New, primitive termites (Isoptera) from Early Cretaceous ambers of France and Lebanon

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A b s t r a c t

Three new genera and species of primitive termites (Isoptera) are described and figured from Early Cretaceous French and Lebanese ambers: *Santonitermes chloeae* Engel, Nel & Perrichot, n. gen., n. sp., from an imago preserved in Charentese amber (Albian–Cenomanian); *Syagriotermes salomeae* Engel, Nel & Perrichot, n. gen., n. sp., from an alate detected in opaque amber from the same locality and reconstructed using synchrotron microtomographic imaging; and *Lebanotermes veltzae* Engel, Azar & Nel, n. gen., n. sp., from an alate preserved in Lebanese amber (Aptian). The three genera exhibit primitive features of the *Meiatermes*-grade of early isopteran genera (sensu Engel et al. 2009). In addition, three further fragmentary specimens from Lebanon amber are reported, each apparently distinct from *Lebanotermes* n. gen. and the previously described *Melqartitermes* Engel et al., 2007. The new fossils further document the diversity and morphological disparity of 'lower' termite groups during the Early Cretaceous, highlighting the importance of palaeontological material for understanding isopteran phylogeny as well as the diversification of Isoptera in the latest Jurassic and Early Cretaceous.

K e y w o r d s : Isoptera, *Meiatermes*-grade, new genera, Early Cretaceous, amber, France, Lebanon.

Z u s a m m e n f a s s u n g

Drei neue Gattungen und Arten ursprünglicher Termiten (Isoptera) werden aus unterkreidezeitlichem Bernstein von Frankreich und dem Libanon beschrieben und abgebildet: *Santonitermes chloeae* Engel, Nel & Perrichot, n. gen., n. sp., nach einer Imago im Bernstein von Charentese (Albium–Cenomanium); *Syagriotermes salomeae* Engel, Nel & Perrichot, n. gen., n. sp., nach einem geflügelten Exemplar in opakem Bernstein derselben Fundstelle, das mittels Synchronton-Microtomographie rekonstruiert werden konnte; und *Lebanotermes veltzae* Engel, Azar & Nel, n. gen., n. sp., nach einem geflügelten Exemplar im Libanon-Bernstein (Aptium). Die drei Gattungen zeigen die ursprünglichen Eigenschaften des *Meiatermes*-Übergangsstadiums innerhalb der frühen Termitengattungen (sensu Engel et al. 2009). Darüber hinaus werden drei weitere, fragmentarische Exemplare aus dem Libanon-Bernstein nachgewiesen, die sich von *Lebanotermes* n. gen. und der früher beschriebenen Gattung *Melqartitermes* Engel et al., 2007 unterscheiden. Die neuen Fossilien dokumentieren weiterhin die Diversität und morphologische Unterschiedlichkeit der „niederen" Termitengruppen in der Unteren Kreidezeit, und betonen dadurch die Bedeutung von paläontologischem Material für das Verständnis der Termitenstammesgeschichte sowie die Diversifizierung der Termiten im Oberen Jura und der Unteren Kreide.

C o n t e n t s

1. Introduction

Our knowledge of Mesozoic Isoptera has increased greatly in recent years, with the discoveries of Martínez-Delclòs & Martinell (1995), Ren (1995), Fontes & Vulcano (1998), Krishna & Grimaldi (2000, 2003), Martins-Neto et al. (2006), Francis & Harland (2006), Bechly (2007), Grimaldi et al. (2008), Engel et al. (2007a, 2009), Vršanský (2008), Poinar (2009), Engel & Delclòs (2010), and Colin et al. (2011). Some of these works report on indirect evidences from trace fossils such as wood borings (Francis & Harland 2006), or coprolites (Colin et al. 2011), which cannot be attributed to any precise family of termites. Direct evidence is provided by compression fossils and amber inclusions, although many of these specimens are more-or-less fragmentary wings or poorly preserved. Notable exceptions include the recently revised diversity from the Crato Formation of Brazil (Grimaldi et al. 2008) as well as species preserved with remarkable fidelity in amber from Lebanon, Myanmar, Spain, New Jersey, and Canada (Krishna & Grimaldi 2000, 2003; Engel et al. 2007a; Engel & Delclòs 2010). These species have proven of considerable value for phylogenetic analyses of Isoptera, highlighting the importance of fossils for

reconstructing relationships in this ecological dominant lineage of insects (Engel et al. 2009; Ware et al. 2010). Accordingly, the discovery of new termites from the Mesozoic is of significance. We report here on new material and taxa preserved in Early Cretaceous amber from France and Lebanon, further highlighting the past geological diversity of this important order.

Acknowledgements

We warmly thank Eric Dépré and his daughters Chloé and Salomé who collected and gave us amber pieces containing some of the specimens described herein. We also thank Gilbert Hodebert (MNHN illustrator) for the drawings. Partial support for this work was provided by the French National Research Agency grant BLAN07-1-184190 (project AMBRACE to D. N.), by the ESRF through attribution of inhouse beamtime on the beamline ID19, by the Lebanese University through the project "Biodiversity: Origin, Structure, Evolution, and Geology" (to D. A.), and by US National Science Foundation grants EF-0341724 HymAToL and DEB-0542909 (both to M. S. E.). This is a contribution of the Division of Entomology, University of Kansas Natural History Museum.

2. Material and methods

Amber pieces that contain the French termites published herein come from the Albian–Cenomanian lignitic clay exposed in the Font-de-Benon Quarry between the villages of Archingeay and Les Nouillers, Charente-Maritime, south-western France. One out of four pieces was collected within the uppermost of two amber-bearing strata occurring in this quarry, i. e. the lithological level A2a (Lower Cenomanian) sensu Gomez et al. (2008). The three other pieces were collected within the lithological level A1sl2 (uppermost Albian–lowermost Cenomanian) sensu Néraudeau et al. (2002) (= A1sl-A sensu Perrichot et al. 2010).

