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Coastal raptors and raiders: new bird tracks in the Pleistocene of SW Iberian Peninsula

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Abstract:	Avian traces occurring in Pleistocene aeolianite and beach deposits are rare and relatively poorly known, despite being good paleoenvironmental indicators. Passeriform and raptorial birds are especially rare in the track fossil record. Exceptional tracksites were found in the Malhão formation, a Pleistocene coastal aeolianite unit from the SW mainland Portugal, with subunits in the interval ~190 to ~27 ka. Two new forms of avian traces were identified, Corvidichnus odemirensis and Buboichnus vicentinus - attributed to the locomotion of Western jackdaw and the locomotion and predation/feeding behaviour of a large Eagle-owl. The last trace fossil may correspond to the first evidence of a raptorial bird-prey interaction found in action in the fossil record. Typical shorebird tracks and trackways attributed to gulls (Laridae) and curlews, and others tentatively compared with Rallidae, such as Eurasian coot, are also discussed within the aeolianite ichnoassemblages. The tracks here described are the first avian ichnotaxa from the Pleistocene of Europe.
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Dear Editor,

We are submitting to QSR our original research entitled “Coastal raptors and raiders: new bird tracks in the Pleistocene of SW Iberian Peninsula”. In this paper we proposed and described the first two bird ichnotaxa from the Pleistocene of Europe, *Corvidichnus odemirensis* and *Buboichnus vicentinus.* Besides erecting the new igenn. et ispp. and providing morphometric comparisons with extant likely producers, among corvids and strigids, we discuss probable behaviors in the context of the coastal aeolianites where these tracks were found. Among them, there is rather interesting evidence of bioturbation produced by a raptorial bird (Eagle Owl)-prey interaction. We discuss the new occurrences and other tracks found under a wider understanding of the shorebird ichnofacies, with the intentional raiding for the abundant food resources of coastal environments by birds not directly related to these habitats. In this work we give a fresh look to the lithostratigraphy of the Pleistocene coastal successions in SW Portugal mainland and provide new OSL and calibrated 14C age estimates for the tracksites under study. We believe that this research provides new data to better understand the ecology of coastal aeolianites between MIS7-to-6 and MIS 3 and can be of great interest to a broad audience of QSR, including Quaternary stratigraphers, vertebrate ichnologists, Quaternary paleontologists and evolutionary paleoecologists.

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We are confident we can develop a great paper with you and the reviewers and we are entirely open for discussion and improvements.

Yours sincerely

The authors

Highlights

Coastal raptors and raiders: new bird tracks in the Pleistocene of SW Iberian Peninsula

- Two new bird tracksites are described from the Middle-to-Late Pleistocene coastal aeolianites of SW Portugal

- *Corvidichnus odemirensis* and *Buboichnus vicentinus* igenn. et ispp. nov. record behaviors of western jackdaw and a large eagle-owl

- Passeriform and raptorial birds are especially rare in the track fossil record

- A trace fossil of raptorial bird-prey interaction is described for the first time

- New OSL age estimate of 187±11 ka (OSL), as well as previous OSL and 14C ages obtained for the aeolianites and now calibrated, show that the bird tracks were printed between MIS7-to-6 and MIS 3

- These tracks are the first avian ichnotaxa from the Pleistocene of Europe.

Coastal raptors and raiders: new bird tracks in the Pleistocene of SW Iberian Peninsula

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Abstract

Avian traces occurring in Pleistocene aeolianite and beach deposits are rare and relatively poorly known, despite being good paleoenvironmental indicators. Passeriform and raptorial birds are especially rare in the track fossil record. Exceptional tracksites were found in the Malhão formation, a Pleistocene coastal aeolianite unit from the SW mainland Portugal, with subunits in the interval ~187 to ~27 ka. Two new forms of avian traces were identified, *Corvidichnus odemirensis* and *Buboichnus vicentinus* - attributed to the locomotion of Western jackdaw and the locomotion and predation/feeding behaviour of a large Eagle-owl. The last trace fossil may correspond to the first evidence of a raptorial bird-prey interaction found in action in the fossil record. Typical shorebird tracks and trackways attributed to gulls (Laridae) and curlews, and others tentatively compared with Rallidae, such as Eurasian coot, are also discussed within the aeolianite ichnoassemblages. The tracks here described are the first avian ichnotaxa from the Pleistocene of Europe.

Key-words: Perching bird tracks; zygodactyl tracks; shorebird tracks; coastal habitat; Pleistocene; SW mainland Portugal

1. Introduction

Birds (Neornithes *sensu stricto*) exhibit a huge variety of morphological patterns, habitat specializations and in consequence many different behaviours. In ecology, such behaviours are related to four main 'substrates': the air (*e.g*., active flight, soaring), the water (*e.g*., swimming, diving), sedimentary environments (*e.g*. courtship, walking), and organic substrates as plants or even animals (*e.g*., nesting, perching); potentially, many of these behaviours may produce an ichnological record (see Belaústegui et al., 2018). Among this record, those traces left on or in soft (bioturbation structures) and hard substrates (bioerosion structures) as well as those produced, accumulated or generated by the birds themselves (biodeposition structures), are especially interesting for ichnologists and paleontologists in general. Among bioturbation structures and due to their abundance worldwide, tracks and trackways are probably the most studied traces within this group of animals. They exhibit a huge morphological variability and consequently, a plethora of ichnospecies (from Mesozoic and Cenozoic strata) have been erected (see Lockley and Harris, 2010). Currently, over 23 ichnogenera and 45 ichnospecies are known as valid in the Cenozoic, according to Lockley and Harris (2010), and several ichnotaxa were erected since their synthesis publication. Relatively common ichnogenera, such as *Phoenicopterichnum* Aramayo & Manera de Bianco, *Charadriipeda* Panin & Avram or *Anatipeda* Panin & Avram, are good examples of this diversity. All these tracks and trackways, ethologically classified as locomotion traces or repichnia (Seilacher, 1953), are the direct result of walking, running and hopping gait behaviours. The general morphological pattern of these tracks varies from imprints of feet usually with three to four digits, wide or slender toes, the presence and magnitude of the hallux imprint and its angular relation to toe III, and the

93 divarication angle pattern between toes, that in turn may or may not possess
94 interdigital webbing (Brown et al., 2002). Additionally, aspects such as the gait,
95 walking speed, anatomical features, pathological malformations and feeding
96 behaviour of the producer may also be inferred from this kind of bioturbation
97 structures.

98 Although diverse for the Cenozoic, avian tracks and trackways are relatively rare
99 and still poorly known in Pleistocene sedimentary successions around the world.
100 The fossil record is dominated by the tracks of shorebirds, with a minor
101 component attributable to large flightless and cursorial forms (i.e., Lockley and
102 Harris, 2010). Among the most famous bird-tracksites is the late Pleistocene
103 Pehuen-Co in Argentina where *Aramayichnus rheae* Aramayo et al.,
104 *Phoenicopterichnum pehuencoensis* Aramayo & Manera de Bianco,
105 *Charadriipeda* isp. and *Gruipeda* isp. were described by Aramayo and Manera
106 de Bianco (1987, 1996) and Aramayo et al. (2015). Also, in Argentina rhea tracks
107 from similar age are known in Monte Hermoso (Aramayo and Manera de Bianco,
108 2009). Another famous tracksite for birds from late Pleistocene is Jeju Island
109 (South Korea) where eight types of avian tracks, including from webbed-foot
110 birds, were identified in volcanoclastic shoreline deposits (Kim et al., 2004; Kim
111 et al., 2009). They are also known from at least seven different track
112 morphologies in 19 different tracksites in a still ongoing study and compared with
113 a small and large wader, gulls (Laridae), Gruidae(?), Numididae or Phasianidae,
114 Steminae, Struthionidae(?), Phoenicopteridae, Anatidae(?), and shorebirds
115 (Charadriidae) from the Cape south coast of South Africa (Roberts, 2008; Helm
116 et al., 2017, 2018, 2020). Bird tracks, some compared with oystercatchers and
117 including ones attributed to dromornithids, were described in Kangaroo Island

and the Coorong coastal plain of western Australia by Camens et al. (2018), and Bell and DeMerlo (1969), Vicker-Rich and Gill (1976) and Belperio and Fotheringham (1990), respectively. Recently, Neto de Carvalho et al. (2020) presents well-preserved trackways of geese and shorebirds from Matalacañas Trampled Surface in SW Spain dated to the Late Pleistocene. Other shorebird tracksites, including tracks attributed to gulls, are known in Bermuda and Bahamas (cf. *Avipeda* Vialov compared to the Willet tracks) by Hearty and Olson (2011), Kindler et al. (2008) and Martin and Whitten (2015); they were described also in SW Portugal under *Charadriipeda* isp. types A and B by Neto de Carvalho et al. (2016) and Figueiredo et al. (2018). In Portugal, the fossil record of Pleistocene birds, composed of bones only, was previously known in mainland only from cave sites (a comprehensive synthesis of all occurrences can be found in Figueiredo, 2010; Figueiredo and Rosa, 2014; Figueiredo, 2018).

The formation of aeolianites has been recorded worldwide (Brooke, 2001) under varying glacio-eustatic and inland climate regimes ranging from intervals of sea-level stability associated with interglacial highstands and periods of relative sea-level change at the end of the stage (Helm et al., 2018). In Portugal, the first record of bird fossil tracks was described by Neto de Carvalho (2011) in the Malhão formation at the Pessegueiro island, a Pleistocene coastal aeolianite unit from the SW mainland Portugal. Another tracksite was identified in a lower level of the aeolianite of Pessegueiro (Figueiredo et al., 2018). Bird tracks and trackways found in the Pessegueiro island were among the first published record of vertebrate locomotory behaviours from the Cenozoic in Portugal (Neto de Carvalho et al., 2003; Neto de Carvalho, 2009). The new tracksites found in the

142 Pleistocene aeolianite unit of Portugal provide a hitherto unreported potential for
143 interpreting the ecology and behaviour of the coeval fossil avifauna (Fig. 1).

144 Here we describe two new forms of bird tracks in sub-optimal preservation
145 according to the principles established by Marchetti et al. (2019). This is an
146 exceptional occurrence since tracks of perching birds, raptors and other groups
147 that are not directly dependent on sedimentary shorelines are quite rare (Lockley
148 and Harris, 2010). In this work we also include previously described tracksites
149 and interpret their expressions of behaviour. Our goal is to define a better
150 stratigraphic and ecological framework for the Pleistocene aeolianites from SW
151 Portugal mainland, emphasizing the importance of this fossil track record as the
152 most recent one in the Iberian Peninsula, with the first two bird ichnotaxa
153 described in the Pleistocene of Europe.

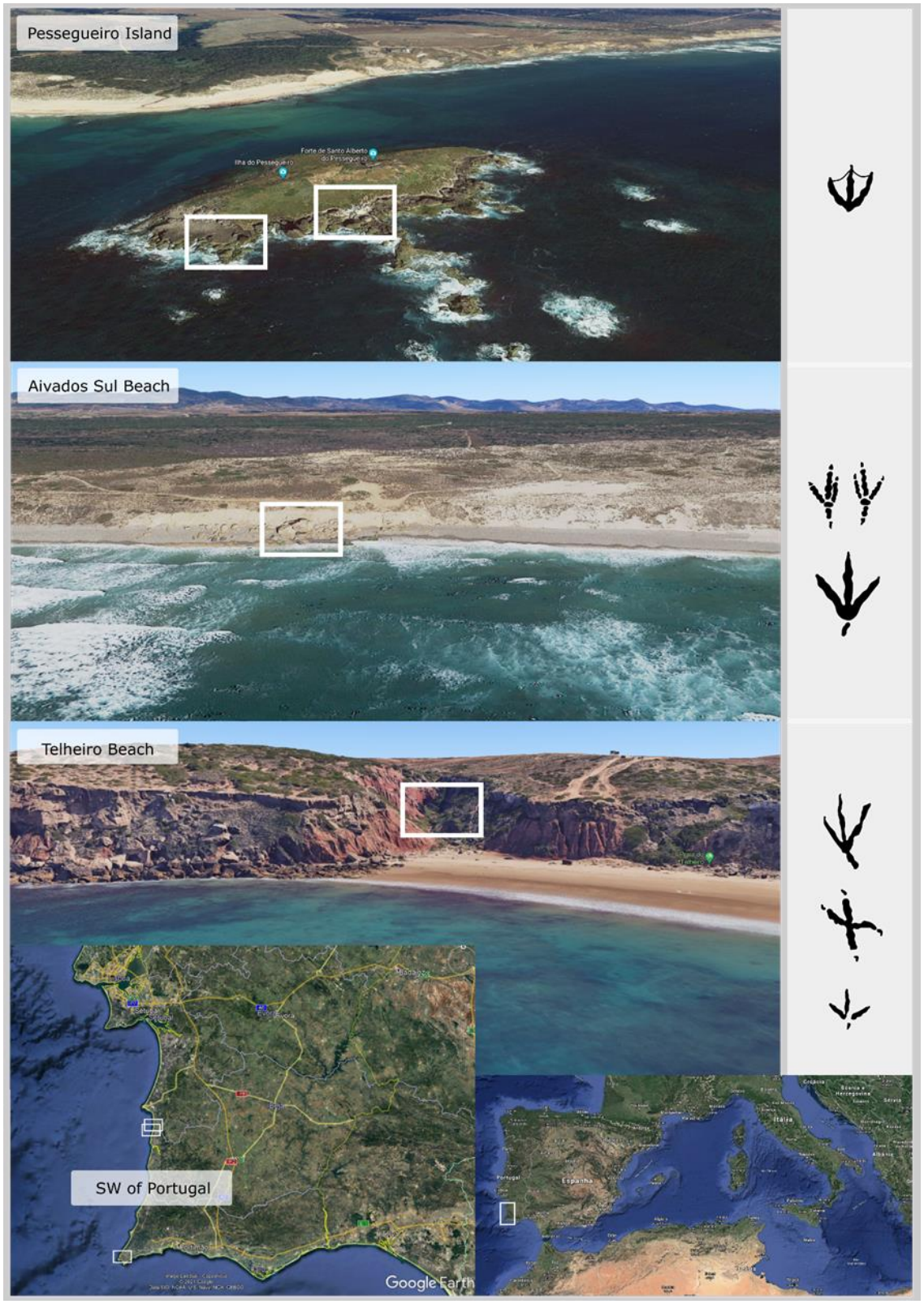


Fig. 1. Location of the tracksites identified so far in the Pleistocene aeolianites of SW Portugal mainland, framing the geographical position of the three sites under study, i.e., from north to south (marked with rectangles in the views and in the

158 maps): Pessegueiro island (37°50'5.05"N, 8°47'52.79"W) with *Charadriipeda* isp.
159 type I; Aivados sul beach (37°47'56.25"N, 8°47'59.18"W) showing *Corvidichnus*
160 *odemirensis* igen. et isp. nov. and *Gruipeda* aff. *maxima*; and Telheiro Beach
161 (37°2'49.98"N, 8°58'40.80"W), with an unnamed large tetradactyl track,
162 *Buboichnus vicentinus* igen. et isp. nov. and *Charadriipeda* type II. Images
163 obtained from Google Maps 3D views and Google Earth (February 2021).

164

165 ## 2. Geological setting

166 ### *2.1. Stratigraphy and chronostratigraphic framework of the aeolianites*

167 A lithostratigraphic scheme comprising up to six stages of aeolian mobilization
168 was proposed for the western coast of mainland Portugal (Pereira, 1990; Pereira
169 and Angelucci, 2004): the oldest from the Middle Pleistocene (ascribed to MIS 6),
170 three being Upper Pleistocene (supposed as MIS 4-3, MIS 3 and MIS 2), and two
171 Holocene (the Pre-Boreal and the last 3 ka). More recently, Costas et al. (2012)
172 studied Holocene aeolian dunes just south of Lisbon and identified five episodes
173 of aeolian deposition interpreted as related with cold events: 12.6 ka, 5.6 ka, 1.2
174 ka, 0.4 ka and 0.3 ka.
175 In mainland Portugal, the Pleistocene aeolianites under study (Malhão formation)
176 crop out with interruptions ~300 km along the western coast (Pereira, 1990;
177 Pereira and Angelucci, 2004; Pereira et al., 2007; Neto de Carvalho, 2009, 2011).
178 This formation, composed of stacked aeolianite sub-units, is frequently covered
179 in disconformity by two main Holocene aeolian sand units, the older containing
180 paleosols and the younger consisting of mobile sand dunes, which can be
181 correlated to the MIS 2-1 (Pereira and Angelucci, 2004). In the study area, the
182 littoral zone has a generally NNE-SSW oriented coastline, which is directly

exposed to the energetic Atlantic swells. The coast has steep cliffs, usually developed in a highly deformed Paleozoic bedrock of schists and metagreywackes discordantly overlain by Late Triassic-to-Late Jurassic sedimentary rocks. The modern abrasion platform is narrow and the littoral zone is dominated by a rocky-shore environment, with coarse sands present at pocket beaches.

On the coastal slopes, the Pleistocene aeolianite unit onlaps older coastal units, namely coastal terrace deposits ascribed from MIS 5 to MIS 13 (Pereira, 1990; Figueiredo et al., 2013, 2015; Ressurreição et al., 2018). A culminant regional wave cut platform, up to 10 km wide and with altitude usually between 40 and 160 m a.s.l., is associated with siliciclastic shallow marine deposits and more inland deltaic and fluvial deposits (Pereira, 1990); it corresponds to the allostratigraphic unit UBS13 (probably age of 3.7 to 1.8 Ma, uppermost Zanclean to Gelasian; Cunha, 2019).

The largest continuous aeolianite outcrop is at the Malhão area, located between São Torpes (N: 37º55') and the Mira River (S), 20 km long and 5 km wide, and including the Pessegueiro island and Aivados Sul Beach (Fig. 1). In the section, the aeolianite unit covers, by disconformity, a marine terrace with *Glycimeris* shells at its basal level (at 17 m of altitude) which were dated, by amino-acid racemization, indicating deposition during the MIS 13 (540-460 ka) (Ressurreição, 2018; Ressurreição et al., 2018). At the Forte do Pessegueiro site, between Pessegueiro island and Aivados sul Beach sections, the sedimentary succession exposed at the coastal comprises: a) a lower unit of beach deposits (a conglomerate, a lumachela and coarse sands); a middle unit of reddish sands with paleosols; c) an upper unit of aeolianite subunits.

Further south, at the Castelejo Beach aeolianite, the gravelly marine terrace located close to the present sea-level has an intercalated sand level which was dated using luminescence to ~110-112 ka; just above this MIS 5 unit, the base of the aeolianite unit was dated as ~90 ka and its upper division as 42.3-38.8 ka cal BP (^{14}C) (Figueiredo et al., 2013, 2015; ^{14}C ages from Martins, 2014).

The Telheiro Beach section shows ^{14}C ages obtained for the aeolianite of 44.7-40.3 ka cal BP (Monge Soares et al., 2012; Martins, 2014). At Sagres, the southernmost section of the Portuguese western coast (37º00'N), ages of 27.8-26.8 cal ka BP were obtained from apparent ^{14}C ages determined for the base and top of the aeolianite unit (Monge Soares et al., 2012; Martins, 2014).

