Geologica Acta, Vol.16, Nº 2, June 2018, 189-213, I-V
DOI: 10.1344/GeologicaActa2018.16.2.5

geologica acta

The *Konservat-Lagerstätte* Menat (Paleocene; France) – an overview and new insights

S. WEDMANN[1] D. UHL[2,3,4] T. LEHMANN[2] R. GARROUSTE[5] A. NEL[5] B. GOMEZ[6] K. SMITH[2] S.F.K. SCHAAL[2]

[1]Senckenberg Forschungsstation Grube Messel, Forschungsinstitut Senckenberg
Markstraße 35, 64409 Messel, Germany. E-mail: sonja.wedmann@senckenberg.de

[2]Senckenberg Forschungsinstitut und Naturmuseum Frankfurt
Senckenberganlage 25, 60325, Frankfurt am Main, Germany. Uhl E-mail: dieter.uhl@senckenberg.de
Lehmann E-mail: thomas.lehmann@senckenberg.de
Smith E-mail: krister.smith@senckenberg.de
Schaal E-mail: stephan.schaal@senckenberg.de

[3]Senckenberg Center for Human Evolution and Palaeoenvironment, Institut für Geowissenschaften, Universität Tübingen
Sigwartstraße 10, 72076, Tübingen, Germany

[4]Programa de Pós-Graduação em Ambiente e Desenvolvimento (PPGAD). Centro Universitário UNIVATES
95.900-000, Lajeado, Rio Grande do Sul, Brazil

[5]Muséum National d'Histoire Naturelle, Institute de Systématique, Evolution, Biodiversité, ISYEB, UMR 7205 CNRS UPMC EPHE, CP50
45 rue Buffon, F-75005 Paris, France. Garrouste E-mail: garroust@mnhn.fr
Nel E-mail: anel@mnhn.fr

[6]Université Lyon 1 (Claude Bernard), ENS Lyon, Observatoire de Lyon, CNRS-UMR
5276 LGL-TPE, Campus de la Doua, bâtiment Géode, 2 rue Raphäel Dubois, F-69622 Villeurbanne, France.
E-mail: bernard.gomez@univ-lyon1.fr

ABSTRACT

The *Konservat-Lagerstätte* Menat (Puy-de-Dôme, France) is an outstanding archive of a Paleocene ecosystem, which was deposited in a former maar lake. Excavations during the last century have yielded an extensive flora and fauna record, therefore an overview of the current state of paleontological investigations is given in this paper. Additionally, new results based on excavations from the years 2012 to 2014 are presented. The preservation of organic matter differed strongly between excavation sites, probably influenced by weathering processes. The stratigraphic succession consists mostly of organic-rich clays, intercalated with hard, silicified claystones. In 2013 and 2014 both impression and compression fossils were collected from different outcrops. Compression fossils from organic-rich clays were exceptionally well-preserved and included three-dimensional plant remains. A new database on insect paleobiodiversity was compiled. The occurrence of charcoal in almost all horizons investigated suggests that paleowildfires were frequent during the Paleocene in the vicinity of the paleolake. The results confirm the high potential of the *Konservat-Lagerstätte* Menat for future paleontological research.

KEYWORDS Menat. Paleocene. *Konservat-Lagerstätte*. Plants. Insects. Vertebrates.

INTRODUCTION

The major biotic turnover that occurred immediately after the Cretaceous–Paleogene boundary (K/Pg, formerly K/T) led to significant extinction of marine and terrestrial taxa (*e.g*. Benton, 1995; Sepkoski, 1996; D'Hondt, 2005; Fastovsky and Sheehan, 2005; Lloyd *et al*., 2008; Longrich *et al*., 2011, 2012). Not all major clades became extinct or showed a marked decline in diversity on a global scale. For instance, insects were seemingly not affected, at least not at systematic levels equal or higher than family (*e.g*. Labandeira and Sepkoski, 1993; Ross *et al*., 2000; Zherikhin, 2002; Nel *et al*., 2010a; Nicholson *et al*., 2015), while plants were only affected temporarily (*e.g*. Sweet *et al*., 1990; Wilf *et al*., 2001, 2003, 2005; Labandeira *et al*., 2002; Wappler *et al*., 2009). Many higher clades of modern aspect appeared after the Cretaceous–Paleogene mass extinction, especially orders of placental mammals (*e.g*. Archibald and Deutschman, 2001; Rose, 2006). However, the evolutionary history of terrestrial taxa during the earliest Paleogene is still poorly known in many parts of the world, including Europe. In particular, the scarcity of well-preserved fossils from the Paleocene obscures the analysis of their evolution and development of their biodiversity.

Plants

Studies on a number of plant-bearing localities from the Late Cretaceous and Early Paleogene indicated that a significant extinction occurred in North America at the K/Pg boundary, with high levels of extinction especially among the broad-leaved evergreen vegetation (*e.g*. Wolfe and Upchurch, 1986; Nichols and Johnson, 2008). Recovery of plant communities in this region was generally slow, and for over 10Ma –*i.e*. the Paleocene– the North American plant fossil record is generally formed by low diverse assemblages (Wing *et al*., 1995; Nichols and Johnson, 2008). However, the highly diverse Paleocene site Castle Rock in Colorado suggests that the recovery may have varied very much geographically (Johnson and Ellis, 2002).

Although the development of terrestrial vegetation during the Paleocene is relatively well studied in North America, our understanding of the western and central European vegetation during this period is seriously hampered by the scarcity of Paleocene sites and because they have not been revised since initial descriptions in the 19th and 20th centuries (*e.g*. Kvaček, 2010). Based on earlier works by Mai and Walther (1978), Mai (1995) used a system of plant assemblages (*Florenkomplexe*) to characterize vegetation development in Europe, but even this system needs to be updated with new data. Dealing with the Paleocene, Mai (1995) distinguished three main floral assemblages in western and central Europe:

i) Eisleben-Roda, based on leaves, fruits and seeds from the Eisleben Basin in Germany (Friedrich, 1883; Knobloch and Mai, 1986; Mai, 1995; Kvaček, 2010),

ii) Gelinden, based on leaf impressions from this locality in Belgium (Saporta and Marion, 1873, 1878; Stockmans, 1932a, b, 1960), which are in urgent need of taxonomic revision, since they include several enigmatic taxa,

iii) Menat, based on the locality of the same name in France, as well as a number of other localities in England, France and Germany (see Mai, 1995). The flora from Menat is known mainly through the publications of Laurent (1909, 1911, 1912a, b, 1919), Laurent and Marty (1910, 1939) and Piton (1940). However, almost no significant research has been undertaken on this flora for almost seven decades.

Insects

Most extant insect families had their origin in the Cretaceous or even earlier (*e.g*. Grimaldi and Engel, 2005; Nicholson *et al*., 2015). However, little is known about their ecological role in the Paleocene. The scarcity of outcrops with well-preserved fossil insects from the Late Cretaceous to the Eocene is the reason that only a few studies compare insect assemblages from different ages. One study, based on Middle Eocene ants (Formicidae) from the Messel maar showed that the dominance and diversity of different subgroups of ants changed substantially from the Middle to the Late Eocene (Dlussky and Wedmann, 2012).

The Paleogene is a crucial period for the evolution of modern insect communities (Zherikhin, 2002, pg.: 387). Nonetheless, only a few Paleocene fossil sites with abundant insects have been found (*e.g*. Grimaldi and Engel, 2005), which results in a clear underrepresentation of the insect fossil record of this stage in comparison with the Eocene. In Europe, the two Paleocene fossil sites rich in insects are Menat in France (Piton, 1940) and the Paleocene-Eocene Fur Formation (Fm.) in Denmark (Rust, 1999). In Asia, Sakhalin amber has yielded numerous insects (Grimaldi and Engel, 2005), and in North America the Paskapoo Fm. of South Central Alberta, Canada, is also significant (Wighton, 1982).

Vertebrates

Aquatic and semiaquatic amphibians appear to have been largely unaffected by the K/Pg event (Bryant, 1989). Thus, a recent study based on salamanders suggested that diversity declined already towards the end of the Cretaceous (Wilson *et al*., 2014). Among lizards and snakes, only Boreoteioidea is thought to have gone extinct at the K/Pg boundary (MacLeod *et al.*, 1997; Evans and Jones, 2010). However, extinction at the species level was shown to be high in geographic areas where a relatively continuous record was available, such as in the western interior of North America (Bryant, 1989; Longrich *et al.*, 2012). Most turtle taxa survived the K/Pg event, although the large and fully terrestrial taxon *Basilemys* went extinct in North America (Bryant, 1989; Lyson and Joyce, 2009; Holroyd *et al.*, 2014). Similarly, extinction among the semiaquatic crocodilians and champsosaurs across the K/Pg boundary was low in the western interior of North America (Bryant, 1989). In sum, the extinction of basal tetrapods was concentrated in terrestrial rather than aquatic forms (Sheehan and Fastovky, 1992).

Mammals were strongly affected by the mass extinction at the K/Pg boundary (Fastovsky and Bercovici, 2016; Longrich *et al.*, 2016), with only one third of the families present in the Cretaceous surviving into the Paleogene (Rose, 2006). Most of them belonged to the multituberculate, eutherian and metatherian clades and, ultimately, gave rise to the diversity of Cenozoic mammals. Soon after the K/Pg, the mammals –especially eutherians– experienced an "explosive" (*i.e.* rapid and extensive) adaptive radiation (*e.g.* McKenna and Bell, 1997; Rose, 2006). Nearly all modern mammal orders, as well as many extinct ones, first appear in the fossil record during the first third of the Cenozoic (Rose and Archibald, 2005), leading Simpson (1967) to label this time as the "Beginning of the Age of Mammals".

Paleocene eutherian and metatherian taxa, often considered primitive or archaic (such as "plesiadapiforms" and "condylarths"; *e.g.* Russell, 1975; Smith *et al.*, 2014), are derived either from Late Cretaceous or other Early Paleocene lineages (Rose, 2006). They were eventually replaced by new Eocene taxa, which constitute the first modern mammals (such as primates, perissodactyls and artiodactyls). The origin of modern mammalian orders is certainly to be found in the Paleocene, but except for some specific clades (*e.g.* carnivoraforms, proboscideans, rodents), unambiguous fossil relatives of this age have not been found yet (Gheerbrant, 2009; Wu *et al.*, 2012; Smith *et al.*, 2014; Solé *et al.*, 2016). While Eocene sites yielding mammals are relatively widespread worldwide (except for Africa), the Paleocene history of mammals is better documented in North America (*e.g.* Bighorn and Wind River basins, Wyoming) and Asia (*e.g.* Mongolia) than in Europe. The few noteworthy European Paleocene localities known include Hainin (Belgium; *e.g.* De Bast *et al.*, 2012; De Bast and Smith, 2017), Walbeck (Germany; *e.g.* Russell, 1964; Rose *et al.*, 2015), the sites around Mont Berru (France; *e.g.* Russell, 1964), the new site of Rivecourt Petit Pâtis (France; *e.g.* Smith *et al.*, 2014), and Menat (France; *e.g.* Piton, 1940). Earliest Paleocene faunas remain largely unknown, but a few exceptions are documented by Peláez-Campomanes *et al.* (2000) and Rose (2006). Because of this rarity, each of the European Paleocene localities represents a cornerstone in the knowledge of the vertebrate fauna from this epoch.

To sum up, the earliest evolution of the Cenozoic flora and fauna in western and central Europe is still poorly understood, making it necessary to increase the paleontological database of the Paleocene. This would enable comparisons with the better-known flora and fauna from the Eocene and Oligocene, such as Messel (*e.g.* Schaal and Ziegler, 1992; Lehmann and Schaal, 2011, 2012; Smith *et al.*, 2018 *[In Press]*) and Enspel (*e.g.* Wuttke *et al.*, 2010, 2015).

STATE OF THE ART OF THE STUDY OF THE FOSSIL SITE MENAT

Location, age and history

The *Konservat-Lagerstätte* Menat is located in the department Puy-de-Dôme of the Auvergne-Rhône-Alpes Region (France), in the northwestern part of the Massif Central (Fig. 1A). The village of Menat is built atop the fossiliferous sedimentary sequence (Fig. 1B). The deposits represent an isolated lake basin that is interpreted as a maar lake (Vincent *et al.*, 1977; Russell, 1982; Michon and Merle, 2001). The chemical composition of the deposits is variable, but previous chemical analysis revealed a composition of 15–25% carbonates, 50–60% silicates, 10–15% aluminum and 2–5% iron oxides (Piton, 1940). According to Dangeard (1934), most of the lacustrine "lignites" and organic-rich deposits of Menat result from the accumulation of remains of a single diatom species, *Amphora subovalis* (Bacillariophyceae). It was suggested that "the siliceous element of the sediment is related to the presence of numerous diatoms as well as to fresh-water sponge spicules" (Russell, 1975, pg.: 36). The outcropping area of these deposits is about 1000m-long and 600m-wide (Fig. 1B; C). The thickness of the lacustrine formation has not been determined exactly, but wells indicate a thickness of up to 250m (S. Hervet, personal observation).

Based on a fossil primate, a horizon of the sedimentary sequence at Menat has been biostratigraphically dated as Mid- to Late-Paleocene, and a palynological study provided a Thanetian age (Russell, 1967); another estimation gives a Selandian age (personal communication of P. Gingerich to T. Wappler, in Wedmann *et al.*, 2009). Radiometric K/Ar-based dating of basalts (whole-rock) and tuffs (hornblende) in the vicinity of Menat yielded an average age for the volcanism in this area of *ca.* 56Ma (Vincent *et al.*, 1977), which is now equivalent

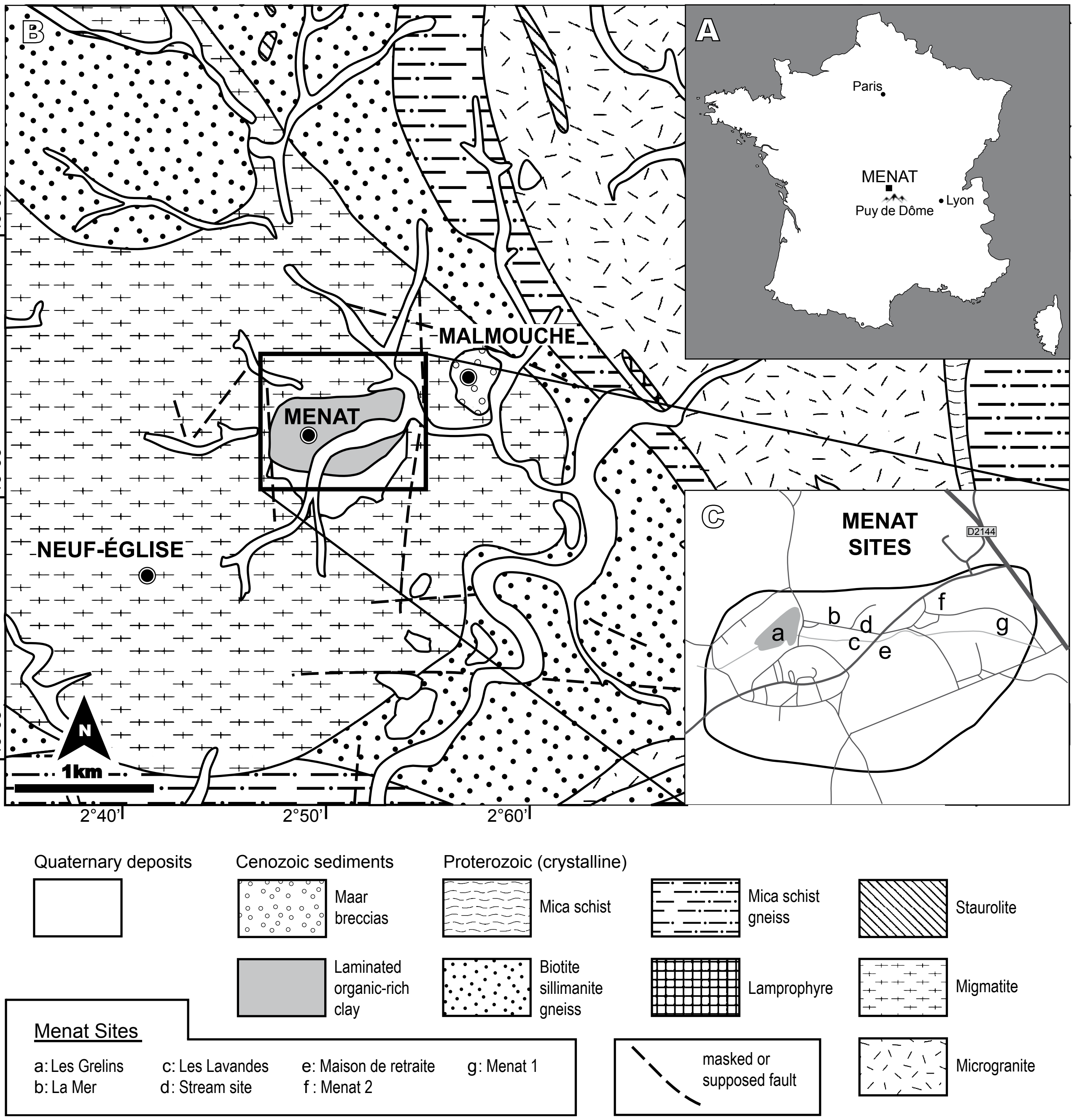

FIGURE 1. Geographic and geological context of the *Konservat-Lagerstätte* Menat. A) General map of France modified from www.d-maps.com. B) Geological map excerpt based on the Geological Map of France, 645 - Gannat - 1/50,000, Feuille XXV-29. C) Specific location map of Menat showing the position of the fossil sites relative to the local road network. The probable outline of the crater is indicated by the black line around the town of Menat. Explanations of the sites: a) historical site "Les Grelins", where many fossils were found, now a lake; b) historical site "La Mer", now backfilled and covered by a road; c) site "Les Lavandes", opened in 2011; d) site "Stream site", surveyed and sampled in 2014; e) site "Maison de retraite", opened mainly between 2004-2008; f) site "Menat 2", excavated in 2013 and 2014; g) site "Menat 1", excavated in 2012.

to the Thanetian-Ypresian boundary. This "average age" has been repeatedly cited as a reliable absolute age for the Menat maar (*e.g.* Russell, 1982), which is highly problematic taking into account the lack of a verified connection of the basalts and tuffs with the maar deposits (Vincent *et al.*, 1977).

