ECOLOGY AND PALEOECOLOGY

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The habitats of the Characeae are mainly freshwater, but some species successfully colonize brackish lagoons, and a few species inhabit the Baltic Sea. The species of the family Characeae are fundamentally aquatic: apart from the oospores and gyrogonites, which can survive desiccation, the only forms that survive as a whole organism when aerially exposed are those that develop on damp ground in special conditions. The thallus of *Nitella hyalina* (DE CANDOLLE) AGARDH is enclosed in a mucilage that maintains sufficient moisture, and *"N. terrestris"* (a *Nitella* species whose taxonomic status is still unclear) grows in the very high atmospheric humidity of the equatorial part of India (IYENGAR, 1958).

Characeae are pioneer species, colonizing environments lacking vegetation, whether new or reworked, before the development of higher plant communities. Subjected to competition from the phanerogams, most of them regress to refuges on open beaches or even disappear from a locality. The positively phototactic fertile tips of branches grow toward the water surface where the orange to red color of the mature gametangia is visually striking and may provide some protection from ultraviolet light.

Regarded as annual, the Characeae possess a vegetative thallus that may, under special conditions, persist during unfavorable seasons. Each individual produces a large number of oogonia and antheridia (often more than a hundred). After fertilization in water, the oospores mature, then break off and fall to the bottom, where they germinate after a period of dormancy. The germinating oospores give rise to a rather dense population, forming a carpet of benthic vegetation. Similarly, the gyrogonites of fossil species, which correspond to the calcified parts of the oogonia, are found in abundance in sediments, allowing statistical estimates of ancient populations.

The Characeae, which are fixed by very thin rhizoids, colonize preferentially quiet waters. In slow currents (5 to 6 m per minute), thalli develop into spindles, which are characterized by the elongation of the internodes and phylloids. Habitats where Characeae grow may be permanent or temporary but must be moist for at least a few months: lakes, salt ponds, rice fields, pisciculture ponds, lagoons, chotts, and water bodies of all sizes. The habitats must not be subject to drainage during the growing period of the protonemata or just before fertilization. The germination potential of some Characeae persists for several years [e.g., *Chara braunii* GMELIN, *Nitella syncarpa* (THUILLER) CHEVALLIER, and *Lamprothamnium succinctum* (A. BRAUN) R. D. WOOD], but dried soil with characean spores must not be subject to extensive mixing, which may bury the oospores too deeply for germination.

WATER QUALITY

Well-mixed waters with high levels of oxygen and carbon dioxide provide the best conditions for respiration and assimilation and thus increase development of the thallus. Moreover, the complex structure of the thallus favors the sedimentation of suspended particles, resulting in clarification of the water. Due to their large biomass, Characeae also contribute to the maintenance of water quality. Most species develop in low-nutrient waters that are oligotrophic, mesotrophic, or slightly eutrophic (IMAHORI, 1954).

SUBSTRATUM

Characeae prefer less dense soils (sand, silt, or mud) that rhizoids can penetrate

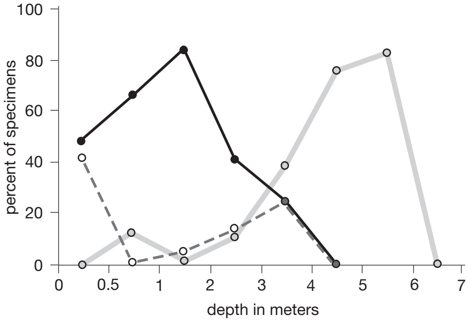

Fig. 20. Vertical range of *Chara globularis* var. *aspera* (Detharding *ex* Willdenow) R. D. Wood (*solid line*), *Chara vulgaris* f. *contraria* (A. Braun *ex* Kützing) R. D. Wood (*dashed line*), and *Nitellopsis obtusa* (Desvaux in Loiseleur-Deslongchamps) J. Groves (*gray line*) in Nors Sø Lake, Denmark (adapted from Olsen, 1944, fig. 36).

more easily. They also root in interstices between stones or gravel or at the bottom of artificial basins covered with a thin film of silt. They do not grow on rocks.

DEPTH

Most Characeae grow in shallow water, between 0.1 and 10 m deep (Fig. 20), but some species are able to survive at greater depth, such as *Nitellopsis obtusa* (Desvaux in Loiseleur-Deslongchamps) J. Groves, which ranges from 1 to 30 m (Stroede, 1933). Deep-dwelling species often grow and form fructifications down to 10 meters depth late in the season. In deep zones, also carpeted by a few species of *Nitella,* individuals remain sterile and persist by vegetative multiplication, as occurs, for example, with *N. flexilis* (L.) Agardh in Pavin Lake in France (Hy, 1913).

LIGHT

Quality and quantity of light affect vegetative growth, especially internode length and phylloid development, and sexual reproduction (development of the gametangia). Light also affects the distribution of species according to depth, resulting in vertical and horizontal zonation of vegetation belts. Finally, in terms of fructification development, species may be classified into short-day (vernal), long-day (estival), or indifferent species. Light largely controls photosynthesis and influences calcification, according to the reaction:

$$Ca^{++} + 2HCO_3^- \rightleftharpoons CaCO_3 + CO_2 + H_2O$$

(Imahori, 1954). The fact that light intensity is a function of latitude explains why most calcified species occur in temperate and subtropical climatic zones.

TEMPERATURE

Some species of Characeae are restricted in climatic zones and are evidently influenced by temperature. Temperature affects significantly both germination and development. Generally in temperate areas, Characeae occur in waters of about 12 °C to 26 °C, but in tropical areas they may survive in waters as warm as 30 °C. Three species grow and fructify in the cold waters (not more than 16 °C) of Grande Terre, the largest of the Kerguelen Islands (Corillion, 1982). Thalli cannot withstand sudden temperature variations, although the species living on the fringes of lakes or ponds are exposed to nychthemeral variations, often over 10 °C in summer, or seasonal variations. Increased water temperature that results in evaporation yields an increased concentration of soluble substances, as well as a decrease in concentration of dissolved gases. As calcification is related to temperature, calcified species prefer biotopes in temperate zones. In contrast, uncalcified species, such as those from the Kerguelen Islands, can tolerate very cold water.

SALINITY

Salinity is thought to be the major factor governing distribution of charophytes (Stroede, 1933). Characeae are mainly lacustrine, but some species tolerate continental brackish waters. In the Baltic Sea, Characeae occur in areas where the percentage of NaCl is not higher than 30 g Cl liter^{-1} (Fig. 21), approximately 30 psu (practical salinity units; UNESCO, 1981).

FIG. 21. Distribution of 6 Characeae species in littoral zones of Scandinavia, in function of salinity; *broken lines,* annual isohaline; *solid lines,* August isohalines; *numbers* refer to salinity in ‰ (adapted from Olsen, 1944; with data from Langangen, 1974, and Blindow & Langangen, 1995).