The Lebanese specimens come from the most fossiliferous amber outcrop of the country, named Mdeyrij-Hammana, in Baabda, Mount Lebanon district. Amber is found in clay-sandstone which is dated as Early Aptian, although possibly Late Barremian (Azar et al. 2010). Details on the age, geological settings, and palaeobiota of the French and Lebanese amber deposits are reviewed in Perrichot et al. (2010) and Azar et al. (2010), respectively.

Morphological terminology used herein generally follows that of Engel et al. (2007a, 2007b, 2009) and Grimaldi et al. (2008). Specimens preserved in more-or-less transparent amber were studied using different stereomicroscopes, and drawings and photographs were made with a camera lucida and a digital camera, respectively, both attached to the stereomicroscopes. One of the new French species is based upon a single specimen preserved in a piece of opaque, milky amber. It was detected during a large survey of the opaque Charentese amber which was performed at beamline ID19 of the European Synchrotron Radiation Facility (ESRF Grenoble, France) using propagation phase contrast X-ray synchrotron microradiography, and then three-dimensionally imaged using microtomography (PPC-SRμCT), following the method described in Lak et al. (2008) and Soriano et al. (2010). The specimen was scanned with a monochromatic beam using a RuB4C multilayer with a set energy of 25 keV. The scan consisted of 1500 images with 0.5 seconds of exposure time each, acquired along a 180 degrees rotation, with a sample/detector distance of 40 mm and a resolution of 7.44 μm for the complete specimen. A scan of the legs was performed to observe the structures with more detail, which was composed of 1500 images with 0.3 seconds of exposure time each, obtained through a 180 degrees rotation of the sample, with a set energy of 25 keV, sample/detector distance of 25 mm and optic resolution of 1.4 μm. All the microtomographic data (original slices, segmentation files, animations, and stereolithographic models) are available at the ESRF paleontological online database (http://paleo.esrf.eu), and 3D models in ABS plastic are deposited with the holotype in University of Rennes 1, in the Entomology Division of the University of Kansas, and at beamline ID19 of the ESRF. All specimens from Charentese amber are housed in the Geology Department of Rennes University, while the Lebanese specimens are housed in the Muséum National d'Histoire Naturelle, Paris, France.

3. Systematic palaeontology

Order Isoptera Brullé, 1832
Family incertae sedis

Genus *Santonitermes* Engel, Nel & Perrichot, n. gen.

Typus generis: *Santonitermes chloeae* n. sp.

Derivatio nomimis: The new genus-group name is a combination of Santones, the name of the Gallic tribe to first inhabit the Saintonge within the region of Poitou-Charentes (their name formed the Roman appellation of the city of Saintes – Mediolanum Santonum), and 'Termes' (Latin, "wood-boring"), the common generic suffix in Isoptera. The name is masculine.

Diagnosis (Imago). – Head rounded, lateral and posterior margins gently rounded; antenna moniliform, with 14 preserved articles (similar to *Mylacrotermes* Engel et al., 2007); compound eyes circular, relatively small; occipital carina present; ventral cervical sclerites absent (present in *Mylacrotermes*), lateral cervical sclerites elongate, without longitudinal groove, lateral parts widening posteriorly to meet relatively large posterior intercervical portion; pronotum about as wide as head; procoxa without keel; tibial spur formula 3-4-4, with closely approximated

subapical spine on mesotibia and two subapical spines on metatibia; tarsi completely pentamerous; arolium absent; forewing Rs with two inferior branches; M with only two branches; CuA well-developed, with numerous posterior branches; wing membrane hyaline, with faint reticulations; apicalmost abdominal sternum large, medioapically with small emargination; cerci five-segmented.

Santonitermes chloeae Engel, Nel & Perrichot, n. sp.
Figs. 1–2

Holotypus: IGR.ARC-328.4 (coll. E. Dépré), an alate missing most of its dorsal surface, preserved in a piece of amber with a Coleoptera: Belidae, a Hymenoptera: Mymarommatidae, and a Raphidioptera: Mesoraphidiidae; deposited in the amber

