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Early Cretaceous amber from south-western France: insight into the Mesozoic litter fauna

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ABSTRACT

The Albian amber of Archingeay (Charente-Maritime, SW France) shows a unique ecological feature among worldwide Cretaceous ambers: a large part of the arthropods trapped in this resin are representatives of the litter biota (i.e. the fauna living on the ground surface). This selective trap sampled the *in situ* fauna, important for the knowledge of the Early Cretaceous forest ecosystem. This exceptional fossilization could be explained by an important fluidity of the resin, which allowed flows from the branches or the trunk to directly contact the soil, instantaneously entrapping organisms crawling on the soil surface as well as the associated plant remains. The plant source of the resin was probably a member of the Araucariaceae, as suggested by SEM analysis of both plant remains trapped in the resin and the abundant lignite associated with the amber in the same strata. This litter-bearing amber exhibits a high diversity of taxa, encompassing 14 of 21 arthropod groups included in this resin: Isopoda, Myriapoda, Acari, Araneae, Pseudoscorpionida, Collembola, Blattodea, Psocoptera, Coleoptera, Homoptera, Heteroptera, Orthoptera, Hymenoptera, and Diptera. In addition to a unique insight into the diversity of a Cretaceous subtropical forest floor, this litter fauna provides valuable paleoclimatic data for the west European Albian coast, suggesting xeric conditions with a probable dry season within the globally warm and wet period of the mid-Cretaceous.

KEYWORDS **Litter biota. Amber. Lower Cretaceous. Albian. France.**

INTRODUCTION

Amber has been collected for trade, principally as ornamental goods, for several millennia. Recently, there has been overdue scientific interest in the study of organic inclusions (Grimaldi, 1996), as there is now recognition of the exceptional preservation of organisms in life-like conditions. Studies of fossil inclusions have never been so extensively pursued as they are now. Consequently, Cretaceous amber has gained a distinctive interest among researchers during the past few decades because of the valuable evolutionary data provided on fossil insects during the ecological expansion and diversification of angiosperms. Several new Cretaceous amber deposits have been discovered recently, although some are poorly fossiliferous. These deposits include the Wealden of England (Jarzembowski, 1999); the Aptian /Albian of Brazil (Castro et al., 1970; Cardoso et al., 2000); the Valanginian of South Africa (Gomez et al., 2002a, b); the Cenomanian of Germany (Schmidt et al., 2001); the Upper Cretaceous of Wyoming, United-States (Grimaldi et al., 2000a); and the Lower Cretaceous of Japan (Grimaldi, 1996). Nevertheless, the recently discovered deposit of southwest France at Archingeay, in Charente-Maritime (Néraudeau et al., 2002), is richer and thus can be included among the seven major fossiliferous Cretaceous amber deposits of the World (Table 1).

TABLE 1 **List of major fossiliferous Cretaceous amber deposits.**

Location	Age	References
New Jersey, USA	Turonian	Grimaldi et al., 2000b; Grimaldi, 1996
Manitoba/Alberta, Canada	Campanian	Pike, 1995; McAlpine and Martin, 1969
Taimyr, Siberia	Cenomanian-Santonian	Zherikhin and Eskov, 1999
Alava, Spain	Aptian	Alonso et al., 2000; Corral et al., 1999
Myanmar (former Burma)	Albian[a]	Cruickshank and Ko, 2002; Grimaldi et al., 2002; Zherikhin and Ross, 2000; Ross and York, 2000
Archingeay, France	Albian	Néraudeau et al., 2002
Jezzine/Hammana, Libanon	Neocomian-Aptian	Azar, 1998, 2000; Poinar and Milki, 2001

[a]: Burmese amber was formerly dated as Cenomanian/Turonian by Zherikhin and Ross (2000) and Grimaldi et al., (2002), but Cruickshank and Ko (2002) recently replaced it in Albian.

A taphonomic analysis and inventory of arthropod inclusions of the amber nodules display a heretofore unrecognized and distinctive feature for a Cretaceous amber. Namely, numerous samples are composed of litter-inhabiting fauna, which were entombed by a resin flowing directly onto the ground from the resin-producing branches of the source tree. Most of the arthropods in this amber are representative of the litter fauna. This provides additional and important data for understanding the Cretaceous forest soil biota and its Mesozoic evolution. Furthermore, these data provide additional paleoclimatic and paleoenvironmental information about the west European Albian coast.

MATERIALS AND METHODS

Recent investigation of the Cretaceous strata from the Charente-Maritime region lead to the discovery of five amber deposits in four years. Two of these deposits are of Cenomanian age and are located on the coast and yield a small amount of poorly fossiliferous amber (Fig. 1, outcrops 4 and 5); the other three occurrences are located in quarries within a sandy lignitic clay of Albian age (Fig. 1, outcrops 1, 2, and 3). Among these latter three deposits, the quarry of Archingeay is the only broadly accessible site. This availability has allowed for regular and careful investigation that has led to the excavation of approximately 90 kg of amber. A large proportion of this amber was recovered during a single field investigation, using the following extracting method:

- the exploitation of the Cenomanian sand involved the excavation on a wide outcrop surface down to the Albian subjacent lignite and amber-bearing strata. Because this horizon is frequently waterlogged by the inflow of the ground water, there was difficulty in retrieving amber from the sandy clay matrix. However, the level of ground water was significantly lowered during a drought in the summer of 1999. The newly exposed bottom of the quarry subsequently was washed with moderate-pressure water. The resulting slurry contained amber pieces that were removed from the surrounding clay matrix and were swept downstream and collected at the end of a channel where a sieve was placed. Size-sortening of the amber fragments resulted in approximately 60 kg that were collected in this manner.

Most of the amber nodules represent fragmented flows of large size, ranging from 50 to 200 mm, many of which were occasionally rounded and bored, dark brown to tan-colored but rarely deep red-colored. Other amber pieces are translucent light yellow to tan-colored flows of smaller size ranging from 5 to 50 mm in diameter. The opacity in the largest pieces complicated the screening for inclusions, and consequently our investigations focused on the amber nodules less than 60 to 70 mm in maximum size. The samples were washed with water and then screened individually under a stereomicroscope. It was sometimes necessary to have a polished surface in order to view the internal aspect of an amber piece. This was made by polishing it on a flat-lap unit with an abrasive disc, followed by buffing on a lightweight felt disc in order to eliminate surface streaks. In addition, because some pieces displayed decreased visibility due to microbubbles within the resin, it was sometimes necessary to trim off the maximum amount of amber surrounding a specimen with a shaving blade. The prepared specimen, then surrounded by the thinnest possible amber layer, was embedded in Canada balsam between cover slips, based on the method from Azar (2000; pers. comm., 2001). When possible, multiple inclusions in a single piece were physically isolated for better observation. Each fossiliferous amber piece was numbered MNHN ARC *n*, and the separated specimens of a single piece were successively lettered from *n.1* to *n.n*. The Archingeay collection is deposited in the paleoentomological section of the Muséum National d'Histoire Naturelle (MNHN), in Paris.

