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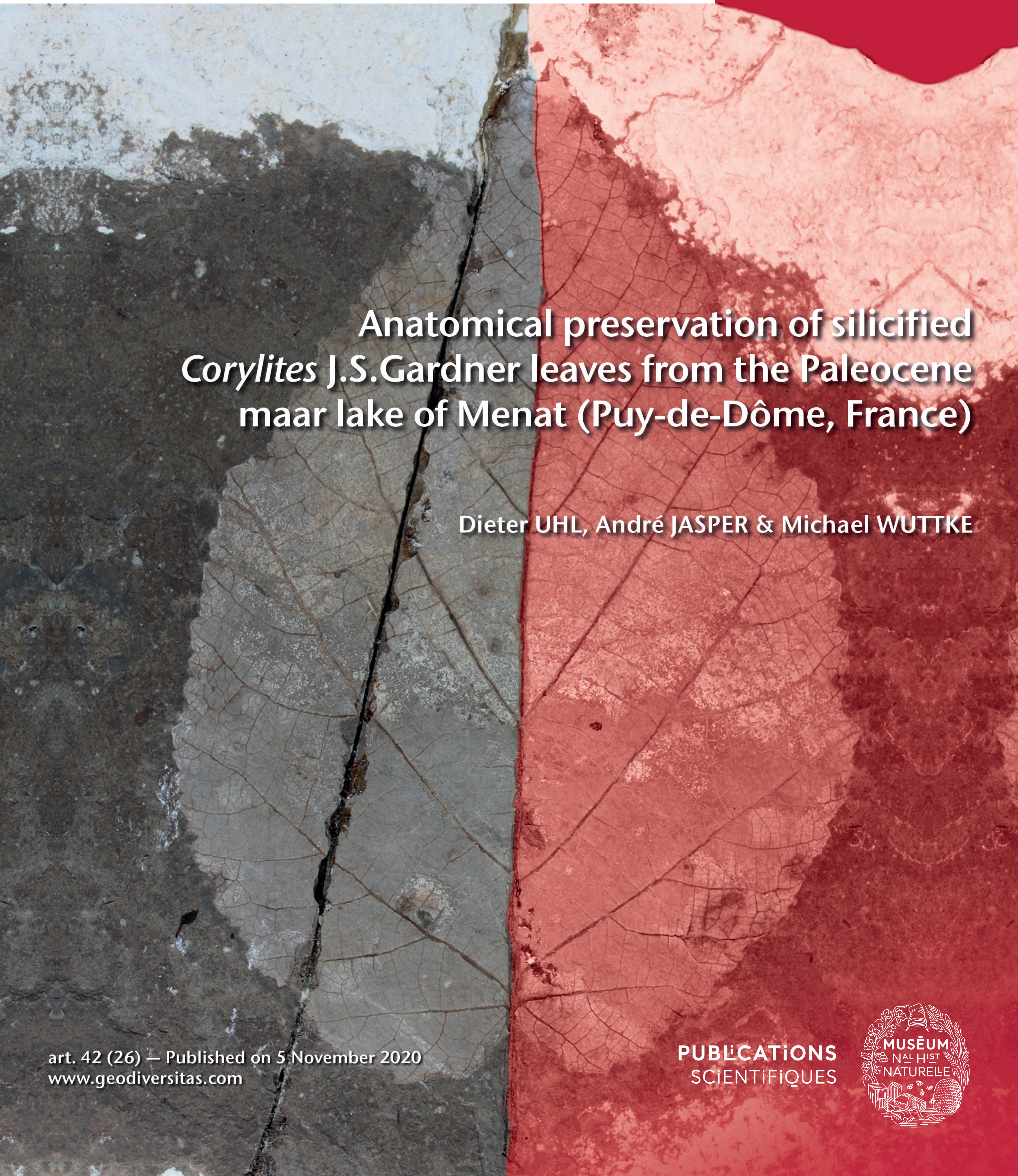

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# Anatomical preservation of silicified *Corylites* J.S.Gardner leaves from the Paleocene maar lake of Menat (Puy-de-Dôme, France)

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**ABSTRACT**
The late Paleocene fossil lagerstätte Menat in France is well known for its wealth of excellently preserved fossil plants and insects. Although the flora from this locality is regarded as characteristic for the late Thanetian in Western and Central Europe, there is a noteworthy lack of modern paleobotanical studies on this locality. The few existing studies on plant megafossils utilized only the gross morphology of leaves and carpological material for taxonomic questions, whereas anatomical data (i.e. from cuticles and permineralizations) have been completely neglected. The present study provides the first data on anatomically preserved internal tissues of leaves assigned to *Corylites macquarrii* (Forbes) Heer from this locality. Cell walls are preserved as silicates, whereas cell lumina are mostly empty. On occasion, cell lumina are filled with foam-like, porous silica. Anatomical preservation of these tissues is probably related to early diagenetic silicification of plant cell walls. Although at the moment nothing can be said about the source of the $SiO_2$ it is likely that it is related to the volcanic origin of the Menat maar and/or volcanic activities in the vicinity of the lake during deposition of the sediments.

