



Hidden termite coprolites revealed by Synchrotron microtomography inside Eocene–Oligocene filled wood-borings from the Malzieu Basin, Lozère, southern France

JEAN-DAVID MOREAU , VINCENT TRINCAL, ANDRE NEL, RÉGINE SIMON-COINÇON, VINCENT SALLÉ, MATTHIEU LE COULS, DIDIER NÉRAUDEAU  AND VINCENT FERNANDEZ

LETHAIA



Moreau, J.-D., Trincal, V., Nel, A., Simon-Coinçon, R., Sallé, V., Le Couls, M., Néraudeau, D. & Fernandez, V. 2019: Hidden termite coprolites revealed by Synchrotron microtomography inside Eocene–Oligocene filled wood-borings from the Malzieu Basin, Lozère, southern France *Lethaia*, <https://doi.org/10.1111/let.12344>.

Fragments of filled wood-borings were recently discovered from the Eocene–Oligocene Conglomerate and Sandstone Formation of the Malzieu Basin (Lozère, southern France). Propagation phase-contrast X-ray synchrotron microtomography (PPC-SRμCT) was used to characterize their hidden inner structures. Virtual 2D sections and 3D reconstructions show that the inner microstructures of borings display a mudstone–wackestone siliceous matrix including tiny coprolites. The hexagonal cross-section of these coprolites is characteristic of termite faecal pellets. Morphology and dimensions of the coprolites share strong similarities with those of extant *Kalotermitidae* (drywood termites). The depositional environment is interpreted as a fluvial valley in which the lenticular sandstone and conglomerate lenses correspond to channels. This discovery complements the record of Palaeogene termites which remain poor in France and throughout the world. □ *Faecal pellets*, *Insecta*, *Kalotermitidae*, *Lozère*, *Palaeogene*, *PPC-SRμCT*.

Jean-David Moreau [jean.david.moreau@gmail.com], CNRS UMR 6538 Laboratoire Géosciences Océan, Centre de Recherche Yves Coppens, Université Bretagne Sud, Campus de Tohannic, rue André Lwoff, Vannes 56017, France; Vincent Trincal [vincenttrincal@gmail.com], LMDC - Laboratoire Matériaux & Durabilité des Constructions, Université de Toulouse, INSA/UPS - 135 av. de Rangueil Toulouse 31077, France; Andre Nel [andre.nel@mnhn.fr], Institut de Systématique, Évolution, Biodiversité, ISYEB-UMR 7205-CNRS, MNHN, UPMC, EPHE, Muséum national d'Histoire naturelle, Sorbonne Universités, 57 rue Cuvier, CP 50, Entomologie ParisF-75005, France; Régine Simon-Coinçon [an.c.77@hotmail.fr], 10, allée du Parchemin Buxerolles 86180, France; Vincent Sallé [salle.vincent@gmail.com], Association Paléontologique des Hauts Plateaux du Languedoc, 14 chemin des Ecureuils Mende 48000, France; Matthieu Le Couls [matthieu.lecouls@wanadoo.fr], Didier Néraudeau [didier.neraudeau@univ-rennes1.fr], CNRS UMR 6118 Géosciences, Université Rennes 1, Campus de Beaulieu, 263 avenue du général Leclerc Rennes Cedex 35042, France; Vincent Fernandez [vinfernand@gmail.com], Imaging and Analysis Centre, Natural History Museum, Cromwell Road London SW7 5BD, UK; Vincent Fernandez [vinfernand@gmail.com], European Synchrotron Radiation Facility, 7 avenue des Martyrs Grenoble 38043, France; manuscript received on 17/01/2019; manuscript accepted on 5/04/2019.

Although the diversity of extant termites (Isoptera) is relatively modest compared with that of other insect major clades, in recent ecosystems they are probably the most ecologically important group of insects besides the bees and ants (Grimaldi & Engel 2005). They constitute recyclers of organic matter essential for carbon mineralization, humification and building of soils (Eggleton 2011). Worldwide, evidence of termites in fossil ecosystems was demonstrated by the discovery of bodies preserved as inclusions in amber (Krishna & Emerson 1983; Krishna & Grimaldi 1991; Poinar 1993; Nel & Bourguet 2006; Krishna *et al.* 2013; Coty *et al.* 2014) and compressions on slabs of sedimentary rocks (e.g. Jarzembowski 1981; Nel & Paicheler 1993). Fossil record also yielded indirect

evidences such as underground nests (Genise 2016 and references therein; Roberts *et al.* 2016), borings in wood (Rohr *et al.* 1986; Genise 1995; Francis & Harland 2006) and coprolites in wood, sediment and amber (Colin *et al.* 2011). Although termite bodies date back to the Jurassic/Cretaceous boundary (Engel *et al.* 2011; Vršanský & Aristov 2014), the record of Palaeogene termites remains sparse, except in Baltic amber. This is particularly true for the Eocene–Oligocene interval which is weakly documented in Europe (Nel & Paicheler 1993; Engel *et al.* 2008).

Recently, fragments of filled borings (inner casts) containing coprolites were discovered in the Eocene–Oligocene deposits from the Malzieu Basin, in Lozère (southern France). Although coprolites of termites

are known since the Early Cretaceous to the Holocene (Rogers 1938; Corbett & Burrell 2001; Sutherland 2003; Nuorteva & Kinnunen 2008; Pires & Sommer 2009; Colin *et al.* 2011; Boucher 2012; Jud *et al.* 2017), this report consists of the first evidence of Eocene–Oligocene termite borings containing coprolites in Europe. The fragments of pellet-filled borings were analysed using a non-destructive imaging technique useful for the observation of inner and hidden structures: propagation phase-contrast X-ray synchrotron microtomography (PPC-SR μ CT). The paper aims to compare specimens from Malzieu with faecal pellets of extinct and extant termites and discuss probable authors of the coprolites as well as taphonomical and palaeoecological implications. Fragments of borings were discovered in the Conglomerate and Sandstone Formation whose age is uncertain and debated since the 19th century (Boule 1888).

Geological setting

The Malzieu basin is located in the south of Massif Central, in the Lozère department, between Mende and Clermont-Ferrand (Fig. 1). Deposits of the basin lie on the 'Granite de la Margeride' basement, a Hercynian porphyritic batholith dated to the Carboniferous (Talbot *et al.* 2005). Numerous studies (Glangeaud 1922; Rey 1949; Bout 1961; Coinçon 1972) tentatively divided the sedimentary series of the Malzieu basin into the seven following formations (Fig. 2), from the oldest to the most recent: the Red Sandstone Formation (RSF), the Conglomerate and Sandstone Formation (CSF), the Red Clay Formation (RCF), the Green Clay Formation (GCF), the Silcrete Formation (SF), the Variegated Sandy Clays Formation (VSCF) and the Chert-bearing Sand Formation (Fy) (or Grey Sand Formation).

The Conglomerate and Sandstone Formation

The filled wood-borings presented herein were collected in the CSF. This formation is 3–10 m thick. It is composed of lenticular channelized conglomerate bearing cross-bedded stratifications (Simon-Coinçon *et al.* 1981) that show marked lateral variation in facies and contain quartz and flint pebbles joined by an orange to reddish arkosic or sandy cement (Colin 1963; Coinçon 1972). Conglomerate alternates with lenses of arkose, siltstone and white argillite. This formation is mainly exposed in the Ganigal forest which is immediately south of Malzieu (Fig. 2) and was formerly used for making millstones (Boule 1888; Couturié 1972; Remy *et al.* 2011). Due to the fault

movements, the CSF is also visible 2 km further north, at the top of the Verdezun hill as well as 8 km to the southwest, near La Chaumette (St-Chély-d'Apcher; Colin 1963; Couturié & Geffroy 1974). The CSF yields abundant plant macroremains, including large trunks preserved as impressions and silicified permineralizations. Their identification and dating were reported in an ancient study (Boule 1888). Based on scanty and fragmented specimens, and by comparison with the regional Cenozoic flora, the author announced an Aquitanian age (Lower Miocene). However, the comparisons were limited and Boule (1888) indicated that this age is only an approximation, even suggesting that the deposit may be more than 10 million years older and dated to the Priabonian (Upper Eocene). Simon-Coinçon *et al.* (1981) indicated that the plant species identified by Boule (1888) are not characteristic of a particular stage and may be dated from the Oligocene to the end of the Miocene.