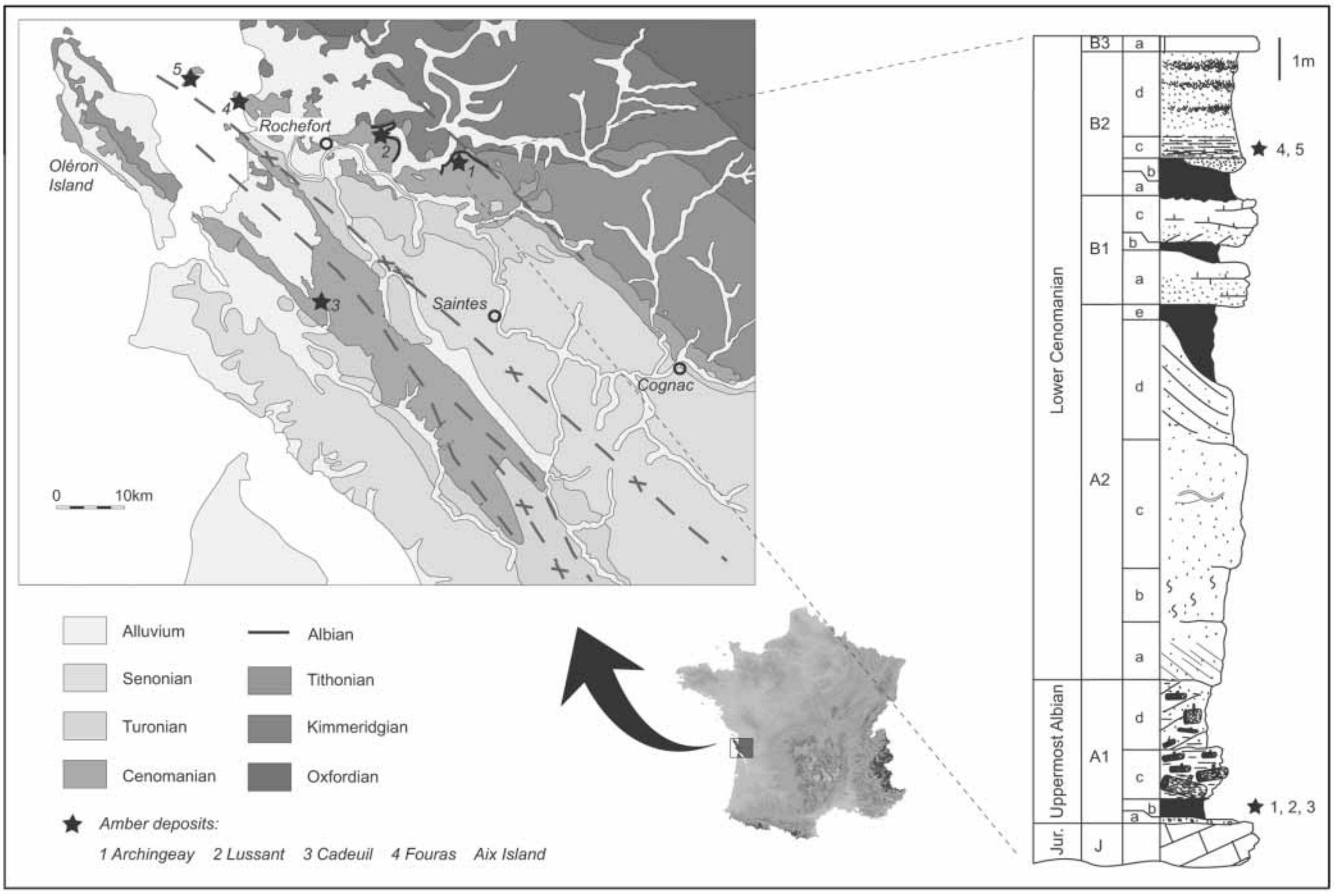

FIGURE 1 **Geological map of Charente-Maritime region (modified from Waterlot and Polvèche, 1958) with a stratigraphic section of the amber outcrop.**

RESULTS

Taphonomic observations

Approximately 1100 amber nodules have been screened, yielding 625 fossil arthropods, including 51 undetermined specimens from fragmentary remains. The diversity of arthropods from this collection is important, representing 21 arthropod orders, of which the Diptera constitutes the most numerous and diverse group (Fig. 2). Inclusions are mainly concentrated in the yellow- to tan-colored amber, where an average of two or three specimens frequently occurs in a single piece. Inclusions have never been found in red-colored lumps despite their transparency.

Some amber pieces have a distinct appearance within the sample. They have flattened and foliated lens-shaped structures, from 20 to 30 cm^3, that show a gradient of transparency ranging from a highly opaque brown side, whose surface is pockmarked by numerous pressure marks of sandstone grains, to a much more translucent yellow side, whose surface is smoother (Fig. 3). This difference is attributable to a greater quantity of impurities in the dark side, such as dust, plant fibres, coprolites and microbubbles, when compared to the purer clear side. The presence of banding probably is the result of successive resin flows and frequently is indicated by a thin crystallization of pyrite that occurs as an interbedded lamina. Arthropod inclusions are generally very abundant in these specific amber nodules, and up to 83 specimens have been documented in a single piece. Six major nodules have yielded 226 arthropods, namely a third of the total recorded number of inclusions in the deposit.

Taxonomic diversity

These six amber pieces are taxonomically varied, including representatives of 14 arthropod orders, as well as a spider web fragment, vertebrate remains (one feather), and plant tissues (Table 2). This sample harbors a diverse assemblage of taxa, and represent a microcosm of the Early Cretaceous litter fauna (Fig. 4). Furthermore, within the total collection of amber pieces, many amber nodules of more typical appearance provided additional documentation for arthropod taxa living in soil habitats (Fig. 2). The most significant groups are summarized below.

