


Research Article

Insect trace fossils as indicators of climatic conditions during the uppermost Pleistocene deposits in southern Brazilian Atlantic coast

Kimberly Silva Ramos^a , Renata Guimarães Netto^a, Daniel Sedorko^{a,b} and Diego Luciano Nascimento^a

^aICHNOS Research Group, Geology Graduate Program, Unisinos University, Av. Unisinos, 950, 93022-750 São Leopoldo, RS, Brazil. and ^bMuseu Nacional, Departamento de Geologia e Paleontologia, Federal University of Rio de Janeiro. Horto Botânico, Parque Quinta da Boa Vista, R. Gen. Herculano Gomes, 1340, São Cristóvão 20940-040, Rio de Janeiro, RJ, Brazil.

Abstract

The Rio Grande do Sul Coastal Plain records sea-level oscillations driven by climatic changes during Quaternary glaciations, represented as four lagoon-barrier systems, the last one forming after the last glacial maximum and still active. Marine trace fossils are reported in the Pleistocene deposits, but terrestrial burrows also occur in the eolian deposits. The insect trace fossil assemblages from the uppermost Pleistocene deposits of the lagoon-barrier system III are used as relative proxies to infer the climate regimes that controlled sedimentation prior to the last glacial maximum. Two suites occur in the eolian deposits: the *Vondrichnus* suite, dominated by structures produced by termites, in the basal eolian beds; and the *Celliforma* suite, dominated by hymenopteran (bees and wasps) structures, in the upper eolian beds. The dominance of termite nests indicates humid conditions. The shift upward to the *Celliforma* suite signals a change in the humidity regime and the prevalence of drier conditions. The stratigraphic position of the ichnoassemblage, above the uppermost Pleistocene marine transgressive beds that formed during the last interglacial and below the record of the last glacial maximum in this coastal plain, suggests that the last glacial interval controlled this humid-dry fluctuation.

Keywords: Trace fossils, Paleoclimate bioindicators, *Termitichnus*, Quaternary icehouse, Coastal dynamics

(Received 6 October 2021; accepted 6 September 2022)

INTRODUCTION

The Rio Grande do Sul Coastal Plain is the geological province that best preserves evidence of climate changes along the Atlantic coast in southernmost Brazil during Quaternary glacial-interglacial cycles. Glacioeustatic sea-level cycles controlled deposition in coastal environments, forming four lagoon-barrier systems (LBS) in southern Brazil (Tomazelli, 1985; Villwock et al., 1986). These LBSs are high-frequency depositional sequences controlled by Quaternary glacioeustatic oscillations (Rosa et al., 2017) that were chronologically correlated to the calibrated $\delta^{18}\text{O}$ curves of Imbrie et al. (1984). Numerical ages obtained by thermoluminescence and optically stimulated luminescence in these deposits allowed chronocorrelation of LBS II to Pleistocene interglacial marine isotope stage (MIS) 7, LBS III to MIS 5, and LBS IV to Holocene interglacial MIS 1 (Buchmann et al., 1998; Buchmann and Tomazelli, 2003; Lopes et al., 2014, 2020). The abundant fossil record of mammals from the Lujanian South American land-mammal age in LBS III (ca. 33 ka; Lopes et al., 2021) also constrains the timing of deposition to the late Pleistocene. The last glacial maximum (LGM) (e.g., Clark et al., 2009) peaked at ca. 20 ka, leading to a sea-level

fall of ~120 m and temperatures between 9 and 6°C colder than today (e.g., Fairbanks, 1989; Peltier and Fairbanks, 2006; Hansen et al., 2013). Although no putative record of this sea-level fall has been claimed yet for Rio Grande do Sul coastal plain, the best record resides in the loess deposits of the Cordão Formation (29–11.7 ka; Lopes et al., 2016). The Cordão Formation overlies LBS II (Lopes et al., 2021) at the southern of PCRS and probably LBS III, considering its age (ca. 120 ka to ca. 33 ka; Rosa et al., 2017; Lopes et al., 2021), its adjacent lateral distribution to the east of LBS II (Fig. 1B), and the ages of the Cordão Formation, deposited during the MIS 2.

Pleistocene deposits of the Rio Grande do Sul Coastal Plain have been extensively studied from sedimentological, stratigraphical, and paleontological approaches (e.g., Tomazelli and Villwock, 2000; Lopes et al., 2014, 2016, 2020, 2021; Rosa et al., 2017). In terms of ichnology, several studies highlighted the presence of trace fossils produced by marine and non-marine organisms on the deposits of LBSs II and III (Berqvist and Maciel, 1994; Gibert et al., 2006; Netto et al., 2007, 2017; Lopes and Pereira, 2019; Freitas et al., 2020; Lopes et al., 2021; Ramos et al., 2021). Trace fossils are chiefly abundant on the LBS III deposits exposed in sand quarries in the Osório region (northern littoral of the Rio Grande do Sul State, Fig. 1). The most outstanding burrows in the marine deposits of LBS III correspond to the ichnogenus *Ophiomorpha* (Gibert et al., 2006; Netto et al., 2017; Freitas et al., 2020), a callianassid crustacean burrow commonly referred to as “*Callichirus* sp.” (e.g., Tomazelli, 1985; Tomazelli

Corresponding author email address: <kimmysramos@gmail.com>.

Cite this article: Ramos KS, Netto RG, Sedorko D, Nascimento DL (2023). Insect trace fossils as indicators of climatic conditions during the uppermost Pleistocene deposits in southern Brazilian Atlantic coast. *Quaternary Research* 113, 134–145. <https://doi.org/10.1017/qua.2022.55>

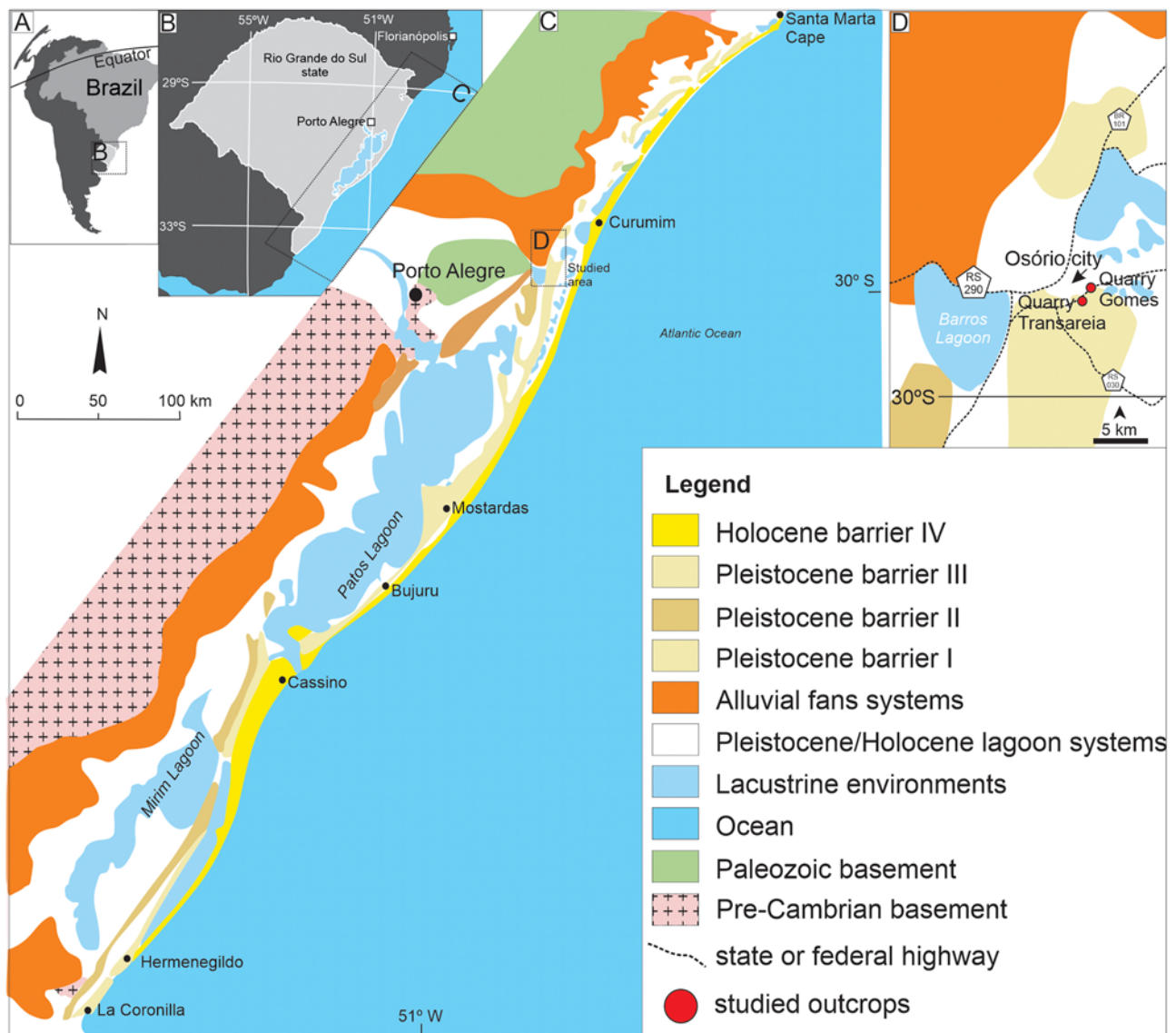


Figure 1. Location map of studied area. (A) Position of studied area in South America. (B) Position of studied outcrops in Rio Grande do Sul Coastal Plain. (C) Distribution of geologic units in the area of the studied outcrops. (D) Detail of studied outcrops close to Osório city. Modified from Lopes et al. (2014) and Ramos et al. (2021).

and Villwock, 2000). *Cylindrichnus helix*, *Diplocraterion parallelum*, *Macaronichnus* sp., and *Rosselia socialis* also occur (Gibert et al., 2006; Netto et al., 2017; Lopes et al., 2021).

