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Fossil charophytes and hydrophytic angiosperms as indicators of lacustrine trophic change. A case study in the Miocene of Catalonia (Spain)

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Abstract — The use of aquatic fossil macrophytes for the determination of ancient trophic situations is explored in the Late Miocene lake of La Cerdanya (Eastern Pyrenees, Catalonia, Spain). Aquatic plant remains occur in a 400 m thick lacustrine succession, Vallesian in age. Palustrine claystones and lignites grade horizontally to open lake diatomites and pass upwards to shallow lacustrine claystones and deltaic arkosic sandstone. Three different aquatic plant assemblages were identified in these facies: (1) Palustrine deposits with abundant fruits and pollen from *Trapa ceretana*, indicative of eutrophic water conditions, (2) Lacustrine diatomites with *Potamogeton orbiculare*, *Ceratophyllum schrotzburgense* macroremains, Nymphaeaceae and *Myriophyllum*. This assemblage is comparable to extant communities of mesotrophic lakes. (3) Deposits of late lacustrine infilling stages contain abundant *Lychnothamnus barbatus* subsp. *megalicarpus* gyrogonites, indicating oligotrophic and alkaline water conditions. The results show how the lake of La Cerdanya was largely eutrophic to mesotrophic in origin but shifted towards more oligotrophic and alkaline conditions in its later infilling stages. The taxonomic status of *Trapa ceretana* is briefly reviewed and an emended diagnosis is provided. Neotypes are erected for this species and for *Potamogeton orbiculare*.

Charophytes / Macrophytes / Neotypes / Limnology / Miocene / Pyrenees

Résumé — Charophytes et angiospermes hydrophytes fossiles comme indicateurs de changement trophique lacustre. Etude de cas dans le Miocène de Catalogne (Espagne). L'intérêt des macrophytes aquatiques fossiles pour la détermination des contextes trophiques anciens est étudié dans le lac Miocène de La Cerdanya (Pyrénées orientales, Catalogne, Espagne). Les plantes aquatiques se trouvent dans une succession lacustre épaisse de 400 m et datée du Vallésien. Les lignites et argiles palustres passent latéralement à des diatomites de lac ouvert. L'ensemble est couvert par des grès arkosiques et des argiles de lac peu profond. Trois assemblages de plantes aquatiques sont décrits : (1) Les dépôts palustres présentent des fruits et pollens de *Trapa ceretana* caractéristiques d'eaux eutrophiques. (2) Les diatomites lacustres contiennent *Potamogeton orbiculare*, *Ceratophyllum schrotzburgense*, Nymphaeaceae et *Myriophyllum*. Cet assemblage est comparable à celui des communautés de lacs mésotrophiques actuels. (3) Les dépôts des derniers stades de remplissage du lac sont dominés par *Lychnothamnus barbatus* subsp.

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megalicarpus, indiquant des conditions alcalines et oligotrophiques. Ces résultats montrent que le lac de La Cerdanya était eutrophique-mésotrophique à l'origine mais a changé vers une situation plus oligotrophique et alcaline. La taxonomie de *Trapa ceretana* est révisée et une nouvelle diagnose est proposée. Des néotypes sont érigés pour *T. ceretana* et *Potamogeton orbiculare*.

Charophytes / Macrophytes / néotypes / limnologie / Miocène / Pyrénées

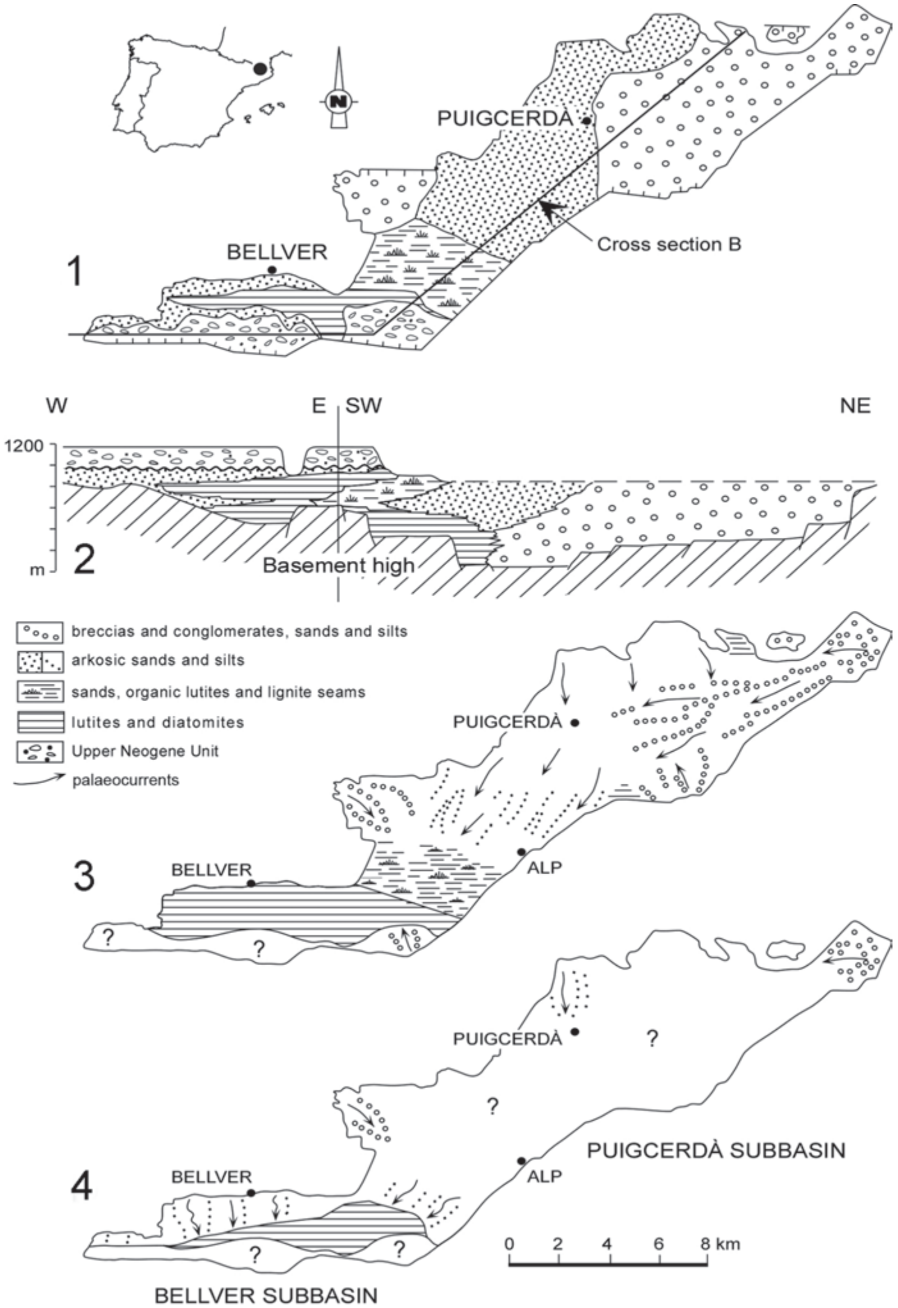
INTRODUCTION

Traditional studies of palaeolimnology have been based on the phytoplankton, mainly diatoms, whereas the use of macrophytic fossils has been comparatively infrequent (Cohen, 2003; Martín-Closas, 2003). However, this approach is being challenged by the use of living macrophytes as indicators of water quality in post-industrial societies (e.g. Simons *et al.*, 1994; Melzer, 1999), which increases the information available about aquatic macrophyte ecology. The aim of this study is to define the limnological changes that occurred in the Miocene lake of La Cerdanya, (Pyrenees, Catalonia, Spain) on the basis of fossil charophyte gyrogonites and aquatic angiosperm pollen, fruits, seeds and leaves. The working hypothesis is that horizontal (coeval) and vertical (successive in time) trophic gradients explain the changes observed in the composition of aquatic macrophyte remains in the fossil lake. This hypothesis will be contrasted by comparison with the ecology of the nearest extant relatives of fossil species.

GEOLOGICAL SETTING

The semi-graben of La Cerdanya is located in the Eastern Pyrenees (Catalonia, Spain) at an altitude of about 1100 m. The origin of this graben can be traced back to the Late Miocene strike-slip movement of the La Tet fault, which cut the Eastern Pyrenees from ENE to WSW (Cabrera *et al.*, 1988, Fig. 1). The stratigraphic record of the La Cerdanya Basin includes two depositional units separated by a major stratigraphic unconformity. The Lower Neogene Unit, with a thickness of 400-800 m, is Vallesian (Late Miocene) in age and represents a fluvio-lacustrine sedimentation (Agustí & Roca, 1987). On the south-western margin of the basin, the Lower Unit is covered by alluvial red conglomerates from the Upper Neogene Unit, which is Turolian, Latest Miocene Zone MN 13 in age (Agustí & Roca, 1987). The present study deals exclusively with lacustrine and palustrine facies of the Lower Unit.

