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CHAROPHYTE FLORA FROM THE OLIGOCENE FOSSIL SITE OF SUCEAG (TRANSYLVANIAN BASIN, ROMANIA)

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Abstract

A charophyte assemblage composed of six species has been recovered from lower Oligocene deposits of the Dâncu Formation at the fossil site of Suceag (Transylvanian Basin, Romania). The assemblage is dominated by the two varieties of the species *Lychnothamnus pinguis* (*L. pinguis* forma *pinguis* and *L. pinguis* forma *major*). Accessory species include *Lychnothamnus* *prealangeri*, *Nitellopsis* (*Tectochara*) *merianii*, and few *Sphaerochara* sp. and *Harrisichara* sp. gyrogonites. *L. pinguis* is the index species of the homonymous Rupelian European biozone which was previously correlated in Western Europe with the Mammal Paleogene Reference Levels of MP21–MP23, and calibrated with the Geomagnetic Polarity Time Scale (GPTS), chrones C13N and C12R. From a paleobiogeographic viewpoint, this study confirms the presence of *L. pinguis* forma *pinguis* and *L. praelangeri* in Romania and in the whole Eastern Europe. Moreover, the charophyte assemblage from Suceag belongs to the Priabonian–Rupelian European charophyte bioprovince. While the vertebrate fossils reported in the same fossil locality indicate that the Dâncu Formation at Suceag sedimented in an estuarine environment, the charophyte assemblage suggests a more complex pattern, with presence of freshwater lakes too.

Keywords: Charophyta, upper Paleogene, biostratigraphy, paleobiogeography, Transylvania, eastern Europe.

1. Introduction

Charophytes represent a group of aquatic plants living in freshwater or brackish water environments. Their calcified fructifications (gyrogonites and utricles) are abundant in non-marine sedimentary rocks as old as Silurian in age (Feist et al., 2005). The high evolutionary rate and the worldwide distribution of this group make them one of main biostratigraphic markers of the Paleogene non-marine sequences.

Previous studies based on Romanian Paleogene charophytes were performed in the northwestern margin of the Transylvanian Basin. Hauer and Stache (1863) already noticed the presence of fossil charophytes in this area. Iva et al. (1970) found populations of *Tectochara meriani meriani* and *T. meriani octospirae*, both being varieties of the accepted species *Nitellopsis* (*Tectochara*) *merianii*. These authors also reported the presence of several species of *Gyrogona* (former *Chara caelata, Chara wrighty* and *Chara medicaginula)*, *Grobesichara distorta* (former *Chara distorta*), *Peckichara coronata* (previously *Aclistochara coronata*) or *Lychnothamnus langeri* (previously *Rhabdochara lengeri*) in the Priabonian deposits of the Turbuța Formation from the Hârtoapelor Valley at Glod (Sălaj District, NW Romania). Later, Iva (1987) identified *Harrisichara ceciliana*, *Sphaerochara cathariensis*, and *Gyrogona caelata* in the Lutetian of the Foidaș Formation (= Lower Gypsum Horizon, or Foidaș Gypsum), from an outcrop exposed by a tributary in the Racova Valley, near Jibou (Sălaj District). Also, in the northwestern side of the Transylvanian Basin, Baciu and Feist (1999) firstly studied the charophyte flora from the early Oligocene of Suceag as well as other fossil sites within the Dâncu Formation. However, these authors did not illustrate, neither described in detail the flora. Baciu and Feist (1999) recovered up to 4 species in Suceag, i.e., *Nitellopsis* (*Tectochara*) *merianii*, *Lychnotahmnus pinguis* forma *major* (previously *Rhabdochara major*), *Sphaerochara ulmensis* var. *bullaefera*, and *Chara media*. This assemblage was included within the former European charophyte *Rhabdochara major* Biozone of Riveline et al. (1996), which belonged to the middle and "non-terminal" late Rupelian. Baciu and Feist (1999) did not mention the actual outcrop location and they only specified that the charophyte-rich samples were collected within the Dâncu Formation, along the Nadăș Valley, as well as in Mera, Suceag, and Cluj-Napoca localities. Later, Baciu (1999, 2003) illustrated and described the charophyte assemblage within his PhD thesis. However, he did not provide a lithological column of the outcrop analyzed near Suceag located along the banks of the Cipcheș Creek. The author provided instead a brief description of the outcrop. Based on this brief description, we were unable to establish whether or not it is the same outcrop as ours, particularly if we have gathered samples from the same level that Baciu referred to.

This study aims to describe the charophyte assemblage from a fossil site that yielded rich vertebrate remains in the past, and to update the already known assemblage from Suceag fossil locality, providing new light about its relative age, paleoecology, and paleogeography. Moreover, the paleobiogeographic distribution of this flora is herein considered, and a possible explanation is provided for the paleogeographic widespread of the taxa. Based on the faunal and floral assemblages and type of facies revealed at Suceag, new interpretations of local paleogeography and paleoecology are also provided.

2. Geological and stratigraphical setting

The Suceag (= Suceagu; Cluj District, Romania) fossil site is located on the north-western side of the Transylvanian Basin, ca. 6 km far from Cluj-Napoca. From the geological viewpoint, it is located in the most extended and illustrative of the areas where Paleogene exposures are noticed. In this region, based on the sedimentary facies distribution (mainly in the upper Eocene–lower Oligocene formations), three Paleogene sedimentary areas were distinguished by Rusu (1970, 1987) and Popescu (1976, 1984). The locality of interest for this study belongs to the Gilău sedimentary area.

This latest Cretaceous–Paleogene sedimentary basin represents the first 'post-Laramian' basin in the Transylvanian Depression (Balintoni et al., 1998) and the largest molasse basin in Romania (Săndulescu, 1984; Săndulescu and Dimitrescu, 2004). The sedimentation in this region occurred as a result of the uplift of the Gilău Mountains. After the erection of this massif, three megacycles of sedimentation occurred (Codrea and Dica, 2005; Fărcaş, 2011), starting from the latest Cretaceous (Codrea and Godefroit, 2008; Codrea and Venczel, 2020) and lasting until the late Miocene (Dumitrescu, 1968, Krézsek and Bally, 2006). The rocks filling this basin concern marine and continental interbeddings (e.g., Mészáros and Moisescu, 1991; Mészáros, 2000;

Codrea and Hosu, 2001; Fărcaş, 2011; Filipescu, 2011; Sabău et al., 2021). Starting from the Gilău Mountains and extending eastwards, a predominantly uniform monoclinic rock system can be observed, the rocks ages becoming younger as they are farther from the basin border (Mészáros and Clichici, 1976; Codrea and Dica, 2005; Fărcaş, 2011). All of the Paleogene rocks from this area are exposed due to Quaternary hydrographic erosion, which has smoothed out most of the hilly relief in the region (Fig. 1).

