

Termite nests in eolian backshore settings: An unusual record throughout the Quaternary in the Neotropical realm

Kimberly Silva Ramos, Renata Guimarães Netto, and Daniel Sedorko

ABSTRACT

In this paper, we report the unusual presence of extant termite nests in frontal beach eolian sandy substrates in the Rio Grande do Sul Coastal Plain (southernmost Brazil) and describe the nest architectures, aiming to compare them with termite fossil nests preserved in Pleistocene backshore deposits of this same coastal plain. Four sites were analyzed along the modern beach, and the architecture of the termite nests was described. The nests are composed of a rounded convex epigeal portion and a hypogeal portion with variable dimensions formed by interconnecting spherical to semi-spherical chambers. Considering that termites are assumed to colonize more mature, vegetated soils due to the need for abundant cellulosic material, the occurrence of termite nests in backshore dunes close to the shoreline opens a discussion about the distribution and habit of termites and the applicability of their trace fossils for paleoenvironmental reconstitutions.

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INTRODUCTION

Termites are social insects within the Blattodea order that construct complex ground nests (Inward et al., 2007). This group occurs in several modern environments, including grasslands and vegetated zones close to or inside tropical forests, and is restricted to the latitudinal interval 0° to 50° in the Northern and Southern hemispheres (Lee and Wood, 1971; Su, 2003). Unlike ants that commonly nest in coastal dunes (e.g., Chen et al., 2015), termites are seldom registered in these settings. A few studies reported termite nests in sandy soils in coastal environments (e.g., Kaiser, 1953; Araújo and Fontes, 1979; Fontes, 1979, 1982, 1992; Vasconcellos et al., 2005; Diehl et al., 2014, 2015; Santos, 2015), mostly in denser vegetated areas of restinga ecosystems (e.g., Moura and Machado, 2017). However, these occurrences are rare compared with termite nests in mature soils (e.g., Martius, 1994; Bandeira et al., 2003; Oliveira et al., 2013; Cancellato et al., 2014; Plaza and Galbiati, 2017). Indeed, termite nests in barely vegetated dunes in backshore settings are virtually unrecorded.

Abundant trace fossils attributed to ants and termites, along with other such insects like beetles, solitary wasps, and cicadas, occur in the Upper Pleistocene eolian deposits of the Rio Grande do Sul Coastal Plain (PCRS, as it is known in Brazil), southernmost Brazil (Gibert et al., 2006). This insect trace fossil assemblage descends from a well-marked Fe-rich surface that suggests a depositional hiatus, leading Netto et al. (2007) to preliminarily infer colonization of more mature soils in alluvial deposits that settled over the eolian dunes due to a significant sea-level fall. Among all insect groups represented in this trace fossil assemblage, only termites do not leave the burrow to feed and necessarily have to construct their nests in vegetated areas or nearby. Thus, they are the best biomarker to characterize the type of paleosol developed at the top of the Pleistocene deposits, which is crucial to understand better the sedimentary dynamics involved in the PCRS evolution during the terminal Pleistocene.

Thus, to test the hypothesis erected by Netto et al. (2007), we performed a search for termite nests in the modern coastal dune deposits of the PCRS (barrier-lagoon system IV, Holocene to recent), which is considered a modern analog for the Upper Pleistocene coastal settings (barrier-lagoon system III) (e.g., Tomazelli and Vilwock, 2000; Carassai, 2013). Surprisingly, this search revealed extant termite nests in the barely vege-

tated frontal eolian dunes in different latitudes along the PCRS and a few meters from the sea. Hence, the objective of this study is threefold: (i) to report the unusual occurrence of termite nests in sandy substrates from frontal beach eolian dunes; (ii) to characterize the architecture of these termite nests for actuopaleontological approaches; and (iii) to highlight the relevance of these occurrences for the insect trace fossil record in paleosols.

BACKGROUND

Social insect nests are distributed in several continental sub-environments, from sparsely vegetated areas to humid soils associated with forests (Genise, 2017). This large distribution allows the application of nest architecture as an auxiliary tool to interpret depositional settings in continental paleoenvironments. Termites (Order Blattodea), which are the object of this study, live in colonies and are organized into castes formed by the breeding couple and sterile individuals, the latter subdivided into workers and soldiers. Workers are responsible for food capture and nest building while soldiers defend the colony (Brusca and Brusca, 2007).

Termites feed mainly from cellulosic material inside the nest. Thus, they tend to nidify in soils rich in grass, herbaceous plants, wood, fungi, excrement, animal remains, lichens, and organic matter. Termites can obtain energy from these materials due to the protozoa present in their intestine (e.g., Lima and Costa, 2007). They also depend on humidity to avoid body desiccation. Thus, unlike other social insects, the termite nest architecture guarantees internal microclimate maintenance, keeping the local humidity and controlling the relative heat (Redford, 1984; Noirot and Darlington, 2000; Genise et al., 2004; Korb, 2011). The termite's constructive behavior changes the substrate, increasing the porosity and mixing minerals, depositing in, or extracting them from the substrate (Wood and Sands, 1978). Termites are ecosystem "engineers", influencing the availability of resources for other organisms and modifying the edaphic trophic relations (Lavelle et al., 1997).

The oldest putative record of termites is from the Lower Cretaceous (Jarzembowski, 1981; Martinez and Martinell, 1995). In the PCRS, social insect nests are common in the eolian deposits of the lagoon-barrier systems III (Upper Pleistocene), represented by the ichnogenera *Termitichnus*, *Vondrichnus*, and *Krausichnus* (Gibert et al., 2006), and IV (Holocene to Recent), represented by their modern counterparts. Ant nests are wide-

spread throughout the east to west modern backshore extension and commonly occur in the foredunes. Termites are less frequent and show a more consistent distribution in the inner portion of the backshore, in vegetated areas that characterize the restinga ecosystem (Diehl et al., 2014, 2015). The occurrence of termite nests in the foredunes was unrecorded until now.

The PCRS is a geological province that characterizes the Atlantic coastal plain of the Rio Grande do Sul State (Figure 1) and comprises the exposed portion of the Pelotas Basin, a marginal rift basin formed due to the South Atlantic Ocean opening in the Cretaceous (Milani et al., 2007). The PCRS is composed mostly of sandy and minor silty deposits accumulated during four previous falling and rising sea-level cycles. Each cycle represents the establishment of a lagoon-barrier system (LBS), the oldest one (LBS I) formed at the end of the Pliocene, the following ones (LBS II-III) during the Pleistocene, and the last (LBS IV) during the Holocene (Tomazelli and Villwock, 2000). The sandy deposits represent beach barriers and show two main sedimentary facies associations: a marine facies that contains deposits formed by the wave and current action in shoreface and foreshore settings, and an eolian facies, representing backshore settings (Gibert et al., 2006).

