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Oocystis lacustris CHOD. (Chlorophyta, Trebouxiophyceae) in Lake Tanganyika (Africa)

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A b s t r a c t : Representatives of the Trebouxiophycean green algal genus *Oocystis* A. Br. 1855 in phytoplankton samples from Lake Tanganyika (Africa) were investigated. Up-to-date taxonomy of most described taxa is problematic and needs revision. Special attention was paid to the general morphology of single cells and colonies of a group of species around *Oocystis lacustris* CHODAT, where many inconsequences of descriptions and drawings, as overlapping of diacritical features exist. The morphological variability of *O. lacustris* and the closely related *O. marssonii* LEMM., *O. parva* W. WEST et G. S. WEST, *O. borgei* SNOW and *O. nephrocytioides* FOTT & ČADO was summarized in a tabular form and combined with figures from different authors. The broad range of morphological variability observed in the Tanganyika material let us decide to identify all the specimens found as belonging to the single species - *O. lacustris* CHODAT, including all other aforementioned taxa as synonyms.

K e y w o r d s : *Oocystis lacustris*, *Oocystis marssonii*, *Oocystis parva*, *Oocystis borgei*, *Oocystis nephrocytioides*; Tanganyika

Introduction

Species belonging to the genus *Oocystis* A. BRAUN 1855 are quite common in different water bodies (particularly in freshwater ecosystems and predominantly in the plankton of small lakes and ponds – VAN DEN HOEK et al. 1995), but occur as well in terrestrial habitats (BOLD & WYNNE 1985; ETTL & GÄRTNER 1995). During recent studies of Lake Tanganyika representatives of *Oocystis* were recognized among the important biomass contributors in the phytoplankton (STOYNEVA et al. 2007). The identification procedure with analysis of preceding taxonomical works and of studies on relevant African material[1], brought us to problems of species delimitation in this genus (particularly in *O. lacustris* CHODAT 1897 group), which show the need for new sharpening of the attention of algologists to the unsatisfactory classification in *Oocystis* and proposal of some operational solutions, which could be used in further limnological studies.

The traditional approach to the species delimitation (which originated mainly from the studies of natural populations) in algology still is based on morphologically derived

[1] including Madagascar

units, nevertheless that at present the species concept in algae and particularly in asexually reproducing organisms is under intensive discussion and some modern methods combined with ecological characteristics are involved (KOMÁREK & ANAGNOSTIDIS 1999). Before going into the 'shifting sands' of using lower taxonomic ranks (MANN 1997) in *O. lacustris*-group it is necessary to make a more detailed introduction, which objectives include: i) characterization of the family Oocystaceae and the genus *Oocystis* together with (ii) a discussion of specific criteria in the genus, combined with (iii) a detailed, illustrated discussion of diacritical features used by different authors in one of the most problematic groups of related species – *O. lacustris* – *O. marssonii* LEMMERMANN 1898 – *O. parva* W. WEST et G.S. WEST 1898 – *O. borgei* SNOW 1902 – *O. nephrocytioides* FOTT & ČADO 1966; and (iv) comments on previous African material from these species.

General notes on *Oocystis* with particular reference to its taxonomy and diagnostic criteria

After its description the genus *Oocystis* was placed among the 21 genera of Palmellaceae (DECAISNE) NÄGELI em. 1847 (e.g. COOKE 1882). DE TONI (1886) and DE WILDEMAN (1896) kept *Oocystis* in the same family, but separated it together with *Nephrocytium* NÄGELI 1849 in the subfamily Nephrocytieae DE TONI 1888. By the work of BOHLIN (1901) *Oocystis* became the type genus of Oocystaceae and since then the last represent a distinct family in most monographs on green (e.g. LEMMERMANN et al. 1915; KORSHIKOV 1953; BOURRELLY 1966, 1988; FOTT 1971; PICKETT-HEAPS 1975; HINDÁK 1977, 1980, 1984, 1988, 1990; KOMÁREK & FOTT 1983), freshwater (LINDAU & MELCHIOR 1930; SMITH 1950; PRESCOTT 1962;) or aerophytic algae (ETTL & GÄRTNER 1995), as well as in some general phycological manuals (IYENGAR 1951; BEGER 1954. LOUIS 1968; PRESCOTT 1969; SILVA 1982; BOLD & WYNNE 1985; LEE 1989). The members of Oocystaceae in recent understanding have more or less spherical, ellipsoidal, fusiform or cylindrical cells and propagate by autosporulation[2], releasing spores by fracture or gelatinization of wall. These characteristics combined with the ultrastructure of multilayered cell walls (where the crystalline cellulose fibrils orientation in each layer is perpendicular to that of the adjoining layers) are well supported by molecular data and recently phylogenetic analysis showed that Oocystaceae are a distinct monophyletic group within the Trebouxiophyceae FRIEDL 1995[3] (HEPPERLE et al. 2000; KRIENITZ et al. 2003).

In 1966, SMITH & BOLD (p. 91) noted the existing of 'a desperate need for detailed comparative morphological and physiological studies of the entire Oocystaceae, with the goals that its genera will be more fully characterized and, perhaps, more serviceably and accurately classified than they are at present'. However, the genera included in Oocystaceae still varied, depending on the author; e.g. SMITH (1950), PRESCOTT (1962), KORSHIKOV (1953), BOURRELLY (1966 1988), COMPÈRE (1976) and MELKONIAN (1983) have broader understanding of the family than BEGER (1954), LINDAU & MELCHIOR

[2] Aplanospore formation (WILLE 1908; PRINTZ 1913; SMITH 1950; PRESCOTT 1969) and sexual reproduction (HALLETT 1962; HINDÁK 1988; HINDÁK & HINDÁKOVA 2003) are still not confirmed for all species of the genus *Oocystis* and for all other members of the family

[3] VAN DEN HOEK et al. (1995) still positioned *Oocystis* in Chlorophyceae

(1930), ETTL & KOMÁREK (1982), KOMÁREK (1983) and KOMÁREK & FOTT (1983). Different opinions about the bulk of taxa included concern also the infrageneric level of the type genus *Oocystis*. This interesting genus, which is 'in some ways intermediate between the coccoid unicellular and coccoid colonial levels of organization' (VAN DEN HOEK et al. 1995, p. 365-366) is recently recognized as a member of subfamily Oocystoideae[4], distinguished from other subfamilies by the peculiarity that adult daughter cells live for a long time in the mother cell wall which becomes distinctly enlarged to a greater or lesser extent (FOTT 1976; KOMÁREK & FOTT 1983).

The first monograph on *Oocystis* was published by PRINTZ (1913)[5] and was followed by many descriptions of new species and varieties (e.g. PLAYFAIR 1916; SMITH 1920; CHODAT 1931; MOEWUS 1951; HORTOBAGYI 1962; HORTOBAGYI & NÉMETH 1963; REISIGL 1964; SKUJA 1964; BATURINA 1966; FOTT & ČADO 1966; PROSHKINA-LAWRENKO 1967; GROOVER & BOLD 1968; GUILLARD et al. 1975; WATANABE 1978; HEGEWALD et al. 1980; HINDÁK 1988, 1990). The biochemical properties and cell ultrastructure with emphasis on cell wall organization have been studied on some *Oocystis* species (ORCUTT & RICHARDSON 1970; ROBINSON & PRESTON 1972; ROBINSON & WHITE 1972; SCHWERTNER et al. 1972[6]; SACHS et al. 1976; ROBINSON & HERZOG 1977; MONTEZINOS & BROWN 1978; QUADER & ROBINSON 1981; LEE & PICARD 1982, 1983; QUADER et al. 1983; QUADER 1986; EMONS et al. 1992; CHANG & SIBLEY 1993), *O. marssonii* among them (PENDLAND & ALDRICH 1972, 1973a, b). The complete 18S rRNA gene sequences based on 3 strains from America and Europe (Peru, France and Germany) have been made for three species – *Oocystis heteromucosa* HEGEWALD 1980, *O. marssonii* LEMMERMANN 1898 and *O. solitaria* WITTROCK 1879 in WITTROCK & NORDSTEDT 1889 (HEPPERLE et al. 2000).

In spite of this complex approach, the taxonomy of *Oocystis* still remained unclear and doubt attaches to many of the more than 90 currently recognized species (JOHN & TSARENKO 2002). In almost each taxonomic monograph the need of more data from various world localities and of more profound studies on each species with the range of its morphological variation is noted especially since the opinions of different authors contradict even on the diacritical features of the species. Nevertheless that it is more and more widely accepted that traditional morphology has often been lacking in value (WATANABE & FLOYD 1996), still the diagnostic features relied upon are generally morphological, all of which could be observed by light microscopy (e.g. JOHN & TSARENKO 2002). Among them the presence or absence of a mucilage envelope and the possibility to use the way of autospore release (through fracture or dissolution of the parent cell wall) for species separation was strongly supported by ŘEHÁKOVÁ (1969)[7].

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[4] Oocysteae – in BRUNNTHALER (1915) and BEGER (1954), distinguished by the absence of spines on cells from Lagerheimieae and by cell shape from Nephrocytieae

[5] Since the diagnoses in generalization of PRINTZ (1913) are more complete than the originals, hereafter we shall refer to his data as to first reliable data

[6] *Oocystis polymorpha* studied in this paper, more recently is referred as a member of genus *Ecdysichlamys* G. S. WEST 1912 (KOMÁREK & FOTT 1983)

[7] Only some years earlier distention of mother cell wall in *Oocystis* accompanied by a gradual dissolution of the wall during release of daughter cells had been mentioned as good differential criteria and had been used by authors for the taxonomic disposition of certain other *Oocystis*-like algal genera with non-distend mother walls where release resulted from daughter cell expansion and subsequent stretching and rupture

FOTT (1976) and TIKKANEN & WILLÉN (1992) used the last feature for distinguishing some closely related species. JOHN & TSARENKO (2002) also applied it, but much more precautiously, in combination with words like 'often', 'usually' and 'only rarely'. However, HINDÁK (1980, 1984) proved that the same species could use different ways for release of autospores and practically the same possibility is shown in the descriptions of JOHN & TSARENKO (2002). Concerning mucilage, HINDÁK (1988, p. 112) underlined that 'a mucous envelope has hitherto been found by the author with each species of *Oocystis/Oocystella*, although in some specimens it was weekly formed, or missing (namely in laboratory cultures)'.

Chloroplast number in each cell has been considered among the primary criteria for classification by majority of the authors. However, this diacritical feature seems also to be quite discussional, since these numbers change by age[8], often overlap and in keys and descriptions the data on chloroplast number are cohabiting by words like 'generally', 'usually' and 'normally', as well as 'depending on age'. The chloroplast descriptions ranged around 'parietal', but the exact shape was rarely mentioned. The need for more precise data on chloroplast numbers and structure for taxonomic purposes was underlined by most of the aforementioned authors and by LEGOVIČ (1962). ŘEHÁKOVÁ (1969) applied the number of chloroplasts in autospores in her key for distinguishing two groups among *Oocystis* species with smooth cell wall – *O. lacustris* and *O. parva* with one, and *O. marssonii* with 1-2 chloroplasts in autospores. FOTT (1976) used this characteristic in his key for separation of *O. marssonii*, *O. lacustris* and *O. parva*, with 1, rare 2 chloroplasts in autospores from *O. solitaria*, with 2 chloroplasts in its autospores. HINDÁK (1980) and KOMÁREK & FOTT (1983) also mentioned it in their descriptions and later on HINDÁK (1988) again suggested to use it for species separation (e.g. *O. marssonii* from *O. lacustris*). In the same time he underlined the need of verification whether this characteristic could be used as a sole reliable differentiating feature.

The most debatable diacritical feature still remains the presence or absence of pyrenoid in the chloroplasts of adult cells (for more details see discussions in KORSHIKOV 1953; HINDÁK 1988; JOHN & TSARENKO 2002). LOUIS (1968) and ŘEHÁKOVÁ (1969) stated that there is always a pyrenoid, KORSHIKOV (1953) noted that he himself had never seen cells without pyrenoids, most of the authors pointed that pyrenoids could be present or absent, while FOTT (1976) and LEE (1989) did not even mention them. HINDÁK (1988) re-established the genus *Oocystella* LEMMERMANN 1903 and transferred to it all species with pyrenoid. This considerably reduced the species within the genus *Oocystis*, in which remained all taxa without pyrenoid, as it was in the original material and description of *O. naegeli* by A. BRAUN (1855). JOHN & TSARENKO (2002) and SHUBERT (2003) did not accept this transformation. The last authors acceded to the formerly expressed opinion by LEMMERMANN et al. (1915), PRESCOTT (1962), KORSHIKOV (1953), BOURRELLY (1966, 1988), COMPÈRE (1976) and KOMÁREK & FOTT (1983), who included *Oocystella* in *Oocystis*. Noteworthy is that 5 years after creating the genus *Oocystella* for the single species *O. natans* with a pyrenoid, LEMMERMANN (1908) himself reclassified it among *Oocystis* and since then it became a synonym of the genus *Oocystis*, or the section

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of the surrounding wall (notably *Siderocelis* FOTT 1934 but also *Eremosphaera* DE BARY 1898 – THOMPSON, 1952; FOTT & ŘEHÁKOVÁ, 1963; SMITH & BOLD, 1966).

[8] the trend of increasing number of chloroplasts by age was strongly underlined as family feature by KOMÁREK (1983)

Oocystella (LEMMERMANN) WILLE 1909 of this genus (e.g. PRINTZ 1913; BRUNNTHALER 1915).

Among the non-debatable diacritic species features still are the cell shape and presence or absence of thickenings on the cell poles (polar nodules). However, studying the morphological variation of *O. marssonii* on different media TSCHERMAK (1942) noticed that cells of *O. marssonii* (reported under the name *O. crassa* var. *marssonii*) kept in acidic culture medium showed fusiform shapes with striking thickenings on the poles, while cells from agar cultures were more rounded and sometimes with nearly not visible polar nodules (Fig. 65). She stated that 'without knowledge of this connection such forms could be identified as different varieties' (TSCHERMAK 1942, p. 586). Later, comparing field and culture material of *O. lacustris* from different localities HINDÁK (1980, p. 91) also showed that 'apical thickenings were somewhere well visible in form of short beak-like extension, or the cell wall was only thickened on the poles or there were no apical thickenings produced at all'. The contradiction of data on polar thickenings could be exemplified on *O. lacustris*: KOMÁREK & FOTT (1983) pointed that polar nodules are not clear and are sometimes present, while for the same species JOHN and TSARENKO (2002) noted that nodules are distinct. SKUJA (1956) underlined the possibility for both presence and absence of polar thickenings in *O. borgei* (Table 1A). SMITH & BOLD (1966, p. 34) noted that 'nodules do not always develop in cells of a given species' and used this to reject the character of polar nodulation as a good but generic criterion for *Oocystis*. The taxonomic importance of cell wall sculpture was recognized years ago by FOTT (1934), KORSHIKOV (1953) and HINDÁK (1977), who established the new genera *Siderocelis* FOTT, *Amphikrikos* KORSHIKOV, *Granulocystopsis* HINDÁK and *Granulocystis* HINDÁK, differentiated by surface granulation and its organization. HEYNIG (1991) accepting the granulated mucilage capsule as a generic feature, in combination with smooth cell wall established a new genus – *Oocystopsis*[9], which is closely related to the genera *Oocystis*, *Granulocystis* and *Granulocystopsis*. ŘEHÁKOVÁ (1969) also used the smooth or granulated character of cell wall, but just to separate some of the species within the genus *Oocystis*.

Asymmetrical cells have been depicted for single cells of *O. lacustris* by WEST (represented as Fig. 96a in BRUNNTHALER (1915) and as Fig. 2b in this paper) and mentioned by JOHN & TSARENKO (2002). By contrast, in KOMÁREK & FOTT (1983) *O. lacustris* was pointed to have symmetrical cells. ŘEHÁKOVÁ (1969) noted the appearance of cell asymmetry in *O. marssonii* and *O. parva*, and HINDÁK (1988) recorded slight asymmetry of cells in *O. borgei*. Asymmetry was underlined by FOTT & ČADO (1966) among the peculiarities of their new species *O. nephrocytioides*, which distinguished it from the resembling species *O. borgei*. Following the description of REISIGL (1964) ETTL & GÄRTNER (1995) used in their key the heteropolarity of cells of *O. alpina* REISIGL for species separation. KOMÁREK & FOTT (1983) suggested transfer of some *Oocystis* species with asymmetrical cells to the genus *Ecdysichlamys* G. S. WEST 1912, but still many questions around this taxon remained.

The size of the cells is still regarded as having important taxonomic significance at species level, nevertheless that most of the diagnoses are brief and incomplete. This could easily be demonstrated in the case of *O. lacustris* and *O. parva*, where an addi-

[9] on the basis of *Oocystis granulata* HORTOBAGYI 1962

tional hitch lies in the fact that CHODAT (1897) did not give information on the cell dimensions in his diagnosis on *O. lacustris*, a year before *O. parva* was published. Therefore, the dimensions accepted for this species varied significantly (Table 1B) and orientation was made generally according to the WEST & WEST (1898) description of *O. parva*.

The position of the cells in the colonies was applied for species delimitation first by PRINTZ (1913) and later on in the keys of KOMÁREK & FOTT (1983) and JOHN & TSARENKO (2002) nevertheless that earlier SMITH & BOLD (1966) both in generic description of *Oocystis* and in general discussion on differences between *Eremosphaera* and *Oocystis* outlined that in the last genus autospores are 'loosely enclosed within a gradually distended mother cell wall' (p. 38) and that 'it is apparent from the literature and from study of few species available that none of them has... daughter cells tightly surrounded by a non-distended mother cell wall' (p. 40). Frequency of formation of solitary cells and colonies is often noted in the descriptions, but was never used as separate specific diacritical feature[10]. FOTT (1976) and KOMÁREK & FOTT (1983) applied the presence or absence of compound colonies in different steps of their keys.

Describing the *Oocystis* generic features KORSHIKOV (1953, p. 252) wrote: 'the systematics of the genus remains in an exceedingly satisfactory state through the superficiality of the descriptions of most of the known species[11]'. Here has to be added the frequent inaccuracy of figures provided by different authors and outlined in the comments by HINDÁK (1988). In spite of some attempts to apply statistic methods for taxonomic decisions (JAVORNICKY & ŘEHÁKOVÁ 1964), still the identification keys on *Oocystis* are not satisfactory. This is due also to the fact that many quantitative characteristics overlap and often reliable species identification requires examination of large populations to observe the full range of potential morphological variation (JOHN & TSARENKO 2002). In contrast to culture material, the field morphological variability of infrageneric taxa of *Oocystis* had rarely been discussed profoundly (e.g. HINDÁK 1980, 1984, 1988), although some short notes on existence of great variability are almost always added in numerous floristic publications. In the same time, as a consequence of making species identifications solely from field material some unicellular morphs of *Oocystis* due to their variable morphology have been misidentified with *Desmodesmus* AN, FRIEDL ET HEGEWALD 1999 (SHUBERT 2003). FOERSTER (1971) reported interesting results on environmentally induced morphological changes in *Oocystis lacustris* (?): after more than one year cultivation and alteration of medium (from a freshwater sample to sea water medium and then to soil-water extract medium 0.03 p.p.m.) a change in morphology of *O. submarina* (?) LAGERH. produced an organism which could be classified as *O. lacustris* (?) CHODAT.

