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The fossil record and evolution of freshwater plants: A review

C. MARTÍN-CLOSAS

Departament d'Estratigrafia, Paleontologia i Geociències Marines, Facultat de Geología, Universitat de Barcelona
c/ Martí i Franquès s/n, 08028 Barcelona, Catalonia (Spain). E-mail: cmartin@natura.geo.ub.es

ABSTRACT

Palaeobotany applied to freshwater plants is an emerging field of palaeontology. Hydrophytic plants reveal evolutionary trends of their own, clearly distinct from those of the terrestrial and marine flora. During the Precambrian, two groups stand out in the fossil record of freshwater plants: the Cyanobacteria (stromatolites) in benthic environments and the prasinophytes (leiosphaeridian acritarchs) in transitional planktonic environments. During the Palaeozoic, green algae (Chlorococcales, Zygnematales, charophytes and some extinct groups) radiated and developed the widest range of morphostructural patterns known for these groups. Between the Permian and Early Cretaceous, charophytes dominated macrophytic associations, with the consequence that over tens of millions of years, freshwater flora bypassed the dominance of vascular plants on land. During the Early Cretaceous, global extension of the freshwater environments is associated with diversification of the flora, including new charophyte families and the appearance of aquatic angiosperms and ferns for the first time. Mesozoic planktonic assemblages retained their ancestral composition that was dominated by coenobial Chlorococcales, until the appearance of freshwater dinoflagellates in the Early Cretaceous. In the Late Cretaceous, freshwater angiosperms dominated almost all macrophytic communities worldwide. The Tertiary was characterised by the diversification of additional angiosperm and aquatic fern lineages, which resulted in the first differentiation of aquatic plant biogeoprovinces. Phytoplankton also diversified during the Eocene with the development of freshwater diatoms and chrysophytes. Diatoms, which were exclusively marine during tens of millions of years, were dominant over the Chlorococcales during Neogene and in later assemblages. During the Quaternary, aquatic plant communities suffered from the effects of eutrophication, paludification and acidification, which were the result of the combined impact of glaciation and anthropogenic disturbance.

KEYWORDS **Freshwater algae. Aquatic angiosperms. Charophytes. Evolution. Palaeoecology.**

INTRODUCTION

The study of plant evolution has been traditionally devoted to the fossil record of terrestrial plants and marine algae, leaving the palaeobotany of freshwater environments largely unexplored. During the twentieth century three main fields of palaeobotany -namely palynology, palaeocarpology (the study of fossil fruits and seeds) and palaeoalgology- focused on the study of freshwater fossil plants, especially diatoms, chrysophytes, chlorophytes and charophytes. An increasing number of studies of freshwater plants were undertaken, principally encouraged by applications to plant evolution (Graham, 1993; Kenrick and Crane, 1997), palaeoecology (Collinson, 1988; Matthiessen et al., 2000), biostratigraphy (Riveline et al., 1996) and organic geochemistry (Peniguel el al., 1989). To date, however, the palaeobotany of aquatic plants remains a largely unexplored domain. The aim of this paper is to summarise the data available on this subject and to analyse the major lines of future research. In order to limit the number of taxa referred to in this study, aquatic plants will be understood as "organisms bearing photosynthetic organs underneath the surface of freshwater bodies" (Cook, 1996). This includes all hydrophytic plants and excludes helophytes (emergent plants rooted in a substrate below standing water).

THE FIRST FRESHWATER PLANTS OF THE PROTEROZOIC AND THEIR PALAEOZOIC DIVERSIFICATION

Freshwater plants of the Proterozoic

Stromatolites have been found in a number of Precambrian continental palaeogeographic contexts including ponds associated with alluvial fans or lakes formed in volcanic calderas (Walter, 1994). Hoffmann (1976) and Hoffmann et al. (1980) described large cup-shaped stromatolitic structures in lacustrine environments dating from the Proterozoic, 2800 to 2700 m.a. ago (Figs. 1A and 1B). These continental stromatolites are morphologically similar to their marine counterparts but it is uncertain whether or not different taxa of Cyanobacteria were growing in both environments. Only in a few cases, such as in the Bitter Springs Chert (Australia), the biological affinity of the bacterial assemblage could be identified (Schopf, 1999). This association, which contains abundant Oscillatoriaceae and Chroococcaceae, bears a striking similarity to extant freshwater cyanobacterial communities. Unfortunately, there are no unequivocal data about the salinity of these facies. Among the oldest eukaryotic algal fossils are smooth organic cysts from the Proterozoic, which were traditionally classified as sphaeromorphic or leiosphaeridian acritarchs. Thus, genus *Leiosphaeridia,* may in fact belong to ancestral tasmanitids, which were prasinophytes. The walls of these cysts are thinner and are not crossed by pores as in typical prasinophyte cysts (Fig. 1C). Bearing in mind that prasinophytes bloom under the influence of continental runoff, some early leiosphaerids may have become adapted to freshwater environments and gave rise to freshwater green algae of the Palaeozoic, for which they are phylogenetically basal.

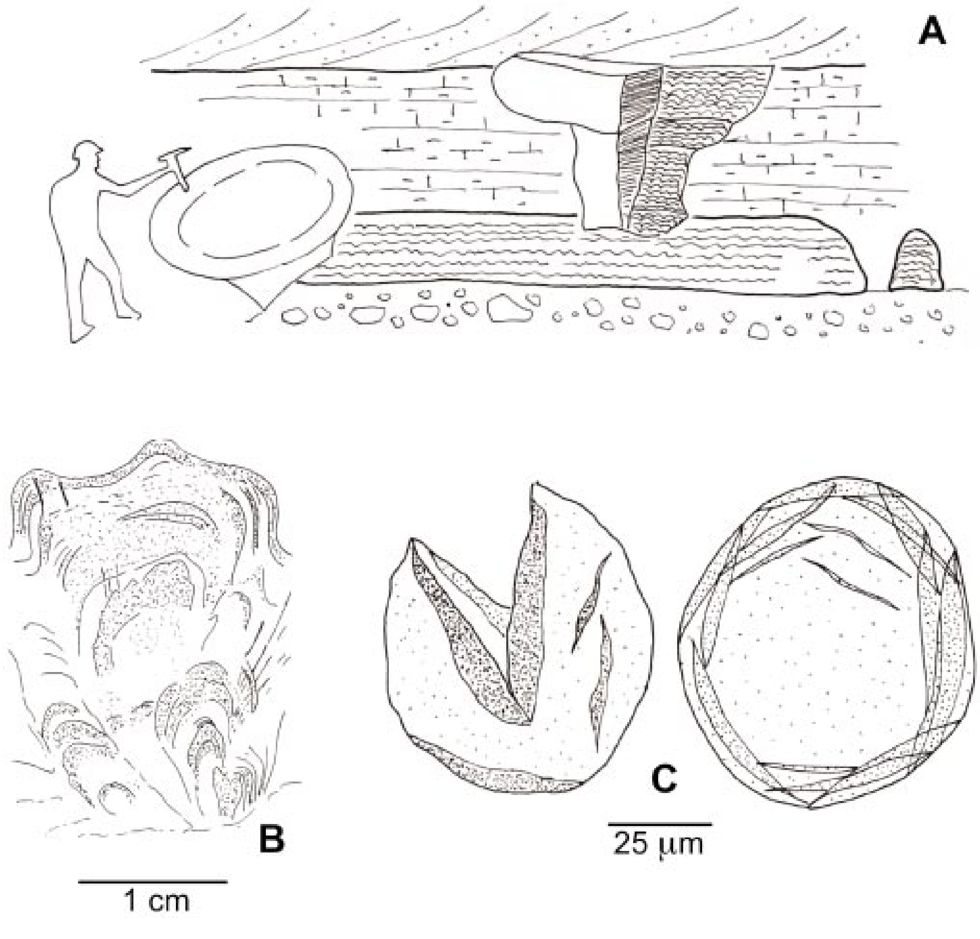

FIGURE 1 **Precambrian freshwater flora. A) Proterozoic freshwater stromatolites from the Murky Formation (Ontario) showing cup-shaped structures growing upon planar stromatolites within a silty lacustrine unit and overlaid by fluvial facies (modified from Hoffmann 1976). B) *Alcheringa narrina* from the Proterozoic of Fortescue Group, Australia, showing columnar growth (modified from Walter 1994). C) *Leiosphaeridia*, possibly a prasinophyte cyst (modified from Tappan 1980).**

In summary, the Precambrian fossil record of freshwater to brackish biota is extremely poor and equivocal from the point of view of water salinity. It was dominated by cyanobacteria and acritarchs, the latter taxonomically assigned to the prasinophytes. This scenario should be taken cautiously since widely accepted phylogenies suggest that other algal groups were already present, albeit without a conclusive fossil record (Perasso et al., 1989).

Diversification of green algae in Palaeozoic lakes

Tasmanitids of genus *Tasmanites* are first known to occur in the Cambrian (Fig. 2A) and show a structure identical to modern prasinophyte cysts (Jux, 1977; Fensome et al., 1990; Guy-Ohlson, 1996). During the Early Palaeozoic the oldest algal blooms recorded in the history of the Earth massively accumulated in transitional, brack-

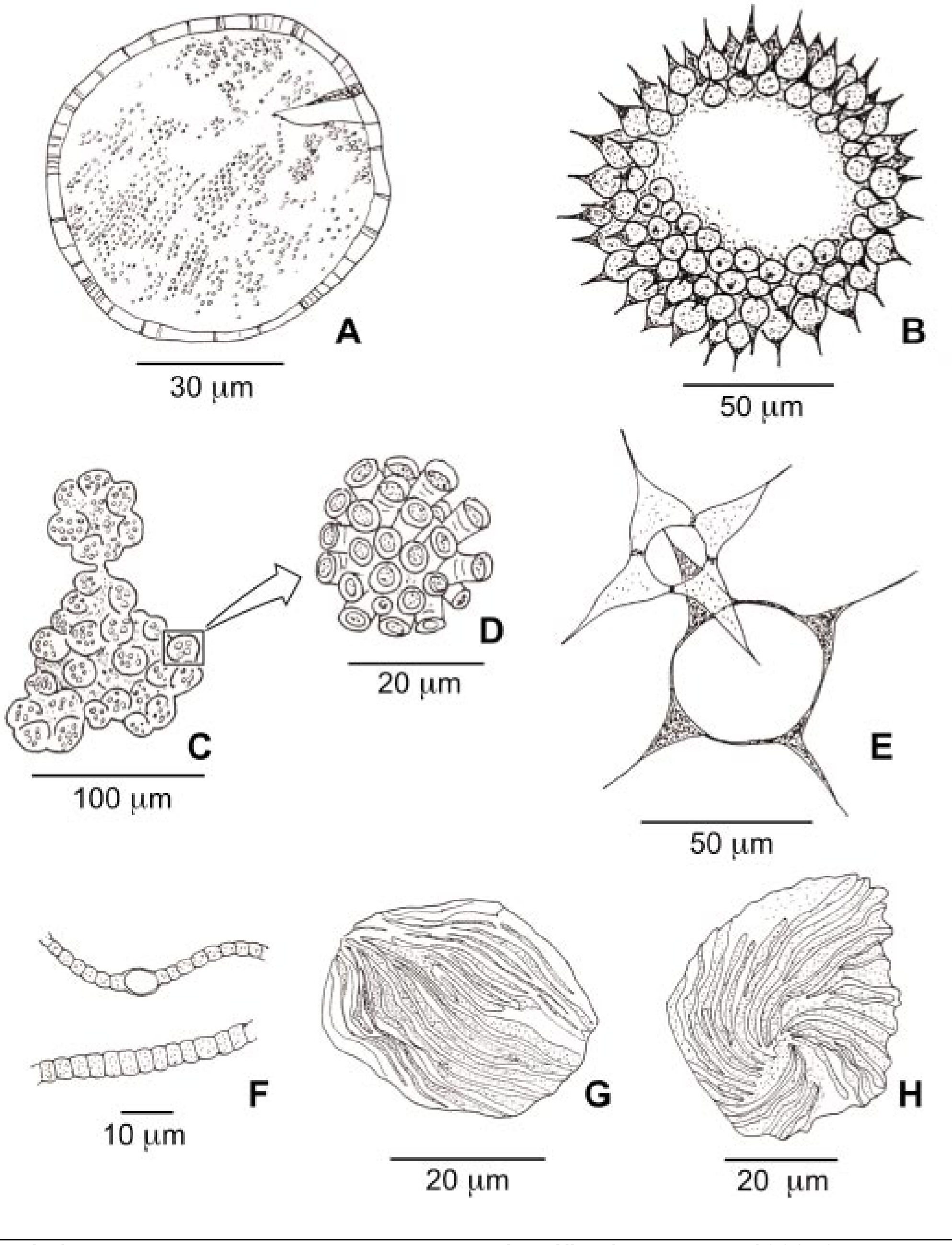

FIGURE 2 **Palaeozoic freshwater chlorophytes and euglenophytes (modified from Tappan, 1980; Gray and Boucot, 1989; and Guy-Ohlson, 1996). A) *Tasmanites* (Prasinophyceae) from the Ordovician of Oklahoma (USA). B) *Eovolvox* (Volvocales) from the Upper Devonian of Poland. C and D) *Botryococcus* (Chlorococcales), showing an entire coenobium and a detail of cup-shaped cells. E) *Deflandrastrum* (Chlorococcales) from the Silurian of Libya. F) *Palaeoedogonium* (Oedogoniales), Middle Devonian, New York (USA). G and H) *Moyeria cabotii* (Euglenophytes) from the United States Ordovician and Silurian.**