2.2. The stratigraphic levels with vertebrate trace fossils

In the study area, 18 stratigraphic levels with vertebrate trace fossils were already found in the Pleistocene aeolianite units. These include tracks and trackways of straight-tusked elephant, red deer, fox, Iberian lynx, rabbit and shorebirds (Neto de Carvalho et al., 2016; Neto de Carvalho and Belo, 2020). Three tracksites show avian tracks and trackways (Fig. 2).

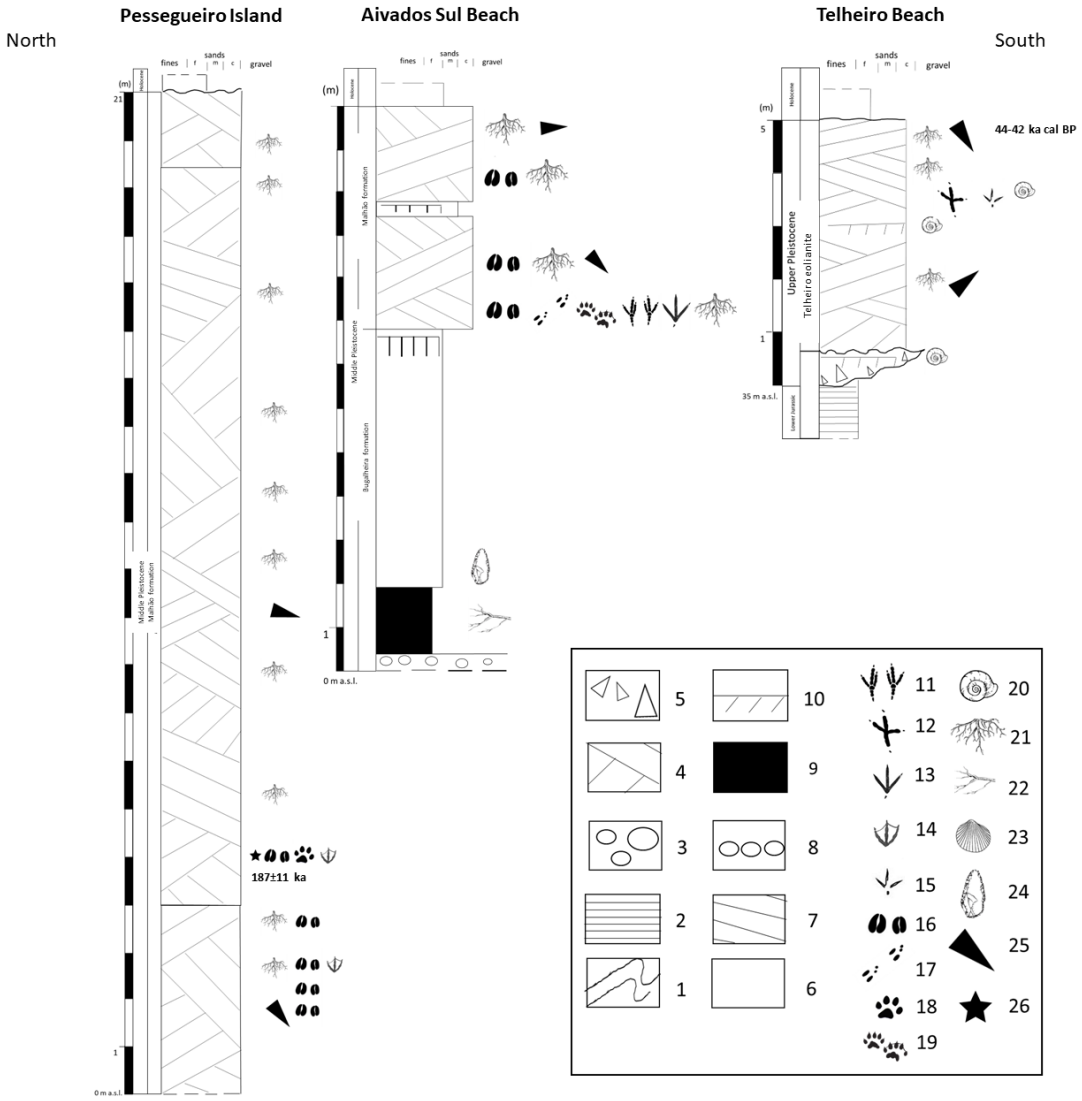
Pessegueiro island is the northernmost site of the study area; the aeolianite unit has a thickness of ~21 m and is composed of several stacked subunits with main changes in the orientation and dip (up to 34º) of the foresets, separated by reactivation surfaces. The aeolianite is heavily bioturbated by rhizoliths, increasing towards the top. They show abundant large deer tracks in several levels, but also rabbit, felid and shorebird tracks. Bird tracks are found in the lower part of the aeolianite unit. In the scope of this study, a trampled bed upper surface with *Charadriipeda*, *Felipeda* Panin & Avram and *Bifidipes* Demathieu et al. tracks

and trackways, located 5 m above the aeolianite unit base, was sampled for OSL dating (see Luminescence dating section; Fig. 2, Tables 1 and 2).

The Aivados Sul Beach section exposes (Fig. 2): a) a wave cut platform cut in the basement covered with a beach gravel deposit (0.4 m thick), followed by a silty layer (1.6 m thick), and a layer of fine to medium sand (6.0 m thick), with a paleosol at the top; b) above a disconformity is the strongly cemented aeolian unit, which is 4.5 m thick and comprising two subunits separated by a reactivaction surface with a well-developed rubefacted paleosol; c) above a disconformity, there are aeolian dune sands. The aeolianite unit shows low angle lamina, wind ripples, rhizoturbation and different types of tracks found both *in situ* and in the scree by the collapse of part of the cliff. The bird tracks are located at several levels of the lower aeolianite subunit and could have approximately the same Middle Pleistocene age obtained for the Pessegueiro island, based on stratigraphic correlation. Also, as in Pessegueiro island, the Aivados Sul Beach sedimentary succession may record interdune and backdune environments (Roberts et al., 2008). Together, we found mustelid and abundant artiodactyl tracks, some of the latter reaching a length of 15 cm; these will be described elsewhere. Together with the new *Corvidichnus odemirensis*, we found a clear trackway with the characteristic gait and track size of the European rabbit *Oryctolagus cuniculus* (Linnaeus), and which is comparable with the previously described new ichnogenus *Leporidichnites malhaoi* (Neto de Carvalho, 2009; Fig. 2).

Finally, the Telheiro Beach section is one of the southwesternmost aeolianites in Europe and covers a small area between two creeks (Fig. 1). At the Quebrada creek, above an angular unconformity with Lower Jurassic limestones, the

aeolianite unit is composed of a lower colluvial layer with a developed rubefacted soil, overlain by the aeolianite unit (~4 m thick). As previously referred, four aeolianite levels were dated here between 44.7 and 40.2 ka cal BP (from ^{14}C ages obtained from marine bioclastic sand fraction by Monge Soares et al., 2012; Martins, 2014). In the studied section, the calibrated age obtained from Martins (2014) was 44.7-42.6 ka cal BP. The aeolianite unit shows several bioturbated levels with bird tracks and other mammal and reptile tracks that, for its intrinsic importance, will be described elsewhere. Tracks of *Buboichnus vicentinus* isp. nov. and *Charadriipeda* isp. type II are described in this section. A single large tetradactyl track, 15 cm long showing low divarication angles between toes with large claw imprints, was also found here but since it is an isolated case, we will not describe it.



271

272 Fig. 2. Stratigraphic logs of the three sections with bird tracks and trackways:
273 from north to south, Pessegueiro island, Aivados sul Beach and Telheiro Beach
274 (SW Portugal). Legend: 1 – Paleozoic turbidites; 2 – Lower Jurassic marls; 3 –
275 conglomerate; maximum clast size = 30-35 cm; 4 – cross-bedded aeolianite; 5 –
276 colluvial deposits; 6 – coarse sandstone; 7 – low-angle laminated sandstone; 8 –
277 gravel lens; 9 – carbonaceous fine sandstone; 10 – paleosol; 11 – *Corvidichnus*
278 *odemirensis*; 12 – *Buboichnus vicentinus*; 13 – *Gruipeda* aff. *maxima*; 14 –
279 *Charadriipeda* isp. type I; 15 – *Charadriipeda* isp. type II; 16 – *Bifidipes* isp.; 17 –
280 *Leporidichnites malhaoi*; 18 - *Felipeda lynxi*; 19 – mustelid track; 20 –land snails;

21 – rhizoliths; 22 – plant remains; 23 - marine bioclasts; 24 – Paleolithic artefacts; 25 - paleowind direction; 26 – OSL and ^{14}C sample ages.

3. Materials and methods

3.1. Preservational conditions of the occurrences

This study used a standard paleontological fieldwork approach, but also involving topography, geomorphology, lithostratigraphy, sedimentology and numerical dating of the Pleistocene aeolianites under study. The aeolianites extend up to 2 km inland. In general, they are lithologically homogeneous, without evident textural and mineralogical contrasts that can be exposed differently by erosion. They comprise bioclastic quartzarenites which are well-sorted, usually medium- to coarse-grained (0.14 to 0.67 mm; Pereira, 1990), with bioclasts representing up to 38% of the total rock (Romariz and Carvalho, 1975). The aeolianites are strongly cemented by a calcite cement.

The bird trackways were found in exposed lamina surfaces of blocks collapsed from the coastal cliffs subjected to wave erosion; the blocks are prone to a quick weathering and erosion. For these reasons, the stratigraphic levels in which tracks were found are located in sections where active erosion by breaking waves or flowing waters in creeks is happening and periodic surveys are necessary.

Delicate tracks can be found in cross-bedding lamina surfaces of the medium to coarse grained aeolianite sandstones. The sand of these ancient dune systems was made cohesive in the superficial layers by rain, coastal fog or marine spray (e.g., McLaren, 1995) or even occasional high phreatic level, preserving sometimes in a quite detailed way the morphology of the tracks, even made by

small and light animals, such as birds (Roberts et al., 2008). Fast and deep cover by aeolian sand and later, an accelerated diagenesis in a seasonal contrasted dry environment, with bioclastic dissolution and reprecipitation in the vadose zone induced by the activity in the rhizosphere, resulted in the lithification of the sand textures and the preservation of the ichnological record.

3.2. Digital photogrammetry and morphometric data acquisition for ichnotaxonomy

For the study of such delicate tracks, we applied current standards of data acquisition and 3D image analysis using photogrammetry, described in Falkingham et al. (2018). Since the type material of the new ichnotaxa, which are located in large slabs are thus uncollectable, was left in the field under fast erosive conditions, 3D models developed and available are considered the "digitypes" (*sensu* Adams et al., 2010; see also Neto de Carvalho et al., 2020); they can be analysed from the Supplementary Material (Sketchfab link: xxxxx).

3D digital modelling is today one of the most used techniques to support paleontological studies (including ichnology). This technique can be applied using different equipment and techniques, which can be used separately or together, such as computed tomography, laser scanning, structured light photogrammetry and digital photogrammetry. Comparing cost, geometric accuracy, radiometric accuracy, time to collect and produce records and equipment portability, each technique has some advantages and disadvantages over the others, considering the goals to be achieved and the characteristics of each site or object of work (see Brecko and Mathys, 2020; Otero et al., 2020). The main advantages of

digital modelling are: (i) its great capacity for the 3D non-intrusive registration of surfaces and objects of interest, portraying the sites / objects of study with realism, high geometric and radiometric precision; (ii) the possibility to survey large areas (e.g. Romilio et al. 2017) and small objects (e.g. Bucchi et al., 2020), at different aerial and terrestrial scales (Romilio et al. 2017, Petti et al., 2018, Lkbir et al., 2020); (iii) the opportunity to analyse in a more appealing and interactive digital environment, enhancing and facilitating the tasks of visual interpretation and measurement and allowing the application of quantitative statistical methods (Belvedere et al. 2018, 2019) and automated data extraction (Lallensack 2019). In addition to the remarkable capacity for enhancing the micro-relief (e.g., Muñiz et al., 2019, Cerrillo-Cuenca et al., 2019), in ichnological studies 3D models provide important ichnotaxonomic information in the track-producer interrelation, facilitating taphonomic, paleoenvironmental (Mujal et al., 2020) and palaeoecological reconstitution (Neto de Carvalho et al., 2020). Among the technologies presented, digital photogrammetry has been one of the most used techniques by paleontologists worldwide, as it is an inexpensive method, relatively fast and simple to perform, whose necessary equipment is very easily transportable (considering the places sometimes distant and difficult to access, where the objects of study are located) but, above all, for the quality of the results obtained (Otero et al., 2020). In this study for the realization of the records, analysis and interpretation of the tracks and trackways of birds in the SW of Portugal, digital photogrammetry was used. The applied methodology was adapted from Mallison and Wings (2014) and Falkingham et al. (2018), and is described below.

For the modelling of the *Charadriipeda* trail, 51 photographs were taken in perpendicular and oblique views (resolution 4608x3456 pixels, in JPG format), using a Nikon Coolpix P510 V1 camera. For *Gruipeda*, *Corvidichnus odemirensis* and *Buboicnus vicentinus* tracks and trackways surveys, 70, 207 and 242 photographs were taken respectively, in perpendicular and oblique views with a focal length of 16 mm (resolution 6480x4320 pixels, in JPG format), using a Camera Samsung NX500 V2 with 16-50 mm lens. Three-dimensional scales were used to improve accuracy along the x, y and z axes. The photogrammetric processing of the tracks and trackways of *Charadriipeda*, *Gruipeda*, *Corvidichnus odemirensis* and *Buboichnus vicentinus*, was carried out with the free open-source software Meshroom 2020.1.1 (© 2010-2019 AliceVision contributors). Photogrammetric processing produces several types of 3D data that can be used for the intended analysis, such as dense point clouds, shadowing surface mesh models and textured mesh models. In this case, the photogrammetric product that we used for the post-processing of the data, were the textured mesh models. Post-processing: the post-processing was carried out using free open-source software MeshLab v2020.12 (Cignoni et al., 2008) and CloudCompare v2.11.0. (CloudCompare, 2020). The post-processing phase involved the analysis, treatment, fixation to the plane, orientation and scale assignment to the textured photogrammetric models obtained. The attribution of techniques that allow the microtopographic enhancement of the tracks and trackways under analysis, substantially facilitate their interpretation and, consequently, the achievement of more precise measurements and angles, often allowing observation of details that, in fact, would not be easy or possible to observe in the field. For the purpose of interpretation and visualization of the new tracks and trackways presented in

this article, we opted for the presentation of 3D models in nadir and oblique views, textured in real color (rgb), in false colors with shadows, representing the altimetric variation (height maps) of the modelled surfaces and enhanced by the Radiance Scaling (Vergne et al., 2010) and Ambient Occlusion PCV ShadeVis (Zhukov et al., 1998) algorithms. 2D visualization and data measurements: after post-processed, conveniently highlighted and analysed data in 3D environment, these were extracted in nadir view, projected orthographically, to illustrate the tracks and trackways and obtain the desired measurements. 2D images obtained, scaled and previously ortho-rectified by photogrammetric processing show metric and cartographic coherence. Measurements of 1) angle of divarication between toes II and III, and II and IV; 2) length of hallux and toes II, III, and IV; 3) track length; 4) track width; 5) pace length; 6) stride length; and 7) angle of divarication from the midline, were performed over the produced images using the free open-source software AragoJ (Aleixo et al., 2020). These measurements were used to describe the tracks and to identify behaviours. The figures presented were compiled in the free open-source software Inkscape v0.92.3 (Inkscape, 2018). The models used are made available as supplementary material, as suggested by Falkingham et al., 2018.

3.3. Luminescence dating

In order to obtain a geochronological control of the tracksites, in the different sections of the Upper Pleistocene aeolianites of the SW Portugal our team is developing a suitable sampling strategy for OSL dating in order to date the most relevant track-bearing stratigraphic surfaces. For the purpose of the present work, a trampled stratigraphic surface at the Pedreira sub-sector of the

Pessegueiro Island (altitude: 5.0 m a.s.l.; L: 37º 50' 05.06'' N; L: 8º 47' 52.86''W), with vertebrate (including bird) tracks and trackways (Fig. 5e), was selected to be dated by OSL. Under protection from sunlight exposure by using a thick black plastic, a block of aeolianite about 20 kg was extracted from the exposure and also covered by the black plastic; the given field code is Pessegueiro-1. An extra sub-sample of the sediment was also collected, in order to be used to measure the field and saturation water contents, respectively.

The preparation of the OSL mineral fractions from the inner part of the aeolianite block was carried out in the sample preparation room of the Dept. of Earth Sciences - University of Coimbra, under subdued red light to prevent resetting of the luminescence signal. After the removal of the ~3 cm external part of the block of sandstone, by dissolution of the carbonate cement under HCl (at 10%) attack, its internal part was also disintegrated by the same procedure. Later, H_2O_2 (at 10%) was used to remove any organic particles (very rare). The sand obtained was then sieved for obtaining several grain-size fractions. The 180-250 μm fraction was then selected to separate the K- rich feldspar fraction from the quartz and silicates fraction, through differential flotation in a heavy liquid solution (sodium polytungstate solution; $\rho = 2.58$ g/cm^3). The quartz-rich fraction ($\rho > 2.58$ g/cm^3) was etched using concentrated (40%) HF for 60 min, to remove the outer alpha-irradiated layer, followed by 10% HCl for 40 min (*e.g.*, Cunha et al., 2019).

Radionuclide concentrations (^{238}U, ^{232}Th and ^{40}K) in the bulk sediment were measured using high-resolution gamma spectrometry. The additional sediment sample associated with the main OSL sample was first dried at 50°C. A subsample of ~250 g was pulverized and homogenized, and then heated to 450ºC for 24 h to remove any organic matter (weight loss recorded). Finally, this

material was cast in wax to prevent radon loss and to provide a reproducible counting geometry. Samples were stored for three weeks to allow ^{222}Rn to reach equilibrium with its parent ^{226}Ra before being measured on a high purity germanium detector for at least 24 h. Details on the gamma spectrometry calibration are given in Murray et al. (2018). The external beta and gamma dose rate is the same to both quartz and K-feldspar grains. For quartz, a small internal dose rate of 0.02±0.01 Gy/ka was assumed, consistent with Vandenberghe et al. (2008). The radionuclide concentrations were converted to dose rate data using the conversion factors from Guérin et al. (2011). The contribution from cosmic radiation to the dose rate was calculated following Prescott and Hutton (1994) assuming an uncertainty of 5%. The long-term water content of each sample was estimated based on the average of the field water content and saturation water content.

Quartz grains were mounted as large (8 mm) aliquots on stainless steel discs or cups. Measurements were carried out on automated Risø TL/OSL (model DA-20) luminescence readers (stimulation with blue diodes for 40 s at 125ºC; preheat and cut-heat temperatures were 260°C /10 s and 22°C /0 s, respectively). A standard single-aliquot regenerative-dose (SAR) protocol was used to estimate the quartz D_e (Wintle and Murray, 2000; Murray and Wintle, 2003); the blue (470±30 nm) stimulated OSL signal was detected through a U-340 filter. All samples had a strong fast component; the net OSL signal was calculated from the initial 0.0–0.32 s of stimulation and an early background between 0.32 and 0.64 s. Dividing the D_e by the environmental dose rate (in Gy/ka) gives the luminescence age of the sediment.

