HELICAL CRUSTACEAN BURROWS: *GYROLITHES* ICHNOFABRICS FROM THE PLIOCENE OF LEPE (HUELVA, SW SPAIN)

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ABSTRACT

Two ichnofabrics characterized by abundant vertical and helical burrows (ichnogenus *Gyrolithes*) are described from the Pliocene siliciclastic facies of the southwestern sector of the Guadalquivir Basin (Lepe, Huelva, SW Spain). These ichnofabrics, associated with shallow and marginal marine environments, characterize two consecutive and concordant stratigraphic units: (1) the lower one is dominated by *G. nodosus* (together with other pellet-lined ichnotaxa), occurs in fine- to medium-grained, massive sands and silty sands, and is characterized by moderate to high bioturbation; (2) the upper ichnofabric is dominated by *G. variabilis* (and other unlined ichnofossils), occurs in sandy silts, and is

characterized by low to high bioturbation. The transition of these two ichnofabrics clearly reflects the ability of an infaunal community to assimilate environmental changes over time. Additionally, new observations at the type locality of *G. nodosus*, the description of a new locality for *G. variabilis* and review of existing literature on this ichnogenus have provided the bases for emending the diagnoses of both ichnospecies, to propose a neotype for *G. nodosus* and to suggest a new type locality for *G. variabilis*. According to the main architectural features of *Gyrolithes* specimens studied herein and by comparison with modern analogues, 'thalassinidean' shrimps are proposed as their most likely tracemakers. Although it is known that these kinds of crustaceans exhibit a great variability in regards to their burrowing behaviors, further study is needed in order to more fully understand the purpose of these helical bioturbation structures.

INTRODUCTION

Several ichnotaxa are characterized by a spiral or helical morphology. Buatois et al. (2017) differentiated between five categories of architectural design, namely: (1) horizontal spiral burrows; (2) burrows with helicoidal spreiten; (3) vertical helicoidal burrows; (4) spiral graphoglyptids; and (5) spiral borings, comprising spiral to helical morphologies. Among the total of thirteen ichnogenera included within these five categories (Buatois et al. 2017), only *Gyrolithes* and *Lapispira* correspond to bioturbation structures that have been confidently attributed to the burrowing activity of decapod crustaceans (e.g., Wetzel et al. 2010; Gibert et al. 2012 and references therein). Several architectural features (e.g., bioglyphs, pelleted linings, etc., see below) may be representative and/or indicative of decapod burrowing behavior. Nevertheless, the vertical disposition of such helical/spiral burrows is a crustacean fingerprint, at least

since the Permian and particularly since the Mesozoic Marine Revolution (Carmona et al. 2004; Buatois et al. 2016; Laing et al. 2018).

Mesozoic and Cenozoic ichnofabrics consisting of and/or dominated by *Gyrolithes* or *Lapispira* are not uncommon in the fossil record. Macsotay (1967) described the transition from an *Ophiomorpha* ichnofabric to a *Gyrolithes* ichnofabric in the Upper Miocene of La Vela Formation (Venezuela). Christiansen and Curran (1995) documented an ichnofabric dominated by *Gyrolithes* from the Miocene St. Mary's Formation of Maryland (USA). Netto and Rossetti (2003) documented the existence of a monospecific ichnofabric of *Gyrolithes* from the Lower Miocene of São Luís Basin (Lower Barreiras Formation, Maranhão, Brazil). Lanés et al. (2007) described an ichnofabric with abundant *Lapispira* from the Lower Jurassic deposits in the Atuel Valley area of the Neuquén Basin (Mendoza, Argentina). Gibert et al. (2012) described an *Ophiomorpha* ichnofabric with common *Lapispira* and rare *Gyrolithes*, both with a pelleted (*nodosus*-like) lining. Desai (2013) recorded the presence of a *Gyrolithes*-*Rhizocorallium* ichnofabric from the Lower Cretaceous of the Ukra Hill Member (Kachchh, India). Belaústegui et al. (2015) described *Gyrolithes* cf. *nodosus* as minor component of an *Ophiomorpha nodosa* ichnofabric from the Middle Miocene of El Camp de Tarragona Basin (NE Spain).

In the present paper, two ichnofabrics characterized by abundant specimens of *Gyrolithes nodosus* or *G. variabilis* from the Pliocene of Lepe (Huelva, SW Spain) are described. One of these ichnofabrics was briefly described previously by Gibert et al. (2001). New observations from the current study have implications for ichnotaxonomy and for the sedimentological, paleoethological and paleoenvironmental significance of these trace fossils. In particular, the transition between these two ichnofabrics reflects

how an infaunal community is able to modify and/or adapt its burrowing behavior to new substrate conditions.

GEOLOGIC AND STRATIGRAPHIC SETTING

The studied ichnofabrics are found in two neighboring areas (Arroyo Valleforero and La Redondela outcrops) situated along the coast of the Huelva province, southwestern Iberian Peninsula. Both outcrops, located in the surroundings of the towns of Lepe and La Redondela, respectively, are part of the Pliocene fill of the western sector of the Guadalquivir Basin (Fig. 1A). This Neogene foreland basin is limited to the south by the External Zone of the Betic Ranges and to the north by the Paleozoic basement of the Iberian Massif (Fig. 1A).

The origin of the Guadalquivir Basin is linked to the collision of the African and Iberian plates during the Neogene, which caused asymmetrical uplift of sediments filling the basin; the easternmost part (currently exposed) was elevated more than the western part (Sanz de Galdeano 1990; Braga et al. 2003). During the Miocene and Pliocene, the northern passive margin and the center of the basin were filled with autochthonous and parautochthonous terrigenous and biogenic deposits. In contrast, the active southern and southeastern margins were filled with allochthonous materials of the olistostrome structural unit (Riaza and Martínez del Olmo 1996; Sierro et al. 1996).

In the Lepe area (Fig. 1B), the Neogene is represented by an array of marginal marine siliciclastic facies (mainly mud, silt, sand and gravel deposits) informally known as the ‘Lepe White Silts’ (Muñiz 1998; Muñiz et al. 2010). The Lepe White Silts (units 1-9 in Fig. 1C) unconformably lie upon Lower Carboniferous greywackes and shales and are erosively topped by Lower Pleistocene sands, gravels and conglomerates interpreted as fluvial terraces (Cáceres 1999). Within these Neogene facies, Muñiz

100 (1998) distinguished between an Upper Miocene interval (units 1 to 5) and a Pliocene
101 interval (units 6 to 9), bounded by an erosive surface. The Pliocene interval corresponds
102 to the so-called 'Arroyo Valleforero' section (Muñiz et al 2010; Belaústegui and Muñiz
103 2016). The ichnofabrics described herein (Figs. 2–8) occur in units 7 (only at Arroyo
104 Valleforero outcrop) and 8 (at Arroyo Valleforero and La Redondela outcrops) of the
105 Pliocene interval (Fig. 1B, C).

106 Unit 6, consisting of medium- to coarse-grained sands and reddish gravels and
107 conglomerates, erosively overlie unit 5 (top of the Miocene interval, not described
108 herein). Lenticular bodies of white clay occur intercalated within coarser-grained facies.
109 This unit has a variable thickness between 2 and 6 m and exhibits common scoured
110 erosive surfaces and cross-bedding. Coarse-grained facies (gravels and conglomerates)
111 include fossils of marine bivalves and gastropods and cetacean remains (see Belaústegui
112 and Muñiz, 2016 and references therein). White clay lenses, between 0.5 and 1.5 m
113 thick, exhibit limited (up to tens of meters) lateral extent; they exhibit parallel
114 lamination and thin sandy and microconglomeratic intercalations. Although fossil fauna
115 is scarce, these clay lenses contain the remains of insects, decapods, asteroideans and
116 bivalves, and some lenses were colonized by pholadoidean bivalves. In contrast,
117 terrestrial plant remains are abundant in this facies (Muñiz et al., 1999; Barrón et al.,
118 2003). Trace fossils are scarce in both the fine and coarse-grained sediments in this unit,
119 although *Ophiomorpha* passively filled with microconglomerates are common (see
120 Belaústegui and Muñiz, 2016).

121 Unit 7 consists of 1-3 m of yellowish, fine- to medium-grained, massive sands
122 and silty sands. The silty sands, located at the base, include a marine fossil fauna of
123 bivalves, gastropods and scaphopods (see Belaústegui and Muñiz, 2016). Bioturbation
124 structures are very abundant.

Unit 8 comprises up to 12 m of white-yellowish sandy silts. Ferruginous horizons, usually linked to thin sandy beds, are common. The upper part of the section contains decimeter-thick medium-grained sand and conglomerate beds. Common sedimentary structures are salt crystal molds, fluid escape structures and ferruginous nodules. Body fossils occur generally associated with the ferruginous horizons and include bivalves, gastropods, scaphopods, cirripedians, chelipeds of decapods, cetacean remains, and wood fragments (see Belaústegui and Muñiz, 2016). Trace fossils are abundant and diverse. Muñiz (1998) and Muñiz et al. (1998) distinguished three ichnoassemblages in this unit, based on the relative abundance of traces, which from base to top are: *Thalassinoides*, *Gyrolithes variabilis* and *Psilonichnus*. The *G. variabilis* ichnofabric described herein corresponds to their lower and middle ichnoassemblages.

