



A new primitive termite (Isoptera) from the Crato Formation, Araripe Basin, Early Cretaceous of South America

Francisco Irineudo Bezerra^{a,*}, Og DeSouza^b, Guilherme Cunha Ribeiro^c, Márcio Mendes^a

^a Departamento de Geologia - Universidade Federal do Ceará, Fortaleza, Ceará, Brazil

^b Departamento de Entomologia, Universidade Federal de Viçosa, Viçosa, Minas Gerais, Brazil

^c Centro de Ciências Naturais e Humanas, Universidade Federal do ABC, Santo André, São Paulo, Brazil

ARTICLE INFO

Keywords:

Fossil insect
Euisoptera
Meiatermes
Group santana
Aptian
Brazil

ABSTRACT

Meiatermes cretacicus n. sp., an alate termite from the Early Cretaceous Crato Formation, Araripe Basin, north-eastern Brazil. The new taxon is similar in many characteristics to other termites from the Araripe Basin, and primitive termites from Spanish amber. The rounded head and pronotum, Y-shaped line, veins Sc, R, Rs and M more heavily sclerotized than CuA, multiple Rs branches, and CuA well-developed are features shared with the basal-most termites belonging to the *Meiatermes*-grade. The Mesozoic record of the Araripe Basin includes six species of termites. Therefore, each discovery of a fossil termite is of high interest, giving new insight into their early evolutionary history and diversity during the Cretaceous of the South America.

1. Introduction

Termites are members of a monophyletic lineage within the order Blattaria (Inward et al., 2007; Engel et al., 2009; Krishna et al., 2013). All the species of the Infraorder Isoptera are highly eusocial (Krishna et al., 2013), living in colonies in which the roles of the individuals are defined by a system of castes that include workers, soldiers, and winged reproductives. Termites are ecologically significant recyclers of organic matter in temperate and tropical ecosystems (Grimaldi and Engel, 2005), where they are particularly abundant in terms of biomass (Eggleton et al., 1996). In these environments, termites play an essential ecological role in the decomposition of extremely abundant, but highly resistant lignocellulose (DeSouza et al., 2009). The success of termites is in part due to their ability to digest poor nutritional lignocellulose but also by the ability to influence their habitat, modifying soil chemical and plant growth rates (Jouquet et al., 2006; Bourguignon et al., 2017; Engel, 2019), often causing damage to human structures (Su and Scheffrahn, 2000).

Termite evolution is one of the most fascinating subjects in entomology, and has attracted the attention of recent studies (Inward et al., 2007; Engel et al., 2009; Buček et al., 2019). The precise timing of the appearance of termites is not well understood, although fossil records do provide a glimpse into their subsequent diversification in the Cretaceous. Vrsanský et al. (2017) provided the appearance time at around

127 Ma (Early Cretaceous). The first undisputed termites evolved from cockroaches, probably derived from Liberiblattinidae (Vrsanský, 2002, 2010; Inward et al., 2007; Engel et al., 2009, 2016; Lo et al., 2000; Vrsanský et al., 2019a,b; Li et al., 2020; Sendi et al., 2020) and eusociality was already present in the Early Cretaceous (Thorne et al., 2000; Engel et al., 2016).

The first Cretaceous termite was described in Labrador's Late Cretaceous (Emerson, 1967). This was followed by the description of four more species from Europe (Jarzembowski, 1981; Lacasa-Ruiz and Martínez-Delclòs, 1986; Schlüter, 1989) and Asia (Ponomarenko, 1988). Later, seven species were described from the Early Cretaceous of China (Ren, 1995) and one in North America (Krishna and Grimaldi, 2000). After the 2000s, the Cretaceous termite record increased considerably, mainly due to discoveries in the amber-bearing deposits of Myanmar, for which 15 species are known (Krishna and Grimaldi, 2003; Engel et al., 2007, 2016; Poinar, 2009; Engel, 2019; Zhao et al., 2019, 2020a; Vrsanský et al., 2019). Also, two new species have been described in Lebanese amber (Engel et al., 2007, 2011); four species in Spanish amber, (Engel and Delclòs, 2010; Sánchez-García et al., 2020); three species in French amber (Engel et al., 2011; Engel, 2014); and three species as fossil compressions in Russia and Mongolia (Engel et al., 2007; Vrsanský and Aristov, 2014).

Fossils belonging to basal lineages provide direct evidence for understanding the early evolution and biogeographic patterns of termites.

* Corresponding author.

E-mail addresses: irineudoufc@gmail.com (F.I. Bezerra), og.souza@ufv.br (O. DeSouza), ribeirogc@gmail.com (G.C. Ribeiro), paleonto@ufc.br (M. Mendes).

<https://doi.org/10.1016/j.jsames.2021.103260>

Received 4 January 2021; Received in revised form 24 February 2021; Accepted 25 February 2021

Available online 8 March 2021

0895-9811/© 2021 Elsevier Ltd. All rights reserved.

For this reason, Crato termites are very valuable, being one of the Mesozoic Gondwanan records of the Isoptera, and one of the oldest in the world. The Crato Formation is considered one of the most important world *Konservat-Lagerstätten* (Martill et al., 2007). The fossil insects of this locality are preserved as three-dimensional, mineralized replicas with details visible at the micrometer scale. Several recent studies have demonstrated that Crato insects have been preserved by iron oxides after framboidal pyrite (Delgado et al., 2014; Osés et al., 2016).

Here, we report a new record of the extinct genus *Meiatermes*: *M. cretacicus* n. sp. from Crato Formation, Early Cretaceous (Aptian) of Brazil, which is of significance for the paleodiversity and paleobiogeographical distribution of primitive termites in the Neotropical region.

