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SPOTLIGHT

A UNIQUE PIECE OF AMBER AND THE COMPLEXITY OF ANCIENT FOREST ECOSYSTEMS

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Studies on amber—fossil resin—have attracted much attention from the scientific community in the last decade. Seven Ph.D. theses with amber as the main material of study recently have been completed (Penney, 1999; Azar, 2000; Schmidt, 2003; Perrichot, 2005; Grund, 2006; Solórzano Kraemer, 2007; Girard, 2008), and two more are currently in progress by Malvina Lak and Jaime Ortega Blanco. From our personal bibliographic databases, we estimate that $>$1080 papers and books on amber have been published between 1999 and 2008 (as of October 2008). These works have dealt not only with the systematics and phylogeny of arthropods, plant remains, and microorganisms preserved as inclusions in the resin but also with the biogeography, taphonomy, paleoecology, paleoenvironmental reconstructions, chemical and physical properties of amber, its archaeological value, and the development of new methodologies for the analysis of its fossil content.

A reason for this recent trend, but a consequence of it, too, was the discovery of several new amber deposits during the last 10 years—from the Triassic of Italy (Roghi et al., 2006), the Jurassic of Thailand (Philippe et al., 2005), the Cretaceous of France, South Africa, Spain, and Wyoming in the United States (Alonso et al., 2000; Grimaldi et al., 2000; Gomez et al., 2002; Néraudeau et al., 2002; Guiliano et al., 2006; Peñalver et al., 2007), the Eocene of France, India, and Italy (Nel et al., 1999; Alimohammadian et al., 2005; Trevisani et al., 2005), and the Miocene of Peru (Antoine et al., 2006).

In France, Didier Néraudeau, professor of paleontology at the University of Rennes 1, revived studies on Cretaceous amber in 1999 when he discovered the deposit of Archingeay–Les Nouillers, in Charentes, which was soon followed by the discovery of five other deposits in the same region (Néraudeau et al., 2002, 2003, 2008; Perrichot et al., 2007a). We subsequently began Ph.D. projects on the paleoecology of these amber deposits, based on the entomofauna and the amber-associated wood flora (Perrichot, 2005), and on microinclusions (Girard, 2008).

Ten years after its discovery, the Albian deposit of Archingeay–Les Nouillers is among the most fossiliferous ones known for the Cretaceous period and has provided the oldest-known fossils for several groups of arthropods (Perrichot et al., 2007b). In addition to the work on its amber content, the deposit is still under study with a combination of various data from stratigraphy, taphonomy, palynology, and paleobotany (Gomez et al., 2004, 2008; Dejax and Masure, 2005; Peyrot et al., 2005; Coiffard et al., 2006, 2008). Apart from the Eocene Baltic, Miocene Dominican, and Oligocene Saxonian ambers, the Albian deposit of Archingeay–Les Nouillers is probably the amber deposit with the widest variety of analyses from different geological disciplines, and this contributes to obtaining the best possible reconstruction of the corresponding forest ecosystem.

Soon after we began work on this deposit, in 2000 one of us (Perrichot) concentrated on a particularly important $5 \times 3 \times 2.5$ cm piece of amber. With an unusual gradient of transparency and foliated aspect, it appeared extremely rich in organic inclusions. At the beginning, only macroinclusions were observed, but later microscopic examinations by us, together with Alexander Schmidt (Museum für Naturkunde Berlin) and other microbiologists, also revealed numerous microorganisms. To date, 274 syninclusions—co-occurrences of more than one type of inclusion—have been found in this single fragment, composed of 86 arthropods, 181 microorganisms, 7 feathers, and various plant remains, including wood fibers and stellate hairs. The arthropods represent 19 families in 13 orders, and the microorganisms at least 25 families in 9 orders. More significant than the exceptional diversity of fossils occurring in this fragment, however, is the mixture of terrestrial and aquatic organisms trapped in a single fragment. Indeed, in addition to inclusions of terrestrial origin that are commonly preserved in amber, this fragment also includes limnetic and marine crustaceans and protists. To find aquatic organisms in the resin exuded by trees is rather rare, but possible, as recently demonstrated by Schmidt and Dilcher (2007). In the case of the French amber, however, the marine organisms and their co-occurrence with animals that fly, live in litter, or crawl on tree bark raises questions about the ecosystem that produced the resin, as well as the mechanisms involved in the trapping this diversity of organisms. The most likely scenario is that the marine

