HAL
open science

Les mondes de l'ambre. Paléobiologie, paléoenvironnements & paléobiogéographie des systèmes résinifères

Vincent Perrichot

To cite this version:

Vincent Perrichot. Les mondes de l'ambre. Paléobiologie, paléoenvironnements & paléobiogéographie des systèmes résinifères. Sciences de la Terre. Université de Rennes 1, 2015. tel-01160063

HAL Id: tel-01160063

https://insu.hal.science/tel-01160063

Submitted on 4 Jun 2015

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.

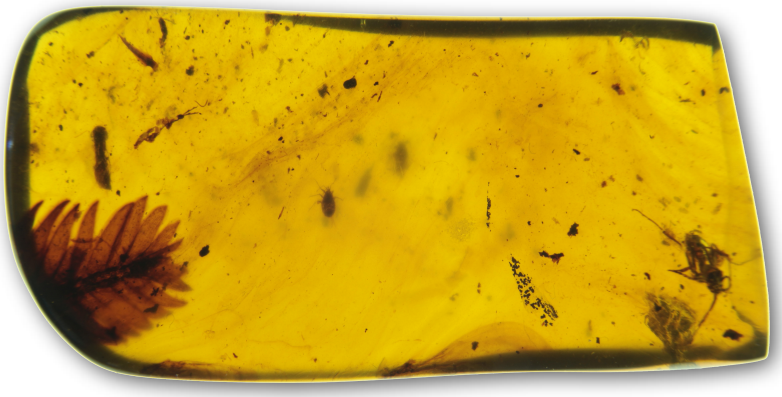
L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Mémoire d'Habilitation à Diriger des Recherches

Soutenance 13 mai 2015

les mondes de l'ambre

paléobiologie, paléoenvironnements & paléobiogéographie des écosystèmes résinifères



Vincent Perrichot
Maître de conférences à l'Université de Rennes 1

UMR CNRS 6118 Géosciences & OSUR
Campus de Beaulieu, Rennes

Habilitation à Diriger des Recherches

Soutenue le 13 mai 2015
À l'Université de Rennes 1

Vincent Perrichot

Les mondes de l'ambre – Paléobiologie, paléoenvironnements & paléobiogéographie des écosystèmes résinifères

Rapporteurs :

Dr. Antonio ARILLO - chercheur
Universidad Complutense de Madrid, Departamento de Zoología y Antropología Física, Facultad de Biología, 28040 Madrid, Espagne
aarillo@teleline.es

Dr. Sylvie CRASQUIN - DR CNRS
Université Paris 6, UMR 7207 CNRS/MNHN/UPMC CR2P (Centre de Recherche sur la Paléobiodiversité & les Paléoenvironnements), Département Histoire de la Terre, 4 Place Jussieu, 75252 Paris cedex 05, France
sylvie.crasquin@upmc.fr

Dr. Philippe GRANDCOLAS - DR CNRS
Muséum National d'Histoire Naturelle, UMR 7205 ISYEB (Institut de Systématique, Evolution, Biodiversité), 45 rue Buffon, 75005 Paris, France
pg@mnhn.fr

Examinateurs :

Dr. Philippe JANVIER - DR émérite
Muséum National d'Histoire Naturelle, UMR 7207 CNRS/MNHN/UPMC, Centre de Recherche sur la Paléobiodiversité & les Paléoenvironnements (CR2P), Département Histoire de la Terre, 8 rue Buffon, 75005 Paris, France
janvier@mnhn.fr

Dr. Loic VILLIER - professeur
Université Paris 6, UMR 7207 CNRS/MNHN/UPMC CR2P (Centre de Recherche sur la Paléobiodiversité & les Paléoenvironnements), 4 Place Jussieu, 75252 Paris cedex 05, France
loic.villier@upmc.fr

Dr. Michel BALLÈVRE - professeur
Université de Rennes 1, UMR CNRS 6118 Géosciences, Campus de Beaulieu bat. 15, 263 avenue du Général Leclerc, 35042 Rennes cedex, France
Michel.Ballevre@univ-rennes1.fr

À Anne & Gaspard...

sommaire

3 Première partie – Dossier scientifique
3 Curriculum vitae
4 Activités d'enseignement
6 Encadrement d'étudiants
9 Activités de recherche
9 Publications
20 Intégration dans les programmes nationaux et internationaux
20 Bourses et subventions
21 Autres activités liées à la recherche
27 Deuxième partie – Synthèse des travaux
29 L'ambre : un fossile et un milieu de fossilisation
29 Contexte géologique
30 Démarche scientifique
30 Axes de recherche
31 Les régions d'intérêt
34 Les groupes d'intérêt
37 L'évolution des insectes
37 Fausses fourmis
39 Fourmis
41 Les écosystèmes résinifères
43 Les préservations exceptionnelles
43 Plumes
44 Champignon carnivore
45 'Coquillages' et crustacés
47 Troisième partie – Projet de recherche
49 Origine et évolution des fourmis
50 Evolution de la production de résine
51 L'ambre en Afrique
53 Références bibliographiques
59 Annexes – Sélection de publications

Première partie

Dossier scientifique

I. Curriculum vitae

Vincent Perrichot
Né le 19 Mai 1976 à Ploërmel (Morbihan, France)
Pacsé, 1 enfant
Maître de Conférences - Paléontologue (section CNU 36)
Université de Rennes 1 – UMR CNRS 6118 Géosciences & OSUR
vincent.perrichot@univ-rennes1.fr ; Tel: 02.23.23.60.26

1.1. Diplômes universitaires

2000-2003 **Doctorat de Biologie** Thèse soutenue le 17 décembre 2003 à l'Université Rennes 1.
Sujet : *Environnements paraliques à ambre et à végétaux du Crétacé nord-aquitain (Charentes, Sud-Ouest de la France).*
Directeurs : D. Néraudeau (Univ. Rennes 1), A. Nel (MNHN), M. Philippe (Univ. Lyon 1).
Mention très honorable.

2000 **DEA Paléontologie, Phylogénie, et Paléobiologie** *Univ. Rennes 1 & Montpellier 2, mention Bien.*

1999 **Maîtrise Sciences de la Terre** *Université Rennes 1.*

1998 **Licence Sciences de la Terre** *Université Rennes 1.*

1997 **DEUG Sciences de la Vie** *Université Rennes 1.*

1.2. Parcours professionnel – *Recherche & enseignement*

Depuis 2009 **Maître de Conférences** *Université Rennes 1*, *CNRS UMR 6118 Géosciences* (équipe Biodiversité : Interactions, Préservation, Evolution).

Depuis 2011 **Chercheur associé** *University of Kansas Biodiversity Institute, Division of Entomology, Lawrence, Kansas, USA* (équipe du Pr. Michael S. Engel).

2009 **Enseignant, *Université du Kansas, Lawrence, USA.***
"Principles and practices of Museum management", Master of Arts in Museum Studies.

2008-2009 **Chercheur post-doc** *Paleontological Institute, University of Kansas, Lawrence, USA* (20 mois ; équipe du Pr. Paul Selden).
Financement Université du Kansas.

2006-2007 **Chercheur post-doc** *Museum für Naturkunde, Berlin, Allemagne* (18 mois ; équipe du Dr. Alexander Schmidt).
Financement Fondation Alexander von Humboldt.

2003-2004 **ATER** en paléontologie, *Université Rennes 1.*

2001-2003 **Vacataire d'enseignement** *Universités Rennes 1 et Bretagne-Sud (Vannes).*

1.3. Distinctions, bourses

2006 Bourse post-doctorale de la fondation Alexander von Humboldt.

2004 Lauréat du prix de thèse de l'Association Paléontologique Française.

II. Activités d'enseignement

*— **9 ans** d'activité, niveau Licence et Master, en France et aux USA —*
*— Volume horaire enseigné **1132h eTD** —*
— Responsable de deux U.E. de Master —

C'est durant ma thèse que j'ai abordé l'enseignement, en tant que vacataire pour les universités de Rennes 1 et de Bretagne Sud, pour dispenser des cours et TP en paléontologie des invertébrés. Puis j'ai enchainé après la thèse par une année d'ATER (1/2 poste) pour des cours, TP, et TD de micropaléontologie, paléontologie des invertébrés, et paléobotanique.

Plus tard à l'occasion de mon séjour post-doctoral à l'université du Kansas, on m'a proposé de prendre en charge un module de master en muséologie, portant sur les principes et pratiques du management de musées (40h). Un challenge à relever compte tenu de mon expérience uniquement dans la pratique de collections paléontologiques, et qui s'est avéré très formateur pour moi. J'ai ainsi organisé le module entre CM, TP, et visites de différents musées locaux animées par les conservateurs en chef des collections (musées des arts, d'ethnographie, et d'entomologie).

Enfin depuis mon recrutement en tant que maître de conférences en 2009, mon activité d'enseignement à l'Université de Rennes 1 s'effectue intégralement en formation initiale dans les licences et masters, essentiellement dans la mention Bio-Agro-Santé (BAS). Je contribue également, pour un volume horaire moindre, à des formations initiales spécialisées dans les mentions Sciences de la Terre (ST) ainsi que Métiers de l'Education à l'Enseignement et à la Formation (MEEF). Tous mes enseignements se font dans le domaine de la paléontologie (tableau 1), avec des thèmes abordés embrassant micropaléontologie, paléobotanique, paléontologie des invertébrés, taphonomie, évolution, phylogénie, paléoenvironnements, et muséologie.

Compte tenu de l'augmentation constante des effectifs d'étudiants dans la plupart des parcours enseignés, depuis mon recrutement en 2009, et des enseignants titulaires dans la discipline 'Paléontologie' à Rennes 1 (3 enseignants-chercheurs et 1 CNRS dans l'équipe BIPE de Géosciences Rennes), mon service est globalement équilibré sur le service statutaire de 192h équivalent TD. J'ai ainsi effectué 182h en 2009-2010, 193h en 2010-2011, 178h en 2011-2012, 191h en 2012-2013, et 209h en 2013-2014.

2.1. Charge et responsabilités

Depuis 2009	Service annuel moyen de 190h eTD, niveau Licence (L2, L3) et Master (M1, M2).
Depuis 2014	Responsable de l'U.E. "Fossilisation et Paléoécologie" (34h eTD par 6 intervenants) du M2 Préhistoire, Paléontologie & Paléoenvironnements, Univ. Rennes 1.
2009	Responsable de l'U.E. MUSE 704 "Principles and practices of Museum management" (40h par 4 intervenants), Master of Arts in Museum Studies, Université du Kansas.

2.2. Descriptif des enseignements

(Volumes horaires en équivalent TD)

— L2 (mention STS, parcours biologie des organismes et parcours SVT ; mention ST) —

CM	Micropaléontologie (6h/an depuis 2009).
TP	Fossilisation, paléobotanique, paléontologie des invertébrés, micropaléontologie (44h en 2009-10, 58h en 2011-12, 50h en 2012-13, 76h en 2013-14).
TD	Paléoenvironnements, biostratigraphie (16h/an depuis 2009).
Terrain	Faluns de Touraine et de Bretagne, Cambrien d'Ille-et-Vilaine (18h/an depuis 2009).

— L3 (mention BAS parcours sciences exactes et naturelles) —

TD	Sujets bibliographiques (6h en 2012 ; 1,5h en 2013 ; 3h en 2014).

— M1 (mention BAS spécialité préhistoire, paléontologie, paléoenvironnement; mention MEEF parcours SVT) —

CM Muséologie, cladisme, paléobotanique, paléoenvironnements (12h/an depuis 2012).

TP/TD Paléontologie des invertébrés, micropaléontologie (30h/an en 2010, 2011 ; 22h depuis 2012).

Terrain 'Ediacarien' et Ordovicien du Massif Armoricain, Jurassique du Calvados et d'Anjou, Jurassique et Crétacé de Charente-Maritime (30h/an depuis 2010).

— M2 (mention BAS : spécialité PPP ; mention MEEF : spécialité SBG) —

CM Micropaléontologie, évolution des insectes, fossilisation, paléoécologie, taphonomie (12h/an en 2012, 2013).

Terrain Aalénien-Bajocien de la Sarthe, Crétacé de Vendée (3h/an depuis 2012).

— Prepa CAPES-AGREG SVT (mention ST) —

TD Micropaléontologie (14h/an en 2009, 2010).

Diplômes	Année	Intitulés des UE	Type	Volume
Licence STS Sc. Terre	L2	Le Temps	CM, TD	62
Licence STS Biologie	L2	Dynamique de la paléobiodiversité	CM, terrain	84
	L2	Ecosystèmes fossiles	TP, TD, terrain	380
	L2	Stratigraphie, paléontologie	TP, terrain	142
	L3	Paléontologie & médiation scientifique	TD	10,5
Licence STS SENA	L3	Ecosystèmes anciens	Terrain	12
	L3	Paléontologie et médiation scientifique	TD	10,5
Master Bio-Agro-Santé	M1	Histoire de la biosphère	TP, terrain	140
	M1	Evolution & paléobiodiversité	CM, TD	35,5
Master Bio-Agro-Santé SBG	M1	Sciences de la Terre	CM, TD	11
Master MEEF	M1	Paléoécologie & paléoenvironnements	CM, terrain	129
Master Bio-Agro-Santé PPP	M2	Evolution & biodiversité quantitative	CM, terrain	18,5
	M2	Fossilisation & paléoécologie	CM, TD	15,5
	M2	Paléoenvironnements & paléoclimats	CM	9
Prépa CAPES-AGREG SVT	M2	Sciences de la Terre	TD	28
M.A. Museum Studies	M1	Principles & practices of Museum management	CM, TP	34

Tableau 1 Synthèse du volume horaire enseigné par diplôme et UE (heures données en équivalent TD).

III. Encadrement d'étudiants

3.1. Doctorat

— Youssef Nohra (2012-2015) —
Sujet de thèse : *Résines végétales actuelles et fossiles : origine, caractérisation chimique, et évolution*.
Financement Fondation Azm et Saadé (Liban), taux d'encadrement 50% (Direction en co-tutelle avec D. Azar, Université Libanaise). Soutenance prévue en mai-juin 2015.
Coproduction scientifique : 2 articles (dont 1 soumis), 7 communications (1 réunion nationale, 5 congrès internationaux).

— Joanna Choufani (2010-2014) —
Sujet de thèse : *Origine, taxinomie, évolution et systématique des Ceratopogonidae (Diptera)*.
Financement Association El-Hajj (Liban), taux d'encadrement 20% (co-encadrants HDR : A. Nel, MNHN ; D. Azar, Université Libanaise). Soutenue le 18-12-2014, mention très honorable.
Coproduction scientifique : 3 articles, 1 communication de congrès international.

3.2. Master 2 / DEA

— Johanne Esnault (2014) — Actuellement en M2 Métiers de l'Archéologie, Université de Nantes
Sujet : *Ambre et plantes associées du Crétacé inférieur du Congo : études systématiques et paléoécologiques*.
Master PPP Univ. Rennes 1 ; taux d'encadrement 50% (co-encadrants : J. Gaillot, Total E&P Pau ; A. Boura, UPMC/MNHN).
Coproduction scientifique : 1 article en préparation.

— Sylvère Poyau (2013) — Situation actuelle inconnue
Sujet : *Les neuroptères fossiles des ambres crétacé et éocène de France (Insecta: Neuroptera)*.
Master PPP Univ. Rennes 1 ; taux d'encadrement 50% (co-encadrant : A. Nel, MNHN).

— Cédric Aria (2010) — Actuellement en thèse au Royal Ontario Museum, Canada
Sujet : *Etude sur les fourmis (Hymenoptera: Formicidae) de l'ambre sparnacien*.
Master PPP Montpellier 2 ; taux d'encadrement 50% (co-encadrant : A. Nel, MNHN).
Coproduction scientifique : 1 article.

— Steffi Struwe (2007) — Actuellement salariée d'une entreprise privée
Sujet : *Microinclusions dans les ambres du Crétacé de Charente-Maritime, France* [en Allemand].
'Diplomarbeit' / Master Biologie, Freie Universität Berlin; taux d'encadrement 50% (co-encadrant : A. R. Schmidt, Museum für Naturkunde Berlin).
Coproduction scientifique : 4 articles, 1 communication de congrès national.

— Malvina Lak (2006) — Actuellement auto-entrepreneur
Sujet : *Détection et imagerie 3D des inclusions fossiles dans l'ambre opaque par contraste de phase en rayonnement X synchrotron*.
Master PPP Univ. Rennes 1 ; taux d'encadrement 33% (co-encadrants : D. Néraudeau, Univ. Rennes 1 ; P. Tafforeau, ESRF Grenoble).
Coproduction scientifique : 3 articles, 5 communications (1 réunion nationale, 4 congrès internationaux).

— Florent Tostain (2004) — Actuellement enseignant en SVT en lycée.
Sujet : *Un assemblage de micro-organismes dans l'ambre albien/cénomanien de Charente-Maritime (gisements d'Archingeay, de Cadeuil et de l'Ile d'Aix, France) - Implications taphonomiques et paléoécologiques.*.
DEA PPP Univ. Rennes 1 ; taux d'encadrement 33% (co-encadrants : D. Néraudeau, Univ. Rennes 1 ; G. Breton, Muséum Le Havre).
Coproduction scientifique : 1 article, 2 communications (1 réunion nationale, 1 symposium international).

3.3. Liste des travaux scientifiques issus d'encadrements

(Les noms des étudiants encadrés sont surlignés en gris)

Articles dans des revues indexées

1. Adl S., Girard V., Breton G., Lak M., Maharning A., Mills A., **Perrichot V**., Trionnaire M., Vullo R., Néraudeau D. (2011) Reconstructing the soil food web of a 100 million-year-old forest: the case of the mid-Cretaceous fossils in the amber of Charentes (SW France). *Soil Biology and Biochemistry*, 43: 726-735.
2. Aria C., **Perrichot V**., Nel A. (2011) Fossil Ponerinae (Hymenoptera: Formicidae) in Early Eocene amber of France. *Zootaxa*, 2870: 53-62.
3. Choufani J., Azar D., **Perrichot V**., Soriano C., Tafforeau P., Nel A. (2011) The genus *Leptoconops* Skuse (Diptera: Ceratopogonidae) in Early Cretaceous Charentese amber. *Palaeobiodiversity and Palaeoenvironments* 91: 285-291.
4. Girard V., Saint Martin S., Saint Martin J.-P., Schmidt A.R., Struwe S., **Perrichot V**., Breton G., Néraudeau D. (2009) Exceptional preservation of marine diatoms in upper Albian amber. *Geology*, 37: 83-86.
5. Girard V., Schmidt A.R., Saint Martin S., Struwe S., **Perrichot V**., Saint Martin J.-P., Breton G., Néraudeau D. (2008) Evidence for marine microfossils from amber. *Proceedings of the National Academy of Sciences of the USA*, 105: 17426-17429.
6. Girard V., Schmidt A.R., Struwe S., **Perrichot V**., Breton G., Néraudeau D. (2009) Taphonomy and palaeoecology of mid-Cretaceous amber-preserved microorganisms from southwestern France. *Geodiversitas*, 31: 152-163.
7. Lak M., Néraudeau D., Nel A., Cloetens P., **Perrichot V**., Tafforeau P. (2008) Phase contrast X-ray synchrotron imaging: opening access to fossil inclusions in opaque amber. *Microscopy & Microanalysis*, 14: 251-259.
8. Néraudeau D., **Perrichot V**., Colin J.-P., Girard V., Gomez B., Guillocheau F., Masure E., Peyrot D., Tostain F., Videt B., Vullo R. (2008) A new amber deposit from the Cretaceous (Uppermost Albian-Lowermost Cenomanian) of southwestern France. *Cretaceous Research*, 29: 925-929.
9. Néraudeau D., Vullo R., Gomez B., Girard V., Lak M., Videt B., Dépré E., **Perrichot V**. (2009) Amber, plant and vertebrate fossils from the Lower Cenomanian paralic facies of Aix Island (Charente-Maritime, SW France). *Geodiversitas*, 31: 13-27.
10. Nohra Y.A., **Perrichot V**., Jeanneau L., Le Polles L., Azar D. Chemical characterization and botanical origin of French ambers. Submitted to *Journal of Natural Products*, 01.2015.
11. Schmidt A.R., Dörfelt H., Struwe S., **Perrichot V**. (2010) Evidence for fungivory in Cretaceous amber forests from Gondwana and Laurasia. *Palaeontographica B*, 283: 157-173.

Articles dans des revues non-indexées, à comité de lecture

1. Choufani J., **Perrichot V**., Azar D., Nel A. (2014) New biting midges (Diptera: Ceratopogonidae) in Late Cretaceous Vendean amber. *Paleontological Contributions*, 10H: 34-40.
2. Nohra Y.A., Azar D., Gèze R., Maksoud S., El Samrani A., **Perrichot V**. (2013) New Jurassic amber outcrops from Lebanon. *Terrestrial Arthropod Reviews*, 6: 27-51.

Actes de congrès, newsletters

1. Choufani J., **Perrichot V**., Girard V., Garrouste R., Azar D., Nel A. (2013) Two new biting midges of the modern type from Santonian amber of France (Diptera: Ceratopogonidae), *in*: Azar D., Engel M.S., Jarzembowski E., Krogmann L., Nel A., Santiago-Blay J. (Eds.), Insect Evolution in an Amberiferous and Stone Alphabet. *Proceedings of the 6th International Congress on Fossil Insects, Arthropods and Amber*. Brill, Leiden, pp. 71-95.
2. Lak M., Tafforeau P., Néraudeau D., **Perrichot V**., Nel A. (2007) Non-destructive study of fossil inclusions in opaque amber using phase contrast X-ray synchrotron imaging. *ESRF Highlights* 2006: 109-110.

Communications en congrès nationaux et internationaux

1. Choufani J., **Perrichot V**., Girard V., Garrouste R., Azar D., Nel A. (2013) Two new biting midges of modern type from the Santonian amber of France (Diptera: Ceratopogonidae). *6th International Congress on Fossil Insects, Arthropods, and Amber*, Byblos, Lebanon, abstract volume p. 53. [Communication orale]
2. Lak M., Tafforeau P., **Perrichot V**., Néraudeau D., Nel A. (2006) Détection et reconstitution 3D d'inclusions dans l'ambre opaque par imagerie à rayonnement X synchrotron. *21ème Réunion des Sciences de la Terre*, Dijon. [Poster]
3. Lak M., Tafforeau P., **Perrichot V**., Néraudeau D., Nel A. (2007) Detection and 3D-reconstruction of inclusions in opaque amber using phase contrast X-ray synchrotron imaging. *4th FossilsX3: Insects, Arthropods, Amber*, Vitoria-Gasteiz, Spain, abstract volume p. 112. [Communication orale]
4. Néraudeau D., Breton G., Colin J.-P., Girard V., Gomez B., Guillocheau F., Lak M., Masure E., Nel A., **Perrichot V**., Platel J.-P., Videt B., Vullo R. (2007) Sequence stratigraphy, palaeogeography and palaeoenvironments of the Cretaceous amber deposits from western France. *4th FossilsX3: Insects, Arthropods, Amber*, Vitoria-Gasteiz, Spain, abstract volume p. 122-123. [Poster]
5. Néraudeau D., Girard V., Gomez B., Lak M., **Perrichot V**., Vullo R. (2009) Mid-Cretaceous terrestrial biota from Charentes, SW France: a synthesis of 10 years of investigation. *10th Mesozoic Terrestrial Ecosystems Symposium*, Teruel, Spain, abstract volume p. 211-212. [Communication orale]
6. Néraudeau D., **Perrichot V**., Tostain F., Videt B., Vullo R. (2005) Insects and micro-organisms from the Late Albian amber of Cadeuil (Charente-Maritime, SW France). *7th International Symposium on the Cretaceous*, Neuchâtel, Switzerland, abstract volume p. 153. [Poster]
7. Néraudeau D., **Perrichot V**., Vullo R., Breton G., Le Diouron T., Gomez B., Peyrot D., Tostain F., Videt B. (2005) L'apport des faciès à ambre insectifère de l'Albien-Cénomanien des Charentes à la connaissance des écosystèmes terrestres du Crétacé européen. *Réunion thématique du Groupe Français du Crétacé: Impact environnemental sur la dynamique des populations au Crétacé*, Ecole des Mines, Paris, volume des résumés p. 29. [Communication orale]
8. Nohra Y., Azar D., Gèze R., El-Samrani A., **Perrichot V**. (2012) Jurassic amber outcrops from Lebanon. *18th LAAS International Science Meeting*, Beirut, Lebanon. [Poster]
9. Nohra Y., Azar D., Gèze R., Maksoud S., El Samrani A., **Perrichot V**. (2013) New Jurassic amber outcrops from Lebanon. *6th International Congress on Fossil Insects, Arthropods, and Amber*, Byblos, Lebanon, abstract volume p. 61. [Communication orale]
10. Nohra Y., Azar D., Gèze R., Maksoud S., El-Samrani A., Perrichot V. (2013) New Jurassic amber outcrops from Lebanon. *Amberif 2013 - International Amber Researcher Symposium*, Gdansk, Poland, abstract volume p. 17. [Communication orale]
11. Nohra Y.A., **Perrichot V**., Boura A., Jeanneau L., Néraudeau D., Thomas R., Azar D. (2014) Cupressacean origin of the Cretaceous Vendean amber (northwestern France): evidence from fossil woods and chemical signatures. *9th European Palaeobotany – Palynology Conference*, Padova, Italy, August 26-31, abstract book p. 189. [Communication orale]
12. Nohra Y.A., **Perrichot V**., Boura A., Jeanneau L., Néraudeau D., Thomas R., Azar D. (2014) Biomarqueurs chimiques et origine botanique des résines fossiles: le cas de l'ambre de Vendée. *2e réunion FROG (French Researchers in Organic Geochemistry)*, Bourget-du-Lac, France, 3-4 Juillet. [Communication orale – Prix meilleure présentation]
13. Nohra Y.A., **Perrichot V**., Jeanneau L., Gèze R., Azar D. (2014) Lebanese Jurassic *versus* Cretaceous amber: Chemical characterization. *20th LAAS International Science Conference*, Hadath, Lebanon, March 27-29, abstract volume p. 865-866. [Poster]
14. **Perrichot V**., Girard V., Lak M., Nel A., Néraudeau D., Saint-Martin S., Schmidt A.R. (2007) Terrestrial and marine inclusions from French Cretaceous amber and their palaeoecological implications. *4th FossilsX3: Insects, Arthropods, Amber*, Vitoria-Gasteiz, Spain, abstract volume p. 128. [Communication orale]
15. **Perrichot V**., Néraudeau D., Girard V., Nel A., Nohra Y., Saint Martin S., Saint Martin J.-P., Schmidt A.R., Dupé F. (2013) Santonian Vendeen amber: large amounts of data from a small sample in north-western France. *6th International Congress on Fossil Insects, Arthropods, and Amber*, Byblos, Lebanon, abstract volume p. 49. [Communication orale]

16. Solórzano Kraemer M., **Perrichot V**., Lak M., Tafforeau P., Soriano C., Néraudeau D. (2010) Aquatic bugs (Heteroptera: Gerromorpha) from Cretaceous amber of France and their palaeoecological implications. *5th FossilsX3: Insects, Arthropods, Amber*, Beijing, China, abstract volume p. 65. [Poster]
17. Struwe S., **Perrichot V**., Schmidt A.R. (2007) Mikroinklusen und die Paläoökologie der kretazischen Bernsteinwälder von Charente-Maritime (Frankreich). *Jahrestagung der Deutschen Paläontologischen Gesellschaft*, 17-19 September 2007, Freiberg, Germany. [Communication orale]

IV. Activités de recherche

*— **14 ans** d'activité, dont + de **3 ans** en Allemagne et aux USA —*
écosystèmes terrestres crétacés, paléogènes et néogènes
paléoenvironnements forestiers à ambre
systématique, phylogénie, paléoécologie, et biogéographie des insectes
systématique et paléoécologie des bois de conifères
taphonomie et chimie de l'ambre

L'ensemble de mes activités de recherche s'articule autour de l'ambre, abordé d'un point de vue à la fois biologique et géologique, deux champs disciplinaires complémentaires à mes yeux. Les différentes thématiques évoquées dans mes publications sont résumées en figure 1. Mes travaux de recherche seront développés en deuxième partie de ce mémoire, à la suite du présent dossier scientifique.

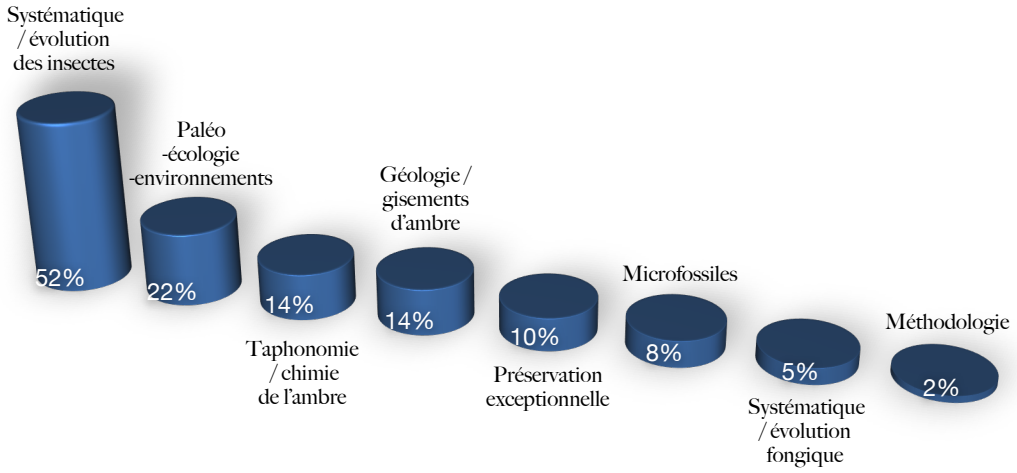


Figure 1 Répartition thématique de mes publications.

4.1. Publications

*— **82 articles** dans des revues internationales, dont **30 en 1er auteur** —*
*— **2 chapitres** d'ouvrages —*
*— **2 ouvrages** édités —*
*— **52 résumés** de congrès nationaux et internationaux —*
*— **h-index: 17** (ISI WoK), **24** (Google Scholar) —*

Bibliographie et bibliométrie :
http://publicationslist.org/vincent.perrichot
www.researchgate.net/profile/Vincent_Perrichot/publications
http://scholar.google.fr/citations?user=ORf7Q8gAAAAJ&hl=en

Articles dans des revues indéxées au JCR (IF 2013)

66 **Perrichot V.** (2015) A new species of *Baikuris* (Hymenoptera: Formicidae: Sphecomyrminae) in mid-Cretaceous amber from France. *Cretaceous Research*, 52B: 585-590. [IF 2,39]

65 Saint Martin S., Saint Martin J.-P., Schmidt A.R., Girard V., Néraudeau D., **Perrichot V.** (2015) The intriguing marine diatom genus *Corethron* in Late Cretaceous amber from Vendée (France). *Cretaceous Research*, 52A: 64-72. [IF 2,39]

64 Dunlop J.A., Kontschán J., Walter D.E., **Perrichot V.** (2014) An ant-associated mesostigmatid mite in Baltic amber. *Biology Letters*, 10: 20140531. [IF 3,425]

63 Nel A., de Ploëg G., **Perrichot V**. (2014) The first ibis fly in mid-Cretaceous amber of France (Diptera: Athericidae). *Zootaxa*, 3768(5): 591-595. [IF 1,060]

62 Peris D., Delclòs X., Soriano C., **Perrichot V**. (2014) The earliest occurrence and remarkable stasis of the family Bostrichidae (Coleoptera: Polyphaga) in Cretaceous Charentes amber. *Palaeontologia Electronica*, 17(1:14A): 8 p. [IF 1,365]

61 **Perrichot V**. (2014) A new species of the Cretaceous ant *Zigrasimecia* based on the worker caste reveals placement of the genus in the Sphecomyrminae (Hymenoptera: Formicidae). *Myrmecological News*, 19: 165-169. [IF 1,582]

60 **Perrichot V.**, Antoine P.-O., Salas-Gismondi R., Flynn J.J., Engel M.S. (2014) The genus *Macroteleia* Westwood in Middle Miocene amber from Peru (Hymenoptera, Platygastridae *s.l.*, Scelioninae). *ZooKeys*, 426: 119-127. [IF 0,917]

59 Rikkinen J., Tuovila H., Beimforde C., Seyfullah L.J., **Perrichot V**., Schmidt A.R. (2014) *Chaenothecopsis neocaledonica* sp. nov.: the first resinicolous mycocalicioid fungus from an araucarian conifer. *Phytotaxa*, 173(1): 49-60. [IF 1,376]

58 Schmidt A.R., Beimforde C., Seyfullah L.J., Wege S.E., Dörfelt H., Girard V., Grabenhorst H., Gube M., Heinrichs J., Nel A., Nel P., **Perrichot V.**, Reitner J., Rikkinen J. (2014) Amber fossils of sooty moulds. *Review of Palaeobotany and Palynology*, 200: 53-64. [IF 1,656]

57 Solórzano Kraemer M.M., **Perrichot V**., Soriano C., Damgaard J. (2014) Fossil water striders in mid-Cretaceous French amber (Heteroptera: Gerromorpha: Mesoveliidae and Veliidae). *Systematic Entomology*, 39(3): 590-605. [IF 2,553]

56 Aquilina L., Girard V., Hénin O., Bouhnik-Le Coz M., Vilbert D., **Perrichot V.**, Néraudeau D. (2013) Amber inorganic geochemistry: new insight into the environmental processes in a Cretaceous forest of France. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 369: 220-227. [IF 2,752]

55 Fate C., **Perrichot V**., Nel A. (2013) A mid-Cretaceous representative of the modern scatopsid genus *Ectaetia* (Diptera: Scatopsidae: Ectaetiinae). *Zootaxa*, 3686(3): 396-400. [IF 1,060]

54 Girard V., Breton G., **Perrichot V.**, Bilotte M., Le Loeuff J., Nel A., Philippe M., Thévenard F. (2013) The Cenomanian amber of Fourtou (Aude, Southern France): Taphonomy and palaeoecological implications. *Annales de Paléontologie*, 99(4): 301-315. [IF 1,091]

53 LaPolla J.S., Dlussky G.M., **Perrichot V**. (2013) Ants and the fossil record. *Annual Review of Entomology*, 58: 609-630. [IF 13,021]

52 Néraudeau D., Redois F., Ballèvre M., Duplessis B., Girard V., Gomez B., Daviero-Gomez V., Mellier B., **Perrichot V**. (2013) L'ambre cénomanien d'Anjou: stratigraphie et paléontologie des carrières du Brouillard et de Hucheloup (Ecouflant, Maine-et-Loire). *Annales de Paléontologie*, 99(4): 361-374. [IF 1,091]

51 **Perrichot V.** (2013) New maimetshid wasps in Cretaceous amber from Myanmar (Insecta: Hymenoptera). *Annales de Paléontologie*, 99: 67-77. [IF 1,091]

50 Pérez-de la Fuente R., **Perrichot V**., Ortega-Blanco J., Delclòs X., Engel M.S. (2012) Description of the male of *Megalava truncata* Perrichot (Hymenoptera: Megalyridae) in Early Cretaceous Spanish amber from El Soplao. *Zootaxa*, 3274: 29-35. [IF 1,060]

49 **Perrichot V.**, Beaucournu J.-C., Velten J. (2012) First extinct genus of a flea (Siphonaptera: Pulicidae) in Miocene amber from the Dominican Republic. *Zootaxa*, 3438: 54-61. [IF 1,060]

48 Adl S., Girard V., Breton G., Lak M., Maharning A., Mills A., **Perrichot V**., Trionnaire M., Vullo R., Néraudeau D. (2011) Reconstructing the soil food web of a 100 million-year-old forest: the case of the mid-Cretaceous fossils in the amber of Charentes (SW France). *Soil Biology and Biochemistry*, 43(4): 726-735. [IF 4,410]

47 Aria C., **Perrichot V**., Nel A. (2011) Fossil Ponerinae (Hymenoptera: Formicidae) in Early Eocene amber of France. *Zootaxa*, 2870: 53-62. [IF 1,060]

46 **Perrichot V.**, Engel M.S. (2011) A new micropterous species of *Embolemus* from Baltic amber (Hymenoptera: Embolemidae). *Annales de Paléontologie*, 97(1-2): 1-7. [IF 1,091]

45 **Perrichot V**., Engel M.S., Nel A., Tafforeau P., Soriano C. (2011) New earwig nymphs (Dermaptera: Pygidicranidae) in mid-Cretaceous amber from France. *Cretaceous Research*, 32(3): 325-330. [IF 2,39]

44 **Perrichot V**., Ortega-Blanco J., McKellar R.C., Delclòs X., Azar D., Nel A., Tafforeau P., Engel M.S. (2011) New and revised maimetshid wasps from Cretaceous ambers (Hymenoptera, Maimetshidae). *ZooKeys*, 130: 421-453. [IF 0,917]

43 Solórzano Kraemer M.M., **Perrichot V**., Brown B.V., Tafforeau P., Soriano C. (2011) A new species of the Cretaceous genus *Prioriphora* (Diptera: Phoridae) in French amber. *Systematic Entomology*, 36(3): 581-588. [IF 2,553]

42 Nel A., Nel P., Petrulevicius J.F., **Perrichot V**., Prokop J., Azar D. (2010) The Wagner Parsimony using morphological characters: a new method for palaeosynecological studies. *Annales de la Société Entomologique de France*, 46(1-2): 276-292. [IF 0,539]

41 Schmidt A.R., Dörfelt H., Struwe S., **Perrichot V**. (2010) Evidence for fungivory in Cretaceous amber forests from Gondwana and Laurasia. *Palaeontographica B*, 283(4-6): 157-173. [IF 0,300]

40 Schmidt A.R., Girard V., **Perrichot V**., Schönborn W. (2010) Testate amoebae from a Cretaceous forest floor microbiocoenosis of France. *Journal of Eukaryotic Microbiology*, 57(3): 245-248. [IF 2,911]

39 Schmidt A.R., **Perrichot V**., Svojtka M., Anderson K.B., Belete K.H., Bussert R., Dörfelt H., Jancke S., Mohr B., Mohrmann E., Nascimbene P.C., Nel A., Nel P., Ragazzi E., Roghi G., Saupe E.E., Schmidt K., Schneider H., Selden P.A., Vávra N. (2010) Cretaceous African life captured in amber. *Proceedings of the National Academy of Sciences of the USA*, 107: 7329-7334. [IF 9,809]

38 Soriano C., Archer M., Azar D., Creaser P., Delclòs X., Godthelp H., Hand S., Jones A., Nel A., Néraudeau D., Ortega-Blanco J., Pérez-de la Fuente R., **Perrichot V**., Saupe E.E., Solórzano Kraemer M.M., Tafforeau P. (2010) Synchrotron X-ray imaging of inclusions in amber. *Comptes Rendus Palevol*, 9(6-7): 361-368. [IF 1,167]

37 Vilhelmsen L., **Perrichot V**., Shaw S.R. (2010) Past and present diversity and distribution in the parasitic wasp family Megalyridae (Insecta: Hymenoptera). *Systematic Entomology*, 35(4): 658-677. [IF 2,553]

36 Girard V., Saint-Martin S., Saint-Martin J.-P., Schmidt A.R., Struwe S., **Perrichot V**., Breton G., Néraudeau D. (2009) Exceptional preservation of marine diatoms in upper Albian amber. *Geology*, 37(1): 83-86. [IF 4,638]

35 Girard V., Schmidt A.R., Struwe S., **Perrichot V**., Breton G., Néraudeau D. (2009) Taphonomy and palaeoecology of mid-Cretaceous amber-preserved microorganisms from southwestern France. *Geodiversitas*, 31(1): 152-163. [IF 0,825]

34 Néraudeau D., Vullo R., Gomez B., Girard V., Lak M., Videt B., Dépré E., **Perrichot V**. (2009) Amber, plant and vertebrate fossils from the Lower Cenomanian paralic facies of Aix Island (Charente-Maritime, SW France). *Geodiversitas*, 31(1): 13-27. [IF 0,825]

33 **Perrichot V**., Girard V. (2009) A unique piece of amber and the complexity of ancient forest ecosystems. *Palaios*, 24(3): 137-139. [IF 1,904]

32 **Perrichot V**., Nel A., Quicke D.L.J. (2009) New braconid wasps from French Cretaceous amber (Hymenoptera, Braconidae): synonymization with Eoichneumonidae and implications for the phylogeny of Ichneumonoidea. *Zoologica Scripta*, 38(1): 79-88. [IF 2,922]

31 Ragazzi E., Giaretta A., **Perrichot V**., Néraudeau D., Schmidt A.R., Roghi G. (2009) Thermal analysis of Cretaceous ambers from southern France. *Geodiversitas*, 31(1): 163-175. [IF 0,825]

30 Girard V., Schmidt A.R., Saint-Martin S., Struwe S., **Perrichot V**., Saint-Martin J.-P., Breton G., Néraudeau D. (2008) Evidence for marine microfossils from amber. *Proceedings of the National Academy of Sciences of the USA*, 105: 17426-17429. [IF 9,809]

29 Lak M., Néraudeau D., Nel A., Cloetens P., **Perrichot V**., Tafforeau P. (2008) Phase contrast X-ray synchrotron imaging: opening access to fossil inclusions in opaque amber. *Microscopy & Microanalysis*, 14(3): 251-259. [IF 2,161]

28 Nel A., Néraudeau D., **Perrichot V**., Girard V., Gomez B. (2008) A new dragonfly family from the Upper Cretaceous of France. *Acta Palaeontologica Polonica*, 53(1): 165-168. [IF 1,722]

27 Néraudeau D., **Perrichot V**., Colin J.-P., Girard V., Gomez B., Guillocheau F., Masure E., Peyrot D., Tostain F., Videt B., Vullo R. (2008) A new amber deposit from the Cretaceous (uppermost Albian-lowermost Cenomanian) of southwestern France. *Cretaceous Research*, 29: 925-929. [IF 2,39]

26 **Perrichot V**., Lacau S., Néraudeau D., Nel A. (2008) Fossil evidence for the early ant evolution. *Naturwissenschaften*, 95(2): 85-90. [IF 1,971]

25 **Perrichot V**., Marion L., Néraudeau D., Vullo R., Tafforeau P. (2008) The early evolution of feathers: fossil evidence from Cretaceous amber of France. *Proceedings of the Royal Society B*, 275: 1197-1202. [IF 5,292]

24 **Perrichot V**., Nel A. (2008) Eocene bethylid wasps from French amber (Hymenoptera: Bethylidae). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 248(1): 91-101. [IF 0,541]

23 **Perrichot V**., Nel A., Néraudeau D., Lacau S., Guyot T. (2008) New fossil ants in French Cretaceous amber (Hymenoptera: Formicidae). *Naturwissenschaften*, 95(2): 91-97. [IF 1,971]

22 Schmidt A.R., Dörfelt H., **Perrichot V**. (2008) *Palaeoanellus dimorphus* gen. et sp. nov. (Deuteromycotina): a Cretaceous predatory fungus. *American Journal of Botany*, 95(10): 1328-1334. [IF 2,463]

21 **Perrichot V**., Engel M.S. (2007) Early Cretaceous snakefly larvae in amber from Lebanon, Myanmar, and France (Raphidioptera). *American Museum Novitates*, 3598: 1-11. [IF 1,636]

20 **Perrichot V**., Nel A., Néraudeau D. (2007) Schizopterid bugs (Insecta: Heteroptera) in mid-Cretaceous ambers from France and Myanmar (Burma). *Palaeontology*, 50(6): 1367-1374. [IF 1,804]

19 **Perrichot V**., Néraudeau D., Nel A., de Ploëg G. (2007) A reassessment of the Cretaceous amber deposits from France and their palaeontological significance. *African Invertebrates* 48(1): 213-227. [IF 0,5]

18 Schmidt A.R., Dörfelt H., **Perrichot V**. (2007) Carnivorous fungi from Cretaceous amber. *Science*, 318: 1743. [IF 31,477]

17 **Perrichot V**., Nel A., Guilbert E., Néraudeau D. (2006) Fossil Tingoidea (Heteroptera: Cimicomorpha) from French Cretaceous amber, including Tingidae and a new family, Ebboidae. *Zootaxa*, 1203: 57-68. [IF 1,060]

16 Nel A., **Perrichot V**., Azar D. (2005) New and poorly known fossil Coniopterygidae in Cretaceous and Cenozoic ambers (Insecta: Neuroptera). *Annales Zoologici* 55(1): 1-7. [IF 0,978]

15 Nel A., **Perrichot V**., Azar D., Néraudeau D. (2005) New Rhachiberothidae (Insecta: Neuroptera) in Early Cretaceous and Early Eocene ambers from France and Lebanon. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 235(1): 51-85. [IF 0,541]

14 Néraudeau D., Vullo R., Gomez B., **Perrichot V**., Videt B. (2005) Stratigraphie et paléontologie (plantes, vertébrés) de la série paralique Albien terminal - Cénomanien basal de Tonnay-Charente (Charente-Maritime, France). *Comptes Rendus Palevol* 4(1-2): 79-93. [IF 1,167]

13 **Perrichot V**., Nel A., Néraudeau D. (2005) Gerromorphan bugs in Early Cretaceous French amber (Insecta: Heteroptera): first representatives of Gerridae and their phylogenetic and palaeoecological implications. *Cretaceous Research* 26(5): 793-800. [IF 2,39]

12 **Perrichot V**., Néraudeau D. (2005) Reptile skin remains in the Cretaceous amber of France. *Comptes Rendus Palevol* 4(1-2): 47-51. [IF 1,167]

11 Nel A., Perrault G., **Perrichot V**., Néraudeau D. (2004) The oldest ant in the Lower Cretaceous amber of Charente-Maritime (SW France) (Insecta: Hymenoptera: Formicidae). *Geologica Acta* 2(1): 23-29.

10 Nel A., **Perrichot V**., Daugeron C., Néraudeau D. (2004) A new *Microphorites* in the Lower Cretaceous amber of the Southwest of France (Diptera: Dolichopodidae, "Microphorinae"). *Annales de la Société Entomologique de France* 40(1): 23-29. [IF 0,539]

9 **Perrichot V**. (2004) Early Cretaceous amber from south-western France: insight into the Mesozoic litter fauna. *Geologica Acta* 2(1): 9-22. [IF 1,483]

8 **Perrichot V**., Nel A., Néraudeau D. (2004) A new, enigmatic, evaniomorphan wasp in the Albian amber of France (Insecta: Hymenoptera). *Journal of Systematic Palaeontology* 2(2): 159-162. [IF 2,852]

7 **Perrichot V**., Nel A., Néraudeau D. (2004) Two new wedge-shaped beetles in Albo-Cenomanian ambers of France (Coleoptera: Ripiphoridae: Ripiphorinae). *European Journal of Entomology* 101(4): 583-589. [IF 1,076]

6 Azar D., **Perrichot V**., Néraudeau D., Nel A. (2003) New psychodids from the Cretaceous ambers of Lebanon and France, with a discussion about *Eophlebotomus connectens* Cockerell, 1920 (Diptera, Psychodidae). *Annals of the Entomological Society of America* 96(2): 117-126. [IF 1,174]

5 Gomez B., Barale G., Saad D., **Perrichot V**. (2003) Santonian angiosperm-dominated leaf-assemblage from Piolenc (Vaucluse, SE France). *Comptes Rendus Palevol* 2(3): 197-204. [IF 1,167]

4 Néraudeau D., Allain R., **Perrichot V**., Videt B., De Broin F., Guillocheau F., Philippe M., Rage J.-C., Vullo R. (2003) Découverte d'un dépôt paralique à bois fossiles, ambre insectifère et restes d'Iguanodontidae (Dinosauria, Ornithopoda) dans le Cénomanien inférieur de Fouras (Charente-Maritime, sud-ouest de la France). *Comptes Rendus Palevol* 2(3): 221-230. [IF 1,167]

3 **Perrichot V**., Azar D., Néraudeau D., Nel A. (2003) New Psocoptera in the Early Cretaceous amber of SW France and Lebanon (Insecta: Psocoptera: Trogiomorpha). *Geological Magazine* 140(6): 669-683. [IF 2,177]

2 Néraudeau D., **Perrichot V**., Dejax J., Masure E., Nel A., Philippe M., Moreau P., Guillocheau F., Guyot T. (2002) Un nouveau gisement à ambre insectifère et à végétaux (Albien terminal probable): Archingeay (Charente-Maritime, France). *Geobios* 35(2): 233-240. [IF 1,187]

1 **Perrichot V**., Néraudeau D., Azar D., Menier J.-J., Nel A. (2002) A new genus and species of fossil mole cricket in the Lower Cretaceous amber of Charente-Maritime, SW France (Insecta: Orthoptera: Gryllotalpidae). *Cretaceous Research* 23(3): 307-314. [IF 2,39]

Articles dans des revues non indéxées, à comité de lecture

16 Azar D., Nel A., **Perrichot V**. (2014) Diverse barklice (Psocodea) from Late Cretaceous Vendean amber. *Paleontological Contributions*, 10C: 9-15.

15 Bennett D. J., **Perrichot V**., Engel M.S. (2014) A new genus and species of pemphredonine wasp (Hymenoptera: Crabronidae) in Late Cretaceous Vendean amber. *Paleontological Contributions*, 10I: 41-45.

14 Choufani J., **Perrichot V**., Azar D., Nel A. (2014) New biting midges (Diptera: Ceratopogonidae) in Late Cretaceous Vendean amber. *Paleontological Contributions*, 10H: 34-40.

13 Engel M.S., **Perrichot V**. (2014) An earwig in Late Cretaceous Vendean amber (Dermaptera). *Paleontological Contributions*, 10D: 16-20.

12 Engel M.S., **Perrichot V**. (2014) The extinct wasp family Serphitidae in Late Cretaceous Vendean amber (Hymenoptera). *Paleontological Contributions*, 10J: 46-51.

11 **Perrichot V**., Engel M.S. (2014) Youngest occurrence of the genus *Microphorites* (Diptera: Dolichopodidae): A new species in Late Cretaceous Vendean amber. *Paleontological Contributions*, 10G: 30-33.

10 **Perrichot V**., Garrouste R., Azar D., Néraudeau D., Nel A. (2014) A new genus of dustywings (Neuroptera: Coniopterygidae) in Late Cretaceous Vendean amber. *Paleontological Contributions*, 10F: 25-29.

9 **Perrichot V**., Néraudeau D. (2014) Introduction to thematic volume "Fossil arthropods in Late Cretaceous Vendean amber (northwestern France)". *Paleontological Contributions*, 10A: 1-5.

8 Nohra Y., Azar D., Gèze R., Maksoud S., El Samrani A., **Perrichot V**. (2013) New Jurassic amber outcrops from Lebabon. *Terrestrial Arthropod Reviews*, 6(1-2): 27-51.

7 Choufani J., Azar D., **Perrichot V**., Soriano S., Tafforeau P., Nel A. (2011) The genus *Leptoconops* Skuse (Diptera: Ceratopogonidae) in Early Cretaceous Charentese amber. *Palaeobiodiversity and Palaeoenvironments*, 91(4): 285-291.

6 Colin J.-P., Néraudeau D., Nel A., **Perrichot V**. (2011) Termite (Insecta: Isoptera) coprolites from the Cretaceous of western France: A palaeoecological insight. *Revue de Micropaléontologie*, 54(3): 129-139.

5 Engel M.S., Nel A., Azar D., Soriano C., Tafforeau P., Néraudeau D., Colin J.-P., **Perrichot V**. (2011) New, primitive termites (Isoptera) from Early Cretaceous ambers of France and Lebanon. *Palaeodiversity*, 4: 39-49.

4 **Perrichot V**. (2009) Long-tailed wasps (Hymenoptera: Megalyridae) from Cretaceous and Paleogene European amber. *Paleontological Contributions*, 1: 1-35.

3 Azar D., Tahchy A., **Perrichot V**. (2007) The oldest Sycoracinae (Diptera: Psychodidae) from the French Cretaceous amber. *Alavesia* 1: 5-10.

2 **Perrichot V**., Nel A., Krzemínski W. (2007) A new crane fly (Diptera: Limoniidae) in Cretaceous amber from France. *Alavesia* 1: 75-80.

1 Nel A., **Perrichot V**., Néraudeau D. (2003) The oldest trigonalid wasp in the Late Albian amber of Charente-Maritime (SW France) (Hymenoptera: Trigonalidae). *Eclogae Geologicae Helvetiae* 96(3): 503-508.

Chapitres d'ouvrages

2 Néraudeau D., **Perrichot V**. (2010) Un exemple du patrimoine de l'Albien : les ambres albiens de France. *In*: Colleté C. (ed.), *Stratotype Albien*. Publications Scientifiques du Muséum, Paris, collection "Patrimoine géologique"; BRGM Editions, Orléans: 298-299.

1 **Perrichot V**., Néraudeau D., Tafforeau P. (2010) Charentese amber. *In*: Penney D. (ed.), *Biodiversity of fossils in amber from the major world deposits*. Siri Scientific Press, Manchester: 192-207.

Volumes thématiques édités

2 **Perrichot V**. (2014) Fossil arthropods in Late Cretaceous Vendean amber (northwestern France). *Paleontological Contributions*, 10: 51 p.

1 **Perrichot V**., Néraudeau D. (2009) Cretaceous ambers from southwestern France: geology, taphonomy, and paleontology. *Geodiversitas*, 31(1): 175 p.

Thèse

Perrichot V. (2005) Environnements paraliques à ambre et végétaux du Crétacé nord-aquitain (Charentes, Sud-Ouest de la France). *Mémoires de Géosciences Rennes*, 118: 310 pp.
http://www.geosciences.univ-rennes1.fr/IMG/pdf/Memoires_GS.pdf

Actes de congrès

1 Choufani J., **Perrichot V.**, Girard V., Garrouste R., Azar D., Nel A. (2013) Two new biting midges of the modern type from Santonian amber of France (Diptera: Ceratopogonidae). *In*: Azar D., Engel M.S., Jarzembowski E., Krogmann L., Nel A., Santiago-Blay J. (Eds), *Insect Evolution in an Amberiferous and Stone Alphabet*. Proceedings of the 6th International Congress on Fossil Insects, Arthropods and Amber. Brill, Leiden, pp. 71-95.

Autres publications

8 Kaulfuss U., Lee D., Bannister J., Lindqvist J., Mildenhall D., **Perrichot V**., Maraun M., Schmidt A. (2011) Discovering the New Zealand amber forest biota. *Geoscience Society of New Zealand Newsletter* 5: 20-25.

7 **Perrichot V**., Marion L., Néraudeau D., Vullo R., Tafforeau P. (2009) Early structure of feathers revealed by phase contrast X-ray synchrotron imaging. *ESRF Highlights* 2008: 115-116.

6 Schmidt A.R., Dörfelt H., **Perrichot V**. (2009) Paleomycology: do we consider extinct lineages in the evaluation of fossil fungi? A reply to Thorn *et al*., 2008. *Mycological Research* 113(3): 275-276.

5 Lak M., Tafforeau P., Néraudeau D., **Perrichot V**., Nel A. (2007) Non-destructive study of fossil inclusions in opaque amber using phase contrast X-ray synchrotron imaging. *ESRF Highlights* 2006: 109-110.

4 Saint-Martin J.-P., Saint-Martin S., Tostain F., **Perrichot V**., Néraudeau D., Breton G. (2006) L'ambre fossile du Crétacé inférieur : un piège pour les diatomées ? *Symbioses* 14: 26.

3 Nel A., **Perrichot V**., Azar D., Néraudeau D. (2005) A replacement name for the neuropteran genus *Eorhachiberotha* Nel *et al*., 2005 (Neuroptera: Rhachiberothidae). *Bulletin de la Société Entomologique de France* 110(2): 128.

2 Guillocheau F., Néraudeau D., Videt B., **Perrichot V**., Vullo R. (2003) La plate-forme carbonatée cénomanienne de Charente : une double approche sédimentologique et paléoécologique. *Livre-excursion du 9ème Congrès français de Sédimentologie, Bordeaux, Octobre 2003*, 35 pp.

1 Le Meur H., Néraudeau D., **Perrichot V**. (2003) D'ambre et d'insectes. *La Recherche* n° 370: 72-79.

Résumés de congrès nationaux

16 **Perrichot V**., Engel M.S., Nel A., Ortega-Blanco J., Delclòs X., Soriano C., Lohrmann V., Tafforeau P. (2014) "False ants" from the Cretaceous (Hymenoptera: Chrysidoidea: Falsiformicidae). *11th Meeting of Hymenopterologists*, Stuttgart, Germany, October 3-5, *Mitteilungen des Entomologischen Vereins Stuttgart*, 49(1): 26.

15 Conran J.G., Busch A., Engel M.S., Kaulfuss U., Kiecksee A.P., Lee D.E., Maraun M., **Perrichot V**., Sadowski E.-M., Schmidt A.R. (2013) The first arthropods from New Zealand amber. *44th Meeting of the Australian Entomological Society*, Adelaide, Australia, September 29 - October 2, abstract book p. 64.

14 Seyfullah L.J., Beimforde C., **Perrichot V**., Rikkinen J., Schmidt A.R. (2013) Why do we have amber forests? Using modern studies to attempt to understand the relationship between resin production and amber deposits. *In*: Rascher J., Rappsilber I. & Wimmer R. (Eds.), Bitterfelder Bernstein und andere fossile Harze aus Mitteldeutschland. *III. Bitterfelder Bernsteinkolloquium*, May 23–25, Bitterfeld, Germany. *Exkursionsführer und Veröffentlichungen der Deutschen Gesellschaft für Geowissenschaften*, 249: 64-67.

13 **Perrichot V.** (2012) Mid-Cretaceous amber forests from France. *In*: Witzmann F. & Aberhan M. (Eds), *Centenary Meeting of the Paläontologische Gesellschaft*, September 24-28, Berlin, Germany. *Terra Nostra*, 2012/3: 133.

12 Seyfullah L.J., Beimforde C., **Perrichot V**., Rikkinen J., Schmidt A.R. (2012) The what and why of amber: attempting to understand the relationship between resin production and amber deposits. *In*: Witzmann F. & Aberhan M. (Eds), *Centenary Meeting of the Paläontologische Gesellschaft*, September 24-28, Berlin, Germany. *Terra Nostra*, 2012/3: 166-167.

11 Peñalver E., Barrón E., Ortega J., **Perrichot V**., Delclòs X. (2008) Taphonomy of kauri resin (*Agathis australis*) from New Zealand as a key for the interpretation of arthropod-bearing amber from the Cretaceous of Spain. *Taphos'08*, June 12-14, Granada, Spain, abstract book p. 86-87.

10 Struwe S., **Perrichot V**., Schmidt A.R. (2007) Mikroinklusen und die Paläoökologie der kretazischen Bernsteinwälder von Charente-Maritime (Frankreich). *In*: Elicki O., Schneider J.W. (eds), "Fossile Ökosysteme". 77th Jahrestagung der Paläontologischen Gesellschaft, Freiberg, Germany, September 17-19, *Wissentschaftliche Mitteilungen des Institutes für Geologie der TU Bergakademie Freiberg*, 36: 150.

9 Lak M., Tafforeau P., **Perrichot V**., Néraudeau D., Nel A. (2006) Détection et reconstitution 3D d'inclusions dans l'ambre opaque par imagerie à rayonnement X synchrotron. *21ème Réunion des Sciences de la Terre*, 05-09 décembre, Dijon, volume des résumés p. 126.

8 Néraudeau D., **Perrichot V**., Vullo R., Breton G., Le Diouron T., Gomez B., Peyrot D., Tostain F., Videt B. (2005) L'apport des faciès à ambre insectifère de l'Albien-Cénomanien des Charentes à la connaissance des écosystèmes terrestres du Crétacé européen. *Réunion thématique du Groupe Français du Crétacé: Impact environnemental sur la dynamique des populations au Crétacé*, Ecole des Mines, Paris, volume des résumés p. 29.

7 **Perrichot V**., De Ploëg G., Philippe M., Delclòs X., Néraudeau D. (2004) Sources botaniques des ambres crétacés de France. *Journée APF: "Faune et flore des bassins paraliques"*, Muséum national d'Histoire Naturelle, Paris, 16 juin, volume des résumés p. 12.

6 Saint Martin J.-P., Saint Martin S., Tostain F., **Perrichot V**., Néraudeau D., Breton G. (2004) L'ambre fossile du Crétacé inférieur: un piège pour les diatomées? *23ème Colloque de l'Association des Diatomistes de Langue Française (ADLAF)*, Muséum d'Histoire Naturelle, Orléans, 14-16 septembre, *Symbioses*, 14: 26.

5 Tostain F., Breton G., Saint-Martin S., **Perrichot V**., Néraudeau D. (2004) Les micro-organismes (cyanobactéries, diatomées, protozoaires…) de l'ambre albien terminal d'Archingeay (Charente-Maritime, France). *Journée APF: "Faune et flore des bassins paraliques"*, Muséum national d'Histoire Naturelle, Paris, 16 juin, volume des résumés p. 16.

4 Gomez B., Thévenard F., **Perrichot V**., Daviero-Gomez V., Coiffard C., Néraudeau D. (2002) Le conifère *Glenrosa* dans l'Albien-Cénomanien de Charente-Maritime (France) : marqueur d'un climat à saison sèche. *Colloque Eclipse: environnement et climat du Passé: histoire et évolution*, CNRS, Paris, 21-22 octobre, volume des résumés p. 70.

3 **Perrichot V**., Dejax J., Masure E., Nel A., Néraudeau D., Philippe M. (2002) Les écosystèmes terrestres du Crétacé ouest-européen : données paléobiologiques des gisements à ambre de Charente-Maritime. *19ème Réunion des Sciences de la Terre*, Faculté des Sciences et Techniques, Nantes, 9-12 avril, volume des résumés p. 194.

2 **Perrichot V**., Nel A., Néraudeau D. (2002) Une faune de litière dans l'Albien de Charente-Maritime: une préservation exceptionnelle dans l'ambre crétacé. *Colloque Eclipse: environnement et climat du Passé: histoire et évolution*, CNRS, Paris, 21-22 octobre, volume des résumés p. 29.

1 **Perrichot V**., Philippe M., Néraudeau D. (2001) Paléoécologie des flores crétacées pré-angiospermiennes: données xylologiques de Charentes. *Séance spécialisée de la Société Géologique de France: "Paléobiodiversité, Crise, Paléoenvironnement"*, Muséum National d'Histoire Naturelle, Paris, volume des résumés p. 69.

Résumés de congrès internationaux

(Les numéros en rouge dénotent des conférences données à l'invitation des organisateurs)

36 Nohra Y.A., **Perrichot V**., Boura A., Jeanneau L., Néraudeau D., Thomas R., Azar D. (2014) Cupressacean origin of the Cretaceous Vendean amber (northwestern France): evidence from fossil woods and chemical signatures. *9th European Palaeobotany-Palynology Conference*, Padova, Italy, August 26-31, abstract book p. 189.

35 Nohra Y.A., **Perrichot V**., Jeanneau L., Gèze R., Azar D. (2014) Lebanese Jurassic *versus* Cretaceous amber: Chemical characterization. *20th LAAS International Science Conference*, Hadath, Lebanon, March 27-29, abstract book p. 865-866.

34 **Perrichot V**. (2014) Fossil *versus* molecular datings of major ant subfamilies. *International Congress of the International Union for the Study of Social Insects*, Cairns, Australia, July 13-18, abstract book p. 92.

33 Schmidt A.R., Kaulfuss U., Borkent A., Busch A., Conran J., D'Haese C.A., Engel M.S., Harvey M., Kerr P., Kettunen E., Kiecksee A.P., Larivière M.-C., Lengeling F., Maraun M., **Perrichot V**., Rikkinen J., Sadowski E.-M., Seyfullah L.J., Lee D.E. (2014) Amber inclusions from New Zealand. *9th European Palaeobotany-Palynology Conference*, Padova, Italy, August 26-31, abstract book p. 245-246.

32 Choufani J., **Perrichot V**., Girard V., Garrouste R., Azar D., Nel A. (2013) Two new biting midges of modern type from the Santonian amber of France (Diptera: Ceratopogonidae). *6th International Congress on Fossil Insects, Arthropods, and Amber*, Byblos, Lebanon, April 14-18, abstract book p. 53.

31 Girard V., Aquilina L., Brossier B., Garrouste R., Nel A., Néraudeau D., Pastor T., **Perrichot V**. (2013) ResPine: A long-term actuotaphonomical survey of organism trapping in plant resins. *6th FossilX3: International Congress on Fossil Insects, Arthropods, and Amber*, Byblos, Lebanon, April 14-18, abstract book p. 65-66.

30 Kaulfuss U., Lee D.E., Bannister J.M., Lindqvist J.K., Conran J.G., Mildenhall D.C., Kennedy E.M., **Perrichot V**., Maraun M., Schmidt A.R. (2013) Foulden Maar and South Island amber (New Zealand) – two exceptional windows into Southern Hemisphere Cenozoic terrestrial ecosystems. *In*: Reitner J., Yang Q., Wang Y., Reich M. (Eds), *Palaeobiology and geobiology of fossil lagerstätten through earth history. A joint conference of the Paläontologische Gesellschaft and the Palaeontological Society of China*, Göttingen, Germany, September 23-27, abstract book p. 84-85.