2. Material and methods

The fossils examined in the present work were gathered from the collections of the Centro de Ciências Naturais e Humanas, Universidade Federal do ABC, Santo André, Brazil (CCNH 73 a/b; CCNH 74; CCNH 75; CCNH 76; CCNH 77; CCNH 78; CCNH 79; CCNH 80; CCNH 81; CCNH 82; CCNH 87; CCNH 88; CCNH 89; CCNH 90; CCNH 91; CCNH 92; CCNH 93 and CCNH 94, see supplementary material) and Laboratório de Paleontologia, Universidade Federal do Ceará, Fortaleza, Brazil (LP/UFC CRT 552, LP/UFC CRT 546, LP/UFC CRT 604 and LP/UFC CRT 605, see supplementary material). The specimens were collected from the Três irmãos quarry in Nova Olinda, Ceará, northeastern Brazil. Fossils were prepared using a fine needle to remove overlying pieces of the carbonatic matrix. All measurements were made using an ocular micrometer and are given in millimeters. All photographs were taken with a Nikon D7100 digital camera. Illustrations were prepared with the aid of a *camera lucida* attached to an Olympus CO11 microscope. Simplified drawings were prepared using Adobe Photoshop and designated

according to the system Comstock-Needham (1898).

3. Geological setting

The Araripe Basin belongs to the Araripe–Potiguar Depression (Mabesoone et al., 1994), located in NE Brazil, at the central part of the Borborema Province (Fig. 1). The pre-Mesozoic basement of this region consists of Precambrian metasedimentary rocks and migmatite terrains. This basement was affected by extensive Jurassic–Cretaceous rifting processes related to the split between South America and Africa during the break-up of Gondwana (Mabesoone, 1994; Ponte and Ponte Filho, 1996). Pre-rift and syn-rift stages took place during Jurassic to Early Cretaceous deposition of alluvial and fluvial-lacustrine successions (Brejo Santo, Missão Velha, and Abaiara Formations). After a significant erosive episode, the Aptian post-rift I sequence (Assine, 2007) corresponds to the Santana Group, which, according to most current interpretations, consist of fluvial, lacustrine, and transitional marine depositions (Barbalha, Crato, Ipubi, and Romualdo Formations, respectively).

Among all the other lithostratigraphic units, the Crato Formation stands out for its fossil fauna and flora, remarkable either in terms of preservation and abundance. The Crato fossil beds represent one of the most productive fossil sites of Gondwana. The Crato Formation consists of micritic laminated limestone layers several meters thick inter-bedded with shales and sandstones, whose origin is attributed to transgressive–regressive events associated with a lacustrine system (Neumann 1999; Neumann et al., 2003). The high-fidelity preservation of the Crato fossils suggests that the depositional environment was restricted and deficient in oxygen avoiding the rapid degradation of the organism tissues (Osés et al., 2016, 2017). According to Martill and Heimhofer (2007), the Crato Formation can be divided into four different members,

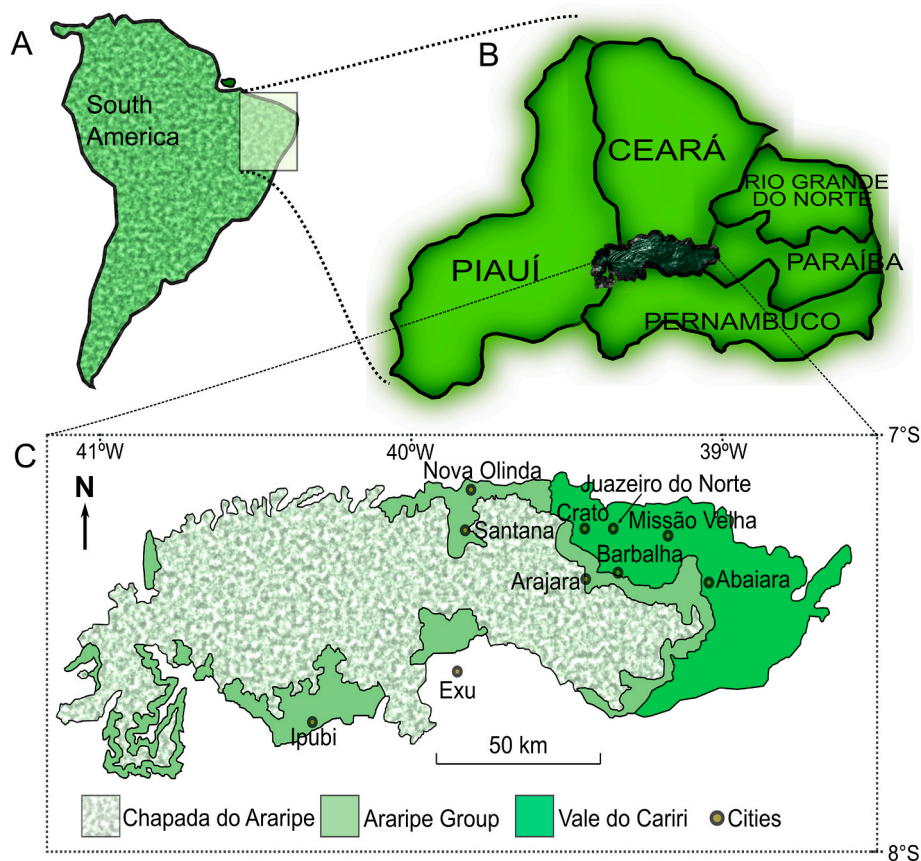


Fig. 1. Simplified map showing the location of the Crato Formation. A. The map of the South American continent shows the position of some states in northeastern Brazil. B. Araripe Basin position on northeastern Brazil. C. Generalized map of the Araripe Basin.

from bottom to top: the Nova Olinda, Caldas, Jamacaru, and Casa de Pedra Members. The Nova Olinda Member represents the lowermost limestone bed and hosts the Crato Fossil Lagerstätte (Heimhofer et al., 2010). According to Neumann et al. (2003), these limestones can be distinguished between two types of carbonate facies: clay-carbonate rhythmites, represented by fine limestones with variable detrital components; and laminated limestone, which represents the very regular limestone banding.

