SILICIFIED TERMITE COPROLITES IN MESQUITE-LIKE WOOD FROM THE MIOCENE OF LA RIOJA, ARGENTINA

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Coprolite-filled borings in fragments of nondecayed wood showing affinity with the mesquite-like morphogenus *Prosopisinoxylon* Martínez are described from Miocene strata from La Rioja, northwestern Argentina. Borings are excavated in the secondary xylem and contain numerous cylindrical coprolites with a characteristic hexagonal shape in cross section. Coprolites are rather inconspicuous and visible only through the exposed ends of the borings. The concealed occurrence of the coprolites inside the borings, the nondecayed state of the mesquite-like wood, and the overall morphology of the fossils suggest dry-wood members of the termite family (Kalotermitidae) as a probable producer. This is the first fossil record of termites from northwestern Argentina and is among the few known from South America, thereby expanding their paleobiogeographic range. The presence of dry-wood termites in the studied deposits is consistent with a forested environment set in an arid tropical to subtropical climate. In this setting termites probably had a significant role in the recycling of organic matter. Their association with mesquite-like wood suggests that the current relationship between termites and members of this genus in modern ecosystems dates back to at least the Late Miocene.

Keywords: fossil wood, coprolites, termites, arthropod-plant interactions, northwestern Argentina

Introduction

Termites are key members of modern terrestrial ecosystems acting as recyclers of organic matter essential for carbon mineralization and humification and building of soils (Eggleton 2011). Their greatest abundance and diversity are in the tropics, where they represent the most important decomposer animal group (Davies et al. 2003). This is due in part to their complex social organization and the multiple symbioses engaging the different termite groups with a variety of microorganisms that aid them in the digestion of vast amounts of plant remains present in soils or as wood (Grimaldi and Engel 2005).

In the Neotropical region of Argentina, termites are represented by four families (Termopsidae, Rhinotermitidae, Termitidae, Kalotermitidae) distributed from northern Patagonia to the northernmost borders of the country (Torales et al. 1997, 2005, 2008). The majority of extant termites known from Argentina are from the eastern-northeastern provinces, whereas only a few records are known from the more arid western-northern regions of the country. In particular, the presence of extant termites in La Rioja Province is represented by only three records known since 2005 (Torales et al. 2005).

The fossil record of termites dates back to the Early Cretaceous on the basis of body fossils and traces of activity (Colin et al. 2011; Engel et al. 2011). Fossil termites in Argentina are represented by traces of their activity in Pliocene and Miocene soils from Buenos Aires and in a permineralized cycad stem from the Cretaceous of Patagonia (Bown and Laza 1990; Genise 1995, 1997; Laza 1995, 2006). Herein we report silicified termite coprolite-filled borings in mesquite-like wood from Miocene deposits in northwestern Argentina and discuss the paleobiologic significance of this record.

Geological Setting

The study area is in the Salar de Pipanaco, a very arid region of northwestern Argentina in northeastern and southeastern La Rioja and Catamarca Provinces, respectively. Coprolite-bearing fossil wood was found in two localities in La Rioja (lat. 28°34’8.64”S, long. 66°29’29.44”W; lat. 28°32’44.28”S, long. 66°29’29.44”W) that are part of the Salicas Formation (fig. 1; Sosic 1973). The Salicas Formation also crops out in the central-northern region of La Rioja and adjacent regions in southern Catamarca, but plant remains are known only from the Salar de Pipanaco area. Coprolite-bearing fossil wood from the Salicas Formation is silicified and occurs loose in small groups of individuals at the top of a short sedimentary succession (~10 m) capped by a massive grayish sandstone that is covered by unconsolidated sand. Exposed sections of the sedimentary succession show alternating massive to slightly stratified sandstones and siltstones that are sometimes mixed with finer clayey and volcaniclastic material and show signs of pedogenesis (i.e., presence of rizoliths), suggesting deposition...
in an alluvial plain influenced by volcanism. Paleontological and sedimentological data from more western outcrops of the Salicas Formation indicate a succession of fluvial horizons deposited in an open semidesertic environment (grasslands with patches of forests) that became gradually more arid (Tauber 2005; Brandoni et al. 2012).

