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Two virtually complete termites in Early Cretaceous (Late Albian) amber from Peñacerrada I outcrop, Spain, are described and figured, representing the most well-preserved Isoptera yet discovered from the Albian stage. The material is described as Ithytermes montoyai, gen. et sp. nov., and is similar in many details to the slightly younger Krishnatermes yoddha Engel, Barden, and Grimaldi of northern Myanmar amber. Given the presence of distinct soldiers in this grade of Cretaceous termites, it is likely that I. montoyai also exhibited such a tripartite caste system. In addition to the type material of I. montoyai, two fragmentary termites are recorded for the first time in Albian amber from the El Soplao outcrop, and in the few preserved details these taxa are not conspecific with the former.

Keywords	Albian; Euisoptera; eusociality; Mesozoic; taxonomy
Taxonomy	Paleontology, Invertebrate Paleontology
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Early Cretaceous termites in amber from northern Spain (Isoptera)

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Abstract Two virtually complete termites in Early Cretaceous (Late Albian) amber from Peñacerrada I outcrop, Spain, are described and figured, representing the most well-preserved Isoptera yet discovered from the Albian stage. The material is described as *Ithytermes montoyai*, gen. et sp. nov., and is similar in many details to the slightly younger *Krishnatermes yoddha* Engel, Barden, and Grimaldi of northern Myanmar amber. Given the presence of distinct soldiers in this grade of Cretaceous termites, it is likely that *I. montoyai* also exhibited such a tripartite caste system. In addition to the type material of *I. montoyai*, two fragmentary termites are recorded for the first time in Albian amber from the El Soplao outcrop, and in the few preserved details these taxa are not conspecific with the former.

Keywords: Albian; Euisoptera; eusociality; Mesozoic; taxonomy

1. Introduction

Termites inspire awe, not the least of which is due to their remarkable societies. All of the more than 3300 species of Isoptera are highly eusocial (Krishna et al., 2013), living in permanent colonies and in which the roles of the society's participants are more or less fixed by a system of castes — workers, soldiers, and winged reproductives. This advanced eusocial syndrome is ancient among termites and, in fact, termites were perhaps first among the social insects (Grimaldi and Engel, 2005). Termite eusociality was already present in the Early Cretaceous (Martínez-Delclòs and Martinell, 1995; Thorne et al., 2000; Engel et al., 2016a), and it is likely that the earliest termite societies were appearing during the latest Jurassic (Ware et al., 2010). Not only were basal termites eusocial, but even the complexities of a tripartite caste system were present by the mid-Cretaceous, and likely also in the Early Cretaceous (Martínez-Delclòs and Martinell, 1995; Engel et al., 2016a). Despite the presence of intricate societies by the Early Cretaceous, eusociality did not confer great ubiquity, and it appears to have been the much later appearance of large colony sizes, supported in part by more developed nests, that permitted termites to achieve the ecological dominance for which they are so famed today (Engel et al., 2009). Nonetheless, while the Termitidae are dominant today and inform us greatly about termite social dynamics and their ecological impact, it remains the frequently smaller societies of the basal families that more closely approximate characteristics likely to have been influential in early isopteran social evolution. Relationships among the basal lineages of termites provide a greater perspective of early termite evolution, and the integration of fossils into this phylogenetic framework provides the only direct evidence for understanding these episodes (Engel et al., 2009, 2016a; Ware et al., 2010; Zhao et al., 2019). As such, the paleontological record of termites is of significance and, in fact, Isoptera are not uncommon in many Cenozoic deposits (e.g., Krishna, 1996; Engel and Krishna, 2007; Engel et al., 2007a, 2011a; Krishna and Grimaldi, 2009). These taxa are, as one would suspect, typically of more derived lineages and while informative of Paleogene and Neogene events, such as biogeographic patterns and climatic changes, they reveal little in terms of divergences among early termites. Relicts do exist within the Cenozoic fauna, such as the diverse and widespread species of *Mastotermes* Froggatt (Emerson, 1965; Krishna and Emerson, 1983; Krishna and Grimaldi, 1991; Wappler and Engel, 2006; Engel et al., 2015), the most basal of living termites and today native to northern Australia (Emerson, 1965; Krishna et al., 2013). These species, however, do not give further refinement to the affinities of mastotermitids among Isoptera. Conversely, Cretaceous termites are more interesting for their unique combinations of traits placing many of them outside of traditional concepts of the modern families and most form a well-circumscribed grade of taxa relative to the basal families (Engel et al., 2009, 2016a). Most Cretaceous Isoptera, particularly those preserved as compression fossils in sedimentary rock, are represented by the shed wings of alates and are therefore of limited phylogenetic value due to the absence of so many critical traits present in the body. Preservation in amber, however, leaves fossilized remains with life-like fidelity and it is from these taxa that we may extract the greatest amount of character and paleobiological information. Termites in Cretaceous amber, however, are not overly abundant, perhaps the sole exception being the abundance of species and individuals in mid-Cretaceous amber from Myanmar. Species are known in most of the major deposits and spanning the breadth of the Cretaceous (Table 1), but these range in degrees of completeness, leaving much to be done on the Mesozoic record of Isoptera. One glimmer of hope rests in the fact that the majority of these taxa have been discovered in the last decade or so, suggesting that continued efforts will reveal an even greater diversity of material from which to revisit and refine our hypotheses.