The morphological variability of *Oocystis* in Africa has never been a subject of entire study, nevertheless that it is one of the most frequently mentioned chlorococcal genera in almost all algological and limnological works and appears among the abundant algae or even as dominant in some water bodies (e.g. WEST 1907; HECKY & KLING 1987;

[10] This cell state together with the size and position of nucleus, as well as with cytoplasm character were proposed by SMITH & BOLD (1966) among the morphological criteria for the separation of *Eremosphaera*, *Oocystis* and the provisional *Eremosphaera oocystoides* group.

[11] citation according to translation by J. W. G. LUND and W. TYLKA in the English version, printed in 1987 by Binen Singh Mahendra Pal Singh and Koeltz Scientific Books

COCQUYT & VYVERMAN 1994; ZOHARY et al. 1995, 1996). Up-to-date about 33 taxa of this genus had been reported for the continent in more than 65 publications, *O. lacustris*, *O. parva*, *O. marssonii* and *O. borgei* among them.

The aim of this paper is to present data on field morphological variability of an important species in the phytoplankton of Lake Tanganyika, *Oocystis lacustris* CHODAT with discussion of its relations with the closely related species *Oocystis borgei*, *O. parva* and *O. marssonii*, as well as with the still uncertain species *O. nephrocytioides*.

The similarities between all these species and possibility of their confusion are underlined in almost all monographs and are well known not only to so-called pure taxonomists but also to each limnologist dealing with quantitative or fixed field material. In order to present a complete summary on diacritical features used by different authors more clearly and concisely than would be possible in a lengthy textual discussion, they are rendered here in chronological order in tabular form (Table 1) and are combined with Figs. 1-20, 29-38, 43-52, 61-67. Therefore in the text below only some comments are provided.

Comments on former descriptions and species delimitation of *Oocystis lacustris - O. parva - O. marssonii – O. borgei* and *O. nephrocytioides*

Originally, all these taxa were described as separate species: *Oocystis lacustris* - by CHODAT in 1897, *Oocystis parva* – one year later by W. et G. S. WEST, just in the same year –1898 – when LEMMERMANN published *Oocystis marssonii*, and *O. borgei* – by SNOW in 1903. Very soon LEMMERMANN (1903) assigned *O. borgei* SNOW as a variety, to *O. gigas* Archer 1877 and PRINTZ (1913) transformed *O. marssonii* LEMMERMANN to a variety of *O. crassa* WITTROCK 1879 in WITTROCK & NORDSTEDT 1889[12]. But following LEMMERMANN, PRINTZ (1913, p. 12) noted that *O. marssonii* (*O. crassa* var. *marssonii* (LEMMERMANN) PRINTZ) is very close to *O. lacustris* and the differences lay generally in cell shapes and in the mother cell wall, as well as in the presence or absence of pyrenoid (Table 1; Figs. 1, 61). He positioned *O. borgei* and *O. crassa* var. *marssonii* in the section *Oocystella* (LEMMERMANN) WILLE 1909, distinguished by the presence of pyrenoid, while *O. lacustris* and *O. parva* remained in the section *Euoocystis* (LEMMERMANN) WILLE 1909, where species did not have such part of the chloroplast (Table 1; Figs. 29, 43, 61). Only two years later BRUNNTHALER (1915) placed all the species mentioned above in the *Euoocystis* section (Table 1; Figs. 2, 30, 44, 62a, b).

SMITH (1950) did not provide species descriptions, but represented the genus *Oocystis* with illustrations on *O. lacustris*, *O. parva*, *O. borgei* (Figs. 3, 31, 45) and *O. crassa*. There: 1) all sporangia (except *O. parva*) were lemon-shaped; 2) *O. borgei*, *O. crassa* and *O. parva* seemed to have pyrenoids; 3) cells in the colonies of *O. borgei* and *O. parva* contained different number of chloroplasts and were without polar thickenings. Mucilage and the way of autospore release were not mentioned in the genus description.

KORSHIKOV (1953), following PRINTZ (1913) accepted the variety status of *O. marssonii* as O. *crassa* var. *marssonii* (LEMMERMANN) PRINTZ (Table 1; Fig. 62a). However, this remained unclear because the number of chloroplasts (6-10 in the key and 4-10 in the

[12] KOMÁREK & FOTT (1983) accepted *O. crassa* as synonym of *O. solitaria* WITTROCK 1879 in WITTROCK & NORDSTEDT 1889

text) separated *O. crassa* from other species, while its var. *marssonii* was pointed to have 1-2 chloroplasts.

SKUJA (1956) depicted *O. lacustris*, *O. borgei* and *O. marssonii* from Swedish freshwaters. Since this regional floristic work followed by SKUJA's publication in 1964 influenced many further algological studies and taxonomic decisions, all data are summarized in Table 1 and in Figs. 6, 7, 48a-c. SKUJA (1956) outlined the similarity between *O. lacustris* and *O. marssonii*, as well as between *O. marssonii* and *O. borgei* (Table 1). He mentioned the degree of visibility of pyrenoids as difference between O. *borgei* and *O. marssonii* (Table 1C).

PRESCOTT (1962) did not discuss *O. marssonii* at all and separated *O. lacustris* from *O. parva* generally by the shape of the cells and their poles (Table 1; Figs. 5, 34). Both species – *O. lacustris* and *O. parva* have the same number and position of chloroplasts (1-3 (rarely 4), parietal). Slight and unsure difference appeared in description of pyrenoids – 'chloroplasts usually containing 1 pyrenoid' for *O. lacustris* and 'pyrenoids sometimes present' in *O. parva*. *O. crassa* (in which *O. marssonii* is often included) is situated in the group of species with polar nodular thickenings of cells (together with *O. lacustris*) and is characterized by the presence of 4-10 relatively large parietal chloroplasts with pyrenoids 'usually present'. The determination of *O. crassa* and *O. lacustris* according to PRESCOTT (1962) is really confusing since the cell shape is almost similar and dimensions, as well as number of chloroplasts obviously overlap (Table 1A-C). The separation of *O. parva* looks clearer due to smaller cell dimensions (4-7.5x6-15.5 μm) and to the absence of nodular thickenings.

FOTT & ČADO (1966) described the species *Oocystis nephrocytioides* (Fig. 67), which in their opinion was quite similar to *O. borgei* but differred by its mucilaginous mother-cell walls, by the asymmetrical shape of its cells (slightly kidney-shaped) and by its manner of autospore formation through complete gelatinization of mother wall. HINDÁK (1977) considered *O. nephrocytioides* as belonging to the genus *Kirchneriella* SCHMIDLE 1893. KOMÁREK & FOTT (1983) positioned it again in genus *Oocystis* but among its unclear species.

SMITH & BOLD (1966) in their comparative studies on morphology and physiology of genera *Eremosphaera* DE BARY 1858 and *Oocystis* used only 3 strains of the last genus. *O. marssonii* was among them and its full description in different culture media was presented and combined with photographs. The small magnification used did not allow us to include them in the figures to this paper, but the summary of the textual description is provided in Table 1.

PHILIPOSE (1967) discussed 12 species from India, among which *O. lacustris* and *O. borgei* were distinguished generally by presence/absence of polar nodules (Table 1). *O. crassa* (to which *O. marssonii* was often assigned) was separated from the closest species *O. lacustris* (Fig. 8) by the inconspicuous polar nodules and by the presence of 4-10 chloroplasts, each with one pyrenoid.

ŘEHÁKOVÁ (1969) made a profound study of culture material and provided many data on cell ontogenesis on 7 species, 2 varieties and 2 forms of *Oocystis*. In this work the differences between *O. lacustris*, *O. parva* and *O. marssonii* have been shown (Table 1; Figs. 10, 33, 63), but *O. borgei* was not discussed at all.

As it was already mentioned, ŘEHÁKOVÁ (1969) emphasized not only on the chloroplast

number but also on the presence/absence of mucilage around cells and on the differences in release of autospores. Since HINDÁK (1980) showed that the last feature varied even among the same species, it could be stated that in terms of ŘEHÁKOVÁ (1969) *O. parva* is differentiated from *O. lacustris* only by the absence of mucilage envelope, *O. borgei* from *O. marssonii* only by the presence of mucilage and *O. borgei* from *O. lacustris* by larger cell dimensions (Table 1). In 1980 HINDÁK still accepted the presence or absence of mucilage as distinguishing feature between *O. lacustris* and *O. parva* (Figs. 11-13). However, in 1984 and in 1988 he pointed that older authors did not pay special attention to the mucilage and usually they did not even mention it, while in his opinion mucous envelope is always present in planktic *Oocystis/Oocystella* species. Therefore HINDÁK (1984) accepted *O. parva* and *O. marssonii* as synonyms of *O. lacustris*, which had great variability in the size of cells and sporangia (Table 1; Figs. 15-17). In 1988, following SMITH (1920) and SKUJA (1964), HINDÁK again differentiated *O. lacustris* from *O. parva* (Fig. 36), this time using only larger dimensions of cells and colonies of *O. lacustris* (Table 1B). In the same publication HINDÁK re-established the genus *Oocystella* LEMMERMANN for species with pyrenoids, to which *Oocystis lacustris*, *O. parva*, *O. marssonii* and *O. borgei* were transferred. In 1988 HINDÁK noted the resemblance between *O. borgei* and *O. marssonii* (Figs. 50, 64) by cell size and by 2-4 chloroplasts in autospores, but found the difference in cell shape (broadly oval to broadly fusiform, mostly without polar thickenings, or only with slight thickenings in *O. borgei* and elongately elliptical with polar nodules in *O. marssonii*) and in the way of expansion of mother cell wall (slight in *O. borgei* and in contrast, marked expansion with forming of composite colonies from 2-3 generations in *O. marssonii*). HINDÁK did not comment the number of chloroplasts (4-16) found in his *O. borgei* material by which these specimens resemble another group of species of the genus *Oocystis* – *O. pelagica* LEMMERMANN 1901 - *O. solitaria* and partially *O. crassa* (if accepted as separate species), which have more chloroplasts. However, in the subsequent comments on *O. marssonii* HINDÁK (1988, p.125) noted: 'According to older literary data, the number of chloroplasts in adult *O. marssonii* cells is indicated as being 8 (or even more)'. Thus, the overlapping in chloroplast number in adult cells of both species is obvious (Table 1C).

FOTT (1976) included all 5 species in his paper, separating them in two groups: a first group containing *O. nephrocytioides* as a single species with dissolved mother cell wall and all other species in a second group with persistent parental wall. According to this author the remaining four species were unified by the peculiarity of lacking compound colonies. The next delimitation is made on the basis of the polar nodules, *O. borgei* pointed to be without them. *O. marssonii*, *O. lacustris* and *O. parva* were included in a group with 1, rare with 2 chloroplasts in autospores and vegetative cells with 2-4, rare more, chloroplasts. Further separation is made according to cell shapes and dimensions – *O. marssonii* with spindle cells up to 14 µm long, while *O. lacustris* and *O. parva* were with ellipsoidal cells less than 14 µm. Finally both *O. lacustris* and *O. parva* were delimitated by their dimensions and mode of autospore release – the first species having greatest cells long 15 µm and releasing daughter cells by gelatinization of cell wall and the second – having cells which are no more than 11 µm long and proliferating after rupture of parent wall (Table 1).

KOMÁREK & FOTT (1983) grouped all the species discussed above[13] (Figs. 14, 33c, d,

[13] including *O. nephrocytioides*

48a-c, 63c-e) firstly due to presence of 1-4-(8-10?) chloroplasts in vegetative cells and 1 chloroplast in autospores and after that in a second group of species which do not form compound colonies of 2-3 generations and are free-laying in the colonies. In this second group the species are separated by cell shape, character of cell ends and presence or absence of polar nodules, dimensions, presence of mucilage and number of released autospores (Table 1). According to them, the only species in a wide mucilage sheet is *O. lacustris* (Table 1; Fig. 14).

DILLARD (1989) divided *Oocystis* species in two groups: first including taxa with more than 4 chloroplasts and second, which contained taxa with 1-4 chloroplasts. *O. lacustris*, *O. parva* and *O. borgei* belonged to the second group. In the next step of the key, *O. lacustris* was separated from *O. parva* and *O. borgei* according to the daughter cells, which retained within a poorly defined and unstratified mucilagineous envelope. *O. parva* and *O. borgei* belonged to the group of species in which daughter cells retained in a sharply defined and often stratified mucilageneous envelope. The further delimitation between *O. parva* and *O. borgei* is made on the basis of cell dimensions (Table 1B).

TIKKANEN & WILLÉN (1992) differentiated *O. lacustris* from *O. parva* mainly by the way of autospore release (Table 1; Figs. 18, 37). When identifying Australian material LING & TYLER (2000) followed the determinations by PHILIPOSE (1967) and KOMÁREK & FOTT (1983) for *O. lacustris*, *O. parva* and *O. borgei* (Table 1; Figs. 19, 38, 52).

JOHN & TSARENKO (2002, p. 374) noted that 'acc. to HINDÁK (1988), the species (*O. lacustris*) can be reliably separated from *O. parva* only by differences in cell size. Despite the considerable overlap in size between *O. lacustris* and *O. marssonii*, it is considered by HINDÁK (1984) and others to be the only reliable character for separating the two species'. About *O. marssonii* JOHN & TSARENKO (2002, p. 374) wrote: 'Several authors have questioned the validity of this species which closely resembles *O. lacustris*...' However, they still distinguished *O. marssonii* from *O. lacustris* by the shape of chloroplasts (with slight difference in the number – Table 1) and by different way of autospore release in their key, while in the text the last difference is with more fuzzed borders (descriptions on p. 374 in JOHN & TSARENKO 2002 and Table 1 in this paper). The other closely related species – *O. parva* is delimited by its bluntly pointed apices, dense packed cells in colonies and presence of pyrenoid. The both species *O. parva* and *O. borgei* are distinguished from *O. lacustris* and *O. marssonii* by the absence of apical thickenings of cell walls (Table 1; Figs. 20, 33b, 48a-c, 63c, e).

KOMÁREK (1983) studied *O. marssonii* and *O. parva* from Cuba, outlining that these specimens were not identical with the European representatives of both species and including them as forms in his systematic list. Due to differences pointed out by KOMÁREK these data are not included in comparative Table 1 but have been taken into account during our work (Figs. 66, 69). Some differences in species features could be found if these descriptions are compared with KOMÁREK & FOTT (1983). The last authors pointed 'narrow or wide ellipsoidal' cell shape and presence of one pyrenoid for *O. parva*, while in KOMÁREK (1983) cells of the same species were mentioned as 'oval' with 'pyrenoid not clearly observed' without special comment. If the first authors placed *O. parva* among the species that do not form compound colonies, KOMÁREK (1983) described compound colonies of 2 generations, which occurred 'sometimes'. KOMÁREK & FOTT (1983) did not mention polar nodules on autosporangial wall, while KOMÁREK (1983) described them as visible polar thickenings. *O. marssonii* from Cuba differed 'mainly by their smaller average dimensions, by the tendency to live mainly in colonies,

by commonly occurring cells with one chloroplast and by the less enlarged mother-cell wall around the daughter cells' (KOMÁREK 1983, p. 108).

Taking into account Australian material from more than 256 samples, in 52 of which forms of *Oocystis* occurred more or less plentifully, PLAYFAIR (1916, p. 110) wrote: '*O. crassa*, *O. lacustris* and *O. parva* seem to me to form but one species; they are only slightly different, and are all plankton forms.' And some pages later (p. 127), he added: '*O. parva* might very well be arranged as a variation of *O. lacustris'*. As a conclusion, PLAYFAIR (1916, p.109) shared extreme opinion on *Oocystis* taxonomy: 'I do not... consider any of the species of *Oocystis* to be biologically distinct, but merely polymorphic forms of one organism'.

Available literature on the karyology of the members of Oocystaceae revealed that 10 species falling under 6 genera have been worked out karyologically, among which 5 species were from the genus *Oocystis* (AGRAWAL 1996). The taxa *O. borgei* and *O. marssonii* showed equal number of chromosomes (n=8) in independently conducted studies – by TSCHERMAK (1942) on *O. marssonii* and by SEDOVA (1969) on *O. borgei.*

Comments on African material:

Species discussed in this paper (except *O. nephrocytioides*) could be found in more than 60 publications concerning African algal flora, but taxonomical notes and figures are rarely provided.

WEST (1907, p. 142) recorded both species *O. lacustris* and *O. parva* in lakes Malawi and Tanganyika. He gave dimensions only for *O. lacustris* (Table 2) with the following notes: 'This alga was very frequent in the plankton, especially in Tanganyika. The envelope surrounding the colonies is always hyaline, and no colonies were observed of more than eight cells. The faint apiculus at each pole is very characteristic, although exceedingly slight. Two chloroplasts were generally present in each cell. The plants observed were identical in every respect with those which occurred in the plankton of certain Irish lakes.." Comparing this material with Australian specimens, PLAYFAIR (1916) noted its general coincidence except that colony dimensions from Africa and Irish lakes were larger.

FRITSCH & RICH (1923) found on the rocks of a quiet pool in the stream Cedara (South Africa) a form of *O. crassa*, approaching *O. marssonii* but without so pronouncedly pointed cells as the typical *marssonii* cells (Table 2).

GAUTHIER-LIÈVRE (1931) reported *O. borgei* (as a variety of *O. gigas*) from lake Freitis and from marsh Bordji-Ali-Bey (Northern Africa) and provided data on cell dimensions from the first locality (Table 2).

BOURRELLY & LEBOIME (1946) recorded the abundance of one small *Oocystis*, 'which resembles *O. parva*, but its cells were elliptical without pointed ends, with 1 chloroplast[14], without pyrenoid, the enlarged membrane was tapered on the poles; it was much more rare in single cells and much more often in 'families' of 2 cells' (Table 2; Fig. 39). The authors noticed the resemblance (even identity) of this species (found in volcanic peat bogs on Tsaratanna Massive in Madagascar) to material from a peat bog in the Alps, without more comments. The species is included in their species list as '*O. parva* W. et G. S. West fa.'

[14] chromatophore in the original text

GAYRAL (1953) provided only a figure of *Oocystis borgei* from the Moroccan lake Daïet er Roumi without other comments (Fig. 53; Table 2). Later, GAYRAL (1954) recorded in Morocco *O. borgei*, *O. marssonii* (as *O. crassa* var. *marsonii*) and *O. parva* and supplied not only taxonomical notes and figures (Table 2; Figs. 40, 54, 58), but also ecological data on these species.

