



## EVIDENCE FOR WILDFIRES DURING DEPOSITION OF THE LATE MIOCENE DIATOMITES OF THE KONSERVAT-LAGERSTÄTTE LAKE SAINT-BAUZILE (ARDÈCHE, FRANCE) – PRELIMINARY RESULTS

This article is dedicated to the late Zlatko Kvaček (1937 – 2020), in honour of his long-term friendship and collegial support.

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**Abstract:** The freshwater diatomite deposits from Saint-Bauzile in the Ardèche (France) represent a first-class Fossil-Lagerstätte of late Miocene, i.e., Tortonian age. A large variety of different animals (i.e., insects, fishes, and mammals) and macro-plants as well as palynomorphs and lacustrine diatoms are known from this locality, in generally excellent preservation. This contribution presents preliminary results on charred plant remains, i.e., charred fern and grass remains, as well as partly charred wood of taxodioid cupressacean affinity, as evidence for the occurrence of wildfire(s) during deposition of the lower part of the diatomite sequence. Previously published volcanological and sedimentological evidence for the interpretation of Lake Saint-Bauzile as a maar is reviewed, re-interpreted, and discussed in combination with new observations.

**Key words:** Tortonian, wildfire, charcoal, fern, grass, wood

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### Introduction

Fire is an important source of disturbance in many modern ecosystems, and a number of ecosystems are even dependent on the regular occurrence of such wildfires (e.g., Scott et al. 2014, and citations therein). Wildfires have become a focus of public and political interest during the last years, especially when seen in connection with ongoing climate and land-use changes, which will probably also lead to changes in fire ecology and fire regimes in several regions (e.g., Cochrane 2019, McLauchlan et al. 2020, Dos Reis et al. 2021).

Naturally ignited wildfires have been a part of continental ecosystems at least since the Late Silurian (Glasspool et al. 2004), and evidence of their occurrence can be found in the fossil record in the form of fossil charcoal (including the pyrogenic coal macerals of the inertinite group) and pyrogenic biomarkers like certain polyaromatic hydrocarbons (e.g., Daubreé 1844, 1846, Potonié 1929, Stutzer 1929, Scott 2000, 2010).

During recent decades, a large number of studies have dealt with such evidence for fire in deep time, especially the

Palaeozoic and Mesozoic (e.g., Scott 2000, 2010, Scott and Glasspool 2006, Belcher and McElwain 2008, Glasspool and Scott 2010, Abu Hamad et al. 2012, Brown et al. 2012, Lu et al. 2021, Jasper et al. 2021, and citations therein) but also Palaeogene and Neogene (e.g., Figueiral et al. 1999, 2002, Figueiral and Mosbrugger 2000, Uhl et al. 2011, 2014, 2020, 2022, Holdgate et al. 2014, Robson et al. 2015, Korasidis et al. 2016, 2017, Sluiter et al. 2016, Kowalski 2017, Uhl and Jasper 2018, Wedmann et al. 2018). Knowledge about Palaeogene and Neogene wildfires is of special interest regarding the evolution of many modern, fire-adapted ecosystems, but so far, comparatively few studies dealing with such wildfires in detail have been published (e.g., Bond 2015).

The diatomites from Saint-Bauzile represent an exceptional Fossil-Lagerstätte of late Miocene (Tortonian) age, which has been known since the 18<sup>th</sup> century (e.g., Faujas de Saint Fond 1778, 1815, Boulay 1887). A large variety of different animals (i.e., insects, fishes, amphibians, reptiles, birds, and mammals) and plants are known from this locality in generally excellent preservation, e.g., insects with preservation of colour and mammals with body outlines and fur (e.g., Mein et al. 1983, Demarcq et al. 1989, Riou

1995, Saint Martin et al. 2017, Métais and Sen 2018). A few scientific studies have been published on plant macrofossils and pollen grains (Grangeon 1960, Brice 1965, Iskandar 1990), and the assemblage of diatoms (Ehrlich 1966, Kuehlthau-Serieyssol 1993).

Here we present a preliminary study of charcoal as evidence for palaeo-wildfires from the late Miocene (Tortonian) diatomites quarried at the Montagne d'Andance, near the village of Saint-Bauzile in Ardèche (France). This study provides preliminary new information on some aspects of the Miocene fire-ecology in Southern Europe, a region which may be plagued more intensively by wildfires due to ongoing climate change (e.g., Jolly et al. 2015, Abatzoglou et al. 2019, Ganteaume et al. 2021). Additionally, we provide a re-interpretation of previously published volcanological and sedimentological evidence from Lake Saint-Bauzile to support its origin as a maar lake.

## Geology and stratigraphy

The diatomite Konservat-Lagerstätte “Lake Saint-Bauzile” occurs on the “Montagne d'Andance”, east of the village Saint-Bauzile (region Auvergne-Rhône-Alpes, Département Ardèche, France). The “Montagne d'Andance” is a steep hill, isolated by erosion from the eastern part of the basaltic plateau of Coiron, situated on its north-eastern margin, 8–9 km southeast of the commune Privas. Cretaceous (Valangian) marls of the Chomérac and St-Lager-Bressac plain form the bedrock sediments of the lower part of the hill (e.g., Ehrlich 1966, Demarcq et al. 1989, Riou 1995). They are underlain by Upper Jurassic limestones, only exposed here in a diatreme breccia (Audra et al. 2002).

Stratigraphically, the main diatomite unit (~30 to 60 m in thickness), which has yielded fossil vertebrates mainly in its basal parts (Riou 1995), lies about 100 m above the marls and is capped by three basaltic flows. It has been exploited for industry since the 1960s (Champreux and Euvrard 1993). During the Pliocene and Pleistocene, the sequence was eroded, giving the present “reversed” relief.

