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SYNONYMY OF DINOFLAGELLATES WITH BASKET-LIKE ENDOSKELETONS: *Monaster*, *Amphilothus* AND *Achradina* (AMPHILOTHALES, DINOPHYCEAE)

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ABSTRACT. The basket-like skeleton-bearing dinoflagellates have been divided into three genera: the little-known *Monaster* as having a skeleton with longitudinal ribs in the epitheca, *Amphilothus* with a dense and geometric skeletal tessellation in the epitheca, and *Achradina* with characteristics intermediate between the other two genera. Cells of different sizes and morphologies corresponding to these genera co-occurred within the same samples from the Mediterranean Sea and South Atlantic Ocean. During cell division, a bigger daughter cell kept the endoskeleton, while the smaller daughter cell formed a new skeleton, beginning with the formation of the hypotheca. The different degree of maturation of the skeleton explained the great intraspecific variability in skeletal morphology. These forms share a distinctive crest-like apical structure with several internal radiating slits. These evidences indicate that the genus *Monaster* corresponds to immature cells with incomplete developed endoskeleton in the epitheca; *Amphilothus* corresponds to the mature cells with more developed epithecal endoskeleton, while *Achradina* shows intermediate morphologies and it is the most common form in the plankton samples. The genera *Achradina*, *Amphilothus* and *Monaster* correspond to a single species, with the name *Monaster rete* having priority.

Keywords: *Amphitholus*, Brazil, Dinoflagellata, Mediterranean Sea, morphological variability, skeleton, South Atlantic Ocean

Sinonimia de dinoflagelados con endoesqueletos en forma de cesta: *Monaster*, *Amphilothus* y *Achradina* (Amphilothales, Dinophyceae)

RESUMEN. Los dinoflagelados caracterizados por endoesqueletos en forma de cesta se han agrupado en tres géneros: *Monaster*, poco conocido y con un esqueleto con arcos longitudinales en la epitheca, *Amphilothus* con el esqueleto de la epiteca densa y geométricamente teselado, y *Achradina* con características intermedias entre los otros dos géneros. Células de diferentes tamaños y morfologías correspondientes a estos géneros coocurren en muestras recolectadas del Mar Mediterráneo y el Océano Atlántico Sur. Durante la división celular, una de las células hija es más grande y mantiene el esqueleto de la célula madre, mientras que la otra célula hija es más pequeña y crea un nuevo esqueleto, comenzando con la formación de la hipoteca. El diferente grado de maduración explica la gran variabilidad en la morfología del esqueleto que se ha observado. Estas formas comparten una distintiva estructura apical en forma de cresta con varias aberturas radiales. Estas evidencias indican que el género *Monaster* corresponde a células inmaduras con un endoesqueleto incompletamente desarrollado en la epitheca, *Amphilothus* corresponde a células maduras con el endoesqueleto de la epitheca más desarrollado, mientras que *Achradina* es la forma más frecuente en las muestras de plancton y engloba a células con una morfología intermedia entre los otros dos géneros. Estas observaciones sugieren que los géneros *Achradina, Amphilothus* y *Monaster* corresponden a una sola especie, con prioridad para el nombre *Monaster rete*.

Palabras clave: *Amphitholus*, Brasil, Dinoflagellata, Mar Mediterráneo, variabilidad morfológica, esqueleto, Océano Atlántico Sur

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INTRODUCTION

Only a handful of dinoflagellates species with skeletal element are known. Heterotrophic dinoflagellates with a basket-like skeleton of variable morphology have been described under the genera *Monaster* F. Schütt, *Amphilothus* Kofoid *ex* Poche and *Achradina* Lohmann (Schütt, 1895; Lohmann, 1903, 1919; Nival, 1969; Sournia, 1986; Fensome *et al*., 1993; Hernández-Becerril and Bravo-Sierra, 2004).

Schütt (1895) described *Monaster rete* and *Amphilothus elegans* as having an identical skeletal meshwork in the hypotheca and a pointed antapex or antapical spine. Later Lohmann (1903, 1919) described the genus *Achradina* with four species, the type *A. pulchra* and *Achradina angusta*, *A. reticulata* and *A. sulcata*. The shape and skeletal meshwork of the hypothecae of *Monaster*, *Amphilothus* and *Achradina* were similar. The differences between *Monaster rete*, *Amphilothus* spp. and *Achradina* spp. were based on the morphology of the epitheca. The skeleton of the epitheca of *Monaster rete* was composed of several longitudinal ribs that converged at the apex. These ribs were illustrated in *Achradina sulcata*; they also occurred in the hypotheca of *Achradina pulchra*, and less notably in the epitheca of *Amphilothus quincuncialis* Kofoid. Schütt (1895) emphasized the longitudinal ribs in the epitheca of *Monaster*, which are typically illustrated in *Achradina*. The epitheca of *Amphilothus elegans* was illustrated as having a honeycomb-like surface in the form of regular hexagons with large internal circles.

The instraspecific variability of dinoflagellates was little known over a century ago when these

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species were described. Consequently, different morphotypes or life stages of a single species were often described as new species. In the case of delicate forms (e.g., *Monaster rete*, *Amphilothus* spp. and *Achradina* spp.), the cells easily lyse and the description could have been based on deteriorated or distorted cells. If the description is based on the endoskeleton, we must keep in mind that dissolution of the skeleton-forming minerals begins immediately after cell death, and so the skeletons described may have been partially dissolved. Moreover, given that one of the daughter cells regenerates a new endoskeleton, different stages in skeleton development may have been recorded. Nival (1969) considered the last three species of *Achradina* as forms of the type, *A. pulchra*, and proposed other new forms based on the high morphological variability of the endoskeletons. Sournia (1986) considered *Monaster* and *Amphilothus* as synonyms. See Appendix (supplementary information) for an account of the taxonomy, nomenclature and synonymy.

MATERIALS AND METHODS

The morphologies of *Monaster*, *Amphilothus* and *Achradina* were examined from live samples collected from the Mediterranean Sea and the South Atlantic Ocean as described in Gómez *et al*. (2016).

