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Is *Macaronichnus* an exclusively small, horizontal and unbranched structure? *Macaronichnus segregatis degiberti* isubsp. nov.

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ABSTRACT

The new ichnosubspecies *Macaronichnus segregatis degiberti* from Miocene deposits of Cádiz, SW Spain, is described. This ichnotaxa shows the characteristic presence of a mineralogical segregation within the tube, with a core made up of low density material, surrounded by a rim of glauconite. However, significant differences in size, orientation and branching with respect to the type species of *Macaronichnus* are observed. *Macaronichnus segregatis degiberti* is characterized by a diameter between 4 mm and 12 mm, with common obliquely and even vertically oriented galeries, and the presence of frequent branching. Different types of branching can be observed, including false, primary/secondary successive, and true, simultaneous branchings. Specimens occur in a wide range of palaeoenvironmental contexts, from inner to outer sliciclastic shelf. This includes deeper and more distal habitats than those usually interpreted for *Macaronichnus*. *Macaronichnus segregatis degiberti* could be produced by a new tracemaker showing a composite behavior, pascichnia being the main strategy and dominichnia/cubichnia or repichnia, a secondary, sporadic one.

Keywords: Trace fossil, *Macaronichnus*, branching, palaeoecology, ethology, Miocene, SW Spain.

RESUMEN

Se describe la nueva icnosubespecie *Macaronichnus segregatis degiberti* en materiales del Mioceno de Cádiz, SO de España. Este icnotaxón posee la característica segregación mineralógica en el interior de la galería, con la presencia de una parte central compuesta por material de baja densidad, rodeada de un halo de glauconita. Sin embargo, se observan diferencias significativas en tamaño, orientación y ramificación respecto de la especie tipo de *Macaronichnus*. *Macaronichnus segregatis degiberti* se caracteriza por poseer un diámetro entre 4 mm y 12 mm, frecuentes orientaciones oblicuas e incluso verticales, y la presencia de distintos tipos de ramificaciones, incluyendo falsas, sucesivas primarias/secundarias, y verdaderas, simultáneas. Se encuentran en un amplio rango paleoambiental, desde ambientes de plataforma interna proximal hasta plataforma externa, ambientes más profundos y distales que los usualmente interpretados para *Macaronichnus*. *Macaronichnus segregatis degiberti* podría haber sido producido por un nuevo organismo, mostrando un comportamiento compuesto, con una estrategia principal de alimentación y otra secundaria de domicilio/reposo o locomoción.

Palabras clave: Traza fósil, *Macaronichnus*, ramificación, paleoecología, etología, Mioceno, SO España.

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1. INTRODUCTION

Macaronichnus is a long-ranging ichnogenus recorded in fine- to medium-grained sandy marine deposits, mostly in high and intermediate latitudes, from Permian onwards (e.g., Clifton & Thompson, 1978; Nara, 1994; Bromley, 1996; Pemberton *et al*., 2001, 2008; Gingras *et al*., 2002; Uchman & Krenmayr, 2004; Bromley *et al*., 2009; Quiroz *et al*., 2010; Seike *et al*., 2011). It is interpreted as a feeding burrow, a grazing trace (pascichnia), produced by deposit-feeding worms, commonly in foreshore and shallow subtidal deposits (Clifton & Thompson, 1978; Saunders & Pemberton, 1986, 1990; Saunders, 1989; Pemberton *et al*., 2001, 2008). Similar feeding structures produced by the opheliid polychaetes *Ophelia limacina* (Clifton & Thompson, 1978) and several species of the genus *Euzonus* (Pemberton *et al*., 2001; Gingras *et al*., 2002; Nara & Seike, 2004; Seike, 2007, 2008, 2009; Dafoe *et al*., 2008a, b; Seike *et al*., 2011) have been observed in recent marine settings.

Since the original description by Clifton & Thompson (1978) of *Macaronichnus*, the type ichnospecies *Macaronichnus segregatis* has been referred to an intrastratal preferentially horizontal trace, non-branching cylindrical structure, 3-5 mm in diameter. *M. segregatis* is characterized by the presence of a mineralogical segregation within the tube. Thus, the tube shows a core made up of low density material, light-colored felsic sand grains surrounded by a rim of high density material, and dark colored mafic sand grains.

Nonetheless, some morphological, compositional, and distributional variations have been recognized: 1) larger specimens (Curran, 1985; Masuda & Yokokawa, 1988; Nara, 1998; Savrda & Uddin, 2005; Aguirre *et al*., 2010; Seike *et al*., 2011); 2) obliquely and even vertically oriented traces (Pollard *et al*., 1993; Bann & Fielding, 2004; Seike, 2007); 3) branched structures (Curran, 1985; Bann & Fielding, 2004; Aguirre *et al*., 2010); 4) a diverse and complex range of burrow infill, including passive, active and meniscated (Bann & Fielding, 2004); 5) latitudinal distribution, with frequent occurrences in tropical settings; and 6) deeper and comparatively more distal habitats, such as from inner and proximal middle shelf (Aguirre *et al*., 2010), some of them probably underestimated.

The upper Miocene-lower Pliocene deposits cropping out along the Atlantic coast of Cádiz, in the Conil-Cabo Roche area, are largely characterized by the pervasive occurrence of *Macaronichnus segregatis*. Aguirre *et al*. (2010) described a *Macaronichnus* ichnofabric dominated by *M. segregatis* as the most abundant ichnotaxa, followed by *Bichodites monastiriensis*, in the lower Pliocene sediments. These authors described *M. segregatis* as a large, unbranched burrow, and highlighted the presence of branched forms. In this paper, we analyze the morphological variations of *Macaronichnus segregatis* found in this area, a study initiated by Jordi M. de Gibert. Although *Macaronichnus* is pervasively present both in the Miocene and in the Pliocene sediments, we will focus on the upper Miocene deposits. Here, we confirm the presence of large, densely-packed traces of *Macaronichnus*, sometimes oblique and even vertical to the bedding plane, and often branched. Based on all these features, we propose a new ichnosubspecies, and discuss the potential implications for understanding the behavior and the ethological interpretation of the producer, as well as for palaeoecological approaches.