The stratigraphic sequence exposed in the Montagne d'Andance is summarized in Ehrlich (1966), Riou (1995), and Métais and Sen (2018). According to Grangeon (1960), the lacustrine sedimentation could be related to a lava flow dam, located in the eastern and southern part of the site. Demarcq et al. (1989) suggested a maar origin, but these authors grouped together basal breccias and overlying hyaloclastites of the sequence as evidence for their maar hypothesis. In reality, these are two petrographically different and temporally clearly separated processes (Demarcq et al. 1989: fig. 2), which cannot be combined to serve as evidence for a maar hypothesis (see below for details).

The diatomite was stratigraphically classified as belonging to the lower Turolian land mammal age (MN 11, ca. 7.5–8.5 Ma; Agusti et al. 2001), based on the evidence of the equid *Hipparion truyolsi*, the murine rodent *Parapodemus lugdunensis*, and the basal bosephine *Graecoryx andancensis* (Demarcq et al. 1989). The top of the diatomitic sequence is incised by channelized conglomerates that have yielded a mammal assemblage taxonomically very close to that of the main diatomite, suggesting a sub-contemporaneous age (Demarcq et al. 1989).

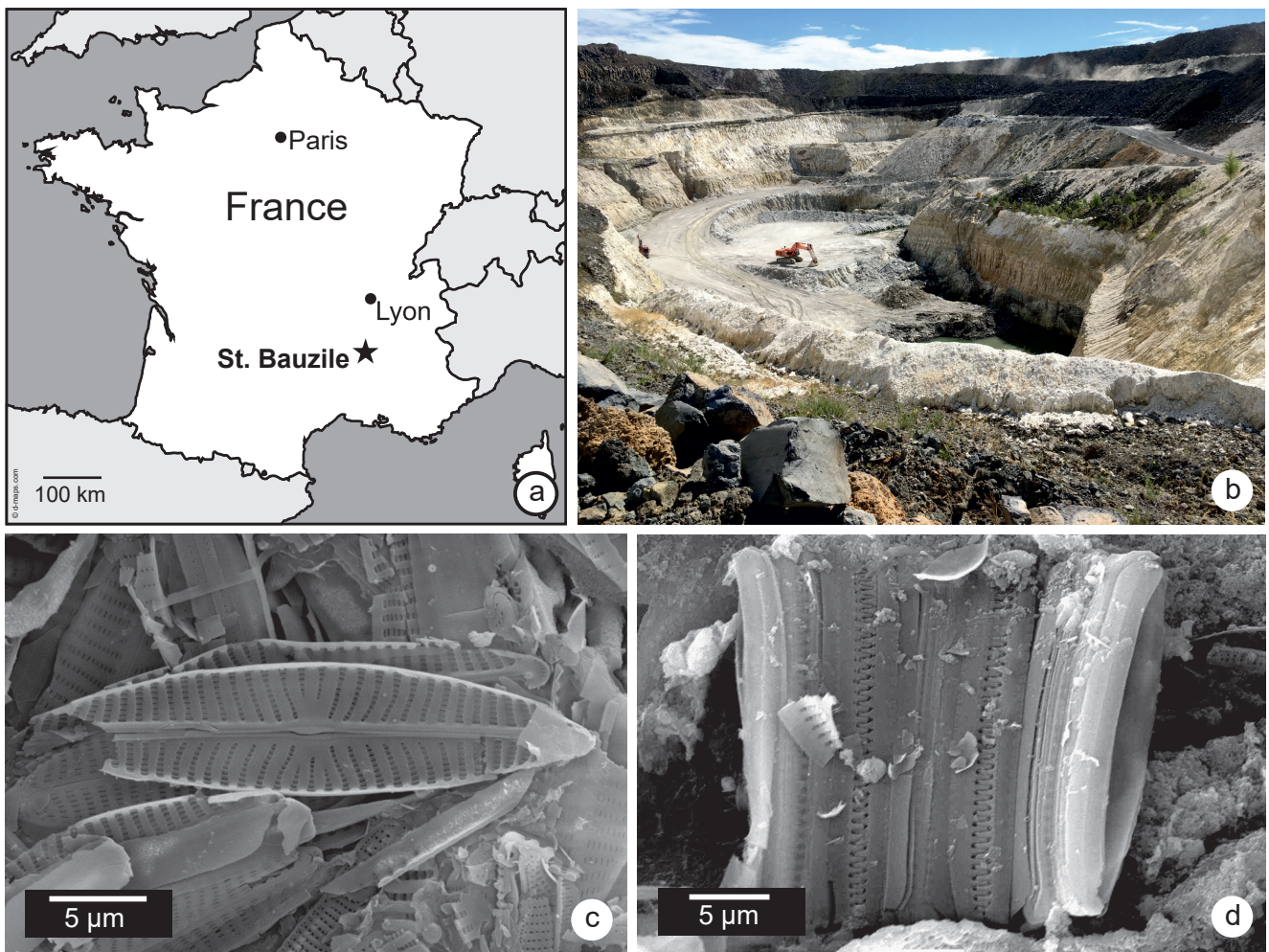
<sup>40</sup>Ar/<sup>39</sup>Ar laser fusion and unspiked K-Ar-Dating of a basal trachytic tephra layer within the main diatomite and of the middle basalt flow topping the sequence enable a chronostratigraphic classification of the diatomite. The basal trachytic tephra is dated at  $7.17 \pm 0.06$  Ma, the covering lava flow at  $7.13 \pm 0.06$  Ma (Pastre et al. 2004: fig.1), implying a sedimentation timeline of about 300 to 400 ky. Finally, it is worth noting that the main diatomite is underlain by ~100 m of peperitic and hyaloclastitic material, each clastite enveloped by diatomitic material. The peperite was formed when a basaltic (basanitoid) lava intruded into diatomaceous muds of Lake Saint-Bauzile. It cannot be said with certainty whether the peperite horizon has the same age as sills within the main diatomite, dated by Pastre et al. (2004) to  $7.17 \pm 0.06$  Ma. However, it can be assumed that these are separate processes, because the peperites/hyaloclastites are basanitic in nature, whereas the sills are tephrites (Grangeon and Michel 1957, Pastre et al. 2004).

