



Termite activity in the mid-Cretaceous of Australia

**Stephen McLoughlin, Artai A. Santos, Sherri Donaldson,
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ABSTRACT

In this paper we provide the oldest evidence of termites in Australia, based on an aggregation of several hundred morphologically distinctive faecal pellets preserved as opalized casts from the Griman Creek Formation (Albian–Cenomanian: c. 100 Ma) at Lightning Ridge, New South Wales, Australia. This trace fossil extends the record of isopterans in Australia around 40 to 50 million years earlier than previously identified termite wing impressions, and indicates that this group was an active component of the detritivorous community in eastern Gondwanan terrestrial ecosystems by the mid-Cretaceous. The distinctive prismatic faecal pellets with hexagonal cross-sections (referable to *Microcarpolithes hexagonalis* Vangerow) were probably produced by kalotermitid or mastotermitid termites. The associated fossil plant assemblage indicates that the producers of the faecal pellets likely fed on conifer wood. Based on the distribution of extant termites, the climate of the Lightning Ridge area (Surat Basin) was probably warm and moist during the mid-Cretaceous. Recognition that termites were well established in Australian terrestrial ecosystems by the Albian–Cenomanian implies that vicariance may have been just as influential as trans-oceanic dispersal in determining the early distribution of major termite clades. Opalization of these delicate faecal pellets highlights the potential for further discoveries of three-dimensionally preserved soft or friable body and trace fossils in the Lightning Ridge opal deposits.

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Final citation: McLoughlin, Stephen, Santos, Artai A., Donaldson, Sherri, Pott, Christian, and McCurry, Matthew. 2024. Termite activity in the mid-Cretaceous of Australia. *Palaeontologia Electronica*, 27(3):a48.

<https://doi.org/10.26879/1420>

palaeo-electronica.org/content/2024/5339-opalized-termite-coprolites

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Keywords: Isoptera; coprolites; opalization; plant-insect interactions; Kalotermitidae, Mastotermitidae

Submission: 13 June 2024. Acceptance: 13 September 2024.

INTRODUCTION

Termites (infraorder Isoptera) are detritivorous insects that play a major role in nutrient cycling in various terrestrial ecosystems on all continents except Antarctica (Eggleton, 2011). They are eusocial insects, known for constructing some of the most complex colonial habitats in the animal kingdom (Noirot, 1970). In turn, numerous ancient and modern invertebrates and vertebrates have adapted to feed specifically or predominantly on termites (Sheppe, 1970; Redford, 1987; Luo and Wible, 2005). Termites and termitophagous animals are prominent components of northern Australian ecosystems; yet, despite their key ecological roles in the landscape, very little is known about the origins of Australasian representatives of this group.

On a global basis, the sedimentary record has yielded numerous occurrences of termite body fossils, coprolites, nests, and borings structures from a broad array of Cenozoic and Cretaceous deposits (e.g., Colin et al., 2011; Engel et al., 2011; Jouault et al., 2021), indicating that the importance of Isoptera in terrestrial ecosystems extends far back in time. Nevertheless, the fossil record highlights some important palaeogeographical and temporal gaps that inhibit reconstruction of the evolutionary history of this group. The origin of termites remains controversial. Classically, a Late Jurassic origin has been proposed for the divergence of Isoptera from their cryptocercid cockroach sister group (Engel et al., 2009; Bourguignon et al. 2014; Legendre et al., 2015). Some controversial features interpreted as termite nests from Upper Triassic and Lower Jurassic deposits have been used to suggest a more ancient origin (Hasiotis and Dubiel, 1995; Bordy et al., 2004, 2009, 2010) but the attribution of these structures to Isoptera is disputed (Genise et al. 2005; Genise, 2017) and some may represent megarhizoliths (Alonso-Zarza et al., 2008; Genise, 2017). An Early Jurassic age for the stem-termite origin and a Late Jurassic age for the crown-termite origin have been proposed based on combined molecular and fossil data (Legendre et

al., 2015). However, other molecular and fossil data have suggested the possibility of a crown isopteran origin around the Triassic-Jurassic boundary (c. 200 Ma) or even older (Davis et al., 2009; Ware et al., 2010; Jouault et al., 2021). The disparity in results regarding the origin and diversification of termites makes the fossil record crucial for understanding the evolutionary history of this important group of insects. Thus far, the oldest convincing body fossils of termites were recovered from Lower Cretaceous deposits of Europe (see Appendix 1), specifically from the Berriasian Doronino Formation (Vršanský and Aristov, 2014) and Zaza Formation (Engel et al., 2007), Russia. The earliest evidence of isopteran coprolites derives from the Berriasian Missão Velha Formation of Brazil (Pires and Sommer, 2009), and over 40 other examples of fossil termite faecal pellets have been documented (see Appendix 2).

Cretaceous body fossils or coprolites of termites are relatively common in Europe (Jarzemowski, 1981; Lacasa-Ruiz and Martínez-Delclós, 1986; Schlueter, 1989; Engel et al., 2007, 2011; Engel and Delclós, 2010; Colin et al., 2011; Engel, 2014; Sánchez-García et al., 2020), Asia (Ren, 1995; Krishna and Grimaldi, 2003; Engel et al., 2007, 2011, 2016; Colin et al., 2011; Zhao et al., 2020; Jouault et al., 2021, 2022a, 2022b; Jouault and Nam, 2023; Engel and Jouault, 2024; Jiang et al., 2024), and the Americas (Krishna, 1990; Fontes and Vulcano, 1998; Krishna and Grimaldi, 2000; Martins-Neto et al., 2006; Bechly, 2007; Grimaldi et al., 2008). There is also evidence of hexagonal isopteran coprolites in various Cretaceous deposits across Africa (Colin et al., 2011 and references therein). By contrast, the Australasian fossil record of Isoptera is depauperate. Previously, the oldest fossil isopteran from this region was a single fragmentary termite forewing described by Riek (1952) from the Paleocene–Eocene (58.5–55 Ma: Langford et al., 1995) Redbank Plains Formation near Ipswich, Queensland, and assigned to *Blattotermes neoxenus* Riek (Mastotermitidae). Kaulfuss et al. (2010) described another solitary

forewing from Lower Miocene deposits of Foulden Maar, Otago, New Zealand, assigning it to *Stolotermites kupe* Kaulfuss, Harris et Lee (Stolotermitidae). McCurry et al. (2022) reported two additional termite (Mastotermitidae) wings from a thinly laminated goethitic siltstone of latest Early to earliest Late Miocene age (c. 16–11 Ma) near Talbragar in central New South Wales. Thus far, these are the only body fossil records of Isoptera from Australasia. In the absence of a rich body fossil record, trace fossils (coprolites, tunnels in wood, and nest structures) offer scope for elucidating the ancient history of termites in this region.

Australia has an extensive record of Cretaceous woods, albeit that few of these materials have been studied and most investigations have focused on the taxonomy and palaeoclimatic implications of these remains. Silicified conifer wood is abundant in eastern Australian Cretaceous basins (White, 1961; Frakes and Francis, 1990; Dettmann et al., 1992; Philippe et al., 2004; Fletcher et al., 2014, 2015; Tosolini et al., 2018). This abundance is probably linked to the release of permineralizing silica from the weathering of volcanic ash derived from the Whitsunday Igneous Province that was emplaced during the breakup of Australia and New Zealand.

In some marine deposits, the wood is entombed in calcareous concretions (Frakes and Francis, 1990) and, in others, (e.g., Western Australian marginal basins) the wood is preserved by silicification and phosphatization via the decomposition of glauconite and apatite in greensands (Simpson, 1912; McLoughlin et al., 1995b; McLoughlin, 1996; McLoughlin and McNamara, 2001; Mory and Hocking, 2017). Mummified, coalified, and charcoalfied woods are also represented in various Australian basins but this material has been understudied (Backhouse et al., 1995; McLoughlin et al., 2002; Carpenter et al., 2016; Tosolini et al., 2018). Thus, there is considerable potential for investigation of termite traces in Australian fossil wood preserved in multiple styles.

Woody axes can have long taphonomic trajectories, acquiring biogenic (bacterial, fungal, arthropod, and molluscan) damage while the tree is alive, as deadwood in the form of stumps and logs on land, during transport in freshwater systems, and as driftwood or submerged log grounds after being washed into marine or lacustrine environments (Philippe et al., 2022). Although some of the published Australian Cretaceous woods contain evidence of fungal attack, especially in the form of pocket rot (McLoughlin, 1996), and other examples

host borings from teredinid bivalves (McLoughlin et al., 1995b) and oribatid mites (Fletcher and Salisbury, 2014), none of the Cretaceous axes has yet revealed termite damage.

Australasian Cenozoic woods have yielded at least two examples of termite faecal pellets within tunnels excavated in wood that is now permineralized. Well-preserved examples include *Neotermes*-like fossil frass documented from mid-Cenozoic permineralized plant litter in central Queensland, Australia (Rozefelds and De Baar, 1991), and *Kalotermes* faecal pellets recorded in Miocene *Avicennia* wood from North Island New Zealand (Sutherland, 2003). Sub-fossil (Pleistocene) termite mounds have also been documented from stabilized sand dune systems in the Simpson Desert, central Australia (Miller, 1989).

There are over 360 extant species of termites in Australia within about five families (Watson and Abbey, 1993). Many Australian species are endemic. They are important ecosystem engineers as various groups have selective feeding patterns and abilities to consume and degrade leaf litter, grass, wood, fungi and diffuse organic matter in soil (Clement et al., 2021), liberating nitrogen, phosphorus and potassium that plants can exploit (Griffiths et al., 2021) and, in the process, contributing to c. 1–3% of the atmospheric CH₄ budget (Sanderson, 1996; Nauer et al., 2018). Extant wood and humic soil-feeding termites are roughly constrained to latitudes between 45° N and 45° S (Hellemans et al., 2022). They are particularly abundant and diverse in moist, warm (tropical) climates, where they constitute c. 10% of animal biomass and are responsible for >55% of organic matter decomposition (Bignell, 2006; Jones and Eggleton, 2011; Griffiths et al., 2019, 2021). They do not live in cool or cold habitats (Sanderson, 1996; Atlas of Living Australia, 2024).

