

**Charophyte flora from the Miocene of Zahle
(Beeka Valley, Lebanon).
Biostratigraphic, palaeoenvironmental
and palaeobiogeographical implications**

Josep SANJUAN & Mohammad ALQUDAH

DIRECTEUR DE LA PUBLICATION : Bruno David,
Président du Muséum national d'Histoire naturelle

RÉDACTEUR EN CHEF / *EDITOR-IN-CHIEF*: Didier Merle

ASSISTANTS DE RÉDACTION / *ASSISTANT EDITORS*: Emmanuel Côté (geodiv@mnhn.fr); Anne Mabilie

MISE EN PAGE / *PAGE LAYOUT*: Emmanuel Côté

COMITÉ SCIENTIFIQUE / *SCIENTIFIC BOARD*:

Christine Argot (MNHN, Paris)
Beatriz Azanza (Museo Nacional de Ciencias Naturales, Madrid)
Raymond L. Bernor (Howard University, Washington DC)
Alain Blicq (USTL, Villeneuve d'Ascq)
Henning Blom (Uppsala University)
Jean Broutin (UPMC, Paris)
Gaël Clément (MNHN, Paris)
Ted Daeschler (Academy of Natural Sciences, Philadelphie)
Bruno David (MNHN, Paris)
Gregory D. Edgecombe (The Natural History Museum, Londres)
Ursula Göhlich (Natural History Museum Vienna)
Jin Meng (American Museum of Natural History, New York)
Brigitte Meyer-Berthaud (CIRAD, Montpellier)
Zhu Min (Chinese Academy of Sciences, Pékin)
Isabelle Rouget (UPMC, Paris)
Sevket Sen (MNHN, Paris)
Stanislav Štámbek (Museum of Eastern Bohemia, Hradec Králové)
Paul Taylor (The Natural History Museum, Londres)

COUVERTURE / *COVER*:

Réalisée à partir des Figures 3, 5 et 7 de cet article/*created from Figures 3, 5 and 7 of this article.*

Geodiversitas est indexé dans / *Geodiversitas is indexed in*:

- Science Citation Index Expanded (SciSearch®)
- ISI Alerting Services®
- Current Contents® / Physical, Chemical, and Earth Sciences®
- Scopus®

Geodiversitas est distribué en version électronique par / *Geodiversitas is distributed electronically by*:

- BioOne® (<http://www.bioone.org>)

Les articles ainsi que les nouveautés nomenclaturales publiés dans *Geodiversitas* sont référencés par /
Articles and nomenclatural novelties published in Geodiversitas are referenced by:

- ZooBank® (<http://zoobank.org>)

Geodiversitas est une revue en flux continu publiée par les Publications scientifiques du Muséum, Paris
Geodiversitas is a fast track journal published by the Museum Science Press, Paris

Les Publications scientifiques du Muséum publient aussi / *The Museum Science Press also publish*:
Adansonia, Zoosystema, Anthropolozologica, European Journal of Taxonomy, Naturae.

Diffusion – Publications scientifiques Muséum national d'Histoire naturelle
CP 41 – 57 rue Cuvier F-75231 Paris cedex 05 (France)
Tél.: 33 (0)1 40 79 48 05 / Fax: 33 (0)1 40 79 38 40
diff.pub@mnhn.fr / <http://sciencepress.mnhn.fr>

© Publications scientifiques du Muséum national d'Histoire naturelle, Paris, 2018
ISSN (imprimé / *print*): 1280-9659/ ISSN (électronique / *electronic*): 1638-9395

Charophyte flora from the Miocene of Zahle (Beeka Valley, Lebanon). Biostratigraphic, palaeoenvironmental and palaeobiogeographical implications

Josep SANJUAN

Department of Geology, American University of Beirut (AUB),
11-0236, Beirut (Lebanon)
js76@aub.edu.lb
josepst.juan@hotmail.com
(corresponding author)

Mohammad ALQUDAH

Yarmouk University, Faculty of Science,
Department of Earth and Environmental Science, 21163 Irbid (Jordan)

Submitted on 20 July 2017 | accepted on 29 January 2018 | published on 24 May 2018

urn:lsid:zoobank.org:pub:64D30CC3-102C-4A1F-A5AF-C9969BDDDFEE

Sanjuan J. & Alqudah M. 2018. — Charophyte flora from the Miocene of Zahle (Beeka Valley, Lebanon). Biostratigraphic, palaeoenvironmental and palaeobiogeographical implications. *Geodiversitas* 40 (10): 195–209. <https://doi.org/10.5252/geodiversitas2018v40a10>. <http://geodiversitas.com/40/10>

ABSTRACT

Neogene lacustrine deposits in Zahle, western margin of the Bekaa Valley (Lebanon), are studied from a biostratigraphic and paleoenvironmental point of view using fossil charophytes. These sediments contain a well-preserved charophyte assemblage described and illustrated here for the first time including the taxa: *Nitellopsis* (*Tectochara*) *merianii* Grambast & Soulié-Märsche, 1972, *Lychnothamnus barbatus* var. *antiquus* Soulié-Märsche, 1989, *Chara* aff. *microcera* Grambast & Paul, 1965 and *Chara* sp. *Nitellopsis* (*T.*) *merianii* has been reported in several European and Asiatic localities ranging in age from Late Eocene to Pliocene, *L. barbatus* var. *antiquus* has been found in several European Miocene localities in Europe and Turkey, while *Chara* aff. *microcera* has been documented from a large number of west European localities ranging in age from Early Oligocene to Early Miocene. Based on these data, we inferred that the basal part of the lacustrine deposits of Zahle is lower Miocene in age which is consistent with isotopic results obtained from basalts located northern, laterally and above the lacustrine sequence of Zahle. The palaeoenvironmental characteristics at the base of these deposits are inferred by comparing of the occurrence of *N. (T.) merianii* and *L. barbatus* var. *antiquus* with the ecological requirements of their nearest living relatives (*Nitellopsis obtusa* and *Lychnothamnus barbatus*). This suggests that the Bekaa Valley was occupied by a permanent, shallow oligotrophic freshwater lake during the Miocene. This study also provides valuable data about the palaeogeographic distribution of Neogene charophyte from Lebanon and the Middle East region.

KEY WORDS

Charophyta,
Bekaa Valley,
Neogene,
Miocene,
biostratigraphy,
palaeoecology.

RÉSUMÉ

Une flore de characées du Miocène de Zahlé (Vallée de Bekaa, Liban). Implications biostratigraphiques, paléoenvironnementales et paléobiogéographiques.

Les dépôts lacustres localisés de la région de Zahlé, dans la marge ouest du bassin de Bekaa (Liban), sont étudiés d'un point de vue biostratigraphique et paléoenvironnemental à partir des characées fossiles. Ces sédiments contiennent un assemblage très bien préservé, décrit et illustré dans ce travail pour la première fois. L'assemblage est composé de quatre espèces, *Nitellopsis* (*Tectochara*) *merianii* Grambast & Soulié-Märsche, 1972, *Lychnothamnus barbatus* var. *antiquus* Soulié-Märsche, 1989, *Chara* aff. *microcera* Grambast & Paul, 1965 et *Chara* sp. La première espèce a été signalée dans plusieurs localités, allant de l'Éocène supérieur au Pliocène, en Europe et en Asie. *Lychnothamnus barbatus* var. *antiquus* a été rapportée de plusieurs localités du Miocène d'Europe et de Turquie. *Chara* aff. *microcera* a été documentée dans un grand nombre de dépôts européens, allant de l'Oligocène inférieur au Miocène inférieur. Sur la base de ces données, nous déduisons que la partie inférieure des dépôts lacustres dans la région de Zahlé est d'âge Miocène inférieur, ce qui est compatible avec les études isotopiques réalisées dans les basaltes d'âge Miocène supérieur qui se trouvent latéralement et au-dessus de ces dépôts, vers le nord. Les caractéristiques du paléoenvironnement à la base des dépôts lacustres de la région de Zahlé peuvent être déduites par comparaison de *N. (T.) merianii* et de *L. barbatus* var. *antiquus* avec l'écologie des représentants vivants plus proches de ces espèces, *Nitellopsis obtusa* et *Lychnothamnus barbatus*. Ces caractéristiques suggèrent que le bassin de Bekaa a été occupé par un lac permanent, peu profond, baigné dans des eaux oligotrophiques. Cette étude fournit des données précieuses sur la distribution paléogéographique des espèces de characées du Néogène du Liban et du Moyen-Orient.

MOTS CLÉS

Charophyta,
bassin de Bekaa,
Néogène,
Miocène,
biostratigraphie,
paléoécologie.

INTRODUCTION

Charophytes represent a group of land plants ancestors living in freshwater or brackish environments. Their calcified fructifications i.e., gyrogonites and utricles, generally fossilize. Fossil gyrogonites have been recovered in non-marine deposits worldwide from the Silurian to the present (Feist *et al.* 2005). These structures have been traditionally used as non-marine biostratigraphic markers due to their specific morphology and relatively high evolutionary rates. Neogene sedimentary rocks from Bekaa Valley (Lebanon) show relative continuous exposures, little lateral facies changes, little post-depositional diagenetic alteration and extremely high content of microfossils. However, these deposits have been poorly studied from the viewpoints of sedimentology, biostratigraphy and palaeoecology. These rocks are exceptionally well-exposed in the western margin of the Bekaa Valley near the village of Zahlé (Fig. 1).

This study documents and describes, for the first time, the charophyte flora from Neogene lacustrine deposits of Lebanon and Middle East, highlighting its palaeoenvironmental and palaeobiogeographic significance and shedding new light on the age of the base of these lacustrine deposits.

MATERIALS AND METHODS

In order to characterize and improve the relative age and palaeoenvironment of these Neogene lacustrine deposits in Zahlé two consecutive field works were performed during October 2016 and May 2017 in the basal part of the lacustrine deposits

of Zahlé located along the western margin of the Bekaa Valley (Fig. 1). This section was sampled for microfossils. Hundreds of well-preserved gyrogonites were obtained from the studied deposits along with other microfossils such as gastropods, ostracods and vertebrate remains.

Fossil remains were recovered from a section stratigraphically located at the lower part of the lacustrine deposits in the village of Zahlé (UTM at the base of the section: 33°59'19.1"N, 35°49'33"E, UTM at the top of section: 33°51'15.12"N, 35°53'49"E). Microfossils were obtained from 4 samples of grey lacustrine marls collected from the aforementioned section (Fig. 2). About 2 kg of sediment per sample were disaggregated in water and later sieved using sieves with mesh apertures of 1.0 cm, 0.85, 0.65, 0.35 and 0.25 mm. Gyrogonites and other microfossils such as gastropods and ostracods were picked out under a light microscope. Selected gyrogonites were measured taking into account the morphometric parameters, i.e., gyrogonite height (µm), gyrogonite width (µm), number of spiral turns observed in lateral view and the isopolarity index (gyrogonite height/gyrogonite width × 100). Gyrogonites were measured using the software Motic Images Plus 2.0 ML in a stereomicroscope Motic BA310 housed in the Departament de Dinàmica de la Terra i de l'Oceà (Facultat de Geologia, Universitat de Barcelona). Selected gyrogonites were photographed using a scanning electronic microscope MIRA 3LMU with OXFORD EDX detector by TESCAN located in the Central Research Science Laboratory (CRSL) of the American University of Beirut. The material is housed in the Geology Museum of the American University of Beirut (acronym AUBGM).

