

Wolf spider burrows from a modern saline sandflat in central Argentina: morphology, taphonomy and clues for recognition of fossil examples

Fatima Mendoza Belmontes¹, Ricardo N. Melchor² and Luis N. Piacentini³

¹ UNLPam, FONCyT doctoral scholar, Santa Rosa, La Pampa, Argentina

² INCITAP- UNLPam, CONICET, Santa Rosa, La Pampa, Argentina

³ Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', CONICET, Buenos Aires, Argentina

ABSTRACT

Pavocosa sp. (Lycosidae) burrows found in an open sparsely vegetated area on the edge of the Gran Salitral saline lake, in central Argentina, are described. Burrows were studied by capturing the occupant and casting them with dental plaster. The hosting sediments and vegetation were also characterized. Inhabited *Pavocosa* sp. burrows display distinctive features as open, cylindrical, nearly vertical, silk lined shafts about 120 mm long, subcircular entrances, a gradual downward widening, and a particularly distinctive surface ornamentation in the form of sets of two linear parallel marks at a high angle to the burrow axis. Instead, casts of vacated *Pavocosa* sp. burrows showed some disturbances caused either by the reoccupation by another organism or by predation of the dweller. Two morphologies are related to reoccupation of burrows: those with a structure in form of an “umbrella” and another with smaller excavations at the bottom of the burrow. Predation by small mammals produces funnel-shaped burrows. Both active and abandoned *Pavocosa* sp. burrow casts are compared with existing ichnogenera and inorganic sedimentary structures, highlighting its distinction. It is argued that key features like the presence of a neck, a downward widening and the described surface texture will allow recognition of wolf spider burrows in the fossil record. However, the putative spider burrows described in the literature either lack the necessary preservational quality or do not show ornamentation similar to the modern wolf spider burrows. Fossil wolf spiders are recorded since the Paleogene (possibly Late Cretaceous), therefore Cenozoic continental rocks can contain wolf spider burrows awaiting recognition. In addition, the particular distribution of *Pavocosa* sp. in saline lakes may imply that this type of burrow is linked to saline environments.

Submitted 9 March 2018

Accepted 2 June 2018

Published 29 June 2018

Corresponding author
Fatima Mendoza Belmontes,
famebel@exactas.unlpam.edu.ar,
fa.belmontes@hotmail.com

Academic editor
Graciela Piñeiro

Additional Information and
Declarations can be found on
page 19

DOI 10.7717/peerj.5054

© Copyright
2018 Mendoza Belmontes et al.

Distributed under
Creative Commons CC-BY 4.0

OPEN ACCESS

Subjects Animal Behavior, Paleontology

Keywords Spider burrow, Wolf spiders, Neoichnology, Predation, Burrow reoccupation, Burrow modifications, Saline lake, Sandflat, Gran Salitral, *Pavocosa* sp.

INTRODUCTION

Araneae (recorded since the Devonian) is the most diverse order within arachnids with around 47,000 described extant species (*World Spider Catalog, 2017*). Due to striking adaptations such as silk production and a complex behavior (e.g., construction of

hunting webs), Araneae has become a highly successful group that is present in almost all environments (Murphy et al., 2006; Garrison et al., 2016). Burrow construction in spiders is considered a primary adaptation as a retreat from high temperatures and dry air conditions typical of arid environments (e.g., Cloudsley-Thompson, 1983; Punzo, 2000). Important functions as dwelling, nesting, mating, breeding, and foraging are also related to burrows (e.g., Marshall, 1996; Aisenberg, Viera & Costa, 2007; Hils & Hembree, 2015; Uchman, Vrenozi & Muceku, 2017).

In general, modern spider burrows consist of vertical or oblique, simple or branched forms, sometimes with a terminal chamber, in some cases silk lined, and structures atop such as trap doors or a turret can be found (e.g., Ratcliffe & Fagerstrom, 1980; Bryson, 1939; Hils & Hembree, 2015; Uchman, Vrenozi & Muceku, 2017). Among the burrowing spiders, those of the wolf spider (Lycosidae) tend to produce a nearly vertical burrow with or without a terminal chamber in flat terrain, whereas many trapdoor spider burrows (families Nemesiidae, Ctenizidae, Antrodiaetidae) are at an oblique angle and located on inclined surfaces (Uchman, Vrenozi & Muceku, 2017). This simple morphology can be comparable to the ichnogenenera *Skolithos* Hadelman, 1840 or *Cylindricum* Linck, 1949 (Smith et al., 2008; Hils & Hembree, 2015), the Y-shaped forms to *Psilonichnus* Fürsich, 1981 (Uchman, Vrenozi & Muceku, 2017), and those with a terminal chamber to *Macanopsis* Macsotay, 1967 (Hasiotis, 2002; Mikuš & Uchman, 2012; Hils & Hembree, 2015; Uchman, Vrenozi & Muceku, 2017).

Significant research related to burrow construction in wolf spiders has been made, but mainly focused on biological and ecological aspects (e.g., Hancock, 1899; Marshall, 1996; Aisenberg, Viera & Costa, 2007; Carrel, 2008; Suter, Stratton & Miller, 2011; De Simone, Aisenberg & Peretti, 2015; Foelix et al., 2016; Foelix et al., 2017; Framenau & Hudson, 2017). In addition to the pioneer contributions by Bryson (1939), Ahlbrandt, Andrews & Gwynne (1978), and Ratcliffe & Fagerstrom (1980), recent neoichnological studies have paid attention to the morphology of spider burrows (Hils & Hembree, 2015; Hembree, 2017; Uchman, Vrenozi & Muceku, 2017). These studies rely essentially on the overall morphology as a clue for recognition of spider burrows in general, including those of Lycosidae.

Similarly, probable spider burrows in the fossil record are scarce and their identification was always based on general morphology. The oldest record is controversial and based on poorly preserved simple vertical hollows from the Eocene of northern France, first considered worm burrows (Polychaeta) and later assigned to trapdoor spiders, in both cases named using biological names for a trace fossil (see details in Dunlop & Braddy, 2011). The same material was later incorrectly referred to as *Oichnus* (Bromley, 1981) by Dunlop & Braddy (2011), an ichnogenus reserved for bioerosion structures on calcareous skeletons (Wisshak et al., 2015). *Skolithos* isp. 1 from the Mio-Pliocene fluvial sediments of Brazil was compared with Lycosidae burrows due to its overall morphology (Fernandes, Borghi & Carvalho, 1992). Pleistocene and Holocene carbonate eolianites from the Bahamas and Yucatán contain *Skolithos linearis* (Haldeman, 1840) that were tentatively assigned to arachnids and/or insects (White & Curran, 1988; Curran & White, 1991; Curran & White,

2001). Finally, a burrow in Pleistocene clastic sediments of the Simpson Desert in Australia (Hasiotis, 2007) was attributed to wolf spiders.

The purposes of this work are (1) the identification of ichnological signatures of the burrows produced by *Pavocosa* sp. (Lycosidae) that may facilitate identification of wolf spider burrows in the fossil record, and (2) to discuss their environmental distribution.

Previous descriptions of modern wolf spider burrows

The first work unequivocally related to burrows of wolf spiders was “The castle –building spider” from Illinois (USA) published by Hancock (1899). This paper describes in detail the burrows produced by *Geolycosa domifex* (Hancock, 1899) (= *Lycosa domifex*), explaining important aspects such as materials and the methods of construction. *Geolycosa domifex* burrows are described as vertical shafts, unless obstacles cause some deviation (Fig. 1A). Ratcliffe & Fagerstrom (1980), in their widely cited work on traces found in Holocene floodplains, described spider burrows in general (assigned to Ctenizidae, Antrodiaetidae, Theraphosidae and Lycosidae) as simple or branched tunnels, sometimes with side chambers that are separated from the main tunnel by hinged doors (Fig. 1B). Burrows of *Geolycosa xera archboldi* (McCrone, 1963) and *G. hubbelli* (Wallace, 1942) from Florida, USA, are illustrated as vertical shafts showing a gradual transition between the shaft and the terminal chamber (Figs. 1C–1D) (Carrel, 2008). *Geolycosa missouriensis* (Banks, 1895) burrows from Mississippi, USA, are described as vertical forms, narrower at the surface and broader near the bottom, sometimes with a conspicuously enlarged chamber at the bottom (Fig. 1E) (Suter, Stratton & Miller, 2011). *Geolycosa* sp. burrows from India, exhibited a contrasting morphology in comparison with previous records of wolf spiders. These burrows were complex with a U-shaped form, two chambers (one located at the entrance and the other at the end of the burrow), and shallow hollows described as drainages or prey traps (Fig. 1F) (Chikhale, Santape & Bodkhe, 2013). Albin, Simó & Aisenberg (2015), reported different burrow morphologies produced by *Allocosa brasiliensis* (Petrunkevitch, 1910) from Uruguay, linking these variations in the morphology to the development stage and sex of the spider that produce them. These authors described burrows with a simple vertical shaft and a terminal chamber produced by adults, shallow capsules by virgin females, and Y-shaped burrows by male juveniles (Fig. 1G). Hils & Hembree (2015), through experimental neoichnological studies, recorded four burrow morphologies produced by *Hogna lenta* (Hentz, 1844) (Lycosidae): vertical shafts, vertical shafts with a terminal chamber, sub-vertical shafts, and Y-shaped burrows (Fig. 1H). *Geolycosa vultuosa* (Koch, 1838) burrows from Albania are characterized as vertical to subvertical, slightly curved or straight shafts with a basal chamber, showing either a gradual transition between the shaft and the basal chamber or a well delineated chamber (Vrenozi & Uchman, 2015). In a taxonomic revision of the halotolerant wolf spider genus *Tetrallycosa* Roewer, 1960 (Framenau & Hudson, 2017), the burrows of three species (*T. alteripa* McKay, 1976, *T. williamsi* Framenau & Hudson, 2017, and *T. eyrei* Hickman, 1944) were described. *Tetrallycosa* burrows are vertical shafts with an offset (a curvature) at mid-depth, which are later modified by backfilling the part above the curvature and creating a new burrow oriented in the opposite direction (Fig. 1I) (Framenau & Hudson,