--Fig. 1 near here--

The fossil site is located at Suceag Village, on the left bank of Nadăş River, upstream of the Cipcheş Creek, between Cere and Baciu forests, at the north-eastern extremity of the golf court of the Sun Garden resort. The outcrop in this area exposes rocks belonging to the Oligocene Dâncu and Gruia formations (Fig. 1), followed by an erosive episode, after covered by boulders mixed with gravels and sand marking the Middle Miocene transgression, in Badenian (Reichenbacher and Codrea, 1999; Fărcaş, 2011; Venczel et al., 2012). The here-studied fossiliferous level is part of the Dâncu Formation as defined by Rusu (1972) and represents the upper portion of the former "Ticu Strata" originally described by Koch (1884). The Dâncu Formation in this outcrop is composed of silty clay beds at the base, followed by intercalations of coaly clays, marly clays, and shelly sandstones (Fig. 2). The studied fossiliferous layer lies in the first marly claystone interval, sandwiched between two intervals of coaly claystone. More details on the characteristic geology of this fossil site can be found in Reichenbacher and Codrea (1999), Fărcaş (2011), and Venczel et al. (2012). Other outcrops located in the same creek can be noticed upstream, as well as on a right small tributary. Moisescu (1975) already described the facies in laterally equivalent outcrops exposed westward, in the Berecoaia Valley. According to this author the thickness and composition of the two coaly strata found in the Suceag fossil site varies significantly in nearby outcrops becoming thicker towards the north, but completely replaced by clays towards the south. In contrast, the thickness of the here-studied marly claystone bed with charophytes displays a constant thickness of ca. 1 m, suggesting that slow and consistent sedimentation prevailed in a wide area. Based on Moisescu's (1975) data, and the thickness of the layer studied in Suceag (ca. 60 cm), we can state that the mouth of the estuary through which the sediment supply originated from was located in the western vicinity of Suceag fossil locality, and that the marly clay and coal layers in Suceag formed on the right side of the flowing water (Nichols and Biggs, 1985), nearby the contact with the open sea.

A similar fossil site of the same age and lithological composition is cropping out on the north-western flank of the same hill, at ca. 1.8 km distance, on the valley of Berecoaia Creek from Mera Village (Reichenbacher and Codrea, 1999; Codrea and Fărcaș, 2002). The Dâncu Formation is also exposed in the Cetățuia Hill (Cluj-Napoca City), at Sânpaul-Aghireș (both localities in Cluj District) and at Ticu (Sălaj District) (Codrea and Fărcaș, 2002) and Almașului Valley (Sălaj District) (Givulescu, 1997; Fărcaș and Codrea, 2008).

---Fig. 2 near here---

Apart from the research carried out on the fossil charophytes from this locality, additional ones were focused on other fossil plants, invertebrates, and vertebrates. The fossil macroflora that was studied by Givulescu (1997) from the Dâncu Formation originates from the Cetății

Valley (tributary of Almaşului Valley). The author mentioned an assemblage including up to 25 taxa, from which species belonging to *Doliostrobus*, *Athrotaxis*, *Myrica*, *Alnus*, *Quercus*, and *Osmunda* are of great interest, clearly describing the coal-generating marshes were these plants accumulated. Based on the whole plant assemblage, the author concluded that warm and wet climate prevailed in the basin during the early Oligocene (Givulescu, 1997; Fărcaș and Codrea, 2008). Petrescu et al. (2002) added a microflora assemblage composed of pteridophyte spores and pollen of conifers and angiosperms from the core samples of the F2 borehole in Feleacului Hill (Cluj-Napoca). These authors concluded that this flora is dominated by thermophilus elements. A little later, Petrescu (2003) refined the climate data based on microflora, indicating that the annual temperature and rainfall in the basin was about 18°C, and ca. 1800 mm in average respectively.

Previous paleontological works in the Suceag outcrop have been focused on fossil vertebrates. For instance, Reichenbacher and Codrea (1999) described an otolith-based fish fauna composed of 7 taxa of freshwater and brackish-water fish including *Enoplophthalmus* sp., *Hemitrichas* sp., *Dapalis angustus*, *D. transylvanicus*, *D.* sp., *Dicentrarchus* (=*Morone*) sp., *Lepidocottus* (="g. *Eleotridarum*") sp., and "g. aff. *Lesueurigobius*" sp. Based on the fossil fish teeth, Trif and Codrea (2019) added 3 batoid species belonging to the family Dasyatidae (*Dasyatis* cf. *rugosa*, *Dasyatis* aff. *Strangulate*, and *Taeniurops cavernosus*). Also, the herpetofauna was studied in detail by Codrea and Fărcaș (2002), Fărcaș (2011), Venczel et al. (2012), and Venczel and Codrea (2018). Amphibians are represented by proteids (*Mioproteus gardneri*, *Latonia* sp.), palaeobatrachians (*Albionbatrachus oligocenicus*), and ranids (*Pelophylax* sp.). Several groups of reptiles are also represented in Suceag including anguids (Anguidae indet.), aniliids (*Eoanilius* sp.), boids (cf. *Bransateryx* sp.), chelonians (*Tryonix* sp., *Chinemys strandi*), and crocodilians (*Diplocynodon* sp.) (Codrea and Fărcaş, 2002; Fărcaş, 2011; Codrea and Venczel, 2020). Bird remains (Anserinae indet. and *Rallicrex kolozsvarensis*) were also reported by Codrea and Fărcaş (2002). The mammals unearthed from the Suceag fossil site are represented by erinaceous insectivores (?*Neurogymnurus* sp.), cricetid rodents (*Paracricetodon* sp.), a pantolestid (*Kochictis centennii*), entelodonts (*Entelodon* aff. *deguilhemi*, Entelodontidae indet. cf. *Paraentelodon* sp.), and anthracotheres (*Antracotherium* sp., *Elomeryx borbonicus*) (Rădulescu and Samson, 1989 and references therein; Codrea and Fărcaş, 2002; Fărcaş, 2011). According to these authors the fossil site of Suceag is assigned to the Mammal Paleogene (MP) 23-24 reference levels (Suevian).

