
The oldest ant in the Lower Cretaceous amber of Charente-Maritime (SW France) (Insecta: Hymenoptera: Formicidae)

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ABSTRACT

Gerontofornica cretacica n. gen., n. sp., until now the oldest known ant, is described after a putative worker specimen, from the Uppermost Albian amber of France. Although its characters are those of modern ants, it does not fit in any recent ant subfamilies.

KEYWORDS | Insecta. Hymenoptera. Formicidae. n. gen., n. sp. Lower Cretaceous amber. France.

INTRODUCTION

Ants are very rare in the Cretaceous. Until now the oldest known ants are a male specimen attributed to the Formicinae or Dolichoderinae from the Lower Cenomanian of France (amber of the Île d'Aix, Charente Maritime) (Lacau et al., submitted) and undescribed 'primitive ants (Formicidae: Ponerinae n. gen. and *Sphecomyrma* n. sp. [Sphecomyrminae])' from the 'probable Turonian-Cenomanian Burmese amber' (Grimaldi et al., 2002, p. 3). Other Upper Cretaceous ants are known from the Turonian amber of New Jersey, Santonian amber of Taimyr, Campanian amber of Alberta, Upper Cretaceous Burmese amber (Dlussky, 1996; Ross and York, 2000; Zherikhin and Ross, 2000; Grimaldi and Agosti, 2000a; Grimaldi et al., 2002). Upper Cretaceous ants comprise Formicinae, Ponerinae, Dolichoderinae

and the fossil subfamily Sphecomyrminae (Dlussky, 1999a; Grimaldi and Agosti, 2000a).

Nevertheless, Poinar et al. (1999, 2000) put in doubt the attribution to ants of the Cretaceous genera *Sphecomyrma* WILSON, CARPENTER and BROWN 1967 and *Brownimecia* GRIMALDI, AGOSTI and CARPENTER 1997 and considered that the ant fauna from the Hat Creek Lower Eocene amber (between 50 and 55 Ma, British Columbia) comprises the oldest record of Formicidae. These authors did not cite the other Upper Cretaceous taxa attributed to ants and a very rich and diverse ant fauna in the Oise amber (- 53 Ma, France) (Nel et al., 1999). The recent discoveries of a true Formicinae in the Turonian New Jersey amber and of a Formicidae in the Cenomanian of France are the final evidences of a probable Lower Cretaceous ant diversification (Grimaldi and Agosti, 2000a).

The position of the Upper and Lower Cretaceous (Barremian to Cenomanian) group Armaniidae is still controversial, either considered as a separate family on the basis of a very thick petiole or ant subfamily (Grimaldi et al., 1997; Dlussky, 1999b; Grimaldi and Agosti, 2000a). The other Lower Cretaceous fossils that have been attributed to Formicidae (from Brazil, Australia and Lebanese amber) are probably not ants (Jell and Duncan, 1986; Brandão et al., 1989; Darling and Sharkey, 1990; Naumann, 1993; Dlussky, 1999b; Poinar and Milki, 2001).

The Upper Albian amber of Archingeay-les-Nouillers (Charente-Maritime, France) has given a very rich and diverse insect fauna, among which we discovered two ants. These specimens are a male and a worker, corresponding to very different taxa. The present discoveries strongly support a Lower Cretaceous age for the origin and first radiation of the Formicidae.

GEOLOGICAL SETTING

The coastal and fluvio-estuarine deposits of the Albo-Cenomanian transgression, eroding on a Kimmeridgian or Tithonian substratum, crop out widely in the Charente-Maritime region of SW France. These transgressive deposits correspond to a sand and laminated lignitic clay complex comprising two main formations (Moreau, 1996): 1) bottom resting on an eroded Jurassic substratum. The Formation is a lenticular lignitic clay containing large lumps of amber and interbedded in sands of varying thickeners; and 2) a younger formation above, with laminated lignitic clay having small lumps of amber, interbedded in fine homogenous sands. The lower Formation is Uppermost Albian in age and the upper Formation is attributed to the Early Cenomanian (Néraudeau et al., 2002).

The amber containing the ant described here was collected from the Albian part of the Archingeay-Les Nouillers quarry, within a lignitic clay lens that ranges from 0.1 to 1 m in thickness. This amber and the associated fossil wood were deposited in a coastal marine area, as indicated by the presence of oysters and terebratulid bivalve holes in the wood and marine foraminifera in the lignitic clay.