ish environments and were formed by tasmanitids (Tappan, 1980). Extensive deposits of these tasmanite-shales are considered to be petroleum source rocks containing prasinophyte cysts as their main constituent (Peniguel et al., 1989). Tasmanitids diversified into a number of green algal groups by the end of the Precambrian. The shortage of algal remains that are neither calcified nor contain a significant amount of sporopollenin accounts for a rather scanty fossil chlorophyte record at the beginning of Palaeozoic. Thus, fossil Volvocales considered as basal chlorophytes, are restricted to *Eovolvox* (Fig. 2B), from the Devonian of Silesia in Poland (Tappan, 1980). The most abundant Palaeozoic freshwater chlorophytes are the Chlorococcales. Planktonic coenobia (colony-like structures) similar to the extant *Botryococcus* algae, are present as early as in the Precambrian of Bohemia (Czech Republic) according to Tappan (1980). However, forms identical to the extant *Botryococcus* do not appear until the Ordovician (Figs. 2C and 2D), when they became dominant as plankton of particular freshwater systems (Batten and Grenfell, 1996; Clausing, 1999). During the Palaeozoic, chlorococcalean colonies diversified, achieving higher levels of organization, such as *Deflandrastrum* from the Libyan Silurian (Fig. 2E), which shows a tetragonal symmetry (Tappan, 1980). Palaeozoic Chlorococcales are occasionally found in nearshore marine environments, where massive accumulations occurred after being laterally transported from freshwater or brackish environments, as it happens in Quaternary environments (Matthiessen et al., 2000). Given their high content of chlorococcalean cytoplasmic lipids, these accumulations produced petroleum source rocks (Peniguel et al., 1989).

Filamentous chlorophytes were only preserved in exceptionally well-preserved sites (Fossil-Lagerstätten), such as the Devonian Rhynie Chert in Scotland, where *Mackiella* and *Rhynchertia* (Ulotrichales) were preserved, permineralised together with cyanobacteria (Edwards and Lyon, 1983). Another of these exceptional sites for early green algae is the Devonian Onondaga Chert of New York state. According to Baschnagel (1942, 1966) these deposits yield *Palaeoedogonium* (Fig. 2F), representing Oedogoniales (or alternatively cyanobacteria according to Zippi, 1998), *Geminella* (Ulotrichales) and Zygnematales.

Palaeozoic representatives from the charophyte lineage

Algal ancestors of land plants were charophytes, Coleochaetales, Zygnematales, Klebsormidiales and Chlorokybales (Graham, 1993). The oldest fossil remains of land plant ancestors are the calcified fructifications of Silurian charophytes (Ishchenko and Ishchenko, 1982). However, the Silurian should be considered the time of charophyte radiation rather than the origin of land plant ancestors, since trilete spores of land plants (bryophytes or early vascular plants), which are a more derived group, were found in Ordovician sediments (Gray 1985; Steemans, 2000). Thus, a Cambrian or Precambrian origin for algal groups that were ancestors to land plants appears to be a highly probable hypothesis. Smooth organic vesicles, ellipsoidal in shape and similar to the conjugate zygospores of *Spirogyra*, already may have been present during the Proterozoic, even if they have been attributed to acritarchs. The first unequivocal occurrence of a fossil zygnematalean thallus belongs to a unicellular species, *Paleoclosterium leptum* from the Middle Devonian of New York state (Fig. 3A) (Baschnagel, 1966).

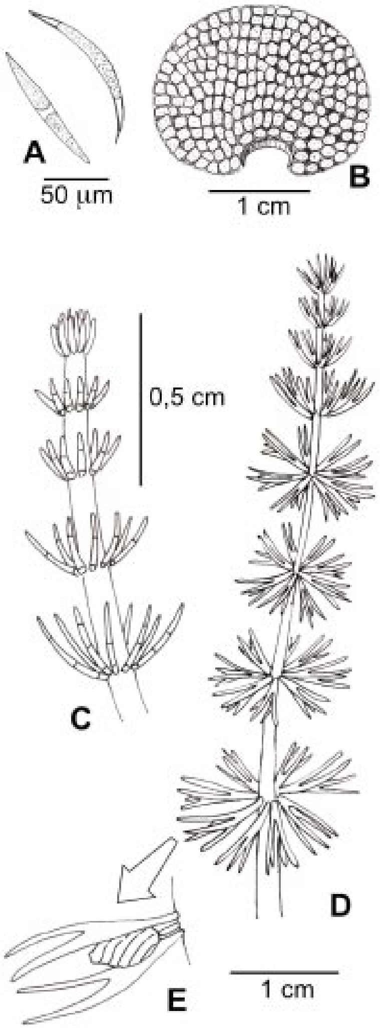

FIGURE 3 **Palaeozoic charophytes and allies (modified from Kidston and Lang, 1921; Tappan, 1980; Hemsley, 1990 and Gess and Hiller, 1995). A) *Palaeoclosterium* (Zygnematales) from the Middle Devonian of New York (USA). B) *Parka decipiens* (Coleochaetales?) from the Lower Devonian of Scotland and the United States. C) Thallus of *Palaeonitella cranii* (Charophyta) from the Devonian Rhynie Chert (Scotland). D and E) Thallus of *Octochara gracilis* (Charophyta) from the Devonian of Grahamstown, South Africa, with a detail of gyrogonite insertion.**

By contrast, the first unmistakable conjugate zygospores are known from the Carboniferous and they already bore a similarity to extant genera (Van Geel and Grenfell, 1996). Carboniferous zygospores of the genera *Tetrasporina*, *Brazilea* and *Lacunalites* are reminiscent of extant *Mougeotia*, *Spirogyra* and *Zygnema*, respectively. The origin of conjugation as a special mechanism for producing zygospores is significant as it represents the first adaptation of a green alga to survive desiccation of ephemeral ponds on land (Stebbins and Hill, 1980). During the Early Permian, Zygnematales underwent a short radiation period, with the appearance of the genera *Peltacystia*, *Aleteverrucosispora*, *Singraulipollenites* and *Kagulubeites*, the two first being similar to the extant *Debarya* (Van Geel and Grenfell, 1996). This Permian radiation may reflect speciation related to the extension of small, ephemeral ponds during this period of general aridity.

The Coleochaetales also are among the algal ancestors of land plants. Presently they are filamentous or thalloid in shape and inhabit ephemeral ponds. This group is significant to the evolution of land plants since some authors, such as Graham (1993), consider them the sister group to the embryophytes (but see Karol et al., 2001 for an alternative interpretation). Only one fossil has been tentatively related to Coleochaetales, namely, *Parka decipiens* from the British and United States Lower Devonian (Fig. 3B) (Niklas, 1976). In spite of their overall similarity, this fossil is significantly different from living Coleochaetales, with a much larger thallus (2-3 cm across) in comparison to the extant *Coleochaete* (1-2 mm across). An ultrastructural study of *Parka*'s spores led Hemsley (1990) to describe this fossil as intermediate between the Coleochaetales and bryophytes. Irrespective of its exact phylogenetic position, *Parka decipiens* may be indicative of a high diversity of fossil taxa in land plant ancestry during the Palaeozoic. No additional fossils have been related to the Coleochaetales in the fossil record.

Among land plants ancestors, charophytes yield the most complete fossil record. This allows for greater detail in assessing the palaeobotany of the group, in contrast to previous taxa. Palaeozoic thalli bear exclusively ecorticate internodes, namely simple cylinders as in *Palaeonitella* from the Devonian Rhynie Chert (Fig. 3C) (Kidston and Lang, 1921) or in *Octochara* and *Hexachara* from the same interval in South Africa (Fig. 3D and 3E; Gess and Hiller, 1995). During the Palaeozoic, calcified fructifications yield extremely diverse structural patterns including helically coiled gyrogonites in the orders Trochiliscales and Charales, and uncoiled fructifications in the order Sycidiales (Fig. 4; Grambast, 1974). Uncoiled fructifications are formed from a number of patterns, ranging from vertical filaments in *Sycidium* to more complicated and branching filaments in *Pinnoputamen*. The uncoiled type of fructification is probably ancestral to the charophytes since it simply results from closing a whorl of branchlets upon an oospore (Fig. 4). Helically coiled gyrogonites were more successful during evolution and all post-Devonian fructifications displayed this pat-

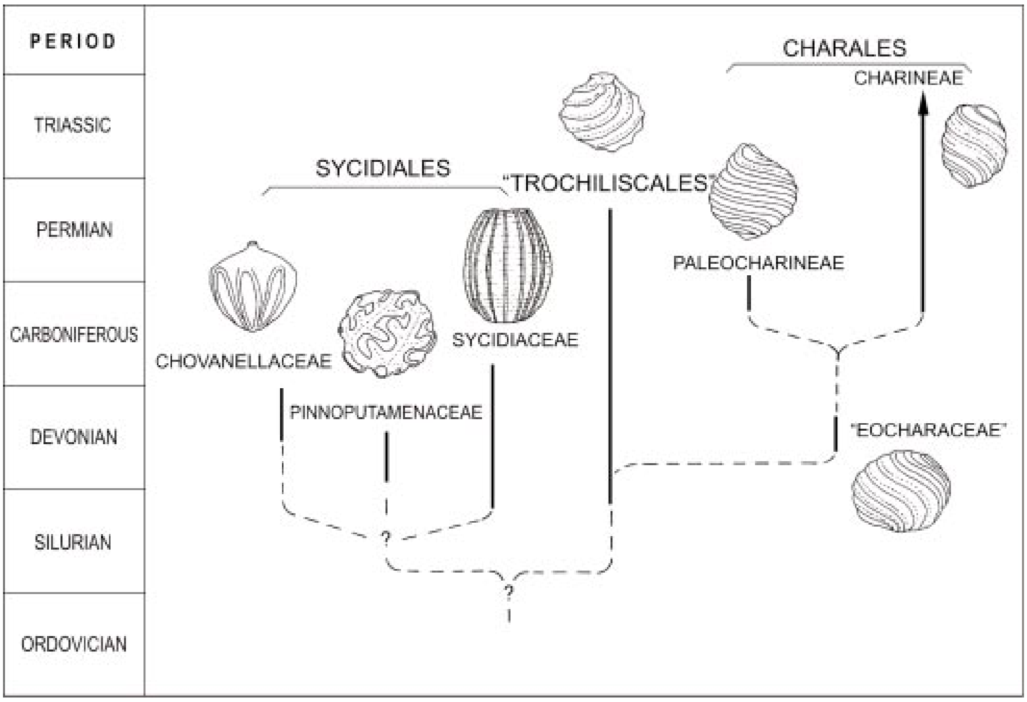

FIGURE 4 **Evolution of Palaeozoic charophyte fructifications (from Martín-Closas et al., 1999).**

tern. During the Palaeozoic, gyrogonites produced up to 15 helical cells in basal groups (Trochiliscales and early Charales) but in the Permian this number was reduced and fixed at 5 (‘Porocharaceae’), which also is the number of helical cells in all post-Palaeozoic gyrogonites (Fig. 4; Grambast, 1974). As demonstrated by Martín-Closas et al. (1999) helically coiled gyrogonites with a reduced number of cells are more resistant to the stronger internal pressures produced during zygote maturation.

