

Swimming in sand: evidence of skink lizard locomotion in Pleistocene aeolianites of Maio Island, Cabo Verde Archipelago

Alfred UCHMAN, Markes E. JOHNSON, Gonçalo C. ÁVILA, Ricardo S. RAMALHO, Esther MARTÍN-GONZÁLEZ, Gustavo M. MARTINS, Ana HIPÓLITO, Sandra MARQUES, Patrícia MADEIRA & Sérgio P. ÁVILA

DIRECTEURS DE LA PUBLICATION / PUBLICATION DIRECTORS :

Gilles Bloch, Président du Muséum national d'Histoire naturelle
Étienne Ghys, Secrétaire perpétuel de l'Académie des sciences

RÉDACTEUR EN CHEF / EDITOR-IN-CHIEF : Michel Laurin (CNRS)

ASSISTANTE DE RÉDACTION / ASSISTANT EDITOR : Adenise Lopes (Académie des sciences ; cr-palevol@academie-sciences.fr)

MISE EN PAGE / PAGE LAYOUT : Audrina Neveu (Muséum national d'Histoire naturelle ; audrina.neveu@mnhn.fr)

RÉVISIONS LINGUISTIQUES DES TEXTES ANGLAIS / ENGLISH LANGUAGE REVISIONS : Kevin Padian (University of California at Berkeley)

RÉDACTEURS ASSOCIÉS / ASSOCIATE EDITORS (*, took charge of the editorial process of the article/a pris en charge le suivi éditorial de l'article):

Micropaléontologie/*Micropalaeontology*

Lorenzo Consorti (Institute of Marine Sciences, Italian National Research Council, Trieste)

Paléobotanique/*Palaeobotany*

Cyrille Prestianni (Royal Belgian Institute of Natural Sciences, Brussels)

Anaïs Boura (Sorbonne Université, Paris)

Métazoaires/*Metazoa*

Annalisa Ferretti* (Università di Modena e Reggio Emilia, Modena)

Paléoichthyologie/*Palaeoichthyology*

Philippe Janvier (Muséum national d'Histoire naturelle, Académie des sciences, Paris)

Amniotes du Mésozoïque/*Mesozoic amniotes*

Hans-Dieter Sues (Smithsonian National Museum of Natural History, Washington)

Tortues/*Turtles*

Walter Joyce (Universität Freiburg, Switzerland)

Lépidosauromorphes/*Lepidosauromorphs*

Hussam Zaher (Universidade de São Paulo)

Oiseaux/*Birds*

Jingmai O'Connor (Field Museum, Chicago)

Paléomammalogie (mammifères de moyenne et grande taille)/*Palaeomammalogy (large and mid-sized mammals)*

Grégoire Métais (CNRS, Muséum national d'Histoire naturelle, Sorbonne Université, Paris)

Paléomammalogie (petits mammifères sauf Euarchontoglires)/*Palaeomammalogy (small mammals except for Euarchontoglires)*

Robert Asher (Cambridge University, Cambridge)

Paléomammalogie (Euarchontoglires)/*Palaeomammalogy (Euarchontoglires)*

K. Christopher Beard (University of Kansas, Lawrence)

Paléoanthropologie/*Palaeoanthropology*

Aurélien Mounier (CNRS/Muséum national d'Histoire naturelle, Paris)

Archéologie préhistorique (Paléolithique et Mésolithique)/*Prehistoric archaeology (Palaeolithic and Mesolithic)*

Nicolas Teyssandier (CNRS/Université de Toulouse, Toulouse)

Archéologie préhistorique (Néolithique et âge du bronze)/*Prehistoric archaeology (Neolithic and Bronze Age)*

Marc Vander Linden (Bournemouth University, Bournemouth)

RÉFÉRÉS / REVIEWERS : <https://sciencepress.mnhn.fr/fr/periodiques/comptes-rendus-palevol/referes-du-journal>

COUVERTURE / COVER :

Made from the Figures of the article.

Comptes Rendus Palevol est indexé dans / *Comptes Rendus Palevol is indexed by:*

- Cambridge Scientific Abstracts
- Current Contents® Physical
- Chemical, and Earth Sciences®
- ISI Alerting Services®
- Geoabstracts, Geobase, Georef, Inspec, Pascal
- Science Citation Index®, Science Citation Index Expanded®
- Scopus®.

Les articles ainsi que les nouveautés nomenclaturales publiés dans *Comptes Rendus Palevol* sont référencés par /
Articles and nomenclatural novelties published in Comptes Rendus Palevol are registered on:

- ZooBank® (<http://zoobank.org>)

Comptes Rendus Palevol est une revue en flux continu publiée par les Publications scientifiques du Muséum, Paris et l'Académie des sciences, Paris
Comptes Rendus Palevol is a fast track journal published by the Museum Science Press, Paris and the Académie des sciences, Paris

Les Publications scientifiques du Muséum publient aussi / *The Museum Science Press also publish:*

Adansonía, Geodiversitas, Zoosystema, Anthropolzoologica, European Journal of Taxonomy, Naturae, Cryptogamie sous-sections *Algologie, Bryologie, Mycologie*.

L'Académie des sciences publie aussi / *The Académie des sciences also publishes:*

Comptes Rendus Mathématique, Comptes Rendus Physique, Comptes Rendus Mécanique, Comptes Rendus Chimie, Comptes Rendus Géoscience, Comptes Rendus Biologies.

Diffusion – Publications scientifiques Muséum national d'Histoire naturelle

CP 41 – 57 rue Cuvier F-75231 Paris cedex 05 (France)

Tél. : 33 (0)1 40 79 48 05 / Fax : 33 (0)1 40 79 38 40

diff.pub@mnhn.fr / <https://sciencepress.mnhn.fr>

Académie des sciences, Institut de France, 23 quai de Conti, 75006 Paris.

© This article is licensed under the Creative Commons Attribution 4.0 International License (<https://creativecommons.org/licenses/by/4.0/>)

ISSN (imprimé / print) : 1631-0683/ ISSN (électronique / electronic) : 1777-571X

Swimming in sand: evidence of skink lizard locomotion in Pleistocene aeolianites of Maio Island, Cabo Verde Archipelago

Alfred UCHMAN

Jagiellonian University, Faculty of Geography and Geology,
Institute of Geological Sciences, Gronostajowa 3a,
30-387 Kraków (Poland)
alfred.uchman@uj.edu.pl (corresponding author)

Markes E. JOHNSON

Department of Geosciences, Williams College, Wachenheim Science Center,
18 Hoxsey Street, Williamstown, MA 01267 (United States)
mjohnson@williams.edu

Gonçalo C. ÁVILA

Faculdade de Ciências e Tecnologia (NOVA), Universidade Nova de Lisboa,
Campus de Caparica, 2829-516 Caparica (Portugal)
and Marine PalaeoBiogeography Lab, CIBIO-Açores, University of the Azores,
Rua da Mãe de Deus, 9501-801 Ponta Delgada, Açores (Portugal)
goncalorenteavila@gmail.com

Ricardo S. RAMALHO

School of Earth and Environmental Sciences, Cardiff University,
Park Place, Cardiff, CF10 3AT (United Kingdom)
and Instituto Dom Luiz, Faculdade de Ciências,
Universidade de Lisboa, C1 Campo Grande,
1746-016 Lisboa (Portugal)
ramalhor@cardiff.ac.uk

Esther MARTÍN-GONZÁLEZ

Museo de Ciencias Naturales de Tenerife,
Santa Cruz de Tenerife, 38003 Canary Islands (Spain)
mmartin@museosdetenerife.org

Gustavo M. MARTINS

Ana HIPÓLITO

Sandra MARQUES

Patrícia MADEIRA

Marine PalaeoBiogeography Lab, CIBIO-Açores,
University of the Azores, Rua da Mãe de Deus,
9501-801 Ponta Delgada, Açores (Portugal)
and CIBIO, Research Centre in Biodiversity and Genetic Resources,
InBio Associate Laboratory, Pólo dos Açores, BIOPOLIS Program in Genomics,
Biodiversity and Land Planning; University of the Azores, Rua da Mãe de Deus,
9500-321 Ponta Delgada (Portugal)
gustavo.om.martins@uac.pt
ana.hipolito80@gmail.com
sandracmarques10@hotmail.com
patricia.ga.madeira@uac.pt

Sérgio P. ÁVILA

Marine Palaeobiogeography Lab, CIBIO-Açores, University of the Azores,
Rua da Mãe de Deus, 9501-801 Ponta Delgada, Açores (Portugal)
and CIBIO, Research Centre in Biodiversity and Genetic Resources, InBio Associate
Laboratory, Pólo dos Açores, BIOPOLIS Program in Genomics, Biodiversity and Land Planning;
University of the Azores, Rua da Mãe de Deus, 9500-321 Ponta Delgada (Portugal)
and Departamento de Biologia, Faculdade de Ciências e Tecnologia da Universidade dos
Açores, 9501-801 Ponta Delgada, Açores (Portugal)
and UNESCO Chair – Land Within Sea: Biodiversity and Sustainability in Atlantic Islands,
Universidade dos Açores, Rua Mãe de Deus 13A, 9500-321 Ponta Delgada (Portugal)
sergio.pa.marques@uac.pt

Submitted on 23 January 2026 | Accepted on 8 April 2026 | Published on 12 October 2026

[urn:lsid:zoobank.org:pub:AB70EDE4-DBE9-4AF5-932C-8C774ED9F2BF](https://doi.org/10.5852/cr-palevol2026v25a20)

Uchman A., Johnson M. E., Ávila G. C., Ramalho R. S., Martín-González E., Martins G. M., Hipólito A., Marques S., Madeira P. & Ávila S. P. 2026. — Swimming in sand: evidence of skink lizard locomotion in Pleistocene aeolianites of Maio Island, Cabo Verde Archipelago. *Comptes Rendus Palevol* 25 (20): 375-389. <https://doi.org/10.5852/cr-palevol2026v25a20>

ABSTRACT

Pleistocene well-sorted bioclastic calcarenites form an aeolian sand-sheet in south-western Maio Island (Cabo Verde Archipelago) that contains distinctive, large, horizontal, sinuous trace fossils attributed to the ichnogenus *Cochlichnus* Hitchcock, 1858. Owing to its size and morphology, this trace is described herein as a new ichnospecies, *Cochlichnus grandis* isp. nov. Morphometric parameters, the sedimentary context, and comparison with modern analogues indicate that the trace was most likely produced by a sand-swimming skink lizard, which was partially buried at the surface or fully subsurface within the sand. To date, traces produced by skinks swimming through loose sand have not been documented in the fossil record even if they have been studied thanks to neoichnological experiments. Preservation of *C. grandis* isp. nov. was facilitated by relatively high substrate moisture in a coastal aeolian setting and by early carbonate cementation – conditions that are rarely met in dry siliciclastic dune systems. This narrow taphonomic window explains the exceptional rarity of fossil traces recording sand-swimming behaviour, despite the wide distribution and long evolutionary history of skinks in arid and semi-arid regions.

KEY WORDS

Ichnology,
ichnotaxonomy,
fossil behaviour,
aeolianites,
West Africa,
new ichnospecies.

RÉSUMÉ

Nager dans le sable : grands terriers sinueux attribués à des scinques dans les éolianites pléistocènes de l'île de Maio, archipel du Cap-Vert.

Les calcarénites bioclastiques bien triées du Pléistocène contribuent à une nappe sableuse éolienne dans le sud-ouest de l'île de Maio (archipel du Cap-Vert), laquelle renferme une trace fossile distinctive, de grande taille, horizontale et sinueuse, attribuée à l'ichnogenre *Cochlichnus* Hitchcock, 1858. En raison de sa taille et de sa morphologie, cette trace est décrite ici comme une nouvelle ichnoespèce, *Cochlichnus grandis* isp. nov. Les paramètres morphométriques, le contexte sédimentaire et la comparaison avec des analogues actuels indiquent que la trace a très probablement été produite par un scinque (Squamata) se déplaçant en nageant dans le sable, qui était partiellement enterré à la surface ou complètement dans le sous-sol. À ce jour, les traces produites par des scinques nageant à l'intérieur de sables meubles n'ont pas été documentées dans le registre fossile, bien qu'elles aient été étudiées grâce à des expériences néoichnologiques. La préservation de *C. grandis* isp. nov. a été favorisée par une humidité relativement élevée du substrat dans un environnement éolien côtier, ainsi que par une cimentation carbonatée précoce – des conditions rarement réunies dans les systèmes dunaires silicoclastiques secs. Cette fenêtre taphonomique étroite explique l'extrême rareté des traces fossiles enregistrant un comportement de nage dans le sable, malgré la large distribution et la longue histoire évolutive des scinques dans les régions arides et semi-arides.