Gibert et al. (2006) also reported an insect-dominated trace fossil assemblage in the overlying eolian facies composed mostly of the ichnogenera *Krausichnus*, *?Vondrichnus*, cf. *Celliforma*, and root traces. Preliminary studies led by Netto et al. (2007) on this assemblage recognized nests attributed to ants, termites, beetles, solitary wasps, and cicadas. Among the abovementioned insects, termites are the unique group that depends on cellulose and humidity in the substrate to construct the nest. Due to this dependence, termite nests are usually interpreted as an indicator of perennially vegetated paleosols, such as those of grasslands and dense forests (Genise et al., 2000). This led Netto et al. (2007) to preliminarily infer more mature soil colonization in back-barrier alluvial settings developed over the eolian dunes, which would imply an abrupt sea-level fall and might represent a forced regression linked to the sea-level fall of the last glacial epoch. However,

Ramos et al. (2021) demonstrated that termite nests occur in the present-day eolian frontal dunes (LBS IV, Holocene to present) in different latitudes throughout the Rio Grande do Sul Coastal Plain. Thus, termite nests might be present in immature soils formed in the coastal eolian deposits of LBS III, not necessarily representing a signature of continental settings.

Insect burrows usually exhibit specific morphologies due to the high speciation capacity of the group, which facilitates identification of the edaphic paleofauna preserved in the geological record, especially after the Cretaceous (Genise, 1995). Climate and environmental conditions play an important role in the biogeographic distribution of many insect groups, particularly termites, bees, and wasps, making their nests good indicators of paleoenvironmental and paleoclimatic conditions (e.g., Genise et al., 2000; Genise, 2017; Sánchez et al., 2021). Considering the remarkable presence of insect trace fossils and rhizoliths in the eolian deposits of LBS III in the Osório region, this study aims to (1) characterize these trace fossil suites, (2) use them as relative proxies to infer the

climate regimes that controlled LBS III sedimentation, and (3) better understand the climate changes that controlled the study area coastal dynamics that culminated in the LGM.

GEOLOGICAL SETTING

The Rio Grande do Sul Coastal Plain extends for ~620 km and covers an area of ~33,000 km² (Fig. 1A, B). It consists of two types of depositional siliciclastic systems—alluvial fan systems and lagoon-barrier systems (Tomazelli and Villwock, 2000). The lagoon-barrier systems characterize ancient coastlines and represent fourth-order depositional sequences formed by successive glacioeustatic-controlled sea-level oscillations during the Pleistocene and Holocene (Rosa et al., 2017). The oldest sequence characterizes lagoon-barrier system (LBS) I, and the youngest characterizes LBS IV, which comprises the present-day coastline (Tomazelli and Villwock, 2000). Except for the last, all others represent the maximums of the postglacial marine transgressions that occurred during the Pleistocene (Villwock and Tomazelli, 1995; Rosa et al., 2011, 2017).

LBS I was established ca. 400 ka and configured the oldest coastal deposits in the Rio Grande do Sul Coastal Plain. Three main transgressive-regressive events that took place on the South Atlantic coast formed LBS II–IV. The timing of LBS III was correlated to Marine Isotope Stage (MIS) 5 of Imbrie et al. (1984) and dated as 120 ka (Villwock and Tomazelli, 1995; Rosa et al., 2011). Thus, this system has been linked to the last transgressive peak of the Pleistocene (Canaanía Transgression; Suguio and Martin, 1978). LBS IV developed during the Holocene, ca. 7 ka due to the last great post-glacial transgression when sea level rose 4–5 m above the current level (Dillenburg et al., 2000; Angulo et al., 2006; Rosa et al., 2011; Santos et al., 2022). Regarding modern climatic patterns in the Rio Grande do

Sul Coastal Plain, temperatures vary during the year from a minimum average of 7.2°C in July (Southern Hemisphere winter) to a maximum average of 31.7°C in January (Southern Hemisphere summer). Rain is well distributed, varying between 74 mm in the driest month and 164 mm in the rainiest month (see Ramos et al., 2021). Wind speeds are constant throughout the year in the entire coastal plain, with average annual winds between 7.0 and 8.0 m/s at 50 m height (Amarante and Silva, 2002). Tide is semi-diurnal and has a mean range of 0.5 m (Dillenburg et al., 2009). Meteorological tides derived by storms can reach up to 1.9 m for short periods (Parise et al., 2009).

Deposits of LBS III can be subdivided into a shallow marine and an eolian facies association (e.g., Tomazelli et al., 2000; Gibert et al., 2006; Tomazelli and Dillenburg, 2007). The shallow marine deposits characterize the lower strata in the studied quarries. They are composed of fine- to medium-grained quartz sand with low-angle cross-lamination, wave-ripple cross-lamination, and planar cross-stratification (interval 0–3 m at Transareia Quarry and interval 0–5.5 m at Gomes Quarry; Fig. 2A, B). *Arenicolites* isp., *Cylindrichnus helix*, *Diplocraterion* isp., *Macaronichnus segregatis*, *Ophiomorpha nodosa*, *Ophiomorpha puerilis*, and *Rosselia socialis* occur in these lower beds, suggesting deposition in shoreface settings (Gibert et al., 2006; Netto et al., 2017). The eolian facies association comprises ~5 m of well-sorted fine-grained quartz sand with parallel lamination interbedded with planar cross-stratification intercalated with several muddy sand horizons each of which is a few centimeters thick. Two strongly weathered horizons consisting of reddish fine- to medium-grained beds characterize ortsteins and occur in the eolian deposits (Fig. 2A, B), from which rhizoliths and predominantly insect nest burrows descend. This eolian ichnoassemblage is the focus of this work and will be discussed here in detail. Due to the proximity among the prospected quarries (Fig. 1), we assume that these

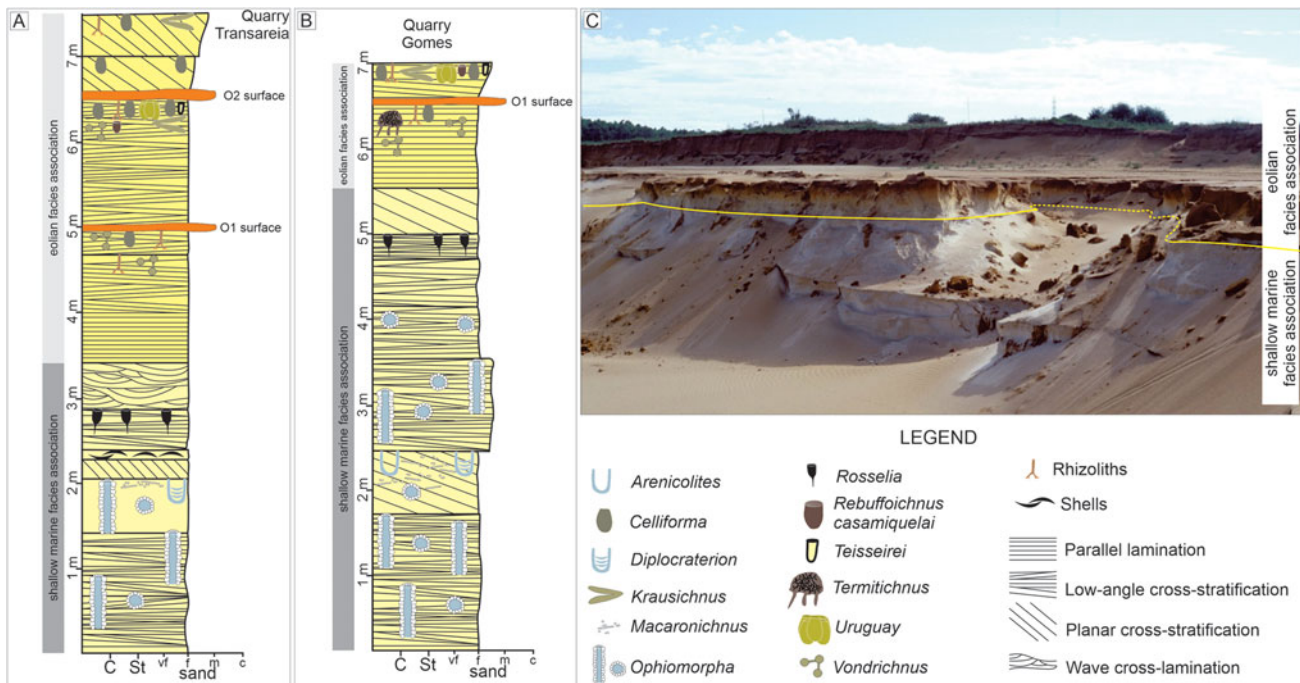


Figure 2. Geologic sections and trace fossils of studied outcrops. (A, B) Geologic sections of Transareia (A) and Gomes (B) quarries. (C) General view of Gomes Quarry with eolian facies overlying marine facies (contact between facies indicated by the yellow line; dashed yellow line indicates sand-covered contact between facies). O1 and O2 surfaces correspond to the pedogenic horizons found in the eolian deposits. Adapted from Gibert et al. (2006).

pedogenic horizons are correlative and used them to understand the vertical stacking of trace fossils.

