



New record of Mastotermitidae from Fonseca Basin, Eocene-Oligocene boundary of southeastern Brazil

Francisco Irineudo Bezerra¹ · Márcio Mendes¹ · Og De Souza²

Received: 10 December 2019 / Accepted: 31 January 2020 / Published online: 14 February 2020
© Institute of Zoology, Slovak Academy of Sciences 2020

Abstract

The first representative of the genus *Mastotermes* Froggatt, 1897 from the Cenozoic of the South America is described here based on seven specimens from the Fonseca Formation, Eocene-Oligocene boundary, Minas Gerais State, southeastern Brazil. Today, *Mastotermes* is geographically restricted to northern Australia, with only one relict species, *Mastotermes darwiniensis* Froggatt, 1897. However, its fossil record clearly shows a global distribution, with species ranging from the Cretaceous of Myanmar, Russia, Mongolia and China, throughout Cenozoic of mainland Europe and Miocene of Africa, Mesoamerica and the Caribbean. Along with *Spagotermes costalimai* Emerson, 1965, *Mastotermes brasiliensis* sp. n. is the second fossil termite recorded in the Fonseca strata. This discovery extends the paleo-distribution of this genus into Neotropical South America during the Paleogene.

Keywords Fossil insect · Mastotermitid · Paleogene · Paleobiogeography · Paleoclimatology

Introduction

Termites generally live in highly organized colonies with morphologically specialized castes (Abe et al. 2000; Bignell et al. 2011). Their colonies range in size from a few hundred to several million individuals. All colonies have fertile males, fertile females, sterile workers and sometimes a soldier caste. Within the colony hard labor is restricted to the workers and soldiers. Termites undergo an incomplete metamorphosis that contains an egg, young nymph, old nymph, worker, soldier, pseudergate and adult stages (Bignell et al. 2011). They are among the most successful groups of insects on Earth extending between the latitudes of 30–45N 40–45S (Antarctica is the only landmass that is not colonized by termites) (Abe et al.

2000). Termites can also play an essential ecological role by recycling lignocellulose, a highly resistant and abundant substance, especially in subtropical and tropical regions (Wood and Sands 1978; Bignell et al. 2011).

Termites otherwise known as Isoptera, are an infraorder within Blattodea (cockroaches) (Engel et al. 2009). Inward et al. (2007) suggested that all termites should be grouped within one superfamily Termitoidea. Termites and cockroaches have close evolutionary ties (Vršanský 2002; Vršanský et al. 2002, 2017, 2019; Wang et al. 2017; Courent et al. 2018). Extant genus *Cryptocercus* Scudder, 1862 has many structural, behavioural and short genome similarities with termites (Bell et al. 2007; Maekawa et al. 2008). The last common ancestor of *Cryptocercus* and termites belonging to the Liberiblattinidae Vršanský, 2002 probably lived during Early Cretaceous (Vršanský et al. 2017, 2019). Termites developed from social cockroaches as is confirmed with both fossil record and molecular results (Engel et al. 2009, 2016; Inward et al. 2007).

Isoptera is likely monophyletic with Mastotermitidae Desneux, 1904 family as one of the most primitive (Emerson 1965; Kambhampati et al. 1996; Donovan et al. 2000; Wappler and Engel 2006; Vršanský et al. 2019). Cratomastotermidae Engel, Grimaldi et Krishna, 2009, Pabuonquedidae (Vršanský et al. 2019) and Mastotermitidae belongs to so-called “lower” termites, which comprise other basal families such as Hodotermitidae Desneux, 1904, Kalotermitidae Froggatt,

✉ Francisco Irineudo Bezerra
irineudoufc@gmail.com

Márcio Mendes
paleonto@ufc.br

Og De Souza
og.souza@ufv.br

¹ Departamento de Geologia, Universidade Federal do Ceará, Fortaleza, Ceará 60440-554, Brazil

² Departamento de Entomologia, Universidade Federal de Viçosa, Viçosa, Minas Gerais 36570-900, Brazil

1896, Archotermopsidae Engel, Grimaldi et Krishna, 2009, Stolotermitidae Engel, Grimaldi et Krishna, 2009, Rhinotermitidae Froggatt, 1897, Stylotermitidae Holmgren et Holmgren, 1917 and Serritermitidae Holmgren, 1910. Mastotermitidae record is well known from Cenozoic deposits all over the world with ambiguous occurrences in the Mesozoic (Ponomarenko 1988; Schlüter 1989; Vršanský and Aristov 2014). The fossil record of this family comprises the extinct genera *Blattotermes* Riek, 1952, *Garmitermes* Engel, Grimaldi et Krishna, 2007, *Idianotermes* Engel, 2008, *Khanitermes* Engel, Grimaldi et Krishna, 2007, *Spargotermes* Emerson, 1965, *Miotermes* von Rosen, 1913, *Valditermes* Jarzembowski, 1981 and extant *Mastotermes*. *Mastotermes* is most numerous in the fossil register (Table 1), represented today by a single species, *Mastotermes darwiniensis* Froggatt, 1897 from tropical Australia. However, during Paleogene this genus had a worldwide distribution. There is general agreement that *Mastotermes* represents a good example of primitive relict anatomy (McKittrick 1965; Emerson 1965; Nalepa and Bandi 2000). *Mastotermes* shares many primitive features with cockroaches such as endosymbiotic flavobacteria in the fat body, packaging of eggs in an oothecal mass, well-developed anal lobe in the hind wing, and similarities in the structure of reproductive organs (McKittrick 1965; Baccetti 1987; Watson and Gay 1991; Nalepa and Lenz 2000; Sacchi et al. 2000). Historically, Mastotermitidae has been considered as a sister family to all other termites (Engel et al. 2009; Engel and Delclòs 2010). Emerson (1942, 1965) theorized that *Archotermopsis* Desneux, 1904 has more primitive features than *Mastotermes*. Based on phylogenetic analysis, Engel

et al. (2009) suggested *Cratomastotermes* Bechly, 2007 as the most basal among Isoptera with *Mastotermes* as a living sister group. Most recently, Vršanský et al. (2019) described the most primitive termite *Pabuonqed* (Pabuonqedidae) from Cretaceous burmite amber.

Plants, fish and insects preserved in the Fonseca beds are often carbonized. Fossil assemblage from this locality contains a rich flora of angiosperms, especially “dicotyledons” (Annonaceae, Lauraceae and Siparunaceae) and “eudicotyledons” (Euphorbiaceae, Fabaceae, Malpighiaceae, Combretaceae, Malvaceae, Melastomataceae, Meliaceae, Myrtaceae, Rutaceae, Sapindaceae, Vochysiaceae, Bignoniaceae, Primulaceae and Sapotaceae) (Gorceix 1884; Berry 1935; Dolianiti 1949; Duarte 1956, 1958; Oliveira-e-Silva 1982; Burnham and Johnson 2004). Besides plants, Fonseca strata also bear an important insect fauna containing remains of Blattodea, Coleoptera, Hemiptera and Hymenoptera (Martins Neto 2005) (Table 2). Many of these insects and leaves decomposed, leaving imprints (impression fossils) into layers of papyraceous shale. Only one species of Isoptera, *Spargotermes costalimai* Emerson, 1965 is formally described so far.

