

Taxonomy, stratigraphic distribution and palaeobiogeography of the Early Cretaceous coral genus *Holocystis*

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ABSTRACT

The Early Cretaceous Scleractinian coral genus Holocystis Lonsdale, 1849 –first reported for southern England and for a long time believed to be restricted to this region– is easy to recognise but it is also rare. Abundant material from the Late Barremian to Early Albian found in Sonora (Mexico) as well as the available type material and additional material from Europe and East Africa allowed a systematic revision. Five species are distinguished. One of them –Holocystis nomikosi– is described as a new species. Three species previously described for other genera were assigned to the genus Holocystis and two species formerly assigned to Holocystis were found to belong to other genera. Two genera (Tetracoenia and Nowakocoenia) are considered junior synonyms of Holocystis. The stratigraphic extent of the genus was limited to the range from the Barremian to the Early Albian. Holocystis is not a common coral genus but occurred in a large geographic area comprising the central Tethys, the Caribbean, and even the eastern to south-eastern Tethys. The genus is restricted to sediments with a certain terrigenous input.

Key words: Scleractinia, Cretaceous, taxonomy, corals, palaeobiogeography.

RESUMEN

El género de corales Holocystis Lonsdale, 1849 del Cretácico Temprano fue reportado por primera vez en el sur de Inglaterra y por mucho tiempo se consideró como restringido a esta región. El género es fácil de reconocer pero es un género raro. Abundantes muestras del Barremiano tardío hasta el Albiano temprano encontradas en Sonora (México), así como el material tipo y muestras adicionales de Europa y África oriental permitieron una revisión sistemática. Se identifican cinco especies. Una especie –Holocystis nomikosi– se describe como especie nueva. Tres especies originalmente asignadas a otros géneros se reasignan a Holocystis, y dos especies originalmente asignadas a este género pertenecen a otros géneros. Dos géneros (Tetracoenia y Nowakocoenia) son considerados como sinónimos de Holocystis. El rango estratigráfico del género es limitado del Barremiano hasta el Albiano temprano. Holocystis no es un género común de coral, pero se encuentra en un área grande que comprende la región central del mar de Tethys, el mar Caribe y también en le este y sureste del mar de Tethys. El género está casi restringido a sedimentos con una cierta influencia terrígena.

Palabras clave: Scleractinia, Cretácico, taxonomía, corales, paleobiogeografía.

INTRODUCTION

The colonial coral genus *Holocystis* Lonsdale, 1849 is an easily recognisable Early Cretaceous genus owing to its tetrameral septal arrangement. It was first described from the Early Aptian of Southern England, with *Cyathophora elegans* Lonsdale, 1849 as type species, and is a common coral in the Lower Greensand at the south coast of the Isle of Wight. Five *Holocystis* species were described subsequently from Lower Cretaceous outcrops in Europe, two of which belong to other genera. Three other species were described under genera different from *Holocystis* but belong to this genus. Only two species are reported commonly in the literature. Except for the study by Ryder (1927), which is restricted to the type species of the genus, the genus has never been considered in detail. New, previously unreported material mainly from the Late Barremian to Early Albian from Mexico, but also from Spain and Greece and the discovery of a new species demand a taxonomical revision of the genus, and also will allow a better limitation of its stratigraphical extent.

MATERIAL

The material comes from various localities. Most of them are listed, commented and provided with additional references in Löser *et al.* (2005); the locality code is provided in parenthesis after the locality name. Herein, details are only provided if not already reported in that publication.

Azerbaijan, Kubatlinskij rajon, Alikuliushagi (AZ.146); Barremian.

France, Dépt. Aube, Les Croûtes (F.417). According to d'Orbigny (1851, p. 165), the locality has an Aptian age, which was later specified by Corroy (1925, p. 456) as Early Aptian. An Aptian age is improbable.

France, Dépt. Yonne, Seignelay. Without stratigraphy mentioned by d'Orbigny (1850, p. 121). Corroy (1925, p. 456) claimed an Early Aptian age, which is improbable according to the geological situation. In this area, which concerns also Les Croûtes, sediments of the Calcaire à Spatangus (Early Hauterivian, zone of *Acanthodiscus radiatus*) crop out (F.418).

Germany, Bavaria, Allgäuer Helvetikum, Tiefenbach (D.256); Schrattenkalk, Early Aptian.

Greece, Viotía, Chiarmena SE Aliartos (GR.537); Evangelistria-Schichten, Late Aptian-Early Albian.

Italy, L'Aquila, Abruzzi, Monti d'Ocre, Fossa Cerasetti (I.1734); Late Aptian.

Mexico, Sonora, Municipio Ures, Cerro de Oro; Cerro de Oro Formation (Late Barremian-Early Aptian) and Cerro La Espina Member, Mural Limestone (Early Albian). Corals are found in two different levels in the area of the small village Cerro de Oro: in the Late Barremian-Early Aptian (zone of *Palorbitolina lenticularis*) of the Cerro de Oro Formation and in the Early Albian of the Cerro La

Espina Member, Mural Limestone (both Bisbee Group; González-León and Lucas, 1995). Two sample locations are distinguished in the Cerro de Oro Formation (CO4 and BZ1) and one sample location in the Cerro La Espina Member (CO5). Lawton *et al.* (2004) claimed a Middle Albian age in comparable sections for the Cerro La Espina Member, which is not well constrained by biostratigraphic data according to the opinion of this author, and therefore was not applied in this paper.

Poland, Malopolskie, Lanckorona, Jastrzebia (PL.1170); Grodziszcz Sandstones, Early Aptian.

Poland, Slaskie, Bielsko-Biala, Rudzica (PL.3627); Late Barremian-Early Aptian.

Romania, Suceava, Pojorîta area, Cîmpulung-Moldovenesc, Valea Seaca and Valea Izvorul Alb (RO.280, RO.827); Wildflysch, Early Aptian.

Serbia, East Serbia, Zljebine (SM.126); Early Aptian.

Spain, Cataluña, Lérida, Com. Alt Urgell, Mun. Cabó, Senyús section (E.2273); Senyús Formation, early Late Aptian.

Spain, Cataluña, Lérida, Com. Alt Urgell, Mun. Coll de Nargó, Set Comelles, El Caso section (E.2040); Font Bordonera Formation, latest Aptian.

Spain, Cataluña, Lérida, Com. La Noguera, Montsec de Rubies, section NW La Cabrua quarry; early Late Aptian. The coral fauna from this locality is still undescribed, but the stratigraphy of the locality was discussed in Löser and Decrouez (2000).

Spain, Murcia, Jumilla, Sierra de Sopalmo; Early Aptian. The locality is described in Morycowa *et al.* (2001).

Spain, Tarragona, Cataluña, Com. Baix Penedés, Mun. Sant Martí Sarroca, Can Grau (E.834); Late Aptian.

Tanzania, Tanganyika, Mtwara, Nambawala plateau, Pilepile (EAT.16); Kiturika member, Late Aptian.

Turkmenistan, Krasnovodskaya oblast, Small Balcan (TUR.137); Early Barremian.

United Kingdom, Isle of Wight, Atherfield (GB.312); Perna Beds, Early Aptian. The locality at the coast has been well known for many years. The localities Atherfield point, coast guard station, Sandown (bay) and Shanklin are close to the type area and of Early Aptian age as well.