SYSTEMATIC PALEONTOLOGY

Order: Hymenoptera LINNAEUS, 1758

Family: Formicidae LATREILLE, 1809

GENUS *Gerontoformica* NEL and PERRAULT n. gen.

Type species: *Gerontoformica cretacica* NEL and PERRAULT n. sp.

Diagnosis (worker characters): Presence of peg-like teeth on labrum and clypeus, made of large, cylindrical setae; mandibles long, strongly curved with a long apical tooth and a strong subapical tooth; masticatory margin not dentate; eyes present; geniculate antenna with twelve articles, with a long scape; propodeal lobes well developed; petiole well defined, pedunculate, with a rather large node and a strong constriction between it and gaster; a differentiated pretergite on first segment of gaster (third abdominal segment); gaster globose, without constriction between the segments; no sting; no acidopore; legs very long.

Etymology: *Geronto* after the very old age of this ant.

Gerontoformica cretacica n. sp.

Figures 1 and 2

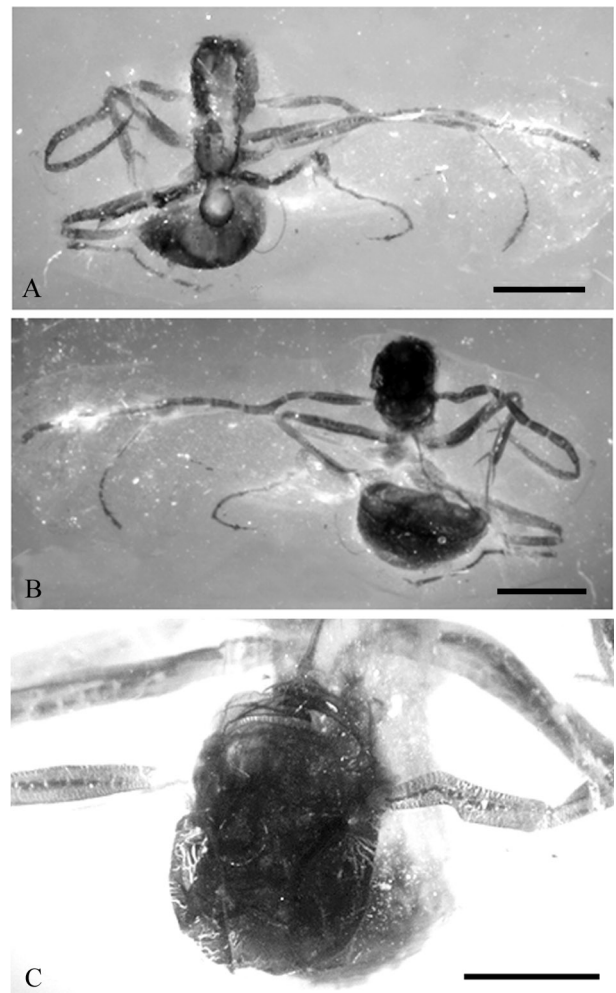


FIGURE 1 | *Gerontoformica cretacica* n. gen., n. sp., holotype specimen ARC 203.1. A) dorsal view. Scale bar: 1 mm. B) ventral view. Scale bar: 1 mm. C) head dorsal view. Scale bar: 0,5 mm.

Material: Holotype specimen ARC 203.1, Laboratoire de Paléontologie, Muséum national d'Histoire naturelle, Paris, France.

Locality deposit: Archingeay-les-Nouillers, Charente-Maritime, France.

Geological age: Lower Cretaceous, Uppermost Albian (approximately 100 Million years). (Néraudeau et al., 2002).

Etymology: After the Cretaceous age of this ant.

Diagnosis: That of the genus.

Description: A nearly complete ant, without any trace of wings, certainly a worker. Only the right metathoracic leg is broken but all appendages are distorted, probably due to desiccation in amber. The metasoma and head are curled up so that the ventral part of the thorax is not visible. Total length of body about 5.4 mm.