Since the beginning of the 19th century, the village of Menat has been known for its diatomite quarries (Monestier and Lavina, 1995; Monpied, 2003). The organic-rich clays and diatomites were exploited by pre-industrial means until around 1873, when a well-equipped factory was built outside the village, mainly to avoid intoxication with noxious fumes, at a place called "La Faye" (Laurent, 1912a). Through different processes (distillation, carbonization), the deposits were treated to obtain the "noir minéral d'Auvergne" (pigment and fertilizer), the "rouge minéral" or "Tripoli" (abrasive) and, later, even a stabilizer for nitro-glycerine in the production of dynamite. The industrial exploitation of the quarries ceased in the 1950s and the factory at "La Faye" was closed in 1964 after a brief conversion to a ceramic-tiles factory. During all these years numerous small collections by miners and amateurs were created.

Most paleontological discoveries were made in the main quarry, called "Les Grelins" (Fig. 1C, site a), located at the northwestern edge of the original maar crater. This quarry was transformed into a pond in the 1960s. Another important quarry, which was situated adjacent to the local river, "La Mer" (Fig. 1C, site b), was backfilled and is now overlain by a road. However, these sites represent only a small portion of the presumed extent of the former maar lake.

Soon after the industrial exploitation ceased, the site of "Les Grelins" was frequented by collectors of fossils. In order to protect the paleontological heritage, the municipal council issued an ordinance in 1979 prohibiting the collection of fossils ("Arrêté municipal du 22 juin 1979"). In parallel, a local museum was created with the support of a local paleontological association (Le Cercle de Paléontologie Bernard Palissy) and the Muséum National d'Histoire Naturelle (MNHN) in Paris. Also, in the 1980s, collection of fossils in the historical quarry of Menat was restricted in order to protect the small site for future scientific excavations. A few excavations were, then, organized by paleontologists from the MNHN (see Russell, 1982), focused on the quarry of "Les Grelins." In 1988, part of the historical site became a Regional Natural Reserve (RNR 84) and, from then on, no institutional excavations have taken place at "Les Grelins".

Between 1996 and 2008, in collaboration with the municipality of Menat, the paleontological association Rhinopolis organized short excavations in the historical quarry. Simultaneously, Rhinopolis opened a new site called "Maison de retraite" (Fig. 1C, site e) between 2004 and 2008. In 2009, the municipality of Menat established a new collaboration with the association Paléovergne for the preservation and enhancement of its paleontological heritage. In the context of this partnership, the two aforementioned sites were visited regularly until 2010, when the "Maison de retraite" site was used to construct a retirement home and a new site, "Les Lavandes" (Fig. 1C, site c), was opened in 2011. These excavations yielded numerous insects and plants but also new fossil birds and fishes (*e.g.* Jensen, 2008; Kirejtshuk *et al.*, 2010; Nel *et al.*, 2010b). Moreover, a well-preserved specimen of a small reptile (choristodere) was found in 2000 at the historical site "Les Grelins" (Matsumoto *et al.*, 2013).

In 2012, a team of the Senckenberg Forschungsinstitut und Naturmuseum Frankfurt, in collaboration with the organizations Eldonia and Epona, investigated a test pit, "Menat 1" (Fig. 1C, site g), at the eastern margin of the former maar lake. These excavations led to measuring the first stratigraphic log in this site and the discovery of new fossils. In 2013 and 2014 another test pit, "Menat 2" (Fig. 1C, site f), was opened at the northeastern margin of the former maar lake. Also in 2014, a few samples of laminated claystones from the so-called "Stream site" (Fig. 1C, site d), were taken. More details on the first results from these excavations are given below, in the section "New data on the fossil site Menat".

The most comprehensive paleontological study of Menat was made by Piton (1940), which provides a good basis for further work, but many of his taxonomic identifications must be revised and updated. Unfortunately, many of the specimens he investigated were lost, especially during World War II. Some holotypes are scattered in different collections, mainly in the Laboratoire de Paléontologie of the Muséum National d'Histoire Naturelle (MNHN) (see Appendix I). To the best of our knowledge, a comprehensive list on the repository institutions of the Menat fossils has not been elaborated before.

Since Piton's (1940) work, several thousands of new fossils have been collected by the Rhinopolis, Paléovergne, and Eldonia organizations, as well as by researchers from the MNHN (A. Nel, R. Garrouste, J. Gaudant), Senckenberg Museum Frankfurt (Germany) and private collectors. Fossils collected by Rhinopolis and Paléovergne are mainly housed in the local Musée de Menat (MNT), while fossils found by the Senckenberg and MNHN research teams are deposited at the Epona building in Menat and at the MNHN (Paris). Fossils from Menat are also housed in the following collections: Muséum d'Histoire Naturelle Henri Lecoq in Clermont-Ferrand (MHNHL), Naturhistorisches Museum Basel (NHM, Switzerland); Collections de Géologie of the Université Lyon 1 (UCBL-FSL), Maarmuseum Manderscheid in Germany, Senckenberg Museum Frankfurt (see Appendix I).

Flora

Fossil plants were reported since the 19th century from Menat (*e.g.* Brongniart, 1828; Lecoq, 1829; Heer, 1859; Saporta and Marion, 1885). A first revision of the flora was published by Laurent (1912a) with only a few subsequent taxonomic additions (*e.g.* Laurent, 1912b, 1919). Besides these studies, there is one more recent revision of the flora by Piton (1940). Part of Piton's plant fossils are now deposited at the MNHN (Wappler *et al.*, 2009 supplement). This flora still forms one of the pillars of our current interpretation of Paleocene vegetation in western and central Europe (Mai, 1995). According to Mai (1995) the flora from Menat represents the first evidence of a supposed invasion of Arcto-Tertiary elements (*e.g. Alnus*, *Corylus*, *Glyptostrobus*, *Lindera*, *Macclintockia*, *Menispermum*, *Platanus*, *Quercus* Sect. Rubrae, *Salix*, *Ulmus*, tilioid and caryoid pollen grains) into European floras as well as the earliest occurrence of a Mixed Mesophytic Forest in Europe. Thus, Menat is considered as a key locality for the understanding of plant evolution in western and central Europe. However, most identifications of plant fossils by Laurent (1912a, 1912b, 1919) and Piton (1940), on which all interpretations are based, must be seen as questionable and/or outdated. In addition, nothing is known about the plant taphonomy of this locality.

The palynology from Menat was investigated by Kedves (1967) and Kedves and Russell (1982), and a first biostratigraphic interpretation by these authors, as well as by Krutzsch (1967), supported a Paleocene age of the sedimentary rocks.

So far, identifications of plant megafossils are solely based on morphological data and no information from fossil cuticles is available in the literature. Most of the material in historical collections derives from relatively hard, partly silicified claystone, which could be collected without difficulty. Fossils originating from clays, which were not silicified, are more difficult to sample because these beds are wet and soft, fossil specimens are fragile and must be dried slowly before they can be integrated into a collection.

A study of the megaflora of Menat and its insect-feeding damage showed that the diversity of both is very high in comparison to coeval North American localities (Wappler *et al.*, 2009). Recent field investigations made by A. Nel and R. Garrouste strongly suggest that this diversity is even higher than what was found on the basis of partial collections, as nearly all the leaves show very diverse traces of insect activities, which is highly unusual by comparison with Late Eocene and Oligocene sites in southern France. Wappler *et al.* (2009) concluded that Paleogene fossil sites of Europe were not very much affected by the end-Cretaceous event, probably due to the large geographical distance to the Chicxulub impact site. This should be tested by work on the Eisleben and Gelinden floras, which are probably older than Menat (Mai, 1995), although Wappler *et al.* (2009) claimed that Menat is the oldest well-preserved Paleocene flora in Europe.

Insects

Menat has yielded fossil insects of varying quality of preservation. Recent investigations have shown that the insect abundance is very high in certain beds (see section "Preservation of plants and insects"). The first insect discoveries were made by Heer (1861, pg.: 117) and Bruyant (1902). The only comprehensive investigation of the insect fauna was presented by Piton (1940). He showed that the insect oryctocoenosis from Menat comprises numerous species, with the most abundant insect groups being beetles (Coleoptera) and cockroaches (Blattodea). The work by Piton (1940) is a good basis for further entomological study, but many of his identifications need revision (*e.g.* Balazuc and Descarpentries, 1964; Nel, 1988, 1992; Boulard and Nel, 1990; Nel and Roy, 1996; Nel and Petrulevicius, 2003).

Mayflies (Ephemeroptera) and all other aquatic insects appear to be rarer in Menat than previously thought (Nel and Roy, 1996). Odonata are quite rare; two fossils were attributed to this order by Piton (1940), *i.e.* a supposed member of Lestidae that is in fact an insect of uncertain affinities and an abdomen of Anisoptera. Additional records of Odonata are the megapodagrionid *Thanetophilosina menatensis* Nel *et al.*, 1997, the 'amphipterygid' *Valerea multicellulata* Garrouste *et al.*, 2016a and a few recently discovered, undescribed wings (A. Nel). Small undescribed trichopteran larval cases, built with quartz grains, are relatively common. Gerrid bugs are also quite common, with at least ten specimens of *Cylindrostethus gaudanti* Hartung *et al.*, 2016, the first cylindrostethine fossil known worldwide. A member of the water-living Gyrinidae (Coleoptera) described by Piton (1940) was revised by Nel (1989). The scarcity of aquatic insects is a general feature of western European Cenozoic-compression entomofaunas (Nel, 1991), including Messel and Enspel (Wedmann, 2000; Wedmann *et al.*, 2010; S. Wedmann, 2015, personal observation).

Nel and Roy (1996) identified several wing fragments that were formerly attributed to mayflies as mantids (Mantodea). Reinvestigation revealed chaeteessid mantids, which today only occur in the Neotropics, but were formerly much more widespread (Nel and Roy, 1996).

Among Hymenoptera (bees, ants and related groups), a fossil horntail wasp was described as an extinct genus (Piton, 1940), but after re-study it could be placed in the living genus *Urocerus* (Nel, 1988). Four records of this horntail wasp species are known now from Menat, which is very unusual and probably indicates that these insects were abundant near the former lake (Wedmann *et al.*, 2014). An isolated insect wing was described as belonging to the assassin bugs (Heteroptera: Reduviidae) by Piton (1940), but Nel (1992) showed that this wing belongs to Argidae or Pterygophoridae, which are basal symphytan hymenopterans. Four other symphytan wasps have been recently discovered by some of the authors (A. Nel and R. Garrouste). *Protobombus hirsutus* Piton, 1940 was originally described as the oldest fossil record of bumblebees (Hymenoptera: Apidae), but Nel and Petrulevicius (2003) showed it to be a megachilid bee. Wedmann *et al.* (2009) indirectly confirmed the presence of megachilid leaf-cutter bees from an excision in a leaf. The fossil bee *Paleohabropoda oudardi*, which was recently described from Menat (Michez *et al.*, 2009), clearly belongs to an extant tribe, and is very close to an extant genus, thus indicating evolution towards modern bee genera as early as in the Paleocene. At least three other bee specimens have been recently discovered by A. Nel and R. Garrouste, and are yet to be described. Nel and Auvray (2006) reported the oldest record of an extant subfamily of wasps (Hymenoptera: Vespidae: Vespinae) based on a fossil from Menat. The same taxon was also recorded from the Eocene Baltic amber and from the Late Eocene of Florissant (North America), which documents a wide geographic distribution in the Paleogene. A wasp fossil awaits further investigation (Fig. 2A). A rhopalosomatid was recorded in Menat illustrates the widespread occurrence of this group in the Paleocene (Nel *et al.*, 2010b). The first Cenozoic roproniid wasp was also recently described under the name of *Paleoropronia salamonei* Garrouste *et al.*, 2016b.

Fossils of flies and midges (Diptera) are very rare in Menat and constitute only about 2% of the insect oryctocoenosis (Nel, 2008). In the Eocene maar lakes of Messel (S. Wedmann, 2017, personal observation) and Eckfeld (Wappler, 2003) they are also very rare, due to taphonomic reasons. Nectoux (1981–1982) recorded a tipulid midge (Diptera) from Menat without providing a more precise determination. A fossil bee fly (Diptera: Bombyliidae) and a species of *Plecia* (Diptera: Bibionidae) have been recorded by Nel (2007, 2008). A well-preserved robber fly (Diptera: Asilidae) was found in recent years but is still undescribed (Fig. 2B).

Plant-hoppers (Hemiptera: Auchenorrhyncha) are more common than flies. Some specimens have been described by Swedo *et al.* (2006) and Stroinski and Swedo (2012).

Beetles (Coleoptera) are among the most common insects, especially weevils (Curculionoidea) (Legalov *et al.*, 2017) and jewel beetles (Buprestidae) (Piton, 1940). Archostematan beetles (Cupedidae) are taxonomically diverse (Kirejtshuk *et al.*, 2010, 2016).

Vertebrates

The most common fossil vertebrates at Menat are fishes (Fig. 3), which have been studied since the early 19th century (*e.g.* Agassiz, 1833–1844; Brongniart, 1880; Priem, 1914; Piton, 1940). Like fossil insects, fossil fishes present different states of preservation, from strongly-weathered specimens in nodules to complete specimens in clay. The ichthyofauna from Menat is less diverse than originally assumed by Piton (1940). Gaudant (1979) revised the fish fauna from Menat and identified three species belonging to Amiidae, Thaumaturidae and Percichthyidae. Two of these groups, Amiidae and Thaumaturidae, are also found in Messel, suggesting that the basic components of the fish fauna in maar lakes were similar from the Paleocene to Late Eocene (Gaudant, 2000). *Cyclurus valenciennesi* is, with a length of 45cm, by far the largest fish from Menat. It was originally assigned to the recent genus *Amia*, but placed in *Cyclurus* by Gaudant (1987). This species is not abundant in Menat and is usually only represented by isolated scales, according to Gaudant (2014, personal communication). The Thaumaturidae show a high variability, which led Piton (1940) to differentiate three species. Gaudant (1979) discussed their diagnostic characters and concluded that only one species occurred, *Thaumaturus brongniarti* (Fig. 3A). The family Percichthyidae is represented by *Properca angusta* (Fig. 3B). *Cyclurus* and *Thaumaturus* point to a limnic context in Menat, whereas *Properca* can also occur in brackish water.

The basal tetrapods of Menat comprise at least six species –an amphibian, a squamate, a choristodere, two turtles and a crocodylian– although half of these specimens are lost. It is noteworthy that most of these tetrapods, with the exception of the squamate, were animals closely associated with freshwater. The amphibian was known from a single anuran skeleton that Piton (1940) had seen but not studied, nor did he know whose collection it belonged to. He recalled that it was about the size of *Rana temporaria* but with longer hindlimbs (femur and tibia) and assigned it to Ranidae. The squamate was also known from a single specimen, a partial mandible (dentary, coronoid and parts of the angular and surangular) briefly described by Piton (1940, fig. 105) as the new species (and *nomen nudum*) *Proiguana loevidens*. The specimen, now presumably lost, had unicuspid teeth and was favorably compared to the Quercy taxon *Proiguana europaea* (now synonymized with *Plesiolacerta lydekkeri*). The choristodere specimen, collection-no. BDL 1819 of the Musée de Menat (MNT), was recently described by Matsumoto *et al.* (2013) and referred to as *Lazarussuchus* sp. based on a large number of cranial and postcranial characters. These authors noted several differences between BDL 1819 and the type species, *L. inexpectatus*, but declined to name a new species due to the inadequate preservation of the former. BDL 1819 is the oldest record of

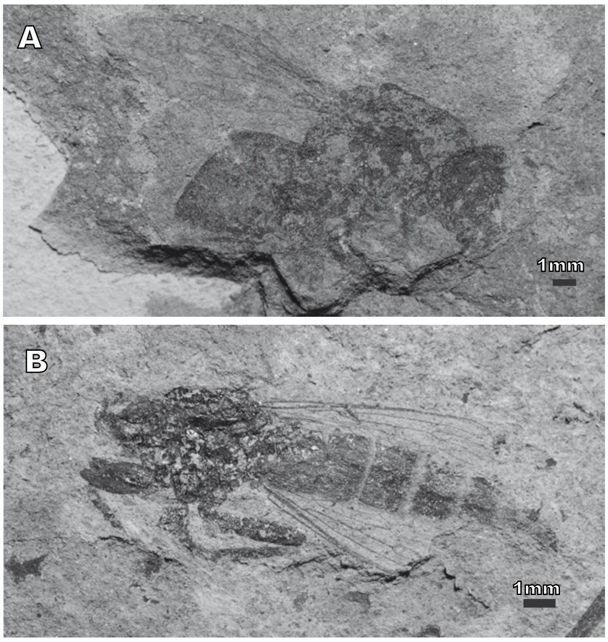

FIGURE 2. Fossil insects from Menat: A) undescribed wasp (Hymenoptera: Vespidae), B) undescribed robber fly (Diptera: Asilidae), both from the collection of the Musée de Menat.

