

The oldest record of North American *Lychnothamnus* (northeastern Sonora, Mexico): Implications for the evolution, ecology, and paleogeographic distribution of the genus

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ARTICLE INFO

Keywords:

Charophytes
Paleobiogeography
Upper Cretaceous
Paleogene
Laramidia
North America

ABSTRACT

A large population of Late Cretaceous *Lychnothamnus tenuis* holding small sized gyrogonites are described after systematically sampling the Fronteras section in the Cabullona Group (northeastern Sonora, Mexico). This discovery represents the oldest record of *Lychnothamnus* in North America and the first record of this genus in Mexico. The sedimentological analyses of the section suggest that Mexican *L. tenuis* grew in fluvial and floodplain ephemeral ponds such as their South American counterparts, *Lychnothamnus barbosa* (oldest known worldwide occurrence of *Lychnothamnus*) and *L. tenuis*, from the Turonian–Santonian and Santonian–lower Campanian respectively. The small sized gyrogonites (calcified fructifications of charophytes) of *L. tenuis* from South America was considered to represent an adaptation to stressful growth conditions since most of the fossil and extant *Lychnothamnus* species are mainly found in freshwater lacustrine deposits. However, this floodplain-type environment has also been described for a small population of *Lychnothamnus* sp. recently recovered from the lower Eocene Claron Formation (Utah, USA) and for extant *Lychnothamnus barbatus* found in Australia, both populations having medium to large gyrogonites. This suggests that rather than being a response to ecological parameters, the gyrogonite size of *Lychnothamnus* is related to the evolutionary trend of the genus, producing smaller gyrogonites when first appeared in the Upper Cretaceous. Finally, the presence of *L. tenuis* in Sonora (North America) suggests a south to north colonization route for *L. tenuis* during the Late Cretaceous.

1. Introduction

Charophytes are an important group of aquatic plants, traditionally considered as green algae that thrive in non-marine fresh and transitional waters since the Silurian (Grambast, 1974). During millions of years, charophytes evolved and branched out resulting in the diversification into several families and genera whose species have been often applied in biostratigraphy, paleoecology and paleogeography (Grambast, 1974; Feist et al., 2005 and references therein). The genus *Lychnothamnus* Ruprecht is a well-known living genus of charophytes representing one of the six extant genera of the Characeae family. The only living species, *Lychnothamnus barbatus* (Meyen) Von Leonhardi, has been found in dense meadows in relatively deep oligo-mesotrophic freshwater lakes (Karczmarz, 1967).

However, this species can survive in a wide array of environments, i.e. subtropical to arid, and can tolerate a number of habitats, i.e. lakes, rivers, creeks, ditches, wet meadows, swamps, and reservoirs (Casanova et al., 2003; García and Chivas, 2006; Sugier et al., 2009). Today, extant *L. barbatus* is restricted to only few localities in Eurasia (Feist et al., 2005 and references therein), Australia (Casanova et al., 2003; García and Chivas, 2006), and North America (Karol et al., 2017). This taxon, it is known since the Miocene where gyrogonites (the calcified fructifications of charophytes) have been recovered from many lacustrine basins in Eurasia, Africa, Middle East, and Australia (Bhatia, 2006; García and Chivas, 2006; Sanjuan and Alqudah, 2018 and references therein). However, the genus *Lychnothamnus* itself has a long evolutionary history, originating in the Late Cretaceous (ca. 70 Ma) and extending to the Quaternary (last 2.6 Ma). Species of this genus

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<https://doi.org/10.1016/j.aquabot.2020.103271>

Received 28 October 2019; Received in revised form 20 June 2020; Accepted 21 June 2020

Available online 23 June 2020

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have been found in the fossil record of Eurasia (Feist et al., 2005, and references therein; Sanjuan and Martín-Closas, 2014, 2015; Vicente et al., 2015, 2016b), the Middle East (Mazzini et al., 2013; Sanjuan and Alqudah, 2018; Sanjuan et al., 2019), North Africa (Soulié-Märtsche in Petit-Maire and Riser, 1981), South America (Musacchio, 1973, 2006, 2010), and now in North America.

Charophyte calcified fructifications (utricles and gyrogonites) are easily fossilized and recognized world-wide in the fossil record enabling charophyte research. However, in comparison with Europa and Asia, which have a long history of charophyte research, the studies on fossil charophytes within North America is sparse with only few well-developed taxonomic studies published in the early 1900s. Some of these analyses involve Cretaceous and Paleogene charophytes from USA where characean genera (not including *Lychnothamnus*) were found, e.g. *Platychara* and *Chara* (Peck, 1941, 1957; Peck and Reker, 1948; Peck and Forester, 1979). From Mexican deposits, the only Late Cretaceous charophytes that are mentioned include *Tolypella* sp. and *Pseudoharrisichara* cf. *tenuis* from the Cabullona Group, northeastern Sonora (Kietzke et al., 1993), and *Platychara* sp. and *Porochara gilde-meisteri* Koch et Blissenbach from the Cerro del Pueblo Formation (Parras Basin), southeastern Coahuila (Aguillón-Martínez, 2010).

In their synthesis of charophyte genera, Feist et al. (2005) characterized *Lychnothamnus* gyrogonites as having a flat apex showing a characteristic periapical furrow and apical nodules, rounded base, pentagonal-shaped basal pore located within a funnel and a simple (unicellular) basal plate. *Lychnothamnus* gyrogonites are usually medium to large in size, often reaching more than 1000 µm in length. However, some species, such as *L. tenuis* found from Late Cretaceous fluvially influenced ponds in Argentina (Musacchio, 1973, 2010), have small gyrogonites with an average length and width of 544 µm and 386 µm respectively. Considering these studies, the diagnosis of *Lychnothamnus* should be modified to include the whole size range of its gyrogonites, i.e. from small to large, instead of the medium to large.

In the previous few decades, a deeper understanding of the evolution and morphological variability of fossil and modern gyrogonites, has resulted in placing the fossil genera *Amblyochara* Grambast, *Rhabdochara* Mädler, *Stephanochara* Grambast, and *Lychnothamnites* Maslov (by Soulié-Märtsche, 1989), and *Pseudoharrisichara* Musacchio (by Musacchio, 2010) in synonymy with *Lychnothamnus*. At the species

level, morphometric analyses including size and shape, degree of calcification, presence/absence of apical nodules, ornamentation and basal pore morphology, has permitted researchers to distinguish interspecific vs. intraspecific variability within *Lychnothamnus* as shown by Soulié-Märtsche (1989); Soulié-Märtsche and Martín-Closas (2003) and Sanjuan and Martín-Closas (2015). In consequence, *Lychnothamnus major* (Grambast & Paul) Soulié-Märtsche and *Lychnothamnus pinguis* (Grambast) Soulié-Märtsche from the Oligocene are now synonymes (Sanjuan and Martín-Closas, 2015), and a new variant, *Lychnothamnus barbatus* ssp. *megalicarpus* Soulié-Märtsche and Martín-Closas from the Miocene was proposed (Soulié-Märtsche and Martín-Closas, 2003).

