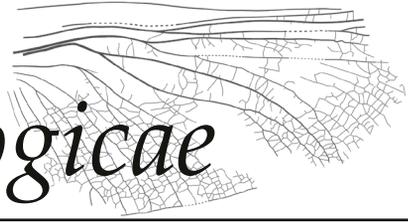


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A new fossil drywood termite species from the Late Eocene of France allied to *Cryptotermes* and *Procryptotermes* (Isoptera: Kalotermitidae)

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Abstract. A new fossil genus and species of drywood termite (Kalotermitidae) is described and figured from the Late Eocene of southern France. *Huguenotermes septimaniensis* Engel & Nel, new genus and species, is closely allied to *Cryptotermes* Banks and *Procryptotermes* Holmgren, perhaps representing part of the stem group leading to the *Cryptotermes-Procryptotermes* clade.

INTRODUCTION

Drywood termites comprise a distinctive clade (Kalotermitidae) among the grade of early-diverging families in the Isoptera (Engel *et al.*, 2009; Ware *et al.*, 2010; Krishna *et al.*, 2013). Although eusocial, like all termites, kalotermitids lack a true worker caste and instead rely upon retinues of pseudergates to undertake those tasks typically enacted by workers. As their name suggests, species establish their nests in undamaged wood, even dry, and do not require contact with soil in order to maintain the colony, relying on adaptive rectal papillae for water conservation in the hind gut (*e.g.*, Collins, 1969). These traits, as well as the ease by which they can produce secondary reproductives via nymphs or retention of alates, has allowed some to become invasive pests in various places around the world, particularly species of the genus *Cryptotermes* Banks

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(e.g., Collins, 1991; Evans *et al.*, 2013), and it is not surprising that many genera and species have broad distributions (Krishna *et al.*, 2013). As would be expected from their phylogenetic position (Engel *et al.*, 2009), kalotermitids are of considerable antiquity among Isoptera, with taxa well documented into the Early Cretaceous (e.g., Engel *et al.*, 2007a) and comparatively modern genera by the Eocene (e.g., Rosen, 1913; Weidner, 1955; Krishna, 1961; Emerson, 1969; Nel & Paicheler, 1993; Nel & Bourguet, 2006; Engel *et al.*, 2007b).

Termites are quite well documented from a diversity of deposits throughout France, and from the Miocene well into the Cretaceous (e.g., Nel & Paicheler, 1993; Nel & Bourguet, 2006; Engel *et al.*, 2011; Engel, 2014), and these include a variety of kalotermitids from the Eocene through Miocene. One French fossil of particular interest was briefly described but not named by Nel & Paicheler (1993) as a kalotermitid of uncertain generic identity (Figs. 1–4). Here we provide a new and formal description of this species and document its affinities to the modern genera *Procryptotermes* Holmgren and *Cryptotermes*.

MATERIAL AND METHODS

For the description we follow the wing terminology of Engel *et al.* (2007a, 2009) and Krishna *et al.* (2013), and the general format used elsewhere for fossil kalotermitid and other primitive species (e.g., Engel & Krishna, 2007; Engel & Delclòs, 2010). Descriptions are provided in the context of improving the elaboration of evolutionary patterns (Grimaldi & Engel, 2007). The classification adopted is that of Krishna *et al.* (2013), including retention of the name Isoptera (as an infraorder) as put forward by Lo *et al.* (2007), Engel *et al.* (2009), Engel (2011), and Krishna *et al.* (2013). Measurements were made with a Nikon SMZ 1500 stereomicroscope, while photographs were prepared with an AxioCam HRc digital camera both dry and with the pieces submerged in ethanol.