**KEY WORDS**
Fossil lagerstätte,
silicification,
taphonomy,
leaf fossilization,
SEM,
EDX.

**RÉSUMÉ**

*Préservation anatomique de feuilles silicifiées de* Corylites *J.S.Gardner du lac Maar du Paléocène de Menat (Puy-de-Dôme, France).*

Le gisement à conservation exceptionnelle du Paléocène supérieur de Menat (France) est réputé pour l'excellente préservation de ses insectes et de ses plantes. Bien que la flore de cette localité soit considérée comme caractéristique du Thanétien supérieur d'Europe occidentale et centrale, il existe un manque notable d'études paléobotaniques modernes sur cette localité. Les quelques rares études existantes sur les mégafossiles de plantes n'ont utilisé que la morphologie générale des feuilles et du matériel carpologique pour les questions taxonomiques, alors que les données anatomiques (à partir des cuticules et des perminéralisations) ont été complètement négligées. La présente étude fournit les premières données sur les tissus internes anatomiquement préservés des feuilles attribuées à *Corylites macquarrii* (Forbes) Heer de cette localité. Les membranes cellulaires sont conservées sous forme de silicates, tandis que les luminescences cellullaires sont pour la plupart vides. Parfois, ces luminescences cellulaires sont remplies de silice poreuse, en forme de mousse. La préservation anatomique de ces tissus est probablement liée à la silicification diagénétique précoce des parois cellulaires des plantes. Bien que pour l'instant on ne puisse rien dire sur la source du $SiO_2$, il est probable qu'elle soit liée à l'origine volcanique du Menat maar et/ou aux activités volcaniques à proximité du lac pendant le dépôt des sédiments.

**MOTS CLÉS**
Gisement à fossiles,
silicification,
taphonomie,
fossilisation des feuilles,
SEM,
EDX.

## INTRODUCTION

The Paleocene (possibly late Thanetian) maar deposits of Menat in France represent a classical fossil lagerstätte, which has been known at least since the 19th century (e.g. Heer 1859; Saporta & Marion 1885). The locality is best known for its wealth of excellently preserved fossil insects (e.g. Piton 1940; Wedmann *et al.* 2018; and citations therein) and its megaflora (e.g. Laurent 1912a, b, 1919; Piton 1940), which is regarded as characteristic for the later part of the Thanetian in Western/Central Europe (e.g. Mai 1995).

The majority of paleobotanical studies on plants from Menat have focused so far on the taxonomy of the fossil leaves (e.g. Laurent 1912a, b, 1919; Piton 1940) and palynomorphs (e.g. Kedves & Russell 1982; Krutzsch 1967), although in recent years, a few studies have examined plant–insect interactions (Wappler *et al.* 2009) and the morphometrics of leaf fossils based on old museum collections (Roth-Nebelsick *et al.* 2017). However, the later studies are mostly based on the outdated taxonomy of the leaves provided by Laurent (1912a, 1919) and Piton (1940) and must therefore be taken with great caution in regard to the taxonomy and systematics of individual taxa.

An overview on the current knowledge of the Menat fossil lagerstätte provided by Wedmann *et al.* (2018) pointed out the fact that plant remains from Menat are not only preserved as impressions, but in a variety of different preservational modes. Some of these modes have the potential to provide information beyond morphological data, which have solely been used for paleobotanical studies on the megaflora from Menat so far (e.g. Laurent 1912a, b, 1919; Piton 1940).

In this short communication, the preliminary results of an in-depth study on the different preservational modes of plant remains from Menat are presented, highlighting the excellent anatomical preservation of some silicified leaves, which are abundant in specific, completely silicified and several cm thick horizons at this locality.