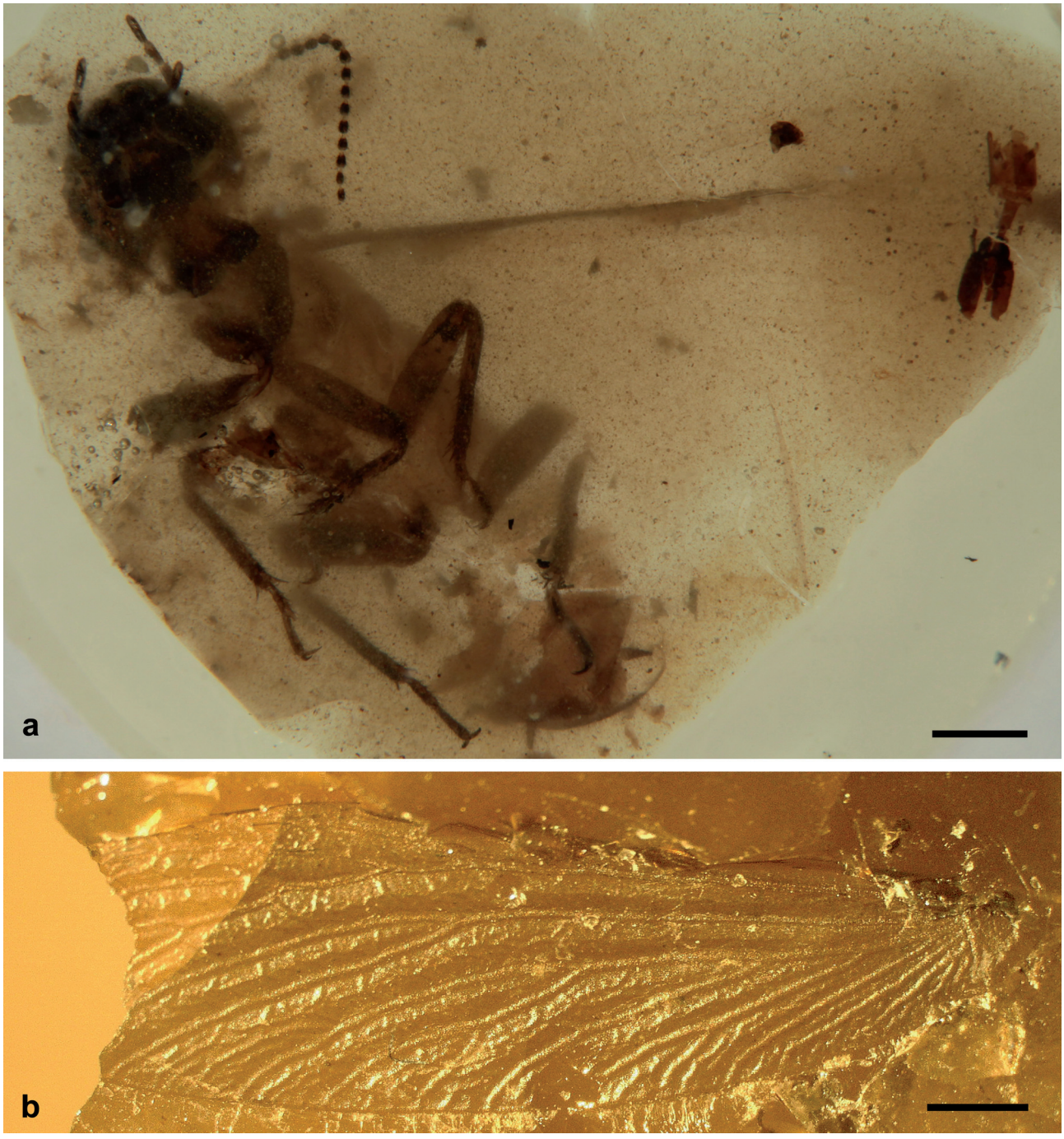

Fig. 1. *Santonitermes chloeae* n. gen., n. sp., holotype IGR.ARC-328.4, in Albian–Cenomanian Charentese amber. – **a**. Habitus in dorsal view. **b**. Imprint of forewing at surface of amber. – Scale bars: 1 mm.

collection of the Department of Geosciences of the University Rennes 1, Rennes, France.

D e r i v a t i o n o m i n i s : The specific epithet is a matronym honoring Chloé Dépré, daughter of the collector of the holotype.

L o c u s t y p i c u s : Font-de-Benon Quarry, 1 km east of Archingeay, Charente-Maritime, France.

S t r a t u m t y p i c u m : Mid-Cretaceous, Uppermost Albian–Lowermost Cenomanian, lithological subunit A1sl-A.

D i a g n o s i s . – As for the genus (vide supra).

D e s c r i p t i o n . – Head, pronotum dark brown; legs brown, lighter than head and pronotum; antennae yellowish brown; wing apparently hyaline; pilosity of body not preserved; wing apparently bare, without nodules or seta, membrane apparently reticulate (faintly preserved in specimen). Head generally round; width with compound eyes nearly equal to length to side base of mandibles (Figs. 1a, 2a); dorsal surface of head not preserved; compound eyes only partly preserved, small, round, moderately convex; mandibles partly visible but dentition not entirely discernable, with at least four teeth (Fig. 2a); antenna moniliform, 14 antennal articles preserved. Main part of pronotum not preserved but at most as broad as head with compound eyes. Procoxa unmodified; tibial spurs 3-4-4; pro- and mesotibia with one visible lateral spine, but none on hind tibia; tarsus pentamerous, basal four tarsomeres with a ventral row of six strong spines (Fig. 2b); pretarsal claws simple, arolium absent. Cerci five-segmented. Forewing membrane with weak reticulation; humeral suture nearly completely missing (only its length can be established, it just reaches the level of the base of the hind wing scale); Sc and R1 scarcely visible, no clear R2+3; Rs with six strong branches, regularly disposed, the two distals reaching apico-posterior margin of wing (Fig. 1b); area between Rs and anterior wing margin 0.7 mm wide; M separated from R in wing scale; M weakly developed, divided into two simple branches in distal two-thirds of wing length; CuA well-developed, with 10 posterior branches, covering main part of wing. Hind wing not preserved. Length of head to side base of mandibles 1.8 mm, width of head 2.0 mm; diameter of compound eye 0.5 mm, length of metatibia 2.0 mm; length of forewing scale about 1.0 mm; length of forewing from suture about 9.0 mm, width of forewing about 3 mm; length of abdomen 5.7 mm.