SYSTEMATIC PALAEOONTOLOGY

The following institutional abbreviations are used: BSP: Bayerische Staatssammlung für Paläontologie und Geologie München, Germany; ERNO: Universidad Nacional Autónoma de México, Instituto de Geología, Estación Regional del Noroeste, Hermosillo, Mexico; GPS: Geologische und Paläontologische Sammlung der Universität Leipzig, Germany; JCSV: Coll. Saldaña-Villodre, San Vicente del Raspeig, Spain; MB: Naturkundemuseum der Humboldt-Universität Berlin, Germany; MGSB: Museo Geológico del Seminario de Barcelona, Spain; MNHN:

Muséum National d'Histoire Naturelle Paris, France; NHM: The Natural History Museum London, United Kingdom; NHMW: Naturhistorisches Museum Wien, Austria; PU: Museo di Geologia e Paleontologia dell'Università di Torino, Italy; TUM: The Tohoku University Museum, Sendai, Japan; UJ: Jagiellonian University, Instytut Nauk Geologicznych, Kraków, Poland.

The following abbreviations are used: c: calicular diameter; ccd: distance of calicular centers; s: number of septa; sc: number of costae; ac: acetate peel; ths: thin section; v = the present author has seen the material belonging to this citation; * = first publication. The term 'cycle' or 'septal cycle' refers to radial elements of equal width and length. The first three cycles are assumed to have formed at the same time (Milne-Edwards 1857, p. 45).

Order Scleractinia Bourne, 1900
 Suborder Stylinina Alloiteau, 1952
 Family Cyathophoridae Vaughan and Wells, 1943
 Genus *Holocystis* Lonsdale, 1849

Type species. *Cyathophora elegans* Lonsdale, 1849, by monotypy, from the Lower Greensand of Atherfield (Isle of Wight, United Kingdom).

Diagnosis. Massive colonial coral with sub-ceroid or plocoid calicular arrangement. Calices round, well distinguished, separated by a mostly narrow coenosteum. Septa short, regular in four systems and up to three septal cycles. A fourth septal cycle may appear, but is invariably incomplete. Septa are thin, compact, invariably free, and broad in their peripheral part. They do not bear auriculae (small winged ornamentations at the inner septal margin; Gill, 1977). A columella is absent. The endotheca consists of regular tabulae and/or dissepiments. The coenosteum consists of dissepiments.

Synonym. *Tetracoenia* (type species *Tetracoenia dupiniana* d'Orbigny, 1850, by monotypy). The types of the type species could not be found recently in the collections of the MNHN. D'Orbigny indicated the species from two localities: Early Aptian of Les Croûtes (Dépt. Aube, France) and from Seignelay (Dépt. Yonne, France; without stratigraphy). Both villages are in areas where only Early Hauterivian sediments typically yield colonial corals. However, *Holocystis* could not be found in Museum collections or in the widely exposed sediments of the Early Hauterivian of the Paris Basin. According to the description and illustration given by d'Orbigny (1851), the genus is most likely synonymous with *Holocystis*. Wery (1954, p. 41) distinguished *Holocystis* and *Tetracoenia* by the extent of their coenosteum. This character may vary within one colony and cannot be used to distinguish these genera. Wery (1954) did not note whether or not he had the type material of *Tetracoenia dupiniana* in hand.

Possible synonym. *Nowakocoenia* Kołodziej and Gedl, 2000 (type species *Nowakocoenia cieszynica* Kołodziej and Gedl, 2000, by original designation). The authors of the genus distinguished it from *Holocystis* on the basis of morphological characteristics of wall formation. The character of the wall was described as "ambiguous, however at least in some places of the colony", and they claimed that it had developed prior to the septa. They did not compare their distinctions with *Holocystis*. It was also claimed that the septal pattern of *Holocystis* was more regular and "different" from that in *Nowakocoenia*, without going into detail. The septal insertion in *Nowakocoenia* is indeed not very regular, but neither is it in *Holocystis*. The main distinguishing feature proposed by the authors of *Nowakocoenia*—the development of the wall before the septa—is based on thin sections showing strongly reduced septa and the presence of the wall (Kołodziej and Gedl, 2000, figs. 9C, D). The extreme reduction of the septa to small ridges is no exception in genera of the Cyathophoridae and Stylinidae. But it cannot be claimed in such cases that the wall developed first and the septa later. Serial sections beginning from the top of the colony would be needed to support these arguments, but no such sections were provided by the authors of *Nowakocoenia*. Until such is proven to be the case in the type material of *Nowakocoenia cieszynica*, it is considered synonymous with *Holocystis dupini*, and therefore the genus is synonymous with *Holocystis*.

Not regarded as synonyms anymore. *Cyathocoenia* de Fromental, 1884 non Duncan, 1867 nec Volz, 1896 (type species *Cryptocoenia neocomiensis* d'Orbigny, 1850, subsequently designated by Wells, 1936) was originally created by de Fromental (1884, p. 541) as a subgenus of *Cyathophora*. It was included in the synonymy of *Holocystis* by Wells (1956, p. 375). The lectotype of *Cryptocoenia neocomiensis* (designated by Wells, 1936; MNHN, Coll. d'Orbigny, no. 5274) belongs to *Cryptocoenia* d'Orbigny, 1849. Therefore *Cyathocoenia* de Fromental, 1884 cannot be a junior synonym of *Holocystis*, but probably of *Cryptocoenia* or *Adelocoenia* (which are probably synonymous genera).

Occurrence. The genus occurs in the Boreal and Tethys realms (from Europe to middle Asia and east Africa) and in the Caribbean province (Mexico). It ranges from the Barremian (Azerbaijan and Turkmenistan) to the Early Albian (Greece and Mexico). *Holocystis* predominantly occurs in siliciclastic deposits or carbonate deposits with an influence of siliciclastic sediments (as lagoonal environments or carbonate ramps). In pure platform carbonates the genus is rare.

Description. Massive sub-ceroid to plocoid corallum with more or less densely arranged calices. Each calice has its own wall. Calicular outline round or slightly quadratic. Septa free, confluent to subconfluent, compact, straight. The septa of the first cycle reach up to 40 percent of the

calicular radius but may be longer. They are commonly wedged-shaped. Those of the second cycle are shorter and reach up to 20 percent of the radius. Those of the third cycle are very short, commonly only represented by ridges. The septa do not have auriculae at their inner margins. The septal flanks and the septal upper border are smooth.

The first and second septal cycles each encompass four septa, the third cycle eight septa, and the fourth up to 16 septa. The last septal cycle may be incomplete. The fourth cycle is in all examined samples incomplete and the maximum number of septa found is 24 (fourth cycle with eight septa). The septa of the different cycles can be easily distinguished by their length and thickness.

The coenosteum consists of the septal costae and dissepiments. It can be strongly reduced. The endotheca is made of tabulae and dissepiments. In some species (such as *H. elegans*), tabulae predominate, in others (such as *H. nomikosi*) dissepiments dominate. The wall is parathecal. Columella, pali and synapicalae are absent. The budding of new calices is extracalicular.

Remarks. Lonsdale (1849, p. 83) established the new genus only provisionally and cited the type species still under the genus *Cyathophora*. Milne-Edwards and Haime (1851, p. lxiv) confirmed the genus and Lonsdale as author. Ryder (1927) considered the ontogenetic stages and the nature of the septal insertion. Observations on the type and additional topotypic material show that the septal insertion is different from the description of Ryder (1927): new calices successively develop the four septa of the first cycle. Four or six septa do not appear at the same time. After the first cycle is completed, the calice gains size, and then the second cycle appears. The third cycle normally appears before the second cycle is completed. Therefore, calices can be found that have reached the average 'adult' calicular diameter with six, eight, ten, 12 or 14 septa.

