

Review

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Review

Trace Fossils on Oceanic Volcanic Islands of Macaronesia: Current State of Knowledge

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Abstract

Ichnological research on trace fossils from the volcanic islands of Macaronesia (North Atlantic) is reviewed in light of significant advances over the past two decades. These studies contribute to the interpretation of paleoenvironments and enhance our understanding of the biota preserved in Miocene–Holocene shallow marine and non-marine deposits across the Azores, Cape Verde, Canary, Madeira, and Salvagens archipelagos. Trace fossils provide evidence of organisms not always known from body fossils, or whose potential tracemakers are absent from the extant island fauna. They include sedimentary burrows, borings in hard substrates, and traces of plant–insect interactions. Some ichnotaxa are widespread and common (e.g., *Bichordites monastiriensis*, *Dactyloidites otto*, *Macaronichnus segregatis*, *Ophiomorpha nodosa*, *Thalassinoides* sp.), whereas others are rare. Several new ichnotaxa have also been described from the islands, including *Alaichnus kabuverdiensis* (cumulative trace of bivalve siphons), *Centrichnus dentatus* (attachment trace of verrucid barnacles), *Diopatrighnus santamariaensis* (polychaete tubes armored with shell debris), *Ericichnus bromleyi* and *E. asgaard* (bioerosion grooves of regular echinoids), and *Rebuffoichnus guanche* (coleopteran pupation chambers). Despite these advances, ichnological research in Macaronesia remains uneven, with many topics still underexplored and significant gaps in the geographic and inventory record.

Keywords: ichnology; ichnotaxonomy; ichnofossils; borings; burrows; cenozoic

1. Introduction

Since Darwin's time, islands isolated from continents by deep seas have been central to understanding the history of life, particularly speciation and the dispersal of biota. Among them, oceanic volcanic islands hold special significance because they arise directly from submarine volcanic activity rather than from continental drift or submergence. Unlike continental fragments, which may already carry biota at the moment of separation, oceanic volcanic islands are initially sterile and must be colonized entirely by incoming organisms [1,2].

Sedimentary rocks are rare or poorly exposed on the emerged surfaces of volcanic islands. For a long time, this led to relatively little attention from geologists and paleontologists, who traditionally focused on sedimentary successions. However, during the past three decades, remarkable progress has been achieved, particularly in the Atlantic archipelagos of Macaronesia, which include the Azores, Madeira, the Salvagens, the Canary Islands, and Cape Verde. Studies have shown that marine deposits on these islands are often fossiliferous. Numerous works have documented body fossils from diverse taxonomic groups in Miocene, Pliocene, and Quaternary deposits, forming a solid basis for palaeoecological and palaeogeographical interpretations [3–5].

Complementing the record of body fossils are trace fossils—the preserved evidence of biological activity that modifies the substrate and typically exhibits recurrent morphological patterns. The organisms that produced them are often absent as body fossils, meaning trace fossils provide essential, and sometimes unique, insights into past environments and biotic interactions. They therefore represent a powerful tool for paleoenvironmental reconstruction [6–8]. Over the last two decades, the ichnological record from Macaronesia has expanded considerably, including the

description of new ichnotaxa. This paper reviews recent advances in the study of trace fossils from these islands and highlights their importance for understanding colonization processes and the ecological history of oceanic volcanic islands.

2. Synopsis of Selected Trace Fossils

The trace fossils preserved in the sedimentary successions of Macaronesia show broadly comparable assemblages across the archipelagos. This chapter outlines the most common and distinctive ichnotaxa. As elsewhere, the ichnological record can be grouped into two main categories: burrows, produced in soft and unconsolidated substrates, and borings, produced in hard substrates such as rocks or skeletal material.

For clarity, the discussion is organized into three parts: marine burrows, marine borings, and trace fossils from continental deposits. The latter include a more diverse range of structures, such as borings, burrows, root traces, and plant-damage traces attributable to insect activity.

2.1. Burrows in Marine Deposits

Bichordites monastiriensis Plaziat & Mahmoudi (Figure 1A) is a horizontal, straight to gently winding, complex burrow characterized by meniscate backfill surrounding a central core, typically with a heart-shaped cross section. The upper surface of the core bears a narrow median furrow, whereas the lower surface displays a longitudinal crest. The core, interpreted as the drainage structure of a burrowing irregular echinoid—most likely of the *Echinocardium* group [9–12]—is preferentially cemented and thus usually much better preserved than the surrounding meniscate fill.

Dactyloidites otto (Geinitz) (Figure 1B) forms nearly complete rosette structures composed of outwardly radiating, horizontal to subhorizontal cylindrical elements, occasionally showing spreiten displacement. It is interpreted as a feeding structure [13], most likely produced by polychaete worms [14,15].