The age of the Salicas Formation is constrained on the basis of its vertebrate fossil content to the Late Miocene (Tauber 2005; Brandoni et al. 2012). So far only mammals, beetle traces, and a mesquite-like wood have been described from the Salicas Formation (Tauber and Mazzoni 2003; Tauber 2005; Pujana 2010; Brandoni et al. 2012).

**Material and Methods**

Fossils were studied from standard thin sections with transmitted light microscopy (Hass and Rowe 1999). Description and classification of coprolites were based on comparisons to modern and fossil examples (Labandeira et al. 1997; Grimaldi and Engel 2005; Taylor et al. 2009). In particular, coprolites were compared to fecal pellets produced by extant termites and especially to the morphologically closer ones produced by three termite species within the family Kalotermitidae (*Neotermes hirtellus*, *Tauritermes taurocephalus*, *Cryptotermes brevis*) from northeastern Argentina. The genera *Neotermes* and *Tauritermes* account for about 70% of the diversity of species of kalotermitids in Argentina, which are mainly distributed in the Chaqueña region (Torales et al. 1997, 2005, 2008). Extant Kalotermitidae pellets were sectioned, mounted on microscopic slides, and examined using light microscopy. Host fossil woods for the coprolite-filled borings are most similar to the morphogenus *Prosopisinoxylon* on the basis of diagnostic anatomical characters (Tortorelli 1956; Castro 1994; Martinez 2010; Pujana 2010). Five different samples of fossil wood filled with coprolites were studied and are deposited under accession numbers CRILAR-Pb 0029, 0031, 0034, 0070, and 0227 in the Geological Sciences Division of the Centro Regional de Investigaciones y Transferencia Tecnológica de La Rioja (CRILAR) in Anillaco, La Rioja, Argentina.

**Fig. 1** Map of Argentina with enlarged region (rectangle) showing the Salar de Pipanaco area. Satellite image of the Salar de Pipanaco depicting the coprolite-bearing localities (stars).

**Fig. 2** Transverse section of fossil wood showing anatomical characters. Scale bar = 500 μm.
Results

This section describes numerous borings filled with coprolites that occur within fragments of wood assignable to the morphogenus *Prosopisinoxylon* (Martínez 2010). Diagnostic characters include vessels of two distinct classes, simple perforation plates, multiseriate rays, and abundant axial parenchyma (fig. 2), on the basis of which affinities to the extant genus *Prosopis* were suggested (Martínez 2010).

Borings consist of small (maximum length, 2.5 cm; width, 0.2–0.5 cm) cavities or small chambers that are at variable angles relative to the fibers’ long axes of the host woods (fig. 3A, 3B). The uncut surface of the host woods shows the exposed ends of the borings, which are elliptical to oval in cross section with rounded borders (fig. 3A). The borings are completely filled with coprolites embedded in an amorphous matrix. In longitudinal section the borings are elongate with slightly irregular borders and fully filled with coprolites (fig. 3B). Thin sections of the borings show a cylindrical to lentil-shaped cross section and an elongate to curved longitudinal section, smooth borders, and rounded ends and the absence of branches (fig. 3C, 3D).

Coprolites occur as tightly packed groups within the borings (fig. 3E). They are cylindrical, sometimes oval shaped (average diameter × length, 453.75 × 911.25 μm; n = 20), with rounded ends. Most are hexagonal and display slightly concave sides in cross section, but some are more rounded in cross section (fig. 3F, 3G). Most coprolites appear as well-delineated individuals displaying a smooth texture and are formed by finely chewed-up material of probable plant origin (fig. 3H). Some coprolites have thin (~1–3-μm diameter) radiating filaments, and others have coarser filaments (5–10-μm diameter) embedded in their bodies (fig. 3I, 3J). Other coprolites are made up of a variety of amorphous and better-defined particles, including very small spherical to irregular particles, including very small spherical to irregular particles (fig. 3K, 3L).

