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Historical biology

The oldest Cenozoic ant fossil: †Tyrannomecia gen. nov. (Formicidae: Myrmeciinae) from the Palaeocene Menat Formation (France)

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ABSTRACT

A new genus and species of myrmeciine ants, also called bulldog ants, is described and illustrated from the Palaeocene of Menat (France) as Tyrannomecia inopinata gen. et sp. nov. This new taxon represents the oldest representative of the subfamily and provides the oldest calibration point for the total clade Myrmeciinae. It shows the apomorphic characters used to define the Myrmeciinae: mandibles elongate such that their length is three-quarters or more of head length, third abdominal segment (AIII) substantially smaller than the fourth abdominal segment (AIV), and with its height distinctly less than that of the fourth one. This new genus is easily differentiated from all the other

myrmeciine ants owing to its petiole with a conspicuous tooth located dorsally on the posterior declivity, and is considered to belong to the stem- Myrmeciinae. Aside from the calibration aspects, this new taxon, possessing a hunter morphology, is used to discuss implications for the recovery of ants after the K/Pg.

KEY WORDS

calibration point; Cenozoic; Formicoidea; fossil record; Insecta

Introduction

The first fossil ants after the K/Pg event are currently of Ypresian age, challenging the understanding of the impact of this crisis on the evolutionary history of ants. They are clearly younger than the ant assemblage described from the mid-Cretaceous Burmese amber encompassing numerous stem-ants (e.g. Boudinot et al. 2020; Perrichot et al. 2020) and hyper-specialised predators. It seems that these stem-ants declined prior or during the K/Pg crisis. Sometimes, they display strange heads with cephalic horns, clypeus and mandibles without modern equivalent, a reflection of ancient diversification ultimately bound for extinction.

The presence of crown-ants in Cretaceous amber (e.g. Grimaldi and Agosti 2000; McKellar et al. 2013; Zheng et al. 2018) suggests that both stem- and crown-ants have lived in similar environments for at least 10 million years. However, most of these earliest crown-representatives were far from being ”apex” predator since possessing relatively small mandibles and being of small sizes. The sole exception is a Cretaceous stem-Ponerinae, not yet described, and possessing long mandibles suggesting active hunting and represent- ing a strictly predatory lineage.

The fossil described herein suggests that posterior to the K/Pg crisis at least one predatory lineage has rapidly emerged (see discussion).

This potential active hunter belongs to the subfamily Myrmeciinae, today restricted to two genera distributed in Australia, New Zealand, and New Caledonia, viz. Myrmecia Fabricius, 1804 – also called ‘bulldog ant’, ‘jack jumper’, and ‘bull ant’ – and Nothomyrmecia (Clark 1934) also called ‘dinosaur ant’ (only present in a restricted area of Australia). Together with the extinct genus Prionomyrmex, Nothomyrmecia forms the tribe Prionomyrmecini, while the genus Myrmecia is placed alone in its own tribe Myrmeciini. The phylogenetic relationships of the sub- family, in regard of other ant subfamilies, are fully resolved point to the subfamily Pseudomyrmecinae as sister lineage of the Myrmeciinae (e.g., Ward and Brady 2003; Brady et al. 2006; Moreau et al. 2006; Branstetter et al. 2017; Borowiec et al. 2019). According to the most recent publications, these subfamilies shared a common ancestor during the late Cretaceous (e.g., Borowiec et al. 2019). The subfamily Myrmeciinae has its crown-group estimated to the mid- dle Eocene (e.g., Borowiec et al. 2019). However, previous studies pointed a possible older age for the (Pseudomyrmecinae + Myrmeciinae) and mainly suggested a Cretaceous age for the separation of both subfamilies (Borowiec et al. 2020: Table. 1). Our discovery suggests that the total and/or crown clade of Myrmeciinae may be older, and can be directly used to calibrate the total Myrmeciinae as already done with younger fossils. In fact, different approaches are used to calibrate the Myrmeciinae or estimate the age of the latter subfamily. Sometimes, without direct calibration within the clade (Economo et al. 2018) or using a calibration for the total Myrmeciinae (e.g., Ypresiomyrma in Borowiec et al. 2019) and additional calibration in the crow-group (e.g., Prionomyrmex in Borowiec et al. 2019). We assume that the new fossil, described in this paper, will have a great influence when used to calibrate the total Myrmeciinae.