Head 1.1 mm long, 0.85 mm wide; no microsculpture on integument; eyes present but rather small and hardly visible; ocelli not visible; frontal carina absent; antennal sockets partly but not completely exposed, they only weakly abut posterior margin of clypeus; postclypeal triangle not visible; clypeus transverse, 0.2 mm long, 0.6 mm wide, with one anterior row of thirty two peg-like teeth, those in median part being the longest; labrum with about sixteen anterior teeth; antennae with twelve articles; antennal scape long (1.0 mm) and narrow (0.16 mm wide, scape length/width = 6.25), not reaching occipital border (scape index: scape length/head width = 1.17), but broken at base so that it is not possible to determine if their radicles deviate much from their long axis; antennal funiculus 3.7 mm long; ratio (scape length/length funiculus) = 0.27; index IK1 (length scape/length antenna) = 0.21; funiculus with eleven segments; not increasing in width apically; funicular segment lengths, without distinct club (basal diameter > apical diameter) 0.3/0.55/0.4/0.38/0.35/0.35/0.3/0.3/0.28/0.28/0.28; both mandibles not triangular in shape, but very long, 0.6 mm wide, and strongly curved, without small masticatory small teeth but with a sharp and long inner tooth, 0.10 mm long, and a sharp apical tooth, 0.25 mm long. Bases of mandibles well separated, 0.6 mm apart; distal halves of mandibles overlapping; maxillary palps not visible hidden under head.

Alitrunk (= mesosoma = thorax + propodeum): about 2.1 mm long; bare and without significant microsculpture; no supplementary sclerite visible; a distinct suture between pronotum and mesonotum; suture between mesonotum and metanotum not visible, partly destroyed

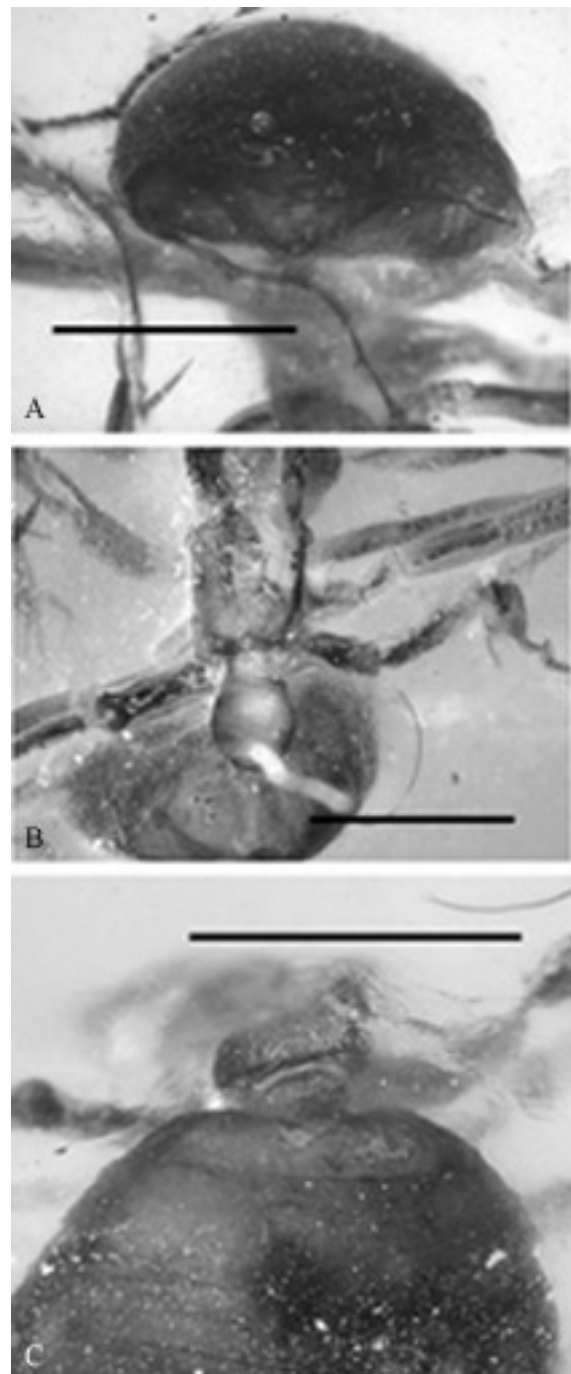


FIGURE 2 | *Gerontoformica cretacica* n. gen., n. sp., holotype specimen ARC 203.1. A) apex of abdomen. B) petiole, dorsal view. C) pretergite of first segment of gaster. Scale bar: 0,5 mm.

except laterally; propodeum elongate with anterior edge probably rather high but partly destroyed; metathoracic spiracles visible, rounded and protruding in anterior part of propodeum; propodeal spiracles not visible; meta-pleural gland orifices not visible, if present hidden by latero-posterior gibbositities; lateral propodeal lobes clearly visible from above, 0.6 mm long.