Ryder (1927) also mentioned the rare existence of a columella. None of the specimens of *Holocystis elegans* from the type locality, which were observed directly, show any trace of a central calicular structure.

Relationship. *Holocystis* can be considered as a successor of the Late Jurassic and Early Cretaceous *Pseudocoenia* d'Orbigny, 1850 (sensu d'Orbigny, 1850; Löser, 1998b) which shows an octamer symmetry. *Holocystis* compares also with the genera *Adelocoenia* and *Cryptocoenia*, which show hexamer symmetry, and with the pentamer *Pentacoenia* d'Orbigny, 1850.

Scleractinian corals with tetramer septal symmetry, as in *Holocystis*, are rare. Besides *Holocystis*, there is one species of *Heterocoenia* (*Heterocoenia tetrasepta* Eguchi, 1951, Aptian of Japan), one species of *Stylina* (*Stylina surensensis* Wells, 1944, Aptian of Venezuela), two –probably synonymous– species of *Paronastraea* (*Paronastraea bassanii* (Prever, 1909), and *Paronastraea serrata* (Prever, 1909), both Late Aptian of Italy), another

species of *Paronastraea* (*P. occulta* Löser, 2006), and finally one still undescribed species of *Enallhelia* (labelled as *Enallhelia rathieri* d'Orbigny, 1850; unpublished specimen TUM without number, depository number D21L-L25, Albian of Japan) with a tetramer symmetry.

Species. So far, six coral species have been assigned to the genus *Holocystis* (*bukowinensis*, *calzadai*, *elegans*, *octolobata*, *polyspathes*, *similis*; Löser *et al.*, 2002; Kuzmicheva, 2002). The species are distinguished on the basis of their calicular diameter and the number of septal cycles. Calicular diameters vary between 1.3 and 4.1 mm. Within one colony, there is a maximum variation of 38 per cent between the smallest and the largest calicular diameter; the average of percentual variation is 20 per cent. The distance of the calices shows a higher variation of up to 53 per cent, the average is 22 per cent. The number of septa varies between 4 and 24. The variation of the number of septa within one colony is low: only half of the material included in the calculation shows any variation. In most cases, the number of septa varies in an interval between eight and 16, rarely between four and eight.

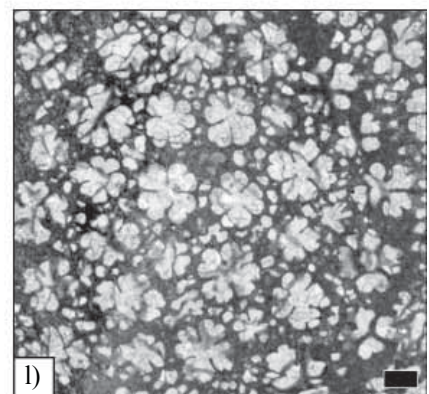
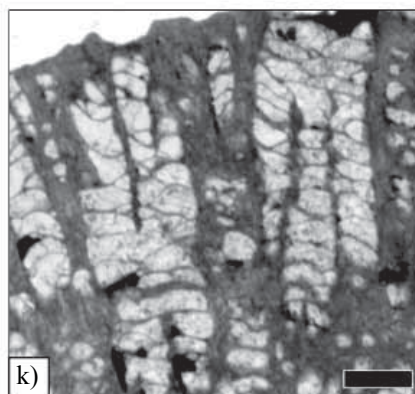
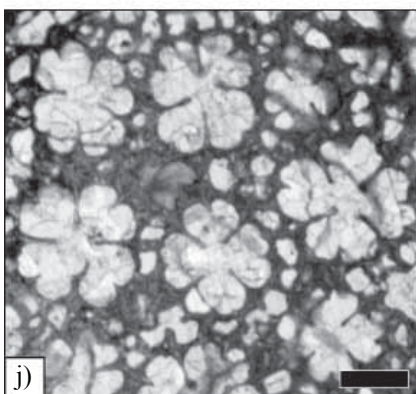
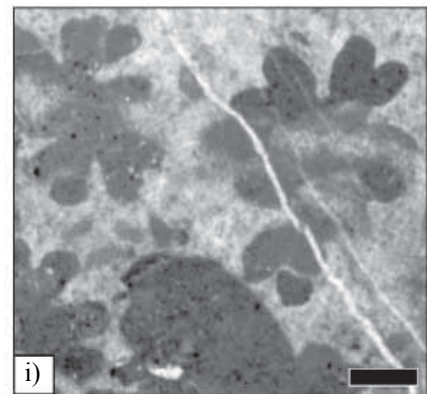
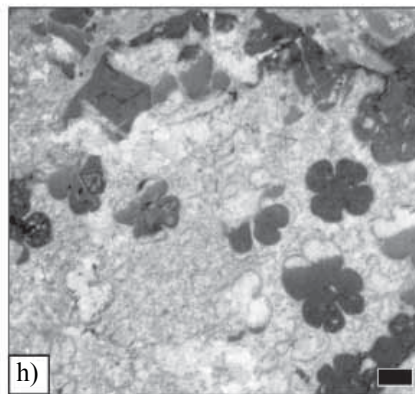
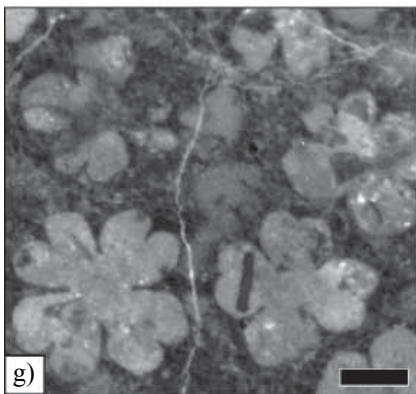
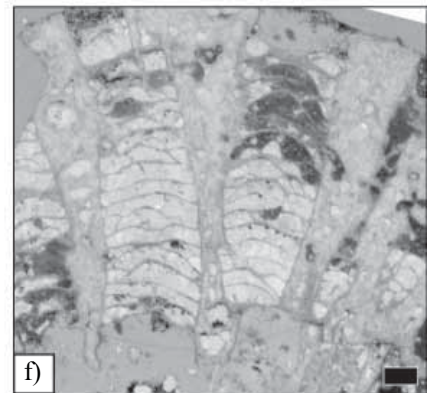
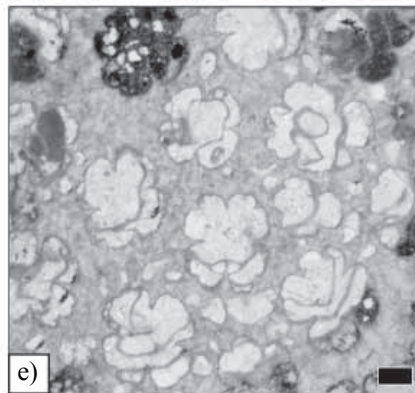
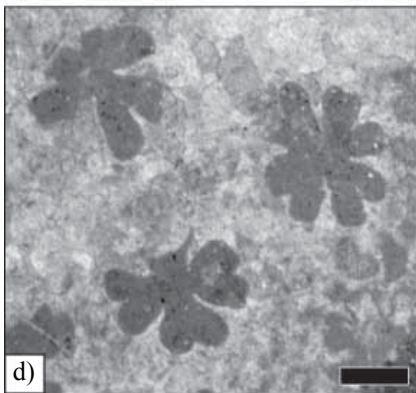
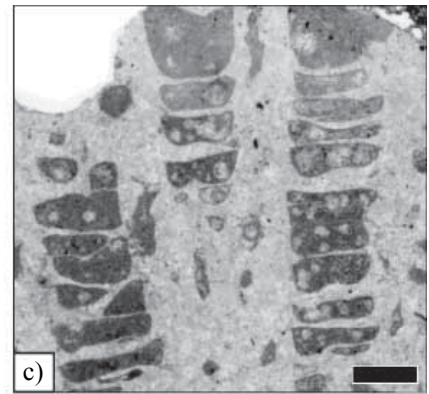
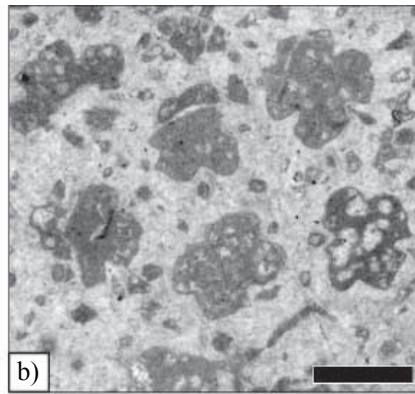
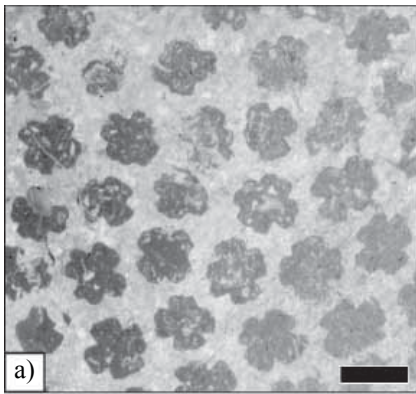
In the following synonymy lists, pure quotations of taxa in the literature are mainly suppressed. First, it cannot be proven whether the concerned quotation belongs to the species or not, and second, the data have been already published elsewhere (Löser *et al.*, 2002). Localities are given only for material that was observed directly, or the description/depiction in the literature allows a sure comparison, and the locality data are precise and reliable.

