

## Did the silicoflagellate genus *Octactis* evolve from *Bachmannocena*?

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**Abstract:** It has long been assumed that *Octactis* and *Stephanocha* (previously known as *Distephanus*) are closely related. Both have apical rings, but with *Octactis* possessing an apical ring of larger diameter relative to the basal ring and made of thinner elements. However, closer examination of the basal rings and double skeletons (doublets) shows other differences that have received little attention. The location of the struts and pikes on each side of the Neogene *Stephanocha* basal ring are consistently rotated towards the basal corners. This establishes a distinct basal element between the struts and pikes that is tilted to form a zig-zag basal design that creates an interlocking of the doublet skeletons. The pikes project into the region of the paired skeleton and the apical ring is also rotated with respect to the basal ring. In contrast, *Octactis* has a flatter basal ring without pikes, and possesses strut attachments located midway between the corners with the doublet held together only by organic material.

Recent examination of living *Octactis* from the Seto Inland Sea of southern Japan provides a better understanding about the variability and structure of *Octactis* skeletons than previously available. Among these are double skeletons that have an incompletely formed daughter that consists only of the basal ring. The older literature includes line drawings that illustrate similar double skeletons, but these have not been previously photographed or adequately understood. Such skeletons are also found singly after disarticulation, and have a strong resemblance to those of fossil *Bachmannocena* (formerly known as *Mesocena*), which also has a flat basal ring lacking apical structures and pikes. The hypothesis that *Octactis* evolved from *Bachmannocena* rather than from *Stephanocha* is presented, with the possible evolution of an apical ring in *Bachmannocena* accounting for the differences between the skeletal morphologies of *Octactis* and *Stephanocha*.

**Keywords:** *Bachmannocena*; *Octactis*; silicoflagellates; *Stephanocha* (*Distephanus*)

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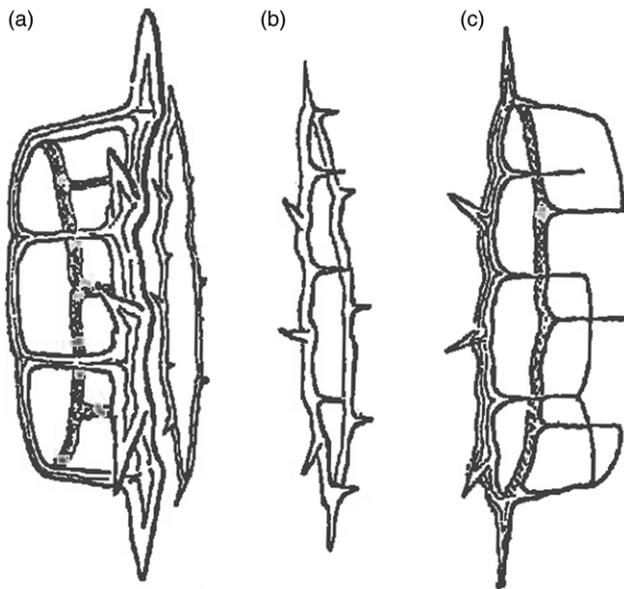
Hovasse (1932; Fig. 1 herein), Deflandre (1950, figs 18, 19, 21) and Gemeinhardt (1930, figs 16, 17) provided line-drawing illustrations of *Octactis* skeletons that had either incomplete apical rings or lacked apical structures altogether. These skeletons occurred singly or as incomplete daughter skeletons of a doublet. We have recently observed and photographed similar specimens. These bear a general resemblance to fossil *Bachmannocena* and may suggest a closer affinity between the two genera than previously thought. *Octactis* has to this point in time been considered to be more closely associated with silicoflagellates that possess an apical structure.

Some biologists place all the modern skeleton-bearing silicoflagellates in a single genus, *Dictyocha* Ehrenberg (e.g. Moestrup & Thomsen 1990; Henriksen *et al.* 1993; Chang 2015), whilst other biologists and all palaeontologists separate these into two or three genera based on skeletal morphology (e.g. Malinverno 2010; Rigual-Hernández *et al.* 2010; McCartney *et al.* 2015). The generally four-sided *Dictyocha* Ehrenberg has an apical bridge and is most abundant in lower latitudes. The apically-ringed and usually six-sided *Stephanocha* McCartney & Jordan (which replaces the invalid *Distephanus* Stöhr; Jordan & McCartney 2015) predominates closer to the poles. The third group is the less well-studied eight-sided *Octactis* Schiller that also has apical rings and is observed in coastal regions (Abe *et al.* 2015).

