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Fossiliferous Holocene tufa of Mende (Lozère, southern France): implication for the Atlantic vegetation of the Causses Basin

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Keywords. – **T**ufas, Holocene, Angiosperms, Leaves, Causses Basin, Lozère

Abstract. – Tufas bearing plant macroremains are uncommon in the Causses Basin (southern France). Here, we report a new fossiliferous tufa deposits at Mende, in Lozère. This palaeontological site is the first Quaternary tufa from the northern part of the Causses Basin that yields such an abundance of plant macroremains. The radiocarbon dating shows that these Holocene deposits are related to the Atlantic period. Geomorphology and mineralogy show that the plant-bearing deposit is a calcareous tufa only composed by calcite, deposited near to an outlet of cool water, linked to the karstic hydrological system of the Causse de Mende. The flora exposed in this article is dominated by angiosperms. Leaves and reproductive structures were assigned to *Acer platanoides*, *Corylus* sp., *Hedera* sp., *Salix* cf. *cinerea*, and *Tilia cordata*. This new palaeobotanical data complements our scarcely knowledge of the Atlantic floras from the Causses Basin. During the Atlantic period, and in the northern part of the basin, whereas *Pinus*-dominated forests and oak groves were probably well-developed, valleys were locally inhabited by diversified wet angiosperm-dominated forests.

Le tuf fossilifère holocène de Mende (Lozère, sud de la France) : implications pour la végétation du Bassin des Causses durant l'Atlantique

Mots-clés. – Tufs, Holocène, Angiospermes, Feuilles, Bassin des Causses, Lozère

Résumé. – Les tufs livrant des macrorestes végétaux sont peu fréquents dans le Bassin des Causses (sud de la France). Nous présentons ici un tuf fossilifère inédit, à Mende, en Lozère. Ce site paléontologique est le premier tuf quaternaire de la partie nord du Bassin des Causses à livrer une telle richesse en macrorestes de plantes. La datation radiocarbone démontre que les dépôts sont d'âge holocène, plus particulièrement de la période Atlantique. La géomorphologie et la minéralogie montrent que le niveau à plantes est un tuf calcaire exclusivement composé de calcite, déposé à proximité d'une source d'eau fraîche reliée au système hydrologique karstique du Causse de Mende. La flore présentée dans cet article est dominée par des angiospermes. Les feuilles et les structures reproductrices sont attribuées à *Acer platanoides*, *Corylus* sp., *Hedera* sp., *Salix* cf. *cinerea*, and *Tilia cordata***.** Ces nouvelles données paléobotaniques complètent notre connaissance encore partielle des flores de l'Atlantique, dans le Bassin des Causses. Cette étude soutient que pendant l'Atlantique, et dans la partie nord du bassin, alors que les forêts de pins et de chênes étaient probablement dominantes, les vallées caussenardes étaient localement habitées par des forêts plus humides, riches en angiospermes.

INTRODUCTION

Tufas consist of carbonate deposits mainly precipitated under subaerial conditions from calcium bicarbonate-rich freshwater [Capezzuoli *et al*., 2014]. Tufas may cover wide areas, however, they are commonly local at such sites as waterfalls and springs [Ford and Pedley, 1996]. In some cases, tufaceous deposits may extremely well-preserved plant impressions and invertebrates [Magnin *et al*., 1991]. Tufas yielding fossil plants were reported from southern France since the XIX^{e} century [Saporta, 1860; Planchon, 1864]. Imprints of megaremains commonly consist of trunks, leaves, and reproductive structures ascribed to angiosperms and conifers [Vernet, 1986; Ali *et al*., 2003a; Limondin-Lozouet *et al*., 2006; Roiron *et al*., 2006]. Based on these fossil plants, tufas allow to obtain crucial information useful for the reconstruction of Quaternary palaeofloras [Roiron, 1997; Ali *et al*., 2014].

Features and evolution of Pleistocene-Holocene vegetation in the Causses Basin (southern France) remain only weakly known [Vernet, 1972]. Our knowledge of the vegetation from this area during the Holocene is mainly based on isolated pollen and charcoal studies [Vernet, 1968, 1972, 1986]. Although Quaternary tufas were reported from diverse localities of the Causses Basin [Rouire and Rousset, 1973; Ambert, 1986; Fabre, 1986 and references therein], only rare of them yielded plant megaremains [Boulay, 1887; Vernet, 1972; Vernet *et al*., 1984, 2008; Ambert *et al*., 1992].

A new tufa bearing abundant and well-preserved leaf imprints was discovered from the northern part of the Causses Basin, in Lozère. Objectives of this work was to: (1)

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determine the age of deposits using isotopic method applied on gastropod shells, and determine the mineralogy of the plant-bearing unit; (2) provide an inventory of the flora; and (3) discuss implications for our knowledge of the Holocene vegetation in the Grands Causses area.

GEOLOGICAL SETTING

Plant fossils were discovered from the Holocene tufa deposits of Mende (Lozère, southern France). The city of Mende is located south of the Massif Central, in the northernmost part of the Causses Basin. This latter is composed of carbonaceous rocks that are mainly Jurassic (fig. 1) [Ciszak *et al*., 1999; Perrissol, 1990; Hamon, 2004]. Fossil plants were collected on a unique outcrop in the valley of the Lot river, 1 km south of the city of Mende. The outcrop is located onto the northwest border of the Causse de Mende (altitude, 762 m a.s.l.). Locally, we have observed saw traces supporting that the tufa of Mende was exploited as a quarry, several decades before (obs. of the authors before 2001). Today, these traces are not accessible being totally covered by vegetation. The main part of the outcrop is not accessible anymore, being nearly totally blocked by screes and vegetation. Our oldest observations show that size of the outcrop was considerably reduced from 2001 to 2016. Today, plant-bearing tufa is only accessible along one dozen of metres long, and one-to-five-metres-high outcrop. The tufa system is not active anymore. Five lithological units were distinguished in a log crossing tufa (U1 to U5; fig. 2). Tufaceous deposits unconformably overlain Middle Jurassic marly limestones locally composing the base of the Causse de Mende (fig. 2, Unit 1). Regionally, these marly limestones were dated to the Aalenian based on rare ammonites such as *Leioceras opalinum* RENNECKE, *Ludwigia* cf. *haugi* DOUVILLÉ and *Ludwigia murchisonae* SOWERBY, and abundant ichnites such as *Zoophycos* MASSALONGO [Briand *et al*., 1979, 1993; Gèze *et al*., 1980; Defaut *et al*., 1990]. Unit 2 consists of screes showing angular, sharp-edged, Middle Jurassic limestone and dolomite blocks embedded inside a brown clayey matrix. Unit 3 consists of cemented-tufa screes. This sedimentary breccia shows angular and up to one decimetre wide limestone blocks. The Unit 4 consists of lenticular, indurated, layered, highly porous, up to two metres thick, and highly fossiliferous tufa facies. This unit yielded abundant plant fossils such as trunk, leave, and fruit imprints. Dimension of impressions varies a lot, from several centimetres wide leave fragments to metric trunks. Leave impressions form remarkable accumulations (fig. 3). Unit 4 also yields some continental gastropods. The Unit 5 consists of the dismantled top part of plant-bearing tufa facies that are overlain by the modern soil.