MATERIAL AND METHODS

The study locale is located in the municipality of Osório (the Rio Grande do Sul State, southernmost Brazil), ~100 km east of Porto Alegre, on two adjacent outcrops in sand quarries, Gomes (29°90'51"S, 50°23'97"W) and Transareia (29°90'06"S, 50°23'06"W) (Figs. 1, 2A, B). The sedimentological analysis considered texture, composition, bed geometry, and primary sedimentary structures and follows Gibert et al. (2006). The morphology of paleosol profiles was described in the field following the nomenclature and procedures from Schoeneberger et al. (2001) and Retallack (2001). The following morphological attributes were described: soil horizon (types and boundaries), soil structure, soil color, bioturbation features (types, patterns, and abundance), and density of trace fossils.

Insect trace fossils are good indicators of climate conditions and are useful for local microclimate determination (e.g., Ekdale et al., 2007; Buatois and Mángano, 2011; Genise, 2017). The body temperature of insects fluctuates with the temperature of their surrounding environment. Thus, insect nesting activity is controlled by regional climate and local microclimate (e.g., Grassé, 1986; Genise et al., 2000, 2004; Düringer et al., 2007). The trace fossil analysis considered structures preserved in the eolian facies of LBS III only and followed the ichnotaxobases approach (Bromley, 1996; Bertling et al., 2006). The ichnotaxonomical identification followed Genise (2017). However, many structures were loose on the substrate due to the present-day wind action that erodes the unlithified deposits of the LBS III. Thus, the original orientation of many burrows with respect to the original soil surface could not be determined.

All the studied trace fossils occur exclusively in the Upper Pleistocene eolian deposits of LBS III that are exposed in the Transareia and Gomes quarries. The 178 collected specimens are housed in the paleontological collection of the Museu da História Natural do Rio Grande do Sul (MHGEO) at Unisinos University, under the numbers ULVG-13129 to ULVG-13349.

RESULTS

The ichnotaxonomy of the trace fossils present in the LBS III eolian deposits is characterized in the Supplemental Material. The ichnoassemblage shows a moderate to high ichnodiversity and a high abundance of burrows. Two trace fossil suites, *Vondrichnus* and *Celliforma*, were identified in the eolian facies.

The *Vondrichnus* suite is characterized by the dominance of spherical to ovoid structures, locally with interconnections and generally presenting walls with reddish color compared to the host rock, which are attributed to *Vondrichnus obovatus* (Fig. 3A–C). Dense galleries with primary and secondary order, identified as *Termitichnus* sp. (Fig. 3D), also occur in this suite. These structures are interbedded to locally dense intervals with rhizoliths. Isolated cells attributed to *Celliforma* sp. (Fig. 3E) and simple tunnels (Fig. 3F) that may be part of the *V. obovatus* connections occur subordinately. This suite is characterized by moderate burrow density and, although ichnodiversity is low, the tiering structure is complete, revealing the varied depth of colonization by different groups of insects. The burrows in this suite descend from the pedogenic horizon O1 (Fig. 2). Abundant rhizocretions and root molds occur mainly in Bhm horizons,

with circular to subcircular forms varying from 0.5 to 2 cm in diameter. They are cemented by iron and show an average length of 20 cm, with dichotomous and herringbone patterns.

The *Celliforma* suite is dominated by several morphologies of isolated cells, identified as *Celliforma* sp. (Fig. 4A), *C. curvata* (Fig. 4B, C), *C. rosellii* (Fig. 4D, E), and *C. spirifer* (Fig. 4F–H), and large, condensed burrows attributed to *Krausichnus* sp. (Fig. 5A, B). Rows of cells identified as *Uruguay* sp. (Fig. 4I–K), chambers attributed to *Rebuffoichnus casamiquelai* (Fig. 4L, M) and *Teisseirei* sp. (Fig. 4N), and less-common spherical to ovoid structures attributed to *V. obovatus* occur as secondary structures. Trace fossils occur in moderate to high density, forming pavements of *Celliforma* and simple tunnels. This suite is more diverse than the *Vondrichnus* suite and has a complete tiering structure, revealing the varied depth of colonization by different insect groups. These insect burrow-rich intervals are interbedded with locally dense intervals with rhizoliths (Fig. 5) below the pedogenic horizon O2 (Fig. 5C) from where the trace fossils descend.

DISCUSSION

Trace fossil suites

The trace fossil suites represent insect activity, which implies sub-aerial exposure and substrate quiescence that allowed colonization by this biologic group (Genise, 2017). These insect populations colonized unlithified, fine-grained sandy soils formed in stabilized coastal eolian dunes. The lower eolian deposits in LBS III (below OS1) were colonized chiefly by termites, while bee and wasp nests dominate in the upper eolian deposits (above OS1 and below OS2).

Insect trace fossils are ecologically controlled, with climate, soil, and vegetation playing a more relevant role in substrate colonization than depositional processes (Genise et al., 2000). Climate also influences the biogeographical distribution of ectotherm organisms, such as insects. Termites and hymenopteran insects (bees and wasps) have been used in the ichnological literature as key indicators of substrate moisture, the former suggesting more humid conditions and the latter drier conditions (e.g., Genise et al., 2000, 2004, 2010; Genise, 2017; Sánchez et al., 2021). The dominance of termite structures has been interpreted as colonization in more humid conditions than those that characterize the *Celliforma*-dominated suites (Genise et al., 2000; Düringer et al., 2007). Thus, the shift of these two trace fossil suites in paleosols might be a good indicator of climatic dynamics.

It has been postulated that trace fossil suites dominated by termites indicate forested, often humid substrates and warm climates in the scope of the *Termitichnus* ichnofacies (e.g., Grassé, 1986; Genise et al., 2000, 2004, 2010; Buatois and Mángano, 2011). However, termite nests are also abundant in settings other than forests in tropical latitudes, including wet and arid lowlands such as the Pantanal wetlands (central-west Brazil), the border of the Namib Desert (Namibia), and the sub-tropical Pampa grasslands in the Rio Grande do Sul State. Although not common, they occur in the restinga-vegetated frontal dunes in the active backshore zone of LBS IV where water sources are available (Ramos et al., 2021). Termites depend on humidity and vegetation to survive; thus, nesting in arid settings requires ecological adaptations such as the excavation of horizontal foraging tunnel systems close to the soil surface to collect plant fragments and vertical tunnels connecting the nest to moist soil at great depths, in addition to nocturnality (Tschinkel, 2010). However, the