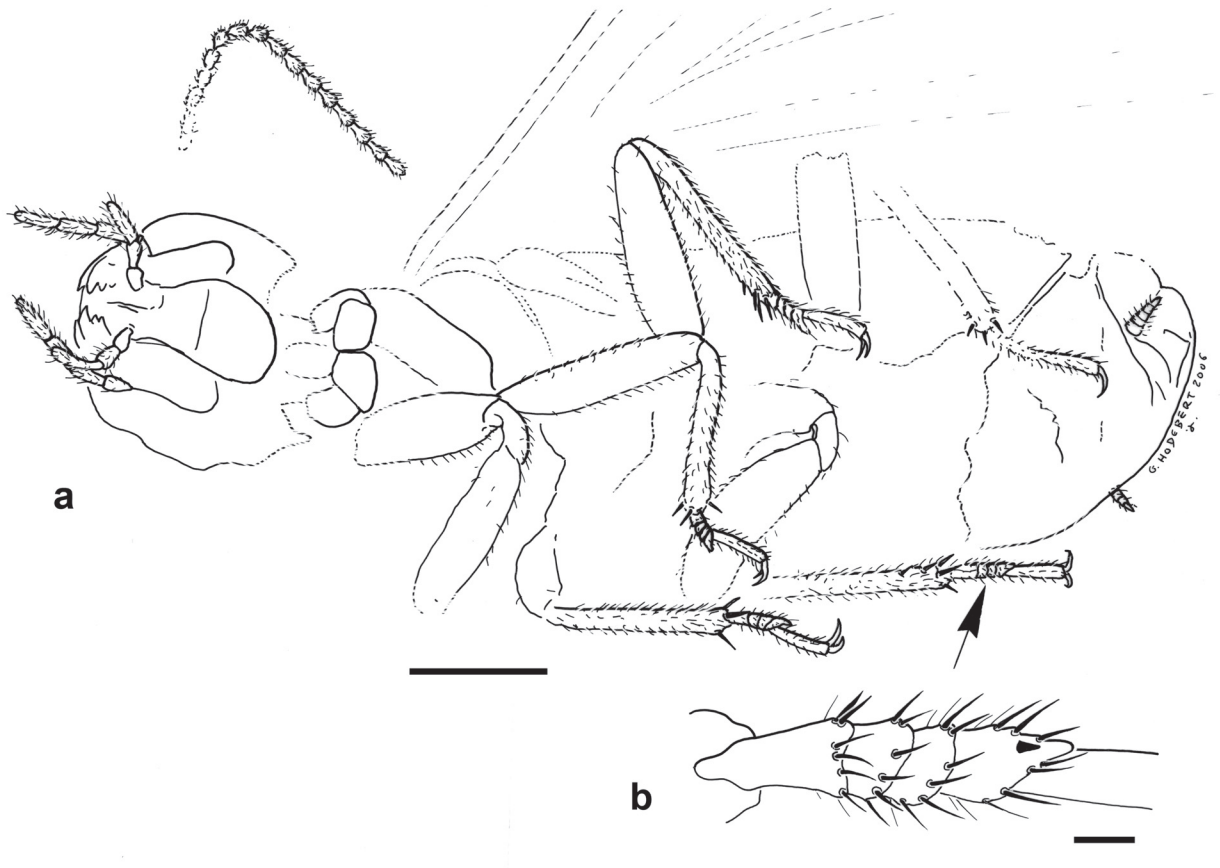

Fig. 2. *Santonitermes chloeae* n. gen., n. sp., holotype IGR.ARC-328.4, in Albian–Cenomanian Charentese amber. – **a**. Habitus diagram in ventral view. **b**. Detail of hind tarsus. – Scale bars: 1 mm and 0.1 mm, respectively.

D i s c u s s i o n . – The affinities of Cretaceous termites have undergone a significant shift owing to revised cladistic work across the order (Engel et al. 2009). The broad radial area with numerous branches of Rs, including some inferior branches, excludes affinities with the Neoisoptera and Archeorhinotermitidae Krishna & Grimaldi, 2003, as well as the Kalotermitidae Froggatt, 1896, based on the latter character (among others). *Santonitermes* n. gen. can similarly be excluded from the basal termite families, except Mastotermitidae Desneux, 1904, owing to the combined presence of the occipital carina and completely pentamerous tarsi. The Mastotermitidae are also excluded owing to the absence of an arolium, the reduced number of antennal articles, the absence of a procoxal keel, more narrow pronotum, and shorter cerci.

Santonitermes is allied to a grade of genera forming a stem series basal in the Euisoptera and relative to the 'lower' termite families (excluding Mastotermitidae) (Engel et al. 2009). Among this grade (the "*Meiatermes*-grade"), *Santonitermes* shares some superficial similarity with *Mylacrotermes* in latest Albian amber from Myanmar (Engel et al. 2007a). However, the former differs from the latter by the absence of ventral cervical sclerites, the posteriorly broadened lateral portion of the lateral cervical sclerites, the absence of procoxal keels, the narrower pronotum, the 3-4-4 tibial spur formula, and the shorter cerci. From *Carinatermes* Krishna & Grimaldi, 2000, in Turonian amber from New Jersey, *Santonitermes* differs in its narrower pronotum and absence of procoxal keels. From *Meiatermes* Lacasa-Ruiz & Martínez-Delclòs, 1986, as revised by Grimaldi et al. (2008), *Santonitermes* differs by smaller number of antennal articles, the absence of arolia (minute in *Meiatermes*), and the pronotum not wider than the head (slightly wider in *Meiatermes*).

Ren (1995) described several Cretaceous genera and species that could be loosely assigned to the "*Meiatermes*-grade". These taxa include *Jitermes tsaii*, *Yanjingtermes giganteus*, *Yondingia opipara*, *Huaxiatermes huangi*, *Asiatermes reticulatus*, *Mesotermopsis incompleta*, and *Mesotermopsis lata* (formerly in the genus *Mesotermes* Ren, 1995) (Engel & Ren 2003). All of these are based solely on wing venation and all differ from *Santonitermes* in a strongly developed vein M, with four or more branches.

Genus and species indeterminate 1
Fig. 3a

M a t e r i a l : Specimen IGR.ARC-383.2, in amber from Font-de-Benon Quarry, 1 km east of Archingeay, Charente-Maritime, France; mid-Cretaceous, Uppermost Albian–Lowermost Cenomanian, lithological subunit A1sl-A. Specimen IGR.ARC-A2-385 (coll. E. Dépré), in amber from Font-de-Benon Quarry, 1 km east of Archingeay, Charente-Maritime, France; mid-Cretaceous, Lowermost Cenomanian, lithological subunit A2a; both deposited in the amber collection of the Department of Geosciences of the University Rennes 1, Rennes, France.