2. GEOLOGICAL SETTING AND STRATIGRAPHY

The study deposits crop out along the coastal cliffs NW of Conil de la Frontera (Cádiz, SW Spain), by the El Roqueo beach (Figs 1a-1b). This area lies at the southwestern margin of the Guadalquivir Basin, the foreland basin of the Betic Cordillera (Sanz de Galdeano & Vera, 1992). The sedimentary infilling of this basin consists of Miocene to Pliocene marine deposits (Aguirre, 1995; Aguirre *et al*., 1995; Sierro *et al*., 1996; Braga *et al*., 2002; Martín *et al*., 2009). The studied deposits are late Tortonian-Messinian (Late Miocene) in age and they are exposed in a continuous succession, dipping ~25º to the southeast, that can be followed for hundreds of meters (Fig. 1b).

The stratigraphic section starts with silts and fine-grained sands with intercalations of medium-grained sandstone beds. Nodular structures due to differential cementation occur in the silts. These deposits are enriched in glauconitic grains. Intervals of large scale trough-cross-bedding are present in this part of the section (Fig. 1c). Occasionally, the foreset beds of the sedimentary structures are slightly deformed. The massive sediments of this interval are pervasively bioturbated, thus disturbing the original sedimentary structures. *Macaronichnus* is the dominant trace fossil, followed by rare *Bichordites*.

In the middle part of the stratigraphic section, beds of marls are intercalated into the silts, thus changing gradually to an interval of massive bluish marls (Fig. 1c). Trace fossils are present in the lower part of this marly interval, where beds densely bioturbated by *Macaronichnus* alternate cyclically with massive, structureless beds.

Higher up in the section, grain size gradually increases, evolving to silts and finally fine-grained sands. Then, some packages of calcarenites, up to 4 m thick, intercalate the silts and sands (Fig. 1c). Calcarenites show trough-cross stratification. The thickness of these carbonate packages

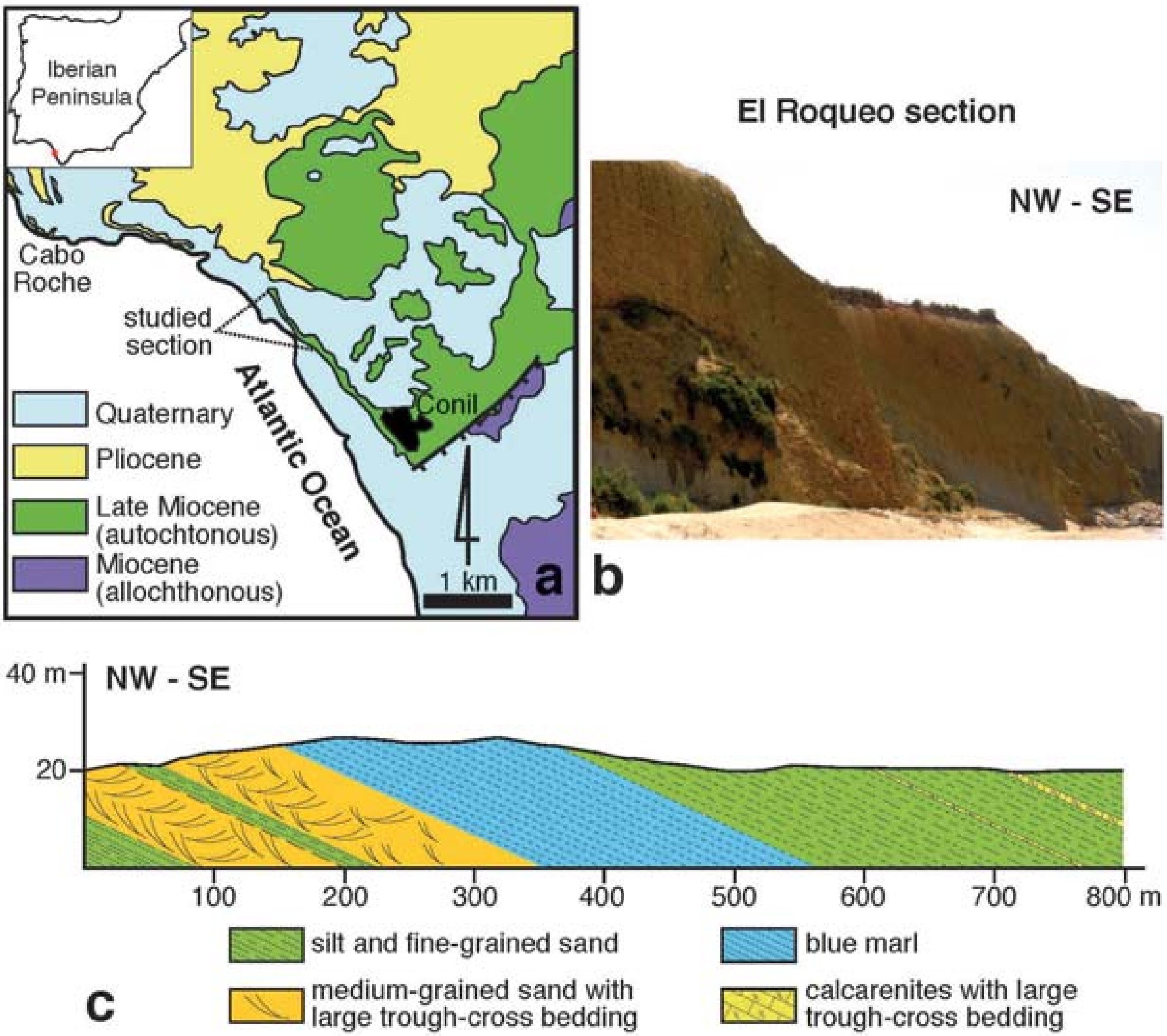

Figure 1. a) Geological map and the studied area. **b)** A panoramic view of the upper Miocene deposits along the El Roqueo beach. **c)** Diagramatic section of the studied deposits along El Roqueo.

increases higher up within the succession, although exposure is very poor.