As previously noted, the fossil record of the Myrmeciinae is rich but the position of one of its putative oldest representatives Cariridris bipetiolata described from the Lower Cretaceous Crato Formation and assumed to be a Myrmeciinae (Brandão et al. 1990), was controversial. Other studies rather argued for its placement in the Ampulicidae (Ohl 2004) or Sphecidae (see additional informa-

tion in the discussion) (Dlussky and Rasnitsyn 2003; Dlussky 2012)). Herein, we do not treat Cariridris as a member of the Myrmeciinae. Another intriguing taxon, Myanmyrma gracilis (Engel and Grimaldi 2005) (mid-Cretaceous Burmese amber), was assumed to share some morphological similarities with the Myrmeciinae (Engel and Grimaldi 2005, p. 16), but its placement was uncertain (Engel and Grimaldi 2005; Grimaldi and Engel 2005; Wilson and Hölldobler 2005). It was latter considered as incertae sedis in Formicidae or in Ponerinae (Barden and Grimaldi 2013), but is now placed in the Sphecomyrminae (Boudinot et al. 2020).

The extant Myrmeciinae show a relict distribution compared to that known in the record fossil. In fact, they were broadly distributed and relatively speciose during the Cenozoic (Table 1) with represen- tatives known from South America, North America and Europe while they are today restricted to the Australasian ecozone. The earliest fossil myrmeciine ants were described from the Eocene Baltic amber (Mayr 1868) and were, since this study, compared to extant representatives of the Myrmeciinae (Mayr 1868, p. 78). Latter, additional work on the genus Prionomyrmex results in pointing resemblances with the genus Nothomyrmecia (e.g. Clark 1934). It was not until the early 2000's that Baroni Urbani (2000) rediscovered the genus and used it to discuss relations within the Myrmeciinae. Following a renewed interest in the study of inclusions in Baltic amber, a new species of Prionomyrmex has also been described: Prionomyrmex gusakovi (Radchenko and Perkovsky 2020), suggest- ing that the myrmeciine diversity through geological time is still underestimated.

During his work on the Eocene of Green River (USA), Cockerell (1923) described the genus Archimyrmex in which several species were placed following descriptions based on material that originate from deposits throughout the world (Table 1). These descriptions highlight the broad distribution of the subfamily during the Eocene. Baroni Urbani (2008) transferred this genus in the Formicidae as incertae sedis, but Dlussky (2012) did not followed this treatment. Similarly, the genus Ypresiomyrma, erected by Archibald et al. (2006) based on fossils from MacAbee (Canada)

and with the inclusion of Y. rebekkae (Ypresian, Denmark), was transferred in the Formicidae as incertae sedis by Baroni Urbani (2008) but this transfer was not followed by Dlussky et al. (2015) when he described a new species from the Priabonian of Russia. Recent discoveries of numerous imprint specimens from the early Eocene serve to increase the past diversity of the subfamily (Archibald et al. 2006) by describing Avitomyrmex, Macabeemyrma and Myrmeciites from the Ypresian of McAbee. These genera were, also, excluded from the Formicidae by Baroni Urbani (2008) and treated as Hymenoptera incertae sedis. However, these placements do not have consensus (Bolton 2021). Therefore, the placement of several fossils in the Myrmeciinae do not make consensus even if those mentioned in Table 1 seem to belong the Myrmeciinae. Finally, the genus Propalosoma, initially placed in the wasp family Rhopalosomatidae (Dlussky and Rasnitsyn 1999), was transferred into the Myrmeciinae by Archibald et al. (2018) but without detailed explanation.

Here, we further expand this fossil record with a new genus and species from the Palaeocene of Menat (ca. 60 Ma), representing the earliest non-dubious species of the subfamily and providing a new calibration point for myrmeciine ants. This new specimen also represents the oldest Cenozoic ant and predates those from the Ypresian of the Fur Formation (ca. 55 Ma), Denmark or of the Oise amber (ca. 53.5 Ma), France (e.g. Archibald et al. 2006; Aria et al. 2011) by at least 5 Ma. In comparison, the oldest ants, that currently all belong to the stem-group, are dated from the mid-Cretaceous from Burmese (ca. 98 Ma) and Charentese amber (ca. 100 Ma) (Barden 2017: tbl. 2).

Material and methods

Specimen origin

The middle Palaeocene Menat fossil site, small outcrop near the southeast of the village of Menat (46°06’ N; 2°54’ E, Menat Basin, Puy-de-Dôme, France), is a volcanic maar containing a rather small paleolake ca. 1 km in diameter, filled with sedimentary rocks (spongo-diatomites) with

remains of diverse aquatic and terrestrial flora and fauna (Piton 1940; Nel 1989, 2008; Nel and Roy 1996). The composition of faunal and floral remains suggests that this lake was surrounded by a forest and that the palaeoenvironment was warm and humid (Wedmann et al. 2018). The age of the Menat outcrop was estimated as ca. 59 Ma after pollen, mammalian stratigraphic, and radiometric K/Ar analyses. (Kedves and Russell 1982; Nel 2008). However, a new estimate based on macroflora study postu- lated its age within 60–61 Ma (Wappler et al. 2009). Several ant morphospecies are present at Menat, but represented by few specimens.