Holocystis ?*bukowinensis* Volz, 1903

Figures 1a-c

- * 1903 *Holocystis bukowinensis*; Volz, p. 27, pl. 4, figs 14-17.
- v 1909 *Polytremacis magnicanaliculata*; Prever, p. 68, pl. 1, fig. 20, fig. 22 a.
- v non 1964 *Holocystis bukowinensis* Volz; Morycowa, p. 25, pl. 3, fig. 3, pl. 5, fig. 1 [= *Holocystis elegans*].
- ? 1971 *Holocystis bukowinensis* Volz; Morycowa, p. 44, pl. 6, fig. 4.
- . 1981 *Holocystis bukowinensis* Volz; Turnšek and Mihajlović, p. 19, pl. 13, figs 5-6.
- non 1987 *Holocystis bukowinensis* Volz; Kuzmicheva, p. 222, pl. 1, fig. 3 [= *Holocystis dupini*].
- non 1988 *Holocystis bukowinensis* Volz; Kuzmicheva and Aliev, p. 157, pl. 1, fig. 4 [= *Holocystis dupini*].
- v non 1989 *Holocystis bukowinensis* Volz; Morycowa, p. 61, pl. 19, fig. 2 [= *Holocystis elegans*].
- non 2002 *Holocystis bukowinensis* Volz; Kuzmicheva, p. 165, pl. 23, fig. 3 [= *Pentacoenia* sp.].

Type. The collection of Wilhelm Volz, held at the former Natural History Museum in Breslau (now: Muzeum



Geologiczne im. Henryka Teisseyre, Instytut Nauk Geologicznych Uniwersytetu Wrocławskiego, Wrocław) was almost completely destroyed during the World War II. The type(s) of *Holocystis bukowinensis* must be considered lost, according to A. Pacholska (personal communication, 2002). A neotype has not yet been selected. Topotypical material could not be made available.

Dimensions. Volz (1903, p. 27) c: 1.3–1.5 mm, ccd: 3.0 mm, s: 8, sc: 16; Morycowa (1971, p. 44) c: 1.3–1.7 mm, ccd: 1.5–2.5 mm, s: 16, sc: 16; present material c: 1.2–1.7 mm, ccd: 1.4–2.4 mm, s: (4) 8–10, sc 16.

Description. Small platy colonies with a cerioid appearance, but sub-cerioid structure. The calices are small and have irregular outlines or are quadratic. There are two cycles of septa. The first cycle remains short and reaches only 15 percent of the calicular diameter. Septa of the second cycle are much shorter and reduced to short ridges. The second cycle is in some cases not complete. Endotheca and coenosteum of the material are known only from sample PU 18118. The coenosteum is formed by sub-confluent to confluent costae, up to 16 per calice. The endotheca is made of strong tabulae and thin dissepiments.

Remarks. The characteristics of the species are presently not clearly known due to the circumstance that the type is lost, and material from the type area contradicts with the original description. Unfortunately, the material described by Morycowa (1971, p. 44) cannot be currently found in the UJ collection. Morycowa confirmed (personal communication, 2005) only that the single specimen described by her was small and poorly preserved. The descriptions given by Volz (1903) and Morycowa (1971) differ in the number of septal cycles. If the number of septa reaches 16, *H. bukowinensis* is close to, perhaps even synonymous with *H. dupini*, and to the material with eight septa the species name *magnicanaliculata* must be applied. If the number of septa is eight, the material previously described by Morycowa (1971) might be assigned to *H. dupini*.

Occurrence. Roadcut near Perachorion, NW Levadia (Viotía, Greece), Early Aptian, BSP 2003 XX 5754; section NW La Cabrua quarry (Montsec de Rubies, Com. La Noguera, Lérida Cataluña, Spain), early Late Aptian, BSP 2003 XX 4200; Fossa Cerasetti, Monti d'Ocre (Abruzzi,

L'Aquila, Italy), Late Aptian, PU18118 (holotype of *Polytremacis magnicanaliculata*).

Occurrences according to the literature. Valea Seaca and Valea Izvorul Alb (Cîmpulung-Moldovenesc, Pojorîta area, Suceava, Romania), Early Aptian; Zljebine (East Serbia), Early Aptian.

***Holocystis dupini* (d'Orbigny, 1850)
emend. de Fromentel, 1861**

Figure 1d

- * 1850 *Tetracoenia Dupiniana* d'Orbigny, p. 121.
- . 1851 *Tetracoenia Dupiniana*; d'Orbigny, p. 166, fig. 303.
- . 1861 *Holocystis Dupini*; de Fromentel, p. 308.
- . 1987 *Holocystis bukowinensis* Volz; Kuzmicheva, p. 222, pl. 1, fig. 3.
- . 1988 *Holocystis bukowinensis* Volz; Kuzmicheva and Aliev, p. 157, pl. 1, fig. 4.
- v. 1995 *Holocystis calzadai* n. sp.; Reig Oriol, p. 8, pl. 1, fig. 1.
- 2000 *Nowakocoenia cieszynica* gen. et sp. nov.; Kołodziej and Gedl, p. 187, figs 3, 8–9.

Type. The type material could not be found in the collections of the MNHN.

Dimensions. (d'Orbigny, 1851, p. 166) c: (1.5) 1.7–2.2 mm, ccd: (1.7) 2.0–2.5 (4.0) mm, s: 8–16, sc: 16; other material c: (1.3) 1.5–2.0 (2.2) mm, ccd: 1.7–3.5 mm, s: 16, sc: 16.