VAN MEEL (1954a) provided data on the distribution of *O. lacustris*, *O. parva*, *O. marssonii* and *O. borgei* in different African lakes. In Tanganyika *O. lacustris* and *O. parva* were recorded and a more detailed distribution by sites and even hours of sampling was given for *O. lacustris*. *O. marssonii* was reported by VAN MEEL (1954a) for lakes Kivu and Edward, while *O. borgei* was recorded by him only in the lakes Ndalaga and Tana. However, the figures provided by VAN MEEL (1954b) for *O. borgei* and *O. lacustris* were not original, but 'after SMITH and PRESCOTT' without indicating the year (Figs. 3a, b, 5 and 47).

SYMOENS (1956, 296) wrote only the following notes on *O. lacustris* from the Lake Tanganyika: 'cells elliptical with rounded ends, solitary or in groups of 2 to 8 inside the enlarged mother cell wall, with few chloroplasts".

COMPÈRE (1967) recorded *O. lacustris* in Lake Chad and gave data on chloroplast, pyrenoid and cell dimensions (Table 2). Later on, COMPÈRE (1976) reported two forms of *O. lacustris* in Lake Chad and its surroundings – one small, corresponding in his opinion to the descriptions by ŘEHÁKOVÁ (1969) and one larger, relevant to data of PHILIPOSE (1967) and PRESCOTT (1951) – Table 2, Figs. 22a, b, as well as *O. parva* (Fig. 41a) and *O. borgei* (Fig. 56). In the same publication COMPÈRE provided a key for identification of *Oocystis* species. In this key *O. marssonii* was not included, but *O. lacustris*, *O. parva* and *O. borgei* were grouped as species with 1-4 chloroplasts in adult cells and 1(-2) in autospores, all having pyrenoids. The further delimitation of species was based on the cell shape and polar nodules, combined with dimensions (Table 2).

In a stream in the Gebel Marra Mountains in West Sudan STARMACH (1975, p. 219) recorded in one sample 'a few typical colonies' of *O. lacustris*. UHERKOVICH & RAI (1977) depicted *O. lacustris* from Bouaké Dam in Ivory Coast (Fig. 21; Table 2). GERRATH & DENNY (1980) recorded *O. borgei* as a rare species from the lakes Gambia and Sonfon (Sierra Leone) and provided notes and one figure (Table 2; Fig. 55). The authors did not comment the number of solitary cells and colonies, but on their figure only a solitary cell is represented. ILTIS (1980) illustrated the genus *Oocystis* from 'Sahelo-Sudanean African waters' by a figure of *O. lacustris* (Fig. 23) without any comment on the species in the text. From the drawing of ILTIS (1980) the presence of 3 parietal chloroplasts with a pyrenoid in each of them is obvious. However, the dimensions of the cell are not clear since there is a scale bar in the plate but without indication of the scale size. KALF & WATSON (1986) reported *O. borgei*, *O. lacustris* and *O. parva* with close spatial and temporal distribution (with general prevalence of *O. lacustris*) in the phytoplankton of the lakes Naivasha and Oloidien (Kenya).

HECKY & KLING (1987) recorded *O. lacustris* in Lakes Tanganyika, Kivu and Malawi, and *O. marssonii* – in lakes Albert and Edward. The authors generally provide comments on ecology, with separate graph of the temporal development of *O. lacustris* in Lake Tanganyika and drawings of the both species (Figs. 24-26, 60; Table 2) without any taxonomical notes.

COMPÈRE (1991) reported *O. lacustris*, *O. parva* and *O. marssonii* from the Lake Guiers

(Senegal), with close spatial distribution and provided both taxonomic notes and figures (Figs. 27, 41, 56, 59). He recorded *O. parva* also in an inundate region of Ndiagène and in a small irrigation canal near Ouali Diaba. It is interesting to note that in his interpretation all the species have pyrenoids and *O. parva* had larger dimensions than *O. lacustris* (Table 2).

The distribution of *O. lacustris*, *O. parva* and *O. borgei* in the East African Great Lakes was summarized in the check-list by COCQUYT et al. (1993) and in the paper by COCQUYT & VYVERMAN (1994) without taxonomical notes on the species.

MPAWENAYO (1996) found *O. parva* in Lake Dogodogo (Burundi) and provided information on dimensions, supplied by a figure (Table. 2; Fig. 42). There are no comments on chloroplasts and pyrenoid.

OUATTARA et al. (2000) reported *O. borgei* and *O. lacustris* from two rivers (Bia and Agnébi) in Ivory Coast. There is an obvious overlap of the dimensions (Table 2), but the difference in both cell and autosporangial shape is clear from their drawings – broadly oval cells with rounded ends for *O. borgei* and ellipsoidal to fusiform cells with tapered ends in lemon-shaped sporangia for *O. lacustris* (Figs. 28, 57).

VUORIO et al. (2003) reported *O. lacustris* and *O.* cf. *marssonii*, as well as *Oocystis* sp. from the phytoplankton of the Lake Tanganyika without any taxonomical note or comment on their spatial or temporal distribution.

Material and methods

A monitoring in two offshore and two more littoral stations of Lake Tanganyika: Kigoma (Tanzania) in the north (04°51.26' S, 29°35.54' E and 4° 51.17’ S 29° 36.61’ E) and Mpulungu (Zambia), in the south (08°43.98' S, 31°02.43' E and 08° 45.23’ S, 31° 05.15’ E), started in February 2002. The standard sampling periodicity was every two weeks. For the present study water samples taken at 20 m depth for the offshore and surface samples for the littoral stations were analysed. For quantitative investigation one liter of lake water was fixed immediately *in situ* with an acid Lugol’s solution, formalin and a 3% sodium thiosulphate solution (method after RASSOULZADEGAN in SHERR & SHERR 1993). Samples were settled during 48 h in the laboratories at Kigoma and Mpulungu. The supernatant was removed and the concentrated sample was transferred to 100-ml bottles, for later transportation to Belgium. Prior to the microscopic analyze, samples were again concentrated in order to fit in 10-ml sedimentation chambers. A Zeiss Axiovert 135 inverted microscope was used to count phytoplankton ≥ 5 µm according to the method of UTHERMÖHL (1931). Simultaneously additional samples were taken with a plankton-net (10 µm mesh width) from the upper water column (50 m). Detailed investigation of *Oocystis* specimens was done with a Leitz Diaplan microscope, equipped with Differential Interference Contrast at a magnification of 1000. Mucilage was stained by Indian Ink and pyrenoids were studied by staining by iodine solutions combined by cell squashing-method of ETTL & GÄRTNER (1988b). Digital photographs were taken with an Olympus DP 50 camera.

Results

Oocystis species were found among the phytoplankton dominants in both northern and southern parts of the Lake Tanganyika during different periods of the both studied years 2002 and 2003 (COCQUYT et al., in prep.). A large range of morphological variability was observed in both quantitative and semi-quantitative samples.

Frequency of solitary cells and colonies

The cells occurred solitary (Figs. 72, 74, 77-124, 268, 269, 274) or in colonies containing 2 or 4 cells (Figs. 75a-f, 76a-f, 133-194, 199-201, 209-268, 270-273, 276-278, 281). Three-celled colonies (Figs. 195-197, 201, 202, 275), as well as compound colonies of 2-3(-4-6) generations were more rare (Figs. 204, 207, 279). Quite often, fungal specimens were observed attached on the walls of the single cells (Figs. 104, 120, 269, 274), of the autosporangia (Figs. 127, 130, 188), of the 2-celled (Figs. 155, 179, 188) and of the 4-celled colonies (Figs. 232, 253, 254, 257, 261).

The relative abundance of different types of colonies and of solitary cells in quantitative samples during 2 years of sampling is represented on Fig. 71. In the text below the general reference is made to the material collected on the same date - 24.06.2003 - in both northern (Kigoma) and southern (Mpulungu) part of the Lake Tanganyika.

Shape of cells and colonies, wall shape and structures:

Solitary cells

The solitary cells generally were ellipsoidal, covering the whole range of shapes between broadly ellipsoidal (Figs. 72b, 77-81, 90, 92, 95-98, 100, 104-108) through narrowly ellipsoidal (Figs. 73, 87, 103, 117) to fusiform (Figs. 72a, c, 82, 83, 94, 99, 127, 128, 268, 269). Seen from the apex, the cells were almost globular (Figs. 84-86, 115, 119). The cell ends of ellipsoidal cells were rounded (Figs. 72b, 78, 80, 92, 98, 103) or tapered (Figs. 72a, c, 82, 83, 87, 93, 94, 99, 118, 121, 123, 128), but in both cases with thickenings on the poles (Figs. 77, 90, 94, 96, 106, 107, 114, 118, 124, 127, 268, 269).

Solitary cells occurred commonly as free single cells (Figs. 72a-d, 77-110, 268, 269) and more rare as cells embedded by a parental wall - tightly (Figs. 111, 112) or freely (Figs. 74, 113-116, 118-124). In very rare occasions two mother walls surrounded one cell (Fig. 117) or several single cells were included in a large common mucilage sheet (Fig. 73). The presence of one cell, embedded in a partially dissolved parental wall (Figs. 127-129) could be explained by the possible release of the other autospores (Figs. 130, 131) while in each of the cases exemplified by Figs. 74, 111-116 and 121-124 the parental wall was intact. The shape of autosporangia varied. They were almost globular (Figs. 112, 122), barrel-shaped (Fig. 124), cordial (Fig. 123), pyriform (Fig. 119), ellipsoidal (Figs. 74, 113, 121) and fusiform (Fig. 111). Generally the parental walls were thickened at their nodules (Figs. 111, 116, 117, 122, 124, 128, 129) but some autosporangial walls were without polar nodules (Figs. 74, 112, 113).

2-celled colonies (incl. cells producing 2 autospores)

The shape of cells was generally ellipsoidal to spindle-shaped (Figs. 75a-f, 134, 135, 145-167, 169-173, 176-182, 198-194) and more rare broadly oval (Figs. 133, 136, 168), while seen from the apex, they looked globular (Figs. 75f, 141-143, 175). Most of the cells had polar thickenings (Figs. 134, 138, 139, 144-154, 166, 171-173, 176-194). Differences appeared more in the type of cell ends – rounded (Figs. 133, 191) or tapered (Figs. 181, 189, 190, 194) and in the position of cells in colonies. There a great variation was found – from cells tightly surrounded by non-distended mother wall (Figs. 75b, 133-160) through closely situated cells within lesser or greater extended wall (Figs. 75c, 169, 173) to freely-laying cells embedded by the distended walls (Figs. 75e, f, 176, 178-186). This feature obviously is related with the autospore production and age of the colonies (Figs. 75f, 189-194). In some colonies (autosporangia) the cells were in different planes, orientated perpendicular to each other and their shapes looked different (Figs. 75f, 137, 140, 144, 151, 163, 176, 178, 183, 184, 187, 188, 271), while in other colonies (autosporangia) cells were more or less in the same plane and looked similar (Figs. 75b, e, 133, 136-139, 145-150, 152-161, 166, 170-174, 177, 179-182, 189-194, 205). In some specimens the cells were oriented perpendicular to each other but laid in the same plane and therefore looked similar (Figs. 75c, 147, 169, 192). Differences occurred also in the shape of sporangia and in their poles. They ranged from almost globular (Figs. 134, 135, 168) and broadly ellipsoidal (Figs. 137, 152, 153, 186) to regularly ellipsoidal (Figs. 75d, e, 140-143, 171-173, 176-181), sometimes with rhomboid outline (Fig. 163, 165) to barrel-shaped (Figs. 145, 174, 184). The poles of autosporangial walls were smoothly rounded (Figs. 133, 136, 176, 180, 183, 187,) or with thickenings, both convexed (Figs. 148, 169, 171) or concaved (Figs. 174, 184), the polar nodules appearing on both poles (Figs. 148, 150, 154, 171) or on one of them (Figs. 159-161). Ovoid sporangia (Figs. 177, 182, 185) as well as sporangia with irregular shape were also found (Figs. 138, 139, 154, 157). Seldom more than one parental wall was observed (Figs. 75a, d, 161-163).

3-celled colonies

This type of colonies was found rarely in both lake parts on 24.06.2003 (Figs. 195-197, 201, 202, 276) as well as on some other sampling dates (Fig. 71). The cells were embedded tightly by the mother wall and there was always one bigger cell with two smaller cells, most probably, a result of just completed division (Fig. 196). The cell poles were rounded, without striking nodules.

4-celled colonies

The shape of cells in the colonies (or autosporangia) composed by four cells was generally ellipsoidal to spindle-shaped (Figs. 76a, 198-200, 211-267, 271, 276, 278, 281) and cells looked almost globular when seen from the apex (Figs. 76d, 208, 245, 247, 259). Differences appeared in the type of cell ends – rounded without polar nodules (Figs. 208, 209, 220, 227, 259) or more or less tapered with polar thickenings (Figs. 198-200, 229-241, 244, 246-249, 252-254, 257, 258, 260-267, 271) and also in the position of cells in colonies. There a great variation was found – from cells tightly embedded by a parent wall (Figs. 198, 199, 208-228, 232-243, 247-251, 255-257, 273, 278, 281) through closely situated cells embedded by a distended wall (Figs. 237, 238, 267, 272) and

through more free-laying cells within slightly enlarged wall (Figs. 246, 251-253, 260, 264) to free-laying cells surrounded by a distended wall (Figs. 200, 245, 254, 261-263a, b, 266, 271). This feature obviously is related with the age and development of colonies. In some colonies the cells were oriented almost perpendicular to each other with different looking shapes (Figs. 220, 225, 244, 245, 247, 251, 259) while in other sporangia or colonies cells were in the same plain and looked similar (Figs. 198-200, 211, 257, 278) or, laying in different plains, the cells had the same orientation and also looked similar (Figs. 257, 261-263a, b, 264, 267, 271). Differences occurred also in the shape of colonies (autosporangia) and their poles. Colonies ranged from almost globular (Figs. 226, 232, 234, 235) and ovoid (Figs. 244, 248, 251, 260, 266) to barrel-shaped (Figs. 228, 233, 237, 245) and ellipsoidal (Figs. 208, 209, 213, 214, 257, 259). The poles of parental walls were smoothly rounded without polar nodules (Figs. 208, 209, 213, 214, 221, 226, 232, 234-236, 252-254, 259, 266) or with thickenings, both convexed (Figs. 210, 240-243, 258, 260, 263a, b) or concaved (Figs. 245, 261, 262, 264, 268). Seldom a second enlarged parental wall was observed (Figs. 255, 256, 265).

Compound colonies of 2-3 generations

Compound colonies were rarely observed in Tanganyika phytoplankton (Fig. 71). They were generally of two types – composed by 2-celled colonies (Figs. 203-206) and composed by 4-celled colonies (Figs. 207a, b, 276, 279). During phytoplankton counts 6-celled colonies were recorded (Fig. 71), however without notes on their exact structure. The greatest number of cells found in compound colony was 18 (on 5.08.2003 - 2-celled colony type), while for 4-celled colony type the highest number was 12 (Fig. 279). Most of the cells of the compound colonies of first type were with rounded ends, without polar nodules, embedded in 2 mother walls with quite regular shape, rounded ends without thickenings (Figs. 203, 204, 206). Nevertheless rare, polar nodules were observed on both first and second parent wall, when parent cells were obviously spindle- shaped (Fig. 205). 4-celled compound colonies generally were not completely developed and contained cells in different reproductive stages (Figs. 207a, b, 276). According to the position and dimensions, the consecutive character of cell division in each mother cell/colony could be followed in both types of compound colonies – in 2-celled colonies (Figs. 203, 205) and in 4-celled colonies (Figs. 207a, b, 276).

Asymmetry of cells and colonies (autosporangia)

Slightly asymmetrical cells were observed rarely among the solitary cells (Figs. 72d, 93, 94, 102, 109, 110), among the cells in 2-celled colonies (Figs. 75c, 139, 167, 171, 190, 192, 194), as well as in 4-celled colonies (Figs. 76b, c, f, 226, 246, 267). Cells of different size were observed in 2-celled autosporangia (Figs. 132, 167).

Asymmetry was found also in the shape of some autosporangia with 2 cells (Figs. 139, 144, 155-157, 159, 160, 161), in all 3-celled colonies or sporangia (Figs. 195-197, 201, 202) and in some 4-celled colonies (Figs. 200, 215, 216, 240, 258, 261).

Seldom both asymmetrical cells and sporangia were observed (Figs. 139, 159). Different shape of first and second parental wall was detected (Figs. 75a, 75d, 117, 161-163, 194, 255, 256).

Dimensions

The cell dimensions ranged as follows: i) length - (10-15)-15.9-(16.3-17.5)-19.1 μm; ii) width – (6.4-7.5)-8-9.5-(10-11.1-12.7) μm. Most of the cells were 8x16 or 9.5x19.1 μm. Generally the length: width ratio was 2:1.

The range of colonial (sporangial) dimensions was: i) length – 16.3-22.3-28.6-31.8-36 μm; ii) width – 10-15.9-27.5-31.8-36 μm.

Chloroplasts and pyrenoids

Number of chloroplasts in solitary cells ranged between 1 (Figs. 74, 81, 95, 104, 111, 114, 268, 269), 2 (Figs. 78, 83, 90, 94, 105, 124), 3 (Figs. 72b, d, 106, 126), 4 (Figs. 72a, c, 77, 108), 5 (Fig. 73) and more (Figs. 89, 109, 117). In autospore-producing cells and in 2-celled colonies the number of chloroplasts also ranged between 1 (Fig. 75c, 133, 138, 140, 146, 154, 157, 175, 176), 2 (Figs. 75b, d, 153, 192, 270), 3 (Fig. 75c, f), 4 (Fig. 75b, e, 179) or more (Figs. 136, 150, 160, 164), being sometimes different even in the same colony (Figs. 75b, c, 144, 153, 192). In 3-celled colonies one chloroplast per cell was visible (Figs. 195-197, 201, 202, 275). In 4-celled colonies the number of chloroplasts ranged from 1 (Fig. 76a-f, 198, 208, 224, 238, 260), 2 (Fig. 217, 229, 253, 259, 263b, 266, 271, 278, 281), 3 (Fig. 76c, 248), 4 (Fig. 76b, c, e, f, 264) and more (Fig. 222, 223, 226, 242, 243, 245, 253, 254). Similarly to the case of 2-celled colonies, in some 4-celled colonies the number of chloroplasts per cell sometimes was different (Fig. 76a-f, 253, 264, 271, 276). Lobed and grooved chloroplasts were observed in many cases. The chloroplast number is obviously related with the cell age and with the preparation for next division (Figs. 75b, c, 76a-f, 205, 207a, b).