In this context, we provide a brief account of termites newly recovered from the Early Cretaceous (Albian) Peñacerrada I (Burgos Province) and El Soplao (Cantabria Province) outcrops in Spain. Previous records of termites from Albian-aged amber in Spain were two species from the deposit of Peñacerrada I and one species from the deposit of San Just (Teruel Province) (Engel and Delclòs, 2010), and those were exceedingly fragmentary. Much is the same for the newly discovered Spanish amber termites from El Soplao. However, one piece from Peñacerrada I nicely preserves two nearly complete alates (imagoes) and from these we can observe more features than from any previously known Albian Isoptera. The Spanish termites, along with those few from Lebanon (Barremian in age), are the earliest termites preserved in amber.

2. Material and methods

The amber pieces MCNA 14936 and CES-446 were cut and embedded in a transparent epoxy resin except the piece CES-552; the preparations were polished once the polymer hardened (Nascimbene and Silverstein, 2000). These three samples were observed under three different lenses, i.e., an Olympus SZX-12 stereomicroscope, and a Motic BA310 compound microscope with reflected and transmitted light. Photomicrographs were taken with a Canon EOS 7D digital camera attached to an Infinity K–2 long-distance microscope lens for general habitus, and a Moticam 2500 camera attached to the Motic BA310 microscope for details. All photographs were arranged and sharpened with Helicon focus and edited with Adobe Photoshop. Illustrations were prepared with the aid of a camera lucida attached to an Olympus BX41 compound microscope.

We have generally followed the classification of termites as presented by Krishna et al. (2013), and categorically reject proposals to eliminate Isoptera as a name for this clade (Lo et al., 2007), preferring the rank of infraorder as advocated by Engel (2011) and others, although the name could equally be used without formal rank, much as is done for Aculeata among the Hymenoptera. Morphological terminology has also generally followed that of Krishna et al. (2013), while the format for the descriptions is analogous to those used elsewhere for basal grade Isoptera (e.g., Engel et al., 2016a). Measurements were taken with the aid of an ocular micrometer on an Olympus SZX-12 stereomicroscope.

Specimen MCNA 14936 is deposited in the Museo de Ciencias Naturales de Álava (Vitoria-Gasteiz, Spain), and specimens CES-446 and CES-552 are deposited in the amber fossil collection of the Laboratory of the El Soplao Cave (Celis, Santander, Spain).

3. Geological and paleontological settings

Peñacerrada I

The Peñacerrada I [=Moraza] amber-bearing outcrop is included within the Utrillas Group *sensu* Barrón et al. (2015) (eastern area of the Basque-Cantabrian Basin, Burgos Province, northern Spain), and dated to the Late Albian (Barrón et al., 2015). This outcrop, together with the Peñacerrada II amber-bearing outcrop in Álava Province, belongs to the so-called ‘Álava amber’. In this area continental-transitional deposits can be differentiated into three subunits that are represented by a deltaic succession, with a vertical tendency toward a regression of the deltaic system in the lower-middle subunits and a vertical transgression in the upper subunit. The amber is found in the middle subunit associated with coal and lignitic beds or organically-rich marl levels, coinciding with the boundary between the maximum regression and the beginning of the transgression, and it is mainly present at the top of filling sequences of interconnected channels within deltaic bays. In general, these two amber deposits of the eastern region of the Basque-Cantabrian Basin represent paralic-swamp environments (Peñalver and Delclòs, 2010). The stratigraphy and taphonomy of the Peñacerrada I deposit are provided by Alonso et al. (2000). Peñacerrada I amber includes a high diversity and abundance of arthropod inclusions. To date, different hexapod orders have been recognized from this deposit (Collembola, Archaeognatha, 'Blattaria', Isoptera, Orthoptera, Psocoptera, Thysanoptera, Hemiptera, Homoptera, Coleoptera, Raphidioptera, Neuroptera, Trichoptera, Lepidoptera, Hymenoptera, and Diptera), as well as crustaceans (Isopoda and Tanaidacea), and chelicerates (Acari, Arachnida and Pseudoscorpionida). Termites are not abundant in Álava amber, with only five specimens collected thus far of the 1500 bioinclusions. *Morazatermes krishnai* Engel and Delclòs, 2010 was described from an imago (and wings of a second specimen), and *Cantabritermes simplex* Engel and Delclòs, 2010 from one isolated forewing (Engel and Delclòs, 2010). Thus, the two imagoes described in this paper correspond to the third isopteran species from Peñacerrada I.

