

Modern algae resembling fossil *Tetraporina*

Svenolov Lindgren

Lindgren, Svenolov (1987). Modern algae resembling fossil *Tetraporina*. *Palaeobotanist* 35(2) : 131-135.

Specimens of *Tetraporina*, usually interpreted as algal microfossils, display similarities to several modern taxa of the Dinophyceae, Xanthophyceae and Chlorophyceae. The quadrangular and tetrahedral cell shape of algae and its variability due to ontogeny and environmental modifications, are reviewed in this article together with taxonomical problems in different classes of modern algae which are relevant to the taxonomy and botanical affinities of fossil *Tetraporina*.

Key-words—Algae, Dinophyceae, Xanthophyceae, Chlorophyceae, *Tetraporina* (Sweden).

Svenolov Lindgren, Department of Geology, University of Stockholm, S-10 691 Stockholm, Sweden.

सारांश

अशिमत टेट्रापोरीना-सदृश वर्तमान शैवाल

स्वेनोलाव लिन्दग्रेन

टेट्रापोरीना के प्रादर्श जिनकी प्रायः सूक्ष्म-शैवालाश्रमों की भाँति व्याख्या की जाती है डाइनोफाइसी, जैन्थोफाइसी एवं क्लोरोफाइसी नामक कुलों के कई वर्तमान वर्गों से समानता प्रदर्शित करते हैं। इस शोध-पत्र में शैवालों की चतुर्भुजी एवं चतुष्फलकीय आकार की कोशाओं में पादप-विकास एवं वातावरणीय परिवर्तनों के फलस्वरूप विभिन्नतायें विवेचित की गई हैं। इसी के साथ-साथ वर्तमान शैवालों के विभिन्न वर्गों में वर्गीकरणिक समस्याओं पर पुनर्विचार किया गया है। ये समस्यायें अशिमत टेट्रापोरीना की वनस्पतिक सजातीयताओं एवं वर्गिकी से सम्बद्ध हैं।

THE general morphology and the cell wall of *Tetraporina* indicate that these microfossils are of algal origin. The genus, however, may be made up out of specimens belonging to different natural taxa. The botanical affinities of fossil *Tetraporina* are discussed in Lindgren (1980, pp. 337-346).

Some specimens of modern algae may be difficult or impossible to assign to appropriate taxa without studying their ontogenetic variability in culture. The classification of fossil algae is further complicated by the restricted number of preserved diagnostic characters.

Modern algae displaying shapes similar to fossil *Tetraporina* occur in several groups, which are recorded in Table 1.

In this article are reviewed the distribution of quadrangular and tetrahedral cell shape in modern algae, and the variability of the cell shape due to ontogeny and environmental modifications, and taxonomical problems in different classes of modern algae which are relevant to the taxonomy of *Tetraporina*.

Table 1—Taxa of modern algae which include forms with shape similar to fossil *Tetraporina*

Class	Order	Family
Dinophyceae	Peridinales	Ceratiales
	Dinococcales	Phytodiniaceae
Xanthophyceae	Mischococcales	Pleurochloridaceae
		Centrictaceae
Chlorophyceae	Volvocales	Tetrasporaceae
		Oocystaceae
	Chlorococcales	Micractiniaceae
		Hydrodictyaceae
		Coelastraceae
	Zygnematales	Zygnemataceae

MORPHOLOGY AND ONTOGENETIC VARIABILITY

Dinophyceae

Some species of *Ceratium* Schrank (Peridinales) often occur in great quantities in lakes and ponds. At the

end of the vegetation period they produce cysts which hibernate in the bottom sediment (Foot, 1959, p. 361). The spores are released through a burst in the cyst wall (Huber-Pestalozzi, 1950, pp. 259, 272). Some resting cysts of *Ceratium* have the same shape as *Tetraporina* and have been misinterpreted as species of the chlorophycean genus *Tetraedron* Kützing (Kováčik, 1975, pp. 384, 386).

Tetradinium Klebs (Dinococcales) comprises tetrahedral cells of the similar shape as *Tetraedron*. The existence of *Tetragonidium* Pascher as a genus comprising pyramidal and tetragonal cells attributed to the Cryptomonadaceae (Cryptophyceae) has been questioned by Fott (1959, p. 368).