3. Materials and Methods

The studied flora was recovered from a marly claystone sequence in the locality of Suceag, coordinates 46°49'00.44"N and 23°29'11.16"E (Fig. 1). About 60 kg of sediment were extracted and processed to recover the microfossils at the *Paleotheriology and Quaternary Geology Laboratory of the Babes-Bolyai University* (hereinafter shortened BBU-PQGL). After the sediment was sundried, it was left two days to disaggregate in a solution of water and 15% hydrogen peroxide. Afterwards, using sieves with mesh apertures of 0.3 mm it was wet-sieved in order to obtain the fossil concentrate. Charophyte remains and other microfossils were sorted using a Motic SMZ 160 TLED microscope binocular. Gyrogonites were selected at BBU-PQGL, and measured using Motic Images Plus 2.0 ML software and a Motic BA310 stereomicroscope coupled to a digital camera located at the *Departament de Dinàmica de la Terra i de l'Oceà, Universitat de Barcelona*. Well-preserved gyrogonites were selected and photographed using the scanning electron microscope Quanta 200 at the *Centres Científics i Tecnològics, Universitat de*

Barcelona (CCiTUB). The material is housed in the *Departament de Dinàmica de la Terra i de l'Oceà, Universitat de Barcelona* and the *Museu Geològic del Seminari Conciliar*, Barcelona. Fossil charophyte systematics follow the works of Horn af Rantzien (1956) and Feist et al. (2005). The biometric parameters considered in this study were the gyrogonite height (µm), gyrogonite width (µm), the number of spiral turns observed in lateral view, and the isopolarity index (gyrogonite height/gyrogonite width × 100).

4. Charophyte systematics

The sample extracted from the Suceag fossil site have yielded a charophyte assemblage composed of up to 6 taxa, 4 of which can be classified into a species level.

Division: CHAROPHYTA Migula, 1897

Class: CHAROPHYCEAE Smith, 1938

Order: CHARALES Lindley, 1836

Family: CHARACEAE Richard ex C.A. Agardh, 1824

Subfamily: NITELLOIDEAE A. Braun in Migula, 1897

Genus: **Lychnothamnus** (Ruprecht, 1845) Leonhardi, 1863. Emended by A. Braun in Braun and Nordstedt (1882)

Lychnothamnus pinguis forma *pinguis* (Grambast, 1958) Soulié-Märsche, 1989. Emended by Sanjuan and Martín-Closas (2015a)

Fig. 3A–D

1958 *Stephanochara pinguis* Grambast, p. 158–159, fig. 68.

1989 *Lychnothamnus pinguis* Soulié-Märsche., p. 158.

2015a *Lychnothamnus pinguis* forma *pinguis* Sanjuan and Martín-Closas, p. 7–9, Fig. 4B, C, E, F, H, I.

Material: Twenty gyrogonites have been recovered from the studied outcrop. Ten complete specimens have been measured (Table S1).

Description: The gyrogonites are medium to large, measuring 785–1031 μm high (mean 932 μm) and 638–837 μm wide (mean 739 μm), and ellipsoidal in shape with an isopolarity index, ranging between 116 and 143 (mean 126). Spiral cells are convex and about 125 μm in height in mean. Seven to nine convolutions (frequently 8) are visible in lateral view. The apex is flat or slightly rounded and generally ornamented with rounded apical tubercles. Spiral cells become thinner in the apical periphery but they do not show constrictions in the apical zone. The base has a small star-shaped basal funnel.

Lychnothamnus pinguis forma *major* (Grambast and Paul, 1965) Soulié-Märsche, 1989.

Emended by Sanjuan and Martín-Closas (2015a)

Fig. 3E, F, and G

1965 *Rhabdochara major* Grambast and Paul, p. 241 and 242, pl. 2, figs 1–4.

1989 *Lychnothamnus major* Soulié-Märsche, p. 159.

2015a *Lychnothamnus pinguis* forma *major* Sanjuan and Martín-Closas, p. 7–9, Fig. 6.

Material: This represents by far the dominant taxa in the studied sample of Suceag. The population is composed of up to 120 specimens. However, many individuals are germinated or broken. Thirty-one complete gyrogonites have been measured in this study (Table S1).

Description: Gyrogonites are medium to large, 784–1019 μm in height (mean 914 μm) and 629–853 μm wide (mean 762 μm), and ellipsoidal in shape with an isopolarity index of 109–129 (mean 120). Spiral cells are always concave and about 131 μm height. The concavity of the spiral cells forms sharp sutures in all gyrogonites. Seven to nine convolutions (frequently 8) are visible in lateral view. The apex is flat, non-ornamented, and without periapical modifications. The base is slightly pointed showing a small basal pore within a star-shaped funnel.

Lychnothamnus praelangeri (Castel, 1967) Soulié-Märsche, 1989.

Fig. 3H

1967 *Rhabdochara praelangeri* Castel, p. 516–517, pl. XX 1–11.

1989 *Lychnothamnus praelangeri* Soulié-Märsche, p. 159.

Material: Few specimens were recovered from the outcrop. Eight gyrogonites were measured in this study (Table S1).

Description: Gyrogonites medium to large, 794–1040 μm in height (mean 882 μm) and 627–877 μm wide (mean 741 μm), and ellipsoidal in shape with an isopolarity index of 104–129 (mean 119). Spiral cells are concave and about 131 μm in height. They display a characteristic ornamentation consisting in vertical ridges arranged along the spiral cell. Seven to nine (frequently 8) convolutions are visible laterally. The apex is flat, non-ornamented, and without periapical modification. The base is generally pointed. Gyrogonites show small basal pores located within a star-shaped funnel.

Genus: **Nitellopsis** Hy, 1889

Subgenus: **Tectochara** Grambast and Grambast, 1954

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

Fig. 3I–L

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

1954 *Tectochara meriani* Grambast and Grambast, p. 668.

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

Material: Twenty specimens were extracted from the Suceag fossil site. Fifteen well-preserved gyrogonites were measured (Table S1).