4. Results

Systematic paleontology.

Infraorder Isoptera Brullé, 1832

Clade Euisoptera Engel et al., 2009

'Meiatermes Grade' (sensu Engel et al., 2007).

Genus *Meiatermes* Lacasa-Ruiz et Martínez-Delclòs (1986).

Type species: *Meiatermes bertrani* Lacasa-Ruiz et Martínez-Delclòs (1986).

Meiatermes cretacicus n. sp. (Figs. 2–5) Figure 2 – 2-column.

4.1. Derivation of name

The specific name refers to the Cretaceous period, the time interval when the fossil species lived, Cretaceous of the Araripe Basin.

4.2. Material

Holotype: Imago, indeterminate (Figs. 2 and 3), specimen CCNH 73 a/b, preserved in dorsal view on two yellow limestone slabs with extended wings, legs, and antenna not preserved. Further specimens are alate with at least one extended wing (visible veins) and poorly preserved body portions. Most of the studied specimens lack enough diagnostic features, we are unable to accurately find out their taxonomic position. CCNH 76, CCNH 77, and CCNH 78 tentatively belong to *Meiatermes* sp., based on their body proportions and venation pattern.

4.3. Type locality and horizon

Chapada do Araripe, vicinity of Nova Olinda, southern Ceará, northeastern Brazil. Laminated limestones, Lower Cretaceous, Group Santana, Upper Aptian, Crato Formation (Assine et al., 2014), Nova Olinda Member (Martill, 2007).

4.4. Diagnosis

Small body-size termite. Head rounded, lateral borders slightly

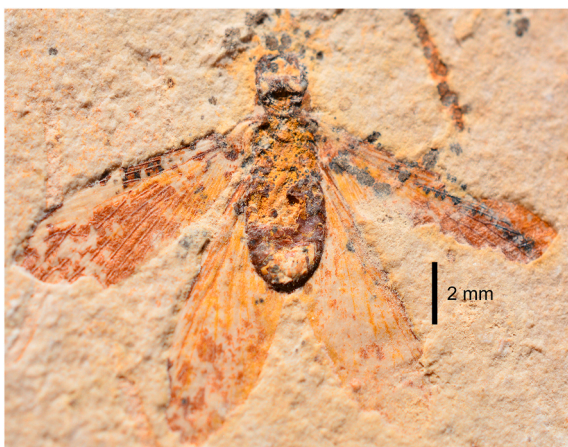


Fig. 2. Photomicrograph of *Meiatermes cretacicus* n. sp. (CCNH 73a).



Fig. 3. Photomicrograph of *Meiatermes cretacicus* n. sp. (CCNH 73 b).

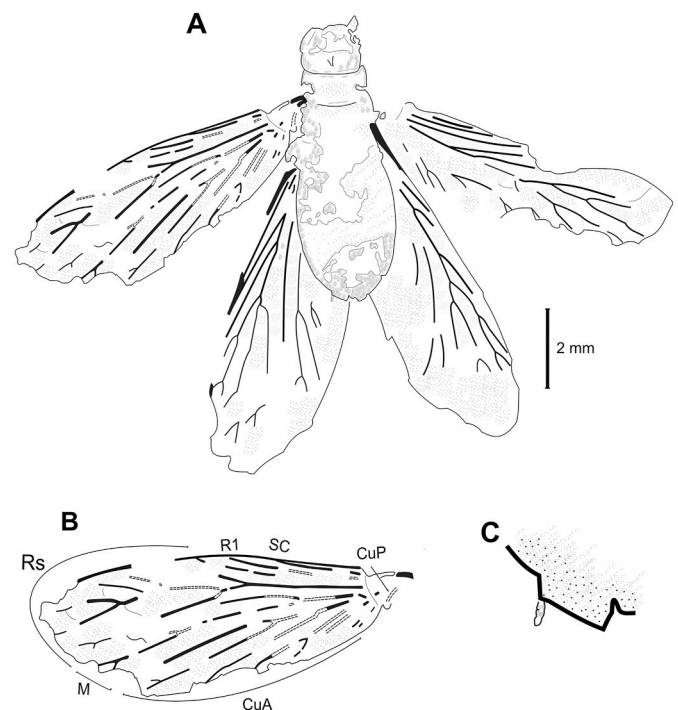


Fig. 4. Camera lucida drawings of *Meiatermes cretacicus* n. sp. (CCNH 73a). A. Holotype specimen. B. Venation of the left forewing. C. Drawing of cercus. Abbreviations: Sc (subcosta); R1 (radius); Rs (radial sector); M (media); CuA (cubitus anterior); CuP (cubitus posterior).

rounded, and Y-shaped line present. Pronotum slightly broader than head, anterior border concave, lateral borders broadly rounded, and posterior border slightly straight. Forewing veins Sc, R, Rs, and M more heavily pigmented than CuA. Rs extensively branched and encompassing majority of the posterior wing margin. M branching near wing midlength with only two branches. CuA well-developed, with modest posterior branches terminating on inner margin of the wing. Cerci short and three-segmented.