3.4. Calibration of radiocarbon ages

453 The previous ^{14}C dates obtained by Martins (2014) were calibrated by using the
454 OxCal 4.4. [152] program provided by the University of Oxford and applying the
455 Marine 20 curve. However, as Martins (2014) clearly states, those dates may be
456 *terminus ante quem* for the deposition of the aeolianites.

457

458 ## 4. Results

459 ### *4.1. OSL dating results for the sampled aeolianite at the Pessegueiro island*

460 The results of quartz OSL dating of the Pessegueiro-1 aeolianite sample,
461 collected immediately bellow the trampled surface located at the lower part of the
462 aeolianite unit at the Pessegueiro Island (Fig. 2) are presented in Tables 1 and
463 2. The quartz OSL signal is pure (no IR sensitivity) and is bright and dominated
464 by a fast component, a prerequisite for accurate De determination using SAR
465 (Wintle and Murray, 2006; Murray et al., 2021). The dose recovery ratio is
466 0.957±0.012 (n=12) suggesting that our SAR protocol is suitable to measure dose
467 given prior to heat treatment in these samples. The measured D_e (92±3 Gy) is
468 smaller than the average characteristic dose value (D_c = 105±3 Gy; Murray et al.,
469 2021) derived from fitting the dose response curve with a single saturating
470 exponential function. So the natural quartz OSL signal lies well below the
471 saturation level of the dose response curve. The resulting quartz OSL age is
472 187±11 ka pointing at deposition towards the end of MIS7 or the beginning of MIS
473 6.

474

475 Table 1 – Dry gamma and beta dose rate components, radionuclide
476 concentrations (^{238}U, ^{226}Ra, ^{210}Pb, ^{232}Th and ^{40}K), burial depth (b.d.) and
477 estimated average water content of the sample during burial (w.c.) used for
478 dose-rate calculations of the luminescence dating ages

NLL code	Field code	Gamma dose rate (Gy/ka)	Beta dose rate Gy/ka)	^{238}U (Bq/kg)	^{226}Ra (Bq/kg)	^{232}Th (Bq/kg)	^{40}K (Bq/kg)	b.d. (cm)	w.c. (%)
202201	Pessegueiro-1	0.184 ±0.004	0.340 ±0.010	9±3	6.8±0.2	5.3±0.2	95±4	1800	10

479

Table 2 - Summary of quartz OSL results. (n) - number of measured and accepted aliquots contributing to the equivalent dose (D_e). Total dose rate to 180-250µm quartz grains assuming 10% water content. Uncertainty (1σ) on the ages incorporates both systematic and random components

Lab code	Field code	Protocol	D_e (Gy)	(n)	Dose rate (Gy/ ka)	OSL age estimate (ka)
202201	Pessegueiro-1	Quartz-OSL	92±3	24	0.51±0.03	187±11

4.2. Systematic Ichnology

Ichnogenus *Corvidichnus* igen. nov.

Type ichnospecies: *Corvidichnus odemirensis* isp. nov.

Derivatio nominis: The ichnogenus name includes the family Corvidae Vigors after the inferred type of producers and “ichnus” for trace. The specific name recalls the Odemira municipality where these tracks were found.

Diagnosis: Bipedal trackway of high pace angulation with mesaxonic tetradactyl, anisodactyl tracks of moderate size with small positive rotation with the midline. Tracks with three compared-sized digits directed forward showing clear phalangeal pad impressions, and a long hallux pointing backward, but slightly offset from the middle line; divarication angles between digits II-IV are small (i.e. ~70º); track length/width ratio less than 2.

Corvidichnus odemirensis isp. nov.

Figs. 3-5a

Holotype: A trackway of 4 footprints left in situ (T1C0 marked with yellow in Fig. 4). 3D digitype available as supplementary material (Sketchfab link: xxxxx).

Diagnosis: Same as for the ichnogenus, for now the only known ichnospecies.

Horizon and locality: Malhão formation located at Aivados Sul beach, coordinates 37º47'26.77''N 8º48'07.58''O; Chibanian (OSL dating of 187±11 ka for the lower part of the Malhão formation at Pessegueiro Island).

Description: The slab TPCorvLmAIVS with an area of 2.8 m^2 (Fig. 4) was found in the scree from the cliff showing two main trackways and few paired tracks, in a total of 12 imprints, preserved as concave epirelief. Description and interpretation is based on the 3D model developed for this study (Fig. 3) because the original specimen was damaged by wave action in less than one year. Two trackways are present, T1Ca and T2Ca, with four tracks each, besides two paired-tracks and one isolated imprint (Fig. 4). Measurements of the tracks and trackways are presented in Table 3. Trackway's breadth is <100 mm and the paired tracks PiCo are 161 mm. Anisodactyl tetradactyl tracks with prominent retroflexed hallux; the central metatarsal area is small. Thick toes with characteristic phalangeal and interphalangeal pad impressions: the mean size of the tracks is 62.8 mm in length and 38.9 mm in width; the mean length of the digits is for digit II, 23mm, for digit III, 28.8 mm, and for digit IV, 22.5 mm, with the hallux measuring 20.8 mm; toe I is slightly offset from central line and shorter than toe III. Divarication angle of the toes II-IV is 69.7 mm; inward rotation of the track with respect to the midline with an average angle of 12º; pace length of 187 mm of and stride length of 368 mm (T2Ca). High pace angulation of 145-150º resulting of each foot swinging around and from behind in arc.

525 

526 Fig. 3. General view of TPCorvLmAIVS; ruler is 24.35 cm long.

527

528 Table 3 – Measurements for *Corvidichnus odemirensis* isp. nov.

	Corvidichnus odemirensis														
	Left Side Pes							Right Side *Pes*							
Track measurements	PiCoPe1	T2CoPe1	T2CoPe2	T1CoPe1	T1CoPe2	PiCoP?1	Mean L	PiCoPd1	T2CoPd1	T2CoPd2	T1CoPd1	T1CoPd2	PiCaP?2	Mean R	Mean
Length (mm)	64	60	70	57	65	71	64,5	67	84	61	54	51	50	57,5	62,8
Width (mm)	40	42	32	59	40	36	41,5	33	46	33	38	32	36	34,5	38,9
Length digit II (mm)	25	26	22	21	20	25?	23,1	26	33	20	19	18	23?	21,5	23
Length digit III (mm)	31	26	32	25	29	23	27,6	31	38	28	27	32	24	29,5	28,8
Length digit IV (mm)	26	19	21	20	22	21?	21,5	21	30	21	24	21	21?	21	22,5
Length of hallux (mm)	20	20	22	22	19	23	21	25	27	19	19	16	18	19	20,8
Divarication between digits II-IV (°)	61	72	64	74	72	84	72	60	76	61	65	77	70	67,5	69,7
Divarication between digits II-III (°)	30	21	22	22	23	36?	22	14	34	46	15	26	35?	26	25,3
Inwards pace rotation (°)	15	13	9	22	12	-	13	11	8	14	**9**	**7**	-	9	**12**

Trackways		Length	Mean
Pace (mm)	T2CoPe1 - T2CoPd1	183	183
	T2CoPd1 - T2CoPe2	187	
	T2CoPe2 - T2CoPd2	166	
	T1CoPd1 - T1CoPe1	186	168
	T1CoPe1 - T1CoPd2	168	
	T1CoPd2 - T1CoP32	128	
Stride (mm)	T2CoPe1 - T2CoPe2	368	352,5
	T2CoPd1 - T2CoPd2	347	
	T1CoPe1 - T1CoPe2	286	
	T1CoPd1 - T1CoPd2	358	
Trackway width (mm)	T1	<100	-
	T2	<100	-
	PiCoPe1 - PiCoPd1	161	-

529

Remarks: By their morphology these are typical tracks of large perching birds, without any doubt compared with corvids (see discussion). The asymmetric ripples and the direction of the trackways indicate that the bird(s) walked following the wind direction. There is also a nice trackway of the rabbit *Oryctolagus cuniculus* that was identified at the near Malhão beach as *Leporidichnites malhaoi* by Neto de Carvalho (2009).

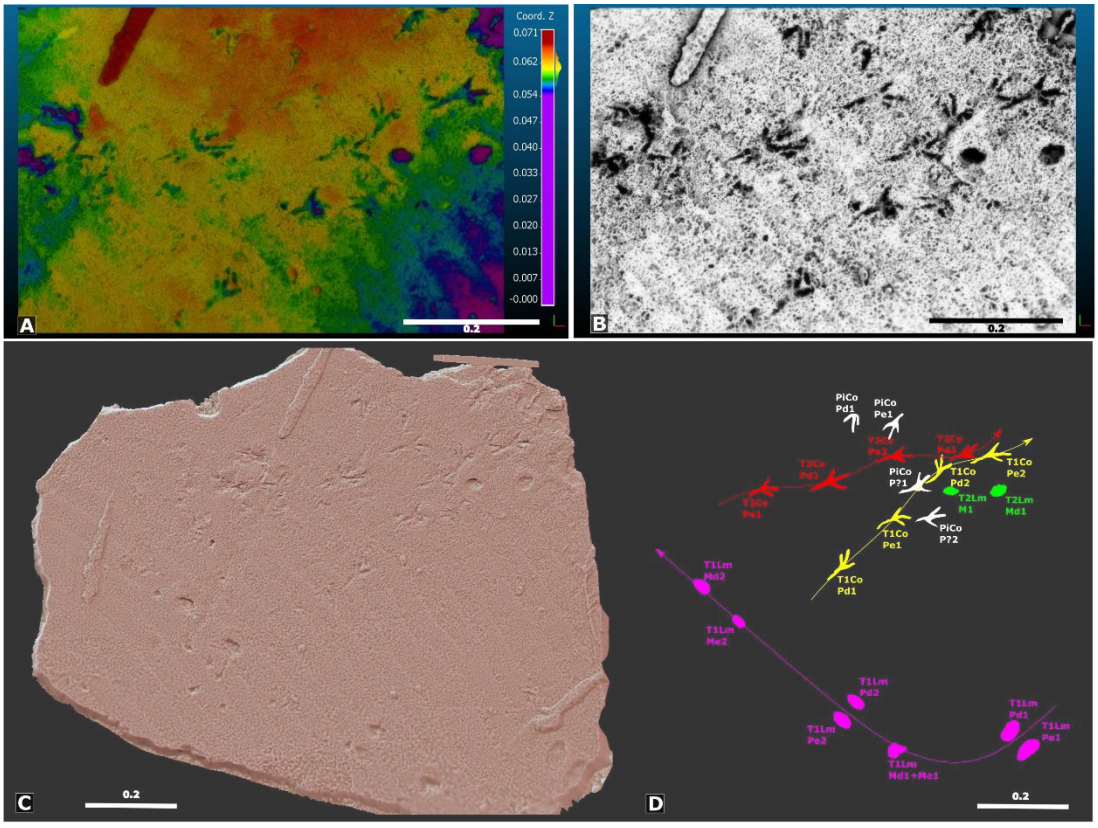
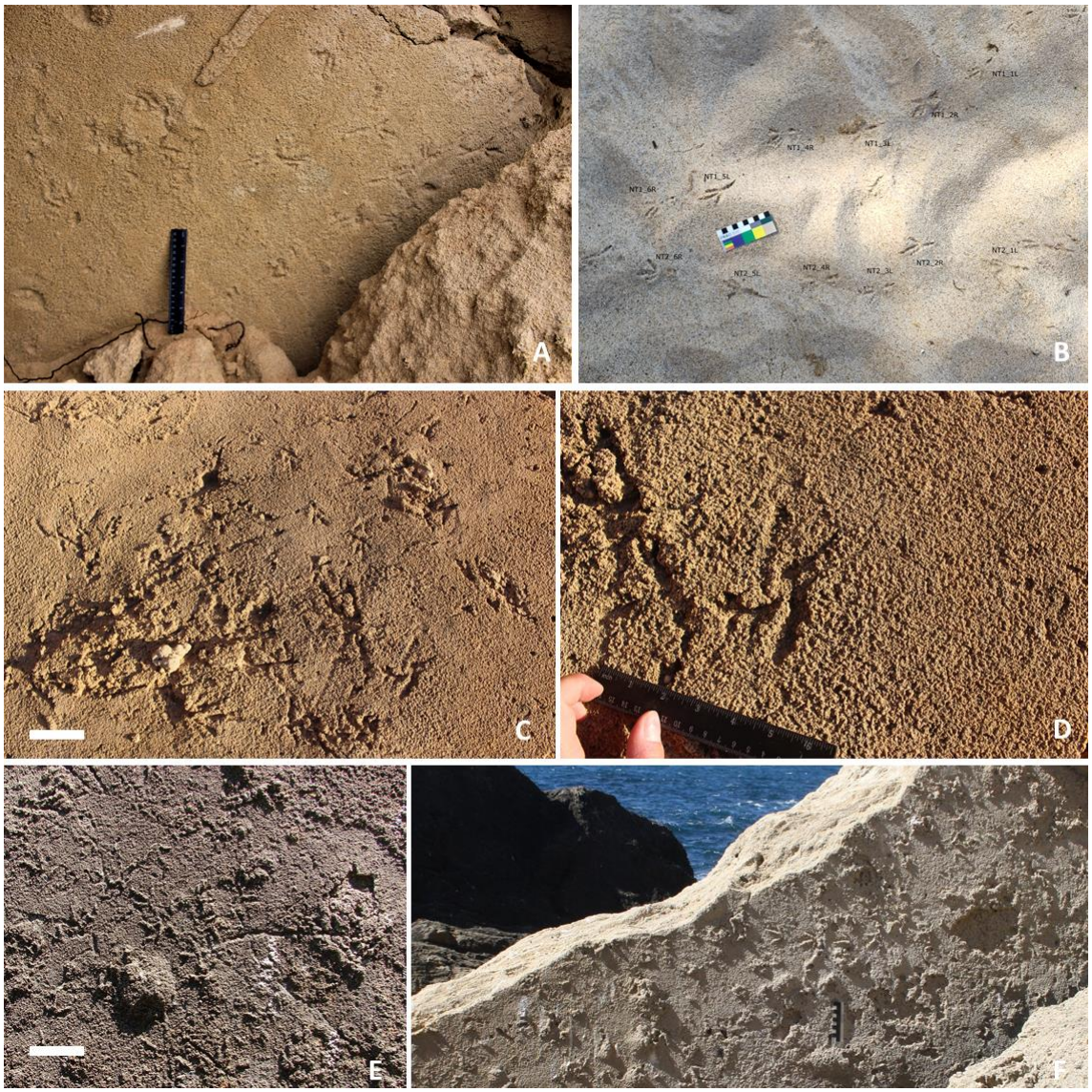


Fig. 4. Corvid (*Corvidichnus odemirensis*) and the rabbit (*Leporidichnites malhaoi*) trackways from TPCorvLmAIVS. A) False color height map (m) of the trackways area. B) Trackways area enhanced by Ambient Occlusion PCV Shade Vis algorithm (Zhukov et al., 1998). C) 3D model improved by Radiance Scaling algorithm (Vergne et al, 2010). D) Interpretative drawing of the tracks and trackways (white color correspond to the isolated tracks and red and yellow to the

543 trackways of *Corvidichnus odemirensis*, the green color corresponds to the
544 isolated tracks and the purple color to the trackways of *Leporidichnites malhaoi*).



545

546 Fig. 5. Avian trackways from the Pleistocene aeolianites of SW Portugal. A –
547 *Corvidichnus odemirensis* from Aivados Sul beach section. B - *Corvus monedula*
548 (Western jackdaw) trackways measured in Aivados beach for comparison with *C.*
549 *odemirensis* (see Table 6). C – *Buboichnus vicentinus* trampled area interpreted
550 as a predation/feeding trace; scale is 10 cm. D – Detail of *B. vicentinus* zygodactyl
551 track in Telheiro beach section. E – Detail of the trackways attributed to
552 *Charadriipeda* isp. type I in the trampled surface of Pedreira in Pessegueiro island

553 section; scale is 10 cm. Main trackway of *Charadriipeda* isp. type I located in
554 Canto da Pedra dos Corvos tracksite, Pessegueiro island section.

555

556 Ichnogenus *Gruipeda* Panin and Avram

557 Diagnosis: Tracks showing four digits, three (II to IV) directed forward and long;
558 toe I pointing backwards, spur-like and short. The interdigital angles between
559 digits II and III and digits III and IV are less than 70º. The axis of digit I does not
560 correspond with that of digit III, the interdigital angle between digits I and II is
561 greater than that between digits I and IV. Webbing absent (emended by Sarjeant
562 and Langston, 1994).

563

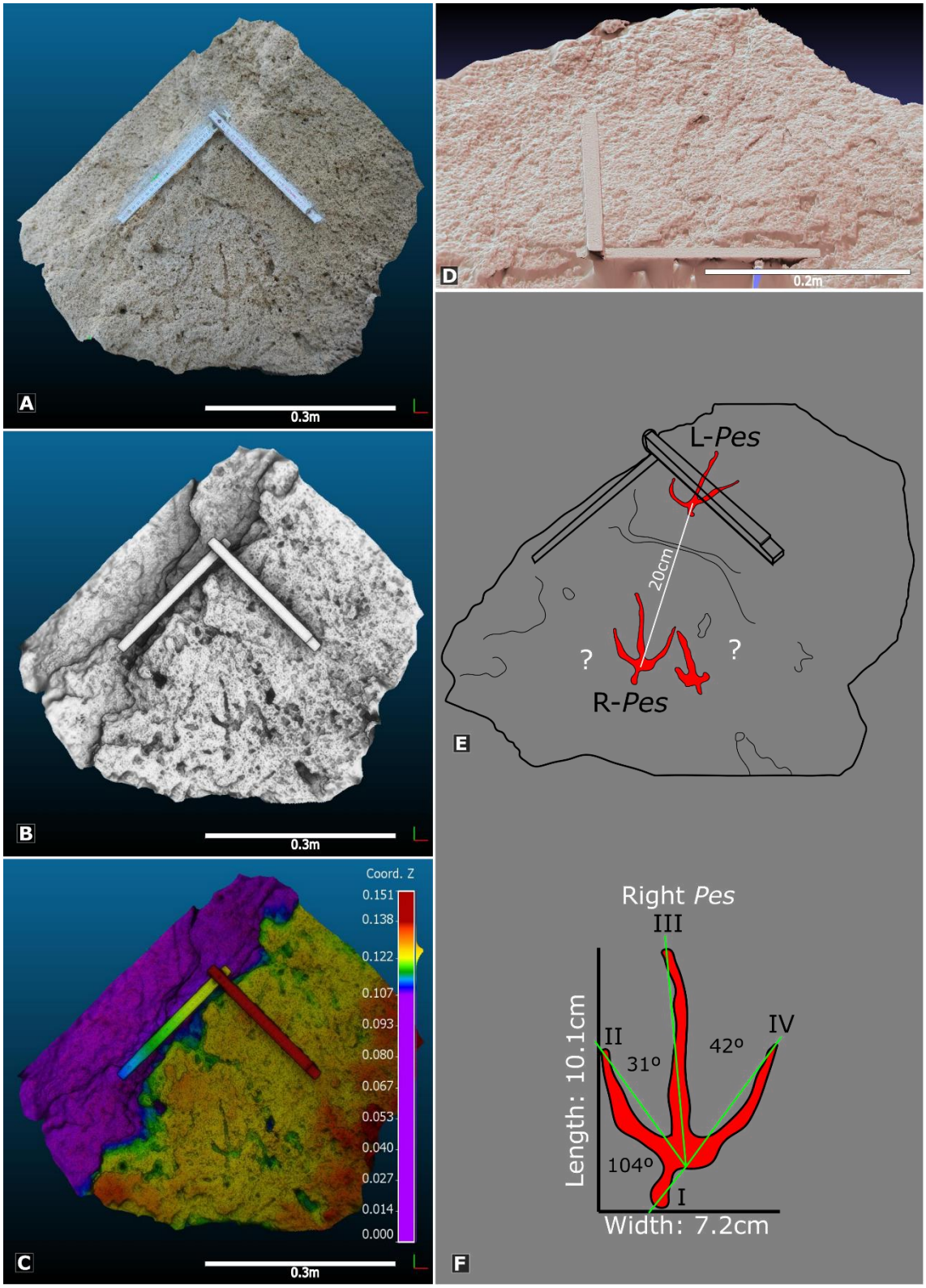
564 *Gruipeda* aff. *maxima* Panin and Avram

565 Fig. 6

566 Description: Tetradactyl anisodactyl tracks longer than wide, of relatively large
567 size, with 10 cm long by 7 cm wide. They exhibit four digits, II and IV directed
568 forward and diverging at an angle of about 65º, digit I directed backwards. Digits
569 II and IV are similar in length, with sides almost parallel for most of their length
570 and tapering abruptly to a pointed tip. Digit I is short, spurlike and tapering; its
571 axis is offset at a low angle to the right from that of digit III. The impressions of
572 digit II and IV are connected proximally; digit I is separate. Webbing absent
573 (Sarjeant and Langston, 1994). Size of the track; length of the middle toe; length
574 and shape of the rear toe; size and angle between outer toes, and whether the
575 toes are long and slender or short and powerful. Digit I is short, makes an angle

with digit III but is not separated which is the result of a deep impression. Digits II and IV bends inwards.