The fossil tufa edifice of Mende is located onto screes composing the piedmont slope in the border of the Causse de Mende. Similarly, several active tufas are known in valleys around Lozerian plateaus [Conservatoire des sites lozériens, 2012]. The Causse de Mende is a greatly karstified limestone plateau showing numerous active sources on its borders. We notice that, currently, some active sources located at the base of the lower Aalenian facies continue to actively produce tufas a few hundreds of metres from the fossil tufa system presented in this study. Outlets are frequent above the Toarcian facies that is characterized by highly impermeable marls [Briand *et al*., 1979]. Location and morphology of sediments support that the plant-bearing deposits of Mende were meteogene calcareous tufas deposited near to an outlet linked to the karstic hydrological system of the Causse de Mende. Although terminology between "tufas" and "travertines" was highly controversial, following the nomenclature of Capezzuoli *et al*. [2014], the relevant term to define plant-bearing sediments of Mende is "tufa"

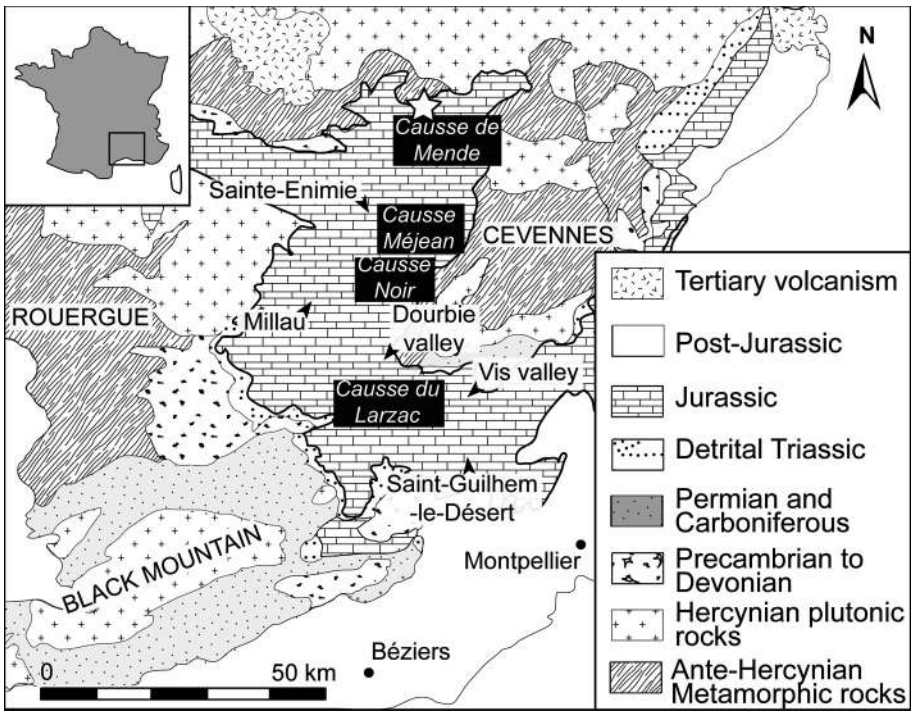

FIG. 1. – Geological map of the Causses Basin. The star indicates the location of the tufa of Mende. Modified from Moreau *et al*. [2014].

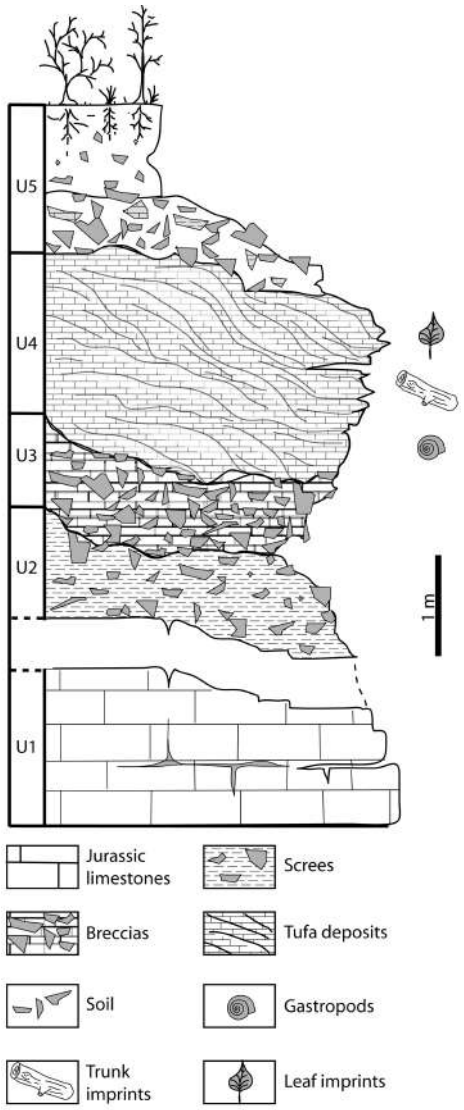

FIG. 2. – Stratigraphic cross-section of the Holocene tufa deposits from Mende. The section is divided in 5 units, U1-U5.