Diopatrachus santamariaensis Uchman, Quintino & Rodrigues, 2017 in [16] (Figure 1C) is a vertical to inclined tube, armored predominantly with crushed or uncrushed bivalve shell valves. The valves are arranged concave-upward and oriented mostly perpendicular to the burrow axis. It is attributed to the activity of polychaetes, comparable to the burrowing behavior of extant *Owenia* [16].

Macaronichnus segregatis Clifton & Thompson (Figure 1D) is a variably oriented, usually straight to winding cylindrical burrow characterized by a light-grained core surrounded by a mantle of darker grains. It is produced by opheliid polychaetes that segregate sand grains, ingesting the lighter fraction—presumably richer in microbial content—while rejecting darker grains [17–19]. Two ichnosubspecies are recognized: the smaller *M. s. segregatis* and the larger *M. s. degiberti* [20].

Ophiomorpha nodosa Lundgren (Figure 1E) is a tubular, rarely branched burrow with walls bearing a distinctly knobby external texture. In some cases, abundant interconnecting branches form a boxwork network. It is interpreted as a dwelling and feeding, or facultative farming, structure produced by decapod crustaceans [6,21–24].

Palaeophycus isp. consists of predominantly horizontal, tubular burrows with smooth walls. It is interpreted as a dwelling and feeding structure, produced by various deposit-feeding or carnivorous invertebrates, most likely polychaetes [25,26].

Piscichnus waitemata Gregory (Figure 1F) is a bowl-shaped depression interpreted as a feeding trace, produced primarily by rays and, in some cases, by mammals hunting invertebrates within the sediment [66].

Thalassinoides isp. (Figure 1G) comprises predominantly horizontal, cylindrical, branched burrows that may form complex networks. It is interpreted as a semi-permanent dwelling and feeding structure, produced mainly by obligatory or facultative deposit-feeding decapod crustaceans [6,27,28].