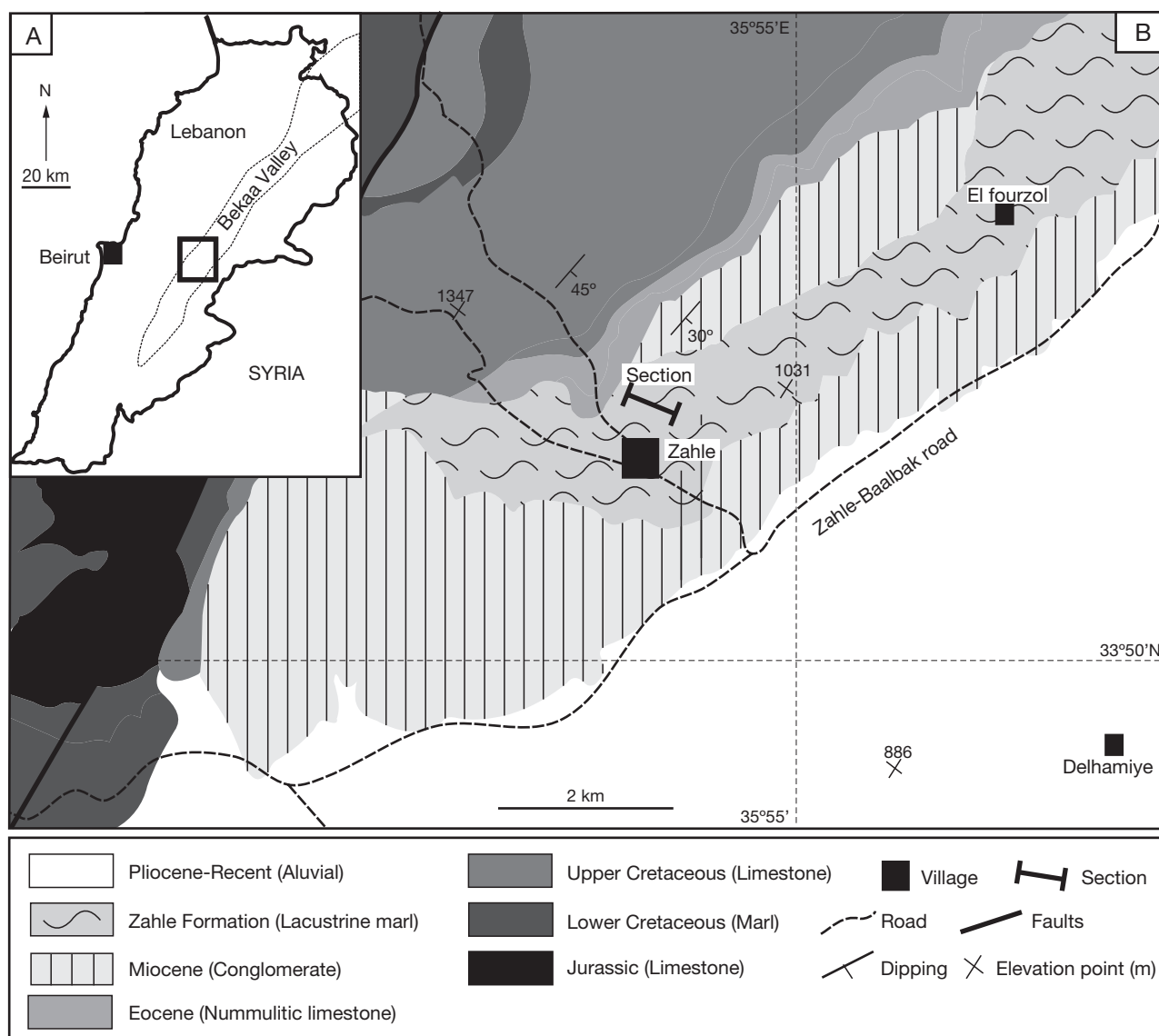


FIG. 1. — Geological sketch of the western part of the Bekaa Valley showing the location of the studied section (modified from Dubertret 1945).

GEOLOGICAL SETTING

The Bekaa Valley is a tectonic basin located in the Levant area (Lebanon) bounded by two anticline-systems i.e., the western Lebanese anticlines forming the Mount Lebanon, and the eastern Lebanese anticline represented by the Anti-Lebanon mountain range. The origin of the Bekaa Valley is related to the folding activity due to the collision between the African-Arabian Plate and the Eurasian Plate from the late Cretaceous (Lateef 2007 and references herein). This tectonic activity also known as the Syrian Arc Event caused an emergence of Mount Lebanon and Anti-Mount Lebanon.

During the late Cretaceous, all the Levant area underwent a period of tectonic compression creating a rugged and undulatory regional topography that lead in the K/Pg boundary the partial emergence of isolated islands encircled by a shallow sea (Ponikarov *et al.* 1967; Sharland *et al.* 2001). During the Early Paleogene, further emergence took place in the area and larger

parts of the low-amplitude anticlines emerged forming longitudinal islands oriented NE-SW within the shallow Tethys Sea. These longitudinal islands represent the young stages of the well-known morphostructural zones of “Mount Lebanon” and “Anti-Lebanon” (Lateef 2007). Paleogene rocks of Bekaa Valley include deposits of marine and non-marine origin. Paleocene and lower/middle Eocene rocks are represented by chalky limestone and marls deposited in a shallow sea environment. Later, during the Late Eocene-Oligocene, a complete retreat of marine conditions took place in the Bekaa Valley due to the crustal shortening process related to the tectonic convergence between the African-Arabian Plate and the Eurasian Plate. This tectonic event produced a regional uplift of the Valley shifting the sedimentary environment conditions from shallow marine to continental, mainly alluvial and lacustrine (Beydoun 1999; Sharland *et al.* 2001). However, the precise date of the continentalization of the basin is unclear due to the scarcity of documentation and difficulties in the recognition of strata

which show monotonous lithologies and are partially covered in some areas. Thus, no Late Eocene/Oligocene/Early Miocene continental deposits have already been identified in the Bekaa Valley until now (Lateef 2007).

The Neogene represents a key-period regarding the geologic evolution of the Bekaa Valley. As a consequence of high tectonic activity associated with the Dead Sea Fault System, an intense synorogenic deposition took place filling the Bekaa Valley as well as other Levant tectonic basins.

During the early Miocene, tectonism affected the Bekaa Valley causing a larger fold amplitude which resulted in an increased erosion, sediment transport and hence more deposition (Lateef 2007). Materials from this period are mainly characterized by conglomerates related to alluvial fan deposits. The Levant Fracture/Dead Sea Fault appeared later in the Middle/Late Miocene. This tectonic event favoured the development of volcanism in the area and the uplift of the Mount Lebanon and the Anti-Lebanon mountain chain (Ponikarov *et al.* 1967). On the other hand, this Miocene tectonic activity deepened the proto-Bekaa Valley resulting in the increase of accommodation space infilled by more synorogenic alluvial and lacustrine deposits. Hence, during the middle Miocene-Late Miocene times the Bekaa Valley hosted a wide-spread lacustrine system. The south and middle areas of Bekaa were occupied by large lakes with high lateral extension, ranging from the closure of southern Bekaa basin i.e., nearby the region of Ghazzah and Mansoura Villages in the south-southwest, to Iaatt Village in the north-northeast. Deposits from this period are characterized by lacustrine marls located in central areas of the basin and thick fluvio-lacustrine conglomerates located in peripheral positions. These deposits are specially well-exposed in the Zahle area (Zahle town), the locality chosen for this micropalaeontological study. A second orogenic phase commenced during the Pliocene- middle Pleistocene time (Lateef 2007). This young tectonic event is characterized by strong faulting, folding and land uplift. The Al Yemmouna fault and associated small pull-apart basins appeared on the scene during this phase on the western flank of the basin.

Neogene rocks of Zahle were first studied by Dubertret (1945, 1955) who identified and described a stratigraphic set of beds termed in French “poudingues et marnes lacustres de Zahle” i.e., conglomerates and lacustrine marls of Zahle. This author defined this interval as a sequence of conglomerates passing upwards to thick, finely stratified marl deposits, rich in gastropods and intercalated with thin layers of lignite. Dubertret (1945) noted that neither vertebrate fossils nor other biostratigraphically useful fossils had been recovered from these lacustrine deposits. However, he was able to infer a relative age of middle-upper Miocene by imprecise lithostratigraphic correlation with similar rocks exposed northwards in the basin, in the areas of Tripoli (north of Lebanon) and Homs (southwest of Syria). Lateef (2003) obtained an absolute age of 10.4 ± 0.37 Ma and 10.87 ± 0.31 Ma for the basalts pouring north of Bekaa Valley situated laterally and above the lacustrine deposits of Zahle, which corresponds to late Miocene age. The charophyte flora reported herein comes from a section located near the village of Zahle, along the western margin of the Bekaa Valley (Fig. 1). The section studied at Zahle shows a 60 m of non-marine deposits

(mainly marls) with abundant fossils. This section is assigned here to the basal part of the informally termed Zahle Formation (Dubertret 1975). These deposits represent a sequence of clastic materials with calcareous breccia and conglomerates, lacustrine marls, limestones and lignite layers that flanks either sides of the Bekaa Valley. This sedimentary sequence has been previously given an imprecise Miocene age. Biostratigraphic significant fossils from these strata were first reported by Kansou (1961) who discovered a horse tooth of *Hipparion* suggesting a Miocene age. Malez & Forsten (1989) described in detail this horse tooth from Zahle and reported a new *Hipparion* fossil locality in the area of Kefraya. López-Antoñanzas *et al.* (2015) recently described in the same deposits of Zahle a mammal assemblage composed of rodents belonging to genera *Proafricanomys* López-Antoñanzas, Knoll, Maksoud & Azar, 2015 and *Progonomys* Schaub, 1938 supporting the correlation with the European Mammal Neogene reference levels MN 10 or MN 11 (late Miocene).

STRATIGRAPHY

The studied section overlies an Eocene nummulitic limestone bed dipping 50° East. The Neogene deposits dip 30° East. Neogene rocks consist of fossiliferous marls, alternated with thin limestone beds and few lignite horizons deposited in a lacustrine environment (Fig. 2). A 30 cm thick dark interval within the marls related to an air-fall ash is also present. Marl beds are monotonous, metric in thickness and light grey to yellowish in colour. Marls and limestones are very rich in well-preserved fossil remains of gastropods, charophytes and ostracods. Small gastropods are especially abundant in most of the intervals, representing by far the dominant fossil of the whole section. The gastropod fauna was already identified by Dubertret (1945) who reported the presence of two main morphotypes belonging to genera *Hydrobia* Hartmann, 1821 and *Melanopsis* Férussac, 1807. Despite the low sedimentological variation, distinctive vertical succession of facies can be observed: metric marl beds, intercalated with centimetric lignite horizons, topped by thin limestone beds (Fig. 2). Marls are organised in gray to yellowish sets of beds ranging in thickness from 1 to 0.3 m. They show diffuse lamination and contain abundant fossil remains, mainly gastropods, and charophytes. Limestone intervals are about 20-50 cm thick showing high concentration of fossils (packstone of gastropods). Lignite layers are 5-10 cm thick showing poorly preserved comminute plant debris. No edaphic features have been observed underlying these lignite layers. A 30 cm thick dark marl interval occurs at the base of the section (Fig. 2).