Mastotermes is documented here for the first time from Eocene-Oligocene boundary of Brazil. The species described herein, *Mastotermes brasiliensis* sp. n., found near Fonseca village, municipality of Alvinópolis, Minas Gerais State, has important implications about the poorly studied palaeontofauna of Fonseca Formation. In addition, this new data provides better understanding of the potential palaeobiogeographic connection between *Mastotermes* from north and south hemisphere during early Cenozoic.

Table 1 List of *Mastotermes* species throughout geological time, together with their geographical distribution

Species	Geological age	Distribution
<i>Mastotermes darwiniensis</i> Froggatt, 1897	Holocene	Australia
† <i>Mastotermes? stuttgartensis</i> Armbruster, 1941	Miocene	Germany
† <i>Mastotermes aethiopicus</i> Engel, Currano et Jacobs, 2015	Miocene	Ethiopia
† <i>Mastotermes minor</i> Pongrácz, 1928	Miocene	Germany
† <i>Mastotermes haidingeri</i> Heer, 1849	Miocene	Croatia
† <i>Mastotermes croaticus</i> Rosen, 1913	Miocene	Croatia
† <i>Mastotermes electrodominicus</i> Krishna et Grimaldi, 1991	Miocene	Dominican Republic
† <i>Mastotermes electromexicus</i> Krishna et Emerson, 1983	Oligocene	Mexico
† <i>Mastotermes? heerii</i> Göppert, 1855	Oligocene	Poland
† <i>Mastotermes gallica</i> Nel, 1986	Oligocene	France
† <i>Mastotermes anglicus</i> Rosen, 1913	Oligocene	England
† <i>Mastotermes picardi</i> Nel et Paicheler, 1993	Oligocene	France
† <i>Mastotermes bournemouthensis</i> Rosen, 1913	Eocene	England
† <i>Mastotermes minutus</i> Nel et Bourguet, 2006	Eocene	France
† <i>Mastotermes krishnorum</i> Wappler et Engel, 2006	Eocene	Germany
† <i>Mastotermes monostichus</i> Zhao et al., 2019	Cretaceous	Myanmar
† <i>Mastotermes sarthensis</i> Schlüter, 1989	Cretaceous	France
† <i>Mastotermes nepropadyom</i> Vršanský et Aristov, 2014	Cretaceous	Russia

Table 2 Checklist of insects described in the Fonseca Formation. The list does not include *M. brasiliensis* sp. n. * *Fonsecablatta patricioi* was placed by Mendes and Pinto (2001) in Blattidae Latreille, 1810. However,

F. patricioi has been placed within Blaberidae Saussure, 1864 on some database websites (e.g. fossilworks). Here, we follow the original publication by Mendes and Pinto (2001)

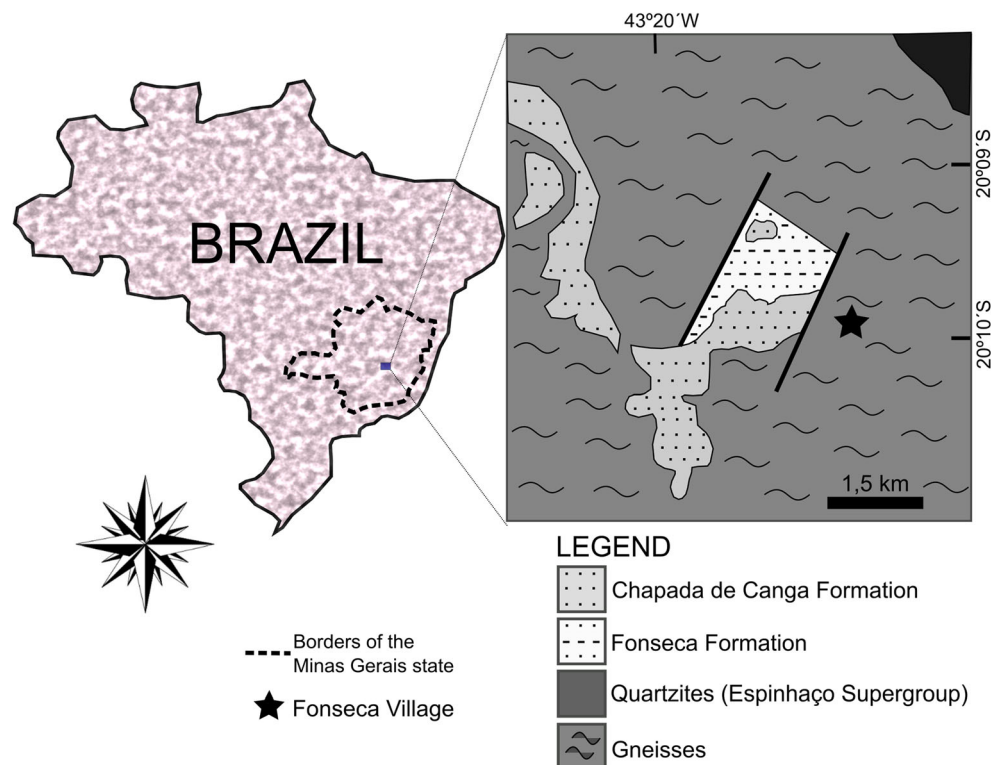
Order	Family	Species
Blattodea	Mastotermitiidae	<i>Spargotermes costalimai</i> Emerson, 1965
Blattodea	Blattidae	<i>Fonsecablatta patricioi</i> Mendes et Pinto, 2001*
Coleoptera	Apionidae?	Undetermined Costa Lima, 1944
Coleoptera	Carabidae	<i>Fonseccarabus placidus</i> Martins-Neto et Mendes, 2002
Coleoptera	Curculionidae	<i>Duartia pulchela</i> Martins-Neto, 2001
Hemiptera	Cicadidae	<i>Fonseccicada mineira</i> Martins-Neto et Mendes, 2002
Hymenoptera	Formicidae	<i>Fonsecahymen stigmata</i> Martins-Neto et Mendes, 2002
Hymenoptera	Pergidae	<i>Fonsecadalius perfectus</i> Mendes, Bezerra et Limaverde, 2015
Hymenoptera	Pergidae	<i>Fonsecadalius propinquus</i> Mendes, Bezerra et Limaverde, 2015

Geological setting

The Fonseca Formation occurs in the form of as relicts restricted to a small graben-like structure within the Precambrian basement in the eastern portion of the village of Fonseca (Fig. 1). This Cenozoic formation occupies about 2.2 km² and is located within the basin of the same name (Sant’Anna 1994). Lithologically, the Fonseca Formation comprises a sedimentary succession dominated by finer rocks, with subordinate medium to fine-grained sandstones and conglomerates (Sant’Anna and Schorscher 1997; Maizatto 2001). In the lower portion of this succession the main facies consist of clast-

supported conglomerates with subangular clasts. The medium portion is made up of coarse to medium-grained sandstones with planar cross-stratification fining up towards medium to fine-grained sandstones, with sparse granules and with horizontal stratification. The upper portion of the formation is characterized by claystones with horizontal lamination, demarcated by brownish and white intercalations and sedimentary boudinage structures. The uppermost portion of this section consist of a lignite layer rich in carbonized leaf impressions. Based on the facies association, the origin of these continental sediments was interpreted as taking place within a fluvial plain, with temporary lakes and wetlands areas,

Fig. 1 Map of Brazil showing the location and simplified geological setting of the Fonseca Formation in the south-east



probably meandering river systems, deposited upon Precambrian basement rocks (Sant’Anna et al. 1997). These Precambrian gneissic rocks are usually fractured and deformed in two main directions, one somewhat N-S and the other E-W (Sant’Anna et al. 1997).

