



Fossil Ponerinae (Hymenoptera: Formicidae) in Early Eocene amber of France

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Abstract

The French Early Eocene (Ypresian, 52–55 million-year-old) amber of Oise contains a rich and well-diversified myrmecofauna, which has remained unstudied until now. A recent survey of these fossil ants revealed 40 different species, among which nine belong to the subfamily Ponerinae. We describe here the two best-preserved morphotypes: a possible ergatoid queen representing the earliest known occurrence of the extant genus *Platythyrea* Roger, and described as a new species *P. dluskyi* **sp. n.**; and a male morphotype related to the equivocal, paraphyletic genus *Pachycondyla* Smith, thus described herein but not formally assigned to genus until the male-based taxonomy of Ponerinae is better established. This fauna provides an ecological context to make inferences about the paleoenvironment of northwestern Europe during the PETM and gives new arguments for a radiation of modern ants at that time.

Key words: Insecta, Hymenoptera, ants, *Platythyrea*, *Pachycondyla*, Eocene, Oise amber

Résumé

L'ambre éocène inférieur (Yprésien, 52–55 millions d'années) de l'Oise contient une myrmécophage riche et diversifiée demeurée inédite jusqu'à présent. Un inventaire récent de ces fourmis fossiles a révélé 40 espèces différentes parmi lesquelles neuf appartiennent à la sous-famille des Ponerinae. Sont décrits ci-après les deux morphotypes les mieux préservés : une possible femelle ergatoïde représentant la plus ancienne occurrence du genre *Platythyrea* Roger, et décrite comme une nouvelle espèce *P. dluskyi* **sp. n.**; et un morphotype mâle rapproché du genre *Pachycondyla* Smith, désormais reconnu comme paraphylétique et actuellement sujet à révision, raison pour laquelle nous nous limitons ici à une description formelle sans attribution à un genre, dans l'attente d'une taxonomie des Ponerinae mâles mieux établie. Les implications écologiques pour le paléoenvironnement Yprésien du nord-ouest de l'Europe ainsi que pour l'évolution des Formicidae sont brièvement discutées.

Introduction

The present paper focuses on material collected from the insect-rich amber of Oise (northern France). The deposit has been the subject of numerous publications over the past decade, although none have focused on ants. With 40 morphotypes identified to date, the Formicidae appear diverse in this amber in comparison to the roughly contemporaneous Chinese amber of Fushun (35 morphotypes according to Hong, 2002), suggesting the group was already of major ecological and taxonomic importance in the Early Eocene. Subfamilies represented in Oise amber include the Dolichoderinae, Formicinae, Myrmeciinae, Myrmicinae, Pseudomyrmecinae, and the Ponerinae we detail herein. Of the nine morphotypes studied to date, seven belong to extant genera, which contrasts with Fushun amber where all morphotypes have been attributed to extinct genera. The recently discovered Early Eocene (50–52 million-year-old) amber of India has been described as having a fauna of 15 ant species of both a cosmopolitan and modern intertropical character (Rust *et al.* 2010), and further descriptions will provide an interesting comparison with the Oise paleofauna.

Over the past few years, the increased use of combined morphological and molecular data has allowed researchers to make substantial progress in inferring how extant ant subfamilies are related. Some controversies still remain, however, particularly among the basal clades. For example, Leptanillinae and the newly discovered subfamily Martialinae have been recovered as sisters to all other ants using molecular data (Brady *et al.* 2006, Moreau *et al.* 2006, Rabeling *et al.* 2008). This result is difficult to interpret because these ants are worker-blind and subterranean, while most ants are epigeaic and highly visual foragers. One possible explanation for the discrepancy is that the basal clades have specialized towards their hypogaecic ecology from 'ancestral' more epigeaic forms that are now extinct. These basal lineages may represent very morphologically-apomorphic survivors (i.e., adapted to strict hypogaecic conditions) of more versatile 'primitive' ants, maybe already found in the fossil record, such as Sphecomyrminae. Regardless of the position of Leptanillinae and Martialinae, a traditional 'plesiomorphic' clade is the Ponerinae, likely representative of the early evolution of ant societies and morphologies.

The Cretaceous fossil record as known today only provides a partial picture of early ant diversity, and the paleontological evidence for the early occurrence of Ponerinae is weak (see Ward [2007] or Perrichot *et al.* [2008] for the latest reviews on the fossil record of ants). Once attributed to Ponerinae, *Canapone dentata* Dlussky, 1999 and *Brownimecia clavata* Grimaldi, Agosti & Carpenter, 1997 were transferred by Bolton (2003) to Ectatomminae and a new Mesozoic subfamily Brownimeciinae, respectively. According to the fossil record, then, the origin of Ponerinae remains ambiguous.