Although there are still no definite studies on a phreatomagmatic origin of Lake-Bauzile, we assume its maar origin, founded on several typical lithofacies sequences and sedimentological indications after the models of, e.g., Pirrung et al. (2003), and Lorenz (2003), based on the volcano-sedimentological profiles published by Demarcq et al. (1989: fig. 2; adapted from the thesis of Romaggi 1987), and Riou (1995). This overall information can be combined to a general indication of the development of the Saint-Bauzile maar lake, but a detailed reconstruction requires further research.

In the Coiron plateau area, with the Montagne d'Andance as a former part of it, volcanism is mainly a fissure-type volcanism which indicates a close connection between tectonics and volcanic activity (Granet et al. 1995, Wilson and Downes 2006, Négrel et al. 2015). The Coiron volcanic field shows pronounced NW-SE trending alignments of eruptive centers, it reflects the orientation of the regional stress field within Europe at that time. This episode of the so-called Miocene “major magmatic event” (Michon and Merle 2001) is spatially and temporally associated with a period of uplift, suggesting a common origin for volcanism and uplift processes (Michon and Merle 2001).

In the Coiron area, where hard rocks from Triassic marly dolomites, and Jurassic limestones to Cretaceous marls form the country rocks, maar-diatreme volcanoes are frequently located in palaeo-valleys (Grangeon 1960), also typical for other volcanic fields in the Massif Central in France (Camus 1975), and, e.g., for the Eifel and Schwäbische Alb Mountains in Germany (e.g., Lorenz 2003, Lorenz and Lange 2020).

The effects of a thermohydraulic explosion in the Montagne d'Andance can be inferred especially by the occurrence of basal breccias of country rocks, consisting of Jurassic limestones and Cretaceous marls. These breccias indicate the lower part of the maar-diatreme filling, however, these would also have to be examined for Triassic marly dolomites and volcanogenic components in the future. Subsequently, limnic sedimentation within the maar crater began with diatomaceous muds, of which about 2.5 m of diatomite have survived undisturbed (Demarcq et al. 1989: fig. 2). Basanitic melts subsequently penetrated the muds of a not-reconstructable thickness of diatomite.



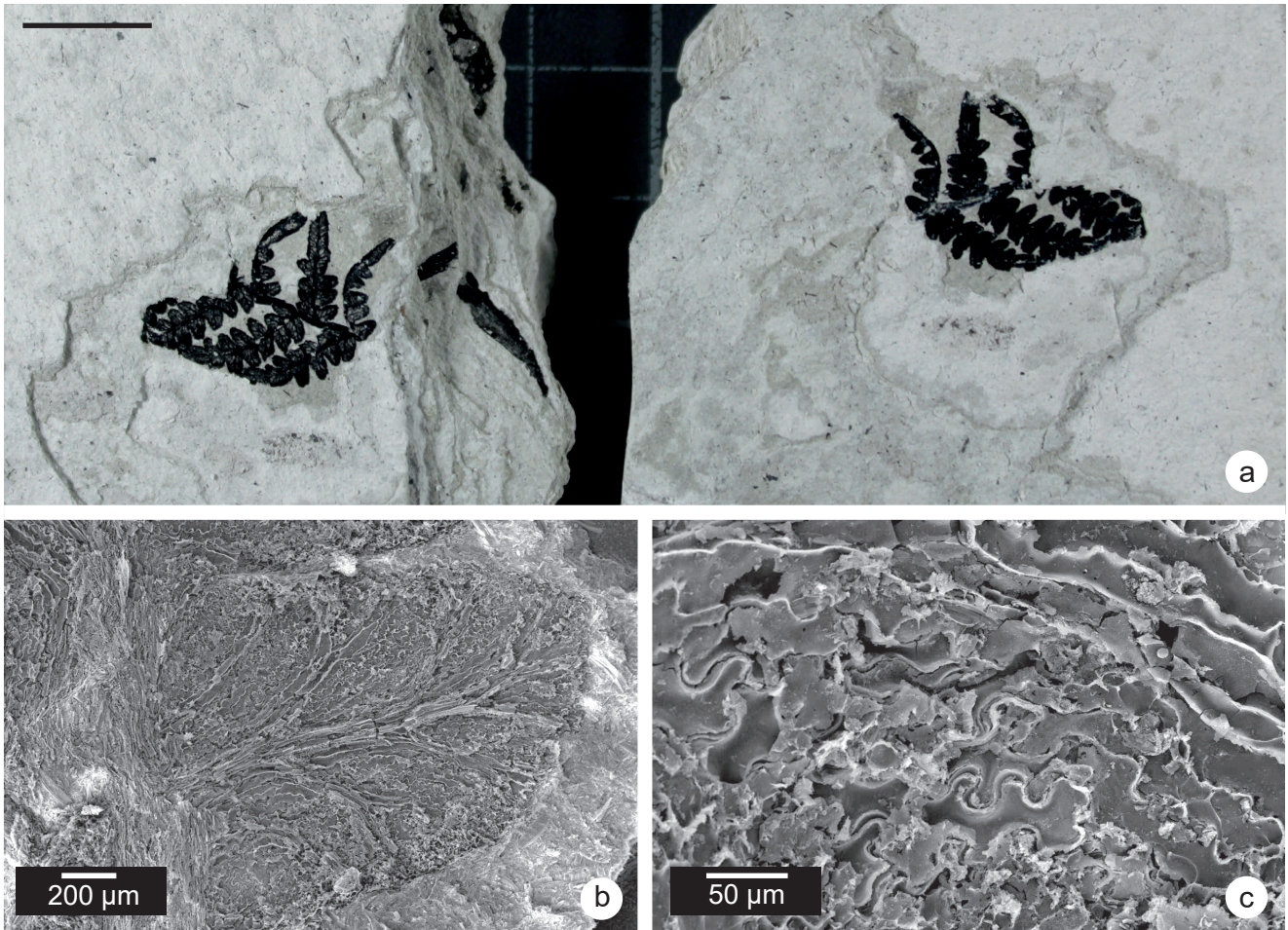
**Text-fig. 1. a:** Map of France showing geographic position of Saint-Bauzile (source: <http://d-maps.com/m/europa/france/france/france09.gif>). **b:** Overview of the active diatomite quarry at the Montagne d'Andance, photograph taken in 2017. **c:** SEM image of a frustule of pennate diatom (cf. *Navicula* sp.) from Saint-Bauzile. **d:** SEM image of frustules forming a colony of centric diatoms (cf. *Diatoma* sp.) from Saint-Bauzile.