RESULTS

Between 2007 and 2011, cells of *Monaster*, *Amphilothus* and *Achradina* were occasionally encountered during the observations of live phytoplankton samples from the sea off Marseilles (Figs. 1–3), Banyuls-sur-Mer (Figs. 4–11) and Villefranche-sur-Mer (Figs. 12–14), and rarely also in the Lugol-fixed samples collected from the open Mediterranean Sea based on Lugol's preserved samples (Fig. 15). There is no doubt that these cells possessed an endoskeleton because it is surrounded by the cell covering. The cell covering is highly delicate and easily lysed during the stress of capture and observation (Figs. 7–8). The endoskeleton was close to the cell covering near the apex and antapex, and often well separated from the cell covering at the level of the cingulum level (Figs. 3, 6–7). Although the skeleton is internal, the observations of cells devoid of the cell covering may induce to consider that the skeleton is external (Fig. 8).

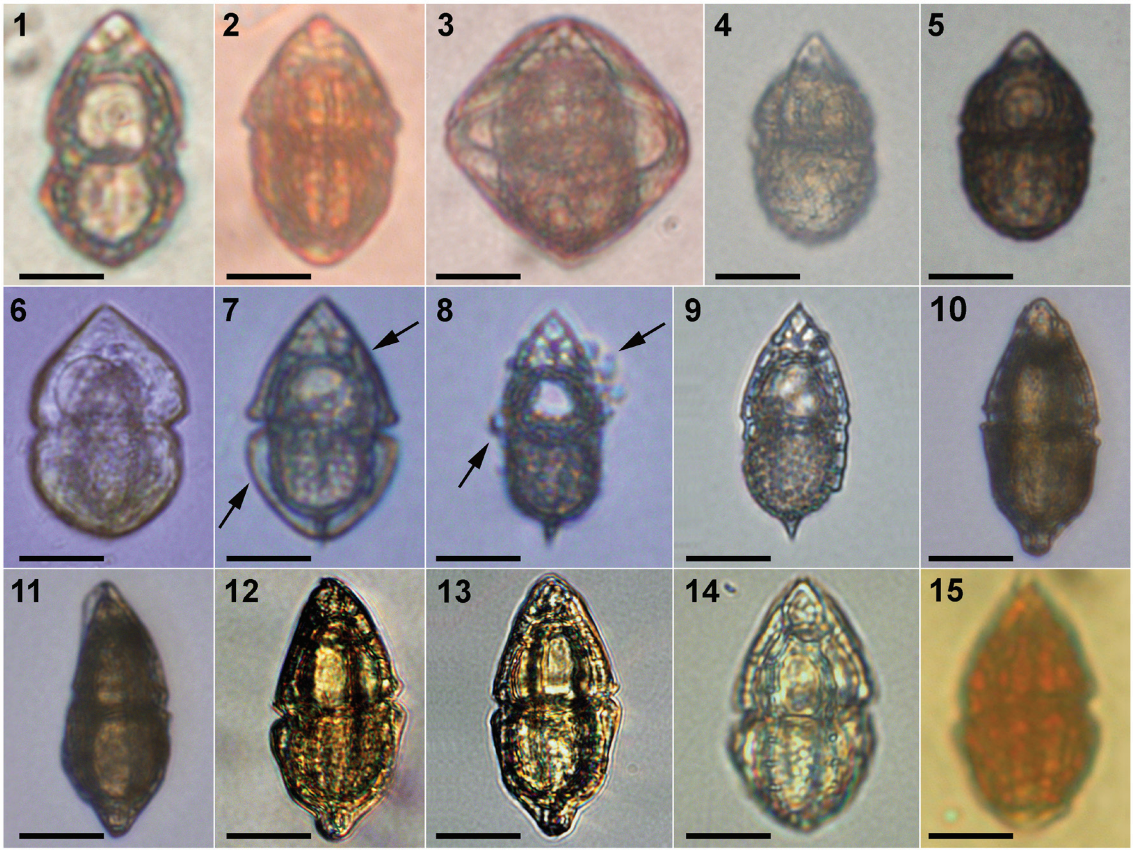
Cells were more common in the samples from offshore Brazil (Figs. 16–39) where sometimes several tens of cells occurred in the same plankton sample. It is common to find cells of different sizes and morphologies corresponding to all these genera in the same sample and sometimes cells under division. The cells were constricted by a well-marked, slightly anterior planar cingulum, with clearly determined epitheca and hypotheca (Figs. 16–39). The outline of the hypotheca tended to be rounder, while the epitheca was conical with a more or less pointed apex. However, it was not possible to determine the location of the flagellar pores, the sulcal groove, the ends of the cingulum, or other structures that could be used to establish the cell's ventral and dorsal surfaces. The cell covering showed different morphologies and usually lysed (Figs. 19–21). The degree of development of the endoskeleton is highly variable (Figs. 16–39). The most common morphology corresponded to forms known as *Achradina* with a characteristic distinctive crest-like structure with several internal radiating slits (Figs. 5–8, 16–23). The little-known *Monaster* was an immature form with an incomplete developed epitheca, with longitudinal ribs in the epitheca (Figs. 9–14, 24–27). In some cells, the distinctive crest-like apical structure was already visible (Figs. 9, 26). These forms known as *Amphilothus* corresponded to mature cells with a dense and geometric skeletal tessellation in the epitheca (Figs. 4–5, 28–30), also including the crest-like apical structure (Fig. 4).

In recently divided cells, the two daughter cells showed different morphologies, with one daughter cell slightly smaller and showing a less-developed endoskeleton (Figs. 31–39). During cell division, two daughter cells of different size and shape were joined. The bigger daughter cell kept the endoskeleton, while the smaller daughter cell showed lesser developed the endoskeleton, especially in the epitheca (Figs. 31–39). These observations showed that one of the daughter cells has to regenerate a new skeleton after each division, explaining the great intraspecific variability in skeletal development and the different sizes (Figs. 37–39).

