



HAL
open science

Beyond Eocene and Oligocene Epochs: The Causses du Quercy Geopark and the Grande Coupure

Thierry Pélissié, Maëva J Orliac, Pierre-Olivier Antoine, Vincent Biot, Gilles Escarguel

► **To cite this version:**

Thierry Pélissié, Maëva J Orliac, Pierre-Olivier Antoine, Vincent Biot, Gilles Escarguel. Beyond Eocene and Oligocene Epochs: The Causses du Quercy Geopark and the Grande Coupure. *Geoconservation Research*, 2021, 4 (2), pp.573-585. 10.30486/GCR.2021.1913051.1050 . hal-03420318

HAL Id: hal-03420318

<https://hal.science/hal-03420318>

Submitted on 9 Nov 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Beyond Eocene and Oligocene Epochs: The Causses du Quercy Geopark and the Grande Coupure

Thierry Pelissié^{1*}, Maëva J. Orliac², Pierre-Olivier Antoine², Vincent Biot¹, Gilles Escarguel³

¹ UNESCO Global Geopark Causses du Quercy, BP 10, 11 rue Traversière, 46240, Labastide-Murat, Cœur de Causses, France

² Institut des Sciences de l'Évolution, UMR 5554, Université de Montpellier-CNRS-IRD-EPHE – CC64, Place Eugène Bataillon, 34095 Montpellier cedex 05, France

³ Laboratoire d'Écologie des Hydrosystèmes Naturels et Anthropisés, UMR CNRS 5023 LEHNA -- Université Claude Bernard Lyon 1, Boulevard du 11 Novembre 1918, F-69622 Villeurbanne Cedex. France

Abstract

Corresponding Author:

Thierry Pelissié
UNESCO Global Geopark Causses du Quercy, BP 10, 11 rue Traversière, 46240, Labastide-Murat, Cœur de Causses, France.
ORCID: 0000-0003-2975-2903
Email: tpelissie@parc-causses-du-quercy.org

The “phosphatières du Quercy” are karstic fillings exploited for phosphate at the end of the 19th century. They yield countless continental fossils through some 30 million years, ranging from late early Eocene to early Miocene. This exceptional paleontological series documents the ‘Grande Coupure’, a major biogeographical event involving a profound renewal of vertebrate faunas, recorded in Eurasia during the Eocene–Oligocene transition. This exceptional fossil record is key to understanding the impact of biotic and abiotic factors during this turbulent time of global change. The presence of natural mummies and the 3D preservation of numerous vertebrate skulls, as well as remains of arthropods and plants, are all attractive means to raise public awareness and promote an internationally unique geoheritage.

Keywords: Paleogene; Eocene–Oligocene Transition; Palaeokarst; Phosphatières; Konzentrat-Lagerstätte; Climate change; Biodiversity; Heritage.

Article information

Received: 2020-10-23

Accepted: 2021-06-26

DOI: 10.30486/GCR.2021.1913051.1050

How to cite: Pelissié T, Orliac MJ, Antoine P-O, Blot V & Escarguel G (2021). Beyond Eocene and Oligocene epochs: The Causses Du Quercy Geopark and the Grande Coupure. *Geoconservation Research*. 4(2):***. doi: 10.30486/gcr.2021.1913051.1050

Geoconservation Research e-ISSN: 2588-7343 p-ISSN: 2645-4661

© Author(s) 2021, this article is published with open access at <http://gcr.khuisf.ac.ir>



This work is licensed under a Creative Commons Attribution 2.0 Generic License.

Introduction

The Causses du Quercy provide nearly 200 paleontological localities that document the ‘Grande Coupure’, an important biological crisis driven by climatic and paleogeographic changes at the Eocene–Oligocene transition, 33.9 million years ago (Ma). This event is marked by drastic changes in climatic and environmental conditions as well as biodiversity. The Geopark is located in south-

western France, on the northern sedimentary edge of the Aquitaine, a site of former phosphate mining on the southern termination of the Causses du Quercy, straddling the Lot and Tarn-et-Garonne departments, with a few sites also in the Aveyron and Tarn departments (Fig. 1). They occupy the southern half of the territory of the UNESCO Causses du Quercy World Geopark.