Xanthophyceae

Tetraedriella and *Tetragoniella* (Pleurochloridaceae) were established by Pascher to comprise tetrahedral cells differing only in their size range. The monotypic genus *Tetragoniella* has been transferred into *Tetraedriella* since the size differences are not sufficient for distinguishing two genera (Smith, 1950, p. 385). The polymorph type species for *Tetraedron* Kützing (Chlorophyceae) has the diagnostic characteristics of *Tetraedriella* and has been transferred into this genus of the Xanthophyceae (Fott, 1967, p. 358).

Certain criteria used to distinguish modern algae from each other cannot be used on fossils since they are not preserved. Thus the modern algae *Tetraedriella* (Xanthophyceae) and *Tetraedron* (Chlorophyceae) can be distinguished from each other only by means of their chromatophors or food storage materials (Pascher, 1939, p. 586).

Species of the xanthophycean genera *Goniochloris* Geitler and *Pseudostaurastrum* Chodat have earlier been assigned to *Tetraedron* Kützing (Chlorophyceae). Some species described as *Tetraedron* are supposed to be misinterpreted representatives of the xanthophycean genera *Ophiocytium* Nägeli and *Tetraplektron* Fott (Kováčik, 1975, pp. 382, 383, 387).

Chlorophyceae

Volvocales

Porochloris Pascher, 1929 (Tetrasporaceae) comprises epiphytic, solitary algae with a thin to very thick cell wall which is distinctly resistant and impregnated by iron-hydroxide. In younger specimens the outline of the cell is round to elliptic whereas in older specimens it is quadrangular, square-shaped, rhomboidal or more or less round-shaped with four thickenings clearly marked on the cell wall.

The quadrangular shape of the cell, which in several instances may deviate, is defined by pores which break the cell wall at the corners. The aperture of the pore is slightly enlarged outwardly and often characterized by early iron-hydroxide precipitates. In one species, *P.*

filamentorum, the pores can be seen only on strongly iron-impregnated specimens. From each pore extend hyaline threads of unknown function, emanating from the protoplast.

The reproduction occurs by zoospores which are released by bursting of the mother cell wall in either an appointed or an indefinite way. Aplanospores were observed as the only resting spores. They are in general larger than the vegetative cells and elliptical in outline. Their membrane is thick and smooth.

Chlorococcales

Tetraedron Kützing (Oocystaceae) originally comprised about 100 species (253 taxa) and represented a complex of various tetraedric algae. A great many of them have turned out to belong to other genera, mainly of the Xanthophyceae and Dinophyceae. Other cells which resemble *Tetraedron* in shape are either cysts or parts of the thallus of other unknown algae, or spores of aquatic hyphomycetes (Kováčik, 1975, p. 355). Many species which were previously referred to *Tetraedron* represent ontogenetic stages of other algae (Migula, 1907, p. 638).

A number of species originally assigned to other genera have been included in *Tetraedron* and many new taxa have been described.

Older investigators classified the algae primarily according to their shape, without recognizing their cytology. The descriptions of new taxa were frequently based on morphological features alone. The number of species, varieties, and forms of *Tetraedron* was reduced to six species (11 taxa) by Korsikov (1953) and later to four species by Kováčik (1975). Most of the remaining species were assumed to belong to the Xanthophyceae.

The type species of *Tetraedron* (*T. regulare* Kützing) has been transferred to *Tetraedriella* Pascher by Fott (1967, p. 358). For that reason the name *Tetraedron* is not valid for a chlorophycean genus. Korsikov (1953, p. 238) used *Tetraedron* exclusive of all xanthophycean species. The use of *Tetraedron* from the nomenclatural point of view is discussed in Komárek and Fott (1983, p. 696).

Despite that the variability of the shape was noticed as early as in 1894 by Lagerheim, and subsequently studied by Tanner (1923), Troitzkaja (1933), and Kováčik (1975), the present knowledge of the variability of the shape during the ontogeny of cells of most representatives of *Tetraedron* is still meagre.