Here, we document opalized casts of clusters of prismatic coprolites from the Albian–Cenomanian Griman Creek Formation at Lightning Ridge that are interpreted to represent the oldest evidence for termites in Australia. We evaluate the probable producers of the coprolites, their importance for interpreting the early radiation of termites, and their role in nutrient recycling in mid-Cretaceous ecosystems.

GEOLOGICAL SETTING

Opal is Australia's official national gemstone, with a significant percentage of commercial extraction occurring at Lightning Ridge in northern New South Wales (Department of Industry, Sci-

ence and Resources, Commonwealth of Australia, 2022). Both precious and non-precious opal has been exploited from this area for over 100 years, with many examples representing replacements of the hard parts of Cretaceous organisms.

The area around Lightning Ridge (centred on $29^{\circ}25'39''S$, $147^{\circ}58'44''E$) is characterized by a low-lying NW–SE trending mesa system in the southern part of the Surat Basin (Herrmann and Maas, 2022; Figure 1A, B). The Griman Creek Formation (Rolling Downs Group) is a sedimentary succession up to 400 m thick, comprising generally thin-bedded, interlaminated, fine- to medium-grained sandstone, siltstone, mudstone, and minor coals, intercalated with thicker (c. 1–1.5 m thick)

cross-bedded sandstones and conglomerates (Green et al., 1997; Payenberg and Reilly, 2004; Bell et al., 2019). The Griman Creek Formation at Lightning Ridge has been divided into two members: the Wallangulla Sandstone Member, comprising chiefly fine-grained, laminated, clay-rich sandstone with discontinuous claystone lenses of the informal ‘Finch clay facies’; and the overlying Coocoran Claystone Member, a claystone unit ≤ 10 m thick (Moore, 2002; Bell et al., 2019). The formation was deposited in low-energy freshwater fluvial and lacustrine systems (coastal plain environments) draining into the epeiric Eromanga Sea to the west (Bell et al., 2019). Laser Ablation Multicollector Inductively Coupled Plasma Mass Spectrom-

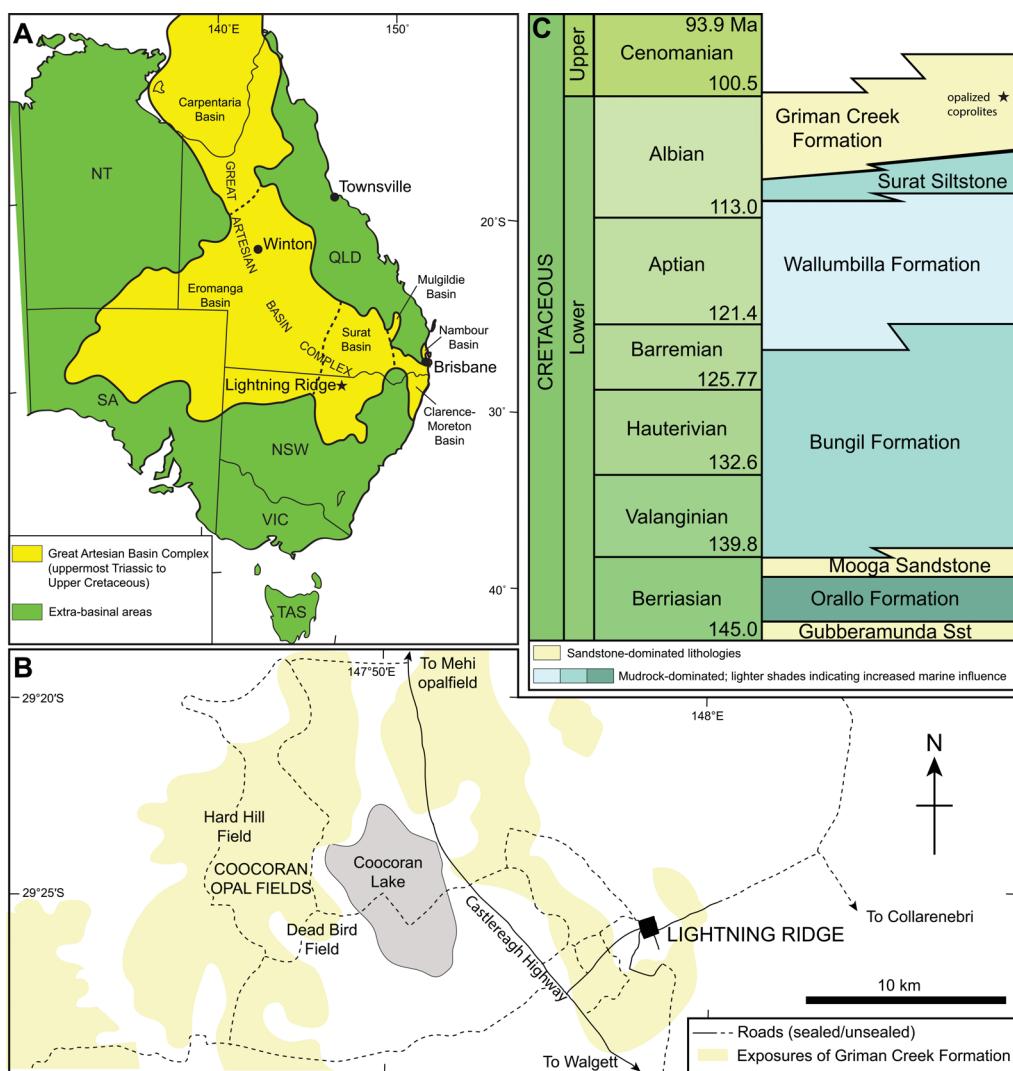


FIGURE 1. Details of the fossil locality. **A**, Map of eastern Australia showing the extent of the Surat Basin within the Great Artesian Basin complex, and the location of Lightning Ridge. **B**, Map showing the location of the Coocoran Opalfield (after Smith and Smith, 1999) and extent of the Griman Creek Formation (after Frauenfelder et al., 2021). **C**, Cretaceous stratigraphy of the southern Surat Basin (after Bell et al., 2019).

try U-Pb-Th radioisotopic dating of detrital zircons recovered from a volcanogenic bentonitic clay bed overlying the ‘Finch clay facies’ at the Hard Hill locality, yielded a range of Cretaceous depositional ages, with opalization of the formation occurring much later, during the Neogene (Bell et al., 2019; Mustoe and Smith, 2023; Figure 1C). More specifically, the suite of clear euhedral to elongate prismatic zircon grains with oscillatory magmatic zoning yielded $^{238}\text{U}/^{206}\text{Pb}$ ages of 117 ± 1.75 to 96.9 ± 1.49 Ma (mid-Aptian to mid-Cenomanian), with the youngest coherent set of grains dated as $98.08 \pm 1.1/-2$ Ma (early Cenomanian: at 95% confidence) and the youngest graphical peak in the population being 101 Ma (latest Albian: Bell et al., 2019). Thus, we interpret the age of the underlying ‘Finch clay facies’ of the Wallangulla Sandstone Member to approximate that of the Albian-Cenomanian boundary (hereafter, informally designated mid-Cretaceous; Figure 1C).

Although there is very little surface expression of the Griman Creek Formation in this region, fossils have been discovered in lenses of the ‘Finch clay facies’, extracted from small-scale subsurface mining activities since the early 1900s (Meakin, 2011). Many of the opal occurrences fill tectonic or dissolution voids in the ‘Finch clay facies’ but some represent casts of invertebrate shells, vertebrate bones or robust plant organs. These do not preserve the calcium carbonate, calcium phosphate, or cellulose/lignin of the original animal and plant remains but represent infilling of voids left by dissolution of the organisms’ hard parts. Dissolution and subsequent infilling of the voids by opaline silica is inferred to be primarily a Neogene phenomenon associated with the development of deep weathering profiles across the region (Herrmann and Maas, 2022; Mustoe and Smith, 2023).

The opalized biota of the Griman Creek Formation is considered to represent one of the most important Cretaceous terrestrial fossil assemblages in Australia, containing a diverse array of vertebrate, invertebrate, and plant fossils preserved as opalized casts (Bell et al., 2019). The rich array of vertebrate remains includes both freshwater and amphibious animals: amiid fishes, dipnoans, lamnid chondrichthyans, chelids, crocodylomorphs, and elasmosaurid plesiosaurs (Kemp and Molnar, 1981; Kear, 2006; Smith, 2010; Smith and Kear, 2013; Hart et al., 2019; Kemp and Berrell, 2020; Berrell et al., 2023). Terrestrial vertebrate fossils include theropods (Bell et al., 2016; Birch et al., 2019, 2020), sauropods (Frauenfelder et al., 2021), ornithopods (Molnar and Galton,

1986; Bell et al., 2018a, 2018b; Kitchener et al., 2019), enantiornithine birds (Molnar, 1999), and monotreme mammals (Archer et al., 1985; Clemens et al., 2003; Flannery et al., 2024). Freshwater invertebrate remains include bivalve and gastropod molluscs, and a single clade of decapod crustaceans (Newton, 1915; Hocknull, 2000; Hamilton-Bruce et al., 2002, 2004; Hamilton-Bruce and Kear, 2006, 2010; Kear and Godthelp, 2008; Bell et al., 2020). The fossil plant suite from the Griman Creek Formation is currently under study by the authors and includes various equisetaleans, ferns, and cupressacean and araucarian conifers, but lacks obvious angiosperm remains (Smith and Smith, 1999).

