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Megaichnus igen. nov.: Giant Paleoburrows Attributed to Extinct Cenozoic Mammals from South America

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ABSTRACT
In the last ten years, more than 1,500 large burrows have been discovered in southern and southeastern Brazil, dug in rocks that include weathered granitic and basaltic rocks, sandstones, and other consolidated sediments. Their presence in geological units of Plio-Pleistocene age suggests that large extinct mammals produced these structures. The internal walls exhibit scratches and grooves left by the animals that inhabited these structures. The burrows are straight or slightly sinuous tunnels that measure up to tens of meters in length. One smaller type measures up to 1.5 meter in diameter, and the larger type can reach 2 meters in height and 4 meters in width, suggesting that such structures have been produced by at least two kinds of organisms. This contribution proposes a classification for these ichnofossils under the generic designation *Megaichnus* igen. nov., consisting of two ichnospecies identified so far: *M. major* and *M. minor* ispp. nov. Although the exact identity of the producers of the burrows is yet unknown, the dimensions and morphology point to ground sloths and giant armadillos.

KEYWORDS
Continental ichnology; Semifossorial mammals; Paleoburrows; *Megaichnus*; Domichnia

Introduction

The production of burrows is a widespread behavior among different types of organisms, ranging from small invertebrates to large mammals and birds. Burrows are usually produced in soft sediments and also in resistant substrates, either firmgrounds (well consolidated sediments) or hardgrounds (rocks or lithified sediments) (Bromley, 1996), therefore being classified as bioerosion traces.

In the fossil record, burrows produced by marine organisms are abundant and are grouped in several ichnofacies, which reflect different behaviors such as feeding and sheltering. In continental settings, such ichnofossils are known to have been produced by Permo-Triassic reptiles (Groenwald, 1991; Modesto and Botha-Brink, 2010), Cretaceous ornithopod dinosaurs (Varricchio et al., 2007; Martin, 2009), and Cenozoic mammals (Martin and Bennett, 1977; Vizcaíno et al., 2001; Hembree and Hasiotis, 2008).

Terrestrial vertebrates can be divided in fossorial (animals that spend all their lives underground, even to obtain food) and semifossorial (those that spend some time inside the burrows but have to go outside to feed) (White, 2005). The burrows produced by semi-fossorial mammals are usually simple tunnels, sometimes with enlarged nesting areas, but those produced by fossorial animals are more complex, often with several interconnected chambers (Jarvis and Sale, 1971; Sheets et al., 1971; Thomas, 1974; Reichmann and Smith, 1990).

It is estimated that about half of the extant mammalian species are semi-fossorial, and about 3.5% are fossorial (Voorhies, 1975; Nevo, 1979). Mammals produce burrows for sheltering, nesting, or feeding purposes; burrows used for shelter are usually simple, formed by a tunnel with one single opening and sometimes with an enlarged area or short ramification for nesting, food storing, or as areas for disposal of feces (Reichman and Smith, 1990). Despite the abundance of fossilized remains of burrowing mammals, records of the burrows themselves are scarce in comparison, probably due to the lack of descriptions in the literature, to the failure in recognizing such structures, or to low preservation potential (Voorhies, 1975).

In the last ten years, hundreds of giant burrows have been discovered in southern and southeastern Brazil and in Argentina (Fig. 1), and possible occurrences were also reported from Paraguay (Ricardo Souberlich, personal communication 2016). The first

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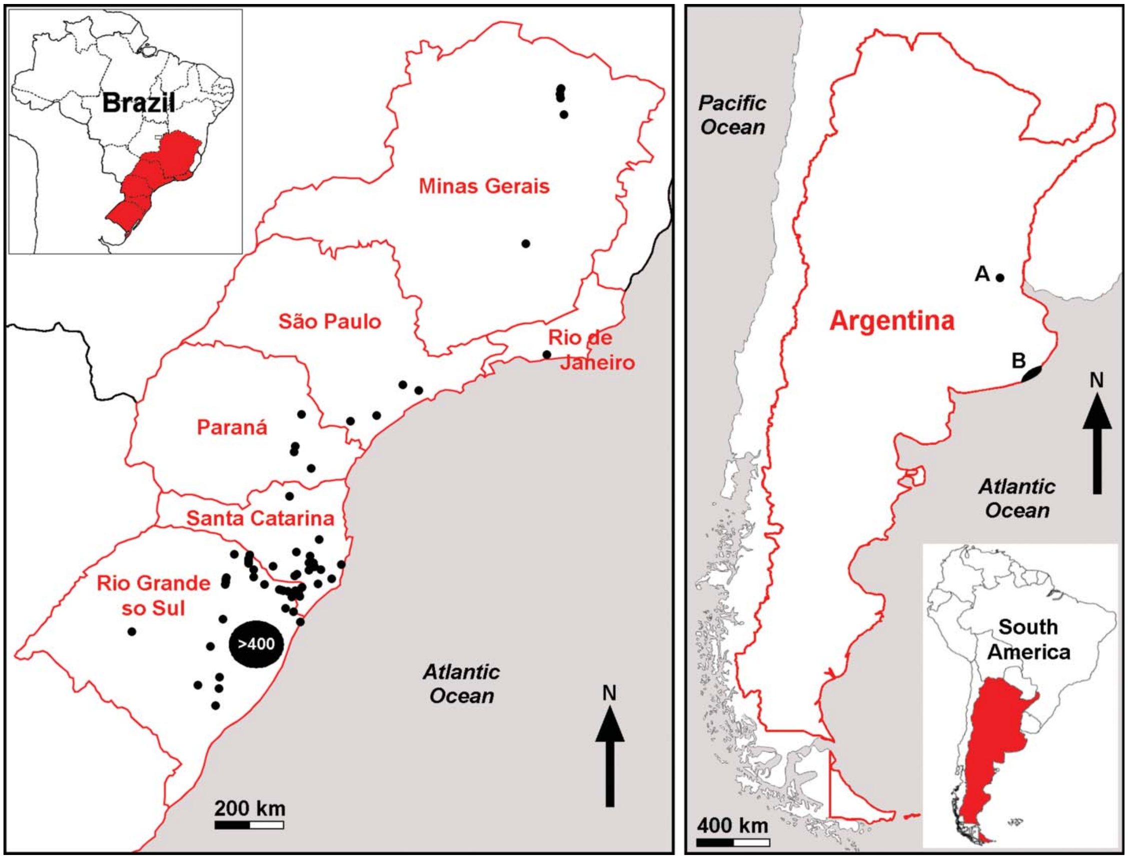

