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RE-EXAMINATION AND NEW DATA FROM THE LAST INTERGLACIAL (EEMIAN) MACROFLORA FROM THE RESSON TUFA, FRANCE

■

Marie-Claude JOLLY-SAAD[1] & Julie DABKOWSKI[2]

ABSTRACT

Due to their nature and the process of their precipitation, tufa deposits offer the potential to serve as sedimentary records of hydrology, climate, ecology, and biodiversity in areas otherwise lacking such archives of past interglacial landscapes. In this study, a flora from Resson tufa (northeastern Paris Basin) assigned to the last interglacial (Eemian) is reinvestigated. The analysis of 52 samples identify 24 taxa including *Acer, Corylus, Fagus,* cf. *Taxus* and other woody shrubs reflecting a forest environment. The abundance of charophytes support the hypothesis that an open aquatic environment existed in the vicinity of the shady wetland forest close to the stream. Most of the taxa are currently present in the area with the exception of *Buxus* and *Taxus*. The description of new palaeobotanical data from this tufa system provides rich information complementing former studies that are used for palaeoenvironmental investigations aimed to the reconstruction of the past landscape during the last Interglacial.

Keywords: Tufa, Late Pleistocene, Interglacial flora, foliar imprints, Paris Basin, Eemian, France

RÉSUMÉ

RÉVISION ET NOUVELLES DONNÉES DE LA MACROFLORE DU DERNIER INTERGLACIAIRE (EEMIEN) DU TUF DE RESSON, FRANCE.
De par leur nature et les processus de précipitation, les dépôts de tufs offrent un fort potentiel d'enregistrement des données hydrologiques, climatiques, écologiques et de biodiversité dans les régions ne possédant pas d'autres archives paléoenvironmentales des périodes interglaciaires. Dans cette étude, la flore fossile préservée dans un tuf daté du dernier interglaciaire (Eemien) localisé à Resson au nord-est du Bassin de Paris, est réétudiée. L'analyse de 52 échantillons a permis l'identification de 24 taxons incluant *Acer, Corylus, Fagus,* cf. *Taxus* ainsi que plusieurs espèces arbustives évoquant un environnement forestier. L'abondance des Charophytes témoigne de la présence d'un milieu aquatique ouvert à proximité d'une forêt humide riveraine. La plupart des taxons sont présents dans la flore actuelle régionale à l'exception de *Buxus* et *Taxus*. La description de ces nouvelles données paléobotaniques apporte de nouvelles données essentielles complétant les études antérieures qui peuvent être très utiles pour les études paléoenvironnementales visant à la reconstruction du paysage passé au cours du dernier interglacaire.

Mots-clés : Tuf, Pléistocène supérieur, flore interglaciaire, empreintes foliaires, Bassin de Paris, Eemien, France

1- INTRODUCTION

This paper presents the rich plant macroremains from the Resson tufa (Aube, Northeastern France). Calcareous tufa deposits result from the dissolution of the carbonate content of the bedrock in the aquifer, favoured by soil and forest development and the resulting groundwater acidification (Pentecost, 1995, 2005). The terms tufa and travertine have been controversially used for decades. Herein we follow Capezuolli *et al.* (2014) who stated that tufa differs from travertine in that the latter is reserved to rocks originating from warm to hot water hydrothermal facies. During tufa formation, when water emerges at a spring, physicochemical parameters and activity of the instream vegetation (especially cyanobacteria, mosses and algae) lead to rapid calcite precipitation. which can lead to the preservation of imprints and incrustations of organic remains and their structures. While the plant remains later decay, the remaining calcite cast can provide sufficient external details to allow specific identification and thus environmental investigations (e.g. Ali *et al*., 2002; Green *et al*., 1984; Field, 1993; Meyrick & Schreve, 2002; Jolly-Saad *et al.,* 2007). While regional vegetation changes during the Quaternary are well documented in western Europe through palynological records, macroflora sites are still rare. However, they can provide a discrete snapshot of the ecology of plants and local plant communities as well as of the geological conditions at the locality (Ambert *et al*. 1995; Roiron, 1997; Roiron *et al.*, 2006; Ali *et al.*, 2002, 2003a,b, 2014).

The tufa deposit at Resson (France) was first studied by Leymerie (1846) who mentioned the presence of numerous aquatic and terrestrial plant imprints, mollusc shells and mammal remains. The site thus became of interest for geologists and palaeontologists (Belgrand, 1869; Meugy, 1877; De Mortillet, 1883). The most detailed investigations were provided by Fliche (1883), who provided a synthesis of earlier studies and a full inventory of palaeontological remains from Resson, especially a list of 35 plant taxa preserved as imprints in the tufa calcite. Furthermore, 8 taxa of molluscs

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(*Cepaea nemoralis, Fruticicola fruticum, Helicella itala, Stagnicola palustris, Galba truncatula, Radix sp., Gyraulus albus, Hippeutis complanatus* and 6 taxa based on vertebrate remains (*Anas boschas, Canis familiaris, Castor fiber, Cervus elaphus, Rhinoceros tichorhinus, Elephas primigenius*) were listed by Fliche (1883). Remains of human skull and bone are also reported from the deposit.

These former studies place the Resson tufa into a Quaternary warm period. In the xxth century, Resson geomorphological position and sedimentology were further discussed and the tufa was assigned to the last interglacial or the Eemian (Marine Isotope Stage or MIS 5) (Tricard, 1952; Michel, 1967). More recent malacological data reveals the presence of *Belgrandia marginata,* a biostratigraphic indicator of Middle to Late Pleistocene interglacial periods (Dabkowski *et al*., 2020). According to Fliche (1883), most of the palaeontological collection from Resson was stored at the *Muséum d'histoire naturelle* in Troyes (Aube, France), now called *Musée de Troyes*, where plant imprints have been retrieved thanks to Ghislain Grégoire, assistant at the museum. The main goal of the present paper is a re-examination of the plant macrofossil specimens in the collection in order to validate their determinations and palaeoenvironmental significances before new field prospections will be untertaken. Knowledge on the Resson tufa system potentially provids a rare but crucial insight into the palaeoclimatology and palaeoecology of a former interglacial. The Eemian in continental Europe could likely serve as fundamental analogue for the current Holocene epoch. In this review, data from Resson is compared with those from other European tufas and long-sequence records.

2 - STUDY SITE INFORMATION

The site (coordinates N 48°32'59'', E 3°29'24; 82 m a.s.l.) is located in the hamlet of Resson, north to La Saulsotte (Aube, France), in the small valley of the Resson river (earlier called La Doué), a tributary of the Seine (fig. 1). Recent human activities have largely modified the landscape which comprises nowadays cultivated fields and few fragmented forest areas. The area has a degraded oceanic climate, that is intermediate between oceanic and continental climate (Pédelaborde, 1957). Mean annual temperature is ca. 11°C and mean seasonal temperatures are around 2-3°C in winter - December, January and February - 16-19°C in summer June, July and August and relatively low mean annual precipitation (less than 700 mm/year). Interannual variability in precipitation rate is minimal while temperature variability is high (Joly *et al*., 2010; Pédelaborde, 1957).

Resson tufa deposit, as shown on the 1:50,000 geological map (Provins section, Lacot, 1967) has an elliptic shape of about 1 km length and 300 m width, oriented NO-SE along the valley. Due to its exploitation

Fig. 1: Geographical location of the Resson tufa outcrops (Aube, France).
Fig. 1 : Localisation géographique des affleurements du tuf de Resson (Aube, France).

as a local building stone quarry since at least the Middle Ages (Gérard *et al*., 1997; Koeniguer, 1996), several profiles are excavated in Resson tufa, which represents an 8-10 m thick deposit.

The general stratigraphy of the Resson tufa was described by Leymerie (1846), Fliche (1883), Tricart (1952) and Michel (1967). Above colluvial and fluvial deposits, the profile shows tufa with subhorizontal layering. The lower part is indurated comprising whitish silty to sandy homogeneous tufa; this facies is called 'white marl' by Michel (1967), alternating with light brown coarse-grained tufa units. According to Michel (1967), these units, especially the uppermost ones, are likely those beds in which locally imprints of leaves of spermatophytes, *Chara* and mosses are preserved, partly composing the collection described by Leymerie (1846) and Fliche (1883). The upper deposit is mostly crumbly and porous, with phytoclasts and detrital sands and gravel (Leymerie, 1846; Michel, 1967). Only remains of monocotyledons are common in both parts. Regarding the stratigraphic information, one may assumed that the macroflora kept at the Musée de Troyes constitutes a coherent assemblage of specimens.

3 - MATERIAL AND METHODS

In palaeobotanical studies, vegetative and reproductive organs are, in most cases, fossilized separately and fossil leave without cuticles are certainly the most common fossil macroremains. In Resson tufa, fossil plants described herein are diverse, preserved as impressions of leaves and few diaspores (fruits and seeds). In addition, vegetative parts such as lignified xylem cells of little twigs (PP 395) or vegetative organs of mosses (PP 395) are described.

The leaf venation pattern and leaf shape provide a set of characters, which allows for accurate identification of taxa. The specimens with well-preserved leaf venations were studied using modern leaf architectural analysis and could be identified to species level. The description of leaf architecture follows the methodology of Mouton (1966), Dilcher (1974), and the publication of the Leaf Architectural Working Group (Ellis *et al*., 2009). Taxonomy follows the most recent update of the Angiosperm Phylogeny Group classification (APG IV, Chase *et al*., 2016), and the system published in Christenhusz *et al*. (2011) for the conifers.

The collection housed at Musée de Troyes comprises 52 fragments of indurated tufa, large of 5 to 15cm, with one or numerous plant imprints on each individual hand specimen. In his monographic description of the Resson flora, Fliche (1883) inventoried 35 taxa including algae, bryophytes, pteridophytes, monocotyledons and dicotyledons (tab. 1). Several examples for these groups are shown on plates 1-4. Generally, the fossils of this collection are not well preserved: complete imprints are rare and for several remains the number of recognizable descriptive features is limited. Their Morphotype Quality Index (MQI) scores being often low (less than the fourth-order veins are preserved in the imprints) (Ellis *et al.*, 2009), this made taxonomic identifications difficult. Some specimens are damaged (PP 409, MR 9523) and thus observable features are insufficient to identify the leaf at the genus or species levels. Among the revised material, taxa from 19 families, 19 genera and 22 species are recognized.