MOTS CLÉS

Ichnologie,
ichnotaxonomie,
comportement fossile,
éolianites,
Afrique de l'Ouest,
nouvelle ichnoespèce.

INTRODUCTION

Some lizards, snakes, and small mammals are capable of swimming within loose sand (e.g., Seymour *et al.* 1998; Hembree & Hasiotis 2007; Maladen *et al.* 2009). In recent years, the mechanics of this mode of locomotion have become better understood and visualised using advanced experimental and imaging techniques (Baumgartner *et al.* 2008; Maladen *et al.* 2009; Sharpe *et al.* 2013, 2015; Astley *et al.* 2020). Among vertebrates, the most efficient and best-known sand swimmers are skinks (Reptilia: Squamata: Scincidae), one of the most diverse squamate families, comprising almost 1 800 species (Uetz *et al.* 2025). Skinks are distributed worldwide, with the most significant expression in arid to semi-arid regions of warm climates (Pasteur 1981; Shenbrot & Krasnov 1997; Vitt & Caldwell 2013; Hedges 2014; Chapple *et al.* 2023). Morphologically, they are characterised by elongate, cylindrical bodies, generally small body size, cone-shaped heads, tapered tails, and reduced or completely lost limbs – features that facilitate fossorial and sand-swimming locomotion (Vitt & Caldwell 2013; Chapple *et al.* 2023).

Despite their ability to disturb sand fabrics during burrowing and swimming, the biogenic structures produced by fossorial skinks are poorly documented in the ichnological literature. Experimental neoichnological studies by Catena & Hembree (2014a, b) described a variety of trails, burrows, and lamina-disrupting structures produced by the skink species *Chalcides ocellatus* (Forskål, 1775) and *Eutropis multifasciata* (Kuhl, 1820) (synonym of *Mabuya multifasciata*). These studies demonstrated that the morphology and preservation potential of skink traces strongly depend on substrate texture and moisture content. In addition, photographs and short, popular videos showing skinks plunging into and moving through loose sand are widely available online. However, traces produced specifically by swimming in sand have not yet been recognised in the fossil record.

In this paper, we describe a relatively large, horizontal, sinuous trace fossil found on Pleistocene consolidated aeolianites exposed in the south-western part of Maio Island (Cabo Verde Archipelago), which we interpret as produced by a sand-swimming skink lizard. To our knowledge, this represents the first fossil example of a trace attributable to this mode of locomotion. Owing to its distinctive size and morphology, the trace is described herein as a new ichnospecies of *Cochlichnus* Hitchcock, 1858. The sedimentological context, morphometric analysis, and comparison with modern analogues provide strong support for this interpretation and offer new insights into the behavioural repertoire of fossorial reptiles and the taphonomic conditions required for preserving sand-swimming traces.

GEOLOGICAL SETTING AND DEPOSITIONAL PALAEOENVIRONMENT

The Cabo Verde Archipelago is a cluster of volcanic islands located 600–900 km off the western coast of continental Africa, between 15° and 17°N in latitude (Fig. 1A, B).

With a complex geological history, the Cabo Verde Islands started to emerge during the Middle to Late Miocene, with the south-westernmost islands of Fogo and Brava emerging later, during the Pleistocene (Ramalho 2011, and references therein). Within this context, the eastern islands of Sal, Maio, and Boa Vista correspond to the oldest volcanic edifices, exhibiting a razed morphology with central residual reliefs surrounded by broad coastal platforms that decrease in elevation towards the coastline. These low-lying coastal platforms correspond to raised marine terraces formed by the combined action of marine erosion during glacio-eustatic oscillations and a slow uplift trend over the last 2–3 Ma, resulting in the formation of a preserved regressive system tract with raised beaches and fossil sand dunes extending several kilometres inland (Zazo *et al.* 2007, 2010; Ramalho *et al.* 2010a, b, c; Ramalho 2011). At Maio Island, these deposits are remarkably well preserved, with a set of Pleistocene raised beaches and their associated aeolian dune systems recognized at elevations of 2 to 6 m, 8 to 12 m, 15 to 20 m, 25 to 40 m, 55 to 65 m, 65 to 75 m, and 80 to 100 m above present sea level (apsl) (Serralheiro 1970; Ramalho *et al.* 2010a; Madeira *et al.* 2020). Deposits mostly correspond to consolidated bioclastic calcarenites (with a significant rhodolith contribution) interpreted as open-shelf to wave-dominated beach deposits (Ramalho *et al.* 2010a; Mayoral *et al.* 2013), topped by, and occasionally interbedded with, well-developed and laterally extensive supra-tidal aeolian deposits up to several metres-thick (Johnson *et al.* 2013; Samrock *et al.* 2018), which attest to the existence of extensive coastal dune fields driven by the steady and strong northeast trade winds that blow in this part of the world, together with the relatively high availability of sand during the periods preceding coastal platforms exposure.

MATERIAL AND METHODS

Four of the Cabo Verdean islands – Sal, Santiago, Maio, and Boa Vista – were surveyed during the 7th International Workshop “Palaeontology in Cabo Verde Archipelago”, which was held in the archipelago in July 2024. All fossiliferous outcrops were studied in detail to reconstruct the overall structure, geometry, and field relations between the various sedimentary sequences. The described trace fossil was found *in situ* in a small quarry (15°08′01″N, 23°11′50″W; Fig. 1C, D), located approximately 1.6 km east of the main square of Vila do Porto Inglês (also known as Vila do Maio) on the southwestern shore of Maio Island, on a raised marine terrace at c. 20–30 m in elevation and whose surface is slightly inclined towards the sea (Fig. 1).

Field investigations were conducted along the entire exposure, which shows variability and facies succession (Fig. 2). Special care was taken to record the geometry and dimensions of observed sedimentary structures, lateral and vertical continuity of facies, and the position and taphonomic aspects of fossil content.

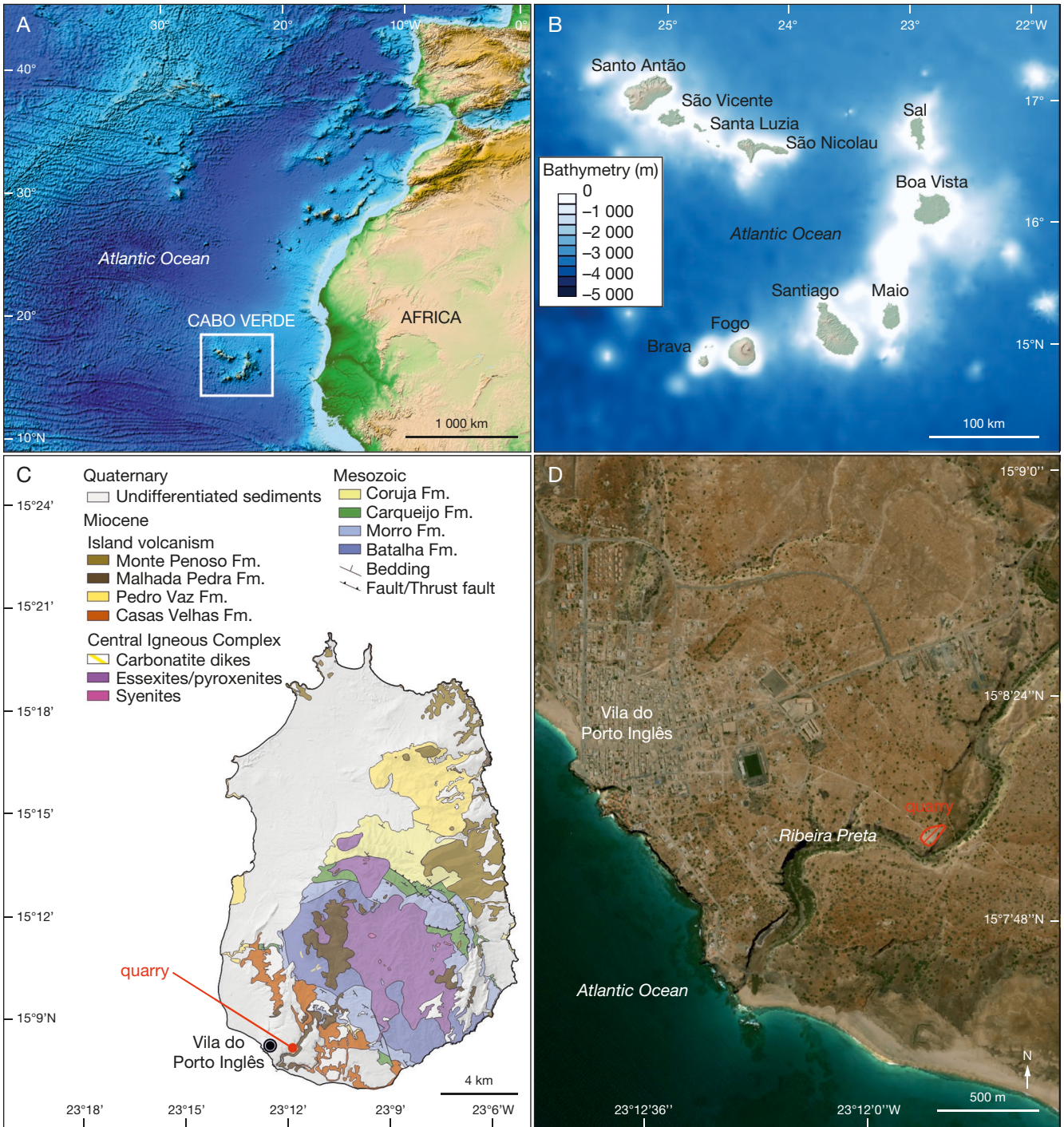


Fig. 1. — Location maps: **A**, general location of the Cabo Verde Archipelago; topography/bathymetry from NOAA National Centers for Environmental Information's 1 arc-minute global relief model ETOPO1 (2009); **B**, the Cabo Verde Archipelago showing main islands; topography from NASA Shuttle Radar Topography Mission (2013) Global 1-arc second and bathymetry from GEBCO (2020); **C**, geological map of Maio Island with indication of the studied quarry; modified from Madeira *et al.* 2020; **D**, satellite image of the study area showing location of the studied quarry; satellite image from Bing Maps (2026) overlaid on a digital elevation model (UCCP/MAHOT 2010) in shaded relief. Credits: compiled by R.S. Ramalho.