According to their salinity tolerance, the Characeae fall into four categories (WINTER, SOULIÉ-MÄRSCHE, & KIRST, 1996.

(1) Strict halophobes or obligatory freshwater species. Salinity 0 to 0.5 psu. This group includes most *Nitella* and a few *Chara.*

(2) Freshwater to brackish-water tolerant species. Salinity 0.5 to 5 psu. Most Characeae occur in these waters: numerous *Chara,* rare *Nitella, Tolypella glomerata* (DESVAUX in LOISELEUR-DESLONGCHAMPS) R. D. WOOD, *Nitellopsis obtusa* (DESVAUX in LOISELEUR-DESLONGCHAMPS) J. GROVES, and *Lychnothamnus barbatus* (MEYEN) LEONHARDI.

(3) Brackish-water species. Salinity 5 to 16 psu. Some *Chara, Lamprothamnium papulosum* (WALLROTH) J. GROVES, *Tolypella nidifica* (MÜLLER) A. BRAUN, and oligobrackish species that withstand brackish waters [*Nitella hyalina* (DE CANDOLLE) AGARDH].

(4) Strict halophilic species. Salinity 16 to 26 psu. *L. papulosum, L. papulosum* f.

macropogon (A. Braun) R. D. Wood, *Chara globularis* var. *aspera* f. *galioides* (De Candolle) R. D. Wood; tolerance of 69 psu has been reported for *Lamprothamnium,* which is the most halophilic extant genus; however, even if the charophyte can remain apparently healthy, photosynthesis and sexual reproduction are inhibited at such salinities (Burne, Bauld, & DeDecker, 1980).

The salinity tolerance of the Characeae has been related to a physiological mechanism that regulates turgor pressure (Winter & Kirst, 1991); there is evidence of a pumping mechanism involving diverse salts, including sodium and potassium chloride (Hutchinson, 1975; Winter, Soulié-Märsche, & Kirst, 1996).

ALKALINITY

Charophytes thrive in pH generally from 5.5 to more than 9. Acid waters with pH as low as 3 containing thriving populations of *Chara fibrosa* (de Candolle) Agardh and *Nitella hyalina,* however, have been reported from rehabilitated mining excavations in Western Australia (Melanie Ward, personal communication, 1996). According to their preferences, Characeae may be categorized into three groups.

Acidophilic: mainly *Nitella* and rare *Chara* species, in waters from pH 5 to 7.

Neutrophilic: mainly *Chara, Nitellopsis,* rare *Nitella.*

Alkaline: *Chara, Tolypella, Lamprothamnium.*

Some species tolerate wide ranges of pH, for example, from 5 to 9.5 for *Nitella translucens* (persoon) Agardh in Denmark (Olsen, 1944).

CONTENT OF LIME IN WATER

The encrustation of the cell walls by calcium carbonate is related to the calcium concentration of the water. For example, *Chara* starts to develop between 15 to 60 mg/l CaO depending on the species and tolerates 200 mg/l CaO to 400 mg/l CaO. Beyond 2,000 mg/l CaO it stops developing. Quantitative analysis and use of X-rays show that the ions are found mainly as insoluble combinations, thus limiting their toxic effect (Walter-Lévy & Strauss, 1974). For uncalcified taxa, the optimal values of hardness are between 0 and 200 mg/l CaO.

MODES OF LIFE OF FOSSIL GENERA

Evidence from the fossil record shows that, like the modern species, fossil charophytes inhabited continental fresh- and brackish waters as well as possibly shallow, low-salinity, sheltered marine habitats. The earliest charophytes known from the upper Silurian and Lower Devonian of Laurentia already occupied different habitats. The Ludlowian Hamra Beds of Gotland, which have yielded *Moellerina laufeldi* Conkin, were deposited in shallow water at the end of the regressive Lau cycle (Jeppsson, 1998), whereas the slightly younger *Praesycidium,* which is associated with land plants in the Ludlowian of Podolia (T. A. Ishchenko & A. A. Ishchenko, 1982), seems to have occupied a freshwater habitat.

FOSSIL GENERA WITH EXTANT REPRESENTATIVES

On the whole, extant genera have modes of life similar to those of their fossil representatives. Fossil *Lamprothamnium,* which are generally found in Upper Cretaceous–Holocene brackish-water deposits, share the same ecological preferences as modern, congeneric species.

Among the Nitelloideae, *Tolypella* and *Sphaerochara* seem to have tolerated a wide range of salinities, like their living descendants. *Tolypella* occurs frequently in brackish-water deposits, such as the Maastrichtian Prince Creek Formation at Ocean Point, Alaska, which has yielded *T. grambasti arctica* (Feist & Brouwers, 1990). The Paleocene *Sphaerochara edda* Soulié-Märsche occurs in brackish and lacustrine facies (Riveline, 1986). The occurrence of *T. caudata* in the freshwater upper Eocene Limnäenmergel of the Rhine graben (BREUER & FEIST, 1986) is an exception.

Chara has been reported from a number of different biotopes. The ecological preferences of *Lychnothamnus* seem comparable for extant and fossil forms, as shown by the lacustrine upper Miocene locality at Asseiceira (Portugal) with *L. barbatus* var. *antiquus* (ANTUNES & others, 1992). Very little is known of the uncalcified *Nitella* as fossils; the exceptional Indian Jurassic locality with *N. sahnii* is thought to be a lake deposit (HORN AF RANTZIEN, 1957).

In the fossil record *Nitellopsis* differs from other genera by its clearly more diverse modes of life than the unique extant species *N. obtusa,* which is restricted to permanent, relatively deep, cold lakes (SOULIÉ-MÄRSCHE, 1991). Most fossil species of *Nitellopsis* occur in lacustrine deposits, such as the upper Oligocene Argile des Milles, with *N.* (*Tectochara*) *meriani* L. & N. GRAMAST accompanied by the freshwater gastropods *Limnaea* and *Planorbis* (FEIST-CASTEL, 1977c). The genus also occurs in brackish-water deposits: for example, *N. (Tectochara) thaleri elongata* FEIST-CASTEL, in the lower Eocene Oyster beds of Corbières and Minervois (southern France), is associated with *Lamprothamnium priscum* CASTEL & GRAMBAST as well as with a brackish-water fauna of foraminifers and ostracodes (TAMBAREAU & others, 1989). In the extant *N. obtusa,* the ability to withstand a low concentration of salt in laboratory experiments (KATSUHARA & TAZAWA, 1986) may be related to the former tolerance of the genus to a higher salinity.

TOTALLY EXTINCT GENERA

Because comparison with living species is not possible, ecological data for extinct genera are based mainly on evidence provided by associated faunas, generally foraminifers, molluscs, ostracodes, echinoderms, and conodonts. SCHUDACK (1993a) evaluated the salinity tolerances of 13 charophyte genera on the basis of more than 500 associations from the Upper Jurassic and Lower Cretaceous of Europe (Fig. 22). We refer readers to this paper for examples from times apart from the Paleozoic Era, which has been the subject of controversy regarding the ecology of the charophytes.