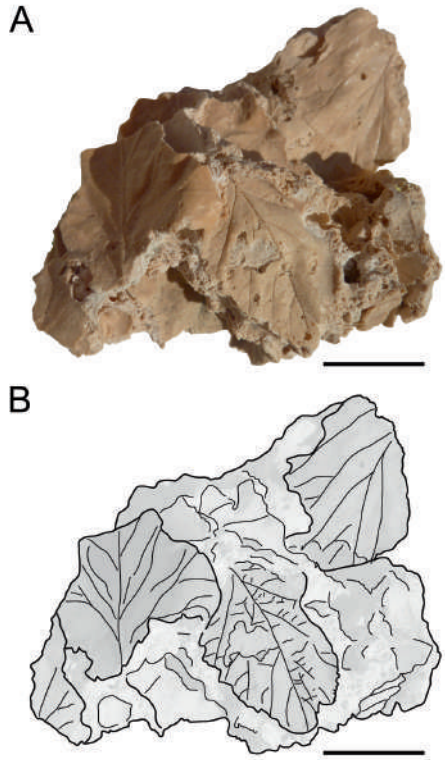

FIG. 3. – Photograph of a block of tufa from the Unit 4, bearing plants and showing accumulation of angiosperm leaves (A), and interpretative sketch (B). Scale bars = 2 cm.

commonly reserved for ambient cool water deposits, rather than "travertine" that is reserved to warm to hot water hydrothermal facies. The term "tufa" refers to continental carbonates composed dominantly of calcite and typical of karstic areas [Capezzuoli *et al.*, 2014].

MATERIAL AND METHODS

Dating and mineralogy features

In order to determine the age of the plant-bearing bed (Unit 4), radiocarbon dating using Accelerator Mass Spectrometer (AMS) method was applied on a unique gastropod shell (*Helicigona lapicida* LINNAEUS, 1758) from the same unit. ^{14}C age was carried out in Beta Analytic Radiocarbon Dating Laboratory (USA) (table I). The radiocarbon age was converted to calendar years using the INTCAL13 database [Reimer *et al.*, 2013] and the Talma and Vogel [1993] calibration scenario.

In order to characterize mineralogy of the tufa of Mende, we used optical microscope coupled with cathodoluminescence using cold cathode equipment operating at 18.5 ± 1.5 keV and 250 ± 50 mA at the University of Franche-Comté (Besançon, France). XRD analyses were recorded on rock sample powder at the University of Franche-Comté (Besançon, France) using a Bruker D8 Advance diffractometer system using Cu-Ka radiation equipped with a fast LynxEye linear detector. The diffractometer was operated at 40 kV and 40 mA; scans were run from 20° to 60°2θ, with a step interval of 0.02°2θ and a goniometry speed of 1 s per step.

Plant remains

All plant specimens studied in this work were collected in the Unit 4. They consist of plant macroremains. Plant

TABLE I. – ^{14}C ages obtained with gastropod shell from the tufa from Mende (Unit 4).

Laboratory number	Radiocarbon age BP	Calibrated age (2σ) (cal. BP)	Calibrated age (2σ) (cal. BC)	Method	Material
Beta-394879	6600 ± 30	7565-7435	5615-5485	AMS	Gastropod shell
		-7485	-5535		

assemblage is dominated by angiosperm vegetative structures such as leave imprints. Some reproductive structures of angiosperms such fruits were also observed. Complete leaves of angiosperms are quite frequent but difficult to observed because they are folded. Preservation is characterized by imprints/impressions of the external gross morphology. Compressions with or without cuticles were never observed. However, impressions excellently preserved tinny details such as leaf veins. This palaeobotanical study was led on twenty, and 10 to 60 cm wide tufa blocks. These blocks were split with hammers and knives. Hundreds of angiosperms leave fragments have been observed. Fossil plants were released with needles to obtain specimens the most entire as possible. Determinations of remains were made using the online database e-ReColNat which includes digital herbariums of national and academic institutions such as those of the Muséum National d'Histoire Naturel (Paris, France). We also used diverse literature sources [e.g., Coombes, 1993; Rameau *et al.*, 1993; Bock, 1997]. Specimens are housed in the collection of the Association Paléontologique des Hauts Plateaux du Languedoc (A.P.H.P.L.; Mende, Lozère, France).

Gastropod remains

After plants, gastropods are the most abundant fossil remains from the Unit 4 (fig. 4). They are often completely entombed in matrix, showing more or less thick layer of

