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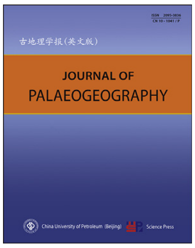

Research article

Rhodoliths and trace fossils record stabilization of a fan-delta system: An example from the Mio-Pliocene deposits of Gran Canaria (Canary Islands, Spain)

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Abstract Fan-delta systems are geomorphological structures and sedimentary records seldom preserved on oceanic volcanic islands. The generally coarse-grained deposits belonging to the Las Palmas Detritic Formation (Mio-Pliocene) at the Las Rehoyas section, NE part of Gran Canaria Island (Canary Islands, Spain), contain abundant but relatively small rhodoliths, non-nucleated, in partly bioturbated (*Skolithos* ichnofacies) sand-dominated strata. This section consists of four sedimentary units deposited in a fan-delta system that developed on a marine platform in the northeastern part of the island. The system was flooded during the late Miocene to early Pliocene, a non-eruptive phase on Gran Canaria Island. Stabilization of the fan delta due to a relative rise in sea level enabled colonization by burrowing organisms and the development of rhodoliths, which were redeposited by storms from the lower shoreface—offshore to the foreshore—middle shoreface environment.

Keywords Coralline red algae, Trace fossil, Palaeoenvironmental interpretation, Volcanic island, Las Palmas Detritic Formation, Macaronesian islands

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1. Introduction

Evidence for the deposition and maintenance of mobile sediment agglomerations (e.g., fan-delta systems) is often lacking around oceanic volcanic islands (Melo *et al.*, 2018). Moreover, coarse-grained, conglomerate-dominated fan deltas are inhospitable habitats for colonization by organisms due to a hard, unstable substrate with a high rate of deposition, and an ephemeral, not rarely catastrophic character. Additionally, fluctuations in salinity resulting from freshwater input or water turbidity contribute to additional constraints (for depositional conditions, refer to Nemec and Steel (1988), Colella and Prior (1990 and references therein), as well as Nemec (1990). However, marine flooding caused by relative sea level rise can lead to some stabilization of the depositional system (e.g., Bardaji *et al.*, 1990; Postma, 1995), alleviation of these unfavourable factors, and the development of variable biota on the sea floor. Furthermore, these factors around volcanic islands need to occur simultaneously with a period of low volcanic activity to allow favourable conditions for biocolonisation. Nonetheless, these aspects of environmental conditions are rarely the target of study and are usually a matter of bayside observations.

The Mio-Pliocene Las Palmas Detritic Formation (LPDF) in Gran Canaria Island offers a 220—280-m-thick succession of fan-delta deposits, whose dominating fossil-barren lower and upper parts are mostly conglomeratic, while the middle fossiliferous part is mostly sandy. Such extraordinary symmetrical development of the succession and the presence of diverse fossils (e.g., rhodoliths, trace fossils, molluscs, bryozoans, and echinoderms) suggest environmental stabilization. In this paper, the middle part of the LPDF from the Las Rehoyas section is presented as a record of such stabilization, with a focus on facies development and analysis of rhodoliths and trace fossils. Such studies enable the formulation of palaeoenvironmental interpretations contributing to the knowledge of the island. Furthermore, this paper contributes to increasing knowledge of the palaeontology and sea level global changes in the Canary Islands.

Palaeontological studies of the Mio-Pliocene marine deposits in this archipelago have been carried out since the nineteenth century. These studies have contributed to the understanding of the region's past climate, focusing on molluscs (Rothpletz and Simonelli, 1890; Martín-González *et al.*, 2018), crustaceans (Betancort *et al.*, 2014), bryozoans (Sendino and Taylor, 2014), and fishes (Betancort *et al.*, 2016). Nevertheless, little remains known about the rhodoliths (free-living nodules of crustose coralline red algae, Rhodophyta) which are abundant at the Mio-Pliocene Las Rehoyas outcrop in the district of Las Palmas on Gran Canaria Island.

Within the Macaronesian archipelagos, rhodolith deposits have been identified, spanning from the Miocene to recent times (Johnson *et al.*, 2011, 2012, 2016, 2018, 2020; Rebelo *et al.*, 2014, 2016, 2018, 2021a, 2022). Rhodoliths and rhodolith beds are a

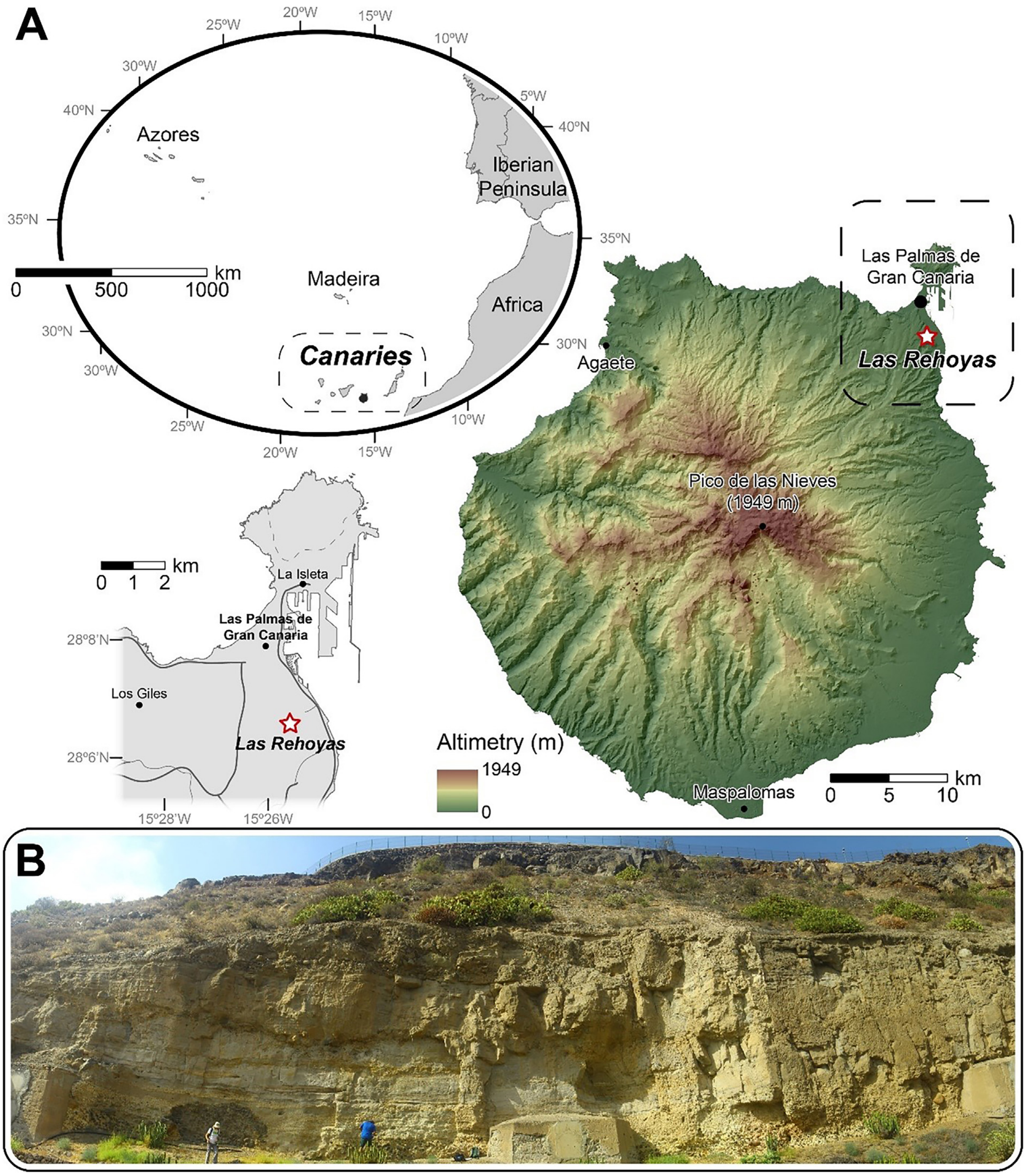

Fig. 1 Location map and exposure. **A)** Location of Gran Canaria Island within the NE Atlantic Ocean (insert); marked with a star is the detailed location of Las Rehoyas palaeontological site; **B)** General view of Las Rehoyas main exposure (investigators measuring ~1.80 m). Coastline in A from the Portuguese Hydrographic Institute free data (https://www.hidrografico.pt/op/33). Digital Elevation Model from Gran Canaria, generated from a 1:5000 scale digital altimetric database (https://opendata.sitcan.es/dataset/base-topografica-5000-20042006).

common feature of modern and ancient carbonate shelves, representing a sedimentary transition from sandy areas to rocky substrates (Riosmena-Rodríguez, 2017). The ecological role of rhodoliths is important in nearshore environments worldwide, from the intertidal to depths of −270 m, the deepest known record for a marine plant (Littler and Littler, 1984). These rhodolith deposits are generally located on older islands with no recent volcanism and a more complex uplift history that contributes to more developed marine shelves (Ramalho *et al.*, 2013). However, there are deposits on younger islands with a poorly developed platform (Rebelo *et al.*, 2018). For example, on the northern coast of Fuerteventura, where the insular platform is wider, there are deposits of rhodoliths, both fossil and contemporary, related to high-intensity waves, currents, and winds (Johnson *et al.*, 2017; Rebelo *et al.*, 2022). Studies on the rhodolith deposits in the Canary Islands, have yet to include details that concern the taxonomic composition or the palaeoecological conditions under which they originated.

Also less studied is the palaeoichnological record of coastal deposits in the Canary Islands (Sánchez-Pinto *et al.*, 2009; Mayoral *et al.*, 2019). However, the presence of ichnofossils in rhodolithic deposits provides additional information about depositional environments, conditions, and evolution over time. Aspects related to the trophism of their producers and their behaviour are essential in interpreting trace fossils, which provides useful information for estimating the depth from the relative position of sea level (Pollard *et al.*, 1993; Uchman and Krenmayr, 2004; Buatois and Mángano, 2011).

2. Geological setting

Gran Canaria Island is located at the centre of the Canarian Archipelago, between latitudes 27°41'44″N—28°12'06″N and longitudes 15°53'30″W—15°20'45″W (Fig. 1A). The Canary Islands, encompassing seven main islands and several islets, are primarily volcanic but, both terrestrial and marine deposits containing tropical biotas characteristic of the Miocene-Pliocene can be found interbedded between the lava flows (Meco *et al.*, 2015 and references therein). The dating of the basaltic flows overlying the fossiliferous levels in the three eastern Canary Islands (Fuerteventura, Lanzarote, and Gran Canaria) (Meco *et al.*, 2015; Carracedo and Troll, 2016) suggests that the age of the fossiliferous deposits is narrowly late Miocene to early Pliocene. The study by Martín-González *et al.* (2018) on gastropod associations from these islands reduces even more this age gap, pointing to the late Miocene (Tortonian) age.

On Gran Canaria Island, a significant volume of sediments deposited as alluvial and fan-delta conglomerates and sandstones, mainly on the N—NE coastal platforms, correspond to the Las Palmas Detritic Formation (LPDF). Cabrera (1985) and Gabaldón *et al.* (1989) distinguished three informal members for the LPDF (Lower, Middle, and Upper) with the Middle Member comprising three main sedimentary environments: beaches, aeolian dunes, and offshore sediments.