## MATERIAL AND METHODS

The leaves analyzed here come from finely laminated, bituminous, dark gray to brown, silicified pelites collected from the former open pit mine in the village of Menat (Fig. 1). Based on their gross morphology, they are assigned to *Corylites macquarrii* (Forbes) Heer, a fossil leaf species that occurs in abundance in the Menat pit (e.g. Saporta & Marion 1885; Laurent 1912a; Piton 1940). According to current interpretations, these sediments were deposited in a maar lake in a volcanically active landscape (cf. Wedmann *et al.* 2018). The exact position of the source strata with fossil leaves within the sedimentary succession in Menat is unknown, a common problem with museum collections from this locality (cf. Wedmann *et al.* 2018). The material studied here is deposited at the Maar Museum Manderscheid, Germany, under accession numbers MMM-2010-012 and MMM-2010-019. For further details on the geology, stratigraphy, and paleontology of the source locality, see Wedmann *et al.* (2018; and citations therein).

For scanning electron microscopy (SEM) and energy dispersive X-ray analysis (EDX), small pieces of the lamina of the leaf were mechanically extracted with the aid of preparation needles and tweezers using a binocular microscope (Leica M80). Extracted samples were mounted on standard stubs with liquid LeitC (Plano, Münster, Germany). Some specimens were sputter-coated with gold and examined with a JEOL JSM 6490 LV Scanning Electron Microscope (SEM; accelerator current 20 kV) equipped with an EDAX-Amatek EDX at the Senckenberg Forschungsinstitut und Naturmuseum Frankfurt, Germany. The specimens used for EDX were analyzed with the same machine, but were not sputter-coated with gold.

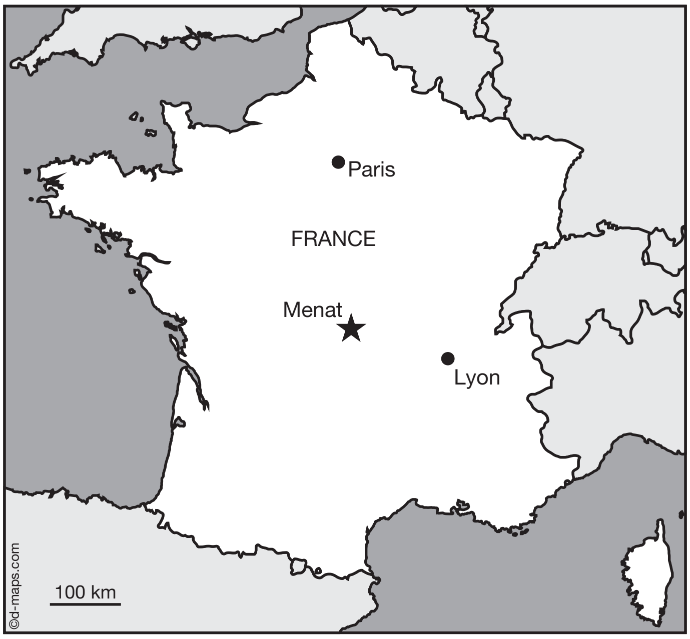


Fig. 1. — Map of France showing the geographic position of Menat. (Source: http://d-maps.com/m/europa/france/france/france09.gif).

## RESULTS

Macroscopically, the leaves analyzed here appear as physically hard, light-colored to white layers on the finely laminated, bituminous, dark gray to brown sediment (Fig. 2). In many cases, the fracture plane of the rock is also covered with a whitish layer (Fig. 2). The sediment itself is extremely hard. A qualitative EDX analysis of the substance of the leaves showed that the white substance is almost purely composed of Si and O, with only minor traces of C and Al (Fig. 3), indicating that the white layer consists of silicates (Figs 4, 5).

In most parts of the leaves, anatomical details are not visible on the surface of the white layer (Fig. 4A). Stomata can be observed on this surface only on occasion (Fig. 3A). In areas where the white layer is split by accident or during preparation, details of the internal anatomy of the leaves can become apparent. Parenchyma cells are irregularly polygonal in shape and have straight cell walls (Fig. 4B, C). Most cell walls consist of solid material, although there are other areas where the remnants of the cell walls consist of foam-like, porous material (Fig. 4B-D). Occasionally, the cell walls seem to be covered by a thin, possibly additional layer of silica (Fig. 4D). On some cell walls, globular structures of 2-3 μm in diameter occur (Fig. 4E). Stomata, as seen from the inner side of the leaf lamina, seem to be anomocytic (Fig. 4F). Preservation and/or silicification of the cell walls may vary on small scales within the leaf lamina, with areas of cellular preservation directly adjacent to areas without cellular preservation (Fig. 5A). Larger veins seem to consist of 10-12 μm wide tracheids with spiral thickenings in the cell walls (Fig. 5A, B). In some cases, the lumina of these tracheids are also filled with foam-like, porous siliceous material (Fig. 5B). In one case, the wall of a tracheid is covered with filamentous structures (Fig. 5C), which resemble hyphae of fungi or filaments of ascomycetes. Within the parenchyma of the leaf lamina, occasional remnants of fine veins are visible (Fig. 5D). These fine veins are composed of 4-6 μm wide tracheids with spiral thickenings in the cell walls (Fig. 5E, F). In most cases, only these spiral thickenings are silicified, whereas the considerably thinner areas of the cell walls between thickenings are only rarely preserved (Fig. 5F).