Figure 1. On the left, localities in southern and southeastern Brazilian states where large paleoburrows have been discovered; the black ellipse indicates the highest density (more than 400 found so far) of burrows, in the surroundings of the city of Porto Alegre. On the right, map of Argentina with indication of areas where paleoburrows have been reported: near the town of San Pedro (**A**); in the coastal area between Mar del Plata and Miramar (**B**).

known record of such structures in Brazil was published by Padberg-Drenkpol (1933), but it was only much later that Bergqvist and Maciel (1994) recognized burrows found in Cenozoic (possibly middle Pleistocene) consolidated sediments in southern Brazil as products of biogenic activity. Although the structures described by those authors consisted of burrows that were filled with sediments (krotovinas, *sensu* Sukachev, 1902, *apud* Andreis, 1981), the shape and dimensions are similar to burrows found in Plio-Pleistocene siltstones of Argentina, known since the early 20th century (Ameghino, 1909). Later, Buchmann et al. (2009) presented the first description of one open burrow, and many more have been discovered in recent years (Frank et al., 2008; 2010a; 2012; 2013; Lopes et al., 2009). These burrows are found in continental settings, in substrates that include consolidated sands, sandstones, and weathered granitic and basaltic rocks ranging in age from the Precambrian to the late Cenozoic. The size of these structures precludes their assignment to any living species, and therefore, they are considered paleoburrows (i.e., produced by extinct organisms). Here we present an overall description and a proposed classification for these ichnofossils. A discussion about the purposes and possible builders of these structures is also included.

Systematic ichnology

Despite the large number of paleoburrows and krotovinas discovered so far (more than 1,500), few have been described in detail. Nevertheless, differences in dimensions and structure of those that are already described allowed distinguishing patterns that suggest the activity of at least two types of burrowing animals. Following this rationale, a formal classification of these ichnofossils is proposed, consisting of two species grouped under one single genus.

Ichnogenus

Megaichnus igen. nov.

***Etymology*:** From the Greek *megas* (= large) and *ichnos* (= trace).

***Diagnosis*:** Large (at least 0.6 meter in diameter), subhorizontal straight to slightly sinuous tunnels, single or branched, with subcircular to subelliptical outline.

Restricted to continental settings, in areas with shallow to relatively high slope. Produced on firmgrounds and hardgrounds that include consolidated sands, weathered volcanic rocks, and sandstones. Digging marks in the form of long and shallow grooves along the walls and ceiling are common features.

***Comments*:** Despite of having been found in substrates ranging in age from the Precambrian to late Cretaceous, these burrows are considered to have been produced by Cenozoic mammals, because they are also found in arkosic sandstone (which constitutes the subaerial portion of the Alluvial Fans depositional system) and consolidated aeolian sands (of the coastal Barrier System I) in the state of Rio Grande do Sul. These units are regarded as of Pliocene and Pleistocene age, respectively (Closs, 1970; Villwock and Tomazelli, 1995).

Type ichnospecies

Megaichnus minor n. isp.

The diagnostic features of this ichnospecies is based on the description of the paleoburrow found in the outskirts of the town of Cristal, in the state of Rio Grande do Sul, Brazil, presented by Buchmann et al. (2009) (Fig. 2A).