PALEOECOLOGY OF PALEOZOIC CHAROPHYTES: WERE THEY MARINE?

The paleoecology of Paleozoic charophytes is far from being completely understood. The salinity preferences of only a few genera have been recognized: *Karpinskya* seems to be euryhaline, *Sycidium* and *Trochiliscus* are freshwater species but occasionally tolerant of brackish water (RACKI, 1982; LANGER, 1976), and *Gemmichara* and *Leonardosia* are strictly freshwater genera (LU & ZHANG, 1990).

The possibility of early charophytes occupying marine habitats has been discussed for a long time, as some of their localities include other kinds of fossils that are thought to have been marine. Major contributions on the subject have been analyzed by RACKI (1982). The main point of the debate bears on the possibility that early charophytes could have been adapted to a wider range of habitats than modern species.

Two hypotheses have been formulated. In the first the association of the two types of organisms is artificial: when gyrogonites are not well preserved and in low abundance, they may have been washed from fresh- or brackish-water swamps into a marine environment by passage through estuaries (HECKEL, 1972); transportation of gyrogonites as far as 80 km from the coast has been noted in the English Channel (MAGNIEZ, RAT, & TINTANT, 1960).

The second hypothesis erected to explain the apparently abnormal assemblages of charophytes and marine organisms requires acceptance that in the past charophytes could have had lifestyles different from those of living ones and might have tolerated

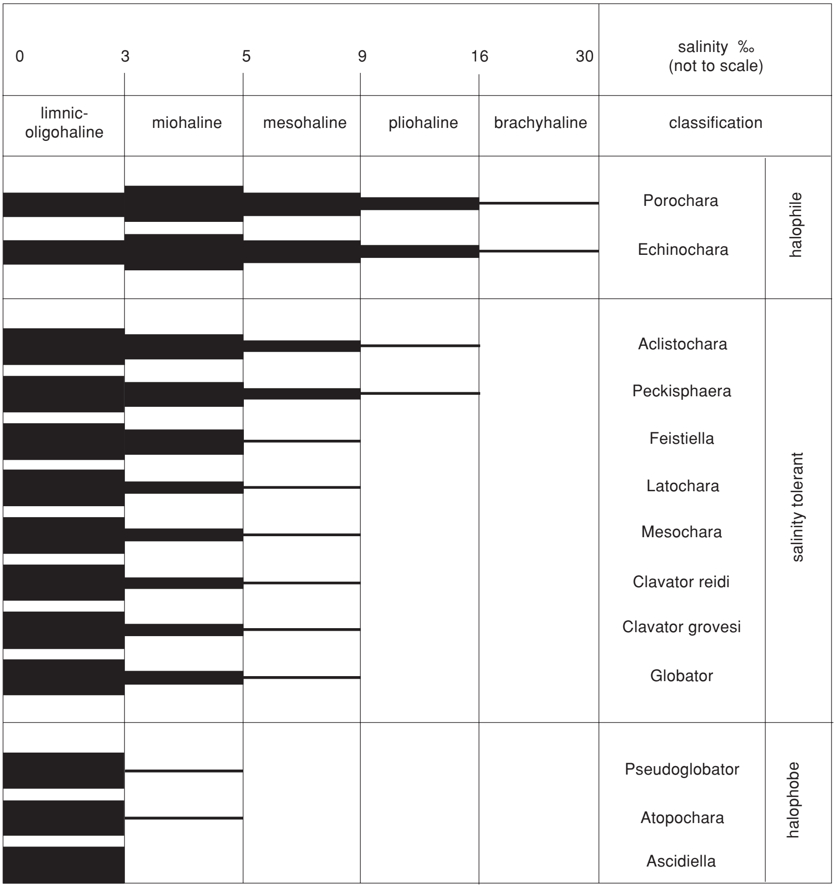

Fig. 22. Integrated interpretation of salinity tolerances of most important Late Jurassic–Early Cretaceous charophyte taxa (adapted from Schudack, 1993a, fig. 10).

open-marine conditions. Nothing in the fossil record except co-occurring marine species, however, suggests the existence of fundamental differences in the constitution of the extant and fossil forms. The thin rhizoids of the Devonian *Palaeonitella* (Kidston & Lang, 1921; Edwards & Lyon, 1983) testify that, as in the modern forms, their ancestors were not floating algae but were fixed to the bottom. More recent work with *Palaeonitella* and the Rhynie Chert (Taylor, Remy, & Hass, 1992) indicates that deposition was in a freshwater oligotrophic peat swamp. We have noted earlier that depths between 0 and 10 m were optimal for light penetration, inducing both photosynthesis and reproduction. Croft (1952) judged that the structure of the gyrogonite, being particularly resistant and able to withstand periods of desiccation, is indicative of adaptation to life in nonmarine environments.

This view is not in contradiction with the presence of several species of Characeae living in the Baltic Sea, which supports the idea that some Paleozoic species might have inhabited marine habitats. Moreover, Paleozoic seas are thought to have had a lower concentration of chlorides, as the Baltic Sea does now (Racki, 1982). The Baltic Characeae live along the coast (Fig. 21) in shallow water where wave action is not strong (Olsen, 1944). This mode of life compares well with some Devonian nearshore marine habitats and possibly also with some Paleozoic epeiric seas, such as the Devonian shallow, offshore deposits of the Holy Cross Mountains (Poland), which have yielded abundant populations of *Karpinskya* (Racki, 1982).

Thus the biology of charophytes does not support the idea of an adaptation of their Paleozoic ancestors to fully marine environments implying tides and high waves, and the presence of abundant gyrogonites in marine sedimentary rocks is evidence of shallow water near the land.

BIOGEOGRAPHY

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INTRODUCTION

The extant charophytes are broadly distributed with respect both to latitude (from 80° N to 50° S) and to altitude (from 0 to more than 4,000 m in the Andes) in habitats where aquatic conditions are permanent or persist for at least a few months. Being aquatic, charophytes often have a rather wide distribution in relation to the relative uniformity of the aquatic environment. Probably their great power of propagation, due to their oospores being protected by resistant walls and characterized by a long viability, also plays a role in their broad distribution, which is effectively cosmopolitan.

CORILLION (1957), WOOD and IMAHORI (1959, 1965 in 1964–1965), and KHAN and SARMA (1984) gave an overview of the distribution of the species in the world. All the continents have been explored, but many areas have been insufficiently sampled, particularly central Africa, South America, central Asia, and many islands; consequently, the reported ranges are certainly smaller than in reality, and the number of endemic taxa has probably been overestimated.