A recent phylogenetic tree of the Dictyochophyceae included three silicoflagellate species (*D. fibula* Ehrenberg, *D. speculum* Ehrenberg, *D. octonaria* Ehrenberg), as well as a closely related naked taxon, *Vicicitus globosa* (Hara & Chihara) Chang, in a single clade (Chang *et al.* 2012). While this confirms that the modern

silicoflagellates are a monophyletic group, there were genetic, ultrastructural and pigment composition differences between *D. fibula* and the other two silicoflagellate species, which could be interpreted as evidence supporting a genus-level separation of *Dictyocha* from *Stephanocha/Octactis*. Although Chang *et al.* (2012) did not illustrate *D. octonaria* in their paper, a photograph of a skeleton from this study (Chang, pers. comm. April 2014) suggests that the culture can be identified as *Octactis pulchra* Schiller, but greater study is needed on the distinctions between *O. pulchra* and *D. octonaria*. Various data suggest that the *D. octonaria* and *D. speculum* studied by Chang *et al.* (2012) represented separate taxa, and small subunit (SSU) rDNA data suggest that *D. octonaria* may be distinguished from both *D. speculum* and *D. fibula* (see Chang 2015).

Thus, the status of *Octactis* is still controversial, with some workers synonymizing *Octactis* with *Distephanus* (now *Stephanocha*), due to the possession of the shared character, the apical ring (e.g. Ling & Takahashi 1985; Dumitrica 2014). However, the construction of the apical ring appears to be different, which has resulted in the continued use of separate genera, particularly among palaeontologists. *Stephanocha* has more robust apical elements with struts that generally slope towards a relatively small apical window, while the struts of *Octactis* taper distally away from the basal ring and trend more steeply to support a fragile apical ring made of thin elements (Fig. 2:1). The *Octactis* morphology developed in the late Miocene to Pliocene (McCartney *et al.* 1995) and thus has neither the long geological record nor the diversity of the other two genera, which diverged during the Eocene (McCartney *et al.* 2015).



**Fig. 1.** Reprint of illustrations from Hovasse (1932) showing *Octactis* with incomplete daughter skeletons. (a) Double skeleton with the daughter (right) consisting only of an apical ring. (b) Isolated daughter skeleton that lacks apical structure. (c) Single *Octactis* skeleton that has an incomplete apical structure. No scale provided in the original illustration.

Discussion on the relationship between *Stephanocha* (as *Distephanus*) and *Octactis* has focused on the apical ring. Bukry (1982) observed that thin apical elements also occur on *Distephanus speculum* subsp. *tenuis* Bukry, which has been used as a biostratigraphic marker for the equatorial late Miocene (McCartney *et al.* 1995). This led Ling & Takahashi (1985) to conclude that *Octactis* should be included in *Distephanus* since they both possess a similar apical structure. Some workers (McCartney *et al.* 1995; Onodera & Takahashi 2007; Takahashi *et al.* 2009) use *Distephanus pulchra* (Schiller) Ling & Takahashi, while others (Barron & Bukry 2007; Rigual-Hernández *et al.* 2010; Martínez-López *et al.* 2012; McCartney *et al.* 2014b) have continued to favour *Octactis pulchra*. In what follows, we will consistently refer to the replacement taxon *Stephanocha*.

A recent study of modern silicoflagellate double skeletons (McCartney *et al.* 2014b) showed pronounced differences in the basal structures of *Stephanocha* and *Octactis*. Neogene skeletons of both *Dictyocha* and *Stephanocha* show a sinistral rotation of the apical structure when seen from apical view, with the strut attachment positions on each basal side moved to the left towards one corner and the pikes towards the right corner. These movements break each basal side into three elements, two of which connect the corners to the strut and pike positions. The medial basal element (this term is formally defined in McCartney & Witkowski, 2016) connects the triple-junctions that include a strut or pike. These elements trend apically towards the strut attachment and abapically towards the pike to produce a zig-zag design on each basal side when viewed laterally (McCartney *et al.* 2014b). This design, in combination with the prominent pike, appears to keep the two skeletons of the doublet in place during the divisional process (Moestrup & Thomsen 1990; McCartney *et al.* 2014b).