El Soplao

The El Soplao amber-bearing outcrop is included within the Las Peñosas Formation and is near the village of Rábago, within the El Soplao Territory (western area of the Basque-Cantabrian Basin, Santander Province, northern Spain). The El Soplao outcrop is dated to the early Albian. The amber is found in a unit of heterolithic sandstone-siltstone and carbonaceous mudstone related to broadly coastal delta-estuarine environments in unit P2 of the Rábago section (*sensu* Najarro et al., 2009), but the depositional environment also exhibits a slight marine influence (Najarro et al., 2010). Together with the amber, there were also dinoflagellate cists, spores of vascular cryptogams, pollen grains of numerous gymnosperms and some angiosperms (the latter poorly represented), abundant gymnosperm cuticle remains, fusainized wood, and marine or brackishwater invertebrates such as gastropods and bivalves (Najarro et al., 2010). The stratigraphy and taphonomy of the El Soplao deposit are provided by Najarro et al. (2009, 2010). Embedded in the amber, 549 bioinclusions have been recorded, including fungi, plants, and diverse arthropods. The hexapod orders hitherto found are Collembola, Blattaria, Isoptera, Psocoptera, Thysanoptera, Raphidioptera, Neuroptera, Hemiptera, Coleoptera, Trichoptera, Lepidoptera, Hymenoptera, Mecoptera, and Diptera (Pérez-de la Fuente, 2012). The record of Isoptera consists of only two fragmentary specimens (one consisting on isolated partial wings) collected thus far of the 549 bioinclusions. However, these bioinclusions represent the first documentation of the order from El Soplao amber.

Institutional abbreviations

CES, Cueva El Soplao, Celis, Cantabria, Spain; MCNA, Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Spain.

4. Systematic paleontology

Infraorder Isoptera Brullé, 1832

Clade Euisoptera Engel et al., 2009

‘*Meiatermes* Grade’

Genus *Ithytermes*, gen. nov.

Type species Ithytermes montoyai, sp. nov.

Diagnosis **Imago.** Large termites, approximately 9.5 mm in length, with comparatively long, erect setae prominent on much of body and wing scales. Head longer than wide; mandible completely covered by labrum (dentition not visible in available material); antenna moniliform, with 20 articles; compound eye circular, without emargination, separated from posterior border of head by more than compound eye length; ocelli absent; fontanelle absent; occipital carina present; subgenal sulcus present; ventral cervical sclerite absent. Pronotum large, slightly broader than head, anterior border concave, posterior border medially straight, lateral borders broadly rounded and slightly convergent posteriorly, apicolateral angles broadly rounded. Procoxa apparently with weak ventral keel; femora not carinate or keeled ventrally; all tarsi wholly pentamerous; tibial apical spur formula 3-4-4, spurs minutely serrate, asymmetrical; tibiae with outer and pre-apical spurs present; pretarsal claws long, arolium present and large. Wing membrane hyaline, reticulate; forewing scale large, greatly overlapping hind wing base, humeral margin convex, basal suture convex, all veins originating within scale, surface of scale tegminous with numerous erect setae, with distinct reticulation in scale posterior to M, CuA, and CuP; CuP arched, termination of CuP (claval fissure) on posterior wing margin basal to basal suture; Sc long; multiple, elongate R veins, extending beyond wing midlength; R_1 apparently simple; R_2 with numerous branches, particularly apically; Rs long, branching in apicalmost part of wing (an indeterminate number of branches but inferior branches lacking); radial field only slightly expanding apically; M branching near wing midlength; CuA extensively branched and apparently encompassing majority of posterior wing margin. Hind wing without defined scale, lacking distinct basal suture, apparently without anal lobe. Abdominal styli prominent, thin, long, projecting beyond abdominal apex; cerci short, with five short and somewhat indistinct cercomeres.

Etymology The new generic name is a combination of *ithyos*, meaning, “upright”, and *termes*, common generic stem meaning, “termite.” The name refers to the comparatively abundant and upright setae of the head and body. The gender of the name is masculine.

Ithytermes montoyai, sp. nov.

(Figs. 1–4)

Holotype Imago (Figs. 1, 2A–C), MCNA 14936, Early Cretaceous, Late Albian, Peñacerrada I outcrop [Peñacerrada I = Moraza], Utrillas Group (Barrón et al., 2015), eastern area of the Basque-Cantabrian Basin, Burgos, northern Spain; deposited in the Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Spain.

Paratype A single imago (Figs. 1, 2D–F, 3, 4), preserved in the same piece of amber with the holotype, and in the same repository.

Other syninclusions include a microlepidopteran and a male ceratopogonid.

Diagnosis As for the genus (*vide supra*).

Description **Imago.** Large, total body length 9.46 mm (from apex of abdomen to tip of labrum); head longer than wide, length of head to apex of labrum 2.30 mm, width across compound eyes 1.50 mm, width posterior to compound eyes 1.15 mm; labrum wider than long, length 0.30 mm, width 0.50 mm; compound eye length 0.50 mm; median length of pronotum 1.08 mm, depth of anterior concavity 0.15 mm (maximum width of pronotum cannot be adequately measured in either specimen but is wider than head); length of metatibia 2.05 mm; length of forewing scale 1.50 mm; forewing length (including scale) at least 9.5 mm (neither individual with completely preserved forewings, but nearly complete, partially folded left forewing of paratype at least 9.5 mm in length and missing portion of apex suggests it could have been perhaps slightly more than 10 mm in life); styli length 0.31 mm; cerci length 0.19 mm.