The upper Miocene sequence ends with calcarenites and calcirudites showing trough-cross-bedding. These sediments are well exposed locally in Conil de la Frontera.

3. *MACARONICHNUS* FROM MIOCENE DEPOSITS OF CÁDIZ, SW SPAIN

3.1. Taxonomic discussion

The presence of a characteristic mantle concentration of glauconite and infilling with clean, non-glauconitic sand, either structureless or faintly backfilled, enables us to clearly assign the trace fossils to *Macaronichnus*. They differ from other morphologically similar non-meniscate ichnogenera, such as *Planolites* and *Palaeophycus*, as well as from meniscate ones, *Muensteria*, *Anchorichnus* and *Scoyenia*, as indicated by Saunders (1989). Differences between *Planolites*, *Palaeophycus* and *Macaronichnus* have been profusely analyzed (Clifton & Thompson, 1978; Pemberton & Frey, 1982; Fillion, 1989; Fillion & Pickerill, 1990; Keighely & Pickerill, 1995). Uchman & Krenmayr (2004) indicated that when heavy minerals are scarce in the sediment, the characteristic segregation observed in *Macaronichnus* is poorly visible, and its separation from *Planolites* may be problematic.

Thus, most of the ichnological features of our specimens agree with those of the standard *Macaronichnus*, including the cylindrical shape, mineral segregation between the tube core and a surrounding rim, or dense distribution. However, several features of the studied *Macaronichnus segregatis*, such as size, orientation and branching, reveal significant differences with respect to the usually assigned forms of this ichnospecies.

3.1.1. Size

Most of *Macaronichnus segregatis* traces are (2)3-5 mm in diameter, which could be considered as the standard dimensions for this taxa. Only occasionally larger specimens, ranging from 5 to 15 mm in diameter, have been reported in Cretaceous (Curran, 1985; Pollard *et al*., 1993), Pliocene (Aguirre *et al*., 2010), and Pleistocene sediments (Masuda & Yokokawa, 1988; Nara, 1998), as well as in Recent settings (Seike *et al*., 2011). Other larger *Macaronichnus*, 4-19 mm, described in Cretaceous sediments (Savrda & Uddin, 2005) should be assigned to *Bichordites* on the basis of shape and internal structure (Seike *et al*., 2011) (see Uchman, 1995 for an emended diagnosis of *Bichordites*). In our study, *Macaronichnus* can be undoubtedly differentiated from the associated *Bichordites monastiriensis* (Aguirre *et al*., 2010). The latter consists of broad structures (4-14 cm wide) and horizontal, meniscate burrows, with a longitudinal median groove (Aguirre *et al*., 2010).

In our case, the size of *M. segregatis* ranges from 4 mm to 12 mm in diameter, with numerous specimens 7-9 mm, and some structures larger than 20 cm long (Figs 2-5). This is clearly within the range of the larger *Macaronichnus*, very different from that of the type ichnospecies.

3.1.2. Orientation

Clifton & Thompson (1978, p. 1293) indicated that *Macaronichnus* traces "*tend to be preferentially oriented about a horizontal plane*". Lately, some authors point out variations of this general pattern. Pollard *et al*. (1993; p. 154) recognized the presence of *Macaronichnus* tubes oblique to bedding in a particular *Ophiomorpha-Macaronichnus* ichnofabric. Uchman & Krenmayr (2004, p. 238; text-fig. 19) stated that these traces are "*mostly horizontal or sub-horizontal*" but show abundant oblique forms in the illustrated examples of crosscutting relations. Bann & Fielding (2004; fig. 16e) and Seike (2007; fig. 4) illustrated variable orientations with frequent oblique and vertical structures. Finally, Pervesler *et al*. (2011; p. 87-89) highlighted that they are "*mostly horizontal and oblique*". In the case study, horizontal forms are dominant, but oblique and vertical specimens are common (Fig. 2).

3.1.3. Branching

Together with the mineralogical segregation between the light-colored sand in the tube core and the dark-colored glauconite-rich sand in the surrounding mantle, the most distinctive feature of the ichnogenus *Macaronichnus* is the absence of real branching. In the original description of *Macaronichnus segregatis*, Clifton & Thompson (1978; p. 1293) stressed, "*the trails interpenetrate but do not branch, tend to be more or less horizontal, and generally occur in dense concentration*s". Subsequently, *Macaronichnus segregatis* has been profusely studied, and some emended diagnoses have been presented. Nevertheless, it has mostly been considered as an unbranched burrow.

Four distinct modes of producing branching in biogenic structures have been described (D'Alessandro & Bromley, 1987; Bromley, 1990, 1996): a) false, as an apparent branching originated by simple intersection and incomplete preservation, b) secondary successive, as a branched structure (false impression, not true) caused by two successive burrowers producing unbranched forms, when a tracemaker enters and follows an earlier, pre-existing burrow, and then deviates from it, c) primary successive, as a branched structure produced by an unbranched burrow through successive probing movements, and d) simultaneous, corresponding to networks where branches were simultaneously open. Of these four different types, the only one held to true branching is the simultaneous sort (Bromley, 1990, 1996).