Description. Small flat colonies with a sub-cerioid to plocooid appearance. The distance between calices may vary giving a different appearances to the calicular arrangement. Calicular outline circular, in places irregular. Septa straight, free and compact. Three septal cycles are developed, the first reaching *ca.* 40 percent of the calicular diameter, the second reaching up to 20 percent, and the third remaining very short, only marked by vertical ridges in calices. In small calices the third cycle may be absent or incomplete. The length of septa may vary. They are much shorter in specimens described as *Nowakocoenia cieszynica*. Sixteen costae can be counted. They are non-confluent to sub-confluent, depending on the calicular distance. The endotheca consists of thin tabulae; the exotheca of dissepiments.

Figure 1. a–c: *Holocystis ?bukowinensis* Volz, 1903. a: BSP 2003 XX 4200, section NW La Cabrua quarry, Montsec de Rubies, Com. La Noguera, Lérida Cataluña, Spain; early Late Aptian; transversal ths; b, c: PU 18118 (holotype of *Polytremacis magnicanaliculata*), Fossa Cerasetti, Monti d'Ocre, Abruzzi, L'Aquila; Late Aptian; b: transversal ap c: longitudinal ap. d: *Holocystis dupini* (d'Orbigny, 1850) emend. de Fromentel, 1861. ERNO L-4378, Cerro de Oro MEX.4419, Municipio Ures, Sonora, Mexico; Cerro de Oro Fm; Late Barremian-Early Aptian; transversal ths. e–g: *Holocystis elegans* (Lonsdale, 1849); e, f: BSP 2003 XX 5431, Atherfield point, Isle of Wight, United Kingdom; Lower Greensand; Early Aptian; e: transversal ths; f: longitudinal ths; g: ERNO L-4380, Cerro de Oro (CO5), Municipio Ures, Sonora, Mexico; Cerro La Espino Member, Early Albian; transversal section. h, i: *Holocystis octolobata* Kuzmicheva, 2002; h: BSP 2003 XX 4023, El Caso section, Set Comelles, Mun. Coll de Nargó, Com. Alt Urgell, Lérida, Cataluña, Spain; Font Bordonera Formation; latest Aptian; transversal ths; i: ERNO L-4313; Cerro de Oro CO4, Municipio Ures, Sonora, Mexico; Cerro de Oro Fm; Late Barremian-Early Aptian; transversal ths. j–l: *Holocystis nomikosi* sp. nov. BSP 2003 XX 6200, holotype, Chiarmena SE Aliartos, Aliartos, Viotia, Greece; Evangelistria-Schichten; Late Aptian-Early Albian; j: transversal ths; k: longitudinal ths; l: transversal ths. Scale bar in all figures 1 mm.

Remarks. D'Orbigny (1850) gave only a very short description. A good illustration is provided in d'Orbigny (1851, p. 166). Since the work of Felix (1914, p. 25), *H. dupini* is considered a junior synonym of *H. elegans*. This cannot be confirmed because *H. dupini* has smaller calicular dimensions.

D'Orbigny (1850, p. 121) indicated two localities for the new species: Les Croûtes (Dépt. Aube, France), and Seignelay (Dépt. Yonne, France), both without stratigraphical data. An Early Aptian age was claimed subsequently (Corroy, 1925, p. 456). Early Aptian coral-bearing sediments were never confirmed in later literature (e.g., Chevalier and Masse, 1980) from the Paris Basin. No coral specimen belonging to *Holocystis* could be found in the collections or during extensive excavations by the author in the Dépt. Yonne (Löser, 2001).

The material described by Kołodziej and Gedl (2000, p. 187) differs from the other material by having a very reduced coenosteum. However, the width of the coenosteum may differ in one and the same colony as it can be recognised for instance in *H. nomikosi* and might not be a specific character. Additionally, the number of septa is greater; the beginning of a fourth cycle can be observed in *Nowakocoenia cieszynica*.

Occurrence. Can Grau (Mun. Sant Martí Sarroca, Com. Baix Penedés, Tarragona, Cataluña, Spain), Late Aptian, MGSB 55820 (holotype of *Holocystis calzadai*); Cerro de Oro (Municipio Ures, Sonora, Mexico), Late Barremian-Early Aptian, ERNO 3032, 3023 (from BZ1), ERNO L-4378 (from CO4).

Occurrences according to the literature. Small Balcan (Krasnovodskaya obl., Turkmenistan), Early Barremian; Alikuliushagi (Kubatlinskij r., Azerbaijan), Barremian; Rudzica (Bielsko-Biala, Slaskie, Poland), Late Barremian-Early Aptian.

Holocystis elegans (Lonsdale, 1849)

Figures 1e-g

- 1847 *Astrea? elegans* Fitton, p. 296 [nomen nudum, non *Astrea elegans* Goldfuss, 1826].
 * v 1849 *Cyathophora? elegans*; Lonsdale, p. 83, pl. 4, figs 12-15.
 . 1851 *Holocystis elegans*; Milne-Edwards *et al.*, p. 70, pl. 10, fig. 5.
 . 1851 *Holocystis elegans*; Bronn, p. 143, pl. 29.4, fig. 13.
 1860 *Holocystis elegans*; Milne-Edwards, (3), p. 326.
 ? 1861 *Holocystis elegans* E. H.; Gümbel, p. 566.
 . 1879 *Holocystis elegans*; Nicholson, (1), p. 211, fig. 102.
 . 1879 *Holocystis elegans*; Quenstedt, p. 454, pl. 158, fig. 20.
 non 1883 *Tetracoenia elegans*; de Fromentel, p. 520, pl. 139, fig. 1 [= *Actinastrea* sp.].

- . 1927 *Holocystis elegans* (Fitton); Ryder, p. 120, figs 1-9
 v ? 1964 *Holocystis bukowinensis* Volz; Morycowa, p. 25, pl. 3, fig. 3, pl. 5, fig. 1.
 v ? 1989 *Holocystis bukowinensis* Volz; Morycowa, p. 61, pl. 19, fig. 2.
 v non 1998 *Holocystis elegans* (Lonsdale, 1849); Schöllhorn, p. 76, figs 36, pl. 18, figs 4-5, pl. 21, figs 1-3, pl. 27, fig. 1 [= *Holocystis octolobata*].
 v. 2003 *Holocystis elegans* (Lonsdale, 1849); Baron-Szabo and González-León, p. 204, figs 6A-B.

Holotype by monotypy. NHM R. 50224 [46800], Lower Greensand, Early Aptian, Atherfield (Isle of Wight, United Kingdom).

Dimensions. Holotype c: 2.2–2.8 mm, ccd: 3.0–3.5 mm, s: 8–16, sc: 16; other material c: (2.0) 2.5–3.0 (3.2) mm, ccd: (2.8) 3.0–3.5 (5.0) mm, s: 8–16, sc 16.

Description. Small rounded colonies. In the type locality they are commonly attached to bivalve shells. The colony appears cerioid, but there is a narrow coenosteum. The calicular outline is round, in small calices quadratic. Septa compact, straight and free. They occur in three cycles. The four septa of the first cycle reach up to 40 percent of the calicular radius. Those of the second cycle are much shorter, reaching only up to ten percent of the radius or only being marked by ridges in the calice. Eight septa of the third cycle are only visible as ridges. Sixteen costae are developed. The peritheca is made of dissepiments and the confluent to subconfluent costae. The endotheca consists of very regular tabulae and some dissepiments. Approximately four tabulae occur within two millimetres of vertical section.

