Compound biogenic structures resulting from ontogenetic variation: An example from a modern dipteran

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ABSTRACT

Several families of Diptera are known to be active burrowers. Fly larvae of the genus *Symplecta* (family Limoniidae) were observed in a sandy substrate of an orange grove in Lepe, SW Spain. Traces produced by *Symplecta* display: (1), a proximal segment characterized by a winding furrow trail; (2), an intermediate part consisting of burrow segments arranged in zigzag; and (3), a distal part formed by a complex U-shaped burrow. The most complex morphology is present in the intermediate zigzag burrow system, which varies from irregularly sinuous and curved in its most proximal part to spiraled. In the fossil record, the trace would be ascribed to different ichnotaxa depending on the part preserved.

RESUMEN

Varias familias de dípteros incluyen excavadores activos. Larvas y pupas de mosca del género *Symplecta* (familia Limoniidae) han sido observadas en el sustrato arenoso de un campo de naranjos en Lepe, SO de España. Sus estructuras biogénicas muestran: (1) una parte proximal caracterizada por un surco sinuoso; (2) una parte intermedia formada por segmentos de madrigueras en zigzag; y (3) una parte distal formada por una madriguera en "U" compleja. La mayor complejidad se da en la parte intermedia, con trayectorias rectas, irregulares, sinuosas o curvas en su parte más proximal, y espirales en la parte distal. Si estas estructuras se encontrasen en el registro fósil, se podrían relacionar

In fact, this is a compound trace recording multiple behavioural patterns. The winding furrow shows affinities with *Helminthopsis*, the zigzag burrows with *Treptichnus*, and the U-shaped burrow with *Arenicolites*. Furthermore, the spiral portion shows some similarities with *Spirophycus* and *Spirodesmos*. Interestingly, formation of these compound traces is connected with different ontogenetic stages of the producer. The winding and zigzag segments are produced, respectively, by *Symplecta* larvae and pupae for feeding purposes, whereas the U-shaped burrow is excavated during the end of pupal stage for protection until adulthood. In the fossil record, this incipient compound trace potentially may occur in lake-margin, fluvio-estuarine and overbank deposits, including levee, crevasse splay and pond deposits, forming part of the *Scoyenia* or the *Mermia* ichnofacies. Structures similar to those produced by modern diptera are known from freshwater ichnofaunas since the Devonian.

con diferentes icnotaxones según la parte conservada. El conjunto es una estructura compuesta que registra múltiples comportamientos: el surco sinuoso muestra afinidades con *Helminthopsis*, las madrigueras en zigzag con *Treptichnus*, la madriguera en "U" con *Arenicolites*, y la parte en espiral con *Spirophycus* y *Spirodesmos*. Su formación está relacionada con diferentes etapas ontogénicas del productor. Tanto los surcos sinuosos como las madrigueras en zigzag son producidas por *Symplecta* en los estadios de larva y pupa respectivamente, para alimentarse; la madriguera en "U", durante la fase terminal de pupa, como protección hasta convertirse en adulto. En materiales antiguos, esta pista compuesta podría aparecer en depósitos lacustres marginales, fluvio-estuarinos y de desbordamiento, incluyendo facies de dique, rotura de dique y charca, formando parte de las icnofacies de *Scoyenia* o de *Mermia*. Estructuras similares aparecen en icnofaunas de agua dulce desde el Devónico.

1. INTRODUCTION

Diptera, or true flies, are a large order containing about 200,000 known species (of which under half of these have been described), grouped in 218 families of which 43 are extinct (Blagoderov *et al.*, 2002). Several families of flies are known to be active burrowers. In particular, neoichnologic studies have documented a wide variety of structures produced by Chironomidae, Ephydridae, Stratiomyidae, Syrphidae, Tabanidae and Tipulidae, among others (Chamberlain, 1975; McLachlan & Cantrell, 1976; McCall & Tevesz, 1982; Metz, 1987a, b; Mángano *et al.*, 1996; Charbonneau & Hare, 1998; Uchman, 2005). Diptera have been suggested as tentative producers of biogenic structures in the palaeoichnologic literature (e.g., Tarr, 1935; Metz, 1987b, 1995, 1996, 2000; Braddy & Briggs, 2002; Uchman *et al.*, 2004; Rindsberg & Kopaska-Merkel, 2005; Mikuláš *et al.*, 2012).