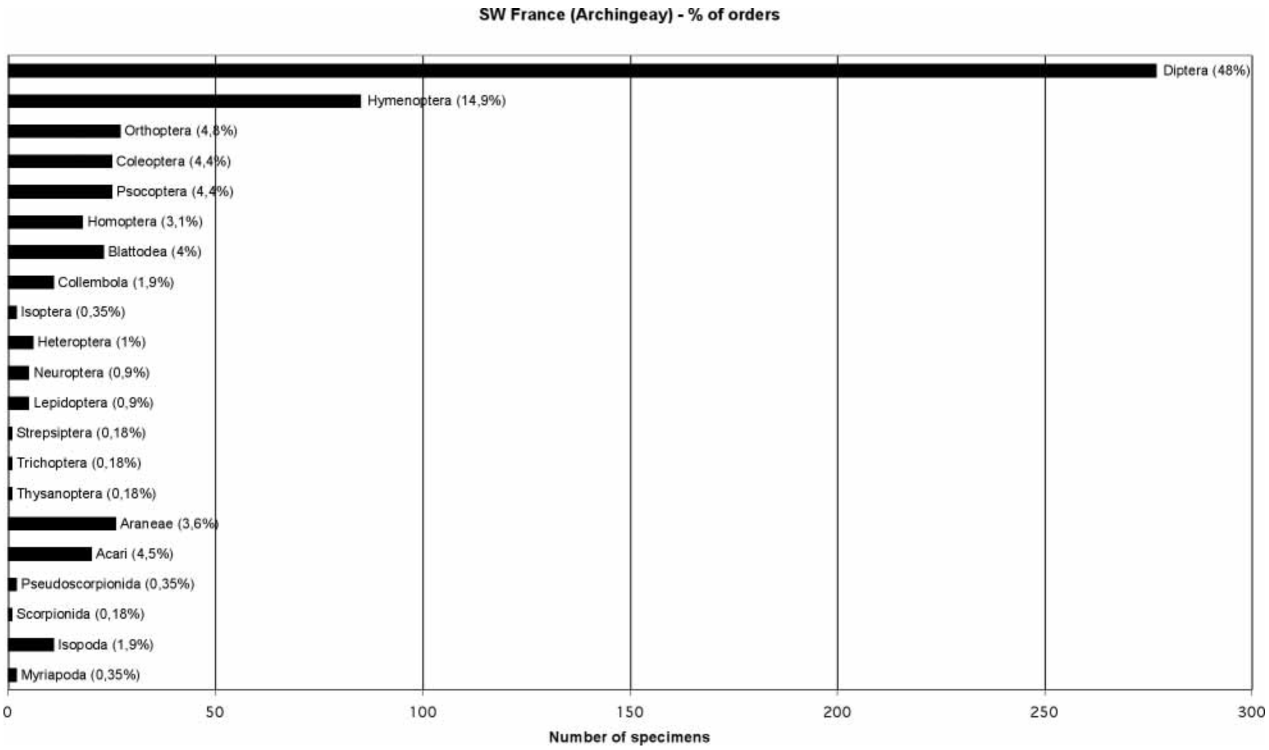

FIGURE 2 **Frequency distribution of arthropods in Archingeay amber.**

Kingdom Plantae

Different types of plant remains are entombed in amber, including small fibres and epidermal cuticular remains that are of difficult determination. Wood fragments also can be embedded within resin either in a more or less pyritized fashion found in lignite (Fig. 3A), or as an imprint on the resin. In the former mode of preservation, microscopic wood structure is anatomically well preserved, which allow for examination under a Scanning Electron Microscope (SEM). In this context, two samples were obtained from litter-bearing amber pieces MNHN ARC 115 and MNHN ARC 226, attributed to the coniferalean family Araucariaceae, with the extinct form-genus *Agathoxylon* HARTIG 1848 (Fig. 5A and 5B).

Kingdom Animalia
Phylum Vertebrata

Vertebrate occurrences in Cretaceous amber are very infrequent. Arnold et al. (2002) described the skin and the claws of a lizard in Neocomian amber from Lebanon, and skin remains of a reptile are cited in Albian amber from Myanmar (= Burmese amber) in Grimaldi et al. (2002). By contrast, feathers are more common; three are cited from Turonian amber of New Jersey (Grimaldi and Case, 1995; Grimaldi et al., 2000b); several fragments are known from Aptian-Albian amber of Álava, Spain (Alonso et al., 2000; Barrón et al., 2001); one piece occurs in Santonian amber of Alberta, Canada, in amber of Kuji, Japan (Grimaldi and Case, 1995), and in amber from Myanmar (Grimaldi et al., 2002); finally several pieces are reported from a single specimen in Lebanese amber (Schlee, 1973). Notably, one of the six previously mentioned litter-bearing amber pieces of Charente-Maritime revealed a portion of a feather (MNHN ARC 115.23),

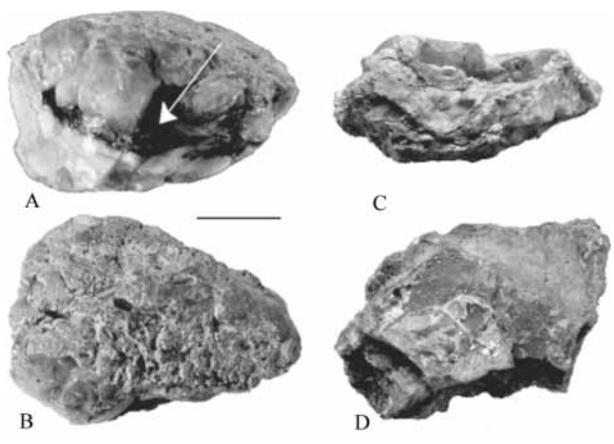

FIGURE 3 **A sample of litter amber showing a typical lamination with an opaque layer on the bottom and a translucent layer on the top. The arrow points out an interbedded wood fragment. MNHN ARC 149. Scale bar: 1 cm.**

consisting of a rhachis and numerous barbules, with two uninterpretable ganglia at the base of the rhachis (Fig. 6B). A careful examination will be needed in order to determine the precise affinity of this feather.

TABLE 2 **List of inclusions of the six samples of litter amber from Archingeay (SW France).**

Group	Taxon	
Sample Arc 115		
Kingdom Plantae		
Conifera	Araucariaceae	many remains
Kingdom Animalia		
Phylum Vertebrata		
Aves (feather)		1
Phylum Arthropoda		
Araneae	indet.	0[a]
Myriapoda	indet	1[b]
Isopoda	indet.	11
Collembola	indet.	6
Blattodea	indet.	2[c]
Coleoptera	indet.	2[c]
Hymenoptera	indet.	2
Homoptera	Fulgoroidea	2[b]
	Membracidae	2
	indet.	1[c]
	TOTAL	5
Orthoptera	Tridactylidae	5[c]
	Gryllotalpidae	2[c,d]
	indet.	3[c]
	TOTAL	10
Diptera	Psychodidae	14[e]
	Tipulidae	1
	Nematocera indet.	2[c]
	Brachycera indet.	9[c]
	TOTAL	26
Insecta	indet.	12[c]
TOTAL, Arthropods		77
Sample Arc 116		
Phylum Arthropoda		
Blattodea	indet.	1[c]
Psocoptera	indet	1[c]
Collembola	indet.	2[c]
Hymenoptera	Formicidae ?	2[c]
Diptera	Brachycera indet.	1[c]
	Nematocera indet.	1[c]
	indet.	2[c]
	TOTAL	4
Insecta	indet.	2[c]
TOTAL, Arthropods		12
Sample Arc 149		
Phylum Arthropoda		
Coleoptera	indet.	1[c]
Orthoptera	Grylloidea.	2[c]
Diptera	Ceratopogonidae	1
	Nematocera indet.	3[c]
	Dolichopodidae	9[f]
	Brachycera indet.	2[c]
	TOTAL	15
TOTAL, Arthropods		18
Sample Arc 186		
Phylum Arthropoda		
Acari	indet.	1
Pseudo-scorpionida	indet.	1
Homoptera	Cercopidae	1
Coleoptera	Elateridae	1[c]
Psocoptera	Prionoglaridae ? or Archaetropidae ?	2[g]
Diptera	Tipulidae	1
	Ceratopogonidae	4
	TOTAL	5
TOTAL, Arthropods		11
Sample Arc 226		
Kingdom Plantae		
Conifera	Araucariaceae	1
Kingdom Animalia		
Phylum Arthropoda		
Araneae	indet.	1
Acari	indet.	6
Heteroptera	indet	1
Hymenoptera Chalcidoidea		2
Blattodea	indet.	1
Psocoptera	indet.	2[c]
Orthoptera	Grylloidea	2
Diptera	Dolichopodidae	12[f]
	Rhagionidae	3
	Brachycera indet.	37[c]
	Ceratopogonidae	8
	Tipulidae	2
	Nematocera indet.	6c
	TOTAL	68
TOTAL, Arthropods		83
Sample Arc 263		
Phylum Arthropoda		
Blattodea	indet.	2[c]
Hymenoptera	Chalcidoidea	2
	indet.	1
	TOTAL	3
Coleoptera	indet.	1[c]
Orthoptera	Grylloidea	2
Diptera	Brachycera indet.	17
TOTAL, Arthropods		25
TOTAL, Arthropods		**226**