Age of the Conglomerate and Sandstone Formation

The age of the CSF has historically been debated because of the lack of biostratigraphical evidence and relationships with the other formations of the Malzieu basin (Coinçon *et al.* 1976). Furthermore, in the current topography, the CSF is located more than 100 m above the sediments that have succeeded them, suggesting a tectonic shift (Boule 1888; Bout 1961; Coinçon *et al.* 1976). The detachment border faults pushed blocks, creating thresholds and collapses (more than 600 m according to the unpublished CFMU drillings). Thus, it is possible to find at the same topographic level formations of different ages. This has misled many authors who thought that the CSF may be at the top of the sedimentary series, and therefore posterior to the VSCF (Glangeaud 1922; Colin 1963; Couturié 1972; Coque-Delhuille & Pigeys 1980), which was dated as Rupelian based on faunas from neighbour basins (e.g. Brons and Vendèze deposits; Rames 1886; Lavocat 1951; Jodot & Rey 1956; Rey 1967; Coinçon 1972; Coinçon *et al.* 1976; Couturié 1972; Jodot & Rey 1956). This hypothesis no longer holds since the discovery of the GCF above the CSF in the La Chaumette outcrop (Couturié & Geffroy 1974).

Located below the RCF and the GCF, and locally lying unconformably on granite, the CSF is probably posterior to the weathering mantles and duricrusts of the RSF (Boule 1888; Coinçon *et al.* 1976). This has, however, not yet been observed in the Malzieu basin (Coinçon *et al.* 1976). Its syntectonic sedimentation could have started after the Ypresian-Lutetian RSF

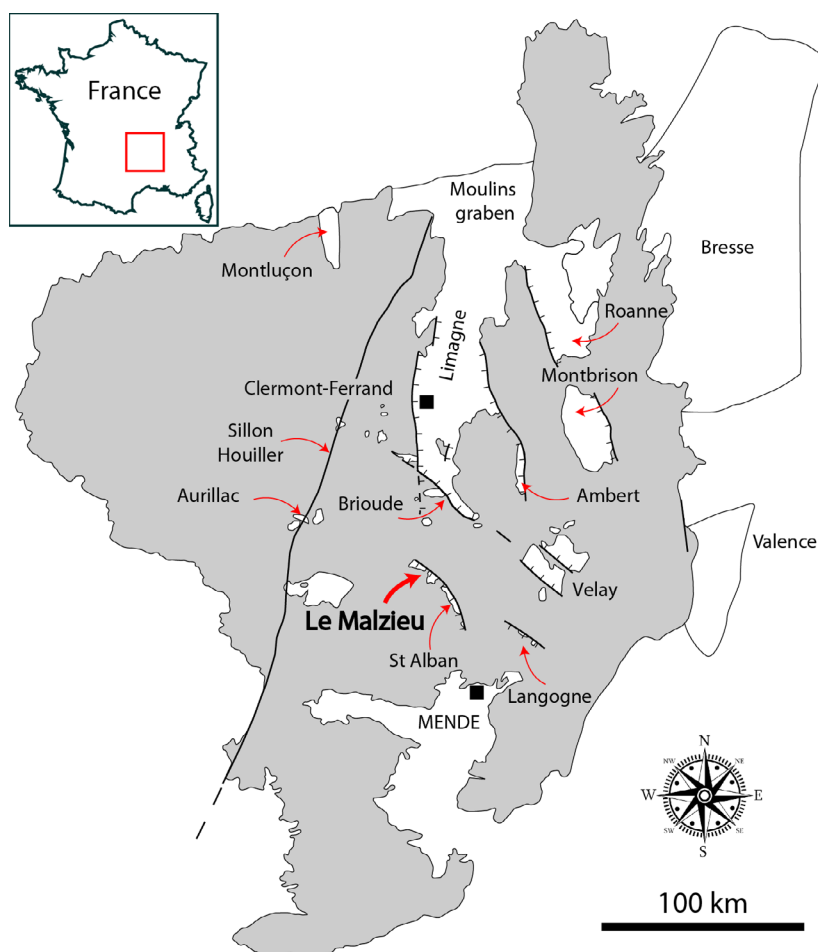


Fig. 1. Geological context, and location of the French Malzieu Basin in the Massif Central (modified after Michon 2000).

(Thiry *et al.* 2006, 2014; Ricordel-Prognon 2007), probably during the lower Bartonian (Auversian) as in basins bordering the Villefranche-de-Rouergue fault in Quercy (Simon-Coinçon *et al.* 1997). The GCF was dated as upper Rupelian by malacology in the St-Alban-sur-Limagnole Basin (i.e. *Limnaea* (*Stagnicola*) *mammertensis* and *Limnaea* (*Stagnicola*) *orelango*; Jodot & Rey 1956). Flint from the SF was formerly exploited for lithic industry and considered Rupelian or latest Eocene/Rupelian (e.g. Fernandes *et al.* 2006, 2008a, 2008b; Raynal *et al.* 2012). The SF yielded a partial right mandible of the perissodactyl *Plagiolophus* sp., possibly *P. annectens* (Astruc *et al.* 2003). The genus *Plagiolophus* is documented in Western Europe from the middle Eocene to mid-Oligocene, probably between -45.2 and -28.3 Ma (Escarguel *et al.* 1997; Remy 2004). *P. annectens* is restricted from upper Barthonian to lower Priabonian; but other more recent lineages of plagiolophes, as *P. minor* of the Lower Oligocene, cannot be excluded for the identification of this fossil (Astruc *et*

al. 2003). We may notice that similar silcretes described in the Massif Central were considered Priabonian in age by Thiry & Turland (1985) and Simon-Coinçon *et al.* (1995, 1997). In conclusion, although Boule (1888) attributed an Aquitanian age for the CSF, its alternative suggestion of a Priabonian age seems more appropriate but uncertain. In the absence of undeniable biochronological evidence, we prefer to moderate the chronostratigraphic assignment of the CSF and propose a lower Bartonian–Rupelian age.

Material and methods

The fragments of pellet-filled borings were collected in 2015 during field prospecting in a small outcrop along the forest path of the ‘Bois de Ganigal’ (Fig. 2). Specimens are three in number. Firstly undetected, it was only in 2016, after microtomographic experiments that the coprolites were identified. The three