4.5. Description

Imago. Total body length without wings 7.0 mm, width without

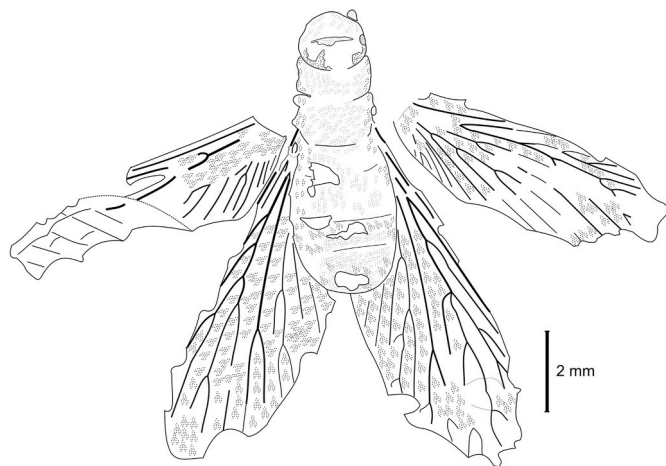


Fig. 5. Camera lucida drawings of *Meiatermes cretacicus* n. sp. (CCNH 73 b).

wings 2.7 mm. Head longer than wide, length of head about 1.9 mm, width 1.7 mm. Head rounded and robust, posterior border gently rounded. Compound eye semicircular, occupying about a half of the lateral edge of the head. Ocelli and fontanelle not visible, or absent. Y-shaped coronal ecdysial cleavage line poorly preserved. Pronotum large, flat, and slightly broader than head, anterior border concave, lateral borders gently convex. Length of forewing 8 mm, veins with reticulations throughout, basal suture weakly convex, Sc, R, and Rs more strongly pigmented than the remainder of veins. Sc simple, terminating on costal margin near one-third. R1 simple terminating on costal margin anteriorly to the wing half. Rs elongate, with at least six and numerous sub-branches, radial field terminating on costal margin and greatly expanded apically. M branching anteriorly to the wing midlength and two primary branches, with two secondary branches, terminating slightly posterior to wing apex. CuA branching across its length. CuP weakly convex. Hindwing without basal suture, Rs elongate, with numerous branches and sub-branches, M elongate, branching just beyond wing midlength. Abdomen relatively cylindrical, styli not present. Cercus very short, three-segmented, cercal articles displaying approximately the same length.

4.6. Remarks

Meiatermes cretacicus n. sp. is placed in the genus *Meiatermes* Ruiz et Martínez-Delclòs (1986) based on overall body-size, head rounded, compound eye semicircular with a moderate size, pronotum slightly wider than the head, venation pattern of the forewing and cerci three-segmented.

Krishna (1990) was the first to propose the presence of the genus *Meiatermes* in the Crato Formation, when he described *Meiatermes araripena*. Fontes and Vulcano (1998, 2004) transferred the species to *Cretatermes* Emerson (1986). Later, Martins-Neto et al. (2006) created a new genus, *Nordestinatermes*, to place this species. After a thorough review, Grimaldi et al. (2008) returned *araripena* to *Meiatermes*. Grimaldi et al. (2008) arguing that prior proposals of new species, or even new subfamilies, have been made by different authors (e.g. Martins-Neto et al., 2006) based on trivial or plastic characters. Based on body size, wing length, pronotal shape, venation pattern and the number of tarsomeres, Grimaldi et al. (2008) considered the species *Caatingatermes megacephalus* Martins-Neto et al. (2006); *Araripetermes nativa* Martins-Neto et al. (2006) (*nomen incorrectum, recte: nativus*) and *Nordestinatermes obesa* Martins-Neto et al. (2006) (*nomen incorrectum, recte: obesus*) as *nomina dubia*, most likely synonyms of *Meiatermes araripena*. In this context, we followed Grimaldi et al. (2008) who accepted that only two species of *Meiatermes* (*M. araripena* and *M. hariolus*) occur in the Araripe Basin.

Meiatermes cretacicus n. sp. exhibits approximately the same proportions as the other termites described for the Crato Formation, except *Cratomastotermitidae*. Features such as wing venation, pronotal shape, wing length, and body proportions make the new taxon similar to *M. araripena*, *M. bertrani* and *M. hariolus*. Despite such similarities, *M. cretacicus* differs from these species by several characters. Within *Meiatermes*, *M. cretacicus* n. sp. can be distinguished from *M. araripena* Krishna (1990) by the body length smaller, pronotal hind margin without a median concavity and cerci short, trimerous, with approximately the same length. It also differs from *M. bertrani* by Sc terminating on costal margin near one-third of the wing length (most of the representatives of *M. bertrani* closer to one-half the wing length), R1 simple without branches and radial field with consistent width. While *M. cretacicus* n. sp. has three cercal articles, *M. hariolus* has five.

5. Discussion

The taxonomy of the Crato termites has been the subject of many problems, most of these mistakes being resolved in a comprehensive review by Grimaldi et al. (2008). The following six species are considered valid for the Crato Formation: *Cratokalotermes santanensis* Bechly (2007), *Cratomastotermes wolfschwenningeri* Bechly (2007), *Cretarhinotermes novaolindense* Bechly (2007), *Mariconitermes talicei* Fontes et Vulcano (1998), *Meiatermes araripena* Krishna (1990) and *Meiatermes hariolus* Grimaldi et al. (2008).

The other taxa (5 species) are considered invalid species because they are based on non-robust characters (Grimaldi et al., 2008). These are: *Araripetermes nativa* Martins-Neto et al., (2006) (*nomen incorrectum, recte: nativus*), *Caatingatermes megacephalus* Martins-Neto et al., (2006), *Cretatermes pereirai* Fontes et Vulcano (1998) and *Nordestinatermes obesa* Martins-Neto et al. (2006) (*nomen incorrectum, recte: obesus*).