Integument dark brown throughout except lighter on antenna, tarsi, and styli; impunctate and generally faintly imbricate except on head distinctly and coarsely imbricate. Integument with scattered, fine, erect to suberect, moderately long setae (setae on average about one half length of compound eye); setae largely pale brown in color except on legs seemingly darker (either dark brown or nearly black); setae particularly prominent on head, pronotum, forewing scale, and abdominal terga; antenna with numerous setae arranged in irregular whorls, setae as long as or slightly longer than individual antennal articles; legs with numerous, erect, stiff, bristle-like setae, particularly prominent on tibiae; forewing scale with scattered, erect, fine, long setae; styli and cerci with numerous, minute, fine, mostly apically-directed or suberect setae.

Head robust, longer than wide, posterior border broadly and gently rounded, lateral borders parallel-sided; mandibles covered entirely by labrum (dentition cannot be discerned as preserved); labrum subquadrate, wider than long; postclypeus flat, transverse, much wider than long; antenna moniliform, with 20 articles (based on right antenna of paratype; left antenna of paratype and both antennae of holotype damaged and incomplete); compound eye without anterior emargination, circular, separated from lower margin of head by slightly more than compound eye diameter, separated from posterior border of head by about 1.5 times compound eye length; ocelli ('ocelloids' sensu Engel et al., 2009) absent; fontanelle absent; Y-shaped ecdysial cleavage scar absent; ventral cervical sclerite absent. Pronotum large, broad, broader than head; anterior border concave, with rounded apicolateral angles, concavity comparatively shallow; lateral borders slightly convergent posteriorly, convex, with posterior corners gently rounded and tapering inward; posterior border medially straight. Procoxa with weak ventral keel; femora not carinate or keeled ventrally; all tarsi wholly pentamerous; tibiae with 2–3 outer spines along length, tibial spur formula 3-4-4, spurs of all legs asymmetrical; arolium present and comparatively large, pretarsal claws long, simple. Wings hyaline, membrane reticulate (faint as preserved but discernible), not pimplate or nodulate. Forewing veins Sc, R, and Rs more strongly pigmented than remainder of veins; forewing scale large, greatly overlapping hind wing base, scale about as long as medial length of pronotum, humeral margin convex, basal suture convex; all major longitudinal veins originating inside wing scale, with strong reticulation between veins posterior to M within scale; Sc long, simple, terminating along anterior wing margin apparently near one-third wing length; R1 simple, terminating slightly proximal wing midlength; Rs elongate, with numerous branches and sub-branches; radial field not greatly expanded apically;M elongate, simple, paralleling and nearest to Rs; CuA branching extensively and across its entire length, CuA field encompassing entire posterior margin of wing. Hind wing without basal suture and without anal lobe. Abdomen somewhat compressed, lateral borders roughly parallel; styli present, thin, slender, projecting beyond abdominal apex; cerci short, distinctly shorter than styli, with five cercomeres.

Etymology The specific epithet honors Dr. Plinio Montoya, Universitat de València (Spain).

Indeterminate (Fig. 5)

Material Imago, CES 552, Early Cretaceous, Albian, Las Peñosas Formation, El Soplao outcrop; deposited in the Laboratory of the El Soplao Cave, Celis, Santander, Spain.

Comments Isolated partial wings.

Indeterminate

Material Imago, CES 446, Early Cretaceous, Albian, Las Peñosas Formation, El Soplao outcrop; deposited in the Laboratory of the El Soplao Cave, Celis, Santander, Spain.

Comments A fragmentary alate largely obscured by fractures and debris but with pentamerous tarsi discernible and about 5 mm in total length. No other meaningful details of this specimen can be observed but it nonetheless records a smaller form of basal grade termite within the El Soplao deposits.

5. Discussion

Ithytermes montoyai gen. et sp. nov. is a comparative large termite, approximating the proportions of other large Cretaceous alates such as those recently described from Cenomanian amber from Myanmar (Engel et al., 2016a). While not as massive as some Tertiary species, such as those of the genus *Gyatermes* Engel and Gross, 2009 which had forewing lengths of about 27–34 mm (Engel and Gross, 2009; Engel and Tanaka, 2015), the present species is still among the larger of fossil termite species. Among described genera, *Ithytermes* gen. nov. appears to share most features in common with *Krishnatermes* Engel, Barden, and Grimaldi, 2016 in Burmese amber (Engel et al., 2016a). Aside from their proportions, both genera have many shared traits, although most are clearly symplesiomorphies shared with other basal lineages including mastotermitids. Like *Krishnatermes*, *Ithytermes* share with mastotermitids the presence of well-developed, asymmetrical tibial spines; a 3-4-4 tibial spur formula; wholly pentamerous tarsi; a large, apicolaterally rounded pronotum; a massive forewing scale with all primary veins originating within, and a dense reticulate pattern present between the veins within the scale; multiple Rs branches within a comparatively narrow radial field along anterior wing margin (not greatly widening toward wing apex); and the absence of a hind wing scale. The presence of styli is another noticeably primitive feature of *Ithytermes*, shared across most basal termite lineages (Krishna et al., 2013). Unfortunately, the mandibles are obscured in the holotype and paratype and it is therefore unknown whether or not a subsidiary tooth was present. Such a tooth is present in Archotermopsidae and some *Meiatermes*-grade genera, where known. However, *Ithytermes* differ from *Krishnatermes* by the presence of a large arolium; distinct subgenal and occipital sulci; long, slender styli; larger number of cercomeres; and the numerous, elongate, erect setae on the head, pronotum, and forewing scale.