The sedimentation of the Lower Neogene Unit was largely controlled by active synsedimentary faults located along the southern margin of the basin and by a basement high, which crosses the basin transversely and separates the Puigcerdà Subbasin in the northwest from the Bellver Subbasin in the southeast (Cabrera *et al.*, 1988). As a result, two sedimentary facies belts developed during the early deposition of the Lower Unit (Figs 2, 3): (1) In the northern subbasin (the Puigcerdà Subbasin), sedimentation was related to alluvial fans and fluvial plains that graded distally into a broad palustrine-deltaic area. In this area,



Figs 1-4. Geological and sedimentological setting of the La Cerdanya Basin (modified from Cabrera *et al.*, 1988). **1.** Geological sketch of the Neogene deposits from the La Cerdanya Basin. **2.** Cross section along the main axis of the basin. **3.** Sedimentological interpretation of the Lower Neogene Unit (Vallesian) during the maximum lacustrine extension. **4.** Sedimentological interpretation of the Lower Neogene Unit during the late lacustrine infilling stages.

sandstone beds, interbedded with organic claystone and lignite, crop out and contain the first set of aquatic macrophyte assemblages studied here. (2) In the southern subbasin (the Bellver Subbasin), the Lower Neogene Unit is formed by an extremely monotonous succession, up to 400 m thick, of laminated claystones and diatomites with phosphatic nodules, which yields an abundance of land plant and insect remains, including the second set of aquatic macrophyte fossils studied. This unit was deposited in a deep, meromictic lake (Anadón *et al.*, 1989).

The diatomitic facies are overlain by up to 30 m of arkosic sandstone intercalated with lignite and claystones, representing the late infilling stages of the lake. This formation records a major progradation event of a large fan delta, which fed into the granitic outcrops of the Puigpedrós massif, located 10 km north of the lake. As a consequence, the lake became shallower and shifted rapidly to the south, narrowing against the active fault (Fig. 4). The claystones of this late, shallow lake supplied the third set of plant macrophytes studied. The final infilling of the lake resulted in its replacement by a fluvial formation (Cabrera *et al.*, 1988).

MATERIAL AND METHODS

This study is based on fossil remains of hydrophytic macrophytes. Helophytic fossils were excluded because their identification was only possible at an approximate taxonomic level. The first set of macrophyte remains studied was obtained by systematic layer-by-layer sampling of the Sanavastre lignite opencast mine (Figs 5, 6). This mine is the only outcrop available from the ancient mining district of La Cerdanya Basin. The second set of remains studied was obtained by systematic sampling of a number of outcrops of the diatomaceous formation, near Bellver (Figs 5, 6). The third set of samples was obtained by systematic sampling of three outcrops of claystones intercalated with arkosic sandstone at Ridolaina, Olià-road and Túnel del Cadí. In these outcrops, microscopic seeds and gyrogonites required the washing and sieving of up to 3 kg of sediment per layer and subsequent picking of fossil remains under a binocular lens. Our analysis is based on the Nearest Living Relative Method to infer palaeoecological parameters by comparison between fossil and extant representatives of a particular taxon (Mosbrugger, 1999).

SYSTEMATIC PALAEONTOLOGY

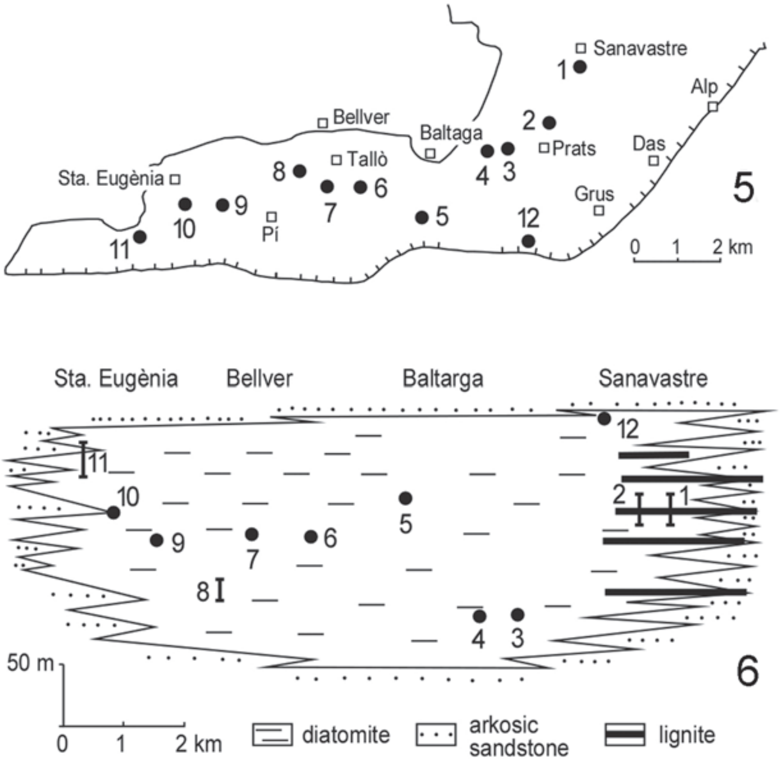
Seven different aquatic macrophyte fossil taxa from six whole-plants were found in the Upper Miocene deposits of La Cerdanya (Table 1). Some of them are well-known and will not be described in detail, while others need a more detailed characterisation.

***Lychnothamnus barbatus* subsp. *megalicarpus* Soulié-Märsche *et* Martín-Closas, 2003** (Figs 7-12)

Gyrogonites from this subspecies were originally described from the overlying Upper Neogene Unit, which is Turolian, about 2.5 million years younger

Table 1. List of aquatic macrophytes from the Vallesian of La Cerdanya.

TAXON	FOSSIL REMAIN FOUND	OUTCROP	REFERENCE FOR DESCRIPTIVE PURPOSES
Division CHAROPHYTA Class CHAROPHYCEAE Order CHARALES Family CHARACEAE Genus *Lychnothamnus* *Lychnothamnus barbatus* (Meyen, 1827) von Leonhardi, 1863. *Lychnothamnus barbatus* subsp. *megalicarpus* Soulié-Märsche & Martín-Closas, 2003.	Calcified thalli, gyrogonites and organic oospores	Ridolaina, Olià-road, Túnel del Cadí	Soulié-Märsche & Martín-Closas (2003)
Division MAGNOLIOPHYTA Class MAGNOLIOPSIDA Order NYMPHAEALES Family CERATOPHYLLACEAE Genus *Ceratophyllum* *Ceratophyllum schrotzburgense* Hantke, 1954.	Apical portions of plant (impressions)	Sanavastre, Camp d'en Mixela, Olià-village	*Nitella pre-flexilis* in Menéndez-Amor (1955) and this study
Family NYMPHAEACEAE Genus and species unknown	Disperse pollen	Sanavastre, Sansor, Camp d'en Mixela	Barrón (1996)
Order MYRTALES Family TRAPACEAE Genus *Trapa* *Trapa ceretana* Rérolle, 1885 emend. Wójcicki & Martin-Closas	Fruits (compressions and impressions)	Sanavastre, Coll de Saig, Camí de Beders, Camp d'en Mixela , Vilella,	This study
Sporotrapoidites carlesii Zetter & Ferguson, 2001	Disperse pollen	Sanavastre, Sansor	Zetter & Ferguson (2001)
Order HALORAGALES Family HALORAGACEAE Genus *Myriophyllum* *Myriophyllum* sp.	Disperse pollen	Sanavastre, Sansor, Camp d'en Mixela, Riu de Santa Maria	Barrón (1996)
Class LILIOPSIDA Order NAJADALES Family NAJADACEAE Genus *Najas* *Najas* cf. *marina* Linnaeus 1753	Seeds (compressions)	Ridolaina	This study
Family POTAMOGETONACEAE Genus *Potamogeton* *Potamogeton orbiculare* Rérolle, 1884	Isolated leaves (impressions) and disperse pollen	Sanavastre, Sansor St. Salvador, Camp d'en Mixela	Leaves: Rérolle (1885) and this study Pollen: Barrón (1996)

