Palaeoecology, taphonomy, and preservation of a lower Pliocene shell bed (coquina) from a volcanic oceanic island (Santa Maria Island, Azores)

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ABSTRACT

Massive fossil shell accumulations require particular conditions to be formed and may provide valuable insights into the sedimentary environments favouring such concentrations. Shallow-water shell beds appear to be particularly rare on reefless volcanic oceanic islands on account of narrow, steep and highly-energetic insular shelves where the potential for preservation is limited. The occurrence of an exceptional coquina (Pedra-que-pica) within the Miocene–Pliocene deposits of Santa Maria Island (Azores), therefore provides a rare opportunity to understand the conditions that led to the formation and preservation of a massive shell bed at mid-ocean insular setting. This study provides a detailed analysis regarding a 10–11 m-thick bivalve-dominated fossil assemblage exposed at Pedra-que-pica on Santa Maria Island in the Azores. Integration of taphonomical, palaeoecological and sedimentological observations are used to reconstruct the genesis of the coquina bed and related events, and to discuss why such exceptional sedimentary bodies are so rare on shelves around reefless volcanic oceanic islands.

The sequence at Pedra-que-pica demonstrates a complex succession of sedimentary environments in response to the drowning of an existing coastline during a period of rapid sea-level rise. The Pedra-que-pica shell bed incorporates storm-related materials and possible debris falls that originated nearby in a shallow and highly productive carbonate factory. Deposition took place below fair-weather wave base, at around 50 m depth, as inferred from the overlying volcanic succession. The preservation of this coquina was favoured by deposition on a platform laterally protected by a rocky spur, combined with rapid burial by water-settled volcanic tuffs and subsequent volcanic effusive sequences. The recent exhumation of the deposit is the result of island uplift and subsequent erosion.

Keywords: Coquina, Sedimentary processes, Palaeoenvironmental reconstruction, Island shelves, Volcanic oceanic islands, Azores.

1. Introduction

Coastlines at volcanic oceanic islands are extremely dynamic geomorphological features, as they are subjected to vertical displacements over time (both subsidence and uplift), to glacio-eustatic sea-level changes, are impacted by high-energy oceanic conditions, and are frequently disturbed by medium- to large-scale geological processes (i.e. landslides, active tectonics, volcanic eruptions, tsunamis, etc.) (Moore et al., 1989; Schmincke, 2004; Felton et al., 2006; Crook and Felton, 2008; Quartau et al., 2010, 2012; Quartau and Mitchell, 2013; Ramalho et al., 2013). Around young and exposed volcanic islands, sediment accommodation space is limited by narrow and shallow shelves. The residence time of sediments on the shelves is very brief due to frequent offshore transport induced by storms and sediment spill-over to the submarine slopes, both reinforced during sea level drops (Tsutsui et al., 1987; Donovan, 2002; Ávila et al., 2008a; Quartau et al., 2010, 2012, 2015; Ávila, 2013; Meireles et al., 2013). Due to the subsidence trend to which most volcanic oceanic islands are subjected and at latitudes where protective coral reef barriers fail to develop, the aforementioned conditions are responsible for the scarcity and relative improbability for the retention of subaerial exposures of thick, well-developed marine shelf deposits within island successions. Only the most erosion-resistant deposits – hydrodynamically-stable coarse sediment deposits such as boulder accumulations or well-lithified deposits – may withstand shoreline transgressive-regressive cycles of sea-level changes (Felton et al., 2006; Ávila et al., 2008a; Quartau et al., 2012). However, looser and finer shelf sediments have the potential to be incorporated into an island edifice by volcanic progradation. The rare islands that experienced uplift trends may thus exhibit well-preserved volcanic and sedimentary marine sequences, thus constituting prime localities to gain insight regarding sedimentation on volcanic island shelves.

The small island of Santa Maria (97 km^2) in the Azores archipelago (North Atlantic Ocean) is one of those exceptional cases. The fortuitous combination of uplift, coastal erosion and volcanism (Serralheiro et al., 1987; Serralheiro and Madeira, 1990; Serralheiro, 2003) resulted in the preservation and exposure of rich Neogene fossiliferous marine sediments (Ferreira, 1955; Zbyszewski and Ferreira, 1962; Ávila et al., 2002, 2009a, 2009b, 2010, 2012; Estevens and Ávila, 2007; Janssen et al., 2008; Kroh et al., 2008; Winkelmann et al., 2010; Madeira et al., 2007, 2011; Meireles et al., 2012), together with marine volcanic sequences (Serralheiro, 2003; Meireles et al., 2013; Ramalho et al., 2013).

The focus of this study is the Pedra-que-pica (literally, "stone that stings") fossiliferous outcrop, which is located on the southeastern coast of Santa Maria Island. Although previous work based on strontium-isotope stratigraphy suggested an uppermost Miocene age for the deposit with an average estimated age of 5.51±0.21 Ma (Kirby et al., 2007), recent K/Ar datings indicate an age ranging between 4.02±0.06 Ma and 3.96±0.06 Ma, thus early Pliocene in age (Sibrant et al., 2015). The sedimentary sequence at Pedra-que-pica comprises a thick coquina unit – a sedimentary rock composed of transported, abraded and mechanically sorted fragments of various origins and entire shells of molluscs and other bioclasts that constitute > 50% of the rock volume (Neuendorf et al., 2005). While such deposits are typically more abundant along continental shores [e.g., east coast of Florida and southeastern North Carolina, both in the USA (Fallaw, 1973); the Guadalquivir Basin, in Cadiz and the southern part of Sevilla province, Spain (Aguirre, 1995)], they are rare in volcanic oceanic islands. In fact, in the Atlantic Ocean, well-developed coquinas are only known from Santiago Island (Cape Verde Archipelago – Serralheiro, 1976) and Santa Maria Island (Azores – Serralheiro et al., 1987; Serralheiro and Madeira, 1990; Serralheiro, 2003; Kirby et al., 2007). To our knowledge, the outcrop at Pedra-que-pica is possibly one of the world's largest coquina shelf deposits in a volcanic oceanic island setting. Therefore, Santa Maria represents an excellent opportunity to gain insights into the sedimentary dynamics leading to coquina-bed formation on the exposed shelves of volcanic oceanic islands and their preservation. To achieve this goal, a comprehensive analysis of the outcrop from an integrated volcanostratigraphic, geomorphological, sedimentological, petrographical, ichnological and palaeontological point of view was performed in order to improve previous interpretations of the coquina (e.g., Kirby et al., 2007) and the physical setting in which it accrued. The main aims of the present study are to reconstruct and interpret the palaeoenvironment of the sedimentary sequence and advance the understanding of the interplay of sedimentological, volcanological and biological processes in producing and preserving such unusual sedimentary bodies on reefless volcanic oceanic island shelves.

2. Geological setting

Located in the NE Atlantic Ocean, the Azores archipelago comprises nine volcanic oceanic islands younger than 6 Ma (Ramalho et al., 2014; Sibrant et al., 2015). The islands represent the emerged tops of larger volcanic edifices superimposed on the Azores Plateau (Needham and Franchetau, 1974; Madeira and Ribeiro, 1990; Beier et al., 2012; Fig. 1), a large area of elevated seafloor adjacent to the triple junction between the Eurasian, Nubian and North American plates (Laughton and Whitmarsh, 1974; Schilling, 1975; Cannat et al., 1999; Gente et al., 2003; Marques et al., 2013). With the exception of the south-eastern-most and oldest island (Santa Maria), none of the other islands record exposed marine fossiliferous sequences (Serralheiro, 2003; Quartau et al., 2014).

Santa Maria was the first island of the Azores to have emerged above sea level during the late Miocene (Abdel-Monem et al., 1975). Its detailed volcanostratigraphic sequence was defined by Serralheiro et al. (1987) and subsequently refined by Serralheiro and Madeira (1990), Serralheiro (2003) and Ávila et al. (2012). The geological evolution of Santa Maria can be summarised as follows (cf. Fig. 2): 1) emergence of the volcanic edifice above sea-level during the Late Miocene (Cabrestantes and Porto formations); 2) construction of a subaerial shield volcano during the Late Miocene (Anjos Complex); 3) subsequent erosion and possible total submersion producing heterogeneous volcaniclastic deposits, with synchronous low-volume submarine lava effusions on the eastern side of the island during the Late Miocene/Early Pliocene (Touril Complex); 4) increase in volcanic activity with a gradual shift from submarine to subaerial eruptions, forming lava deltas along coeval coastlines – and emergence of an elongated NNW-SSE-trending edifice during the Early Pliocene (Facho-Pico Alto Complex); 5) subaerial and littoral erosion followed by low-volume volcanism, forming a sequence of monogenetic cinder cones, during the Late Pliocene (Feteiras Formation); and 6) uplift and erosion of the edifice from Early Pleistocene to the present.

3. Materials and methods

3.1. Sedimentological, taphonomical and palaeoecological analysis

The outcrop at Pedra-que-pica was studied in detail to understand its overall structure, geometry and field relationships between the sedimentary deposit and the underlying and overlying volcanic sequences. A general geomorphological survey of the local palaeotopography was conducted in order to assess the physical setting in which the coquina was trapped. Special care was taken to record the lateral and vertical facies changes, the sedimentary structures, the spatial disposition of the fossils, and the position, identification, and taphonomical aspects of trace fossils. Data were collected with the objective of constructing detailed cross sections and stratigraphic columns. Fossils and bulk rock samples for micropalaeontological study were collected. Macrofossils were photographed in the field, measured, and classified to genus and species level whenever possible. Eight randomly selected quadrats of 1 m^2 were placed on horizontal surfaces of the outcrop and all fossils within the quadrat were identified and counted; taphonomic parameters (articulation of the valves, degree of fragmentation, bioerosion signs and encrustations) were measured for 164 shells. The outcrop was exhaustively surveyed for *Gigantopecten latissimus* (Brocchi, 1814), a large bivalve mollusc that may reach a maximum length of ≈25 cm. All exposed specimens of this species were counted and their shell settlement position (concave up/down, oblique/vertical position) was recorded, as well as the articulation state of the valves (articulated/disarticulated).

Because part of the coquina is presently underwater, the actual size of the outcrop was examined by SCUBA diving. The sublittoral rocky substrate east of the presently exposed area of the outcrop was surveyed and samples were collected and later examined for the presence of carbonate sediments. From the exposed area of the outcrop, representative samples of all main subunits of the deposit were collected for petrographic investigations to identify structures, micro textures, mineralogy, and microfossil content.

In compliance with the legislation of the Regional Government of the Azores, all fossil specimens collected during this study were deposited in the Fossil Collection at the Department of Biology of the University of the Azores (DBUA-F).

4. Results

4.1. Geomorphology of pre-existing topography

A prominent spur system composed of massive pillow lavas projects seaward perpendicular from the shore, now subaerially exposed over a distance of 115 m adjacent to the western edge of the Pedra-que-pica outcrop (Fig. 3). The existing spur system attains a maximum elevation of 9 m above present sea level (apsl) on its western side (2^{nd} rocky spur of Fig. 3A, B), and is flanked by an irregular surface contiguous to the east, eroded in the pillow lavas (1^{st} rocky spur of Fig. 3A, B); the sedimentary sequence rests unconformably on this surface and abuts against the 1^{st} rocky spur to the west. The unconformity between the eroded pillows and the overlying sediments is exposed within the present-day tidal range, being visible around the margins of the coquina outcrop and at several openings (blow holes) formed by wave erosion.