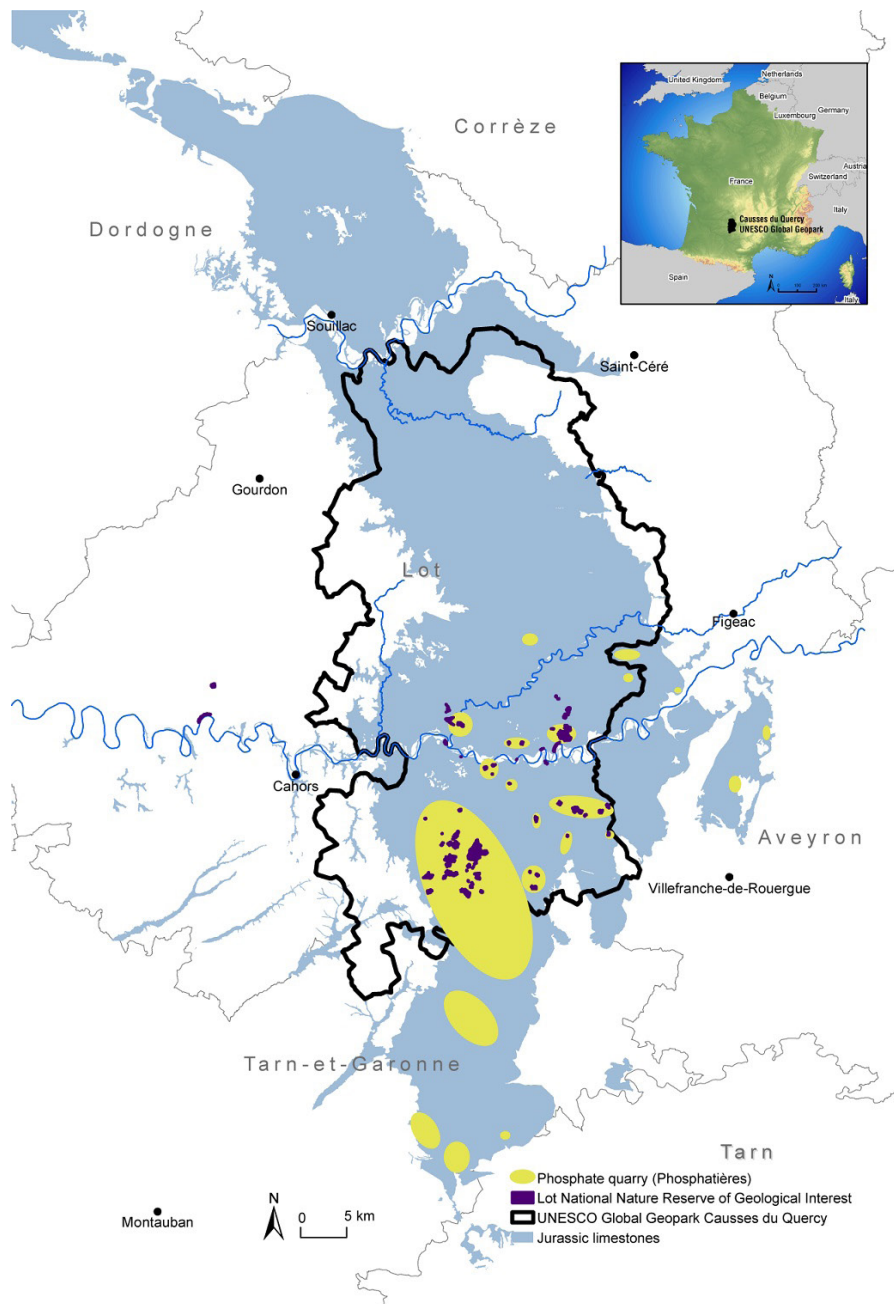


Figure 1. Geographical location and geological context of the Causses du Quercy area in southwestern France.

The key importance of the site includes its documentation of the Grand Coupure, which was enabled by three other elements.

First, the Jurassic carbonate substratum has experienced karstic erosion since the Campanian–Maastrichtian, about 70 Ma. Limited surface weathering since then means that paleokarstic fillings of very different ages, ranging from 52 Ma to the present, may be seen, including a continuous, highly fossiliferous series from the late middle Eocene to the late Oligocene (39–24 Ma).

Second, the karstic cavities form sedimentary traps and specific habitats. The remains of living organisms accumulated in the caves, whatever their size: large elements brought by floods, prey dragged into their dens by predators, pellets of raptors, corpses of cave-dwellers, etc. The filling was instantaneous geologically speaking, and fossils thus give a relatively accurate and unbiased picture of the ecosystems around the landscape above the karst.

Third, phosphate is omnipresent in these fillings. Even if the mechanisms, probably bacterial, allowing its mobilization remain poorly understood, they allowed flash fossilization of exceptional quality. This is evidenced by the preservation of skulls in 3D (especially as delicate as those of bats) and the presence of amphibian mummies, mummified arthropods, and phosphatized seeds, fruits and flowers.

Scientific Importance of the Causses du Quercy Geopark

The Causses du Quercy Geopark has no equivalent worldwide in preserving a unique abundance of highly fossiliferous paleokarst (a multi-site Konzentrats-Lagerstätte) recording local fossil assemblages covering a total time interval of more than 30 million years (52–19 Ma) among which ca. 15 myr is very densely documented (39–24 Ma) with excellent biochronological resolution (Escarguel *et al.* 1997) in a context of drastic global climatic and environmental changes.

The dense, almost continuous fossil record at Quercy gives access to a dynamic image of vertebrate faunas (Fig. 2), with an unparalleled taxonomic diversity of amphibians (frogs and newts), squamates (lizards and snakes), turtles, crocodylians, birds (with for example parrots and birds of prey), and, above all, mammals, including marsupials, pangolins, flesh-eaters, insectivores, odd- and even-toed ungulates, bats, rodents, and primates (Pélissié and Sigé 2006). Hence, this fossil assemblage offers a unique window on Eocene–Oligocene biodiversity in Europe (Legendre 1989; Escarguel *et al.* 2008, 2011).

