

# **Palaeoecology of Middle Miocene charophytes from the Vallès–Penedès and Vilanova basins (Catalonia, Spain)**

Josep Sanjuan<sup>1,2\*</sup>, Damià Matamoros<sup>3</sup>, Isaac Casanovas-Vilar<sup>4</sup>, Alba Vicente<sup>1,2,5</sup>, Josep Anton Moreno-Bedmar<sup>6</sup>, Jonathan Holmes<sup>7</sup>, Carles Martín-Closas<sup>1,2</sup>

<sup>1</sup> Departament de Dinàmica de la Terra i de l'Oceà, Facultat de Ciències de la Terra, Universitat de Barcelona-UB, 08028 Barcelona, Catalonia (Spain)

<sup>2</sup> Institut de Recerca de la Biodiversitat (IRBio). Universitat de Barcelona-UB, 08028 Barcelona, Catalonia (Spain)

<sup>3</sup> Dianastrasse 10a, 9200 Gossau SG, Switzerland

<sup>4</sup> Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Edifici ICTA-ICP, c/Columnes s/n, Campus de la UAB, 08193 Cerdanyola del Vallès, Barcelona, Catalonia (Spain)

<sup>5</sup> Instituto Politécnico Nacional. Av. IPN s/N, Col. Playa Palo de Santa Rita. C.P. 23096, La Paz, BCS, Mexico

<sup>6</sup> Instituto de Geología, Universidad Nacional Autónoma de México, Ciudad Universitaria, Coyoacán, 04510, Ciudad de México, Mexico

<sup>7</sup> Environmental Change Research Centre, Department of Geography, University College London, London WC1E 6BT, United Kingdom

\*Corresponding author: josepsanjuan@ub.edu

## **Abstract**

A diverse charophyte assemblage from the Early-Middle Miocene of the Vallès–Penedès and Vilanova basins (Catalonia, NE Spain) is here described and illustrated for the first time. This flora has been recovered from three localities: els Casots (Subirats), Vilobí del Penedès, and Mas de l'Alonso–el Pi Gros (Vilanova i La Geltrú). The charophyte assemblages comprise ten different species distributed among three distinctive aquatic environments, and are approximately simultaneous to major fossil vertebrate sites of these basins. *Sphaerochara ulmensis*, *Chara* cf. *vulgaris*, *Chara molassica* var. *notata*,

*Lychnothamnus barbatus* var. *antiquus*, *Lychnothamnus* sp., *Nitellopsis* (*Tectochara*) *merianii*, and *Nitellopsis* sp. occur associated to abraded benthic foraminifera in organic-rich claystones related to palustrine and shallow freshwater coastal lakes. *Lamprothamnium papulosum* forms monospecific assemblages in gypsum-claystone alternations attributed to a coastal brackish water salina. *Chara* cf. *hispida* and *Chara* sp. are found associated with ostracods in marls and limestones related to a permanent oligohaline and alkaline lake. The discovery of this aquatic flora sheds new light on the palaeoenvironmental conditions that prevailed in the Vallès–Penedès Basin during the Langhian in the context of the Mid-Miocene Climatic Optimum and in the Vilanova Basin during the Serravalian.

**Keywords:** Charophyta; Neogene; Aragonian; palaeolimnology; paleolake; palaeoecology

## Introduction

In this work we describe three Miocene charophyte assemblages from the Vallès–Penedès and Vilanova i la Geltrú basins (Catalonia), which are near the northeastern coast of Spain.

The Vallès–Penedès Basin is one of the best known Miocene basins of eastern Iberia, mostly famous by its dense and continuous land mammal record that comprises hundreds of localities and thousands of specimens (see Casanovas-Vilar et al. 2016a and references therein). A relatively rich fossil pollen and leaf flora has also been documented from this basin (Bessedik 1985; Sanz de Siria Catalán 1993, 1994, respectively), allowing for a comparison with other Southern European floras. Despite its rich continental record, quite surprisingly fossil charophytes have yet to be reported from this area.

In the Iberian Peninsula Miocene charophytes have been described in detail from several basins, including the Ebro Basin (e.g., Feist et al. 1994), the Loranca Basin (e.g., Julià de

Agar 1991), the Teruel Basin in the Iberian Chain (e.g., Ludwig 1987) and the Portuguese part of the Tagus Basin (Soulié-Märsche 1978). Less remarkable records include the Intermediary Depression in Central Spain (Ortíz et al. 1998), La Cerdanya Basin in the Eastern Pyrenees (e.g., Soulié-Märsche and Martín-Closas 2003) and from the Balearic Islands (Martín-Closas and Ramos 2005). The state of the art about Iberian Miocene charophytes surprisingly contrasts with the lack of charophytes studies from the Vallès–Penedès Basin, and more considering that both land vertebrates and marine mollusks have been thoroughly studied since the late 19<sup>th</sup> Century.

In this work we describe the first fossil charophyte assemblages from the Vallès–Penedès Basin and use them to provide accurate palaeoenvironmental reconstructions of Miocene continental aquatic environments. These derive from three distinct localities, els Casots and Vilobí del Penedès, located in the southern sector (Penedès) of the Basin, and Mas de l’Alonso–el Pi Gros, located in the western sector of the Vilanova i La Geltrú sub-basin (Fig. 1). The els Casots and Vilobí del Penedès localities have been accurately dated by means of bio- and magnetostratigraphy to about 16 Ma (see following section), that is coinciding with the onset of the Miocene Climatic Optimum (MCO). The MCO represented a brief greenhouse interval between ~17 and 15 Ma characterized by an interruption of the Antarctic icesheet build up (Zachos et al. 2001, 2008; Foster et al. 2012) and mid-latitude temperatures as much as 3 °C (You et al. 2009) or even 7 °C (Steinthorsdottir et al. 2020) higher than present. Fossil charophytes from both localities (els Casots and Vilobí del Penedès) not only represent the first charophyte assemblages from the Vallès–Penedès, but also provide new palaeoenvironmental information on continental aquatic environments during the MCO in the western Mediterranean. The sites from the Vilanova Basin i.e. Mas de l’Alonso and el Pi Gros date back to the

Serravallian (see below), that is, they postdate the MCO and coincides with a time of gradual cooling (see Zachos et al., 2001, 2008; Steinthorsdottir et al., 2020).

The three outcrops studied, els Casots, Vilobí del Penedès and Mas de l'Alonso–el Pi Gros correspond to three different palaeoenvironments, ranging from the late Burdigalian to the Serravalian. They record a diverse charophyte flora and show the potential interest that the study of fossil charophytes has for the understanding of the Vallès–Penedès non-marine palaeoenvironments. The presence of other microfossils (foraminifers and ostracods) provide further information on the palaeoenvironments associated to the charophyte flora.

## **Geological setting**

The Vallès–Penedès Basin is part of a large system of Neogene grabens that mark the present eastern Iberian coastline, continuing further offshore (Roca and Guimerà 1992; Roca et al. 1999; Cabrera et al. 2004). These basins are part of the so-called València Trough which originated because of the opening of the western Mediterranean during the late Oligocene and Miocene (Roca et al. 1999; Roca 2001).

The Vallès–Penedès Basin is bounded by NE-SW oriented normal faults that formed after the tectonic inversion of ancient alpine compressional structures during the late Oligocene to Early Miocene (Fontboté 1954; Roca and Guimerà 1992). These limit the basin, which is 100 km long by 12-14 km wide, with the surrounding horsts of the Catalan Litoral Ranges. The Vallès-Penedès main fault is located in its northwestern margin, where the basement is attained at up to 4000 m depth (Bartrina et al. 1992; Roca et al. 1999). Basin basement, and corresponding sediment thickness, gently grades far away from the active margin towards the southeastern margin of the basin to just a few meters (Cabrera et al. 1991). The southwestern margin of the basin is only affected by minor faults which were overlapped by Early to Middle Miocene sedimentary sequences (Cabrera 1981a; Cabrera



and Calvet 1996). These were later fractured as result of minor fault reactivations (Cabrera 1981a; Cabrera and Calvet 1996). The basin is divided into two distinct sectors or sub-basins, Vallès and Penedès, by the NW-SE oriented Llobregat fault (Fontboté 1954; Cabrera and Calvet 1996). The semi-graben also shows a strong internal compartmentation due to the occurrence of small horsts and grabens, broadly parallel to the main fault (Permanyer 1990; Cabrera and Calvet 1996).

The Miocene record of the Vallès-Penedès basin has been subdivided into four main lithostratigraphic units which have been dated combining bio- and magnetostratigraphy (Agustí et al. 1985; Cabrera and Calvet 1996; Cabrera et al. 1991; Casanovas-Vilar et al. 2016b; de Gibert and Casanovas-Vilar 2011):

(1) Basal Breccia Unit. This consists of monogenic conglomerates and breccias and crops out only at a few points in the Garraf-Montnegre horst. It dates back to the Ramblian mammal age (early Burdigalian) in the Vallès sector and it is younger in the Penedès, dating back to the early Aragonian (late Burdigalian and earliest Langhian; de Gibert and Casanovas-Vilar 2011; Casanovas-Vilar et al. 2022).

(2) Lower Continental Units. Consist of alluvial fan red beds, including conglomerates, sandstones, and siltstones. Older alluvial fan deposits within this unit were sourced from the southeastern basin margin, while younger ones were also sourced from the northwestern reliefs and expanded in the lowlands covering wider areas. Shallow carbonate and evaporite lacustrine systems developed in zones of the southeastern part of the basin (Cabrera et al. 1979; Cabrera 1981a, b), such as the Subirats detritic-carbonatic system, which includes the site of els Casots (see Casanovas-Vilar et al. 2022). This unit mainly covers the Burdigalian (Early Miocene) and coincides with the rifting phase in the Vallès–Penedès Basin (Cabrera et al. 2004). The els Casots site has been dated to the earliest Langhian (15.9 Ma).

(3) The Marine and Transitional Units. These developed during the late Burdigalian to the early Serravallian and were related to a global sea-level rise that took place in the context of the MCO between 17 and 15 Ma (Miller et al. 2020). These also coincide with the beginning of the post-rift phase, when the faults that bounded the southeastern margin of the basin became inactive and were overlapped and overlapped by the sedimentary infill (Cabrera and Calvet 1996; Cabrera et al. 1991, 2004; Roca et al. 1999). At least three episodes of marine transgression and regression are recorded in the basin: late Burdigalian, Langhian and early Serravallian (Cabrera et al. 1991; Cabrera and Calvet 1996; Roca et al. 1999; de Gibert and Casanovas-Vilar 2011; Casanovas-Vilar et al. 2016b). Coastal saline lakes (sabkhas) developed just below the marine units in the area of Vilobí del Penedès, which represents a lifted block of the basin basement (Permanyer 1990). A diverse set of gypsum deposits up to 60 m thick developed in these sabkhas (Ortí and Pueyo 1976; Agustí et al. 1990). These gypsum deposits are overlain by claystones, which have yielded various charophyte assemblages, that are ultimately covered by oyster-rich greyish claystones and bioclastic limestones corresponding to the Langhian transgression. The gypsum units have been generally correlated to the late Burdigalian (Ortí and Pueyo 1976; Agustí et al. 1990; de Gibert and Casanovas-Vilar 2011), while the overlying claystones, which include small mammal fossils, indicate a younger, earliest Langhian, age (Jovells-Vaqué, 2020).

(3) Upper Continental Units. These cover the Serravallian and Tortonian and represent the late post-rift phase in the basin (Cabrera et al. 2004). They consist of alluvial fan deposits that were sourced from the reliefs in the northwestern margin while the Vallès-Penedès main fault remained active (Agustí et al. 1985, 1997; Cabrera and Calvet 1996; Roca et al. 1999; Casanovas-Vilar et al. 2016a, b; de Gibert and Casanovas-Vilar 2011). Most of the fossil vertebrate sites of the Vallès-Penedès Basin are located in the distal to marginal

facies of alluvial fan systems (Casanovas-Vilar et al. 2016 a, b), but this unit has not yielded charophyte localities thus far.

There are several smaller grabens next to the coast, south of the Garraf-Montnegre horst of the Catalan Coastal Ranges. These include the Pla de Barcelona, Baix Llobregat, Sant Andreu de la Barca, Olesa de Bonesvalls and Vilanova basins, and all formed in the context of the same extensional processes that originated the Vallès-Penedès Basin.

The Vilanova basin is about 5 km wide by 11 km long (Fig. 1). Same as the Vallès-Penedès, its northwestern margin is limited by a major normal fault affecting the pre-Miocene basement, while the southeastern margin is defined by minor normal faults that are overlapped by Quaternary sediments or are currently under sea in most of the basin (Ramos-Guerrero et al. 1996). Ramos-Guerrero et al. (1996) defined up to four lithostratigraphic units attaining a maximum thickness of about 400 m. The oldest unit (M0) is represented by the marginal complex (breccias) associated and genetically related to the main faults that bound the basin. The other three units show a vertical evolution from continental alluvial environments at the base (M1), freshwater and brackishwater lacustrine facies (M2), to marine (littoral and restricted shelf-bay) at the top (M3). The charophyte assemblages studied here (localities of Mas de l'Alonso and el Pi Gros) have been recovered from the M2 unit (Intermediate Detrital-Carbonate Unit) which is mainly composed of lacustrine marls and limestones. These lithostratigraphic units have been correlated to the Serravallian, although the lowermost alluvial conglomeratic units may correspond to Langhian (Cabrera et al. 2004).

-----Figure 1 near here-----

## Materials and methods

The fossil flora herein studied has been recovered from soft rocks (claystones and marls) from three distinct localities: els Casots, Vilobí del Penedès, in the Penedès sub-basin and Mas de l'Alonso–el Pi Gros, in the Vilanova i la Geltrú sub-basin (Fig. 1). The coordinates of these localities are: els Casots (Subirats), 41°24'56.57"N 01°48'41.78"E; Vilobí del Penedès, 41°23'15.24"N, 01°39'10.90"E; Mas de l'Alonso (Vilanova i la Geltrú), 41°14'57.28"N, 1°43'39.59"E, and el Pi Gros (Vilanova i la Geltrú), 41°14'52.57"N, 01°42'50.09"E.

In total, 12 samples of 2 kg each one were treated to extract the microfossils. Samples were disaggregated in water, hydroxide peroxide and sodium carbonate and later wet-sieved using sieves with mesh apertures of 1, 0.5, and 0.3 mm. In case of Vilobí del Penedès (sample V6/7), about 2000 kg of sediments were screen-washed during a field campaign undertaken by the Institut Català de Paleontologia (ICP) in the 1990s. The field campaign focused on the recovery of microvertebrate remains and the smallest mesh aperture used during the sieving process was 0.5 mm. In April 2021, 2 kg of sediments were taken from the same outcrop to recover a smaller microfossil fraction (200 – 500 µm), which was lost in the previous campaign because a larger mesh size was used.

Nine out of the twelve studied samples yielded microfossils including gyrogonites, ostracod carapaces, skeletons of foraminifera, and fish teeth (Fig. 2). Microfossils were sorted after inspecting the residue washed sediment under a light microscope. Selected gyrogonites were measured using the software Motic Images Plus 2.0 ML in a stereomicroscope Motic BA310 with a built-in digital camera housed in the Departament de Dinàmica de la Terra i de l'Oceà (Facultat de Ciències de la Terra), Universitat de Barcelona). The biometric parameters considered were the gyrogonite height (µm), the gyrogonite width (µm), the number of spiral turns observed in lateral view and the isopolarity index (gyrogonite height/gyrogonite width × 100). Well-preserved

microfossils were selected and photographed using the scanning electronic microscope (SEM) QUANTA 200 located at the Centres Científics i Tecnològics, Universitat de Barcelona (CCiTUB). Thin-sections, ca. 30 µm in thickness, were prepared from four limestone beds from els Casots and Mas de l'Alonso-el Pi Gros localities (Fig. 2). The microfossils illustrated herein are curated at the Institut Català de Paleontologia Miquel Crusafont (ICP) at Sabadell (Catalonia, Spain) with catalogue numbers IPS122528, IPS122530 and IPS127514 to IPS127517.