RESULTS

STRATIGRAPHICAL, SEDIMENTOLOGICAL AND PALAEOLOGICAL CHARACTERISATION

The measured section in the western part of the quarry is 3.05 m thick (Fig. 2A). Its lower part (1.15 m thick) consists

of very fine-grained, parallel-laminated, platy calcarenite, with a few horizons of small-scale ripple cross-lamination arranged in sets up to 2.5 cm thick (Fig. 2B, C). Parting lineation is commonly developed. The calcarenite is porous and composed of well-sorted carbonate grains, mostly *c.* 0.2–0.25 mm in size, consisting predominantly of shell debris

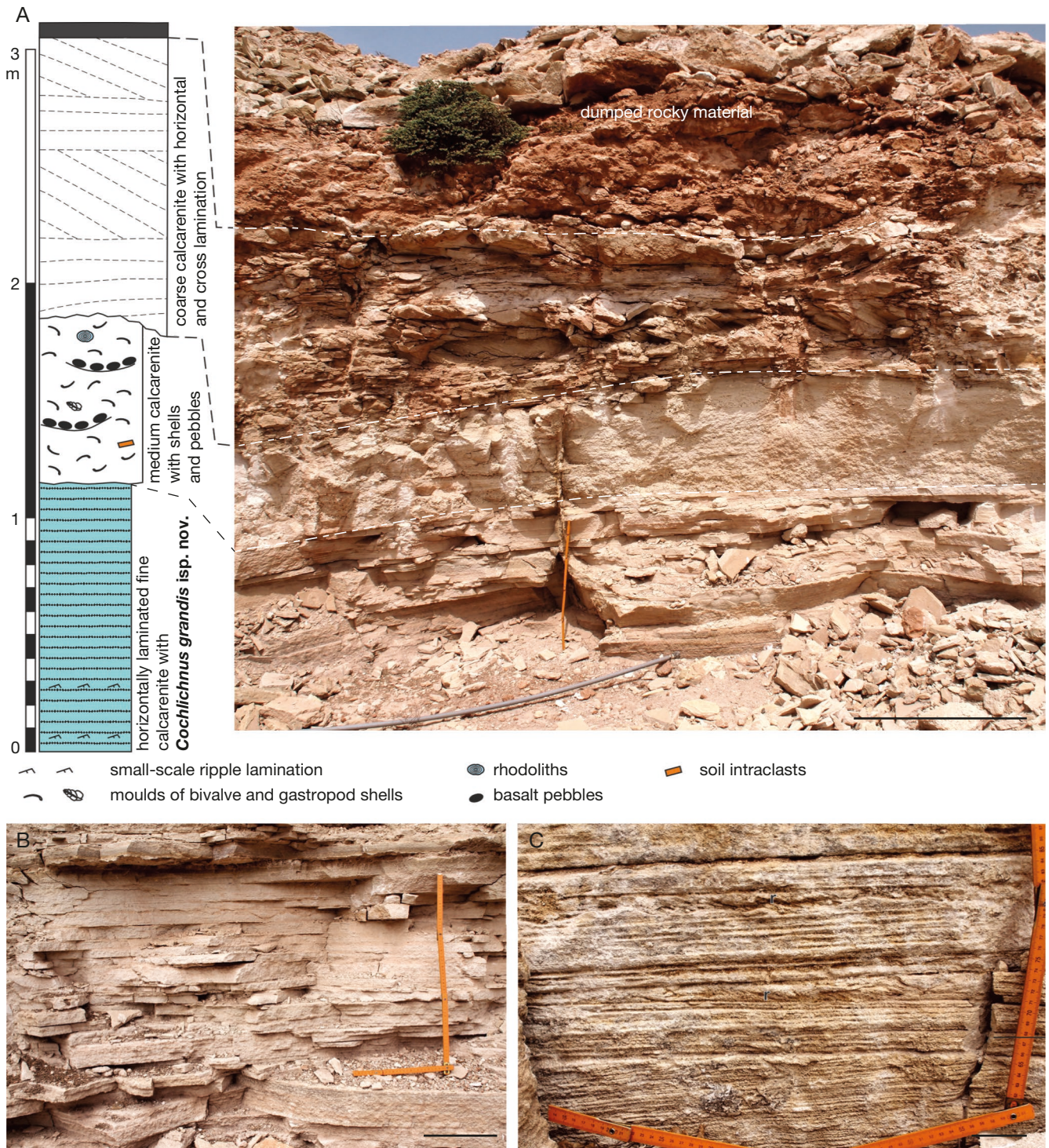


FIG. 2. — Quarry section and facies: **A**, quarry section correlated with a view of the quarry wall (boundaries of divisions marked by white dashed lines on the photograph); **B**, fine-grained, platy calcarenites in the lower part of the section; **C**, weathered wall of the fine-grained, platy calcarenites showing small ripple horizons (r). Scale bars: A, 1 m; B, 20 cm; C, 5 cm. Credits: Alfred Uchman.

and coralline algae fragments that show varying degrees of abrasion (Fig. 3A-C). Recrystallisation and micritisation of grains are common. In addition, dispersed tests of benthic calcareous foraminifers, mainly miliolids, and very rare bryozoans are present. Lamination reflects subtle variations in grain size and composition; some laminae contain slightly

coarser material with a higher proportion of shell debris and miliolid tests. Slabs derived from this calcarenite level contain the trace fossil described in this paper.

The fine-grained calcarenite is overlain by a sharply bounded unit of medium-grained calcarenite (70-80 cm thick). This unit locally preserves crude parallel or cross-lamination and

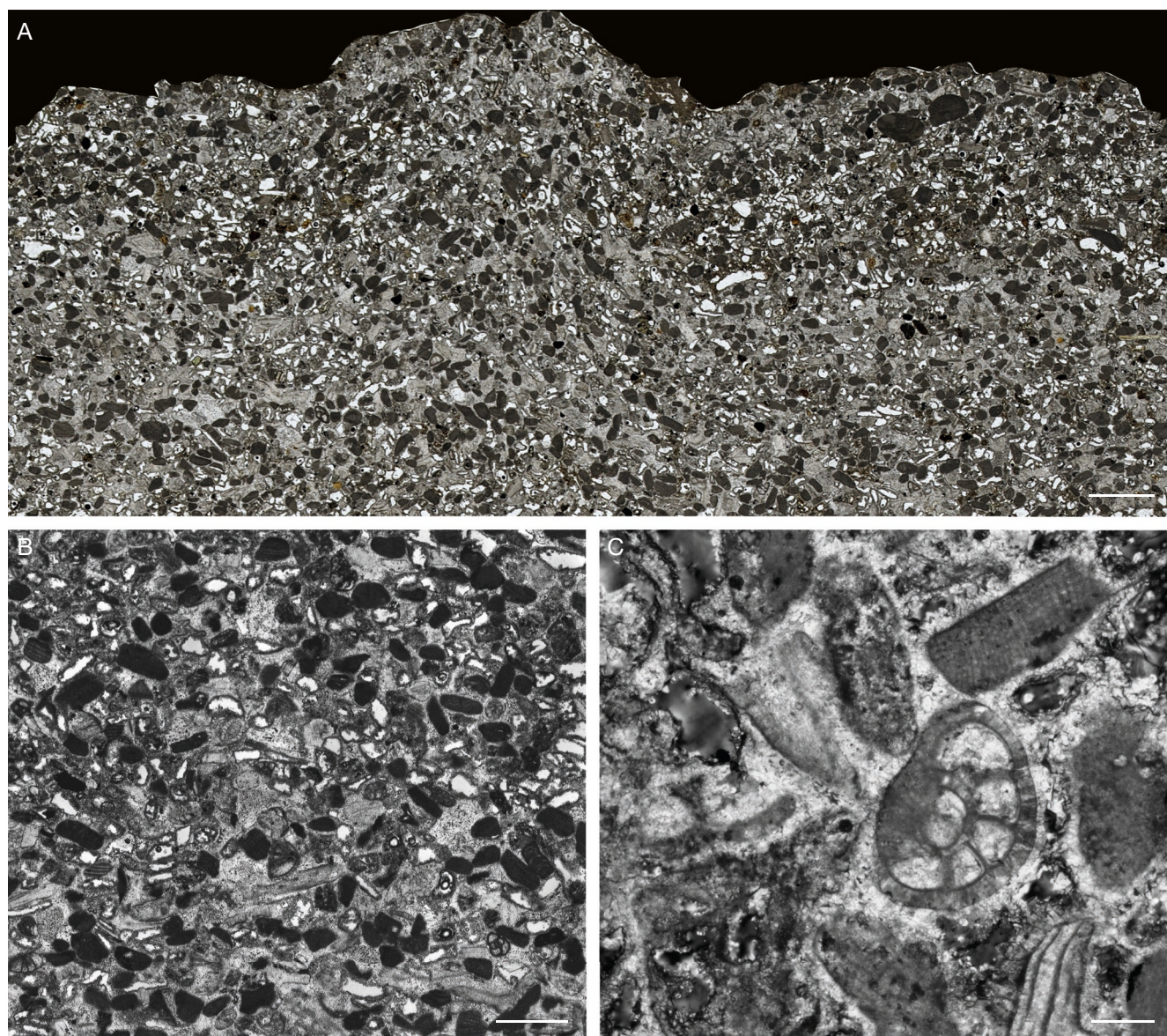


FIG. 3. — Microfacies of the calcarenite bearing the holotype of the new trace fossil: **A**, scan of a thin section crossing the trace fossil, showing fine, well-sorted biocalcarene with variable grain packing and locally steeply oriented elongate grains; **B**, closer view of the biocalcarene; dark grains represent coralline algae bioclasts, white spots are pores; **C**, abraded coralline algae bioclasts, pores, and a benthic foraminifer (photograph under crossed nicols). Scale bars: A, 1 mm; B, 0.5 mm; C, 0.2 mm. Credits: Alfred Uchman.

contains dispersed Pectinidae bivalves and small moulds of unidentified bivalve shells. More rarely, *Conus* gastropod shells are also present, mostly crushed and preserved as moulds. Small rhodoliths occur sporadically. The calcarenite includes several scouring surfaces paved with rounded basalt pebbles up to 10 cm in diameter. In its lower part, a few red intraclasts of possible palaeosol origin, up to 6 cm in size, are present. This unit is overlain by an erosional boundary and a coarse-grained calcarenite displaying cross and horizontal lamination in sets less than 20 cm thick, capped by recent soil and quarry debris.

The precise age of the investigated deposits remains uncertain. Based on their relative position within the series of Quaternary marine terraces, they are more likely to be Middle/Upper Pleistocene than Early Pleistocene in age.

THE TRACE FOSSIL

Several well-preserved examples of the new trace fossil described in this paper have been observed in slabs used as paving stones, walls, and other architectural elements in Vila do Porto Inglês, including the patio of the Casa Évora Hotel, the main square, and the fencing walls around the local school. All such slabs are derived from the same quarry. Their common origin is confirmed by the distinctive fabric of the rock and by information obtained from interviews with local residents.

A limited number of specimens were collected directly from the quarry. The specimens are housed in the collections of the Institute of Geological Sciences of the Jagiellonian University in Kraków, Poland, and are displayed at the Nature Education Centre of the Jagiellonian University

(CEP) – the Museum of Geology in Kraków (institutional abbreviation and prefix INGJ249P). Additional specimens are housed in the fossil collection of the Department of Biology of the University of the Azores in Ponta Delgada (prefix DBUA-F).

Ichnogenus *Cochlichnus* Hitchcock, 1858

Cochlichnus Hitchcock, 1858: 161.

TYPE ICHNOSPECIES. — *Cochlichnus anguineus* Hitchcock, 1858.

EMENDED DIAGNOSIS. — Unbranched, regular, sinusoidal, horizontal trails and burrows (partly modified from Głuszek 1995, and references therein).

REMARKS

Głuszek (1995: 184) compiled the diagnosis of *Cochlichnus* based on Hitchcock (1858), Häntzschel (1962), and Fillion & Pickerill (1990), defining it as “regular, sinusoidal, horizontal trails and burrows resembling a compressed and stretched corkscrew,” with the overall width of an individual trace potentially changing progressively. In this diagnosis, the corkscrew-like aspect is emphasised; however, this feature is not apparent in many specimens. Including it as an obligatory diagnostic criterion may therefore unnecessarily restrict ichnogenus-level determinations. Likewise, progressive changes in width are not universally present. For these reasons, we propose that both features be removed from the ichnogenus diagnosis and retained instead as non-obligatory characteristics in the diagnosis of *C. anguineus*.

The proposed diagnosis closely follows the concept of Häntzschel (1975: W52), who described *Cochlichnus* as “regularly meandering trails, resembling a sine curve”. Removing the terms “meandering” and “resembling” results in a more concise and operational diagnosis. Furthermore, the ichnogenus *Sinusichnus* Gibert, 1996, typified by *S. sinuosus*, also exhibits a sinuous course similar to *Cochlichnus* but differs in being branched (Belaústegui *et al.* 2014). To emphasise this distinction, we explicitly include the term “unbranched” in the revised diagnosis.

Rindsberg (1994) proposed the ichnogenus *Cymatulus* for horizontal burrows displaying a sinuous course, similar to those of *Cochlichnus*, thereby restricting *Cochlichnus* to surface trails. However, distinguishing between fossil burrows and trails is problematic in many cases, and this approach has been rejected by most subsequent authors (cf. Stanley & Pickerill 1998; but see Gougeon *et al.* 2025).

