
The French ambers: a general conspectus and the Lowermost Eocene amber deposit of Le Quesnoy in the Paris Basin

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ABSTRACT

A conspectus of the current knowledge on the French ambers is proposed. France is a very rich country with more than seventy localities known after the 'old' literature, especially from the Jurassic, Cretaceous and Paleogene. A more detailed new insectiferous amber locality is given for the amber from Le Quesnoy (Lowermost Eocene, Oise department, Paris Basin, France). After the preliminary survey of the flora and the vertebrate and arthropod faunas, we propose a reconstruction of a fluvio-lacustrine palaeoenvironment with a forest, under a warm and wet seasonal climate. This site is outstanding because of the richness, diversity and the state of preservation of the fossils. The present discovery opens a remarkable window on the terrestrial life during the earliest Eocene. It shows that future researches on the 'old' French amber localities shall be crucial for our knowledge on the evolution and diversity of the insects during the Mesozoic and Early Cenozoic.

KEYWORDS | Amber. Mesozoic. Cenozoic. France. Palaeofauna. Palaeoflora. Palaeoenvironment.

INTRODUCTION

Outcrops with fossiliferous amber are rare enough to render any new discovery in the field noticeable. If, furthermore, the amber is in its primary deposit and associated with a rich flora and vertebrate fauna, this discovery can be qualified as a major one. France is a country rather rich for amber, with numerous localities (Fig. 1).

In the present work, we present the state of the art on French ambers, followed by a more precise development on the Lowermost Eocene amber of the Oise department.

THE FRENCH AMBERS

Lacroix (1910) cited seventy-five localities or regions with amber, ranging from the Carboniferous to the Cenozoic. Schlüter (1978, pp. 13-14) gave a list of sixty-two

localities, without indication of age, mainly after Lacroix. Other data in the literature have nearly always been taken from the original work of Lacroix (Krumbiegel and Krumbiegel, 1994; Eskov, 2002), without further field research. Little has been done up to the present to collect these ambers and their inclusions.

Noticeable works on the French ambers are rare. Galippe (1920) made an analysis of the microfossils in several French ambers. Savkevitch and Popkova (1978) compared the mineralogy and chemical composition of several French ambers. Schlüter (1975, 1978, 1983, 1989) made a rather extensive study of the Cenomanian amber from the Sarthe Department and its fauna. Breton et al. (1998) studied the microfossils from a Sparnacian amber from the Corbières (South France).

We began to collect and study fossiliferous French ambers in 1996, after the discovery of an important out-