Crato termites are one of the oldest in the world – being only younger than the termites from the Lebanese amber (Barremian), Baissa and Chernovskie Kopi localities (Engel et al., 2007; Vršanský and Aristov, 2014) and Weald Formation from the Hauterivian of the United Kingdom (Jarzembowski, 1981; Engel et al., 2007, 2011). *Baissatermes lapideus*, *Mastotermes nepropadyom* and *Santonitermes transbaikalicus* from Baissa and Chernovskie Kopi localities, respectively, were thought to be Jurassic in age, but recent works have shown that they are younger, from the Early Cretaceous, still older than the Isoptera representatives of the Crato Formation (Engel et al., 2007; Vršanský and Aristov, 2014; Wolfe et al., 2016). Although phylogenetic studies suggest the origin of the termites in the Late-Middle Jurassic or earlier (Engel et al., 2009; 2016; Ware et al., 2010; Buček et al., 2019; Zhao et al., 2019), it is in the Cretaceous when they appear in the fossil record, already showing substantial diversity. The high diversity of termites can be confirmed in the Hukawng Valley in the amber mines in Kachin state, Cenomanian of the Myanmar (Zhao et al., 2020a, 2020b).

All Crato species are large-bodied termites and present pronotum that are as wide or wider than the head, except *Cratokalotermes santanensis*. Broader pronotum and larger body are features that strongly place them within lower termite taxa. *Cratomastotermes wolfschwenningeri* has one of the largest pronota among all termites. The large size, well-developed pronotal lobes, wing venation, and the broad hind wings with anal fan strongly suggest affinities with *Mastotermitidae*. However, phylogenetic analyses have supported *Cratomastotermes* as more basal and one of the first branches in the termite lineage (Engel et al., 2007, 2016). Even though it is the most primitive of the Crato termites, *Cratomastotermes* is still a monotypic genus and is extremely scarce. On the other hand, *Meiatermes* is distinctly more abundant in number of individuals than all the other Crato termite genera and shows substantial morphological plasticity (mainly *M. araripena*). *M. araripena* displays a very large intraspecific variation in wing venation. For example, R2 can be present or absent; Rs with one or two inferior branches or sometimes none; M branching near, occasionally, beyond wing midlength with one or two primary branches and sometimes with

secondary branches; and CuA with numerous branches, sometimes with secondary branches. A striking feature of *M. cretacicus* forewing is the presence of vein deformities. These deformities in the veins indicate the occurrence of significant mass mutations, which apparently appear in response to environmental stress (Vršanský, 2005; Vršanský et al., 2017).

Regarding the wings, Crato termites share specific traits with other basal termites such as dense reticulate pattern between the veins; multiple Rs branches with a comparatively extensive field (except for *C. novaolindense*); M having at least two branches (Fig. 6). These features are plesiomorphic in Isoptera (Engel et al., 2007, 2016; Grimaldi et al., 2008). They were derived most basally along with cratomastotermes, mastotermes and pabuonqed (Vršanský et al., 2019a, 2019b). The presense of other primitive termites discovered in Burmese, Lebanese and Spanish ambers (Engel and Delclòs, 2010; Engel et al., 2011; Sánchez-García et al., 2020; Zhao et al., 2020a, 2020b) and Transbaikalia (Engel et al., 2007), suggests that there was a well diversified and widely distributed grade of basal termites during the

Cretaceous.

6. Conclusion

A new species of *Meiatermes cretacicus* n. sp., is described for the Crato Formation, Araripe Basin, Aptian of Brazil. Its discovery is important as it improves our knowledge on the diversity of primitive termites in the Early Cretaceous of Gondwana. The new taxon shares features with the basal-most termites belonging to the *Meiatermes*-grade. The presence of several different primitive termites in amber-bearing deposits (Albian and Cenomanian) of Europe and Asia has shown that Isoptera was rather diverse and abundant during the Cretaceous, shortly after they diverged from their roach relatives in the Late-Middle Jurassic/Early Cretaceous. The taxonomy of Crato termites has always been the subject of debate, more studies and new specimens will hopefully provide a more complete understanding of their taxonomy, relationships to other isopteran lineages, and paleoecology.