In addition to *Cochlichnus anguineus*, fourteen ichnospecies have been proposed or assigned to *Cochlichnus*. These include *C. antarcticus* Tasch, 1968; *C. serpens* Webby, 1970; *C. gracilis* Vialov, 1979; *C. kochi* (Ludwig, 1869); *C. surpuliformis* Yang & Hu in Yang *et al.*, 1987; *C. lagartensis* Muniz, 1980; *C. duomaensis* Yang in Yang *et al.*, 1983; *C. sousensis* Muniz, 1985; *C. annulatus* Orłowski, 1989; *C. luguanensis* Zhang, 1991; *C. xinhuaensis* Zhang, 1991; *C. ciliensis* Zhang & Wang, 1996; *Cochlichnus* [sic] *hanyangensis* Yang, Zhang

& Yang, 2004; and *C. karlae* Zessin, 2009. Most of these ichnospecies, together with *Helminthopsis regularis* Crimes & Crossley, 1991, were synonymised with *C. anguineus* by Stanley & Pickerill (1998), who also regarded *Cymatulus undulatus* Rindsberg, 1994 as an ichnospecies of *Cochlichnus*. In addition, *Gracilichnus sinualis* Yang & Shen, 1999 was tentatively included in *C. anguineus* by Uchman *et al.* (2004).

Gougeon *et al.* (2025) provided an extensive review of *Cochlichnus* ichnospecies. The same authors concluded that only *C. anguineus*, *C. annulatus*, *C. antarcticus*, *C. gracilis*, and *C. luguanensis* are sufficiently distinct to remain useful. Among these, *C. annulatus* is characterised by annulations, and *C. antarcticus* by lateral marks. The remaining ichnospecies are smooth and relatively small, with wavelengths not exceeding those typical of *C. anguineus*.

To clarify the meaning of the type ichnospecies, an emended diagnosis is here proposed.

Cochlichnus anguineus Hitchcock, 1858

Cochlichnus anguineus Hitchcock, 1858: 161.

EMENDED DIAGNOSIS. — Relatively small (wavelength usually much less than 50 mm), unbranched, regular, sinusoidal, horizontal trails and burrows. They may resemble a compressed and stretched corkscrew and may show progressive changes in width (modified from Głuszek 1995; see discussion under the ichnogenus).

REMARKS

As *Cochlichnus anguineus* is the type ichnospecies of *Cochlichnus*, its diagnosis requires emendation to avoid overlap with the diagnosis of the new ichnospecies described herein. Won & Kong (2023: 402) diagnosed *C. anguineus* as “unbranched, continuously and regularly meandering grooves or ridges that resemble at least one full sine wave”, noting that successive waves may gradually diminish in amplitude. However, the requirement of “at least one full sine wave” cannot be retained, because single sine-wave elements also occur as components of several other trace fossils, including *Cosmorhaphis*, *Phycosiphon* (e.g., Uchman 1998), and *Sinusichnus* (e.g., Gibert 1996).

The inclusion of size as a diagnostic parameter is justified by the morphometric analysis presented in the subsequent sections of this paper. Fossil specimens assigned to *C. anguineus* consistently show smaller wavelengths and amplitudes than those of the new ichnospecies described below, allowing the two forms to be distinguished on objective morphometric grounds, in addition to the other diagnostic features.

Cochlichnus grandis isp. nov.

(Figs 4–6)

urn:lsid:zoobank.org:act:8499A1F5-E3B6-47C8-9F5D-0B39F7776F7D

DERIVATION OF NAME. — *Grandis* (Latin), meaning “large” or “big”, in reference to the size of the trace.

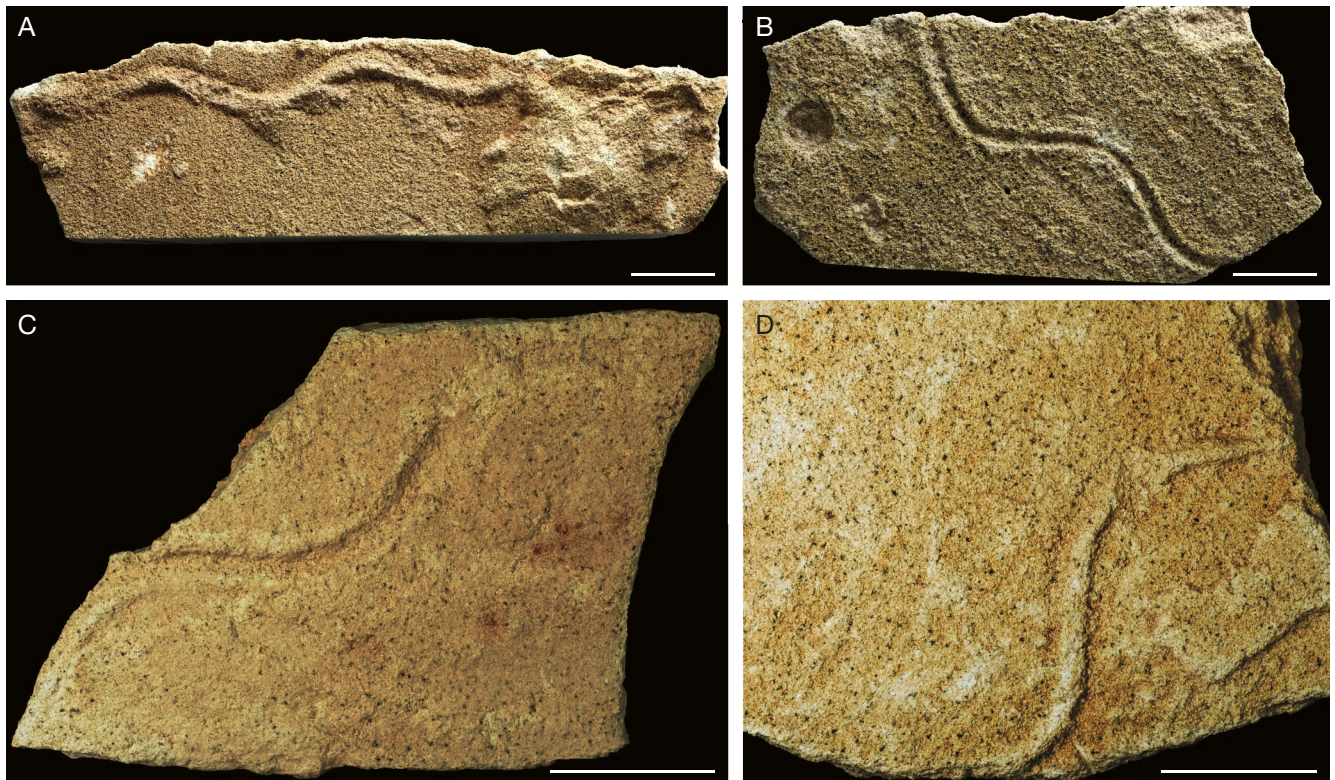


FIG. 4. — The nomenclatural types of *Cochlichnus grandis* isp. nov. from Pleistocene calcarenites, Maio Island, Cabo Verde Archipelago: **A**, holotype, INGUJ249P115; **B**, paratype 1, INGUJ249P116; **C**, paratype 2, DBUA-F 1682-2_MPB_5222; **D**, paratype 3, DBUA-F 1682-3_MPB_5218. Scale bars: 3 cm. Credits: Alfred Uchman.

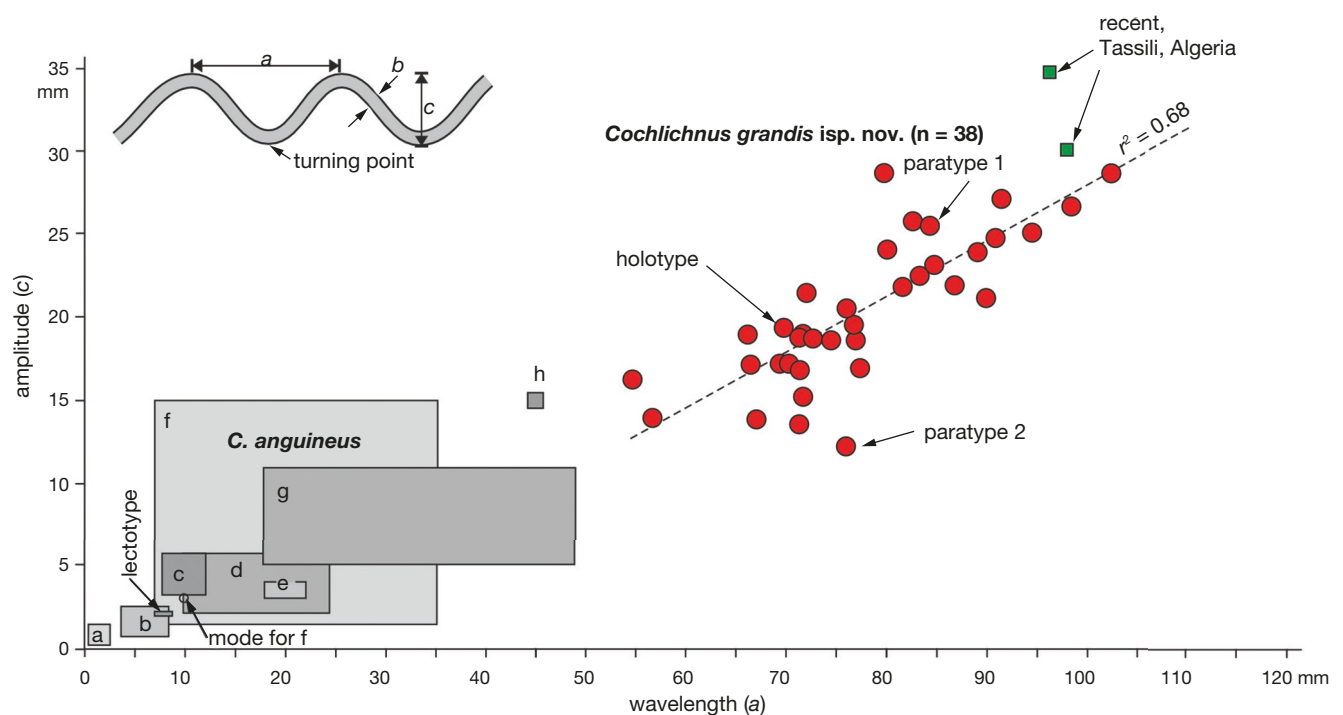


FIG. 5. — Morphometric plot of *Cochlichnus* Hitchcock, 1858, including *C. anguineus* Hitchcock, 1858 (grey squares) and *C. grandis* isp. nov. (red circles): **a**, *C. anguineus*, Oligocene fluvial plain, Switzerland (Uchman *et al.* 2004); **b**, *C. anguineus*, terrestrial Permian, Argentina (Buatois *et al.* 1997); **c**, *C. anguineus*, terrestrial and marine upper Carboniferous, Ukraine (Dernov 2023); **d**, larger *C. anguineus*, terrestrial Permian, Argentina (Buatois *et al.* 1997); **e**, *Cochlichnus* (no species determination), terrestrial(?) upper Carboniferous, United Kingdom (Jarzemkowski 1989: fig. 4); **f**, *C. anguineus*, terrestrial upper Carboniferous, Poland (Głuszek 1995); **g**, *C. anguineus*, fluvial Cretaceous, South Korea (Kim *et al.* 2002); **h**, *Cochlichnus* isp., subtidal Ordovician, Ontario, Canada (Stanley & Pickerill 1998). Data for the *C. anguineus* lectotype measured from Rainforth (2005: fig. 19a). Parameters of two modern skink lizard swimming traces from Tassili (Algeria) have been added (green quadrangles).