[a] Based on a web fragment. [b] Indicates that specimens are larvae. [c] Some specimens are based on fragmentary remains only (antennae, legs, wings, etc.). [d] *Marchandia magnifica* (PERRICHOT et al. 2002). [e] *Eophlebotomus carentonensis* (AZAR et al., 2003). [f] *Microphorites deploegi* (NEL et al., in press), [g] *Proprionoglaris guyoti*, *Prospeleketor albianensis* (PERRICHOT et al. 2003).

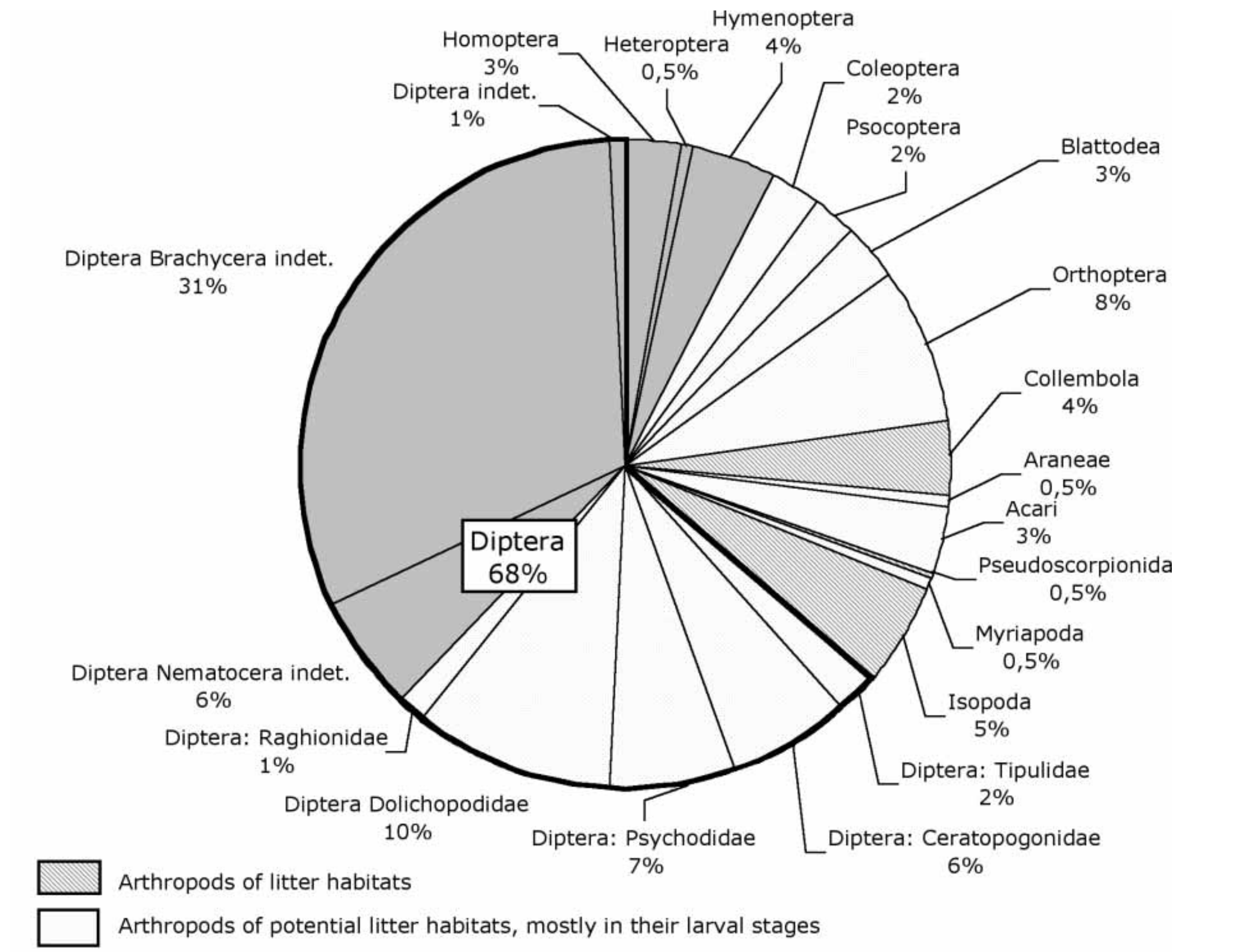

FIGURE 4 **Percentage distribution of arthropods in the six samples of litter amber, with potential affinities for the litter habitat.**

Phylum Arthropoda
Class Arachnida
Order Pseudoscorpionida/Chelonethi

Mesozoic pseudoscorpions also are documented in Archingeay amber. These chelicerate arthropods live in the litter or under the bark of trees where they can be trapped by the resin. The most abundant pseudoscorpion fauna is documented from Myanmar amber; Judson (2000) redescribed a specimen previously described by Cockerell (1917) and attributed it to the family Cheiridiidae. Moreover, 38 and 11 undescribed specimens are catalogued in the collections of the Natural History Museum of London (NHML) and the American Museum of Natural History (AMNH) respectively (Grimaldi et al., 2002). Three specimens are cited from Lebanese amber (Azar, 2000); four from New Jersey amber (Grimaldi et al., 2002); and one from Canadian amber (Schawaller, 1991). The litter-bearing amber of Charente-Maritime provides a single representative of this group (MNHN ARC 186.1), and a second specimen was found in a more typically hued amber piece (MNHN ARC 76). Studies are in progress by M. Judson (MNHN) for the identifications of these specimens.

Order Scorpionida

Scorpions are very rare in the Mesozoic fossil record. Only one specimen has been described from Lebanese amber (Lourenço, 2001) and another one is documented from amber of Myanmar (Lourenço, 2002), although Grimaldi et al. (2002) cited three fragmentary individuals from the same locality. Recently one scorpion was found in the Charente-Maritime amber (MNHN ARC 236.2). This scorpion, belonging to the Chactoidea, was a probable inhabitant of the litter (Lourenço, 2003).

Order Acari

The Acari are probably present in all Cretaceous ambers but they are difficult to locate as inclusions because of their small size, especially in opaque resins. The amber from Myanmar undoubtedly provides the most abundant fauna, with 371 specimens allocated to at least 8 families (Grimaldi et al., 2002). Eighteen acari are catalogued from Charente-Maritime amber (Fig. 6C), and are awaiting a taxonomic study.