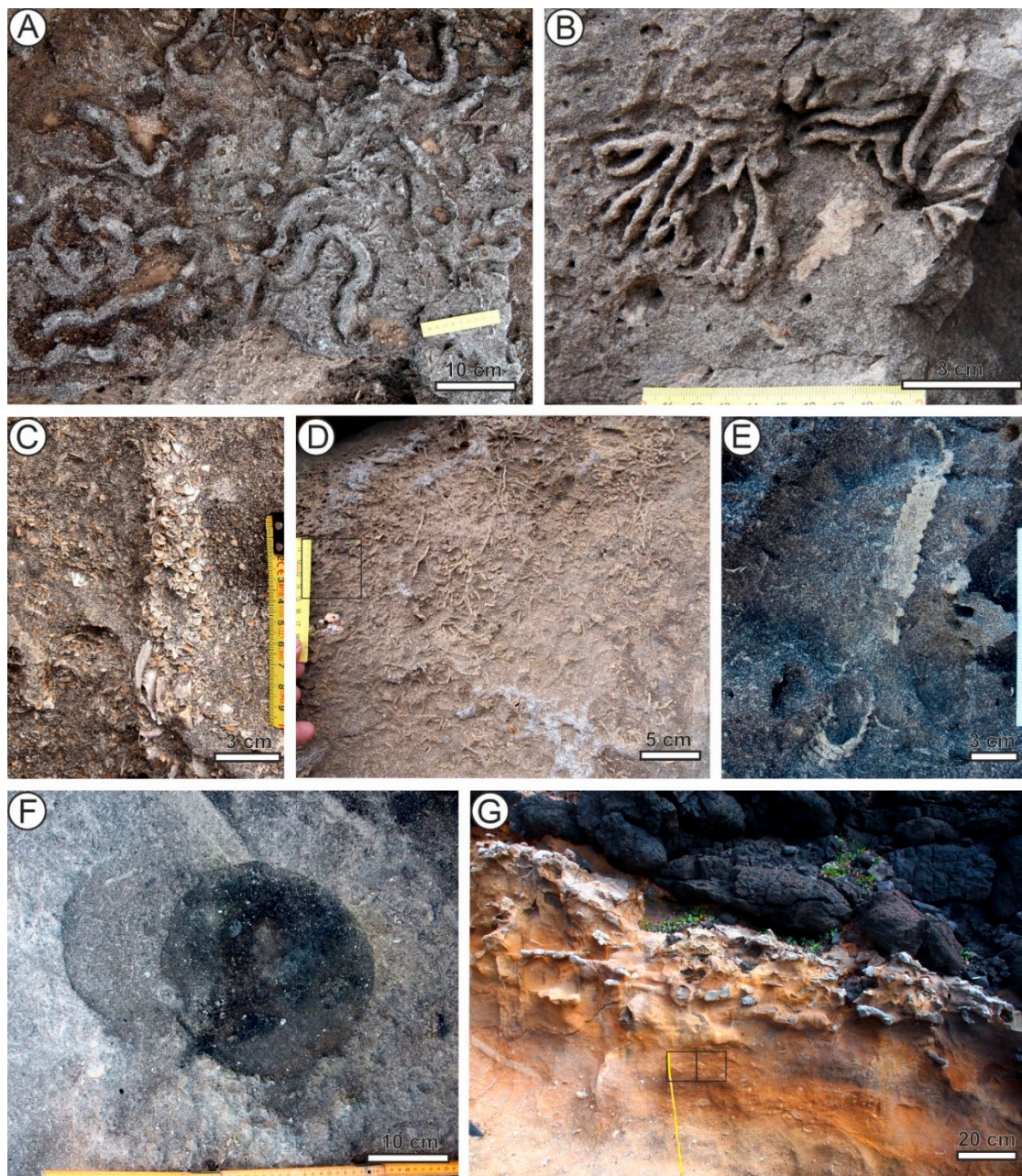


Figure 1. Trace fossils (fossil burrows) in Pliocene calcarenites-sandstones of Santa Maria, Azores. **A.** *Bichordites monastiriensis*. **B.** *Dacyloidites ottoii*. **C.** *Diopatrighnus santamariaensis*. **D.** *Macaronichnus segregatis*. **E.** *Ophiomorpha nodosa*. **F.** *Piscichnus waitemata*. **G.** *Thalassinoides* isp. A-F –Malbusca; G – Castillo.

2.2. Marine Borings

Caulostrepsis spp. (Figure 2A) are U-shaped galleries, commonly interconnected by a vane and forming pouch-shaped structures. They are borings with a single entrance or embedment structure, wider in the distal portion than at the apertural part and typically display elliptical to dumbbell-shaped cross sections. These structures are produced mainly by spionid polychaetes of the genus *Polydora*, and less frequently by some eunicid polychaetes [29,30].

Centrichnus dentatus Uchman, Wisshak, Madeira, Melo, Sacchetti, Ávila & Ávila (Figure 2B) is a small, symmetric or asymmetric depression on shells, circular or elliptical in outline, and bounded by a groove and/or a series of pits. It is interpreted as an attachment trace produced by verrucid barnacles [31].