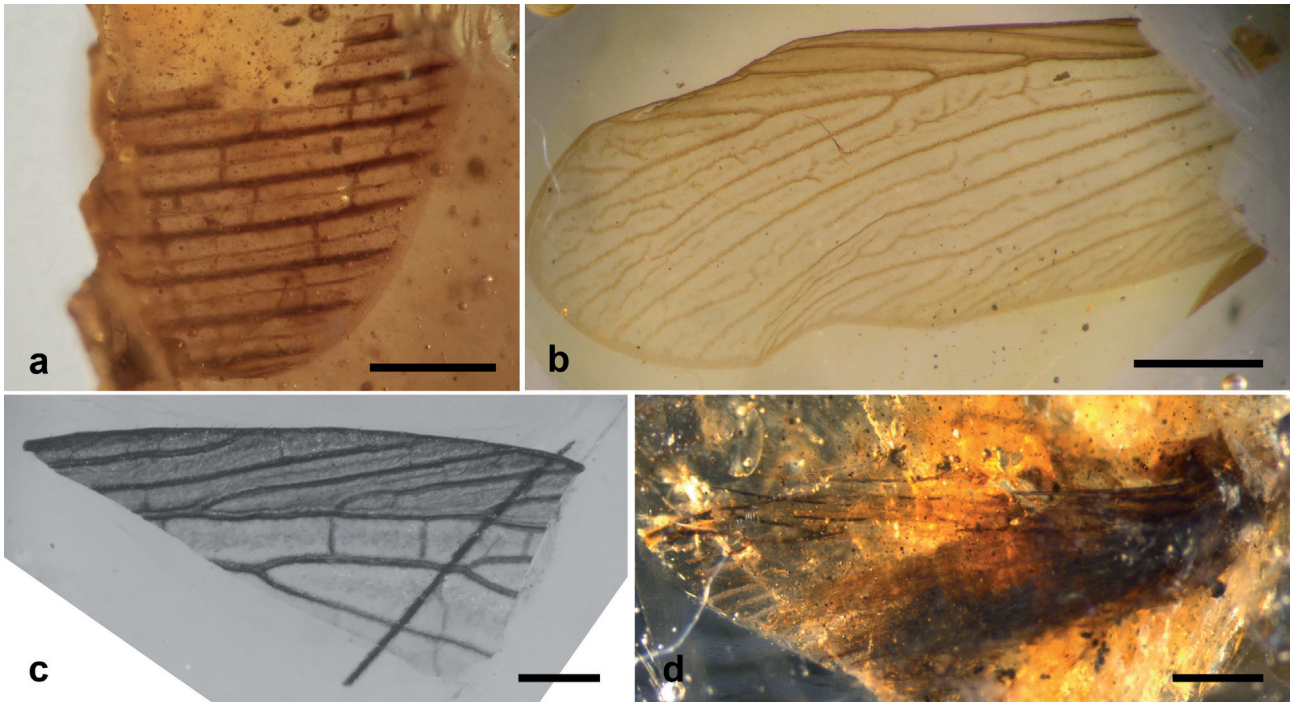

Fig. 3. Wings fragments of undetermined termites from Lower Cretaceous amber. – **a**. Specimen IGR.ARC-A2-385, in Albian–Cenomanian Charentese amber. **b**. Specimen 679. **c**. Specimen 732. **d**. Specimen 1283, in Aptian Lebanese amber. – Scale bars: 0.5 mm.

C o m m e n t s . – These pieces include minute shreds of the fore- and hind wing of termites, none of which are sufficiently large to determine them to any level of certainty, or even to ascribe them to a morphospecies. From the fragments it is clear that the wing membrane was reticulate and there was a relatively dense venation pattern, as is found in many (if not most) Cretaceous termite genera. These might be fragments of further *Santonitermes chloeae* specimens but there is no way this could be determined with any level of confidence.

Genus *Syagriotermes* Engel, Nel & Perrichot, n. gen.

T y p u s g e n e r i s : *Syagriotermes salomeae* n. sp.

D e r i v a t i o n o m i n i s : The new genus-group name is a combination of Syagrius (430–486/7 AD), the last Roman 'magister militum' of ancient Gaul (eventually being overrun by Clovis I of the Salian Franks), and 'Termes', common generic suffix in the Isoptera. The name is masculine.

D i a g n o s i s (Alate). –Pronotum apparently as wide as head (based on preserved fragments of posterior border of head and anterior of pronotum). Tibial spur formula apparently 3-4-4; tibiae without outer spines; all tarsi pentamerous; pretarsal claws simple, arolium present and large. Forewing with membrane highly reticulate and

Fig. 4. *Syagriotermes salomeae* n. gen., n. sp., holotype IGR.ARC-284.1, in Albian–Cenomanian Charentese amber. Synchrotron microtomographic 3D rendering of the habitus (a–e) and right legs (f–h). – **a**. Dorsal view. **b**. Right lateral view. **c**. Left lateral view. **d**. Ventral view. **e**. Posterior view. **f**. Fore leg. **g**. Mid leg. **h**. Hind leg. – Scale bars: 1 mm.

rounded apex; forewing scale large, easily overlapping hind wing scale, basal suture convex; all veins originating inside wing scale; termination of CuP (claval fissure) on posterior margin apparently prior to basal suture; Sc terminating in basal quarter of wing length; R1 apparently simple, terminating at about one-third wing length; Rs with six superior branches, no inferior branches, terminating before wing apex, radial field relatively narrow and equally wide across entire length; M simple for most of its length, running about midway between Rs and CuA in basal half of wing and then slightly diverging from CuA more apically, branching in apical one-fifth of wing length, encompassing wing apex; CuA extending to point tangential with Rs apical termination, highly-branched, at least eight primary branches encompassing entire posterior wing margin. Abdomen relatively narrow as preserved, cylindrical; cerci not evident.

Syagriotermes salomeae Engel, Nel & Perrichot, n. sp.
Fig. 4

Holotypus: IGR.ARC-284.1, preserved in a piece of fully opaque amber, visualized using; deposited along with its 3D printout in the amber collection of the Department of Geosciences of the University Rennes 1, Rennes, France.

Derivatio nominis: The specific epithet is a matronym honoring Salomé Dépré, second daughter of Eric Dépré, the most prolific collector of amber from Charentes.