SYSTEMATIC PALEONTOLOGY

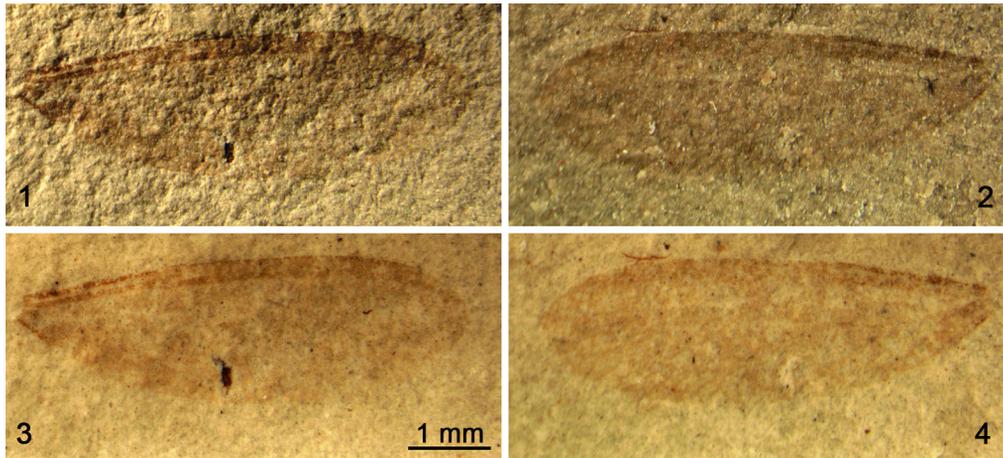
Family Kalotermitidae Froggatt

Huguenotermes Engel & Nel, new genus

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TYPE SPECIES: *Huguenotermes septimaniensis* Engel & Nel, new species.

DIAGNOSIS: The new genus, like *Cryptotermes* and *Procryptotermes*, has the hind wing with Sc absent (presumably fused to C), and M poorly sclerotized and diverging from Rs apical to but near the basal scale, then apically arcs anteriorly to terminate into Rs beyond the wing midlength (Fig. 5) (this form of M is a synapomorphy for *Procryptotermes* + *Cryptotermes*; there is an unrelated genus, *Rugitermes* Holmgren, in which M emerges and fuses with Rs but the condition is quite different whereby M is absent in the hind wing and in the forewing M terminates into Rs basal in the wing and just apical to the scale, often prior to the termination tangent of Sc, *vide* Krishna, 1961). From both genera, *Huguenotermes* differs in the probably plesiomorphic retention of a greater number of Rs branches, with eight branches (including the apicalmost extension of the stem) rather than the 3–4 in *Cryptotermes* and 4–5 in *Procryptotermes*. In this regard, the new genus has Rs more extensively developed as in genera such as *Epicalotermes*



Figures 1–4. Photographs of holotype (IPM-R.54350) hind wing of *Huguenotermes septimaniensis*, new genus and species, from the late Eocene (Priabonian) of southern France. **1.** Part as preserved. **2.** Counterpart as preserved. **3.** Part under ethanol. **4.** Counterpart under ethanol. All photos to the same scale.

Silvestri. As in *Procryptotermes*, the hind wing R1 terminates into the costal margin in the basal half of the wing, often around one-third wing length, and well prior to the tangent at which M fuses with Rs (Fig. 5), while in *Cryptotermes* R1 is frequently much longer, extending to about wing midlength or further and terminating into the costal margin near the tangent of the Rs-M fusion (Krishna, 1961).

ETYMOLOGY: The new genus-group name is a combination of the name Huguenot, the group of French Protestants who fled France in the late 17th Century after the Edict of Fontainebleau, and *termes*, meaning “termite”. For a period of time after the Edict of Nantes (1598), Alès (near the type locality), was granted to the Huguenots as a secure home, although by 1629 their religious freedoms were slowly eroding. The senior author is a direct descendant of two Huguenots, Pierre Fauré (1675–1745) of Auvergne, who left France for England with his wife Elizabeth and son Jean, departing Kensington 18 January 1701 aboard ‘la Nasseau’, arriving in Virginia 5 March 1701 and settling in Manakin, and Jean Pierre Bondurant (1677–1734) of Génolhac and who escaped to Manakin as well, via Switzerland (Brock, 1886; Jones, 1928; Warren, 2009). The gender of the name is masculine.