4.2. Facies description, stratigraphy and sedimentological structures

4.2.1. Pliocene sedimentary succession

The main outcrop at Pedra-que-pica consists of a 10 to 11 m thick succession of marine fossiliferous sediments, of which only the uppermost 3 to 4 m are presently exposed above sea level. These sediments are intercalated between an underlying volcanic sequence and an overlying volcano-sedimentary sequence (Fig. 4A, B). The base of the section is formed by pillow lavas (facies 1) which are truncated by an erosional surface dipping towards ENE down to a depth of 6–7 m below mean sea-level (bmsl). Locally, limited remains of strata that predate the coquina can be found in spaces in between the pillow lavas, forming sandstone pockets composed of fine-grained, light grey calcarenites (facies 2; Fig. 5). These calcarenites occupy a corner of the eroded lava platform at its junction with the rocky spur system. Larger somatofossils are absent from the calcarenites, but trace fossils belonging to *Macaronichnus segregatis* Clifton and Thompson, 1978 are abundant (Figs. 3A, 6A, B), with rare ?*Ophiomorpha* isp. (misidentified as *Thalassinoides* isp. by Kirby et al., 2007). Pockets of calcareous sand among the pillow structures above this level and located on the flanks of the spur system at a present height of 9 m apsl (white stars in Fig. 3A) also feature additional examples of *M. segregatis*. Thin neptunian dikes filled with calcareous sand are a prominent feature across the spur adjacent to the fossiliferous sediments. *M. segregatis* occupies the sediments in these dikes, which can be traced through a continuous vertical distance of 4 m (Fig. 6C, D). The calcarenite (facies 2; Fig. 5) is unconformably truncated by an irregular erosion surface and covered by a 3-4 m thick unstructured coquina (facies 3a–c; Figs. 5, 7A–E, 8A, B).

The lower part of the coquina is submerged below present-day sea level. By scuba-diving, we estimated its total area to be 23,463 m^2 (continuous hard white line in Fig. 3A). The intermediate part of the sequence is exposed at the intertidal zone as a shore platform, extending for 3,179 m^2, whereas the upper part extends below the slope deposits at the base of the present seacliff (Fig. 4A, B). The top of the coquina may be traced laterally to a position near the adjacent spur (cf. Fig. 3), where it abuts against the ravinement cut into the underlying calcarenites. About 1.0 m above the base of the coquina it is possible to observe a 30 to 60 cm thick, discontinuous bed of subangular to subrounded volcanic cobbles and boulders (facies 3b; Figs. 5, 7A, D), followed by another unstructured, massive layer of coquina up to 2.6 m thick (facies 3c; Fig. 5). The very poorly-sorted coquina-rudstone layers (facies 3a and 3c; Fig. 9A, B) are rich in large, disarticulated bivalves (dominated by ostreids, pectinids and spondylids). It also contains fewer echinoids (Fig. 8C), barnacles, brachiopods, bryozoans, calcareous algae (rhodoliths) and small stony-corals. Teeth of bony fishes and sharks as well as moulds of large gastropods (*Persististrombus* sp.) are rare, while whale bones are extremely rare. The matrix of the coquina is predominantly composed of moderately sorted, sand-size skeletal bioclasts (fragments of bivalves, echinoids, coralline algae, bryozoans as well as benthic and planktonic foraminifers) with a smaller percentage of well-rounded volcaniclasts (coarse palagonitic ash and tachylitic to lithic clasts) cemented by sparry calcite (Fig. 9C, D).

Close to the top, the coquina contains rhodoliths (Fig. 8D) and abundant bryoliths (i.e., nodules composed of bryozoans; Fig. 8E), as well as colonies of bryozoans with an erect rigid growth form; these can be found within a fining upward to faintly bedded calcarenite devoid of large clasts (facies 3d; Figs. 5, 8F). These calcarenites are ≈10 to 60 cm thick, show a sub-horizontal, very regular top, and are partly bioturbated throughout the deposit. The most common trace fossil is *Asterosoma* isp., composed of a cluster of concentrically layered spindle-shaped tubes, which diverge radially upward from a common stem (Fig. 8G). Less common is a tubular backfill structure with a central rod, ascribed to *Bichordites* isp., which occurs in the eastern part of the outcrop, within the upper 1 to 2 cm of the calcarenite (Fig. 8H). The topmost 10 cm contain abundant spines of the echinoid *Eucidaris tribuloides* (Lamarck, 1816) and fragments of the coral *Porites* sp. The top of the calcarenite is locally scoured and some trace fossils are truncated.

Abruptly overlying the bioturbated calcarenite (facies 3d) there follows a ≈36 m thick unit of well-stratified, fine- to coarse-grained, vitric ash tuffs (facies 4a; Figs. 4, 10A; Kirby et al., 2007). The boundary between the two units is sharp. The basal 20–30 cm of the tuffs are characterized by relatively fine grain-sizes (fine ash) and by the presence of water-escape structures (Fig. 10B). None of these structures appear to penetrate the underlying calcarenites. Likewise, none of the calcarenite material is incorporated in the basal tuff layers. Tuffitic material, however, infills the bioturbation canaliculated conducts opened on the top of the calcarenite.

Sedimentary structures within the tuffs include thin planar lamination to medium-thick bedding, low-angle cross-bedding, internal erosional surfaces where the planar bedding is discordant and multiple reverse and normal graded beds. The tuff is a matrix-supported fine-grained ash, locally palagonitised and cemented by micro zeolites. Clasts are quite variable in size (0.25–2.5 mm) and consist of moderately rounded and weathered lava clasts, and angular fragments and euhedral loose crystals (plagioclases, olivines and clinopyroxenes). Fractures are cemented by secondary calcite (sparite) (Fig. 9E). A single external mould of a bivalve (5.5 cm in length) was found within the tuff, circa 20 cm above the contact with the calcarenite (Fig. 10C). Very rare angular lava clasts (10–15 cm in size), are scattered within this unit (Fig. 10D). In addition to these clasts of volcanic origin, a subordinate amount of lithic clasts (2–20 cm) of sedimentary rock (Fig. 9F–H) are present within the tuffs. These clasts are represented by a variety of different lithologies, ranging from bioclastic tuffaceous sandstone to almost pure limestone (grainstone or rudstone with sparitic cement with a subordinate amount of volcaniclastic fragments).

The tuffs are overlain by a <0.5 m thick conglomerate horizon (facies 4b; Fig. 4B) that is followed by a thick lava-delta sequence composed of foresets of pillow lavas and hyaloclastites (facies 4c) and a topset of flat-lying subaerial flows (facies 4d). The passage zone between the subaerial and submarine flows marks the coeval sea level and is nowadays located ≈50 m apsl. Towards the top of the cliff, the sequence is mostly effusive and subaerial with the exception of occasional surtseyan tuff layers (facies 4e and 4g), and a small set of submarine lava flows (facies 4f; Fig. 4B).

4.2.2. Pleistocene sedimentary succession

At the section locality (Fig. 4A, B), the tuffaceous sequence (facies 4a) is truncated by a Pleistocene (MIS 5e; Ávila et al., 2008b, 2015) shore platform that reduced its thickness to ≈4 m. The erosional unconformity and the overlying 0.5 to 1 m thick boulder beach conglomerate (facies 5; Figs. 4B, 5) ends against a visible shore angle, which is exposed ≈50 m to the east (Fig. 4B). The conglomerate is topped by a >20 m thick, wedge-shaped terrigenous talus deposit (colluvium), consisting predominantly of boulder breccias (facies 6; Figs. 4B, 5).

4.3. Palaeoecology and taphonomy of the coquina layers

The vast majority of the macrofossils in the coquina (facies 3a and 3c; Fig. 5) consist of bivalve molluscs: *Chlamys hartungi* (Mayer, 1864), *Talochlamys abscondita* (Fischer in Locard, 1898) [= *Hinnites ercolanianus* (Cocconi, 1873)], *Aequipecten opercularis* (Linnaeus, 1758), *Pecten dunkeri* Mayer, 1864, *Argopecten* cf. *levicostatus* Toula, 1909 [= *Pecten* cf. *laevicostatus* (Soweby, 1844)], *Manupecten pesfelis* (Linnaeus, 1758), *Gigantopecten latissimus* (Brocchi, 1814), *Arca noae* Linnaeus, 1758, *Anadara* sp., *Cubitostrea frondosa* (de Serres, 1829) [= *Ostrea frondosa* de Serres, 1829], *Ostrea* cf. *edulis* Linnaeus, 1758 [= *O*. cf. *lamellosa* Brocchi, 1814], *Lopha plicatuloides* (Mayer, 1864), *Spondylus gaederopus* Linnaeus, 1758, *Spondylus* cf. *concentricus* Bronn, 1831, and the boring bivalve *Myoforceps aristatus* (Dillwyn, 1817).

The results of surface-abundance counts on eight 1-m^2 quadrats show that *Ostrea* spp. are the dominant species, ranging from 69 to 89%, with *Spondylus* spp. (4–9%), *Manupecten pesfelis* (1–6%), *Chlamys hartungi* (1–9%), *Pecten dunkeri* (1–4%) and the endemic *Lopha plicatuloides* (2–6%) as accessory species; *Gigantopecten latissimus* ranges from 0 to 2%. Fossils of aragonitic gastropods and bivalves are nearly absent from Pedra-que-pica, probably due to the preferential dissolution of aragonitic shells during diagenesis (Valentine *et al.,* 2006). The only exceptions are a few poorly preserved moulds of *Persististrombus* sp., *Conus* sp. and *Cheilea equestris* (Linnaeus, 1758).

In total, 70 different taxa could be determined: 38 bryozoans, 18 species of molluscs (15 bivalves and 3 gastropods), 6 echinoids, 3 gnathostomata (two sharks and one teleost), 2 balanid crustaceans, 1 brachiopod, 1 cnidarian and 1 mammal (an unidentified whale) (Table 1).

Throughout the coquina, the majority of the larger pectinid shells (e.g., *Gigantopecten* longer than 10 cm) are concordant, lodged in a stable concave-down position. The analysis of all the valves of *G. latissimus* visible on the coquina surface (394 specimens) found that 389 were single disarticulated valves (98.7%) and only five shells were still articulated (1.3%). Of the disarticulated shells, 347 valves were concordant (286 in a stable concave-down position and 61 showed a concave-up orientation), 25 were obliquely oriented – 15 of which with the concavity downwards (3.8%) and 10 with the concavity upwards (2.5%) – and 17 were perpendicular (that is, in a vertical position – 4.3%). Of the five articulated shells, three were preserved in a concordant position (0.8%) and two in a perpendicular position (0.5%).

The orientation of the smaller bivalves, mainly composed by ostreids having all valves disarticulated, was studied along three vertical profiles each 25 cm wide and 1.75

m, 2.50 and 2.75 m in height, respectively (Fig. 11A–C). A total of 1,482 ostreid shells were counted, and their angles measured. The resulting rose diagrams (Fig. 11A–C) demonstrate the main differences in the chaotic disposition of the smaller ostreids, with most shells in concordant – either stable (concave-down) or unstable (concave-up) (horizontal/sub-horizontal) – positions but with somewhat lesser numbers of valves in perpendicular (vertical/subvertical) positions. In contrast, the large *Gigantopecten* (389 valves analysed) are predominantly in concordant (stable horizontal/subhorizontal) positions (Fig. 11D). A further representative sample of 164 bivalves dominated by *Ostrea* spp. (51.2%) and with subordinate amounts of *Lopha plicatuloides* (12.8%), *Chlamys* spp (10.4%), *Spondylus* spp. (8.5%), *Pecten dunkeri* (7.3%), *Gigantopecten latissimus* (4.9%), *Manupecten pesfelis* (4.3%) and *Arca noae* (0.6%) was examined for taphonomical traits. All shells are disarticulated (100%, n= 164), 76.8% are fragmented mostly on the edges (either on the umbo, dorsal or ventral margins), 68.9% show signs of bioerosion and 82.3% have encrustations. Most bivalve shells are heavily bioeroded on the external side of the valves (mostly *Gastrochaenolites* isp. produced by bivalves, *Entobia* isp. by clionaid sponges, and *Caulostrepsis* isp. by spionid polychaetes), and are commonly encrusted by bryozoans, balanids, oysters, serpulids and calcareous red algae (listed in order of decreasing abundance). Despite this, they are generally well preserved, with fragile skeletal elements still present (e.g., external ornamentation of bivalves). Similarly, the tests of delicate echinoderms such as *Echinoneus* cf. *cyclostomus* Leske, 1778 are also well preserved (Madeira et al., 2011).

The inner sides of most bivalves are usually encrusted by cheilostome and, to a lesser degree, cyclostome bryozoans (cf. Table 1). Most, if not all, of these bryozoan species are new to science and will be described elsewhere. The most ubiquitous bryozoan species is *Onychocella* cf. *angulosa* (Reuss, 1847), which may cover large parts of or even entire shells.