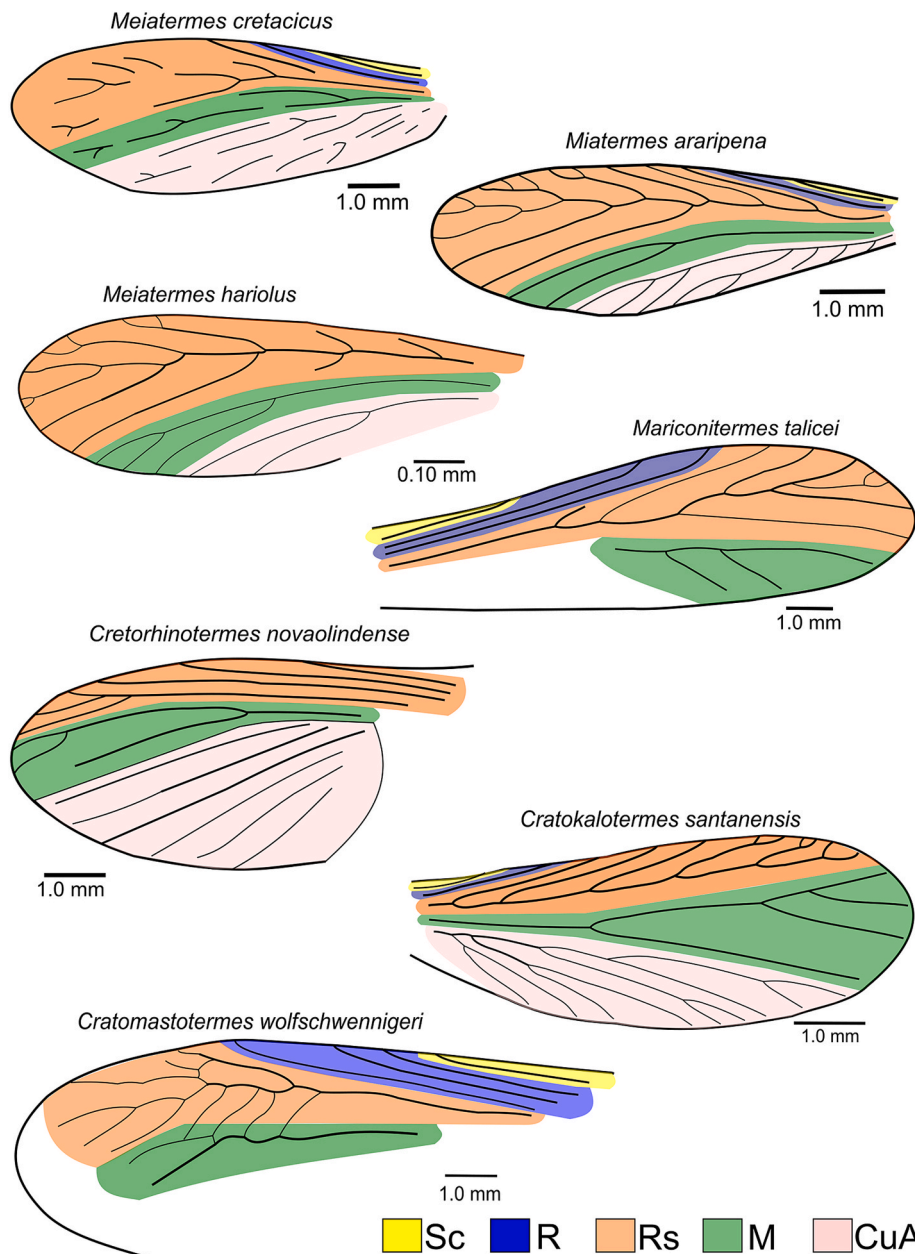


Fig. 6. Forewing venation patterns (without reticulated veins) of the termites from the Cretaceous Crato Formation. Redrawn from Grimaldi et al. (2008).

Author contributions

Francisco Irineudo Bezerra: Conceptualization, Methodology, Software, Formal analysis, Writing – original draft. Og DeSouza: Validation, Writing – review & editing, Visualization. Guilherme Cunha Ribeiro: Data curation, Writing – review & editing, Visualization, Project administration, Funding acquisition. Márcio Mendes: Data curation, Supervision, Project administration, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

This study was financed in part by 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 holds a CNPq fellowship (# 307990-2017-6). GCR is grateful to Irma Tie Yamamoto, chief of the paleontological division of the Brazilian National Mining Agency (ANM), for assistance during the process of getting permits for collecting fossils in the Crato Formation. We also thank José Artur Andrade (ANM) for all his help and assistance during the several trips to the city of Crato (Brazil), and to São Paulo State Research Agency (FAPESP; grant number 20/02844–5).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jsames.2021.103260>.