The best-preserved samples were identified with references to botanical materiel held in the online Herbarium (e-ReColNat, MNHN, Paris) and systematics literature (Coste, 1937; Cronquist, 1981; Rameau, 1993).

Several bryophyte samples (MR5432, MR5442, MR5433, PP 395 and PP 417) are reported to the Bryaceae (pl. 1, pics. 5-15). These samples form tufts and patches up to several centimetres high (4-12 cm) which have an important role in the deposition and consolidation of tufas (pl. 2, pics. 5-15). Calcified moss remains are coarse without microanatomical features. The precise shape of the limb, the midvein height and leaf cell organization are not preserved in the different available moulds. Only, the biggest specimen, PP 395, was sampled and studied after dissolution of carbonates with diluated HCL (10 %). This bryophyte remain is observed with optical microscopy and described herein. The identification of one bryophyte fragment was facilitated by the modern standard floras (Smith, 1978; Douin, 1986).

All other specimens were examined with a Nikon stereo microscope with illumination by a fibre-optic lamp and photographed using Nikon camera. Digital images of macrospecimens were obtained by Carole Bell the photographer of the *Musée de Troyes* with a camera Canon EOS 5 using low-angle incident lighting from different directions to best enhance leaf venation features.

4 - RESULTS: DESCRIPTION OF TAXA

The new list described below in alphabetical order of families, genera and species is also summarised in table 1.

4.1 - ALGAE

Order: Charales Dumort. 1829

Family: Characeae S.F. Gray 1821

Chara L. 1753

Chara sp. cf. *C. vulgaris*

pl. 1, pics. 1-4

Samples: pp 400, pp 401, pp 415, pp 416, pp 418, pp 420, mr 9524, MR 5890.

The states of preservation and the degree of calcification are variable from one sample to another. The 8 fossil samples consists of dense encrusted stems differentiated into nodes and internodes, dimorphic branches (long branches of unlimited growth and short branches of limited growth). The branching system of the fossil specimens is complex with branches derived from apical cells which cut off segments at the base to form nodal and internodal cells alternately. Stems are corticated (pl. 1, pic. 4) with sizes up to 11-12 cm length; most of the stems are truncated, they were probably longer than 12 cm. Apex and rhizoids are not distinct. Axis diameters including incrustation are 1-1.5 mm, the diameter of the vegetal matrix was approximately 0.5 mm (pl. 1, pic. 4). Axes at internodes are 0.9-1.3 mm wide. Branchlets are distinct with 8-10 segments. Stipulodes and acicles are indistinct on all fossil samples (pl. 1, pic. 2). No gyrogonites and oospores are not observed in these samples (Soulié-Märsche & García, 2015).

The fossil stems differentiated into nodes and internodes, dimorphic branches are similar to the Characeae family. It is a small family divided in two tribes: the Chareae with four genus (*Chara*, *Nitellopsis, Lamprothamnium* and *Lychnothamnus*) and the Nittelleae with two genus *Nitella* and *Tolypella*. Among the different genus of Chareae and Nittelleae only the genus *Chara* has corticated stems (Bailly & Schaefer, 2010). Due to their strong calcification, the identification of *Chara* species is particularly difficult on tufa samples. In the former studies at Resson, two species were reported: *Chara foetida* Al. Braun and *Chara hispida,* L. var. *Brachyphyla* (Fliche, 1883). Only one species was found at the Musée de Troyes. Anatomical features of the different samples with branchlets of 8-10 segments, thin axe (0.4mm) have more affinity with *Chara* sp. cf. *C. vulgaris*. All these fossil samples differ from *Chara hispida* which is scarcely branched, with robust axes 0.7-1.5 mm in diameter (Corillion, 1957, 1975; Moore, 1986; Bailly & Schaefer, 2010). Oospores, the reproductive structures, which would be complementary diagnostic features to improve Charophytes identification (Soulié-Märsche & García, 2015) are not observed in Resson samples.

	FAMILY	FLICHE (1883)	THIS REVIEW	ORGANS	SAMPLES	Pl.S & FIGURES
ALGAE	Characeae	*Chara foetida* Al. Braun *Chara hispida* L. var. *brachyphyla*	*Chara* cf. *C. vulgaris*	M	MR 5890	Pl. 1, pics. 1-4
BRYOPHYTES	Bryaceae	*Bryum bimum* Schreb.	*Bryum pseudotriquetum* (Hedw.) G. Gaertn., B. Mey. & Scherb.	M	PP 395	Pl. 1, pics. 9-15
		Unidentifiable Bryophytes	Unidentifiable Bryophytes	M	MR 5432-MR 5433-MR 5442	Pl. 1, pics. 5-8
PTERIDOPHYTES	Aspleniaceae	*Scolopendrium vulgare* Symons	*Asplenium scolopendrium* L.	Im	PP 111-PP 404	Pl. 2, pics. 5-6
MONOCOTYLEDONS	Poaceae	*Phragmites communis* Trin.	*Phragmites* sp.	Im	PP 414	Pl. 4, pics. 1-3
	Cyperaceae	*Scirpus* sp.	Uncertain	Im		
		Carex glauca Scop.				
		Carex maxima Scop.				
		Carex flava L.				
	Typhaceae	*Typha* sp.		Im		
			Unidentifiable Monocotyledons	Im	PP 110 - Br 1084	Pl. 4, pics. 12b & 13
DICOTYLEDONS	Betulaceae	*Betula alba* L.	*Betula/Populus*			
		Betula alba L. var. *papyrifera* Spach		Im		
		Alnus glutinosa Gartn.	*Alnus* cf. *A.glutinosa*	Im	MR 9523- PP 413	Pl. 3, pic. 8 ; Pl. 4, pic. 6
		Alnus incana DC. ?				
	Salicaceae	*Populus canescens* Sm				
		Populus tremula L.				
		Salix purpurea L.	*Salix* sp.	Im	PP 396	Pl. 2, pic. 12
		Salix cinerea L.	*Salix* sp. cf. *S. cinerea*	Im	PP 110	Pl. 2, pic. 12
		Salix grandifolia Sér.?				
			Salix sp. *cf. S. caprea*	Im	PP 145	Pl. 2, pic. 9 ; Pl. 4, pic. 12a
		Salix nigricans Sm. ?				
	Corylaceae	*Corylus avellana* L.	*Corylus avellana* L.	Im/W/M	PP 145-PP 413	Pl. 2, pic. 15 ; Pl. 4, pic. 5
	Fagaceae	*Fagus sylvatica* L.	*Fagus sylvatica* L.	Im		Pl. 3, pics. 5 & 6
	Juglandaceae	*Juglans regia* L.				
	Buxaceae	*Buxus sempervirens* L	*Buxus sempervirens* L	Im	PP 296	Pl. 2, pic. 10
	Oleaceae	*Ligustrum vulgare* L.	*Ligustrum vulgare* L.	Im		
			Fraxinus cf. *F. excelsior*	Im		
	Cornaceae	*Cornus sanguinea* L.				
	Araliaceae	*Hedera helix* L.	*Hedera helix* L.	Im	BR 1084 & PP 294	Pl. 3, pics. 7 & 12
	Apiaceae	*Heracleum spondylium* L.	Incertae sedis	Im		
	Rosaceae	*Rubus fruticosus* L.				
		Cerasus padus D.G.				
			Sorbus aria (L.) Crantz	Im	PP 138 b- PP 145	Pl. 3, pic. 11b ; Pl. 4, pic. 7
	Rhamnaceae	*Rhamnus frangula* L.				
	Tiliaceae	*Tilia platyphylla* Scop. ?				
				Im		
	Sapindaceae	*Acer campestre* L.	*Acer* cf. *A. campestre*	Im	PP 402	Pl. 2, pic. 14
		Acer platanoïdes L.	*Acer* cf. *A. pseudoplatanus*	Im	PP 136	Pl. 2, pics. 7, 8 & 11
		Acer opulifolium Vill.				
			Acer sp.	Im	PP 402-PP 410- PP 413	Pl. 3, pics. 14-16 - Pl. 4, pic. 11
	Renonculaceae	*Clematis vitalba* L.	*Clematis* cf. *C. vitalba*	Im	PP 178	Pl. 3, pics. 1-3
	Celastraceae		*Euonymus europeus* L.	Im	PP 138a	Pl. 3, pics. 9-10
PINOPHYTES	Taxaceae		*Taxus* cf. *T. baccata*	Im		
SPHENOPHYTES	Equisetaceae		*Equisetum* sp.	M	PP 390	Pl. 2, pics. 1-4
INCERTAE SEDIS 1				Im	PP 138a	Pl. 3, pic. 13
INCERTAE SEDIS 2						
INCERTAE SEDIS 3				Im	PP 414	Pl. 4, pic. 4
INCERTAE SEDIS 4				Im	PP 227	Pl. 4, pic. 10

Tab. 1: Fossil taxa flora from Resson tufa (Aube, France) as described by Fliche (1883) compare to the revision of this study.
M/ Mold, Im/ Imprint, W/ Wood.
Tab. 1 : Flore fossile du tuf de Resson (Aube, France) décrite par Fliche (1883) comparée à la présente révision. M/ Moulage, Im/ Empreinte, W/ Bois.

4.2 - MOSSES

Order: bryales fleisch 1904

Family: Muscineae Bisch

bryum hedw. 1801

Bryum pseudotriquetum (Hedw.) Gaertn., B. Mey. et Schern.

pl. 1, pics. 9-15

sample: pp 395

The fossil sample is characterized, amongst other things, by his tufts up to several centimetres tall (12-15 cm). The stems are brown-reddish. The leaves are ovate-lanceolate and entire, they are 2-3.5 mm long with a strong vein ending in the tip (pl. 1, pic. 14). An unistratose border of narrow cells is visible at the margin of the leaf. A thick nerve is usually shortly excurrent on this specimen. Most plants have leaves with a base that runs down onto the stem. Basal cells are rectangular.

The well preserved plant remains with brown-reddish stem, ovate-lanceolate leaves, strong nerve shortly excurrent and an unistratose border were reported to the species *Bryum pseudotriquetum*.