If the closely attached cells in the colonies could be accepted as autospores, from our observations it could be stated that the number of chloroplasts in autospores varied generally between 1 and 4 (Figs.75a, b, d, 76d, e). The same statement could be made according to observations of autosporangia with fractures, fissures, etc. (Figs. 75f, 125-132, 168, 230).

Almost always parietal, chloroplasts represented different shapes, which were obviously related with their number. The variation was from thorough single chloroplast through 2-4-(5) band-like chloroplasts to numerous discoid and densely arranged chloroplasts.

In general, pyrenoids were not easily visible without staining due to presence of many oil droplets in cell content. When stained, one large pyrenoid in each chloroplast became visible (Figs. 268-281). In more rare cases and under higher magnifications pyrenoids were visible without staining (Figs. 72a, c, 73, 75a, f, 76f, 192, 195-198). By the method of squashing-out of the cells the presence of continuous starch sheath was detected.

Mucilage

Wide, but hyaline, structureless mucilage envelope was recorded around some of the solitary cells and around the colonies as well (e.g. Fig. 73). It is to be noted that the mucilage was easily visible only when there were sedimentated particles on it (Figs. 121, 124, 126, 187, 209, 214, 251, 264) and not well visible without specific staining (Indian Ink).

Autospores and their release

Generally formation of both two (Figs. 75d, f, 159-161, 163, 168, 188, 205) and four autospores was observed (Figs. 207a, b, 212, 217, 230, 265, 276, 277, 280). Formation of four spores and degradation of two of the cells could precede formation of two autospores (Fig. 244). Presence of one autospore (one cell?) was detected in an intact parental wall (Figs. 74, 111-116, 121-124) or walls (Fig. 117) as well.

The release of autospores was by partial dissolution of cell wall (Figs. 127-132, 277), by its fracture (Figs. 75f, 212, 217, 280), through fissure combined with a slight wall invagination (Figs. 156, 164, 168) or through simple fissure (Figs. 120, 125, 126, 188, 230). Joint release of autospores in a tight common wall through partially dissolved second (older) parental wall was observed also (Figs. 265, 277).

Discussion

SCHEINER et al. (1991) and SCHEINER (1993) distinguished two types of environmentally induced variation: phenotypic plasticity and developmental noise as independent properties that are both trait and environment specific. At least part of the variability in morphology is accounted for the developmental noise, which entails changes in developmental pathways due to random internal events and may broaden the ranges of taxonomically important morphological characters and thus lower the diagnostic value in identifying species.

The detected polymorphism of *Oocystis* specimens showed almost continuous character in each of the samples studied and in the whole amount of samples from the lake. The ranges of cell shapes and of the shapes of colonies (autosporangia) were similar in cases of solitary cells, of 2- and 4-celled colonies, as well as in compound colonies. The variability included the whole range from broadly oval cells / colonies without polar nodules to spindle-shaped cells / colonies with pronounced thickenings. Here it is worthy to remind the aforementioned data of TSCHERMAK (1942), SKUJA (1956) and HINDÁK (1980), according to which polar nodules could be both present or absent in *O. marssonii* (Fig. 65), *O. lacustris* and *O. borgei*. Nevertheless quite rare, some of the found sporangia were rhomboid in outline and resembled a small part of the variability described for *Oocystis rhomboidea* FOTT 1934 (*Oocystella rhomboidea* (FOTT) HINDÁK 1988 - Fig. 70). KOMÁREK & FOTT (1983) considered this species as closely related to *O. parva.*

Careful investigation of specific descriptions of different authors reveals the overlapping of morphological features and different understanding of the species boundaries in *Oocystis lacustris* group, as well as some contradictions. This is obvious if data from Tables 1-2 and Figs. 1-64 are compared. The same tables reveal the superficiality of some of the descriptions and even lack of important characters in some of them, as it was noted previously by PLAYFAIR (1916), KORSHIKOV (1953), HINDÁK (1984, 1988) and JOHN & TSARENKO (2002). If data of different authors are summarized the common features become evident and according to this summary the material found in Lake Tanganyika could be classified as each of the species of the *O. lacustris*-group, nevertheless has it been described from Africa or other continents. The broad range of morphological variability observed in the material from Lake Tanganyika at present

state-of-art let us decide to identify all the specimens found as belonging to one species – *O. lacustris*, which is the earliest described taxon among the group. By this we accede the opinions expressed before by PLAYFAIR (1916) and HINDÁK (1984) and enlarge them by including *O. borgei.* This we would suggest to all further working limnologists instead of giving 4-5 different names (depending on the available identification books) until a critical re-evaluation of the whole genus using modern methods is made.

An indirect confirmation of our opinion could also be find in the observed fungal parasitism on all types of cells and colonies (autosporangia) and in the lack of visible high degree of specifity. MANN (1999) pointed that parasites and particularly chytridial fungi can discriminate between morphologically similar demes of what have traditionally been considered single species among diatoms. In the material from Lake Tanganyika fungal parasites were observed on all types of cells and colonies with relatively equal frequency. The only un-affected cells were the asymmetrical cells and colonies (autosporangia) and particularly these, which mostly resemble the representatives of the genus *Ecdysichlamys*. However, the last cells were in so low frequency that it is difficult to make more solid statement. Up-to now there is one detailed paper on fungal parasitism on *Oocystis* (ARAUZO et al. 1987), where the host was identified as *O. borgei.*

The essential difference between the material from Lake Tanganyika and the other described material is the observed presence of compound colonies. The lack of composite colonies was strongly supported previously by FOTT (1976) and later on by KOMÁREK & FOTT (1983) in their world-wide used manual on coccal green algae as characteristic for all the species discussed in this paper. However it met contradictory opinion of one of the authors, who himself described compound colonies in *O. parva* from Cuba (KOMÁREK 1983). The occurrence of compound colonies in American and European material was noted earlier for *O. parva* by PRESCOTT (1962), for *O. lacustris* by SKUJA (1956, 1964 – Figs. 6, 7) and later on by ŘEHÁKOVÁ (1969), HINDÁK (1984, 1988) and JOHN & TSARENKO (2002) for *O. lacustris* and for *O. marssonii* – Table 1A.

A perpendicular to each other position of the autospores was described by FOTT & ČADO (1966) for *Oocystis nephrocytioides* as 'crossed disposition'. A part of the material found in Lake Tanganyika resembled this species, where cells were single or in groups of 2 by chloroplast shape, position and presence of pyrenoid, by presence of asymmetrical cells, by dimensions, by frequent crossed position of autospores, but completely differs in the way of autospore release.

The temporal distribution of solitary cells and *Oocystis* colonies with different number of cells suggests some reproductive trends, since appearance of 6-celled and other compound colonies generally follows the occurrence of solitary cells and 2-celled colonies (autosporangia) – Fig. 71. Such statement certainly requires further confirmation from more quantitative investigations from different world localities.

Nevertheless that 3-celled colonies were found among the bulk of *Oocystis* specimens in Lake Tanganyika, we consider this more as a reproductive phase than as a stable colonial stage. The occurrence of 3-celled colonies (formed by one big and two smaller cells) was detected by TSCHERMAK (1942) in culture of *O. marssonii*. She considered it as a result of degenerative development and formation of pycnotic nucleus in the bigger cell. The appearance of the 3-celled colonies (cell groups) in combination with the observations on the morphology of cells in compound colonies in Tanganyika allows us to suggest the consecutive character of cell division during autospore production as additional

possibility or as a variety of general successive type of autospore production outlined by ETTL & GÄRTNER (1988a) for Chlorococcales. This conclusion is in coincidence with the opinion of TSCHERMAK (1942) that autospore formation in the genus *Oocystis* has a consecutive character. SEDOVA (1969) detected the same character of the cytokinesis in cultures of *O. borgei*, but for *O. marssonii* she described simultaneous division.

It is worthy of special note that during this study all range between tightly surrounded cells to freely-laying cells embedded in a distended autosporangial wall was observed together with all possible ways for the release of the autospores – by partial dissolving of the parental wall, by its rupture or through fissure (simple or combined with slight wall invagination). The observations on autospore release were not so numerous to lead to firm statements, but it has to be mentioned that fractures were observed quite rare and only in cases of tightly embedded cells, while more distended walls underwent partial dissolution, slight invagination or had simple fissures.

Peculiar embedment of one cell in one parent wall was depicted only once in the literature studied (HINDÁK (1980) for *Oocystis lacustris* - Fig. 13b). The disposition in two parent walls was depicted by the same author for the same species 4 years later (Fig. 15). KORSHIKOV (1953) noted that in some cases solitary cells were embedded in 2-3 times larger outer walls (Table 1). Nevertheless that no relevant drawings were provided, the text of KORSHIKOV suggests that he had observed cells similar to these found by us (Figs. 111, 112). Similar pictures could be found for *Ecdysichlamys obliqua* G. S. WEST (WEST 1912; KOMÁREK & COMAS 1984) where one autospore is surrounded by one (Fig. 70a) or more parent walls (Fig. 70b).

Similarity of our material with *Ecdysichlamys* existed also in occurrence of asymmetrical cells and autosporangia (particularly these on Figs. 72d, 75c, 76c, d, f, 139, 159-161). The small amount of these cells and work with fixed material does not allow us to take final decision about the co-existence of both genera and is beyond the scope of this study. However, finding of these rare cells among the bulk of *Oocystis* specimens has to be noted and taken into account in future studies on these problematic genera. More, we have to underline the similarity of *Ecdysichlamys obliqua* photographed by KOMÁREK & COMAS (1984) and illustrated by their Tab. II, Figs. 15a-d, g, i with a part of the material found in Lake Tanganyika. This similarity concerns cell shape and dimensions, presences of a parietal chloroplast and of a tight mother wall around the autospores.

When studying the chloroplast ultrastructure of *O. marssonii*, PENDLAND & ALDRICH (1973a, p. 307) wrote 'in the typical cell... the single chloroplast fills most of the cytoplasm'. According to our observations, the number of chloroplasts ranged in the same way in the solitary cells and in the cells of different colonies – from a single parietal chloroplast to numerous smaller discoid chloroplasts. This number was obviously related with cell age and the consecutive character of chloroplast division seemed clear, particularly in cases when two small and one big chloroplasts were observed (e.g. Figs. 72b, d). The prevailing practice in *Oocystis* (and almost whole algal) systematics was to attribute great weight to chloroplast number and morphology since especially after the work by STARR (1955) it was believed that chloroplasts are genetically determined and thus unchangeable. However, there are recent genetic and molecular evidences that even in algae, for which the number of chloroplasts has been considered a primary classification criterion, the reorganization of photosynthetic apparatus is reversible and quick not only depending on growing conditions in cultures, but also in nature, where

changes in chloroplast number could be encountered as normal phenomenon. Moreover, this reconstruction (which involves the replacement of one big structure, such as single chloroplast, with two smaller ones) is not coupled with any changes in the cell morphology or irregularity of karyo- or cytokineses (e.g. ZAKRYŚ et al., 2002). As it was mentioned in the results, the number of chloroplasts ranged in all observed cells and finding of cells with one big chloroplast and several smaller ones suggests their consecutive division. Therefore we propose this number to be applied in a precise and careful way among the generic, but not among the specific diacritical features until more profound study on the genus *Oocystis* is carried out.

BROWN & MCLEAN (1969) were the first who used the structure of the pyrenoid as a means of classifying various *Chlorococcum* species and extended it to other green algae. Since then the type of pyrenoids was recognized among the key-structure features used in green algal taxonomy (INGOLIĆ & GÄRTNER 2002). As it was noted in the introduction to this paper, the presence or absence of pyrenoid in *Oocystis/Oocystella* is among the most debatable features for delimitation on genus level. Nevertheless, still the presence/absence of the pyrenoid is always mentioned among the key characters, even by authors who did not took this feature as sufficient enough to warrant such separation (e.g. JOHN & TSARENKO 2002). In the type species *Oocystis naegeli* A. BRAUN 1855 a pyrenoid is missing, but in the generic diagnosis of *Oocystis* provided by PRINTZ (1913) species could be with or without pyrenoid. The presence of pyrenoid had been proved by electron micrsocopy for *O. marssonii* by PENDLAND & ALDRICH (1973a) without detailed description and for *O. apiculata* as falling 'in the category with "fragmentated starch plate penetrated by a simple tubular thylakoid system"' (ROBINSON & WHITE 1972, p. 111). This type of pyrenoid was pointed to be embedded in a central position in the plastid and to be usual for coccal green algae (DODGE 1973). It is also known that development of pyrenoids takes place in several ways and in many green algae the pyrenoids disappear during cell division and are then reformed in daughter cells (DODGE 1973). The first detailed study on this was carried out on *Scenedesmus* (BISALPUTRA & WEIER 1964 – cited after DODGE 1973), who proved that just before division the pyrenoid is very large with a distinct starch sheath but the whole structure disappears as the cell divides. Both genera *Scenedesmus* and *Oocystis* are similar in the general way of reproduction by autospores and in their pyrenoids (when they have been studied in *Oocystis*). Therefore it could be proposed that the situation with pyrenoids of *Oocystis* is somewhat similar and they could disappear at the division nevertheless that TSCHERMAK (1942) stated that pyrenoids were not dissolved during the cytokinesis of *O. marssonii*. However, SEDOVA (1969) reported about the possibility of disappearance of the pyrenoid during the second and the third cell division in *O. borgei*. Since it is 'difficult to be certain when a pyrenoid is really absent for it is not easy to say when a rather uniformly granular area of stroma has become a simple pyrenoid' (DODGE 1973, 124) and the fact that pyrenoids are sometimes known to be present at only some stages of life cycle, in our opinion a transmission electron microscopic investigation is required during the study of the life history of *Oocystis* species for solving the problem of taxonomical implication of the presence or absence of the pyrenoid. Until this is properly done and doubts attaches absence of this chloroplast structure, we could not accept using of presence or absence of the pyrenoid as sufficient generic criterion. Therefore we classify our material in the earlier described genus *Oocystis* and not in *Oocystella* in spite of the fact that iodine staining and cell-squashing method (ETTL & GÄRTNER 1988b) revealed a

large central pyrenoid in each chloroplast with a continuous starch sheath.

The observed morphological variability of *Oocystis* specimens in Tanganyika covers practically all previously known polymorphism from different world localities and cultures. Similar range of variability was noted by THOMASSON (1955) for *Pediastrum clathratum* (SCHROEDER) LEMMERMANN in Lake Victoria – Nyanza and he related it either with the old age of the lake or with the particularly favorable environment for such forms. Since Lake Tanganyika is well known for its peculiar limnology and old age (e.g. HUTCHINSON 1957; TALLING & TALLING 1965; BEADLE 1974 among the many others), it could be proposed with a high probability that its stable features support all types of morphological variability which appeared and are stabilized in generations due to asexual reproduction of *Oocystis* species.

As is often the case of studies of the type here undertaken, more questions can be asked than have been answered. From the all above comments the evident need of critical re-evaluation of the genus *Oocystis* becomes clear. It is well known that often it is difficult to understand whether two populations that differ slightly are two different species or varieties of the same species and nevertheless that this species problem has been realized by systematics since the early 19th century a solution has not been achieved to date (SCHLEGEL & MEISTERFIELD 2003). It is beyond the scope of this study to discuss the species problem, especially in the line of asexually reproducing organisms for which the outstanding biological species concept of MAYR (1963, 1998) is not applicable, but which however evolved as successfully as sexually outcrossing species. In 1957, SONNEBORN already assumed that most fundamental for organism's evolutionary success was its ability to maximize reproduction and to maintain enough genetic variability to respond to demands of changing environment and that asexually reproducing forms could also built discrete evolving groups. Basically he postulated that species in asexual and sexual organisms could be defined on essentially the same principle, which is the surpassing of a threshold of minimal irreversible evolutionary divergence. SONNEBORN (1957) suggested that means to ascertain such differences for asexual organisms were to be found in detailed studies on life cycles, morphology, cytology, physiology and ecology. Recent understanding of problem of clones and real existing or not of their genetic fidelity also showed the need to learn more about the nature of eukaryotic clonal organisms (as asexual lineages of a stem parent), including their levels of variance (LOXDALE & LUSHAI 2003). Therefore of particular need for future research on *Oocystis* are the following: i) ontogenetic studies with special attention to chloroplast and pyrenoid development combined with transmission electron micrsocopic data; 2) comparative genetic studies on different *Oocystis* populations; 3) comparison between field and culture variability in the genus. Doubtless, the same type of investigation is needed to verify the separation of *Oocystis* from some closely related genera (e.g. *Ecdysichlamys*). This is in coincidence with the fact that with increasingly robust hypotheses for the higher level questions of green algal evolution, more and more attention will be focused on resolution of lower level taxonomic questions (WATERS & CHAPMAN 1996).

In conclusion, it can be said that data obtained from the present study could conduce to the more and more needed amounts of comparative data on *Oocystis* from different world localities and it is hoped that the small contribution herein has served its purpose.

Zusammenfassung

Vertreter der Grünalgengattung *Oocystis* A. BR. 1855 in Phytoplanktonproben aus dem Tanganyika See (Afrika) wurden lichtmikroskopisch untersucht. Die Taxonomie der meisten beschriebenen Taxa ist bis heute problematisch und revisionsbedürftig. Im Rahmen dieser Studie wurde ein Schwerpunkt auf die allgemeine Morphologie der Einzelzellen und Zellkolonien von Vertretern der Artengruppe um *O. lacustris* CHODAT gelegt, deren Beschreibungen und Abbildungen sehr variieren und deren diakritische Merkmale sich zum Teil überlappen. In Tabellenform ist die morphologische Variabilität von *O. lacustris* und ihrer verwandten Sippen *O. marssonii* LEMM., *O. parva* W. WEST et G. S. WEST, *O. borgei* SNOW und *O. nephrocytioides* FOTT & ČADO zusammengefasst und mit Abbildungen verschiedener Autoren ergänzt. Die weitgestreute morphologische Variabilität des Probenmaterials aus dem Tanganyika See veranlasste die Autoren, alle gefundenen Sippen als Vertreter einer einzigen Art – *O. lacustris* CHOD. – zu identifizieren und alle oben erwähnten Taxa als Synonyma dieserArt zu führen.