## **Results**

### ***Depositional setting and age***

#### ***Els Casots (Subirats)***

Els Casots is a key vertebrate fossil site situated in the municipality of Subirats, in the south-western margin of the Penedès sub-basin (Fig. 1). The Miocene succession at els Casots area directly overlies the basement, which consists of Mesozoic (mainly Early Cretaceous) marine carbonates (Casanovas-Vilar et al. 2022). The Miocene succession was studied by means of geological core sampling and is described in detail in Casanovas-Vilar et al. (2022). The core records a basal breccia followed by a 25 m-thick, cyclically-arranged mudstone/limestone succession that at the bottom includes thin (mm to dm thick) sub-bituminous coal deposits. The upper part of the cycle is a carbonate term that includes a variety of bioclastic- to micrite-dominated limestones that range from a few centimetres to a maximum of a couple of meters thick. The carbonate facies include bioclastic laminae alternated with very thin tufa-like carbonates (Cabrera 1979). Thin ferruginous laminae are associated to some of the bioclastic facies. Both carbonates and siliciclastic mudstones may include abundant plant fragments and freshwater gastropod shells or casts. The stratigraphic succession indicates lacustrine to palustrine environments with cyclically oscillating water level. This lacustrine/marshy succession

has yielded abundant and remarkably complete terrestrial vertebrate fossils in the excavated area of the site. The vertebrate fauna comprises up to 75 different vertebrate species including amphibians, reptiles, birds and mostly mammals. The finding of several articulated partial skeletons indicate that the site records an autochthonous to parautochthonous vertebrate assemblage (Casanovas-Vilar et al. 2022). The charophyte flora studied here was recovered from a 3.5 m thick section laterally equivalent to the vertebrate-bearing lacustrine/marshy layers (samples C1-C4 in Fig. 2). This consists of organic-rich claystones alternated with marls and a limestone bed (Figs 2 and 3A–B). Claystone beds range from 10 to 50 cm thick and show strong color variation from yellowish, gray to dark gray (Figs 2 and 3A–B). Some organic-rich claystones have yielded abundant plant remains such as leaf fragments of helophytic plants, e.g., *Typha*, well-preserved charophyte gyrogonites, abraded benthic foraminifera, plus vertebrate bones, sometimes in anatomical connection. Some claystone intervals present root marks. In some horizons abundant and irregular carbonate nodules occur (Fig. 3A). A 20 cm thick limestone bed with packstone texture includes mollusk shell fragments, 150 µm thin carbonate planar crusts (Fig. 3C–H) and oncoids (Fig. 3G), both interpreted as of cyanobacterial origin.

Claystones at els Casots are attributed to deposition in a quiet and shallow lake. The presence of nodular carbonates, mottling and root marks suggests that the original lacustrine sediments were subject to fluctuations of the water table leading eventually to subaerial exposure with a development of pedogenetic features, similar to those described elsewhere by Alonso-Zarza and Wright (2010) and references herein. Limited oxygen levels and rapid burial at the lake margins favored the preservation of mammal remains and helophytic plant leaves found in darker claystone intervals. Charophytes from these claystones grew under shallow lake conditions, while abraded remains of foraminifera

were probably whashed in from nearby marine settings. The limestone layer studied at els Casots is interpreted as deposited in a shallow pond. The occurrence of oncoids and abundant mollusk-shell fragments suggest that higher hydrodynamic conditions and perhaps trampling prevailed during its deposition. Moreover, the abundance of cyanobacterial crusts and absence of charophyte remains in the same limestone bed suggest that the water was eutrophic (Martín-Closas, 1999).

The lacustrine succession at els Casots ends rather abruptly and is followed by reddish and mottled mudstones and sandstones that record subaerial distal channelized alluvial fan facies. The continental deposits are in turn overlain by an oyster coquina and a bioclastic quartzarenite, which marks the early Langhian transgressive surface in this sector of the Vallès-Penedès Basin.

The age of els Casots is well constrained thanks to bio- and magnetostratigraphic data (see Casanovas-Vilar et al. 2022). For a long time, this site was correlated to the latest Early Miocene European mammal Neogene zone MN4, but the recent data indicate a correlation to Aragonian subzone Cb, which corresponds to the earliest MN5. Magnetostratigraphic data from the 30-m-thick els Casots succession indicate reverse polarity which, coupled with the correlation to Aragonian subzone Cb (16.15–15.94 Ma; boundaries after Van der Meulen et al. 2012), results in an estimated age of ~15.9 Ma for the site of els Casots. Therefore, els Casots would coincides with the onset of the Miocene Climatic Optimum (Zachos et al. 2001, 2008; Holbourn et al. 2015). Overall, sedimentological, palaeobotanical (scarce macroflora remains) and faunal data indicate that els Casots corresponds to an ancient freshwater lacustrine or palustrine environment that developed in a tropical-subtropical climate with rainfall seasonality (Casanovas-Vilar et al. 2022).

278 -----Figure 2 near here-----

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283 -----Figure 4 near here-----

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### 285 *Vilobí del Penedès*

286 The section studied at Vilobí del Penedès overlies unconformably the Cretaceous  
287 limestone substrate (Fig. 1). The base of the sequence is represented by non-marine  
288 breccias, detritic red beds and limestones of the Lower Continental System, which in turn  
289 are overlain by a 60 m thick evaporitic sequence mainly composed of secondary gypsum  
290 but showing primary gypsarenite at the top (Ortí and Pueyo 1976; Ortí 1990). The  
291 succession follows with a 7-m-thick interval dominated by reddish and grey claystones  
292 which have yielded the charophyte flora studied herein (samples V1-V6/7 in Fig. 2.2) and  
293 micromammal remains that had been previously attributed to the early Aragonian, MN4  
294 zone, corresponding to the latest Early Miocene (Agustí et al. 1985, 1990; Casanovas-  
295 Vilar et al. 2016a). However, the rodent fauna includes the same cricetid species recorded  
296 at els Casots (Jovells-Vaqué and Casanovas-Vilar 2021) and amongst the eomyids only  
297 the species *Ligerimys ellipticus* is present (Jovells-Vaquè 2020). Consequently, this  
298 favors a correlation with Aragonian subzone Cb and indicate an early Middle Miocene  
299 age (MN5) for the site instead (Jovells-Vaqué 2020). Therefore, it would be  
300 chronologically very close to other sites of the Vallès-Penedès Basin immediately before



the Langhian regional marine transgression, such as els Casots or Sant Mamet (Sant Cugat del Vallès).

The upper part of the Vilobí del Penedès succession, which has been studied here in more detail, can be subdivided into three intervals. The first one is 2.5 m thick and overlies a laminated gypsarenite (Fig. 4A). It is composed of an alternation of primary gypsum and greenish claystones rich in charophytes and ostracods. Up to 4 parasequences of gypsum-claystone alternations can be distinguished (Fig. 4B). A semi covered greenish claystone bed, 1.5 m thick, lays over the gypsum-claystone alternation and yielded a second, species-rich charophyte assemblage (Fig. 4C). The second interval is represented by 2.5 m of reddish claystone covered by an oyster bank that marks the base of the third interval (Fig. 4D), which is dominated by grey marls and bioclastic limestones rich in marine fossils such as echinoderms and coralline rhodophytes.

The evaporitic succession at Vilobí del Penedès has been interpreted by Bitzer (2004) and references therein as having been deposited in a restricted coastal lake or salina (sabkha).

The facies alternation of gypsum and claystone horizons with charophytes observed above the evaporitic unit, suggests that sediments settled under fluctuating salinity conditions within the coastal salina. Gypsum layers precipitated in hypersaline conditions, of up to 110‰ according to Bitzer (2004), while claystone layers were deposited in more diluted conditions, corresponding to brackish water, as shown herein.

Each gypsum-claystone parasequence can be interpreted as small transgressive-regressive cycle within the salina (Fig. 2). The absence of evaporites and the presence of a diverse charophyte assemblage in the overlying grey claystone beds indicate that diluted conditions finally prevailed, corresponding probably to a coastal freshwater lake (Fig. 4C). Finally, the oyster bank and the bioclastic limestone located atop of the section marks the onset of the Langhian regional marine transgression (Fig. 4D).

*Mas de l'Alonso–el Pi Gros (Vilanova i la Geltrú):*

The studied succession is located at the western margin of the Vilanova i la Geltrú basin (Fig. 1) and corresponds to the Intermediate Detrital-Carbonate Unit (M2) of Ramos-Guerrero et al. (1996). The outcrop at Mas de l'Alonso consists of dark grey organic-rich claystones with charophytes topped by a metric yellowish lacustrine limestone bed (Fig. 2.4). Two samples provided charophytes (samples MA1 and MA2 in Fig. 2.4). About 1 km westwards, at the el Pi Gros locality, a lateral equivalent of the same non-marine sequence crops out and shows a 3.5 m succession of yellowish limestone alternated with marls, claystones, and siltstones (Figs 2.3 and 5). Four horizons yielded charophytes, i.e., samples PG1-PG4 in Fig. 2.3. Light grey to yellowish limestone beds at the base of the el Pi Gros section range in thickness from 10 to 30 cm. They display wackstone-packstone textures and contain abundant microfossils such as ostracods and gyrogonites (Fig. 5C–H). These limestones are overlain by two parasequences of limestone beds with stromatolitic lamination covered by reddish bioturbated claystones (Figs 2.3 and 5B). The upper part of the section at el Pi Gros shows 0.5 m-thick cross-bedded calcarenite and is topped by a 0.6 m limestone bed displaying packstone textures rich in gyrogonites, charophyte thalli, dasycladaleans, ostracods, and potamidid gastropods (Fig. 2.3). Above these materials marine facies of the M3 Unit of Ramos-Guerrero et al. (1996) crop out. Despite some authors suggested that the M2 unit is Langhian in age (Batllori and Moreno 2003), the micromammals from fossil sites located within this unit indicate younger ages (Serravalian). The site of los Viñedos (Sant Pere de Ribes), yielded small vertebrate remains that are succinctly reported in Ramos-Guerrero et al. (1996). The revised faunal list includes the cricetids *Megacricetodon crusafonti* and *Hispanomys* cf. *decedens* which would indicate a correlation with the *Megacricetodon crusafonti* + *Democricetodon larteti* Concurrent Range Subzone of the Vallès-Penedès Basin (Casanovas-Vilar et al.

2016b), thus indicating an age closer to 12.4–12.5 Ma, that is late Aragonian (chronologically equivalent to the late Serravallian). A second site, Sant Pere de Ribes 1, located at the Can Mestre quarry (Ramos-Guerrero et al. 1996), has yielded additional small mammal remains. These include just a few teeth that are assigned to *Democricetodon crusafonti* (referred to as *Renzimys bilobatus* in Ramos-Guerrero et al. 1996) a species that is first recorded during the late Aragonian in the Vallès-Penedès at 11.88 Ma (Casanovas-Vilar et al. 2016b) and slightly earlier (12.4 Ma) in the Calatayud-Montalbán Basin (Aragon; Van Dam et al. 2014). Therefore, unit M3 would belong to the late Serravallian as well.

According to Ramos-Guerrero et al. (1996), the sequence integrating the M2 and M3 units grades upwards from lacustrine to brackish and finally marine environments. The lacustrine conditions of Unit M2 were inferred because of the presence of freshwater gastropods, helophytic plant stems, and charophyte remains (Batllori and Moreno 2003 and references therein). The locality of el Pi Gros is well known by the diverse and rich mollusk fauna preserved as molds, and the bioerosion ichnofossils, both found in the overlying marine M3 Unit (Batllori and Moreno 2003; Belaústegui et al. 2018). In contrast, the fossils of the M2 Unit are poorly known.

Microfossils recovered from the lower marls at Mas de l'Alonso (sample MA-1, Fig. 3 and Table 1) and el Pi Gros (sample PG-2, Fig. 3, Table 1) are well preserved and do not show signs of fragmentation or abrasion. Moreover, ostracod carapaces frequently appear with the two valves articulated suggesting that they were buried *in situ*. The absence of charophyte thalli in these marls suggest that there was a certain selection of the original plant remains, and that gyrogonites may have been laterally transported from the shallower areas of the lake where they grew. The occurrence of rare and abraded foraminifera at Mas de l'Alonso is interpreted as result of transport from a nearby marine

coastal area. Altogether these data suggest that the depositional environment of these marls corresponded to a relatively deeper part of a freshwater lake. The overlying charophyte-rich limestones were deposited in shallower freshwater environments, where lime-producing organisms thrived. Wackestone–packstone textures suggest the prevalence of sublittoral lacustrine conditions (e.g., Gierlowski-Kordesch 2010). Higher in the series, the substitution of charophyte-rich marl and limestones by stromatolite limestones and reddish claystone suggest that palaeoenvironmental conditions changed, difficulting the growth of charophytes. The occurrence of the terrigenous red claystone atop of the stromatolite, probably indicating deposition in a floodplain, suggest that the nutrient input to the lake may have increased during the development of stromatolites, hindering the development of charophytes.

-----Figure 5 near here-----

## **Systematic palaeobotany (Charophytes)**

Division Charophyta Migula, 1897

Class Charophyceae Smith, 1938

Order Charales Lindley, 1836

Family Characeae Richard ex C. Agardh, 1824

Subfamily Nitelloideae A. Braun in Migula, 1897

Genus *Sphaerochara* (Mädler, 1952) emend. Soulié-Märsche, 1989

*Sphaerochara ulmensis* (Straub, 1952) comb. nov. Grambast, 1962

Fig. 6A–I

399 1952. *Chara ulmensis* Straub, p. 470, pl. A, fig. 19.

400 1962. *Sphaerochara ulmensis* Grambast, p. 77.

401 *Material:* This species occurs at Vilobí del Penedès and Mas de l'Alonso–el Pi Gros  
402 (Table 1). Twenty-three gyrogonites were measured in sample MA1 and nine specimens  
403 in sample V6/7 (Table 2 in supplementary data).

404 *Description:* Gyrogonites from MA1 are small, 398–477  $\mu\text{m}$  high (mean 437  $\mu\text{m}$ ) and  
405 330–431  $\mu\text{m}$  wide (mean 391  $\mu\text{m}$ ), prolate spheroidal in shape, with an isopolarity index  
406 of 112 (mean). Nine to ten spiral turns are visible in lateral view. Spiral cells are 53  $\mu\text{m}$   
407 high in average and ornamented with an irregular mid-cellular crest (Fig. 6F–H). The  
408 thickness of the mid-cellular crest can vary significantly, and it can stretch the complete  
409 width of the spiral cell (Fig. 6B, C and C–E). The apex is rounded in lateral view. The  
410 apical end of each spiral cell is ornamented with a small, individualized coma-shaped  
411 nodule (Fig. 6A). The basal plate is visible from the outside and it is located within a large  
412 pentagonal basal pore of  $\sim 75$   $\mu\text{m}$  across (Fig. 6D and I). The external part of the basal  
413 plate bears a central nodule (Fig. 6D and I). Gyrogonites from the sample V6/7 at Vilobí  
414 del Penedés (Fig. 6A–D) are  $\sim 175$   $\mu\text{m}$  larger and wider than specimens extracted from  
415 Mas de l'Alonso.

416 *Remarks:* This species shows strong morphological similarities to other ornamented  
417 *Sphaerochara* gyrogonites from the European Paleogene displaying mid-cellular crests  
418 such as *S. hirmeri* (Rasky 1945) Mädlar 1952 and *S. labellata* Feist and Ringeade 1977.  
419 Gyrogonites of *S. ulmensis* are longer and show a higher ISI index than the two  
420 aforementioned taxa. Moreover, this species displays a thicker and more prominent mid-  
421 cellular crest. The subtle differences between these three coeval ornamented  
422 *Sphaerochara* species suggest that a comprehensive taxonomic revision should be  
423 conducted in future studies.

*Fossil record and distribution:* This taxon has been reported in several Paleogene and Neogene basins worldwide i.e., Europe, Middle East, and China mainly in sedimentary sequences ranging in age from the upper Rupelian (early Oligocene) to the Tortonian (Late Miocene). In Europe it is reported from several basins such as the Rhine Graben in North and Central Germany (Straub 1952; Schwarz 1997 and references therein); the Alpine Molasse in South Germany (Mädler 1955; Horn af Rantzen, 1959; Reichenbacher and Schwarz 1997); the Provence (Feist-Castel 1977), and the Languedoc, both in France (Chellai et al. 1982); the Ebro Basin in Catalonia (Feist et al. 1994); and the Cluj Basin in Romania (Baciu and Feist 1999). *S. ulmensis* has also been reported by Mädler and Staesche (1979) from several basins of Central Anatolia (Turkey), and Knobloch (1979) further recovered *S. ulmensis* in Neogene rocks from Iraq. In China, *S. ulmensis* is found in Oligocene deposits from the Bohai coastal region (Xinlun 1978) as well as in several Chinese provinces, such as Sichuan (Huang et al. 1988), Yunnan (Liu 1989), Xinjiang (Lu and Luo 1990) and Qinghai (Tang and Di 1991).

*Palaeoecology:* *S. ulmensis* is found in limestones attributed to well-developed lacustrine systems, e.g., the Trévaresse limestone Formation in Aix-en-Provence, France (Feist-Castel 1977). Based on the associated microfossils, Reichenbacher and Schwarz (1997) concluded that *S. ulmensis* was a halophobous taxon, adapted exclusively to freshwater habitats.

Subfamily Charoideae A. Braun in Migula 1897

Genus *Chara* Linnæus, 1753

*Chara* cf. *vulgaris* Linnæus, 1753

Fig. 6 J–N

1753. *Chara vulgaris* Linnæus, p. 1156

448 1989. *Chara vulgaris* var. *vulgaris* Soulié-Märsche, p. 97, pl. 22

449 *Material:* This taxon dominates the flora in the sample C4 from els Casots (Table 1). Fifty  
450 gyrogonites were measured (Table 2 in supplementary data).