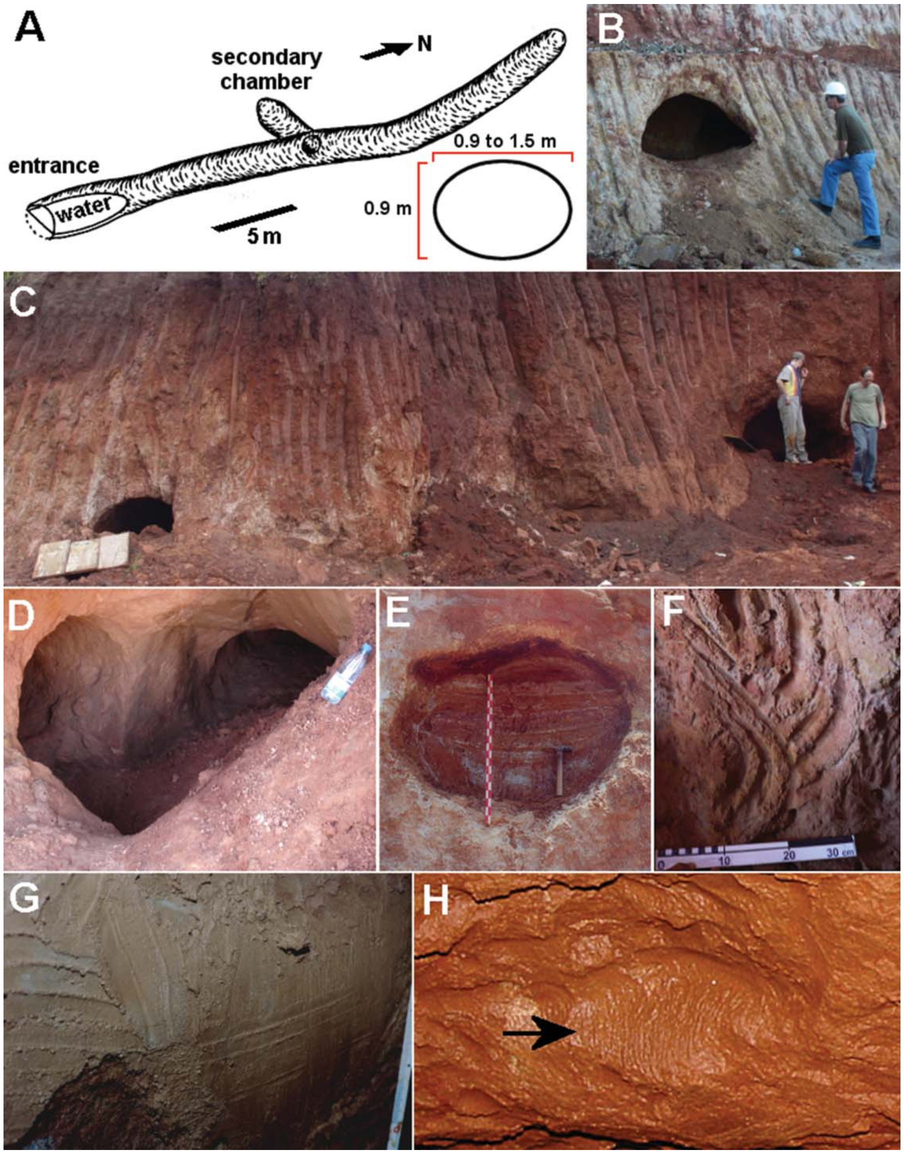

Figure 2. Schematics of the paleoburrow found near the town of Cristal (modified from Buchmann et al., 2009) (**A**). Specimen of *Megaichnus minor* exposed on a roadside; the vertical grooves are machinery scrape marks not related to the burrows (**B**). Two *M. minor* exposed on the same outcrop (**C**). Intersection between two paleoburrows (**D**). One completely filled krotovina, the scale measures 1 meter (**E**). Claw impressions inside one *M. minor* (**F**). Osteoderm imprints along the wall (**G**). Possible fur impression on the ceiling (indicated by the arrow) of one *M. minor* (**H**).

Diagnosis: Subcircular to subelliptical burrows (Fig. 2B), that form two groups: one ranging from 0.6 to 0.9 meter in width and 0.5 to 0.7 meter in height, and other ranging from 1.2 to 1.5 meters in width and about 0.9 in height. The total length can reach 30 meters at least (but see the Discussion below) and the burrows can be horizontal to sloped. The walls and ceiling are arched, but the floor is often flat because of the partial infilling by sediments. Most are single tunnels, but smaller ramifications/chambers have been observed. These burrows are often found on hillsides; at some outcrops several burrows are found, with two or more intersecting each other (Fig. 2C,D). About 90% of this species consist of krotovinas (Fig. 2E), and so far no fossils have been found inside the open burrows. Short and long grooves observed along the walls and ceiling (Fig. 2F) are evidences of digging by the animals that produced or re-occupied the burrows. Other traces imprinted along the walls were long shallow grooves separated by thin ridges, which are consistent with osteoderms of the mobile belt of a giant armadillo (Fig. 2G), and rugosities on the ceiling that suggest fur impressions (Fig. 2H). Some burrows exhibit several enlarged portions intercalated with slightly narrower passages, suggesting that the animal stopped and resumed the excavation several times.

Occurrence: The entrances of most of these paleoburrows are covered by sediments and vegetation, and only become exposed during excavations for construction purposes such as roads, parking lots and buildings, among others. They occur in firmgrounds (consolidated sediments and weathered volcanic rocks) of Cenozoic age (Plio-Pleistocene?) and hardgrounds (sandstones) of Cretaceous and Jurassic age, in terrains with moderate slope, usually close to a water source. This ichnospecies is also found in Plio-Pleistocene loessoid sediments near the town of San Pedro and in the coast of the Buenos Aires Province of Argentina (Vizcaíno et al., 2001; Dondas et al., 2009; Cenizo, 2011).

Megaichnus major n. isp.

This ichnospecies consist of large burrows (also called “megatunnels”), whose type specimen is the larger burrow described by Frank et al. (2013) in the locality of Boqueirão do Leão (Fig. 3A).

Diagnosis: Large (about 2 meters in height and up to 4 meters in width), subelliptical paleoburrows (Fig. 3B) that can surpass 50 meters in length and become narrower towards their ends. These megatunnels are subhorizontal; so far, no body fossils have been found inside, but scratches produced by the diggers are present along the walls (Fig. 3C); most (about 70%) are found partially filled by allochthonous sediments and rock fragments (Fig. 3D). Besides scratches, smooth surfaces are also observed along the arched ceiling and walls (Fig. 3E). One remarkable feature found in some of these paleoburrows are large elliptical smooth surfaces on the floor and lower wall (Fig. 3F) that could have been used as resting places for large animals.

Occurrence: So far, this ichnospecies was found only in Brazil, in hardgrounds such as weathered Proterozoic banded iron formations (BIFs), Jurassic-Cretaceous sandstones, and Cretaceous weathered volcanic rocks. It is found in low to moderately steep terrains such as the slopes of plateaus and ridges. Most of these paleoburrows are hard to find because their entrances are covered by vegetation or rubble from landslides or rock collapse. The height and width of *M. major* are larger than those of the giant burrows found in Argentina (Zárate et al., 1998; Dondas et al., 2009), which may reflect the action of different builders (see Discussion).

Discussion

Identification of Megaichnus

The paleoburrows found in South America are possibly the largest ichnofossils known so far. In Brazil, these burrows have been described in the early 1930s, but they have been considered as archaeological structures (Padberg-Drenkpol, 1933; Rohr, 1971; Prous, 1991). Although they have been overlooked and misinterpreted by scientists for so many years, the ichnofossils *Megaichnus major* with clear entrances are well known by the people that live in their vicinity, and several curious stories have been created to explain these structures. One legend told by local people says that these burrows are the places where the Curupira (a mythical being from the mythology of Tupi-Guarani tribes) hides the weapons stolen from hunters until a tribute of beverage is paid. According to other native legend they are the lair of a giant snake (called Boiúna), while stories that emerged among European settlers tell that they are the hiding places of treasures left by the Jesuits.

The large burrows (probably *M. minor*) found in the cliffs of Mar del Plata, Argentina, are often found with mammalian remains preserved inside and, therefore, have been recognized as of biogenic origin for decades (Ameghino, 1909; Vizcaíno et al., 2001). The absence of mentions of such large and conspicuous structures in the Brazilian geological and paleontological literature prior to the 1990s is apparently related to the failure in recognizing them as biogenic structures. In fact, *M. major* can easily be misinterpreted as natural caves or lava tubes (Fig. 4).