Vincent Perrichot (left) received his Master's degree in geology and Ph.D. in biology from the University of Rennes, advised by Didier Néraudeau, André Nel (Museum of Natural History, Paris), and Marc Philippe (University of Lyon) on the Mesozoic amber deposits from France and their corresponding forest ecosystems. He spent 2 years at the Berlin Museum of Natural History working with Alexander Schmidt on the combined analysis of arthropods and microorganisms fossilized in amber. Currently a postdoctoral fellow at the Paleontological Institute of the University of Kansas, he works on the systematics, phylogeny, and biogeography of hymenopterans using living species and fossils from various Mesozoic and Cenozoic ambers. He also works on actuopaleontology in tropical and subtropical resin-producing forests. Vincent Girard (right) received an M.S. in geology from the University of Lyon, studying the diversity and paleoecology of early angiosperm woods from the Cretaceous of southeastern France with Marc Philippe. He just received his Ph.D. from the University of Rennes with Didier Néraudeau and Gérard Breton, investigating amber microorganisms and their paleoecological implications. He spent 4 months at Dalhousie University of Halifax comparing a food web of modern soil with that preserved in French amber. He is now a teacher assistant at the University of Rennes.

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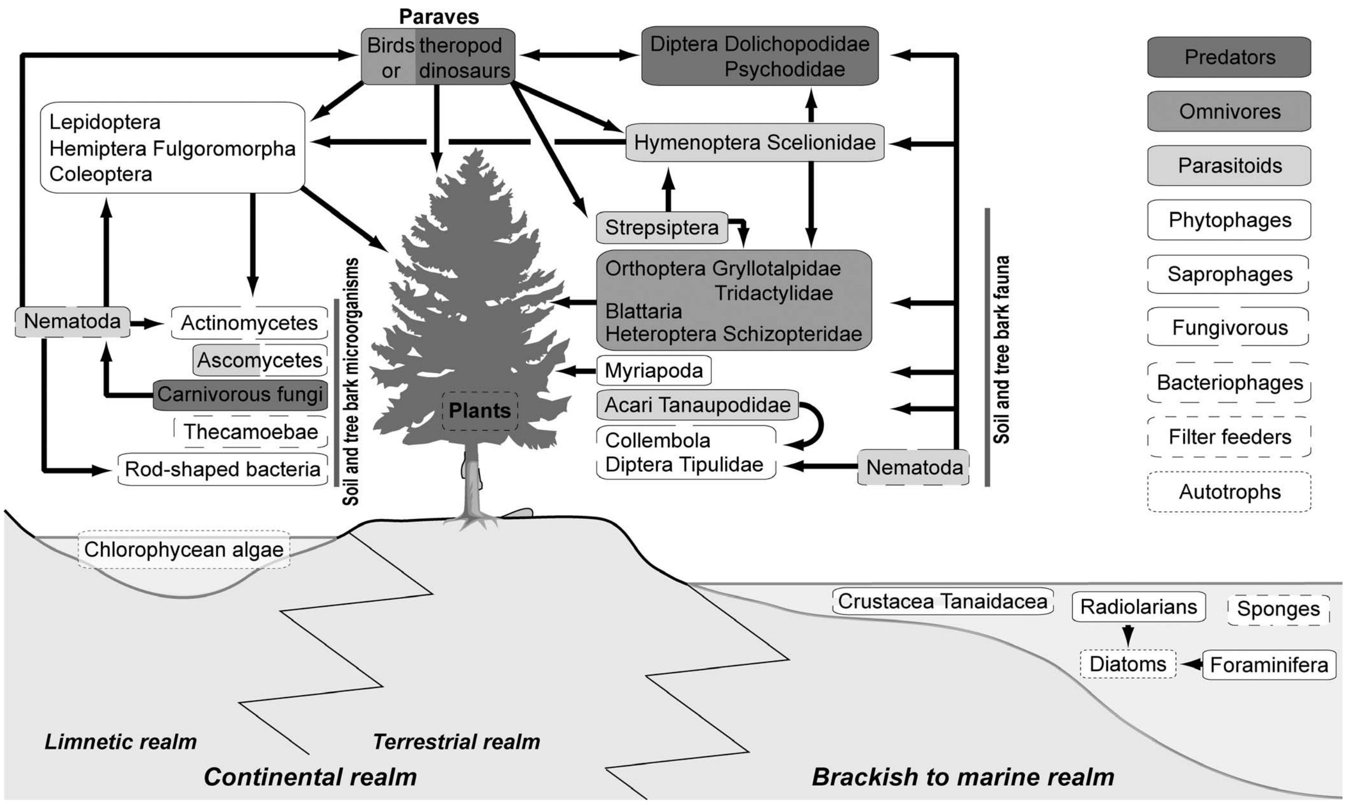