The Lower Member, up to 120 m thick, is mostly conglomeratic, although it also includes sandy and silty greyish deposits. It has been inferred that they were deposited in an alluvial fan filling a palaeorelief characterised by large gullies (Cabrera, 1985; Gabaldón *et al.*, 1989). At the top, there occurs a rubefacted cobble level with reddish-orange patina-covered cobbles and traces of coastal honeycomb erosion, indicating a marine incursion. Rhodoliths are scarce.

The Middle Member, up to 30 m thick, also referred to as Facies Santidad (Balcells *et al.*, 1992), is in concordance with the Lower Member, and its base is marked by a fossiliferous level of marine organisms which lies just above the rubefacted level. This member comprises alluvial phonolitic conglomerates and sandstones overlain by clays, volcanic ashes, and shallow-water marine sediments containing molluscs, rhodoliths, bryozoans, and echinoids (Meco *et al.*, 2007). They show significant lateral variability and are referred to as foreshore, shoreface, beaches, eolian dunes, and distal alluvial fan depositional settings. Locally, these deposits are intensively bioturbated, especially in the shoreface and foreshore facies.

The Upper Member is transitional to the felsic pyroclastic materials of the Roque Nublo Group. Elevations of Miocene—Pliocene marine deposits on Gran Canaria range from 50 m to 120 m apsl (above present sea level), which indicate post-depositional uplift movements. Menéndez *et al.* (2008) calculated a mean uplift rate between 0.013 and 0.030 mm/yr in the northeastern sector of Gran Canaria, in the range of those inferred from the raised Pliocene sea-level markers in the same area (0.021—0.024 mm/yr; Pérez-Torrado *et al.*, 2002).

The Las Rehoyas section represents mostly the Middle Member of LPDF. It is located in the municipality of Las Palmas de Gran Canaria (Fig. 1) between latitudes 28°06'32″N—28°06'28″N and longitudes 15°25'40″W—15°25'33″W. Its exposure, oriented NW—SE, forms a transect of the LPDF parallel to the present-day coastline.

3. Methods

A detailed log was measured from the stratigraphic section at Las Rehoyas, and the main facies were described during fieldwork. In addition to rhodoliths, shelly macrofossils and trace fossils were recorded. The echinoderms and molluscs collected are housed in the marine fossil collection of the Museum of Natural Sciences of Tenerife, Canary Islands (TFMCFO) under

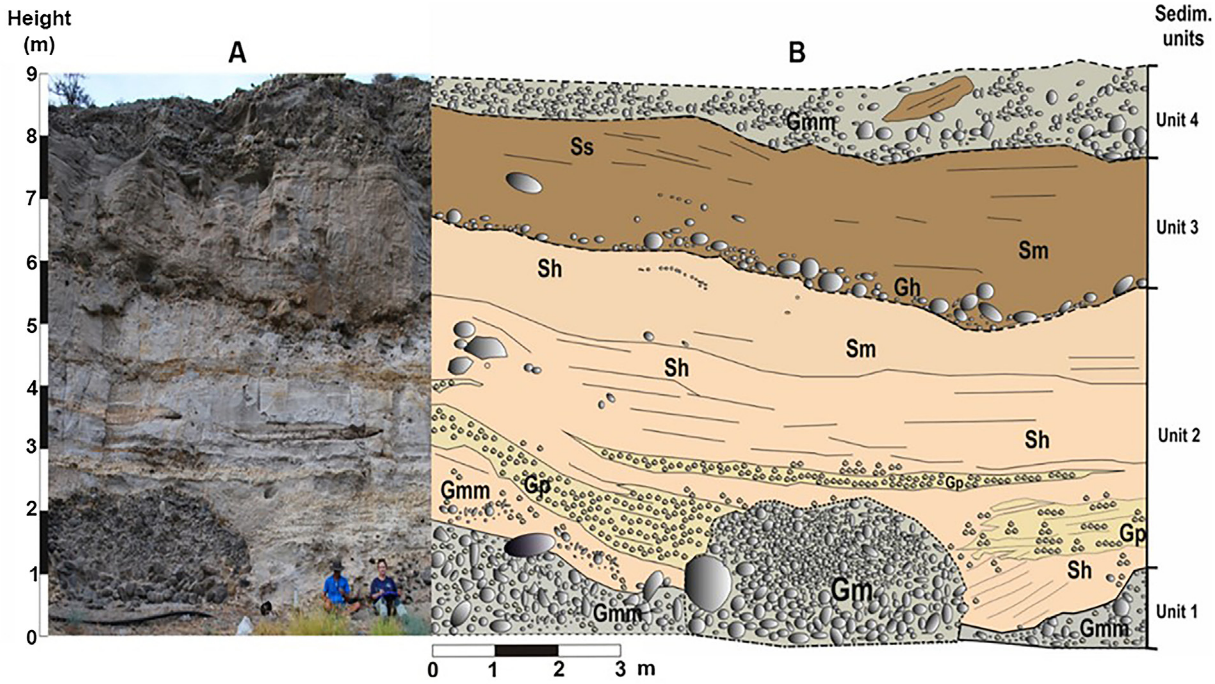

Fig. 2 The studied Las Rehoyas site. **A)** General view of the exposure; **B)** Graphical expression of the exposure with the indication of facies code by Miall (1978, 1996). Gmm: clast-supported, massive conglomerate; Gm: block-supported and imbricated conglomerate; Gp: cross-bedded rhodolith conglomertes; Gh: lag deposits made by boulders and blocks of epiclastic conglomerates; Sm: massive laminated coarse sandstone; Ss: slightly laminated medium to coarse sandstone; Sh: biogenic cross-laminated sandstone beds.

TFMCFO-1302 to TFMCFO-1341, TFMCFO-2537, TFMCFO-5940 and TFMCFO 6145 to TFMCFO-6156. For every horizon within Unit 2 depicted in the stratigraphic section (Figs. 2 and 3), a thorough examination of 30 rhodoliths was conducted. Rhodoliths were measured on-site across three main axes (long, intermediate, and short). All measurements were plotted on a triangular plot among spherical, ellipsoidal, and discoidal shapes (e.g., Bosence, 1976, 1983). Size and rhodolith frequency were also subject to analysis using bar graphs for comparison among horizons 1—3. Once measured, each rhodolith was broken apart to determine the nature of its core. A random subset of rhodoliths was later selected for taxonomic studies. Seven thin sections were studied under a compound polarizing microscope (Leica DM750P) equipped with a digital camera (Leica ICC50W). Anatomical and taxonomical terminologies on corallines conform to the works by Braga *et al.* (1993), Irvine and Chamberlain (1994), Rasser and Piller (1999), and Hrabovský *et al.* (2016); growth form terminology follows Woelkerling *et al.* (1993), and branching density follows Bosence (1983). Cell and conceptacle dimensions were measured according to Rasser and Piller (1999) using *ImageJ*. Mean (M) and standard deviation (SD) were calculated for both cells and conceptacles, whenever the number of measurements allowed (n = 5).

4. Results

4.1. *Sedimentary units and facies analysis*

The outcropping succession of the Las Rehoyas fossiliferous sequence is approximately 200 m in length and ca. 9 m in overall thickness. Lateral facies changes are frequent in this section (Fig. 2). The synthetic stratigraphic column illustrated in Fig. 3 outlines four main sedimentary units, characterised by differences in lithology, grain size, sedimentary structures, textures, color, and fossil content (summarized in Table 1). The main facies associations were used for the interpretation of depositional environments. The top of the sequence is then covered by Pliocene basaltic lavas dated 3.9 Ma to 3.0 Ma (Pérez-Torrado *et al.*, 1995). The base of the sequence is not visible at this site, but Unit 1 most likely corresponds to the first level of weathered phonolithic conglomerates included in the Lower Member of the LPDF, indicated on the Geological Map of Las Palmas de Gran Canaria as Unit 6 (Barrera and Balcells, 1989), whereas the remaining units correspond to the Middle Member of the LPDF, composed of conglomerates and marine sands (Gabaldón *et al.*, 1989), indicated as Unit 7 in the Geological Map (Barrera and Balcells, 1989). The

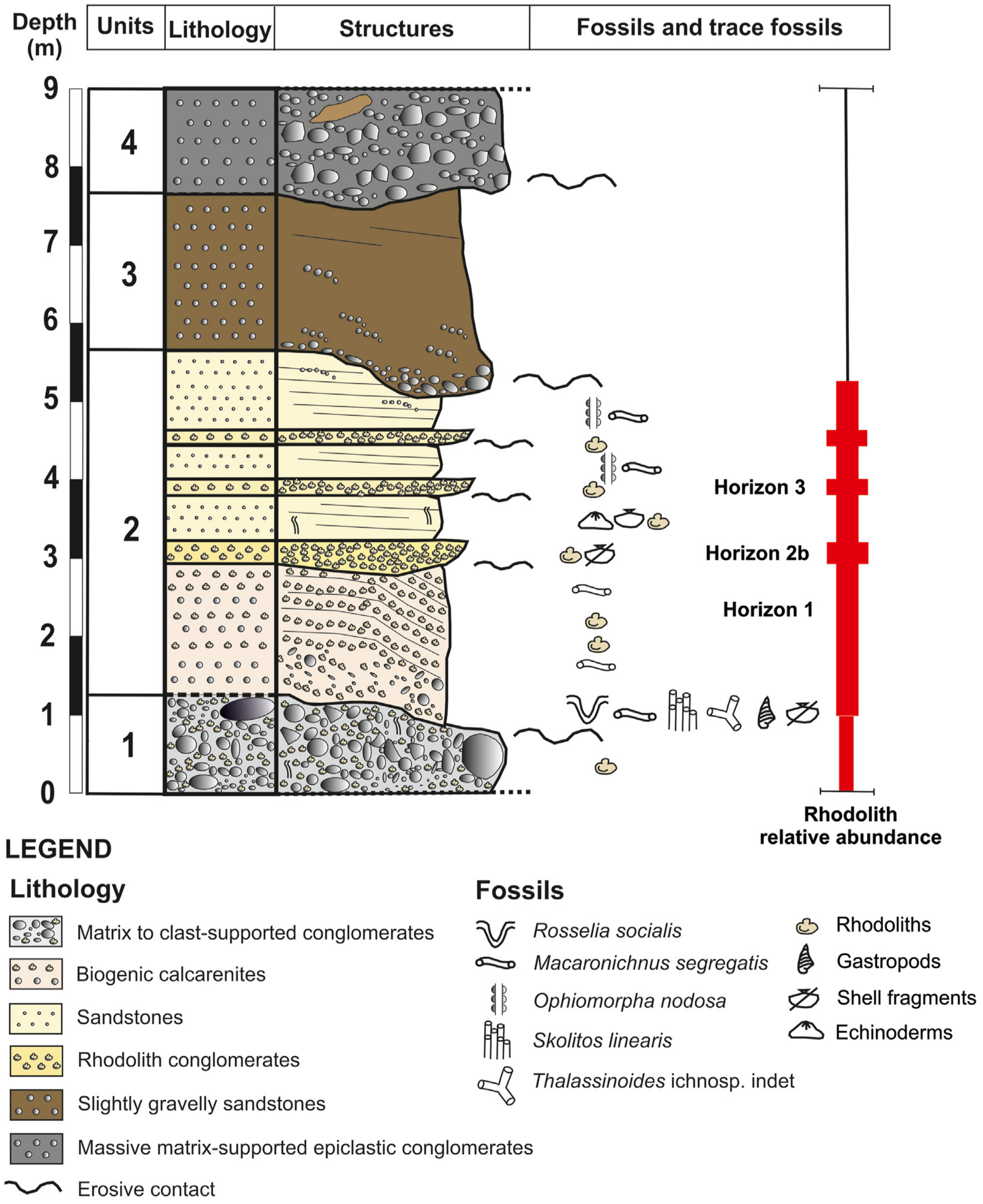

Fig. 3 Synthetic stratigraphic column from the Las Rehoyas section and palaeontological site, Gran Canaria Island.

upper part of the sequence at Las Rehoyas is partially covered by a slope deposit and by Pliocene subaerial basalts corresponding to Unit 9 of the geological map (Barrera and Balcells, 1989).