It is evident that most of the illustrated branched *M. segregatis*, whether Recent or fossil counterparts, show a cross-cutting relationship, thus representing false branching due to intersections of different burrows (i.e., Fürsich, 1984; fig. 3b; Curran, 1985; plate 1B; Uchman & Krenmayr, 2004; text-fig. 7B; Seike, 2007; figs. 3-4; Dafoe *et al*., 2008a, b; fig. 1A; Seike, 2009; fig. 6D; Quiroz *et al*., 2010; figs. 3B, C; Pervesler *et al*., 2011; fig. 2F; Seike *et al*., 2011; fig. 1A; among others). Presence of interpenetrating *Macaronichnus* is especially evident in the ichnospecies *Macaronichnus simplicatus* of Saunders (1989; fig. 27, plate 11; see also fig. 103 in Pemberton *et al*., 2001), and in the ichnosubspecies *Macaronichnus segregatis spiriformis* of Bromley *et al*. (2009). In other instances, however, specimens illustrated show branching structures that could not be definitively assigned to false branching, as in the papers by Curran (1985; plate 1C), MacEachern & Pemberton (1992; fig.7b) and Bann & Fielding (2004; figs. 6e and 7b).

In addition to the figured specimen, there are occasional references in the literature stressing that the observed branchings might not be true ramifications of the trace and could be due to cross-cuttings (e.g., Curran, 1985; Gingras *et al*., 2002; Uchman & Krenmayr, 2004). Curran (1985) indicated that "*burrows tend to be densely packed, and normally are unbranched, but branching can occur*" (p. 263). He illustrated a branching form (Curran, 1985; plate 1C), and differentiated it from common burrow crossovers (Curran, 1985; plate 1B). Bromley (1990, 1996), however, indicated, "*Curran (1985) identified a similar trace fossil as* M. segregatis*, but illustrated a Y-shaped*

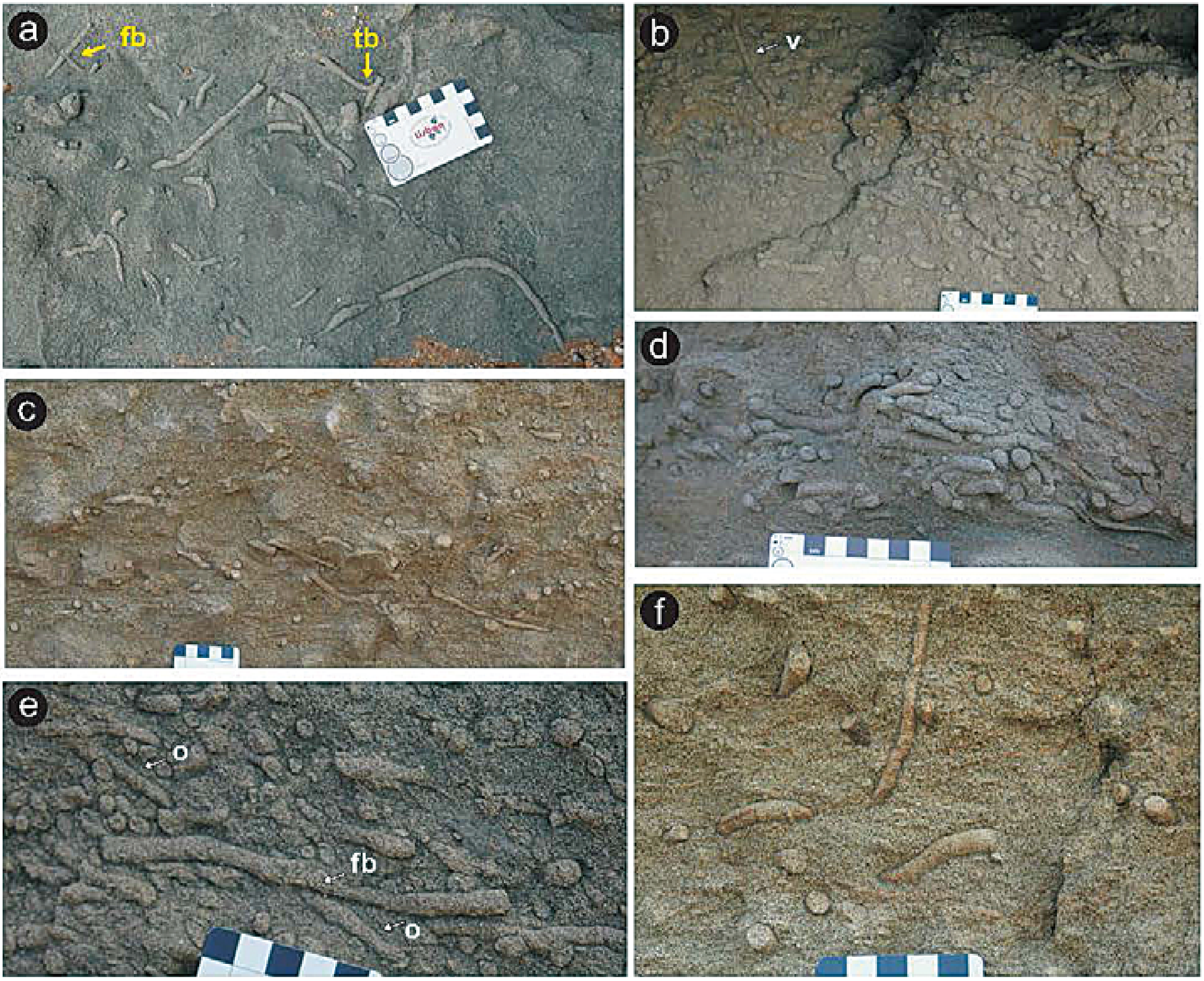

Figure 2. Outcrop views of *Macaronichnus segregatis degiberti* isubsp. nov. Rodríguez-Tovar & Aguirre. **a)** Horizontal section showing straight and sinuous forms, as well as false (fb) and true (tb) branchings (see Fig. 5a for close-up view). **b-f)** Vertical sections. **(b)** *Macaronichnus*-bearing horizon with dominance of horizontal burrows and a nearly vertical (v) form, **(c)** dispersed *Macaronichnus* showing large horizontal forms**, (d)** high concentration of *Macaronichnus* showing intersections of burrows, **(e)** concentration of *Macaronichnus* with obliquely (o) oriented forms and false branching (fb), and **(f)** disperse *Macaronichnus* with vertical specimens. Note scale in centimeters to evidence large diameters of burrows.