The palaeoecology of Palaeozoic charophytes has been a matter of controversy. A number of Palaeozoic (mostly Devonian) sites that yield gyrogonite assemblages are found in marine rocks and are associated with marine invertebrates such as brachiopods, tentaculitids or crinoids (Choquette, 1956). Consequently some authors have suggested a marine habitat for Palaeozoic charophytes (Racki, 1982) or even that the entire group originated in the sea (Berger, 2002). In opposition to this point of view, taphonomic evidence such as erosion and fragmentation, suggests that these charophyte fructifications were transported into the marine environment, perhaps from supratidal ponds. The seaward transport of large amounts of such tiny, spheroidal bodies could well have been possible for dozens of kilometres along gently sloping Devonian ramp-type shelves. Also, marine assemblages of Devonian charophyte fructifications are always devoid of vegetative remains, the latter being found exclusively in freshwater deposits of the same age. In addition, Palaeozoic assemblages of charophyte thalli display a wide range of preservations such as silicification (Kidston and Lang, 1921), compression (Gess and Hiller, 1995) or lime-encrustation (Hill and El-Khayal, 1983). This excludes that they were only preserved under unique diagenetic circumstances.

The evolutionary history of Palaeozoic charophytes shows an early diversification at the beginning of the Devonian (Grambast, 1974). Tappan (1980) related this to the spread of oligotrophic freshwater systems, after nutrients were retained within the first well-developed soils recorded on land. In addition, the Devonian greenhouse environmental effect probably promoted the calcification of charophyte fructifications and the development of alkaline supratidal marshes, which was an optimal environment for charophytes. By way of contrast, the late Palaeozoic was more critical for charophytes. Carboniferous freshwater environments were rich in helophytic vascular plants such as arborescent lycophytes and sphenophytes but poor in hydrophytic plants. As in all forested swamps, Carboniferous coal swamps supplied a large amount of suspended organic matter and dissolved humic acids, which resulted in aphotic lake bottoms and acidic lake water. These circumstances may explain, as suggested by Tappan (1980), charophyte turnover during the Late Devonian and Carboniferous. Thus, the Sycidiales disappeared in the Early Carboniferous and Charales diversified during the same period. The fossil record of charophytes was poor during the Permian, when the Trochiliscales finally became extinct and only five-celled coiled gyrogonites survived into the Mesozoic.

More diversity in Palaeozoic lakes

In addition to chlorophytes and charophytes, other freshwater plants were present in the Palaeozoic aquatic systems. This is the case for *Moyeria*, a problematic organic-walled microfossil (20 x 40 µm in size) found in the Ordovician and Silurian of Pennsylvania (United States) and Gotland (Sweden). *Moyeria*, with a unique bihelical architecture composed of fused bands (Figs. 2G and 2H), was related to the euglenophytes by Gray and Boucot (1989). Irrespective of its precise biological affinity, *Moyeria* again provides evidence of the high diversity of Palaeozoic freshwater biota. Embryophytes were excluded from the aquatic (hydrophytic) habitat during the Palaeozoic, with perhaps the exception of a few bryophytes. *Protosphagnum*, from the Russian Permian is a genus that superficially resembles the extant bog-moss *Sphagnum* and possibly grew in swampy environments (Krassilov and Schuster, 1984; Meyen, 1987).

TRIASSIC TO LOWER CRETACEOUS FRESHWATER MACROPHYTES

A number of biological and geological factors favoured charophyte dominance into Triassic to Lower Cretaceous lacustrine macrophytic assemblages. From a geological perpective, Triassic to Lower Cretaceous freshwater deposits developed in intraplate rift-basins on topographically flat continents (Salas and Casas, 1993; Ziegler et al., 2001). Depending on climate, sea-level changes and terrigenous supply, alkaline and oligotrophic lakes and marshes developed, which enhanced the development of charophytes. Also the first well-documented aquatic bryophytes date from the Triassic (Krassilov and Schuster, 1984). From the palaeobiological point of view it is significant that only a few free-sporing vascular plants (mainly ferns and selaginellaceans) were hydrophytes at the end of this period (Collinson, 1988). Isoetales inhabited freshwater swamps from the Devonian onwards and also appeared in Triassic to Lower Cretaceous swamps (Batten and Kovach, 1993), but were probably helophytes rather than hydrophytes (Retallack, 1997). On the other hand, gymnospermous seed plants never developed hydrophytic representatives. This meant that macrophytic associations from the Triassic, Jurassic and Early Cretaceous conserved their ancestral, Palaeozoic physiognomy, and specifically were dominated by charophytes

(Martín-Closas and Serra-Kiel, 1991; Martín-Closas and Diéguez, 1998).

The Triassic lacustrine benthos

Triassic macrophytic assemblages dominated by charophytes have been found principally in freshwater-to-brackish limestone and marl from the Keuper facies (Late Triassic) in northern Europe (Bilan, 1988; Breuer, 1988) and Russia (Saidakovski, 1966). Similar assemblages occur in the United States (Peck and Eyer, 1963) and China (Lu and Luo, 1984). These assemblages have been particularly studied owing to their biostratigraphic interest. Triassic charophytes are usually assigned to the paraphyletic family 'Porocharaceae' (Fig. 5), which is characterised by gyrogonites of the genera *Porochara* and *Feistiella* with five clockwise-coiled spiral cells and an apical pore (Grambast, 1974). From the Triassic onwards, charophytes possess two types of basal plates, either unicellular or multicellular (Fig. 5). In the latter case two out of three cells are preserved. Basal plates resulting from the calcification of residual cells formed during oospore gametogenesis and, according to Soulié Märsche (1989) and Martín-Closas and Schudack (1991), they indicate that two major lineages occur in charophytes at least since the Permian. In terrigenous facies of mainly fluvial silts and sandstones, charophytes were rare whereas early isoetaleans were better represented. Genera such as *Isoetites*, *Annalepis* or *Tomiostrobus* are not only similar to the extant Isoetales from the point of view of overall morphology but also show an ultrastructural affinity (Retallack, 1997; Lugardon et al., 2000). The hydrophytic character of the early isoetaleans was suggested by Hickey (1986) on the basis of neontologic phylogenies, but this is not supported by the data available from the fossil record, which indicate instead that the first Isoetales were helophytes (Retallack, 1997). In the Triassic, the first unequivocal aquatic liverwort, *Naiadita lanceolata*, occurs. According to Krassilov and Schuster (1984) it was remotely allied to *Riella*, Sphaerocarpales. Possible aquatic mosses have been documented in the Triassic too. Schuster (1970) reports a sporomorph assemblage rich in *Sphagnum*-like spores of genus *Stereisporites* in the German Triassic. In addition, *Muscites fontinaloides*, perhaps related to extant *Fontinalis*, was reported from the Triassic of South Africa by Krassilov and Schuster (1984). Triassic Zygnematales display similar evolutionary trends to the charophytes, even though they rarely constituted a significant part of the freshwater assemblage. Brenner and Foster (1994) describe one such case from the Triassic of Northwest Australia, which contained the genera *Tetraporina* and *Circulisporites*, and are probably related to extant *Mougeotia* and *Spirogyra* respectively.

Jurassic and Lower Cretaceous charophytes and allies

Few macrophytic assemblages from the Early and Middle Jurassic are recorded, owing to the general rise in sea level that occurred during this period (Ziegler, 1988).

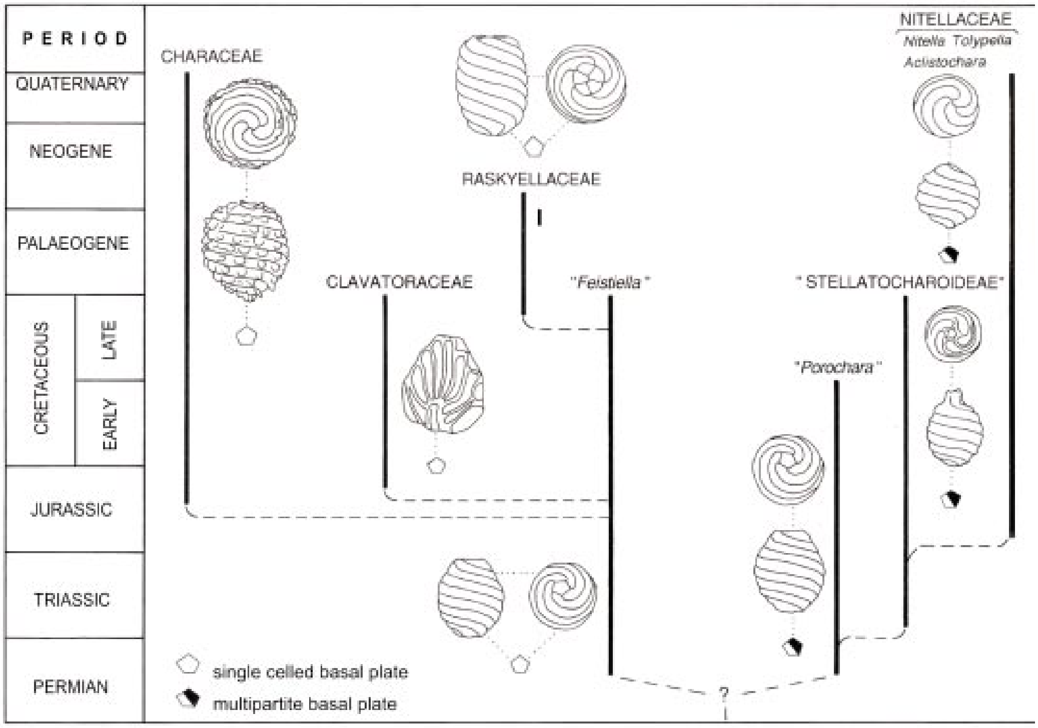

FIGURE 5 **Evolution of post-Palaeozoic charophyte fructifications.**

However, a number of freshwater basins in China indicate that charophyte assemblages were dominant and were comprised of porocharaceans (genus *Porochara*) and the first nitellaceans, which are assigned to the genus *Aclistochara* (Fig. 5). These charophytes bore gyrogonites with a composite basal plate and closed apex (Wang et al., 1976; Yang, 1985). The latter characteristic may reflect adaptation to ephemeral freshwater environments such as intermittent ponds associated with fluvial floodplains (Martín-Closas and Serra-Kiel, 1991).