CORILLION (1957) has reviewed the modes of dispersion of the Characeae. The oospores, bulbils, and nodes of the thallus are transported mainly by water currents or by animals. Species that grow along the banks of rivers and their estuaries are disseminated during floods. Animals can transport the organs of reproduction to considerable distances. The oogonia, protected by their resistant wall, can pass through the digestive canals of water birds without damage, or, together with vegetative fragments, can be present in mud adhering to their feet and wings, thus being distributed along migration routes (PROCTOR, 1962). KRASSAVINA (1971) has reported oogonia of *Nitellopsis obtusa* (DESVAUX in LOISELEUR-DESLONGCHAMPS) J. GROVES in the stomach of a duck. Oogonia and vegetative parts are also transported by frogs and toads and by large and small mammals. RIDLEY (1930) observed the occurrence of *Nitella furcata* subsp. *mucronata* var. *sieberi* f. *microcarpa* (A. BRAUN) R. D. WOOD in the footprints of a rhinoceros.

Human intervention also has its effects as a result of artificial habitats favorable to such species as *Lamprothamnium papulosum* (WALLROTH) J. GROVES, which has established itself on European coasts as a result of the formation of salt marshes in past centuries. Human activity can result also in the destruction of natural habitats through draining and management of especially sensitive aquatic environments (GUERLESQUIN, 1986), leading to the increasing rarity and finally the disappearance of species in some areas. To prevent this, species that are especially at risk have been accorded protected status, for example *L. papulosum* in Great Britain (MOORE, 1991) and *Lychnothamnus barbatus* (MEYEN) LEONARDI in Australia (CASANOVA, 1997). Other species are reported as rare or endangered in Sweden (BLINDOW, 1994) and in Germany (KRAUSE, 1984). Elsewhere, programs for the amelioration of water quality have recently allowed the return of species to some localities from which they had disappeared several years previously (SIMONS & others, 1994).

AREAS OF DISTRIBUTION

The concepts of areas of distribution and endemism can be interpreted in different ways. Thus endemism may perhaps be defined as the presence of a taxon either in a single very restricted area or, following KHAN and SARMA (1984), over all of a continent. Between these two extremes are other possibilities of grouping charophyte species in isolated geographic entities, such as the Indian subcontinent, Japan, and southern Africa.

Table 1. Number of microspecies known in the different genera by continent (*sensu* Wood & Imahori, 1965 in 1964–1965).

Continent	Chara	Nitella	Tolypella & Sphaerochara	Lamprothamnium	Nitellopsis	Lychnothamnus
Africa	53	48	4	3	0	0
North America	59	31	5	0	0	0
South America	50	38	4	2	1	0
Asia	77	105	6	3	1	1
Australia s.l.	21	39	3	3	0	1
Europe	46	21	9	2	1	1

The number of taxa known in each continent varies according to the size. Asia, by far the largest, has the greatest number, while Europe, being much smaller, has the fewest. The number of species in the genera varies among continents (Table 1). The proportion of endemics, highly variable, is least in Europe and highest in southern Africa and Japan (Table 2).

COSMOPOLITAN SPECIES

We have seen that the characteristics of charophytes allow their dispersion over great distances. The percentage of cosmopolitan species, i.e., occupying four or five continents, is nine percent among living species. These are generally species with great tolerance to variations in physicochemical factors as well as having long-lived oospores. This group comprises especially those species that populate regions that are isolated geographically such as Greenland, Iceland, Newfoundland, and some Pacific islands (Hawaii, Fiji, New Caledonia).

SUBCOSMOPOLITAN SPECIES

Containing 41 percent of species, this group of species, which are present on two or three continents, occupies an important place in the characean flora. These species are environmentally less tolerant or sometimes ancient species, the area of distribution of which has been reduced and broken up.

ENDEMIC SPECIES sensu lato

This group comprises 50 percent of the total number of species. These have ecological preferences that limit them to a single continent, to a broad area, or to a limited region with a highly variable landscape.

CLIMATICALLY CONTROLLED SPECIES

For some species, climate is the essential factor, as for *Chara zeylanica,* the tropical species par excellence (Zaneveld, 1940), which occurs between 40° N and 30° S (Fig. 23). It is worth noting that in the complex *C. zeylanica,* the variety *diaphana* f. *diaphana* (Meyen) R. D. Wood has the broadest distribution; two other subspecies each occupy a more or less restricted climatic area. In other instances local ecological conditions allow species to flourish in climatic zones to which they are not adapted otherwise. In some, it is altitude, giving a cooler and more humid climate, that allows species from temperate zones to live in subtropical regions. Conversely, southern species may benefit from local shelter from the cold (Proctor, 1962). Thus *Chara canescens* Desvaux & Loiseleur-Deslongchamps is able to live in Spitzbergen (79° N) in hot springs (Langangen, 1979).

DISTRIBUTIONS OF GENERA AND SPECIES

The distribution of the seven extant genera is unequal on the various continents and independent of their surface features. Africa and North America have four genera; South

Table 2. Percentages of endemic and worldwide species in the continents (new).

Continent	% endemics	% worldwide
Africa	20	6
North America	15	4
South America	24	4
Asia	23	13
Australia	13	2
Europe	7	2

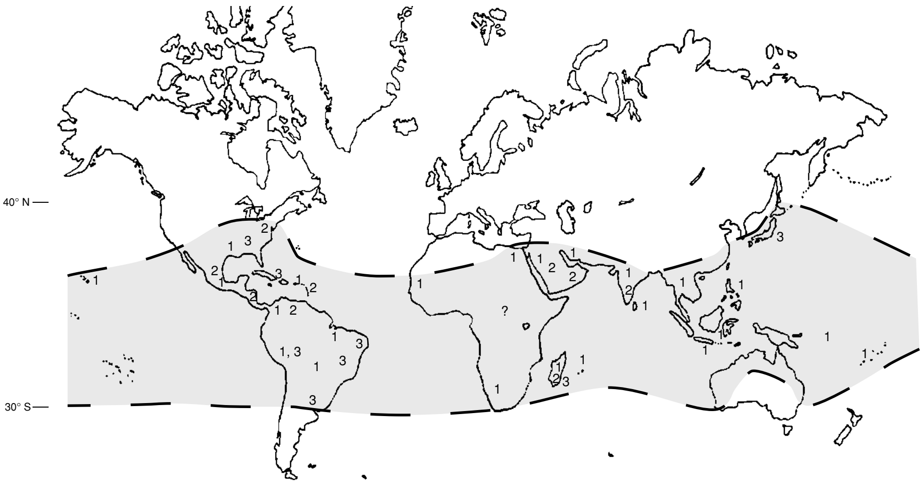

FIG. 23. Repartition area of 3 microspecies (*sensu* WOOD & IMAHORI, 1965 in 1964–1965) of *Chara zeylanica; 1, Chara zeylanica* var. *diaphana* forma *diaphana* (MEYEN) R. D. WOOD; *2, Chara zeylanica* var. *diaphana* forma *oerstediana* (BRAUN) R. D. WOOD; *3, Chara zeylanica* var. *sejuncta* (BRAUN) R. D. WOOD (new).