4.2. Rhodolith taxonomy

Phylum Rhodophyta Wettstein, 1901
Class Florideophyceae Cronquist, 1960
Subclass Corallinophycidae Le Gall and Saunders, 2007
Order Corallinales PSilva and Johansen, 1986
Family Mastophoraceae Townsend and Huisman, 2018
Subfamily Mastophoroideae Setchell, 1943
Genus *Lithoporella* (Foslie) Foslie (1909).
Lithoporella sp.
Fig. 4A and B.

Table 1 Summary of facies association and their description at Las Rehoyas section (Las Palmas, Gran Canaria Island).

Sedimentary units	Facies association	Description
Unit 4	Gmm	Massive matrix-supported conglomerates. Erosive base.
Unit 3	Gh, Sm, Ss	Slightly gravelly sandstone beds. Lag deposit over an eroded surface. Imbricated clasts and large-scale cross-lamination.
Unit 2	Sh, Sm	Biogenic cross-laminated sandy beds (sedarenites) interspersed with rhodoliths gravel-sized cross-bedded forming bars. Trace fossils (*C. conicus, M. segregatis, O. nodosa, S. linearis, Thalassinoides* isp. indet.) are abundant in the bottom part of this unit.
	Gm, Gp	Clast-supported epiclastic conglomerates. Gravels to boulder size and imbricated clasts.
Unit 1	Gmm, Gm	Massive matrix-supported epiclastic conglomerates made of basaltic and phonolotic blocks with rhodolith matrix. Channel filled with clast-supported epiclastic conglomerates and imbricated clasts.

Description: Encrusting thin thallus with applanate branches growing interspersed with other coralline thalli. Thallus dorsiventral and dimerous; core region unistratose, filaments composed of palisade cells; thallus 1—3 cells thick. Cells are rectangular in section, and their size ranges from 7 to 14 μm (M = 10; SD = 3) in diameter and 17—32 μm (M = 23; SD = 4) in length. Cell fusions are present. Two conceptacles completely raised above the thallus surface are 177—256 μm in diameter and 87—99 μm in height. The roof thickness is 33 μm. No pore canals were visible.

Remarks: The genus *Lithoporella* is characterized by having: (i) bi/tetrasporangial conceptacles with roofs developed from filaments peripheral to the fertile area and interspersed among sporangial initials, (ii) the thin thallus with dimerous construction, (iii) palisade cells in primigenous filaments, (iv) laterally connected cells with fusions, and (v) trichocytes arranged in solitary or in groups (Hrabovský *et al.*, 2016 and references therein).

In the present work, *Lithoporella* sp. was identified based on the presence of cell fusions and the thin thallus with dimerous construction and large palisade cells. However, because the only two conceptacles present do not have visible pores, it is not possible to further identify the species.

Lithoporella sauvageaui (Foslie) W.H. Adey is the only species of the genus modernly documented for the Canary coasts. It is a species still morphologically poorly known, which was originally described as *Litholepis sauvageaui* by Foslie (1905) from some tiny plants collected by Sauvageau in Puerto Orotava (now Puerto de la Cruz) in Tenerife. According to Lemoine and Mme (1929), who also documented it for Gran Canaria around Las Palmas, it is a tiny but relatively common species. It was later found in the Cabo Verde Islands (Lemoine and Mme, 1964). On the other hand, *Lithophyllum geometricum* Lemoine and Mme (1929), a modern species described for the Canary Islands, appears to exhibit no discernible differences from *Lithoporella sauvageaui* (Afonso-Carrillo and Sansón, 1999).

Thin section studied: RO-1/RH/1, RO-1/RH/3, RO-1/RH/4, RO-1/RH/5.

Order Hapalidiales W.A. Nelson, J.E. Sutherland, T.J. Farr and H.S. Yoon, 2015

Genus *Boreolithothamnion* P.W. Gabrielson, Maneveld, Hughey and V. Peña (2023).

Boreolithothamnion sonderi (Hauck) P.W. Gabrielson, Maneveldt, Hughey and V. Peña (2023).

Fig. 4C—E.

Description: The growth form is encrusting. The thin thallus has a dorsiventral organization and monomerous construction with non-coaxial core filaments. Thallus thickness is 0.3—0.4 mm, becoming 0.6 mm when conceptacles are present. Cells are rectangular, both in the core and peripheral filaments. The core region is 65—163 μm in thickness, and the core cells are 6—14 μm (M = 10; SD = 2) in diameter and 10—18 μm (M = 14; SD = 2) in length. Cells of peripheral filaments are 7—13 μm (M = 9; SD = 1) in diameter and 11—22 μm (M = 17; SD = 3) in length. Cell fusions are present in both the core and peripheral regions. Multiporate conceptacles raised above the thallus surface without raised rims and slightly arched roofs are 377—673 μm in diameter and 108—235 μm high. Roof thickness is 48—61 μm. The pore canals vary from 9 μm to 30 μm (M = 15; SD = 5) in diameter and are 33—49 μm (M = 42; SD = 5) in height. Epithallial cells are flattened and seem to be flared.

Remarks: The thallus type, the presence of cell fusions, the flat and flared epithallial cells, and the multiporate conceptacles with flat and slightly arched roofs without raised rims indicate the genus *Lithothamnion* to be identified (Braga *et al.*, 1993; Irvine and Chamberlain, 1994). However, recently, Gabrielson *et al.* (2023), based on phylogenetic analyses, redefined the genus *Lithothamnion*, and all its

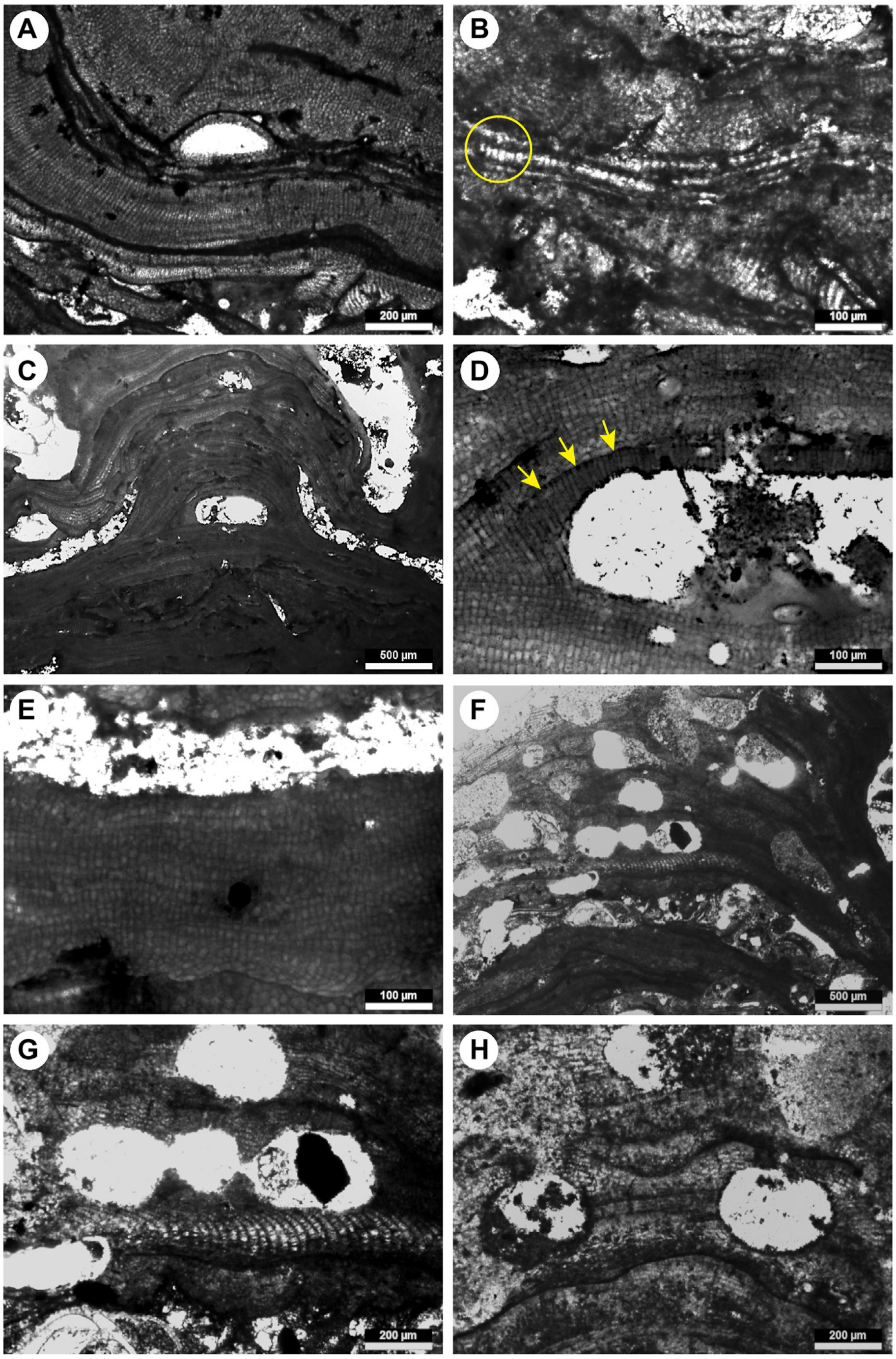

Fig. 4 Representative rhodolith forming crustose coralline algae from the Las Rehoyas section, Gran Canaria Island. **A—B)** *Lithoporella* sp.; cell fusions are marked by the yellow circle (B); **C—E)** *Boreolithothamnion sonderi*; epithallial cells are marked by yellow arrows (D); **F—H)** *Mesophyllum* sp.

seven species, *L. glaciale* (the generitype), *L. lemoineae*, *L. soriferum*, *L. tophiforme*, *L. giganteum*, *L. phymatodeum*, and *L. sonderi*, which have been transferred to the genus *Boreolithothamnion*. *Lithothamnion sonderi*, which is now *Boreolithothamnion sonderi*, was identified here based on the subepithallial initials that are similar in size to the subtending cortical cells and a single layer of conspicuously flared epithallial cells (Chamberlain, 1992; Gabrielson *et al.*, 2023).