The aim of this study is to present for the first time the occurrence of fossil *Lychnothamnus* in Mexico. This enables discussing its historical evolution, geographical distribution, ecological requirements, and possible routes of North American colonization. The large population of *L. tenuis* described in the Late Cretaceous deposits of the Cabullona Group in Fronteras (northeastern Sonora, Mexico), is the oldest record of the genus in the southern part of Laramidia (the late Cretaceous landmass corresponding to present western North America). The Mexican gyrogonites of *L. tenuis* are compared with *L. tenuis* from South America, and with an additional population of *Lychnothamnus* sp. recently discovered in lower Eocene deposits of the Claron Formation (southwestern Utah, USA; Sanjuan et al., 2020, in press). Both taxa, *L. tenuis* and *Lychnothamnus* sp., are here fully described and illustrated.

2. Material and methods

2.1. Study sites

2.1.1. Cabullona Group, Sonora, Mexico (Late Cretaceous)

The studied sedimentary sequence is located in the proximity of the town of Fronteras (30° 53' 13.3091" N, 109° 32' 55.4266" W base and 30° 53' 12.8" N, 109° 32' 06.6" W top coordinates) near the border with the USA and in the southern part of the well-known Cabullona Basin. The section selected for this study is ca. 470 m thick and was measured and systematically sampled for microfossils (Fig. 1).

The Cabullona Basin underwent syntectonic sedimentation from the Campanian to the lower Maastrichtian and is associated with the uplift of the Sierra Anibacachi (González-León et al., 2017 and references

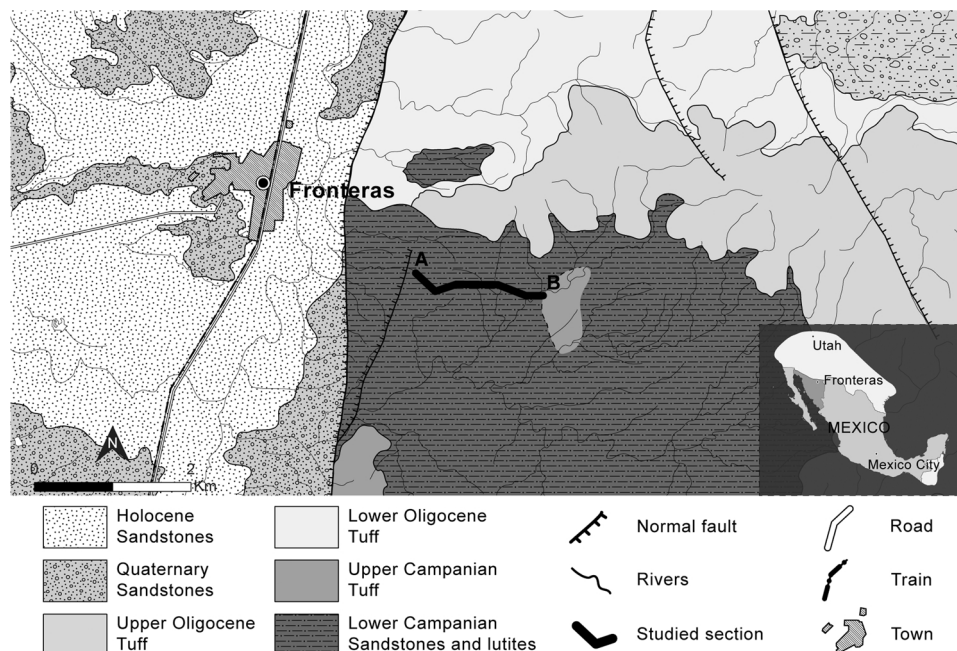


Fig. 1. Geologic map of the western part of Sonora (Mexico) showing the location of the studied section at Fronteras. “A” marks the base of the section and “B” the top. Modified from Robles Zavala and Ortega Carmona (2016).

therein). The infilling of this basin corresponds to the Cabullona Group sedimentary sequence (González-León et al., 2017) which has been recognized as a fluvio-lacustrine deposit and divided into four units (González-León et al., 2017 and references therein). The chronostratigraphy of these units has been improved recently by the use of the U/Pb dating method on samples obtained from tuff beds found in several sections of the Cabullona Basin including rhyolites from the uppermost part of the Fronteras section, dated at 76.7 ± 0.7 Ma (González-León et al., 2017). However, the uppermost part of the Cabullona Group elsewhere has dates ranging ca. 81.9 ± 0.7 to 69.8 ± 0.7 Ma (early Campanian–early Maastrichtian).

The fossils found in the Fronteras section are very diverse including charophytes, aquatic gastropods, bivalves (pelecypod), ostracod carapaces, fish, turtles, and dinosaurs amongst others. The Cabullona Group also contain continental palynomorphs (Villanueva-Amadoz et al., 2014). Most of the sediments of this group were deposited under continental conditions, but two minor marine incursions have recently been identified in the Corral de Enmedio Formation (Naco Section) which contains marine fossils and euryhaline charophytes related to the Porcharaceae (Duarte-Bigurra, 2018).

2.1.2. Claron Formation. Utah, USA (early Eocene)

The Claron Formation contains a small *Lychnothamnus* sp. population within its lower three units of a ca. 450 m thick stratigraphic section present in the southern part of the Aquarius Plateau, southwestern Utah, USA (see Fig. 2 in Sanjuan et al., 2020, in press). Orange-tan fluvial-related deposits of the Claron Formation (Fig. 2 in Eaton et al., 2018) compose the majority of the section. The charophytes were recovered from insect bioturbated siltstones. The upper part of the Claron Formation was dated as early Eocene in age based on the presence of fossil mammals (Eaton et al., 2018). Hence, the *Lychnothamnus* beds from the lower Claron Formation are no younger than early Eocene, but could possibly be as old as late Paleocene. This formation provides a rich and diverse microfossil assemblage dominated by freshwater charophytes, including *Lychnothamnus* sp. reported here, but also ostracods and gastropods.