It was recently documented that at least some species of the *Meiatermes* grade had tripartite castes and specialized soldiers, representing a dramatic degree of specialization among early termite societies (Engel et al., 2016a). Given the phylogenetic placement of these genera relative to Mastotermitidae, Archotermopsidae, and Hodotermitidae, families in which well-developed soldiers are present, and the presence of similar soldiers in at least *Krishnatermes yoddha* Engel, Barden, and Grimaldi, 2016 and *Ginormotermes rex* (Engel, Barden, and Grimaldi, 2016) (Engel et al., 2016a, b), it is reasonable to conclude that all *Meiatermes*-grade species had such castes. Thus, this would be true for the present species as well.

Collectively, the Cretaceous record of termites, inclusive of those known less completely from compression fossils, reveals a considerable diversity and one that was scarcely hinted at merely 20 years ago, particularly those from the Early Cretaceous (e.g., Thorne et al., 2000; Engel et al., 2007b; Grimaldi et al., 2008). Although termites were not abundant at the time and their colonies were likely small, the group had nonetheless experienced considerable cladogenesis such that disparate species could be found throughout the world (Engel et al., 2009, 2016a; Krishna et al., 2013). From this diversity and the specialization of their societal structures, it is apparent that termites were under considerable influence from their surroundings and likely interactions with other organisms such that there was selective maintenance for complex systems of colony defense. This pressure could have been from vertebrate predators that would see a colony as a concentration of resources, but also from other social lineages such as ants, the present-day rivals of the termites. Indeed, advanced eusocial ants and termites co-existed during the Cretaceous (Barden and Grimaldi, 2016; Engel et al., 2016a), but the latter certainly predated the former as did their societies (Engel et al., 2009; Ware et al., 2010). In fact, while termites extend well into the Early Cretaceous and were likely already present in the latest Jurassic (Engel et al., 2007b; Grimaldi et al., 2008; Ware et al., 2010), the earliest occurrences of true ants are from the earliest Cenomanian, although they most certainly must have been present during at least the Albian (Perrichot, et al., 2008a; LaPolla et al., 2013; Barden and Grimaldi, 2016; Barden, 2017). It is therefore fascinating that termites are the sole social insects known from Spanish amber. Arthropod inclusions are abundant from the varied Albian amber deposits across the Iberian Peninsula, and most of the major orders of hexapods are represented (e.g., Delclòs et al., 2007; Peñalver and Delclòs, 2010; Pérez-de la Fuente, 2012; Engel et al., 2015b; Sánchez-García et al., 2015; Sánchez-García and Engel, 2016a, b). Termites have been previously described from the Peñacerrada I locality (Engel and Delclòs, 2010), and those together with the present material document a rather diverse representation of basal Euisoptera within the fauna at that time. Termites are also present in the slightly younger, Early Cenomanian deposits of nearby localities in France (e.g., Engel et al., 2011b), and those taxa also belong to the basal *Meiatermes* grade of genera. Further afield geographically but roughly coeval with the deposits of France, there is also a diverse termite fauna present in the amber of northern Myanmar (Engel et al., 2007b, 2016a). In the Burmese and French deposits ants are similarly well represented (e.g., Engel and Grimaldi, 2005; Perrichot et al., 2008b; Perrichot, 2014, 2015; Barden and Grimaldi, 2016; Barden, 2017). However, no ants have been recovered from any of the Spanish localities and this absence is striking given the close geographic and temporal proximity to deposits with significant myrmecofaunas.

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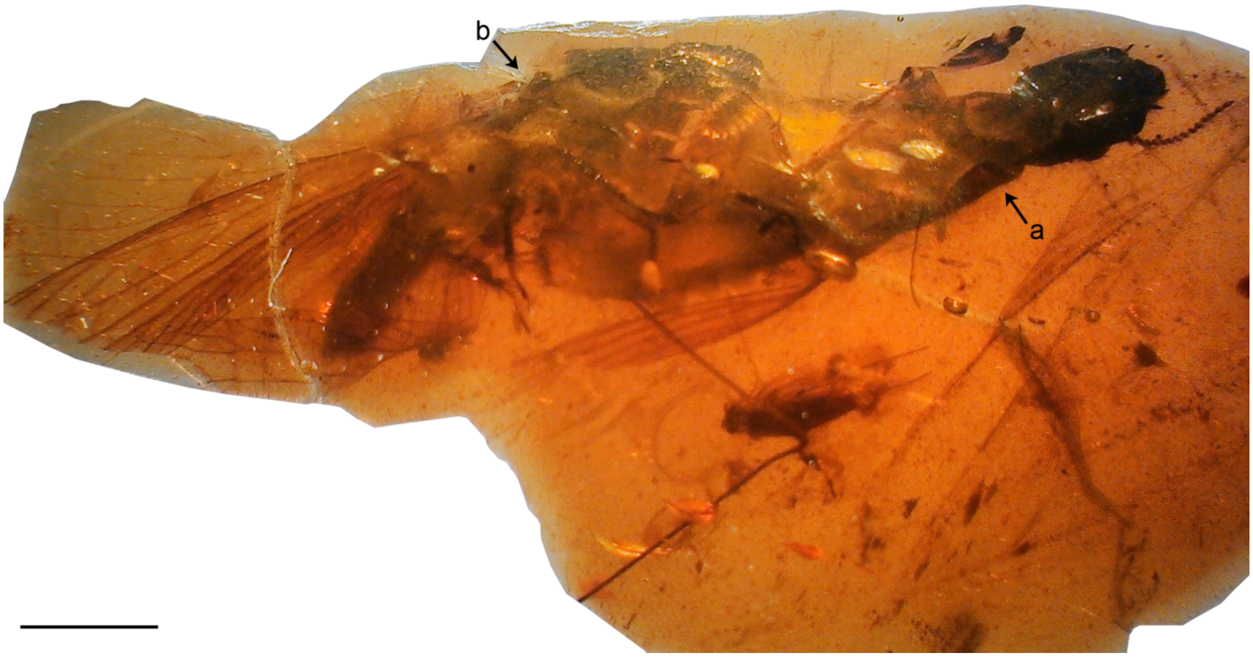