The LBS IV characterizes the modern beach deposits in the littoral. The LBS IV backshore deposits are composed exclusively of fine-grained, well-sorted quartz sand, except for shell fragments blown by the wind from the foreshore to the foredunes. The backshore extension is variable throughout the PCRS, narrower in the NNE and wider in SSW. Vegetation is generally scarce in the foredunes and restricted to areas where some water supply exists. Vegetation is represented mostly by xerophytic grasses, but other groups of herbaceous angiosperm plants and ferns from the dune pioneer vegetation also occur. The phreatic line is shallow in the backshore zone and oscillates according to storm surges and exceptional tides. Tides range from 30 to 50 cm on average, characterizing a micro-tidal regime (Netto and Grangeiro, 2009). Regarding climatic pattern, temperatures are variable throughout the year in the PCRS, with the minimal average recorded in site D (7.2 °C in July, South Hemisphere winter) and maximum average record in site C (31.7 °C in January, South Hemisphere summer) (Table 1). Rain is well-distributed, oscillating between 74 mm in the drier month and 164 mm in the rainiest month (Table 1). The winds are constant along the year in the whole coastal plain, with average annual winds between

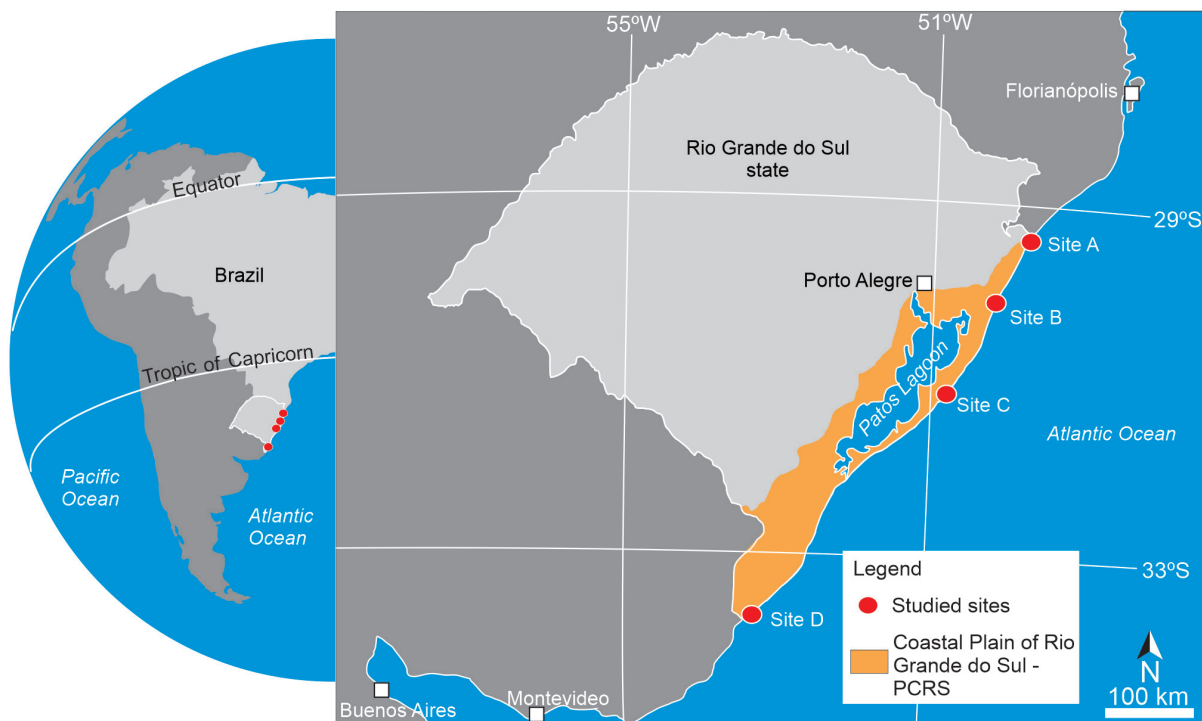


FIGURE 1. Schematic map of studied areas (red circles). In this study only coastal occurrences of termite nests were considered. Site A: 29°23'3.26"S, 49°45'29.94"W; Site B: 30° 5'21.61"S, 50°10'9.26"W; Site C: 31° 9'34.00"S, 50°49'0.12"W; Site D: 33°43'40.44"S, 53°21'3.80"W. Modified from Google Earth.

TABLE 1. Climatological average based on 30 years of data (1981-2010), using official stations at INMET (National Institute of Meteorology) as available in IRGA (2021).

Site (city)	Minimum temperature average (°C)	Maximum temperature average(°C)	Less raining month (mm)	More raining month (mm)
A (Torres)	July (10.7)	February (27)	December (95.3)	February (164)
B (Tramandaí)	July (11.7)	January (29.6) and February (29.6)	December (74)	February (133.3)
C (Mostardas)	July (11.2)	January (31.7)	March (74.5)	June (138.3)
D (Chuí)	July (7.2)	January (27.7)	November (76.6)	February (150.7)

7.0 to 8.0 m/s in 50 m height (Amarante and Silva, 2002).

MATERIAL AND METHODS

Four equidistant localities were selected for prospection throughout the eolian deposits of the PCRS (sites A, B, C, and D, Figure 1). Termite nests were found in all sites and analyzed in situ, being numbered according to the site of occurrence (e.g., A.1, A.2, A.3 for site A). The nest architecture was described, and internal morphological variations were accessed by successive cuts in the nest structure and casting. Nest casts were made in sites B and D using an orthophthalic resin catalyzed by butanox 5%. The entire nest architecture was characterized; however, the deeper portions received more attention for comparison purposes with the fossil nests due to their higher fossilization potential. Comparisons between the modern and ancient nest architectures were based on Genise (2017). Termites were collected and identified at the family level (identification key of Constantino, 1999).

RESULTS

Field Observations

While ant nests are abundant and widespread in the eolian dunes of the PCRS, termite nests are less abundant and restricted to vegetated areas associated with some freshwater supply in the surrounding zone. All observed nests present a dome-shape with no open chimneys, varying in diameter, height, and depth as detailed below.

Site A. Termite nests from site A (Itapeva Beach; Figure 1) form dense patches of nests in frontal eolian dunes where water supply is available in the interdunes (Figure 2D), and the patches are ~30 m distant from the high tide line. Angiosperms from the families Gramineae, Hypericaceae, Araliaceae, Asteraceae, Juncaceae, and some ferns (family Equisetaceae and others) constitute the vegetation

of the foredunes. Termite nest concentration is higher where vegetation is denser, with ferns predominating (Figure 3C).

The hypogeal nest portion exhibits a gradual downward reduction in diameter, finishing in few horizontally-oriented passages that reach 60 cm in length. Some passages are produced inside the roots that the termites ate. The average nest mound diameter in site A is 21.27 cm, and the average height is 21.15 cm. The depth of the nest below the surface is 54.23 cm (Table 2). One nest showed a large and empty chamber in which coleopterian larvae were observed (Figure 3A-B). Termites were active in all levels of the nest.

Site B. Only five termite nests sparsely distributed along the eolian dunes were observed in site B (Tramandaí Beach; Figure 1). The nest closest to the shoreline was casted, while the others were only measured (Table 2). The termite nests from site B also occur in the foredunes and are ~50 m from the high tide line (Figure 4D). Angiosperms from the families Gramineae, Araliaceae, and Juncaceae characterize the primary vegetation in site B (Figure 4A).

The hypogeal nest portion exhibits a gradual downward reduction in diameter, finishing in a few horizontally-oriented passages that can reach 70 cm in length, mostly produced inside roots consumed by the termites. The average mound diameter in site B is 23.42 cm, and the average height is 19.56 cm. The nest reaches 94.5 cm in depth below the surface (Table 2), but only one nest was excavated in this locality (Figure 4). Termites were active in all levels of the nest.