4.3 - FERNS AND HORSETAILS

4.3.1 - Samples PP 227, 389, 391, 399, 404, 406 and 111

Order: Polypodiales Link 1833

Family: Aspleniaceae Newman 1840

Asplenium L. 1753

Asplenium scolopendrium L. 1753 (syn: *Phillytis scolopendrium* L. Newman)

pl. 2, pics. 5 & 6

Eight samples with numerous undivided frond fragments of different sizes are present in the collection. The frond is simple, longer than wide with strap-shaped or lanceolate, heart-shaped base. The margin is entire and becomes slightly wavy as the frond ages. The primary vein is pinnate. Secondary veins are free and numerous, they arise at 60° to the midvein. Associated to sterile frond one fertile frond with sori is observed. Sori are characterized by lines along the vein, and arranged with an angle of 25-30 degrees and up to 50 degrees (pl. 2, pic. 6).

Fossil samples with long and simple frond longer than wide and entire margin are reported to *Asplenium scolopendrium,* a fern with long frond (20-60 cm). Populations of this species are relatively common and occasionally abundant in French Pleistocene tufas from Caours (Somme) and la Celle-sous-Moret (Seine-et-Marne) (Jolly-Saad *et al*., 2007).

4.3.2 - Sample PP 390

Order: Equisetales Dumort. 1829

Family: Equisetaceae ex DC. 1804

Equisetum L. 1753

Equisetum sp.

pl. 2, pics. 1-4

The specimen PP 390 was not identified in previous studies, it consists of very small fragments of rounded culms with a moderate diameter of 2-5 mm observed (pl. 2, pic. 2). These tubular moulds reflected articulated stems bearing regular whorls with 4-6 scars of non-preserved branches and ca.18-25 longitudinal striations (pl. 2, pic. 3). Some transverse sections show large hollow pits surrounded by a row of vallecular canals (air canals) which are arranged at the margin of the stem in the parenchymatous cortex (pl. 2, pic. 3) and carinal canals which are smaller and are not distinct on this sample.

To further identify the macroremains, the rootstock and basal stem characters of all herbaceous vascular plants was considered. The fossils are not typical of Cyperaceae or Poaceae, which are tufted, scaly stoloniferous, scaly narrow to stoutly rhizomatous with or without subterranean branching. Amongst the Liliaceae, leaves arise from a bulb or corm, not from the aerial stem. Members of the Juncaceae (rushes) have several clasping basal leaves around the culms but their removal reveals only a single abscission scar. The fossil sample showing tubular moulds with impressions of internal striations, nodes and a large central cavity in the stem was identified to represent a horsetail rhizom (*Equisetum*). The characters found in the fossil specimen, such as thin stems and thin numerous striations and a large pit in the middle of the stem indicate the species affiliation of *Equisetum sp*. (Coste, 1937).

4.4 - CONIFERS

Subclass: Pinidae Cronquist, Takht. & Zimmerm. (1966)

Order: cf. Cupressales Link. 1929 (Christenhusz *et al*., 2011)

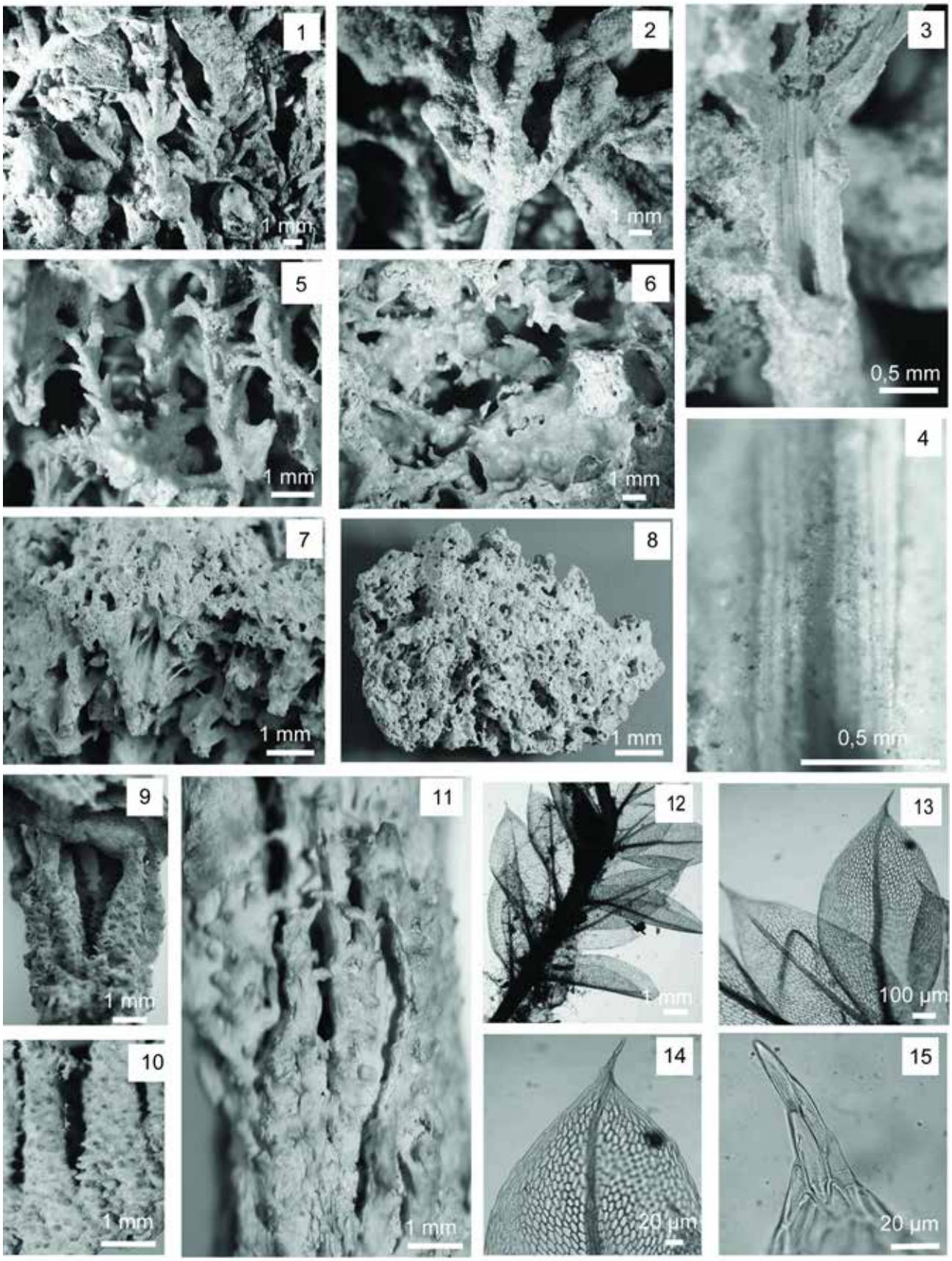
or Order: Pinales Gorozh. (1904): Pinaceae. Abietales Link, (1829), Abietaceae. Family 7. Pinaceae Spreng. (1830), nom. cons. T.: *Pinus* L. (Christenhusz *et al*., 2011)

Sample: pp 410

Note: The mould of the needles was lost during the study because of the delicate nature of tufa and its susceptibility to deformation that resulted in the loss of fossil structure integrity.

Only one needle fragment with a linear shape and parallel margins has been ientified. The mould preserved the lower face of the needles. The venation observed is hypodromous type with the midrib clearly visible and right. Apex and base of the needle are not preserved, the petiole is absent. Fragment is 19 mm length, and 2 mm width.

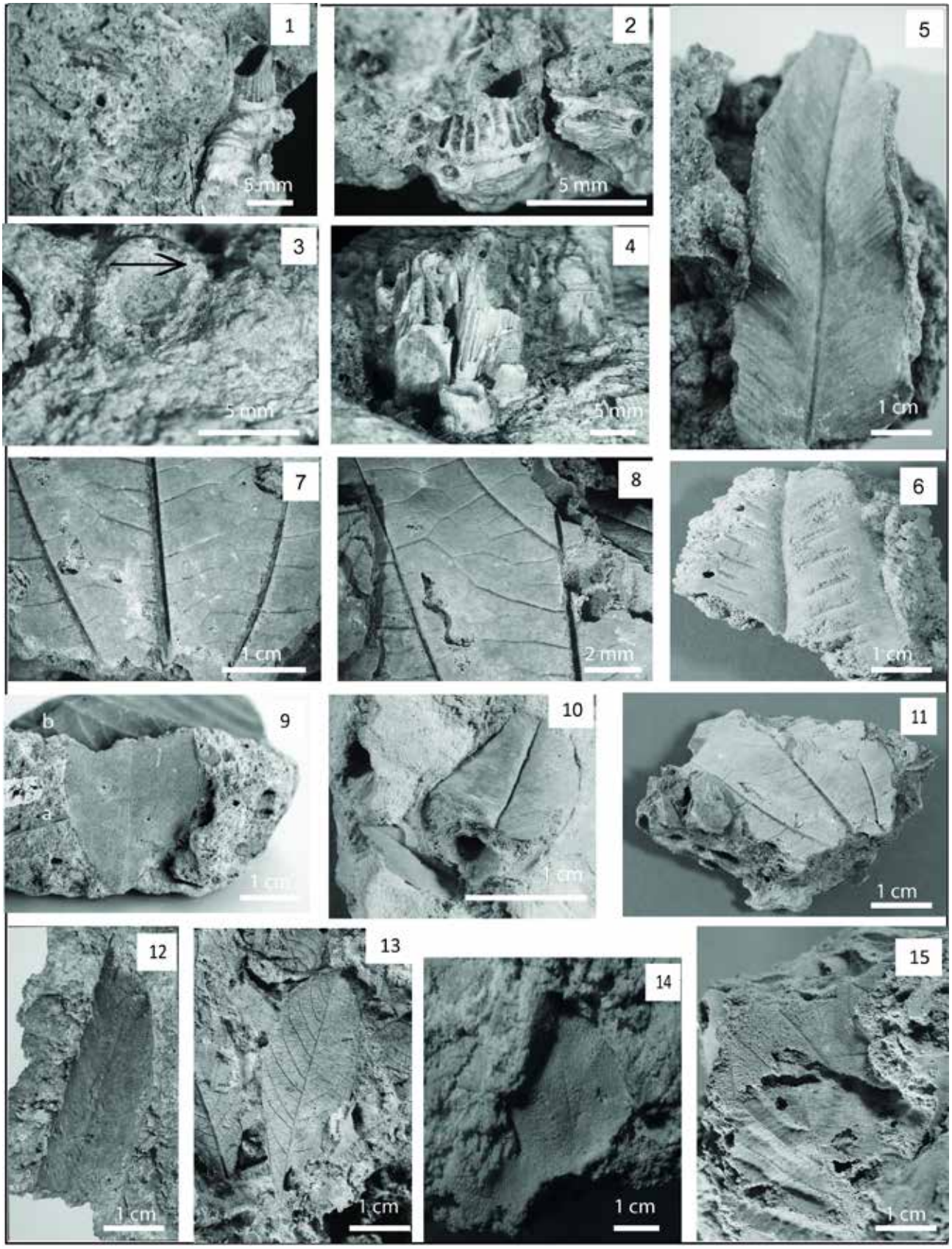
The fossil PP 410 is likely to be fragment of a conifer needle, while conifers were not described previously in this locality. A proper identification of conifer based on a single and badly preserved imprint is hardly possible, without apex and base. The size and shape of the needle is similar to *Abies* or *Taxus*. *Abies* needles are 15-30 mm long. Apex is emarginated or acuminated and the base is ended by a small bulb, the two features



Pl. 1: Characeae and Bryophytes.