## DISCUSSION

The data presented here demonstrate that at least some leaves, in this particular case, those of *Corylites macquarrii*, from certain silicified layers of the Paleocene lake deposits in Menat have silicified cell walls that preserve evidence of their internal anatomy. Mineralization by silica must have happened very rapidly after deposition of the leaves in the lake sediments, because even fine anatomical details, such as stomata and the spiral thickenings of tracheids, were preserved and thus retain their original, three-dimensional structure. This indicates that silicification must have occurred in a window of time before the leaves underwent significant microbial decay, that is, in an anaerobic zone at the bottom of the maar lake, and before the compaction of sediments at the lake bottom could compress the cells of the leaf. There must have been a high content of silica gels from unknown sources within the upper layers of the lake beds, due to high alkaline conditions. It can be assumed that the pH dropped sharply to increased acidity because of the decomposition of dispersed organic matter and the *Corylites* leaves within the sediment, as it is described from the sediments of modern lakes (Hesse 1989). Although a large body of literature exists on the silicification of wood (e.g. Buurman

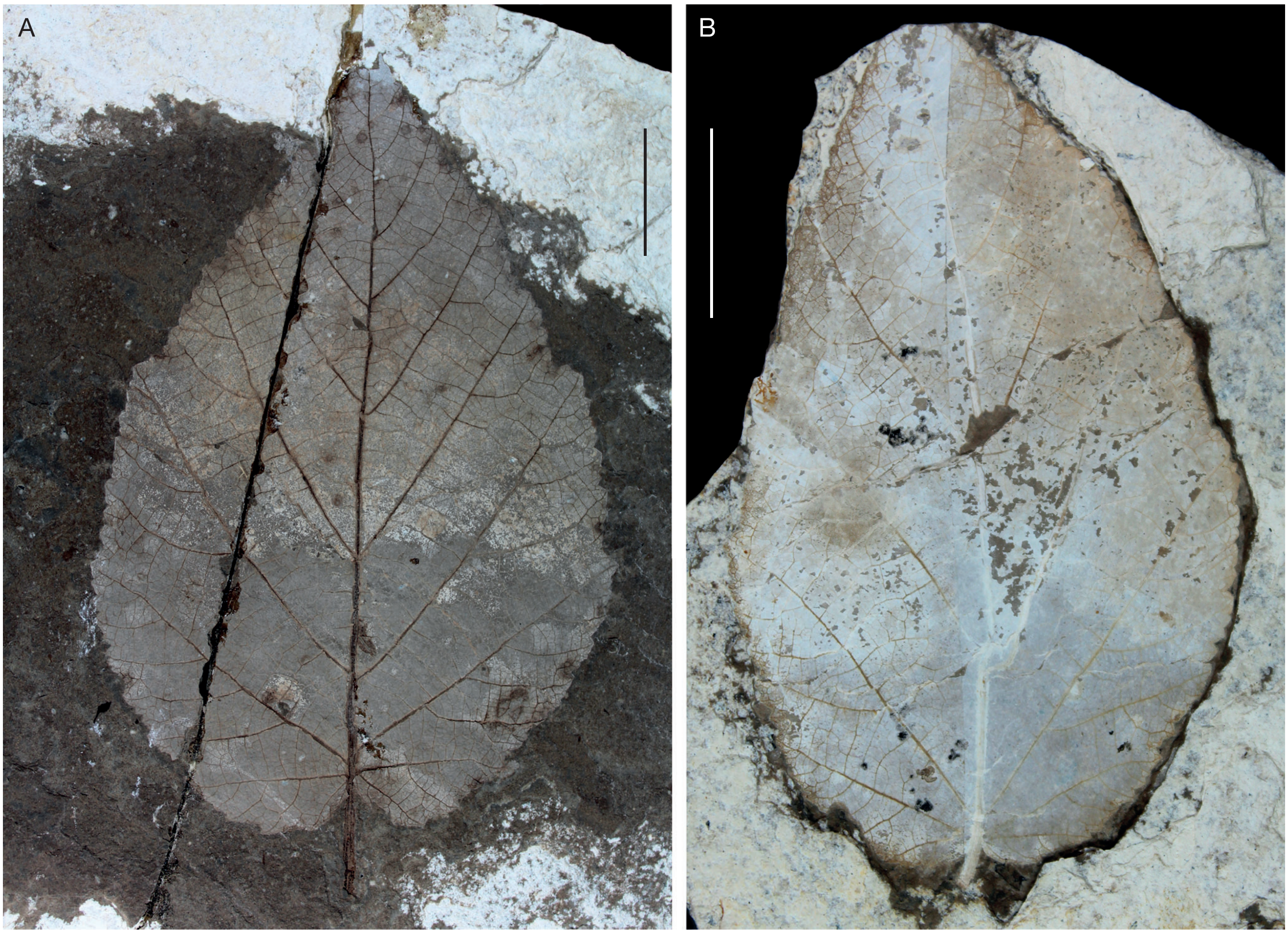


FIG. 2. — Examples of silicified leaves from the Paleocene of Menat: **A**, *Corylites macquarrii* (Forbes) Heer, Inv.-No. MMM-2010-019; **B**, cf. *Corylites macquarrii* (Forbes) Heer, Inv.-No. MMM-2010-012. Scale bars: 2 cm.

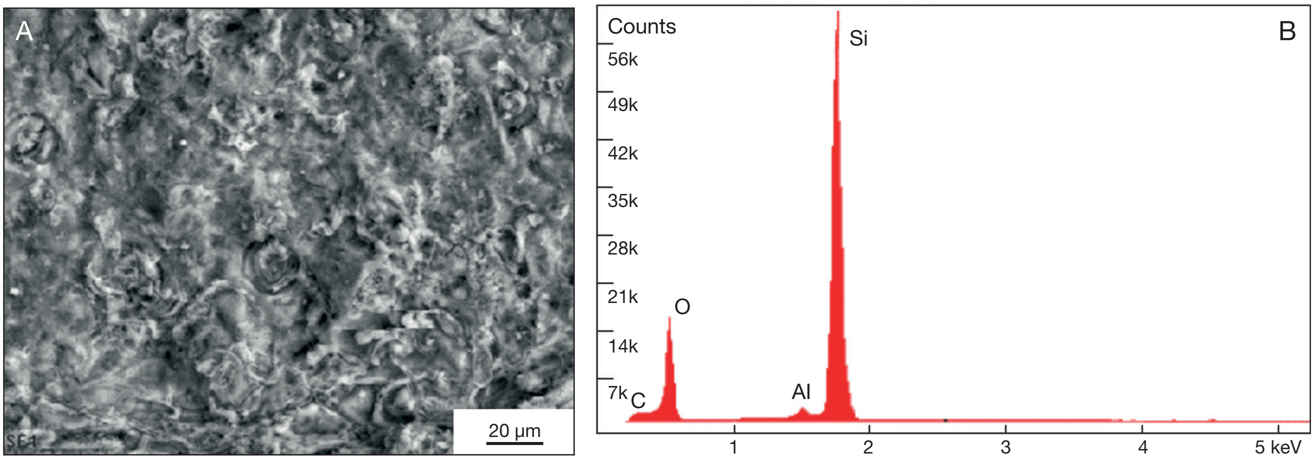


FIG. 3. — Results of a qualitative EDX analysis of a silicified leaf of *Corylites macquarrii* (FORBES) HEER from Menat (Inv.-No. MMM-2010-019): **A**, SEM image of the same area of the silicified leaf analyzed by EDX; **B**, qualitative EDX spectrum of the area shown in A, exhibiting strong **Si** and **O** peaks, together with minor **C** and **Al** peaks. Spectrum is cut off at 5 kV, as no further peaks appeared beyond this value.