The Late Jurassic to Early Cretaceous interval correspond to a renewed phase in the subsidence of intraplate sedimentary basins in many continents (Ziegler et al., 2001). This, combined with a low sea level and a prevalence of a humid climate, resulted in the extension of lacustrine systems worldwide. In Europe the Purbeck and Wealden facies belong to this period, as also the Morrison Formation of the Western interior in the United States; other stratigraphic units of South America and Asia present similar facies for the same period. This extension of freshwater systems, produced that the charophyte flora also radiated (Martín-Closas and Serra-Kiel, 1991). Two new charophyte families, the Characeae and Clavatoraceae, developed during the Oxfordian (Fig. 5). Both were derived from an ancestral stock of porocharaceans, with gyrogonites bearing a unicellular basal plate (Martín-Closas and Schudack, 1991). *Mesochara*, the earliest known Characeae genus, closed the ancestral apical pore of the gyrogonite by a simple junction of the spiral cells. The Clavatoraceae lost the capacity to calcify the gyrogonite, or calcified it only weakly, but nevertheless developed a calcitic utricle between the gyrogonite and an external coat of vegetative cells (Pia, 1927; Grambast, 1968). These utricles exhibited a gradual change among anagenetic lineages, which are useful for biostratigraphic purposes (Grambast, 1974; Wang and Lu, 1982; Riveline et al., 1996). Little is known of the thalli of the Upper Jurassic and Lower Cretaceous charophytes. Their remains are well preserved only in exceptional cases. Silicified thalli of Clavatoraceae were described by Harris (1939) in the English Berriasian, by Peck (1957) in the Kimmeridgian of the United States and by Musacchio (1971) in the Barremian of Argentina. Martín-Closas and Diéguez (1998) described a lime-incrusted assemblage of charophyte thalli from the upper Barremian of the Iberian Chain (Central Spain). Some of these thalli, assigned to the genus *Clavatoraxis*, displayed a heavy coat of spine cell rosettes, which were probably an adaptation against herbivory (Fig. 6A). Similar adaptations are found in the extant characeans (Proctor, 1999). The Clavatoraceae appear to dominate all macrophytic associations, at least from the Berriasian until the Aptian, in the tropical Tethyan biogeographic province, where oligotrophic and alkaline lacustrine systems were abundant (Martín-Closas and Serra-Kiel, 1991). This resulted in ecological relegation of the porocharaceans to brackish environments (Mojon, 1989) and to higher latitudes (Schudack et al., 1998). Clavatoraceans were also absent in carbonate fluvial deposits and during lacustrine eutrophication events, when Cyanobacteria were dominant (Martín-Closas, 1999).

Like charophytes, the Zygnematales diversified during the Jurassic and Early Cretaceous. Genera such as *Lecaniella, Schizosporis, Ovoidites, Schizocystia* and *Mougeotia* are recorded from this time (Fig. 7; Van Geel and Grenfell, 1996; Zippi, 1998). *Lecaniella* is possibly related to the extant genus *Debarya*. *Schizosporis* and *Ovoidites* are similar to *Spirogyra*, whereas *Schizocystia* may be related to *Mougeotia* or *Zygogonium*. Also the oldest unequivocal representatives of aquatic Ricciaceae (bryophytes) are considered to be Early Jurassic in age. They are assigned to genus *Ricciopsis* and were found in roof strata of coal beds in Sweden and Iran (Hoffman and Stockey, 1997).

The origin of aquatic angiosperms and ferns

The most significant event in the Early Cretaceous history of freshwater flora was the colonisation of lakes and ponds by the first vascular plants, specifically hydrophytic angiosperms and free-sporing plants. This occurred in parallel to the extinction of the Lower Cretaceous charophytes and represented a complete renovation of the freshwater macrophyte flora. In just one step, freshwater assemblages passed from their ancestral, Palaeozoic charophyte dominance to a modern physiognomy typified by angiosperms. This means that freshwater plant evolution bypassed two of the main events in the evolution of terrestrial plants, namely, the dominance of free-sporing vascular plants (‘pteridophytes’) in the Palaeozoic, and the dominance of gymnospermous seed plants in the Mesozoic.

The Chinese Neocomian yields the oldest family of freshwater vascular plants, called Archaefructaceae, an extinct family with seeds similar to angiosperms (Sun et al., 2002). These plants already present typical adaptations to the hydrophytic habitat, such as swollen petiole bases for flotation and highly dissected leaves. A more diverse assemblage of aquatic angiosperms is known from the Spanish Barremian (Fig. 6), with an aquatic buttercup-like plant assigned to the genus *Ranunculus (R. ferreri)* by Blanc-Louvel (1984), a waterlily-like plant of the genus *Proteaephyllum* and a very conspicuous but little known plant, *Montsechia vidali*, first assigned to the aquatic bryophytes (Jungermanniales) by Blanc-Louvel (1991), but which may have been an angiosperm, on the basis of reproductive structures (Martín-Closas et al., 2002). During the Aptian and Albian, the fossil record for freshwater angiosperms extended worldwide and increased in diversity. In the lower Aptian of Portugal, Nymphaeales relatives have been documented both on the basis of sterile and floral fossils (Saporta, 1894; Friis et al., 2000, 2001). In the Aptian and Albian Potomac Formation (United States) possible aquatic angiosperms have

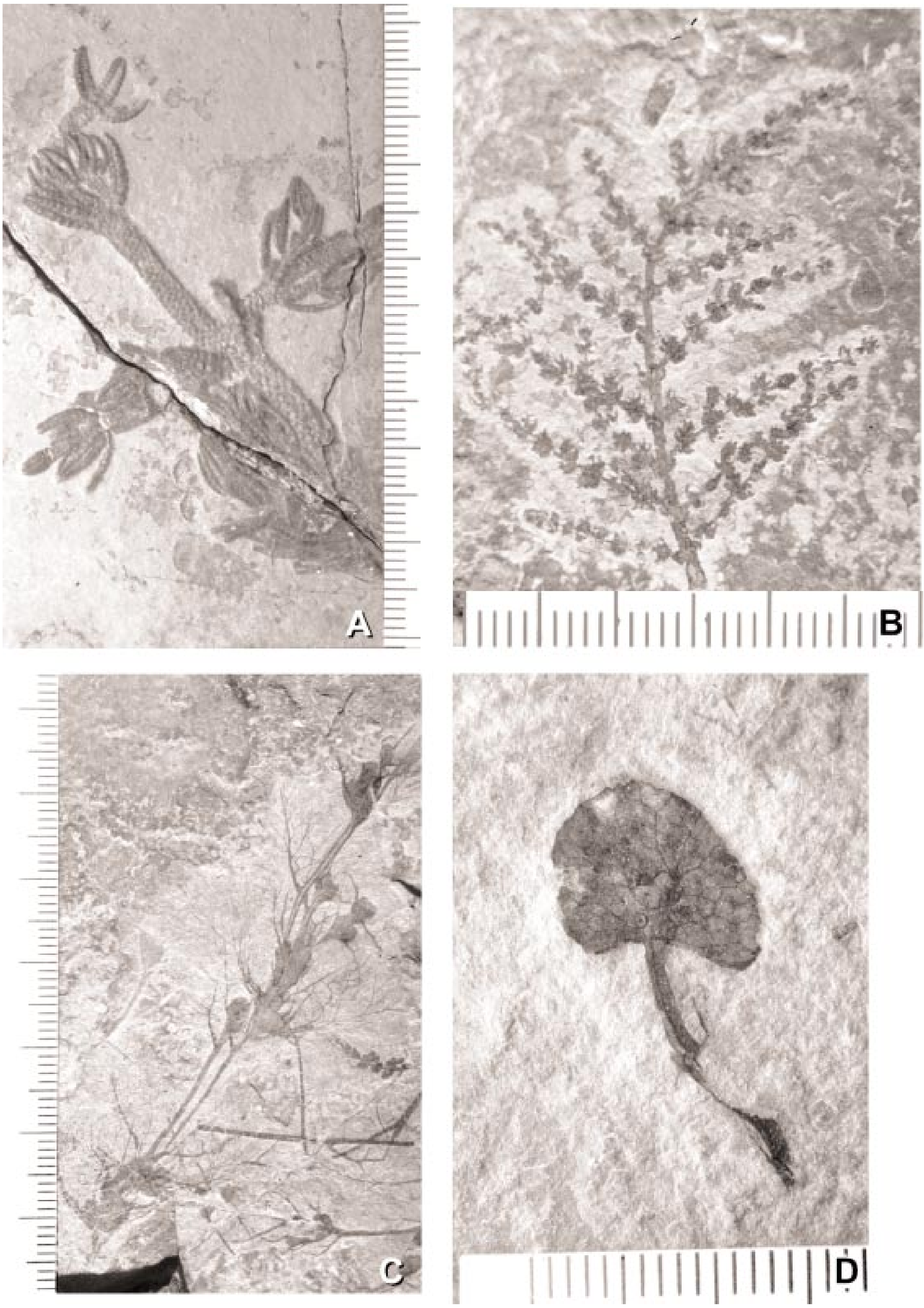

FIGURE 6 **Lower Cretaceous macrophyte assemblage from Las Hoyas and El Montsec (Barremian, Spain). A) *Clavatoraxis robustus*. B) *Montsechia vidali*. C) *Ranunculus ferreri*. D) *Proteaephyllum* sp. Scale bar in millimetres.**

been reported by Doyle and Hickey (1976) and Hickey and Doyle (1977). These taxa belong to *Plantaginopsis* sp., *Alismaphyllum victor-masoni*, *Proteaephyllum cissiforme*, *Vitiphyllum multifidum*, *Hydrocotylophyllum lusitanicum* and *Menispermites curringtonii* (Fig. 8). These fossil remains are exclusively sterile and their precise systematic affinity is unknown. Mai (1985) considered their hydrophytic habit to be uncertain. Among Gondwanian continents, freshwater angiosperms are documented from the Aptian of Victoria, Australia (Vasil'ev, 1967), the Albian of Brazil (Mohr and Friis, 2000) and the upper Aptian-lower Albian of North Africa (Barale and Ouaja, 2001). In the Aptian and Albian, a radiation of aquatic angiosperms occurred in siliciclastic and brackish environments (Retallack and Dilcher, 1986), which may have been an opportunistic strategy to avoid the selective pressure of charophytes in the permanent alkaline lakes.

Freshwater angiosperms are among the first angiosperms reported from the fossil record. This may be just a taphonomic artifact related to their habitat in environments with good preservation potential or, on the contrary, may reflect a real affinity for freshwater by the early angiosperms (Sun et al., 2002). The latter hypothesis appears to be correct and is even in agreement with some molecular phylogenies, which show typically aquatic taxa, such as *Ceratophyllum* or *Nymphaea*, at the base of the angiosperm clades (Sytsma and Baum, 1996). Aquatic angiosperms are also included in the palaeoherbs or ANITA grade (*Amborella*-Nymphaeales-Illiciales-Trimeniaceae-*Austrobaileya* clade) which are considered by some authors to be basal to angiosperms together with Ceratophyllaceae, Chloranthaceae and magnoliids (Leitch and Hanson, 2002)

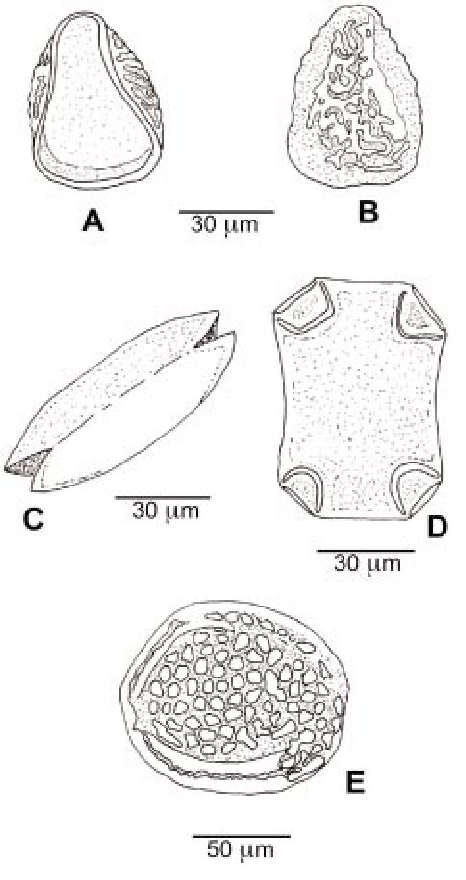

FIGURE 7| **Zygnematalean assemblage from the Albian of Ontario (Canada) (redrawn from Zippi, 1998). A and B) *Lecaniella irregularis*. C) *Ovoidites parvus*. D) *Schizocystia rugosa*. E) *Schizosporis reticulatus*.**

Aquatic ferns colonised freshwater at about the same time as angiosperms. The first recognized water ferns are from the Late Jurassic to Neocomian and bear megaspores such as *Arcellites*, *Ariadnaesporites* or *Molaspora* (Hall, 1969; Collinson, 1980, 1988, 1996; Batten and Kovach, 1993). *Ariadnaesporites* may be assigned to a separate order related to the Salviniaceae, whereas *Arcellites* and *Molaspora* are extinct genera related to the Marsileaceae (Collinson, 1996). Also related to Marsileaceae is the recently described new genus *Regnellites*, from the Upper Jurassic to Neocomian (Berriasian?) of the Kiyosue Formation, Western Japan (Yamada and Kato, 2002). This is the oldest known macrofossil of a water fern. It was a creeping plant with petioles bearing one axilar, short stalked sporocarp and one pair of leaflets like in *Regnellidium*. The venation is dichotomous-anastomosing like in extant Marsileaceae, but lacks a marginal vein. The first freshwater ferns probably lived in mesotrophic-to-eutrophic systems since they are found in deltaic-lacustrine facies or in fluvial floodplains and do not occur in association with charophytes. Other free-sporing plant remains, mainly lycophytes, were more abundant than ferns in the Lower Cretaceous freshwater deposits and record a diversification by that time (Batten and Kovach, 1993). These are isoetalean thalli and megaspores, referred to as *Isoetites* (Barale, 1999) and *Minerisporites* (Collinson, 1988), respectively, and selaginellalean megaspores, such as *Thomsonia* (Mädler, 1954). It is uncertain whether these are hydrophyte or helophyte remains. In the case of selaginellacean megaspores, the presence of long filaments or 'barbae', on the surface is thought to be an adaptation for anchoring the gametophyte in freshwater environments (Fig. 9), which is indicative of a hydrophytic habitat (Collinson, 1988; Hemsley et al., 1999).