All legs deformed but very long; no trochantellus visible; pretarsal claws simple but long, 0.1 mm. Spur formula 1:2:2. Medium and hind leg with major tibial spur finely pectinate, that of hind legs corresponding to a setose area on distal end of tibia; all tarsomeres with two inner rows of small setae and three strong apical setae; lengths of leg segments (in order of trochanter-femur-tibia-basitarsomere-tarsi 2 to 5 in mm): fore leg, 0.25/1.35/1.1/?; mid leg, 0.25/1.35/1.3/0.75/0.8; unknown in hind leg.

Petiole well distinct from propodeum and gaster, 0.75 mm long, with an anterior peduncle, 0.25 mm wide, and a strong posterior dorsal node, 0.3 mm high and 0.47 mm wide; it is not possible to determine if a tergo-sternal fusion is present or not; a strong posterior constriction of petiole present at its attachment on gaster, posterior foramen 0.18 mm wide; pretergite of first segment of gaster clearly visible in posterior foramen of petiole, 0.2 mm wide, without a dorsal notch.

Gaster strongly deformed, but globose, about 1.5 mm long, 1.7 mm maximum wide; last metasomal segments retracted; no constrictions between gastral segments; first segment of gaster about the same length as segments 2 and 3; spiracles not visible; hypopygium lacking an acidopore; both hypopygium and pygidium not strongly sclerotized, with a row of short setae; no sting visible, even though cuticle between hypopygium and pygidium is transparent.

Relationships with the Formicidae

Very few synapomorphies can be found to affirm the membership with ants of this unique worker incompletely preserved by fossilization. The general habitus of this fossil is similar to that of an ant worker, more precisely that of a Formicinae or a Dolichoderinae, but some characters exclude affinities with these subfamilies (see below). It can be included in Formicidae because of the following characters: head probably prognathous with geniculate antennae and relatively long scape not reaching occipital border (Baroni-Urbani, 1989; Baroni-Urbani et al., 1992). Unfortunately, the presence of a metapleural gland cannot be ascertained in our fossil. Gauld and Bolton (1988) considered this character as a synapomorphy of the Formicidae. Grimaldi et al. (1997) and Grimaldi and Agosti (2000b, p. 691) emphasized its importance, but its orifice is not always visible outside (Gauld and Bolton, 1988), as it is in the recent genera *Oecophylla*, *Camponotus*, *Polyrachis*, *Phasmomyrmex* and *Dendromyrmex* that have no visible gland orifice (that does not signify the absence of the metapleural gland).

The first segment of the metasoma (true abdominal segment II) of *Gerontoformica* n. gen. is a well-differentiated

petiole, with a peduncle and a high node, and it is distinctly separated from the gaster by a deep constriction. A pretergite is easily recognisable in front of the second abdominal segment of the metasoma (true abdominal segment III). Nevertheless, the presence of a differentiated petiole cannot be considered a formicid synapomorphy because it is present in other hymenopteran families, in particular *Apterogyna* in the Bradynobaenidae, though *Apterogyna* is hypognathous.

A more interesting character is the presence of comb-like or pectinate spurs on the second and third tibiae (the pectinate spur and the simple spur of the middle right leg are particularly well preserved; the pectinate spur of the right hind legs is embedded in turbid amber). According to Brothers (1975), a comb-like calcar (the pectinate spur) on the hind legs occurs only in some Formicidae and Methocidae. The latter cannot be confused with ants based on other characters (no petiole, scape very short).

Relationships with recent formicid subfamilies

Many of the characters used in recent phylogenetic analyses of the Formicidae (Taylor, 1978; Ward, 1990; Bolton, 1990a, b; Shattuck, 1992; Baroni-Urbani et al., 1992; Grimaldi et al., 1997) indicate affinities of *Gerontoformica* n. gen. with the Formicinae and Dolichoderinae, i.e. the absence of a sting, the presence of a well defined petiole (Bolton, 1994) and the presence of a pectinate tibial spur on the middle and hind legs (Brothers, 1975). The fact that some recent Dolichoderinae (*Dolichoderus bidens*) have a very atrophied sting, hardly visible under dissection is not contradictory, even if it would be the case for *Gerontoformica* n. gen.