Remarks. Lonsdale used Fitton as author of the type species. Although Fitton (1847, p. 296) was the first author to use the name *Astrea? elegans*, he mentioned only the name. The first description and illustration was given by Lonsdale (1849, p. 83).

Corroy (1925) mentioned the species from various outcrops of the Early Hauterivian and Early Aptian of the Paris Basin, but his collection could not be found, and no material belonging to *Holocystis* was found from the indicated localities.

The species does not occur at the locality Cerro de la Espina (Sonora, Mexico) as indicated by Baron-Szabo and González-León (2003, p. 204). The original sampling list and the material were both in hand and indicate that all *Holocystis* samples described by Baron-Szabo and González-León (2003) are from the locality Cerro de Oro (Sonora, Mexico; sample locality BZ1).

The material mentioned by Gümbel (1861, p. 566) could not be found in the collection of the BSP. A recent revision of the corals from the Allgäu area (Baron-Szabo, 1997) did not report the occurrence of *Holocystis*, and also

the author's own excavations in the outcrop area did not yield any *Holocystis*.

The material depicted by Morycowa (1964) as *Holocystis bukowinensis* shows a slightly larger calicular diameter and the beginning of a fourth septal cycle. The largest measured calicular diameter is 4.1 mm, the highest number of septa 24. These values make its assignment even to the species with the largest dimensions (*Holocystis elegans*) unsure.

Occurrence. Atherfield (Isle of Wight, United Kingdom), Early Aptian, NHM R. 50224 [46800] (holotype); Atherfield point (Isle of Wight, United Kingdom), Early Aptian, BSP 2003 XX 5431, 6044-6047, GPS FLX 2092; Cerro de Oro (Municipio Ures, Sonora, Mexico), Late Barremian-Early Aptian, ERNO 3018 (from BZ1), ERNO L-4313, L-4317, L-4324 (from CO4); Cerro de Oro (Municipio Ures, Sonora, Mexico), Early Albian, ERNO L-4339, L-4344, L-4345, L-4349, L-4380 (from CO5); Sierra de Sopalmo, Early Aptian (JCSV C3).

Occurrence unsure. Jastrzebia (Lanckorona, Malopolskie, Poland), Early Aptian, UJ 4P nn.

Occurrence according to the literature. Rye, Peasemarsch (Sussex, United Kingdom), Early Aptian; Coast-Guard Station; Atherfield, Redhill cutting; Sandown bay, Shanklin (all Isle of Wight, United Kingdom) Early Aptian.

Holocystis octolobata Kuzmicheva, 2002

Figures 1h-i

v. 1998 *Holocystis elegans* (Lonsdale 1849); Schöllhorn, p. 76, fig. 36, pl. 18, figs 4-5, pl. 21, figs 1-3, pl. 27, fig. 1.

* 2002 *Holocystis octolobata* Kuzmicheva, p. 166, pl. 23, figs 4-5.

Type. Holotype PIN 4768/127 (by original designation), Barremian, Akkyr (Turkmenistan).

Dimensions. c: (1.8) 2.2–3.0 (3.2) mm, ccd: 2.5–4.0 mm, s: 4–8.

Description. Small rounded colonies with calices on all sides. Calicular arrangement sub-ceroid to plocoid. The calices have a quadratic form. The compact, straight and free septa appear in two cycles. The septa of the first cycle are long (half of the radius of the calice), those of the second cycle are very short and in some cases hardly recognisable. Eight costae can be found. The endotheca is well developed and consists of thin tabulae, which are slightly convex. Approximately six tabulae can be counted at a distance of two millimetres in a vertical section. The exotheca consists of dissepiments.

Remarks. The description and illustration differ from each other in Kuzmicheva (2002, p. 166). In the text, the calicular diameter is indicated as 3.0–3.5 mm, the illustrations show a diameter of 2.2–3.0 mm (fig. 4) and 2.8–3.2 mm (fig. 5). It is not clear whether *H. octolobata* represents an independent species or is synonymous with *H. elegans*. In its dimensions, it does not differ much from the latter; only the lower number of septa is a clear difference.

Occurrence. Senyús section (Mun. Cabó, Com. Alt Urgell, Lérida, Cataluña, Spain), early Late Aptian, BSP 2003 XX 4052; El Caso section (Set Comelles, Mun. Coll de Nargó, Com. Alt Urgell, Lérida, Cataluña, Spain), latest Aptian, BSP 2003 XX 4023.

Occurrence according to the literature. Akkyr (Turkmenistan), Barremian.

Holocystis nomikosi sp. nov.

Figures 1j-l

v. 1926 *Cyathophora* sp.; Dietrich, p. 66, pl. 6, fig. 3.

Derivation of name. After D. Nomikos, the owner of the tomato puree company where the type locality is located.

Holotype. BSP 2003 XX 6200.

Paratypes. BSP 2003 XX 6172, 6173, 6199, 6207, 6215.

Type locality. North of the Chiarmena SE Aliartos, on the grounds of the tomato puree company of D. Nomikos, located at the eastern end of Aliartos on the road to Thiva, (Viotía, Greece); WGS84 position Lat 38°22'50" N, Long 23°8'25" E. Evangelistria-conglomerates of Late Aptian-Early Albian age based on the occurrence of the microfossils *Pseudocyclamina vasconica*, *Trocholina aptiensis*, *Mesorbitolina texana* and *Simplorbitolina conulus* (see Löser and Raeder, 1995).

Material. Holotype with two thin sections, and five paratypes from the type locality. One specimen from Tanzania.

Diagnosis. *Holocystis* with a calicular diameter of 1.5–1.9 mm and a number of septa of 10–14. The third cycle is always present, but never completed.

Dimensions. c: 1.5–1.9 (2.0) mm, ccd: 2.0–2.5 (3.2) mm, s: 10–14, sc: 16.

Description. Small rounded colonies (20–30 mm diameter). The calicular arrangement appears ceroid at the outer surface. The thin section shows that each calice has its own wall, and a narrow coenosteum occurs. The outlines of calices are round or slightly quadratic. They are regular in

size, but larger calices occur. Septa are thin, straight, free and compact. They appear in three cycles. The first cycle consists of four septa, reaching almost to the centre of the calices (*ca.* 80 per cent of the radius of the calice). The septa have a slightly broader peripheral part, therefore appearing wedge-shaped. Four septa of the second cycle are short (*ca.* 20 per cent of the radius of the calice). The third cycle with up to six septa is only developed as ridges on the inner calicular wall. Normally, only two septa of the third cycle are visible in the calices. There are invariably 16 costae. The coenosteum is made of confluent or subconfluent costae and dissepiments, which extend from the calice. The endotheca consists of tabulae and dissepiments. Both are thin, and dissepiments dominate. About six to eight endothelial elements occur in two millimetres of vertical section.

Comparison and remarks. *H. elegans* has larger dimensions. *H. dupini* shows a higher calicular diameter and a completed third cycle, at least in mature calices, whereas the third cycle is in no case complete in the new species. *H. bukowinensis* is the most similar species, but shows a slightly smaller calicular diameter and a smaller number of septa (Figure 2).

The material described by Dietrich (1926, p. 66) is only well preserved on the surface; the inside is completely recrystallized and does not show any details.

Occurrence. Pilepile, Nambawala plateau (Mtwara, Tanganyika, Tanzania), Late Aptian, MB K 1398; Chiarmena SE Aliartos, Aliartos (Viotia, Greece), Late Aptian-Early Albian, BSP 2003 XX 6172, 6173, 6199, 6200, 6207, 6215.

Stratigraphical range. Late Aptian-Early Albian.