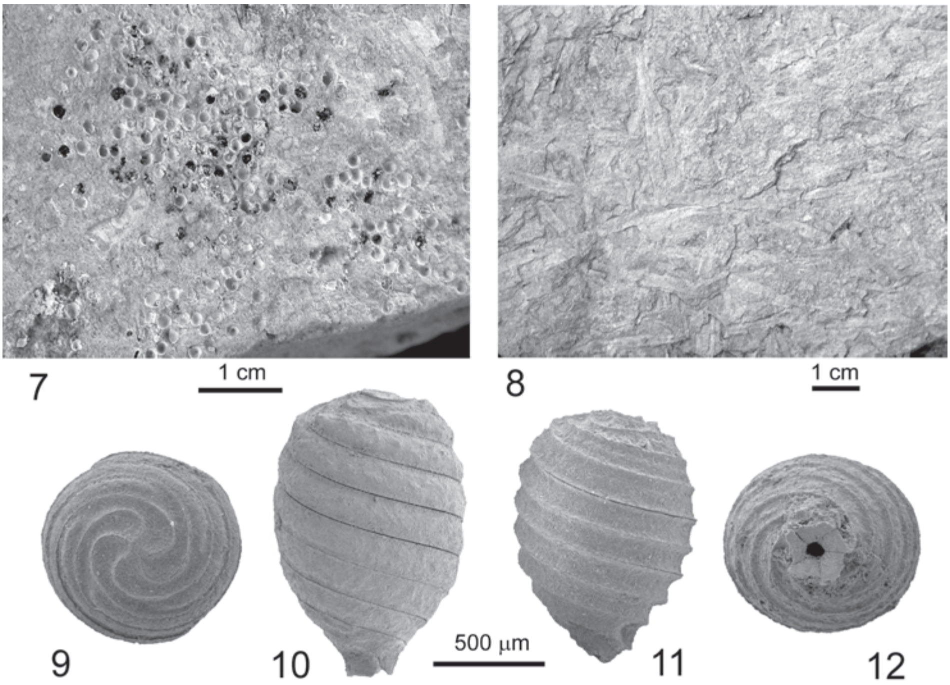


Figs 5, 6. Location of samples studied. **5.** Geographic location of outcrops sampled (dots). **6.** Approximate stratigraphic position of outcrops. 1–2. Outcrops from the palustrine lignites and claystones: 1. Sanavastre, 2. Sansor. 3–10 Outcrops from the lacustrine diatomites: 3. Sant Salvador, 4. Coll de Saig, 5. Camí de Beders, 6. Riu de Santa Maria, 7. Vilella, 8. Camp d'En Mixela, also known as Torrent de Pí, 9. Olià-village. 10–12 Outcrops from the claystones intercalated with arkosic sandstone of late lacustrine infilling stages: 10. Olià-road, 11. Ridolaina, 12. Túnel del Cadí.

than the layers, where the present material was found. Both the populations from the Lower and Upper Neogene Units show similar gyrogonite features. The equivalence between fossil and extant gyrogonites of *L. barbatus* (Meyen) Leonhardi was documented by Soulié-Märsche (1989). In contrast with the *locus typicus* of this subspecies, the layers studied in the Lower Neogene Unit have provided organic oospores and lime-encrusted ecorticate thalli together with gyrogonites.

Ceratophyllum schrotzburgense **Hantke, 1954** (Figs 13-15)

The fossils found include apical portions of the plant up to 8 cm long, showing closely arranged whorls, up to 3 cm wide, bearing 2.5 cm long, laciniate, dichotomously forking leaves with 2-3 dichotomies. The leaf margin is entire and generally toothless, although some specimens bear small teeth in the apical leaf segments (Fig. 14). No details of the cuticle structure were preserved.

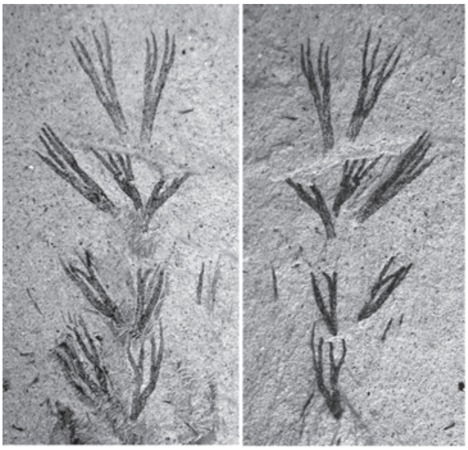


Figs 7-12. *Lychnothamnus barbatus* subsp. *megalicarpus* Soulié-Märsche *et* Martín-Closas. **7.** Bedding surface with abundant gyrogonites containing oospores (black dots). Specimen DEPGM-UB PB0028, Ridolaina. **8.** Assemblage of calcified ecorticate thalli. Specimen DEPGM-UB PB0029, Ridolaina. **9.** Apex of gyrogonite showing thinning of spiral cells. **10.** Lateral view of gyrogonite showing convex spiral cells with incipient tubercules. **11.** Lateral view of gyrogonite showing concave spiral cells. **12.** Base of gyrogonite showing funnel. (9)-(12) DEPGM (C. Martín-Closas Collection) AC-1, Túnel del Cadí.

This species was not reported from the basin in previous studies. Menéndez-Amor (1955: 29-30, pl. 14, fig. 3) confused this fossil with the charophyte genus *Nitella* and created the new species *N. pre-flexilis* to include it. The large size of the preserved stem portions, the leaves gradually narrowing towards the apex and the presence of rare marginal teeth allow us to discard this taxonomic attribution. *Ceratophyllum schrotzburgense* is similar to extant *C. demersum* and some authors have attributed its remains to this latter species (e.g. Leroy & Roiron, 1996). The abundance of non-rooting stem portions, presumably from free floating plants, the reduced number of leaf furcation, the occasional presence of teeth and the overall rigid aspect of the plant would be compatible with this species, but the fruits are necessary to confirm this affinity.

Family Nymphaeaceae

Pollen from this family was reported from organic claystones intercalated with lignites at Sanavastre and Sansor by Bessedik (1985) and Barrón (1996, 1997a, b) and from a number of localities of diatomitic claystones (Barrón, 1996, 1999). No seeds or unequivocal leaf remains have been found so far. The pollen



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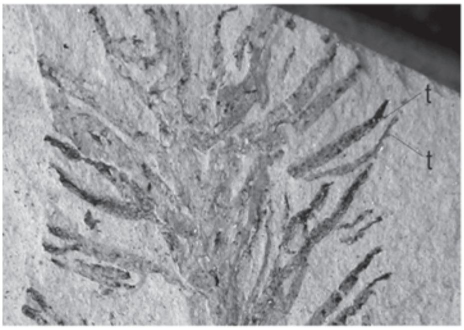

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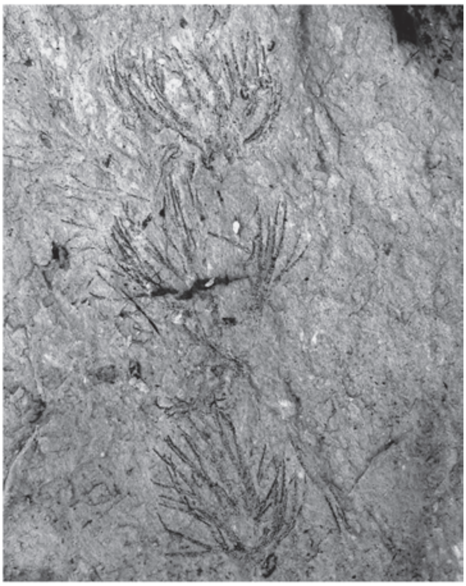