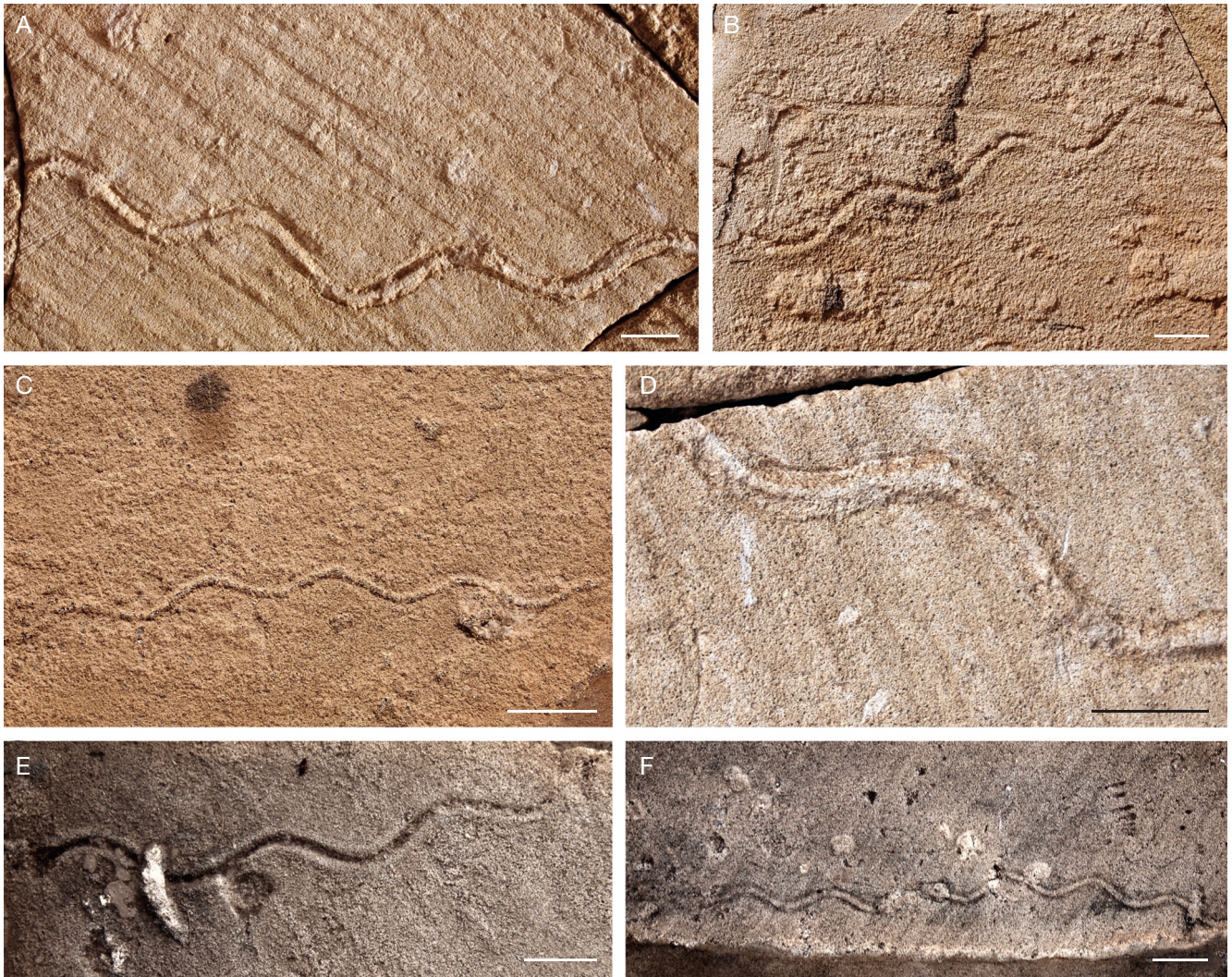


FIG. 6. — *Cochlichnus grandis* isp. nov. from Pleistocene calcarenites, Maio Island, Cabo Verde Archipelago. Photographs of slabs incorporated into the architectural element of the Vila do Porto Inglês: **A**, trace with a distinct moat and local mantle on a surface with well-developed current lineation; **B**, trace preserved as a furrow with levees; **C**, trace preserved as semicircular ridge; **D**, trace with a distinct mantle, locally showing oblique striations; **E**, trace preserved as a furrow with levee, crosscut by a short ridge plunging into the slab and associated with knobs; **F**, long trace with a moat, associated with knobs. Scale bars: A, B, D, E, 3 cm; C, F, 5 cm. Credits: Alfred Uchman.

TYPES AND OTHER MATERIALS. — **Cabo Verde • Maio**, a quarry 1.6 km east of the main square of Vila do Porto Inglês; Slab INGUJ249P115 contains the holotype (Fig. 4A); INGUJ249P116 contains paratype 1 (Fig. 4B); DBUA-F 1682-2_MPB_5222 contains paratype 2 (Fig. 4C); and DBUA-F 1682-3_MPB_5218 contains paratype 3 (Fig. 4D). Thin section Ma1 was prepared from the slab containing the holotype. In addition, 43 photographs of traces preserved in architectural elements within Vila do Porto Inglês were examined; 38 of these specimens were sufficiently complete to allow detailed morphometric measurements.

DIAGNOSIS. — Relatively large (wavelength > 50 mm), unbranched, regular, sinusoidal, horizontal burrow. It may display a low levee (raised lateral margin of the trace) or a mantle.

TYPE LOCALITY. — Cabo Verde, Maio, 1.6 km east of the main square of Vila do Porto Inglês.

DESCRIPTION

The trace fossil occurs as horizontal, sinuous ridges or grooves preserved on flat surfaces of slabs of very fine-grained calcarenite. Individual traces are 3.0–13.3 mm wide (mean 6.6 mm;

$n = 38$). Wavelengths range from 54.5 to 102.3 mm (mean 77.3 mm; $n = 38$), and amplitudes from 12.1 to 28.5 mm (mean 20.2 mm; $n = 38$). The number of waves per specimen varies from 2 to 13, with a mean of 6–7 ($n = 43$). Morphometric parameters are generally stable within individual specimens, and the overall course of the trace is approximately straight.

Mean wavelength is strongly correlated with mean amplitude (Pearson correlation coefficient $r = 0.82$; coefficient of determination $r^2 = 0.68$; Fig. 5). In contrast, mean wavelength shows only a weak relationship with mean width ($r = 0.34$; $r^2 = 0.12$), whereas mean amplitude displays a moderate correlation with mean width ($r = 0.56$; $r^2 = 0.32$).

Most ridges and grooves are unornamented and roughly semicircular in cross-section. Grooves may be bordered by a narrow, smooth levee (Figs 4B, C; 6B, E), whereas ridges may be surrounded by a mantle (Figs 4D; 6A, D). The mantle is commonly thin but may locally attain up to half the width of the ridge (Fig. 4D). In rare cases, its width equals that of the

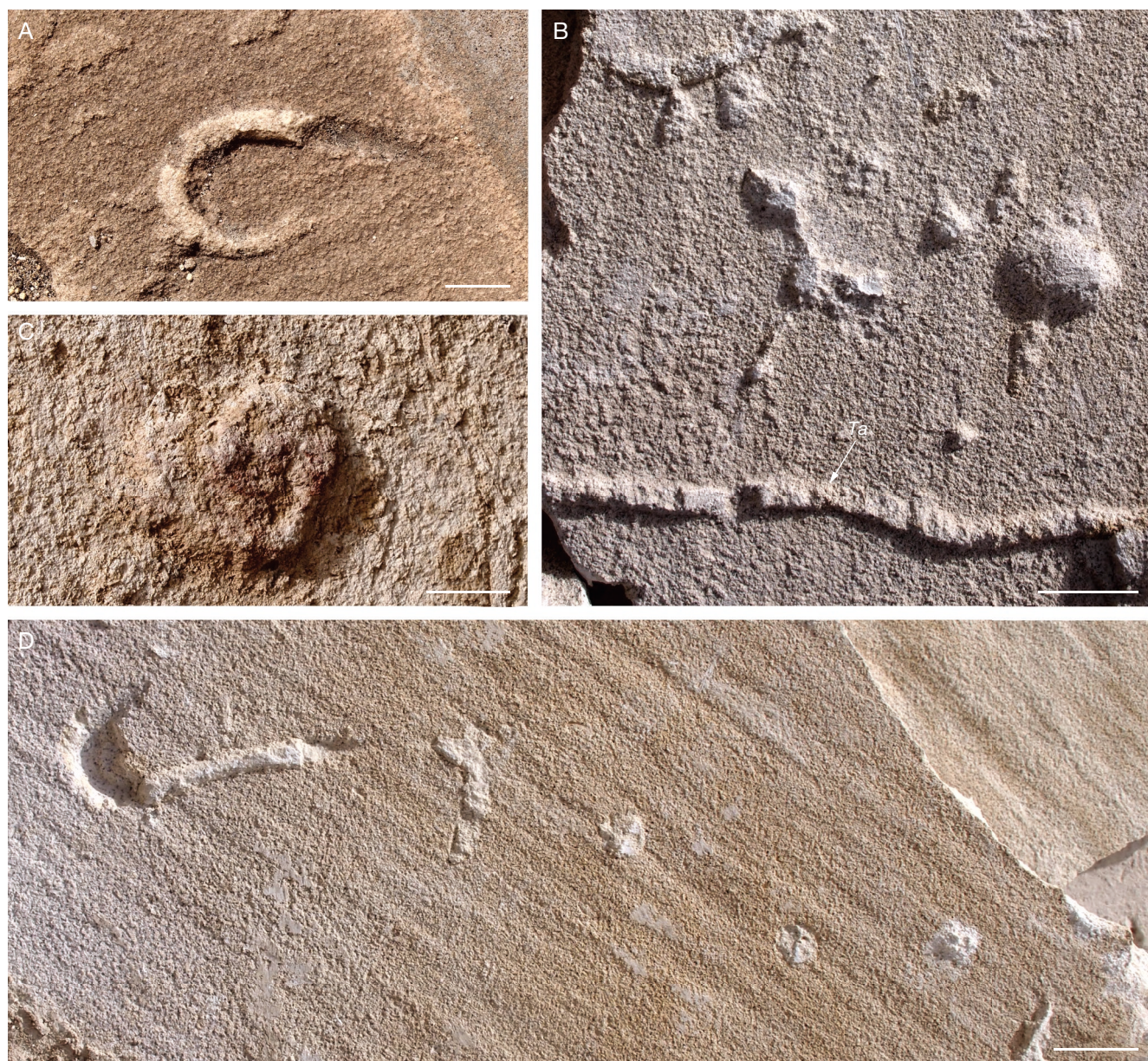


FIG. 7. — Traces associated with *Cochlichnus grandis* isp. nov. in Pleistocene calcarenites, Maio Island, Cabo Verde Archipelago (field photographs): **A**, looping ridge; **B**, *Taenidium* isp. (*Ta*), irregular ridges and mounds; **C**, spiral ridge; **D**, deeply meandering ridge associated with a set of knobs. Scale bars: A, C, 2 cm; B, D, 3 cm. Credits: Alfred Uchman.

ridge and may display indistinct oblique striations (Fig. 6D). In some specimens, the mantle is slightly depressed relative to the slab surface, forming a shallow moat flanking the ridge (Fig. 6A).

The ridges are preserved in full relief and are filled with material identical to that of the host rock. The mantle is composed of the same lithology, although subtle textural differences make it discernible. In cross-section, the trace fossil is nearly invisible. Thin-section observations reveal a localised steep alignment of elongate grains within the trace (Fig. 3A).

REMARKS

The levee observed in some specimens may result from the splitting of slabs and could represent the counterpart expression of the mantle. Smoothing of levees may reflect

abrasion during slab separation. It is therefore possible that a mantle is present along at least part of the perimeter of most observed traces.

ASSOCIATED TRACES

In addition to *Cochlichnus grandis* isp. nov., the slabs from the original quarry locally preserve other trace fossils, some of which are dispersed and difficult to identify taxonomically. These include a looping ridge, up to 10 mm wide, plunging into the bed (Fig. 7A), and a spiral ridge, 7 mm wide, forming one complete whorl and continuing away, plunging into the bed (Fig. 7C). One slab contains a slightly winding, meniscate-like ridge, 5 mm wide, tentatively attributed to *Taenidium* isp. or *Entradichnus* isp.

(Fig. 7B), acknowledging that the diagnostic features distinguishing these ichnogenera are unclear (Lucas 2024; Uchman *et al.* 2024).

Several slabs also exhibit short, straight or curved ridges (5–10 mm wide) and associated knobs of comparable width, occasionally larger (Figs 4B; 6E, F; 7C). In one specimen, a deeply meandering ridge is associated with a set of knobs, suggesting that they may belong to a single trace (Fig. 7D).