Traces of fly larvae and pupae of the genus *Symplecta* (family Limoniidae, subfamily Chioneinae) were observed on a wet, sandy substrate of an orange grove in the town of Lepe, Huelva, SW Spain. The main objectives of this study are to: (1), document recent compound traces produced by Diptera; and (2), interpret these traces in connection to ontogenetic stages of the producer. In addition, we discuss the ichnotaxonomic implications of our finding, and we place the described biogenic structures within the evolutionary framework of the Diptera.

2. STUDY AREA AND METHODS

The zone studied is located in an area known as Arroyo Valleforero, 3 km west of the town of Lepe (Huelva Province, southwestern Spain) (Fig. 1a). Arroyo Valleforero is dominated by a landscape of gullies produced from the erosion of silt and sandy sediment of Early Pliocene age (Muñiz Guinea, 1998). This soft substrate is appropriate for intense agricultural activities in connection with orange production (Fig. 1b). In particular, our observations were made on a 100 m^2 area in an orange grove (*Citrus sinensis* Osbeck). Over 20 specimens producing compound traces were studied (Fig. 1c). Samples and photographs of specimens in larval and pupal stages were taken for classification and illustration. Observations were made between November and March.

3. DESCRIPTION OF BIOGENIC STRUCTURES

Three distinct morphologies are recognized from the proximal to the distal end of the trace:

