

Review

Diatoms with studied sexual reproduction

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Abstract: Diatoms (Bacillariophyta) are unicellular organisms with extremely high species diversity. According to AlgaeBase, the names of approximately 17 thousand species are currently considered to be taxonomically accepted. It is assumed that there are about 100,000 species of diatoms on the planet. Sexual reproduction is an obligatory stage of the life cycle in many diatoms due to specific structure of their frustules and the mode of reduction and restoration of the latter. At the same time, analysis of literature showed that over the entire three-century history of the study, data (in some cases very incomplete) have been accumulated on the sexual reproduction of approximately 350 species. There are about 1000 literature sources providing information about sexual reproduction of diatoms. Here, we present a summary of those species of Bacillariophyta for which data on sexual reproduction are available. The degree of knowledge of the particular classes of diatoms was analysed.

Key words: diatoms, number of species, sexual reproduction

INTRODUCTION

The first data on sexual reproduction of diatoms were published 175 years ago. The article by G. Thwaites was very short; it was only one page (THWAITES 1847). Since then, the number of works on reproductive behaviour, as well as on diatoms in general, has been continuously growing. The list of publications describing (with varying degree of details) sexual reproduction of diatoms is presently close to 1000. By now, the basic principles and rules of the reproductive biology of diatoms have been established, main features of their life cycle have been elucidated, and classifications of the types of the sexual process have been proposed (KARSTEN 1899; MERESCHKOWSKY 1903; GEITLER 1932, 1973; FRITSCH 1935; DREBES 1977; ROUND et al. 1990; ROSHCHIN 1994; EDLUND & STOERMER 1997; ROSHCHIN & CHEPURNOV 1999; CHEPURNOV et al. 2004; MIZUNO 2006; DAVIDOVICH 2010; MANN 2011; KACZMARSKA et al. 2013; GASTINEAU et al. 2014; DAVIDOVICH et al. 2015; MANN et al. 2017; POULÍČKOVÁ & MANN 2019; etc.).

The reproductive phase is apparently a mandatory stage in the life cycle of the vast majority of diatoms. This is due to peculiarities of the structure and the mode of formation of the siliceous frustule of the diatom cells. The interested reader can find the necessary details following the above references. Our aim was to compile the

most complete list of diatoms for which information on sexual reproduction and auxosporulation was obtained, as well as to analyze the degree of knowledge of this phenomenon in relation to particular groups.

MATERIAL AND METHODS

We have been collecting information on publications describing sexual reproduction in diatoms since 1986. Over the past time, a list of publications has been compiled, which includes about 1000 sources. The sources of information for the list were references to the literature in the articles. At the moment, collecting of early publications is close to completion, since unaccounted articles in the bibliographies are almost never found. New articles are collected as they are published. Internet resources, including search engines and databases hosted on various sites, were used to find relevant articles. The list of keywords used to search for documents on sexual reproduction of diatoms is given in Supplementary Table 1. In the original publications, a number of species had other names being currently regarded as synonyms. In cases of synonymy, we provide the species names in accordance with the AlgaeBase. In particular cases, we have kept the initial names used in the original sources. Relation of the examined species to the salinity (general environment) was assessed following AlgaeBase and literature data. Diatoms tolerant to a broad range of salinity and occurred in both fresh or brackish water and marine environment were designated as “freshwatermarine”.

RESULTS AND DISCUSSION

The compiled data are presented in the table (Supplementary Table 2), that embraces 355 taxa (including species, varieties and forms) of 140 genera, which is 2.1% of the total number of known diatoms catalogued in AlgaeBase (GUIRY & GUIRY 2021, <https://www.algaebase.org>). According to AlgaeBase, the names of approximately 17 thousand species of diatoms are currently considered to be taxonomically accepted. Thus, the sexual process remains unexplored in 98% of the known taxa. Less taxa, especially those taxonomically accepted are currently included in the DiatomBase (<https://diatombase.org/aphia.php?p=stats>). Search for the rank “species” returned ca. 6,000 matching records (searched on 21 February 2022).

If compare the degree of knowledge on sexual reproduction related to different groups of diatoms, the following can be noted (Table 1). The largest number of species (a little more than half of those in which sexual process was observed) are raphid pennates. Approximately one fifth is represented by diatoms belonging to the class Mediophyceae, which combines polar centric and Thalassiosirales in the Medlin and Kaczmarska system (MEDLIN & KACZMARSKA 2004). The smallest amount of species (only 10% of investigated) for which data on sexual reproduction are available are in the paraphyletic group of araphid pennates. If we consider raphid and araphid pennates together as the class Bacillariophyceae, it turns out that the number of species with described sexual reproduction in this class counts to 2/3 of the total number of diatoms with studied sexual reproduction. A different picture arises if we consider the extent of study of sexual reproduction separately for each group. In relative units, Mediophyceae has been investigated most of all (4.9% of the total species in the group). The class Coscinodiscophyceae has been slightly less studied (3.5%). Among Bacillariophyceae, sexual reproduction was investigated in 2.7% of araphid and only 1.6% of raphid pennates; when combined, this is 4.3% percent