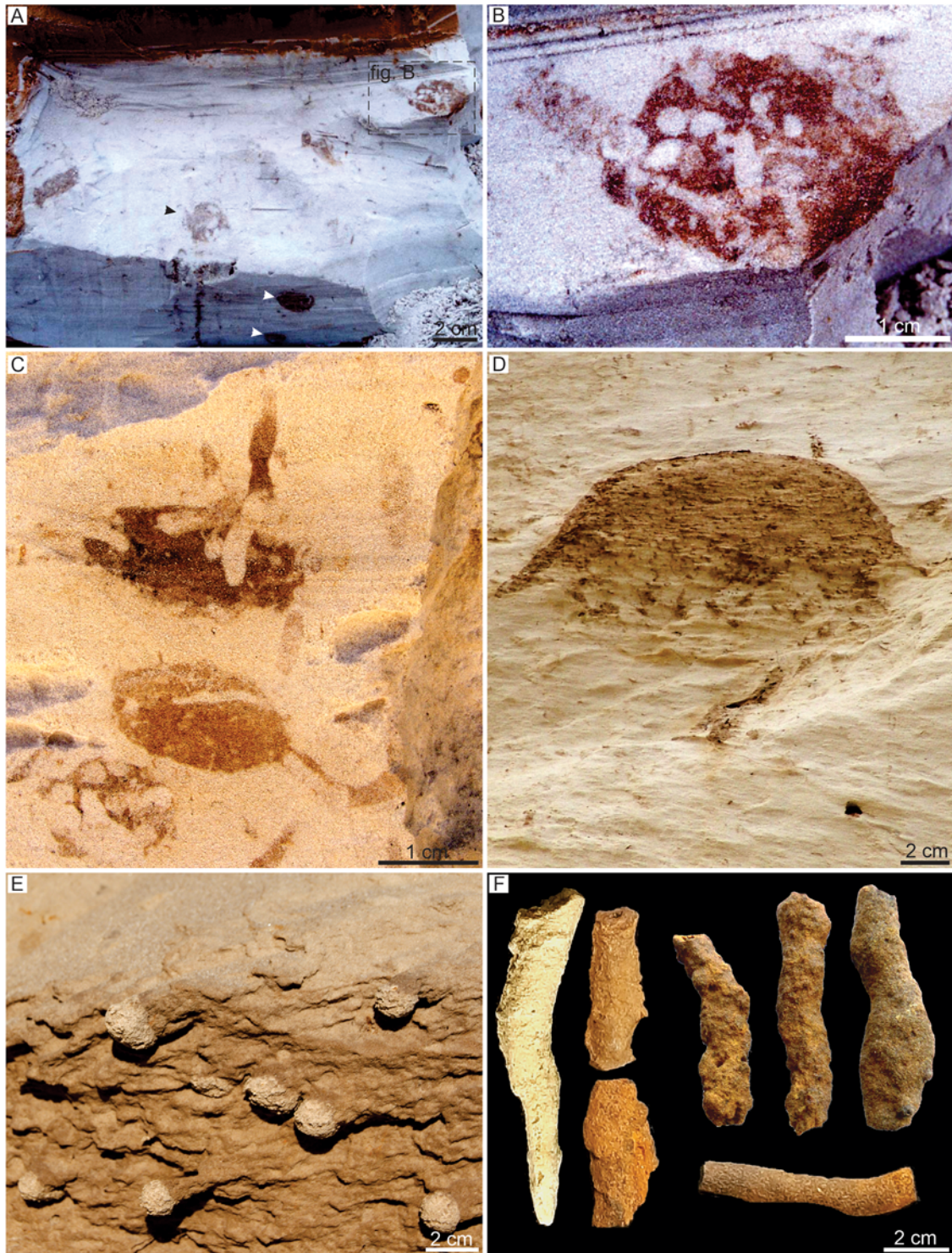


Figure 3. In situ trace fossils from studied sections. (A–C) Krausichnidae: *Vondrichnus obovatus*; note the wall lined by oxides with sharp contact with surrounding substrate, the disposition in different planes (black and white arrows in A), and the alveolar filling of the structure (B, C) (D) *Termitichnus* isp. with a wall lined by oxides with sharp contact with surrounding substrate. (E) Celliformidae: *Celliforma* isp. showing the isolated cells. (F) Simple tunnels with walls lined by oxides.

architecture of these nests differs completely from those found in the eolian beds of LBS III.

While termite nests shelter a colony that cares for their larvae, most ground-nesting bees and wasps do not care for their offspring after sealing the provision-rich brood cells (Antoine and

Forrest, 2021). Thus, the females must find a high-quality substrate for nest construction to guarantee larval survival. Protection against harsh weather conditions and excessive humidity is imperative for larvae development (Roulston and Goodell, 2011). Unlike termites, adult bees can thermoregulate, allowing

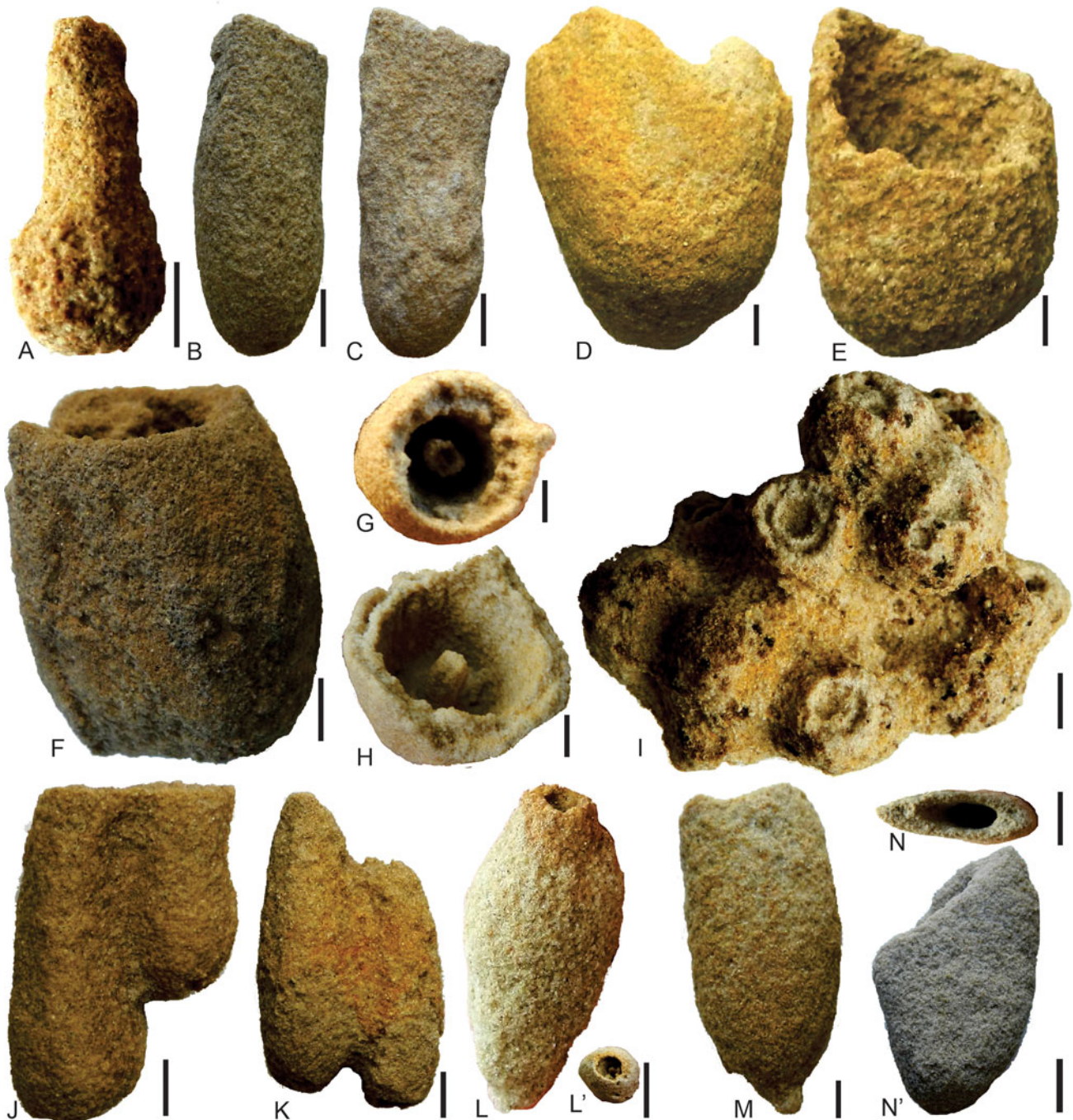


Figure 4. Morphological variation of Celliformidae and Coprinisphaeridae specimens. (A–K) Celliformidae: (A) *Celliforma* isp. with a rounded base and a flat top with a constriction near the top. (B, C) Elongated specimens with curved necks, attributed to *C. curvata*. (D, E) *Celliforma rosellii* with rounded bottom end and rough microstructure walls. (F–H) *Celliforma spirifer* cells with a central stem resembling an eroded spiral closure. (I–K) Clustered cells attributed to *Uruguay* isp. (L–N') Coprinisphaeridae: (L–M) Morphological aspects of *Rebuffoichnus casamiquelai*, characterized by oblate chambers with rough external wall, that may preserve a terminal circular aperture (L, L'). (N, N') Morphological aspects of *Teisseirei*. Scale bars = 5 mm.

some ground-nesting species (e.g., *Bombus polaris*) to adapt to low temperatures.

Ants are adapted to various habitat types and can rapidly excavate a new nest to move their colonies according to soil moisture changes (e.g., Lamb et al., 2020). Ant mounds were found in Holocene outlet glaciers in southern Norway (Hill et al., 2018), proving they can survive in cold climates and adverse soil conditions. Ground-nesting beetles are also widely distributed

throughout the globe (Genise, 2017) and are mainly controlled by temperature (Ernst and Buddle, 2015). Although their richness decreases towards high latitudes, they occur in high arctic locations (Ernst and Buddle, 2015). Thus, ant and beetle structures are not good indicators of climate-related changes in soil abiotic conditions.

The predominance of termite nests in the *Vondrichnus* suite, together with the restricted presence of bee cells (e.g.,



Figure 5. In situ trace fossils from studied sections. (A, B) Krausichnidae: *Krausichnus* isp. exhibiting ovoid (A) and conical (B) morphologies. (C) Rhizoliths lined by oxides. (D) General view of O1 surface with rhizoliths.

Celliforma) and the absence of ant structures, suggests the prevalence of more humid and warmer conditions during colonization of the paleosols capped by OS1. In contrast, the abundance of hymenopteran (mostly bee structures, mainly represented by *C. curvata*) in the *Celliforma* suite indicates drier climate conditions during colonization of the podzols below OS2 (e.g., Genise et al., 2000; Düringer et al., 2007).

The local abundance of rhizoliths in these paleosols suggests periods of relatively high water tables (Hesp, 1991; Bonilha

et al., 2012; Marques et al., 2015). The root decay provides organic matter for soil development and is an important food source for soil macrofauna. The thick, cemented horizon observed on the O2 surface represents a longer time hiatus for weathering (compared to the thin horizon observed on the O1 surface), allowing establishment of a *Celliforma* suite with a higher ichnodiversity than the *Vondrichnus* suite.

The subordinate presence of termite and ant nests in the *Celliforma* suite and the absence of calcareous soils preclude a

precise attribution of this suite to the *Celliforma* ichnofacies (e.g., Buatois and Mángano, 2011; Genise, 2017). The *Vondrichnus* suite might be an expression of *Coprinisphaera* ichnofacies (e.g., Genise et al., 2000), but the restricted occurrence of coprinisphaerid structures also precludes this attribution.