1-4/ Characeae facies, Sample MR 5890, *Chara* cf. *C. vulgaris*, 1-2/ General view of branching organization, 3-4/ Microanatomical stem details, 5/ Sample MR 5432: unidentifiable Bryophytes, 6/ Sample PI 5433: unidentifiable Bryophytes, 7-8/ Unidentifiable Bryophytes, sample MR 5442, 9-15/ *Bryum pseudotriquetum* (Muscineae), sample PP 395, 9-15/ General view of calcified samples. 11-15/ Micro anatomical details of *Bryum pseudotriquetum* remains preserved in calcification.

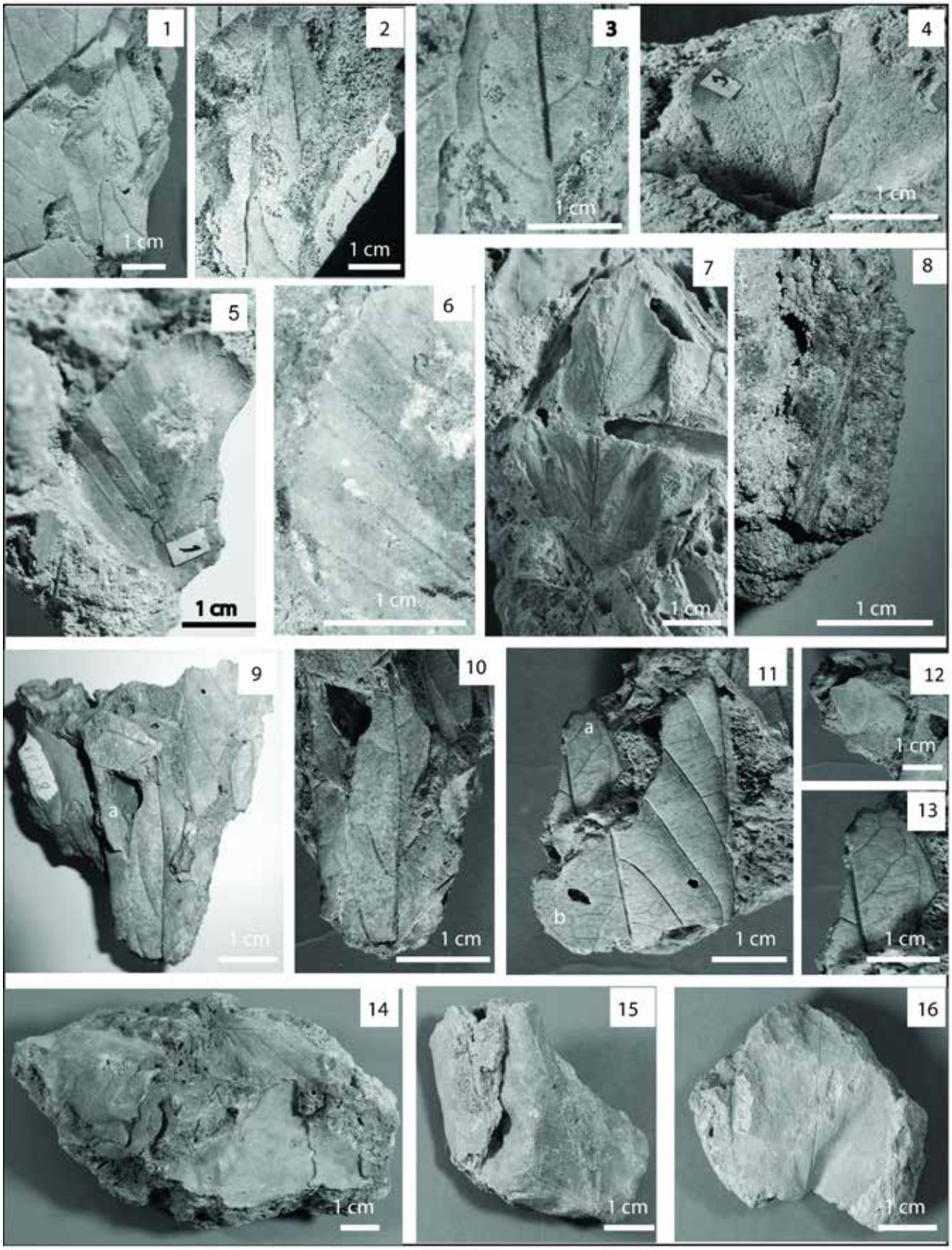
Pl. 1 : Characeae et Bryophytes. 1-4/ Faciès à Characeae, échantillon MR 5890, Chara cf. C. vulgaris, 1-2/ Vue générale de l'organisation vegetative, axe primaire et verticilles, 3-4/ Détails microanatomiques de la tige, 5/ Échantillon MR 5432: Bryophytes non identifiables, 6/ Sample PI 5433 : Bryophytes non identifiables, 7-8/ Bryophytes non identifiables, échantillon MR 5442, 9-15/ Bryum pseudotriquetum (Muscineae), échantillon PP 395, 9-15/ Vue générale de l'échantillon carbonaté. 11-15/ Détails micro anatomiques de Bryum pseudotriquetum conservé dans la calcification.



Pl. 2: Equisetaceae and Dicotyledons.

1-4/ *Equisetum* facies, Sample PP 390, 1-2/ *Equisetum* rhizome and stem, 2/ *Equisetum* sp. (Equisetaceae), detail view, nodes with a grooved stem, 2/ Tranverse section with large pit surround by a row of vallecular canals (arrow), 4/ *Equisetum* sp. (Equisetaceae), tuft, general view, 5-6/ *Asplenium scolopendrium* (Aspleniaceae), samples PP 404 and PP 111, 7-8-11/ *Acer* cf. *A. pseudoplatanus* L. (Sapindaceae), sample PP 136, 9/ *Salix* cf. *S. caprea* (Salicaceae), sample PP 145a, 10/ *Buxus sempervirens* L. (Buxaceae), sample PP 296, 12/ *Salix sp.* (Salicaceae), sample PP 396, 13/ *Salix* cf. *S. cinerea* (Salicaceae), sample PP 110, 14/ *Acer* cf. *A. campestre* (Sapindaceae), sample PP 402, 15/ *Corylus avellana* L. (Betulaceae), sample PP 145.

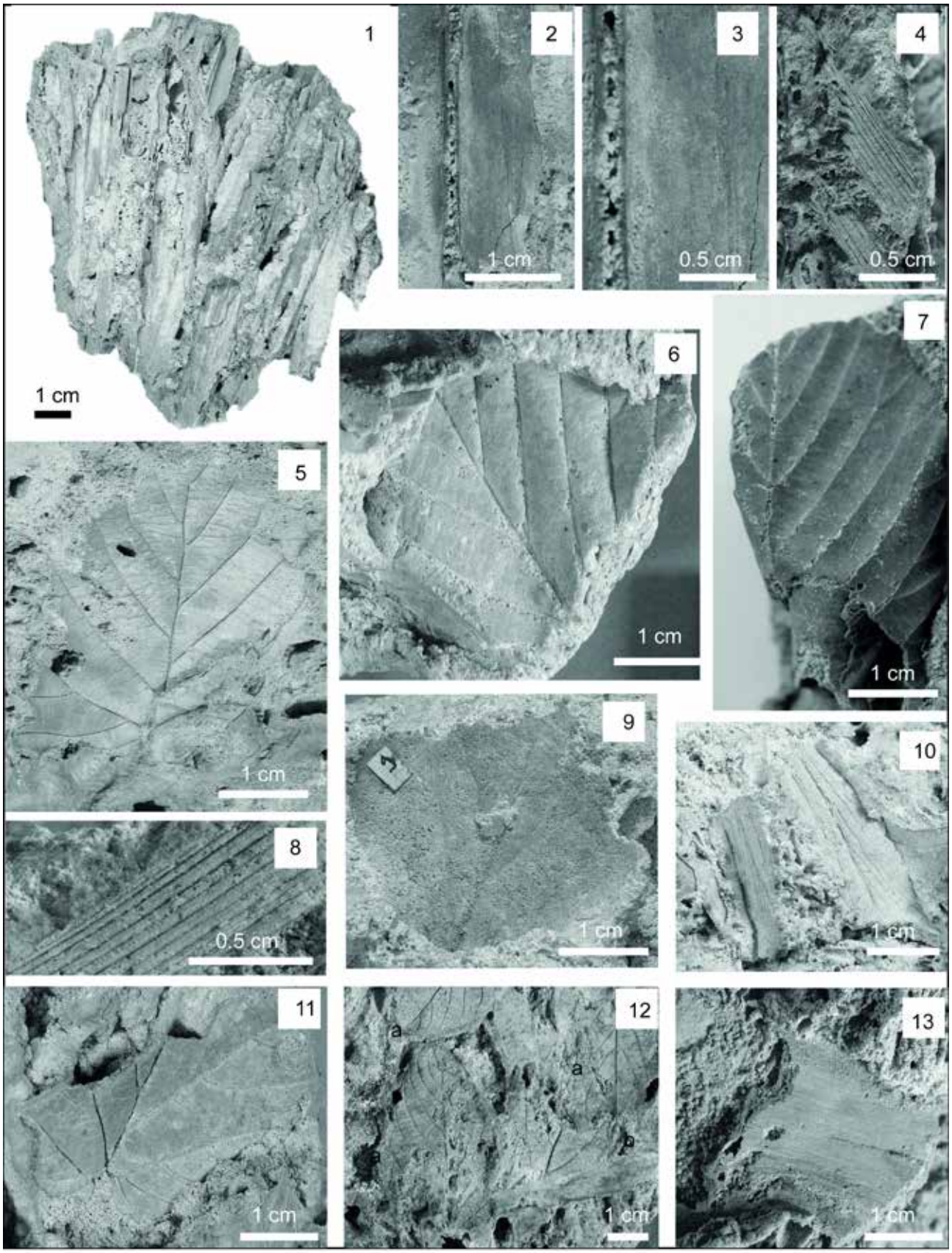
Pl. 2 : Équisetaceae et Dicotyledons. 1-4/ Faciès à Equisetum, échantillon Sample PP 390, 1-2/ Rhizome et tige d'Equisetum, 2/ Equisetum sp. (Equisetaceae), detail de la tige et des noeuds, 2/ Section tranversale montrant une large cavité entourée d'une rangée de canaux valléculaires (flèche), 4/ Equisetum sp. (Equisetaceae), vue générale d'une touffe, 5-6/ Asplenium scolopendrium (Aspleniaceae), échantillons PP 404 and PP 111, 7-8-11/ Acer cf. A. pseudoplatanus L. (Sapindaceae), échantillon PP 136, 9/ Salix cf. S. caprea (Salicaceae), échantillon PP 145a, 10/ Buxus sempervirens L. (Buxaceae), échantillon PP 296, 12/ Salix sp. (Salicaceae), échantillon PP 396, 13/ Salix cf. S. cinerea (Salicaceae), échantillon PP 110, 14/ Acer cf. A. campestre (Sapindaceae), échantillon PP 402, 15/ Corylus avellana L. (Betulaceae), échantillon PP 145.