simultaneous branching point. Thus, this structure cannot be considered trophically or ichnotaxonomically equivalent to M. segregatis. *In vertical section, and therefore in core, however, these structures would be indistinguishable. Branching is vitally important, but is not easy to see in vertical section*" (Bromley, 1990; p. 179; Bromley, 1996; p. 204). In turn, Gingras *et al*. (2002), working on magnetic resonance images of recent *Macaronichnus segregatis*, indicated, "*as noted from the hand sample, branching is not present. An exception to this may be imaged in Figure 3E, but the apparent branch there could also be explained as a composite of two out-of-plane burrows, which is expected inasmuch as each image slice represents a section of the medium approximately 0.5 mm thick. Plan-view images demonstrate more clearly the sinuous nature of the burrows (Fig. 4D, E; white arrows)*" (Gingras *et al*., 2002; p. 553). Finally, Uchman & Krenmayr (2004), studying monotypic ichnofabric formed by *Macaronichnus*, indicated that "*the cross cuttings of* Macaronichnus *can give the impression of branches, but they are false branches sensu D'Alessandro & Bromley (1987)*" (Uchman & Krenmayr, 2004; p. 245).

In our study, several types of branching were differentiated:

a) False branching is dominant, showing interpenetrating burrows in variable orientations, from perpendicular to near tangential (Fig. 3).

b) Differentiation between secondary successive, primary successive and simultaneous is no easy matter, especially when the direction of the movement cannot be approached due to the absence of meniscus orientation. In secondary successive branching, the organism reworks the backfill of the pre-existing burrow and, in many cases, the movement is opposite in the two burrows. When movements are concordant, however, it is difficult to distinguish this style from the primary successive (D'Alessandro & Bromley, 1987). Primary successive shows a characteristic backfilling, and in the simultaneous branching, the true branching, the fill must be emplaced by different means and a characteristic meniscus orientation cannot be defined (D'Alessandro & Bromley, 1987; Bromley, 1990, 1996). In the studied *Macaronichnus*, the absence of meniscate structures excludes the use of this feature for distinguishing among the different branching patterns. Therefore, other features must be considered. Apart from the meniscus orientation, both secondary successive and primary successive styles show a clear differentiation between the burrow walls corresponding to the two different burrows in the case of the secondary successive style, or to the burrows corresponding to the several probes originated by the same animal in the case of the primary successive style. In the study case, different burrow walls in a unique structure have been occasionally recognized, proving the existence of primary and/or secondary branching. The absence of meniscus precludes any definitive differentiation between the two types; yet the presence of only one branch, not several probes, could be indicative of secondary successive branching (Fig. 4).

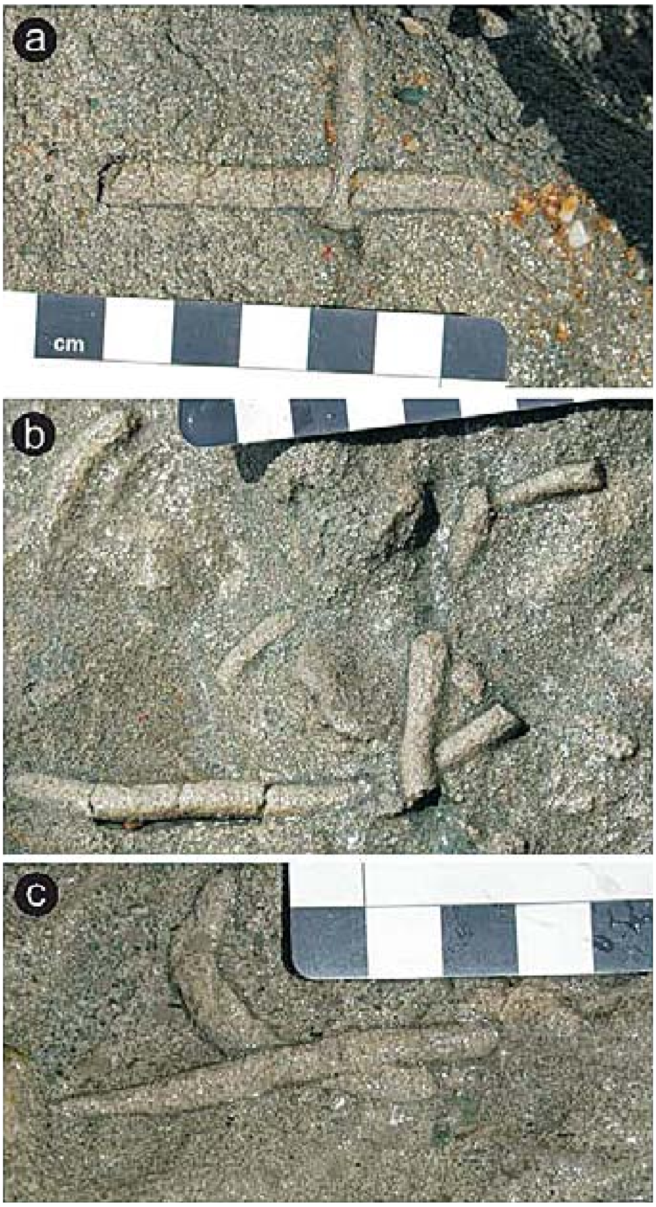

Figure 3. False branching of *Macaronichnus segregatis degiberti* isubsp. nov. Rodríguez-Tovar & Aguirre, with examples of perpendicular **(a)**, oblique **(b)** and near tangential **(c)** intersections. Note green halo to evidence the cross-cutting relationships. Scale is in centimeters to evidence large diameters of burrows.

c) Apart from the aforementioned types of branching, in several cases the observed branched forms do not display different burrow mantles associated to primary or secondary branching, but rather a clear continuity in the burrow infill in the entire structure (from the main burrow to the branch) (Fig. 5). A single branch is usually recognized in the branching structure, but occasionally several small branches have been observed in the same structure (Figs 5d-5f). In these cases two possibilities could be considered: i) a true, simultaneous branching, and ii) a secondary successive branching without burrow mantle in the intersection of the corresponding two different burrows. In this second possibility, the worm ingests in a pre-existing *Macaronichnus* burrow in which the infilling material have not mafic grains because they constitute the mantle of the previous burrow (Seike, per. com.). Thus, dark colored mantle is not produced at the intersection of the two burrows. The use of a pre-existing *Macaronichnus* burrow would reflect; either a re-exploitation by the tracemaker for food of the infilling material (pascichnia behavior) in a material previously ingested and then with lower organic matter content, that appears profitableness, or a locomotion trace. This latter alternative involves a change of the tracemaker behavior from pascichnia to repichnia.