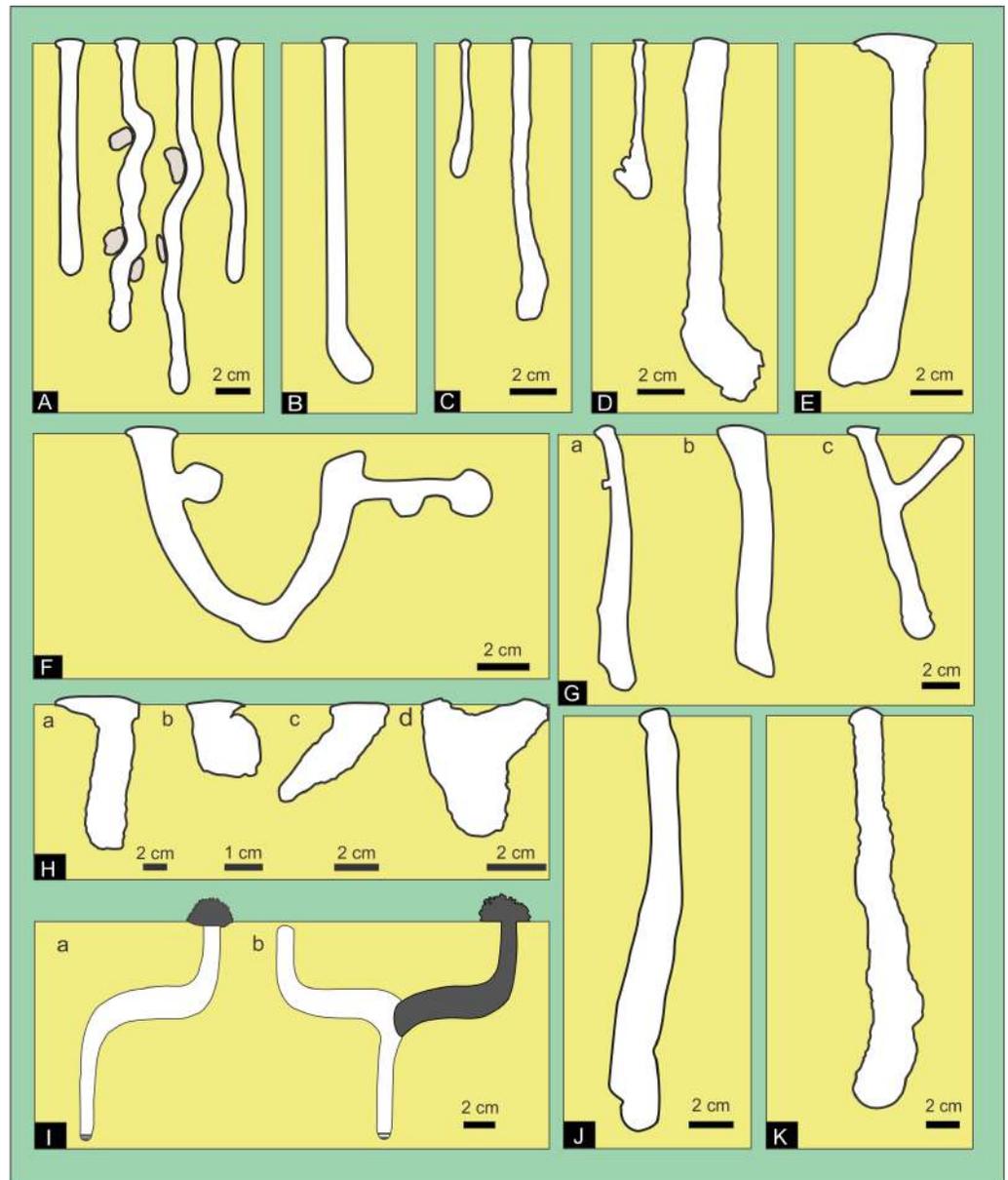


Figure 1 Compilation of previous descriptions of wolf spider burrows. (A) *Geolycosa domifex* (Hancock, 1899; fig. Pl II). (B) Generalized shape of spider burrows (Ctenizidae, Antrodiaetidae, Theraphosidae and Lycosidae. Ratcliffe & Fagerstrom (1980, fig. 1B). Not to scale. (C) *Geolycosa xera archboldi* and (D) *G. hubbelli* burrows by Carrel (2008), fig. 1). (E) *Geolycosa missouriensis* burrow (Suter, Stratton & Miller, 2011, fig. 1). (F) *Geolycosa* sp. (Chikhale, Santape & Bodkhe, 2013, fig. 7); (G) *Allocosa brasiliensis*: Produced by: a. Females, b. Males, and c. Juveniles (Albín, Simó & Aisenberg, 2015, fig. 1). (H) *Hogna lenta*: a. vertical shaft (fig. 12-2), b. vertical shaft with a terminal chamber (14-4), c. subvertical shaft (fig. 13-4), and d. Y-shaped burrow (fig. 15-1) (Hils & Hembree, 2015) (I) *Tetrallycosa* burrow showing (a) offset burrow and (b) with original burrow backfilled ((Framenau & Hudson, 2017), fig. 3). (J) *Allocosa senex* (Foelix et al., 2017; fig. 16); (K) *Trochosa hispanica* (Uchman, Vrenozzi & Muceku, 2017; fig. 6A). Image credit: Fatima Mendoza-Belmontes.

Full-size DOI: 10.7717/peerj.5054/fig-1

2017). *Allocosa senex* (Mello-Leitão, 1945) burrows from Uruguay are also simple vertical shafts with a downward widening (Fig. 1J) (Foelix et al., 2017). Finally, the burrows of *Trochosa hispanica* (Simon, 1870) from Albania (Fig. 1K) were described as simple, vertical shafts with a terminal chamber (Uchman, Vrenozzi & Muceku, 2017).

From the previous account, it is clear that the most common form in wolf-spider burrow are almost vertical cylinders with a rounded end that increase progressively in width downward, vertical shafts with a terminal chamber, and Y shaped burrows. Hasiotis & Bourke (2006) also suggested that horizontal burrows systems with a pustulose ornamentation are produced by spiders, however, the illustrated burrow system (Hasiotis, 2002, p. 114, figure B) is typical of surface burrows produced by Grillotalpidae (e.g., Chamberlain, 1975). Figure 1 also highlights that the burrows produced under experimental conditions (Fig. 1H) contrast markedly with the remaining ones excavated in natural conditions.

MATERIALS AND METHODS

We studied burrows produced by *Pavocosa* sp. found on the edge of sparsely vegetated sandflats of the Gran Salitral saline lake located in southwest La Pampa Province, Argentina (37°24'18.40"S, 67°12'13.57"W) (Figs. 2A–2B). This saline lake is placed in the subregion of alluvial plains of the Atuel-Salado rivers, characterized by a flat relief and sandy sediments, under a semiarid climate and with halophyte vegetation (Fig. 2C) (INTA, La Pampa, UNLPam, 1980). The Gran Salitral saline lake is the terminal part of an endorheic drainage system that occasionally receives waters from the Atuel- Salado rivers. Modern brines exhibit a concentration ranging from 213 to 252 g/l and the near-surface sediments of the saline lake attest for hydrological variations during the Holocene, including fluctuations in brine salinity and lake level (Melchor & Casadío, 2000). The mean monthly temperature ranges between 6.9 °C in July and 24.6 °C in January, and the mean annual precipitation is 340 mm, in both cases for the period 1961–1980 (INTA, La Pampa, UNLPam, 1980).

Observations were conducted during three field trips in October 2016 (early spring, mean monthly temperature for 2016: 15.4 °C, and the total monthly precipitation was 140 mm), December 2017 (late spring, mean monthly temperature for 2016: 23.1 °C, with no precipitations) and February 2017 (summer, mean monthly temperature for 2017: 24.7 °C, and precipitation was 22 mm). Rain data were obtained from *Policía de la Provincia de la Pampa* (2017) (<http://www.policia.lapampa.gov.ar/contenidos/ver/lluvias>), and temperature data from *Servicio Meteorológico Nacional* (2017) (<http://www.smn.gov.ar>), in both cases for the nearby 25 de Mayo and Puelén towns.

Sandflat sediments were logged in a shallow pit using standard sedimentological methods, and samples were taken for grain size and carbonate content analysis. Carbonate content of sediment samples was estimated using the Digital Calcimeter “NETTO” that indicates the total percent amount of calcium and magnesium carbonates. Grain size analyses of sediment samples were obtained by the laser particle size counter Malvern Mastersizer 2000[®] (Malvern, UK), prior to elimination of organic matter and carbonates, at the Laboratorio de Sedimentología of the Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa.

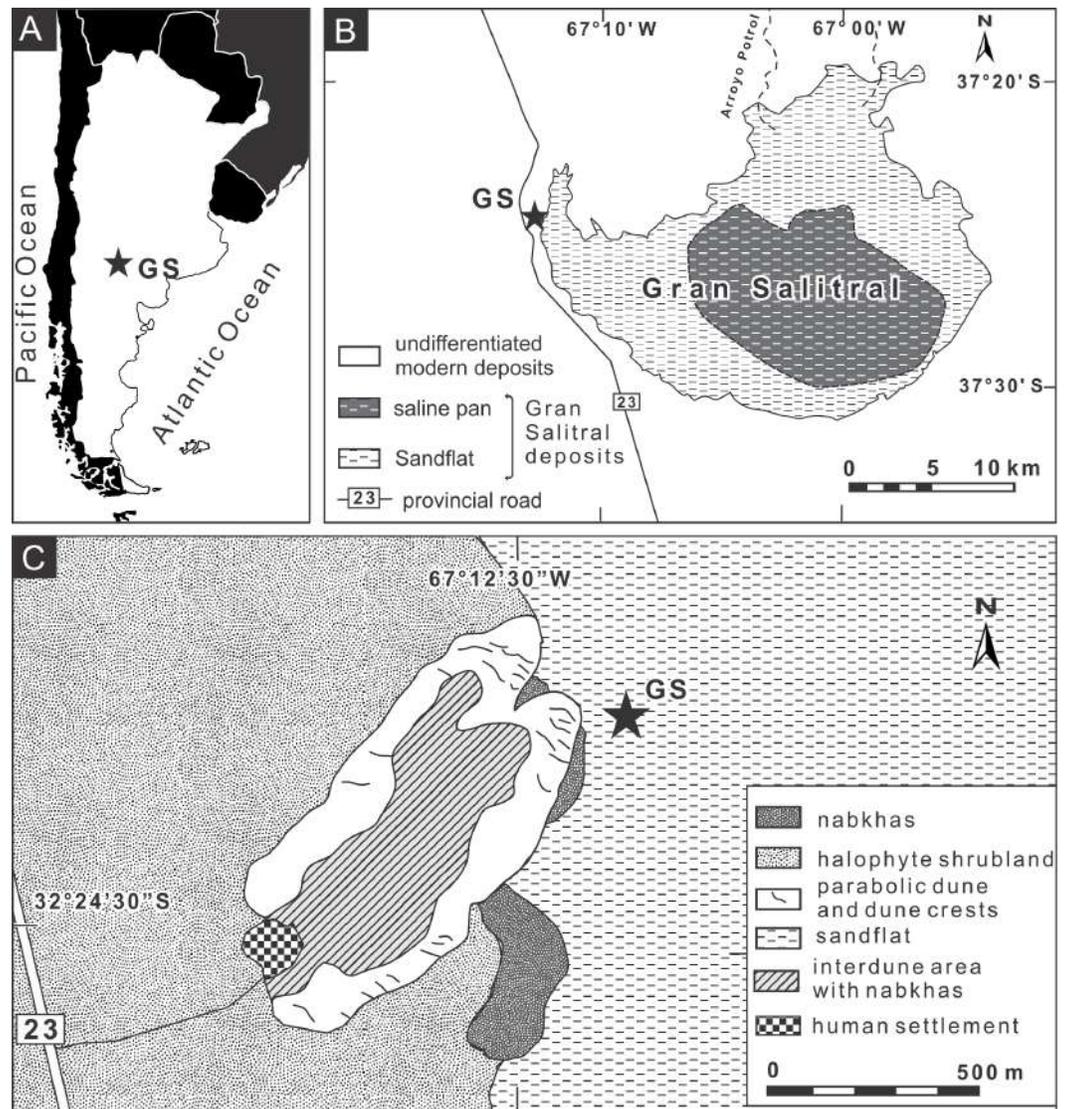


Figure 2 Location map of the study area. (A–B) Site of study in the “Gran Salitral” in La Pampa Province, Argentina; (C) Geomorphologic map of the Gran Salitral area and location of *Pavocosa* sp. burrows (GS). Modified from Melchor et al. (2012). Image credit: Ricardo Melchor.