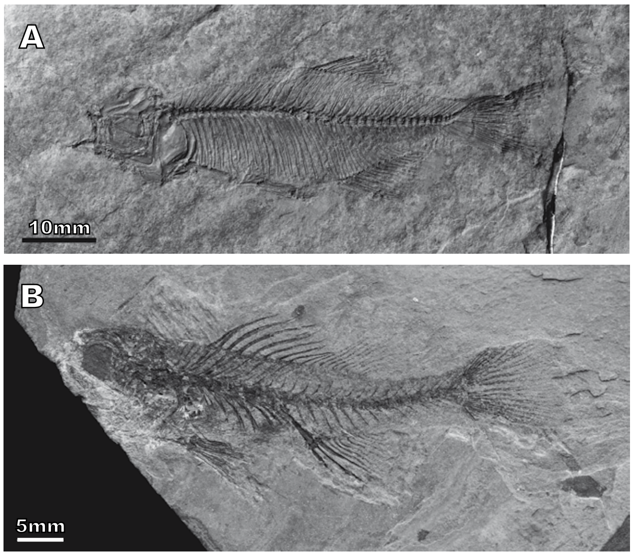

FIGURE 3. Fossil fishes from Menat: A) *Thaumaturus brongniarti*, found in a silicified claystone at "Menat 1", collection no. SMF-P-10094. B) *Properca angusta*, from organic-rich clay at "Stream site", collection no. MNT-14-7565a.

the genus, while the lineage of choristoderes extends back to the uppermost Jurassic (Matsumoto *et al.*, 2013). The only crocodylian reported from Menat was a partial skeleton that Piton (1937) described as *Menatalligator bergouniouxi* (Fig. 4A, modified from a photograph, pl. XXII in Piton, 1940). The type and only known specimen has been lost, but he regarded it as similar to, but more primitive than, the Oligocene *Diplocynodon* from the Massif Central. Notably, the specimen had remains of a fish ("*Amia*") in its stomach. *Menatalligator* was very briefly discussed by Martin *et al*. (2014).

The fossil turtles of Menat have a complicated history. Piton (1937, 1940) briefly described three specimens, all of which he assigned to *Trionyx* sp. and only one of which can presently be accounted for. These specimens are now recognized as belonging to two unrelated taxa. The first species is represented by a single specimen, FSL 532 267, one of Piton's (1940) two partial carapaces. It was later re-identified as *Compsemys cf. victa* (De Broin, 1977) and recently described as the holotype of the new species *Berruchelus russelli* by Pérez-García (2012). *Berruchelus russelli* is diagnosed by several autapomorphies of the shell and interpreted as the sister-lineage of North American *Compsemys victa*, and more distantly to Baenidae. The second species is undoubtedly referable to Trionychidae. Piton (1940, pl. XVI, fig. 1, reproduced here as Fig. 4B) illustrated the skull of one specimen and stated that a partial shell, poorly preserved, was associated with it. The specimen is presumed to be lost.

Although many early bird lineages became extinct at the K/Pg event, modern birds underwent a radiation after that event, filling available niches and contributing to the ecological diversification process (*e.g*. Longrich *et al*., 2011; Brusatte *et al*., 2015). This is noticeable also at Menat, where up to ten bird specimens were discovered (Launay, 1908; Piton, 1940; Jensen, 2008; Mayr *et al*., 2018). In a Master's Thesis by Jensen (2008) seven specimens were recorded, of which one was considered lost. Unfortunately, the preservation is often fragmentary. Some specimens show feathers, which were preserved as carbonaceous impressions. The poor preservation did not allow a reliable identification. Some characters suggested that the fossil birds comprise both aquatic, semi-aquatic and terrestrial taxa (Jensen, 2008). New taxonomic records are given by Mayr *et al*. (2018).

Very few fossil mammals are known from Menat (see Piton, 1940; Guth, 1962), most of them were found during the first half of the 20th century; the youngest was first described in the 1960's. Their articulated skeletons, together with the preservation of body outlines and hair (Figs. 5 and 6), led some French paleontologists (E. Gheerbrant, S. Steyer from the MNHN, personal communication, 2012) to give the nickname "French Messel" to the paleontological site Menat. Doubtless, the most controversial fossil mammal is *Menatotherium insigne* Piton, 1940 (Fig. 5A–C). This specimen consists of two parts, one of which is housed in the Natural History Museum of Basel (Switzerland), while the other is on loan to the MNHN, corresponding to a partial skeleton with preserved skull and with remains of the fur. Simpson (1948) expressed doubts about its classification as a tillodont by Piton (1940) and Russell (1967) subsequently recognized its affinities with the genus *Plesiadapis*, a plesiadapiform (stem primate). In particular, the enlarged, procumbent and pointed lower central incisors, the procumbent multi-cusped upper incisors, the reduced (upper) and absent (lower) canines, well-developed talonid basins on the lower molars, the enlarged hypoconulid on m3, the presence of a postprotocingulum on the P4 (termed “fort bourrelet postérieur” by Russell, 1967, pg.: 485), and the lack of a postorbital bar are characteristics of plesiadapids (see Silcox and Gunnell, 2008 and references therein). Moreover, according to Russell (1967), this fossil alone would support a Paleocene age for the fossil site.

Another exceptional specimen, now in the collection of the MNHN, was found after Piton’s (1940) Thesis and was described by Guth (1962). It consists of a complete, articulated skeleton with fur outline (single hairs can be distinguished in places) and with stomach contents that were never analyzed (Fig. 6A; B). But if at first sight only the tip of the snout seems to be missing, closer examination reveals that most of the bones are not preserved, but only their external molds. The specimen was originally described as an “insectivore” close to the genus “*Ictops*” (=*Leptictis*), a leptictid known from North America (*e.g.* Gunnell *et al.*, 2008). However, preliminary work on photographic material casts some doubts on this identification, in particular the limb proportions are evidence of immaturity of the individual. A re-evaluation of the specimen, including additional comparative material –particularly postcrania of leptictids (see Rose, 1999) and eulipotyphlans, especially those of Amphilemuridae (Maier, 1979; Dunn and Rasmussen, 2009)– would be advisable. In addition to *Plesiadapis insigne* and this “insectivore”, Piton (1940) reported two other mammals, a presumed carnivore, *Cynodictis* sp. (collection of UCBL-FSL, Lyon; Fig. 5D) and a presumed rodent, *Sciuroides* sp. (collection of MNHN; Fig. 6C; D). However, both specimens lack the skull, making identifications by Piton (1940) very problematic.

NEW DATA ON THE FOSSIL SITE MENAT

Lithology

The site “Menat 1”, located near the eastern border of the former maar lake (Fig. 1C, site g), was investigated in collaboration with the organization Eldonia and the support of Epona. The first geological profile for the site “Menat 1” was compiled in 2012 and is shown in Figure 7. Previously, the fossils from Menat were collected without supplying any stratigraphic information. For instance, in the case of the specimens housed in the collection of the local Musée de Menat, the names of localities are given without further stratigraphic information.

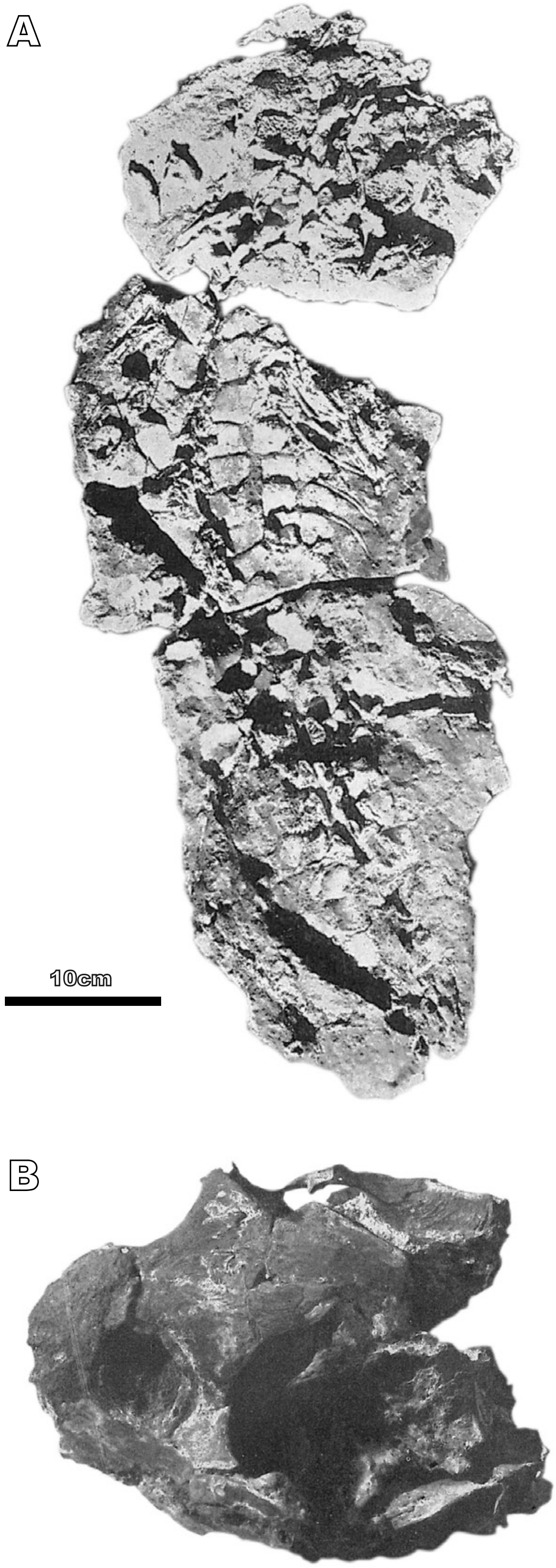

FIGURE 4. Fossil reptiles from Menat described and figured by Piton (1940), which are presumably lost. A) Crocodylian, described as *Menatalligator bergouniouxi*, body in dorsal view; B) Trionychid turtle skull in left dorso-lateral view (no scale bar published, skull length of approximately 7cm) (Piton 1940, pg.: 276).

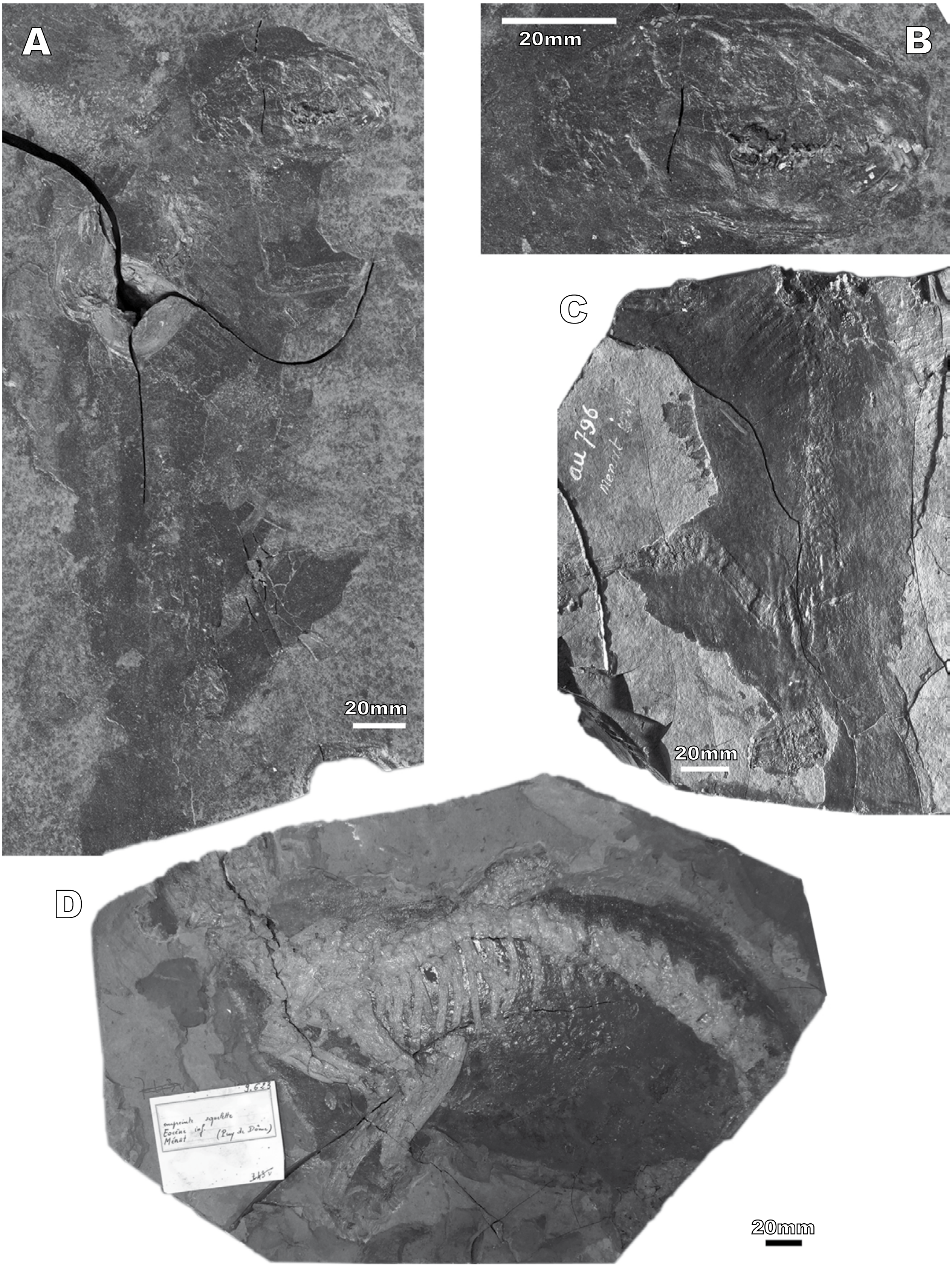

FIGURE 5. Fossil mammals from Menat. A) Plate A (MNHN Paris), with B) details of the head, and C) Plate B (NHM Basel) of *Plesiadapis* (*Menatotherium*) *insigne*; D) A putative carnivoran (?*Cynodictis*). Photographs A and B by P. Loubry. Photograph C by S. Hervet. Photograph D by S. Schaal.

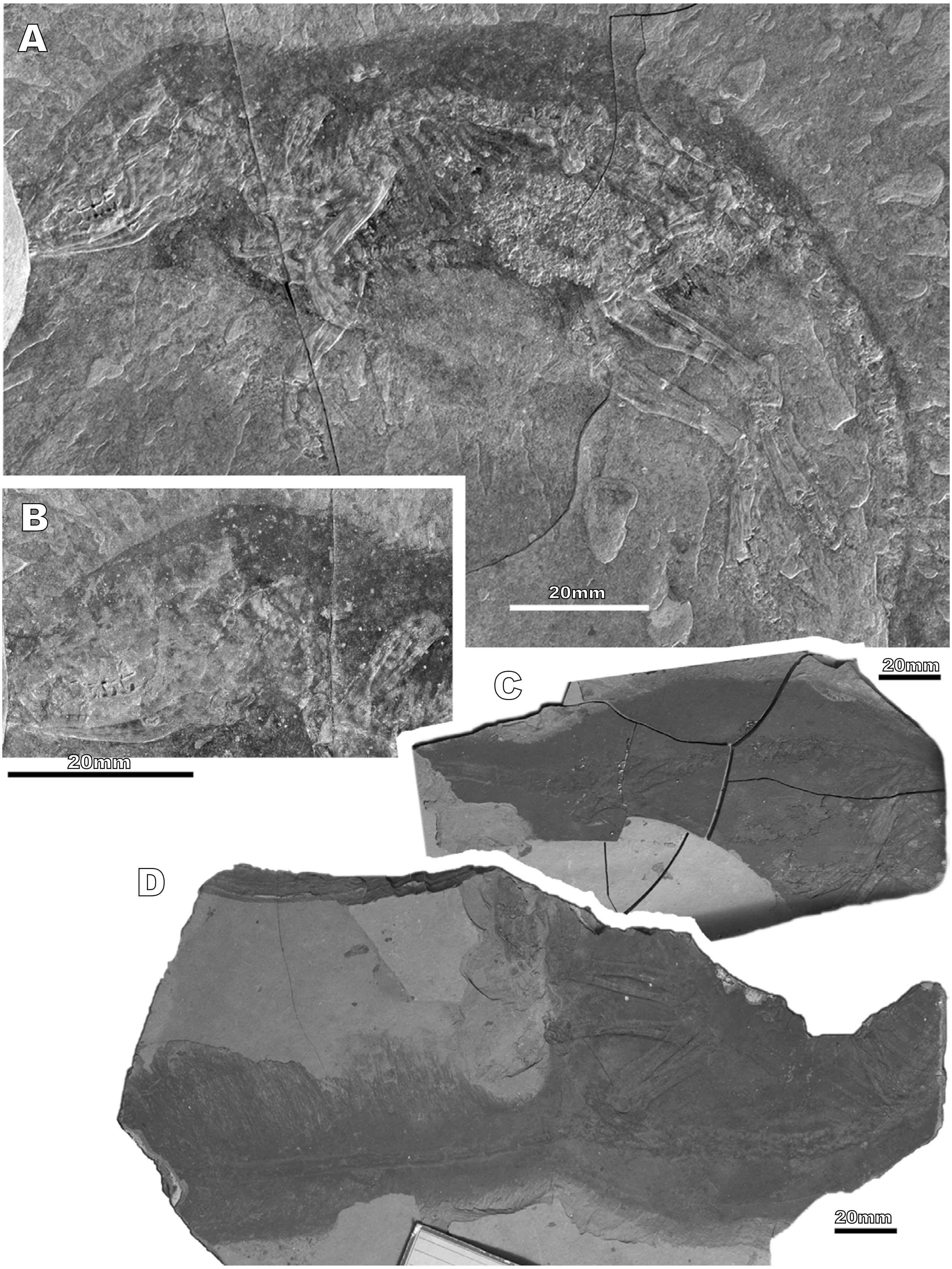

FIGURE 6. Fossil mammals from Menat. A and B) Full specimen and details of the head of the "insectivore" (?*Leptictis*); C and D) Plate A and B of a putative rodent (?*Sciuroides*). Photographs A and B by P. Loubry. Photographs C and D by S. Hervet.