Site C. This site (Mostardas Beach; Figure 1) has the smallest density of termite nests among the studied areas; only three nests were found. The termite nest closest to the coastline was located 174 m from the high tide line, next to a freshwater stream in the interdune zone (Figure 5). The primary vegetation explored by termites in these nests is grass (Gramineae). However, plants from

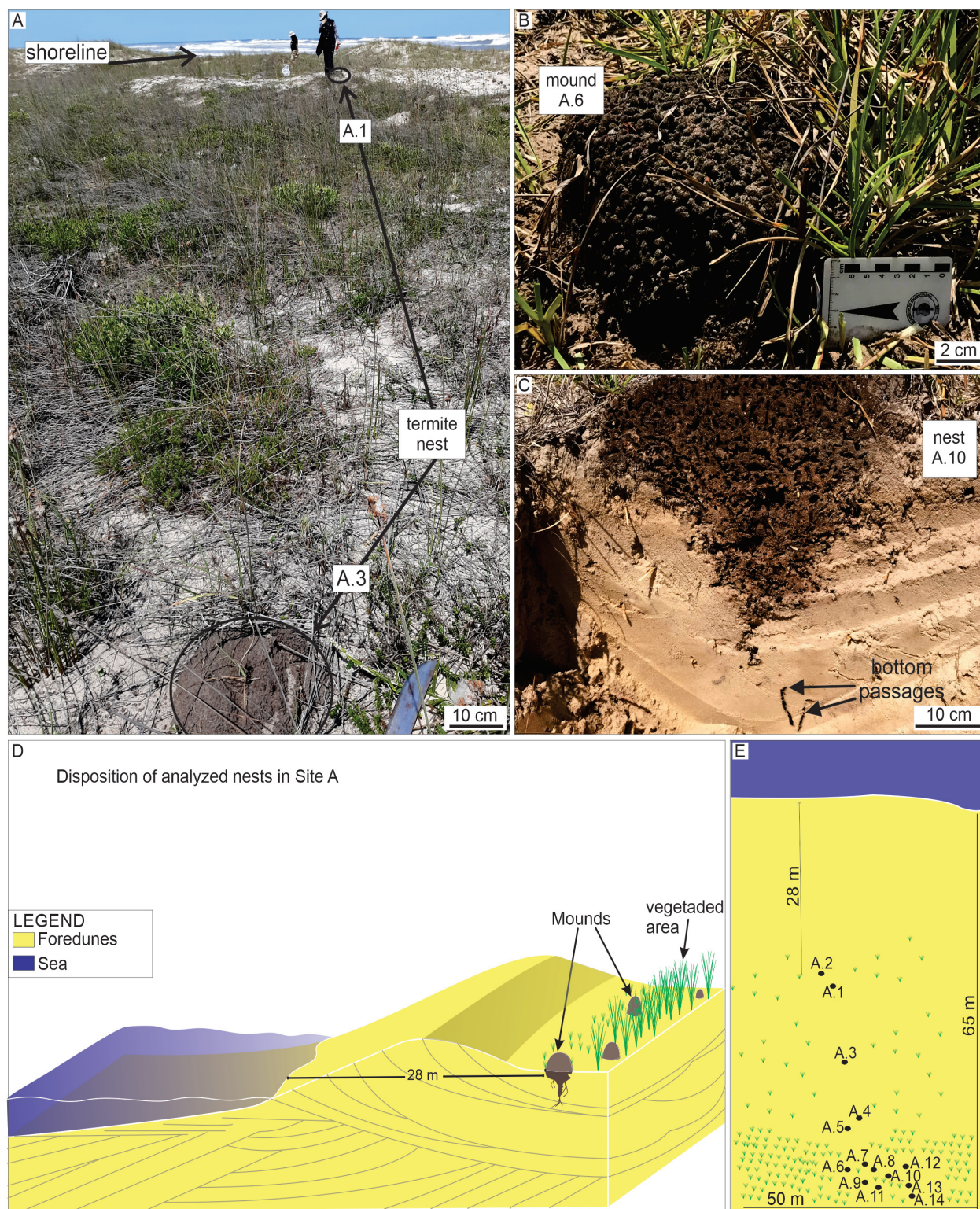


FIGURE 2. Termite nests from site A. General view of the nests close to the shoreline (a), with sparse vegetation of grasses and ferns around the mounds, and detail of external nest morphology with no open chimneys (b) (nest A.6). The hypogean portion of nest A.10 with bottom passages vertically oriented is shown in (c). The schematic disposition of termite nests in site A allow observing that the closest nest is less than 30 m from shoreline (d), and nest's concentration in the flat areas of foredunes (e), almost 60 m far from shoreline.

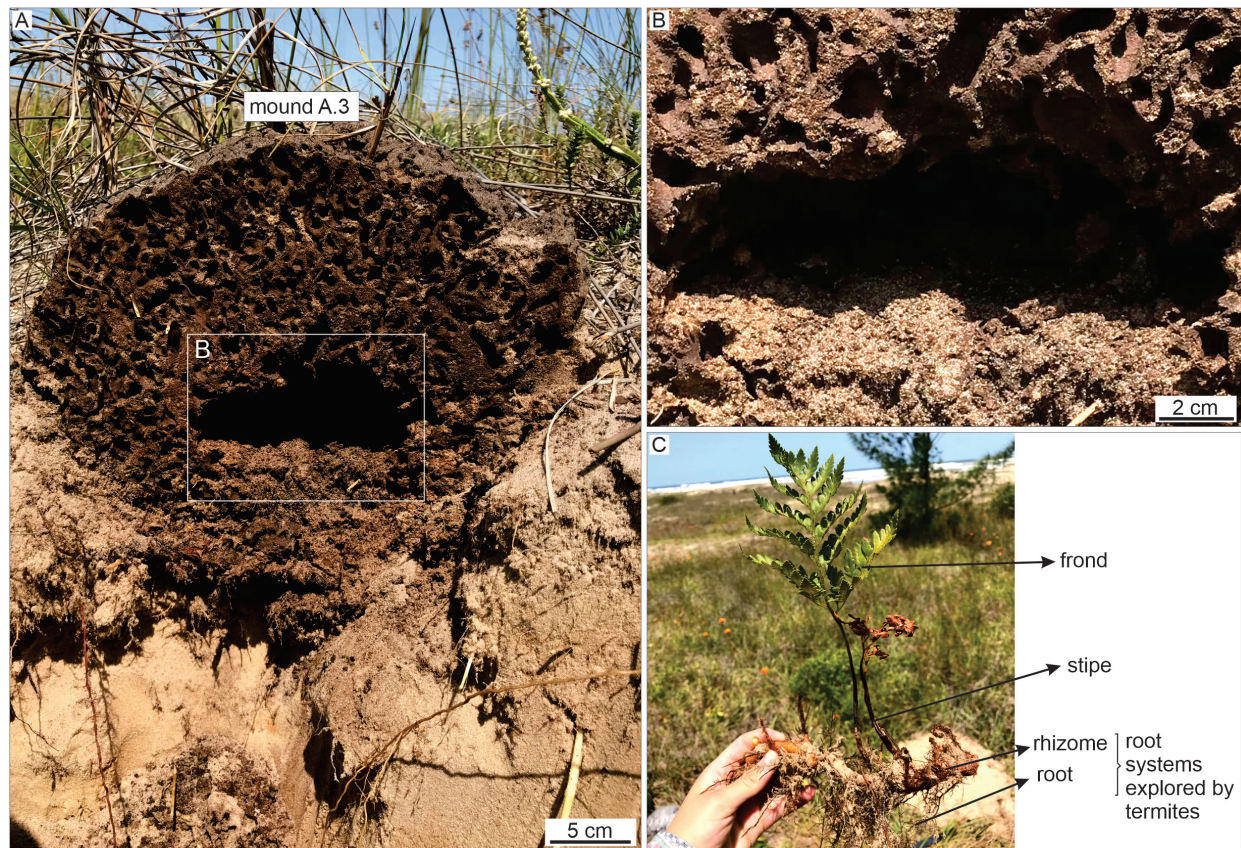


FIGURE 3. Detail of the internal chamber found in nest A.3 (a, b) and the rhizome of ferns used by termites (c).

the family Juncaceae and other angiosperm taxa also occur on the stream edges.

The nest mounds are very small (4.36 cm high on average) compared to the other sites' nests (Table 2). However, the nests show a downward enlargement below the general funnel that characterizes the bottom of the termite nests in the PCRS, resembling a downward helicoidal pattern in passages distribution (Figure 6). This particular architectural detail was observed exclusively in site C. Termites were active in all nest levels.

Site D. The termite nests from site D (Barra do Chuí Beach; Figure 1) are ~58 m from the high tide line and are common along the foredunes, mostly in lee side and interdunes, concentrated in the sand strip between 60 and 80 m from the sea (Figure 7E). The surrounding vegetation is primarily of plants from families Gramineae and Araliaceae.