29 Kaulfuss U., Lee D.E., Bannister J. M., **Perrichot V**., Schmidt A.R. (2013) Discovering the New Zealand amber forest biota. *In*: Dickinson K., Lee B. (Eds), *Southern lands and southern oceans: life on the edge? VII Southern Connection Congress*, Dunedin, New Zealand, January 21-25, abstract book p. 57.

28 Nohra Y., Azar D., Gèze R., Maksoud S., El-Samrani A., **Perrichot V.** (2013) New Jurassic amber outcrops from Lebanon. *Amberif 2013 - International Amber Researcher Symposium*, Gdansk, Poland, March 22-23, abstract book p. 17.

27 Nohra Y., Azar D., Gèze R., Maksoud S., El Samrani A., **Perrichot V**. (2013) New Jurassic amber outcrops from Lebabon. *6th FossilX3: International Congress on Fossil Insects, Arthropods, and Amber*, Byblos, Lebanon, April 14-18, abstract book p 61.

26 **Perrichot V**., Néraudeau D., Girard V., Nel A., Nohra Y., Saint Martin S., Saint Martin J.-P., Schmidt A.R., Dupé F. (2013) Santonian Vendeen amber: large amounts of data from a small sample in northwestern France. *6th FossilX3International Congress on Fossil Insects, Arthropods, and Amber*, Byblos, Lebanon, April 14-18, abstract book p 49.

25 Sánchez-García A., Peñalver E., Peris D., **Perrichot V**., Delclòs X. (2013) Diverse assemblages of tanaids (Crustacea) related to Albian-Cenomanian resin-producing forests in Western Europe and their paleobiological implications. *6th FossilX3: International Congress on Fossil Insects, Arthropods, and Amber*, Byblos, Lebanon, April 14-18, abstract book p. 47-48.

24 **Perrichot V**., Fisher B.L. (2012) AntWeb: digitizing Recent and fossil insects for an online database of the ants of the world. *1st DigitalFossil Conference*, September 24-26, Berlin, Germany. Online abstract www.naturkundemuseum-berlin.de/forschung/tagungen/digitalfossil-berlin-2012/home/abstracts-of-presentations/#c24995

23 **Perrichot V.**, Tafforeau P., Soriano C. (2012) Synchrotron imaging as a tool for the survey of amber inclusions. *1st DigitalFossil Conference*, September 24-26, Berlin, Germany. Online abstract www.naturkundemuseum-berlin.de/forschung/tagungen/digitalfossil-berlin-2012/home/abstracts-of-presentations/#c24994

22 Seyfullah L.J., Beimforde C., **Perrichot V**., Rikkinen J., Schmidt A.R. (2012) Resin production in Araucariaceae: enlightening amber deposition? *9th International Organization of Palaeobotany Congress*, Tokyo, Japan, August 23-30, *Japanese Journal of Palynology,* 58: 210.

21 **Perrichot V**. (2011) Mid-Cretaceous insect evolution in the context of changing vegetation. *Biosystematics 2011, 7th International Congress of Systematic and Evolutionary Biology*, Berlin, Germany, February 21-27, abstract book p. 287.

20 Aquilina L., Girard V., Bouhnik-Le Coz M., Henin O., Perrichot V., Vilbert D., Néraudeau D. (2010) Geochemistry of amber and resin: new perspectives. *5th FossilX3: Insects, Arthropods, Amber*, Beijing, China, August 20-25, abstract book p. 36-37.

19 Ortega-Blanco J., Delclòs X., Engel M.S., McKellar R., Peñalver E., Pérez de la Fuente R., **Perrichot V**., Rasnitsyn A.P., Soriano C. (2010) Diversity of hymenopteran families in the Early Cretaceous amber from Spain. *5th FossilX3: Insects, Arthropods, Amber*, Beijing, China, August 20-25, abstract book p. 60.

18 Nel A., Nel P., Petrulevicius J. F., **Perrichot V**., Prokop J., Azar D. (2010) The Wagner Parsimony using morphological characters: a new method for palaeosynecological studies. *5th FossilX3: Insects, Arthropods, Amber*, Beijing, China, August 20-25, abstract book p. 88.

17 **Perrichot V**., Fisher B.L., Schmidt A.R., Svojtka M., Tafforeau P., Ward P.S. (2010) The early evolution of ants: fossil *versus* molecular evidence. *5th FossilX3: Insects, Arthropods, Amber*, Beijing, China, August 20-25, abstract book p. 161.

16 Schmidt A.R., **Perrichot V**., and 18 others (2010) The Ethiopian amber forest. *5th FossilX3: Insects, Arthropods, Amber*, Beijing, China, August 20-25, abstract book p. 166-167.

15 Solórzano Kraemer M., **Perrichot V**., Lak M., Tafforeau P., Soriano C., Néraudeau D. (2010) Aquatic bugs (Heteroptera: Gerromorpha) from Cretaceous amber of France and their palaeoecological implications. *5th FossilX3: Insects, Arthropods, Amber*, Beijing, China, August 20-25, abstract book p. 65.

14 Soriano C., Nel A., Néraudeau D., **Perrichot V**., Saupe E.E., Solórzano Kraemer M., Tafforeau P. (2010) Latest discoveries with X-Ray Synchrotron imaging techniques on the Cretaceous French amber. *5th FossilX3: Insects, Arthropods, Amber*, Beijing, China, August 20-25, abstract book p. 70.

13 Néraudeau D., Girard V., Gomez B., Lak M., **Perrichot V**., Vullo R. (2009) Mid-Cretaceous terrestrial biota from Charentes, SW France: A synthesis of 10 years of investigation. *10th Mesozoic Terrestrial Ecosystems Symposium*, Teruel, Spain, septembre 17-21, abstract book p. 211-212.

12 **Perrichot V**., Ward P.S. (2009) The early evolution of ants: fossil *versus* molecular evidence. *10th Mesozoic Terrestrial Ecosystems Symposium*, Teruel, Spain, September 17-21, abstract book p. 59-60.

11 Girard V., Struwe S., Saint Martin S., Saint Martin J.-P., **Perrichot V**., Breton G., Néraudeau D. (2008) Mid-Cretaceous marine microfossils preserved in fossil tree resin. *8th International Organization of Palaeobotany Congress*, Bonn, Germany, August 30- September 5. *Terra Nostra* 2008/2: 94.

10 Struwe S., Girard V., **Perrichot V**., Schmidt A.R. (2008) Reconstruction of a diverse soil microbiocoenosis from French Cretaceous amber. *8th International Organization of Palaeobotany Congress*, Bonn, Germany, August 30- September 5. *Terra Nostra* 2008/2: 271.

9 Girard V., Saint-Martin S., Breton G., Néraudeau D., **Perrichot V.**, Saint-Martin J.-P., Schmidt A.R. (2007) An exceptional preservation of marine diatoms in Late Albian French amber. *4th FossilsX3: Insects, Arthropods, Amber*, Vitoria-Gasteiz, Spain, May 4-9, abstract book p. 80.

8 Lak M., Tafforeau P., Perrichot V., Néraudeau D., Nel A. (2007) Detection and 3D-reconstruction of inclusions in opaque amber using phase contrast X-ray synchrotron imaging. *4th FossilsX3: Insects, Arthropods, Amber*, Vitoria-Gasteiz, Spain, May 4-9, abstract book p. 112.

7 Néraudeau D., Breton G., Colin J.-P., Girard V., Gomez B., Guillocheau F., Lak M., Masure E., Nel A., **Perrichot V**., Platel J.-P., Videt B., Vullo R. (2007) Sequence stratigraphy, palaeogeography and palaeoenvironments of the Cretaceous amber deposits from western France. *4th FossilsX3: Insects, Arthropods, Amber*, Vitoria-Gasteiz, Spain, May 4-9, abstract book p. 122-123.

6 **Perrichot V**., Girard V., Lak M., Nel A., Néraudeau D., Saint-Martin S., Schmidt A.R. (2007) Terrestrial and marine inclusions from French Cretaceous amber and their palaeoecological implications. *4th FossilsX3: Insects, Arthropods, Amber*, Vitoria-Gasteiz, Spain, May 4-9, abstract book p. 128.

5 **Perrichot V**., Nel A. & Quicke D.L.J. (2007) Protothyssalinae and allies: towards an improved understanding of basal braconid wasps relationships (Hymenoptera). *4th FossilsX3: Insects, Arthropods, Amber*, Vitoria-Gasteiz, Spain, May 4-9, abstract book p. 236.

4 Néraudeau D., **Perrichot V**., Tostain F., Videt B., Vullo R., Gomez B. (2005) Insects and micro-organisms from the Late Albian amber of Cadeuil (Charente-Maritime, SW France). *7th International Symposium on the Cretaceous*, Neuchâtel, Switzerland, September 7-9, abstract book p. 153.

3 **Perrichot V**. (2005) The underestimated importance of the Cretaceous amber of France. *3rd FossilsX3: Insects, Arthropods, Amber*, Pretoria, South Africa, February 7-11, abstract book p. 27.

2 **Perrichot V**., Nel A. (2005) Hymenopteran inclusions from the Cretaceous amber of France. *3rd FossilsX3: Insects, Arthropods, Amber*, Pretoria, South Africa, February 7-11, abstract book p. 49-50.

1 **Perrichot V**., Néraudeau D., Philippe M., Gomez B., Nel A. (2002) Insects and plant remains from the oldest French amber locality: a new insight into an Early Cretaceous terrestrial ecosystem. *8th International Symposium on Mesozoic Terrestrial Ecosystem*, Cape Town, South Africa, July 21-26, abstract book p.42.

4.2. Intégration dans les programmes nationaux et internationaux

Co-responsable de projet

2011-2012 NOVAMBRE : Programme INSU Interrvie. Coordonnateurs: D. Néraudeau et V. Perrichot (Univ. Rennes 1).

Participant

2008-2011 AMBRACE : Evolution faunique, floristique et paléoclimatique des ambres crétacés de France. Programme ANR n° BLAN07-1-184190. Coordonnateur : D. Néraudeau (Univ. Rennes 1).

2009-2011 Cretaceous insects and the origins of modern insect diversity. Programme HymAToL (Assembling the Tree of Life - Hymenoptera) de la Fondation américaine pour les Sciences (NSF) n° DEB-0542909. Coordonnateur: M. S. Engel (Univ. Kansas).

2007-2008 Systématique, taphonomie et paléoécologie des microorganismes fossiles de l'ambre. Programme de la Fondation allemande de la Recherche (DFG) n° SCHM 2152/1-1. Coordonnateur : A. R. Schmidt (MfN Berlin).

2005-2006 Evolution paléobiologique et paléo-environnementale des gisements à ambre du Crétacé de France et d'Espagne. Programme Egide d'action intégrée franco-espagnole PICASSO n° 09045SE, Coordonnateurs : X. Delclòs (Univ. Barcelone) et D. Néraudeau (Univ. Rennes 1).

2004-2005 Interactions entre biodiversité végétale et changement global durant la transition Crétacé inférieur/Crétacé supérieur en Europe de l'Ouest. Programme "Biodiversité et Changement Global" de l'Institut Français de Biodiversité. Coordonnateurs : F. Thévenard (Univ. Lyon 1) et B. Gomez (Univ. Rennes 1).

2004-2005 Environnements et climats du Crétacé. Programme CNRS ECLIPSE II. Coordonnateur : F. Guillocheau (Univ. Rennes 1).

2001-2003 Interactions Climat / Ecosystèmes entre l'Aptien et le Paléocène. Programme CNRS ECLIPSE. Coordonnateur : D. Néraudeau (Univ. Rennes 1).

4.3. Bourses et subventions

2015 Bourse 'visiting professor' de l'Académie chinoise des Sciences (CAS), Nanjing Institute of Geology and Palaeontology. Projet : "Etude des fourmis fossiles des ambres du Crétacé du Myanmar et de l'Eocène de Chine".

2013 Subvention OSUR sur appel à projets pour l'accueil d'un chercheur étranger (T. Wappler, Univ. Bonn); "Interactions plantes – insectes dans le Cénomanien basal des Charentes : implications paléoécologiques et paléoclimatiques". (1450 €)

2013 Bourse SYNTHESYS pour un séjour d'étude des collections d'insectes fossiles du Muséum d'Histoire Naturelle de Londres, janvier 2013.

2012 Subvention TGIR pour utilisation de la plateforme RMN-THC de Lille (UCCS-UGSF) ; "RMN 1H haut champ et MAS haute vitesse pour la caractérisation d'ambres d'origines géologiques variées".

2012 Subvention ESRF sur appel à projets, ligne de lumière ID19 ; "Imagerie 3D par rayonnement X synchrotron de fourmis fossilisées dans l'ambre crétacé du Myanmar".

2012 Subvention OSUR sur appel à projets impliquant plusieurs équipes ; "Caractérisation physico-chimique des résines végétales fossiles et actuelles". (2625 €)

2011 Subvention OSUR sur appel à projets pouvant déboucher sur projet ANR ; "Actuo-paléontologie dans les forêts modernes productrices de résine: implications pour l'étude des écosystèmes forestiers à ambre". (2500 €)

2010 Subvention ESRF sur appel à projets, ligne de lumière ID19 ; "Imagerie 3D par rayonnement X synchrotron d'inclusions fossiles dans l'ambre crétacé de France".

2008 Subvention KUBI (Kansas University Biodiversity Institute) pour participation au workshop Ant Course de l'Académie des Sciences de Californie (CAS), Station Biologique Rancho Grande, Vénézuela, août 2008. (1000 US$)

2006 Bourse post-doctorale de la Fondation Alexander von Humboldt. (72.000 €)

4.4. Autres activités liées à la recherche

Gestion de collections et de bases de données

Depuis 2011 Conservateur de la collection d'ambre du Crétacé de France, mêlant les fonds de Géosciences Rennes et du Muséum national d'Histoire Naturelle (ce dernier mis en dépôt à Géosciences Rennes par convention entre le MNHN et l'université de Rennes 1).

Depuis 2009 Conservateur de la collection d'ambre du Musée de Géologie de l'Université de Rennes 1 (fig. 2).

Depuis 2009 Correspondant local *Trans'Tyfipal* (http://transtyfipal.u-bourgogne.fr/acPalFr.shtml : catalogue électronique national des types et figurés présents dans les collections paléontologiques des universités et muséums français).

Charge : imagerie et mise à jour permanente du catalogue électronique de la typothèque du Musée de Géologie de l'Université Rennes 1 (fig. 3).

Depuis 2013 Administrateur des données 'fossiles' du site internet *AntCat* (http://www.antcat.org : catalogue électronique mondial des fourmis actuelles et fossiles).

Charge : mise à jour permanente du catalogue fossile et de la bibliographie associée (fig. 4).

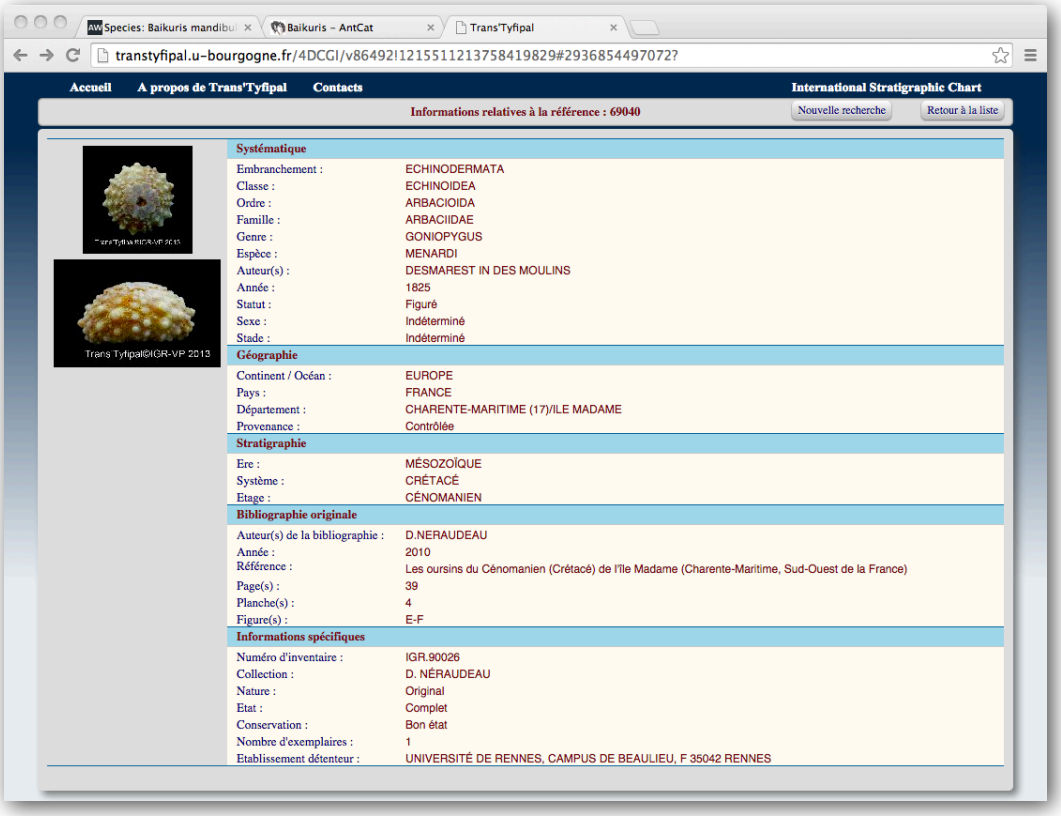
Depuis 2008 Créateur et administrateur de la base de données 'fourmis fossiles' du site internet *AntWeb* (http://www.antweb.org/fossil.jsp : catalogue mondial illustré et géoréférencé des fourmis actuelles et fossiles, en lien avec *AntCat*).

Charge : création et mise à jour permanente du catalogue fossile ; imagerie des spécimens pour chaque espèce fossile (fig. 5).

Les responsabilités inhérentes à ma charge de conservation de la collection d'ambre, qui représente environ 10% de mon temps de travail, sont les suivantes :

- préparation, étiquetage, et conditionnement pour conservation durable des spécimens ;
- informatisation de la collection ;
- réception des visiteurs : 11 chercheurs depuis 2009, en moyenne 12 jours de visite par an ;
- gestion des prêts à destination des chercheurs ;
- valorisation de la collection par des publications.

Figure 2
Un aperçu de la collection d'ambre de Géosciences Rennes.



Species: Baikuris mandibul | Baikuris - AntCat | Trans'Tyfipal

transtyfipal.u-bourgogne.fr/4DCGI/v86492!1215511213758419829#29368544970727

Accueil | A propos de Trans'Tyfipal | Contacts | International Stratigraphic Chart

Informations relatives à la référence : 69040 — Nouvelle recherche — Retour à la liste

Trans Tyfipal©IGR-VP 2013

Systématique	
Embranchement :	ECHINODERMATA
Classe :	ECHINOIDEA
Ordre :	ARBACIOIDA
Famille :	ARBACIIDAE
Genre :	GONIOPYGUS
Espèce :	MENARDI
Auteur(s) :	DESMAREST IN DES MOULINS
Année :	1825
Statut :	Figuré
Sexe :	Indéterminé
Stade :	Indéterminé
Géographie	
Continent / Océan :	EUROPE
Pays :	FRANCE
Département :	CHARENTE-MARITIME (17)/ILE MADAME
Provenance :	Contrôlée
Stratigraphie	
Ere :	MÉSOZOÏQUE
Système :	CRÉTACÉ
Etage :	CÉNOMANIEN
Bibliographie originale	
Auteur(s) de la bibliographie :	D.NERAUDEAU
Année :	2010
Référence :	Les oursins du Cénomanien (Crétacé) de l'Ile Madame (Charente-Maritime, Sud-Ouest de la France)
Page(s) :	39
Planche(s) :	4
Figure(s) :	E-F
Informations spécifiques	
Numéro d'inventaire :	IGR.90026
Collection :	D. NÉRAUDEAU
Nature :	Original
Etat :	Complet
Conservation :	Bon état
Nombre d'exemplaires :	1
Etablissement détenteur :	UNIVERSITÉ DE RENNES, CAMPUS DE BEAULIEU, F 35042 RENNES

Figure 3
Un extrait du catalogue Trans'Tyfipal pour un spécimen figuré de la collection de Géosciences Rennes.

Figure 4
Un extrait de la section fossile du catalogue électronique AntCat.

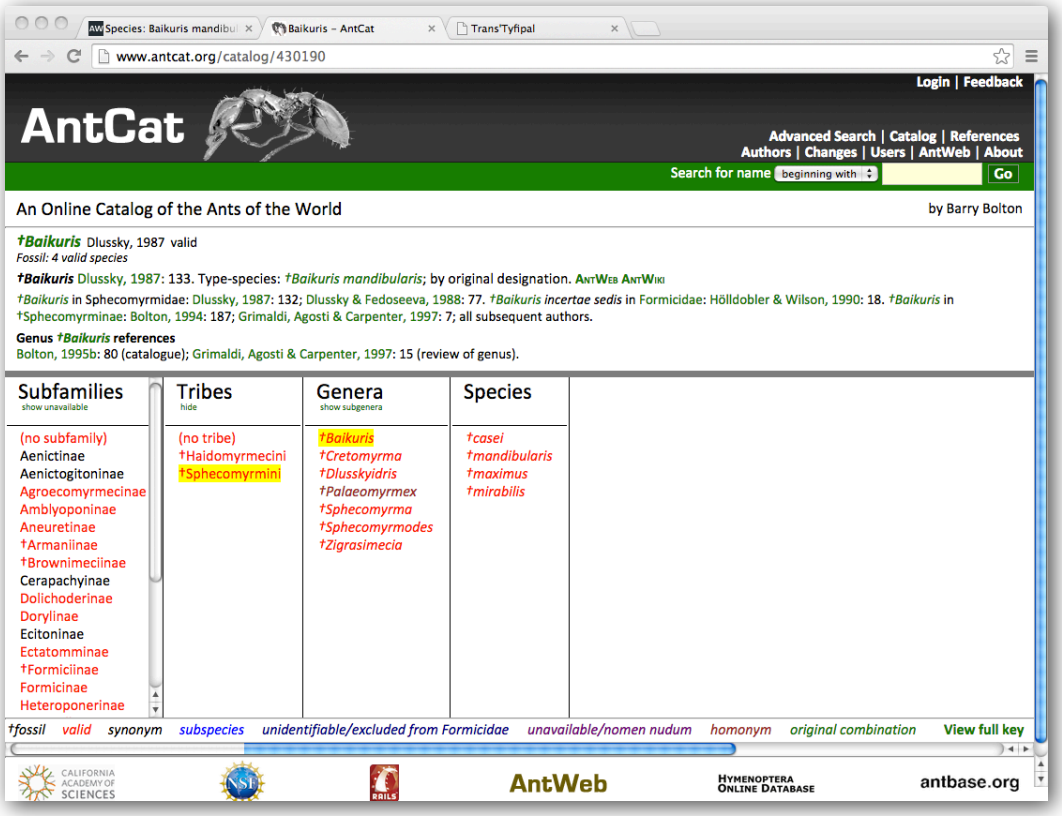
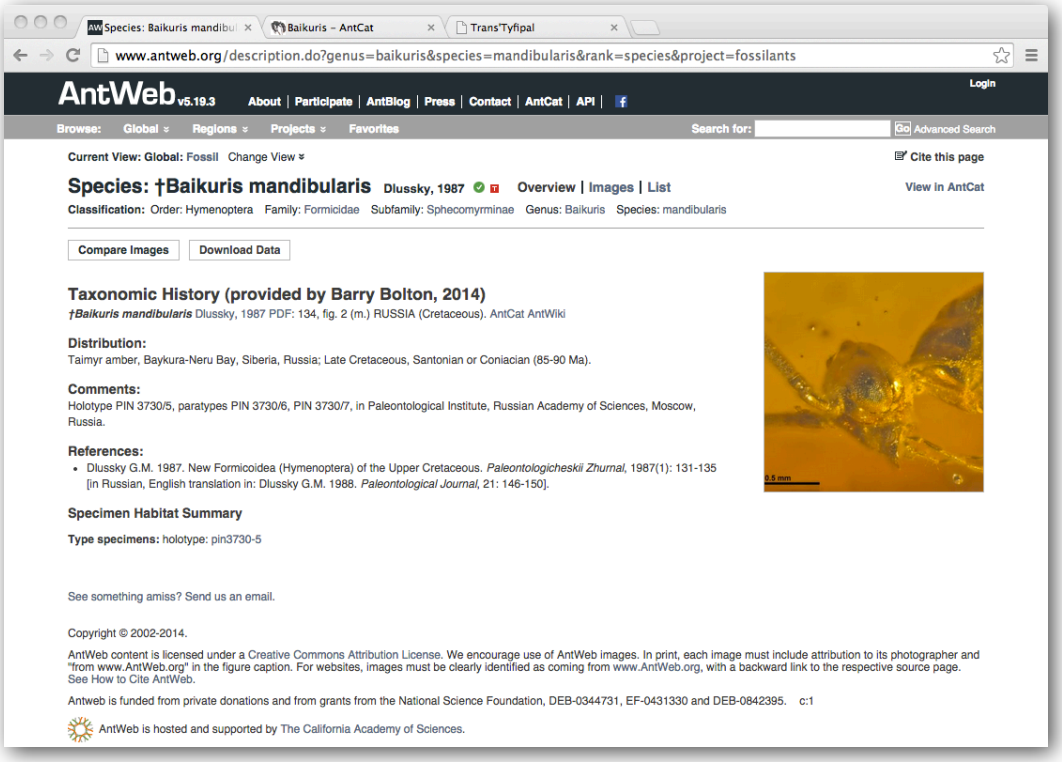


Figure 5
Un extrait de la section fossile du catalogue électronique AntWeb.



Expertises scientifiques

- Rapporteur de 46 articles scientifiques pour des revues en sciences multidisciplinaires ou bien spécialisées (tableau 2), avec une moyenne de 6 articles par an depuis 5 ans.
- Rapporteur de 4 projets de recherche pour : Fondation Estonienne de la Recherche ; Fondation Tchèque de la Recherche ; bourses Sepkoski (Paleontological Society International Research Program).

Catégories	Revues
Paléontologie	Acta Palaeontologica Polonica (2) Alcheringa (1) Annales de Paléontologie (1) Comptes Rendus Palevol (8) Geodiversitas (1) Journal of Paleontology (1) Journal of Systematic Palaeontology (3) Neues Jahrbuch für Geologie und Paläontologie (1) Palaeodiversity (1) Paläontologische Zeitschrift (1) Paleontological Contributions (1)
Entomologie	Alavesia (2) Annales de la Société Entomologique de France (1) Bulletin of the British Arachnological Society (1) Deutsche Entomologische Zeitschrift (1) Insect Systematics and Evolution (1) Systematic Entomology (1)
Géologie / Géosciences multidisciplinaires	Bulletin of Geosciences (1) Cretaceous Research (4) Geomicrobiology Journal (1)
Sciences multidisciplinaires	Naturwissenschaften (2) PLoS One (1) PNAS (1)
Zoologie	American Museum Novitates (2) ZooKeys (2) Zootaxa (3) Sociobiology (1)

Tableau 2
Synthèse des revues pour lesquelles j'ai été rapporteur de manuscrits (nombre d'articles donné entre parenthèses).

Jurys / comités scientifiques

- 2 jurys de thèse (J. Ortega-Blanco, 2010, Univ. Barcelone [*Président du jury*] ; J. Choufani, 2014, MNHN [co-directeur]).
- 1 comité de suivi de thèse (J.-D. Moreau, 2011-2014).
- 5 comités de sélection de postes MCF, sections CNU 35-36 et 67 (2012, 2013 : MNHN, UMRs 7205 et 7207 ; 2013, 2014 : Univ. Angers, UMR 6112).
- 1 comité de sélection des postes d'ATER, section CNU 35-36 (2012 : Géosciences Rennes).

Activités éditoriales

- Editeur associé de la revue *Paleontological Contributions* depuis 2012.
- Coordonnateur de deux volumes thématiques sur les ambres de France (fig. 6) : Perrichot V. & Néraudeau D. (eds.), 2009, *Geodiversitas,* vol. 31 ; Perrichot V. (ed.), 2014, *Paleontological Contributions*, vol. 10.

Vulgarisation scientifique

- Consultant scientifique pour l'exposition *1000 milliards de fourmis* (Palais de la découverte, Paris, octobre 2013 – août 2014 ; Espace des Sciences, Rennes, septembre 2014 – mai 2015).
- 2nd Fushun Amber Festival, Fushun City, Liaoning, Chine, septembre 2014 (une conférence).
- Diverses conférences publiques en métropole rennaise (Mardis de l'Espace des Sciences 2015 ; Fête de la science 2002, 2003 ; Festival des sciences 2010, 2012 ; Kiosque Citoyen 2012).
- Divers séminaires de laboratoires en France et à l'étranger (Nanjing Institute of Geology and Palaeontology, Chine, 2014; Univ. Pierre et Marie Curie, 2014 ; California Academy of Sciences, San Francisco, 2009 ; Univ. Kansas, 2008 ; Univ. Copenhague, 2007 ; Museum de Berlin, 2006 ; Univ. Bonn, 2006 ; Univ. Lyon 1, 2002).
- Conférences pour des associations naturalistes de l'Ouest de la France (Géocontact, 2014 ; SSNOF, 2002 ; AGMFO, 2001 ; CNER, 2000).
- Animation d'un stand de découverte des insectes fossiles pour la nuit des musées (*Die Lange Nacht*) au Muséum d'Histoire Naturelle de Berlin, 2007.
- Intervenant dans 2 reportages TV sur l'ambre ("Charentic Park", reportage pour les émissions *Bonjour l'ancêtre* (France 3) et *Les dessous de la Terre*, (la Cinquième), 2001 ; "L'ambre des dinosaures", rubrique Sciences de *Télématin* (France 2), 2010).

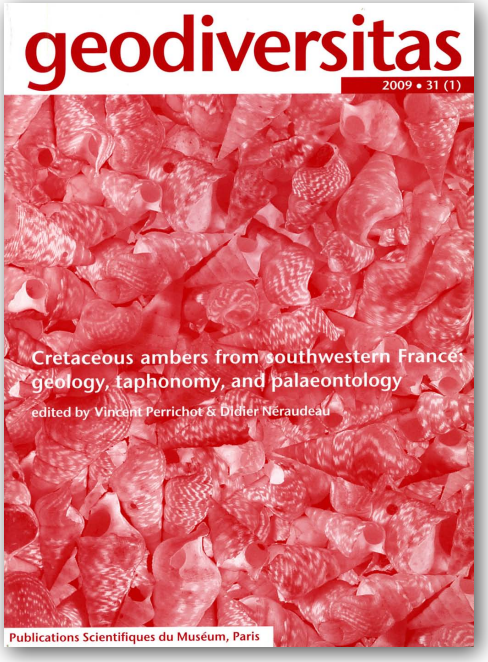


Figure 6 Premières de couvertures des deux volumes thématiques édités.

Deuxième partie

Synthèse des travaux

I. L'ambre : un fossile et un milieu de fossilisation

L'ambre est le produit fossile des résines exsudées à l'origine par des plantes, solidifiées au contact de l'air, puis altérées diagénétiquement par polymérisation et perte de composés volatiles (terpènes). La composition chimique des résines varie considérablement selon la nature des arbres producteurs, et la caractérisation de l'ambre en géochimie organique renseigne donc sur ses sources végétales et sur l'évolution paléobotanique des écosystèmes terrestres (Beck *et al*., 1964 ; Langenheim, 1969). L'ambre peut également préserver un signal géochimique inorganique (isotopes stables, éléments traces) et ainsi renseigner sur les conditions environnementales dans les écosystèmes résinifères (Nissenbaum *et al*., 2005 ; Aquilina *et al*., 2013).

Outre cet intérêt paléobotanique et celui paléoenvironnemental, liés à l'objet en lui-même, l'ambre présente également un grand intérêt paléontologique en tant que milieu de fossilisation car il peut contenir une grande variété d'inclusions organiques fossiles. Arthropodes, micro-organismes, feuilles, plumes, peaux, poils... ont parfois été emprisonnés il y a des millions d'années dans de la résine fraichement coulée, et nous sont aujourd'hui restitués dans l'ambre avec une qualité de préservation et une précision anatomique sans pareille dans le registre fossile. Ainsi les parties molles de certains organismes, habituellement détruites lors des processus de fossilisation, sont parfois conservées. Ces inclusions livrent des témoignages fossiles uniques de processus évolutifs précoces, par exemple un stade intermédiaire de développement des plumes (Perrichot *et al*., 2008), ou le cycle de vie de dinoflagellés (Masure *et al*., 2013).

L'ambre constitue ainsi une fenêtre exceptionnelle sur les écosystèmes du passé, et son étude peut intéresser des disciplines aussi variées que la (paléo)botanique, la (paléo)entomologie, la (paléo)microbiologie, ou la géochimie organique et inorganique.

II. Contexte géologique

L'ambre apparait dans le registre fossile dès le Carbonifère, sous forme de gouttelettes microscopiques visibles au sein des structures anatomiques de fougères à graines ou de Cordaïtales, plus rarement sous forme de grains millimétriques parsemés dans des blocs de charbon ou dans les sédiments (van Bergen *et al*., 1995 ; Bray & Anderson, 2009). Il se trouve toutefois en quantités infimes et dépourvu d'inclusions fossiles, dans le Carbonifère supérieur des Etats-Unis, d'Ecosse, de France, ou de République Tchèque (Smith, 1896 ; Lacroix, 1910 ; Jehlicka *et al*., 2004 ; Nel *et al*., 2004 ; Bray & Anderson, 2009 ; Onoratini *et al*., 2009). La formation d'ambre reste semble t'il marginale jusqu'au Crétacé (fig. 7) : quelques rares morceaux isolés ont été signalés dans le Permien d'Italie et de Russie (Grimaldi, 1996 ; Trevisani & Ragazzi, 2013) ; de rares localités sont signalées au Trias, et seul un gisement carnien d'Italie a livré une grande quantité de gouttelettes fossilifères, contenant de nombreux micro-organismes mais de rares arthropodes (Schmidt *et al*., 2006, 2012) ; enfin, quelques gisements sont mentionnés dans le Jurassique mais ne livrent que de faibles quantités non fossilifères (Philippe *et al*., 2005 ; Azar *et al*., 2010a ; Nohra *et al*., 2012 ; Trevisani & Ragazzi, 2013). Finalement ce sont les gisements du Crétacé inférieur proche-oriental (Liban, Jordanie) qui constituent les premiers ambres vraiment riches en arthropodes fossiles (Poinar & Milki, 2001 ; Kaddumi, 2005 ; Azar *et al*., 2010b). Dans l'ensemble le Crétacé a été la première période favorable à la formation et la préservation abondante d'ambre, puisque plusieurs gisements très fossilifères sont répertoriés entre le Barrémien et le Campanien. Les gisements cénomaniens du Myanmar sont les plus riches du Crétacé. Ils sont aussi les plus anciens à pouvoir être exploités industriellement, tant pour leur contenu paléontologique que pour la joaillerie, l'art décoratif, et de prétendues vertus médicinales. Suite à cette période faste, peu de données sont disponibles autour de la transition Crétacé-Tertiaire (Maastrichtien-Paléocène), et seul un gisement russe de l'île de Sakhalin a livré des arthropodes fossiles (Zherikhin & Eskov, 1999). Une deuxième période majeure pour l'ambre intervient à l'Eocène, visiblement la plus prolifique de tous les temps. En région balte, où l'ambre éocène est extrait depuis plus de 150 ans, la quantité encore disponible aujourd'hui dans la seule région de Yantarnyi, en province russe du Samland, est estimée à 640000 tonnes (Weitschat & Wichard, 2002) ! Pas moins de 510 tonnes ont été extraites pour la seule année 2000 et, actuellement, environ 2 millions d'inclusions fossiles nouvelles sont potentiellement disponibles chaque année pour étude, selon une estimation (Clark, 2010). Enfin, un dernier épisode majeur de production d'ambre apparait au Miocène.

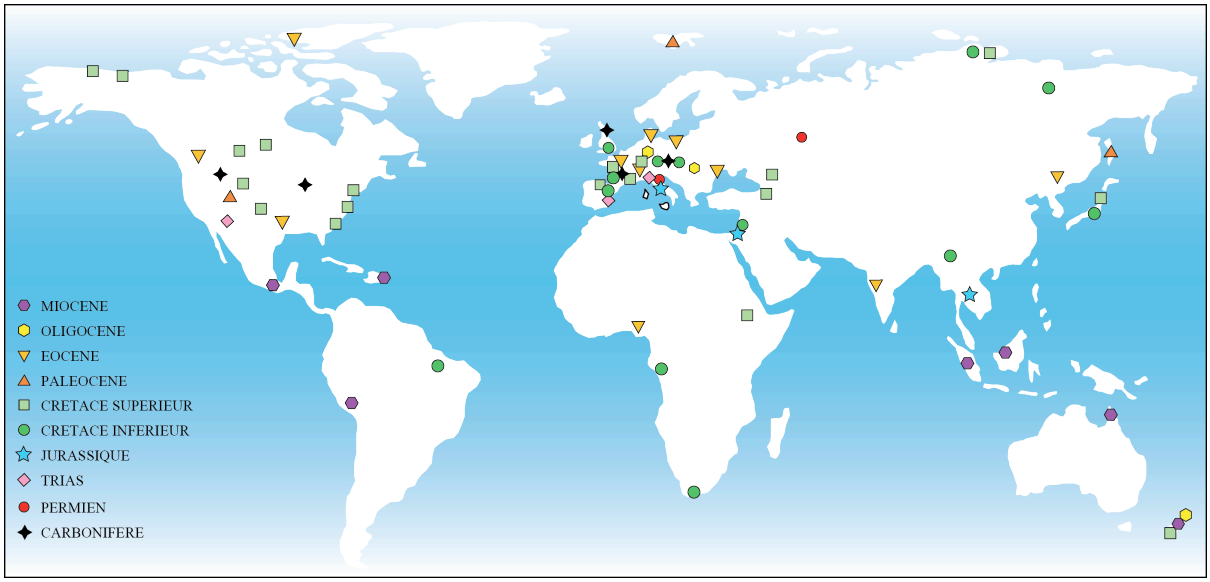


Figure 7 Distribution géographique et stratigraphique des gisements d'ambre dans le monde.

III. Démarche scientifique

3.1. Axes de recherche

Au vu du contexte géologique, les géochimistes s'intéresseront à tout type d'ambre quel que soit son âge, alors que les paléontologues seront davantage restreints à l'étude des ambres fossilifères. Ma démarche depuis bientôt 15 ans s'inscrit surtout dans ce dernier cas. Mes travaux ont porté majoritairement sur des aspects biologiques et géologiques, et je me suis particulièrement intéressé : 1/ à l'origine et l'histoire évolutive des insectes ; 2/ à l'évolution des écosystèmes résinifères ; et 3/ à des préservations exceptionnelles trouvées dans l'ambre.

J'ai abordé l'histoire évolutive des insectes au travers des nombreuses inclusions fossiles mises à jour dans l'ambre. J'ai eu l'opportunité de travailler sur plusieurs gisements inédits et provenant de régions jusqu'alors dépourvues de données paléoentomologiques, aussi la presque totalité des arthropodes fossilisés en inclusions que j'ai pu découvrir étaient nouveaux pour la science. Comme évoqué en première partie de ce mémoire (fig. 1), une large part de mes activités a donc consisté en la description systématique de taxons nouveaux, un préalable nécessaire à toute analyse phylogénétique, paléobiologique, paléoécologique, ou encore paléobiogéographique. Dans la mesure du possible, je me suis efforcé chaque fois de replacer ces insectes dans un contexte global relativement à leur groupe d'appartenance, réunissant les données fossiles et actuelles afin d'extraire les informations d'ordre évolutif.

Dans la suite logique de cette démarche, et toujours dans l'optique de mieux cerner l'histoire évolutive des insectes, j'ai cherché à replacer ces entomofaunes dans leurs écosystèmes. J'ai collaboré pour cela avec des microbiologistes afin d'analyser le contenu des ambres en micro-organismes, qui sont d'excellents marqueurs de leur environnement. Leur paléoécologie permet bien souvent de préciser le type d'environnement dans lequel la résine a été produite, et donc de situer les écosystèmes forestiers résinifères dans leur milieu de vie plutôt que le milieu de dépôt de l'ambre (ce dernier étant plutôt appréhendé par des analyses sédimentologiques des gisements). L'étude combinée des arthropodes et des micro-organismes de l'ambre des Charentes était par exemple l'objet principal de mes recherches post-doctorales avec Alexander Schmidt, au Muséum d'histoire naturelle de Berlin. Nous avons complété nos analyses avec des études taphonomiques (actuo-paléontologie dans des forêts résinifères actuelles) afin de comprendre les processus de production de résine et de piégeage d'organismes dans différents types d'environnements forestiers.

Une autre étape dans la reconstitution des écosystèmes consiste à identifier les plantes productrices de la résine. Je me suis appuyé d'une part sur les données associées à l'ambre (restes de plantes fossilisées en inclusion ou dans les sédiments encaissants) et fournies par les paléobotanistes, d'autre part sur la chimie de

l'ambre. C'est la raison pour laquelle j'encadre actuellement une thèse portant sur la "caractérisation chimique des résines végétales actuelles et fossiles" (thèse en co-tutelle France/Liban, par Youssef Nohra).

Enfin en certaines occasions, j'ai été confronté à des cas de préservation à caractère exceptionnel, quasi exclusif à l'ambre (restes de vertébrés, champignons, organismes aquatiques). L'étude de ces inclusions m'est apparue importante d'un point de vue paléontologique, fournissant des éléments primordiaux sur certains processus évolutifs ou bien d'ordre paléoécologique. Elle constituait aussi un défi personnel très stimulant sur des organismes hors de mon champ d'expertise habituel.

La variété des thématiques abordées au cours de mes recherches m'a conduit à développer un certain nombre de coopérations nationales et internationales, dont les principales sont résumées ci-dessous (tableau 3).

Discipline/chercheur	Affiliation actuelle	Etudes conjointes
Entomologie		
André Nel	MNHN, Paris	Insectes des ambres de France
Dany Azar	Univ. Libanaise, Beyrouth	Diptères, Neuroptères, Psocoptères (ambre de France, du Liban)
Michael Engel	Univ. Kansas, USA	Hyménoptères, Dermaptères (ambres crétacés, tertiaires)
Xavier Delclòs	Univ. Barcelone, Espagne	Hyménoptères (ambre d'Espagne)
Jaume Ortega-Blanco	Univ. Barcelone, Espagne	Hyménoptères (ambre d'Espagne)
Uwe Kaulfuss	Univ. d'Otago, Nouvelle-Zélande	Hyménoptères (ambre de Nouvelle-Zélande)
Microbiologie		
Alexander Schmidt	Univ. Göttingen, Allemagne	Champignons, amibes, diatomées (ambre de France, d'Ethiopie)
Vincent Girard	Univ. Montpellier 2	Microalgues des ambres de France
Simona Saint Martin	MNHN, Paris	Diatomées des ambres de France
Géologie		
Didier Néraudeau	Univ. Rennes 1	Gisements de France
Vincent Delhaye-Prat	Total E&P Congo	Gisements du Congo
Paléobotanique		
Anais Boura	MNHN/UPMC, Paris	Bois fossiles (gisements de France, du Congo)
Marc Philippe	Univ. Lyon 1	Bois fossiles (gisements de France)
Taphonomie		
Alexander Schmidt	Univ. Göttingen, Allemagne	Ecosystèmes résinifères (Nouvelle-Calédonie, Nouvelle-Zélande)
Chimie de l'ambre		
Laurent Jeanneau	Univ. Rennes 1	Py-GC-MS
Laurent Le Polles	ENS Chimie, Rennes	RMN ^{13}C et ^{1}H
Eugenio Ragazzi	Univ. Padoue, Italie	Thermogravimétrie
Tomographie RX		
Paul Tafforeau	ESRF Grenoble	Imagerie 3D des inclusions de l'ambre
Carmen Soriano	Argonne National Lab, Chicago	Imagerie 3D des insectes de l'ambre

Tableau 3 Principales coopérations nationales et internationales développées au cours de mes recherches.

3.2. Les régions d'intérêt

La paléoentomologie est une discipline ancienne initiée dans la première moitié du 19e siècle (Curtis, 1829 ; Berendt, 1830) mais qui s'est globalisée depuis les années 1990 seulement (Nel *et al.*, 2010). Les insectes carbonifères et cénozoïques étaient relativement bien documentés dès le début du 20e siècle mais les données sur les entomofaunes crétacées sont restées très lacunaires jusque récemment (Szwedo & Nel, 2015). La découverte de nombreux gisements insectifères (ambre ou empreintes dans les roches) depuis 20 ans comble progressivement ces lacunes, mais de manière très inégale selon les régions biogéographiques.

En France, il faut attendre les années 70 pour voir les premières descriptions taxonomiques d'insectes crétacés, et au total moins de 40 espèces furent publiées, exclusivement de l'ambre cénomanien d'Anjou (Kühne *et al.*, 1973 ; Schlüter, 1978, 1989). Les empreintes dans les roches sont encore plus rares, puisque

seuls une dizaine de fossiles ont été récemment trouvés dans deux gisements cénomaniens en Charente-Maritime et dans la Vienne (Nel *et al*., 2008, 2015). Une étude plus poussée des gisements insectifères français prenait donc tout son sens afin de documenter une lacune tant géographique que stratigraphique dans l'histoire des arthropodes terrestres. Mes travaux en DEA et en thèse ont focalisé exclusivement sur les ambres du Crétacé des Charentes, mentionnés dès le 19e siècle (Fleuriau de Bellevue, 1823 ; Coquand, 1856) mais dont le potentiel fossilifère n'a étrangement été découvert qu'en 1999. L'exploitation de ces gisements s'est faite conjointement avec l'équipe de paléoentomologie du MNHN (A. Nel, G. de Ploëg) qui entamait parallèlement l'étude des gisements éocènes de l'Oise (Nel *et al*., 1999). Les équipes de Géosciences Rennes et du MNHN ont alors entamé une vaste prospection des gisements d'ambres français, qui a abouti à la découverte ou la re-découverte de 10 gisements crétacés fossilifères à ce jour (Néraudeau *et al*., 2002, 2003, 2008 ; Perrichot *et al*., 2007a ; Girard *et al*., 2013 ; Perrichot & Néraudeau, 2014). Leur étude a livré environ 2000 arthropodes fossiles, principalement dans l'ambre albien-cénomanien des Charentes. J'ai ainsi montré que les gisements charentais constituent l'un des gisements majeurs d'ambre crétacé dans le monde (Perrichot *et al*., 2007b, 2010).

Par la suite, j'ai élargi mes investigations à une quinzaine de gisements mésozoïques et cénozoïques à travers le monde, particulièrement ceux du Crétacé moyen et de l'Eocène, et dans une moindre mesure ceux du Miocène (figs. 8, 9). A la faveur de mes travaux post-doctoraux, des opportunités se sont présentées d'étudier des insectes, surtout hyménoptères, répertoriés dans des collections préexistantes de divers gisements. J'ai particulièrement développé l'étude de gisements proches des ambres de France temporellement ou géographiquement (Crétacé d'Espagne et du Myanmar; Eocène d'Europe) afin d'en extraire des informations sur l'évolution biogéographique des entomofaunes. Pour les ambres cénozoïques, c'est surtout l'étude de l'évolution des hyménoptères qui a motivé mes contributions.

Enfin j'ai été sollicité pour participer à l'étude globale de deux gisements récemment découverts en Afrique (Ethiopie et Congo). Les paléoentomofaunes africaines sont encore particulièrement méconnues puisqu'à l'exception de l'ambre néocomien du Liban (alors rattaché au continent africain), seuls deux autres gisements ont jusqu'à présent livré un nombre conséquent d'insectes en empreintes, dans le Trias d'Afrique du Sud et le Turonien du Botswana (Brothers & Rasnitsyn, 2003 ; Schlüter, 2003). La découverte de nouveaux jalons fossiles sur le continent africain est donc primordiale.

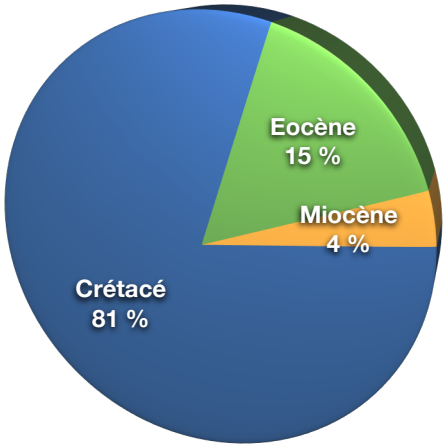
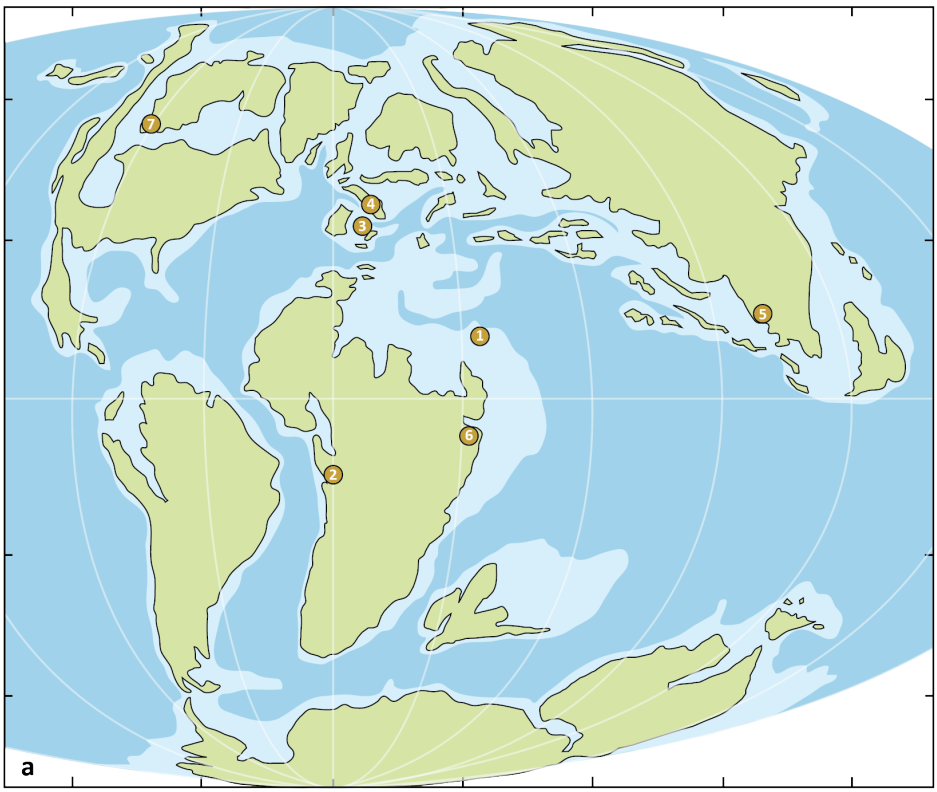
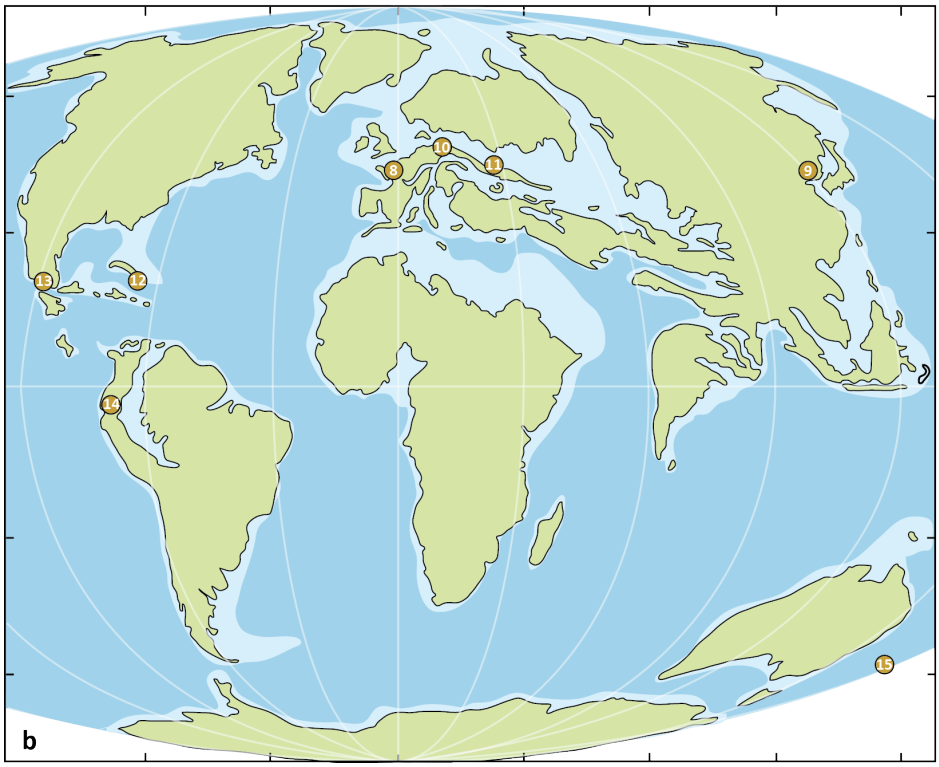


Figure 8
Proportions relatives des époques géologiques considérées dans mes travaux.

Figure 9, page de gauche
Distribution paléogéographique et stratigraphique des gisements étudiés au cours de mes recherches, positionnés **a/** sur une carte du Crétacé moyen (Albien, 105 Ma) ; **b/** sur une carte de l'Eocène inférieur (50 Ma) – cartes modifiées d'après Blakey (2011).



1 Liban (120-130 Ma)
2 Congo (113-117 Ma)
3 Espagne (110 Ma)
4 France (85, 95, et 100 Ma)
5 Myanmar (100 Ma)
6 Ethiopie (93-95 Ma)
7 Canada (78-79 Ma)



8 France (53 Ma)
9 Chine (50-53 Ma)
10 Baltique (37-45 Ma)
11 Ukraine (37-45 Ma)
12 Rép. Dominicaine (16-19 Ma)
13 Mexique (16-19 Ma)
14 Pérou (12-15 Ma)
15 Nouvelle-Zélande (17-23 Ma)

3.3. Les groupes d'intérêt

Durant ma thèse, j'ai été formé à la fois à la taxonomie des bois de conifères et à celle des insectes. Par la suite, j'ai centré mes travaux taxonomiques presque exclusivement sur les insectes, à l'exception de quelques crustacés et champignons trouvés en inclusions dans l'ambre (fig. 10a).

Les insectes (classe des Hexapodes) représentent environ 55% de la biodiversité actuelle, 85% de celle des animaux (Grimaldi & Engel, 2005). Leur extraordinaire diversité leur permet d'occuper une place prépondérante dans les écosystèmes terrestres. Au vu des spécificités anatomiques, biologiques, et écologiques de chaque ordre, les (paléo)entomologistes se spécialisent le plus souvent sur l'un ou quelques uns d'entre eux. J'ai débuté comme "généraliste" sans ordre privilégié, plutôt guidé par le fil de mes découvertes dans les gisements français étudiés, puis j'ai eu un intérêt grandissant pour les hyménoptères (fig. 10b). Mes recherches post-doctorales à l'Université du Kansas focalisaient ainsi sur l'origine et l'évolution de cet ordre. Guêpes et fourmis sont aujourd'hui mes groupes de prédilection sur les études que je supervise, même si je participe encore à l'étude d'autres ordres en coopération avec leurs différents spécialistes (tableau 4).

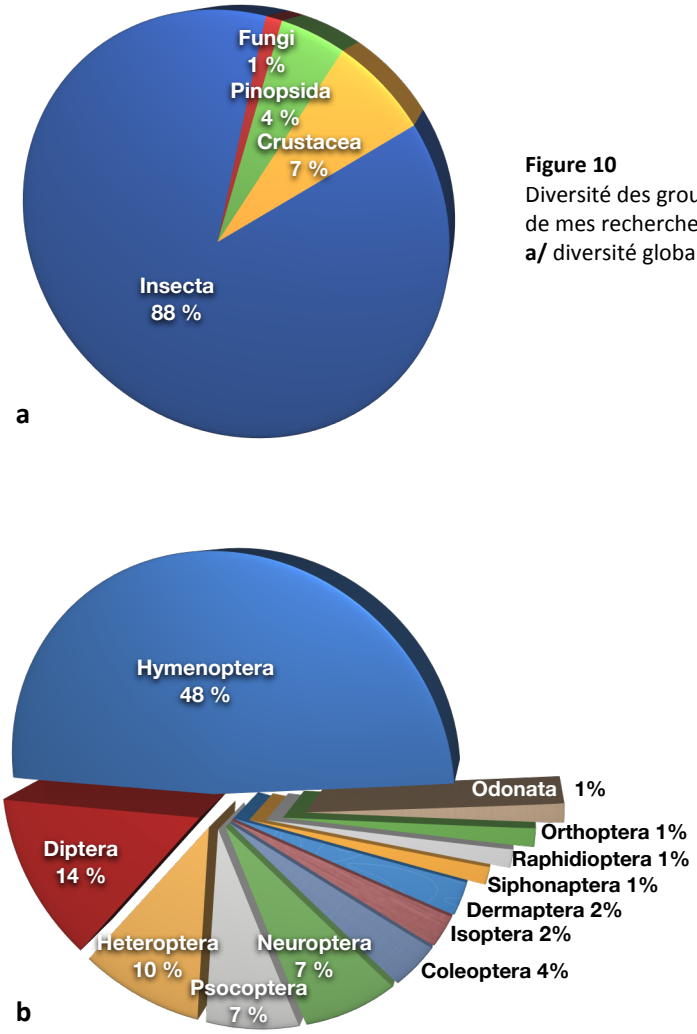


Figure 10
Diversité des groupes taxonomiques étudiés au cours de mes recherches.
a/ diversité globale ; **b/** ordres d'insectes.

Phylum Ordre	Famille	Taxon	Gisement
Fungi			
Deuteromycotina		*Palaeoanellus dimorphus* Schmidt, Dörfelt & Perrichot 2008	Charentes [C1-2]
Arthropoda			
Crustacea			
Tanaidacea	Alavatanaidae	*Eurotanais* sp. A Sánchez-García, Peñalver & Perrichot 2015	Pyrénées [C2]
		Eurotanais sp. B Sánchez-García, Peñalver & Perrichot 2015	Vendée [C2]
		Gen. A sp. A Sánchez-García, Peñalver & Perrichot 2015	Charentes [C1-2]
	Paratanaidae	Gen. B sp. A Sánchez-García, Peñalver & Perrichot 2015	Pyrénées [C2]
		Gen. B sp. B Sánchez-García, Peñalver & Perrichot 2015	Charentes [C1-2]
		Gen. C sp. A Sánchez-García, Peñalver & Perrichot 2015	Pyrénées [C2]
Insecta			
Coleoptera	Bostrichidae	*Stephanopachys vetus* Peris, Delclòs & Perrichot, 2014	Charentes [C1-2]
	Ripiphoridae	*Macrosiagon ebboi* Perrichot, Nel & Néraudeau 2004	Provence [C2}
		Paleoripiphorus deploegi Perrichot, Nel & Néraudeau 2004	Charentes [C1-2]
Dermaptera	Pygidicranidae	*Gallinympha walleri* Perrichot & Engel 2011	Charentes [C1-2]
	Indet.	*Vendeenympha gravesi* Engel & Perrichot 2014	Vendée [C2]
Diptera	Athericidae	*Galloatherix incompletus* Nel, de Ploëg & Perrichot 2014	Charentes [C1-2]
	Ceratopogonidae	*Culicoides doyeni* Choufani, Perrichot, Azar & Nel 2014	Vendée [C2]
		Leptoconops gravesi Choufani, Perrichot, Azar & Nel 2014	Vendée [C2]
		Leptoconops sp. A Choufani, Perrichot, Azar & Nel 2014	Vendée [C2]
	Dolichopodidae	*Microphorites deploegi* Nel, Perrichot, Daugeron & Néraudeau 2004	Charentes [C1-2]
		Microphorites magaliae Perrichot & Engel 2014	Vendée [C2]
	Limoniidae	*Antodicranomyia azari* Perrichot, Nel & Krzeminski 2007	Charentes [C1-2]
	Phoridae	*Prioriphora schroederhohenwarthi* Solórzano Kraemer & Perrichot 2011	Charentes [C1-2]
	Psychodidae	*Eophlebotomus carentonensis* Azar, Perrichot, Néraudeau & Nel 2003	Charentes [C1-2]
		Sycorax neli Azar, Tahchy & Perrichot 2007	Charentes [C1-2]
	Scatopsidae	*Ectaetia capdoliensis* Fate, Perrichot & Nel 2013	Charentes [C1-2]
Heteroptera	Ebboidae	*Ebboa areolata* Perrichot, Nel, Guilbert & Néraudeau 2006	Charentes, Provence [C2]
	Gerridae	*Cretogerris albianus* Perrichot, Nel & Néraudeau 2005	Charentes [C1-2]
	Mesoveliidae	*Emilianovelia audax* Solórzano Kraemer & Perrichot 2014	Charentes [C1-2]
		Malenavelia videris Solórzano Kraemer & Perrichot 2014	Charentes [C1-2]
	Schizopteridae	*Buzinia couillardi* Perrichot, Nel & Néraudeau 2007	Charentes [C1-2]
		Tanaia burmitica Perrichot, Nel & Néraudeau 2007	Myanmar [C1-2]
	Tingidae	*Ambarcader eugenei* Perrichot, Nel & Guilbert 2005	Charentes [C1-2]
	Veliidae	*Arcantivelia petraudi* Solórzano Kraemer & Perrichot 2014	Charentes [C1-2]
Hymenoptera	Bethylidae	*Electroepyris magnificus* Perrichot & Nel 2008	Oise [E]
		Rhabdepyris gallicus Perrichot & Nel 2008	Oise [E]
		Epyrini indet. Perrichot & Nel 2008	Oise [E]
	Braconidae	*Aenigmabracon capdoliensis* Perrichot, Nel & Quicke 2009	Charentes [C1-2]
		Protorhyssalodes arnaudi Perrichot, Nel & Quicke 2009	Charentes [C1-2]
	Crabronidae	*Menopsila dupeae* Bennett, Perrichot & Engel, 2014	Vendée [C2]
	Diapriidae	*Gaugainia electrogallica* Perrichot & Nel 2008	Charentes [C1-2]
	Embolemidae	*Embolemus excitus* Perrichot & Engel 2011	Baltique [E]
	Falsiformicidae	Sous-famille n. Perrichot & Engel 2015	Liban [C1]
		Gen. A sp. A Perrichot & Engel 2015	Liban [C1]
		Gen. B sp. A Perrichot & Engel 2015	Myanmar [C1-2]
		Gen. B sp. B Ortega Blanco, Perrichot & Engel 2015	Espagne [C1]
		Falsiformica sp. A Perrichot, Nel & Engel 2015	Pyrénées [C2]
...		*Falsiformica* sp. B Perrichot & Nel 2015	Charentes [C1-2]

Tableau 4 Liste des taxons nouveaux décrits au cours de mes recherches et leur provenance (taxons surlignés ; Abbréviations : C1, Crétacé inférieur ; C1-2, limite Crétacé inférieur / supérieur ; C2, Crétacé supérieur ; E, Eocène ; M, Miocène).