Sommer and Lima (1967) treated Fonseca Formation as Miocene in age. However, palynological biozones of *Retibrevitricolpites triangulatus* (late Eocene) and *Dacrydiumites florinii* (early Oligocene) lowered the age to Eocene – Oligocene (Maizatto 2001; Maizatto et al. 2008).

Material and methods

The specimens were found four kilometres away from Fonseca village, Alvinópolis city, Minas Gerais State, Brazil. Fossils were collected on an outcrop alongside the Fonseca creek, a private property owned by CENIBRA – Celulose Nipo-Brasileira. Code numbers were assigned to all specimens (LP/UFC CRT 2595; LP/UFC CRT 2791; LP/UFC CRT 2792; LP/UFC CRT 2793; LP/UFC CRT 2794; LP/UFC CRT 2796 and LP/UFC CRT 2797) and are deposited in the paleontological collection of Universidade Federal do Ceará (UFC), Ceará State, Brazil. Fossils were prepared using a fine needle to remove overlying pieces of host matrix. Representative samples were preserved as carbonized impressions on the surface of fissile shales, which have a tendency to split. In order to avoid damage, a strong adhesive was added on both sides of the shale. In addition, it was necessary to isolate the fossils from atmospheric oxygen. A thin coverage of fixative varnish was added to avoid volatilization. Drawings of the specimens were made using microscope with an attached camera lucida serving as a drawing aid.

Class Insecta Linnaeus, 1758

Order Blattaria Latreille, 1810

Family Mastotermitidae Desneux, 1904

Genus Mastotermes Froggatt, 1897

Type species: *Mastotermes darwiniensis* Froggatt, 1897, p. 519, a living species, northern Australia.

Genus representatives. *Mastotermes aethiopicus*, *Mastotermes anglicus*, *Mastotermes bournemouthisensis*, *Mastotermes croaticus*, *Mastotermes darwiniensis*, *Mastotermes electrodominicus*, *Mastotermes electromexicus*, *Mastotermes gallica*, *Mastotermes haidingeri*, *Mastotermes heerii*, *Mastotermes krishnorum*, *Mastotermes minor*, *Mastotermes minutus*, *Mastotermes monostichus*, *Mastotermes nepropadyom*, *Mastotermes picardi*, *Mastotermes sarthensis*, *Mastotermes stuttgartensis*.

Stratigraphic range of the genus. Holocene of Australia; Miocene of Croatia, Dominican Republic and Ethiopia; Oligocene of France, Poland, Mexico and England; Eocene of France, Germany and England; Cretaceous of France, Russian and Myanmar.

***Mastotermes brasiliensis* sp. n.** urn:lsid:zoobank.org:pub:6635B00E-F83A-4C65-8048-AF3066182807

Diagnosis. Species (head length 1.8 mm; head width 4.0 mm; forewing 24.0 mm in length, as preserved; total length 30.0 mm). Mandible well developed with outer margin of the apical tooth curved. Pronotum arched with a long line in the middle. Forewing Sc simple, R1 simple, branching from Rs. Rs branching before M. M richly branched, initial branching near to wing base. CuA well developed, branching dichotomous. CuP weak with at least three branches joining the lower margin, branching relatively basally, first branching before first fork of CuA.

Description. Imago (Fig. 2), total length with wings 35.0 mm, without wings 24.0 mm, length of head to mandible base 3.0 mm, length of head to apex of labrum 4.3 mm, head width 4.2 mm, oval in shape. Compound eyes small, roundish, moderately convex almost touching the antennal fossa, ocelli indistinct. Anterior margin slightly depressed. Y-ecdysial cleavage present. Posterior margin of head slightly rounded and moderately convex. Dentition of mandibles preserved, right mandible with apical teeth well developed. Antenna moniliform, incomplete, second segment slightly longer than

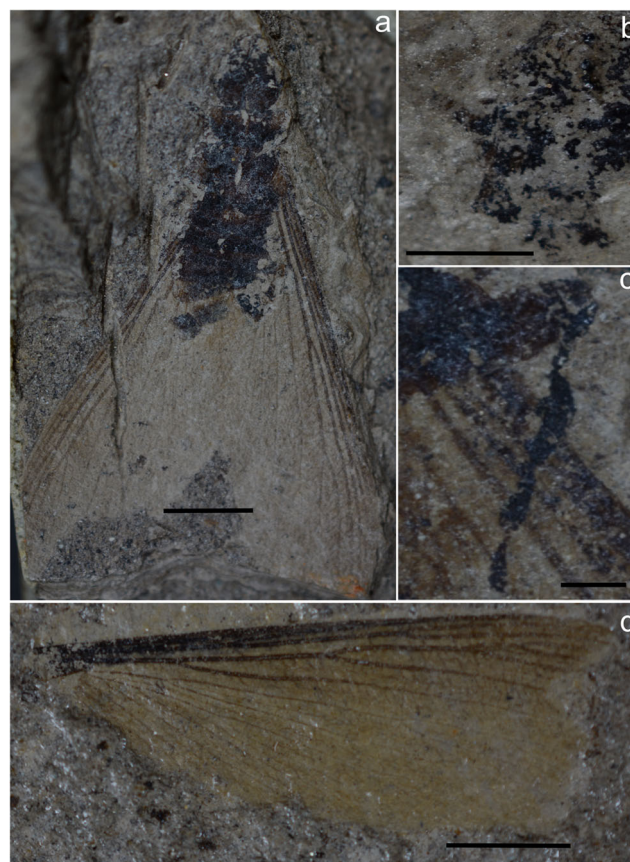


Fig. 2 Photographs of *Mastotermes brasiliensis* sp. n. **a** Specimen almost complete (holotype LP/UFC CRT 2595), scale bar = 10 mm; **b** head with antennomeres, paratype 2796, scale bar = 1 mm; **c** hind leg of paratype LP/UFC 2794, scale bar = 2 mm; **d** forewing fragment (Paratype LP/UFC CRT 2797), scale bar = 10 mm

third. Pronotum (0.9 mm in length; 3.2 mm in width) is significantly concave, arched, and wider than the head. Hind margin shorter and arched compared to front margin. Pronotum with posterior margin straight and median carina poorly visible. Thorax surface rough and slightly depressed. Abdomen incomplete with six segments preserved. Abdominal segment 6 fragmented. Protibia with at least three terminal spurs. Metatibia length 1.4 mm, basal portion of metatibia with at least three lateral spurs. Last metatarsal segment with claws. Arolium present. Humeral suture arcuate. Forewing with simple subcosta (Sc) sclerotized. First radius (R1) simple, branching from Radial sector (Rs) and joining the costal margin in anteriormost part of wing. Rs branching basally, anteriormost branch running close to and parallel with costal border, posteriormost branching twice along preserved length. Rs extending nearly to the tip of wing with three branches reaching the apex border. Media (M) branches on the first half of the wing scale, first branching slightly beyond second fork of Rs, posteriormost branch forking slightly before first fork in posterior branch of Rs. M with at least three branches reaching the outer margin of wing. Anterior Cubitus (CuA) well developed, at least four branches preserved. Posterior cubitus (CuP) with three inferior branches joining lower margin. First branching of CuP appears before the first branching of CuA. A with at least three straight branches preserved. Intercalaries and cross veins present.