of the total number of species in the class. Freshwater diatoms account for only 40% of the total number of the studied taxa (Fig. 1). Marine and brackish diatoms are better studied, totaling 58%. Genetic sequences are available in GenBank (<https://www.ncbi.nlm.nih.gov/Taxonomy/Browser/wwwtax.cgi>) for 248 of 355 examined species (see Supplementary table 2). Among sequenced species, more than a half belong to raphid pennates (Fig. 2).

In general, all Coscinodiscophyceae and Mediophyceae, with the exception of Toxariales (DAVIDOVICH et al. 2017), demonstrate an oogamous type of the sexual process. Depending on the species, one or two large egg cells are produced by the female gametangial cell, and from four to 128 single-flagellate motile spermatozoa are formed in the male gametangium. In contrast to centric diatoms, no one case of oogamy was recorded in araphid and raphid pennates. Their sexual process is isogamous in terms of the gamete sizes. However, anisogamy is also a characteristic of some pennates, because of the mode of formation and behaviour of their gametes. For example, in representatives of the genera *Tabularia* (Kützinger) D.M. Williams et Round and *Ulnaria* (Kützinger) Compère, male gametes are formed through transapical division of the cell protoplast, while during the formation of female gametes, the protoplast divides in the apical plane (DAVIDOVICH & DAVIDOVICH 2010; PODUNAY et al. 2014). The *cis*-anisogamous behaviour of gametes (see, for example, DAVIDOVICH & BATES 1998) makes it possible to distinguish not only two mating types, but two sexes, implying that the gametes are active in males and passive in females. In terms of sex determining genetic factors, the heterogametic character of male clones has been proven in a number of morphologically and behaviourally anisogamous pennates (DAVIDOVICH 2002; DAVIDOVICH et al. 2006, 2010; DAVIDOVICH & DAVIDOVICH 2010; PODUNAY et al. 2014).

Toxariids represent an original line of evolution. Similar to pennates, they evolved nonoogamous type of sexual reproduction (DAVIDOVICH et al. 2017). That sharply distinguishes them from all other Mediophyceae,

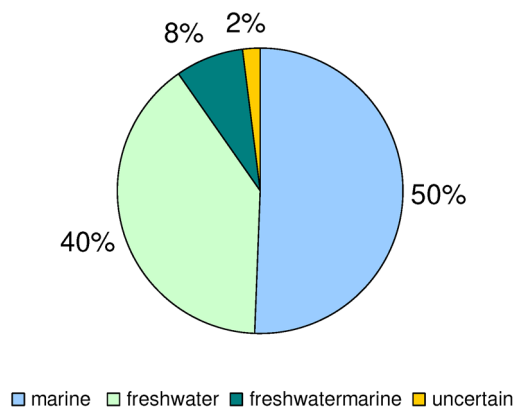


Fig. 1. Relation of the examined diatoms (N=355) to the salinity of the environment.

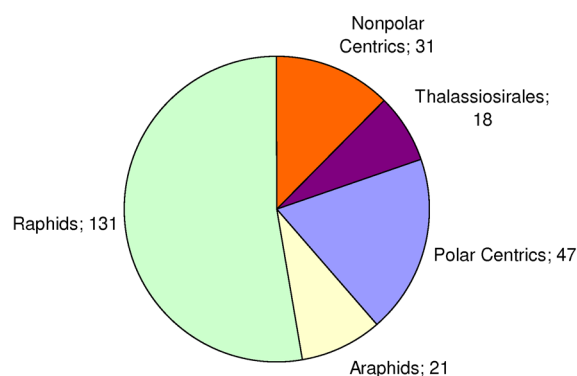


Fig. 2. Number of diatoms with studied sexual reproduction for which genetic sequences are available in GenBank.

where toxariids are placed according to genetic and to some extent morphological data. This is the first and so far the only fact of the parallel (convergent) evolution of non–oogamous sexual reproduction in diatoms.

Among empiric regularities is the generic character of the pattern of sexual reproduction. As a rule, all members of a particular genus are uniform in relation to the model of their sexual behaviour. Exceptions are those species of the genus which breeding system allows both hetero– and homothallic reproduction. The types of the sexual process in these cases can be radically different. For example, we can observe in the same species the normal type of the sexual process during heterothallic reproduction and automixis at homothally. In some species, two different types of sexual behaviour relate exclusively to one of the sexes, as only one sex reveals an ability to reproduce both homo– and heterothallically (DAVIDOVICH 2002; PODUNAY et al. 2014). Thus, as we suppose, the dominant type of sexual reproduction is a generic trait, but additionally to the basic pattern, accessory models of sexual behaviour may exist in some species.