Phylum Ordre	Famille	Taxon	Gisement
Hymenoptera (suite)	Formicidae	*Baikuris maximus* Perrichot 2014	Charentes [C1-2]
		Gen. A sp. A Perrichot & Engel 2015	Myanmar [C1-2]
		Haidomyrmodes mammuthus Perrichot *et al.* 2008	Charentes [C1-2]
		Platythyrea dlusskyi Aria, Perrichot & Nel 2011	Oise [E]
		Ponerinae gen. et sp. indet. Aria, Perrichot & Nel 2011	Oise [E]
		Sphecomyrmodes occidentalis Perrichot *et al.* 2008	Charentes [C1-2]
		Technomyrmex sp. A Perrichot & Engel 2015	Ethiopie [M]
		Zigrasimecia ferox Perrichot 2014	Myanmar [C1-2]
	Maimetshidae	*Ahiromaimetsha najlae* Perrichot, Azar, Nel & Engel 2011	Liban [C1]
		Burmaimetsha concava Perrichot 2013	Myanmar [C1-2]
		Guyotemaimetsha enigmatica Perrichot, Nel & Néraudeau 2004	Charentes [C1-2]
		Iberomaimetsha rasnitsyni Ortega-Blanco, Perrichot & Engel, 2011	Espagne [C1]
		Maimetshasia kachinensis Perrichot 2013	Myanmar [C1-2]
	Megalyridae	*Megallica parva* Perrichot 2009	Charentes [C1-2]
		Megazar elegans Perrichot 2009	Charentes [C1-2]
		Megalava truncata Perrichot 2009	Espagne [C1]
		Prodinapsis eosiensis Perrichot 2009	Oise [E]
		Prodinapsis pumilio Perrichot 2009	Baltique [E]
		Prodinapsis janzeni Perrichot 2009	Baltique [E]
		Rubes bruesi Perrichot 2009	Baltique [E]
		Ukrainosa prolata Perrichot & Perkovsky 2009	Ukraine [E]
		Valaa delclosi Perrichot 2009	Espagne [C1]
	Platygastridae	*Macroteleia yaguarum* Perrichot & Engel 2014	Pérou [M]
	Trigonalyidae	*Albiogonalys elongatus* Nel, Perrichot & Néraudeau 2003	Charentes [C1-2]
	Serphitidae	*Serphites fannyae* Engel & Perrichot 2014	Vendée [C2]
Isoptera		*Santonitermes chloeae* Engel, Nel & Perrichot 2011	Charentes [C1-2]
		Syagryotermes salomeae Engel, Nel & Perrichot 2011	Charentes [C1-2]
Neuroptera	Rhachiberothidae	Paraberothinae Nel, Perrichot, Azar & Néraudeau 2005	Charentes [C1-2]
		Alboberotha petrulevicii Nel, Perrichot, Azar & Néraudeau 2005	Charentes [C1-2]
		Chimerhachiberotha acrasarii Nel, Perrichot, Azar & Néraudeau 2005	Liban [C1]
		Oisea celinea Nel, Perrichot, Azar & Néraudeau 2005	Oise [E]
		Spinoberotha mickaelacrai Nel, Perrichot, Azar & Néraudeau 2005	Liban [C1]
	Coniopterygidae	*Alboconis cretacica* Nel, Perrichot & Azar 2005	Charentes [C1-2]
		Garnaconis dupeorum Perrichot & Nel 2014	Vendée [C2]
Odonata	Enigmaeshnidae	*Enigmaeshna deprei* Nel *et al.* 2008	Charentes [C1-2]
Orthoptera	Gryllotalpidae	*Marchandia magnifica* Perrichot *et al.* 2002	Charentes [C1-2]
Psocoptera	Archaeatropidae	*Proprionoglaris axioperierga* Azar, Nel & Perrichot 2014	Vendée [C2]
		Proprionoglaris guyoti Perrichot, Azar, Néraudeau & Nel 2003	Charentes [C1-2]
		Prospeleketor albianensis Perrichot, Azar, Néraudeau & Nel 2003	Charentes [C1-2]
		Parapsyllipsocus vergereaui Perrichot, Azar, Néraudeau & Nel 2003	Charentes [C1-2]
	Compsocidae	*Scocompus atelisus* Azar, Nel & Perrichot 2014	Vendée [C2]
	Mesopsocidae	*Mesopsocoides dupei* Azar, Nel & Perrichot 2014	Vendée [C2]
Raphidioptera	Mesoraphidiidae	sp. A Perrichot & Engel 2007	Charentes [C1-2]
Siphonaptera	Pulicidae	*Eospilopsyllus kobberti* Beaucournu & Perrichot 2012	Rép. Dominicaine [M]
TOTAL, décrits	**2 familles**	**2 sous-familles, 54 genres, 86 espèces**	

Tableau 4 (suite) Liste des taxons nouveaux décrits au cours de mes recherches et leur provenance (taxons surlignés ; Abbréviations : C1, Crétacé inférieur ; C1-2, limite Crétacé inférieur / supérieur ; C2, Crétacé supérieur ; E, Eocène ; M, Miocène).

IV. L'évolution des insectes

Notre connaissance des insectes et de leur histoire évolutive s'est véritablement accrue depuis 20 ans grâce au développement d'analyses phylogénétiques des caractères morphologiques et/ou moléculaires, et grâce à la découverte de plusieurs gisements fournissant une pléthore d'arthropodes fossiles (Lagerstätten). Depuis leur origine, vraisemblablement au cours du Dévonien inférieur (Engel & Grimaldi, 2005 ; Garrouste *et al*., 2012), l'évolution des insectes a procédé de quatre innovations majeures, chacune suivie d'une phase de diversification remarquable : 1/ l'apparition de l'aile et du vol au Dévonien (Misof *et al*., 2014) ; 2/ le développement du stade nymphal (holométabolie) au Carbonifère (Nel *et al*., 2013) ; 3/ le développement de la pollinisation liée aux angiospermes au Crétacé inférieur (Hu *et al*., 2008 ; Labandeira & Currano, 2013); et 4/ le développement de l'eusocialité au Crétacé inférieur (Wilson & Hölldobler, 2005). La transition Crétacé inférieur – Crétacé supérieur est donc une période cruciale dans l'évolution des insectes, marquée par la coexistence des dernières familles 'primitives' aujourd'hui éteintes et l'apparition de la plupart des familles modernes. Les genres modernes apparaissent quant à eux plutôt à partir de l'Eocène. L'ambre fournit des jalons fossiles à divers moments du Crétacé et du Cénozoïque, entre 130 et 12 millions d'années, livrant ainsi des informations sur les phases 'modernes' de l'évolution des entomofaunes. Quelques exemples de mes travaux sont présentés ci-après, sur l'évolution crétacée de deux familles d'hyménoptères au destin opposé.

4.1. Fausses fourmis

Les Falsiformicidae sont une famille de guêpes crétacées, connue jusqu'à présent par la seule espèce *Falsiformica cretacea* Rasnitsyn, 1975, et décrite sur la base de deux spécimens incomplets fossilisés dans l'ambre cénomanien du Taimyr, en Russie (Rasnitsyn, 1975). L'holotype femelle manque la tête alors que le paratype mâle manque les ailes, la partie postéro-dorsale du thorax, et tout l'abdomen. L'affinité précise des Falsiformicidae était alors compliquée à établir. Selon Rasnitsyn (1975), les Falsiformicidae possédaient des caractères des guêpes Chrysidoidea, mais il pensait leur affinité plus grande avec les 'Scolioidea' (= Vespoidea *partim*.). Malgré la présence d'un pétiole bien défini et d'antennes coudées après le premier segment (fig. 11), deux caractéres diagnostiques des fourmis, Rasnitsyn (1975) considérait que la famille n'était pas immédiatement liée aux fourmis, d'où son choix du nom 'fausses fourmis'. Mais les Scolioidea étant un groupe paraphylétique dans le système de classification de Rasnitsyn, ce dernier notait plus tard (Rasnitsyn, 2002) la possibilité que la lignée soit un groupe-frère des fourmis (Formicidae *s.l*. [= Formicidae *s.str*. + Armaniidae]).

Au cours de mes recherches, j'ai eu la surprise de découvrir de nouveaux spécimens de Falsiformicidae dans l'ambre albien-cénomanien des Charentes et l'ambre cénomanien de l'Aude. Puis des investigations complémentaires dans les collections d'autres institutions ont révélé la présence de cette famille dans les ambres du Liban (Barrémien-Aptien), d'Espagne (Albien), et du Myanmar (Cénomanien). Au total plus de 40 spécimens supplémentaires ont été découverts, attribuables à deux nouveaux genres et cinq nouvelles espèces dont deux de *Falsiformica* (Perrichot *et al*., soumis). Plusieurs de ces spécimens ont été scannés en microtomographie par rayons X et des reconstructions virtuelles 3D ont été réalisées (fig. 11), permettant de visualiser et coder un grand nombre de caractères morphologiques pour une analyse phylogénétique de la famille. Les résultats indiquent que les Falsiformicidae sont clairement apparentés aux Chrysidoidea plutôt qu'aux Vespoidea (fig. 12), et que les caractères partagés avec les fourmis résultent d'une convergence morphologique.

Ces fossiles supplémentaires indiquent que la lignée des Falsiformicidae a existé pendant au moins 35 millions d'années autour de la transition Crétacé inférieur – Crétacé supérieur, avec une large distribution géographique, principalement eurasiatique. La chronologie de leur origine reste énigmatique puisqu'ils sont totalement absents des gisements pourtant riches de la fin du Jurassique supérieur et du début du Crétacé inférieur, mais ces gisements livrent des empreintes dans les roches et les Falsiformicidae ne sont jusqu'à présent fossilisés que dans l'ambre. Leur présence dans l'ambre du Liban suggère qu'ils pouvaient être plus largement répartis en Afrique, mais les rares gisements crétacés africains en sont dépourvus. De même, leur absence dans les ambres d'Amérique du Nord (Turonien du New Jersey et Campanien du Canada) pourrait indiquer qu'ils étaient restreints à la partie eurasiatique de Laurasie, mais leur absence dans les gisements eurasiatiques post-cénomaniens (Santonien de Vendée, de Provence, de Russie ; Turonien du Kazakhstan)

suggère une possible extinction entre le Cénomanien et le Santonien. Finalement les Falsiformicidae auront été un groupe un temps florissant de guêpes vraisemblablement parasitoïdes mais ne s'étant pas adapté aux changements globaux des écosystèmes terrestres initiés à la fin du Crétacé inférieur.

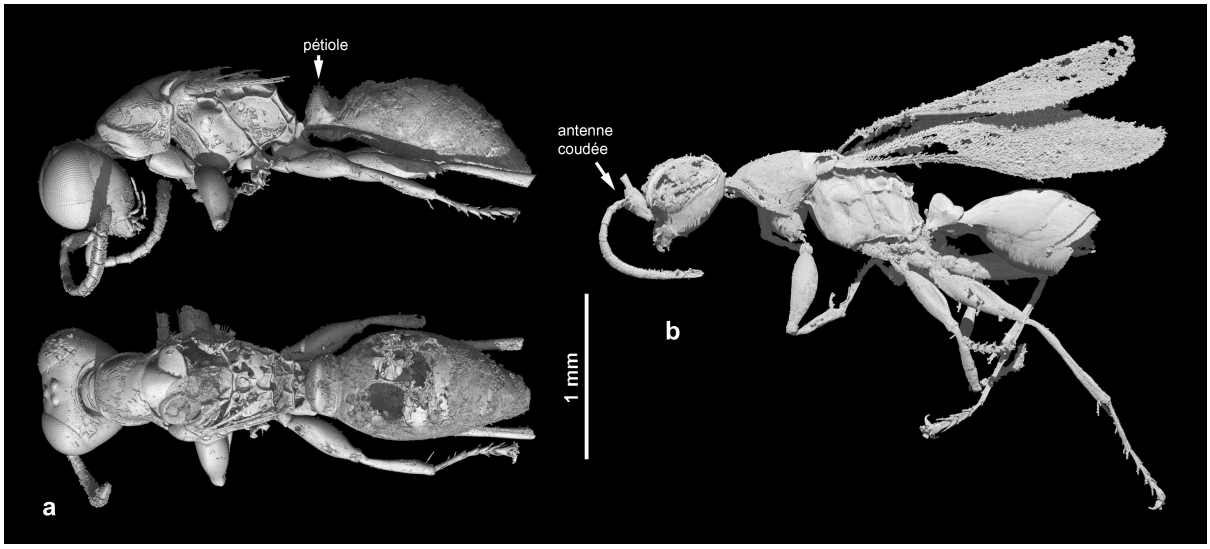


Figure 11 Reconstructions 3D de guêpes Falsiformicidae (Hymenoptera) fossilisées dans l'ambre crétacé de France (images ESRF). **a/** *Falsiformica* sp. A, ambre albien-cénomanien de Charente-Maritime, vues dorsale et latérale (ailes omises) ; **b/** *Falsiformica* sp. B, ambre cénomanien de l'Aude, vue latérale.

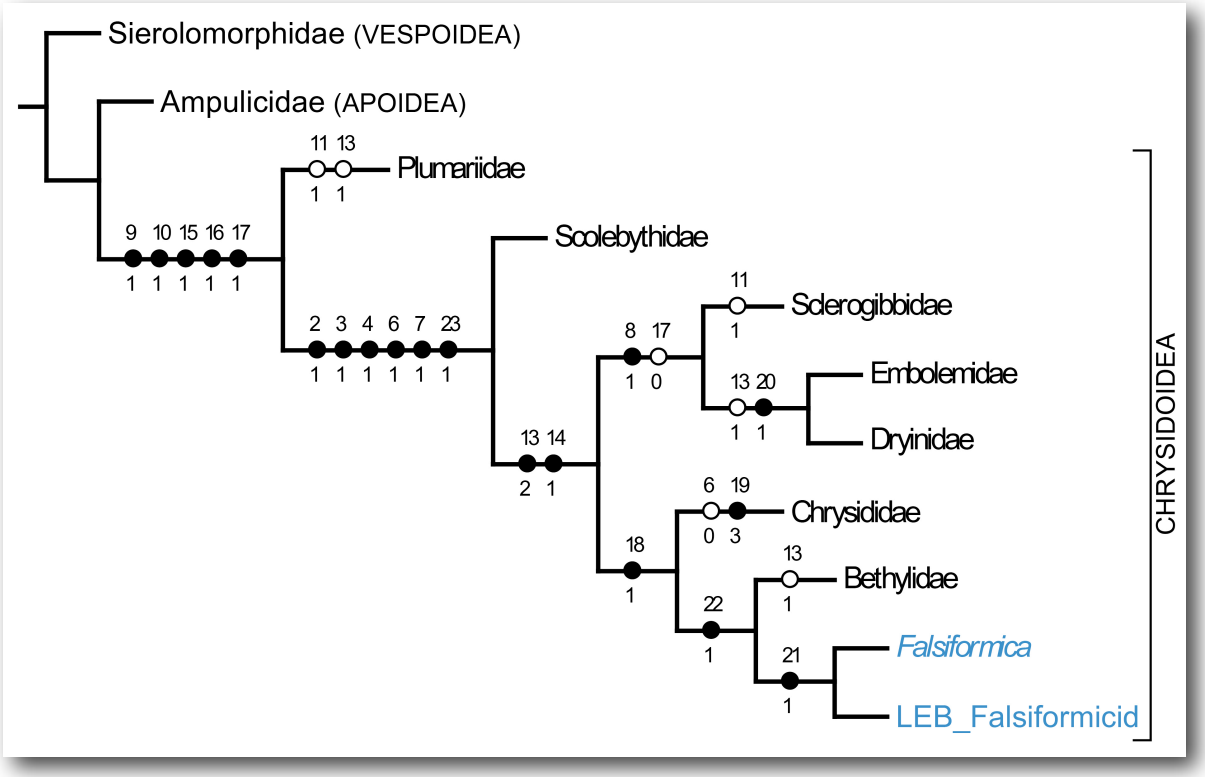


Figure 12 Relations de parentés des Falsiformicidae au sein des hyménoptères (arbre de consensus strict, L: 34 ; CI: 79 ; RI: 83).

4.2. Fourmis

Depuis des débuts modestes au Crétacé inférieur, vraisemblablement vers 120-130 millions d'années, les fourmis (Hymenoptera: Formicidae) se sont largement diversifiées jusqu'à devenir aujourd'hui les insectes sociaux les plus abondants, présents dans la plupart des écosystèmes terrestres et à l'impact écologique majeur. On dénombre environ 13000 espèces actuelles (mais leur nombre réel pourrait être 2 à 3 fois plus élevé) et 700 espèces fossiles (Bolton, 2014). Les fossiles de fourmis sont abondants à partir de l'Eocène, tant en empreintes que dans les gisements d'ambre (fig. 13). Les fossiles crétacés restent encore peu nombreux, connus entre 100 et 78 millions d'années, et appartiennent majoritairement à des lignées éteintes, les sous-familles Sphecomyrminae et Brownimeciinae (fig. 14a). Seuls deux fossiles sont attribués à des sous-familles modernes : une Dolichoderinae dans l'ambre campanien du Canada (78-79 Ma), et une Formicinae dans l'ambre turonien du New Jersey (92 Ma). La première moitié de l'histoire des fourmis reste donc assez peu documentée par les archives fossiles. Mais la première fourmi crétacée fut découverte il y a moins de 50 ans (Wilson *et al.*, 1967), dans le Turonien du New Jersey, et les découvertes se sont enchainées depuis un peu moins de deux décennies, qui ont permis une progression spectaculaire de notre connaissance de leur histoire précoce.

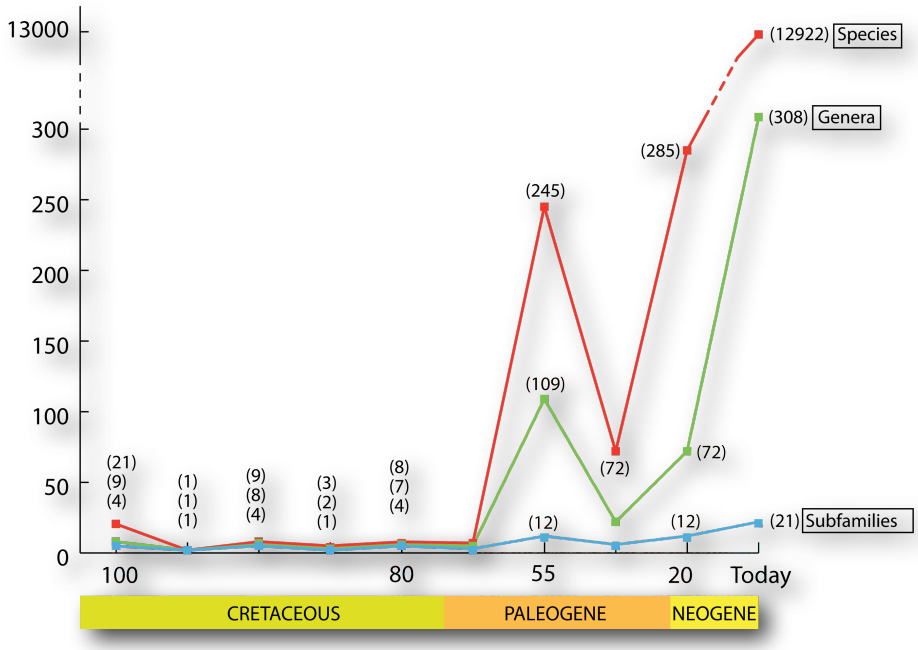


Figure 13
Diversité des fourmis au cours du temps.

J'ai contribué à l'apport de ces données crétacées avec la découverte de diverses fossiles dans l'ambre albien-cénomanien des Charentes et du Myanmar (100 Ma), qui constituent les plus anciennes fourmis connues à ce jour (figs. 14b, 14c). A l'exception d'un spécimen qu'il n'a pas été possible de placer dans une sous-famille existante (Nel *et al.*, 2004), tous les fossiles décrits appartiennent à la sous-famille la plus basale et exclusivement crétacée, les Sphecomyrminae (Perrichot *et al.*, 2008a ; Perrichot, 2014 – article en annexe ; Perrichot, 2015a). Ajoutées aux autres Sphecomyrminae décrites dans le Cénomanien du Myanmar, le Turonien du New Jersey, le Santonien de Sibérie, et le Campanien du Canada (Dlussky, 1996, 1999 ; Engel & Grimaldi, 2005 ; Barden & Grimaldi, 2012, 2013, 2014 ; McKellar *et al.*, 2013a, 2013b), ces fossiles montrent que les Sphecomyrminae étaient étonnamment diversifiées et largement distribuées au sein de la Laurasie (fig. 15). Les découvertes les plus récentes confortent la suggestion d'une origine et une dispersion antérieures à l'insularisation de la région ouest-européenne de Laurasie, au plus tard vers 120 millions d'années (Perrichot *et al.*, 2008b – article en annexe).

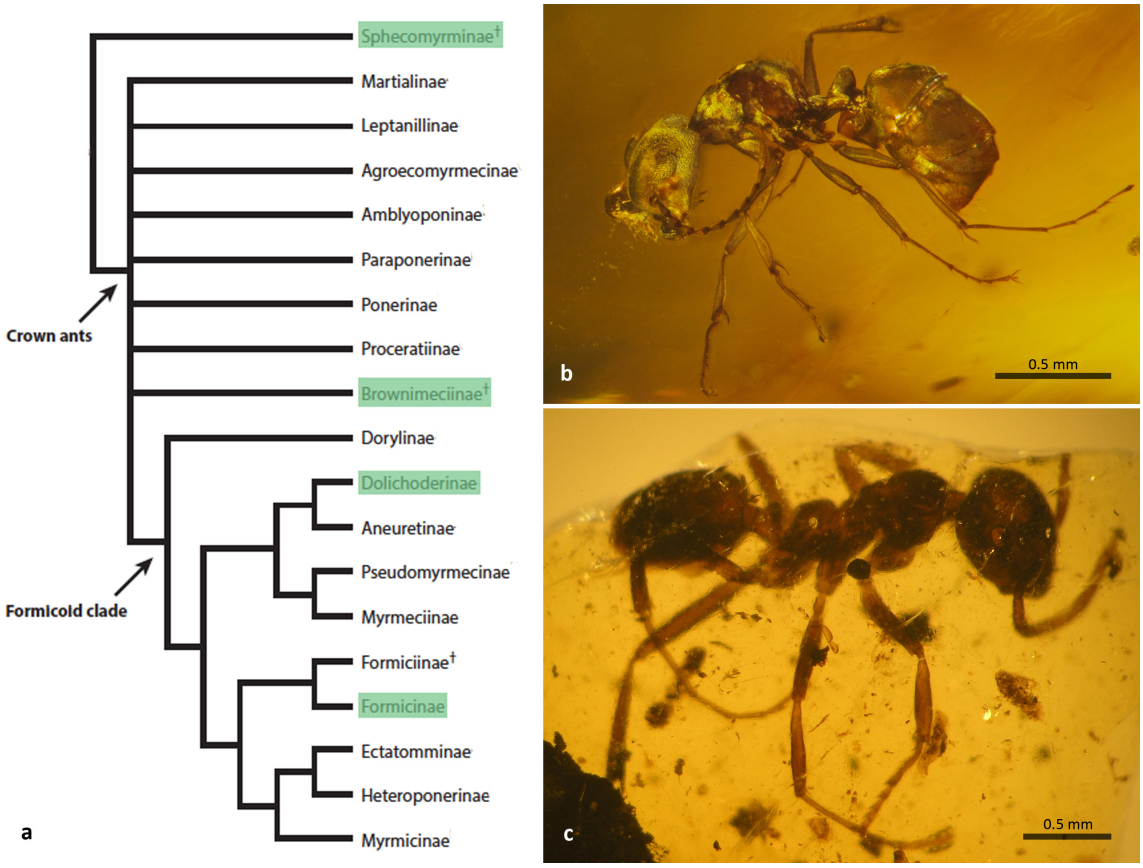


Figure 14 a/ Sous-familles de fourmis connues au Crétacé (en vert), et leurs relations avec les autres sous-familles (modifié d'après Ward, 2014) ; **b/** *Zigracimecia ferox* Perrichot, 2014, Cénomanien du Myanmar ; **c/** *Sphecomyrmodes occidentalis* Perrichot *et al*., 2008, Cénomanien des Charentes.

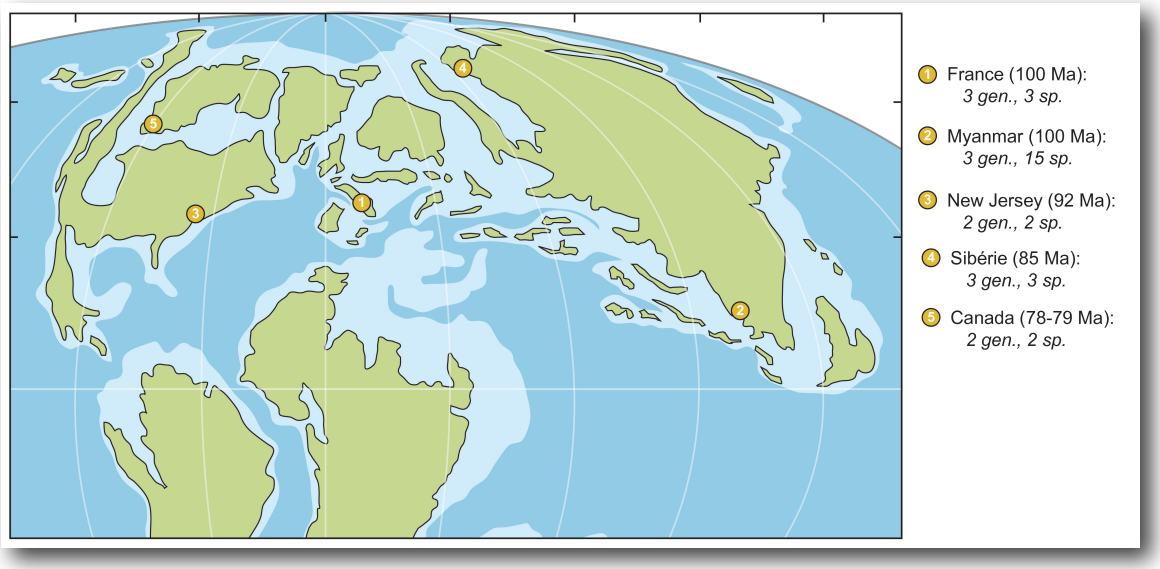


Figure 15 Distribution des Sphecomyrminae au cours du Crétacé (carte du Crétacé moyen modifiée d'après Blakey, 2011).

Parallèlement à ces travaux taxonomiques et paléobiogéographiques, mon intérêt croissant pour les fourmis m'a conduit à intégrer en 2008 l'équipe des créateurs et administrateurs du catalogue électronique AntWeb (www.antweb.org, California Academy of Sciences) pour créer et alimenter la section fossile du catalogue illustré mondial des fourmis. J'ai ensuite utiliser la base de données constituant ce catalogue fossile pour intégrer deux études sur l'histoire évolutive des fourmis : d'abord un article de synthèse sur le registre fossile global des fourmis et son implication pour leur évolution (LaPolla *et al*., 2013 – article en annexe) ; puis une étude macroécologique intégrant les données de distribution fossile et actuelle pour les genres actuels, à partir de l'Eocène (Guénard *et al*., soumis). Les résultats suggèrent par exemple une large distribution actuelle des genres holarctiques du Paléogène et Néogène, mais surtout de fortes affinités entre les myrmécofaunes du Paléogène et Néogène d'Europe et les myrmécofaunes actuelles de la région indomalayenne, et dans une moindre mesure celles de la région australasienne (fig. 16).

Figure 16 Similitude générique entre les faunes de fourmis fossiles et actuelles pour chaque région biogéographique. Les couleurs claires indiquent une plus grande similitude. Les valeurs vont de 0 (pas de genre en commun) à 1 (tous les genres connus sont partagés).

Modern Ant Faunas

Fossil Ant Faunas	Carribean	Nearctic	Neotropical	Afrotropical	Malagasy	West Palearctic	East Palearctic	Indo-Malayan	Australasian
Carribean Miocene	0.75	0.88	0.98	0.46	0.42	0.38	0.46	0.54	0.52
Nearctic Miocene	0.86	1.00	0.95	0.50	0.50	0.50	0.64	0.64	0.55
Nearctic Eocene	0.64	1.00	0.82	0.36	0.36	0.73	0.82	0.82	0.45
East Palearctic Miocene	0.46	0.69	0.69	0.38	0.46	0.62	0.85	1.00	0.77
West Palearctic Miocene	0.37	0.63	0.58	0.53	0.42	0.68	0.95	0.95	0.79
West Palearctic Oligocene	0.46	0.69	0.69	0.38	0.46	0.62	0.85	1.00	0.77
West Palearctic Eocene	0.53	0.72	0.66	0.59	0.47	0.66	0.91	1.00	0.75

V. Les écosystèmes résinifères

Depuis le début de mes travaux de recherche, j'ai été fasciné par le potentiel inouï de l'ambre à capturer des portions d'écosystèmes anciens. Un gisement très fossilifère fournit des milliers d'inclusions fossiles qui, prises en compte dans leur ensemble, renseignent sur la diversité du biotope mais sans certitude de la durée pendant laquelle le piégeage s'est effectué, donc sans certitude que tous ces organismes ont réellement vécu en même temps. En effet il n'est pas possible d'évaluer si l'ensemble des morceaux de résine accumulés dans un gisement ont été formés durant 1 an, 1000 ans, ou plus. En revanche, un seul morceau d'ambre peut contenir de multiples inclusions (= syninclusions) dont on sait alors qu'elles ont vécu au même moment. Ces morceaux sont particulièrement informatifs pour restituer la paléoécologie et les paléoenvironnements des écosystèmes résinifères.

L'étude de morceaux d'ambre des Charentes particulièrement riches en syninclusions a occupé une large place dans mes travaux de thèse et de post-doc au Muséum de Berlin. Dans un premier temps, j'ai noté la proportion importante et inhabituelle d'arthropodes issus de la faune épigée, avec par exemple la fossilisation excessivement rare d'un grillon-taupe (Perrichot *et al*., 2002). Cette particularité, inédite dans la bibliographie consacrée aux ambres, traduit des coulées de résine effectuées directement au sol et que j'ai appelées "ambre

de litière" (Perrichot, 2004 – article en annexe). Cet ambre très caractéristique montre un aspect feuilleté et un gradient de transparence entre la première coulée en contact avec le sol, et les coulées suivantes (fig. 17). Elles piègent successivement les éléments constitutifs du sol, et de nombreux arthropodes rampant ou volant en surface de la litière. La préservation exceptionnelle de véritables portions du sol des forêts par la résine a ainsi été mise en évidence pour la première fois.

Figure 17
Aspect caractéristique d'un échantillon d'ambre de litière (échelle = 20 mm).

Avec des collègues microbiologistes, nous avons ensuite dressé l'inventaire taxonomique des micro-inclusions présentes dans ces morceaux. Ces travaux ont montré la présence inédite de micro-organismes marins, en particulier des diatomées et foraminifères (Girard *et al*., 2008, 2009a, 2009b). L'assemblage le plus remarquable était constitué d'un morceau contenant 275 spécimens représentant 45 familles d'arthropodes, microalgues, champignons, végétaux, ainsi que des plumes (fig. 18) : une oryctocénose très particulière associant organismes aquatiques marins ou non et organismes terrestres de différentes strates écologiques (épigée, arborée). Le scénario taphonomique le plus vraisemblable est que les éléments marins ont été déposés sur le sol de la forêt lors d'une très haute marée, une tempête, ou par les embruns, puis rapidement piégés avec divers organismes terrestres dans de la résine coulée depuis des branches ou un tronc. Ceci impliquait donc la présence d'eau marine ou saumâtre à proximité immédiate des arbres producteurs de la résine, et précisait l'existence d'une vaste forêt côtière. En outre, ce type d'assemblage fossile exceptionnellement préservé et diversifié indique la complexité des réseaux trophiques dans ces écosystèmes forestiers anciens (Perrichot & Girard, 2009 – article en annexe) (fig. 19).

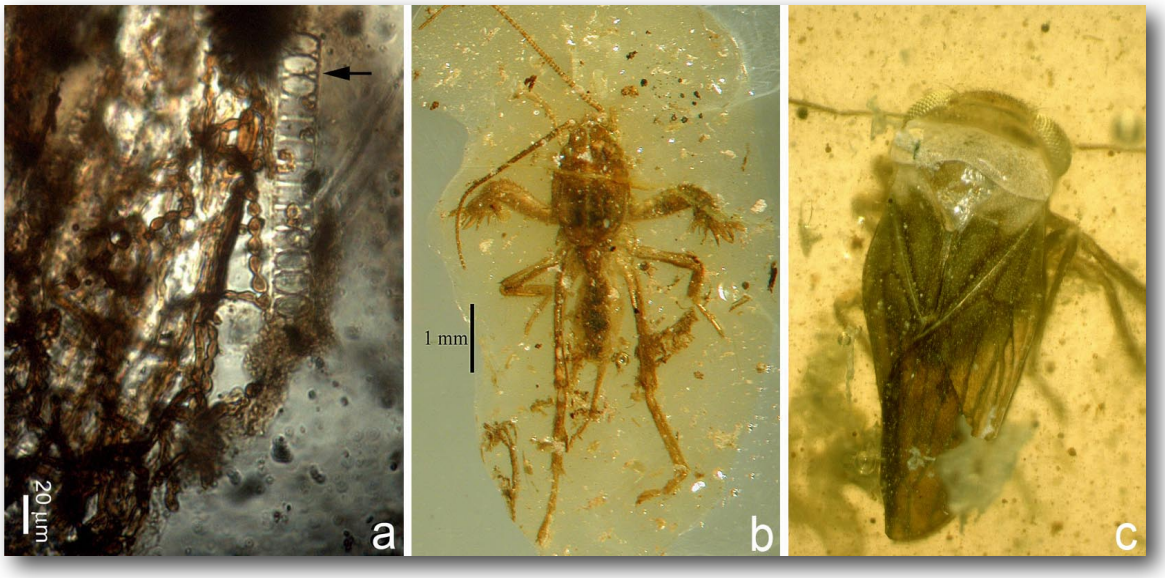


Figure 18 Syninclusions dans l'ambre albien-cénomanien des Charentes. **a/** filaments mycéliens corticoles (Ascomycota : Metacapnodiaceae) et diatomées marines *Hemiaulus* sp. (flèche) ; **b/** Orthoptère Gryllotalpidae, *Marchandia magnifica* Perrichot *et al*., 2002 ; **c/** Hétéroptère Schizopteridae, *Buzinia couillardi* Perrichot, Nel & Néraudeau, 2007.

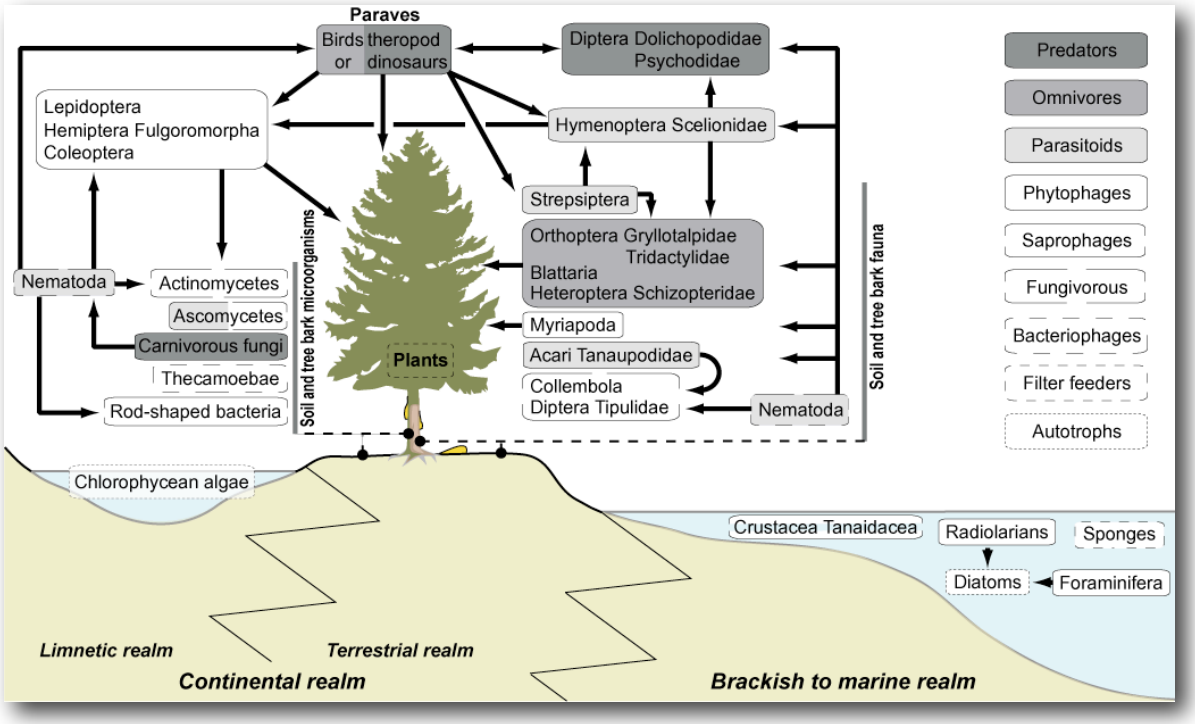


Figure 19 Réseau trophique d'un environnement forestier côtier de l'Albien-Cénomanien du Sud-Ouest de la France, reconstruit à partir d'un assemblage d'organismes fossilisés dans un morceau d'ambre des Charentes.

VI. Les préservations exceptionnelles

Généralement sécrétée par les arbres suite à des traumatismes (blessures mécaniques, attaques d'insectes ou de parasites, feux, ...), la résine protège les zones de lésions contre les agents pathogènes (Langenheim, 1994, 2003). Encore fraîche et poisseuse, elle agit comme un piège quasi instantané pour les organismes et les soustrait alors à presque toute putréfaction ultérieure. Il en résulte la préservation exceptionnelle d'organismes ou parties d'organismes à composés essentiellement labiles qui, en d'autres circonstances, sont le plus souvent dégradés avant fossilisation : fragments végétaux ou mycéliens (Girard *et al.*, 2009a ; Sadowski *et al.*, 2012 ; Schmidt *et al.*, 2014), organismes à corps mou (Poinar *et al.*, 1993; Poinar, 2003), ou encore téguments de vertébrés tels que plumes (Schlee, 1973 ; Grimaldi & Case, 1995 ; McKellar *et al.*, 2011), poils (Vullo *et al.*, 2010), et peaux (Lazell, 1965 ; Perrichot & Néraudeau, 2005 ; Arnold *et al.*, 2008).

Autre type de préservation exceptionnelle : la présence d'organismes aquatiques, en particulier marins, dans une matière formée en domaine continental, qui plus est hydrophobe lorsqu'elle est fraiche. L'une des explications tient au piégeage d'organismes déposés par l'eau en surface du sol, au pied des arbres résinifères (cf. paragraphe précédent). Dans d'autres cas les micro-organismes sont projetés avec les embruns contre des coulées de résine fraiche (observations personnelles dans les forêts côtières de Nouvelle-Calédonie, 2011). Enfin, des coulées de résine immergées temporairement peuvent piéger des micro-organismes ou des arthropodes aquatiques selon des processus particuliers à chacun de ces groupes, comme indiqué par des études taphonomiques menées dans des forêts actuelles marécageuses (Schmidt & Dilcher, 2007).

Toutes ces inclusions dans l'ambre constituent des jalons fossiles inestimables pour préciser l'histoire évolutive des groupes considérés. Parmi les cas rencontrés au cours de mes travaux sur les ambres crétacés de France, voici des exemples pertinents qu'avec divers collaborateurs nous avons jugés opportun d'étudier.

6.1. Plumes

– Etude menée avec des paléontologues (R. Vullo & D. Néraudeau) et un ornithologue (L. Marion) à l'Université de Rennes 1; imagerie synchrotron réalisée à l'ESRF de Grenoble –

Un ensemble de plumes à la structure jusqu'alors inédite a été trouvé dans l'ambre albien-cénomanien des Charentes (Perrichot *et al.*, 2008c – article en annexe). La taille minuscule de ces fragments de plumes combinée à leur enchevêtrement dans l'ambre rendant leur observation difficile (fig. 20a), elles ont été scannées en holotomographie synchrotron à rayons X et l'une d'elle a été reconstruite en 3D (fig. 20b). La comparaison de sa structure avec celles des plumes actuelles et d'autres plumes fossiles a révélé un stade de développement intermédiaire jamais évoqué dans les modèles évolutifs. Les barbes sont partiellement fusionnées à leur base pour former une ébauche de rachis (fig. 19c), un stade précurseur de la disposition en deux vanes planes de par et d'autre d'un rachis bien individualisé, condition nécessaire au vol.

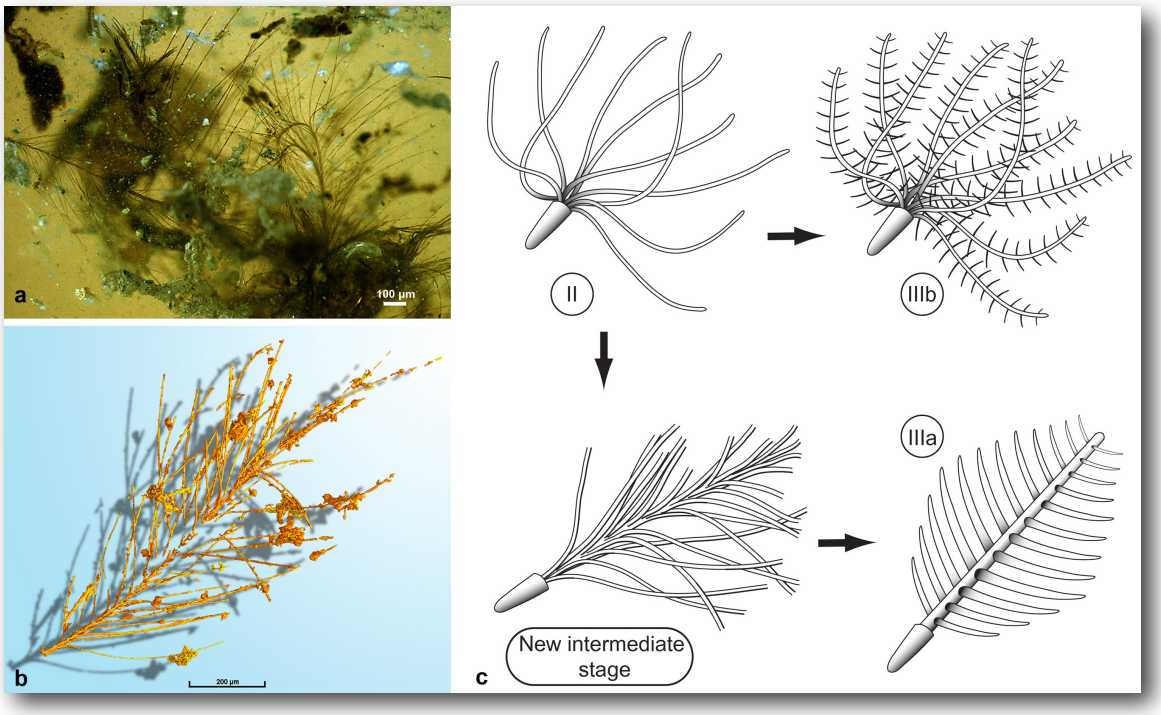


Figure 20 a/ Plumes fossilisées dans l'ambre albien-cénomanien (100 Ma) des Charentes **; b/** reconstitution 3D de l'une des plumes en holotomographie (image ESRF) **; c/** place dans le modèle de développement des plumes.

6.2. Champignon carnivore

– Etude menée avec un microbiologiste (A. Schmidt) lors de mon post-doc au Muséum de Berlin –

Les filaments mycéliens constituent un autre de ces cas de fossilisation exceptionnelle dans l'ambre charentais, et la découverte la plus remarquable est sans doute celle d'un champignon carnivore, vraisemblablement nématophage, qui reste à ce jour l'unique témoin fossile d'un comportement prédateur chez les champignons (Schmidt *et al.*, 2007 – article en annexe ; Schmidt *et al.*, 2008). Filament capable de générer des anneaux gluants pour capturer et digérer des organismes mobiles dans le sol comme les nématodes (fig. 21), ce fossile montre que les champignons avaient déjà développé des systèmes de pièges complèxes au Crétacé. Comme dans les écosystèmes modernes, les champignons carnivores formaient un groupe écologique spécialisé dans la consommation de petits métazoaires ou protozoaires. Aujourd'hui cette niche écologique est occupée par plus de 200 espèces de Zygomycètes, Ascomycètes et Basidiomycètes. Le fossile n'a pu être assigné à aucun de ces groupes récents de champignons, suggérant qu'au moins un groupe différent a occupé cette niche écologique par le passé, et qu'un tel système de piège a été développé indépendamment à plusieurs reprises dans l'histoire de la Terre.

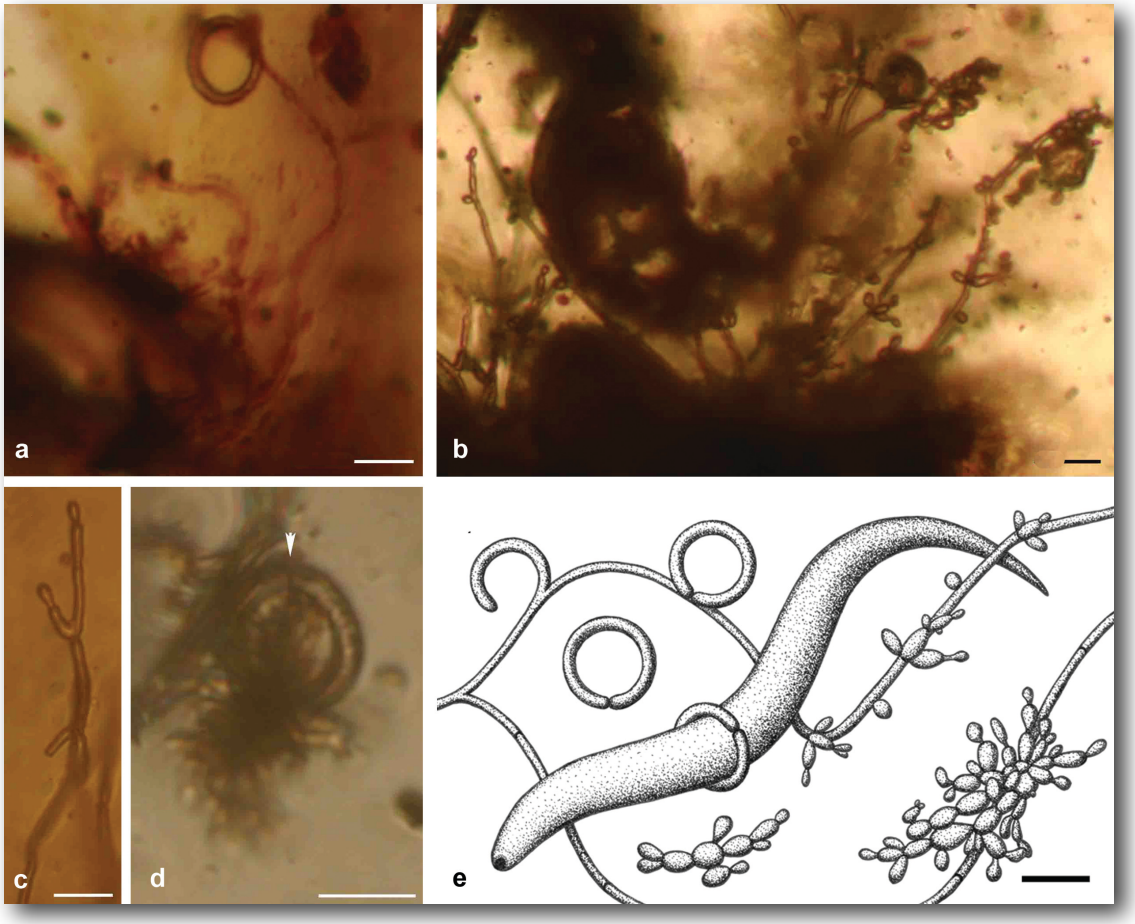


Figure 21 Champignon prédateur fossilisé dans l'ambre albien-cénomanien (100 Ma) des Charentes. **a-d/** détails de différents anneaux, filaments, et spores ; e/ reconstruction du champignon à différents stades de développement des anneaux et spores, et avec un nématode piégé dans un anneau (Barres d'échelle 10 µm).

6.3. 'Coquillages' et crustacés

– Etudes menées avec des microbiologistes (V. Girard, Géosciences Rennes ; S. Saint Martin, MNHN ; A. Schmidt, Muséum de Berlin) lors de mon post-doc à Berlin –

Diatomées centrales, foraminifères, radiolaires, ou encore spicules de spongiaires : des éléments marins a priori improbables en inclusions dans l'ambre... Et pourtant ces 'microcoquilles' sont bel et bien fossilisées dans l'ambre albien-cénomanien des Charentes (Girard *et al*., 2008 – article en annexe ; Girard *et al*., 2009b) et l'ambre crétacé supérieur de Vendée (Saint Martin *et al*., 2015) (fig. 22a-c). Retrouvées le plus souvent en syninclusion avec des arthropodes terrestres, elles indiquent alors un piégeage hors de l'eau, dans la résine coulée le long des arbres ou en surface du sol, et donc dans une forêt littorale soumise à l'influence marine.

– Etude menée dans le cadre d'une thèse sur les arthropodes aquatiques fossiles dans l'ambre (A. Sánchez-García, Univ. Barcelone) –

Les petits crustacés aquatiques à carapace fine sont habituellement rapidement dégradés post-mortem et donc excessivement rarement fossilisés dans les sédiments. Deux groupes de ces crustacés ont été trouvés fossilisés dans divers ambres crétacés de France (fig. 22d-g). Parmi eux, des Tanaidaceae vraisemblablement marins, dont un spécimen femelle conservé avec sa poche marsupiale et son contenu. Le stade marsupial existe chez la plupart des Tanaidaceae modernes, et ce fossile unique atteste d'un processus biologique resté inchangé dans ce groupe de crustacés depuis au moins 100 millions d'années (Sánchez-García *et al*., soumis).

Figure 22 Organismes aquatiques dans l'ambre crétacé de France. **a/** foraminifère, ambre albien-cénomanien des Charentes (Girard *et al*., 2009b) ; **b/** *Corethron* sp., diatomée centrale, ambre crétacé supérieur de Vendée (Saint Martin *et al*., 2015) ; **c/** spicule de spongiaire, ambre crétacé supérieur de Vendée ; **d-g/** Crustacé Tanaidacé, femelle **(d)** préservée avec sa poche marsupiale (**e**) contenant des oeufs (**f**), ambre cénomanien des Charentes ; **g/** Crustacé Isopode indéterminé, ambre crétacé supérieur de Vendée.

Troisième partie

Projet de recherche

Mon projet de recherche pour les années à venir est discuté ci-dessous. Il est en continuité avec les travaux réalisés auparavant mais plus spécialisé, avec des champs d'investigation restreints à certains groupes taxonomiques. En ce qui concerne les insectes, j'ambitionne de me concentrer exclusivement sur les fourmis. Pour les écosystèmes résinifères, je veux me focaliser sur l'évolution de la production de résine. Enfin, sans délaisser les gisements en cours d'étude, je souhaite accentuer mon travail sur les gisements d'ambre dans des régions encore trop méconnues pour ce qui concerne les entomofaunes, particulièrement en Afrique.

I. Origine et évolution des fourmis

Des progrès substantiels ont été faits depuis une décennie concernant la phylogénie interne des fourmis (arrangement des sous-familles). Des modèles phylogénétiques proposés auparavant à partir de la morphologie ont été confirmés ou corrigés grâce à l'apport de données moléculaires toujours plus riches et des dernières découvertes fossiles. Les analyses moléculaires (e.g., Brady *et al*., 2006 ; Moreau *et al.*, 2006 ; Moreau & Bell, 2013) utilisent des fossiles comme points de calibration pour estimer les dates de divergences des lignées et proposer une chronologie de la diversification des fourmis. Mais les fossiles crétacés manquent cruellement pour les sous-familles modernes, alors même que ces lignées ont pour la plupart une origine estimée au Crétacé dans les dernières analyses moléculaires (fig. 23). Même lorsque de rares données crétacées existent, elles ne sont pas toujours prises en compte. Par exemple dans une analyse de la sous-famille Dolichoderinae, Ward *et al*. (2010) utilisent pour calibrer le clade le plus basal un fossile signalé mais non décrit dans l'ambre éocène du Canada (55 Ma), alors qu'un fossile est décrit du Campanien (78-79 Ma) du Canada (Dlussky, 1999). Il en résulte un âge estimé de 65 Ma pour l'origine des Dolichoderinae ('crown group'), et de 95 Ma pour leur ancêtre le plus proche apparenté ('stem group').

J'ai accès depuis peu à une nouvelle collection d'ambre cénomanien (100 Ma) du Myanmar, au *Nanjing Institute of Paleontology and Geology*, qui contient un nombre remarquable de fourmis fossiles (> 50 spécimens alors que moins de 10% de la collection a été examinée). Beaucoup sont des Sphecomyrminae, et leur étude complètera significativement la connaissance de cette sous-famille crétacée, la plus basale des lignées de fourmis. Mais plus intéressant encore, j'ai découvert des spécimens attribuables à trois des quatres principales sous-familles modernes : une Ponerinae, deux Dolichoderinae, et trois Formicinae. Ces fossiles sont ainsi les plus anciens réprésentants connus de chacune des trois sous-familles. Leur étude détaillée dira s'ils sont à placer comme 'crown group' ou bien comme 'stem group' de leur lignée, mais ils précèdent déjà les âges estimés de leur origine respective (fig. 23).

Dès 2015, je vais m'attacher à décrire ces fossiles de première importance en les plaçant dans des analyses phylogénétiques des caractères morphologiques. Ensuite une coopération est envisagée avec Corrie Moreau (Field Museum of Natural History, Chicago) pour intégrer ces fossiles dans de nouvelles analyses phylogénétiques moléculaires. Utilisés comme les premiers points de calibration crétacés (exception faite des Formicinae qui ont un fossile connu dans le Turonien), ils devraient logiquement bouleverser les chronologies établies jusqu'à présent, peut-être même appuyer l'hypothèse d'une origine des fourmis au Jurassique terminal (Crozier *et al*., 1997 ; Moreau & Bell, 2013) plutôt qu'au Crétacé inférieur.

Outre les fourmis crétacées, je souhaite m'investir davantage sur l'étude taxonomique, phylogénetique, et biogéographique des myrmécofaunes cénozoïques. Un grand nombre d'espèces fossiles sont déjà connues de gisements insectifères historiques, mais d'autres gisements découverts plus récemment sont riches en fossiles de fourmis encore inédites : ambre éocène de l'Oise et de Chine, ambre miocène du Pérou et de Nouvelle-Zélande, compressions miocènes de Nouvelle-Zélande. Les conservateurs de ces collections m'ont déjà confié du matériel, en cours ou en attente d'analyse.

Même les gisements historiques abondamment étudiés sont encore pourvoyeurs de nouveaux taxons. A l'exception de l'ambre balte dont le contenu fossilifère a attiré l'attention des naturalistes dès le 18e siècle (Sendel, 1742), la majeure partie des études sur les inclusions de l'ambre s'est faite durant les quatre dernières décennies. Même pour l'ambre balte, duquel près de 3500 espèces d'arthropodes ont été décrites (Weitschat & Wichard 2010), la quantité d'inclusions disponible est telle que des dizaines d'espèces nouvelles sont encore décrites chaque année. Pour le seul groupe des fourmis qui représente environ 5% des inclusions dans l'ambre balte, 130 espèces ont été décrites à ce jour (Perrichot, 2015b) mais une estimation statistique suggère qu'environ 29% de la myrmécofaune reste à découvrir (Penney & Preziosi, 2014). Aucun gisement d'ambre

aussi étudié soit il n'a donc encore livré tous ses secrets et les données fossiles de toute région biogéographique sont donc d'intérêt.

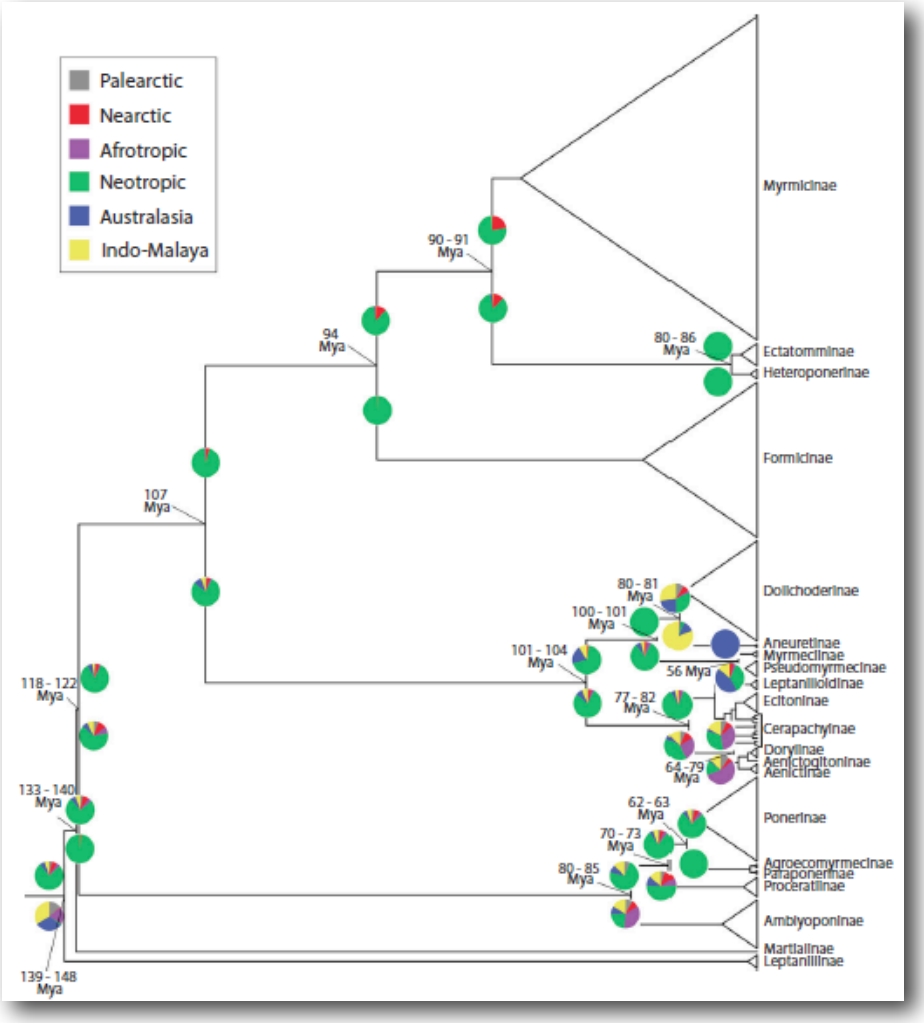


Figure 23
Relations de parentés des sous-familles actuelles de fourmis et âges estimés de leur origine respective ('crown-groups') (source: Moreau & Bell, 2013).

II. Evolution de la production de résine

Comme précédemment évoqué dans la synthèse de mes travaux de recherche, la production de résine végétale est un mécanisme très ancien attesté par des traces fossiles dès le Carbonifère. A cette époque, et au moins jusqu'à la fin du Paléozoïque, les résines semblent principalement produites en faible quantité par des fougères à graines (Ptéridospermophytes) et des Cordaïtales (Gymnospermes). Puis avec le Mésozoïque arrive "l'âge d'or" des conifères (Gymnospermes) et une production beaucoup plus massive de résine par certains d'entre eux. Toutefois, bien que la plupart des familles de conifères résinifères existent dès le Trias supérieur ou le Jurassique, la formation de grands gisements d'ambre est surtout observée au Crétacé. De la même manière, au Cénozoïque, des résines sont abondamment produites par des conifères et certaines familles de plantes à fleurs (Angiospermes), mais la formation d'ambre est principalement restreinte à l'Eocène et au Miocène. Il apparait donc plusieurs époques géologiques sans préservation d'ambre alors qu'existaient des plantes résinifères : l'ensemble du Jurassique, le début et la fin du Crétacé (Berriasien–Hauterivien et Maastrichtien), le Paléocène, ou l'Oligocène. Il serait par exemple logique de trouver de l'ambre oligocène issu des Fabaceae, puisque cette famille d'angiospermes a produit de copieuses quantités de résine à l'Eocène (ambre de l'Oise) et au Miocène (ambres du Mexique, de République Dominicaine).

Dans les prochaines années je souhaite m'investir sur deux questions liées à la production de résine :

- les lacunes traduisent-elles des conditions défavorables à la production de résine (e.g., changements climatiques), ou bien défavorables à la préservation de l'ambre (e.g., non-dépôt, érosion ultérieure) ?
- dans quelle mesure les Cheirolepidiaceae (famille éteinte de conifères, connue du Trias supérieur au Maastrichtien) ont-elles participé à la production de résine ? Parmi les conifères régulièrement évoqués comme sources possibles d'ambre mésozoïque, la contribution des Cheirolepidiaceae reste obscure. Elles sont vraisemblablement à l'origine de l'ambre du Trias d'Italie (Schmidt *et al*., 2012), et elles sont régulièrement associées à l'ambre (bois, feuilles, pollen) dans les gisements crétacés, sans toutefois pouvoir affirmer qu'elles en sont la source. En effet, elles partagent de nombreuses affinités avec une autre famille de conifères, les Araucariaceae, à tel point que leur bois ne sont pas toujours discernables (e.g. *Agathoxylon* Hartig) et qu'il n'a pas encore été possible de distinguer les deux ambres chimiquement. Identifier un biomarqueur chimique des Cheirolepidiaceae permettrait donc de mieux cerner le rôle de cette lignée éteinte de conifères dans la production de résine au Mésozoïque.

III. L'ambre en Afrique

L'Afrique fait partie de ces régions biogéographiques où les entomofaunes fossiles sont largement méconnues, aussi bien pour le Paléozoïque que le Mésozoïque et le Cénozoïque. Seul l'ambre du Liban est fortement insectifère, et les sites livrant un nombre significatif d'insectes en empreintes sont à peine plus nombreux (Schlüter, 2003 ; Engel *et al*., 2012). Ces dernières années ont toutefois montré le potentiel pour la découverte d'autres gisements d'ambre fossilifère, et il est enthousiasmant de penser que tout reste à faire :

- en 2010, une équipe internationale dont je faisais partie publiait la découverte du premier ambre fossilifère africain dans le Crétacé supérieur d'Ethiopie (Schmidt *et al*., 2010). Ce papier portait sur un premier lot de matériel fossile qui avait livré une quarantaine d'arthropodes et de multiples micro-organismes en inclusions dans l'ambre, ainsi que des palynomorphes associés dans le sédiment encaissant. Nos différentes analyses (palynomorphes, chimie de l'ambre, arthropodes, géologie) convergeaient vers un âge Cénomanien (≈ 95 Ma) malgré quelques éléments contradictoires. En 2014, nous avons eu accès à du matériel supplémentaire contenant de nouveaux arthropodes qui excluent l'âge crétacé, et une nouvelle interprétation des palynomorphes nous a été proposée, qui contredit également l'âge crétacé et suggère plutôt un âge miocène (≈ 15 Ma) ! Des analyses complémentaires sont en cours, qui vont permettre de publier un correctif sur ce gisement (Perrichot *et al*., en préparation). Ironiquement, et malgré la déconvenue, les arthropodes de l'ambre d'Ethiopie deviennent les premiers jalons cénozoïques africains et cette nouvelle datation est donc tout aussi intéressante pour la connaissance des paléoentomofaunes.
- en 2012, un géologue de Total Exploration & Production Congo contactait Didier Néraudeau à Géosciences Rennes pour lui faire part de la découverte d'ambre dans le Crétacé inférieur du Congo. Un premier lot d'échantillons nous est parvenu, et j'ai effectué une mission de collecte sur place en 2013 (fig. 24a). Un total de 3 kg d'ambre a été collecté jusqu'à présent, représentant plus de 5000 morceaux de résine fossile (fig. 24b). Une étude préliminaire a été réalisée dans le cadre d'un stage de recherche de Master 2 que j'ai supervisé (Esnault, 2014), qui a permis de préciser l'âge aptien moyen (113-117 Ma) et de trouver les premiers arthropodes fossiles en inclusions (fig. 24c). L'étude va se poursuivre dans les années à venir, notamment l'investigation par imagerie synchrotron des inclusions fossiles dans les morceaux d'ambre trop foncé pour une étude en microscopie classique (30% des morceaux). Au moins une nouvelle mission de fouilles est également envisagée. Il reste donc un travail considérable à mener dans les prochaines années, et je projette de superviser une thèse sur ces gisements à ambre d'Afrique (candidate pressentie : J. Esnault).

En complément de ces deux gisements déjà en cours d'étude, des missions d'exploration sont envisagées dans d'autres localités africaines, notamment dans des zones où est implanté Total E&P (Gabon, etc...). Une meilleure connaissance des paléo-entomofaunes africaines est primordiale pour mieux appréhender la phylogénie, la paléobiogéographie, et plus globalement l'histoire évolutive des insectes.

Figure 24 L'ambre aptien du Congo. **a/** zone d'affleurement ; **b/** un aperçu de l'ambre ; **c/** exemple d'insecte trouvé en inclusion : une guêpe Platygastridae (Hymenoptera).

En conclusion de ce mémoire, l'avenir des recherches sur l'ambre semble plus prometteur que jamais. La multiplication des découvertes de gisements depuis une quinzaine d'années, le développement de techniques d'imagerie adaptées à l'examen détaillé des inclusions (CT-scan, micro- et holotomographie par rayons X synchrotron), et le développement des études multidisciplinaires ayant de l'ambre pour matériau de base, témoignent d'un domaine de recherche actuellement en plein essor.

Références bibliographiques

Aquilina L., Girard V., Hénin O., Bouhnik-Le Coz M., Vilbert D., Perrichot V., Néraudeau D. (2013) Amber inorganic geochemistry: new insight into the environmental processes in a Cretaceous forest of France. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 369: 220-227.

Arnold E.N., Poinar G. (2008) A 100 million year old gecko with sophisticated adhesive toe pads, preserved in amber from Myanmar. *Zootaxa*, 1847: 62-68.

Azar D., Gèze R., El-Samrani A., Maalouly J., Nel A. (2010a) Jurassic amber in Lebanon. *Acta Geologica Sinica*, 84: 977-983.

Azar D., Gèze R., Acra F. (2010b) Lebanese amber. *In*: Penney D. (ed.), *Biodiversity of fossils in amber from the major world deposits*. Siri Scientific Press, Manchester: 271-298

Barden P., Grimaldi D.A. (2012) Rediscovery of the bizarre Cretaceous ant *Haidomyrmex* Dlussky (Hymenoptera: Formicidae), with two new species. *American Museum Novitates*, 3755: 1-16.