Figure 4. Secondary successive branching in *Macaronichnus segregatis degiberti* isubsp. nov. Rodríguez-Tovar & Aguirre. Note variability in the angle of branching, and differentiation (cross-cutting relationships) of burrow walls with the characteristic mantle concentration of green glauconite (white arrows).

4. *MACARONICHNUS SEGREGATIS DEGIBERTI* ISUBSP. NOV.

Since the original designation of *Macaronichnus segregatis* by Clifton & Thompson (1978), the ichnotaxonomical subdivision of *Macaronichnus* has scarcely been approached. Several emendations and new diagnoses have been proposed (Saunders, 1989; Saunders & Pemberton, 1990; Bromley *et al*., 2009). Moreover, ichnotaxonomical descriptions have been confusing in some cases. Thus, for example, Saunders (1989; fig. 27) figured an exemplar of *Macaronichnus simplicatus* that was later referred to as *Planolites* sp. in fig. 1 by Saunders & Pemberton (1990; text-fig. 13), and finally illustrated again as *Macaronichnus simplicatus* by Pemberton *et al*. (2001; fig. 103).

In his M.Sc. thesis, Saunders (1989) revised the ichnogenus *Macaronichnus*, and included an emended diagnosis, recognizing three distinct forms of *Macaronichnus* based on the foraging pathway configurations (fig. 27 in Saunders, 1989; see also fig. 103 in Pemberton *et al*., 2001). He distinguished two ichnospecies, *Macaronichnus segregatis*, with two varieties or ichnosubspecies named *M. segregatis segregatis* and *M. segregatis spiralis*, and *M. simplicatus*. *M. segregatis segregatis* is characterized by random burrows but with no interpenetration structures. *M. segregatis spiralis* shows distinct planispiral arrangement configurations. Finally, the ichnospecies *Macaronichnus simplicatus* is characterized by random interpenetrating burrows. This subdivision has been subsequently used by several authors (e.g., Pemberton, 1992; Pemberton *et al*., 2001; Bann & Fielding, 2004; Bann *et al*., 2004; Gordon *et al*., 2010).

In a new reassessment of the ichnogenus *Macaronichnus*, Saunders & Pemberton (1990) changed the status of the two ichnosubspecies described by Saunders (1989) to species level. Thus, they proposed the ichnospecies *M. segregatis*, which corresponds with the definition of *M. segregatis segregatis* of Saunders (1989), and the new ichnoespecies *M. spiralis*, corresponding to the ichnosubspecies variety of *M. segregatis spiralis* in Saunders (1989). However, no reference to this change in the taxonomical assignation is presented by Saunders & Pemberton (1990).

Bromley *et al*. (2009) made another detailed revision of *Macaronichnus*, providing a new diagnosis for the type ichnospecies *M. segregatis*, and described three new ichnosubspecies, *M. segregatis lineiformis*, *M. segregatis spiriformis* and *M. segregatis maeadriformis*. These three new ichnotaxa are described at ichnosubspecies rank on the basis of the different degrees of spirality and meandering. These morphotypes of *M. segregatis* probably represent foraging optimization under different regimes of porewater movement, even other hypothesis has been proposed; Seike (2008) interpreted that the tracemaker also modified behavioral patterns in response to the beach topographical changes due to wave conditions. With the designation of