Order Araneae

The diversity of Cretaceous spiders is still poorly known, but new specimens were discovered recently in many amber deposits, including those from Lebanon (Azar, 2000; Penney and Selden, 2002); Myanmar (Grimaldi et al., 2002; Penney, 2003); New Jersey, USA (Penney, in press; Grimaldi et al., 2000b); Canada (Pike, 1995); Taimyr, Russia (Zherikhin and Eskov, 1999; Eskov and Wunderlich, 1994); Álava, Spain (Alonso et al., 2000); Isle of Wight, United Kingdom (Selden, 2002); and France (Schlüter, 1978). The amber of Archingeay provided 25 spiders (Figs. 6D and 6E). Studies are in progress by A. Canard, University of Rennes 1. A preliminary examination shows a significant level of diversity, and some specimens undoubtedly represent oldest occurrences of some families, such as Salticidae and Zodariidae.

Class Crustacea
Order Isopoda

The Crustacea, particularly the Isopoda, are infrequently encountered in Cretaceous ambers. Alonso et al. (2000) mentioned only a few occurrences in Spanish amber of Álava. Eleven sowbugs were found in the Charente-Maritime amber, all associated in a single piece (MNHN ARC 115). Individuals are congregated and have a ghostly appearance, which makes their study difficult.

Class Insecta
Order Collembola

Although they first occur in the Lower Devonian (Hirst and Maulik, 1926), Collembola (springtails) have few Mesozoic representatives, all of which have been reported from Cretaceous ambers. Christiansen and Pike (2002) described 78 specimens from Late Cretaceous Canadian amber of Grassy Lake, Alberta, and cited two others in amber of Cedar Lake, Manitoba. Seven springtails are mentioned in the Lebanese deposits of Jezzine and Hammana (Azar, 2000), 109 from Myanmar amber (Grimaldi et al., 2002) and approximately ten in Spanish amber of Álava (Alonso et al., 2000). Eleven collembolan specimens were collected from Charente-Maritime amber, and almost all are represented by abdominal or furcal fragments (Fig. 6F). Eight specimens were present in two pieces of litter-bearing amber (six and two respectively in the samples MNHN ARC 115 and MNHN ARC 116).

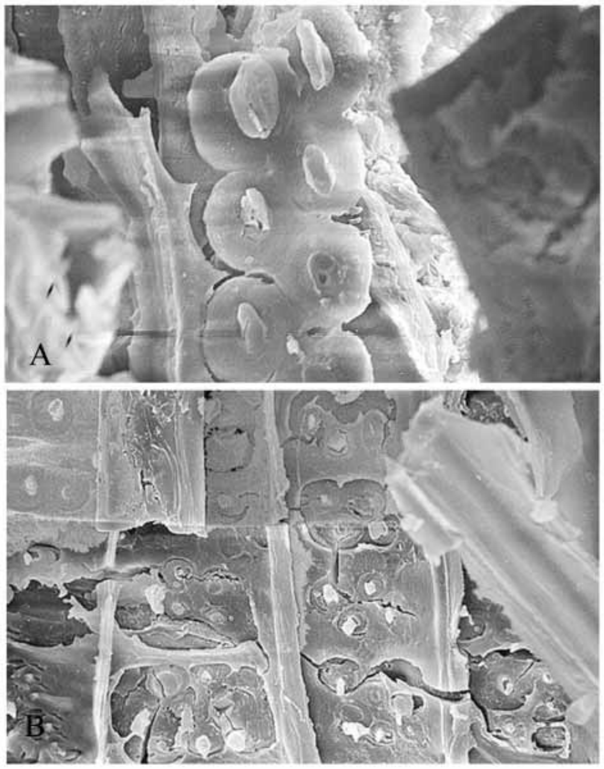

FIGURE 5 **Scanning electron photomicrographs of a wood fragment attributed to an Araucariaceae (*Agathoxylon* HARTIG 1848), in the sample of litter amber MNHN ARC 226. A) Radial view of typically araucariaceous biseriate and alternately imbricated radial pits; B) Radial view of typically araucariaceous cross-field pits, including 6 to 9 cupressoid oculipores.**

Poinar and Milki (2001) thought that the low proportion of springtails in amber is due to their habitat requirements within the litter or under the bark of the trees. However, some modern species are aquatic; others live on the trees, so this explanation is not really valuable.

Order Orthoptera

Orthoptera are particularly infrequent in Cretaceous ambers, where they always represent less than 1% of all inclusions. Eight specimens were found in Myanmar amber, among which three Grylloidea (Grimaldi et al., 2002); one undetermined specimen were also found in Álava amber (Alonso et al., 2000); two undetermined nymphs in New Jersey amber (Grimaldi et al., 2000b); and one Grylloidea in Lebanese amber from Hammana (Azar, 2000). No Orthoptera have been cited from the ambers of Russia and Canada. With twenty-seven specimens catalogued, that is to say about 5% of all inclusions, the Charente-Maritime amber is the richest for any Cretaceous deposit, and the most diversified as well. Sixteen specimens occur in the previously discussed six pieces of litter-bearing amber: two Gryllotalpidae (Fig. 6A) namely