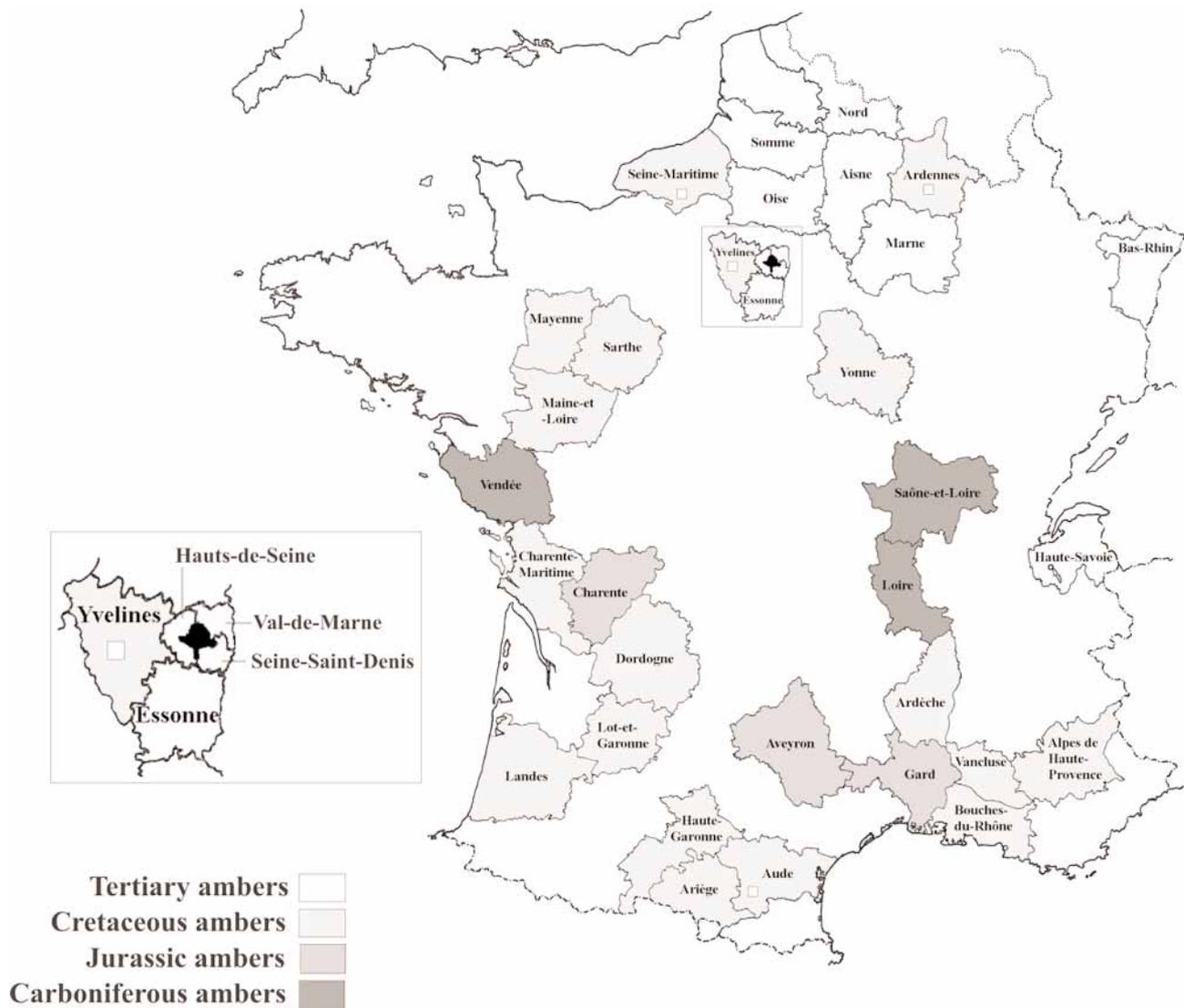


FIGURE 1 | Map of the French departments that include Carboniferous to Tertiary amber localities. The white square corresponds to some departments where also several Tertiary localities occur. Most of the Tertiary localities are Palaeocene-Eocene in age, whereas localities in Bas-Rhin and Haute Savoie are Oligocene and Miocene, respectively.

crop of Lowermost Eocene amber in the Oise department. Also the discovery of an Upper Albian locality at Archingeay, near Rochefort (Charente-Maritime) provided an opportunity to create national collection of inclusions of about 20,000 specimens for the Oise amber and 300 for the amber of Archingeay. We also collected Albo-Cenomanian ambers with inclusions at Fourtou and Cubières (ten inclusions, Jean Le Loeuff leg., Corbières) and Salignac (twenty four inclusions, in marine deposits with ammonites and ichthyosaurs, Luc Ebbo leg., Alpes-de-Haute-Provence), but also Santonian ambers at Piolenc (in fluvial or estuarine deposit, eight inclusions, Christian Delvaque leg., Drome) and La Bouilladise (in estuarine and marine deposit, Daniel Roggero leg., Bouches-du-Rhône).

We have rechecked the list of amber localities of Lacroix (1910). Lacroix cited the presence of Carboniferous 'amber' in small drops. More interesting for the potential inclusions are the citations of Jurassic ambers. More precisely, an amber locality is cited near Le Vigan (Gard), which should be Bathonian (geological map B.R.G.M. 672 'Le Vigan', 1985), and another locality should be near Roumazière (Charente). It has given yellow amber and should be Toarcian (geological map B.R.G.M. 686 'La Roche Foucauld', 1983). Pre-Cretaceous ambers are not frequent around the World (Triassic of Mutxamiel, Alicante Province, Spain; Swiss, Triassic; Arizona, Triassic; Italy, Triassic; Lebanon, Jurassic) (Krumbiegel and Krumbiegel, 1994; Gianolla et al., 1998; Peñalver, pers. comm.).