Holotype. Specimen LP/UFC CRT 2595 (Fig. 3) almost completely preserved adult in dorsal view. The fossil is housed in the paleontological collection of Universidade Federal do Ceará, Ceará State, Brazil.

Locality and horizon. Papyraceous shale, Fonseca Formation, four kilometres from Fonseca village, on the bank of the Fonseca creek (20°09'–20°10'S/43°15'–43°20'W), Minas Gerais State, Brazil, late Eocene – early Oligocene.

Character of preservation. Six additional specimens were also identified as *M. brasiliensis*. Paratypes: LP/UFC CRT 2796 preserved in dorsal view (Fig. 2b); LP/UFC CRT 2794 preserved in ventral view; LP/UFC CRT 2793 (Fig. 2c) partially preserved without abdomen; LP/UFC CRT 2797 (Fig. 2d) forewing fragment, length of preserved portion 25.5 mm, most of veins clearly visible; LP/UFC CRT 2792 incomplete specimen, missing head; and LP/UFC CRT 2791 almost complete specimen.

Derivation of name. The specific epithet refers to the origin of the fossil. The name *brasiliensis* means fossil from Brazil (Latin).

Differential diagnosis. *Mastotermes brasiliensis* sp. n. is placed within the genus *Mastotermes* on the basis of numerous characters such as overall body size, antennal fossa almost touching eyes, Y-shaped cleavage line, large pronotum, anterior margin of pronotum broad and concave, large forewing scale, forewing venation, arcuate humeral suture, broad costal area, veins Sc, R, Rs and M more heavily sclerotized than

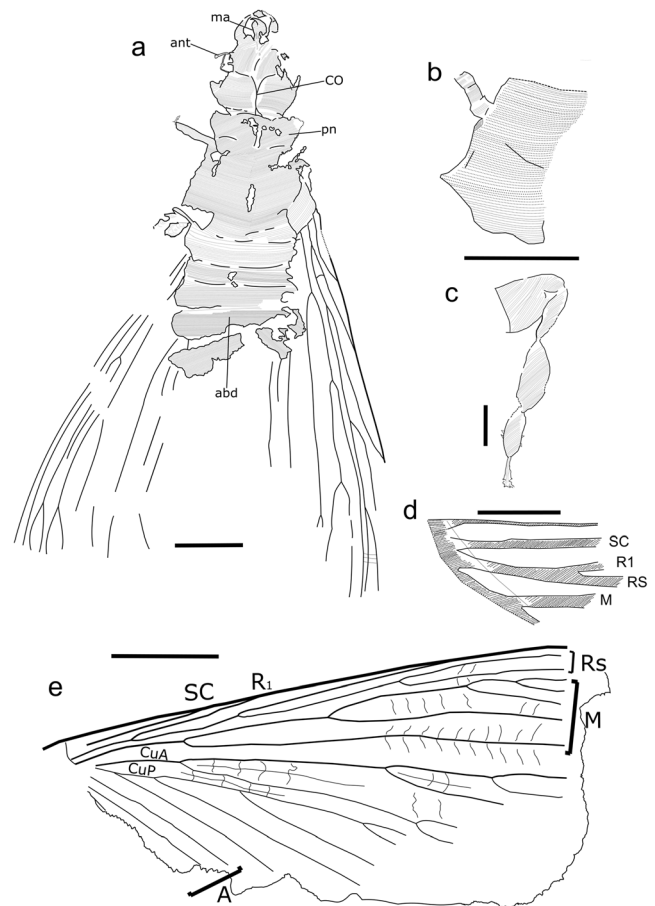


Fig. 3 Camera lucida drawings of *Mastotermes brasiliensis* sp. n. **a** Holotype specimen (LP/UFC CRT 2595), scale bar = 10 mm; **b** head with basal antennomeres, paratype 2796, scale bar = 1 mm; **c** basal part of forewing (holotype) with humeral suture, scale bar = 1 mm; **d** hind leg of the paratype LP/UFC 2794, scale bar = 2 mm; **e** paratype forewing fragment (LP/UFC CRT 2797), scale bar = 10 mm. Abbreviations: abd (abdomen), ant (antenna), co (coronal line), pn (pronotum), ma (mandible), A (anal), CuA (anterior cubitus), CuP (posterior cubitus), M (media), R1 (first radius), Rs (radial sector), SC (subcosta)

CuA. *Mastotermes brasiliensis* adds to the diversity of this genus and offers us a chance to compare it with the only living extant species. For example, *M. brasiliensis* shares many characters with *M. darwiniensis* such as a slightly depressed head, similar forewing size, arched pronotum, wider than head and with a medial line. *Mastotermes brasiliensis* head is similar in width to that of *M. electromexicus* but wider than that of *M. darwiniensis*. Mandible with outer margin less sharply curved than in *M. darwiniensis*. Pronotum is more narrow than that of *M. krishnorum*. Wing venation is reduced as in *M. nepropadyom*, *M. anglicus* and *M. minutus*. In *M. brasiliensis* the first branching of Rs is before that of M as opposed to *M. electrodominicus* where it is after. In *M. brasiliensis*, Rs is somewhat reticulated as in *M. nepropadyom* and *M. croaticus*. The Brazilian species can be distinguished from *M. gallica* by the more developed Rs system. *Mastotermes monostichus* can be easily

distinguished from *M. brasiliensis* by Rs containing five main branches. RS is more simplified in *M. brasiliensis* than in *M. sarthensis* and *M. bournemouthisensis*. From M the new species resembles *M. aethiopicus*, *M. gallica*, *M. monostichus* and *M. picardi* by branching near to the wing base. M system is lesser extensively branched in *M. minor* than in *M. brasiliensis*. The posteriormost branch of M in *M. haidingeri* is simple, while posterior branch of M is clearly branched in *M. brasiliensis*. *Mastotermes brasiliensis* can be distinguished from *M. picardi* by the more simplified medial system. CuP in the new species has four branches at least, while *M. eletrodominicus* it is short and reduced. Like *M. brasiliensis*, the contemporary *S. costalimai* lacks a convex humeral margin on the wing scale. In contrast to *M. brasiliensis*, *S. costalimai* has a straight costal border extending three-fourths of the wing length and is not thickened. The veins starting at the humeral suture include a short first radius, a short second and third radius branching into separate veins as they reach the costal border, a diffuse radial sector and a CuA with several straight branches not curved inward. The presence of intercalaries and cross-veins evidence that the *M. brasiliensis* flew for a prolonged period (Dirks and Taylor 2012; Vršanský and Aristov 2014). Another remarkable and intriguing feature of *M. brasiliensis* is the absence of wing vein deformities. According to Vršanský (2005), the insect wing deformities indicate the occurrence of significant mass mutations, which apparently appear in response to environmental changes.