The Ponerinae have also been extensively studied as an ecological model of early insect societies, as most species display simple colonial organizations and limited polyphenism/polyethism. Even though they are distributed world-wide, the vast majority are concentrated in the soil and litter of tropical and subtropical forests as insectivorous predators and direct competitors of many Myrmicinae, the most diverse and abundant ant subfamily in the world. This has raised questions about the historical succession of subfamilies and the sharing of niches (Wilson & Hölldobler 2005). Dlussky and Rasnitsyn (2007) suggested the present-day fauna arose later than the Early Eocene, e.g. after the Paleocene–Eocene thermal maximum (PETM) event. However, ant fossils from around the PETM were particularly scarce until now, with no information on diversity and abundance other than from Fushun amber. Fossils from the Ypresian Oise amber are thus of particular interest and should help clarify the ant evolution in the post-Cretaceous.

Material and methods

The amber material originates from a Lowermost Eocene (Ypresian) stratum dated to *ca.* 55/52 Myr, e.g. the Sparnacian level MP7 of the mammal fauna of Dormaal (Nel *et al.* 1999, De Franceschi & De Ploëg 2003, Brasero *et al.* 2009). The material was excavated at the Le Quesnoy farm, Chevrière, in the region of Creil, Oise department (north of France). The ant fauna comprises 375 ants (out of nearly 20,000 arthropods), totalling 40 morphotypes among six subfamilies. The subfamily Ponerinae is represented by nine morphotypes and 15 specimens. Seven morphotypes suffered from taphonomic conditions and await further examination, whereas two of them were comparatively well preserved and are described here.

The amber pieces were polished to remove the opaque weathered surface. Some fragments were embedded in Canada balsam between microscopic slides or immersed in water or 60–70% glucose solutions to minimize light scattering during study and image capture. Several stereomicroscopes magnifying up to X200 were used to examine the specimens. Photographs were taken with a Leica DC300 camera coupled with a Leica MZ APO stereomicroscope. HeliconFocus v.4.45 software was used to build composite photographs from a series of photographs taken by focal scanning of the field depth. Colour images of the type material are available on the fossil section of AntWeb (www.antweb.org/fossil.jsp). Camera lucida drawings are by Gilbert Hodebert (MNHN illustrator). The material is housed in the amber collection of the Department 'Histoire de la Terre', Muséum National d'Histoire Naturelle, Paris, France (MNHN).

Acronyms for measurements (all in mm) and indices are listed below. The first four measurements were taken in the same plane, i.e. with the head in full-frontal view. HL: head length, in a straight line from the mid-point of anterior clypeal margin to the mid-point of the occipital margin; HW: maximum head width measured behind the eyes; MFC: maximum distance between frontal carinae; SL: the maximum straight-line length of the scape, excluding radicle; ED: maximum diameter of eye as measured in lateral view of the head to show full surface of eye; AL:

mesosoma length in dorsal view, from juncture with the petiole to anterior border of pronotum; PW: maximum width of pronotum; PtL: length of petiole in lateral view; PtH: height of petiole in lateral view; FL: length of profemur, measured along its long axis in posterior view; CI: cephalic index (HW/HL x 100); FCI: frontal carinae index (MFC/HW x 100); SI: scape index (SL/HW x 100); OI: ocular index (ED/HL x 100); PtI: petiolar index (PtH/PtL x 100); FI: profemur index (FL/AL x 100); AI: mesosoma index (PW/AL x 100).

Systematic Paleontology

Order Hymenoptera Linnaeus, 1758

Family Formicidae Latreille, 1809

Subfamily Ponerinae Lepeletier de Saint-Fargeau, 1835

Genus *Platythyrea* Roger, 1863

Platythyrea dluskyi sp. n.

(Figures 1, 3A–B)

Material examined. Holotype MNHN A32915 (PA7873, worker).

Etymology. The specific epithet is a patronym honoring our colleague Gennady Dlussky, a world authority on fossil ants, for his many contributions to the subject.

Diagnosis. Ponerine ant worker or ergatoid queen with the following characters: head longer than wide, in frontal view with anterior clypeal margin and sides convex, posterior margin nearly straight; posterior clypeal margin strongly convex medially between frontal lobes; mandibles with 10–11 blunt denticles on masticatory margin, with external margin slightly concave medially; antennal sockets widely separated; antenna with scape slightly surpassing the occipital margin, evenly curved; first funicular segment smaller than second. Propodeal dorsum posteriorly with two blunt teeth each prolonged in a concave carina laterally on declivitous face. Petiole longer than high and broad, its dorsal sclerite roughly parallelepipedic in shape, with a small tooth at anterolateral corners, anterior and dorsal margins evenly convex, posterior margin slightly concave, with a pronounced lobe projecting posteriorly above anterior sides of helcium at posterolateral corners.