The vertical succession of facies from marls with some lignite intervals grading upwards to limestones can be interpreted as the increasing activity of lime-producing organisms in the shallower and well-illuminated environments located in the margin of a paleolake. Marls were deposited in more distal and deeper lacustrine facies than limestones. Despite the high content of fossils in the marl interval, they show diffuse lamination and they contain few lignite horizons suggesting that the lake bottom was occasionally anoxic, hindering bioturbation and preserving the plant remains (Gierlowski-Kordesch 2010).

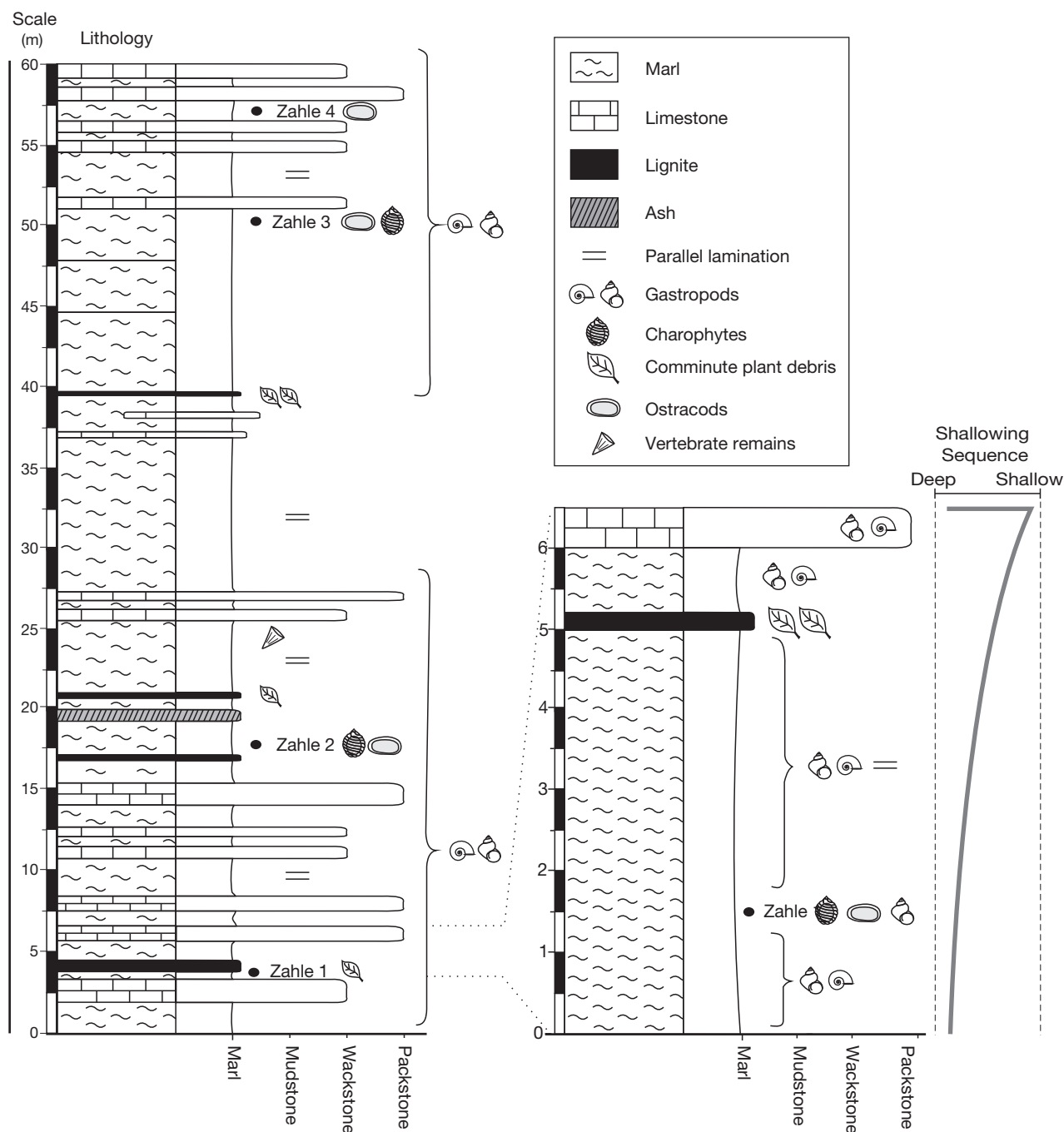


FIG. 2. — Stratigraphic log for Zahle section (base of the lacustrine deposits of Zahle) showing a detail of a shallowing sedimentary cycle.

Lignite horizons show poorly-preserved comminute plant remains. Moreover, no edaphic features have been observed underlying lignite layers indicating that plant remains were eventually transported and sank to form an allochthonous assemblage in the lake bottom. Microfossil content is composed of charophytes (four species here illustrated and described), ostracods belonging to the *Cyprideis* Jones, 1857 genera and a diverse assemblage of mollusks. Freshwater gastropods belonging to Hydrobiidae family are especially abundant in the studied samples. Fossils are extremely well-preserved and charophytes show their mineralogical constituents (endocalcine

and ectocalcine), without any trace of dissolution or corrosion. Gyrogonites do not show any evidence of fragmentation or erosion and they occur in association with fragments of thalli. These evidences suggest that fossils were buried *in situ* or after gentle transport from the original growing locality. Fossils occur in both marls and limestones and from the sedimentological viewpoint they correspond to biogenic carbonate producers in well-oxygenated and well-illuminated shallow permanent lake bottoms. Moreover, the absence of ripples and broken fossils suggesting a quite environment, without the action of strong waves or currents.

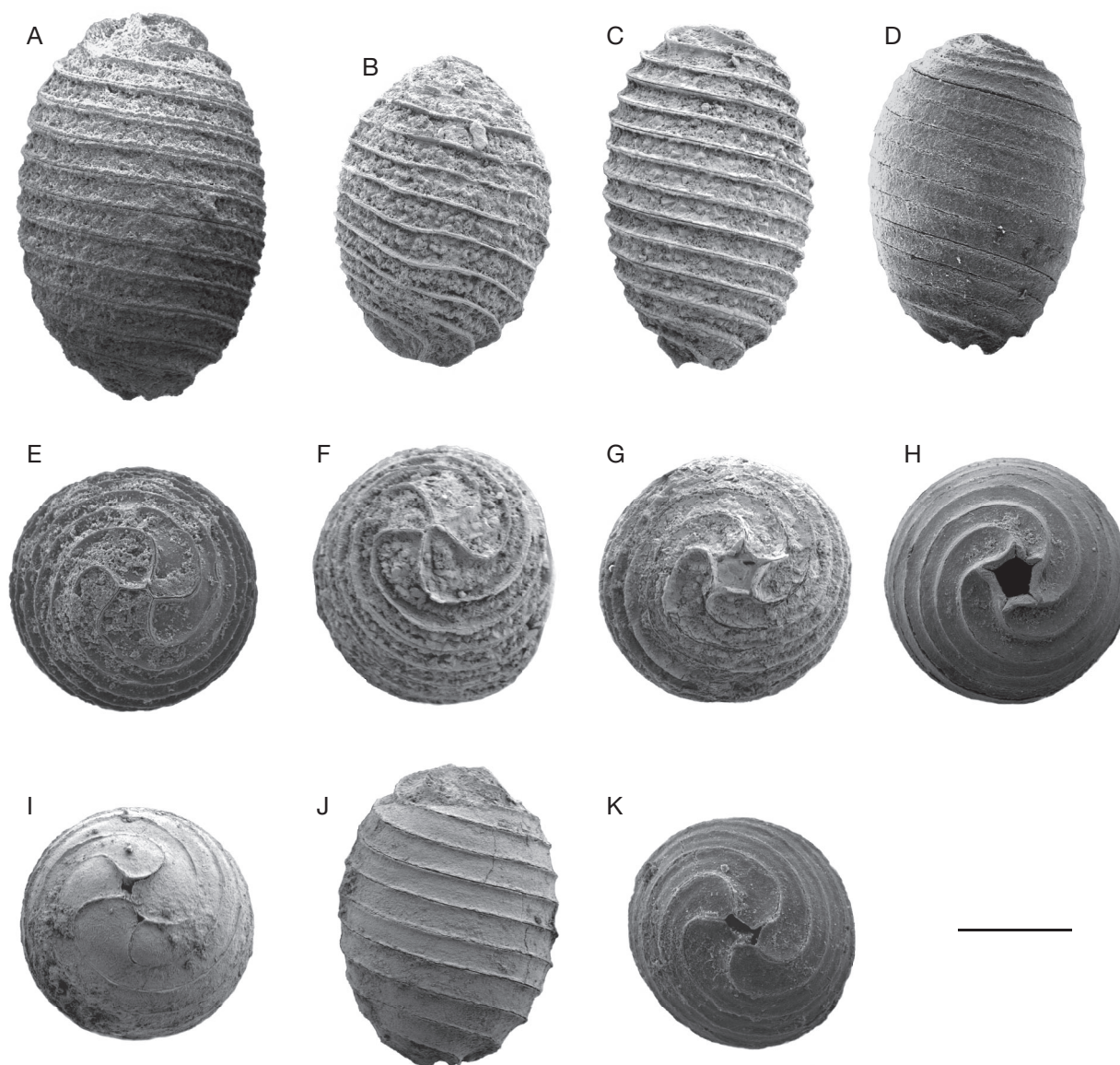


FIG. 3. — Charophytes from the lacustrine deposits of Zahle, sample Zahle 1: **A-H**, *Chara* aff. *microcera* Grambast & Paul, 1965; **A**, lateral view, no. 2017001 AUBGM; **B**, lateral view, no. 2017002 AUBGM; **C**, lateral view, no. 2017003 AUBGM; **D**, lateral view, no. 2017004 AUBGM; **E**, apical view, no. 2017004 AUBGM; **F**, apical view, no. 2017002 AUBGM; **G**, basal view, no. 2017005 AUBGM; **H**, basal view, no. 2017006 AUBGM; **I-K**, *Chara* sp.; **I**, apical view, no. 2017007 AUBGM; **J**, lateral view, no. 2017008 AUBGM; **K**, basal view, no. 2017009 AUBGM. Scale bar: 200 µm.

SYSTEMATIC PALAEOBOTANY

Division CHAROPHYTA Migula, 1890
 Class CHAROPHYCEAE Smith, 1938
 Order CHARALES Lindley, 1836
 Family CHARACEAE Richard, 1815 *ex* Agardh, 1824
 Genus *Chara* Vaillant, 1719

Chara aff. *microcera* Grambast & Paul, 1965
 (Figs 3A-H; 4)

Chara aff. *microcera* Grambast & Paul, 1965: 244, pl. 2, figs 10-14.

MATERIAL EXAMINED. — 39 well-preserved gyrogonites have been recovered from sample Zahle 1.

