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Charophyta: their use in paleolimnology *

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Abstract

Charophyta are common algae in limnic waters from many regions and are an interesting group from an evolutionary point-of-view, as they are believed to be related to the Chlorophyceae and land plants. Paleontological-botanical systematics are discussed, taking into consideration some new advances. Charophytes live in all types of inland waters and are sensitive to ecological change, and so they are very useful paleolimnological markers. Gaps concerning gyrogonite morphology in extant taxa and their responses to different environmental conditions must be described. This paper discusses data concerning ecological factors affecting the distribution of Argentinian Charophyta (principally distributed between 30° S and 40° S), gyrogonite morphology related to different ecological conditions, and the way that Charophyta can modify the environment.

Introduction

The charophytes are green macroscopic algae, characterized by their very complex thallus and reproductive organs, biflagellate spermatozoids and the development of protonema when oospores germinate. They have chlorophylls *a* and *b* (as Chlorophyta and higher plants), the thylakoids form grana (as in higher plants) and starch is the storage product. The continued growth is provided by an initial apical cell and their thallus is formed by cladomes (Chadefaud, 1979), with uninucleate cell nodes and plurinucleate, coenocitic internodal cells. Stipulodes and spiral cells are also multinucleate and nuclei fragmentation, as in internodal cells, is produced by amitosis (Cáceres & Parodi, 1985). The only motile cells, the spermatozoids, are helicoidal with two unequal flagella (very similar to those of Bryophyta and some Pteridophyta) and have an assymetrical microtubular cytoskeleton and rhombic scales (Moestrup, 1970; Cocucci & Cáceres, 1976). The oosphere is protected by sterile cells (as in *Coleochaete* and higher plants) and after fertilization several complex changes occur in the walls that protect the zygote, and in some genera and species, the content of the spiral cells can calcify and form the gyrogonite. In fossils, vegetative parts or oospores are only rarely found, although oospores and external calcareous remains covering the thallus are frequently found in Quaternary sediments. The sculpture of the external wall, called the ectosporostine, is useful in systematics; but the only structure well represented as fossil are the gyrogonites, on which paleontological systematics of the Charophyta is based. Grambast (1974) agreed to place the group in a separate division, suggesting that the charophytes were well differentiated since their appearance in the Upper Silurian.

Charophyta reproduction is oogamous, a characteristic also acquired by *Coleochaete* spp. and all Cormophyta. The life cycle is monogenetic haplophasic.

Pickett-Heaps & Marchant (1972) and Pickett-Heaps (1974, 1975, 1976, 1979) using TEM (transmission electron microscopy) demonstrated in Charophyta the presence of a persistent interzonal spindle and the formation of a phragmoplast during the bipartition of the cells, also present in the Chlorophyta genera *Stichococcus*, *Raphidonema*, *Klebsormidium*, *Chaetospheridium* and *Coleochaete*, and typical in the cytokinesis of the higher plants. Stewart & Mattox

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* This is the fifth in a series of papers published in this issue on 'Paleolimnology in Southern South America'. Dr C. A. Fernández served as guest editor for these papers.

(1975) suggested the establishment of four classes of advanced green algae. Cáceres (1989) reviewed the advances in algal systematics, and the orders Coleochaetales, Charales, Chlorokybales and Klebsormidiales were included in the Class Charophyceae.

Guerlesquin (1990) analyzed the available evidence that relates the charophytes with some chlorophytes and higher plants. She said that if charophytes had anything to do with the evolution of land plants, it is impossible to state it at the present time.

According to Grambast (1974), the group is treated as Charophyta because evidence exists to segregate these algae from advanced Chlorophyceae and primitive higher plants, and because these differences appeared very early in the Earth's history.

Some important characteristics that make the Charophyta useful in paleolimnology are:

The spiral cells surrounding the zygote can become calcified in several taxa, so they remain in the sediments as fossils. Sometimes, the oospores or parts of the oospore walls, can be found, especially in Quaternary sediments. These gyrogonite and oosporal remains can be very abundant in lacustrine sediments. Fossil thalli are rare but vegetative remains such as calcareous tubes or nodes are frequently found in younger sediments (Fig. 1).

The charophytes are widely distributed in limnic sediments since the Upper Silurian. Most taxa indicate age and environment, and stratigraphic correlations can be made. They can also provide inferences of paleolimnological and paleoclimatic conditions.

Charophytes are sensitive to environmental change. They inhabit most types of non-marine habitats, from fresh to hyperhaline waters, between the coast to inland lakes. Each genus, species and morphotype indicates different ecological conditions, such as ephemeral or permanent waterbodies, acid to alkaline waters, littoral or deeper zones, gravel to slimy bottoms, high or low temperatures, lentic or lotic water-bodies, ionic composition and principally different degree of salinity.