5. Discussion

5.1. Palaeoenvironmental reconstructions

Foremost consideration is given to the pre-existing topography. Similar to the present day, it featured a prominent spur system, formed by pillow-lavas emplaced in latest Miocene time that advanced to the south in a direction perpendicular to the present shore (cf. Figs. 2, 3). An erosional platform was cut into the pillow-lava pile to form an accumulation zone. Thereby, the spur system acted as an effective trap capable of accommodating and retaining a considerable volume of bioclastic materials in the littoral environment (Fig. 3A). This prominent coastal feature played a key role in preventing the offshore transport of sediments, thus allowing accumulation of sediments.

A lowering in sea level must have occurred after the emplacement of the submarine lavas, because planation of the spur system's east flank took place under intertidal conditions, incising a typical gently sloping (4°) shore platform where the coquina now sits. Hence, the angle between the shore platform and the proximal spur, define a north-south oriented palaeoshore that was subsequently drowned by a rise in sea level. The original width of the eroded surface embraces the entire lava platform underneath the adjacent coquina deposit, immediately to the east. The relief of the spur above the flat platform now remains more than 9 m in height.

Remnants of the earliest phase of sedimentation covering the platform's shoreward margin are represented by pockets of bioturbated calcarenite that include the trace fossil

Macaronichnus segregatis (Fig. 6A–D). Highly bioturbated sandstones with *Macaronichnus* and mostly vertical, sparse crustacean burrows typically occur in upper foreshore environments (e.g., Pemberton et al., 2001). Incipient *Macaronichnus* traces are known to be produced today on sandy beaches by some ophelid polychaetes such as those belonging to the genus *Euzonus* (Nara and Seike, 2004; Seike, 2007). Thus, mass occurrences of this trace fossil are generally regarded as an excellent indicator of intertidal to shallow subtidal conditions (i.e., upper foreshore). *Macaronichnus* isp. is also recorded from shoreface settings in the Cape Verde Archipelago (Mayoral et al., 2013; see also Bromley et al., 2009 for discussion of environmental range of *Macaronichnus*), but as far as known, its occurrence within calcarenite sediments in neptunian dikes such as the ones that dissect the spur adjacent to Pedra-que-pica is unique (cf. Fig. 6C, D). The continuous representation of these fossil traces through a vertical space of 4 m suggests a coeval sea-level rise. Moreover, as pockets of similar carbonate sandstone are retained on the flanks of the parallel spur that is now 9 m apsl, it is inferred that a minimum change in local sea level amounted to at least 9 m during the early stages of this succession. Therefore, we infer a coeval increase in water depth above the adjacent coastal platform to become entirely subtidal. The fact that the leading edge of the coquina partially truncates and cuts across the earlier calcarenites (Fig. 6A), over a ravined morphology, is also interpreted as a result of this transgressive regime.

The coquina appears to have been formed by at least three events, as indicated by the occurrence of two shell beds (facies 3a and 3c), separated by a semi-continuous layer of basaltic gravel (facies 3b; Figs. 5, 7D). This structure is interpreted to reflect discrete pulses of material deposited under high-energy conditions, despite the lack of other obvious internal stratification or structuring. A final resting place for this tri-part deposit (shell bed, conglomerate, and shell bed) was effectively constrained by a natural submarine configuration where the materials became trapped.

The abundant occurrence of bioeroded exterior and bryozoan-encrusted interior valves of ostreids and pectinids argue for a primary (living bivalves) and secondary origin (when post-mortem bioerosion and encrustation took place) of the Pedra-que-pica coquina constituents, prior to final deposition. Whereas bioerosion primarily takes place on upward-facing surfaces in the euphotic zone (Wisshak et al., 2010, 2011), most bryozoans are cryptobionts and preferentially settle on the concave interior of shells, which, in its energetically stable position, is facing downwards. In this way, boring organisms and competition with fast growing photoautotrophs are avoided by the bryozoan colonies (McKinney and Jackson, 1989; Wisshak et al., 2014). However, in this outcrop, the bryozoan-encrusted concave side of many of the small ostreid and pectinid valves face upward, which contrasts with the energetically stable position taken by the majority of the large *Gigantopecten* valves (cf. Fig. 11). This bimodal distribution occurs throughout the whole vertical section of the deposit, and thus must be related to intrinsic characteristics of the process of deposition at this depth. The bimodality might be explained by a debris fall sensu Titschack et al. (2005), with different hydrodynamic behaviours of shells according to their size and shape. The smaller and more convex shells (like the ostreids) might settle from suspension in the concave-up position, exhibiting greater lift-to-drag ratio than the bigger and flatter shells (like the *Gigantopecten*), and thus may be more prone to movement by rolling, whereas the larger and flatter shells are transported by a sliding process along the slope which might favour a deposition in more stable positions (see Oliveira and Wood, 1997). An alternative explanation is that bottom current velocities during storm events were high enough to overturn the large and heavy recently deposited *Gigantopecten* shells to their most stable position (concave-down) and that these high velocities induced a chaotic deposition of the smaller and much more abundant ostreids shells, which were quickly covered (and thus locked in unstable positions) by successive layers of new shells. In detail, however, this deposition model needs to be refined and the cause for the bimodality further investigated.

The trigger mechanism for such energetic depositional conditions is not entirely clear. The coquina lacks most of the features diagnostic of (shelly) storm beds/tempestites, such as grading and sole structures, as defined in Reineck and Singh (1973) or Aigner (1987), possibly due to the coarse grain size. Earthquakes and storms could be responsible for triggering these re-depositional events. Since earthquakes are much less frequent than large storms in the region, storms are the most probable initiators of the redeposition.

The fossil assemblages at Pedra-que-pica indicate a shallow-marine source: the balanids *Zullobalanus santamariaensis* Buckeridge and Winkelmann, 2010 and the bivalve *Gigantopecten latissimus* predominantly inhabited agitated shallow-water environments (e.g., Bongrain, 1988; Harzhauser et al., 2003; Winkelmann et al., 2010); rhodoliths require at least periodically prevailing high-energy conditions and the former require habitats within the photic zone (Piller and Rasser, 1996); extant clypeasteroids close to *Clypeaster altus* (Leske, 1778), as well as extant cidarids such as *Eucidaris tribuloides* (Lamarck, 1816) are predominantly littoral inhabitants, being most common above 50 m water depth (Madeira et al., 2011); *Myoforceps aristatus* is an extant boring bivalve that lives in calcareous substrates commonly just below the low tide mark. This bivalve does not occur in the Azores today due to the lack of appropriate substrate (Ávila et al., 2010), as it is not able to bore lava and carbonate production is very limited, but it was a very common species at Santa Maria during the formation of the

Pedra-que-pica deposit, boring rhodoliths and bryoliths, as well as bivalve shells. The borings *Gastrochaenolites*, *Entobia* and *Caulostrepsis*, are typical members of the *Entobia* ichnofacies, whose formation requires exposition of the substrate for months, if not years (Bromley, 1992). These borings occur mostly in the deeper intertidal and shallow subtidal zones (Ekdale et al., 1984), typically on upward-facing surfaces of shells (Wisshak et al., 2010). Most fossils (especially the bivalve shells and their encrusting bryozoans), exhibit a low degree of fragmentation (mostly limited to the edges of the shell), abrasion and/or reworking, which – together with the poor sorting – indicates a proximal provenance followed by transport and deposition of the coquina into somewhat deeper waters below fair-weather wave base, where low-energy conditions prevented further reworking and fragmentation of the shell material. Therefore, the fossil assemblage at Pedra-que-pica represents an allochthonous fauna generated at a highly productive carbonate factory at shallower levels, later transported (as argued above) to a calmer, deeper depocenter.

The occurrence of just only five paired *Gigantopecten* valves (<1.3%), together with the degree of shell fragmentation and sorting, also indicates a swift removal and rapid transport of the shell accumulation from a nearby source. With the exception of bioclasts of the stony coral *Porites* (which are mainly composed of aragonite), the lack of other aragonitic bioclasts and the predominance of oysters, echinoids, pectinids, barnacles, and other calcitic taxa in the coquina is interpreted as a taphonomical artefact due to early diagenetic dissolution of shell aragonite prior to lithification.

In temperate latitudes, post-mortem disarticulation of pectinid shells due to the decay of the organic ligaments occurs in a matter of months to years (Christmas et al., 1997; Best, 2008). At the time of deposition, the palaeoclimatic conditions around Santa Maria would have been typical of a tropical environment, thus the degradation of soft tissues and the consequent disarticulation of the pectinid valves would have been faster (weeks to months) than in a more temperate climate (Best et al., 2004). We infer tropical sea-surface temperatures (SST's) based on the high frequency of the shallow *Gigantopecten latissimus* and *Clypeaster altus*, as well as on the presence of *Persististrombus* sp., *Ficus* sp., *Conus* spp., *Xenophora* sp. and *Porites* sp. The first three taxa were the most important warm-water taxa of the "Mediterranean Plio-Pleistocene Molluscan Unit 1" (Raffi and Monegatti, 1993; Monegatti and Raffi, 2001; Landau et al., 2011), a Zanclean-mid Piacenzian ecostratigraphical unit based on molluscs (Monegatti and Raffi, 2007). The common occurrence of specimens of *Persististrombus* at Pedra-que-pica further points towards much higher SST's than the present minimum sea-surface temperature in the Azores around 14°C in the winter period (Wisshak et al., 2010). Indeed, according to several authors, the presence of *Persististrombus* requires mean annual SST around 23–24°C, and winter SST not below 19-21°C (Bardají et al., 2009; Zazo et al., 2010). Thus, we infer that at the time of deposition of the coquina at Pedra-que-pica, tropical conditions were prevalent, with minimum sea-surface palaeotemperatures (at least) over 19°C, which is five degrees higher than nowadays.

In summary, we interpret the fossiliferous sequence at Pedra-que-pica to represent a succession of several debris-fall deposits (sensu Titschack et al., 2005) whose redeposition was triggered by major storm events that removed the sediments from its original nearshore setting (Fig. 12B) to a higher gradient area of the shelf. These events brought shell materials to a local depocenter below fair-weather wave base (cf. Figs. 2, 12C), where the lava spur system acted like a protective coastal groin. The accumulation of fine sediments continued during subsequent fair–weather conditions, when the calcarenite at the top of the coquina was colonised by invertebrate settlers. As a result, it shows increased bioturbation by polychaetes and large spatangoid echinoids, which produced *Asterosoma* isp. and *Bichordites* isp., respectively (Fig. 12D; Uchman, 1995, 1998). *Asterosoma* and *Bichordites* can be ascribed to the impoverished archetypal *Cruziana* ichnofacies, which is typical of shoreface-offshore transition and upper offshore, below the fair-weather wave base (e.g., Pemberton et al., 2001). The impoverishment can be caused by the shelly ground below the calcarenites, preventing deep burrowing, and by small scale scouring before deposition of water-settled tuff, which might erosionally remove some shallower burrows (see section 5.3).

5.3. Preservation of the deposit and subsequent events

The sharp transition between the calcarenite and overlying water-settled tuff (facies 4a, Fig. 4B; facies 4, Fig. 5) demonstrates an abrupt change in sediment supply, related to the onset of a new volcanic phase in this area, probably from the Rocha Alta volcanic cone, located ≈600 m to the west of Pedra-que-pica. Prior to this eruption, part of the top of the calcarenite was removed, probably by a storm. This reasoning is based on the *Bichordites* isp. (Fig. 8G) that was typically produced by spatangoid echinoderms, usually at depths of 5 to 50 cm from the top of the sediment surface (Bromley *et al.,* 1997). As this ichnofossil is at a depth of only 1 to 2 cm from the contact between the calcarenite and water-settled tuff, it is inferred that several centimetres of sediment were removed. Rapid and voluminous accumulation of loose lapilli- to ash-sized pyroclastic particles subsequently sealed the remaining sediments below, and thus favoured their preservation.