Barden P., Grimaldi D. (2013) A new genus of highly specialized ants in Cretaceous Burmese amber (Hymenoptera: Formicidae). *Zootaxa*, 3681: 405-412.

Barden P., Grimaldi D. (2014) A diverse ant fauna from the mid-Cretaceous of Myanmar (Hymenoptera: Formicidae). *PLoS One*, 9: e93627.

Beck C.W., Wilbur E., Meret S. (1964) Infrared spectra and the origin of amber. *Nature*, 201: 256-257.

Berendt G.C. (1830) *Die Insekten im Bersntein. Ein Beitrag zur Thiergeschichte der Vorwelt*. Nicolai Publ., Danzig, 39 p.

Blakey R.C. (2011) Global Paleogeography, Mollewide Globes. Late Early Cretaceous (105Ma) http://cpgeosystems.com/105moll.jpg and Eocene (50 Ma) http://cpgeosystems.com/50moll.jpg [accès mars 2012].

Bolton B. (2014) An online catalog of the ants of the world. Available from http://antcat.org [accès 12.2014].

Brady S.G., Schultz T.R., Fisher B.L., Ward P.S. (2006) Evaluating alternative hypotheses for the early evolution and diversification of ants. *Proceedings of the National Academy of Sciences of the USA*, 103: 18172-18177.

Bray P.S., Anderson K.B. (2009) Identification of Carboniferous (320 Million Years Old) class Ic amber. *Science*, 326: 132-134.

Brothers D.J., Rasnitsyn A.P. (2003) Diversity of Hymenoptera and other insects in the Late Cretaceous (Turonian) deposits at Orapa, Botswana: a preliminary review. *African Entomology*, 11: 221-226.

Clark N.D.L. (2010) *Amber – Tears of the Gods*. Dunedin Academic Press, Edinburgh, 118 p.

Coquand H. (1856) Notice sur la formation crétacée du département de la Charente. *Bulletin de la Société Géologique de France*, série 2, 14: 55-98.

Curtis J. (1829) Observations upon a collection of fossil insects discovered near Aix in Provence in the summer of 1828 by R.J. Murchison and Lyell C. Edinburgh New Philosophical Journal, April-October 1829: 295-297.

Crozier R.H., Jermiin L.S., Chiotis M. (1997) Molecular evidence for a Jurassic origin of ants. *Naturwissenschaften*, 84: 22-23.

Dlussky G.M. (1996) Ants (Hymenoptera: Formicidae) from Burmese amber. *Paleontological Journal*, 30: 449-454.

Dlussky G.M. (1999) New ants (Hymenoptera, Formicidae) from Canadian amber. *Paleontological Journal*, 33: 409-412.

Engel M.S., Grimaldi D.A. (2005) Primitive new ants in Cretaceous amber from Myanmar, New Jersey, and Canada (Hymenoptera, Formicidae). *American Museum Novitates*, 3485: 1-23.

Engel M.S., McKellar R.C., Gibb S., Chatterton B.D.E. (2012) A new Cenomanian–Turonian (Late Cretaceous) insect assemblage from southeastern Morocco. *Cretaceous Research*, 35: 88-93.

Esnault J. (2014) Ambre et plantes associées du Crétacé inférieur du Congo : études systématiques et paléoécologiques. Mémoire de recherche inédit de Master 2 PPP, Université Rennes 1, 39 p. + 8 pl. + annexes.

Fleuriau de Bellevue L.B. (1823) Description de la forêt sous-marine de l'île d'Aix. *In*: Brongniart A., *Dictionnaire des Sciences naturelles*. Tome 26. Levrault éditeur, Paris: 368.

Garrouste R., Clément G., Nel P., Engel M.S., Grandcolas P., D'Haese C., Lagebro L., Denayer J., Gueriau P., Lafaite P., Olive S., Prestianni C., Nel A. (2012) A complete insect from the Late Devonian period. *Nature*, 488: 82-85.

Girard V., Breton G., Brient L., Néraudeau D. (2009a) Sheathed prokaryotic filaments, major components of mid-Cretaceous French amber microcoenosis. *Journal of Paleolimnology*, 42: 437-447.

Girard V., Breton G., Perrichot V., Bilotte M., Le Loeuff J., Nel A., Philippe M., Thévenard F. (2013) The Cenomanian amber of Fourtou (Aude, Southern France): Taphonomy and palaeoecological implications. *Annales de Paléontologie*, 99: 301-315.

Girard V., Saint Martin S., Saint Martin J.-P., Schmidt A.R., Struwe S., Perrichot V., Breton G., Néraudeau D. (2009b) Exceptional preservation of marine diatoms in upper Albian amber. *Geology*, 37: 83-86.

Girard V., Schmidt A.R., Saint Martin S., Struwe S., Perrichot V., Saint Martin J.-P., Breton G., Néraudeau D. (2008) Evidence for marine microfossils from amber. *Proceedings of the National Academy of Sciences of the USA*, 105: 17426-17429.

Grimaldi D.A. (1996) *Amber: window to the Past*. Harry N. Abrams Inc., New York, 216 p.

Grimaldi D.A., Case G.R. (1995) A feather in amber from the Upper Cretaceous of New Jersey. *American Museum Novitates*, 3126: 1-6.

Grimaldi D.A., Engel M.S. (2005) *Evolution of the insects*. Cambridge University Press, 655 p.

Guénard B., Perrichot V., Economo E.P. Integration of global fossil and modern biodiversity data reveals dynamism and stasis in ant macroecological patterns. [Soumis à *Journal of Biogeography*, 12.2014].

Hu S., Dilcher D.L., Jarzen D.M., Taylor D.W. (2008) Early steps of angiosperm–pollinator coevolution. *Proceedings of the National Academy of Sciences of the USA*, 105: 240-245.

Jehlicka J., Jorge Villar S.E., Edwards H.G.M. (2004) Fourier transform Raman spectra of Czech and Moravian fossil resins from freshwater sediments. *Journal of Raman Spectroscopy*, 35: 761-767.

Kaddumi H.F. (2005) *Amber of Jordan*. Eternal River Museum of Natural History, Amman, 224 p.

Kühne W.G., Kubig L., Schlüter T. (1973) Eine Micropterygide (Lepidoptera) aus mittelcretazischem Harz Nordwestfrankreichs. *Mitteilungen der Deutschen Entomologischen Gesellschaft*, 32: 61-64.

Labandeira C.C., Currano E.D. (2013) The fossil record of plant-insect dynamics. *Annual Review of Earth and Planetary Sciences*, 41: 287-311.

Lacroix A. (1910) Groupe des résines fossiles. *Minéralogie de la France*, 4: 637-645.

Langenheim J.H. (1969) Amber: a botanical inquiry. *Science*, 163: 1157-1169.

Langenheim J.H. (1994) Higher plant terpenoids: a phytocentric overview of their ecological roles. *Journal of Chemical Ecology*, 20: 1223-1280.

Langenheim J.H. (2003) *Plant resins: chemistry, evolution, ecology, and ethnobotany*. Timber Press, Cambridge, 586 p.

LaPolla J.S., Dlussky G.M., Perrichot V. (2013) Ants and the fossil record. *Annual Review of Entomology*, 58: 609-630.

Lazell J.D. (1965) An *Anolis* (Sauria, Iguanidae) in amber. *Journal of Paleontology*, 39: 379-382.

Masure E., Dejax J., de Ploëg G. (2013) Blowin' in the wind… 100 Ma old multi-staged dinoflagellate with sexual fusion trapped in amber: Marine-freshwater transition. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 388: 128-144.

McKellar R.C., Chatterton B.D.E., Wolfe A.P., Currie P.J. (2011) A diverse assemblage of Late Cretaceous dinosaur and bird feathers from Canadian amber. *Science*, 333: 1619-1622.

McKellar R.C., Glasier J.R.N., Engel M.S. (2013a) A new trap-jawed ant (Hymenoptera: Formicidae: Haidomyrmecini) from Canadian Late Cretaceous amber. *The Canadian Entomologist*, 145: 454-465.

McKellar R.C., Glasier J.R.N., Engel M.S. (2013b) New ants (Hymenoptera: Formicidae: Dolichoderinae) from Canadian Late Cretaceous amber. *Bulletin of Geosciences*, 88: 583-594.

Misof B., Liu S., Meusemann K., Peters R.S., Donath A., *et al*. (2014) Phylogenomics resolves the timing and pattern of insect evolution. *Science*, 346, 763-767.

Moreau C.S., Bell C.D. (2013) Testing the museum versus cradle tropical biological diversity hypothesis: phylogeny, diversification, and ancestral biogeographic range evolution of the ants. *Evolution*, 67: 2240-2257.

Moreau C.S., Bell C.D., Vila R., Archibald S.B., Pierce N.E. (2006) Phylogeny of the ants: diversification in the age of angiosperms. *Science*, 312: 101-104.

Nel A., de Ploëg G., Dejax J., Dutheil D., de Franceschi D., Gheerbrant E., Godinot M., Hervet S., Menier J.-J., Auge M., Bignot G., Cavagnetto C., Duffaud S., Gaudant J., Hua S., Jossang A., de Lapparent de Broin F., Pozzi J.-P., Paicheler J.-C., Beuchet F., Rage J.-C. (1999) Un gisement sparnacien exceptionnel à plantes, arthropodes et vertébrés (Eocène basal, MP7): Le Quesnoy (Oise, France). *Comptes Rendus de l'Académie des Sciences, Paris, série IIa*, 329: 65-72.

Nel A., de Ploëg G., Millet J., Menier J.-J., Waller A. (2004) The French ambers: a general conspectus and the Lowermost Eocene amber deposit of Le Quesnoy in the Paris Basin. *Geologica Acta*, 2: 3-8.

Nel A., Fleck G., Garcia G., Gomez B., Ferchaud P., Valentin X. (2015) New dragonflies from the lower Cenomanian of France enlighten the timing of the odonatan turnover at the Early – Late Cretaceous boundary. *Cretaceous Research*, 52: 118-126.

Nel A., Néraudeau D., Perrichot V., Girard V., Gomez B. (2008) A new dragonfly family from the Upper Cretaceous of France. *Acta Palaeontologica Polonica*, 53: 165-168.

Nel A., Perrault G., Perrichot V., Néraudeau D. (2004) The oldest ant in the Lower Cretaceous amber of Charente-Maritime (SW France) (Insecta: Hymenoptera: Formicidae). *Geologica Acta*, 2: 23-29

Nel A., Petrulevicius J.F., Azar D. (2010) Palaeoentomology, a young old field of science. *Annales de la Société Entomologique de France*, 46: 1-3.

Nel A., Roques P., Nel P., Prokin A.A., Bourgoin T., Prokop J., Szwedo J., Azar D., Desutter-Grandcolas L., Wappler T., Garrouste R., Coty D., Huang D., Engel M.S., Kirejtshuk A.G. (2013) The earliest known holometabolous insects. *Nature*, 503: 257-261.

Néraudeau D., Allain R., Perrichot V., Videt B., de Broin F., Guillocheau F., Philippe M., Rage J.-C., Vullo R. (2003) Découverte d'un dépôt paralique à bois fossiles, ambre insectifère et restes d'Iguanodontidae (Dinosauria, Ornithopoda) dans le Cénomanien inférieur de Fouras (Charente-Maritime, Sud-Ouest de la France). *Comptes Rendus Palevol*, 2: 221-230.

Néraudeau D., Perrichot V., Dejax J., Masure E., Nel A., Philippe M., Moreau P., Guillocheau F., Guyot T. (2002) Un nouveau gisement à ambre insectifère et à végétaux (Albien terminal probable): Archingeay (Charente-Maritime, France). *Geobios*, 35: 233-240.

Néraudeau D., Perrichot V., Colin J.-P., Girard V., Gomez B., Guillocheau F., Masure E., Peyrot D., Tostain F., Videt B., Vullo R. (2008) A new amber deposit from the Cretaceous (Uppermost Albian-Lowermost Cenomanian) of southwestern France. Cretaceous Research, 29: 925-929.

Nissenbaum A., Yakir D., Langenheim J.H. (2005) Bulk carbon, oxygen, and hydrogen stable isotope composition of recent resins from amber-producing *Hymenaea*. *Naturwissenschaften*, 92: 26-29.

Nohra Y., Azar D., Gèze R., Maksoud S., El Samrani A., Perrichot V. (2013) New Jurassic amber outcrops from Lebanon. *Terrestrial Arthropod Reviews*, 6: 27-51.

Onoratini G., Guiliano M., Asia L., Mille G., Simon P. (2009) L'ambre dans le Sud-Est de la France, ressources géologiques et utilisation archéologique. *Bulletin du Musée d'Anthropologie préhistorique de Monaco*, 49: 3-20.

Penney D., Preziosi R.F. (2014) Estimating fossil ant species richness in Eocene Baltic amber. *Acta Palaeontologica Polonica*, 59: 927-929.

Perrichot V. (2004) Early Cretaceous amber from south-western France: insight into the Mesozoic litter fauna. *Geologica Acta*, 2: 9-22.

Perrichot V. (2014) A new species of the Cretaceous ant *Zigrasimecia* based on the worker caste reveals placement of the genus in the Sphecomyrminae (Hymenoptera: Formicidae). *Myrmecological News*, 19: 165-169.

Perrichot V. (2015a) A new species of *Baikuris* (Hymenoptera: Formicidae: Sphecomyrminae) in mid-Cretaceous amber from France. *Cretaceous Research*, 52: 585-590.

Perrichot V. (2015b) AntWeb: Fossil Ants. http://www.antweb.org/taxonomicPage.do?rank=species&project=fossilants [accès 8.01.2015]

Perrichot V., Girard V. (2009) A unique piece of amber and the complexity of ancient forest ecosystems. *Palaios*, 24: 137-139.

Perrichot V., Engel M. S., Nel A., Ortega-Blanco J., Delclòs X., Soriano C., Tafforeau P. – In search of ant ancestors: Ruling out the Falsiformicidae (Hymenoptera: Chrysidoidea). [Soumis à *Systematic Entomology*, 12.2014].

Perrichot V., Lacau S., Néraudeau D., Nel A. (2008b) Fossil evidence for the early ant evolution. *Naturwissenschaften*, 95: 85-90.

Perrichot V., Marion L., Néraudeau D., Vullo R., Tafforeau P. (2008c) The early evolution of feathers: fossil evidence from Cretaceous amber of France. *Proceedings of the Royal Society B: Biological Sciences*, 275: 1197-1202.

Perrichot V., Nel A., Néraudeau D. (2007a) Schizopterid bugs (Insecta: Heteroptera) in mid-Cretaceous ambers from France and Myanmar (Burma). *Palaeontology*, 50: 1367-1374.

Perrichot V., Nel A., Néraudeau D., Lacau S., Guyot T. (2008a) New fossil ants in French Cretaceous amber (Hymenoptera: Formicidae). *Naturwissenschaften*, 95: 91-97.

Perrichot V., Néraudeau D. (2005) Reptile skin remains in the Cretaceous amber of France. *Comptes Rendus Palevol*, 4: 47-51.

Perrichot V., Néraudeau D. (2014) Introduction to thematic volume "Fossil arthropods in Late Cretaceous Vendean amber (northwestern France)" *Paleontological Contributions*, 10A: 1-4.

Perrichot V., Néraudeau D., Azar D., Menier J.-J., Nel A. (2002) A new genus and species of fossil mole cricket in the Lower Cretaceous amber of Charente-Maritime, SW France (Insecta: Orthoptera: Gryllotalpidae). *Cretaceous Research*, 23: 307-314.

Perrichot V., Néraudeau D., Nel A., de Ploëg G. (2007b) A reassessment of the Cretaceous amber deposits from France and their palaeontological significance. *African Invertebrates*, 48: 213-227.

Perrichot V., Néraudeau D., Tafforeau P. (2010) Charentese amber. *In*: Penney D. (ed.), *Biodiversity of fossils in amber from the major world deposits*. Siri Scientific Press, Manchester: 192-207.

Philippe M., Cuny G., Suteethorn V., Teerarungsigul N., Barale G., Thévenard F., Le Loeuff J., Buffetaut E., Gaona T., Košir A., Tong H. (2005) A Jurassic amber deposit in Southern Thailand. *Historical Biology*, 17: 1-6.

Poinar G.O. Jr. (2003) A rhabdocoel turbellarian (Platyhelminthes, Typhloplanoida) in Baltic amber with a review of fossil and sub-fossil platyhelminths. *Invertebrate Biology*, 122: 308-312.

Poinar G.O. Jr., Milki R. (2001) *Lebanese amber. The oldest insect ecosystem in fossilized resin*. Oregon State University Press, Corvallis, 96 p.

Poinar G.O.Jr., Waggoner B.M., Bauer U.-C. (1993) Terrestrial soft-bodied protists and other micro-organisms in Triassic amber. *Science*, 259: 222-224.

Rasnitsyn A.P. (1975) Hymenoptera Apocrita of Mesozoic. *Trudy Paleontologicheskogo Instituta, Akademii Nauk SSSR*, 147, 1-134 [in Russian].

Rasnitsyn A.P. (2002) Superorder Vespidea Laicharting, 1781. Order Hymenoptera Linné, 1758 (= Vespida Laicharting, 1781). *In*: Rasnitsyn A.P., Quicke D.L.J. (eds.), *History of insects*. Kluwer Academic Publishers, Dordrecht, The Netherlands, 242-254.

Sadowski E.-M., Beimforde C., Gube M., Rikkinen J., Singh H., Seyfullah L.J., Heinrichs J., Nascimbene P.C., Reitner J., Schmidt A.R. (2012) The anamorphic genus *Monotosporella* (Ascomycota) from Eocene amber and from modern *Agathis* resin. *Fungal Biology*, 116: 1099-1110.

Saint Martin S., Saint Martin J.-P., Schmidt A.R., Girard V., Néraudeau D., Perrichot V. (2015) The intriguing marine diatom genus *Corethron* in Late Cretaceous amber from Vendée (France). *Cretaceous Research*, 52: 64-72.

Sánchez-García A., Peñalver E., Bird G.J., Perrichot V., Delclòs X. – Paleobiology of tanaids (Crustacea: Tanaidomorpha) from Cretaceous French ambers: The earliest record of marsupial brood-care in crustaceans. [Soumis à *Journal of Systematic Palaeontology*, 01.2015]

Schlee D. (1973) Harzkonserviertefossile Vogelfedern aus untersten Kreide. *Journal of Ornithology*, 114: 207-219.

Schlüter T. (1978) Zur Systematik und Palökologie harzkonservierter Arthropoda einer Taphozönose aus dem Cenomanium von NW-Frankreich. *Berliner Geowissenschaftliche Abhandlungen (A)*, 9: 1-150

Schlüter T. (1989) Neue daten über harzkonservierte arthropoden aus dem Cenomanium NW-Frankreichs. *Documenta Naturae*, 56: 59-70.

Schlüter T. (2003) Fossil insects in Gondwana - localities and palaeodiversity trends. *Acta Zoologica Cracoviensia*, 46: 345-371.

Schmidt A.R., Beimforde C., Seyfullah L.J., Wege S.E., Dörfelt H., Girard V., Grabenhorst H., Gube M., Heinrichs J., Nel A., Nel P., Perrichot V., Reitner J., Rikkinen J. (2014) Amber fossils of sooty moulds. *Review of Palaeobotany and Palynology*, 200: 53-64.

Schmidt A.R., Dilcher D.L. (2007) Aquatic organisms as amber inclusions and examples from a modern swamp forest. *Proceedings of the National Academy of Sciences of the USA*, 104:16581-16585.

Schmidt A.R., Dörfelt H., Perrichot V. (2007) Carnivorous fungi from Cretaceous amber. *Science*, 318: 1743.

Schmidt A.R., Dörfelt H., Perrichot V. (2008) *Palaeoanellus dimorphus* gen. et sp. nov. (Deuteromycotina): a Cretaceous predatory fungus. *American Journal of Botany*, 95:1 328-1334.

Schmidt A.R., Jancke S., Lindquist E.E., Ragazzi E., Roghi G., Nascimbene P.C., Schmidt K., Wappler T., Grimaldi D.A. (2012) Arthropods in amber from the Triassic Period. *Proceedings of the National Academy of Sciences of the USA*, 109: 14796-14801.

Schmidt A.R., Perrichot V., Svojtka M., Anderson K.B., Belete K.H., Bussert R., Dörfelt H., Jancke S., Mohr B., Mohrmann E., Nascimbene P.C., Nel A., Nel P., Ragazzi E., Roghi G., Saupe E.E., Schmidt K., Schneider H., Selden P.A., Vávra N. (2010) Cretaceous African life captured in amber. *Proceedings of the National Academy of Sciences of the USA*, 107: 7329-7334.

Schmidt A.R., Ragazzi E., Coppellotti O., Roghi G. (2006) A microworld in Triassic amber. *Nature*, 444: 835.

Sendel N. (1742) *Historia succinorum corpora aliena involventium et naturae opere pictorum et caelatorum ex Augustorum I et II cimeliis Dresdae conditis aeri insculptorum*. Gleditsch, Leipzig, 328 p.

Smith J. (1896) On the discovery of fossil microscopic plants in the fossil amber of the Ayrshire coal-field. *Transactions of the Geological Society of Glasgow*, 10: 318-322.

Szwedo J., Nel A. (2015) The Cretaceous insects: a promising state of the art. *Cretaceous Research*, 52: 628-630.

Trevisani E., Ragazzi E. (2013) L'ambra nelle Alpi Meridionali: stato delle conoscenze. *Quaderni del Museo di Storia Naturale di Ferrara*, 1: 25-32.

van Bergen P.F., Collinson M.E., Scott A.C., de Leeuw J.W. (1995) Unusual resin chemistry from Upper Carboniferous pteridosperm resin rodlets. *American Chemical Society Symposium Series*, 617: 149-169.

Vullo R., Girard V., Azar D., Néraudeau D. (201). Mammalian hairs in Early Cretaceous amber. *Naturwissenschaften*, 97: 683-687.

Ward P.S. (2014) The phylogeny and evolution of ants. *Annual Review of Ecology, Evolution, and Systematics*, 45: 23-43.

Ward P.S., Brady S.G., Fisher B.L., Schultz T.R. (2010) Phylogeny and biogeography of dolichoderine ants: effects of data partitioning and relict taxa on historical inference. *Systematic Biology*, 59: 342-362.

Weitschat W., Wichard W. (2002) *Atlas of Plants and Animals in Baltic amber*. Verlag Dr. Friedrich Pfeil, München, 256 p.

Weitschat, W. Wichard, W. (2010) Baltic amber. *In*: D. Penney (ed.), *Biodiversity of Fossils in Amber from the Major World Deposits*. Siri Scientific Press, Manchester: 80-115.

Wilson E.O., Carpenter F.M., Brown W.L.Jr. (1967) The first Mesozoic ants. *Science*, 157: 1038-1040.

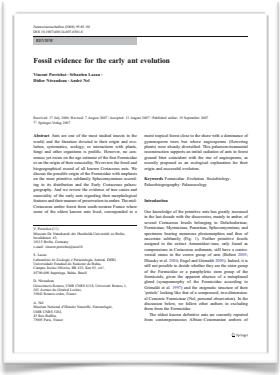
Wilson E.O., Hölldobler B. (2005) Eusociality: origin and consequences. *Proceedings of the National Academy of Sciences of the USA*, 102: 13367-13371.

Zherikhin V.V., Eskov K.Y. (1999) Mesozoic and Lower Tertiary resins in former USSR. *Estudios del Museo de Ciencias Naturales de Alava*, 14: 119-131.

Annexes

Sélection de publications

Evolution des insectes



Perrichot V., Lacau S., Néraudeau D., Nel A. 2008
Fossil evidence for the early ant evolution. *Naturwissenschaften*, 95:85-90.

Perrichot V. 2014 A new species of the Cretaceous ant *Zigrasimecia* based on the worker caste reveals placement of the genus in the Sphecomyrminae (Hymenoptera: Formicidae). *Myrmecological News*, 19, 165-169.

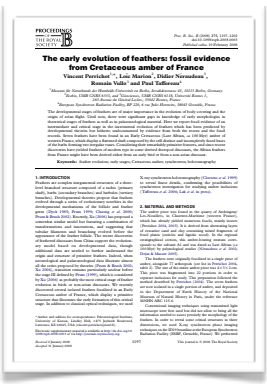
LaPolla J. S., Dlussky G. M., Perrichot V. 2013
Ants and the fossil record. *Annual Review of Entomology*, 58: 609-630.

Ecosystèmes résinifères

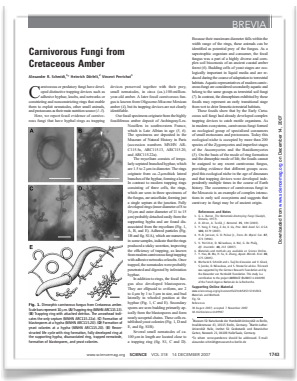
Perrichot V. 2004
Early Cretaceous amber from south-western France: Insight into the Mesozoic litter fauna. *Geologica Acta*, 2: 9-22.

Perrichot V., Girard V. 2009
A unique piece of amber and the complexity of ancient forest ecosystems. *Palaios*, 24: 137-139.

Préservations exceptionnelles



Perrichot V., Marion L., Néraudeau D., Vullo R., Tafforeau P. 2008
The early evolution of feathers: fossil evidence from Cretaceous amber of France. *Proceedings of the Royal Society B*, 275: 1197-1202.



Schmidt A.R., Dörfelt H., Perrichot V. 2007
Carnivorous fungi from Cretaceous amber. *Science*, 318: 1743.

Girard V., Schmidt A.R., Saint Martin S., Struwe S., Perrichot V., Saint Martin J.-P., Breton G., Néraudeau D. 2008
Evidence for marine microfossils from amber. *PNAS*, 105: 17426-17429.

Naturwissenschaften (2008) 95:85–90
DOI 10.1007/s00114-007-0301-8

REVIEW

Fossil evidence for the early ant evolution

Vincent Perrichot · Sébastien Lacau · Didier Néraudeau · André Nel

Received: 17 July 2006 / Revised: 7 August 2007 / Accepted: 11 August 2007 / Published online: 19 September 2007
© Springer-Verlag 2007

Abstract Ants are one of the most studied insects in the world; and the literature devoted to their origin and evolution, systematics, ecology, or interactions with plants, fungi and other organisms is prolific. However, no consensus yet exists on the age estimate of the first Formicidae or on the origin of their eusociality. We review the fossil and biogeographical record of all known Cretaceous ants. We discuss the possible origin of the Formicidae with emphasis on the most primitive subfamily Sphecomyrminae according to its distribution and the Early Cretaceous palaeogeography. And we review the evidence of true castes and eusociality of the early ants regarding their morphological features and their manner of preservation in amber. The mid-Cretaceous amber forest from south-western France where some of the oldest known ants lived, corresponded to a moist tropical forest close to the shore with a dominance of gymnosperm trees but where angiosperms (flowering plants) were already diversified. This palaeoenvironmental reconstruction supports an initial radiation of ants in forest ground litter coincident with the rise of angiosperms, as recently proposed as an ecological explanation for their origin and successful evolution.

Keywords Formicidae · Evolution · Sociobiology · Palaeobiogeography · Palaeoecology

V. Perrichot (✉)
Museum für Naturkunde der Humboldt-Universität zu Berlin,
Invalidenstr. 43,
10115 Berlin, Germany
e-mail: vincent.perrichot@neuf.fr

S. Lacau
Laboratório de Zoologia e Parasitologia Animal, DEBI,
Universidade Estadual do Sudoeste da Bahia,
Campus Juvino Oliveira, BR 415, Km 03, s/n°,
45700-000 Itapetinga, Bahia, Brazil

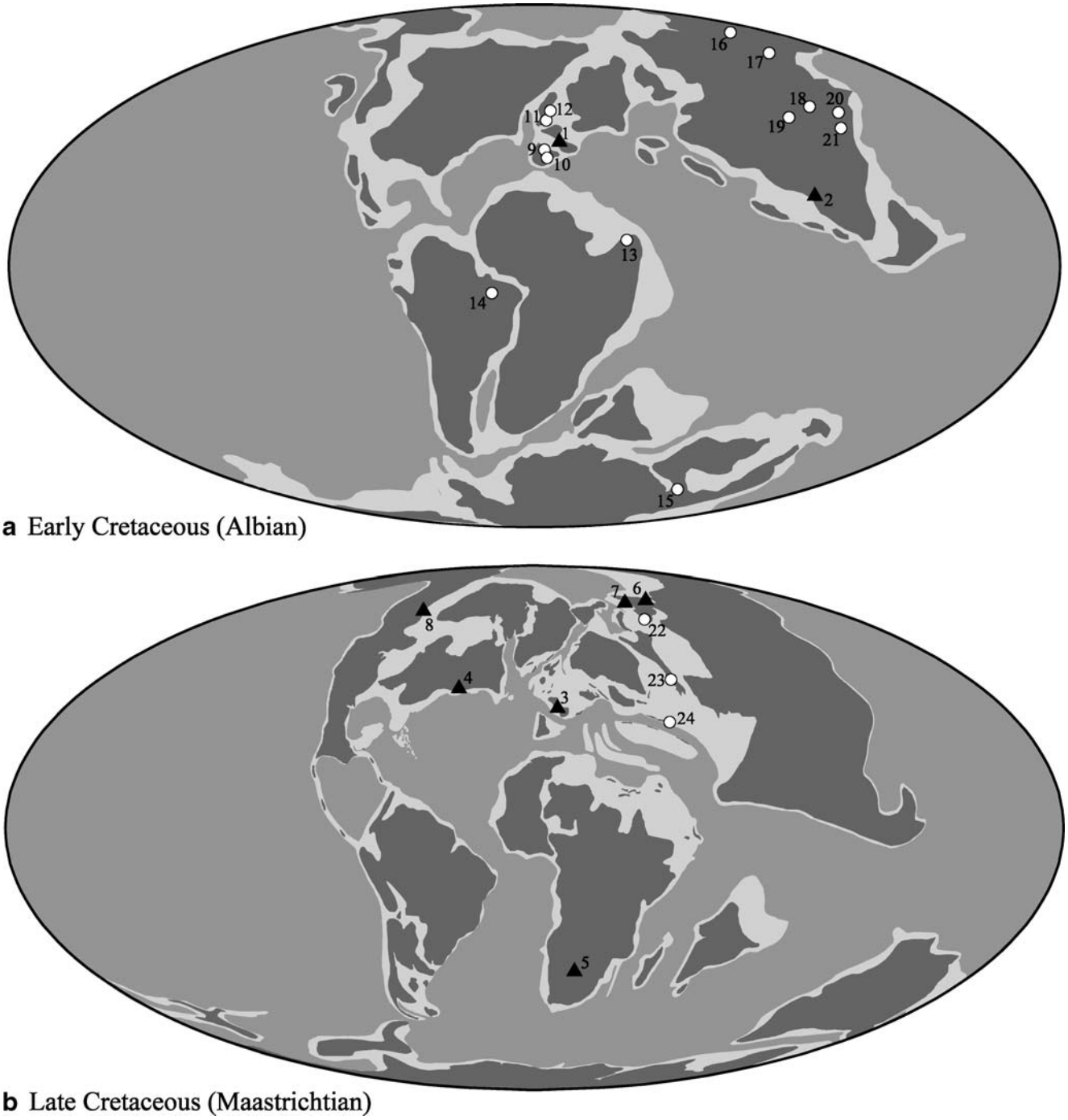
D. Néraudeau
Géosciences Rennes, UMR CNRS 6118, Université Rennes 1,
263 Avenue du Général Leclerc,
35042 Rennes cedex, France

A. Nel
Muséum National d'Histoire Naturelle, Entomologie,
UMR CNRS 5202,
45 Rue Buffon,
75005 Paris, France

Introduction

Our knowledge of the primitive ants has greatly increased in the last decade with the discoveries, mainly in amber, of several Cretaceous fossils belonging to Dolichoderinae, Formicinae, Myrmicinae, Ponerinae, Sphecomyrminae, and specimens bearing numerous plesiomorphies and thus of uncertain subfamily (Fig. 1). Further primitive fossils assigned to the extinct Armaniidae/-inae, only found as compressions in Cretaceous sediments, still have a controversial status in the crown group of ants (Bolton 2003; Dlussky et al. 2004; Engel and Grimaldi 2005). Indeed, it is still not possible to decide whether they are the sister group of the Formicidae or a paraphyletic stem group of the formicoids, given the apparent absence of a metapleural gland (synapomorphy of the Formicidae according to Grimaldi et al. 1997) and the enigmatic structure of their 'petiole' looking like that of a compressed, two-dimensional Cenozoic Formicinae (Nel, personal observation). In the discussion below, we follow other authors in excluding them from the Formicidae.

The oldest known definitive ants are currently reported from contemporaneous Albian–Cenomanian ambers of



France and Myanmar and are either considered as incertae sedis within the formicid subfamilies or belong to the extinct Sphecomyrminae (Dlussky 1996; Nel et al. 2004; Engel and Grimaldi 2005; Perrichot et al. 2007a). However, this Cretaceous subfamily is largely based on plesiomorphic characters and needs substantial additional fossils before being more accurately defined and its monophyly confidently stated.

In this paper, we discuss the possible geographical and ecological origin of the first Formicidae with an emphasis on the Sphecomyrminae, based on the biogeographical record of all known Cretaceous ants and their supposed habitat as reconstructed for the Cretaceous amber forest from south-western France. We also discuss the eusociality of these primitive ants as evidenced by their morphological features and their manner of preservation within the fossil record.

◀ **Fig. 1** Palaeogeographical distribution of Early (**a**) and Late (**b**) Cretaceous ants (indicated by *triangles*) and major insect fossil sites (indicated by *circles*, >100 insects, after Eskov 2002; Rasnitsyn and Zherikhin 2002; maps modified from Scotese 2001 and Ziegler and Rowley 1998). *1 Gerontoformica cretacica*, subfamily uncertain; *Haidomyrmodes mammuthus*, Sphecomyrminae; Late Albian, Charente-Maritime, France (Nel et al. 2004; Perrichot et al. 2007a). *2 Burmomyrma rossi*, *Myanmyrma gracilis*, subfamilies uncertain; *Haidomyrmex cerberus*, *Sphecomyrmodes orientalis*, *Sphecomyrma* sp., Sphecomyrminae; Late Albian, Myanmar (Dlussky 1996; Grimaldi et al. 2002; Grimaldi and Engel 2005). *3 Haidomyrmodes mammuthus*, *Sphecomyrmodes occidentalis*, Sphecomyrminae; Early Cenomanian, Charente-Maritime, France (Perrichot et al. 2007a). *4 Sphecomyrma freyi*, *Sphecomyrma mesaki*, *Sphecomyrma* sp., *Baikuris casei*, Sphecomyrminae; *Brownimecia clavata*, Ponerinae; *Kyromyrma neffi*, Formicinae; Turonian, New Jersey (Wilson et al. 1967; Grimaldi et al. 1997; Grimaldi and Agosti 2000; Engel and Grimaldi 2005). *5 Afropone oculata*, *A. orapa*, *Afromyrma petrosa*, subfamilies uncertain; Turonian, Orapa, Botswana (Dlussky et al. 2004; Archibald et al. 2006). *6 Cretomyrma arnoldi*, *C. unicornis*, *Dlusskyidris zherichini*, Sphecomyrminae; Santonian, Yantardakh, Taimyr peninsula, Siberia (Dlussky 1975). *7 Baikuris mandibularis*, *B. mirabilis*, Sphecomyrminae; Santonian? Taimyr Lake, Siberia (Dlussky 1987); *8 Sphecomyrma canadensis*, Sphecomyrminae; *Canapone dentata*, Ponerinae; *Eotapinoma macalpini*, Dolichoderinae?; *Cananeuretus occidentalis*, Aneuretinae?; Campanian, Alberta, Canada (Wilson 1985; Dlussky 1999; Engel and Grimaldi 2005). *9* Álava amber, Spain, Late Aptian–Early Albian; *10* Montsec, Spain, Berriasian–Valanginian; *11* Purbeck Group, England, Berriasian; *12* Wealden Supergroup, England, Hauterivian–Barremian; *13* Lebanese amber, Hauterivian–Aptian; *14* Santana Fm, Brazil, Aptian; *15* Koonwarra beds, Australia, Aptian; *16* Khetana, East Siberia, Middle Albian; *17* Baissa, Central Siberia, Neocomian; *18* Khutel-Khara, Mongolia, Early Cretaceous; *19* Bon-Tsagan, Mongolia, Barremian–Aptian; *20* Yixian Fm, China, Barremian; *21* Laiyang Fm, China, Early Neocomian; *22* Agapa, Siberia, Late Cenomanian; *23* Kzyl-Zhar, Kazakhstan, Turonian; *24* Agdzakend, Azerbaijan, Cenomanian

Origin of ants

As shown by the oldest known fossils recently discovered in French and Burmese ambers, the Early/mid-Cretaceous ants appear to be unexpectedly diversified with seven distinct genera within at least two subfamilies recorded from these two ambers: *Haidomyrmodes*, *Haidomyrmex*, *Sphecomyrma* and *Sphecomyrmodes* in the Sphecomyrminae; *Burmomyrma*, *Gerontoformica* and *Myanmyrma* in uncertain subfamilies. Important morphological differences between them represent a strong evolution from the primitive shape of their common ancestor. Furthermore, the contemporaneous occurrence of *Haidomyrmodes*, *Haidomyrmex* and *Sphecomyrmodes* in French and Burmese mid-Cretaceous ambers implies a wide distribution of ants at this time and an earlier origin of the tribes Haidomyrmecini and Sphecomyrmini on a same palaeocontinent. According to palaeogeographical maps (Ziegler 1990; Masse et al. 1993; Scotese 2001 and http://www.scotese.com as accessed in April 2007), the western part of Laurasia, including France, was fragmented in insular landmasses and separated from Eastern Laurasia by epicontinental seas since at least the Early Aptian (ca. 120 Ma) till the Maastrichtian (ca. 70 Ma). Therefore, the Sphecomyrminae would have originated no later than the Early Aptian. These results on the high morphological disparity and wide distribution of early ants well agree with an Earliest Cretaceous age of the Formicidae, as estimated from the fossil record of ants and their vespoid relatives (Grimaldi and Engel 2005). Some molecular phylogenetic studies suggested that the first ants arose much earlier in the Earliest Cretaceous or the Jurassic with an estimated minimum/maximum age of 140/168 Ma (Crozier et al. 1997; Moreau et al. 2006). According to Brady et al. (2006), however, a Jurassic origin is highly unlikely. They estimated an age of 115/140 Ma for the crown group ants, based on a wider molecular analysis and incorporation of the fossil record of ants and other aculeate Hymenoptera. So far, fossil ants do not occur before the Albian. Owing to the relative scarcity of Early Cretaceous fossil insect sites, this absence of ant anteriorly to the Albian certainly reflects a bias in the fossil record. However, the fact that they were not collected yet in the very rich fossil deposits of Australia, Brazil, China, England, Lebanon, Russia and Spain (Table 1) likely corresponds to their absence in the corresponding ecosystems and well agrees with the hypothesis that ant subfamilies mainly diverged since the Albian and through the Turonian, coinciding with the rise of angiosperms (Dlussky et al. 2004; Grimaldi and Agosti 2000; Moreau et al. 2006; Ward and Brady 2003; Wilson and Hölldobler 2005a). Because they were already widespread and rather well-diversified at the end of the Albian, it is expected to find fossil ants earlier in the Cretaceous, even if rare and thus with a low probability of being fossilized.

Despite the present and updated data on French and Burmese Albian ants, it is still difficult to estimate the ancestral subfamily. Haidomyrmecini are apparently not basal in ant phylogeny (Bolton 2003), and *Burmomyrma*, *Myanmyrma* and *Gerontoformica* currently remain of uncertain affinities. Given its combination of characters, however, *Gerontoformica* could be close to an "ancestor" of the two subfamilies Formicinae and Dolichoderinae (Nel et al. 2004).

Palaeobiogeography and palaeoecology

Extant Formicidae are cosmopolitan, but numerous lineages show a continental endemism (Bolton 1995). According to Grimaldi and Agosti (2000), ancestors could have been isolated on different landmasses after the Early Cretaceous fragmentation of Pangaea, and then diversified independently. However, the Early Cretaceous occurrence of ants and 'formicoids' on Gondwana is not yet assessed; some fossils found in Australia, Brazil and Lebanon were attributed to

Table 1 Proportions of Hymenoptera and Formicidae for major fossiliferous Cretaceous deposits

Fossil deposits	A/C	Age	Total insects	Total Hymenoptera	Total ants	References
Lebanon[a]	A	Hauterivian/ Barremian	2,837	250	0	Azar (2000)
Baissa, Siberia	C	Neocomian	>20,000	?	0	Zherikhin et al. (1999); Rasnitsyn and Zherikhin (2002)
Montsec, Spain	C	Berriasian/ Valanginian	900	30	0	Delclòs, personal communication; Rasnitsyn and Martínez-Delclòs (2000)
Las Hoyas, Spain	C	Barremian	1,300	6	0	Delclòs, personal communication
China[b]	C	Neocomian	>580	>72	0	Ren, personal communication
England[c]	C	Neocomian	13,000	48	0	Rasnitsyn et al. (1998)
Australia[d]	C	Aptian	300	10	0	Jell and Duncan (1986)
Ceará, Brazil	C	Aptian	>3,000	26	0	Darling and Sharkey (1990)
Álava, Spain	A	Aptian/Albian	2,300	500	0	Delclòs et al. (2007)
Myanmar	A	Albian	4,210	364	9	Grimaldi et al. (2002)
Charente, France	A	Albian/ Cenomanian	911	135	17	Perrichot et al. (2007b)
Agapa, Siberia	A	Cenomanian	>700	?	0	Eskov (2002)
New Jersey, USA	A	Turonian	>1,100	250	8	Grimaldi et al. (2000)
Orapa, Botswana	C	Turonian	641	108	4	Brothers and Rasnitsyn (2003)
				86	10	Dlussky et al. (2004)
Taimyr, Siberia	A	Santonian	>3,000	?	9	Eskov (2002); Dlussky (1975, 1987)
Alberta, Canada	A	Campanian	>3,000	>300	6	Pike (1994)

A: amber, *C*: compression
[a] Hammana, Jezzine and Bcharré
[b] Yixian and Laiyang Fms
[c] Purbeck and Wealden groups
[d] Koonwarra beds

Formicidae, but this attribution was later revised and the fossils assigned to other hymenopteran families (Jell and Duncan 1986; Brandão et al. 1989; Darling and Sharkey 1990; Naumann 1993; Dlussky 1999; Poinar and Milki 2001). The oldest accurate record of Gondwanan ants is from the Turonian of Botswana (Fig. 1b) with a rather diverse fauna of Formicidae of uncertain subfamilies (Dlussky et al. 2004; Archibald et al. 2006). If not a bias of the fossil record, and given that ants and Armaniidae are lacking in the three rich Early Cretaceous Gondwanan deposits, this may indicate an earlier diversification of ants on Laurasia. It is interesting to note that the earliest known Armaniidae occur in distinct Barremian/Aptian, Albian and Cenomanian deposits of Russia (Dlussky 1983, 1999), so that there is still no fossil evidence that Armaniidae and Formicidae have co-existed before the Turonian—e.g. in Kazakhstan (Dlussky 1975). Formicidae and Armaniidae (if the later is monophyletic) could have evolved independently on distinct Laurasian insular landmasses, rendering difficult the colonisation of other islands, which could explain their absence in other highly fossiliferous Laurasian outcrops from Spain, England, Russia or China.

Finally, the extreme scarcity of Early Cretaceous ants could also be related to peculiar, confined habitats of the primitive ants, which would have limited the possibility of fossilisation. Wilson and Hölldobler (2005a) have suggested that the first ants arose and radiated in forest ground litter and soil with the rise of angiosperms. The presence of ants in the arthropod fauna of the Cretaceous French amber strongly supports this scenario, as it probably stems from the unusual preservation of litter-inhabiting species in addition to organisms living on trees (Perrichot 2004, 2005). The corresponding palaeoenvironment is estimated to have been a tropical moist forest growing near the shore in a mosaic of estuarine and mangrove-like context, and thus with a marine influence (Perrichot 2005). The amber-producer (Araucariaceae or the extinct gymnosperm family Cheirolepidiaceae) was likely the dominant tree of this ecosystem but various angiosperms were also present in some confined, limnetic environments (Gomez et al. 2004).

Conclusion

Haidomyrmodes mammuthus is the first Cretaceous ant species known by both the gyne and worker (Perrichot et al. 2007a). This provides evidence for the true sociality of

primitive ants based on the differentiation of two morphological castes, which was hitherto suggested by the existence of workers in other Cretaceous genera, but where the gyne remained unknown. Further evidences of eusociality for the early ants are based on morphological characters such as the metapleural gland or the structure and relative length of antennal segments (Grimaldi et al. 1997). Dlussky (1996) suggested semi-sociality for *Haidomyrmex* with its highly specialized craniomandibular system "which has arisen only in a specialized hunter providing its progeny with food". Engel and Grimaldi (2005) suggested that the type specimen of *Haidomyrmex* could be a kind of "major" worker, unable to feed itself, which implies the presence of "minor" workers with mandibles of different shape. Only workers and gyne (but not males) of the recent genus *Harpegnathos* have rather similar mandibles with distal half curved upward (but distinctly less than in the Haidomyrmecini) and a tooth at elbow (Emery 1911, internet site http://www.antweb.org/world.jsp from April 2007). *Harpegnathos* species are predaceous and the workers can feed themselves (Hölldobler and Wilson 1990: 569–570). It is also notable that workers have ocelli, which is rare in Ponerinae. *Haidomyrmodes* is represented by workers with ocelli and an alate gyne with distinct antennal scapes, both having mandibles rather similar to those of the type specimen of *Haidomyrmex*. This suggests that these mandibles were likely functional for hunting in all castes. It remains that a social organisation is strongly suggested for the Early Cretaceous ant genus *Haidomyrmodes*.

Primitive ants from Cretaceous amber of France now include an alate gyne in one genus (*Haidomyrmodes*) and workers in three distinct genera (*Haidomyrmodes*, *Sphecomyrmodes* and *Gerontoformica*). Furthermore, the occurrence of two workers of *Sphecomyrmodes* in a single piece of amber suggests that they were foraging socially, as is the case for workers of *Sphecomyrma* in Turonian New Jersey amber (Grimaldi and Engel 2005). In addition, the oldest known spiders of the family Zodariidae are fossilised in the same amber from Archingeay/Les-Nouillers (Perrichot 2005). It is interesting to note that these fossils possess characteristics of modern representatives, which are highly specialized predators feeding exclusively on ants (Pekár and Král 2002). Such a specialization implies that prey were rather abundant and possessed effective methods of defence. If the strict myrmecophagous habit assumed for these Cretaceous zodariids is valid, then their occurrence may indicate a relative abundance of ants in Western Europe as soon as the Late Albian.

Other eusocial insect lineages such as termites, wasps and bees also developed during the Early Cretaceous (Grimaldi and Engel 2005; Poinar and Danforth 2006). Wilson and Hölldobler (2005b) have discussed and proposed a new model for the origin of the insect eusociality, but the fact that this phenomenon apparently occurred in a relatively short period during the Early Cretaceous in insect clades of different ecologies remains largely unexplained.

Acknowledgements We thank Thierry Guyot and Eric Depré who gave some of the fossil ants discussed in this paper; Alain Canard (Univ. Rennes 1) for the preliminary comments on the zodariid fossil spiders; Carl Findley for checking the English; and the anonymous reviewers for the useful comments on the manuscript. This work was supported by the CNRS programme ECLIPSE II on "Cretaceous climates and ecosystems" and by Alexander von Humboldt Foundation for VP.

References

Archibald SB, Cover SP, Moreau CS (2006) Bulldog ants of the Eocene Okanagan Highlands and history of the subfamily (Hymenoptera: Formicidae: Myrmeciinae). Ann Entomol Soc Am 99:487–523

Azar D (2000) Les ambres mésozoïques du Liban. Ph.D. dissertation, University Paris XI, Orsay, Paris, pp 1–164

Bolton B (1995) A taxonomic and zoogeographical census of the extant ant taxa (Hymenoptera: Formicidae). J Nat Hist 29:1037–1056

Bolton B (2003) Synopsis and classification of Formicidae. Mem Am Entomol Inst 71:1–370

Brady SG, Schultz TR, Fisher B, Ward PS (2006) Evaluating alternative hypotheses for the early evolution and diversification of ants. Proc Natl Acad Sci USA 103:18172–18177

Brandão CRF, Martins-Neto RG, Vulcano MA (1989) The earliest known fossil ant (first Southern Hemisphere Mesozoic record) (Hymenoptera, Formicidae, Myrmicinae). Psyche 96:195–208

Brothers DJ, Rasnitsyn AP (2003) Diversity of Hymenoptera and other insects in the Late Cretaceous (Turonian) deposits at Orapa, Botswana: a preliminary review. Afr Entomol 11:221–226

Crozier RH, Jermiin LS, Chiotis M (1997) Molecular evidence for a Jurassic origin of ants. Naturwissenschaften 84:22–23

Darling DC, Sharkey MJ (1990) Order Hymenoptera. In: Grimaldi DA (ed) Insects from the Santana Formation, Lower Cretaceous, of Brazil. Bull Am Mus Nat Hist 195:123–153

Delclòs X, Arillo A, Peñalver E, Barrón E, Soriano C, López Del Valle R, Bernárdez E, Corral C, Ortuño VM (2007) Fossiliferous amber deposits from the Cretaceous (Albian) of Spain. Comptes Rendus Palevol 6:135–149

Dlussky GM (1975) Superfamily Formicoidea Latreille, 1802. Family Formicidae Latreille, 1802. In: Rasnitsyn AP (ed) Hymenoptera Apocrita of the Mesozoic. Trans Paleontol Inst Acad Sci USSR 147:114–122 (in Russian)

Dlussky GM (1983) A new family of Upper Cretaceous Hymenoptera: an "intermediate link" between the ants and the scolioids. Paleontol Z 3:65–78 (in Russian, English translation in 1984, Paleontol J 17:63–76)

Dlussky GM (1987) New Formicoidea (Hymenoptera) of the Upper Cretaceous. Paleontol Z 1987(1):131–135 (in Russian, English translation in 1988, Palaeontol J 21:146–150)

Dlussky GM (1996) Ants (Hymenoptera: Formicidae) from Burmese amber. Paleontol J 30:449–454

Dlussky GM (1999) The first find of the Formicoidea (Hymenoptera) in the Lower Cretaceous of the Northern Hemisphere. Paleontolol J 33:274–277

Dlussky GM, Brothers DJ, Rasnitsyn AP (2004) The first Late Cretaceous ants (Hymenoptera: Formicidae) from southern Africa, with comments on the origin of the Myrmicinae. Insect Syst Evol 35:1–13

Emery C (1911) Hymenoptera fam. Formicidae subfam. Ponerinae. Genera Insectorum 118:1–125

Engel MS, Grimaldi DA (2005) Primitive new ants in Cretaceous amber from Myanmar, New Jersey, and Canada (Hymenoptera: Formicidae). Am Mus Novit 3485:1–23

Eskov KY (2002) Alphabetic list of selected insect fossil sites. 4.2. Fossil resins. In: Rasnitsyn AP, Quicke DLJ (eds) History of insects. Kluwer, Dordrecht, The Netherlands, pp 444–446

Gomez B, Daviero-Gomez V, Perrichot V, Thévenard F, Coiffard C, Philippe M, Néraudeau D (2004) Assemblages floristiques de l'Albien-Cénomanien de Charente-Maritime (SO France). Ann Paléontol 90:147–159

Grimaldi DA, Agosti D (2000) A formicine in New Jersey Cretaceous amber (Hymenoptera: Formicidae) and early evolution of the ants. Proc Natl Acad Sci USA 97:13678–13683

Grimaldi DA, Engel MS (2005) Evolution of the insects. Cambridge University Press, New York

Grimaldi DA, Agosti D, Carpenter JM (1997) New and rediscovered primitive ants (Hymenoptera: Formicidae) in Cretaceous amber from New Jersey, and their phylogenetics relationships. Am Mus Novit 3208:1–43

Grimaldi DA, Shedrinsky AM, Wampler TP (2000) A remarkable deposit of fossiliferous amber from the Upper Cretaceous (Turonian) of New Jersey. In: Grimaldi DA (ed) Studies on fossils in amber, with particular reference to the Cretaceous of New Jersey. Backhuys Publishers, Leiden, pp 1–76

Grimaldi DA, Engel MS, Nascimbene PC (2002) Fossiliferous Cretaceous amber from Myanmar (Burma): its rediscovery, biotic diversity, and paleontological significance. Am Mus Novit 3361:1–71

Hölldobler B, Wilson EO (1990) The ants. Harvard University Press, Cambridge

Jell PA, Duncan PM (1986) Invertebrates, mainly insects, from the freshwater, Lower Cretaceous, Koonwarra fossil bed, (Korumburra Group), South Gippsland, Victoria. In: Jell PW, Roberts J (eds) Plants and invertebrates from the Lower Cretaceous Koonwarra fossil bed, South Gippsland, Victoria. Mem Assoc Australas Palaeontol 3:111–205

Masse JP, Bellion Y, Benkhelil J, Dercourt J, Guiraud R, Ricou LE (1993) Lower Aptian (114–112 Ma). In: Dercourt J, Ricou LE, Vrielynck B (eds) Atlas Tethys, palaeoenvironmental maps. Gauthier-Villars, Paris, pp 135–152+1 map

Moreau CS, Bell CD, Vila R, Archibald SB, Pierce NE (2006) Phylogeny of the ants: diversification in the age of angiosperms. Science 312:101–104

Naumann ID (1993) The supposed Cretaceous ant *Cretacoformica explicata* Jell and Duncan. J Aust Entomol Soc 32:353–356

Nel A, Perrault G, Perrichot V, Néraudeau D (2004) The oldest ant in the Lower Cretaceous amber of Charente-Maritime (SW France) (Insecta: Hymenoptera: Formicidae). Geologica Acta 2:23–29

Pekár S, Král J (2002) Mimicry complex in two central European zodariid spiders (Araneae: Zodariidae): how *Zodarion* deceives ants. Biol J Linn Soc 75:517–532

Perrichot V (2004) Early Cretaceous amber from south-western France: insight into the Mesozoic litter fauna. Geologica Acta 2:9–22

Perrichot V (2005) Environnements paraliques à ambre et à végétaux du Crétacé nord-aquitain (Charentes, Sud-Ouest de la France). Mém Géosciences Rennes 118:1–310

Perrichot V, Nel A, Néraudeau D, Lacau S, Guyot T (2007a) New fossil ants in French Cretaceous amber (Hymenoptera: Formicidae). Naturwissenschaften DOI 10.1007/s00114-007-302-7

Perrichot V, Néraudeau D, Nel A, De Ploëg G (2007b) A reassessment of the Cretaceous amber deposits from France and their palaeontological significance. African Invertebrates 48:213–227

Pike EM (1994) Historical changes in insect community structure as indicated by hexapods of Upper Cretaceous Alberta (Grassy Lake) amber. Can Entomol 126:695–702

Poinar GO, Danforth BN (2006) A fossil bee from Early Cretaceous Burmese amber. Science 314:614

Poinar GO, Milki R (2001) Lebanese amber. The oldest ecosystem in fossilized resin. Oregon State University Press, Corvallis

Rasnitsyn AP, Martínez-Delclòs X (2000) Wasps (Insecta: Vespida = Hymenoptera) from the Early Cretaceous of Spain. Acta Geol Hisp 35:65–95

Rasnitsyn AP, Zherikhin VV (2002) Alphabetic list of selected insect fossil sites. 4.1. Impression fossils. In: Rasnitsyn AP, Quicke DLJ (eds) History of insects. Kluwer, Dordrecht, the Netherlands, pp 437–444

Rasnitsyn AP, Jarzembowski EA, Ross AJ (1998) Wasps (Insecta: Vespida = Hymenoptera) from the Purbeck and Wealden (Lower Cretaceous) of southern England and their biostratigraphical and palaeoenvironmental significance. Cretac Res 19:329–391

Scotese CR (2001) Atlas of earth history, vol 1. PALEOMAP Project, Arlington, Texas

Ward PS, Brady SG (2003) Phylogeny and biogeography of the ant subfamily Myrmeciinae (Hymenoptera: Formicidae). Invertebrate Systematics 17:361–386

Wilson EO (1985) Ants from the Cretaceous and Eocene amber of North America. Psyche 92:205–216

Wilson EO, Hölldobler B (2005a) The rise of the ants: a phylogenetic and ecological explanation. Proc Natl Acad Sci USA 102:7411–7414

Wilson EO, Hölldobler B (2005b) Eusociality: origin and consequences. Proc Natl Acad Sci USA 102:13367–13371

Wilson EO, Carpenter FM, Brown WL Jr (1967) The first Mesozoic ants, with the description of a new subfamily. Psyche 74:1–19

Zherikhin VV, Mostovski MB, Vršanský P, Blagoderov VA, Lukashevich ED (1999) The unique Lower Cretaceous locality Baissa and other contemporaneous fossil insect sites in North and West Transbaikalia. In: Vršanský P (ed.) Proceedings of the First Palaeoentomological Conference, Moscow, 1998. AMBA Projects, Bratislava, Slovakia, pp 185–191

Ziegler PA (1990) Geological atlas of western and central Europe, 2nd ed. Shell International Petroleum, Geological Society, London

Ziegler AM, Rowley DB (1998) The vanishing record of epeiric seas with emphasis on the Late Cretaceous "Hudson Seaway". In: Crowley TJ, Burke K (eds) Tectonic boundary conditions for climate reconstructions. Oxford University Press, Oxford, pp 147–165

Myrmecological News	19	165-169	Vienna, January 2014

A new species of the Cretaceous ant *Zigrasimecia* based on the worker caste reveals placement of the genus in the Sphecomyrminae (Hymenoptera: Formicidae)

Vincent PERRICHOT

Abstract

Zigrasimecia ferox sp.n. is described and illustrated based on workers fossilized in 99 million-year-old Burmese amber. The new specimens allow the confident assignment of *Zigrasimecia* BARDEN & GRIMALDI, 2013, a genus recently described based upon a gyne from the same amber deposit, to the extinct subfamily Sphecomyrminae, and more specifically to the tribe Sphecomyrmini.

Key words: Stem-group ants, Formicidae, Sphecomyrmini, amber, Myanmar, Cenomanian.

Myrmecol. News 19: 165-169
ISSN 1994-4136 (print), ISSN 1997-3500 (online)

Received 16 July 2013; revision received 10 October 2013; accepted 24 October 2013
Subject Editor: Herbert Zettel

Vincent Perrichot, Géosciences Rennes & OSUR, UMR CNRS 6118, Université de Rennes 1, Campus de Beaulieu bat. 15, 263 avenue du Général Leclerc, 35042 Rennes cedex, France. E-mail: vincent.perrichot@univ-rennes1.fr

Introduction

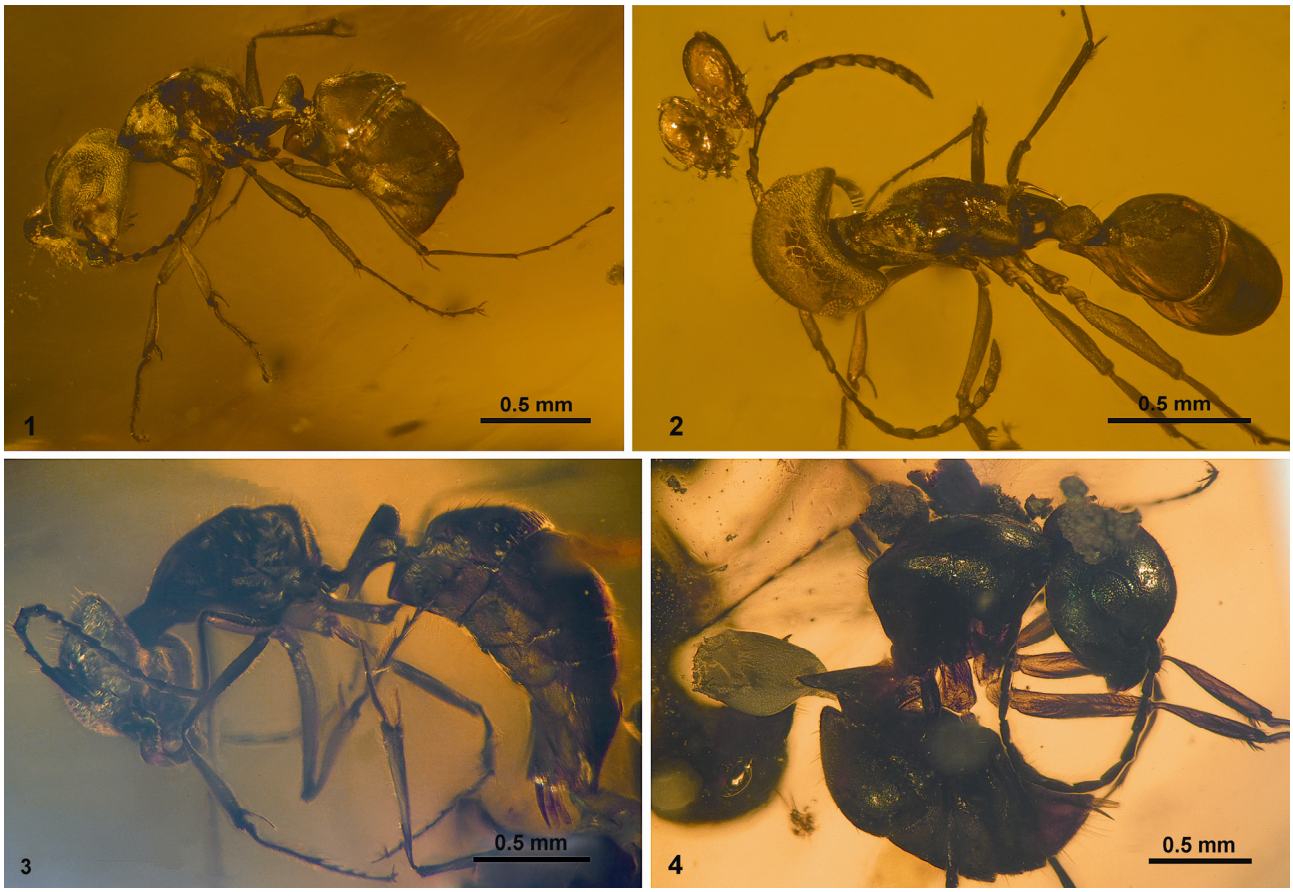
Ants are a rare component of the Cretaceous paleoentomofauna. Since the first description of *Sphecomyrma*, from 92 million-year-old (Myo) New Jersey amber, 46 years ago by WILSON & al. (1967), only a few other Cretaceous ants have been discovered totalling no more than 28 species described in 22 genera (LAPOLLA & al. 2013: tab. 1; with addition of BARDEN & GRIMALDI 2013, MCKELLAR & al. 2013a, b). More than half of these species were described in the last decade (DLUSSKY & al. 2004, NEL & al. 2004, ENGEL & GRIMALDI 2005, PERRICHOT & al. 2008, BARDEN & GRIMALDI 2012, 2013, MCKELLAR & al. 2013a, b), reflecting the renewed interest in paleontological research on the origins of ants.

The greatest diversity of Cretaceous ants occurs in amber from Myanmar (ca. 99 Myo) and Canada (79 Myo). The latter is the only deposit revealing potential crown-group ants in the Aneuretinae, Dolichoderinae, and Ectatomminae, though the exact affinities of these fossils are still debated (DLUSSKY 1999, ENGEL & GRIMALDI 2005, MCKELLAR & al. 2013a). Most of the ants found in Burmese amber belong in the Sphecomyrminae, an exclusively Cretaceous and yet enigmatic subfamily, but a couple of fossils cannot be assigned to any extant or extinct subfamily. Among these, the latest contribution made recently by BARDEN & GRIMALDI (2013) depicted the gyne of *Zigrasimecia*, a new genus of highly specialized ants that they could not assign to any of the known subfamilies. Instead, they suggested possible affinities with the genera *Sphecomyrmodes* ENGEL & GRIMALDI, 2005 (Sphecomyrminae) and *Gerontoformica* NEL & PERRAULT, 2004 (subfamily incertae sedis). I was astonished when *Zigrasimecia* was published earlier this year, because at the same time I was completing a manuscript dealing with the description of a very similar morphotype, although from the worker caste. Owing to the few occurrences of Cretaceous ants, this is a very rare case of concurrent and synchronous research work based on material from the same fossil deposit. I provide herein the supplemental description and illustration of the worker caste of *Zigrasimecia*, with the description of a new species, and a further discussion on its affinities within the Formicidae.

Material and methods

The present study comprises six new specimens originally preserved in two pieces of burmite, the Cretaceous amber from the State of Kachin in northern Myanmar. These were obtained at a mine near Tanai village, in the Hukawng Valley. A radiometric age of 98.79 ± 0.62 Ma (earliest Cenomanian) was recently established for burmite using U-Pb dating of zircons contained in volcanic rock clasts from the surrounding sediment (SHI & al. 2012).