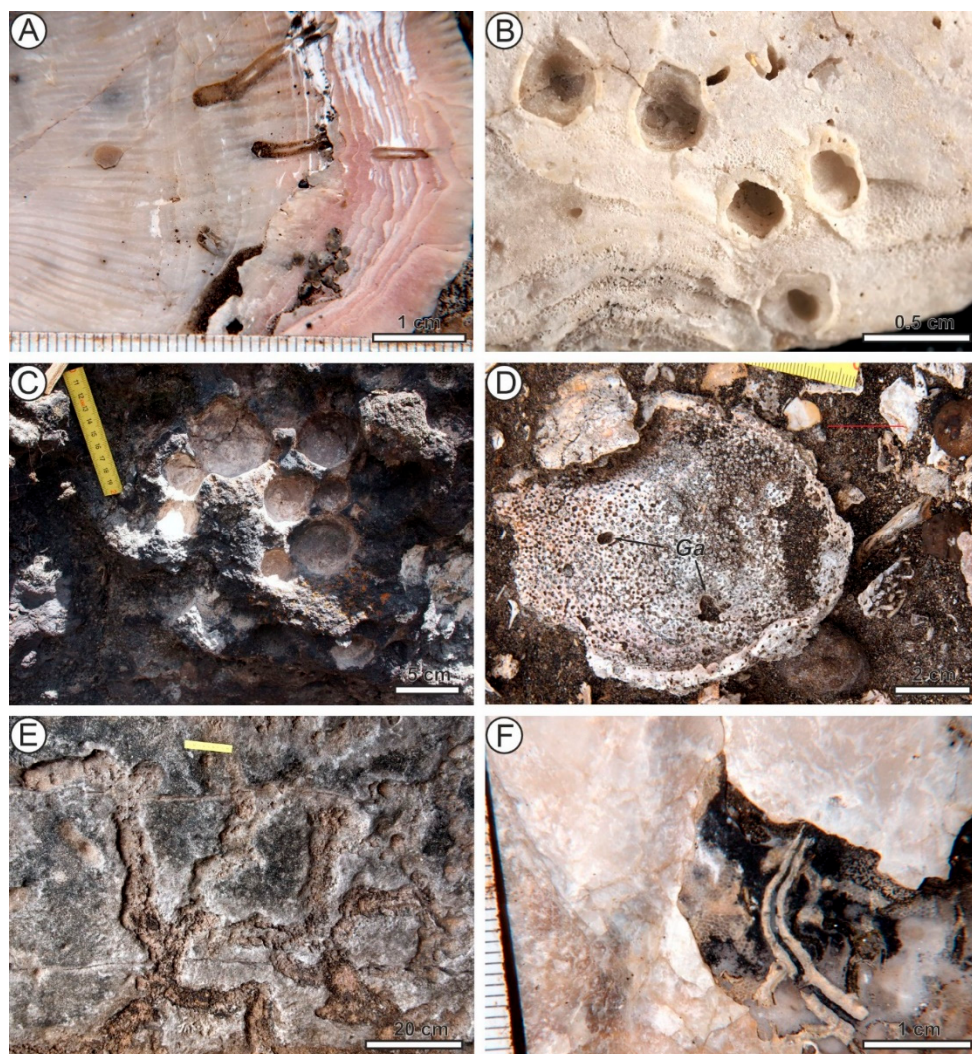


Figure 2. Trace fossils (borings) from Santa Maria, Azores. **A.** *Caulostrepis* isp. in *Spondylus* shell valve, Pliocene, Baía de Nossa Senhora. **B.** *Centrarchus dentatus* in an oyster shell valve, Pliocene, Pdara-que-pica. **C.** *Circolites kotouensis* in basalt, Pleistocene, Prainha. **D.** *Entobia* isp. and *Gastrochaenolites* isp. (Ga) in a bivalve shell, Pliocene, Malbusca. **E.** *Ericichnus bromleyi* in calcarenite, Pleistocene, Ichnofossil Cave. **F.** *Maeandropolydora* isp., Pliocene, Baía de Nossa Senhora.

Circolites kotouensis Mikuláš (Figure 2C) are bowl-shaped structures formed in rocky substrates, including basalts. They are interpreted as traces produced by regular echinoids, and in modern Macaronesia by *Paracentrotus lividus* [32,33].

Entobia spp. (Figure 2D) are branched systems of galleries composed of small chambers interconnected by tunnels and opening to the surface. They are produced by clionaid sponges in calcareous hard substrates, most commonly in mollusk shells [34]. Several ichnospecies of *Entobia* are distinguished based on morphological details.

Ericichnus bromleyi Santos et al. (Figure 2E) is an irregularly sinuous grooves on the rock surfaces, which may converge or diverge, and form irregular networks. It is produced by regular echinoids [57].

Gastrochaenolites spp. (Figure 2D) are flask-shaped cavities in hard substrates, consisting of a chamber and a neck. They are interpreted as borings produced by bivalves [35].

Maeandropolydora spp. (Figure 2F) are long, sinuous, and typically contorted cylindrical galleries in hard calcareous substrates, opening to the surface. The limbs of the galleries may be interconnected. They are interpreted as borings produced by suspension-feeding spionid polychaetes [29].

2.3. Trace Fossils in Continental Deposits

Cuniculonomus isp. is a linear, undulating to sinuous leaf mine, of uniform width or with a slight terminal widening [36,37]. It is interpreted as the feeding trace of flies (*Agromyzidae*) or moths (*Gracillariidae*) [38].

Palmiraichnus castellanosi (Roselli) is an ovoid to subcylindrical structure with a smooth, shiny chamber. It is straight or slightly curved, concave or truncated on one side, and rounded on the other, where a spiral closure separates the main chamber from the ante-chamber. The ante-chamber may be filled with structureless sediment. This trace fossil occurs in palaeosols and is interpreted as the nesting burrow of solitary bees of the family *Andrenidae* [39,40].

Phagophytichnus ekowskii van Amerom consists of semicircular excisions along the margins of plant leaves that do not reach the midrib, forming an incomplete oval to elliptical outline. It is interpreted as a feeding trace produced by butterfly caterpillars or locust larvae [37].

Rebuffoichnus guanche Genise et al. (Figure 3) comprises subovoid to subcylindrical structures composed of a chamber and a wall. The outer wall surface is rough and lumpy, whereas the inner surface is smooth or nearly smooth. The chamber is ellipsoid in outline and circular in cross section. The wall may exhibit a rounded opening [41].



Figure 3. Three specimens of *Rebuffoichnus Guanche*. Top view in the upper row and side view in the lower row. Pleistocene, Altillo, Gran Canaria, Canary Islands.