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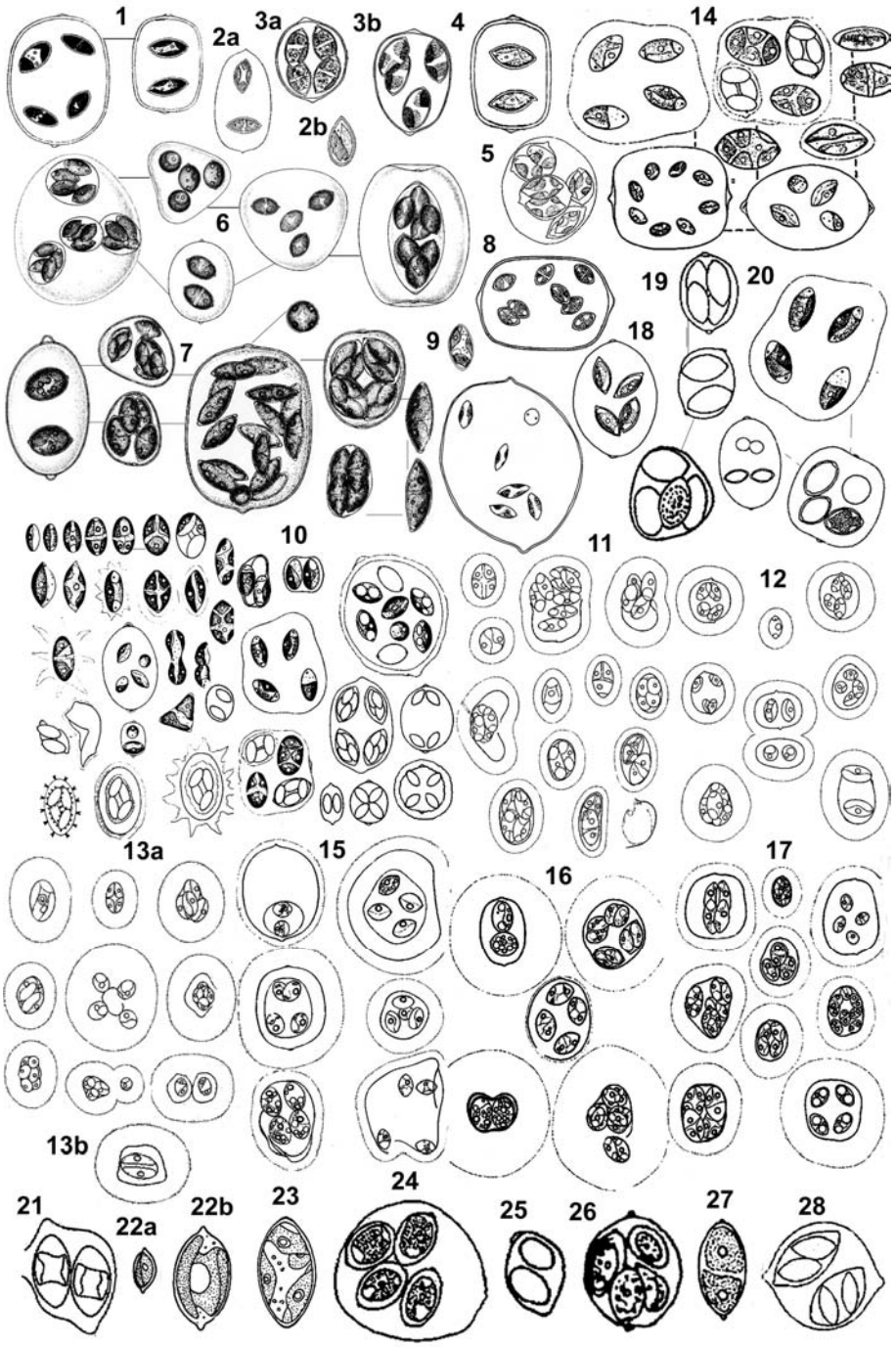
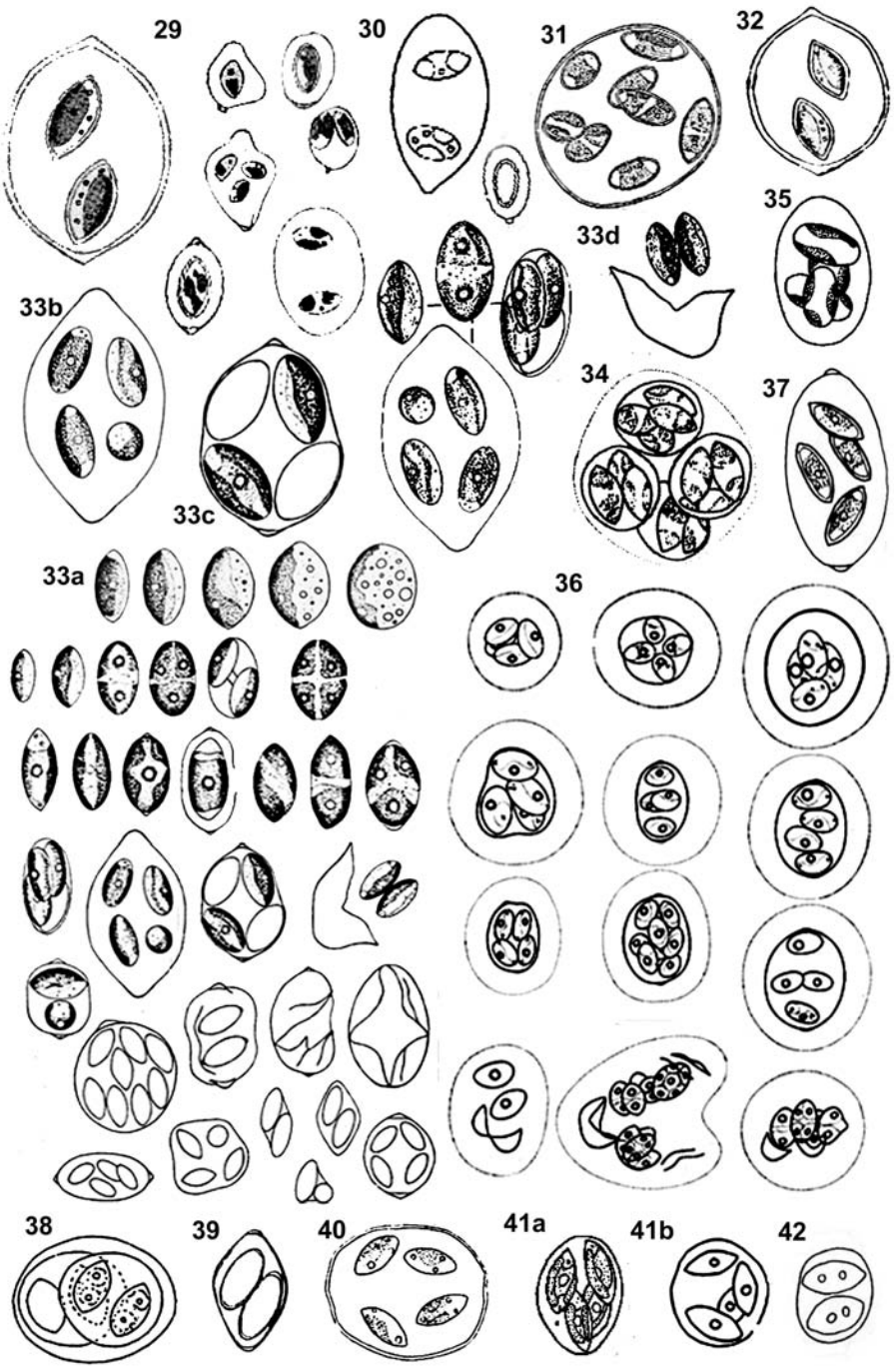
Figs 1-20: Shape of cells and colonies of *Oocystis lacustris* CHODAT as represented in the most important identification books, papers and monographs: (**1**) in PRINTZ (1913); (**2**) in BRUNNTHALER (1915 – 'after CHODAT'); (**3**) a: in SMITH (1950) and in VAN MEEL (1954b); b: in VAN MEEL (1954b – 'after SMITH'); (**4**) in KORSHIKOV (1953 – 'after CHODAT'); (**5**) in PRESCOTT (1962) and in DILLARD (1989); (**6**) in SKUJA (1956); (**7**) in SKUJA (1964); (**8**) in PHILIPOSE (1967); (**9**) in BOURRELLY (1966) and SHEATH & WEHR (2003); (**10**) in ŘEHÁKOVÁ (1969); (**11 – 13a, b**) in HINDÁK (1980); (**14**) in KOMÁREK & FOTT (1983, incl. figs of NYGAARD 1949); (**15-17**) in HINDÁK (1984); (**18**) in TIKKANEN & WILLÉN (1992); (**19**) in LING & TYLER (2000); (**20**) in JOHN & TSARENKO (2002).

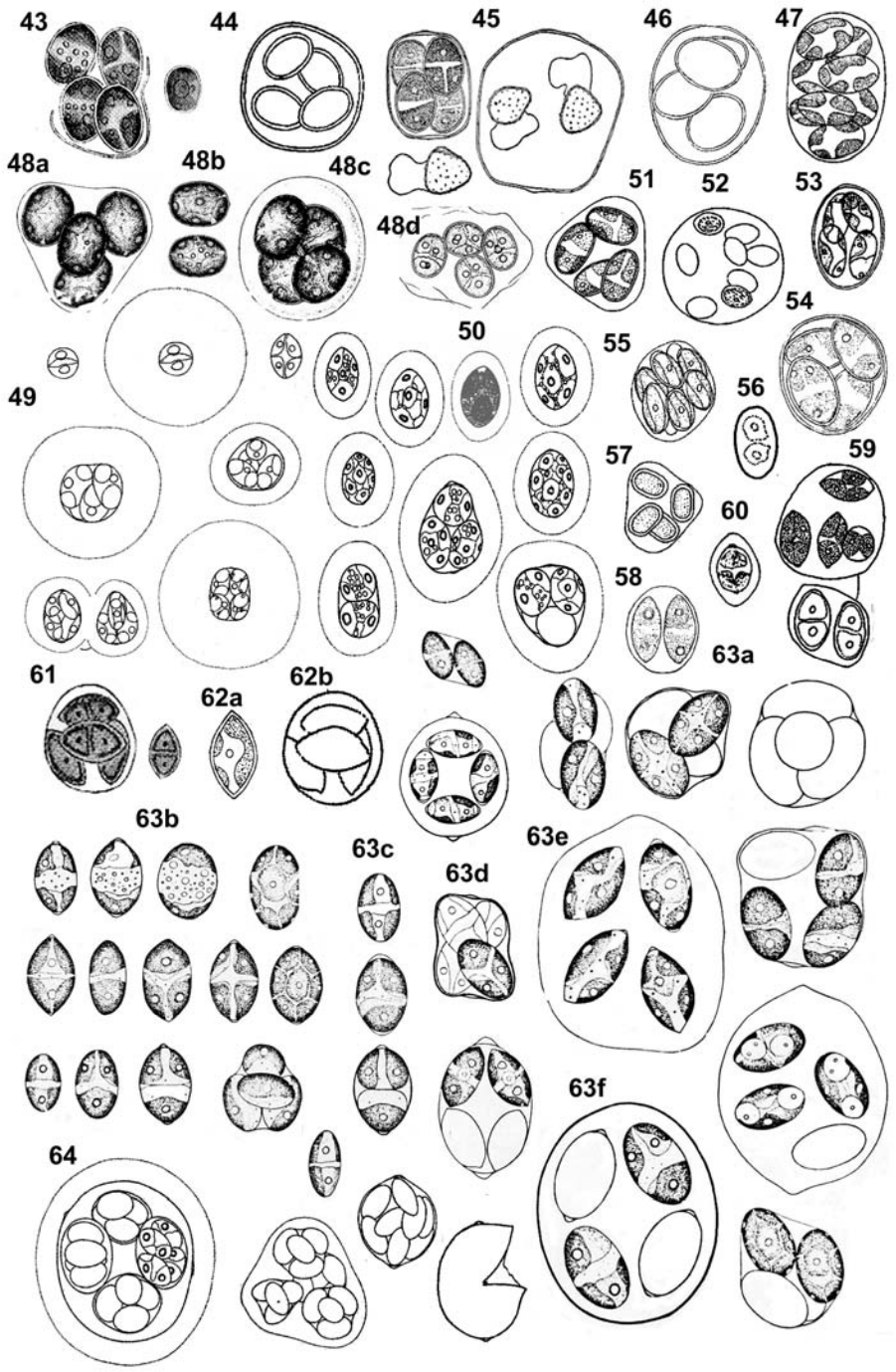
Figs 21-28: Shape of cells and colonies of *Oocystis lacustris* CHODAT from Africa depicted by: (**21**) UHERKOVICH & RAI (1977); (**22a**) COMPÈRE (1967; small form); (**22b**) COMPÈRE (1967; big form); (**23**) ILTIS (1980); (**24**) HECKY & KLING (1987; specimen from Lake Edward); (**25**) HECKY & KLING (1987; specimen from Lake Kivu); (**26**) HECKY & KLING (1987; specimen from Lake Malawi); (**27**) COMPÈRE (1991); (**28**) OUATTARA et al. (2000).



Figs 29-38: Shape of cells and colonies of *Oocystis parva* WEST & WEST as represented in the most important identification books, papers and monographs: (**29**) in PRINTZ (1913); (**30**) in BRUNNTHALER (1915 – 'after WEST'); (**31**) in SMITH (1950); (**32**) in KORSHIKOV (1953 – 'after the WESTS'); (**33a**) in ŘEHÁKOVÁ (1969); (**33b**) in ŘEHÁKOVÁ (1969) and in JOHN & TSARENKO (2002); (**33c**) in ŘEHÁKOVÁ (1969), in KOMÁREK & FOTT (1983) and in JOHN & TSARENKO (2002); (**33d**) in ŘEHÁKOVÁ (1969) and in KOMÁREK & FOTT (1983); (**34**) in PRESCOTT (1962) and DILLARD (1989); (**35**) in PRESCOTT (1969); (**36**) in HINDÁK (1988); (**37**) in TIKKANEN & WILLÉN (1992); (**38**) in LING & TYLER (2000).

Figs 39-42: Shape of cells and colonies of *Oocystis parva* WEST & WEST from Africa depicted by: (**39**) BOURRELLY & LEBOIME (1946 – forma); (**40**) GAYRAL (1954); (**41a**) COMPÈRE (1976), (**41b**) COMPÈRE (1991); (**42**) MPAWENAYO (1996).



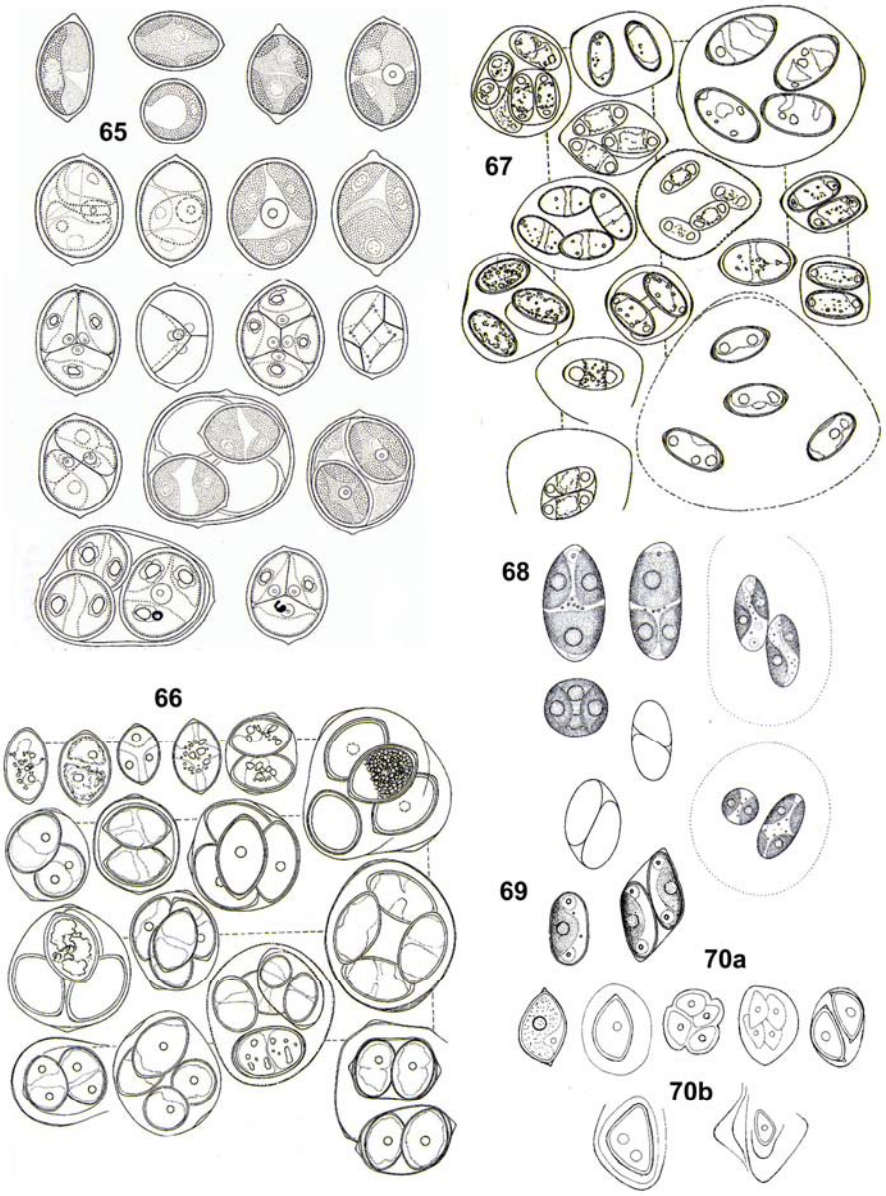


Figs 43-52: Shape of cells and colonies of *Oocystis borgei* SNOW as represented in the most important identification books, papers and monographs: (**43**) in PRINTZ (1913); (**44**) in BRUNNTHALER (1915 – 'after BORGE'); (**45**) in SMITH (1950); (**46**) in KORSHIKOV (1953 – 'after SNOW'); (**47**) in PRESCOTT (1962); (**48a**) in SKUJA (1956), in KOMÁREK & FOTT (1983), in DILLARD (1989) and in JOHN & TSARENKO (2002); (**48b, c**) in SKUJA (1956), in KOMÁREK & FOTT (1983) and in JOHN & TSARENKO (2002); (**48d**) in KOMÁREK & FOTT (1983 – 'after NYGAARD 1949'); (**49**) in HINDÁK (1980); (**50**) in HINDÁK (1988); (**51**) in TIKKANEN & WILLEN (1992); (**52**) in LING & TYLER (2000).

Figs 53-56: Shape of cells and colonies of *Oocystis borgei* SNOW from Africa depicted by: (**53**) GAYRAL (1953); (**54**) GAYRAL (1954); (**55**) COMPÈRE (1976); (**56**) GERRATH & DENNY (1980); (**57**) OUATTARA et al. (2000).

Figs 57-60: Shape of cells and colonies of *Oocystis marssonii* LEMMERMANN from Africa depicted by: (**58**) GAYRAL (1953); (**59**) COMPÈRE (1991); (**60**) HECKY & KLING (1987; specimen from Lake Albert).