Description: Gyrogonites are very large, measuring 1009–1226 μm in height (mean of 1105 μm) and 842–1168 μm in width (mean of 968 μm). They show a rounded ovoidal or subspherical shape, with an isopolarity index ranging between 103 and 126, mean of 114. The number of convolutions observed in lateral view ranges between 7 and 9 (frequently 8). Spiral cells are concave to convex, with an average high of 149 μm. Gyrogonites display a nitellopsidoid apex, i.e., spiral cells are thinner and narrower at the apical periphery. The apex is slightly rounded and some specimens bear apical nodules. The base generally displays a rounded profile, and shows a small basal pore within a pentagonal or star-shaped funnel.

Associated to the aforementioned species, few gyrogonites of two accessory species have also been extracted and illustrated herein. Only one gyrogonite belonging to the genus *Harrisichara* was found. This gyrogonite displays strong affinity to the well-known European and North American Priabonian–Rupelian taxon *H. tuberculata* (Lyell, 1826) Grambast, 1957 (Fig. 3M). Also, 3 gyrogonites of the genus *Sphaerochara* were identified in the sample. It shows resemblance to the European species *S. hirmerii* (Rásky, 1945) Mädler, 1952 (Fig. 3N–P).

---Fig. 3 near here---

5. Discussions

Age and distribution of the charophyte flora from the Suceag fossil site

The here recovered flora indicate that the Dâncu Formation at Suceag is lower–middle Rupelian in age (Fig. 4). This flora has already been found in several European and Asiatic localities (Table 1). *Lychnothamnus pinguis* forma *pinguis* represents a common taxon in the Rupelian deposits of western European basins including Hampshire, Paris, Rhine Graben, and the Iberian Chain (Grambast 1958; Riveline 1986; Schwarz 1997, Adrover et al., 1983). *L. pinguis* forma *major* has also been recovered in the Rupelian of Western Europe, i.e., basins of Languedoc, Provence, Aquitaine, and Ebro (Grambast and Paul, 1965; Feist-Castel, 1977; Feist et al., 1994; Sanjuan and Martín-Closas, 2014). This variety (previously named *Rhabdochara major*) was reported in Romania near the Suceag fossil site by Baciu and Feist (1999). Recently, this species has been found out the European continent, i.e., in the Oligocene of the Qaidam Basin (NE China) by (Xing et al., 2023). *L. pinguis* is the index species of the homonymous European biozone, defined by Riveline et al. (1996) and modified by Sanjuan and Martín-Closas (2015a). This biozone was correlated in the Ebro Basin (NE Spain) with the Mammal Paleogene Reference Levels MP21, MP22, and MP23, and calibrated with the Geomagnetic Polarity Time Scale (GPTS) C13N and C12R chrons (absolute age of 31,1–33,8 Ma). *Lychnothamnus praelangeri* has been recovered in the middle–upper Rupelian to lowermost Aquitanian sedimentary sequences of several south western European basins, i.e., Marseille, Aquitaine, Provence, north of the Pyrenees, and Paris (Riveline, 1986 and references therein). Reichenbacher and Schwarz (1997) and Schwarz (1997) found this species in the Molasse Basin in Switzerland. Martín-Closas and Ramos (2005) found several specimens of this taxon in the late Oligocene of Mallorca (Balearic Islands, Spain). Gyrogonites attributed to *Nitellopsis* (*T.*)

merianii were already found in the Transylvanian Basin by Baciu and Feist (1999) and by Baciu (2003) in Suceag. *Nitellopsis* (*T.*) *merianii* is a well-known Eurasian taxon distributed over the Oligocene, Miocene, and Pliocene (Sanjuan and Martín-Closas, 2015b and references therein). According to these authors, *N.* (*T.*) *merianii* appears to be exclusive to Western and Eastern Europe during the upper Eocene (upper Priabonian) and lower Oligocene (Rupelian). During the uppermost Oligocene–lower Miocene, this species expanded from Europe across the Paratethys realm to NE China and SE Asia, ranging from latitude 18°N to 50°N (Sanjuan and Martín-Closas, 2015b). The two accessory species illustrated herein (*Harrisichara* aff. *tuberculata* and *Sphaerochara* aff. *hirmerii*) display a concordant biostratigraphic range with the other 4 species constituting the assemblage. *H. tuberculata* was already reported in the Suceag fossil site by Baciu and Feist (1999). It is a widely distributed taxon occurring in upper Priabonian–middle Rupelian deposits of Europe and North America (Sanjuan et al., 2017 and references therein). *S. hirmerii* is a common taxon in the Western Europe Priabonian, Rupelian, and Chattian. It has been found in continental deposits of the Paris Basin, the Rhine Graben, the Hampshire Basin, the Languadoc Basin, and the Provence Basin (Riveline, 1986). Martín-Closas and Ramos (2005) reported *S. hirmerii* in the Rupelian of the Balearic Islands. Mojon et al. (2018) found gyrogonites of this species in the Oligocene of the Molasse Basin in Switzerland.

From the paleobiogeographic viewpoint, the charophyte assemblage from Suceag is composed by characteristic species included within the European Priabonian–Rupelian charophyte bioprovince defined by Sanjuan and Martín-Closas (2014) (Table 1).

--Table 1 near here--

Moreover, this study reports, for the first time in Romania, the presence of the species *Lychnothamnus pinguis* forma *pinguis* and *L. praelangueri*. The first species occurs mainly in north-western European basins such as Hampshire, Paris, and the Rhine Graben while it is rare in southern European basins and it has never been found before in Eastern Europe (Sanjuan and Martín-Closas, 2015a and references therein). Also, the species *L. praelangeri* is a common taxon of western European basins and it has never been recovered in the east of Europe. The dispersion vectors (W-E) of the charophyte species during the Rupelian could be tentatively compared with the dispersion routes of their dispersers such as waterfowl bird. In fact, bones attributed to waterfowl birds of the anserinae subfamily (Noordhuis et al., 2002) have been found within the Dâncu Formation (Codrea and Fărcaş, 2002). These latter authors reported the presence of Anserinae indet. and *Rallicrex kolozsvarensis*. However, this comparison would raise other questions regarding the west-east trended migration of the birds, since there are no actual representatives that follow such a path.