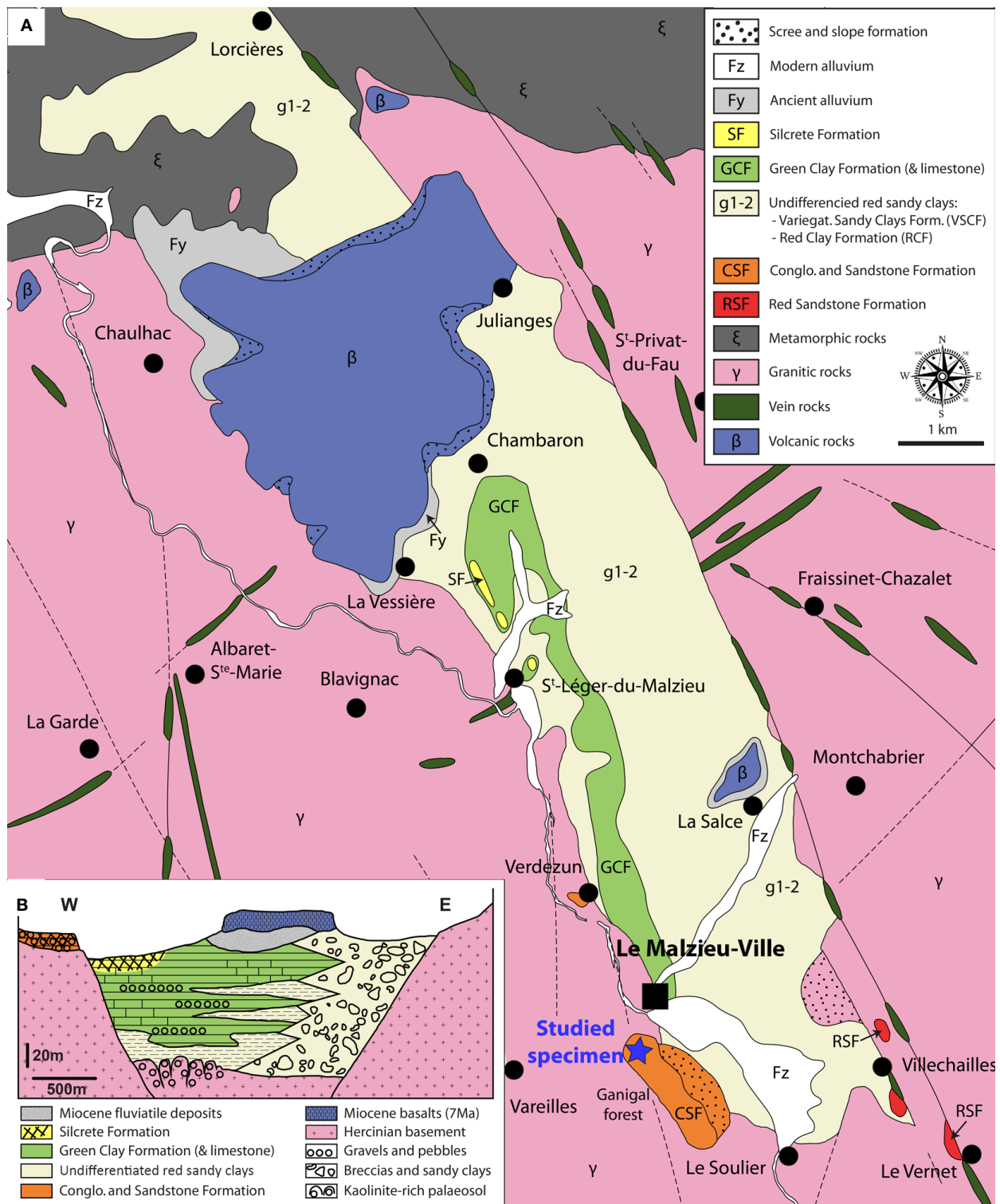


Fig. 2. A, geological map of the Malzieu Basin and location of the study area (modified after Couturié 1972). B, synthetic E-W transversal section of the Malzieu Basin (Modified after Simon-Coinçon *et al.* 1997).

specimens were examined at the beamline ID19, at the European Synchrotron Radiation Facility (ESRF, Grenoble, France) using PPC-SR μ CT and an

isotropic voxel size of 2.26 μ m (Tafforeau *et al.* 2006). A propagation distance of 0.8 m between the specimen and the detector was chosen to use the

properties of the propagation phase contrast. Phase contrast significantly increases the contrast compared with that strictly due to the variation of absorption by the specimen. This approach enables the reconstruction of virtual sections and 3D renderings of the specimen and their inner microstructures (Figs 3–6). We used an effective energy of 125 keV based on the white beam spectrum of a W150b wiggler set to a gap of 35 mm and filtered with 6 mm of copper. We used a PCO.edge 4.2 camera mounted on lens-based optical system coupled with a 200- μ m-thick LuAG scintillator. In order to increase the reconstructed horizontal field of view, the scans were performed in continuous rotation mode over 360°, in half-acquisition mode (centre of rotation shifted near the edge of the detector). Scans were performed using 6000 projections and an exposure time of 0.01 s per projection. The scans were reconstructed using a back-projection algorithm implemented in the PyHST2 software (High Speed Tomography in python version, ESRF, Mirone *et al.* 2014). It was coupled with single distance phase retrieval process modified from Paganin's algorithm (Paganin *et al.* 2002) to incorporate an unsharp mask applied to the retrieved phase maps (Sanchez *et al.* 2012). Data were finally converted into a 16 bit tiff stack of slices corrected for residual ring artefacts (Lyckegaard *et al.* 2011) and cropped. The three-dimensional reconstructions of specimens were achieved with the software VG Studio Max 2.2 (Volume Graphics, Heidelberg, Germany). The virtual dissection and segmentation were made using 3D region growing and manual selections. The specimens are deposited in the collection of Musée du Gévaudan (Mende, France).

Filled borings and coprolites

Description

The fragments of filled borings containing coprolites are up to 3.5 cm long (Fig. 3). Surface of the borings shows longitudinal imprints of wood fibres. It bears desiccation cracks preserved as inverted relief. The sediment filling the cracks is similar to those filling the borings. The tomographic virtual 2D sections show that inner microstructures of borings are composed of a mudstone–wackestone siliceous matrix including tiny coprolites and wood debris (Figs 3–6). They are <1 mm to more than 6 mm long. The poor preservation of the wood debris and the technical limitation do not allow us to clearly characterize tracheids, rays or pits and thus do not permit a determination of the wood.

Coprolites are dispersed inside the matrix, not in contact with each other and randomly oriented (Figs 3, 4). Two kinds of coprolite preservations are reported. In the first case, they are entirely or partially preserved showing various degrees of fragmentation probably induced by desiccation. The second case consists of empty moulds (dark on the tomographic 2D reconstructions; Figs 4, 5). In both cases, they are uncompacted and fully preserved in 3D. The coprolites share identical morphologies. They are oblong in shape, 470–615 μ m long and 220–325 μ m in diameter. One end is blunt, whereas the other is more pointed. Coprolites display a characteristic hexagonal cross-section with slightly rounded edges, sometimes with a shallow central dimple. Sides of coprolites are commonly straight, but among some specimens, they are slightly concave. Coprolites do not display internal structures.

Remarks

Gross morphology, shape of the cross-section and range size of coprolites from Malzieu are similar to *Microcarpolithes hexagonalis* which was described in diverse Cretaceous deposits worldwide (see Colin *et al.* 2011 and references therein). Based on material from the Senonian of the Netherlands, the genus *Microcarpolithes* was firstly interpreted as angiosperm seeds. After Knobloch (1970, 1971, 1977) recognized insect coprolites, Kovach & Dilcher (1988) ascribed *M. hexagonalis* to termite coprolites.

Discussion

Comparison with faecal pellets of extinct and extant termites, and probable borers

Worldwide, termite coprolites are rather uncommon in the Eocene–Oligocene fossil record. In the Eocene, such pellets are frequent in the Ypresian amber from the Paris Basin (Oise; Colin *et al.* 2011), the Lutetian Baltic amber (Nuorteva & Kinnunen 2008), and the Priabonian from Central Europe and southern England (Schultze-Dewitz & Süss 1988; Hooker *et al.* 1995). In the Oligocene, termite coprolites were reported from Australia (Rozefelds 1990; Rozefelds & de Baar 1991) and United States of America (Viney 2008).