Discussion

Discovery of *M. brasiliensis* is proof that the paleoentomological potential of the Fonseca Basin has been little explored to date. In fact, only a small number of insect species have been described in this unit (Table 2). The Fonseca paleontomofauna contains representatives of Coleoptera, Blattodea, Homoptera and Hymenoptera. The ecological implications of these insect groups point to an extremely dynamic environment. For example, Carabidae Latreille, 1802 were predators in both adult and larval stage; Blattidae were omnivorous and inhabited dimly lit places; the families Cicadidae Westwood, 1840 and Curculionidae Latreille, 1802 were phytophagous; Formicidae Latreille, 1809 probably fed on nectar (Fanton et al. 2014). The presence of Mastotermitidae (*S. costalimai* and *M. brasiliensis* sp.n.) suggests availability of wooden resources. Fossil assemblage from the Fonseca formation points to a humid tropical forest dominated by angiosperms and ground densely covered by wood/leaf litter, serving as shelter and food for many insects. Like other Paleogene floras, Fonseca paleoflora points to higher temperatures than those recorded today, at equivalent latitudes (Fanton et al. 2014). Past climatic shifts provide

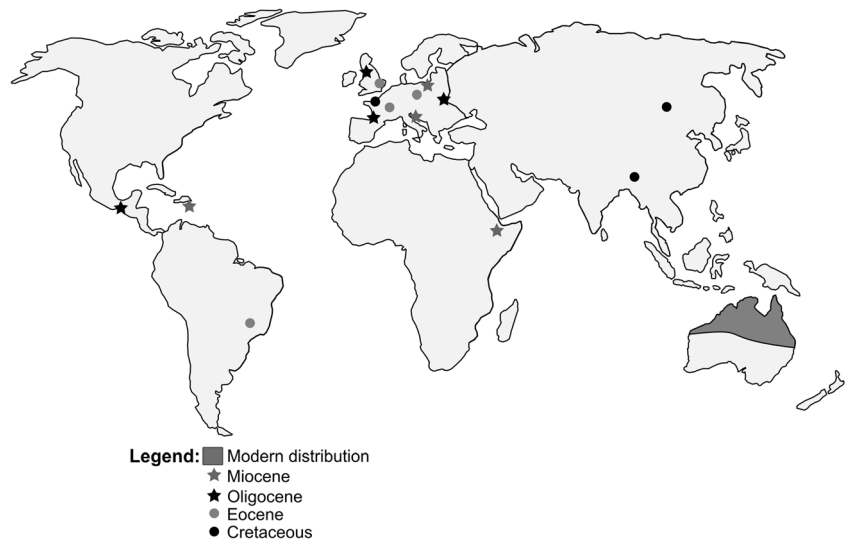
additional insight into the redistribution of the termites. Assuming temperature alone to be a strong driver of termite geographic distribution, we could conclude that general cooling of previous habitats, throughout the Cenozoic, could have contributed to the decline of Mastotermitidae, particularly *Mastotermes*.

Palaeoclimatical and palaeobiogeographical implications from *Mastotermes*

Mastotermitids extend from Cretaceous to the present. The only extant species of *Mastotermes* is restricted exclusively to northern Australia. In contrast, its fossil record is abundant (Fig. 4), with fossil representatives found on all continents (except Antarctica), occurring mainly in the Palearctic ecozone. They are also recorded in others terrestrial ecozones such as Neotropic, Afrotropic and Australasia. The oldest mastotermitid was recovered from Cretaceous age (near 127 Ma) deposits of Chernovskie Kopi, eastern Transbaikalia (Vršanský and Aristov 2014; Vršanský et al. 2017, 2019). This locality is characterized by a complex rhythmical association of volcanic-sedimentary rocks, with lakes that were periodically covered by volcanic ash (Stupak et al. 2018). Reconstructed palaeoenvironment consisted of high-mountain, caldera lakes characterized by punctuated populations and surrounding vegetation consisting mostly of horsetails.

Cretaceous paleoflora from this area was similar to that of the Siberian-Canadian realm with warm moderate climate, enriched by subtropical elements from the Euro-Sinian realm (Kirillova et al. 2000). *Mastotermes* was also recorded from Cretaceous (Cenomanian) amber of France and Myanmar (Schlüter 1989; Zhao et al. 2019). Later part of Mesozoic is a crucial period in termite evolution. It has long been understood that all termites derived from Blattaria, especially *Cryptocercus* wood roaches (Inward et al. 2007; Engel et al. 2009; Wang et al. 2017). Nonetheless, Vršanský et al. (2019) suggested *Cryptocercus* as a true termite. According to Vršanský et al. (2019), the discovery of Pabuonqedidae confirms this relationship and indicates an explosive termite radiation from a transitional form. *Mastotermes* and *Cryptocercus* have an intimate relationship (see Courrent et al. 2018). This would make termites the oldest group of eusocial animals (Engel et al. 2009; Vršanský 2010). According to Zhao et al. (2019), the scarce occurrence of *Mastotermes* in the Cretaceous is possibly due to taphonomic bias. The large size of the body and strongly sclerotized wings facilitated their escape from the resin flow. Therefore, it is likely that few *Mastotermes* were trapped and preserved within amber inclusions. In contrast, the close relationship between *Mastotermes* and *Cratomastotermes* and the occurrence of the later in the Aptian of Brazil points to a higher abundance of mastotermitids in the Cretaceous.

Fig. 4 World map showing distribution of modern and fossil *Mastotermites*. Dark gray area indicates distribution of extant *Mastotermites*. The icons correspond to fossils and the shades of gray represent different ages. All occurrences shown here are listed in Table 1



Mastotermitids occur almost exclusively in Europe during the Cenozoic (exceptions are: *M. electromexicus* and *M. electrodominicus* from the Late Oligocene – Early Miocene Mexican and Dominican ambers; *M. aethiopicus*, early Miocene of Ethiopia; and the new fossil described here from Eocene-Oligocene of Brazil). The beginning of Paleogene was marked by global warming period which high temperatures, creating mild and humid environments (Pearson et al. 2001) and in turn causing tropical forests to spread across Europe. *Mastotermites minutus* from Early Eocene Oise amber of France, lived in an arborescent subtropical forest characterized by hot climate with a wet season (De Franceschi and De Ploëg 2003). *Mastotermites bournemouthisensis* from the upper Eocene of Hampshire, England, survived a rhythmic alternation of wetter-drier climatic periods. Mean annual temperature in the Eckfeld Maar (middle Eocene fossil locality in central Europe where *M. krishnorum* was described) was ca. 22 °C based on the macrobotanical record (Wappler et al. 2012).

Mastotermites was present on the Central American continent in the late Oligocene – middle Miocene. *M. electromexicus* and *M. electrodominicus* belong to Mexican and Dominican ambers, respectively. The Dominican amber forest has already been characterized as a lowland, interior Neotropical rainforest (Grimaldi 1996) and Mexican amber forest as a lowland forest in close vicinity to coastal mangrove forests (Solórzano Kraemer 2007).