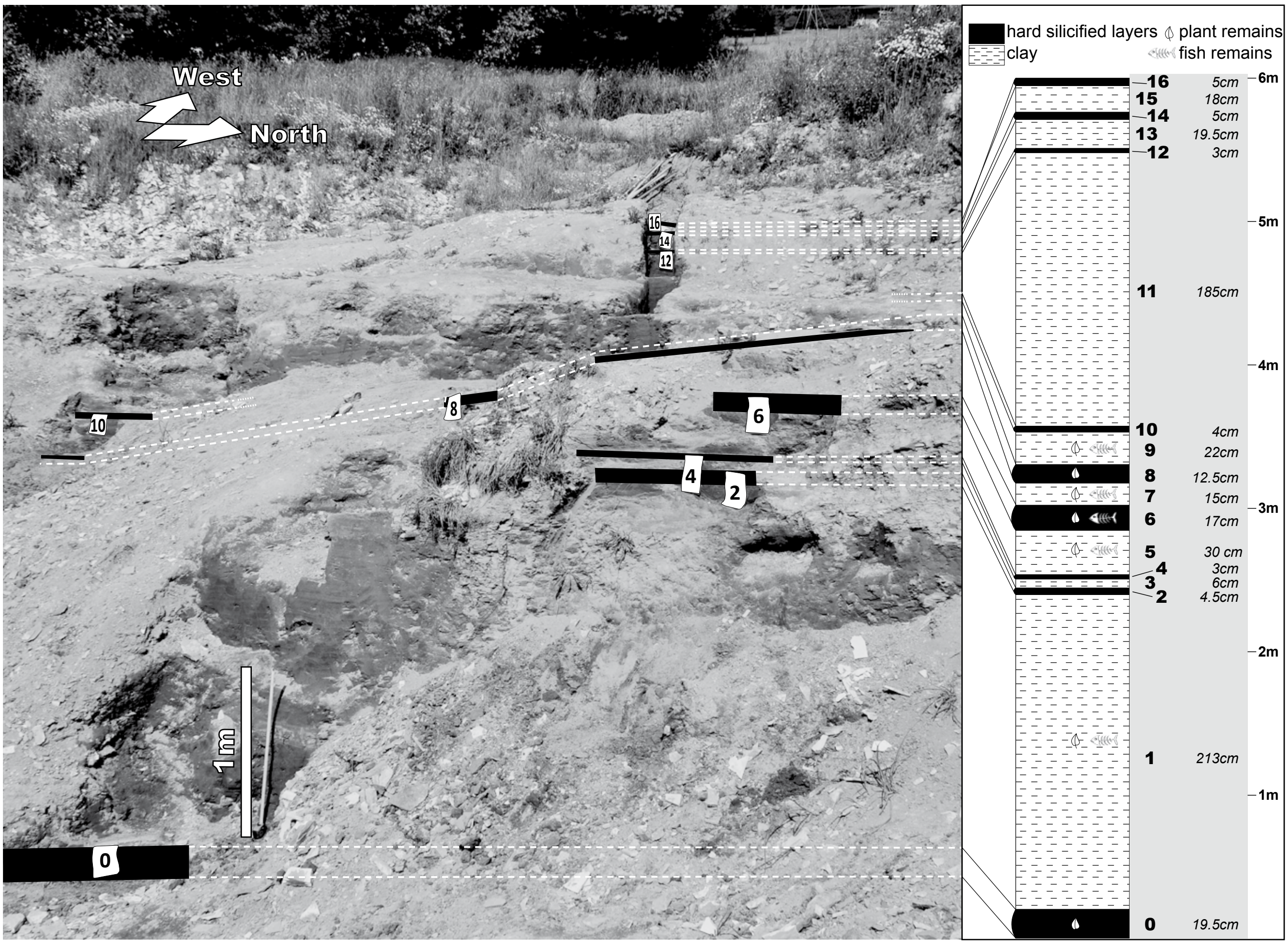

FIGURE 7. Stratigraphic log of site "Menat 1", done in June 2012. Hard silicified claystone (even numbers) and clay beds (odd numbers) have different consistent thicknesses. The white pieces scattered all over the site are touch-dry plates of silicified claystone.

"Menat 1" shows an intercalation of clay with nine hard, silicified claystone beds, 3 to 20cm-thick (Fig. 7). The stratigraphic log shows a thickness of 5.82m and can be followed laterally throughout the digging site. Clay beds are strongly weathered at the top. The originally organic-rich black clay, known from the outcrop "Stream site" (see below), shows a brownish color in the whole excavation site "Menat 1". The hard silicified claystones are greyish, shifting into light grey to white. While, in terms of morphology, the preservation of plants and fishes in silicified beds is quite good, it is poor in weathered clay.

In 2013 and 2014 field excavations were conducted at the new site "Menat 2", located near the eastern entrance to the village Menat at 46°06'21.9"N, 002°54'38.0"E, (Fig. 1C, site f). Wet chunks of clay were extracted and dried under tents for several days before they could be split and examined for fossils. In the upper beds of the stratigraphic log, unconsolidated clays were strongly weathered and broken up by numerous minor joints. As expected, the degree of weathering of the clay diminished noticeably in deeper levels.

Fossils recovered during these excavations were housed in the Epona building in Menat. They comprise over 1000 specimens, mainly plants (about 80%) and, to a much lesser extent, insects (less than 10%) and coprolites and fish remains (both about 5%). The preservation quality of the fossils, in general, is rather poor, as discussed in more detail below.

Correlation suggests that the deposits of "Menat 2" are about 20m above those of "Menat 1". The stratigraphic log of site "Menat 2" is 6m-thick (Fig. 8) and deeply weathered at the top. Below this weathered horizon, we divided the stratigraphic log into three intervals; A, B and C. In the basalmost interval A, from 0 to 1.68m, clays are dark grey to black, finely laminated and can easily be split without drying. These dark grey to black clays seem to be only weakly weathered. Interval B, from 1.68m to 3.05m, is formed by grey to dark grey clay. At 3.05m, the clay was interrupted by a hard-silicified claystone only a few centimeters-thick, called level BC. Such hard beds occur at different excavation sites and stratigraphic positions in Menat (*e.g.* the stratigraphic log of "Menat 1") and probably do not

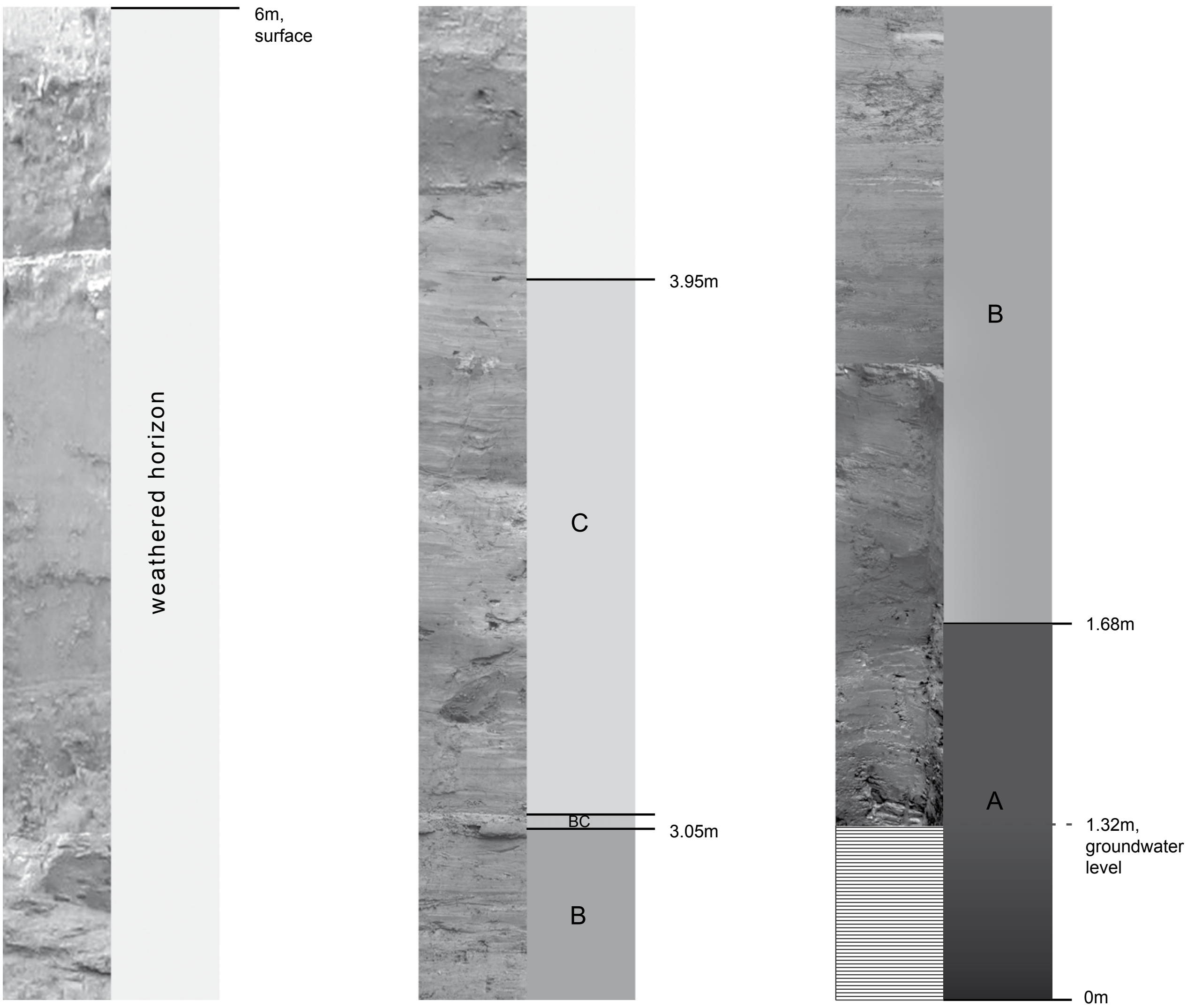

FIGURE 8. Exposed deposits of excavation site "Menat 2" illustrated as a stratigraphic column, presented here in three rows. The basalmost section was below the water level. The sequence is divided into the three intervals A, B, C (differentiated in the text) and the uppermost strongly weathered horizon.

correspond to diatomites, as they show no evidence of diatoms neither under light-microscope nor under the Scanning Electron Microscope (SEM). In interval C, from about 3 to 3.95m in the stratigraphic log, the lamination is recognizable and the clays could be split quite well after a few days of drying. The uppermost clay of this excavation site is brownish and strongly weathered, the organic content appears to decrease and the lamination is only recognizable after drying.

The preservation of organic matter differs strongly between different sites and stratigraphic levels. At "Menat 2", the uppermost 2–3m were in an advanced state of soil development and few fossils could be collected. They were mostly limited to impressions of plant and insect fossils, without any trace of organic matter. In lower levels, the lamination and fossil preservation became better, particularly in level A, where a higher number of fossils preserved organic matter.

During a field survey in 2014, another site was identified near the small stream traversing the village. Some samples of organic-rich clays were collected at 46°06.282'N, 002°54.370'E with permission of the municipality of Menat. At this survey point, which we call the "Stream site," the preservation of the fossils was much better than in the test sites "Menat 1" and "Menat 2". Most likely, this new site is correlated with the section excavated in the quarry "Les Grelins" and the quarry "La Mer", now overlain by a road, on the other river side.

Preservation of plants and insects

In all weathered deposits exposed near the surface, as well as in the silicified claystone, most plant fossils are preserved as impressions, with virtually no organic matter. Examples are leaves of *cf. Quercus* sp. (Fig. 9A), "*Cinnamonum*" *martyi* Fritel (Fig. 9B), *Dryophyllum dewalquei* Saporta et Marion (Fig. 9C), and "*Corylus*" *macquarrii* (Forbes) Heer (Fig. 9D) from localities "Menat 1" and "Menat 2."

In contrast, charcoal occurs mostly as compressions, even in weathered levels, since it is chemically stable and can be less easily oxidized and dissolved than other organic remains. Large pieces of charred wood, up to 15cm across, with excellent anatomical preservation (Fig. 10A; B), were found in some horizons, whereas smaller pieces, down to isolated tracheids of fragmented charcoal (Fig. 10C), were frequent in all lithologies analyzed so far. Investigated with SEM, specimens show homogenized cell walls, a feature characteristic of charred plant remains (Scott, 2000, 2010). In many horizons, charcoal is impregnated with silica, hampering a more detailed anatomical study. All charcoal samples investigated so far represent most probably conifers. A number of fern remains are also preserved as charcoal (Fig. 10D), with excellently preserved anatomical details (Fig. 10E).

Non-weathered deposits, such as organic-rich clay cropping out in horizons A and B from "Menat 2" (Fig. 8), contain cuticles and other organic remains (Figs. 9E and 11). Examples are an achene of a plant originally described from Menat as *Atriplex borealis* (Heer) Laurent (Fig. 9E), which probably represents *Palaeocarpinus* Crane

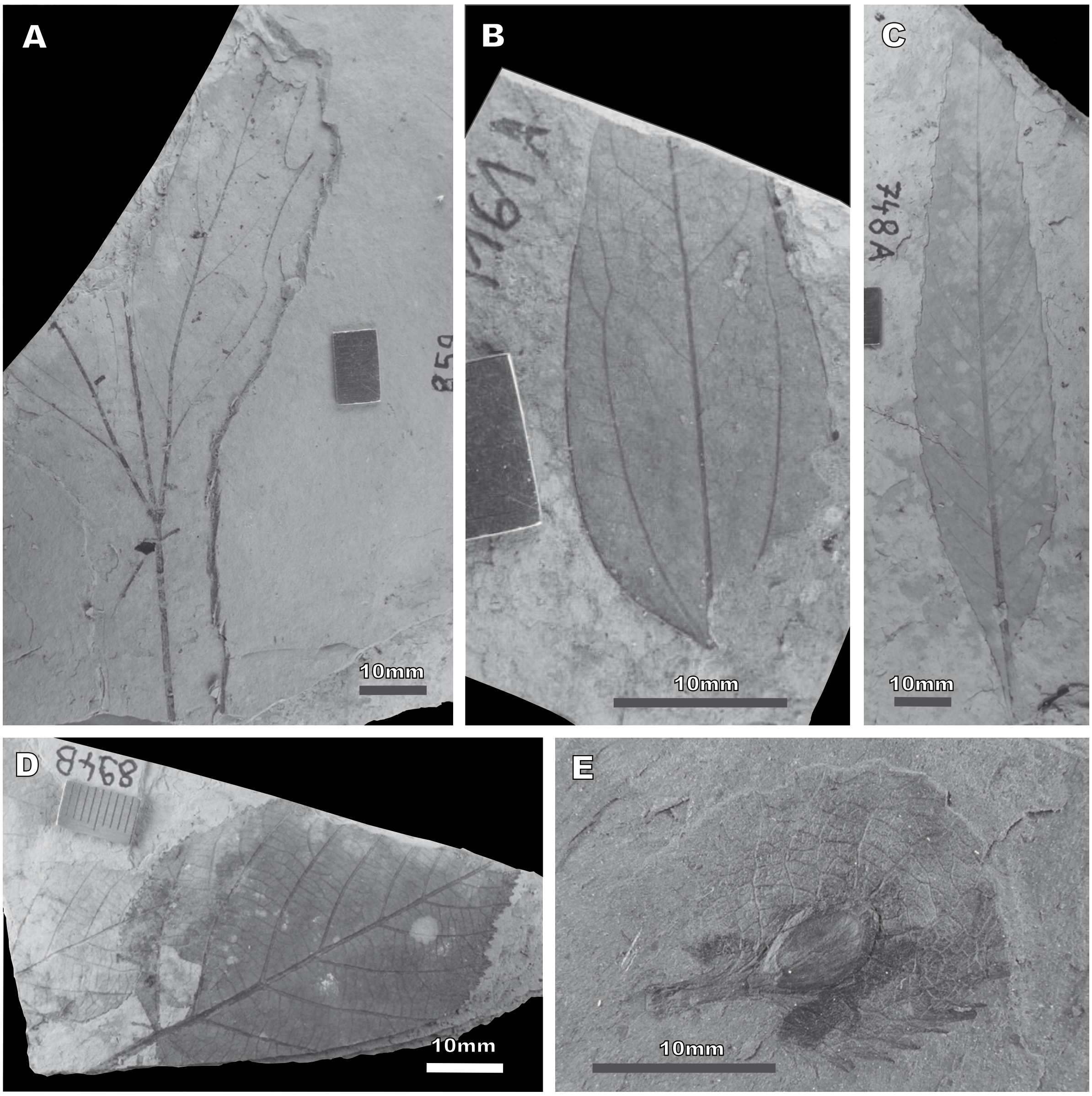

FIGURE 9. Fossil angiosperms from Menat. A) *cf. Quercus* sp.; B) "*Cinnamonum*" *martyi* Fritel; C) *Dryophyllum dewalquei* Saporta and Marion; D) "*Corylus*" *macquarrii* (Forbes) Heer; E) "*Atriplex*" *borealis* Heer (*cf. Palaeocarpinus* sp.); A–D housed in the Epona building in Menat, E housed in the Musée de Menat.

and a short shoot of *cf. Sequoia langsdorffii* (Brongniart) Heer (Fig. 11C) from the "Stream site".