Locus typicus: Font-de-Benon Quarry, 1 km east of Archingeay, Charente-Maritime, France.

Stratum typicum: Mid-Cretaceous, Uppermost Albian–Lowermost Cenomanian, lithological subunit A1sl-A.

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

Description. – The following description provides minor metrics as a supplement to the generic diagnosis: Total body length as preserved 4 mm; forewing length 5.8 mm, maximum width 1.5 mm; abdominal length as preserved 2.24 mm, maximum width 1.1 mm; metafemur length 0.68 mm, maximum width 0.3 mm; metatibial length 0.8 mm.

Discussion. – Unfortunately, the head of this fossil is largely missing and significant portions of the thorax are similarly partially preserved. Details of the legs, abdomen, and wings were easily visualized from the 3D reconstructions permitting a careful comparison of this species with other Cretaceous taxa. The relatively narrow radial field which does not encompass the wing apex is similar to several other Early Cretaceous genera such as *Cratokalotermes* Bechly, 2007, *Cantabritermes* Engel & Delclòs, 2010, and *Aragonitermes* Engel & Delclòs, 2010, also sharing with these genera a highly reticulate wing membrane. From *Cratokalotermes* the new genus differs in the more elongate R_1 and the less expansive M, differing in this last character also from *Cantabritermes* and *Aragonitermes*. The genus differs further from *Aragonitermes* in the absence Rs_2 and of inferior branches on Rs (both present in *Aragonitermes*).

Genus *Lebanotermes* Engel, Azar & Nel, n. gen.

Typus generis: *Lebanotermes veltzae* n. sp.

Derivatio nominis: The new genus-group name is a combination of Lebanon and 'Termes' (Latin, "wood-boring"), the common generic suffix in Isoptera. The name is masculine.

Diagnosis. – Pronotum about as wide as head. Procoxa with small keel; tibial spur formula 3-4-4; meso- and metatibia with three lateral spines; tarsus completely pentamerous; arolium absent. Forewing Sc short; fore- and hind wing Rs with numerous anterior branches, M with four branches; hind wing cubito-anal area very broad, without anal fan; wing membranes with reticulations. Cerci five-segmented.

Lebanotermes veltzae Engel, Azar & Nel, n. sp.
Figs. 5–6

Holotypus: Specimen 341C, coll. Azar, an alate missing posterodorsal surface of head and a dorsal portion of pronotum, bearing 13 phoretic astigmatan Acari, and also preserved with a Hemiptera: Aleyrodidae and a Diptera: Chironomidae; provisionally deposited in the Muséum National d'Histoire Naturelle, Paris.

Derivatio nominis: The specific epithet is a matronym honoring colleague Dr. Isabelle Veltz.

Stratum typicum: Lower Cretaceous, Lower Aptian.

Locus typicus: Mdeyrij-Hammana, Caza Baabda, Mount Lebanon district, Lebanon.

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

Description. – Head, pronotum dark brown; legs brown, lighter than head and pronotum (Fig. 5). Dorsal surface of head partly destroyed; ocelli not visible, maybe not preserved; 32 antennal segments, all with two rows of rather long setae, as long as width of the segments, with first to third segments equal in length, slightly longer than the others (Fig. 6b, 6c); labial palpus three-segmented; maxillary palpus with three visible segments; labrum rounded anteriorly; clypeus shorter than labrum; gula broad and short, with a median narrowing; pronotum nearly as wide as head; prothorax moderately pilose, with small bristles on ventral part; pronotum about as wide as head; prothorax moderately pilose, with small bristles on ventral part; wings apparently bare. Procoxa with small keel (Fig. 6d); profemur with groove running along inner margin; tibial spur formula 3-4-4; meso- and metatibia with three lateral spines; tarsi completely pentamerous (Figs. 6e, 6f); arolium absent. Cerci five-segmented. Wing membrane with well-developed reticulation, apparently bare; scales of wings not preserved; forewing with Sc, R1, R2+3, and Rs strongly and evenly sclerotized relative to each other;

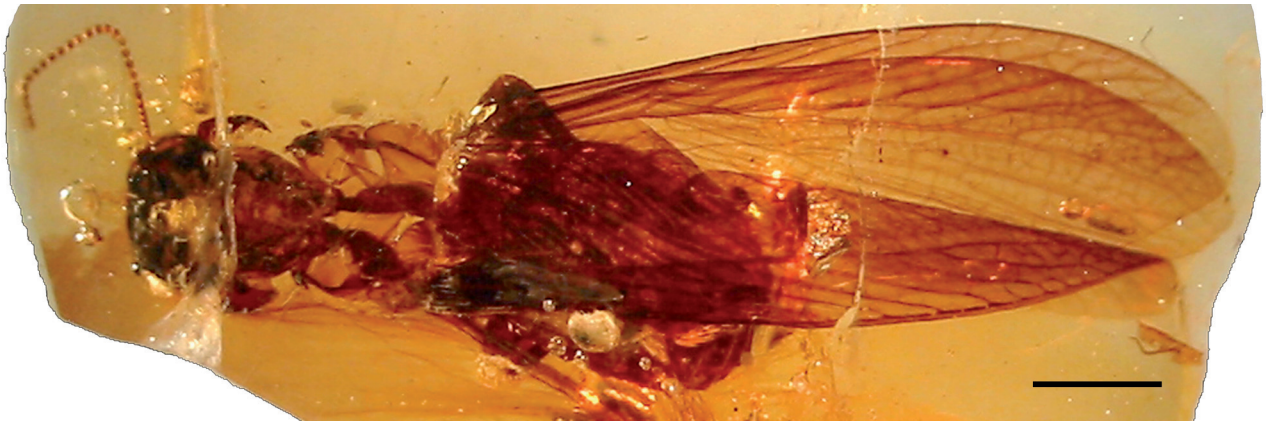

Fig. 5. *Lebanotermes veltzae* n. gen., n. sp., holotype specimen 341C, in Aptian Lebanese amber, habitus in dorsal view. – Scale bar: 2 mm.