The distinction between these paleoburrows and natural cavities is made on the basis of the observed physical

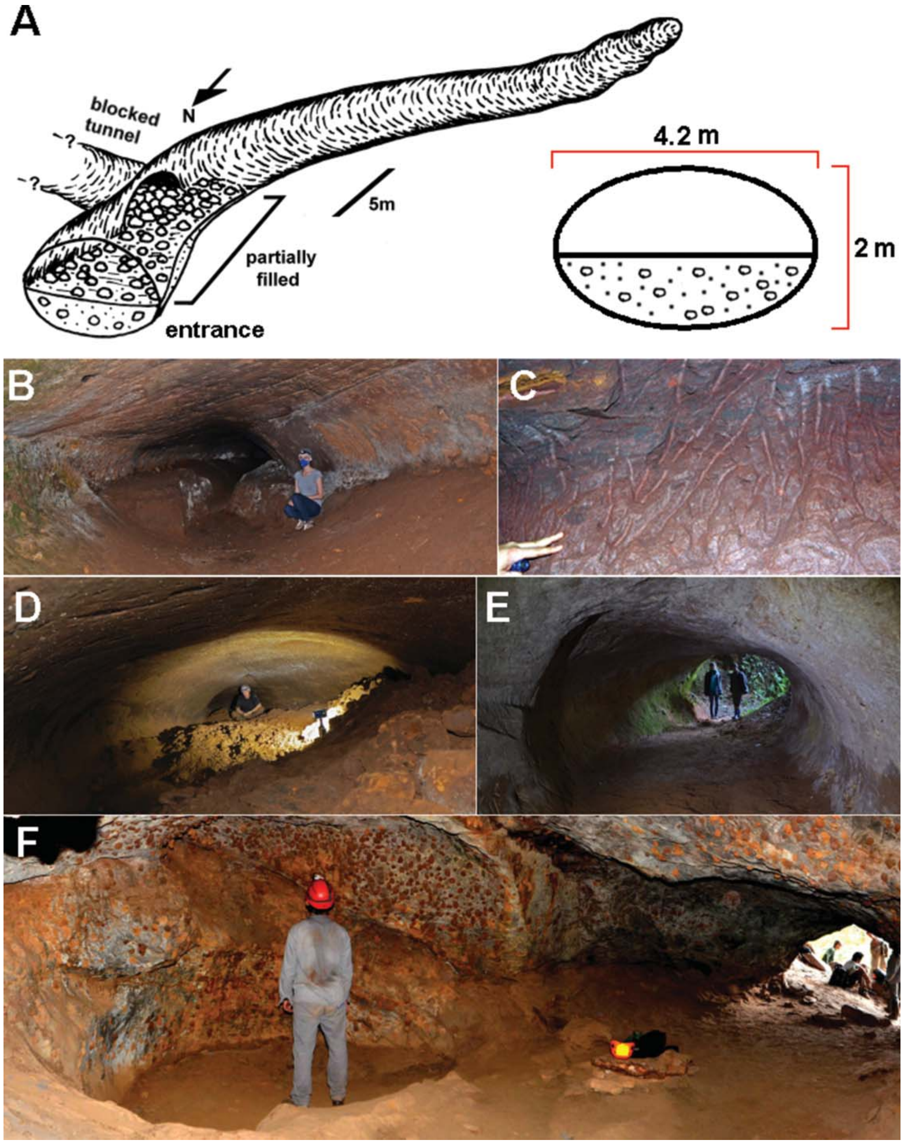

Figure 3. Schematics of the type specimen of *Megaichnus major* (modified from Frank et al., 2013) (**A**). Interior of one *M. major* dug in aeolian sandstone of the Botucatu Formation (**B**). Scratches on the wall produced by the animals that inhabited these burrows (**C**). *M. major* partially filled by sediments and rock debris (**D**). Smooth surfaces of the walls (**E**). Large elliptical smoothing on the wall and floor of one *M. major* (**F**).

features. *M. minor* is characterized by its well-defined subelliptical to subcircular outline, and its presence cannot be related to any features that could produce cavities in the hosting rock such as faultings, fractures, or flowing water. Krotovinas of this species are easily identified, because the sediment that fills them usually exhibit laminations or textural and color differences from the hosting rock. The paleoburrows *M. major* dug in sedimentary rocks are more difficult to distinguish from natural cavities produced by rock collapse, but whereas this process tends to occur along weak points that follow the bedding planes of the rock, the surfaces of the burrows are usually discordant in relation to the rock structure.

Other features that distinguish these ichnofossils are the smooth internal surfaces. These are common in the large megatunnels, even in those produced in weathered granitic rocks. The absence of evidences of strong water flows inside the burrows or other form of natural erosion indicates that this smoothing was produced by organisms, either on purpose or unintentionally. These surfaces could have resulted from the friction against the walls produced when the animals moved inside the burrows. In Triassic tetrapod burrows of Morocco, for example, the smooth floor is interpreted as the result of frequent movement of the burrowers to the outside in order to forage (Voigt, 2011). The large subelliptical smooth surfaces at specific areas inside some *M. major* (see Fig. 3D) suggest preferential use of this space, possibly as a resting area, for long periods. Other possibility is that the smoothing was intentional, produced by the

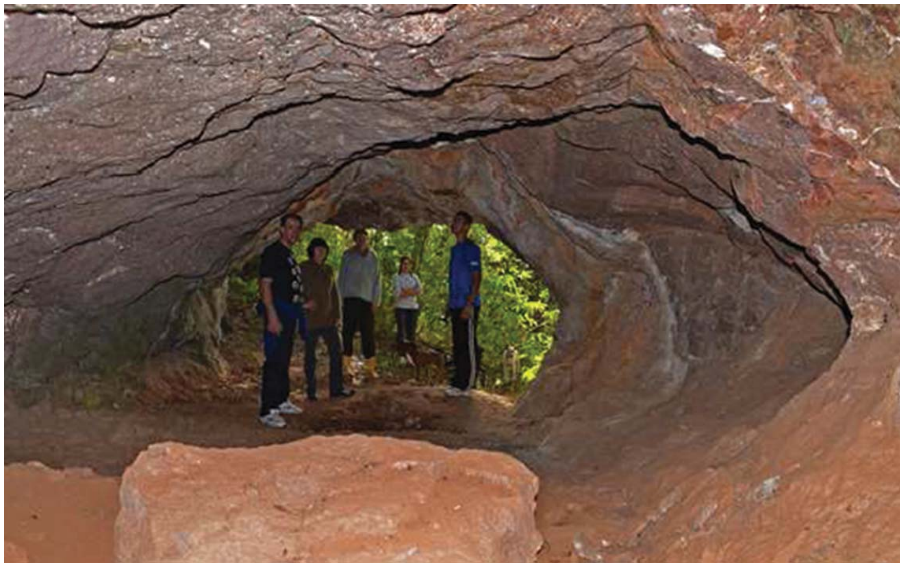

Figure 4. Interior of a lava tube in basaltic rock of the Serra Geral Formation.

animals rubbing against the walls on purpose, to remove parasites or scratch their itches. Large mammals such as elephants usually rub themselves against trees or rocks to remove parasites or to stop itching (Haynes, 2006). The smooth surfaces found high above the ground in some rocks from California were possibly produced by the rubbing of mammoths (Parkman, 2007).