The foliar physiognomy and floristic composition of Fonseca paleoflora indicate that its mean annual temperature (MAT) was <26 °C (Fanton et al. 2014). This area has generally been attributed to lowlands during the Paleogene. Today, the region exhibits uneven relief where the MAT is >20 °C. As with other species of *Mastotermites*, the environment in which *M. brasiliensis* sp. n. lived might have been warmer in the past. The hypothesis that the *Mastotermites* (or even the whole Mastotermitidae family) is an indicator of warm climate is reinforced by one recent species constricted to the warm

climate of Australia north of tropic of Capricorn. The absence of *Mastotermites* from temperate faunas (e.g., Florissant shale, Colorado) was also noticed (Emerson 1965). However, they are recorded from outcrops throughout all the European Cenozoic, indicating a fauna that lived in a more temperate climate, such as *M. anglicus* (Oligocene, Isle of Wight, England). *Mastotermites haidingeri* and *M. croaticus* were recorded from Radoboj shale (Croatia) in association with other taxa (e.g., *Reticulitermes*), which are indicators of essentially temperate climate. Nel (1997), based on probabilistic phylogenetic inferences, suggested that Cenozoic *Mastotermites* are less sensitive temperature indicators than other insects. This genus is well documented from Paleogene faunas of Europe, but its absence in the Baltic amber fauna has always been considered enigmatic. One other genus, *Garmitermes*, closely related to *Mastotermites*, was recorded from Baltic amber (Engel et al. 2007).

Geographical distribution along with primitive structures and venation of wings might suggest that the mastotermitids originated in Eurasia (where they occur commonly in Mesozoic-Paleogene strata) during middle Mesozoic (Bourguignon et al. 2015). Both fragmentary fossil record and phylogenetic inferences are inconclusive in precisely determining the time and origin of this genus. However, the northern occurrences indicate dispersal from Northern to Southern Hemisphere (Bourguignon et al. 2015). The presence of *M. brasiliensis* in Brazil during Late Eocene would indicate that *Mastotermites* was already established in South America prior to its Miocene occurrence in Mexico and the Dominican Republic. The presence of *Cratomastotermites* in Gondwana already in Lower Cretaceous supports this hypothesis. Newest geographic range of known Paleogene *Mastotermites* fossils includes Europe and South America, indicating a broad distribution prior to the breakup of Pangaea as well as and both temperate and tropical habitats.

Extant *Mastotermes* is restricted to the Southern Hemisphere while its fossils are common throughout Cenozoic of Europe and other parts of Northern Hemisphere. This shortage of fossils from the Southern Hemisphere occurs also in other insect groups. Temperature requirements of these termites correspond with reconstructed Paleogene climate conditions based on macrobotanical record. Increasingly warm climate during lower to middle Paleogene probably influenced the widespread distribution of *Mastotermes*. However, during Oligocene the earth's climate began shifting towards cooler temperatures due to Antarctic glaciation. Tropical plant diversity declined during the Eocene-Oligocene boundary in South America (Jaramillo et al. 2006; Woodburne et al. 2013). Presence of Ephedraceae in the Fonseca strata is most likely an indicator of dry climates. In addition, sedimentary record of the Fonseca Basin does not provide clues or evidence for dry climatic scenarios. Likewise, there is no clear evidence for dry environments from sedimentary record of the Bonfim Basin (São Paulo State) (Garcia et al. 2016). The transition from late Eocene to Oligocene of Itaquaquecetuba Formation (São Paulo Basin), Oligocene of Tremembé Formation (Taubaté Basin) and occurrence of *Podocarpidites* and *Dacrydiumites* in great abundances (Lima et al. 1985; Santos et al. 2010) suggests cooler phases. South, in Alexandra Formation, the presence of arkose sediments supports dry climate scenarios. On the other hand, the presence of a fossil termite nest, *Tacuruichnus farinai* from Barranca de Los Lobos Formation, late Pliocene of Argentina is congruent with the warm and wet conditions (Genise 1997). Thus, we interpret that late Oligocene to Miocene climate had some drier phases but was overall cooler compared to Eocene of southeastern Brazil. Paleobotanical record of South America seemingly responded in accordance with the global climate pattern during Cenozoic.

The extant distribution of *M. darwiniensis* could give us answers about ecological requirements of the fossil species. During II World War, *M. darwiniensis* was introduced into New Guinea, where annual rainfall is higher than Australia. According to Evans et al. (2013), *Mastotermes* is able to survive in more humid climates, but without thriving. In other words, the extinct species of *Mastotermes* were possibly better capable of populating more wet environments. Preference of *M. darwiniensis* for drier environments may be an adaptation acquired during a dramatically cooling-drying event in the Miocene-Pliocene. Except for *M. darwiniensis*, the *Mastotermes* extinction can probably be dated from late Miocene and early Pliocene. This period corresponds to important cooling alongside rising continental land masses (Zachos et al. 2001). At this time other termites, especially Termitidae, were undergoing widely successful radiation in Africa and South America. Finally, the inability to adapt to an increasingly colder climate, and possibly a concomitant

change in competitive pressures influenced extinction of *Mastotermes* species around the world.

Acknowledgments This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Finance Code 001. FIB is grateful for your doctorate scholarship (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, Brasil - CAPES, process 88882.454892/2019-01). ODS is supported by a Fellowship from the Brazilian National Council for Scientific and Technological Development (CNPq, process 307990/2017-6).

Author's contributions FIB designed research, analyzed data and wrote the manuscript; MM made substantial contributions to the conception or design of the work, interpreted the data, contributed to writing the manuscript; ODS revised the work, approved the version to be published critically for important intellectual content, approved the version to be published.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval Ethical standards were adhered to in this study and in the production of this manuscript.

References

- Abe T, Bignell DE, Higashi M (2000) Termites: evolution, sociality, symbiosis, ecology. Springer, Dordrecht
- Baccetti B (1987) Spermatozoa and phylogeny in orthopteroid insects. In: Baccetti BM (ed), Evolutionary biology of orthopteroid insects, John Wiley & Sons, Chichester, pp 12–112
- Bell WJ, Roth LM, Nalepa CA (2007) Cockroaches: ecology, behaviour and natural history. The Johns Hopkins University Press, Baltimore
- Berry EW (1935) Tertiary plants from Brazil. Proc Am Philos Soc 75: 565–590
- Bignell DE, Roisin Y, Lo N (2011) Biology of termites: a modern synthesis. Springer, Dordrecht
- Bourguignon T, Lo N, Cameron SL, Šobotnik J, Yoshinobu Hayashi Y, Shigenobu S, Watanabe D, Roisin Y, Miura T, Evans TA (2015) The evolutionary history of termites as inferred from 66 mitochondrial genomes. Mol Biol Evol 32(2):406–421. <https://doi.org/10.1093/molbev/msu308>
- Burnham RJ, Johnson KR (2004) South American palaeobotany and the origins of neotropical rainforests. Philos Trans R Soc Lond Ser B Biol Sci 359:1595–1610. <https://doi.org/10.1098/rstb.2004.1531>
- Courrent A, Quenedey A, Nalepa CA, Robert A, Lenz M, Bor-dereau C (2018) The fine structure of collateral glands in two cock-roaches and three termites, including a detailed study of *Cryptocercus punctulatus* (Blattaria, Cryptocercidae) and *Mastotermes darwiniensis* (Isoptera, Mastotermitidae). Arthropod Struct Dev 37:55–66. <https://doi.org/10.1016/j.asd.2007.03.004>
- De Franceschi D, De Ploëg G (2003) Origine de l'ambre des faciès sparnaciens (Eocène inférieur) du bassin de Paris: le bois de l'arbre producteur. Geodiversitas 25:663–647
- Dirks JH, Taylor D (2012) Veins improve fracture toughness of insect wings. PLoS One 7(8):e43411. <https://doi.org/10.1371/journal.pone.0171111>
- Doliani E (1949) Contribuição a flora pliocênica de Fonseca, Minas Gerais. An Acad Bras Ciênc 21:239–244