2.2. Field collection, processing of sediments, and taphonomic considerations

During the fieldwork in the Fronteras section, 25 samples of a normalized weight of 3 kg were collected from gray and ochre lutite and siltstone intervals. These samples were treated with a solution of hydrogen peroxide (H_2O_2) and water. In order to deflocculate the clay, 5–10 g of anhydrous sodium carbonate (Na_2CO_3) were added to the solution. The sediment was then washed on sieves with mesh sizes of 180, 500, and 1000 μm . In order to avoid contamination, before washing each sample, the sieves were cleaned, dried, and dyed with methylene blue. Charophyte fructifications were handpicked using a binocular Zeiss Stemi 508 at the ERNO-IGL-UNAM (Estación Regional del Noroeste-Instituto de Geología-Universidad Nacional Autónoma de México, Hermosillo, Sonora, Mexico). The section from Utah was randomly sampled generally taking larger samples than those from Fronteras. The sediment was later washed through a set of three nested screens (mesh sizes of 200, 500, and 1000 μm). Screens were dried and washed after each processing to avoid contaminations. Gyrogonites were handpicked under a Meiji EMZ stereo microscope. All specimens were measured using the software Motic Image Plus 2.0 ML in a binocular Wild Heerbrugg attached to a Moticam 5 housed in the DDTO-UB (Departament de Dinàmica de la Terra i de l'Oceà-Universitat de Barcelona, Barcelona, Catalonia, Spain). Selected gyrogonites from the Fronteras section were photographed using the Hitachi TM3030Plus Tabletop Scanning Electron Microscope (SEM) at the Laboratorio Nacional de Geoquímica y Mineralogía (LANGEM) at the ERNO-IGL-UNAM. The charophyte remains found in the Cabullona Group are stored in the

paleontological collections of the ERNO-IGL-UNAM. The gyrogonites of *Lychnothamnus* sp. from the Claron Formation (southwestern Utah, USA) included in this study for comparison, are stored at the Natural History Museum of Utah-UMNH (Utah, USA).

The taxonomic studies are based on the biometric data obtained by measuring a large gyrogonite population (100 individuals when possible) for each species. Moreover, taphonomic features such as abrasion, chemical corrosion and fragmentation of the gyrogonites have been considered here since might indicate a possible reworking or transport from the original depositional environment.

3. Results

3.1. Sedimentology, taphonomy, and paleoecology

This study focuses on the sediments of the ca. 460 m thick succession of the Cabullona Group. These deposits are mostly composed of light to dark gray and ochre mudstone and siltstone strata alternating with channelized sandstone beds, sometimes with erosive bases and cross-bedding stratification. Some thin marl beds occur sporadically at the base and top of the section. Several mudstone and siltstone intervals display edaphic features such as mottled colors, carbonate nodules, root marks and bioturbation. The fossil assemblage has been recovered from the ochre, gray, and dark gray mudstone and siltstone beds and was mainly composed of charophyte fructifications, freshwater mollusks (mainly gastropods and rarely bivalves) with many of the shells fragmented, and ostracods. However, microgastropods and ostracods appear complete, with the ostracods often found with the valves still attached. At the base and top of the section, other remains include fragmented turtle shells, fish teeth, and dinosaur bones. In the upper part of the sequence, a few 10–20 cm thick fossiliferous marl intervals occur, containing large gastropod shells (2–3 cm length). Gyrogonites of the genus *Lychnothamnus*, along with other charophyte species, are usually well-preserved, although there are some corroded individuals. Thick channelized sandstone beds occur overlying and underlying these fossiliferous marl intervals, displaying erosive bases and cross-bedding stratification, and containing three silicified fossil trunks, some of them up to 14 m in length.

The sedimentary succession found in the Fronteras section has been interpreted as fluvial in origin with abundant turbulent and lower regime detrital flows. Gray mudstones and siltstones suggest the presence of fluvial influenced shallow ponds rich in charophytes, microgastropods, and ostracods.

Taphonomic evidence suggest that well-established populations of *L. tenuis* along with mollusks developed in temporary fluvial shallow ponds, subjected to low energy transport in a floodplain context. Occasionally, these ponds became more stable enabling large gastropods, fishes and turtles to thrive. The presence of edaphic features such as mottled colors, calcium carbonate nodules, and root marks indicate the presence of paleosols (Kraus and Aslan, 1993). The corrosion observed in the gyrogonites has been interpreted as a diagenetic feature, probably due to the presence of slightly acid fluids, which are commonly associated with volcanoclastic horizons.

The sediments of the lower Eocene Claron Formation form a thick continental formation, subdivided in the study area in eight informal lithostratigraphic units. The charophyte flora has been found in the three lower units of the Claron Formation, which consists generally of well-oxidized (orange to red) and bioturbated mudstones alternating with sandstones and lacustrine carbonates. Trace fossils, charophytes, gastropods, and ostracods are the most common fossil elements in the formation (Eaton et al., 2018; Sanjuan et al., 2020, in press). Rare gray floodplain mudstones contain vertebrate fossils (Eaton et al., 2018). The presence of insect bioturbated mudstones and siltstones has been interpreted as floodplain deposits (Eaton et al., 2018) that was periodically flooded causing the development of small ponds.

3.2. Systematic paleontology

Division CHAROPHYTA Migula, 1897

Class CHAROPHYCEAE Smith, 1938

Order CHARALES Lindley, 1836

Family CHARACEAE Richard ex C. Agardh, 1824

Subfamily Charoidae Al. Braun in Migula, 1897

Genus *Lychnothamnus* Ruprecht, 1845

Lychnothamnus tenuis (Musacchio, 1973) Musacchio, 2010

Fig. 2, A–E.

Material. Hundreds of gyrogonites were collected from samples Fro.c-10a and Fro.c-11a of the Fronteras section (Cabullona Group, Sonora, Mexico). Dozens of gyrogonites were collected through the section in samples Dinosaur Outcrop 2, Fro.c-3a, Fro.c-06, Fro.c-6a, Fro.c-08, Fro.c-010, Fro.c-7a, and Fro.c-8a.

Description. Gyrogonites are small to medium in size with 469–725 μm (mean 604 μm) in length and 388–613 μm (mean 530 μm) in width (Fig. 3). The gyrogonites have an isopolarity index (ISI) ranging from 99–149 (mean 114) indicating an oblate spheroidal to prolate, mainly subprolate, shape (Figs. 2 and 3). Six to eight, most frequently seven,

spiral turns are visible in lateral view (Figs. 2 and 3) with cells about 56–100 μm (mean 82 μm) in width. Spiral cells are concave, usually with a bicarinate suture (Fig. 2B). In some cases, spiral cells show a poorly marked reticulated ornamentation formed by small perpendicular rods placed between both sides of the suture. The apex is psilocharoid, flat or slightly rounded, with slightly periapical thinning and without apical nodules (Fig. 2D). The base is pointed and ends forming a small pentagonal pore about 38–100 μm in diameter (mean 72 μm) usually showing a funnel (Fig. 2E). The basal plate cannot be observed; however, this genus usually presents simple and conical basal plates.