*Octactis* does not have these features. The strut attachment positions are located midway between the corners so that each basal side has only two elements that connect the strut attachment to adjacent basal corners. The *Octactis* basal ring has a much flatter appearance than that of *Stephanocha*, and also lacks pikes. These differences led McCartney *et al.* (2014b) to suggest that *Octactis* and *Stephanocha* should remain in separate genera and to reject a proposal by Dumitrica (2014) that *Octactis* should replace the

invalid *Distephanus* (Jordan & McCartney 2015). The photographs used in the McCartney *et al.* (2014b) study also led Abe *et al.* (2015) to examine *Octactis* and its double skeletons more closely. As a result of these two studies we now realize that some incompletely formed skeletons of *Octactis pulchra* have similarities to another genus, *Bachmannocena* Bukry. The aims of this paper are to investigate the relationship between these two genera and to discuss the potential consequences for silicoflagellate evolution.

## Materials and methods

The *Octactis* specimens examined in this study come from the Seto Inland Sea, located between Honshu, Shikoku and Kyushu islands in southern Japan. The sea surface water samples were collected during the Bosei-maru Cruise (26 April 2008–2 May 2008) of the Department of Ocean Science, Tokai University, in collaboration with Yamagata University. Information concerning the geographical locations and ecological conditions in which these were collected are presented in a separate study (Abe *et al.* 2015). Details on the preparation of the samples for study in the scanning electron microscope (SEM) and of SEM micrographs are described in Abe *et al.* (2015) and also included in the supplementary material in McCartney *et al.* (2014b). For definitions and illustrations of the silicoflagellate descriptive terminology used in this study, see McCartney & Witkowski (2016).