The basanitic melts possibly originate from a subaquatic diatreme wall eruption within the maar crater. Peperitic textures, hyaloclastites and intraformational volcanic bombs were produced by subsequent interaction between magma and wet sediment, displayed by volcanic components enveloped by diatomaceous material (Grangeon and Michel 1957). This mixture filled up the maar crater with about 90m of volcanoclastic material. Thereafter, the filling up lowered the water depth within the maar-diatreme to such an extent that siltation started, documented by approx. 2.5 m of lignite. Because of post-eruptive diagenesis, the diatreme fill was subject to an ongoing period of compaction, and was therefore influenced by syn- and post-sedimentary subsidence (compare, e.g., Suhr et al. 2006), combined with a deepening of the water. Sedimentation of diatoms started again, documented by about 30 to 60 m of diatomite (depending on the variable morphology of the peperitic lake bottom), which is mined today.

A trachytic tephra layer just below the mined diatomite, combined with about twenty basaltic tephra layers within this sequence, make it possible to date and subdivide the diatomitic sequence (Riou 1995, Pastre et al. 2004). About 340,000 years (radiometric age; Pastre et al. 2004) after sedimentation of this sequence started, syn-sedimentary

tephritic magmas intruded into the diatomites and were replaced in form of dykes and sills (Mein et al. 1983: fig. 2, Pastre et al. 2004).

Based on diatoms, Ehrlich (1966) concluded that Lake Saint-Bauzile was “undoubtedly shallow (constant presence of a small number of benthic forms), with very low to no salinity and an alkaline pH”. Kuehlthau-Serieyssol (1993) has been able to demonstrate a series of changes in the associations of the diatoms through time. These are probably due to fluctuations in the environmental conditions, or to a change in the ratio of precipitation to evaporation. We agree with Ehrlich (1966) that Lake Saint-Bauzile was relatively shallow during deposition of the entire upper diatomitic sequence, which is also reflected by repeated siltation, which resulted in the formation of a two- to three-meter-thick lignite at the top of the diatomitic sequence. This is followed by several meters of river deposits, which locally also eroded the lignite, down to the upper parts of the diatomite. As a result of persistent subsidence of the diatreme filling, a new sedimentation of about 5 m of diatomaceous mud took place, followed by the washing in of several meters of red clays. Some volcanic eruptions in the vicinity of the Montagne d'Andance lake led to the alternating deposition of lapilli tuffs with a total of three alkali-basaltic



**Text-fig. 2.** Charred fern from diatomite of Saint-Bauzile. **a:** Overview of diatomite slab with large fragment of charred fern; SM.B 22258; scale bar = 1 cm. **b:** SEM overview image of charred fern pinnule. **c:** Enlargement of (b) showing details of undulating anticlinal walls of the epidermis.

lava flows, which finally capped sedimentation in the maar ( $7.13 \pm 0.06$  Ma, Pastre et al. 2004). For this contribution, only material from the basal parts of the diatomite (some meters above the 2.5 m lignite) was analyzed. This material is still mined today.