Suceag paleoecology and paleogeography

Based on the fossil charophyte assemblage, the associated faunal remains, and the type of facies studied in the Suceag fossiliferous bed, new data about the Rupelian regional paleoecology and paleogeography is now available. At the beginning of the Oligocene, the Paratethys Sea was splitting into smaller basins, bounding few local bodies of water (Rögl, 1998). During this time span, the Solenovian Sea developed in the Transylvanian Basin and to the east (Mészáros et al., 1989). The facies of the Suceag section and coeval nearby deposits has been related to nearshore depositional environments.

The facies assemblage at the lower part of the section of Suceag is constituted by fossiliferous marly claystones, coaly claystones, and lumachelic sandstones. The marly claystone interval studied herein is light grey in colour and 0.6 m thick. This interval provided the charophyte assemblage studied herein as well as other fossils related to freshwater and brackish water environments. The gyrogonites found in this interval are well-preserved without fragmentation or erosion features. However, no charophyte thalli have been found associated to the gyrogonites suggesting that they were transported from nearby localities (parautocthonous). The ecological requirements of the charophyte assemblage found in this interval indicate that freshwater lakes occurred in the area. In general, both *Lychnothamnus* taxa, i.e., the dominant *Lychnothamnus pinguis* and *L. praelangeri* have been recovered in facies attributed to freshwater lakes subjected to siliciclastic inputs (Riveline, 1986; Martín-Closas and Ramos, 2005). Sanjuan and Martín-Closas (2012) indicated that the species *Nitellopsis* (T.) *merianii* and *Harrisichara tuberculata* thrived in freshwater perennial lakes located in distal alluvial plains. Other freshwater elements, additionally to charophytes, were previously recovered from the same interval. Reichenbacher and Codrea (1999) found remains of freshwater fishes such as *Dapalis angustus*, and other anadromous nut also specific for coastal freshwaters, brackish, and estuarine environments (i.e., *Enoplophthalmus* sp. and *Hemitrichas* sp.). These authors also recovered taxa related to marine and brackish water environments, i.e., *Dapalis transylvanicus*, *Dapalis* sp., *Dicentrarchus* (=*Morone*) sp., *Lepidocottus* (="g. *Eleotridarum*") sp. and "g. aff. *Lesueurigobius*" sp.. At a family level, most of these fish and also the batoids reported by Trif and Codrea (2019) are indicative of tropical and subtropical waters, while others are tropical and temperate sea-dwellers (Nelson et al., 2016). Thus, the fossiliferous marly claystone interval studied herein was deposited under a tropical – subtropical climate, which is in agreement with the average temperature proposed by Petrescu (2003). The facies and the fossil content suggest that this interval was deposited in a calm nearshore environment subjected to salinity fluctuations. The amphibian and the charophyte assemblage indicate that freshwater ponds or lakes occurred adjacent to the estuary. Two dark grey coaly claystone beds are represented in the section and they are located above and below the fossiliferous marly claystone bed. They have a thickness of 0.3 m and include an abundance of plant remnants. No root marks neither burrows were observed at their base suggesting that plant debris were transported from nearby marshy localities. Overlying the upper coaly claystone bed, a 5 cm thick lumachel sandstone layer can be observed. Dominant shells belong to disjointed valves of the freshwater bivalve *Unio wolffi*. Almost all valves are arranged in huge majority with the convex sides upwards which clearly indicate selection and transport.

Considering the whole micropaleontological and sedimentological data as well as the regional geology we can conclude that the fossiliferous interval at Suceag was deposited within an estuary, a transitional environment located at a river mouth, and that was receiving both fresh and marine water sources. The fluvial waters drained westwards from the already erected Gilău Mountains. The charophyte assemblage studied herein demonstrates that freshwater bodies occurred in the floodplain, either in connection with the running waters, or as distinct bounded ones on the floodplains, where heavy rains could have periodically connected the lakes/oxbows with the main channel (Scanes et al., 2017).

--Fig. 4 near here--

---Fig. 5 near here---

Conclusions

Six charophyte species have been extracted from the Suceag fossil site (Transylvanian Basin, Romania). Among the charophyte assemblage, only 4 taxa are characterized by populations of several individuals allowing a clear taxonomic determination. Part of this flora was already reported by previous authors i.e., *Lychnothamnus pinguis* var. *major* (previously *Rhabdochara major*), and *Nitellopsis* (*T.*) *merianii*, while others are here firstly reported in Romania and in the whole Eastern Europe (*Lychnothamnus pinguis* forma *pinguis* and *L. praelangueri*). Two other species are included in the assemblage but the low number of gyrogonites represented hinders a clear taxonomic attribution (*Harrisichara* sp. and *Sphaerochara* sp.). The charophyte flora from Suceag can be included within the European charophyte Lychnothamnus pinguis Biozone (early–middle Rupelian in age) previously correlated with the Mammal Paleogene Reference Levels of MP21–MP23, and calibrated with the GPTS chrones C13N and C12R. From the paleobiogeographic viewpoint, this charophyte assemblage can be included within the Priabonian–Rupelian European charophyte bioprovince. The fossil site of Suceag has previously been related to an estuary environment. Despite charophyte gyrogonites are well-preserved in general, the absence of charophyte thalli suggest parautochtony. The facies and the fossil content recovered from the Suceag marly claystone interval suggest that a calm nearshore environment subjected to salinity fluctuations prevailed in the area during the mid-Rupelian. Moreover, the charophyte assemblage indicates that freshwater ponds or lakes occurred adjacent to the estuary.

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Fig. 1. Geological map of the studied region within Romania (modified after Rusu et al., 2018).

Fig. 2. Lithological column of the Dâncu Formation, Suceag fossil site – Cipcheș Valley (redrawn after Fărcaș, 2011; Venczel et al., 2012). The charophyte symbol represents the location of the here-studied samples.

Fig. 3. Fossil charophytes from the Suceag fossil site. *Lychnothamnus pinguis* forma *pinguis* (A-D): A – apical view; B and C – lateral views; D – basal view. *Lychnothamnus pinguis* forma *major* (E-G): E – apical view; F – lateral view; G – basal view. *Lychnothamnus praelangeri* (H) in lateral view. *Nitellopsis* (*Tectochara*) *merianii* (I-L): I – apical view; J and K – lateral views;

L – basal view. *Harrisichara* sp. (M) in lateral view. *Sphaerochara* sp. (N-P): N – apical view; O – lateral view; P – basal view.

Fig. 4. Biostratigraphic chart showing the relative age suggested by the identified species of fossil charophytes in Suceag (Transylvanian Basin, Romania).