Xyloniichnus trypetus Genise consists of a boxwork of anastomosing longitudinal, tangential, and radial tunnels, rectangular to circular in cross section, developed at various depths within the xylem. The tunnels may be filled with frass. This trace is interpreted as the work of buprestid beetles or termites [37].

3. Ichnological Investigations in Macaronesia

3.1. Burrows in Marine Deposits

Exposed marine deposits in the Macaronesian islands are almost exclusively restricted to shallow-marine Miocene–Holocene facies, influenced primarily by wave and storm activity. These deposits, typically lacking quartz grains, consist mainly of rocks ranging from calcarenites to lithic sandstones, with variable contributions from volcanic-derived components. Conglomerates also occur, mostly in fan deltas and fossil beach deposits. Characteristic depositional architectures include shoreface-to-backshore sheet-like covers or patches (at outcrop scale) preserved in cliffs and marine terraces, clinoforms prograding into the open ocean, and fan-delta cones. In several cases, sedimentary lithosomes are encapsulated between lava flows. Trace fossils are common and locally abundant in Miocene and Pleistocene calcarenite–sandstone exposures. The most widespread

ichnotaxa include *Macaronichnus segregatis*, *Bichordites monastiriensis*, *Thalassinoides* isp., *Ophiomorpha nodosa*, and *Dactyloidites otto*, with other forms occurring more sporadically.

The first comprehensive ichnological study of marine sediments on volcanic islands was conducted by Mayoral et al. [42], who examined Miocene and Pleistocene deposits of the Cape Verde Archipelago. Some ichnotaxa had already been reported in related papers from the same period [43–46]. For example, *Sinusichnus* isp. was documented from São Nicolau Island [46]. Mayoral et al. [42] recognized two principal ichnoassociations: (1) a Miocene *Thalassinoides* ichnoassociation (restricted to Maio Island) and (2) a Pleistocene *Macaronichnus*–*Dactyloidites* ichnoassociation (Santiago, Maio, São Nicolau). Within the latter, mostly horizontal trace fossils such as *Dactyloidites otto*, *Dactyloidites* isp., *Bichordites monastiriensis*, *Bichordites* isp., *Cardioichnus* isp., *Phycodes* isp., *Teichichnus rectus*, aff. *Taenidium* isp., and *Palaeophycus tubularis* were assigned to the proximal Cruziana ichnofacies. In contrast, *Macaronichnus* and vertical burrows including *Skolithos*, *Conichnus conicus*, *Ophiomorpha nodosa*, and *Ophiomorpha* isp. were referred to the Skolithos ichnofacies. Importantly, based on the geometric relationship between submarine and subaerial lava flows, as well as the stratigraphic distribution of ichnofossil-bearing deposits, Mayoral et al. [42] calibrated the transition from the proximal Cruziana ichnosubfacies to the Skolithos ichnofacies at water depths of approximately 12–18 m.

The Miocene *Thalassinoides* ichnoassociation comprises *Thalassinoides suevicus*, *Thalassinoides* isp., *Conichnus conicus*, *Dactyloidites otto*, and *Macaronichnus segregatis*, and belongs to the proximal Cruziana ichnofacies. In addition, a *Psilonichnus* ichnofacies, represented by a monospecific assemblage of *Psilonichnus upsilon* (produced by crabs), was recognized in a Pleistocene section of Maio Island, indicating an upper foreshore–backshore setting. At the Nossa Senhora da Luz section (Santiago), protected-bay sediments contain almost exclusively *Thalassinoides* [47].

Mayoral et al. [48] described thin pockets of Upper Pleistocene biocalcirudites encapsulated between lava flows on Santiago Island. These contained *Thalassinoides*, *Rhizocorallium commune irregulare*, *Rhizocorallium jenense versum* (a new ichnosubspecies), *Alaichnus kabuverdiensis* (a new ichnogenus and ichnospecies, interpreted as a cumulative trace of bivalve siphons), and cf. *Dactyloidites*. Taphonomic analysis allowed interpretation of erosion–sedimentation events, colonization sequences, and estimates of erosion depth during deposition.

In the Canary Islands, ichnological investigations are less numerous. Sánchez-Pinto et al. [50] reported *Dactyloidites otto* from Pliocene deposits of Fuerteventura, also mentioned by Martín González [50] and Martín González & Castillo [51]. Schneider et al. [52] described Skolithos ichnofacies traces in Miocene–Pliocene fan-delta deposits of the Cuevas los Guinchos section, Las Palmas Detritic Formation, Gran Canaria. Mayoral et al. [53] recognized *Rosselia socialis*, *Macaronichnus segregatis*, *Bichordites monastiriensis*, and *Ophiomorpha nodosa* in the same formation, assigning them to the Skolithos and proximal Cruziana ichnofacies. Uchman et al. [54] reinterpreted these assemblages in terms of sedimentation dynamics within a transgressive–regressive cycle of fan-delta progradation, rather than as indicators of bathymetric change. At the Las Rehoyas section of the same formation, *Macaronichnus segregatis*, *Ophiomorpha nodosa*, *Rosselia socialis*, *Skolithos linearis*, and indeterminate *Thalassinoides* have been described, assigned to the Skolithos ichnofacies, and interpreted as evidence of seafloor stabilization within sand-dominated intervals of a conglomeratic fan-delta system [55].