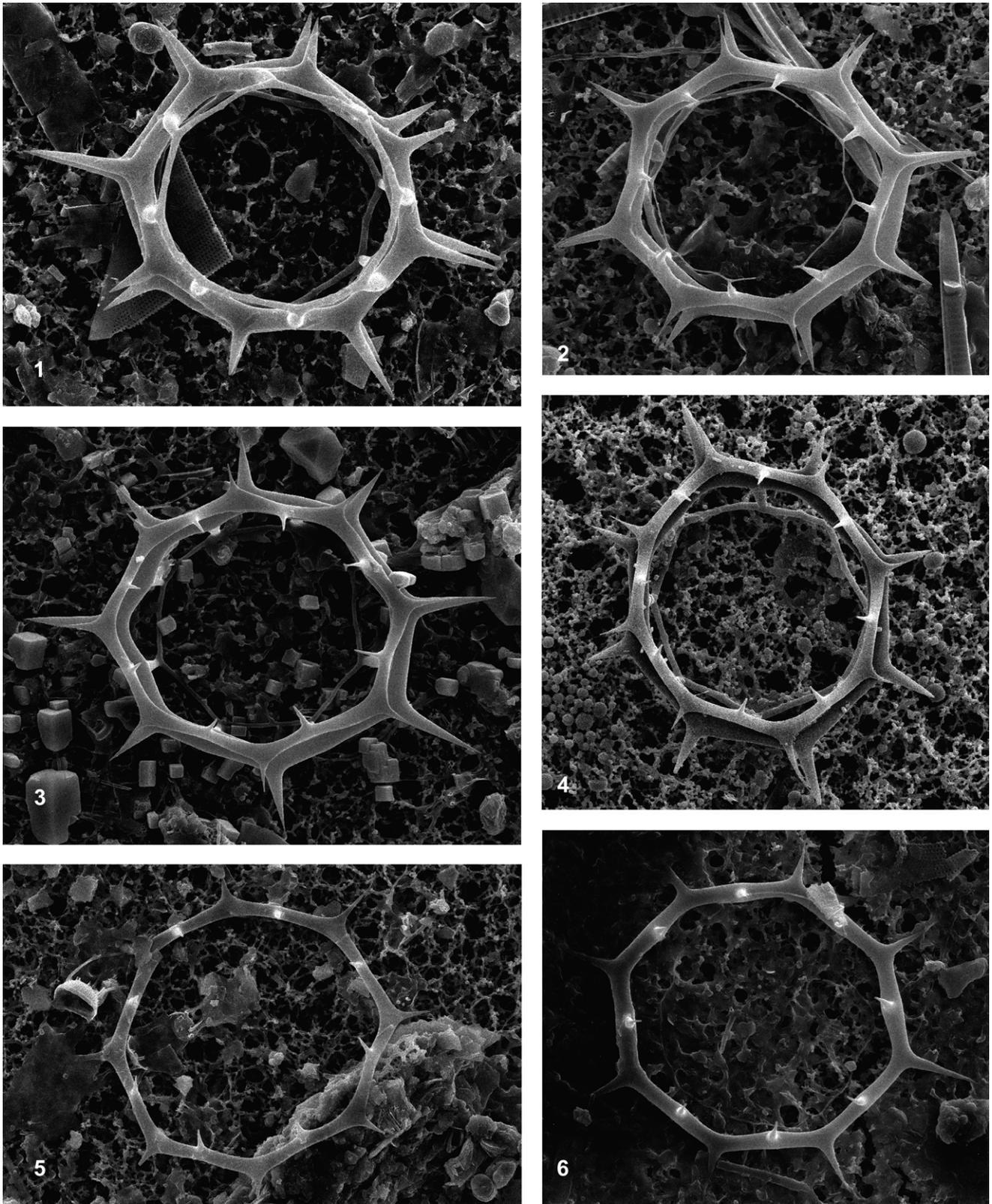
## Results and discussion

### *Octactis* doublets with daughter skeletons that lack an apical structure

Of 256 *Octactis* specimens observed from the Seto Inland Sea by Abe *et al.* (2015), 70 were double skeletons (Figs 2:1, 2:2, 2:3 and 2:4). The specimens were identified as belonging to two taxa, *O. pulchra* var. *pulchra* Schiller, which predominated in the Seto Inland Sea and *O. pulchra* var. *takahashii* McCartney, Abe & Jordan, which has a more fragile appearance with longer spines, and predominated in lower abundances in the less nutrient-rich water of the Kuroshio, SE of Shikoku Island. The *O. pulchra* var. *pulchra* skeletal morphology is by far the better known and occurs in coastal areas and inlets such as the Gulf of California (Murray & Schrader 1983; Martínez-López *et al.* 2012) and Adriatic Sea (Rigual-Hernández *et al.* 2010), and has been observed off the coast of Panama (Takahashi 1991). This variety is also known from deep ocean sediments of the equatorial Pacific Ocean (e.g. Bukry & Foster 1973; Bukry 1983; McCartney *et al.* 1995) and is the subject of all the *Octactis* photographs included in this study.

Usually the double skeletons observed from the Seto Inland Sea were slightly disarticulated and lay flat upon the apical ring of the distal paired skeleton (thus, the pair is in apical axis view, see McCartney *et al.* 2014b). When single skeletons are seen in apical or abapical view, the basal sides appear to be linear with all sides being in a basal plane, but when double skeletons are viewed obliquely, the sides are observed to slightly arch apically so that there is a gap between the strut attachments of the paired skeletons (McCartney *et al.* 2014b). The basal spines are relatively thick near the basal ring and taper distally without being in contact with the paired basal spine. Thus, the main points of contact between the two members of a double skeleton are at the abbasal surfaces of the basal corners (Abe *et al.* 2015).