DESCRIPTION

Small to medium sized gyrogonites, very variable in size, 475-720 µm high (mean 617 µm) and 340-474 µm wide (mean 414 µm), elongate, prolate to perprolate in shape, with an isopolarity index ranging from 120 to 179 (mean 144) (Fig. 4). Ten to thirteen (frequently eleven) convolutions are visible in lateral view (52 µm high in mean value). Spiral cells are generally concave. The 48% of the population display a characteristic ornamentation consisting in isolated small tubercles irregularly arranged along the spiral cells following one or two rows (Fig. 3B, C). The apex is psilocharoid, prominent, sometimes ornamented with isolated small tubercles. The base is rounded or slightly pointed showing a shallow pentagonal basal pore.

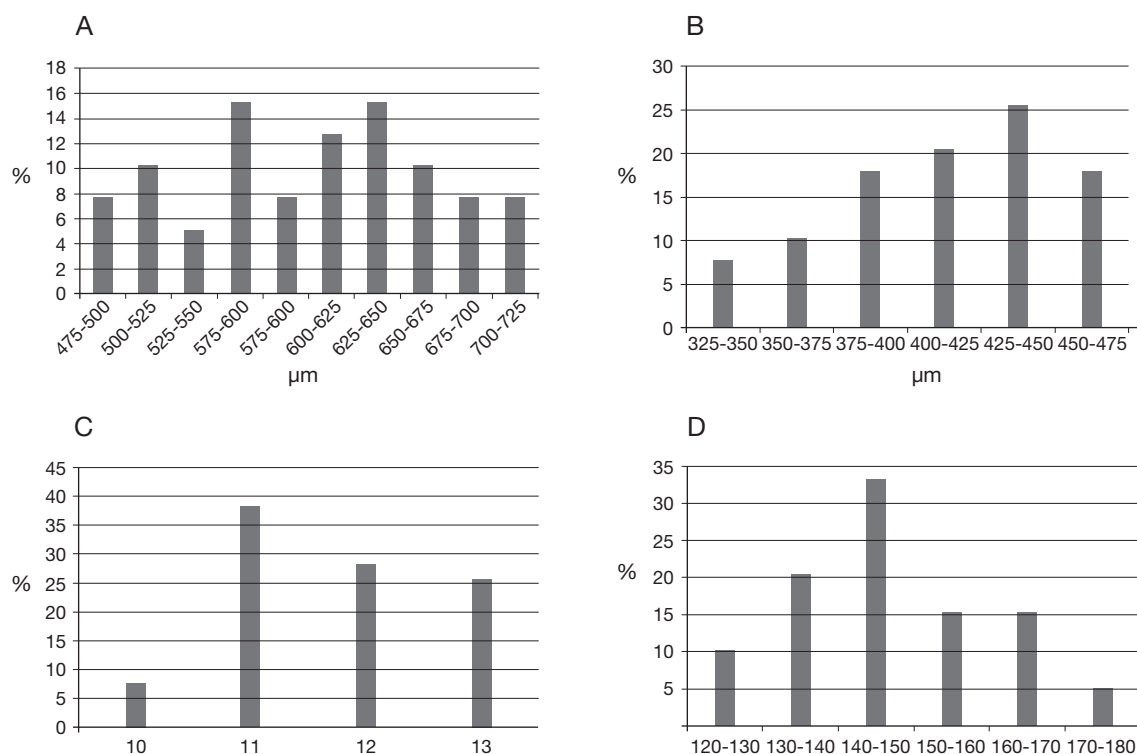


FIG. 4. — Biometric values of *Chara* aff. *microcera* Grambast & Paul, 1965 from sample Zahle 1 (n = 39 gyrogonites): **A**, gyrogonite height (µm); **B**, gyrogonite width (µm); **C**, number of convolutions visible in lateral view; **D**, isopolarity index (ISI = $h/w \times 100$).

BIOSTRATIGRAPHY

The biostratigraphic distribution of *Chara* aff. *microcera* in Europe is quite wide ranging in age from the Lower Oligocene (middle Rupelian) to Lower Miocene (Burdigalian).

PALAEOECOLOGY

Sedimentological analysis coupled with taphonomical studies is a powerful tool to infer the palaeoenvironmental requirements of fossil charophytes. Well-preserved gyrogonite populations of *Chara* aff. *microcera* have traditionally been recovered from thick marl/limestone deposits related to well-developed lacustrine systems such as in limestones from Étampes in the Paris basin (France) or Tàrrega in the Ebro basin (Spain) (Grambast & Paul 1965; Sanjuan *et al.* 2014). The gyrogonite population from Zahle does not show any evidence of fragmentation or erosion preserving their delicate ornamentation which suggest that gyrogonites were buried in situ. The samples have been collected within a thick marl layer with abundant freshwater gastropods and other lacustrine-related charophyte species. Taphonomic and sedimentologic evidence, together with the abundance of other charophyte species which their extant representatives are related to perennial lake facies i.e., *Nitellopsis* (*T.*) *merianii* and *Lychnothamnus barbatus*, suggests that *Chara* aff. *microcera* also grew in well-developed perennial freshwater lakes.

DISTRIBUTION

Chara aff. *microcera* has been recorded from a large number of west European localities in many Paleogene/Neogene

basins i.e., France (Paris, Aquitaine, Provence), Switzerland (Swiss Molasse), Germany (Rhine Graben) and Spain (Ebro and Tajo), (Riveline 1986; Sanjuan & Martín-Closas 2014 and references herein). The occurrence of *Chara* aff. *microcera* in lacustrine deposits from Zahle represents its easternmost locality.

Chara sp.
(Fig. 3I-K)

MATERIAL EXAMINED. — 10 well-preserved gyrogonites have been recovered from sample Zahle 1.

DESCRIPTION

Small to medium sized gyrogonites, 486–637 µm high (mean 555 µm) and 375–456 µm wide (mean 416 µm), elongate and prolate in shape, with an isopolarity index ranging from 120 to 144 (mean 130). Nine to eleven convolutions are visible in lateral view in mean value). Spiral cells flat to concave, about 54 µm wide and without ornamentation. Apex psilocharoid and prominent. Base rounded to slightly pointed showing a small pentagonal basal pore.

REMARKS

This population from Zahle 1 belongs to the genus *Chara*, although the reduced number of specimens found hinders at present their specific attribution.

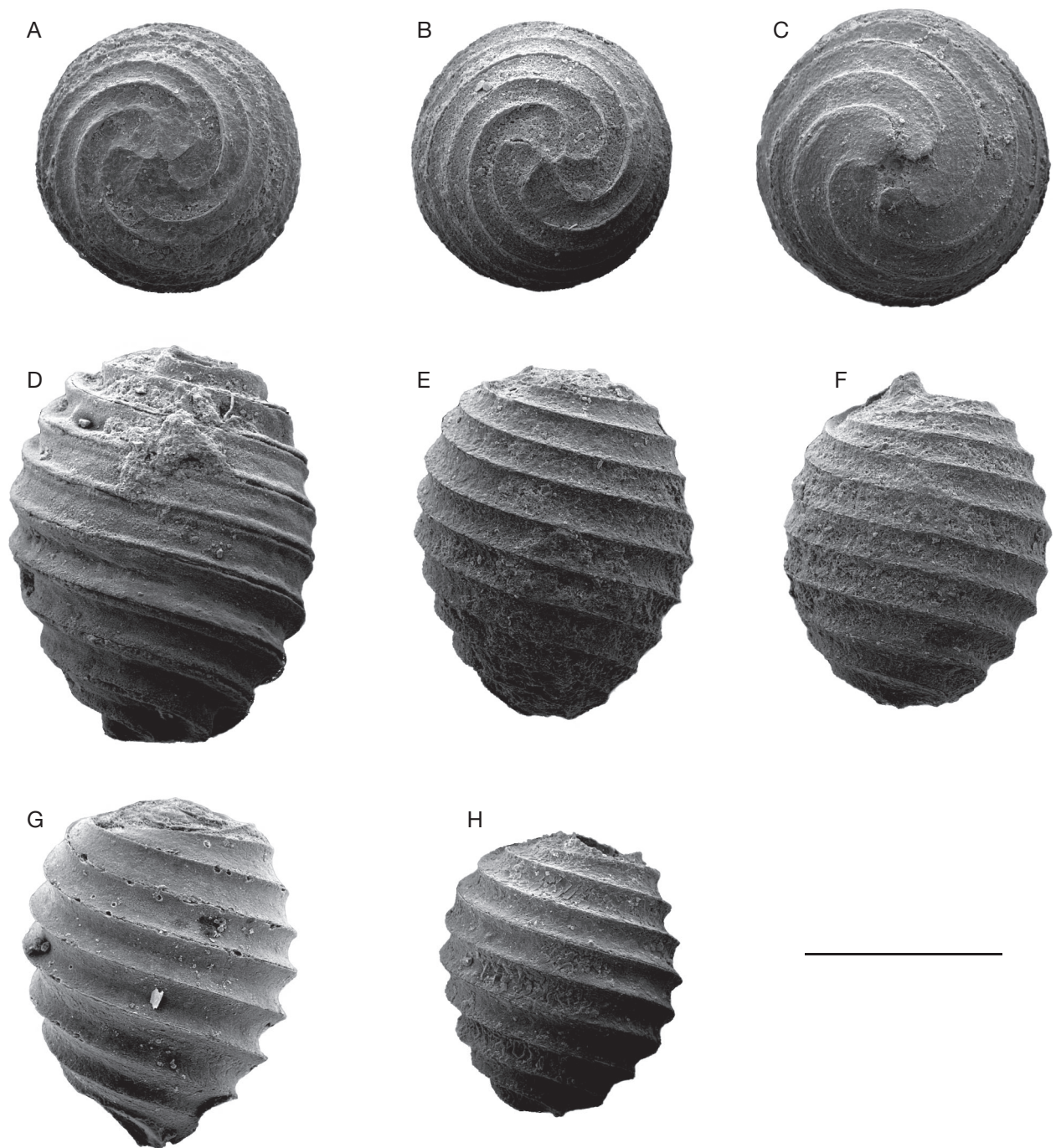


FIG. 5. — Charophytes from the lacustrine deposits of Zahle, sample Zahle 2: **A-H**, *Lychnothamnus barbatus* var. *antiquus* Soulié-Märsche, 1989; **A**, apical view, no. 2017010 AUBGM; **B**, apical view, no. 2017011 AUBGM; **C**, basal view, no. 2017012 AUBGM; **D**, lateral view, no. 2017013 AUBGM; **E**, lateral view, no. 2017014 AUBGM; **F**, lateral view, no. 2017015 AUBGM; **G**, lateral view, no. 2017016 AUBGM; **H**, lateral view, no. 2017017 AUBGM. Scale bar: 500 μ m.

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

Lychnothamnus barbatus (Meyen, 1827) Leonhardi, 1863

Lychnothamnus barbatus var. *antiquus*
Soulié-Märsche, 1989
(Figs 5; 6)

Lychnothamnus barbatus var. *antiquus* Soulié-Märsche, 1989: 155,
pl. XXXVII, figs 1-6.

MATERIAL EXAMINED. — 40 well-preserved gyrogonites have been recovered from sample Zahle 2.