- Donovan SE, Jones DT, Sands WA, Eggleton P (2000) Morphological phylogenetics of termites (Isoptera). *Biol J Linn Soc* 70:467–513. <https://doi.org/10.1111/j.1095-8312.2000.tb01235.x>
- Duarte L (1956) Melastomataceae fósseis da bacia terciária de Fonseca, MG. *Boletim da Divisão de Geologia e Mineralogia DNPM-Rio de Janeiro* 161:7–32
- Duarte L (1958) Annonaceae fósseis da bacia terciária de Fonseca, MG. *Boletim da Divisão de Geologia e Mineralogia DNPM-Rio de Janeiro* 178:7–33
- Emerson AE (1942) The relations of a relict south African termite (Isoptera, Hodotermitidae, Stolotermes). *Am Mus Novit* 1187:1–12
- Emerson AE (1965) A review of the Mastotermitidae (Isoptera), including a new fossil genus from Brazil. *Am Mus Novit* 2236:1–46
- Engel MS, Delclòs X (2010) Primitive termites in cretaceous Amber from Spain and Canada (Isoptera). *J Kansas Entomol Soc* 83(2):111–128. <https://doi.org/10.2317/JKES0908.06.1>
- Engel MS, Grimaldi DA, Krishna K (2007) A synopsis of Baltic amber termites (Isoptera). *Stuttg Beitr Naturk B* 372:1–20
- Engel MS, Grimaldi DA, Krishna K (2009) Termites (Isoptera): their phylogeny, classification, and rise to ecological dominance. *Am Mus Novit* 3659:1–27. <https://doi.org/10.1206/651.1>
- Engel MS, Barden P, Riccio ML, Grimaldi DA (2016) Morphologically specialized termite castes and advanced sociality in the early cretaceous. *Curr Biol* 26:522–530. <https://doi.org/10.1016/j.cub.2015.12.061>
- Evans TA, Forschler BT, Grace JK (2013) Biology of invasive termites: a worldwide review. *Annu Rev Entomol* 58:455–474. <https://doi.org/10.1146/annurev-ento-120811-153554>
- Fanton JC, Ricardi-Branco F, Mendes M (2014) As paleofloras de Fonseca e Gandarela revisadas e insetos associados: Paleógeno do Sudeste brasileiro. In: Carvalho IS, Gárcia MJ, Lana CC, Strohschoen O (eds) *Paleontologia: Cenários de vida – Paleoclima*. Interciência, Rio de Janeiro, pp 241–253
- Froggatt WW (1897) Australian Termitidae, Part II. *Proc Linn Soc New South Wales* 21:510–552
- Garcia MJ, Premaor E, Deoliveira PE, Bernardes-de-Oliveira MEC, Rodolfo D, Antonioli L, De Menezes JB (2016) Cenozoic distribution of *Ephedripites* Bolkhovitina (1953) ex Potonié (1958) emend. Krutzsch (1961) in Brazil. *Grana* 55:52–70. <https://doi.org/10.1080/00173134.2015.1119882>
- Genise JF (1997) A fossil termite nest from the Marplatense stage (late Pliocene) of Argentina: palaeoclimatic indicator. *Palaeogeogr Palaeoclimatol Palaeoecol* 136:139–144. [https://doi.org/10.1016/S0031-0182\(97\)00077-1](https://doi.org/10.1016/S0031-0182(97)00077-1)
- Gorceix H (1884) Bacia terciária d'água doce nos arredores de Ouro Preto (Gandarela e Fonseca), Minas Gerais, Brasil. *Anais da Escola de Minas* 3:75–92
- Grimaldi DA (1996) *Amber: window to the past*. Harry N. Abrams, New York
- Inward DJ, Beccaloni G, Eggleton P (2007) Death of an order: a comprehensive molecular phylogenetic study confirms that termites are eusocial cockroaches. *Biol Lett* 3(3):331–335. <https://doi.org/10.1098/rsbl.2007.0102>
- Jaramillo CA, Rueda MJ, Mora G (2006) Cenozoic plant diversity in the Neotropics. *Science* 311:1893–1896. <https://doi.org/10.1126/science.1121380>
- Kambhampati S, Kjer KM, Thorne BL (1996) Phylogenetic relationship among termite families based on DNA sequence of mitochondrial 16S rRNA gene. *Insect Mol Biol* 5:229–238. <https://doi.org/10.1111/j.1365-2583.1996.tb00097.x>
- Kirillova GL, Markevitch VS, Belyi VF (2000) Cretaceous environmental changes of East Russia. *Dev Palaeontol Stratigr* 17:1–47. [https://doi.org/10.1016/S0920-5446\(00\)80023-0](https://doi.org/10.1016/S0920-5446(00)80023-0)
- Lima MR, Salard-Cheboldaeff M, Suguio K (1985) Étude palynologique de la Formation Tremembé, Tertiaire du Bassin de Taubaté (état de São Paulo, Brésil), d'après les échantillons du sondagen. 42 du CNP. Coletânea de Trabalhos Paleontológicos, Série Geologia, Seção de Paleontologia e Estratigrafia 2:379–393
- Maekawa K, Matsumoto T, Nalepa CA (2008) Social biology of the wood-feeding cockroach genus *Salganea* (Dictyoptera:Blaberidae: Panesthiinae): did ovoviviparity prevent the evolution of eusociality in the lineage? *Insect Soc* 55:107–114. <https://doi.org/10.1007/s00040-008-0997-2>
- Maizatto JR (2001) Análise bioestratigráfica, paleoecológica e sedimentológica das bacias terciárias de Gandarela e Fonseca, Quadrilátero Ferrífero, Minas Gerais, com base nos aspectos palinológicos e sedimentares. Dissertation, Universidade Federal de Ouro Preto
- Maizatto JR, Regali MSP, Castro PTA (2008) Análise bioestratigráfica e paleoclimática das bacias paleógenas e neógenas do Gandarela e Fonseca- Quadrilátero Ferrífero- Minas Gerais, Brasil: 12º Simposio Brasileiro de Paleobotânica e Palinologia, Florianópolis, Boletim de Resumos 1:133
- Martins Neto RG (2005) Estágio atual da paleoartropodologia brasileira: hexápodes, miriápodes, crustáceos (Isopoda, Decapoda, Eucrustacea e Copepoda) e quelicerados. *Arquivos do Museu Nacional* 63:471–494
- Mckittrick FA (1965) A contribution to the understanding of cockroach-termites affinities. *Ann Entomol Soc Am* 58:18–22. <https://doi.org/10.1093/aesa/58.1.18>
- Mendes M, Pinto ID (2001) The first findings of Blattodea (Insecta, Blattellidae) from the Fonseca formation, Oligocene period, Minas Gerais, in the south east of Brazil. *Acta Geol Leopold* 24:283–290
- Nalepa CA, Bandi C (2000) Characterizing the ancestors: paedomorphosis and termite evolution. In: Abe T, Bignell DE, Higashi M (eds) *Termites: evolution, sociality, symbiosis, ecology*, 1st edn. Springer, Dordrecht, pp 53–75
- Nalepa CA, Lenz M (2000) The oötheca of *Mastotermes darwiniensis* Froggatt (Isoptera: Mastotermitidae): homology with cockroaches. *Proc R Soc Lond Ser B* 267:1809–1813. <https://doi.org/10.1098/rspb.2000.1214>
- Nel A (1997) The probabilistic inference of unknown data in phylogenetic analysis. In: Gracolas P (ed) *The origin of biodiversity in insects: phylogenetic tests of evolutionary scenarios* (Memoires du Museum National d'Histoire Naturelle), Éditions du Muséum, Paris, pp 305–327
- Oliveira-e-Silva MIMN (1982) Flórua da Bacia de Fonseca, Minas Gerais, Brasil. Dissertation, Universidade Federal do Rio de Janeiro
- Pearson PN, Ditchfield PW, Singano J, Harcourt-Brown KG, Nicholas CJ, Olsson RK, Shackleton NJ, Hall MA (2001) Warm tropical sea surface temperatures in the late cretaceous and Eocene epochs. *Nature* 413:481–487. <https://doi.org/10.1038/35097000>
- Ponomarenko AG (1988) New Mesozoic insects. *Trudy, Sovmestnaya Sovetsko-Mongol 'Skaya Paleontologicheskaya Ekspeditsiya* 33: 71–80
- Sacchi L, Nalepa CA, Lenz M, Bandi C, Corona S, Grigolo A, Bigliardi E (2000) Transovarial transmission of symbiotic bacteria in *Mastotermes darwiniensis* (Isoptera: Mastotermitidae): Ultrastructural aspects and phylogenetic implications. *Ann Entomol Soc Am* 93:1308–1313. [https://doi.org/10.1603/0013-8746\(2000\)093\[1308:TTOSBJ\]2.0.CO;2](https://doi.org/10.1603/0013-8746(2000)093[1308:TTOSBJ]2.0.CO;2)
- Sant'Anna, LG (1994) Mineralogia das argilas e evolução geológica da Bacia de Fonseca, Minas Gerais. Dissertation, Universidade de São Paulo
- Sant'Anna LG, Schorscher HD (1997) Estratigrafia e mineralogia dos depósitos cenozóicos da região da Bacia de Fonseca, Estado de Minas Gerais. *An Acad Bras Ciênc* 69:211–226
- Sant'Anna LG, Schorscher HD, Riccomini C (1997) Cenozoic tectonics of the Fonseca Basin region, eastern Quadrilátero Ferrífero, MG, Brazil. *J S Am Earth Sci* 10:275–284. [https://doi.org/10.1016/S0895-9811\(97\)00016-3](https://doi.org/10.1016/S0895-9811(97)00016-3)