Fig. 1. Photograph of the holotype (specimen MCNA 14936a) and paratype (specimen MCNA 14936b) of *Ithytermes montoyai* gen. et sp. nov. in Peñacerrada amber. Scale bar: 2 mm.

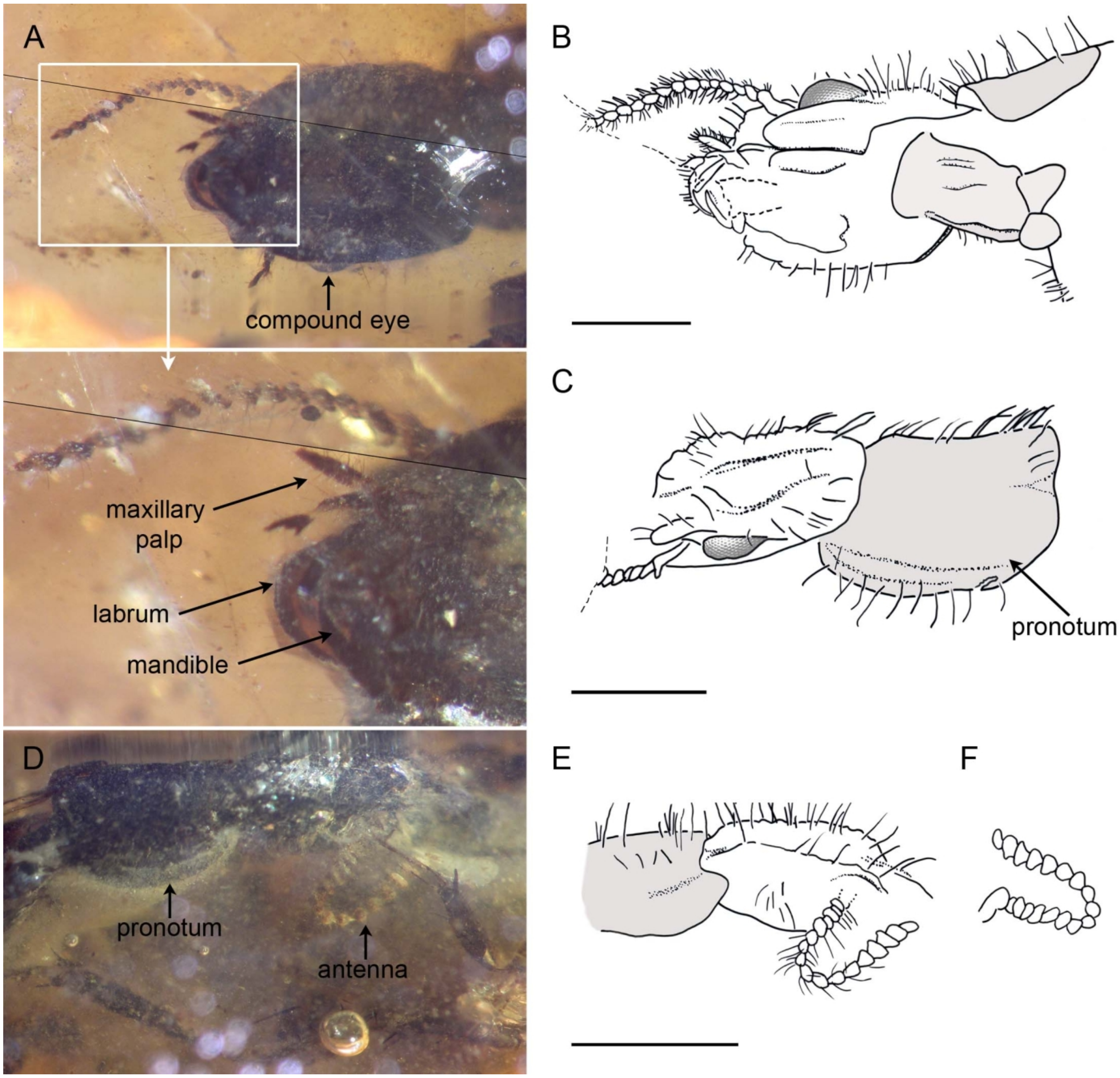

Fig. 2. Details of the holotype (subfigures A, B, C, specimen MCNA 14936a) and paratype (subfigures D, E, F, specimen MCNA 14936b) of *Ithytermes montoyai* gen. et sp. nov. A, microphotograph of head in ventral view showing details of left antenna and mouthparts (magnified area). B, camera lucida drawing of head in ventrolateral view. C, camera lucida drawing of head and pronotum in dorsolateral view. D, microphotograph of head and pronotum in lateral view. E, camera lucida drawing of head and pronotum in lateral view. F, camera lucida