MATERIAL AND METHODS

The single available specimen was photographed using an Apple iPhone 12 dual camera system with primary 12 megapixel sensor with 1.4 μm pixels and 26 mm equivalent f/1.6 lens. SEM micrographs were acquired of the uncoated specimen using a JEOL NeoScope JCM-7000 Benchtop SEM at the Australian Museum, Sydney, employing an acceleration voltage of 15.0 kv under low-vacuum mode, with EDS acquisition under high-vacuum mode. Tomography was undertaken using a Nikon XT H 225 ST X-ray CT system at 130 kV and 70 μA with a resulting voxel size of 6.069 μm that was reconstructed in VGstudio Max V2023.3. The studied specimen is registered as AM F 128064 and stored at the Australian Museum, Sydney, where it was received as a donation by E. Smith in 2004.

SYSTEMATIC PALEONTOLOGY

Ichnogenus *MICROCARPOLITHES* Vangerow, 1954

Type ichnospecies. *Microcarpolithes hexagonalis* Vangerow, 1954; by subsequent designation of Hall (1963).

Microcarpolithes hexagonalis Vangerow, 1954
Figure 2A–J

Description. The specimen consists of an aggregation of several hundred hexagonally prismatic opaline pellets; the block is 27 mm long, 16 mm wide, and 10 mm thick (Figure 2A–D). Individual pellets are oblong, 0.97–(1.33)–1.62 mm long ($n=40$), 0.59–(0.76)–1.00 mm in transverse diameter ($n=40$), and conspicuously hexagonal in cross-section (Figure 2E–G), with smoothly faceted surfaces (Figure 2H–J), and truncate to broadly

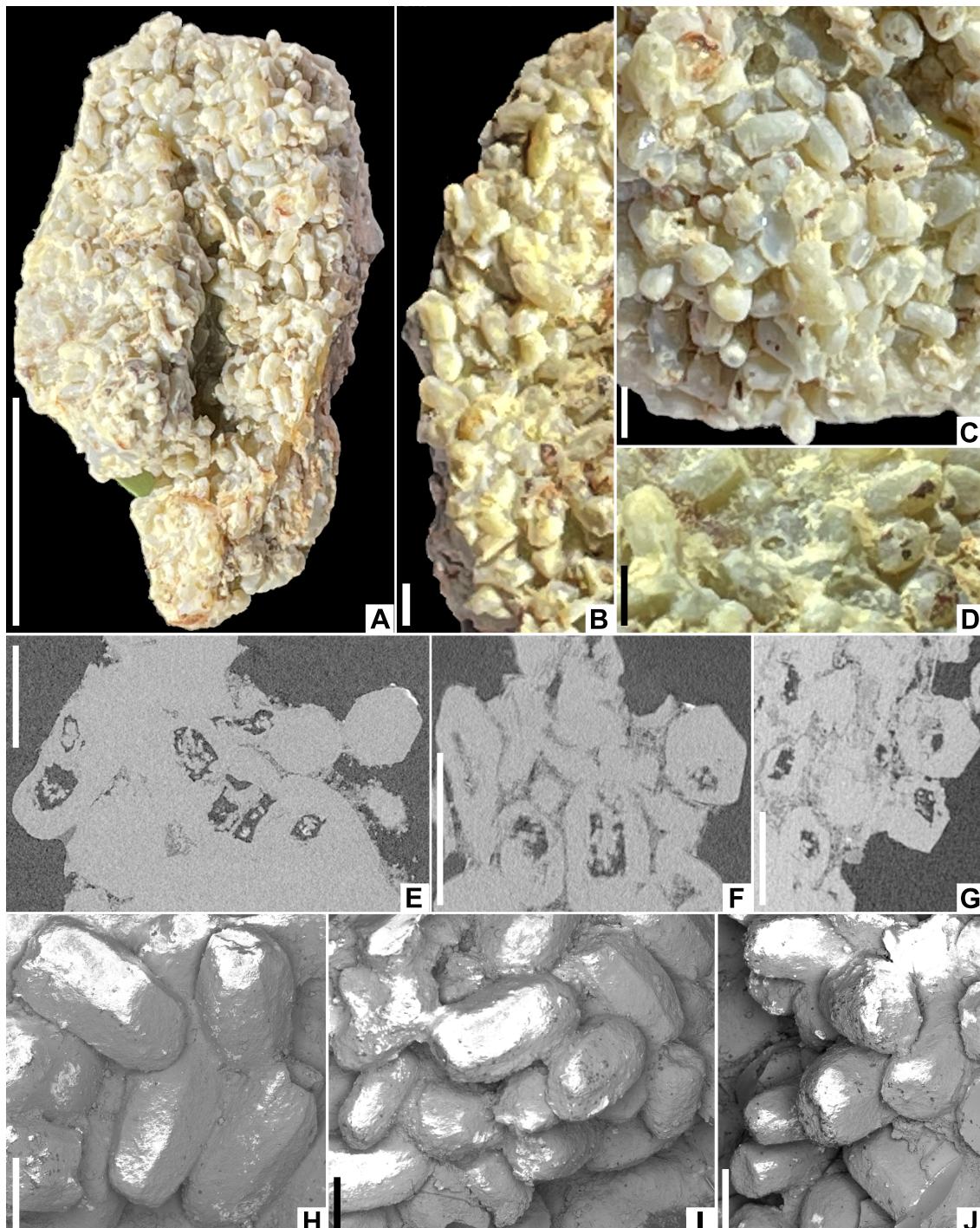


FIGURE 2. Illustrations of opalized termite coprolites from the Griman Creek Formation, Lightning Ridge (all images of specimen AM F 128064). **A**, Overview of specimen. **B**, Details of irregularly arranged pellets. **C**, Details of hexagonally prismatic faecal pellets. **D**, Details of faecal pellets and remnants of intervening clays and opaline silica. **E**, Greyscale tomographic (μ CT) reconstruction of fossil frass showing a mix of pellets with uniform and hollow interiors; hexagonal shape is evident in the cross-section in the coprolite on the right. **F**, Greyscale tomographic reconstruction of fossil frass showing pellets in longitudinal (oblong) and transverse (hexagonal) section. **G**, Greyscale tomographic (μ CT) reconstruction of fossil frass showing pellets held together by porous clays or opaline silica. **H**, Scanning electron micrograph of hexagonally prismatic coprolites. **I**, Scanning electron micrograph of hexagonally prismatic coprolites with blunt termini. **J**, Scanning electron micrograph of coprolites showing details of truncate termini. Scale bars equal 10 mm for A; 1 mm for B–G; 500 μ m for H–J.

rounded ends. Tomographic analysis reveals that individual coprolites have either a uniform finely granular internal composition (Figure 2E) or have an equivalent uniform outer rind and an internal cavity or porous region constituting one- to two-thirds of the pellet diameter (Figure 2F–G). The cavities locally contain irregularly arranged minute flecks of detritus. The coprolites lack any obvious regular organization or common orientation (Figure 2C). They are bound together by porous interstitial clays or opaline silica (Figures 2D, I, 3).

Remarks. The structures described in this study differ from replacements of euhedral quartz crystals by their bluntly rounded termini (at both ends of the pellets) and irregular arrangement. These mid-Cretaceous structures are interpreted to be termite coprolites based on their equivalency in shape and cross-section to termite coprolites assigned to *Microcarpolithes hexagonalis* Vangerow, from the Late Cretaceous of the Netherlands (Vangerow, 1954; Colin et al., 2011). *Microcarpolithes hexagonalis* was originally considered to represent angiosperm seeds but later reinterpreted by Kovach and Dilcher (1988) as termite coprolites (Colin et al., 2011; Moreau et al., 2019). Here we follow the criteria of Colin et al. (2011) who proposed that *Microcarpolithes hexagonalis* “must be used to uniquely designate termite coprolites that are cylindrical in shape and with a conspicuous hexagonal section, making it clearly distinct from some coprolites of curculionid weevil larvae that occasionally produce subhexagonal pellets.” Although the Australian Cretaceous coprolites are slightly longer than the

type specimen of *M. hexagonalis* from Europe, we do not regard this small difference (less than 1 mm) to be taxonomically significant for a trace fossil, which is in line with the proposal that size should not be considered primary criteria for differentiating ichnotaxa (Bertling et al., 2022).

DISCUSSION

Prismatic faecal pellets with sharply hexagonal cross-sections are atypical among insects, being produced by some groups of termites and some anobiid beetles, although those produced by coleopterans are typically much larger and less regular than pellets produced by isopterans (Weidner, 1956; Sutherland, 2003). Termopsidae, Kalotermitidae Archotermopsidae, and Mastotermitidae termites generate oblong pellets (Rohr et al., 1986; Colin et al., 2011; Moreau et al., 2019; Dong et al., 2022), whereas some other termite clades (e.g., Rhinotermitidae) produce amorphous, liquid, or gelatinous faeces (Arquette and Rodriguez, 2011; Colin et al., 2011). Termopsid pellets are generally larger and less regular than those of kalotermitids and mastotermitids (Light, 1934), and they lack surficial striate. Kalotermitids and mastotermitids are the most common producers of prismatic/faceted (hexagonal in cross-section) faecal pellets (Colin et al., 2011; Lewis et al., 2014) and, consequently, are the most likely producers of the Australian Cretaceous coprolites. The fecal pellets of some extant Kalotermitidae (*Kalotermes*) are smaller than those produced by the single extant