The French Cretaceous ambers are mainly Albian (twelve localities) and Cenomanian (thirty two localities), with few localities dated from the Turonian (two outcrops in Bouches-du-Rhône), Santonian (two outcrops in the Bouches-du-Rhône and one in the Drome department), and Maestrichian (five outcrops in Corbières, Emmanuel Gheerbrandt leg., one in Ariège).

French Cenozoic ambers are mainly Upper Paleocene to Lowermost Eocene (Lower Sparnacian). They were very numerous in the Paris Basin during the 19th century and the first half of 20th century, but they were located in lignite, potash, and alum quarries that are now closed. There is only one citation of an Oligocene outcrop from Alsace (Bas-Rhin) and one from the Aquitanian of Haute-Savoie (Lacroix, 1910).

Some general remarks can be made concerning the French amber outcrops. First, all the French Cretaceous ambers that have been analysed were produced by gymnosperms, probably by Araucariaceae (Schlüter, 1978; Néreaudau et al., 2002). The French Eocene amber is of angiosperm origin (see below), unlike the well-known Baltic amber. The sediments of some Cenomanian amber localities were deposited under the sea, especially those around Sisteron (Alpes-de-Haute-Provence). Other French Cretaceous outcrops are of fluvial or estuarine origin, similarly to many amber deposits around the World. Perrichot (2004) gives a more precise conspectus on the Albian amber of Archingeay.

THE LOWERMOST EOCENE AMBER OF LE QUESNOY ("AMBRE DE L'OISE")

The new Le Quesnoy locality, near Houdancourt (Oise), has yielded fossiliferous amber associated with abundant plant remains and a diverse vertebrate fauna in sediments. Nel et al. (1999) proposed a first analysis of the palaeoenvironment, herein summarized. The strata, typical 'Argiles à Lignite du Soissonnais', are at the bottom of two channels cutting into the underlying Thanetian marine greensands. They prograde toward the north-east and were discovered under the River Oise Quaternary deposits. These Sparnacian beds are made of a succession of lenticular bodies showing two main facies: 1) clayed sands rich in frequently pyritised lignite, together with amber; 2) grey clayey sands with less lignite (1 to 12 % of the sediment), with continental vertebrate fauna. These facies, the rarity of mollusc shells and charophytes, probably due to decarbonation and the occurrence of pyrrhotite, reflect a hypoxic environment.

The infrared spectra (KBr) of Le Quesnoy and Baltic ambers are very different, that of the former is more simi-

lar to the Recent *Hymenaea* copals. The Le Quesnoy amber is very clear yellow. The pieces are of medium size. Spherical pearls are very abundant. There is at least one inclusion in nearly all the flows.

The microflora is rather rich, with some taxa typical of the Early Eocene. It is dominated by angiosperm-like pollen, mainly dicotyledons (including Juglandaceae, Myricaceae and/or Symplocaceae, Celastraceae, Apocynaceae and/or Tiliaceae). This palynological association is similar to contemporaneous associations of the Paris Basin (in a broad sense) and Central Europe. The amber contains isolated grains or clusters of pollen grains at the interfaces between successive flows, coming from taxa in large part also present in the sediment.