Preparation, examination and illustration

The holotype of †Tyrannomecia inopinata gen. et sp. nov. (Figures 1–2) is housed in the Palaeontological collection of the Muséum national d'Histoire naturelle in Paris (MNHN. F). It was prepared by removing the rock around the fossil using a pneumatic micro-firing pin and light air puff. The specimen was studied using a stereomicroscope Nikon SMZ25 in the MNHN. Photographs were taken with a Nikon D800 and the images treated with graphic software. All images are digitally stacked photomicrographic com- posites of several individual focal planes, which were obtained using Helicon Focus 6.7. The figures were composed with Adobe Illustrator CC2019 and Photoshop CC2019 software.

Published work and nomenclatural acts are registered in ZooBank (http://zoobank.org/, last access: 16 November 2021), with the following LSID (reference): urn:lsid:zoobank.org: pub:5E9607E2-DDCE-40FE-B21E-33EDC09433D0.

Systematic paleontology

Class Insecta Linnaeus, 1758

Order Hymenoptera Linnaeus, 1758

Family Formicidae Latreille, 1809

Subfamily Myrmeciinae Emery, 1877

***Tyrannomecia* gen. nov.**

urn:lsid:zoobank.org:act:C8DFF49D-104C-4066-8066-60EE6579BF56

Type species

Tyrannomecia inopinata sp. nov.

Diagnosis

Worker. Head slightly longer than wide (ca. 1.20 ×); eyes large (0.26 × head length), located anteriad head mid-length, near epistomal (clypeal) margin; mandibles elongate (not triangular), shorter than head (ca. 0.61 × as long as head length), not broadly crossing apically (sensu Bolton 2003), with small tubercles/teeth along masticatory margin (as in Nothomyrmecia); propodeum smooth (without propodeal tooth); petiole short, dorsal surface broadly rounded, posterior surface with a conspicuous tooth; sternite of AIII without visible prora (if present, not in form of a longitudinal keel); AIII and AIV separated by a constriction.

Etymology

The genus name is a combination of the Latin word *tyrannus*, from the ancient Greek τύραννος meaning absolute ruler, and the suffix ‘mecia’, often used for ant genus names. Gender feminine.

Tyrannomecia inopinata sp. nov. (Figs. 1-2)

urn:lsid:zoobank.org:act:DA568D60-0C56-4C59-8298-C2BAFEB72C98

Etymology

The specific name derived from the Latin word inopinatus, meaning ”unexpected”. The epithet refers to the rather unexpected nature of the discovery in Menat deposit.

Type material

Holotype MNHN.FA71374 (Oli 435, collection Philippe Olivier, both sides), deposited in the Muséum national d’Histoire naturelle in Paris.

Type locality

Historical quarry of ‘Noir d’Auvergne’, Menat, Puy-de-Dôme, France.

Type horizon

Middle Paleocene (ca. 60 Ma), Menat Basin.

Diagnosis

As for the genus (*vide supra*).

Description

Worker. Head slightly longer than wide (ca. 1.2 × longer than wide), 4.80 mm long and ca. 4.20 mm wide, sides rounded, occiput rounded; antennae not preserved; mandibles elongate, ca. 2.92 mm long, without conspicuous teeth, with parallel and touching masticatory margin when closed, broader basally, tapering towards apex, not broadly crossing apically; eyes conspicuous, ovoid, ca. 1.28 mm long and 0.94 mm wide, located slightly anterior to head mid-length.

Mesosoma. Quite robust, elongate, ca. 7.05 mm long; dorsal surface slightly convex; pronotum slightly convex in lateral view, with posterior margin convex; propleuron visible laterally (but difficult to describe); pro-mesonotal articulation slightly impressed, presence or absence of fusion

uncertain; mesonotum indistinct (poorly preserved); mesopleuron distinct, ovoid, elongate towards insertion of third pair of legs; metanotal groove apparently well impressed; propodeum long, unarmed (without tooth), with dorsal surface convex, propodeal declivity without strong angle with dorsal surface, propodeal lobes apparently small. Legs not preserved.

Petiole. In lateral view, longer than high, bell-shaped, anterior surface short, slightly concave, dorsal surface broadly rounded, posterior surface dorsally with a blunt tooth located near mid- length (not an artefact of preservation since recorded in part and counterpart and not corresponding with petiolar collar visible just behind), subpetiolar process, if present, not visible, helcium clearly visible and strongly constricted between petiole and AIII.

Gaster. Medium size, longer than mesosoma, ca. 10.80 mm long, distinctly constricted between AIII and AIV; separations between tergites and sternites visible; sternite of AIII without visible prora; first two segments the longest, then decreasing in length, second segment the widest, length of segments from base to apex (in mm): ca. 3.36, 3.55, 2.88, 2.00, 1.56; sting not visible.