## Material and methods

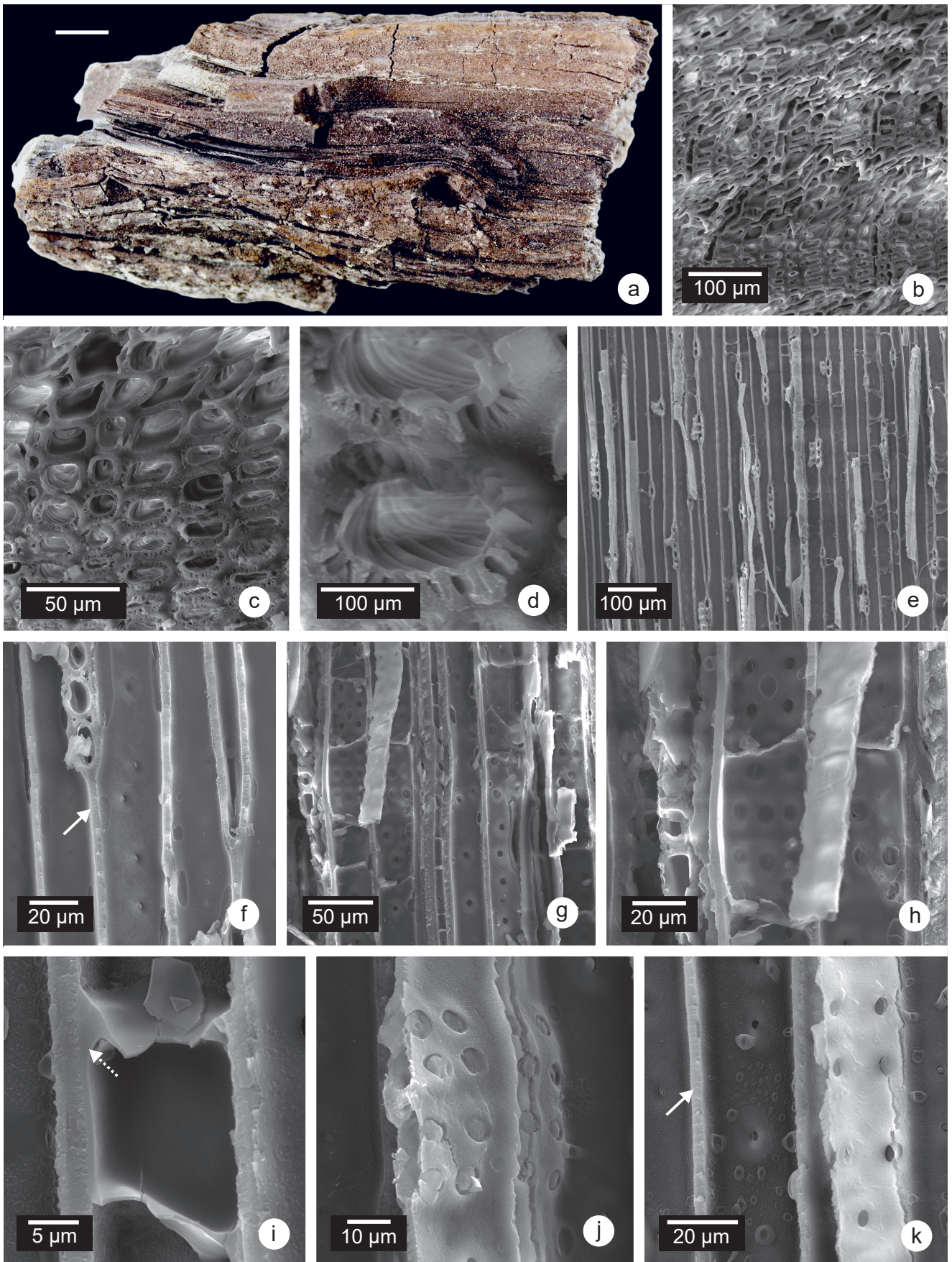
The active open-cast mine that exploits the diatomite deposits of the former maar lake of Saint-Bauzile is situated at the top of an isolated hill, called “Montagne d’Andance”, near the village Saint-Bauzile (region Auvergne-Rhône-Alpes, Département Ardèche, France). It lies on the northeastern margin of the vast basaltic plateau of Coiron (about 20 km long and 10 km wide, latitude: 44.6802, longitude: 4.6859; Text-fig. 1a).

Sediment samples with plant remains, i.e., putative charcoal, exposed on bedding surfaces, ranging from micro-charcoal to relatively large fragments (Text-figs 2a, 4a)

fragments, as well as several specimens resembling partly charred wood have been collected on stock piles (not in situ) from the open-cast mine during prospecting for charcoal-bearing fossil deposits in 2017, at the diatomite quarry at the top of the Montagne d’Andance by MW. The material comes from the lowest mining-level of the quarry. The material analysed for the present study is stored in the palaeobotanical collection of the Senckenberg Forschungsinstitut und Naturmuseum Frankfurt, under collection numbers SM.B 22258 – SM.B 22298.

Selected small diatomite samples with charcoal exposed on bedding surfaces ( $n = 2$ ) and pieces taken from larger charred wood specimens (several cm in diameter) ( $n = 2$ ) were mounted on standard stubs with LeitC (Plano, Münster, Germany), and subsequently examined with the aid of a JEOL JSM 6490 LV Scanning Electron Microscope (SEM; accelerator current 20 kV) at the Senckenberg Forschungsinstitut und Naturmuseum Frankfurt (Germany).

**Text-fig. 3.** Partly charred wood from diatomite of Saint-Bauzile. **a:** Overview of the wood specimen in tangential view; SM.B 22259; scale bar = 1 cm. **b:** Cross-section showing two growth rings. **c:** Detail of late-wood in cross-section. **d:** Close-up of late-wood cells exhibiting hollow (?) helical structures in cell wall. **e:** Early wood in tangential view with tracheids, rays and axial parenchyma.



**f:** Detail of ray with triangular intercellular spaces between ray cells and uniseriate bordered pits on tracheid wall (arrow points to homogenized cell wall). **g:** Tracheids and axial parenchyma in radial view with uni- to triseriate pits. **h:** Close-up of triseriate pits in parenchyma cells. **i:** Tracheid with resin (?) adhering to cell wall and forming plates (dotted arrow). **j:** Taxodioid crossfield pits. **k:** Uniseriate pits on tangential tracheid wall and biseriate pits on turned down radial tracheid wall (right). Arrow points to homogenized cell wall.

## Results

Black plant fragments, ranging from small micro-charcoal fragments to relatively large, up to  $12 \times 6 \times 4$  cm, (partly) charred wood specimens, are exposed (Text-figs 2a, 3a, 4a) on almost all diatomite bedding planes inspected so far (e.g., after splitting larger blocks of diatomite). This material exhibits a silky lustre and a black streak on touch, as well as homogenized cell-walls (e.g., Text-fig. 3f, k) and excellently preserved internal anatomy under the SEM (Text-figs 2–4). These characters are usually considered typical for charcoal, as the result of incomplete combustion of plants (e.g., Scott 2000, 2010). Larger wood specimens (Text-fig. 3a) exhibit these characters only in peripheral areas, and large parts of such wood specimens exhibit mostly a brown colour and non-homogenized cell-walls. It seems likely that these specimens represent partly charred wood, which is often found in natural fires (e.g., Komarek et al. 1973, Scott 2000). Charred fern remains (Text-fig. 2), partly charred coniferous wood (Text-fig. 3) and a charred grass leaf (Text-fig. 4) have been studied by SEM.