451 *Description:* Gyrogonites are of medium size, 378–584  $\mu\text{m}$  high (mean 466  $\mu\text{m}$ ) and 256–  
452 430  $\mu\text{m}$  wide (mean 352  $\mu\text{m}$ ), showing a prolate to perprolate shape and an isopolarity  
453 index ranging between 112 and 166 (mean 133). Ten to thirteen (mainly eleven)  
454 convolutions are visible in lateral view (Fig. 6K–M). Spiral cells are flat to concave, non-  
455 ornamented and  $\sim 44$   $\mu\text{m}$  in height. Spiral cells expand at the apical area (Fig. 6J) forming  
456 a psilocharoid apex type (Feist et al. 2005). The base is rounded or slightly pointed  
457 showing a small pentagonal basal pore of  $\sim 48$   $\mu\text{m}$  in diameter (Fig. 6N).

458 *Remarks:* The population described herein is remarkably similar to gyrogonites of living  
459 *C. vulgaris* in morphological characters such as the apical and basal structure, gyrogonite  
460 width and convolution number in lateral view (Soulié-Märsché 1989; Sanjuan et al.  
461 2017). However, the studied fossil sample shows gyrogonite heights  $\sim 100$ – $150$   $\mu\text{m}$   
462 shorter than living populations.

463 *Fossil record and distribution:* Fossils of *C. vulgaris* are poorly known in Neogene  
464 sedimentary sequences. Ghetti et al. (2002) reported gyrogonites of *C. vulgaris* from Late  
465 Miocene (early Messinian) rocks of the Velona Basin (Siena, Central Italy). Bathia et al.  
466 (1998) found this species in the Plio-Pleistocene intermountainous Himalayan basins  
467 (Kashmir, India). Fan et al. (1996) also recovered gyrogonites attributed to this taxon in  
468 upper Pleistocene lacustrine facies in the Bangong Co Basin (Western Tibet). Large  
469 samples of *C. vulgaris* were recovered by Soulié-Märsche (1991) and Soulié-Märsche et  
470 al. (2010) from Pleistocene/Holocene paleolakes from Chad, Algeria and Sudan (Africa).

*Palaeoecology: Chara vulgaris* thrives in many kinds of shallow non-marine waterbodies worldwide (Corillion 1972). This taxon grows in temporary ponds or permanent lakes from the depth of several centimeters to up to 1 m (Krause 1997). It can live in freshwater to oligohaline conditions, but calcified gyrogonites are only formed at salinities below 5 ‰ and in alkaline water (Ghetti et al. 2002 and references therein). It has also a wide tolerance to different trophic conditions including eutrophic water (Korsch 2016).

*Chara molassica* var. *notata* (Straub, 1952) comb. nov. Soulié-Märsche, 1989

Fig. 6O–U

1952. *Chara molassica* forma a Straub, p. 467, pl. A, fig. 4–5

1965. *Chara notata* Grambast and Paul, p. 245

1989. *Chara molassica* var. *notata* Soulié-Märsche, p. 146

**Material:** Fifty specimens were extracted from Vilobí del Penedès and fifteen gyrogonites from els Casots (Table 1). Thirty-five specimens were measured from the sample V6/7 (Table 2 in supplementary data).

**Description:** Gyrogonites are of medium size, 498–599 µm high (mean 520 µm) and 320–416 µm wide (mean 377 µm). They are subprolate in shape and display a wide isopolarity index value, ranging between 108 and 161 (mean 138). Eight to twelve (commonly ten) convolutions are visible in lateral view. Mean high of spiral cells is ~59 µm and they are concave and ornamented with isolated small tubercles regularly arranged in row (Fig. 6I, Q and T). Gyrogonites display a prominent psilocharoid-type apex (Fig. 6O and S). The apex is ornamented with enlarged apical tubercles (Fig. 6S). The base is rounded or slightly pointed showing a shallow pentagonal basal pore of ~36 µm in diameter (Fig. 6R and U).



*Fossil record and distribution:* *Chara molassica* var. *notata* has been recovered in latest Oligocene (Chattian) to Late Miocene (Tortonian) sedimentary sequences in Europe. Feist-Castel (1977) and Feist and Ringeade (1977) described populations of this taxon from the latest Oligocene/Early Miocene (Aquitanian) of the Provence and Aquitaine basins in France respectively. Large samples of *C. molassica* var. *notata* were later recovered in Aquitanian-aged rocks of the Alpine Molasse Basin in Switzerland (Berger 1983; Schwarz and Reichenbacher 1989). This variety is also well represented in the latest Oligocene/Early Miocene of the Rhine Graben, Germany (Schwarz 1997 and references therein). Julià de Agar (1991) reported this taxon from the Loranca Basin (Tagus Basin, Spain). In the Ebro Basin (NE Spain) *C. molassica* var. *notata* is well represented in Chattian to Tortonian non-marine deposits (Feist et al. 1994; González-Pardo 2012). This species was also reported from the Middle East by Knobloch (1979) who found it in the Miocene Fars Formation (Iraq).

*Palaeoecology:* Previous studies report this species in freshwater lacustrine facies (e.g., Feist and Ringeade 1977).

-----Figure 6 near here-----

*Chara* cf. *hispida* Linnæus, 1753

Fig. 7A–H

1753. *Chara hispida* Linnæus, p. 1156–1157

1989. *Chara hispida* var. *major* Soulié-Märsche, p. 92, pl. 23

1999. *Chara* cf. *hispida* var. *major* García, p. 311, Fig. 4a–e

*Material:* Hundreds of well-preserved gyrogonites have been recovered in the el Pi Gros section (Table 1). One hundred specimens were measured from the sample PG2 (Table 2 in supplementary data).

*Description:* Gyrogonites are medium- to large-sized, ranging between 540–891  $\mu\text{m}$  in height (mean 726  $\mu\text{m}$ ) and 352–621  $\mu\text{m}$  in width (mean 500  $\mu\text{m}$ ). The dominant gyrogonite shape is prolate spheroidal to perprolate (Feist et al. 2005), with an isopolarity index ranging between 106 and 206 (mean 145). Nine to twelve (commonly ten) spiral cells are visible in lateral view (Fig. 7A–D). Spiral cells are flat to convex, about 88  $\mu\text{m}$  wide and without ornamentation. They become thinner towards the periphery of the apex. The apex is psilocharoid and prominent, generally pointed (Fig. 7E–F). The base is also pointed showing a small pentagonal basal pore of  $\sim 59$   $\mu\text{m}$  in diameter (Fig. 7G–H).

*Remarks:* The population at el Pi Gros displays smaller gyrogonites ( $\sim 180$   $\mu\text{m}$  in length and  $\sim 85$   $\mu\text{m}$  in width) than recent populations of *C. hispida* studied by Soulié-Marshé (1989) or Détriché et al. (2009).

*Fossil record and distribution:* Fossils of *Chara hispida* have been described from Quaternary sedimentary sequences of Europe, Africa and South America. Anadón et al. (1987) reported gyrogonites of this species from the Pleistocene of the Guadix-Baza Basin (SE Spain). Fossil samples are also reported from the Holocene lacustrine sediments from the Wadi Shaw (Sudan) and intermountainous basins in the Middle Atlas of Morocco (Soulié-Marsche 1991; Détriché et al. 2009). García (1999 and references therein) reported gyrogonites of *C. hispida* from several Quaternary localities from Argentina, i.e., Quebrada del Zonda (Province of San Juan), Laguna Salada Grande (Buenos Aires Province), and Laguna del Bebedero (San Luis Province).

*Palaeoecology:* Extant *C. hispida* is a subcosmopolitan species thriving in lakes from nearly all states in Europe, and a few localities in North Africa, the Caucasus, Central

Asia, and Eastern Siberia (Corillion 1972; Barinova et al. 2014 and references therein). It dwells in alkaline permanent and well-oxygenated lakes at depths of up to 15 m. However, this species mostly occurs between 0.5 and 7 m depth (Krause 1997). In spite that preferred habitats of *C. hispida* are freshwater lakes, it can tolerate brackish water (Mannschreck 2003). In agreement with habitat requirements of extant *C. hispida*, the gyrogonite assemblage studied here would also be indicative of permanent and stable freshwater lake conditions.

*Chara* sp.

Fig. 7I–M

**Material:** A few gyrogonites were found at el Pi Gros locality (Table 1). Three specimens were measured in sample PG2 (Table 2 in supplementary data).

**Description:** Gyrogonites are very variable in size ranging between 612–825  $\mu\text{m}$  in height and 350–400  $\mu\text{m}$  in width. The dominant gyrogonite shape is perprolate, with a very high isopolarity index ranging between 161 and 206. Six to seven spiral cells are visible in lateral view (Fig. 7J–L). Spiral cells are convex, without ornamentation. The apex is psilocharoid and very prominent, generally pointed (Fig. 7I). The base is also pointed showing a very small basal pore (Fig. 7M).

**Remarks:** This material could belong to extreme polymorphs of *Chara hispida*, with which it cooccurs in the same samples but in a lower proportion (Table 1). Stressful environmental conditions are well known to result in the development of extreme polymorphs in extant *Chara* species (e.g., Pukacz et al. 2012).

Genus *Lamprothamnium* J. Groves, 1916

*Lamprothamnium papulosum* (Wallroth, 1833) comb. nov. Groves, 1916

Fig. 7N–U

567 1833. *Chara papulosa* Wallroth, p. 107

568 1916. *Lamprothamnium papulosum* Groves, p. 336

569 1969. *Lamprothamnium priscum* Castel and Grambast, p. 940–941, pl. XXXII, figs 4–7

570 1989. *Lamprothamnium papulosum* Soulié-Märsche, p. 150–153, pl. XXXII

571

572 *Material:* Many gyrogonites were recovered from several samples at the base of the  
573 Vilobí del Penedès section (Table 1). Sixty specimens were measured from the sample  
574 V5 (Table 2 in supplementary data).

575 *Description:* Gyrogonites are of medium size, 569–711  $\mu\text{m}$  high (mean 631  $\mu\text{m}$ ) and 348–  
576 542  $\mu\text{m}$  wide (mean 469  $\mu\text{m}$ ), cylindrical or prolate in shape (Fig. 7N–Q), with an  
577 isopolarity index ranging from 113 to 177 (mean 135). Gyrogonites show a prominent  
578 apex of lamprothamnoid type (Fig. 7R–S), i.e., displaying a well-marked periapical  
579 depression (Feist et al. 2005). Seven to eleven (commonly 9) spiral cells are visible in  
580 lateral view. Spiral cells are concave, flat, or convex depending on the calcification degree  
581 and  $\sim 81 \mu\text{m}$  high. Gyrogonites are not ornamented. The base of the gyrogonite is rounded  
582 or slightly pointed with a small pentagonal pore, ranging in diameter from 40 to 60  $\mu\text{m}$   
583 (Fig. 7T–U).

584 *Remarks:* Fossil gyrogonites of *L. papulosum* from Vilobí del Penedès are  $\sim 75 \mu\text{m}$   
585 wider and display a reduced number of spiral cells in lateral view than gyrogonites from  
586 the living populations of the same species from brackish waters of southern France  
587 studied by Soulié-Märsché (1989). The studied gyrogonites are morphologically closer to  
588 *Lamprothamnium priscum* Castel and Grambast, 1969, a fossil species synonymized with  
589 *L. papulosum* by Soulié-Märsché (1989).

*Fossil record and distribution:* Extant *Lamprothamnium papulosum* is a quasi-cosmopolitan species distributed throughout the world except in North and Central America (Corillion 1972; García and Chivas 2004). The oldest known *L. papulosum* was reported by Castel and Grambast (1969) and referred to as *L. priscum*, from the early Eocene deposits from the Corbières mountains (southern France) and further from the early Eocene of Ksour Mountains in Algeria (Mennad et al. 2021). *Lamprothamnium papulosum* has been found in several Quaternary deposits of North Africa (Soulié-Märsche 1982, 1998, 2007).

*Palaeoecology:* *L. papulosum* is adapted to aquatic environments subject to salinity fluctuations and can thrive in sub-saline to hyper-saline waters up to 68‰ in salinity (Burne et al. 1980). Despite *Lamprothamnium* can live in hypersaline conditions, the required salinity to produce oospores and gyrogonites should be 20–40‰ (Soulié-Märsche 1998 and references therein). However, short periods of salinity close to 10‰ are also tolerated for germination of oospores and gyrogonites (Dubois, 1968).

-----Figure 7 near here-----

Genus *Lychnothamnus* (Ruprecht, 1845) von Leonhardi, 1863 emend. A. Braun in  
Braun et Nordstedt, 1882

*Lychnothamnus barbatus* (Meyen, 1827) comb. nov. von Leonhardi, 1863

*Lychnothamnus barbatus* var. *antiquus* Soulié-Märsche, 1989

Fig. 8A–C

1827. *Chara barbata* Meyen, p. 75, pl. e, figs 7 and 8.

1863. *Lychnothamnus barbatus* Leonhardi, p. 72.

1989. *Lychnothamnus barbatus* var. *antiquus* Soulié-Märsche, p. 155, pl. 37, figs 1–6.

*Material:* A few specimens were recovered from the sample V6/7 at Vilobí del Penedès (Table 1). Three gyrogonites were measured (Table 2 in supplementary data).

*Description:* Gyrogonites are large (878  $\mu\text{m}$  high and 733  $\mu\text{m}$  wide), ellipsoidal in shape with an isopolarity index of 120. In the few gyrogonites recovered, spiral cells do not display any modification in the width or thickness at the periphery of the apex (Fig. 8A). The apex is flat, and the base is tapered showing a small basal pore. Nine or ten concave spiral cells in lateral view separated by bicarinate sutures can be clearly observed near the base (Fig. 8B). They are 120  $\mu\text{m}$  high and devoid of ornamentation.

*Fossil record and distribution:* *Lychnothamnus barbatus* var. *antiquus* has been found in several Miocene/Pliocene peri-Mediterranean lacustrine basins from Europe, North Africa, and the Middle East. It has been reported from the Ebro and the Cerdanya basins (NE Spain), Rio Maior (Portugal), Provence (France), Maoče (Montenegro), Çankırı (Turkey) and Bekaa in Lebanon (Sanjuan and Alqudah 2018 and references therein).

*Palaeoecology:* The living species *L. barbatus* mainly thrives in permanent lakes of northern Europe (Corillion 1972) where it forms dense meadows at depths ranging between 2 and 8 m. These extant populations grow in cold and oligo-mesotrophic waters of freshwater lakes, frequently associated to phreatic sources (Krause 1997; Brzozowski et al. 2019).

*Lychnothamnus* sp.

Fig. 8D–F

*Material:* Only one complete specimen has been found. This gyrogonite and other fragments attributed to this taxon were recovered from sample MA1 at Mas de l'Alonso (Table 1 and Table 2 in supplementary data).

*Description:* Gyrogonites are large, 1022  $\mu\text{m}$  high and 777  $\mu\text{m}$  wide, cylindrical in shape with an isopolarity index of 131. Spiral cells are ornamented with a characteristic midcelular crest (Fig. 8E). Spiral cells do not show any modification at the periphery of the apex and show a constant width. The apex is flat and ornamented with coma-shaped tubercles (Fig. 8D). The base is tapered showing a star-shaped basal funnel (Fig. 8F). Eight concave spiral cells are visible laterally, being separated by bicarinate sutures. This character can be clearly observed near the base.

*Remarks:* The small number of recovered specimens hinders their identification to the species level, but the ornamentation of this gyrogonite suggests affinities with species formerly attributed to the fossil genus *Stephanochara* Grambast, which was synonymized with *Lychnothamnus* by Soulié-Märsche (1989).

#### Genus *Nitellopsis* Hy, 1889

##### Subgenus *Tectochara* Grambast and Grambast-Fessard, 1954

*Nitellopsis (Tectochara) merianii* (Al. Braun ex Unger, 1852) comb. nov. Grambast and Soulié-Märsche, 1972

#### Fig. 8G–N

1852. *Chara merianii* Unger, p. 82, pl. 25, figs 10–12.

1954. *Tectochara merianii* Grambast et Grambast-Fessard, p. 668.

1972. *Nitellopsis (Tectochara) merianii* Grambast et Soulié-Märsche, p. 11.

*Material:* Fifty gyrogonites were recovered from sample V6/7 at Vilobí del Penedès and few fragments attributed to this taxon were found in sample MA1 (Table 1). Thirty-five specimens were measured (Table 2 in supplementary data).

*Description:* Gyrogonites are large, ovoidal (Fig. 8K–N), 781–1120 µm high (mean 958 µm) and 656–957 µm wide (mean 824 µm), with an isopolarity index ranging between 104 and 135 (mean 116). Spiral cells are flat to convex. Seven to nine (frequently eight) spiral cells are visible in lateral view (116 µm high). Gyrogonites display a nitellopsidoid apex (Fig. 8G–H), i.e., spiral cells become thinner and narrower at the periapical zone (Hornaf Rantzien 1959). The apex is flat and ornamented with large apical nodules. The basal pole is conical showing a basal pore within a wide pentagonal funnel, 292 µm in diameter (Fig. 8I–J), sometimes star-shaped (Fig. 8J).