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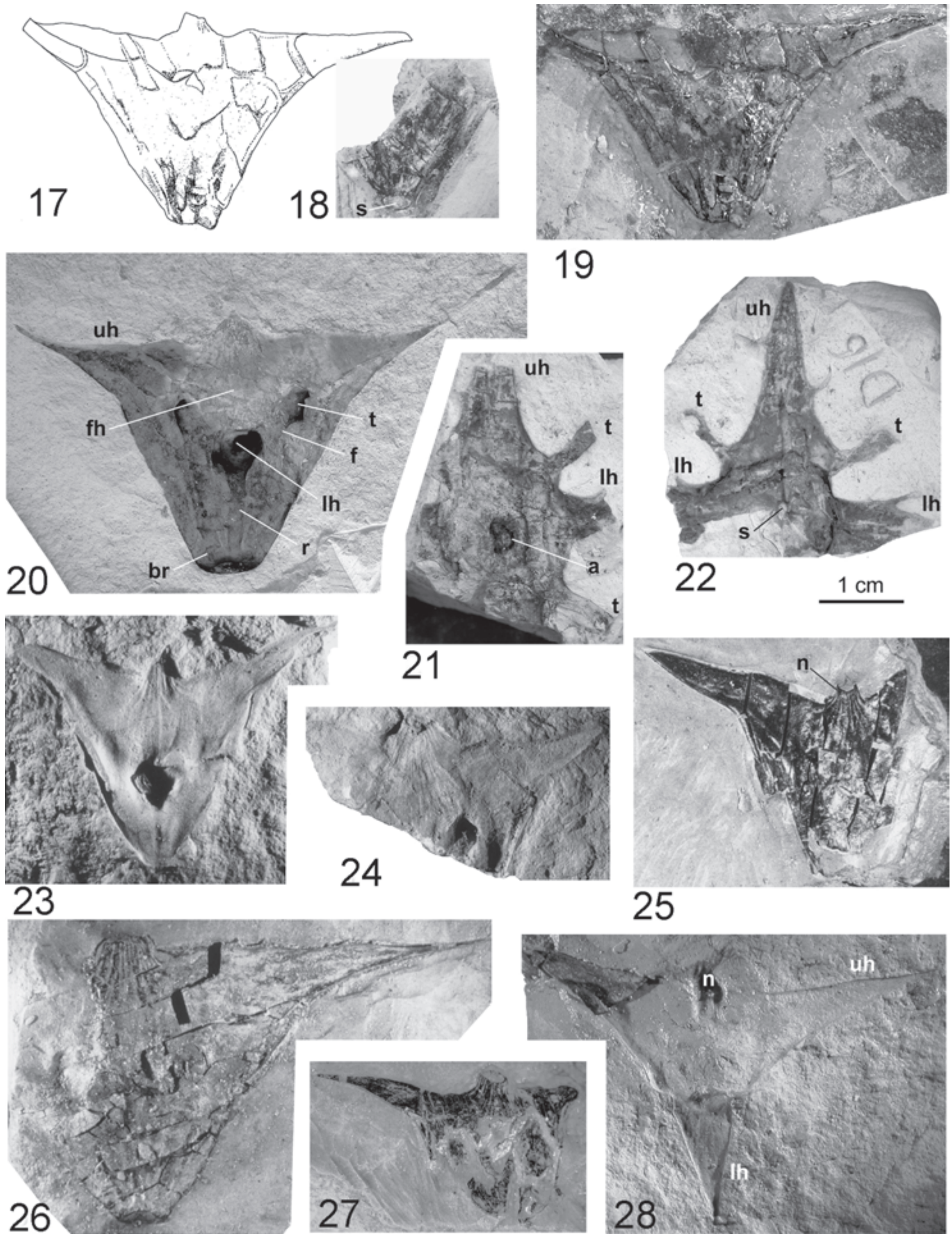
Figs 13-16. *Ceratophyllum schrotzburgense* Hantke. **13.** Part and counterpart of specimen MGSC-67775, from Sanavastre, showing whorls composed of twice forking leaves. **14.** Apical part of specimen MGSCB-67776, from Camp d'en Mixela, showing small teeth (t). **15.** Central part of mature stem showing three whorls of leaves (MGSCB-67777) from Camp d'En Mixela. **16.** Seed of *Najas* cf. *marina* L. from Ridolaina (specimen DEPGM-UB PB0030).

characteristics indicated by Barrón (1996) do not allow more precision than comparison at the family level.

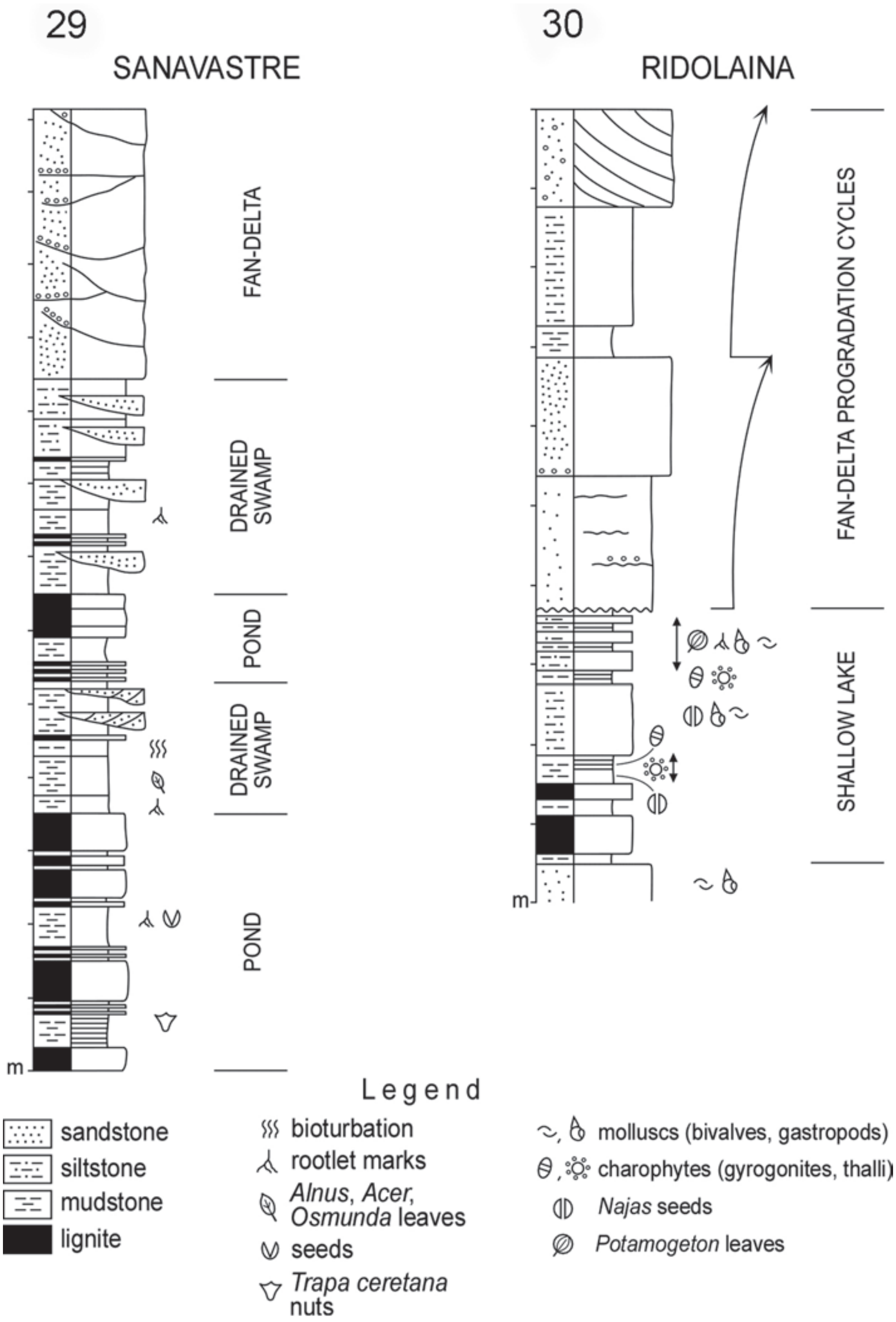
***Trapa ceretana* Rérolle, 1885 emend. Wójcicki & Martín-Closas** (Figs 17-28)

The original diagnosis of *Trapa ceretana* given by Rérolle (1885: 378) is incomplete and may lead to confusion. Thus, an emendation and new circumscription of this species is necessary. Because all syntypes provided by Rérolle (1885) in the protologue are missing, a neotype should be designated, in accordance with Art. 9.6 of ICBN (Greuter *et al.*, 2000).

Type locality and layer. Sanavastre lignite opencast mine, La Cerdanya, Eastern Pyrenees, Catalonia, Spain. Organic clays bearing *Trapa* fruits at the base of the outcrop (Fig. 29).



Figs 17-28. *Trapa ceretana* Rérolle emend. Wójcicki & Martín-Closas. **17.** Drawing of neotype, specimen MGSCB-6772. **18.** MGSCB-67763. **19.** neotype MGSCB-6772. **20.** MGSCB-67771. **21.** MGSCB-67764. **22.** MGSCB-67765. **23.** MGSCB-67766. **24.** MGSCB-67767. **25.** MGSCB-67768. **26.** MGSB-67769. **27.** MGSCB-67770. **28.** KRAM-P 248/1. Location: (18), (19), (23), (25)-(28) from Sanavastre lignite opencast mine; (20), (24) from Coll de Saig; (21), (22) from Vilella. Legend: (a) apical aperture, (br) ring, (f) frame, (fh) head, (h) head, (lh) lower horn, (n) neck, (r) rib, (s) scar, (t) tubercle, (uh) upper horn.