There are three important gaps that still require considerable research before charophytes can be applied more effectively to paleolimnology. One is our incomplete knowledge about the oospores and gyrogonites of extant taxa, which is necessary for the study of forms collected in younger sediments, their correct taxonomic determinations, and the recognition of extinct taxa. The second gap concerns our still poor knowledge of the ecological conditions that influence their geographic distribution. Finally, we must learn more about charophyte physiology, both measured in the field and in laboratory cultures.

The gyrogonite

The process of oospore and gyrogonite formation is very complex: once fertilization occurs, two zygotal walls surrounding the fertilized oosphere are differentiated: the endosporine and the ectosporine. Overlying these two zygotal walls, there are two other external walls, the endosporostine and the ectosporostine originated by the adaxial wall of the spiral cells with a multilayered structure. All these walls constitute the oospore, and in some taxa the spiral cells themselves can calcify, forming the gyrogonite (Fig. 1). Thus, the observation of living gyrogonites from Argentina, together with Horn af Rantzien (1956) and Dyck (1970), shows that the external oospore membranes originate from the adaxial wall of the spiral cells, which differs from Soulié-Märsche's (1979, 1989) observations. She suggests that these walls originate from intercellular substances.

Since the systematics of charophytes is generally based on 'the soft parts' (vegetative structures, oogonium, oospores and antheridia) and in general the gyrogonite is not even mentioned, the paleontologist cannot fully answer the following questions: a) Do changes in gyrogonites represent genetic changes occurring in charophytes? b) Is the gyrogonite a reliable structure on which paleontological systematics could be based?

Horn af Rantzien (1959) was the first to analyze systematically the morphology and characteristics of living oosporangias, gyrogonites and oospores. He recorded the morphology of oosporangia and oospores of 23 taxa, 10 of which produced gyrogonites. He used the parameters (Horn af Rantzien, 1956) LPA (largest polar axis), LED (largest equatorial diameter), *n* (number of spiral cells), ISI (isopolarity index: LPA/LED.100), ANI (anisopolarity index: the distance from the apical pole to the LED/LPA. 100). Other measurements used were the width of spiral cells at the equator, the width of basal pores and the characteristics of the basal plugs.

Soulié-Märsche (1979, 1989) compared 50–100 gyrogonites from 39 species, 20 of which were calcified. She deduced reliable patterns of variability, suggesting that, in some species, the variability was related to ecological changes. She also proposed a phylogenetic scheme.

García (1987) studied 23 extant taxa from Argentina (15 with gyrogonites) from a botanical and pa-