The scratches interpreted as digging marks found along the walls and ceiling are also a common feature seen in most of the paleoburrows. Although not described in detail yet, thousands have been observed, and some distinct characteristics of these traces are apparent. Most consist of long, shallow grooves parallel to each other, grouped (Fig. 5A) and apparently produced by 2 or 3 claws. Good estimates of the number of grooves and their relation with each other is difficult, because most of them overlap each other. Most are straight, but curved grooves are common (see Fig. 2F). Their width and depth do not seem to be related to the hardness of the substrate, because thin/shallow and large/deep grooves are observed in *M. major* dug in hardgrounds and in *M. minor* dug in softer firmgrounds. These grooves are mostly smooth (Fig. 5B), but some irregular ones may have been produced by broken claws (Fig. 5C).

Several paleoburrows have been found after indication by local public health agencies. These agencies search and monitor for areas used as refuges for haematophagous bats, which can transmit diseases such as rabies, and these animals are often found in the large paleoburrows. Other hazards associated with the paleoburrows are fungi, venomous spiders, and leprosy, caused by bacteria carried by armadillos that use the burrows today (Frank et al., 2010b; Landell et al., 2010).

Other important information about the presence of these ichnofossils is gathered through the "Paleoburrows Project" (www.ufrgs.br/paleotocas). Besides the study of the burrows, the other main goal of this project is the public awareness about their existence, origin, and potential hazards. The information has been released not only through the homepage of the project, but also by radio and broadcasts and television news, which resulted in an increase of 5 to 28 known large burrows only in the first year of the project, mostly by communication from local people (Frank et al., 2010c).

The origin and purpose of Megaichnus

Although the identification of the organisms responsible for the ichnofossils found in the geological record can be very difficult and in most cases impossible (Bromley, 1996), one cannot avoid speculating about the organisms that could have produced the remarkable paleoburrows found in South America. No body fossils have been found inside the Brazilian paleoburrows so far, but the presence of *M. minor* in Cenozoic (Plio-Pleistocene) sedimentites indicates that they are the product of mammals. In Argentina, however, there are plenty of records of mammalian fossils inside paleoburrows, including adult individuals with cubs (Soibelzon et al., 2009; Safer et al., 2014), which suggests their use as nesting areas.

So far, *M. major* has been found only in older rocks, of Precambrian to Cretaceous age, but the claw impressions similar to those found in *M. minor* and the large size of the burrows also suggest mammals as the possible diggers. Today, there are no mammals living in South America that could have produced such large-sized structures, but during the Cenozoic, however, the

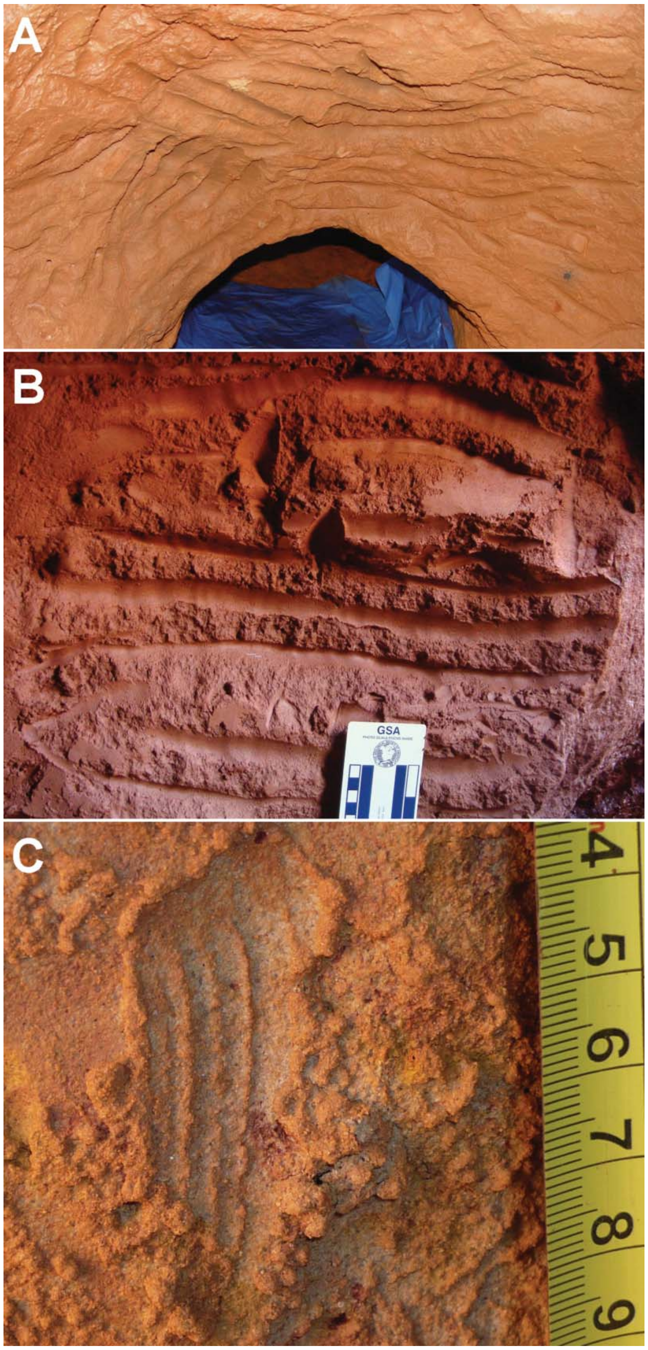

Figure 5. Digging marks scratches at the end of one *M. minor*; the opening at the bottom of the picture is the entrance to a smaller chamber (**A**). Large smooth scratches in clayey substrate, parallel to the direction of the burrow (**B**). Irregular grooves, possibly produced by a broken claw (the scale is in centimeters) (**C**).

continent was inhabited by several species of large mammals. The gigantism trend among South American mammals reached its acme in the Quaternary, most notably among Pleistocene xenarthrans (Fariña et al., 1998; 2013; Vizcaíno et al., 2012).