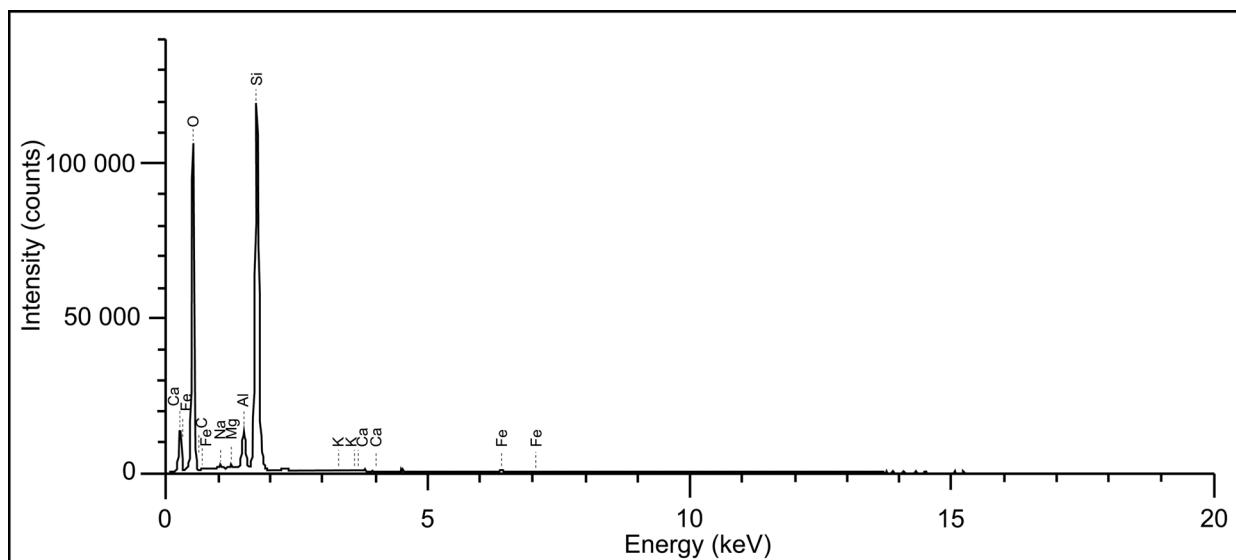


FIGURE 3. Energy-Dispersive X-ray Spectroscopy (EDS) plot for coprolites showing overwhelming dominance of silicon and oxygen X-ray counts denoting opaline composition of the fossils.

species of Mastotermitidae (*Mastotermes darwiniensis* Froggatt). Although the mid-Cretaceous coprolites described here are more consistent with the size of the pellets produced by *M. darwiniensis* (1–1.2 mm long according to Colin et al. 2011), the dimensional range and shapes of the Lightning Ridge coprolites are not sufficiently distinctive to exclude production by either mastotermitid or kalotermitid termites.

The hexagonal cross-section of termite dung is generated via pressure from six muscle bands that squeeze moisture out of the faecal mass in the rectum in order to collect water in the rectal grooves for retention by the insect (Child, 1934). The precise shape of the faecal pellet may also be influenced by the diet items and their moisture content (Lance, 1946). The cavities within some of the Lightning Ridge coprolites (Figure 2E–G) probably reflect incomplete opal casting of the pellet rather than constituting a primary textural or compositional character.

We interpret the dense arrangement of the Lightning Ridge coprolites to be the result of packing within a confined space, e.g., in a gallery formerly excavated within wood or within a termite mound or subterranean tunnel. The kalotermitid faecal pellets described from mid-Cenozoic (?Oligocene) deposits of central Queensland occur as masses in galleries within conifer wood or as free masses preserved in a silicified rainforest leaf litter assemblage (Rozefelds and De Baar, 1991). Those pellets are similar to the Lightning Ridge coprolites in being oblong and hexagonal in cross-section, but they are slightly larger (2.0–2.6 mm long and 0.8–1.0 mm wide). However, pellet size may be influenced by the availability and type of food or other ecological constraints (Rozefelds and De Baar, 1991). Apart from the slightly smaller size and more sharply defined hexagonally prismatic form of the Lightning Ridge coprolites, there is little to differentiate these from the central Queensland material, which supports a kalotermitid affinity for the new material and denotes a long (>100-million-year) history for this isopteran family in Australia.

The fossil flora of the Lightning Ridge opal fields is currently under study by the authors. Preliminary results indicate that the Albian–Cenomanian woody vegetation of this area was dominated by cupressacean and araucariacean conifers. The Lightning Ridge plant assemblage shares several taxa with the slightly younger Winton Formation flora of the Eromanga Basin to the north, in western Queensland (McLoughlin et al., 1995a, 2010). The former differs mainly in the

apparent absence of angiosperms; hence, we infer that, like the Oligocene examples from Queensland (Rozefelds and De Baar, 1991), the Lightning Ridge mid-Cretaceous termites were probably feeding primarily on coniferous wood.

The Lightning Ridge specimen is not the only example of an opalized mass of termite coprolites. Rogers (1928, 1938) documented termite coprolites in Pliocene opalized wood from Santa Barbara, California. They are of similar size and shape to the Lightning Ridge material but more loosely aggregated and bound by interstitial opal and colloform lussatite.

Given that extant termites do not live in cool or cold habitats, it is likely that the climate experienced at Lightning Ridge during the late Early Cretaceous was fairly warm, despite the region's relatively high (c. 60° S) palaeolatitude (Burgener et al., 2023). In addition, permineralized woods preserved at Lightning Ridge have marked growth ring boundaries suggesting strong seasonality in productivity. A relatively warm climate is supported by the presence of crocodilians and the diverse range of fossil organisms found in the opalized assemblages at Lightning Ridge (Smith and Smith, 1999; Bell et al., 2019). This is consistent with inferred global stepwise warming through the Albian–Turonian interval (Dettmann et al., 1992; Forster et al., 2007; Bottini and Erba, 2018; Huber et al., 2018; Burgener et al., 2023).

In North America, at least one archaic mammal (*Fruitafossor windscheffeli* Luo and Wible, 2005) had, by the Late Jurassic, developed fore-limb adaptations for digging and specialized dentition consistent with feeding on termites, other insects or soft plant matter. However, similar adaptations can develop among vermivorous mammals (Charles et al., 2013). Among extant Australian animals, the numbat (*Myrmecobius fasciatus*: Marsupialia), short-beaked echidna (*Tachyglossus aculeatus*: Monotremata), and at least 16 species of lizards specialize in feeding on termites (Abensperg-Traun and Steven, 1997). As yet, no lizard or marsupial fossils have been recovered from the Griman Creek Formation at Lightning Ridge. Recent work has uncovered six species of monotremes from this deposit (Flannery et al., 2024). Among these, *Opalios splendens* Flannery et al. 2024 has some features reminiscent of adaptations to termitivory (e.g., long, slender jaws, reduced teeth with simplified crown shape, and inter-molar or -premolar diastemata) although these might, alternatively, have been adaptations to feeding on vermiform invertebrates. Although isopterans were

clearly widespread by this time, whether any vertebrates targeted termites as a food source as early as the mid-Cretaceous in Australia remains speculative.

Mastotermitids and kalotermitids are relatively basal in at least some phylogenies of Isoptera, suggesting divergence early in the history of this order (Legendre et al., 2008; Lo and Eggleton, 2011). Owing to the relatively poor body fossil record of termites and recent discoveries of isopteran body and trace fossils extending back to, at latest, the Early Cretaceous on multiple continents (Jarzembski, 1981; Rohr et al., 1986; Martínez-Delclòs and Martinell, 1995; Francis and Harland, 2006; Pires and Sommer, 2009; Colin et al., 2011; Dong et al., 2022; Greppi et al., 2023), we suggest that the ancient distribution of many termite clades remains inadequately constrained and poorly dated. Thus, biogeographic hypotheses invoking long-distance dispersal for the distribution of many termite groups (Emerson, 1955, 1969; Bourguignon et al., 2016; Buček et al., 2022) are probably premature. It is clear that isopterans have a fossil record extending back to the mid-Mesozoic, before the major phase of Pangean breakup (McLoughlin, 2001) and, on that basis, vicariance related to continental separation may have played an important role in the distribution of termite groups through time.

CONCLUSIONS

The distinctive opal-replaced, clustered, hexagonally prismatic coprolites with blunt termini from the Griman Creek Formation at Lightning Ridge, Surat Basin, New South Wales, are tentatively

assigned to kalotermitid or mastotermitid termites. Being dated to c. 100 Ma, they represent the oldest evidence of termites in Australasia, pre-dating previous body and trace fossil records by c. 40–50 million years. These coprolites demonstrate the presence of termite activity in mid-Cretaceous continental ecosystems of eastern Australia, suggesting that these organisms were already important detritivores of dead, probably coniferous wood before the diversification of angiosperms. Mineral replacement of this delicate frass cluster, presumably representing faeces backfilling a bored cavity within wood, highlights the possibility of discovering additional opalized delicate body and trace fossils at Lightning Ridge that will provide a more complete understanding of the structure, biotic interactions and energy flow within the mid-Cretaceous coastal plain ecosystems of eastern Australia. Based on the modern climatic preferences of kalotermitid and mastotermitid termites, along with co-preserved crocodilians, a relatively warm climate is invoked for the high-latitude southern Surat Basin around the Albian–Cenomanian transition. The growing number of Mesozoic body and trace fossil records from multiple continents suggests that isopterans were widely established around the world before the major phase of Pangean breakup.

ACKNOWLEDGEMENTS

This research was funded by a Swedish Research Council VR grant (number 2022-03920) to SM. Specimen AM F 128064 was donated to the Australian Museum by E. Smith. We thank the editor and reviewers for their constructive comments on the manuscript.

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APPENDIX 1.

Global Jurassic–Cretaceous body fossil records of Isoptera. Appendices are available for download at
<https://palaeo-electronica.org/content/2024/5339-opalized-termite-coprolites>.