Angular lithic clasts of marine sedimentary origin and isolated gastropods within the water-settled tuffs (Fig. 9F–H) are classified as “accidental clasts” (cf. Fisher and Schmincke, 1984) that were produced and became entrained by the disruption of pre-existing, lithified country rocks at the seafloor during explosive hydromagmatic eruptions. Their angular clast shapes indicate that such volcaniclastic calcarenites were already lithified at the time of the eruption and that transportation distances were short. Some clasts are composed of material similar to the matrix of the coquina and the overlying calcarenite. Others, however, are very pure, well cemented limestone with subordinate volcano-detritic content and abundant gastropods (cf. Fig. 8H), i.e. aragonitic shells are preserved, which indicates that the source is different than that of Pedra-que-pica, where aragonite was dissolved prior to lithification. The single external mould of a bivalve (Fig. 10C) is also an "accidental clast". It is interpreted as a shell that, projected together with the pyroclasts, became entrained in the volcanic plume from the sea floor, and was thus deposited together with the water-settled tuffs.

The absence of bioturbational structures, prominent unconformities, or larger intercalations of epiclastic material within the tuffs indicates rapid deposition and a continuous and voluminous supply of pyroclastic material in a relatively short period of time. The massive provision of loose tuffaceous material caused the sedimentary system to switch from retrogradational to progradational.

The deformed structures at the base of the tuffs are interpreted as fluid-escape structures (Fig. 10B). They might be attributed to sediment liquefaction during earthquakes, when localised fluid-escape velocities are higher than those needed for minimum sediment fluidisation (Judd and Hoveland, 2007). Alternatively, they could be indicative of an abrupt overburden, and thus a rapid deposition of the tuffs, which caused the underlying, fluid-saturated sediment to dewater due to sedimentary overload.

The absence of ballistic emplacement structures of volcanic bombs and blocks (e.g., impact pits, bomb sags) suggests a submarine origin for these pyroclasts, classifying them as water-settled surtseyan tuffs formed by hydromagmatic volcanic activity in relatively shallow waters (Fisher and Schmincke, 1984). The subaquatic deposition of the tuff layers is further corroborated by the common occurrence of cross-bedding and small cross-cutting channels, as we interpret these sedimentary structures not as primary structures typical of surge (diluted turbulent pyroclastic flow) deposits, common in surtseyan eruptions (as they would be if subaerial and related to the deposition of the tuffs), but as secondary structures related to the marine environment and the rapid resedimentation of the tuffs.

At an elevation of ≈35 m apsl, the top of tuffaceous unit is overlain by a thin (<1 m) conglomerate bed (facies 4b; Fig. 4B). The unconformity and the overlying conglomerate indicate erosion and reworking in comparatively shallow water. Following the formation of the conglomerate on top of the tuffs, another period of volcanism emplaced the overlying lava delta (facies 4c and 4d; Fig. 4B). Low palaeo-relief characterises the transition between the conglomerate and the submarine volcanics, which indicates a short hiatus due to sediment reworking. Pillows and palagonitised hyaloclastites constitute the basal part (facies 4c; Fig. 4B), indicating submarine volcanism. The submarine lavas are topped by massive subaerial flows (facies 4d; Fig. 4B), with the transition between submarine and subaerial environments occuring at an altitude of ≈50 m apsl, marking very accurately the position of coeval sea-level (Fig. 4B). Thus, the volcano-sedimentary sequence overlying the fossiliferous sediments further attests to a sea-level rise of around 50 m.

5.4. Sedimentation on the shelves of volcanic oceanic islands

In the highly dynamic environment of volcanic oceanic islands, it is unusual to find marine sediments preserved in bulk, although carbonate may be abundantly produced by a range of benthic organisms in euphotic to aphotic conditions (Wisshak et al., 2014). Island shelves in these settings are typically very narrow and steep, exposed to high-wave energy and, thus, offer little accommodation space compared to continental shelves (Ávila et al., 2008a; Quartau et al., 2010, 2012). Present-day submarine deposits on such island shelves are affected by strong, offshore-directed, downwelling currents that form to compensate coastal setup of storm surges (Tsutsui et al., 1987; Chiocci and Romagnoli, 2004; Quartau et al., 2010, 2012, 2015; Meireles et al., 2013).

The typical morphology of these shelves and the exposure to high-energy conditions are unfavourable for preservation of depositional sequences older than those dating from the present highstand. As shorelines migrate downwards across the shelf during sea-level drops, downwelling currents are more likely to transport sediments over the shelf edge where they are ultimately lost to the deep-island slopes (Ávila et al., 2008a, 2010; Quartau et al., 2012). Occasionally, chances for preservation may be enhanced by adequate geomorphological features (e.g. natural barriers, bays, channels, gullies, depressions, etc.), sediment textures (coarse deposits) and lithification (Quartau et al., 2012). However, the single most important contributor to preservation is volcanic capping. Exposure, on the other hand, is only possible on islands that experience uplift (or eventually vertical stability and sea-level fall). That is why other marine deposits have been described from Atlantic islands such as Madeira, Porto Santo and Selvagens (Mayer, 1864; Cotter, 1892; Gerber, 1989; Johnson et al., 2011; Santos et al., 2011; Baarli et al., 2014; Ramalho et al., 2015), as well as the Canary (Zazo et al., 2002) and Cape Verde archipelagos (Zazo et al., 2007, 2010; Ramalho et al., 2010; Ramalho, 2011; Johnson et al., 2012; Baarli et al., 2013). All these islands experienced uplift episodes during their geological history, and sea-level fall relative to the Last Interglacial period. Therefore, to find well-preserved shell accumulations on reefless volcanic oceanic islands is unusual, as only a few experienced the necessary conditions for preservation and exposure.

Additionally, massive fossil accumulations preferentially form when sedimentation is reduced, i.e., during transgressions (Kidwell et al., 1986; Kidwell, 1991). However, these condensed sections are less likely to be preserved in the geological record of continental margins (Scarponi et al., 2013) and even less likely on insular shelves (Ávila, 2008a; Quartau et al., 2012; Meireles et al., 2013). Fortunately, in volcanic settings, eruptions may locally entomb marine deposits through rapid and abrupt burial, thus locally preserving the transgressive sedimentary record. Consequently, volcanic events have the potential to interrupt carbonate production but also provide the hard substrata for a diverse benthic ecosystem and development of an offshore carbonate factory in the first place (e.g. Wisshak et al., 2010). Volcanoes also can be responsible for the effective preservation of marine deposits on oceanic-island shelves (cf. Meireles et al., 2013).

6. Conclusions

The sedimentary deposits at Pedra-que-pica are the result of localised biotic and abiotic factors that operated under a rare confluence of the following events:

1. Sea-surface temperatures above 19°C and sunlight worked to elevate productivity in a nearshore shelf setting around Santa Maria Island, with the resulting development of a shallow carbonate factory;
2. A natural coastal groin formed by a resistant spur of basalt perpendicular to the island’s south shore and adjacent to a shore platform where deposition was

already present in the Pliocene; the angle between the spur and the platform demarks a palaeoshore;

3. The first depositional event on this shore platform was the accumulation of carbonate sand in an intertidal to very shallow water setting. This depositional depth is inferred by the presence of neptunian dikes filled with carbonate sand that hosted intertidal organisms that left behind the trace fossil *Macaronichnus segregatis*. The continuous migration of the trace maker in vertical dikes reaching upward for 4 m represents a rise in relative sea level. The sea-level continued to rise to a level deep enough to accommodate the next depositional sequence (coquina);
4. Through a succession of no less than three debris-fall events initially triggered by storms, the deepening accommodation space on the platform received a tri-part accumulation of sediment that formed a shell coquina, a conglomerate, and a second shell coquina;
5. The coquina deposit is formed by disarticulated bivalve shells (dominated by *Ostrea* spp. as much as 89% by count), has an overall preserved thickness of several meters (at least 11 m) and covers an uneven platform inferred to be over 23,400 m^2 in area;
6. The deposition of shells and other biological material occurred below fair-weather wave base, where low-energy conditions prevented reworking and shell fragmentation;
7. Erosion of the calcarenites on top of the coquina took place prior to emplacement of the water-settled tuffs, which were capped by a lava delta sequence that effectively sealed the fossiliferous succession from any further disturbance until its relatively recent exhumation due to uplift and erosion.

This study contributes to the understanding of processes responsible for the transport and sedimentation on the shelves that surround reefless volcanic oceanic islands. It also highlights the importance of the Pedra-que-pica coquina within an oceanic island context, because very special conditions are required for the preservation and exposure of similar deposits on shelf environments of reefless volcanic oceanic islands. The same exciting avenue of research may be advanced by similar studies in other archipelagos. Finally, the extreme rarity and hence the international interest in this deposit calls for a reinforcement of its legal protection and continuation of further studies at Pedra-que-pica.

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Figures and tables

Fig. 1. Location maps. **Insert.** Location of the Azores Archipelago within the NE Atlantic. MAR = Mid-Atlantic Ridge; NA = North American plate; Nu – Nubian (African) plate; Eu = Eurasian plate. Location of Santa Maria, within the Azores Archipelago.

Fig. 2. A. Simplified geological map of Santa Maria (Serralheiro et al., 1987; Serralheiro, 2003). **B.** Profile of Santa Maria Island (vertical amplification = 3x). **C.** Pedra-que-pica on SE Santa Maria (white rectangle).

Fig. 3. A–B. Position of the rocky spurs in relation to the Pedra-que-pica fossiliferous sediments. **A.** White asterisks mark the position of the calcareous sand inclusions, some of which feature examples of the trace fossil *Macaronichnus segregatis*, on the rocky spurs. The four red flags indicate the location of the diving where rock samples were collected. Hatch white line represents the present exposed area of the coquina. Continuous hard white line represents the total inferred area of the coquina. **B.** Pedra-que-pica seen from the east (lateral view).

Fig. 4. Stratigraphy and sedimentological structures at Pedra-que-pica. **A.** General cross-section of Pedra-que-pica volcano-sedimentary sequence, showing the volcanostratigraphic setting of the basal sedimentary sequence, and location of the passage zone between subaerial and submarine flows (representing coeval sea-level) within the overlying lava delta sequence. **B.** Stratigraphic framework and interpretation of the Pedra-que-pica lithological succession. The numbers depicted in black circles

correspond to facies 1–8, which are described in the text. The scale bar indicates the location of the detailed composite profile (see Figure 5).

Fig. 5. Detailed composite stratigraphic column at Pedra-que-pica (N36°55.806'', W25°01.482''). The numbers depicted in black circles correspond to facies 1–6, which are described in the text.

Fig. 6. Remnant sediments and their trace fossils on the pre-existing topography, below the coquina. **A–B.** Light grey calcarenites forming sandstone pockets up to 1 m thick, bioturbated with abundant *Macaronichnus segregatis* and rare ?*Ophiomorpha* isp., rest directly on the bedrock. Note that part of the sediments (the shell rich parts), belong to the overlaying coquina. **C–D.** Neptunian dikes filled with calcareous sand and bioturbated by *Macaronichnus segregatis*.

Fig. 7. Selected sedimentary features of the coquina and associated deposits. **A.** General view of the coquina at Pedra-que-pica seen from the west. **B.** Coquina resting directly on top of the basal pillow lavas of the Touril Complex (eastern section of the outcrop). **C.** General view of the first coquina layer (facies 3a) seen from the east. Note the chaotic disposition of the smaller ostreid shells and the valve of a large *Gigantopecten latissimus* in a vertical position (center of the photo). **D.** Closer view of the conglomerate layer that separates coquina deposits formed by two debris-fall events. The conglomerate is a moderately-sorted, component-supported volcaniclastic pebble to cobble sediment (facies 3b) located ~1 m from the base of the sedimentary Touril succession at Pedra-que-Pica. The intermediate conglomerate contains a volcaniclastic

calcarenite matrix, similar to the matrix of the overlying coquina. **E.** General view of the second coquina layer (facies 3c) seen from the west.