Measurements. HL 1.65, HW 1.30, MFC 0.45, SL 1.55, ED 0.40, AL 2.45, PW 0.93, PtL 0.90, PtH 0.67, FL 1.57, CI 79, FCI 35, SI 119, OI 24, PtI 74, FI 64, AI 38.

Description. *Worker or ergatoid queen.* Body length around 8.00 mm; nearly completely glabrous, apparently mostly smooth except rough punctuation of small shallow foveolae limited to mandibles, mesosoma and petiole; head 1.3 times longer than wide, with sides convex, anterior clypeal margin distinctly convex, posterior (occipital) margin nearly straight; central part of head including frontal carinae, frontal triangle and clypeus prominent; posterior clypeal area rather broad and strongly convex medially between frontal lobes; minute setae on mandibles and antennae; mandibles triangular, curved in lateral view, their external margin slightly concave medially, with 10–11 blunt denticles and setae on masticatory margin; clypeus almost glabrous, with only four fine setae along anterior margin; frontal lobes moderately expanded laterally, covering at most half the antennal sockets; frontal carinae well-separated from compound eyes, barely diverging posteriorly. Antenna 12-segmented; scape surpassing the occipital margin for a distance equal to its maximum width, slightly curved; first funicular segment smaller than second, which is a little more than twice as long as broad; other funicular segments decreasing progressively in size. Eyes of moderate size compared to head width, rounded, slightly bulged, situated anteriorly around midlength of head. Ocelli vestigial, removed far posteriorly from compound eyes. Mesosoma long, with dorsal surface rather flat; promesonotal suture conspicuous; anterior margin of mesonotum projecting forward over suture of pronotum; mesonotum and propodeum dorsally fused, mesopropodeal suture present although weakly visible in lateral view; propodeum with a pair of blunt teeth laterally at juncture of dorsal and declivitous faces, the teeth prolonged in concave carina along propodeal declivity; propodeal spiracles relatively small, rounded, situated on metasternal margin, slightly behind midlength of propodeal sides; metapleural lobes large, with rounded orifice. Legs long, glabrous, except scarce setae on tip of tibia and tarsi; protibia with one long pectinate spur, mesotibia with two finely

pectinate spurs, one slightly shorter than the other; metatibiae not preserved after first half; claws missing. Petiole 0.75 times as high as long; dorsal sclerite in lateral view roughly parallelepipedic, with a small tooth at anterolateral corners, anterior and dorsal margins evenly convex, posterior margin slightly concave, with a pronounced lobe projecting posteriorly above anterior sides of helcium at posterolateral corners; ventral sclerite with a small ventral tooth at about midlength of petiole. Gaster relatively short, distinctly constricted between abdominal segments III and IV; segments III and IV covering V and partly VI; tip of gaster pubescent; sting not visible, if present.