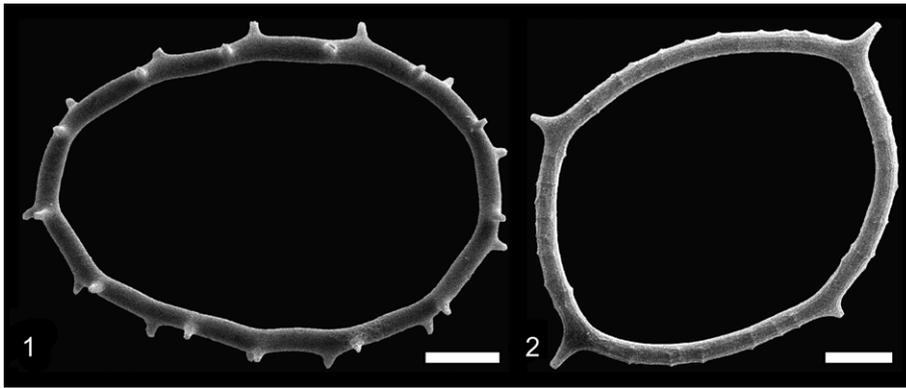
In a recent study of a culture of *Octactis pulchra* (identified as *Dictyocha octonaria*), skeleton-bearing cells were shown to discard their parent skeleton before dividing into two daughter cells and forming new skeletons (Chang 2015). Thus, double skeletons were presumed to be the result of a failed separation of the two daughter cells. However, it is possible that two scenarios exist for double



**Fig. 2.** Scanning electron microscope photographs of *Octactis pulchra* var. *pulchra* (scale bar 10  $\mu$ m). **1.** Double skeleton, apical axis view, sample Seto-49. **2.** Double skeleton, with daughter skeleton in forefront, apical axis view, sample Seto-65. **3.** Double skeleton, with daughter skeleton in forefront lacking an apical ring, apical axis view, sample Seto-51. **4.** Double skeleton, with daughter skeleton in forefront lacking an apical ring, apical axis view, sample Seto-59. **5.** Single skeleton, a daughter specimen lacking an apical ring, sample Seto-49. **6.** Single skeleton, a daughter specimen lacking an apical ring, sample Seto-43.

skeletons, whereby (1) the parent skeleton fails to be discarded and is adopted by one of the daughter cells, with the other daughter

skeleton is discarded and the two daughter cells fail to separate, but have identical skeletons. Both of these scenarios may occur, as seen in the dataset of [Abe \*et al.\* \(2015\)](#).



**Fig. 3.** Scanning electron microscope photographs of *Bachmannocena* (scale bar 10 µm) from Moron, Spain (middle or late Miocene): **1.** *Bachmannocena circulus* (Ehrenberg) Bukry; **2.** *B. quadrangula* (Ehrenberg ex Haeckel) Bukry.

Many of the double skeletons observed by Abe *et al.* (2015) consist of two essentially equivalent skeletons, although the daughter skeleton can sometimes be identified by the possession of thinner basal elements, shorter spines (Fig. 2:2), or thinner apical ring elements, compared to the other (mother) skeleton. However, those double skeletons most relevant to this paper are examples that show incomplete formation of the daughter skeleton, which in some cases consists only of a basal ring, with short terminated struts and no apical ring (Fig. 2:3 and 2:4). These daughter basal ring skeletons that lack an apical ring may also be found singly (Fig. 2:5 and 2:6). While aberrant (teratoid) double skeletons are known (McCartney *et al.* 2014a), an absent apical ring is not a common aberrant morphology (see McCartney & Wise 1990). The doublets have less well-developed basal spines on the skeleton with an absent basal ring, which suggests that this is an incompletely formed daughter rather than an aberrant.

The member of the double skeleton pair that lacks an apical ring could simply be the result of death that occurred prior to the formation of the second apical ring. However, such basal rings that lack apical structures have not been generally observed for species of either *Dictyochoa* or *Stephanocha*, which suggests that *Octactis* may not be directly related to other late Cenozoic or modern silicoflagellates that possess apical structures. Significant numbers of *S. speculum* subsp. *tenuis* specimens were observed by McCartney *et al.* (1995), without the observed presence of basal rings that lacked structures, although it should be mentioned that there was no reason at the time to be looking for these. Plainly, the assumption by both biologists and palaeontologists that *Octactis* and *Stephanocha* are closely related is now in question.