TAXA	PERIOD/ EPOCH	AGE	COUNTRY	LOCATION/ BASIN	FORMATION/ SECTION	REFERENCES
<i>Santonitermes transbaikalicus</i>	latest Jurassic or Early Cretaceous	latest Jurassic or Early Cretaceous	Russia	Chernovskie Kopi in Transbaikalian Siberia	Doronino Formation	Vršanský, P., and Aristov, D. 2014. Termites (Isoptera) from the Jurassic/Cretaceous boundary: evidence for the longevity of their earliest genera. European Journal of Entomology, 111:137–141.
<i>Mastotermes nepropadyom</i>	latest Jurassic or Early Cretaceous	latest Jurassic or Early Cretaceous	Russia	Chernovskie Kopi in Transbaikalian Siberia	Doronino Formation	Vršanský, P., and Aristov, D. 2014. Termites (Isoptera) from the Jurassic/Cretaceous boundary: evidence for the longevity of their earliest genera. European Journal of Entomology, 111:137–141.
<i>Baissatermes lapideus</i>	Early Cretaceous	Berriasian	Russia	Saissa	Zaza Formation	Engel, M.S., Grimaldi, D., Krishna, K. 2007. Primitive termites from the Early Cretaceous of Asia (Isoptera). Staatl. Museum für Naturkd., 371, 1–32.
<i>Valditermes brenanae</i>	Early Cretaceous	Hauterivian	U.K.	Wealden, England	Weald Clay Formation	Jarzembowski, E.A. 1981. An Early Cretaceous termite from southern england (Isoptera: Hodotermitidae). Systematic Entomology, 6:91–96.
<i>Meiatermes bertrani</i>	Early Cretaceous	Barremian	Spain	Lleida	Montsec	Lacasa-Ruiz, A., and Martínez-Delclòs, X. 1986. Meiatermes: Nuevo género fosil de insecto isóptero, Hodotermitidae, de las calizas Neocomienses del Monsec, Provincia de Lérida, España. 1986, 65 pp.
<i>Huaxitermes huangi</i>	Early Cretaceous	Barremian	China	Beijing	Lushangfen	Ren, D. 1995. Isoptera Comstock, 1895. In Ren, D., Lu, L., Guo, Z., and Ji, S. (eds): Fauna and Stratigraphy of Jurassic-Cretaceous in Beijing and the Adjacent Areas. Seismic Publishing House, Beijing, pp. 56-61
<i>Yanjingtermes giganteus</i>	Early Cretaceous	Barremian	China	Beijing	Lushangfen	Ren, D. 1995. Isoptera Comstock, 1895. In Ren, D., Lu, L., Guo, Z., and Ji, S. (eds): Fauna and Stratigraphy of Jurassic-Cretaceous in Beijing and the Adjacent Areas. Seismic Publishing House, Beijing, pp. 56-62

TAXA	PERIOD/EPOCH	AGE	COUNTRY	LOCATION/BASIN	FORMATION/SECTION	REFERENCES
<i>Yongdingia opipara</i>	Early Cretaceous	Barremian	China	Beijing	Lushangfen	Ren, D. 1995. Isoptera Comstock, 1895. In Ren, D., Lu, L., Guo, Z., and Ji, S. (eds): Fauna and Stratigraphy of Jurassic-Cretaceous in Beijing and the Adjacent Areas. Seismic Publishing House, Beijing, pp. 56-63
<i>Asiatermes reticulatus</i>	Early Cretaceous	Barremian	China	Beijing	Lushangfen	Ren, D. 1995. Isoptera Comstock, 1895. In Ren, D., Lu, L., Guo, Z., and Ji, S. (eds): Fauna and Stratigraphy of Jurassic-Cretaceous in Beijing and the Adjacent Areas. Seismic Publishing House, Beijing, pp. 56-64
<i>Mesotermopsis incompleta</i>	Early Cretaceous	Barremian	China	Beijing	Lushangfen	Ren, D. 1995. Isoptera Comstock, 1895. In Ren, D., Lu, L., Guo, Z., and Ji, S. (eds): Fauna and Stratigraphy of Jurassic-Cretaceous in Beijing and the Adjacent Areas. Seismic Publishing House, Beijing, pp. 56-65
<i>Mesotermopsis lata</i>	Early Cretaceous	Barremian	China	Beijing	Lushangfen	Ren, D. 1995. Isoptera Comstock, 1895. In Ren, D., Lu, L., Guo, Z., and Ji, S. (eds): Fauna and Stratigraphy of Jurassic-Cretaceous in Beijing and the Adjacent Areas. Seismic Publishing House, Beijing, pp. 56-66
<i>Melqartitermes myrrheus</i>	Early Cretaceous	Late Barremian–Early Aptian	Lebanon	Mdeyrif-Hammana, Mount Lebanon district	Lebanese amber	Engel, M.S., Grimaldi, D., and Krishna, K. 2007. Primitive termites from the Early Cretaceous of Asia (Isoptera). Staatl. Museum für Naturkd., 371, 1–32.
<i>Lebanotermes veltzae</i>	Early Cretaceous	Late Barremian–Early Aptian	Lebanon	Mdeyrif-Hammana, Mount Lebanon district	Lebanese amber	Engel, M.S., Nel, A., Azar, D., Soriano, C., Tafforeau, P., Néraudeau, D., Colin, J.-P., and Perrichot, V. 2011. New, primitive termites (Isoptera) from Early Cretaceous ambers of France and Lebanon. Palaeodiversity 4:39–49
<i>Isoptera indet</i>	Early Cretaceous	Late Barremian–Early Aptian	Lebanon	Mdeyrif-Hammana, Mount Lebanon district	Lebanese amber	Engel, M.S., Nel, A., Azar, D., Soriano, C., Tafforeau, P., Néraudeau, D., Colin, J.-P., and Perrichot, V. 2011. New, primitive termites (Isoptera) from Early Cretaceous ambers of France and Lebanon. Palaeodiversity 4:39–49.

TAXA	PERIOD/EPOCH	AGE	COUNTRY	LOCATION/BASIN	FORMATION/SECTION	REFERENCES
<i>Isoptera indet</i>	Early Cretaceous	Late Barremian–Early Aptian	Lebanon	Mdeyrif-Hammana, Mount Lebanon district	Lebanese amber	Engel, M.S., Nel, A., Azar, D., Soriano, C., Tafforeau, P., Néraudeau, D., Colin, J.-P., and Perrichot, V. 2011. New, primitive termites (Isoptera) from Early Cretaceous ambers of France and Lebanon. Palaeodiversity 4:39–49.
<i>Cratokaloterms santanensis</i>	Early Cretaceous	Aptian	Brazil	Araripe Basin	Crato Formation	Bechly, G. 2007. Isoptera, termites. In Martill, D.M., Bechly, G., and Loveridge, R.F. (eds), The Crato fossil beds of Brazil: Chap. 11.9: 249–262. New York: Cambridge University Press, 624 pp.
<i>Khanitermes acutipennis</i>	Early Cretaceous	Aptian	Mongolia	Shar-Tologoy	Shar-Tologoy Formation	Engel, M.S., Grimaldi, D., Krishna, K. 2007. Primitive termites from the Early Cretaceous of Asia (Isoptera). Staatl. Museum für Naturkd., 371:1–32.
<i>Meiatermes araripena</i>	Early Cretaceous	Aptian	Brazil	Santana, Brazil	Crato Formation	Krishna, K. 1990. Isoptera. In Grimaldi, D. (ed.), Insects from the Santana Formation, Lower Cretaceous, of Brazil. Bulletin of the American Museum of Natural History 195: chap. 5: 76–81.
<i>Cretatermes pereirai</i>	Early Cretaceous	Aptian	Brazil	Santana, Brazil	Crato Formation	Fontes, L.R., and Vulcano, M.A. 1998. Cupins fosseis do Novo Mundo. In Fontes, L.R. and Filho, E.B. (eds.), Cupins: o desafio do conhecimento: 243–295. Piracicaba, Brazil: FEALZ, 512 pp
<i>Mariconitermes talicei</i>	Early Cretaceous	Aptian	Brazil	Santana, Brazil	Crato Formation	Fontes, L.R., and Vulcano, M.A. 1998. Cupins fosseis do Novo Mundo. In Fontes, L.R. and Filho, E.B. (eds.), Cupins: o desafio do conhecimento: 243–295. Piracicaba, Brazil: FEALZ, 512 pp
<i>Caatingatermes megacephalus</i>	Early Cretaceous	Aptian	Brazil	Santana, Brazil	Crato Formation	Martins-Neto, R.G., Ribeiro-Júnior, C., and 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.

TAXA	PERIOD/EPOCH	AGE	COUNTRY	LOCATION/BASIN	FORMATION/SECTION	REFERENCES
<i>Arariptermes nativa</i>	Early Cretaceous	Aptian	Brazil	Santana, Brazil	Crato Formation	Martins-Neto, R.G., Ribeiro-Júnior, C., and 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. <i>Sociobiology</i> , 47:125–134.
<i>Nordestinatermes obesa</i>	Early Cretaceous	Aptian	Brazil	Santana, Brazil	Crato Formation	Martins-Neto, R.G., Ribeiro-Júnior, C., and 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. <i>Sociobiology</i> , 47:125–134.
<i>Meiatermes hariolus</i>	Early Cretaceous	Aptian	Brazil	Santana, Brazil	Crato Formation	Grimaldi, D.A., Engel, M.S., & Krishna, K. 2008. The species of Isoptera (Insecta) from the early Cretaceous Crato Formation: a revision. <i>American Museum Novitates</i> , 2008(3626):1–30.
<i>Cratomastotermes wolfschwenningeri</i>	Early Cretaceous	Aptian	Brazil	Santana, Brazil	Crato Formation	Bechly, G. 2007. Isoptera, termites. In Martill, D.M., Bechly, G., and Loveridge, R.F. (eds), <i>The Crato fossil beds of Brazil: Chap. 11.9:249–262</i> . New York: Cambridge University Press, 624 pp.
<i>Ithytermes montoyai</i>	Early Cretaceous	Albian	Spain	El Soplao amber	Peñacerrada I	Sánchez-García, A., Peñalver, E., Delclòs, X., and Engel, M.S. 2020. Early Cretaceous termites in amber from northern Spain (Isoptera). <i>Cretaceous Research</i> , 110:104385.
<i>Sclerotermes samsiki</i>	Early Cretaceous	early Albian	South Korea	Jinju city	Jinju Formation at the Jeongchon section	Jouault, C., and Nam, G.S. 2023. A new primitive termite from the lower cretaceous (Albian) Jinju Formation of Korea. <i>Historical Biology</i> , 35:1522–1527.
<i>Morazatermes Krishnai</i>	Early Cretaceous	Albian	Spain	Burgos	Peñacerrada	Engel, M.S. and Delclòs, X. 2010. Primitive termites in Cretaceous amber from Spain and Canada (Isoptera). <i>Journal of the Kansas Entomological Society</i> , 83:111–128.
<i>Aragonitermes teruelensis</i>	Early Cretaceous	Albian	Spain	Teruel	San Just outcrop	Engel, M.S. and Delclòs, X. 2010. Primitive termites in Cretaceous amber from Spain and Canada (Isoptera). <i>Journal of the Kansas Entomological Society</i> , 83:111–128.