America and Australasia have five. All seven genera are present in Europe and Asia (Table 1). *Chara* and *Nitella* have a global distribution, and these genera are also the richest in species. *Tolypella* is represented in different parts of the world but with gaps in its distribution. *Lamprothamnium,* confined to saline continental environments or exceptional instances in marine environments (e.g., the Baltic Sea), is unknown in North America and barely represented in Australia; it is absent from most of Africa. The reduction of areas of distribution in geologic time, most evident in *Nitellopsis* and *Lychnothamnus,* indicates genera on the decline.

Even in the widespread genera *Chara* and *Nitella,* several species have quite disjunct distributions. These are usually interpreted as corresponding to relict areas. Thus *Chara baueri* A. BRAUN occurs exclusively in Europe, Kazakhstan, and Australasia in regions that are always subject to similarly temperate climatic conditions. In other instances, for example such species as *Nitella tenuissima* f. *transilis* (T. F. ALLEN) R. D. WOOD, present in rare and sparse localities in India (Bihar) and the northeastern part of North America including Cuba, our present knowledge does not allow us to propose a satisfactory explanation.

To assess the affinities of regions to each other on the basis of their charophyte floras, we should examine geographically circumscribed regions (Table 3) with significantly large areas and with great floral richness. India, which harbors 40 percent of the total characean flora, seems to be a good example in this respect. Affinities are closest with other tropical regions, specifically neighboring regions of Asia and South America. Few species occur both in India and Africa, despite the geographic proximity of the two regions in former times. *Chara setosa* f. *pseudobrachypus* (J. GROVES & STEPHENS) R. D. WOOD, reported from both India (Maharastra) and southern Africa, is an example.

TABLE 3. Percentages of endemic and worldwide species in isolated regions (new).

Region	% endemics	% worldwide
India	14	6
Japan	30	6
New Zealand	11	1
Peri-Antarctic zone (Tierra del Fuego, Kerguelen Islands)	25	0.3
South Africa	31	5.5
Tasmania	20	2

STRATIGRAPHIC DISTRIBUTION AND PALEOBIOGEOGRAPHY

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Charophytes are essentially continental, living in freshwater or brackish water with land nearby. The changes induced by movement of the continents during the past 420 million years have certainly influenced the distribution of species and is thus accountable for some stages of their evolution, including periods of diversification or extinction.

The ecological factors that control the distribution of recent forms are mainly water clarity, temperature, pH, and percentage of dissolved salts; among these, the presence of calcium carbonate is the most important because it is essential for the calcified forms, which form most of the fossil record. At present, charophytes occur at nearly every altitude and at every latitude, polar regions excepted. Species and genera are widely distributed geographically. The greatest barriers to their dispersal are the deep oceans, deserts, and glaciers.

The information supplied by living forms is indispensable for the interpretation of the distribution of fossil forms; however, this information cannot be applied directly, as the factors that affect species distributions may have differed through geological time. Concerning charophyte dispersal, for example, birds did not exist during the Paleozoic and early Mesozoic. On the other hand, until the Late Cretaceous, charophytes were not competing with angiosperms in aquatic environments. The water chemistry may also have differed; as indicated in the Ecology chapter (herein, p. 34), a lower salinity of seawater might have allowed some Paleozoic forms to live in marine environments in coastal areas (RACKI, 1982). Moreover, the distribution of the continents, which was different in the past, induced the establishment of climatic conditions often more homogenous than at present, thus favoring cosmopolitan distribution. The distribution of the continents, winds, and marine currents, which are important factors for the transportation of propagules, may have varied in direction and intensity in the geological past. Variations in sea level have certainly played a leading role in the distribution of fossils. The periods of transgression, such as the Early Jurassic and Coniacian, were unfavorable; conversely, times of emergence such as the late Silurian and Early Cretaceous must have allowed these pioneering species to establish themselves in newly emerged continental areas. Cosmic events have been proposed to explain times of mass extinction, such as at the Cretaceous-Tertiary boundary (ALVAREZ & others, 1980), but these are not treated herein. We do not comment about the hypothetical causes of extinction (cosmic events, volcanism, and so on). Phases of charophyte extinction and recovery are treated in Evolution of Charophyte Biodiversity in the chapter on Evolutionary History (herein, p. 74).

PALEOZOIC

SILURIAN

Charophytes are known with certainty in the upper Silurian. *Moellerina laufeldi,* the most ancient, comes from the Ludlowian Stage of Gotland (Sweden; CONKIN & CONKIN, 1992), and *Sycidium* (*Praesycidium*) is from the Ludlow Slasky Formation of Ukraine (ISHCHENKO & ISHCHENKO, 1982). *Primochara* is of Pridolian age (ISHCHENKO & SAIDAKOVSKY, 1975). In the paleogeographical reconstructions of SCOTESE (1997) all the charophytes from the upper Silurian come from the same paleogeographic province, Baltica. The presumed order Sycidiales from the lower Silurian (Llandovery-Wenlock boundary) of Quebec (MAMET & others, 1992), comes from Avalonia, located southwest of Baltica. If the affinity of this taxon to the charophytes were confirmed, the nearshore marine character of the Anticosti and Gotland deposits would indicate a migration toward Baltica by marine currents through the Rheic Ocean.

DEVONIAN

The charophytes diversified during the Devonian. The three orders of the group, Sycidiales, Moellerinales, and Charales, were represented as early as the Middle Devonian with seven widely distributed genera (Fig. 24). This phase of expansion went on until the Late Devonian.

In the Early Devonian, possibly from dispersal centers in the Silurian of Sweden (Conkin & Conkin, 1992) and Ukraine (Ishchenko & Ishchenko, 1982), the genera *Moellerina* and *Sycidium* extended onto the Euramerican continent (present USA, Canada, and Spitsbergen). The presence of *Moellerina* in the Early Devonian might be explained by migration in epeiric seas at the northern boundary of Gondwana. Similarly, the genera *Sycidium* and *Pinnoputamen* might have reached South China and, in the case of *Sycidium,* as far as Australia during the Late Devonian. Only a few deposits with charophytes are known from the Early Devonian, although their disjointed but wide distribution implies a much larger original area of distribution.

In the Middle Devonian the genera *Sycidium* and *Moellerina* are the best-documented examples of the number of species and localities. *Sycidium* is present in the Middle Devonian of South China, central and northern Europe, Iran, and Australia. It is missing from North America where it is noted only in the Lower Mississippian. The genus *Moellerina,* which occurs less frequently, had a much wider distribution: during the Middle Devonian it was present in South China, central Europe, east-central North America, and Australia.