Most remarkably, the time interval covered by the Quercy localities includes a major global climate aridification and cooling event at the Eocene–Oligocene transition (EOT). This event relates to the onset of an Antarctic icecap in response to the slow decrease in atmospheric CO₂ concentration during the late Eocene combined with the opening of the Drake Passage by the latest Eocene (Zachos *et al.*, 2008). Beyond the geologically abrupt switch from a Greenhouse to an Icehouse Earth, such a global climate change has profound biogeographical consequences following a major drop in sea level worldwide resulting from the onset of ice sheets. In Eurasia, the EOT thus corresponds to a major faunal turnover called the ‘Grande Coupure’ (Stehlin 1910), where about half the European placental mammal species disappeared, while many clades of Asian or North American origin immigrate (Legendre and Hartenberger 1992).

In this context, the Quercy fossil record offers a unique integrated perspective on the deep-time local to regional evolutionary and ecological dynamics of vertebrate communities in the context of a global crisis. For instance, Legendre (1989) and Escarguel *et al.* (2008) show through ceno-gram analyses how the EOT deeply affected local mammal communities from both taxonomic composition and richness points of view, whereas Escarguel *et al.* (2008, 2011) showed an entirely distinct impact of the EOT at the regional meta-

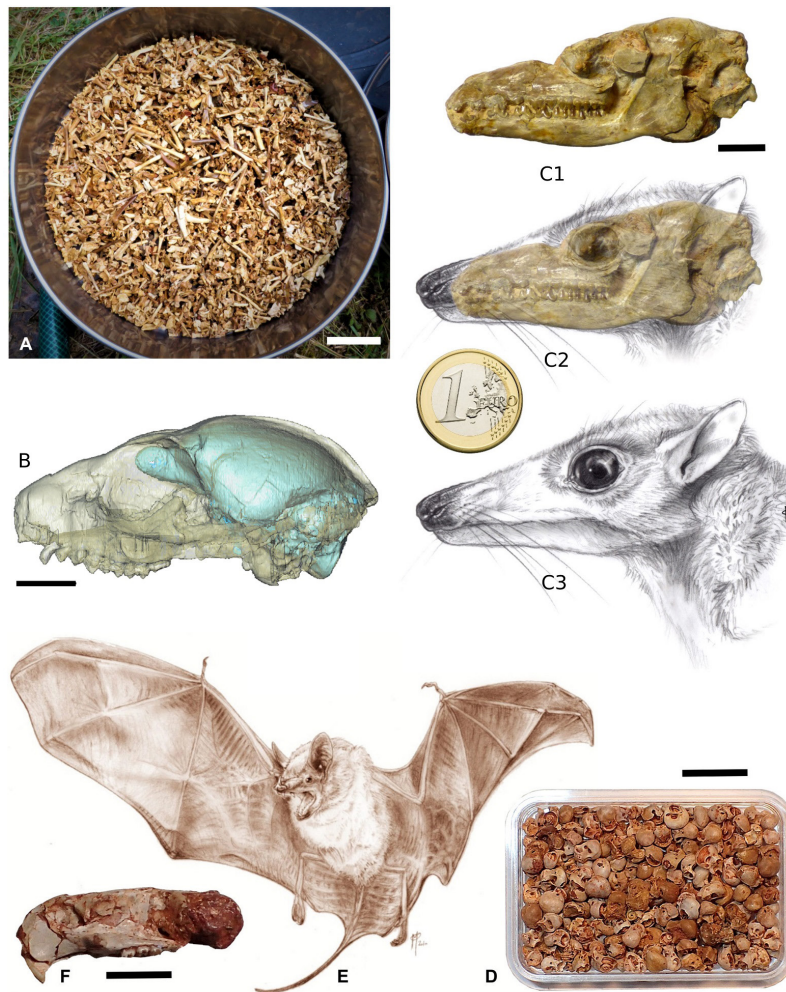


Figure 2. Selected Eocene–Oligocene phosphatized fossils and life reconstructions from the Causses du Quercy Geopark. A) Screen-washing residue of the new Dams locality, latest Eocene. B) Skull of the small primate *Microchoerus eracinus* showing the molding of its cranial cavity, latest Eocene. C) Life reconstruction of the late Eocene artiodactyl *Mouillacitherium elegans*, named after the local Mouillac village. Reconstructions by Maëva J. Orliac. D) Bat petrosal bones from Sainte Néboule locality, late Eocene. E) Life reconstruction of the early Oligocene hipposiderid bat *Vaylatsia*, named after the local Vaylats village. Reconstruction by Maëva J. Orliac. F) Skull of the late Eocene–earliest Oligocene theridomorph rodent *Suevosciurus*, a genus known from several fossil localities in the Quercy before and after the ‘Grande Coupure’. Scale bars = 5 cm (A), 1 cm (B, C), 5 mm (D, F).

community level (Fig. 3). Focusing on late Eocene and early Oligocene even-toed ungulates for which a comprehensive fossil record is available from the Quercy localities, the ongoing “Dead-ender” research project led by one of us (MJO), and funded by the ANR, aims to characterize and

contrast the biological characteristics and evolutionary dynamics of European endemic ‘archaic’ Eocene clades and Asian ‘modern’ clades which dispersed into Europe during the ‘Grande Coupure’.