Pl. 3: Dicotyledons.

1-3/ *Clematis* cf. *C.vitalba* (Ranunculaceae), sample PP 178, 1-2/ General view, 3/ Vein detail. 4/ *Populus/Betula* (Betulaceae), sample PP 227b, 5-6/ *Fagus sylvatica* L. (Fagacae), sample PP 398, 5/ General view of the limb, 6/ Detail of the leaf margin, 7/ *Hedera helix* L. (Araliaceae), samples BR 1084 and PP 294, 8/ *Alnus* cf. *A. glutinosa* (L.) Gaertn. (Betulaceae) fruit, sample MR 9523, 9/ *Euonymus europeus* L. (Celastraceae), sample PP 138b, 10/ *Euonymus europeus* L. (Celastraceae), leaf detail, sample PP 138, 11a-13/ Incertae sedis, sample PP 138, 11 général view and 13 detail of the unidentified leave, 11b/ *Sorbus aria* L. (Rosaceae), sample PP 138b, 14/ *Acer* sp. (Sapindaceae), sample PP 402, 15-16/ *Acer* sp., sample PP 410.

Pl. 3 : Dicotylédones. 1-3/ Clematis cf. C. vitalba (Ranunculaceae), échantillon PP 178, 1-2/ Vue générale, 3/ Detail de la nervation. 4/ Populus/ Betula (Betulaceae), échantillon PP 227b, 5-6/ Fagus sylvatica L. (Fagacae), échantillon PP 398, 5/ Vue générale du limbe, 6/ Detail de la marge du limbe, 7/ Hedera helix L. (Araliaceae), échantillon BR 1084 and PP 294, 8/ Alnus cf. A. glutinosa (L.) Gaertn. (Betulaceae) fruit, échantillon MR 9523, 9/ Euonymus europeus L. (Celastraceae), échantillon PP 138b, 10/ Euonymus europeus L. (Celastraceae), detail de la feuille, sample PP 138, 11a-13/ Incertae sedis, échantillon PP 138, 11 vue générale et 13 détail d'une feuille non identifiée, 11b/ Sorbus aria L. (Rosaceae), échantillon PP 138b, 14/ Acer sp. (Sapindaceae), échantillon PP 402, 15-16/ Acer sp., échantillon PP 410.



Pl. 4: Monocotyledones and Dicotyledons.

1-3/ aff. *Phragmites* sp. (Poaceae), sample PP 414, 1/ Tuft, general view. 2-3/ Detail of leaf veination showing parallel major linear veins with midrib,. 4/ Unidentified stem epidermis, sample PP 414, 5/ *Corylus avellana* (Corylaceae) leaf, sample PP 413, 6/ *Alnus* cf. *A. glutinosa* (Betulaceae) leaf, sample PP 413, 7/ *Sorbus aria L.* (Rosaceae), sample PP 145, 8/ Epidermis unidentifiable, sample PP 414, 9/ *Betula/Populus* sp. (Betulaceae), sample PP 227, 10/ Incertae sedis, sample PP 227, 11/ *Acer* sp. (Tiliaceae), fossil leaf, sample PP 413, 12a/ *Salix* cf. *S. caprea*, 12b/ unidentifiable Monocotyledons leaf, sample PP 110, 13/ unidentifiable Monocotyledons leaf, sample BR 1084.

Pl. 4 : Monocotyledones et Dicotyledons. 1-3/ aff. Phragmites sp. (Poaceae), échantillon PP 414, 1/ Tuft, general view. 2-3/ Detail de la nervation d'une feuille avec nervation paralèlle et nervation centrale bien identifiée. 4/ Unidentified stem epidermis, échantillon PP 414, 5/ feuille de Corylus avellana L. (Corylaceae), échantillon PP 413, 6/ feuille d'Alnus cf. A. glutinosa (Betulaceae), échantillon PP 413, 7/ Sorbus aria L. (Rosaceae), échantillon PP 145, 8/ Épiderme non identifiable, échantillon PP 414, 9/ Betula/Populus sp. (Betulaceae), échantillon PP 227, 10/ Incertae sedis, échantillon PP 227, 11/ feuille fossile d'Acer sp. (Tiliaceae), échantillon PP 413, 12a/ Salix cf. S. caprea, 12b/ Fragment de feuille de Monocotylédons non identifiable, échantillon PP 110, 13/ Fragment de feuille de Monocotylédons non identifiable, échantillon BR 1084.

cannot be evaluated on this fossil sample only partly preserved.,*Taxus* has different anatomical features which are also indistinct on this sample; the apex is acute and the base is continued along the axis. On the basis of the morphological and anatomical characters, it is not possible to identify this taxon. However, from an ecological point of view the presence of *Taxus* is more likely than the presence of *Abies*. It is commonly assumed on the basis of the modern distribution that *A. alba* is the most widespread species, it prefers cool and rather moist habitats (Jacomon, 2001; Ellenberg, 2009). Other *Abies* are more limited in their distribution. The Mediterranean species of *Abies* are most likely relicts of a more diverse conifer flora in Europa which started to become depleted by ice ages during the Pleistocene (Farjon & Filer, 2013). *Taxus baccata* sensu stricto is classified as an European temperate species by Preston & Hill (1997). It exhibits a large ecological amplitude (Jacamon, 2001). In mainland Europe, ecological barriers limiting its distribution are: low temperatures in the north, severe continental climate in the Baltic countries and Poland in the east, long droughts in Turkey to the south-east, and drought and high temperatures in North Africa (Thomas & Polvart, 2003). Near these climatic extremes, *T. baccata* becomes more restricted to moist niches.

4.5 - MONOCOTS

4.5.1 - Samples PP 110, 395, 396, 398, 411, BR 1084, MR 5445, 5447, 9526

The different paralleli-veined carbonated structures representing the macroplant are reported to incomplete Monocotyledonous angiosperms. These fossils are herbaceous in their small size and morphology.

Unidentifiable Monocotyledons

pl. 4, pics. 12b & 13

Leaf remains consisting of linear, parallel-margined varying from 1-3 cm in width are poorly preserved leaf fragments having a characteristic parallel venation.

The parallel venation extends longitudinally through the lamina ressembling the leaves of monocotyledons. Since inflorescences are lacking, it is not possible to determine with precision the species, genus, family or order with certainty.

4.5.2 - Sample PP 414

Order: Cyperales (Poales APG III, 2009)

Family: Poaceae (r.br.) Barnh. 1895

Genus: *Phragmites* Adans 1763

Species: *Phragmites* sp.

pl. 4, pic. 1-3

Leaves are simple, linear in shape with parallel margin. Major linear veins are parallel, irregularly spaced, with 5-10 minor linear veins running parallel and evenly spaced in between each major linear vein. No cross veins are observed. The midrib is well distinct.

The fossil sample is characterized by parallel linear veins, the presence of a midrib and no cross veins. These features are similar to the descriptions of modern *Phragmites* leaves suggesting that this morphotype is a member of the genus *Phragmites*. However, reproductive material was not found and it is not possible to classify this morphotype to the species level.

4.6 - ANGIOSPERMS DICOTYLEDONS

4.6.1 - Samples PP 398 and 227

Eudicots

Order: Fagales Engl. 1892 or Malpighiales Mart. 1835

Family: Betulaceae Gray 1821 or Salicaceae Mirb. 1815

Betula L. 1753 or *Populus* L. 1753

pl 4, pic. 9

The samples show microphyllous leaf imprints, the petiole is not preserved. Apex is acute and the base is partly hidden in the sediment. Lamina margin is indistinct. Primary venation is pinnate and straight. Secondary venation (n=3 distinct on the fossil) are craspedodromous with irregular spacing. They emerge at acute angle from the midvein 60° at the base and to 30° near the apex with straight courses. Tertiary veins slightly marked, opposite percurrent between adjacent secondary veins in parallel paths without branching. They are straight. Angles between primary vein and the secondary veins are 80-90°. Quaternary venation is indistinct.