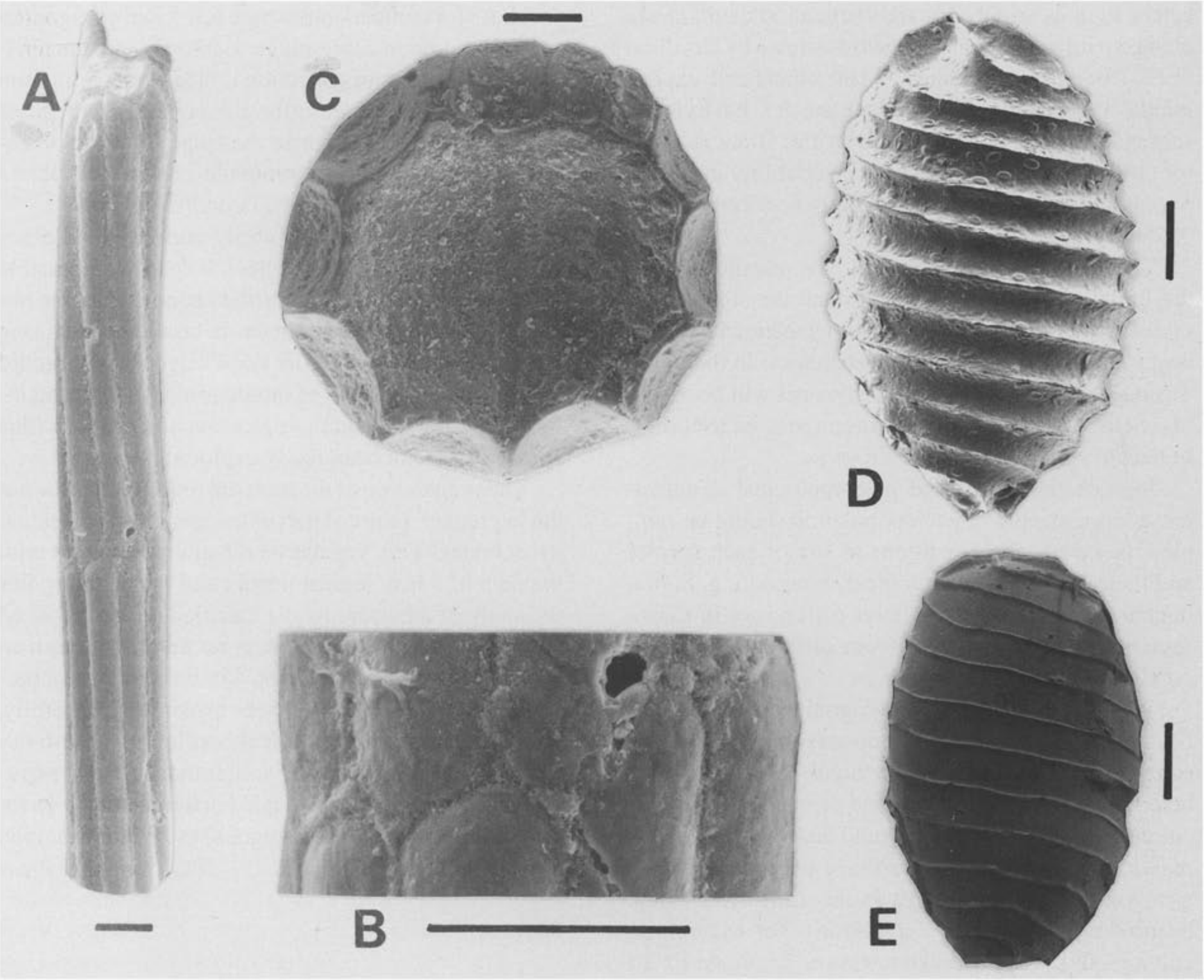

Fig. 1. A-C. Vegetative remains of *Chara* sp., Holocene from Punta Hermengo, Province of Buenos Aires. A. Corticated branchlet, 75×. B. Section of corticated branchlet, 350×. C. Axial node, with two central cells, 100×. D-E. Reproductive charophyte remains of *Chara vulgaris* L. D. Gyrogonite, lateral view, 100×. E. Oospore, lateral view, 100×. Scales: 100 µm.

leontological point-of-view (systematics, ecology, geographical distribution, Quaternary forms). The analysis of 100 gyrogonites of extant species allowed the comparison of both systematics, and provided the basis for the discrimination of Quaternary and Neogene or older gyrogonites.

Very important results were obtained by the above authors: the oospores and the gyrogonites appear to be dependable structures that reflect genetic changes, but paleontologist should be careful about several aspects.

If possible, at least 100 gyrogonites of each taxon are needed in order to recognize intra-populational variability, distinguish teratological forms (deformed forms produced under stressed conditions), and show real patterns of comparison with qualitative and quantitative data. Furthermore, paleontologists should not forget that the gyrogonite is only the calcified remain of the fertilized female gametangium; only one plant (depending on what species) could give more than 100 gyrogonites and calcification occurs at different times in the same plant. Different times of maturation in upper-lower whorls and their position on branchlet nodes can be detected. Pedrola & Acuña (1986) found the last variation to be non-significant.

From a botanical point-of-view, several systematic questions need to be raised. Some advances have been made towards changing the concept of Charophyta species and the value of vegetative characters used in botanical classification. Grant & Proctor (1972) and Proctor (1975, 1980) have demonstrated that characters such as stipulodes and cortication could easily change with ecological changes (as shown by Corillion (1957) for cultured species). On the other hand, experimental hybridizations of the same species, but living in segregated areas, were not interfertile. Grant & Proctor (1989) observed large genetic variability in natural populations of *Chara haitensis* Turper collected across 35 degree latitude.

These results lead to several new questions about the limits of Charophyta species and the significance of cosmopolitan taxa, and also which elements are the best to consider in botanical systematics. In this sense neontological-paleontological advances will be of mutual help, as paleontological criteria may be useful for botanical systematics, and vice versa.

In both, botanical and paleontological systematics, a large sample of each population should be sampled as well as the conditions of life of each species and their responses to ecological changes (e.g. Subramanian (1989) found vegetative differences in *Chara zeylanica* Klein ex Willd. from different ecological conditions).

When studying fossil gyrogonites, care should be taken to differentiate biocoenoses from thanatocoenoses (the first by a high number of specimens, heterogeneity of sizes, and good preservation); different degrees of calcification could be found in a single plant, which can modify the shape of spiral cells and gyrogonite outline; changes in the dimensions could be produced by stressed conditions (for example in cultures, this was observed in *Chara contraria* Br. ex Kütz., *s.l.*). Another example is *C. aspera* Deth. ex Willd., which is more elongated in fresher waters, as shown by Soulié-Märsche (1991). Mojon (1989) analyzed the variability of gyrogonites in extant *Lamprothamnium papulosum* Groves and compared them to the variability found in gyrogonites of Porocharaceae from Jurassic sediments. Both groups were found in saline environments. Based on the gyrogonite variability he detected in extant forms, the author could infer environmental changes for the Mesozoic sediments.