*Fossil record and distribution:* This species has been widely reported from several Paleogene/Neogene basins from Europe, North Africa, the Middle East and Asia (Sanjuan and Alqudah 2018 and references therein). The oldest representatives of this species were discovered in latest Eocene (late Priabonian) deposits of the Ebro Basin (Sanjuan and Martín-Closas 2014). Later, this species expanded its biogeographic range following 4 distributional phases to become finally subcosmopolitan in the Northern Hemisphere during the Miocene (Soulié-Märsche et al. 1997; Soulié-Märsche et al. 2002; Sanjuan and Martín-Closas 2015).

*Palaeoecology:* *Nitellopsis (T) merianii* is considered the ancestor of the living species *Nitellopsis obtusa* (Sanjuan and Martín-Closas 2015). This taxon thrives in permanent, cold, and deep alkaline lakes at a depth range between 4–12 m, in large lakes of northern Europe, Asia and North America (Corillion 1972). This species cannot tolerate salinities higher than 5‰ (Katsuhara and Tazawa 1986).

*Nitellopsis* sp.



*Material:* A few abraded gyrogonites were recovered from sample V6/7, Vilobí del Penedès. Only two specimens were measured (Table 2 in supplementary data).

*Description:* Gyrogonites are very large (1289  $\mu\text{m}$  high and 1051  $\mu\text{m}$  wide), ovoidal, with an isopolarity index of 123. Spiral cells are flat and ornamented with a nodular mid-cellular crest (Fig. 8P). Eight or nine spiral cells are visible in lateral view (155  $\mu\text{m}$  high). The apex is flat and of nitellopsidoid type (Horn af Rantzien 1959), ornamented with small apical nodules (Fig. 8O). The basal pole is conical showing a small basal pore, 97  $\mu\text{m}$  within a star-shaped funnel (Fig. 8Q).

*Remarks:* The main difference between this species and *N. (T) merianii* is the size and the ornamentation. However, the small number of recovered specimens hinders their identification to the species level.

-----Figure 8 near here-----

## Discussion

### *Charophyte taphonomy and palaeoecology*

The non-marine deposits from els Casots, Vilobí del Penedès, and Mas de l'Alonso–el Pi Gros studied in this work have yielded a diverse number of charophyte and two ostracode species which have characteristic palaeoenvironmental distributions. Several of them have living representatives, which allow for more accurated palaeolimnological inferences for the wetlands developed in the Vallès-Penedès and Vilanova i la Geltrú basins during the Langhian and Serravalian.

707 We distinguish three different assemblages in the depositional environments studied:

708 *Charophytes from shallow lakes*: The microfossil assemblage associated to shallow lakes  
 709 varies locally. Charophyte assemblages at els Casots are dominated by *Chara* cf. *vulgaris*.  
 710 This living species has wide ecological tolerance and lives in brackish or freshwater  
 711 environments (estuaries, rivers, springs, ponds and lakes). It mostly occurs at very  
 712 shallow depths, from several centimeters up to 1 m and can live in eutrophic water  
 713 (Krause 1997). This species can withstand oligohaline conditions and it only produces  
 714 gyrogonites at salinities up to 5 ‰ (Ghetti et al. 2002). Associated taxa include *C.*  
 715 *molassica* var. *notata* and abraded tests of *Ammonia* sp. rotraliid foraminifera. *C.*  
 716 *molassica* var. *notata* is an extinct species related to freshwater lakes. The dominance of  
 717 *C. vulgaris* suggests very shallow water and that water trophism may have been high in  
 718 the paleolake of els Casots.

719 The flora in the upper part of the Vilobí del Penedès section (samples V5 and V6/7)  
 720 corresponds to a shallow lake as well. In this case the charophyte assemblage is dominated  
 721 by *C. molassica* var. *notata*. Other, less abundant, species include *Sphaerochara*  
 722 *ulmensis*, *Nitellopsis* (*Tectochara*) *merianii*, and *Lychnothamnus barbatus* var. *antiquus*.  
 723 A few poorly-preserved skeletons of rotraliid foraminifera (*Ammonia* sp.) also occur and  
 724 are considered allochthonous to the lake. Charophytes indicate the prevalence of  
 725 freshwater conditions. The occurrence of *Nitellopsis* (*Tectochara*) *merianii* and  
 726 *Lychnothamnus barbatus* var. *antiquus* (ancestors of the extant species *Nitellopsis obtusa*  
 727 and *Lychnothamnus barbatus*, respectively) thrive today in permanent, relatively deep  
 728 (2–8m), oligotrophic lakes with salinities not exceeding 5‰. The ecological requirements  
 729 of the charophyte assemblage at Vilobí del Penedès suggest that the lake was more stable  
 730 and oligotrophic than the contemporary lake of els Casots.

Finally, the assemblage from Mas de l'Alonso (sample MA1) also corresponds to shallow lacustrine conditions. In spite of the scarce material recovered the charophyte assemblage is quite diverse and also includes rare *Ammonia* sp. foraminifera. The charophyte assemblage is constituted by *Sphaerochara ulmensis*, *Chara* cf. *hispida*, *Lychnothamnus* sp. and fragmented gyrogonites attributed to *Nitellopsis* (*Tectochara*) *merianii*. This assemblage indicates the prevalence of shallow freshwater conditions. *Ammonia* sp. tests show evident signs of abrasion and are considered allochthonous, being probably transported from nearby marine settings.

*Charophytes from coastal salinas:* Assemblages from Vilobí del Penedès (lower part of the section) are dominated by the charophyte species *Lamprothamnium papulosum*, which occurs associated to abraded ostracod carapaces. *L. papulosum* is the most halotolerant species among living charophytes, surviving at salinities up to 70‰ (Burne et al. 1980). Despite withstanding such hypersaline conditions, living populations of *L. papulosum* require salinities around 20‰ (maximum 40‰) to produce gyrogonites (Soulié-Märsche 1998 and references therein). The presence of monospecific assemblages of *L. papulosum* at Vilobí del Penedès indicates the prevalence of brackish water conditions, limiting the development of other charophyte species (Fig. 10). Several germinated gyrogonites indicate that seasonally the palaeosalinity could have been going down to 10‰ for short periods of time.

-----Figure 9 near here-----

*Charophytes from permanent lakes:* Based on the assemblages from el Pí Gros, two charophyte species, *Chara* cf. *hispida* and *Chara* sp., and two ostracod taxa, *Heterocypris*

*salina* Brady 1868 (Fig. 9A–D) and a probable leptocytherid (Fig. 9E–J) are present. The presence of articulated valves suggests *in situ* burial. Gyrogonites of *Chara* cf. *hispida* are by far the dominant charophyte remains. Living meadows of *C. hispida* mainly grow in alkaline permanent freshwater lakes at a depth up to 15 m, mainly between 0.5 and 7 m (Krause 1997). This is an eurythermal species preferring calcareous and well-oxygenated waters (Barinova et al. 2014 and references therein), which can also tolerate brackish water conditions, as reported from the Baltic Sea (Mannschreck 2003).. *Chara hispida* shares similar habitat preferences with other *Chara* species and with *Nitellopsis obtusa* (Barinova et al. 2014). While charophyte thalli are absent in the marls, charophyte gyrogonites are very well preserved showing the endocalcine and ectocalcine layers intact, without traces of corrosion or dissolution, thus evidencing that they were buried *in situ* or near the production area. The ostracods found in these lacustrine facies provide significant information about the characteristics of the palaeo-waterbody at el Pi Gros. The leptocytherid species is similar to *Leptocythere* gr. *psammophila* in Gliozzi et al (2005). *Heterocypris salina* Brady, 1868 is widely distributed across Europe, West Asia, and North Africa inhabiting several types of waterbodies, from freshwater springs and wells to littoral zones of seas (Meisch, 2000; Gusakov et al. 2021). This species is found in slightly saline coastal and continental waters with salinities ranging from 5 to 35‰ (Gusakov et al. 2021), although Meisch (2000) reports that it is more usually associated with oligosaline waters, with an optimum salinity preference of around 6 ‰. Meisch (2000) further maintains that the species can also live in freshwater so that its presence should not be regarded as indicative of a saline waterbody in the absence of supporting evidence. Although Miocene leptocytherids have been reported from both marine brackish and athalassic saline environments (Gliozzi et al. 2005), the co-occurrence of the specimens with *H. salina*, together with additional micropalaeontological evidence,

suggests that el Pi Gros corresponds to lacustrine and oligohaline waterbody (Fig. 10). This interpretation is consistent with the conclusions of Gliozzi et al (2005), who have previously reported the co-occurrence of leptocytherids, including *Leptocythere* gr. *psammophila* with *Heterocypris salina* from Serravallian lacustrine or palustrine sediments from the Iberian Peninsula.

-----Figure 10 near here-----

## Conclusions

Middle Miocene (Langhian–Serravallian) lacustrine deposits of the Vallès–Penedès and Vilanova i la Geltrú basins (SW of Barcelona) are here analyzed from the sedimentological and palaeoenvironmental viewpoints. The three localities studied, i.e., els Casots (Subirats), Vilobí del Penedès, and Mas de l'Alonso–el Pi Gros (Vilanova i la Geltrú), yielded a well-preserved charophyte assemblage comprising ten different species. The recovered flora shows a characteristic palaeoenvironmental distribution and sheds new light on the prevailing palaeolimnological characteristics of the wetlands in the coastal basins of NE Iberia during the Middle Miocene. Facies analysis, taphonomy and palaeoecology of the recovered taxa allows for the distinction of three different palaeoenvironmental settings: shallow lake, coastal salina, and permanent stable lake. Claystones related to shallow lakes occur in the three studied localities and have yielded *Sphaerochara ulmensis*, *Chara* cf. *vulgaris*, *Chara molassica* var. *notata*, *Lychnothamnus barbatus* var. *antiquus*, *Lychnothamnus* sp., *Nitellopsis* (*Tectochara*) *merianii*, and *Nitellopsis* sp. This flora is unevenly distributed owing to local palaeolimnological conditions. Mesotrophic to eutrophic conditions dominated the

Langhian palaeolake at els Casots, while more oligotrophic and stable conditions might have prevailed at the upper part of the Vilobí del Penedès (Langhian) section and at Mas de l'Alonso (Serravallian). The occurrence of abraded tests of benthic foraminifera suggests that these freshwater lakes were situated close to the coastline. Facies related to coastal salinas are only found at the base of the Vilobí del Penedès section (Langhian) and are characterized by primary gypsum beds alternated with greenish claystones rich in *Lamprothamnium papulosum*. Monospecific populations of this halotolerant taxon indicate the prevalence of brackish waters with salinity fluctuations from low to hypersaline concentrations. However salinities of around 20‰ are needed for the production of gyrogonites. Finally, charophytes found in marls and limestones attributed to permanent stable lakes occurs at el Pi Gros (Serravallian). The lake was inhabited by *Chara* cf. *hispid*a and *Chara* sp. as well as the ostracod species ?*Leptocythere* gr. *psammophila* and *Heterocypris salina*, indicating the prevalence of oligohaline and well oxygenated waters.

This is the first in-depth study of the charophytes from the Vallès-Penedès and Vilanova basins. The results presented here show that charophytes are crucial for accurately reconstructing palaeolimnological conditions, such as the water salinity, trophism or depth. The combined study of charophytes and other microfossils, such as ostracods and foraminifera, even improve such palaeoenvironmental inferences, especially regarding salinity.

This study provides just a limited view of the total range of palaeoenvironments recorded in this area. The whole Vallès sector and other associated sub-basins such as Sant Andreu de la Barca, which contains mainly fluvio-lacustrine facies, have yet to be studied but preliminary results indicate that they are also rich in charophyte fossils. Perhaps more importantly, the combined continental record of these Catalan coastal basins covers

almost the entire Miocene, therefore allowing for the study of the evolution of terrestrial wetland ecosystems along protracted time intervals.

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## Figure captions

Figure 1. Geological map of the study area. Red stars represent the location of the three studied localities in the Vallès-Penedès and Vilanova i la Geltrú basins. V=Vilobí; E.C=els Casots; M.A= Mas de l'Alonso; P.G=el Pí Gros. Modified from ICC (2021).

Figure 2. Stratigraphic logs of the 4 studied localities. 1) els Casots (Subirats); 2) Vilobí del Penedès; 3) el Pí Gros (Vilanova i la Geltrú); 4) Mas de l'Alonso (Vilanova i la Geltrú).

Figure 3. Facies and microfacies from els Casots (Subirats). A–B. Field photos of the stratigraphic section. A. organic-claystones with pedogenetic features, see the location of the sample C4. B. limestone interval from where the samples C2 was extracted. C–H. Microphotographs of the limestone sample C2. C. Packstone of cyanobacterial crusts. D. subrounded oncolite. E. fragments of mollusk shells (m.s). F. detail of a mollusk shell. G. well-developed oncolite (Onc). H. detail of cyanobacterial crusts.

Figure 4. Field photos of the section at Vilobí del Penedès. A. laminated gypsarenite interval at the base of the section. B. gypsum (G) and claystone alternation at the base of the section, see the position of samples yielding charophytes V1, V3, and V4. C. Partially covered greenish claystones, see the position of the sample V5. D. Oyster bank at the top of the section.

Figure 5. Facies and microfacies from the el Pí Gros locality (Vilanova i la Geltrú). A–B. Field photos of the stratigraphic section. A. general overview of the upper half section. B. facies showing a shallowing upward cycle from base to top; marly limestone (M), wackestone-packstone limestone (W-P. L), stromatolitic limestone (S.L) and bioturbated claystone (B.C). C–F. Microphotographs of the sample PG1. C. wackestone with gyrogonites (Gyr). D. Detail of a *Chara* gyrogonite showing the basal plate (B.P). E. wackestone–packstone with ostracods (ostr). F. wackestone–packstone with charophytes



1232 showing diagenetic dissolution. G–H. Microphotographs of PG4 sample, wackestone–  
1233 packstone with ostracods (ostr), gyrogonites (gyr), and thalli.

1234 Figure 6. Fossil charophytes from the Vallès-Penedès and Vilanova i la Geltrú basins. A–  
1235 D. *Sphaerochara ulmensis* from sample V6/7. A. apical view, IPS122528.1; B. lateral  
1236 view, IPS122528.2; C. lateral views; IPS122528.3; D. basal view, IPS122528.4. E–I.  
1237 *Sphaerochara ulmensis* from sample MA1, Mas de l'Alonso. E. apical view,  
1238 IPS127516.1; F. lateral view, IPS127516.1; G. lateral view, IPS127516.2; H. lateral view,  
1239 IPS127516.3; I. basal view, IPS127516.4; J–N. *Chara* cf. *vulgaris* from sample C4, els  
1240 Casots. J. apical view, IPS127515.1; K. lateral view, IPS127515.2; L. lateral view,  
1241 IPS127515.3; M. lateral view, IPS127515.4; N. basal view, IPS127515.5; O–R. *Chara*  
1242 *molassica* var. *notata* from sample C4, els Casots. O. apical view, IPS127515.6; P. lateral  
1243 view, IPS127515.7; Q. lateral view, IPS127515.8; R. basal view, IPS IPS127515.8; S–U.  
1244 *Chara molassica* var. *notata* from sample V6/7, Vilobí del Penedès. S. apical view,  
1245 IPS122528.5; T. lateral view, IPS122528.6; U. basal view, IPS122528.7

1246 Figure 7. Fossil charophyte assemblage from the Vallès-Penedès and Vilanova i la Geltrú  
1247 basins (continued). A–H. *Chara* cf. *hispidia* from sample PG2. A. lateral view,  
1248 IPS127517.1; B. lateral view, IPS127517.2; C. lateral view, IPS127517.3; D. lateral view,  
1249 IPS127517.4; E. apical view, IPS127517.5; F. apical view, IPS127517.6; G. basal view,  
1250 IPS127517.7; H. basal view, IPS127517.8; I–M. *Chara* sp. from sample PG2. I. apical  
1251 view, IPS127517.9; J. lateral view, IPS127517.10; K. lateral view, IPS127517.11; L.  
1252 lateral view, IPS127517.12; M. basal view, IPS127517.13; N–U. *Lamprothamnium*  
1253 *papulosum* from sample V5, Vilobí del Penedès. N. lateral view, IPS127514.1; O. lateral  
1254 view, IPS127514.2; P. lateral view, IPS127514.3; Q. lateral view, IPS127514.4; R. apical  
1255 view, IPS127514.5; S. apical view, IPS127514.6; T. basal view, IPS127514.7; U. basal  
1256 view, IPS127514.8.