Fig. 5. Paleogeographic map (Oligocene) showing the distribution of the here studied species in Eurasia (map modified after Popov et al., 2004).

Table 1. Paleobiogeographic distribution of the charophyte flora from the fossil site of Suceag (Transylvanian Basin, Romania) during Late Eocene (Priabonian) and Early Oligocene (Rupelian).

Table S1. List of measurements of the charophyte populations from Suceag (Transylvanian Basin, Romania).

Declaration of interests

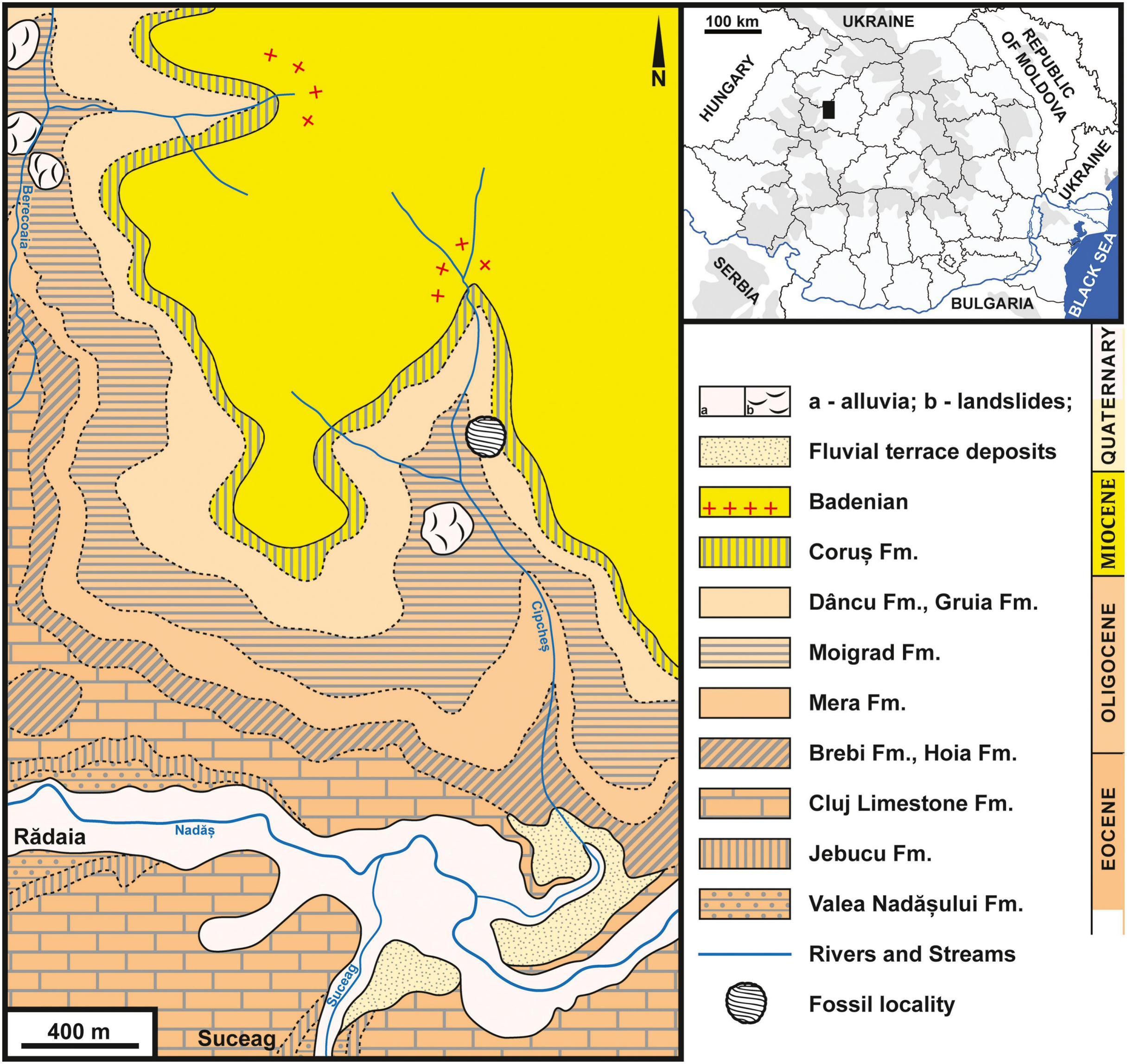
☒The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Basin/Species	***Lychnothamnus pinguis* forma *pinguis***	***Lychnothamnus pinguis* forma *major***	***Lychnothamnus praelangeri***	***Nitellopsis* (*Tectochara*) *meriani***
***This study* Transylvanian, (Romania)**	x	x	x	x
Ebro (Spain)		x		x
Mallorca (Spain)			x	
Loranca (Spain)				x
Paris (France)	x	x	x	x
Languedoc (France)		x		x
Provence (France)		x	x	x
Aquitaine (France)		x	x	x
Marseille (France)			x	
Rhine Graben (Germany)	x			x
Swiss Molasse (Switzerland)			x	x
Hampshire (UK)	x			
Qaidam (NE China)		x		

Table 1. Paleobiogeographic distribution of the charophyte flora from the fossil site of Suceag (Transylvanian Basin, Romania) during Late Eocene (Priabonian) and Early Oligocene (Rupelian).

- Charophytes from Central-Eastern Europe give new data about freshwater environments
- *Lychnothamnus pinguis* forma *pinguis* and *L. praelangeri* are common in most Europe
- Suceag fossil site (Romania) resembles estuarine environments with freshwater influence
- Paleogeographical information about Suceag fossil locality was obtained from the charophyte and faunal associations.