In the quadrangular-shaped species of modern *Tetraedron* opposite cell sides have equally concave curvature or are flat. The curvature of the cell sides disappears with the ageing so that young cells with two deep and two shallow concavities develop slightly concave, flat or even convex sides with different curvature on neighbouring sides. Young cells are tetrahedral and flat, older cells are round or spherical. In *Tetraedron minimum* (Braun) Hansgirg the corners of

the young cells have a papilla at the angles. With proceeding growth the angles become more rounded and papillae disappear so that older cells exhibit only their traces or a smooth surface. *Tetraedron incus* (Teiling) Smith have angular processes which are thin in young cells but thickening in older cells (Kováčik, 1975, pp. 364-368, 373).

The characteristic cell wall feature is the surface pattern network which is formed by the corrugation of the two outer cell wall layers. This structure changes during the ontogeny and the corrugated surface evens out with the cell ageing. "In young cells the periphery of the middle layer is abundantly folded and the network is very dense. In older cells the corrugated surface of the outer layers evens out, the network thins out and is composed of larger, often interlocked meshes. The middle layer is only slightly wavy. In old, large, rounded cells the network is reduced or the cell surface is completely smooth... The outer layer, although it forms the outer contours of the network, retains the same thickness throughout the whole process" while the thickness of the middle layer varies considerably. The disappearance of the surface structure of cell wall during ontogeny is supposed to be due to cell growth (Kováčik & Kalina, 1975, p. 438).

The release of autospores causes a rupture of the mother cell wall. In *Tetraedron minimum* var. *scrobiculatum* Lagerheim this rupture always occurs outside the deep concave indentations of the cell sides (Kováčik, 1975, p. 368).

In classifying fossil algae it must be born in mind that mutually different morphological types can be developed during the life cycles. *Tetraedron*-like stages will occur in several genera of the Chlorococcales, e.g. *Coelastrum* Nägeli, *Hydrodictyon* Roth, *Oocystis* Nägeli, and *Pediastrum* Meyen (Pringsheim, 1861, p. 781; Migula, 1907, p. 638; Wille, 1908, p. 816; Smith, 1950, p. 244; Kováčik, 1975, p. 386).

Plaesiodyctyon mosellanum Wille, 1970 from the lower Keuper of Luxemburg was interpreted as a chlorophycean algae consisting of "plane, onelayered aggregations of a binary number of rectangular cells, which are arranged in a checker-board pattern". It has remarkable similarities to the modern genus *Pediastrum* (Wille, 1970, p. 283). The individual cells of *Plaesiodyctyon* are cushion-shaped. Their angles are generally somewhat thickened as far as they are in contact with the margin of the coenobium and frequently growing into bud-shaped protuberances. There are no thickenings at the corners of the cells in the interior of the coenobium. The four corner cells of the coenobium are specially differentiated insofar as their free ends are most frequently prolonged into more or less distinct lobes.

Zygnematales

Some *Tetraporina*-like species assigned to the

desmidiacean genera *Arthrodesmus* Ehrenberg, *Micrasterias* Agardh, and *Staurastrum* Meyen are misinterpreted representatives of *Tetraedron* and *Tetraedron*-like genera of the Xanthophyceae (Kováčik, 1975, pp. 367, 381, 384).

Strikingly *Tetraporina*-like fossils have been observed in a Bronze-Age settlement deposit in the Netherlands by Van Geel (1976, p. 337) and in Columbian Quaternary sediments by Van Geel & Van der Hammen (1978, p. 383), who have interpreted them as zygospores of *Mougeotia* Agardh (Zygnemataceae). Van Geel (1979, p. 467) has pointed out that spores related with those of the modern *Mougeotia* have been described as *Tetraporina*, *Tetrapidites* and *Tetraporopollenites*.

In the Zygnemataceae the ripe zygospore is quadrangular in the genera *Debarya* Wittrock, *Mougeotia* Agardh, *Temnogametum* West, and *Zygnemopsis* (Skuja) Transeau. For the identification and classification of modern taxa the shape, size and pigmentation of the zygospores and the ornamentation of the spore wall are main characters.