DISCUSSION

The dinoflagellates with a basket-like skeleton (*Monaster*, *Amphilothu*s and *Achradina*) have remained a mystery for more than a century (Sournia, 1986; Fensome *et al*., 1993). The delicate cells easily lysed and the endoskeleton readily dissolved after cell death. During cell division, one of the daughter cells retained the old endoskeleton, while the other daughter cell regenerated a new one (Figs. 31–39). The morphological variability of the skeletons is due partly to the natural maturation along the life cycle of the cell, and partly due to the artificial partial dissolution of the skeleton after cell death.

Appendix reproduces the descriptions of the basket-like skeleton-bearing dinoflagellates. *Monaster*, *Amphilothus* and *Achradina* showed identical cell shape, similar shape and ornamentation of the hypotheca, a well-marked cingulum, and no visible sulcus. The morphology of the epitheca was the main difference among the genera. In the earlier description, Schütt (1895) over-emphasized the epithecal longitudinal ribs in *Monaster* and the epithecal honeycomb tessellation in *Amphilothus.* The later descriptions of *Achradina* species were more detailed and corresponded to the more common appearance of the cells (Lohmann, 1903, 1919). Consequently,



Figures 1–15. Light microscopy images of live cells of *Monaster* (=*Amphilothus*, *Achradina*) from the northwestern Mediterranean Sea at Marseilles (**1–3**), Banyuls-sur-Mer (**4–11**), Villefranche-sur-Mer (**12–14**) and a Lugol-fixed cell collected off Minorca (**15**). *Achradina* (**1–3, 6–9, 15**), *Amphilothus* (**4–5**) and *Monaster* (**12–14**). **7–9.** The arrow points the cell covering before and after lysis. Scale bar 20 µm.

further records have been ascribed to *Achradina*, while *Monaster* and *Amphilothus* disappeared from the literature (Appendix). The observations suggested that *Monaster* and *Amphilothus* represented morphological variants of *Achradina*. The observed morphological variability, even between daughter cells, showed that we are dealing with a single species. These three genera should be considered synonyms, with *Monaster* as the senior name (see Appendix).

The synonymy is updated as follows:

Order Amphilothales (Kofoid & Swezy 1921) Lindemann 1928

Family Amphilothaceae Lindemann 1928, p. 68.

Genus *Monaster* F. Schütt 1895 (non *Monaster* Etheridge Jr. 1892, a fossil starfish).

Generic synonyms: ‘*Amphitholus*’ F. Schütt 1895 *nom. rej.* pro *Amphilothus* Kofoid *ex* Poche, *Achradina* Lohmann 1903, *Amphilothus* Kofoid 1907 *ex* Poche 1913

Type species: *Monaster rete* F. Schütt 1895.

Synonyms of the type: *Achradina pulchra* Lohmann 1903, *A. pulchra* f. *aciculata* Nival 1969, *A. pulchra* f. *angustata* (Lohmann) Nival 1969, *A. pulchra* f. *nervosa* Nival 1969, *A. pulchra* f. *reticulata* (Lohmann) Nival 1969, *A. pulchra* f. *truncata* Nival 1969, *A. pulchra* f. *spatulata* Nival 1969, *A. pulchra* f. *sulcata* (Lohmann) Nival 1969, *Amphilothus quincuncialis* (Kofoid 1907) Poche 1913 (=*Amphitholus quincuncialis* Kofoid in Kofoid and Michener 1911), *Achradina angusta* Lohmann 1919, *A. reticulata* Lohmann 1919, *A. sulcata* Lohmann 1919, *Amphilothus elegans* (F. Schütt 1895) Er. Lindemann 1928 (= ‘*Amphitholus*’ *elegans* F. Schütt).

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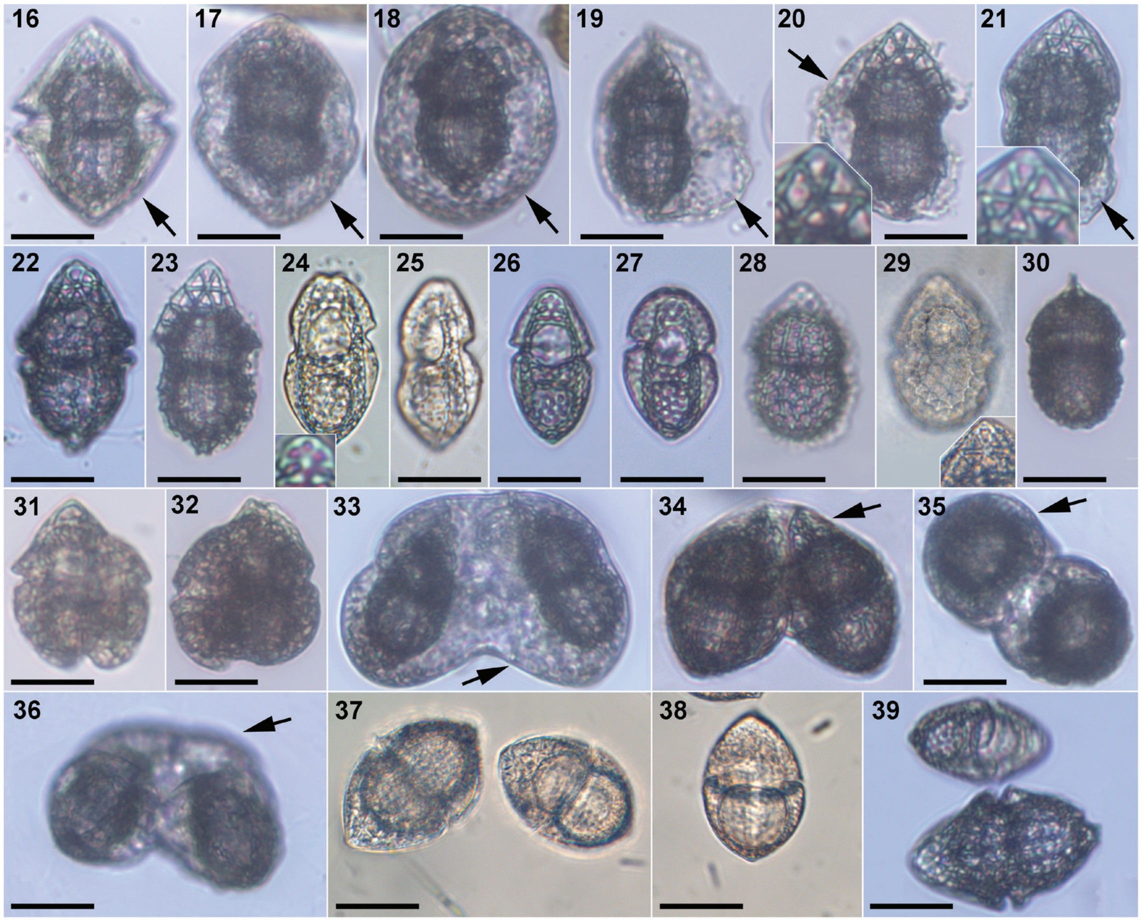