Integument without visible sculpturing nor colouration pattern. Body dark brown to brown.

Remark: When we refer to the mandibles, teeth designate sharp, acute cuticular structures along the masticatory margin of the mandible while tubercles refer to small, blunt structures/teeth along the masticatory margin of the mandible. The large eyes recorded in the genus are sufficient to rule out affinities with the majority of ant genera (extant and extinct). Some formicine genera also possess similar large eyes (*Myrmoteras* and *Gigantiops*), but in the latter, they are always longer than half the head length (vs. 0.26 × head length in the new species). Representatives of the Pseudomyrmecinae also possess large eyes but they are rapidly distinguished from the new genus owing to their distinctly nodi- form postpetiole. The genus Harpegnathos (Ponerinae) is superficially similar to the new genus but differs from the latter in having up-curved mandibles as long or longer than the head (vs. conspicuously shorter than the head and without apparent curva- tion in the new genus); presence of a huge gap between clypeus and beggining of the masticatory

margin while the gap presents in the part and counterpart is only due to damages caused during the preparation process; head quadrate (vs. clearly rounded), and the petiole is dorsally slightly bulging posteriorly in workers or queen (vs. with a clear rounded dorsal surface, and a nearly straight posterior dorsal surface). The genus *Aquilomyrmex* (Haidomyrmecinae) also possesses large eyes but it is easily distinguished from the new genus, at least, owing to the presence of a cephalic horn (absent in the new genus). The sole extant Myrmeciinae genus possessing similar eyes is *Myrmecia* but it differs from *Tyrannomecia* at least owing to the presence of strong teeth along the masticatory margin (see additional comparisons in discussion).

Discussion

Systematic placement

At first we used the identification key for ant subfamilies based on the external morphology proposed by Bolton (1994) even though we know that identification keys are not necessarily based on apomorphic characters. Note that apomorphic characters, as interpreted by Bolton, are recorded in Bolton (2003, p. 29–30). Following the aforementionned key, this fossil keys out in the subfamily Myrmeciinae because of the following couplets: body with two reduced or isolated segments (the petiole and post-petiole) between alitrunk and gaster: either both segments are much reduced or the second is somewhat larger than the first, and if the latter then the post-petiole is distinctly smaller than the first gastral segment and separated from it by an extensive, deep girdling constriction; pygidium transversely rounded, may be very small, not armed laterally or posteriorly with a row of short spines or peg-like teeth (note that even if poorly preserved we have compared the pygidium with that of representatives of the genus *Chrysapace* that possess a flat armed pygidium and found no correspondence between the structure, therefore we interpreted the pygidium as being rounded, possibly quite small, and not armed with peg-like teeth or setae); frontal lobes either absent or very reduced and vertical; in either case the antennal sockets are completely exposed in full-face view

and are not concealed or covered by the frontal lobes (we interpreted the frontal lobes as being reduced even if not preserved, additionally the exposition of the antennal sockets is not describable on the specimen since not preserved); promesonotal suture vestigial to absent (due to presence of a clear metanotal groove, we follow the dichotomy of the key as stated above but the true configuration of the suture is impossible to determine due to the preservation). Due to the presence of the putative apomorphic characters identified by Ward and Brady (2003) for the subfamily Myrmeciinae, we placed the new fossil without any doubt in the Myrmeciinae: mandibles elongate such that their length is three-quarters or more of head length, third abdominal segment (AIII) substan- tially smaller that fourth abdominal segment (AIV), and with its height distinctly less than that of the fourth one. The sole subfamily that may render difficult the attribution of the fossil to the Myrmeciinae is the subfamily Ponerinae (following classification of Bolton 2003) because of the 'similar' shape of the abdomen when preserved in compression or imprints. However, the AIII is nearly equal or substantially greater in height than AIV in most of the ponerine species. In lateral view, ponerines have a segment AIII with a strongly vertical anterior dorsal surface and a flat dorsal surface, both surfaces being separated by a distinct angle, the AIII looks like a block (except in Paraponera, and representative of the subfamily Proceratiinae; Bolton 2003), whereas AIII is always cone/bell-shaped in Myrmeciinae, as in the new fossil. The head, longer than wide (vs. nearly square), the elongate mandibles (vs. small not projected anteriorly), the lack of a hatchet-shaped petiole (unique feature in both females and males *Paraponera*: Boudinot 2015; Boudinot et al. 2020), the apparently quite large eyes, located in anterior half of the head (vs. smaller eyes that are set just in the posterior half of the head) are sufficient differences to rule out the genus *Paraponera*. The Proceratiinae are minute ants that clearly differ from the new specimen owing to the presence of highly reduced eyes and anterior-facing abdomen apex (the latter character being present in *Discothyrea*, *Proceratium*, and †*Bradoponera* but is absent in *Probolomyrmex*). Today, eight fossil genera are accepted within the Myrmeciinae: *Archimyrmex*, *Avitomyrmex*, *Cariridris*,