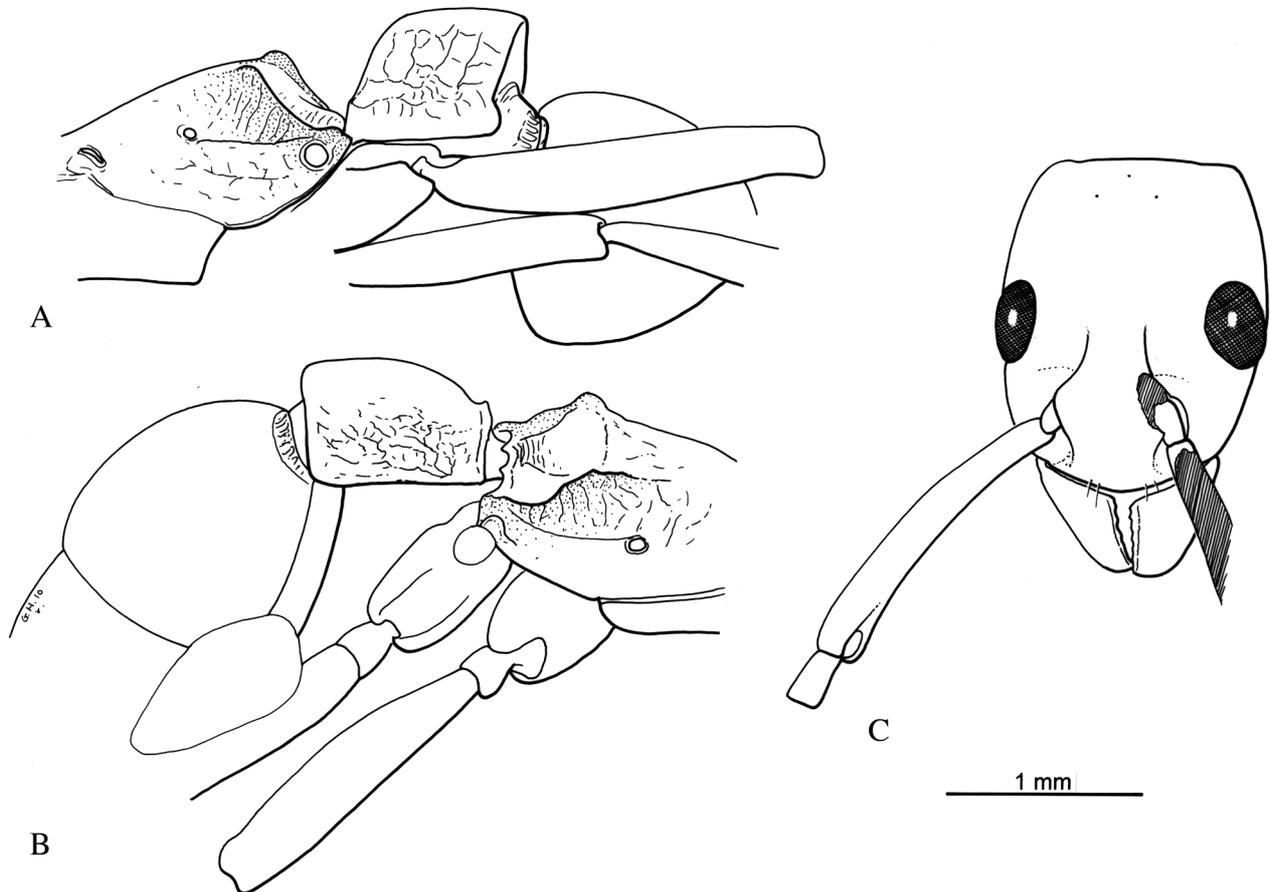


FIGURE 1. *Platythyrea dlusskyi* sp. n., reconstruction of the holotype (worker or ergatoid queen) MNHN A32915. A. Left profile view of propodeum, petiole and first segment of gaster. B. Right dorsolateral view showing the articulation of the central body part. C. Head in frontal view.

Discussion. This fossil possesses all diagnostic characters of the *Platythyreini* as proposed by Bolton (2003), and it falls in the genus *Platythyrea* after the regional Ponerinae keys of Bolton (1994).

In addition to the 37 extant species, five fossil species have been described in the genus *Platythyrea*. The Late Eocene Baltic amber *P. primaeva* Wheeler, 1915, redescribed by Dlussky (2009), differs from our fossil by its smaller size (body length of worker and gyne 5.5–6 mm, respectively, versus 8 mm in *P. dlusskyi*), its cubic petiole with a postero-dorsal tooth-like projection (parallelepipedic and without projection in *P. dlusskyi*), and the antennae with second funicular segment relatively shorter ('only slightly longer than broad', versus twice as long as broad in *P. dlusskyi*). The four other fossil species are from Miocene Dominican amber (Lattke 2003, De Andrade 2004): *P. dlusskyi* sp. nov. is easily distinguishable from *P. scalprum* Lattke, 2003 and *P. pumilio* De Andrade, 2004 in its larger size (body length 3.8 mm in workers of *P. scalprum* and *P. pumilio*), its scape and second funicular segments relatively longer (SI 67 in *P. scalprum*, 58.6 in *P. pumilio*, 119 in *P. dlusskyi*), and from *P. scalprum* in its petiolar shape ('petiole elongate', 0.44 times as high as long in *P. scalprum*, 0.75 times in *P. dlusskyi*). The dorsally-pointing propodeal denticles on the third species, *P. procera* Lattke, 2003, seem to represent a significant structural difference from our fossil, *P. dlusskyi*. Finally, *P. dentata* Lattke, 2003, although based on a wingless queen, is similar to our fossil in its dentate mandibles, but it differs by having a nearly straight anterior clypeal margin, a posterior petiolar margin with a dorsal lobe, and the metacoxa with a triangular dorsal tooth.

Our fossil does not fit either with any of the extant *Platythyrea* species in Brown's (1975) identification keys to Africa (petiole neither armed nor toothless) or Indo-Australia (petiolar node neither higher than long, nor bearing three teeth). The key to New World *Platythyrea* species by De Andrade (2004) would place *P. dluskyi* near the extant *P. lenca* De Andrade, 2004, *P. prizo* Kugler, 1977 and probably the extinct *P. dentata*. The synapomorphy uniting these species is the presence of teeth on the mandibles, which has been proposed as a possible plesiomorphic state (Lattke 2003). The fact that the oldest *Platythyrea* species displays mandibular teeth may support this hypothesis, although convergence is still highly probable for traits of this type. Furthermore, the size and length of the funiculus in *P. dluskyi* resemble that of the extant *P. lenca* and *P. prizo* rather than *P. dentata*.