Figs 29, 30. Stratigraphic log and sedimentological interpretation of the sections cropping out in the Sanavastre opencast mine (**29**) and in Ridolaina (**30**). Left column of logs represents lithology, whilst bedforms are represented in the right column.

Neotype (designated here). Specimen nº 67762 from the Collection of the Museu Geològic del Seminari Conciliar de Barcelona (MGSCB) illustrated in Figs 17, 19.

Additional material. (1) Sanavastre lignite opencast mine: Museu Geologic del Seminari Conciliar de Barcelona MGSCB-67762, 67763, 67766, 67768–67770; Departament d'Estratigrafia, Paleontologia i Geociències Marines, Universitat de Barcelona (DEPGM-UB) numbers PB0010-PB0017; Palaeobotanical Collection of the W. Szafer Institute of Botany, Polish Academy of Sciences (KRAM-P 248). (2) Coll de Saig: MGSCB-67767, 67771, DEPGM-UB numbers PB0019–PB0022; Palaeontological Collection of the British Museum (Natural History) (BMNH): coll. F. M. Wonnacott 1962-63 (BMNH V.35892, V.51435, 51436 — part and counterpart). (3) Vilella, layer D: MGSCB-67764, 67765. (4) Camí de Beders: DEPGM-UB number PB-0023. (4) Camp d'en Mixela/ Torrent de Pí: MGSCB-697A (Magné collection), DEPGM-UB number PB0024-PB0027.

Emended diagnosis and description. Fruits massive, 20-32 mm high (including neck), width of fruit at the level of the upper horns 37-62 mm; fruit about 1.6-2.4 times as wide as high; fruit head pronounced, 9-14 mm high, its upper end located somewhat below the line joining slightly raised bases of the upper horns; fruit head usually gradually attenuating into a conical, truncate neck of up to 3 mm high; corona lacking; a ring of upward pointing hairs closing the apical aperture sometimes visible; surface of the fruit head and neck finely ribbed; upper horns solid, regularly triangular in outline, ascending or widely expanded (60º-85º), 15-25 mm long, at least slightly raised at base, gradually attenuated into straight elongated, thin, spine-like tips, with a smooth surface except for 10 (25) mm long, retrorsely barbed spines (harpoons); presence of mat areas (structures present in some *Trapa* species at the base and/or abaxial part of the upper horns) excluded; lower horns massive, straight, regularly triangular in outline, up to 14 mm long and up to 8 mm broad at the base, expanded, located approximately in the centre of the fruit body or somewhat above; at the base of the lower horn a small cavity is usually developed; frame of the fruit (protruding rib between upper and lower horns framing the fruit head) well pronounced, with solid straight tubercles located between the upper and lower horns; tubercles up to 7 mm long and up to 3.5 mm wide near the base, their upper part gently rounded; lower part of the fruit body truncate, regularly obtriangular in outline, bearing on one side of the surface, five protruding longitudinal ribs; fruit base with a small smooth ring, up to 2 mm high; basal scar up to 3(4) mm in diameter.

Remarks. Some relatively well-preserved fruit compressions/impressions along the plane of lower horns, obliquely along the plane of upper horns (Fig. 28) from the apex (Fig. 21) and scar (Fig. 22) clearly document the presence of stout lower horns in this species. Traces of lower horns are also well visible in most of the fruit impressions along the plane of the upper horns (Figs 19, 20, 23). According to Rérolle (1885), the fruit of *T. ceretana* bears only an upper pair of horns despite the appearance of a trace of the lower horn being properly marked on his drawing. In addition, the presence of characteristic solid tubercles located on the fruit frame between the lower and upper horns (Figs 20-22, 24) has been confirmed, constituting a new diagnostic feature of *T. ceretana*. Their presence is supported by well-marked traces of tubercle bases in most of the specimens. Traces of the tubercles are correctly marked on the drawing given by Rérolle (1885, Pl. 14, fig. 11) but are not mentioned in the protologue.

Trapa ceretana is a well-defined fossil species (cf. Kovar-Eder *et al.*, 2005). In contrast to other species, like *T. silesiaca* Goeppert emend. Wójcicki &

Zastawniak, which are widely distributed in the Upper Miocene of Europe (Wójcicki & Zastawniak, 2002), *T. ceretana* is known exclusively from the La Cerdanya Basin. Thus, the species was probably endemic to that region.

In gross morphology *T. ceretana* shows some similarity to the extant fruit morphotype known from Mantua, Italy, which is probably an extreme form of *T. natans* L. Despite obvious morphological differences it is also slightly similar to relict *T. muzzanensis* (Jäggi) Szafer, Kulczynki *et* Pawlowski from Lake Muzzano, Switzerland, in that it has solid tubercles between the lower and upper horns.

Sporotrapoidites carlesii **Zetter & Ferguson, 2001**

This taxon includes the pollen attributed to the same plant that bears the *Trapa ceretana* fruits described above. It is abundant in the basal layers of the Sanavastre opencast mine, which is the *locus typicus* of this species. Barrón (1997b) reports the same pollen from the neighbouring locality of Sansor. This pollen was not found in the diatomic claystones (Barrón, 1999). Diagnostic characters observed at the SEM by Zetter & Ferguson (2001) allow us to distinguish this species from other trapaceous pollen of the Miocene of Europe, which supports the case for the independent status of the Pyrenean species.

Myriophyllum **sp.**

Pollen from this genus was reported and described from the palustrine lignites and claystones in Sanavastre and Sansor by Barrón (1996, 1997a, b). It is possible that equivalent material from the same localities was attributed to *Haloragis* by Bessedik (1984), but he did not provide any description to support this attribution. Further records of this type of pollen were found by Barrón (1996) in diatomitic claystones. According to this author, the pollen features allow for comparison with extant *Myriophyllum spicatum* L. No seeds or leaves have been found in the La Cerdanya Basin so far.

Najas **cf.** ***marina*** **Linnaeus, 1753** (Fig. 16)

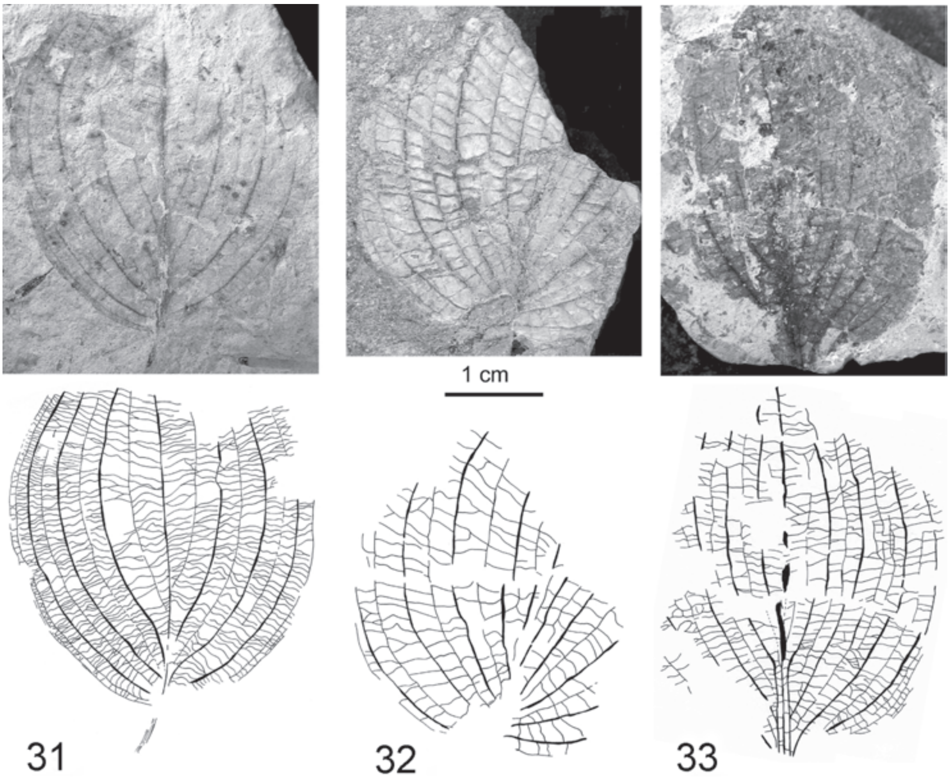
Seeds are 3.0-3.5 (4.5) mm long and 1.1–1.8 mm wide, ovate or elliptical in outline, at least slightly asymmetrical and gradually narrowing towards the subacute apex. The seed base is gently truncate or rounded. The surface of seeds lacks the characteristic areolation, which is diagnostic of the *Najas* species (e.g. Haynes, 1979). In general morphology they resemble the extant, cosmopolitan *N. marina* but some diagnostic features are not visible, due to poor preservation. In size and shape the *Najas* seeds from Ridolaina are most similar to *Najas* cf. *marina* seeds reported from the late Miocene of S Moldova and SW Ukraine (Negru, 1970) as well as to those described as *N. marina* by Dorofeev (1966) from the Pliocene of S Russia. They also remarkably resemble the extinct *N. major-pliocenica* Dorofeev ex Velichkevich from the Pliocene of SE Belarus (Velichkevich & Zastawniak, 2003) suggesting wider differentiation of the subgenus *Najas* in the European Late Neogene.