Macabeemyrma, *Myrmeciites*, *Prionomyrmex*, *Propalosoma*, and *Ypresiomyrma* (Bolton 2021). Note that some genera herein integrated in the Myrmeciinae (following Bolton 2021) are debated. The new specimen differs from the representatives of the genus *Archimyrmex* at least based on the lack of coarse obtuse teeth on mandibles (vs. present), petiole relatively short (vs. elongate) (Dlussky and Rasnitsyn 2003). The stout habitus (vs. slender) and the elongate mandibles (vs. short and triangular) of our specimen allow us to clearly differentiate it from the genus *Avitomyrmex* (Archibald et al. 2006). Note that *Avitomyrmex* is treated as *incertae sedis* in Hymenoptera by Baroni Urbani (2008, p. 6–7). However, since we follow the classification of Bolton (2021), we proposed a discussion to differentiate the new specimen from *Avitomyrmex*. The genus *Cariridris* as a long taxonomic history since it was first assumed to be a Formicidae (Brandão et al. 1990), or placed in the Ampulicidae by Ohl (2004) or treated as a Sphecidae (Dlussky and Rasnitsyn 2003; Dlussky 2012). In 2007, new material was examined (Osten 2007), and *Cariridris* was replaced within the subfamily Myrmeciinae but without justification nor proper illustration of the details allowing this hypothesis. Herein, we do not treat the genus *Cariridris* as a member of the Myrmeciinae. Nevertheless, the new specimen differs from *Cariridris* in the shape of its petiole (massive, relatively high vs. elongated, thin and apparently rather low) (Osten 2007: figs 11.77, pl. 15 m). The genus *Macabeemyrma* (McAbee, British Columbia, Canada) is treated as *incertae sedis* in the Hymenoptera by Baroni Urbani (2008, p. 6–7). However, since we follow the classification of Bolton (2021) we proposed a discussion to differentiate the new specimen from Macabeemyrma. The genus *Macabeemyrma* differs from the new specimen in its size, assumed to be equal to ca. 25 mm ‘in life’ vs. ca. 27 mm in the new fossil. *Macabeemyrma* has a head about ca. 1.5 times longer than wide (versus ca. 1.2 in the new specimen) and lacks a distinctive constriction between AIII and AIV (Archibald et al. 2006: fig 11), while the constriction is evident in the new specimen. The genus *Myrmeciites* is referred as a collective group without a proper diagnosis (Archibald et al. 2006, p. 500). Note that *Myrmeciites* is treated as *incertae sedis* in the Hymenoptera by Baroni

Urbani (2008, p. 6–7). However, since we follow the classification of Bolton (2021) we proposed a discussion to differentiate the new specimen from *Myrmeciites*. The most striking character that can be used to separate the new fossil from the representatives of *Myrmeciites* is the shape of the petiole with a reduced bell-shape (less high and with an elongate anterior surface vs. high with an anterior surface less elongate and more abrupt in the new specimen). However, it is important to mention that comparison with representatives of the latter genus are nearly impossible since this genus is not clearly defined. The genus *Prionomyrmex* is without doubt the best documented fossil genus of Myrmeciinae due to the discoveries of numerous specimens in amber that facilitate morphological study. *Prionomyrmex* species can be differentiated from the new specimen on the basis of the length of their mandibles that are equal to the head-length or slightly longer while they are clearly shorter in the new fossil. Note that we interpret, in the new fossil, the complete structure in front of the head, and separated from the latter by a damaged part as the mandibles. Mainly because we cannot identify a clear delineation between the lateral portion of the clypeus (since not preserved) and putative bases of the mandibles. *Prionomyrmex* can also be easily differentiated from the new fossil owing to the presence of propodeal teeth (Baroni Urbani 2000; 2003; Radchenko and Perkovsky 2020: fig. 6) that are absent in *Tyrannomecia* gen. nov. The genus *Propalosoma* was initially placed within the Rhopalosomatidae (Dlussky and Rasnitsyn 1999), but Archibald et al. (2018) moved it into the subfamily Myrmeciinae. The specimens of *Propalosoma* are not sufficiently well preserved to propose an in-deep comparison with the new specimen but they differ, at least, in the shape of their petiole with a broadly rounded dorsal surface in the new fossil while it is angled (between anterior and dorsal surface) in *Propalosoma* (Dlussky and Rasnitsyn: Fig. 1). The mandibles of *Propalosoma* are also much shorter than that of *Tyrannomecia* gen. nov. and resembles that of ‘classic’ formicids, viz. short triangular with a masticatory margin with numerous teeth, while they are elongate without tooth in *Tyrannomecia* gen. nov. The genus *Ypresiomyrma* (Archibald et al. 2006) is maybe the compression/imprint of a myrmeciine ant that is the most easily distinguishable