Unit 9, the uppermost Pliocene unit, consists of 1-4 m of brownish medium- to coarse-grained sands, silts and white kaolinitic sands. Sands are concentrated mostly in the lower part where they locally exhibit small-scale channel-like morphologies, cross-bedding, current cross-lamination, and hummocky cross-stratification (Abad et al., 2013). Body fossils are absent but marine trace fossils are present, mainly *Rosselia*, *Skolithos* and *Diplocraterion*. This unit is erosively covered by Pleistocene fluvial coarse-grained terrigenous sediments (Cáceres, 1999).

SYSTEMATIC ICHNOLOGY

According to the latest reviews of the ichnogenus *Gyrolithes* Saporta 1884 (see Uchman and Hanken 2013; Laing et al. 2018 and references therein), fifteen ichnospecies are currently accepted as valid: *G. davreuxi* Saporta 1884 (type ichnospecies); *G. cycloides* (Mikuláš and Pek 1994); *G. gyratus* (Hofmann 1979), *G.*

krameri (von Ammon 1900); *G. krymensis* Vyalov 1969; *G. lorcaensis* Uchman and Hanken 2013; *G. marylandicus* (Mansfield 1927); *G. mexicanus* (Mansfield 1930); *G. nodosus* Mayoral and Muñiz 1998; *G. okinawaensis* (Myint and Noda 2000); *G. polonicus* Fedonkin 1981; *G. saxonicus* (Häntzschel 1934); *G. scintillus* Laing *et al*. 2018; *G. suprajurassicus* (Schneid 1938); and *G. variabilis* Mayoral and Muñiz 1995. Uchman and Hanken (2013) proposed *G. bularti* Macsotay 1967, *G. vidali* Mayoral 1986, *G. valeroi* Mendiola et al. 1998, and *G. clarcki* (Mansfield 1930) as junior subjective synonyms of *G. krameri* (von Ammon 1900). At the Arroyo Valleforero and La Redondela outcrops, the ichnospecies *G. nodosus* and *G. variabilis* are identified. They are abundant and very well preserved, providing an opportunity to address new observations about their architecture, to emend their respective diagnoses, to propose a neotype for *G. nodosus*, and to describe a new locality (La Redondela) for *G. variabilis*.

Gyrolithes **Saporta 1884**

Diagnosis: "Rarely branched, spiraled burrows; helix essentially vertical, consisting of dextral, sinistral or reversing coils, which are not in contact" (Uchman and Hanken 2013, modified from Bromley and Frey 1974).

Gyrolithes variabilis **Mayoral and Muñiz 1995**

(Figs. 2, 3, 7)

Emended diagnosis: Smooth *Gyrolithes* describing a dextral or sinistral path with the coiling axis close to vertical. Radius of whorls and distance between whorls are clearly variable, so each of these dimensions (individually or jointly) can decrease or maintain their value as the structure penetrates into the sediment. Burrow width is more or less constant (after Mayoral and Muñiz 1995 and Uchman and Hanken 2013).

175 *Type locality:* Unfortunately, the type locality of *G. variabilis* no longer exists; it
176 was destroyed during the construction of an industrial building in the early 2000s. For
177 this reason, Arroyo Valleforero (Lepe, Huelva, SW Spain) is proposed as the new type
178 locality of this ichnospecies (37º14'59"N 7º13'30"W).

179 *Description:* Bioturbation structures studied herein consist of vertical, dextrally or
180 sinistrally spiraled burrows preserved as full reliefs. Cross-sections are subcircular to
181 ellipsoidal. Tunnels are passively filled by sediments with similar composition to that of
182 the host sediment. Bioglyphs (pairs of simple and short scratches) are locally observed on
183 the outer perimeter of the burrows. Partial or complete ferruginization (diagenetic) of
184 burrows is common; occasionally, a thin ferruginous lining can be observed.

185 Maximum width of the burrows ranges from 7 to 36 mm, and the radius of whorls
186 ranges from 13.5 to 32.5 mm. Both the burrow width and the radius of whorls slightly
187 decrease from top to bottom along the helix (from this point and in order to avoid
188 confusion, all explanations are referred to vertical structures perpendicular to bedding).
189 Space among whorls (or interwhorl distance) may decrease downwards or remain constant.
190 A maximum of seven whorls have been observed in a single specimen.

191 Based on morphological variations observed in *G. variabilis*, Mayoral and Muñiz
192 (1995) differentiated between four morphotypes (A to D). Three of which are recognized
193 in the current study. In Morphotype A, whorl radius gradually decreases downwards, and
194 burrow width and interwhorl distance are constant. Specimens of Morphotype B have
195 constant whorl radius and burrow width, and interwhorl distance gradually decreases
196 downwards. In Morphotype C, whorl radius and interwhorl distance decrease downwards,
197 whereas burrow width is constant. Based on the relationship between burrow width and
198 whorl radius, Uchman and Hanken (2013) differentiated among three lineages of
199 *Gyrolithes* ichnospecies. Following this classification, the specimens studied herein are

200 included within the '*variabilis* lineage'; i.e., they are narrow forms (small whorl radius to
201 burrow width ratio). Subsequently, Laing et al. (2018; based on De Renzi et al. 2017)
202 supported the idea of 'lineages', but they altered the ichnospecies components of each
203 'lineage' based on mathematical analysis. In turn, Laing et al. (2018) noted the term
204 'lineage' should be replaced by 'group', given that 'lineages' were purely morphometric
205 and had no evolutionary merit.

206 Specimens from Valleforero and La Redondela are always associated with
207 complex burrow systems that exhibit horizontal to vertical branched galleries
208 (*Thalassinoides* isp.) that may be connected to the uppermost or lowermost whorl of the
209 helical burrows.

210

211 ***Gyrolithes nodosus* Mayoral and Muñiz 1998**

212 (Figs. 4–6)

213 *Emended diagnosis: Gyrolithes* describing a dextral or sinistral path with the
214 coiling axis close to vertical. The burrow is characterized by a knobby (nodose) lining
215 homogeneously arranged around the whole spiral system. The relation between radius
216 of whorls and interwhorl distance tends to decrease simultaneously with depth but
217 burrow width is constant (after Mayoral and Muñiz 1998 and Uchman and Hanken
218 2013).

219 *Type material:* the specimen selected as holotype (LE16/Gn6) and housed in the
220 'Museo de Geología de la Universidad de Sevilla' (Geology Museum of the University
221 of Seville; SW Spain) by Mayoral and Muñiz (1998) is currently lost. For this reason, a
222 new specimen from the type locality has been selected as Neotype (MGUS-1110) and
223 housed in the same institution (Fig. 6A).

224 *Description:* These structures, only identified at the Valleforero outcrop, consist
225 of vertical, helical burrows preserved as full reliefs. Both dextral or sinistral coiling are
226 observed. Burrows vary from circular to elliptical in cross-section and widths range
227 from 8 to 35 mm in width. Whorl radius varies from 10 to 40 mm, and the interwhorl
228 distance decreases downwards. A maximum of six whorls have been observed.
229 The characteristic lining of these bioturbation structures is formed of a single
230 layer of cylindrical and ellipsoidal pellets oriented parallel, oblique, or perpendicular to
231 the burrow axis; in cross-section, the lining is externally knobby and internally smooth.
232 Linings, which range from 1 to 5 mm thick, commonly appear lighter than host
233 sediments due to their higher silt content.
234 Burrows typically are passively filled (with local lamination, Fig. 6A–C) with
235 sediment similar to that of the host sediments. However, fills are locally finer, grayish
236 silt. A retrusive spreite is observed in one specimen (Fig. 6C), a feature described for
237 the first time in the fossil record. As with *G. variabilis*, *G. nodosus* are part of complex
238 burrow systems and are commonly interconnected with *Ophiomorpha nodosa*.
239
240 ## *GYROLITHES* ICHNOFABRICS
241 Two main ichnofabrics have been identified in the studied outcrops (i.e., Arroyo
242 Valleforero and La Redondela), and both are characterized by a particularly high
243 abundance of the ichnogenus *Gyrolithes*. In particular, it is possible to distinguish: (1) a
244 lower ichnofabric characterized by the presence of the ichnospecies *Gyrolithes nodosus*
245 included within unit 7; and (2) an upper ichnofabric (unit 8) with abundant specimens of
246 *G. variabilis*. Only the *G. variabilis* ichnofabric can be observed at the La Redondela
247 outcrop, whereas a gradual transition between these ichnofabrics is identifiable at the

Arroyo Valleforero outcrop. In both outcrops, only the lower and middle parts of unit 8 have been studied in detail.