The nests present a bigger epigeal portion than the other sites' nests, reaching 1.10 m in high and going deeper into the substrate (Table 2). The nest structure is characterized by dense passages regularly distributed in the epigeal portion. However, in the hypogeal portion, it assumes a less dense distribution with thicker passages. The black

color of D.4 nest is due to the occurrence of Pleistocene peat deposits buried 2 m below the substrate surface (Figure 8). Termites were active in all levels of the nest.

Nest Morphology and Casts

The hypogeal portion of nests B.1 and D.4 was cast by resin to highlight the underground structures that present higher fossilization potential. The casts revealed a similar architecture in both nests, except for more passages inside roots in nest B.1 (Figure 4C) than in D.4 (Figure 8).

A general downward funnel-shaped structure characterizes the hypogeal portion in both casted nests, with condensed passages (Figure 9A-D) from epigeal portion converging to horizontally-oriented passages presenting larger diameters. In nest D.4, the deepest structures spread from this condensed part (Figure 9A), reaching 132.5 cm in depth. The nests present lateral projections that can reach 70 cm in length, following the root systems. Some of the horizontal passages contain small chambers connected (up to 5 cm in diameter; Figure 9A). Successive cuts evidenced the hypogeal architecture in the nest C.1, which differs from

TABLE 2. Dimensions of observed termite nests and average per site. (-) not observed.

Site/Nest	Diameter of mounds (cm)	Height of mounds (cm)	Maximum depth (cm)
A.1	18.2	24.5	-
A.2	12.5	28.2	-
A.3	31	14.5	36.1
A.4	24.5	20	-
A.5	20.4	18.7	-
A.6	20.1	30.5	57.5
A.7	18	12.4	-
A.8	26.5	15	-
A.9	12	8.9	37.4
A.10	35.7	20.2	-
A.11	23	25.5	-
A.12	40.5	35.9	67.8
A.13	17	20.8	-
A.14	25.8	21	-
<i>average</i>	<i>23.2 (n = 14)</i>	<i>21.1 (n = 14)</i>	<i>49.7 (n = 4)</i>
B.1	26.2	19.1	94.5
B.2	18.7	15.6	-
B.3	28.5	25.1	-
B.4	31.5	28	-
B.5	12.2	9.4	-
<i>average</i>	<i>23.4 (n = 5)</i>	<i>19.6 (n = 5)</i>	<i>94.5 (n = 1)</i>
C.1	8.2	4.4	39.5
C.2	27.3	3.9	58.5
C.3	12.4	4.8	-
<i>average</i>	<i>20.0 (n = 3)</i>	<i>4.4 (n = 3)</i>	<i>49.0 (n = 2)</i>
D.1	80.2	98.8	-
D.2	57.8	107.7	-
D.3	65.8	103.5	-
D.4	53.3	52.9	132.5
D.5	52.5	89.9	-
D.6	63.7	110.6	107.8
D.7	48.5	65.8	-
D.8	54.5	72.1	98.5
<i>average</i>	<i>59.5 (n = 8)</i>	<i>87.7 (n = 8)</i>	<i>112.9 (n = 3)</i>

casted nests by the general helicoidal downward arrangement (Figure 6) and absence of lateral projections. In all observed nests, the sediment used by termites is predominantly quartz-sand, while the passages are revested by dark, thinner sediment with organic matter (Figure 9D). Termites were present in every level of the casted nests.

Successive cuts allowed accessing the architecture of the epigeal portion of the nests. Except for nest A.3 (Figure 3A-B), the epigeal passages'

disposition is similar in all analyzed nests. The nest A.3 presents a large chamber in the middle of the epigeal portion (Figure 3A). The main difference between all mounds resides in their dimensions, mostly the nest height, which varies from 4 cm (nest C.1) to 110 cm (nest D.6) (Table 2).

The collected specimens were mostly composed of workers. However, the occasional presence of soldiers allowed attribution to the family Termitidae (Figure 10).

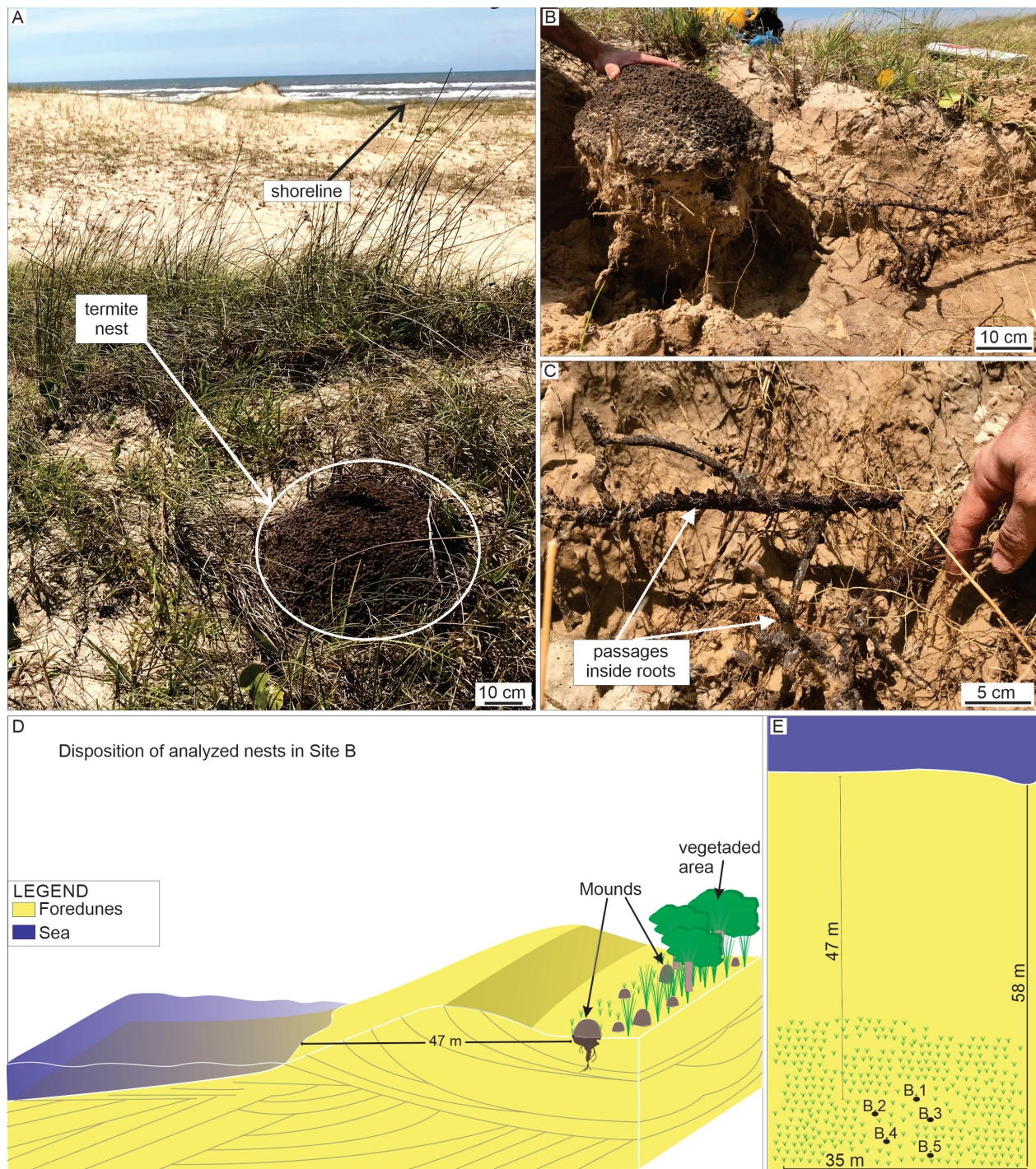


FIGURE 4. Termite nests from site B. General view of nest B.1 (a) and proximity to the shoreline; sparse vegetation of grasses and ferns around the mound. Detailed view of B.1 nest cast (b) and lateral projections mostly inside roots. Detail of the passages inside roots (c), cast by resin. Schematic disposition of termite nests in cross-section (d) and in plan view (e); closest nest is nearly 50 m from shoreline, where the nests are concentrated in interdune settings in the frontal dune zone.