According to the plate-tectonic reconstruction proposed by Scotese (1997) for the Devonian at 390 Ma, the two genera occupied Baltica and the northern margin of Gondwana and extended onto Laurentia. These areas lay in the subtropical zone, suggesting a sufficiently warm climate to allow the calcification of the gyrogonites. Conversely, the deposits with Eocharaceae from the Upper Devonian of South Africa, at that time quite near the pole, have produced only impressions of thalli and fructifications (Gess & Hiller, 1995). This exceptional type of fossilization shows that the Eocharaceae included noncalcified species. This might explain the apparent highly disjunct areal distribution of the Eocharaceae as well as the long time gap that separated the different genera of this family. First described from the Middle Devonian of Canada (Choquette, 1956), the family has been reported since from the Upper Devonian of South Africa (Gess & Hiller, 1995), and its last occurrence was 100 million years later in the Triassic of central Europe (Kisielevsky, 1996).

EARLY CARBONIFEROUS

The early Carboniferous was a time of clear reduction of the number and occurrences of taxa. The area of distribution was reduced to North America (*Sycidium, Karpinskya;* Peck & Morales, 1966) and South China (*Xinjiangochara, Gemmichara;* Yang & Zhou, 1990; Lu & Zhang, 1990). Only *Moellerina* was common to the two areas (Conkin & others, 1974; Lu & Luo, 1990). In Europe, lacustrine sedimentary rock is rare and limited to the cratonic northern areas where the detrital formations contain rare carbonates but are often rich in organic matter; no charophytes are known from the lower Carboniferous rocks.

LATE CARBONIFEROUS

After the extinction of Trochiliscales and Sycidiales, a new order and two families originated, the Palaeocharaceae and Porocharaceae. Within this last family, a new morphological type appeared: gyrogonites with five sinistral spiral cells (Charinae), which persists to the present time.

Palaeochara is known from only two localities, one in Canada (Bell, 1922; Peck & Eyer, 1963a), the other in northern China

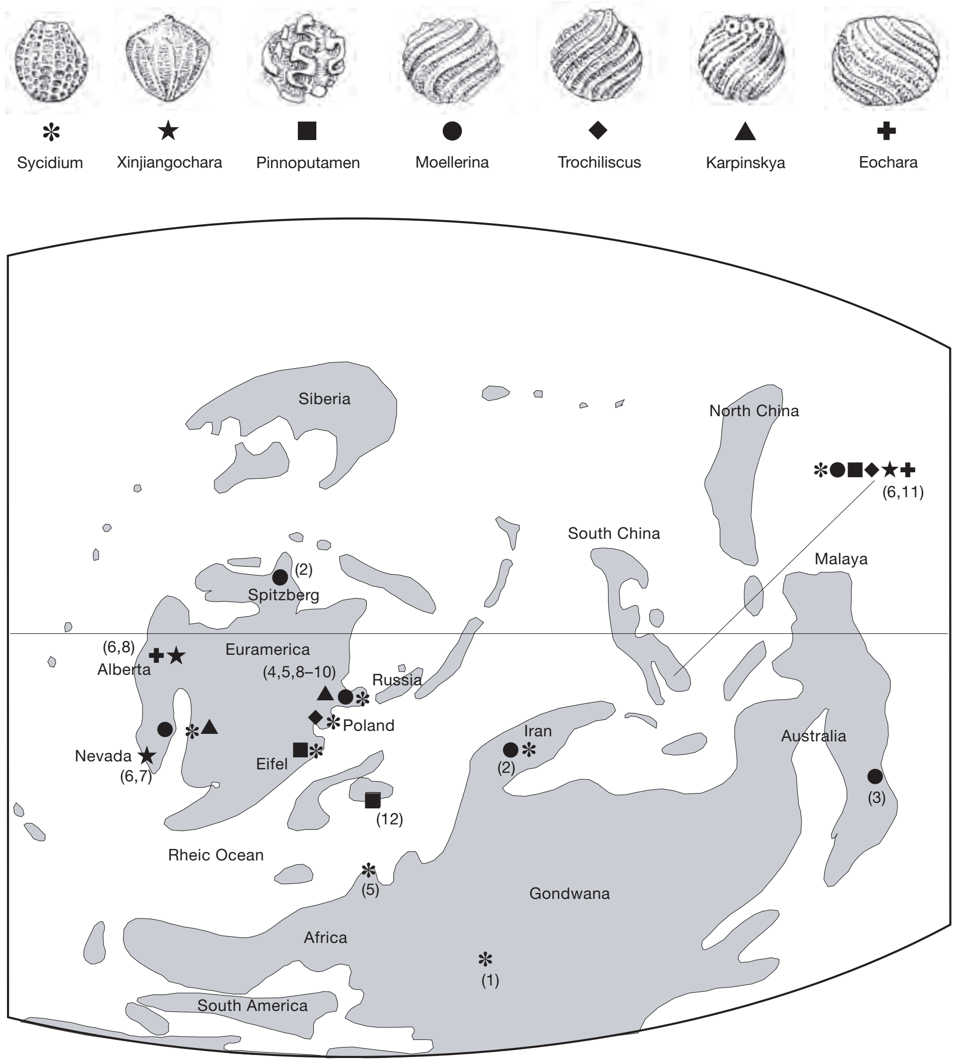

FIG. 24. Distribution of charophyte genera during the Lower and Middle Devonian on the paleogeographic map schematized after SCOTESE (1997); *1,* Choubert, 1932; *2,* Feist & Grambast-Fessard, 1985; *3,* Feist in Talent & others, 2000; *4,* Karpinsky, 1906; *5,* Langer, 1991; *6,* Lu, Soulié-Märsche, & Wang, 1996; *7,* Peck & Eyer, 1963a; *8,* Peck & Morales, 1966; *9,* Racki & Racka, 1981; *10,* Samoilova, 1961; *11,* Z. Wang & Lu, 1980; *12,* M. Feist & R. Feist, 1997 (new).

(LU & LUO, 1990). *Stomochara,* the first representative of the family Porocharaceae, was present in different localities of North America (PECK & EYER, 1963b) and Europe (SHAIKIN, 1966; KISIELEVSKY, 1980; GEBHARDT & SCHNEIDER, 1985; SAIDAKOVSKY, 1989). *Gemmichara,* which was present in the early Carboniferous and occurs in the Permian (Z. WANG, 1984), must also have lived during the late Carboniferous, although it has not yet been discovered.

At the end of the early Carboniferous, the principal continents (Euramerica and Gondwana) were joined, and what would later constitute Europe was the site of the Variscan orogeny. Conditions prevailing within the paralic basins formed in this new continental configuration were certainly catastrophic for the charophytes, as evidenced by the scarcity of deposits with charophytes during this time. Charophytes must have entered into competition with higher plants that were then spreading profusely. In the rare instances when calcified structures might occur, they could seldom be preserved owing to the acidity of the entrophic lacustrine medium. It is noteworthy that during this crisis, which led to the extinction of two entire orders, new taxa appeared, characterized by a morphological change, the realization of the modern type of gyrogonite with five spiral cells, regarded as an innovation.