3.1. Winding furrow trail (Figs 2a-b)

Unbranched, horizontal, unlined slightly sinuous furrows. Structures indicative of motion of the organism (such as
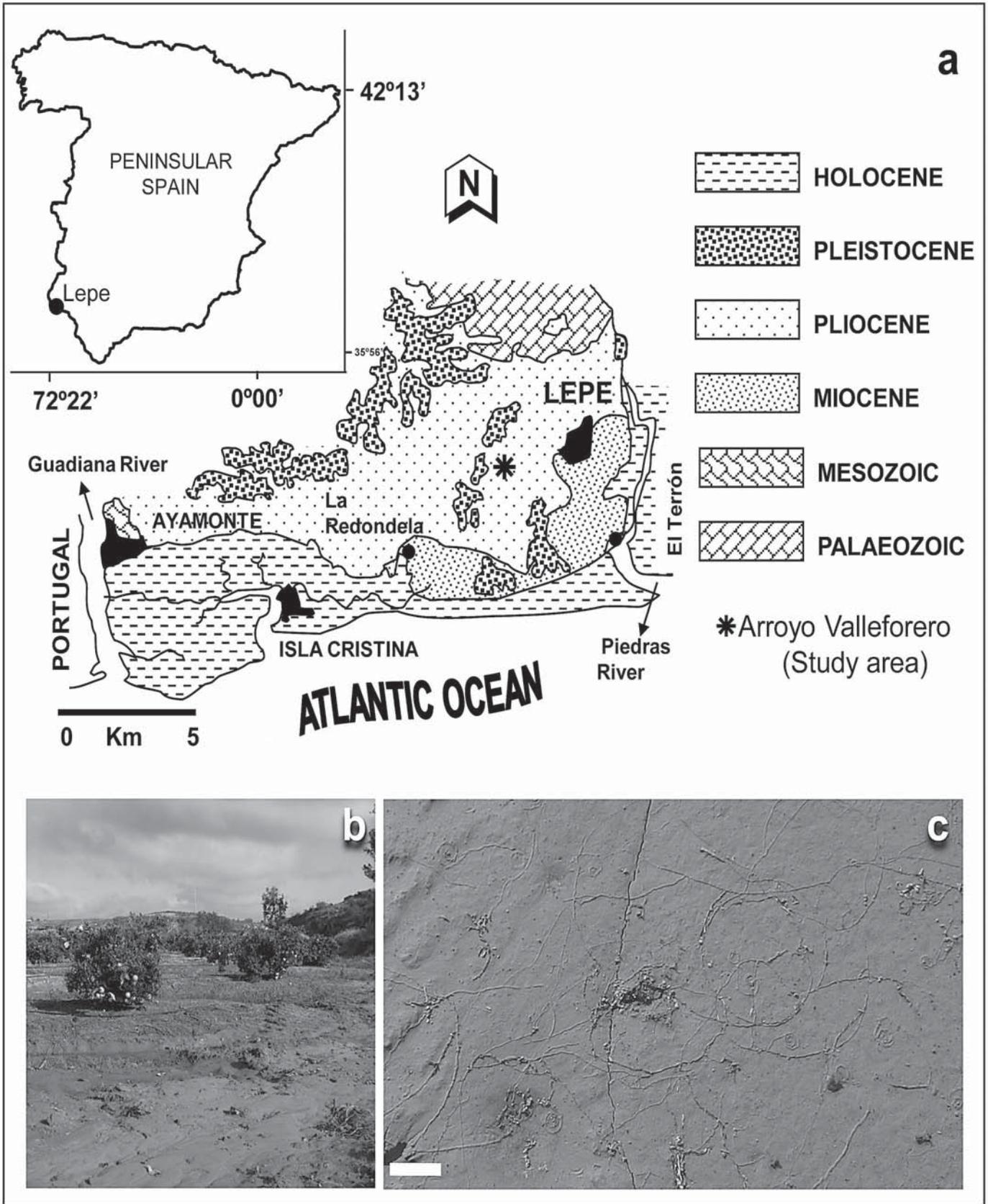
Figure 1. a) Geological map with location of the study area. **b)** Orange grove where the study was performed. **c)** General view of grove soil showing the density of occupation by bioturbating dipterans at various ontogenetic stages. Scale bar, 10 cm.
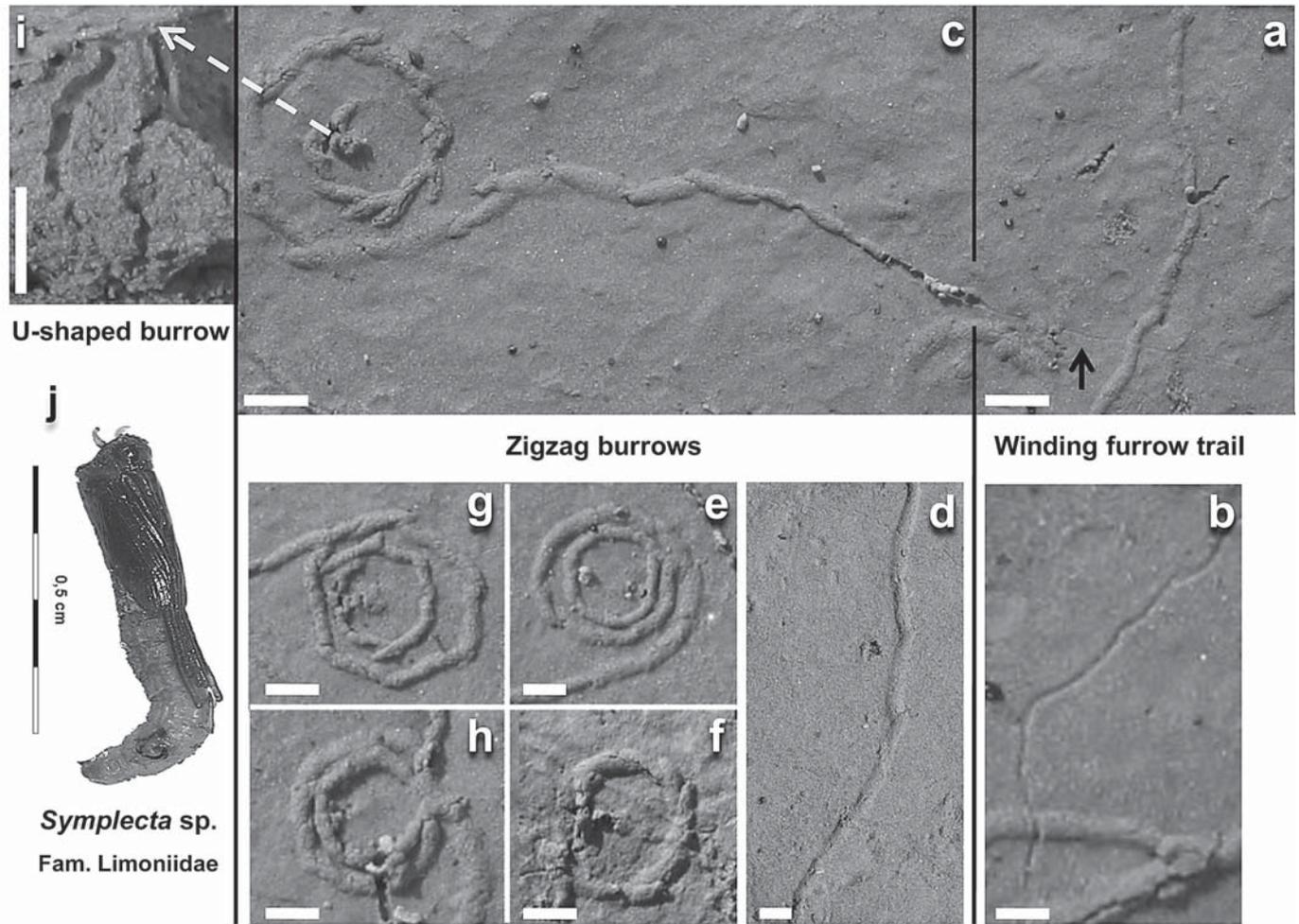
Figure 2. Different morphologies of fly larval and pupal traces, Lepe (Huelva, SW Spain). **a)** A winding trail (incipient *Helminthopsis*). **b)** Close-up of a winding trail. **c)** Straight to dextrorsal spiral zigzag burrow segment (incipient *Treptichnus*). **d)** Close-up of zigzag burrow with straight spindle-shaped segments. **e)** Sinistrorse spiral-shaped burrow (incipient aff. *Spirophycus*/aff. *Spirodesmos*). **f)** Dextrorse spiral zigzag burrows. **g)** Dextrorse spiral zigzag burrows. **h)** Sinistrorse spiral-shaped burrow. **i)** U-shaped vertical burrow (incipient *Arenicolites*). **j)** Fly pupa specimen belonging to *Symplecta* sp. (family Limoniidae). Scale bars in a-i, 1 cm.
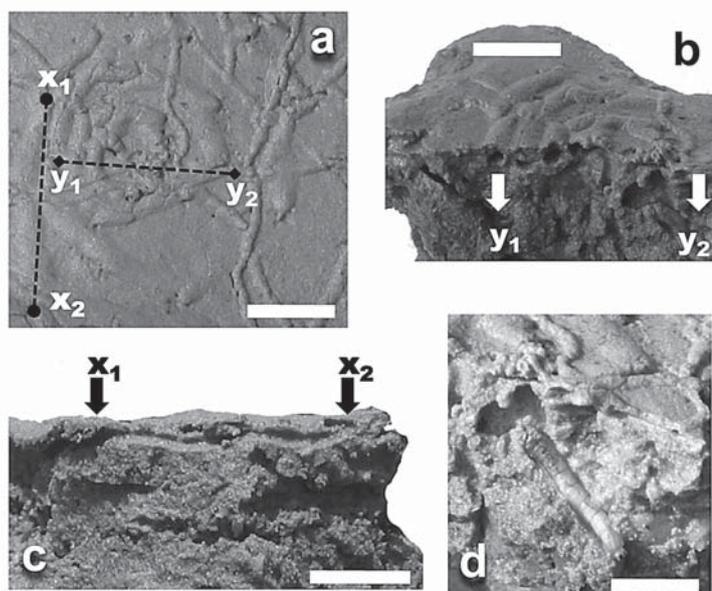