FIGURE 1—Schematic food web reconstructed from organic inclusions fossilized in the piece of amber no. Arc115, from the late Albian of Archingeay–Les Nouillers in southwestern France.

organisms accumulated on the forest ground after a high tide or a storm and then were trapped in a resin outflow together with other terrestrial organisms.

By its richness, this piece of amber alone could constitute the subject of a Ph.D. thesis! While important work has yet to be done on some inclusions, 10 papers have already resulted from the collaborative work of several French and foreign researchers on this exceptional piece of amber. Some of these describe new arthropods of the following families: Diptera: Psychodidae (Azar et al., 2003); Heteroptera: Schizopteridae (Perrichot et al., 2007a); Orthoptera: Gryllotalpidae (Perrichot et al., 2002); and Acari: Tanaupodidae (Judson and Makol, 2009). Other papers deal with diatoms (Girard et al., 2009) and such diverse aquatic protists as foraminiferans, chlorophycean algae, and radiolarians, as well as sponge spicules (Girard et al., 2008). Among other outstanding findings are also a carnivorous fungus (Schmidt et al., 2007, 2008) and some unique feathers belonging either to a bird or a nonavian dinosaur (Perrichot et al., 2008). In addition to these taxonomic contributions, we have also published papers in which the taphonomic, paleoecological, and stratigraphical implications of this atypical assemblage are analyzed and discussed (Perrichot, 2004; Girard et al., 2008, 2009), revealing the previously unreported fossilization of portions of the forest floor and forest litter in addition to the biota living along tree trunks and branches.

More indirectly, the evident richness of this rather opaque piece of amber led to the development of a new methodology for the detection and high-resolution three-dimensional reconstruction of inclusions preserved in such murky amber. Indeed, almost 80% of the total volume of Albian and Cenomanian amber from France is partially or totally opaque, as is the case for several other Cretaceous deposits, which causes a very important bias in evaluating the faunal spectra of the different deposits. In order to overcome this problem, a specific method for analyzing opaque amber in phase-contrast X-ray synchrotron imaging was performed at the European Synchrotron Radiation Facility of Grenoble, France (Tafforeau et al., 2006; Lak et al., 2008), and Malvina Lak is currently working on a Ph.D. thesis on this project. This method can be applied to every kind of amber and allows a nondestructive access to sections and internal structures of fossils. It will certainly constitute an invaluable tool for future systematic and phylogenetic studies of amber inclusions.

In addition to the taphonomic, paleoecological, and analytical implications of this particular piece of amber, the included organisms suggest a possible means of improving the exact dating of amber deposits. Since several amber accumulations were evidently redeposited, they were given only a minimal age. Using the new techniques to image amber, especially opaque ambers, may reveal hitherto unsuspected abundant and diversified marine microinclusions. These could serve as possible biostratigraphic markers for obtaining a more confident age for the amber (Girard et al., 2009). Investigations of protists in fossil resins are thus highly relevant, although still largely unperformed.

Finally, through this single small piece of amber, an extensive trophic chain (Fig. 1), entrapped by resin in a very short time, reveals the complex relationships of an ancient coastal forest ecosystem from 100 Ma.

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