### **The similarity in skeletal morphology of *Bachmannocena* and *Octactis***

*Bachmannocena* (synonym *Mesocena* Ehrenberg), characterized by possessing skeletons that lack an apical structure, is possibly a polyphyletic genus in the Cenozoic (Gleser 1966, p. 233; Perch-Nielsen 1975), which has a long geological history that first appears near the Paleocene/Eocene boundary (McCartney & Witkowski, unpublished data). Basal-ringed species that lack apical structures are also associated with Cretaceous *Arctyochoa* Bukry (McCartney *et al.* 2011). The term ‘mesocenid’ is still applied to skeletal morphologies that consist only of a basal structure of three to many sides, generally with spines on the corners (e.g. Perch-Nielsen 1975; Bukry 1978; McCartney *et al.* 1995). There are also round- to oval-shaped morphologies, often with two spines on the major axis (*B. diodon* (Ehrenberg) Bukry), but which can have zero to many basal spines, sometimes not parallel to the basal plane.

There is a record of mesocenid silicoflagellates that have apical structures and vice versa. Some authors (e.g. Gemeinhardt 1930; Yanagisawa 1943; Tsumura 1963) have observed seven- and eight-sided skeletons that lacked an apical ring and placed these in

*Mesocena polymorpha* Lemmermann. These were associated with skeletal morphologies of similar basal morphology that included apical rings that were identified as varieties of *Distephanus speculum*. McCartney *et al.* (1995; see also Bukry 1982) noted variants of *Bachmannocena diodon* subsp. *nodosa* (Bukry) Bukry in the late Miocene that had an apical bridge and Bukry (1983, pl. 9, figs 9–11) has illustrated variants of *B. quadrangula* that have a bridge across one of the basal corners. Dumitrică (1973) has illustrated mesocenid forms of *Dictyochoa fibula* Ehrenberg and has also noted similarities between the many-sided *Stephanocha polyactis* and large mesocenid morphologies that occur in the same sediments (see also Frenguelli 1940, fig. 7f–g).

It has been generally assumed that *Stephanocha* and *Octactis* are directly related evolutionarily, since both have apical rings, and both genera have been placed in the family Distephanaceae Locker (Prema 1996; Thronsdon 1997). The unusual incomplete daughter skeletons that are often part of doublets in the Seto Inland Sea provide an alternative explanation for the origin of *Octactis*. The remarkable aspect of these is that the daughter skeletons may consist only of a basal ring and suggests that this ring is completed prior to any development of the apical structure. Occurrences of isolated basal rings similar to co-occurring *Stephanocha* appear to be more rare, either as part of double skeletons or individually. This may suggest a different ontogenetic sequence for *Stephanocha* by which the basal and apical structures form at more nearly the same time.

There are several candidate species for a *Bachmannocena* ancestor that have overlapping geological ranges with *Octactis pulchra*. *Bachmannocena circulus* (Ehrenberg) Bukry (Fig. 3:1 herein) is quite variable with a generally circular ring with short spines (see Bukry 1979, pl. 6, figs 1–2; 1980, pl. 7, figs 5–7; Perch-Nielsen 1975, pl. 11, fig. 12). Bukry & Foster (1973) and Bukry (1976, 1983) observed that *B. circulus* consistently occurs in the early to late Pliocene of the Panama Basin, eastern tropical Pacific. Bukry (1979) has noted mid-latitude occurrences as high as the Pliocene–Pleistocene boundary and McCartney *et al.* (1995) have observed rare occurrences as late as the Pleistocene. Alternative ancestors that have polygonal basal rings with more pronounced spines include *B. dumitricae* (Perch-Nielsen 1975, pl. 11, figs 1, 5–8) and *B. quadrangula* (Ehrenberg ex Haeckel) Bukry (Fig. 3:2 herein), which has a more consistent shape with four basal sides and prominent corner spines (see Bukry 1980, pl. 7, figs 9–17; 1983, pl. 8, figs 8–10). *B. dumitricae* is observed in the late Miocene to Pliocene of Site 278 (Perch-Nielsen 1975) and *B. quadrangula* is a biostratigraphic marker in the Pleistocene (Bukry 1985; McCartney *et al.* 1995). There have been scattered reports of the genus in the Recent (Deflandre 1950, fig. 22; Thronsdon 1997) although no recent reports or photographs are known.

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