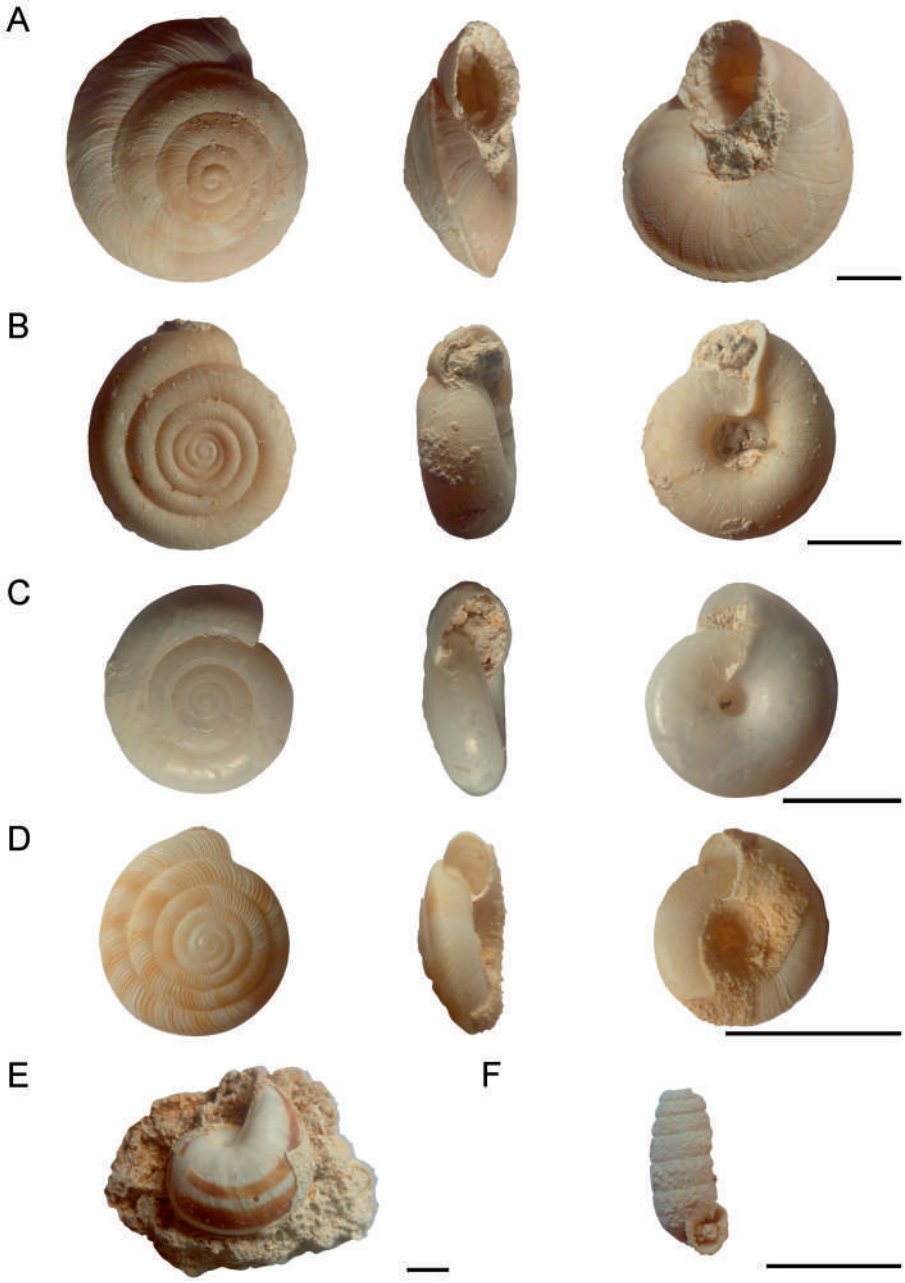

FIG. 4. – Gastropods from the lithological unit bearing plants (Unit 4). A, *Helicigona lapicida* (LINNAEUS, 1758). B, *Helicodonta obvoluta* (MÜLLER, 1774). C, *Oxychilus* (FITZINGER, 1833). D, *Discus rotundatus* (MÜLLER, 1774). E, *Eobania vermiculata* (MÜLLER, 1774). F, *Abida* cf. *secale* (DRAPARNAUD, 1801). Scale bars = 0.5 mm.

calcite on the shell surface. Complete shells are frequent, preserving the apex and the lips around the aperture. In some cases color patterns are preserved. Dozens of gastropod shells have been observed. The palaeomalacological study was led on twenty eight complete specimens. They were extracted from the matrix using needles. Determinations of shells were made using identification guides [e.g., Kerney and Cameron, 2015] and comparing with living taxa, including specimens from the study area. Specimens are housed in the collection of the Association Paléontologique des Hauts Plateaux du Languedoc (A.P.H.P.L.; Mende, Lozère, France).

RESULTS

Age and mineralogy of the plant-bearing tufa

Radiocarbon dating on gastropod shell provided an age of 7485 cal. yr BP (6600 ± 30 BP) for tufa formation, corresponding to the Atlantic period of the Holocene [c. 8000 to 4700 years before present *in* Callec *et al.*, 2006]. Mineralogical study performed with X-ray diffraction reveals that this rock is only constituted by calcite, without aragonite and dolomite occurrence (fig. 5). However, cathodo-luminescence and optical microscopies reveal two crystallisation calcite types such as micrite and sparite. They are clearly distinguished, forming laminations of alternating dark (micrite) and white (sparite) fringes (fig. 6). Calcite spar occurs as coarse cements with well-developed rhomboidal crystals showing palisade and micro dog-tooth morphologies. They are commonly directly in contact with plant imprints that consist of empty external casts (fig. 6). The spar is covered by well-developed, parallel, micritic cement showing fine and clotted to grummose texture.

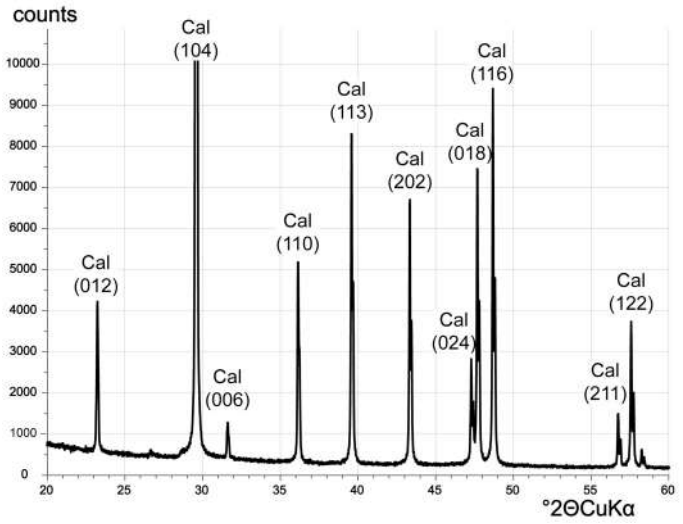

FIG. 5. – Representative tufa from Mende (Unit 4) XRD spectrum with calcite (Cal) and (hkl) Miller indices.