Remarks. The gyrogonites found in the Cabullona Group, correspond to *Lychnothamnus tenuis*, a species previously only known from Upper Cretaceous deposits of the Neuquén Basin in Argentina (Musacchio, 2006, 2010). Gyrogonites of the Mexican *L. tenuis* differ from the South American *L. tenuis* in being slightly longer, defining a more sub-prolate shape (Table 1). Mexican *L. tenuis* is slightly longer, wider, and with a lower number of convolutions visible in lateral view than *L. barbosa* from the Upper Cretaceous non-marine deposits of South America (Musacchio, 2010; Table 1). However, despite these minor differences, the two Upper Cretaceous North and South American

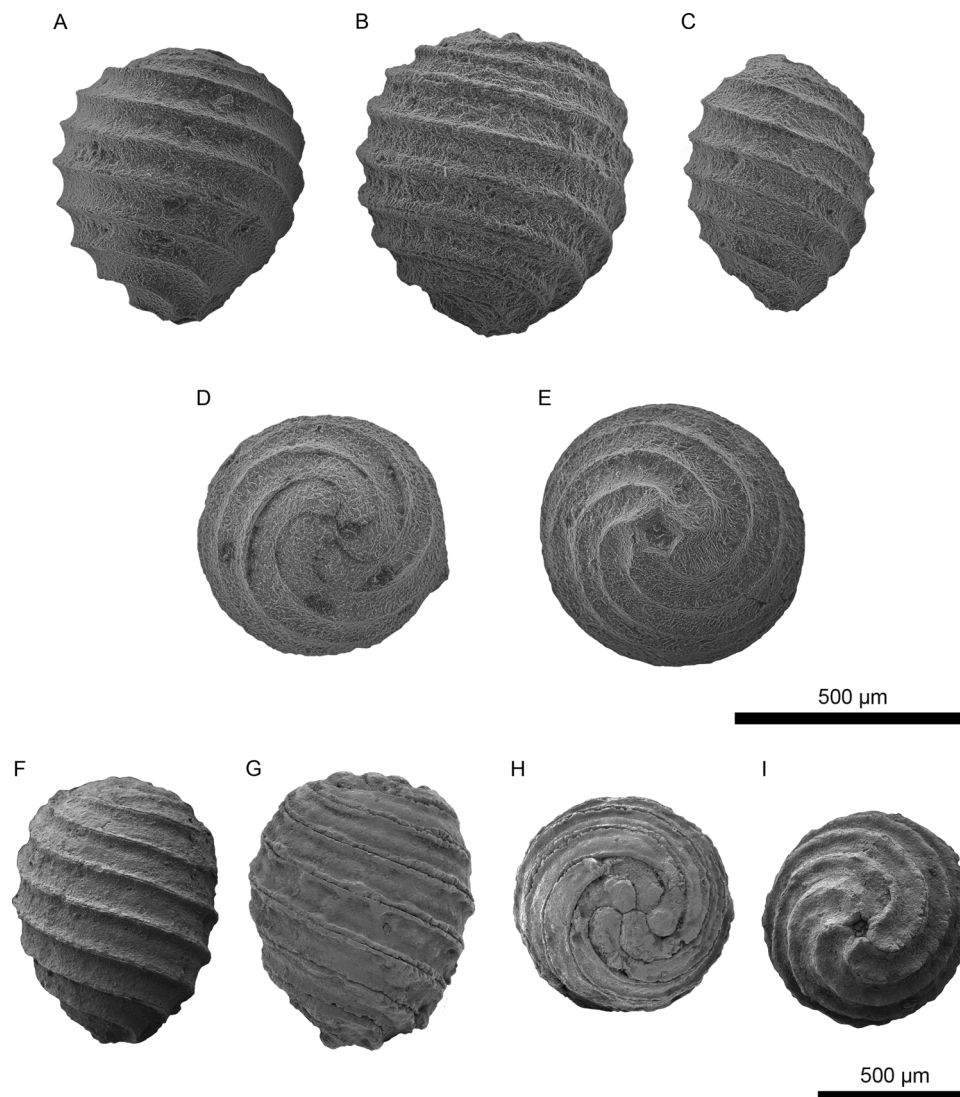


Fig. 2. SEM images of North American *Lychnothamnus*. A–E, *L. tenuis* (specimens no. ERNO-UX0011 to ERNO-UX0015) from the Fronteras section (northeastern Sonora, Mexico). A–C, lateral view; D, apical view; E, basal view. Sample Fro.c-10a. F–I, *Lychnothamnus* sp. from the Claron Formation (southwestern Utah, USA; From Sanjuan et al., 2020, in press). F–G, lateral view. Samples UMNH PB 4035 Loc. 117 and sample UMNH PB 3807 Loc. 107 respectively; H, apical view. Sample UMNH PB 3807 Loc. 107; I, basal view. Sample UMNH PB 4035 Loc. 117.