Figures 16–39. Light microscopy images of live cells of *Monaster* (=*Amphilothus*, *Achradina*) from the São Sebastião Channel, São Paulo State, Brazil. **16–23.** *Achradina*. **24–27.** *Monaster.* **28–30.** *Amphilothus*. **31–39.** Cells during and after division. **16–21, 33–36.** The arrow points the cell covering. The insets show the apical crest. Scale bar 20 µm.

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APPENDIX

TAXONOMY, NOMENCLATURE AND SYNONYMY OF *Monaster rete*, *Amphilothus* spp. AND *Achradina* spp.

ORIGINAL DESCRIPTIONS

The dinoflagellate *Actiniscus pentasterias* (Ehrenb.) Ehrenb. was first described as a fossil skeleton and classified as a silicoflagellate until Schütt (1891) observed the gymnodinioid morphology of its living cells. Later Schütt (1895) observed dinoflagellates with other type of endoskeleton and described *Monaster rete* F. Schütt and '*Amphitholus*' *elegans* F. Schütt from the Atlantic Ocean or the Gulf of Naples. Kofoid (1907) described *Amphilothus quincuncialis* Kofoid from Panama. Lohmann (1903) described *Achradina pulchra* from the Atlantic Ocean and from the Mediterranean off Sicily, and later *Achradina angusta* Lohmann from the equatorial Atlantic Ocean, *Achradina reticulata* Lohmann from the Gulf Stream in the Atlantic Ocean, and *Achradina sulcata* Lohmann from off Brazil (Lohmann, 1919). The original line drawings are reported in figure 1. Nival (1969) considered the last three species as forms of the type, *Achradina pulchra*, and proposed other new forms based on the high morphological variability of the endoskeletons (Fig. 2).

Schütt (1895) described numerous delicate unarmoured dinoflagellates that are usually too distorted or lost under fixation techniques routinely employed by planktologists. Schütt (1895) did not report the type locality of his new species. The original illustration of *Monaster* showed a cell with one flagellum, an organelle rarely preserved in fixed material. Schütt observed live plankton from the Gulf of Naples. Consequently, the Gulf of Naples could be the type locality of *Monaster* and *Amphilothus*. Lohmann developed methods to collect and concentrate plankton in a gentle fashion. The name *Achradina* derives from that of the coastal district around the city of Syracuse, Sicily. Lohmann (1903) observed live plankton off Syracuse, not far from Naples. Kofoid (1907) described numerous new species of thecate dinoflagellates from a cruise in the open Pacific Ocean. However, Kofoid (1907) did not describe *Amphilothus quincuncialis* from the preserved net samples collected in the open ocean, but from material collected when the ship was anchored off Panama City. Nival (1969) studied the intraspecific variability of the skeletons based on fresh material collected in the Bay of Villefranche-sur-Mer (Fig. 2). All these studies shared a common pattern: *Monaster*, *Amphilothus* and *Achradina* are observed from fresh, unpreserved material, rather than from formaldehyde-fixed material. The cells of *Monaster*, *Amphilothus* and *Achradina* may preserved in Lugol's solution, but the skeleton dissolves. As the endoskeleton is the main diagnostic character, the cells could be easily mistaken for species of unarmoured dinoflagellates by non-expert observers. Consequently, the distribution of *Monaster*, *Amphilothus* and *Achradina* clearly has been underestimated, especially in the open ocean, where on-board microscopical observation of live material is more limited.

SPELLING OF *Amphitholus*

Schütt (1895) erected the genus '*Amphitholus*', the etymology of which refers to a double dome. Kofoid (1907) erroneously introduced the name *Amphilothus* as a *lapsus* for '*Amphitholus*' F. Schütt. [–Tholus– has not any especial meaning within the dinoflagellate context. –Tholus– coincided with the name of a king of the Picts, a tribe of Ancient Scotia and it could go easily confused with –lotus–, a flower]. Kofoid and Michener (1911) corrected the error and used Schütt's original spelling, '*Amphitholus*'. Poche (1913) noted the homonymy of '*Amphitholus*' F. Schütt 1895 and the radiolarian *Amphitholus* Haeckel 1887. Poche (1913) continued Kofoid's *lapsus* and proposed *Amphilothus quincuncialis* (Kofoid) Poche. Later Kofoid and Swezy (1921, p. 107) used the name *Amphilothus* (Schütt). Lindemann (1928) proposed *Amphilothus elegans* (F. Schütt) Er. Lindemann. The controversy on the spelling '*Amphitholus*' F. Schütt and *Amphilothus* Kofoid *ex* Poche was dealt in Silva (1980a, b). He proposed to reject '*Amphitholus*' F. Schütt and to conserve *Amphilothus* Kofoid *ex* Poche. Sournia (1984) and Fensome *et al*. (1993) disagreed and considered that '*Amphitholus*' F. Schütt was a legitimate name under botanical nomenclature and must take priory over later names. Proposal no. 478 was accepted. *Amphilothus* Kofoid *ex* Poche 1913 *nom. cons.* was conserved and '*Amphitholus*' F. Schütt, *nom. rej*., was rejected as reported in `*Nomina generica conservanda et rejicienda*´ in the Appendix III A6 of the International Code of Nomenclature, Vienna Code (McNeill *et al*., 2006). The correct generic and specific names are *Amphilothus* Kofoid *ex* Poche, *Amphilothus elegans* (F. Schütt) Er. Lindemann and *Amphilothus quincuncialis* (Kofoid) Poche.