Arroyo Valleforero

At this outcrop, both ichnofabrics can be identified. In unit 7, the ichnofabric is characterized by moderate to high bioturbation (ichnofabric index, ii, 3/4 *sensu* Droser and Bottjer 1986; see fig. 6.1 of Marenco and Bottjer 2011 for comparison of the 'ii' values with those of the 'bioturbation index, BI' of Taylor and Goldring 1993) and the absence of primary sedimentary structures. This ichnofabric, the subject of a preliminary study by Gibert et al. (2001), is mainly constituted by pellet-lined burrows: *Gyrolithes nodosus, Ophiomorpha nodosa* and *Teichichnus nodosus* (Figs. 4–6). These three ichnotaxa are part of compound burrow systems consisting of branching horizontal and inclined tunnels, vertical shafts and spiral galleries. Other common trace fossils are vertical, concentrically lined burrows, cf. *Rosselia* (up to 29.8 mm in diameter and 28.6 cm of maximum observed length; Figs. 4A, C–E, 6P), and *Cylindrichnus concentricus* (up to 15.7 mm in diameter; Fig. 6M). Due to their respective linings that enhance their visibility, all these ichnotaxa are preserved as elite trace fossils *sensu* Bromley (1990). The ichnofabric is dominated by cross-sections of these ichnofossils. In vertical exposures perpendicular to bedding, vertical and longitudinal cross-sections of *O. nodosa* and *G. nodosus* are dominant (up to 31 mm and 35 mm in diameter, respectively); eight longitudinal sections of *G. nodosus* were recorded in one of these vertical exposed surfaces (9 m long and 1.8 m high). By contrast, *T. nodosus* commonly occurs as horizontal-to-subhorizontal longitudinal cross-sections (up to 22.3 mm in diameter) with retrusive spreiten that may reach heights of up to 61 mm. The most abundant ichnotaxon is *O. nodosa*, the systems of which

include horizontal, oblique and vertical tunnels that may be connected with *G. nodosus* and/or *T. nodosus*; vertical shafts commonly contain a laminated passive fill (Figs. 5A, E, 6G, H). Reworked *Ophiomorpha sensu* Löwemark et al. (2016) also are observed (Fig. 6J, K). Background fabrics lack any primary sedimentary structure but contain abundant *Planolites* isp. and *Teichichnus rectus* and rare *Palaeophycus* isp., *Skolithos* isp. and *Thalassinoides* isp. *Thalassinoides* specimens are only visible when they intersect other traces (Fig. 6N). Bedding-parallel exposures are very rare in this outcrop.

This ichnofabric, gradually transitions into the second ichnofabric at the bottom of unit 8. This second ichnofabric is dominated by *Thalassinoides* isp.*, Teichichnus rectus,* and *Gyrolithes variabilis*. Bioturbation structures are very abundant and diverse in this unit (ii 4/5, *sensu* Droser and Bottjer 1986). High bioturbation intensity locally hampers the identification of the various ichnotaxa present in this ichnofabric. Ichnofossils are commonly preserved as sand-filled full reliefs with a strong ferruginization at and below thin ferruginized surfaces, usually sandy in composition. As in the previous ichnofabric, vertical surfaces perpendicular to the bedding have been studied. Ichnofossils mostly occur as transverse cross-sections (circular to subcircular; up to 26.9 mm in diameter) that mainly correspond to horizontal and subhorizontal *Thalassinoides* (Fig. 7), which is the most common ichnogenus. Locally, laminated passive fills are observed in the vertical and longitudinal sections of some *Thalassinoides* specimens. More rarely and after weathering, some of these bioturbation structures may be preserved as three-dimensional casts protruding from the exposed surface (Fig. 7D). Other ichnotaxa identified in unit 8, although rare, include *Ophiomorpha* isp., *Palaeophycus* (*P. heberti, P. tubularis* and *P.* isp), *Spongeliomorpha* (*S. chevronensis* and *S. sinuostriata*) and *Teichichnus* (*T. rectus* and *T.* isp) (Fig. 7C, E; Muñiz 1998; Belaústegui and Muñiz 2016).

As noted above, the transition between the two ichnofabrics at the Arroyo Valleforero outcrop is gradual. Notably, in this transition, several discrete biogenic structures change from unlined (*Thalassinoides*) to pellet-lined (*Ophiomorpha*) as they pass downward from unit 8 into unit 7 (Fig. 8B, C).

La Redondela

At the La Redondela outcrop, only unit 8 is observed. The ichnofabric is dominated by *Thalassionides paradoxicus, T. suevicus,* and *Gyrolithes variabilis*, and is characterized by low to moderate bioturbation (ii, 2/3 *sensu* Droser and Bottjer 1986). Trace fossils are strongly ferruginized and crop out as three-dimensional full reliefs (in some cases almost completely exposed by weathering; Figs. 2, 3). This mode of preservation allows analysis of the overall architecture of the specimens. Locally, trace fossils may occur associated with vertical ferruginized surfaces generated from metric diaclases (or joints) (Fig. 2A–C). This outcrop shows the highest abundance of *G. variabilis.* Twenty eight longitudinal sections were recorded in one vertical surface (12 m long and 2 m high). These helical traces are commonly associated with vertical-to-horizontal *Thalassinoides* (up to 31.6 mm in diameter). Other identified ichnotaxa, although rare, are *Planolites* isp. and cf. *Teichichnus* (Fig. 7). Ichnodiversity of this ichnofabric is low.

Tiering structure

Two different tiering structures have been recognized in units 7 and 8 (Fig. 9). The transition (from bottom to top) between these units display a clear change in the vertical partitioning of the infaunal ecospace, passing from a diverse infaunal community in unit 7 to a more impoverished one in unit 8. In unit 7 (Arroyo Valleforero

outcrop), eight tiers and three ichnoguilds are represented (Fig. 9A), including a *Planolites-Skolithos* ichnoguild consisting of vagile and sessile, shallow tier, deposit- and suspension-feeder structures; a *Gyrolithes-Rosselia-Cylindrichnus* ichnoguild that includes sessile and semi-vagile, shallow- to middle-tier, deposit- and suspension feeder structures; and an *Ophiomorpha-Teichichnus-Thalassinoides* ichnoguild comprising stationary and semi-vagile, middle- to deep-tier, deposit-feeder structures. In unit 8 (Arroyo Valleforero and La Redondela outcrops), four tiers and two ichnoguilds have been recognized (Fig. 9B). This tiered ichnocoenosis includes a *Palaeophycus* ichnoguild that includes vagile, shallow-tier, deposit-feeder structures, and a *Gyrolithes-Thalassinoides-Teichichnus* ichnoguild consisting of stationary and semi-vagile, middle- to deep-tier, deposit-feeder structures.

Lower ichnofabric indices and ichnodiversity, together with the lower number of tiers and ichnoguilds in unit 8 could reflect a more restricted brackish depositional environment. Oxygen or salinity conditions may have been more favorable (perhaps reflecting more open-marine conditions) during unit 7 deposition, resulting in a more diverse ichnocommunity. In both units, the sedimentation rate would have been low. In the case of unit 8, wherein ferruginous crusts has been interpreted as diastemic surfaces recording sea-level pulses (Muñiz, 1998; Muñiz et al., 1998), sedimentation was likely discontinuous.

TRACEMAKER, CONSTRUCTION AND FUNCTION

The ichnogenus *Gyrolithes* ranges from the Ediacaran-Cambrian boundary (Laing et al. 2018) to the Holocene (e.g. Dworschak and Rodrigues 1997). Given such wide chronostratigraphic distribution, many organisms could be considered as possible tracemakers. However, at least since the Permian onwards, decapod crustaceans are

accepted as the most likely producers (Uchman and Hanken 2013; Laing et al. 2018). This interpretation is supported by the common connection of *Gyrolithes* with *Thalassinoides, Spongeliomorpha* and/or *Ophiomorpha*, ichnotaxa typically assigned to the burrowing activity of decapods (e.g. Bromley and Frey 1974; Mayoral and Muñiz 1993, 1995, 1998; Grimm and Föllmi 1994).

Among the Order Decapoda, 'thalassinidean shrimps' (now gebiideans and axiideans, following De Grave et al. 2009 and Dworschak et al. 2012) are considered as the most likely tracemakers. In particular, the modern species *Axianassa australis* Rodrigues and Shimizu 1992 can excavate complex burrow systems with vertical helical galleries identical to those belonging to the ichnogenus *Gyrolithes* (see Dworschak and Rodrigues 1997). Wetzel et al. (2010) recorded the presence of subrecent *Gyrolithes* in Holocene estuarine incised-valley fill deposits of southern Vietnam and interpreted these to have been produced by 'thalassinidean' shrimps based on wall ornamentation. Additionally, other 'thalassinideans' together with other groups of modern decapods, are also capable of excavating simple spiral burrows (e.g. Pervesler and Dworschak 1985; Dworschak and Pervesler 1988; Dworschak and Ott 1993). Among the latter, brachyuran crabs (Ocypodidae) are the best known (e.g. Lisenmair 1967; Vannini 1980; Schober and Christy 1993; Dworschak and Rodrigues 1997; Clayton 2005; Gibert et al. 2013).