The well-preserved woody remains in sediments mainly correspond to dicotyledons, but Monocotyledons (Arecaceae) and Gymnosperms are also present. The most common plant in the whole locality is the amber-producing tree (fragments associated with amber), related to the dicotyledon *Aulacoxylon sparnacense* COMBES 1907, described from the Sparnacian facies of Paris. After studying the new material, the structure of this wood appears very similar to that of extant Combretaceae and Leguminosae-Caesalpiniaceae of the genus *Daniellia* (De Franceschi and De Ploëg, pers. comm.). Various plant structures are preserved in lignite: twigs, bulbs, and insect galls. Among the fossils in amber, some Lauraceae leaf fragments, numerous flowers, and various types of pollen and young fruits of Caesalpiniaceae are present. Several hundred pyritised or lignitised seeds were found in the sediment, among them taxa close to the Icacinaceae, Menispermaceae and Vitaceae, which are also present in the London Clay, Messel (Germany) and Prémontré (Aisne, Paris Basin). Several seeds were bored by insects and it was also possible to remove some pollen with organites preserved. (De Franceschi et al., 2000).

The vertebrate fauna found in sediments is very diversified, with 66 listed species. Nearly all the groups of the earliest Eocene reference locality (MP7) of Dormaal (Belgium) are present. The remains consist of bones, teeth, and numerous coprolites. There are some exceptional fossils embedded in both amber and coprolites, feathers and hair in the former, bones, teeth and skin cast in the latter. Many teeth show corrosion, probably due to digestion by crocodiles.

Elasmobranches are identified by well-preserved teeth. All the taxa found in the continental beds are probably reworked from the Thanetian greensands. This fauna is very close to that of Dormaal. Some elements of the actinopterygian suggest the presence of stagnant freshwater.

The amphibian remains in the sediments are rare, dominated by urodeles, with *a priori* forms characteristic of the Lower Paleogene (Paleocene - Early Eocene). These taxa confirm the presence of freshwater.

The 22 species of reptiles identified so far were previously known in the European Eocene, with the exception of a Late Paleocene chelydroid-like turtle. This turtle fauna suggests an earliest Eocene age. Among the crocodiles, *Allognathosuchus* does not extend beyond the Lower Eocene. Aff. *Diplocynodon* sp. is a new species also found at Dormaal. These taxa are either freshwater, amphibious, or terrestrial. The trionychids lived in lakes or rivers, and the large *Palaeotrionyx* in large streams. This fauna corresponds to a warm and wet palaeoclimate (Nel et al., 1999).

The mammalian fauna is very diversified (24 species and 20 families). The fauna is one of the oldest known from the Eocene of the Paris Basin. Its precise position relative to Dormaal remains to be determined. It shares with Dormaal several taxa but the structure of the Le Quesnoy fauna is different from that of Dormaal. Even if this taphocoenosis concentrates species from different biotas, the high diversity and the quality of the material suggest that the mammal association is not very much biased.

In the nearly 20,000 specimens of amber collected, more than three hundred different forms of arthropod were recognized. They are mainly hexapods, mites, spiders and two pseudoscorpions. Scorpions and myriapods are still unknown. Nearly all the recent orders of Hexapoda have been found. The most noteworthy taxa are an Odonata: Libelluloidea (very rare in ambers) (Fleck et al., 2000), three Dermaptera, and two Mantodea, one with several 'blattoid' characters. The presence of some Isoptera (families Mastotermitidae and Kalotermitidae), Diptera Bibionidae, such as *Plecia* spp. (Gee et al., 2001), and of some Coleoptera (Buprestidae) supports a warm and wet climate. The Mastotermitidae are now restricted to Northern Australia. The discovery of a Hymenoptera Scolybythidae, to date known only in Madagascar, Brazil, Australia and Southern Africa, is of the greatest palaeobiogeographic and palaeoclimatic interest (Lacau et al., 2000). The main modern subfamilies of the Hymenoptera Formicidae (such as Formicinae, Myrmicinae, Dolichoderinae, and Ponerinae) are present, suggesting that this group diversified during the Upper Cretaceous. Adult insects whose larvae are aquatic are frequent and diverse, suggesting the presence of fresh running water near the resin producing trees.

Several biological interactions have been discovered, i.e. Acarina and Mallophaga on mammalian hairs, parasitoid Hymenoptera with their hosts in the same pieces of amber, a spider's web with trapped insects, mating Diptera, etc. Hymenoptera Apoidea are rare but

Microlepidoptera are frequent. Several caterpillars are present and their predators and parasitoids are abundant. Some xylophagous insects (such as Coleoptera: Cerambycidae and Buprestidae, Isoptera, etc.) with their larvae and excrements are imbedded in the amber. Detritivorous Collembola and Blattodea are frequent.