Material and methods

For the study of Quaternary and Neogene charophytes (and earlier ones) a methodogical analysis of extant populations has been followed. As the gyrogonites of extant taxa must be well known, at least 100 gyrogonites of each taxon were separated directly from the plants (García, 1987). This method assures a reliable data base for comparisons where few fossil gyrogonites were found in an assemblage. Ecological characteristics from the sites of collection is at least the minimum information to help describe the ecological range of each species, and recognize the response of the vegetative parts and the gyrogonite morphology in species which live in a broad range of conditions.

As charophytes can be easily cultured (and especially the cosmopolitan species), it should be possible to cultivate them under controlled conditions. The objective will be to find, for each taxon, the limiting conditions for growth. This knowledge and the record of the gyrogonite changes should provide important information for paleolimnological reconstructions (this approach has not been really explored thus far).

The preparation of the material requires to draw out the 'tegument' (abaxial part of the spiral cells) in extant gyrogonites. This vegetative remain is removed with the help of a histological needle and fine pincers. For the study of the oospore, the calcified part is removed with diluted HCl, and the oospores are put through an alcohol series for dehydration. For basal plug recuperation, some gyrogonites must be broken very carefully, with the help of an histological needle and a brush (all instruments are kept wet). For the study of fossil populations, the sediments are treated in the same way as for calcareous microfossils, using 200 to 500 g of sample.

Results

Several questions concerning charophytes must be answered before they can be used as ecological indicators: How do ecological factors influence the distribution of charophytes? How do charophytes modify the environment? Which characteristics can be observed in fossil gyrogonite populations that can be used to infer environmental conditions?

How do ecological factors influence the distribution of charophytes?

The charophytes live in all types of non-marine environments: lentic (pools, ponds, lakes, lagoons) or lotic (creeks, rivers, alluvial plains) systems. Using data about living species studied by Zaneveld (1940), Corillion (1957) and from Argentinian Charophyta (García, 1987), we described the temperature, energy, salinity, ionic composition, pH and substrate influences on geographic distributions.

Temperature

This factor influences all aspects of the life cycle, *i.e.* germination, sexual maturation, death. Gradient temperature changes could be latitudinal, altitudinal, or by water depth. Thus, some taxa are typically circumtropical and temperate, as *Chara zeylanica* which is not found in Europe but widely distributed in all circumtropical areas. *Tolypella intricata* (Trent. ex Roth.) Leonh. var. *apiculata* (A.Br.) Wood has a South American distribution and is not found beyond 37°S.

Another temperature gradient is represented by depth. Some species prefer littoral, warmer waters, such as *Nitella hyalina* (DC) Ag., which is different from other littoral forms, where the temperature is, in some respects, controlled by the movement of the water, e.g. *Chara braunii* Gmel., *C. halina* García, *Nitella clavata* Kütz., *Tolypella intricata* var. *apiculata* and *Lamprothamnium haesseliae* Donterberg. In deeper waters, temperature is low, and *Nitella opaca* (Bruz,) Ag. and *Chara bulbillifera* (Dont.) García can be found. With respect to altitude, some taxa live above 4000 m, e.g. *Chara baltica* Bruz., *Lamprothamnium succinctum* (A. Br. in Asch.) Wood. Cosmopolitan species such as *Chara contraria*, *C. vulgaris* L. and *C. globularis* Thuill. live in a wide range of latitudes, altitudes and depths (0.2–30 m), and so they can withstand wide changes in temperature. *Chara globularis* and *C. contraria* can even tolerate freezing.

Energy

Water energy can be a limiting factor for charophytes growth, specially turbulence (suspended sediments carried by affluents, winds or the turbulence produced by man, *i.e.* nautic). Charophytes prefer quiet waters where they can develop large populations, e.g. *Chara contraria*, *C. vulgaris*, *C. globularis*, *C. braunii*, *C. leptosperma*, *C. baltica*, *C. zeylanica*, *C. rusbyana* Howe, *Nitella hyalina*, *N. clavata*, *Tolypella intricata*. There are taxa that prefer or, at least withstand, moving waters, as Zaneveld (1940) has remarked. In waters with unidirectional movement, predominant cosmopolitan taxa and *Chara leptosperma*, *T. intricata* var. *apiculata* and *Nitella clavata* predominate. In habitats where the wind produces waves frequently in one direction, it is possible to find *Chara baltica*, *C. halina*, *C. bulbillifera*, *Lamprothamnium haesseliae*.

pH

Species which calcify are only found in alkaline waters, e.g. *Chara contraria*, *C. vulgaris*, *C. globularis*. *Nitella hyalina* can live in alkaline or slightly acid waters. *Chara halina*, *Lamprothamnium haesseliae* and *Tolypella intricata* var. *apiculata* are found in very alkaline waters. The majority of Nitellas and some Charas that do not calcify (e.g. *Nitella clavata*, *Nitella opaca* and *Chara braunii*) can live in slightly acid waters. In the analysis of fossil populations, dissolution of the gyrogonite by acid conditions was observed in *Tolypella intricata* var. *apiculata* from Holocene sediments near La Plata city (García, in preparation).

