

Taxonomy and Phylogeny of *Scenedesmus*

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The first taxa of the genus *Scenedesmus* were described in 1828 and studied for more than one hundred years only by light microscopy. The position, delimitation and subdivision of the genus has often been changed. The study of the cell wall structures in the transmission electron microscopy and finally DNA studies (G/C content, homologies, reassociation, sequence analyses) have been very important for progress in the taxonomy of the genus. The combined studies of light and electron microscopy and of DNA studies resulted in a better understanding of the relationship of taxa. Besides overinterpreted variability, polymorphism occurs with the switching of qualitatively different cell wall ultrastructures with the following generation. According to recent publications the genus is now divided into only two subgenera. Several taxa from the former family Chlorellaceae (now classes Trebouxiophyceae) were transferred to *Scenedesmus* and the genera *Tetradesmus* and *Enallax* should become retransferred to *Scenedesmus*.

Key Words: *Chlorella*, *Dicloster*, DNA, electron microscopy, light microscopy, morphology, phylogeny, physiology, *Scenedesmus*, taxonomy, *Tetradesmus*

INTRODUCTION

The first species of the genus *Scenedesmus* were described by Turpin (1828) and placed by him in the diatoms, later by Ehrenberg (1834) in the Desmidiaceae, by Nägeli (1849) in the Chlorococcales, family Hydrodictyaceae, and finally by Oltsmanns (1904) in the family Scenedesmaceae. The genus name was created by Meyen (1829). For this genus Hegewald and Silva (1988) enumerated about 800 taxa or combinations. The most important monographs are: Smith (1916), Chodat (1926), Kiriakov (1977), Komárek and Fott (1983) and Uherkovich *et al.* (1995) and for Korea: An (1989). Only Komárek and Fott (1983) and An (1989) considered also electron microscopy, all other monographs are exclusively based on light microscopy.

According to Komárek and Fott (1983) the family Scenedesmaceae has 6 subfamilies, the genus *Scenedesmus* belongs to the subfamily Scenedesmoideae. It includes 8 genera: *Pseudotetradesmus* Hirose *et*

Akiyama, *Enallax* Pascher, *Tetradesmus* G.M. Smith, *Didymocystis* Korschikov, *Dicloster* Jao, Wei *et* Hu, *Neodesmus* Hindák, *Scenedesmus* Meyen and *Westellopsis* Jao. Of these the genus *Pseudotetradesmus* with its single species was transferred as a synonym to *Scenedesmus* (Hegewald *et al.* 1988) and the genus *Didymocystis* was transferred to the Oocystaceae (Hegewald 1988b). However, the genus *Pseudodidymocystis* Hegewald *et* Deason (Hegewald and Deason 1989), which belongs to Scenedesmaceae was split from *Didymocystis*.

According to Komárek and Fott (1983) the genus *Scenedesmus* is defined by flat coenobia of 2-32 cells, arranged in 1 or 2 rows, cells of different shape, but always elongate, with cell poles from acute to truncate/obtuse, cell wall smooth or with different sculptures, with or without spines, with 1 chloroplast and 1 pyrenoid. Reproduction by autospores, which are arranged within the mother cell into a new coenobium (Trainor 1996: autocoenobium).

Besides autospores, zoospores were first mentioned by Valz (1870) and later produced in culture (Trainor 1963, 1993, 1996), however, they could not be produced in any other laboratory. Trainor (1996) also reported the production and germination of zygotes. Since Valz (1879) we have only one doubtful record for zoospores in outdoor mass cultures (Lukavský 1991; Cepak 1993). Hence

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we conclude that, if sexuality occurs, it is negligible and reproduction is generally, in culture as in nature, by autospores. That means that all mutations occurring which do not significantly influence growth and competition will last and cannot be lost by genetic processes. So it is easy to understand that most of the occurring morphological mutations survive and hence that the genus has an enormous variability.