Tridimensional woody remains like shoots (Fig. 11) are also preserved in the same deposits. Plant cell structures, such as stomata, epidermal and mesophyll cells, can be also observed in impressions and, in several cases, plant fossils are permineralized by yellow to reddish minerals (Fig. 11C; D).

Impressions of flowers in different lithologies have long been known from the outcrops of Menat (*e.g.* Laurent, 1912a; Piton, 1940), but detailed studies of such remains were not carried out yet. Flowers can bear excellently preserved pollen in their anthers (Fig. 11A; B). In sum, plant impressions, anatomically preserved plant remains, and *in situ* pollen suggest that there is a high potential for further study.

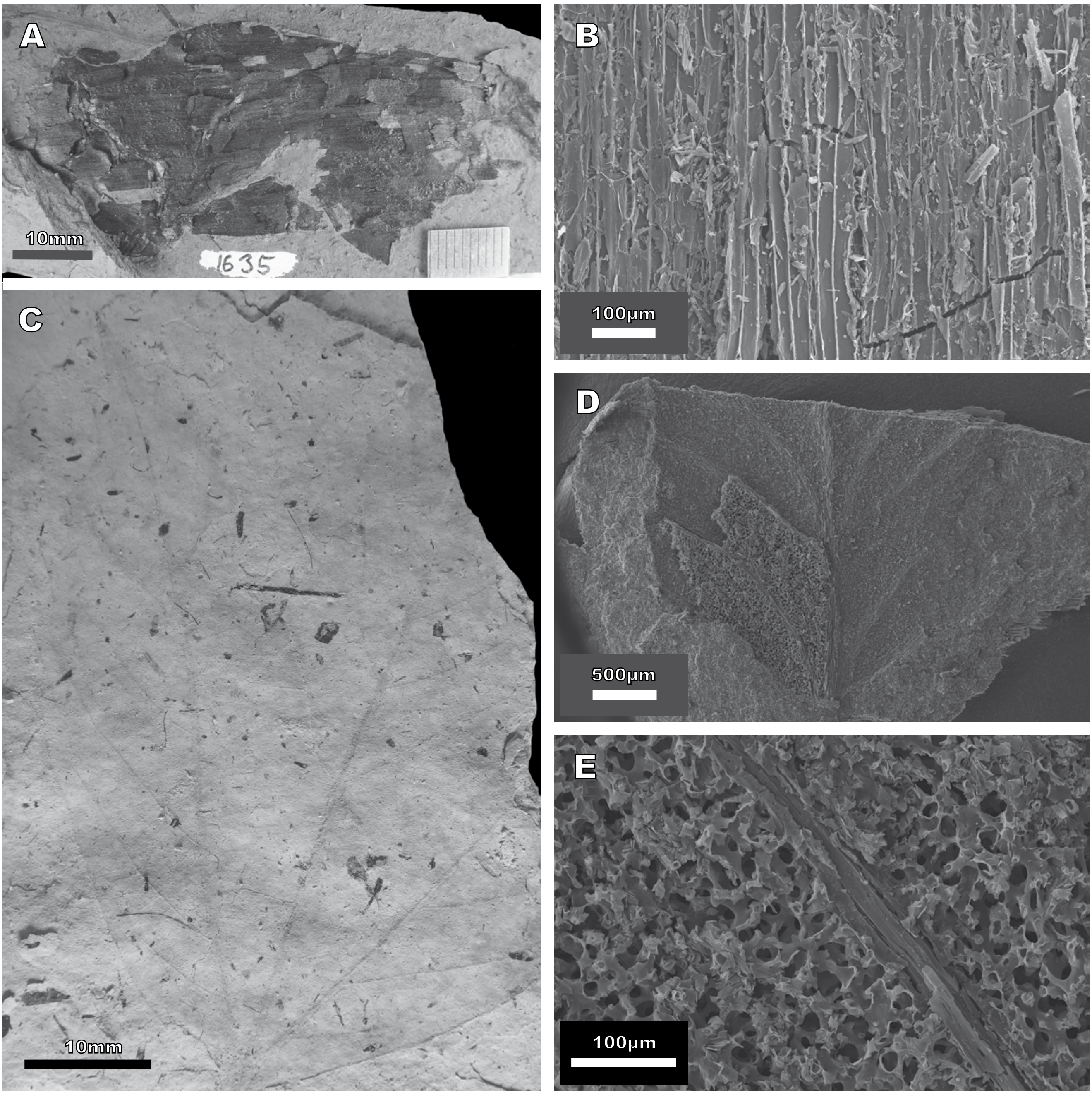

FIGURE 10. Various plant fossils from Menat. A) Large piece of woody charcoal; B) SEM microphotograph of charred wood in tangential view; C) Impression of *cf. Platanus schimperi* (Heer) Saporta and Marion with numerous small pieces of charcoal; D) SEM microphotograph of a fragment of a charred fern pinnule; E) Detail of D showing three-dimensionally preserved parenchyma and veins. All fossils are housed in the Epona building in Menat.

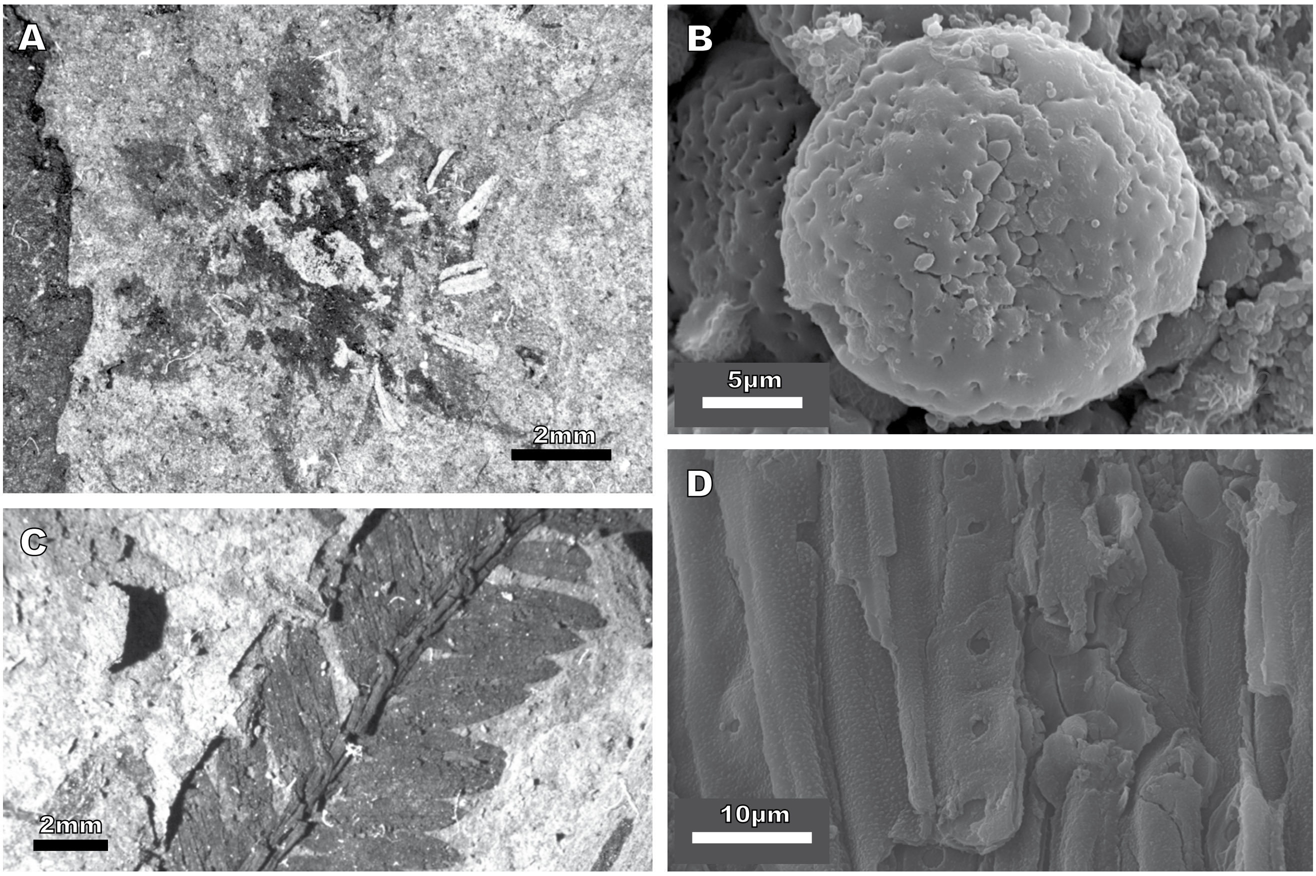

FIGURE 11. Fossil plants from Menat. A) Flower with pollen in anthers; B) SEM microphotograph of *in situ* pollen from specimen figured in A; C) Conifer remain with three-dimensional preservation, *cf. Sequoia langsdorffi* (Brongniart) Heer; D) SEM microphotograph of tracheids from specimen figured in C). All fossils are housed in the Musée de Menat.

During the excavations at "Menat 2" insects were not abundant and often not well-preserved. Most of them are impressions with little or without organic matter, but preserving sometimes rich details (Fig. 12). However, in level A at "Menat 2" the proportion of insects with organic matter increased. As for plants, the degree of preservation of organic matter in insects is correlated with the weathering degree of the different horizons.

Among the insects found on-site at "Menat 1" and "Menat 2", a significant proportion were beetles (Coleoptera), commonly weevils (Curculionoidea) (Fig. 12A; B), leaf beetles (Chrysomelidae) (Fig. 12E) and jewel beetles (Buprestidae). There was one rare record of an isolated wing of a woodwasp (Hymenoptera, Siricidae) (Fig. 12D) probably *Urocerus ligniticus* (Piton, 1940) based on wing venation. Woodwasps are generally very rare, but in Menat they appear to be more abundant (Wedmann *et al.*, 2014).

Investigations of slabs of clay from the historical quarry "Les Grelins" and from "Maison de retraite", which were dried for several weeks before splitting them, showed that the insect richness can be extraordinarily high. We estimate that *ca.* 3000 insects can be found in one cubic meter of these deposits, which is an order of magnitude higher than in the well-known Oligocene locality of Céreste (southern France) (R. Garrouste and A. Nel, 2017, personal observation).

Samples collected at the new "Stream site" outcrop display a better preservation than those from "Menat 2" (Fig. 13). The insect body is well-preserved as an organic film (*e.g.* Fig. 13A), and well-preserved wing venation allowed for determination of a mydid fly (Diptera, Mydidae) (Fig. 13B).

New data on insects

A database of 4622 insects has been created at MNHN (A. Nel and R. Garrouste) including specimens from the MNT and recent MNHN collections. The database provides the systematic placement of the fossil at order and family levels, and the outcrop from which it was collected. Coleoptera was the dominant order with 77.5% of the specimens collected, and consisting of very small specimens (2–6mm), with an overrepresentation of Curculionoidea (about 50%). Surprisingly, Hemiptera are the second most-abundant group, with 8% of specimens. With more than 6% of specimens, Blattodea are also well represented. Other orders are Orthoptera (2.5%), Hymenoptera (2.1%), Lepidoptera (1.8%, with some doubtful specimens), and Diptera (1.8%). Orders with less than 1% are: Odonata, Trichoptera, Ephemeroptera, Dermaptera, Mantodea, Neuroptera and, perhaps, one specimen from Isoptera.

Taphonomy, rather than community functioning, is the main influence for this unusual composition, with beetles strongly dominating over all other orders.

New data on fishes and turtles

Only 10% of the fossil specimens collected at "Menat 1" and "Menat 2" between 2012 and 2014, which are now housed in the Epona building in Menat, are fishes. The family Percichthyidae, represented by *Properca angusta*, represents more than 50% of these fishes. *Thaumaturus brongniarti* was also commonly found, with dozens of specimens of up to 7.5cm-long. Specimens of *Cyclurus valenciennesi* are rarely found

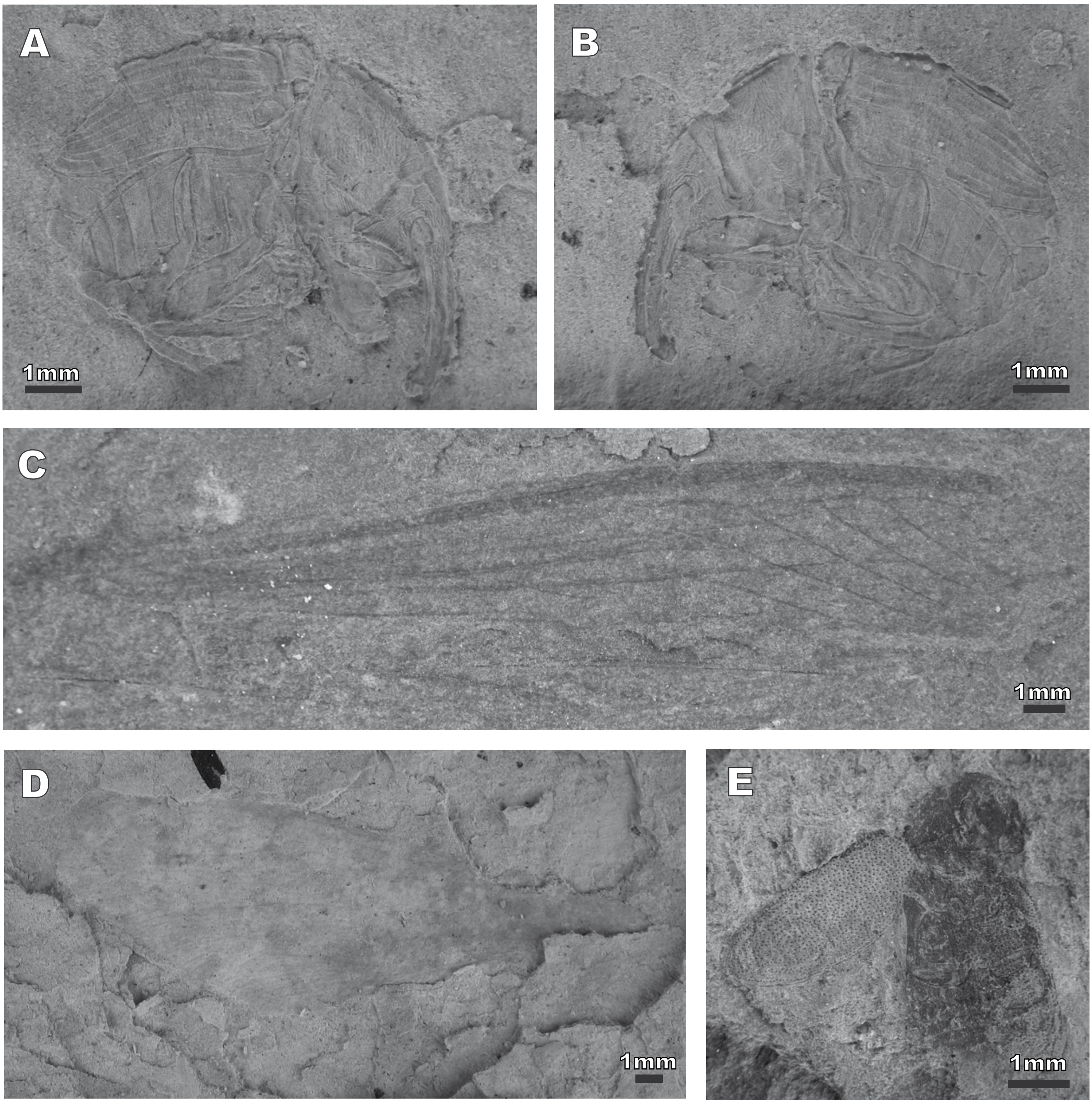

FIGURE 12. Fossil insects from Menat. A and B) Imprint of an undescribed weevil (Coleoptera: Curculionoidea). C) Wing remain of a grasshopper (Orthoptera: Caelifera). D) Wing remain of a wood wasp (Hymenoptera: Siricidae). E) Leaf beetle (Coleoptera: Chrysomelidae). All fossils are housed in the Epona building in Menat.