The coprolites share identical morphologies (cylindrical shape with rounded ends and a hexagonal section with concave sides between ridges) with the three extant species examined. They were more similar in size (average diameter × length, 398.6 × 815 μm; n = 20) to *Tauritermes taurocephalus* (fig. 4A, 4B) than to the other two extant species examined (657.25 × 815 μm in *Cryptotermes brevis* and 623 × 875 μm in *Neotermes birtellus*; n = 20). Feces of all three extant species examined contained very finely masticated plant material, but *N. birtellus* also contained some larger organic fragments including fungal spores and hyphae (fig. 4C, 4D).

Discussion and Conclusions

Termites have provided a wealth of evidence of their occurrence in ancient ecosystems, including numerous body fossils and traces of their building and eating behaviors, such as the presence of feces inside nests built in soils and wood (Rohr et al. 1986; Düringer et al. 2006; Poinar 2009). However, a large part of this information is from well-studied amber-bearing or other deposits primarily in the Northern Hemisphere, whereas the fossil record of termites from the Southern Hemisphere, and, in particular, that from Argentina, is relatively sparse (Grimaldi and Engel 2005). Therefore, despite the ecological significance of termites in modern tropical and subtropical regions such as northern Argentina, their fossil record is of limited significance regarding their paleodiversity, paleoecology, and paleodistribution. The record presented here of coprolites inside borings excavated in mesquite-like (aff. *Prosopis*) wood is the first fossil record of termites from northwestern Argentina, thus filling a gap for the distribution of the group in Neogene deposits from this region.

The characteristics of the borings from the Salicas Formation and the fine preservation of the fragments of the mesquite-like wood where these were excavated are probably the products of the activity of kalotermitid termites. Kalotermitids, also referred to as dry-wood termites, live entirely and inconspicuously inside their woody substrates, where they excavate chambers of variable size and form that are connected to one another by small tunnels or galleries (Nutting 1966; Ebeling 1975; Hasiotis 2003; Lafont 2005). This concealed life mode typical of kalotermitids allows the colony to live off the moisture obtained from the wood they inhabit. As a result, dry-wood termites are very inconspicuous unless evidence of their presence, commonly from the occurrence of tiny holes excavated to the outside of the nest to discard their feces produced inside, is observed (Grace 2009). Feces are also accumulated in unused gallery sections and chambers (Nutting 1966; Ebeling 1975; Hasiotis 2003). The exposed ends of the fossil borings described here are variable in form and dimensions and are completely filled with coprolites, which suggests that they might represent the most external parts of a larger nest (not preserved) related to the deposition of feces to the exterior, much like the holes excavated with a similar objective by extant kalotermitids. This habit maximizes the use of moisture present in the host wood, which allows dry-wood termites to live in very arid regions (Grimaldi and Engel 2005).