### Fern

The charred fern remains resemble '*Pteris*' *oeningiensis* (Text-fig. 2a), a taxon that is known from other Cenozoic localities in the form of charred specimens (e.g., Paleocene of Menat/France; Uhl, unpublished results). The epidermal cells of the pinnules exhibit strongly undulating anticlinal cell walls (Text-fig. 2b, c).

### Coniferous wood

The coniferous wood specimen analysed so far by means of SEM is well preserved (Text-fig. 3), consisting of a pycnoxylic secondary xylem with marked growth rings (Text-fig. 3b). The transition from early wood to late wood is abrupt (Text-fig. 3b). In the late wood, the walls of tracheids have hollow (?) helical structures in the cell walls, which give the cell walls a perforated look when seen in cross-section (Text-fig. 3c, d). Rays are uniseriate (one cell wide) and two to six cells high (Text-fig. 3e), with triangular intercellular spaces between ray cells (Text-fig. 3f). Crossfields have 4(–6?) taxodioid (?) pits (Text-fig. 3j). Bordered pits on tangential tracheid walls are uniseriate (Text-fig. 3f, k), while they are uni- and bi- to tri-seriate on radial tracheid walls, probably abietinean-like distributed (Text-fig. 3g, h, k). Sanio's rims were not seen. Axial parenchyma is present, consisting of relatively short cells with a rectangular outline in tangential view; transverse walls between these cells seem to be smooth (Text-fig. 3e, g, h). Within the axial parenchyma, resin (?) plates and resin (?) adhering to the cell walls (Text-fig. 3i) are present.

The wood charcoal exhibits characteristics, i.e., the bi- (to tri-)seriate pitting on radial tracheid walls, an abrupt transition from early to late wood, axial parenchyma with resin infills, which are considered typical for some taxodioid Cupressaceae (e.g., IAWA Committee 2004, Akkemik et al. 2005). Wood belonging to this group, i.e., *Taxodioxydon grangeonii* PRIVÉ, has previously been described from the diatomites of Saint-Bauzile (Privé 1975). However, several characters of that wood taxon have not been observed in the

charred wood described here. Furthermore, wood shrinks during charring (e.g., Osterkamp et al. 2018, Rößler et al. 2021), and some anatomical features, like cross-field pitting, may completely change their characteristics (e.g., Gerards et al. 2007). Therefore, we refrain from identifying the charred wood described here with the taxon described by Privé (1975) or any other taxon described in the literature for the time being.

Triangular intercellular spaces in the rays are known from different conifer taxa. In the past a number of authors have attempted to use this feature for the taxonomic separation of certain conifer taxa (e.g., Van der Burgh 1973, Visscher and Jagels 2003). However, according to Larson (1994), such triangular spaces may occur in the wood of several (unspecified) species when these grow in wet habitats. From this, he assumed that this may be a general feature, more related to habitat conditions than to taxonomy. The formation of such structures during charring seems unlikely, as such changes have never been described in studies dealing with the experimental production of charcoal. Taken together the potential affiliation of this wood to taxodioid Cupressaceae and such an ecological interpretation of the triangular spaces in the rays, suggest that the partly charred wood analysed here originated from a plant that probably grew in the wettest vegetation belt, directly bordering the lake.

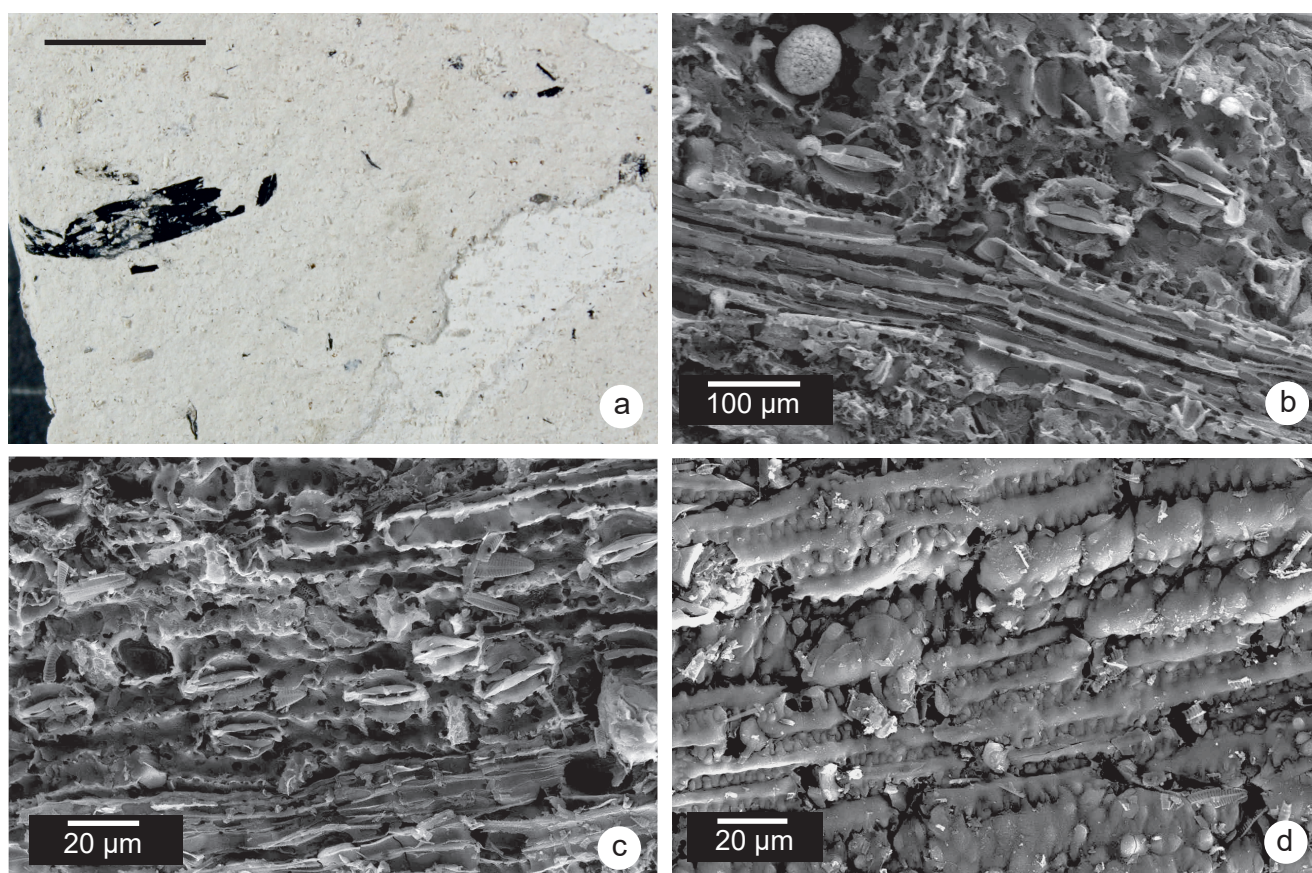
The helical structures observed in the tracheid walls of the charred wood resemble somewhat the cell-walls in compression wood (cf. Jane 1956). Collinson et al. (1999) interpreted comparable checking of cell walls seen in fossil charcoal from the Cretaceous as being indicative for compression wood, and not necessarily drying out prior to charring, as suggested by other authors (e.g., Jones 1993).