TAXA	PERIOD/EPOCH	AGE	COUNTRY	LOCATION/BASIN	FORMATION/SECTION	REFERENCES
<i>Cantabritermes simplex</i>	Early Cretaceous	Albian	Spain	Burgos	Peñacerrada	Engel, M.S. and Delclòs, X. 2010. Primitive termites in Cretaceous amber from Spain and Canada (Isoptera). Journal of the Kansas Entomological Society, 83:111–128.
<i>Isoptera indet</i>	Early Cretaceous	Albian	Spain	El Soplao amber	Peñacerrada I	Sánchez-García, A., Peñalver, E., Delclòs, X., and Engel, M.S. 2020. Early Cretaceous termites in amber from northern Spain (Isoptera). Cretaceous Research, 110:104385.
<i>Isoptera indet</i>	Early Cretaceous	Albian	Spain	El Soplao amber	Peñacerrada I	Sánchez-García, A., Peñalver, E., Delclòs, X., and Engel, M.S. 2020. Early Cretaceous termites in amber from northern Spain (Isoptera). Cretaceous Research, 110:104385.
<i>Mylacrotomes cordatus</i>	Early Cretaceous	latest Albian	Myanmar	Burmese amber	Tanai Village	Engel, M.S., Grimaldi, D., and Krishna, K. 2007. Primitive termites from the early Cretaceous of Asia (Isoptera). Staatl. Museum für Naturkd., 371, 1–32.
<i>Dharmatermes avernalis</i>	Early Cretaceous	latest Albian	Myanmar	Burmese amber	Tanai Village	Engel, M.S., Grimaldi, D., and Krishna, K. 2007. Primitive termites from the early Cretaceous of Asia (Isoptera). Staatl. Museum für Naturkd., 371, 1–32.
<i>Proelectrotermes swinhoei</i>	Early Cretaceous	latest Albian	Myanmar	Burmese amber	Tanai Village	Engel, M.S., Grimaldi, D., and Krishna, K. 2007. Primitive termites from the early Cretaceous of Asia (Isoptera). Staatl. Museum für Naturkd., 371, 1–32.
<i>Proelectrotermes holmgreni</i>	Early Cretaceous	latest Albian	Myanmar	Burmese amber	Tanai Village	Engel, M.S., Grimaldi, D., and Krishna, K. 2007. Primitive termites from the early Cretaceous of Asia (Isoptera). Staatl. Museum für Naturkd., 371, 1–32.
<i>Kachinitermes tristis</i>	Early Cretaceous	latest Albian	Myanmar	Burmese amber	Tanai Village	Engel, M.S., Grimaldi, D., and Krishna, K. 2007. Primitive termites from the early Cretaceous of Asia (Isoptera). Staatl. Museum für Naturkd., 371, 1–32.
<i>Tanytermes anawrahtai</i>	Early Cretaceous	latest Albian	Myanmar	Burmese amber	Tanai Village	Engel, M.S., Grimaldi, D., and Krishna, K. 2007. Primitive termites from the early Cretaceous of Asia (Isoptera). Staatl. Museum für Naturkd., 371, 1–32.

TAXA	PERIOD/EPOCH	AGE	COUNTRY	LOCATION/BASIN	FORMATION/SECTION	REFERENCES
<i>Archeorhinotermes rossi</i>	Early Cretaceous	latest Albian	Myanmar	Burmese amber	Tanai Village	Krishna, K., and Grimaldi, D.A. 2003. The first Cretaceous Rhinotermitidae (Isoptera): a new species, genus, and subfamily in Burmese amber. American Museum Novitates, 2003(3390):1–10.
<i>Santonitermes chloaeae</i>	mid-Cretaceous	Albian–Cenomanian	France	Charentese amber	Charentese amber	Engel, M.S., Nel, A., Azar, D., Soriano, C., Tafforeau, P., Néraudeau, D., Colin, J.-P., and Perrichot, V. 2011. New, primitive termites (Isoptera) from Early Cretaceous ambers of France and Lebanon. Palaeodiversity 4:39–49.
<i>Syagriotermes salomeae</i>	mid-Cretaceous	Albian–Cenomanian	France	Charentese amber	Charentese amber	Engel, M.S., Nel, A., Azar, D., Soriano, C., Tafforeau, P., Néraudeau, D., Colin, J.-P., and Perrichot, V. 2011. New, primitive termites (Isoptera) from Early Cretaceous ambers of France and Lebanon. Palaeodiversity 4:39–49.
<i>Anisotermes bourguignoni</i>	mid-Cretaceous	Albian–Cenomanian	Myanmar	Burmese amber	Hukawng Valley	Jouault, C., Engel, M.S., Legendre, F., Huang, D., Grandcolas, P., and Nel, A. 2022. Incrementing and clarifying the diversity and early evolution of termites (Blattodea: Isoptera). Zoological Journal of the Linnean Society, 196:608–629.
<i>Longitermes pulcher</i>	mid-Cretaceous	Albian–Cenomanian	Myanmar	Burmese amber	Hukawng Valley	Jouault, C., Engel, M.S., Legendre, F., Huang, D., Grandcolas, P., and Nel, A. 2022. Incrementing and clarifying the diversity and early evolution of termites (Blattodea: Isoptera). Zoological Journal of the Linnean Society, 196:608–629.
<i>Mastotermes myanmarensis</i>	mid-Cretaceous	Albian–Cenomanian	Myanmar	Burmese amber	Hukawng Valley	Jouault, C., Engel, M.S., Legendre, F., Huang, D., Grandcolas, P., and Nel, A. 2022. Incrementing and clarifying the diversity and early evolution of termites (Blattodea: Isoptera). Zoological Journal of the Linnean Society, 196:608–629.
<i>Magnifitermes Krishnai</i>	mid-Cretaceous	Albian–Cenomanian	Myanmar	Burmese amber	Hukawng Valley	Jouault, C., Engel, M.S., Legendre, F., Huang, D., Grandcolas, P., and Nel, A. 2022. Incrementing and clarifying the diversity and early evolution of termites (Blattodea: Isoptera). Zoological Journal of the Linnean Society, 196:608–629.

TAXA	PERIOD/EPOCH	AGE	COUNTRY	LOCATION/BASIN	FORMATION/SECTION	REFERENCES
<i>Kachinitermopsis burmensis</i> (syn= <i>Kalotermes burmensis</i>)	Late Cretaceous	early Cenomanian	Myanmar	Burmese amber	Hukawng Valley	Poinar, G.O. 2009. Description of an early Cretaceous termite (Isoptera: Kalotermitidae) and its associated intestinal protozoa, with comments on their co-evolution. Parasites & Vectors, 2:1–17.
<i>Gigantotermes rex</i>	Late Cretaceous	early Cenomanian	Myanmar	Burmese amber	Hukawng Valley	Engel, M.S., Barden, P., Riccio, M.L., and Grimaldi, D.A. 2016. Morphologically specialized termite castes and advanced sociality in the Early Cretaceous. Current Biology, 26:522–530.
<i>Krishnatermes yoddha</i>	Late Cretaceous	early Cenomanian	Myanmar	Burmese amber	Hukawng Valley	Engel, M.S., Barden, P., Riccio, M.L., and Grimaldi, D.A. 2016. Morphologically specialized termite castes and advanced sociality in the Early Cretaceous. Current Biology, 26:522–530.
<i>Valkyritermes inopinatus</i>	Late Cretaceous	early Cenomanian	Myanmar	Burmese amber	Hukawng Valley	Jouault, C., Engel, M.S., Huang, D., Berger, J., Grandcolas, P., Perkovsky, E.E., Legendre, F., and Nel, A. 2022a. Termite Valkyries: soldier-like alate termites from the Cretaceous and task specialization in the Early evolution of Isoptera. Frontiers in Ecology and Evolution, 10:737367.
<i>Milesitermes engeli</i>	Late Cretaceous	early Cenomanian	Myanmar	Burmese amber	Hukawng Valley	Jouault, C., Legendre, F., Grandcolas, P., and Nel, A. 2021. Revising dating estimates and the antiquity of eusociality in termites using the fossilized birth–death process. Systematic Entomology, 46:592–610.
<i>Angustitermes reflexus</i>	Late Cretaceous	Cenomanian	Myanmar	Burmese amber	Hukawng Valley	Jiang, Y., Deng, X., Shih, C., Zhao, Y., Ren, D., and Zhao, Z. 2024. Primitive new termites (Blattodea, Termitoidae) in Cretaceous amber from Myanmar. ZooKeys, 1197:115.
<i>Mastotermes reticulatus</i>	Late Cretaceous	Cenomanian	Myanmar	Burmese amber	Hukawng Valley	Jiang, Y., Deng, X., Shih, C., Zhao, Y., Ren, D., and Zhao, Z. 2024. Primitive new termites (Blattodea, Termitoidae) in Cretaceous amber from Myanmar. ZooKeys, 1197:115.
<i>Tyrannotermes spinifer</i>	Late Cretaceous	Cenomanian	Myanmar	Burmese amber	Hukawng Valley	Engel, M.S. and Jouault, C. 2024. Hodoteropsid termites from the mid-Cretaceous Hkamti and Kachin ambers (Isoptera: Hodoteropsidae). Palaeoentomology, 7:80–91.