drawing of right antenna. Scale bars: A, B – 1 mm (both to the same scale); C, 1 mm; D, E, F – 1 mm (all to the same scale).

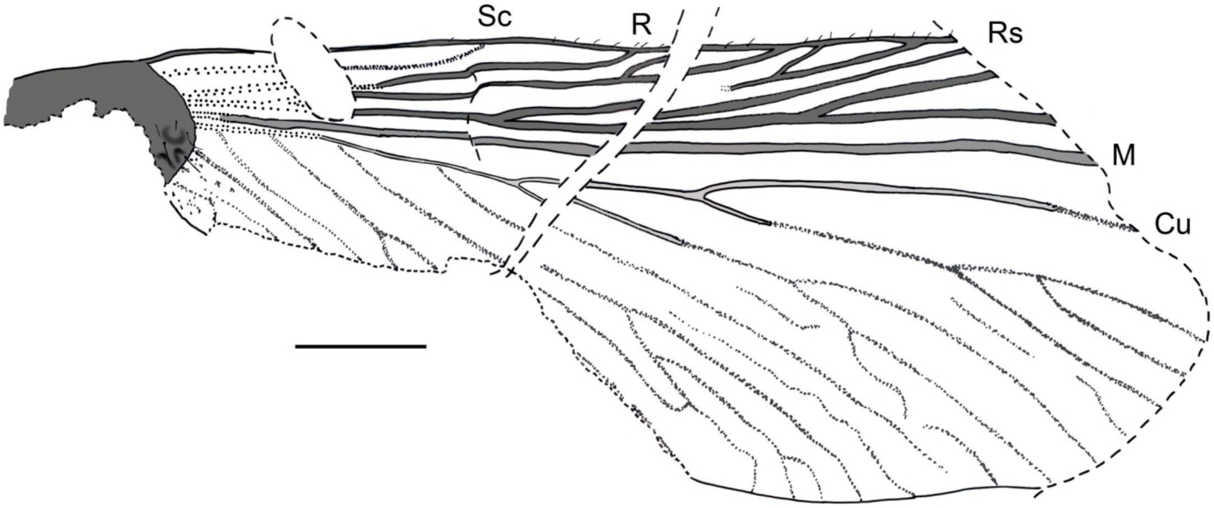

Fig. 3. Camera lucida drawing of the right forewing of the paratype of *Ithytermes montoyai* gen. et sp. nov., specimen MCNA 14936b.