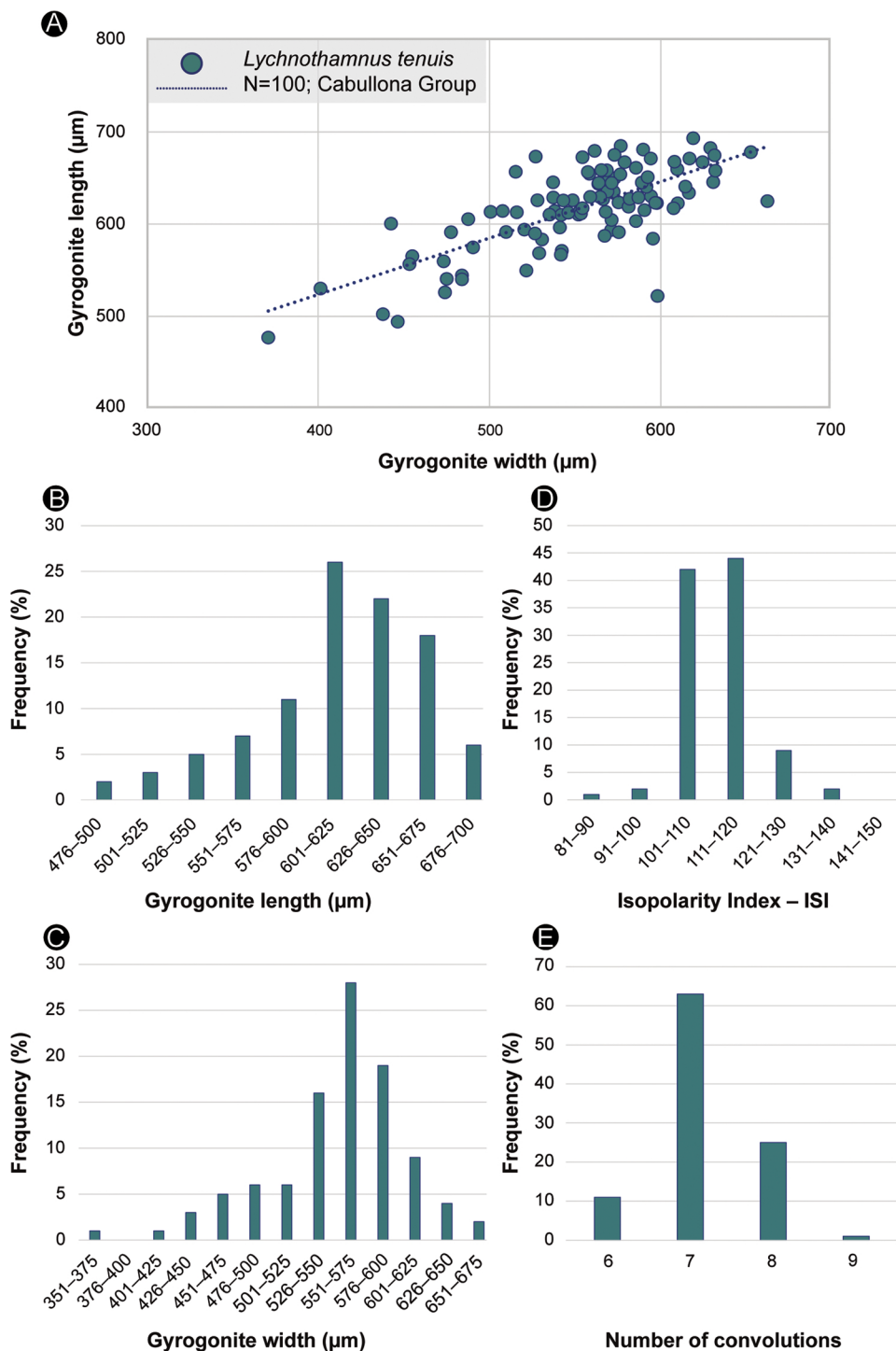


Fig. 3. Biometric analyses of the North American Upper Cretaceous *Lychnothamnus tenuis*. A. Scatter graphs considering gyrogonite length (µm)/Gyrogonite width (µm). Frequency distributions of gyrogonite length (B), gyrogonite width (C), isopolarity index (D), and number of convolutions visible in lateral view (E).

Lychnothamnus species are characterized by the smaller size of their gyrogonites, attributed by Musacchio (2010) to environmental constraints.

Distribution. *L. tenuis* has been reported only in the Santonian–lower Campanian deposits of the South American Neuquén Basin in Argentina (Musacchio, 1973, 2010) and in the upper Campanian non-marine deposits of the Cabullona Basin (North America) as reported here.

Paleoecology. The sediments bearing the Mexican *L. tenuis* have been interpreted as palustrine shallow ponds formed in a floodplain.

Sedimentological analyses suggest that these ponds had abundant terrigenous input and with a low calcium carbonate content.

Lychnothamnus sp.
 Fig. 2, F–I.

Material. Few gyrogonites (20) from samples UMNH PB 3801/4037 Loc. 107; UMNH PB 3807/4035 Loc. 117, and UMNH PB 3806/4035 Loc. 116 from the lower part of the Claron Formation has been included in this study. Only five gyrogonites were adequately preserved to be useful in the biometric measurements.

Description. Gyrogonites are medium to large in size with 778–961

Table 1Morphometric comparison between different populations of *Lychnothamnus*. Abbreviations: L. length; W. width; n. number of convolutions; e. spiral cell width.

Data from	<i>Lychnothamnus tenuis</i> (Musacchio, 1973) Musacchio, 2010 Musacchio, 1973 n = 20	<i>Lychnothamnus tenuis</i> (Musacchio, 1973) Musacchio, 2010 Musacchio, 2010 n = 111 (Zampal 48.b1)	<i>Lychnothamnus tenuis</i> (Musacchio, 1973) Musacchio, 2010 Musacchio, 2010 n = 69 (Zampal 48.b2)	<i>Lychnothamnus barbatus antiquus</i> Soulié-Märsche, 1989 Soulié-Märsche, 1989 n = 150
Shape	Sub-prolate to prolate mainly prolate	Sub-prolate to prolate, mainly sub-prolate	Oblate spheroidal to prolate, mainly sub-prolate	Sub-prolate
Size				
L (µm)	495–615 (mean 544)	455–630 (mean 614)	386–648 (mean 551)	Mean 774
W (µm)	365–460 (mean 386)	325–499 (mean 431)	326–489 (mean 419)	Mean 671
n	7–12	4–10 (mean 10,2)	9–13 (mean 10,4)	8–11
e (µm)	Unknown	Unknown	Unknown	Unknown
ISI (Isopolarity index)	126–155 (mean 141)	114–152 (mean 131)	95–171 (mean 121,8)	Mean 116
Apex	Weakly periapical depression	Sub-truncated to rounded	Sub-truncated to rounded	Sub-rounded
Base	Asymmetrically tapered	Asymmetrically tapered	Asymmetrically tapered	Weakly protruded
Locality (basin)	Neuquén Basin, Argentina	Neuquén Basin, Argentina	Neuquén Basin, Argentina	Veyran (France)
Biostratigraphic range	Santonian–early Campanian	Santonian–early Campanian	Santonian–early Campanian	Miocene

µm (mean 860 µm) in length and 599–790 µm (mean 702 µm) in width. The gyrogonites have an isopolarity index (ISI) ranging from 115–130 (mean 123) and mostly a sub-prolate shape (Figs. 2F and 2 G). Eight, convolutions are visible in lateral view with cells about 104–128 µm (mean 118 µm) in width (Figs. 2F and 2 G). Spiral cells are concave to convex depending on the degree of calcification. Concave cells usually show a bicarinate suture (Fig. 2G). Sometimes highly calcified gyrogonites have slightly undulated and convex spiral cells. The apex is psilocharoid, flat or slightly rounded, with periapical thinning and usually show marked apical nodules, mostly found in highly calcified gyrogonites (Fig. 2H). The base is pointed, without a column, and terminates forming a small pentagonal pore (Fig. 2I) about 63–189 µm in diameter (mean 126 µm). As occurs with *L. tenuis*, the basal plate cannot be observed but it should be simple and conical as generally occur in this genus.

Remarks. The gyrogonites of early Eocene *Lychnothamnus* sp. differs from *L. tenuis* by their larger size, marked apical nodules, and usually convex and undulated spiral cells. These features resemble other Paleogene and Neogene *Lychnothamnus* such as *L. vectensis* (Groves) Soulié-Märsche, *L. stockmansii* (Grambast) Soulié-Märsche and *L. pinguis*. However, the small number of specimens recovered from these Paleogene deposits hinders their specific attribution.