By contrast, extensive ichnological studies have been carried out on Santa Maria Island (Azores), well known for its fossiliferous formations. Meireles et al. [56] reported *Diplocraterion*, *Crossopodia*, *Rhizocorallium*, *Ophiomorpha*, and *Thalassinoides* from storm-influenced Miocene–Pliocene sandy deposits of the Castello section, though the presence of the first three ichnotaxa is doubtful based on later observations. In the Ichnofossil Cave, Santos et al. [57] documented *Arenicolites* isp., *Bichordites* isp., *Macaronichnus segregatis*, *Dactyloidites otto*, and *Ophiomorpha nodosa* from Miocene–Pliocene deposits [see also 58]. In the Pedra-que-pica section, associated with an exceptional coquina, assemblages include *Macaronichnus segregatis*, ?*Ophiomorpha* isp. (misidentified as *Thalassinoides* isp.

by Kirby et al. [59]), *Asterosoma* isp., and *Bichordites* isp. [60,61]. These traces helped refine the palaeoenvironmental interpretation and stratigraphic position of the coquina.

Uchman et al. [62,63] described unusual vertically oriented *Macaronichnus segregatis* from Miocene–Pliocene calcarenites and sandstones of Santa Maria. These deposits, formed on an erosionally truncated island surface and prograding clinoforms on its southern coast, are interpreted as reflecting vertical migration of trace makers following the mixing zone of fresh and marine waters. This ichnotaxon cooccurs with *Piscichnus* isp., *Diopatrighnus* isp., *?Palaeophycus* isp., *?Parmaichnus* isp., *Thalassinoides* isp., *Ophiomorpha nodosa*, *?Pylonichnus* isp., *Asterosoma* isp., and *Dactyloidites otto*, associated with *Pylonichnus*, *Skolithos*, and *Cruziana* ichnofacies, confirming shallow-water deposition [64]. A similar assemblage, including *?Scolicia* isp. and *?Curvolithus* isp., is linked to a major hurricane bed in the Malbusca section [65]. *Diopatrighnus santamariaensis* [16], a new ichnospecies from Santa Maria, is a vertical tube armored with shell fragments, interpreted as the trace of owenid polychaetes. *Piscichnus waitemata*, produced mainly by hunting rays, is abundant in the sediment cover of the truncated island but less common in clinoform deposits on the island's flanks, probably due to lower temperatures and reduced preservation potential [66]. Subtidal clinoforms encapsulated between lava flows on the eastern margin of the island yielded *Thalassinoides*, *Scolicia* isp., *Palaeophycus* isp., *Diopatrighnus santamariaensis*, *Macaronichnus segregatis*, *Ophiomorpha* isp., and *Piscichnus waitemata*, which refine interpretations of depositional environments [67]. The presence of crustacean burrows (*Ophiomorpha* isp., *Ophiomorpha nodosa*, *Thalassinoides* isp., *?Pylonichnus* isp., *?Parmaichnus* isp.) has further clarified the diversity of burrowing decapods in the Pliocene–Pleistocene of Santa Maria [68].

In contrast, information about fossil burrows from Madeira and the Salvagens is scarce. From middle Miocene calcarenites of the Madeira Archipelago, *Thalassinoides* was reported from Ilhéu de Cima [33], and *Bichordites* isp. and *Dactyloidites* isp. from Ilhéu de Baixo [69].

3.2. Marine Bioerosion Structures

Marine bioerosion structures in Macaronesia occur mostly on rocky substrates—typically calcareous, more rarely volcanic—and on skeletal elements, especially mollusk shells.