Among vertebrates, the fossorial mammals are highly specialized for the subterranean mode of life, but semi-fossorial ones also exhibit morphological modifications for digging. Most of these are concentrated in the fore limbs, which often exhibit large, laterally compressed claws, well-developed olecranon process of the ulna, and large muscle insertions (Nevo, 1979; Reichman and Smith, 1990; Bargo et al., 2000; Vizcaíno and Milne, 2002). Such modifications exclude several groups as the possible builders of the paleoburrows, leaving armadillos and ground sloths as the most probable candidates.

The most notorious burrowing mammals of South America are the armadillos, with 20 extant species that are fossorial or semi-fossorial (Vizcaíno and Milne, 2002). These animals dig their burrows preferentially in low elevations with well-drained soils, in higher grounds above the water table, close to a water source. As a result, it is common to find several burrows clustered in relatively small areas (Taber, 1945; Clark, 1951; Abba et al., 2005; Arteaga and Venticinque, 2008).

The largest extant species of armadillo, *Priodontes maximus*, dig burrows that reach up to 45 centimeters in width and 35 centimeters in height, with slope angle between 34° and 47°, in terrains with average slope of 25°, and this species uses the burrows for longer periods than smaller armadillos (Carter and Encarnação, 1983; Cerezoli and Fernandez-Duque, 2012). Although the general morphology, claw impressions, and osteoderm imprints found inside the paleoburrows are consistent with armadillos, the specimens of *M. minor* described so far are more than twice as large as those of *P. maximus*, which seem to indicate giant extinct armadillos as the probable builders of these burrows. In Argentina, burrows of similar dimensions have been attributed to pampatheriid cingulates such as the dasypodids *Propraopus* and *Eutatus* and *pampatheriids* such as *Pampatherium* sp. (Quintana., 1992; Dondas et al., 2009). The impressions found inside the paleoburrow at Cristal (Buchmann et al., 2009; see Fig. 2G) are similar to the osteoderms of the mobile belt of the carapace of *Propraopus*, an extinct dasypodid with widespread fossil records in Brazil (Pitana and Ribeiro, 2007). Some large, smooth, and semicylindrical claw impressions found inside some *M. minor* (Fig. 6A) seem to have been produced by blunt claws, which is consistent with the morphology of the hands of pampatheriid cingulates (Cartelle et al., 1989).

Few paleoburrows exhibit erosional features produced by water (Fig. 6B). Today, water flowing inside the paleoburrows is common and the interior is damp because of rainwater percolating through the substrate they were dug in. It seems unlikely that the animals could have stayed inside the burrows for long periods under such conditions; extant armadillos usually dig burrows in places above the water table to avoid flooding (Taber, 1945; Clark, 1951). Nevertheless, some paleoburrows were dug

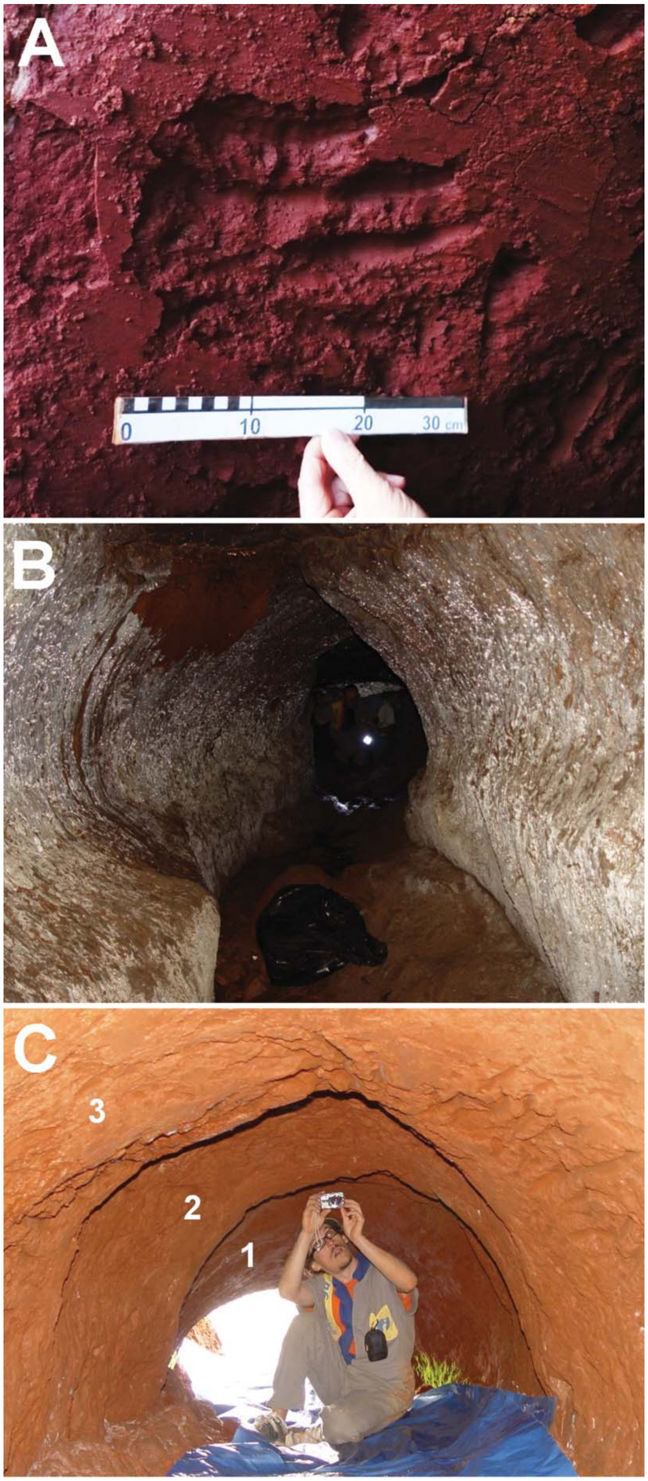

Figure 6. Set of claw impressions possibly produced by pampatheriids (**A**). *M. minor* with floor eroded by flowing water (**B**). View towards the entrance of one *M. minor*, showing three successive chambers, indicated by numbers (**C**).

in ascending angles of about 10° (Buchmann et al., 2009), probably to avoid variations of the phreactic level. By contrast, armadillos that inhabit dry, semiarid areas dig their burrows in descending angles (Abba et al., 2005).