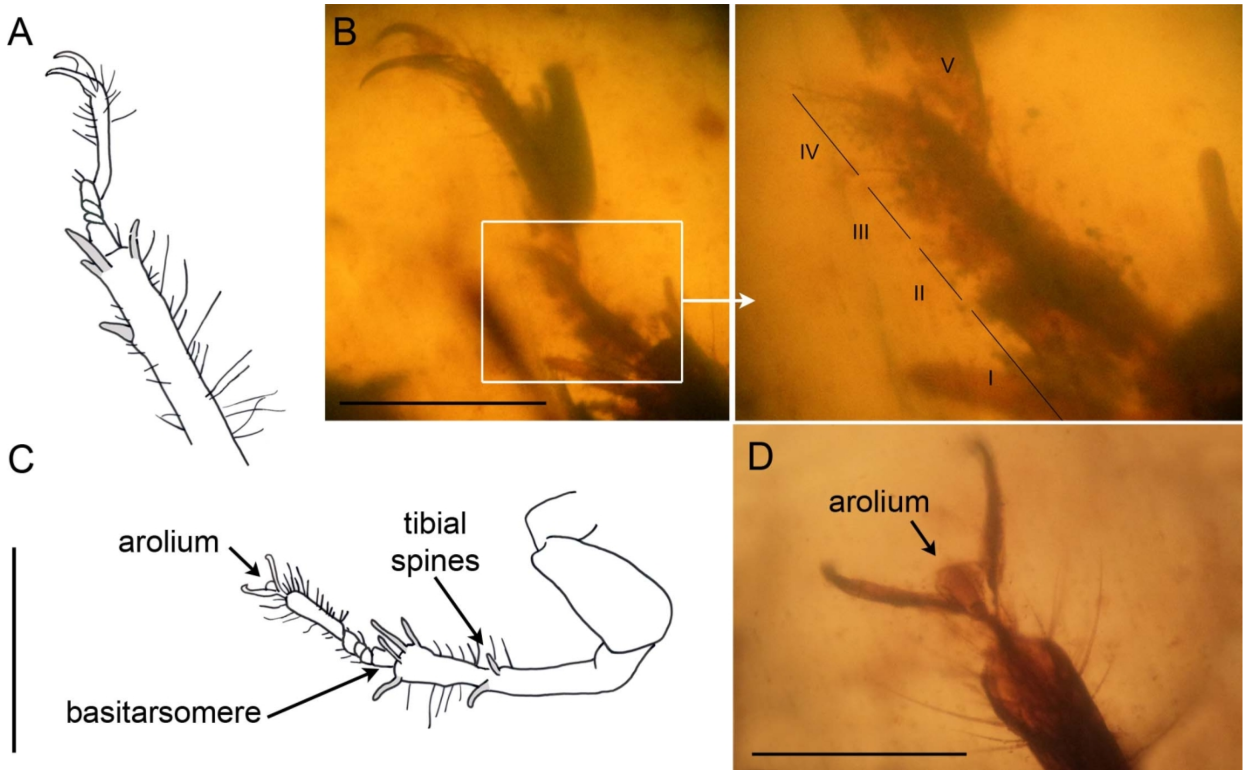

Fig. 4. Details of the paratype of *Ithytermes montoyai* gen. et sp. nov., specimen MCNA 14936b. A, Camera lucida drawing of right metatibial apex, metatarsus, and metapretarsus, lateral view. B, microphotographs of right metatarsus, and metapretarsus, lateral view. See detail of tarsal segmentation in the magnified area. C, Camera lucida drawing of entire right midleg showing stout femur and tibia, spination, and tarsal segmentation. D, microphotograph of arolium. Scale bars: A, C – 1 mm (both to the same scale); B – 0.5 mm; D – 0.25 mm.

Fig. 5. Photograph of Indeterminate specimen CES 552 in El Soplao amber.

Table 1. Described Cretaceous amber termites (Isoptera).

Species	**Locality**	**Age**
Melqartitermes myrrheus Engel, Grimaldi & Krishna, 2007	Lebanon	Barremian
Lebanotermes veltzae Engel, Azar & Nel, 2011	Mdeyrij-Hammana, Lebanon	Barremian
Indeterminate (Engel et al., 2011)	Mdeyrij-Hammana, Lebanon	Barremian
Indeterminate (Engel et al., 2011)	Mdeyrij-Hammana, Lebanon	Barremian
Indeterminate (Engel et al., 2011)	Mdeyrij-Hammana, Lebanon	Barremian
***Ithytermes montoyai*, gen. et sp. nov.**	**Peñacerrada I, Spain**	**Albian**
Cantabritermes simplex Engel & Delclòs, 2010	Peñacerrada I, Spain	Albian

Morazatermes krishnai Engel & Delclòs, 2010	Peñacerrada I, Spain	Albian
Indeterminate (herein)	**El Soplao, Spain**	**Albian**
Indeterminate (herein)	**El Soplao, Spain**	**Albian**
Aragonitermes teruelensis Engel & Delclòs, 2010	San Just, Spain	Albian
Anisotermes xiai Zhao, Eggleton & Ren, 2019	Kachin, Myanmar	Cenomanian
Archeorhinotermes rossi Krishna & Grimaldi, 2003	Kachin, Myanmar	Cenomanian
Dharmatermes avernalis Engel, Grimaldi & Krishna, 2007	Kachin, Myanmar	Cenomanian
Ginormotermes rex (Engel, Barden & Grimaldi, 2016)	Kachin, Myanmar	Cenomanian
Kachinitermes tristis (Cockerell, 1917)	Kachin, Myanmar	Cenomanian
Kachinitermopsis burmensis (Poinar, 2009)	Kachin, Myanmar	Cenomanian
Krishnatermes yoddha Engel, Barden & Grimaldi, 2016	Kachin, Myanmar	Cenomanian
Mastotermes monostichus Zhao, Eggleton & Ren, 2019	Kachin, Myanmar	Cenomanian
Mylacrotermes cordatus Engel, Grimaldi & Krishna, 2007	Kachin, Myanmar	Cenomanian
Proelectrotermes holmgreni Engel, Grimaldi & Krishna, 2007	Kachin, Myanmar	Cenomanian
Proelectrotermes swinhoei (Cockerell, 1916)	Kachin, Myanmar	Cenomanian
Tanytermes anawrahtai Engel, Grimaldi & Krishna, 2007	Kachin, Myanmar	Cenomanian
Lutetiatermes priscus Schlüter, 1989	Bezonnais, France	Cenomanian
Mastotermes sarthensis Schlüter, 1989	Bezonnais, France	Cenomanian
Santonitermes chloeae Engel, Nel & Perrichot, 2011	Archingeay, France	Cenomanian
Syagriotermes salomeae Engel, Nel & Perrichot, 2011	Archingeay, France	Cenomanian
Indeterminate (Engel et al., 2011)	Archingeay, France	Cenomanian
Carinatermes nascimbenei Krishna & Grimaldi, 2000	New Jersey, USA	Turonian
Termitotron vendeense Engel, 2014	Garnache 1, France	Turonian
Indeterminate (Engel & Delclòs, 2010)	Grassy Lake, Canada	Campanian