1972; Leo & Barghoorn 1976; Ballhaus *et al.* 2012; Hellawell *et al.* 2015; Mustoe 2017; Trümper *et al.* 2018; and citations therein), soft-tissues in stems (e.g. Channing & Edwards 2009a, b; Läbe *et al.* 2012), and on peat or peat-like substrates (e.g. Mustoe 2011, 2017; Trewin *et al.* 2003; Trewin & Fayers 2016; and citations therein), there is a lack of studies on the silicification of individual leaves in lake sediments, such as in certain layers in Menat. Most studies dealing with silicified

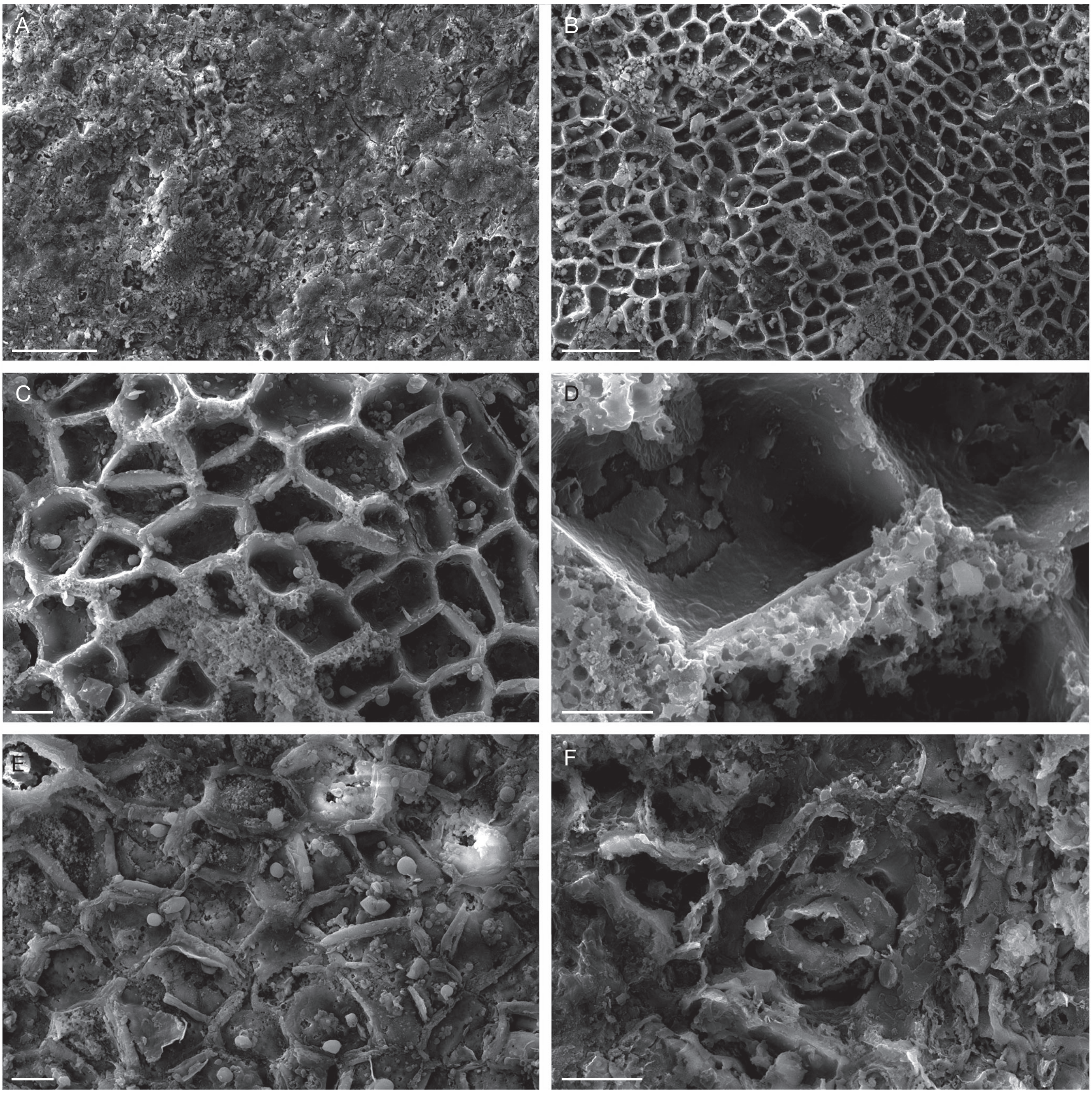


Fig. 4. — SEM images of anatomical details of a silicified leaf of *Corylites macquarrii* (Forbes) Heer shown in Fig. 2A from the Paleocene of Menat (Inv.-No. MMM-2010-019): **A**, overview of leaf surface; **B**, overview of possible epidermal cells with silicified cell walls; **C**, detail of B; **D**, close-up of a cell wall; note the difference between the homogenous silica on one side of the cell wall and the honeycomb-like material on the other side; **E**, detail of cells with an additional layer of silica on cell walls; **F**, close-up of silicified stoma. Scale bars: A, B, 50 µm; C, E, F, 10 µm; D, 5 µm.

leaves are based on material from massively silicified cherts (e.g. Galtier 2008; Pigg & DeVore 2016; Sagasti *et al.* 2016).