Fig. 8. Selected sedimentary features of the coquina and associated deposits. **A.** Broken test of an echinoderm *Clypeaster altus*. **B.** Rhodolith. **C.** Bryolith bioeroded by the bivalve *Myoforceps aristatus*. **D.** The coquina seen from the above. **E.** One of the very rare *Gigantopecten latissimus* with the two valves still articulated. **F.** Calcarenite (topmost section of the coquina). **G.** *Bichordites* isp., a trace fossil produced by burrowing spatangoid echinoids. **H.** Sandstones bioturbated by *Asterosoma* isp. (eastern section of Pedra-que-pica).

Fig. 9. A–B. Cross sections of bulk samples of the coquina. **A.** submarine sample. **B.** Subaerial sample. **C–H.** Thin sections illustrating the lithologies found in facies 3 and 4. **C–D.** Volcaniclastic calcarenite matrix of the coquina-rudstone. **E.** Matrix (tuffaceous sandstone) of the water settled tuff. **F–H.** Sections of lithoclasts floating in the water-settled tuff matrix. **F.** Mudstone/siltstone lithoclast with numerous bioclasts and lithic fragments. **G.** Volcaniclastic sandstone with abundant bioclasts. **H.** Limestone lithoclast (coarse biosparite with subordinate lithic fragments). Aragonite gastropods are visible in the center of the photo. Scale bars equal to 1 mm.

Fig. 10. A. Coquina (light yellow, bottom unit) overlaid by well-stratified, fine- to coarse-grained vitric ash to lapilli water-settled tuffs. **B.** Fluid-escape structure (facies 4) at the base of the tuffs. **C.** External mould of a bivalve (facies 4). **D.** Non-ballistically emplaced pebble (facies 4).

Fig. 11. Stratigraphic logs covering the shell accumulations in the coquina. A bimodal distribution is clearly visible, with most of the big bivalve *Gigantopecten* valves concordant (oriented concave-down) and with the small valves of *Ostrea* spp. and of other bivalve species mainly concordant but with high numbers of valves also in unstable positions (perpendicular and oblique). **A-C.** Rose diagrams for the 1,482 valves of ostreids (counted on the three vertical logs). **D.** Rose diagram for the 389 valves of *Gigantopecten latissimus* (counted along the entire outcrop; top right). The angles of the shells for the construction of the rose diagrams were measured according to the figure. The tallest person (in grey) is about 1.80 m.

Fig. 12. Depositional model inferred for the formation of a coquina in the context of an insular shelf using Pedra-que-pica as an example (figure not to scale). **A.** Formation of the basal carbonate sand with abundant *Macaronichnus segregatis* Clifton and Thompson, 1978, during lower but rapidly rising relative sea-level. **B.** Sea-level rise and establishment of a shallow-water carbonate factory during stand-still. Debris-fall transport from shallow-water carbonate factory onto deeper parts of the shelf (~50 m depth) possibly triggered by storm events. **C.** Waning of storm event and gradual establishment of fair-weather conditions allowing the deposition of finer sediments (fine sand), thickening against the rocky spur that acts like a coastal groin. **D.** Fair-weather conditions. Bioturbation of the top calcarenites by opportunistic invertebrate organisms.

Table 1. Taxa found at Pedra-que-pica outcrop.

Table 1: Taxa of fossils found at Pedra-que-pica outcrop.

GROUP	Taxa
Brachiopoda	*Novocrania turbinata* (Poli, 1795)
Bryozoa	*Antropora* sp.
	Biflustra sp.
	Bryopesanser sp.
	Buffonellaria sp.
	Caberea sp.
	Calloporina sp.
	Celleporidae indet.
	Chaperiidae indet.
	Chaperiopsis sp.
	Cheiloporina sp.
	Chorizopora sp.
	? *Crassimarginatella* sp.
	Crepidacantha sp.
	Cryptosula sp.
	Escharella sp.
	Escharina sp.
	Escharoides sp.
	Figularia cf. *figularis* (Johnston, 1847)
	Hincksina sp.
	? *Hippaliosina* sp.
	Hippopleurifera sp.
	Metroperiella sp.
	Microporella sp. 1
	Microporella sp. 2
	"Myriozoum" cf. *marionense* Busk, 1884
	Onychocella cf. *angulosa* (Reuss, 1847)
	? *Plesiocleidochasma* sp.
	Puellina (*Glabrilaria*) sp.
	Puellina (*Puellina*) sp. 1
	Puellina (*Puellina*) sp. 2
	Reteporella sp.
	Saevitella sp.
	Schizomavella cf. *triaviculata* (Calvet, 1903)
	Schizotheca sp.
	Scrupocellaria sp.
	Smittoidea sp.
	Therenia sp.
	?*Umbonula* sp.
Cnidaria, Anthozoa	*Porites* sp.
Crustacea	? *Megabalanus* sp.
	Zullobalanus santamariaensis Buckeridge & Winkelmann, 2010
Echinodermata	*Clypeaster altus* (Leske, 1778)

	Echinocyamus pusillus (Müller, 1776)
	Echinoneus cf. *cyclostomus* Leske, 1778
	Eucidaris tribuloides (Lamarck, 1816)
	Schizobrissus sp.
	Spatangoida indet.
Mollusca, Gastropoda	*Cheilea equestris* (Linnaeus, 1758)
	Cirsotrema cf. *cochlea* (G. B. Sowerby II, 1844)
	Persististrombus sp.
Mollusca, Bivalvia	*Aequipecten opercularis* (Linnaeus, 1758)
	Anadara sp.
	Arca noae Linnaeus, 1758
	Argopecten cf. *levicostatus* Toula, 1909 = *Pecten* cf. *laevicostatus* (G. B. Sowerby II, 1844,)
	*Chlamys hartungi (*Mayer, 1864)
	Cubitostrea frondosa (de Serres, 1829) = *Ostrea frondosa* de Serres, 1829
	Gigantopecten latissimus (Brocchi, 1814)
	Lopha plicatuloides (Mayer, 1864)
	Manupecten pesfelis (Linnaeus, 1758)
	Myoforceps aristatus (Dillwyn, 1817)
	Ostrea cf. *lamellosa* Brocchi, 1814
	Pecten dunkeri Mayer, 1864
	Spondylus cf. *concentricus* Bronn, 1831
	Spondylus gaederopus Linnaeus, 1758
	Talochlamys abscondita (Fischer in Locard, 1898) = *Hinnites ercolanianus* (Cocconi, 1873)
Chordata, Actinopterygii	*Sparus cinctus* Agassiz, 1839
Chordata, Elasmobranchii	*Carcharhinus* cf. *leucas* (Valenciennes, 1839 in Müller and Henle, 1839–1841)
	Cosmopolitodus hastalis (Agassiz, 1833)
Chordata, Mammalia	Cetacea indet.

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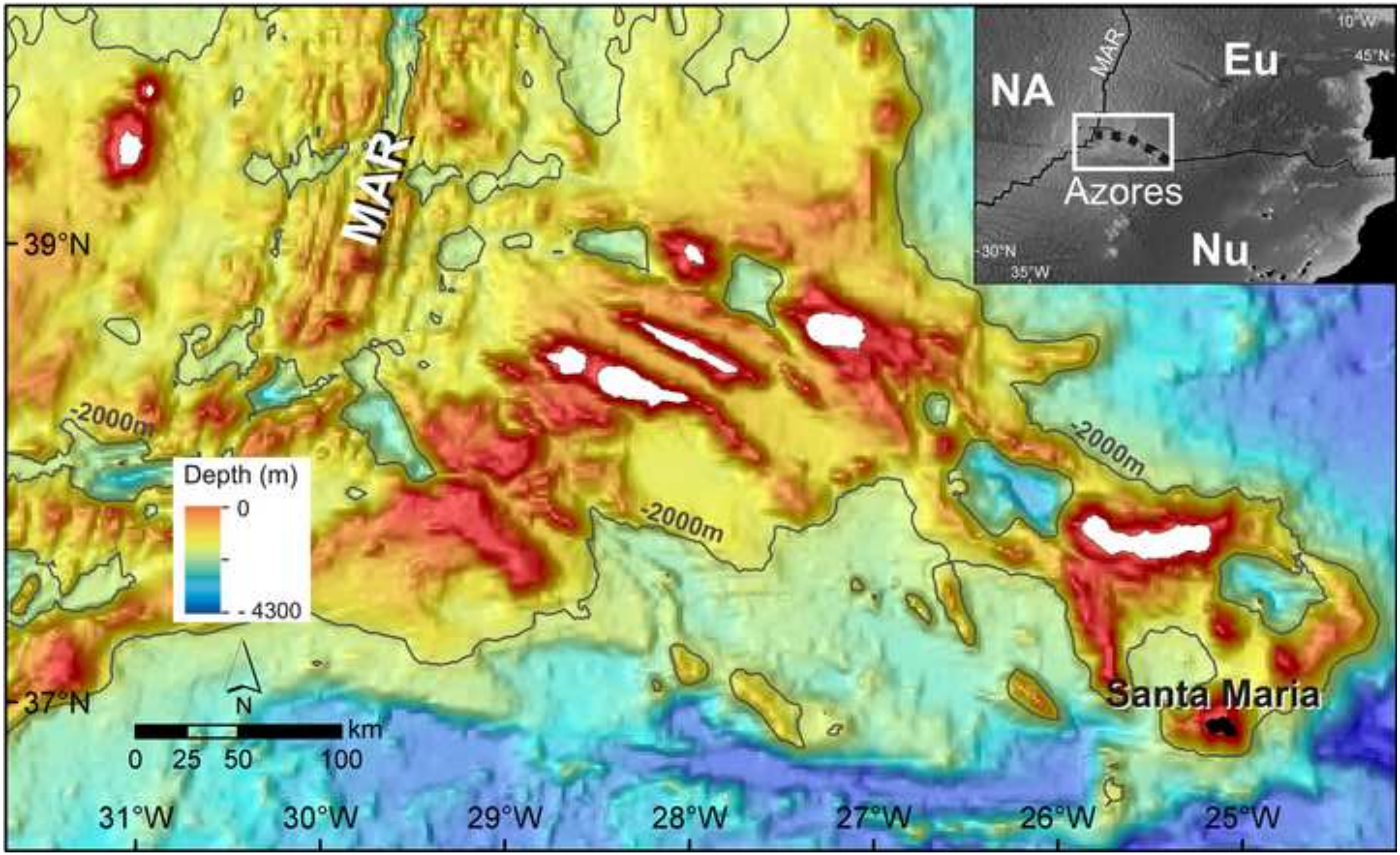