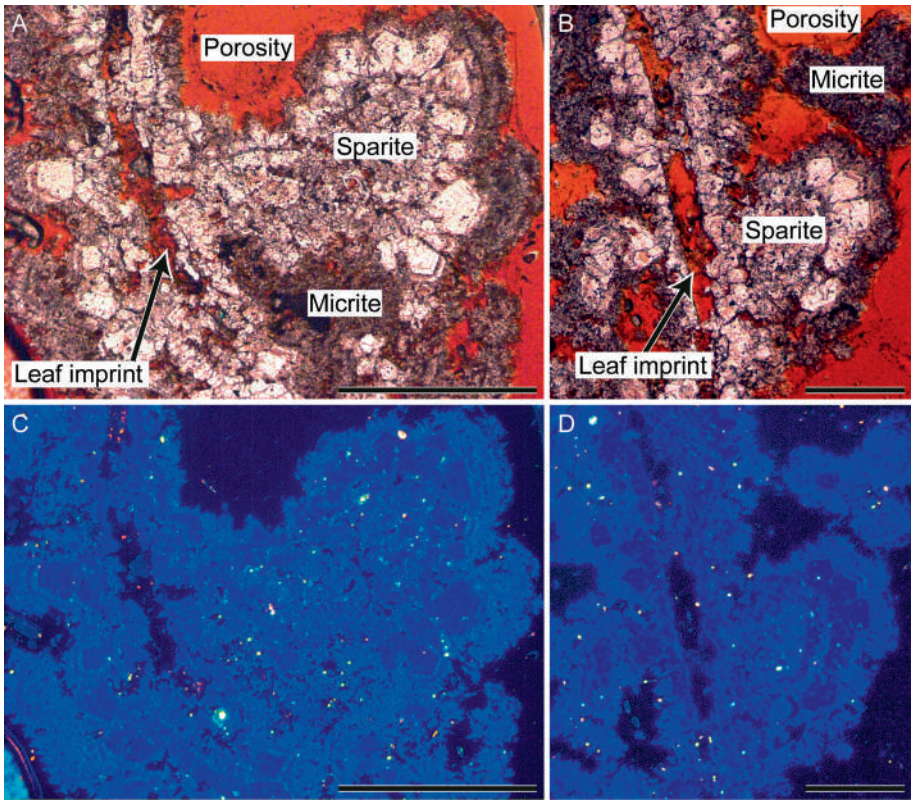

FIG. 6. – Microscopic (A-B) and cathodo-luminescence (C-D) images of the tufa from Mende (Unit 4) showing both micrite and sparite calcite around leaf imprints. Scale bars, A and C = 500 µm, B and D = 250 µm.

Palaeontology

Plants

Angiosperm leaves

Order Malpighiales Mart. 1835
Genus *Salix* L. 1753
Salix cf. *cinerea* L. 1753
fig. 7A-B

Material. APHPL_TME1

Description. The leaf is simple, petiolate, up to 20 mm wide and probably lanceolate. The base is cuneate and symmetric. Lamina displays entire margins. The primary venation is well-marked and pinnate. The primary veins are slightly curved and large (c. 1 mm). The secondary venation is semicraspedodromous. The secondary veins are well-marked, suboppositely to alternately arranged, and slightly curved. They form moderate angles compared to primary vein (35-60 degrees). The tertiary venation is mixed irregular reticular. Tertiaries consist of straight to sinuous veins. Quaternary venation is reticulate.

Remarks. The genus *Salix* is represented by a unique and fragmented leaf. However, it consists of the single

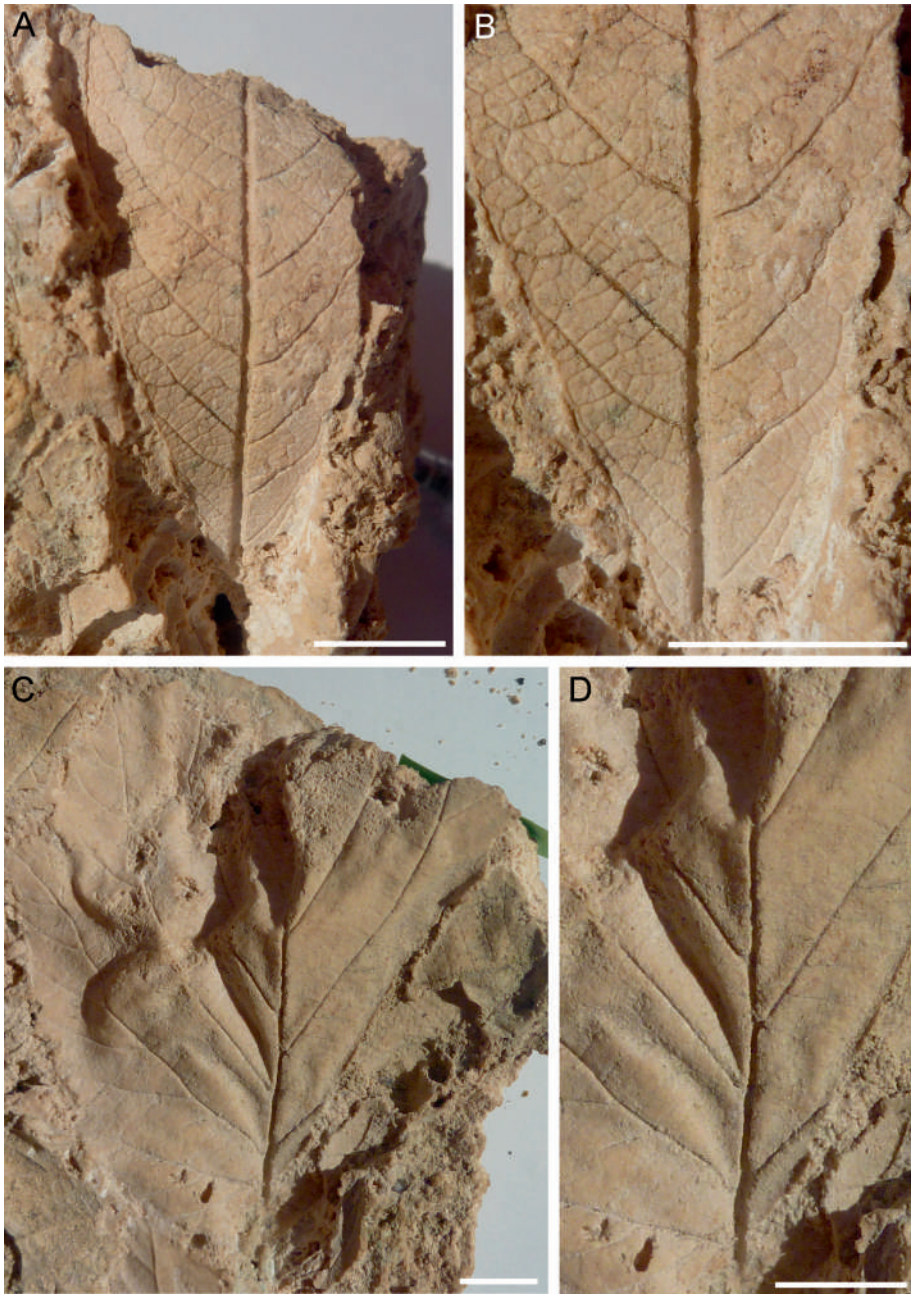

FIG. 7. – Leaves of angiosperms. A–B, *Salix* L. 1753, simple leaf with cuneate and symmetric base, lamina with entire margins, and pinnate primary venation is well-marked. C–D, *Corylus* L. 1753, simple leaf with deeply cordate and asymmetric base, lamina with serrated margins, and pinnate primary venation. Scale bars = 10 mm.