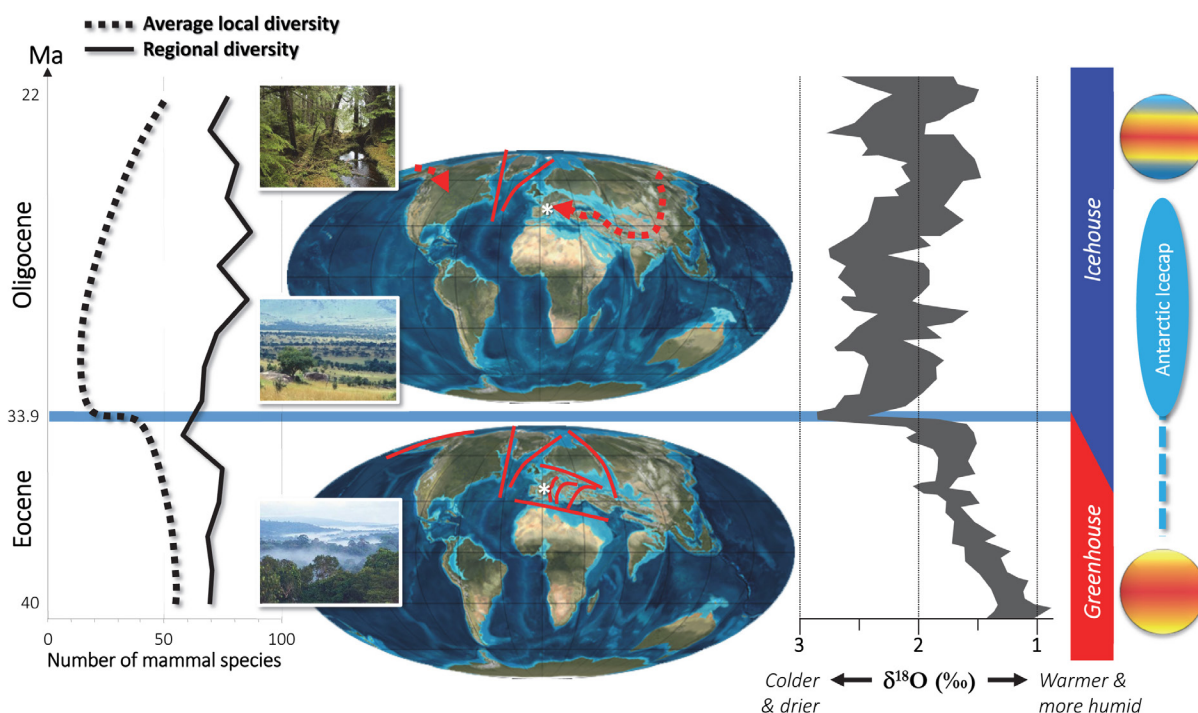


Figure 3. Fossil localities from the Causses du Quercy Geopark illustrate the deep-time evolutionary and biodiversity dynamics of terrestrial environments in a geographically and climatically changing world. The blue line at 33.9 Ma (Eocene-Oligocene transition) indicates Stehlin’s ‘Grande Coupure’, a major Northern-hemisphere biogeographical event resulting from the onset of an Antarctic icecap in the context of a Greenhouse to Icehouse global climate change. The white star on the paleomaps locates the Causses du Quercy area. Evolution of the local and regional number of mammal species after Escarguel *et al.* (2008); Paleomaps by Ron Blakey 2016; $\delta^{18}\text{O}$ curve and global climate after Zachos *et al.* (2008).

In addition to vertebrates, the Quercy localities also yield invertebrate and plants remains, enhancing the value of the sites in providing snapshots of past terrestrial ecosystems. Insects, plants, and some amphibians are preserved as “phosphatized mummies”, with finest details and soft body parts, resulting from a rapid permineralization process that remains to be elucidated. These exceptionally preserved past organisms are very rare worldwide, especially for this time interval.

Although 3D batrachian remains (Fig. 4) were mentioned and depicted in very early years (Filhol 1873), their real nature, as simple molds or mummies, was long debated. It was not until the use of CT Scan- and Synchrotron-aided imagery (Laloy *et al.* 2013; Tissier *et al.* 2016) that the question was settled. Three-dimensional tissue preserva-

tion is truly outstanding in some cases: a *Phosphotriton sigei* salamander preserves the lungs, spinal cord, muscles, urogenital organs, and digestive tract. In the latter organ, the perfectly identifiable remains of a frog, further testify to the animal’s last meal. This is the oldest known example of 3D preservation of vertebrate internal organs to date (Tissier *et al.* 2017).