Paleoclimatic and stratigraphic implications

Netto et al. (2007) preliminarily inferred that the insect trace fossil assemblage preserved in LBS III aeolian strata represents soil colonization in alluvial plains formed by global sea-level lowering of ~120 m during the last glacial period. This inference considered the abundance of termite nests, chiefly *Vondrichnus*, in these beds and the environmental distribution of the insect-dominated ichnofaunas, as expressed by Genise et al. (2000). However, *Termitichnus*-like termite nests occur in eolian dunes that formed very close to the marine shoreline in LBS IV (the present-day active beach; Fig. 1), indicating that termites can colonize incipient soils in backshore settings (Ramos et al., 2021). Although not abundant, several closely spaced nests may occur in sparsely vegetated areas with nearby water sources. Thus, termite nests are not exclusive of continental settings and can be found in frontal eolian dunes in the Rio Grande do Sul Coastal Plain.

Nonetheless, the abundance and diversity of termite nests were higher in the LBS III eolian deposits than in those of LBS IV, suggesting a warmer and humid climate than during colder and drier intervals of the last glacial epoch, and more hospitable ecological conditions during soil colonization than today. Palynological and isotopic data indicate that climate conditions during this interglacial interval were wetter than today in southern Brazil (e.g., Clapperton, 1993; Ledru et al., 1996; Behling, 2002; Leite et al., 2016). Thus, the *Vondrichnus* suite may be a good indicator of soil colonization by termites during periods of humid conditions.

On the other hand, the *Celliforma* suite indicates the dominance of drier conditions than represented by the *Vondrichnus*

suite. Flooding events or rainfall periods are not suitable for emplacement of bees and dung beetles in the substrates because excessive moisture can generate poor oxygen diffusion, resulting in death; flooding events or rainfall periods also increase liquefaction of the substrate and/or decay by fungal attack (Genise, 2017). Thus, these tracemakers generally prefer well-drained substrates for colonization; in fact, the diversity and abundance of bees are better registered in warm-temperate xeric regions worldwide (Stephen et al., 1969; Michener, 2007). Additionally, bee cells are lined with water-repellent lipids to maintain the moisture conditions, allowing short-term survival from occasional floods (Michener, 2007). However, the termite structure *Vondrichnus* is a subordinate trace in the *Celliforma* suite, occurring below the O2 surface (Fig. 5C), suggesting seasonal climate oscillation during the colonization window.

Deposits of LBS III were formed during the global transgressive event that reached a maximum ca. 120 ka and represent active coastal sedimentation during the interglacial epoch that preceded the last glacial maximum (LGM) (e.g., Tomazelli and Villwock, 2000; Rosa et al., 2011). The climate during the late Pleistocene was marked by a glacial cycle; almost 30% of the globe was covered by ice, forming ice sheets that could extend up to 40°N latitude (e.g., Ehlers and Gibbard, 2008). Due to the smaller extent of continental masses compared to the Northern Hemisphere, the record of ice sheets in South America is restricted to the Andes and the southernmost areas of Patagonia (e.g., Hulton et al., 2002; Ehlers and Gibbard, 2008).

The drier conditions that preceded the LGM allowed development of extensive eolian dune fields in the Pampa and Chaco regions (mid-latitudinal South America), spreading out to the southeast of the Rio Grande do Sul, forming vast loess deposits (Clapperton, 1993). These deposits characterize the Cordão Formation, which overlies LBS II deposits in the southern portion of the Rio Grande do Sul Coastal Plain and correlates with Marine Isotope Stage (MIS) 2 (Lopes et al., 2021). Although the Cordão

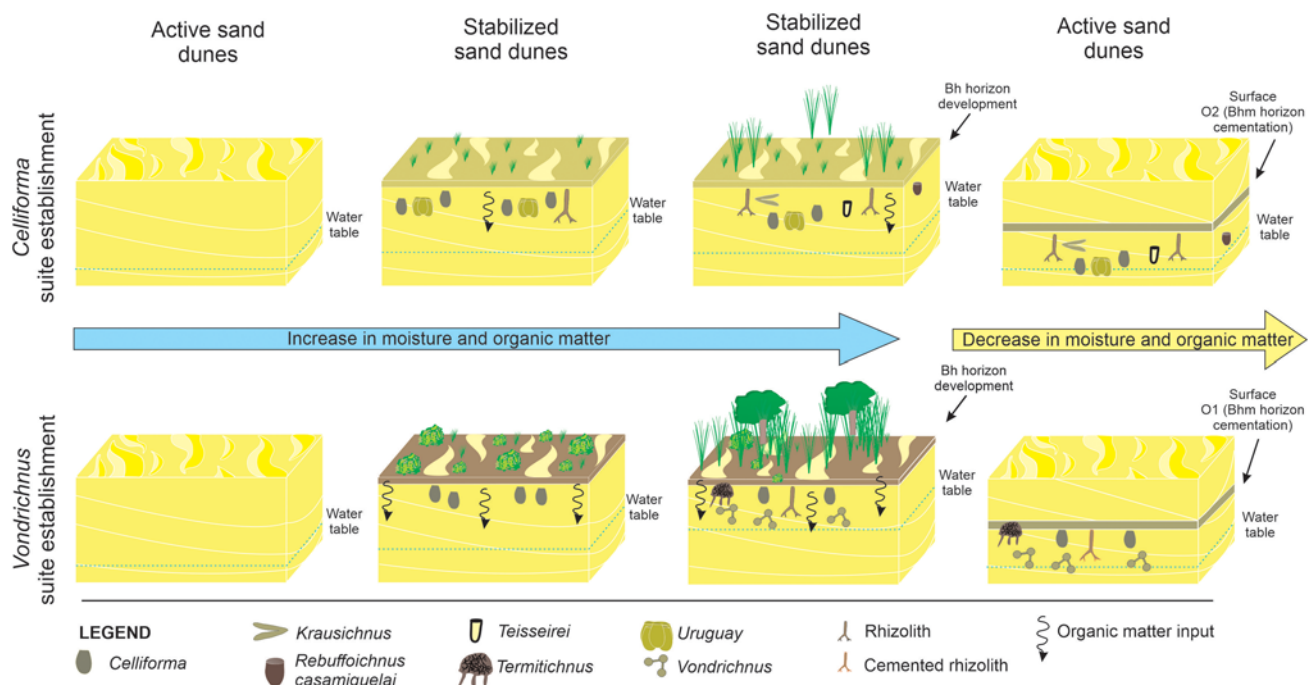


Figure 6. Inferred colonization sequence of trace fossils in LBS III deposits. Note that the sequence of climatic variation was similar in both suites (i.e., increase in moisture and organic matter followed by subsequent decreases of both), but the *Celliforma* suite indicates drier conditions than the *Vondrichnus* suite.

Formation does not occur in the study area, its age and position in the Rio Grande do Sul Coastal Plain stratigraphic framework indicate that they also overlay LBS III deposits (Fig. 1), being removed by weathering or erosion. Thus, the orsteins formed in the eolian deposits of LBS III might represent phreatic oscillation due to a shift in humid-dry climate conditions during the last Pleistocene interglacial stage, with a prevalence of drier conditions towards the LGM.

Diets inferred from $\delta^{13}\text{C}$ in fossil teeth from extinct mammalian herbivores in chrono-correlated deposits (late Pleistocene) indicate that they fed on a mixture of C3 (herbs, shrubs, and/or trees) and C4 (grasses) plants, which suggests open grasslands with sparse trees and shrubs, very similar to the modern local subenvironments (e.g., Oliveira, 1999; Lopes et al., 2013). Based

on late Quaternary palynological data, Behling (2002) concluded that the areas occupied by the Atlantic rainforest were significantly reduced in southernmost Brazil during the glacial periods and replaced by cold-adapted forest taxa or grassland. Grasslands dominated the landscape during the late Pleistocene in southern Brazil, even in the highlands; climates were markedly drier and temperatures 5–7°C cooler than today (Behling, 2002). According to Tomazelli et al. (2000), the cyclic alternation of humid and arid conditions, and possibly shorter oscillations, controlled sedimentation during the Quaternary in the Rio Grande do Sul Coastal Plain (e.g., Rodrigues et al., 2020; Leal et al., 2022). Calcareous and ferruginous pedogenic concretions occur in the lagoon deposits of LBS I, II, and III, locally in high concentration, forming Ca-rich layers up to 1 m thick. These deposits led