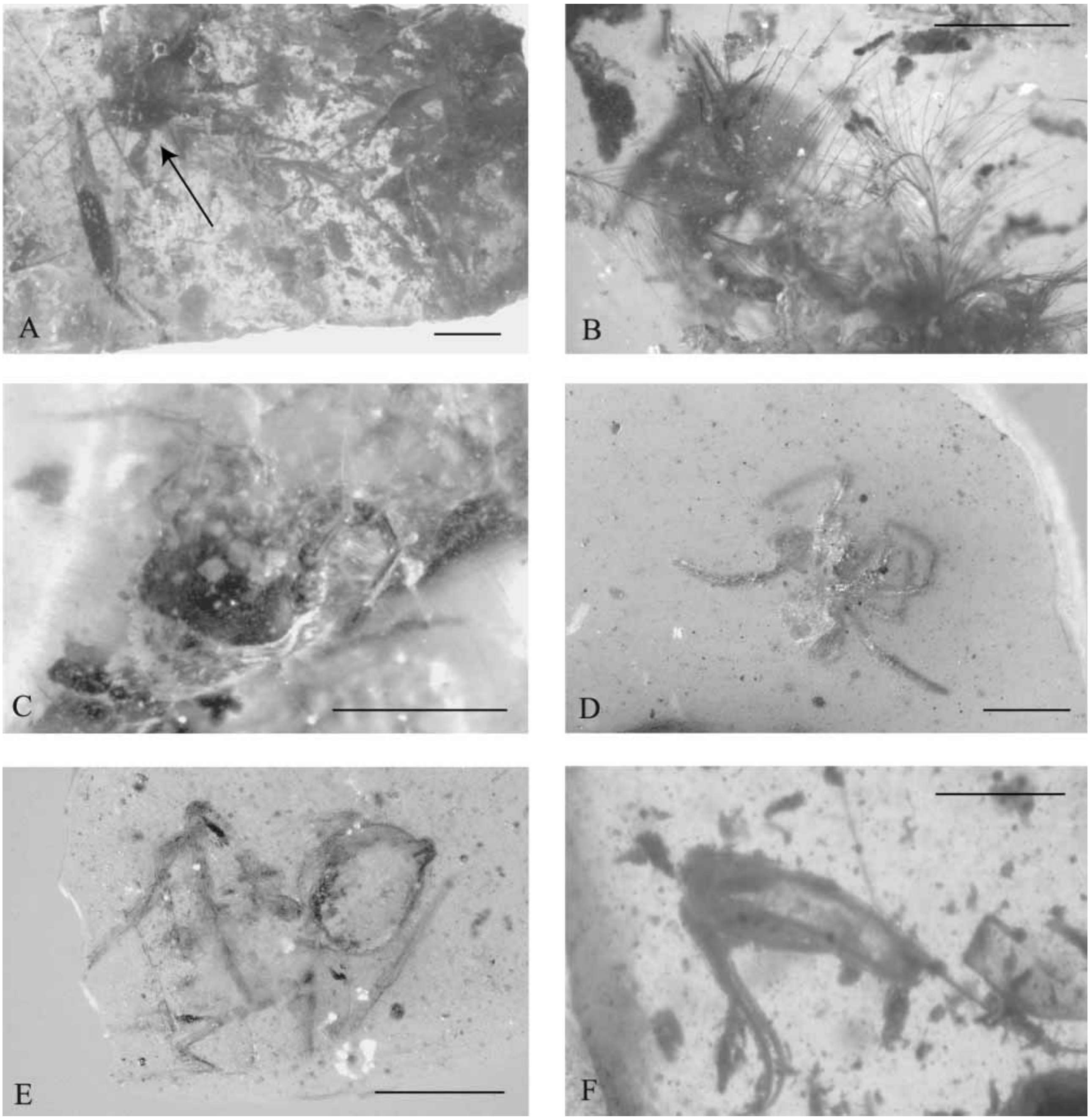

FIGURE 6 **Various inclusions in the French Lower Cretaceous amber of Archingeay. A) MNHN ARC 115: a sample of litter-bearing amber, showing plant remains and one Orthoptera: Gryllotalpidae (arrow). Scale bar 2 mm; B) MNHN ARC 115.23: fragments of feather from an indeterminate animal. Scale bar 2 mm; C) MNHN ARC 226.16: Acari, family indet. Scale bar 1 mm; D and E) MNHN ARC 226.41, MNHN ARC 189: Aranea, families indet. Scale bar 0.5 mm; F) MNHN ARC 115.18: fragment of Collembola showing furca. Scale bar 0.5 mm.**

a complete specimen and two metathoracic legs of a second one (Perrichot et al., 2002); five Tridactylidae comprising an adult female, two nymphs, and two right metathoracic legs; six nymphs of Grylloidea (Figs. 7A and 7B); and the remains of three undetermined Orthoptera. The other eleven specimens are referable to two possible Acridoidea, two Grylloidea, and two Tridactylidae; the fragments of five undetermined Orthoptera have been also identified.

Order Planipennia

Among Cretaceous ambers, those of New Jersey and Myanmar provide the most diversified planipennian fau-

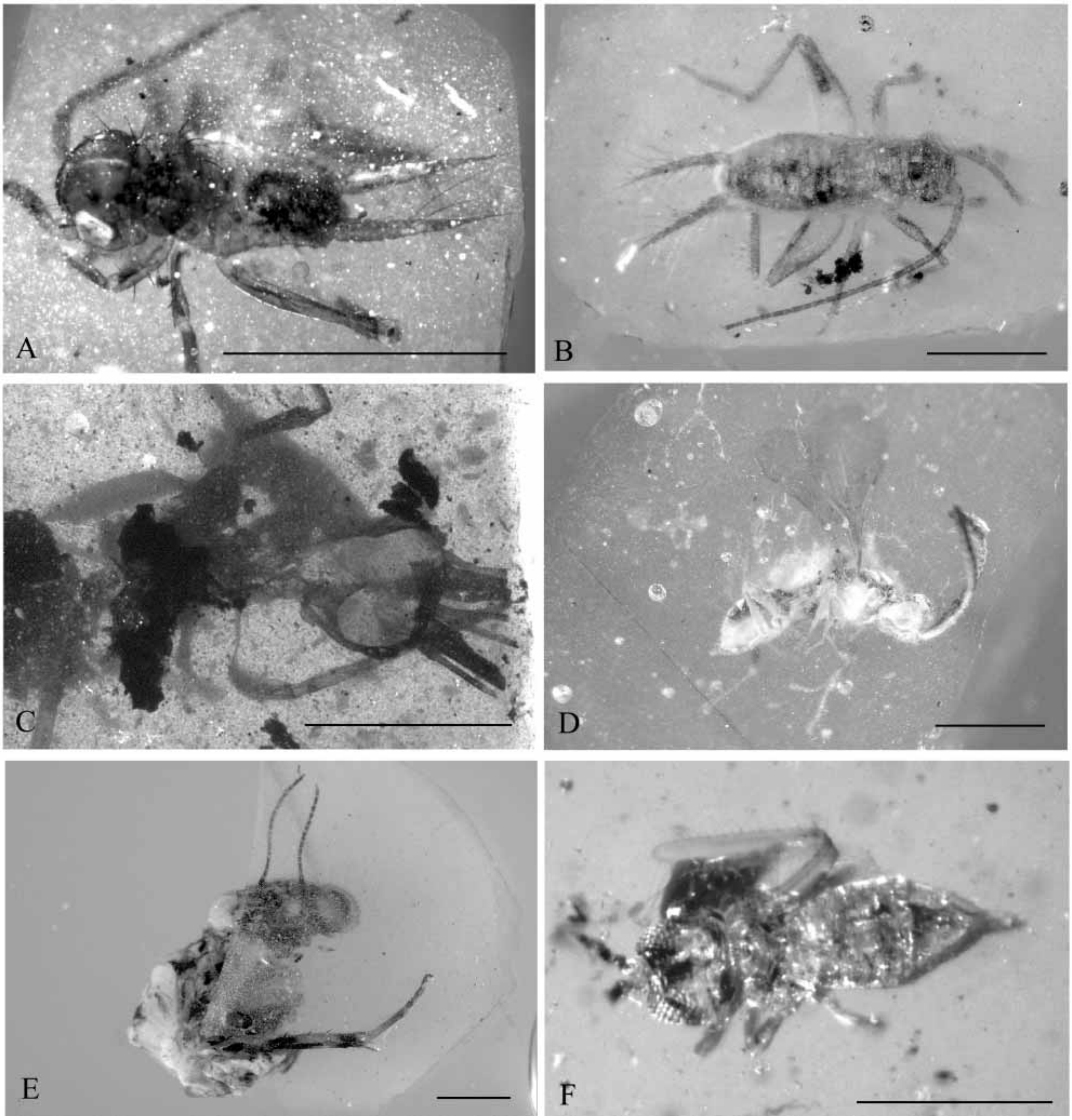

FIGURE 7 **Various inclusions in the French Lower Cretaceous amber of Archingeay. A and B) MNHN ARC 149.2, MNHN ARC 263.6: Orthoptera: Grylloidea (nymph). Scale bar 1 mm; C) MNHN ARC 152.3: head and thorax of Planipennia, family indet. (larva). Scale bar 1 mm; D) MNHN ARC 263.1: Hymenoptera: Chalcidoidea, family indet. (adult). Scale bar 0.5 mm; E) MNHN ARC 264.2: head of Blattodea (nymph). Scale bar 1 mm; F) MNHN ARC 18: Thysanoptera (adult). Scale bar 0.25 mm.**