In almost all species the zygospores are constant in shape. The quadrangular zygospores show a number of variations in respect of the corners, the convexity and

Table 2—The characters of the corners in relation to different wall sculptures in the quadrangular zygnematacean zygospores with straight, concave, deeply concave or convex sides according to Randhawa (1959)

Wall sculpture	Corners
punctate	produced and truncate retuse rounded truncate with horn-like processes
scrobiculate	bulging obtuse produced into rounded horns produced and truncate retuse rounded truncate
smooth	apiculate produced and truncate retuse rounded truncate with horn-like processes with rounded process with thickened wall
verrucose	retuse
granulose	no record
reticulate	no record

concavity of the sides and the ornamentation of the spore wall. In most species the zygospores are smooth, reticulate, punctate or pitted while other kinds of ornamentation is rather uncommon (Randhawa, 1959, p. 100). Among the quadrangular forms the scrobiculate ornamentation is frequent but the pitted is absent. In the quadrangular zygnematacean zygospores with straight, concave, deeply concave or convex sides the characters of the corners in relation to different wall sculptures are recorded in Table 2.

In *Mougeotia* the zygospore wall is composed of an outer chitinous layer which is ornamented, and an inner transparent layer. In *Temnogametum* the spore wall consists of three layers of which the outer and inner are thin and hyaline, and the median is layered, chitinous, and ornamented (Randhawa, 1959, pp. 84, 87).

ENVIRONMENTAL MODIFICATION

The morphogenesis of algal cells is affected by nutritional and environmental factors such as chemical composition and temperature of the medium.

Nutritional influences

"Several inorganic elements or organic compounds trigger pronounced structural changes. For the inorganic nutrients the phenomena involved are : control of cell size and shape, wall ornamentation, unicell production, colony formation, sheath and mucilage formation...and auxospore formation. With organic compounds some organisms can form spines, produce unicells rather than colonies, or develop into a palmelloid state" (Trainor, 1970, p. 755).

The morphogenesis in strains of the acid resistant *Scenedesmus* Meyen under different environmental conditions has been studied by several authors. Forms which produce sporopollenins and have trilaminar wall sheaths are known in this genus (Atkinson *et al.*, 1972, p. 22; Staehelin & Pikett-Heaps, 1975, p. 167). The ratio between coenobia and unicells is affected by the phosphate uptake; the formation of unicells increases with an increase in the phosphate concentration of the medium (Overbeck & Stange-Bursche, 1965, p. 362). The development of bristles was shown to be due to influence of ammonia. When grown in the presence of ammonium at pH 8.5 or above the organism would be unicellular with numerous bristles like *Franceia* Lemmermann, but in a medium without ammonium spiny colonies were abundant (Trainor & Roskosky, 1967, p. 1661).

Soil bacteria can influence colonial or unicellular growth and the development of setae. A *Scenedesmus* culture isolated from soil developed colonies when grown in a soil extract medium. By addition of a soil bacteria the culture became unicellular (Trainor &

Rowland, 1968, p. 315). Ovoid unicells with four or many setae, like *Chodatella*, were mostly developed when soil extract was added to a culture medium (Swale, 1967, p. 287), but without soil extract the same strain did not develop unicells (Trainor, 1970, p. 752). When thiamine was added to a dilute inorganic medium *Chodatella*-like unicells were formed (Trainor, 1970, p. 752). In media with low concentrations of iron and calcium, growth was promoted but spines were not formed on coenobia. Spines were formed when the level of either iron or calcium was increased (Trainor, 1969, p. 188).

It appears from the aforementioned examples that *Scenedesmus* is pleomorphic and that the pleomorphism can be developed under the influence of various nutritional factors. It is not known in detail how the development of the specimens of this and other algal genera is influenced or what controls the formation of the unicellular specimens in nature (Trainor & Rowland, 1968, p. 311). It does not seem to be any connection between the formation of spiny unicells and colonies lacking spines, both of which are produced by the same *Scenedesmus* culture (Trainor, 1969, p. 189).

Temperature influences

It has been shown that the morphology of algae is influenced by water temperature. In many cases an increase of temperature can be accompanied by decrease of size of the algae and production of unicells instead of coenobia (Grimas, 1974, p. 45). In other cases the situation is the other way round.

Scenedesmus quadricauda (Turpin) Brebisson develops larger coenobia at lower temperatures. Below 20°C normal four-cell coenobia and a great share of eight-cell coenobia are developed. At 30°C about 80 per cent of the coenobia are two-celled. *Ankistrodesmus falcatus* (Corda) Ralfs produced large colonies below 20°C but only unicells at higher temperatures. The shape and size of *Oocystis submarina* Lagerheim seem on the other hand to be independent of temperature (Grimas, 1974, p. 43).