In the **Cape Verde Archipelago**, Santos et al. [70] reported *Gastrochaenolites* isp. in Pliocene–Pleistocene limestones, corals, and basalt boulders at Tarrafal outcrop and Ponta das Bicudas (Santiago Island). Mayoral et al. [42] described *Circolites kotoucensis* (echinoid boring, also found in basalt), bivalve borings (*Gastrochaenolites torpedo*, *G. cluniformis*, *Gastrochaenolites* isp.), and sponge borings (*Entobia* isp.) developed on the Miocene–Pleistocene unconformity of Maio Island and on basaltic paleocliffs at Ponta das Bicudas, Santiago [see also 48]. These assemblages belong to the *Entobia* ichnofacies. Baarli et al. [47] also documented *Gastrochaenolites* isp. and *C. kotoucensis* on Santiago, noting that *Gastrochaenolites* penetrated through hydrozoan *Millepora alaicornis* into the underlying basalt. *C. kotoucensis* has also been recorded from São Nicolau [45,57], Sal, and Santo Antão (in basalts), and Brava (in phonolites) [58,72].

In the **Canary Islands**, Martín-González et al. [72] reported *Entobia*, *Gastrochaenolites*, and probable vermetid borings in Pliocene mollusk shells from Fuerteventura. Verde et al. [73] introduced *Santichnus mayoralis* as a new ichnogenus and ichnospecies representing the attachment trace of vermetid gastropods, identified in Miocene–Pliocene mollusk shells from Fuerteventura and La Graciosa (near Lanzarote).

In the **Madeira Archipelago**, Santos et al. [74] documented *Gastrochaenolites torpedo*, *G. vivus*, *G. lapidicus*, and *Entobia* isp. in Miocene algal crusts and corals on a basaltic rocky shore at Ilhéu de Cima near Porto Santo; notably, *G. lapidicus* also penetrated into basalt. Subsequent work at the same locality revealed *G. ornatus*, which likewise entered basalt [70]. Additional *Gastrochaenolites* isp. were found in Miocene corals and rhodoliths [75]. Santos et al. [76] also described *Imbutichnus costatum*, a bioclastration structure resulting from overgrowth of a Miocene hermatypic coral on a pyrgomatid barnacle. However, bioclastration features are no longer regarded as trace fossils [77,78].

In the **Azores**, records are concentrated on Santa Maria Island, with only rare finds from other islands. Boring traces by regular echinoids—now recognized as *Circolites kotoucensis*—were first reported from Holocene basalts of São Miguel [79,80]. Ávila et al. [81] described Pleistocene *Circolites kotoucensis* (Figure 2C) in basalts and *Gastrochaenolites* produced by *Leiosolenus ariestatus* in algal limestones at Prainha (Santa Maria). In the Ichnofossil Cave (Santa Maria), Santos et al. [57] distinguished two new ichnospecies of echinoid grazing grooves, *Ericichnus bromleyi* (Figure 2E) and *E. asgaardi*, as well as *C. kotoucensis*. Similar grooves were reported from tuffites in Sal (Cape Verde). Ávila et al. [58,61] noted *Gastrochaenolites* isp., *Entobia* isp., and *Caulostrepsis* isp. in bivalve shells from the Pliocene coquina of the Pedra-que-pica geosite and the Ponta do Cedro section [67]. *Gastrochaenolites* and *Entobia* also occur in a paleocliff below a large storm bed at Malbusca [82] and in shells armoring *Diopatrachus santamariaensis* (Figure 1C) [16]. *Gastrochaenolites* cf. *torpedo* (produced by *Leiosolenus ariestatus*) was reported in bioclasts, rhodoliths, and algal encrustations at Ponta do Cedro [67]. This boring, along with *Entobia*, is also present in rhodoliths of Malbusca [65] and in Pleistocene (MIS 5e) algal buildups [83].

A new ichnospecies, *Centrichnus dentatus* (Figure 2B), was described from the Pedra-que-pica coquina [31]. Produced by the barnacle *Verruca spengleri* in oyster shells, it co-occurs with *Talpina* isp., *Entobia* isp., *Maeandropolydora* isp., and *Gastrochaenolites* isp. The assemblage was assigned to the *Gnathichnus* ichnofacies, reflecting early colonization of hard substrates, often within months.

Dávid et al. [84] recorded 22 ichnotaxa of bioerosion structures in Lower Pliocene deposits of the Baía de Nossa Senhora section (Santa Maria). The assemblage is dominated by well-preserved *Entobia*, but also includes *Gastrochaenolites*, *Caulostrepsis*, *Maeandropolydora*, *Trypanites* (sipunculid worms), *Talpina* (phoronid worms), and *Iramena* (ctenostome bryozoans). These borings, belonging to the *Entobia* ichnofacies, closely resemble assemblages from the Paratethys, Mediterranean, and eastern Atlantic regions—consistent with the general Neogene shallow-water faunal affinities of the Azores.