Further records and geographical distribution

As reported above the records of *Monaster*, *Amphilothus* and *Achradina* are underestimated because the delicacy of the cells and its endoskeleton. *Monaster* is known only from its original 1895 description, and *Amphilothus* has been very rarely reported (Kofoid, 1907; Durán *et al*., 1956; de la Cruz 1971; Cortés-Altamirano & Pastén-Miranda, 1982), but commonly alongside *Achradina* (Konovalova 2000; Table 1). *Achradina pulchra* is most commonly found in warm ocean waters and more sporadically in cold waters (Baltic Sea, sub-Antarctic Ocean) (Table 1).

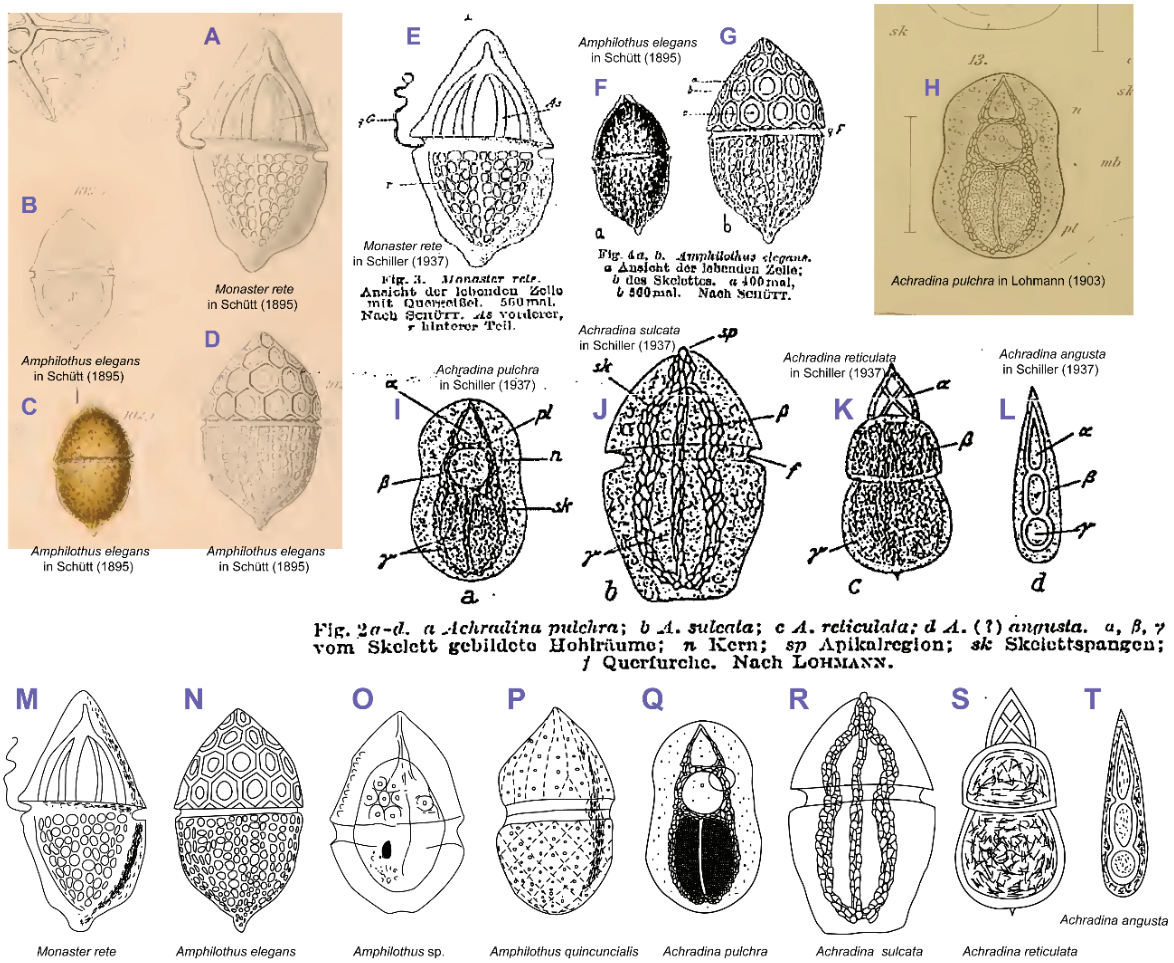

Figure 1. A. Line drawings of basket-like skeleton-bearing dinoflagellates from the literature. **A**. *Monaster rete*, in Schütt (1895). **B–D**. *Amphilothus elegans*, in Schütt (1895). **E**. *Monaster rete*, in Schiller (1937). **F–G**. *Amphilothus elegans*, in Schütt (1895). **H**. *Achradina pulchra*, in Lohmann (1903). **I**. *Achradina pulchra*, in Schiller (1933). **J**. *Achradina sulcata*, in Schiller (1933). **K**. *Achradina reticulata*, in Schiller (1933). **L**. *Achradina angusta*, in Schiller (1933). **M**. *Monaster rete*, redrawn from Schütt (1895). **N**. *Amphilothus elegans*, redrawn from Schütt (1895). **O**. *Amphilothus elegans*, redrawn from Durán *et al.* (1956). **P**. *Amphilothus quincuncialis*, redrawn from Kofoid (1907). **Q**. *Achradina pulchra*, redrawn from Lohmann (1903). **R**. *Achradina sulcata*, redrawn from Lohmann (1919). **S**. *Achradina reticulata*, redrawn from Lohmann (1919). **T**. *Achradina angusta*, redrawn from Lohmann (1919).