The only modern identification of this species in the Canary Islands is due to Lemoine and Mme (1929), who documented it based on samples collected by Børgesen in Tenerife (as *Lithothamnion sonderi* Hauck). All subsequent reports are based on Lemoine data. Some of the plants studied by Lemoine were

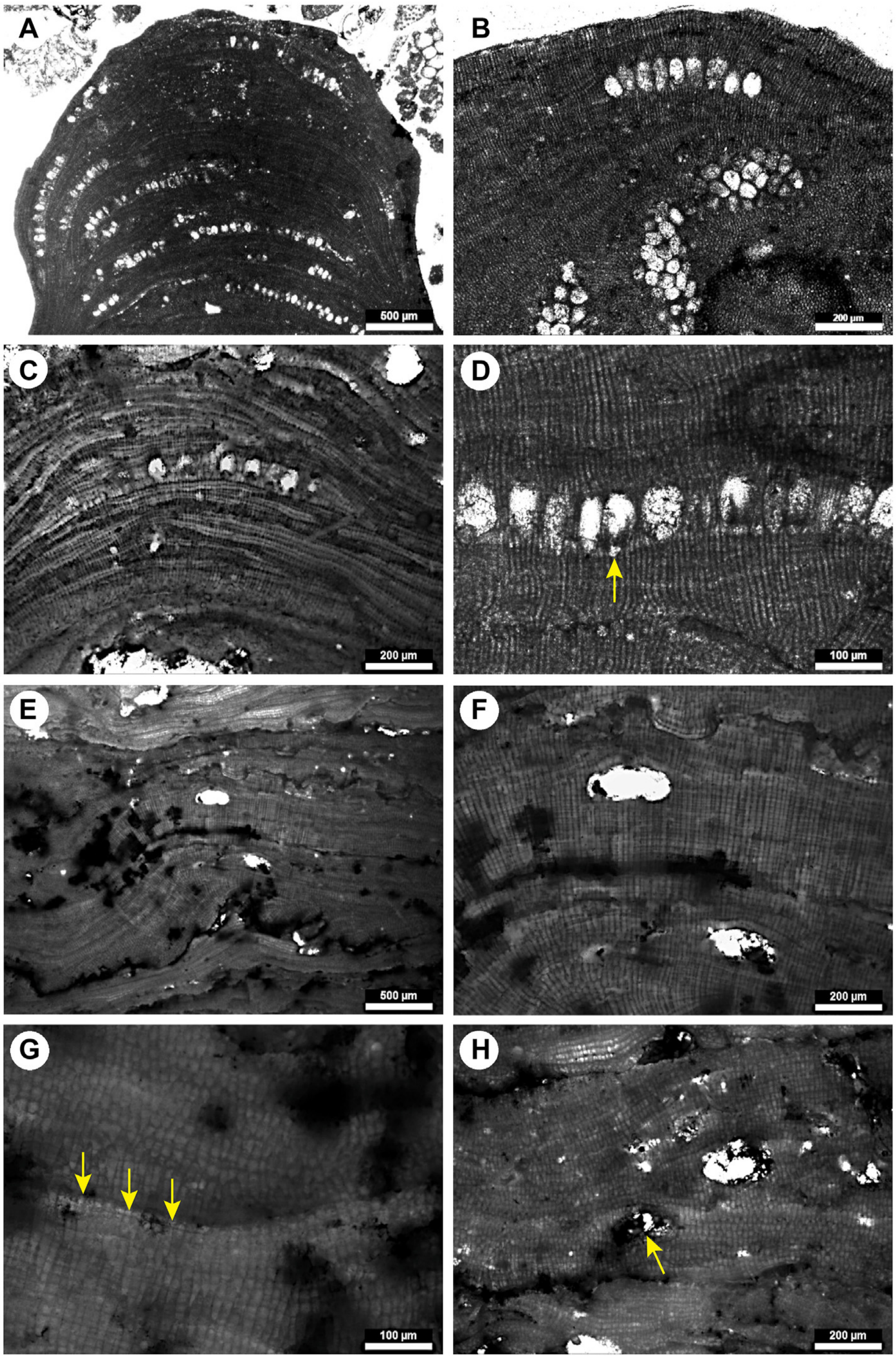

Fig. 5 Representative rhodolith-forming crustose coralline algae (cont.) from the Las Rehoyas section, Gran Canaria Island. **A—D)** *Sporolithon* sp.; yellow arrow points to a line of stalk cells (D); **E—H)** ?*Lithophyllum* sp.; arrows point to epithallial cells (G); single arrow points to a columella (H).

anatomically examined and illustrated by Afonso-Carrillo (1982).

Thin section studied: RO-1/RH/2, RO-1/RH/4.

Genus *Mesophyllum* Me. Lemoine, 1928
Mesophyllum sp.
Fig. 4F—H.

Description: Very thin thallus with monomerous dorsiventral construction and a coaxial continuous ventral core. Thalli are 0.25—0.33 mm in thickness, becoming 0.55 mm thick where there are conceptacles. The core region is very well developed, consisting of the majority of the thallus. The peripheral region is only visible around the conceptacles. The core thickness is 134—192 μm (M = 162; SD = 17). The core cells are trapezoidal in shape, measuring 7—13 μm (M = 10; SD = 2) in diameter and 18—29 μm (M = 25; SD = 4) in length. They are arranged in concentric arcs with good alignment of cells in adjacent filaments. Cell fusions are present. Small multiporate conceptacles with raised rims protrude at the thallus surface and then become buried in the thallus. The conceptacles are 338—499 μm in diameter and 217—263 μm in height. The pore canals are conical in shape and measuring 12—23 μm (M = 18; SD = 3) in diameter and 51—66 μm (M = 59; SD = 3) in height. The conceptacles' roofs are 6 or 7 cells thick.

Remarks: The multiporate conceptacles, the cell fusions, and the coaxial core indicate the genera *Mesophyllum* and *Synathrophyton*. Because these two genera are separated based on their spermatangial filaments, which are only rarely observed in fossil material, we delimited here the genus *Mesophyllum* in its traditional palaeontological sense, in which coaxial growth occurs (Iryu *et al.*, 2009, 2012; Guiry and Guiry, 2023). The peripheral filaments were only observed around the conceptacles, and their poor preservation hindered further species identification. *Mesophyllum expansum* (Philippi) Cabioch and Mendoza is the most common modern species of the genus *Mesophyllum* on the coasts of the Canary Islands, where it has been repeatedly documented mainly as *Mesophyllum lichenoides* (Lemoine and Mme, 1929; Afonso-Carrillo, 1982; Afonso-Carrillo *et al.*, 1985). Athanasiadis and Neto (2010) showed that the Canary Islands plants belonged to the next *M. expansum*. Peña *et al.* (2015) carried out an integrative systematic approach to species diversity and distribution in the genus *Mesophyllum* in the northeastern Atlantic and Mediterranean, confirming that *M. expansum* is a common species in the Azores and the Canaries archipelagos.

Thin section studied: RO-1/RH/3.

Order Sporolithales Le Gall and G.W. Saunders, 2010

Family Sporolithaceae Verheij, 1993

Genus *Sporolithon* Heydrich, 1897

Sporolithon sp.

Fig. 5A—D.

Description: Growth forms from encrusting to lumpy. Thallus monomerous, dorsiventral with non-coaxial core filaments, thallus 0.4—3.15 mm long with protuberances up to 3.09 mm wide. The core region is 84—108 μm thick, and the cells are 6—13 μm (M = 8; SD = 2) in diameter and 8—19 μm (M = 14; SD = 4) in length. The peripheral region shows horizontal layers of cells that are squarish to rectangular, measuring 5—11 μm (M = 8; SD = 2) in diameter and 8—20 μm (M = 15; SD = 3) in length.

Tetra/bisporangial conceptacles arranged in sori are buried in the thallus. Sporangial compartments are 29—58 μm (M = 46; SD = 6) in diameter and 65—106 μm (M = 80; SD = 10) in height. Stalk cells are trapezoidal in shape.

Remarks: *Sporolithon* includes all species of Sporolithaceae in which the tetrasporangial compartments are not surrounded by a pseudoparenchymatous wall (involucre), and in which tetrasporangia are borne on single-celled stalks (Iryu *et al.*, 2012). *Sporolithon africanum* is the only known species occurring nowadays in the Canary Islands (Haroun *et al.*, 2002; Afonso-Carrillo, 2014). The identification of this species, however, remains in open nomenclature, as no matching description was found to fit the species described here.

Sporolithon africanum was originally described as *Archaeolithothamnion africanum* by Foslie (1906), with a very succinct diagnosis from a sample collected by Sauvageau in Puerto Orotava (Puerto de la Cruz) in Tenerife. Lemoine and Mme (1929) searched unsuccessfully for individuals of this species in samples collected by Børgesen in the Canary Islands. Afonso-Carrillo (1982) did not find it in his samples either, but he examined the type material deposited in the Foslie Herbarium (TRH) in Trondheim, resulting in a rather confusing sample because it was covered by crusts of other species. The slide prepared by Foslie and preserved with the tipus includes anatomical sections in which the characteristic sporangial sori close to the surface are evident. According to the rules of nomenclature, *Sporolithon* has preference over *Archaeolithothamnion*, and Afonso-Carrillo (1984) proposed the new combination. This species has not been collected and documented again in the Canary Islands, and all recent references are based on Foslie's original description (Afonso-Carrillo and Sansón, 1999; Haroun *et al.*, 2002; Afonso-Carrillo, 2014; Gallardo *et al.*, 2016). Lemoine and Mme (1964) reported it for the Cabo Verde Archipelago.

Thin sections studied: Rehoyas CG, RO-1/RH/2, RO-1/RH/6.

?*Lithophyllum* sp.

Fig. 5E—H.