Armadillos are very sensitive to low temperatures, and stay inside the burrows during the cooler parts of the day, and long periods of severe aridity seem to have a negative effect on their populations, in part because the soil becomes harder and more difficult to probe for food (Taber, 1945; Clark, 1951). Although the lack of absolute ages do not allow to make more precise correlations with paleoclimate conditions, the extinct animals that dug the paleoburrows could have used them as shelters for aestivation during epochs of seasonal droughts. The process of aestivation is a common part of the life cycle of organisms that inhabit seasonally dry areas, and is triggered when environmental conditions are dry and/or warm and there is a shortage of food and water supply (Secor and Linot, 2010). In the fossil record, evidences of aestivation are known for Devonian-Cretaceous lungfishes, Permian lysorophs, Permo-Triassic dicynodonts, and Miocene beavers (Meyer, 1999; Hembree, 2010). Although torpor (and hibernation) are not known among most of the extant xenarthrans, one armadillo, the pichi (*Zaedyus pichiy*), that inhabits Argentina and Chile to the south of 32°S under temperate conditions, enters periods of daily torpor and also hibernates (Superina and Boily, 2007).

The burrows of pichis described by those authors were progressively deeper towards higher latitudes, indicating that climatic conditions influence the patterns of burrowing. One advantage of burrows is that the subterranean environment is relatively stable in terms of moisture and temperature relative to the surface (Reichmann and Smith, 1990; White, 2005). If a similar relationship stands true for the paleoburrows of South America, then variations in length among these structures may reflect variations in climatic conditions, i.e., during colder periods the burrows must have been longer (i.e., deeper) to maintain suitable conditions than during warmer periods. Unfortunately, much paleoburrows are discovered during excavations that inadvertently destroy them. The paleoburrow in the outskirts of the town of Cristal, for example, originally would have measured about 60 meters, but only 32 meters survived excavation (Buchmann et al., 2009).

Observations of living armadillos show that these animals usually inhabit one burrow, but also can produce several other secondary ones; besides, they can quickly dig a new one to escape from predators if the soil is soft enough (Clark, 1951). The size and structure of the paleoburrows, however, suggest that they were semipermanent shelters and are, therefore, considered to represent the Domichnia ethological class (Buchmann et al., 2009). Several *M. minor* seem to consist of interconnected enlarged chambers separated by slightly narrower passages (Fig. 6C), which suggests that the chambers were

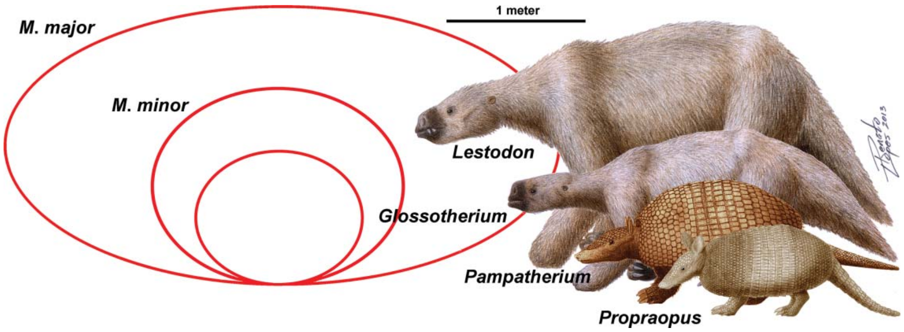

Figure 7. Size comparison between the diameters of *M. major* and *M. minor*, and reconstructions of some of their possible builders (all drawn to the same scale).

dug in successive stages (Frank et al., 2012). The interruptions are likely to represent periods of feeding, drinking, sleeping, breeding, and/or periods of torpor related to aestivation; therefore, the building of these structures took a long time, indicating that they were occupied for long periods. Another possible explanation is that the burrows were successively occupied by other members of the same species, which extended the burrows at different stages. An apparent evidence of reoccupation is seen in Figure 5A, which shows a chamber of smaller diameter than the original burrow dug at the end of the latter.

In several outcrops, three or more *M. minor* are found, forming large burrow systems that can reach estimated densities of one system per km^2. This indicates that the burrowers preferred some types of terrain just like extant armadillos. It is not clear, however, if each burrow was produced by one animal or if all were produced by the same individual as secondary burrows. While most of the burrows are not interconnected or branched, there are examples of several burrows leading to one single large chamber (Frank et al., 2012). The presence of bears, different types of sloths, cingulates, and marsupials in the paleoburrows of Argentina indicates that they were reoccupied after the individuals that dug them died or moved away (Vizcaíno et al., 2001; Dondas et al., 2009).

Although the krotovinas described by Bergqvist and Maciel (1994) were found in deposits regarded as of middle Pleistocene age (about 400 ka BP according to Villwock and Tomazelli, 1995), and the burrows in the coast of Argentina occur in Plio-Pleistocene deposits (Cenizo, 2011), most specimens of *M. minor* from Brazil are found in sediments regarded as of Pliocene age, that overlie Miocene marine deposits (Closs, 1970). Without any fossil evidence to validate or invalidate the proposed Pleistocene age for the paleoburrows found in southern Brazil, the possibility that those ichnofossils may be older cannot be ruled out. Body fossils of mammals older than Pleistocene age are virtually unknown from the areas where the Brazilian paleoburrows occur.

The larger *M. major* does not seem compatible with the work of any known species of armadillo (Fig. 7), but its large dimensions are compatible with the large body size of some species of ground sloths that became gigantic during the middle-late Pleistocene (Vizcaíno et al., 2012). In Argentina, large paleoburrows similar in size to *M. minor* have been attributed to the work of mylodontid ground sloths such as *Glossotherium* and *Scelidotherium* (Zárate et al., 1998; Vizcaíno et al., 2001; Isla and Dondas, 2001; Dondas et al., 2009). *Glossotherium* is well-known from several fossil localities in southern Brazil (Pitana, 2011). Although *Scelidotherium* has not been found in Brazil so far, there are two morphologically similar species, *Catonyx cuvieri*, and *Valgipes bucklandii*, known from several localities from northeastern to southern Brazil (Lopes and Pereira, 2010; Miño-Boilini, 2013; Pereira et al., 2013).