The Dolichoderinae generally have a pectinate spur on the middle and hind legs (Emery, 1912) as it is the case in *Gerontoformica* n. gen., but a 1,2,2 formula with three pectinate spurs is not rare in ants and thus not significant. *Paraponera clavata* (FABRICIUS 1775) for instance has the same formula.

But *Gerontoformica* n. gen. has well-developed, clearly visible, propodeal lobes, which would exclude affinities with recent Dolichoderinae, Formicinae and Aneuretinae (Shattuck, 1992). The Formicinae would be also excluded because of the absence of an acidopore, and the Dolichoderinae because of the absence of pretergal notch on the first segment of the gaster (segment III).

Peg-like teeth are present on the clypeus of Amblyoponini, except *Amblyopone mutica* (SANTSCHI 1914). It is described by Ward (1994) and considered by Grimaldi et al. (1997) as an autapomorphy of this tribe. The presence of peg-like teeth on the labrum and not on the clypeus is a character of the Apomyrminae [*Apomyrma stygia* BROWN,

GOTWALD and LÉVIEUX 1971] and of the Probolomyrmicinae [*Probolomyrmex guineensis* (PERRAULT 2000)]. But no recent ant has the combination of these two characters. Some ants have a denticulate clypeus, but it is not comprised of isolated setae as in *Gerontoformica* n. gen.

Finally, *Gerontoformica* n. gen. does not fit into any recent ant subfamilies. Though it has characters of modern ants, even if in a unique combination. It remains possible that propodeal lobes could have been present in an extinct dolichoderine lineage. *Gerontoformica* n. gen. has no pretergal notch on the first segment of the gaster (true abdominal segment III) but it is also the case in modern Aneuretinae.

Because of the preliminary state of ant phylogeny and the clearly incomplete fossil record, especially for Cretaceous taxa, it is best not to create a new suprageneric taxon for this fossil.

Comparison with workers and female of known fossil subfamilies

Gerontoformica cretacica n. gen., n. sp., has a petiole distinctly higher and with a larger node than in *Sphecomyrma* and Bradynobaenidae. The shape of the petiole is in fact highly polymorphic in ants. The IK1 index (= 21%) of *Gerontoformica* n. gen. is very low for a ant (ranging between 30-40%, after Grimaldi et al. (1997, p. 8), but these authors put in doubt the value of this index proposed by Dlussky. In the Upper Cretaceous ant *Sphecomyrma freyi* WILSON et al. 1967 this index is 22%. A more interesting character is the long scape of *Gerontoformica* n. gen. and *Sphecomyrma*, also shared by recent ants.

Gerontoformica n. gen. differs from the rather poorly known Middle Eocene Formiciinae Lutz (1986) by having mandibles with only two strong teeth, long tarsi and probably a longer petiole (but the Formiciinae are only known from alates) (Lutz, 1986). Among Upper Cretaceous ants, *Gerontoformica* n. gen. cannot be attributed to the subfamily Sphecomyrminae and to the enigmatic genus *Haidomyrmex* DLUSSKY 1996 (Burmese amber, attributed to the Sphecomyrminae by this author but considered of 'obscure' position by Grimaldi et al., 1997), because of its higher petiole, absence of a tooth on pretarsal claws, a peduncle distinctly longer than wide, absence of sting, very strong mandible teeth, second funicular segment not distinctly longer than others (Dlussky, 1975, 1987, 1996; Grimaldi et al., 1997, p. 8). *Gerontoformica* n. gen. differs from the Cretaceous formicine genus *Kyromyrma* GRIMALDI and AGOSTI 2000 in its mandible structure and absence of an acidopore. It differs from the Cretaceous genera *Brownimecia* GRIMALDI et al. 1997 and *Canapone* DLUSSKY 1999 in the absence

of a constriction between the first and second segments of the gaster. It differs from the rather poorly preserved Cretaceous dolichoderine *Eotapinoma macalpini* DLUSSKY 1999, by the high petiole.