Description: Thallus with encrusting growth form and 0.49—1.28 mm thick. The conceptacles are, depending on the section view, either well-rounded or in a more or less flask-shape, measuring 208—254 μm (M = 231; SD = 18) in diameter and 83—116 μm (M = 101; SD = 17) in height. The roof is 33—55 μm thick. One visible pore is 58 μm in diameter

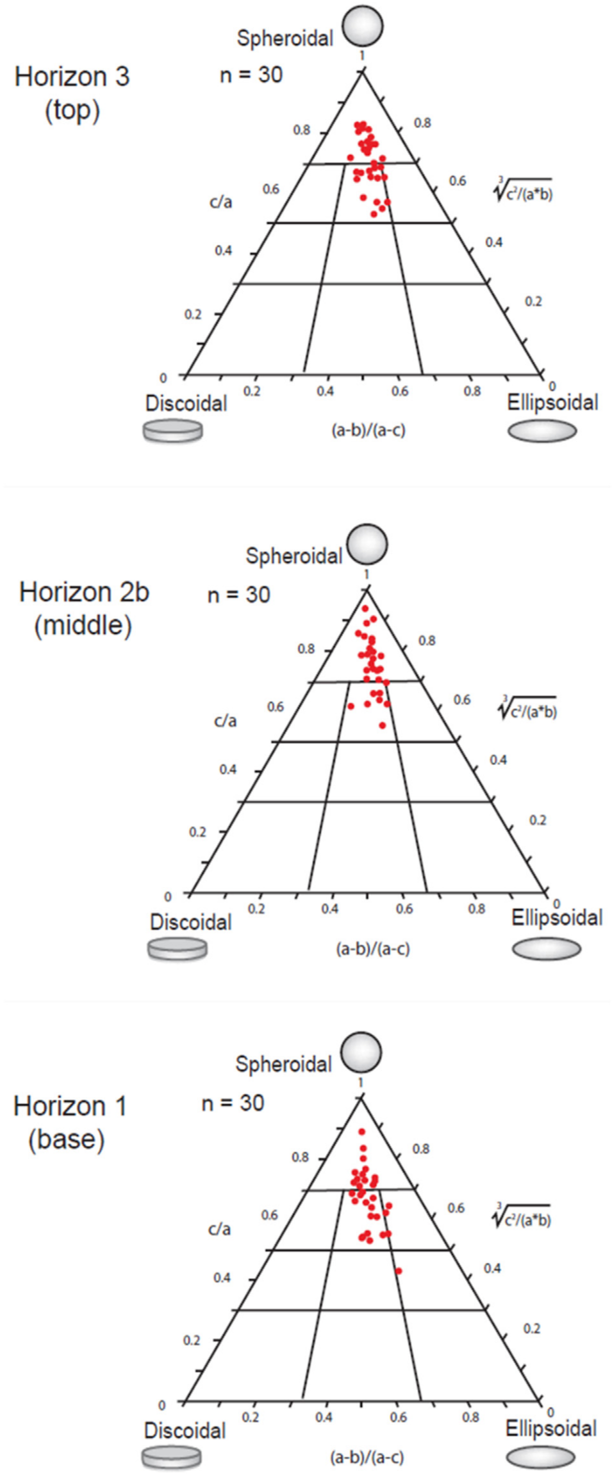

Fig. 6 Shape analyses for fossil rhodoliths sampled at different horizons of Unit 2, from the Las Rehoyas section, Gran Canaria Island.

and 53 μm in height. Some conceptacles show remnants of a columella. Cells have an irregular shape, changing from squarish-rectangular to diamond-shaped. Cells are 9–17 μm (M = 13; SD = 2) in

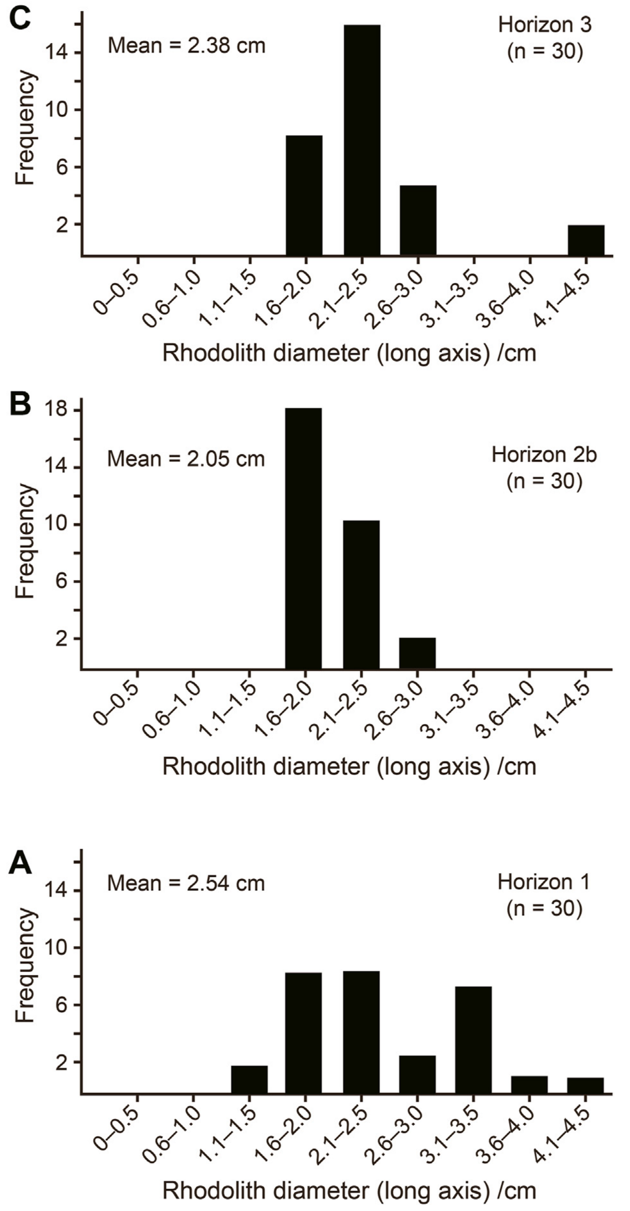

Fig. 7 Distribution in diameter size of rhodoliths from the three horizons, based on the long axis. **A)** Horizon 1; **B)** Horizon 2b; **C)** Horizon 3. See the horizon location in Fig. 3.

diameter and 16–21 μm (M = 18; SD = 2) in length. Epithallial cells are flat and rounded. The well-defined cell walls separating adjacent filaments suggest the absence of cell fusions.

Remarks: The thalli containing uniporate conceptacles are in the same rhodolith containing thalli with sori and multiporate conceptacles, and one other rhodolith containing only sori, therefore could be the carposporangial thalli of *Sporolithon*. However, the arrangement of the cells within the thallus, the shape

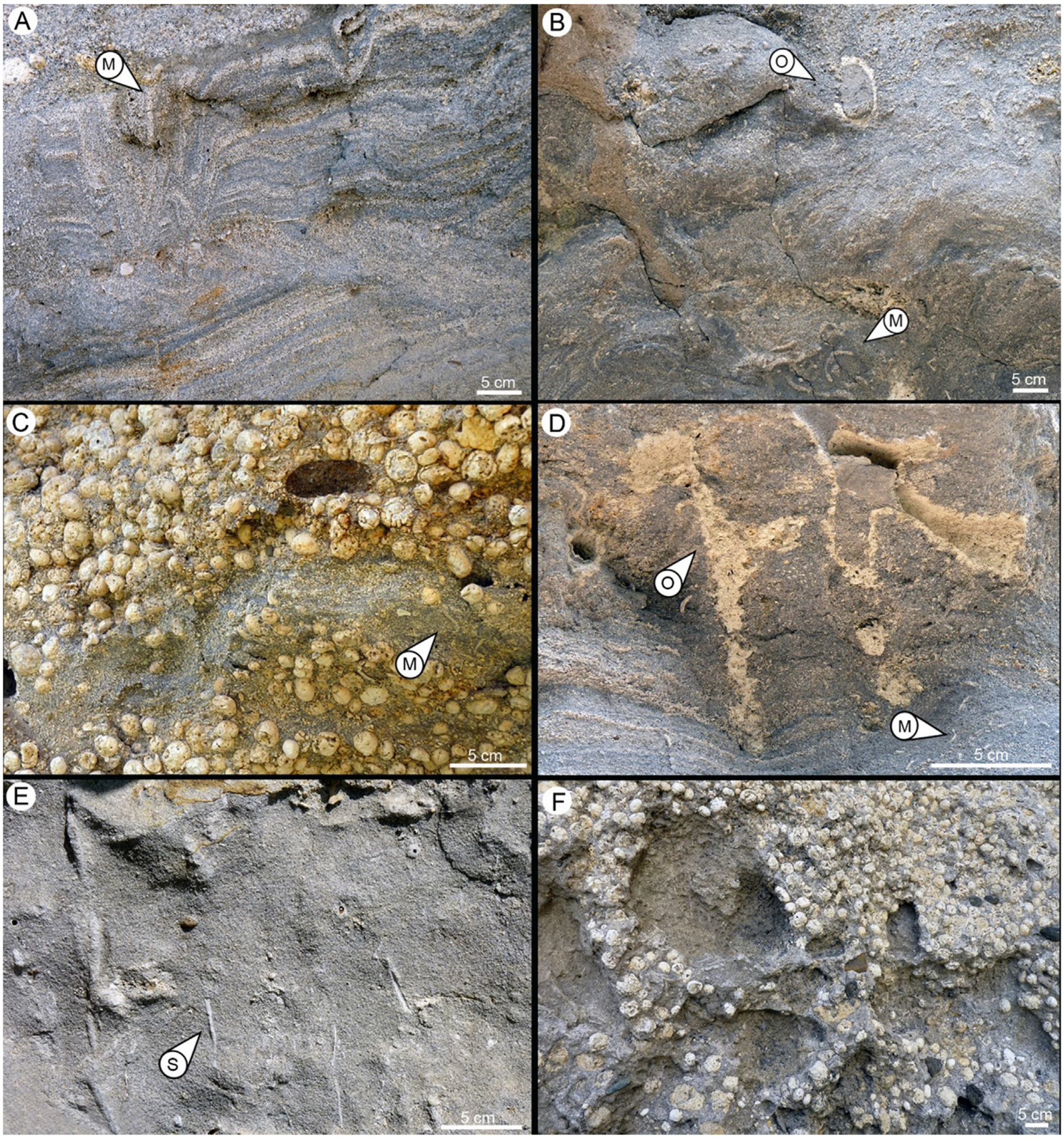

Fig. 8 Trace fossils of Unit 2 in the Las Rehoyas section. **A)** *Rosselia socialis*— equilibrichnium structure burrowed with *Macaronichnus segregatis* (M); **B)** Cross-section of *Ophiomorpha nodosa* (O) associated with *Macaronichnus segregatis* (M); **C)** Rhodolith beds intercalated with sandy gravels burrowed with *Macaronichnus* (M); **D)** Cross-sections of branched *Ophiomorpha nodosa* (O) together with *Macaronichnus segregatis* (M); **E)** *Skolithos linearis* (S) in a sandy gravel matrix; **F)** *Thalassinoides* isp. indet. filled by rhodoliths from an overlying level. All pictures are vertical cross-sections except for B, where the view is from the bottom (in the foreground with *Macaronichnus*) to the top.

of the epithallial cells, and the absence of obvious cell fusions are indicative of the genus *Lithophyllum*. For this reason, we prefer to use open nomenclature and refer to this specimen as ?*Lithophyllum* sp.

Thin sections studied: RO-1/RH/2, RO-1/RH/6.

4.3. Rhodolith shape and size analyses

The sphericity analysis of the rhodoliths shows a highly persistent pattern for extremely well-rounded growths through three distinct horizons sampled in

Unit 2 (Fig. 3). Roughly half of the 30 samples in each collection are plotted into the top tier of the greater triangle reserved for spheroidal shapes (Fig. 6). With a few exceptions, the other half of the plotted points are sub-spheroidal to sub-ellipsoidal. Those few points concentrated in the lower right-hand corner of the second tier's central block (Horizon 2b) show a slight tendency towards a more ellipsoidal shape (Fig. 6).

Moreover, none of the sampled rhodoliths revealed a central nucleus derived from the erosion of igneous rocks. Taken as a whole, the unambiguous result shows that the sustained growth of coralline red algae forming the Las Rehoyas rhodoliths adapted to a regular spherical shape was entirely self-nucleated and capable of rolling in any direction influenced by prevailing wave action and/or bioturbation.

Bar graphs exhibit the maximum diameters of the rhodoliths for each of the three horizons (Fig. 7). The rhodoliths' diameter is the widest in the first stratigraphic horizon-bearing rhodoliths (Fig. 7A). The range extends from 1.4 cm to 4.1 cm, with an average value of 2.54 cm. The maximum diameter range is more restricted in the next sample horizon, running from 1.8 cm to 2.6 cm, with an average value of 2.05 m (Fig. 7B). From the uppermost horizon sampled for rhodoliths, the maximum diameter range extends from 1.6 cm to 4.5 cm, with an average value of 2.38 cm (Fig. 7C). Although the distributions are variable, the difference between the largest and smallest average values among the three horizons differs by only a half-centimetre.