The radiation of freshwater angiosperms and water ferns apparently determined the extinction of a number of charophyte species (Fig. 8). However, the turnover of charophyte floras between the Cenomanian and Santonian probably is also influenced by the high sea-level of this period (Martín-Closas and Serra-Kiel, 1991). In fact, the sea-level highstand of the Cenomanian-Turonian was the highest since the Devonian and produced a gap in the charophyte fossil record (but see Feist, 1981, for an exception). After this crisis, charophyte associations were dominated by the Characeae in the Campanian, whereas only three species of Clavatoraceae and a few porocharaceans survived in Eurasia until the Maastrichtian (Grambast, 1974; Grambast and Gutiérrez, 1977).

LACUSTRINE PHYTOPLANKTON DURING THE MESOZOIC

During the Triassic and Jurassic, lacustrine phytoplankton maintained their ancestral composition, with the Chlorococcales dominating assemblages, but showing increased diversity. An association from the Australian Triassic has been described by Brenner and Foster (1994), which illustrates this situation. Among the solitary forms there are species possibly related to Chlorellaceae, such as *Bartenia*, and others of problematic affinity such as *Palaeoraphidia* or *Eupoikilofusa*. Coenobial forms include *Plaesiodictyon* (Hydrodictyaceae), *Tetrastrum* and *Crucigeniella* (Scenedesmaceae), along with other genera of problematic affinity (Fig. 10). *Plaesiodictyon* is characteristic of the Triassic worldwide. It is recorded in Europe (Wille, 1970), Texas (Wood and Benson, 1991), and Australia (Brenner and Foster, 1994). The coenobium of these forms has a shape similar to the *Pediastrum* (Hydrodictyaceae) but Brenner and Foster (1994) showed that its growth pattern (ontogeny) was closer to the extant *Scenedesmus* (Scenedesmaceae).

The Chlorococcales continued to dominate the fossil assemblages of freshwater phytoplankton during the Early Cretaceous. Batten and Lister (1988), Batten (1996) and Zippi (1998) report from the British and North American Lower Cretaceous the first unequivocal representatives of *Pediastrum* (Hydrodictyaceae), *Scenedesmus* (Scenedesmaceae), *Coelastrum* (Coelastraceae) and *Tetraedron* (Chlorococcaceae) along with other chlorococcalean genera such as *Botryococcus* and *Tetrastrum* (Fig. 10). Floating filamentous algae of the genus *Oedogonium* (Oedogoniales) were reported by Zippi (1998) from the Albian of Ontario (Canada). All these associations were probably developed in mesotrophic to eutrophic habitats.

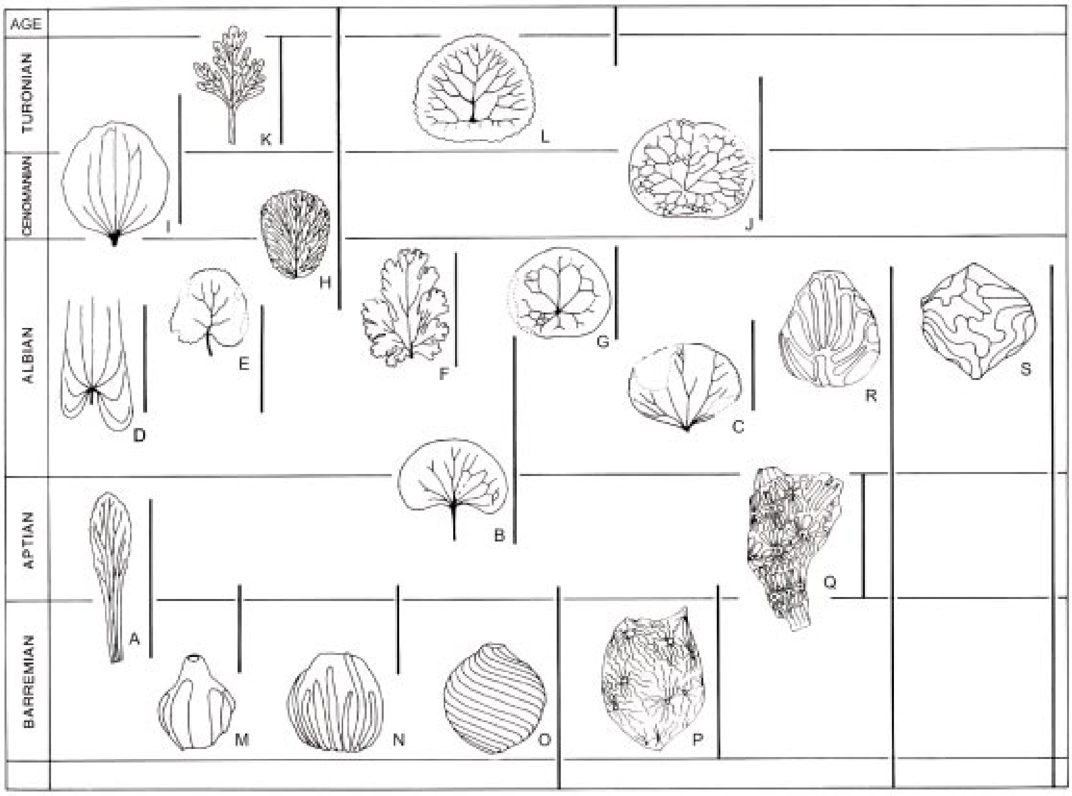

FIGURE 8| **Extinction of Clavatoraceae associated with first occurrences of early aquatic angiosperms (modified from Mai, 1985). A) *Plantaginopsis* sp. B) *Proteaephyllum reniforme*. C) *Menispermites carringtonii*. D) *Alismaphyllum victor-masoni*. E) *Hydrocotylophyllum lusitanicum*. F) *Vitiphyllum multifidum*. G) *Nelumbites tenuinervis*. H) *Quereuxia angulata*. I) *Menispermites potomacensis*. J) *Nelumbites minimus*. K) *Proteophyllum cissiforme*. L) *Nelumbites* sp. M) *Pseudoglobator paucibracteautus*. N) *Pseudoglobator fourcadei*. O) *Globator maillardii* var. *trochiliscoides*. P) *Ascidiella iberica* var. *inflata*. Q) *Ascidiella iberica* var. *iberica*. R) *Clavator harrisii*. S) *Clavator grovesii* var. *corrugatus*.**

The principal macroevolutionary event in the Lower Cretaceous fossil record for phytoplankton is the appearance of the first freshwater dinoflagellates in Barremian deltaic ponds (Batten, 1989). The first freshwater dinoflagellate cysts form low diverse assemblages of species from the ceratioid group, belonging to genera such as *Nyktercysta* and *Balmula* (Fig. 10; Zippi, 1998). We do not know the reasons for the extraordinary delay in the appearance of the first freshwater dinocysts in comparison to their long record in marine facies. If we take into account that marine dinoflagellates have been known from at least the Triassic (Traverse, 1988) but possibly even from the Palaeozoic or earlier (Butterfield and Rainbird, 1998), this delay may involve more than a hundred million years. The thin cyst wall of lacustrine dinocysts, which may be different in composition from their marine counterparts (Harding and Allen, 1995), may have prevented their preservation earlier in the fossil record. However, a late adaptation to the freshwater environment cannot be excluded. At the very least, structural and biochemical changes were required in order to adapt marine dinocysts to low levels of lake turbulence.

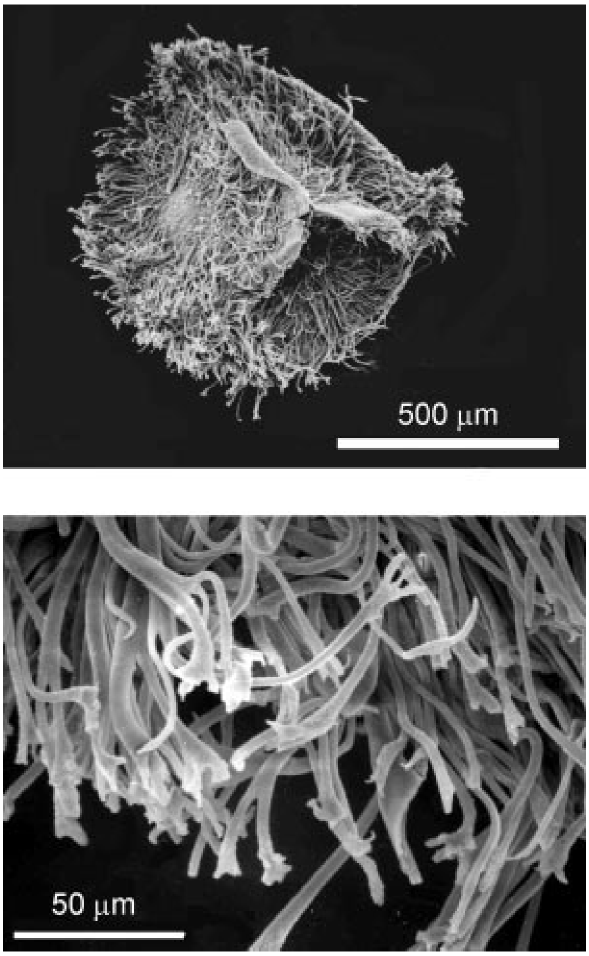

FIGURE 9 **Selaginellacean megaspores (*Thomsonia* sp.) from the Barremian of Buenache (Spain) showing large barbae both on the distal and proximal areas of the megaspore. These filaments are characteristic of freshwater free-sporing plants.**

THE UPPER CRETACEOUS AND TERTIARY MACROPHYTES

During the Late Cretaceous the radiation of freshwater angiosperms and aquatic ferns continued, while charophyte assemblages became completely dominated by the Characeae. The Cretaceous –Tertiary boundary only represented a minor change in the composition of aquatic macrophyte assemblages. The ensuing Cenozoic evolution of freshwater plants was mainly determined by global climate changes. However, the freshwater flora changed later and more slowly in comparison to the terrestrial floras, which would appear to indicate that freshwater plant evolution has been very conservative during the Cenozoic (Mai, 1985).