Insect remains have also been reported for a long time. For instance, Thévenin (1903) wrote “The insects, which are quite numerous in phosphorites and often very delicately preserved, would deserve special study”. This task was initiated four decades later (Handschin 1944) with a remarkable apprehension of internal structures of pupae through progressive wear and tear. Once again, recent investigation methods using high-energy scanners opened new lines of investigation, nota-

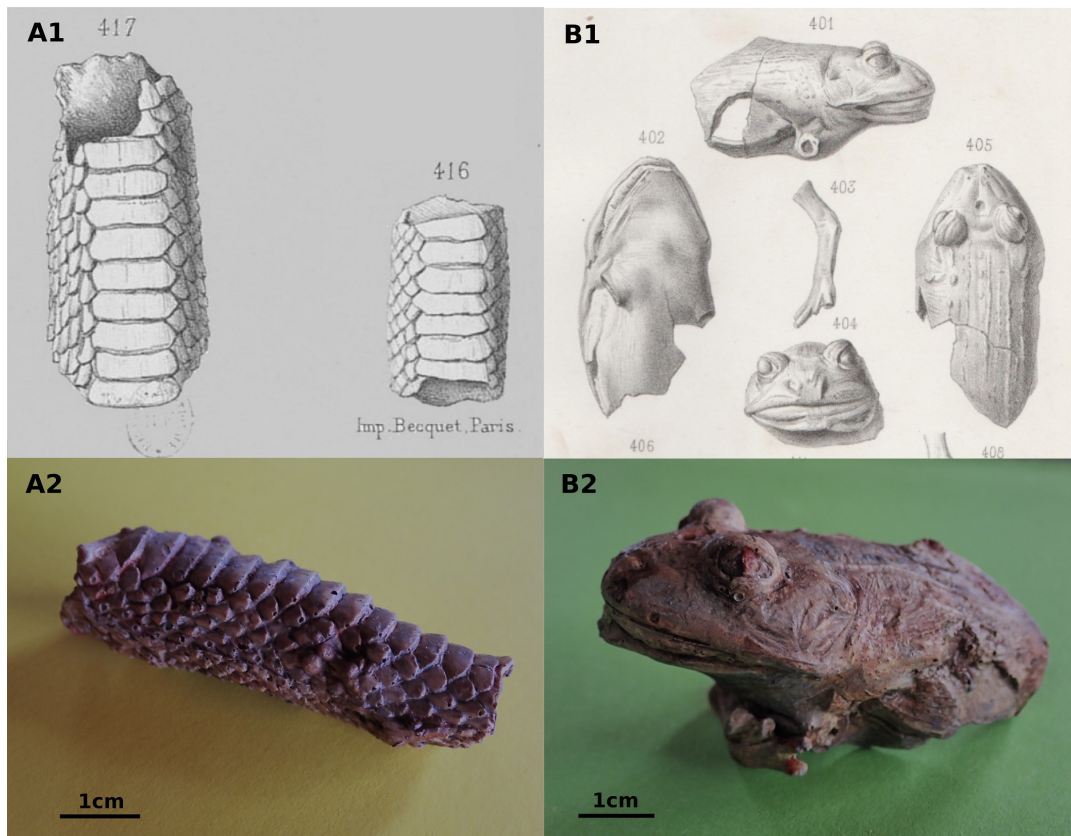


Figure 4. Squamate mummies from the Causses du Quercy Global Geopark. A) *Coluber* sp. B) *Thaumastosaurus gezei*. A1, B1, drawings published by Filhol (1873). A2, B2, moldings made by the MNHN Paris.

bly in unveiling early examples of parasitism in arthropods (Schwermann *et al.* 2016 a,b; van de Kamp *et al.* 2018). Nevertheless, if the data until now have been investigated from undated old collections, recent field work has revealed several well-identified and biochronologically-constrained localities that yield such phosphatized mummies (Fig. 5).

The presence of plant remains in the Quercy localities was only explicitly mentioned in the last decades (De Franceschi *et al.* 2006). The diversity of wood fragments, buds, seeds, and fruits is considerable (Fig. 6), with each field season bringing numerous new specimens. All these fascinating discoveries open up new research avenues for the phosphorites of Quercy.

Thousands of spectacular fossils were discovered during the intense mining activity for phosphate

exploitation in the second half of the 19th century and bought by museums. Fossils from Quercy are today curated by major museums around the world, such as the Muséum National d'Histoire Naturelle in Paris (20,000 specimens), the Natural History Museum in London, and the American Museum of Natural History in New York. From 1965, paleontological fieldwork at Quercy by academics from various French institutions led to the collection of over 100,000 referenced specimens (actually, several millions, if the fragmented and unnumbered elements are taken into account) in well-constrained stratigraphic, biochronological and taphonomic contexts. Rich in about 500 mammalian fossil species described to date for nearly 700 vertebrate species, the Quercy mammalian paleofauna now unsurprisingly constitutes a worldwide Paleogene reference, with five European Mammalian Paleogene reference levels (MP) defined after localities situated in the Quer-



Figure 5. Arthropod mummies from the Causses du Quercy Global Geopark. Top line: beetles; middle line, myriapods; bottom line, undetermined insects.

cy area, including three from the Causses du Quercy Geopark (Biochrom'97 1997).