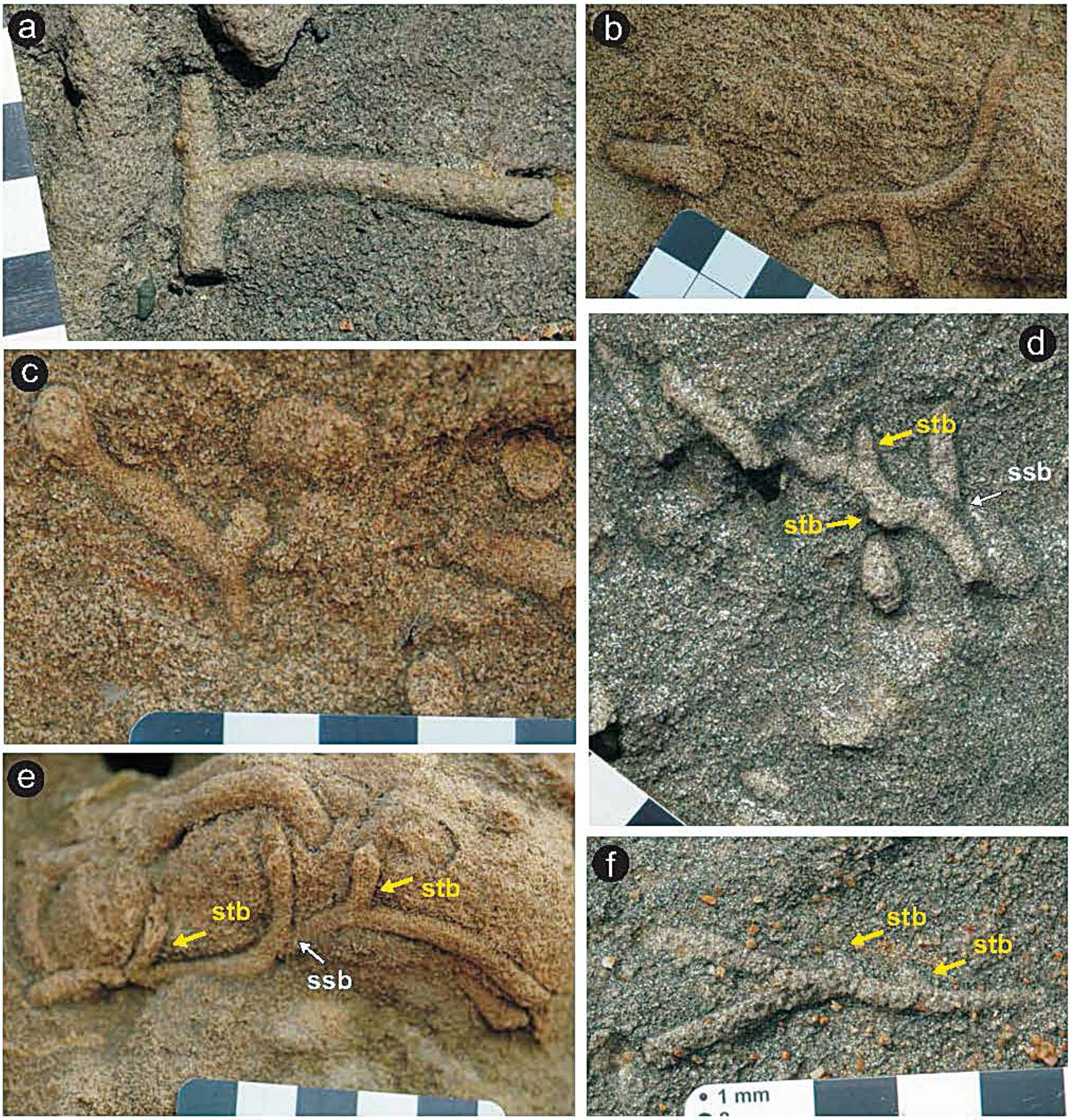

Figure 5. True branching in *Macaronichnus segregatis degiberti* isubsp. nov. Rodríguez-Tovar & Aguirre. **a, b, c)** Specimens showing variability in the angle of true branching or of secondary successive branching without mantle differentiation, and in the length of branches. Note the absence of differentiation of burrow mantle, and the characteristic mantle concentration of branching. **d, e, f)** Specimens showing secondary successive branching (ssb, white arrows) and small true branches (stb, yellow arrows) in the same structure.

these three new ichnosubspecies, Bromley *et al*. (2009) considered the originally described *M. segregatis* by Clifton & Thompson (1978) as another ichnosubspecies, *M. segregatis segregatis*. Bromley and coauthors considered that the three morphological varieties represent different ichnosubspecies, because they share the core-and-mantle organization that characterizes *M. segregatis*. In addition, Bromley *et al*. (2009, p. 117) stated that the ichnospecies *Macaronichnus spiralis* distinguished by Saunders & Pemberton (1986) (see Saunders & Pemberton, 1990; fig. 1, and MacEachern & Pemberton, 1992; fig. 6D) must be considered a *nomen nudum* because it was described in field guidebooks that cannot be recognized as publications according with the ICZN (1999), and thus the name remains informal.

Seike *et al*. (2011) emphasized the importance of the size of *Macaronichnus* (small and large burrows) for reconstructing detailed palaeoenvironments. However, they did not distinguish any new taxa for the large present-day *Macaronichnus* isp. produced by *Travisia japonica*, because according to Bertling *et al*. (2006) the size of the traces is not a valid characteristic in ichnotaxonomy.

Clifton & Thompson (1978; p. 1295), when describing the trace fossil *Macaronichnus segregatis* n. ichnogen., n. ichnosp., indicated that the "generic term *Macaronichnus* is from the Italian "maccaroni" and refers to the size and shape. The trivial term *segregatis*, from the Latin "segregare", refers to the fact that "the trail is defined by mineralogic segregation within the host sand". Accordingly, we consider that the morphological differences in the studied *Macaronichnus* —the large size, the diverse orientation, and the conspicuous branching pattern— could be significant for the definition of a new species of *Macaronichnus*. Nonetheless, taking into account that mineralogic segregation is recognized as a major feature of the type ichnospecies, we consider the designation of a new ichnosubspecies within *Macaronichnus segregatis*.

Macaronichnus segregatis degiberti isubsp. nov.
Rodríguez-Tovar & Aguirre
(Figs 2-4)

Diagnosis. Large *Macaronichnus segregatis* (4-12 mm in diameter) with occasional true branching and locally showing obliquely to vertically oriented galeries with respect to bedding.

Deriviation of name. In honor of Jordi Maria de Gibert, 2012, a well-known and widely reputed Spanish palaeoichnologist who first dealt with the problem of branching in *Macaronichnus* from the studied area.

Description. *Macaronichnus segregatis degiberti* is characterized by a larger diameter (4-12 mm in diameter, with common structures in the range of 7-9 mm, and occasionally longer than 20 cm) than the standard *Macaronichnus segregatis* (3-5 mm in diameter). True branching is often observed. This ichnosubspecies is mostly horizontally arranged, with the tubes parallel to bedding. However, obliquely and vertically oriented traces can be sometimes recognized.

Syntypes. Since *Macaronichnus segregatis degiberti* isubsp. nov. Rodríguez-Tovar & Aguirre consists of specimens with variable distinctive features, such as different size, and horizontal to vertical, unbranched and branched forms, we cannot differentiate a single specimen (holotype) as the name-bearing type. All the characteristic features for identifying the ichnotaxon are observable in the type locality; that is, the upper Miocene deposits cropping out along the sea cliffs of El Roqueo, NW of Conil de la Frontera (Fig. 1). According to the ICZN 1999 (Art.73.2), we consider as the most appropriate strategy to define *Macaronichnus segregatis degiberti* isubsp. nov. Rodríguez-Tovar & Aguirre would be the use of syntypes in reference to all specimens of the type series that collectively constitute the name-bearing type. Selected syntypes are housed at the Department of Stratigraphy and Palaeontology, University of Granada, Spain, under the general label ROQ.