References

- Assine, M.L., 2007. Araripe basin. *Bol. Geociencias Petrobras* 15, 371–389.
- Assine, M.L., Perinotto, J.A.J., Neumann, V.H.M., Custódio, M.A., Varejão, F.G., Mescolotti, P.C., 2014. Sequências Depositionais do Andar Alagoas (Aptiano superior) da Bacia do Araripe, Nordeste do Brasil. *Bol. Geociencias Petrobras* 22, 3–28.
- Bechly, G., 2007. Isoptera: termites. In: Martill, D.M., Bechly, G., Loveridge, R.F. (Eds.), *The Crato Fossil Beds of Brazil: Window into an Ancient World*. Cambridge University Press, Cambridge, pp. 249–262.
- Bourguignon, T., Lo, N., Sobotník, J., Ho, S., Naeem Iqbal, N., Coissac, E., Lee, M., Jendryka, M.M., Sillam-Dusse's, D., Krížková, B., Roisin, Y., Evans, T.A., 2017. Mitochondrial phylogenomics resolves the global spread of higher termites, ecosystem engineers of the tropics. *Mol. Biol. Evol.* 34, 589–597.
- Buček, A., Šobotník, J., He, S., Shi, M., McMahon, D.P., Holmes, E.C., Roisin, Y., Lo, N., Bourguignon, T., 2019. Evolution of termite symbiosis informed by transcriptome-based phylogenies. *Curr. Biol.* 29, 3728–3734.
- Comstock, J.H., Needham, J.G., 1898. The wings of insects (continued). *Am. Nat.* 32, 413–424.
- Delgado, A. de O., Buck, P.V., Osés, G.L., Ghilardi, R.P., Rangel, E.C., Pacheco, M.L.A.F., 2014. Paleometry: a brand new area in Brazilian science. *Mater. Res.* 17, 1434–1441.
- DeSouza, O., Araújo, A.P.A., Reis Jr., R., 2009. Trophic controls delaying foraging by termites: reasons for the ground being brown? *Bull. Entomol. Res.* 99, 603–609.
- Eggleton, P., Bignell, D.E., Sands, W.A., Mawdsley, N.A., Lawton, J.H., Wood, T.G., Bignell, N.C., 1996. The diversity, abundance and biomass of termites under differing levels of disturbance in the Mbalmayo Forest Reserve, southern Cameroon. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 51, 51–68.
- Emerson, A.E., 1967. A new genus and species of termite (Isoptera: hodotermitidae). *Psyche* 74, 276–289.
- Engel, M.S., 2014. A termite (Isoptera) in late cretaceous amber from vendée, northwestern France. *Paleontological Contributions* 10, 21–24.
- Engel, M.S., 2019. Termite evolution: a primal knock on wood or a hearty mouthful of dirt. *Curr. Biol.* 29, R1126–R1129.
- Engel, M.S., Delclòs, X., 2010. Primitive termites in cretaceous amber from Spain and Canada (Isoptera). *J. Kans. Entomol. Soc.* 83 (2), 111–128.
- Engel, M.S., Grimaldi, D.A., Krishna, K., 2007. Primitive termites from the early cretaceous of Asia (Isoptera). *Stuttg. Beitr. Naturkd. B* 371, 1–32.
- Engel, M.S., Nel, A., Azar, D., Soriano, C., Tafforeau, P., Néraudeau, D., Colin, J.-P., Perrichot, V., 2011. New, primitive termites (Isoptera) from early cretaceous, ambers of France and Lebanon. *Palaeodiversity* 4, 39–49.
- Engel, M.S., Barden, P., Riccio, M.L., Grimaldi, D.A., 2016. Morphologically specialized termite castes and advanced sociality in the early cretaceous. *Curr. Biol.* 26, 522–530.
- Fontes, L.R., Vulcano, M.A., 1998. Cupins fósseis do novo mundo. In: Fontes, L.R., Filho, E.B. (Eds.), *Cupins: o desafio do conhecimento: Fundação de Estudos Agrários Luiz de Queiroz*. São Paulo, Brazil, pp. 243–295.
- Fontes, L.R., Vulcano, M.A., 2004. Catalogue of the fossil Isoptera of the new world. *Sociobiology* 44, 345–364.
- Grimaldi, D., Engel, M.S., 2005. *Evolution of the Insects*. Cambridge University Press, Cambridge.
- Grimaldi, D.A., Engel, M.S., Krishna, K., 2008. The species of Isoptera (insecta) from the early cretaceous Crato Formation: a revision. *Am. Mus. Novit.* 3626, 1–30.
- Heimhofer, U., Ariztegui, D., Lenniger, M., Hesselbo, S.P., Martill, D.M., Rios-Netto, A. M., 2010. Deciphering the depositional environment of the laminated Crato fossil beds (early cretaceous, Araripe Basin, north-eastern Brazil). *Sedimentology* 57, 677–694.
- Inward, D., Beccaloni, G., Eggleton, P., 2007. Death of an order: a comprehensive molecular phylogenetic study confirms that termites are eusocial cockroaches. *Biol. Lett.* 3, 331–335.
- Jarzewowski, E.A., 1981. An early cretaceous termite from southern england (Isoptera: hodotermitidae). *Syst. Entomol.* 6, 91–96.
- Jouquet, P., Dauber, J., Lagerlo, J., Lavelle, P., Lepage, M., 2006. Soil invertebrates as ecosystem engineers: intended and accidental effects on soil and feedback loops. *Appl. Soil Ecol.* 32, 153–164.
- Krishna, K., 1990. Isoptera. In: Grimaldi, D.A. (Ed.), *Insects from the Santana Formation, Lower Cretaceous, of Brazil*. Bulletin of the American Museum of Natural History 195, New York, United States, pp. 76–81.
- Krishna, K., Grimaldi, D., 2000. A new subfamily, genus, and species of termite (Isoptera) from New Jersey Cretaceous amber. In: Grimaldi, D. (Ed.), *Studies on Fossils in Amber, with Particular Reference to the Cretaceous of New Jersey*. Backhuys Publishers, Leiden, pp. 133–140.
- Krishna, K., Grimaldi, D., 2003. The first Cretaceous Rhinotermitidae (Isoptera): a new species, genus, and subfamily in Burmese amber. *Am. Mus. Novit.* 3390, 1–10.
- Krishna, K., Grimaldi, D.A., Engel, M.S., 2013. Treatise on the Isoptera of the world: vol 1, introduction. *Bull. Am. Mus. Nat. Hist.* 377, 1–200.
- Lacasa-Ruiz, A., Martínez-Delclòs, X., 1986. Meiatermes, nuevo género fósil de insecto Isóptero (Hodotermitidae) de las calizas Neocomienses del Montsec (Provincia de Lérida, España). *Lleida. Institut d'Estudis Ilerdencs*.
- Li, J., Zhao, X., Gao, Y., Wang, B., Xiao, C., 2020. Cockroach *Stavba jarzewowskii* sp. nov. (Blattaria: liberiblattidae) from mid-Cretaceous Burmese amber. *Cretac. Res.* 115, 104531.
- Lo, N., Tokuda, G., Watanabe, H., Rose, H., Slaytor, M., Maekawa, K., Bandi, C., Noda, H., 2000. Evidence from multiple gene sequences indicates that termites evolved from wood-feeding cockroaches. *Curr. Biol.* 10, 801–804.
- Mabesoone, J.M., Viana, M.S., Lima Filho, M.F., 1994. Sedimentary fill of the araripe-potiguar depression (NE Brazil). Abstracts, 14th Intern. Sedim. Cong., Recife-Brazil. Universidade Federal de Pernambuco, Pernambuco, Brazil, pp. 46–47.
- Martill, D.M., Heimhofer, U., 2007. Stratigraphy of the Crato Formation. In: Martill, D. M., Bechly, G., Loveridge, R.F. (Eds.), *The Crato Fossil Beds of Brazil – Window into an Ancient World*. Cambridge University Press, Cambridge, pp. 25–43.
- Martins-Neto, R.G., Ribeiro-Júnior, C., Prezoto, F., 2006. New fossils (Isoptera: hodotermitidae) from the Santana formation (lower cretaceous, Araripe Basin, northeast Brazil), with descriptions of new taxa including a new subfamily. *Sociobiology* 47, 125–134.
- Neumann, V.H., 1999. Estratigrafia, Sedimentología, Geoquímica y Diagénesis de los Sistemas Lacustres Aptienses-Albienses de la Cuenca de Araripe (Nororreste do Brasil). Ph.D. thesis. Universitat de Barcelona.
- Neumann, V.H., Borrego, A.G., Cabrera, L., Dino, R., 2003. Organic matter composition and distribution through the Aptian-Albian lacustrine sequences of the Araripe Basin, northeastern Brazil. *Int. J. Coal Geol.* 54, 21–40.
- Osés, G.L., Petri, S., Becker-Kerber, B., Romero, G.R., Rizzutto, M.A., Rodrigues, F., Galante, D., Silva, T.F., Curado, J.F., Rangel, E.C., Ribeiro, R.P., Pacheco, M.L., 2016. Deciphering the preservation of fossil insects: a case study from the Crato Member, Early Cretaceous of Brazil. *PeerJ* 4, 1e28.
- Poinar, G.O., 2009. Description of an Early Cretaceous termite (Isoptera: kalotermitidae) and its associated intestinal Protozoa, with comments on their coevolution. *Parasites Vectors* 2, 12.
- Ponomarenko, A.G., 1988. New mesozoic insects. *Transactions of the Joint Soviet-Mongolian Paleontological Expedition* 33, 71–80.
- Ponte, F.C., Ponte Filho, F.C., 1996. Evolução tectônica e classificação da Bacia do Araripe. 4th Simp. Cretáceo Brasil, Boletim, Rio Claro. Universidade Estadual Paulista, Rio Claro, Brazil, pp. 123–133.
- Ren, D., 1995. Isoptera. In: Ren, D., Lu, L., Guo, Z., Ji, S. (Eds.), *Fauna and Stratigraphy of Jurassic-Cretaceous in Beijing and the Adjacent Areas*. Seismic Publishing House, Beijing, pp. 56–61.
- Sánchez-García, A., Peñalver, E., Delclòs, X., Engel, M.S., 2020. Early Cretaceous, termites in amber from northern Spain (Isoptera). *Cretac. Res.*, 104385 (in press).
- Sendi, H., Hinkelmann, J., Vršanská, L., Kúdelová, T., Kúdelá, M., Zuber, M., Thomas van de Kamp, Vršanský, P., 2020. Roach nectarivory, gymnosperm and earliest flower pollination evidence from Cretaceous ambers. *Biologia* 75, 1613–1630.
- Su, N.Y., Scheffrahn, R.H., 2000. Termites as pests of buildings. In: Abe, T., Bignell, D.E., Higashi, M. (Eds.), *Termites: Evolution, Sociality, Symbioses, Ecology*. Kluwer Academic Publishers, Dordrecht, pp. 437–453.
- Thorne, B.L., Grimaldi, D.A., Krishna, K., 2000. Early fossil history of the termites. *Vršanský, P., 2002. Origin and the early evolution of Mantises. Amba Projects* 6, 1–16.