Substrate

Charophytes prefer fine sediments, but some taxa can be found growing over gravel (e.g. *Chara andina* (Braun) Cáceres), with very long rizhoids supported in the interstitial fine sediments, or in artificial waterbodies where sediments form a thin layer on the bottom (e.g. *Chara globularis*, *C. rusbyana* or *Nitella hyalina*). The sediments may also be predominantly slimy-clays (e.g. *Chara contraria*, *C. globularis*, *C. vulgaris*, *C. braunii*, *C. bulbillifera*, *C. longifolia*, *C. rusbyana*, *Nitella hyalina*, *N. clavata*), sometimes with organic matter (e.g. *Chara contraria*, *C. vulgaris*, *C. braunii*, *Lamprothamnium haesseliae*) or with calcareous remains (e.g. *Chara globularis*, *C. leptosperma*, *Tolypella intricata* var. *apiculata*, *Nitella hyalina*). In sandy or sandy-slimy bottoms, *Chara halina* and *Lamprothamnium haesseliae* were found. In some cases the sediments can cover the plants, after a flood for example, but the plants were still healthy, such as *Nitella clavata* from Arroyo Los Cueros, Province of Buenos Aires.

Depth

Depth is closely related to other variables, such as light penetration and temperature. Littoral species are frequently exposed to the air by water level fluctuations, so, as in *Nitella hyalina*, they develop mucus on the upper whorls to protect them from desiccation, and for other functions, such as protection from grazing invertebrates (Proctor, 1989). There are several heliophilic taxa (*i.e. Chara halina*, *Lamprothamnium haesseliae* and *Nitella hyalina*). Other taxa are frequently found in waters up to 2 m deep, such as *Chara contraria*, *C. vulgaris*, *C. globularis*, but they can survive to 10

m. Species that prefer deeper waters include *Nitella opaca*, down to 40 m, *Chara bulbillifera*, from 2–14 m, *C. contraria* to 30 m, *C. globularis* to 10 m (see Fig. 2). This scheme is based on Argentinian taxa and Corillion (1957).

Salinity

Salinity is, to the best of my knowledge, the strongest ecological factor affecting the distribution of Argentinian Charophyta (Fig. 3).

In fresh-oligohaline water-bodies (0–5 g l^{-1}), principally located in the wet Pampa, *Chara contraria*, *C. vulgaris*, *C. globularis*, *C. braunii*, *C. leptosperma*, *Tolypella intricata* var. *apiculata*, *Nitella hyalina* and *Nitella clavata* were found. Cosmopolitan taxa tolerate changes in salinity, as was found for *C. contraria s.l.* in artificial channels from Pedro Luro, Province of Buenos Aires with 12 g l^{-1}. In fresh-oligohaline waters, located in arid areas, such as Lago Pellegrini, Province of Río Negro and Embalse E. R. Mexía, Province of Río Negro and Neuquén, *C. contraria*, *C. vulgaris*, *C. globularis*, *C. bulbillifera*, *C. longifolia*, *Nitella hyalina*, *N. clavata* and *N. opaca* were found.

A particular zone with a characteristic flora represents the ecotone with a semiarid climate, located to the North of the Río Colorado and follows the Río Desaguadero, between the Pampa and arid Patagonia. In this area, I studied water-bodies with mesohaline (5-18 g l^{-1} to polyhaline (18–40 g l^{-1}) to hyperhaline (more than 40 g l^{-1}) waters. Laguna La Salada, Province of Buenos Aires (11–23 g l^{-1} recorded in different years), Laguna La Amarga, Province of La Pampa (36 g l^{-1} recorded) and Arroyo Bebedero, Province of San Luis (without data but with very saline waters), are characterized by the presence of *Chara halina* and *Lamprothamnium haesseliae*, accompanied by Foraminifera and saline ostracods). On the other hand, but not found living yet, gyrogonites of *Lamp. succinctum* were found in Holocene sediments of Argentina, *i.e.* Laguna del Siasgo, Laguna Mar Chiquita and Laguna Salada Grande, all in the Province of Buenos Aires and Salinas del Bebedero, Province of San Luis. According to these observations the genus *Lamprothamnium* is typically found in saline habitats, as recorded for different localities in the world (Corillion, 1957; Burne *et al.*, 1981; Soulié-Märsche, 1982, 1991; García, 1993).

Chara hornemannii Wallmann is another inhabitant of saline environments. Not recorded living yet in Argentina, this taxon, with an apparently exclusive American distribution, was found in Quaternary sediments of Salinas del Bebedero, Province of San Luis and in a core from the Province of Mendoza. *C. baltica*, a species distributed in Europe, Africa and South America, lives in salinities of 7–30 g l^{-1} (Corillion, 1957) and was found in localities near the shore, *i.e.* some ponds near Bahía Blanca and Gorchs, Province of Buenos Aires (García, 1993) and inland saline waters from Bolivia (unpublished).