Among extant termites, two families display faecal pellets sharing morphological features with coprolites from Malzieu, the Kalotermitidae ('drywood termites'; e.g. *Kalotermes*) and the Mastotermitidae (e.g. *Mastotermes*). Both produce solid pellets more favourable to the fossilization, whereas other families

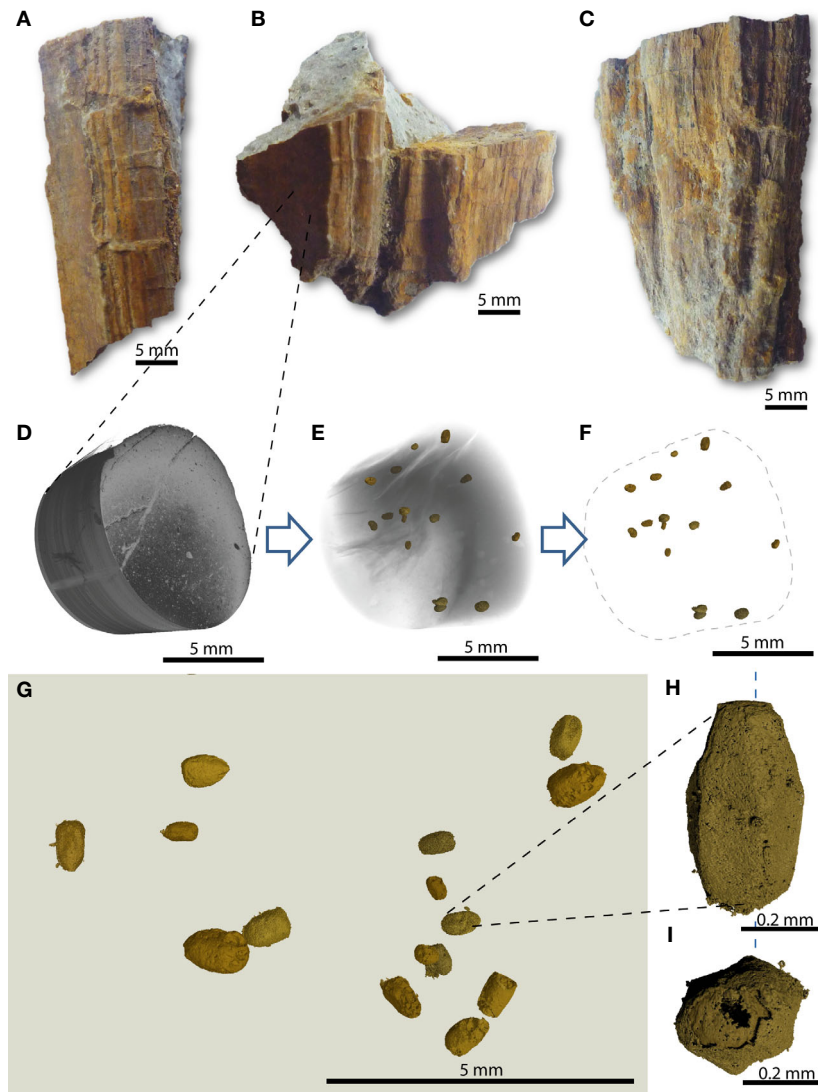


Fig. 3. Filled borings and virtual dissection of inner structures. A–C, photographs of the three fragments of filled borings. D–F, PPC-SRμCT, 3D renderings showing abundant termite coprolites inside a boring. G, PPC-SRμCT, 3D rendering showing the random arrangement of termite coprolites inside matrix. H–I, PPC-SRμCT, zoom on a coprolite showing the characteristic oblong shape and the hexagonal section, lateral view (H) and apical view (I); voxel size, 2.26 μm .

produce pasty to liquid faeces (Rohr *et al.* 1986). Similarly to coprolites from Malzieu, the pellets of the recent taxa *Mastotermes darwiniensis* (Mastotermitidae) and *Kaloterme*s (Kalotermitidae) display an oblong shape, a hexagonal cross-section, and a blunt apex, whereas the other is more pointed. The size range of *Kaloterme*s (i.e. 0.65 mm long and 0.3 mm wide according to Colin *et al.* 2011) is similar to those of fossil coprolites from Malzieu, whereas those of *M. darwiniensis* are clearly larger (i.e. 1.0 to 1.2 mm long according to Colin *et al.* 2011). The habitat of Kalotermitidae is exclusively inside wood pieces in contrast with that of Mastotermitidae (and other families such as Hodotermitidae, Rhinotermitidae and many Termitidae) foraging on or in soil

(Noirot & Darlington 2000). All these arguments suggest that Kalotermitidae, which were already diversified since the Upper Eocene (Nel & Paicheler 1993; Engel & Nel 2015), may have been at the origin of borings from Malzieu. However, although specimens from Malzieu and *Kaloterme*s pellets are very similar, apices of the second are more rounded. We may notice that pellets of the Termopsidae (damp-wood termites) also show hexagonal cross-section. But, they commonly quickly lose this shape and form amorphous clumps (Colin *et al.* 2011). Pellets of Termopsidae only rarely conserve the hexagonal shape (e.g. *Zootermopsis*; Colin *et al.* 2011). This shape which is so characteristic of termite faecal pellets is explained by the pressure of six bands of

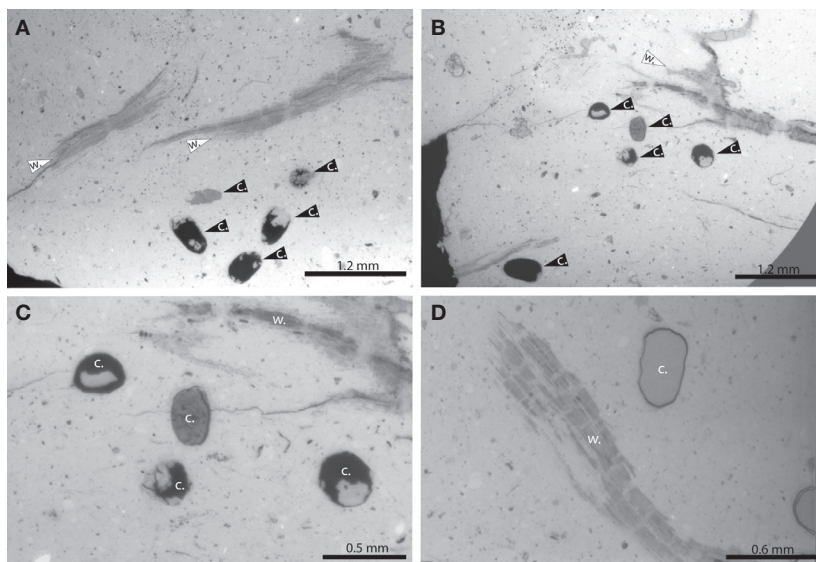


Fig. 4. PPC-SRμCT, virtual 2D sections inside borings. A–D, co-occurrence of termite coprolites and woods debris randomly arranged in the matrix; two kinds of coprolite preservations are visible, some are entirely or partially preserved (white-grey coprolites on tomographic reconstructions), and others are preserved as empty external casts (black coprolites on tomographic reconstructions). Key: C., coprolites; W., wood debris. Voxel size, 2.26 μm .