- Vršanský, P., 2005. Mass mutations of insects at the Jurassic/Cretaceous boundary? *Geol. Carpathica* 6, 473–481.
- Vršanský, P., 2010. Cockroach as the earliest eusocial animal. *Acta Geol. Sin.* 84, 793–808.
- 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.
- Vršanský, P., Oružinský, R., Aristov, D., Wei, D., Vidlička, L., Ren, D., 2017. Temporary deleterious mass mutations relate to originations of cockroach families. *Biologia* 72, 886–912.
- Vršanský, P., Koubová, I., Vršanská, L., Hinkelman, J., Kúdela, M., Kúdelova, T., Liang, J., Xia, F., Lei, X., Ren, X., Vidlička, L., Bao, T., Ellenberger, S., Šmídová, L., Barclay, M., 2019a. Early wood-boring 'mole roach' reveals eusociality 'missing ring. *Amba projekty* 9, 1–28.
- Vršanský, P., Sendi, H., Aristov, D., Bechly, G., Müller, P., Ellenberger, S., Azar, D., Ueda, K., Barna, P., Gárcia, T., 2019b. Ancient roaches further exemplify 'no land return' in aquatic insects. *Cretac. Res.* 68, 22–33.
- Wolfe, J.M., Daley, A.C., Legg, D.A., Edgecombe, G.D., 2016. Fossil calibrations for the arthropod tree of life. *Earth Sci. Rev.* 160, 43–110.
- Zhao, Z., Eggleton, P., Yin, X., Gao, T., Shih, C., Ren, D., 2019. The oldest known mastotermitids (Blattodea: termitoidae) and phylogeny of basal termites. *Syst. Entomol.* 44 (3), 612–623.
- Zhao, Z., Yin, X., Shih, C.K., Gao, T., Ren, D., 2020a. Termite colonies from mid-Cretaceous Myanmar demonstrate their early eusocial lifestyle in damp wood. *Nat. Sci. Rev.* 7, 381–390.
- Zhao, Z., Shih, C.K., Gao, T., Ren, D., 2020b. Termite communities and their early evolution and ecology trapped in Cretaceous Amber. *Cretac. Res.* 104612 (in press).