Full-size [DOI: 10.7717/peerj.5054/fig-2](https://doi.org/10.7717/peerj.5054/fig-2)

A total of nine burrows were casted using dental plaster and three spiders found inside the burrows were collected for identification. Measurements on casts taken were the total length (L), neck length (NL), the minimum (mD) and maximum diameter (MD), and the angle of inclination (A). The measures on the sets of surface ridges preserved on the casts, were the length, the width, and the orientation in relation to the principal axis of the burrow (See Fig. 3). We also measured the entrance diameter (ED) from field photographs.

A 3D model of the burrows was generated based on photographs taken with a Lumix DMC-FZ70 camera (Panasonic, Osaka, Japan) and processed in the software Agisoft Photoscan Professional v.1.4.6. The resulting models were exported in OBJ files to Adobe

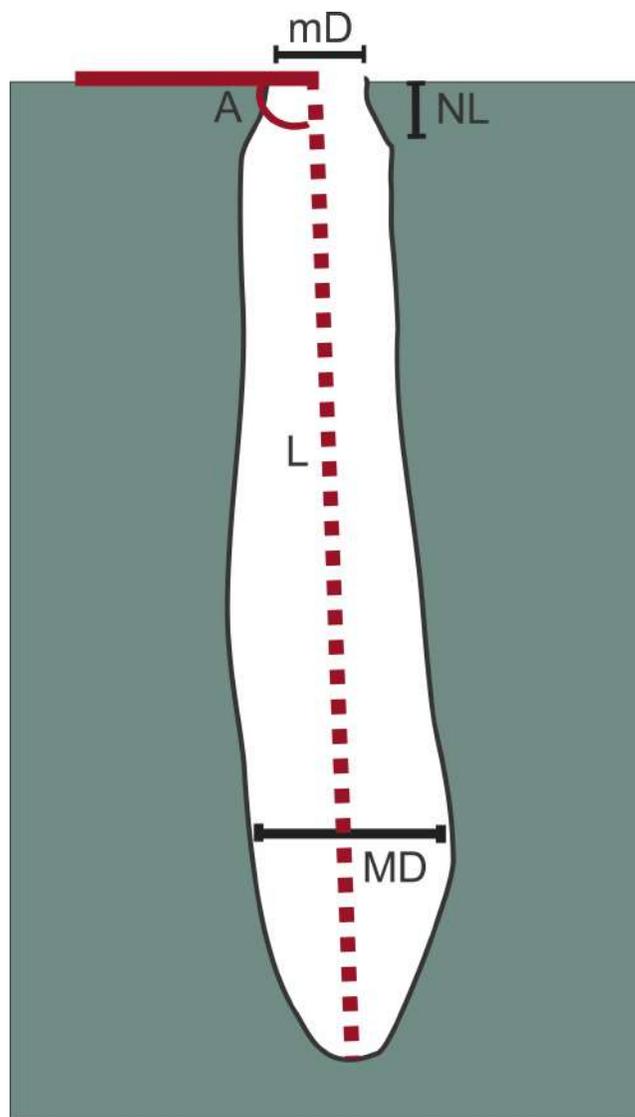


Figure 3 Measures taken on burrows. Length (L), neck length (NL), minimum (mD) and maximum diameter (MD), angle of inclination (A). Image credit: Fatima Mendoza-Belmontes.

Full-size  DOI: [10.7717/peerj.5054/fig-3](https://doi.org/10.7717/peerj.5054/fig-3)

Photoshop CC 2017 (TM) and converted to U3D files (a standard format for 3D), to compose a PDF file for easier visualization.

The casts and spider specimens collected were stored in the “Colección Paleontológica de la Facultad de Ciencias Exactas y Naturales” of the Universidad Nacional de La Pampa (acronym GHUNLPam), and one of the *Pavocosa* sp. specimens in the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (acronym MACN-Ar). The specimens were preserved in EtOH 80%; photographs of preserved specimens were taken with a Leica DFC 290 digital camera mounted on a Leica M165 C stereoscopic microscope (Wetzlar, Germany). Images taken in different focal planes were combined with Helicon Focus 4.62

Pro (<http://www.heliconsoft.com>). The width between the fangs of chelicera in collected spider specimens was measured for comparison with the marks preserved in the casts.

RESULTS

Occurrence of *Pavocosa* sp. burrows

In early spring (October 2016) abundant burrow entrances of similar size were observed in the sandflat surface. Spider burrows were found in a sparsely vegetated sandflat (0 to 10% of plant coverage), with the only presence of the small halophyte shrub *Heterostachys ritteriana* Ungern-Sternberg, 1876 (Fig. 4A). The burrows were simple vertical and silk lined forms (Fig. 4B), appearing either open and covered with a thin ring of silk (Fig. 4C) or partially closed with a plug of silk and sediment pellets (Fig. 4D). Surrounding the burrow (in a radius of up to 64 cm) abundant small spherical sediment pellets were observed (with a density of up to 290 pellets/m²) (Fig. 4F), and at this time no casts were made. In late spring (December 2016) burrow density was lower, and they were restricted to a small area on the edge of the saline lake with sparse vegetation at the boundary with the bare sandflat. A total of eight casts were obtained, five were inhabited burrows, while the remaining were abandoned. The inhabited burrows showed up to two sacs of eggs in the lowermost part (Fig. 4E). During the field trip conducted in summer (February 2017), very few burrows were observed, all open and partially filled with some sand, and they seemed to be uninhabited for a long time. At this time only one uninhabited burrow was casted.

Sandflat sediments

The pit dug in the saline sandflat where the burrows occur was 60 cm deep (Fig. 5A). The uppermost bed (# 1) is 13 cm thick and mainly composed of poorly-sorted pale yellowish brown (10 YR 6/2) silty sand containing 0.9% of carbonate (Figs. 5B, 5C). The lower 5 cm of bed 1 exhibits thin diffuse evaporite laminae and a mud lamina. This bed contained the studied *Pavocosa* sp. burrows. Bed 2 (7 cm thick) is poorly-sorted moderate yellowish brown (10 YR 5/4) silty sand, with massive structure and 0.8% of carbonate. Bed 3 (5 cm thick) is very poorly-sorted, dark yellowish brown (10 YR 4/2), silty sand with massive structure, containing 1.4% of carbonate and small (2 mm) gastropod shells comparable with *Heleobia* (Stimpson, 1865). The 27 cm thick bed 4 is very poorly-sorted, massive, moderate brown (5 YR 4/4), sandy silt containing 0.6% CO₃. The 6 cm thick lowermost bed (# 5), is mainly composed of fine-grained, pale yellowish brown (10 YR 6/2) sand with abundant carbonate cement that matches with the water table. Field work was conducted in rainy days, however, the water table was well below the bottom of *Pavocosa* sp. burrows (about 40–45 cm below the bottom of the burrows).

Producer of the burrows: *Pavocosa* sp.

Although the genus *Pavocosa* (Roewer, 1960) was never reviewed, and its composition was recently questioned (Toscano-Gadea & Costa, 2016), the inclusion of the material studied as an undescribed species of *Pavocosa* was possible through the comparison of the males and females of *Pavocosa gallopavo* (Mello-Leitão, 1941) (Figs. 6A, 6C), the type species of the genus. The male holotype of *P. gallopavo* (MLP-15065) and females from MACN

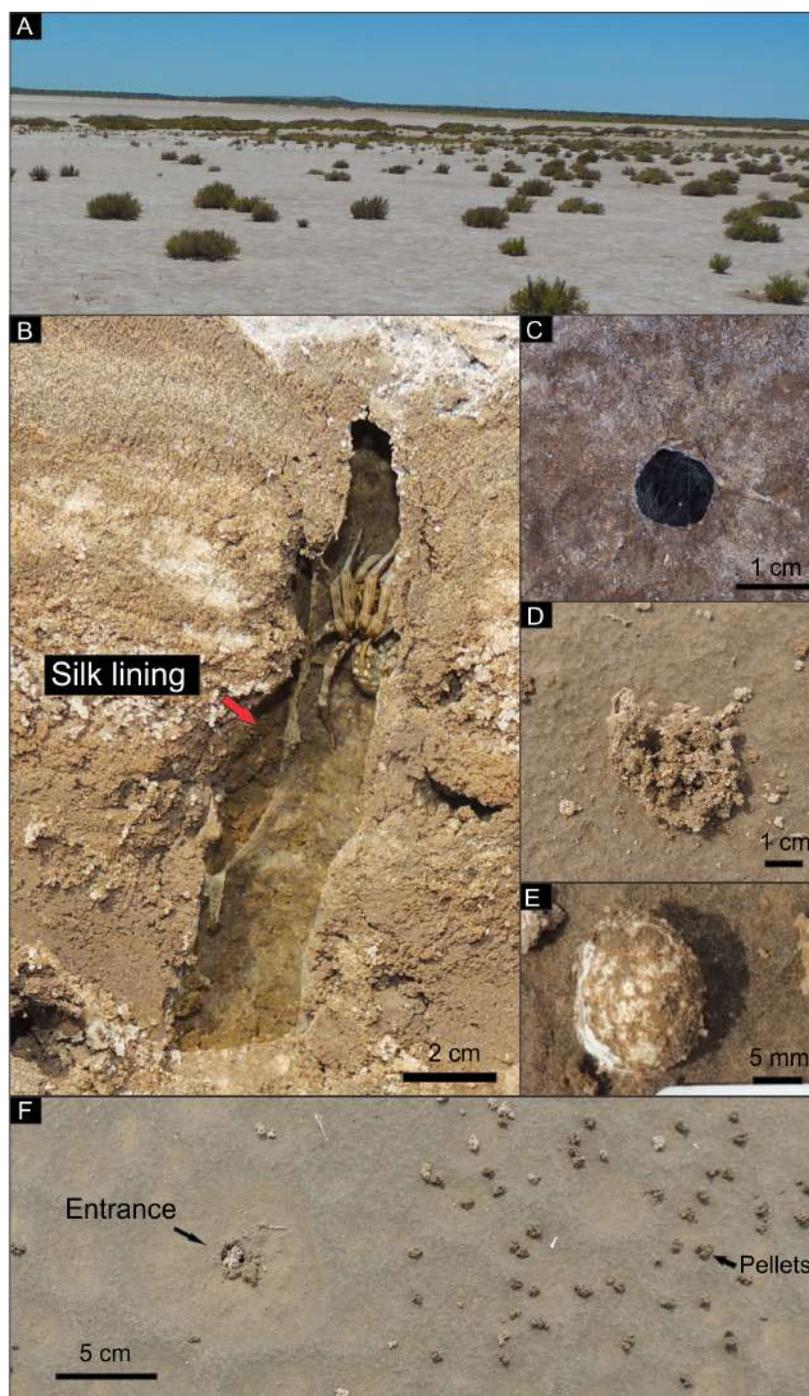


Figure 4 View of *Pavocosa* sp. burrows in the field and location of the study area. (A) Site of observation of burrows in an open area with sparse vegetation (*Heterostachys ritteriana*). (B) Longitudinal section of an inhabited burrow with silk lining. Scale divisions in centimeters. (C) Entrance covered with a thin layer of silk. (D) Burrow partially closed with a cap of silk and sediment pellets; (E) Sac of eggs found inside the burrow. Scale divisions in millimetres. (F) Partially plugged entrance and sediment pellets dispersed on the surface of the sandflat. Photo and image credit: Ricardo Melchor and Fatima Mendoza-Belmontes.