4.4. Ichnofossils and their ichnotaxonomy

Ichnofossils were mainly identified in the field, and ichnotaxonomic analysis was complemented by photographs. Ichnotaxa are arranged alphabetically, and their analysis includes a brief discussion about ichnotaxonomy, stratigraphic range and environment, and the ethology of probable trace makers.

The majority of the specimens were identified at the ichnospecific level. However, open nomenclature is used when ichnofossils show incomplete morphologies, making it difficult to assign them to defined ichnospecies.

Ichnogenus *Macaronichnus* Clifton and Thompson, 1978.

Macaronichnus segregatis Clifton and Thompson (1978).

Fig. 8A—C.

Description: Horizontal to subhorizontal, cylindrical, non-branching burrows, 1.2 to 6.2 (mean 2.4) mm in diameter, at least 87 mm long. They consist of a light-coloured core enveloped by a dark mantle composed generally of dark mafic. Most of them are observed in cross-section.

Remarks: The smaller burrows, up to 3 mm in diameter, which prevail, belong to *Macaronichnus segregatis segregatis* Clifton and Thompson (1978), and the larger burrows belong to *M. s. degiberti* Rodríguez-Tovar and Aguirre (2014). *Macaronichnus segregatis* is produced by infaunal polychaetes feeding on epigranular organic film, which develops preferentially on light grains; hence the segregation of light grains in the burrow core (Clifton and Thompson, 1978). In recent sediments, *M. s. segregatis* is produced by the polychaete *Thoracophelia* Ehlers, 1897 (formerly *Euzonus* Grube, 1866; Nara and Seike, 2004, 2019; Seike, 2007) or *Ophelia* Savigny, 1822 (Clifton and Thompson, 1978), and *M. s. degiberti* by *Travisia* Johnston (1840) (Seike *et al.*, 2011). Abundant occurrences of *M. s. segregatis* are typical of the upper foreshore (Pemberton *et al.*, 2001), although less abundant occurrences may extend to the well-oxygenated shoreface sands (Uchman and Krenmayr, 2004; Bromley *et al.*, 2009). *M. s. degiberti* has a wider bathymetric range and can be common in deeper shelf sands (Seike *et al.*, 2011; Nara and Seike, 2019).

In the investigated section, *Macaronichnus segregatis* is abundant in the sandy beds intercalated with rhodoliths in the lower part of Unit 2 (Fig. 8C) and frequently co-occurs with *Ophiomorpha nodosa* Lundgren (1891) through the higher parts of this unit (Fig. 8B). Occasionally, it cross-cuts *Rosselia socialis*. *Macaronichnus segregatis* is additionally reported from multiple fossiliferous outcrops within the Pliocene of Santa Maria Island, Azores Archipelago (Ávila *et al.*, 2015, 2018; Rebelo *et al.*, 2016; Uchman *et al.*, 2016, 2018, 2020), as well as in Miocene to Pleistocene sediments of the Cabo Verde Archipelago (Mayoral *et al.*, 2013).

Ichnogenus *Ophiomorpha* Lundgren, 1891.

Ophiomorpha nodosa Lundgren (1891).

Fig. 8D.

Description: Inclined to vertical cylindrical, occasionally branched burrows with a granulated wall. They are 2.5 cm in average diameter. Y-shaped branches are frequent (Fig. 8D). The wall consists of dense, irregular ovoid pellets, about 4 mm long, regularly distributed and arranged in a single layer. The burrow fill is structureless and similar to the surrounding matrix. Locally, the fill can contain clasts and/or rhodoliths from the overlying horizons.

Remarks: *Ophiomorpha nodosa* has been interpreted as a dwelling or feeding—dwelling structure produced by callianassid decapods, recently mainly by

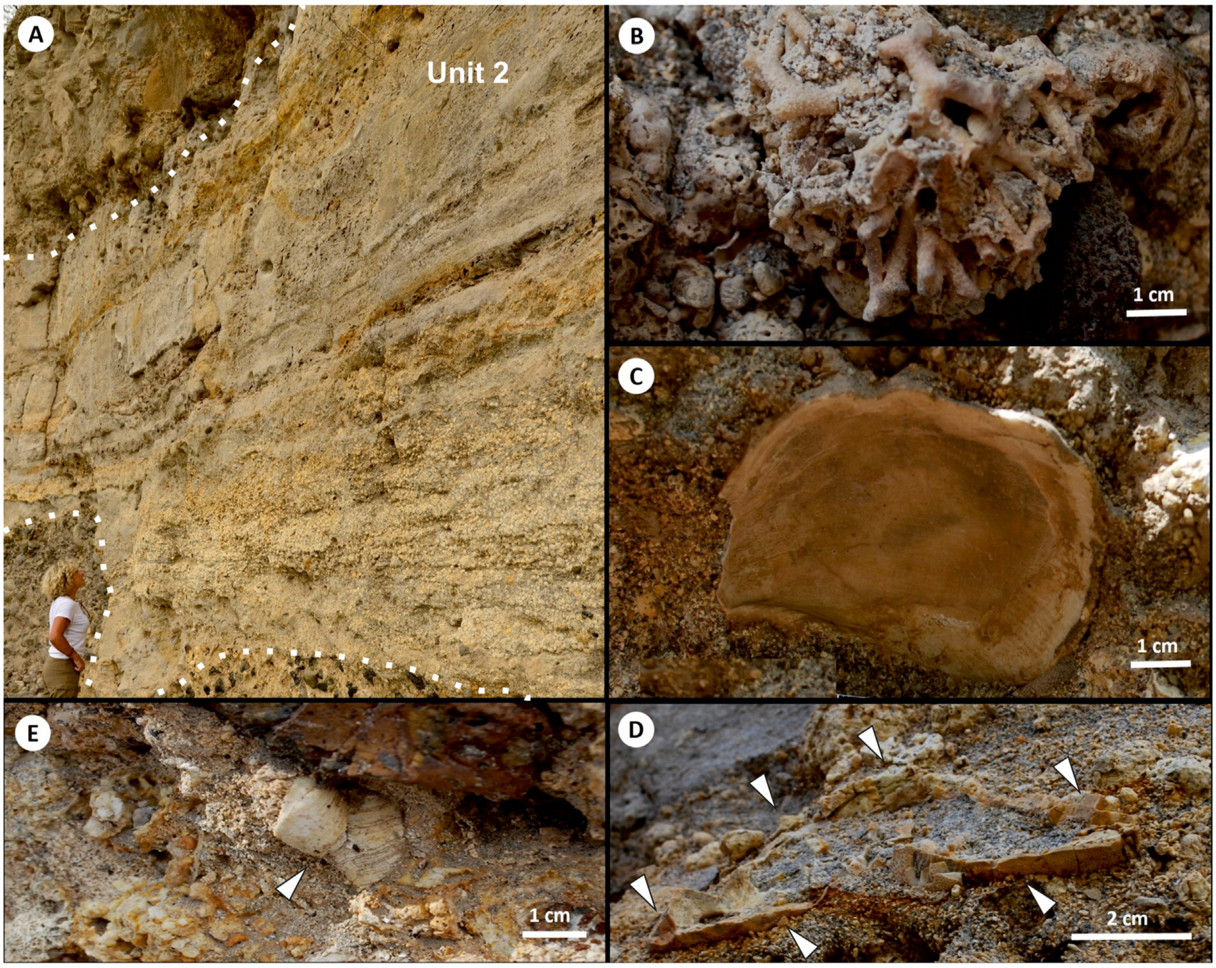

Fig. 9 Macrofossils characteristic of Units 1 and 2 of the Las Rehoyas section. **A)** Rhodolith sublevels in Unit 2; **B)** Celleporiform bryozoan colony; **C)** Valve of the bivalve species *Talochlamys ercolaniana*; **D)** Fossil remains of the echinoderm *Clypeaster* sp. (arrows); **E)** Shells of the Canarian fossil endemic gastropod *Rothpletzia rudista* (arrow).

Callichiurus major in littoral and sublittoral sandy deposits (e.g., Kennedy and Sellwood, 1970; Frey *et al.*, 1978; Pollard *et al.*, 1993). Its abundant occurrences are typical of the lower foreshore—upper shoreface (Pemberton *et al.*, 2001). *O. nodosa* occurs throughout Unit 2, especially in its upper—middle parts, where it co-occurs with *Macaronichnus*. *Ophiomorpha nodosa* is also reported from several fossiliferous outcrops in the Pliocene of Santa Maria Island, Azores Archipelago (Rebelo *et al.*, 2016; Uchman *et al.*, 2018).

Ichnogenus *Rosselia* Dahmer, 1937.
Rosselia socialis Dahmer (1937).
Fig. 8A.

Description: Conical, subcylindrical funnel-shaped, vertical, concentric burrow with a faint core corresponding to a skinny cylindrical central tube. The width at the top is from 3.0 cm to 10.0 cm, an average of 5.4 cm; the width at the base is from 0.8 cm to 2.0 cm, an average of 1.3 cm. Length can reach from 5.0 cm to 18.0 cm, an average of 11.1 cm.

Remarks: *Rosselia socialis* has been interpreted in many different ways. Thus, Chamberlain (1971) interpreted it as a feeding trace produced by a worm or worm-like organism moving repeatedly around a central axis, swallowing the organic material in the sediment. In this sense, Nara (1995) did not rule out the possibility that the trace-maker of *Rosselia* was possibly a detritus feeder related to terebellid polychaetes, as well as McIlroy (2007) that interpreted the producer as a sediment processor in highly bioturbated sandstone strata. However, some interpretations associate *Rosselia* with a dwelling structure of a probable infaunal, detritus-feeding terebellid polychaete (Nara, 1995; Hofmann *et al.*, 2012; Mello *et al.*, 2021). Nevertheless, several studies demonstrated that *Rosselia* commonly reflects adjustments of the burrow in response to depositional

Table 2 Composition and palaeoenvironmental characteristics of the macrofossils present in the Las Rehoyas site.