Three complete worker specimens as well as fragments of two other workers (nine legs and two gastral apices preserved at surface of amber, revealing internal structures) were preserved within a piece of clear yellow amber along with four midges (Nematocera), one wasp (Platygastridae), two cockroaches (Blattaria), and eight mites (Acari). The presence of these syninclusions as well as organic debris made the detailed observation of each specimen difficult, so the piece has been cut into three parts then polished on all sides, with two complete and two fragmentary ants now in one small block and one complete ant in another block. A sixth, fragmentary (only the head and mesosoma preserved) specimen was found in another piece of clear yellow amber, with five workers of *Sphecomyrmodes orientalis* ENGEL & GRIMALDI, 2005 as syninclusions. All material is in the private collection of Jens-Wilhelm Janzen (Germany) but should be ultimately purchased by an academic institution.



Figs. 1 - 4: Photographs of worker specimens of *Zigrasimecia ferox* sp.n. (1) Paratype JWJ-Bu17, profile view. (2) Paratype JWJ-Bu17, dorsal view.(3) Holotype JWJ-Bu18a, profile view. (4) Paratype JWJ-Bu18b, profile view.

The fossils were examined under incident and transmitted light using a Leica MZ APO stereomicroscope, and imaged with the aid of an attached Canon 5D Mark II camera. Stacks of photographs taken at different depths of field were merged using HeliconFocus 5.2 software. Photographs and final repository data will be available on AntWeb (http://www.antweb.org). Measurements were taken at 63× and 80× magnification using a dual-axis micrometer.

Systematic paleontology

Sphecomyrminae WILSON & BROWN, 1967

Sphecomyrmini WILSON & BROWN, 1967

***Zigrasimecia* BARDEN & GRIMALDI, 2013**

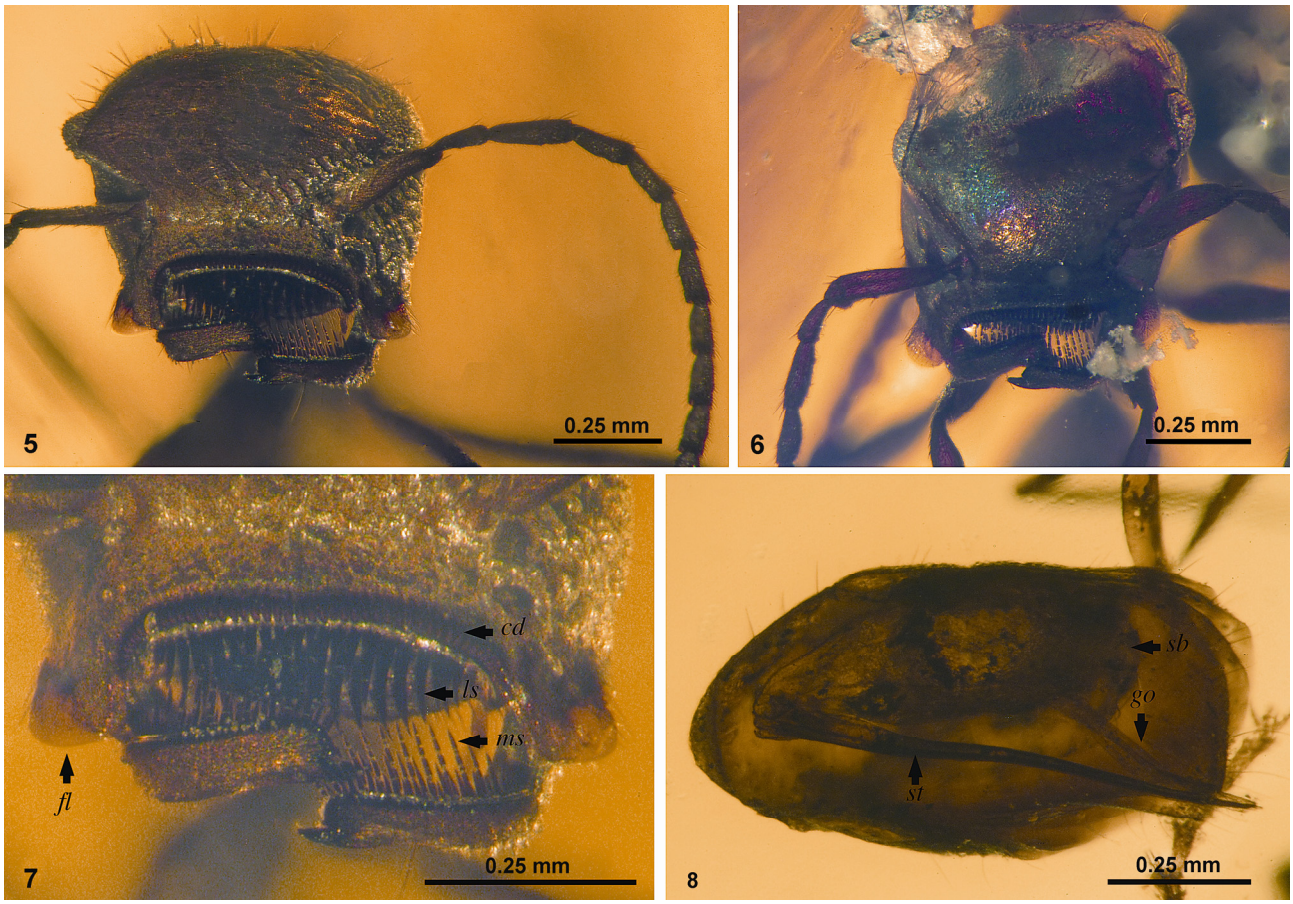
Supplemental diagnosis, worker: Small wingless females of varied body length (2.0 - 2.8 mm) without remarkable cuticular sculpturing. Head very similar to that of gyne (see BARDEN & GRIMALDI, 2013) but without ocelli and without rugose patches on vertex; with toruli ring-like, not raised; with a single row of clypeal denticles (i.e., no rows of subclypeal combs); with vertexal (posterodorsal) margin strongly concave. Mesosoma entirely smooth, without distinctive spine, foveae, or carinae; promesonotal suture indistinct, in profile view dorsal mesosomal surface a continuous curve; posterior (declivous) propodeal surface distinctly concave, high, strongly angled with dorsal propodeal surface; bulla hemispherical. All legs with femur and tibia dorso-ventrally flattened, tibiae carinate anteriorly and posteriorly; tibial spur formula 3 - 2 - 2. Petiole consists of high scale strongly inclined posteriorly, with anterior surface flat, posterior surface convex and nearly half as tall; subpetiolar process present, in profile view a moderately high, short longitudinal lamella pointing anteroventrally. Gaster with five visible segments (abdominal segments AIII-AVII); tergite of AIII with anterior surface vertical, sternite of AIII anteriorly with large medial longitudinal flange protruding underneath helcium; tergite IV largest abdominal sclerite; sting large, retractable, external part basally enclosed by gonostyli.

***Zigrasimecia ferox* sp.n.** (Figs. 1 - 10)

Type material: Holotype JWJ-Bu18a, paratypes JWJ-Bu17, JWJ-Bu18b, three complete workers; paratypes JWJ-Bu18c and JWJ-Bu18d, two partial workers preserved by legs and gastral apices; paratype JWJ-Bu23, a partial worker missing the metasoma. In amber from early Late Cretaceous (Earliest Cenomanian, 98.79 ± 0.62 Ma) of Hukawng Valley, Kachin State, northern Myanmar. Provisionally in J.-W. Janzen collection.

Diagnosis, worker: As for the genus.

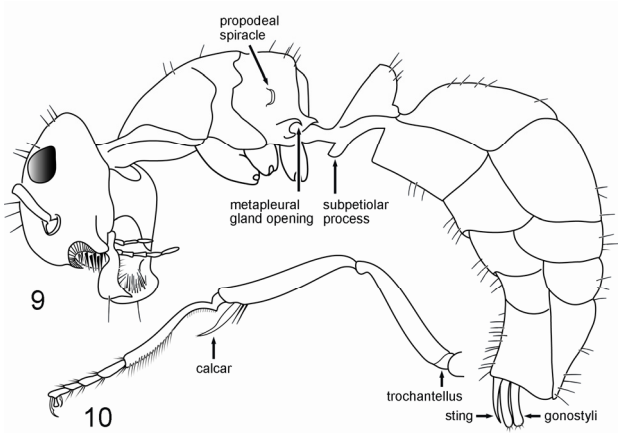
Description: Head broad, crescent-shaped in dorsal view, with frons strongly convex and vertexal (posterodorsal) margin strongly and regularly concave. In full-face view the anterior clypeal margin broad, concave; sides con-



Figs. 5 - 8: Photographs of worker specimens of *Zigrasimecia ferox* sp.n. (5) Holotype JWJ-Bu18a, full-face view. (6) Paratype JWJ-Bu18b, full-face view. (7) Holotype JWJ-Bu18a, close-up of the mouthparts. (8) paratype JWJ-Bu18c, detail of gaster preserved at amber surface, showing the sting apparatus. Abbreviations: cd, clypeal denticles; go, gonostyli; fl, hypostomal flange; ls, labral spicules; ms, mandibular spicules; sb, sting bulb; st, sting shaft.

vex, with small protruding eyes located posteriorly to midlength of head; posterior corners broadly rounded; base of mandibles concealed by large anterior genal expansion (hypostomal flange). Clypeus shallow, transverse, 8× wider than high; anterior clypeal margin entirely lined with 48 contiguous denticles decreasing in length laterally; denticles peg-shaped, with rounded apices. Labrum covered with dense brush of spine-like setae arranged in three transverse rows; each row with approximately 20 setae stouter (about twice as broad basally) and increasingly longer (2× longer in row immediately ventral to clypeus, 3× longer in third row) than clypeal denticles, tapered. Mandibles barely overlapping medially, with one large apical tooth and one smaller subapical tooth; outside surface with one long decumbent seta medially; oral surface covered with dense brush of stiff, sharp, spicule-like setae, inner setae 4× longer than outer setae. Palps very short, maxillary palps with five segments, labial palps apparently with three segments. Frontal carinae absent. Antennae well-separated; toruli not significantly raised, ring-like, directed laterad; antennal scrobes shallow, projecting outward laterally from bases of antennae to ventral margin of eyes; antenna with 12 antennomeres: scape short, barely twice as long as pedicel, third and last antennomeres longest flagellar articles.

Mesosoma at most half as broad as head in dorsal view. Neck long. Junction of mesoscutellum and dorsal surface of propodeum mostly indistinct, only slightly angled on specimens JWJ-Bu18a and JWJ-Bu23 (where dorsal propodeal surface is short, about 0.25× length of mesosoma excluding neck); posterior margin of propodeal dorsum distinctly concave. In profile view, propleuron well developed; mesopleuron fully separated from the rest of the mesosoma by distinct sulci, distinctly higher than long. Propodeum high, declivity steep; propodeal spiracle slit-like, facing posteriad, located around midpoint of propodeal sides; metapleural gland opening semicircular, facing posteroventrad; metapleural bulla developed, roughly hemispherical. Legs: all femora and tibiae dorso-ventrally flattened, tibiae with anterior and posterior margins bordered by a carina; small trochantellus present on all legs; foreleg with patch of dense, elongate setae on ventral surface of tibia (apically) and basitarsomere (entire length following strigil); protibia with three spurs apically on ventral margin, large one ("calcar") gently curved, with minute setae apically, two other ones about half as long as calcar, straight and simple; protarsomere I with "antennal cleaner" (strigil) a velvety notch proximally on ventral margin; tarsomeres I - IV of all legs with two pairs of stiff setae apically on ventral surface; mesotibial apex with two simple spurs straigth and subequal in length; metatibial apex with one large pectinate spur gently curved apically and one small, straight and simple spur; pretarsal claws with minute subapical tooth.



Figs. 9 - 10: Drawings of holotype of *Zigrasimecia ferox* sp.n. (9) Habitus without legs in profile view. (10) Left foreleg in dorsal view.

Gastral segments sometimes telescoped, with apparent small constriction between segments I and II (AIII - AIV) likely an artefact of preservation; anterior flange of sternite of AIII lamellar, with anterior and ventral margins straight and right angled. Sting long but largely internalized, stout, slightly upcurved apically, externalized part basally enclosed by sting sheaths (gonostyli); sting bulb (visible on two fragmentary specimens with mesosoma "opened" by the polishing of the amber surface) large.

Integument minutely rugose throughout except legs and gaster smooth; dorsofrontal portion of head and dorsal surfaces of mesosoma, petiole, and gaster sparsely covered by fine erect hairs; slightly longer and decumbent hairs present ventrally on mesosoma and gaster; apical segment of gaster more densely setose, with longer decumbent hairs.

Measurements (in millimetres) for smallest (paratype JWJ-Bu17) and largest (holotype JWJ-Bu18a, in brackets, {}) specimens: body length 2.00 {2.80}; head length (from vertex to clypeal margin) 0.52 {0.66}, width (excluding eyes) 0.56 {0.70}; maximum diameter of eye 0.15; length of antennomeres: scape 0.19 {0.27}, pedicel 0.10 {0.12}, flagellomeres I - X 0.12, 0.10, 0.09, 0.09, 0.08, 0.06, 0.06, 0.06, 0.05, 0.12 {0.19, 0.14, 0.12, 0.12, 0.12, 0.12, 0.11, 0.11, 0.11, 0.19}, respectively; mesosomal length 0.66 {0.87}, maximum width 0.30; petiole length 0.21 {0.36}, height (including subpetiolar process) 0.33 {0.41}; gastral length (excluding sting) 0.82 {1.36}.

Etymology: The specific epithet is taken from the Latin word ferox, meaning "fierce", and refers to the head appearence of this ant.

Discussion

The new worker specimens are atttributed to *Zigrasimecia* based on the similar, very peculiar head, particularly the unique structures of the mouthparts with clypeal denticles, labral and mandibular spine-like setae, and large hypostomal flange (the latter is absent in figure 2c of BARDEN & GRIMALDI (2013), but is visible in figure 1c). Both morphotypes also have the mandibles, antennae, pronotal neck, propodeal spiracle, propodeum, and petiole of similar shape (though the subpetiolar process was not seen in the gyne of *Z. tonsora*, but this may be a matter of observation – see BARDEN & GRIMALDI 2013: fig. 2a, the anteroventral part of petiole is hidden by right metacoxa). However, the workers differ from the gyne of *Z. tonsora* by the following features, regarded here as species-specific: clypeal margin with more peg-like denticles (48 as opposed to 30 in *Z. tonsora*), denticles decreasing in size laterally (as opposed to subequal in length); labral spicules apparently stouter; mandibular spicules apparently longer; absence of V-shaped groove above clypeus; toruli not raised; antenna with scape and apical flagellomere relatively longer (scape index SI = scape length / head width: 34 - 38 as opposed to 29 in *Z. tonsora*; flagellomere X as long as flagellomere I in *Z. ferox* sp.n., as long as flagellomere II in *Z. tonsora*); legs with femora and tibiae flattened, tibiae carinate; propodeal dorsum without median concavity. The absence of ocelli and head rugosities, and the simplified mesosoma without suture or foveae may be regarded as differences of conspecific castes, with alate specimens having larger mesosomal segments due to flight muscles. But what we know of Cretaceous ant castes so far and basal ant lineages today (e.g., Leptanillinae and poneromorph subfamilies), merely suggests the new specimens represent workers of a distinct species. For example, in *Haidomyrmodes* PERRICHOT & al., 2008, workers and gyne identified as conspecific vary mostly in size but are otherwise remarkably similar in their components, with ocelli and same mesosomal sutures or foveae present in both castes. In the present case, the worker specimens vary quite significantly from the described gyne of *Z. tonsora*, and are thus considered a closely related but distinct species.

BARDEN & GRIMALDI (2013) were equivocal on the exact placement of *Zigrasimecia*, as they suggested affinities with the Sphecomyrminae but without formally assigning it to this subfamily. Instead, they emphasized a close relationship with the sphecomyrmine genus *Sphecomyrmodes* and the enigmatic genus *Gerontoformica*, which both possess a similar row of stout, peg-like setae along the anterior clypeal margin. Another similarity with *Gerontoformica* pointed out by these authors would include the presence of peg-like setae on the labrum. But I have reexamined the type of *Gerontoformica cretacica* and there are no such labral setae: apparently these features were erroneously reported in the original account by NEL & al. (2004). Recently, I also discovered an additional, partial specimen of *Gerontoformica* which provides strong support for the placement of this genus within the Sphecomyrminae (Vincent Perrichot, unpubl.). Therefore, there is little doubt that *Zigrasimecia* also belongs in the Sphecomyrminae, and more specifically, the tribe Sphecomyrmini. With respect to the Sphecomyrminae, it possesses most of the worker characteristics given by BOLTON (2003), viz. the antennae are geniculate and with relatively short antennal scapes, the funiculus is filiform, the propodeal lobes are absent, the mesotibia and metatibia each bear two spurs, the pretarsal claws have a preapical tooth, the petiole is nodiform with a short anterior peduncle, and a distinct sting is present. Assignment of *Zigrasimecia* to the tribe Sphecomyrmini is also supported by the female mandible with only two teeth, the antennal segment III elongate, and the anterior surface of AIII vertical. Another diagnostic feature of the tribe as proposed by BOLTON (2003) was the presence of ocelli, a character missing in workers of *Zigrasimecia*, but this is also variable among genera of the other tribe Haidomyrmecini (e.g., ocelli present in workers of

Haidomyrmodes, but absent in workers of *Haidoterminus* McKellar, Glasier & Engel, 2013, and *Haidomyrmex* Dlussky, 1996). The dorsal surface of the mesosoma being continuously curved is a unique feature among Sphecomyrminae and even among Cretaceous ants, strikingly similar to what is seen in the Formicinae with the genus *Camponotus* Mayr, 1861. But contrary to *Camponotus*, the promesonotal suture is indistinct in *Zigrasimecia*. Finally, the protibiae with three spurs and gonostyli apically externalized are unique characters not seen in any extinct or modern ant so far, thus with potential phylogenetic value.

The simultaneous presence of a partial specimen of *Zigrasimecia* and several workers of *Sphecomyrmodes* in a same piece of amber demonstrates that these two genera were present at exactly the same time, ruling out the diachronism that is always a minor concern with amber deposits. It also suggests that both taxa shared at least a part of their ecological niche, and even possibly fought against each other. Burmese amber provides some of the earliest known ants, yet with a surprising diversity for the time. Sphecomyrmines remain the most enigmatic of these early ants, as they display a wide array of specialized morphologies, and any new discovery challenges the definition and monophyly of this subfamily.

Acknowledgements

I am grateful to Jens-Wilhelm Janzen (Seevetal, Germany) who made possible the study of these ant specimens from his collection. Comments by Ryan McKellar and two other anonymous reviewers significantly improved this manuscript. This work was partly supported by the program Interrvie (research project NOVAMBRE 2 to D. Néraudeau, Univ. Rennes 1) from the French National Institute for Universe Sciences (CNRS-INSU).

References

Barden, P. & Grimaldi, D. 2012: Rediscovery of the bizarre Cretaceous ant *Haidomyrmex* Dlussky (Hymenoptera: Formicidae), with two new species. – American Museum Novitates 3755: 1-16.

Barden, P. & Grimaldi, D. 2013: A new genus of highly specialized ants in Cretaceous Burmese amber (Hymenoptera: Formicidae). – Zootaxa 3681: 405-412.

Bolton, B. 2003: Synopsis and classification of Formicidae. – Memoirs of the American Entomological Institute 71: 1-370.

Dlussky, G.M. 1999: New ants (Hymenoptera: Formicidae) from Canadian amber. – Paleontological Journal 33: 409-412. (translation of original Russian text published in Paleontologicheskii Zhurnal 1999(4): 73-76)

Dlussky, G.M., Brothers, D.J. & Rasnitsyn, A.P. 2004: The first Late Cretaceous ants (Hymenoptera: Formicidae) from southern Africa, with comments on the origin of the Myrmicinae. – Insect Systematics and Evolution 35: 1-13.

Engel, M.S. & Grimaldi, D.A. 2005: Primitive new ants in Cretaceous amber from Myanmar, New Jersey, and Canada (Hymenoptera: Formicidae). – American Museum Novitates 3485: 1-23.

LaPolla, J.S., Dlussky, G.M. & Perrichot, V. 2013: Ants and the fossil record. – Annual Review of Entomology 58: 609-630.

McKellar, R.C., Glasier, J. & Engel, M.S. 2013a: New ants (Hymenoptera: Formicidae: Dolichoderinae) from Canadian Late Cretaceous amber. – Bulletin of Geosciences 88: 583-594.

McKellar, R.C., Glasier, J. & Engel, M.S. 2013b: A new trap-jawed ant (Hymenoptera: Formicidae: Haidomyrmecini) from Canadian Late Cretaceous amber. – The Canadian Entomologist 145: 454-465.

Nel, A., Perrault, G., Perrichot, V. & Néraudeau, D. 2004: The oldest ant in the Lower Cretaceous amber of Charente-Maritime (SW France) (Insecta: Hymenoptera: Formicidae). – Geologica Acta 2: 23-29.

Perrichot, V., Nel, A., Néraudeau, D., Lacau, S. & Guyot, T. 2008: New fossil ants in French Cretaceous amber (Hymenoptera: Formicidae). – Naturwissenschaften 95: 91-97.

Shi, G., Grimaldi, D.A., Harlow, G.E., Wang, J., Wang, J., Yang, M., Lei, W., Li, Q. & Li, X. 2012: Age constraint on Burmese amber based on U-Pb dating of zircons. – Cretaceous Research 37: 155-163.

Wilson, E.O., Carpenter, F.M. & Brown, W.L. Jr. 1967: The first Mesozoic ants. – Science 157: 1038-1040.

Annu. Rev. Entomol. 2013.58:609-630. Downloaded from www.annualreviews.org
by ${individualUser.displayName} on 01/14/13. For personal use only.

Ants and the Fossil Record

John S. LaPolla,[1,*] Gennady M. Dlussky,[2] and Vincent Perrichot[3]

[1]Department of Biological Sciences, Towson University, Towson, Maryland 21252; email: jlapolla@towson.edu

[2]Department of Evolution, Biological Faculty, M.V. Lomonosov Moscow State University, Vorobjovy gory, 119992, Moscow, Russia; email: dlusskye@mail.ru

[3]Laboratoire Géosciences & Observatoire des Sciences de l'Univers de Rennes, Université Rennes 1, 35042 Rennes, France; email: vincent.perrichot@univ-rennes1.fr

Annu. Rev. Entomol. 2013. 58:609–30

The *Annual Review of Entomology* is online at ento.annualreviews.org

This article's doi: 10.1146/annurev-ento-120710-100600

Copyright © 2013 by Annual Reviews. All rights reserved

*Corresponding author

Keywords

Armaniidae, Cretaceous, Eusocial, Formicidae, Insect, Sphecomyrminae

Abstract

The dominance of ants in the terrestrial biosphere has few equals among animals today, but this was not always the case. The oldest ants appear in the fossil record 100 million years ago, but given the scarcity of their fossils, it is presumed they were relatively minor components of Mesozoic insect life. The ant fossil record consists of two primary types of fossils, each with inherent biases: as imprints in rock and as inclusions in fossilized resins (amber). New imaging technology allows ancient ant fossils to be examined in ways never before possible. This is particularly helpful because it can be difficult to distinguish true ants from non-ants in Mesozoic fossils. Fossil discoveries continue to inform our understanding of ancient ant morphological diversity, as well as provide insights into their paleobiology.

Annu. Rev. Entomol. 2013.58:609-630. Downloaded from www.annualreviews.org
by ${individualUser.displayName} on 01/14/13. For personal use only.

INTRODUCTION

Ant worker: the wingless, typically sterile, female caste of an ant colony; sometimes differentiated into major and minor workers

Eusociality: a quality of some animals with (*a*) a reproductive division of labor, (*b*) overlapping generations, (*c*) cooperative care of young

Crown group: a recently evolved, monophyletic lineage

my: million years

mya: million years ago

myo: million year(s) old

Ants are among the most successful, some would argue *the* most successful, groups of insects to ever live. In terms of both sheer species diversity (7, 81) and ecological impacts on terrestrial systems, the importance of ants cannot be overstated. Ant colonies are often called superorganisms (53) because of the collective functioning of a colony. In tropical forests, ants can comprise upward of 15%–20% of the animal biomass (52). Owing to their eusociality, the impact of ants on their surroundings far exceeds that expected from the relatively small size of individual workers. However, despite their presence on Earth for over 100 million years and despite their current ubiquity, it was apparently not until approximately 50 million years ago that ants achieved the ecological dominance we observe today (9, 28, 76) (**Figure 1**). From beautiful pieces of amber, sometimes with spectacularly preserved specimens entombed within showing the finest details of cuticular sculpturing, to the often shadowy outlines hinting at a structure that seems just out of view provided by an imprint fossil, the ant fossil record offers a tantalizing glimpse of ant diversity at various points in the past.

HISTORY OF PALEOMYRMECOLOGY

The study of fossil ants began primarily with inclusions in Eocene Baltic amber, with the first fossils illustrated as early as 1742 by Sendel (101) in his magnificent folio volume "*Historia Succinorum.*" Following this pioneering work, the first series of papers to discuss this fossiliferous deposit, which were published during 1819–1840 (e.g., 39, 98), were of rather poorly described species of uncertain generic placement. Heer (49) described in 1850 the first fossil ants from Radoboj (Croatia) and Oeningen (Germany), which Mayr (69) later revised. In 1868, Mayr (70) published the first large treatment of Baltic amber ants. It was this publication that stimulated other myrmecologists to study amber ants as well as imprint fossils. In 1915, Wheeler (111) produced his now classic monograph on the ants of the Baltic amber.

Following Wheeler's comprehensive monograph, several studies between 1915 and 1937 investigated ant imprint fossils. The most interesting faunas were described from the Late Eocene–Early Oligocene deposits of Florissant and Bembridge Marls and from the Oligocene deposits of Kleinkems and some localities in eastern France. Cockerell (15) first studied the ant fossils of the Bembridge Marls, followed later by the work of Donisthorpe (32). In 1930, Carpenter (13) reviewed fossil ants described from North American deposits. In the 1930s, Théobald (106) described a diverse Oligocene ant fauna from Aix-en-Provence, France, and Kleinkems, Germany, and also revised several species described by Förster (37) from Brunstatt, France. For the next 30 years, however, fossil ant work basically came to halt, probably due in part to the fact that the deposits known at the time were no older than the Late Eocene and most of the species in these deposits belonged to extant genera. In fact, some species in these deposits do not appear much different from extant species. As a result, the fossil record from that time period told us little about the early evolution of ants, and interest in fossil ants waned.

This changed in 1967 with the discovery of *Sphecomyrma freyi* from Cretaceous (Turonian, ca. 92 mya) New Jersey amber. Wilson et al. (115) described an intriguing combination of morphological features that did start to tell us something about how early ants evolved. It also sparked renewed interest in fossil ants. Since then, a diversity of Cretaceous ants have been discovered. These include species described by Dlussky from Taimyr (18–20) and Canadian ambers (23), discoveries from New Jersey amber (35, 41), and surveys of the ancient ants of Burmese and French ambers (22, 35, 43, 77, 84, 118). More recently the oldest definitive crown-group ant was discovered

Annu. Rev. Entomol. 2013.58:609-630. Downloaded from www.annualreviews.org
by ${individualUser.displayName} on 01/14/13. For personal use only.

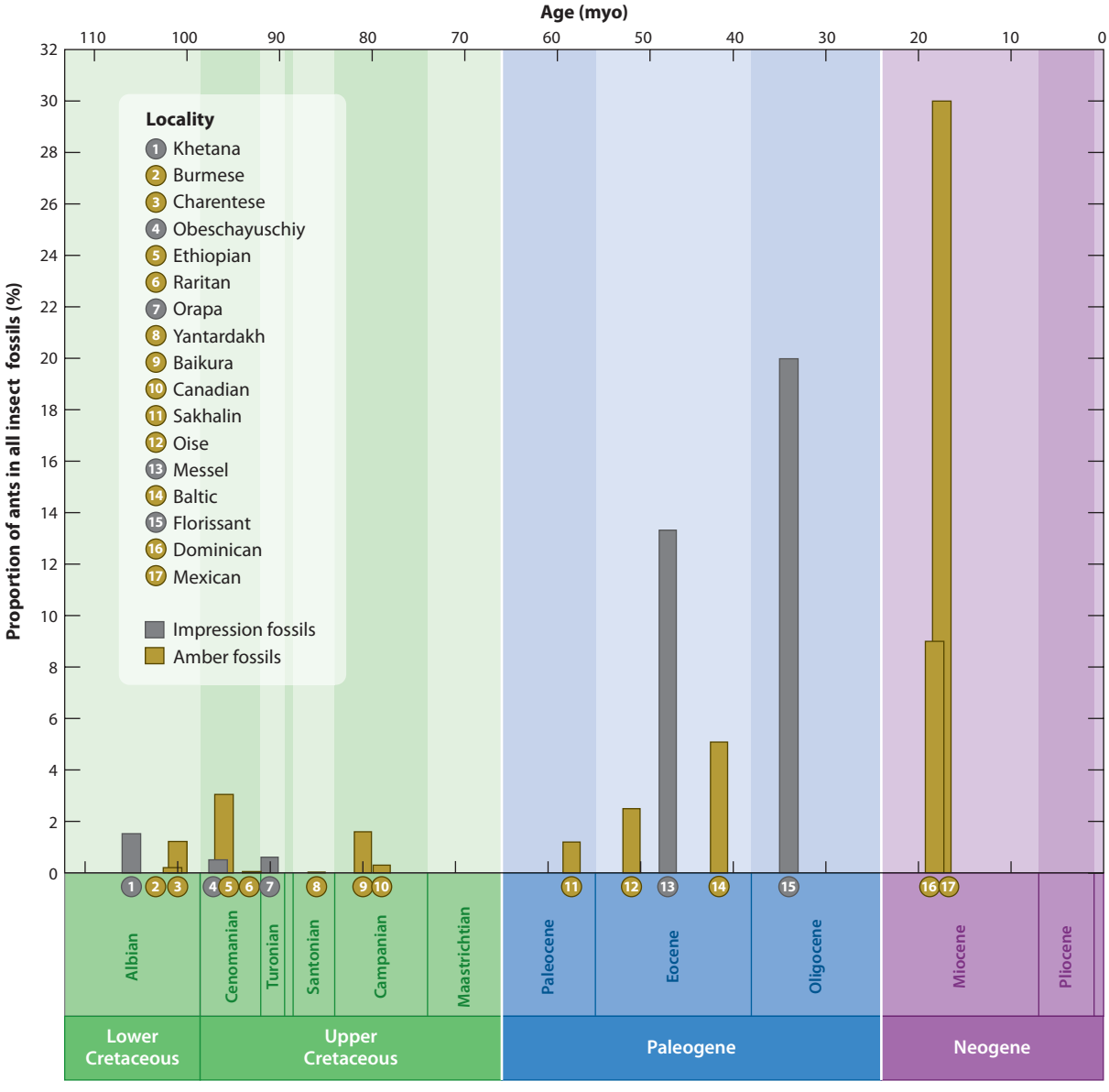


Figure 1

Percentage of ants as a total of all insect fossils from various fossil deposits. Note that the Dominican amber deposit is the average of two different estimates of the proportion of ants as a total of insect fossils (see References 45 and 59).

in Late Cenomanian amber of Ethiopia (96). These Cretaceous age fossils have increased our understanding of early ant evolution while raising a series of new questions. At present, there are 52 fossil deposits known to contain at least one fossil ant specimen (**Table 1**) (**Supplemental Figure 1, Supplemental Figure 2**; follow the **Supplemental Material link** from the Annual Reviews home page at **http://www.annualreviews.org**).

Supplemental Material

Annu. Rev. Entomol. 2013.58:609-630. Downloaded from www.annualreviews.org
by ${individualUser.displayName} on 01/14/13. For personal use only.

PRESERVATION AND METHODOLOGY

Amber Ant Fossils

Fossilized ant bodies come in two forms: as inclusions entombed in amber (the polymerized form of fossil tree resin) (**Supplemental Figure 3**) or as imprints in rock (**Supplemental Figure 4**). Burial conditions differ between the two kinds of fossils, and both have inherent biases as to what

Table 1 List of major ant fossil deposits from the Mesozoic and Cenozoic

Major Mesozoic ant deposits					
Deposit name	**Location**	**Brief geological details**	**Age**	**Percentage of insect fossils that are ants**	**Ant taxa known**
Burmese amber	Northern Myanmar	Inclusions in coniferous fossil resin (Burmite)	Early Cenomanian (98.79 ± 0.62 mya) (93, 102)	0.2% (44)	*Haidomyrmex*, *Sphecomyrmodes* (Sphecomyrminae), *Myanmyrma* (uncertain subfamily), *Burmomyrma* (possibly Aneuretinae) (22, 118)
Charentese amber	Charente-Maritime, France	Inclusions in coniferous fossil resin	Late Albian to Early Cenomanian (99–100 mya) (77)	1.2% (85)	*Gerontoformica* (uncertain subfamily), *Haidomyrmodes*, *Sphecomyrmodes* (Sphecomyrminae) (77, 84)
Ethiopian amber	Wenchit River, central Ethiopia	Inclusions in coniferous fossil resin	Late Cenomanian (93–95 mya) (96)	3% (96)	A fossil taxon yet undescribed in Dolichoderinae
Raritan (New Jersey) amber	Several localities in the Atlantic Coastal Plain	Inclusions in coniferous fossil resin	Turonian (92 mya) (46)	0.05% (46)	*Sphecomyrma*, *Baikuris* (Sphecomyrminae), *Brownimecia* (Brownimeciinae), *Kyromyrma* (Formicinae) (40, 41, 45, 46)
Orapa	Orapa, Botswana	Imprints in mudstone	Turonian (91 mya) (28)	0.6% (28)	*Afropone* (Ponerinae, but see text), *Afromyrma* (Myrmicinae, but see text) (26)
Kzyl-Zhar	Kzyl-Orda Region, Kazakhstan	Imprints in mudstone lenses in fluvial deposits	Turonian (90 mya) (28)	N/A	*Cretopone*, *Petropone* (poneromorphs, incertae sedis) (28)
Yantardakh	East Taimyr Peninsula, North Siberia, Russia	Inclusions in coniferous fossil resin (retinite)	Santonian (85 mya) (36)	0.001% (18)	*Cretomyrma*, *Dlusskyidris* (Sphecomyrminae) (18)

(*Continued*)

Table 1 (*Continued*)

Major Mesozoic ant deposits					
Deposit name	**Location**	**Brief geological details**	**Age**	**Percentage of insect fossils that are ants**	**Ant taxa known**
Baikura	Taimyr Peninsula, North Siberia, Russia	Inclusions in coniferous fossil resin (retinite)	Unclear position within Late Cretaceous, provisionally Campanian-Maastrichtian (ca. 80 mya) (28)	1.6% (90)	*Baikuris* (Sphecomyrminae) (20)
Canadian amber	Grassy Lake, northern Alberta, Canada	Inclusions in coniferous fossil resin (chemavinite)	Campanian (78–79 mya) (72)	0.3% (72)	*Sphecomyrma* (Sphecomyrminae), *Canapone* (Ectatomminae), *Eotapinoma* (Dolichoderinae), *Cananeuretus* (Aneuretinae) (24, 35)
Major Cenozoic ant deposits					
Deposit name	**Location**	**Brief geological details**	**Age**	**Percentage of insect fossils that are ants**	**Ant taxa known**
Sakhalin amber	Sakhalin Island near Starodubskoye, Russia	Inclusions in fossil resin (rumanite-type)	Paleocene (56–59 mya) (36)	1.2% (28)	*Aneuretellus* (Aneuretinae), *Protopone* (Ponerinae), *Eotapinoma*, *Zherichinius* (Dolichoderinae), *Chimaeromyrma* (Formicinae) (21)
Oise amber	Oise Department, France	Inclusions in angiosper-mous fossil resin	Early Eocene, Ypresian (52–55 mya) (4)	2.5% (4)	*Platythyrea* (Ponerinae), *Gesomyrmex* (Formicinae), *Tetraponera* (Pseudomyrmecinae), and 37 other morphotypes (4)
Mo-Clay	Denmark (Jutland)	Imprints in marine diatomites	Early Ypresian (52–55 mya) (94)	N/A	*Ypresiomyrma* (Myrmeciinae) (1, 94)
Cambay amber	Gujarat State, western India	Inclusions in angiosper-mous fossil resin	Early Eocene, Ypresian (50-52 mya) (95)	N/A	Several taxa yet undescribed in Dolichoderinae, Formicinae, Ponerinae, Pseudomyrmecinae (95)
Fushun amber	Fushun City, Liaoning Province, China	Inclusions in fossil resin	Early Eocene, Ypresian (50–52 mya) (52)	N/A	Many taxa listed (54), but see text

(*Continued*)

Annu. Rev. Entomol. 2013.58:609-630. Downloaded from www.annualreviews.org
by ${individualUser.displayName} on 01/14/13. For personal use only.

Table 1 (*Continued*)

Major Cenozoic ant deposits					
Deposit name	**Location**	**Brief geological details**	**Age**	**Percentage of insect fossils that are ants**	**Ant taxa known**
Green River	Widespread across western United States (northeastern Utah, northwestern Colorado, and southwestern Wyoming). Best collected are deposits from the Piceance Creek Basin	Imprints in lacustrine oil shales and calcareous mudstone	Early Eocene (49–54 mya) (103)	6.9% (28)	Species from Aneuretinae, Dolichoderinae, Myrmeciinae, Myrmicinae, Ponerinae, uncertain subfamily (27), Formiciinae (3)
McAbee	British Columbia, Canada	Imprints in lacustrine shale	Early Eocene, Ypresian (51 mya) (1)	N/A	*Ypresiomyrma* (Myrmeciinae) (1)
Messel	Grube Messel, near Darmstadt, Hesse, Germany	Imprints in bituminous claystone	Middle Eocene (47 mya) (74)	13.1% (67)	*Titanomyrma* (Formiciinae), *Gesomyrmex*, *Oecophylla* (Formicinae) (29, 30, 66)
Eckfeld	Eckfeld Maar	Imprints in lacustrine deposits	Middle Eocene (44 mya) (74)	3.9% (28)	*Gesomyrmex* and *Oecophylla* (30, 31). Also present are Formiciinae, Ponerinae, Formicinae, Dolichoderinae and Myrmicinae
Baltic amber	South coast of Baltic Sea from Poland to Estonia	Inclusions in fossil coniferous resin (succinite)	Middle to Late Eocene (37–42 mya) (109)	5% (28)	Many taxa (29)
Bembridge	Several sites along the coast of Isle of Wight	3D impressions in limestone	Late Eocene (34 mya) (55)	N/A	Many taxa (15, 32)
Florissant	Florissant, Colorado	Imprints in lacustrine shale (diatomite)	Eocene/Oligocene boundary (34 mya) (75)	20% (75)	Species from Aneuretinae, Dolichoderinae, Formicinae, Myrmicinae, Ponerinae, and Pseudoponerinae (12)
Bitterfeld amber	Bitterfeld, Lower Saxony, Germany	Inclusions in coniferous fossil resin	Late Oligocene (23 mya) (33)	N/A	Many taxa (26)

(*Continued*)

Annu. Rev. Entomol. 2013.58:609-630. Downloaded from www.annualreviews.org
by ${individualUser.displayName} on 01/14/13. For personal use only.

Table 1 (*Continued*)

Major Cenozoic ant deposits					
Deposit name	**Location**	**Brief geological details**	**Age**	**Percentage of insect fossils that are ants**	**Ant taxa known**
Aix-en-Provence	Bouches-du-Rhône, France	Imprints in gypsum-bearing marls	Late Oligocene (29 mya)	N/A	Many taxa (106), but in need of revision
Dominican amber	Several sites in Dominican Republic	Inclusions in angiosper-mous fossil resin	Early Miocene (16–19 mya) (40)	24% (42) or 36% (28)	Many taxa
Mexican amber	Simojovel, Chiapas, Mexico	Inclusions in angiosper-mous fossil resin	Early Miocene (15–20 mya) (104)	9% (104)	Many taxa (104)
Radoboj	Radoboj, Croatia	Imprints in freshwater limestones	Early Miocene (19 mya) (49, 68)	N/A	Many taxa (49), but see text
Sicilian amber	Sicily, Italy	Inclusions in angiosper-mous fossil resin (simetite)	Unclear position within Oligocene-Miocene, likely Early Miocene (16–23 mya)	N/A	14 species from 13 genera (11, 34)

Annu. Rev. Entomol. 2013.58:609-630. Downloaded from www.annualreviews.org
by ${individualUser.displayName} on 01/14/13. For personal use only.

kinds of ants tend to become fossilized. Ants in amber tend to be species that foraged on trees or on the ground near trees. They are as a general rule smaller species (10 mm or less in length) presumably because small species were less able to free themselves from the viscous resin. Rare exceptions include *Paraponera dieteri* in Miocene Dominican amber (ca. 20 mm), *Prionomyrmex* species in Eocene Baltic amber (up to 15 mm), and an undescribed myrmeciine worker in Eocene Oise amber (ca. 20 mm). Subterranean ant species that lived in the leaf litter or soil are also rare as amber fossils. When we do find these species in amber, they are almost always winged reproductives that were captured in the resin during their mating flights. An exception is the Early Cretaceous (Late Albian, ca. 100 mya) Charentese amber, which uniquely preserved a high proportion of the litter biota (82). Because there are many similarities between the ant fauna of Burmese and Charentese ambers, it is also possible that the Burmese amber ants were foraging on the soil rather than along the tree trunks.

Imprint Fossils

Mating flight: reproductive phase of some ant colonies, which typically involves the mass emergence of winged, virgin queens and males

Imprints in rocks were formed mostly in lake deposits, where the preservation of microscopic features requires the presence of fine-grained sediment such as diatomites, micritic muds, or volcanic tuffs. Such imprints mainly preserve winged reproductives that fell into the water during their mating flights. Although complete bodies may be found, imprint fossils generally fall into two categories: detached wings or body fragments lacking wings and other appendages. Mating behavior affects the likelihood of fossil preservation. Species that fly high and far from their birth

Ant queen: the egg-laying caste of an ant colony; also called a gyne

Paleosol: fossilized soil

nests have the greatest chance of burial in lake deposits. Species that spend most of their time searching and mating on the ground are far less commonly encountered as imprint fossils. In contrast to amber fossils, imprint fossils generally preserve larger ant species. Imprint fossils are found by splitting stones, and as a consequence, small specimens are easily overlooked. It is perhaps not surprising then that most ant imprints are dominated by species with large queens, such as *Oecophylla* in Bembridge deposits and the giant *Titanomyrma* in Messel and Green River deposits (up to 60 mm long!).

Ichnofossils

In addition to body fossils, the presence of ants can be recorded through ichnofossils (or trace fossils), i.e., the traces of their activity in paleosols such as burrows and nests. In the case of recent taxa, the nest architecture can be very distinctive (107), but such architectures are not found in Mesozoic ichnofossils. The identification of ant nests from the Mesozoic is particularly important because they potentially predate the earliest occurrence of body fossils. Unless body fossils are found associated within such nests, however, it remains virtually impossible to identify the kind of ant that built the nest and even to determine whether the tracemaker was an ant, because different groups of animals may have evolved similar burrowing techniques (100). For instance, distinguishing between traces of social insects such as ants and termites can be particularly difficult (38). The oldest trace fossils that have been suggested to be ant ichnofossils are from the Late Jurassic of Colorado (47, 48), but this remains highly controversial and was later dismissed by other authors (10, 38). The oldest nest that seems attributable to ants is from the Late Cretaceous of Utah (92).

New Imaging Techniques

Traditional light microscopy has long been the only technique available to study fossil insects preserved as imprints or amber inclusions. It is still largely in use because it allows for the observation of most external characters. But critical structures can be inaccessible owing to the position of the specimen or, in the case of amber, they can be hidden by turbidity, debris, bubbles, or other inclusions between the amber surface and the insect. Imaging techniques such as X-ray computed tomography (CT) or microtomography (μ-CT) are now increasingly used in amber studies, which provide a three-dimensional virtual reconstruction of the fossils (17, 45, 51). Propagation phase-contrast X-ray synchrotron imaging (PPC-SRμCT), which has been developed specifically for amber inclusions (60, 105), allows for high-resolution reconstructions as well as virtual dissections (**Supplemental Figure 5**), thus providing access to all external and internal features (80). The increasing use of PPC-SRμCT might help reduce the gap between fossils, especially controversial Cretaceous fossils, and extant species of ants.

Supplemental Material

THE PROBLEM OF RECOGNIZING TRUE ANTS IN THE EARLY FOSSIL RECORD

A critical discussion of ant fossils first needs to establish what synapomorphies are used to define the family Formicidae. For examination of fossils these are largely going to be morphological, although, as seen below, behavioral synapomorphies can be inferred from fossils as well. There are generally four widely accepted morphological synapomorphies that define modern ants (considered here as ants from the Tertiary to recent periods). These are an elongated scape, geniculate antennae, petiole, and metapleural gland. The elbowed (geniculate) shape of the ant

Annu. Rev. Entomol. 2013.58:609-630. Downloaded from www.annualreviews.org
by ${individualUser.displayName} on 01/14/13. For personal use only.

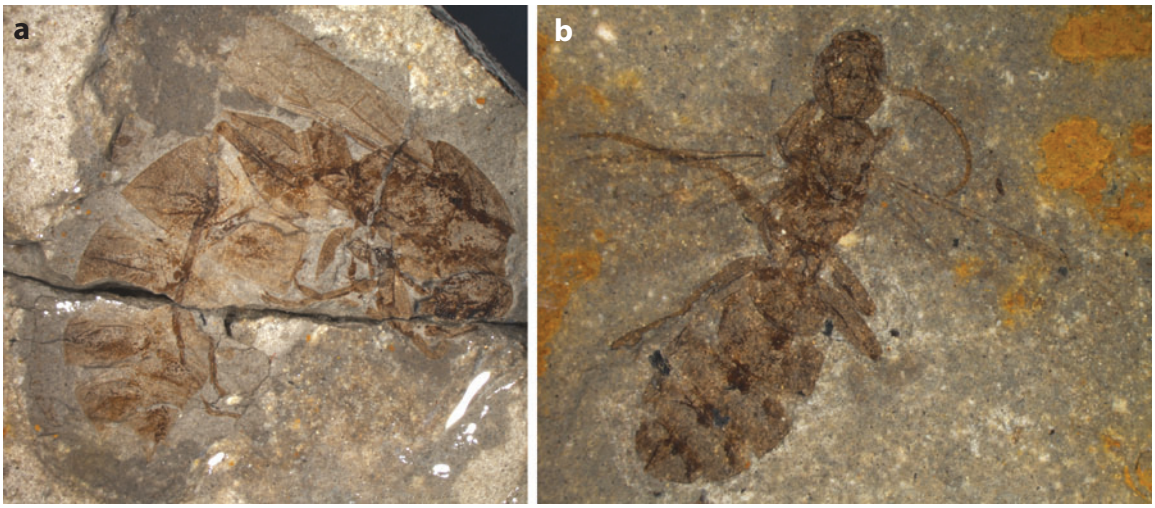


Figure 2

Armaniidae imprint fossils from Cretaceous of Siberia, Russia. (*a*) *Armania robusta*. (*b*) *Pseudarmania rasnitsyni*. Both fossils are from 95 myo mudstone of Obeschayuschiy. (Images courtesy of G. Dlussky)

antenna is formed by the elongation of the first segment (the scape) and the distinct bend that separates it from the remainder of the antenna (the segmented funiculus). The petiole is the modification of abdominal segment II and in some ant groups segment III is further developed into a postpetiole. The metapleural gland is often considered the major feature used to define the Formicidae (52) because it is unique to ants and nothing even closely equivalent exists in any other group of hymenopterans. The gland appears to secrete antimicrobial and, in some cases, alarm substances (117). It has been secondarily lost in some, largely arboreal or socially parasitic, groups, particularly in the subfamilies Formicinae and Myrmicinae (6). The metapleural gland is usually absent in male ants. A nonmorphological synapomorphy for ants is eusocial behavior, which is expressed morphologically in females by the differentiation of the queen and worker castes (although in some socially parasitic taxa, the worker caste has been secondarily lost).

The Cretaceous specimens have elicited the most debate because with these fossils we can ask, When do the first "true" ants appear? In other words, what among bizarre Cretaceous ant-like hymenopterans is a true ant? Dlussky (19) first described the Armaniidae as an intermediate link between ants and scoliid wasps. There has been considerable discussion of whether this group should be given family rank (1, 6, 19, 26, 41, 42, 83, 89, 108, 114), but the most recent action by Bolton (6) classified them as a subfamily. Here we do not follow this recommendation and consider them at the family rank for the remainder of our discussion (see reasons below). Armaniids are known exclusively as imprint fossils that are poorly preserved (**Figure 2**), making the critical areas of the body difficult or impossible to observe (e.g., seeing whether a metapleural gland is present or not). Still, what we know of them is that armaniids possessed a broadly attached, but poorly developed, petiole, very short scapes, and females do appear queen-like (19). Although Dlussky (19) reported the presence of a metapleural gland in some armaniids, others have questioned this interpretation (41, 77). It is this lack of a definitive metapleural gland that has led some authors to consider the armaniids at the family rank and therefore not true ants (35, 84, 116). In addition to only being known from fragmentary imprint fossils, another major complicating factor in determining whether armaniids are true ants is that no specimens have been found with individuals

Annu. Rev. Entomol. 2013.58:609-630. Downloaded from www.annualreviews.org
by ${individualUser.displayName} on 01/14/13. For personal use only.

that could be construed as workers. Armaniids possess vespoid-like mandibles that either are bidentate (19) or have only an apical tooth present (however, this may be a result of preservation).

Stem group: a paraphyletic assemblage composed of taxa more closely related to the crown group than to any other extant taxon

Supplemental Material

The debate about whether armaniids are true ants hinges mainly on just how many synapomorphies of modern ants need to be present in order for the group to be considered an ant. A striking example is a bizarre family of Cretaceous wasps described by Rasnitsyn (88) as the Falsiformicidae, or "false ants." Like Armaniidae, these wasps possessed geniculate antennae with a short scape, a broadly attached petiole, and females with a roughly queen-like appearance (**Supplemental Figure 6**). But no workers have been found, and most importantly, they distinctly lack the metapleural gland and share numerous features with Chrysidoidea. In his description, Rasnitsyn (88) noted that, as indicated by his name for the family, the falsiformicids were distinct from ants despite the presence of a petiole and geniculate antennae. He suggested that the family might be the sister group to the Formicidae s.l. (= Formicidae s.s. + Armaniidae), but additional falsiformicid species recently discovered by Vincent Perrichot from various Cretaceous ambers demonstrate that the family actually belongs in the Chrysidoidea. Therefore, the only definitive synapomorphies that can be used to define true ants seem to be the presence of the metapleural gland, a distinct petiole weakly attached posteriorly, and the differentiation of females into queen and worker castes. As such, and unless the presence of the metapleural gland can be clearly observed, Armaniidae should not be considered true ants.

Another less controversial example in the Cretaceous is the Sphecomyrminae. When Wilson et al. (115) first described *Sphecomyrma freyi* from 92 myo New Jersey amber, it created a sensation in myrmecological circles. Why? Here was an ancient fossilized ant-like organism that possessed a metapleural gland and a distinct petiole weakly attached posteriorly, two synapomorphies that define modern, crown-group ants. Much later, eusociality was inferred on the basis of the discovery of additional sphecomyrmine fossils. Both Grimaldi & Engel (42) and Perrichot et al. (84) used the presence of two wingless female individuals (inferred to be workers) preserved together in the same piece of amber to conclude sphecomyrmines were eusocial, on the basis of the inference that because Cretaceous ant specimens are so rarely encountered, it would be unlikely for two of them to be trapped together unless they were foraging nestmates. The sphecomyrmine *Haidomyrmodes mammuthus* is the first Cretaceous species known in which both queen and worker castes are described (84), perhaps settling the debate of whether sphecomyrmines were eusocial. Of the definitive morphological ant synapomorphies, sphecomyrmines lack only the elongated scapes, and it is the lack of this morphological trait that led Poinar et al. (87) to consider sphecomyrmines not ants, i.e., Sphecomyrmidae. Almost all other authors, however, have considered sphecomyrmines ants (9, 22, 41, 84, 116), and when looking at a *Sphecomyrma* or *Sphecomyrmodes* worker (**Figure 3**), one can easily appreciate most of the general traits of an ant that cannot be confounded with any other insect group. This is somewhat less convincing when observing *Haidomyrmex* or *Haidomyrmodes*, given their very peculiar head morphology (**Figure 4**); however, they clearly possess a metapleural gland and a distinct petiole, and at least *Haidomyrmodes* has females differentiated into castes. Therefore, Sphecomyrminae can readily be considered true ants, and the elongated scape remains a debatable synapomorphy related to how someone classifies crown-group versus stem-group ants (108).

CRETACEOUS ANT FOSSILS

The earliest known ants or ant-like fossils come from the Albian period (100–112 mya) of the Cretaceous. Cretaceous age specimens include a mixture of stem-group and crown-group ants (**Table 1**). Sphecomyrminae appear to be the closest known relatives to extant ants (41, 108, 116). They were present for at least 20 million years in the Cretaceous, with 8 genera and 15 species

Annu. Rev. Entomol. 2013.58:609-630. Downloaded from www.annualreviews.org
by ${individualUser.displayName} on 01/14/13. For personal use only.

Annu. Rev. Entomol. 2013.58:609-630. Downloaded from www.annualreviews.org
by ${individualUser.displayName} on 01/14/13. For personal use only.

Figure 3

Sphecomyrmodes occidentalis, a worker in mid-Cretaceous (99 myo) Charentese amber, southwestern France (lateral view). (Image courtesy of V. Perrichot)

known exclusively in amber (**Table 1**). They had a wide distribution although apparently restricted to Laurasia, with records in the mid-Cretaceous ambers of Burmese and French ambers, and the Late Cretaceous ambers of New Jersey, Siberia, and Canada (18, 20, 22, 23, 37, 41, 84, 116, 118). Among these, the Sphecomyrmini, comprising *Baikuris*, *Cretomyrma*, *Dlusskyidris*, *Sphecomyrma*, and *Sphecomyrmodes*, had a general morphology very similar to that of living ants, except for their relatively short scapes (**Figure 3**). The Burmese and French Haidomyrmecini, comprising *Haidomyrmex* and *Haidomyrmodes*, had the most peculiar head morphology of perhaps any ant, extinct or extant. The face exhibits a high, unusually concave surface surmounted posteriorly by a small lobe covered by a brush of stiff setae (**Figure 4**), and it is yet unclear if the clypeus is composed of both the concave surface and the brushy lobe or if it is only the lobe. The elbowed, sickle-shaped mandibles give Haidomyrmecini a fierce appearance (**Figure 4**) and were assumed to act as trap-jaws uniquely moving in a plane oblique to the dorsoventral and horizontal axes of the body, so they might have been highly specialized predators (22, 35, 84, 118). More generally, sphecomyrmines were likely foragers on the coniferous trees that produced the resin and on the soil surface of the amber forests. These were tropical to warm temperate forests in a coastal marine setting subject to tidal influences, dominated by gymnosperms but with an understory of ferns, cycads, and sparse, although relatively diversified, angiosperms (44, 72, 85). Sphecomyrmines had already developed eusocial traits, as evidenced by the differentiation of the worker caste and the trapping of several workers in the same amber piece, thus suggesting they were foraging together (84).

Laurasia: large northern continent that existed until the Paleocene consisting of Asia (minus India), Europe, Greenland, and North America

Annu. Rev. Entomol. 2013.58:609-630. Downloaded from www.annualreviews.org
by ${individualUser.displayName} on 01/14/13. For personal use only.

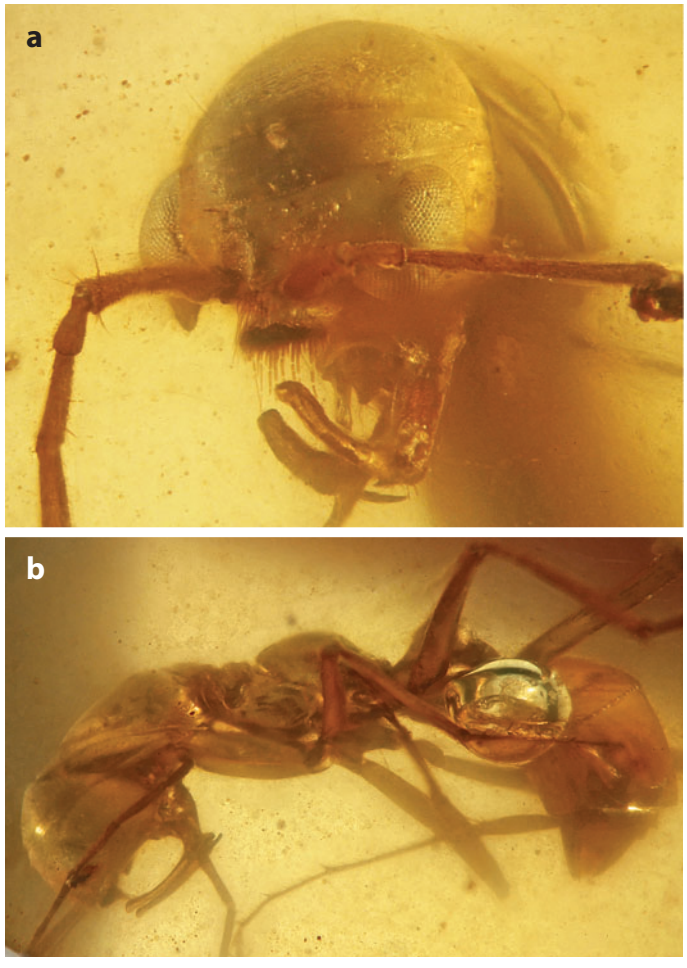


Figure 4

Haidomyrmex sp., a wingless female in mid-Cretaceous (99 myo) Burmese amber. (*a*) Head in frontal view. (*b*) Body in lateral view. (Images courtesy of V. Perrichot)

Kyromyrma neffi, from 92 myo New Jersey amber, is clearly a member of the crown-group ants (Formicinae) (40). The formicines have an easily identifiable synapomorphy that instantly separates them from other ant subfamilies: the acidopore. The acidopore is typically a circular, nozzle-like structure found on the terminal gastral segment of formicine ants (56) that is used to spray formic acid. The single known specimen of *K. neffi* clearly displays an acidopore. In many respects, its overall morphology is that of a fairly generalized formicine, possessing the plesiomorphic states for many characters. The Formicinae are the second most species-rich group of extant ants (6), and they include many examples of trophobiotic ants, those species that gather the exudate from groups of Sternorrhyncha hemipterans such as aphids and scale insects. The presence of formicines in the Cretaceous leaves open the possibility of an early origin of trophobiotic relationships involving ants.

When originally described from the same New Jersey amber, *Brownimecia clavata* was placed incertae sedis within the Ponerinae owing to the presence of a gastral constriction (41). At that time, the ponerines were still broadly defined and, as we now know, also paraphyletic (6, 58, 59).

Following the splitting of the old Ponerinae, Bolton (6) placed *B. clavata* in its own monotypic subfamily (Brownimeciinae), observing that the species did not easily fit into any recognized subfamilies. *B. clavata* has falcate, edentate mandibles, unusual for ants and often associated with dulotic behavior (6). Unlike the armaniids and sphecomyrmines, and more like crown-group ants, *B. clavata* possesses a relatively elongate scape (41). Another interesting morphological feature of *B. clavata* is the presence of clubbed antennae, which, although not uncommon among modern ants, is the only known instance among Cretaceous ants (6).

Two other Cretaceous amber deposits (Burmese and Canadian) are of particular recent interest because they contain, in addition to sphecomyrmines, several fossils that very likely belong to the ant crown group. A possible aneuretine, *Burmomyrma rossi* (22), and a possible myrmeciine (although considered incertae sedis), *Myanmyrma gracilis* (35), from 99 myo Burmese amber have been described. The single known specimen of *B. rossi* is a headless alate. Dlussky (22) considered its general morphology and wing venation to be consistent with the crown-group subfamily Aneuretinae. Another fossil from younger Cretaceous Canadian amber (Campanian, ca. 78 myo), *Cananeuretus occidentalis*, has also been tentatively placed within the Aneuretinae (35). The subfamily Aneuretinae is represented today by a single, presumably relict species, *Aneuretus simoni*, found only on the island of Sri Lanka. Engel & Grimaldi (35) considered *Myanmyrma gracilis* either to be within the poneroid grade or to belong to the Myrmeciinae. The species possesses a gastral constriction, which places it within the poneroid grade, but it shares several other morphological features with the myrmeciines (35). Archibald et al. (1) thought that given the lack of character support and poor specimen preservation, *M. gracilis* was likely not a myrmeciine. They also observed that the short scapes are known only in stem-group ants; however, the strong constriction between abdominal segments III and IV is not known from any stem-group ant.

Discovered in Charentese amber (ca. 100 myo), *Gerontoformica cretacica* is of uncertain taxonomic placement due to the high distortion of the specimen (77), although it is likely a crown-group ant. Nel et al. (77) suggested it is reminiscent of either the Dolichoderinae or the Formicinae on the basis of general habitus. The specimen does have a relatively long scape and the antenna is not clubbed, which suggests it is not a sphecomyrmine or a brownimeciine.

Two other fossils have been assigned to the crown-group ants, *Afropone* to the Ponerinae and *Afromyrma* to the Myrmicinae, on the basis of imprints from Orapa, Botswana (26). The specimens are in poor condition and their assignment to an ant crown group has been questioned (1, 116).

CENOZOIC ANT FOSSILS

The end of the Mesozoic 65 mya, marked by a well-known mass extinction event, also may have brought about the end of both the armaniids and sphecomyrmines—although the times of their extinctions remain unclear. The last armaniids occur about 91 mya in the Turonian of Botswana; however, insect-rich rock deposits are desperately lacking between 55 and 90 mya. Similarly, the last occurrence of sphecomyrmines is from the Campanian Canadian amber, but insect amber deposits are lacking in the Maastrichtian and Paleocene, so the possibility that sphecomyrmines survived until the Paleocene cannot be excluded. This is unlikely, however, given that the only known early Cenozoic deposit contains clearly identifiable and diverse crown-group ant fossils, and no sphecomyrmines. Dlussky (21) studied Sakhalin amber and found that, as in Cretaceous deposits, ants are rare (just 9 specimens), composing only 1.2% of all insect fossils, and belong to extinct genera from modern subfamilies (Dolichoderinae, Aneuretinae, Formicinae, and Ponerinae). Sakhalin amber finds do, however, demonstrate that Paleocene ants occupied various levels in the ecosystem, perhaps the beginnings of the various niches occupied by modern ants (28). For example, based on their morphology, *Aneuretellus* and *Protopone* likely lived in soil or leaf litter

Annu. Rev. Entomol. 2013.58:609-630. Downloaded from www.annualreviews.org
by ${individualUser.displayName} on 01/14/13. For personal use only.

(21). They had small eyes displaced forward and thickening terminal segments of the funiculus. *Zherichinius* had an elongated body and long legs and antennae, and was perhaps arboreal (21).

From the Ypresian stage (50–55 mya) of the Early Eocene, three amber deposits are known (**Table 1**) that contain diverse ants. From French amber of Oise, two ponerines have been described, one in the extant genus *Platythyrea* (with the oldest report of a possible ergatoid condition), and one a close relative of *Pachycondyla*, and 38 other morphotypes are mentioned in Formicinae, Dolichoderinae, Pseudomyrmecinae, Myrmeciinae, and Myrmicinae (4). In Indian amber of Cambay, a preliminary investigation revealed Formicinae, Dolichoderinae, Pseudomyrmecinae, and Myrmicinae (95). These two deposits apparently contain a mixture of extinct and extant genera (4, 95), which contrasts with the Chinese amber from Fushun in which the 35 known taxa were described exclusively from extinct genera (54). However, the identifications are disputable, the descriptions are in Chinese, and the illustrations are low quality; this material clearly needs additional study. All three deposits are of major significance because they provide the only clues for the transitional composition in ant diversity following the Paleocene-Eocene thermal maximum (PETM) 56 mya. With an estimated increase of 5°C–8°C globally, the PETM was a key period of drastic changes in the terrestrial biosphere (14, 71), and it is likely that many modern ant genera evolved during or shortly after this time (4).

It is during the Eocene and beyond that the number of ant fossils increased significantly, with ants in several deposits composing more than 20% of the insect species present. Mo-Clay (Fur and Ølst Formations in Denmark) is one of the earliest Eocene deposits (55 myo), and a myrmeciine, *Ypresiomyrma rebekkae*, is known from this locality. Rust & Andersen (94) discovered 101 body specimens or isolated body parts of ant queen and male *Y. rebekkae* [originally placed in *Pachycondyla* but later moved to the Myrmeciinae by Archibald et al. (1)]. No other ants have been found in this deposit. It is assumed that insect layers from Mo-Clay were formed in a marine environment and at a distance of about 100 km from the nearest coast (94). This is the earliest evidence we have of mating swarm behavior in ants.