Synonymy of *Monaster rete*, *Amphilothus* spp. and *Achradina* spp.

The instraspecific variability of dinoflagellates was little known a century ago. Consequently, different morphotypes or life stages of a single species were often described as new species (see examples in Kofoid & Swezy, 1921; Gómez *et al*., 2015). In the case of delicate forms (e.g., *Monaster rete*, *Amphilothus* spp. and *Achradina* spp.), the cells easily lyse and the description could have been based on deteriorated or distorted cells. If the description is based on endoskeleton, we must keep in mind that dissolution of the skeleton-forming minerals begins immediately after cell death, and so the skeletons described may have been partially dissolved. On the other hand, given that one of the daughter cells regenerates a new endoskeleton, different stages in skeleton development may have been recorded.

Monaster is known only from the original description, and *Amphilothus* has been rarely reported (Table 1). However, our observations showed that *Monaster* and *Amphilothus* have not disappeared from the oceans, or that Schütt did not erect spurious new taxa. The illustrations of *Monaster* and *Amphilothus* by Schütt (1895) did not reflect the most typical morphology of these cells, and the further descriptions under the name *Achradina* by Lohmann (1903, 1919) fit better with the most typical morphology of this species. Consequently, authors have used *Achradina* instead of *Monaster* or *Amphilothus.*

The original illustration of *Monaster* showed the cell covering, and even one of the flagella, while the original illustration of *Amphilothus* showed a cell lacking a cell covering, probably after a recent cell

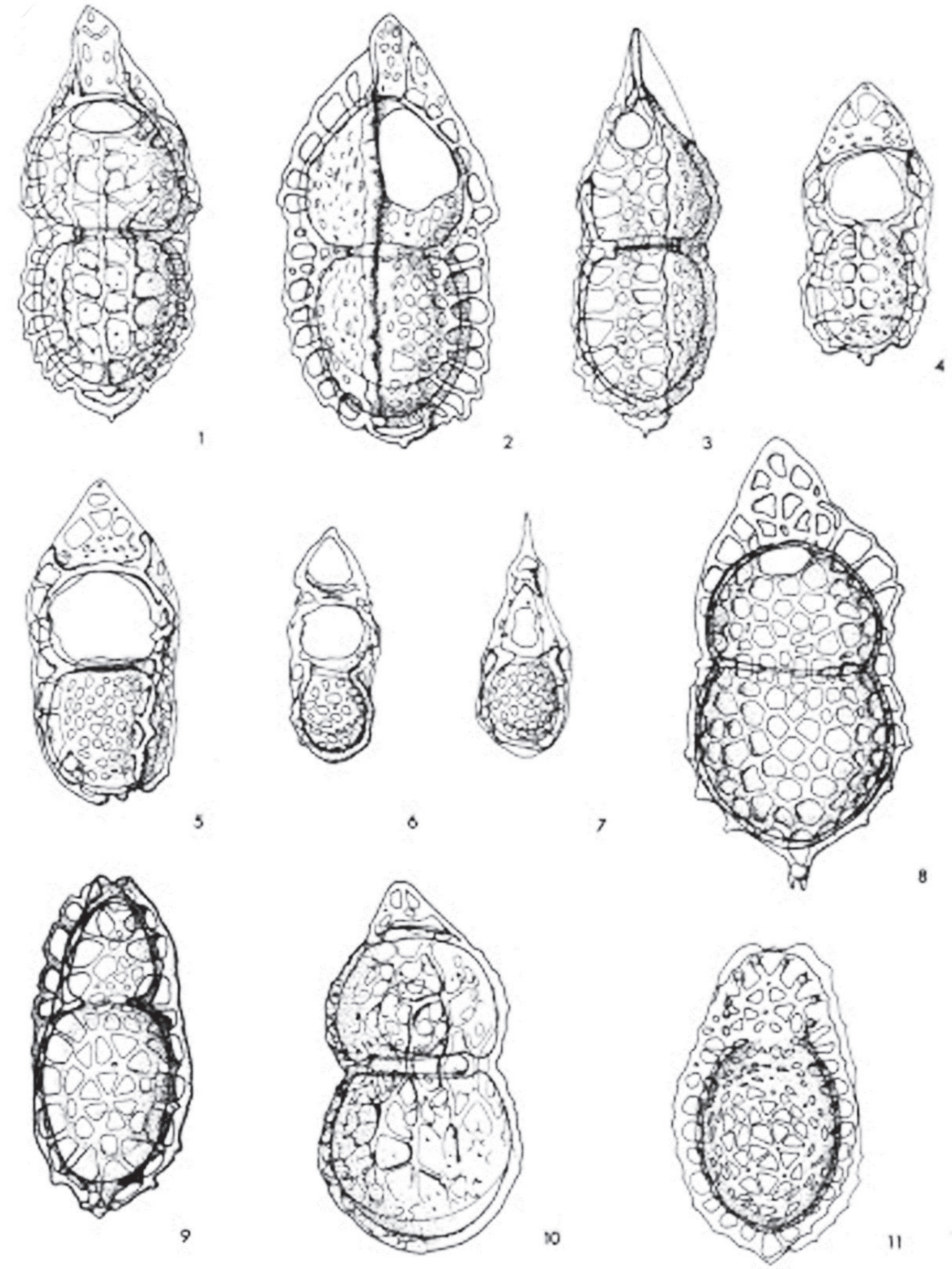

Figure 2. Forms of *Achradina pulchra* in Nival (1969).

lysis. Schütt (1895) illustrated cells of *Monaster* and *Amphilothus* with unusual epitheca development representing unusual morphologies of the species.

Schütt (1895) described *Monaster rete* and *Amphilothus elegans* as having an identical skeletal meshwork in the hypotheca and a pointed antapex or antapical spine. The shape and skeletal meshwork of the hypothecae of *Monaster*, *Amphilothus* and *Achradina* were similar (Fig. 1). The differences between *Monaster rete*, *Amphilothus* spp. and *Achradina* spp. were based on the morphology of

Table 1. Literature records of *Monaster*, *Amphilothus* and *Achradina* in the world's oceans.