PERMIAN

In the Permian *Palaeochara, Gemmichara,* and *Stomochara* were extant from the previous periods, the last of them with a wide distribution in North America, Europe, and China. Other representatives of the Porocharaceae appeared. *Porochara* and *Leonardosia* were present in Europe and China; *Leonardosia* was also present in the upper Permian of Brazil, *L. langei* being the only charophyte representative known from the Paleozoic of South America. In the late Permian, from this same family, *Clavatorites* (synonym: *Cuneatochara*) and *Stellatochara* occurred in Europe (SAIDAKOVSKY, 1968; KOZUR, 1974; BILAN, 1988; KISIELEVSKY, 1993c). The Permian was thus a period of diversification.

The widespread distribution of genera in North and South America, Africa, and Europe was probably favored by the vast nonmarine areas of Pangaea. Connections with Asia may have occurred through present-day Russia where several Permian species have been described.

MESOZOIC

TRIASSIC

Following the close of the Permian, new occurrences of charophytes took place at the beginning of the Triassic, probably in relation with the regression at the beginning of this period. The well-calcified, large-sized Paleozoic genera were replaced by generally small genera, frequently with concave cells. This reduction of calcified structures may be related to the drop of temperatures resulting from the late Permian glaciations. The boundary between the Paleozoic and the Mesozoic thus seems relatively well marked in charophytes. The persistence of two-thirds of the Permian genera into the Triassic shows, however, that this break was not really abrupt. The same holds true with respect to terrestrial plants and freshwater fishes (KNOLL, 1984; BRIGGS, 1995) that similarly were not drastically affected by the end-Permian events.

Baltica and China seem to have been the dispersion centers of charophytes during the Triassic as they were during the late Permian. Apart from these regions, the sole records are from the North American Upper Triassic (PECK & EYER, 1963b).

During the Triassic, three families existed: the Porocharaceae, which were dominant both in number of taxa and localities; the Characeae, which had their earliest occurrence with *Aclistochara,* first reported from the Upper Triassic of South China (LIU & CHEN, 1992); and a unique representative of the ancient family Eocharaceae, last known from the Middle Devonian (CHOQUETTE, 1956) and having persisted in a refuge in Kazakhstan (KISIELEVSKY, 1996).

JURASSIC

During the Early Jurassic, the distribution of charophytes was restricted to a few localities in China, India, and Europe (FEIST & CUBAYNES, 1984; FEIST, BHATIA, & YADAGIRI, 1991; LU & YUAN, 1991; LIU & CHEN, 1992). The extinctions at the end of the Triassic led to an impoverishment that was not compensated by evolution of new forms during the Early Jurassic; the four genera recorded from this epoch were present already in the Early Triassic. The Early Jurassic was one of the most critical times in the evolution of the group, perhaps in relation to the disjunct distribution of landmasses that interrupted paths of migration.

The Middle Jurassic was marked by a renewal. Three new genera arose, and charophytes reached North America as well as Africa. A number of localities with *Porochara* species have been reported worldwide from the Bathonian; this coincided with an episode of regression (Feist & Grambast-Fessard, 1984; Charrière & others, 1994).

During the Late Jurassic, the expansion phase continued. Newly emerging lands in Laurasia (now North America, Europe, Central Asia, and China) as well as in northern Gondwana (Algeria, Tanzania) certainly favored the worldwide spread of charophytes (Lu & Luo, 1990; Feist, Lake, & Wood, 1995; Schudack, Turner, & Peterson, 1998; Schudack, 1999). A new family, the Clavatoraceae, evolved, initially with seven genera. The same number of new genera also evolved in the Characeae, while the Porocharaceae persisted from previous periods without renewal.

CRETACEOUS

During the Early Cretaceous, charophyte floras diversified on the lands that had emerged since the Late Jurassic (Martin-Closas & Serra-Kiel, 1991). Nine new genera of the Characeae evolved and eleven of the Clavatoraceae but none of the Porocharaceae. The Early Cretaceous was a time of vast geographical expansion. Some species, such as *Atopochara trivolvis* Peck and *Flabellochara harrisii* Peck, have a cosmopolitan distribution (Sirna, 1968). Eighty-six percent of genera in the Clavatoraceae and 31 percent in the Characeae, however, went extinct during the Albian. This extinction phase may be attributed to the opening of the Atlantic Ocean, which must have interrupted migration routes and brought about climatic variations, disturbing the aquatic habitats where charophytes were growing. Another factor that may have contributed to the alteration of the charophyte flora was the increasing development of the angiosperms during the Albian and Cenomanian. The Clavatoraceae, which favored calcareous environments owing to their multilayered utricles, were more sensitive than the Characeae to the eutrophication and acidification that resulted from accumulation of organic matter.

During the Late Cretaceous, the Characeae, taking advantage of vacant niches, radiated dramatically with the occurrences of 21 new genera in this family. Only two genera of Clavatoraceae lived during the Cenomanian: *Embergerella* and *Atopochara.* After the Coniacian to Santonian, where the fossil record of charophytes is nearly nonexistent, the family was represented again by only two genera, a new one, *Septorella* Grambast, and *Atopochara* Peck, which persisted from the Early Cretaceous. No change occurred in the Porocharaceae, but the Raskyellaceae, which appeared during the Late Cretaceous, are thought to have evolved from members of this family, presumably the *Feistiella* group, which exhibits undivided basal plates.

Late Cretaceous genera are reported as showing provincial differentiation as a result of the fragmentation of Pangaea. As in other periods, however, the charophyte flora included subcosmopolitan genera that occurred on at least three continents. Among the Porocharaceae, both *Porochara* and *Feistiella* were widely distributed during the Cretaceous. The same was true for *Atopochara* (Clavatoraceae) until the Turonian and for the Characeae *Amblyochara, Chara, Charites, Lamprothamnium, Microchara, Peckisphaera, Platychara, Sphaerochara,* and *Strobilochara* as well as for the Raskyellaceae *Saportanella.*

During the Late Cretaceous, charophytes were distributed in four main zones.

Eurasia

With five genera recorded only from China and Mongolia (*Collichara, Mongolichara, Neochara, Pseudolatochara,* and *Zhejiangella*), this province has a high degree of endemism; Eurasia was also a refuge for the last representatives of *Latochara, Atopochara,* and *Aclistochara.*

Southern Europe

This area was a center of dispersion of *Dughiella* and *Nitellopsis;* southern Europe also yielded three endemic genera: *Embergerella, Septorella,* and *Bysmochara.*

North and South America

The fossil record is very poor in North America from the Turonian onward. According to the record of *Tolypella* (*sensu stricto*) from the Late Cretaceous of Argentina (Uliana & Musacchio, 1978) and Alaska (Feist & Brouwers, 1990), North America and South America seem to have been centers of dispersal of the genus, which is found only from the Eocene onward in other continents. *Nothochara* is endemic to South America.