Neoichnological studies indicate that vertical (although also oblique to horizontal), helical burrows that share diagnostic features with *Gyrolithes* may be excavated by polychaetes (Capitellidae, Maldanidae and Nereidae) and hemichordates (Enteropneusta: Harrimaniidae) (e.g., Van Der Horst 1934, 1940; Howard and Frey 1975; Powell 1977; Bromley 1996; Gingras et al. 1999; Hauck et al. 2009). Hence, such organisms cannot be ruled out as potential tracemakers. However, in the case of the

current study, features clearly point to 'thalassinidean' crustaceans as the most likely tracemakers. These include: (1) the pelleted lining; (2) the presence of bioglyphs; (3) the vertical orientation of the helix; and (4) the recurrent connections with *Thalassinoides* and *Ophiomorpha.*

Different hypotheses have been proposed to explain the purpose of spiral/helical burrows (see Belaústegui et al. 2014): (1) deterrence and/or protection against predation; (2) courtship; (3) adaptation to salinity changes; (4) facilitation of in-burrow locomotion; (5) microbial farming; (6) exploitation of food resources; (7) providing pore-water exchange; (8) symmetric or asymmetric producers (unequal handedness); (9) in-sediment anchoring; and (10) response to high-population densities (e.g. Toots 1963; Linsenmair 1967; Farrow 1971; Beynon and Pemberton 1992; Schober and Christy 1993; Dworschak and Rodrigues 1997; Felder 2001; Clayton 2005; Netto et al. 2007; Seilacher 2007; Gingras et al. 2008; Gibert et al. 2012). However, exactly how and why helical burrows are produced still remains unclear. Further work on the physiological ecology and ethology of their modern producers is needed.

Notably, at Valleforero and La Redondela outcrops, the presence of *Gyrolithes* specimens exclusively differentiated by size (e.g. burrow width ranging from 7 mm to 36 mm) could be indicative of different ontogenetic stages of the burrowing 'thalassinidean' shrimps. In this particular case, the juvenile 'thalassinideans' were able to build the same helical structures as adults.

PALEOENVIRONMENTAL SIGNIFICANCE

Permian to Cenozoic *Gyrolithes* typically occur in brackish-water marginal-marine environments (typically as an element of the depauperate *Cruziana* ichnofacies) or under fully marine, shallow-water conditions forming part of the *Skolithos* or

398 *Cruziana* ichnofacies (Pemberton et al. 2001; Wetzel et al. 2010; Buatois and Mángano,
399 2011; Uchman and Hanken 2013; and references therein).
400 The Pliocene interval (units 6 to 9; Fig. 1C) of the study area has been
401 interpreted, from base to top, as the transition from: (1) marine deposits affected by
402 fluvial processes (unit 6), through (2) sublittoral fully-marine deposits (unit 7), to (3)
403 more restricted/marginal marine deposits (unit 8 and base of unit 9) (very likely
404 associated to an estuarine setting; Muñiz 1998; Muñiz et al. 2010; Belaústegui and
405 Muñiz 2016). In particular, the lowermost unit 6 has both continental (fluvial) and
406 marine signatures, which suggests that this unit was deposited in the proximal part of an
407 estuary where fluvial sediment input and processes were still dominant. Sand and gravel
408 sedimentation took place by bedform migration in channels, while white clay lenses
409 probably correspond to ponds formed between bars or in abandoned channels. The
410 abundance of well-preserved macrofloral remains supports the proximity of the
411 continent and indicates a calid, subtropical paleoclimate with periods of drought
412 (Barrón et al., 2003). However, the presence of marine invertebrate and vertebrate
413 fossils and ichnofossils demonstrates periodic marine influence during the deposition of
414 this unit. The overlying fine- to medium-grained, massive sands and silty sands of unit
415 7, defined by a *G. nodosus* ichnofabric (see also Muñiz 1998; Muñiz et al. 1998, 2010),
416 were deposited in a sublittoral, fully-marine setting, which indicates a relative rise of
417 sea-level with respect to unit 6; the maximum flooding surface associated with this
418 transgressive pulse would be placed on top of unit 7 (Muñiz et al. 1998; Muñiz et al.
419 2010; Belaústegui and Muñiz 2016). The subsequent deposition of the sandy silts of
420 unit 8, which likely occurred in a lower-nergy estuarine setting, reflects a regressive
421 phase. This regressive trend is also evidenced by the presence of a *Psilonichnus*
422 ichnoassemblage (typically indicative of coastal environments: backshore areas,

washover fans, coastal dunes and supratidal flats; Buatois and Mángano, 2011 and references therein) in the upper part of this unit (Muñiz 1998; Muñiz et al. 1998; Muñiz et al. 2010 and Belaústegui and Muñiz 2016). Regression probably continued during deposition of the overlying unit 9, which records higher energy sedimentation, probably in an intertidal-littoral setting.

The contact between units 7 and 8 is concordant. Sediments of unit 7 were deposited under quiet to moderate energy conditions that allowed the colonization of this sandy bottom by 'thalassinidean' shrimps (the likely tracemakers of *G. nodosus*, *O. nodosa*, *T. nodosus* and *Thalassinoides* isp.) and annelid polychaetes (probable tracemakers of *C. concentricus*, *Palaeophycus* isp., *Planolites* isp., *Skolithos* isp. and cf. *Rosselia*). The activities of these organisms resulted in intense bioturbation. The transition to finer-grained sediments (sandy silts) in unit 8 reflects decreasing energy conditions, which was accompanied by a decrease in abundance and diversity of ichnotaxa (Belaústegui and Muñiz 2016).

Substrate composition and consistency (e.g. grain size, sorting, water content, organic matter content, mucus binding) are extrinsic factors controlling burrowing technique and infaunal community composition (Bromley 1990, 1996). A series of stages have been defined for carbonate and siliciclastic sediments based on their degree of consolidation (see Buatois and Mángano 2011 and references therein): soupground (saturated in water and incompetent), softground (unconsolidated sediment, mud and silt), looseground (unconsolidated sediment, sand and gravel), stiffground (stiff but not fully compacted mud), firmground (compacted and dewatered sediment) and hardground (cemented substrates). The transition from unit 7 to 8 reflects a clear example of substrate-controlled behaviors. The massive sands and silty sands of unit 7 would have represented a looseground in which burrows with knobby and thick linings

were produced (*O. nodosa*, *G. nodosus* and *T. nodosus*). Subsequent deposition of the sandy silts of unit 8 resulted in unconsolidated fine sediment i.e. softgrounds hosting a large number of unlined traces (*G. variabilis*, *T. paradoxicus*, *T. suevicus*, *Thalassinoides* isp. and *T. rectus*) (Fig. 8). Consequently, changes in lithology and consistency of the substrate clearly affected the behavior of burrowing organisms.

Given the above, it is possible to speculate that different ichnotaxa prevalent in units 7 and 8 may have been produced by the same organisms (at least those attributed to decapod crustaceans) and that their variable burrowing techniques record the ethologic response to new substrate conditions. That is, *G. nodosus*, *O. nodosa* and *T. nodosus* in unit 7 could be considered as 'equivalent' ichnotaxa of *G. variabilis*, *Thalassinoides* isp. and *T. rectus* in unit 8, respectively. This is plausible given that among modern decapod crustaceans, 'thalassinidean' shrimp exhibit great versatility in regards to their burrowing behaviors that result in significant variability in burrow systems and architectures (Gibert et al. 2012 and references therein).

CONCLUSIONS

Vertical and helical burrows (ichnogenus *Gyrolithes*) in Permian and younger strata exhibit a series of morphological and architectural features that allow attribution to burrowing activity by decapod crustaceans, in particular 'thalassinidean' shrimps. However, further neoichnological studies focused on physiological ecology and ethology of modern analogues are needed to better understand the purpose of helical burrows.

Two ichnofabrics, dominated by the ichnospecies *Gyrolithes nodosus* and *G. variabilis*, are described from two Pliocene sections in Lepe (Huelva, SW Spain); the previously known Arroyo Valleforero outcrop and the new section at La Redondela.

Excellent preservation of *Gyrolithes* specimens in both sections has allowed new observations on burrow architecture, the emending of diagnoses for the two recognized *Gyrolithes* ichnospecies, and the proposal of a neotype for *G. nodosus*.

Based on a combination of stratigraphic, sedimentological, paleontological and ichnological data the studied Pliocene succession (units 6 to 9) contains a fining- and deepening-upward, transgressive sequence (i.e. from fluvially-influenced unit 6 to open-marine unit 7) overlain by a coarsening- and shallowing-upward, regressive sequence (i.e. from restricted-marine unit 8 to coastal-marine unit 9, both likely associated with an estuarine setting). This succession is manifest in the transition from the pellet-lined (unit 7) to unlined (unit 8) ichnofabrics described herein. This architectural change exemplifies the plasticity and/or versatility of the burrowing behavior of 'thalassinideans' and how they may record adaptations to environmental changes.