The presence of ocelli among *Platythyrea* is uncommon, although present in the queen of the extinct morphotype *P. dentata*, and 'probably present' in the ergatoid female of *P. primaeva* (see Wheeler, 1915: p. 37). The possession of ocelli is often related to an improved flight vision (Kastberger 1990), either in alate sexuals or vestigially in ergatoid specimens, as could be the case in our fossil. There is only one *Platythyrea* species with ergatoid queens in extant faunas, *P. conradti* Emery, 1899, but all individuals lack ocelli according to Molet and Peeters (2005) who present a brief morphological comparison between the ergatoid and the worker, which we cannot use since we only have one specimen. Therefore, it is difficult to decide whether this fossil is a worker, an ergatoid sexual or even a gamergate. We leave the caste in the diagnosis as an open question.

Platythyrea are predominantly humid intertropical ants living in twigs, fallen dead trees and other cavities or, for larger subtropical African species, underground (Brown 1975). Members of this group actively run over tree trunks during foraging activities, which may be what the fossil specimens were doing in the Early Eocene forest ecosystem of Oise, leaving them susceptible to capture by fresh resin. *Platythyrea* probably played an important role in the ecosystem and may have competed with other arboreal ants such as *Gesomyrmex* or *Tetraponera*, also found in Oise amber (Aria *et al.* in prep.). These associations reinforce the hypothesis that a humid, warm forest was spread near the northern coast of France during the earliest Eocene.

Genus and species indet.

(Figures 2, 3C–F)

Material examined. Specimens MNHN A32917 (PA2509 1/2), A32918 (PA 307) and A32919 (PA 776), all alate males.

Measurements. HL 0.62, HW 0.66, ED 0.36, SL 0.11, AL 1.22, PtL 0.32, PtH 0.42, CI 106, SI 16.7, OI 58, PtI 131.2.

Description. *Male.* Body length ca. 3.40 mm; mostly shagreened, densely covered by minute setae; vertex and dorsal mesosomal surface with sparse, erect setae of moderate length; gaster with erect setae increasing in length and density towards apex. Head sub-oval, slightly broader than long, with posterior margin rounded in frontal view; compound eyes large and prominent, oval, with anterior margin strongly approximating mandibles; ocelli large and prominent, their diameter subequal to interocellar distance; frons smooth; clypeus convex, with a longitudinal median carina slightly prominent; anterior and posterior clypeal margins distinctly rounded; mandibles reduced, sub-rectangular, probably with an apical tooth but with masticatory margin apparently smooth; maxillary palpi 5-segmented, long, surpassing the occipital orifice; labial palpi 3-segmented, less than half length of maxillary palps; antennae 13-segmented, very long, reaching basal third of second gastral segment; scape short, slightly longer than wide; second funicular segment slender, more than three times longer than scape. Alitrunk robust, higher than head; pronotum transverse; mesonotum anteriorly convex and rather flat dorsally; dorsal part of scutum rather flat; notauli deep; from side view, epimeral lobe present; propodeum sub-angular in lateral view, with dorsal and declivitous faces slightly convex, the declivity bordered by a small carina. Legs moderately long; middle and hind tibiae with two apical spurs, a small simple one and a larger pectinate one. Forewing cells 1+2r, 3r, rm, mcu, and cua closed; cell 3r nearly four times as long as wide; vein rs-m longer than vein 2M; junction of r-rs with RS proximal to that of rs-m, with a section of RS between these two points; mcu pentagonal; 1RS more than twice shorter than 1M; junction of veins cu-a and M+Cu nearly at the same point as that between veins 1M and 1Cu; apical part of veins M and Cu as very short stubs not reaching the apical margin. Hind wing with jugal lobe present. Petiole node-like, higher than long, as high as propodeum, in lateral view with anterior face oblique, the dorsal face distinctly convex, and the posterior face vertical; helcium in profile attached very low on first abdominal segment,

the latter with a high vertical anterior face above the helcium. Gaster with a distinct constriction between abdominal segments III and IV; abdominal tergite VIII differentiated into a strongly down-curved spine. Pygostyles present, small.