TAXA	PERIOD/EPOCH	AGE	COUNTRY	LOCATION/BASIN	FORMATION/SECTION	REFERENCES
<i>Hodotermopsisella novella</i>	Late Cretaceous	Cenomanian	Myanmar	Burmese amber	Hukawng Valley	Engel, M.S. and Joault, C. 2024. Hodotermitopsid termites from the mid-Cretaceous Hkamti and Kachin ambers (Isoptera: Hodotermitidae). <i>Palaeoentomology</i> , 7:80–91.
<i>Mastotermes sartensis</i>	Late Cretaceous	Cenomanian	France	French amber	NW France	Schlüter, T. 1989. Neue Daten über harzkonservierte Arthropoden aus dem Cenomanium NW-Frankreichs. <i>Documenta naturae</i> , 56:59–70.
<i>Lutetiatermes priscus</i>	Late Cretaceous	Cenomanian	France	French amber	NW France	Schlüter, T. 1989. Neue Daten über harzkonservierte Arthropoden aus dem Cenomanium NW-Frankreichs. <i>Documenta naturae</i> , 56:59–70.
<i>Cretatermes carpenteri</i>	Late Cretaceous	Cenomanian	Canada	Canadian amber	Labrador	Emerson, A.E. 1965. A review of the Mastotermitidae (Isoptera), including a new fossil genus from Brazil. <i>American Museum Novitates</i> , 2236:1–46
<i>Anisotermes xiai</i>	Late Cretaceous	Cenomanian	Myanmar	Burmese amber	Kachin	Zhao, Z., Eggleton, P., Yin, X., Gao, T., Shih, C., and Ren, D. 2019. The oldest known mastotermitids (Blattodea: Termitidae) and phylogeny of basal termites. <i>Systematic Entomology</i> , 44:612–623.
<i>Cosmotermes multus</i>	Late Cretaceous	Cenomanian	Myanmar	Burmese amber	Kachin	Zhao, Z., Yin, X., Shih, C., Gao, T., and Ren, D. 2020. Termite colonies from mid-Cretaceous Myanmar demonstrate their early eusocial lifestyle in damp wood. <i>National Science Review</i> , 7:381–390.
<i>Cosmotermes opacus</i>	Late Cretaceous	Cenomanian	Myanmar	Burmese amber	Kachin	Zhao, Z., Yin, X., Shih, C., Gao, T., and Ren, D. 2020. Termite colonies from mid-Cretaceous Myanmar demonstrate their early eusocial lifestyle in damp wood. <i>National Science Review</i> , 7:381–390.
<i>Mastotermes monostichus</i>	Late Cretaceous	Cenomanian	Myanmar	Burmese amber	Kachin	Zhao, Z., Eggleton, P., Yin, X., Gao, T., Shih, C., and Ren, D. 2019. The oldest known mastotermitids (Blattodea: Termitidae) and phylogeny of basal termites. <i>Systematic Entomology</i> , 44:612–623.
<i>Termitotron vendeeense</i>	Late Cretaceous	middle Cenomanian–early Santonian	France	Vendean amber	La Garnache, Vendée	Engel, M.S. 2014. A termite (Isoptera) in Late Cretaceous amber from Vendée, northwestern France. <i>Paleontological Contributions</i> , 2014(10E):21–24.

TAXA	PERIOD/ EPOCH	AGE	COUNTRY	LOCATION/ BASIN	FORMATION/ SECTION	REFERENCES
<i>Carinatermes nascimbenei</i>	Late Cretaceous	Turonian	U.S.A.	New Jersey	New Jersey amber	Krishna, K. and Grimaldi, D. 2000. A new subfamily, genus, and species of termite (Isoptera) from New Jersey Cretaceous amber. Studies on Fossils in Amber, with Particular Reference to the Cretaceous of New Jersey. Backhuys Publishers, Leiden, The Netherlands, 133–140.

APPENDIX 2.

Examples of fossil isopteran faecal pellets (coprolites). Appendices are available for download at <https://palaeo-electronica.org/content/2024/5339-opalized-termite-coprolites>.

TRACE	PERIOD/EPOCH	STAGE	COUNTRY	BASIN/LOCATION	FORMATION/SECTION	REFERENCES
Coprolites	Early Cretaceous	Berriasian	Brazil	Araripe Basin	Missão Velha Fm	Pires, E.F. and Sommer, M.G. 2009. Plant–arthropod interaction in the Early Cretaceous (Berriasian) of the Araripe Basin, Brazil. <i>Journal of South American Earth Sciences</i> , 27:50–59.
Coprolites	Early Cretaceous	Valanginian–Albian	South Africa	Algoa Basin	Sundays River Fm	Dale D.C. and McMillan, I.K. 2002. When the South Atlantic broke open, 25. <i>Earthyear, the Essential Environmental Guide</i> , Johannesburg. pp. 77. McMillan, I. K. (2003). Foraminifera defined biostratigraphic episodes and sedimentation pattern of the Cretaceous drift succession (Early Barremian to Late Maastrichtian) in seven basins on the South African and southern Namibian continental margin. <i>South African Journal of Science</i> , 99:537–576.
Coprolites	Early Cretaceous	Hauterivian–Barremian	U.K.	Weald Clay	Weald Clay Fm	Batten, D.J. (1998). Palaeoenvironmental implications of plant, insect and other organic-walled microfossils in the Weald Clay Formation (Lower Cretaceous) of southeast England. <i>Cretaceous Research</i> , 19:279–315.
Coprolites	Early Cretaceous	Hauterivian–Barremian	France	Angeac, Charente	Unnamed?	Colin, J.P., Néraudeau, D., Nel, A., and Perrichot, V. 2011. Termite coprolites (Insecta: Isoptera) from the Cretaceous of western France: A palaeoecological insight. <i>Revue de micropaléontologie</i> , 54:129–139.
Coprolites	Early Cretaceous	Barremian	U.K.	Isle of Wight	Wessex Fm	Sweetman, S.C. and Insole, A.N. 2010. The plant debris beds of the Early Cretaceous (Barremian) Wessex Formation of the Isle of Wight, southern England: their genesis and palaeontological significance. <i>Palaeogeography, Palaeoclimatology, Palaeoecology</i> , 292:409–424.
Coprolites	Early Cretaceous	Barremian–Aptian	China	Huolinhe Basin, Inner Mongolia	Huolinhe Fm	Dong, C., Shi, G.L., Wang, Z.X., and Huang, D.Y. 2022. Termite coprolites (Blattodea: Isoptera) from the Early Cretaceous of eastern Inner Mongolia, Northeast China. <i>Palaeoentomology</i> , 5:1–14.
Coprolites	Early Cretaceous	Barremian–Aptian	Canada	East coast of Nova Scotia	Chaswood Fm	Scott, A.C. and Stea, R. 2002. Fires sweep across the Mid-Cretaceous landscapes of Nova Scotia. <i>Geoscientist</i> , 12:4–6.
Coprolites	Early Cretaceous	Aptian	Germany	Sauerland	?	Huckriede, R. and Feist, M. 1982. Die unterkretazische Karsthöhlen-Füllung von Nehden im Sauerland. I: Geologische, paläozoologische und paläobotanische Befunde und Datierung. <i>Geologica et Palaeontologica</i> , 16:182–242.
Coprolites	Early Cretaceous	Aptian	U.S.A.	Utah	Cedar Mountain Fm	Dayvault, R.D. and Hatch, H.S. 2005. Cycads from the Upper Jurassic and Lower Cretaceous rocks of Southeastern Utah. <i>Rocks & Minerals</i> , 80:412–432.
Coprolites	Early Cretaceous	Albian	Argentina	Patagonia	Kachaike Fm	Greppi, C.D., Massini, J.L.G., Rombola, C.F., and Pujana, R.R. 2023. Borings and coprolites of termites in fossil woods from the Lower Cretaceous (Kachaike Formation) of Argentinean Patagonia. <i>Review of Palaeobotany and Palynology</i> , 308:104800.
Coprolites	Early Cretaceous	Albian	Canada	Alberta	Moosebar Fm	McLean, J.R. and Wall, J.H. 1981. The Early Cretaceous Moosebar Sea in Alberta. <i>Bulletin of Canadian Petroleum Geology</i> , 29:334–377.
Coprolites	Early Cretaceous	uppermost Albian	France	Charente-Maritime	Unnamed	Colin, J.P., Néraudeau, D., Nel, A., and Perrichot, V. 2011. Termite coprolites (Insecta: Isoptera) from the Cretaceous of western France: A palaeoecological insight. <i>Revue de micropaléontologie</i> , 54:129–139.
Coprolites	Late Cretaceous	Cenomanian	France	Charentes	Unnamed	Colin, J.P., Néraudeau, D., Nel, A., and Perrichot, V. 2011. Termite coprolites (Insecta: Isoptera) from the Cretaceous of western France: A palaeoecological insight. <i>Revue de micropaléontologie</i> , 54:129–139.