A number of studies has demonstrated that silicification of wood often starts with the deposition of silica within cell walls, leaving cell lumina empty during early stages of silicification (e.g. Leo & Barghoorn 1976; Ballhaus *et al.* 2012; Läbe *et al.* 2012; Hellawell *et al.* 2015; Mustoe 2017). Layers of silicates replacing cell walls, as seen in the leaves from Menat, or of siliceous lumina casts, have also been observed in silicified wood (cf. Buurman 1972).

The initial precipitation of silica may happen very quickly under conditions of low oxygen availability, maybe related to the (microbial) decay of the organic cell wall material (e.g. Leo & Barghoorn 1976; Trümper *et al.* 2018). The preservation of delicate fungal hyphae can also probably be considered as an indicator for an early diagenetic and rapid silicification of the leaves (cf. Krings *et al.* 2017). Such rapid silicification can happen even under temperatures below 250°C if the silica is derived from fluids that are supersatured with silica (cf. Ballhaus *et al.* 2012; Läbe *et al.* 2012; Hellawell

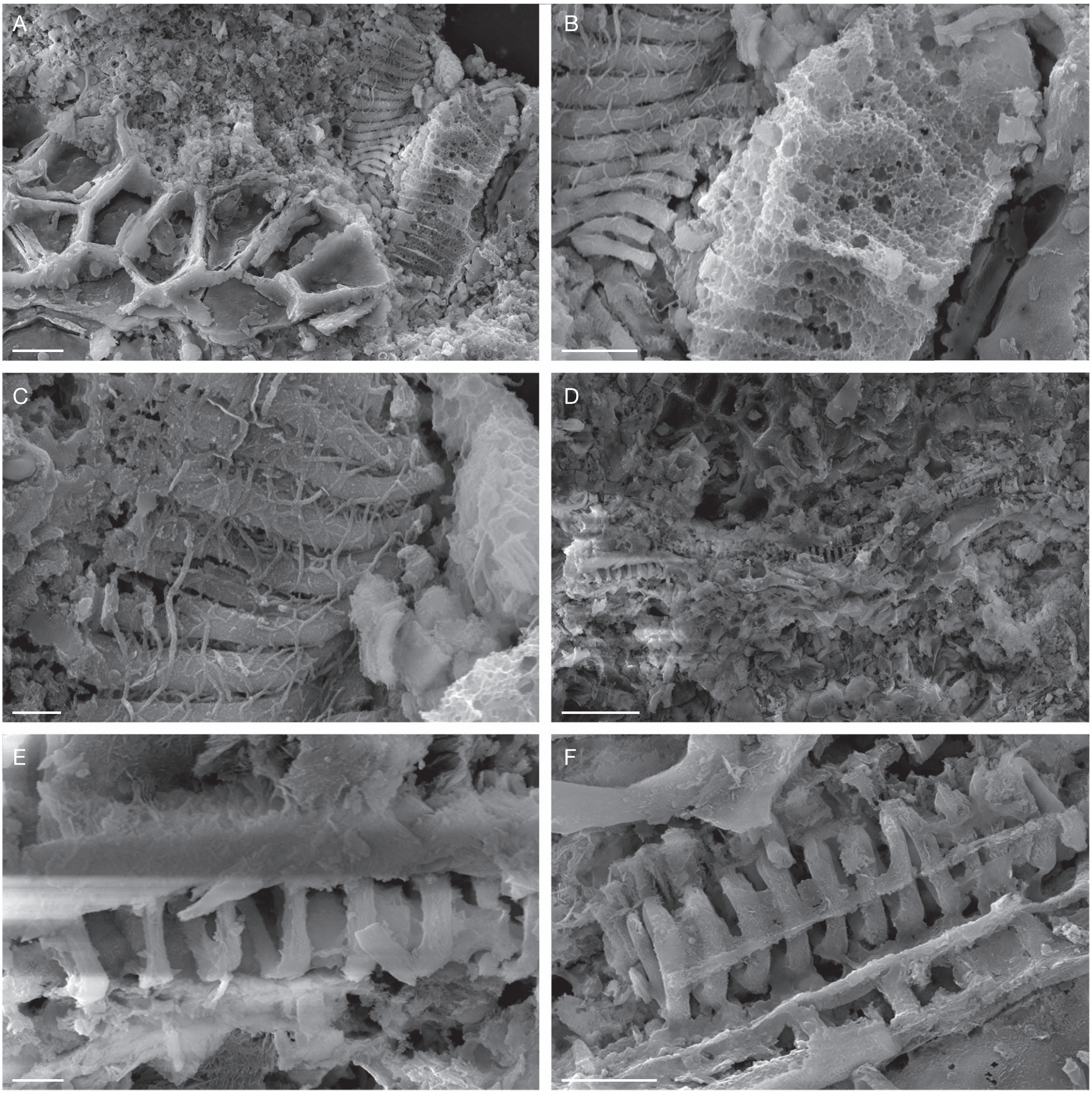


Fig. 5. — SEM images of anatomical details of the silicified leaf of *Corylites macquarrii* (Forbes) Heer shown in Fig. 2A from the Paleocene of Menat (Inv.-No. MMM-2010-019): **A**, overview of an area with parenchymatic cells and tracheids (top right); **B**, close-up of tracheids; to the left, a tracheid with a silicified scalariform pitted cell wall, to the right the honeycomb-like infilling of a tracheid; **C**, detail of the tracheid with scalariform pitting, exhibiting silicified fungal hyphae or ascomycete filaments; **D**, overview of an area with a minor tracheid; **E**, detail of a minor tracheid where only former spiral thickenings of the cell walls have been silicified; **F**, detail of a minor tracheid where only small areas of the thin cell wall areas have been silicified between spiral thickenings of the cell walls. Scale bars: A, 10 µm; B, F, 5 µm; C, E, 2 µm; D, 20 µm.

*et al.* 2015; Matysová *et al.* 2017; Trümper *et al.* 2018; and citations therein).

Biomineralization mediated by microbes, i.e. bacteria and cyanobacteria, is well studied in geothermal hot-springs containing water super-saturated with silica (e.g. McKenzie *et al.* 2001; Benning *et al.* 2005; Kyle *et al.* 2007), although such hot-springs are not neccesarily good analogs for the situation in the former maar-lake of Menat. There are some indications that microbial decay of the leaves started before silicification, such as in the filamentous structures on the tracheid walls, which probably represent remnants of fungal hyphae or ascomycete filaments. Another potential indicator for microbial colonization of the dead leaves is the foam-like, porous silica occurring within tracheid lumina and in the area of some former cell walls. This material resembles "honeycomb" opal A, which has been reported as a result of the silicification of microbial mats (e.g. McKenzie *et al.