Given the exceptional geographical and temporal density of its highly fossiliferous localities, the Causses du Quercy Geopark can barely be compared to other fossil-yielding areas around the world. In France, no region among the most fossiliferous (e.g., Eastern Occitania or the Paris Basin) offers such a quantity and quality of fossil record over such a long period of time. In Eu-

rope, the fossil-bearing levels of the Geiseltal coal mines in Saxony-Anhalt, Germany, have provided a magnificent fossil record, including hundreds of complete vertebrate skeletons, covering a much shorter, mid-Eocene time interval (48–42 Ma). Nevertheless, these fossiliferous levels are no longer accessible, the entire pit mine having been flooded by a large artificial lake in the 2000s to create recreational and natural areas. On the other hand, the Madrid, Calatayud-Daroca and Teruel sedimentary basins in Central Spain offer an



Figure 6. Vegetal remains from the Causses du Quercy Global Geopark. A) Fragments of branches. B1 to 3) Various seeds. C) Bud in lateral (1) and apical view (2).

impressive but size-biased micro-vertebrate fossil record spanning ca. 20 myr from the latest Oligocene to the early Pliocene, but here scattered over a much larger and composite geographical area than in Quercy. Outside Europe, the Cretaceous-Paleogene sedimentary basins in the northwestern USA

(e.g., the Bighorn Basin in Wyoming) as well as the Mongolian Plateau in Asia provide outstanding vertebrate fossil records through hundreds of fossiliferous localities over longer time intervals than for the Quercy, but these records do not offer the spatiotemporal density achieved in the Quercy area.

The fossiliferous complex most directly comparable to the Causses du Quercy Geopark in terms of quality, quantity and density of fossils and fossil localities is the Riversleigh UNESCO World Heritage area in NW Queensland, NE Australia (Archer *et al.* 2000). Fossil sites at Riversleigh document freshwater limestones deposited in lime-rich pools as well as cave and fissure-filling deposits. The Riversleigh vertebrate fauna includes exquisitely preserved fossils of monotreme and marsupial mammals as well as birds and reptiles from about 200 fossil localities ranging from the late Oligocene to the late Miocene (ca. 25–5 Ma). Beyond obvious faunal differences between Europe and Australia, the main difference between the Causses du Quercy Geopark and the Riversleigh World Heritage area is the surface occupied by the Australian sites, about 100 km², thus preventing the integration of local biodiversity variations at an ecologically and evolutionarily relevant regional scale.

Geotouristic Valorization of the “Phosphatières”

Over the last decade, many nations have become interested in geotourism. With the UNESCO World Geopark label obtained in 2017, the Causses du Quercy Regional Natural Park wanted to give genuine recognition to its geological heritage, of which phosphate deposits are the jewel in the crown. However, the Causses du Quercy did not wait until this label was obtained to promote some of its geosites and to make them accessible to the public. At the initiative of various public or private players, four phosphate deposits have been developed and interpreted.

(a) Guided tour of the Cloup d’Aural phosphatières. Developed and managed by the Quercy Phosphate Association, they opened to the public in 2000. This tourist site offers visitors the opportunity to descend, via a comfortable path, to the bottom of a phosphatière, the visit being guided. Excavations are organized every summer in the surrounding phosphatières; the

Cloup d’Aural is then the base camp for processing these localities (room made available for screenwashing, sieving, and picking fossil remains under a battery of stereomicroscopes). With 14,000 annual visitors, the Cloup d’Aural phosphatières are a geosite actively participating in the economic development of southern Lot with four permanent jobs. It is the fifth most visited natural cavity (behind the Padirac chasm and the Pech Merle caves) in the Lot Département. Since 2019, the community of communes of the Pays de Lalbenque-Limogne has taken over the management and tourist exploitation of this unique site. It is currently the subject of an ambitious four-year program to upgrade the site’s tourist facilities to extend the visitor route and improve the experience on the one hand, and to strengthen the surface interpretation facilities on the other.

b) Free access to the phosphatières des Tempories. In addition to the Cloup d’Aural phosphate quarries, the Parc naturel régional des Causses du Quercy, in conjunction with the local authorities, wanted to develop freely accessible phosphatières. The Geosite of Tempories, which still contains some traces of its mining operations, was selected for this project. This choice was motivated by the fact that it is a reference paleontological geosite whose fillings were dated at 34.4 Ma, i.e. just before the ‘Grande Coupure’. The approach to the phosphatières has been secured and observation platforms have been installed. In addition, an interpretation panel presents the site.

c) Phosphate mound and caving at the Factor’s igue. This atypical geosite provides access to beautifully concretioned underground galleries, following its historical excavation pathway. It is a site prized by speleologists for the initiation and discovery of the underground environment. It is valued by the Lot Département as part of its policy of sensitive natural

areas (ENS) and is a point of interest on the caselle interpretation trail, a trail about cultural and natural heritage with many small drystone huts.

d) The karstic path of Crégols. In partnership with speleologists, an interpretation trail has been created on the theme of water catchments in limestone environments. It integrates the Crégols phosphatière which, in addition to its interest as an aquifer resource, illustrates the conservation role of karst.