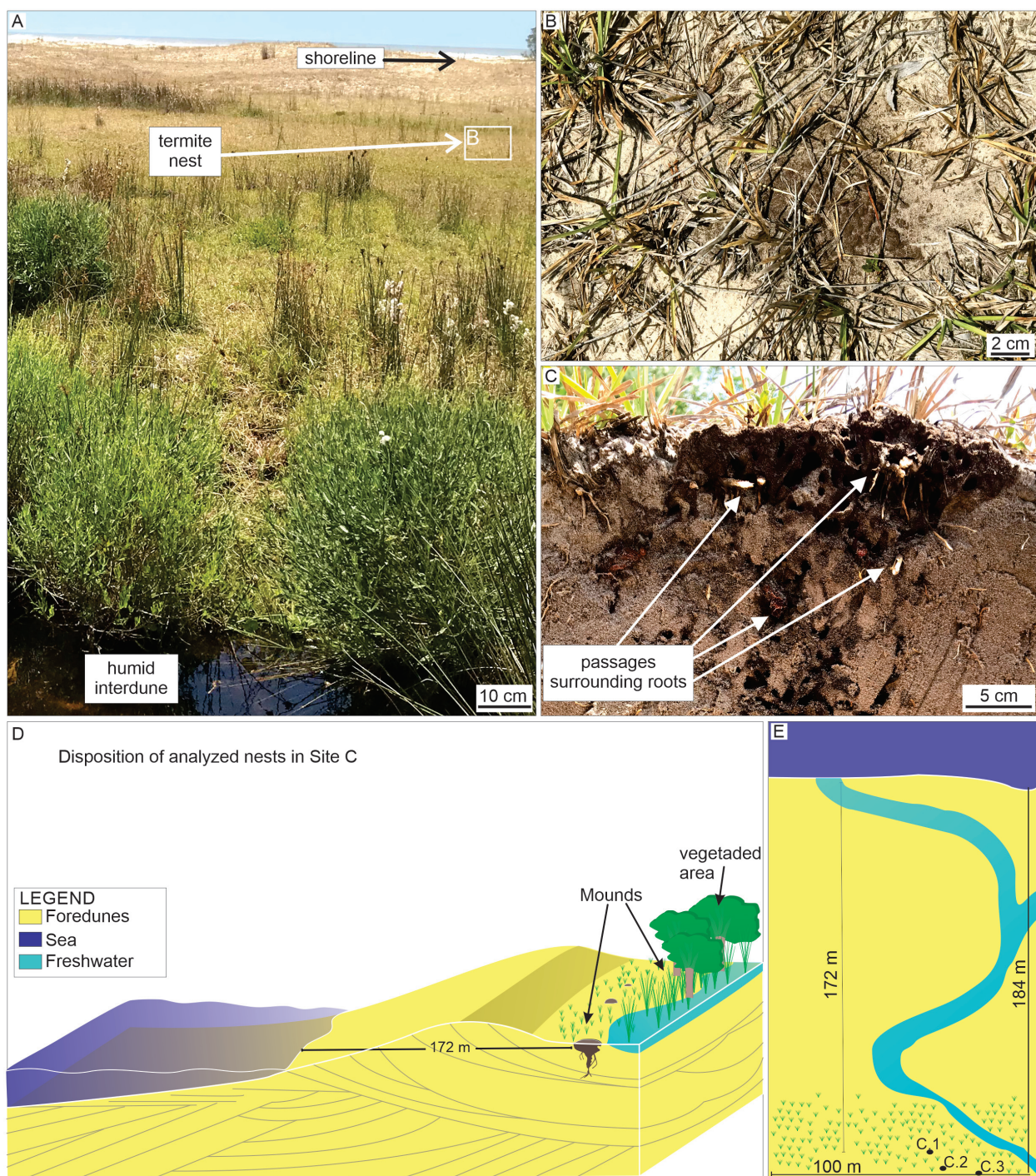


FIGURE 5. Termite nests from site C. General view of nest C.1, next to a stream (a); it seems a diverse vegetation close to the permanent stream, but the termite nests are restricted to grass. Detail of nest C.1 surrounded by grass (b). Detail of the inner passages of nest C.2 surrounded by grass roots (c). Schematic disposition of the termite nests in cross-section (d) and plan view (e); closest nest is approximately 170 m from the shoreline, where the nests are concentrated in the wet interdune zone.

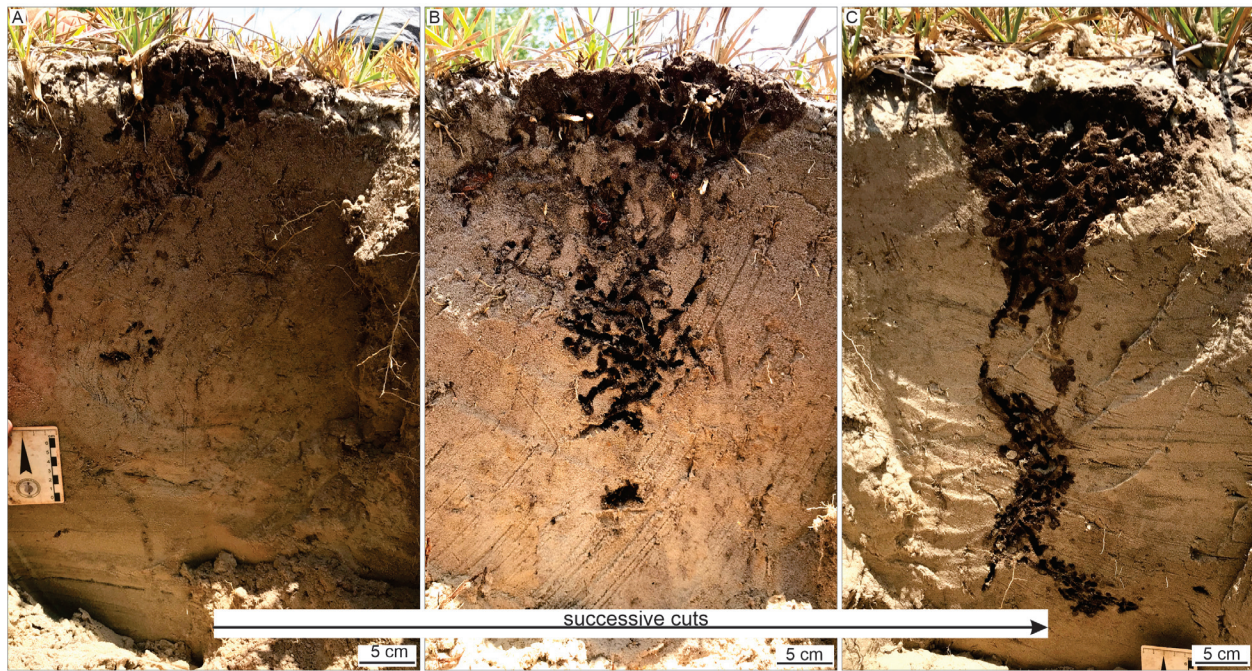


FIGURE 6. Successive cuts in nest C.2 (a-c). Observe a second enlargement below the general funnel in the central portion of the nest (c), while the margins present only a general downward reduction in size (a, b).