Distribution. *Lychnothamnus* sp. has been only found in the lower part of the Claron Formation in North America, and underlie a horizon dated as early Eocene by Eaton et al. (2018).

Paleoecology. The gyrogonites recovered from the Claron Formation come from beds containing mainly thin thalli, ostracods, gastropods and trace fossils that were interpreted as representing floodplain environments. Hence, *Lychnothamnus* sp. probably grew in fluvial influenced ponds formed in these floodplains.

4. Discussion

4.1. Fossil and extant *Lychnothamnus*: evolution, ecology, and geographical distribution

Gyrogonites attributed to the genus *Lychnothamnus* are found in the fossil record since the Upper Cretaceous, 100.5–66 Ma (Feist et al., 2005 and references therein), but despite its long history, its worldwide distribution is relatively sparse when compared with other Characeae (Sugier et al., 2009).

The first records of *Lychnothamnus* species are from the Late Cretaceous from South America. These *Lychnothamnus* thrived in fluvial-palustrine environments and are characterized by producing small gyrogonites (Dias-Brito et al., 2001; Musacchio, 2010). This is the case for *Lychnothamnus barbatus*, which was recovered from Turonian–Santonian sedimentary rocks of the Adamantina Formation in

Brazil (Dias-Brito et al., 2001) and from Turonian–Coniacian fluvial-lacustrine deposits of the Neuquén Basin in Argentina (Musacchio, 2006, 2010). Musacchio (2010) also described the first occurrence of small gyrogonites of *Lychnothamnus tenuis* in slightly younger lacustrine and palustrine deposits (Santonian–lower Campanian) from the Neuquén Basin.

The discovery of *L. tenuis* in the upper Campanian Fronteras section (northeastern Sonora, Mexico) located in the southern part of the Cretaceous Laramidia landmass (Fig. 4) extends the biochron and geographical distribution of this species during the Late Cretaceous.

At the same time, sedimentological and paleontological evidence indicates that the Mexican *L. tenuis* grew in similar ecological conditions to that of *L. barbatus* and *L. tenuis* described from South America. The continental beds of the Fronteras section of the Cabullona Group are interpreted as fluvial deposits formed under turbulent but with a low energetic stream flows regime. The gray mudstone and siltstone intervals, rich in freshwater related microfossils (charophytes, microgastropods, and ostracods), indicate the presence of fluvially influenced shallow and well-oxygenated ponds.

In younger sedimentary sequences, at the end of the Paleocene and especially during the Eocene, *Lychnothamnus* diversifies and evolves, with at least eight species reported in Europe and sixteen in China, most of them characterized by producing medium to large fructifications and by thriving in freshwater lakes (Riveline, 1986; Feist et al., 2005 and references therein). The diversification of *Lychnothamnus* during the Eocene combined with the restricted stratigraphic range of several species resulted in the use of some *Lychnothamnus* taxa as index species of charophyte biozonations for this period of time (Sanjuan et al., 2014).

The discovery of *Lychnothamnus* sp. in early Eocene sediments from the Claron Formation (southwestern Utah, USA), represents the first report of this genus for the Paleogene in North America (Sanjuan et al., 2020, in press; Fig. 4). *Lychnothamnus* sp. is characterized by having medium sized gyrogonites, as occurs in other Eocene species found in Eurasia (e.g. *L. vectensis* or *L. stockmansii*), but this taxon grew in temporary freshwater ponds developed in floodplains with large fluvial incursions which is in contrast with the common habitat of Cenozoic *Lychnothamnus*.

During the Oligocene *Lychnothamnus* started to decline with only four species reported in Europe (Riveline, 1986). In the Neogene, this decline continued but the first record of the extant *Lychnothamnus barbatus* occurred. During the Miocene and Pliocene, *L. barbatus* is found in sequences from Europe and the Middle East, i.e. Spain, southern France, Portugal, Montenegro, Turkey, and Lebanon (Sanjuan and Alqudah, 2018 and references therein). This species became extinct before the Quaternary in some geographic areas such as south European countries (e.g. Spain) and the Middle East (Bhatia, 2006; Sanjuan and

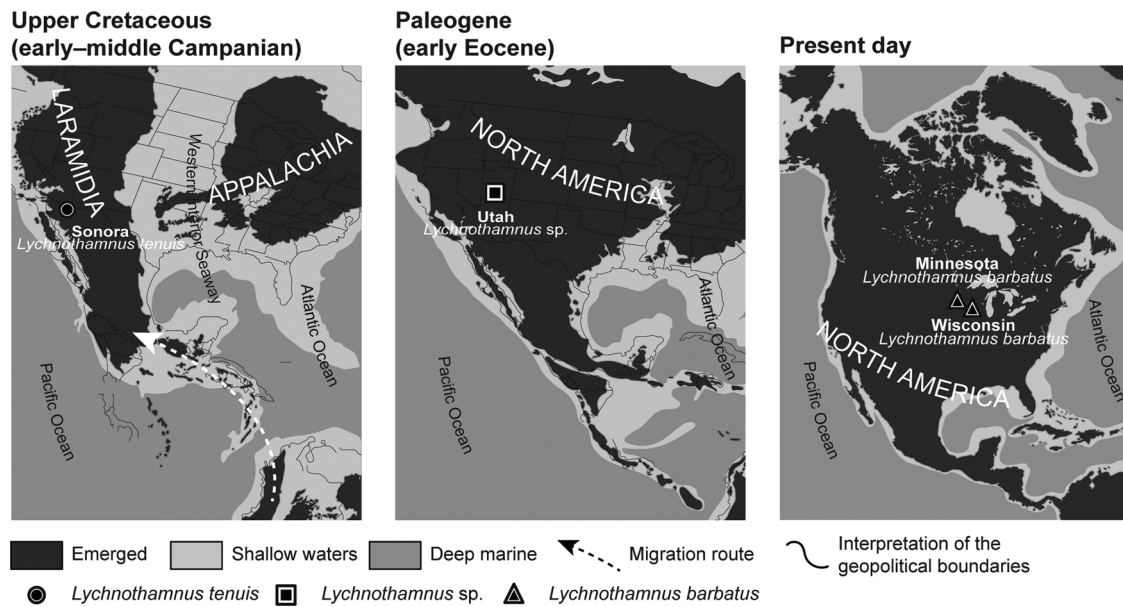


Fig. 4. Biogeographic distribution of the genus *Lychnothamnus* in North America from the Late Cretaceous to the present. Late Cretaceous and Paleogene maps are modified from Scotese (2001).