Full-size  DOI: [10.7717/peerj.5054/fig-4](https://doi.org/10.7717/peerj.5054/fig-4)

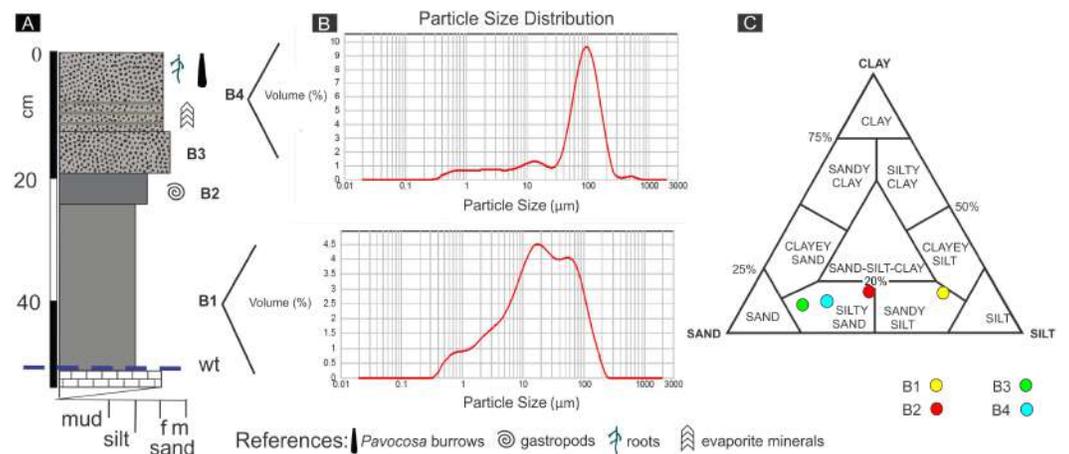


Figure 5 Sediments of the sandflat. (A) Detailed section of the sediments observed at the pit, wt, water table. (B) Representative grain size distribution of sediment samples. (C) Classification of sediment samples after Shepard (1954). Image credit: Ricardo Melchor and Fatima Mendoza-Belmontes.

Full-size [DOI: 10.7717/peerj.5054/fig-5](https://doi.org/10.7717/peerj.5054/fig-5)

collection were examined and they share with *Pavocosa* sp. (Figs. 6B, 6D) the presence of deep furrows on the atrium, parallel to the median septum of the female epigyne and the coloration pattern (Figs. 6A, 6B), characteristics probably diagnostic of the genus (L Piacentini, personal observations). The enlarged posterior eyes in *Pavocosa* sp. and the shape of the genitalia are clearly distinctive from *P. gallopavo*. The fangs of specimens captured inside the burrows ($n = 3$) are separated about 3.9–4.6 mm (Fig. 7H). The environmental distribution of *Pavocosa* is little known, although it seems to prefer bare patches in sandy grassland soils (L. Piacentini, pers. obs., 2014–2017).

Additional material of the described species from Córdoba (Salinas Grandes, 29°50′39″S, 64°40′16″W), Santiago del Estero and San Luis (Pampa de las Salinas; 32°12′19″S, 64°39′13″W) were recorded from MACN-Ar collection (23503, 23505 to 23513, 24096, and 38710), all from saline environments. The burrows of *Pavocosa* sp. from Córdoba (A Peretti, C Mattoni and M Izquierdo, pers. comm., 2008) and San Luis (M Ramírez, pers. comm., 2016) are very similar to those described in this work.

Pavocosa sp. burrows

The inhabited burrows ($n = 5$) (Figs. 7A–7E) are simple, vertical and circular shafts with an inclination of the main axis of 72°–88° (average: 80°), the length ranges from 115 to 130 mm (average: 120 mm). The diameter gradually increases from an upper narrow neck that is 12 to 15 mm wide (average 14 mm) and 5–8 mm long (average 6 mm), to a maximum diameter in the lower half ranging from 18 to 28 mm (average 23 mm). The outline of the entrance and cross-section of the maximum diameter of the burrows are subcircular. In average, the widest part of the burrow is 64% larger than the neck. The burrow cast surface of five burrow casts exhibits sparse ornamentation in the form sets of two linear parallel ridges (Figs. 7F–7G) about 2.8–4.4 mm long (average 3.4 mm, $n = 16$) and 2.2–4.5 mm wide (average: 3.4 mm, $n = 14$) aligned oblique to perpendicular (range: 42°–89°, average:



Figure 6 Comparison between type material of *Pavocosa gallopavo* and *Pavocosa* sp. (A) Female epigyne of *Pavocosa gallopavo* (MACN-Ar 13208), arrow pointing deep furrows on the atrium. (B) Female epigyne of *Pavocosa* sp. (MACN-Ar 38582), arrow pointing deep furrows on the atrium. (C) Dorsal view of *Pavocosa gallopavo* (MACN-Ar 13208). (D) Dorsal view of *Pavocosa* sp. (MACN-Ar 38582). Image credit: Luis Piacentini.

Full-size  DOI: 10.7717/peerj.5054/fig-6

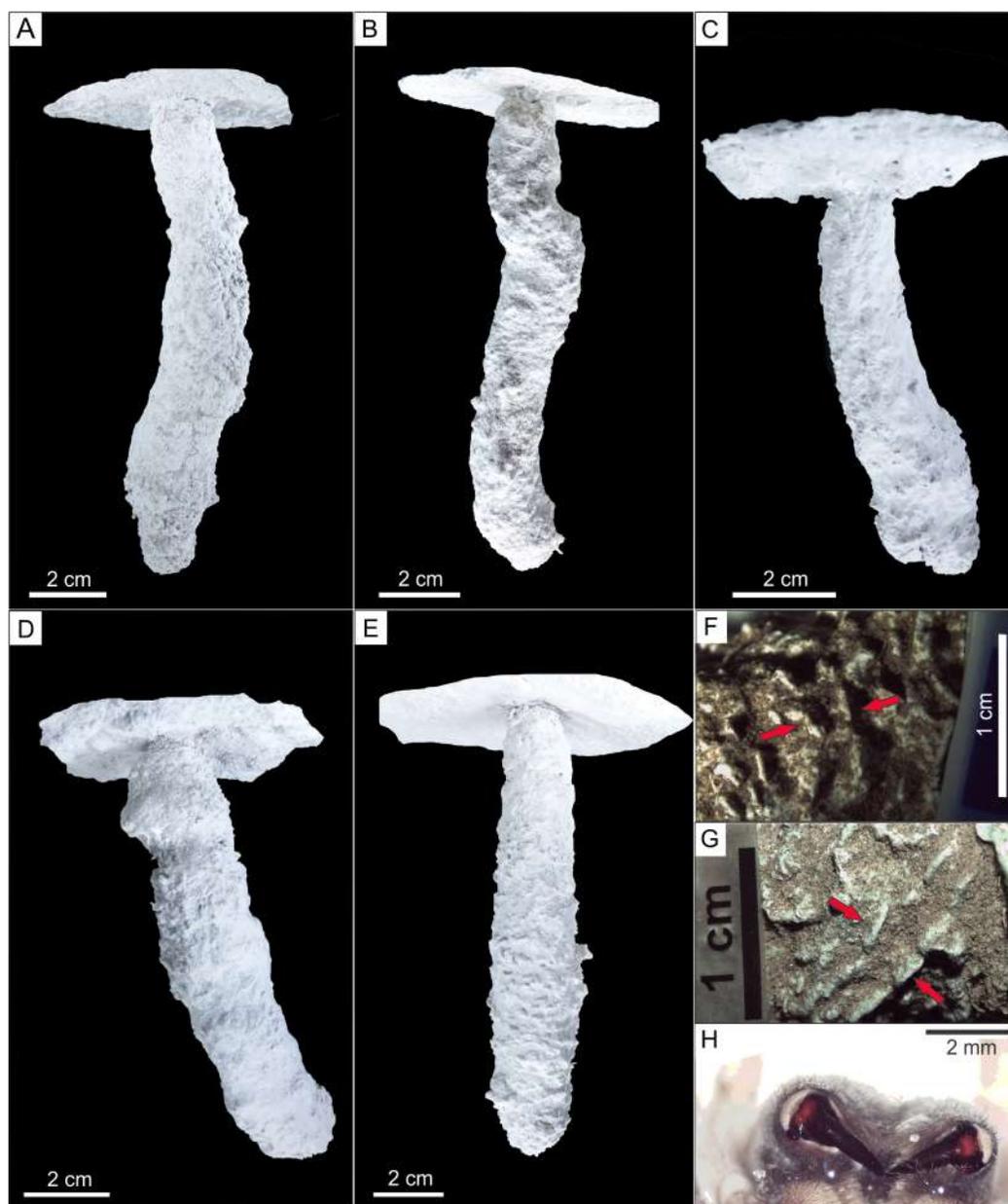


Figure 7 Plaster casts of *Pavocosa* sp. burrows and details of surface ornamentation.

(A) GHUNLPam-4771. Dweller captured *Pavocosa* sp. (GHUNLPam -4780). (B) GHUNLPam -4772 (C) GHUNLPam -4773. Dweller captured. *Pavocosa* sp and an egg sac found at the bottom (GHUNLPam -4770). (D) GHUNLPam -4774. Egg sac found at the bottom (E) GHUNLPam -4775. (F–G) Surface texture of burrow casts in the form of sets of two linear parallel ridges (arrows) (H) View of cheliceral fangs of *Pavocosa* sp. (specimen GHUNLPam -4780). Photo and image credit: Fatima Mendoza-Belmontes.

Full-size  DOI: [10.7717/peerj.5054/fig-7](https://doi.org/10.7717/peerj.5054/fig-7)