Figs 61-64: Shape of cells and colonies of *Oocystis marssonii* LEMMERMANN as represented in the most important identification books, papers and monographs: (**61**) in PRINTZ (1913); (**62a**) in BRUNNTHALER (1915 – 'after LEMMERMANN') and in KORSHIKOV (1953 – 'after LEMMERMANN'); (**62b**) in BRUNNTHALER (1915 – 'after LEMMERMANN'); (**63a, b**) in ŘEHÁKOVÁ (1969); (**63c**) in ŘEHÁKOVÁ (1969), in KOMÁREK & FOTT (1983) and in JOHN & TSARENKO (2002); (**63d**) in ŘEHÁKOVÁ (1969) and in KOMÁREK & FOTT (1983); (**63e**) in ŘEHÁKOVÁ (1969), in KOMÁREK & FOTT (1983), in TIKKANEN & WILLÉN (1992) and in JOHN & TSARENKO (2002); (**63f**) in ŘEHÁKOVÁ (1969) and in KOMÁREK & FOTT (1983); (**64**) in HINDÁK (1988).



Figs 65-70: *Oocystis* and *Ecdysichlamys*: (**65**) *O. marssonii* LEMMERMANN sensu TSCHERMAK (1942 – as *O. crassa* var. *marssonii*); (**66**) *O. marssonii* LEMMERMANN forma from Cuba sensu KOMÁREK (1983); (**67**) *O. parva* W. et G. S. WEST forma from Cuba sensu KOMÁREK (1983); (**68**) *O. nephrocytioides* FOTT & ČADO 1966; (**69**) *O. rhomboidea* FOTT in FOTT (1976) and in KOMÁREK & FOTT (1983 – 'after FOTT 1976'); (**70**) *Ecdysichlamys* obliqua G. S. WEST in KOMÁREK & COMAS (1983 – 'acc. to G. S. WEST 1912').

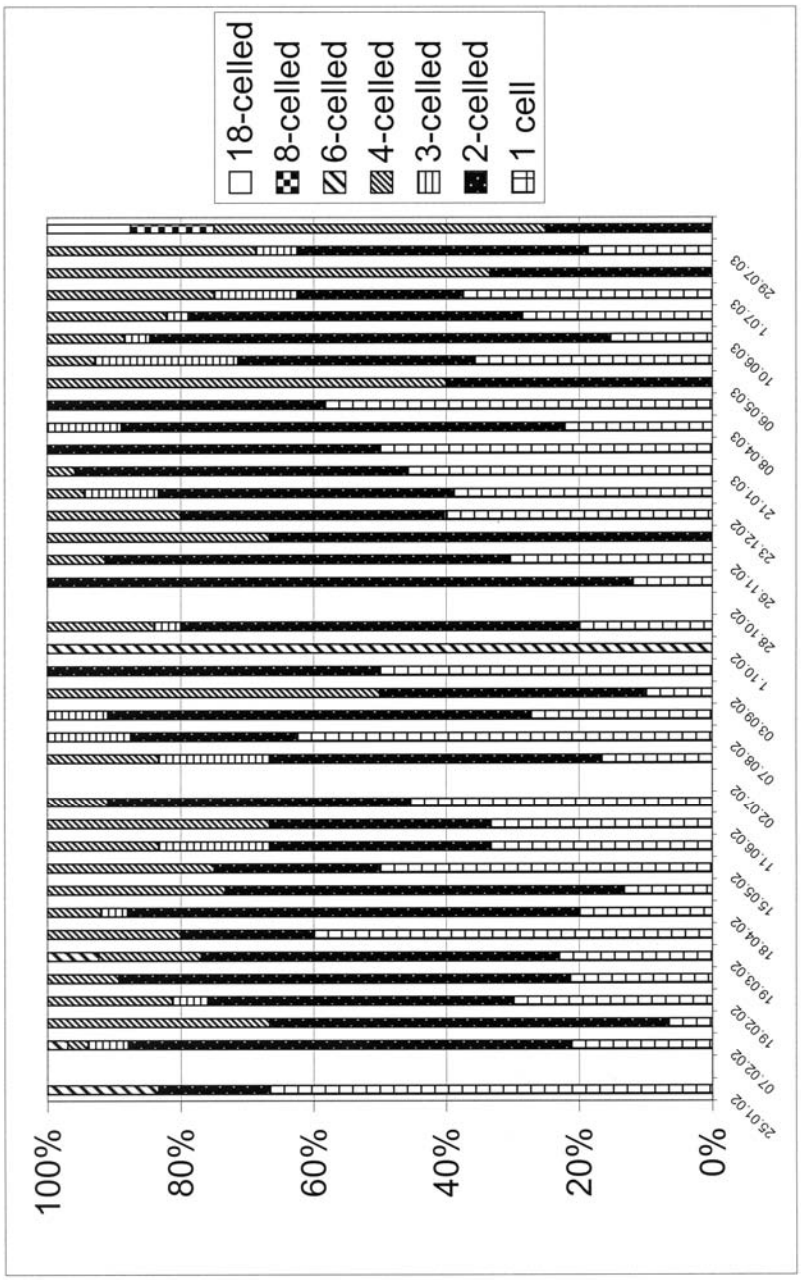
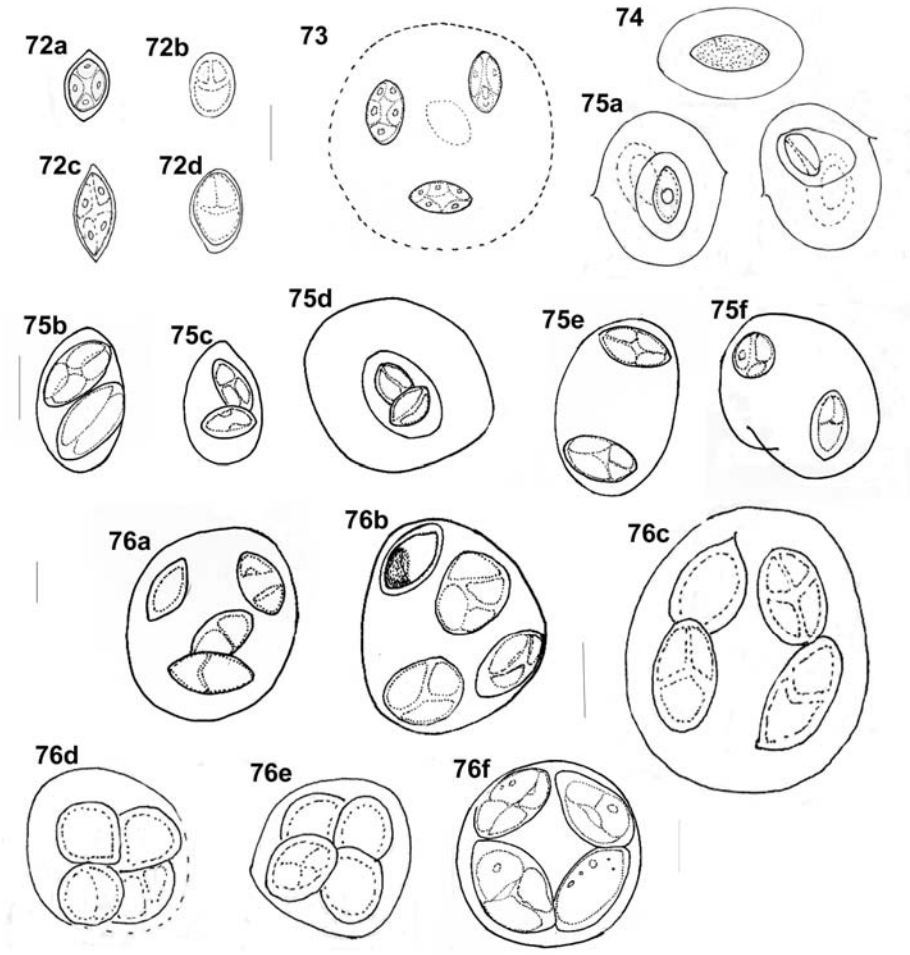
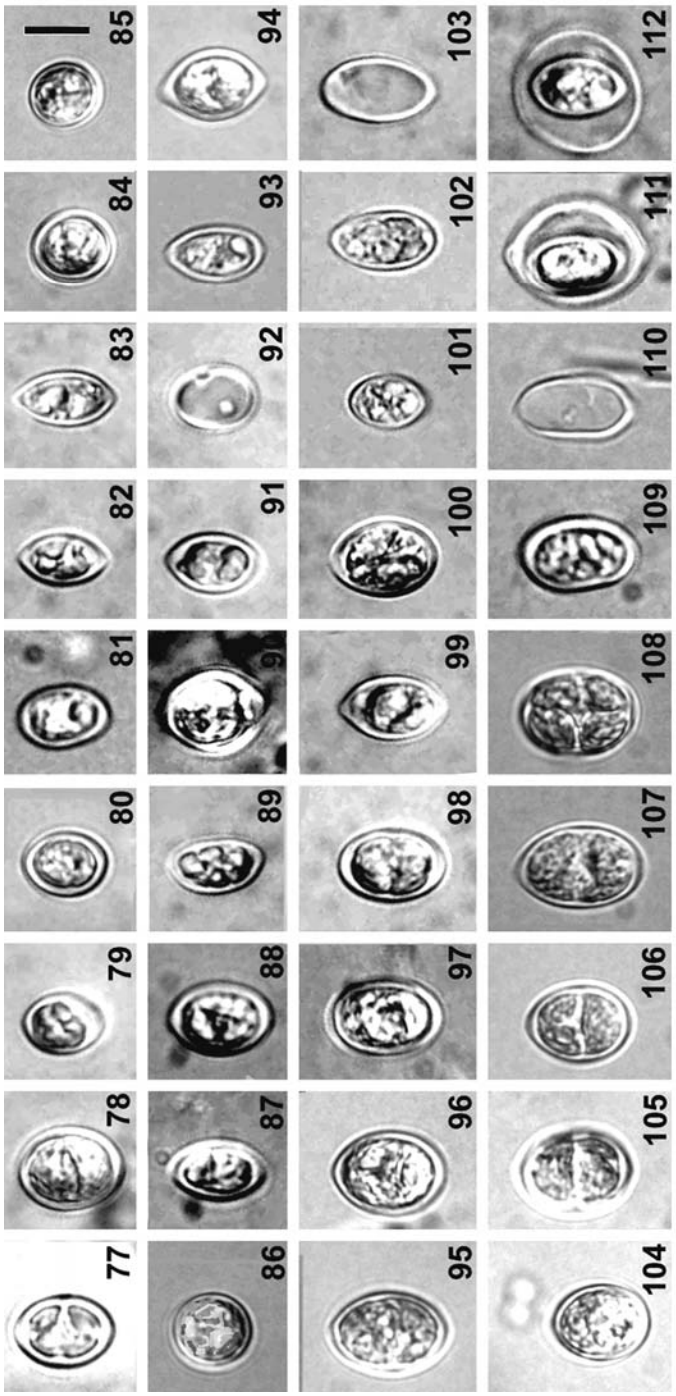


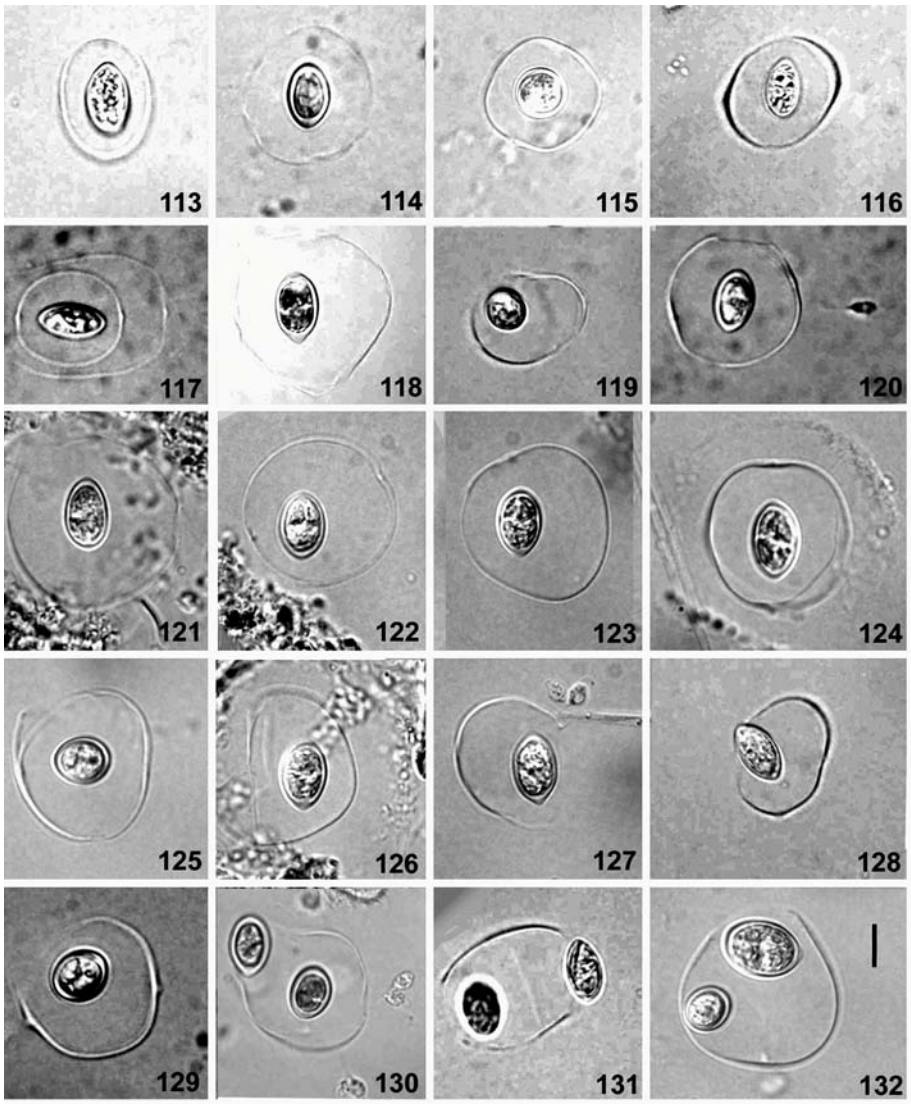
Fig. 71: Temporal distribution of solitary cell and colonies with different cell number in the phytoplankton of the Lake Tanganyika in 2002-2003.



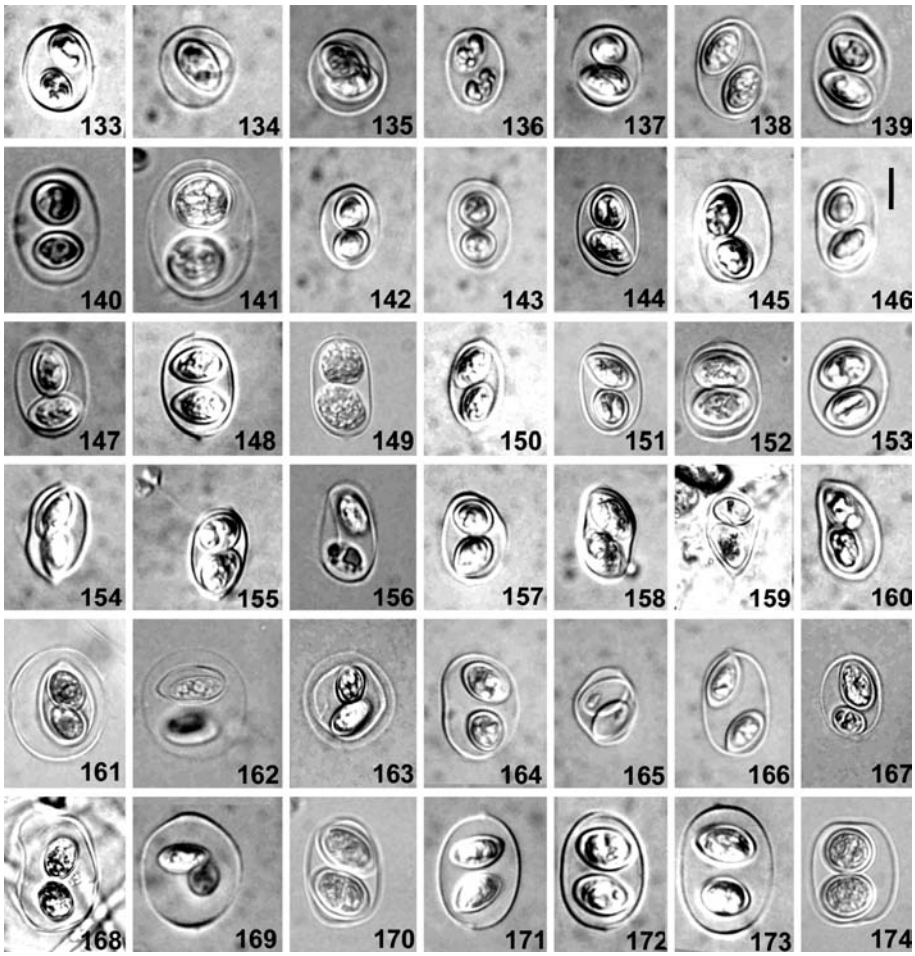
Figs 72-76: *Oocystis lacustris* CHODAT from Lake Tanganyika: Scale bar: 10 µm (original).