DESCRIPTION

Gyrogonites large, very variable in size, 619-901 μ m high (mean 773 μ m) and 521-739 μ m wide (mean 613 μ m), ellipsoidal in shape with an isopolarity index ranging from 108 to 144 (average 125). Spiral cells in the apical zone show a remarkably constant width, which results in a flat apex (Fig. 5A, B). The base is tapered with a star-shaped basal pore, about

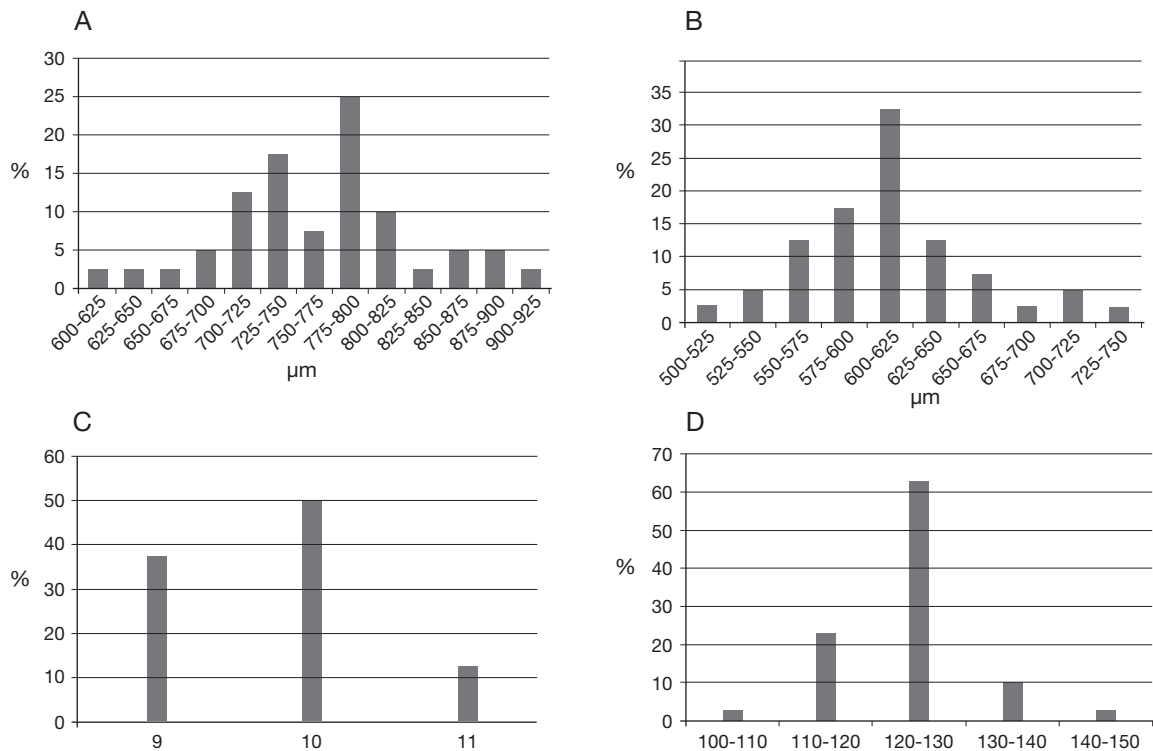


FIG. 6. — Biometric values of *Lychnothamnus barbatus* var. *antiquus* Soulié-Märsche, 1989 from sample Zahle 2 (n = 40 gyrogonites): **A**, gyrogonite height (μm); **B**, gyrogonite width (μm); **C**, number of convolutions visible in lateral view; **D**, isopolarity index (ISI = $h/w \times 100$).

80 μm in diameter (Fig. 5C). Nine to eleven (frequently ten) cells visible laterally (Fig. 5D-H). These are normally concave ranging from 62 to 115 μm in height (mean 84 μm), non-ornamented and separated by prominent sutures, sometime bicarinated (Fig. 5D).

BIOSTRATIGRAPHY

This species is known from the Miocene in Europe and extends through the Pliocene up to recent times (Soulié-Märsche 1989).

PALAEOECOLOGY

Inferred through comparison with the ecological requirements of its single living representative *Lychnothamnus barbatus* (check the chapter charophyte palaeoecology).

DISTRIBUTION

Lychnothamnus barbatus var. *antiquus* has hitherto been recorded from numerous Miocene European localities i.e., Spain (González-Pardos 2012; Suárez-Hernando *et al.* 2013), southern France (Soulié-Märsche 1989), Portugal (Antunes *et al.* 1992), Montenegro (Krstić *et al.* 2010) and Turkey (Mazzini *et al.* 2013). The extant representative i.e., *L. barbatus* is a common species of the moraine lakes of Northern Europe (Karczmarz 1967). It was formerly known from Germany, Poland, France, Italy and Austria (Migula 1897; Corillion 1972; Krause 1986). *Lychnothamnus barbatus* has been also recorded in the Balkans area (Blaženčić *et al.* 2006), Poland (Sugier *et al.*

2010) and Ukraine (Borisova & Yakushenko 2008). This species has been rarely found growing in other areas out of Europe such as Asia (Gollerbach & Krasavina 1983), Australia (Casanova *et al.* 2003) and North America (Karol *et al.* 2017).

Genus *Nitellopsis* Hy, 1889

Subgenus *Tectochara* Grambast & Grambast-Fessard, 1954

Nitellopsis (*Tectochara*) *merianii*

(Al. Braun ex Unger, 1852)

Grambast & Soulié-Märsche, 1972

(Figs 7; 8)

Chara merianii Unger, 1852: 82, pl. 25, figs 10-12.

Tectochara merianii – Grambast & Grambast-Fessard 1954: 668.

Nitellopsis (*Tectochara*) *merianii* – Grambast & Soulié-Märsche 1972: 11.

MATERIAL EXAMINED. — Dozens of well-preserved gyrogonites have been recovered from sample Zahle 1. Hundreds of well-preserved gyrogonites from locality Zahle 2 and Zahle 3. One hundred well-preserved specimens have been measured from sample Zahle 2.

DESCRIPTION

Gyrogonites very large and variable in size, ovoid in general shape 1071-1440 μm high (mean 1265 μm) and 828-1222 μm wide (mean 1035 μm), with isopolarity index

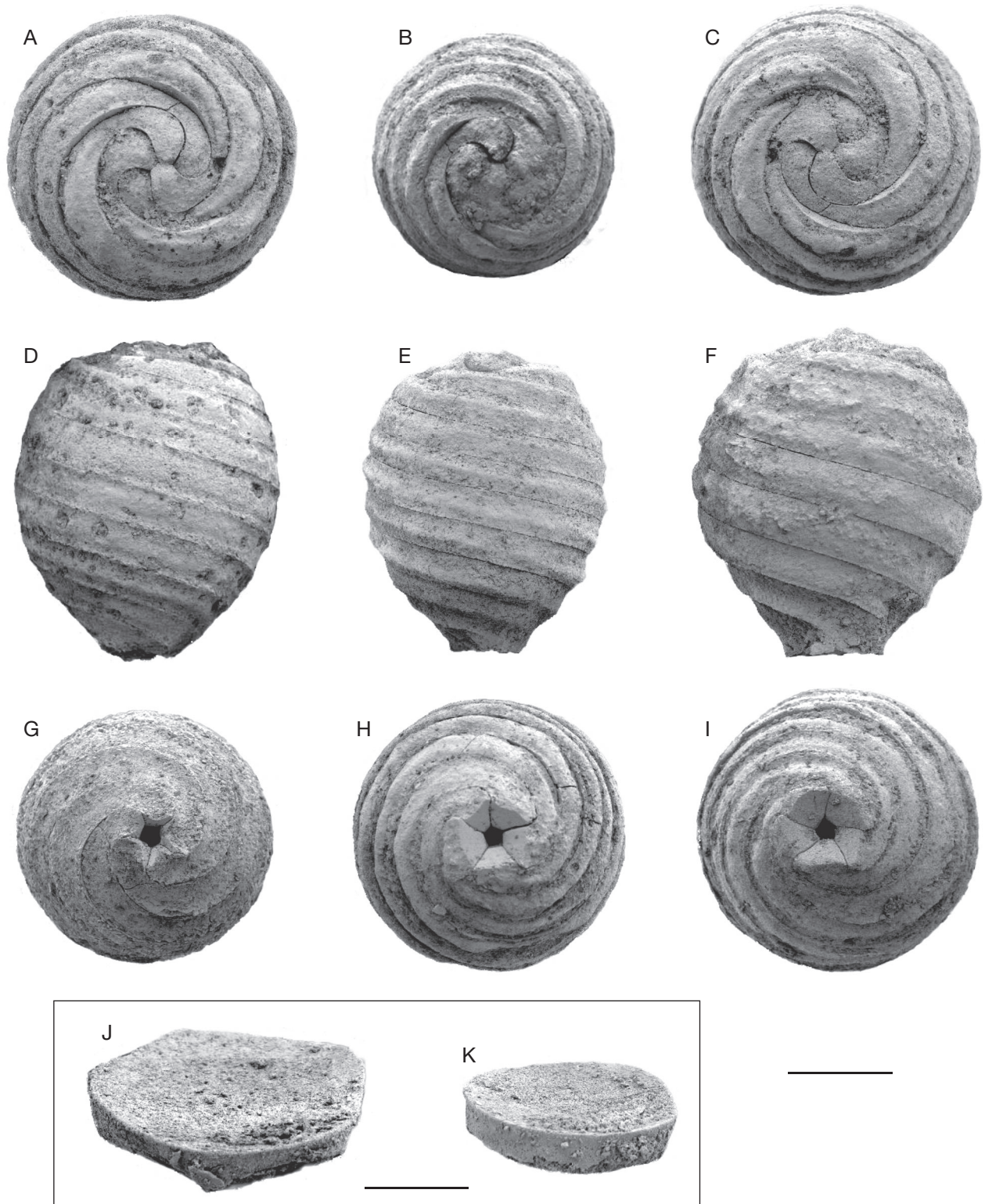


FIG. 7. — Charophytes from the lacustrine deposits of Zahle, sample Zahle 2: **A-H**, *Nitellopsis* (*T.*) *merianii* (Al. Braun ex Unger, 1852) Grambast & Soulié-Märsche, 1972; **A**, apical view, no. 2017019 AUBGM; **B**, apical view, no. 2017020 AUBGM; **C**, apical view, no. 2017021 AUBGM; **D**, lateral view, no. 2017022 AUBGM; **E**, lateral view, no. 2017023 AUBGM; **F**, lateral view, no. 2017024 AUBGM; **G**, basal view, no. 2017025 AUBGM; **H**, basal view, no. 2017026 AUBGM; **I**, basal view, no. 2017027 AUBGM; **J, K**, basal plates of *Nitellopsis* (*T.*) *merianii*; **J**, basal plate, no. 2017028 AUBGM; **K**, basal plate, no. 2017029 AUBGM. Scale bars: A-H, 400 µm; J-K, 100 µm.

ranging between 107 and 147 (mean 123) (Figs 7; 8). Spiral cells concave to convex. Eight to ten (frequently nine) convolutions are visible in lateral view (154 µm high

in mean value) (Fig. 7D-F). Apex nitellopsidoid according the terminology of Horn af Rantzien (1959), flat to slightly convex or sub-rounded, with thinning and narrowing of