DISCUSSION

The architecture of the termite nests constructed in the modern foredunes comprises three main elements: a thick-walled mound, one or more chambers, and a root-like tunnel system. The number of chambers per nest and their size and the size of the nest are variable. According to Korb (2011), the mound's architecture is conditioned by balancing the need for ventilation and thermoregulation. Some fungus-growing termites construct thick-walled mounds to reduce heat loss to the outside, an adaptation to cooler conditions. The ventilation mechanism is more debated; in general, it is triggered by temperature gradients within the mound and between the mound and its exterior environment, resulting in heat convection (Korb, 2011). Considering that the average temperature in the studied sites is low compared with most soils where termites occur in Brazil, the thick walls found in the epigeal mound might be a strategy for thermoregulation. However, these variations might also be linked to colony's size and the time of colonization, as size variations are observed in nests constructed in the same site (e.g., sites A and B).

The smallest mounds occur in site C, which is also the less dense site. Although this site is located close to a large dune field (Mostardas dunes), the humidity was not a restricting factor for the colonies' maturity because site C has a peren-

nial stream nearby. Similarly, the substrate composition is mostly quartz-sand in all sites. We attribute the small dimensions to the dominance of grasses and an inferred absence of organic bed below the surface. The general low density can be attributed to intermittent dune migration, which precludes perennial colonization of the mounds. Similarly, site B also presents a few termite nests and is located close to a dune field (Tramandaí dunes). We discard anthropic degradation as responsible for the small size because all four sites occur in low anthropized dune fields in the periphery of urban areas.

Medium-sized mounds occur in sites A and B, and although they are also close to dune fields, the vegetation is more diverse than in site C. Thus, we infer that this richness in cellulosic source allowed better development of the colonies. The central chamber in nest A.3, a feature not observed in any of the other described nests, suggests a ventilation structure.

The larger mound is from site D, reaching 1.10 m in height. We attributed it to the association of taller and denser vegetation in site D than in other sites and an organic-rich bed 2 m below the surface, from where the colony catches sediments to build the nests or feed the larvae. These attributes allowed the development of long-term colonization.

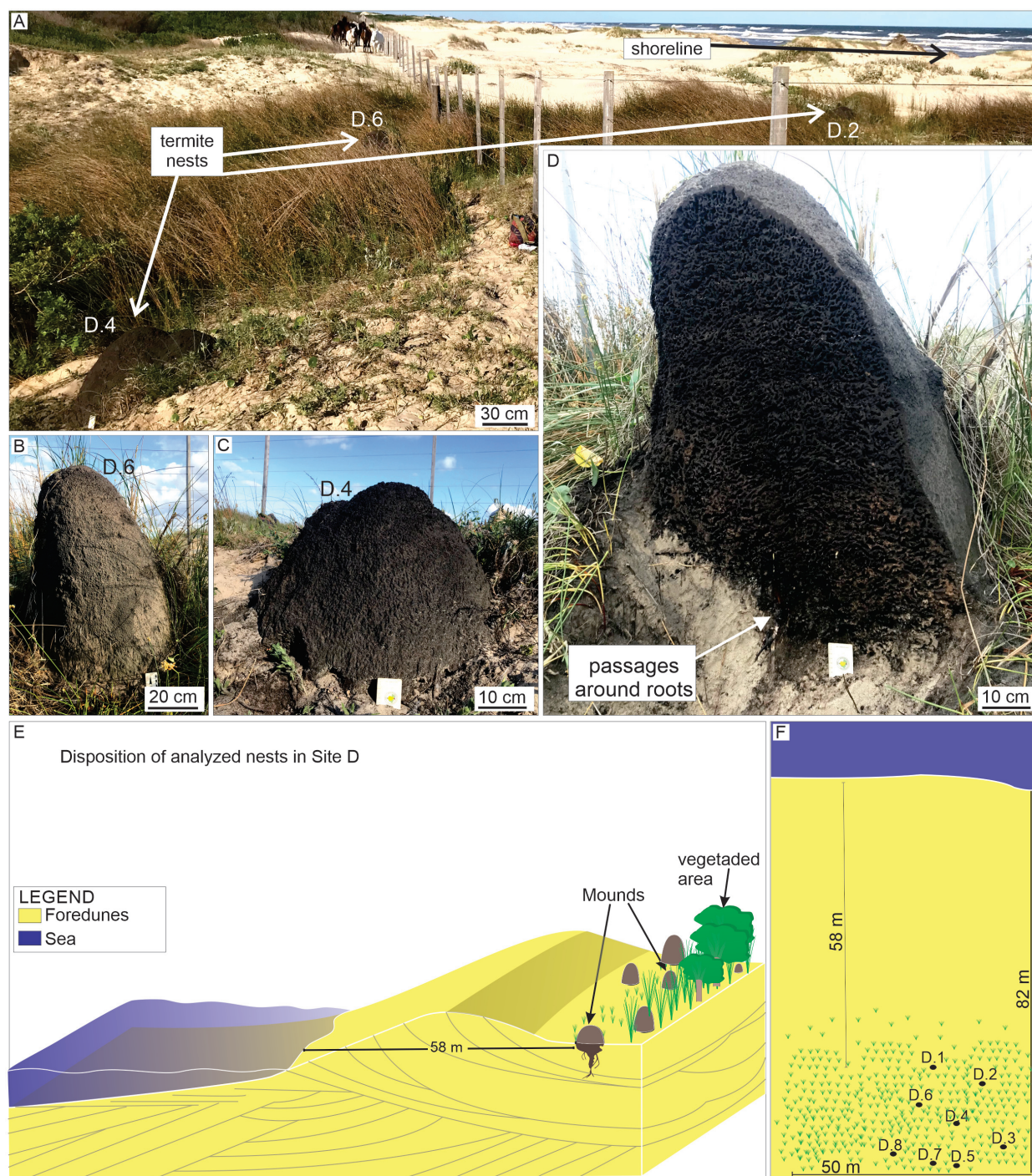


FIGURE 7. Termite nests from site D. General view of nests close to the shoreline (a); grass around the mounds. Detail of big epigeal portion in D.6 (b). Details of the cast nest D.4 (c). Detail of passages of epigeal portion and the surrounding roots in the bottom portion (d). Schematic disposition of termite nests in cross-section (e) and plan view (f); the closest nest is ca. 58 m from shoreline.

Contrary to the general assumption that termites are consumers of wood, they can feed from different organic content disposed in the substrate, in various stages of decomposition, such as wood (live or dead), grasses, herbaceous plants, fungi,

nests built by other species of termites, animal droppings and carcasses, and organic material present in the soil (Noirot, 1992; Sleaford et al., 1996; Miura and Matsumoto, 1997; Donovan et al., 2001). Thus, termite nests are not restricted to veg-