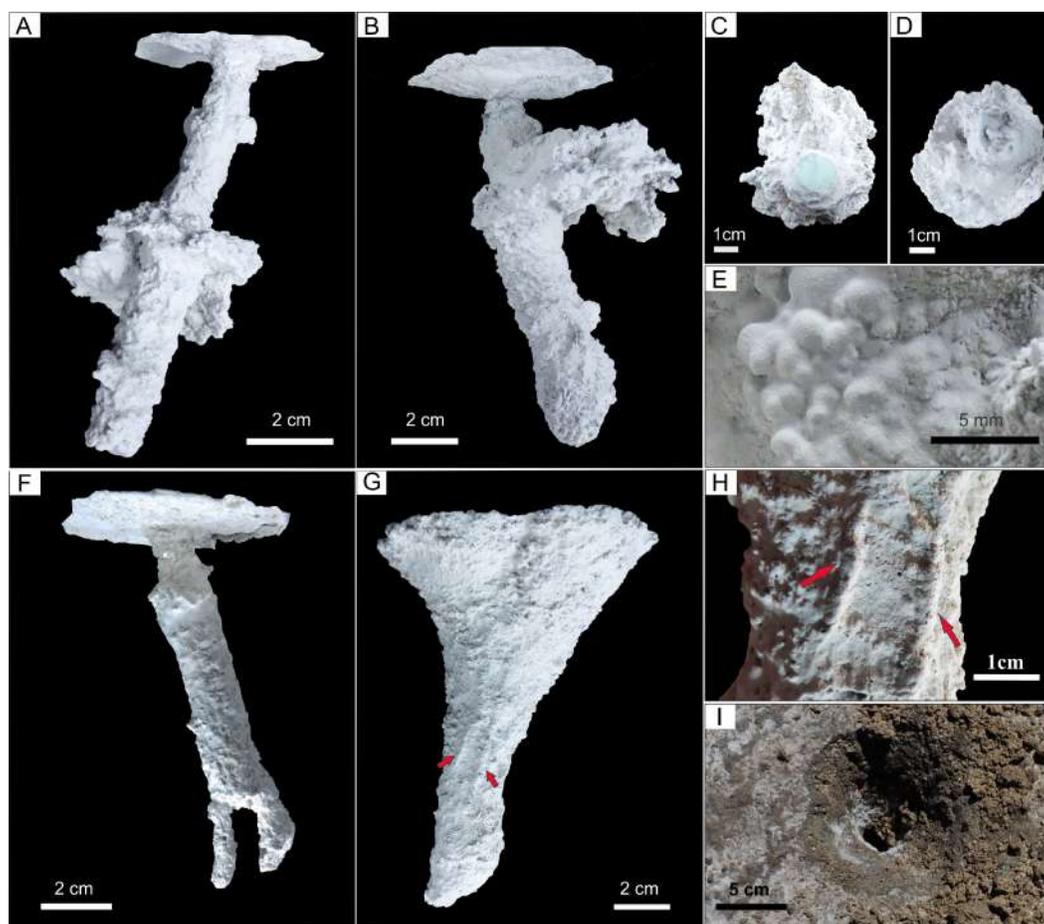


Figure 8 Plaster casts of modified *Pavocosa* sp. burrows. (A–B) Burrows with umbrella-like structures in the middle part, probably produced by reoccupation by ants (GHUNLPam-4776 and 4777). (C–D) Plan view showing umbrella shape from burrow casts GHUNLPam-4776 and 4777. (E) Detail of the knobby surface texture of the umbrella-like structure. (F) Cast showing two smaller burrows arising from the bottom of the wolf spider burrow (GHUNLPam -4778). (G) Funnel-shaped burrow cast as result of predation by a small armadillo (GHUNLPam -4779). Arrows point to set of two parallel ridges. (H) Detail of the set of two linear parallel ridges (arrows). (I) Field view of burrow modified by predation by armadillos (cast figured in G). Note brecciated fragments produced during excavation by the armadillo. Photo and image credit: Ricardo Melchor and Fatima Mendoza-Belmontes.

Full-size DOI: 10.7717/peerj.5054/fig-8

64°, $n = 14$) to the main axis of the burrow. The [Supplemental Information](#) contains interactive PDF files of each of the *Pavocosa* sp. burrow casts.

Modified *Pavocosa* sp. burrows

Uninhabited *Pavocosa* sp. burrows ($n = 4$) display some kind of modification in their overall form (Figs. 8A, 8B, 8F, 8G) (see [Supplemental Information](#) for interactive 3D models of each cast). All are composed of a highly inclined shaft (range: 78°–87°; average: 84.5°), with an upper constriction and an average maximum diameter ranging from 15 to 22 mm (average 19 mm). Three types of modifications were identified. (1) Subcylindrical burrows (108–116 mm long by 15–22 mm wide) with a subhorizontal expansion in the

middle part forming an "umbrella" (Figs. 8A–8B). The shaft boundary exhibit scarce ornamentation in the form of sets of two linear parallel ridges similar to those of the inhabited *Pavocosa* sp. burrows. The "umbrella" structure shows an oval to lobed shape in the plan view (Figs. 8C–8D), with a minimum diameter of 47–54 mm and a maximum diameter of 59–66 mm. The "umbrella" surface exhibits an ornamentation in form of small (1.4 mm in diameter) rounded knobs (Fig. 8E). The burrow bottom is rounded or partially filled with sediments. (2) Subcylindrical burrow about 116 mm long and 21 mm wide with two smaller burrows (8 mm of diameter) arising at the bottom of the larger burrow (Fig. 8F). (3) A third form is a 143 mm high and 101 mm wide funnel that ends in a 24 mm wide cylindrical shaft with an oblique bottom (Fig. 8G). The surface of the funnel exhibits sets of two parallel ridges (about 21 mm long and 9.2 mm wide) running oblique to the major axis (Fig. 8H).

DISCUSSION

Clues for identification of wolf-spider burrows in the fossil record

Pavocosa sp. produces open burrows with distinctive features as cylindrical, nearly vertical, silk lined shaft showing a gradual downward widening, a neck in the top and a rounded end, the entrance sometimes plugged with a cap of silk and sediment pellets, and a particularly distinctive surface ornamentation on the burrow margin. Most of these features are shared with other wolf spider burrows documented in the literature (Fig. 1) (Hancock, 1899; Ratcliffe & Fagerstrom, 1980; Carrel, 2008; Suter, Stratton & Miller, 2011; Albín, Simó & Aisenberg, 2015; Hils & Hembree, 2015; Vrenozi & Uchman, 2015; Foelix et al., 2017; Uchman, Vrenozi & Muceku, 2017). In particular, the presence of a neck and downward widening seem to be a common feature in wolf spider burrows found in natural settings. For *Pavocosa* sp. burrows this widening is about 64%, whereas it is 52% for *Trochosa hispanica* (Uchman, Vrenozi & Muceku, 2017).

Another highly distinctive feature of *Pavocosa* sp. burrows is their surface ornamentation in the form of two short parallel ridges oblique to perpendicular with the burrow axis that appear in most burrow casts (Figs. 7F–7G). Although this surface ornamentation was not recorded in some casts, probably due to the presence of the silk lining, all the burrow casts with delicate preservation of the surface texture exhibit these paired ridges. This feature was not identified in previous studies of wolf spider burrows and is potentially related to the burrowing technique used by *Pavocosa* sp. Spiders use two main mechanisms of excavation: (1) by pushing and compressing sediment using the pedipalps (Hils & Hembree, 2015) and (2) by scraping the soil with help of fangs from chelicerae (Stokes, 1884; Suter, Stratton & Miller, 2011; Hils & Hembree, 2015; Foelix et al., 2016). Although we have not observed *Pavocosa* sp. during digging, the sets of two linear parallel ridges observed on the surface of the better preserved burrow casts are similar in form and shape with the arrangement of fangs of collected specimens. The distance between fangs (3.9–4.6 mm) overlaps with the distance between ridges within a set (2.2–4.5 mm). Thus we propose that excavation in *Pavocosa* sp. involves the use of fangs, as in the type 2 excavation mechanism mentioned above.

Silk lined burrows are unique in spiders and essentially impart stability in soft substrates to prevent collapse (Ratcliffe & Fagerstrom, 1980; Foelix et al., 2017; Hils & Hembree, 2015). The presence of organic matter in the form of a silk lining increase the potential of preservation of wolf spider burrows (Uchman, Vrenozi & Muceku, 2017), well above those of all others arthropods that in habit the same environment.

Spider burrows may be modified by reoccupation or predation, as well as by environmental changes. Reoccupation of abandoned lycosid and mygalomorph burrows by lizards, centipedes, moths, wasps, beetles and ants have been documented (e.g., Fellows, Fenner & Bull, 2009). Ants have been also observed invading occupied wolf spider burrows with the purpose of prey piracy (Marshall, 1995). However, it has not been documented if the reoccupation results in any change in the morphology of the burrow. Common spider burrow disturbances caused by predation includes those produced by pompilid wasps that prey the spider and occasionally dig a tunnel perpendicular to the spider burrow (Gwynne, 1979; Costa, Pérez-Miles & Mignone, 2004), and excavation of the upper part of the burrows by armadillos (Suter, Stratton & Miller, 2011).

Most of *Pavocosa* sp. burrows are susceptible to go through a large amount of disturbances, including those caused by the reoccupation by another organism (Figs. 8A–8B and 8F) and predation of the dweller (Fig. 8G). Two kinds of burrow modifications observed during this study are tentatively related to reoccupation of burrows: those with an expansion in the middle part as a kind of “umbrella” (Figs. 8A–8B) and those with smaller excavations at the bottom of the burrow (Fig. 8F). Even if we cannot discard an inorganic origin (i.e., evaporite leaching) for the “umbrella” structure seen in some casts, it is highly reminiscent of oval to lobed ant nest chambers (Tschinkel, 2003). Although no ants were recorded when making the casts, they were commonly seen in the sandflat surface constructing nests within vertebrate footprints and abandoned burrows, presumably to avoid the hard efflorescent salt crust of the sandflat surface. The producer of the smaller burrows at the bottom of *Pavocosa* sp. burrow is unknown. Funnel shaped burrows (Fig. 8G) are similar to the probing marks related to predation by small mammals, and similar structures are described in the literature including Sarzetti & Genise (2011) from northern Argentina, Suter, Stratton & Miller (2011): Fig. 2), and Platt (2014), the latter two from Mississippi, USA. Small mammals found in this area with similar behaviours are the armadillos and skunks. The more likely producer is a small armadillo as suggested by the size of the funnel and most importantly by the presence of sets of two large ridges in the cast surface (compare Platt, 2014), interpreted as scratch marks (Fig. 8H).

Preservation of burrows in the margin of saline lakes, including those of wolf spiders, is affected by environmental factors like early cementation by evaporites and swelling of expansive clays during flooding (e.g., Scott, Renaut & Owen, 2010). Cementation by evaporites favors preservation, whereas wetting and drying cycles of swelling clays can destroy the burrows.

Both the original *Pavocosa* sp. burrows and those modified by reoccupation or predation can be compared with known ichnogenera. The simple vertical forms are grossly comparable with *Skolithos* (see Alpert, 1974; Schirf, 2000); some significant differences are the presence of a constriction or neck, the downward widening and the surface texture. These features

are potentially significant ichnotaxonomically (Schlirf & Uchman, 2005), although no proposed ichnotaxon match them. Slight variations in burrow diameter are allowed in *Skolithos* (Alpert, 1974; Schlirf, 2000), although the observed differences in *Pavocosa* sp. burrow diameter are significant and repetitive. There are a few examples of ornamented *Skolithos*, all of them from continental settings and tentatively assigned to insects or spiders, but they are not comparable to that observed in *Pavocosa* sp. burrows (Bromley & Asgaard, 1979; Schlirf, Uchman & Kummel, 2001; Netto, 2007). These ornamented *Skolithos* exhibit indistinct striations, except for the example described by Netto (2007) that display horizontal striae forming a circular ring. In consequence, there is no known fossil burrow with all the features described for the studied wolf spider burrows.

Modified *Pavocosa* sp. burrows with an “umbrella” if fossilized can be confused with *Daimoniobarax* (Smith et al., 2011); in particular, the umbrella is comparable with chambers and the vertical burrow of the spider is comparable with the shaft connecting the chambers in *Daimoniobarax*. A potential difference is the considerably larger diameter of the burrow connecting the chambers that averages 40% of chamber diameter in the modified *Pavocosa* sp. burrow and 10% in *Daimoniobarax* (Smith et al., 2011). The modified *Pavocosa* sp. burrow with smaller burrows arising from the bottom can be confused with a downward bifurcation as seen in rhizoliths (Klappa, 1980), a roughly similar rhizolith was figured by Melchor, Genise & Miquel (2002), Fig. 3B). Finally, funnel shaped burrows can be compared with several ichnogenera including *Monocraterion* (Torell, 1870); *Conostichnus* (Lesquereux, 1876); *Rosselia* (Dahmer, 1937); *Conichnus* (Männil, 1966); and *Cornulatichnus* (Carroll & Trewin, 1995) (see also Platt, 2014). A fundamental difference with these ichnogenera is the lack of large paired surface ridges, as seen in the predated *Pavocosa* sp. burrow. Further differences are: (1) *Monocraterion* shows smaller radial burrows arising from the central funnel (Jensen, 1997); (2) *Conostichnus* exhibits a duodecimal symmetry and transverse and longitudinal ridges and furrows (Pemberton, Frey & Bromley, 1988); (3) *Rosselia* is a bulbous structure with a concentrically laminated fill (Schlirf, Nara & Uchman, 2002); (4) *Conichnus* exhibits a rounded apex and common chevron-like fill (Pemberton, Frey & Bromley, 1988); and (5) *Cornulatichnus* has a well-developed lining (Carroll & Trewin, 1995). Conical sedimentary structures of inorganic origin can also resemble *Pavocosa* sp. burrows modified by predation. Buck & Goldring (2003) identified two main inorganic processes that produced conical sedimentary structures: collapse and dewatering. The former is distinguished by V or U shaped downwarping of lamination and the latter by deformed lamination and massive zone at the base of the cone (Buck & Goldring, 2003). These features allow distinction from the predated (i.e., funnel-shaped) *Pavocosa* sp. burrow, that would have a massive fill.