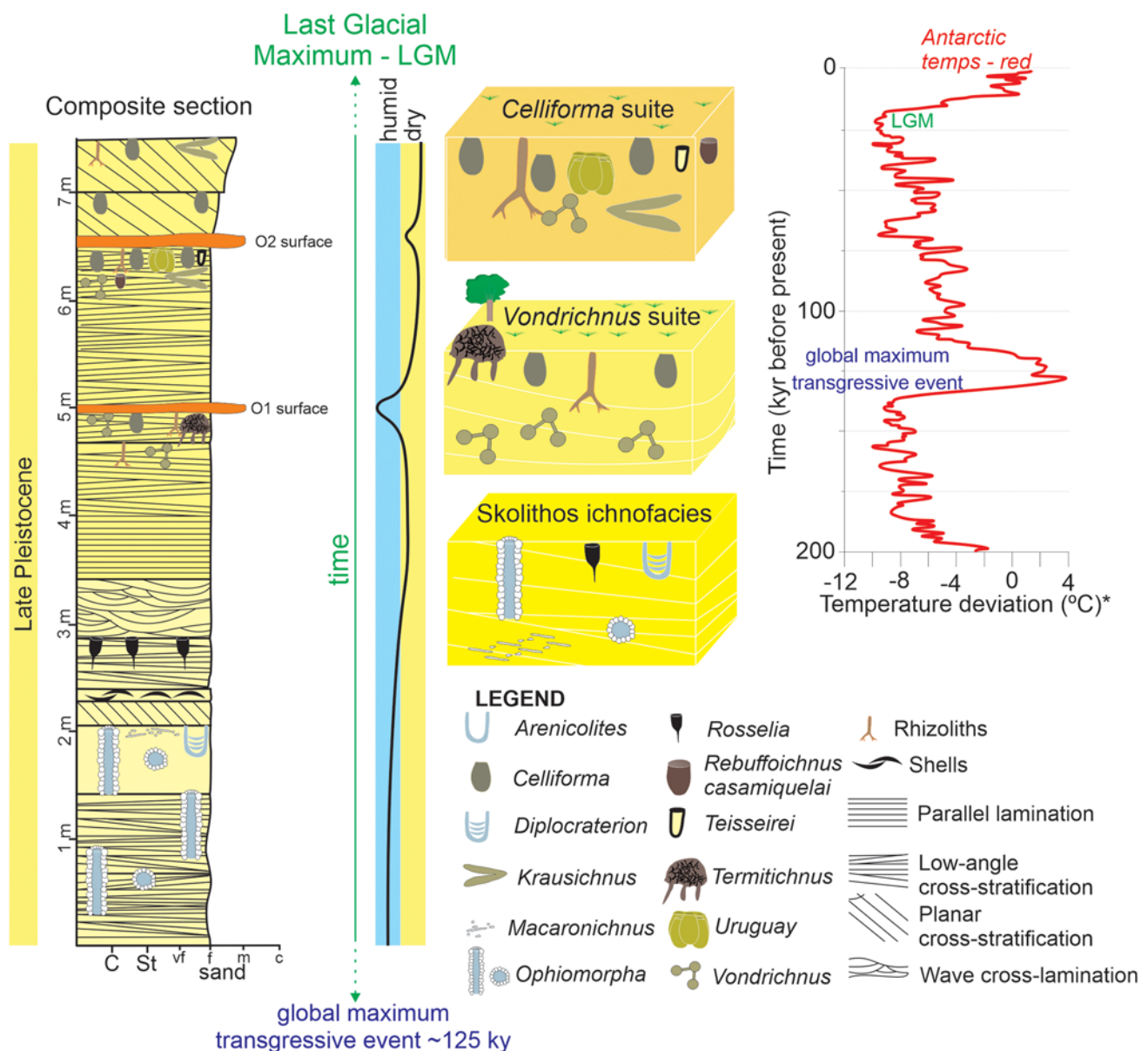


Figure 7. Distribution of trace fossils in a composite section from LBS III deposits. The regressive trend of these deposits evinces a shallow marine setting (Skolithos ichnofacies) overlapped by a *Vondrichnus* suite representing more humid conditions (O1 surface), and finally superimposed by a *Celliforma* suite representing drier conditions (O2 surface). This replacement in trace fossil suite is concomitant with the general reduction in average temperature (red line). *Temperature deviation adapted from Ellis and Palmer (2016).

Tomazelli et al. (2000) to conclude that alternations between wet and dry periods prevailed in the region during the Pleistocene.

Quaternary eolian deposits from the western Mediterranean, for example, also accumulated during lower sea-level periods characterized by colder and arid conditions, whereas pedogenic processes are inferred to be more significant during warm-wet climates linked to interglacial periods (Fornós et al., 2009; Muhs et al., 2010; del Valle et al., 2020). In this sense, the recurrence of horizons colonized by insect trace fossils observed in the studied area, limited by paleosol surfaces and the replacement of a *Vondrichnus* suite by a *Celliforma* suite, signals wet and dry periods, common in the late Pleistocene, but with increasing drier conditions towards the top.

In terms of stratigraphy, the LBSs represent high-frequency (fourth-order) depositional sequences generated by sea-level highstands, controlled by Pleistocene–Holocene glacioeustatic oscillations (e.g., Rosa et al., 2011, 2017), forming a prograding trend. Trace fossils also reflect this trend in the LBS III deposits exposed in the Transareia and Gomes quarries. According to Gibert et al. (2006), trace fossils indicative of shoreface (e.g., *Diplocraterion*, *Cylindrichnus*, *Ophiomorpha*, *Rosselia*) shift upward to monotypic colonization in foreshore (*Macaronichnus*) in the marine facies association. The marine paleoichnocoenosis is abruptly replaced by continental suites in the eolian facies association, and above, the *Vondrichnus* suite gives way upward to the *Celliforma* suite. The establishment of the *Celliforma* suite at the top of these deposits may indicate a regressive phase in the LBS III, linked to drier climate conditions during the late Upper Pleistocene.

Thus, the presence of termite nests overlying marine deposits does not imply a significant sea-level fall for the LBS III eolian deposits because this suite can occur in coastal environments, as reported from the Rio Grande do Sul Coastal Plain in the present day (e.g., Ramos et al., 2021). In terms of colonization pattern, the lower eolian interval was only colonized during more humid conditions, resulting in the dominance of termite structures (*Vondrichnus* suite) and rhizoliths descending from the O1 surface (Figs. 5D, 6). The second eolian interval also indicates dominance of drier conditions during deposition (Fig. 6). However, the O2 surface (Figs. 2, 6) represents less humid conditions than the lower period, expressed by the dominance of the *Celliforma* suite and very rare specimens of *Vondrichnus*. Therefore, the O1 surface associated with the *Vondrichnus* suite can be attributed to a humid period during the late Pleistocene (e.g., Clapperton, 1993). Similarly, humid and warmer conditions were assumed for the Pliocene–Pleistocene strata of the Buenos Aires Province coastal plain (latitudes 38°16'17"–38°00'08"S), based on the occurrence of termite nests (Genise, 1997; Laza, 2006). In this sense, the O1 surface with termite and other insect nests suggests a seasonal climate, with marked rainy and dry seasons (Fig. 7). The O2 surface associated with the *Celliforma* suite is linked to drier conditions in the late Pleistocene, possibly because of the reduction in temperature and precipitation (Fig. 7). Stepped warming starting at ca. 17 ka led to deglaciation, causing an abrupt sea-level rise between 15–14 ka (Hulton et al., 2002).

CONCLUSIONS

The paleoichnocoenosis present in the eolian deposits of LBS III associated with laterally extensive horizons with root traces and forming ortsteins are diagnostic of soil formation in eolian dunes in the Rio Grande do Sul Coastal Plain during the late

Pleistocene. The prevalence of callichnia burrows indicates substrate stabilization by vegetation and immature soil formation, possibly triggered by periods of higher water table in wetter climate conditions. The presence of the *Vondrichnus* and *Celliforma* suites indicates a variation between humid and dry climates throughout LBS III sedimentation. These suites reinforces the hypothesis that a relatively dry climate controlled the coastal dynamics in the Rio Grande do Sul Coastal Plain during the last glacial cycle. The prevalence of the *Celliforma* suite at the top of the eolian deposits indicates the intensification of a drier climate, possibly due to late Pleistocene cooling.

Thus, the *Celliforma* suite indicates drier conditions, while the *Vondrichnus* suite indicates humid conditions for the studied sections. The *Vondrichnus* suite is interpreted to be a common assemblage in coastal settings of the study area, with its distribution controlled by biologic aspects of pioneer colonizers.

Acknowledgments. The authors thank the Brazilian Council for Scientific and Technological Development (CNPq) for the research grant 424237/2018-0 that supported this research. KSR thanks CNPq for the Master of Science fellowship (grant 130470/2019-8) and FAPERGS/CAPES Consortium (Edital 03/2018 - PRÓ-EQUIPAMENTOS; grant 18/2551-0000429-4), which provided logistical support for this work. RGN thanks CNPq for research fellow grants 303863/2016-1 and 310377/2019-6. DS thanks CNPq for the post-doctoral fellowship (grant 159548/2018-7). DLN thanks CNPq for the Doctoral fellowship (grant 140807/2017-9). This paper is a contribution to the BRASILEX Project from Unisinos University.

Supplementary Material. The supplementary material for this article can be found at <https://doi.org/10.1017/qua.2022.55>

REFERENCES

- Amarante, O.A.C., Silva, F.J.L., 2002. *Atlas Eólico: Rio Grande do Sul*. Secretaria de Energia Minas e Comunicações. Porto Alegre: SEMC. 70 pp. <http://www.isl2024.org.br/sistema/uploads/postagens/55/arquivos/atlas-eolico-rs.pdf>.
- Angulo, R.J., Lessa, G.C., de Souza, M.C., 2006. A critical review of mid- to late-Holocene sea-level fluctuations on the eastern Brazilian coastline. *Quaternary Science Review* 25, 486–506.
- Antoine, C.M., Forrest, J.R.K., 2021. Nesting habitat of ground-nesting bees: a review. *Ecological Entomology* 46, 143–159.
- Behling, H., 2002. South and southeast Brazilian grasslands during late Quaternary times: a synthesis. *Palaeogeography, Palaeoclimatology, Palaeoecology* 177, 19–27.
- Bergqvist, L.P., Maciel, L., 1994. Icnofósseis de mamíferos (crotovinas) na planície costeira do Rio Grande do Sul. *Anais da Academia Brasileira de Ciências* 66, 189–197.
- Bertling, M., Braddy, S.J., Bromley, R.G., Demathieu, G.R., Genise, J., Mikuláš, R., Nielsen, J.K., et al., 2006. Names for trace fossils: a uniform approach. *Lethaia* 39, 265–286.
- Bonilha, R.M., Casagrande, J.C., Soares, M.R., Reis-Duarte, R.M., 2012. Characterization of the soil fertility and root system of restinga forests. *Revista Brasileira de Ciência do Solo* 36, 1804–1813.
- Bromley, R.G., 1996. *Trace Fossils. Biology, Taphonomy and Applications*. Chapman and Hall, London, 361 pp.
- Buatois, L.A., Mángano, M.G., 2011. *Ichnology: Organism-Substrate Interactions in Space and Time*. Cambridge University Press, Cambridge, UK, 358 pp.
- Buchmann, F.S.C., Barbosa V.P., Villwock J.A., 1998. Sedimentologia e paleoecologia durante o máximo transgressivo holocênico na Lagoa Mirim, RS, Brasil. *Acta Geológica Leopoldensia* 21, 21–26.
- Buchmann F.S.C., Tomazelli L.J., 2003. Relict nearshore shoals of Rio Grande do Sul, southern Brazil: origin and effects on nearby modern beaches. *Journal of Coastal Research* 35, 318–322.