Huguenotermes septimaniensis Engel & Nel, new species

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(Figs. 1–5)

Kalotermitidae espèce J: Nel & Paicheler, 1993: 130, figs. 42, 43.

DIAGNOSIS: As for the genus (*vide supra*).

DESCRIPTION: Imago (hind wing). Length 5.60 mm as preserved, maximum width 1.95 mm; costal area darker (Figs. 1–4) than remainder of wing which is straw yellow; Sc presumably fused with costal margin; all veins except M originating outside of scale (Fig. 5); R1 and R2 more distinctly sclerotized, M and CuA unsclerotized and weak, particularly apically; R1 simple, comparatively short, extending to slightly more than one-third wing length (Fig. 5), length 2.0 mm; Rs running parallel with

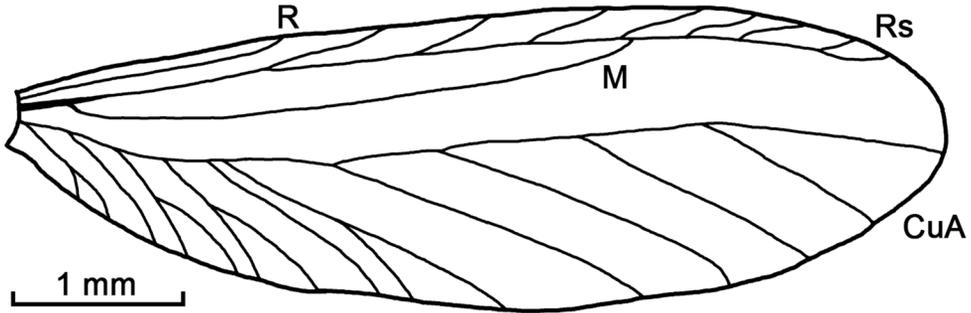


Figure 5. Reconstruction of hind wing venation from holotype (IPM-R.54350) of *Huguenotermes septimaniensis*, new genus and species (redrawn from Nel & Paicheler, 1993).

costal margin, terminating before wing apex, with eight branches (including apical portion of stem), all branches simple (Fig. 5), first branch originating slightly before tangent with termination of R1, *ca.* 1.45 mm from base; M diverging from stem of Rs near base, *ca.* 0.4 mm from preserved base, running slightly closer to Rs than CuA, gently arcing anteriorly and terminating into Rs at apical third of wing length near origin of fourth Rs branch (Fig. 5); CuA fainter apically (typical for many kalotermitids), terminating immediately posterior to wing apex, with numerous, largely simple branches (Fig. 5), a few in basal half with subsidiary forks, CuA field encompassing at least one half of wing width.

HOLOTYPE: Imago wing, IPM-R.54350 [part (Figs. 1, 3) and counterpart (Figs. 2, 4)], Early Priabonian (Early Ludien), Late Eocene, Monteils, Alès, Gard, Languedoc-Roussillon, France; deposited in the Muséum national d'Histoire naturelle, Paris, France.

ETYMOLOGY: The specific epithet refers to the Roman province of Septimania, which generally corresponds to the Languedoc-Roussillon region in modern France.