Modern bioerosion has also been studied. Wisshak et al. [85] conducted in-situ experiments on the submarine slope of Faial Island, spanning intertidal to bathyal depths. They identified 43 ichnotaxa, including microborings produced by cyanobacteria, chlorophytes, fungi, and other chemotrophs; attachment scars of diatoms, foraminifera, bryozoans, cirripeds [see also 31], gastropods, bivalves, and brachiopods; grazing traces from gastropod radulae and echinoids; and several macroborings (*Entobia* isp., *Caulostrepsis taeniola*, *Maeandropolydora decipiens*, *Talpina ramosa*).

3.3. Trace Fossils in Continental Environments

Insect nests have been reported from the Canary Islands for over a century, primarily in Pleistocene and Holocene sandy dunes, sandy silts associated with palaeosols, and calcretes of Lanzarote and Fuerteventura (40,86–92 and references therein). These structures were initially attributed to *Celliforma* and interpreted as nests of solitary bees. Genise [94], however, suggested alternative interpretations as coleopteran pupal chambers or lepidopteran cocoons.

Further studies by Meco et al. [94,95] described mass occurrences of these traces in the Pliocene, Pleistocene, and Holocene of Fuerteventura, interpreting them as evidence of episodic locust invasions. Later analyses of material from the island recognized bee nests attributed to *Palmiraichnus* or to an undescribed ichnogenus of the Celliformidae, as well as coleopteran pupal cells (*Rebuffoichnus*), both produced under semiarid paleoclimatic conditions during wetter intervals [96]. *Rebuffoichnus* isp. was subsequently documented in association with megarrhizoliths in Pleistocene aeolianites of Gran Canaria [97]. Genise et al. [40] introduced the new ichnospecies *Rebuffoichnus guanche*, interpreted as pupation chambers of coleopterans (Curculionidae or Scarabaeidae). *Palmiraichnus castellanosi* has also been reported from the Pleistocene and Holocene of Fuerteventura, Lanzarote, and Gran Canaria [39].

The distribution of insect nests across the archipelago is uneven. Genise et al. [40] noted abundant occurrences in the eastern islands (Fuerteventura and Lanzarote) but only sporadic records

in the western islands (Tenerife, La Palma, La Gomera, El Hierro), where suitable deposits are scarce. Comparable fossils from the more remote Macaronesian archipelagos remain undocumented.

A more recent ichnological development in Macaronesia concerns traces of **plant–insect interactions**. Pokorný & Borges [98] reported *Phagophytichnus ekowskii* (marginal feeding traces on leaves), *Cuniculonomus* isp. (leaf-mining traces; see also [98]), and *Xylonichnus trypetus* (wood borings) from Quaternary plant collections in the Azores (São Miguel, Terceira, Faial). These findings have since been critically reviewed by Gois-Marques et al. [99].

Borings produced by insects in bones have been examined experimentally in Gran Canaria [100]. However, no evidence of insect borings in fossil bones has yet been reported from Macaronesia.

Plant root structures occupy a conceptual “grey zone” between trace fossils, plant body fossils, and diagenetic features. Root-induced deformations can represent genuine bioturbation, but differentiating them from abiotic structures is often challenging [78,79]. This issue has been addressed in studies of Pleistocene root structures in Gran Canaria and Tenerife (97,101–103). Similar interpretative difficulties have been noted for rhizobial nodules from the Pleistocene of Madeira [104].

4. Concluding Remarks

The review demonstrates that ichnological research in Macaronesia has made substantial progress over the past two decades, establishing the archipelago as the best-ichnologically studied among volcanic islands. Many islands have been investigated for the first time, often through initiatives led by the University of the Azores. Consequently, the known list of ichnotaxa has expanded considerably, including numerous new ichnogenera and ichnospecies, and understanding of the distribution of trace fossils and their palaeoenvironmental significance has improved markedly. These studies also show that a variety of burrowing and boring animals can colonize newly emerged volcanic islands, even when their extant representatives are not present locally.

Nevertheless, important gaps remain. Microborings in the fossil record of Macaronesia have not yet been studied. Continental ichnology is largely restricted to insect nests in the Canary Islands [39,40] and plant–insect interaction traces [98]. Neoichnological research—such as studies of bioerosion traces [85] and ray-fish burrows [66]—has begun, but much more remains to be done. Fossil burrows are entirely unknown from the Madeira and Salvagens archipelagos. It is also unclear whether the widespread occurrence of the ray-fish hunting burrow *Piscichnus waitemata* in Santa Maria extends to other islands. In general, geographic trends in trace fossil distribution are poorly understood, and several islands remain completely unexplored ichnologically.

These gaps highlight the need for continued ichnological studies, integrated with other palaeobiological and sedimentological research, to better understand the colonization history and palaeoecology of biota on Macaronesia’s volcanic islands.

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