The genus *Scenedesmus* was divided into 2-6 subgenera or "groups" by Chodat (1926), Hegewald (1978), Hindák (1990), Kiriakov (1977), Komárek and Fott (1983), Lagerheim (1882) and Uherkovich (1966). We distinguish three groups, treated as subgenera in Hegewald (1978) and Kiriakov (1977), one group has acute cell poles (subgenus *Acutodesmus* Hegewald = subgenus *Fusodesmus* Kiriakov nom. inval.), another group has obtuse or truncate cell poles without spines (subgenus *Seenedesmus*) and the last group also has obtuse to truncate cell poles but the coenobia have spines and/or cell wall structures (subgenus *Desmodesmus* Chodat). We will discuss these subgenera separately.

The Subgenus *Acutodesmus* under the Light (LM) and Electron Microscope (EM)

The taxonomy of the subgenus *Acutodesmus* is mainly based on the cell form and cell arrangement, because only few other characteristics are available. An additional taxonomically useful characteristic was found by Krienitz (1987) in growth at high temperature (35°C). High temperature taxa were hitherto known from *Chlorella* Beijerinck (Kessler 1976) but for *Scenedesmus* only high-temperature strains were found (Hegewald 1984). By high temperature resistance Krienitz (1987) was able to separate e.g. *S. obtusiusculus* Chodat from *S. obliquus* (Turpin) Kützing, which otherwise could not be separated by Hegewald (1982). Both taxa are morphologically similar, *S. obtusiusculus* is usually single-celled and smaller than *S. obliquus*, which generally produces coenobia. However, many strains of *S. obliquus* can produce up to 100% single cells and these are smaller than coenobial cells (Hegewald 1982). The production of single cells is common in many *Scenedesmus* species, the coenobia of the species of the subgenus *Acutodesmus* generally disrupt into single cells before cell division. The release of single cells instead of coenobia from a mother cell depends on strain and environmental conditions. If growth conditions are good and the algae are growing fast (e.g. production of more than 8 daughter cells), they often produce only single cells. However, there are many

other factors of influence, e.g. suboptimal growth conditions or special accompanying bacteria. When Egan and Trainor (1989) postulate that low cell density is the unifying principle for unicell development in *Scenedesmus*, they are right because low cell density means good growth conditions (e.g. more light per cell) hence fast growth, however, the cell density itself is not a unifying principle for unicell development.

The recent revision of the subgenus *Acutodesmus* by Holtmann (1994) gives more weight to the twisting of the plane of coenobia and of cells and to the manner of attachment of cells, as well as to the difference of the cell length of outer and inner cells within a coenobium. Based on this revision a key for the taxa is given as an appendix.

A genus morphologically very close to *Scenedesmus* subgenus *Acutodesmus* is *Dicloster*, described by Jao *et al.* (1976). The tropically/subtropically distributed taxon can be distinguished by the arrangement of 2 and 2 cells above each other and by 2 pyrenoids per cell. However, 2-celled coenobia with one pyrenoid per cell are often found in nature (Hegewald 1988a; Hortobágyi 1969 sub nom. *S. acuminatus* var. *elongatus* G.M. Smith, Schmidt *et al.* 1997) and these coenobia can hardly be distinguished from 2-celled *S. acuminatus* (Lagerheim) Chodat. Another related genus is *Tetradismus* with a bundle-like arrangement of cells, which is the only distinguishing characteristic from the subgenus *Acutodesmus*. The genus was transferred to *Scenedesmus* by Chodat (1913) and this was accepted by several authors, however, in Komárek and Fott (1983) the genus *Tetradismus* has been established again. One taxon, described as a variety of *Scenedesmus* (*Tetradismus*) *wisconsinensis* (G.M. Smith) Chodat, is var. *reginae* Holtmann (1994). This taxon has a cell arrangement as *Dicloster* but has only one pyrenoid and much shorter cells. Hence the placement of the taxon is doubtful.

To the subgenus *Acutodesmus* also belongs a species with rib-like structure: *Scenedesmus acutiformis* Schröder. This structure, which is best visible under the EM, is formed by the hemicellulosic cell wall layer, different from the structures in the other subgenera. Because of this structure the species was transferred to the genus *Enallax* by Hindák (1990). However, one or several weakly developed longitudinal ribs are usually found in other species of the subgenus *Acutodesmus*.

The Subgenus *Scenedesmus* under the LM and EM

The subgenus *Scenedesmus* includes all spineless