Class	Species	Composition	Life habit	Substrate	Diet
Echinodermata	*Clypeaster* sp.	High-Mg calcite	Semi-infaunal	Soft	Detritivore
	Schizobrissus sp.	High-Mg calcite	Infaunal	Soft	Deposit feeder, detritivore
Gastropoda	*Haliotis coccinea* Reeve (1846)	Aragonite, low-Mg calcite	Epifaunal	Hard	Phytophagous
	Nerita martiniana Bonci et al. (2000)	Aragonite, low-Mg calcite	Epifaunal	Hard	Carnivore, Phytophagous
	Thericium vulgatum Bruguière, 1792	Aragonite	Epifaunal	Soft	Detritivore, phytophagous
	Tenagodus obtusus (Schumacher, 1817)	Aragonite	Epifaunal	Soft	Suspension feeder
	Turritella turris (Basterot, 1825)	Aragonite	Semi-infaunal	Soft	Suspension feeder
	Zaria subangulata (Brocchi, 1814)	Aragonite	Semi-infaunal	Soft	Suspension feeder
	Petaloconchus glomeratus (Linnaeus, 1758)	Aragonite	Epifaunal	Hard	Suspension feder
	Rothpletzia rudista Simonelli, 1892	Aragonite	Epifaunal	Hard	Detritivore
	Cheilea sp.	Aragonite	Epifaunal	Hard	Phytophagous, suspension feeder
	Niveria avellana meridionalis (J. de C. Sowerby, 1822)	Aragonite	Epifaunal	Hard	Carnivore
	Luria fortunatarum (Schilder, 1928)	Aragonite	Epifaunal	Hard	Omnivore
	Zonaria hesperidum (Schilder, 1928)	Aragonite	Epifaunal	Hard	Carnivore, phytophagous
	Thetystrombus coronatus (Defrance, 1827)	Aragonite	Epifaunal	Hard	Detritivore, carnivore, phytophagous
	Semicassis grateloupi (Deshayes, 1853)	Aragonite	Epifaunal	Soft	Carnivore
	Aspa marginata (Gmelin, 1791)	Aragonite	Epifaunal	Soft	Carnivore
	Prunum augustiforis (Rothpletz and Simonelli, 1890)	Aragonite	Epifaunal	Hard	Carnivore
	Ancilla patula (Döderlein, in Bellardi, 1882)	Aragonite	Epifaunal	Soft	Carnivore
	Ancilla glandiformis (Lamarck, 1810)	Aragonite	Epifaunal	Soft	Carnivore
	Olivella longispira (Bellardi, 1882)	Aragonite	Epifaunal	Soft	Carnivore
	Conilithes exaltatus (Eichwald, 1830) = *Conus dujardini* Deshayes, 1845	Aragonite	Epifaunal	Soft, semi-soft	Carnivore
	Conus virginalis Brocchi, 1814	Aragonite	Epifaunal	Soft, semi-soft	Carnivore
	Conus mercati Brocchi, 1814	Aragonite	Epifaunal	Soft, semi-soft	Carnivore
Bivalvia	*Glycymeris bimaculata* (Poli, 1795)	Aragonite	Infaunal	Soft	Suspension feeder
	Glycymeris glycymeris (Linnaeus, 1758)	Aragonite	Infaunal	Soft	Suspension feeder
	Lima lima (Linnaeus, 1758)	Aragonite	Epifaunal	Hard	Suspension feeder
	Crassostrea sp.	Low-Mg calcite	Epifaunal	Hard	Suspension feeder
	Isognomon maxillatus (Lamarck, 1801)	Aragonite	Epifaunal	Hard, semi-soft	Suspension feeder
	Perapecten scabrellus Lamarck, 1819	Low-Mg calcite	Epifaunal	Soft, semi-soft	Suspension feeder
	Talochlamys ercolaniana (Cocconi, 1873)	Low-Mg calcite	Epifaunal	Soft, semi-soft	Suspension feeder
	Gigantopecten latissimus Brocchi, 1814	Low-Mg calcite	Epifaunal	Soft, semi-soft	Suspension feeder
	Talochlamys multistriata (Poli, 1795)	Low-Mg calcite	Epifaunal	Hard	Suspension feeder
	Spondylus cf. *gaederopus* Linnaeus, 1758	Aragonite	Epifaunal	Hard	Suspension feeder
	Laevicardium sp.	Aragonite	Infaunal	Soft	Suspension feeder

events and is therefore considered to be an equilibrium trace fossil (e.g., Nara, 1997, 2002; Pemberton *et al.*, 2001; Campbell *et al.*, 2006; Netto *et al.*, 2014; Buatois *et al.*, 2016).

Ichnogenus *Skolithos* Haldemann, 1840.
Skolithos linearis Haldemann (1840).
Fig. 8E.

Description: Vertical to slightly inclined, cylindrical, unbranched shafts, circular in cross-section, 0.1 to 0.52 (mean 0.25) cm in diameter and 2 to 21 (mean 7.3) cm in length. The burrow margins are smooth and generally indistinct. The fill is homogeneous and similar to the surrounding deposit.

Remarks: *Skolithos* is a dwelling structure (ethological category domichnia) of suspension- or deposit-feeding worms, most likely phoronids or polychaetes (e.g., Alpert, 1974; Sundberg, 1983; Pemberton and Frey, 1984; Desjardins *et al.*, 2010; Knaust *et al.*, 2018). *Skolithos* has been recorded in various sedimentary settings, from tide-dominated environments to offshore settings through shallow marine high-energy deposits and upper—middle shoreface (Frey *et al.*, 1990; Buatois and Mángano, 2011). However, it is most typical of the *Skolithos* ichnofacies, which is typical of the lower foreshore and upper shoreface (Pemberton *et al.*, 2001).

In the studied section, *Skolithos* occurs exclusively in the lower part of Unit 2, together with isolated specimens of *Ophiomorpha* and *Macaronichnus*. Its density is six specimens per 750 cm^2 of horizontal surface.

Ichnogenus *Thalassinoides* Ehrenberg, 1944.
Thalassinoides ichnosp. indet.
Fig. 8F.

Description: An irregular network of cylindrical, branched, smooth, unlined galleries and shafts, which are 7.1—12.1 (mean 9.8) cm in diameter. T-shaped and Y-shaped (130°—135°) branchings are common. The sandy filling differs in size and composition from the surrounding deposits; and it contains rhodoliths from an overlying level.

Remarks: As the trace fossil was observed mostly in cross sections, its three-dimensional geometry detection is incomplete. This prevents its determination at the ichnospecies level. *Thalassinoides* is usually attributed to the activity of suspension- and deposit-feeding endobenthic decapod crustaceans in well-oxygenated sediments (e.g., Bromley and Frey, 1974; Ekdale, 1992; Bromley, 1996; Pemberton *et al.*, 2001). *Thalassinoides* has a wide bathymetric range of distribution, from shallow marine (O'Byrne and Flint, 1995; Sharafi *et al.*, 2012) to deep-sea settings (Uchman, 1995); however, it is most characteristic of the *Cruziana* ichnofacies within the middle shoreface—upper offshore zone (Pemberton *et al.*, 1992). In the investigated section, *Thalassinoides* occurs in the basal part of Unit 2, in cross-bedded rhodolithic sandy beds. *Thalassinoides* isp. is also reported from several fossiliferous outcrops in the Pliocene of Santa Maria Island, Azores Archipelago (Rebelo *et al.*, 2016; Uchman *et al.*, 2016, 2018, 2020; Johnson *et al.*, 2017; Ávila *et al.*, 2018).

4.5. Palaeontological association

In the Las Rehoyas section, several species of molluscs, echinoderms, and bryozoans occur dispersed among the rhodolith levels and between them (Fig. 9). Most of the macrofossil taxa are originally composed of aragonite, which is highly dissoluble during diagenesis or even pre-burial. Therefore, they are preserved only in the form of moulds, and this adds an important bias in the investigated faunal composition (Table 2). The bivalve shells are disarticulated and disturbed from their life positions. The internal skeletons and isolated spines of the echinoderms *Clypeaster altus* (Leske, 1778) and *Schizobrissus* sp. are also present. Betancort *et al.* (2014) cited several species of crustaceans, including decapod crustaceans from the Las Rehoyas section.

5. Discussion

5.1. Rhodolith taxonomic composition and bathymetric range

All studied rhodoliths from the Las Rehoyas section were shown to be multispecific, composed of more than one genus of coralline red algae, without any general trend from the nucleus to the surface. They are composed of species from the genera *Boreolithothamnion*, *Hydrolithon*, *Lithoporella*, *Sporolithon*, and ?*Lithophyllum*. No dominant genus was observed. The genera are typical of somewhat deep water in both temperate and reefal carbonates (Aguirre *et al.*, 2017 and references therein). This suggests that the rhodoliths were formed at a water depth of ~50 m.

While recent rhodoliths are widely recognized to inhabit the areas surrounding the Canary Islands, ranging from intertidal zones to depths of at least 40 m, particularly on sandy substrate bottoms (e.g., Otero-Ferrer *et al.*, 2020; Rebelo *et al.*, 2022), there remains limited understanding regarding their distribution and species composition. Studies on the current coralline algae of the Canary Islands are scarce, and not all islands have been studied uniformly. Their occurrences in Tenerife and Gran Canaria are the best documented, but in both cases only based on a very small number of localities and a few floristic studies (see Foslie, 1906, 1909; Lemoine and Mme, 1929; Afonso-Carrillo, 1982). Given the proximity of the islands to each other, a relatively similar distribution of species on the different islands can be expected, especially between Tenerife and Gran Canaria, which are nearby. Afonso-Carrillo (2021) gave information on the current state of knowledge about coralline algae in the Canary Islands.

All the fossil corallines identified from the Las Rehoyas section are known to occur presently in the Canary Islands (Haroun *et al.*, 2002; Afonso-Carrillo, 2014). However, the genera *Boreolithothamnion* (as *Lithothamnion*) and *Sporolithon*, although present in other Canarian islands, are not known to occur currently at Gran Canaria.

5.2. Accumulation and resedimentation of the rhodolith deposits

Among the Canary, Azores, Madeira, and Cabo Verde archipelagos in the NE Atlantic Ocean, several islands are known to host living populations of rhodoliths (Rebelo *et al.*, 2021b) as well as significant deposits formed almost exclusively by fossil rhodoliths (Johnson *et al.*, 2011, 2017). Additional supporting evidence can be inferred through comparisons with fossil and modern deposits on other islands and continental Iberia (Indemares project, 2009—2014).

The morphological analysis of the three horizons of rhodoliths within Unit 2 of the Las Rehoyas section (Fig. 3), coupled with the absence of a distinct, well-defined sharp transition between them, indicates the presence of a singular population of rhodoliths in this unit. The stratigraphic beds appear to represent different pulses of the same stage of facies development. The presence or absence of a rock core within rhodoliths depends on the availability of clastic particles supplied from shallower zones. Generally, the size of clastic particles and their movement by waves and currents tend to diminish with the distance from the shore, and usually concomitant increases in water depth. However, during major storms, waves reach greater depths as a function of orbital movement with increasing wavelength. Large rhodoliths with cobble nuclei from the middle Miocene on Madeira's Porto Santo Island are interpreted to have lived in areas close to basaltic cliffs (Santos *et al.*, 2012). Some equally large rhodoliths from a coeval deposit on the opposite side of the same palaeoisland have no rock cores and are interpreted as having originated in deeper waters and redeposited on a palaeoshore by storms of nearly hurricane intensity (Johnson *et al.*, 2011). In contrast, the rhodoliths from the Las Rehoyas section are uniformly small without clast nuclei. The absence of clast nuclei suggests a very reduced supply of coarser clasts. Their formation was possible because of the deepening and quick relocation of the shoreline inland caused by the relative sea level rise, which is recorded in deposits of Unit 2 (see discussion in section 5.3) when the terrigenous sediment input to the depositional system was significantly reduced and its delivery to the shoreface was markedly smaller. The water depth of ~50 m inferred from the taxonomic analysis of the rhodoliths (see section 5.1) corroborates this interpretation. The relatively small size of the rhodoliths studied suggests their shorter and/or slower growth. The shorter growth can be related to regular redepositional/burial events occurring in more or less the same time intervals, taking into account the uniformity of size. However, the slower growth is better explained by reduced light in deeper water, a reduced supply of nutrients during flooding, or still less favourable conditions in the fan-delta environment than in other optimal environments. Otero-Ferrer *et al.* (2020) showed that the living rhodoliths off Gando Bay at Gran Canaria Island, distributed along three different depths: 18 m, 25 m, and 40 m, varied in size with depth, being the largest ones (~5 cm) living at 25 m depth. Both extant Gran Canaria and the fossil rhodolith specimens collected in Las Rehoyas section share a predominantly spheroidal shape morphology.