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FIGURE CAPTIONS

FIG. 1.–Geographic and geologic setting of the studied area. **A**) Simplified geologic map of the Guadalquivir Basin and surrounding areas and its location on the Iberian Peninsula. **B**) Geologic map of the study area. White stars show the locations of 'Arroyo Valleforero' and 'La Redondela' outcrops (VF and LR, respectively). **C**) Synthetic Neogene stratigraphic section of the Lepe area (abbreviations: M, medium; C, coarse; VC, very coarse; CN, carbonate nodules; FC, ferruginous crusts; K, kaolinitic; IC, interbedded clays; CN9 (upper Tortonian–Messinian, upper Miocene) and CN11 (upper Zanclean, lower Pliocene) biozones of Okada and Bukry, 1980). White stars show the locations of the *Gyrolithes* ichnofabrics dominated by *G. variabilis* (iGv) and *G. nodosus* (iGn).

FIG. 2.–Ichnofabric of *Gyrolithes variabilis* from La Redondela outcrop. **A**) Overall view of a vertical section. **B–F**) Details of several specimens of *G. variabilis* in connection with *Thalassinoides* burrows. Scale bars are 5 cm long.

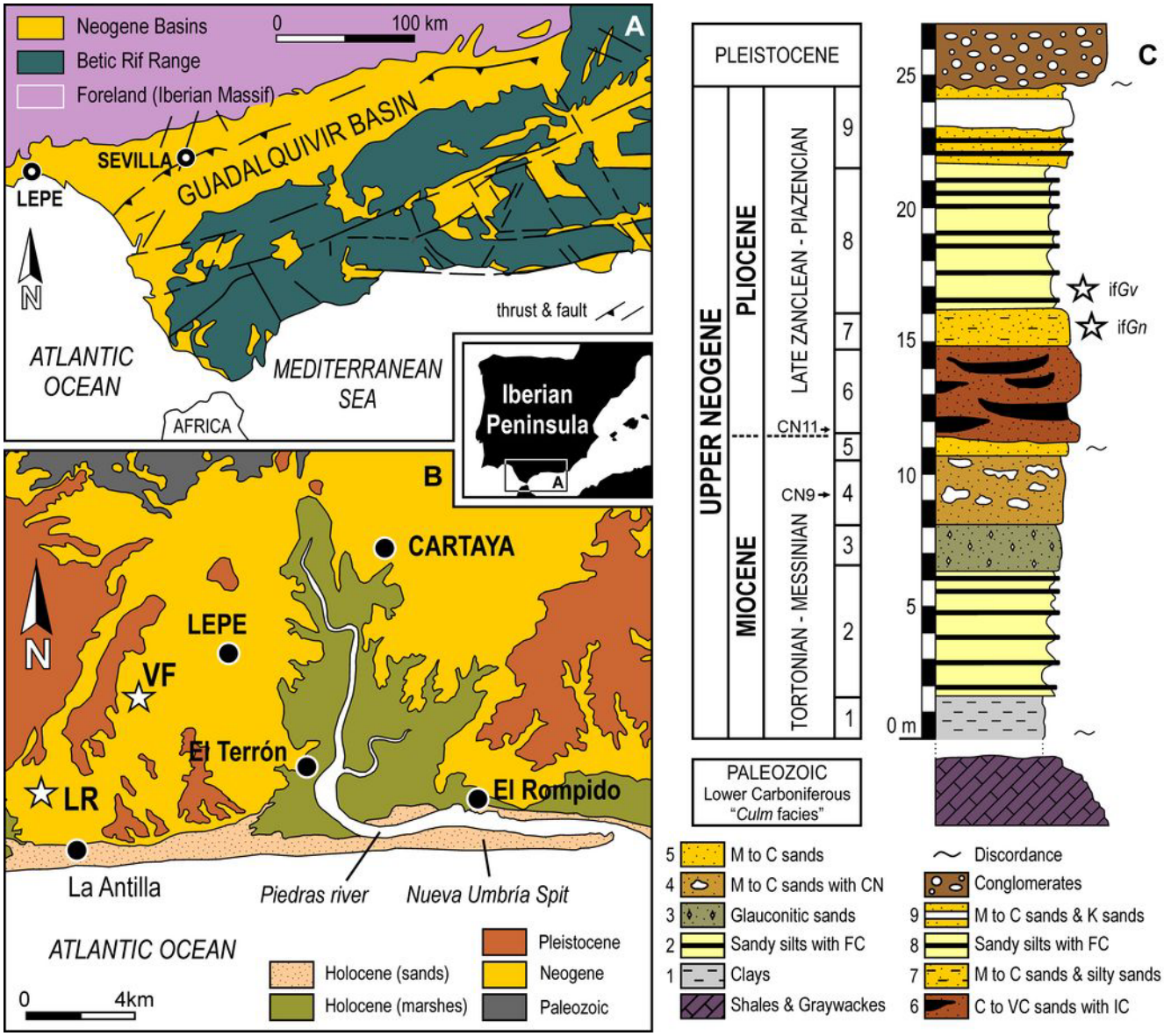
FIG. 3.–*Gyrolithes variabilis* from La Redondela outcrop. **A–F**) Details of different specimens. Scale bars are 5 cm long, except in D, where scale is 1 cm long.

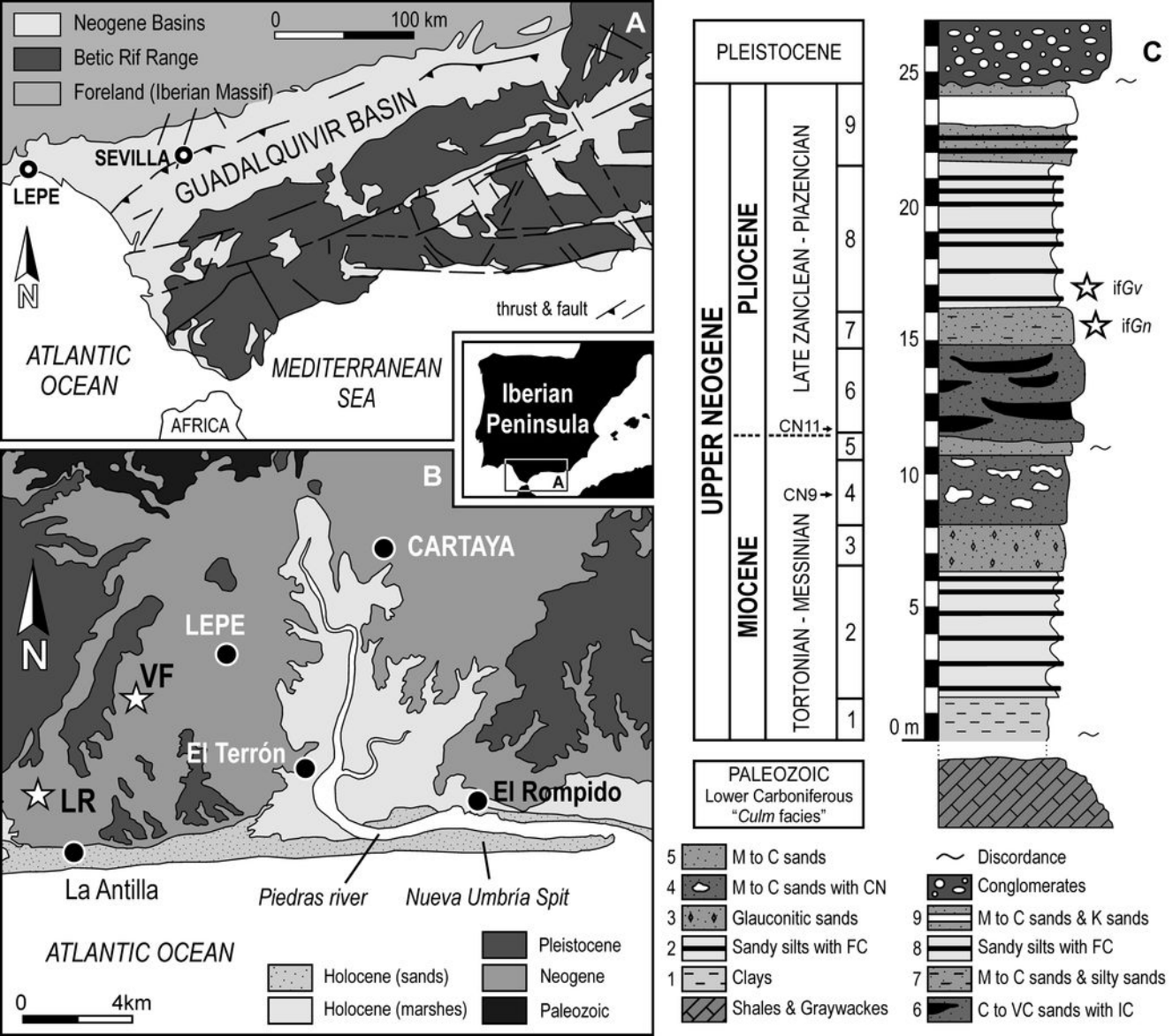
765 FIG. 4.–Ichnofabric of *Gyrolithes nodosus* from Arroyo Valleforero outcrop. **A**) Overall
766 view of a vertical section. **B, C**) Details of A; in B, laminated passive fills (lpf)
767 are observed in some horizontal and oblique *Ophiomorpha.* **D, E**) Details
768 showing vertical burrow sections belonging to *Gyrolithes* (Gy), *Ophiomorpha*
769 (Op)*, Skolithos* (Sk) and cf. *Rosselia* (Ro). (Te: *Teichichnus;* Th:
770 *Thalassinoides*). Scale bars are 5 cm.
771
772 FIG. 5.–Ichnofabric of *Gyrolithes nodosus* from Arroyo Valleforero outcrop. **A–E**)
773 Details of different specimens of *Ophiomorpha nodosa*; laminated passive fills
774 (lpf) are common. **B, C**) Detail of *Teichichnus nodosus*; the retrusive spreite has
775 been intersected by a vertical *O. nodosa*. (Gy: *Gyrolithes*). Scale bars are 5 cm.
776
777 FIG. 6.–*Gyrolithes nodosus* from Arroyo Valleforero outcrop. **A**) Neotype (MGUS-
778 1110) of *G. nodosus* Mayoral and Muñiz, 1998. **B–D**) *G. nodosus* specimens:
779 specimen in C shows a retrusive spreite. **E**) *Ophiomorpha nodosa* showing the
780 outer perimeter of the pelleted lining. **F–H**) Vertical and longitudinal sections of
781 *O. nodosa* showing laminated passive fills. **I**) Obique to transverse section of *O.*
782 *nodosa*. **J, K**) Reworked *Ophiomorpha sensu* Löwemark et al. (2016). **L**)
783 Vertical burrow (*Thalassinoides*-like) filled with cylindrical pellets. **M**)
784 Subcircular cross-section of *Cylindrichnus concentricus*. **N**) *Thalassinoides* isp.
785 intersecting *O. nododsa*. **O**) Branching point of *O. nodosa*. **P**) Vertical and
786 longitudinal section of cf. *Rosselia*. Scale bars are 1 cm long in C, D, G, H, I, K,
787 L, M,N, and 5 cm long in A, B, E, F, J, O, P.
788