Ionic composition

The influence of ionic composition of the water on charophyte distribution is still poorly understood. Calciphile species include *Chara contraria*, *C. vulgaris*, *C. globularis*, *C. leptosperma*, *Nitella hyalina*, and *Tolypella intricata*. The majority of *Nitella* and species of *Chara* that do not form gyrogonites are calciphobes. The Argentinian localities have a predominance of sodium chloride waters, with varying concentrations of these ions.

It is easily recognized that cosmopolitan taxa (*i.e. Chara contraria*, *C. vulgaris*, *C. globularis*) are the most plastic species (Corillion, 1957; Soulié-Märsche, 1991) and this plasticity allows them to live in all continents. On the other hand, cosmopolitan species such as *Chara braunii* and *Nitella hyalina* indicate more restricted conditions. In taxa with restricted distributions and endemics, the requirements are variable. Some are stenotopic (e.g. *Chara halina*, *C. bulbillifera*) while others are relatively plastic, such as *Chara leptosperma*. In cosmopolitan species, the ecological plasticity is reflected in phenotypic changes, and generally different degrees of calcification could be detected in the gyrogonites.

How do charophytes modify the environment?

The charophytes represent, in several cases, the most important hydrophytes in subaquatic habitats. They develop a large biomass over a short time period, e.g. channels near Pedro Luro, Province of Buenos Aires, with predominance of *Chara contraria s.l.*. Consequently, they can play an important role in O_2 production and Ca consumption. The formation of the extracellular calcite deposits is a by-product of HCO_3^{-1} uptake during photosynthesis (Borowitzka, 1982; McConnaughey and Falk, 1991; McConnaughey, 1991). A calcareous cover may reduce grazing pressure (Borowitzka, 1982). Intracellular calcification processes occurring in spiral cells when the gyrogonite