determined specimen from the tufa of Mende showing such details of quaternary venations. The entire margins and the particularly well-marked and thick veins remind *Salix cinerea*. In absence of the top of the lamina, we cannot indisputably ascribe the specimen to this species.

Order Fagales Engl. 1892
Genus *Corylus* L. 1753
Corylus sp.
fig. 7C-D

Material. APHPL_TME2; APHPL_TME3; APHPL_TME4; APHPL_TME4; APHPL_TME6; APHPL_TME7

Description. Leaves are simple, petiolate, ovate, with deeply cordate and asymmetric base. Largest specimen is 40 mm wide. Petiole is up to 1 mm wide. Lamina displays serrate margins. The primary venation is well-marked and pinnate. The primary vein runs straight. The secondary venation is craspedodromous. The secondary veins are alternately arranged and straight. They form moderate to fairly broad angles with midvein (up to 87 degrees at the base, and up to 35 degrees near to the apex degrees). Compound agrophic veins are basally present. Tertiaries are mixed opposite/alternate percurrent. Tertiaries consist of straight to sinuous veins.

Remarks. This taxon is one of the main components of the flora from the tufa of Mende. Details are missing to propose determination at the species level.

Order Sapindales Juss. ex Bercht. & J. Presl 1820
Genus *Acer* L. 1753
Acer platanoides L. 1753
fig. 8A

Material. APHPL_TME8; APHPL_TME9

Description. Leaves are palmately lobed, petiolate, with symmetric cordate base. Largest specimen is 50 mm wide. Petiole is up to 2.3 mm wide and shows a large 0.5 mm wide groove. Primary venation is palmate, basal actinodromous, with nine veins arising from the base. They are straight and diverge at an angle up to 45°. Secondary veins are alternately arranged, and straight to curve. They diverge at an angle up to 55° from the primary veins.

Second-order veins are thicker than primary veins. Tertiary venation is mixed opposite/alternate percurrent. The tertiary veins are mainly straight to sinuous.

Remarks. This taxon is only represented by three highly fragmented leaves. However, the nine primary veins, the hastate base and the entire margins allowed to ascribe specimens to *Acer platanoides*.

Order Malvales Juss. ex Bercht. & J. Presl 1820
Genus *Tilia* L. 1753
Tilia cordata Mill. 1768
fig. 8B

Material. APHPL_TME10; APHPL_TME11; APHPL_TME12; APHPL_TME13; APHPL_TME14; APHPL_TME15

Description. Leaves are simple, petiolate, ovate, with a cordate, asymmetric base and an acuminate apex. Largest specimen is 60 mm wide. Lamina displays serrate margins except the base that shows entire margin. Petiole is up to 15 mm long and up to 0.9 mm wide. Primary venation is palmate, basal actinodromous, with five straight to slightly curved veins arising from the base. They diverge at an angle up to 53°. Secondary veins are highly curve, alternately arranged, regularly spaced, and seem to reach the margin. They form a moderate angle with the primary veins (up to 45°). Compound agrophic veins are present, with minor secondaries arising proximally from the basal veins. Tertiary venation is mixed opposite/alternate percurrent. The tertiary veins are mainly straight to sinuous.

Remarks. This taxon is one of the main components of the flora from the tufa of Mende. The dimensions of specimens, the ovate lamina and serrate margins allow the species *Tilia cordata* to be determined.

FIG. 8. – A, *Acer platanoides* L. 1753, palmately lobed leaf with cordate and symmetric base, and well-marked, palmate primary venation. B, *Tilia cordata* MILL. 1768, simple leaf with cordate and symmetric base, lamina with entire margin, and palmate primary venation. C–D, *Hedera* L. 1753, simple leaf with entire margin and palmate primary venation. Scale bars = 10 mm.

Order Apiales Nakai 1930
Genus *Hedera* L. 1753
Hedera sp.
fig. 8C-D

Material. APHPL_TME16

Description. Leave is simple and petiolate. Petiole is 13 mm long and 2 mm wide. Lamina displays a large base and entire margins. The primary venation is well-marked, palmate, basal actinodromous. The primary vein runs straight.

Remarks. This taxon is only known by a unique and greatly partial specimen that cannot be identified at the species level.

Angiosperm reproductive structures

Order Fagales Engl. 1892
Genus *Corylus* L. 1753
Corylus sp.
fig. 9A

Material. APHPL_TME17; APHPL_TME18; APHPL_TME19

Description. Ovoid, up to 21 mm long, and 17 mm wide nuts. They show elongated, thin, and weakly marked traces.

Remarks. Similarly to leaves, nuts are only known by external moldings. Here, they consist of empty casts.

Order Malvales Juss. ex Bercht. & J. Presl 1820
Genus *Tilia* L. 1753
Tilia cf *cordata* Mill. 1768
fig. 9B-D

Material. APHPL_TME20; APHPL_TME21; APHPL_TME22

Description. Samara (winged achene) consists of a lanceolate, up to 85 mm long, and up to 18 mm wide wing that bears an elongate and up to 22 mm long peduncle. One specimen shows a peduncle bearing a unique spherical fruit 8 mm in diameter and supported by a rounded, 3 mm wide receptacle.