Angiosperms

In contrast to the Lower Cretaceous fossils, Upper Cretaceous freshwater angiosperms already bore some affinity to modern families. According to Mai (1985), well-documented taxa from the Late Cretaceous include Sparganiaceae, *Pistia* (Araceae), *Nelumbites* (Nelumbonaceae), *Nymphaeites* (Nymphaeaceae), *Palaeoaldrovanda* (Droseraceae), as well as other taxa belonging to helophytic plants. Heredeen et al. (1990) and Dilcher (1991) reports the presence of *Ceratophyllum*-like fruits, *Nelumbites*, and Alismatales-like leaves in the Cenomanian Dakota Formation of the United States. In some cases their affinity to modern families has been questioned. Thus, fossils considered to belong to the early Trapaceae, such as *Quereuxia* from the Cenomanian of the Russian Pacific Coast and North America (Vachrameev et al., 1978; Mai, 1995) and leaves of the genus *Trapago* with associated (but not attached) nuts from the Maastrichtian of Alberta (Canada) are significantly different from the extant *Trapa* (Stockey and Rothwell, 1997) and may belong to a different family (Fig. 11A). Fossil remains attributed unequivocally to the genus *Trapa* do not appear in the fossil record until the Oligocene (Wójcicki and Szafer, 2000).

Palaeogene freshwater angiosperms formed rich assemblages and are especially known for their seeds (Fig. 12). Many of the extant families of freshwater angiosperms have already been recorded in the Palaeogene (see Mai, 1985, 1995 for a summary). In some other cases fossil taxa bear characteristics intermediate between two extant families. This case is well documented in *Limnobiophyllum scutatum* from the Palaeocene of Alberta (Canada), which represents an intermediate clade between *Pistia* and *Lemna* (Fig. 11C) (Stockey et al., 1997).

From the Eocene onwards freshwater plants are of palaeoclimatic and palaeogeographic interest. In Europe, Mai (1985) and Collinson (1988) recognised representatives of extant tropical genera such as *Eichhornia* (Pontederiaceae), *Vallisneria* and *Ottelia* (Hydrocharitaceae) or *Ammania* and *Decodon* (Lythraceae). Other exclusively fossil genera such as *Palaeolythrum* (Lythraceae) and *Limnocarpus* (Potamogetonaceae) have been recorded as well. The Eocene-Oligocene climatic changes did not reduce the diversity of the freshwater communities and during the Oligocene it is possible to distinguish, for the first time, freshwater angiosperm bioprovinces by recording the geographic distribution of seeds (Mai, 1985, 1995). The European Neogene exhibits significant changes in the composition of freshwater floras. On the one hand, climatic cooling resulted in the demise of tropical species and the arrival of circumboreal species such as *Ceratophyllum demersum* or *Menyanthes trifoliata*. On the other hand, palaeogeographic changes produced the fragmentation of the huge Palaeogene bioprovinces into small Neogene provinces separated by Alpine chains and

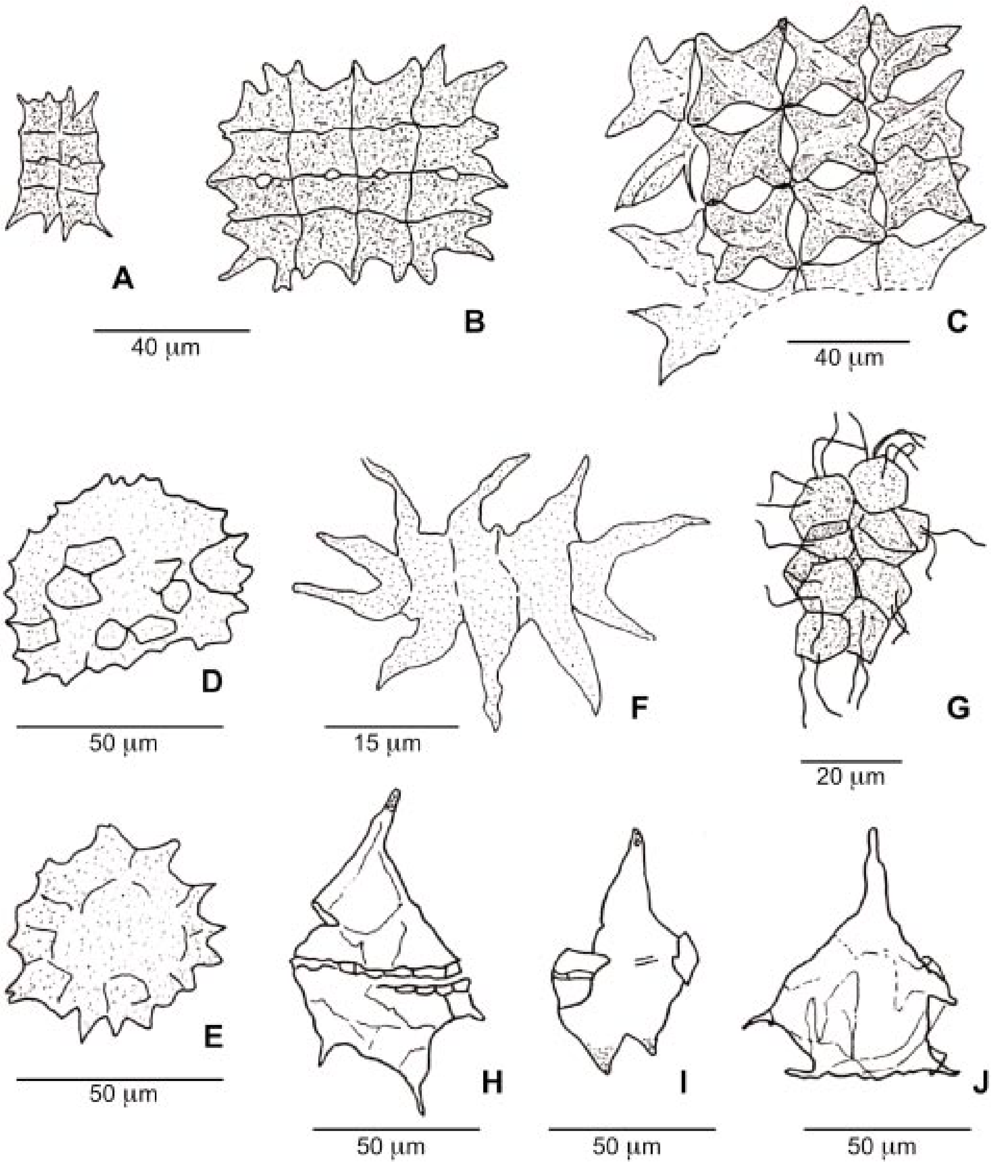

FIGURE 10 **Mesozoic planktonic algae (redrawn from Brenner and Foster, 1994; Batten, 1996 and Zippi, 1998). A and B) Two growth stages of the coenobium of *Plaesiodictyon mosellanum*, Triassic of Australia. C) *Plaesiodictyon decussatum*, Triassic of Australia. D and E) *Pediastrum boryanum*, Albian of Ontario (Canada), showing poor cell definition. F) *Scenedesmus bifidus*, Lower Cretaceous of England. G) *Tetrastrum multiflorum*, Triassic of Australia. H and I) *Nycterikista lacustra*, Albian of Ontario (Canada). J) *Balmula* sp., Albian of Ontario (Canada).**

epeiric seas (Mai, 1985, 1995). These provinces may be distinguished by vicariant species of the genera *Aldrovanda, Brasenia, Ceratophyllum, Potamogeton, Sparganium* and *Stratiotes*. Neogene species are easily compared with extant relatives, which permits their use as palaeolimnological indicators (Fig. 13). Thus the association of *Vallisneria-Ottelia* developed in warm and eutrophic systems while the assemblage of *Potamogeton–Najas* is more abundant in relatively cool and mesotrophic water. Eutrophic water rich in sulfate result in assemblages dominated by *Trapa* or *Hemitrapa* (Mai, 1995; Zetter and Ferguson, 2001).

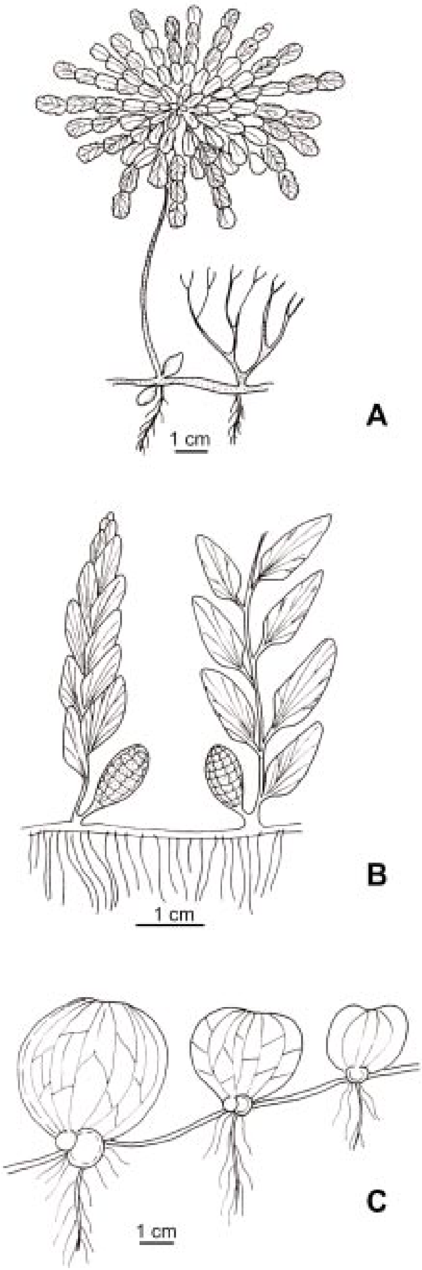

FIGURE 11 **Reconstructions of some Upper Cretaceous and Palaeocene freshwater ferns and angiosperms (modified from Rothwell and Stockey, 1994 and Stockey et al., 1997). A) *Trapago angulata* showing polymorphism in floating and submerged leaves. B) *Hydropteris pinnata* from the Maastrichtian of Alberta (Canada) showing pinnules with basal sporocarps. C) *Limnobiophyllum scutatum* from the uppermost Cretaceous and Palaeocene of North America and East Russia.**

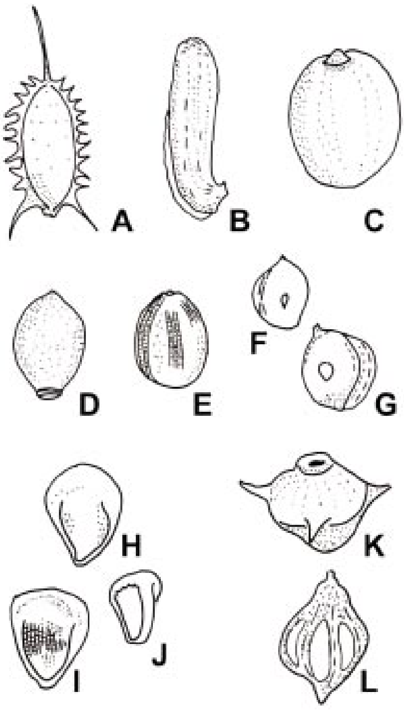

FIGURE 12 **Seeds from Tertiary freshwater plants (redrawn from Mai, 1985). A) *Ceratophyllum*. B) *Stratiotes*. C) *Brasenia*. D) *Aldrovanda*. E) *Nymphaea*. F and G) *Decodon*. H, I and J) *Potamogeton*. K) *Trapa*. L) *Sparganium*. Not to scale.**

Water ferns

During the Late Cretaceous the most primitive (plesiomorphic) representatives of Salviniaceae and Marsileaceae are recorded (Collinson, 1996). Rothwell and Stockey (1994) reported *Hydropteris* from the uppermost Cretaceous of Canada (Fig. 11B). This fossil plant shows vegetative affinity with *Marsilea* but bears megaspores (genus *Parazolla*) and microspores similar to Salviniaceae. Consequently, it was assigned to an extinct family, called Hydropteridaceae, which is considered basal to Salviniaceae and the sister group of Marsileaceae. Fossil megaspores of the genus *Azolla* and related fossil genera (*Azinia, Azollopsis* and *Glomerisporites*) have been widely documented in the Late Cretaceous (Collinson, 1996). They are characterised by a floating apparatus which assisted in the dispersion of megaspores within an aquatic system. Fossils of this age attributed to *Salvinia* include one specimen from Mexico with leaves and attached sporocarps and sterile fossil leaves, whereas the first unequivocal dispersed megaspores appear later during the earliest Palaeocene (Collinson, 1996). Marsileaceae were described by Skog and Dilcher (1992, 1994) from the Cenomanian of the Dakota Formation, Kansas. These were fossil pinnules related to the genus *Marsilea,* bearing megaspores of genus *Molaspora*.