The comparison of *Gerontoformica* n. gen. with the Armaniidae is much more delicate because all the taxa attributed to this group are described from impressions in sedimentary rock. An additional difficulty is that they are alates, though many characters of the worker are similar in the female alates, except for the thorax. Dlussky (1983) proposed the following diagnosis of Armaniidae: 1) (geniculate antennae) with scape very short, approximately equal to the third segment in the female. In *Gerontoformica* n. gen., the third antennal segment is distinctly shorter than the scape; 2) peduncle very short, approximately as long as wide in female. In *Gerontoformica* n. gen., the peduncle is very long, but some recent ants have also very short peduncle; 3) mandible short, without masticatory margin, bidentate with apical and preapical teeth in female alates. In *Gerontoformica* n. gen., the mandibles are long, but they have the same organization of teeth (see Dlussky, 1983, fig. 3b). Dlussky (1999, p. 274) considered such bidentate mandibles similar to those of primitive solitary wasps, but as noted above, similar mandibles occur in recent ants; 4) metapleural glands developed, at least in some species, but its orifice is very difficult to observe in many recent ants and in amber fossils. Grimaldi and Agosti (2000a, fig. 2) put in doubt its presence in Armaniidae and recent inspection of armaniids in the PIN collection (Moscow) by D. Grimaldi (pers. comm.) revealed that preservation is insufficient to determine the presence or absence of a metapleural gland in these fossils; 5) hind leg with trochantellus. After Wilson (1987, p. 50), this character would be erroneous, but Grimaldi et al. (1997, pp. 18-19) noted the presence of a genuine Cretaceous ant with a trochantellus. Furthermore, it is probably very difficult to observe such a small structure in impressions, so this character is too uncertain to be used in the diagnosis of Armaniidae. *Gerontoformica* n. gen. has no visible trochantellus; 6) spur formula 1:2:2, as in *Gerontoformica* n. gen. but also in many recent ants; 7) sting developed; and 8) petiole very thick, i.e. broadly attached to gaster. This character is difficult to establish for fossils preserved in impression because of the deformations due to compression. Nevertheless, the petioles of *Armania robusta* DLUSSKY 1983 and other Armaniidae indeed appear more broadly attached to the gaster than in *Gerontoformica* n. gen. and recent ants (see Wilson, 1987, fig. 4B; Dlussky, 1983, 1999b).

Gerontoformica n. gen. only shares with at least some Armaniidae (this character is unknown in many species) bidentate mandibles, though they are large, not short. The petiole of Armaniidae seems to be in a more plesiomorphic condition than in *Gerontoformica* n. gen. and Formi-

cidae *sensu stricto* (Grimaldi and Agosti, 2000a). *Gerontoformica* n. gen. cannot be considered as an Armaniidae.

In conclusion, *Gerontoformica* n. gen. is one of the oldest known true ant, dated from the Uppermost Albian. Its strongly acute, large mandibles, combined with peg-like teeth on the clypeus and on the labrum, and its long legs seem to be well adapted to a predaceous life. The present discovery is not very surprising as Lacau et al. (submitted) described an ant related to Formicinae and Dolichoderinae in the Cenomanian of France and Grimaldi and Agosti (2000a) a Formicinae in the Turonian. The high diversity of these Cretaceous ants is more surprising. We have also discovered an alate ant very closely related to *Haidomyrmex* DLUSSKY 1996 in the same amber outcrop with *Gerontoformica*, which suggests a similar Albian age for the Burmese amber, as indicated by Grimaldi (pers. comm.). All these discoveries strongly support a very older age for the 'first' ant, probably before the Albian, in which case the lack of ants in the very rich Lebanese amber is surprising. Maybe the formicid lineage had not appeared in the palaeocontinent of Gondwana, to which Lebanon was connected during the Lower Cretaceous. But the lack of Lower Cretaceous ant in diverse northern deposits of Siberia, England and Spain suggests that the earliest radiation of ants may have been quite sudden or that the first ants occupied very particular biotas and escaped fossilisation.

ACKNOWLEDGMENTS

We thank Dr Villemant-Lemkaden Claire for her help in the consultation of the collections of the Laboratoire d'Entomologie, MNHN, Paris, and M. Gaël de Ploëg for the very delicate preparation of the type specimen. We also thank Dr Cesare Baroni-Urbani and Dr David Grimaldi for their useful comments on the first version of this paper. This paper is a contribution to the 'ECLIPSE' CNRS project 'Interactions Climat/Ecosystèmes entre l'Aptien et Paléocène'.

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Manuscript received June 2002;
revision accepted October 2002.