Alqudah, 2018). However, *L. barbatus* reached Australian waterbodies during the Pleistocene (Quaternary) as indicate their presence in the freshwater lacustrine deposits of the Gulf of Carpentaria (García and Chivas, 2006). The absence of Paleogene–Neogene charophytes studies, especially from the Americas, Africa, and Australia, makes difficult the development of well-constrained paleobiogeographic maps for this genus. However, it is important to remark that extant *L. barbatus*, although having disjunct populations, is found today in Europe, Asia, and Australia (Karczmarz, 1967; Bhatia, 2006; Sugier et al., 2009; Brzozowski et al., 2019 and references therein) and more recently in North America (Karol et al., 2017; Fig. 4). The lack of fossil *Lychnothamnus* records in North America was used as an argument to suggest that the controversial presence of *L. barbatus* in Minnesota and Wisconsin (USA) was the result of a recent introduction (Karol et al., 2017). However, the presence of *L. tenuis* in the Late Cretaceous Fronteras section and *Lychnothamnus* sp. in the early Eocene Claron Formation, suggest that at least, this genus was present in North America during those times.

The comparison between the ecological preferences of the Late Cretaceous *Lychnothamnus* species with small gyrogonites and the Cenozoic species, characterized by having medium to large gyrogonites, suggests that through time *Lychnothamnus* colonized new habitats such as freshwater lakes, expanding their geographical distribution and becoming more diversified.

At present, *L. barbatus*, with medium to large gyrogonites, is found in a wide array of environments, climate types and habitats, some of them located in subtropical to arid areas; with permanent to more temporary waterbodies, i.e. lakes, rivers, creeks, ditches, wet meadows, swamps, and water reservoirs. It is worth to note that extant *L. barbatus* from northern Australia grows today in fluvial, palustrine, and floodplain areas (Casanova et al., 2003), the same type of environment established for the Late Cretaceous *L. barbatus* (South America) and *L. tenuis* (South and North America) and early Eocene *Lychnothamnus* sp. (North America). However, the earliest record of *L. barbatus* in Australia was in a Pleistocene, when was thriving in the freshwater Carpentaria paleolake (García and Chivas, 2006). Since most extant *L. barbatus* localities occur mainly in freshwater lakes.

Ecological studies of *L. barbatus* have recently shown that the demise or even disappearance from many European freshwater lakes is due to anthropogenic water eutrophication (Pelechaty et al., 2017)

rather than to an ecological constraint. This large area reduction in the geographic distribution of the species prompted the designation of *L. barbatus* as an endangered species in many countries and geographic areas such as Lithuania, Poland, Germany, the Balkans, and Australia (Sugier et al., 2009; Brzozowski et al., 2019). These studies also show that a change is observed in the habitat preferences of *Lychnothamnus* through time, passing from thriving in floodplain ponds to mainly colonizing freshwater lakes after the Eocene, with the exception of the extant Australian *Lychnothamnus* populations. Despite this, all living and fossil *Lychnothamnus* have been found in deposits related to freshwater environments, which makes this genus a valuable paleoenvironmental proxy to identify past freshwater conditions.

4.2. Hypothesis for *Lychnothamnus* colonization of North America: a paleobiogeographical approach

The breakup of the Pangea supercontinent and the subsequent opening of the Atlantic Ocean occurred from the late Paleozoic to the Early Cretaceous, resulting in the separation of the two large landmasses of Laurasia (i.e. North America and Eurasia) and Gondwana (i.e. South America, Africa, India, Antarctica, and Australia), and later, in the splitting of South and North America. However, it was not until the Early Cretaceous that American continents were completely separated by the Proto-Caribbean Sea (Boschman et al., 2014 and references therein). As North America moved northward, the distance between North and South America increased, hindering the migration of terrestrial organisms between both land masses. At the same time, a continuous subduction of the Farallon Plate under the North and South American plates occurs, resulting in the formation of an orogeny and magmatism that were related to the development of a foreland basin and the Western Interior Seaway during the middle Cretaceous (ca. 100.5 Ma). This marine corridor separated the large Laramidia (west North America) and Appalachia (east North America) islands, reducing the emerged landmass of North America (Fig. 4).

Musacchio (2000) already suggested that charophytes could have migrate from the South American Andean Province (western South America) to the north even though there was an apparent lack of terrestrial connection between North and South America. The discovery of upper Campanian *L. tenuis* from the Cabullona Basin (southern part of the Laramidia Island; Fig. 4) suggests that indeed, South American

Lychnothamnus from the Santonian–lower Campanian Neuquén Basin migrated toward the north. It was approximately during that time (Campanian) that the Greater Antilles Arc, located between Yucatán (southern Mexico) and northern South America, was formed as a result of the subduction between the Caribbean and the American plates (Boschman et al., 2014 and references therein). This formed an island archipelago connecting the northern part of the South American Andean Province and the southern Laramidia Island that could act as a connecting bridge for a south to north dispersal during the Late Cretaceous. Birds, especially waterbirds, have been traditionally considered as a key dispersal vector in supra-continental charophyte colonization through time as has been previously suggested in *Lychnothamnus* dispersal theories (Sanjuan and Martín-Closas, 2015). These authors suggest that migratory aquatic birds from the Anatidae family, important charophyte dispersers today, were involved in the west to east dispersion of Eocene–Oligocene *L. stockmansii* (Sanjuan and Martín-Closas, 2015 and references therein). However, the first records of ducks occur later during the earliest Oligocene (Sanjuan and Martín-Closas, 2015 and references therein). Other charophyte-eating birds or flying animals such as pterosaurs could be probably responsible for charophyte dispersal since they show a great dispersal potential enabling to cross large distances and marine barriers during the Cretaceous using north–south migratory routes just as birds do today. In fact, during this period, birds already displayed advanced skeletal modifications that improve locomotion suggesting that they could have been adapted to long-distant flights similar to those of extant migratory birds like some ducks. Non-flying herbivorous or piscivorous animals such as some dinosaurs cannot be excluded as charophyte dispersal vectors, however, this hypothesis has not been proved yet. On the other hand, biological features such as the monoecious reproduction of *Lychnothamnus* and the taxon's ability to thrive in unstable environments such as fluvial systems with variable water regimes allowing the development of floodplains, could be key factors that helped *Lychnothamnus* colonize both American landmasses during the Late Cretaceous.

4.3. Final remarks

Fossil gyrogonites of the genus *Lychnothamnus* have been described for the first time in Mexico after a systematical sampling of the upper Campanian (Upper Cretaceous) Fronteras section in the Cabullona Basin (northeastern Sonora, Mexico). The charophyte assemblage recovered from this section is dominated by the small gyrogonites of *L. tenuis*. Recent analyses of the continental deposits from the lower Eocene Claron Formation (Utah, USA), also provide a record of a small population of *Lychnothamnus* sp. having slightly larger sized gyrogonites.