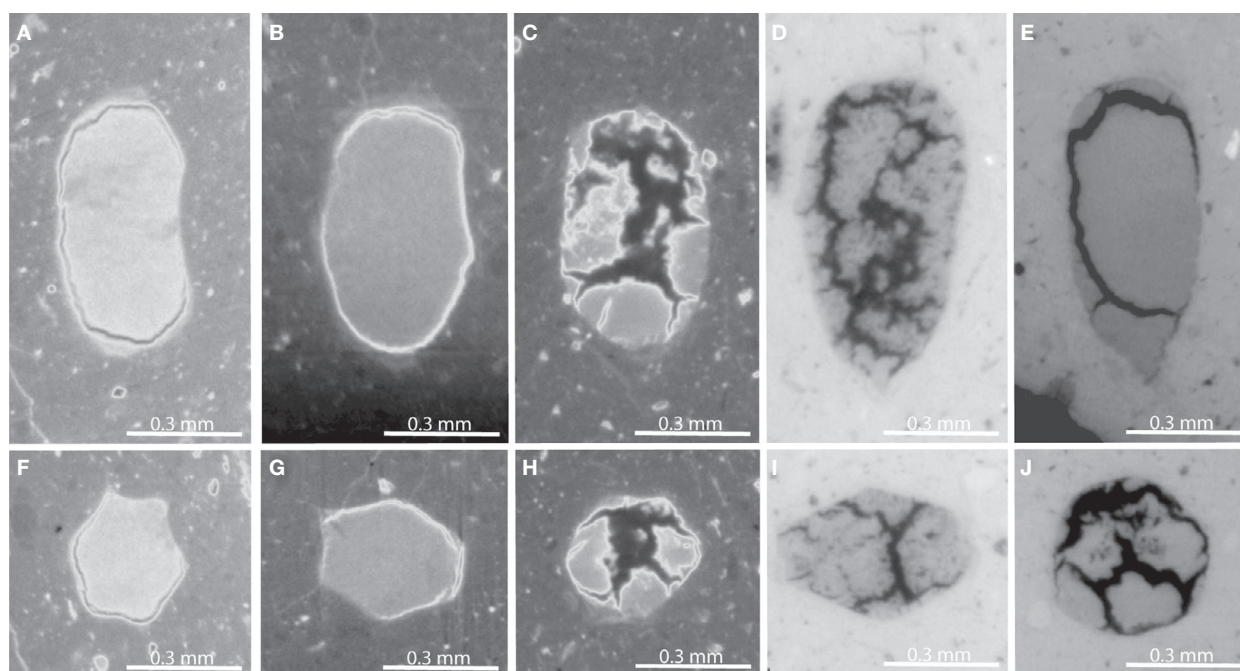


Fig. 5. PPC-SRμCT, virtual 2D sections of coprolites. A–E, longitudinal section showing the oblong shape and one end blunt (A–C) whereas the other is more pointed (D, E). F–J, transversal section showing hexagonal to rounded shape. Voxel size, 2.26 μm .

muscle which squeeze liquid out of the faecal mass in the rectum for the water retention (Sutherland 2003).

During the Eocene–Oligocene interval, Kalotermitidae and Mastotermitidae were diversified families throughout the world (see Thorne *et al.* 2000 and references therein). Although Palaeogene termites remain uncommon in France, the Eocene amber

from the Paris Basin yielded inclusions ascribed to two termite species, *Electrotermes flecki* and *Mastotermes minutus* which are included in the Kalotermitidae and the Mastotermitidae families, respectively (Nel & Bourguet 2006). In the other hand, Eocene deposits from Gard (southern France) yielded an isolated wing of Kalotermitidae ascribed

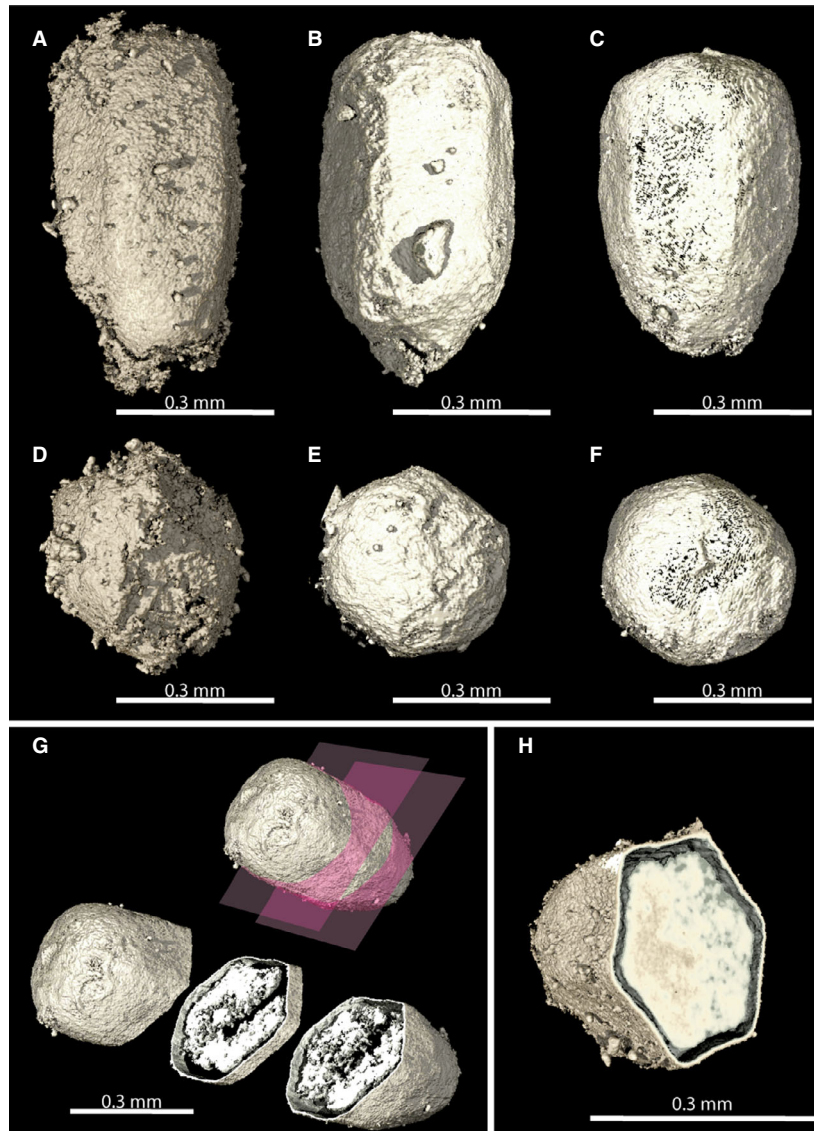


Fig. 6. PPC-SR μ CT, 3D renderings of coprolites. A–C, lateral view showing the oblong shape. D–F, apical view showing hexagonal to rounded shape. G–H, virtual cross-section showing the characteristic hexagonal shape. Voxel size, 2.26 μ m.

to *Huguenotermes septimaniensis* (Nel & Paicheler 1993; Engel & Nel 2015). In the French Oligocene deposits, termites are represented by Mastotermitidae such as *Mastotermes* (Nel 1986; Nel & Paicheler 1993; Nel & Arillo 1995) and *Blattotermes* (Nel 1986; Nel & Paicheler 1993) as well as Termopsidae such as *Paleotermopsis* and Hodotermitidae such as *Ulmeriella* (Nel 1986; Nel & Paicheler 1993). ‘Higher’ termite families (Termitidae, etc.) are recorded in the latest Oligocene only in this area. Regionally, after the single termite wing reported from the Eocene of Gard, the filled borings containing coprolites from Malzieu confirm the presence of termites in the Palaeogene ecosystems from the Massif Central.

Taphonomy

The genesis of the filled borings containing coprolites is questionable. The imprints of wood fibres on the surface of specimens attest that these would be remains of wood-borings (Steps 1 and 2 in Fig. 7). Borings filled with sediment might be a part of a nest inside a large piece of wood (Steps 3 and 4 in Fig. 7). However, it is not possible to attest the degree of complexity of the nest. When preserved *in situ*, termite coprolites commonly form accumulations in their nest (see Rozefelds & de Baar 1991; Francis & Harland 2006). In the filled borings from Malzieu, the coprolites are isolated in the matrix, not in

contact and without a particular arrangement. It suggests that they were probably a bit reworked in their nest before being trapped (reworking of trunk by water before being deposited and/or reworking of coprolites during the injection of sediment in borings). The coprolites and the coprolite moulds are well preserved (not compacted, always entire), suggesting that the sediment was injected when or a short time after the cavities were inhabited by termites (i.e. during the sedimentation or the early stages of the diagenesis). The presence of desiccation cracks on the surface of filled wood-borings demonstrates that the wood was already very dry when the holes were filled-in with sediment. The cracks are not diagenetic and were already formed before injection of sediment because they are filled by the same sedimentological material that those filling the inner structure of borings. It could be consistent with the hypothesis supporting that *Kalotermitidae* produced the coprolites under dry conditions. The borings from Malzieu were found isolated in sediment, suggesting that the wood was destroyed during the diagenesis, after lithification of filled borings (Step 4 in Fig. 7).

Palaeoenvironmental insights

The sedimentological features of the Conglomerate and Sandstone Formation from Malzieu suggest a continental palaeoenvironment. Near Malzieu, the area along the palaeo-Truyère river was a floodplain in which fluvial channels periodically occurred. Lenticular sandstone and conglomerate levels showing cross and oblique stratifications correspond to channels, whereas the argillites represent temporary low-energy deposits. The abundance of plant macroremains in both sandstone and argillite layers suggests that the environment was inhabited by a dense riparian flora. Boule (1888) mentioned angiosperm leaves and woods, including Lauraceae, Platanaceae and possible *Alnus*, *Myrica* and *Quercus*. Locally, we have noted abundant macroremains of conifers including vegetative and reproductive structures (J-DM and VT, personal observations).