from *Tyrannomecia* gen. nov. since possessing mandibles with eight to 12 coarse (not spiniform) teeth (vs. only minute teeth visible), and a AIII without constriction at junction with AIV (Archibald et al. 2006, p. 492) while the constriction is remarkable in the new specimen. *Tyrannomecia* gen. nov. cannot be attributed to the genus *Myrmecia*, at least, because it possess mandibles that do not broadly cross apically (vs. broadly crossing in *Myrmecia*), mandibles with minute teeth along the masticatory margin (vs. with strong and sharp teeth along the masticatory margin) and a less marked constriction between AIII and AIV (Taylor 2015: figs. 4–6). The genus *Nothomyrmecia* does not match for the new specimen since it possesses an elongate anterior petiolar surface (Ward and Brady 2003: Fig. 1) vs. short in the new fossil. *Nothomyrmecia* also have a subpetiolar process and an anterior process on sternite of AIII (Ward and Brady 2003: Fig. 1) while they both appear to be absent on the new specimen. Lastly the new specimen has a clear constriction between the AIII and the AIV, while it is not present in *Nothomyrmecia* (Ward and Brady 2003: Fig. 1). Based on these comparisons, we create a new genus to accommodate this specimen. This new genus is also supported by the posterior surface of the petiole with a tooth, a character not recorded in other genera of the subfamily.

Potential calibration point

Dated phylogenies are a key element to decipher the evolutionary histories of clades. They allow to place the relationships between lineages in a temporal context and permit to propose hypotheses on the correlation between past events (e.g. climatic changes) and the diversification or extinction recorded in the deep past. These phylogenies rely on fossil calibration (node-dating) in which the fossils are not directly integrated into the tree topology, as they are in tip- or total-evidence dating approaches (e.g. Ronquist et al. 2012; Jouault et al. 2021). In node-dating approach, the fossils are used to calibrate a node within the topology based on the ages of the fossils. To date the calibrations used to constrain the minimum temporal range of the total Myrmeciinae or the stem-Myrmeciinae

are based on species described by Archibald et al. (2006) and dated ca. 54.5 Ma (in Moreau and Bell 2013), or on a different species from Mo-Clay ca. 53.5 Ma: *Ypresiomyrma* Rust and Andersen 1999 in Borowiec et al. (2019). Here we propose a new older fossil, possessing the putative apomorphies of the Myrmeciinae, as a new calibration point for a stem node calibration (i.e., for the Myrmeciomorpha, or Myrmeciinae + Pseudomyrmecinae). Therefore, we push back from 53.5–54.5 Ma to 60 Ma the age to be used to calibrate the stem-Myrmeciinae.

Implications for ants after the K/Pg crisis

The particular morphology of *Tyrannomecia inopinata* gen. et sp. nov. i.e. with elongate mandibles and large eyes, suggests that it may have been an active and efficient hunter, and represented a strictly predatory lineage. This combination of morphological features with the particular age of this new genus (ca. 60 Ma) i.e. being a few million years younger than the K/Pg crisis, may suggest that insect biomass recovered quickly after this event. At least, the insect biomass was sufficient and the trophic chains sufficiently elaborate to be able to withstand the diversification of a strictly predatory clade, in accordance with the previous results of Wappler et al. (2009). Therefore, the description of *Tyrannomecia inopinata* gen. et sp. nov. raises the question of whether (and how many) of the Myrmeciinae survived the end- Cretaceous event. In fact, if they were present during the Cretaceous, they have not suffered the K/Pg crisis in the same way as the others predatory ant lineages that did not survive the great extinction (e.g., Haidomyrmecinae, Zigrasimeciinae). It seems that the ant subfamilies have followed different patterns of diversifications and dynamics since the beginnings of the evolutionary history of the clade. However, it remains to decipher clearly this period and to better document the Palaeocene to be able to provide a robust scenario.

Conclusion

The description of *Tyrannomecia inopinata* gen. et sp. nov. shows that the myrmeciine ants were already present in Europe before the Eocene and older than previously thought. This new genus displays a new combination of characters, some already known from other myrmeciine genera and other never recorded in extant or fossil Myrmeciinae, i.e. petiole with a tooth on the posterior dorsal declivity. *Tyrannomecia inopinata* gen. et sp. nov. is aging the total clade Myrmeciinae, but at present its relationships with the two crown-group genera are uncertain. Therefore, it can be used to calibrate the stem-Myrmeciinae, and pushes back the age used to calibrate the total Myrmeciinae from ca. 54 Ma to 60 Ma. As for many extant lineages, the phylogeny of the subfamily Myrmeciinae must be studied using the new techniques of total-evidence dating or tip-dating to refine the time divergence esti- mates and be able to provide robust scenarios for the evolution of the clade by integrating the fossil record. This new description has also major implications for the recovery of ants after the K/Pg crisis suggesting that insect biomass recovered quickly after this event, if impacted, and was sufficient to withstand the diversification of a strictly predatory clade.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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Figure captions

Table 1. Fossil record of the subfamily Myrmeciinae (*Cariridris* excluded due to the lack of justification for its placement).