Remarks: The slab PsAvipAIVS corresponds to a small block (~0.6m^2), with three poorly preserved tracks. Two of the tracks belong to a trackway. Only one track could be detected without 3D image analysis. This is the second morphotype attributed to birds recognized at the Aivados sul section. The ichnogenus *Ardeipeda* Panin and Avram shows tetradactyl tracks with wider divarication angles between digits than the tracks of Aivados sul (see Sarjeant and Langston, 1994). *Leptoptilostipus pyrenaicus* (Payros et al., 2000) reveals similarities with our tracks, namely the digits II and IV bending upwards and small digit divarication, with a long and slender digit III, but in the Portuguese tracks lacks the impression of the membrane. Therefore, the large tracks from Aivados sul are better compared with *Gruipeda maxima*.



591

592 Fig. 6. *Gruipeda* aff. *maxima* from the upper Pleistocene of Aivados sul; ruler is
593 25 cm. A) Real colors textured 3D model. B) 3D model enhanced with the
594 Ambient Occlusion PCV ShadeVis algorithm (Zhukov et al., 1998). C) False color

595 height map (m) of the 3D model. D) Oblique views of the 3D model highlighted
596 by Radiance Scaling algorithm (Vergne et al, 2010). E) Interpretative draw of the
597 tracks and trackway. F) Dimensions and divarication angles of the right *pes*.

598

599 Ichnogenus *Buboichnus* igen. nov.

600 Type ichnospecies: *Buboichnus vicentinus* isp. nov.

601 *Derivatio nominis*: The ichnogenus name after the species *Bubo bubo* (Linnaeus),
602 the likely producer, and “ichnus” for trace. The specific name recalls to cape São
603 Vicente where these tracks were found.

604 Diagnosis: Moderate-sized tetradactyl zygodactyl tracks with well-developed
605 hallux impression; digital pads recognizable and with claw marks attached or
606 independent. Digits II and III point anteriorly with digits I and IV pointing
607 posteriorly with variable divarication angle, but showing mesaxonic symmetry.

608 *Buboichnus vicentinus* isp. nov.

609 Figs. 5c-d, Figs. 7-9

610 Holotype: Paired-tracks TZTrk006L and TZTrk007/8R in Fig. 7. 3D digitype
611 available as Supplementary Material (Sketchfab link xxxx).

612 Diagnosis: The same as for the ichnogenus.

613 Horizon and locality: Telheiro aeolianite located in the Quebrada creek close to
614 the beach, coordinates 37º02’51.07’’N 8º58’12.79’’O. Taking in account that the
615 horizon with the bird tracks is located between dated levels by ^{14}C dating (44.7

and 40.3 ka cal BP; Monge Soares et al., 2012; Martins, 2014) it is likely that these tracks have a depositional age of, at least, ca. 45-43 ka (MIS 3).

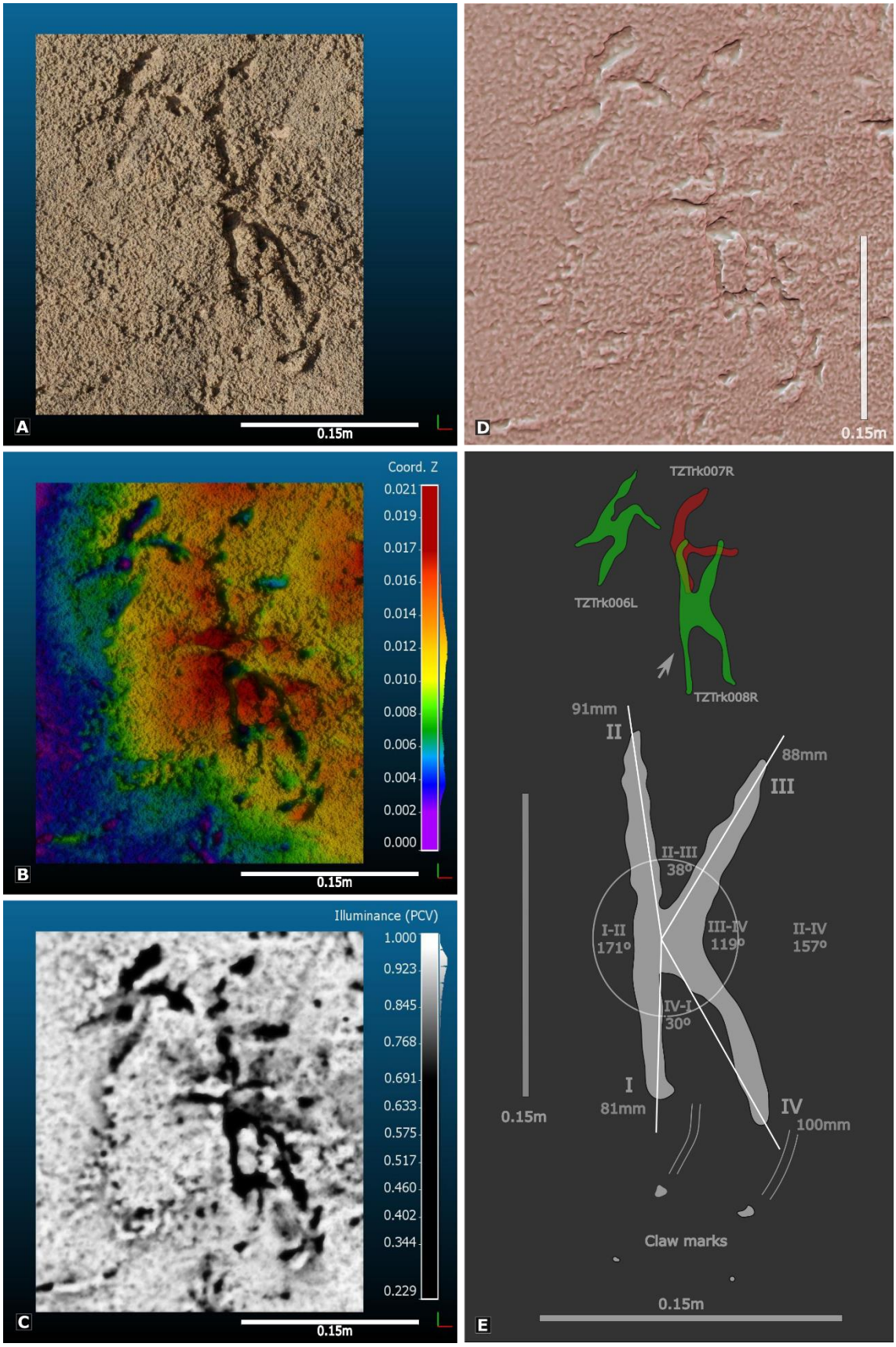
Description: Zygodactyl four-toed tracks with a mean length of 113 mm and width 57 mm. Measurements of the ten tracks identified can be found in Table 4. Digits II and III pointing forward and I and IV pointing backwards. Toes are long and powerful except in a few cases, probably due to preservational reasons. Digits I-IV show a mean length of 37.9 mm, 49.5 mm, 50.8 mm and 44.7 mm, respectively. Divarication angles of digits II-IV and II-III are 164.4º and 43.5º, respectively. Claw marks are detached from the track in the holotype. Toe pad impressions are identified (Fig. 7). High pace angulation in defined short trackway, with a pace length of 39.2 cm and stride length of 67.7 cm in TZTrl.

Table 4 – Measurements for *Buboichnus vicentinus* isp. nov.

Buboichnus vicentinus

Side	Left Side *Pes*					Right Side *Pes*							
Track measurements	TZTrk001L	TZTrl004L	TZTrk006L	TZTrk009L	Mean L	TZTrk002R	TZTrl003R	TZTrl005R	TZTrk007R	TZTrk008R	TZTrk010R	Mean R	Mean LR
Length (mm)	106	137	103	118	112	102	70	141	-	137	102	110,4	112,9
Width (mm)	33	65	56	48	52	41	53	68	67	53	55	54	53,9
Length digit II (mm)	40	58	46	51	48,5	43	37	61	55	50	54	52	49,5
Length digit III (mm)	46	55	51	49	50	39	41	67	50	64	46	48	50,8
Length digit IV (mm)	41	54	41	55	47,5	48	33	65	-	64	46	51,2	44,7
Length of hallux (mm)	26	39	41	30	34,5	42	27	43	-	58	35	41	37,9
Divarication between digits II-IV (°)	180	>180	162	178	175	160	175	160	-	157	128	156	164,4
Divarication between digits II-III (°)	18	47	60	36	41,5	30	49	40	68	37	50	44,5	43,5

Trackway		Length	Mean
Pace (mm)	TZTrl003R - TZTrl004L	285	338,5
	TZTrl004L - TZTrl005R	392	
Stride (mm)	TZTrl003R - TZTrl005R	677	-
Trackway width (mm)	TZTrl003004005	<80	-


A
0.15m
D
0.15m
B
Coord. Z
0.021
0.019
0.017
0.016
0.014
0.012
0.010
0.008
0.006
0.004
0.002
0.000
0.15m
C
Illuminance (PCV)
1.000
0.923
0.845
0.768
0.691
0.633
0.575
0.517
0.460
0.402
0.344
0.229
0.15m
E
TZTrk007R
TZTrk006L
TZTrk008R
91mm
II
88mm
III
II-III
38°
I-II
171°
III-IV
119°
II-IV
157°
IV-I
30°
I
81mm
IV
100mm
0.15m
Claw marks
0.15m

630

631

Fig. 7. *Buboichnus vicentinus* holotype. A) Real colors textured 3D model; B) False color height map of the 3D model; C) 3D model enhanced with the Ambient Occlusion PCV ShadeVis algorithm (Zhukov et al., 1998). D) Map highlighted by Radiance Scaling algorithm (Vergne et al, 2010), of the type material of *Buboichnus vicentinus* igen. et isp. nov. evidencing the morphology of the track TZTrk008R; E) Interpretation drawing of the previous figures, with the location of the paired-tracks, with the measurements of the toes I-IV and the divarication angles between toes.

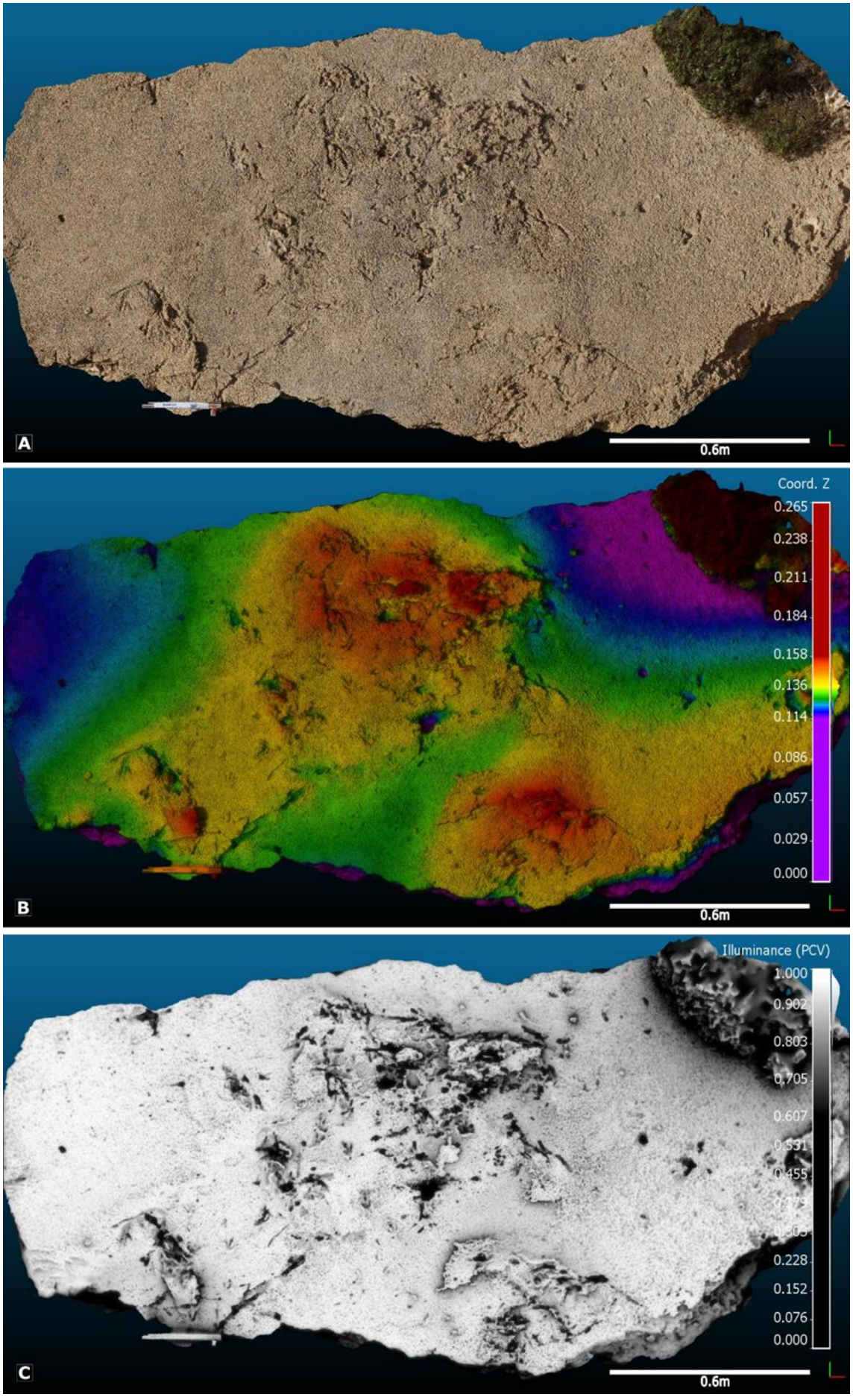

A
0.6m
Coord. Z
0.265
0.238
0.211
0.184
0.158
0.136
0.114
0.086
0.057
0.029
0.000
B
0.6m
Illuminance (PCV)
1.000
0.902
0.803
0.705
0.607
0.531
0.455
0.228
0.152
0.076
0.000
C
0.6m

Fig. 8. General view of the localized trampled block. A) Orthophoto of the real colours textured 3D model. B) DSM False color height map of the 3D model, C) PCV 3D model enhanced with the Ambient Occlusion PCV ShadeVis algorithm (Zhukov et al., 1998).

Remarks: In a very localized area 10 zygodactyl tracks are recognized surrounding the completely bioturbated substrate (Figs. 5c, 8). Due to this preservation, only three tracks are clear individualized. We interpreted the organization of the short trackways and tracks in multiple directions surrounding a completely trampled area as evidence of predation (see Discussion and Fig. 9). The two trackways of shorebirds converging to the trampled area can be just a coincidence and may be made some hours before the disturbing action of the larger bird.

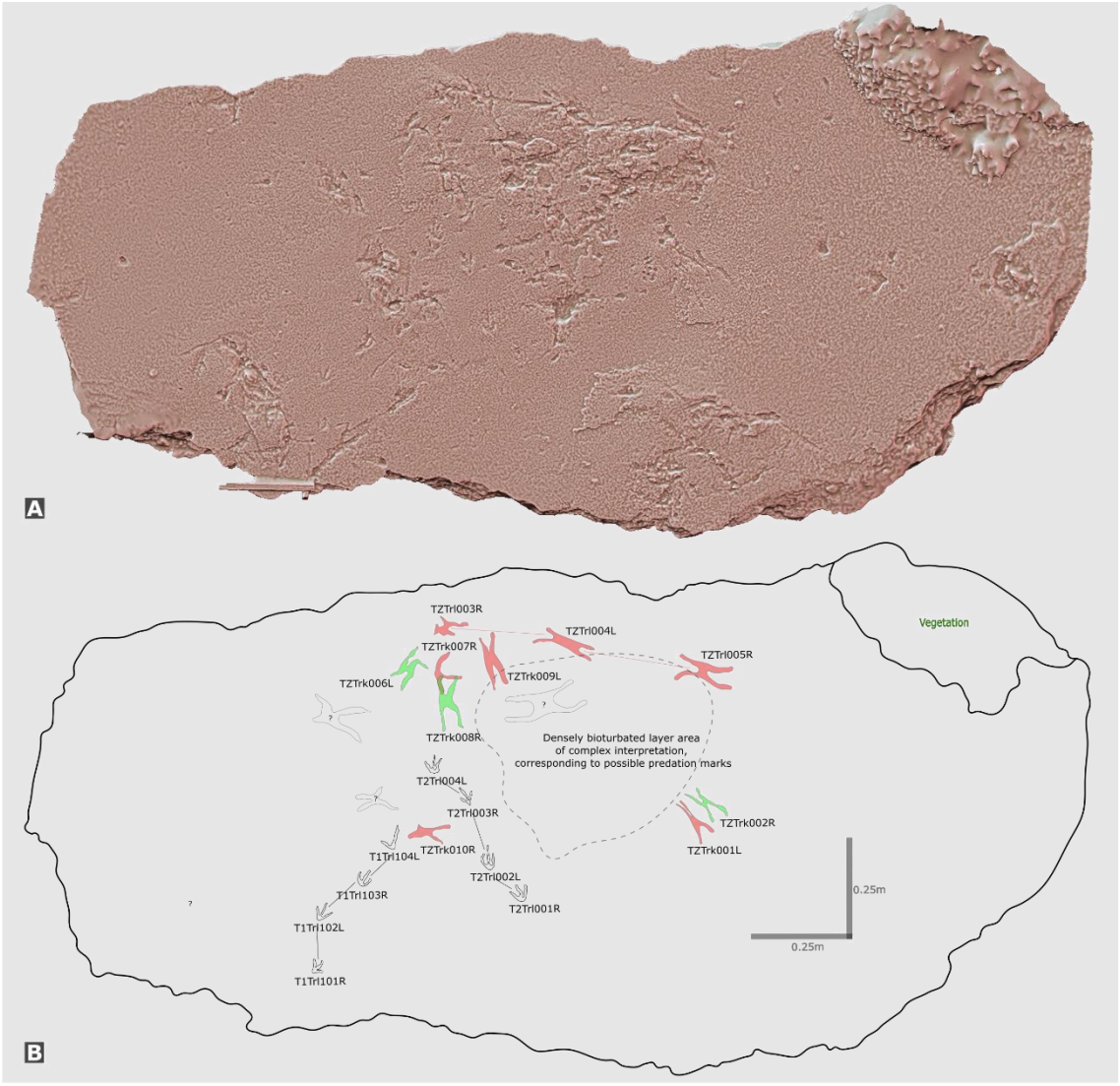


Fig. 9. A) High-resolution 3D vertical view of the track surface (improved by Radiance Scaling algorithm (Vergne et al., 2010). The sediment disturbance occurred possibly resulting from the preying action of the producer of *Buboichnus vicentinus* intersecting two trackways converging to the same area (see the interpretation scheme B). Present vegetation interferes in the upper right part of the model.