Several authors have delineated the main characteristics of the coprolites produced by different arthropods throughout the fossil record (Scott and Taylor 1983; Labandeira et al. 1997, 2004). With regard to these characteristics, which include size, shape, texture, and contents, the coprolites found in the borings in the mesquite wood from the Salicas Formation are most similar to those of termites. In particular, shape, size, and cross section of the coprolites from the Miocene of La Rioja are comparable to the feces of extant kalotermitid and termopsid termites (Labandeira et al. 1997, 2004; Hasiotis 2003; Grimaldi and Engel 2005). Termopsid feces are larger and have a more variable shape and cross section (more commonly circular rather than hexagonal) than those of kalotermitids because they possess different rectal pads that mold the extruded pellet (Noirot and Noirot-Timorhée 1977). Kalotermitid feces are cylindrical with rounded ends, and they have a consistent hexagonal shape with slightly concave sides, much like the fossils from La Rioja. Morphological comparison to the feces of three kalotermitids (*Cryptotermes brevis*, *Neotermes birtellus*, *Tauritermes taurocephalus*) found in different kinds of woody substrates from Corrientes Province in northeastern Argentina (Toroles et al. 1997, 2005, 2008) shows no differences between the coprolites from La Rioja and their extant relatives. The characteristic morphology of the feces of kalotermitids is a consequence of a six-padded rectum specialized to reabsorb moisture from...
Fig. 3 Silicified termite coprolites from the Miocene of northwestern Argentina. A, Uncut surface of the secondary xylem of fragments of mesquite-like wood with parallelly arranged termite borings (arrowheads). Scale bar = 2 cm. B, Uncut surface of the secondary xylem of mesquite-like wood with transversely arranged termite borings (arrowheads). Scale bar = 1 cm. C, Elliptical to lentil-shaped cross section of termite borings in mesquite-like wood. Scale bar = 0.5 cm. D, Elongate to slightly irregular longitudinal section of termite borings in mesquite-like wood. Scale bar = 0.5 cm. E, Close-up of a termite boring completely filled with coprolites. Scale bar = 0.25 cm. F, Close-up of a group of coprolites with a characteristic cylindrical shape. Scale bar = 500 μm. G, Close-up of a group of coprolites displaying a typical hexagonal section.
Several coprolites are made up of a variety of amorphous and better-defined particles, including thin, radiating, and coarser filaments and small spheres of uncertain affinity. Morphologically, these structures are very simple and do not provide enough characters for taxonomic assignment, although one possibility is that they represent fungal remains that were part of the termite’s diet. Although kalotermitids are more common in nondecayed wood, they can consume fungally degraded wood, and fungi have been found inside their nests (Nutting 1966; Moein and Rust 1992; Brune 2006). In addition, two Neogene records, from Germany and Australia, found fungal hyphae associated with kalotermitid coprolites (Brues 1936; Sutherland 2003), and we detected fungal hyphae and spores in the feces of an extant kalotermitid (*N. hirtellus*). Such occurrences could represent either consumption of fungi or secondary colonization of the feces by a saprotrophic fungus. Regardless, these data show that it is possible to find fungi associated with termite feces. Therefore, the filaments and small spheres in the coprolites from the Salicas Formation could be fungal hyphae and unicellular spores, more likely of a secondary colonizer than part of the termite’s diet.

An alternative is that the fungal-like coprolite contents are remains of the termite-gut microflora, including flagellate protozoans and bacteria, both of which are lost during molting (Margulis et al. 1998; Radek 1999). Identification of protozoans and bacteria within the digestive systems of termites is rarely achieved on the basis of solely gross morphology. Regardless, the remains in coprolites from La Rioja are reminiscent of the protozoan and bacterial cysts and filaments previously found in the guts and feces of extant and fossil termites, including kalotermitids (Margulis et al. 1990, 1998; Wier et al. 2002; Dolan et al. 2004; Poinar 2009). Moreover, the abundance of possible protist cysts in some of the coprolites from La Rioja may be related to a hypothesized mode of gut-microbiota transmission by coprophagy between termites (Poinar 2009).

Cylindrical coprolites with a hexagonal shape similar to the fossils described here have been documented from Cretaceous and younger strata worldwide (Colin et al. 2011). Their possible affinity to termopsids and kalotermitids has been discussed, but in most cases they are considered products of the latter (Rozefelds and De Baar 1991; Sutherland 2003). Only one of these records, possible kalotermitid coprolites in a cycad stem from the Upper Cretaceous of Patagonia (Genise 1995), was known for Argentina before the current record from the Miocene of La Rioja. It is probable that the current sparse record from South America (Fontes and Vulcano 2004; Grimaldi et al. 2008; Pires and Sommer 2009), including Argentina, is a result of insufficient search.

Termites are the most important macroinvertebrate decomposers in tropical deserts, where common recyclers of organic matter in other ecosystems, fungi and bacteria, are limited in activity, especially during the dry, hot season (Whitford 2011).
kalotermitids in the area is extinction as a result of anthropogenic pressure on the scarce resources, especially wood (Torales et al. 2005; Villagra et al. 2009). Alternatively, they still occur in the region but have simply gone undetected.

In summary, this is the first record of coprolites assignable to kalotermitid termites in northwestern Argentina. This expands the paleobiogeographic record of the family and provides evidence of interaction with mesquite-like trees during the Miocene. Kalotermitids would have been very well adapted to the arid Salar de Pipanaco area, where they probably were significant members of the ecosystem acting as recyclers of organic matter, especially of woody substrates.

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