Several important Middle Eocene deposits are known: Green River (27) and Okanagan Highlands (1) in North America, and Messel and Eckfeld (30, 31, 66) in Europe. Compared with earlier deposits, the percentage of insects that are ants rises substantially: at Green River 6.9% and at Messel 13.1%. Middle Eocene deposits are dominated by genera that are extinct, but we do see several extant ant genera appear during this period. Among those are *Dolichoderus* in Green River, *Oecophylla* and *Gesomyrmex* in Messel and Eckfeld, and *Pachycondyla* in Green River and Messel (27, 30, 31). Another interesting feature is that several species are represented by numerous specimens, in stark contrast to earlier deposits. Imprints of *Eoformica pinguis* and *Dolichoderus kohlsi* constitute 40% and 25%, respectively, of all ants in Green River (27); *Titanomyrma gigantea* and *T. simillima* constitute nearly 50% of ants in Messel (45). Four subfamilies dominate these fossil deposits: Aneuretinae, Dolichoderinae, Formicinae, and Formiciinae at Green River (85.6% of all ants) and Messel (90.3% of all ants). Interestingly, the Myrmicinae are quite rare in these deposits, composing just 1.9% of ants in Green River and 1.6% of ants in Messel.

Supplemental Material

One subfamily of ants, the Formiciinae (not to be confused with the Formicinae), appears in the Early Eocene and disappears in the Middle Eocene (**Supplemental Figure 7**). They were originally known only from forewing fossils (12, 110) and initially were not even placed in the Formicidae (110); Lutz (66) later revised the group. A number of remarkable formiciine fossils have been discovered. Formiciine queens were very large; in fact they are the largest ants to have ever lived, with individuals reaching body lengths of 6 cm and possessing wingspans of up to 13 cm (66). In one species, *Titanomyrma lubei*, the body of the queen is larger than the rufous hummingbird (*Selasphorus rufus*) common to North America (3). Unfortunately, workers of these ants remain unknown. Formiciines are known from both European and North American deposits.

Annu. Rev. Entomol. 2013.58:609-630. Downloaded from www.annualreviews.org
by ${individualUser.displayName} on 01/14/13. For personal use only.

One of the best-studied ant fossil deposits dates from the Middle to Late Eocene period (34–42 myo): the Baltic amber. Mayr (70) and Wheeler (111) produced the first taxonomic treatments, but a host of more recent studies have followed. This deposit is important from a number of perspectives, such as its high species diversity (with 118 species; 29), and a significant portion of its identified genera (9%; 29) known today only from the tropics, including *Oecophylla*, *Gesomyrmex*, *Pristomyrmex*, and *Tetraponera*, among others. Wheeler (112) first noted that the Baltic amber was unusual in part because it contains a mixture of both thermophilic and temperate genera. Archibald & Farrell (2) addressed this observation, considering two possibilities that either the Baltic amber forests were tropical/subtropical or that there was less pronounced seasonality in this area than is observed today (the area had milder winters). They concluded that the latter hypothesis was more likely the explanation for this seemingly strange mixture of ant faunas. This is an interesting observation because it implies that what are considered tropical ant genera today may in fact have been associated originally with a more mild, temperate climate.

The first record of polymorphism among worker ants is noted in specimens from Baltic amber. Dimorphic worker specimens (majors and minors) of *Gesomyrmex hoernesi* and *Pheidologeton* sp. have been discovered (31, 111). Ergatoid conditions have been reported for both a male ant (*Anonychomyrma constricta*; 111) and a gyne (*Plagiolepis klinsmanni*; 25) from Baltic amber fossils. Baltic amber fossils have also given insights into other aspects of ant biology. For instance, several fossil ant species (*Ctenobethylus goepperti*, *Lasius schiefferdeckeri*, *Prenolepis henschei*, and *Monomorium mayrianum*) have been found as syninclusions with aphids (Hemiptera: Aphididae: *Germaraphis*), which may be an indication of trophobiotic interactions between the ants and the aphids (e.g., 79). However, due to the presence of wax-secreting structures on the aphids, some authors have doubted that the ants and aphids were associated (50). Wheeler (112) reported a mite on *L. schiefferdeckeri*.

If we examine the three most-speciose extant ant subfamilies (Dolichoderinae, Formicinae, and Myrmicinae), approximately 50% or more of the species from the Eocene are from genera that are extant (**Supplemental Figure 8**). In fact, some fossil species look remarkably similar to extant species. A classic example involving apparent morphological stasis in worker morphology from the Eocene is observed in the common Baltic amber species *Prenolepis henschei*. Wheeler (112) was the first to note that workers of this species looked morphologically very similar to the extant and widespread Nearctic *Prenolepis imparis* (which is also incidentally morphologically very similar to the extant European *Prenolepis* species, *P. nitens*). LaPolla & Dlussky (64) noted differences between the male genitalic structures of *P. henschei* and *P. imparis*, but the morphological similarities among the workers of these two species broadly links the modern fauna back to the Eocene.

From the Oligocene onward (23–34 myo) the percentage of ants as a total of insects found in fossil deposits rises. In the Florissant shale, 20% of insects are ants (13). Carpenter (13) reports a dominance of two subfamilies in the Florissant: Dolichoderinae (ca. 63%) and Formicinae (ca. 33%). In the French deposit of Aix-en-Provence, the Dolichoderinae and Myrmicinae are among the most common ants, each composing approximately 36% of the ants. The Formicinae are the third most commonly encountered ants (ca. 27%) (106).

The Dominican amber (16–19 myo) found in Hispaniola is arguably the best-studied ant fossil deposit in the world. In fact, ants are the largest single group of arthropods known from Dominican amber, with upward of 24%–36% of all fossil insects being ants. Dominican amber in many respects is essentially a modern ant fauna, but there have been notable extinctions since the amber was formed (113). Although fewer than 10% of the genera known from Dominican amber are globally extinct (113), some groups that existed on Hispaniola in the Miocene are absent today. For instance, there were army ants on Hispaniola in the Miocene, but today army ants are not found in the Greater Antilles (113). An interesting dolichoderine putatively placed in the genus *Leptomyrmex* (*L. neotropicus*) was discovered from Dominican amber (5). Today *Leptomyrmex* is

Annu. Rev. Entomol. 2013.58:609-630. Downloaded from www.annualreviews.org
by ${individualUser.displayName} on 01/14/13. For personal use only.

found only in the wet forests of Australia, New Guinea, and New Caledonia, so the presence of the Dominican amber fossil species has presented a biogeographical puzzle since its discovery. Lucky (65) suggested that the fossil species is a stem lineage of *Leptomyrmex*, and does not belong to the crown group of modern *Leptomyrmex* species. This conclusion was based on the dating of the divergence of *Leptomyrmex* from its extant sister group, which is found in the New World.

Trophobiosis: relationship in which ants receive honeydew from sternorrhynchans or caterpillars, which in return are protected by the ants

Undoubtedly, in part because of their sheer abundance as amber inclusions, which overall increases the chances of syninclusions, ants in Dominican amber have provided insights into understanding complex interspecific interactions. This can be illustrated by examining evidence for trophobiosis among Dominican amber ants. The first definitive cases of trophobiosis have been observed in Dominican amber (although see Baltic amber, above), one case by inference from the syninclusions of both trophobiotic partners, and the other example with the ants actually carrying the trophobionts involved in the trophobiosis (57, 63). In one spectacular fossil, an *Acropyga* winged queen is still clutching a mealybug between her mandibles, a behavior termed trophophoresy that is unique to this genus (61–63, 97). Other complex symbiotic relationships have been preserved in Dominican amber as well. Fungus-growing ants (Myrmicinae: Attini) are unique to the New World and have been the focus of intense study regarding the nature of the symbiosis between the ants, the fungus they grow in their gardens, and other associated organisms. We know that fungus-growing ants were common since at least the early Miocene because five attine species from three genera have been found in Dominican amber (99).

Mexican amber is of approximately the same age as Dominican amber (**Table 1**) but has received comparatively less study. It is known that ants compose nearly 10% of insect specimens from this deposit (104). Several studies have examined the species composition of Mexican amber (**Table 1**). Given the biogeographic affinities of southern Mexico and Hispaniola in modern times, a comparison of the amber ant fauna from these two regions could prove illuminating. There are other fossil deposits of younger age, but generally they are either poorly known or contain relatively few ants (**Supplemental Figure 1, Supplemental Figure 2**). One exception is Sicilian amber, the exact age of which remains unclear within the Oligocene-Miocene boundary. This deposit possesses some unique, extinct genera as the unusual formicine *Sicilomyrmex corniger* (11, 34). Notably, most inclusions belong to genera not found in other European deposits, which led Dlussky & Rasnitsyn (28) to conclude this fauna was essentially Afrotropical. Another fossil deposit of early Miocene age (19 myo) is Radoboj in Croatia, from which many ant species were described in the nineteenth century by Heer (49), but because it has not been revised in over 100 years, much of the taxonomy of these fossils is woefully out of date.

Supplemental Material

Annu. Rev. Entomol. 2013.58:609-630. Downloaded from www.annualreviews.org
by ${individualUser.displayName} on 01/14/13. For personal use only.

AGE OF ANTS

Both Wilson & Hölldobler (116) and Moreau et al. (76) correlated the diversification of ants in the Eocene with the rise of angiosperm-dominated forests and their correspondingly more complex leaf-litter layers. The diversification of other insect lineages, such as the phytophagous beetles (73), has been correlated with the rise of the angiosperms as well. However, the role of angiosperms in the diversification of ants has been challenged (86), and previous attempts to correlate their rise with ant diversification have been characterized as artifacts of incomplete taxon sampling. Pie & Tschá (86) found that ants have displayed a constant rate of lineage expansion, rather than a single burst, which might be expected if correlated with the radiation of angiosperms.

The age of ants has been a focus of several studies. Wilson et al. (115), as discussed above, discovered the first Mesozoic ant, leading them to speculate that ants originated 100 mya. Crozier et al. (16) challenged this age using a molecular study that questioned whether ants evolved concurrently with their first appearance in the fossil record. These authors (16) were the first to

use molecular techniques to infer an age for ants and from their data estimated a Late Jurassic (ca. 185 mya +/− 36 my) origin. The fossil used in the calibration was *Cariridris bipetiolata* (8), at the time considered a myrmeciine. However, subsequently *C. bipetiolata* was found not to be an ant (and was placed in the Ampulicidae), rendering the calibration incorrect. Two large molecular studies undertook the task of estimating the age of ants (9, 76). These two studies, however, came to different age estimates. Moreau et al. (76) inferred an age of 140–168 myo, and Brady et al. (9) inferred an age of 115–135 myo. Brady et al. (9) further inferred an age of 137–143 myo for crown-group ants plus sphecomyrmines. How do we reconcile this range of dates? Differences in how fossil deposits were calibrated, as well as what fossils were utilized in the analysis, may explain the discrepancy. For instance, Brady et al. (9) utilized a much more complete range of aculeate fossils to calibrate a series of multiple outgroup nodes.

Gondwana: supercontinent that existed in the Mesozoic consisting of Africa, Antarctica, Arabia, Australia, India, Madagascar, New Zealand, and South America

The age estimates of both Moreau et al. (76) and Brady et al. (9) are older than what the fossil record reveals, but given the rarity of Mesozoic ants (**Figure 1**) this is perhaps not surprising. What we do know is that since the discovery of *Sphecomyrma freyi*, myriad fossil discoveries have shown that there was a rather diverse sphecomyrmine fauna in the Cretaceous and that definitive crown-group ants (*Kyromyrma neffi* and the Ethiopian dolichoderine) existed concurrently with them. The apparent absence of ants from Early Cretaceous insect-rich deposits such as the Spanish and Lebanese ambers (110 to 125 mya), the Santana Formation of Brazil (120 mya), and the Chinese Yixian Formation (140–145 mya) suggests ants did not originate before 110–120 mya. The question of the age of ants, however, does demonstrate the necessity of combining fossil ants with molecular divergence dating techniques because fossils provide the critical minimum age estimates for the lineages in question. As divergence dating becomes ever more popular, the need for accurately identified and classified fossil specimens will only increase. Investigations for additional Cretaceous fossils, particularly from ancient Gondwanan localities, will help elucidate the timing of the origin and radiation of these highly successful insects.

SUMMARY POINTS

1. Ants have existed on Earth for at least 100 million years and, based on the fossil record, probably evolved somewhere between 110 and 120 mya.
2. The taxonomic placement of the extinct, ant-like Armaniidae, which are likely the closest relatives of the Formicidae, has been controversial, but there are compelling arguments for why they should not be considered formicids.
3. Although the first Mesozoic ant was discovered in 1967, it was not until the past two decades that a number of important Mesozoic ant discoveries have been made, including, most recently, the discovery of a 93–95 myo crown-group ant assignable to the Dolichoderinae from the Cretaceous of Africa.
4. Recent discoveries have shown that the Cretaceous stem group, Sphecomyrminae, although rare as fossils, was surprisingly diverse morphologically, which implies a diverse array of ancient sphecomyrmine behaviors as well.
5. Despite their appearance in the Cretaceous, it was not until the Eocene that ants became common as fossils, and presumably this increase in fossilized remains is correlated with an increase in the general abundance and ecological dominance of ants.
6. Molecular divergence dating techniques are growing in popularity, and the need for accurate fossil ant identification will only become more acute as more studies rely on fossils for calibration of datasets.

Annu. Rev. Entomol. 2013.58:609-630. Downloaded from www.annualreviews.org
by ${individualUser.displayName} on 01/14/13. For personal use only.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

We thank Seán Brady and Robert Kallal for comments on earlier drafts of this manuscript. JSL was supported by the National Science Foundation under grant DEB-0743542; GMD was supported by the Russian Foundation for Basic Research under grant 11-04-00421; VP was supported by the French National Institute for Universe Sciences under grant Interrvie NOVAMBRE.

LITERATURE CITED

1. Archibald SB, Cover SP, Moreau CS. 2006. Bulldog ants of the Eocene Okanagan Highlands and history of the subfamily (Hymenoptera: Formicidae: Myrmeciinae). *Ann. Entomol. Soc. Am.* 99:487–523
2. Archibald SB, Farrell BD. 2003. Wheeler's dilemma: Proceedings of the Second Paleoentomological Congress. *Acta Zool. Cracov.* 46(Suppl.-Fossil Insects):17–23
3. Archibald SB, Johnson KR, Mathewes RW, Greenwood DR. 2011. Intercontinental dispersal of giant thermophilic ants across the Arctic during early Eocene hyperthermals. *Proc. R. Soc. B* 278:3679–86
4. Aria C, Perrichot V, Nel A. 2011. Fossil Ponerinae (Hymenoptera: Formicidae) in Early Eocene amber of France. *Zootaxa* 2870:53–62
5. Baroni Urbani C, Wilson EO. 1987. The fossil members of the ant tribe Leptomyrmecini (Hymenoptera: Formicidae). *Psyche* 94:1–8
6. Bolton B. 2003. Synopsis and classification of Formicidae. *Mem. Am. Entomol. Inst.* 71:1–370
7. Bolton B. 2012. *AntCat: An Online Catalog of the Ants of the World.* **http://www.antcat.org**
8. Brandão CR, Martins-Neto R, Vulcano VA. 1989. The earliest known fossil ant (first Southern Hemisphere Mesozoic record) (Hymenoptera: Formicidae: Myrmeciinae). *Psyche* 96:195–208
9. Brady SG, Schultz TR, Fisher BL, Ward PS. 2006. Evaluating alternative hypotheses for the early evolution and diversification of ants. *Proc. Natl. Acad. Sci. USA* 103:18172–77
10. Bromley RG, Buatois LA, Genise JF, Labandeira CC, Mángano MG, et al. 2007. Comments on the paper "Reconnaissance of Upper Jurassic Morrison Formation ichnofossils, Rocky Mountain Region, USA: paleoenvironmental, stratigraphic, and paleoclimatic significance of terrestrial and freshwater ichnocoenoses" by Stephen T. Hasiotis. *Sediment. Geol.* 200:141–50
11. Brown WL Jr, Carpenter FM. 1978. A restudy of two ants from the Sicilian amber. *Psyche* 85:417–23
12. Carpenter FM. 1929. A fossil ant from the Lower Eocene (Wilcox) of Tennessee. *J. Wash. Acad. Sci.* 19:300–1
13. Carpenter FM. 1930. The fossil ants of North America. *Bull. Mus. Comp. Zool. Harv.* 70:1–66
14. Clementz M, Bajpai S, Ravikant V, Thewissen JGM, Saravanan N, et al. 2011. Early Eocene warming events and the timing of terrestrial faunal exchange between India and Asia. *Geology* 39:15–18
15. Cockerell TDA. 1915. British fossil insects. *Proc. U.S. Natl. Mus.* 49:469–99
16. Crozier RH, Jermiin LS, Chiotis M. 1997. Molecular evidence for a Jurassic origin of ants. *Naturwissenschaften* 84:22–23
17. Dierick M, Cnudde V, Masschaele B, Vlassenbroeck J, Van Hoorebeke L, Jacobs P. 2007. Micro-CT of fossils preserved in amber. *Nucl. Instrum. Methods Phys. Res. A* 580:641–43
18. Dlussky GM. 1975. Superfamily Formicoidea. See Ref. 88, pp. 114–22
19. **Dlussky GM. 1983. A new family of Upper Cretaceous Hymenoptera: an "intermediate link" between ants and Scolioidea. *Paleontol. J.* 17:63–76**
20. Dlussky GM. 1987. New Formicoidea (Hymenoptera) of the Upper Cretaceous. *Paleontol. J.* 20:146–50
21. Dlussky GM. 1988. Ants from (Paleocene?) Sakhalin amber. *Paleontol. J.* 22:50–61

19. First description of the Armaniidae.

Annu. Rev. Entomol. 2013.58:609-630. Downloaded from www.annualreviews.org
by ${individualUser.displayName} on 01/14/13. For personal use only.

22. Dlussky GM. 1996. Ants (Hymenoptera: Formicidae) from Burmese amber. *Paleontol. J.* 30:449–54
23. Dlussky GM. 1999. New ants (Hymenoptera, Formicidae) from Canadian amber. *Paleontol. J.* 33:409–12
24. Dlussky GM. 1999. The first find of the Formicoidea (Hymenoptera) in the Lower Cretaceous of the Northern Hemisphere. *Paleontol. J.* 33:274–77
25. Dlussky GM. 2010. Ants of the genus *Plagiolepis* Mayr (Hymenoptera, Formicidae) from Late Eocene ambers of Europe. *Paleontol. J.* 44:546–55
26. Dlussky GM, Brothers DJ, Rasnitsyn AP. 2004. The first Late Cretaceous ants (Hymenoptera, Formicidae) from southern Africa, with comments on the origin of the Myrmicinae. *Insect Syst. Evol.* 35:1–13
27. Dlussky GM, Rasnitsyn AP. 2003. Ants (Hymenoptera: Formicidae) of Formation Green River and some other Middle Eocene deposits of North America. *Russ. Entomol. J.* 11:411–36
28. Dlussky GM, Rasnitsyn AP. 2007. Paleontological record and stages of ant evolution. *Uspehi Sovrem. Biol.* 127:118–34
29. Dlussky GM, Rasnitsyn AP. 2009. Ants (Insecta: Vespida: Formicidae) in the Upper Eocene amber of Central and Eastern Europe. *Paleontol. J.* 43:1024–42
30. Dlussky GM, Wappler T, Wedmann S. 2008. New Middle Eocene formicid species from Germany and the evolution of weaver ants. *Acta Palaeontol. Pol.* 53:615–26
31. Dlussky GM, Wappler T, Wedmann S. 2009. Fossil ants of the genus *Gesomyrmex* Mayr (Hymenoptera, Formicidae) from the Eocene of Europe and remarks on the evolution of arboreal ant communities. *Zootaxa* 2031:1–20
32. Donisthorpe H. 1920. British Oligocene ants. *Ann. Mag. Nat. Hist.* 9:81–94
33. Dunlop JA. 2010. Bitterfeld amber. See Ref. 78, pp. 57–68
34. Emery C. 1891. Le formiche dell'ambra Siciliana nel Museo Mineralogico dell'Universita di Bologna. *Mem. R. Accad. Sci. Inst. Bologna* 5:141–65
35. Engel MS, Grimaldi DA. 2005. Primitive new ants in Cretaceous amber from Myanmar, New Jersey and Canada. *Am. Mus. Novit.* 3485:1–23
36. Eskov KY. 2002. Appendix: alphabetic list of selected insect fossil sites. 4.2. Fossil resins. See Ref. 91, pp. 444–46
37. Förster B. 1891. Die Insekten des "Plattigen Steinmergels" von Brunnstatt. *Abh. Geol. Spec. Elsass-Lothr.* 3:333–59
38. Genise JF, Bellosi ES, Melchor RN, Cosarinsky MA. 2005. Comment—advanced Early Jurassic termite (Insecta: Isoptera) nests: evidence from the Clarens Formation in the Tuli Basin, Southern Africa (Bordy et al., 2004). *Palaios* 20:303–8
39. Germar EF. 1837. Fauna insectorum Europae. Fasciculus 19. Insectorum protogaeae specimen sistens insecta carbonum fossilium. Halle, Ger.: Kümmel. 1–25 pp.
40. Grimaldi DA, Agosti D. 2000. A formicine in New Jersey Cretaceous amber and early evolution of ants. *Proc. Natl. Acad. Sci. USA* 97:13678–83
41. Grimaldi DA, Agosti D, Carpenter JM. 1997. New and rediscovered primitive ants in Cretaceous amber from New Jersey, and their phylogenetic relationships. *Am. Mus. Novit.* 3208:1–43
42. Grimaldi DA, Engel MS. 2005. *Evolution of the Insects*. New York: Cambridge Univ. Press. 755 pp.
43. Grimaldi DA, Engel MS, Nascimbene PC. 2002. Fossiliferous Cretaceous amber from Myanmar (Burma): its rediscovery, biotic diversity, and paleontological significance. *Am. Mus. Novit.* 3361:1–71
44. Grimaldi DA, Nascimbene PC. 2010. Raritan (New Jersey) amber. See Ref. 78, pp. 167–91
45. Grimaldi DA, Nguyen T, Ketcham R. 2000. Ultra-high-resolution X-ray computed tomography (UHR CT) and the study of fossils in amber. In *Studies on Fossils in Amber, with Particular Reference to the Cretaceous of New Jersey*, ed. DA Grimaldi, pp. 77–91. Leiden: Backhuys Publ.
46. Grimaldi D, Shedrinsky AM, Wampler TP. 2000. A remarkable deposit of fossiliferous amber from the Upper Cretaceous (Turonian) of New Jersey. In *Studies on Fossils in Amber, with Particular Reference to the Cretaceous of New Jersey*, ed. DA Grimaldi, pp. 1–76. Leiden: Backhuys Publ.
47. Halfen AF, Hasiotis ST. 2010. Neoichnological study of the traces and burrowing behaviors of the western harvester ant *Pogonomyrmex occidentalis* (Insecta: Hymenoptera: Formicidae): paleopedogenic and paleoecological implications. *Palaios* 25:703–20

23. First description of species from the morphologically bizarre Haidomyrmecini (Sphecomyrminae).

26. Detailed fossil discoveries from Botswana that challenged the notion of a Laurasian origin for ants.

40. First description of a definitive crown-group ant.

Annu. Rev. Entomol. 2013.58:609-630. Downloaded from www.annualreviews.org by ${individualUser.displayName} on 01/14/13. For personal use only.

Annu. Rev. Entomol. 2013.58:609-630. Downloaded from www.annualreviews.org
by ${individualUser.displayName} on 01/14/13. For personal use only.

48. Hasiotis ST. 2004. Reconnaissance of Upper Jurassic Morrison Formation ichnofossils, Rocky Mountain Region, USA: paleoenvironmental, stratigraphic, and paleoclimatic significance of terrestrial and freshwater ichnocoenoses. *Sediment. Geol.* 167:177–268
49. Heer O. 1850. Die Insektenfauna der Tertiargebilde von Oeningen und von Radoboj in Croatien. Zweite Abtheilung: Heuschrecken, Florfliegen, Aderfluger, Schmetterlinge und Fliegen. *Neue Denkschr. Allg. Schweiz. Ges. Gesammten Naturwiss.* 11:1–264
50. Heie OE. 1987. Palaeontology and phylogeny. In *Aphids: Their Biology, Natural Enemies, and Control*, ed. AK Minks, P Harrewijn, 2A:367–91. Amsterdam: Elsevier
51. Henderickx H, Cnudde V, Masschaele B, Dierick M, Vlassenbroeck J, Van Hoorebeke L. 2006. Description of a new fossil *Pseudogarypus* (Pseudoscorpiones: Pseudogarypidae) with the use of X-ray micro-CT to penetrate opaque amber. *Zootaxa* 1305:41–50
52. Hölldobler B, Wilson EO. 1990. *The Ants*. Cambridge, MA: Harvard Univ. Press. 732 pp.
53. Hölldobler B, Wilson EO. 2008. *The Superorganism: The Beauty, Elegance, and Strangeness of Insect Societies*. New York: WW Norton & Co. 522 pp.
54. Hong YC. 2002. *Amber Insects of China*. Beijing: Sci. Technic Publ. House. 653 pp.
55. Hooker J, Grimes ST, Mattey DP, Collinson ME, Sheldon ND. 2009. Refined correlation of the UK Late Eocene–Early Oligocene Solent Group and timing of its climate history. *Geol. Soc. Am. Spec. Pap.* 452:179–95
56. Hung ACF, Brown WL. 1966. Structure of gastric apex as a subfamily character of the Formicinae. *J. N.Y. Entomol. Soc.* 74:198–200
57. Johnson C, Agosti D, Delabie JH, Dumpert K, Williams DJ, et al. 2001. *Acropyga* and *Azteca* ants (Hymenoptera: Formicidae) with scale insects (Sternorrhyncha: Coccoidea): 20 million years of intimate symbiosis. *Am. Mus. Novit.* 3335:1–18
58. Keller RA. 2000. Cladistics of the tribe Ectatommini (Hymenoptera: Formicidae): a reappraisal. *Insect Syst. Evol.* 31:59–69
59. Keller RA. 2011. A phylogenetic analysis of ant morphology (Hymenoptera: Formicidae) with special reference to the poneromorph subfamilies. *Bull. Am. Mus. Nat. Hist.* 355:1–90
60. Lak M, Néraudeau D, Nel A, Cloetens P, Perrichot V, Tafforeau P. 2008. Phase contrast X-ray synchrotron imaging: opening access to fossil inclusions in opaque amber. *Microsc. Microanal.* 14:251–59
61. LaPolla JS. 2004. *Acropyga* (Hymenoptera: Formicidae) of the World. *Contrib. Am. Entomol. Inst.* 33:1–130
62. LaPolla JS. 2005. Ancient trophophoresy: a fossil *Acropyga* (Hymenoptera: Formicidae) from Dominican amber. *Trans. Am. Entomol. Soc.* 131:21–28
63. LaPolla JS, Cover SP, Mueller UG. 2002. Natural history and distribution notes on the mealybug-tending ant *Acropyga epedana*, with descriptions of the male and queen castes. *Trans. Am. Entomol. Soc.* 128:367–76
64. LaPolla JS, Dlussky GM. 2010. Review of fossil *Prenolepis* genus-group species. *Proc. Entomol. Soc. Wash.* 112:258–73
65. Lucky A. 2011. Molecular phylogeny and biogeography of the spider ants, genus *Leptomyrmex* Mayr (Hymenoptera: Formicidae). *Mol. Phylogenet. Evol.* 59:281–92
66. Lutz H. 1986. Eine neue Unterfamilie der Formicidae (Insecta: Hymenoptera) aus dem mitteleozänen Ölschiefer der "Grube Messel" bei Darmstadt (Deutschland, S-Hessen). *Senckenberg. Lethaea* 67:177–218
67. Lutz H. 1990. Systematische und palökologische Untersuchungen an Insekten aus dem Mittel-Eozän der Grube Messel bei Darmstadt. *Cour. Forschungsinst. Senckenberg* 124:1–165
68. Lutz H. 1997. Taphozönosen terrestrischer Insekten in aquatischen Sedimenten—ein Beitrag zur Rekonstruktion des Paläoenvironments. *Neues Jahrb. Geol. Palaontol. Abh.* 203:173–210
69. Mayr GL. 1867. Vorläufige Studien über die Radoboj-Formiciden, in der Sammlung der k.k. geologischen Reichsanstalt. *Jahrb. K. K. Geol. Reichs.* 17:47–62
70. Mayr GL. 1868. Die Ameisen des Baltischen Bernstein. *Beitr. Naturk. Preuss. Königsberg* 1:1–102
71. McInerney FA, Wing SL. 2011. The Paleocene-Eocene thermal maximum: a perturbation of carbon cycle, climate, and biosphere with implications for the future. *Annu. Rev. Earth Planet. Sci.* 39:489–516

66. Recognized the giant ants of the Eocene, the Formiciinae, as a distinct lineage.

70. First monograph of a fossil ant fauna and first attempts at reconstruction of incomplete fossil specimens.

72. McKellar RC, Engel MS. 2012. Hymenoptera in Canadian Cretaceous amber (Insecta). *Cretac. Res.* 35:258–79
73. McKenna DD, Farrell BD. 2006. Tropical forests are both evolutionary cradles and museums of leaf beetle diversity. *Proc. Natl. Acad. Sci. USA* 103:10947–51
74. Mertz DF, Renne PR. 2005. A numerical age for the Messel fossil deposit (UNESCO World Heritage Site) derived from 40Ar/39Ar dating on a basaltic rock fragment. *Cour. Forschungsinst. Senckenberg* 255:67–75
75. Meyer HW. 2003. *The Fossils of Florissant*. Washington, DC/London: Smithson. Books. 258 pp.
76. Moreau CS, Bell CD, Vila R, Archibald SB, Pierce NE. 2006. Phylogeny of the ants: diversification in the age of angiosperms. *Science* 312:101–4
77. Nel A, Perrault G, Perrichot V, Néraudeau D. 2004. The oldest ant in the Lower Cretaceous amber of Charente-Maritime (SW France) (Insecta: Hymenoptera: Formicidae). *Geol. Acta* 2:23–29
78. Penney D, ed. 2010. *Biodiversity of Fossils in Amber from the Major World Deposits*. Manchester, UK: Siri Sci. Press
79. Perkovski EE. 2007. Syninclusions of ant *Lasius schiefferdeckeri* (Hymenoptera, Formicidae) and aphid *Germaraphis* (Homoptera, Aphidinae) in Rovno and Saxonian ambers. *Vestn. Zool.* 41:181–85
80. Perreau M, Tafforeau P. 2011. Virtual dissection using phase-contrast X-ray synchrotron microtomography: reducing the gap between fossils and extant species. *Syst. Entomol.* 36:573–80
81. Perrichot V. 2012. *AntWeb. Fossil ants.* **http://www.antweb.org/fossil.jsp**
82. Perrichot V, Girard V. 2009. A unique piece of amber and the complexity of ancient forest ecosystems. *Palaios* 24:137–39
83. **Perrichot V, Lacau S, Néraudeau D, Nel A. 2008. Fossil evidence for the early ant evolution. *Naturwissenschaften* 95:85–90**
84. Perrichot V, Nel A, Néraudeau D, Lacau S, Guyot T. 2008. New fossil ants in French Cretaceous amber (Hymenoptera: Formicidae). *Naturwissenschaften* 95:91–97
85. Perrichot V, Néraudeau D, Tafforeau P. 2010. Charentese amber. See Ref. 78, pp. 192–207
86. Pie MR, Tschá MK. 2009. The macroevolutionary dynamics of ant diversification. *Evolution* 63:3023–30
87. Poinar GO Jr, Archibald B, Brown A. 1999. New amber deposit provides evidence of Early Paleogene extinctions, paleoclimates and past distributions. *Can. Entomol.* 131:171–77
88. Rasnitsyn AP. 1975. Hymenoptera Apocrita of Mesozoic. *Trans. Paleontol. Inst. Acad. Sci. USSR* 147:1–134 [in Russian]
89. Rasnitsyn AP. 2002. Superorder Vespidea Laicharting, 1781. Order Hymenoptera Linné, 1758 (= Vespida Laicharting, 1781). See Ref. 91, pp. 242–54
90. Rasnitsyn AP, Kulicka R. 1990. Hymenopteran insects in Baltic amber with respect to the overall history of the order. *Prace Muz. Ziemi* 41:53–64
91. Rasnitsyn AP, Quicke DLJ, eds. 2002. *History of Insects*. Dordrecht, The Neth.: Kluwer Acad. Publ.
92. Roberts EM, Tapanila L. 2006. A new social insect nest from the Upper Cretaceous Kaiparowits Formation of southern Utah. *J. Paleontol.* 80:768–74
93. Ross A, Mellish C, York P, Crighton B. 2010. Burmese amber. See Ref. 78, pp. 208–35
94. Rust J, Andersen NM. 1999. Giant ants from the Paleogene of Denmark with a discussion of the fossil history and early evolution of ants (Hymenoptera: Formicidae). *Zool. J. Linn. Soc.* 125:331–48
95. Rust J, Singh H, Rana RS, McCann T, Singh L, et al. 2010. Biogeographic and evolutionary implications of a diverse paleobiota in amber from the early Eocene of India. *Proc. Natl. Acad. Sci. USA* 107:18360–65
96. Schmidt AR, Perrichot V, Svojtka M, Anderson KB, Belete KH, et al. 2010. Cretaceous African life captured in amber. *Proc. Natl. Acad. Sci. USA* 107:7329–34
97. Schneider SA, LaPolla JS. 2011. Systematics of the mealybug tribe Xenococcini (Hemiptera: Coccoidea: Pseudococcidae) with a discussion of trophobiotic associations with *Acropyga* Roger ants. *Syst. Entomol.* 36:57–82
98. Schweigger AF. 1819. *Beobachtungen auf naturhistorischen Reisen. Anatomisch-physiologische Untersüchungen über Corallen; nebst einem Anhange, Bemerkungen über den Bernstein enthaldend*. Reimer, Berlin. 127 pp.
99. Schultz TR. 2007. The fungus-growing ant genus *Apterostigma* in Dominican amber. In *Advances in Ant Systematics: Homage to E.O. Wilson—50 Years of Contributions*, ed. RR Snelling, BL Fisher, PS Ward. *Mem. Am. Entomol. Inst.* 80:425–36

83. Utilized the emerging diverse Cretaceous age fossil record to discuss the origins and paleobiogeography of ants.

Annu. Rev. Entomol. 2013.58:609-630. Downloaded from www.annualreviews.org
by ${individualUser.displayName} on 01/14/13. For personal use only.

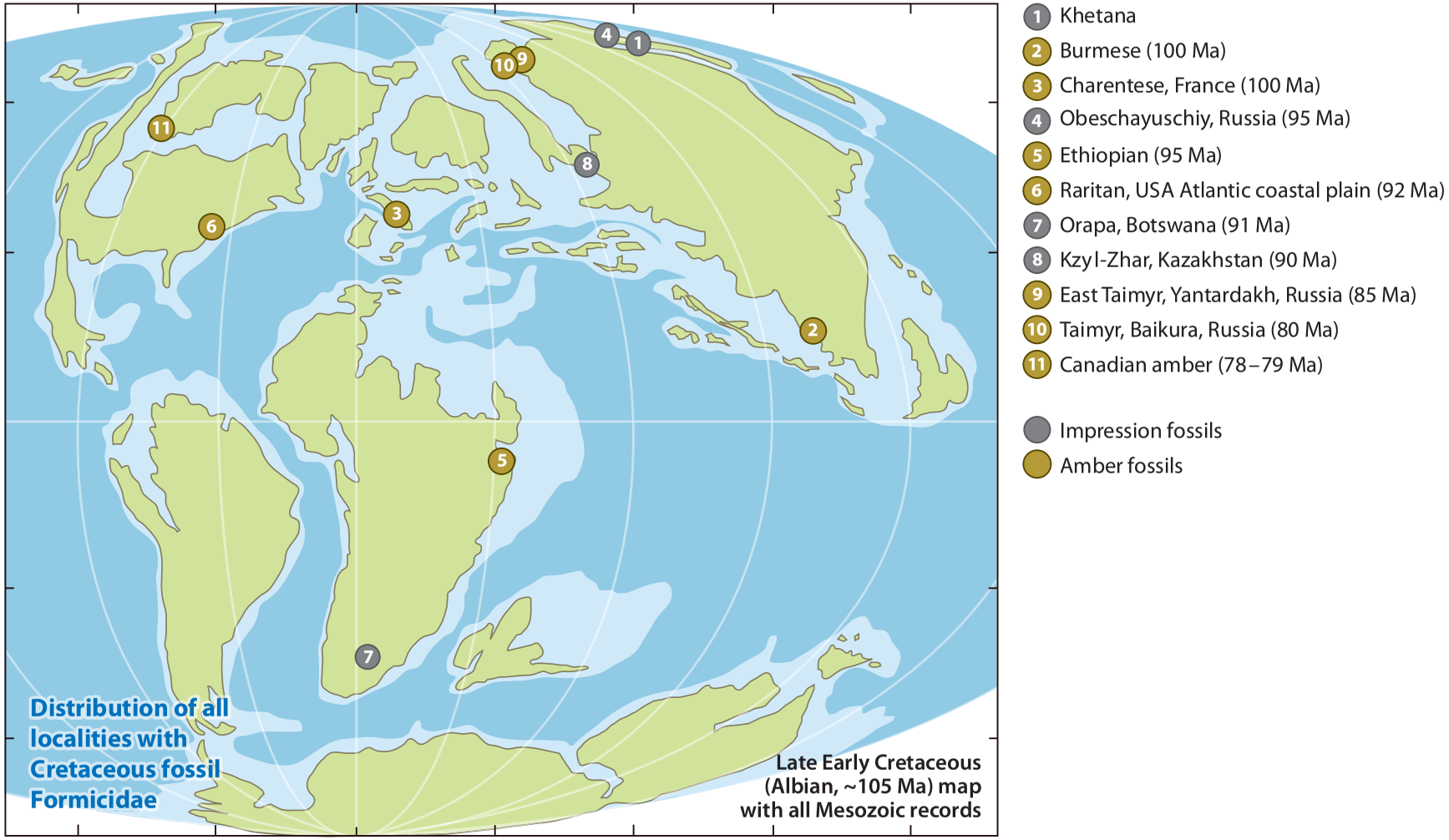
100. Seilacher A. 2007. Arthropod tunnel systems. In *Trace Fossil Analysis*, ed. A Seilacher, pp. 45–60. Berlin/Heidelberg: Springer
101. Sendel N. 1742. *Historia succinorum corpora aliena involventium et naturae opere pictorum et caelatorum ex Augustorum I et II cimeliis Dresdae conditis aeri insculptorum*. Leipzig, Ger.: Gleditsch. 328 pp.
102. Shi G, Grimaldi DA, Harlow GE, Wang Jing, Wang Jun, et al. 2012. Age constraint on Burmese amber based on U-Pb dating of zircons. *Cretac. Res.* 37:155–63
103. Smith ME, Singer BS, Carroll AR. 2008 Synoptic reconstruction of a major ancient lake system: Eocene Green River Formation, western United States. *Geol. Soc. Am. Bull.* 120:54–84
104. Solórzano Kraemer MM. 2007. Systematic, palaeoecology, and palaeobiogeography of the insect fauna from the Mexican amber. *Palaeontogr. A* 282:1–133
105. Soriano C, Archer M, Azar D, Creaser P, Delclòs X, et al. 2010. Synchrotron X-ray imaging of inclusions in amber. *C.R. Palevol.* 9:361–68
106. Théobald N. 1937. Les insectes fossiles des terrains oligocènes de France. *Mém. Soc. Sci. Nancy* 2:1–473
107. Tschinkel WR. 2003. Subterranean ant nests: trace fossils past and future? *Palaeogeogr. Palaeoclim. Palaeoecol.* 192:321–33
108. Ward PS. 2007. Phylogeny, classification, and species-level taxonomy of ants (Hymenoptera: Formicidae). *Zootaxa* 1668:549–63
109. Weitschat W, Wichard W. 2010. Baltic amber. See Ref. 78, pp. 50–83
110. Westwood JO. 1854. Contributions to fossil entomology. *Q. J. Geol. Soc. Lond.* 10:378–96
111. Wheeler WM. 1915. The ants of the Baltic amber. *Schrift. Phys. Ökonom. Ges. Königsberg* 55:1–142
112. Wheeler WM. 1930. The ant *Prenolepis imparis* Say. *Ann. Entomol. Soc. Am.* 23:1–26
113. Wilson EO. 1985. Invasion and extinction in the West Indian ant fauna: evidence from the Dominican amber. *Science* 229:265–67
114. Wilson EO. 1987. The earliest known ants: an analysis of the Cretaceous species and an inference concerning their social organization. *Paleobiology* 13:44–53
115. Wilson EO, Carpenter FM, Brown WL Jr. 1967. The first Mesozoic ants, with the description of a new subfamily. *Psyche* 74:1–19
116. Wilson EO, Hölldobler B. 2005. The rise of the ants: a phylogenetic and ecological explanation. *Proc. Natl. Acad. Sci. USA* 202:7411–14
117. Yek SH, Mueller UG. 2011. The metapleural gland of ants. *Biol. Rev.* 86:774–91
118. Barden P, Grimaldi D. 2012. Rediscovery of the bizarre Cretaceous ant *Haidomyrmex* Dlussky (Hymenoptera: Formicidae), with two new species. *Am. Mus. Novit.* 3755:1–16

111. Groundbreaking monograph of the Baltic amber ants; for many years the gold standard for fossil ant study.

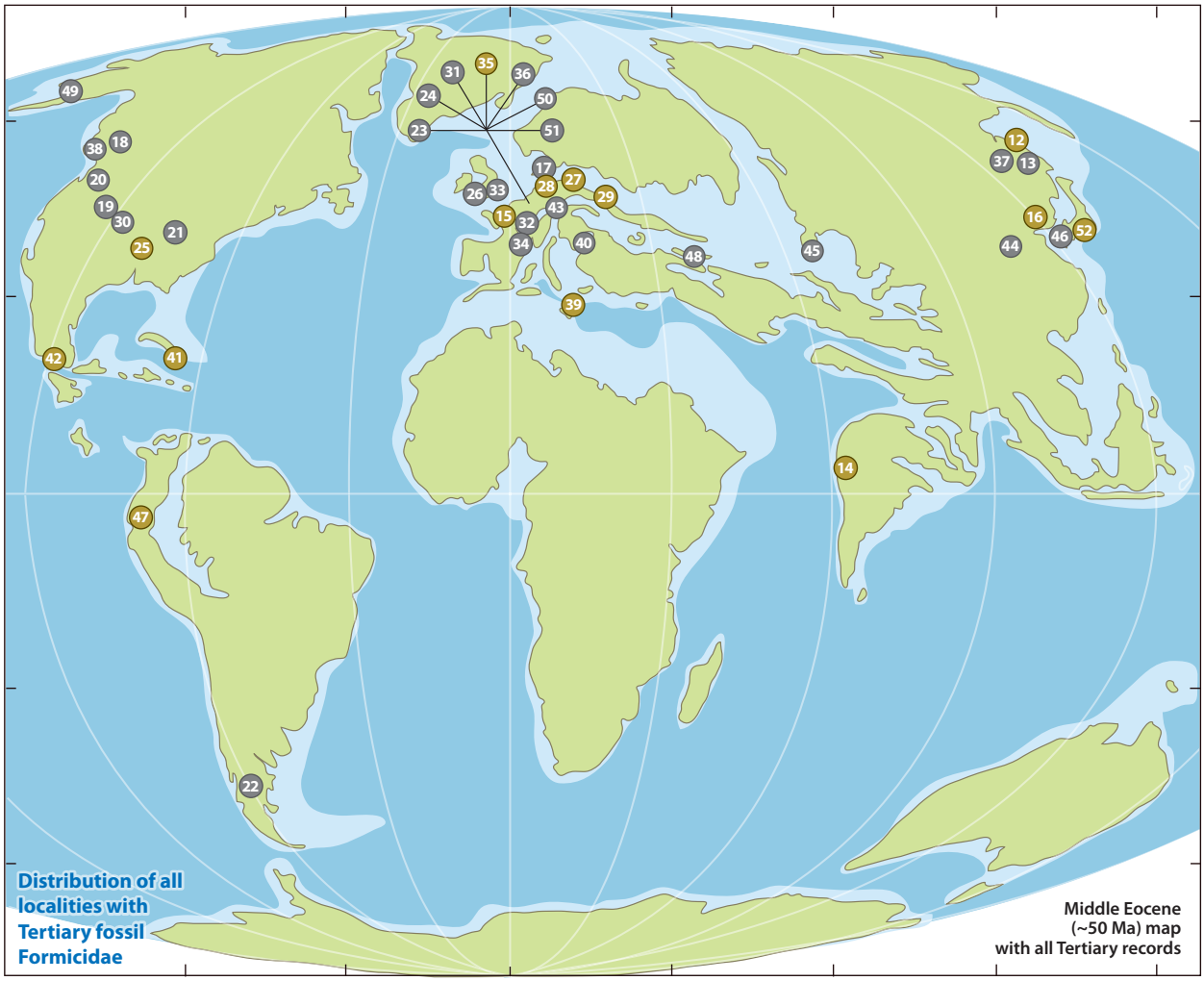
115. Discovery of first Mesozoic ant.

Annu. Rev. Entomol. 2013.58:609-630. Downloaded from www.annualreviews.org
by ${individualUser.displayName} on 01/14/13. For personal use only.

Supplemental Material: Annu. Rev. Entomol. 2013. 58:609-30
doi: 10.1146/annurev-ento-120710-100600
Ants and the Fossil Record
LaPolla, Dlussky, and Perrichot



Supplemental Figure 1. Distribution of all Cretaceous localities with fossil Formicidae (maps modified from Blakey RC. 2011. Library of Paleogeography, Colorado Plateau Geosystems, Inc. Mollewide Globes, Late Early Cretaceous (105 mya). http://cpgeosystems.com/105moll.jpg.



Paleocene

12 Sakhalin amber, Russia (56–59 Ma)
13 Tadushi Formation
14 Cambay, India (56 Ma)

Eocene

15 Oise, France (53–55 Ma)
16 Fushun, China (49–56 Ma)
17 Mo-Clay, Denmark (55 Ma)
18 Okanagan Highlands, Canada (51 Ma)
19 Green River Formation, USA (50 Ma)
20 Republic, Washington, USA (49 Ma)
21 Wilcox Formation, USA (49 Ma)
22 Ventana Fm., Confluencia, Argentina (48 Ma)
23 Messel, Germany (47 Ma)
24 Eckfeld, Germany (44 Ma)
25 Arkansas, USA (40–48 Ma)

Eocene (continued)

26 Dorset, England (37–40 Ma)
27 Baltic (34–42 Ma)
28 Scandinavian, Denmark
29 Rovno, Ukraine (34–37 Ma)
30 Florissant, Colorado, USA (34 Ma)

Oligocene

31 Kleinkems, Germany (33 Ma)
32 Brunstatt, France (30–34 Ma)
33 Bembridge, Isle of Wight, England (28 Ma)
34 Aix-en-Provence, France (28 Ma)
35 Bitterfeld, Germany (23 Ma)
36 Rott, Germany (23 Ma)
37 Bol'Shaya Svetlovodnaya, Russia

Impression fossils
Amber fossils

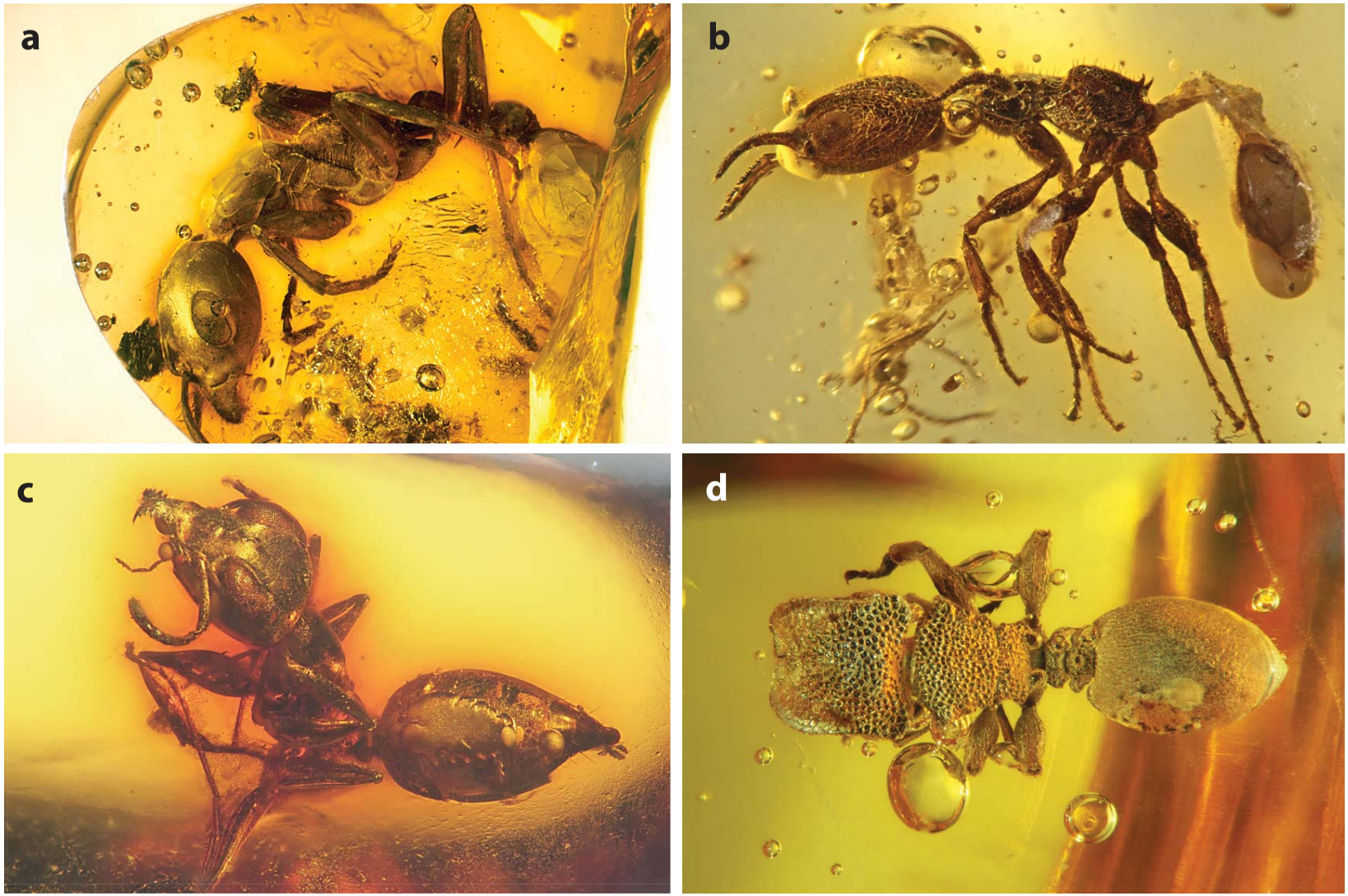
Miocene

38 Quesnel, Br. Columbia, Canada (20–23 Ma)
39 Sicilian (16-23 Ma)
40 Radoboj, Croatia (19 Ma)
41 Dominican (16–19 Ma)
42 Mexican (16–19 Ma)
43 Krottensee, Czech Republic (16–18 Ma)
44 Shanwang, China (17 Ma)
45 Chon-Tuz, Kyrgyzstan (12–16 Ma)
46 Chojaburu, Japan (12–16 Ma)
47 Peruvian (12–15 Ma)
48 Stavropol, Russia (11–16 Ma)
49 Central Alaska (6.7 Ma)
50 Oeningen, Germany (5–7 Ma)

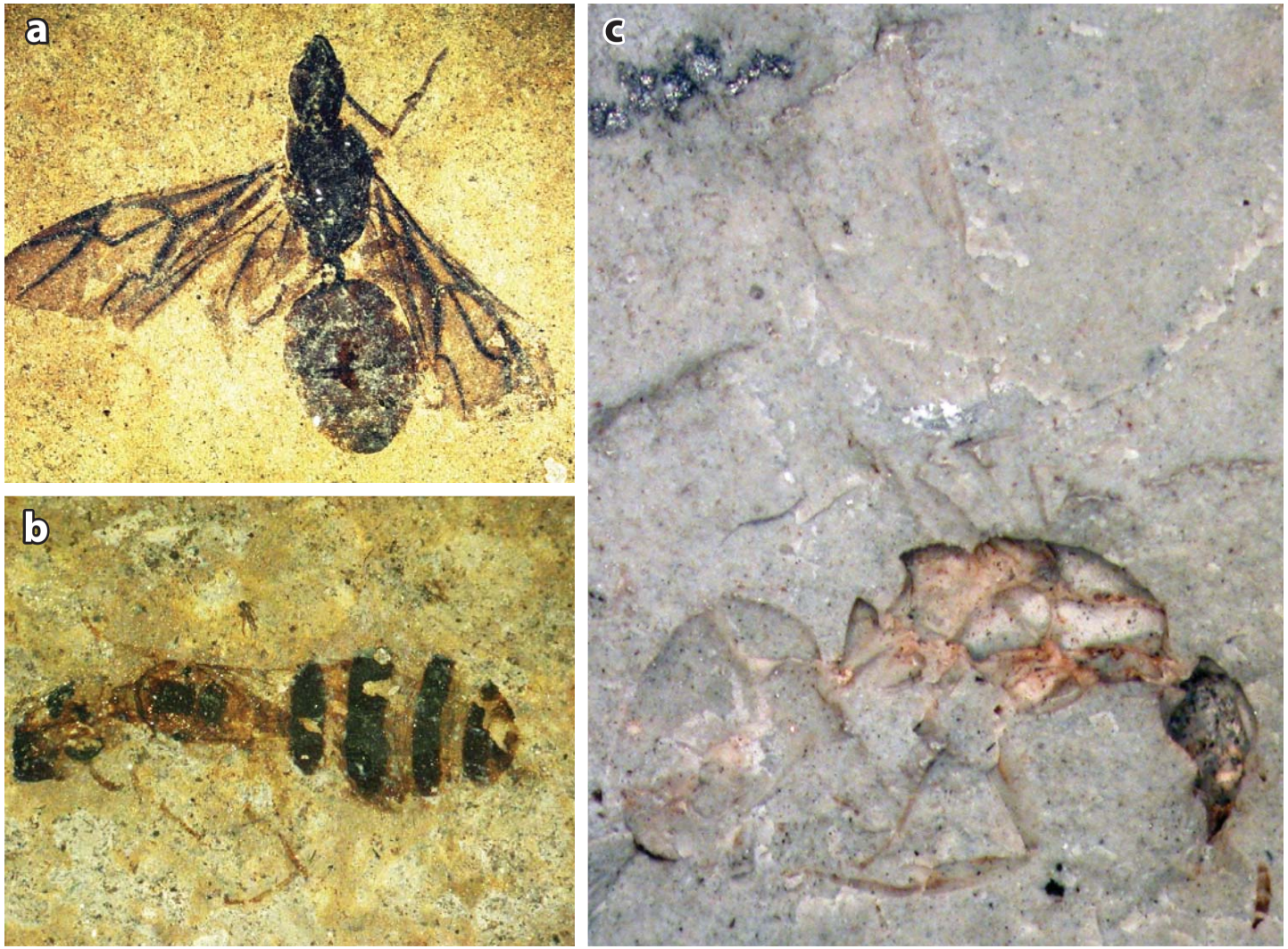
Pliocene

51 Willershausen, Germany (2–2.5 Ma)
52 Mizunami, Japan (1 Ma)

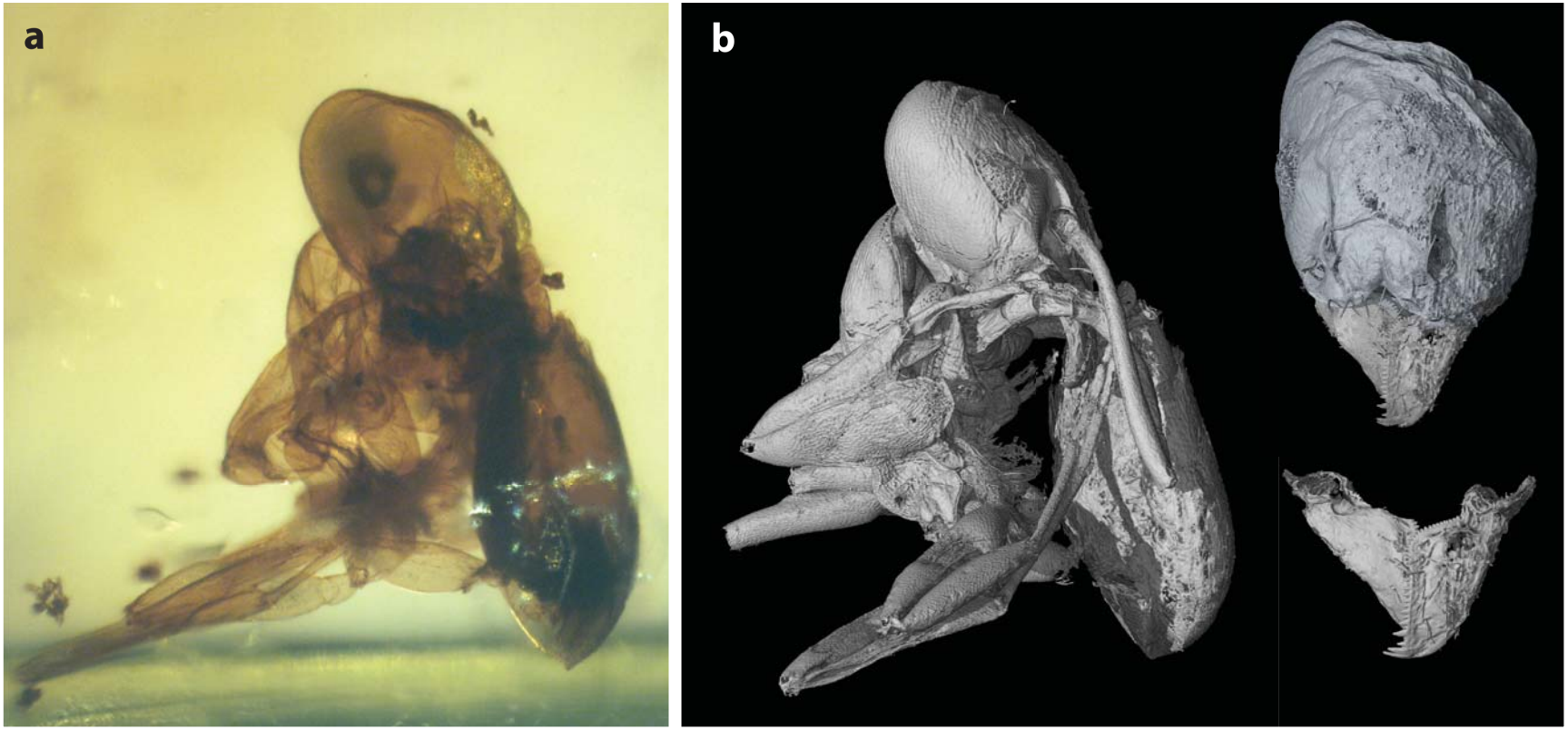
Supplemental Figure 2. Distribution of all Cenozoic localities with fossil Formicidae (maps modified from Blakey RC. 2011. Library of Paleogeography, Colorado Plateau Geosystems, Inc. Mollewide Globes) Eocene (50 mya). http://cpgeosystems.com/50moll.jpg.



Supplemental Figure 3. Examples of amber ants. (*a*) *Tetraponera* sp., in Eocene Oise amber; (*b*) *Electromyrmex klebsi*, in Eocene Baltic amber; (*c*) *Gesomyrmex* sp., in Oligocene Bitterfeld amber; (*d*) *Cephalotes serratus*, in Miocene Dominican amber. Images courtesy of V. Perrichot/Antweb.



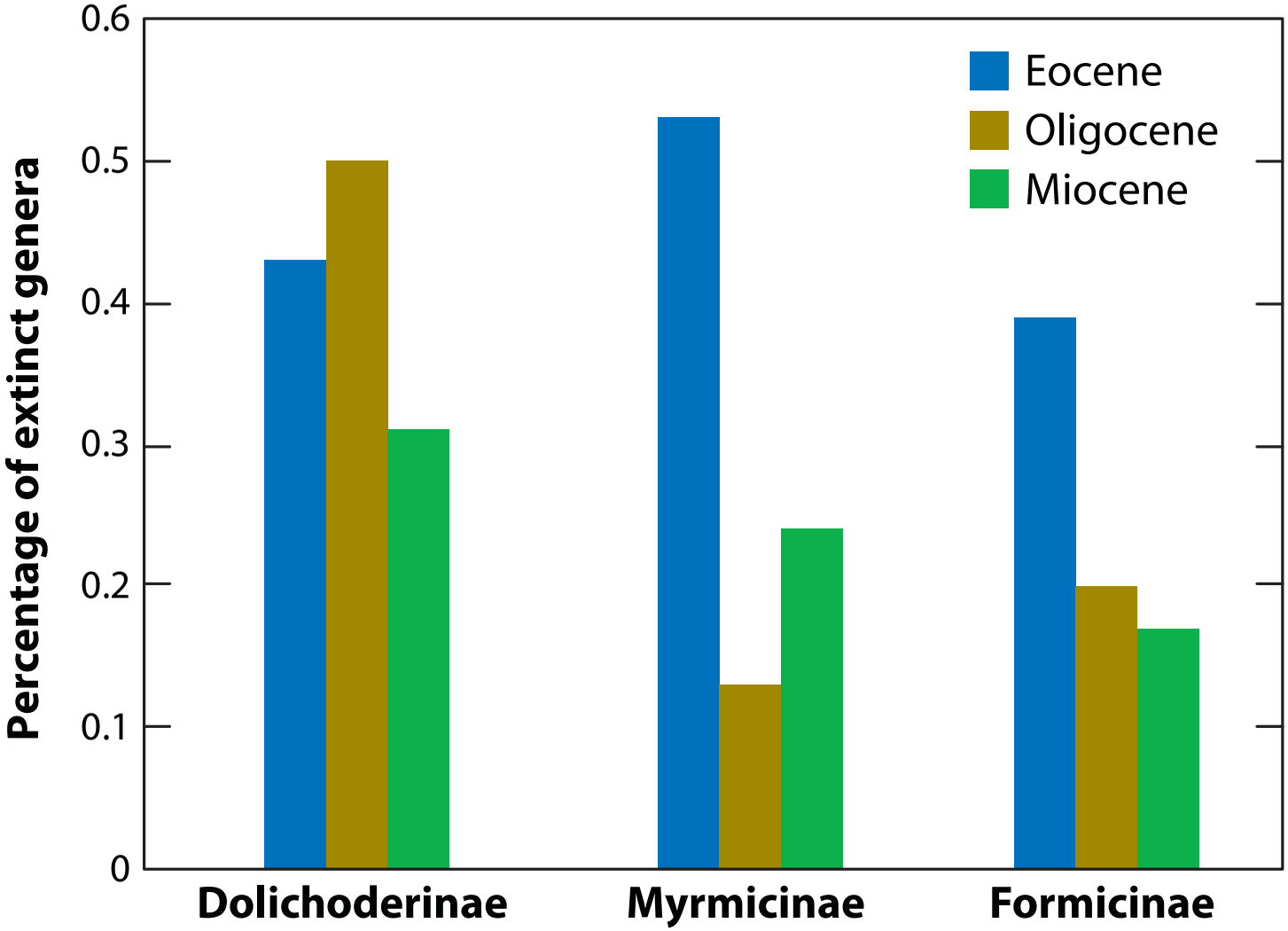
Supplemental Figure 4. Examples of ant imprint fossils. (*a*) *Oecophylla longiceps*, in Eocene bituminous claystone from Messel, Germany; (*b*) *Gesomyrmex breviceps*, from Messel, Germany; (*c*) *Dolichoderus vectensis*, in Eocene limestone from Bembridge, Isle of Wight, United Kingdom. Images courtesy of G. Dlussky.



Supplemental Figure 5. (*a*) A worker ant from 95 Myo amber of Ethiopia. The fossil is curled, which made the observation of many diagnostic features and thus the identification impossible using conventional light microscopes. (*b*) Three-dimensional virtual reconstruction in phase contrast synchrotron microtomography, followed by a virtual dissection, allows access to all morphological features, as detailed here with the head and mandibles, and identification of a Dolichoderinae (taxon currently under study). Images courtesy of V. Perrichot/C. Soriano/P. Tafforeau/ESRF.

Supplemental Figure 6. A “false ant” (Hymenoptera: Falsiformicidae) in mid-Cretaceous (100 Myo) Charentese amber, SW France, showing geniculate antennae with a short scape and a petiole broadly attached to abdominal segment III. Three-dimensional virtual reconstruction in phase contrast synchrotron microtomography, wings partially removed. Image courtesy of V. Perrichot/C. Soriano/P.Tafforeau/ESRF.

Supplemental Figure 7. *Titanomyrma similima*, a giant ant imprint fossil in 47 Myo claystone from Messel, Germany. Image V. Perrichot/AntWeb.



Supplemental Figure 8. Percentage of extinct genera as a total of all ant genera known to exist at a particular time period; for genera that are extant, they are considered to remain present from their first appearance in a fossil deposit even if no representatives of those genera are known from younger deposits.