Ichnogenus *Charadriipeda* Panin and Avram (1962)

Charadriipeda isp.

Figs. 5e-f, Figs. 10, 11.

Description: Tridactyl anisodactyl and mesaxonic tracks, of moderate size and slender digits, commonly showing claw marks. The first morphotype (type I) was previously described in two different tracksites found at the Pessegueiro Island (Figueiredo et al., 2018; Figs. 10, 11). In the trampled surface found at Pedreira tracksite (Fig. 5e), 10 trackways plus 3 isolated prints were identified; three trackways, the longer composed of 10 tracks, and some apparently isolated tracks were found in the same level at Canto da Pedra dos Corvos tracksite (Fig. 5e). These are formed by a longer digit III (30 to 55 mm), with divarication angles with toes II and IV of between 30º and 42º. Digit II measures 15 to 30 mm and digit IV, between 18 and 38 cm. These two digits are linear or bend upwards. There is no impression of the hallux. The flat areas identified by 3D image analysis are related to interdigital webbing. According to the emended diagnosis of Sarjeant and Langston (1994), the ichnogenus *Charadriipeda* include avian footprints having only three digits (II–IV), directed forward and showing interdigital angles of less than 70°, connected by webbing from their proximal end almost to their tips. However, these features are not common in some of the ichnospecies of *Charadriipeda*. Meanwhile, Sarjeant and Reynolds (2001) emended its diagnosis to avian footprints showing four digits, with a spur-like hallux being preserved in some ichnospecies. Because the ichnogenus needs a solid revision, we do not intend in this study to differentiate ichnospecies despite the sub-optimal preservation of the material.

Webbing seems to be one of the main characteristics to discriminate this morphotype from the two trackways found at Telheiro tracksite (morphotype II;

Fig. 11). Table 5 presents the measurements made to the two trackways included in type II. Those are composed of four tracks each, smaller than type I (41.1 mm long and 27.6 mm wide), displaced in a zigzag pattern and a narrow gauge, showing also low divarication angles but the imprint of a spur-like hallux in just one of the tracks (T2Trl003R). There is an isolated track on the same surface which is larger, with a longer hallux, and therefore could be a different morphotype from the previously described forms.

Table 5 – Measurements of *Charadriipeda* isp. type II from Telheiro beach section

***Charadriipeda* isp. type II**											
	Left side *Pes*					**Right Side Pes**					
Track measurements	**T1Trl102L**	**T1Trl104L**	**T2Trl002L**	**T2Trl004L**	**Mean L**	**T1Trl101R**	**T1Trl103R**	**T2Trl001R**	**T2Trl003R**	**Mean R**	**Mean LR**
Length (mm)	48	27	51	35	41,5	34	42	41	51	42	41,12
Width (mm)	29	21	26	30	26,5	-	-	32	28	30	27,6
Length digit II (mm)	36	18	31	27	28	26	28	28	23	26,25	27,12
Length digit III (mm)	48	27	51	35	41,5	34	42	41	33	37,5	38,8
Length digit IV (mm)	28	11	27	23	25	-	-	27	24	25,5	23,3
Length of hallux (mm)	-	-	-	-	-	-	-	-	13	-	-
Divarication between digits II-IV (°)	49	76	53	60	56,5	-	-	66	50	58	59
Divarication between digits II-III (°)	**24**	**33**	**23**	**25**	**24,5**	**50**	**-**	**-**	**30**	**40**	**30,8**

Trackways		Length	Mean
Pace (mm)	T1Trl101R - T1Trl102L	116	123,6
	T1Trl102L - T1Trl103R	141	
	T1Trl103R - T1Trl104L	114	
	T2Trl001R - T2Trl002L	115	135,3
	T2Trl002L - T2Trl003R	174	
	T2Trl003R - T2Trl004L	117	
Stride (mm)	T1Trl101R - T1Trl103R	230	225,5
	T1Trl102L - T1Trl104L	221	
	T2Trl001R - T2Trl003R	281	286
	T2Trl002L - T2Trl004L	291	
Trackway width (mm)	T1Trl	96	-
	T2Trl	77	-

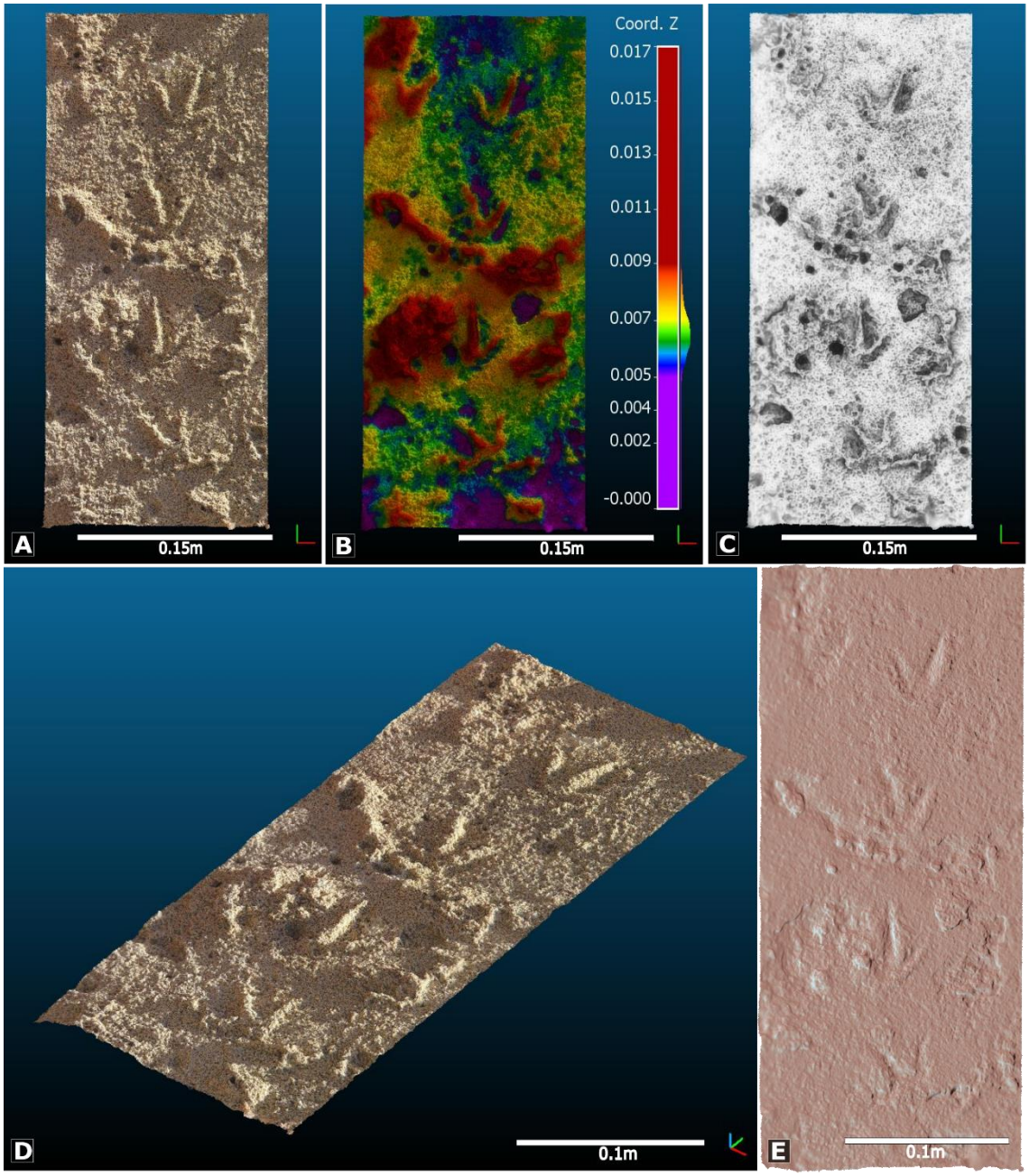
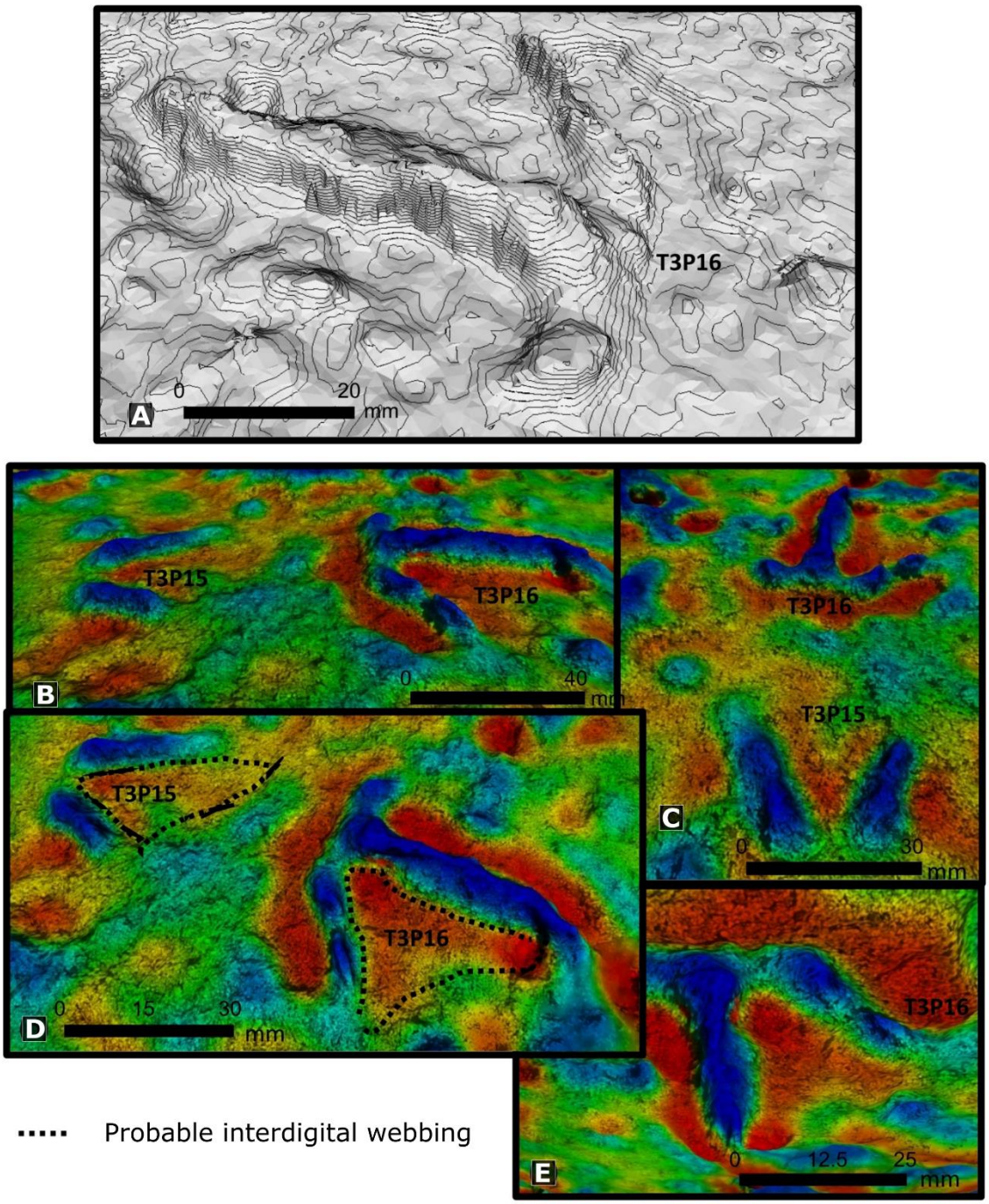


Fig. 10. A and D) Nadir and oblique views of the real colors 3D textured model of *Charadriipeda* type I; scale is 0.15 m, except for D and E which is 0.1m. B) False color height map (m) of the 3D model. C) 3D model enhanced with the Ambient Occlusion PCV ShadeVis algorithm (Zhukov et al., 1998). E) 3D model improved by Radiance Scaling algorithm (Vergne et al., 2010).



709

710 Fig. 11. Gull tracks interpretation based on digital image analysis. A) 3D surface
711 of the track T3P16 made of contour lines to enhance morphological features
712 described. B) to E) 3D surface of the tracks T3P15 and T3P16, viewed from
713 different angles by curvature algorithm (cold colors correspond to the convex
714 features and hot colors to the concave features). The flat areas between digits

715 (evidenced in red) indicated a webbing impression (from Neto de Carvalho et al.,
716 2016).

717

718 5. Discussion: The track producers and associated behaviors

719 *5.1.* Corvidichnus odemirensis *compared to Western jackdaw*

720 The tracks TPCorvLmAIVS of Aivados Sul section can be attributed to perching
721 birds due to the asymmetrical toe alignment. The imprint of toe III tends to turn
722 under and inwards, which is obvious and characteristic in corvid tracks (Brown et
723 al. 2002). Crow and raven tracks have a distinctive digital segmented
724 appearance. In corvids the three forward-pointing toes are often asymmetrical,
725 with different lengths and arranged at different angles from each other; the hind
726 toe points straight back and is almost as long as the front centre toe.

727 The fossil record of corvids extends since the Middle Miocene (Kessler, 2020).
728 According to comprehensive databases such as ebird.org and BirdLife, four
729 species of corvids have their present distribution covering the territory of Portugal:
730 *Corvus corax* Linnaeus, *C. corone* Linnaeus, *Corvus monedula* Linnaeus and
731 *Pyrrhocorax pyrrhocorax* (Linnaeus). During the Middle and Late Pleistocene,
732 besides these species, *Corvus antecorax* Mourer-Chauviré, *C. frugilegus*
733 (Linnaeus) and *Pyrrhocorax graculus* (Linnaeus) are known from the Paleolithic
734 cave records in Portugal (Figueiredo, 2010, 2018; Figueiredo and Rosa, 2014).
735 Carrion crow (*Corvus corone*) tracks are up to 140 mm long and 70 mm wide with
736 walking strides between 400 and 650 mm (Brown et al. 2002). Together with the
737 Common raven they are some of the largest corvids existing. The Rook is also a
738 large corvid that lives nowadays in North and Central Europe. The Alpine chough

739 (or yellow-billed chough) and the Red-billed chough are in present typical from
740 mountain ecosystems but could also be present in other areas during the glacial
741 conditions interpreted for the MIS 6. Moreover, the Alpine chough was found in
742 the Upper Pleistocene deposits of the Furninha coastal cave (central Portugal),
743 which are much younger than the ages now obtained for the Pessegueiro island-
744 Aivados sul beach (Brugal et al., 2012; Figueiredo et al. 2017). Being not
745 possible to dismiss the Alpine chough as a possible producer of *Corvidichnus*
746 *odemirensis*, the size of these tracks fits closer with the Western jackdaw (*Corvus*
747 *monedula*), the second smallest member of the corvids, which is very common
748 among the Pleistocene birds record of Portugal (Figueiredo, 2010; Brugal et al.,
749 2012; Figueiredo and Rosa, 2014; Figueiredo, 2018; Figueiredo et al., 2017,
750 2018) and still lives nowadays in the coastal areas of SW Portugal, including the
751 area, visiting beaches and the dune systems on a daily basis foraging food.
752 These animals are opportunist omnivorous also searching for live invertebrates
753 such as echinoderms and carrion in the surf line, as well as beetles, snails,
754 spiders, eggs and chicks of birds that they can find in the dunes (Sievers et al.,
755 2014). The difference in size between hind toes in paired tracks (shorter) and in
756 trackways (longer) is clearly related to dragging during walking. The claw on toe
757 I is much longer and sharp and can thus also extend the size of this toe print.
758 Large passerines such as corvids walk and hop. Walking prints appear in a zigzag
759 or sometimes in a line. Paired tracks are associated to take-off or landing.
760 However, in corvids side by side tracks may indicate the bird was hopping along.
761 Table 6 presents the measurements made for two trackways of *C. monedula* in
762 the Aivados Sul section. Comparing with the data obtained from *Corvidichnus*
763 *odemirensis* in Table 3 (Figs. 5a, b), it is clear that proportions of track and toes,

764 divarication angles, trackway width and pace rotation are comparable, the
765 somewhat larger pace length and clearly larger stride length could be explained
766 by faster walking or walking-hopping following the wind direction in *Corvidichnus*
767 *odemirensis*. Changing pace in the fossil trackway marked yellow in Fig. 4, from
768 186 mm to 128 mm, indicates slowing down.

