *Synactinea micrantha* - d’Orbigny, (2), p. 94
1850b *Centrastraella collinaria* - d’Orbigny, p. 177
1850b *Synactinea micrantha* - d’Orbigny, p. 178
1851 *Astrea micrantha* Roemer - Milne-Edwards and Haim, p. 99
1851 *Thamnastrea? collinaria* - Milne-Edwards and Verrill, p. 112
1851 *Thamnastrea ? micrantha* - Milne-Edwards and

<table>
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<th>Maximum value (mm)</th>
<th>Average (mm)</th>
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<td>0.269</td>
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</table>
The Early Cretaceous coral genus Holocoenia

1857 Holocoenia micrantha - de Fromentel, p. 53
v 1857 Holocoenia collinaria - de Fromentel, p. 54, pl. 7: 9, 10
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 Holocaenia 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
? 1887 Centrastraea collinaria - Mallada, p. 170, pl. 62: 4
non v 1909 Holocoenia micrantha - Prever, p. 128, pl. 14: 8 [= Styлина sp.]
? 1937 Centrastraea collinaria d’Orbigny, 1849 - Bataller, p. 201
1952 Holocaenia 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 Stereocoenia collinaria de From. sp. - Alloiteau, fig. 272-274, pl. 19: 4, non pl. 1: 10 [= Mesomorpha or Thamnasteria sp.]
? 1978 cf. Holocoenia micrantha (Roemer) - Wingfield, Evans and Deegan, p. 30
non 1980 Stereocoenia collinaria (Fromentel, 1857) - Kuzmicheva, p. 100, pl. 37: 2 [= Mesomorpha sp.]
non 1983 Stereocoenia collinaria (Fromentel, 1857) - Kuzmicheva, p. 34, pl. 3: 4 [not pl. 2: 4 as indicated] [= Mesomorpha or Thamnasteria sp.]
non 1987 Stereocoenia collinaria (d’Orbigny, 1850) - Kuzmicheva, p. 246, pl. 5: 3 [= Mesomorpha sp.]
non 1988 Stereocoenia collinaria (Fromentel, 1857) - Kuzmicheva and Aliev, p. 168, pl. 5: 3 [= Mesomorpha sp.]
v 1995 Stereocoenia (= 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 Stereocoenia collinaria (d’Orbigny, 1850) - Löser et al., p. 616 [detailed synonymy here]
2002 Stereocoenia 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 Stereocoenia 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 3677, but was not available for study.

Synonyms. Centrastraea collinaria d’Orbigny, 1850; Stereocoenia 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 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 Fromentel (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 Fromentel (1887) is poor and the description is incomplete since it starts on the very last page of the 16th (and last) installment 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 described by Hauterivian (Götz et al., 2005), but new material kindly provided by S. Tomás (Barcelona) included a Felixíxira species, a genus which is absent in the Hauterivian elsewhere.

**Occurrence.** *Astrea micrantha* Roemer, 1841: Early Valanganinian of Arzier, La Violette quarries (Vaud, Switzerland); Latest Valanganinian to Earliest Hauterivian (late Paucinodum / early Amblygonium zone) of Apelstedt and Berklingen near Braunschweig (Lower Saxon, Germany); Early Hauterivian (Radiatus zone) of the various outcrops near the villages Fontevey, Gy-l’Évêque, and Les Saints (Yonne, France) and near Vallières and Marolles (Aube, France); Hauterivian (?Barremian) of the La Avellà section near Cati (Valencia, Castellón, Spain; FGUB AV-C-6); Late Barremian of Pont de Laval near St.Reméze (Ardèche, France); Latest Barremian to Early Aptian (Weissi zone) of the outcrops Mahdical, Mitteleck, Obere Gottesackerwinde, Scealpe 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.** Valanganinian 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’Orbigny - 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 *Stereocenia triboleti* (Koby, 1896) - Morycowa, p. 77, pl. 23: 1-3
v 1970 *Stereocenia 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 *Stereocenia triboleti* (Koby, 1896) - Morycowa, p. 65, pl. 27: 1, 2
non 1996 *Paretallonia bendukidzeae* Sikharulidze, 1972 - Császár and Turnšek, p. 434, fig. 4 [= *Cryptocoenia* 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 *Stereocenia 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 Museum 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 Le loux (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’Évèque (Yonne, France); Hauterivian of Shkmeri (Racha, Georgia); Kvemo-Chalovani and Sachkhere (Imerti, Georgia); Wieliczka, Buków (Malopolskie, Wieliczka, Poland). Hauterivian (?Barremian) of the La Avellà section near Catí (Valencia, Castellón, Spain); Barremian of Morteau (Doubes, 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-Toure 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 (? 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 *Columnocoeia*.
- *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 *Columnocoeia* 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 Haim, 1851 was assigned by Beauvais (1966) to *Stereocaeenia*. *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 centrals 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 (*Stereocaeenia, 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.

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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.

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