The modification of shape and size is possibly an adaptation to the density of water, which is correlated to the temperature. The surface-to-volume ratio, morphology, size adaptation, and colony formation and their interactions with the physical environment are discussed by Tappan and Loeblich (1973, p. 211).

The approximate size range of some modern algae and fossil *Tetraporina* is listed in Lindgren (1980, p. 345, table 3).

CONCLUSION

Forms which are morphologically similar to fossil *Tetraporina* occur in several modern algal taxa. The origin of the *Tetraporina*-species can be sought for

among unicellular forms, solitary forms which can also develop coenobia, coenobia which have disintegrated into individual cells, and resting spores.

It does not seem possible to assign the fossil form genus *Tetraporina* to any modern algal genus. The closest similarities seem to occur with cysts of the Dinophyceae, zygospores of the Zygnemataceae, individual cells of the coenobium of *Pediastrum*, and with specimens of *Porochloris*, *Tetradinium*, *Tetraedron* and *Tetraedriella*.

The great difficulties and diverse interpretations in classifying the modern quadrangular and tetrahedral algae demonstrates the impossibility of assigning their fossil counterparts to appropriate natural taxa, even at the rank of class.

ACKNOWLEDGEMENTS

The manuscript has been reviewed by Dr Kuno Thomasson, University of Uppsala.