India

Besides cosmopolitan genera (*Chara, Microchara*), India shares the genus *Nemegtichara* with China and Mongolia; *Peckichara* is common to Asia and Europe; and *Nodosochara* is common to Europe and South America. Thus, at the generic level charophytes do not provide clear indications on the position of the Indian subcontinent at the end of the Cretaceous.

Bhatia and Rana (1984) reported, however, an Upper Cretaceous–Eocene assemblage from intertrappean beds, including *Platychara perlata* (Peck & Reker) Grambast, *Peckichara varians* Grambast, and ostracodes. According to these authors, this assemblage has floral and faunal affinities with the northern Asian part of India, and thus its distribution is not in accordance with paleogeographic reconstructions where the Indian plate is isolated from other continuous landmasses.

CRETACEOUS-TERTIARY BOUNDARY

The end of the Cretaceous was a time of marked importance for the charophytes (see Stratigraphic Range Chart, herein p. 148). The events triggering the K-T crisis must have been fatal to the last representatives of the Clavatoraceae, already severely impoverished by the extinctions during the early Late Cretaceous. In the sections calibrated by magnetostratigraphy (Galbrun & others, 1993; Westphal & Durand, 1990) the last *Septorella* became extinct about two million years before the beginning of the Danian.

The episodes of cooling during the Maastrichtian pointed out by Médus and others (1988) may have caused a decrease in the amount of calcium carbonate precipitation, thus inhibiting the development of calcified utricles.

The diversity of Porocharaceae had remained unchanged with the persistence of the same three genera, *Latochara, Porochara,* and *Feistella,* since the Early Cretaceous. The family crossed over the K-T boundary but was already very much impoverished and disappeared during the Eocene.

The K-T boundary is well marked in the Characeae, as 40 percent of the genera became extinct. In this family, the crisis did not result in a complete extinction and coincided with the family's major stage of expansion. This scenario is similar to that of the early Carboniferous when the expanding Porocharaceae allowed the survival of the charophytes.

It appears thus that the K-T boundary marks a break within the charophytes but not really a mass-extinction phenomenon. The most outstanding consequences occurred after the K-T crisis. Indeed, the extinctions at the end of the Cretaceous were not balanced by an equivalent number of newly appearing genera (see Fig. 40). This resulted in a drastic reduction in diversity during the Cenozoic. We suppose that the expansion of the aquatic angiosperms was a factor limiting the recovery of the charophytes.

CENOZOIC

PALEOCENE

After the extinctions at the end of the Cretaceous, the charophytes included 21 genera. The Paleocene assemblages, however, have an entirely distinct appearance due to the evolution of many new species in the Danian (Feist & Colombo, 1983). At the generic level, only *Rhabdochara* originated in the late Paleocene (Hao & others, 1983). One genus, *Platychara,* disappeared at the end of the Danian, and the last occurrence of *Collichara* is in uppermost Paleocene rocks of the Jiangsu (China; Lu, 1997). In addition, the Porocharaceae nearly became extinct before the Eocene; to date, a single occurrence of the family has been mentioned in the Eocene (Shaikin, 1977).

The provincial differentiation that started during the Late Cretaceous persisted throughout the Paleocene. Asia became a new center of endemism for several genera: *Collichara, Nemegtichara,* and *Neochara. Tolypella* was still restricted to North America (Feist & Brouwers, 1990); this is consistent with its American origin suggested by its occurrences in both North and South America during the Late Cretaceous. The Paleocene Epoch included also five widely distributed genera: *Feistiella, Harrisichara,* and *Dughiella,* as well as *Platychara* and *Peckichara,* both cosmopolitan.

EOCENE

After the extinction of most Porocharaceae, the charophyte flora included only two families: the Characeae, which was the most important in both the number of genera and localities, and the Raskyellaceae. In the earliest Eocene, 19 genera were in existence. *Raskyella* evolved in North Africa during the early to middle Eocene (Mebrouk & others, 1997); *Psilochara* evolved in Europe in the middle Eocene (Feist-Castel, 1971); and *Linyechara, Lychnothamnus,* and *Shandongochara* evolved in China during the late Eocene. The last occurrence of *Peckichara, Maedleriella, Microchara, Nodosochara,* and *Raskyella* is in the upper Eocene.

The persistence of paleogeographic provinces is illustrated by Asiatic endemism. New migration routes resulting from continental collisions, however, must have favored the geographical dispersion of several genera. The most widely distributed were *Nitellopsis, Harrisichara, Maedleriella, Peckichara,* and *Stephanochara,* suggesting migration between Europe, China, India, and North Africa.

OLIGOCENE

As the extinctions at the end of the Eocene were not compensated by evolution of new taxa, the Oligocene was a time of impoverishment. This decline is shown moreover by the reduction of areas of distribution. The number of genera, initially 15, was reduced by the extinction of *Harrisichara* and *Shandongochara.* The genus *Gyrogona,* absent from Europe from the middle Oligocene onward, persisted in China until the late Miocene (Lu & Luo, 1990). During the late Oligocene there was a renewal, marked by the evolution of new species within several genera (*Chara, Nemegtichara, Nitellopsis, Rhabdochara,* and *Sphaerochara*). Oligocene charophytes have been reported mostly from Europe and Asia.

MIOCENE

The diversification phase continued during the early Miocene: a new genus, *Rantzieniella,* evolved; and areas of distribution became more extended, especially of *Chara* and *Nitellopsis.* Reports of the last occurrence of *Grovesichara* at the end of the early Miocene (Tang & Di, 1991) as well as of *Gyrogona* and *Psilochara* before the end of the Miocene mark the end of this period of diversification, which was the last one for the charophytes.

PLIOCENE

The decline of the charophytes is underlined by the extinction during the Pliocene of *Amblyochara* and *Rantzieniella,* the last representative of the Raskyellaceae. *Nemegtichara, Stephanochara,* and *Rhabdochara* also became extinct before the end of the Pliocene. As during the Oligocene, areas of distribution were reduced and restricted mainly to Europe and Asia. Two cosmopolitan genera were an exception: *Chara* and *Lamprothamnium.* The latter of these, however, has not been reported so far from North America in rocks above the Lower Cretaceous.

PLEISTOCENE

The charophyte flora of the Pleistocene resembled that of the modern world. Only one genus reported from the Pleistocene, *Hornichara,* does not live at the present time. All the extant genera are represented but in some instances with a different distribution. *Lychnothamnus* has been reported from Africa (Soulié-Märsche, 1981) where it is unknown today, and *Nitellopsis* was spread over a greater area than at present. *Chara* and *Sphaerochara* were cosmopolitan. The area of distribution of the halophilous genus *Lamprothamnium* was also very wide but localized in particular biotopes generally near the shoreline.

Genera with uncalcified fructifications are poorly represented. Thus a single locality in the middle Pleistocene of Russia has been reported for the genus *Nitella* (Krassavina, 1966).