Some larger specimens (4.3–4.5 mm long and 1.7–1.8 mm wide) found in the material studied suggest that another species may be present, which is similar to extant *N. major* Allioni, distributed in the Atlantic and Mediterranean Europe and in Asia (e.g. Kolesnikova, 1965; Tzvelev, 1987). However, precise delimitation of fossil species within this morphologically plastic genus is still unsatisfactory and requires further studies.

***Potamogeton orbiculare* Rérolle, 1884a** (Figs 31-33)

Original diagnosis. "Axis of P. [*Potamogeton*] geniculate and flexible, stipules lanceolate, leaves largely rounded-ovate, margin entire, lateral veins, circa 8-10 in number at each side, convergent, with alternating thinner and thicker veins, transverse venation form a delicate, generally reticulate, network" (translated from the Latin diagnosis given by Rérolle, 1884a: 185).

Description. Leaves oval to rounded in shape, up to 9.5 cm long and 4 cm wide. Apex obtuse. Base attenuated or decurrent. Venation acrodromous, suprabasal, with a central midrib and up to five lateral veins alternating on each side. Thinner, lateral veins are intercalated between the latter in single or double rows. Secondary venation made up of small veins orthogonal to the lateral veins forming a dense network (Fig. 31). Petioles short, up to 2 cm long, rarely



Figs 31-33. *Potamogeton orbiculare* Rérolle. Photograph and camera lucida drawing of: **31.** Neotype (MGSCB-67772), compressed leaf from Sant Salvador, showing acrodromous venation with well developed central vein and alternating veins of second and third order. **32.** Lime-incrusted leaf (MGSCB-67773), from Ridolaina, showing acrodromous venation without central vein. **33.** Compressed leaf (MGSCB-67774), from Camp d'En Mixela, showing three parallel veins in the leaf base.

preserved. In some specimens without a midrib, all lateral veins appear to arise from the leaf base (Fig. 32). In other specimens, the midrib and two lateral veins, one on each side of the midrib, form a three-veined basal parallel venation (Fig. 33). Rérolle (1884a: 185–187, Pl. III, figs 7 and 7') reported and illustrated articulated stems with attached leaves and stipules. This type of preservation was not found in modern excavations.

Neotypification. Because all syntypes described by Rérolle (1885) are missing, a neotype should be designated in accordance with Art. 9.6 of ICBN (Greuter *et al.*, 2000). The neotype (Fig. 31) is selected from several specimens recently collected in Sant Salvador. The outcrop, formed by greyish siltstones, 100 m to the south of the Sant Salvador church, near Prats, probably corresponds to the type locality and stratum indicated by Rérolle (1885: 185). The neotype specimen is housed in the collection of the Museu Geològic del Seminari Conciliar, Barcelona (MGSCB nº 67772), which contains other specimens of the same species (MGSCB 21775, 31216, 40448, 67773, 67774).

Remarks. This species has been compared with a number of recent broad-leaved pondweeds, and according to Rérolle (1884a) and Barrón (1996) the most similar species would be *P. natans* L. However, as long as seeds are not found, this comparison remains hypothetical. The pollen from *Potamogeton* reported both from the palustrine claystones and lignites by Bessedik (1984) and Barrón (1996, 1997a, b) and from the lacustrine diatomitic claystones (Barrón, 1999) does not allow for further taxonomic precision.

SEDIMENTOLOGY, TAPHONOMY AND PALAEOECOLOGY

Aquatic plants in organic claystones of the palustrine belt

Fossil hydrophytes from the palustrine claystones and lignites were studied in the Sanavastre opencast mine (municipality of Das). The series cropping out in this mine shows an alternation of lignite seams up to one metre thick and intercalated organic claystones in the base, which pass upward to siltstones and massive sandstones (Fig. 29). Lignites at the base of the series contain abundant macerals of the exinite group, which are related to cuticular plant tissues (Permanyer *et al.*, 1998). The base of the lignites lacks rooting structures, whilst the roof-shales show an accumulation of elongated stems up to 1 cm thick with parallel venation, probably belonging to helophytic plants. Claystones intercalated with lignites may show lamination or alternatively are massive and show rootlet-marks. This part of the Sanavastre section is interpreted as the decantation of clays and deposition of plant debris in shallow ponds of a palustrine area. Coal macerals and taphonomic data suggest that the coal was mainly formed by accumulation of poorly lignified stems of helophytic plants. This conclusion is supported by a regular pollen content of 5–15% Poaceae and up to a 65% Sparganiaceae–Typhaceae (Barrón, 1997). Massive sandstones of the upper part of the section are attributed to fan-deltaic deposits on the basis of massive bedding and poor grain size sorting.

Hydrophytic macrophyte remains found in organic claystones intercalated with lignites are predominately fruits and pollen from *Trapa ceretana*. Water chestnut fruits occur massively (up to 150 fruits/m^2 in particular bedding surfaces) and were extremely well preserved as compressions, including the two long and delicate lateral horns. Pollen grains (*Sporotrapoidites carlesii*) reach up to 3% of total pollen in some layers (Barrón, 1997). The association of abundant fruits and pollen and the presence of rootlet traces in claystones suggest that this plant was autochthonous and dominant in the palustrine ponds. Rare macroscopic remains of *Ceratophyllum schrotzburgense* and pollen from Nymphaeaceae, *Myriophyllum* and *Potamogeton* together with abundant conjugate zygospores of the genus *Spyrogyra* occur in some beds of the section (Bessedik, 1985; Barron, 1997; Martín-Closas *et al.*, 2005). There are no taphonomic data available to ascertain whether these sporomorphs were produced by plants growing in the palustrine ponds.

Aquatic plants in lacustrine diatomites

Lacustrine diatomites and claystones are the main formation cropping out in the Bellver Subbasin. The study of fossil diatoms showed that the lake was deep and meromictic (Margalef, 1957; Haworth & Sabater 1993). Geochemical and sedimentological data indicate that water stratification resulted in low-oxygenation conditions, preservation of lacustrine varves, high organic content including sapropelic organic matter, and low sulphate concentration at the lake bottom (De las Heras *et al.*, 1989; Martín-Closas *et al.*, 2005). The thick diatomitic unit and associated claystones yielded a rich leaf and seed flora of terrestrial plants, studied by Rérolle (1884a, b, 1885), Menéndez-Amor (1955), Álvarez-Ramis & Golpe-Posse (1981), Bessedik, (1985), and Barrón (1996). This fossil flora is estimated at about 150 different species of a mixed montane forest (*Fagus, Quercus, Castanea, Betula, Carpinus, Cathaya*) with rare termophyllous elements (Lauraceae, Fabaceae, Araliaceae, Arecaceae, Taxodiaceae). The contributions of riparian communities (*Alnus, Acer, Zelkova, Ulmus*) and helophytic plants (*Typha,* Poaceae) were significant in some layers. In contrast to this diverse land flora only a few aquatic macrophytes were recorded in the diatomites. All macroscopic remains belong to leaves from pondweeds (*Potamogeton orbiculare*), twigs from hornworts (*Ceratophyllum schrotzburgense*) and rare *Trapa ceretana* fruits. Pollen corresponds to rare Nymphaeaceae, *Myriophyllum* and more abundant *Potamogeton* (Barrón, 1999).

Pondweed leaves and pollen were abundant in some outcrops located near the ancient lakeshores, such as in Sant Salvador, where in some layers they comprise up to 20% of the total macroremains. In the same beds pondweed remains occur associated with other lakeshore elements, such as stems of helophytic plants (*Typha latissima* Al. Br.) and trichopteran insect cases. Terrestrial plant remains from the same layers show taphonomic features typical of lakeshores, such as leaf tearing produced by running water transport (Martín-Closas *et al.*, 2005). In outcrops of the diatomitic unit that correspond to deeper lake facies, pondweed remains were rare. These data suggest that pondweeds were growing on the diatomitic lake margins and that isolated floating leaves occasionally reached the open lake, where they sank and were deposited post-mortem.