Type horizon and locality. Miocene deposits cropping out along the cliffs between Conil and the Cabo Roche area, along the Atlantic coast of Cádiz (Fig. 1).

Discussion. The presence of the characteristic halo and the difference between the filling material and the host sediment support assignment to *Macaronichnus segregatis* in view of other morphologically similar meniscate and non-meniscate structures. Larger size, common oblique and even vertical orientation, and presence of true branching, not discarding a secondary successive branching without dark mantle in the intersection of the corresponding two different burrows, allow for differentiation from the standard *Macaronichnus segregatis*.

5. PALAEOBIOLOGICAL AND PALAEOECOLOGICAL IMPLICATIONS

The palaeoecological and paleoenvironmental significance of *Macaronichnus segregatis* may be an indicator of ancient sea level, shoreline orientation, and beach morphodynamics (Nara, 1998; Nara & Seike, 2004; Seike, 2007, 2008, 2009, and references therein). Nonetheless, Bromley *et al*. (2009) underline that the literature dealing with the environmental range of *Macaronichnus* is confusing.

Quiroz *et al*. (2010) have recently suggested that this trace fossil is typically associated with upwelling conditions in tropical settings that causes strong seasonality of cold waters and replenishes the surface waters with nutrients. The ichnospecies and ichnosubspecies of *Macaronichnus* proposed by Saunders (1989) —*Macaronichnus simplicatus*, *M. segregatis segregatis* and *M. segregatis spiralis*— were interpreted to be related to increasing foraging optimizations (fig. 27 in Saunders, 1989). The three ichnosubspecies of Bromley *et al*. (2009) —*M. segregatis lineiformis*, *M. segregatis meandriformis*, and *M. segregatis spiriformis*— were contrastively interpreted to be linked to different pore-water flow related to seasonal (winter and summer) conditions (fig. 15 in Bromley *et al*., 2009).

Furthermore, based on the distribution of the modern *Euzonus* worm (a possible producer of *Macaronichnus* trace fossils), two aspects have been addressed: a) the variation of burrowing behavior of the tracemaker in response to the magnitude of beach topographical changes due to wave conditions (Seike, 2008), and b) the relationship between the vertical thickness of *Macaronichnus segregatis*-bearing beds and the ancient beach morphodynamics; a greater bed thickness being associated with decreasing beach-face gradient (Seike, 2009).

As indicated by Seike *et al*. (2011), the differentiation of large *Macaronichnus* has significant palaeoenvironmental implications. According to the distribution of the different producers (*Ophelia limacina*, *Euzonus* spp, and *Travisia* spp) recognized in modern settings, ecological and depositional differences can be envisaged. Thus, the standard (small) *M. segregatis* is commonly related to high energy environments in foreshore and shallow subtidal settings, while large *Macaronichnus* could be associated with a wider range of depositional environments and bathymetry, including tidal flats, upper-lower shoreface, continental shelf, and possibly even deep-sea floor (Seike *et al*., 2011).

In the context of our study, significant differences can be surmised in the palaeoenvironment with respect to that usually interpreted for *Macaronichnus*. As occurs for the *Macaronichnus* assemblages previously described in Pliocene deposits (Aguirre *et al*., 2010), the studied succession represents middle to outer shelf environments. Hence the habitat of *Macaronichnus* tracemaker must be extended to deeper and comparatively more distal areas than those usually proposed for this trace. Two possible interpretations are proposed: a) a different distribution of the producers of *Macaronichnus* (*Ophelia limacina*, *Euzonus* spp, and *Travisia* spp) during Pliocene and Miocene times; and b) different *Macaronichnus* tracemakers than those proposed, adapted to the ecological and depositional conditions typical of deeper and more distal environments.

In short, *Macaronichnus* represents the activity of deposit-feeder worms in well-oxygenated sediments, at a depth usually below 20 cm from the water-sediment interface, allowing a deep-tier position (Saunders & Pemberton, 1986; Pemberton *et al*., 2001; Bann and Fielding, 2004; Bromley *et al*., 2009).

An important unresolved question resides in the presence of true branching in structures associated with pascichnia behavior. As indicated by Bromley (1996; p. 202), "*repichnia and pascichnia cannot truly be branched*". Nevertheless, it has indeed been recognized on occasion, as in the well-known *Planolites*, interpreted as pascichnion and referred to polyphyletic vermiform deposit-feeders producing active backfilling, which is rarely branched (Pemberton & Frey, 1982; Fillion & Pickerill, 1990; Uchman, 1995; Stanley & Pickerill, 1998). A possible interpretation is that these short branches represent semi-permanent domiciles (domichnia behavior) or even resting traces (cubichnia) during continuous feeding locomotion. In this event, the presence of small true branches (Figs 5d-5f) in *Macaronichnus segregatis degiberti* could reveal a composite behavior, pascichnia being the main strategy, together with dominichnia/cubichnia as a secondary, sporadic one. Accordingly, any of the traditionally assigned producers of short and large *Macaronichnus* must be discarded, and a new tracemaker, with a new behavior, must be considered. As indicated above, Bann & Fielding (2004) observed structures assigned to *Macaronichnus* isp. with branches and containing a diverse and complex range of burrow infill. The authors interpreted these features as representing different components of the same biogenic structure. For these authors, those parts of the burrow passively infilled appear to have been lined and then remained open, while the ones actively filled represent backfilled or waste-stuffed chambers. This interpretation is significantly different from the traditional proposals, and, as we propose, supports a complex and variable behavior of the tracemakers. In case that these branches were considered as secondary successive branching without dark mantle, the re-exploitation for food of a previously ingested material could be interpreted as revealing a change of the behavior tracemaker from pacichnia to a probably repichnia.

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