Taxa	Place	Reference
Monaster rete	Atlantic or Gulf of Naples	Schütt (1895)
Amphilothus elegans	Atlantic or Gulf of Naples	Schütt (1895)
Amphilothus elegans	Russian Pacific Ocean	Konovalova (2000)
Amphilothus sp.	Mediterranean Sea	Durán *et al.* (1956)
Amphilothus sp.	Mexican Pacific Ocean	Cortés-Altamirano & Pastén-Miranda (1982)
A. quincuncialis	NE Pacific at Panama	Kofoid (1907)
A. quincuncialis	Caribbean Sea	de la Cruz (1971)
Achradina pulchra	Mediterranean and Atlantic	Lohmann (1903)
Achradina angusta	Equatorial Atlantic	Lohmann (1919)
Achradina reticulata	Gulf Stream, North Atlantic	Lohmann (1919)
Achradina sulcata	South Atlantic at Brazil	Lohmann (1919)
Achradina pulchra	Mediterranean Sea	Nival (1969)
Achradina pulchra	Mediterranean Sea	Gómez (2003)
Achradina pulchra	Mediterranean Sea	This study
Achradina pulchra	Black Sea	Gómez & Boicenco (2004)
Achradina pulchra	NE Atlantic at Portugal	Moita & Vilarinho (1999)
Achradina pulchra	NE Atlantic at Skagerrak	ICES (2005)
Achradina pulchra	Baltic Sea	Eker-Develi *et al.* (2008)
Achradina pulchra	South Atlantic at Namibia	Schweikert & Elbrächter (2006)
Achradina pulchra	Gulf of México	Muciño-Márquez *et al.* (2011)
Achradina pulchra	Gulf of México	Zamudio-Reséndiz *et al.* (2013)
Achradina pulchra	Mexican Pacific Ocean	Hernández-Becerril & Bravo-Sierra (2004)
Achradina pulchra	Mexican Pacific Ocean	Meave del Castillo *et al.* (2012)
Achradina pulchra	Mexican Pacific Ocean	Gárate-Lizárraga (2014)
Achradina pulchra	NW Pacific Ocean	Omura *et al.* (2012)
Achradina pulchra	Russian Pacific Ocean	Konovalova (1998, 2010)
Achradina pulchra	Subantarctic Ocean	Henjes (2007)
Achradina pulchra	Subantarctic Ocean	Malinverno *et al.* (2016)

the epitheca. The skeleton of the epitheca of *Monaster rete* was composed of several longitudinal ribs that converged at the apex. These ribs were illustrated in *Achradina sulcata*; they also occurred in the hypotheca of *Achradina pulchra*, and less notably in the epitheca of *Amphilothus quincuncialis* (Fig. 1). Schütt (1895) emphasized the longitudinal ribs in the epitheca of *Monaster*, which are typically illustrated in *Achradina*. The epitheca of *Amphilothus elegans* was illustrated as having a honeycomb-like surface in the form of regular hexagons with large internal circles. However, it seems that Schütt (1895) exaggerated the meshwork, accentuating the angles and the regular geometric contours. In this study, a high variable meshwork was revealed by light microscopy of live cells.

The illustrations of *Achradina pulchra* and *A. sulcata* by Lohmann correspond to the most typical morphology that we found in this species. Lohmann developed a gentle method for the collection and concentration of plankton. *Achradina*, which is delicate and easily lysed, benefitted from this method. Lohmann's cells illustrated as the names *Achradina reticulata* and *A. angusta* correspond to cells of *A. pulchra* that are devoid of the cell covering due to sample treatment (Fig. 1). Nival (1969) observed a high diversity in shape and reticulation of fresh material from Villefranche-sur-Mer (Fig. 2). Nival (1969) proposed *A. sulcata*, *A. reticulata* and *A. sulcata* as morphotypes of *Achradina pulchra*, and this was accepted by later authors.

During this study, more than one thousand live or recently lysed cells of *Achradina* have been observed. *Achradina* appeared sporadically, with the two morphotypes with the morphologies of *Achradina pulchra* and *A. sulcata* dominant; and, more rare were cells with the morphology of *Amphilothus* (dense tessellation), and *Monaster* (with prominent ribs). This study illustrates divi ding cells of *Achradina* for the first time. Our observations of daughter still joined confirmed the variability in size and shape to be intraspecific. One of the daughter cells kept the complete endoskeleton, while the other regenerated a new endoskeleton. Consequently, we find cells with different degrees of maturation of the endoskeleton, related to stage in the life cycle and to cell age. Other physiological or environmental factors could determinate the thickness or the degree of elaboration of the tessellation in the endoskeleton. Such variability is also introduced artificially due to the partial dissolution of the endoskeleton after cell death. These factors explain the high morphological variability in the morphology of the endoskeletons as also reported by Nival (1969). Sournia (1986) previously considered *Monaster* and *Amphilothus* as synonyms. However, misunderstandings in the chemical composition of the endoskeleton of *Achradina* were used to support the split between *Monaster* and *Amphilothus* on the one hand and *Achradina* on the other. Schütt reported that the endoskeletons of *Monaster* and *Amphilothus* were soluble in acetic acid without effervescence, and consequently these structures are not composed of silica or calcium carbonate. We can find incorrect comments in the literature, such as "The skeleton of *Achradina* is insoluble in acetic acid" by Loeblich & Loeblich (1966, p. 7). This comment persuaded authors (i.e. Sournia 1986) to consider that the skeleton of *Achradina* and that of *Monaster/Amphilothus* have different compositions, and consequently that these taxa could not be related, retaining them as separate genera, or even to classify them in different orders (Fensome *et al.*, 1993). The observations show that the genera *Monaster*, *Amphilothus* and *Achradina* should be considered synonyms.

Priority among *Monaster rete*, *Amphilothus* spp. and *Achradina* spp.