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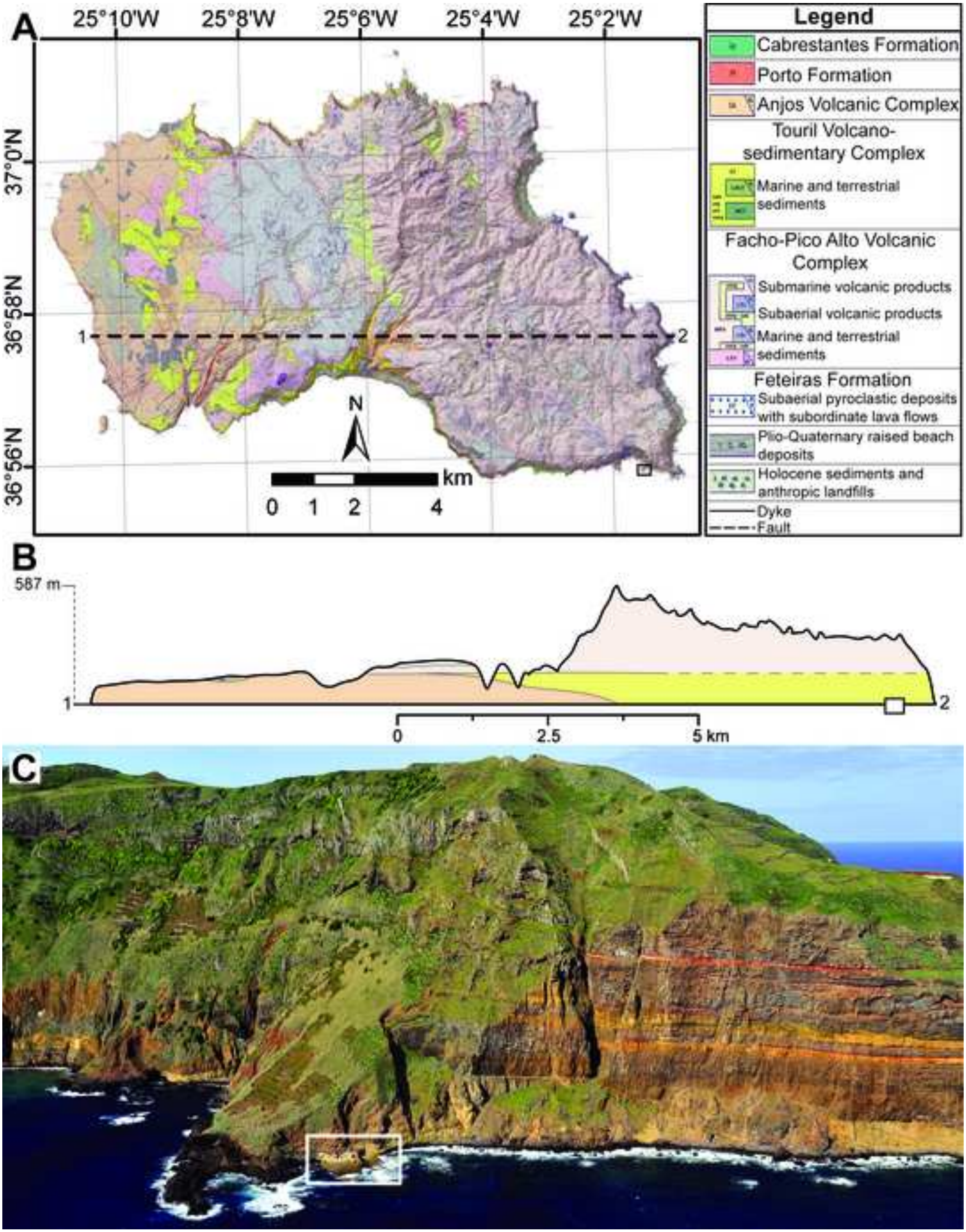

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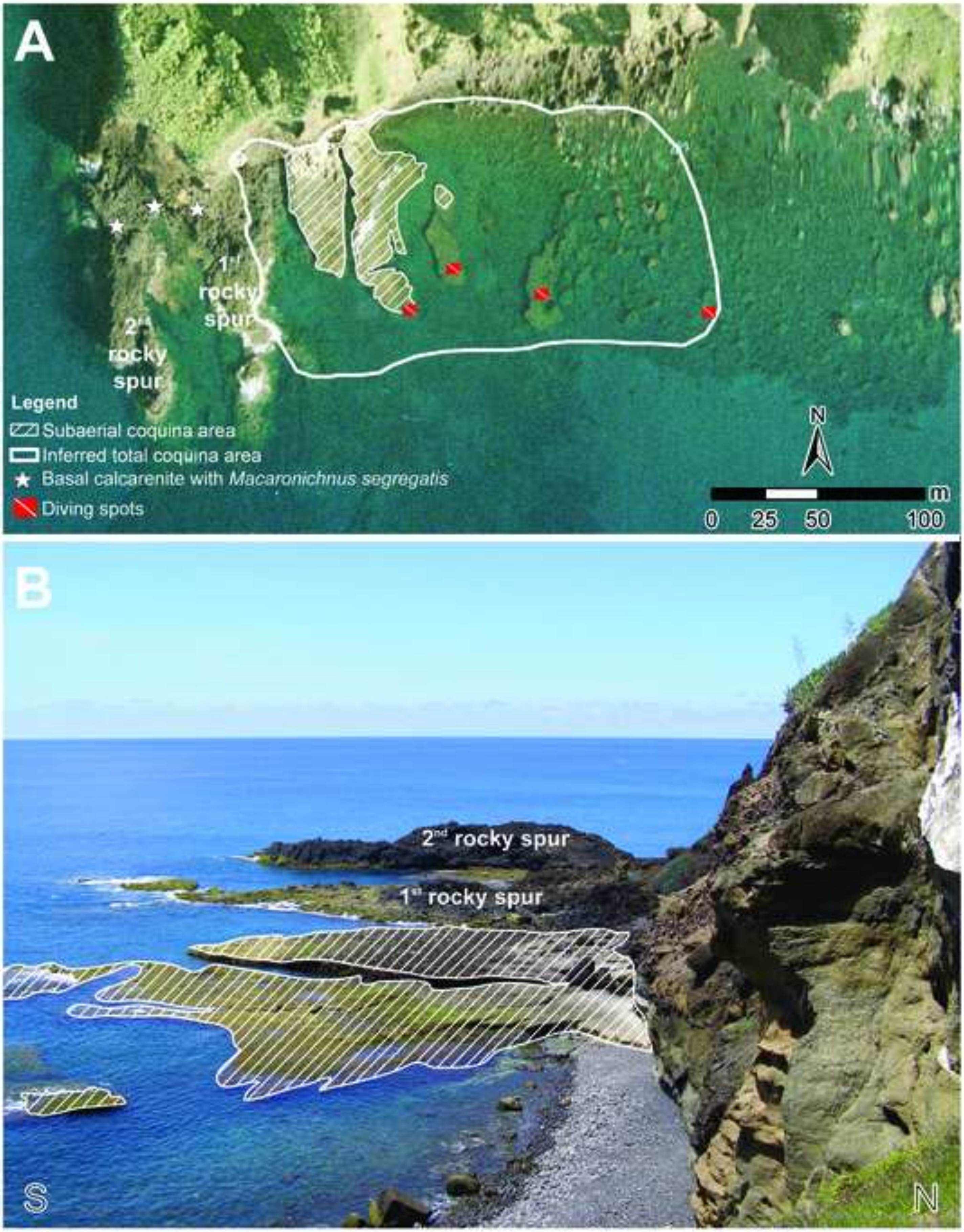

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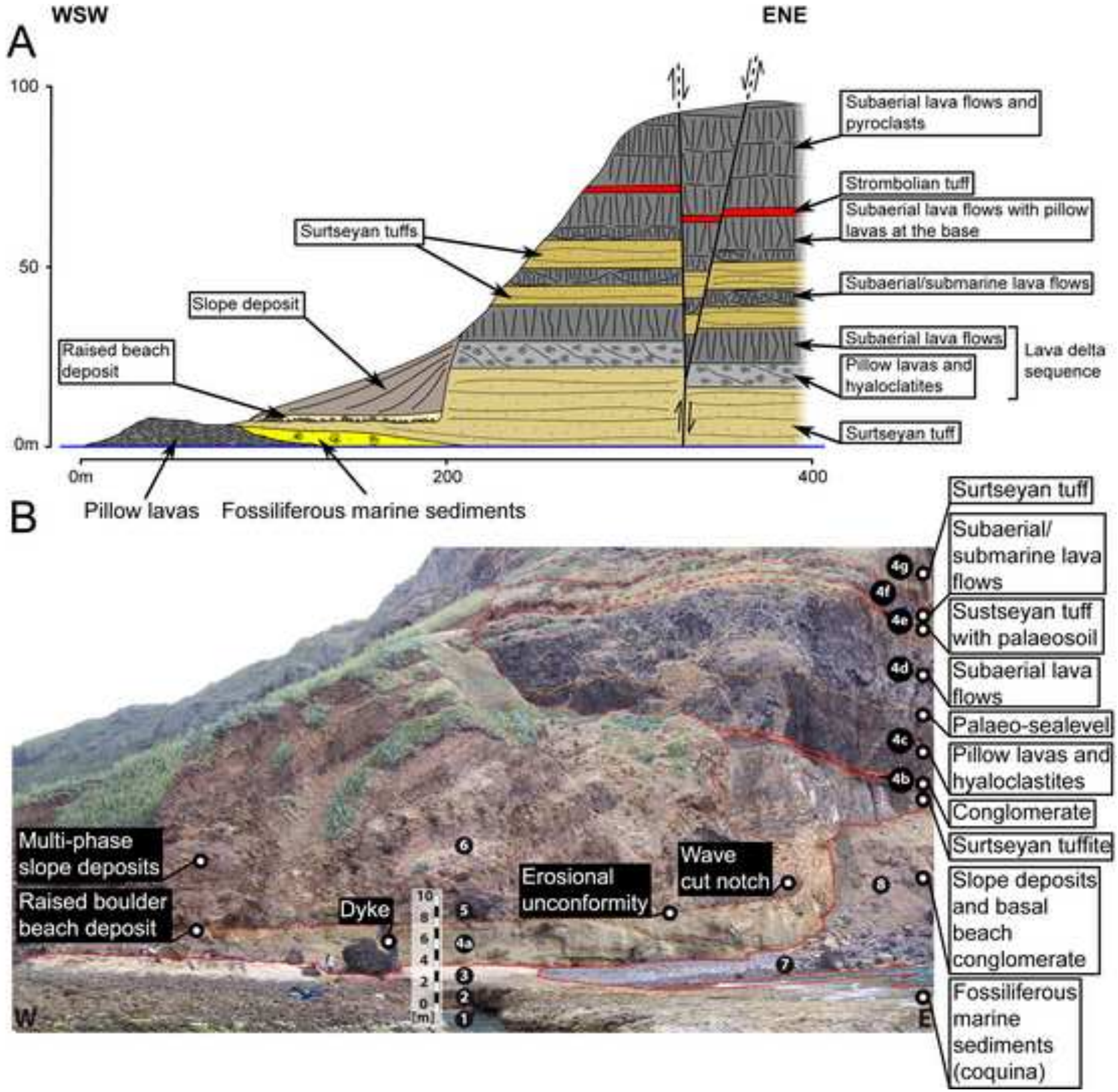

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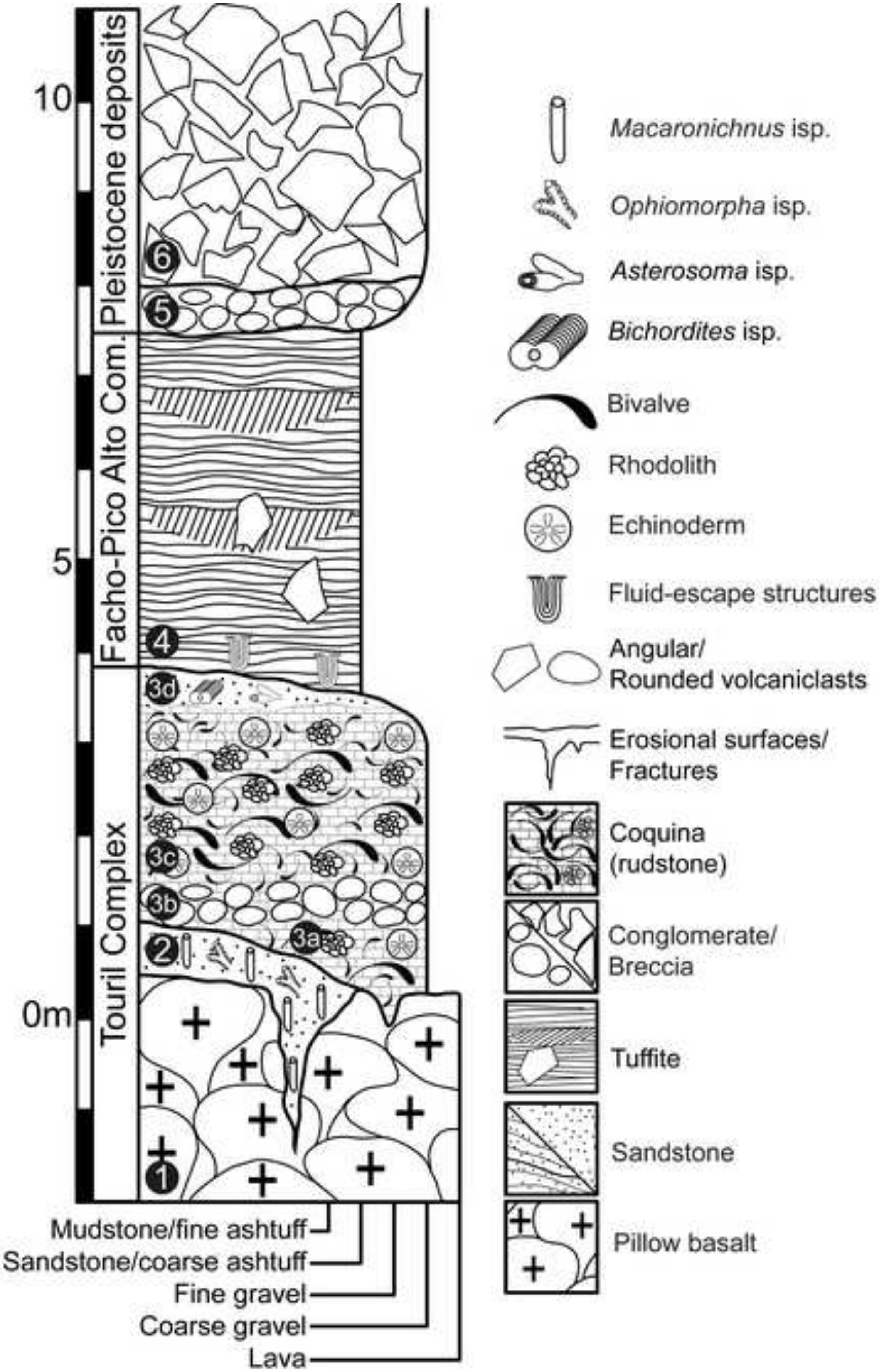