Figure 8. Fossil charophyte assemblage from the Vallès-Penedès and Vilanova i la Geltrú basins (continued). A–C. *Lychnothamnus barbatus* var. *antiquus* from sample V6/7, Vilobí del Penedès. A. apical view, IPS122528.8; B. lateral view, IPS122528.9; C. basal view, IPS122528.10; D–F. *Lychnothamnus* sp. from sample MA1, Mas de l'Alonso. D. apical view, IPS127516.5; E. lateral view, IPS127516.5; F. basal view, IPS127516.6; G–N. *Nitellopsis (Tectochara) merianii* from sample V6/7, Vilobí del Penedès. G. apical view, IPS122530.1; H. apical view, IPS122530.2; I. basal view, IPS122530.3; J. basal view, IPS122530.4; K. lateral view, IPS122530.5; L. lateral view, IPS122530.6; M. lateral view, IPS122530.7; N. lateral view, IPS122530.8; O–Q. *Nitellopsis* sp. from sample V6/7, Vilobí del Penedès. O. apical view, IPS122528.11; P. lateral view, IPS122528.11; Q. basal view. IPS122528.12.

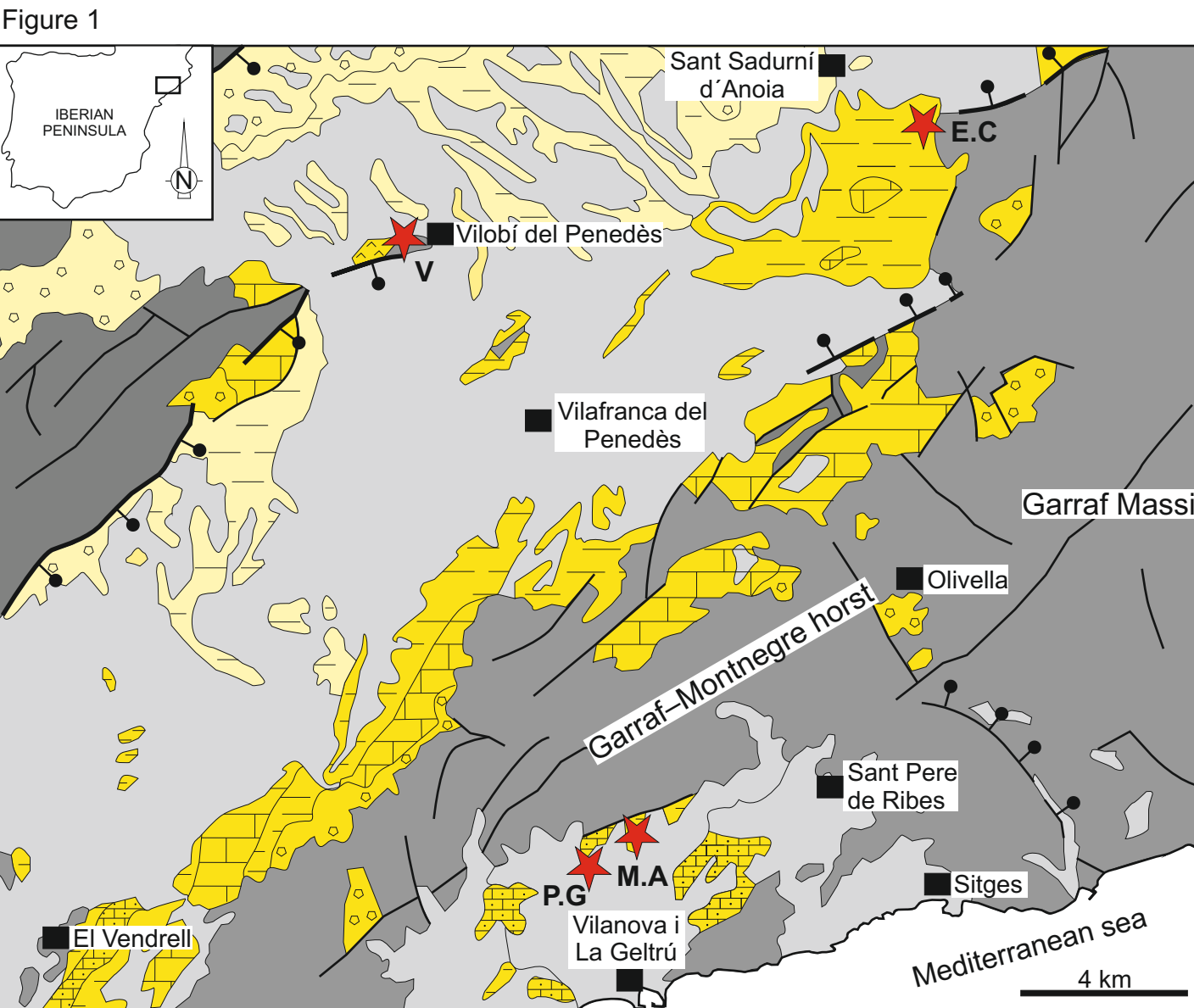
Figure 9. Fossil ostracods and foraminifera from Vallès-Penedès and Vilanova i la Geltrú basins. A–D. *Heterocypris salina* from sample PG2, el Pi Gros locality. A. external view of a right valve, IPS127517.14; B. internal view of a right valve, IPS127517.15; C. dorsal view of carapace, IPS127517.16; D. ventral view of carapace, IPS127517.17; E–J. *?Leptocythere* gr. *L. psammophila* from sample PG2, el Pi Gros locality. E. external view of a left valve, IPS127517.18; F. external view of a left valve, IPS127517.19; G. external view of a right valve, IPS127517.20; H. opened carapaces from the ventral view, IPS127517.21; I. dorsal view of carapace, IPS127517.22; J. ventral view of carapace, IPS127517.23; K–M. *Ammonia* sp. from sample C4, els Casots. K. umbilical view, IPS127515.9; L. umbilical view, IPS127515.10; M. spiral view, IPS127515.11.

Figure 10. Palaeoenvironmental model showing the distribution of the charophyte taxa and the distinguished depositional environments in the Vallès-Penedès and Vilanova i la Geltrú basins. Note that this is not a palaeoenvironmental reconstruction, as the Vallès-Penedès sites date back to the Langhian while those from the Vilanova i la Geltrú date

1282 back to the Serravallian. The figure is meant to illustrate the range of wetland  
1283 environments occurring in these coastal basins during the Middle Miocene.

1284 Table 1. List of microfossils and their relative abundances based on a semi-quantitative  
1285 visual estimation.

1286 Table 2 (in supplementary data). Biometric measurements of the studied charophyte  
1287 samples from the Middle Miocene deposits of the E Vallès-Penedès and Vilanova i la  
1288 Geltrú basins.

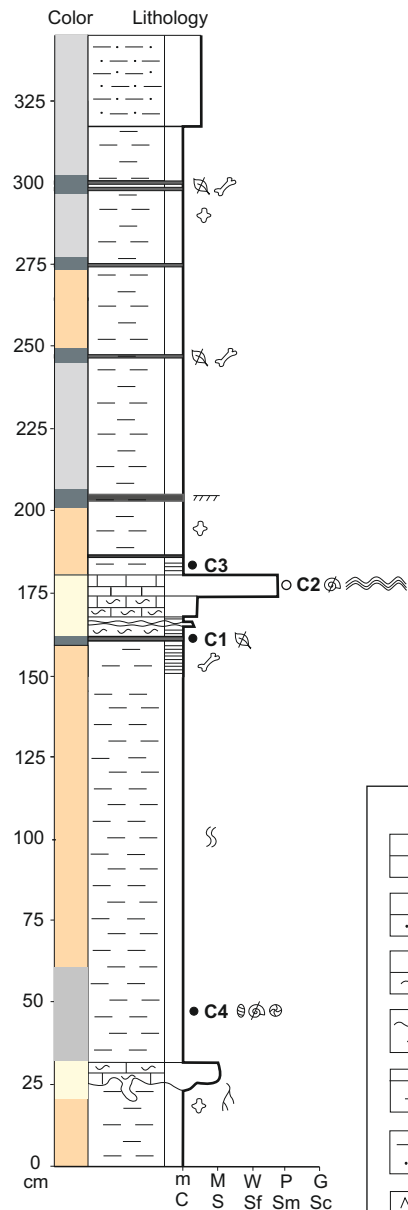


Legend

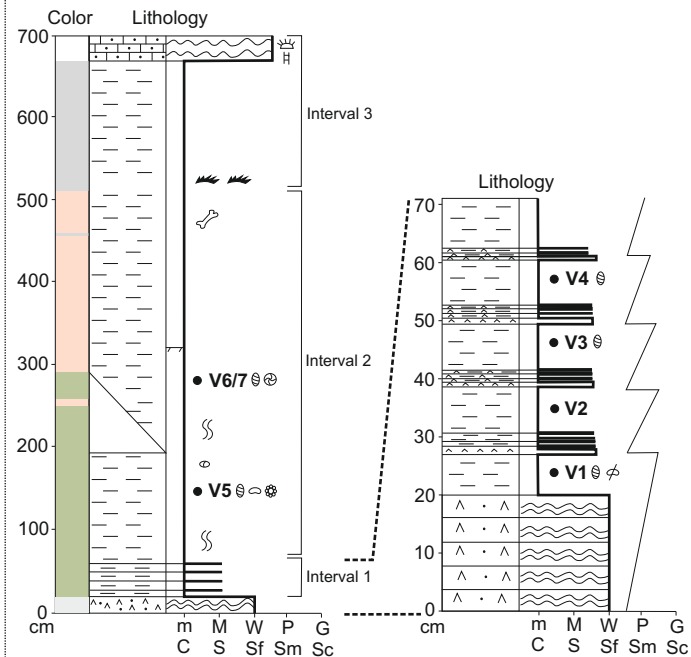
- |                        |                                                     |                                             |
|------------------------|-----------------------------------------------------|---------------------------------------------|
| ■ Village              | □ Quaternary (fluvial, alluvial and beach deposits) | □ Middle/Late Miocene (conglomerate)        |
| ★ Section location     | □ Early Miocene (conglomerate and coarse sandstone) | □ Middle/Late Miocene (marls and mudstone)  |
| —● Major normal faults | □ Early Miocene (marls and mudstone)                | □ Jurassic and Cretaceous rocks (limestone) |
| — Minor faults         | □ Early Miocene (reefal limestone)                  |                                             |
|                        | □ Early/Middle Miocene (bioclastic limestone)       |                                             |
|                        | □ Early Miocene (gypsum)                            |                                             |

Figure 2

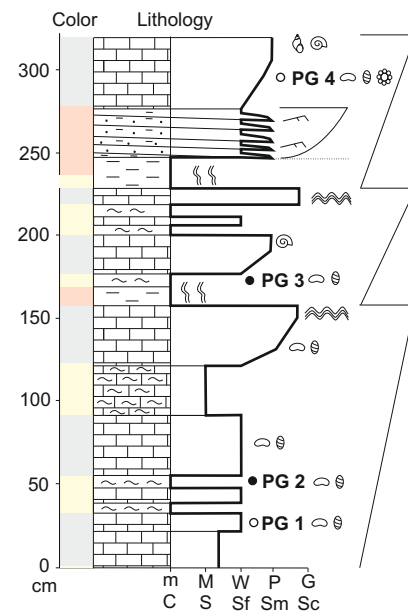
## 1. ELS CASOTS (SUBIRATS)



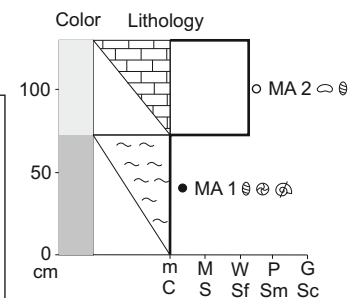
## 2. VILOBÍ DEL PENEDÈS



## 3. PI GROS (VILANOVA I LA GELTRÚ)



## 4. MAS DE L'ALONSO (VILANOVA I LA GELTRÚ)



## Legend

|  |                      |  |                                 |  |                       |
|--|----------------------|--|---------------------------------|--|-----------------------|
|  | Limestone            |  | Ripples                         |  | Gyrogonites           |
|  | Bioclastic limestone |  | Limonite horizon                |  | Charophyte thalli     |
|  | Marly limestone      |  | Bioturbation                    |  | Ostracods             |
|  | Marlstone            |  | Plant remains                   |  | Ostracod fragments    |
|  | Claystone            |  | Carbonate nodules               |  | Freshwater gastropods |
|  | Siltstone            |  | Cyanobacterial crusts           |  | Potamidid gastropods  |
|  | Gypsarenite          |  | Root marks                      |  | Mollusk's fragments   |
|  | Gypsum               |  | Nodule                          |  | Vertebrate remains    |
|  | Lignites             |  | Soft Samples<br>C / V / PG / MA |  | Oysters               |
|  |                      |  | Hard Samples<br>C / PG / MA     |  | Foraminifera          |
|  |                      |  |                                 |  | Equinoids             |
|  |                      |  |                                 |  | Rodophytes            |