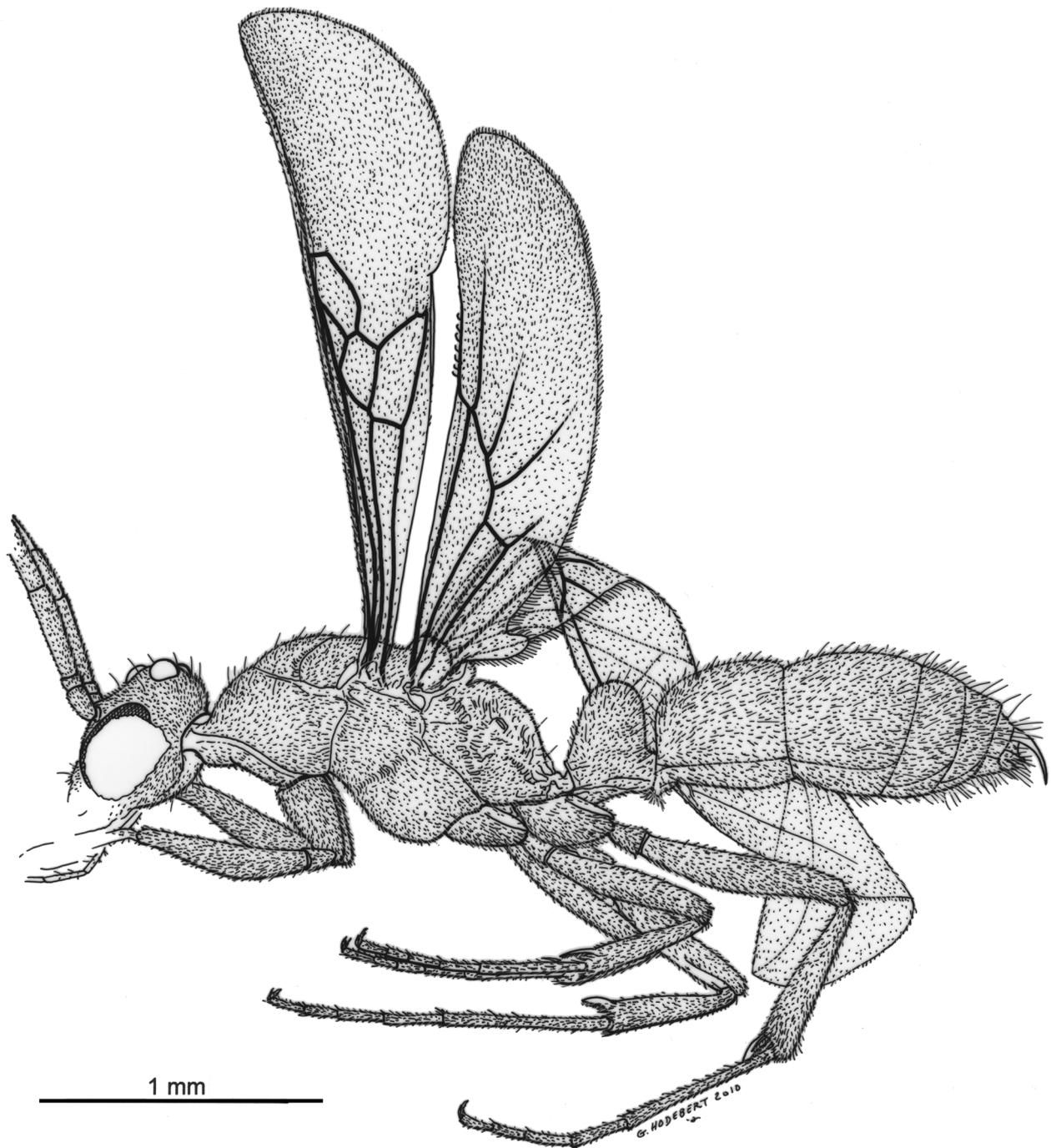


FIGURE 2. Reconstruction of an undetermined ponerine male, specimen MNHN A32917, habitus in profile view.

Discussion. Male-based keys to recent ponerines have been proposed by Yoshimura and Onoyama (2002) for Japan and by Yoshimura and Fisher (2007) for the Malagasy region. Using these keys leads to the attribution of our fossil to the now equivocal genus *Pachycondyla*, a result also obtained with Dlussky's key (2009) for Baltic amber male ponerines. *Pachycondyla* in its current sense (*sensu* Bolton 1995) is evidently paraphyletic, however, and an ongoing revision of the generic composition will alter the group's composition (Schmidt and Shattuck, in prep.). Since this work has not yet been published, we describe and discuss this fossil to witness its existence during a time

interval important for the evolution of modern ants, while awaiting reclassification of *Pachycondyla* to propose a relevant taxonomic name. Comparisons are made nevertheless with other fossil *Pachycondyla* to facilitate the use of existing references.