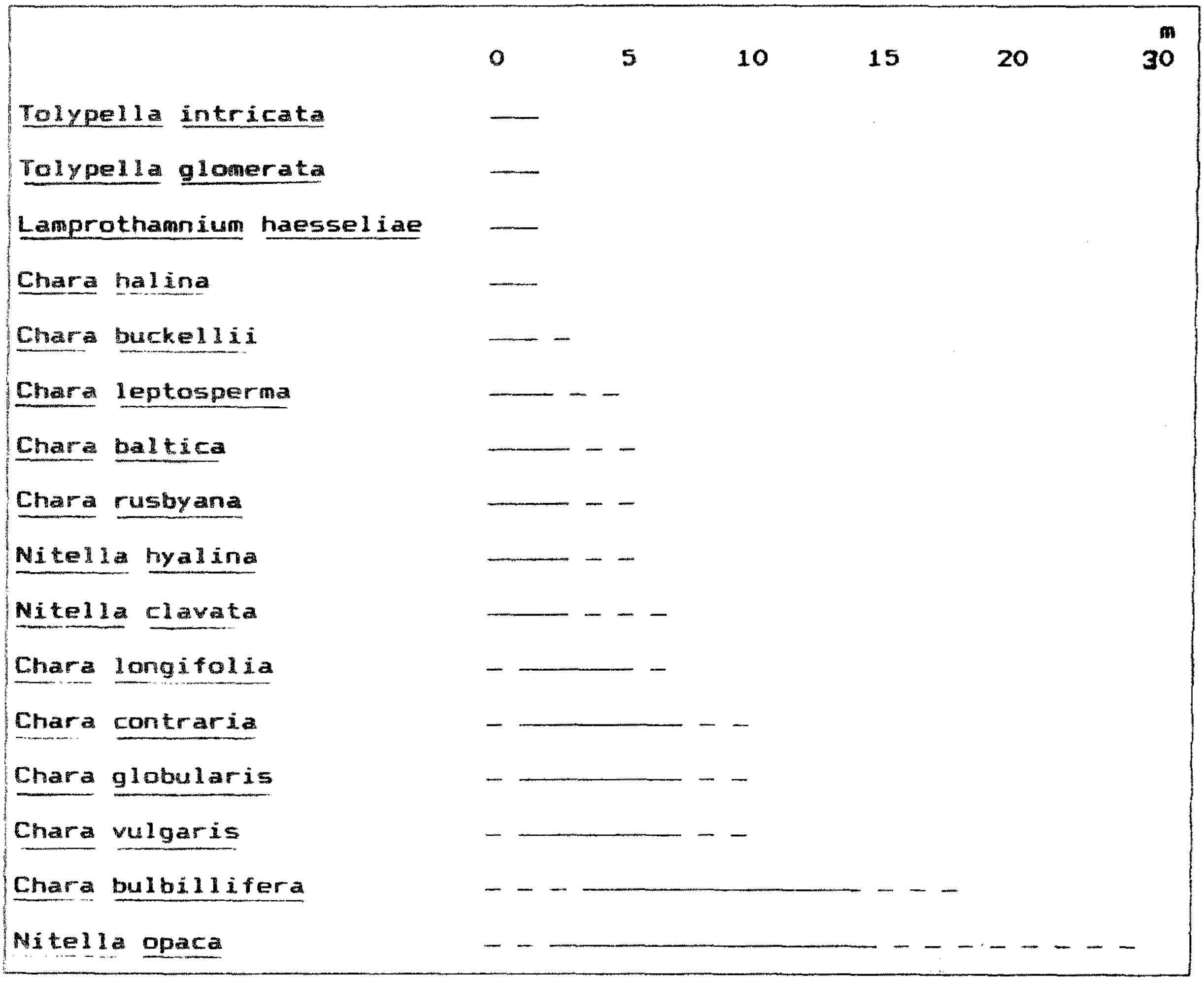

Fig. 2. Charophyta distribution in relation to depth.

is forming have not been studied yet.

Charophytes represent an important source of food for birds, fish and molluscs (Proctor, 1962; Guerlesquin & Podlejsky, 1980; Conkin & Conkin, 1989). They support large populations of epiphytes (e.g. diatoms) which are eaten by small organisms such as ostracods and snails, which are eaten in turn by birds and fish. Hence, they play an important role in the trophic chain.

By retaining sediments in their whorls, charophytes diminish the turbidity of the water, as has been observed by Zaneveld (1940). In Arroyo Los Cueros, Province of Buenos Aires, *Nitella clavata* appears totally covered by sediments, but it retains its photosyntetic ability and the plants are green and healthy.

The charophytes serve as protection for the zoobenthos. Grigelis (1973) in Guerlesquin & Podlejski (1980) observed the ratio 1:16 for zoobenthos population in habitats without or with charophytes. In the case of Foraminifera, most of which live in the sea but with a few genera found in inland saline waters, Cann & DeDeckker (1981) found specimens of *Elphidium* sp. living in wet sediments under a 'coat' of dried charophytes in waterbodies that dry out in summer. This may explain the presence of Foraminifera in Quaternary sediments from Salinas del Bebedero. Province of San Luis. They may have been transported through a set of ponds from the shore to inland sites (González *et al.*, 1981), and could be carried by birds together with the charophytes and eggs of ostracods.