During the Palaeogene, *Azolla* megaspores are frequent and display up to 24 floats, which are structures adapted to dispersion in aquatic environments (Collinson, 1980). An evolutionary trend towards a reduction in the number of floats has been described for this genus (Hall, 1969) and appears to be useful for biostratigraphical purposes (Fig. 14; Mai, 1985, 1995). However some authors

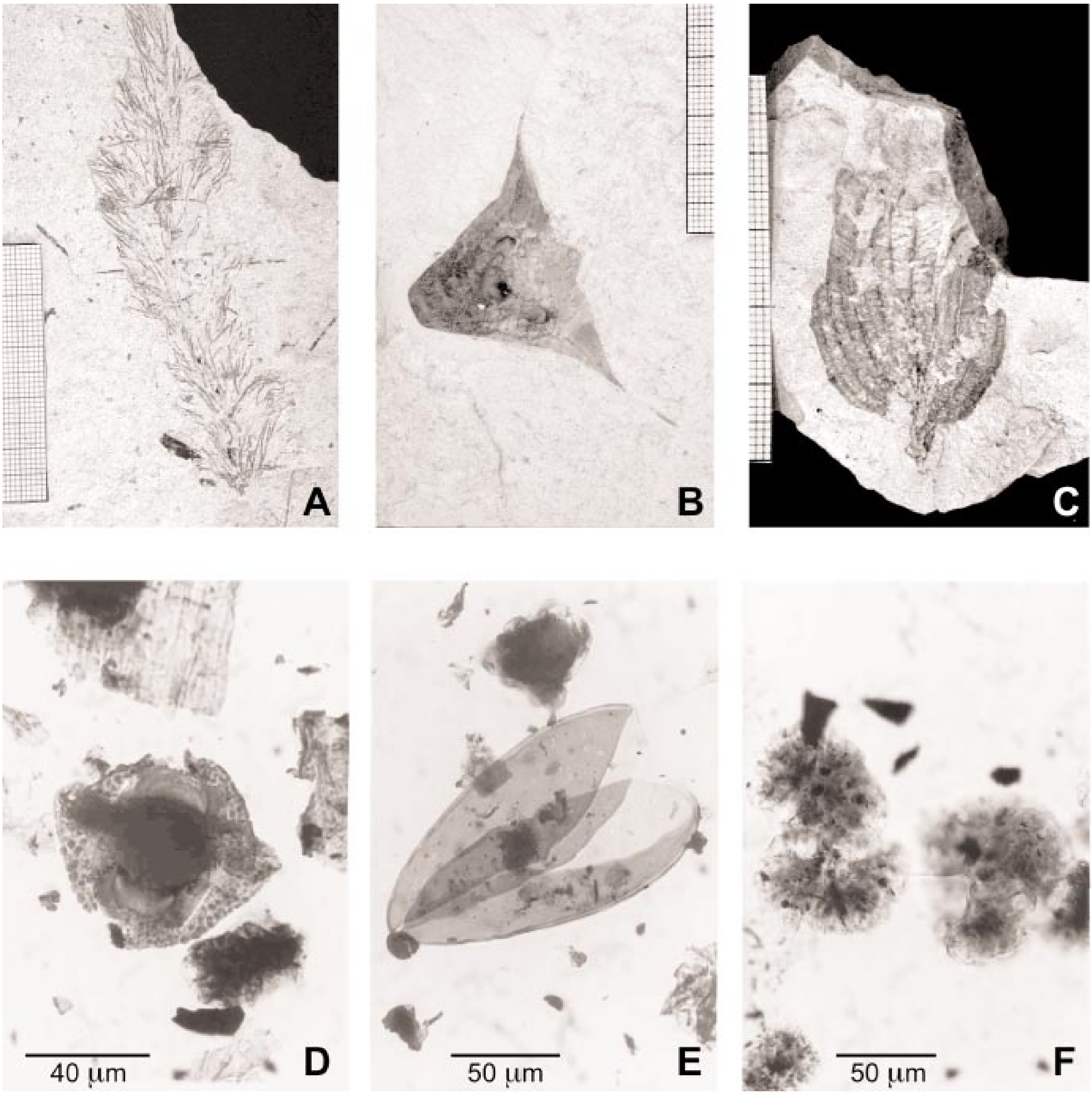

FIGURE 13 **Freshwater plant assemblage from the Upper Miocene of La Cerdanya (Pyrenees, Catalonia, Spain), which indicates a mesotrophic to eutrophic status for the palaeolake. A) Stem of *Ceratophyllum* sp. B) Nut of *Trapa ceretana*. C) Leaf of *Potamogeton orbiculare*. D) Pollen of *Trapa* (*Sporotrapoidites carlesii*). E) Zygospore of *Spirogyra* sp. F) Coenobium of *Botryococcus* sp. Scale bar in A, B and C is in millimetres.**

point out that this is not a general trend in the hydropteridaceans, which instead exhibit a large disparity in the number of floats from as early as the Late Cretaceous and later a loss of species bearing a high number of floats (Archangelsky et al., 1999). Megaspores attributed to the modern marsileacean genera *Regnellidium*, *Marsilea* and *Pilularia* have been reported, respectively, from the Eocene, Oligocene and Miocene.

Charophytes and allies

At the Cretaceous-Tertiary boundary, the Characeae underwent minor extinction, which meant a replacement within the family (Feist and Colombo, 1983; Riveline, 1986, Feist in Galbrun et al., 1993; Li, 1998). During the Eocene, the same family underwent a radiation with the development of heavily calcified and ornamented gyrogonites. Lutetian and Bartonian assemblages are especially diverse with some characean genera such as *Maedleriella* and *Harrisichara* being widely distributed. *Raskyella peckii* (Raskyellaceae) also has been recorded worldwide for these stages. Great diversity, high evolutionary rates, and widespread distribution have permitted Tertiary charophytes to be used for biostratigraphical purposes (Riveline et al., 1996). A progressive extinction of Palaeogene genera occurred during the Oligocene and in the Early Miocene. From this perspective it is significant that the extinction of the genus *Rantzieniella*, the last representative of Raskyellaceae, occurred in the Early Miocene (Fig. 5; Berger, 1986). After the Oligocene, the calcification and ornamentation of gyrogonites decreased and there was a trend towards smooth, homeomorphic gyrogonites. Thus, some Neogene and Quaternary charophyte associations are known exclusively from their organic oospores (Haas, 1994). However, the difficulty that Neogene charophytes had in calcification, which was related to global cooling and a general decrease in atmospheric pCO_2, may have also played a role in our perception of poorly diversified charophyte assemblages for this interval.

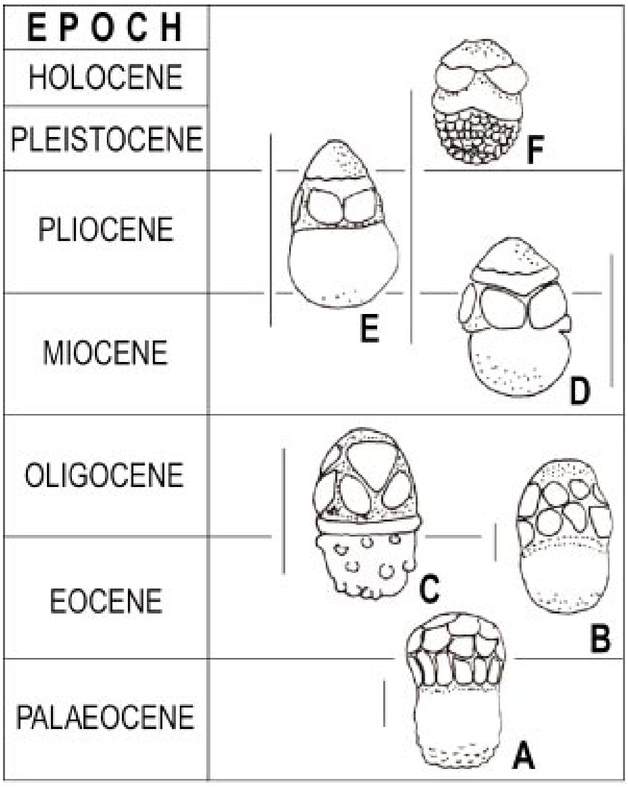

FIGURE 14 **Selected Tertiary megaspores of genus *Azolla* to illustrate the evolutionary trend towards reduction of floats (modified from Mai, 1995). A) *Azolla teschiana*. B) *A. colwellensis*. C) *A. prisca*. D) *A. aspera*. E) *A. tegeliensis*. F) *A. interglacialica*. Bars indicate stratigraphic range.**

Tertiary Zygnematales already show morphologies similar to extant genera to which they can be assigned. *Spirogyra* and *Mougeotia* were especially abundant in the Tertiary fossil record. For the Neogene and the Quaternary, the Zygnematales are useful as indicators of early colonisation of freshwater substrates (Van Geel and Grenfell, 1996).

Aquatic bryophytes assigned to *Ricciopsis* or *Riccia* (Ricciaceae) were described from the Maastrichtian of Madhya Pradesh, India, the Palaeocene of Alberta, Canada, and the Miocene of Bohemia, Czech Republic (Hoffman and Stockey, 1997). They were often found in facies attributed to shallow lakes or taxodiaceous swamps. During the Cenozoic aquatic bryophytes of this genus may become dominant in such environments (Mai, 1995).

RENEWAL OF THE LACUSTRINE PHYTOPLANKTON DURING THE TERTIARY

Freshwater algal evolution is marked during the Tertiary by the arrival and diversification of chromists in the continental realm. Two groups, the diatoms and the chrysophytes, were prominent in freshwater environments. This is in contrast to the long fossil record of chromists in the marine realm, which may have begun in the Cambrian (Allison and Hilgert, 1986) and was evident in the Triassic (Lipps, 1993). The Chlorococcales continued to be abundant in particular freshwater environments.

Chrysophytes

This group of problematic taxonomy is understood here in the sense of Van den Hoek et al. (1995) and it includes, at present, principally planktonic freshwater forms belonging to a number of orders such as

Ochromonadales and Mallomonadales. Freshwater chrysophyte cysts, especially siliceous ochromonadalean statospores that are 3-35 µm in diameter, are relatively abundant in the fossil record (Sandgren, 1991). They are known in marine sediments from the Cretaceous to the Recent (Cornell, 1972; Lipps, 1993), but only since the Eocene in freshwater facies (Tappan, 1980; Travé et al., 1996). These cysts are difficult to relate to living species and are usually classified according to a non-Linnean system (Cronberg and Sandgren, 1986; Ryback et al., 1987). The old taxonomic separation between the Archaeomonadales and Chrysostomatales used in the palaeontologic literature to distinguish marine from freshwater siliceous statospores is no longer applicable. Freshwater chrysophyceans may be found in a number of palaeoenvironments; however, they appear to be dominant in acidic and oligotrophic bogs, where siliceous cysts may accumulate massively, up to 30000 units per cm^3 (Adam and Mahood, 1981).

Diatoms

Bacillariophytes are the most important group of chromists in freshwater systems. Relatively eutrophic fresh water with a high silicic acid content is the environment preferred by diatoms for massive growth (Lipps, 1993). Their siliceous frustules have been known in marine facies since the Early Jurassic (Toarcian). During the Jurassic and most of the Cretaceous, they are only represented by centric diatoms (Order Centrales). Pennate diatoms of Order Pennales appeared in Late Cretaceous marine environments. The first freshwater diatoms were also pennate forms, recorded in the Russian Palaeocene (Lipps, 1993). The reason why diatoms did not colonise the freshwater realm until the Tertiary is unknown but may be related to the general oligotrophic character of the Mesozoic lakes. Freshwater diatoms first diversified during the Oligocene, but during the Miocene planktic centric diatoms experienced a number of radiations in continental facies, which have been related to a significant increase in the supply of silica due to active intraplate volcanism (Lipps, 1993). Specific Miocene lacustrine diatoms belonging to the centric genera *Aulacoseira* or *Melosira* may accumulate massively to form diatomites or ‘Kieselguhr’, which are rocks quarried for the production of industrial liquid filters, for the insulation of furnaces (Lee, 1989) and for a wide range of other applications, such as abrasives or explosives. Non-marine diatoms are useful in Tertiary palaeolimnology as indicators of pH, water acidity and alkalinity, salinity, depth, turbidity, water stratification and especially trophic status (Bradbury, 1988). For instance, the Centrales/Pennales ratio is indicative of trophism, since Centrales require higher levels of nutrients than Pennales to bloom (Sommer, 1988).