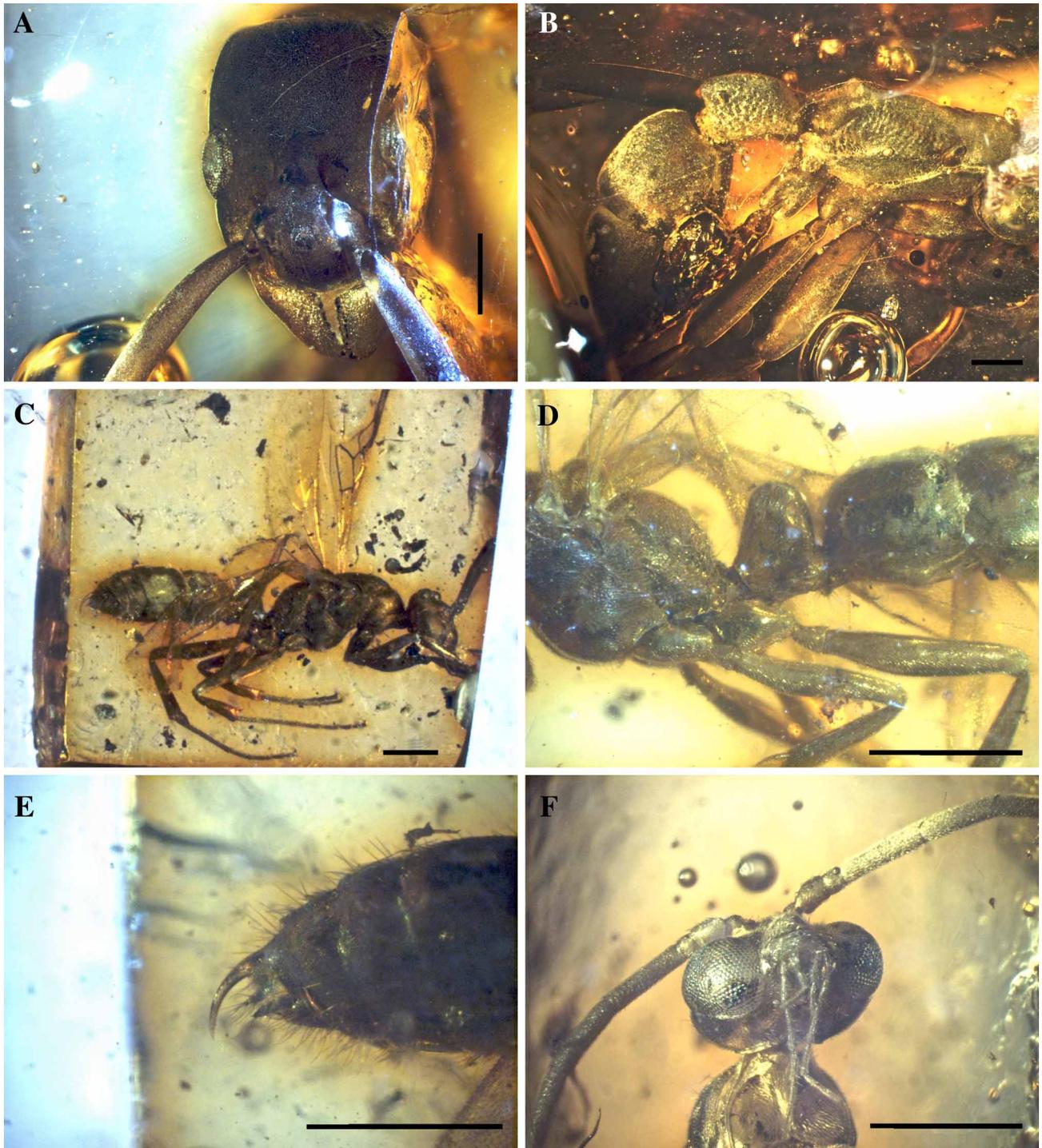


FIGURE 3. Photographs of the ponerine ants from Early Eocene French amber. A–B: *Platythyrea dluskyi* sp. n., holotype worker or ergatoid queen MNHN A32915; A. Head in frontal view. B. Right profile of the body, excluding head. C–E: Male undetermined, specimen MNHN A32917. C. Habitus in profile view. D. Detail of the central part of body in left lateral view. E. Apical part of gaster in lateral view. F. Male undetermined, specimen MNHN A32918, detail of head in ventral view. All scale bars: 0.5 mm.

Among the fossil ponerines with known males discussed by Wheeler (1915) and Dlussky (2009), the new ant shares the following characters with *Pachycondyla baltica* Dlussky, 2002: clypeus with a median carina, dorsal

part of scutum rather flat, propodeum subangular in lateral view, forewing cell 3r four times as long as wide. But the new fossil differs from *P. baltica* by its longer antennae and maxillary palpi, larger ocelli, and the eyes nearly touching the mandibles. Our fossil shares the latter two characters with *P. conservata* Dlussky, 2009 but it differs in its clypeus with a median carina, longer maxillary palpi, a propodeum subangular in lateral view, and a shorter forewing cell 3r. It differs from *P. succinea* (Mayr, 1868) by its clypeus with a median carina, the eyes nearly touching mandibles, the antennae reaching basal third of fourth abdominal segment, the first funicular segment twice as short as scape, the maxillary palpi surpassing the occipital orifice, the petiole nearly as high as propodeum.