Geologica Acta, Vol.2, N°1, 2004, 9-22
Available online at www.geologica-acta.com

geologica acta

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

V. PERRICHOT

Géosciences, Université Rennes I and CNRS UMR 6118
Bat. 15, 263 avenue du Général Leclerc, 35042 Rennes Cedex, Francia. E-mail: Vincent.Perrichot@univ-rennes1.fr

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).

© UB-ICTJA

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.

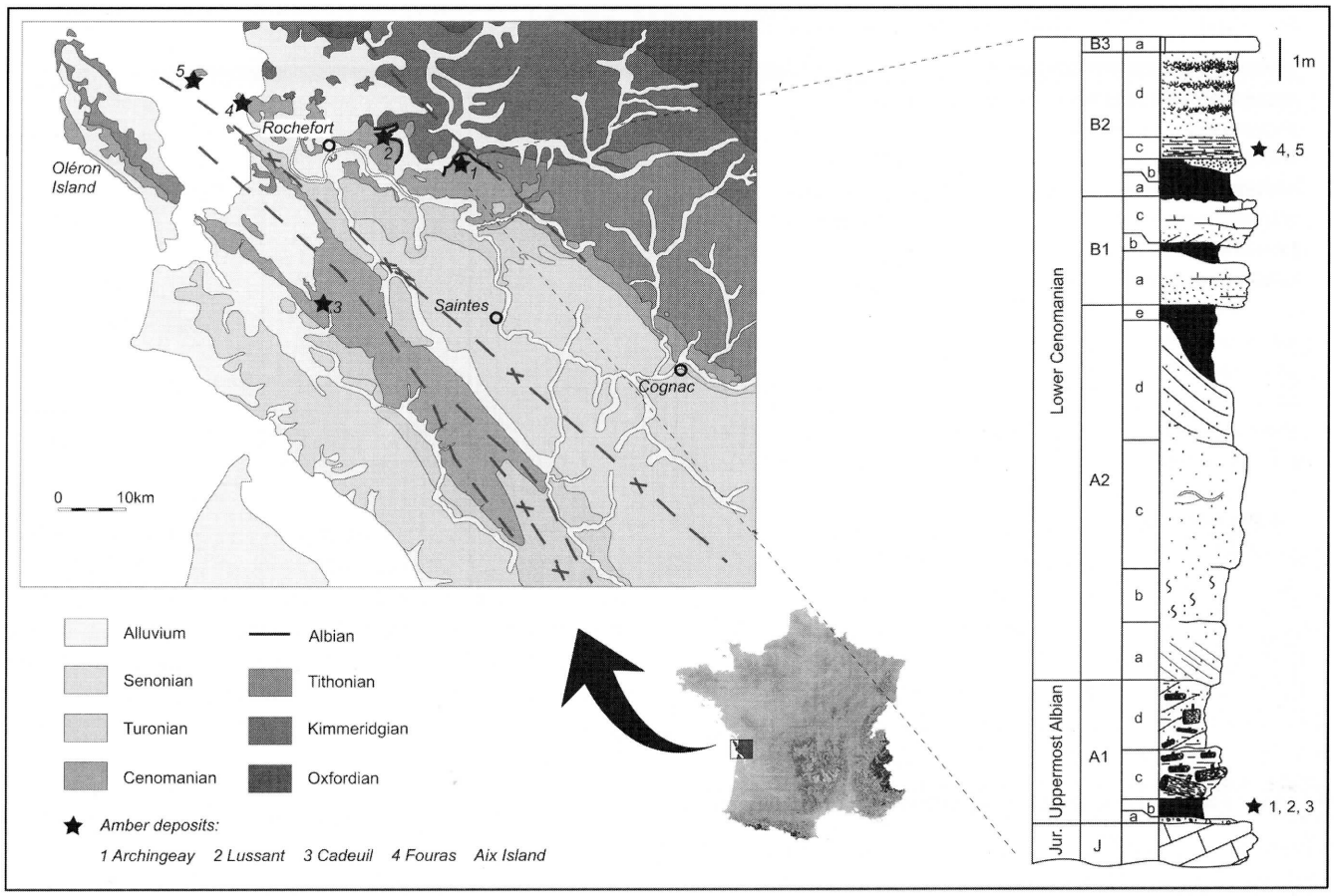


FIGURE 1 | **Geological map of Charente-Maritime region (modified from Waterlot and Polvèche, 1958) with a stratigraphic section of the amber outcrop.**

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.

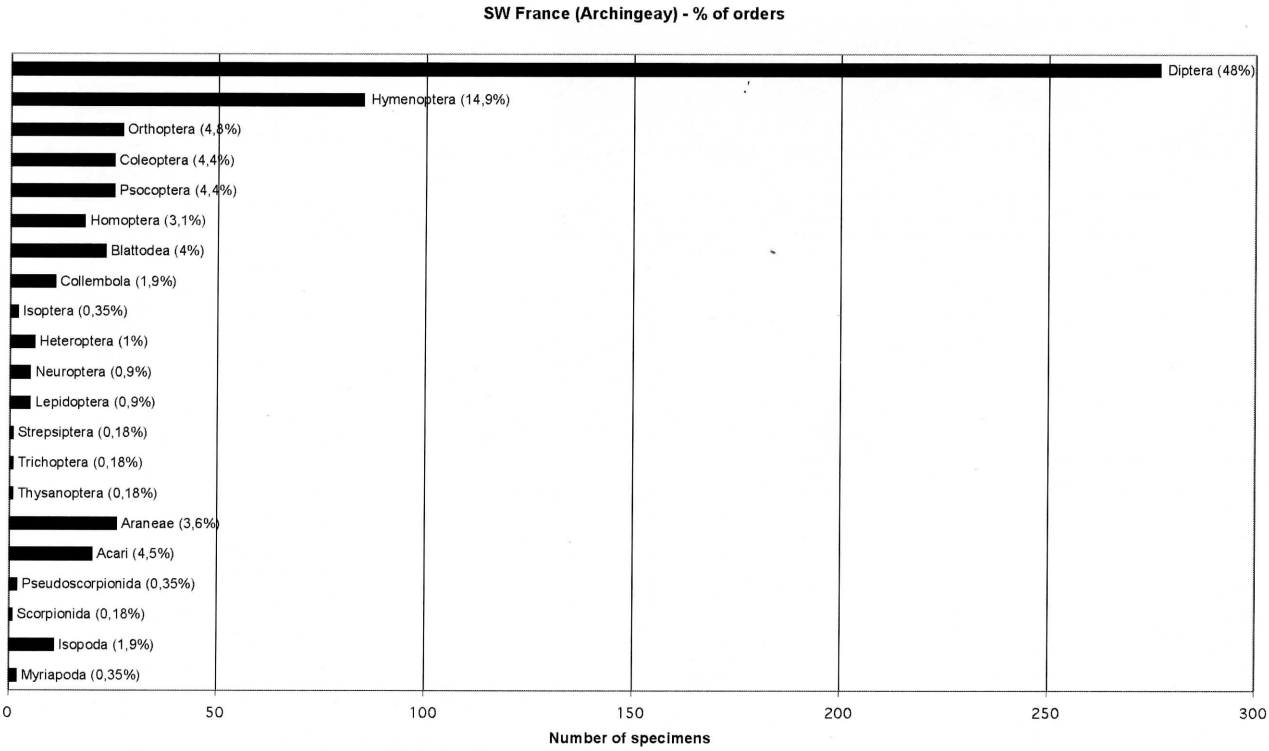


FIGURE 2 | **Frequency distribution of arthropods in Archingeay amber.**

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),

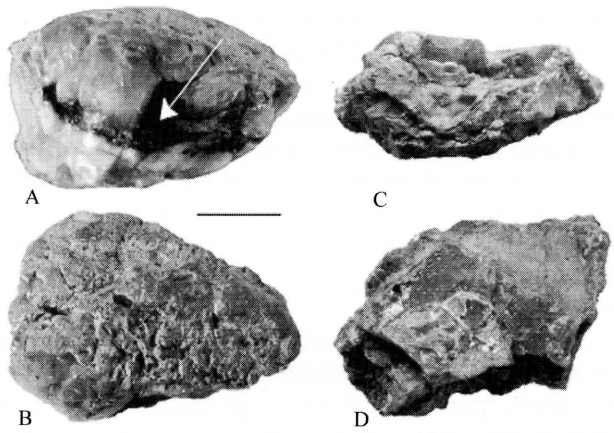


FIGURE 3 | **A sample of litter amber showing a typical lamination with an opaque layer on the bottom and a translucent layer on the top. The arrow points out an interbedded wood fragment. MNHN ARC 149. Scale bar: 1 cm.**

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).

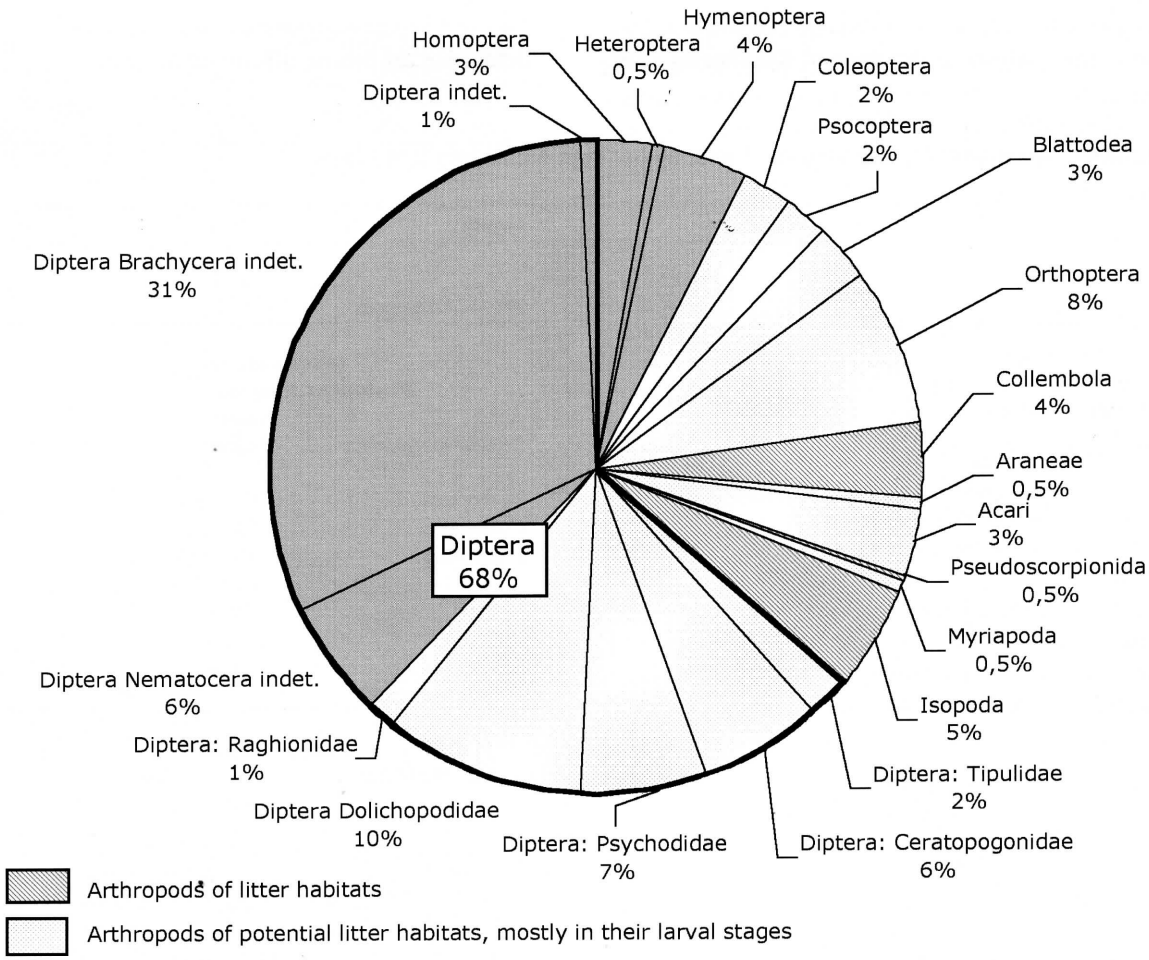


FIGURE 4 **Percentage distribution of arthropods in the six samples of litter amber, with potential affinities for the litter habitat.**

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).

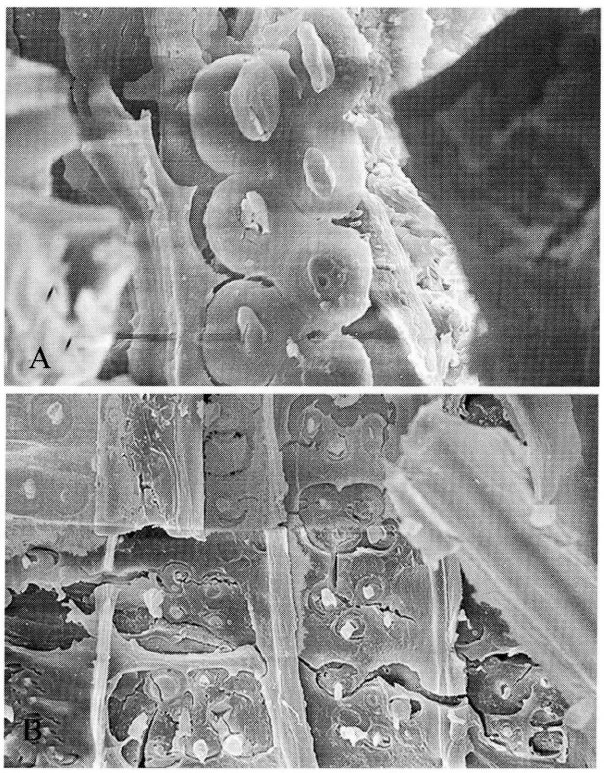


FIGURE 5 | **Scanning electron photomicrographs of a wood fragment attributed to an Araucariaceae (*Agathoxylon* HARTIG 1848), in the sample of litter amber MNHN ARC 226. A) Radial view of typically araucariaceous biseriate and alternately imbricated radial pits; B) Radial view of typically araucariaceous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

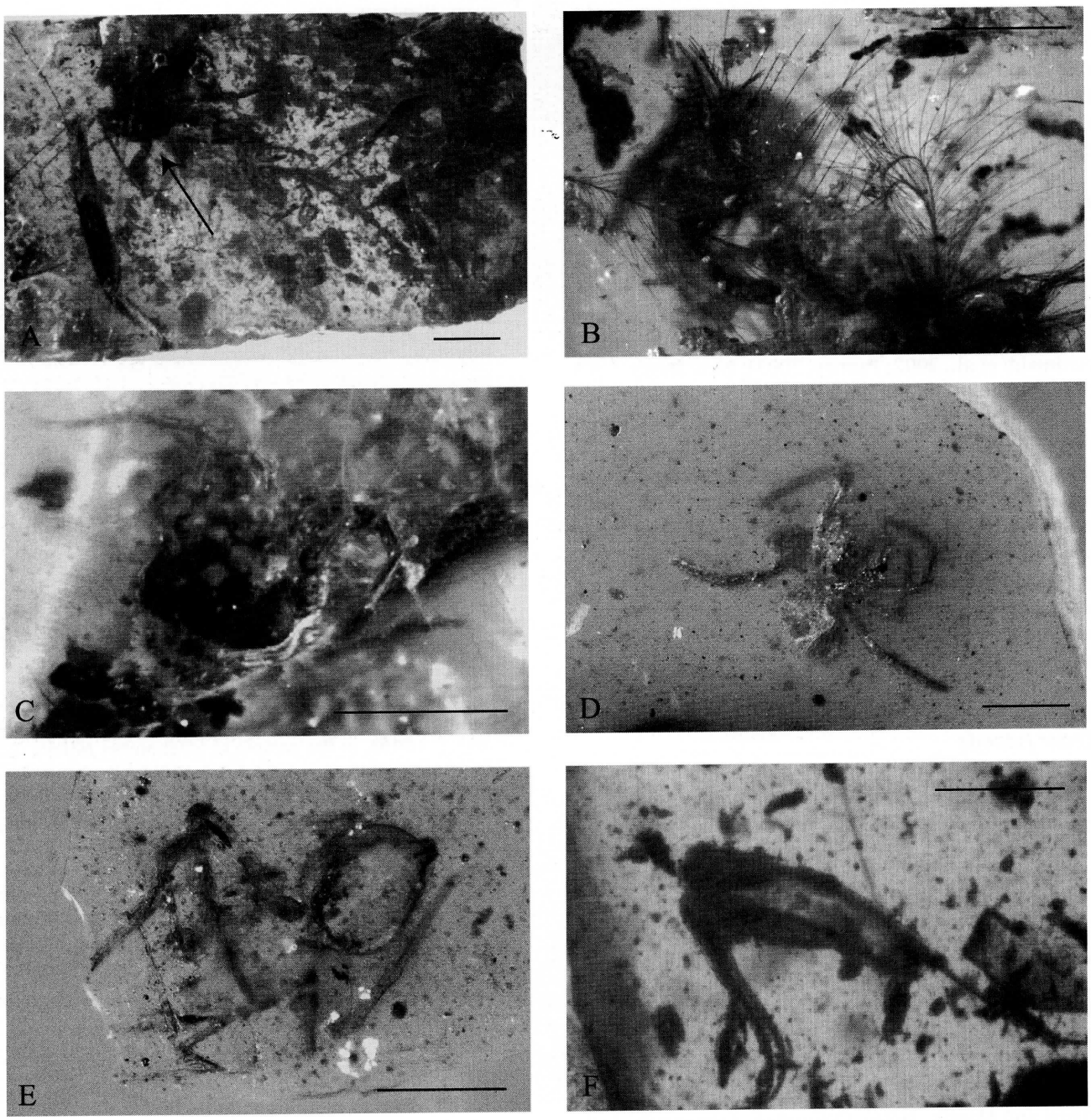


FIGURE 6 **Various inclusions in the French Lower Cretaceous amber of Archingeay. A) MNHN ARC 115: a sample of litter-bearing amber, showing plant remains and one Orthoptera: Gryllotalpidae (arrow). Scale bar 2 mm; B) MNHN ARC 115.23: fragments of feather from an indeterminate animal. Scale bar 2 mm; 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-

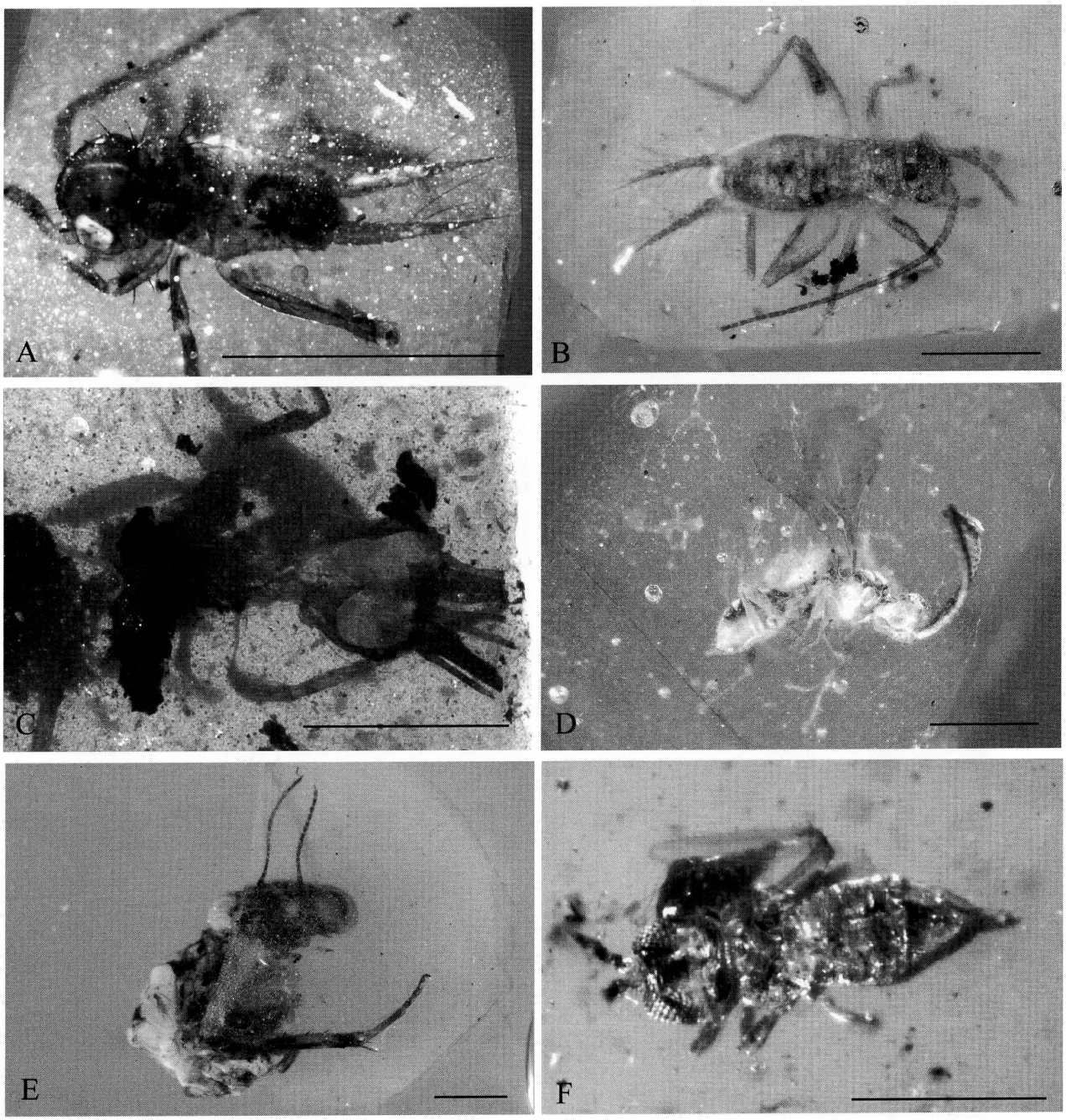


FIGURE 7 **Various inclusions in the French Lower Cretaceous amber of Archingeay. A and B) MNHN ARC 149.2, MNHN ARC 263.6: Orthoptera: Grylloidea (nymph). Scale bar 1 mm; C) MNHN ARC 152.3: head and thorax of Planipennia, family indet. (larva). Scale bar 1 mm; D) MNHN ARC 263.1: Hymenoptera: Chalcidoidea,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

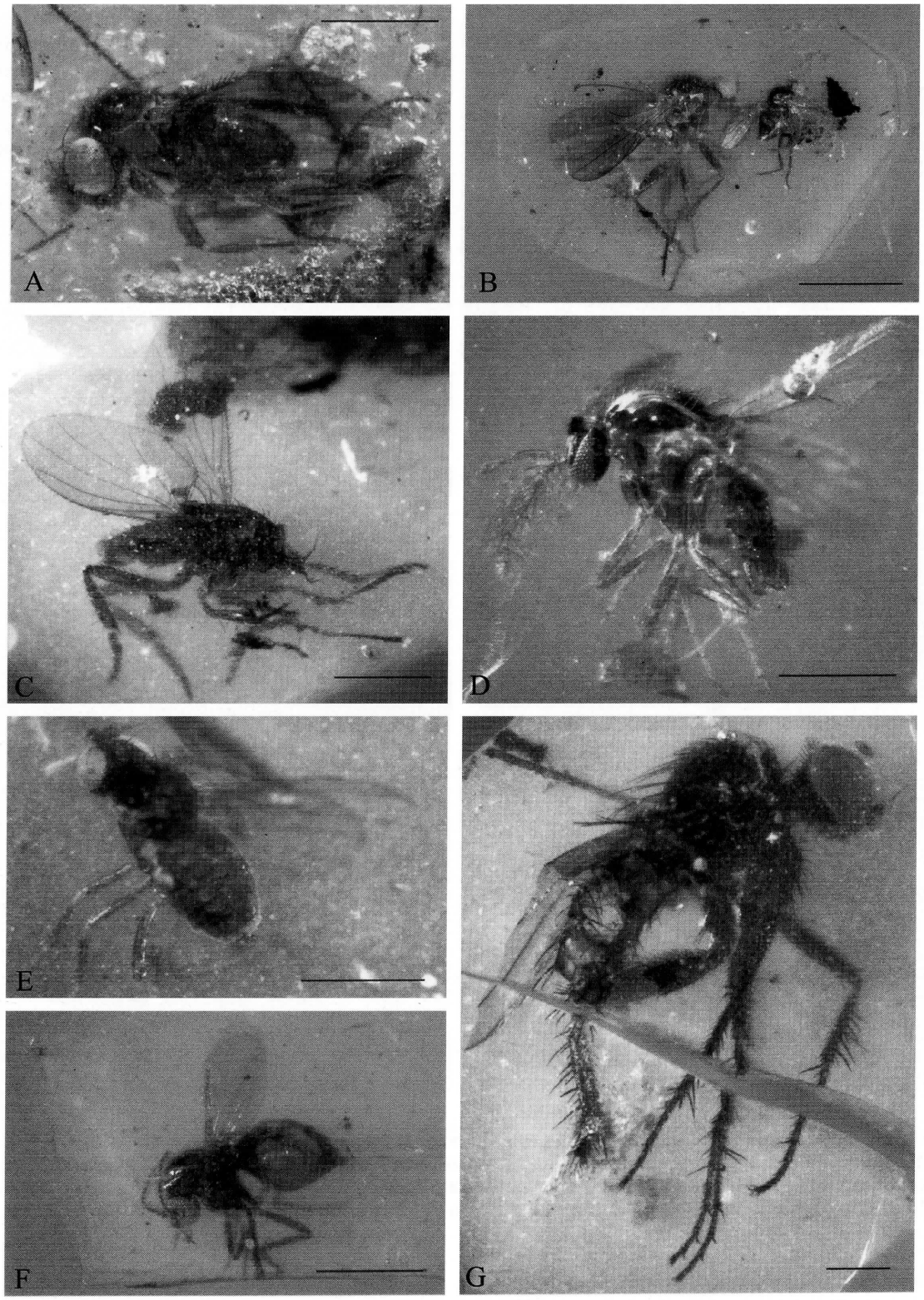


FIGURE 8 | **Assorted Diptera from the French Cretaceous amber of Archingeay. a) MNHN ARC 263.14: Brachycera, family indet. Scale bar 1 mm; b) MNHN ARC 226.38: Left: Rhagionidae (male); Right: Dolichopodidae: Microphorinae: *Microphorites deploegi*. Scale bar 2mm; c) MNHN ARC 226.12: Dolichopodidae. 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.

ACKNOWLEDGMENTS

Foremost, my sincere thanks go to Ms. Anne Vidy for her support and understanding during both the preparation of this paper and the numerous hours devoted to my thesis. I am grateful to Didier Néraudeau (University of Rennes), André Nel (MNHN), Marc Philippe (University of Lyon), Dany Azar and Gaël de Ploëg (MNHN) for their support and major contributions to the study of the French Cretaceous amber deposits during the past two years. This paper would have been impossible without them. Bernard Gomez (University of Leeds) provided useful discussions on taphonomic processes and climatic interpretations. I also acknowledge Thierry Guyot who generously donated us his collection of fossil inclusions from Archingeay, among which the extraordinary sample n° ARC 226 was. The manuscript benefited significantly from the critical revision of André Nel, Michael S. Engel (University of Kansas) and Conrad Labandeira (Smithsonian Institution, Washington). This paper is a contribution to the ECLIPSE (Environnement et Climat du Passé: Histoire et Evolution) program of the Centre National de la Recherche Scientifique (CNRS): "Interactions Climat /Ecosystèmes entre Aptien et Paléocène".

REFERENCES

Alonso, J., Arillo, A., Barrón, E., Corral, C.J., Grimalt, J., López, J.F., López, R., Martínez-Delclòs, X., Ortuño, V.M., Peñalver, E., Trincão, P.R., 2000. A new fossil resin with biological inclusions in Lower Cretaceous deposits from Álava (Northern Spain, Basque-Cantabrian Basin). Journal of Paleontology, 74, 158-178.

Arnold, E.N., Azar, D., Ineich, I., Nel, A., 2002. The oldest reptile in amber: a 120 million year old lizard from Lebanon. Journal of Zoology, 258, 7-10.

Azar, D., 1998. Lebanese amber. Meganeura, 1, 26-27.

Azar, D., 2000. Les ambres mésozoïques du Liban. Doctoral thesis. Université Paris XI Orsay, 164 pp.

Azar, D., Perrichot, V., Néraudeau, D., Nel, A., 2003. New psy-

chodids from the Cretaceous ambers of Lebanon and France, with a discussion about *Eophlebotomus connectens* Cockerell, 1920 (Diptera, Psychodidae). Annals of the Entomological Society of America, 96, 117-126.

Barrón, E., Comas-Renfigo, M.J., Ecorza, L., 2001. Contribuciones al estudio palinológico del Cretácico Inferior de la Cuenca Vasco-Cantábrica: los afloramientos ambarígenos de Peñacerrada (España). Coloquios de Paleontología, 52, 135-156.

Cardoso, A.H., Saraiva, A.A.F., Nuvens, P.C., Andrade, J.A.F.G., 2000. Ocorrência de resina fossil na Formação Santana, XVI Congreso Brasileiro de Paleontologia. Bulletin de Resumos, p. 32.

Castro, de C., Menor, E.A., Campanha, V.A., 1970. Descoberta de resina fósseis na Chapada do Araripe, Municipio de Porteira - Ceará, Universidade Federal de Pernambuco - Instituto Geociencias. Notas Previas.1, 1-12

Christiansen, K., Pike, E.M., 2002. Cretaceous Collembola (Arthropoda: Hexapoda) from the Upper Cretaceous of Canada. Cretaceous Research, 23, 165-188.

Cockerell, T.D.A., 1917. Arthropods in Burmese amber. American Journal of Science, 44, 135-138.

Corral, C.J., López del Valle, R., Alonso, J., 1999. El ámbar Cretácico de Álava (Cuenca Vasco-Cantábrica, Norte de España) su colecta y preparación. Estudios del Museo de Ciencias Naturales de Álava, 14(2), 7-21.

Cruickshank, R.D., Ko, K., 2003. Geology of an amber locality in the Hukawng Valley, Northern Myanmar. Journal of Asian Earth Sciences, 21, 441-455.

Engel, M.S., 2002. A new dustywing (Neuroptera: Coniopterygidae) in Turonian amber from New Jersey, with a reassessment of *Glaesoconis* in Neocomian amber from Libanon. Journal of the Kansas Entomological Society, 75, 38-42.

Eskov, K.Y., Wunderlich, J., 1994. On the spiders from Taymir ambers, Siberia, with the description of a new family and with general notes on the spiders from the Cretaceous resins. Beiträge zur Araneologie, 4, 95-107.

Evenhuis, N.L., 1994. Catalogue of the fossil flies of the World (Insecta: Diptera). Leiden, Backhuys Publishers, 600 pp.

Frakes, L.A., 1979. The Cretaceous period. In: Frakes, L.A. (ed.). Climates throughout geological time. Amsterdam, Elsevier Scientific Publishing Company, 168-178.

Gomez, B., 2002. A new species of *Mirovia* (Coniferales, Miroviaceae) from the Lower Cretaceous of the Iberian Ranges (Spain). Cretaceous Research, 23, 761-773

Gomez, B., Bamford, M., Martínez-Delclòs, X., 2002a. Lower Cretaceous plant cuticles and amber (Kirkwood Formation, South Africa). Comptes Rendus Palevol, 1, 1-5.

Gomez, B., Martínez-Delclòs, X., Bamford, M., Philippe, M., 2002b. Taphonomy and palaeoecology of plant remains from the oldest African Early Cretaceous amber locality. Lethaia, 35, 300-308.

Gomez, B., Thévenard, F., Perrichot, V., Daviero-Gomez, V., Coiffard, C., Néraudeau D., 2002c. Le conifère *Glenrosa* dans l'Albien-Cénomanien de Charente-Maritime (France): marqueur d'un climat à saison sèche. Colloque Eclipse: environnement et climat du Passé: histoire et évolution, 21-22 octobre 2002, CNRS, Paris.

Grimaldi, D.A., 1996. Amber: window to the past. New York, Harry, N. Abrams, Inc., 216 pp.

Grimaldi, D.A., 2000. A diverse fauna of Neuropterodea in amber from the Cretaceous of New Jersey. In: Grimaldi, D.A. (ed.). Studies on fossils in amber, with particular reference to the Cretaceous of New Jersey. Leiden, Backhuys Publishers, 259-303.

Grimaldi, D.A., Case G.R., 1995. A feather in amber from the Upper Cretaceous of New Jersey. American Museum Novitates, 3126, 6 pp.

Grimaldi, D.A., Engel, M.S., Nascimbene, P.C., 2002. Fossiliferous Cretaceous amber from Myanmar (Burma): its rediscovery, biotic diversity, and paleontological significance. American Museum Novitates, 3361, 71 pp.

Grimaldi, D.A., Lillegraven, J.A., Wampler, T.W., Bookwalter, D., Shedrinsky, A.M., 2000a. Amber from Upper Cretaceous through Paleocene strata of the Hanna Basin, Wyoming, with evidence for source and taphonomy of fossil resins. Rocky Mountain Geology, 35, 163-204.

Grimaldi, D.A., Shedrinsky, A.M., Wampler, T.P., 2000b. A remarkable deposit of fossiliferous amber from the Upper Cretaceous (Turonian) of New Jersey. In: Grimaldi, D.A. (ed.). Studies on fossils in amber, with particular reference to the Cretaceous of New Jersey. Leiden, Backhuys Publishers, 1-76.

Hirst, S., Maulik, S., 1926. On some arthropod remains from the Rhynie Chert (Old Red Sandstone). Geological Magazine, 63, 69-71.

Jarzembowski, E.A., 1999. British amber: a little-known resource. Estudios del Museo de Ciencias Naturales de Álava, 14, 133-140.

Jenkyns, H.C., Gale, A.S., Corfield, R.M., 1994. Carbon- and oxygen-isotope stratigraphy of the English Chalk and Italian Scaglia and its palaeoclimatic significance. Geological Magazine, 131, 1-34.

Judson, M.L.I., 2000. *Electrobisium acutum* Cockerell, a cheiridiid pseudoscorpion from Burmese amber, with remarks on the validity of the Cheiridioidea (Arachnida, Chelonethi). Bulletin of the Natural History Museum of London (Geology), 56, 79-83.

Lambert, J.B., Jonhson, S.C., Poinar, G.O. Jr., 1996. Nuclear magnetic resonance characterization of Cretaceous amber. Archaeometry, 38, 325-335.

Lambert, J.B., Poinar, G.O. Jr., 2002. Amber: the organic gemstone. Accounts of Chemical Research, 35, 628-636.

Lourenço, W.R., 2001. A remarkable scorpion fossil from the amber of Lebanon. Implications for the phylogeny of Buthoidea. Comptes-Rendus de l'Académie des Sciences, Paris, série IIa, 332, 641-646.

Lourenço, W.R., 2002. The first scorpion fossil from the Cretaceous amber of Myanmar (Burma). New implications for the phylogeny of Buthoidea. Comptes Rendus Palevol, 1, 97-101.

Lourenço, W.R., 2003. The first scorpion fossil from the Cretaceous amber of France. New implications for the phylogeny

of Chactoidea. Comptes Rendus Palevol, 2, 213-219.

Manum, S.B., Van Konijnenburg-Van Cittert, J.H.A., Wilde, V., 2000. *Tritaenia* Maegdefrau et Rudolf, Mesozoic '*Sciadopitys*-like' leaves in mass accumulations. Review of Palaeobotany and Palynology, 109, 255-269.

McAlpine, J.F., Martin, J.E.H., 1969. Canadian amber: a palaeontological treasure chest. Canadian Entomologist, 101, 819-838.

Nel, A., Perrichot ,V., Daugeron, C., Néraudeau, D., in press. A new *Microphorites* in the Lower Cretaceous amber of the Southwest of France (Insecta: Diptera: Dolichopodidae: 'Microphorinae'). Annales de la Société Entomologique de France.

Néraudeau, D., Perrichot, V., Dejax, J., Masure, E., Nel, A., Philippe, M., Moreau, P., Guillocheau, F., Guyot, T., 2002. Un nouveau gisement à ambre insectifère et à végétaux (Albien terminal probable): Archingeay (Charente-Maritime, France). Geobios, 35, 233-240.

Otto, A., Simoneit, B.R.T., Wilde, V., Kunzmann, L., Püttmann, W., 2002. Terpenoid composition of three fossil resins from Cretaceous and Tertiary conifers. Review of Palaeobotany and Palynology, 120, 203-215.

Penney, D., 2002. Spiders in Upper Cretaceous amber from New Jersey (Arthropoda: Araneae). Palaeontology, 45, 709-724.

Penney, D., 2003. *Afrarchaea grimaldii*, a new species of Archaeidae (Araneae) in Cretaceous Burmese amber. Journal of Arachnology, 31, 122-130.

Penney, D., in press. New spiders in Upper Cretaceous amber from New Jersey in the American Museum of Natural History (Arthropoda, Araneae). Palaeontology.

Penney, D., Selden, P.A., 2002. The oldest linyphiid spider, in Lower Cretaceous Lebanese amber (Araneae, Linyphiidae, Linyphiinae). Journal of Arachnology, 30, 487-493.

Perrichot, V., Azar, D., Néraudeau, D., Nel, A., 2003. New Psocoptera in the Early Cretaceous ambers of SW France and Lebanon (Insecta: Psocoptera: Trogiomorpha). Geological Magazine, 140, 627-641.

Perrichot, V., Néraudeau, D., Azar, D., Menier, J.-J., Nel, A., 2002. A new genus and species of fossil mole cricket in the Lower Cretaceous amber of Charente-Maritime, SW France (Insecta: Orthoptera: Gryllotalpidae). Cretaceous Research, 23, 307-314.

Pike, E.M., 1995. Amber taphonomy and the Grassy Lake, Alberta amber fauna. PhD.thesis. University of Calgary, 264 pp.

Poinar, G.O. Jr., Milki, R., 2001. Lebanese amber. The oldest insect ecosystem in fossilized resin. Corvallis, Oregon State University Press, 96 pp.

Ross, A.J., York, P.V., 2000. A list of type and figured specimens of insects and other inclusions in Burmese amber. Bulletin of the Natural History Museum of London (Geology), 56, 11-20.

Schawaller, W., 1991. The first Mesozoic pseudoscorpion, from Cretaceous Canadian amber. Palaeontology, 34, 971-976.

Schlee, D., 1973. Harzkonserviertefossile Vogelfedern aus untersten Kreide. Journal of Ornithology, 114, 207-219.

Schlüter, T., 1978. Zur Systematik und Palökologie harzkonservierter Arthropoda einer Taphozönose aus dem Cenomanium von NW-Frankreich. Berliner Geowissenschaftliche Abhandlungen (A), 9, 1-150.

Schmidt, A.R., Von Eynatten, H., Wagreich, M., 2001. The Mesozoic amber of Schliersee (southern Germany) is Cretaceous in age. Cretaceous Research, 22, 423-428.

Selden, P.A., 2002. First British Mesozoic spider, from Cretaceous amber of the Isle of Wight, Southern England. Palaeontology, 45, 973-983.

Szadziewski, R., Schlüter, T., 1992. Biting midges (Diptera: Ceratopogonida) from Upper Cretaceous (Cenomanian) amber of France. Annales de la Société Entomologique de France, 28, 73-81.

Waterlot, G., Polvèche, J., 1958. Carte géologique. Scale: 1:80.000, 2d edition, n° 152, La Rochelle, ed. BRGM.

Watson, J., Lydon, S.J., Harrison, N.A., 2001. A revision of the English Wealden Flora, III: Czekanowskiales, Ginkgoales and allied Coniferales. Bulletin of the Natural History Museum of London (Geology), 57, 29-82.

Zherikhin, V.V., Eskov, K.Y., 1999. Mesozoic and lower Tertiary resins in former USSR. Estudios del Museo de Ciencias Naturales de Álava, 14, 119-131.

Zherikhin, V.V., Ross, A.J., 2000. A review of the history, geology and age of Burmese amber (Burmite). Bulletin of the Natural History Museum of London (Geology), 56, 3-10.

Manuscript received July 2002;
revision accepted December 2002.

PALAIOS
Emphasizing the impact of life on Earth's history

PALAIOS, 2009, v. 24, p. 137–139
Spotlight
DOI: 10.2110/palo.2009.S02

SPOTLIGHT

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

VINCENT PERRICHOT[1]* and VINCENT GIRARD[2]

[1]*University of Kansas, Paleontological Institute, Lindley Hall, 1475 Jayhawk Boulevard, room 119, Lawrence, Kansas 66045, USA, e-mail: vperri@ku.edu;*
[2]*Université Rennes 1, UMR CNRS 6118, 263 avenue du Général Leclerc, 35042 Rennes, France, e-mail: vincent.girard@univ-rennes1.fr*

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 × 3 × 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.

* Corresponding author.

Copyright © 2009, SEPM (Society for Sedimentary Geology) 0883-1351/09/0024-0137/$3.00

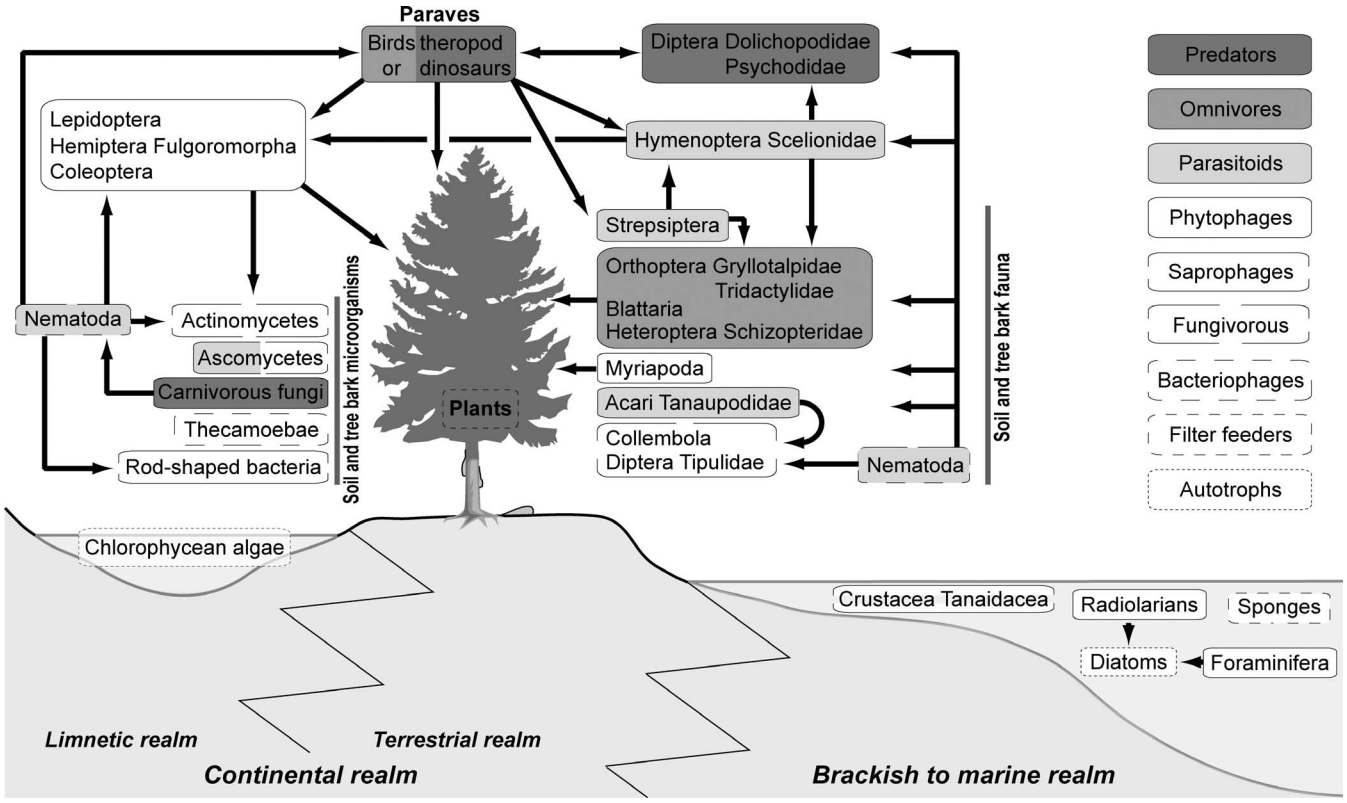


FIGURE 1—Schematic food web reconstructed from organic inclusions fossilized in the piece of amber no. Arc115, from the late Albian of Archingeay–Les Nouillers in southwestern France.

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.

REFERENCES

Alimohammadian, H., Sahni, A., Patnaik, R., Rana, R. S., and Singh, H., 2005, First record of an exceptionally diverse and well preserved amber-embedded biota from Lower Eocene (~ 52 Ma) lignites, Vastan, Gujarat: Current Science, v. 89, p. 1328–1330.

Alonso, J., Arillo, A., Barrón, E., Corral, C.J., Grimalt, J., Lopez, J.F., Lopez, R., Martínez-Delclòs, X., Ortuño, V.M., Peñalver, E., and Trincao, P.R., 2000, A new fossil resin with biological inclusions in Lower Cretaceous deposits from Alava (Northern Spain, Basque–Cantabrian Basin): Journal of Paleontology, v. 74, p. 158–178.

Antoine, P.-O., De Franceschi, D., Flynn, J.J., Nel, A., Baby, P., Benammi, M., Calderón, Y., Espurt, N., Goswami, A., and Salas-Gismondi, R., 2006, Amber from western Amazonia reveals Neotropical diversity during the middle Miocene: Proceedings of the National Academy of Sciences, USA, v. 103, p. 13,595–13,600.

Azar, D., 2000, Les ambres mésozoïques du Liban: Unpublished Ph.D. dissertation, University Paris XI-Orsay, Paris, France, 164 p.

Azar, D., Perrichot, V., Néraudeau, D., and Nel, A., 2003, New psychodids from the Cretaceous ambers of Lebanon and France, with a discussion of *Eophlebotomus connectens* Cockerell, 1920 (Diptera, Psychodidae): Annals of the Entomological Society of America, v. 96, p. 117–126.

Coiffard, C., Gomez, B., Kvacek, J., and Thévenard, F., 2006, Early angiosperm ecology: Evidence from the Albian–Cenomanian of Europe: Annals of Botany, v. 98, p. 495–502.

Coiffard, C., Gomez, B., Nel, A., Kvacek, J., Néraudeau, D., and Thévenard, F., 2008, Application of the Wagner's Parsimony Method in fossil plant assemblages from the Cretaceous of Europe: Review of Palaeobotany and Palynology, v. 148, p. 1–12.

Dejax, J., and Masure, E., 2005, Analyse palynologique de l'argile lignitifère à ambre de l'Albien terminal d'Archingeay (Charente-Maritime, France): Comptes Rendus Palevol, v. 4, p. 53–65.

Girard, V., 2008, Microcénoses des ambres médio-crétacés français. Taphonomie, systématique, paléoécologie et reconstitution du paléoenvironnement: Unpublished Ph.D. dissertation, University of Rennes 1, Rennes, France, 294 p.

Girard, V., Saint-Martin, S., Saint-Martin, J.-P., Schmidt, A.R., Struwe, S., Perrichot, V., Néraudeau, D., and Breton, G., 2009, Exceptional preservation of marine diatoms in Upper Albian amber: Geology, v. 37, p. 83–86.

Girard, V., Schmidt, A.R., Saint-Martin, S., Struwe, S., Perrichot, V., Saint-Martin, J.-P., Breton, G., and Néraudeau, D., 2008, First evidence for marine microfossils from amber: Proceedings of the National Academy of Sciences of the USA, v. 105, p. 17,426–17,429, DOI: 10.1073/pnas.0804980105.

Gomez, B., Bamford, M., and Martínez-Delclòs, X., 2002, Lower Cretaceous plant cuticles and amber (Kirkwood Formation, South Africa): Comptes Rendus Palevol, v. 1, p. 83–87.

Gomez, B., Coiffard, C., Dépré, E., Daviero-Gomez, V., and Néraudeau, D., 2008, Diversity and histology of a plant litter bed from the Cenomanian of Archingeay–Les Nouillers (southwestern France): Comptes Rendus Palevol, v. 7, p. 135–144.

Gomez, B., Daviero-Gomez, V., Perrichot, V., Thévenard, F., Coiffard, C., Philippe, M., and Néraudeau, D., 2004, Assemblages floristiques de l'Albien–Cénomanien de Charente-Maritime (SO France): Annales de Paléontologie, v. 90, p. 147–159.

Grimaldi, D.A., Lillegraven, J.A., Wampler, T.W., Bookwalter, D., and Shedrinsky, A.M., 2000, Amber from Upper Cretaceous through Paleocene strata of the Hanna Basin, Wyoming, with evidence for source and taphonomy of fossil resins: Rocky Mountain Geology, v. 35, p. 163–204.

Grund, M., 2006, Zuckmücken (Chironomidae) und ihre Syninklusen in Dominikanischem Bernstein: Eine Analyse der Diversität, Biogeographie, Paläoökologie und Stabilität der fossilen Fauna und Vergleich mit der heutigen Lebewelt: Unpublished Ph.D. dissertation, Friedrich-Wilhelms-Universität, Bonn, Germany, 118 p.

Guiliano, M., Mille, G., Onoratini, G., and Simon, P., 2006, Présence d'ambre dans le Crétacé supérieur (Santonien) de La Mède à Martigues (Sud-Est de la France): Caractérisation IRTF: Comptes Rendus Palevol, v. 5, p. 851–858.

Judson, M.L.I., and Makol, J., 2009, A mite of the family Tanaupodidae (Acari, Parasitengona) from the Lower Cretaceous of France, *in* Perrichot, V., and Néraudeau, D., eds., Cretaceous amber deposits from southwestern France: Sedimentology, taphonomy, paleontology: Geodiversitas, v. 31(1), in press.

Lak, M., Néraudeau, D., Nel, A., Cloetens, P., Perrichot, V., and Tafforeau, P., 2008, Phase contrast X-ray synchrotron imaging: Opening access to fossil inclusions in opaque amber: Microscopy and Microanalysis, v. 14, p. 251–259.

Nel, A., De Ploëg, G., Dejax, J., Dutheil, D., De Franceschi, D., Gheerbrant, E., Godinot, M., Hervet, S., Menier, J.-J., Auge, M., Bignot, G., Cavagnetto, C., Duffaud, S., Gaudant, J., Hua, S., Jossang, A., De Lapparent De Broin, F., Pozzi, J.-P., Paicheler, J.-C., Beuchet, F., and Rage, J.-C., 1999, Un gisement sparnacien exceptionnel à plantes, arthropodes et vertébrés (Eocène basal, MP7): Le Quesnoy (Oise, France): Comptes Rendus de l'Académie des Sciences, Paris, ser. 2a, v. 329, p. 65–72.

Néraudeau, D., Allain, R., Perrichot, V., Videt, B., De Broin, F., Guillocheau, F., Philippe, M., Rage, J.-C., and Vullo, R., 2003, Découverte d'un dépôt paralique à bois fossiles, ambre insectifère et restes d'Iguanodontidae (Dinosauria, Ornithopoda) dans le Cénomanien inférieur de Fouras (Charente-Maritime, Sud-Ouest de la France): Comptes Rendus Palevol, v. 2, p. 221–230.

Néraudeau, D., Perrichot, V., Colin, J.-P., Girard, V., Gomez, B., Guillocheau, F., Masure, E., Peyrot, D., Tostain, F., Videt, B., and Vullo, R., 2008, A new amber deposit from the Cretaceous (Uppermost Albian–Lowermost Cenomanian) of southwestern France: Cretaceous Research, v. 29, p. 925–929.

Néraudeau, D., Perrichot, V., Dejax, J., Masure, E., Nel, A., Philippe, M., Moreau, P., Guillocheau, F., and Guyot, T., 2002, Un nouveau gisement à ambre insectifère et à végétaux (Albien terminal probable): Archingeay (Charente-Maritime, France): Geobios, v. 35, p. 233–240.

Néraudeau, D., Vullo, R., Girard, V., Gomez, B., Perrichot, V., and Videt, B., in press, Amber, plants and vertebrates from the paralic Lower Cenomanian deposits of Aix Island (Charente-Maritime, France), *in* Perrichot, V., and Néraudeau, D., eds., Cretaceous amber deposits from southwestern France: Sedimentology, taphonomy, paleontology: Geodiversitas, v. 31.

Peñalver, E., Delclòs, X., and Soriano, C., 2007, A new rich amber outcrop with palaeobiological inclusions in the Lower Cretaceous of Spain: Cretaceous Research, v. 28, p. 791–802.

Penney, D., 1999, Dominican Republic amber spiders and their contribution to fossil and Recent ecology: Unpublished Ph.D. dissertation, University of Manchester, Manchester, UK, 377 p.

Perrichot, V., 2004, Early Cretaceous amber from south-western France: Insight into the Mesozoic litter fauna: Geologica Acta, v. 2, p. 9–22.

Perrichot, V., 2005, Environnements paraliques à ambre et à végétaux du Crétacé nord-aquitain (Charentes, Sud-Ouest de la France): Mémoires de Géosciences Rennes, v. 118, p. 1–310.

Perrichot, V., Marion, L., Néraudeau, D., Vullo, R., and Tafforeau, P., 2008, The early evolution of feathers: Fossil evidence from Cretaceous amber of France: Proceedings of the Royal Society, ser. B, Biological Sciences, v. 275, p. 1197–1202.

Perrichot, V., Nel, A., and Néraudeau, D., 2007a, Schizopterid bugs (Insecta: Heteroptera) in mid-Cretaceous ambers from France and Myanmar (Burma): Palaeontology, v. 50, p. 1367–1374.

Perrichot, V., Néraudeau, D., Azar, D., Menier, J.-J., and Nel, A., 2002, A new genus and species of fossil mole cricket in the Lower Cretaceous amber of Charente-Maritime, SW France (Insecta: Orthoptera: Gryllotalpidae): Cretaceous Research, v. 23, p. 307–314.

Perrichot, V., Néraudeau, D., Nel, A., and De Ploëg, G., 2007b, A reassessment of the Cretaceous amber deposits from France and their palaeontological significance: African Invertebrates, v. 48, p. 213–227.

Peyrot, D., Jolly, D., and Barron, E., 2005, Apports de données palynologiques à la reconstruction paléoenvironnementales de l'Albo–Cénomanien des Charentes (Sud-Ouest de la France): Comptes Rendus Palevol, v. 4, p. 151–166.

Philippe, M., Cuny, G., Suteethorn, V., Teerarungsigul, N., Barale, G., Thévenard, F., Le Loeuff, J., Buffetaut, E., Gaona, T., Košir, A., and Tong, H., 2005, A Jurassic amber deposit in Southern Thailand: Historical Biology, v. 17, p. 1–6.

Roghi, G., Ragazzi, E., and Gianolla, P., 2006, Triassic amber of the Southern Alps (Italy): PALAIOS, v. 21, p. 143–154.

Schmidt, A.R., 2003, Das fossile Harz von Schliersee (Bayerische Alpen) und seine Mikroinklusen: Unpublished Ph.D. dissertation, Friedrich-Schiller-Universität, Jena, Germany, 195 p.

Schmidt, A.R., and Dilcher, D.L., 2007, Aquatic organisms as amber inclusions and examples from a modern swamp forest: Proceedings of the National Academy of Sciences, USA, v. 104, p. 16,581–16,585.

Schmidt, A.R., Dörfelt, H., and Perrichot, V., 2007, Carnivorous fungi from Cretaceous amber: Science, v. 318, p. 1743.

Schmidt, A.R., Dörfelt, H., and Perrichot, V., 2008, *Palaeoanellus dimorphus* gen. et sp. nov. (Deuteromycotina): A Cretaceous predatory fungus: American Journal of Botany, v. 95, p. 1328–1334.

Solórzano Kraemer, M.M., 2007, Systematic, palaeoecology, and palaeobiogeography of the insect fauna from the Mexican amber: Palaeontographica, ser. A, v. 282, p. 1–133.

Tafforeau, P., Boistel, R., Boller, E., Bravin, A., Brunet, M., Chaimanee, Y., Cloetens, P., Feist, M., Hoszowska, J., Jaeger, J.-J., Kay, R.F., Lazzari, V., Marivaux, L., Nel, A., Nemoz, C., Thibault, X., Vignaud, P., and Zabler, S., 2006, Applications of X-ray synchrotron microtomography for non-destructive 3D studies of paleontological specimens: Applied Physics, ser. A, Materials Science and Processing, v. 83, p. 195–202.

Trevisani, E., Papazzoni, C.A., Ragazzi, E., and Roghi, G., 2005, Early Eocene amber from the "Pesciara di Bolca" (Lessini Mountains, Northern Italy): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 223, p. 260–274.

PROCEEDINGS OF THE ROYAL SOCIETY B

Proc. R. Soc. B (2008) **275**, 1197–1202
doi:10.1098/rspb.2008.0003
Published online 19 February 2008

The early evolution of feathers: fossil evidence from Cretaceous amber of France

Vincent Perrichot[1,*], Loïc Marion[2], Didier Néraudeau[3], Romain Vullo[3] and Paul Tafforeau[4]

[1]*Museum für Naturkunde der Humboldt-Universität zu Berlin, Invalidenstrasse 43, 10115 Berlin, Germany*
[2]*Ecobio, UMR CNRS 6553, and* [3]*Géosciences, UMR CNRS 6118, Université Rennes 1, 263 Avenue du Général Leclerc, 35042 Rennes, France*
[4]*European Synchrotron Radiation Facility, BP 220, 6 rue Jules Horowitz, 38043 Grenoble, France*

The developmental stages of feathers are of major importance in the evolution of body covering and the origin of avian flight. Until now, there were significant gaps in knowledge of early morphologies in theoretical stages of feathers as well as in palaeontological material. Here we report fossil evidence of an intermediate and critical stage in the incremental evolution of feathers which has been predicted by developmental theories but hitherto undocumented by evidence from both the recent and the fossil records. Seven feathers have been found in an Early Cretaceous (Late Albian, *ca* 100 Myr) amber of western France, which display a flattened shaft composed by the still distinct and incompletely fused bases of the barbs forming two irregular vanes. Considering their remarkably primitive features, and since recent discoveries have yielded feathers of modern type in some derived theropod dinosaurs, the Albian feathers from France might have been derived either from an early bird or from a non-avian dinosaur.

Keywords: feather evolution; early stages; Cretaceous amber; synchrotron; holotomography

1. INTRODUCTION

Feathers are complex integumental structures of a three-level branched structure composed of a rachis (primary shaft), barbs (secondary branches) and barbules (tertiary branches). Developmental theories propose that feathers evolved through a series of evolutionary novelties in the developmental mechanisms of the follicle and feather germ (Dyck 1985; Prum 1999; Chuong *et al.* 2000; Prum & Brush 2002). Recently, Xu (2006) has proposed a somewhat similar model but featuring a combination of transformations and innovations, and suggesting that tubular filaments and branching evolved before the appearance of the feather follicle. The recent discoveries of feathered dinosaurs from China support the evolutionary model based on developmental data, though additional data are needed to further understand the origin and structure of primitive feathers. Indeed, when neontological and palaeontological data illustrate almost all the series proposed by theories (Prum & Brush 2002; Xu 2006), transition remains particularly unclear before the stage III defined by Prum (1999), which is considered by Xu (2006) as probably the most critical stage of feather evolution in birds or non-avian dinosaurs. We recently discovered several isolated feathers fossilized in an Early Cretaceous amber of France, which display a primitive structure that illustrates the early formation of this critical stage. In addition to classical optical techniques, we used X-ray synchrotron holotomography (Cloetens *et al.* 1999) to reveal finest details, confirming the possibilities of synchrotron investigation for studying amber inclusions (Tafforeau *et al.* 2006; Lak *et al.* in press).

2. MATERIAL AND METHODS

The amber piece was found in the quarry of Archingeay/Les-Nouillers, in Charente-Maritime (western France), which has already yielded numerous fossils, mainly insects (Perrichot 2004, 2005). It is derived from alternating layers of estuarine sand and clay containing mixed fragments of fossil plants (cuticles and lignitic wood). In the regional stratigraphical section, this amber-bearing stratum corresponds to the subunit A1 and was dated as Late Albian (*ca* 100 Myr) by palynological studies (Néraudeau *et al.* 2002; Dejax & Masure 2005).

The feathers were originally fossilized in a single piece of amber, alongside 77 arthropods (see list in Perrichot 2004, table 2). The size of the entire amber piece was 4×3×2 cm. This piece was fragmented into 22 portions in order to separate inclusions for study. This preparation followed the method described by Perrichot (2004). The seven feathers are now isolated in a single portion of amber, and deposited in the Department of Earth History of the National Museum of Natural History in Paris, under the reference MNHN ARC 115.6.

Conventional imaging techniques using transmitted light microscope were first used but did not allow to bring all the information needed to assess precisely the morphology of the feathers. In order to reveal some critical structures in three dimensions, we used X-ray synchrotron phase imaging techniques on the ID19 beamline at the European Synchrotron Radiation Facility (ESRF, Grenoble, France). We performed

* Author and address for correspondence: Paleontological Institute, University of Kansas, Lindley Hall, 1475 Jayhawk Boulevard, Lawrence, KS 66045, USA (vincent.perrichot@neuf.fr).

Electronic supplementary material is available at http://dx.doi.org/10.1098/rspb.2008.0003 or via http://journals.royalsociety.org.

Received 2 January 2008
Accepted 31 January 2008

This journal is © 2008 The Royal Society

several propagation phase contrast microtomography and holotomography tests (Cloetens *et al.* 1999, 2006; Tafforeau *et al.* 2006; Lak *et al.* in press) using various configurations in order to define the optimal parameters to reveal the feathers clearly. As the feathers present a relatively large extension in regard to the size of each barb, it was necessary to combine high-resolution imaging with quite a large field of view. We used an optical magnification system coupled with a CCD FReLoN (Fast Readout Low Noise) camera (Labiche *et al.* 2007) providing an isotropic voxel size of 0.7 μm. In order to cover a large enough area of the amber piece, six scans of contiguous parts (two scans per line on three lines) were taken using local phase microtomography (propagation distance of 100 mm) in continuous acquisition mode (see Lak *et al.* in press) with a 30 keV monochromatic beam. Using 0.3 s of exposure time, 1500 projections were taken over 180°.

Being thin structures, feathers are very difficult to extract from these scans, so we used a single-distance holotomographic reconstruction of each scan after filtering of all the projection (subtraction of a blurred copy of the picture using a 10-pixel Gaussian filter), following the protocol described in Tafforeau *et al.* (2007). The data preparation allowed enhancement of the visibility of the feathers and other fine structures relative to larger ones. After correction of the strong ring artefacts (Tafforeau *et al.* 2006) on the reconstructed holotomographic slices, the six scans were assembled in order to obtain a single volume covering $1\times2\times3$ mm with a voxel size of 0.7 μm.

Owing to the large size of the data (40 Gb), a three-step segmentation protocol was used to limit the processing time. As the feathers appeared as white structures in the grey matrix of resin, the whole dataset was reduced by a linear factor of 8 (corresponding to a reduction by 512 of the volume) using binning by maximum. Each 5.6 μm voxel of the new volume was attributed the maximum value of all the corresponding 0.7 μm original voxels. That new volume was visualized and segmented in three dimensions using VGStudioMax v. 1.2 (Volume Graphics, Heidelberg, Germany) in order to obtain a rough extraction of the feathers. The binary segmentation mask was then exported, extrapolated to fit with the original dataset, and applied to it. The area containing the most visible feather was selected on that new volume and a fine segmentation was performed in order to prepare three-dimensional renderings.

3. RESULTS

Seven identical feathers are lying side by side in the amber piece (figure 1*a*) and very probably originate from a single individual. Like the rare fossil feathers previously known from amber, they are perfectly preserved, although probably incomplete in their basal part since there is no visible calamus. The tangle of these feathers, their three-dimensional disposition in amber, and numerous dust grains hinder the observation of some of them. The following description is mainly based on the three best visible. These are 2.3, 1.6 and 1.1 mm long as measured along the rachis. Filamentous, long and free barbs lacking barbules are inserted opposite to each other on each side of a rather flattened rachis and form two vanes (figure 2). The diameter of the rachis is constant, approximately 0.01 mm. The number of barbs is 40 per vane mm^{-1} of rachis; that is approximately 180 for the longest feather. Barbs are approximately 0.60 mm long near the basal part of the rachis, and 0.50 mm long near the distal tip. However, it is somewhat difficult to observe their point of insertion precisely, as they border the rachis before diverging, while their base is hidden by the more basal barbs (figures 1*b* and 2*a*,*d*). In fact, they fuse progressively to compose the rachis, and lack the complete fusion that is observed in the rachis of all other fossils and almost all modern feathers. The vanes observed on these feathers result from the insertion of barbs on the two opposite sides of the flattened rachis. These feathers are morphologically close to the down, ornamental or afterfeathers, and not to the contour, remiges or rectrices. However, they have a thick and long rachis, unlike classical down feathers whose barbs generally diverge from the very short apex of the rachis.