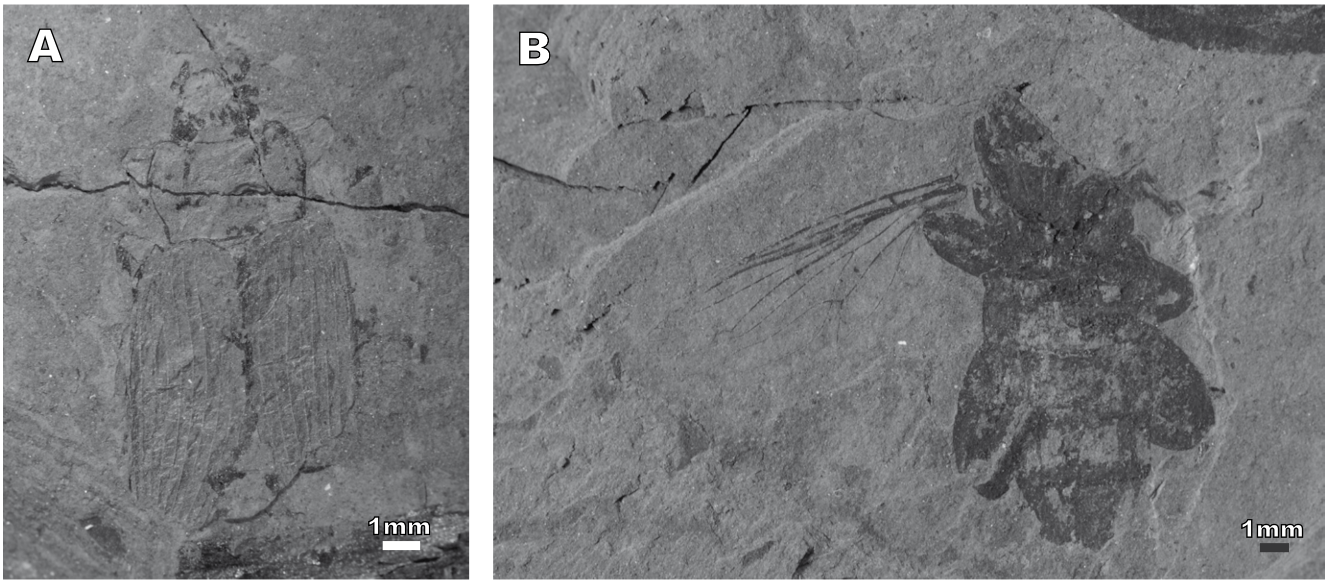

FIGURE 13. Fossil insects from Menat. A) undescribed ground beetle (Coleoptera: Carabidae); B) undescribed fly (Diptera: Mydidae). Both fossils are from the collection of the Musée de Menat.

and usually only represented by isolated scales, as identified by J. Gaudant (2014, personal communication). One individual of this species, of an estimated length of 30cm, consists of a part of the torso, backbone with scales and intestine contents.

A new turtle specimen was discovered and is deposited in the private collection Escuillié at Gannat (France). The distinctive pit-and-ridge sculpturing of the carapace elements (Fig. 14A; B) and the loss of the peripheral bones demonstrate that it belongs to the clade Trionychidae. Large portions of the plastron are preserved and seen in dorsal view, as well as a few poorly-preserved remnants of the carapace cover the plastron and the limb bones in places (Fig. 14C; D). The left posterolateral limb of the entoplastron is narrow and, were it complete, probably boomerang-shaped. Its proportions are similar to those in extant *Apalone*, which lacks a callosity. The hyoplastron and hypoplastron are fused, unlike in specimens referred to *Rafaetoides* (Karl, 1998). Their medial margins, especially that of the right element, are poorly-preserved but, assuming they are not significantly displaced, they did not contact one another along the midline. The medial margin of the left element shows a strong bulge at mid-length. The lateral hyoplastral process appears to be single, as in *Apalone*, whereas the lateral hypoplastral process is double, which corresponds to the primitive condition. The anterior margin of the hyoplastron and posterior margin of the hypoplastron are strongly concave, as in Trionychinae. The xiphiplastra are separate. The articulation with the hypoplastron appears to be of the trionychine type (Meylan, 1987), with the xiphiplastra lateral to the hypoplastra, as indicated by the combined morphology of the left and right elements. The xiphiplastra articulated with one another anteriorly along a short zone of interdigitation. Each possesses a long, tapering, posteromedial process, as in *Apalone* but not *Pelodiscus*. The left femur is well-preserved. The right hindlimb is more complete, comprising pubis, femur, tibia and fibula, but these bones are not well exposed.

Paleoenvironment

The occurrence of soot and charcoal in almost all horizons at Menat testifies the frequent occurrence of wildfires during the Paleocene in the vicinity of the Menat lake. So far, there are only a few records of Paleocene wildfires and they are mostly restricted to coal forming environments (Collinson *et al*., 2007, 2009; Diessel, 2010; Robson *et al*., 2015). Studies on profiles spanning the Paleocene–Eocene boundary have shown that fire regimes changed during this period, leading to less frequent but more serious fires during the Eocene (*e.g*. Collinson *et al*., 2007, 2009; Robson *et al*., 2015). Therefore, Menat is an excellent locality in which to study the regional development of fire regimes during the Paleocene and its relationships to climatic and other environmental changes.

CONCLUSIONS

Menat is a significant Paleocene *Konservat-Lagerstätte* in Europe, yielding well-preserved plant, invertebrate and vertebrate fossils. The different fossil collections from Menat, partly historical and partly recent, come from different excavation sites and beds that are difficult to correlate with each other. The historical collections were investigated in the first half of the 20th century, but these studies are now outdated and need revision. As regards fossil plants, new data suggest that the potential for taxonomic studies based on modern techniques, such as cuticule analysis or *in situ* pollen analysis, is high.

More research has been done on insects in the last decades; several selected groups of insects have been studied after Piton (1940), but an updated comprehensive study of the rich insect oryctocoenoses is missing. Among vertebrates, fishes are the most frequent fossils, whereas tetrapods are very rare. Although meager in quantity, the quality of preservation of the fossil tetrapods from Menat bears a potential for groundbreaking discoveries. For example, one out of the four mammal fossils found in Menat is a primate, significant for research on primate evolution worldwide.

In order to understand the long-term development of the maar lake of Menat, a scientific drilling project should be conducted to reach the oldest known strata (as visible, for example, at "Menat 2") and going, probably, at least 300m-Sdeep. The resulting borehole will be crucial for new and high-resolution studies on the sedimentology, taphonomy, and palynology of the site. This would also enable the distinction of possible key horizons to correlate the different excavation sites with each other, as done before in the Messel Fossil Pit (Schaal and Ziegler, 1992). After this drilling project, and armed with a better knowledge of the stratigraphy of the maar, large-scale scientific excavations could be strategically planned in beds deep enough to skip the superficial weathering. There, organic-rich clay, which provides the best preservation quality for fossil plants, insects, and vertebrates, would be reached. Such excavations would dramatically increase the probability to find very rare taxa, such as mammals.

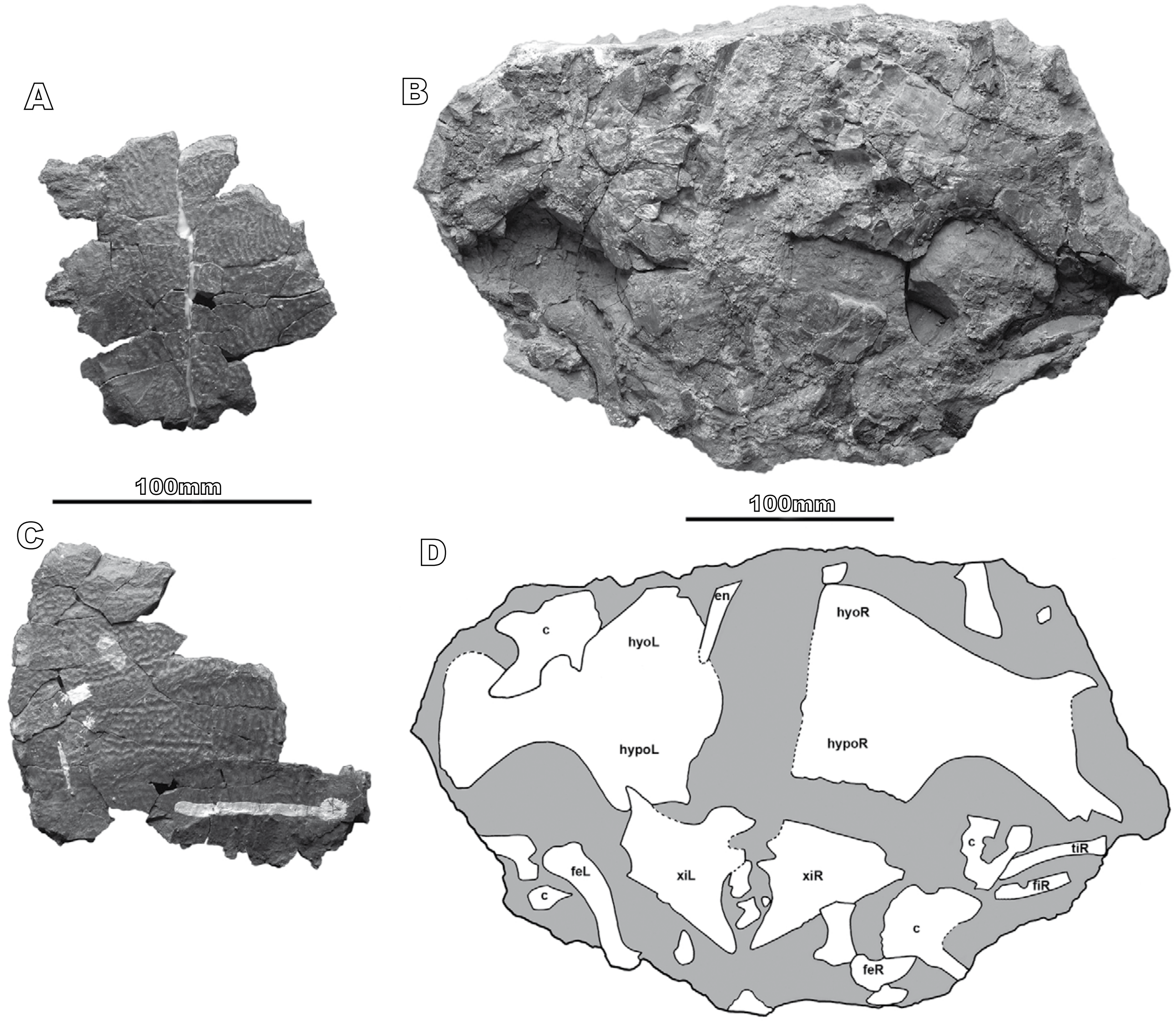

FIGURE 14. Fossil trionychid turtle specimen from Menat, housed in the private collection Escuillié, Gannat. A and B) Two portions of the carapace, showing the distinctive pit-and-ridge sculpturing of the dorsal surface; C and D) Nodule containing much of the plastron (seen in dorsal view), as well as parts of the carapace and hind-limbs. Abbreviations: c, carapace; en, entoplastron; fe, femur; fi, fibula; hyo, hyoplastron; hypo, hypoplastron; ti, tibia; xi, xiphiplastron; L and R, left and right element, respectively. Same scale bar applies to A and C.

ACKNOWLEDGMENTS

S. Wedmann, D. Uhl, T. Lehmann and S. Schaal thank the Deutsche Forschungsgemeinschaft for financial support of their work in Menat (DFG UH 122/6–1, WE 2942/7–1). R. Garrouste and A. Nel thank UMR 7205 "ISyEb" and MNHN for support, and also Mme Valère for information and collection management. Most sincere thanks of all authors go to Epona and Eldonia, especially to Dr. *h.c.* Burkhard Pohl, and Francois Escuillié for their generous support of our stay and fieldwork in Menat and for the access to their fossils. J.-M. Pouillon, associated with Rhinopolis and Epona, was very helpful for logistic questions and fieldwork whenever his advice was needed. We want to sincerely thank the mayor D. Mazuel and the municipality of Menat for their cooperation and, also, especially Dr. S. Hervet, associated with the Musée de Menat, for her help. We also want to thank the Communauté de Commune du Pays de Menat. Dr. S. Pelucchi is thanked for granting access to the fossil insect collections at the Muséum d'Histoire Naturelle Henri Lecoq, Clermont-Ferrand (MHNHL). Senckenberg Research Institute thanks private collector K.D. Weiß, Fischbach, for the loan of fossil fishes from Menat for scientific analysis and donation to the Senckenberg collection.

All participants in the 2012, 2013 and 2014 field seasons are thanked for their support. In particular, we acknowledge the crucial help provided by the technical assistants and preparators from the Senckenberg Research Institute, as well as the enthusiasm of the French and German students who participated in the 2014 excavations.

We would like to thank Dr. E. de Bast, an anonymous reviewer, and the editor Dr. C. Martín-Closas for their thorough revision of the manuscript.

REFERENCES

Agassiz, L., 1833–44. Recherches sur les poissons fossiles. Petitpierre, Neuchâtel, 5 vols.

Archibald, J.D., Deutschman, D.H., 2001. Quantitative analysis of the timing of the origin and diversification of extant placental orders. Journal of Mammalian Evolution, 8(2), 107-124.

Balazuc, J., Descarpentries, A., 1964. Sur *Lampra gautieri* Bruyant et quelque autres Buprestidae fossiles des schistes de Menat. Bulletin de la Société Entomologique de France, 69, 47-56, 101-108.

Benton, M.J., 1995. Diversification and extinction in the History of Life. Science, 268, 52-58.

Boulard, M., Nel, A., 1990. Sur deux cigales fossiles des terrains tertiaires de la France (Homoptera, Cicadoidea). Revue Française d'Entomologie, (Nouvelle Serie), 12(1), 37-45.

Brongniart, A., 1828. Prodrome d'une histoire des végétaux fossiles. París, F.G. Levrault publisher, 223pp.

Brongniart, Ch., 1880. Notice sur quelques poissons des lignites de Menat. Bulletin de la Société Linnéenne de Normandie, IV, 353-358.

Brusatte, S.L., O'Connor, J.K., Jarvis, E.D., 2015. The origin and diversification of birds. Current Biology, 25(19), R888–R898.

Bruyant, C., 1902. Bupreste fossile des lignites de Menat, *Lampra gautieri* . Revue Scientifique du Bourbonnais et du Centre de la France, 15, 63-65.

Bryant, L.J., 1989. Non-dinosaurian lower vertebrates across the Cretaceous-Tertiary boundary in northeastern Montana. University of California Publications in Geological Sciences, 134, 1-107.

Collinson, M., Steart, D.C., Scott, A.C., Glasspool, I.J., Hooker, J.J., 2007. Episodic fire, runoff and deposition at the Palaeocene-Eocene boundary. Journal of the Geological Society, 164, 87-97.

Collinson, M.E., Steart, D.C., Harrington, G.J., Hooker, J.J., Scott, A.C., Allen, L.O., Glasspool, I.J., Gibbons, S.J., 2009. Palynological evidence of vegetation dynamics in response to palaeoenvironmental change across the onset of the Paleocene-Eocene Thermal Maximum at Cobham, Southern England. Grana, 48, 38-66.

Dangeard, L., 1934. Observations sur les schistes bitumineux de Menat et sur une roche à grains de pollen du Puy de Mur et de Gergovie. Bulletin de la Société d'Histoire Naturelle d'Auvergne, 22, 26-32.

De Bast, E., Smith, T., 2017. The oldest Cenozoic mammal fauna of Europe: implication of the Hainin reference fauna for mammalian evolution and dispersals during the Paleocene. Journal of Systematic Palaeontology, 15(9), 741-785.

De Bast, E., Smith, T., Sigé, B., 2012. Diversity of the adapisoriculid mammals from the early Palaeocene of Hainin, Belgium. Acta Palaeontologica Polonica, 57(1), 35-52.

De Broin, F., 1977. Contribution à l'étude des chéloniens: chéloniens continentaux du Crétacé et du Tertiaire de France. Mémoires du Muséum national d'Histoire Naturelle, n.s., C 38, 1-366, pls. I-XXXVIII.

De Launay, L., 1908. La fourrure d'un écureuil tertiaire. La Nature (Paris), 36, 393-395.

Diessel, C.F.K., 2010. The stratigraphic distribution of inertinite. International Journal of Coal Geology, 81, 251-268.

Dlussky, G.M., Wedmann S., 2012. Poneromorph ants (Hymenoptera, Formicidae: Amblyoponinae, Ectatomminae, Ponerinae) of Grube Messel, Germany: Diversification during the Eocene. Journal of Systematic Palaeontology, 10, 725-753.

D'Hondt, S., 2005. Consequences of the Cretaceous/Paleogene mass extinction for marine ecosystems. Annual Review of Ecology and Evolutionary Systematics, 36, 295-317.

Dunn, R.H., Rasmussen, D.T., 2009. Skeletal Morphology of a new genus of Eocene insectivore (Mammalia, Erinaceomorpha) from Utah. Journal of Mammalogy, 90(2), 321-331.

Evans, S.E., Jones, M.E.H., 2010. The origin, early history and diversification of lepidosauromorph reptiles. In: Bandyopadhyay, S. (ed.). New Aspects of Mesozoic Biodiversity. Heidelberg, Germany, Springer, 27-44.

Fastovsky, D.E., Sheehan, P.M., 2005. The extinction of the dinosaurs in North America. GSA Today, 15, 4-10.

Fastovsky, D.E., Bercovici, A., 2016. The Hell Creek Formation and its contribution to the Cretaceous–Paleogene extinction: A short primer. Cretaceous Research, 57, 368-390.

Friedrich, F., 1883. Beiträge zur Kenntnis der Tertiärflora der Provinz Sachsen. Abhandlungen zur Geologischen Specialkarte Preussens, 4, 1-305.

Garrouste, R., Wedmann, S., Pouillon, J.-M., Nel, A., 2016a. The oldest 'amphipterygid' damselfly of tropical affinities in the Paleocene of Menat (Zygoptera: Eucaloptera). Historical Biology, 29, 818-821. DOI: 10.1080/08912963.2016.1247448

Garrouste, R., Pouillon, J.-M., Nel, A., 2016b. The first Cenozoic roproniid wasp from the Paleocene of Menat, France (Hymenoptera, Proctotrupoidea). European Journal of Taxonomy, 239, 1-9.

Gaudant, J., 1979. Mise au point sur l'ichthyofaune paléocène de Menat (Puy-de-Dôme). Comptes rendus de l'Académie des Sciences, 288, 1461-1464.

Gaudant, J., 1987. Mise au point sur certains poissons Amiidae du Cénozoic européen: Le genre *Cyclurus* AGASSIZ (=*Kindleia* JORDAN). Paläontologische Zeitschrift, 61(3/4), 321-330.