FIG. 7.–Ichnofabric of *Gyrolithes variabilis* from unit 8 at the Arroyo Valleforero outcrop. **A, C, E, F**) Different overall views of vertical sections of ichnofabric (Te, *Teichichnus*; Gy, *Gyrolithes*; Pa, *Palaeophycus;* lpf, laminated passive fill). **B**) Detail of *Gyrolithes variabilis* in A. **C**) Abundant *Thalassinoides*-like structures (mainly transverse and horizontal sections) together with less frequent *Teichichnus*. **D**) *Gyrolithes* specimens preserved as three-dimensional positive cast protruding from the exposed surface by weathering. **E**) *Teichichnus rectus*. Scale bars are 5 cm, except (D) that is 1 cm.

FIG. 8.–Transition between the ichnofabric dominated by *Gyrolithes nodosus* to that dominated by *G. variabilis* (i.e. from unit 7 to 8) at the Arroyo Valleforero outcrop. **A**) Overall view. **B, C**) Details of A showing an oblique burrow (*Thalassinoides*-like) with a laminated passive fill and without lining (unit 8) changing (downward) to *Ophiomorpha* with a pelleted lining (unit 7). Scale bars are 5 cm.

FIG. 9.–Tiering structures and ichnoguilds of units 7 (**A**; Arroyo Valleforero outcrop) and 8 (**B**; Arroyo Valleforero and La Redondela outcrops) from the Pliocene of Lepe (Huelva, SW Spain). (Cy, *Cylindrichnus*; Gy, *Gyrolithes*;Pa, *Palaeophycus*; Pl, *Planolites*; Op, *Ophiomorpha*; Ro, *Rosselia*; Sp, *Spongeliomorpha*; Sk, *Skolithos*; Te, *Teichichnus*; Th, *Thalassinoides*).


Neogene Basins
Betic Rif Range
Foreland (Iberian Massif)
0
100 km
A
SEVILLA
GUADALQUIVIR BASIN
LEPE
N
thrust & fault
ATLANTIC OCEAN
MEDITERRANEAN SEA
AFRICA
Iberian Peninsula
A
B
CARTAYA
LEPE
N
VF
El Terrón
LR
El Rompido
La Antilla
Piedras river
Nueva Umbría Spit
ATLANTIC OCEAN
0
4km
Holocene (sands)
Holocene (marshes)
Pleistocene
Neogene
Paleozoic
PLEISTOCENE
UPPER NEOGENE
PLIOCENE
MIOCENE
LATE ZANCLEAN - PIACENCIAN
TORTONIAN - MESSINIAN
CN11
CN9
9
8
7
6
5
4
3
2
1
PALEOZOIC
Lower Carboniferous
"Culm facies"
5 M to C sands
4 M to C sands with CN
3 Glauconitic sands
2 Sandy silts with FC
1 Clays
Shales & Graywackes
C
25
20
15
10
5
0 m
ifGv
ifGn
Discordance
Conglomerates
9 M to C sands & K sands
8 Sandy silts with FC
7 M to C sands & silty sands
6 C to VC sands with IC


A
Neogene Basins
Betic Rif Range
Foreland (Iberian Massif)
0
100 km
SEVILLA
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LEPE
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thrust & fault
ATLANTIC OCEAN
MEDITERRANEAN SEA
AFRICA
Iberian Peninsula
A
B
CARTAYA
LEPE
N
VF
El Terrón
LR
El Rompido
La Antilla
Piedras river
Nueva Umbría Spit
ATLANTIC OCEAN
0
4km
Holocene (sands)
Holocene (marshes)
Pleistocene
Neogene
Paleozoic
PLEISTOCENE
UPPER NEOGENE
PLIOCENE
MIOCENE
LATE ZANCLEAN - PIAZENCIAN
TORTONIAN - MESSINIAN
CN11
CN9
9
8
7
6
5
4
3
2
1
PALEOZOIC
Lower Carboniferous
"Culm facies"
C
25
20
15
10
5
0 m
ifGv
ifGn
5 M to C sands
4 M to C sands with CN
3 Glauconitic sands
2 Sandy silts with FC
1 Clays
Shales & Graywackes
Discordance
Conglomerates
9 M to C sands & K sands
8 Sandy silts with FC
7 M to C sands & silty sands
6 C to VC sands with IC