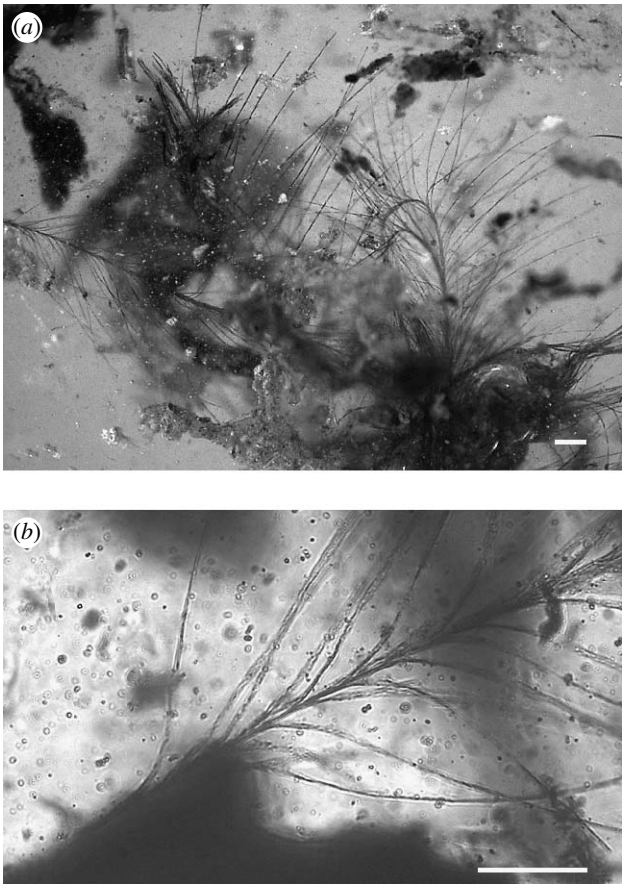


Figure 1. Fossil feathers from the Early Cretaceous amber of France (MNHN ARC 115.6): (*a*) seven feathers are preserved in a single piece of amber; (*b*) their excellent quality of preservation allows observation of fine structures using transmitted light microscope. Scale bars, 0.1 mm.

4. DISCUSSION

According to developmental theories, the rachis is the result of a complete fusion of the barbs, even in down feathers with a small basic rachis, and a planar form of feathers results from the helical growth of barb ridges within the follicle and interlocking between neighbouring barbs to create the vane (Dyck 1985; Griffiths 1996; Prum 1999; Chuong *et al.* 2000; Prum & Brush 2002; Xu 2006). A shaft consisting of incompletely fused, still distinguishable, partially superimposed barbs is not considered in feather evolution, although this stage would logically have existed with regard to the formation of feathers in the

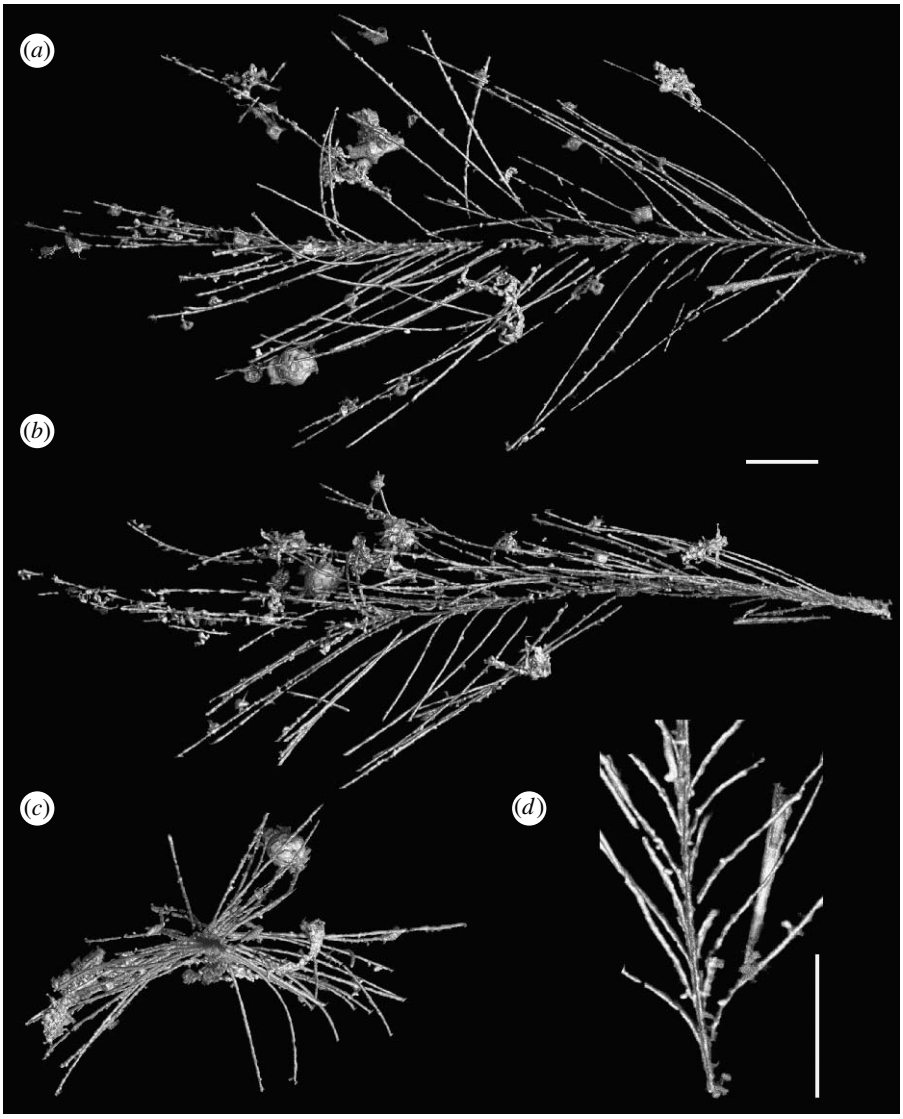


Figure 2. Three-dimensional virtual reconstruction of one fossil feather in phase contrast microtomography: (*a*–*c*) long barbs form two vanes on each side of a relatively flattened shaft; (*d*) the shaft is flattened and composed by the still incompletely fused bases of the barbs, a stage in feather evolution that was hitherto unknown in fossil and recent records. Scale bars, 100 μm.

follicle. The structure observed in these specimens from French amber therefore represents the first fossil evidence of the intermediate stage between the very distinct stages II and IIIa defined by Prum (1999) in his theory of evolutionary diversification of feathers. Stage II is characterized by non-ramified barbs attached at their base to the calamus, without barbules. Stage IIIa corresponds to the appearance of a central shaft formed by the fusion of non-ramified barbs and the appearance of the planar form. Stage IIIb exhibits barbules without differentiation between basal or distal part of the feather, unlike in stage IV (figure 3). Similarly, the new fossils take place between stages II and III defined by Xu (2006), and more precisely correspond to the early phase of stage III. The present discovery, therefore, sheds new light on the idealized nature of the developmental stages of feather evolution. Indeed, with a long rachis appearing before the barbules, it emphasizes stage IIIb as unlikely and stage IIIa as more likely evolving after stage II. We prefer not to create a new stage for this morphology, as it merely illustrates a transition between two well-established stages rather than a distinct, stable stage. According to Prum (1999), Bock (2000) and Prum & Brush (2002), such evidence for primitive feathers (excluding simple filaments or 'protofeathers') was hitherto desperately missing in the fossil record to augment theories on the origin of feathers.

Fossil feathers are essentially preserved as carbonized imprints in sedimentary rocks (Davis & Briggs 1995) and are rather rare in amber, even in abundant and rich Palaeogene ambers. The fossils we report here are only the sixth occurrence of feathers in Cretaceous amber, together with those from Lebanon (Schlee 1973; Schlee & Glöckner 1978), Myanmar (Grimaldi *et al.* 2002), Spain (Alonso *et al.* 2000; Delclòs *et al.* 2007) and the USA (Grimaldi & Case 1995). Further fossils mentioned from the Late Cretaceous ambers of Canada, Japan and Siberia (Kurochkin 1985; Grimaldi & Case 1995) have yet to be properly described or illustrated. Amber fossils are characterized by an exceptional quality of preservation that allows a detailed observation of all tiny structures. Those found in the Neocomian amber of Lebanon (Schlee & Glöckner 1978, fig. 6, pl. 3), the Aptian–Albian amber of Spain (Alonso *et al.* 2000, fig. 9.2; Delclòs *et al.* 2007, fig. 4N) and the Albian amber of Myanmar (Grimaldi *et al.* 2002, fig. 14e) clearly differ from the French fossils, featuring barbs and barbules organized in asymmetrical

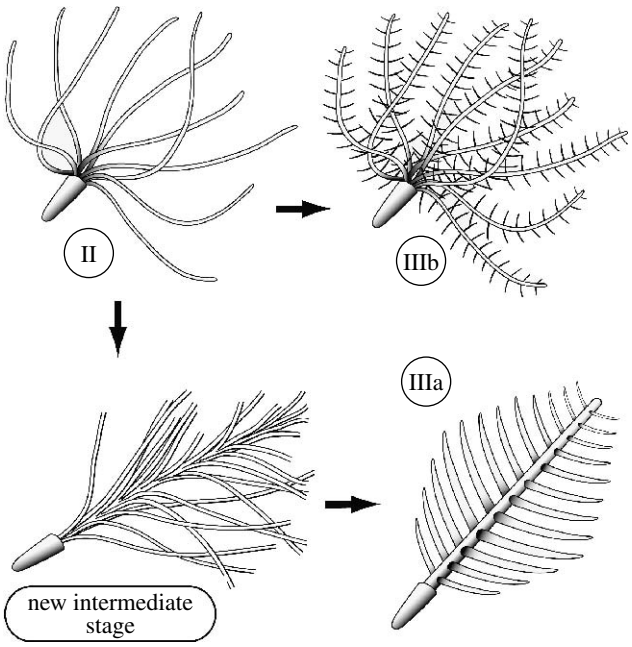


Figure 3. Feathers from French amber take place between the very distinct stages II and IIIa proposed in the developmental model of Prum (1999).

vanes, and thus similar to the contour feathers of stage IV of Prum's model (1999). Grimaldi & Case (1995) described a semiplume almost similar in aspect to our fossils, preserved in the Turonian amber of New Jersey, USA (Raritan-Magothy Formation, *ca* 90–94 Myr). However, it differs from the amber feathers from France by its larger size (7.5 mm long) and a cylindrical rachis decreasing in diameter from base to apex (Grimaldi & Case 1995, fig. 1).

In addition to the above-mentioned Spanish amber fossils, only two other feathers are mentioned in the Cretaceous of Europe, preserved as carbonized imprints: those from the Barremian limestones of Spain show a basal branching of filaments without apparent rachis (Sanz *et al.* 1988, fig. 1) and thus similar to stage II defined by Xu (2006); and those from the Santonian–Campanian of Slovenia display features of pennaceous feathers of stage IV, though barbules and hooklets are not visible but only inferred from the general morphology (Buffetaut *et al.* 2002, fig. 2).

Grimaldi & Case (1995) considered the semiplume from New Jersey as the oldest record of a bird in North America. However, feathers were still considered unique to birds at that time, and this is now known to be incorrect since the subsequent discovery of feathers in non-avian theropod dinosaurs in the Cretaceous of China (Chen *et al.* 1998; Xu *et al.* 1999*a*,*b*, 2000, 2001, 2003, 2004; Zhang & Zhou 2000; Ji *et al.* 2001, 2005; Norell *et al.* 2002; Xu & Zhang 2005). The oldest known birds, for example, *Archaeopteryx* from Germany and *Confuciusornis* from China, have modern-type feathers that are similar to those of extant birds, although they are significantly older (150–124 Myr) than the feathers from New Jersey and France. The latter have a much more primitive structure and are intermediate between the stages II and III of Prum (1999) and Xu (2006). They are also very distinct from the most derived feathers of stage V, which show asymmetrical vanes on each side of the rachis and barbules. According to Prum & Brush (2002), filamentous feathers of stage II, with a tuft of barbs fused basally (such as modern down feathers), would have appeared alongside simple filaments, or protofeathers, in the theropod dinosaur *Sinosauropteryx* (145 Myr; Chen *et al.* 1998). However, the presence of such protofeathers in *Sinosauropteryx* remains unclear, being reinterpreted as collagen fibres by Lingham-Soliar *et al.* (2007). The presence of true feathers is less equivocal in some other theropods: the recently described *Pedopenna*, from China (Xu & Zhang 2005), shows long pennaceous feathers of stage IV attached to its legs. *Caudipteryx* and *Protarchaeopteryx*, described by Ji *et al.* (1998; see also Dyke & Norell 2005), also have pennaceous feathers of stage IV. Xu *et al.* (2000) and Norell *et al.* (2002) found dromaeosaurs (e.g. *Microraptor*) with modern feathers of stage V (remiges), a character that was hitherto considered to be unique to birds (Prum & Brush 2002) and now is recognized to have a more ancient origin among non-avian dinosaurs (Sereno 2004). *Jinfengopteryx*, though formerly assigned to an avialan bird (Ji *et al.* 2005), is more likely a troodontid with pennaceous feathers of stage IV (Xu & Norell 2006). Finally, Ji *et al.* (2001) and Xu *et al.* (2001) inferred the existence of a rachis in a pattern of branched barbs for the dromaeosaur *Sinornithosaurus* and a still unnamed Chinese theropod ('filaments jointed at their bases along a central filament' and 'filaments appearing to be around a central rachis', respectively). The morphology of the new fossils described herein, with a rachis forming 'primitive' vanes without barbules, is entirely consistent with the shafted feathers displayed by these two theropods. According to this, and to the current evolutionary model of increasing complexity in feather morphologies (Norell & Xu 2005; Xu 2006; Xu & Norell 2006; Zhang *et al.* 2006), the French amber feathers may thus belong to a non-avian theropod dinosaur. It is noteworthy that isolated teeth of troodontids were recovered from the amber deposit considered here (Vullo *et al.* 2007). Indeed, they were found in a slightly younger geological level of earliest Cenomanian age, located approximately 10 m above the amber-bearing level. Further teeth of troodontids and dromaeosaurids were also found in the same Cenomanian level from other nearby fossil localities of the Charentes region (Vullo *et al.* 2007). These two non-avian dinosaur clades are currently known to be feathered and are thus possibly related to the fossil feathers from France. But the poor early feather record still prevents a complete reconstruction of the distribution pattern of morphologies among non-avian coelurosaurs and basal birds, and the possibility that they are derived from an early bird cannot be excluded.

We thank Philippe Janvier, Ronan Allain (MNHN), Alexander Schmidt (MfN, Berlin) and two anonymous reviewers for their useful critical comments of the manuscript; Carl Findley (Chicago) and Paul Selden (University of Kansas) for checking the usage of English and Dany Azar (Lebanese University, Beirut) for his help in the preparation of the fossils. We are grateful to the ID19 staff and users of the ESRF for the given beamtime on their experiments to perform the different synchrotron imaging tests. This work was partially sponsored by the Alexander von Humboldt Foundation (to V.P.) and is a contribution to the ANR project AMBRACE no. BLAN07-1-184190.

REFERENCES

Alonso, J. *et al.* 2000 A new fossil resin with biological inclusions in Lower Cretaceous deposits from Alava (northern Spain, Basque-Cantabrian Basin). *J. Paleontol.* **74**, 158–178. (doi:10.1666/0022-3360(2000)074<0158:ANFRWB>2.0.CO;2)

Bock, W. J. 2000 Explanatory history of the origin of the feathers. *Am. Zool.* **40**, 478–485. (doi:10.1668/0003-1569(2000)040[0478:EHOTOO]2.0.CO;2)

Buffetaut, E., Jurkovšek, B. & Kolar-Jurkovšek, T. 2002 A fossil feather from the Upper Cretaceous of Kras (Slovenia). *CR Palevol.* **1**, 705–710. (doi:10.1016/S1631-0683(02)00079-9)

Chen, P. J., Dong, Z. M. & Zhen, S. N. 1998 An exceptionally well-preserved theropod dinosaur from the Yixian Formation of China. *Nature* **391**, 147–152. (doi:10.1038/34356)

Chuong, C. M., Chodankar, R., Widelitz, R. B. & Jiang, T. X. 2000 Evo–devo of feathers and scales: building complex epithelial appendages. *Curr. Opin. Genet. Dev.* **10**, 449–456. (doi:10.1016/S0959-437X(00)00111-8)

Cloetens, P., Baruchel, J., Van Dyck, D., Van Landuyt, J., Guigay, J.-P. & Schlenker, M. 1999 Holotomography: quantitative phase tomography with micrometer resolution using hard synchrotron radiation X rays. *Appl. Phys. Lett.* **75**, 2912–2914. (doi:10.1063/1.125225)

Cloetens, P., Mache, R., Schlenker, M. & Lerbs-Mache, S. 2006 Quantitative phase tomography of *Arabidopsis* seeds reveals intercellular void network. *Proc. Natl Acad. Sci. USA* **103**, 14 626–14 630. (doi:10.1073/pnas.0603490103)

Davis, P. G. & Briggs, D. E. G. 1995 Fossilization of feathers. *Geology* **23**, 783–786. (doi:10.1130/0091-7613(1995)023<0783:FOF>2.3.CO;2)

Dejax, J. & Masure, E. 2005 Analyse palynologique de l'argile lignitifère à ambre de l'Albien terminal d'Archingeay (Charente-Maritime, France). *CR Palevol.* **4**, 53–65. (doi:10.1016/j.crpv.2004.12.002)

Delclòs, X., Arillo, A., Peñalver, E., Barrón, E., Soriano, C., López Del Valle, R., Bernárdez, E., Corral, C. & Ortuño, V. M. 2007 Fossiliferous amber deposits from the Cretaceous (Albian) of Spain. *CR Palevol.* **6**, 135–149. (doi:10.1016/j.crpv.2006.09.003)

Dyck, J. 1985 The evolution of feathers. *Zool. Scr.* **14**, 137–154. (doi:10.1111/j.1463-6409.1985.tb00184.x)

Dyke, G. J. & Norell, M. A. 2005 *Caudipteryx* as a non-avialan theropod rather than a flightless bird. *Acta Palaeontol. Pol.* **50**, 101–116.

Griffiths, P. J. 1996 The isolated *Archaeopteryx* feather. *Archaeopteryx* **14**, 1–26.

Grimaldi, D. A. & Case, G. R. 1995 A feather in amber from the Upper Cretaceous of New Jersey. *Am. Mus. Novit.* **3126**, 1–6.

Grimaldi, D. A., Engel, M. S. & Nascimbene, P. C. 2002 Fossiliferous Cretaceous amber from Myanmar (Burma): its rediscovery, biotic diversity, and paleontological significance. *Am. Mus. Novit.* **3361**, 1–71doi:10.1206/0003-0082(2002)361<0001:FCAFMB>2.0.CO;2.

Ji, Q., Currie, P. J., Norell, M. A. & Ji, S. A. 1998 Two feathered dinosaurs from northeastern China. *Nature* **393**, 753–761. (doi:10.1038/31635)

Ji, Q., Norell, M. A., Gao, K. Q., Ji, S. A. & Ren, D. 2001 The distribution of integumentary structures in a feathered dinosaur. *Nature* **410**, 1084–1088. (doi:10.1038/35074079)

Ji, Q., Ji, S. A., Lü, J. C., You, H. L., Chen, W., Liu, Y. Q. & Liu, Y. X. 2005 First avialan bird from China. *Geol. Bull. China* **24**, 197–205.

Kurochkin, E. N. 1985 A true carinate bird from Lower Cretaceous deposits in Mongolia and other evidence of Early Cretaceous birds in Asia. *Cretaceous Res.* **6**, 271–278. (doi:10.1016/0195-6671(85)90050-3)

Labiche, J.-C., Mathon, O., Pascarelli, S., Newton, M. A., Ferre, G. G., Curfs, C., Vaughan, G., Homs, A. & Fernandez Carreiras, D. 2007 The fast readout low noise camera as a versatile X-ray detector for time resolved dispersive extended X-ray absorption fine structure and diffraction studies of dynamic problems in materials science, chemistry, and catalysis. *Rev. Sci. Instrum.* **78**, 091301. (doi:10.1063/1.2783112)

Lak, M., Néraudeau, D., Nel, A., Cloetens, P., Perrichot, V. & Tafforeau, P. In press. Phase contrast X-ray synchrotron imaging: opening access to fossil inclusions in opaque amber. *Microsc. Microanal.* **14**. (doi:10.1017/S1431927608080264)

Lingham-Soliar, T., Feduccia, A. & Wang, X. 2007 A new Chinese specimen indicates that 'protofeathers' in the Early Cretaceous theropod dinosaur *Sinosauropteryx* are degraded collagen fibres. *Proc. R. Soc. B* **274**, 1823–1829. (doi:10.1098/rspb.2007.0352)

Néraudeau, D., Perrichot, V., Dejax, J., Masure, E., Nel, A., Philippe, M., Moreau, P., Guillocheau, F. & Guyot, T. 2002 Un nouveau gisement à ambre insectifère et à végétaux (Albien terminal probable): Archingeay (Charente-Maritime, France). *Geobios* **35**, 233–240. (doi:10.1016/S0016-6995(02)00024-4)

Norell, M. A. & Xu, X. 2005 Feathered dinosaurs. *Annu. Rev. Earth Planet. Sci.* **33**, 277–299. (doi:10.1146/annurev.earth.33.092203.122511)

Norell, M. A., Ji, Q., Gao, K. Q., Yuan, C., Zhao, Y. & Wang, L. 2002 'Modern' feathers on a non-avian dinosaur. *Nature* **416**, 36–37. (doi:10.1038/416036a)

Perrichot, V. 2004 Early Cretaceous amber from south-western France: insight into the Mesozoic litter fauna. *Geol. Acta* **2**, 9–22.

Perrichot, V. 2005 Environnements paraliques à ambre et à végétaux du Crétacé nord-aquitain (Charentes, Sud-Ouest de la France). *Mém Géosciences Rennes* **118**, 1–310.

Prum, R. O. 1999 Development and evolutionary origin of feathers. *J. Exp. Zool. B (Mol. Dev. Evol.)* **285**, 291–306. (doi:10.1002/(SICI)1097-010X(19991215)285:4<291::AID-JEZ1>3.0.CO;2-9)

Prum, R. O. & Brush, A. H. 2002 The evolutionary origin and diversification of feathers. *Q. Rev. Biol.* **77**, 261–295. (doi:10.1086/341993)

Sanz, J. L., Bonaparte, J. F. & Lacasa, A. 1988 Unusual Early Cretaceous birds from Spain. *Nature* **331**, 433–435. (doi:10.1038/331433a0)

Schlee, D. 1973 Harzkonserviertefossile Vogelfedern aus untersten Kreide. *J. Ornithol.* **114**, 207–219. (doi:10.1007/BF01641171)

Schlee, D. & Glöckner, W. 1978 Bernstein. *Stutt Beitr Naturk C* **8**, 1–72.

Sereno, P. C. 2004 Birds as dinosaurs. *Acta Zool. Sin.* **50**, 991–1001.

Tafforeau, P. *et al.* 2006 Applications of X-ray synchrotron microtomography for non-destructive 3D studies of paleontological specimens. *Appl. Phys. A: Mater. Sci. Process* **83**, 195–202. (doi:10.1007/s00339-006-3507-2)

Tafforeau, P., Bentaleb, I., Jaeger, J.-J. & Martin, C. 2007 Nature of enamel laminations and mineralization in rhinoceros enamel using histology and X-ray synchrotron microtomography: potential implications for palaeo-environmental isotopic studies. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **246**, 206–227. (doi:10.1016/j.palaeo.2006.10.001)

Vullo, R., Néraudeau, D. & Lenglet, T. 2007 Dinosaur teeth from the Cenomanian of Charentes, western France:

evidence for a mixed Laurasian–Gondwanan assemblage. *J. Vertebr. Paleontol.* **27**, 931–943. (doi:10.1671/0272-4634(2007)27[931:DTFTCO]2.0.CO;2)

Xu, X. 2006 Feathered dinosaurs from China and the evolution of major avian characters. *Integr. Zool.* **1**, 4–11.

Xu, X. & Norell, M. A. 2006 Non-avian dinosaur fossils from the Lower Cretaceous Jehol Group of western Liaoning, China. *Geol. J.* **41**, 419–437. (doi:10.1002/gj.1051)

Xu, X. & Zhang, F. 2005 A new maniraptoran dinosaur from China with long feathers on the metatarsus. *Naturwissenschaften* **92**, 173–177. (doi:10.1007/s00114-004-0604-y)

Xu, X., Tang, Z. L. & Wang, X. L. 1999*a* A therizinosauroid dinosaur with integumentary structures from China. *Nature* **399**, 350–354. (doi:10.1038/20670)

Xu, X., Wang, X. L. & Wu, X. C. 1999*b* A dromaeosaurid dinosaur with a filamentous integument from the Yixian Formation of China. *Nature* **401**, 262–266. (doi:10.1038/45769)

Xu, X., Zhou, Z. & Wang, X. L. 2000 The smallest known non-avian theropod dinosaur. *Nature* **408**, 705–708. (doi:10.1038/35047056)

Xu, X., Zhou, Z. & Prum, R. O. 2001 Branched integumental structures in *Sinornithosaurus* and the origin of feathers. *Nature* **410**, 200–204. (doi:10.1038/35065589)

Xu, X., Zhou, Z., Wang, X. L., Kuang, X., Zhang, F. & Du, X. 2003 Four-winged dinosaurs from China. *Nature* **421**, 335–340. (doi:10.1038/nature01342)

Xu, X., Norell, M. A., Kuang, X., Wang, X., Zhao, Q. & Jia, C. 2004 Basal tyrannosauroids from China and evidence for protofeathers in tyrannosauroids. *Nature* **431**, 680–684. (doi:10.1038/nature02855)

Zhang, F. & Zhou, Z. 2000 A primitive enantiornithine bird and the origin of feathers. *Science* **290**, 1955–1959. (doi:10.1126/science.290.5498.1955)

Zhang, F., Zhou, Z. & Dyke, G. 2006 Feathers and feather-like integumentary structures in Liaoning birds and dinosaurs. *Geol. J.* **41**, 395–404. (doi:10.1002/gj.1057)

Carnivorous Fungi from Cretaceous Amber

Alexander R. Schmidt,[1]* Heinrich Dörfelt,[2] Vincent Perrichot[1]

Carnivorous or predatory fungi have developed distinctive trapping devices such as adhesive hyphae, knobs, and networks or constricting and nonconstricting rings that enable them to exploit nematodes, other small animals, and protozoans as their main nutrition source (*1*–*3*).

Here, we report fossil evidence of carnivorous fungi that have hyphal rings as trapping devices preserved together with their prey, small nematodes, in circa (ca.)-100-million-year-old amber. A later fossil carnivorous fungus is known from Oligocene-Miocene Mexican amber (*4*), but its trapping devices are not clearly identifiable.

Our fossil specimens originate from the highly fossiliferous amber deposit of Archingeay/Les-Nouillers in southwestern France, which is Late Albian in age (*5*, *6*). The specimens are deposited in the Museum of Natural History in Paris (accession numbers MNHN ARC115.5a, ARC115.13, ARC115.20, and ARC115.22a).

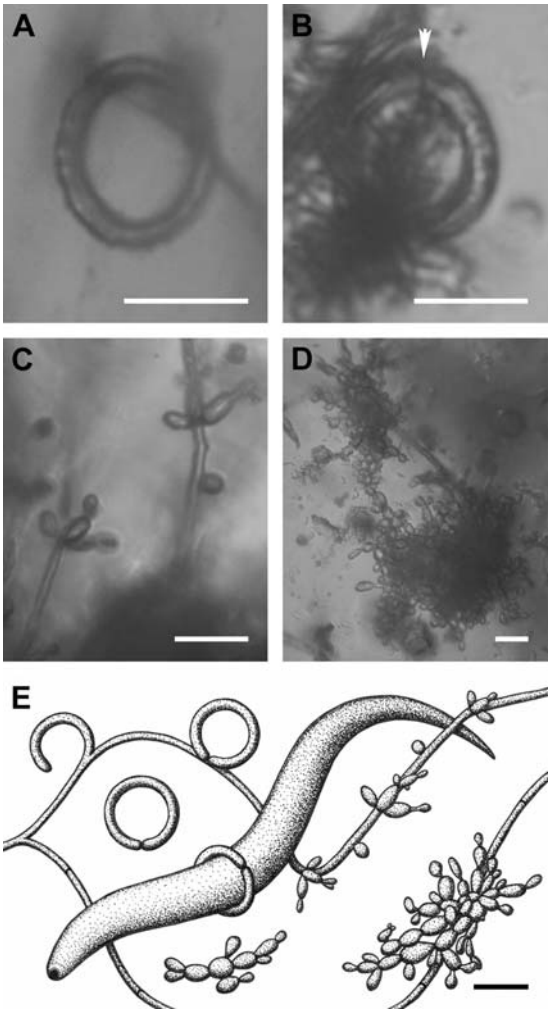


Fig. 1. Dimorphic carnivorous fungus from Cretaceous amber. Scale bars represent 10 μm. (**A**) Trapping ring (MNHN ARC115.13). (**B**) Trapping ring with attached detritus. The arrowhead indicates the only septum (MNHN ARC115.22a). (**C**) Formation of blastospores at a hypha (MNHN ARC115.20). (**D**) Formation of yeast colonies at a hypha (MNHN ARC115.20). (**E**) Reconstructed life cycle with ring formation, fully developed ring at the supporting hypha, disassociated ring, trapped nematode, formation of blastospores, and yeast colonies.

The mycelium consists of irregularly septated branched hyphae, which are 1.5 to 2 μm in diameter. The rings originate from ca.-2-μm-thick lateral branches of the hyphae, forming a loop. In contrast to modern trapping rings consisting of three cells, the rings, which are seen in three specimens of the fungus, are unicellular, forming just a single septum at the junction. Fully developed rings (inner diameter of 8 to 10 μm and outer diameter of 11 to 15 μm) probably detached easily from the supporting hypha and are found disassociated from the mycelium (Fig. 1, A, B, and E). Adhered particles (Fig. 1B and fig. S1A), which are numerous in some samples, indicate that the rings produced a sticky secretion, improving the efficiency of trapping, as known from modern carnivorous fungi trapping with adhesive networks or knobs. Once trapped, the nematodes were probably penetrated and digested by infestation hyphae.

In addition to rings, the fossil fungus also developed blastospores. They are ellipsoid to oviform, are 2 to 4 μm by 1 to 3 μm in size, and bud laterally in whorled position at the hyphae (Fig. 1, C and E). Secondary spores are seen budding primarily apically from the blastospores and form nearly acropetal chains. These cells established yeast colonies (Fig. 1, D and E, and fig. S1B).

Several small nematodes of ca. 100 μm in length are located close to a trapping ring (fig. S1, C and D). Because their maximum diameter falls within the width range of the rings, these animals can be identified as potential prey of the fungus. As a saprotrophic organism and consumer, the fossil fungus was a part of a highly diverse and complex soil biocenosis of an ancient coastal amber forest (*6*). Budding cells of yeast stages are ecologically important in liquid media and are reduced during the course of adaptation to terrestrial habitats. Aquatic representatives of modern carnivorous fungi are considered secondarily aquatic and belong to the same groups as terrestrial soil fungi (*7*). In contrast, the dimorphism exhibited by these fossils may represent an early transitional stage from wet to drier limnetic-terrestrial habitats.

These fossils show that by the Early Cretaceous soil fungi had already developed complex trapping devices to catch motile organisms. As in modern ecosystems, carnivorous fungi formed an ecological group of specialized consumers of small metazoans and protozoans. Today this ecological niche is occupied by more than 200 species of the Zygomycetes and imperfect stages of the Ascomycetes and the Basidiomycetes (*3*). On the basis of the mode of ring formation and the dimorphic mode of life, the fossils cannot be assigned to any recent carnivorous fungus, providing evidence that different groups occupied this ecological niche in the age of dinosaurs and that trapping devices were developed independently multiple times in the course of Earth history. The occurrence of carnivorous fungi in the Mesozoic is an example of complex interactions in early soil ecosystems and suggests that carnivory in fungi may be of ancient origin.

References and Notes

1. G. L. Barron, *The Nematode-Destroying Fungi* (Guelph, Ontario, 1977).
2. D. Ahren, A. Tunlid, *J. Nematol.* **35**, 194 (2003).
3. Y. Yang, E. Yang, Z. An, X. Liu, *Proc. Natl. Acad. Sci. U.S.A.* **104**, 8379 (2007).
4. H.-B. Jansson, G. O. Poinar Jr., *Trans. Br. Mycol. Soc.* **87**, 471 (1986).
5. V. Perrichot, D. Néraudeau, A. Nel, G. De Ploëg, *Afr. Invertebr.* **48**, 213 (2007).
6. Materials and methods are available on *Science* Online.
7. Y. Hao, M. Mo, H. Su, K. Zhang, *Aquat. Microb. Ecol.* **40**, 175 (2005).
8. We thank K. Schmidt and L. Tsuji for discussion and V. Girard, S. Jancke, D. Néraudeau, and S. Struwe for advice. This work was supported by the German Research Foundation and by the Alexander von Humboldt Foundation. This study is a contribution to the project AMBRACE (BLAN07-1-184190) of the French Agence Nationale de la Recherche.

Supporting Online Material
www.sciencemag.org/cgi/content/full/318/5857/1743/DC1
Materials and Methods
Fig. S1
References

30 August 2007; accepted 7 November 2007
10.1126/science.1149947

[1]Museum für Naturkunde der Humboldt-Universität zu Berlin, Invalidenstrasse 43, 10115 Berlin, Germany. [2]Martin-Luther-Universität Halle, Institut für Geobotanik und Botanischer Garten, Neuwerk 21, 06108 Halle/Saale, Germany.

*To whom correspondence should be addressed. E-mail: alexander.schmidt@museum.hu-berlin.de

Downloaded from www.sciencemag.org on December 14, 2007

Supporting Online Material for

Carnivorous Fungi from Cretaceous Amber

A. R. Schmidt, H. Dörfelt, V. Perrichot

Materials and Methods

Amber piece no. ARC 115 was found in the Archingeay/Les-Nouillers quarry in Charente-Maritime (southwestern France), which has already produced numerous fossils, mainly insects (*S1, S2*). The amber is derived from alternating layers of estuarine sand and clay containing mixed fragments of fossil plants (cuticles and lignitic wood). In the regional stratigraphical section, this amber-bearing stratum corresponds to the subunit A1 (*S3*) and was dated as Late Albian (ca 100 million years old) by palynological studies (*S4, S5*). The reconstructed paleoenvironment corresponds to a coastal tropical forest and representatives of the Araucariaceae were probably the main resin-producing trees (*S1, S6*).

The carnivorous fungi were originally fossilized in a single piece of amber (ARC 115) alongside 79 arthropods and numerous microorganisms such as bacteria, algae and testate amoebae. Most arthropods are litter-living taxa. The find of a mole cricket, in particular, indicates that the resin solidified in a soil habitat, not at the tree bark (*S7*). The original 4 x 3 x 2 cm piece of amber was divided into 31 pieces in order to separate the inclusions for investigation. This preparation followed the method described by Perrichot (*S1*). The polished amber pieces were investigated using transmitted-light differential-interference-contrast microscopes.

The four fungi-containing amber fragments are deposited in the amber collection of the Department of Earth History in the National Museum of Natural History in Paris. MNHN ARC115.13 contains a fragment of decomposed wood with a mycelium and the trapping ring shown in Figs. 1A and S1D as well as dispersed yeast cells and several nematodes. MNHN ARC115.22a contains a mycelium with two trapping rings (Figs. 1B and S1A) and yeast cells. MNHN ARC115.20 yields mycelia as well as a loop representing an initial stage of ring formation. Attached to a piece of detritus, several hyphae forming blastospores and secondary spores are preserved (Fig. 1C). A plethora of yeast colonies is preserved, some of which are still connected to hyphae (Fig. 1D). MNHN ARC115.5a contains a mycelium and numerous small yeast colonies as well as several nematodes (Fig. S1, B and C).

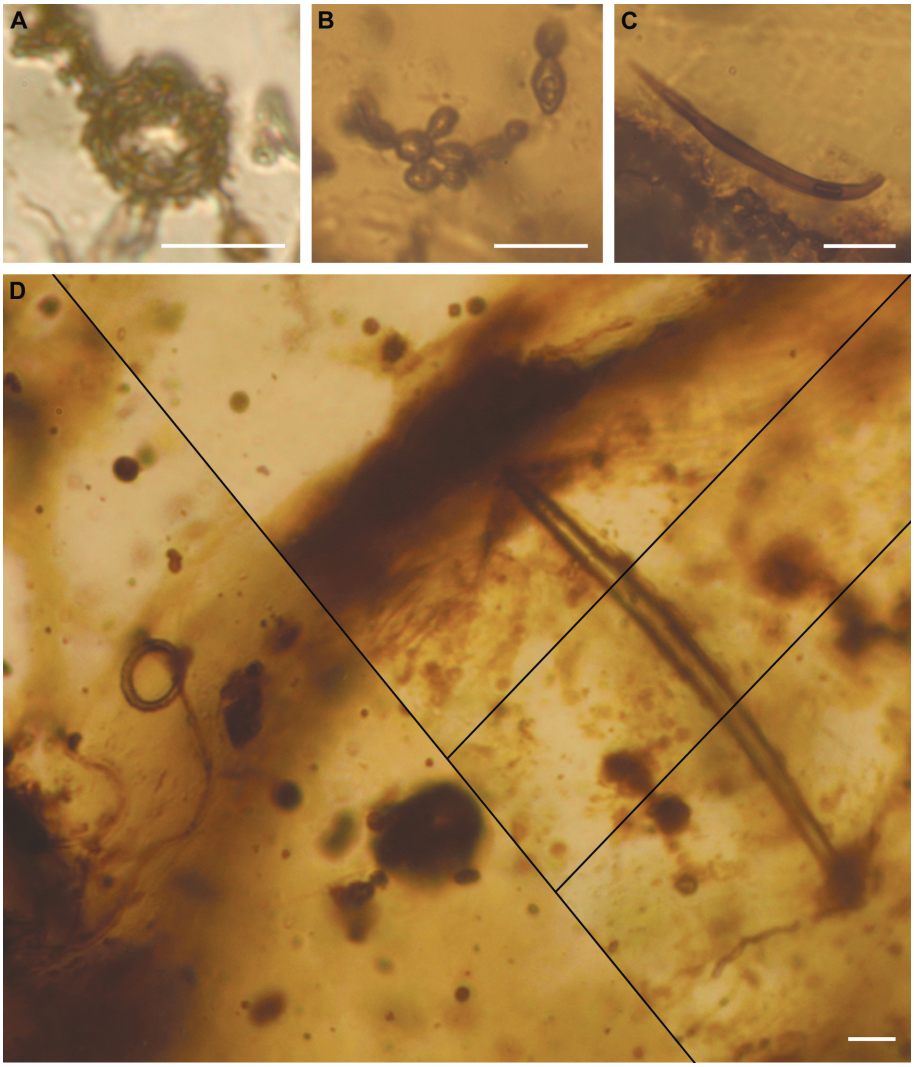


Fig. S1. Dimorphic carnivorous fungus from Cretaceous amber with its prey. (**A**) Trapping ring polluted by tiny detritus particles indicating that the rings were sticky (MNHN ARC115.22a). (**B**) Yeast colony disassociated from the hypha (MNHN ARC115.5a). (**C**) Syninclusion of a small nematode (MNHN ARC115.5a). (**D**) View of a trapping ring and a nematode close to it reconstructed from four optical sections (MNHN ARC115.13). Scale bars represent 10 µm.

Supplementary References

S1. V. Perrichot, *Geol. Acta* **2**, 9 (2004).
S2. V. Perrichot, D. Néraudeau, A. Nel, G. De Ploëg, *Afr. Invert.* **48**, 213 (2007).
S3. D. Néraudeau, P. Moreau, *Geobios* **22**, 293 (1989).
S4. D. Néraudeau, V. Perrichot, J. Dejax, E. Masure, A. Nel, M. Philippe, P. Moreau, F. Guillocheau, T. Guyot, *Geobios* **35**, 233 (2002).
S5. J. Dejax, E. Masure, *C R Palevol* **4**, 53 (2005).
S6. V. Perrichot, *Mém. Géosciences Rennes* **118**, 1 (2005).
S7. V. Perrichot, D. Néraudeau, D. Azar, J.-J. Menier, A. Nel, *Cretaceous Res.* **23**, 307 (2002).

Evidence for marine microfossils from amber

Vincent Girard[a,1], Alexander R. Schmidt[b,c,1], Simona Saint Martin[d,e], Steffi Struwe[c], Vincent Perrichot[f], Jean-Paul Saint Martin[d], Danièle Grosheny[g], Gérard Breton[a], and Didier Néraudeau[a]

[a]Université de Rennes 1, Unité Mixte de Recherche Centre National de la Recherche Scientifique 6118, 263 avenue du Général Leclerc, F-35042 Rennes Cedex, France; [b]Courant Research Centre Geobiology, Georg-August-Universität Göttingen, Goldschmidtstrasse 3, D-37077 Göttingen, Germany; [c]Museum für Naturkunde der Humboldt-Universität zu Berlin, Invalidenstrasse 43, D-10115 Berlin, Germany; [d]Muséum National d'Histoire Naturelle, Unité Mixte de Recherche Centre National de la Recherche Scientifique 5143, 8 rue Buffon, F-75231 Paris Cedex 05, France; [e]Facultatea de Geologie si Geofizica, Universitatea din Bucuresti, bulevardul N. Balcescu no. 1, Bucuresti, Romania; [f]Paleontological Institute, University of Kansas, Lindley Hall, 1475 Jayhawk Boulevard, Lawrence, KS 66045; and [g]Université Louis Pasteur, Strasbourg 1, Ecole et Observatoire des Sciences de la Terre, Unité Mixte de Recherche Centre National de la Recherche Scientifique 7517, 1 rue Blessig, F-67084 Strasbourg Cedex, France

Edited by Xavier Delclos, Universitat de Barcelona, and accepted by the Editorial Board September 26, 2008 (received for review May 22, 2008)

Amber usually contains inclusions of terrestrial and rarely limnetic organisms that were embedded in the places were they lived in the amber forests. Therefore, it has been supposed that amber could not have preserved marine organisms. Here, we report the discovery amber-preserved marine microfossils. Diverse marine diatoms as well as radiolarians, sponge spicules, a foraminifer, and a spine of a larval echinoderm were found in Late Albian and Early Cenomanian amber samples of southwestern France. The highly fossiliferous resin samples solidified ≈100 million years ago on the floor of coastal mixed forests dominated by conifers. The amber forests of southwestern France grew directly along the coast of the Atlantic Ocean and were influenced by the nearby sea: shells and remnants of marine organisms were probably introduced by wind, spray, or high tide from the beach or the sea onto the resin flows.

Cretaceous | palaeoecology | taphonomy | fossil resin | SW France

Amber contains some of the best preserved fossils of terrestrial arthropods, microorganisms, and plants remains (1). Deposits of fossil resins are therefore considered exceptional Lagerstätten (2) that provide important data on the paleoecology of Triassic to Neogene forests (3–8). The presence of marine organisms in tree resin, however, seemed highly unlikely, and the absence of marine inclusions, which could serve as index fossils for dating of amber, had been emphasized in previous literature (6). Very few amber-preserved arthropods have been attributed to littoral or marine habitats so far (1, 9), but there are just speculations how they got trapped in the resin.

Here, we present the discovery of marine microinclusions in a fossil resin: diatoms, radiolarians, sponge spicules, a foraminifer, and a larval spicule of a sea urchin were found in 100 million-year-old amber from southwestern France. Our fossils originate from the Late Albian amber deposit of Archingeay/Les-Nouillers (10, 11) and from the Early Cenomanian deposit of La Buzinie (11, 12; Fig. 1). The amber inclusions discovered provide fresh insight into the paleoecology of the Cretaceous amber forests, and suggest that the dating of amber by marine inclusions might become relevant in the future.

Results and Discussion

Marine Microfossils. All fossils described herein were found inside the amber pieces and were entirely surrounded by the fossil resin. None of the specimens was located in microfissures or at the surface of the amber pieces. Moreover, few specimens were found in contact with filaments of fossil fungi that are preserved on arthropods. Consequently, our fossils are true amber inclusions that were enclosed by the resin in its liquid stage in the amber forests. Thus, any post-Cretaceous contamination can be excluded. Furthermore, the quarries with the amber-bearing sediments are ≈30 and 100 km far from the sea, which makes it unlikely to find remnants of modern marine organisms attached to the amber pieces from Archingeay/Les-Nouillers and from La Buzinie.

Planktonic colonial centric diatoms were the most diverse marine inclusions in the investigated amber samples (Fig. 2). Approximately 70 specimens have been confidently attributed to 9 genera. The most diverse representatives are elliptical frustules of the genus *Hemiaulus*, which are connected by long horns (Fig. 2*A*). The most abundant diatom inclusions are frustules of the genus *Stephanopyxis* ranging from 8 to 20 μm in diameter (Fig. 2*B*). Other subspherical, discoid, or cylindrical frustules were assignable to the genera *Basilicostephanus*, *Coscinodiscus*, *Melosira*, *Paralia*, *Rhizosolenia*, *Skeletonema*, and *Trochosira*. These discoveries extend the fossil record of the genera *Paralia*, *Rhizosolenia*, *Skeletonema*, and *Trochosira* from the Late into the Early Cretaceous, whereas *Basilicostephanus*, *Coscinodiscus*, *Hemiaulus*, *Melosira*, and *Stephanopyxis* were already known from marine Aptian-Albian sediments (13). Some specimens could only be tentatively attributed to particular genera. A small diatom of 6 μm diameter with a strong central process of 16–18 μm length and 2 small marginal spines of 6–7 μm length resembles the genus *Syndetocystis* (Fig. 2*D*). A centric diatom of 40 μm in diameter possesses strong costae on its edges; based on these features, which are visible in the valval view, it has been tentatively assigned to the Thalassiosirales (Fig. 2*E*). Cylindrical diatoms of 10 μm diameter with flat valve faces and a marginal ring of short spines resemble the genus *Aulacoseira*. Other diatoms were not identifiable because they are largely covered by organic debris (see, e.g., Fig. 2*C*).

Fossil and modern representatives of the amber-preserved diatom genera are typical taxa of marine nearshore shallow waters. These colonial genera are largely preserved as solitary frustules or as short-chain fragments of 2 or 3 cells. Rarely, longer filaments of up to 20 frustules were found in the genera *Paralia* and *Stephanopyxis* (Fig. 2*B*).

Other marine inclusions include a young foraminifer whose shell is not mineralized; it was found embedded in organic debris in the highly fossiliferous amber piece ARC115 from Archingeay/Les-Nouillers (Fig. 3*A*). It is weakly elongated in 1 direction, 35 μm × 29 μm, and is composed of 6 membranous rolled chambers. The panispiral shape of this foraminifer suggests that it belongs to the Nodosariidae (small benthic foraminifers). This amber piece also contains 2 specimens of marine radiolarians resembling the genera *Acanthosphaera* and *Carposphaera* (Fig. 3*B*). The spheres are 16 μm in diameter and possess a regular subhexagonal areolae network. Small spines are

Author contributions: A.R.S., G.B., and D.N. designed research; V.G., A.R.S., S.S., and V.P. performed research; V.G. and V.P. contributed new reagents/analytic tools; V.G., A.R.S., S.S.M., S.S., V.P., J.-P.S.M., D.G., and D.N. analyzed data; and V.G. and A.R.S. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission. X.D. is a guest editor invited by the Editorial Board.

[1]To whom correspondence may be addressed. E-mail: vincent.girard@univ-rennes1.fr or alexander.schmidt@geo.uni-goettingen.de.

© 2008 by The National Academy of Sciences of the USA

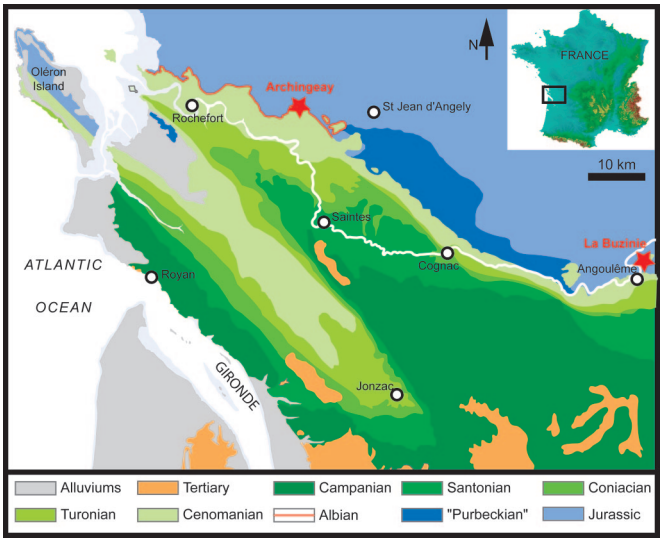


Fig. 1. Geological map of Charentes (southwestern France) showing both mid-Cretaceous amber localities with marine microfossils.

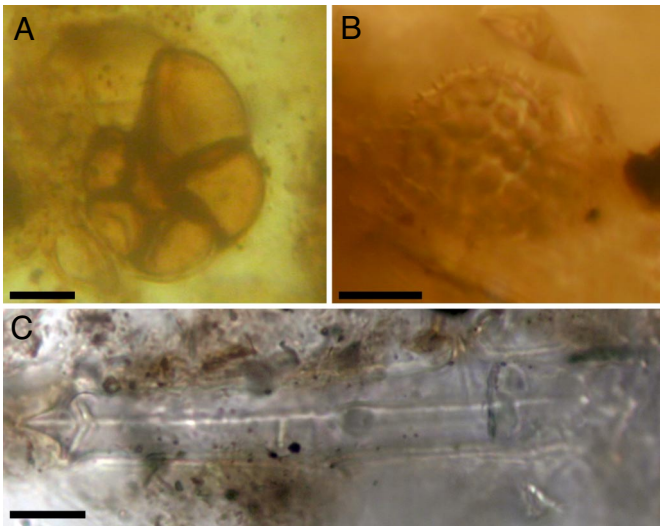


Fig. 3. Diverse marine microfossils from mid-Cretaceous amber of southwestern France. (*A*) Foraminifer (MNHN ARC115.1). (*B*) Radiolarian (MNHN ARC115.20). (*C*) Larval spine of a sea urchin (MNHN ARC115.24). (Scale bar: 10 μm.)

visible on their surface. One elongate calcitic inclusion of ARC115 has been identified as a spine of an echinopluteus, the planktotrophic larva of sea urchins (Fig. 3*C*). This spiny siliceous inclusion has a central canal of 1 μm diameter that branches several times into lateral canals that are 0.6–0.7 μm wide and reach the edges of the inclusion. Siliceous sponge spicules are the most abundant marine microfossils from the mid-Cretaceous French amber. Most of them correspond to oxea of demosponges (Fig. 4*A*) from which 2 different kinds could be distinguished. Eighty to 100 of these more-or-less curved spiny inclusions have been found in the 6 amber pieces containing marine fossils. One type is 7–12 μm, and the other 17–24 μm in diameter. Their length ranges from 160 to 350 μm but they are mainly 230–290 μm long. Two acanthostyles have also been found. One is a 70- to 75-μm-long curved siliceous inclusion (Fig. 4*B*) of 5–6 μm diameter. This inclusion has a central canal of 1–1.2 μm width that divides regularly into lateral canals of 0.35–0.4 μm width. The second has numerous small spines on its surface (Fig. 4*C*) and is just 50–55 μm long and 5–5.5 μm in diameter. Apart from these monoaxone spicules, an apparent triaxone sponge spicule has been found (Fig. 4*D*). Each large spine of these inclusions is 20–22 μm long and has a maximum diameter of 2 μm at its base. Detailed observation of this inclusion, however, revealed a very short spine emerging from the junction. We therefore interpret this fossil as a tetraxone calthrops with a reduced axis. A microsclere is also present in French amber. This multispiny inclusion is 35 × 24 μm in size. Because all spines are carried by a very small axis, this fossil is assignable to the strepaster type.

Numerous siliceous shell fragments and spicules are associated with these microfossils, but they remain unidentifiable.

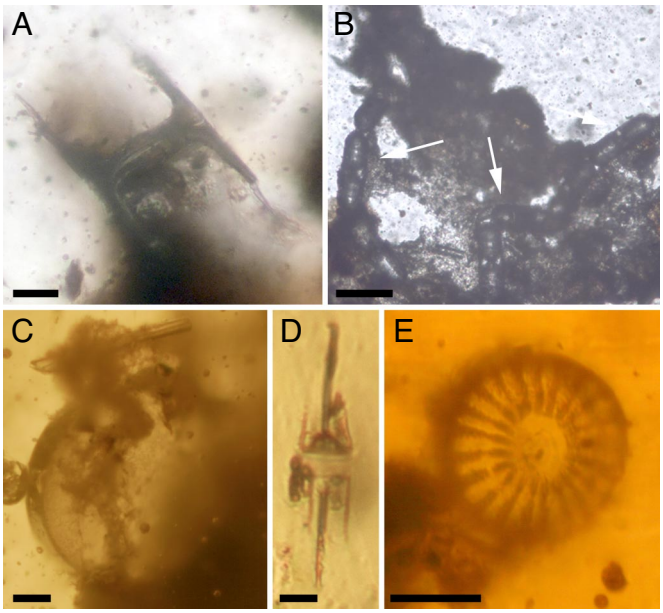


Fig. 2. Marine diatoms preserved in the mid-Cretaceous amber of southwestern France. (*A*) Diatom genus *Hemiaulus* [National Museum of Natural History (MNHN) ARC263.9]. (*B*) An 18-cell chain of *Stephanopyxis* (arrows; collection Géosciences Rennes BUZ1.1). (*C*) Centric diatom attached to organic debris (MNHN ARC115.19). (*D*) Centric diatom morphologically close to the genus *Syndetocytis* (MNHN ARC115.22). (*E*) Centric diatom belonging to Thalassiosirales (MNHN ARC115.13). (Scale bar: *B*, 100 μm; *A*, *C*, and *E*, 20 μm; and *D*, 5 μm.)

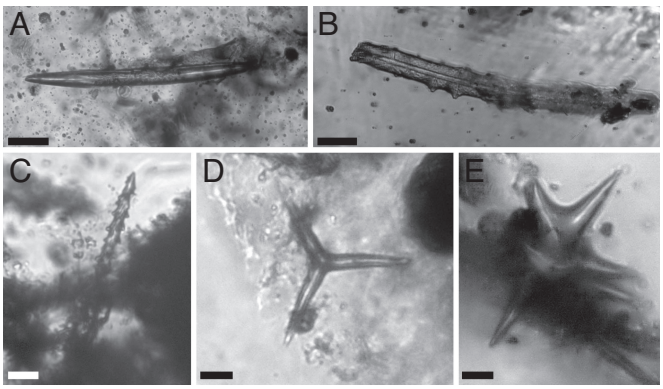


Fig. 4. Spicules of demonsponges from mid-Cretaceous amber of southwestern France. (*A*) Slightly curved oxea (MNHN ARC226.36). (*B*) Acanthostyle with a central canal (MNHN ARC115.12). (*C*) Spiny acanthostyle (MNHN ARC115.26). (*D*) Tetraxone calthrops (ARC60). (*E*) Microsclere (strepaster, ARC115.2). (Scale bar: *A*, 50 μm; *B* and *C*, 15 μm; and *D* and E, 5 μm.)

Paleoecology and Taphonomy. The sources of the amber were mixed coastal forests at the eastern rim of the young Atlantic Ocean (2, 14). These woods were dominated by the conifer families Araucariaceae and Cheirolepidiaceae (15–17). Furthermore, various representatives of the Ginkgoales and Lauraceae grew in these forests (15). All of the different marine microfossils described above have been found in litter amber samples (14). Numerous syninclusions of litter- and soil-dwelling arthropods and microorganisms (14, 18, 19) indicate that this resin flowed and solidified on the forest floor and not on the trees.

The occurrence of marine microfossils in the resin suggests that the amber forests were temporarily influenced by the nearby sea. Analysis of the depositional environment also supports the model of an estuarine, coastal landscape for the mid-Cretaceous amber forests of southwestern France. It has been suggested that a mangrove environment *sensu stricto* probably did not exist as early as the Albian-Cenomanian (20). But the French Cretaceous amber forests were clearly very close to the seashore as also indicated by syninclusions of mangrove bugs whose modern representatives forage on forest floors during low tides (12). Also, teeth of sharks that are typical for mangroves occur in the amber-bearing layer (21). It has been shown that mangrove-like vegetation already existed at that time (20). Representatives of the Cheirolepidiaceae that are very abundant in the amber-bearing strata are considered to be the dominant trees in these Cretaceous mangroves. Under these conditions, different processes could have easily transported marine microorganisms to the forest floor where they were embedded in fresh resin flows. Marine organisms or their shells and spicules could have been introduced together with attached organic debris during high tides or by spray; later they became engulfed by tree resin. Because the inclusions occur in layers of successive resin flows within a single piece of amber, we assume that the introduction of marine debris to the forest was a continuous process, rather than a single event. Because most marine microfossils are attached to tiny pieces of organic debris, it is likely that dried, marine organic matter with siliceous microfossil remnants was blown from the beach into the nearby woods. In this way, even long cell chains (see Fig. 2*B*) could have been transported onto the resin flows by attachment to detritus particles. Today, similar coastal resinous forests are difficult to find and only a few places in the world can be considered as a modern analogue. The *Araucaria columnaris* forests of New Caledonia (Fig. 5) may be a modern equivalent of the mid-Cretaceous amber forest of southwestern France. Some of these forests are growing directly at the seashore. In this environment, wind, spray, and high tides may easily transport shells and microremnants of marine organisms from the beach and sea onto the abundant resin flows of these woods.

Conclusions

Our findings show that tree resin of coastal forests is not exclusively a trap for terrestrial and limnetic organisms, and that the occurrence of marine fossils should seriously be considered when interpreting amber inclusions. Dating of ambers and their terrestrial inclusions is often difficult because they may be redeposited in sedimentary rocks that are younger than the fossil resin itself (e.g., ref. 22). These marine microorganisms reveal that, contrary to common opinion, dating of amber by enclosed index fossils might become relevant in the future.

Fig. 5. A possible modern analogue of the Cretaceous amber forest of southwestern France: a coastal forest of *Araucaria columnaris* at Maré, New Caledonia. Shells and remnants of marine microorganisms can be introduced by wind, spray, or high tide from the beach or seawater onto the resin flows in the nearby woods.

Materials and Methods

The amber pieces nos. ARC60, ARC115, ARC226, and ARC263 were found in the quarry of Archingeay/Les-Nouillers in Charente-Maritime, and the amber pieces no. BUZ1 and BUZ2 were collected in 2002–2003 during road works near the locality of La Buzinie in Charente (southwestern France). The amber is derived from alternating layers of estuarine sand and clay containing mixed fragments of fossil plants (cuticles and lignitic wood). The amber-bearing stratum from Archingeay/Les-Nouillers corresponds to the regional stratigraphic subunit A1 and was dated as latemost Albian (10), whereas the amber-bearing stratum from La Buzinie corresponds to the subunit B2 and is dated as mid Early Cenomanian (12). The reconstructed paleoenvironment corresponds to a coastal tropical forest, and representatives of the Araucariaceae and Cheirolepidiaceae were probably the main resin-producing trees (18).

The marine microfossils were found in the 6 highly fossiliferous amber pieces mentioned above. These pieces also contained >200 arthropods and numerous microorganisms such as bacteria, algae, and testate amoebae. Most syninclusions of arthropods and microorganisms are litter- and soil-dwelling taxa. In particular, the finds of a mole cricket (23), carnivorous soil fungi and nematodes (19), and actinomycetes indicate that the resin solidified in a soil habitat, not on the tree bark. The different pieces of amber were fragmented into smaller portions to separate the inclusions for investigation. This preparation followed the method described by Perrichot (12). The polished fragments were investigated by using transmitted-light differential-interference-contrast microscopes. The siliceous or calcitic nature of the microfossils described above has been proofed under a polarized microscope at the University of Rennes 1.

The different amber fragments containing the marine microfossils are deposited in the amber collection of the Department of Earth History in the National Museum of Natural History (MNHN) in Paris and in the collection of the Geosciences Laboratory of the University of Rennes 1.

ACKNOWLEDGMENTS. We thank Taniel Danelian (Paris) for his help in identifying the radiolarians, Kerstin Schmidt (Jena) for discussion, and Erin Saupe (Lawrence) for checking the usage of English. This work was supported by the French National Research Agency project AMBRACE, BLAN07–1-184190, by the German Research Foundation, and by the Alexander von Humboldt Foundation.

1. Poinar GO Jr, Poinar R (1999) *The Amber Forest. A Reconstruction of a Vanished World* (Princeton Univ Press, Princeton).
2. Néraudeau D (2005) Fauna and flora of paralic basins. *C R Palevol* 4:1–6.
3. Schmidt AR, Ragazzi E, Coppellotti O, Roghi G (2006) A microworld in Triassic amber. *Nature* 444:835.
4. Azar D (2007) Lebanese amber: Latest news and discoveries. *Abstract Volume, the Fossils X3 Congress: Insects, Arthropods, Amber* (Diputación Foral de Alava, Vitoria-Gasteiz), p 62.
5. Peñalver E, Delclòs X, Soriano C (2007) A new rich amber outcrop with palaeobiological inclusions in the Lower Cretaceous of Spain. *Cretac Res* 28:791–802.
6. Weitschat W, Wichard W (2002) *Atlas of Plants and Animals in Baltic Amber* (Verlag Dr. Friedrich Pfeil, München).
7. Nel A, de Ploëg G, Millet J, Menier J-J, Waller A (2004) The French ambers: A general conspectus and the Lowermost Eocene amber deposit of Le Quesnoy in the Paris basin. *Geol Acta* 2:3–8.

8. Antoine P-O, *et al*. (2006) Amber from western Amazonia reveals Neotropical diversity during the middle Miocene. *Proc Natl Acad Sci USA* 103:13595–13600.
9. Vonk R, Schram FR (2007) Three new tanaid species (Crustacea, Peracarida, Tanaidacea) from the Lower Cretaceous Álava amber in Northern Spain. *J Paleontol* 81:1502–1509.
10. Néraudeau D, *et al*. (2002) A new fossil locality with insects in amber and plants (likely Uppermost Albian): Archingeay (Charente-Maritime, France). *Geobios* 35:233–240 (in French).
11. Perrichot V, Néraudeau D, Nel A, de Ploëg G (2007) A reassessment of the Cretaceous amber deposits from France and their palaeontological significance. *Afr Invertebr* 48:213–227.
12. Perrichot V, Néraudeau D, Nel A (2007) Schizopterid bugs (Insecta: Heteroptera) in Mid-Cretaceous ambers from France and Myanmar (Burma). *Palaeontology* 48:1367–1374.
13. Gersonde R, Harwood DM (1990) 25. Lower Cretaceous diatoms from ODP LEG 113 Site 693 (Weddel sea). Part 1: Vegetative cells. *Proc ODP Sci Res* 113:365–402.
14. Perrichot V (2004) Early Cretaceous amber from south-western France: Insight into the Mesozoic litter fauna. *Geol Acta* 2:9–22.
15. Peyrot D, Jolly D, Barrón E (2005) Contribution of palynological data to the paleoenvironmental reconstitutions of the Albian-Cenomanian of Charentes (Southwest France). *C R Palevol* 4:151–165 (in French).
16. Gomez B, *et al*. (2004) Floristic assemblage from the Albian-Cenomanian of Charente-Maritime (SW France). *Ann Paleontol* 90:147–159 (in French).
17. Gomez B, Coiffard C, Depré E, Daviero-Gomez V, Néraudeau D (2008) Diversity and histology of a plant litter bed from the Cenomanian of Archigeay-les Nouillers (south-western France). *C R Palevol* 7:135–144.
18. Perrichot V (2005) Amber- and plant-bearing paralic environments from the Cretaceous of northern Aquitain (Charentes, SW France). *Mém Géosci Rennes* 118:1–310 (in French).
19. Schmidt AR, Dörfelt H, Perrichot V (2007) Carnivorous fungi from Cretaceous amber. *Science* 318:1743.
20. Plaziat JC, Cavagnetto C, Koeniguer JC, Baltzer F (2001) History and biogeography of the mangrove ecosystem, based on a critical reassessment of the paleontological record. *Wet Ecol Manage* 9:161–179.
21. Vullo R, Cappetta H, Néraudeau D (2007) New sharks and rays from the Cenomanian and Turonian of Charentes, France. *Acta Pal Pol* 52:99–116.
22. Grimaldi DA, Engel MS, Nascimbene PC (2002) Fossiliferous Cretaceous amber from Myanmar (Burma): Its rediscovery, biotic diversity, and paleontological significance. *Am Mus Novit* 3361:1–72.
23. Perrichot V, Néraudeau D, Azar D, Menier J-J, Nel A (2002) A new genus and species of fossil mole cricket in the Lower Cretaceous amber of Charente-Maritime, SW France (Insecta: Orthoptera: Gryllotappidae). *Cretac Res* 23:307–314.