Conservation of Phosphatières-related Geopatrimony

The phosphatières located within the perimeter of the Causses du Quercy Regional Nature Park benefit from double protection.

First is classification as a National Geological Nature Reserve. This classification, initiated by the French State in 2015, provides strong protection and is endowed with dedicated funding and human resources. Any geosite sampling is subject to authorization following the advice of a dedicated Scientific Council. Whatever their nature, dumping of waste is strictly forbidden. The agents of the Reserve have police powers, but their work includes above all an important information and awareness-raising component aimed at the inhabitants and users of the territory, local elected representatives, tourists, and especially schoolchildren. In parallel, the Reserve coordinates the ongoing scientific research activities in the phosphatières and indexes in its collection of all the specimens collected.

Older collections were built up during the industrial exploitation of these sites at the end of the 19th century and during excavations prior to its creation. The Reserve endeavors to complete an exhaustive inventory, but this is a difficult task, as fossils are scattered in numerous public and private collections all over the world. In the long term, it is planned to archive as many CT scans

as possible of the major specimens, particularly holotype and figured specimens, to produce 3D prints of them and to enhance their value through a museographical structure set up, with the Maison de la Réserve on the Cloup d'Aural site.

A second level of protection comes through the GGU label of the Causses du Quercy. This is intended to enable the inhabitants to better appropriate this still little-known heritage and to become its guarantors (Fig. 7). They are closely linked to the projects carried out by the GGU, often in partnership with approved structures such as the Cloup d'Aural geosite and the "Les phosphatières du Quercy" association. For schools, we note the "Graines de paléontologues" (seeds of palaeontologists) program, in which fossiliferous sediment is handed over to the schools that sort it, with all the fossils collected in this way enriching the material available to paleontologists (Peigné *et al.* 2014). For its part, the operation "My village, my fossil" aims to create, in consultation with the inhabitants, a mascot promoting extinct animals whose name derives from that of the village, such as *Bachitherium* for Bach or *Vaylatsia* for Vaylats (Fig. 2).

The boundaries of the Geopark are currently limited to the Lot Department, and some phosphate quarries, particularly in the Tarn-et-Garonne Department, are excluded. Contacts with local elected officials are underway for a possible extension of the Reserve, or even the Geopark in the long term, to ensure sustainable conservation.

Summary

Since their discovery in the 1870s, the Phosphatières du Quercy has never ceased to provide abundant and diverse Paleogene fossil material including vertebrates, molluscs, arthropods, and plant remains. After a few decades of relative oblivion following the abandonment of mining activities in the early 20th century, the renewal of modern paleontological research in the Causses du Quercy in the mid-1960s, which has been uninterrupted ever since, has demonstrated the



Figure 7. On the Cloup d'Aural geosite, each year, more than 14.000 adults and children discover the "Phosphatières du Quercy" through specific animations.

extreme richness of the Quercy fossil-yielding sites, combined with the exceptional preservation of very delicate specimens (e.g., bat and rodent skulls, petrosal and middle-ear bones) as well as "mummified" organisms preserving petrified soft tissues. This makes Quercy one of the most exceptional fossil-yielding areas at the world scale – a genuine multi-site *Konzentrat-Lagerstätte* including about 200 fossil localities known to date. New localities are discovered and sampled every year, and thoroughly associated with the geological and sedimentological study of fossiliferous fillings. As such, the Phosphatières du Quercy allow for a diachronic analysis of local-regional terrestrial communities, their dynamics, and their environment over more than 15 myr, in a context of major climatic and biogeographical changes (around the Eocene-Oligocene transition).

Building on previous scientific results and ongoing research projects, the long-term scientific potential of this area is indisputable and future stud-

ies of fauna and flora dynamics will certainly be of considerable help for understanding the evolution of organisms during times of drastic global changes. Forthcoming projects may tackle questions related to absolute radiometric dating of fossils and sediments to improve the biochronological resolution of the entire time series, karst dynamics and phosphatization processes. On the other hand, focusing on specific, well-sampled clades or trophic levels will provide a more detailed understanding of the evolutionary and ecological dynamics of inter-organismal interactions in the ancient ecosystems.

Concerning land development, a Reserve House will be created on the Cloup d'Aural site, a phosphatière-museum open to the public since 2000. This structure devoted to the reserve and the geopark will include a conservation area for the collections (currently scattered in different academic institutions) and a public-dedicated museographic structure, part of which will be

outdoors. A series of short video presentations about the geosites has already been initiated (<https://www.facebook.com/parcdescausses-duquercy/videos/331979104694995>) and will be expanded. These actions result from the constant desire to involve the inhabitants in the management of a geo-heritage unique in the world.