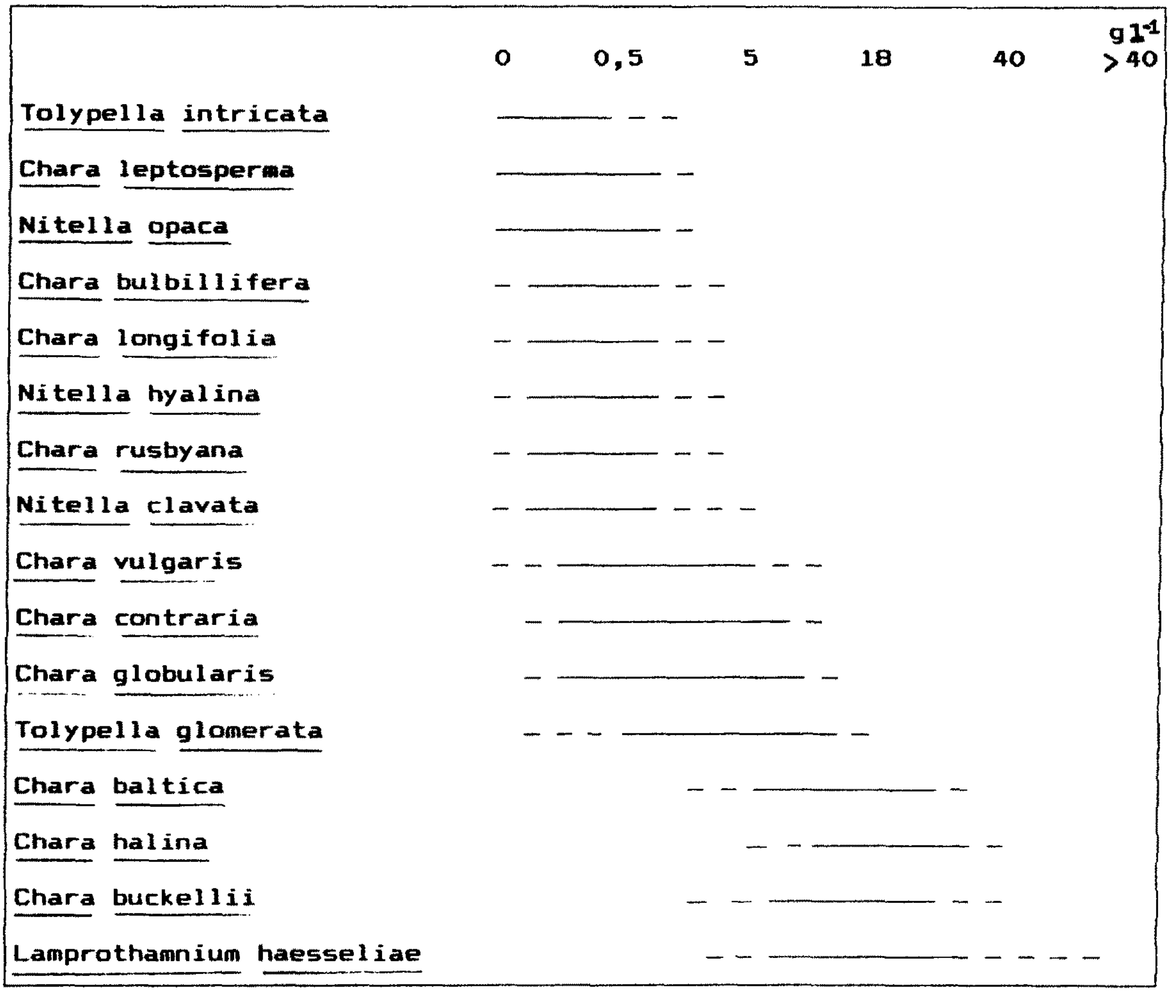

Fig. 3. Charophyta distribution related to salinity.

Which characteristics could be observed in gyrogonite populations that provide information about the environment?

Even without specific determinations, some characteristics of the gyrogonite population can provide information about the environment. The low number of specimens can indicate rheophile conditions and the degree of preservation can indicate the degree of energy. The selection of size could represent a thanathocoenosis, but it becomes difficult to distinguish this parameter in charophytes. It is safe to define a biocoenosis on the basis of a large number of gyrogonites deposited in calm waters and with intrapopulational variability.

The colour of the gyrogonites is important. Black ones could indicate reducing conditions (*i.e.* personal observations on *Lamprothamnium haesseliae* found in Quaternary sediments of Mar de Cobo, Province of Buenos Aires, associated to *Cyprideis* sp., *Cypridopsis* sp. and *Limnocythere* sp.). On the other hand, brown to reddish colour could indicate very oxidizing conditions. These different conditions can occur together in the same profile, indicating moments of shallow or deeper waters, and habitats with FeS and Fe present.

If the gyrogonites collected in one locality have a constant degree of calcification which differs of others collected in other localities, this could be related to different salinities, which in turn could be a response to changes in temperature. This was observed in *Chara contraria* and *C. papillosa* from Holocene sediments from Quebrada del Zonda, Provincia de San Juan, which were weakly calcified, probably related to fresh and cold water with low content of calcium carbonate and other salts.

Discussion

The utility of charophytes in paleolimnology is clear. Multidisciplinary studies are needed for paleolimnological reconstructions and charophytes represent one such indicator group.

Different steps should be considered with charophytes, when evaluating past environments. An adequate database constructed from 100 or more gyrogonites is an adequate reference for recognizing Neogene and Quaternary taxa. In Argentina, at the present time, all Quaternary taxa have extant representatives. With ecological data about extant populations, the paleoecological extrapolations can be made with a certain degree of confidence. On the other hand, experimental cultures under controlled conditions of temperature, pH, salinity, ionic composition, and exposure to light could help provide for each taxon the ecological optima and tolerances under which they live, and their morphological responses to ecological changes. Thus, environmental conditions could be inferred from fossil populations. Dubois (1968) in Soulié-Märsche (1991) found the typical halophilic species *Lamprothamnium papulosum* germinating in fresh water when the waterbody was filled by water after dessication, although the salinity increased subsequently and the species grows normally in mesohaline to hyperhaline waters. In Argentina, *Lamp. haesseliae* was found in saline ponds affected by desiccation (García, unpublished data).

Conclusions

This paper contains only a brief account of some of the possible applications of charophytes to paleolimnology. They still represent a relatively unexplored group of paleoindicators. Once more detailed information is available for the different species, they will be even more biomarkers. Charophytes may be ideal indicators of salinity, depth, temperature, energy, substrate and ionic composition. At the same time, urgent ecological data for species level changes are required. Data about their role in aquatic ecosystems are important in understanding paleolimnological conditions. There are many interesting possibilities; for example, the degree of calcification with respect to the chemistry of the water or the relation between water chemistry and the gyrogonite, on the basis of isotopic and trace elements, such as was done with ostracods (Chivas *et al.*, 1985, 1986). The finding of elements that help in the reconstruction and interpretation of lake histories can, in turn, help in the understanding and reconstruction of inland paleoclimatic processes.

The origin of the charophytes in the Upper Silurian, their abundance in non-marine sediments, and the existence of taxa with short life-spans, make them useful paleoindicators for the study of chronology, stratigraphy and paleoenvironmental reconstructions.

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