The sample PP 398 with a more or less triangular shape has similarities with the genus *Betula and Populus. Populus* is basally subactinodromous. The veins are pinnate distally and secondary brochidodromous or semicraspedodromous. All these features are not visible on the specimen. The bad preservation of the studied specimen makes difficult to detect the category and the number of higher-order veins and so a more precise identification. It is thus reported to *Betula/Populus*.

4.6.2 - Samples MR 9523 and PP 413

Order: Fagales Engl. 1892

Family: Betulaceae Gray 1821

Alnus Miller 1754

Alnus sp. cf. *A. glutinosa* (L.) J. Gaertn. 1790

pl. 3, pic. 8 & pl. 4, pic. 6

The fossil specimen MR 9523 is a f**ruit** (pl. 3, pic. 8)**,** a woody cone-like with peduncle 1 cm long. With an egg-shaped, it contains many small winged nutlets. The second specimen, PP 413, is a little fragment of leaf (2,5 cm high and 4 cm wide) with pinnate and straight primary vein of moderate thickness. Secondary venation are simple craspedodromous, preserving 4 to 5 pairs straight veins. Secondary veins diverge from midvein at an angle of 60°-80° near leaf base, 45°-60°. More precise lower venation features are indistinct on the fossil sample.

The woody cone is similar to *Alnus cf. A. glutinosa* (L.) J. Gaertn. 1790. Leaf fragment has similarities with *Corylus* and *Alnus,* with higher angles between primary and secondary venation. It is also reported to *Alnus.*

4.6.3 - Samples PP 110 and 145

Order: Malpighiales Mart. 1835, APG III 2009 (ex Salicales Lindl. 1833)

Family: Salicaceae Mirb. 1815

Salix L. 1753

Salix cf. *S. cinerea* and *S.* cf. *caprea*

pl. 2, pic. 9 & 13, pl. 4, pic. 12a

Leaves or leaf fragments are simple oblong-ovate and symmetrical. Petiole and apex are not preserved. Lamina displays an entire margin. The Base is cuneate and symmetric. Primary venation is pinnate, well marked and straight and thin. Secondary veins are brochidodromous, spacing 0.7-1.0mm, without intercalary veins. They emerge from the midvein at acute angle 60° at the base to 40° towards the apex. Tertiary veins cross between adjacent secondary veins in parallel paths with sometimes a furcating pathway, their courses are sinuous. Quaternary veins are not distinct.

The fossil specimen is reported to *Salix*. Salicaceae is a family that unites all potential difficulties for diagnosis. Hybrid and foliar polymorphism are very frequent in the genus, which makes the discrimination between species difficult. However, the two morphotypes from Resson tufa are similar to *Salix* cf. *S cinerea* for the narrowest leaf, sample PP 110 and the wider to *S.* cf. *Caprea,* samples PP 145 and PP 110.

4.6.4 - Sample PP 396

Salix sp.

pl. 2, pic. 12

Lamina fragment linear is about 2.5 cm long and 1 cm wide. Petiole, base and apex are not preserved. Margin show distinctly shaped teeth with rounded sinus. Primary venation is pinnate and straight. Secondary veins show regular spacing of about 0.5mm. Tertiary and quaternary veins are indistinct.

The characteristics of this specimen (PP 396) are not distinctive enough to assign the fossil to a particular species**.** It is reported to the genus *Salix*.

4.6.5 - Samples PP 136, 402, 409 and 410a

Samples: PP 136, PP 409 (two fragments), PP 402 (1 fragment), PP 410a: short fragment of leaf.

Order: Sapindales Juss. ex Bercht & J. Presl 1820

Family: Sapindaceae Juss. 1789

Acer L.

Acer cf. *A. pseudoplatanus* L.

pl. 2, pic. 7, 8 & 11

The fossil samples are macrophyll fragments of simple lamina. The base, apex and margin are indistinct. Base angle is wide and obtuse. Secondary veins are craspedodromous, arising at 27-45° from the main veins with straight courses. They are spacing irregularly and increasing towards the base. Intersecondary veins are present. Tertiary veins mixed opposite/alternate percurrent with sinuous course. They have an angle to primary vein obtuse. Higher-order veins not preserved.

This taxon is only represented by four highly fragmented leaves. The specimens have similarities with *Acer* cf. *A. pseudoplatanus*.

4.6.6 - Sample PP 402

Acer cf. *A. campestre*

pl. 2, pic. 14

Microphyll is incomplete with one probably apical lobe of a probably simple, palmately lobed leaf. Apex shape is convex with an angle obtuse forming simple rounded apices. The venation of the this specimen is indistinct.

The fragment of foliar imprint has an affinity with *Acer campestre* L. and *Acer Monspessulanum* but due to the rounded apical the fossil sample is more similar to *A.* cf. *Acer campestre*.

4.6.7 - Sample: pp 136 and 178

Order: Ranunculales Juss. Ex Bercht & J. Presl. 1820

Family: Ranunculaceae Juss. 1789

Clematis L. 1753

Clematis cf. *C. vitalba*

pl. 3, pic. 1-3

Incomplete and simple microphyll, base and petiole are absent. The margin is entire. The primary vein is thick, the upper part of the leaf shows four pairs of brochidodromous secondary veins which are slightly arched or straight. The secondary veins are thinner than the primary veins. Tertiary veins alternate percurrent. Quaternary veins are indistinct.

The fragment corresponds to the upper portion of a leaf. It bears alternate or subopposite, remote secondaries veins which arch by a large curve far within the margin and have provide with two distinct series of large loops outside. These features are similar to the extant leaf of the genus *Clematis.* Among the different species it is very similar with *Clematis* cf. *C. vitalba,* a species with a very thick midvein clearly marked on the fossil sample.

4.6.8 - Sample: PP 138

Order: Celastrales Link 1829

Family: Celastraceae R. Br 1814

Euonymus L. 1753

Euonymus europeus L. 1753

pl. 3, pic. 9-10

The microphyll is oblong-ovate, symmetrical, about 2 cm long and 1 cm wide. Petiole and apex are not preserved. Margin is entire. Primary venation is pinnate and straight hile secondary veins (n=3) are brochidodromous, spacing 0.5-0.6mm, without intercalary veins. Emerging at acute angle from the midvein 28-30°. Tertiary veins slightly marked. Quaternary veins are not distinct.

The fossil features are similar to *Euonymus europeus* L.

4.6.9 - Samples PP178 and 410

Order: Scrofulariales Juss. 1789

Family: Oleaceae Hoffmanns & Link 1809

Fraxinus L. 1753

Fraxinus cf. *F. excelsior*

Two leaflets of *Fraxinus* are recognized. The most complete leaf is 4.5 cm long and 2.5 cm wide. Margins are unlobed, crenate/serrate. Apices are acuminate. Primary venation framework is pinnate and straight in course. Secondary venation is scalloped semicraspedodromous an angle to the midvein of 30°. Secondary veins are decurrent, irregularly spaced, with inconsistent angles. A few inter secondary veins are present. Lower order venation is indistinct.

The specimen is poorly preserved and shows only higher-order venation resembling *Fraxinus* cf. *F. excelsior.*

4.6.10 - Samples PP 410b and 294

Order: Apiales Nakai 1930

Family: Araliaceae Juss. 1789

Hedera L. 1753

Hedera cf. *H. helix*

pl. 3, pic. 7 & 12

The species is represented by a small piece of leaf, from which base and apex are absent. Venation actinodromous with three basal or suprabasal primary veins ramified and anastomosed. The three primary vein runs straight. Tertiary venation is sinuous and forked.

The sample PP 410b is very poorly preserved and is only known by a sole and greatly fragmented specimen. The shape of the limb and the venation type suggest affinities with the leaves of fertile stem of Araliaceae. The species is frequent in humid undergrowth. The site has not yielded the 3-5 lobed leaves of sterile stems characteristic of the species.

4.6.11 - Samples pp 145 and 413

Order: Fagales Engl. 1892

Family: Betulaceae Gray 1821

Corylus L. 1753

Corylus avellana L. 1753

pl. 2, pic. 15 & pl. 4, pic. 5

Leaves are simple, ovate with cordate symmetrical base, about 6 cm long and 4 cm wide. Leave bases are symmetrical cordate rounded and apex acuminate. The lamina displays serrate margin. Primary venation is pinnate, well-marked and straight. Secondary venation (n=6) is craspedodromous with compound agrophic veins basally present. They emerge at acute angle from the midvein (70° at the base and 30° near apex), their courses is straight.. Spacings between secondaries are irregular and gently curving toward the apex. Tertiary veins are opposite or mixed opposite/alternate percurrent between adjacent secondary veins; they are organized in parallel paths without branching. They are straight or with arches forms. Angle with the secondary veins is 90°. Quaternary venation is indistinct.

Fossil leaves on PP 413 and PP 402 fossil leaves were previously identified as *Corylus avellana*, because they are virtually indistinguishable from those of the extant genus. They differ from *Rubus* and more particularly from *Rubus ulmifolia* which has less spaced tertiary veins, more common and much more pronounced dichotomy of secondary veins.

In the specimen pp 395, few little branches are perfectly preserved in tufas. In transverse section, the wood is diffuse-porous. Pores are in rather wide radial groups. In tangential section rays are composed of 1-3 seriate rays; vessels have scalariform perforations and spiral thickenings; microanatomical wood features thus indicate *Corylus avellana* wood. This taxon is locally present and it is one of the main components of the flora from the tufa of Resson.

4.6.12 - Sample PP 398

Family: Fagaceae Dumort. 1829

Fagus L. 1753

Fagus sylvatica L.

pl. 3, pics. 5-6

An unique leaf was described by Fliche (1883).

The Leave is oblong-ovate, symmetrical, about 3.5cm long and 2cm wide. The petiole and apex are not preserved. The base is rounded. Margin is not well preserved, not entire. Primary venation, is partially visible, with thin pinnate that seems straight. Secondary veins (n=12) are craspedodromous with large and regular spacing. They emerge from the midvein at acute angle from 44° at the base and 25-30° near apex with straight courses. Tertiary and quaternary veins are not distinct.