- Santos DB, Garcia MJ, Saad AR, Bistrichi CA (2010) Palinoestratigrafia da Formação Itaquaquecetuba, Bacia de São Paulo, Brasil. *Rev Bras Paleontol* 13:205–220. <https://doi.org/10.4072/rbp.2010.3.05>
- Schlüter T (1989) Neue Daten über harzkonservierte Arthropoden aus dem Cenomanium NW-Frankreichs. *Doc Nat* 56:59–70
- Solórzano Kraemer MM (2007) Systematic, palaeoecology, and palaeobiogeography of the insect fauna from Mexican amber. *Palaeontogr Abt A* 282:1–133. <https://doi.org/10.1127/pala/282/2007/1>
- Sommer FW, Lima CD (1967) Contribuição a paleoflora de Fonseca, Minas Gerais. *An Acad Bras Ciênc* 39:537–538
- Stupak FM, Kudryashova EA, Lebedev VA, Gol'tsman YV (2018) The structure, composition, and conditions of generation for the early cretaceous Mongolia–east-Transbaikalia volcanic belt: the Durulgui–Torei area (southern Transbaikalia, Russia). *J Volcanol Seismol* 12(1):34–46. <https://doi.org/10.1134/S0742046318010074>
- Vršanský P (2002) Origin and the early evolution of mantises. *Amba Projekty* 6:1–16
- Vršanský P (2005) Mass mutations of insects at the Jurassic/cretaceous boundary? *Geol Carpath* 56:473–481
- Vršanský P (2010) Cockroach as the earliest eusocial animal. *Acta Geol Sin* 84:793–808. <https://doi.org/10.1111/j.1755-6724.2010.00261.x>
- Vršanský P, Aristov D (2014) Termites (Isoptera) from the Jurassic/cretaceous boundary: evidence for the longevity of their earliest genera. *Eur J Entomol* 111:137–141. <https://doi.org/10.14411/eje.2014.014>
- Vršanský P, Vishniakova VN, Rasnitsyn AP (2002) Order Blattida Latreille, 1810. The cockroaches. In: Rasnitsyn AP, Quicke DLJ (eds) *History of insects*. Kluwer Academic Publisher, Dordrecht, pp 263–271
- Vršanský P, Oružinský R, Aristov D, Wei DD, Vidlička L, Ren D (2017) Temporary deleterious mass mutations relate to originations of cockroach families. *Biologia* 72(8):886–912. <https://doi.org/10.1515/biolog-2017-0096>
- Vršanský P, Koubova I, Vršanská L, Hinkelman J, Kudela M, Kudelova T, Liang J-H, Xia F, Lei XJ, Ren XY, Vidlička L, Bao T, Ellenberger S, Šmidová L, Barclay M (2019) Early wood-boring ‘mole roach’ reveals eusociality “missing ring”. *Amba Projekty* 9(1):1–28
- Wang Z, Shi Y, Qiu Z, Che Y, Lo N (2017) Reconstructing the phylogeny of Blattodea: robust support for interfamilial relationships and major clades. *Sci Rep* 7:3093. <https://doi.org/10.1038/s41598-017-04243-1>
- Wappler T, Engel MS (2006) A new record of *Mastoterms* from the Eocene of Germany (Isoptera: Mastotermitidae). *J Paleontol* 80:380–385. [https://doi.org/10.1666/0022-3360\(2006\)080\[0380:ANROMF\]2.0.CO;2](https://doi.org/10.1666/0022-3360(2006)080[0380:ANROMF]2.0.CO;2)
- Wappler T, Labandeira CC, Rust J, Frankenhäuser H, Wilde V (2012) Testing for the effects and consequences of mid Paleogene climate change on insect herbivory. *PLoS One* 7:e40744. <https://doi.org/10.1371/journal.pone.0040744>
- Watson JAL, Gay FJ (1991) Isoptera (termites). In: CSIRO (ed) *The insects of Australia*. 2nd edn. Melbourne University Press, Carlton, pp 330–347
- Wood TG, Sands WA (1978) The role of termites in ecosystems. In: Brain MV (ed) *Production ecology of ants and termites*. University Press, Cambridge, pp 245–292
- Woodburne MO, Goin FJ, Bond M, Carlini AA, Gelfo JN, López GM, Iglesias A, Zimicz NA (2013) Paleogene land mammal faunas of South America; a response to global climatic changes and indigenous floral diversity. *J Mamm Evol* 21(1):1–73. <https://doi.org/10.1007/s10914-012-9222-1>
- Zachos J, Pagani M, Sloan L, Thomas E, Billups K (2001) Trends, rhythms and aberrations in global climate 65 ma to present. *Science* 292:686–693. <https://doi.org/10.1126/science.1059412>
- Zhao Z, Leggleton P, Chuyin X, Gao T, Shih C, Ren D (2019) The oldest known mastotermitids (Blattodea: Termitoidea) and phylogeny of basal termites. *Syst Entomol* 44:612–623. <https://doi.org/10.1111/syen.12344>

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.