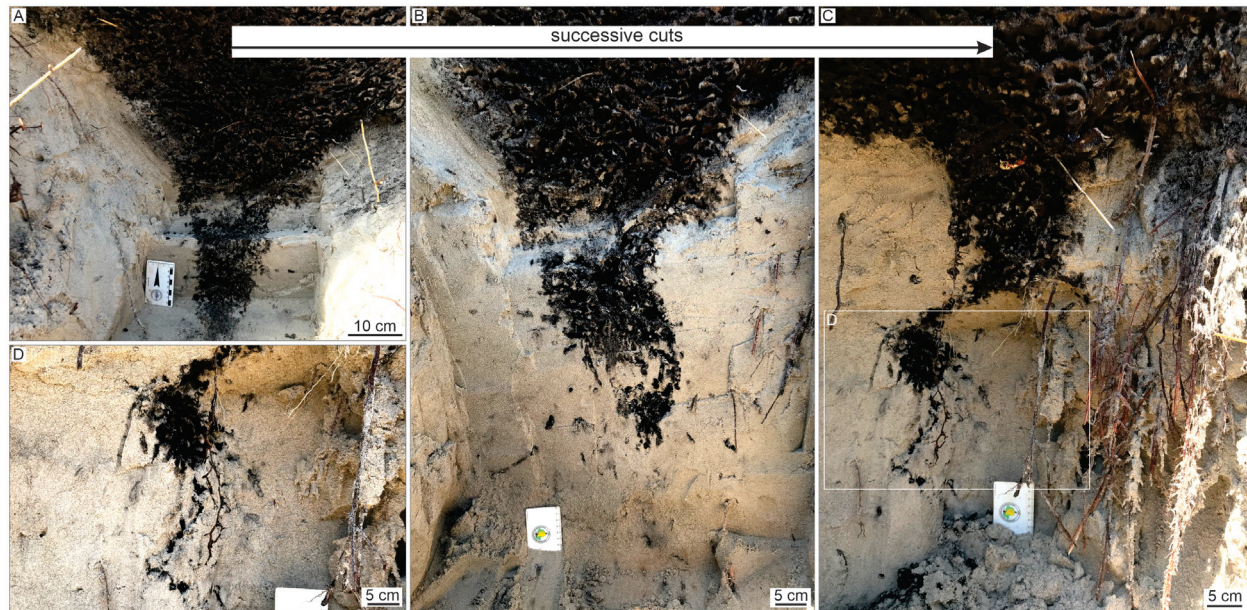


FIGURE 8. Hypogean structures in nest D.4. Successive cuts evidencing a general funnel shape (a, b) and agglomerated passages (c, d) as a lateral projection.

etated areas; well-developed nests also occur in organic-rich soils (as described for site D). The reworking of deeper sediments to the surface has been reported in Rhinotermitidae and Termitidae families (Nutting et al., 1987), but in all sites we only identified Termitidae specimens.

Dune pioneer vegetation is the main food source for termites in all studied sites, although ferns also occur. Their root systems and rhizomes are frequently found inside the nests, allowing us to infer that the termites nesting in the PCRS modern foredunes are mostly cellulosic feeders. According to Diehl et al. (2015), the termites that inhabit the areas close to the shoreline in the surroundings of site A are wood-feeders, humus-feeders, and intermediate in feeding habits. Thus, the presence of roots and rhizomes inside the nests and the poor-organic richness of the sandy substrate suggest a wood-feeder trophic habit. However, the thick-walled mounds point to a fungus-growing habit for these termites as well (Korb, 2011).

The distribution of termite nests in sandy, nutrient-poor substrates along the ~600 km of extension of the PCRS suggests that this is not an accidental occurrence. Termites have been recorded in Brazilian coastal areas, in the so-called restinga ecosystems, but always associated with arboreal vegetation (e.g., Kaiser, 1953; Araújo and Fontes, 1979; Fontes, 1979, 1982, 1992; Vasconcellos et al., 2005; Santos, 2015). Termites from the families Kalotermitidae and Termitidae were

also reported in the PCRS by Diehl et al. (2014, 2015), mostly in the non-marine zones, except in Torres (Figure 1) where termites occur closer to the shoreline in vegetated areas. The areas sampled by Diehl et al. (2014, 2015) in Torres are a few kilometers north of Itapeva Beach (site A, Figure 1) and contain termites from the species *Rugitermes* sp., *Anoplotermes* sp., *Aparatermes* sp., and *Araujotermes caissara* (Diehl et al., 2015). However, no detail about the nest architecture of these species was mentioned. In our study, only termitids were found associated with dunes close to the shoreline.

Termite nests were confidently reported in the fossil record since the Late Cretaceous (e.g., Genise, 2017). Based on the average distribution and biology of extant termites, they have been used as a bioindicator of mature paleosols (e.g., Smith et al., 1993; Genise et al., 2000). The presence of termite nests in loose sediments of foredunes places new light on this paradigm and expands the paleoecological discussion regarding this insect group.

Termite nests have a high potential for fossilization, considering that they can reach up to 1 m depth. The mixture of sediment, feces, and spittle used to construct the nest chambers provides a strong cement that protects the nest from erosion, even in loose substrates (Ferreira et al., 2011). Unlike ants, termites rarely go outside the nest to collect their food. Thus, the nests need to be constructed in substrates that provide their food,

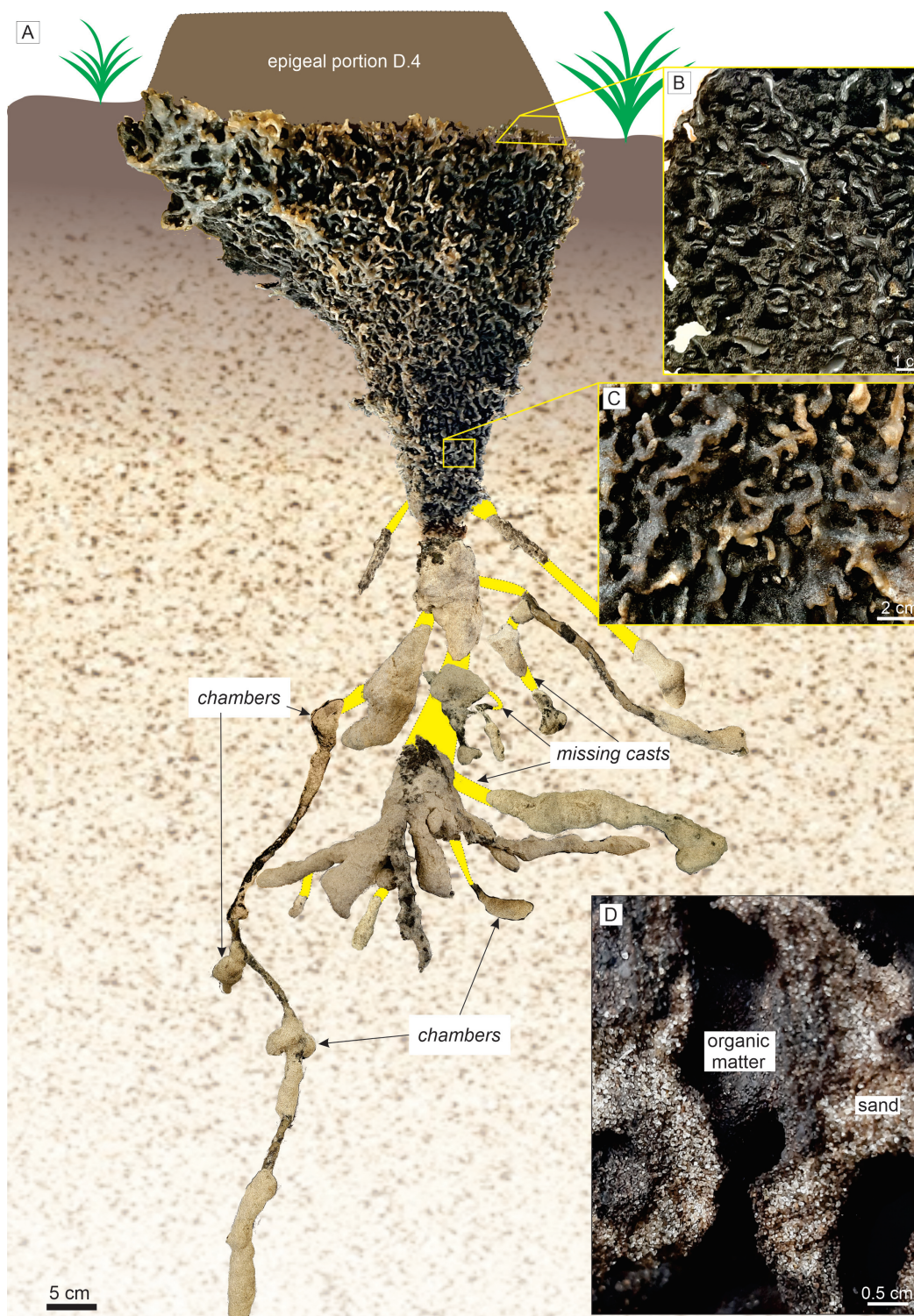


FIGURE 9. Features of the casted nests. A. Photomosaic evidencing the hypogean portion of nest D.4; observe that the structure present two main disposition of passages, with concentrated passages very similar to epigeal portion going up to ~70 deep, and elongated passages mostly vertically-oriented with lateral chambers occurring only in deeper part of the structure; horizontally-oriented passages are more common in the middle of the underground portion, with local globous chambers. Dotted lines colored in yellow represent inferred connections, lost during removal of the cast. B. Plan view of the bottom of epigeal portion, with concentrated pattern of passages (central chamber is absent). C. Casted concentrated passages evidencing a random distribution. D. Walls of passages in epigeal portion, showing high concentration of sand lined by organic matter in its interior (this sample was not casted).