A
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B
C
D
E
F


A
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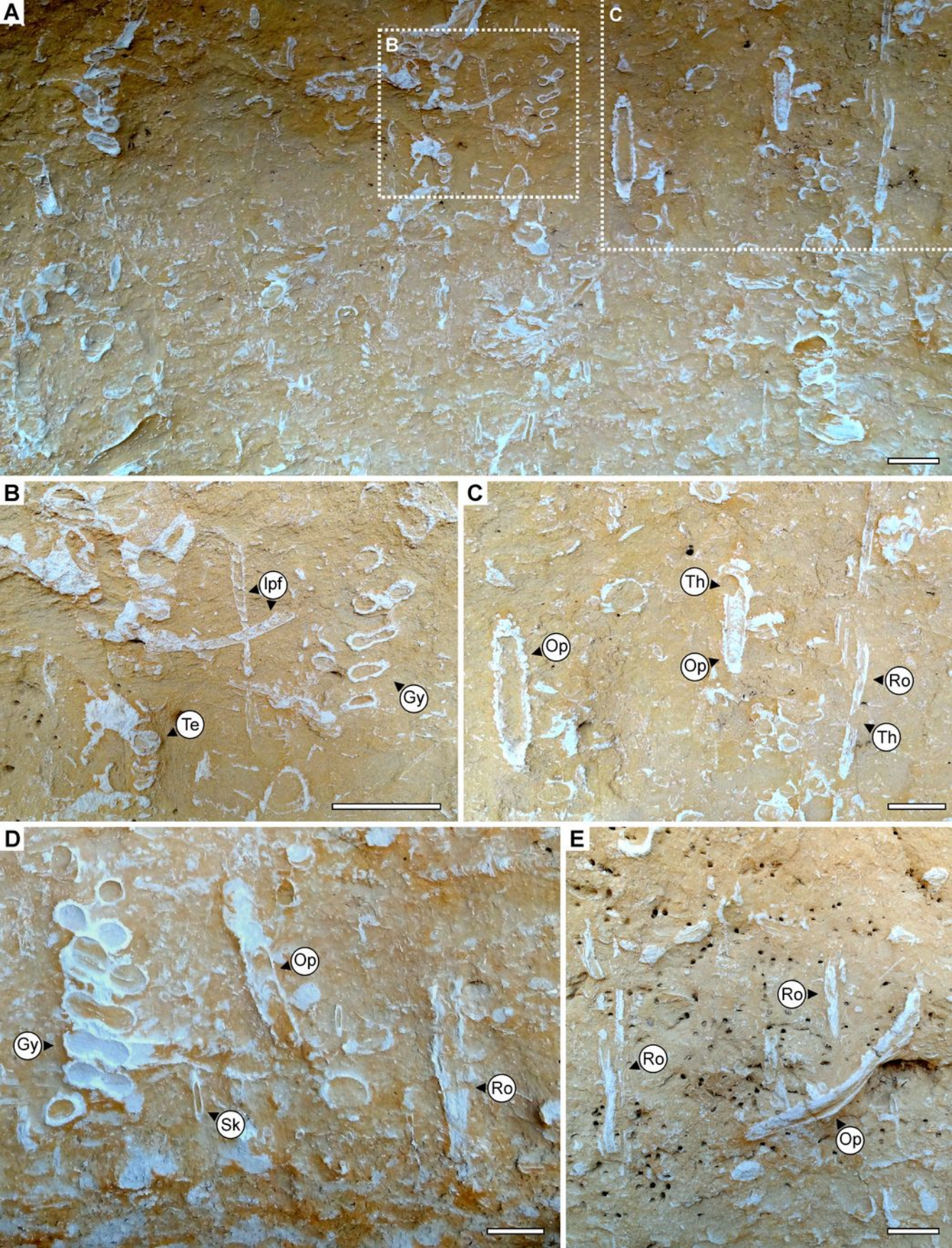
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lpf
Gy
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Op
Ro
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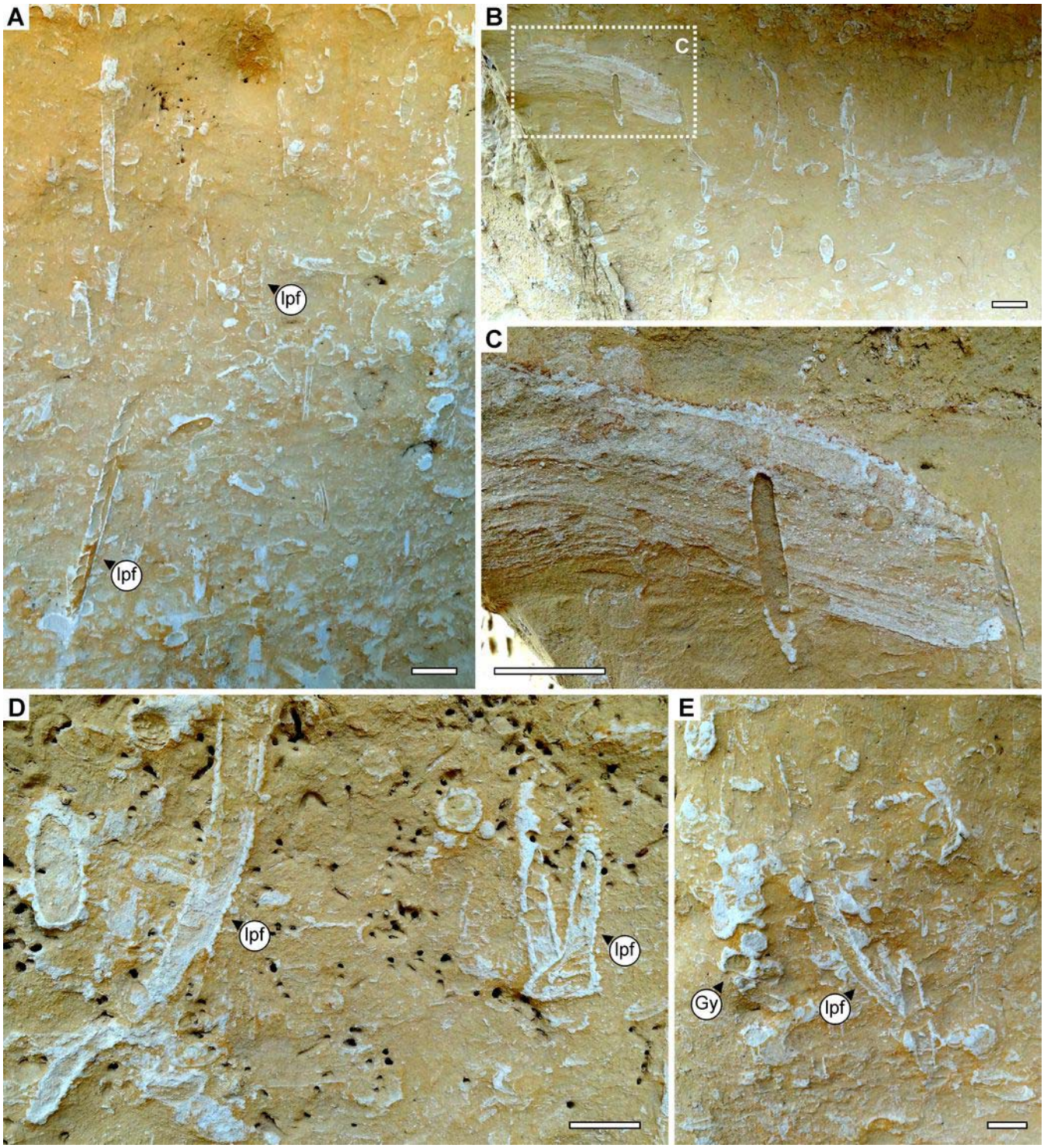
Ro
Ro
Op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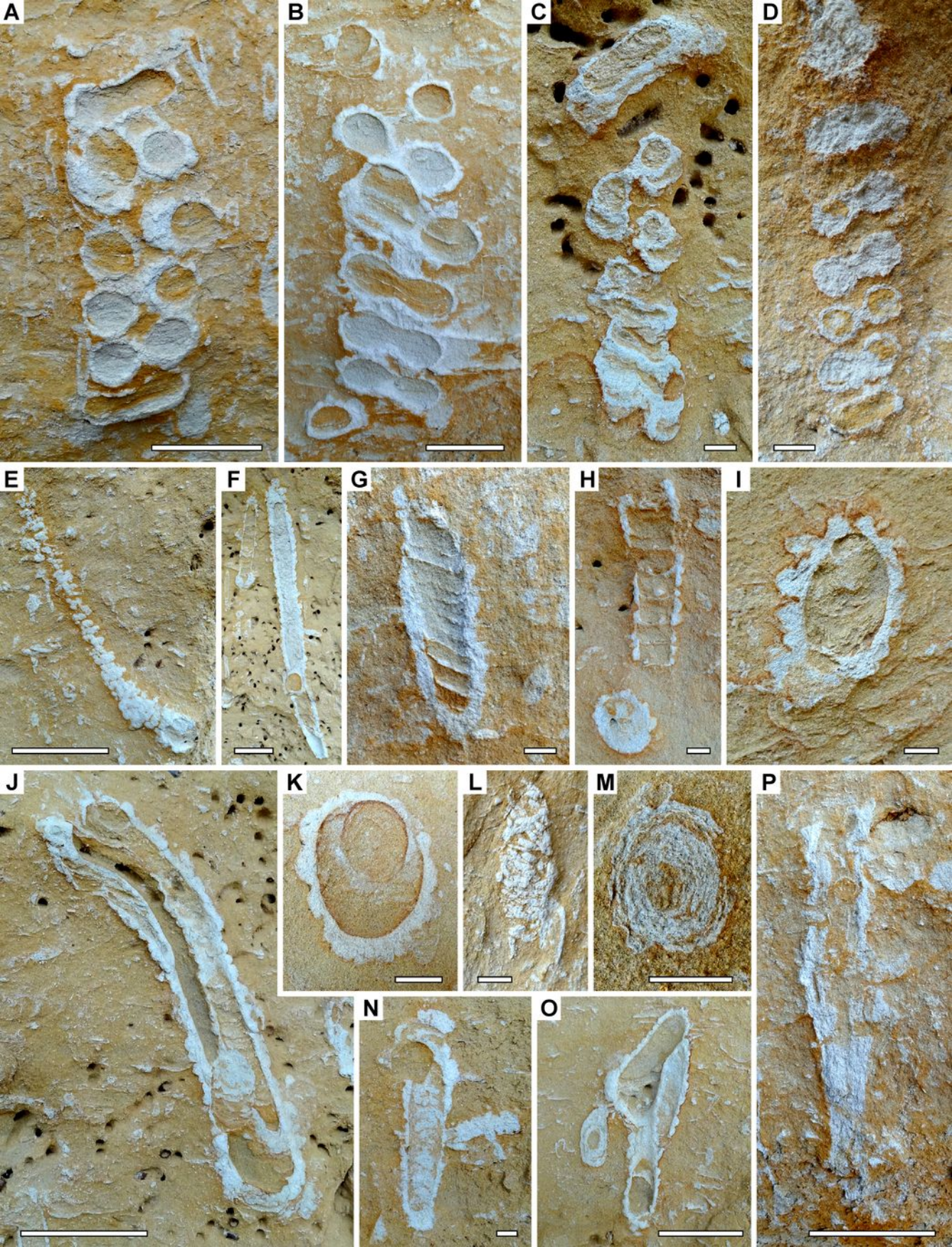
Gy
lpf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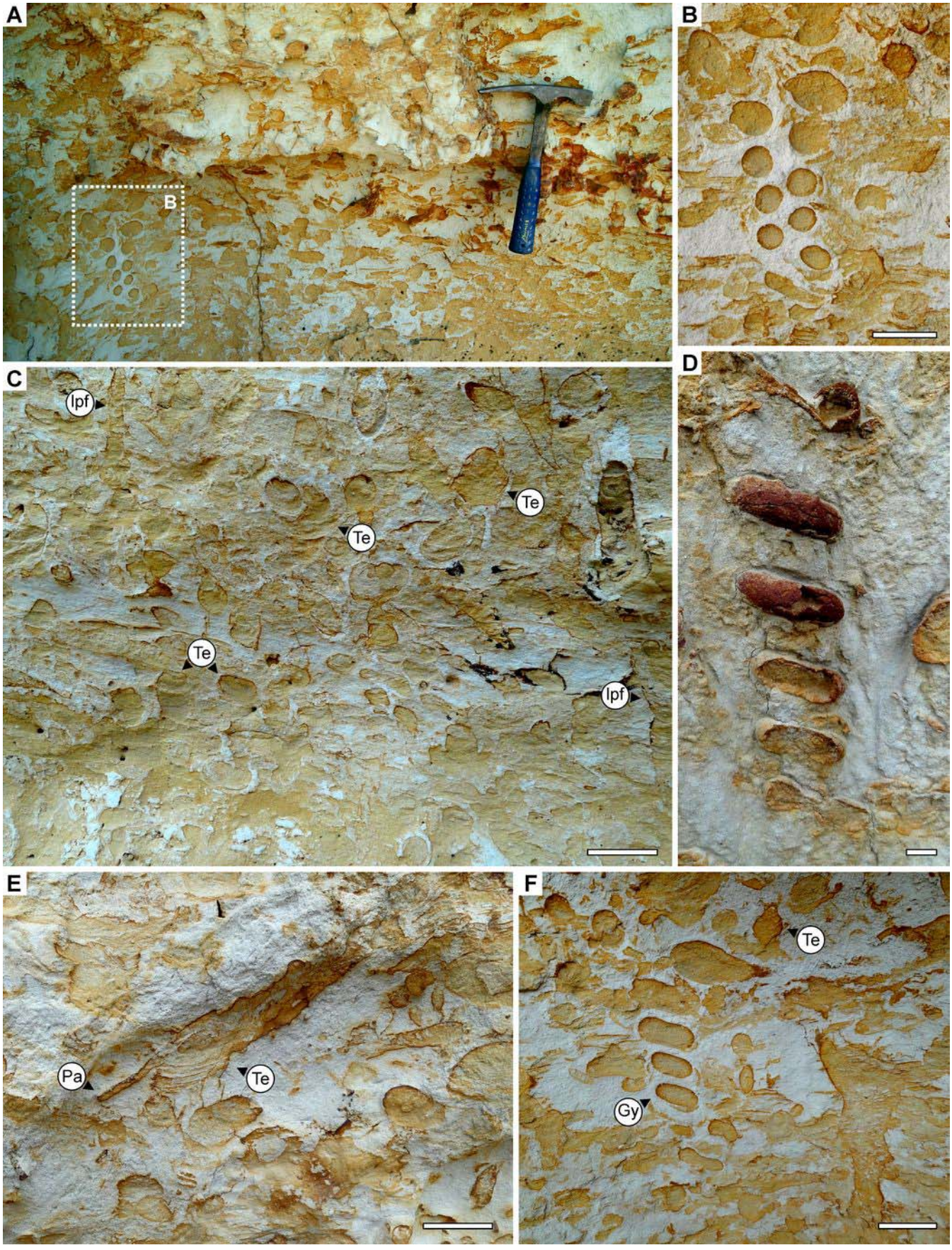