Burrowing spiders belong to Mesothelae and Opisthothelae (Coddington, 2005). Although Mesothelae dates back to the Late Carboniferous, the only known burrowing group (Liphistiidae) has no fossil record (Dunlop, Penney & Jekel, 2017). Within Opisthothelae, burrowing spiders are found in the Middle Triassic to Recent Mygalomorphae, which includes the tarantulas and trapdoor spiders, and in the Cretaceous to Recent Lycosoidea (included in Araneomorphae) that comprises the wolf spiders (Dunlop, 2010; Dunlop, Penney & Jekel, 2017). The oldest putative example of Lycosoidea

comes from Turonian beds of Botswana (*Selden, Anderson & Anderson, 2009*), which is close to the age of the superfamily suggested by phylogenetic studies (70 Ma, after *Garrison et al., 2016*), although most fossil records are from the Paleogene to Recent (*Dunlop, Penney & Jekel, 2017*). In addition, phylogenetic studies on web type suggest that the spider common ancestor likely foraged from a subterranean burrow, mostly sealed by a trapdoor (*Garrison et al., 2016*). In consequence, the record of spider burrows can be traced back at least to the Middle Triassic (and probably to the Late Carboniferous) and lycosid burrows to the Late Cretaceous or Cenozoic.

The use of fossils to calibrate molecular phylogenies is an uprising topic in spider biology (*Planas, Fernández-Montraveta & Ribera, 2013; Wood et al., 2013; Moradmand, Schönhofer & Jäger, 2014*). The absence of reliable fossil record, such as in Lycosidae (*Penney, 2001*), is an important impediment and the potential identification of wolf spider burrows on the fossil record, with the clues provided herein, can be a useful alternative source of data.

Environmental distribution of *Pavocosa* sp. burrows

The sediments of the sandflat containing the *Pavocosa* sp. burrows reflect the interaction between the nearby eolian and lacustrine settings. The two upper beds are essentially sandy deposits with a mixture of dominant fine sand and silt (samples S1 and S2; Fig. 5). The dominance of the coarse fraction (fine sand), poor sorting and the frequency distribution are comparable with those of modern interdune deposits (e.g., *Ahlbrandt, 1979*). Poorly defined laminae with evaporites in bed 1 are interpreted as the result of capillary rise and precipitation from brines. The sandy nature of the material where *Pavocosa* sp. excavated the burrows and their location 40 cm above the water table suggests preference for well-drained substrates. In contrast, the lowermost silty beds (samples S3 and S4; Fig. 5) are interpreted as dominantly lacustrine deposits, on the basis of the fine grain size and the presence of gastropods shells. *Heleobia* is a very common extant gastropod in South America recorded in estuarine and continental settings, including saline lakes (see review in *Cazzaniga, 2011*). In consequence, the logged section reflects the migration of the parabolic dune towards the northeast over the Gran Salitral lacustrine sediments (for a more detailed interpretation of dune deposits see *Melchor et al., 2012*). The presence of abundant *Pavocosa* sp. burrows in the well-drained sandflat deposits of the Gran Salitral and similar occurrences reported in the literature (e.g., *Hudson & Adams, 1996*) suggest that wolf spider colonization of saline lakes occur preferentially during dry periods of the lake.

Wolf spiders (Lycosidae) are one of the most successful spider families distributed in most of the habitats around the world (*World Spider Catalog, 2017*). Lycosids display a wide range of prey-capture strategies from web builders to burrow-dwellers or vagrant species. The use of burrows in wolf spiders can be in some cases obligatory, temporary in male juveniles, and as brood care in females (*Logunov, 2011*), or merely facultative in absence of objects as a rock that serves as a retreat. In general, burrows in wolf spiders are related to open areas of xerothermic habitats with sparse or no vegetation (e.g., sandy seashores, dune heaths, limestone areas and desert nanophanerophyte steppe) (*Logunov, 2011*). Some wolf spider species have specific habit preferences, as is the case of halotolerant species that inhabit the surface of salt lakes, most of them included in *Tetrallycosa* and other species

as *Lycosa salifodina* (McKay, 1976) from Australia (Hudson & Adams, 1996; Framenau & Leung, 2013), and two other Argentinian species including *Pavocosa* sp. In particular, *Pavocosa* sp. has been documented in saline lakes of Cordoba, Santiago del Estero, San Luis and La Pampa. In consequence, it is likely that the described burrows are typical of saline environments.

CONCLUSIONS

Observations on the burrows of the wolf spider *Pavocosa* sp. in the coast of a saline lake in central Argentina suggest that:

(1) *Pavocosa* sp. produces burrows with recognizable features as open, cylindrical, nearly vertical, silk lined shafts, showing a gradual downward widening, with a neck and the entrance and a rounded end, and a particularly distinctive surface ornamentation on the burrow margin. These features are considered typical of wolf spider burrows.

(2) Burrows are susceptible to go through a large amount of disturbances, including reoccupation by another organism or by predation of the dweller. Two types of modified *Pavocosa* sp. are related to reoccupation of burrows: those with a lateral expansion in the middle part as a kind of "umbrella" and another with smaller excavations at the bottom of the burrow. Predation by small mammals results in funnel-shaped burrows.

(3) *Pavocosa* sp. burrows have significant differences with those found in the *Skolithos* ichnospecies. Such features as the presence of a neck, a downward widening and the surface texture make them identifiable in the fossil record. The modified *Pavocosa* sp. burrows can be confused with *Daimoniobarax*, rhizoliths, and several conical sedimentary structures, although some key aspects allow their distinction.

(4) The features of *Pavocosa* sp. burrows that are considered diagnostic of wolf spider burrows are not identified to date in any published description of fossil examples.

(5) *Pavocosa* sp. colonized well drained sandy substrates of eolian origin on the margin of a saline lake. Known occurrences of this species suggest that it is a halotolerant wolf spider that inhabits the surface of saline lakes. Furthermore, as the wolf spiders avoid flooded substrates, it is suggested that the occurrence of wolf spider burrows in saline lakes is probably related to dry periods.

(6) The potential record of wolf spider burrows dates back to the Paleogene (possibly to the Late Cretaceous). The presence of silk lining increases its potential of preservation and the typical morphology and the surface texture render them recognizable in the fossil record.

ACKNOWLEDGEMENTS

Silverio Feola, Mauricio Fernández, Sofía Mulatero, Luis Torres and Angélica Tamame helped during field work. The landowner of Puesto La Porfía, Mr Tránsito Cerda, is thanked for permission to work on his property.

ADDITIONAL INFORMATION AND DECLARATIONS

Funding

This research was supported by projects PICT 2013-1129 (from Agencia Nacional de Investigaciones Científicas y Tecnológicas); PIP 2014-2016 11220130100005CO (from CONICET), and project PI09G (from Universidad Nacional de La Pampa) to Ricardo N Melchor. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Grant Disclosures

The following grant information was disclosed by the authors:

Agencia Nacional de Investigaciones Científicas y Tecnológicas: 2013-1129.

CONICET: PIP 2014-2016 11220130100005CO.

Universidad Nacional de La Pampa: PI09G.

Competing Interests

The authors declare there are no competing interests.

Author Contributions

- Fatima Mendoza Belmontes and Ricardo N. Melchor conceived and designed the experiments, performed the experiments, analyzed the data, contributed materials/analysis tools, prepared figures and/or tables, authored or reviewed drafts of the paper, approved the final draft.
- Luis N. Piacentini prepared figures and/or tables, authored or reviewed drafts of the paper, approved the final draft.

Data Availability

The following information was supplied regarding data availability:

The casts and spider specimens collected were stored in the “Colección Paleontológica de la Facultad de Ciencias Exactas y Naturales” of the Universidad Nacional de La Pampa (acronym GHUNLPam 4770 -4780), and one of the Pavocosa sp. specimens in the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (acronym MACN- Ar 38582). Additionally, the raw data are available as [Supplementary Data Files](#).

Supplemental Information

Supplemental information for this article can be found online at <http://dx.doi.org/10.7717/peerj.5054#supplemental-information>.

REFERENCES

- Ahlbrandt TS. 1979.** Textural parameters of eolian sands. A study of global sand seas. *Geological Survey Professional Paper* **1052**:21–52.
- Ahlbrandt TS, Andrews S, Gwynne DT. 1978.** Bioturbation in eolian deposits. *Journal of Sedimentary Petrology* **48**:839–848.

- Aisenberg A, Viera C, Costa FG. 2007.** Daring females, devoted males, and reversed sexual size dimorphism in the sand-dwelling spider *Allocosa brasiliensis* (Araneae, Lycosidae). *Behavioral Ecology and Sociobiology* **62**:29–35
[DOI 10.1007/s00265-007-0435-x](https://doi.org/10.1007/s00265-007-0435-x).
- Albín A, Simó M, Aisenberg A. 2015.** Characterisation of burrow architecture under natural conditions in the sand-dwelling wolf spider *Allocosa brasiliensis*. *Journal of Natural History* **50**:201–209 [DOI 10.1080/00222933.2015.1068395](https://doi.org/10.1080/00222933.2015.1068395).
- Alpert SP. 1974.** Systematic review of the genus *Skolithos*. *Journal of Paleontology* **48**(4):661–669.
- Banks N. 1895.** Some Missouri spiders. *Entomological News* **6**:204–207.
- Bromley RG. 1981.** Concepts in ichnology illustrated by small round holes in shells. *Acta Geológica Hispánica* **16**:55–64.
- Bromley RG, Asgaard U. 1979.** Triassic freshwater ichnocoenoses from Carlsberg Fjord. *Palaeogeography, Palaeoclimatology, Palaeoecology* **28**:39–80
[DOI 10.1016/0031-0182\(79\)90112-3](https://doi.org/10.1016/0031-0182(79)90112-3).
- Bryson HR. 1939.** Identification of soil insects by their burrow characteristics. *Transactions of the Kansas Academy of Science* **42**:245–253.
- Buck SG, Goldring R. 2003.** Conical sedimentary structures, trace fossils or not? Observations, experiments, and review. *Journal of Sedimentary Research* **73**:338–353
[DOI 10.1306/091602730338](https://doi.org/10.1306/091602730338).
- Carrel JE. 2008.** Differential survival of *Geolycosa xera archboldi* and *G. hubbelli* (Araneae, Lycosidae) after fire in Florida scrub. *Journal of Arachnology* **36**:595–599
[DOI 10.1636/T08-14.1](https://doi.org/10.1636/T08-14.1).
- Carroll S, Trewin NH. 1995.** *Cornulatichnus*: a new trace fossil from the Old Red Sandstone of Orkney. *Scottish Journal of Geology* **31**:37–41 [DOI 10.1144/sjg31010037](https://doi.org/10.1144/sjg31010037).
- Cazzaniga N. 2011.** El género *Heleobia* (Caenogastropoda: Cochliopidae) en América del Sur. In: *Amici Molluscarum special number: 11-48*. Viña del Mar: Sociedad Malacológica de Chile.
- Chamberlain CK. 1975.** Recent Lebensspuren in non-marine environments. In: *The study of trace fossils*. New York: Springer-Verlag, 431–438.
- Chikhale MP, Santape GB, Bodkhe AK. 2013.** Some observations on burrow architecture of burrowing spider *Geolycosa* Montgomery, 1904 (Araneae, Lycosidae) At Vairat, Melghat Tiger Reserve, Maharashtra, India. *Indian Journal of Arachnology* **2**:34–38.
- Cloudsley-Thompson JL. 1983.** Desert adaptation in spiders. *Journal of Arid Environments* **4**:307–317.
- Coddington JA. 2005.** Phylogeny and classification of spiders. In: Ubick D, Paquin P, Cushing PE, Roth V, eds. *Spiders of North America: an identification manual*. Columbia: American Arachnological Society, 18–24.
- Costa FG, Pérez-Miles F, Mignone A. 2004.** Pompilid wasp interactions with burrowing tarantulas: *Pepsis cupripennis* versus *Eupalaestrus weijenberghi* and *Acanthoscurria suina* (Araneae, Theraphosidae). *Studies on Neotropical Fauna and Environment* **39**(1):37–43 [DOI 10.1080/01650520412331270945](https://doi.org/10.1080/01650520412331270945).