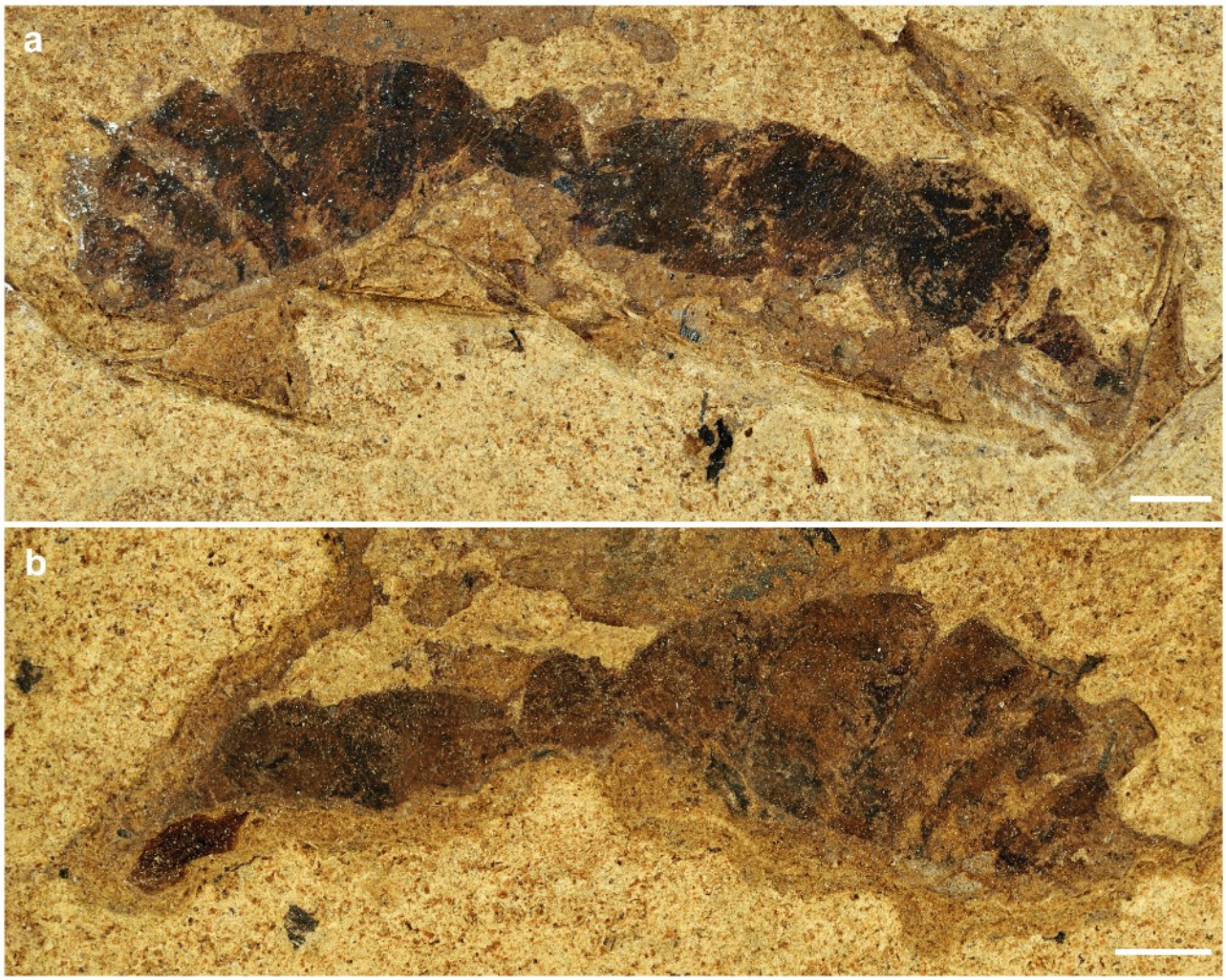


Figure 1. *Tyrannomecia inopinata* gen. et sp. nov., holotype MNHN.FA71374. Photographs. (a) habitus on part; (b) habitus on counterpart. Scale bars = 2mm.