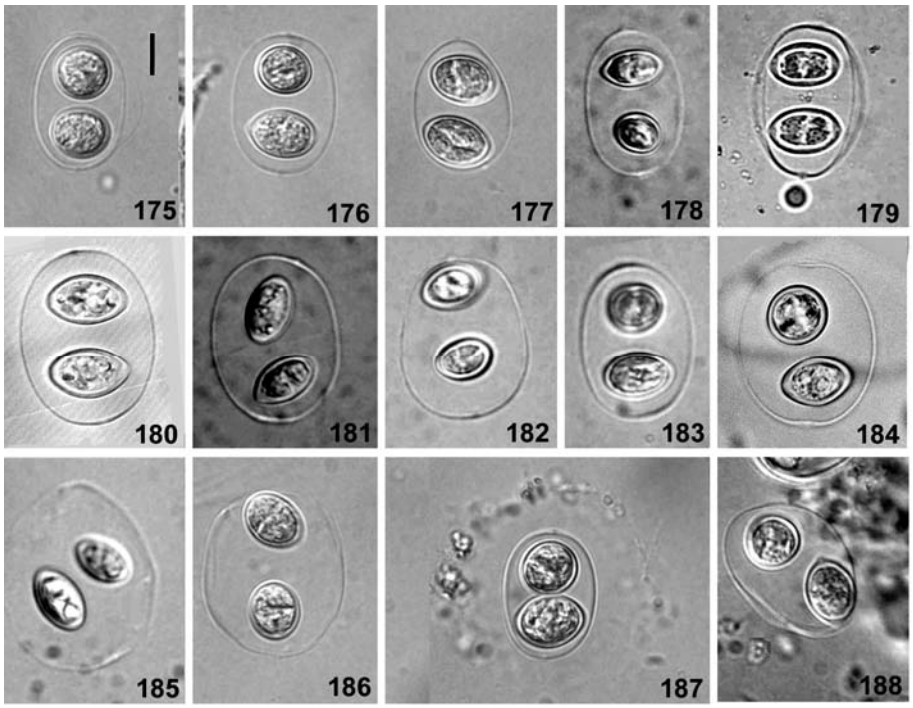
Figs 77-112: Solitary cells of *Oocystis lacustris* CHODAT from Lake Tanganyika. Scale bar – 5 µm



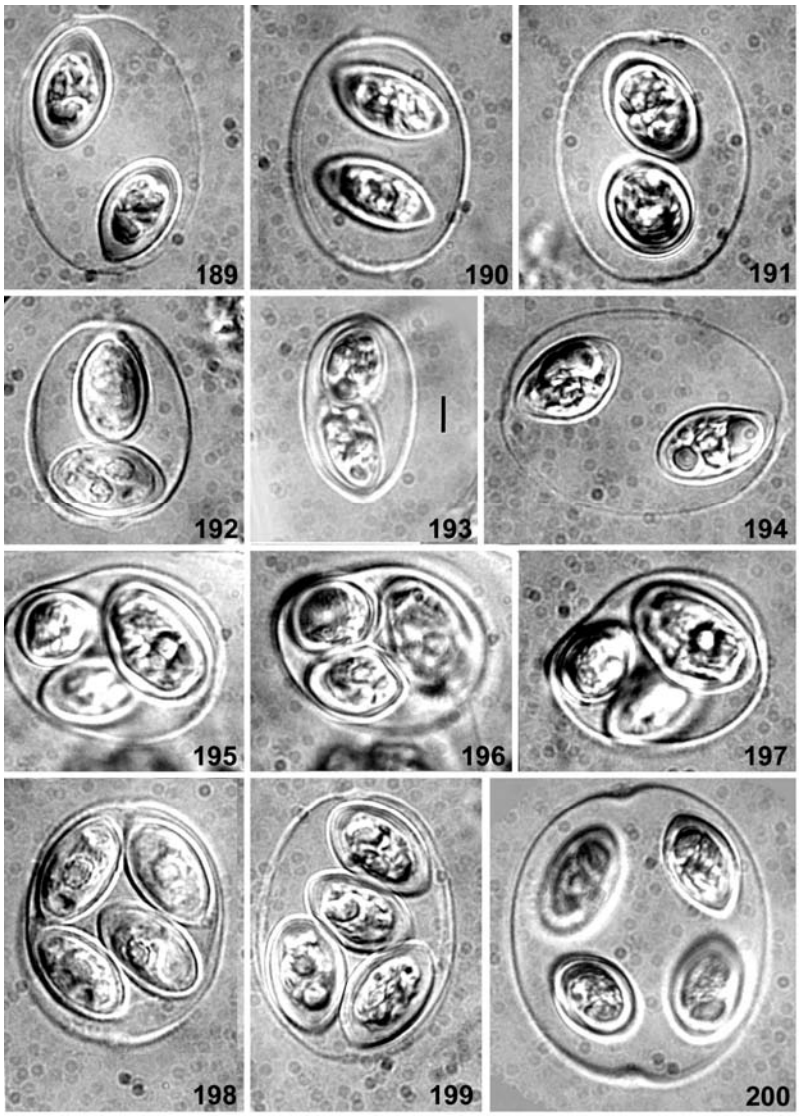
Figs 113-132: Solitary cells and autospores of *Oocystis lacustris* CHODAT from Lake Tanganyika. Scale bar – 10 µm.



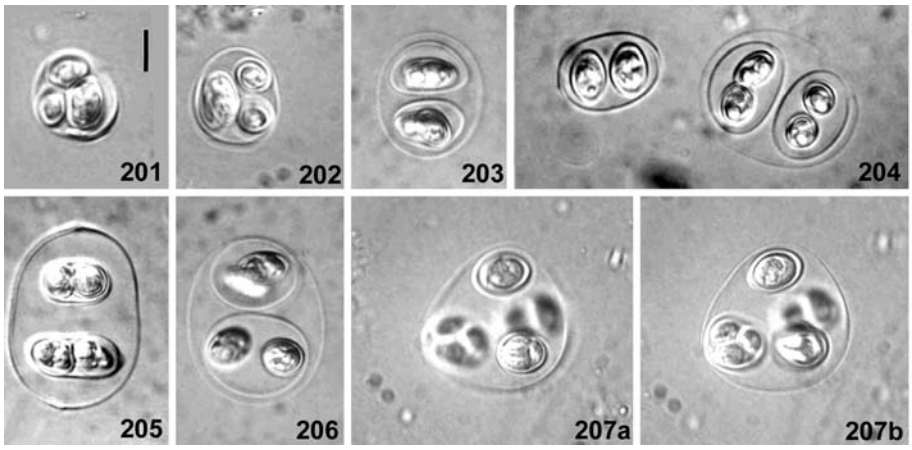
Figs 133-174: Two-celled colonies and autosporangia of *Oocystis lacustris* CHODAT from Lake Tanganyika. Scale bar – 10 µm.



Figs 175-188: Two-celled colonies of *Oocystis lacustris* CHODAT from Lake Tanganyika. Scale bar – 5 µm.

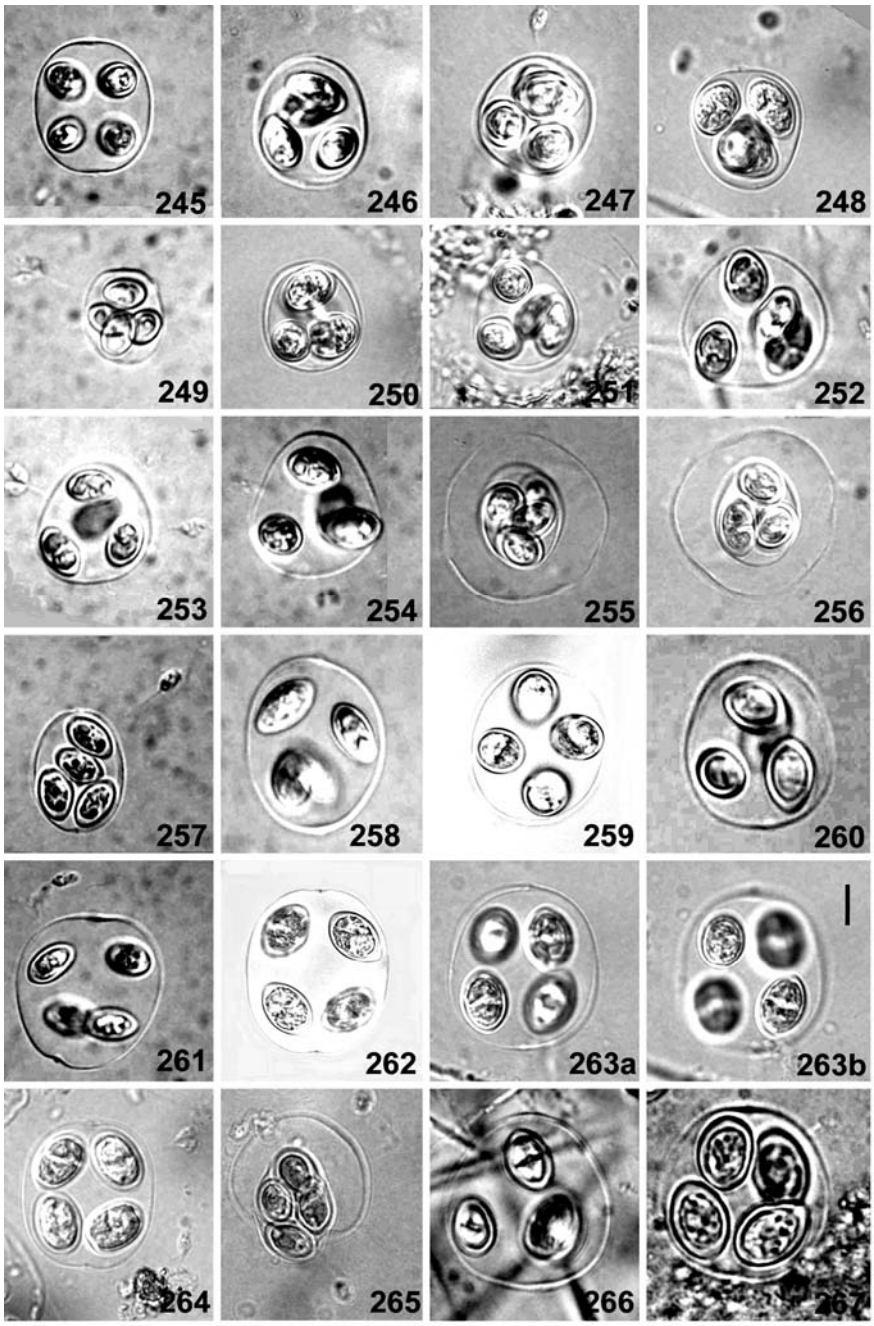


Figs 189-200: Colonies and autosporangia with 2, 3 and 4 cells of *Oocystis lacustris* CHODAT from Lake Tanganyika. Scale bar – 5 µm.

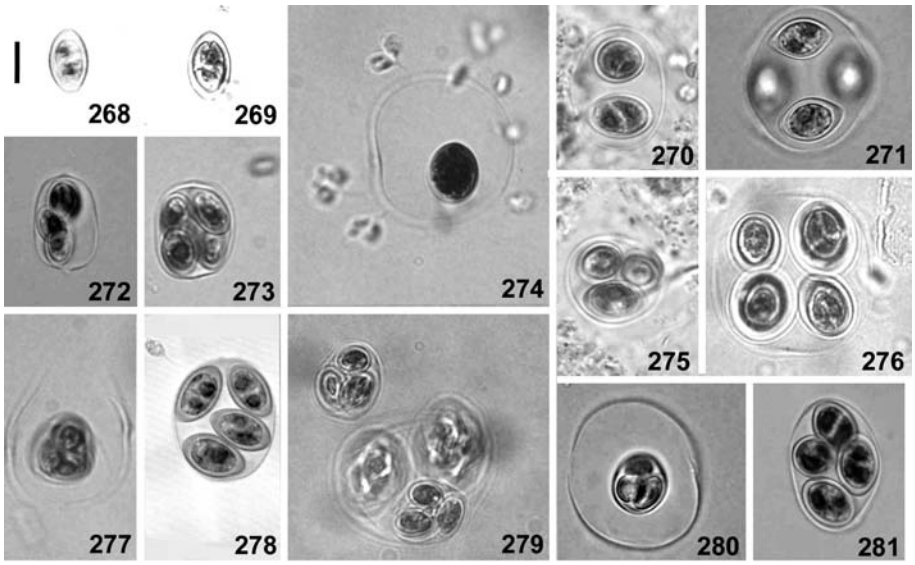


Figs 201-207: Three-celled and compound colonies and autosporangia of *Oocystis lacustris* CHODAT from Lake Tanganyika. Scale bar – 10 µm.

Figs 208-244: Four-celled colonies and autosporangia of *Oocystis lacustris* CHODAT from Lake Tanganyika. Scale bar – 10 µm.



Figs 245-267: Four-celled colonies and autosporangia of *Oocystis lacustris* CHODAT from Lake Tanganyika. Scale bar – 10 µm.



Figs 268-281: Solitary cells and colonies of *Oocystis lacustris* CHODAT from Lake Tanganyika after iodine staining. Scale bar – 5 µm.

Table 1A: Diacritical features in species of *Oocystis lacustris* CHODAT group in most used taxonomical literature (references in the text; K – in the key; T – in the text): cell morphology.

Author	Cell shape	Cell ends / poles	Polar thickenings nodules	Parental wall	Poles of parental wall	Number of cells in colonies	Position of cells in colonies	Single (solitary) cells	Number of autospores	Release of autospores
O. lacustris										
PRINTZ (1913)	K: fusiform; T: ellipsoidal or wide fusiform, 11.5x longer than wide	slightly acuminate (tapering gradually) at both poles	slightly pronounced	gelatinous, wide, enlarged	sometimes present and then obvious					
BRUNNTHALER (1915)	ellipsoidal	tapered	slightly pronounced		tapered thickenings					
KORSHIKOV (1953)	broadly fusiform to almost oval, length 1.5x breadth		present		distinct	2-4-8		not usual		
SKUJA (1956)	wide and short fusiform	tapered	present	ellipsoidic or tetrahedrial	slightly concaved with central polar nodules	2-4-8		occur (more rare than colonies)	2-4-8	
PRESCOTT (1962)	K: elliposoid or ovate, 1.5x their diameter in length; T: broadly elliptic or moniliform		large nodular thickenings, projecting outward (sometimes with a slight inner swelling also) at both poles	enlarged, oval	nodules sometimes present	2-8		not usual		
SKUJA (1964)	narrow or wide ellipsoidal	'+/-' tapered, sometimes asymmetrically sharpened on one of the poles, while the other is rounded	present	thick, gelatinous, smooth	present, sometimes formed as end papillae	4-16		not usual		
PHILIPOSE (1967)	ellipsoid; 1.5x longer than broad	somewhat pointed			with polar nodules	4-8				
REHAKOVA (1969)	length 1.1-3x width	rounded or tapered/sharpe	absent?			4-24 (2 or 3 generations)	free-laying	occur (?in the same frequency as colonies)		gelatinization of mother cell wall
LINDAU & MELCHIOR (1971)	fusiform		present			2-8		occur		
FOTT (1976)	ellipsoidal		present			<16	free-laying	occur (in the same frequency as colonies)		gradual dissolu-tion of mother cell wall

Author	Cell shape	Cell ends / poles	Polar thickenings nodules	Parental wall	Poles of parental wall	Number of cells in colonies	Position of cells in colonies	Single (solitary) cells	Number of autospores	Release of autospores
HINDAK (1980)	oval to slightly fusiform		somewhere visible as a short beak-like extension, somewhere only the cell wall was thickened, somewhere not at all	thick (<7 in 2celled colonies), widened conspicuously before autospore release				more often than colonies	2-4-8	complete gelatinization of the mother cell wall but by its splitting asunder beneath the apical thickening
KOMAREK & FOTT (1983)	K: fusiform to oval, symmetrical; T: narrow or wide ellipsoidal, rarely slightly asymmetrical	'+/-' rounded with clear tapered poles	sometimes, not clear		tapered	2-8, rare 24	free-laying	rare	2-4-8	
HINDAK (1984)						<16, compound colonies formed				
DILLARD (1989)	narrowly to broadly ellipsoid		present			2-8(-24)		not usual		
TIKKANEN & WILLEN (1992)	ellipsoidal					2-8		occur		
JOHN & TSARENKO (2002)	narrow to broadly ellipsoidal or spindle-shaped, slightly asymmetrical, about twice as long as broad	apices rounded to obtuse	distinct	with age slightly or markedly expanding		2-4-8, sometimes containing up to 3 generations	occasionally cells in tiers		2, 4 or 8 per sporangium	by gelatinization of mother wall and only rarely by its breakage
O. marssonii										
PRINTZ (1913)	K: fusiform; oval or fusiform, T: 1-1.5x longer than wide	sharpened, some times rounded	pronounced	thin						
KORSHIKOV (1953)	wide fusiform	acute, more rarely obtuse	present			(?<) 8				
SKUJA (1956)	wide and short fusiform	tapered	present	distended or nondistended	with nodules	2-8 (in last case often 2-cells are destroyed and 6-celled colonies appear)	both tightly and loosely arranged		1 (or more rare 2 or 8)	
SMITH & BOLD (1966)	ovate to medium fusiform		not evident	slightly distended		2-4-8, but more rare than solitary cells		usual	2-4-8	gradual dissolution of mother wall

Author	Cell shape	Cell ends / poles	Polar thickenings nodules	Parental wall	Poles of parental wall	Number of cells in colonies	Position of cells in colonies	Single (solitary) cells	Number of autospores	Release of autospores
REHAKOVA (1969)	narrow or wide-ellipsoidal, sometimes asymmetric, length 1.1-2.2 to width	rounded or sharpened		tetrahedrical		2-4-8, more rare compound colonies with 2-3 generations (only in old cultures)		occur (?in the same frequency as colonies)		
LINDAU & MELCHIOR (1971)	ellipsoidal	tapered	present			2-8		occur		
FOTT (1976)	wide fusiform, convexed at the long side		present			not more than 16		occur (in the same frequency as colonies)		
KOMAREK & FOTT (1983)	K: fusiform or ellipsoidal; T: wide fusiform to wide oval	more or less rounded or with slightly tapered ends	present			2 to 4 to 8	free-laying, close to each other or not	occur	(2 to) 4 (to 8)	
HINDAK (1988)	elongately elliptic		present		present	composite colonies with 2 or 3 generations				
TIKKANEN & WILLEN (1992)	wide fusiform			markedly expanding		2-4		occur		
JOHN & TSARENKO (2002)	broadly spindle-shaped to almost ovoid	each apex narrow, obtuse or slightly rounded	present			2-4-8; sometimes containing <3 generations	initially laying against mother cell wall	more often than colonies	2, 4 or 8 per sporangium	by fracture of mother cell wall
O. parva										
WEST & WEST (1898)	ellipsoid									
PRINTZ (1913)	wide fusiform to ellipsoidal	tapered	generally not present, or sometimes slightly pronounced with the development of cells	thin and smooth	small	2 to 4	tight	very often, almost always		
BRUNNTHALER (1915)								almost always		
KORSHIKOV (1953)	thick fusiform, length 1.25-1.75x breadth	narrowed acutely	present or the thickenings insignificant (sometimes present in daughter cells)			2-4		more usual than colonies		

Author	Cell shape	Cell ends / poles	Polar thickenings nodules	Parental wall	Poles of parental wall	Number of cells in colonies	Position of cells in colonies	Single (solitary) cells	Number of autospores	Release of autospores
PRESCOTT (1962)	K: narrowly elliptic; T: ellipsoid or fusiform	pointed poles	without definite polar nodules		not present (acc. to fig.)	2-8, 2-4 generations sometimes involved		usually		
REHAKOVA (1969)	narrow or wide ellipsoidal, sometimes slightly asymmetric, length 1.1-3x width	rounded or sharpened ends	sometimes with polar thickenings			2-4-8		occur (? in the same frequency as colonies)		
FOTT (1976)	ellipsoidal to broadly spindleshaped, 1.5 to almost twice as long as broad		present			<16	?free-laying	occur (in the same frequency as colonies)		rupture of mother cell wall
KOMAREK & FOTT (1983)	narrow or wide ellipsoidal	more or less rounded or with slightly tapered ends				2-4-8	free-laying	present	2-4-(8)	
HINDAK (1988)	ellipsoid		mostly not developed		mostly not developed, small but distinct in some colonies					
DILLARD (1989)	narrowly to broadly ellipsoid		without			2-4-8		as often as colonies		
TIKKANEN & WILLEN (1992)	elliptic					2-8		present		
JOHN & TSARENKO (2002)	ellipsoidal to broadly spindle-shaped, 1.5 to almost twice as long as broad	apices rounded or bluntly pointed	distinct, nipple-shaped thickening which often developes during autospore formation			2-4-8	densely packed, in contact by their long axes	as often as colonies	2, 4 or 8 per cell	by fracture of mother wall
O. borgei										
PRINTZ (1913)	oval	widely rounded	normally not, but possible in adult cells	thin	not thickened	2-8		in the same frequency as colonies		
BRUNNTHALER (1915)	wide elliptic	widely rounded	never						4	

Author	Cell shape	Cell ends / poles	Polar thickenings nodules	Parental wall	Poles of parental wall	Number of cells in colonies	Position of cells in colonies	Single (solitary) cells	Number of autospores	Release of autospores
KORSHIKOV (1953)	broadly oval, the length approx. 1.5x the breadth	widely rounded	without			2-4-8		not as usual as colonies		
SKUJA (1956)	wide oval	rounded		rounded, roundedellipsoi-dic or tetrahedrial		4-8	tight	occur (in the same frequency as colonies)	4 or more rarely 8	
PRESCOTT (1962)	ellipsoid or ovate	broadly rounded and smooth	without		rounded, not thickened or sharpened (acc. to fig.)	2-8	close to each other (acc. to fig.)	common		
PHILIPOSE (1967)	broadly ellipsoid to round about 1.25-1.5 x longer than broad		without	more or less round and narrow		2-8	narrowly embedded	not as usual as colonies		
FOTT (1976)	wide ellipsoidic		without							
HINDAK (1980)	oval to widely oval, also more elongate		without apical thickenings or with small apical thickenings			4, never composite colonies			4, usually or 2-4	
KOMAREK & FOTT (1983)	wide oval	widely rounded	absent			2-4-8	free-laying; close to each other or tetrahedrically arranged	rare	2-4-(8)	
HINDAK (1988)	broadly oval to broadly spindle-shaped; some-times slightly asymmetric		without or with neglible polar thickenings; only small on autospores		?only small	2-4; composite colonies not seen	densely pressed	often		
DILLARD (1989)	broadly ellipsoid		without			2-4-8		not as usual as colonies		
TIKKANEN & WILLEN (1992)	wide ellipsoidal			rounded triangular shape		2-8		as usual as colonies		
LING & TYLER (2000)	broadly ellipsoid	rounded	poles not thickened	more or less round		2-8				
JOHN & TSARENKO (2002)	broadly ovoid or ellipsoidal, usually <1.5x longer than broad	apices broadly rounded	usually without (reported to have small cell wall thickenings at apices)			2-4-8	densely packed, tetrahedrally arranged	as usual as colonies	2, 4 or 8 per sporangium	by fracture or slightly inflated mother cell wall

Table 1B: Diacritical features in species of *Oocystis lacustris* CHODAT group in most used taxonomical literature (references in the text; K – in the key; T – in the text): dimensions.