Figure 3

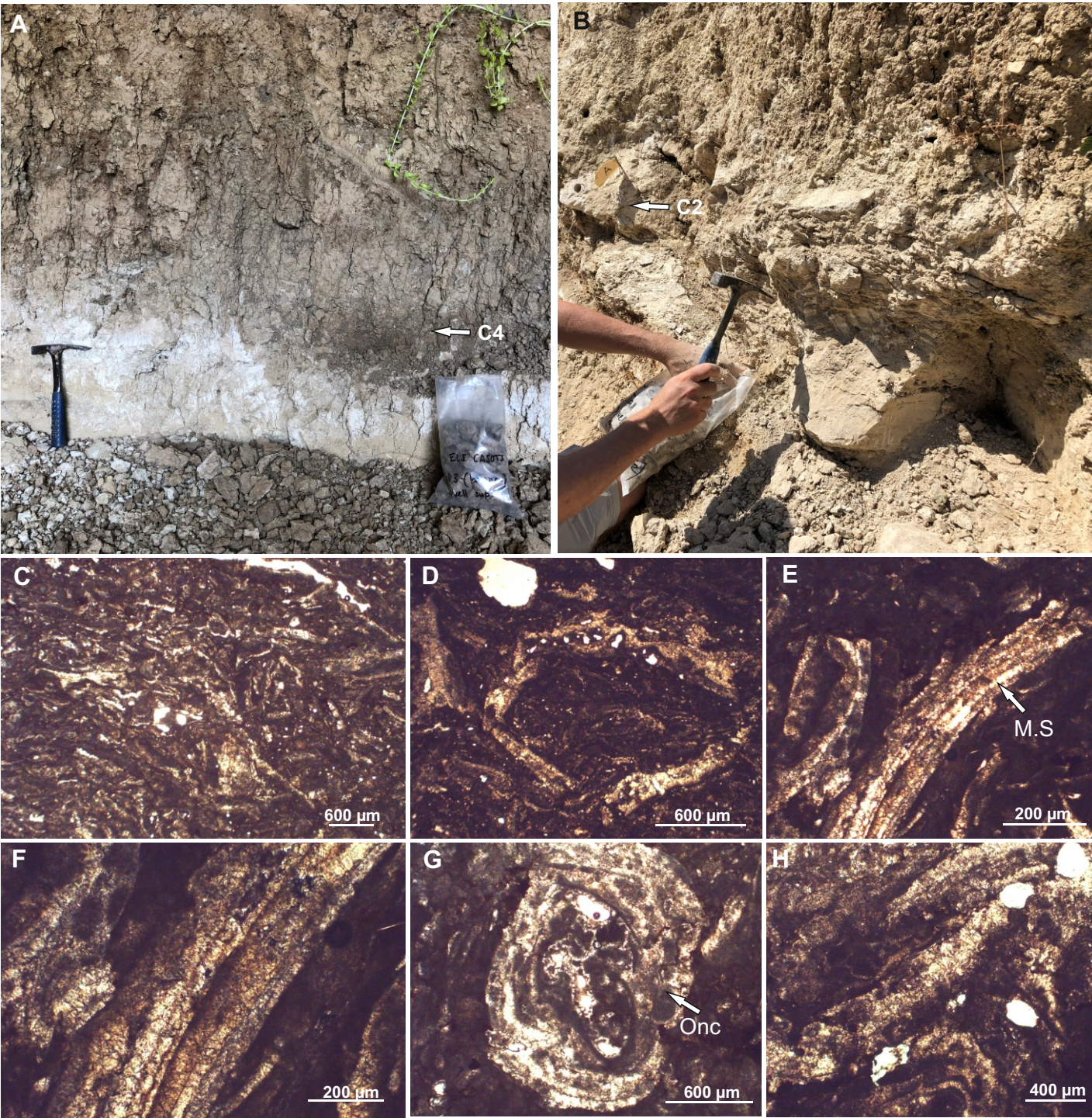




Figure 4

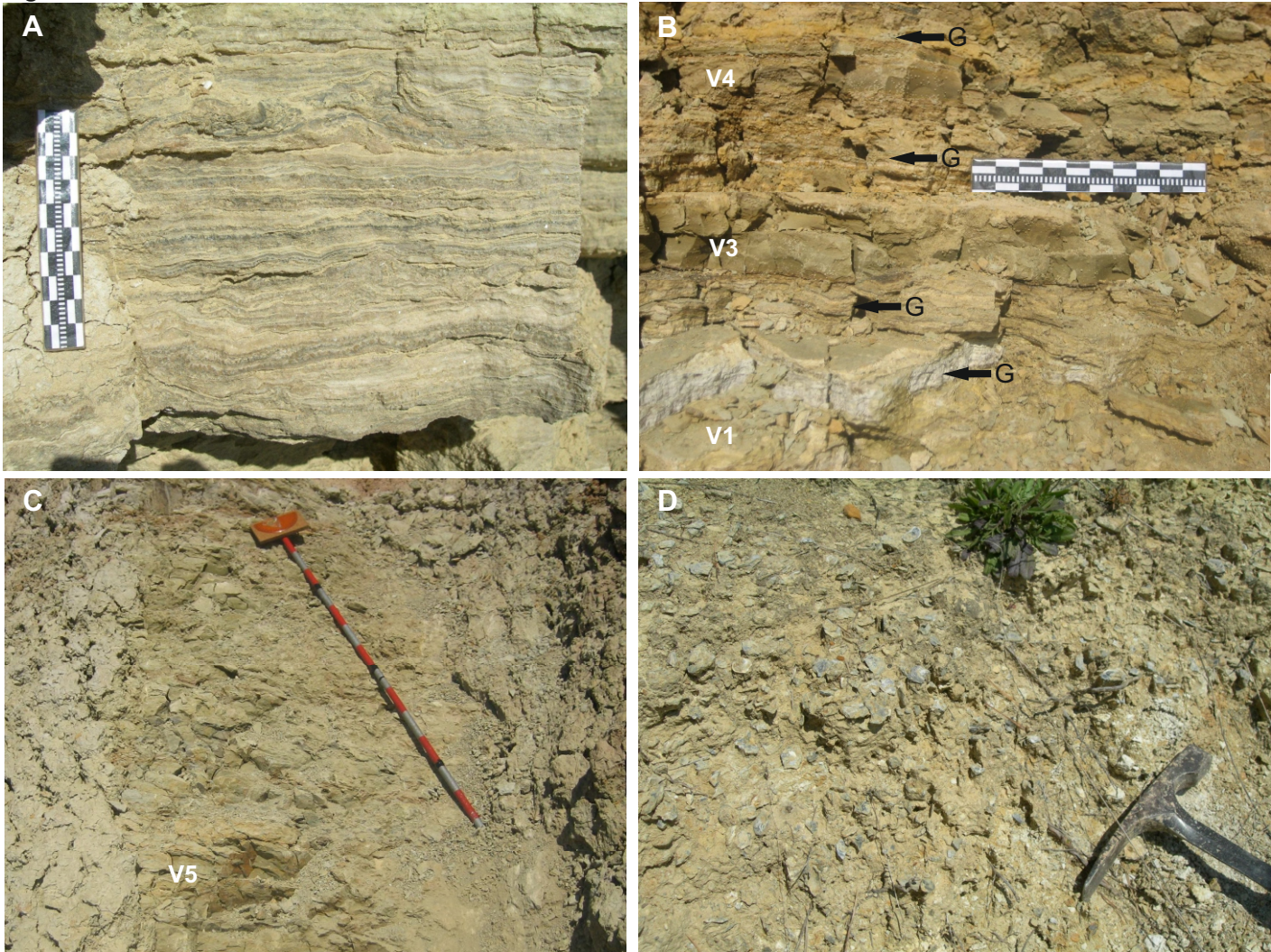




Figure 5

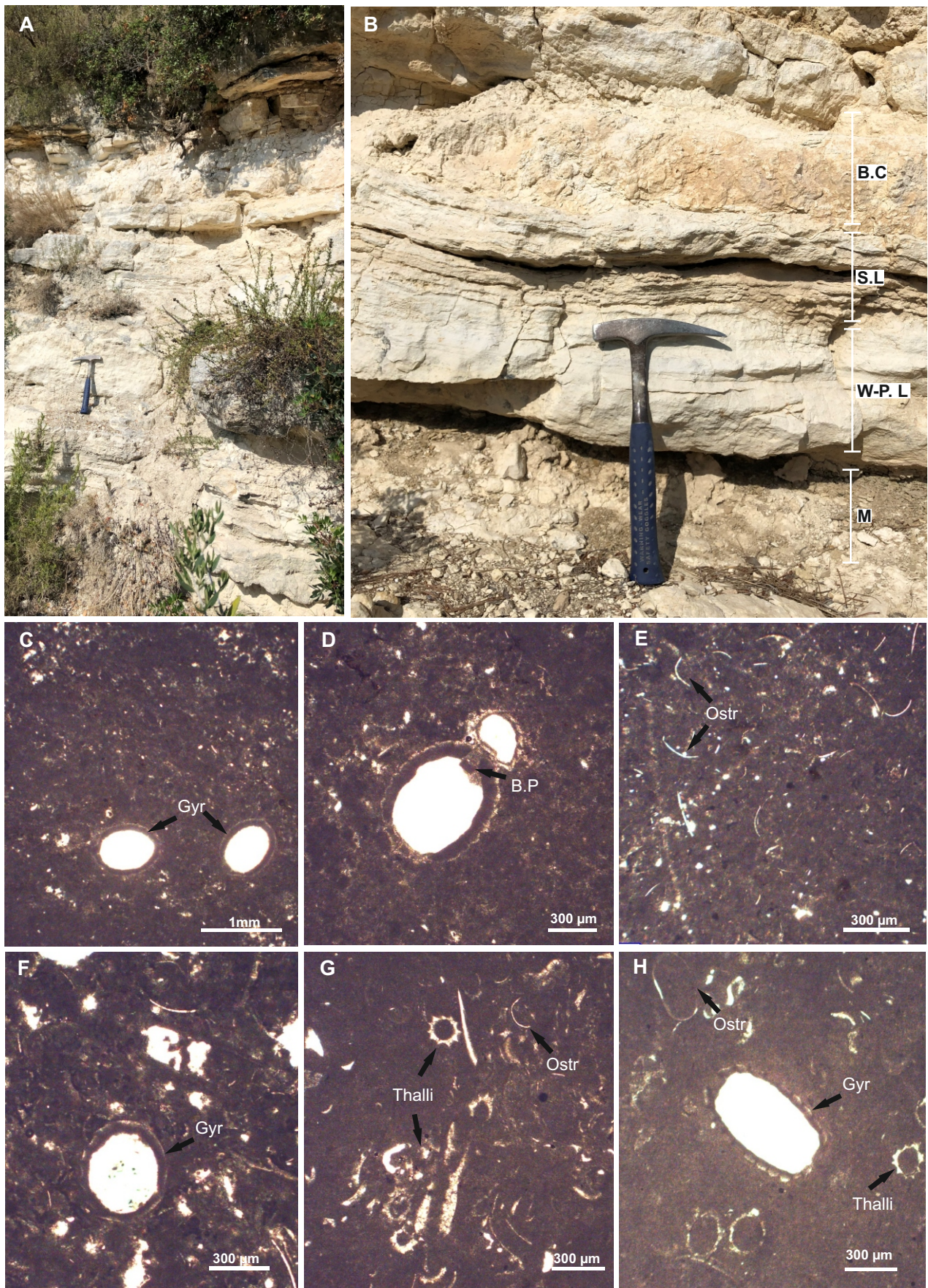




Figure 6

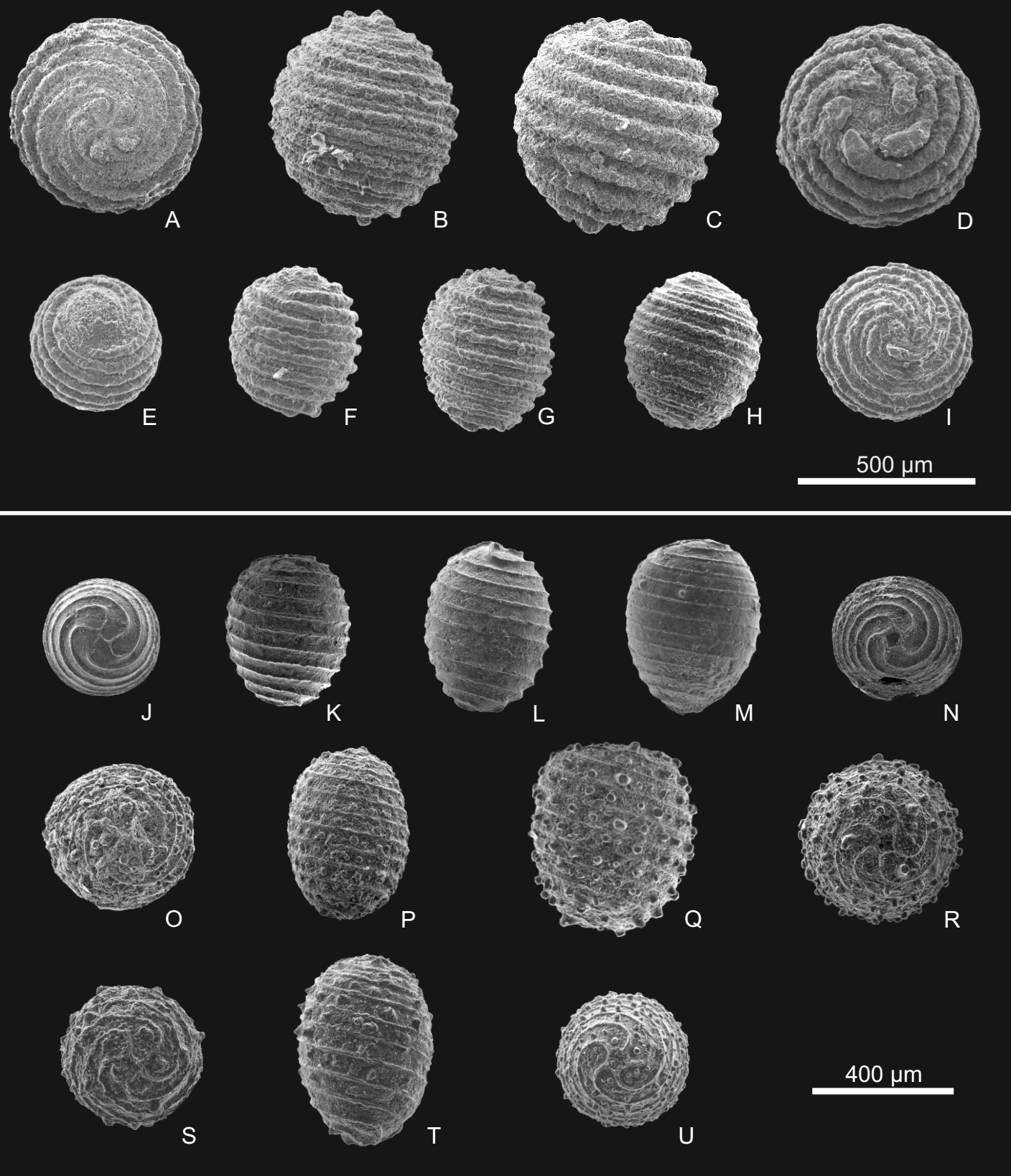


Figure 7

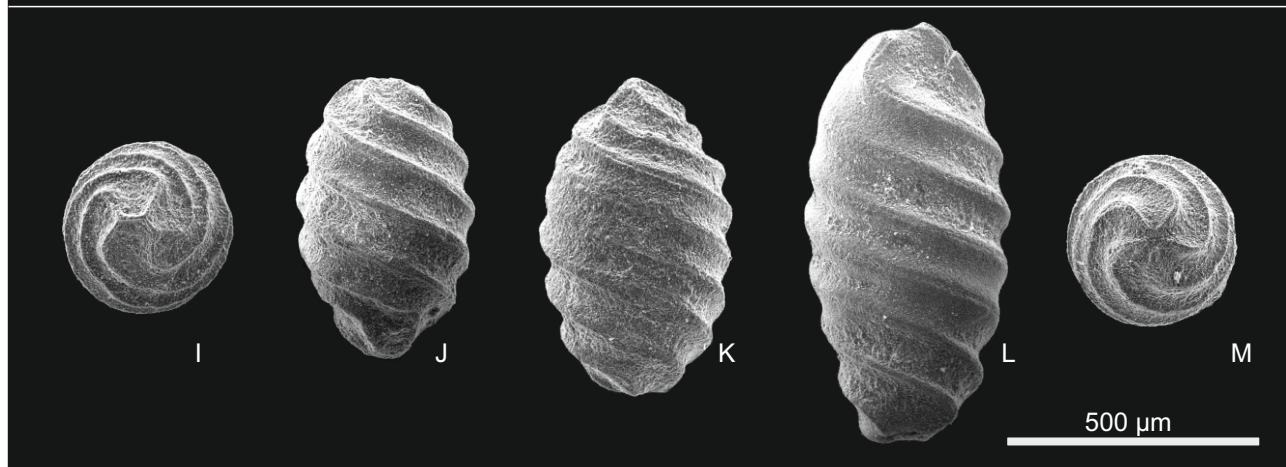
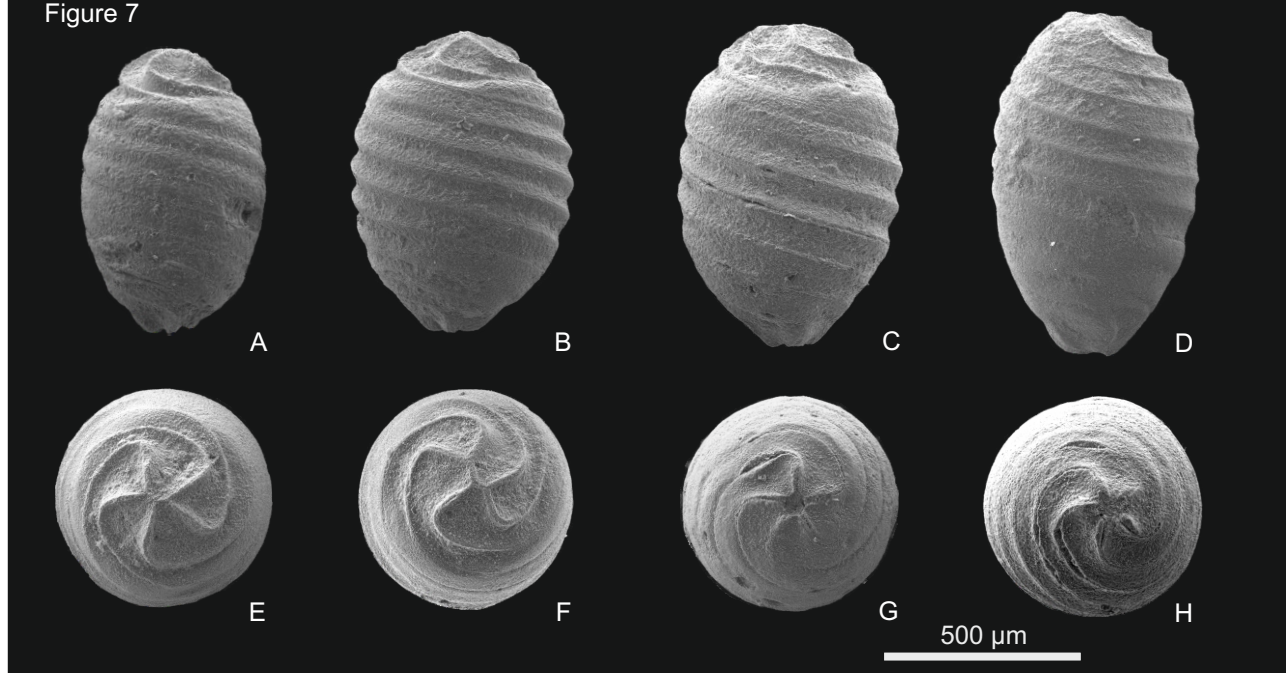