- Curran HA, White B. 1991.** Trace fossils of shallow subtidal to dunal ichnofacies in Bahamian Quaternary carbonates. *Palaios* **6**:498–510 DOI [10.2307/3514987](https://doi.org/10.2307/3514987).
- Curran HA, White B. 2001.** Ichnology of Holocene carbonate eolianites of the Bahamas. *Society of Economic Paleontologists and Mineralogists, Special Publication* **71**:47–55.
- Dahmer G. 1937.** Lebensspuren aus dem Taunusquarzit und den Siegener Schichten (Unterdevon). *Preussischen Geologischen Landesanstalt zu Berlin Jahrbuch* **1936** **57**:523–539.
- De Simone GA, Aisenberg A, Peretti AV. 2015.** Female and juvenile burrow digging in *Allocosa brasiliensis*, a South American sand-dwelling wolf spider. *Arachnology* **16**(8):276–280 DOI [10.13156/arac.2015.16.8.276](https://doi.org/10.13156/arac.2015.16.8.276).
- Dunlop JA. 2010.** Geological history and phylogeny of Chelicerata. *Arthropod Structure and Development* **39**:124–142 DOI [10.1016/j.asd.2010.01.003](https://doi.org/10.1016/j.asd.2010.01.003).
- Dunlop JA, Braddy SJ. 2011.** *Cteniza bavincourti* and the nomenclature of arachnid-related trace fossils. *The Journal of Arachnology* **39**:250–257 DOI [10.1636/CHa10-70.1](https://doi.org/10.1636/CHa10-70.1).
- Dunlop JA, Penney D, Jekel D. 2017.** A summary list of fossil spiders and their relatives. In World Spider Catalog. Natural History Museum Bern. version 18.5. Available at <http://wsc.nmbe.ch> (accessed on 11 September 2017).
- Fellows HL, Fenner AL, Bull CM. 2009.** Spiders provide important resources for an endangered lizard. *Journal of Zoology* **279**(2):156–163 DOI [10.1111/j.1469-7998.2009.00600.x](https://doi.org/10.1111/j.1469-7998.2009.00600.x).
- Fernandes ACS, Borghi L, Carvalho IS. 1992.** Icnofósseis de Artropodes na Formação Resende (Bacia de Resende, RJ). *Academia Brasileira de Ciências* **64**:269–275.
- Foelix R, Rechenberg I, Erb B, Albin A, Aisenberg A. 2017.** Sand transport and burrow construction in sparassid and lycosid spiders. *Journal of Arachnology* **45**:255–264 DOI [10.1636/JoA-S-16-058.1](https://doi.org/10.1636/JoA-S-16-058.1).
- Foelix R, Rechenberg I, Erb B, Joel AC. 2016.** Über den Bau der Wohnröhren bei wüstenlebenden Spinnen. *Arachne* **21**:4–17.
- Framenau VW, Hudson P. 2017.** Taxonomy, systematics and biology of the Australian halotolerant wolf spider genus *Tetrallycosa* (Araneae: Lycosidae: Artoriinae). *European Journal of Taxonomy* **335**:1–72 DOI [10.5852/ejt.2017.335](https://doi.org/10.5852/ejt.2017.335).
- Framenau VW, Leung AE. 2013.** *Costacosa*, a new genus of wolf spider (Araneae, Lycosidae) from coastal north-west Western Australia. *Records of the Western Australian Museum* **83**:173–184 DOI [10.18195/issn.0313-122x.83.2013.173-184](https://doi.org/10.18195/issn.0313-122x.83.2013.173-184).
- Fürsich FT. 1981.** Invertebrate trace fossils from the upper Jurassic of Portugal. *Comunicacoes Servicos Geologicos de Portugal* **67**:153–168.
- Garrison NL, Rodriguez J, Agnarsson I, Coddington JA, Griswold CE, Hamilton CA, Hedin M, Kocot KM, Ledford JM, Bond JE. 2016.** Spider phylogenomics: untangling the Spider Tree of Life. *PeerJ* **4**:e1719 DOI [10.7717/peerj.1719](https://doi.org/10.7717/peerj.1719).
- Gwynne DT. 1979.** Nesting biology of the spider wasps (Hymenoptera: Pompilidae) which prey on burrowing wolf spiders (Araneae: Lycosidae, *Geolycosa*). *Journal of Natural History* **13**:681–692 DOI [10.1080/00222937900770511](https://doi.org/10.1080/00222937900770511).
- Haldeman SS. 1840.** Supplement to number one of ‘A monograph of the Limniades, and other freshwater bivalve shells of the apparently new animals in different classes,

- and names and characters of the subgenera in *Paludina* and *Anculosa*. J. Dobson, Philadelphia. 3 pp.
- Hancock JL. 1899.** The castle-building spider. *Entomological News* **10**:23–29.
- Hasiotis ST. 2002.** Continental trace fossils. In: *SEPM Society for Sedimentary geology, Short Course Notes 51*. Tulsa: Oklahoma, 134 p.
- Hasiotis ST. 2007.** Continental ichnology: fundamental processes and controls on trace fossil distribution. The continental realm. In: Miller III W, ed. *Trace fossils: concepts, problems, prospects*. Amsterdam: Elsevier Sci, 268–284
DOI [10.1016/B978-044452949-7/50142-X](https://doi.org/10.1016/B978-044452949-7/50142-X).
- Hasiotis ST, Bourke MC. 2006.** Continental trace fossils and museum exhibits: displaying burrows as organism behaviour frozen in time. *The Geological Curator* **8**(5):211–226.
- Hembree DI. 2017.** Neoichnology of tarantulas (Araneae: Theraphosidae): criteria for recognizing spider burrows in the fossil record. *Palaeontologia Electronica* **20.3.45A**:1–30 DOI [10.26879/780](https://doi.org/10.26879/780).
- Hentz NM. 1844.** Descriptions and figures of the araneides of the United States. *Boston Journal of Natural History* **4**:386–396 DOI [10.5962/bhl.part.16998](https://doi.org/10.5962/bhl.part.16998).
- Hickman VV. 1944.** Scorpions and spiders. The simpson desert expedition, 1939- scientific reports no. 1, biology. *Transactions of the Royal Society of South Australia* **68**:18–48.
- Hils JM, Hembree DI. 2015.** Neoichnology of the burrowing spiders *Gorgyrella inermis* (Mygalomorphae: Idiopidae) and *Hogna lenta* (Araneomorphae: Lycosidae). *Palaeontologia Electronica* **18.1.7A**:1–62 DOI [10.26879/500](https://doi.org/10.26879/500).
- Hudson P, Adams M. 1996.** Allozyme characterisation of the salt lake spiders (*Lycosa*: Lycosidae: Araneae) of southern Australia: Systematic and population genetic Implications. *Australian Journal of Zoology* **44**:535–567 DOI [10.1071/ZO9960535](https://doi.org/10.1071/ZO9960535).
- INTA, La Pampa, UNLPam. 1980.** Inventario integrado de los recursos naturales de la provincia de La Pampa. In: *Clima, Geomorfología, Suelo y vegetación*. Buenos Aires, 491 p.
- Jensen S. 1997.** Trace fossils from the Lower Cambrian Mickwitzia sandstone, south-central Sweden. *Fossils and Strata* **42**:111.
- Klappa CF. 1980.** Rhizoliths in terrestrial carbonates: classification, recognition, genesis and significance. *Sedimentology* **27**:613–629 DOI [10.1111/j.1365-3091.1980.tb01651.x](https://doi.org/10.1111/j.1365-3091.1980.tb01651.x).
- Koch CL. 1838.** . Die Arachniden. NÄijrnberg, Vierter Band, 109-144, Funfter Band. 1–124.
- Lesquereux L. 1876.** Species of fossil marine plants from the Carboniferous Measures. *Geological Survey of Indiana, Annual Report* **7**:134–145.
- Linck O. 1949.** Lebens-Spuren aus dem Schilfsandstein (Mittl Keuper, km 2) NW-Württembergs und ihre Bedeutung für die Bildungsgeschichte der Stufe. *Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg* **97–101**:1–100.
- Logunov DV. 2011.** Sexual size dimorphism in burrowing wolf spiders (Araneae: Lycosidae). *Proceedings of the Zoological Institute RAS* **315**:274–288.
- Macotay O. 1967.** Huellas problemáticas y su valor paleoecológico en Venezuela. *GEOS Revista Venezolana de Ciencias de la Tierra* **16**:1–87.