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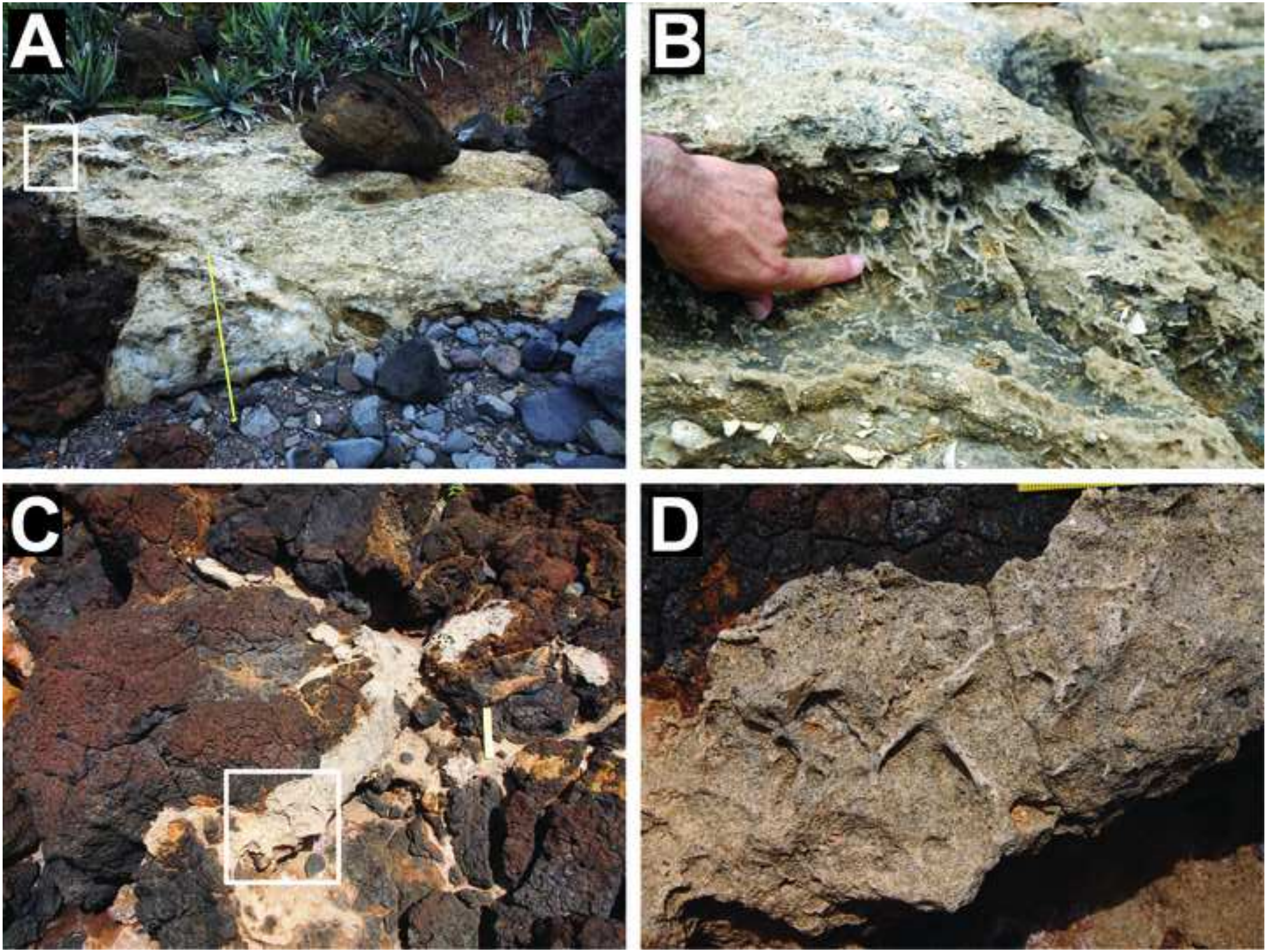

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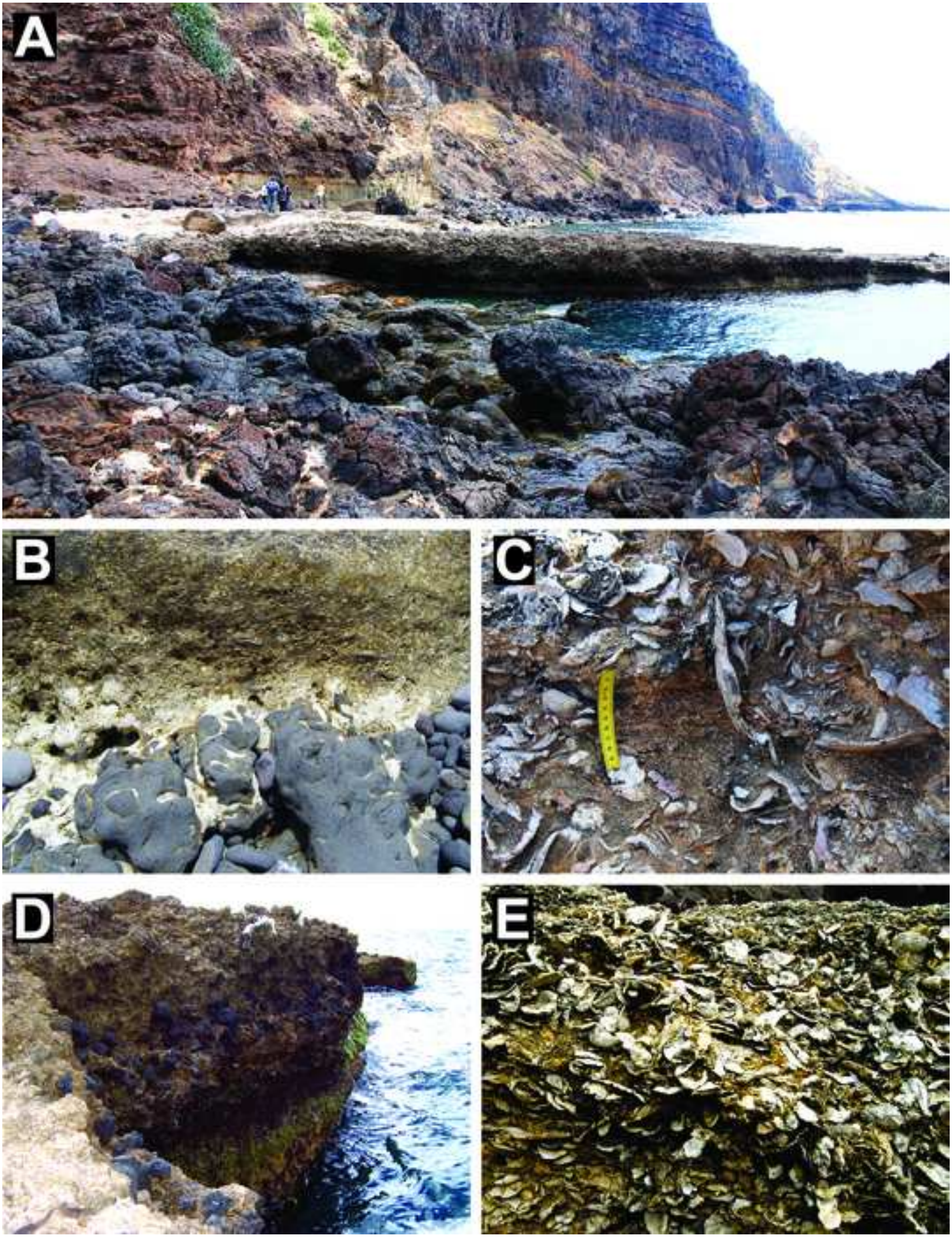

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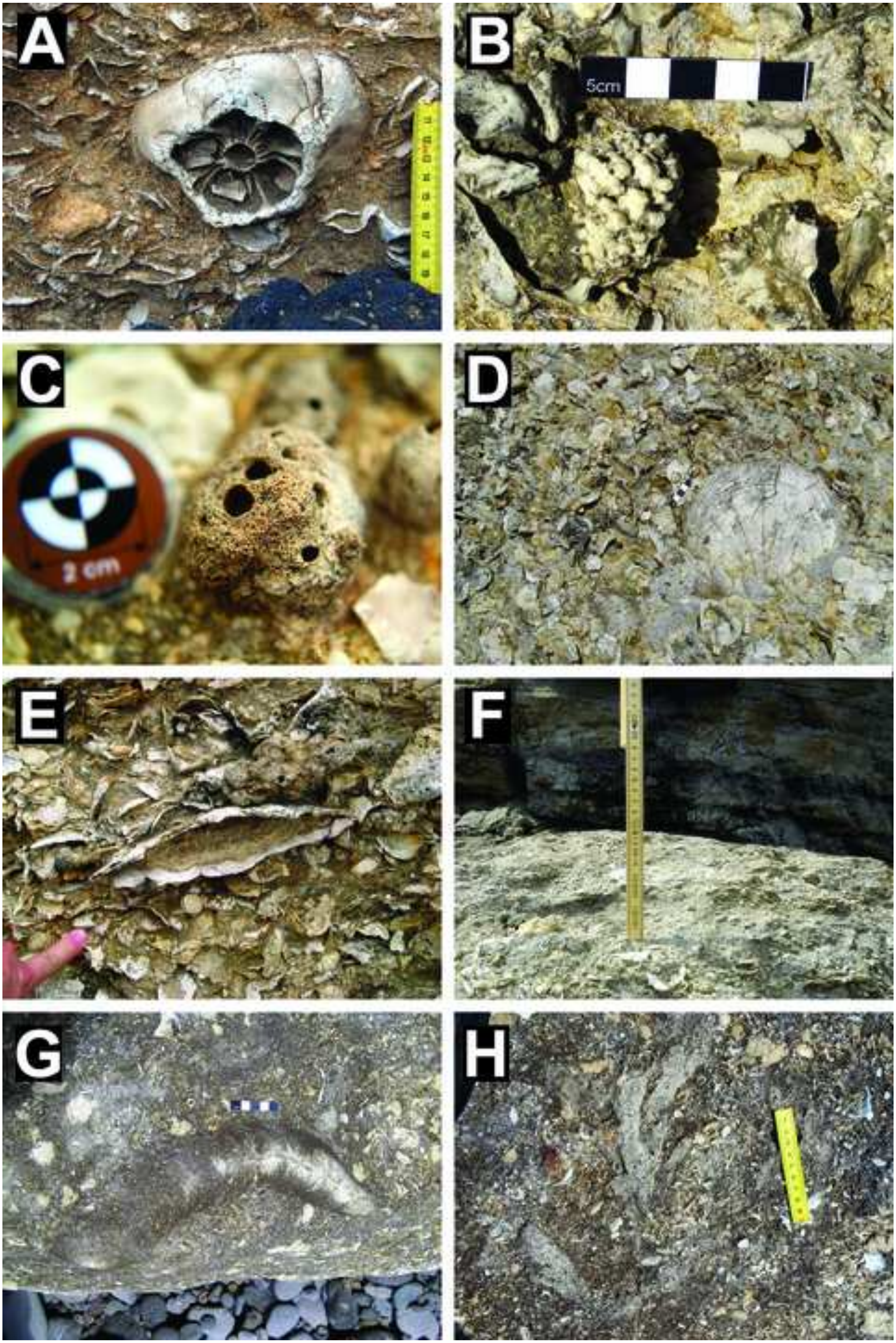