A strong fossil analogue can be drawn from a study of Miocene rhodoliths in the Algarve region of southern Portugal (Marques da Silva *et al.*, 2019). In this study, small and similarly shaped, non-nucleated rhodoliths accumulated in repetitive layers as much as a metre in thickness. As the red coralline algae that form rhodoliths are unable to grow in the absence of sunlight when buried at the bottom of a substantial deposit, it is supposed that these were washed shoreward in large numbers under the influence of storm waves readily capable of moving unattached spherical objects.

Another modern analogue for the Pliocene rhodoliths at Las Rehoyas section derives from rhodoliths deposited in an extensive subaerial embankment at Caleta del Bajo Mejillón on the northern coast of Fuerteventura in the Canary Islands. Multispecific rhodoliths attributed to the genera *Lithothamnion*, *Lithoporella*, and *Hydrolithon* (Johnson *et al.*, 2012; Rebelo *et al.*, 2022) are small in size, mostly between 1 cm and 3 cm in diameter (Johnson *et al.*, 2012: their Fig. 4). They also conform to a shape pattern similar to those from the Las Rehoyas section.

The large sample of modern rhodoliths includes only a few that extend toward the ellipsoidal morphotype beyond those identified at Las Rehoyas section. The deposit at Caleta del Bajo Mejillón on Fuerteventura extends for 120 m parallel to the shore. It sits above the landward termination of a wide wave-cut platform exposed in the seaward direction for 130 m during low tide. It means that the subaerial beach deposit estimated to contain six million rhodoliths was transported across the wave-cut platform during storm events from their original offshore habitat (Johnson *et al.*, 2012; Rebelo *et al.*, 2022). The analogue examples raise the question of whether the rhodoliths from the Las Rehoyas section are redeposited or they are *in situ*, i.e., in the setting located at a depth of ~50 m. The answer comes from the analysis of ichnofacies (section 5.3).

Not all redeposited rhodoliths are small and non-nucleated, e.g., those from the extensive Holocene rhodolith deposits stranded on the northern coast of Maio Island and the eastern shore of Sal Island in the Cabo Verde Archipelago (Johnson *et al.*, 2018). In both cases, large, non-nucleated rhodoliths exceeding 12 cm in diameter formed extensive subaerial deposits attributed to shoreward transport by major storm events. The wave action during such storms would need to be more powerful to displace larger rhodoliths from their natural habitat and carry them to deeper waters further from the shore. Moreover, these storms were probably less frequent, allowing the living rhodolith beds to remain undisturbed for longer periods and support continuous growth.

5.3. Palaeoenvironmental interpretations

The fossiliferous deposits in the Las Rehoyas section are considered to have formed in a marine environment.

Unit 1: Interpreted as having a high epiclastic input with debris flow reworked in the backshore, shoreface, and gravel channels. This unit represents proximal deposits of the marine part of a fan-delta system that developed during the erosive period and coeval stage of the relative lower sea level. Deposits accumulated on slopes and a high-energy submarine platform formed in the NW part of the island. Some rhodoliths present between rock boulders indicate areas stable enough for colonization by coralline algae.

Unit 2: Richest in rhodoliths, generally becoming finer towards the top. Formed during further stabilization of the depositional system, with peak calcium carbonate production. The concentration of rhodoliths in three horizons, some with erosive bases, suggests re-deposition. The rhodoliths are non-nucleated, indicating that they likely originated from a deeper sandy bottom (~50 m depth). This unit displays substantial trace fossils, crucial for estimating the palaeodepth of the deposit. The ichnoassemblage includes *Rosselia socialis*, *Macaronichnus segregatis*, *Ophiomorpha nodosa*, *Skolithos linearis*, and *Thalassinoides* isp. indet. The association of *O. nodosa* and *S. linearis* indicates the *Skolithos* ichnofacies, typical of the foreshore to middle shoreface (Pemberton *et al.*, 2001). The ichnologically interpreted zones are generally shallower than 50 m, supporting the hypothesis that rhodoliths were redeposited from lower shoreface to shallower zones by storm surges.

Unit 3: Represents the recurrence of a highly erosive phase on the island and the onset of a regressive phase that caused the shift of the sedimentary environment into the proximal zones of a marine fan-delta system. The facies migrated across the marine platform towards the sea and partly eroded sediments in Unit 2, as marked by channelized incisions (Figs. 2 and 3).

Unit 4: Interpreted as debris-flow and gravity-flow deposits occurring during periods of higher energy and further progradation of the fan delta, causing partial erosion of Unit 3. Unit 4 generally indicates a continued decrease in relative sea level.

The fossil assemblage of molluscs from the Las Rehoyas section shows a certain affinity for soft and semi-soft substrates of the meso-infralittoral environment under certain energy conditions (e.g., the echinoderms *Clypeaster altus* Leske, 1778 and *Schizobrissus* sp.; the gastropods *Cerithium vulgatum* Bruguière, 1789, *Tenagodus obtusus* (Schumacher, 1817), *Turritella turris* (Basterot, 1825), *Zaria subangulata* (Brocchi, 1814), *Semicassis grateoloupi* (Deshayes, 1853), *Aspa marginata* (Gmelin, 1791), *Ancilla patula* (Döderlein, in Bellardi, 1882), *Ancilla glandiformis* (Lamarck, 1810) and *Olivella longispira* (Bellardi, 1882); and the bivalves *Glycymeris bimaculatus* (Poli, 1795), *Glycymeris glycymeris* (Linnaeus, 1758) and *Gigantopecten latissimus* (Brocchi, 1814) — cf. Table 2), which is in agreement with the already inferred palaeoecological environment necessary for the development of a rhodalgal facies. Some shells can be redeposited, as species typical of hard substrates (e.g., *Rothpletzia rudista* Simonelli, 1892; *Cheilea* sp.) are also present. Echinoderms, represented by the remains of clypeasteroids, denote a soft and semi-soft meso-infralittoral environment, as they are more common above 50 m of water depth (Madeira *et al.*, 2011).

Meco *et al.* (2007, 2015) indicated that *Tethystrombus coronatus* or *Ancilla glandiformis* are indicative of tropical climatic conditions. Of the 35 specific taxa listed (Table 2), 20 are considered typical of tropical climatic environments and were distributed during the late Miocene and early Pliocene in the European basins. Five are endemic to the Canary Islands Neogene deposits (Martín-González, 2016) and 8 are also reported from Santa Maria Island (Madeira *et al.*, 2011; Ávila *et al.*, 2015, 2016; Sacchetti *et al.*, 2023). The data here presented are congruent with previous inferences for higher sea surface temperatures (SSTs) during the Mio-Pliocene in the Macaronsesian archipelagos, thus a warmer climate was in place in the Canaries Archipelago during this time (Meco *et al.*, 2005, 2007; Sendino and Taylor, 2014; Martín-González *et al.*, 2018). The high values in the SSTs during this period in the NE Atlantic allowed for the range expansion, arrival, and settlement of viable populations of tropical, shallow-water species to higher latitudes, such as the echinoderms *Clypeaster altus* and *Schizobrissus* sp., the gastropods *Tenagodus obtusus* and *Thetystrombus coronatus*, and the bivalve *Gigantopecten latissimus*, as is the case of the Azores Archipelago (Santa Maria Island; Madeira *et al.*, 2011; Ávila *et al.*, 2015, 2016; Sacchetti *et al.*, 2023). Most of these thermophilic species locally disappeared from Canaries or even went extinct (e.g., the echinoid *Clypeaster altus*, and the gastropod *Rothpletzia rudista*) as a result of the global climatic deterioration that was caused by a series of cooling events that started in the mid-Pliocene (Raffi and Monegatti, 1993; Monegatti and Raffi, 2001, 2007; Landau *et al.*, 2007, 2011).

In summary, the roughly symmetrical facies development from Unit 1 to Unit 4 records a relative sea level rise (Units 1 and 2) and fall (Units 3 and 4), in a coarse-grained fan-delta depositional system. The facies that we see in Units 1 and 2 are very similar to those in the Pleistocene fan delta in SE Spain, which is interpreted as a result of sea level rise (Bardaji *et al.*, 1990). The marine flood that ensued led to the inland shifting of the shoreline, a decrease in sediment supply to the system, sediment fining, and ultimately, stabilization. This enabled colonization by epi- and infaunal variable organisms, which resulted in increased production of calcium carbonate. The stabilization was already initiated during the deposition of Unit 1 and reached its maximum during the deposition of Unit 2. The maximum flooding stage is probably not preserved due to erosion at the base of Unit 3. The cause of the relative sea level rise remains unclear, as it could be attributed to eustatic changes in the sea level or to the vertical uplift of the island induced by volcanic events or geotectonic forces. Unfortunately, the imprecise dating of the section does not allow adjustment to the sea-level curve. Nevertheless, the Las Rehoyas section serves as a noteworthy example illustrating the stabilization of the fan delta resulting from the rise in relative sea level.

6. Conclusions

1) The sedimentary deposits of the Las Rehoyas section accumulated in a generally coarse-grained fan-delta system located on the northeastern margin of the Gran Canaria marine platform during the late Miocene to early Pliocene. The investigated section forms a symmetrical succession, which starts with conglomerates and continues through sandstones with conglomerate intercalations back to conglomerates.
2) The investigated sandy interval of the section contains abundant, relatively small, mostly spherical rhodoliths of uniform size, without rocky nuclei. They were built by multispecific coralline algae that lived at a water depth of ~50 m.
3) The sandy interval contains trace fossils of the *Skolithos* ichnofacies, which is typical of the foreshore to the middle shoreface. This interval also contains variable, mostly tropical molluscs, and echinoderms, which live usually above 50 m of water depth.
4) The rhodoliths were re-deposited from the lower shoreface—offshore to the foreshore—middle shoreface zone by storms.
5) The sandy portion of the section documents the stabilization of the fan-delta system, attributed to a relative sea level rise. This phenomenon occurred as sediment input to the system decreased, creating conditions conducive to the colonization by diverse organisms. The stabilization process initiated at the upper part of the underlying conglomerate and ceased due to a subsequent relative sea level drop. This drop triggered the progradation of the coarse fan delta, leading to the deposition of conglomerates on an erosive surface. The specific origin of the relative sea level rise remains undetermined, with uncertainty regarding whether it was of eustatic or tectonic origin.

CRediT authorship contribution statement

ACR, AU, MEJ, and EMG conceived the idea and conceptualized it: original draft, writing, review, and editing. MEJ, CSM, JV, IG, EM, AS, and EMG contributed to field work, sample collecting, and processing. AGR, JAC, and SPA contributed to the writing, review, and

editing. All authors read and approved the final manuscript.

Availability of data and material

The data that support the findings of this study are available on request from the corresponding author, ACR.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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