- Clapperton, C.M., 1993. Nature of environmental changes in South America at the last glacial maximum. *Palaeogeography, Palaeoclimatology, Palaeoecology* **101**, 189–208.
- Clark, P.U., Dykejeremy, A.S., Shakunanders, D., Carlsonjorie, E., Wohlfarthjerry, C., Mitrovicasteven, X., Hostetlerand, W., Mccabe, A.M., 2009. The last glacial maximum. *Science* **325**, 710–714.
- del Valle, L., Genise, J.F., Pons, G.X., Pomar, F., Vicens, D., Fornós, J.J., 2020. Insect trace fossils in Pleistocene deposits from the Pityusic Islands (Balearic Archipelago, Western Mediterranean): ichnotaxonomy and palaeoenvironmental significance. *Quaternary International* **553**, 83–93.
- Dillenburg, S.R., Barboza, E.G., Tomazelli, L.J., Hesp, P.A., Clerot, L.C.P., Ayup-Zouain, R.N., 2009. The Holocene coastal barriers of Rio Grande do Sul. In: Dillenburg, S.R., Hesp, P.A. (Eds.), *Geology and Geomorphology of Holocene Coastal Barrier of Brazil*. Lecture Notes in Earth Science **107**, pp. 53–91.
- Dillenburg, S.R., Roy, P.S., Cowell, P.J., Tomazelli, L.J., 2000. Influence of antecedent topography on coastal evolution as tested by the shoreface translation-barrier model (STM). *Journal of Coastal Research* **16**, 71–81.
- Duringer, P., Schuster, M., Genise, J.F., Mackaye, H.T., Vignaud, P., Brunet, M., 2007. New termite trace fossils: Galleries, nests and fungus combs from the Chad basin of Africa (Upper Miocene–Lower Pliocene). *Palaeogeography, Palaeoclimatology, Palaeoecology* **251**, 323–353.
- Ehlers, J., Gibbard, P., 2008. Extent and chronology of Quaternary glaciation. *Episodes* **31**, 211–218.
- Ekdale, A.A., Bromley, R.G., Loope, D.B., 2007. Ichnofacies of an ancient erg: a climatically influenced trace fossil association in the Jurassic Navajo Sandstone, southern Utah, USA. In: Miller, W., III, (Ed.), *Trace Fossils. Concepts, Problems, Prospects*. Elsevier, Amsterdam, pp. 562–564.
- Ellis, R., Palmer, M., 2016. Modulation of ice ages via precession and dust-albedo feedbacks. *Geoscience Frontiers* **7**, 891–909.
- Ernst, C.M., Buddle, C.M., 2015. Drivers and patterns of ground-dwelling beetle biodiversity across northern Canada. *PLoS ONE* **10**, e0122163. <https://doi.org/10.1371/journal.pone.0122163>.
- Fairbanks, R.G. 1989. A 17,000-year glacio-eustatic sea-level record: influence of glacial melting rates on the younger rates on the Younger Dryas event and deep-ocean circulation. *Nature* **342**, 637–642.
- Fornós, J.J., Clemmensen, L.B., Gómez-Pujol, L., Murray, A., 2009. Late Pleistocene carbonate aeolianites on Mallorca, western Mediterranean: a luminescence chronology. *Quaternary Science Reviews* **28**, 2697–2709.
- Freitas, G.P., Francischini, H., Tãmega, F.T.S., Spotorno-Oliveira, P., Dentzien-Dias, P., 2020. On ex situ *Ophiomorpha* and other burrow fragments from the Rio Grande do Sul Coastal Plain, Brazil: paleobiological and taphonomic remarks. *Journal of Paleontology* **94**, 1148–1164.
- Genise, J.F., 1995. Upper Cretaceous trace fossils in permineralized plant remains from Patagonian, Argentina. *Ichnos* **3**, 287–299.
- Genise, J.F., 1997. A fossil termite nest from the Marplatán Stage (Late Pliocene) of Argentina: palaeoclimatic indicator. *Palaeogeography, Palaeoclimatology, Palaeoecology* **136**, 139–144.
- Genise, J.F., 2017. *Ichnoentomology: Insect Traces in Soils and Paleosols*. Topics in Geobiology 37. Springer, New York, 695 pp.
- Genise, J.F., Alonso-Zarza, A.M., Krause, J.M., Sánchez, M.V., Sarzetti, L.C., Farina, J.L., González, M.G., Cosarinsky, M., Belloso, E.S., 2010. Rhizolith balls from the Lower Cretaceous of Patagonia: just roots or the oldest evidence of insect agriculture? *Palaeogeography, Palaeoclimatology, Palaeoecology* **287**, 128–142.
- Genise, J.F., Belloso, E.S., Gonzalez M.G., 2004. An approach to the description and interpretation of ichnofabrics in paleosols. In: McIlroy, D. (Ed.), *The Application of Ichnology to Palaeoenvironmental and Stratigraphic Analysis*. Geological Society, London Special Publication **228**, 355–382.
- Genise, J.F., Mángano, M.G., Buatois, L.A., Laza, J.H., Verde, M., 2000. Insect trace fossil associations in paleosols: the Coprinisphaera ichnofacies. *Palaios* **15**, 49–64.
- Gibert, J.M. de, Netto, R.G., Tognoli, F.M.W., Grangeiro, M.E., 2006. Commensal worm traces and possible juvenile thalassinidean burrows associated with *Ophiomorpha nodosa*, Pleistocene, southern Brazil. *Palaeogeography, Palaeoclimatology, Palaeoecology* **230**, 70–84.
- Grassé, P., 1986. *Termitologia, Tome III: Anatomie, Physiologie, Biologie, Systématique des Termites*. Masson, Paris, 715 pp.
- Hansen, J., Sato, M., Russell, G., Kharecha, P., 2013. Climate sensitivity, sea level and atmospheric carbon dioxide. *Philosophic Transactions of the Royal Society A* **371**, 20120294. <https://doi.org/10.1098/rsta.2012.0294>.
- Hesp, P.A., 1991. Ecological processes and plant adaptations on coastal dunes. *Journal of Arid Environments* **21**, 165–191.
- Hill, J.L., Vater, A.E., Geary, A.P., Matthews, J.A., 2018. Chronosequences of ant nest mounds from glacier forelands of Jostedalbreen, southern Norway: insights into the distribution, succession and geo-ecology of red wood ants (*Formica lugubris* and *F. aquilonia*). *The Holocene* **28**, 1113–1130.
- Hulton, N.R.J., Purves, R.S., McCulloch, R.D., Sugden, D.E., Bentley, M.J., 2002. The last glacial maximum and deglaciation in southern South America. *Quaternary Science Reviews* **21**, 233–241.
- Imbrie, J.D., Hays, J.D., Martinson, D.G., McIntyre, A., Mix, A.C., Morley, J.J., Pisias, N.G., Prell, W.L., Shackleton, N.J., 1984. The orbital theory of Pleistocene climate: support from a revised chronology of the marine $\delta^{18}\text{O}$ record. In: Berger, A.L., Imbrie, J., Hays, J., Kukla, G., Saltzman, B. (Eds.), *Milankovitch, and Climate. Part 1*. D. Reidel Publishing Company, Dordrecht, pp. 269–305.
- Lamb, S.D., McCombe, G.G.I., Lawrence, E., Macwan, R., Mayer, T., Jandt, J.M., 2020. Subterranean nesting behaviour in response to soil moisture conditions in the southern ant, *Monomorium antarcticum* Smith (Hymenoptera: Formicidae). *New Zealand Entomologist* **43**, 33–43.
- Laza, J.H., 2006. Termiteros del Plioceno y Pleistoceno de la Provincia de Buenos Aires, República Argentina. Significación paleoambiental y paleozoogeográfica. *Ameghiniana* **43**, 641–648.
- Leal, R.A., Barboza, E.G., Bitencourt, V.J.B., 2022. Interdecadal climate variability identified in aeolian deposits in southern Santa Catarina, Brazil. *Journal of South American Earth Sciences* **113**, 103636. <https://doi.org/10.1016/j.jsames.2021.103636>.
- Ledru, M.-P., Braga, P.I.S., Soubiès, F., Fournier, M., Martin, L., Suguio, K., Turcq, B., 1996. The last 50,000 years in the Neotropics (Southern Brazil): evolution of vegetation and climate. *Palaeogeography, Palaeoclimatology, Palaeoecology* **123**, 239–257.
- Leite, Y.L.R., Costa, L.P., Loss, A.C., Rocha, R.G., Batalha-Filho, H., Bastos, A.C., Quaresma, V.S., et al., 2016. Neotropical forest expansion during the last glacial period challenges refuge hypothesis. *PNAS* **113**, 1008–1013.
- Lopes, R.P., Dillenburg, S.R., Savian, J.F., Pereira, J.C., 2021. The Santa Vitória Alloformation: an update on a Pleistocene fossil-rich unit in Southern Brazil. *Brazilian Journal of Geology* **51**, e2020065. <https://doi.org/10.1590/2317-4889202120200065>.
- Lopes, R.P., Dillenburg, S.R., Schultz, C.L., 2016. Cordão Formation: loess deposits in the southern coastal plain of the state of Rio Grande do Sul, Brazil. *Anais da Academia Brasileira de Ciências* **88**, 2143–2166.
- Lopes, R.P., Dillenburg, S.R., Schultz, C.L., Ferigolo, J., Ribeiro, A.M., Pereira, J.C., Holanda, E.Z., Pitana, V.G., Kerber, L., 2014. The sea-level highstand correlated to marine isotope stage (MIS) 7 in the coastal plain of the state of Rio Grande do Sul, Brazil. *Anais da Academia Brasileira de Ciências* **86**, 1573–1595.
- Lopes, R.P., Pereira, J.C., 2019. Molluscan grazing traces (ichnogenus *Radulichnus* Voigt, 1977) on a Pleistocene bivalve from Southern Brazil, with the proposal of a new ichnospecies. *Ichnos* **26**, 141–157.
- Lopes R.P., Pereira J.C., Kinoshita A., Molleberg M., Barbosa F., Jr., Baffa O., 2020. Geological and taphonomic significance of electron spin resonance (ESR) ages of Middle–Late Pleistocene marine shells from barrier-lagoon systems of Southern Brazil. *Journal of South American Earth Sciences* **101**, 102605. <https://doi.org/10.1016/j.jsames.2020.102605>.
- Lopes, R.P., Ribeiro, A.M., Dillenburg, S.R., Schultz, C.L., 2013. Late Middle to Late Pleistocene paleoecology and paleoenvironments in the coastal plain of Rio Grande do Sul state, Southern Brazil, from stable isotopes in fossils of *Toxodon* and *Stegomastodon*. *Palaeogeography, Palaeoclimatology, Palaeoecology* **369**, 385–394.
- Marques, M.C., Silva, S.M., Liebsch, D., 2015. Coastal plain forests in southern and southeastern Brazil: ecological drivers, floristic patterns, and conservation status. *Brazilian Journal of Botany* **38**, 1–18.
- Michener, C.D., 2007. *The Bees of the World*. John Hopkins University Press, Baltimore, MD, 953 pp.