The specimen is similar to the extant leaf of *Fagus sylvatica* L. and *Carpinus betulus*, with a margin not serrate and large spacing between secondary veins, the specimen appears more similar to the extant leaf of *Fagus sylvatica* L.

4.6.13 - Samples PP 145, 227, 410 and BR 1084

Only few small fragments for PP410.

Order: Rosales Perleb 1826

Family: Rosaceae Juss. 1789

Sorbus L. 1753

Sorbus aria (L.) Crantz 1763

pl. 4, pic. 7 & pl. 3, pic 11b

Leaves are simple, incomplete and oval in shape. Lamina are symmetrical. Apex and base are not distinct. Margin is double-serrate, three teeth per cm, tooth shape straight for the apical and concave for the basal side, sinus rounded. Primary venation is pinnate and straight. Secondary venation is craspedodromous with presence of agrophic veins (angles 30°). Intersecondary veins absent. The course of secondary veins is straight and slightly curved towards the margin. Secondary vein angle acute (30°) to primary veins Tertiary venation clearly distinct, curved with an angle of 6° to secondary veins.

The simple leave with regular craspedodromous pattern and regular percurrent tertiary veins well marked is similar to *Sorbus aria*.

4.6.14 - Sample BR 1084

Order: Scrofulariales Juss. 1789

Family: Oleaceae Hoffmanns & Link 1809

Ligustrum L. *1753*

Ligustrum vulgare L. 1753

The fossil specimen is a fragment of leaf simple, microphyll, elliptic in shape and symmetrical. Margin is entire, the petiole is absent. Apex acuminate with acute angle, venation pinnate, straight and wide. Secondary venation are brochidodromous, veins are not numerous (n= 4-5), regularly spaced and almost indistinguishable. This imprint has close affinity with *Ligustrum type vulgare a* deciduous to semi-evergreen shrub found as a native in hedgerows, woodland and scrub, preferring well-drained, calcareous or base-rich soils. The species is very common on tufa.

4.6.15 - Sample PP 410 & 296

Order: Buxales Takht. ex. Reveal 1996

Family: Buxaceae Dumort. 1822

Buxus L. 1753

Buxus sempervirens (syn. *Buxus arborescens* (L.) Mill, *Buxus colchica* Pojark., *Buxus hyrcana* Pojark.)

pl. 2, pic. 10

Fragment of microphyll, more or less oval in shape with an entire margin. Apex is rounded, texture subcoriaceous. The primary venation is pinnate and coarse. Secondary veins are uniform and brochidodromous with numerous, nearly parallel, partly ramified veins which are thin and not protruding.

The leaf is attributed to the *Buxus sempervirens* L. *Buxu*s is a common and widespread species in numerous Late Pleistocene floras.

4.6.16 - Sample PI 5891

Incertae sedis

The sample PI 5891 is probably a large colony of the filamentous Algae. The algae are regularly calcified forming spongy travertine. This organism is characterized by tubular and linear filaments without branches. Dissolution of the mineral with acid did not allow to highlight the organism. We refrain here from a definite assignment to this species.

4.6.17 - Sample PP 138

Incertae sedis 1

pl. 3, pics. 11a-13

Microphyll**,** broadly oval in its general outline, with a rounded apex, the base of the specimen is indistinct. Length about 1.5 cm; maximum width, in the middle part of the leaf, about 1 cm. Margins are entire, evenly rounded. Midrib stout. Secondaries thin, three or four alternate pairs, diverging from the midrib at angles of about 39° to 40°, curving upward almost immediately in a broad, sweeping curve, becoming subparallel with the lateral margins, along which they arch camptodromely. Tertiaries thin, not closely set, subparallel, mostly percurrent at right angles to the midrib.

The fossil leaf could not be identified.

4.6.18 - Sample PP 227

Incertae sedis 2

pl. 4, pic. 10

A very tiny and incomplete fragment of leaf, oblong in outline, 7 mm long and 4 mm broad. Apex and base are not preserved, margin is entire. The nervation is dichotomous at the ends of the veins and resemble to petal or sepal.

This fragment affinity cannot be specified.

5 - DISCUSSION: RECONSTRUCTION OF PALEOVEGETATION

5.1 - FLORISTIC ELEMENTS

The revision of Resson macroflora provides a new list of species (tab. 1) including Characeae (n=1), Bryophytes (n=1), Pteridophytes (1), Monocotyledonous Angiosperms (n=3) and Dicotyledonous Angiosperms (n=22). The list established by Fliche in the 1880s (tab. 1) has been enriched by the determination of new families, new species and new genera, namely *Fraxinus* cf. *F. excelsior* L., cf. *Taxus baccata* L*., Equisetum* sp.

Conversely, it appears that several taxa previously determined and listed by Fliche (1883) are absent from the revision (tab. 1). Specifically, a first group of Monocotyledons including *Scirpus* sp., *Carex glauca* Scop., *C. maxima* Scop., *C. flava* L., cannot be identified on the basis of their anatomical epidermis. Some other species (*Cerasus padus* D.G., *Rubus fruticosus* L., *Rhamnus frangula* L., *Acer platanoïdes* L., *Acer opulifolium* Vill., *Betula alba* L*., Betula alba* L., var. *papyrifera*, Spach, *Populus tremula* L., *Alnus incana*, DC. ?*Populus canescens* Sm., *Salix grandifolia* Sér.?, *Salix nigricans* Sm. ?, *Cornus sanguinea* L., *Juglans regia* L. and ?*Tilia platyphylla* Scop. are lacking in the collection preserved at the *Musée de Troyes*. Some of them are referred to as “Chertier collection” in Fliche (1883). Jules-Louis Chertier was a local savant who collected most of Resson palaeontological specimens. It is unfortunately possible that part of the collection of leaf prints from Resson remained private and is now lost.

5.2 - ECOLOGICAL AND PHYTOSOCIOLOGICAL CONSIDERATIONS

Macrofossil investigations on the terrestrial carbonates of Resson yielded a rare data set for palaeoenvironment reconstruction of the Last Interglacial, a warm stage without human impact on climate and vegetation and, at the same time,. Importantly, it represents the first and unique descriptions of large and diversified fossil leaf

associations from the Late Pleistocene from northern France.

The diversity and heterogeneity of the fossil flora have extant representatives in the vegetation serving as a reference for their ecological characteristics and suggest that these assemblages reflect azonal and zonal vegetation (zonal vegetation is only subject to (regional) climatic conditions while azonal vegetation is constrained by local conditions as well as the presence of a watercourse). Three relatively specific plant communities can be described: they differ in their species compositions (depending on specific ecological conditions of biotopes) and merge into one another at their ecotones.

Aquatic paleohabitats are represented by a mass accumulation of Charophytes remains. The collection was related, in former studies, to *Chara* cf. *vulgaris* L. (syn. *C. foetida* A. Br. 1864) and *Chara hispida,* L. var. *brachyphyla* (Fliche, 1883).

In phytosociological terms, a characteristic feature of charophyte communities is the simple community structure, usually with only one dominant species. Charophytes carpets are essentially composed of *Chara* species, generally considered to be the ancestral group within Chlorophyta that gave rise to the lands plants (Karol *et al*., 2001; McCourt *et al*., 2004). The biotope of Charophytes is generally undisturbed ground in clear, oxygenated water bodies where transport of plant debris probably played, if at all, a minor role. They are among the first macrophytes to colonize a water body after major perturbations (Corillion, 1957, 1975; Crawford, 1977; Moore, 1986; Bailly & Schaefer, 2010). *Chara* grows in alkaline habitats with a range of concentration between 55 to 200mg/l CaCO3 (Schneider *et al*., 2015).

Open conditions are also indicated by some moss species occuring in tufts and patches up to several centimetres tall (4-12 cm) and which play an important role in the deposition and construction of tufa deposits. The identified species, *Bryum pseudotriticum* (Hedw.) G. Gaertn., B. Mey. & Scherb. is an abundant *Bryum* species in marshes, fens, and foodplains. It also occurs in damp soil near lakes, in dune slacks, and on wet rocks on cliffs. *Bryum pseudotriquetrum* prefers a rather moister substrate and grows along the margins of streams. Unfortunately, other moss specimens with different morphological incrustation are too small for dissolution and could not be identified.

The second plant community, bordering the aquatic habitats, is characterized by some hygrophytes, mainly grasses and horsetails, which permanently occupy waterlogged substrates. Ecologically, all species of horsetails are considered mesophytes or hygrophytes. *Equisetum* species prefer calcareous soils and frequently colonize substrat newly formed. *Equisetum* grows in a wide variety of aquatic, semi-aquatic or humid habitats like ditches, small ponds and sheltered rivers. It tolerates a remarkable range of water and substrate pH, nutrient levels, substrate type and water depth, and is often a pioneer species in freshwater successions. Adjacent to the stream, an assemblage of abundant Monocots, *Phragmites* sp. and other unidentifiable Monocotyledon Angiosperms are described.

Some foliar imprints from woodland species are representative of wet soils in temperate riparian forests with a dominance of deciduous elements in the surrounding area. Mesophytic elements, such as *Alnus glutinosa*, *Acer* sp., *Fraxinus excelsior*, *Betul*a sp., and an abundant *Asplenium scolopendrium* occupied open moist habitats but did not tolerate waterlogged conditions.

In the drained areas, a temperate deciduous forest was mainly composed of the *Fagus sylvatica, Corylus avellana* and *Taxus.* Beech, the diagnostic species for Fagion *sylvaticae* alliance (Luquet, 1926), is a very competitive oceanic and sub-oceanic species with the need of 800-1000 mm precipitation and high atmospheric humidity. It prefers moist, well-aerated, often calcific and humus and mineral rich soils but avoids waterlogged as well as dry soil conditions. It is sensitive to drought and late frost. *Taxus* often associated with *Fagus* has the same niche in its natural distribution it is also mainly confined to soils on limestone and other types of well-drained, base-rich soils. *Corylus* is represented with abundant leaf imprints and some little stems which are perfectly preserved in the tufa deposits. *Corylus* is a deciduous suckering shrub of dry to wet, calcareous to mildly acidic soils, but favouring moist, base-rich conditions (Jacamon, 2001). Hazel tree is locally present in the sampling area and one of the main components of the local flora from Resson.