### Grasses

A number of fragmentary macro-charcoal specimens belonging to grasses (Text-fig. 4a) of so far unknown taxonomic affinity can be observed on different slabs of diatomite. These specimens exhibit a parallel venation, and under the SEM it can be seen that epidermal cells as well as stomata are oriented in longitudinal rows (or bands) that run parallel to veins (Text-fig. 4b, c). Also, the apertures of the individual stomata are oriented along the long axis of a leaf (Text-fig. 4b, c). In the intercostal areas, the epidermis consists of rectangular, elongated cells with strongly undulating margins (Text-fig. 4c, d). Due to the small size of the specimens and the fact that only a few anatomical details can be seen in the single grass leaf analysed so far by SEM, it is not possible to infer a more specific taxonomic affinity for these specimens.

### Micro-charcoal

Most of the micro-charcoal remains that are visible on the surfaces of different sediment slabs have a highly elongated form (Text-figs 2a, 4a), taken as indicative for a possible origin from grasses by some authors (e.g., Umbanhowar and McGrath 1998). However, as demonstrated by Crawford et al. (2018) such a morphometric interpretation of charcoal particles can be misleading, and depending on the charring temperature, other plant groups, like conifers, can also lead



**Text-fig. 4.** Charred grass from diatomite of Saint-Bauzile. **a:** Overview of diatomite slab with one larger specimen of charred grass (left) and several smaller, lath-shaped charcoal fragments; SM.B 22260; scale bar = 1 cm. **b:** Detail of vein exhibited on split grass blade, with stomata oriented parallel to vein. **c:** Stomata oriented in rows and bands parallel to veins exposed on split grass blade. **d:** Surface of grass leaf with rectangular, elongated cells with strongly undulating margins in an intercostal area.

to the production of wood micro-charcoal fragments with similar/comparable dimensions.

## Discussion

The presence of micro- as well as macro-charcoal, as well as partly charred wood remains indicate that the terrestrial ecosystems around the maar lake of Saint-Bauzile experienced wildfires during the deposition of the lower part of the diatomite sequence. The numerous micro-charcoal remains, occurring on different bedding planes of the diatomite, which can also be observed on fossil bearing sediment specimens from this locality figured in the literature (e.g., Saint Martin et al. 2017, Tanrattana et al. 2020), provide evidence that these ecosystems were repeatedly affected by wildfires.

Kidder and Gierlowski-Kordes (2005) suggested that the extensive formation of Miocene non-marine diatomite deposits is related to the rapid expansion of grasslands during this period, which also lead to changes in the silica cycle. According to interpretations based on palaeobotanical and palynological data (e.g., Brice 1965, Iskandar 1990), the lake of Saint-Bauzile was surrounded by a forested belt, with riparian taxa (*Populus*, *Salix*, *Liquidambar*, taxodioid Cupressaceae) growing at the water-land interface. Beyond this riparian zone, there was a mixed mesophytic forest belt with tree taxa like *Carya* and other Juglandaceae,

*Castanea*, *Cinnamomum*, as well as other Lauraceae, *Parrotia*, *Platanus*, *Zelkova*, and a variety of other conifers, together with an undergrowth of ferns, mosses and epiphytic lianas. This forest belt around the lake was probably surrounded by a kind of drier, open grassland of unknown spatial extent, serving as a grazing grounds for antelopes and horses (Mein et al. 1983, Iskandar 1990, Métais and Sen 2018).

Charred fern remains are common constituents of many Mesozoic (e.g., Harris 1981, Brown et al. 2012, Uhl et al. 2019) and a few Cenozoic floras (e.g., Wedmann et al. 2018), and some taxa are repeatedly preserved as charcoal, suggesting that they were adapted to recurring wildfires (Watson and Alvin 1996). Such Mesozoic fire-adapted ferns probably grew on fire-prone fern prairies or in the undergrowth of fire-prone coniferous forests (e.g., Watson and Alvin 1996, Brown et al. 2012). In some cases, such charred ferns, i.e., some occurrences of charred *Weichselia reticulata*, are also interpreted as evidence for a regular occurrence of wildfires in a rather wet mangrove-like vegetation bordering the Mesozoic seas (e.g., Abu Hamad et al. 2016, El Atfy et al. 2019).