Chlorococcales

During the Tertiary, diatoms progressively dominated the lacustrine plankton, replacing the planktonic chlorophytes. However in particular locations, such as in Lake Messel (Eocene of Germany), Chlorococcales of the genus *Tetraedron* constituted a significant part of the lacustrine oil shales and dominated the diatom flora (Goth, 1990). Diatom domination was more widespread in Neogene than in Palaeogene lakes. In present-day lakes, when Chlorococcales co-exist with diatoms, they bloom during later stages of lacustrine succession, as nutrients become depleted and diatoms decline (Happey-Wood, 1988). This ecological subordination may date from the Neogene, when lacustrine diatoms became abundant and Chlorococcales had to compete with them for resources.

FRESHWATER PLANTS AND QUATERNARY ENVIRONMENTAL CHANGE

Two major events influenced the evolution of freshwater plants during the Quaternary: glaciations and human impact.

Effects of Quaternary glaciations on aquatic plants

A progressive loss of thermophilous species has been noted in temperate lakes of the world during successive glacial intervals (Mai, 1985). Interstadial temperature amelioration resulted in a recolonisation of lakes and ponds by plants which survived in refugia. Some of these dominated opportunistically after the disappearance of their competitors, even under atmospheric temperatures lower than the minimum required for these species in question to grow. Thus, some thermophilous macrophytes (for example Mai’s *Brasenia*- complex, 1995) survived until the last glaciation in Europe, when all terrestrial thermophilous plants vanished. This was probably attributable to the persistence of lacustrine glacial refugia that were not iced over throughout the entire year –even if surrounded by glacial open landscapes devoid of vegetation–, and shows once more the reluctance of freshwater plants to environmental change.

In contrast to higher latitudes, subtropical regions (present day subtropical deserts) were wetter than today and allowed for the development of lacustrine flora during the early Holocene. This could be the result of the installation of wide atmospheric high-pressure belts at higher latitudes and an associated southward shift by the humid westerlies in the northern hemisphere (Tallis, 1991). However, Gasse (2000) considers that the hydrology of the Sahara and the Sahel after the Last Glacial Maximum was the result of complex climatic interactions between atmosphere, ocean, vegetation cover and phreatic water. Thus, in the Sahara and the Sahel, a number of early Holocene lakes contain charophytes, such as *Lychnothamnus barbatus,* which would indicate deep and cool water, probably phreatic in origin (Petit-Maire and Riser, 1981; Kröpelin and Soulié-Märsche, 1991).

Human impact on aquatic plants

Human influence on the freshwater environment has been recorded from the very beginning of the Holocene. Long-term human habitation near a freshwater system results in three main types of impact: lake eutrophication, paludification and lake acidification.

Lake eutrophication

At the beginning of the Holocene, moderate lake eutrophication was a natural process resulting from climatic amelioration and the subsequent development of land-plant communities on lakeshores (Brugam, 1978). Dramatic human-induced eutrophication began later and was usually associated with an increase in the mineral input to lakes, which reflected forest clearing and eventually led to the introduction of agricultural species. Eastwood et al. (1999), for instance, reported the substitution of rich macrophytic vegetation by chlorococcalean algae 3300 years ago in Southwest Turkey, during the development of the Minoan culture on the Eastern Mediterranean coast. In the Fertile Crescent, ranging from the Eastern Mediterranean to the Zagros Mountains of Iran, these changes occurred even earlier, as documented by Pollinger (1986). In Central Europe they were delayed until the Middle Ages (Ahmad-Reza et al., 1986). Modelling of the human-induced eutrophication of lakes has been carried out for the English Moorlands (Harper, 1992) and describes three phases in the development of the macrophytic vegetation. The first phase, with less than 50 μgl^{-1} of total dissolved phosphorus, is characterised by a charophyte-dominated vegetation. The second phase, between 50-80 μgl^{-1} of total dissolved phosphorus, presents a diverse macrophytic angiosperm community that may become gradually impoverished if eutrophication persists, and eventually leads to the dominance of one or two macrophytic species, such as, for example, *Potamogeton pectinatus*. Finally, with more than 100 μgl^{-1} of total dissolved phosphorus, the system lacks a macrophytic benthos and is dominated by planktonic algae (diatoms or chlorococcaleans). In Holland, human management (‘biomanipulation’) of the trophic status of freshwater systems, which consists in the removal of excess nutrients, resulted in the recovery of the initial oligotrophic conditions (Van den Berg et al., 1998).

Paludification and lake acidification

Paludification may be also a natural process which results from the infilling of lakes and leads to a succession of vegetation known as a hydrosere (Rieley and Page, 1990). However some of the supposedly natural hydroseres were in fact of human origin, as shown by Jackson et al. (1988) in Miller Woods Pond, Lake Michigan (USA). This pond was supposedly a complete hydrosere, owing to the long-standing history of ponds peripheral to Lake Michigan and to its present-day vegetation, which is dominated by helophytes. However, pollen analysis of a borehole in the Miller Woods Pond showed that for 2700 years the lacustrine vegetation remained hydrophytic and surprisingly homogeneous until the construction of a railway in the 19th century, when the area was partially drained.

Natural acidification of lakes has been extensively documented for some topographically elevated lakes, such as those of the Adirondack Mountains in New York state (USA). Studies by Charles (1985) and Whitehead et al. (1986) showed that natural acidification after the last deglaciation produced pH shifts from 7.5 down to 5. The effects of acidification were recorded by changes in the composition of acid-prone algae, such as particular diatoms and especially chrysophytes (Smol et al., 1984). This process was related to increasing weathering of the surrounding siliclastic rocks associated with weather amelioration. In the same region acidification progressed in the last century due to human influence, mainly in relation to acid rain (Davis, 1987). This process continues even if the cause of the acid rain has been controlled (Majewski and Cumming, 1999).

CONCLUSIONS

The study of the evolution of freshwater plants is an emerging and largely unexplored field of palaeobotany. Available data indicate that freshwater plant evolution had patterns of its own, clearly differentiated from those observed for terrestrial or marine floras (Fig. 15). Differences included the late arrival of some of the major plant groups (dinoflagellates, diatoms, ferns), or even complete failure by other taxa to develop hydrophytic species, such as all ‘gymnosperms’. In contrast, other groups such as Chlorococcales or Charophyta were abundant in freshwater systems from the beginning of their fossil record. As a matter of fact, plant evolution in freshwater systems bypassed two of the main steps in terrestrial macroevolution: 1) the dominance of free-sporing vascular plants (‘pteridophytes’) during most of the Palaeozoic and 2) the dominance of the gymnospermous seed plants during most of the Mesozoic. Hydrophytic floral assemblages already present in the Early Palaeozoic, characterised by charophytes and chlorophytes, bypassed all the changes in terrestrial floras until the Early Cretaceous, when early angiosperms radiated and colonised freshwater systems (Fig. 15). Another very marked tendency in the history of freshwater plants was their reluctance to adapt to environmental change. This has been documented for the glacial intervals of Europe, when thermophilous aquatic plants survived even after all warm-adapted terrestrial elements had vanished.

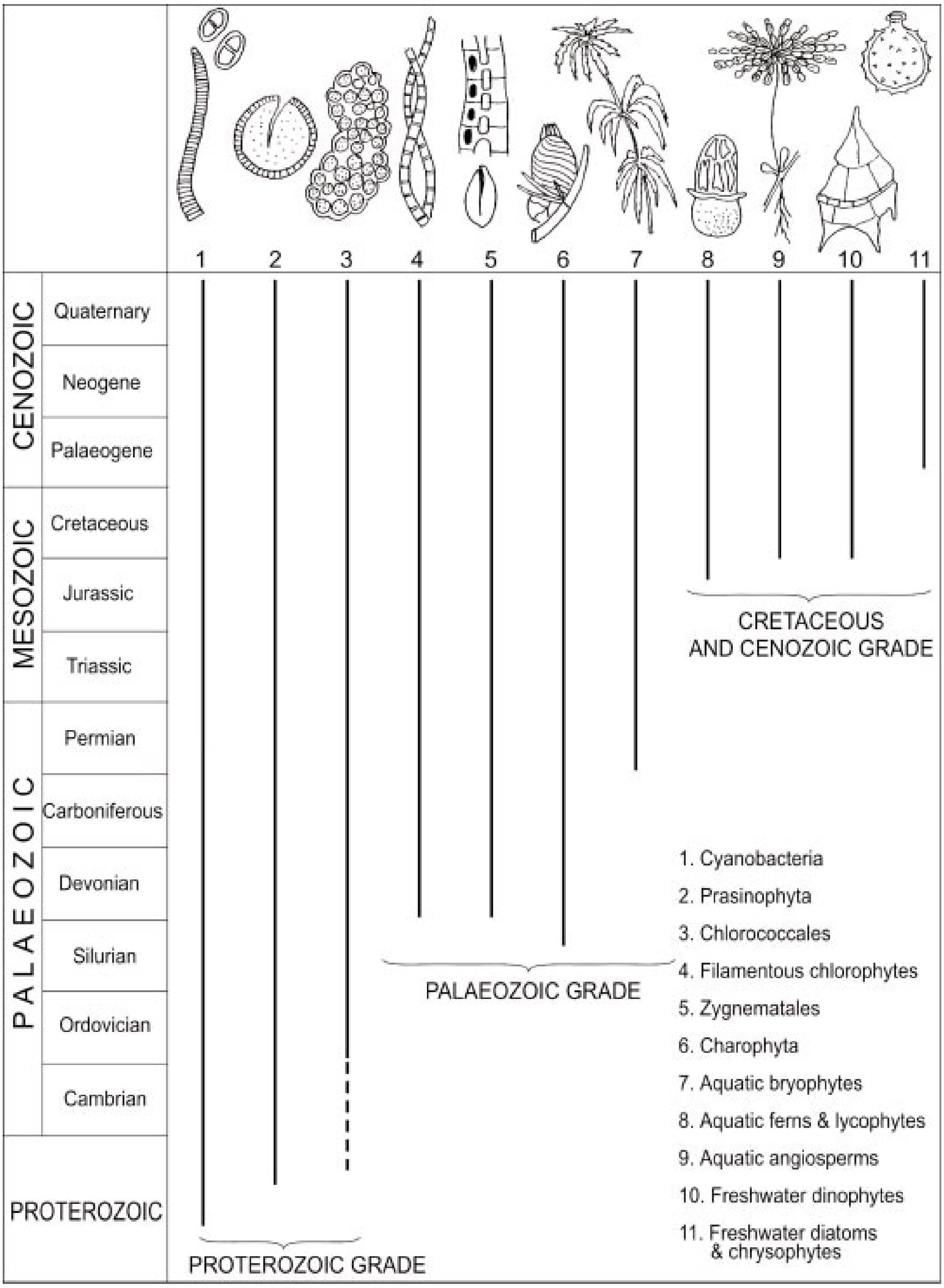

FIGURE 15 | **Chronostratigraphic ranges of major freshwater plant groups. The three main stages (“grades”) in freshwater plant evolution have been indicated. Legend of drawings: 1: *Cephalophytarion* and *Eozygion*; 2: *Tasmanites*; 3. *Botryococcus*; 4: *Oedogonium*; 5: *Spirogyra*; 6: *Chara*; 7: *Sphagnum*; 8: *Parazolla*; 9: *Trapago*; 10: *Nykterikista*; 11: *Clericia*.**

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