DISCUSSION

Today the *Cryptotermes-Procryptotermes* clade comprises 73 known species (14 in *Procryptotermes*, 69 in *Cryptotermes*), distributed throughout the world but not well represented in the Palearctic (Krishna *et al.*, 2013). Prior to the present species, there were three fossil species recorded for the group, all in *Cryptotermes*. *Cryptotermes bath-eri* (Rosen) is known from Pleistocene (or perhaps even younger) East African copal. This taxon is perhaps representative of a living species and might well be considered a subfossil. The other two fossils are *C. yamini* Krishna & Bacchus and *C. glaesarius* Engel & Krishna, both in Early Miocene amber from the Dominican Republic (Krishna & Bacchus, 1987; Engel & Krishna, 2007). *Huguenotermes* is the earliest documented evidence of this clade, extending the lineage back by at least 15 million years. In the Late Eocene, portions of southern Europe remained as archipelagos along the Tethys seaway that was gradually closing, and southern France had a subtropical, warm, humid climate with most localities not too distant from the seashore (Ollivier-Pierre *et al.*, 1987; Vianey-Liaud, 1991; Zachos *et al.*, 2001; Pagani *et al.*, 2005; Nel *et al.*, 2008), all as the dramatic cooling and aridification of the Eocene-Oligocene transition was poised to take place. This near coastal habitat is rather consistent with that of most species of *Procryptotermes* (e.g., Scheffrahn & Krecke, 2001), a group that is largely defined

by plesiomorphies relative to *Cryptotermes* and may even be paraphyletic to the latter (Krishna, 1961). Thus, the habitat preferences of *Procryptotermes* are likely ancestral for the larger group that includes *Huguenotermes*, and they are certainly consistent with the environment in which the younger fossil species of *Cryptotermes* would have lived. Nonetheless, the local paleoenvironment of the Monteils deposits was a lacustrine marl, with a comparatively poor fish fauna. Although the Eocene-Oligocene transition was great, the local climate in the region was comparatively stable between the latest Eocene and Oligocene as evidenced by the persistence of a comparatively similar forest and insect fauna at Monteils with those of Céreste (Lubéron) and Camoins-les-Bains (Marseille Basin) (Rousset *et al.*, 1996; Collomb *et al.*, 2008; Nel *et al.*, 2008), but admittedly the floras of these sites are in need of modern revision. At Monteils there is a taphonomic bias toward insects that are comparatively tiny, the preserved fauna consisting largely of aphids, psyllids, and minute flies (Nel, pers. obs.), and it appears as though the fauna represents individuals transported by wind to the paleolake, similar to what has been observed in the Oligocene deposits of Potasse d'Alsace (Quiévreux, 1935).

Interestingly, despite the large number of termites known from other Eocene sites across mainland Europe (*e.g.*, Nel & Paicheler, 1993; Wappler & Engel, 2006; Nel & Bourguet, 2006; Engel *et al.*, 2007b; Engel, 2008), those kalotermitids known are largely of the seemingly closely related genera *Electrotermes* Rosen and *Proelectrotermes* Rosen. Although putative species of *Kalotermes* Hagen are documented from the Eocene of the Bembridge Marls (Cockerell, 1917; Jarzembowski, 1980), other lineages of the Kalotermitidae have not yet been recorded, and it will be interesting to see if this pattern of diversity persists as more material is uncovered. Hopefully, future excavations will discover more complete specimens and allow a further characterization of this interesting genus, allowing for reconstruction of paleobiogeographical patterns among the Kalotermitidae.

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This small note is dedicated to the memory of Kumar Krishna (1926–2014), world's greatest authority of the Isoptera and whose loving generosity toward all whom he met so positively influenced the field of termite studies. He is missed. We are grateful to two reviewers for providing helpful comments on the manuscript. This is a contribution of the Division of Entomology, University of Kansas Natural History Museum.

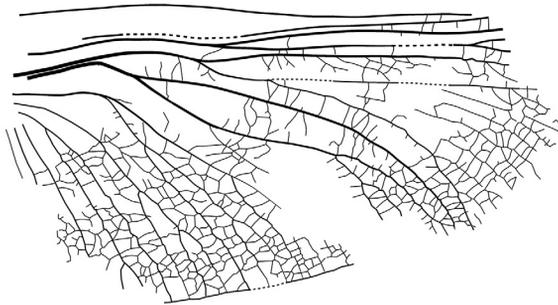
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Pharciphyzelus lacefieldi Beckemeyer & Engel, 2011

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