Figure 8

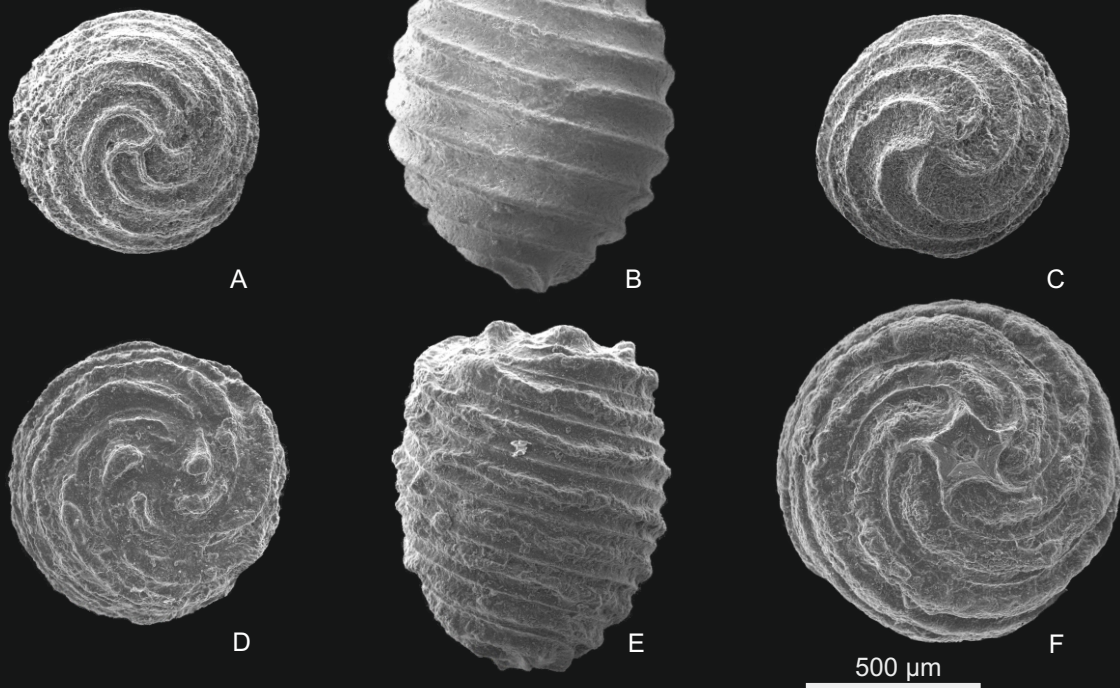


Figure 9

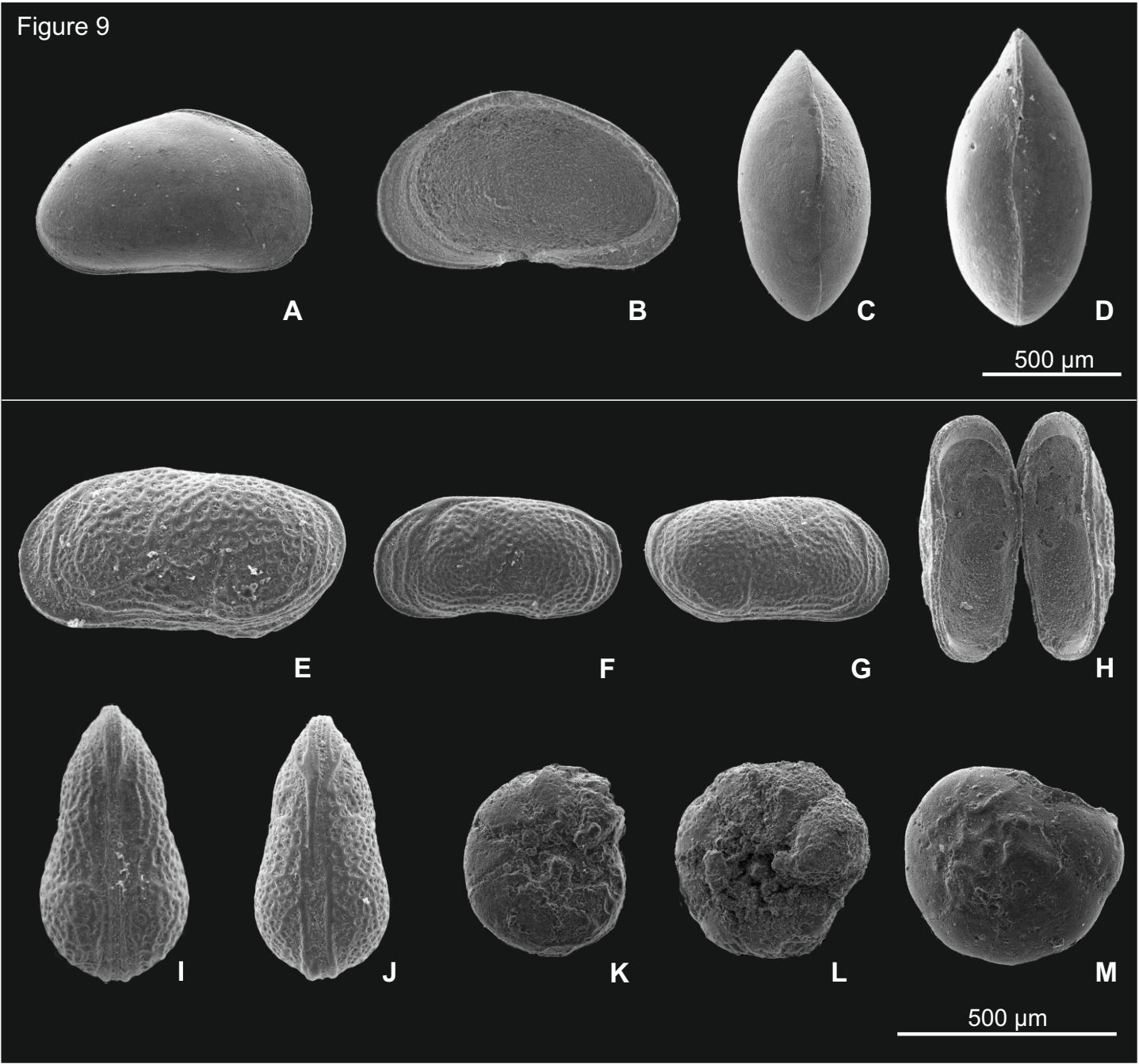
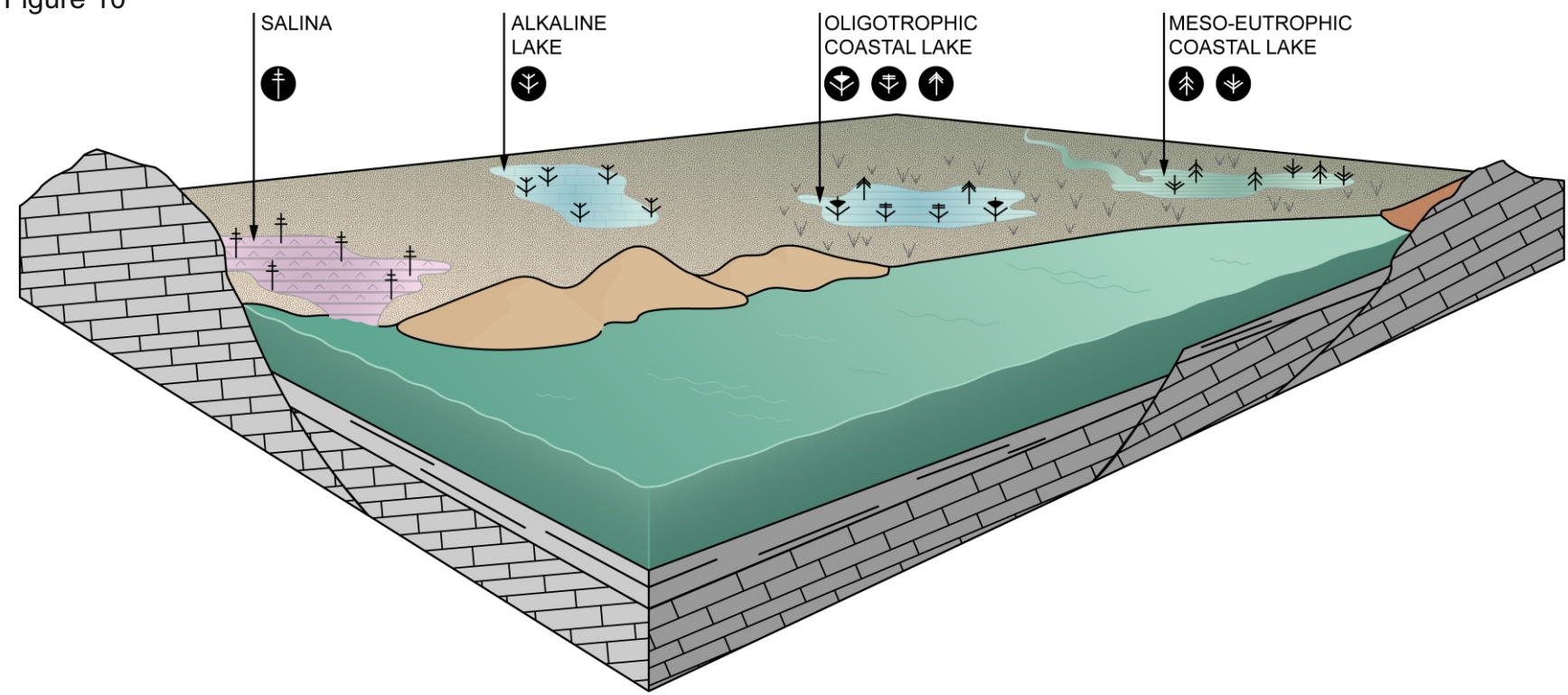


Figure 10



- |                                   |                                             |                                   |                                                      |
|-----------------------------------|---------------------------------------------|-----------------------------------|------------------------------------------------------|
| ⚡ Helophytic plants               | ⚡ <i>Chara molassica</i> var. <i>notata</i> | ⚡ <i>Chara</i> cf. <i>hispida</i> | ↑ <i>Lychnothamnus barbatus</i> var. <i>antiquus</i> |
| † <i>Lamprothamnium papulosum</i> | ⚡ <i>Chara</i> cf. <i>vulgaris</i>          | ⚡ <i>Sphaerochara ulmensis</i>    | ⚡ <i>Nitellopsis merianii</i>                        |

Table 1

| Sample \ Species   |       | Charophytes                             |                        |                                              |                          |                                  |                                           |                                 |                  |                              |                                 | Ostracods                                    | Foraminifera               | Fish teeth         |        |
|--------------------|-------|-----------------------------------------|------------------------|----------------------------------------------|--------------------------|----------------------------------|-------------------------------------------|---------------------------------|------------------|------------------------------|---------------------------------|----------------------------------------------|----------------------------|--------------------|--------|
|                    |       | <i>Nitellopsis</i> (T.) <i>merianii</i> | <i>Nitellopsis</i> sp. | <i>Lychno. barbatus</i> var. <i>antiquus</i> | <i>Lychnothamnus</i> sp. | <i>Chara</i> cf. <i>vulgaris</i> | <i>Chara molassica</i> var. <i>notata</i> | <i>Chara</i> cf. <i>hispida</i> | <i>Chara</i> sp. | <i>Sphaerochara ulmensis</i> | <i>Lamprothamnium papulosum</i> | ? <i>Leptocythere</i> gr. <i>psammophila</i> | <i>Heterocypris salina</i> | <i>Ammonia</i> sp. | indet. |
| El Pi Gros         | PG 3  |                                         |                        |                                              |                          |                                  |                                           | ●                               | ●                |                              |                                 | ●                                            | ●                          |                    |        |
|                    | PG 2  |                                         |                        |                                              |                          |                                  |                                           | ●                               | ●                |                              |                                 | ●                                            | ●                          |                    |        |
| Mas de l´Alonso    | MA 1  | ●                                       |                        |                                              | ●                        |                                  |                                           | ●                               |                  | ●                            |                                 |                                              |                            | ●                  | ●      |
| Vilobí del Penedès | V 6/7 | ●                                       | ●                      | ●                                            |                          |                                  | ●                                         |                                 |                  | ●                            |                                 |                                              |                            | ●                  |        |
|                    | V 5   |                                         |                        |                                              |                          |                                  |                                           |                                 |                  |                              | ●                               |                                              |                            |                    |        |
|                    | V 4   |                                         |                        |                                              |                          |                                  |                                           |                                 |                  |                              | ●                               |                                              |                            |                    |        |
|                    | V 3   |                                         |                        |                                              |                          |                                  |                                           |                                 |                  |                              | ●                               |                                              |                            |                    |        |
|                    | V 1   |                                         |                        |                                              |                          |                                  |                                           |                                 |                  |                              | ●                               |                                              |                            |                    |        |
| els Casots         | C 4   |                                         |                        |                                              |                          | ●                                | ●                                         |                                 |                  |                              |                                 |                                              |                            | ●                  | ●      |

Relative abundance    ● rare    ● abundant    ● rich



Table 2 (supplementary data).

**H**=gyrogonite height,  $\mu\text{m}$ **W**=gyrogonite width,  $\mu\text{m}$ **C.N**=convolution number in lateral view**S.C.H**=spiral cell height,  $\mu\text{m}$ **ISI**=Isopolarity index.  $H/W \times 100$ **ELS CASOTS***Chara molassica* var. *notata*. Sample C4

| H   | W   | C.N | S.C.H | ISI |      |
|-----|-----|-----|-------|-----|------|
| 550 | 439 | 10  | 56    | 125 |      |
| 491 | 369 | 11  | 44    | 133 |      |
| 641 | 404 | 11  | 54    | 159 |      |
| 538 | 418 | 11  | 44    | 129 |      |
| 555 | 408 | 11  | 50    | 136 | mean |
| 491 | 369 | 10  | 44    | 125 | min  |
| 641 | 439 | 11  | 56    | 159 | max  |

*Chara* cf. *vulgaris*. Sample C4

| H   | W   | C.N | S.C.H | ISI |  |
|-----|-----|-----|-------|-----|--|
| 419 | 335 | 11  | 31    | 125 |  |
| 475 | 375 | 12  | 53    | 127 |  |
| 454 | 325 | 10  | 42    | 140 |  |
| 501 | 305 | 10  | 33    | 164 |  |
| 504 | 391 | 12  | 43    | 129 |  |
| 520 | 365 | 11  | 38    | 142 |  |
| 486 | 347 | 11  | 49    | 140 |  |
| 435 | 386 | 10  | 53    | 113 |  |
| 513 | 430 | 11  | 43    | 119 |  |
| 483 | 359 | 10  | 42    | 135 |  |
| 401 | 289 | 12  | 42    | 139 |  |
| 455 | 371 | 11  | 52    | 123 |  |
| 451 | 390 | 13  | 51    | 116 |  |
| 552 | 359 | 11  | 38    | 154 |  |
| 482 | 384 | 11  | 46    | 126 |  |
| 460 | 402 | 11  | 44    | 114 |  |
| 533 | 414 | 13  | 45    | 129 |  |
| 529 | 429 | 12  | 49    | 123 |  |
| 495 | 356 | 13  | 41    | 139 |  |
| 473 | 357 | 11  | 49    | 132 |  |
| 584 | 406 | 12  | 54    | 144 |  |
| 446 | 360 | 11  | 41    | 124 |  |
| 414 | 370 | 10  | 45    | 112 |  |
| 437 | 355 | 11  | 37    | 123 |  |
| 382 | 336 | 12  | 38    | 114 |  |
| 468 | 374 | 11  | 44    | 125 |  |

Table 2 (supplementary data).

|     |     |    |    |     |      |
|-----|-----|----|----|-----|------|
| 456 | 293 | 12 | 40 | 156 |      |
| 465 | 359 | 10 | 41 | 130 |      |
| 481 | 375 | 10 | 54 | 128 |      |
| 442 | 377 | 10 | 60 | 117 |      |
| 470 | 299 | 10 | 48 | 157 |      |
| 444 | 346 | 11 | 45 | 128 |      |
| 456 | 333 | 10 | 39 | 137 |      |
| 481 | 350 | 10 | 33 | 137 |      |
| 474 | 301 | 11 | 42 | 157 |      |
| 378 | 323 | 11 | 48 | 117 |      |
| 435 | 345 | 12 | 43 | 126 |      |
| 487 | 352 | 12 | 37 | 138 |      |
| 468 | 323 | 11 | 48 | 145 |      |
| 543 | 357 | 10 | 53 | 152 |      |
| 492 | 330 | 10 | 57 | 149 |      |
| 426 | 256 | 10 | 39 | 166 |      |
| 449 | 325 | 12 | 40 | 138 |      |
| 428 | 334 | 11 | 37 | 128 |      |
| 386 | 319 | 10 | 39 | 121 |      |
| 470 | 347 | 10 | 45 | 135 |      |
| 467 | 361 | 12 | 46 | 129 |      |
| 501 | 333 | 12 | 43 | 150 |      |
| 419 | 325 | 10 | 42 | 129 |      |
| 421 | 363 | 12 | 46 | 116 |      |
| 466 | 352 | 11 | 44 | 133 | mean |
| 378 | 256 | 10 | 31 | 112 | min  |
| 584 | 430 | 13 | 60 | 166 | max  |