Previously in France, Eocene–Oligocene termite remains described by Nel (1986), Nel & Paicheler (1993), Nel & Arillo (1995), Nel & Bourguet (2006) and Engel & Nel (2015) were collected in sediments deposited in diverse depositional palaeoenvironments.

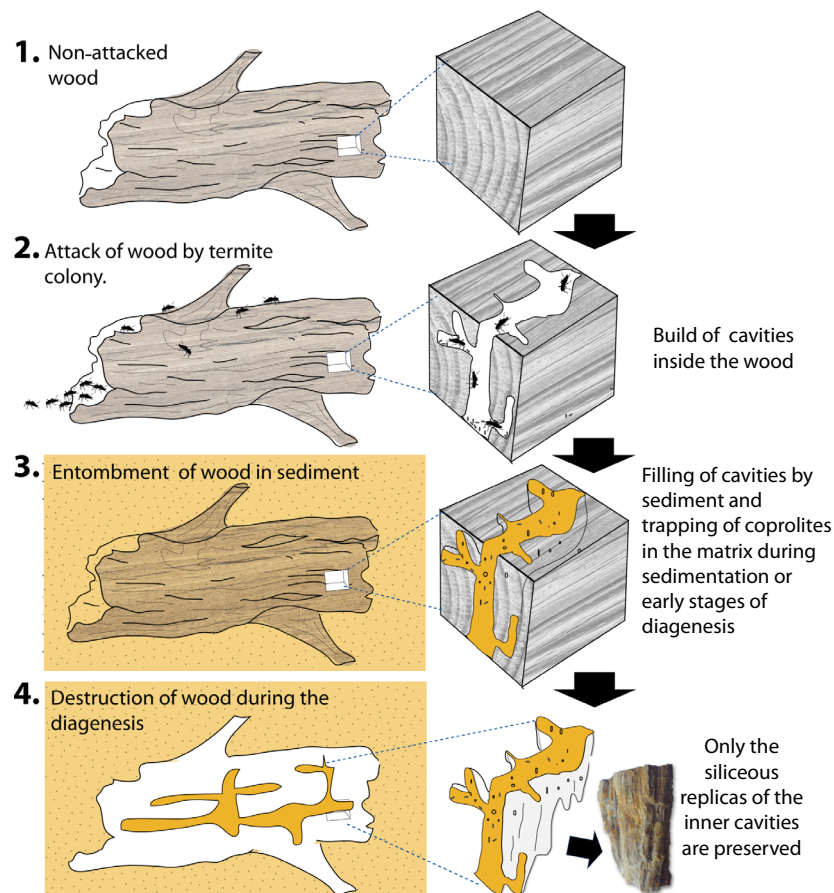


Fig. 7. Hypothetical steps explaining the preservation of the boring replicas.

The filled wood-borings from Malzieu complement this record, demonstrating that in France and during the Eocene–Oligocene interval, termite colonies have occupied diverse environments including marginal-littoral domains as well as innermost continental areas. Although, our knowledge of the flora contained in the Conglomerate and Sandstone Formation from the Malzieu Basin remains very poor, it suggests a warm temperate climate.

Conclusions

PPC-SR μ CT revealed that the fragments of borings from the Malzieu Basin contain abundant hidden tiny coprolites clearly attributable to termites. Pellets are characteristically hexagonal in cross-section. After comparison with extant termites, these coprolites share strong similarities with those of *Kalotermitidae* also called ‘drywood termites’. Although borings are only preserved as replicas, the taphonomic analysis attests that the specimens consist of fragments of wood-borings dug by termites and then filled by sediment. The depositional environment of the Conglomerate and Sandstone Formation is interpreted as a fluvial valley in which the lenticular sandstone and conglomerate lenses correspond to channels, in a probably warm environment.

Acknowledgements. – We thank the European Synchrotron Radiation Facility (ESRF) and particularly the ID19 beamline for the beam time and the material support. We thank P. Tafforeau who provided useful help during tomographic experiments. We express our gratitude to Jorge F. Genise and Marc Philippe who provided useful comments and suggestions. This paper is a contribution of the project EC-412 financed in 2016 by the ESRF. J-DM and ML received financial support from the CNRS-UMR6118. This project was supported by the Association Paléontologie des Hauts Plateaux du Languedoc (A.P.H.P.L., Mende, Lozère). We thank Cécile Fort, archivist at IMT Lille-Douai, for her bibliographical research and the time spent digitizing these publications.

References

- Astruc, J.G., Hugueney, M., Escarguel, G., Legendre, S., Rage, J.-C., Simon-Coinçon, R. & Sigé, B. 2003: Puycelci, a new vertebrate-bearing locality in the Aquitaine molassic basin. Density and continuity of the Paleogene biochronologic record in the Quercy and peripheral basins area. *Geobios* 36, 629–648.
- Boucher, L.D. 2012: Three-dimensional modeling of termite galleries in Cretaceous silicified wood. *Japanese Journal of Palynology* 58, 22.
- Boule, M. 1888: Note sur le bassin tertiaire de Malzieu (Lozère). *Bulletin de la société géologique de France* 13, 341–345.
- Bout, P. 1961: Le remplissage du bassin du Malzieu (Lozère) et ses enseignements sur la morphogénèse du Massif Central. *Revue d'Auvergne* 76, 11–26.
- Coinçon, R. 1972: La bordure occidentale de la Margeride de Neussargues à Saint-Alban, étude géomorphologique: sédimentologie des bassins, problème du modelé et de l'altération du granite de la Margeride. Unpublished Doctoral Thesis. Blaise Pascal University.
- Coinçon, R., Tardy, Y. & Godard, A. 1976: Les enseignements d'ordre morphogénique et paléoclimatique apportés par l'étude des bassins de l'ouest de la Margeride. *Revue de géomorphologie Dynamique* 3, 81–91.
- Colin, F. 1963: Le Plateau de Julianges et ses bordures (Lozère). *Bulletin du laboratoire de géologie et de préhistoire du musée de Mende* 3, 5–19.
- Colin, J.-P., Néraudeau, D., Nel, A. & Perrichot, V. 2011: Termite coprolites (Insecta: Isoptera) from the Cretaceous of western France: A palaeoecological insight. *Revue de micropaléontologie* 54, 129–139.
- Coque-Delhuille, B. & Pigeire, H. 1980: Enseignements d'un sondage dans le bassin de Saint-Alban (Lozère): comportement du socle du centre du Massif Central à l'Oligocène. *Comptes Rendus de l'Académie des Sciences Série D* 290, 1401–1404.
- Corbett, I. & Burrell, B. 2001: The earliest Pleistocene (?) Orange River fan-delta: an example of successful exploration delivery aided by applied Quaternary research in diamond placer sedimentology and palaeontology. *Quaternary International* 82, 63–73.
- Coty, D., Aria, C., Garrouste, R., Wils, P., Legendre, F. & Nel, A. 2014: The first ant-termite syninclusion in amber with CT-scan analysis of taphonomy. *PLoS ONE* 9, e104410.
- Couturié, J.-P. 1972: *Notice de la carte géologique au 1/50 000e de la France, feuille de Saugues*, 10 pp. Bureau de Recherches Géologiques et Minières, Orléans.
- Couturié, J.-P. & Geffroy, J. 1974: *Notice de la carte géologique au 1/50 000e de la France, feuille de Saint-Chély-d'Archer*, 10 pp. Bureau de Recherches Géologiques et Minières, Orléans.
- Eggleton, P. 2011: An introduction to termites: biology, taxonomy and functional morphology. In Bignell, D.E., Roisin, Y. & Lo, N. (eds): *Biology of Termites: A Modern Synthesis*, 1–26. Springer, Dordrecht.
- Engel, M.S. & Nel, A. 2015: A new fossil drywood termite species from the Late Eocene of France allied to *Cryptotermes* and *Pro-cryptotermes* (Isoptera: Kalotermitidae). *Novitates Paleontologicae* 11, 1–7.
- Engel, M.S., Grimaldi, D.A. & Krishna, K. 2008: A synopsis of Baltic amber termites (Isoptera). *Stuttgarter Beiträge zur Naturkunde, Serie B* 372, 1–20.
- Engel, M.S., Nel, A., Azar, D., Soriano, C., Tafforeau, P., Néraudeau, D., Colin, J.-P. & Perrichot, V. 2011: New, primitive termites (Isoptera) from Early Cretaceous ambers of France and Lebanon. *Palaeodiversity* 4, 39–49.
- Escarguel, G., Marandat, B. & Legendre, S. 1997: Sur l'âge numérique des faunes de mammifères du Paléogène d'Europe occidentale, en particulier celles de l'Eocène inférieur et moyen. *Mémoires et Travaux de l'EPHE, Institut de Montpellier* 21, 443–460.
- Fernandes, P., Raynal, J.-P. & Moncel, M.-H. 2006: L'espace minéral au Paléolithique moyen dans le Sud du Massif Central: premiers résultats pétroarchéologiques. *Comptes Rendus Palevol* 5, 981–993.
- Fernandes, P., Raynal, J.-P. & Moncel, Marie-Hélène. 2008a: Middle Palaeolithic raw material gathering territories and human mobility in the southern Massif Central, France: first results from a petro-archaeological study on flint. *Journal of Archaeological Science* 35, 2357–2370.
- Fernandes, P., Piboule, M., Raynal, J.-P. & Tuffery, C. 2008b: *L'espace minéral au Paléolithique moyen dans le sud du massif central (volet Lozère), synthèse 2006–2008*, 1–43 pp. Direction des Affaires Culturelles de Languedoc Roussillon, Montpellier.
- Francis, J.E. & Harland, B.M. 2006: Termite borings in Early Cretaceous fossil wood, Isle of Wight, UK. *Cretaceous Research* 27, 773–777.
- Genise, J.F. 1995: Upper Cretaceous trace fossils in permineralized plant remains from Patagonia, Argentina. *Ichnos* 3, 287–299.
- Genise, J.F. 2016: *Ichnoentomology: Insect Traces in Soils and Paleosols*. Springer, Dordrecht.