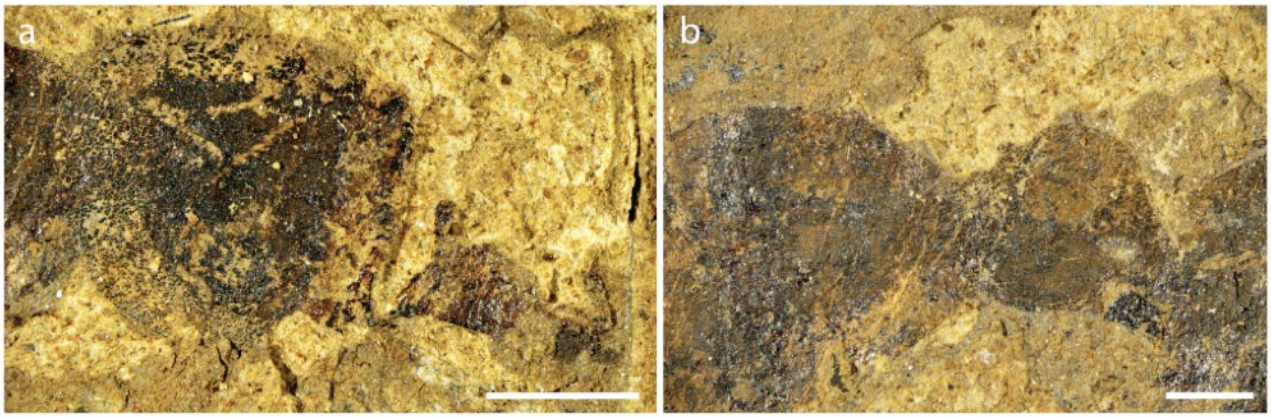


Figure 2. *Tyrannomecia inopinata* gen. et sp. nov., holotype MNHN.FA71374. Photographs. (a) head; (b) petiolar region. Scale bars = 2 mm (a), 1 mm (b).

Genus	Species	Country	Age	Locality / Formation	Reference
Archimyrmex					
	A. piatnitzkyi Viana and Haedo Rossi, 1957	Argentina	Lutetian	Pilcaniyeu road / Ventana Formation	Viana and Haedo Rossi, 1957
	A. rostratus Cockerill, 1923	USA	Bridgerian	Ute Trail, Roan Plateau / Green River Formation	Cockerell, 1923
	A. smekali Rossi de Garcia, 1983	Argentina	Lutetian	Confluencia / Ventana Formation	Rossi de Garcia, 1983
	A. wedmannae Dlussky, 2012	Germany	Lutetian / Ypresian	Grube Messel Pit / Messel Formation	Dlussky, 2012
Avitomyrmex					
	A. elongatus Archibald et al., 2006	Canada	Ypresian	McAbee	Archibald et al., 2006
	A. mastax Archibald et al., 2006	Canada	Ypresian	McAbee	Archibald et al., 2006

	A. systenus Archibald et al., 2006	Canada	Ypresian	McAbee	Archibald et al., 2006
Macabeemyrma					
	M. ovata Archibald et al., 2006	Canada	Ypresian	McAbee	Archibald et al., 2006
Myrmeciites					
	M. goliath Archibald et al., 2006	Canada	Ypresian	McAbee	Archibald et al., 2006
	M. herculeanus Archibald et al., 2006	Canada	Ypresian	McAbee	Archibald et al., 2006
	M. tabanifluviensis Archibald et al., 2006	Canada	Ypresian	Black Creek Road Locality (Horsefly River)	Archibald et al., 2006
Prionomyrmex					
	P. gusakovi Radchenko and Perkovsky, 2020	Russia	Priabonian	Baltic amber / Yantarnyi, Kaliningrad Region	Radchenko and Perkovsky, 2020
	P. janzeni Baroni Urbani, 2000	Russia	Priabonian	Baltic amber	Baroni Urbani, 2000
	P. longiceps Mayr, 1868	Baltic Sea region	Priabonian	Baltic amber	Mayr, 1868
	P. wappleri Dlussky, 2012	Germany	Oligocene	Rott	Dlussky, 2012
Propalosoma					
	P. gutierrezae Dlussky and Rasnitsyn, 1999	USA	Ypresian	Republic, locality B4131 / Klondike Mountain Formation	Dlussky and Rasnitsyn, 1999

Tyrannomecia gen. nov.					
	T. inopinata sp. nov.	France	Selandian	Old quarry / Menat	This study
Ypresiomyrma					
	Y. bartletti Archibald et al., 2006	Canada	Ypresian	McAbee	Archibald et al., 2006
	Y. orbiculata Archibald et al., 2006	Canada	Ypresian	McAbee	Archibald et al., 2006
	Y. orientalis Dlussky et al., 2015	Russia	Priabonian	Bolshaya Svetlovodnaya, Biamo, layer 1	Dlussky et al., 2015
	Y. rebekkae Rust and Andersen, 1999	Denmark	Ypresian	Stolleklint / Fur Formation	Rust and Andersen, 1999