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B
B
C
lpf
Te
Te
Te
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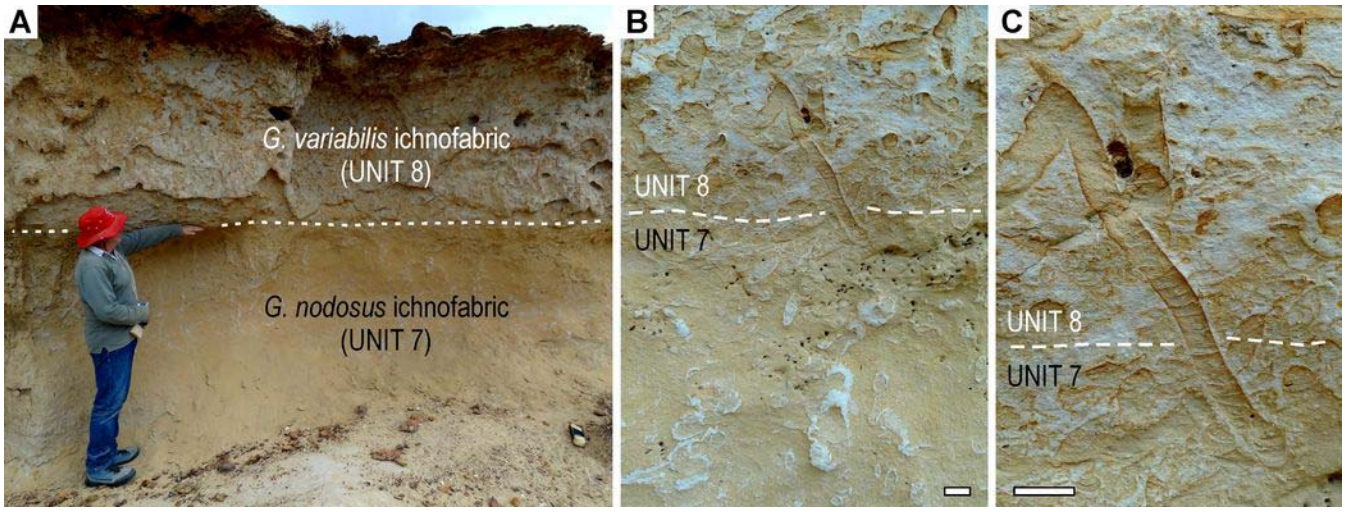
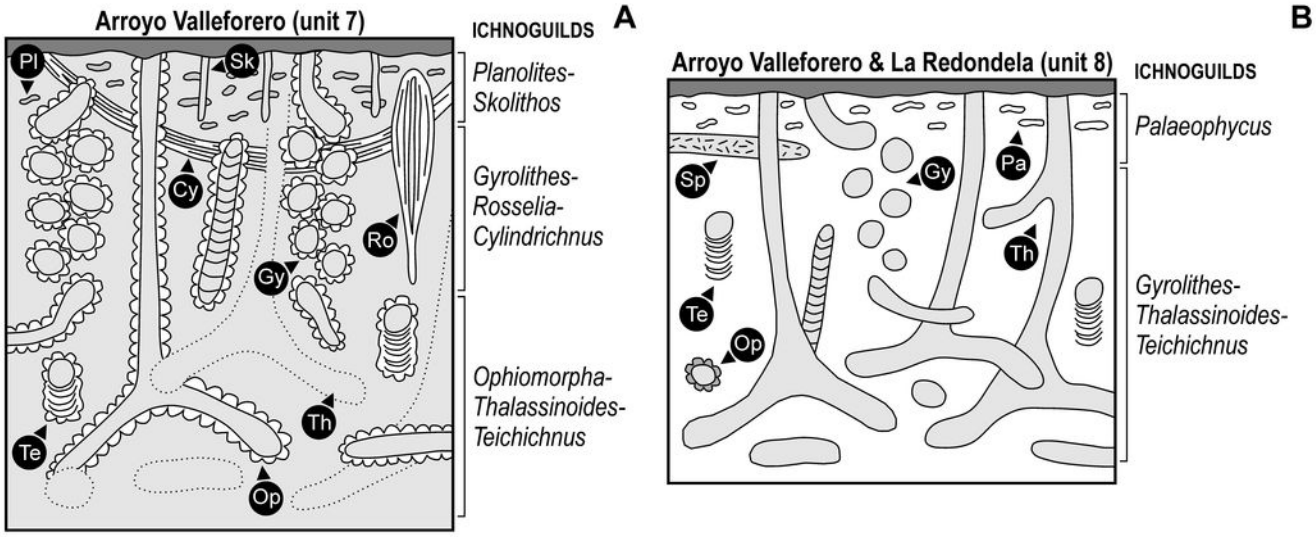
D
E
Pa
Te
F
Te
Gy


A
G. variabilis ichnofabric
(UNIT 8)
G. nodosus ichnofabric
(UNIT 7)
B
UNIT 8
UNIT 7
C
UNIT 8
UNIT 7


A
Arroyo Valleforero (unit 7)
ICHNOGUILDS
Pl
Sk
Cy
Ro
Gy
Th
Te
Op
Planolites-
Skolithos
Gyrolithes-
Rosselia-
Cylindrichnus
Ophiomorpha-
Thalassinoides-
Teichichnus
B
Arroyo Valleforero & La Redondela (unit 8)
ICHNOGUILDS
Sp
Gy
Pa
Th
Te
Op
Palaeophycus
Gyrolithes-
Thalassinoides-
Teichichnus