- Glangeaud, P. 1922: Le bassin oligocène effondré de Saint-Flour (Cantal) - Malzieu (Lozère). La Truyère miocène affluent de l'Allier. *Compte rendus des séances de l'Académie des Sciences* 174, 401–404.
- Grimaldi, D. & Engel, M.S. 2005: *Evolution of the Insects*. Cambridge University Press, New York, NY.
- Hooker, J.J., Collinson, M.E., van Bergen, P.F., Singer, R.L., de Leuw, J.W. & Jones, T.P. 1995: Reconstruction of land and freshwater palaeoenvironments near the Eocene-Oligocene boundary, southern England. *Journal of the Geological Society London* 152, 449–468.
- Jarzemowski, E.A. 1981: An early Cretaceous termite from southern England (Isoptera: Hodotermitidae). *Systematic Entomology* 6, 91–96.
- Jodot, P. & Rey, R. 1956: Observations stratigraphiques et malacologiques sur les bassins lacustres de Saint-Alban-sur-Limagnole (Lozère) et de Massiac (Cantal). *Bulletin de la Société Géologique de France* 6, 937–968.
- Jud, N.A., Wheeler, E.A., Rothwell, G.W. & Stockey, R.A. 2017: Angiosperm wood from the Upper Cretaceous (Coniacian) of British Columbia, Canada. *IAWA Journal* 38, 141–161.
- Knobloch, E. 1970: Ermöglicht die Paläokarpologie Aussagen zur Genese und Biostratigraphie der jungen Flyschsedimente. *Bayrischen Staatssammlung für Paläontologie und historische Geologie* 10, 297–308.
- Knobloch, E. 1971: Fossile Früchte und Samen aus der Flyschzone der mährischen Karpathen. *Sbornik Geologických Ved: Paleontologie* 13, 7–43.
- Knobloch, E. 1977: Paläokarpologische Charakteristik der Flyschzone der mährischen Karpaten. *Sbornik Geologických Ved: Paleontologie* 19, 79–137.
- Kovach, W.L. & Dilcher, D.L. 1988: Megaspores and other dispersed plant remains from the Dakota Formation (Cenomanian) of Kansas, USA. *Palynology* 12, 89–119.
- Krishna, K. & Emerson, A.E. 1983: A new fossil species of termite from Mexican amber, *Mastotermes electromexicus* (Isoptera, Mastotermitidae). *American Museum Novitates* 2767, 1–8.
- Krishna, K. & Grimaldi, D.A. 1991: A new fossil species from Dominican amber of the living Australian termite genus *Mastotermes* (Isoptera, Mastotermitidae). *American Museum Novitates* 3021, 1–10.
- Krishna, K., Engel, M.S., Grimaldi, D.A. & Krishna, V. 2013: Treatise on the Isoptera of the world. *Bulletin of the American Museum of Natural History* 377, 1–2704.
- Lavocat, R. 1951: *Révision de la faune des mammifères oligocènes d'Auvergne et du Velay*, 154 pp. Sciences et Avenir, Paris.
- Lyckegaard, A., Johnson, G. & Tafforeau, P. 2011: Correction of ring artifacts in X-ray tomographic images. *International Journal of Tomography and Statistics* 18, 1–9.
- Michon, L. 2000: Dynamique de l'extension continentale: application au Rift Ouest-Européen par l'étude de la province du Massif Central. Unpublished Doctoral thesis, Blaise Pascal University, Clermont-Ferrand.
- Mirone, A., Brun, E., Goullart, E., Tafforeau, P. & Kieffer, J. 2014: The PyHST2 hybrid distributed code for high speed tomographic reconstruction with iterative reconstruction and a priori knowledge capabilities. *Nuclear Instruments and Methods in Physics Research Section B: Beam Interactions with Materials and Atoms* 324, 41–48.
- Nel, A. 1986: Sur trois espèces nouvelles de termites fossiles du Stampien d'Aix-en-Provence (Bouches-du-Rhône) (Dictyoptera, Hodotermitidae, Mastotermitidae). *L'Entomologiste* 42, 271–278.
- Nel, A. & Arillo, A. 1995: Révision de *Mastotermes haidingeri* (Heer, 1849). Description de deux nouveaux *Mastotermes* de l'Oligocène de France et d'Espagne (Isoptera, Mastotermitidae). *Bulletin de la Société entomologique de France* 100, 67–74.
- Nel, A. & Bourguet, E. 2006: Termite of the Early Eocene amber of France (Isoptera: Mastotermitidae, Kalotermitidae). *Neues Jahrbuch für Geologie und Paläontologie* 2, 101–115.
- Nel, A. & Paicheler, J.-C. 1993: Les Isoptera fossiles (Insecta: Dictyoptera). In Nel, A., Martinez-Delclos, X. & Paicheler, J.-C. (eds): *Essai de révision des Aeschnidioidea, (Insecta, Odonata, Anisoptera)*, 103–179. CNRS Editions (Cahiers de Paléontologie), Paris.
- Noirot, C. & Darlington, J.P. 2000: Termite nests: architecture, regulation and defence. In Abe, T., Bignell, D.E. & Higashi, M. (eds): *Termites: Evolution, Sociality, Symbioses, Ecology*, 121–139. Springer, Dordrecht.
- Nuorteva, M. & Kinnunen, K.A. 2008: Insect frass in Baltic amber. *Bulletin of the Geological Society of Finland* 80, 105–124.
- Paganin, D., Mayo, S.C., Gureyev, T.E., Miller, P.R. & Wilkins, S.W. 2002: Simultaneous phase and amplitude extraction from a single defocused image of a homogeneous object. *Journal of Microscopy* 206, 33–40.
- Pires, E.F. & Sommer, M.G. 2009: Plant-arthropod interaction in the Early Cretaceous (Berriasian) of the Araripe Basin, Brazil. *Journal of South American Earth Sciences* 27, 50–59.
- Poinar, G.O. Jr 1993: Insects in amber. *Annual Review of Entomology* 38, 145–159.
- Rames, M.B. 1886: Note sur l'âge des argiles du Cantal et sur les débris fossiles qu'elles ont fournis. *Bulletin de la Société Géologique de France* 3, 357–360.
- Raynal, J.-P., Moncel, M.-H., Daujeard, C., Fernandes, P., Fiore, I., Tagliacozzo, A., Lecorre-Le Beux, M., Navarro, G.C. & Theodoropoulou, A. 2012: Neanderthal land-use and related tool-kits at the MIS 5/4 boundary in the South-East portion of the French Massif Central. In Ruebens, K., Romanowska, I. & Bynoe, R. (eds): *Unravelling the Palaeolithic: Ten Years of research at the Centre for the Archaeology of Human Origins (CAHO, University of Southampton)*, 53–72. Archaeopress, Oxford.
- Remy, J.A. 2004: Le genre *Plagiolophus* (Palaeotheriidae, Perissodactyla, Mammalia): révision systématique, morphologie et histologie dentaires, anatomie crânienne, essai d'interprétation fonctionnelle. *Palaeovertebrata* 33, 17–281.
- Remy, I., Caillet, M., Femenias, J.-M., Thuaudet, O. & Trincal, V. 2011: *Lozère, Apcher, le château, rapport intermédiaire de fouilles programmées - Intervention sur la zone 8: Le Logis 4 (le secteur 6), le bâtiment 5 (secteurs 7 et 8) et la cour*, 101 pp. Service régional de l'archéologie de Languedoc-Roussillon direction régionale des affaires culturelles, Montpellier.
- Rey, J. 1949: Stratigraphie des bassins tertiaires de Saint-Alban, le Malzieu, Saint-Flour et Neussargues. *Comptes Rendus de l'Académie des Sciences* 229, 63–66.
- Rey, R. 1967: Les formations sédimentaires à l'Est et à l'Ouest du massif du Cantal. *Revue de la Haute Auvergne* 40, 616–621.
- Ricordel-Prognon, C. 2007: Datations par paléomagnétisme des paléoolterations du Massif Central et de ses bordures: implications géodynamiques. Unpublished Doctoral dissertation, Ecole Nationale Supérieure des Mines de Paris.
- Roberts, E.M., Todd, C.N., Aanen, D.K., Nobre, T., Hilbert-Wolf, H.L., O'Connor, P.M., Tapanila, L., Mtelela, C. & Stevens, N.J. 2016: Oligocene termite nests with *in situ* fungus gardens from the Rukwa Rift Basin, Tanzania, support a Paleogene African origin for insect agriculture. *PLoS ONE* 11, e0156847.
- Rogers, A.F. 1938: Fossil termite pellets in opalized wood from Santa Maria, California. *American Journal of Science* 36, 389–392.
- Rohr, D.M., Boucot, A.J., Miller, J. & Abbott, M. 1986: Oldest termite nest from the Upper Cretaceous of west Texas. *Geology* 14, 87–88.
- Rozefelds, A.C. 1990: A mid-Tertiary rainforest flora from Capella, central Queensland. In Douglas, J.G. & Christophel, D. (eds): *Proceedings of the Third International Symposium on Palaeobotany*, 123–136. A-Z Printers, Melbourne, Vic.
- Rozefelds, A.C. & de Baar, M. 1991: Silicified Kalotermitidae (Isoptera) frass in conifer wood from a mid-Tertiary rainforest in central Queensland, Australia. *Lethaia* 24, 439–442.
- Sanchez, S., Ahlberg, P.E., Trinajstić, K., Mirone, A. & Tafforeau, P. 2012: Three dimensional synchrotron virtual paleohistology: a new insight into the world of fossil bone microstructures. *Microscopy and Microanalysis* 18, 1095–1105.
- Schultze-Dewitz, G. & Süß, H. 1988: Fossiler Termitenfrass an Holzresten aus dem Tertiär von Staré Sedlo (CSSR). Ein