M and CuA less distinctly sclerotized; forewing Sc rather short, simple, about 0.25 mm long; R1 and R2+3 separate and unbranched, about 0.30 mm and 0.35 mm long, respectively; Rs with seven anterior branches meeting costal margin, without inferior branches; radial area relatively broad, 1.0 mm wide; M emerging independently from R within scale, running midway between Rs and CuA, with four branches; CuA with five posterior branches. Hind wing without anal fan, M branching from Rs close to wing scale; cubito-anal area very broad, with numerous parallel branches (similar to Mastotermitidae). Head about 2.5 mm long, 2.5 mm wide; pronotum 2.0 mm long, 2.5 mm wide; metatibia length 2.1 mm; forewing length from suture 12.0 mm, width about 2.3 mm; hind wing length from suture 12.0 mm, width 2.3 mm; abdomen about 3.5 mm long, 2.7 mm wide.

D i s c u s s i o n . – The broad radial area with numerous branches of Rs and the presence of a procoxal keel excludes affinity with Stolotermitidae, Kalotermitidae, Archeorhinotermitidae, and the Neoisoptera (Engel et al. 2009). The absence of an anal fan excludes a relationship with Mastotermitidae, despite the broadened cubito-anal area. The absence of inferior branches to Rs also excludes a relationship with Termopsidae, Cratomastotermitidae,

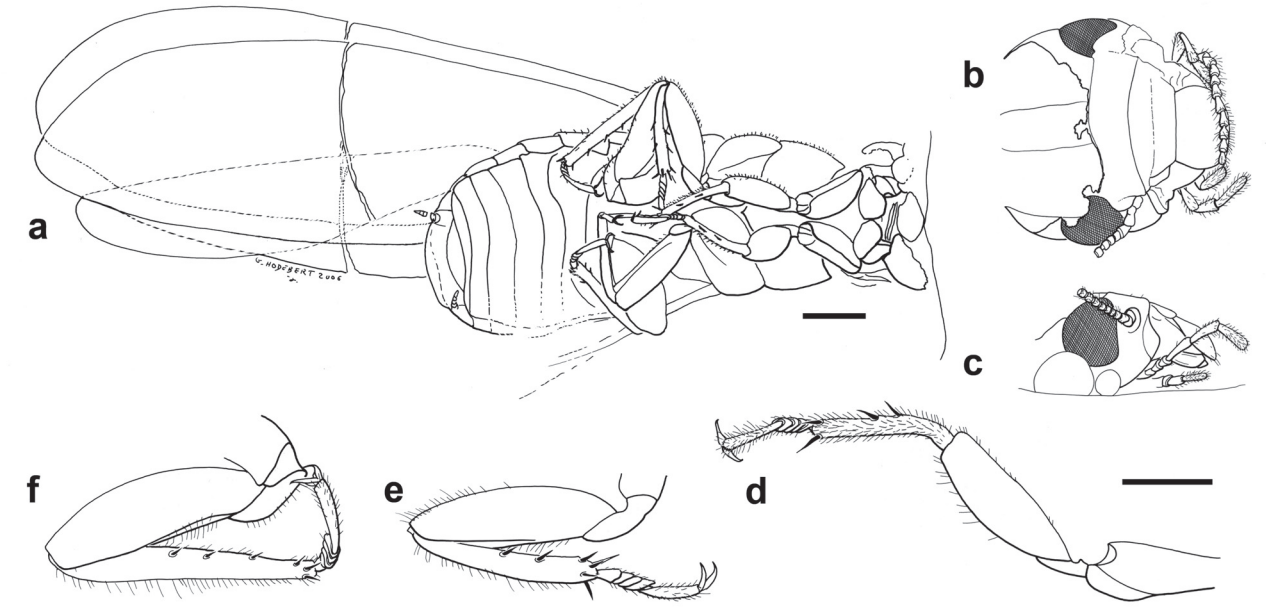

Fig. 6. *Lebanotermes veltzae* n. gen., n. sp., holotype specimen 341C, in Aptian Lebanese amber. – **a**. Habitus diagram in ventral view. **b**. Head in dorsal view. **c**. Head in lateral view. **d**. Left fore leg. **e**. Mid leg. **f**. Hind leg. – Scale bars: 1 mm.

many Mastotermitidae, and genera such as *Meiatermes*. The procoxal keel seen in *Lebanotermes* is a plesiomorphic feature among several primitive termite genera, such as *Carinatermes*. *Lebanotermes* also shares with *Carinatermes* the forewing media branches occupying a large area, the pronotum about as wide as the head, the profemur with a groove along its inner margin, the absence of arolia, pentamerous tarsi, and five-segmented cerci. The former differs from this genus in the forewing radial area without clear inferior branches, the 3-4-4 tibial spur formula (3-3-3 in *Carinatermes*), and presence of two thick lateral spines on the meso- and metatibia (only one in *Carinatermes*).

Lebanotermes differs from the only other formally described genus of Lebanese amber termites, *Melqartitermes* (Engel et al. 2007a), by the absence of arolia, the short Sc (elongate in *Melqartitermes*), R1 and R2+3 separate for entire length, the presence of the procoxal keel, and the presence of the ventral profemoral groove. Otherwise *Lebanotermes* and *Melqartitermes* have some similarities in wing venation (e. g., cf. Engel et al. 2007a, text-fig. 4).