These associated traces indicate the presence of other burrowing organisms, possibly small lizards or insects, operating under slightly different sediment conditions (e.g., higher moisture preventing sand-swimming behaviour). Overall, the assemblage, including *Cochlichnus grandis* isp. nov., fits within the *Entradichnus-Octopodichnus* ichnofacies typical of coastal aeolian and shallow marginal-marine sands (Buatois & Mángano 2008, 2011).

DISCUSSION

DEPOSITIONAL ENVIRONMENT

The very fine-grained, parallel-laminated, platy calcarenite forming the lower part of the section is interpreted as an aeolianised beach deposit. Although the bioclastic composition indicates a marine origin of the grains, the presence of continuous, horizontal lamination – rather than the low-angle lamination typical of the upper foreshore (Clifton 1969; Reineck & Singh 2012) – indicates significant aeolian reworking. This is further demonstrated by thorough sorting and the absence of complete mollusc shells and basalt pebbles, which are abundant in the overlying units. The lack of large-scale cross-sets typical of dune deposits and the localised extent of this unit suggest deposition as an aeolian sand-sheet of limited lateral extent (for sand-sheet deposits, see Kocurek & Nielson 1986).

The overlying medium-grained, cross-bedded calcarenite containing pebbles and mollusc shells is interpreted as a shallow-marine, high-energy deposit, probably corresponding to the upper shoreface (cf. Reineck & Singh 2012). Foreshore deposits that generally would be expected below this unit were likely removed by erosion, as indicated by the sharp basal contact and the presence of possible palaeosol intraclasts. Overall, the section records a transgressive succession developed during a sea-level highstand, during which the marine terrace was formed. The coarse-grained calcarenite at the top of the section, bounded by an erosional surface, may represent a higher-order, incomplete depositional cycle.

THE TRACE MAKER

Recent *Cochlichnus anguineus* is produced by nematodes, chironomids, and some fly larvae (e.g., Uchman *et al.* 2004; Kimitsuki *et al.* 2025). Probably similar trace makers produced this ichnogenus in the past, especially in Mesozoic and Cenozoic continental settings. Paleozoic *C. anguineus*, which is usually larger than younger representatives, was likely made by worm-shaped organisms, typically associated with muddy substrates.

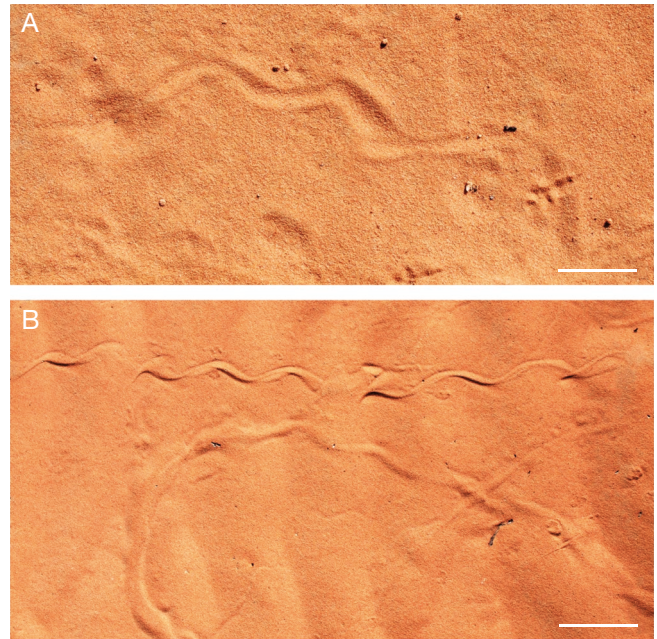


FIG. 8. — Recent skink traces in sand dunes, Tassili, southern Algeria, November 2025: **A**, surface groove with levees; **B**, sinuous ridge with local sand displacement (upper part) and a curved, subsurface sinuous trace. Scale bars: A, 5 cm; B, 10 cm. Credits: Alfred Uchman.

In contrast, *Cochlichnus grandis* isp. nov. is distinctly larger and occurs in sandy substrate interpreted as an aeolian sand sheet in a coastal setting. Skink lizards match the trace in size, mode of locomotion, and palaeoenvironment. Recent skink traces observed by A.U. in the Tassil mountains, Sahara (southern Algeria; Fig. 8), show sinuosity and dimensions comparable to those of *C. grandis* isp. nov. For example, the average wavelength of sand-swimming in the North African sandfish skink *Scincus scincus* (Linnaeus, 1758) reaches 10.6 cm, close to the range of *C. grandis* isp. nov. (Sharpe *et al.* 2015; cf. Fig. 5).

Skinks swim through loose sand, either partially buried at the surface or fully subsurface, using lateral undulations with or without leg movements (Baumgartner *et al.* 2008; Maladen *et al.* 2009; Sharpe *et al.* 2013, 2015; Catena & Hembree 2014a, b; Astley *et al.* 2020). The mantle observed in *Cochlichnus grandis* isp. nov. likely results from leg dragging, friction along the body, or a combination of both. Its discontinuous, variable thickness reflects local differences in interaction strength between the animal and the sand (Astley *et al.* 2020). Levees along the traces result from the pressure of the animal's body on the substrate. The trace described was probably produced in the shallow subsurface or fully within the subsurface. The latter interpretation is supported by well-preserved traces occurring similarly on both counterparts of split slabs, where the pressure exerted by the body on the sediment was relatively uniform in all directions. In contrast, specimens with pronounced levees suggest a shallower position, where the sediment was displaced predominantly laterally. In the Cabo Verde Archipelago, 13 species of skinks (Scincidae) are currently recognised (Miralles *et al.* 2011).

All are endemic and assigned to the genus *Chioninia* Gray, 1845, of which 11 are extant and two are extinct (*Chioninia coctei* Duméril & Bibron, 1839 and *Chioninia magna* Mateo *et al.*, 2022). *Chioninia coctei* is the largest of all Cabo Verdean skinks and has been considered extinct since the early 20th century (Angel 1935), whereas *Ch. magna* was last observed between AD 1450–1700 at the time of the arrival of the Portuguese (Fernández-Palacios *et al.* 2025).

Skink diversity in the archipelago is characterised by pronounced island endemism and strong geographic structuring. On the island of Maio, at least three well-differentiated lineages occur: the widely distributed species *Chioninia delalandii* (Duméril & Bibron, 1839), the island-restricted form *Chioninia spinalis maioensis* (Mertens, 1955), and *Chioninia vaillanti* (Boulenger, 1887), whose distribution is limited to the eastern sector of the archipelago. Additionally, on Maio, bones of the species *Ch. magna* are easily and abundantly found in sandy areas such as Praia Santana, where seabird colonies are concentrated (Mateo *et al.* 2022).

This assemblage highlights the role of Maio as a key island for understanding processes of diversification, isolation, and the long-term persistence of ancient lineages among Cabo Verdean skinks, in contrast to other islands, where species richness is lower or dominated by a single taxon (Vasconcelos *et al.* 2013).

Species of the genus *Chioninia* exhibit considerable ecological plasticity and occupy a wide range of habitats across the Cape Verde Islands. Although some populations show preferences for particular microhabitats – such as stony ground, scree slopes, or coastal rocky environments (Moravec 2023; Moravec & Moravcová 2025) – several studies indicate that they also occur on sandy substrates, along dune margins, within xerophilous vegetation, and in more open habitats with soft soils (Mateo *et al.* 1997; Köhler *et al.* 2007; Carretero *et al.* 2016). This broad habitat use appears to be influenced by local factors including the availability of refuges, vegetation structure, and aridity, suggesting that many species within the genus exploit mosaics of adjacent microhabitats rather than strictly bounded environments. Overall, *Chioninia* can be regarded as an ecologically flexible group of lizards within the arid and coastal ecosystems of the Cape Verde Archipelago (Vasconcelos *et al.* 2013).

Our knowledge of Pleistocene skinks on Maio Island is probably incomplete. Nevertheless, the most probable trace maker of *Cochlichnus grandis* isp. nov. was related to the genus *Chioninia*, considering the dominant role of these endemic lizards within the Cabo Verde Archipelago.

PRESERVATION

Despite the widespread occurrence of skinks, fossil traces of sand-swimming are extremely rare. The main factor limiting preservation is the homogeneity and loose texture of sand, in which subtle biogenic disturbance is often invisible in lithified sediments.

On the marine terrace documented on the south-western part of Maio Island, preservation of *C. grandis* isp. nov. was facilitated by relatively high substrate humidity. Vertebrate

and invertebrate traces are better preserved in moist than in dry, loose sand (Ahlbrandt *et al.* 1978; Milán & Loope 2007; Good & Ekdale 2014; Carvalho & Leonardi 2021). The sand sheet was likely close to the water table, providing ideal conditions for trace formation. For fossorial lizards in Florida, optimal water saturation ranges from 23 to 42% (Lee 1969). Additional moisture from rainfall, dew, fog, or high tides, combined with early diagenetic carbonate cementation, stabilised the traces. A thin section of the slab bearing the holotype shows grains “floating” in cement and epitaxial growth of isopachous calcite on bioclasts (Fig. 3), indicating early cementation, whereas observed porosity (Fig. 3B) likely reflects secondary dissolution (Longman 1980).

This narrow taphonomic window explains why fossil traces of sand-swimming lizards are so scarce, despite skinks being widespread in semi-arid and arid environments (Hedges 2014) and known from the Cretaceous onwards (Estes 1969; Wellstead 1982; Martin *et al.* 2004). Coastal carbonate sands provide a higher preservation potential than inland siliciclastic aeolian deposits.

REMARKS ON THE ASSOCIATED TRACES

The looping, short, straight, or curved ridges and associated knobs (Figs 6E, F; 7A–D) may have been produced by burrowing lizards other than sand-swimming skinks, by skinks swimming in overly moist sand, or by insects. The comparable widths to *C. grandis* isp. nov. suggest small lizards as likely trace makers. *Taenidium* isp. and *Entradichnus* isp. are typical traces in aeolian deposits, produced by insect larvae or adults (Lucas 2024; Uchman *et al.* 2024). Together with *C. grandis* isp. nov., these traces belong to the *Entradichnus-Octopodichnus* ichnofacies (Buatois & Mángano 2008, 2011), which is characteristic of aeolian environments.

CONCLUSIONS

Cochlichnus grandis isp. nov. is a large, horizontal, sinuous trace fossil with wavelengths exceeding 50 mm, interpreted as produced by a skink lizard swimming in loose sand. The trace occurs in well-sorted bioclastic calcarenites deposited as a coastal aeolian sand-sheet. A narrow taphonomic window facilitated its preservation: increased substrate humidity, combined with early carbonate cementation, which fixed the trace. Morphometric analysis shows stable parameters across specimens, with unbranched sinusoidal patterns, variable amplitude, and occasional mantles or levees, likely produced by leg drag or friction along the body. Associated traces, including looping, curved, or short ridges, may represent burrowing activity by skinks or other small vertebrates. Together with *C. grandis* isp. nov., they belong to the *Entradichnus-Octopodichnus* ichnofacies. The discovery of *C. grandis* isp. nov. provides the first fossil evidence of sand-swimming behaviour in lizards and underscores the role of taphonomic conditions in preserving such delicate traces in the fossil record.

Acknowledgements

S.P.A. and P.M. acknowledge contracts with project M1.1.A/INFRAEST CIENT/A/001/2021 – Base de Dados da PaleoBiodiversidade da Macaronésia, funded by the Regional Government of the Azores. SPA also acknowledges his current FCT/2023.07418 CEECIND research contract with BIOPOLIS: <https://doi.org/10.54499/2023.07418.CEECIND/CP2845/CT0001>.

S.M. acknowledges her PhD grant FCT 2025.04385.BD for the project “The impact of interglacial-glacial cycles on the Pleistocene marine biota of the Cabo Verde Archipelago: The past as a window to understand current climate change effects on the marine ecosystems”.

This work benefited from FEDER funds, through the Operational Program for Competitiveness Factors – COMPETE, and from National Funds, through FCT (UIDB/50027/2020, POCI-01–0145-FEDER-006821, UIDB/00153/2020, LA/P/0048/2020), as well as through the Regional Government of the Azores (M1.1.a/005/FuncionamentoC-/2016, CIBIO-A; M1.1.A/INFRAEST CIENT/A/001/2021; M3.3.B/ORG.R.C./005/2021). Finally, this work received support from FEDER funds (85%) and from the Regional Government of the Azores (15%) through the project M1.1.A/INFRAEST CIENT/A/001/2021 – Base de Dados da PaleoBiodiversidade da Macaronésia. A.U. was additionally supported by a grant from the Faculty of Geography and Geology under Priority Research Area (Anthropocene) of the Strategic Programme Excellence Initiative at Jagiellonian University. We acknowledge Radek Mikuláš (Prague) and one Anonymous Reviewer for comments which helped to improve the paper.