na, with more than five families and about 40 inclusions in both of these resins (Grimaldi, 2000; Engel, 2002; Grimaldi et al., 2002). Ambers from Lebanon, Russia, and Canada are less abundant, with only a few specimens. Six planipennians were collected in Charente-Maritime amber: one specimen of the family Rhachiberotidae; one larva of the Coniopterygidae: Aleuropteryginae; another larva of either the Ascalaphidae or the Myrmeleontidae (antlions); the head and a portion of the thorax of an undetermined larva (Fig. 7C); the mandibles of an undetermined larva; and an undetermined forewing.

Order Diptera

The Diptera is the most abundant group of insects in Cretaceous ambers. Although detailed study of each

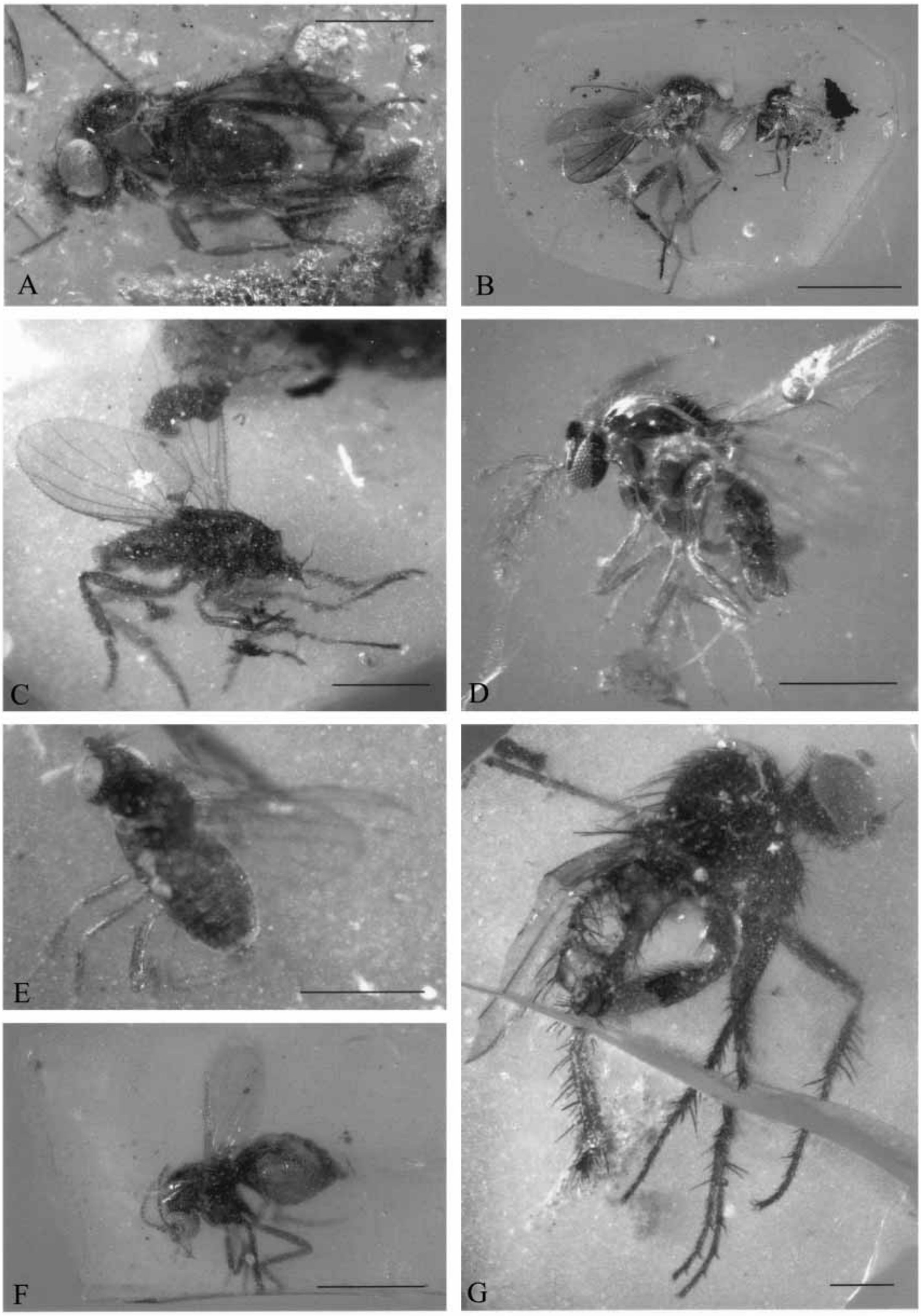

FIGURE 8 **Assorted Diptera from the French Cretaceous amber of Archingeay. a) MNHN ARC 263.14: Brachycera, family indet. Scale bar 1 mm; b) MNHN ARC 226.38: Left: Rhagionidae (male); Right: Dolichopodidae: Microphorinae: *Microphorites deploegi*. Scale bar 2mm; c) MNHN ARC 226.12: Dolichopodidae. Scale bar 1 mm; d) MNHN ARC 20.2: Ceratopogonidae (male). Scale bar 0.5 mm; e) MNHN ARC 226.2: Dolichopodidae. Scale bar 0.5 mm; f) MNHN ARC 226.15: Ceratopogonidae (female). Scale bar 0.5 mm; G) MNHN ARC 226.1: Rhagionidae. Scale bar 0.5 mm.**

dipteran specimen will be necessary in order to appreciate the diversity of the Charente-Maritime sample, an initial evaluation shows that there are significant similarities with other Cretaceous ambers. Ceratopogonidae (biting midges), Psychodidae (moth flies) and Dolichopodidae (long-legged flies) are the dominant families (Fig. 8), as in the amber of Myanmar (Grimaldi et al., 2002), Lebanon (Azar, 2000), New Jersey (Grimaldi et al., 2000b), Canada (Pike, 1995), Russia (Siberia) (Zherikhin and Eskov, 1999), and Spain (Alonso et al., 2000). Numerous representatives from these three families are associated with the litter amber from Archingeay (Table 2; Fig. 4), as are in particular specimens of the genera *Eophlebotomus* (Azar et al., 2003) and *Microphorites* (Nel et al., in press). The following nematoceran families were also identified from the entire collection: Chironomidae (aquatic midges), Cecidomyiidae (gall midges), Tipulidae (crane flies), and Mycetophylidae (fungus gnats). Ceratopogonidae and Cecidomyiidae previously have been mentioned in French Cenomanian amber (Schlüter, 1978; Szadziewski and Schlüter, 1992). For the brachyceran families, Rhagionidae (snipe flies) and Phoridae (scuttle flies), which also are present, further examination of this suite of specimens will be needed. It is expected that the number of families will increase.