In other cases, deviations from the general scheme, if they are observed in probable representatives of a particular genus, rather indicate that these representatives do not belong to it. Most likely, they should be assigned to another genus. For example, this can be illustrated by separation of the genus *Pseudo-nitzschia* H. Peragallo from *Nitzschia* Hassall (HASLE 1994). The separation was based on morphological and ecological characteristics and the ability to form chain colonies. At the same time, the difference between these genera becomes even more obvious if we take into account the type of sexual process characteristic of their representatives. The reproduction is trans–anisogamous accompanied with the formation of copulation canals in true *Nitzschia* (MANN 1986), and cis–anisogamous without any copulation structures in *Pseudo-nitzschia* (DAVIDOVICH & BATES 1998).

Due to its conservative evolution, the scheme of

the sexual behaviour guarantees the unity of the species and the continuity of generations. Significant deviations in the mode of sexual reproduction may indicate an essential evolutionary divergence. Among the closely related genera *Berkeleya* Greville, *Mastogloia* Thwaites ex W. Smith, *Climaconeis* Grunow, *Frustulia* Rabenhorst, and *Amphipleura* Kützinger, the first two are relatively older according to the available molecular data (NAKOV et al. 2018). Morphological and behavioural isogamy was found in two investigated representatives of the genus *Berkeleya* (TSCHERMAK–WOESS 1973; DAVIDOVICH 2001). It should be noted that one of them was initially included in the genus *Amphipleura* (TSCHERMAK–WOESS 1973). A little later, after the evolutionary history of the genus *Berkeleya* began, the genus *Climaconeis* split from it. Morphological and behavioural isogamy was observed in *C. scalaris* (DAVIDOVICH et al. 2019). Thereafter, the genera *Frustulia* and *Amphipleura* appeared; they are the youngest in the considered evolutionary branch. Their sexual process is fundamentally different; they demonstrate trans–anisogamous reproduction (GEITLER 1949, 1952). In both cases the formation of copulation canals connecting gametangial cells was described. Gamete interchange takes place through these copulation canals, which is similar to the process of syngamy in *Nitzschia* sensu stricto (MANN 1986). The genus *Mastogloia*, which apparently had a common ancestor with the genus *Berkeleya*, evolved in a different way from *Climaconeis* – *Frustulia* – *Amphipleura*. *Mastogloia* also came to anisogamy, but of the cis–type (STICKLE 1986).

The considered sequence of evolutionary changes suggests that the trans–anisogamous type of sexual process could be regarded progressive, as it appeared later and spread within two relatively younger genera. The formation of copulation canals is obviously extreme specialization. However, it should be noted that the genera *Mastogloia* and *Berkeleya*, which had a common, most likely isogamous ancestor, came to completely different

Table 1. Distribution by classes of the diatoms which sexual reproduction has been discovered.

Group	Number of species*	% of the total number of species	Number of taxa which sexual reproduction has been determined	Taxa with discovered sexual reproduction	
				% of the total number of taxa with discovered reproduction	% of the total number of species in the group
Coscinodiscophyceae	1323	8.0	46	13.0	3.5
Mediophyceae	1644	9.9	81	22.8	4.9
Bacillariophyceae (araphid)	1230	7.4	33	9.3	2.7
Bacillariophyceae (raphid)	12436	74.7	195	54.9	1.6
Sum	16633	100	355	100	

Note. * – According to AlgaeBase, <http://www.algaebase.org>; searched on 31 October 2021 (Guiry & Guiry, 2021).

results during the same time of evolution. Based on this, we can conclude that isogamy and anisogamy have equal adaptive value, since they both enabled the existence of these genera in many generations over the same (or similar) and sufficiently long evolutionary time. It remains unclear at what stage of evolution such serious differences appeared in individual genera. In particular, did the genus *Mastogloia* acquired cis-anisogamy immediately after separation from the ancestor common with *Berkeleya*, or the transformation took place some time later?

Attempts to analyze evolution of breeding behaviour are largely theoretical and speculative. As before, we have too little information to reconstruct the evolutionary history of sexual reproduction in diatoms in general, or even in particular phylogenetic branches. Sexual reproduction remains the most intimate and poorly understood stage of the diatom life cycle. In many genera, sexual reproduction has not been studied in any of their representatives. Therefore, investigation of sexual behaviour of individual species is still a relevant task.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Key words used for searching documents on sexual reproduction in diatoms.

Table S2. Diatoms which sexual reproduction was observed and described (with varying degrees of details)

Supplementary references

This material is available as part of the online article (<http://fottea.czechphycology.cz/contents>)