The males of the two other European amber species remain unknown: *P. gracilicornis* (Mayr, 1868) is based on a worker and *P. tristis* Dlussky, 2009 on a gyne, making them impossible to compare to the new fossil. *P. labandei-rai* Dlussky and Rasnitsyn, 2002, from the Eocene Green River Formation (USA), is also based on a female and lacks the petiole and gaster (Dlussky & Rasnitsyn 2002). *P. globiventris* (Théobald, 1937) and *P. dubia* (Théobald, 1937), from the Oligocene of Kleinkems, Germany, are based on winged gynes without a visible petiole and a clear constriction between abdominal segments III and IV (Théobald 1937: 196, 198, pl. 4, fig. 15, pl. 13, fig. 16). Taphonomic distortions can easily cause displacements of the third abdominal segment in ants fossilized in lacustrine sediments, mimicking a typical ponerine constriction (Nel, pers. obs.). This phenomenon may have occurred in both fossils above (*P. globiventris* and *P. dubia*), suggesting that their attribution to Ponerinae is weakly supported. The same remarks apply to *P. crawleyi* (Donisthorpe, 1920) from the Oligocene of the Isle of Wight (Donisthorpe 1920: pl. 5, fig. 3). Finally *P. calcarea* (Théobald, 1937), also from Kleinkems, has the petiole and gaster resembling those of the Ponerinae, but the specimen does not show enough characters to be compared to our fossil.

Pachycondyla in its current broad sense comprises more than 200 extant species worldwide, occupying various ecological habits ranging from 'cryptobiotic leaf litter inhabitants to large, aggressive epigaeic and arboreal ants' (Wild 2002). This broad ecological and geographical range supports the emerging consensus that *Pachycondyla* is not a single clade.

Conclusion

In their 'Dynastic-Succession' hypothesis, Wilson and Hölldobler (2005) proposed that Ponerinae first occupied the new, complex forest soil formed by the continued expansion of angiosperms during the Paleocene/Early Eocene, and experienced the radiation towards the modern-day fauna by that time. Myrmicinae, Dolichoderinae, and Formicinae then radiated successively during the first half of the Eocene by adapting to new niches such as the canopy, which was made possible due to a change of diet. Dlussky and Rasnitsyn (2007) suggested that this diversification of modern ants did not take place before the middle Eocene. But the fossil record, including new data recorded from Oise amber and in some extent from Indian amber, gives a new window to this key period. First, all Cretaceous fossils that were tentatively attributed to the Ponerinae were later removed and placed as stem-group ants (i.e., Armaniidae or Brownimeciinae) or left as *incertae subfamiliae* in poneromorphs (Bolton 2003, Archibald *et al.* 2006). Second, and although Paleocene ants are largely missing for a good estimate of the post-Cretaceous diversity, the few fossils known for this time are exclusively old lineages: only seven species have been described in Aneuretinae, Formicinae, Dolichoderinae, and Ponerinae, from the Russian Sakhalin amber (Late Paleocene, 56–59 million-year-old) (Dlussky 1988), but all belonged in five extinct genera and one genus even survived the Cretaceous (i.e., *Eotapinoma* Dlussky, 1988, also recorded from Campanian amber of Canada [Dlussky 1999]). Finally, fossil data recorded from Oise and Indian amber show the presence of all major ant subfamilies as soon as in the Early Eocene, and preliminary accounts indicate the generic diversity was already important and with a modern character (this paper and Rust *et al.* 2010). Therefore, a first important shift from extinct to modern genera likely took place at or shortly after the Paleocene–Eocene boundary, but not only for Ponerinae as suggested by Wilson and Hölldobler (2005).

The etiology and validity of this burst of diversity remains an open question. We suggest that the climatic optimum, expansion of intertropical biomes, and overall increase of ecological diversity of the PETM event was the primary driver enhancing the adaptive radiation of modern ants, particularly for intertropical forms such as the Ponerinae.

Acknowledgments

We thank the company Lafarge-Granulat for help with sampling the amber and the Langlois-Meurinne family for authorization to work on their property; Gael De Ploëg for the preparation of some material; Gilbert Hodebert (MNHN) for the drawings of the specimens; and Erin Saupe (Univ. Kansas) and Brioch Hemmings (Univ. Bristol) for checking the usage of English. The manuscript greatly benefited from criticism and helpful suggestions of John T. Longino, Chris Schmidt, and an anonymous reviewer.

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