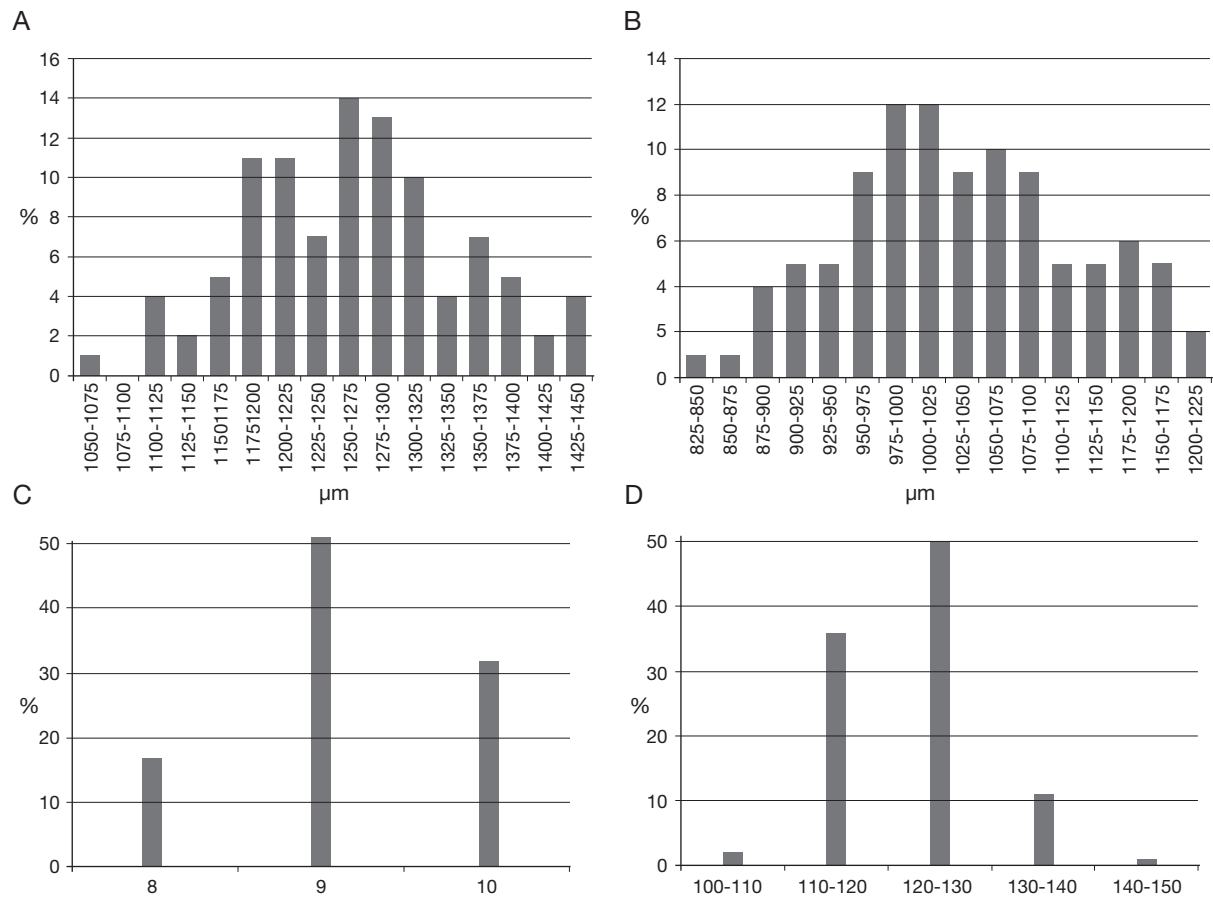


FIG. 8. — Biometric values of *Nitellopsis* (*T.*) *merianii* (Al. Braun ex Unger, 1852) Grambast & Soulié-Märsche, 1972 from sample Zahle 2 (n = 100 gyrogonites): **A**, gyrogonite height (μm); **B**, gyrogonite width (μm); **C**, number of convolutions visible in lateral view; **D**, isopolarity index (ISI = h/w × 100).

the spiral cells in the periapical zone (Fig. 7A-C). Apical nodules present in the 30% of the population. Apical nodules are variable in height from few μm to 97 μm (50 μm high in mean value). The basal pole is rounded or slightly conical with large basal pore, 80 μm across, and located within a characteristic pentagonal funnel (Fig. 7G-I). The basal plate shows a characteristic discoidal shape and it is very thin (Fig. 7J, K).

BIOSTRATIGRAPHY

This species is known all over the Oligocene, Miocene and Pliocene age sediments from Europe and Asia (Soulié-Märsche 1989).

PALAEOECOLOGY

Inferred through comparison with the ecological requirements of its single living representative *Nitellopsis obtusa* (check the chapter charophyte palaeoecology).

DISTRIBUTION

Fossil *Nitellopsis* (*Tectochara*) *merianii* represents the ancestor of the extant species *Nitellopsis obtusa* (Soulié-Märsche *et al.* 2002). These authors linked both species in an evolutionary lineage that ranges from the Uppermost Eocene

(Upper Priabonian) to Quaternary. This species followed four distributional phases (Soulié-Märsche *et al.* 1997; Soulié-Märsche *et al.* 2002; Sanjuan & Martín-Closas 2015): 1) *Nitellopsis* (*Tectochara*) *merianii* appears to be an exclusive Europe species during the uppermost Eocene (Upper Priabonian) and Early Oligocene (Rupelian); 2) During the uppermost Oligocene-Early Miocene, it expanded from Western Europe across the Paratethys realm reaching NE China and SE Asia. Fossil populations covered the entire Eurasian landmass during this time span comprising a range of latitudes from 18°N to 50°N; 3) During the upper Miocene-Pliocene *Nitellopsis* (*T.*) *merianii*-*N. obtusa* lineage maintained its Eurasian distribution; and 4) The last episode in the biogeographic history of this lineage is represented by the living species *Nitellopsis obtusa* that has been recovered from lacustrine deposits ranging in age from the Early Quaternary to the present. *Nitellopsis obtusa* is considered a boreal lake species, displaying since the Quaternary to the present, similar Eurasian distribution to *N. (T.) merianii* which during the Neogene, is recorded from the west coast of Europe to Japan. In recent years Sleith *et al.* (2015) found *N. obtusa* in North America (USA) but at the moment is considered the product of introduction by humans and not a native taxon.

CHAROPHYTE BIOSTRATIGRAPHY

The species *Nitellopsis* (*T.*) *merianii* and *Lychnothamnus barbatus* var. *antiquus* are of limited biostratigraphic value. *Nitellopsis* (*T.*) *merianii* has a broad stratigraphic and geographic distribution in all Eurasia and it has been recovered in deposits ranging in age from the Uppermost Eocene (Upper Priabonian) to the Pliocene (Soulié-Märsche *et al.* 1997; Sanjuan *et al.* 2014; Sanjuan & Martín-Closas 2015 and references herein). *Lychnothamnus barbatus* var. *antiquus* is known from Miocene, Pliocene and Holocene sediments in Europe (Soulié-Märsche 1989; Bahtia *et al.* 1998; Mazzini *et al.* 2013). The biostratigraphic distribution of *Chara* aff. *microcera* in Europe is quite wide ranging in age from the Lower Oligocene (middle Rupelian) to Lower Miocene (Burdigalian). This species has a biostratigraphic interest since it represents the key species for the homonymous biozone of the Oligocene. This biozone was defined by Riveline *et al.* (1996) as the interval from the first occurrence of *Chara* aff. *microcera* to the first occurrence of *Lychnothamnus ungeri*. Sanjuan *et al.* (2014) correlated the lower limit of this biozone, and hence the first occurrence of *Chara* aff. *microcera* in the Ebro Basin (Spain) with the MP23 European mammal reference level and calibrated it with the reversed magnetozone of chron C12 (C12r), providing an age of *c.* 31 Ma. The last occurrence of this species in Europe is recorded in lower Miocene deposits (Burdigalian) from the Aquitaine basin, France (Feist & Ringeade 1977; Riveline 1986). Hence the presence of *Ch. microcera* together with *N. (T.) merianii* and *L. barbatus* var. *antiquus* suggests that the base of the lacustrine deposits of Zahle may be Early Miocene in age (Fig. 9). However, it is difficult to provide a precise age for the base of this lacustrine sequence based solely on a reduced number of charophyte species.

CHAROPHYTE PALAEOECOLOGY

Gyrogonites provide valuable information of the palaeoecology of lacustrine environments. The charophyte assemblage composed of 4 well-preserved species clearly refers to freshwater environments. The presence of the species *Nitellopsis* (*T.*) *merianii* and *Lychnothamnus barbatus* var. *antiquus* is of special interest from the palaeoecological viewpoint since both species have living representatives i.e., *Nitellopsis obtusa* and *Lychnothamnus barbatus* respectively. Hence, palaeolimnological characteristics of the lake area from Zahle can be tentatively reconstructed by comparison with the ecological requirements of their extant counterparts. The typical depth range of *Lychnothamnus barbatus* in Europe is from 2 to 8 m where it forms dense meadows of up to 1 m high plants (Krause 1986). This endangered species represents a characteristic feature for strictly cold and oligotrophic freshwaters usually associated to phreatic origin from northern Europe (Krause 1997; Soulié-Märsche & Martín-Closas 2003). Previous palaeoecological studies in Miocene lacustrine deposits of Catalonia (Spain) demonstrate that fossil *L. barbatus* had similar ecological requirements to its living representative (Martín-Closas *et al.* 2006). These authors suggested that this

species grew under mesotrophic-oligotrophic conditions by the comparison with other groups of fossil aquatic plants and diatoms. *Lychnothamnus barbatus* has never been reported from brackish water. However, recent botanical studies in the Lake Kuźnickie (central-western Poland) demonstrated that this species is able to grow and overwinter under eutrophic conditions (Pelechaty *et al.* 2017). On the other hand *Nitellopsis obtusa* has an optimal growth in permanent, cold, alkaline freshwater lakes at a depth range of 4–12 m (Krause 1985; Soulié-Märsche *et al.* 2002). In these conditions plants can reach a length of 2 m. *Nitellopsis obtusa* can thrive in mesotrophic waters but collapses at salinities higher than 5‰ (Katsuhara & Tazawa 1986). *Nitellopsis obtusa* is currently classified as a boreal species since it is exclusive distributed in deep and shallow large lakes of northern Europe (Scandinavia, Poland and Russia), Asia and in North America, Great Lake area, (Corillion 1972; Soulié-Märsche *et al.* 2002). In these permanent lacustrine habitats *N. obtusa* forms large and dense meadows covering the lake ground and tends to reproduce vegetatively instead of sexually (Soulié-Märsche *et al.* 2002). Thus, sexual propagules, i.e., oogonia or gyrogonites, are very unusual. Rey-Boissezon & Auderset (2015) recently noticed the presence of a large number of gyrogonites of *N. obtusa* in a very shallow and small pond from Switzerland. These authors suggested that this unusual gyrogonite production could represent an adaptive ability of this species to change its reproductive strategy in response to high luminosity and high temperature, parameters that can be related to shallower waters.