Conflict of Interest

The authors declare that they have no conflicts of interest concerning this article

References

- Archer M, Hand SJ & Godthelp H (2000). Australia's lost world: Riversleigh. Reed, Sydney : World Heritage Site.
- De Franceschi D, Le Gall C, Escarguel G, Huguency M, Legendre S, Simon Coinçon R, Pélissié T & Sigé B (2006). Une paléoflore des phosphatières karstiques du Quercy (Sud-Ouest France): première découverte, résultats et perspectives. In: 30 millions d'années de biodiversité dynamique dans le paléokarst du Quercy, Journées Bernard Gèze. Strata (sér. 1) 13:97–101.
- Escarguel G, Fara E, Brayard A & Legendre S (2011). Biodiversity is not (and never has been) a bed of roses! *Comptes Rendus Biologies* 334:351–359.
- Escarguel G, Legendre S & Sigé B (2008). Unearthing deep-time biodiversity changes: The Palaeogene mammalian metacommunity of the Quercy and Limagne area (Massif Central, France). *Comptes Rendus Geoscience* 340:602–614.
- 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. In Aguilar J-P, Legendre S, Michaux J (Eds.), *Actes du congrès Biochrom'97* (pp 443–460), Mem. et trav. E.P.H.E., Inst. Montpellier 21.
- Filhol H (1873). Sur des pièces fossiles provenant de Batraciens, de Lacertiens et d'Ophidiens, trouvés dans les dépôts de phosphates de chaux de l'Aveyron. *Comptes Rendus de l'Académie des Sciences, Paris*. 77:1556–1557.
- Handschin E (1944). Insekten aus den Phosphoriten des Quercy. *Schweizerische Paläontologische Abhandlungen*. 64:1–23.
- Laloy F, Rage J-C, Evans SE, Boistel R, Lenoir N & Laurin, M (2013). A re-interpretation of the Eocene anuran *Thaumastosaurus* based on microCT examination of a 'mummified' specimen. *PLOS ONE* 8(12): 10.1371/annotation/f7988d67-24b9-493c-9aef-c5c715948a1e.
- Legendre S (1989). Les communautés de mammifères du Paléogène (Éocène supérieur et Oligocène) d'Europe occidentale: structures, milieux et évolution. *Münchener Geowissenschaftliche Abhandlungen A* 16:1–110.
- Legendre S & Hartenberger J-L (1992). Evolution of mammalian faunas in Europe during the Eocene and Oligocene. In Prothero DR & Berggren WA (Eds.), *Eocene/Oligocene climatic and biotic evolution*, (pp. 516–528), Princeton, NJ, USA: Princeton University Press.
- Peigné S, Vianey-Liaud M, Pélissié T & Sigé B (2014). Valbro: un nouveau site à vertébrés de l'Oligocène inférieur (MP22) de France (Quercy). I – Contexte géologique; Mammalia : Rodentia, Hyaenodontida, Carnivora. *Annales de Paléontologie*. 100:1–45.
- Pélissié T & Sigé B (2006). 30 millions d'années de biodiversité dynamique dans le paléokarst du Quercy. *Journées Bernard Gèze. Strata (sér. 1) 13*: 284.
- Schwermann AH, Wuttke M, dos Santos Rolo T, Caterino MS, Bechly G, Schmied H, Baumbach T & van de Kamp T (2016a). The fossil insects of the Quercy region: a historical review. *Entomologie Heute*. 28:127–142.
- Schwermann AH, dos Santos Rolo T, Caterino MS, Bechly G, Schmied H, Baumbach T & van de Kamp T (2016b). Preservation of three-dimensional anatomy in phosphatized fossil arthropods enriches evo-

- lutionary inference eLife. 5:e12129.
- Stehlin HG (1910). Remarques sur les faunules de mammifères des couches éocènes et oligocènes du Bassin de Paris. Bulletin de la Société Géologique de France. 9:488–520.
- Thévenin A (1903). Etude géologique de la bordure Sud-Ouest du Massif Central. Bulletin du Service du Carte Géologique de France. 14(95):353–554.
- Tissier J, Rage J-C, Boistel R, Fernandez V, Pollet N, Garcia G & Laurin M (2016). Synchrotron analysis of a ‘mummified’ salamander (Vertebrata: Caudata) from the Eocene of Quercy, France. Zoological Journal of the Linnean Society. 177:147–164.
- Tissier J, Rage J-C & Laurin M (2017) Exceptional soft tissues preservation in a mummified frog-eating Eocene salamander. PeerJ 5:e3861
- Van de Kamp T, Schwermann AH, dos Santos Rolo T, Lösel PD, Engler T, Etter W, Faragó T, Göttlicher J, Heuveline V, Kopmann A, Mähler B, Mör, T, Odar J, Rust J, Jerome NT, Vogelgesang M, Baumbach T & Krogmann L (2018). Parasitoid biology preserved in mineralized fossils. Nature Communications. 9:3325.
- Zachos J, Dickens G & Zeebe R (2008). An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. Nature. 451:279–283.