Hornworts occur in small quantities in many diatomitic outcrops irrespective of their palaeogeographic location. In contrast to pondweeds, hornworts are represented by well articulated stem portions rather than by isolated leaves or small fragments. This preservation state and their wide distribution in the palaeolake are interpreted as the result of dispersal of whole plants by flotation when still alive, rather than to a post-mortem lateral transport. This dispersal strategy is typical of extant *Ceratophyllum demersum*.

Rare, isolated fruits from *Trapa ceretana* that were found in the diatomitic formation are interpreted as having been laterally transported from the palustrine belt, where they occur massively.

Together with aquatic macrophytes, two planktonic algae occur in lacustrine diatomites. According to Haworth & Sabater (1993), diatomites themselves are made up of diatom assemblages dominated by the centric, planktonic *Aulacoseira ceretana*. The planktonic chlorophyte *Botryococcus* sp. is abundant in the same sediments (Martín-Closas *et al.*, 2005). These planktonic algae are interpreted as growing in the open lake.

Aquatic plants in deposits of late infilling stages

The late infilling stages of La Cerdanya Lake show an intercalation of arkosic sandstone with organic claystone and lignite. The outcrop at Ridolaina allows for detailed sedimentological and taphonomic analyses (Fig. 30).

The base is formed by lacustrine organic claystones with thin lignite intercalations. Lignites do not show rootlet marks at their base. On the basal organic layers, an alternation of beige, massive siltstone with grey, laminated, micaeous claystones occurs. The laminated rock contains a monospecific assemblage of gyrogonites and organic oospores of *Lychnothamnus barbatus* subsp. *megalicarpus*, with up to 70 gyrogonites per cm^2 of bedding surface (Fig. 7). In some beds, these remains are associated with poorly-preserved, lime-incrusted, ecorticate thalli, probably belonging to the same charophyte species (Fig. 8). Monospecific meadows of *L. barbatus* are common in Neogene to extant lakes, in contrast to Palaeogene lakes, which included a variety of charophyte species together with those of the genus *Lychnothamnus* (Martín-Closas & Ramos, 2005). In contrast to previous layers, the massive siltstone contains abundant, compressed seeds from *Najas* cf. *marina* (up to 5 seeds per dm^2 of bedding surface), rare gyrogonites and some mollusc shells (planorbids, lymnaeids and bivalves). The uppermost siltstone contains abundant remains of *Potamogeton orbiculare*, horizontal rootlet-casts, and strap-shaped leaves. The latter two remains are related to a helophytic plant. Mollusc shells (planorbids, lymnaeids) also occur in these beds.

This part of the sequence is interpreted as having been formed in a shallow lake during a short lacustrine deepening event, as evidenced by the thinning upwards stacking pattern of layers. The basal claystones and lignite indicate deposition of suspended mud and plant debris in anoxic lake bottom conditions. Siltstone layers with *Potamogeton* and *Najas* seeds were deposited relatively close to the sedimentary supply, i.e. in relatively shallower parts of the lake. In contrast, the laminated mud with *Lychnothamnus* corresponds to deposition under calm hydrodynamic conditions during still stands of deltaic progradation or in places away from the coarser sediment supply, i.e. in deeper facies.

The upper part of the outcrop at Ridolaina was formed by two coarsening and thickening sequences. Massive siltstone or fine sandstone at the base passes upwards to coarse, arkosic sandstone, which may be cross-bedded. These deposits are interpreted as corresponding to mouth bars of small deltaic lobes, with increasing tractional flow towards the top. They are devoid of fossil remains.

Lychnothamnus barbatus subsp. *megalicarpus* gyrogonites are well preserved in their original mineralogical constituents (endocalcine and ectocalcine). Even the organic oospore is preserved within some gyrogonites (Fig. 7). The gyrogonites do not show any evidence of fragmentation or erosion, which indicates that they were buried *in situ* or after gentle transport from the original growth location. The abundance of gyrogonites and their association with the corresponding thalli is generally considered an indication of autochthony. Few taphonomic data are available about *Najas* cf. *marina* seeds, but Dieffenbacher-Krall & Halteman (2000) concluded that this type of seed is rarely transported. *Potamogeton orbiculare* leaves were lime-incrusted in this outcrop (Fig. 32). This particular type of preservation, previously described by Kovar-Eder (1992) in the Miocene of Austria, allows for the recognition of turgor pressure in the fossil record. The abundance and excellent preservation of some of these rigid and extremely fragile lime-incrusted leaves suggest that this plant was growing *in situ* on the silts where the leaves appear.

The succession of assemblages observed in the central part of the Ridolaina outcrop is informative as to plant habitats by correlation with the sedimentary sequence (Fig. 30). Charophytes were growing in the deeper parts of the shallow lake, where only the suspended clay was deposited. By way of comparison, extant *Lychnothamnus barbatus*, grows in depths of up to 4 m (Karczmarz & Krause, 1979). In relatively shallower facies *Najas* sp. was growing, associated with aquatic molluscs. Last, *Potamogeton* was growing closer to the lakeshore, beside the active deltaic lobes, probably under more turbid water conditions, associated with helophytic plants. This zonation may have been determined by depth and reduction of light intensity by the suspended sediment in an active lacustrine delta.

As a conclusion of the taphonomic and palaeoecological analyses, two contrasting plant ecological contexts were found in the Vallesian lake of La Cerdanya (Fig. 34). Each of these situations is characterised by a particular downslope plant zonation: (1) the shallower facies of the main lacustrine unit (i.e. palustrine ponds with lignite and organic claystones) contain an assemblage dominated by *Trapa ceretana* and subsidiary Nymphaeaceae, *Myriophyllum* and *Potamogeton*, whereas in deeper facies (fossil remains preserved in diatomites) the hydrophytic assemblage was dominated by *Ceratophyllum schrotzburgense* and *Potamogeton orbiculare* with minor contributions of Nymphaeaceae and *Myriophyllum*. (2) In the upper part of the unit, which corresponds to the late infilling stages of the lake, shallower facies were dominated by *Potamogeton orbiculare* passing downslope to *Najas* sp. and finally to meadows of the charophyte *Lychnothamnus barbatus* subsp. *megalicarpus*. In the next section, these two ecological contexts will be compared with extant associations in terms of contrasting limnological parameters, especially water trophism.

TROPHIC STATUS AND EVOLUTION OF THE LA CERDANYA LAKE

Ponds of the palustrine area, which were dominated by one species of *Trapa*, are similar to extant *Trapetum natantis*, which develops in shallow, eutrophic ponds (Fig. 34). *Trapa natans*, for instance, requires total phosphorous concentrations that vary between 120-660 μgP^{-1}, which occur in brownish water

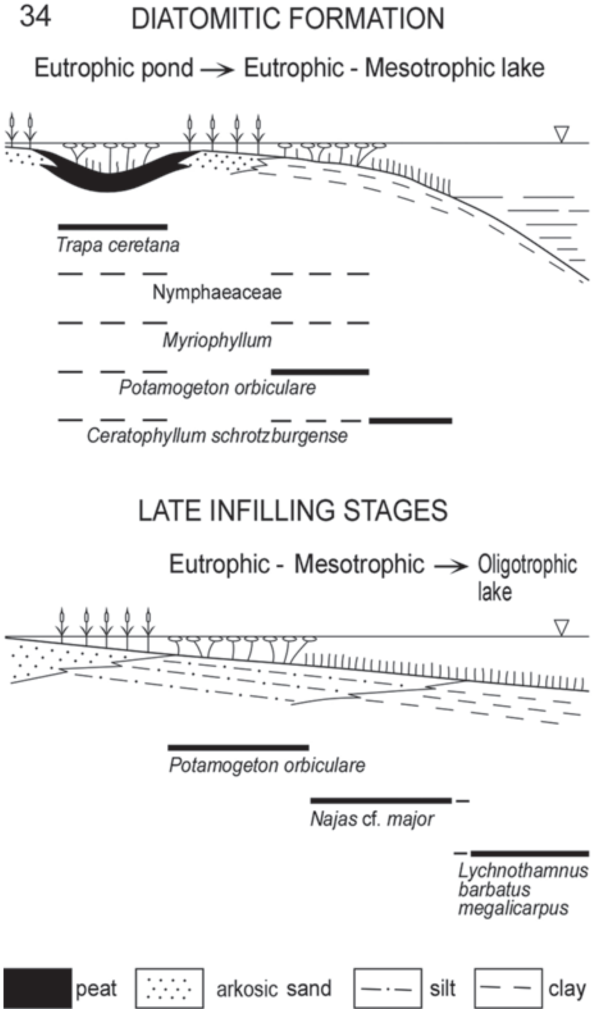


Fig. 34. The two stages in the evolution of the Miocene lake of La Cerdanya. An eutrophic-mesotrophic vegetation characterises the diatomitic stage whilst a mesotrophic-oligotrophic vegetation occurs during late infilling stages.

with a very shallow Secchi depth (Klosowski, 1995). The water chestnut is usually growing in water with a comparatively low ammonium content (120–880 $\mu gNH4^{+}.l^{-1}$), usually below 250 $\mu gNH4^{+}.l^{-1}$ (Jorga *et al.*, 1982; Klosowski, 1995). These conditions are similar for other extant species of *Trapa* and probably correspond as well to the water parameters of fossil *Trapa ceretana*. The association of *Trapa* with other hydrophytic angiosperms, such as *Nymphaea, Nuphar* and particular species of *Potamogeton* is not uncommon and has been reported, for instance, by Karhola & Tikkanen (1997) from Finland.