REFERENCES

- AHLBRANDT T. S., ANDREWS S. & GWYNNE D. T. 1978. — Bio-turbation in eolian deposits. *Journal of Sedimentary Research* 48 (3): 839–848. <https://doi.org/10.1306/212F7586-2B24-11D7-8648000102C1865D>
- ANGEL F. 1935. — Lézards des îles du Cap-Vert, rapportés par M. le Professeur Chevalier. Description d'espèces nouvelles. *Bulletin du Muséum national d'Histoire naturelle, Paris*, série 2, 7: 165–169.
- ASTLEY H. C., MENDELSON J. R. III, DAI J., GONG C., CHONG B., RIESER J. M., SCHIEBEL P. E., SHARPE S. S., HATTON R. L., CHOSSET H. & GOLDMAN D. I. 2020. — Surprising simplicities and syntheses in limbless self-propulsion in sand. *Journal of Experimental Biology* 223 (5): jeb103564. <https://doi.org/10.1242/jeb.103564>
- BAUMGARTNER W., FIDLER F., WETH A., HABBECKE M., JAKOB P., BUTENWEG C. & BÖHME W. 2008. — Investigating the locomotion of the sandfish in desert sand using NMR imaging. *PLoS ONE* 3 (10): e3309. <https://doi.org/10.1371/journal.pone.0003309>
- BELAÚSTEGUI Z., DE GIBERT J. M., LÓPEZ-BLANCO M. & BAJO I. 2014. — Recurrent constructional pattern of the crustacean burrow *Sinusichnus sinuosus* from the Paleogene and Neogene of Spain. *Acta Palaeontologica Polonica* 59 (2): 461–474. <https://doi.org/10.4202/app.2012.0092>
- BING MAPS 2026. — *Satellite Imagery of Maio Island*. Available at: <http://binged.it/Q06Ih9> (last accessed on 4 January 2026).
- BUATOIS L. A. & MÁNGANO M. G. 2008. — Continental ichnology and the marine–nonmarine transition, in UCHMAN A. (ed.), *Second International Congress on Ichnology*. Polish Geological Institute, Warszawa: 22.
- BUATOIS L. A. & MÁNGANO M. G. 2011. — *Ichnology: Organism–Substrate Interactions in Space and Time*. Cambridge University Press, Cambridge, 358 p.
- BUATOIS L. A., JALFIN G. & ACENÓLAZA F. G. 1997. — Permian nonmarine invertebrate trace fossils from southern Patagonia, Argentina: ichnologic signatures of substrate consolidation and colonization sequences. *Journal of Paleontology* 71 (2): 324–336. <https://doi.org/10.1017/S0022336000039238>
- CARRETERO M. A., LOPES E. P. & VASCONCELOS R. 2016. — An ecophysiological background for biogeographic patterns of two island lizards? *The Science of Nature* 103: 97. <https://doi.org/10.1007/s00114-016-1422-8>
- CARVALHO I. S. & LEONARDI G. 2021. — Fossil footprints as biosedimentary structures for paleoenvironmental interpretation: examples from Gondwana. *Journal of South American Earth Sciences* 106: 102936. <https://doi.org/10.1016/j.jsames.2020.102936>
- CATENA A. M. & HEMBREE D. I. 2014a. — Swimming through the substrate: the neoichnology of *Chalcides ocellatus* and biogenic structures of sand-swimming vertebrates. *Palaeontologia Electronica* 17: 37A, 19 p. <https://doi.org/10.26879/463>
- CATENA A. M. & HEMBREE D. I. 2014b. — Biogenic structures of burrowing skinks: neoichnology of *Mabuya multifasciata* (Squamata: Scincidae), in HEMBREE D. I., PLATT B. F. & SMITH J. J. (eds), *Experimental Approaches to Understanding Fossil Organisms. Topics in Geobiology*. Vol. 41. Springer, Dordrecht: 343–369. https://doi.org/10.1007/978-94-017-8721-5_14
- CHAPPLE D. G., SLAVENKO A., TINGLEY R., FARQUHAR J. E., CAMAITI M., ROLL U. & MEIRI S. 2023. — Built for success: distribution, morphology, ecology and life history of the world's skinks. *Ecology and Evolution* 13 (12): e10791. <https://doi.org/10.1002/ece3.10791>
- CLIFTON H. E. 1969. — Beach lamination: nature and origin. *Marine Geology* 7 (6): 553–559. [https://doi.org/10.1016/0025-3227\(69\)90023-1](https://doi.org/10.1016/0025-3227(69)90023-1)
- CRIMES T. P. & CROSSLEY J. D. 1991. — A diverse ichnofauna from Silurian flysch of the Aberystwyth Grits Formation, Wales. *Geological Journal* 26 (1): 27–64. <https://doi.org/10.1002/gj.3350260104>
- DERNOV V. 2023. — First record of the trace fossil *Cochlichnus* from the Pennsylvanian continental and marine deposits of the Donets Basin (Ukraine). *Geo&Bio* 25: 109–120.
- ESTES R. 1969. — A scincoid lizard from the Cretaceous and Paleocene of Montana. *Breviora* 331: 1–9. <https://doi.org/10.5281/zenodo.16432838>
- FERNÁNDEZ-PALACIOS J. M., FRUCTUOSO M., ILLERA J. C., RANDO J. C., DE NASCIMENTO L., FERNÁNDEZ-PALACIOS E., PATIÑO J., OTTO R., CASTILLA-BELTRÁN A., MARTÍN-GONZÁLEZ E., ORIHUELA-RIVERO R., ALCOVER J. A. & WHITTAKER R. J. 2025. — A synthesis of terrestrial species extinctions in the Macaronesian Islands and their correspondence with human occupancy. *PNAS Nexus* 4 (8): pgaf215. <https://doi.org/10.1093/pnasnexus/pgaf215>
- FILLION D. & PICKERILL R. K. 1990. — Ichnology of the Upper Cambrian? to Lower Ordovician Bell Island and Wabana groups of eastern Newfoundland, Canada. *Palaeontographica Canadiana* 7, 119 p.
- GEBCO 2020. — *GEBCO Compilation Group. Grid*. Available at: <https://doi.org/10.5285/f98b053b-0c3c-6c23-e053-6c86abc0af7b> [last accessed on 20 November 2020].
- GIBERT J. M. DE 1996. — A new decapod burrow system from the NW Mediterranean Pliocene. *Revista Española de Paleontología* 11: 251–254.
- GLUSZEK A. 1995. — Invertebrate trace fossils in the continental deposits of an Upper Carboniferous coal-bearing succession, Upper Silesia, Poland. *Studia Geologica Polonica* 108: 171–202.
- GOOD T. R. & EKDALE A. A. 2014. — Paleocology and taphonomy of trace fossils in the eolian Upper Triassic/Lower Jurassic Nugget Sandstone, northeastern Utah. *Palaio* 29: 401–413. <https://doi.org/10.2110/palo.2014.013>

- GOUGEON R., MÁNGANO M. G., BUATOIS L. A., NARBONNE G. M., LAING B. A. & PAZ M. 2025. — Ichnology of the Ediacaran–Cambrian Chapel Island Formation of Newfoundland, Canada: unravelling bioturbation at the onset of the Cambrian Explosion. *Fossils and Strata* 72: 1–215. <https://doi.org/10.18261/9788294167128-2025-01>
- HÄNTZSCHEL W. 1962. — Trace fossils and problematica, in MOORE R. C. (ed.), *Treatise on Invertebrate Paleontology, part W, Miscellaneous*. Geological Society of America and University of Kansas, New York & Lawrence: W177–W245.
- HÄNTZSCHEL W. 1975. — Trace fossils and problematica, in TEICHERT C. (ed.), *Treatise on Invertebrate Paleontology, part W, Miscellaneous, Supplement I*. Geological Society of America and University of Kansas, Boulder & Lawrence: W1–W269.
- HEDGES S. B. 2014. — The high-level classification of skinks (Reptilia, Squamata, Scincomorpha). *Zootaxa* 3765 (4): 317–338. <https://doi.org/10.11646/zootaxa.3765.4.2>
- HEMBREE D. I. & HASIOTIS S. T. 2007. — Biogenic structures produced by sand-swimming snakes: a modern analog for interpreting continental ichnofossils. *Journal of Sedimentary Research* 77: 389–397. <https://doi.org/10.2110/jsr.2007.034>
- HITCHCOCK E. 1858. — *Ichnology of New England. A Report on the Sandstone of the Connecticut Valley, Especially its Fossil Footmarks*. W. White, Boston, 220 p.
- JARZEMBOWSKI E. A. 1989. — Writhlington Geological Nature Reserve. *Proceedings of the Geologists' Association* 100: 219–234. [https://doi.org/10.1016/S0016-7878\(89\)80012-4](https://doi.org/10.1016/S0016-7878(89)80012-4)
- JOHNSON M., BAARLI G., DA SILVA C. M., CACHÃO M., RAMALHO R., LEDESMA-VÁSQUEZ J. & MAYORAL E. 2013. — Coastal dunes with high content of rhodolith (coralline red algae) bioclasts: Pleistocene formations on Maio and São Nicolau in the Cape Verde Archipelago. *Aeolian Research* 8: 1–9. <https://doi.org/10.1016/j.aeolia.2012.10.008>
- KIM J. Y., KIM K.-S. & PICKERILL R. K. 2002. — Cretaceous nonmarine trace fossils from the Hasandong and Jinju formations of the Namhae area, Kyongsangnamdo, Southeast Korea. *Ichnos* 9: 41–60.
- KIMITSUKI R., PROCTOR H. & GINGRAS M. K. 2025. — *Cochlichnus*-like traces produced by chironomid midge larvae (Diptera: Chironomidae: Orthoclaadiinae) and a summary of traces produced by modern chironomids. *Ichnos* 32 (4): 355–363. <https://doi.org/10.1080/10420940.2025.2549832>
- KOCUREK G. & NIELSON J. 1986. — Conditions favourable for the formation of warm-climate aeolian sand sheets. *Sedimentology* 33 (6): 795–816. <https://doi.org/10.1111/j.1365-3091.1986.tb00983.x>
- KÖHLER G., HERTZ A., SUNYER J., SEIPP R. & MONTEIRO A. 2007. — Herpetologische forschungen auf den Kapverden unter besonderer berücksichtigung des Kapverdischen Riesenskinks, *Macrosclincus coctei*. *Elaphe* 15: 75–79.
- LEE D. S. 1969. — Moisture toleration: a possible key to dispersal ability in three fossorial lizards. *Bulletin of the Maryland Herpetological Society* 5: 53–56.
- LONGMAN M. W. 1980. — Carbonate diagenetic textures from near-surface diagenetic environments. *AAPG Bulletin* 64 (4): 461–487. <https://doi.org/10.1306/2F918A63-16CE-11D7-8645000102C1865D>
- LUCAS S. G. 2024. — A critical review of eolian ichnofacies. *Geosciences* 14 (9): 246. <https://doi.org/10.3390/geosciences14090246>
- MADEIRA J., RAMALHO R. S., HOFFMANN D. L., MATA J. & MOREIRA M. 2020. — A geological record of multiple Pleistocene tsunami inundations in an oceanic island: the case of Maio, Cape Verde. *Sedimentology* 67 (2): 1529–1552. <https://doi.org/10.1111/sed.12612>
- MALADEN R. D., DING Y., LI C. & GOLDMAN D. I. 2009. — Undulatory swimming in sand: subsurface locomotion of the sandfish lizard. *Science* 325 (5938): 314–318. <https://doi.org/10.1126/science.1172490>
- MARTIN J. E., HUTCHINSON M. N., MEREDITH R., CASE J. A. & PLEDGE N. S. 2004. — The oldest genus of scincid lizard (Squamata) from the Tertiary Etadunna Formation of South Australia. *Journal of Herpetology* 38 (2): 180–187. <https://doi.org/10.1670/25-03A>
- MATEO J. A., GARCÍA-MÁRQUEZ M., LÓPEZ-JURADO L. F. & PETHER J. 1997. — Nuevas observaciones herpetológicas en las Islas Desertas (Archipelago de Cabo Verde). *Boletín de la Asociación Herpetológica Española* 8: 8–11.
- MATEO J. A., GENIEZ P., VEIRET P. & LÓPEZ-JURADO L. F. 2022. — *Reptiles de Macaronesia. Azores–Madeira–Salvajes–Canarias–Cabo Verde*. Asociación Herpetológica Española, Madrid, 473 p.
- MAYORAL E., LEDESMA-VÁSQUEZ J., BAARLI G., SANTOS A., RAMALHO R., CACHÃO M., DA SILVA C. M. & JOHNSON M. 2013. — Ichnology in oceanic islands: case studies from the Cape Verde Archipelago. *Palaeogeography, Palaeoclimatology, Palaeoecology* 381–382: 47–66. <https://doi.org/10.1016/j.palaeo.2013.04.014>
- MILÁN J. & LOOPE D. B. 2007. — Preservation and erosion of theropod tracks in eolian deposits: examples from the Middle Jurassic Entrada Sandstone, Utah, USA. *Journal of Geology* 115: 375–386. <https://doi.org/10.1086/512758>
- MIRALLES A., VASCONCELOS R., PERERA A., HARRIS D. J. & CARRANZA S. 2011. — An integrative taxonomic revision of the Cape Verdean skinks (Squamata, Scincidae). *Zoologica Scripta* 40 (1): 16–44. <https://doi.org/10.1111/j.1463-6409.2010.00453.x>
- MORAVEC J. 2023. — Herpetological notes from the islands of São Vicente and Santo Antão, Cabo Verde. *Zoologia Caboverdiana* 11: 3–9.
- MORAVEC J. & MORAVCOVÁ L. 2025. — First observation of pollen transport in endemic Cape Verdean *Chioninia* scincid lizards (Scincidae). *Journal of the National Museum (Prague), Natural History Series* 194 (1): 5–12. <https://doi.org/10.37520/jnmpnhs.2025.002>
- MUNIZ G. C. B. 1980. — *Cochlichnus lagartensis* ichnosp. nov., ichnofóssil da Formação Lagarto, Grupo Estância, Estado de Sergipe. *Anais da Academia Brasileira de Ciências* 52: 101–103.
- MUNIZ G. C. B. 1985. — *Cochlichnus sousensis*, icnoespécie da Formação Sousa, Grupo Rio do Peixe, Estado da Paraíba, in *Coletânea de Trabalhos Paleontológicos, VIII Congresso Brasileiro de Paleontologia*. DNPM, Brasília: 239–241.
- NASA JPL 2013. — *NASA Shuttle Radar Topography Mission Global 1 arc second Topography*. NASA JPL.
- NOAA NATIONAL CENTERS FOR ENVIRONMENTAL INFORMATION 2009. — *ETOPO1 1 Arc-Minute Global Relief Model*. NOAA National Centers for Environmental Information. Available at: <https://doi.org/10.7289/V5C8276M> [last accessed on 4 January 2026].
- ORŁOWSKI S. 1989. — Trace fossils in the Lower Cambrian sequence in the Świętokrzyskie Mountains, central Poland. *Acta Palaeontologica Polonica* 34: 211–231.
- PASTEUR G. 1981. — A survey of the species groups of the Old World scincid genus *Chalcides*. *Journal of Herpetology* 15: 1–16. <https://doi.org/10.2307/156340>
- RAINFORTH E. C. 2005. — *Ichnotaxonomy of the fossil footprints of the Connecticut Valley (Early Jurassic, Newark Supergroup, Connecticut and Massachusetts)*. PhD dissertation, Columbia University, 1302 p.
- RAMALHO R. 2011. — *Building the Cape Verde Islands*. Springer, Berlin–Heidelberg, 207 p. https://doi.org/10.1007/978-3-642-19103-9_5
- RAMALHO R., HELFFRICH G., COSCA M., VANCE D., HOFFMANN D. & SCHMIDT D. N. 2010a. — Vertical movements of ocean island volcanoes: insights from a stationary plate. *Marine Geology* 275 (1–4): 84–95. <https://doi.org/10.1016/j.margeo.2010.04.009>
- RAMALHO R., HELFFRICH G., COSCA M., VANCE D., HOFFMANN D. & SCHMIDT D. N. 2010b. — Episodic hotspot swell growth inferred from variable uplift from the Cape Verde hotspot islands. *Nature Geoscience* 3: 774–777. <https://doi.org/10.1038/ngeo982>