TRACE	PERIOD/EPOCH	STAGE	COUNTRY	BASIN/LOCATION	FORMATION/SECTION	REFERENCES
Coprolites	Late Cretaceous	Cenomanian	U.S.A	Kansas	Dakota Fm	Kovach, W.L. and Dilcher, D.L. 1988. Megasporites and other dispersed plant remains from the Dakota Formation (Cenomanian) of Kansas, USA. <i>Palynology</i> , 12:89–119.
Coprolites	Late Cretaceous	Cenomanian	U.S.A	Iowa	Dakota Fm	Hall, J.W. 1963. Megasporites and other fossils in the Dakota Formation (Cenomanian) of Iowa, (USA). <i>Pollen et Spores</i> , 5:425–443.
Coprolites	Late Cretaceous	Cenomanian	France	Dordogne	Lignites du Sarladais	Colin, J.P. and Médus, J. 1972. Un gisement de lignite du Sarladais d'âge cénomanien; données palynostatigraphiques. <i>Compte Rendu Sommaire des Séances de la Société Géologique de France</i> , 6:22.
Coprolites	Late Cretaceous	late Turonian	France	Dordogne	?	Colin, J.P. 1973. Microfossiles végétaux dans le Cénomanien et le Turonien de Dordogne (SO France). <i>Palaeontographica Abteilung B</i> , 143:106–119.
Coprolites	Late Cretaceous	Cenomanian–Lower Campanian	South Africa	Transkei	Mzamba Fm	Stevenson, I.R. and McMillan, I.K. 2004. Incised valley fill stratigraphy of the Upper Cretaceous succession, proximal Orange Basin, Atlantic margin of southern Africa. <i>Journal of the Geological Society</i> , 161:185–208.
Coprolites	Late Cretaceous	Coniacian	Namibia	Orange River fan-delta	?	Corbett, I. and Burrell, B. 2001. The earliest Pleistocene (?) Orange River fan-delta: an example of successful exploration delivery aided by applied Quaternary research in diamond placer sedimentology and palaeontology. <i>Quaternary International</i> , 82:63–73.
Coprolites	Late Cretaceous	Santonian	Germany	Westphalia	Aachen Fm	Vangerow, E.F. 1954. Megasporites und andere pflanzliche Mikrofossilien aus der Aachener Kreide. <i>Palaeontographica Abteilung B</i> , 96:24–38.
Coprolites	Late Cretaceous	Late Cretaceous	Czech Republic	Carpathian Mountains	?	Knobloch, E. 1964. Neuen Pflanzenfunden aus dem südböhmischen Senon. <i>Jahrbuch des Staatlichen Museums für Mineralogie und Geologie zu Dresden</i> , 1964, pp. 133–201. Knobloch, E. 1971. Fossile Früchte und Samen aus der Flyschzone der mährischen Karpaten. <i>Sbornik Geologickych Ved: Paleontologie</i> , 13:7–43.
Coprolites	Late Cretaceous	Late Cretaceous	U.S.A.	Brewster County, Texas	Javelina Formation	Rohr, D.M., Boucot, A.J., Miller, J., and Abbott, M. 1986. Oldest termite nest from the Upper Cretaceous of west Texas. <i>Geology</i> , 14:87–88.
Coprolites	Late Cretaceous	Turonian–lower Campanian	Canada	Vancouver Island, British Columbia	Dunsmuir Member, Comox Formation	Jud, N.A., Wheeler, E.A., Rothwell, G.W., and Stockey, R.A. 2017. Angiosperm wood from the Upper Cretaceous (Coniacian) of British Columbia, Canada. <i>IAWA J.</i> , 38:141–161.
Coprolites	Late Cretaceous	Coniacian–Santonian	Austria	Gosau	?	Huckriede, R. and Feist, M. 1982. Die unterkretazische Karsthöhlen-Füllung von Nehden im Sauerland. I: Geologische, paläozoologische und paläobotanische Befunde und Datierung. <i>Geologica et Palaeontologica</i> , 16:182–242.
Coprolites	Late Cretaceous	Maastrichtian	Congo	offshore Congo	?	Massala, A. 1992. Le Crétacé supérieur et le Tertiaire du bassin côtier congolais. Biochronologie et stratigraphie séquentielle. Ph.D. thesis, Université de Bourgogne, Dijon, 326 pp. (unpublished).
Coprolites	Late Cretaceous	late Maastrichtian	Spain	Spanish Pyrenees	?	Liebau, A. 1973. El Maastrichtense lagunar (Garumniense) de Isona. XIII Coloquio Europeo de Micropaleontología, C.N.G. Enadisma, Madrid, 87–112.
Coprolites	Late Cretaceous	Late Cretaceous	Argentina	Patagonia	unnamed Upper Cretaceous Fm	Genise, J.F. 1995. Upper Cretaceous trace fossils in permineralized plant remains from Patagonia, Argentina. <i>Ichnos: An International Journal of Plant & Animal</i> , 3:287–299.
Coprolites	Late Cretaceous	Maastrichtian	Canada	British Columbia	?	Colin, J.P., Néraudeau, D., Nel, A., and Perrichot, V. 2011. Termite coprolites (Insecta: Isoptera) from the Cretaceous of western France: A palaeoecological insight. <i>Revue de micropaléontologie</i> , 54:129–139.
Coprolites	Late Cretaceous	late Maastrichtian	U.S.A	Texas	Javelina Fm	Grimaldi, D. and Engel, M.S. 2005. Evolution of the Insects. Cambridge University Press. New York , 755 pp.

TRACE	PERIOD/EPOCH	STAGE	COUNTRY	BASIN/LOCATION	FORMATION/SECTION	REFERENCES
Coprolites	Palaeocene	Palaeocene	U.K.	England	?	Collinson, M.E. 1999. Plants and animal diets, p. 316–319. In Jones, T.P. and Rowe, N.P. (eds.), <i>Fossil Plants and Spores: modern techniques</i> . Geological Society, London.
Coprolites	Palaeocene	Danian	Belgium	Hainin Fm	Hainin Fm	Colin, J.P., Néraudeau, D., Nel, A., and Perrichot, V. 2011. Termite coprolites (Insecta: Isoptera) from the Cretaceous of western France: A palaeoecological insight. <i>Revue de micropaléontologie</i> , 54:129–139.
Coprolites	Eocene	Lutetian	Poland and Lithuania	Baltic amber	Unknow	Nuorteva, M. and Kinnunen, K.A. 2008. Insect frass in Baltic amber. <i>Bulletin of the Geological Society of Finland</i> , 80:105–124.
Coprolites	Eocene	Priabonian	Central Europe	Staré Sedlo	?	Schultze-Dewitz, G. and Süß, H. 1988. Fossiler Termitenfrass an Holzresten aus dem Tertiär von Staré Sedlo (CSSR). Ein Beitrag zu den Termiten der Vorwelt. <i>Zeitschrift für geologische Wissenschaften</i> , 16:169–173.
Coprolites	Eocene	Priabonian	U.K.:	England	Bembridge Limestone Fm	Hooker, J.J., Collinson, M.E., Van Bergen, P.F., Singer, R.L., De Leeuw, J.W., and Jones, T.P. 1995. Reconstruction of land and freshwater palaeoenvironments near the Eocene-Oligocene boundary, southern England. <i>Journal of the Geological Society</i> , 152:449–468.
Coprolites	Eocene–Oligocene	Eocene–Oligocene	France	Malzieu Basin	Lozère, southern France	Moreau, J.D., Trincal, V., Nel, A., Simon-Coinçon, R., Sallé, V., Le Couls, M., Néraudeau, D., and Fernandez, V. 2020. Hidden termite coprolites revealed by synchrotron microtomography inside Eocene–Oligocene filled wood-borings from the Malzieu Basin, Lozère, southern France. <i>Lethaia</i> , 53:106–117.
Coprolites	Oligocene	Oligocene	Australia	Queensland	nearby Gordon Downs and Selma Station	Rozefelds, A.C. and Baar, M.D. 1991. Silicified Kalotermitidae (Isoptera) frass in conifer wood from a mid-Tertiary rainforest in central Queensland, Australia. <i>Lethaia</i> , 24:439–442.
Coprolites	Oligocene	Chattian	U.S.A.	Louisiana	Catahoula Fm	Colin, J.P., Néraudeau, D., Nel, A., and Perrichot, V. 2011. Termite coprolites (Insecta: Isoptera) from the Cretaceous of western France: A palaeoecological insight. <i>Revue de micropaléontologie</i> , 54:129–139.
Coprolites	Miocene	Early Miocene	New Zealand	Hukatere Peninsula	Kaipara Harbour, North Auckland,	Sutherland, J.I. 2003. Miocene petrified wood and associated borings and termite faecal pellets from Hukatere Peninsula, Kaipara Harbour, North Auckland, New Zealand. <i>Journal of the Royal Society of New Zealand</i> , 33:395–414.
Coprolites	Miocene	Miocene	Dominican Republic	Dominican amber	?	Baroni-Urbani, C. and Saunders, J.B. 1980. The fauna of the Dominican Republic amber: the present status of knowledge. In <i>Proceedings of the Ninth Caribbean Geological Conference</i> (Santo Domingo, August 1980), 213–223.
Coprolites	Miocene	Miocene	Argentina	La Rioja	Salica Fm	García Massini, J.L. and Pujana, R.R. 2013. Silicified termite coprolites in mesquite-like wood from the Miocene of La Rioja, Argentina. <i>International Journal of Plant Sciences</i> , 174:585–591.
Coprolites	Miocene	Miocene	Czech Republic	Pannonian Basin	?	Knobloch, E. 1989. Biometrie und Morphologie der Samen von <i>Stratiotes kaltennordheimensis</i> und <i>S. tuberculatus</i> aus dem mitteleuropäischen Neogen. <i>Sborník Geologických Ved: Paleontologie</i> , 30:159–173.
Coprolites	Pliocene	Pliocene	U.S.A.	California	Fernando Fm	Rogers, A.F. 1938. Fossil termite pellets in opalized wood from Santa Maria, California. <i>American Journal of Science</i> , 5:389–392.
Coprolites	Pleistocene	Pleistocene	U.S.A.	Florida	?	Colin, J.P., Néraudeau, D., Nel, A., and Perrichot, V. 2011. Termite coprolites (Insecta: Isoptera) from the Cretaceous of western France: A palaeoecological insight. <i>Revue de micropaléontologie</i> , 54:129–139.
Coprolites	Pleistocene	Pleistocene	U.S.A.	California	Carpinteria Fm	Lance, J.F. 1946. Fossil arthropods of California. 9. Evidence of termites in the Pleistocene asphalt of Carpinteria, California. <i>Southern California Academy of Sciences Bulletin</i> , 45:21–27.