Author	Cell length	Cell width	Colony width	Colony length	Mucilage
O. lacustris					
PRINTZ (1913)	14-32	8-22	43	65	
PLAYFAIR (1916)	9-18	5-9	22	24-30	
KORSHIKOV (1953)		≤ 6-10			
PRESCOTT (1962)	16-28	12-20			
SKUJA (1956)	9-20	5-14	30-80-150	30-80-150	
SKUJA (1964)	10-25	7-15	26-36 (66)	31-39 (90)	
PHILIPOSE (1967)	13-32	8-22	26; 26-43	32-37; 30-75	
REHAKOVA (1969)	K: 5-14, T: 6.4-11.2 in mass, 4.8-14.4 as extremes	K: 2-8; T: 3.2-6.4 in mass, 1.6-8 as extremes			present
FOTT (1976)	K: ≤ 14 in the 1st step and ≤ 15 in the 2nd step				
HINDAK (1980)	4-8	2-4 (6)	≤ 10	≤ 11	3-5 µm around the cells
KOMAREK & FOTT (1983)	K: 4.8-14.4; T: (4) 6.4-11.2 (-14.4)	K: 1.6-8; T: (1.6)-3.2-6.4-(10)			present, wide
HINDAK (1984)	(9) 12-17 (18)	6-8 (10)	15-40	22-55	5-10, 10-15, or 3-20 µm
HINDAK (1988)	8-26	6-7 - 12-15	12-40	20-55	5-10
DILLARD (1989)	(4)-6-12-(15)	(2)-3-7-(10)			unstratified and not sharply defined
TIKKANEN & WILLEN (1992)	(4)-6-11-(14)	(2)-3-6-(10)			
LING & TYLER (2000)	9-13	5-7			
JOHN & TSARENKO (2002)	(9-) 10.5-16 (-20)	(1.5) 3.2-9.2 (-10)			
O. marssonii					
PRINTZ (1913)	8-14	5-8	21	28	
BRUNNTHALER (1915)		1-2			
KORSHIKOV (1953)	5-8	8-14	21	28	
SKUJA (1956)	10-16	5-10	19-40	19-40	?present
SMITH & BOLD (1966)	6	4			without
REHAKOVA (1969)	K: 6-21; T: 9.6-16 in mass and 6.4-20.8 as extremes	K: 5-14; T: 6.4-11.2 in mass, 4.8-14.4 as extremes			without
FOTT (1976)	≤ 14				
KOMAREK & FOTT (1983)	K: 10-25; T: 6.4-25 (-32)	K: 6 to 14; T: 4-14(-22?)			
HINDAK (1988)	10-13 for autospores; not indicated for adult cells	6-8 for autospores; not indicated for adult cells	43	40	7 µm wide

Author	Cell length	Cell width	Colony width	Colony length	Mucilage
TIKKANEN & WILLEN (1992)	7-25-(32)	3-9			
JOHN & TSARENKO (2002)	(6.4-) 8.5-18 (-20.8)	(4-) 6.3-12 (-14.4)			
O. parva					
WEST & WEST (1898)	13.5-29	4-7			
PRINTZ (1913)	6-12	4-7	10.5-18	13.5-29	
BRUNNTHALER (1915)		2-3			
PLAYFAIR (1916)	10-12	8	12-18-24-30-48-54	12-18-22-24-42-48	
KORSHIKOV (1953)	6-12 (13.5-29 for the outer wall of solitary cells)	4-7 (10.5-18 for the outer wall of solitary cells)			
SKUJA (1964)	10-25	7-15	26-36 (66)	31-39 (90)	
REHAKOVA (1969)	3-11	2-6			never formed
FOTT (1976)	≤ 11				
KOMAREK & FOTT (1983)	K: ≤ 12 (?); T: 3.2-12- (17)	1.5-6.4-(8)			
HINDAK (1988)	6-12	(3) 4-7	(6) 10.5-18	(8-12)-13.5-29	2-4 (6) µm
DILLARD (1989)	3-12-(17)	1.5-6.5-(8)			stratified and sharply defined
TIKKANEN & WILLEN (1992)	3-12-(17)	2-6-(8)			
LING & TYLER (2000)	14-15	7-8			
JOHN & TSARENKO (2002)	(6.4-) 8.5-18 (-20.8)	(4-)6.3-12(-14.4)			
O. borgei					
PRINTZ (1913)	9-17	9-13	30-40	30-40	
BRUNNTHALER (1915)	13-17	9-13	35-36	35-36	
KORSHIKOFF (1953)	9-17	9-13			
SKUJA (1956)	12-23 (< 28 before autospore production)	10-17 (≤ 21 before autospore production)	30-60	30-60	
PRESCOTT (1962)	(9)-10-19	(9)-12-13	31	46	
PHILIPOSE (1967)	9-19	9-14			
FOTT (1976)	≤ 23				
HINDAK (1980)	5-9, 9-16	6-12, 12-18	12-20	17-20 (25)	hyaline, structureless, 4-20 mkm wide around cells
KOMAREK & FOTT (1983)	K: 9-20; T: 9-23	K: 8.5-13; T: 8.5-17 (-20?)			
HINDAK (1988)	12-16	9-14	31	35	hyaline, structureless, 4-7 mkm wide around cells
DILLARD (1989)	9-23	8.5-17-?			stratified and sharply defined
TIKKANEN & WILLEN (1992)	9-22	9-17			
LING & TYLER (2000)	10-12	7-8			
JOHN & TSARENKO (2002)	(9) 10.5-16 (-20)	(6) 8.5-17(-20)			

Table 1C: Diacritical features in species of *Oocystis lacustris* CHODAT group in most used taxonomical literature (references in the text; K – in the key; T – in the text): chloroplasts and pyrenoids.

Author	Number of chloroplasts in vegetative cells	Number of chloroplasts in autospores	Position and shape of chloroplasts	Pyrenoids
O. lacustris				
PRINTZ (1913)	1-3 (in adult cells)		big, blade-like and parietal, with entire ends or very rarely lobated	absent
BRUNNTHALER (1915)	1-2		parietal	K: not; T: not mentioned
PLAYFAIR (1916)	1-2		laminar	often present
KORSHIKOV (1953)	1-3			without pyrenoids (?)'
SKUJA (1956)	1 (rare 2)		parietal or oriented to cell poles	usually present, but sometimes without
PRESCOTT (1962)	K: 1 or 3 (rarely 4); T: 1 or 3		parietal plates	usually 1
PHILIPOSE (1967)	1-3		laminate	without
REHAKOVA (1969)	1-2 (K: ≤ 12 before autospore formation; T: ≤ 8 before autospore formation)	1	parietal, blade-like (in cross-section - halfcrossed)	1
LINDAU & MELCHIOR (1971)	1 or 2			
FOTT (1976)	2-4 (rare more)	1 (rare 2)		
HINDAK (1980)			parietal, initially troughy, later in shape of wide H	1, large, in the centre
KOMAREK & FOTT (1983)	1, splitted in 2 or 4	1		1 in each part of chloroplast
HINDAK (1984)	2-4	1, always		
HINDAK (1988)				has to be due to referring to *Oocystella*, but not mentioned in the text
DILLARD (1989)	1-4			1 in each chloroplast
TIKKANEN & WILLEN (1992)	1 in young, 2-4 in older cells	1, rarely 2		
JOHN & TSARENKO (2002)	1 (increasing to 4 by age)	1	through-shaped and not grooved	1 in each chloroplast
O. marssonii				
PRINTZ (1913)	1-2		big, blade-like, parietal	1, pronounced
BRUNNTHALER (1915)	1-2			?
KORSHIKOV (1953)	1-2			with pyrenoids'
SKUJA (1956)	2-4		parietal, plate-like	1, in central part (slightly pronounced and difficultly visible, sometimes nearly not visible)
SMITH & BOLD (1966)	1-2		parietal laminae	1, often occult in each chloroplast
REHAKOVA (1969)	2-4-8 (4-8-12 before autospore formation)	1-2	parietal, blade-like	1 in each chloroplast
LINDAU & MELCHIOR (1971)	1 or 2			
FOTT (1976)	4-8 (rare more)	1 (rare 2)		

Author	Number of chloroplasts in vegetative cells	Number of chloroplasts in autospores	Position and shape of chloroplasts	Pyrenoids
KOMAREK & FOTT (1983)	(1)-2-4	1		1
HINDAK (1988)	1-2 in young cells and ≤ 8 (or even more?) in adult cells	(1) 2 (4)		has to be due to referring to *Oocystella*, but is not mentioned in the text
TIKKANEN & WILLEN (1992)	1-2 in young, 2-8 in older cells	1, rarely 2		
JOHN & TSARENKO (2002)	2-4-(8)	1	grooved	1 in each chloroplast
O. parva				
PRINTZ (1913)	1-3		blade-like, parietal	lacking
BRUNNTHALER (1915)	2-3			?
KORSHIKOV (1953)	1-3			absent
PRESCOTT (1962)	K: 1-3 (rarely 4); T: 1-3		parietal discs	sometimes present
REHAKOVA (1969)	(1) 2 (K: ≤ 12 before autospore formation; T: ≤ 8 before autospore formation)	1-2		1 in each chloroplast
FOTT (1976)	4-8 (rarely more)	1 (rare 2)		
KOMAREK & Fott (1983)	1 in young cells, later splitted in 2 or 4	1		1
HINDAK (1988)	1		parietal	1, central
DILLARD (1989)	1-4			each with (?or without) pyrenoid'
TIKKANEN & WILLEN (1992)	1in young, 2-4 in older cells	1, rarely 2		
JOHN & TSARENKO (2002)	1 (2-4 by age)	1		1
O. borgei				
PRINTZ (1913)	1or very rare 2 or 4 (just before cell division)		bell-shaped	1, pronounced
KORSHIKOV (1953)	1-2-4, depending on age			present
SKUJA (1956)	normally 2-4, rare 1 (in young cells)	1	parietal	1, rounded or ellipsoidic (present also in autospores) and well pronounced
PRESCOTT (1962)	1, or as many as 4		parietal plates	1 in each chloroplast
PHILIPOSE (1967)	1-4			1 in each chloroplast
FOTT (1976)	normally 4			
HINDAK (1980)	1	often 2 or 4	in form of broad H, parietal	1, in the median portion
KOMAREK & FOTT (1983)	1-2-4	1		1
HINDAK (1984)				
HINDAK (1988)	4-16	2-4	parietal, sometimes with irregular borders, disciform	1, central
DILLARD (1989)	1-3			1 in each chloroplast
TIKKANEN & WILLEN (1992)	(1-) 4	1, rarely 2		
LING & TYLER (2000)		1-4	parietal	1 in each chloroplast
JOHN & TSARENKO (2002)	1-4 (depending on age)	1	grooved	1 in each chloroplast

Table 2A: Diacritical features in species of *Oocystis lacustris* CHODAT group in literature on African material (references in the text): cell morphology.

Author	Cell shape	Cell ends/poles	polar thickenings/ nodules	mother (autosporangial) wall	poles of autosporangial wall	Number of cells in colonies	Position of cells in colonies	Single (solitary) cells	Number of autospores	Realization of autospores
O. lacustris										
WEST (1907)			faint, exceedingly slight			≤ 8				
SYMOENS (1956)	ellipsoidal	rounded				2-8				
COMPÈRE (1976)	ellipsoidal		present, as nodules					with the same frequency as colonies		
UHERKOVICH & RAI (1977) - acc. to drawing	ellipsoidal	rounded	without		tapered					?by gelatinization of the part of the wall
HECKY & KLING (1987) -acc. to figs.	broadly oval to ellipsoidal		with or without			2-4				
COMPÈRE (1991)	ellipsoidal	rounded or sharpened				4-8		more rare than colonies		
O. marssonii										
FRITSCH & RICH (1923) - forma		either rounded, or more or less pointed	slightly thickened			8	close-fitting to each other	with the same frequency as colonies		
GAYRAL (1954)	ellipsoidal	widely pointed		thin		2		with the same frequency as colonies		
COMPERE (1991)	ellipsoidal	rounded, or more often sharpened/tapered				4-8		with the same frequency as colonies		

Author	Cell shape	Cell ends/poles	polar thickenings/ nodules	mother (autosporangial) wall	poles of autosporangial wall	Number of cells in colonies	Position of cells in colonies	Single (solitary) cells	Number of autospores	Realization of autospores
O. parva										
BOURRELLY & LEBOIME (1946) - f.	ellipsoidal	not pointed			thickened	2		very rare		
GAYRAL (1954)	small, ellipsoidal	tapered								
COMPÈRE (1976)	ellipsoidal	tapered/pointed	present			2-8		with the same frequency as colonies		
COMPÈRE (1991)	ovoid or ellipsoidal	rounded or sharpened				4-8		with the same frequency as colonies		
MPAWENAYO (1996)	ellipsoidal (acc. to the drawing)	tapered	absent			2 (acc. to the drawing)				
O. borgei										
GAYRAL (1954)	oval					4		with the same frequency as colonies		
COMPÈRE (1976)	ellipsoidal	rounded	present, as nodules			2, 4 or 8		not mentioned		
GERRATH & DENNY (1980)	broadly ellipsoidal		absent							

Table 2B: Diacritical features in species of *Oocystis lacustris* CHODAT group in literature on African material (references in the text): dimensions

Author	Cell length	Cell width	Colony (autosporangia) width	Colony (autosporangia) length	Mucilage
O. lacustris					
WEST (1907)	12-20	7-13	39-54	39-54	
COMPÈRE (1967)	27	13			
COMPÈRE (1976) - forma I	8-14	4-7			
COMPÈRE (1976) - forma II	20-30	11-20			
COMPÈRE (1976)	5-30	2-20			
COMPÈRE (1991)	5-9	4-5			
O. marssonii					
FRITSCH & RICH (1923) - forma	16-21	10-13	32 (for 8-celled colony)	32 (for 8-celled colony)	
GAYRAL (1954)	10-14	6-8			
COMPÈRE (1991)	12-23	8-15			
O. parva					
BOURRELLY & LEBOIME (1946) -forma	10	5			
GAYRAL (1954)	6-12	4-6			
COMPÈRE (1976)	4-16	2-8			
COMPÈRE (1991)	6-10	2.5-6			
MPAWENAYO (1996)	11	5-6			
O. borgei					
GAUTHIER-LIEVRE (1931)	18	12			
GAYRAL (1954)	15	10-11			
COMPÈRE (1976)	9-29	7-14			
GERRATH & DENNY (1980)	18,5	11			

Table 2C: Diacritical features in species of *Oocystis lacustris* CHODAT group in literature on African material (references in the text): chloroplasts and pyrenoids.

Author	Number of chloroplasts in vegetative cells	Position and shape of chloroplasts	Pyrenoids
O. lacustris			
WEST (1907)	2		
SYMOENS (1956)	few ?		
COMPÈRE (1967)	1	parietal	1, in each chloroplast
COMPÈRE (1976) - forma I			
COMPÈRE (1976) - forma II			
COMPÈRE (1976)	1-2 (-4)	parietal	generally 1, in each chloroplast
UHERKOVICH & RAI (1977) - acc. to drawing	1	parietal, half-ring	without
HECKY & KLING (1987) - acc. to the drawings	>2		without
COMPÈRE (1991)	1-4	parietal (acc. to the drawing)	1, in each chloroplast
O. marssonii			
FRITSCH & RICH (1923) - forma	usually about 4 per cell		
GAYRAL (1954)	2	parietal	1, in each chloroplast
HECKY & KLING (1987) - acc. to the drawings	1	parietal	1, central
COMPÈRE (1991)	1-4	parietal (acc. to the drawing)	1, in each chloroplast
O. parva			
BOURRELLY & LEBOIME (1946) - forma	1		without
GAYRAL (1954)	1-3	parietal (acc. to the drawing)	without
COMPÈRE (1976)	1-2 (-4)	parietal	generally 1
COMPÈRE (1991)	1		1, in each chloroplast
O. borgei			
GAYRAL (1954)	1, more rare 2-4		1, in each chloroplast
COMPÈRE (1976)	1-4		1, in each chloroplast
GERRATH & DENNY (1980)	2-4	parietal	1, in each chloroplast