REFERENCES

- Atkinson, Jr., A. W., Gunning, B. E. S. & John, P. C. L. 1972. Sporopollenin in the cell wall of *Chlorella* and other algae: ultrastructure, chemistry, and incorporation of ¹⁴C-acetate, studied in synchronous cultures. *Planta* **107** : 1-32. Berlin.
- Fott, B. 1959. Algenkunde. *Fischer, Jena*, 482 p.
- Fott, B. 1967. Taxonomische Übertragungen und Namensänderungen unter den Algen, II. *Prestia*, **39** : 352-364. Prague.
- Geel, B. van 1976. Fossil spores of Zygnemataceae in ditches of a prehistoric settlement in Hoogkarspel (the Netherlands). *Rev. Palaeobot. Palyno.* **22** : 337-344. Amsterdam.
- Geel, B. van 1979. Preliminary report on the history of Zygnemataceae and the use of their spores as ecological markers. *Proc. IV int. palynol. Conf., Lucknow (1976-77)* **1** : 467-469. Birbal Sahni Institute of Palaeobotany, Lucknow.
- Geel, B. van & Hammen, T. van der 1978. Zygnemataceae in Quaternary Colombian sediments. *Rev. Palaeobot. Palynol.* **25** : 377-392. Amsterdam.
- Grimas, U. 1974. Värmeeffekter på skilda nivåer i ekosystemet (in Swedish), in: *Kylvatten-effekter på miljön. Liber, Solna* : 37-73.
- Huber-Pestalozzi, G. 1950. Das Phytoplankton des Süßwassers. 3. Teil, in: *Die Binnengewässer*, **16**. Schweizerbart, Stuttgart, 310 p.
- Komárek, J. & Fott, B. 1983. Das Phytoplankton des Süßwassers. 7 : 1. Chlorophyceae (Grünalgen), Ordnung Chlorococcales. *Binnengewässer*, **16**(7 : 1) : 1-1044. Stuttgart.
- Korsikov, O. A. 1953. Vznachnik pryisnovodnikh vodorostej Ukrayinskoy RSR. V. (in *Ukrainian, Flora of fresh-water plants of the URSR V.*). Kiev, 439 p.
- Kováčik, L. 1975. Taxonomic review of the genus *Tetraedron* (Chlorococcales). *Arch. Hydrobiol., Suppl.* **46** (Algol. Stud., 13) : 354-391. Stuttgart.
- Kováčik, L. & Kalina, T. 1975. Ultrastructure of the cell wall of some species in the genus *Tetraedron*. *Arch. Hydrobiol., Suppl.* **46** (Algol. Stud., 13) : 433-444. Stuttgart.
- Lagerheim, G. 1894. Studien über arktische Cryptogamen. I. Über die Entwicklung von *Tetraedron* Kütz. und *Euastropsis* Lagerh., eine neue Gattung der Hydrodictyceen. *Tromsø Mus. Aarsbfter* **17** : 1-24. Tromsø.
- Lindgren, S. 1980. Algal microfossils of the form genus *Tetraporina* from Upper Cretaceous clays, southern Sweden. *Rev. Palaeobot. Palynol.* **30** : 333-359. Amsterdam.
- Migula, W. 1907. Kryptogamen-Flora. Band II, Algen. 1. Teil, in : *Thomé's Flora von Deutschland, Österreich und der Schweiz, 1904-1907*, **6**. F. von Zezschwitz, Gera, 918 p.
- Overbeck, J. & Stange-Bursche, E.-M. 1965. Experimentelle Untersuchungen zum Coenobienformwechsel von *Scenedesmus quadricauda* (Turp.) Bréb. *Ber. Dtsch. Bot. Ges.*, **78** : 357-372. Berlin.
- Pascher, A. 1929. *Porochloris*, eine eigenartige, epiphytische Grünalge aus der Verwandtschaft der Tetrasporalen. *Arch. Protistenkd.*, **68** : 427-450. Jena.
- Pascher, A. 1939. Heterokonten, in : Dr. L. Rabenhorst's *Kryptogamen-Flora*, **11**. Akad. Verlagsges. M.B.H., Leipzig, ed. 2, 1092 p.
- Pringsheim, N. 1861. Die Dauerschwärmer des Wassernetzes und einige ihnen verwandte Bildungen. *Monatsber. Preuss. Akad. Wiss. Berl.*, **1860** : 775-794. Berlin.
- Randhawa, M. S. 1959. *Zygnemataceae*. Indian Counc. Agric. Res., New Delhi, 478 p.
- Smith, G. M. 1950. *The fresh-water algae of the United States*. Mc Graw-Hill, New York, 2 ed., 719 p.
- Stæhelin, L. A. & Pickett-Heaps, J. D. 1975. The ultrastructure of *Scenedesmus* (Chlorophyceae). I. Species with the "reticulate" or "warted" type of ornamental layer. *J. Phycol.*, **11** : 163-185. Baltimore.
- Swale, E. M. F. 1967. A clone of *Scenedesmus* with *Chodatella* stages. *Br. Phycol. Bull.* **3** : 281-293. Glasgow.
- Tanner, H. 1923. La protéolyse par les algues et le polymorphisme du *Tetraedron minimum*. *Univ. Genève, Thèse*, **728** : 1-36.
- Tappan, H. & Loeblich Jr., A. R. 1973. Evolution of the oceanic plankton. *Earth-Sci. Rev.* **9** : 207-240. Amsterdam.
- Trainor, F. R. 1969. *Scenedesmus* morphogenesis. Trace elements and spine formation. *J. Phycol.* **5** : 185-190. Baltimore.
- Trainor, F. R. 1970. Algal morphogenesis: nutritional factors. *Ann. N. Y. Acad. Sci.* **175** : 749-756. New York.
- Trainor, F. R. & Roskosky, F. G. 1967. Control of unicell formation in a soil *Scenedesmus*. *Can. J. Bot.* **45** : 1657-1664. Ottawa.
- Trainor, F. R. & Rowland, H. L. 1968. Control of colony and unicell formation in a synchronized *Scenedesmus*. *J. Phycol.* **4** : 310-317. Baltimore.
- Troitzkaja, O. W. 1933. Über die morphologische Variabilität bei den Protococcales (in Russian, summary in German). *Trudy Bot. Inst. Akad. Nauk SSSR*, Ser. **2**(1) : 115-242. Leningrad.
- Wille, N. 1908. Zur Entwicklungsgeschichte der Gattung *Oocystis*. *Ber. Dtsch. Bot. Ges.*, **26a** : 812-822. Berlin.
- Wille, W. 1970. *Plaesiodyctyon mosellanum* n. g., n. sp., eine mehrzellige Grünalge aus dem Unteren Keuper von Luxemburg. *Neues Jb. Geol. Paläontol. Mb.*, **5** : 283-310. Stuttgart.