N
Berecoaia
Cipcheș
Nadăș
Rădaia
Suceag
Suceag
400 m
100 km
UKRAINE
HUNGARY
REPUBLIC OF MOLDOVA
UKRAINE
SERBIA
BULGARIA
BLACK SEA
a - alluvia; b - landslides;
Fluvial terrace deposits
Badenian
Coruș Fm.
Dâncu Fm., Gruia Fm.
Moigrad Fm.
Mera Fm.
Brebi Fm., Hoia Fm.
Cluj Limestone Fm.
Jebucu Fm.
Valea Nadășului Fm.
Rivers and Streams
Fossil locality
QUATERNARY
MIOCENE
OLIGOCENE
EOCENE

Figure 1

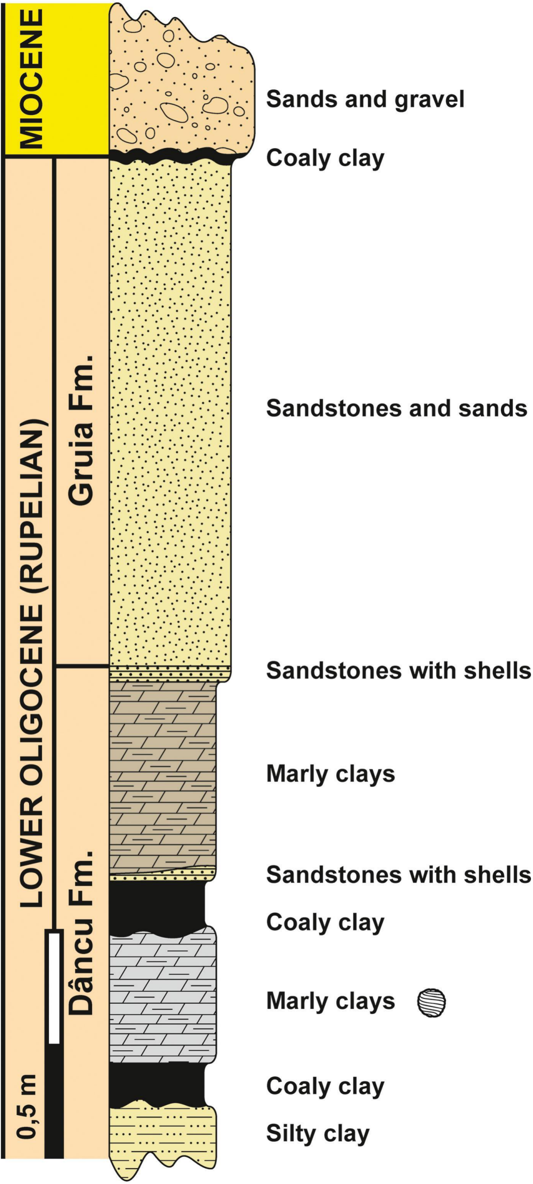

MIOCENE
LOWER OLIGOCENE (RUPELIAN)
Gruia Fm.
Dâncu Fm.
0,5 m
Sands and gravel
Coaly clay
Sandstones and sands
Sandstones with shells
Marly clays
Sandstones with shells
Coaly clay
Marly clays
Coaly clay
Silty clay