Remarks. Specimens are exquisitely preserved, often complete, with well-connected wing and fruit. Surface of wing shows very thin details of the venation. The dimension and the shape of wings and fruits, as well as the absence of marked ornamentation remind *Tilia cordata.*

Other organisms: gastropods

The main component of the gastropod assemblage consists of *Helicigona lapicida* which is characterized by flattened, lens shaped, and strongly keeled shell (fig. 4). *Discus rotundatus* (MÜLLER, 1774), *Helicodonta obvoluta* (MÜLLER, 1774), *Oxychilus* sp. (FITZINGER, 1833) and rare specimens ascribed to *Abida* cf. *secale* (DRAPARNAUD 1801) and *Eobania vermiculata* (MÜLLER, 1774) were also reported from the Unit 4 (fig. 4).

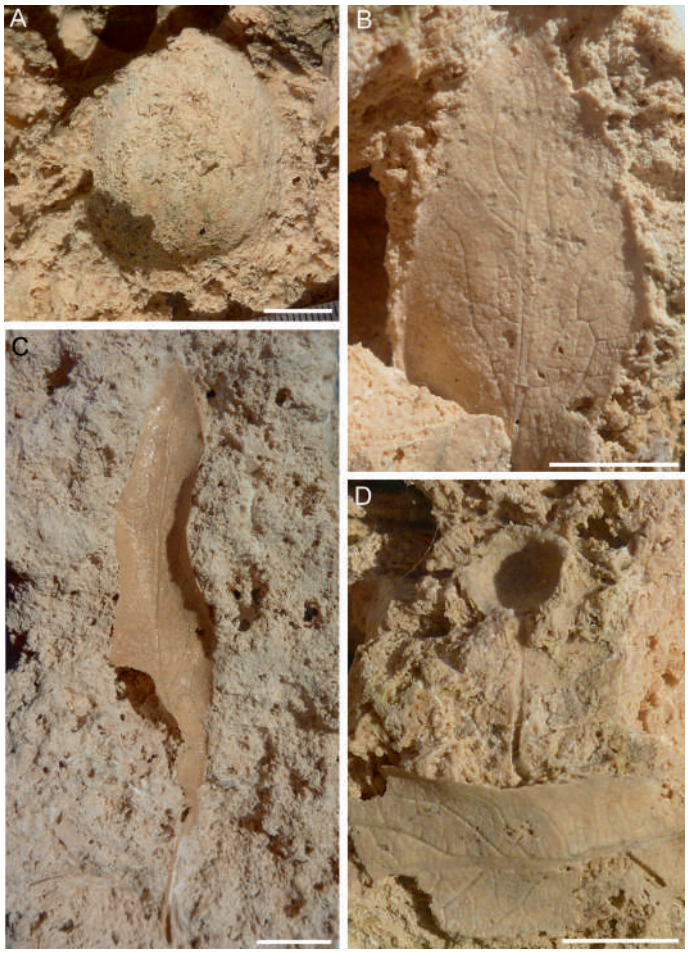

FIG. 9. – A, *Corylus* L. 1753, ovoid nut. B-D, Samara of *Tilia* L. 1753 showing elongated wing (B-C) and a spheroid fruit supported by an elongated peduncle (D). Scale bars = 10 mm.

DISCUSSION

Chronological and geological data

During sampling, no burrow or other reworking figure was observed in tufa, which suggests that gastropod fossils are contemporary to this formation. Dating was performed on a unique gastropod shell with a sufficient material to obtain a good analytical accuracy. It was carefully cleaned before analysis to avoid pollution by the surrounding limestone. However, although no evidence lets us predict, calcite pollution by recent organic matter could lead to erroneously 'young' ^{14}C dates [Ali *et al*., 2003b]. $^{13}C/^{12}C$ isotopic analysis should be performed on these gastropod shells to exclude this possibility. Furthermore, it would be interesting to carry out new dating, e.g. in the top and in the bottom of the unit to estimate precipitation rate of tufa.

Pedley [2000] explained that the precipitation of tufa deposits is the result of both abiotic and biological processes. Spar fringes are well-developed proximal to sources

and produced by physico-chemical precipitation linked with active agitation and cooling of water, and degassing of CO_2 [Pedley, 1992, 1994, 2000]. This kind of abiotic calcite is commonly formed on all surfaces exposed to flow in sites proximal to groundwater resurgences enriched with calcium carbonates. By contrast, as explained by Pedley [1994, 2000], micrite formation is always related to biogenic precipitation and/or trapping associated with biofilm colonisation, i.e. formed by microbial communities generally dominated by diatoms, filamentous green algae, coccoid cyanobacteria and heterotrophic bacteria [Ford and Pedley, 1996 and references therein]. Micrite is commonly formed on surfaces with slow flowing and static water system [Pedley, 2000].

Thus, in the tufa from Mende, we can distinguish two alternately phases of formation. The first implicated physico-chemical (abiotic) processes associated with sparite production during periods of high activity of the source. The second implicated biogenic processes (and micro-organisms) linked with the micrite production during lower activity of the source. Precipitates from both processes frequently alternate, even during the sparite cristals growth inducing zoning (fig. 6) and rapidly overlain plant or gastropod remains.

A new fossiliferous tufa from the Causses Basin

Southern France shows numerous Pleistocene and Holocene tufas [Magnin *et al*., 1990; Vaudour, 1994; Ambert *et al*., 1995; Mlakar *et al*., 1999; Ali *et al*., 2002, 2003b; Hoffmann, 2006; Ollivier *et al*., 2006; Roiron *et al*., 2006]. However, only few of them are highly fossiliferous. Although some Holocene tufas bearing plants were reported from the Alpes, Pre-Alpes and Provence, those from the Causses Basin remain extremely uncommon. Until now, Holocene plant megaremains inside tufas were only reported from the southern part of the basin, in the Tarn valley near Millau (Aveyron, fig. 1) [Ambert *et al*., 1992], then in the Vis valley (Gard, Hérault) [Vernet, 1986], and near to Saint-Guilhem-le-Désert (Hérault, fig. 1) [Ali *et al*., 2008]. In the northern part of the basin, although some tufas were previously and briefly reported from Lozère [Brouder *et al*., 1977; Gèze *et al*., 1980; Fabre, 1986], they never yielded megaremains of fossil floras.