Questionable species

Holocystis polyspathes Gümbel, 1861 was only once listed (Gümbel, 1861, p. 566) and not described or depicted afterwards. The type material could not be found at the BSP. The species must be considered *nomen nudum*. In a recent revision (Baron-Szabo, 1997) of the corals from the Allgäu area, *Holocystis* was not indicated.

The following species were previously or currently assigned to *Holocystis*, but belong to other genera.

The holotype (by monotypy, NHMW, without number) of *Holocystis similis* Toulà, 1877 from Kalna (Sveti-Nikola-Balkan, East Serbia) with Early Aptian belongs to the genus *Hydnophoraraea*.

The holotype (by monotypy, NHMW 1998z0054/0001) of *Holocystis tenuis* Toulà, 1878 from Vratsa (Vrachanska oblast, Bulgaria) with Late Barremian to Early Aptian was originally assigned to *Holocystis*, but correctly reassigned to the genus *Felixigyra* by Masse and Morycowa (1994).

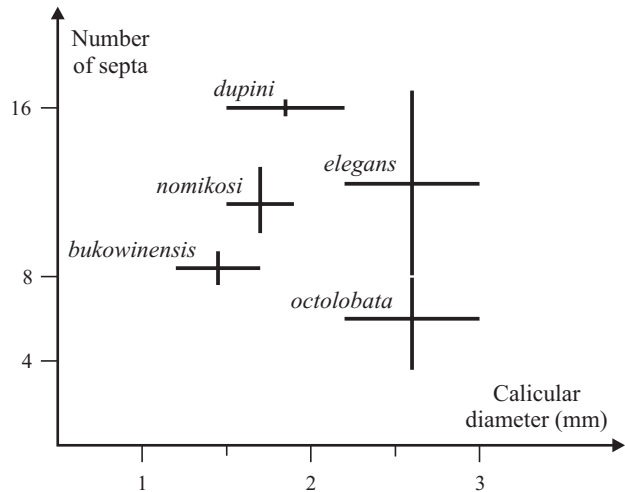


Figure 2. Comparison of morphometric data of the *Holocystis* species.

DISCUSSION

Stratigraphical distribution

The genus *Holocystis* is limited to the Barremian to Early Albian (Figure 3). It appeared with three species in the Barremian, had its maximum of four species in the Late Aptian, and disappeared in the Early Albian, with only two species. The temporal distribution reflects the general abundance of corals in the Cretaceous (Löser, 1998a, fig. 1): increasing values until the Early Aptian and a slight drop in the Early Albian. The sudden disappearance of the genus is probably linked to global anoxic events during the Albian. Almost no hermatypic coral faunas are known from the Middle Albian, and numerous genera disappeared together with *Holocystis* before the Cenomanian (Löser, 2005). Middle and Late Albian faunas with corals are less numerous in species and are dominated by solitary, most likely ahermatypic corals. Such faunas are mainly known

Species \ Stages	Barrem.		Aptian		Albian
	E.	Late	Early	Late	Early
<i>bukowinensis</i>			█	█	
<i>dupini</i>	█	█	█		
<i>elegans</i>			█		█
<i>nomikosi</i>				█	█
<i>octolobata</i>		█		█	

Figure 3. Stratigraphical distribution of *Holocystis* species. The thickness of lines corresponds to the number of different regions where the species were indicated.

from Texas (USA; Wells, 1933). Colonial coral faunas from the Middle to Late Albian are known from southern England (Jukes-Browne, 1900), southern India (Stoliczka, 1873), northern Spain (Reitner, 1987) and New Mexico (USA; Turnšek *et al.*, 2003). They do not contain *Holocystis*.

Palaeobiogeography

The genus is known from only three large regions: the central Tethys, the Caribbean and the southern Tethys (Figure 4). It is unknown from the Tibetan or Japanese faunas. There is no regular pattern in the palaeobiogeographic distribution of the genus. In the majority of the localities, two species co-occur, but there is no repeating combination pattern that could indicate that those two species are synonymous.

The occurrence of *Holocystis* in the New World seems problematic: it is restricted to two different levels (Late Barremian-Early Aptian Cerro de Oro Formation, Early Albian Cerro La Espina Member) within a geographic distance of less than one kilometre within one locality (Cerro de Oro) in Sonora, Mexico. There are numerous outcrops within the Cerro La Espina Member (Mural Limestone) with various coral faunas, but *Holocystis* could not be found in any of these faunas. A confusion of samples can be excluded, since samples were also collected recently

by the author. Both formations are well distinguished in a tectonically relatively calm region. Between both levels is a succession of clastic sediments with a time span of about five Ma. A local persistence –the only explanation of this phenomenon– of coral species over a relatively long time span is rarely observed due to the rarity of sections with a comparable (coral bearing) facies over such a long time period. Comparable situations where species persisted, although rare elsewhere, are known from the Early and Late Cenomanian (Dixon zone, Geslinianum zone; Löser, 1989) of Germany (*Colonicyathus geinitzi*, *Mesomorpha minima*, *Stylohelia granulata*), or from the Early and late Late Aptian of Spain (Schöllhorn, 1998; cf. *Comalia* sp., *Holocystis elegans*). In the latter region, again a *Holocystis* species persisted over a longer time span in the same region.

Palaeoecology

The genus occurred preferably in a siliclastic or at least siliclastic-influenced facies type. The type locality of *Holocystis elegans*, the Perna Beds of the Isle of Wright, is marked by sandstones and sandy clays. Localities in Greece are all in the Evangelistria conglomerates, a clastic sediment with coarse ophiolite pebbles as components. The material from Spain and Mexico occurs in argillaceous limestones. The material from Poland comes from conglomeratic sand-