Gaudant, J., 2000. Nouvelles observations sur quelques Percoidei (Poissons téléostéens) des eaux douces et saumâtres du Cénozoïque européen. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen, 217(2), 199-244.

Gheerbrant, E., 2009. Paleocene emergence of elephant relatives and the rapid radiation of African ungulates. Proceedings of the National Academy of Sciences, 106(26), 10717-10721.

Grimaldi, D., Engel, M.S., 2005. Evolution of the insects. Cambridge University Press, Cambridge, New York, 755pp.

Gunnell, G.F., Bown, T.M., Bloch, J.I., 2008. Leptictida. In: Janis C.M., Gunnell, G.F., Uhen, M.D. (eds.). Evolution of Tertiary Mammals of North America Vol. 2: Marine Mammals and Smaller Terrestrial Mammals. Cambridge, Cambridge University Press, 82-88.

Guth, C., 1962. Un insectivore de Menat. Annales de Paléontologie, 48, 1-10.

Hartung, V., Garrouste, R., Pouillon, J.-M., Nel, A., 2016. First fossil of Cylindrostethinae (Heteroptera: Gerromorpha: Gerridae) in the Paleocene of Menat, France. Palaeontologia Electronica, 19.3.33A, 1-10.

Heer, O., 1859. Flora tertiara Helvetiae III. Verlag von Wurster und Comp., Winterthur, 378pp.

Heer, O., 1861. Recherche sur le climat et la végétation du pays tertiaire. Editeurs Jean Wurster and Comp., Winterthur, xxii + 220pp.

Holroyd, P.A., Wilson, G.P., Hutchison, J.H., 2014. Temporal changes within the latest Cretaceous and early Paleogene turtle faunas of northeastern Montana. Geological Society of America Special Paper, 503, 299-312.

Jensen, M.S., 2008. The radiation and diversification of birds after the Cretaceous/Paleogene boundary. Seven new avian fossils from late Palaeocene Menat in Auvergne, France. Unpublished Master Thesis, Geological Museum and Geological Institute, Copenhagen, Denmark, 71pp.

Johnson, K., Ellis, B., 2002. A tropical rainforest in Colorado 1.4 million years after the Cretaceous-Tertiary boundary. Science, 296, 2379-2383.

Karl, H.-V., 1998. Zur Taxonomie der känozoischen Weichschildkröten Österreichs und Deutschlands (Trionychidae: Trionychinae). Mitteilungen der Abteilung Geologie und Paläontologie, Joanneum, 56, 273-328.

Kedves, M., 1967. Quelques types de sporomorphes du bassin lignitifères de Menat. Acta Biologica Szegediensis, 13, 11-23.

Kedves, M., Russell, D.E., 1982. Palynology of the Thanetian layers of Menat. The geology of the Menat Basin, France. Palaeontographica Abt. B, 182, 87-150.

Kirejtshuk, A.G., Nel, A., Collomb, F.-M., 2010. New Archostemata (Insecta: Coleoptera) from the French Paleocene and Early Eocene, with a note on the composition of the suborder. Annales de la Société Entomologique de France (Nouvelle Serie), 46, 216-227.

Kirejtshuk, A.G., Nel, A., Kirejtshuk, P.A., 2016. Taxonomy of the reticulate beetles of the subfamily Cupedinae (Coleoptera: Archostemata), with a review of the historical development. Invertebrate Zoology, 13(2), 61-190.

Knobloch, E., Mai, H.D., 1986. Monographie der Früchte und Samen in der Kreide von Mitteleuropa. Rozpravy Ústředního ústavu geologického, 47, 1-221.

Krutzsch, W., 1967. Der Florenwechsel im Alttertiär Mitteleuropa auf Grund von sporenpaläontologischen Untersuchungen. Abhandlungen des Zentralen Geologischen Instituts, 10, 17-37.

Kvaček, Z., 2010. Forest flora and vegetation of the European early Palaeogene – a review. Bulletin of Geosciences, 85, 63-76.

Labandeira, C.C., Sepkoski, J.J., 1993. Insect diversity in the fossil record. Science, 261, 310-315.

Labandeira, C.C., Johnson, K.R., Wilf, P., 2002. Impact of the terminal Cretaceous event on plant–insect associations. PNAS, 99, 2061-2066.

Laurent, L., 1909. Contribution à la flore fossile du centre de la France: Un *Menispermum* nouveau (*M. europaeum*) dans les schistes de Menat. Annales de la Faculté des Sciences de Marseille, 18, 1-14.

Laurent, L., 1911. A propos des échantillons des schistes à végétaux de Menat (Puy-de-Dôme) faisant partie de la collection Tribolet. Société Neuchâteloise des Sciences Naturelles, 39, 121-136.

Laurent, L., 1912a. Flore fossile des schistes de Menat (Puy-de-Dôme). Annales du Musée d'Histoire Naturelle de Marseille, 14, 1-246.

Laurent, L., 1912b. Sur la présence du genre "*Atriplex*" dans la flore fossile de Menat (Puy-De-Dôme). Comptes rendus de l'Association Française pour l'Avancement des Sciences, Congrès de Dijon 1911, 40, 379-385.

Laurent, L., 1919. Contribution à l'étude des flores fossiles du Centre de la France. Addition à la flore des schistes de Menat (Puy-de-Dôme). Annales du Musée d'Histoire naturelle de Marseille, 17, 1-8.

Laurent, L., Marty, P., 1910. Note sur le *Castanea arvernensis* Sap. de Menat. Comptes Rendus de l'Association Française pour l'Avancement des Sciences, Congrès de Lille 1909, 38, 607-615.

Laurent, L., Marty, P., 1939. Flore fossile du Puy-de-Mur (Puy-de-Dôme) et liste des espèces végétales fossiles des Schistes de Menat. Avec une introduction géologique par A. Rudel. Annales de la Faculté des Sciences de Marseille, 12(2), 99-132.

Lecoq, H., 1829. Description géologique du bassin de Menat. Annales de la Société industrielle et statistique de l'Auvergne, 11, 433-447. [Publiées par l'Académie des Sciences, Belles-Lettres et Arts de Clermont]

Legalov A.A., Nel, A., Kirejtshuk, A.G., 2017. New and little known weevils (Coleoptera: Curculionoidea) from the Paleocene of Menat (France). Comptes Rendus Palevol, 16(3), 248-256.

Lehmann, T, Schaal, S. (eds.), 2011. The world at the time of Messel: Puzzles in Palaeobiology, Palaeoenvironment, and the history of early Primates. Conference Volume 22nd International Senckenberg Conference, 15th–19th November 2011, Frankfurt am Main, 202pp.

Lehmann, T. Schaal, S. (eds.), 2012. Special Issue: Messel and the terrestrial Eocene. Proceedings of the 22nd Senckenberg Conference. Palaeobiodiversity and Palaeoenvironments, 92, 397-663.

Lloyd, G.T., Davis, K.E., Pisani, D., Tarver, J.E., Ruta, M., Sakamoto, M., Hone, D.W.S., Jennings, R., Benton, M.J., 2008. Dinosaurs and the Cretaceous terrestrial revolution. Proceedings of the Royal Society B, 275, 2483-2490.

Longrich, N.L., Tokaryk, T., Field, D.J., 2011. Mass extinction of birds at the Cretaceous–Paleogene (K–Pg) boundary. Proceedings of the National Academy of Sciences U.S.A,. 108, 15253-15257.

Longrich, N.L., Bhullar, B.A.S., Gauthier, J.A., 2012. Mass extinction of lizards and snakes at the Cretaceous–Paleogene boundary. Proceedings of the National Academy of Sciences U.S.A., 109, 21396-21401.

Longrich, N.L., Scriberas, J., Wills, M.A., 2016. Severe extinction and rapid recovery of mammals across the Cretaceous–Palaeogene boundary, and the effects of rarity on patterns of extinction and recovery. Journal of Evolutionary Biology, 29(8), 1495-1512.

Lyson, T.R., Joyce, W.G., 2009. A revision of *Plesiobaena* (Testudines: Baenidae) and an assessment of baenid ecology across the K/T boundary. Journal of Paleontology, 83, 833-853.

MacLeod, N., Rawson, P.F., Forey, P., Banner, F.T., Boudagher-Fadel, M.K., Bown, P.R., Burnett, J.A., Chambers, P., Culver, S.J., Evans, S.E., Jeffery, C.H., Kaminski, M.A., Lord, A.R., Milner, A.C., Milner, A.R., Morris, N., Owen, E., Rosen, B.R., Smith, A.B., Taylor, P.D., Urquhart, E., Young, J.R., 1997. The Cretaceous-Tertiary biotic transition. Journal of the Geological Society, 154, 265-292.

Mai, D.H., 1995. Tertiäre Vegetationsgeschichte Europas. Gustav Fischer Verlag, Jena, Stuttgart and New York, 681pp.

Mai, D.H., Walther, H., 1978. Die Floren der Haselbacher Serie im Weißelster-Becken (Bezirk Leipzig, DDR). Abhandlungen des Staatlichen Museums für Mineralogie und Geologie zu Dresden, 28, 1-200.

Maier, W., 1979. *Macrocranion tupaiodon*, an adapisoricid (?) insectivore from the Eocene of 'Grube Messel'(Western Germany). Paläontologische Zeitschrift, 53(1-2), 38-62.

Martin, J.E., Smith, T., de Lapparent de Broin, F., Escuillié, F., Delfino, M., 2014. Late Palaeocene eusuchian remains from Mont de Berru, France, and the origin of the alligatoroid Diplocynodon. Zoological Journal of the Linnean Society, 172(4), 867-891.

Matsumoto, R., Buffetaut, E., Escuillié, F., Hervet, S., Evans, S.E., 2013. New material of the choristodere *Lazarussuchus* (Diapsida, Choristodera) from the Paleocene of France. Journal of Vertebrate Paleontology, 33(2), 319-339.

Mayr, G., Hervet, S., Buffetaut, E., 2018. On the diverse and widely ignored Paleocene avifauna of Menat (Puy-de-Dôme, France): new taxonomic records and unusual soft tissue preservation. Geological Magazine, 1-13. DOI: 10.1017/S0016756818000080

McKenna, M.C., Bell, S.K., 1997. Classification of mammals above the species level. Columbia University Press, New York, 631pp.

Meylan, P.A., 1987. The phylogenetic relationships of the soft-shelled turtles (family Trionychidae). Bulletin of the American Museum of Natural History, 186, 1-101.

Michez, D., de Meulemeester, T., Rasmont, P., Nel, A., Patiny, S., 2009. New fossil evidence of the early diversification of bees: *Paleohabropoda oudardi* from the French Paleocene (Hymenoptera, Apidae, Anthophorini). Zoologica Scripta, 38, 171-181.

Michon, L., Merle, O., 2001. The evolution of the Massif Central rift: spatio-temporal distribution of the volcanism. Bulletin de la Société Géologique de France, 172(2), 201-211.

Monestier H., Lavina, P., 1995. Géologie et minéralogie: histoire des mines. Combrailles et Patrimoine, Syndicat mixte pour l'aménagement et le développement des Combrailles (SMADC), 96pp.

Monpied, E., 2003. La production de noir animal à Menat. Combronde: Brayauds et Combrailles, 40pp.

Nabozhenko, M.V., Kirejtshuk, A.G., 2014. *Cryptohelops menaticus*–a new genus and species of the tribe Helopini (Coleoptera: Tenebrionidae) from the Palaeocene of Menat (France). Comptes Rendus Palevol, 13(2), 65-71.

Nectoux, P., 1981–1982. Sur un Diptère Nématocère des schistes bitumineux éocènes de Menat (Puy-de-Dome). Société d'Histoire Naturelle du Creusot, Bulletin, 38, 12-14.

Nel, A., 1988. Redescription de *Eosirex ligniticus* Piton, 1940 (Hymenoptera Symphyta Siricidae) L'Entomologiste, 44(5), 287-292.

Nel, A., 1989. Les Gyrinidae fossiles de France (Coleoptera). Annales de la Société Entomologique de France (Nouvelle Serie), 25(3), 321-330.

Nel, A., 1991. Analyse d'Entomofaunes cénozoïques. Intérêt de la Paléoentomologie pour les Sciences de la Terre et de la Vie. Unpublished Thèse de Doctorat (nouveau régime), Université de Reims-Champagne-Ardenne, France, 882pp.

Nel, A., 1992. Révision du statut de *Manevalia pachyliformis* Piton, 1940 (Insecta, Heteroptera, Hymenoptera). Entomologica Gallica, 3(2), 76-77.

Nel, A., 2007. Les Bibionidae du Paléocène de Menat (Puy-de-Dôme, France) (Diptera). Bulletin de la Société Entomologique de France, 112(3), 369-370.

Nel, A., 2008. The oldest bee fly in the French Paleocene (Diptera: Bombylidae). Comptes Rendus Palevol, 7, 401-405.

Nel. A., Roy, R., 1996. Revision of the fossil "mantid" and "ephemerid" species described by Piton from the Palaeocene of Menat (France) (Mantodea: Chaeteessidae, Mantidae; Ensifera: Tettigonioidae. European Journal of Entomology, 93, 223-234.

Nel, A., Petrulevicius, J.F., 2003. New Palaeogene bees from Europe and Asia. Alcheringa, 27, 227-293.

Nel, A., Auvray, F., 2006. The oldest Vespinae from the Paleocene of Menat (France) (Hymenoptera: Vespidae). Zootaxa, 1344, 59-62.

Nel, A., Martínez-Delclòs, X., Papier, F., Oudard, J., 1997. New Tertiary fossil Odonata from France. (Sieblosiidae, Lestidae, Coenagrioniidae, Megapodagrionidae, Libellulidae). Deutsche Entomologische Zeitschrift, 44(2), 231-258.

Nel, A., Nel, P., Petruleviius, J.F., Perrichot, V., Prokop, J., Azar, D., 2010a. The Wagner Parsimony using Morphological Characters: a new method for palaeosynecological studies. Annales de la Société Entomologique de France, (Nouvelle Serie), 46(1-2), 276-292.

Nel, A., Azar, D., Hervet, S., 2010b. A new rhopalosomatid wasps in the Paleocene of France (Hymenoptera). Annales de la Société Entomologique de France, (Nouvelle Serie), 46, 211-215.

Nichols, D.J., Johnson, K.R., 2008. Plants and the K-T Boundary. Cambridge, Cambridge University Press, X + 280pp.

Nicholson D.B., Mayhew P.J., Ross A.J., 2015. Changes to the Fossil Record of Insects through Fifteen Years of Discovery. PLoS ONE, 10(7), e0128554. DOI: 10.1371/journal.pone.0128554

Peláez-Campomanes, P., López-Martínez, N., Álvarez-Sierra, M.A., Daams, R., 2000. The earliest mammal of the European Paleocene: the multituberculate Hainina. Journal of Paleontology, 74(4), 701-711.

Pérez-García, A., 2012. *Berruchelus russelli*, gen. et sp. nov., a paracryptodiran turtle from the Cenozoic of Europe. Journal of Vertebrate Paleontology, 32(3), 545-556.

Piton, L., 1936. Les Hémipteres fossiles de l'Eocene de Menat. *Miscellanea Entomologica*, 37, 93-94.

Piton, L., 1937. Les reptiles fossiles de Menat. Revue scientifique du Bourbonnais et du Centre de la France, 50, 15-18.

Piton, L., 1940. Paléontologie du gisement Èocène de Menat (Puy-de-Dôme) (Faune et Flore). Mémoire de la Société d'Histoire Naturelle d'Auvergne, Clermont-Ferrand, 1, 1-303.

Piton, L., Théobald, N., 1937. Les Lignites et Schistes bitumineux de Menat (Puy-de-Dôme). II: Les insectes fossiles de Menat. Revue des Sciences naturelles d'Auvergne, 3, 9-21.

Priem, F., 1914. Sur des Poissons fossiles des terrains tertiaires d'eau douce et d'eau saumâtre de France et de Suisse. Mémoires de la Société Géologique de France, Paléontologie, 50, 1-17.

Robson, B., Collinson, M., Riegel, W., Wilde, V., Scott, A., Pancost, R., 2015. Early Paleogene wildfires in peat-forming environments at Schöningen, Germany. Palaeogeography, Palaeoclimatology, Palaeoecology, 437, 53-62.

Ross, A.J., Jarzembowski, E.A., Brooks, S.J., 2000. The Cretaceous and Cenozoic record of insects (Hexapoda) with regard to global change, In: Culver, S.J., Rawson, P.F. (eds.). Biotic response to global change - The last 145 million years. Cambridge University Press, Cambridge, 288-302.

Rose, K.D., 1999. Postcranial skeleton of Eocene Leptictidae (Mammalia) and its implications for behavior and relationships. Journal of Vertebrate Paleontology, 19, 355-372.

Rose, K.D., 2006. The beginning of the age of mammals. The John Hopkins University Press, Baltimore, 448pp.

Rose, K.D., Archibald, J.D. (eds.), 2005. The rise of placental mammals: origins and relationships of the major extant clades. The John Hopkins University Press, Baltimore, 259pp.

Rose, K.D., Storch, G., Krohmann, K., 2015. Small-mammal postcrania from the middle Paleocene of Walbeck, Germany. Paläontologische Zeitschrift, 89(1), 95-124.

Russell, D.E., 1964. Les mammifères Paléocènes d'Europe. Mémoires du Muséum National d'Histoire Naturelle Série C, Sciences de la Terre, tome XIII, 1-324.