The *M. major* found in Brazil are larger than the paleoburrows found in Argentina and attributed to *Glossotherium* and *Scelidotherium*. Smooth surfaces are found along the walls and at the highest portion of the ceilings inside the megatunnels (see Fig. 3), located about 2 meters above the ground. These surfaces do not exhibit claw impressions, and their origin is attributed to the friction produced by constant rubbing of the animals against the walls and ceiling (Frank et al., 2013). The smoothing along the approx. 2 meter-high ceiling precludes armadillos, *Glossotherium*, and *Scelidotherium* as its producers, therefore suggesting that the *M. major* found in southern Brazil were produced by sloths larger than those two genera, which would include the mylodontids *Lestodon* and the megatheriids *Megatherium* and *Eremotherium*. These three genera would have possessed poor digging abilities, judging by the morphology of their arms (Bargo et al., 2000); besides, the hands of megatheriids would be unsuitable for digging because of the restricted range of movement (Tito and De Iuliis, 2003), and their arms would be better suited for speed rather than strenuous activities such as digging (Fariña and Blanco, 1996).

Lestodon is well-known from several localities in Argentina, Uruguay, and southern Brazil; its northernmost known occurrence is in the state of São Paulo (SE Brazil, ~23°S). However, the presence of megatunnels farther to the north, in the Brazilian intertropical region (BIR), may indicate that either *Lestodon* had a greater distribution range, or that the tunnels found in the BIR were produced by morphologically similar sloths such as *Ocnotherium giganteum* (Cartelle, 2012). Although *Lestodon* (and probably other similar species) is regarded as a poor digger based on limb proportions (Bargo et al., 2000; Vizcaíno et al., 2008), it seems plausible that these animals could have produced the megatunnels by removing large chunks of rock rather than digging in the hardground, taking advantage of preexistent cavities, fissures, and faulting in the rock by expanding them according to their needs.

Because of the high energetic costs of burrowing, the tunnels tend not to exceed much the width of the burrowers' bodies (White, 2005). The known specimens of *M. major* (and the larger *M. minor*) are usually wider than taller; this could have provided space for the horizontal rotation of large-bodied sloths. In ground sloths, the vertebral column had poor dorsal and lateral flexibility due to the presence of additional articular facets in terminal dorsal and lumbar vertebrae (Flower, 1882; Toledo, 1998; Gaudin, 1999); therefore, these animals would require additional horizontal space for maneuvering inside the burrows. Armadillos, on the other hand, retained higher ventral flexibility in their backbones (Gaudin and Biewener, 1992), most notably in the genus *Tolypeutes* that can curl themselves into a ball and, therefore, do not require spaces much larger than their body diameter to maneuver inside the burrows.

The cave-dwelling habit of ground sloths is well-known from several fossil localities (Emperaire and Laming-Emperaire, 1954; Toomey, 1994). The accumulations of sloth dung at certain parts of the caves indicate that those animals used them constantly for sheltering (Hansen, 1978; Thompson et al., 1980), and the large smooth elliptical surfaces found inside *M. major* (see Fig. 3F) probably result from long-term use of those spaces as resting places. In the Brazilian intertropical region, fossil remains of ground sloths have been discovered in several caves, but the association with fossils of other mammal groups leaves open the question of whether those sloths inhabited the caves or their carcasses were transported to the caves by flowing water prior to the decomposition of the soft tissues (Cartelle, 2012).

Ground sloths could have been opportunistic, inhabiting caves when these were available, but also could have dug their own burrows in areas without caves but with appropriate soil. The structure of the limb bones of giant sloths, with very low ratio of radius to wall thickness (i.e., marrow cavity greatly reduced or absent) indicates that their long bones were resistant to axial compressive forces, to which the limbs are subject when performing slow movements. Besides, the anterior portion of the body shows morphological modifications that allowed these animals to perform strong anteroposterior movements of the arms (Toledo, 1998) and, therefore, would be suitable for digging even in hardgrounds. The anatomical modifications for power rather than speed also suggest that giant sloths had low metabolic rates, which could have required periodical torpor under certain environmental conditions. The extant sloths have poor temperature regulation and their respiratory metabolism decreases following the reduction of air temperature (Irving et al., 1942; Gilmore et al., 2008). Direct comparisons between extinct ground sloths and living tree sloths are very limited due to the unique physiological adaptations of the latter to a sedentary lifestyle (Gilmore et al., 2008). Nevertheless, if ground sloths also had low metabolism and poor thermoregulation, as suggested by their skeletal anatomy (Toledo, 1998), then the lower temperatures during glacial epochs could have triggered a torpor/hibernation mechanism that forced those animals to search for caves or dig burrows for shelter against cold. Therefore, it is possible that the burrowing habit could have been a behavioral novelty developed to cope with the harsher (cold and dry) conditions related to the glacial epochs of the Quaternary.

It is remarkable that late middle to late Pleistocene fossils of the xenarthrans proposed as the producers of the paleoburrows are found in the coastal area of southern Brazil (Cartelle and Fonseca, 1981; Oliveira and Pereira, 2009; Lopes and Pereira, 2010; Pitana, 2011), which is a low relief area consisting of semiconsolidated to loose quartz sand deposits with small amounts of clay (Villwock and Tomazelli, 1995), too unstable for building those large structures. If the paleoburrows were indeed produced by the same species found as fossils, it would indicate that the animals changed their habits from area to area, possibly according to the topography and physical properties of the soils.

For decades, the large burrows found in southern Brazil have been regarded as structures produced by paleoindians (Padberg-Drenkpol, 1933; Prous, 1991). Although re-occupation of the burrows by other organisms such as bears (Soibelzon et al., 2009), marsupials, and small rodents (Cenizo et al., 2015), very few of the paleoburrows show evidences of occupation by humans; therefore, the most likely explanation is that humans occupied some of the burrows after the original producers were gone. Besides, a large number of people using simple stone tools would be required to modify the hard rock, which is inconsistent with the available archaeological evidence (Prous, 1991; Schmitz, 1991).

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