- Muhs, D.R., Budahn, J., Avila, A., Skipp, G., Freeman, J., Patterson, D., 2010. The role of African dust in the formation of Quaternary soils on Mallorca, Spain and implications for the genesis of red Mediterranean soils. *Quaternary Science Reviews* **29**, 2518–2543.
- Netto, R.G., Curran, H. A., Belaustegui, Z., Tognoli, F.M.W., 2017. Solving a cold case: new occurrences reinforce juvenile callianassids as the *Ophiomorpha puerilis* tracemakers. *Palaeogeography, Palaeoclimatology, Palaeoecology* **475**, 93–105.
- Netto, R.G., Tognoli, F.M.W., Gibert, J.M., Oliveira, M.Z., 2007. Paleosol evolution in nearshore fluvial Pleistocene deposits of the Chuí Formation, south of Brazil. 5^a Reunión Argentina de Icnología y 3^a Reunión de Icnología del Mercosur, Ushuaia, Resúmenes, p. 55.
- Oliveira, E.V., 1999. Quaternary vertebrates and climates of southern Brazil. In: Rabassa, J., Salemme, M. (Eds.), *Quaternary of South America and Antarctic Peninsula*. Balkema, Rotterdam, **12**, 61–73.
- Parise, C.K., Calliari, L.J., Krusche, N., 2009. Extreme storm surges in the south of Brazil: atmospheric conditions and shore erosion. *Brazilian Journal of Oceanography* **57**, 175–188.
- Peltier, W.R., Fairbanks, R.G., 2006. Global glacial ice volume and last glacial maximum duration from an extended Barbados sea level record. *Quaternary Science Reviews* **25**, 3322–3337.
- Ramos, K.S., Netto, R.G., Sedorko, D., 2021. Termite nests in eolian back-shore settings: an unusual record throughout the Quaternary in the Neotropical realm. *Palaeontologia Electronica* **24**, a15. <https://doi.org/10.26879/1146>.
- Retallack, G.J., 2001. *Soils of the Past. An Introduction to Paleopedology*. Blackwell, Oxford, 552 pp.
- Rodrigues, F.C.G., Giannini, P.C.F., Fornari, M., Sawakuchi, A.O., 2020. Deglacial climate and relative sea level changes forced the shift from eolian sandsheets to dunefields in southern Brazilian coast. *Geomorphology* **365**, 107252. <https://doi.org/10.1016/j.geomorph.2020.107252>.
- Rosa, M.L.C.C., Barboza, E.G., Abreu, V.S., Tomazelli, L.J., Dillenburg, S.R., 2017. High-frequency sequences in the Quaternary of Pelotas Basin (coastal plain): a record of degradational stacking as a function of longer-term base-level fall. *Brazilian Journal of Geology* **47**, 183–207.
- Rosa, M.L.C.C., Barboza, E.G., Dillenburg, S.R., Tomazelli, L.J., Ayup-Zouain, R.N., 2011. The Rio Grande do Sul (Brazil) shoreline behavior during the Quaternary: a chronostratigraphic analysis. *Journal of Coastal Research, Special Issue* **64**, 686–690.
- Roulston, T.H., Goodell, K., 2011. The role of resources and risks in regulating wild bee populations. *Annual Review of Entomology* **56**, 293–312.
- Sánchez, M.V., Bellosi, E.S., Genise, J.F., Kramarz, A., Sarzetti, L.C., 2021. An assemblage of large-sized insect traces in paleosols from the Middle Miocene of northern Patagonia related to the climatic optimum. *Journal of South American Earth Sciences* **109**, 103249. <https://doi.org/10.1016/j.jsames.2021.103249>.
- Santos, N.B., Lavina, E.L.C., Paim, P.S.G., Tatumi, S.H., Yeec, M., Santos, V.O., Kern, H.P., 2022. Relative sea level and wave energy changes recorded in a micro-tidal barrier in southern Brazil. *Quaternary Research*. <https://doi.org/10.1017/qua.2022.23>.
- Schoeneberger, P.J., Wysocki, D.A., Benham, E.C., Broderson, W.D., 2001. *Field Book for Describing and Sampling Soils*. USDA-NRCS, National Soil Survey Center, Books Express Publishing, 298 pp.
- Stephen, W.P., Bohart, G.E., Torchio, P.F., 1969. *The Biology and External Morphology of Bees, with a Synopsis of the Genera of Northwestern America*. Agricultural Experimental Station, Oregon State University, Corvallis, Oregon, 140 pp.
- Suguio, K., Martin, L., 1978. *Quaternary Marine Formations of the States of São Paulo and Southern Rio de Janeiro*. International Symposium on Coastal Evolution in the Quaternary, IGCP Project 61, Special Publication 1, São Paulo, 55 pp.
- Tomazelli, L.J., 1985. Contribuição ao conhecimento das fácies de ambiente praial a partir de elementos do Pleistoceno Costeiro do Rio Grande do Sul. *Anais, 2nd Simpósio Sul-Brasileiro de Geologia*, **28**, Florianópolis, Sociedade Brasileira de Geologia, pp. 325–338.
- Tomazelli, L.J., Dillenburg, S.R., 2007. Sedimentary facies and stratigraphy of a last interglacial coastal barrier in south Brazil. *Marine Geology*, **244**: 33–45.
- Tomazelli, L.J., Dillenburg, S.R., Villwock, J.A., 2000. Late Quaternary geological history of Rio Grande do Sul Coastal Plain, southern Brazil. *Revista Brasileira de Geociências* **30**, 474–476.
- Tomazelli, L.J., Villwock, J.A., 2000. O Cenozóico no Rio Grande do Sul: Geologia da Planície Costeira. In: Holz, M., De Ros, L.F. (Eds.), *Geologia do Rio Grande do Sul*. Edição CIGO/ UFRGS, Porto Alegre, pp. 375–406.
- Tschinkel, W.R., 2010. The foraging tunnel system of the Namibian Desert termite, *Baukaliotermes hainesi*. *Journal of Insect Science* **10**, 65. <https://doi.org/10.1673/031.010.6501>.
- Villwock J.A., Tomazelli L.J., 1995. Geologia Costeira do RS. *Notas Técnicas* **8**, 1–45.
- Villwock, J.A., Tomazelli, L.J., Loss, E.L., Dehnhardt, E.A., Horn, N.O., Bachi, F.A., Dehnhardt, B.A., 1986. Geology of the Rio Grande do Sul Coastal Province. In: Rabassa, J. (Ed.), *Quaternary of South America and Antarctic Peninsula*. A.A. Balkema, Rotterdam, pp. 79–97.