The predominance of this species in samples Zahle 1, 2 and 3, suggests that hydrological conditions were especially favourable for *Nitellopsis* (*T.*) *merianii*. Hence, through comparison with the ecology of *N. obtusa* and *Lychnothamnus barbatus* as modern analogues and in agreement with facies analysis, rocks from the base of the lacustrine sequence of Zahle were formed in a large lake, with permanent, cold and oligotrophic water. Moreover, the presence of a large number of gyrogonites of the species *N. (T.) merianii* recovered from Zahle 2 could suggest periods with an increase of light irradiance and temperature probably due to the fluctuation of the water table of the lake related to seasonality. However, the large number of gyrogonites of this species also could be explained for the latitudinal position of the Bekaa Valley (37°N) which implies a higher solar irradiance compared to north European localities where *N. obtusa* grows nowadays. Large number of gyrogonites of this species were also recovered from Holocene lacustrine deposits in North Africa (Kröpelin & Soulié-Märsche 1991; Soulié-Märsche 1993). This large amount of gyrogonites in lacustrine deposits from low latitude basins reinforce the idea that high light irradiances could favour the productivity of gyrogonites in the *Nitellopsis* (*T.*) *merianii-obtusa* lineage.

CHAROPHYTE PALAEOBIOGEOGRAPHY

Because of its geographic position between Europe and Asia, where fossil charophytes have been more intensely studied, Lebanon and the whole Middle East region represents a very

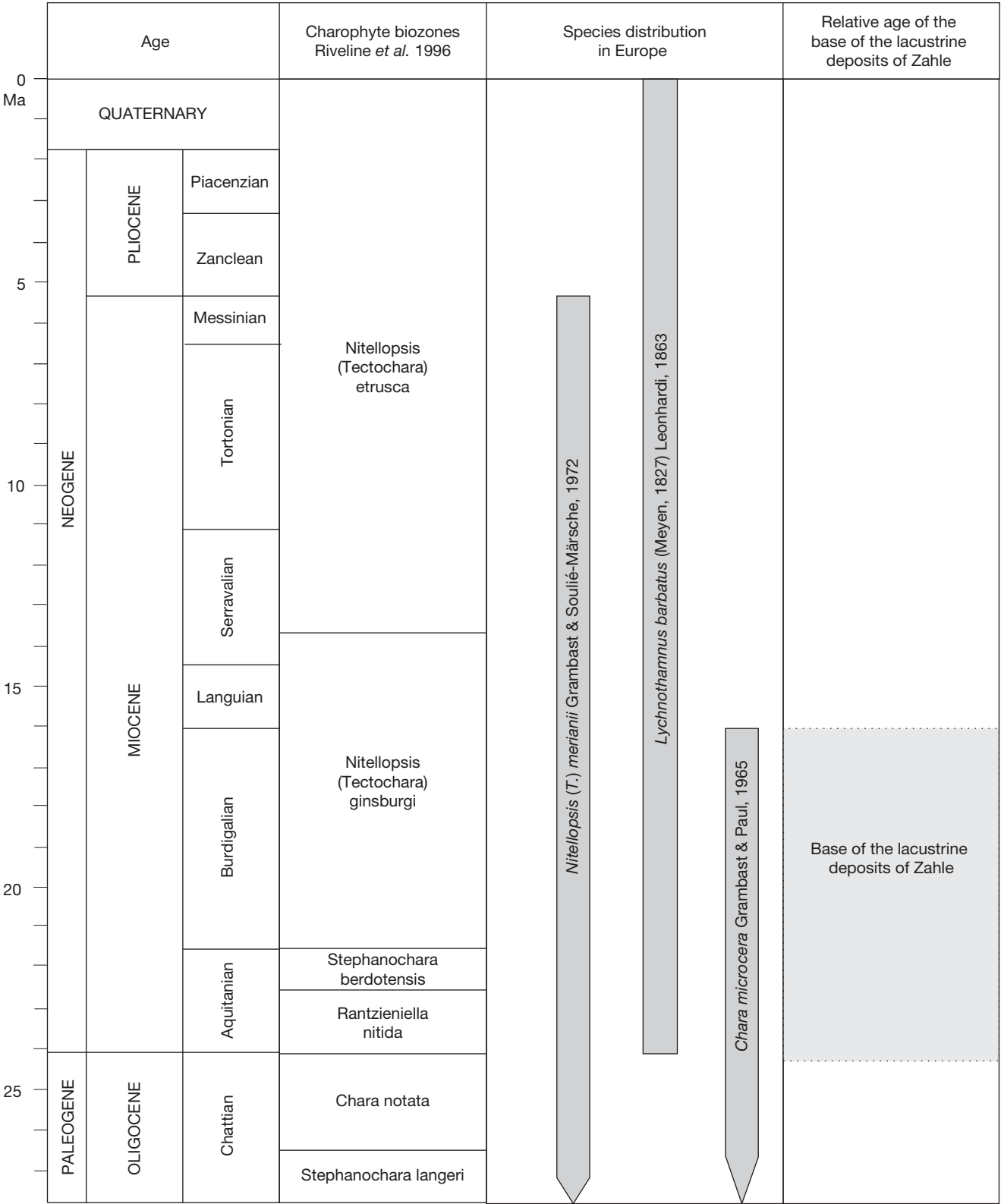


Fig. 9. — Neogene chronostratigraphy. Suggested age of the base of the lacustrine deposits of Zahle according to the charophyte assemblage. European charophyte biozonations and distribution of species are after Riveline et al. (1996).

interesting area for the biogeography of extant and fossil charophyte taxa. The fossil charophyte assemblage recovered from Miocene deposit of Zahle is composed of well-known European

species that have been recognized for the first time in Lebanon and in the Middle East. The Zahle section represents one of the southernmost localities providing a complete fossil assemblage of

the boreal species *Nitellopsis merianii-obtusa* and *Lychnothamnus barbatus*. Moreover, the occurrence of *Chara* aff. *microcera* in the Middle East region is significant since it is a characteristic species, of Oligocene/Early Miocene European basins that has been now found outside Europe for the first time. The presence of this significant species in the Middle East may lay the basis for future biostratigraphic correlations between non-marine distant Paleogene/Neogene basins of Europe and the Middle East.

CONCLUSIONS

The lacustrine deposits of Zahle has yielded four charophyte species identified as *Nitellopsis (Tectochara) merianii*, *Lychnothamnus barbatus* var. *antiquus*, *Chara* aff. *microcera* and *Chara* sp. which provide valuable palaeoecological, palaeobiogeographical and biostratigraphical data. The biostratigraphic distribution in Europe of the assemblage here described and illustrated suggests that the lower part of the lacustrine sequence of Zahle is Miocene in age. The presence of the species *Chara* aff. *microcera* in sample Zahle 1 supports that the lowermost part of this lacustrine interval may be Lower Miocene in age, which is in agreement with the maximum age of the overlying basalts located northwards of the studied area (Upper Miocene, based on isotopic data). However, this age assignment is not consistent with recent studies based on fossil micromammals which supported that these lacustrine deposits are Upper Miocene in age. The occurrence of the fossil species *Nitellopsis (Tectochara) merianii* and *Lychnothamnus barbatus* var. *antiquus* is significant from the palaeoecological (paleolimnological) and evolutive point of view since they represent the ancestors of the extant species *Nitellopsis obtusa* and *Lychnothamnus barbatus* respectively. In agreement with the ecological requirements of the extant species and the facies analysis, we can infer that the lake that stood in the Bekaa Valley during the Miocene was relatively deep (2-8 m deep), permanent and containing cold and oligotrophic waters that may had experienced periods of fluctuation of the water table. This study provides new data about the palaeogeographic distribution of Neogene charophyte species, representing at the same time the first study of Neogene fossil charophytes from Lebanon and the Middle East.

Acknowledgements

This study was funded by the URB project of the American University of Beirut entitled: "Fossil Charophytes from Lebanon" (Project number AUB-23936). We acknowledge Dr Ingeborg Soulié-Märsche and Dr Carles Martín-Closas for their help in charophyte systematics. We thank the *Departament de Dinàmica de la Terra i de l'Oceà (Facultat de Geologia, Universitat de Barcelona)* for offering us technical assistance during a research stage during the summer of 2017. We are also very thankful to the Central Research Science Laboratory (CRSL) of the American University of Beirut and especially to Ms Rania Shatila for their help and technical support during the SEM sessions. Dr Carles Martín-Closas and Dr Adriana Garcia greatly improved the manuscript during the peer review process.

REFERENCES

- ANTUNES M. T., SOULIÉ-MÄRSCHÉ I., MEIN P. & PAIS J. 1992. — Le gisement de Asseiceira, Portugal (Miocène supérieur). Données complémentaires sur Freiria de Rio Maior. *Ciências da Terra (UNL)* 11: 219-253. <http://hdl.handle.net/10362/4493>
- BHATIA S. B., SOULIÉ-MÄRSCHÉ I. & GEMAYEL P. 1998. — Late Pliocene and Early Pleistocene charophyte floras of the Hirpur Formation, Karewa Group, Kashmir, India. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 210 (2): 185-209. <https://doi.org/10.1127/njgpa/210/1998/185>
- BEYDOUN Z. R. 1999. — Evolution and development of the Levant (Dead Sea Rift) Transform System: a historical-chronological review of a structural controversy, in MAC NIOCAILL C. & RAYAN P. D. (eds), *Continental Tectonics*. Geological Society, London, Special Publication 164: 239-255. <https://doi.org/10.1144/GSL.SP.1999.164.01.12>
- BLAŽENČIĆ J., STEVANOVIĆ B., BLAŽENČIĆ Ž. & STEVANOVIĆ V. 2006. — Red Data List of Charophytes in the Balkans. *Biodiversity and Conservation* 15: 3445-3457. <https://doi.org/10.1007/s10531-005-2008-5>
- BORISOVA O. V. & YAKUSHENKO D. M. 2008. — Communities of Charophytes in the south-western part of Lake Svityaz (Valyn Polissia). *Ukrainian Botanical Journal* 2: 226-233.
- CASANOVA M. T., GARCIA A. & PORTER J. L. 2003. — Charophyte rediscovers in Australia; What and why? *Acta Micropalaeontologica Sinica* 20 (2): 129-138.
- CORILLION R. 1972. — *Les Charophycées de France et d'Europe Occidentale*. Travaux du Laboratoire de Botanique de la Faculté des Sciences d'Angers, Angers, vol. 11-12, 499 p.
- DUBERTRET L. 1945. — *Carte géologique au 50 000 – Feuille de Zahle*. République libanaise, Ministère des Travaux publics.
- DUBERTRET L. 1955. — *Carte géologique au 200 000 – Feuille de Beyrouth*. République libanaise, Ministère des Travaux publics.
- DUBERTRET L. 1975. — Introduction à la carte géologique au 1/50 000 du Liban. *Notes et Mémoires sur le Moyen-Orient* 23: 345-403.
- FEIST M. & RINGEADÉ M. 1977. — Étude biostratigraphique et paléobotanique (charophytes) des formations continentales d'Aquitaine, de l'Éocène supérieur au Miocène inférieur. *Bulletin de la Société géologique de France* 7: 341-354. <https://doi.org/10.2113/gssgfbull.S7-XIX.2.341>
- FEIST M., GRAMBAST-FESSARD N., GUERLESQUIN M., KAROL K., LU H., MCCOURT R. M., WANG Q. & SHENZEN Z. 2005. — *Treatise on Invertebrate Paleontology. Part B, Protoctista 1. Charophyta*. The Geological Society of America, Kansas, 170 p.
- GIERLOWSKI-KORDESCH E. H. 2010. — Lacustrine carbonates, in ALONSO-ZARZA A. M. & TANNER L. H. (eds), *Carbonates in Continental Settings. Facies, Environments and Processes: Developments in Sedimentology*, 61. Amsterdam, Elsevier: 1-101. [https://doi.org/10.1016/S0070-4571\(09\)06101-9](https://doi.org/10.1016/S0070-4571(09)06101-9)
- GOLLERBAKH M. & KRASAVINA L. 1983. — *Determination Key for Freshwater Algae of USSR*. vol. 14. *Charophyta*. Nauka, Leningrad, 190 p. (in Russian).
- GONZÁLEZ-PARDOS M. 2012. — *Carófitos del Mioceno Inferior de la Formación Tudela (Cuenca del Ebro, Navarra)*. Master's Thesis, Universitat de València, 68 p.
- GRAMBAST L. & GRAMBAST-FESSARD N. 1954. — Sur la position systématique de quelques charophytes tertiaires. *Revue Générale de Botanique* 61: 665-771
- GRAMBAST L. & PAUL P. 1965. — Observations nouvelles sur la flore de charophytes du Stampien du bassin de Paris. *Bulletin de la Société géologique de France* 7: 239-247. <https://doi.org/10.2113/gssgfbull.S7-VII.2.239>
- GRAMBAST L. & SOULIÉ-MÄRSCHÉ I. 1972. — Sur l'ancienneté et la diversification des *Nitellopsis* (Charophytes). *Paléobiologie continentale* 3: 1-14.
- HORN AF RANTZIEN H. 1959. — Morphological types and organ-genera of Tertiary Charophyte fructifications. *Stockholm Contributions in Geology* 4: 45-197.