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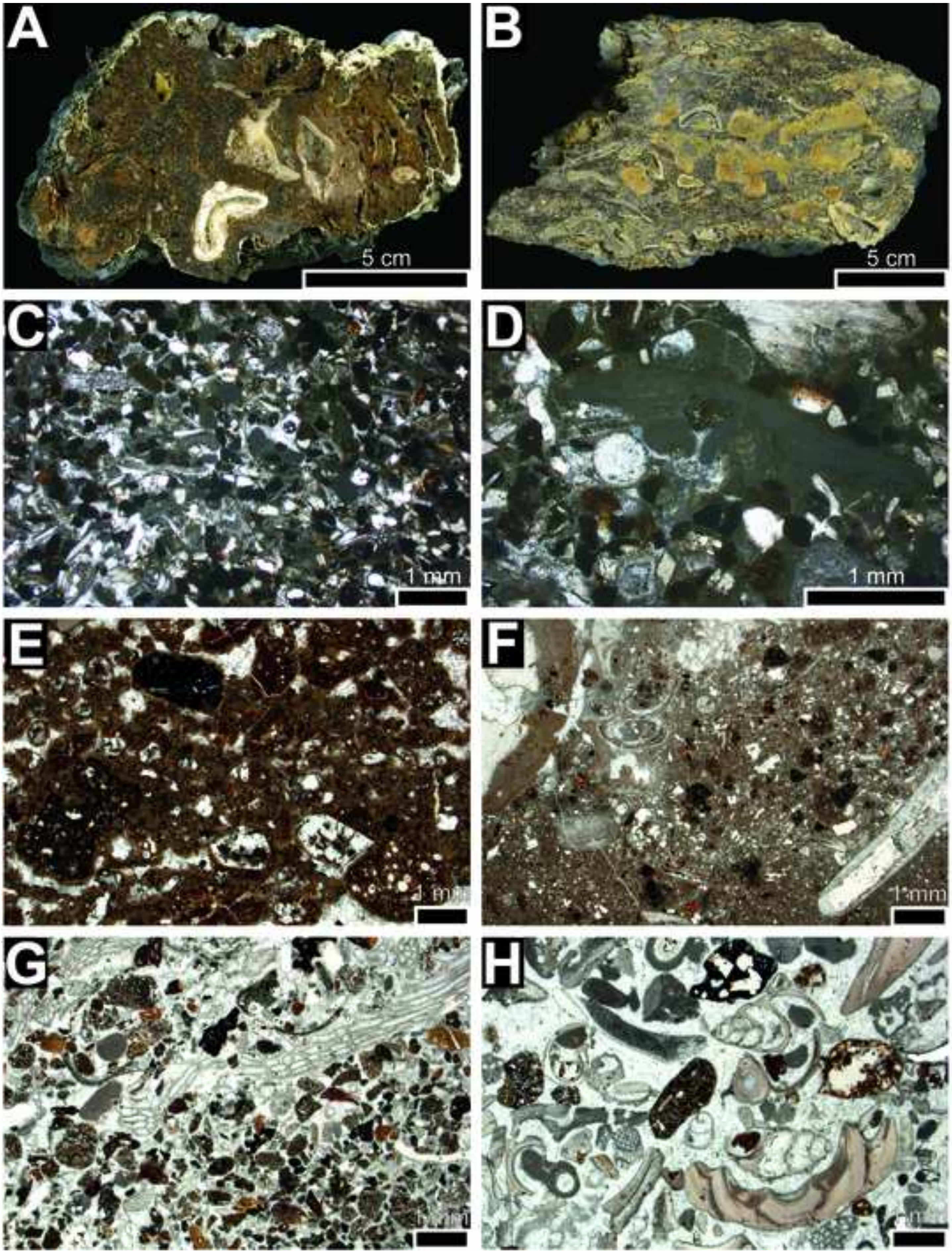

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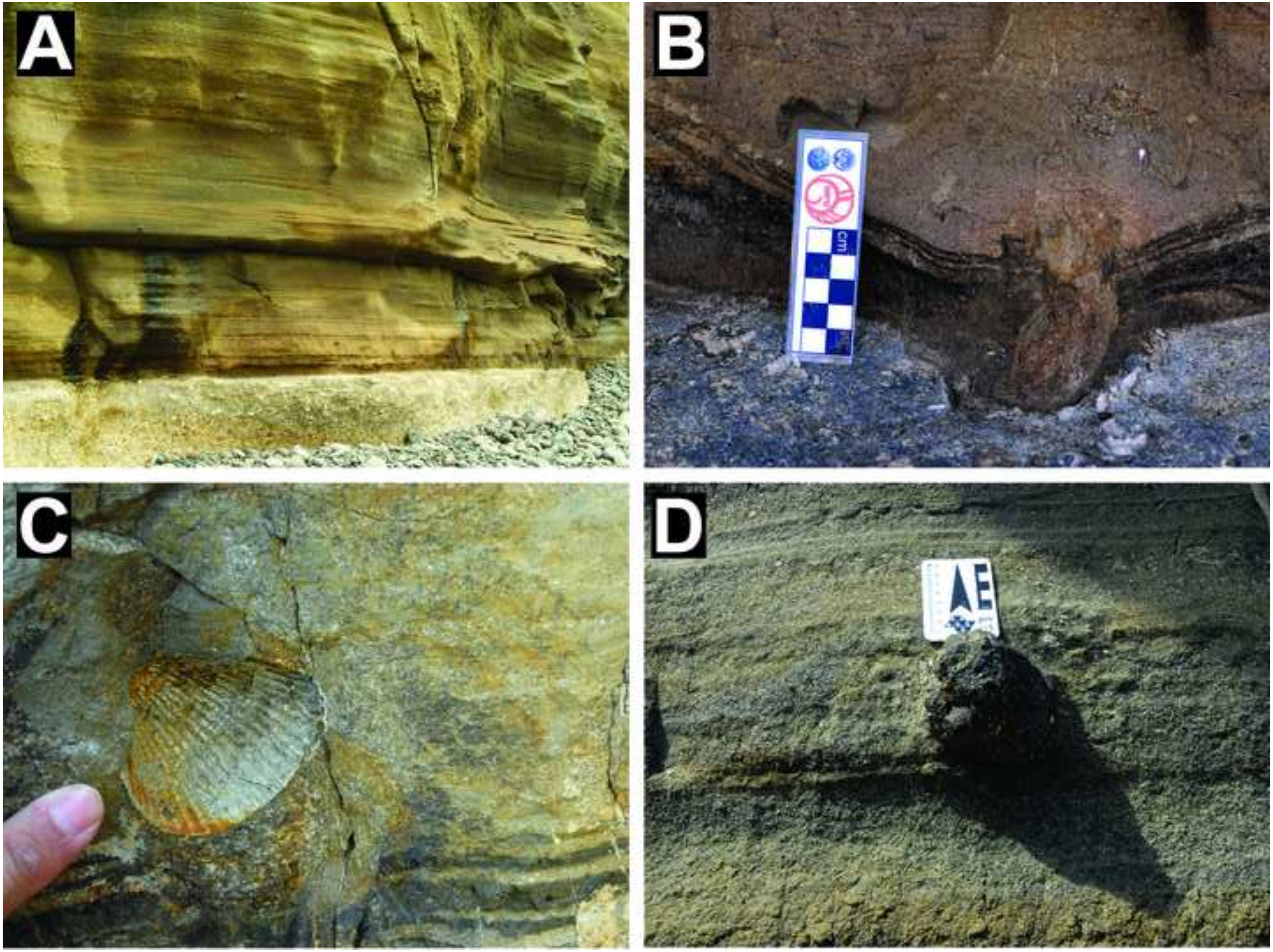

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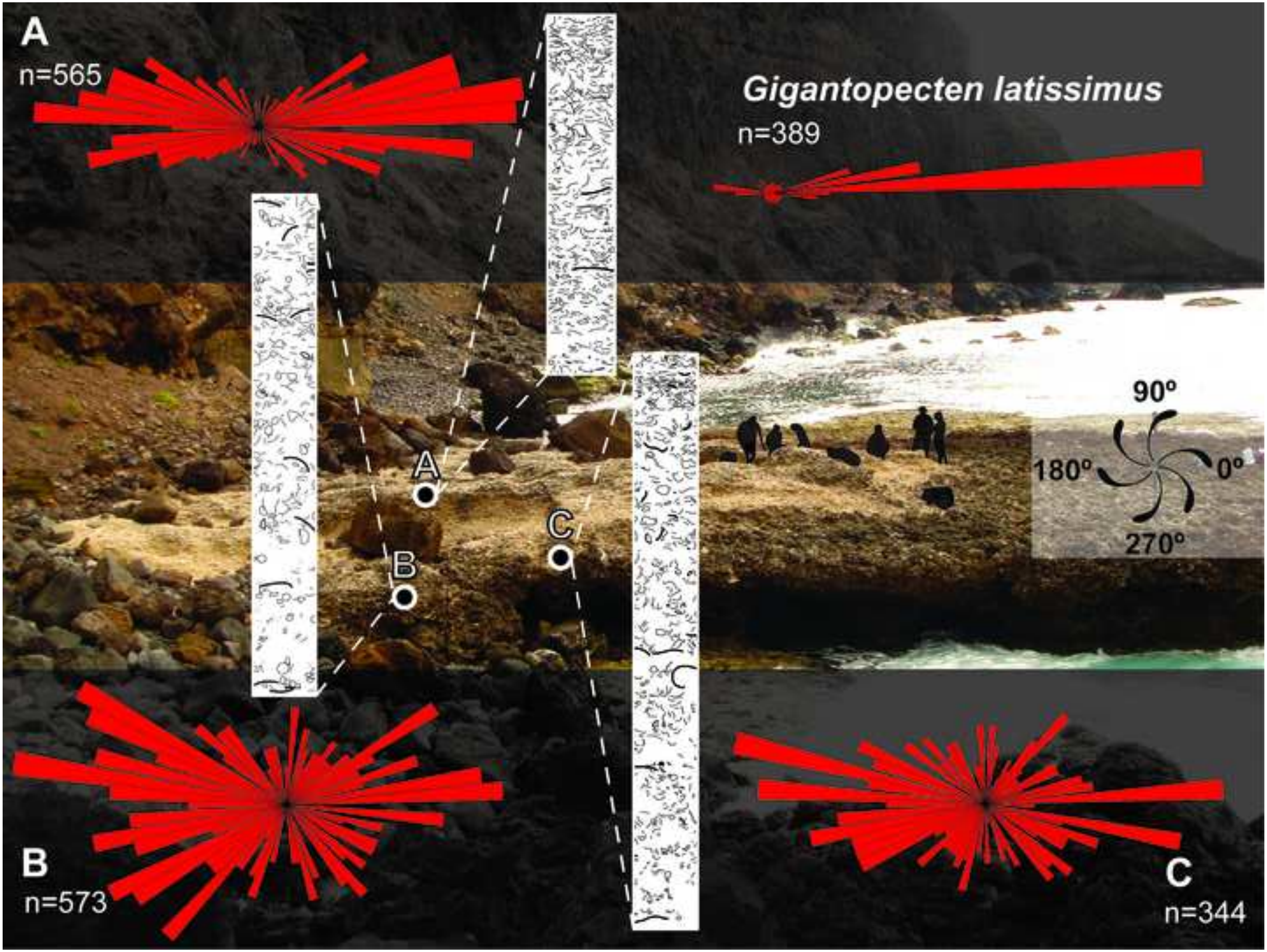

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