Most of the plant macro-remains, amber and vertebrates were only locally transported, however a significant proportion of carbonized wood is rolled. The sedimentology, vegetation and the abundance of vertebrates and insects linked to freshwater support the local importance of the aquatic environment: a fluvial network with multiple arms and standing waters, in a flat landscape, and apparently without marine influence.

The occurrence of Isoptera Mastotermitidae, many reptiles and some plant families such as Areaceae, Caesalpiniaceae, Combretaceae, Icacinaceae and Menispermaceae, etc., suggests a warm climate, with wet and dry seasons. The palaeoflora can be divided into several phytocoenoses. A great part of the terrestrial palynomorphs might originate from a swampy forest. The apparent dominance of an arborescent amber-producing species and the presence of freshwater suggest a semi-deciduous forest. The ligneous remains reflect seasonal alternations and the presence of dry periods (De Franceschi, pers. comm.). On the basis of these preliminary indicators, we can interpolate that, some 53 Myr ago, there existed a wet river forest surrounded by semi-deciduous or deciduous woodland, which was more affected by dry periods.

All the insect species are new. This entomofauna is unique to the Paleocene/Eocene of Western Europe. The systematic studies already achieved on these Lower Eocene insects show that some taxa are very close to their extant relatives, i.e. the Psocoptera: Liposcelididae, Lepidopsocidae and Archipsocidae, while others are either highly specialized with no modern relatives in some aspects (the dermapteran *Chelisoficula caussaneli* NEL et al., 2003) or in a very basal position within their lineage (the Heteroptera Piesmatidae Nel et al., 2004c). Also, this Lower Eocene fauna seems to have no species and very few genera in common with that of the Upper Eocene – Lower Oligocene Baltic amber.

The combination of a diverse arthropod and vertebrate fauna together with a rich flora makes Le Quesnoy a locality of unique scientific interest. The study of this fauna is just at its beginning with the current series of papers.

In conclusion, the example of the amber of Le Quesnoy demonstrates that all or nearly all the fossil insects of a new amber locality can be new. The situation was the same for the Lower Cretaceous amber of Peñacerrada (Álava, Spain) (Alonso et al., 2000) or for the amber of

Archingeay (Néraudeau et al., 2002). Thus, it is of crucial importance for our knowledge of the insect evolution and diversity during the Mesozoic and Paleogene to collect new material in the 'old' French amber localities.

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Appendix. List of described fossil insects from the Paris amber

- Dermaptera: *incertae familiae Chelisoficula caussaneli*
Dermaptera: *incertae familiae Chelisoficula caussaneli*
NEL et al. 2003 (Nel et al., 2003a)
- Dermaptera: *incertae familiae* (2 species) (Nel et al., 2003b)
- Psocoptera: Liposcelididae (Nel et al., 2004a)
- Heteroptera: Tingidae (Nel et al., 2004b)
- Heteroptera: Thaumastocoridae (Nel et al., 2004d)
- Heteroptera: Piesmatidae (Nel et al., 2004c)
- Neuroptera: Sisyridae *Paleosisyra eocenica* NEL et al. 2003 (Nel et al., 2003a)
- Diptera: Bibionidae *Plecia parisiensis* GEE et al. 2001.
- Diptera: Bombyliidae: Toxophorinae (Nel and De Ploëg, 2004)
- Diptera: Mythicomyiidae (Nel and De Ploëg, 2004)
- Megaloptera: Sialidae *Eosialis dorisi* NEL et al. 2002. (Nel et al., 2002b)
- Hymenoptera: Scolebythidae *Eobythus patriciae* LACAU et al. 2000.
- Hymenoptera: Evaniidae *Eoevania magnifica* NEL et al. 2002. (Nel et al., 2002c)
- Hymenoptera: Ichneumonidae *Palaeometopijs eocenicus*