769 Table 6 – Measurements for recent trackways of the Western jackdaw

							Corvus monedula								
Side	Left Side Pes							Right Side *Pes*							
Track measurements	NT1_1L	NT1_3L	NT1_5L	NT2_1L	NT2_3L	NT2_5L	Mean L	NT1_2R	NT1_4R	NT1_6R	NT2_2R	NT2_4R	NT2_6R	Mean R	Mean LR
Length (mm)	56	67	60	76	57	70	63,5	56	49	61	63	68	67	62	62,0
Width (mm)	26	41	30	27	33	35	31,5	31	31	28	30	33	39	31	31,0
Length digit II (mm)	26	25	25	29	26	25	25,5	21	21	23	21	29	22	21,5	25,0
Length digit III (mm)	33	33	32	40	27	30	32,5	27	25	24	35	36	31	29	31,5
Length digit IV (mm)	24	24	22	18	26	24	24	21	20	22	21	26	23	21,5	22,5
ength of hallux (mm)	15	26	18	22	19	28	20,5	17	15	24	20	19	22	19,5	19,5
rication between digits II-IV (°)	55	92	58	49	50	56	55,5	68	70	56	65	58	71	66,5	58,0
rication between digits II-III (°)	14	49	17	6	14	7	14	23	23	16	17	45	22	22,5	17,0
wards pace rotation (°)	7	10	19	20	13	18	15,5	12	20	10	**22**	**15**	**9**	**13,5**	**14**

Trackways		Length	Mean
Pace (mm)	NT1_1L - NT1_2R	127	127
	NT1_2R - NT1_3L	120	
	NT1_3L - NT1_4R	142	
	NT1_4R - NT1_5L	147	
	NT1_5L - NT1_6R	110	
	NT2_1L - NT2_2R	160	145
	NT2_2R - NT2_3L	104	
	NT2_3L - NT2_4R	103	
	NT2_4R - NT2_5L	145	
	NT2_5L - NT2_6R	160	
Stride (mm)	NT1_1L - NT1_3L	244	254,5
	NT1_2R - NT1_4R	258	
	NT1_3L - NT1_5L	271	
	NT1_4R - Nt1_6R	251	
	NT2_1L - NT2_3L	229	236,5
	NT2_2R - NT2_4R	188	
	NT2_3L - NT2_5L	244	
	NT2_4R - NT2_6R	290	
Trackway width (mm)	NT1	68	-
	NT2	96	-

770

771 *5.2. The first evidence of a raptorial bird-prey interaction preserved in action*

772 Arboreal birds show a K- or X-like pattern in track morphology. The only
773 zygodactyl tracks comparable with *Buboichnus vicentinus* found in the fossil
774 record is *Shandongornipes muxiai* from the Lower Cretaceous of China described
775 by Rihui et al. (2005). These are smaller tracks with mesaxonic asymmetry, digits
776 II, III and IV pointing anteriorly and not united in the centre. Mainly for those

777 morphological differences and the sub-optimal preservation conditions, the new
778 zygodactyl tracks from Telheiro deserve to be placed in a new ichnogenus.

779 The Eurasian eagle-owl is one of the largest species of owl, and females can
780 grow to a total length of 75 cm, being larger than males (Voous, 1988). They are
781 also one of the most widely distributed of all species. Owl tracks usually show two
782 toes pointing forward, one to the side and a very short toe pointing to the rear or
783 off to the side. The toes are thick and powerful, usually ending with sharp claws.
784 Owl feet is spread because both the inner and outer toe can function as a versatile
785 toe and work together with the rear toe (Brown et al. 2002). They use their feet to
786 constrict their prey to death, the talons serving only to hold the prey in place (Ward
787 et al., 2002). In average, Eurasian eagle-owls track length is up to 105 mm
788 (without claw marks) with an average toe III length of 49-62 mm (Brown et al.
789 2002). Toe I and claw are sometimes indistinct, with the claw print extending
790 significantly the print. Also, the tracks tend to be dragged when the bird first lands
791 (Brown et al. 2002). The normal gait is a running hop, with the straddled tracks
792 almost in pairs and strides of 150 mm to 400 mm between them (Brown et al,
793 2002). The size and morphology of *Buboichnus vicentinus* fit conveniently in the
794 tracks of the Eagle-owl. The fossil tracks are also well inside the geographic area
795 of the modern *Bubo bubo* in the Iberian Peninsula (Graciá et al., 2015), which
796 can be compared with the Pleistocene fossil record distribution of this species in
797 Portugal (Fig. 12). Although the tracks and stride length apparently oversize the
798 average measurements known for *B. bubo* (Linnaeus) it is known that some of
799 these animals can grow larger, with a female in Britain having the middle toe
800 measured to 57.9 mm (MacGillivry, 1836). The only owl species slightly larger
801 than the Eagle-owl is the Great-grey-owl *Strix nebulosa*, presently living in

802 northern latitudes (Voous, 1988). However, there is no record of the species in
803 SW Europe, both as fossils or living. During the Middle Pleistocene (Mindel
804 glaciation), Eagle-owls of southern France were 6–10% larger than recent
805 individuals (*Bubo bubo davidi* Mourer-Chauviré), and a still larger *Bubo*
806 *binagadensis* Burchak-Abramovich existed in Azerbaijan but disappeared in the
807 Late Pleistocene (Penteriani and Kenward, 2007). Eagle-owls have long and
808 robust claws, especially in toes II and IV. In a soft substrate, like the sand dune,
809 the deeper impression of the feet can increase the apparent size of the digits
810 because the claw marks cannot be distinguished.

811 Eagle-owls are typical of rocky areas, near woodland and shrubby zones
812 (Martinez et al., 2003). The landscape of the surrounding area to the Telheiro
813 beach section may have been completely different ca. 45-43 ka ago. The area
814 may have been covered by forest and the rhizoliths provide evidence for shrub
815 vegetation stabilizing the secondary dune; Eagle-owls could breed at the cliff
816 edges (Penteriani and Delgado, 2019) of the high coastline found towards the
817 north. These animals are nocturnal predators, hunting for a range of different prey
818 species, from rodents, rabbits and larger mammals, but also birds of varying size
819 (Penteriani and Delgado, 2019). Their feeding activity is focused in the first few
820 hours after sunset and last few hours before sunrise (Delgado and Penteriani,
821 2007). At the Telheiro Beach tracksite we find Eagle-owl like tracks associated to
822 a confined irregular patch of heavy sediment trampling to where two shorebird
823 trackways converge (marked with a dashed line in Fig. 9), which we interpret as
824 new evidence of predation/feeding behaviour preserved as a trace fossil
825 snapshot. The action may have happened during or after the shorebirds visited
826 the place foraging for food, likely during the day. According to our interpretation,

827 just after the sunset, the large Eagle-owl caught a prey and brought it to this place
828 or constricted the prey right here (if it was the shorebird represented in the two
829 trackways). The disturbed sediment, including a concentration of large zygodactyl
830 tracks, with different directions, and track overprinting (Fig. 8), resulted from the
831 constricting to death of the prey and/or its manipulation during feeding. Except
832 for functional morphological evidence like bone accumulations (Worthy and
833 Holdaway, 1994; Berger and Clarke, 1995) and digestichnia commonly preserved
834 as owl pellets (e.g., Tobien, 1977; Andrews, 1991) and regurgitates (e.g.,
835 Seersholm et al., 2021), bird predation trace fossils are rare, and mostly restricted
836 to bill dabbling, scything, pecking and probing behaviors (Yang et al., 1995;
837 Fiorillo et al., 2011; Melchor et al., 2012; Falk et al., 2014 and references therein;
838 Abassi et al., 2016; Helm et al., 2020). The trace fossil of predator-prey interaction
839 of raptorial birds described in this study has a rare potential to be preserved,
840 making the example of Telheiro's finding singular and as far could be determined
841 the first example on the fossil record.

842

843 *5.3. The shorebird track record*

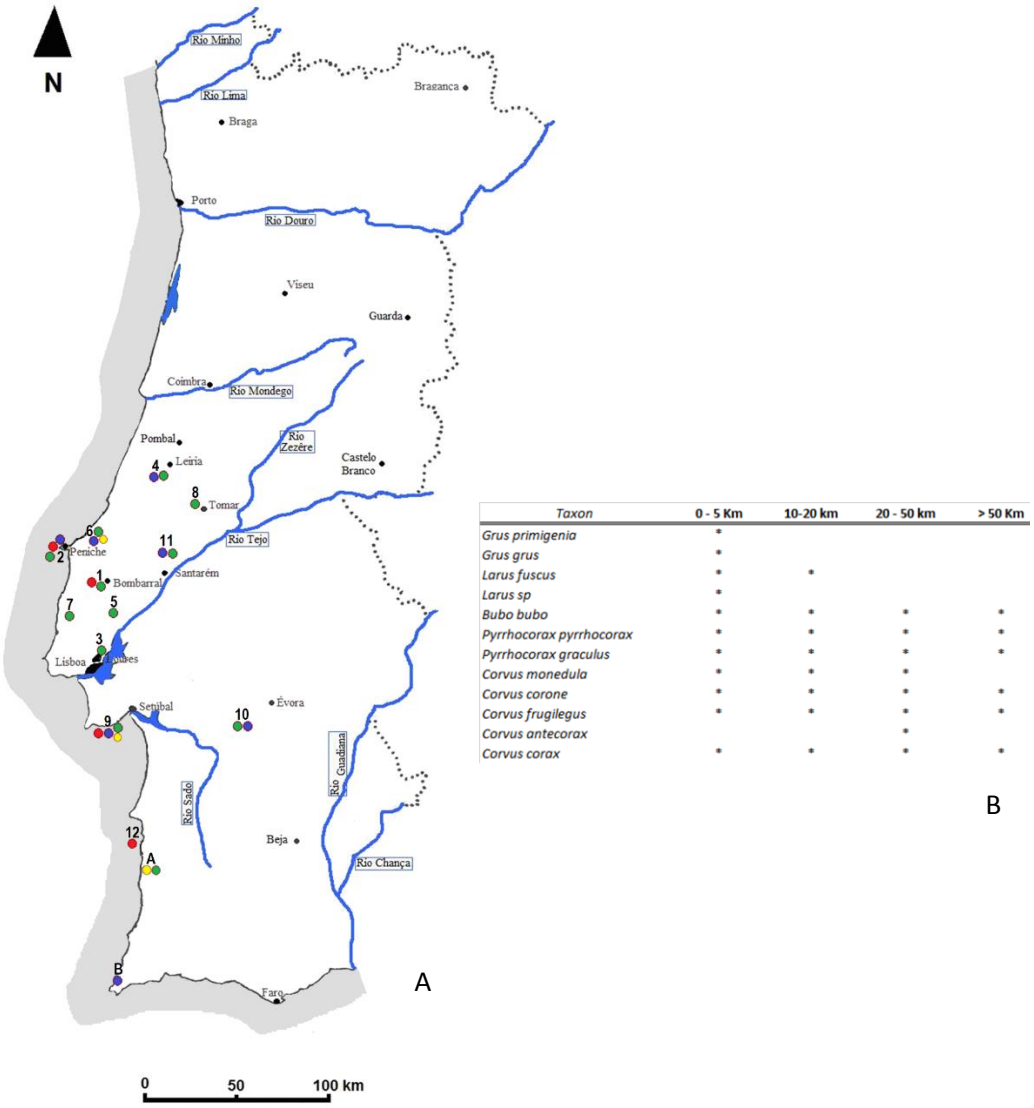
844 The shorebird tracks described in the aeolianite of Pessegueiro island by Neto
845 de Carvalho (2009), Neto de Carvalho et al. (2016) and Figueiredo et al. (2018),
846 are now dated by luminescence to 187±11 ka, very late MIS7 or very early MIS
847 6. The two trackways found in the stratigraphic surface at the Pessegueiro island
848 are composed of tracks with long and slender forward toes, with a moderate to
849 wide divarication and absence of hallux print, features that are found in shorebirds
850 from the order Charadriiformes. This order is nowadays represented in Portugal
851 by over 50 species belonging to 9 families, which typically live in the coastal area

and commonly are seen looking for protection from storms and strong winds on the beach and among the dunes. Shorebirds and especially gulls have long and slender digits, widely open and connected by the interdigital web, which reveal to be adaptations for efficient swimming and walking in soft, sandy substrates. We attributed the variably sized web-prints of *Charadriipeda* isp. type I to different species of Charadriiformes, especially gulls (Figueiredo et al., 2018).

The two trackways defined as *Charadriipeda* isp. type II are different from the webbed-type gull tracks described before. Considering the morphology and size of the tracks, the apparent lack of web, but also the dune habitat and the expected species found there by comparison with the present coastal dune environments found in SW Portugal, any shorebird species such as *Charadrius morinellus* Linnaeus, *C. alexandrinus* Linnaeus, *Pluvialis apricaria* (Linnaeus), *Burhinus oedicnemus* Linnaeus, *Limosa lapponica* (Linnaeus), and *Numenius phaeopus* Linnaeus, could have produced these tracks.

The poorly preserved large tracks of Aivados Sul Beach tracksite have slender toes with short divarication angles, and a spur-like hallux, strongly reminding the tracks of rallids. The Eurasian coot (*Fulica atra* (Linnaeus)) is member of the family Rallidae. This omnivorous waterbird can still be found in coastal lagoons and estuaries of the area where the tracks were found. They are medium-sized, 38 to 50 cm in length, robust birds with short legs and large feet. Coot shows divarication angles of toes II-III and III-IV, 45º and 35º respectively. Toe III is in average 75 mm long (Brown et al., 2002). As in Aivados Sul, coot tracks show evidence of connection of all the digits by the metatarsal imprint. The metatarsal impression is the result of a plantigrade with the full length of the metatarsus in contact with the ground.

The shorebird ichnofacies described by Doyle et al. (2000) comprises ichnocoenoses attributable to Charadriiformes, Anseriiformes and Ciconiiformes, and has been interpreted as effectively lacustrine ichnofacies, although associated with coastal environments. The *Gruipeda* tracks attributed to Eurasian coots reinforce this ecological association. The identification of tracks of the ichnogenus *Gruipeda* in Aivados Sul Beach section is consistent with the fossil record of coastal deposits with body remains of Pleistocene birds in Portugal: in the Gruta da Figueira-Brava (Setúbal), a scapula of *Grus primigenia* was identified (Mourer-Chauvirè & Antunes, 2000) and in the Gruta da Casa da Moura (Óbidos) was identified a tibiotarsus of *Grus grus* (Figueiredo, 2010; Figueiredo and Rosa, 2014). The presence of corvid and strigid tracks reflects however the proximity of rocky areas, near the varied woodland edge and shrubby areas both with openings and/or wetlands where Eagle-owls hunt most of their prey; *Corvus monedula* are omnivorous and opportunists. This species was common in the coastal areas of Portugal mainland during the Pleistocene (Fig. 12) (Figueiredo, 2010, 2018; Figueiredo and Rosa, 2014; Figueiredo et al., 2017, 2018) and presently, although more common in hinterland areas (BirdLife.org), it is frequent to find them in coastal dunes and beaches of SW Portugal raiding in large groups for food. The moderate diversity of tracks found in the Middle and Late Pleistocene aeolianites of SW Portugal reflects an ecological mosaic that still can be found in the area nowadays.



900

901 Fig. 12. A. Distribution of the occurrence of Paleolithic sites with the probable
902 producers of the tracks in the Pleistocene of Portugal. A and B – New tracksites
903 presented in this work: A – Aivados Sul Beach section; B – Telheiro Beach
904 section; 1 – 12: Previously known sites. 1 to 11 – Bone assemblages in caves: 1
905 – Gruta Nova da Columbeira; 2 - Gruta da Furninha; 3 - Gruta de Salemas; 4 -
906 Abrigo do Lagar Velho; 5 - Gruta das Fontainhas; 6 - Gruta da Casa da Moura; 7
907 - Lapa da Rainha; 8 - Gruta do Caldeirão; 9 - Gruta da Figueira-brava; 10 - Gruta
908 do Escoural; 11 - Grutas do Almonda; 12 – Tracksite previously described –
909 Pessegueiro island. Taxonomic information: Yellow circles - Gruiformes; red

910 circles – Charadriiformes; blue circles – Strigiformes; Green circle - Corvidae
911 (adapted from Figueiredo, 2018, Fig. 1). B - Distance to the coast of the
912 archeological occurrences of the bird species from the Pleistocene of Portugal
913 that are compared with the tracks described in this work (adapted from
914 Figueiredo, 2010).

915

916 ## 6. Conclusions

917 The Pleistocene avifauna of mainland Portugal was previously and mostly known
918 from bone assemblages in cave sites. In the outbreak of the new wave of
919 ichnological research on Pleistocene coastal aeolianites 20 years ago, the first
920 Cenozoic vertebrate tracks from Portugal were described in 2003. Since then, 11
921 sections were recognized with vertebrate tracks, documented by 18 stratigraphic
922 levels. The Pessegueiro island sector included the first bird tracks described in
923 Portugal. New tracksites with avian trackways and tracks from the Middle and
924 Upper Pleistocene coastal aeolianites were described in this study for three
925 sections in SW Portugal: Pessegueiro island, Aivados Sul Beach and Telheiro
926 Beachs. According to the luminescence age of 187±11 ka in the Pessegueiro
927 island, as well as previous OSL and ^{14}C ages obtained, the aeolianite levels with
928 the bird tracks were deposited in several aeolian depositional episodes ranging
929 from the MIS 7/6 transition to the MIS 3. The tracksite in the aeolianite unit at
930 Praia do Telheiro site, with an apparent depositional age of ~45-43 ka (MIS 3), is
931 now the most recent fossil record of avian tracks in the Iberian Peninsula.

932 Two new ichnotaxa are described for the first time in the Pleistocene of Europe,
933 *Corvidichnus odemirensis* and *Buboichnus vicentinus*, attributed to corvids and a

large Eagle-owl. Western jackdaw is the likely producer of *Corvidichnus odemirensis* based on the direct morphometric comparison with tracks on beach sands made by this animal still living in region, but the Alpine chough cannot be dismissed as a likely producer since archeological evidence point to their existence in the coast of central Portugal during the same period. In the younger aeolianite of Telheiro Beach (~45-43 ka cal BP), a new predation/feeding trace is described, with the multiple orientation and concentration of Eagle-owl tracks, together with two converging trackways of shorebirds, defining a snapshot of active catching and manipulation of prey by the Eagle-owl. The rarity of perching and raptorial bird behaviors in the fossil record give a special meaning to this study with compelling evidence of their presence, together with Charadriiformes (including Laridae), shorebirds and possibly coots, as well as small and large mammals, that lived or raided for food in the wider coastal habitats of the Late Pleistocene.

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Carlos Neto de Carvalho: Conceptualization; Carlos Neto de Carvalho, João Belo, Silvério Figueiredo, Pedro Proença Cunha, Andrew Murray, Jan-Pieter Buylaert: Data curation; Carlos Neto de Carvalho, João Belo, Silvério Figueiredo, Pedro Proença Cunha, Fernando Muñiz, Zain Belaústegui, Andrea Baucon: Formal analysis; All authors: Funding acquisition; Carlos Neto de Carvalho, João Belo, Silvério Figueiredo, Pedro Proença Cunha, Fernando Muñiz, Zain Belaústegui, Andrea Baucon: Investigation; João Belo, Pedro Proença Cunha: Methodology; Carlos Neto de Carvalho: Project administration; João Belo: Software; Carlos Neto de Carvalho: Supervision; Pedro Proença Cunha, Fernando Muñiz, Mário Cachão: Validation; Carlos Neto de Carvalho, João Belo, Silvério Figueiredo, Pedro Proença Cunha, Fernando Muñiz, Zain Belaústegui, Andrea Baucon; Writing - original draft; All authors: Writing - review & editing.

Declaration of interest

The authors declare that they hold no competing financial or non-financial interests.