- Männil R. 1966.** O vertikalnykh norkakh zaryvaniya v ordovikskikh izvestnyakakh Pribaltiki. In: Hecker RF, ed. *Organizm i sreda v geologicheskome proshlom*. Akademiya Nauk SSSR. St. Petersburg: Paleontologicheskij Institut, 200–207.
- Marshall SD. 1995.** Natural history, activity patterns, and relocation rates of a burrowing wolf spider: *Geolycosa xera archboldi* (Araneae, Lycosidae). *Journal of Arachnology* 23:65–70.
- Marshall SD. 1996.** Evidence for territorial behavior in a burrowing wolf spider. *Ethology* 102:32–39.
- McCrone JD. 1963.** Taxonomic status and evolutionary history of the *Geolycosa pikei* complex in the Southeastern United States (Araneae, Lycosidae). *American Midland Naturalist* 70:47–73 DOI 10.2307/2422771.
- McKay RJ. 1976.** The wolf spiders of Australia (Araneae: Lycosidae): 8. Two new species inhabiting salt lakes of Western Australia. *Memoirs of the Queensland Museum* 17:417–423.
- Melchor RN, Casadío S. 2000.** Descripción Geológica de la Hoja 3766-III “La Reforma” (1:250.000), Provincia de la Pampa. *Boletín del Servicio Geológico Minero Argentino* 295:1–70.
- Melchor RN, Genise JF, Miquel SE. 2002.** Ichnology, sedimentology and paleontology of Eocene calcareous paleosols from a palustrine sequence, Argentina. *Palaios* 17:16–35 DOI 10.1669/0883-1351(2002)017<0016:ISAPOE>2.0.CO;2.
- Melchor RN, Genise JF, Umazano AM, Superina M. 2012.** Pink fairy armadillo meniscate burrows and ichnofabrics from Miocene and Holocene interdune deposits of Argentina: palaeoenvironmental and palaeoecological significance. *Palaeogeography, Palaeoclimatology, Palaeoecology* 350–352:149–170 DOI 10.1016/j.palaeo.2012.06.026.
- Mello-Leitão CF de. 1941.** Las arañas de la provincia de Santa Fe colectadas por el Profesor Birabén. *Revista del Museo de La Plata* 2:199–225.
- Mello-Leitão CF de. 1945.** Arañas de Misiones, Corrientes y Entre Ríos. *Revista del Museo de La Plata* 4:213–302.
- Mikuš P, Uchman A. 2012.** Beetle burrows with a terminal chamber: a contribution to the knowledge of the trace fossil *Macanopsis* in continental sediments. *Palaios* 28:403–413 DOI 10.2110/palo.2012.p12-129r.
- Moradmand M, Schönhofer A, Jäger P. 2014.** Molecular phylogeny of the spider family Sparassidae with focus on the genus *Eusparassus* and notes on the RTA-clade and ‘Laterigradae’. *Molecular Phylogenetics and Evolution* 74:48–65 DOI 10.1016/j.ympev.2014.01.021.
- Murphy NP, Framenau VW, Donnellan SC, Harvey MS, Park YC, Austin AD. 2006.** Phylogenetic reconstruction of the wolf spiders (Araneae: Lycosidae) using sequences from the 12S rRNA, 28S rRNA, and NADH1 genes: Implications for classification, biogeography, and the evolution of web building behavior. *Molecular Phylogenetics and Evolution* 38:583–602 DOI 10.1016/j.ympev.2005.09.004.
- Netto RG. 2007.** Skolithos-dominated piperock in non-marine environments: an example from the Triassic Caturrita Formation, southern Brazil. In: Bromley

- RG, Buatois LA, Mángano MG, Genise JF, Melchor RN, eds. *Sediment- organism interactions: a multifaceted ichnology*. 88. SEPM, Special Publication, 109–121.
- Pemberton SG, Frey RW, Bromley RG. 1988.** The ichnotaxonomy of *Conostichus* and other plug-shaped ichnofossils. *Canadian Journal of Earth Sciences* **25**:886–892.
- Penney D. 2001.** Advances in the taxonomy of spiders in Miocene amber from the Dominican Republic (Arthropoda: Araneae). *Palaeontology* **44**:987–1009 DOI [10.1111/1475-4983.00211](https://doi.org/10.1111/1475-4983.00211).
- Petrunkevitch A. 1910.** Some new or little known American Spiders. *Annals of the New York Academy of Science* **19**:205–224.
- Planas E, Fernández-Montraveta C, Ribera C. 2013.** Molecular systematics of the wolf spider genus *Lycosa* (Araneae: Lycosidae) in the Western Mediterranean Basin. *Molecular Phylogenetics and Evolution* **67**:414–428 DOI [10.1016/j.ympev.2013.02.006](https://doi.org/10.1016/j.ympev.2013.02.006).
- Platt BF. 2014.** The foraging pits of the nine-banded armadillo, *Dasypus novemcinctus* (Mammalia: Xenarthra: Dasypodidae), and implications for interpreting conical trace fossils. *Palaeontologia Electronica* **17.3.46A**:1–17.
- Policía de la Provincia de la Pampa. 2017.** Registros Pluviales para el Departamento Puelén. Available at <http://www.policia.lapampa.gov.ar/contenidos/ver/lluvias>.
- Punzo F. 2000.** *Desert arthropods: life history variations*. Berlin: Springer –Verlag, 230 p.
- Ratcliffe BC, Fagerstrom JA. 1980.** Invertebrate lebensspuren of Holocene floodplains: their morphology, origin and paleoecological significance. *Journal of Paleontology* **54**:614–630.
- Roewer CF. 1960.** Araneae Lycosaeformia II (Lycosidae) (Fortsetzung und Schluss). *Exploration du Parc National de l'Upemba, Mission G. F. de Witte* **55**:519–1040.
- Sarzetti LC, Genise JF. 2011.** Predation of soil-nesting *Centris muralis* (Insecta: Apidae) by armadillos (*Zaedyus pichiy*) (Mammalia: Cingulata) in La Rioja Province, Northwestern Argentina. *Journal of the Kansas Entomological Society* DOI [10.2317/JKES100412.1](https://doi.org/10.2317/JKES100412.1).
- Schlirf M. 2000.** Upper Jurassic trace fossils from the Boulonnais (northern France). *Geologica et Palaeontologica* **34**:145–213.
- Schlirf M, Nara M, Uchman A. 2002.** Invertebraten-Spurenfossilien aus dem aunosquarzit (Siegen, Unterdevon) von der 'Rossel' nahe Rudesheim. *Jahrbucher des Nassauischen Vereins für Naturkunde* **123**:43–63.
- Schlirf M, Uchman A. 2005.** Revision of the ichnogenus *Sabellarifex* Richter, 1921 and its relationship to *Skolithos* Haldeman, 1840 and *Polykladichnus* Fürsich, 1981. *Journal of Systematic Palaeontology* **3**:115–131 DOI [10.1017/S1477201905001550](https://doi.org/10.1017/S1477201905001550).
- Schlirf M, Uchman A, Kümmel M. 2001.** Upper Triassic (Keuper) non-marine trace fossils from the Haßberge area (Franconia, south-eastern Germany). *Paläontologische Zeitschrift* **75**:71–96 DOI [10.1007/BF03022599](https://doi.org/10.1007/BF03022599).
- Scott JJ, Renaut RW, Owen RB. 2010.** Taphonomic controls on animal tracks at saline, alkaline lake Bogoria, Kenya rift valley: impact of salt efflorescence and clay mineralogy. *Journal of Sedimentary Research* **80**:639–665 DOI [10.2110/jsr.2010.057](https://doi.org/10.2110/jsr.2010.057).
- Selden PA, Anderson HM, Anderson JM. 2009.** A review of the fossil record of spiders (Araneae) with special reference to Africa, and description of a new specimen from

- the Triassic Molteno Formation of South Africa. *African Invertebrates* **50**:105–116 DOI [10.5733/afin.050.0103](https://doi.org/10.5733/afin.050.0103).
- Servicio Meteorológico Nacional.** 2017. Meteorological station Neuquén Aero, Period 2016–2017. Available at <http://www.smn.gov.ar/>.
- Shepard FP.** 1954. Nomenclature based on sand-silt-clay ratios. *Journal of Sedimentary Research* **24**:151–158.
- Simon E.** 1870. Aranéides nouveaux ou peu connus du midi de l'Europe. *Mémoires de la Société Royale des Sciences de Liège* **2**(3):271–358.
- Smith JJ, Hasiotis ST, Kraus MJ, Woody DT.** 2008. Relationship of floodplain ichno-coenoses to paleopedology, paleohydrology, and paleoclimate in the Willwood Formation, Wyoming, during the Paleocene-Eocene Thermal Maximum. *Palaios* **23**:683–699 DOI [10.2110/palo.2007.p07-080r](https://doi.org/10.2110/palo.2007.p07-080r).
- Smith JJ, Platt BF, Ludvigson GA, Thomasson JR.** 2011. Ant-nest ichnofossils in honeycomb calcretes, Neogene Ogallala formation, high Plains region of western Kansas, U.S.A. *Palaeogeography, Palaeoecology, Palaeoclimatology* **308**:383–394 DOI [10.1016/j.palaeo.2011.05.046](https://doi.org/10.1016/j.palaeo.2011.05.046).
- Stimpson W.** 1865. Researches upon the Hydrobiinae and allied forms; chiefly made upon materials in the Museum of the Smithsonian Institution. *Smithsonian Miscellaneous Collections* **201**:1–59.
- Stokes AC.** 1884. A burrowing spider. *Science* **4**:114–116.
- Suter RB, Stratton GE, Miller PR.** 2011. Mechanics and energetics of excavation by burrowing wolf spiders, *Geolycosa* spp. *Journal of Insect Science* **11**:22 DOI [10.1673/031.011.0122](https://doi.org/10.1673/031.011.0122).
- Torell O.** 1870. Petrificata Suecana Formationis Cambricae. *Lunds Universitet Arsskrift* **6**:1–14.
- Toscano-Gadea CA, Costa FG.** 2016. Description of the sexual behavior of the Neotropical wolf spider *Pavocosa gallopavo* (Araneae: Lycosidae), with comments on sexual cannibalism. *Journal of Arachnology* **44**:412–416 DOI [10.1636/J15-75.1](https://doi.org/10.1636/J15-75.1).
- Tschinkel WR.** 2003. Subterranean ant nests: trace fossils past and future? *Palaeogeography, Palaeoecology, Palaeoclimatology* **192**:321–333 DOI [10.1016/S0031-0182\(02\)00690-9](https://doi.org/10.1016/S0031-0182(02)00690-9).
- Uchman A, Vrenozi B, Muceku B.** 2017. Spider burrows in ichnological context: a review of literature data and burrows of the wolf spider *Trochosa hispanica* Simon, 1870 from Albania B. *Rendiconti Lincei. Scienze Fisiche e Naturali* **29**:67–79 DOI [10.1007/s12210-017-0662-7](https://doi.org/10.1007/s12210-017-0662-7).
- Ungern-Sternberg F.** 1876. *Salicorniarum Synopsis. Atti del congresso internazionale botanico tenuto in Firenze nel mese di maggio 1874.* 1: 8, Firenze, 259–343.
- Vrenozi B, Uchman A.** 2015. Data on the burrows of the wolf spider *Geolycosa vultuosa* (CL Koch, 1838), the first record for Albania. In: *First International Congress on Continental Ichnology Abstracts*. 69–70.
- Wallace HK.** 1942. A revision of the burrowing spiders of the genus *Geolycosa* (Araneae, Lycosidae). *American Midland Naturalist* **27**:1–62 DOI [10.2307/2421024](https://doi.org/10.2307/2421024).

- White B, Curran HA. 1988.** Mesoscale physical sedimentary structures and trace fossils in Holocene carbonate eolianites from San Salvador Island, Bahamas. *Sedimentary Geology* **55**:163–184 DOI [10.1016/0037-0738\(88\)90095-4](https://doi.org/10.1016/0037-0738(88)90095-4).
- Wisshak M, Kroh A, Bertling M, Knaust D, Nielsen JK, Jagt JWM, Neumann C, Nielsen KSS. 2015.** In defence of an iconic ichnogenus –*Oichnus* Bromley, 1981. *Annales Societatis Geologorum Poloniae* **85**:445–451.
- Wood HM, Matzke NJ, Gillespie RG, Griswold CE. 2013.** Treating fossils as terminal taxa in divergence time estimation reveals ancient vicariance patterns in the palpi-manoid spiders. *Systematic Biology* **62**:264–284 DOI [10.1093/sysbio/sys092](https://doi.org/10.1093/sysbio/sys092).
- World Spider Catalog. 2017.** World Spider Catalog. Natural History Museum Bern. version 18.5. Available at <http://wsc.nmbe.ch> (accessed on 11 September 2017).