Russell, D.E., 1967. Sur *Menatotherium* et l´âge paléocène du gisement de Menat (Puy-de-Dôme). Problèmes actuels de Paléontologie (Evolution des Vertébrés), Colloques Internationaux du CNRS, 163, 483-489.

Russell, D.E., 1975. Paleoecology of the Paleocene-Eocene transition in Europe. In: Szalay, F. (ed.). Approaches to Primate Paleobiology, Contributions to Primatology, 5, Karger, Basel, 28-61.

Russell, D.E., 1982. The geology of the Menat Basin, France. Palaeontographica (B), 182, 89-90.

Rust, J., 1999. Biologie der Insekten aus dem ältesten Tertiär Nordeuropas. Unpublished Habilitation thesis, Georg-August-Universität Göttingen, Germany, 482pp.

Saporta, G. de, Marion, A.F., 1873. Essai sur l'état de la végétation à l'époque des Marnes Heersiennes de Gelinden. Mémoires Couronnés et Mémoires des Savants Etrangers publiés par l'Académie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique, 37, 1-94.

Saporta, G. de, Marion, A.F., 1878. Révision de la flore Heersienne de Gelinden. Mémoires Couronnés et Mémoires des Savants Etrangers publiés par l'Académie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique, 41, 1-112.

Saporta, G. de, Marion, A.F., 1885. L'évolution du règne végétal. Les Phanérogames. Tome 2. Bibliothèque Scientifique Internationale publiée sous la direction de M. Ém. Alglave, 53, 1-248.

Schaal, S., Ziegler, W. (eds.), 1992. Messel. An insight into the history of life and of the Earth. Clarendon press, Oxford, 322pp.

Scott, A.C., 2000. The pre-quaternary history of fire. Palaeogeography, Palaeoclimatology, Palaeoecology, 164, 281-329.

Scott, A.C., 2010. Charcoal recognition, taphonomy and uses in palaeoenvironmental analysis. Palaeogeography, Palaeoclimatology, Palaeoecology, 291, 11-39.

Sepkoski, J.J.Jr., 1996. Patterns of Phanerozoic extinctions: a perspective from global databases. In: Walliser, O.H. (ed.). Global events and event stratigraphy. Springer, Berlin, 35-52.

Sheehan, P.M., Fastovsky, D.E., 1992. Major extinctions of land-dwelling vertebrates at the Cretaceous-Tertiary boundary, eastern Montana. Geology, 20, 556-560.

Silcox, M.T., Gunnell, G.F., 2008. Plesiadapiformes. In: Janis, C.M., Gunnell, G.F., Uhen, M.D. (eds.). Evolution of Tertiary Mammals of North America. Vol. 2: Marine Mammals and Smaller Terrestrial Mammals. Cambridge University Press, Cambridge, 207-238.

Simpson, G.G., 1948. *Menatotherium*, Eocene mammal from France. American Journal of Science, 246(3), 165-170.

Simpson, G.G., 1967. The meaning of evolution: a study of the history of life and of its significance for man. 2nd Edition. Yale University Press, New Haven, 368pp.

Smith, K.T., Schaal, S.F.K., Habersetzer, J. (eds.), 2018. Messel: An Ancient Greenhouse Ecosystem. Schweizerbart, Stuttgart. [*In Press*]

Smith, T., Quesnel, F., De Plöeg, G., De Franceschi, D., Métais, G., De Bast, E., Solé, F., Folie, A., Boura, A., Claude, J., Dupuis, C., Gagnaison, C., Iakovleva, A., Martin, J., Maubert, F., Prieur, J., Roche, E., Storme, J.-Y., Thomas, R., Tong, H., Yans, J., Buffetaut, E., 2014. First Clarkforkian Equivalent Land Mammal Age in the Latest Paleocene Basal Sparnacian Facies of Europe: Fauna, Flora, Paleoenvironment and (Bio) stratigraphy. PLoS ONE 9(1), e86229. DOI: 10.1371/journal.pone.0086229

Solé, F., Smith, T., De Bast, E., Codrea, V., Gheerbrant, E., 2016. New carnivora forms from the latest Paleocene of Europe and their bearing on the origin and radiation of Carnivoraforms (Carnivoramorpha, Mammalia). Journal of Vertebrate Paleontology, 36(2), e1082480, 1-19. DOI: 10.1080/02724634.2016.1082480

Stockmans, F., 1932a. *Posidonia perforata* Saporta et Marion des Marnes de Gelinden. Bulletin du Musée royal d'Histoire naturelle de Belgique, Bruxelles, 8(27), 1-9.

Stockmans, F., 1932b. Sur les épidermes de dicotylédonées (*Dewalquea gelindenensis* Saporta et Marion et *Litsea elatinervis* Saporta et Marion) des Marnes de Gelinden (Paléocène). Bulletin du Musée royal d'Histoire naturelle de Belgique, Bruxelles, 8(9), 1-10.

Stockmans, F., 1960. Initiation à la Paléobotanique stratigraphique de la Belgique. Guide de la salle des végétaux fossiles. Institut royal des Sciences naturelles de Belgique, Bruxelles, 222pp.

Stroinski, A., Swedo, J., 2012. The oldest known Lophopidae planthopper (Hemiptera: Fulgoromorpha) from the European Palaeocene. Geobios, 45, 413-420.

Swedo, J., Bourgoin, T., Lefebvre, F., 2006. New Mnemosynini taxa (Hemiptera, Fulgoromorpha: Cixiidae) from the Palaeogene of France with notes on their early association with host plants. Zootaxa, 1122, 25-45.

Sweet, A.R., Braman, D.R., Lerbekmo, J.F., 1990. Palynofloral response to K/T boundary events: a transitory interruption within a dynamic system. Geological Society of America Special Paper, 247, 457-469.

Vincent, P.M., Aubert, M., Boivin, P., Cantagrel, J.M., Lenat, J.F., 1977. Découverte d'un volcanisme paléocène en Auvergne: les maars de Menat et leurs annexes; étude géologique et géophysique. Bulletin de la Société Géologique de France, S7, 19(5), 1057-1070. DOI: 10.2113gssgfbull.S7_XIX.5.1057

Wappler, T., 2003. Die Insekten aus dem Mittel-Eozän des Eckfelder Maares, Vulkaneifel. Mainzer Naturwissenschaftliches Archiv, Beiheft, 27, 1-234.

Wappler, T., Currano, E.D., Wilf, P., Rust, J., Labandeira, C.C., 2009. No post-Cretaceous ecosystem depression in European forests? Rich insect-feeding damage on diverse middle Palaeocene plants at Menat, France. Proceedings of the Royal Society of London, B, 276, 4271-4277.

Wedmann, S., 2000. Die Insekten der oberoligozänen Fossillagerstätte Enspel (Westerwald, Deutschland): Systematik, Biostratinomie und Paläoökologie. Mainzer naturwissenschaftliches Archiv, Beiheft, 23, 1-154.

Wedmann, S., Wappler, T., Engel, M.S., 2009. Direct and indirect fossil records of megachilid bees from the Paleogene of Central Europe (Hymenoptera: Megachilidae). Naturwissenschaften, 96, 703-712.

Wedmann, S., Poschmann, M., Hörnschemeyer, T., 2010. Fossil insects from the late Oligocene Enspel Lagerstätte and their palaeobiogeographic and palaeoclimatic significance. Palaeobiodiversity and Palaeoenvironments, 90, 49-58.

Wedmann, S., Pouillon J.-M., Nel, A., 2014. New Palaeogene horntail wasps (Hymenoptera, Siricidae) and a discussion of their fossil record. Zootaxa, 3869(1), 33-43.

Wighton, D.C., 1982. Middle Paleocene insect fossils from South-central Alberta. Proceedings of the third North American Paleontological Convention, 1, 577-578.

Wilf, P., Labandeira, C.C., Johnson, K.R., Coleyi, P.D., Cutter, A.D., 2001. Insect herbivory, plant defense, and early Cenozoic climate change. PNAS, 98, 6221-6226.

Wilf, P., Johnson, K.R., Huber, B.T., 2003. Correlated terrestrial and marine evidence for global climate changes before mass extinction at the Cretaceous–Paleogene boundary. PNAS, 100, 599-604.

Wilf, P., Labandeira, C.C., Johnson, K.R., Cúneo, R.N., 2005. Richness of plant–insect associations in Eocene Patagonia: A legacy for South American biodiversity. PNAS, 102, 8944-8948.

Wilson, G.P., DeMar, D.G., Carter, G., 2014. Extinction and survival of salamander and salamander-like amphibians across the Cretaceous-Paleogene boundary in northeastern Montana, USA. Geological Society of America Special Papers, 503, 271-297.

Wing, S.L., Alroy, J., Hickey, L.J., 1995. Plant and mammal diversity in the Paleocene to early Eocene of the Bighorn Basin. Palaeogeography, Palaeoclimatology Palaeoecology, 115, 117-155.

Wolfe, J.A., Upchurch, G.R., 1986. Vegetation, climatic and floral changes at the Cretaceous–Tertiary boundary. Nature, 324, 148-152.

Wu, S., Wu, W., Zhang, F., Ye, J., Ni, X., Sun, J., Edwards, S., Meng, J., Organ, C.L., 2012. Molecular and paleontological evidence for a post-Cretaceous origin of rodents. PLoS One, 7(10), e46445, 1-11. DOI: 10.1371/journal.pone.0046445

Wuttke, M., Uhl, D., Schindler, T. (eds.), 2010. Special Issue: Fossil-Lagerstätte Enspel - exceptional preservation in an Upper Oligocene maar. Palaeobiodiversity and Palaeoenvironments, 90, 1-98.

Wuttke, M., Schindler, T., Smith, K.T. (eds.), 2015. Special Issue: The Fossil-Lagerstätte Enspel - reconstructing the palaeoenvironment with new data on fossils and geology. Palaeobiodiversity and Palaeoenvironments, 95, 1-147.

Zherikhin, V.V., 2002. Ecological history of terrestrial insects, In: Rasnitsyn, A., Quicke, D.L.J. (eds.). History of insects. Kluwer Academic Publishers, Dordrecht, Boston, London, 331-388.

Manuscript received August 2017;
revision accepted February 2018;
published Online May 2018.

APPENDIX I

Depositories of menat specimens. Tables I, II and III.

TABLE I. List of museums housing fossil specimens from Menat

Museum	Plants	Vertebrates	Insects
Muséum National d'Histoire Naturelle (MNHN), Paris	X	X	X
Musée de Menat (MNT)	X	X	X
Epona building, Menat	X	X	X
Muséum d'Histoire Naturelle Henri Lecoq (MHNHL), Clermont-Ferrand			X
Collections de Géologie, UMR 5276 LGLTPE – CERESE, Université Lyon 1, UCB–FSL, Lyon	X	X	X
Naturhistorisches Museum Basel (NHM)		X	
Maarmuseum Manderscheid, Germany	X		X
Senckenberg Museum, Frankfurt (SMF)		X	

TABLE II. List of insect types from Menat deposited at the Muséum National d'Histoire Naturelle, Paris, France (MNHN), at the Muséum d'Histoire Naturelle Henri Lecoq, Clermont-Ferrand, France (MHNHL), and at the Musée de Menat, France (MNT)

Species name, describer + year	Collection, coll-no
Acmaeodera perreaui PITON, 1940	MNHN R07007
Adelocera jungi PITON, 1940	MNHN R06687
Agonum antiquum PITON, 1940	MNHN R07013
Ancistrocerus berlandi PITON, 1940	MNHN R07000
Ancistrocerus eocenicus PITON, 1940	MNHN R07006
Ancylocheira metallica PITON, 1940	MNHN R07018
Ancylocheira octomaculata PITON, 1940	MNHN R07037 (type), MNHN R07049 (figured)
Ancylocheira oligostriata PITON AND THEOBALD, 1937	MHNHL, coll. des Forest
Ancylocheira pinguis PITON, 1940	MNHN R07038
Ancylocheira violaceocyanescens PITON, 1940	MNHN R06993
Anthaxia biimpressa PITON, 1940	MNHN R07040
Aphodius charauxi PITON, 1940	MNHN R07029
Archaeophlebia enigmatica PITON, 1940	MNHN R06999
Arvernineura insignis PITON, 1940	MNHN R07020
Balaninus elegans PITON, 1940	MNHN R07010
Bembedium cyaneomicans PITON, 1940	MNHN R07231
Bolboceras inermis PITON, 1940	MNHN R07232
Chlorida magnifica PITON, 1940	MNHN R06997
Chrysochroa punctata PITON, 1940	MNHN R06994
Chrysops seguyi PITON, 1940	MNHN R07014
Cintux menatensis STROINSKI AND SWEDO, 2012	MNHN F.A45773
Conocephalus martyi PITON, 1940	MNHN R07019
Cryptohelops menaticus NABOZHENKO AND KIREJTSHUK, 2014	MNT-05-712A
Cupes manifestus NEL AND COLLOMB, 2010 in Kirejtshuk *et al.*, 2010	MNT-06-902
Cupes orbiculatus NEL AND COLLOMB, 2010 in Kirejtshuk *et al.*, 2010	MNT-05-198
Deryeuma primordialis PITON, 1940	MNHN R07042

TABLE II. (Cont.)

Species name, describer + year	Collection, coll-no
Dictyophara scudderi PITON, 1940	MNHN R07032
Ectobia menatensis PITON, 1940	MNHN R07046
Eoplaneta des foresti PITON AND THEOBALD, 1937	MHNHL, coll. des Forest
Euchroma arvernica PITON, 1940	MNHN R06995
Eurythyrea micropunctata PITON, 1940	MNHN R07033
Gorytes statzi PITON, 1940	MNHN R07009
Gyna obesa PITON, 1940	MNHN R06689
Gyretes giganteus PITON, 1940	MNHN R06998
Hammapterix eocenicus PITON, 1940	MNHN R07891
Hipporhinus ventricosus PITON, 1940	MNHN R06684
Iridotaenia hovassei PITON, 1940	MNHN R06991
Limnobia theobaldi PITON, 1940	MNHN R07008
Manevalia pachyliformis PITON, 1940	MNHN R07024
Meuniera haupti PITON, 1936	MNHN R07890
Monohammus orientalis PITON, 1940	MNHN R07237
Mnasthaia arverniorum SWEDO, BOURGOIN AND LEFEBVRE, 2006	MNHN-LP-R63851
Myrmosa brunnea PITON, 1940	MNHN R07044
Ochrilidia lineata PITON, 1940	MNHN R07043
Odynerus manevali PITON, 1940	MNHN R07011
Orectochilus sp. (in Nel, 1989)	MNHN R07723
Orthacanthacris incertus PITON, 1940	MNHN R07017
Oxyporus impressus PITON, 1940	MNHN R07021
Palaeoncoderes eocenicus PITON AND THEOBALD, 1937	MNHN R06992 (type), MNHN R07254 (figured)
Paleohabropoda oudardi MICHEZ AND RASMONT, 2009 in Michez *et al*., 2009	MNHN-LP-R63891
Paleolomatia menatensis NEL, 2008	MNHN-LP-R63892
Paleorhopalosoma menatensis NEL, AZAR AND HERVET, 2010	MNT-06-3533

TABLE II. (Cont.)

Species name, describer + year	Collection, coll-no
Paleovespa menatensis NEL AND AUVRAY, 2006	MNHN 21.6 Auvray coll.
Periplaneta houlberti PITON, 1940	MNHN R07034
Plecia sp indet., recorded by NEL, 2007	MNHN-LP-R63888
Phryganaea nigripennis PITON, 1940	MNHN R07046
Polybothris primordialis PITON, 1940	MNHN R07023
Prionus sinuatus PITON, 1940	MNHN R07045
Probombus hirsutus PITON, 1940	MNHN R07030
Prochaeradodis enigmaticus PITON, 1940	MNHN R07003
Prohepialus incertus PITON, 1940	MNHN R07025
Prolamioides bituminosus PITON AND THEOBALD,1937	MNHN R04016
Prolamioides brunneus PITON, 1940	MNHN R07031
Prophasgonura lineatocollis PITON, 1940	MNHN R07050
Protectobia primordialis PITON, 1940	MNHN R07233
Protempusa incerta PITON, 1940	MNHN R07035
Protostylopyga gigantea PITON, 1940	MNHN R07039
Pycanum griseum PITON, 1940	MNHN R54266
Rygchium andrei PITON, 1940	MNHN R07047
Semiotus menatensis PITON, 1940	MNHN R07236
Stigmodera unicolor PITON, 1940	MNHN R07022
Termopsis piacentinii PITON AND THEOBALD,1937	MNHN R07027
Thanetophilosina menatensis NEL *et al.*, 1997	MNHN R55172
Urocerus ligniticus (PITON, 1940), described in *Eosirex*	MNHN R07004 (type), MNHN B47308, MNHN R07722 (figured)
Zeunera madeleinae PITON, 1936	MNHN R07028, MNHN B47309 (figured)
Zeunera superba PITON, 1940	MNHN R07235 (type), MNHN R07234 (figured)
Zonabris immaculatus PITON, 1940	MNHN R07012

TABLE III. List of mammal specimens from Menat and the known repository institutions (as of June 2017): Muséum National d'Histoire Naturelle (MNHN), Paris; Naturhistorisches Museum Basel (NHM); Collections de Géologie, UMR 5276 LGLTPE - CERESE, Université Lyon 1 (acronyme UCBL-FSL)

Taxon	Current collection
Plesiadapis "Menatotherium" insigne PITON, 1940)	MNHN, Paris (Plate A); NHM, Basel (Plate B)
"Insectivore" (*Leptictis?)*	MNHN, Paris
"Rodent" (*Sciuroides?)*	MNHN, Paris
"Carnivore" (*Cynodictis?)*	UCBL-FSL, Lyon