Trophism of the deeper hydrophytic assemblage of the main lacustrine unit is interpreted on the basis of the possible equivalence of *Ceratophyllum* *schrotzburgense* with the extant subcosmopolitan species *C. demersum*. The latter species lives in water with total dissolved phosphorous concentrations of around 100-125 µgP^{-1} (Harper, 1992). However, the main nutrient limiting the germination of this species appears to be dissolved nitrogen, with water concentrations of 760-1370 µgN.l^{-1} in Lake Wigra, Switzerland (Nichols & Keeney, 1976) but varying in other lakes between 490-2240 µgN.l^{-1} (Blüm *et al.*, 1997). Other limnological features of *C. demersum* are relatively high alkalinity of water (Blüm *et al.*, 1997) and preference for turbid environments (Dierberg *et al.*, 2002). The pondweed *Potamogeton orbiculare*, which is also abundant in the deeper facies of the main lacustrine unit, is unfortunately less helpful for the determination of limnological values, since its affinity with extant species is unknown and pondweeds do not present homogeneous limnological ranges at the genus level (Preston, 1995). Other components found in the same facies (Nymphaeaceae and *Myriophyllum*) are characteristic of lakes with a relatively high nutrient content. In conclusion, the whole assemblage found in the deeper facies of the main lacustrine unit appears to indicate mesotrophic to eutrophic water conditions (Fig. 34).

The late lacustrine infilling materials appear to correspond to a different limnological situation. The stonewort *Lychnothamnus barbatus* subsp. *megalicarpus* of the relatively deep parts of the late lake is comparable to its extant relative, *Lychnothamnus barbatus*. This species has wide trophic tolerance and has been described equally from oligotrophic environments (Krause, 1997), oligotrophic-mesotrophic lakes (Karczmarz, 1967) and from mesotrophic to eutrophic water (Karczmarz & Krause, 1979; Blaženčić & Blaženčić, 1983). However, in the eutrophic Lake Zaglebocze (Poland), *L. barbatus* developed only immature spores even when the thallus showed healthy growth (Karczmarz & Krause, 1979), whilst the production of calcified gyrogonites appears to be high only in oligotrophic lakes submitted to a strong fluctuation of the water table (Krause, 1997; Casanova *et al.*, 2003). This species also has a wide tolerance to different ranges of water turbidity and light intensity (Kaczmarz & Krause, 1979; Casanova *et al.*, 2003). In conclusion, the trophic status attributed to the deeper parts of the late lacustrine unit in La Cerdanya, where *L. barbatus* subsp. *megalicarpus* grew and produced abundant gyrogonites, is oligotrophy with wide water table fluctuations. The upslope change from stonewort vegetation to populations dominated first by *Najas* cf. *marina* and then by *Potamogeton orbiculare* may be attributed to an increase in water turbidity and in water trophism (Fig. 34). Mesotrophic to eutrophic conditions appear to be well-suited for the normal development of *Najas marina* (Simons *et al.*, 1994; Bennike *et al.*, 2001). Water turbidity was probably a significant factor in this zonation. In fact, the competition between extant *Chara* and broad-leaved *Potamogeton* species has been shown to occur mainly in terms of light intensity (van den Berg *et al.*, 1999).

DISCUSSION

The trophic evolution of the Miocene (Vallesian) lake of La Cerdanya includes two phases: (1) the main lacustrine development occurred under eutrophic to mesotrophic water conditions. In palustrine ponds (lignites and organic claystones), the hydrophytic vegetation was characterised by the dominance of the water chestnut *Trapa ceretana* together with subsidiary Nymphaeaceae, *Potamogeton* and *Myriophyllum*, whereas on the margins of the open lake *Potamogeton orbiculare* and *Ceratophyllum schrotzburgense* dominated. (2) During the late infilling stages of the lake (claystones intercalated with arkosic sandstone) the trophic conditions shifted towards oligotrophic conditions and strong fluctuation of the watertable with charophytes (*Lychnothamnus barbatus* subsp. *megalicarpus*) dominating the open lake bottom. However on the lakeshores *Najas* cf. *marina* and *Potamogeton orbiculare* suggest that a more mesotrophic to eutrophic and turbid situation occurred. These changes were also related to an increase in the water alkalinity, as shown by the strong lime incrustation of plant remains. The high calcium carbonate content of the late shallow lake could not be provided by surface water, because we know from the arkosic nature of sediment that the delta inlets fed into the granite massif of Puigpedrós, located to the North. Hence, a supplementary subsurface feeding of this lake by karstic water coming from the South (Devonian and Eocene limestones of the Cadí-Moixeró Mountains) is proposed as a hypothesis for future investigation.

The comparison of these results with the only study available on the trophic evolution of the Miocene lake of La Cerdanya (Margalef, 1957) is difficult. This study was based on fossil diatoms and contains stratigraphic and taxonomic confusion. An incorrect stratigraphic location of samples, due to a lack of knowledge of the Miocene stratigraphy of La Cerdanya in the mid 20th century, makes the vertical (time) evolution of diatom floras flawed. Thus, outcrops located by Margalef (1957) at the base of the stratigraphic series, such as Vilella, Padró and Santa Eugènia, correspond in fact to localities on the southern margin of the basin, where the uppermost sediments of the diatomites crop out. Other samples from localities near the base of the Miocene deposits, such as Coll de Saig, were incorrectly located at the top. On the other hand, taxonomic revision of the fossil diatoms of La Cerdanya by Haworth & Sabater (1993) showed that a single taxon, *Aulacoseira ceretana*, probably accommodates several of the diatom species from Margalef's study. Thus, new palaeoecological studies on fossil diatoms of La Cerdanya are needed before a comparison with the results drawn from aquatic macrophytes is possible.

CONCLUSIONS

1. Seven different aquatic macrophytes were described from the Vallesian rocks of the La Cerdanya basin (Pyrenees, Catalonia, Spain): *Lynchnothamnus barbatus* subsp. *megalicarpus*, *Ceratophyllum schrotzburgense*, Nymphaeaceae, *Trapa ceretana* (including *Sporotrapoidites carlesii*), *Myriophyllum* sp., *Najas* cf. *marina* and *Potamogeton orbiculare*. A neotype and an emended diagnosis of *Trapa ceretana*, a species probably endemic to the region, has been provided. For *Potamogeton orbiculare* a neotype has also been selected.

2. Claystones with intercalated lignites at Sanavastre were dominated by *Trapa ceretana* fruits and *Sporotrapoidites carlesii* pollen with subsidiary Nymphaeaceae, *Potamogeton* and *Myriophyllum* pollen. Taphonomic and palaeoecological data suggest that at least *Trapa ceretana* was growing in the depositional setting, which corresponded to eutrophic shallow ponds of the lake margins.

3. Diatomitic claystones in the Bellver Subbasin, which correspond to open lacustrine facies, contain isolated floating leaves of *Potamogeton orbiculare* and *Potamogeton* pollen along with *Ceratophyllum schrotzburgense* twigs. Rare *Trapa ceretana* fruits, Nymphaeaceae and *Myriophyllum* pollen occur as well in this facies. Taphonomic and palaeoecological analyses show that these remains were transported to the open lake, where they sank and were deposited on the anoxic lake bottom. These plants grew in the lakeshores and indicate eutrophic to mesotrophic water conditions.

4. Claystones intercalated with arkosic sandstone of the late infilling stages of the lake indicate that the late lacustrine phases were shallow and strongly influenced by deltaic inlets. Sedimentological and taphonomic analyses show a downslope zonation with *Potamogeton orbiculare* and *Najas* cf. *marina* growing near the turbid lakeshores, whereas *Lychnothamnus barbatus* subsp. *megalicarpus* grew in progressively deeper and more transparent water. Palaeoecology of the assemblage indicates that the lake shifted towards more alkaline conditions in these later phases and that oligotrophy was the rule in the central lake whilst nutrients increased near deltaic inlets.

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