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Figure 1

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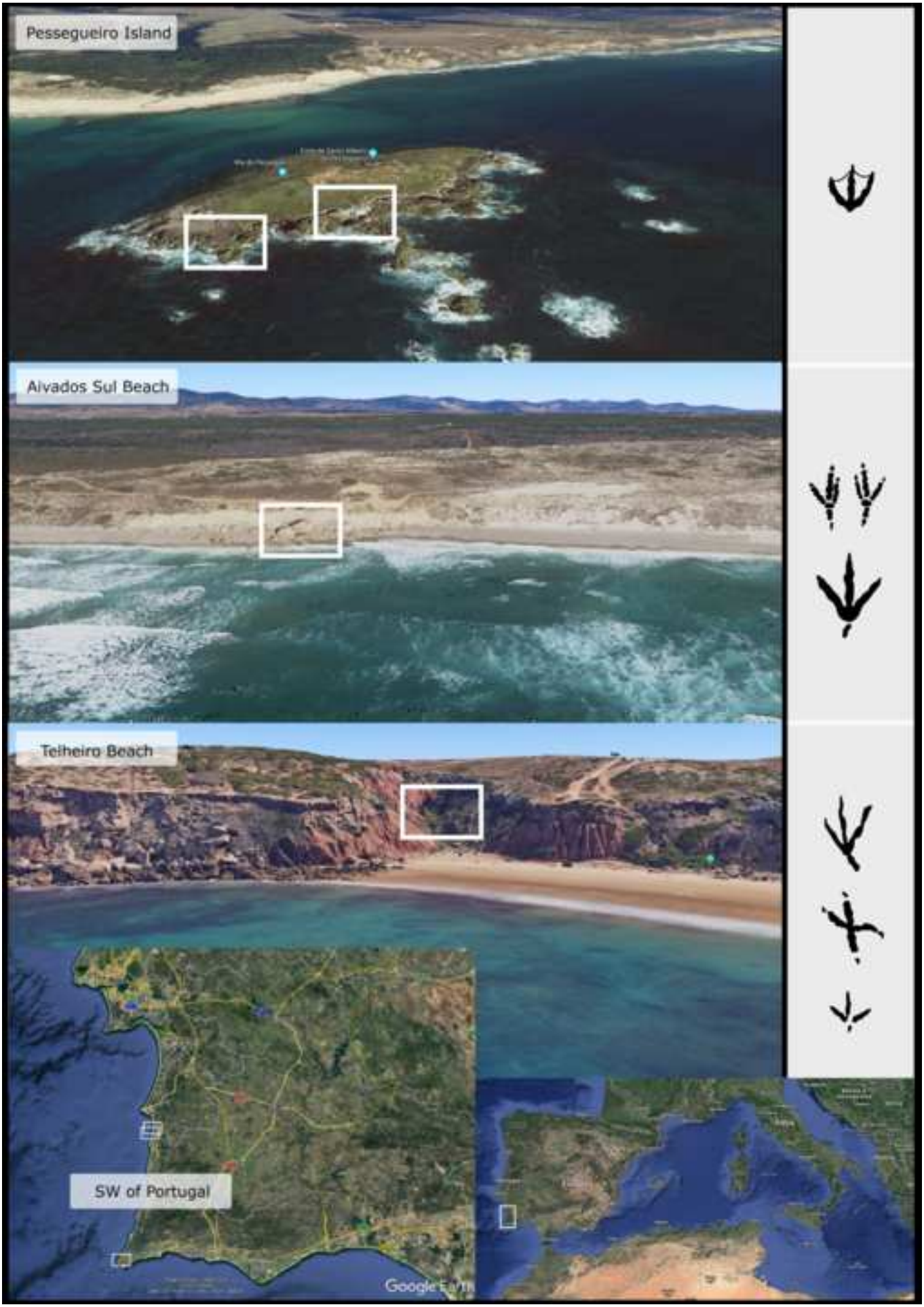

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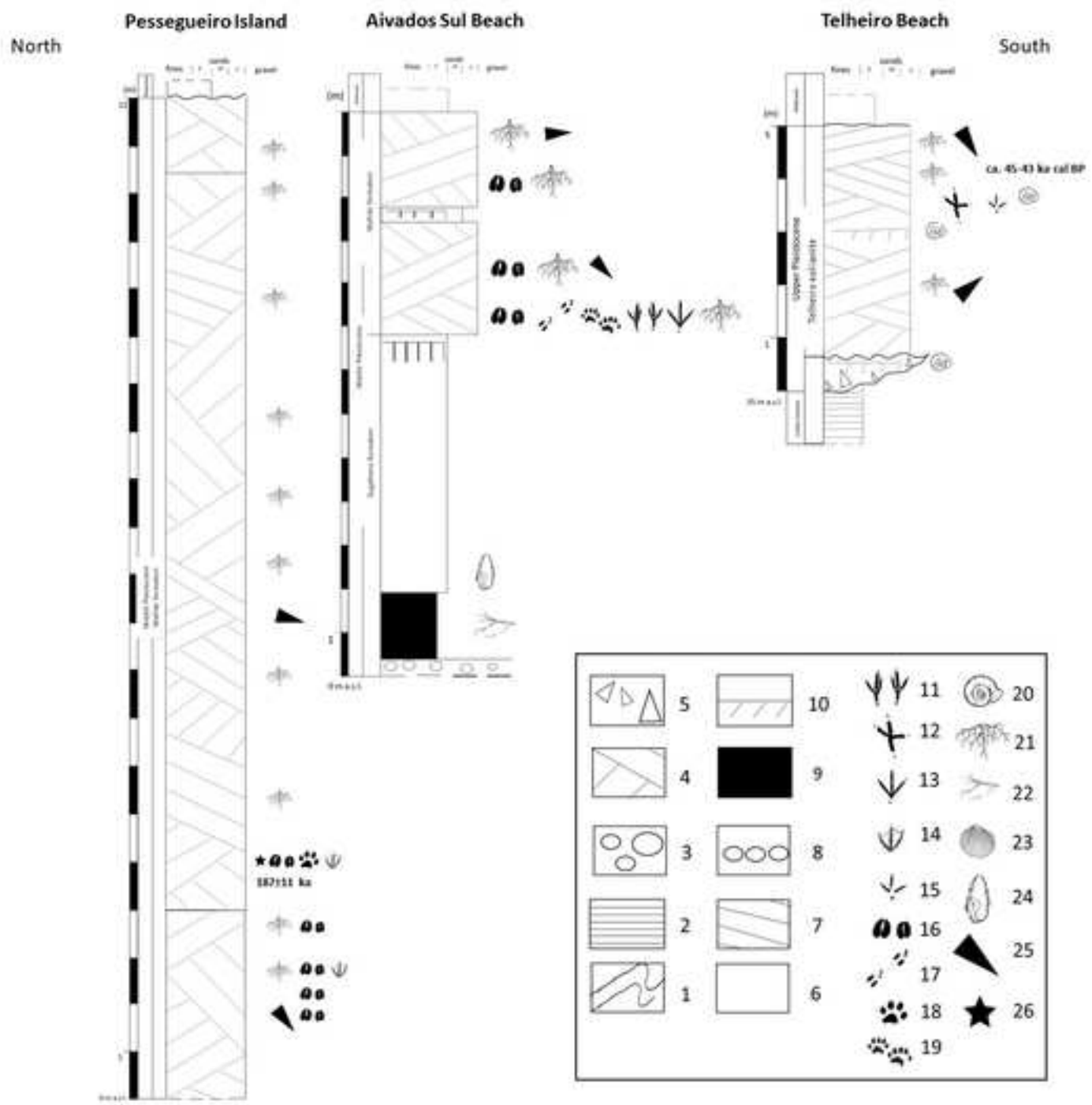

Figure 3

Figure 4

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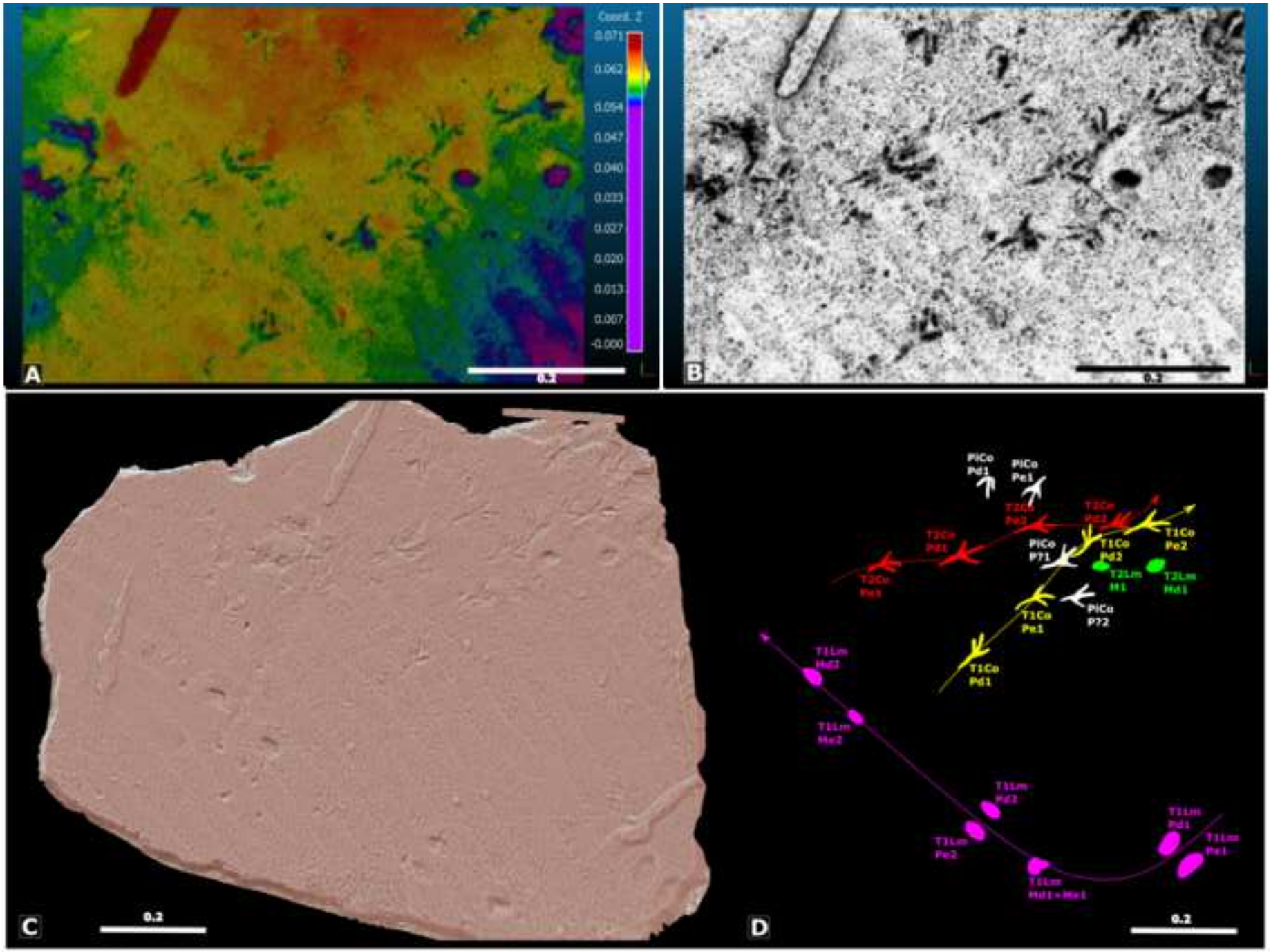

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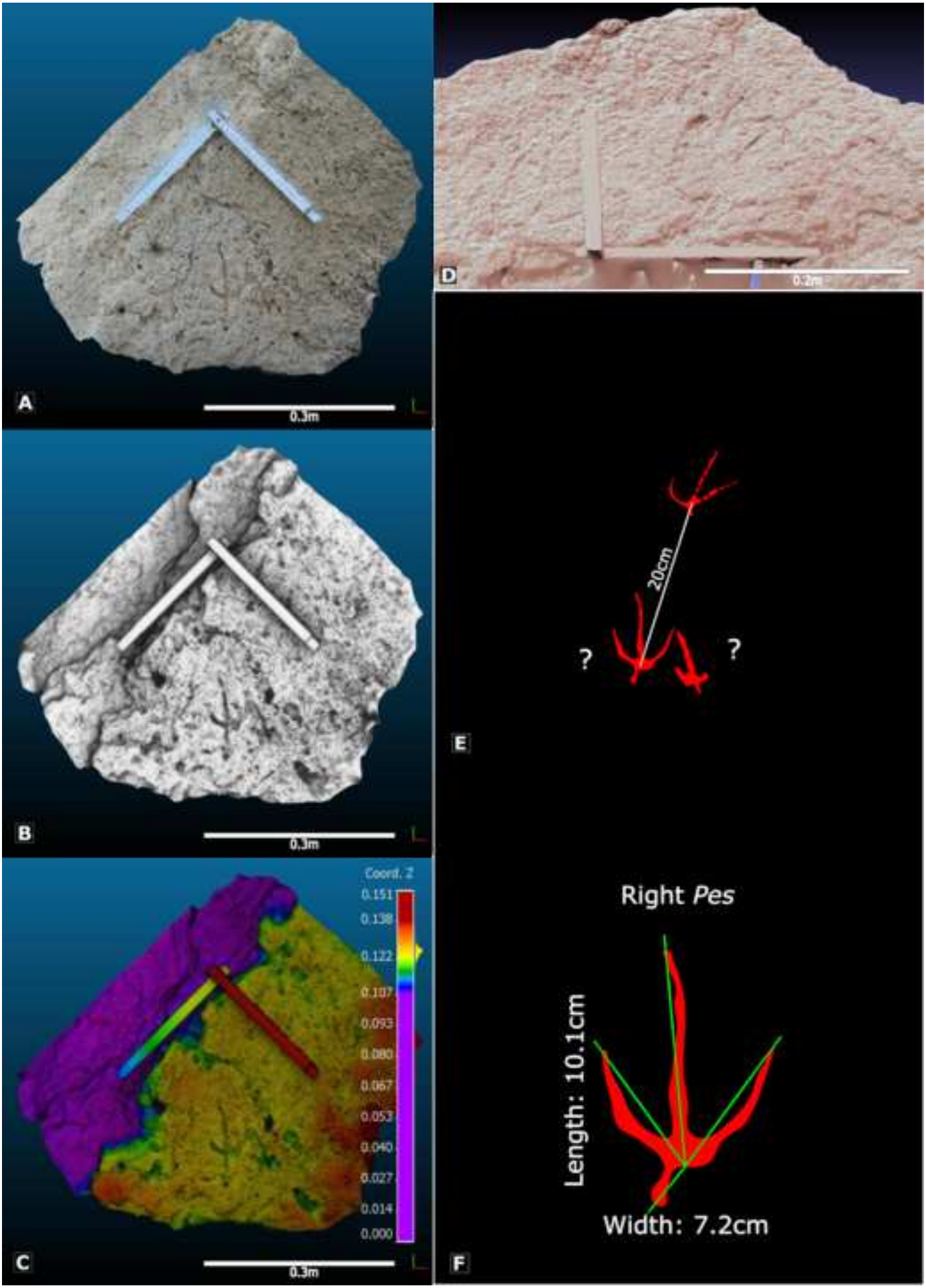

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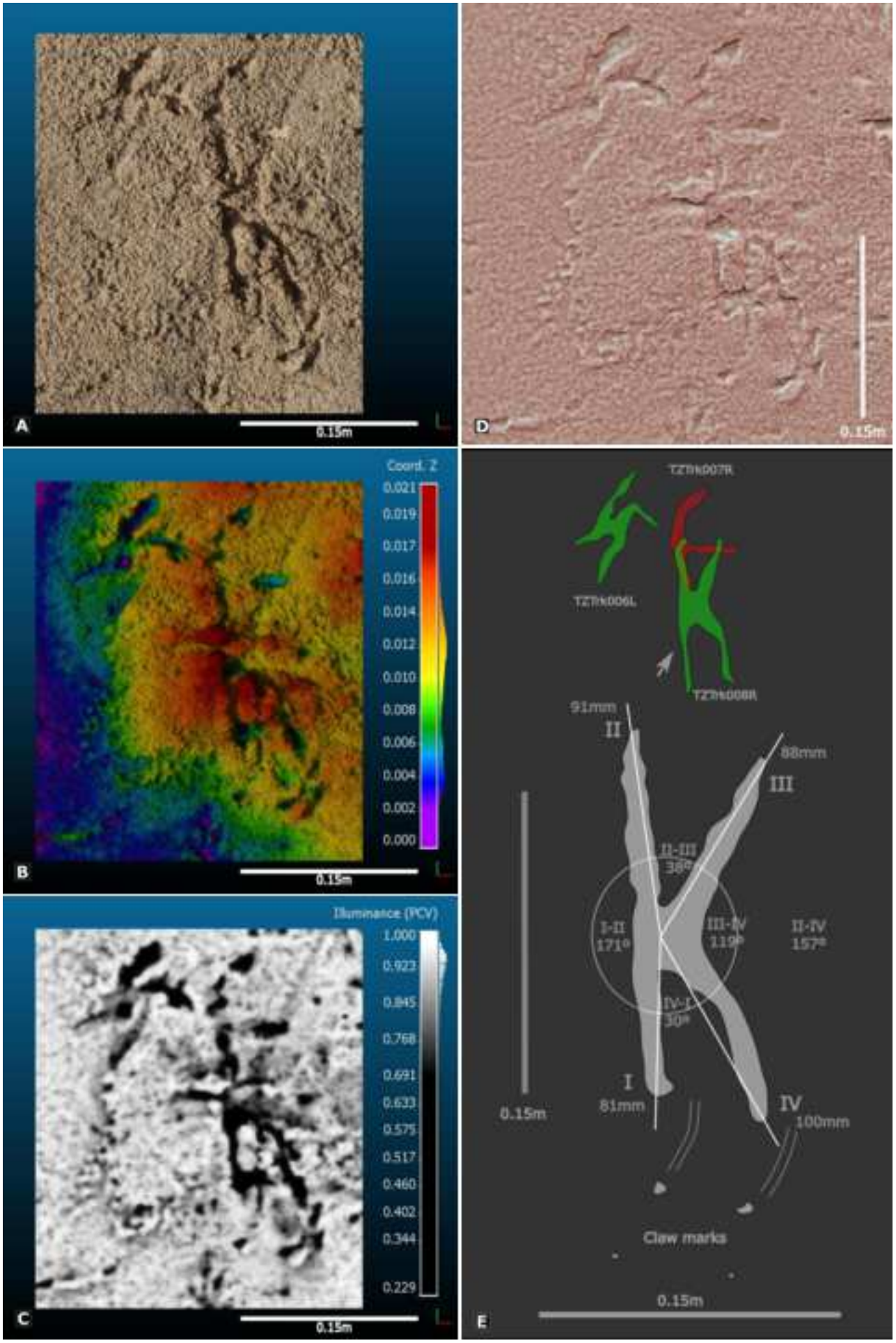