- RAMALHO R., HELFFRICH G., SCHMIDT D. N. & VANCE D. 2010c. — Tracers of uplift and subsidence in the Cape Verde Archipelago. *Journal of the Geological Society* 167: 519–538. <https://doi.org/10.1144/0016-76492009-056>
- REINECK H. E. & SINGH I. B. 2012. — *Depositional Sedimentary Environments: with Reference to Terrigenous Clastics*, 2nd ed. Springer, Berlin, 550 p. <https://doi.org/10.1007/978-3-642-81498-3>
- RINDSBERG A. K. 1994. — Ichnology of the Upper Mississippian Hartselle Sandstone of Alabama, with notes on other Carboniferous formations. *Geological Survey of Alabama Bulletin* 158: 1–107.
- SAMROCK L. K., DULLO W. C. & HANSTEEN T. H. 2018. — Large-scale fossil dune on Maio, Cape Verde. *International Journal of Earth Sciences* 107: 2931–2932. <https://doi.org/10.1007/s00531-018-1622-x>
- SERRALHEIRO A. 1970. — *Geologia da Ilha de Maio (Cabo Verde)*. Junta de Investigações do Ultramar, Lisboa, 103 p.
- SEYMOUR R. S., WITHERS P. C. & WEATHERS W. W. 1998. — Energetics of burrowing, running and free-living in the Namib Desert golden mole (*Eremitalpa namibensis*). *Journal of Zoology* 244 (1): 107–117. <https://doi.org/10.1111/j.1469-7998.1998.tb00012.x>
- SHARPE S. S., DING Y. & GOLDMAN D. I. 2013. — Environmental interaction influences muscle activation strategy during sand-swimming in the sandfish lizard *Scincus scincus*. *Journal of Experimental Biology* 216 (2): 260–274.
- SHARPE S. S., KOEHLER S. A., KUCKUK R. M., SERRANO M., VELA P. A., MENDELSON J. III & GOLDMAN D. I. 2015. — Locomotor benefits of being a slender and slick sand swimmer. *Journal of Experimental Biology* 218 (3): 440–450. <https://doi.org/10.1242/jeb.108357>
- SHENBROT G. & KRASNOV B. 1997. — Habitat relationships of the lizard fauna in the Ramon erosion cirque, Negev Highlands (Israel). *Journal of Zoology* 241 (3): 429–440. <https://doi.org/10.1111/j.1469-7998.1997.tb04835.x>
- STANLEY D. C. A. & PICKERILL R. K. 1998. — Systematic ichnology of the Late Ordovician Georgian Bay Formation of southern Ontario, eastern Canada. *Royal Ontario Museum Life Sciences Contributions* 162: 1–55. <https://doi.org/10.5962/bhl.title.53483>
- TASCH P. 1968. — A Permian trace fossil from the Antarctic Ohio Range. *Transactions of the Kansas Academy of Science* 71 (1): 33–37. <https://doi.org/10.2307/3627396>
- UCCP/MAHOT 2010. — *Unidade de Coordenação do Cadastro Predial (UCCP)/Ministério do Ambiente, Habitação e Ordenamento do Território (MAHOT), República de Cabo Verde* [Digital elevation model at 1:5000 scale of Maio Island].
- UCHMAN A. 1998. — Taxonomy and ethology of flysch trace fossils: A revision of the Marian Książkiewicz collection and studies of complementary material. *Annales Societatis Geologorum Poloniae* 68 (2–3): 105–218.
- UCHMAN A., PIKA-BIOLZI M. & HOCHULI P. A. 2004. — Oligocene trace fossils from temporary fluvial plain ponds: an example from the Freshwater Molasse of Switzerland. *Eclogae Geologicae Helvetiae* 97 (1): 133–148. <https://doi.org/10.1007/s00015-004-1111-z>
- UCHMAN A., HSIEH S., NINARD K., ŁAPCIK P. & ŁASKA W. 2024. — Bioturbation in stabilized Quaternary inland dunes of the European Sand Belt in Poland. *Palaeogeography, Palaeoclimatology, Palaeoecology* 640: 112091. <https://doi.org/10.1016/j.palaeo.2024.112091>
- UETZ P., FREED P., AGUILAR R., REYES F., KUDERA J. & HOŠEK J. (eds) 2025. — *The Reptile Database*. Available at: <http://www.reptile-database.org> [last accessed on 12 January 2026].
- VASCONCELOS R., BRITO J. C., CARRANZA S. & HARRIS D. J. 2013. — Review of the distribution and conservation status of the terrestrial reptiles of the Cape Verde Islands. *Oryx* 47: 77–87. <https://doi.org/10.1017/S0030605311001438>
- VIALOV O. S. 1979. — New bioglyphs and problematics from Middle Asia. *Paleontologicheskii Sbornik* 16: 80–89.
- VITT L. J. & CALDWELL J. P. 2013. — *Herpetology: An Introductory Biology of Amphibians and Reptiles*. 4th ed., Academic Press, London, 776 p.
- WEBBY B. D. 1970. — Late Precambrian trace fossils from New South Wales. *Lethaia* 3 (1): 79–109. <https://doi.org/10.1111/j.1502-3931.1970.tb01265.x>
- WELLSTEAD C. F. 1982. — Lizards from the Lower Valentine Formation (Miocene) of northern Nebraska, USA. *Journal of Herpetology* 16: 364–375. <https://doi.org/10.2307/1563566>
- WON S. & KONG D. Y. 2023. — Application of RTI to improve image clarity of a trace fossil *Cochlichnus* from the Jinju and Haman formations. *Economic and Environmental Geology* 56 (4): 397–408. <https://doi.org/10.9719/EEG.2023.56.4.397>
- YANG S. & SHEN Y. 1999. — Early Tertiary trace fossils from King George Island, West Antarctica. *Acta Palaeontologica Sinica* 38: 203–217.
- YANG S., SONG Z. & LIANG D. 1983. — Late Carboniferous–Early Permian flysch trace fossils from Ali, Xizang (Tibet), China. *Earth Science, Journal of the Wuhan College of Geology* 1: 93–103.
- YANG S., HU C. & SUN Y. 1987. — Discovery of Late Devonian trace fossils from the Guodingshan district, Hanyang, China and its significance. *Earth Science, Journal of the Wuhan College of Geology* 12: 1–8.
- ZAZO C., GOY J. L., DABRIO C. J., SOLER V., HILLAIRE-MARCEL C., GHALEB B., GONZÁLEZ-DELGADO J. A., BARDAJÍ T. & CABERO A. 2007. — Quaternary marine terraces on Sal Island (Cape Verde Archipelago). *Quaternary Science Reviews* 26 (11–12): 876–893. <https://doi.org/10.1016/j.quascirev.2006.12.014>
- ZAZO C., GOY J. L., HILLAIRE-MARCEL C., DABRIO C. J., GONZÁLEZ-DELGADO J. A., CABERO A., BARDAJÍ T., GHALEB B. & SOLER V. 2010. — Sea-level changes during the last and present interglacials in Sal Island (Cape Verde Archipelago). *Global and Planetary Change* 72: 302–317. <https://doi.org/10.1016/j.gloplacha.2010.01.006>
- ZHANG X. 1991. — Trace fossils from the Tiaomajian Formation (Middle Devonian) in Xinhua, Xiangtan and adjacent areas. *Hunan Geology* 10: 97–104.
- ZHANG X.-P. & WANG D.-R. 1996. — A restudy on Silurian–Devonian ichnofossils from northwestern Hunan area. *Acta Palaeontologica Sinica* 35: 475–489.

Submitted on 23 January 2026;
accepted on 8 April 2026;
published on 12 October 2026.