**VILOBÍ DEL PENEDÈS***Chara molassica* var. *notata*. Sample V6/7

| H   | W   | C.N | S.C.H | ISI |
|-----|-----|-----|-------|-----|
| 488 | 320 | 11  | 53    | 153 |
| 570 | 402 | 11  | 56    | 142 |
| 542 | 383 | 10  | 68    | 142 |
| 517 | 331 | 9   | 60    | 156 |
| 498 | 411 | 10  | 52    | 121 |
| 544 | 389 | 9   | 71    | 140 |
| 531 | 368 | 10  | 51    | 144 |
| 557 | 384 | 9   | 72    | 145 |
| 547 | 368 | 11  | 51    | 149 |
| 468 | 333 | 10  | 58    | 141 |
| 523 | 386 | 10  | 57    | 135 |
| 478 | 398 | 10  | 64    | 120 |
| 509 | 344 | 9   | 60    | 148 |
| 558 | 367 | 10  | 50    | 152 |
| 451 | 416 | 8   | 69    | 108 |



Table 2 (supplementary data).

|     |     |    |    |     |      |
|-----|-----|----|----|-----|------|
| 599 | 407 | 10 | 60 | 147 |      |
| 508 | 375 | 9  | 59 | 135 |      |
| 513 | 412 | 8  | 53 | 125 |      |
| 438 | 336 | 10 | 51 | 130 |      |
| 519 | 407 | 10 | 61 | 128 |      |
| 527 | 398 | 9  | 69 | 132 |      |
| 580 | 363 | 11 | 46 | 160 |      |
| 513 | 407 | 9  | 52 | 126 |      |
| 480 | 353 | 10 | 47 | 136 |      |
| 551 | 415 | 9  | 69 | 133 |      |
| 536 | 401 | 9  | 61 | 134 |      |
| 452 | 343 | 9  | 66 | 132 |      |
| 491 | 347 | 10 | 54 | 141 |      |
| 527 | 375 | 11 | 57 | 141 |      |
| 584 | 362 | 12 | 51 | 161 |      |
| 517 | 396 | 9  | 69 | 131 |      |
| 520 | 377 | 10 | 59 | 138 | mean |
| 599 | 416 | 12 | 72 | 161 | max  |
| 438 | 320 | 8  | 46 | 108 | min  |

*Sphaerochara ulmensis*. Sample V6/7

| H   | W   | C.N | S.C.H | ISI |      |
|-----|-----|-----|-------|-----|------|
| 590 | 576 | 10  | 62    | 102 |      |
| 630 | 619 | 9   | 73    | 102 |      |
| 652 | 564 | 9   | 84    | 116 |      |
| 623 | 569 | 9   | 74    | 109 |      |
| 596 | 582 | 9   | 79    | 102 |      |
| 622 | 567 | 10  | 73    | 110 |      |
| 614 | 514 | 10  | 64    | 119 |      |
| 571 | 514 | 10  | 63    | 111 |      |
| 607 | 578 | 10  | 71    | 105 |      |
| 612 | 565 | 10  | 71    | 109 | mean |
| 652 | 619 | 10  | 84    | 119 | max  |
| 571 | 514 | 9   | 62    | 102 | min  |

*Nitellopsis (Tectochara) merianii*. Sample V6/7

| H    | W   | number conv. | conv H | ISI |  |
|------|-----|--------------|--------|-----|--|
| 986  | 863 | 9            | 130    | 114 |  |
| 964  | 856 | 9            | 161    | 113 |  |
| 969  | 790 | 8            | 149    | 123 |  |
| 1035 | 767 | 9            | 130    | 135 |  |
| 907  | 832 | 8            | 145    | 109 |  |
| 781  | 656 | 8            | 104    | 119 |  |
| 914  | 774 | 8            | 170    | 118 |  |
| 1004 | 786 | 7            | 158    | 128 |  |
| 1120 | 957 | 8            | 171    | 117 |  |

Table 2 (supplementary data).

|      |     |   |     |     |      |
|------|-----|---|-----|-----|------|
| 997  | 818 | 7 | 183 | 122 |      |
| 998  | 856 | 7 | 145 | 117 |      |
| 1079 | 914 | 8 | 141 | 118 |      |
| 947  | 867 | 8 | 149 | 109 |      |
| 922  | 886 | 7 | 179 | 104 |      |
| 933  | 852 | 7 | 158 | 110 |      |
| 843  | 786 | 9 | 107 | 107 |      |
| 894  | 810 | 7 | 137 | 110 |      |
| 958  | 866 | 8 | 130 | 111 |      |
| 1023 | 815 | 7 | 123 | 126 |      |
| 804  | 676 | 7 | 104 | 119 |      |
| 955  | 811 | 7 | 158 | 118 |      |
| 854  | 709 | 7 | 118 | 120 |      |
| 959  | 847 | 7 | 131 | 113 |      |
| 1036 | 904 | 8 | 131 | 115 |      |
| 1066 | 913 | 9 | 181 | 117 |      |
| 1004 | 865 | 8 | 152 | 116 |      |
| 899  | 816 | 7 | 130 | 110 |      |
| 943  | 813 | 7 | 164 | 116 |      |
| 988  | 838 | 7 | 139 | 118 |      |
| 928  | 697 | 7 | 131 | 133 |      |
| 951  | 878 | 9 | 114 | 108 |      |
| 1060 | 914 | 9 | 134 | 116 |      |
| 914  | 841 | 8 | 129 | 109 |      |
| 981  | 836 | 9 | 122 | 117 |      |
| 900  | 740 | 8 | 140 | 122 |      |
| 958  | 824 | 8 | 141 | 116 | mean |
| 1120 | 957 | 9 | 183 | 135 | max  |
| 781  | 656 | 7 | 104 | 104 | min  |

*Nitellopsis* sp. Sample V6/7

| H    | W    | C.N | S.C.H | ISI |      |
|------|------|-----|-------|-----|------|
| 1335 | 1053 | 8   | 164   | 127 |      |
| 1243 | 1048 | 9   | 146   | 119 |      |
| 1289 | 1051 | 9   | 155   | 123 | mean |

*Lychnothamnus barbatus* var. *antiquus*. Sample V6/7

| H   | W   | C.N | S.C.H | ISI |      |
|-----|-----|-----|-------|-----|------|
| 934 | 787 | 10  | 113   | 119 |      |
| 726 | 600 | 9   | 107   | 121 |      |
| 974 | 812 | 10  | 153   | 120 |      |
| 878 | 733 | 10  | 124   | 120 | mean |

*Lamprothamnium papulosum*. Sample V5

| H   | W   | C.N | S.C.H | ISI |  |
|-----|-----|-----|-------|-----|--|
| 592 | 464 | 10  | 88    | 128 |  |

Table 2 (supplementary data).

|     |     |    |     |     |
|-----|-----|----|-----|-----|
| 639 | 506 | 10 | 85  | 126 |
| 583 | 491 | 9  | 85  | 119 |
| 700 | 486 | 11 | 70  | 144 |
| 632 | 504 | 10 | 75  | 125 |
| 653 | 490 | 10 | 85  | 133 |
| 608 | 460 | 10 | 63  | 132 |
| 663 | 542 | 11 | 78  | 122 |
| 638 | 495 | 11 | 85  | 129 |
| 634 | 459 | 10 | 86  | 138 |
| 613 | 488 | 11 | 85  | 126 |
| 653 | 484 | 10 | 82  | 135 |
| 598 | 446 | 11 | 68  | 134 |
| 581 | 486 | 10 | 68  | 120 |
| 638 | 499 | 9  | 87  | 128 |
| 627 | 442 | 10 | 73  | 142 |
| 658 | 455 | 10 | 67  | 145 |
| 591 | 458 | 9  | 78  | 129 |
| 650 | 507 | 9  | 73  | 128 |
| 583 | 478 | 9  | 94  | 122 |
| 569 | 431 | 9  | 87  | 132 |
| 639 | 455 | 10 | 88  | 140 |
| 604 | 479 | 9  | 89  | 126 |
| 628 | 528 | 9  | 76  | 119 |
| 657 | 422 | 8  | 100 | 156 |
| 666 | 452 | 8  | 73  | 147 |
| 606 | 460 | 8  | 76  | 132 |
| 610 | 538 | 8  | 93  | 113 |
| 651 | 499 | 9  | 84  | 130 |
| 640 | 460 | 9  | 96  | 139 |
| 619 | 478 | 9  | 87  | 129 |
| 649 | 505 | 9  | 95  | 129 |
| 617 | 467 | 9  | 89  | 132 |
| 639 | 457 | 8  | 85  | 140 |
| 637 | 510 | 8  | 70  | 125 |
| 636 | 447 | 8  | 85  | 142 |
| 625 | 444 | 8  | 71  | 141 |
| 589 | 441 | 9  | 95  | 134 |
| 620 | 484 | 10 | 92  | 128 |
| 586 | 422 | 9  | 87  | 139 |
| 591 | 413 | 8  | 85  | 143 |
| 629 | 433 | 9  | 67  | 145 |
| 690 | 436 | 9  | 72  | 158 |
| 610 | 455 | 9  | 75  | 134 |
| 616 | 462 | 11 | 76  | 133 |
| 599 | 460 | 9  | 78  | 130 |
| 663 | 373 | 9  | 73  | 178 |

Table 2 (supplementary data).

|     |     |    |     |     |      |
|-----|-----|----|-----|-----|------|
| 631 | 511 | 10 | 90  | 123 |      |
| 661 | 448 | 8  | 75  | 148 |      |
| 638 | 501 | 9  | 84  | 127 |      |
| 601 | 474 | 8  | 89  | 127 |      |
| 571 | 391 | 8  | 95  | 146 |      |
| 649 | 506 | 10 | 62  | 128 |      |
| 677 | 459 | 9  | 73  | 147 |      |
| 622 | 459 | 9  | 78  | 136 |      |
| 701 | 528 | 9  | 81  | 133 |      |
| 682 | 519 | 8  | 86  | 131 |      |
| 711 | 452 | 9  | 86  | 157 |      |
| 682 | 480 | 9  | 96  | 142 |      |
| 585 | 348 | 8  | 75  | 168 |      |
| 631 | 469 | 9  | 81  | 135 | mean |
| 711 | 542 | 11 | 100 | 178 | max  |
| 569 | 348 | 8  | 62  | 113 | min  |

**MAS DE L'ALONSO-EL PI GROS***Chara cf. hispida*. Sample PG2

| H   | W   | C.N | S.C.H | ISI |
|-----|-----|-----|-------|-----|
| 783 | 540 | 10  | 80    | 145 |
| 783 | 540 | 9   | 88    | 145 |
| 783 | 513 | 10  | 104   | 153 |
| 783 | 540 | 10  | 88    | 145 |
| 783 | 567 | 9   |       | 138 |
| 567 | 378 | 8   |       | 150 |
| 810 | 540 | 10  |       | 150 |
| 621 | 432 | 10  |       | 144 |
| 621 | 459 | 9   |       | 135 |
| 810 | 540 | 10  |       | 150 |
| 864 | 567 | 8   |       | 152 |
| 594 | 378 | 8   |       | 157 |
| 783 | 540 | 10  |       | 145 |
| 756 | 486 | 9   |       | 156 |
| 810 | 567 | 10  |       | 143 |
| 810 | 540 | 11  |       | 150 |
| 648 | 405 | 10  |       | 160 |
| 540 | 432 | 12  |       | 125 |
| 594 | 405 |     |       | 147 |
| 810 | 567 |     |       | 143 |
| 675 | 351 |     |       | 192 |
| 810 | 540 |     |       | 150 |
| 756 | 567 |     |       | 133 |
| 729 | 540 |     |       | 135 |
| 756 | 540 |     |       | 140 |
| 729 | 513 |     |       | 142 |

Table 2 (supplementary data).

|     |     |     |
|-----|-----|-----|
| 729 | 513 | 142 |
| 756 | 540 | 140 |
| 540 | 405 | 133 |
| 783 | 540 | 145 |
| 810 | 567 | 143 |
| 675 | 486 | 139 |
| 648 | 405 | 160 |
| 702 | 540 | 130 |
| 810 | 540 | 150 |
| 702 | 432 | 163 |
| 891 | 439 | 203 |
| 648 | 567 | 114 |
| 675 | 540 | 125 |
| 540 | 432 | 125 |
| 648 | 432 | 150 |
| 810 | 540 | 150 |
| 567 | 405 | 140 |
| 702 | 567 | 124 |
| 724 | 540 | 134 |
| 756 | 513 | 147 |
| 702 | 432 | 163 |
| 756 | 513 | 147 |
| 648 | 405 | 160 |
| 837 | 540 | 155 |
| 783 | 540 | 145 |
| 702 | 486 | 144 |
| 756 | 459 | 165 |
| 783 | 486 | 161 |
| 675 | 513 | 132 |
| 810 | 567 | 143 |
| 783 | 540 | 145 |
| 783 | 540 | 145 |
| 648 | 405 | 160 |
| 621 | 405 | 153 |
| 702 | 486 | 144 |
| 810 | 567 | 143 |
| 756 | 513 | 147 |
| 540 | 351 | 154 |
| 783 | 540 | 145 |
| 702 | 486 | 144 |
| 594 | 540 | 110 |
| 783 | 567 | 138 |
| 810 | 513 | 158 |
| 810 | 513 | 158 |
| 621 | 486 | 128 |
| 756 | 459 | 165 |

Table 2 (supplementary data).

|     |     |     |    |     |      |
|-----|-----|-----|----|-----|------|
| 594 | 432 |     |    | 138 |      |
| 756 | 513 |     |    | 147 |      |
| 567 | 432 |     |    | 131 |      |
| 594 | 405 |     |    | 147 |      |
| 837 | 405 |     |    | 207 |      |
| 810 | 621 |     |    | 130 |      |
| 756 | 486 |     |    | 156 |      |
| 783 | 567 |     |    | 138 |      |
| 687 | 540 |     |    | 127 |      |
| 756 | 486 |     |    | 156 |      |
| 729 | 486 |     |    | 150 |      |
| 729 | 513 |     |    | 142 |      |
| 702 | 540 |     |    | 130 |      |
| 810 | 540 |     |    | 150 |      |
| 702 | 540 |     |    | 130 |      |
| 783 | 567 |     |    | 138 |      |
| 540 | 378 |     |    | 143 |      |
| 675 | 540 |     |    | 125 |      |
| 810 | 540 |     |    | 150 |      |
| 810 | 540 |     |    | 150 |      |
| 729 | 540 |     |    | 135 |      |
| 621 | 486 |     |    | 128 |      |
| 756 | 540 |     |    | 140 |      |
| 810 | 459 |     |    | 176 |      |
| 726 | 467 |     |    | 155 |      |
| 774 | 548 |     |    | 141 |      |
| 806 | 572 |     |    | 141 |      |
| 854 | 516 |     |    | 166 |      |
| 726 | 500 | 9,6 | 90 | 145 | mean |
| 891 | 621 |     |    | 207 | max  |
| 540 | 351 |     |    | 110 | min  |

*Chara* sp. Sample PG2

| H   | W   | C.N | S.C.H | ISI |      |
|-----|-----|-----|-------|-----|------|
| 612 | 350 | 6   | 100   | 175 |      |
| 625 | 387 | 7   | 75    | 161 |      |
| 825 | 400 | 7   | 112   | 206 |      |
| 687 | 379 | 7   | 96    | 181 | mean |

*Sphaerochara ulmensis*. Sample MA1

| H   | W   | C.N | S.C.H | ISI |  |
|-----|-----|-----|-------|-----|--|
| 477 | 431 | 9   | 50    | 111 |  |
| 433 | 407 | 10  | 41    | 106 |  |
| 413 | 330 | 10  | 39    | 125 |  |
| 413 | 378 | 9   | 43    | 109 |  |
| 446 | 385 | 10  | 43    | 116 |  |

Table 2 (supplementary data).

|     |     |    |    |     |      |
|-----|-----|----|----|-----|------|
| 398 | 374 | 9  | 53 | 106 |      |
| 447 | 379 | 9  | 44 | 118 |      |
| 447 | 363 | 9  | 54 | 123 |      |
| 449 | 409 | 10 | 61 | 110 |      |
| 446 | 410 | 10 | 52 | 109 |      |
| 418 | 375 | 10 | 43 | 111 |      |
| 447 | 421 | 10 | 66 | 106 |      |
| 442 | 404 | 9  | 45 | 109 |      |
| 426 | 383 | 9  | 60 | 111 |      |
| 466 | 402 | 9  | 53 | 116 |      |
| 460 | 417 | 9  | 57 | 110 |      |
| 410 | 388 | 9  | 62 | 106 |      |
| 437 | 397 | 10 | 48 | 110 |      |
| 424 | 402 | 10 | 57 | 105 |      |
| 436 | 406 | 9  | 63 | 107 |      |
| 421 | 375 | 9  | 62 | 112 |      |
| 453 | 378 | 10 | 54 | 120 |      |
| 437 | 390 | 9  | 51 | 112 |      |
| 437 | 391 | 9  | 52 | 112 | mean |
| 477 | 431 | 10 | 66 | 125 | max  |
| 398 | 330 | 9  | 39 | 105 | min  |

*Lychnothamnus* sp. Sample MA1

| H    | W   | C.N | S.C.H | ISI |
|------|-----|-----|-------|-----|
| 1022 | 777 | 8   | 70    | 131 |