The charred ferns from the diatomite of Saint-Bauzile may either represent an (so far hypothetical) older dry- and/or fire-adapted lineage/ecotype, which was still part of the grassland habitat, or the ecotone between forest and grassland, which may have been affected by fires from time

to time. Or they provide evidence, together with the partly charred wood of taxodioid affinity, that fires sometimes also reached the forest and even the wettest riparian zone of this forest belt. But based on the small amount of remains analysed so far, no reliable interpretation of the habitat of these ferns can be given at the moment.

Macro-remains of taxodioid Cupressaceae, i.e., wood belonging to *Taxodioxydon grangeonii*, have previously been described from the Montagne d'Andance (cf. Privé 1975), and foliar remains attributed to the genera *Sequoia* and *Callitris* have been described from other Late Miocene localities of the Coiron massive (e.g., Grangeon 1958). Pollen, which has been attributed to different genera of taxodioid Cupressaceae, is quite common in the Saint-Bauzile diatomite deposits (Iskandar 1990). Although Iskandar (1990) interpreted the taxodioid Cupressaceae as part of the wettest vegetation belt directly bordering the lake, growing on permanently water-logged soils, this is not necessarily the case, as plants belonging to this sub-family can occupy a wide range of ecological niches (e.g., Bouchal and Denk 2020, and citations therein).

Today, fire is an integral part of many types of grassland worldwide, and is often even necessary to maintain such an open landscape (e.g., Beerling and Osborne 2006, Scott et al. 2014). The presence of some kind of drier, open grassland of unknown spatial extent in the vicinity of the lake was previously postulated, based on the ecological demands of grazing mammals, which are also known from the lake deposits (Mein et al. 1983, Iskandar 1990, Métais and Sen 2018). However, charred grass remains can be transported over comparatively large distances as they are easily lifted high in the air by updrafts produced by a fire itself, thus providing information about the occurrence of wildfires on a regional scale (e.g., Umbanhowar and McGrath 1998, Scott et al. 2014, Leys et al. 2015), whereas the large specimens of partly charred wood can probably be seen as evidence of wildfire(s) in the direct vicinity of the palaeo-lake of Saint-Bauzile.

Considering the palaeoclimate during deposition of the diatomites of Saint-Bauzile, Brice (1965) estimated mean annual temperature (MAT) to be around 15–20 °C, with a higher precipitation than today, based on comparisons with nearest living relatives (NLRs) of the macroflora of Saint-Bauzile. Subsequently, Iskandar (1990) reconstructed a warm and humid climate based on the palynoflora from this locality. Also, Quan et al. (2014) reconstructed a warm and humid climate by applying the Coexistence Approach, a quantitative technique based on comparisons with NLRs (cf. Mosbrugger and Utescher 1997), to the palynoflora from this locality. Recently, Tanrattana et al. (2020) reconstructed a humid, warm, temperate to subtropical climate, with a MAT of 14–16 °C and a mean annual precipitation (MAP) of 1,200–1,900 mm without considerable seasonality, based on a leaf physiognomic analysis of the flora from Saint-Bauzile. In general, the results obtained by these authors are comparable to other quantitative reconstructions based on European (i.e., Central Europe, Eastern Mediterranean and Spain) floras from the late Miocene (e.g., Mosbrugger et al. 2005, Bruch et al. 2007, 2011, Quan et al. 2014). However, the results of all palaeobotanical studies indicate more

humid conditions than multi-proxy reconstructions (mainly based on mammals) for the vicinity of Saint-Bauzile, which suggested rather dry environments during deposition of the diatomites of Saint-Bauzile (e.g., Demarcq et al. 1989, Métais and Sen 2018). On a larger scale, there is evidence that a subhumid to humid climate prevailed all over Europe during the Tortonian (e.g., Bruch et al. 2007, 2011, Quan et al. 2014), and a Mediterranean climate, with dry summers, had not yet been established along the northern coast of the Mediterranean during this period (Quan et al. 2014).

The frequent occurrence of charcoal, at least in the studied layers of the diatomites of Saint-Bauzile, is somewhat contradictory to the relatively humid palaeoclimate reconstructions based on palaeobotanical proxies, as the occurrence of massive and regular fires, producing large amounts of charcoal, is often connected to a pronounced dry season, or at occasional least dry spells (e.g., Scott et al. 2014). However, it may be noteworthy that in maar deposits from the Paleocene locality Menat in the Auvergne, micro- as well as macro-charcoal is also rather abundant (e.g., Wedmann et al. 2018, Uhl, unpublished results). Also, for this locality Tanrattana et al. (2020) reconstructed humid conditions with very high precipitation values based on the macro-flora. In both cases it seems possible that the vegetation in the region surrounding the maar lake was, probably due to edaphic factors, a kind of mosaic of different vegetation types, which may have included more fire-prone vegetation types, e.g., on larger grass “islands” on drier soils (maybe on the Coiron basalt plateau?). Based on the existing, preliminary data, it is unfortunately not yet possible to provide definite answers to solve this problem.

Further research at the locality Montagne d'Andance at Saint-Bauzile, especially a high-resolution analysis of micro-charcoal together with palynomorphs (to reconstruct potential short term changes in palaeoclimatic conditions) over the diatomite profile, supplemented by an anatomical/botanical analyses of macro-charcoal specimens, is expected to provide more detailed information about the fire regime in the Saint-Bauzile region during the Tortonian, and its potential connection with climatic conditions.

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