- Beitrag zu den Termiten der Vorwelt. *Zeitschrift für Geologische Wissenschaften* 16, 169–173.
- Simon-Coinçon, R., Goër de Herve, A. & Ginsburg, L. 1981: Première découverte d'un fragment de rhinocérotype dans les « sables à chailles » du bassin de Saint-Flour (Cantal). *Revue des sciences naturelles d'Auvergne* 47, 31–42.
- Simon-Coinçon, R., Thiry, M., Schmitt, J.M., Legendre, S. & Astruc, J.G. 1995: From inland paleosurfaces towards sedimentary basins: the example of southwestern French Massif Central. 16th IAS Regional Meeting of sedimentary–5ème Congrès Français de sédimentologie-ASF, field trip book. Paris, France.
- Simon-Coinçon, R., Thiry, M. & Schmitt, J.-M. 1997: Variety and relationships of weathering features along the early Tertiary palaeosurface in the southwestern French Massif Central and the nearby Aquitaine Basin. *Palaeogeography, Palaeoclimatology, Palaeoecology* 129, 51–79.
- Sutherland, J.I. 2003: Miocene petrified wood and associated borings and termite faecal pellets from Ukateri Peninsula, Kaipara Harbour, North Auckland, New Zealand. *Journal of the Royal Society of New Zealand* 33, 395–414.
- Tafforeau, P., Boistel, R., Boller, E., Bravin, A., Brunet, M., Chaimanee, Y., Cloetens, P., Feist, M., Hozowska, J., Jaeger, J.-J., Kay, R.F., Lazzari, V., Marivaux, L., Nel, A., Nemoz, C., Thibault, X., Vignaud, P. & Zabler, S. 2006: Applications of X-ray synchrotron microtomography for nondestructive 3D studies of paleontological specimens. *Applied Physics A Materials Science & Processing* 83, 195–202.
- Talbot, J.-Y., Faure, M., Chen, Y. & Martelet, G. 2005: Pull-apart emplacement of the Margeride granitic complex (French Massif Central). Implications for the late evolution of the Variscan orogen. *Journal of Structural Geology* 27, 1610–1629.
- Thiry, M. & Turland, M. 1985: Paléotoposéquences de sols ferrugineux et de cuirassements siliceux dans le Siderolithique du nord du Massif central (bassin de Montluçon-Domérat). *Géologie de la France* 2, 175–192.
- Thiry, M., Simon-Coinçon, R., Ricordel, C., Parcerisa, D. & Bruxelles, L. 2006: *Paléosurfaces et paléoreliefs mésozoïques et cénozoïques du Massif Central : décryptage d'un transect Nord-Sud*, 102 pp. Ecole des Mines de Paris, Fontainebleau.
- Thiry, M., Théveniaut, H., Simon-Coinçon, R., Ricordel-Prognon, C., Lenoire, F. & Lacroix, F. 2014: Persistent paléosurfaces in the basement of French Massif Central: geodynamic implications. *Association des Sédimentologues Français (ASF)* 75, 113–117.
- Thorne, B.L., Grimaldi, D.A. & Krishna, K. 2000: Early fossil history of the termites. In Abe, T., Bignell, D.E. & Higashi, M. (eds): *Termites: Evolution, Sociality, Symbioses, Ecology*, 77–93. Springer, Dordrecht.
- Viney, M. 2008: The virtual petrified wood museum. Retrieved from <http://petrifiedwoodmuseum.org/TraceFossils.htm>. Accessed on 6 December 2018.
- Vršanský, P. & Aristov, D. 2014: Termites (Isoptera) from the Jurassic/Cretaceous boundary: Evidence for the longevity of their earliest genera. *European Journal of Entomology* 111, 137–141.