* 2001; Kyle *et al.* 2007; Wang *et al.* 2017). Similar structures, identified as opal A, have also been identified within the lumina of silicified wood (e.g. Leo & Barghoorn 1976; Scurfield & Segnit 1984).

From this, it seems possible that the silicification of leaves in Menat was at least partly mediated by microbial activity and that this process was probably more or less analogous to processes suggested for the silicification of fossil wood (e.g. Buurman 1972; Leo & Barghoorn 1976; Mustoe 2017; Trümper *et al.* 2018; and citations therein). However, at the moment nothing can be said with any degree of certainty about the physicochemical conditions under which this silicification must have happened in the Menat lake and it is absolutely unclear whether microbes have played a role in silicification or not.

In Menat, the lake sediments have been quarried for diatomite (Wedmann *et al.* 2018), and Piton (1940) mentioned that some layers of the lake consist of siliceous diatom sclerites and/or sponge spicules. However, so far no detailed descriptions of these layers have been published, and we found no anatomical evidence for diatom sclerites or sponge spicules in the silicified sediments containing the leaves analyzed here. In other horizons that are not silicified, rare molds of individual sponge spicules have been observed with the SEM (Uhl & Wuttke, pers. observation). The partly massive occurrence of diatoms and sponges indicates that silica was abundant within the water of the lake. However, in the layers analyzed, the remains of diatoms or sponges have not been detected.

Although geochemical studies are lacking so far, it is likely that the source of the silicates within the Menat lake can be traced back to the volcanic origin of the maar itself or to volcanic activity in the surrounding of the maar. In the vicinity of the maar, several occurrences of volcanic rocks are known that provide evidence for volcanic activity in this region lasting at least from 64 ± 2 My (Danian) up to 51 ± 2 My (Ypresian) (e.g. Vincent *et al.* 1977).

Our data on the *Corylites* leaves indicate that such silicified leaves and probably other plant organs from the Paleocene maar lake of Menat offer a large potential for further anatomical studies at this locality. Additionally there is a great potential for further studies on the silicification pathway(s) which have led to the permineralization of individual leaves and entire layers of the sediments deposited within the lake.

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