DISCUSSION

Because of the unique preservational qualities of the six amber nodules described above, as well as the diversity and the taxonomic composition of its inclusions, this resin is thought to have flowed directly on the ground, from the branches of the source tree. An initial flow, being in contact with the ground surface, engulfed surface elements of the litter biota; this corresponds to the dark-brown side of the amber nodules. Subsequently, new resin flows followed onto another, providing the characteristic foliated appearance of these pieces. These latter flows remained more translucent because they did not touch the soil directly. Each subsequent resin flow trapped arthropods crawling on the litter surface, and insects flying immediately above the soil surface. The high abundance number of Psychodidae, Ceratopogonidae, and Dolichopodidae, could be due to swarm flights of these flies, whose larvae notably live in moist soil (Evenhuis, 1994). Their abundance thus is not inconsistent with derivation from the associated litter fauna.

Analysis of the Charente-Maritime amber using infrared spectroscopy is in progress, in order to elucidate the botanical source of this amber. However, the data provided both by the plant inclusions and the abundant remains of lignite associated in the sandy clay (Fig. 1, Albian strata A1; Néraudeau et al., 2002), show a probable araucarian origin (*Agathoxylon*). Furthermore, past studies on French Cretaceous amber support an araucarian affinity for the resin. Schlüter (1978) analysed amber from the Cenomanian of the Paris Basin (Ecommoy locality) and Aquitain Basin (Fouras locality) by infrared spectroscopy; Lambert et al. (1996) re-examined a portion of this material, from an unknown locality (Lambert, pers. comm., 2002), and analysed it using nuclear magnetic resonance (NMR) spectroscopy. They attributed its botanical source to the araucarian genus *Agathis*, particularly resins of group A according to Lambert and Poinar (2002), although the presence of fossils of this genus have never been established in the Charente-Maritime region during the Cretaceous.

In Queensland, Australia, the litter of the extant *Agathis* forests shows a slow degradation of plant remains and an accumulation of millimetric resin droplets, spherical to lenticular in shape (Philippe, pers. comm., 2002). Moreover, a fossil litter accumulation in a Berriasian strata south of Hanover, Germany, consists of a thin accumulation of leaves with resin accumulated in their internal tissues and additional small drops of resin embedded in the coaly matrix (Otto et al., 2002). These plant remains were attributed to *Tritaenia linkii* (ROEMER) MAEGDEFRAU and RUDOLF, a taxa of still controversial affinity: Watson et al. (2001) placed it in the Ginkgoaceae, whereas Manum et al. (2000) and Gomez (2002) attributed this genus to the extinct coniferal family Miroviaceae. Otto et al. (2002) analyzed the resin by gas chromatography-mass spectrometry (GC-MS), and concluded that it was modified by elevated oxidative and microbial alteration. This confirms the possible location of the resin in a degraded litter. Two processes could explain the larger size of the litter amber pieces in the Charente-Maritime deposit: either the resin could have been exuded in large quantities by the source tree, or it is possible that the fluidity of the resin increased with the high temperatures of the mid-Cretaceous, the warmest period of Earth history (Frakes, 1979; Jenkyns et al., 1994).

Despite the occurrence of plant remains in the litter amber pieces, they remain quite infrequent. Seemingly, the resin flowing on the soil should contain many fragments of litter through the degradation process. Similarly, no fungi, spores or pollen have been discovered in this amber to date. This could spotlight a relative aridity in the Western European coast during the Albian. If so, the resin should exude and flow during a markedly dry season, as in summer, when the soil is depleted in altered organic matter. By contrast, the lack of pollen could be explained by a pollination seasonality, reaching a peak during the spring, and different from the resin production period. A more detailed determination of arthropod families and genera could test for this inference of an arid environment. This hypothesis could confirm work based on plant cuticles fossilized with amber and lignite in the same deposits of Archingeay and Lussant, where there is a distinctive conifer adapted to xeric conditions (Gomez et al., 2002c). A second hypothesis, which states that in a deltaic environmental context the soil of this Cretaceous coastal forest was essentially composed of sand particles, could explain the absence of plant remains. The hypothesis is supported by a large part of the entomofauna, which shows affinities for sandy habitats adjacent to streams, swamps or ponds, including the following taxa: Orthoptera (Gryllotalpidae and Tridactylidae); planipennian larvae; Diptera (Dolichopodidae, Microphorinae: *Microphorites*, Psychodidae, Ceratopogonidae, Tipulidae, and Rhagionidae) and Collembola.

Until now, no study of Cretaceous amber suggested the possibility of trapping the sylvan litter fauna. Grimaldi et al. (2002) mentioned a variety of similarly flattened, lens-shaped amber pieces in Myanmar, but according to the authors they rarely contained insects, unlike the French amber pieces at Archingeay. However, collections of Myanmar amber at both the AMNH and NHML yielded many arthropod taxa from the litter fauna inhabiting such as Collembola, Scorpionida, Pseudoscorpionida, and neuropteran larvae. New Jersey amber also exhibits variety of levels of transparency, but Grimaldi et al. (2000b) thought this was attributable to successive flows along the trunks of source trees. Although Alonso et al. (2000) did not mention a similar variety in amber of Álava; they did show nodules with pressure marks of sandstone grains on one side, which could indicate a contact of fresh resin with the soil surface. Additionally, the occurrence of Collembola and Crustacea in this Spanish amber could attest to the presence of litter-bearing amber.

CONCLUSIONS

Albian amber from Charente-Maritime exhibits a diversified fauna, with 21 arthropods orders represented among 625 inclusions. Thus it is one of the most diverse of Cretaceous ambers, despite a lower number of recorded specimens. Half of the Cretaceous ambers supplies 16 to 17 Orders for an average of 1500 inclusions: Taimyr in Russia (reported in Grimaldi et al., 2000b), Canada (Pike, 1995), and Spain (Alonso et al., 1999). Other ambers are considerably more abundant, with 23 orders in 1258 inclusions from Hammana, Lebanon (Azar, 2000), 25 orders in 1045 inclusions from New Jersey (Grimaldi et al., 2000b), and 33 orders in 3100 inclusions from Myanmar (Grimaldi et al., 2002). Much additional material needs to be examined from Archingeay, and it is suspected that new discoveries will not only increase the diversity, but also make this deposit one of the most fossiliferous of Cretaceous deposits.

Among the sampled insect fauna in amber of Archingeay, numerous arthropods are representatives of a litter inhabiting biota. These data provide a unique insight regarding edaphic arthropod biodiversity in western European Albian forests. This deposit also supports a deltaic sandy environment as well as an indication for probable aridity within a globally warm and wet context generally proposed for the Cretaceous period (Frakes, 1979; Jenkyns et al., 1994). It will be interesting to compare with additional details the insect fauna from French amber with those of the geographically and stratigraphically proximal Spanish deposit at Álava, as well as with amber from Myanmar, whose recent dating as Albian (Cruickshank and Ko, 2003) makes it the most contemporaneous deposit with French amber.

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