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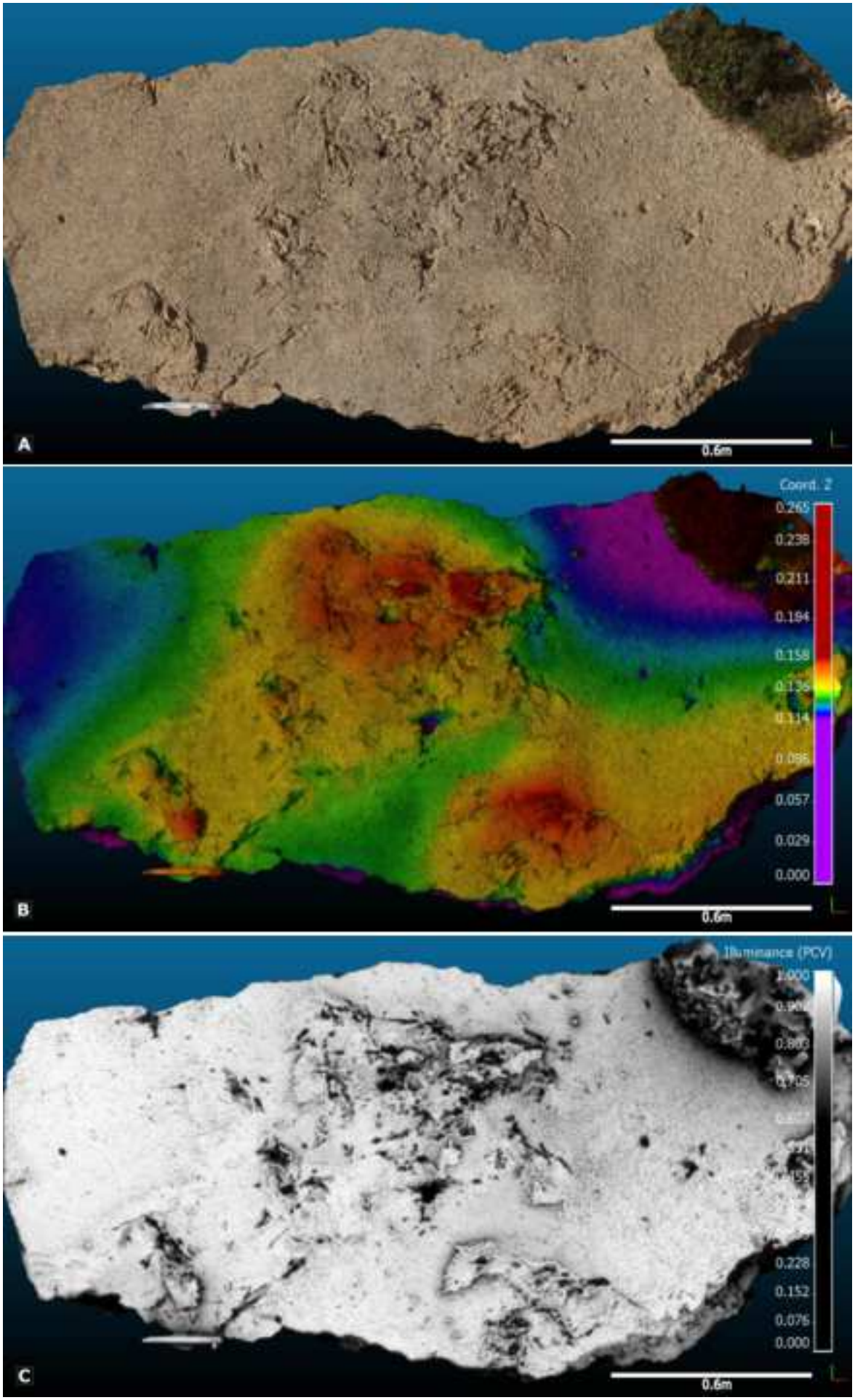

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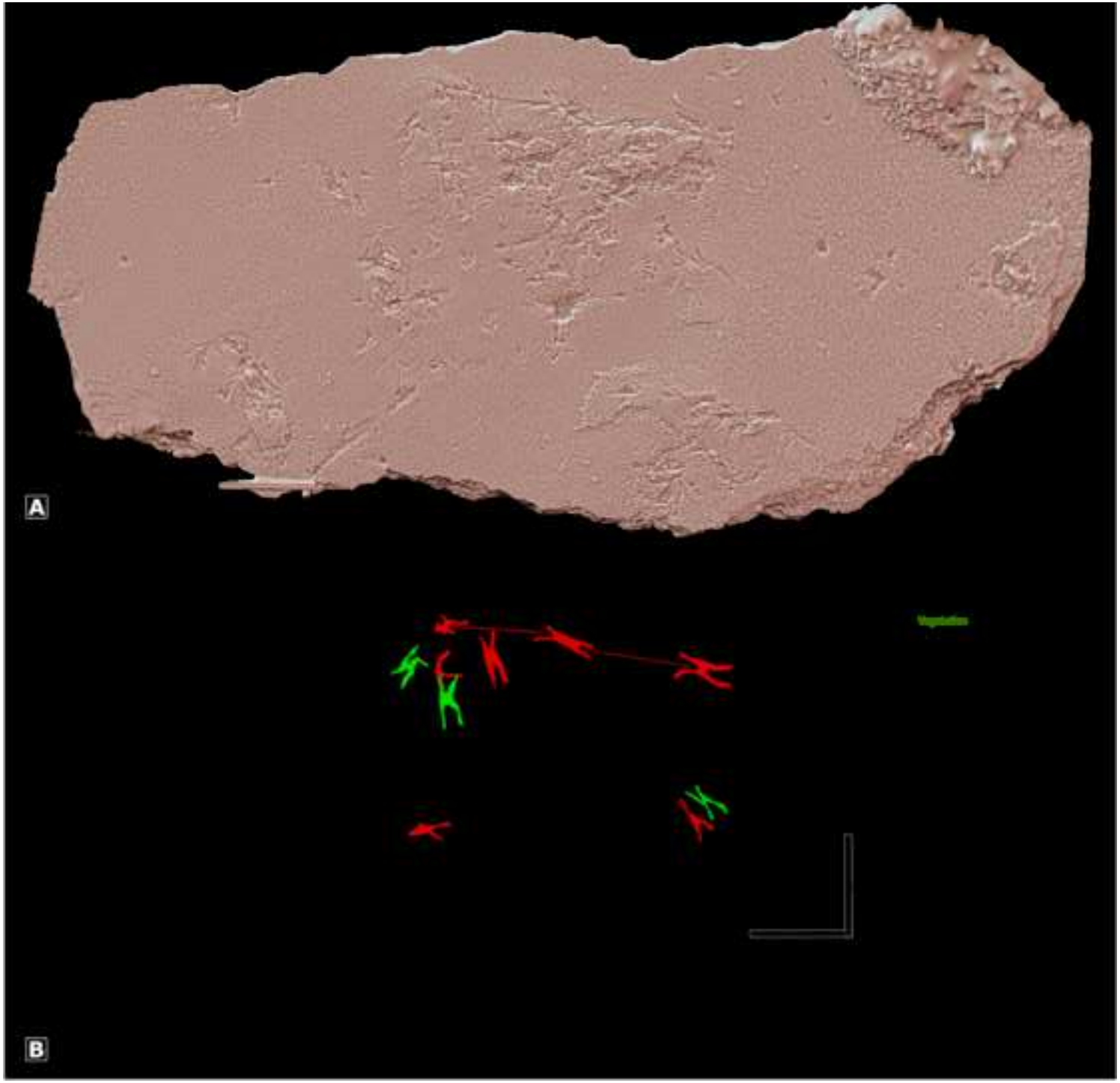

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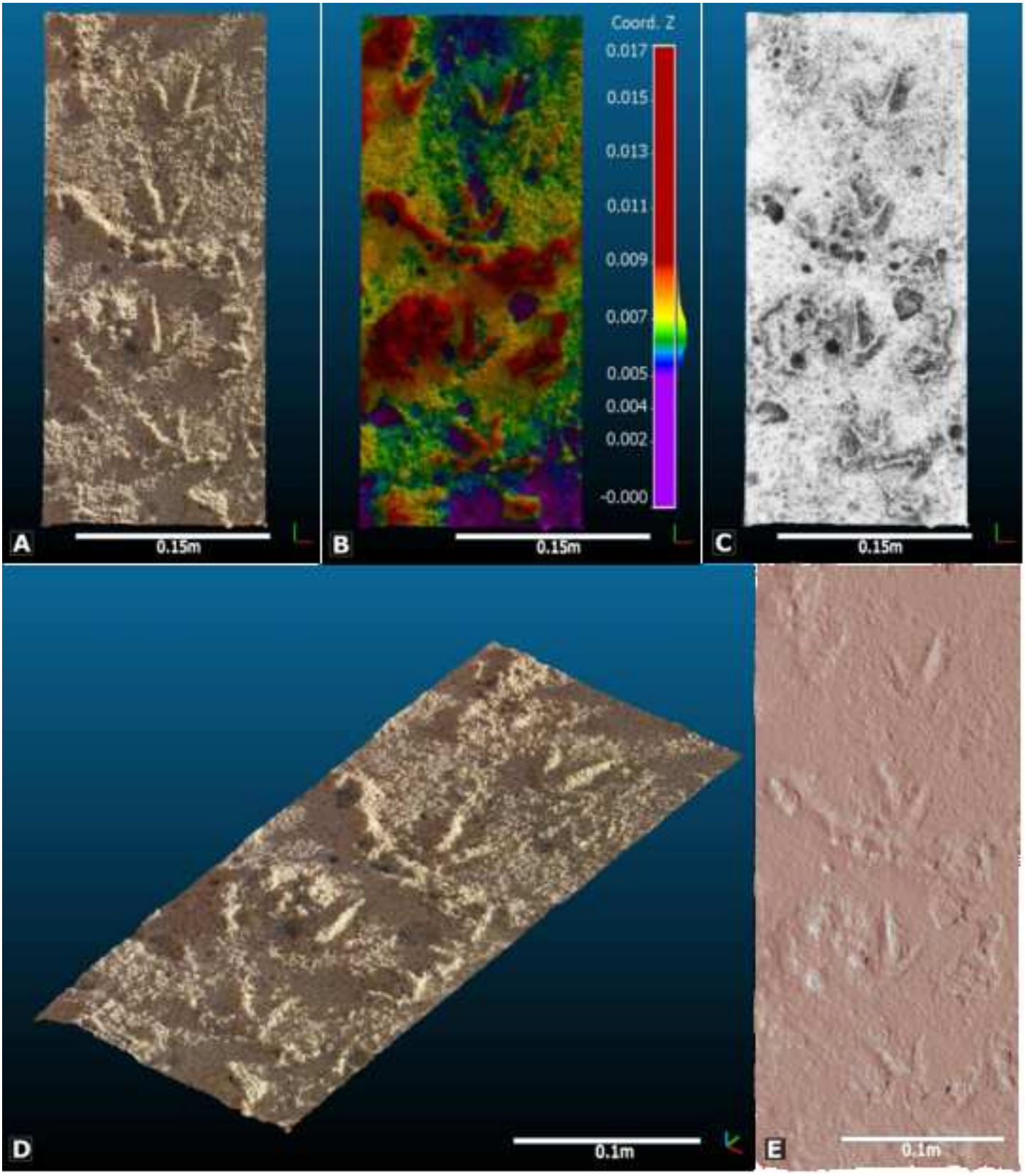

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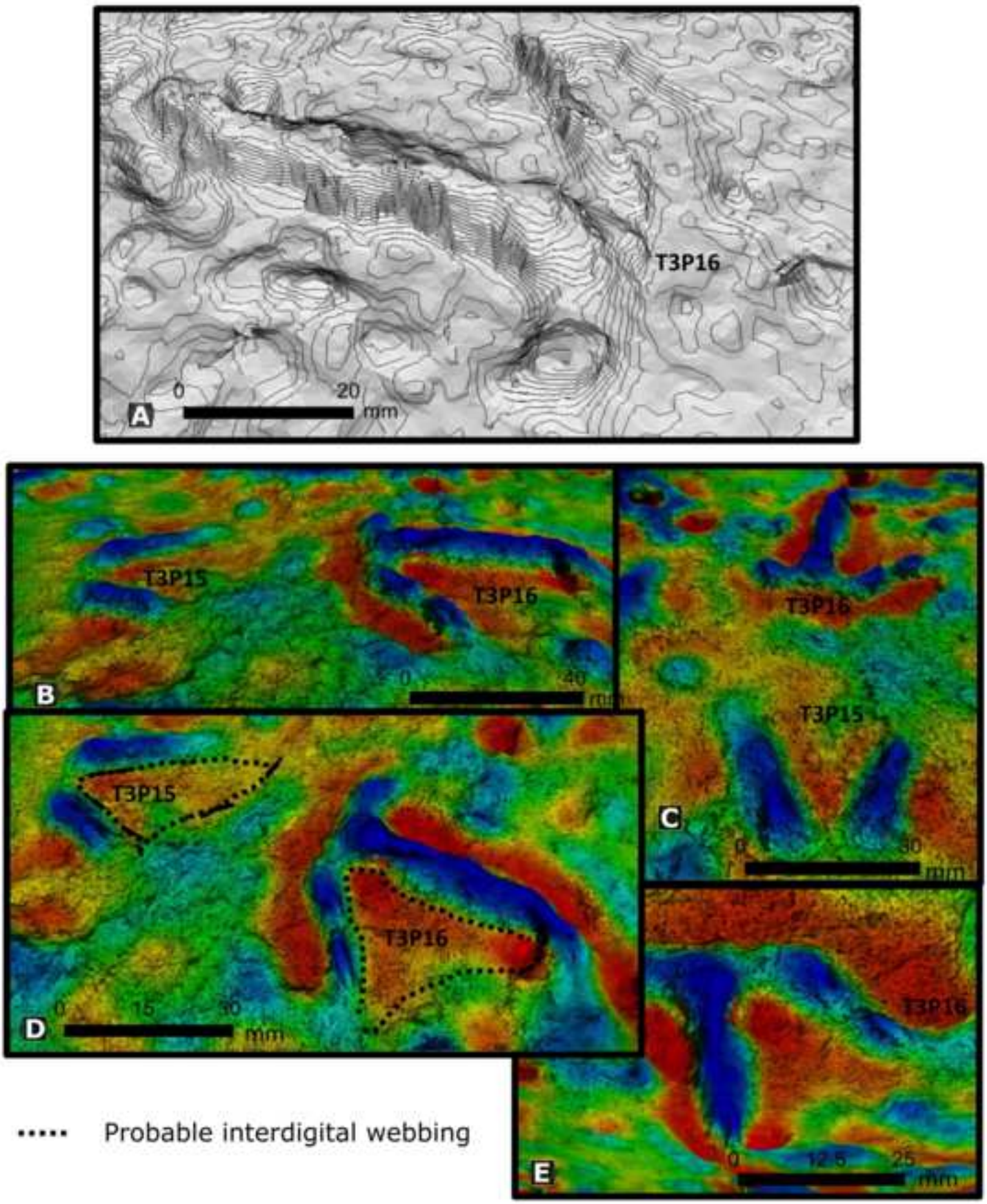

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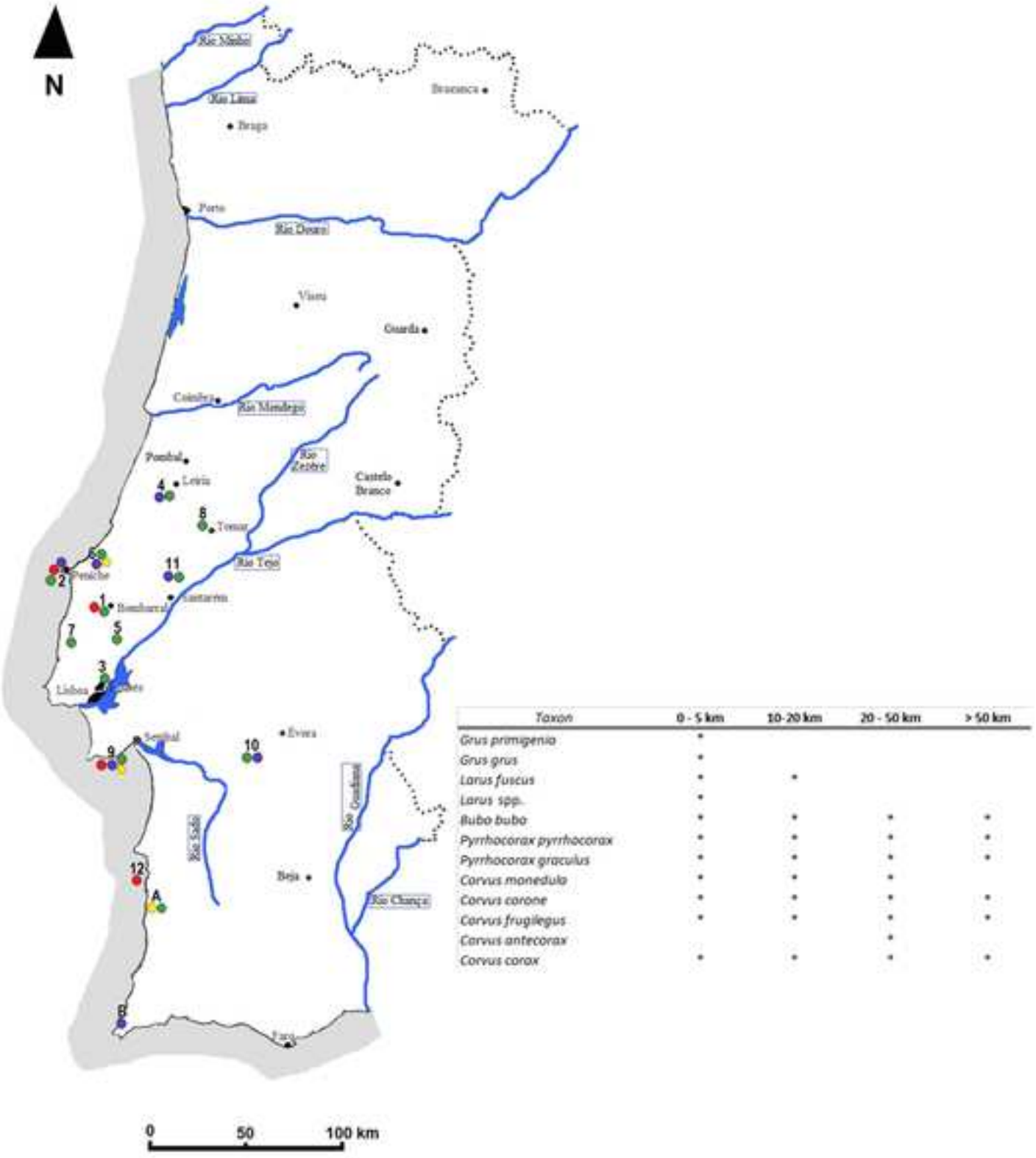

Taxon	0 - 5 km	10-20 km	20 - 50 km	> 50 km
Grus primigenia	•			
Grus grus	•			
Larus fuscus	•	•		
Larus spp.	•			
Bubo bubo	•	•	•	•
Pyrrhocorax pyrrhocorax	•	•	•	•
Pyrrhocorax graculus	•	•	•	•
Corvus monedula	•	•	•	
Corvus corone	•	•	•	•
Corvus frugilegus	•	•	•	•
Corvus antecorax			•	
Corvus corax	•	•	•	•

Declaration of interests

☒ 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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