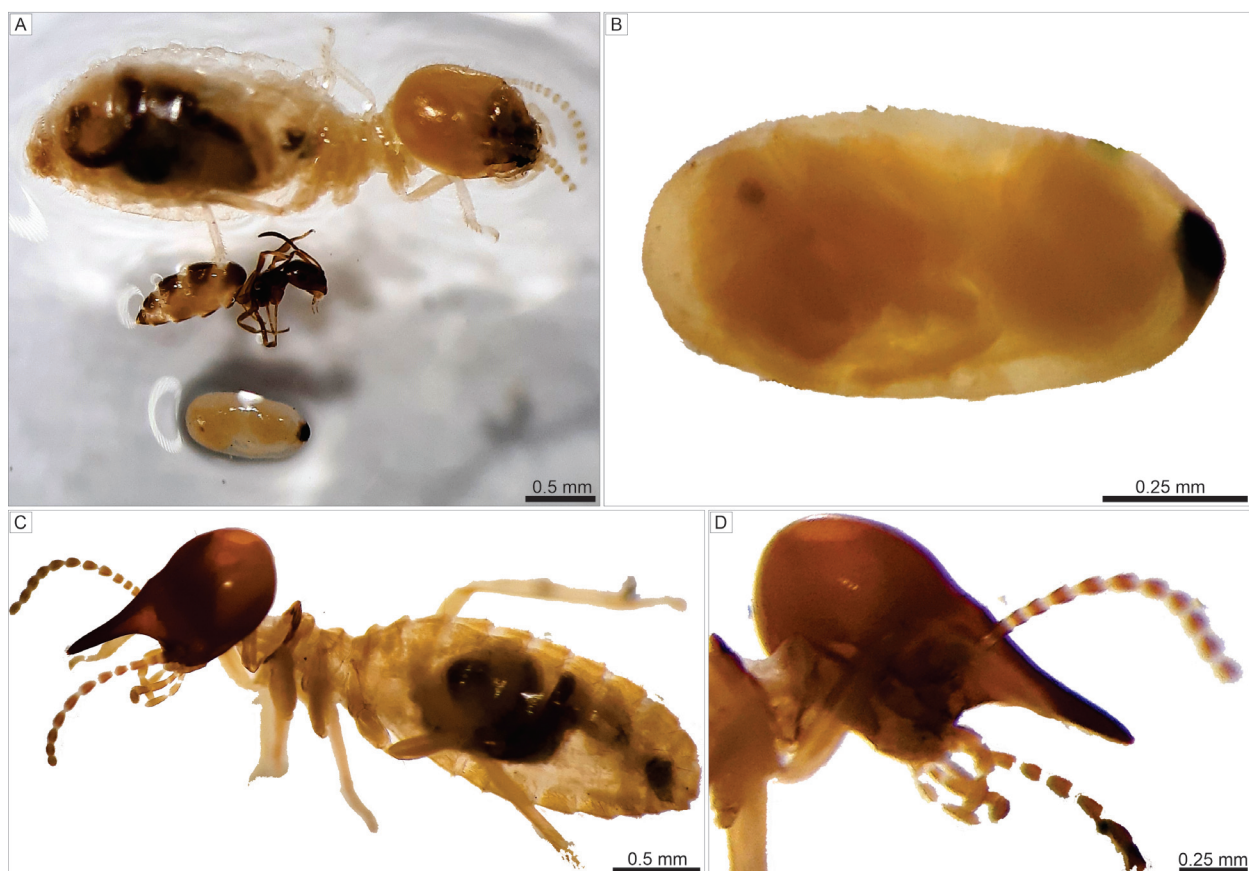


FIGURE 10. Termites collected in site A, identified as Termitidae. Other investigated sites are also represented by termitids. A. General view of an egg (below), a minor worker and a bigger worker (above). B. Detail of an egg with visible termite inside. C. General view of a Termitidae soldier. D. Detail of a soldier with rounded cephalic capsule bearing a conical frontal tube (nasus), with fine extremity.

mostly root systems or organic-rich soils, and a fair amount of humidity for fungi cultivation (Ferreira et al., 2011). However, in eolian substrates, humidity is low, and root systems are superficial and have a low preservation potential. Then, with rare exceptions, the presence of termite nests in ancient eolian deposits is not considered.

Fossil termite nests were reported in the Late Pleistocene deposits of the PCRS by Gibert et al. (2006) and Netto et al. (2012), represented by the ichnogenera *Krausichnus* (later discussed by Genise et al., 2013, as potential ant structures), *?Vondrichnus*, and *Termitichnus*. These trace fossils occur together with other ichnotaxa representing insect nests or breeding chambers (e.g., ichnogenera *Celliforma*, *Coprinisphaera*, *Tesseirei*) in eolian sandy deposits formed in backshore settings. Rhizobioturbation is discrete in the stratigraphic levels containing insect trace fossils. However, root casts are abundant in upper levels (Netto et al., 2012, figure 17A-B). The morphology

of the epigeal portion of the extant nests found in the backshore deposits of the PCRS and the downward funnel-shaped condensed passages resemble *Termitichnus*. Additionally, they are similar in size and share the same sub-spherical to ovoid chamber pattern connected in the bottom by primary and secondary burrows (e.g., Genise, 2017) (Figure 9). Nests with architecture similar to the ichnogenus *Vondrichnus* were not found in the modern deposits of the PCRS.

Although modern architecture and building strategies of termite nests are known, few studies focused on comparison with analogous trace fossils (e.g., Genise, 2017). Modern nests are investigated mostly in search of similarities between structures and taxonomic groups to infer whether morphology reflects the taxa. For example, *Amitermes meridionalis* and *A. laurensis* from Australia have mounds oriented to the solar light to keep the structures warm (Jacklyn, 1992). However, the potential of fossilization of the epigeal portion is

low. If preserved, this ichnoassemblage would be represented by the prevalence of termite nests (ant nests are usually shallow in this environment, reworking less than 20 cm).

Ichnoassemblages dominated by termite structures were referred to represent the *Termitichnus* ichnofacies and are assumed as restricted to paleosols of forest environments (e.g., Genise and Bown, 1994; Genise et al., 2000). However, considering that termite nests can occur in several sub-environments (for example, as part of *Coprini-sphaera* ichnofacies), the occurrence exclusively of termite structures is not an unequivocal indication of the *Termitichnus* ichnofacies (Genise, 2017). Thus, more neoichnological studies involving termite nests are crucial to improve their value for paleoenvironmental reconstructions and stratigraphic applications, and also to refine the significance of the *Termitichnus* ichnofacies.

CONCLUSION

This study reports termite nests associated with foredunes in shoreline settings along the PCRS (southern Brazil). The presence of nests with similar architecture and located in a similar environment along ~600 km corroborates that termites can colonize poorly vegetated sandy substrates close to high-tide level. Besides the

biological significance, the reported *Termitichnus*-like nests in modern backshore dunes close to the shoreline opens a discussion related to the *Termitichnus* ichnofacies, for now defined by the dominance of termite trace fossils in well-vegetated continental settings.

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