Tree species are accompanied by diverse shrubs (*Ligustrum vulgare L.*, *Euonymus europeus* L., *Buxus sempervirens* L., *Sorbus aria* (L.) Crantz, the lianas *Clematis vitalba* and *Hedera helix and s*mall to medium-sized deciduous and mesophilous trees or shrubs that grow up to 5-15 m tall, in semi-shade habitats, open deciduous woodlands or scrublands. *Sorbus aria* (L.) Crantz, is also characteristic of thermophilous-basiphytic mixed beech forest on shallow calcareous soils on steep slopes and at relatively dry and warm sites, commonly with *Tilia* sp., *Carpinus betulus* and *Quercus* sp., in the shrub layer with *Ligustrum vulgare* and *Cornus mas* (Jacamon, 2001).

Macroremain data from Resson point that the palaeovegation has great similarities with the extant vegetation found in the vicinity of the area but differs with the presence of *Buxus* and *Taxus* which are characteristics of Middle to late Pleistocene, and *Juglans* (this last taxa is reported by Fliche in 1883 but not revised in this work). *Buxus* is considered as a thermophilous (sub-) mediterranean but this species is actually widespread with a wide ecological niche and shows an unique and well-known set of plant traits which demonstrate a great adaptability to changing climate, light, soil and community structure, especially with respect to resilience to frost conditions (Hormaetxe *et al*., 2004) and determines its diffusion during past and future changes of climate and habitat. It is today absent in vast areas where suitable habitats are present. It shows a centre of continuity, abundance and frequency

in the Pyrenees, Southern France, French Prealps, central France and all around the Jura Monts. Exiguous stands are located in Britain, Belgium, Luxembourg, Germany, Sardinia, Montenegro and southern European Peninsulas (Iberian, Italian, and Balkan) (Jacomon, 2001). Then, the presence of *Taxus* implies wetter conditions during the Last Interglacial than today.

5.3 - COMPARISON WITH SELECTED EUROPEAN MACROFOSSIL AND MICROFOSSIL RECORDS

In Northern France, there are only few tufa or travertine sites with preserved palaeofloras in contrast to Southern France where numerous Pleistocene and Holocene tufas exist (Boulay, 1887; Magnin *et al.*, 1990; Ambert *et al*., 1992, 1995; Mlakar *et al*., 1999; Ali *et al*., 2002, 2003a, b, 2014; Hoffmann, 2006; Ollivier *et al*., 2006; Roiron *et al.,* 2006; Bourel *et al*., 2016). Few of them are fossiliferous and most of them are Holocene. The travertine of Millau (SW of France) is the oldest Quaternary tufas dated up to c.a. 300,000 years located in the Causses Basin that yields diverse plant megaremains assigned to cones of conifers such as *Pinus* with leaves of *Acer*, *Corylus* and *Salix* (Ambert *et al*., 1992; Vernet *et al*., 1984; Vernet *et al*., 2008). Well-dated Pleistocene macrofloras allowing comparisons with the Resson macroflora are very rare. In Caours (Somme, France), tufa deposits dated from ca. 125 ka (Antoine *et al*., 2006; Bahain *et al.,* 2010) yieded poorly preserved foliar imprints including: 3 Salix species (*Salix cf. S. cinerea, S. cf. S. caprea and S. sp.), Fraxinus* cf. *F. excelsior*, *Hedera helix*, *Corylus avellana*, *Quercus* sp. and *Asplenium scolopendrium* L. characteristic of riverine communities and rocky soils which are all present in Resson tufas. La Celle tufa (MIS 11) provides the largest collection of plants from northern France so far, with a total of 24 Dicotyledons including leaves, seeds and fruits. This assemblage differs from Resson and Caours tufa, specifically with *Celtis australis, Ficus carica* and *Cercis siliquastrum* (Munier-Chalmas, 1903) while *Buxus* is recorded both at sites La Celle (Jolly-Saad *et al*., 2007) and Resson.

In Germany, deposits from the Last Interglacial have been intensively studied, the Ehringsdorf tufa dated from ca. 111 ± 47 ka (Blackwell & Schwarcz, 1986) contains important plant impressions: 37 taxa distributed in two different units. The floristic composition, at least at the the species and generic level, is more diversified. With 8 shared taxa (*Corylus avellana*, *Alnus* sp., *Tilia cordata*, *Acer campestre Salix caprea/cinerea*, *Ligustrum vulgare, Euonymus*, and *Buxus*, it nevertheless differs from Resson in the presence of three *Quercus* species (*Q*. cf. *petrea*, *Q. robur*, *Q. virgiliana*), *Berberis* cf. *vugaris*, *Ribes* sp., *Rosa* sp. *Cotoneaster* cf. *integerrimus, Rhamnus carthatica*, *Vitis* sp, *Syringa* and *Lonicera* (Steiner, 1979). Conversely, *Fagus* and *Taxus* are not reported from the Ehringsdorf macroflora nor is *Carpinus*.

At Stuttgart-Untertürkheims tufa, a diversified assemblage of the temperate deciduous forest consistent with Resson macroflora. The 31 taxa are *Populus alba*, *Populus nigra,* 4 species of *Salix* (*S. caprea*, *S. cinerea*, *S. viminalis*, *Salix* sp.), *Corylus avellana, Ulmus* sp*., Acer pseudoplatanus, Frangula alnus, Rhamnus catharticus, Rhamnus saxatilis, Tilia cordata, Quercus robur, Euonymus europeus, Crataegus laevigata, Crataegus monogyna, Malus sylvestris, Ribes uva-crispa, Rubus idaeus, Prunus spinosa, Cornus sanguinea, Lonicera arborea, Lonicera xylosteum, Myriophyllum, sp., Fraxinus excelsior, Schoenoplectus lacustris, Phragmites australis*, Poaceae, Characeae (Schweigert, 1991). *Fagus* is absent in Stuttgart-Untertürkheims deposits.

Finally, the Eemian site of Burgtonna (Vent, 1978, Brunnacker *et al*., 1983) has yielded leaf macroreamains of 26 taxa including thermophilous Mediterranean species now occurring now futher south and not recorded elsewhere nor in Resson deposits, e.g. *Acer Monspessulanum*, *Mespilus germanica.* They are associated with species characteristic of the temperate deciduous forest similar as Resson flora and with atlantic species such as *Phylitis scolopendrium* (syn. *Asplenium scolopendrium*), *Fraxinus excelsior* and *Acer campestre*.

5.4 - COMPARISON WITH EEMIAN PALYNOLOGICAL RECORD FROM NORTHWESTERN EUROPE

In western Europe there are only a few rather palynological sequences that demonstrate a more or less complete Eemian flora record. A number of these flora assemblages come from France : Les Echets (De Beaulieu & Reille, 1984), la Grande Pile (Woillard, 1975, 1978; De Beaulieu & Reille, 1992) and the Plateau de Devès (Reille & Beaulieu, 1990). In Netherlands, the main sequences are those from Amersfoot (Zagwijn, 1961) defined as the Eemian stratopype , and the Kreftenheye Formation (Van der Hammen *et al*., 2008). In Germany, a number of sites have yielded pollen diagrams covering the entire interglacial cycle, particularly Quakenbrück (Hahne *et al*., 1994) Gröbern and Grabschütz (Litt, 1990) and Oerel site (Behre & Hölzer, 2005). The more striking characteristics of these well dated pollen records are the strong similarity in the development of dominant taxa in NW Europe. In almost all pollen diagrams, the earliest temperate deciduous taxa to appear is *Ulmus* followed by *Quercus*, *Corylus* and *Tilia*. *Taxus* and *Buxus* are clearly significant components of the vegetation which are consistent with Resson macrofossils. A highly characteristic signature of the middle part of the Eemian is the dominance of *Carpinus* in all aeras of the north European plains, generally correlated with Marine Isotope Stage 5e (Martinson *et al*., 1987). *Carpinus* is not recognized in Resson palaeobotanical data and in macrobotanical records from other northwestern macrobotanical localities. In long sequences *Carpinus* succeeds to broadleaved forest trees such as oak and elm forests, unlie the Holocene in which it them. At “les Echets” the occurrence of *Fagus* is only visible in the regressive phase of *Carpinus* corresponding to the

Saint-Germain I and dated c*a*. 115,000 which make it equivalents of MIS 5c which is one of its few record in the Pleistocene. *Fagus* percentages reach 40 % reflecting the presence of beech in the immediate surroundings of the lake.

Concerning, the floral remains from Resson with the identification of *Buxus, Taxus* and *Hedera* the results seem more consistent with the records of the optima of the Eemian (MIS 5e) than the isotopic stages 5c where thermophilous taxa are not recorded in long sequences with more lower frequences. The presence of *Fagus* probably demonstrate that Resson layers cover a long part of the development of the interglacial including it's decline (Dabkowski *et al*., 2020).

6 - CONCLUSIONS

The re-examination of the macroflora collection of Resson yields new data for reconstruction of the main palaeoenvironments and the associated palaeoclimate inferences during Late and Middle Quaternary Interglacials in northern France. Specifically, the recognized assemblages were associated with the Eemian, the last interglacial on the base of geomorphological data in older literature. The deposit has allowed identifying 24 taxa including some families, species and genera that were not listed by earlier authors including Charophytes, Bryophytes, Pteridophytes and Angiosperms (Monocotyledons, Dicotyledons). The abundance of leaves, stems and reproductive structures ascribed to *Fagus*, *Taxus*, *Acer*, *Corylus*, *Tilia*, and diverse shrubs clearly reflects a forest environment. The abundance of Charophytes indicates an open aquatic environment in the vicinity of a wet shady forest. We notice that the angiosperms observed in Resson tufa are currently still present in the area with the exception of *Buxus* and *Taxus* despite suitable habitats are today present. The reconstructed vegetation is thus interpreted as temperate with the predominance of deciduous elements principally in moist habitats. The comparison with other western European Late Pleistocene macroflora indicates that the Resson flora is coherent with an attribution to the Eemian, as already suggested by former authors and recent review (Dabkowski *et al*., 2020). Further description of additional fossil samples complemented by geochemical and geochronological data will contribute to a better understanding of the ecosystem that prevailed at Resson during the last interglacial period.

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