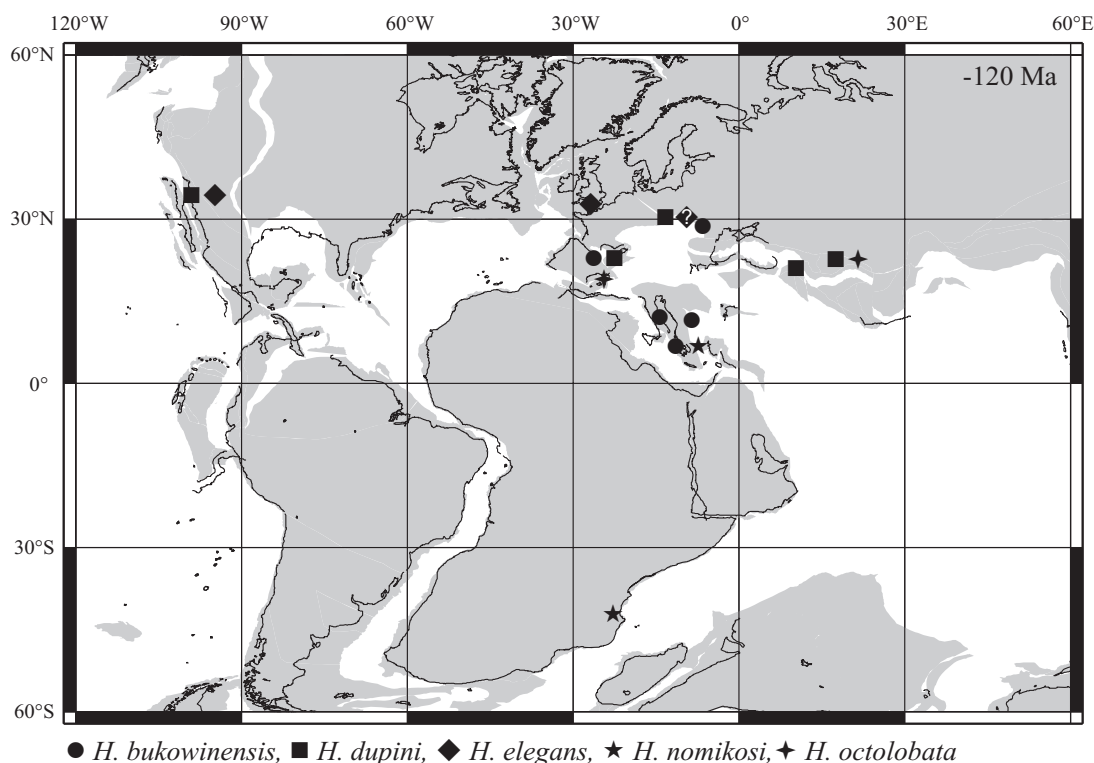


Figure 4. Palaeobiogeographic distribution of the various species of *Holocystis*. Plate tectonic reconstruction (120 Ma) with plates moved relative to the magnetic reference frame (created using the Advanced Plate Tectonic Reconstruction Service, Ocean Drilling Stratigraphic Network, <http://www.odsn.de>); present day shorelines in black, plate fragments in grey.

stones. The isolated colony from Tanzania shows a pale white colour but no attached sediment, and could therefore come from a carbonate facies. Samples from the same locality, for which an Urgonian facies was claimed by Dietrich (1926), show different matrix, such as limestones and sandstones. The unique specimen from Italy was found in carbonatic sediments. *Holocystis* can be found in localities poor in species (such as Can Grau in Spain, Atherfield in the United Kingdom) and in localities rich in species, such as the outcrops in Greece, Mexico, Poland, Romania, Serbia or the localities in Lérida (Spain). Where they occur, coral colonies of the genus are not rare. At least the outcrops in Aliartos (Greece), near Atherfield (United Kinddom), close to Montsec de Rubies (Spain), and in Sonora (Mexico) have yielded numerous specimens, whereas other species are less abundant.

Evolution

Traditionally, the suborder Stylinina is subdivided into three families: Stylinidae d’Orbigny, 1850, Cyathophoridae Vaughan and Wells, 1943, and Agatheliidae Beauvais and Beauvais, 1975. Other families based on genera currently assigned to the suborder Stylinina (such as Euheliidae, Pseudocoeniidae, Cladophylliidae, Stylosmiliidae) comprise only one genus, which would not be very helpful for classification. Whereas the Agatheliidae differ by their irregular septal symmetry and the formation of the coenosteum, the Stylinidae and Cyathophoridae are distinguished by the presence or absence of a columella. Auriculae are present in the Stylinidae, but in the Cyathophoridae they are generally (not always) absent. This feature can also be

linked to the presence of the columella. Members of the two families also differ in the size of their coenosteum (small in Cyathophoridae, large in Stylinidae), the number of costae (in Stylinidae they are often more numerous) and the wall formation (parathecal in Cyathophoridae, para-septothecal in Stylinidae).

Another concept for distinguishing the two families is put forward in Pandey *et al.* (2002) but not confirmed by appropriate type material and therefore doubtful. Both families comprise genera that form plocoid corals with a regular septal symmetry, using different systems (*Cryptocoenia*, *Holocystis*, *Pentacoenia*, *Pseudocoenia* in the Cyathophoridae; *Acanthocoenia*, *Enallhelia*, *Heliocoenia*, *Stylangia*, *Stylina* in the Stylinidae). In both families, corals may show a tetrameral, pentameral, hexameral, octomeral or decameral symmetry. Genera within the Cyathophoridae are traditionally distinguished by their symmetry, while in the Stylinidae all plocoid forms are referred to as *Enallhelia*, *Heliocoenia*, *Stylangia*, *Stylina*, depending on the growth form and the form of the columella. This does not apply, however, to *Acanthocoenia*, the genus with a columella and a pentameral symmetry.

Cyathophoridae and Stylinidae both originated in the Middle Jurassic (Lathuilière, 1989); their plocoid colonies show hexameral, octomeral and decameral symmetries (*e.g.*, Beauvais, 1964). Species older than Early Cretaceous with a tetrameral or pentameral symmetry are unknown in both families. Species with a pentameral symmetry suddenly appeared in both families in the Hauterivian, and those with a tetrameral symmetry in the Barremian (Figure 5). However, this experiment did not last long. In the Albian, the tetrameral and pentameral members disappeared in both families. The octomeral species became moreover

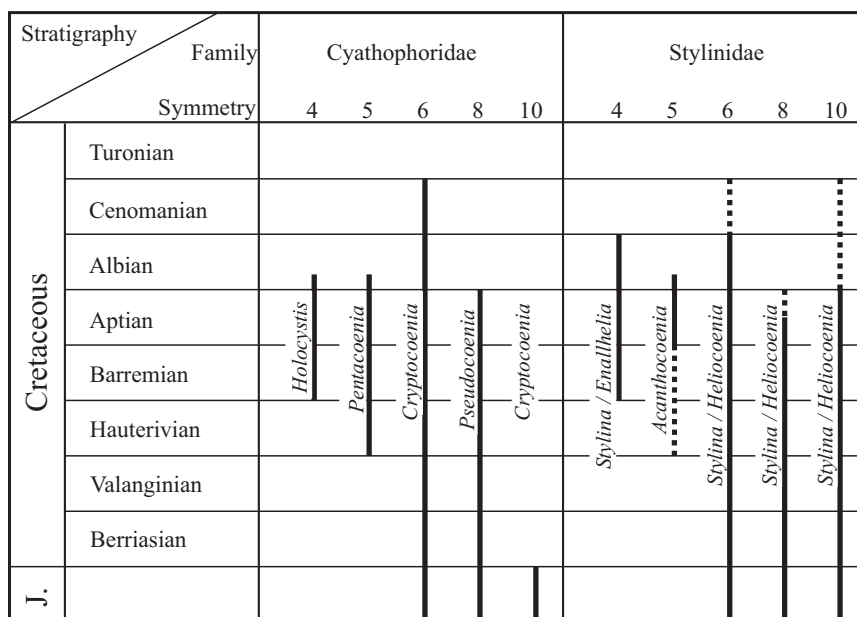


Figure 5. Ranges of genera of the Cyathophoridae and Stylinidae families.

extinct in both families at the end of the Aptian. With the exception of the decamerall forms, genera showing the same symmetry also died out in both families at the same time. In both families, species with a hexamerall symmetry are much more common than species with a septal symmetry not based on six, and pentamerall and tetramerall species are few and far between.

The formation of the columella is, at least in the Stylinidae, a constant feature. Though its form may vary within one colony between lamellar and styliform (making the distinction between *Heliocoenia* and *Stylinia* a rather vague one), its presence or absence is a stable characteristic. Species of Cyathophoridae and Stylinidae may occur together, but none of them have the same calicular diameter and the same number of septa, differing only in the presence or absence of the columella. The two families are considered two different phylogenetic lines.

The surprising parallelism in the sudden variation of the basic number of septal symmetry in the early Cretaceous Cyathophoridae and Stylinidae is not considered just an experiment but is thought to relate to environmental conditions. The growth form of the colony, the size of the calices, the septal perforation and the formation of pennulae have been thoroughly discussed as being indicators of environmental changes (e.g., Dupraz and Strasser, 2002; Sanders and Baron-Szabo, 2005), but changes in the septal symmetry as a possible reaction have been unknown up to now.

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