- KANSOU M. 1961. — Découverte de vertébrés pontiens au Liban dans la plaine de la Bekaa. *Bulletin scientifique (Conseil des Académies de la RPF de Yougoslavie)* 6: 65.
- KARCZMARZ K. 1967. — Variabilité et distribution géographique de *Lychnothamnus barbatus* (Meyen) Leonh. *Acta Societatis Botanicorum Poloniae* 35 (3): 431–439.
- KAROL K. G., SKAWINSKI P. M., MCCOURT R. M., NAULT M. E., EVANS R., BARTON M. E., BERG M. S., PERLEBERG D. J. & HALL J. 2017. — First discovery of the charophycean green alga *Lychnothamnus barbatus* (Charophyceae) extant in the New World. *American Journal of Botany* 104 (7): 1106–1116. <https://doi.org/10.3732/ajb.1700172>
- KATSUHARA M. & TAZAWA M. 1986. — Salt tolerance in *Nitellopsis obtusa*. *Protoplasma* 135: 155–161. <https://doi.org/10.1007/BF01277008>
- KRAUSE W. 1985. — Über die Standortsansprüche und das Ausbreitungsverhalten der Stern-Armleuchter-alge *Nitellopsis obtusa* (Desvaux) J. Groves. *Carolinea* 42: 31–42.
- KRAUSE W. 1986. — Die Bart-Armleuchteralge *Lychnothamnus barbatus* im Klopeiner See. *Carinthia* 176: 337–354.
- KRAUSE W. 1997. — *Charales (Charophyceae). Süßwasserflora von Mitteleuropa. Band 18*. Gustav Fischer Verlag, Jena, 202 p.
- KRÖPELIN S. & SOULIÉ-MÄRSCHÉ I. 1991. — Charophyte remains from Wadi Howar as evidence for deep mid-Holocene freshwater lakes in Eastern Sahara (NW Sudan). *Quaternary Research* 36: 210–223. [https://doi.org/10.1016/0033-5894\(91\)90026-2](https://doi.org/10.1016/0033-5894(91)90026-2)
- KRSTIĆ N., SOULIÉ-MÄRSCHÉ I., ŽIC J., ĐORĐEVIĆ-MILUTINOVIĆ D. & SAVIĆ L. 2010. — Miocene Charophyta of Maoče, Pljevlja (Northern Montenegro), in Proceedings of the XIX CBGA Congress, Aristotle University of Thessaloniki. *Scientific Annals of the School of Geology* 99: 85–90.
- LATEEF A. S. 2003. — Quaternary terrestrial stratigraphic correlations between the Levant and the circum-North Atlantic region: current knowledge and constraints. *Studia Quaternaria* 20: 61–72.
- LATEEF A. S. 2007. — *Geological History of the Bekaa Valley*. Second International Conference on the Geology of the Tethys, Cairo University, 391–402.
- LÓPEZ-ANTOÑANZAS R., KNOLL F., MAKSOUD S. & AZAR D. 2015. — First Miocene rodent from Lebanon provides the ‘missing link’ between Asian and African gundis (Rodentia: Ctenodactylidae). *Scientific Reports* 5, article 12871. <https://doi.org/10.1038/srep12871>
- MALEZ M. & FORSTEN A. 1989. — *Hipparion* from the Bekaa valley of Lebanon. *Geobios* 22 (5): 665–670. [https://doi.org/10.1016/S0016-6995\(89\)80119-6](https://doi.org/10.1016/S0016-6995(89)80119-6)
- MARTÍN-CLOSAS C., WOJCICKY J. J. & FONOLLA L. 2006. — Fossil charophytes and hydrophytic angiosperms as indicators of lacustrine trophic change. A case study in the Miocene of Catalonia (Spain). *Cryptogamie-Algologie* 27: 357–379.
- MAZZINI I., HUDÁČKOVÁ N., JONIAK P., KOVÁČOVÁ M., MIKES T., MULCH A., ROJAY B., LUCI-FORA S., ESU D. & SOULIÉ-MÄRSCHÉ I. 2013. — Palaeoenvironmental and chronological constraints on the Tuğlu Formation (Çankırı Basin, Central Anatolia, Turkey). *Turkish Journal of Earth Sciences* 22: 1–31.
- MIGULA W. 1897. — Die Characeen, in RABENHORST L. (ed.), *Kryptogamen-Flora von Deutschland, Oesterreich und der Schweiz*. E. Kummer, Leipzig, 772 p.
- PELECHATY M., BROZOWSKI M. & KAROL P. 2017. — Overwintering and gyrogonite formation by the rare and endangered indicative macroalga *Lychnothamnus barbatus* (Meyen) Leonh. in eutrophic conditions. *Aquatic Botany* 139: 19–24. <https://doi.org/10.1016/j.aquabot.2017.02.005>
- PONIKAROV, KAZMIN V. G., MIKHAILOV I. A., RAZVALYAEV A. V., KRASHENINNIKOV V. A., KOZLOV V. V., SOULIDI-KONDRAT'EV E. D., MIKHAILOV K. YA, KULAKOV V. V., FARADZHEV V. A. & MIRZAEV K. M. V. P. 1967. — *The Geology of Syria: Explanatory Notes on the Geologic Map of Syria, Scale 1:500 000*. Part I. Stratigraphy, igneous rocks and tectonics. Ministry of Industry, Damascus, 230 p.
- REY-BOISSEZON A. & AUDERSET D. 2015. — Habitat requirements of charophytes. Evidence of species discrimination through distribution analysis. *Aquatic Botany* 120 (A): 84–91. <https://doi.org/10.1016/j.aquabot.2014.05.007>
- RIVELINE J. 1986. — *Les Charophytes du Paléogène et du Miocène inférieur d'Europe occidentale*. Éditions du Centre national de la Recherche scientifique, Paris, 227 p. (Cahiers de Paléontologie; 8).
- RIVELINE J., BERGER J.-P., FEIST M., MARTÍN-CLOSAS C., SCHUDACK M. & SOULIÉ-MÄRSCHÉ I. 1996. — European Mesozoic-Cenozoic charophyte biozonation. *Bulletin de la Société géologique de France* 167: 437–468.
- SANJUAN J. & MARTÍN-CLOSAS C. 2014. — Taxonomy and palaeobiogeography of charophytes from the Upper Eocene-Lower Oligocene of the Eastern Ebro Basin (Catalonia, NE Spain). *Geodiversitas* 36 (3): 385–420. <https://doi.org/10.5252/g2014n3a3>
- SANJUAN J. & MARTÍN-CLOSAS C. 2015. — Biogeographic history of two Eurasian Cenozoic charophyte lineages. *Aquatic Botany* 120 (A): 18–30. <https://doi.org/10.1016/j.aquabot.2014.05.018>
- SANJUAN J., MARTÍN-CLOSAS C., COSTA E., BARBERÀ X. & GARCÉS M. 2014. — Calibration of Eocene-Oligocene charophyte biozones in the Eastern Ebro Basin (Catalonia, Spain). *Stratigraphy* 11 (1): 61–81.
- SHARLAND P. R., ARCHER R., CASEY D. M., DAVIES R. B., HALL S. H., HEWARD A. P., HORBURY A. D. & SIMMONS M. D. 2001. — Arabian Plate Sequence Stratigraphy. *GeoArabia Special Publication* 2, 321 p.
- SLEITH R., HAVENS A. J., STEWART R. A. & KAROL K. G. 2015. — Distribution of *Nitellopsis obtusa* (Characeae) in New York, U.S.A. *Brittonia* 67 (2): 166–172. <https://doi.org/10.1007/s12228-015-9372-6>
- SOULIÉ-MÄRSCHÉ I. 1989. — *Étude comparée de gyrogonites de charophytes actuelles et fossiles et phylogénie des genres actuels*. Millau, Imprimerie des Tilleuls, 237 p.
- SOULIÉ-MÄRSCHÉ I. 1993. — Diversity of aquatic environments in NE Africa as shown by fossil charophytes, in THORWEIHE H. & SCHANDELMEIER R. (eds), *Geoscientific Research in Northeast Africa*. Taylor & Francis, Abingdon: 575–579.
- SOULIÉ-MÄRSCHÉ I. & MARTÍN-CLOSAS C. 2003. — *Lychnothamnus barbatus* (charophytes) from the upper Miocene of la Cerdanya (Catalonia, Spain): Taxonomic and palaeoecological implications. *Acta Micropalaeontologica Sinica* 20 (2): 156–164.
- SOULIÉ-MÄRSCHÉ I., GEMAYEL P., CHAIMANEE Y., SUTEETHORN V., JAEGER J. J. & DUCROCQ S. 1997. — *Nitellopsis* (Charophyta) from the Miocene of northern Thailand. *Alcheringa* 21: 141–156. <https://doi.org/10.1080/03115519708619181>
- SOULIÉ-MÄRSCHÉ I., BENAMMI M. & GEMAYEL P. 2002. — Biogeography of living and fossil *Nitellopsis* (Charophyta) in relationship to new finds from Morocco. *Journal of Biogeography* 29: 1703–1711. <https://doi.org/10.1046/j.1365-2699.2002.00749.x>
- SUÁREZ-HERNANDO O., MARTÍNEZ-GARCÍA B., GONZÁLEZ-PARDOS M., PASCUAL A., LARRAZ M., RUÍZ-SÁNCHEZ F. J., CRUZ-LARRASOANA J. & MURELAGA X. 2013. — Preliminary palaeontological data from the Loma Negra section (Bardenas Reales de Navarra, Lower-Middle Miocene). *Geogaceta* 54: 63–66.
- SUGIER P., PELECHATY M., GABKA M., OWSIANNY P., PUKACZ A., CIECIERSKA H. & KOLADA A. 2010. — *Lychnothamnus barbatus*: global history and distribution in Poland. *Charophytes* 2: 19–24.

Submitted on 20 July 2017;
accepted on 29 January 2018;
published on 24 May 2018.