Lebanotermes differs from *Cretatermes*, *Meiatermes* (and the probable synonyms *Caatingatermes*, *Araripetermes*, *Nordestinatermes*: Grimaldi et al. 2008), *Khanitermes*, *Yanjingtermes*, *Yongdingia*, and *Asiatermes* in the absence of inferior branches of Rs. The forewing venation of *Lutetiatermes* shows some similarities with *Lebanotermes*, but the former has apparently tetramerous tarsi (Schlüter 1989, text-fig. 4). The three remaining Chinese genera *Mesotermopsis*, *Huaxiatermes*, and *Jitermes* have a wing venation similar to that of *Lebanotermes*. All these taxa are based on more-or-less complete wings. *Huaxiatermes huangi*, type species of *Huaxiatermes*, is likely a hind wing as its median vein emerges from Rs distal of the scale. The differences between *Mesotermopsis lata*, *Mesotermopsis incompleta*, *Jitermes tsaii*, and *H. huangi* are small variations of one branch in the median or the cubital veins and could well correspond to the same genus, if not the same species, based on known variability in wing venation within lower termites. In particular, *Jitermes tsaii* and *Mesotermopsis incompleta*, type species of the genus, are wings of nearly the same size and pattern of wing venation, and we accordingly suggest that they should be synonymized under the name *Jitermes tsaii*.

Note. – Kaddumi (2005) described the genus and species *Ardatermes hudaludi* from Lower Cretaceous Jordan amber, which he tentatively attributed to the Kalotermitidae (where it is certainly misplaced) but the type specimen needs to be revised and the name validated (the name is unavailable as no type species was explicitly designated, an ICZN requirement for all names after 1999). This fossil differs from *Lebanotermes* in its smaller size and only 16–17 antennal segments.

Genus and species indeterminate 2
Fig. 3b

Material: Specimen 679, coll. Azar, provisionally deposited in the Muséum National d'Histoire Naturelle, Paris.

Stratum typicum: Lower Cretaceous, Lower Aptian.

Locus typicus: Mdeyrij-Hammana, Caza Baabda, Mount Lebanon district, Lebanon.

Description. – Fragment of anterior margin of forewing, 3.0 mm wide as preserved; Rs with one inferior, one apical, and four superior branches; M with two branches; two other longitudinal veins, probably branches of CuA, visible; width of radial area 0.6 mm.

Discussion. – This specimen is clearly distinct from *Lebanotermes veltzae* n. sp. by the presence of an inferior branch on Rs. Such inferior branches are common among various primitive termite genera (e. g., *Meiatermes*, *Mariconitermes*, *Termopsis*, and the recent Hodotermitidae). Until more complete material is recovered, however, it is not possible to make a definitive statement as to the placement of this fragment.

Genus and species indeterminate 3
Fig. 3c

Material: Specimen 732, coll. Azar, provisionally deposited in the Muséum National d'Histoire Naturelle, Paris.

Stratum typicum: Lower Cretaceous, Lower Aptian.

Locus typicus: Mdeyrij-Hammana, Caza Baabda, Mount Lebanon district, Lebanon.

Description. – Fragment of anterior margin of forewing, with part of Rs (six anterior branches) and M (three branches); branches of Rs regularly disposed; width of radial area 0.5 mm.

Discussion. – This specimen is specifically distinct from *Lebanotermes veltzae* n. gen., n. sp. as evidenced by its considerably narrower radial area. The narrow radial area and the branches of Rs regularly disposed suggest that it could be related to the Kalotermitidae or the Stolotermitidae, *Cratokalotermes* (sensu Grimaldi et al. 2008), *Tanytermes* Engel et al., or *Dharmatermes* Engel et al. (Engel et al. 2007a). Hopefully more complete material will be recovered eventually so that this taxon can be fully characterized and its affinities clarified.

Genus and species indeterminate 4
Fig. 3d

Material: Specimen 1283, coll. Azar, provisionally deposited in the Department Histoire de la Terre, Muséum National d'Histoire Naturelle, Paris.

Stratum typicum: Lower Cretaceous, Lower Aptian.

Locus typicus: Mdeyrij-Hammana, Caza Baabda, Mount Lebanon district, Lebanon.

D e s c r i p t i o n . – A poorly preserved body with the head and pronotum partly visible. Only the fore wing and a fore(?) leg are relatively well preserved. Length of wing 4.5 mm, width 1.2 mm; Rs with one posterior, one apical, and four anterior branches; M with two branches; three branches of Cu visible; width of radial area 0.3 mm; five-segmented tarsus, with strong teeth but no arolia; tibia with two visible apical spurs.

D i s c u s s i o n . – The broad radial area with numerous branches of Rs excludes affinities with the Rhinotermitidae, Serritermitidae, and Termitidae. The Mastotermitidae and Termopsinae can also be excluded owing to the absence of an arolium. Affinities with the Kalotermitidae are excluded on the basis of pattern of radial veins, with some branches of Rs ending on posterior wing margin in this fossil. This wing is distinctly smaller than all other Isoptera from Hammana and certainly corresponds to a different species, still with primitive features of the "*Meiatermes*-grade" of early isopteran genera.

4. Conclusion

The presence of several different representatives of primitive termite lineages in Albian and Cenomanian ambers demonstrates that Isoptera were rather diverse during this period, albeit their abundance was apparently limited (Engel et al. 2009). It remains that several Cretaceous taxa, based on badly preserved or incomplete fossils, are enigmatic and of uncertain position. Unfortunately, these taxa are likely to remain of indeterminate position. Nonetheless, the growing number of well preserved specimens, particularly in amber, from the Cretaceous is gradually revising our understanding of early termite evolution and diversity (e. g., Engel et al. 2007a; Engel & Delclòs 2010; Grimaldi et al. 2008; those species described herein). The morphological disparity among these groups is also notably high, a situation similar to that observed among Mesozoic Odonata in which the diversity and disparity at the (sub)-family level is greater in the Mesozoic than in the Cenozoic. This suggests a diversification into numerous niches, each with considerable anatomical adaptations, followed by subsequent radiation (sometimes decoupled by a time lag) within each of these lineages. The absence of Jurassic termites in the fossil record remains surprising, even if some controversial structures have been interpreted erroneously as termite nests (Bordy et al. 2004, 2005; Genise et al. 2005). The next great challenge will be the discovery of Jurassic termites or cryptocercid-isopteran-like taxa (stem-group Isoptera) from this same period.

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