The tufa of Millau is one of the oldest Quaternary tufas of the Causses Basin yielding diverse plant megaremains [Ambert *et al*., 1992; Vernet *et al*., 2008]. Age of the plant-bearing deposits is up to c.a. 300,000 years. Pleistocene imprints were mainly assigned to cones of conifers such as *Pinus* L. 1753 then leaves of angiosperms such as *Acer*, *Corylus* and *Salix*. The plant impressions from Saint-Guilhem-le-Désert are also older than the flora from tufa of Mende [Ali *et al*., 2008], being linked to the Boreal period [c. 9000 to 8000 years before present *in* Callec *et al*., 2006]. Fossil remains consist of leaves of flowering plants and rare cones of conifers. Like the tufa from Mende, tufa from the Vis valley are related to the Atlantic period (6100 +/– 120 BP and 6200 +/– 100 BP) [Farizier, 1980 *in* Vernet, 1986], and yielded abundant leaf assemblages. Thus, in the Causses Basin, except the tufa from Mende, only one other tufaceous formation is known to yield abundant leaf impressions from the Atlantic period. The plant remains described in the tufa from Mende consist of the unique Quaternary leaf assemblage described in the northern part of the Causses Basin. It is a new opportunity to better understand Holocene vegetation that remains weakly known in this area.

Similarly to plants, malacofaunas were only rarely mentioned in Holocene tufas from the Causses Basin (e.g., Saint-Guilhem-le-Désert, the Vis valley). They consist of diverse gastropods from aquatic to continental assemblages [Ambert, 1986; Ali *et al*., 2008].

Implications for the Atlantic vegetation of the Causses Basin

Although Holocene plant megaremains (trunks, leaves, and reproductive structures) inside tufas have never been characterized in the northern part of the Causses Basin, several studies based of charcoals and pollen have contributed to define the evolution of Holocene vegetation in this area [Vernet, 1968, 1972, 1986; Quilès *et al*., 2002]. Charcoals related to the Atlantic period and from the Causse Noir (fig. 1) were ascribed to *Pinus* and *Quercus* L. 1753 (e.g., Puechmargues shelter II and Rodier cave, Aveyron) [Vernet, 1968]. Pollen linked to these two taxa were also reported in coeval deposits from the Causses Basin [Vernet, 1972]. They are commonly associated with pollen of *Corylus* [Vernet, 1972]. According to Vernet [1968], during the Atlantic period, the main part of the Causses Basin was inhabited by vast *Pinus*- and *Quercus*-dominated forests. In the central part of the basin (Causse du Larzac), and during the Atlantic period, based on charcoals, Vernet [1972] noticed that conifer-dominated forests also show some angiosperms such as *Acer*, *Buxus* L. 1753, *Quercus*, *Fraxinus* L. 1753, and *Ulmus* L. 1753.

In the northern part of the Causses basin and during the Atlantic/Sub-Boreal boundary, vegetation seems to be dominated by conifers at the top of plateaus (e.g., Causse Méjean, fig. 1) and by *Quercus* in the valleys (e.g., charcoal study from la Caze, near Sainte-Enimie, Lozère) [Vernet, 1968]. This observation was also supported by data from the middle part of the basin where *Quercus* reaches 80% of the charcoal assemblage from the Atlantic period (e.g., Dourbie valley) [Vernet, 1968]. Concerning the Sub-Boreal period, Vernet [1968] identified *Pinus*- and *Quercus*-dominated charcoal assemblage from Lozère (Causse Méjean, southern part of the Causses Basin).

In contrast, the plant impressions from Mende show that during the Altantic period, the northernmost area of the Causses Basin was not only limited to *Pinus*- and *Quercus*-dominated forests, especially in valleys along plateaus. By contrast with the palynological data that reflect floras at a broader geographical scale, foliar remains from the tufa of Mende represent a riparian flora, only at a local scale. Both approaches are complementary. The palaeobotanical data presented here indicate that during the Atlantic period, the vegetation was locally, in valleys, composed by angiosperm-dominated floras. However, the flora from Mende shows that during the Atlantic, in the northernmost part of the Causses Basin, the flowering plants were not systematically dominated by oak (oak groves), showing other taxa such as *Acer*, *Corylus*, *Hedera*, *Salix*, and *Tillia.*

The presence of angiosperm-dominated floras is also supported by the coeval Holocene tufas (Atlantic) from the Vis valley, which show abundant angiosperm leaf imprints ascribed to *Corylus*, *Fagus* L. 1753, *Ficus* L. 1753, *Ilex* L.

1753, *Laurus* L. 1753, *Phillyrea* L. 1753, *Quercus*, *Tillia* [Boulay, 1887; Farizier, 1980 *in* Verner, 1986]. The slightly older flora (Boreal) from the tufa of Saint-Guilhem-le-Désert shows mesohygrophilous taxa such as *Salix* and *Populus* L. 1753, then mesophilous taxa such as *Sambucus* L. 1753, *Ulmus*, *Hedera*, *Sorbus* L. 1753 and *Vitis* L. 1753. Charcoal analyses led on the deposits of Saint-Guilhem-le-Désert show the abundance of *Pinus* (*sylvetris* type) from the Boreal period to the Sub-Atlantic period [Ali *et al*., 2008]. They also show occurrences of *Buxus* and *Quercus* mainly since the Atlantic period, and occurrences of *Acer* and *Corylus* since the Sub-Boreal period [Ali *et al*., 2008].

In the tufa of Mende, the abundance of leaves and reproductive structures ascribed to *Acer*, *Corylus*, *Salix*, and *Tilia* clearly reflects a forest environment. Among gastropods, although *Discus rotundatus* and *Oxychilus* can be observed from wet to dry environments, the abundance *Helicodonta obvoluta* supported the hypothesis of a wet shady forest [Kerney and Cameron, 2015]. The specimens ascribed to *Abida* cf. *secale* support that more dry rocky environment were not so far (e.g. Jurassic limestone cliffs of the Causse de Mende). We notice that the angiosperms observed in the tufa from Mende are currently still present in the Lot valley, especially *Acer*, *Corylus*, *Hedera,* and *Tillia* which live near the outcrop. Although the tufa of Mende yields an isolated plant assemblage, it supports that Atlantic and living floras from valleys between limestone plateaus probably share strong similarities.

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