Figure 2

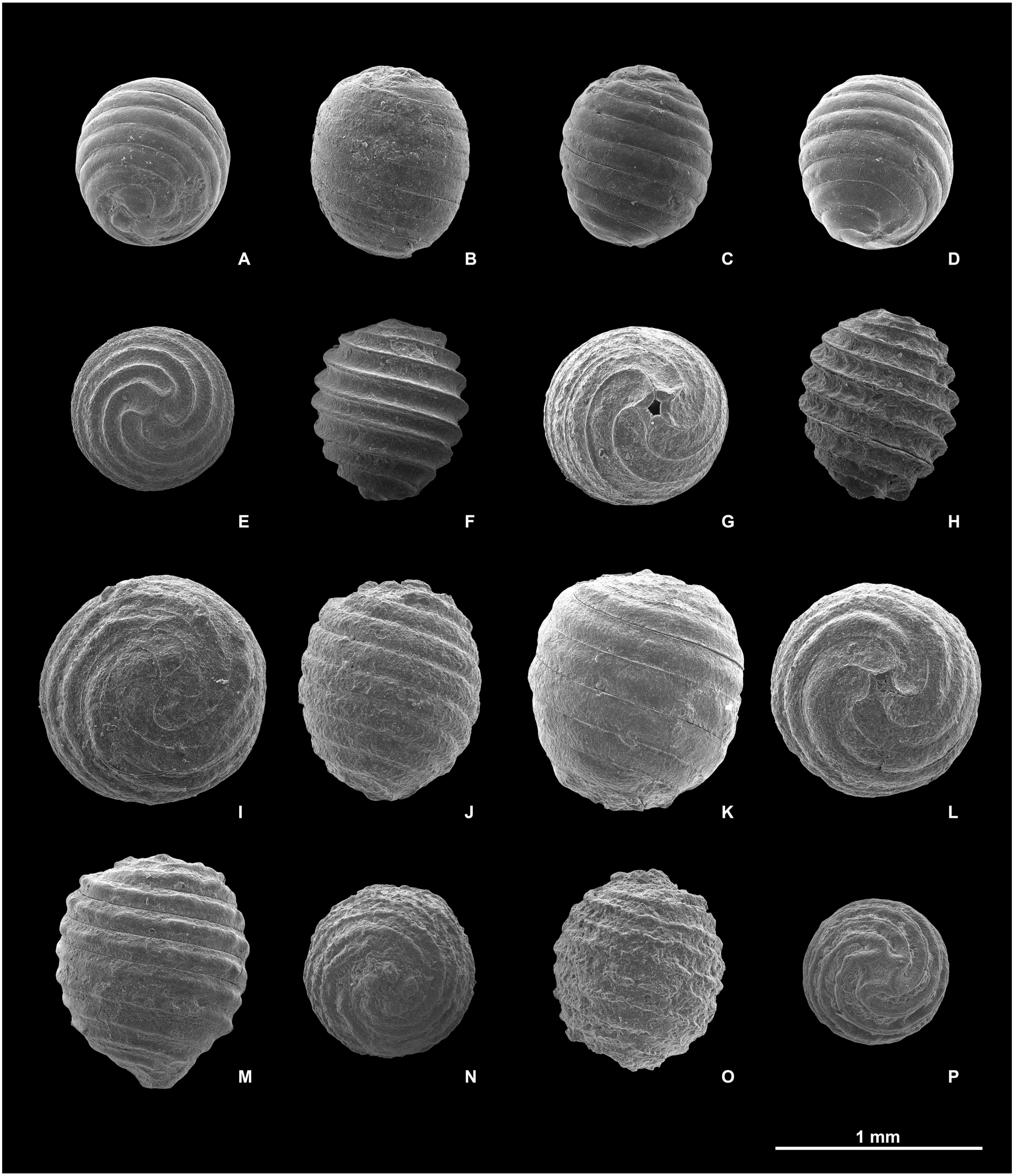


Figure 3

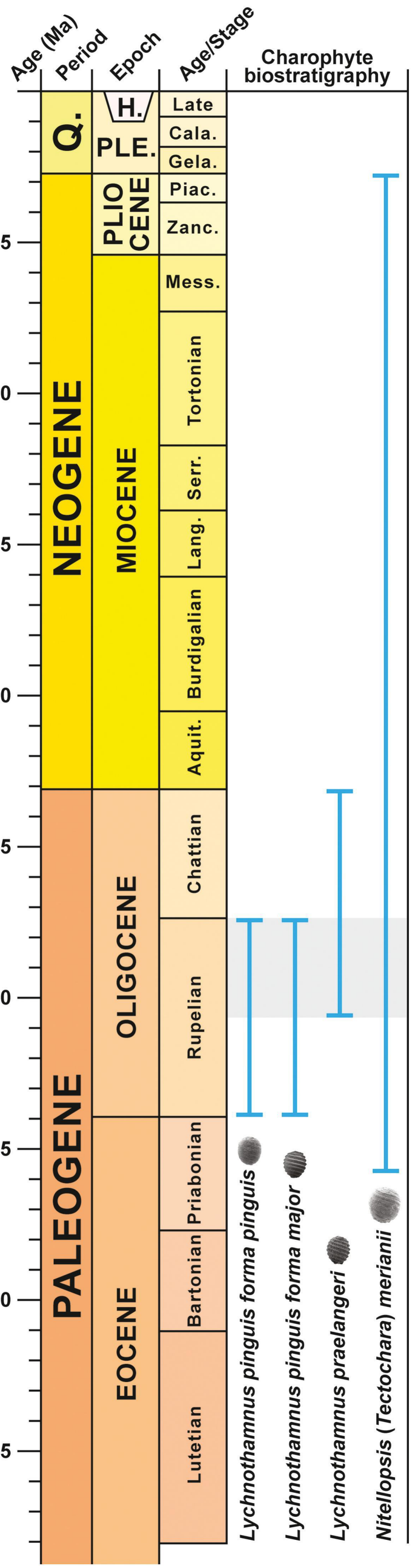

Age (Ma)
Period
Epoch
Age/Stage
Charophyte biostratigraphy
Q.
H.
PLE.
Late
Cala.
Gela.
PLIO CENE
Piac.
Zanc.
5
Mess.
10
Tortonian
NEOGENE
MIOCENE
Serr.
15
Lang.
Burdigalian
20
Aquit.
25
Chattian
OLIGOCENE
30
Rupelian
PALEOGENE
35
Priabonian
Bartonian
40
EOCENE
Lutetian
45
Lychnothamnus pinguis forma pinguis
Lychnothamnus pinguis forma major
Lychnothamnus praelangeri
Nitellopsis (Tectochara) merianii

Figure 4

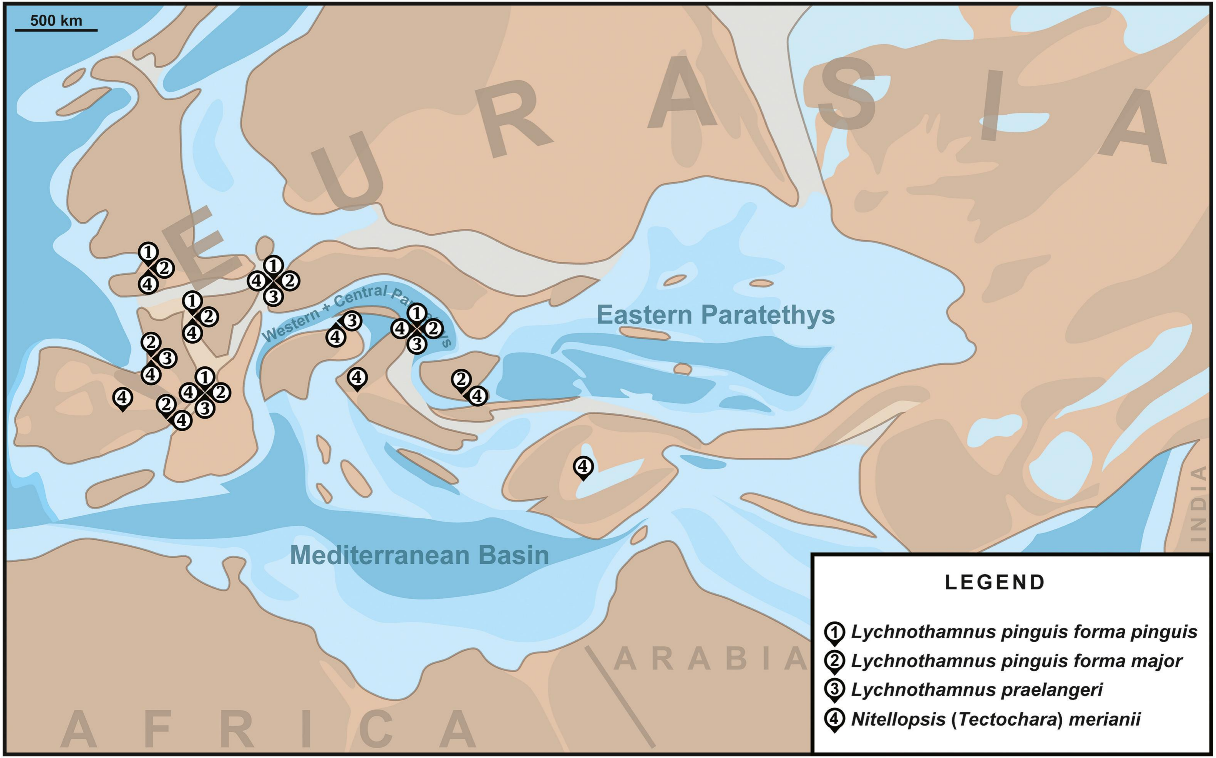

500 km
E U R A S I A
Eastern Paratethys
Western + Central Paratethys
Mediterranean Basin
A R A B I A
A F R I C A
INDIA
LEGEND
1 Lychnothamnus pinguis forma pinguis
2 Lychnothamnus pinguis forma major
3 Lychnothamnus praelangeri
4 Nitellopsis (Tectochara) merianii

Figure 5