The names *Monaster* and *Amphilothus* have disappeared from the literature, while *Achradina* is commonly used. This could be used as a reason to propose the conservation of the name *Achradina*. However, at the present we must follow the rules of the priority according to the article 11.5 of the International Code of Nomenclature for algae, fungi, and plants (I.C.N., Melbourne Code, McNeill *et al.* 2012). The type species of these genera are *Monaster rete* F. Schütt (1895 p. 33, fig. 101), *Amphilothus elegans* (F. Schütt 1895) Er. Lindemann 1928 for which basionym is '*Amphitholus*' *elegans* F. Schütt 1895, p. 34, fig. 102), and *Achradina pulchra* Lohmann 1903. The name *Monaster* was proposed in 1895 and the name '*Amphilothus*' F. Schütt 1895 has been rejected (McNeill *et al.*, 2006). The name *Amphitholus* first appeared in Kofoid (1907), and both names are a source of frequent misspellings ('*Amphilophus*' in Calkins, 1926; '*Amphitolus*' in Delage & Herouard, 1896; '*Amphitolus*' in Adl *et al.*, 2012). The use of *Monaster* avoids the misspelling problems associated with *Amphilothus*/'*Amphilothus*'. From the etymological point of view, the term 'monaster' is used in cell biology for the mother star, as a single star figure at the end of prophase in mitosis. Within the context of the dinoflagellates, *Monaster* refers to a single skeleton when compared to the two "pentasters" of the skeleton of *Actiniscus*, a genus also reported under the name *Diaster* Meunier 1919 (= two stars). The genus *Monaster* Etheridge 1892 is a rarely cited fossil starfish under the zoological nomenclature. *Monaster* F. Schütt 1895 is a legitimate name under the I.C.N. This study propose the priority for the genus *Monaster* F. Schütt, and *Amphilothus* Kofoid 1907 *ex* Poche 1913 (= '*Amphitholus*' F. Schütt) and *Achradina* Lohmann 1903 as synonyms based on the article 11.5 of the I.C.N (McNeill *et al.*, 2012).

Suprageneric classification of *Monaster*

The genus *Actiniscus* was first classified as a silicoflagellate for some time, and Kofoid and Swezy (1921, p. 107) had doubts about the affinity of *Actiniscus*, *Monaster*, *Amphilothus* and *Achradina* with dinoflagellates. The heterotrophic behaviour, the encapsulated nucleus and particularly the presence of siliceous endoskeletons in some species were used to suggest a phylogenetic relationship between dinoflagellates and radiolarians (Zimmermann, 1930; Hovasse, 1934; Hollande *et al.*, 1962).

Following the rules of the zoological nomenclature, Kofoid & Swezy (1921) proposed Amphilothioidae for the genera *Actiniscus* (as *Gymnaster* F. Schütt), *Monaster* and *Achradina*. Lindemann (1928) placed these genera in their own order Amphilothales, while other authors regarded them as member of the naked dinoflagellates within the Gymnodiniales (Schiller, 1937; Tappan, 1980). Sournia (1984) erected the new order Actiniscales for *Actiniscus*, *Achradina*, and *Monaster* as a synonym of *Amphilothus* (Sournia, 1986). *Actiniscus* is a gymnodinioid dinoflagellate and distantly related to *Monaster* (Hansen, 1993). The main feature in common between these genera was the supposed siliceous composition of the endoskeleton of *Monaster*, *Amphilothus* and *Achradina*.

Fensome *et al.* (1993) placed *Actiniscus* and *Dicroerisma* within the Gymnodiniales, and *Achradina*, *Amphilothus* and *Monaster* within the order Ptychodiscales as naked dinoflagellates with a pellicle exceptionally developed into a peripheral, discontinuous basket-like skeleton. The Ptychodiscales also included the unarmoured genera *Balechina* Loebl. & A.R. Loebl., and *Ptychodiscus* F. Stein (Fensome *et al.*, 1993; Adl *et al.*, 2012).

Fensome *et al.* (1993) discussed the suprageneric names for the family containing *Monaster*, *Amphilothus* and *Achradina*. They proposed Amphitholaceae Poche 1913 *ex* Fensome *et al.* 1993 because they used '*Amphitholus*' F. Schütt instead of *Amphitholus* Kofoid *ex* Poche. The name '*Amphitholus*' F. Schütt has subsequently been formally rejected under the I.C.N. and the suprageneric names should be derived from *Amphitholus* Kofoid *ex* Poche. According to I.C.N. Art. 18.1 note 2 and Art. 18.3 names of families cannot be based on an illegitimate genus name. The correct family name is Amphilothaceae. However, it is more difficult is to establish the place of publication due to the combination of orthographical variants and names proposed under both zoological and botanical nomenclature (Table 2). Amphilothidae Poche was proposed under the zoological nomenclature. The name Amphilothaceae Lindemann 1928 appeared on page 34 as *nomen nudum*, and a description was provided in page 68. The correct place of publication of the family is Amphilothaceae Lindemann 1928, p. 68.

At the ordinal level, Kofoid & Swezy (1921) erected Amphilothioidae Kofoid & Swezy under the zoological nomenclature, and Lindemann (1928) proposed Amphilothales (Kofoid & Swezy) Lindemann under the rules of the botanical nomenclature. The order name is not free of misspellings. Nival (1969) in the title of his article misspelled the order name as 'Amphilotales'.

Table 2. Family names derived from *Amphilothus* and '*Amphitholus*' and place of publication.

Amphilothidae Kofoid 1907, p. 165.
Amphitholidae Kofoid & Michener 1911, p. 269.
Amphilothidae Poche 1913, p. 164.
Amphilothiidae Kofoid & Swezy 1921, p. 107.
Amphilothaceae Lindemann 1928, p. 68.
Amphitholaceae Lindemann 1928 *ex* Taylor 1976, p. 54.
Amphitholaceae Kofoid & Michener 1911 *ex* Silva 1980, p. 57–58.
Amphilothaceae Poche 1913 *ex* Silva 1980, p. 57.
Amphitholaceae Poche 1993 *ex* Fensome *et al.* 1993, p. 55.

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