Differences observed in the gyrogonite size of *Lychnothamnus* shed light on the evolution of this genus. The early evolutionary stages occurred during the Late Cretaceous of South and North America are characterized by the small sized gyrogonites of *L. barbosa* (Brazil) and *L. tenuis* (Argentina and Mexico). These species are replaced during the Cenozoic by taxa producing medium to large size gyrogonites (i.e. Paleogene *Lychnothamnus* sp. from USA and modern *L. barbatus*).

The small fossil gyrogonites were recently interpreted as an adaptation to stressful environments, such as fluvial influenced ponds, ponds subjected to increasing detrital input, shallow ponds or event ponds suffering long dry periods (Vicente et al., 2016a). Musacchio (2010) suggested that these environmental constraints were the reason for the smallest gyrogonite size known for *L. tenuis* found in the Neuquén Basin (Argentina) compared to the other, mainly Cenozoic, larger *Lychnothamnus* species. Recent analyses carried out on extant *Chara vulgaris* var. *longibracteata* (Kützing) Groves et Bullock-Webster, confirm that this species can reduce their gyrogonite size as an adaptation to the habitat to ensure their survival in stressful environments (Sanjuan et al., 2017). In accordance with this, the production and gyrogonite size of

extant *L. barbatus* can vary according to the environmental conditions, mainly water depth and light availability (Brzozowski et al., 2019). This species develops smaller gyrogonites, within the *L. barbatus* length and width range of 700–1075 μm and 550–836 μm respectively, and produce more fructifications in deeper and darker areas of lakes following a life strategy that permits them to tolerate the stress (Brzozowski et al., 2019).

The sedimentological interpretations carried out of the Fronteras section (northern Mexico) enabled the description of the paleoecological preferences of upper Campanian *L. tenuis* which includes fluvial influenced shallow ponds with abundant detrital input. The ecological preferences and the gyrogonite size observed in *L. tenuis* from Fronteras agrees with the theory that small gyrogonites reflects an adaptation to stressful environments. However, similar environmental conditions have been proposed for the early Eocene *Lychnothamnus* sp. found in the Claron Formation (southwestern Utah, USA) and in extant *L. barbatus* found in fluvial and floodplain environments from Australia which have medium to large sized gyrogonites. Although the biometric analyses from *Lychnothamnus* sp. are based on a very small sample, the progressive increase of the gyrogonite size of *Lychnothamnus* from the small Cretaceous forms to the larger Cenozoic fructifications, could be the result of the evolutionary trend followed by this genus rather than exclusively an ecological adaptation. This tendency agrees with the evolutionary trend observed in other characean and clavatracean extinct lineages, which are characterized by the increasing size and globularity of their fructifications through time (Martín-Closas et al., 1999).

The ecological constraints observed in *Lychnothamnus* have been suggested as the main cause of the disjunctive paleogeographical distribution of the genus, and especially for the extant *L. barbatus*. Previous research supported this idea, e.g. the presence of *L. barbatus* in Holocene cold and deep lakes of North Africa where it is absent today (Soulié-Märtsche, 1991), or the significant reduction of extant *L. barbatus* sites in northern Europe, due to water eutrophication (Pelechaty et al., 2017). However, this statement is challenged as new discoveries showed that fossil and extant *Lychnothamnus* occur in a wide array of environments from fluvial, as indicated by the North American Cretaceous–Paleogene *L. barbosa* and *L. tenuis* and the Australian extant *L. barbatus*, to freshwater oligo-mesotrophic lakes found mainly in Eurasia. The tolerance of these species to thrive in stressful environments, along with their monoecious reproduction, might enable their dispersal from Turonian–Santonian *L. barbosa*, to the Santonian–early Campanian *L. tenuis*, which later migrates to the north colonizing fluvial ponds in the middle Campanian until the early Eocene. The current paleobiogeographic distribution of *Lychnothamnus* suggests that during the latest Cretaceous, this genus also migrated to the east and during the Pleistocene it reached Australia following an east to southeast Asian colonization route (Bhatia, 2006).

The presence of *Lychnothamnus* in Utah (USA) suggests that this genus remained in North America, at least until the early Eocene, representing the continuation of the south to north dispersal. Its absence from the later Eocene to possibly the present indicates that this genus probably became extinct at some time after the early Eocene. This hypothesis could support the idea that extant populations thriving in North American lakes are the product of recent anthropic introductions (Karol et al., 2017), although, the possibility that *Lychnothamnus* remained after the Eocene as relict populations, cannot be excluded.

5. Author statement

Dr. Alba Vicente: She pursued the fieldwork, processed the samples in the laboratory and analyzed the data for the Mexican material, under the postdoctoral project of the *Universidad Nacional Autónoma de México*. She also wrote the manuscript and designed the tables and figures.

Dr. Josep Sanjuan: He analyzed and studied the Claron Formation samples and wrote part of the manuscript.

Dr. Jeffrey Eaton: He pursued the fieldwork and collection of the Claron Formation *Lychnothamnus*. He collaborated in the sedimentological/paleoecological chapter on the material from the Claron Formation.

Dr. Uxue Villanueva-Amadoz: She collaborated in the fieldwork on the Fronteras section and provided part of the funding's with a project from the Mexican government. She also reviewed the text.

Acknowledgments

This study was funded by the project CONACyT 220368 (Mexican government), and is part of the Vicente's postdoctoral fellowship (DGAPA-UNAM). This study is also a contribution of the URB project AUB-23936 (American University of Beirut). We thank the *Consejo de Paleontología* of the *Instituto Nacional de Antropología e Historia-INAH* (project 401.1S.3-2018/065), M.Sc. Ruben Duarte Bigurra, Mr. Luis Francisco López and Mr. Roy David Clinch Armenta and the Fronteras town council for their assistance and logistical support during the fieldwork. We are grateful to the USDA Forest Service allowing fieldwork Utah (USA) federal lands, and the Natural History Museum of Utah for their help in curation the specimens from USA. Finally, we thank the *Departament de Dinàmica de la Terra i de l'Oceà (Facultat de Geologia, Universitat de Barcelona)* for their technical assistance (October of 2018), and to the *Laboratorio Nacional de Geoquímica y Mineralogía (LANGEM)* for providing access to the Hitachi TM3030Plus Tabletop Scanning Electron Microscope (SEM). We acknowledge Dr. Adriana García (University of Wollongong, Australia), an anonymous reviewer, and the editor Dr. Elisabeth Gross for their constructive observations and criticism provided during the peer-review process, and by their valuable advice which greatly improved the manuscript.

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