Figure 3. Sections of pupal burrows of *Symplecta*. **a)** Top view of zigzag burrows with a dextrorse spiral pattern. Two lines are indicated for sectioning the soft sediment. **b)** Circular cross sections of several zigzag burrow segments coiled in spiral (shown on "a"). **c)** Vertical longitudinal section of two zigzag segments approaching the spiral sector shown in "a". Note that path along the section is slightly sinuous, and show penetration into the sediment. **d)** Transitional state between the larval and pupal stages of the fly, exposed to the air after sectioning its burrow at the transitional sector between the winding furrow trail and the zigzag burrows. Scale bars, 0.5 cm.

sidelong, sediment accumulation or basal menisci) are absent. Width varies with ontogeny, from 0.2 mm in the proximal part up to 1.1 mm in the distal one. Maximum observed length is 13-15 cm. Preservation is as concave epirelief.

3.2. Zigzag burrows (Figs 2c-h)

Horizontal, unbranched traces consisting of short, spindle-shaped segments irregularly organized into a continuous zigzag pattern. The path is also irregular, evolving from straight-sinuous in its proximal part to spiral (either dextrorse Figs 2c-g-f or sinistrorse Figs 2e-h) in its distal part. Vertical longitudinal sections of the segments are slightly sinuous, and show penetration into the sediment (Fig. 3). Cross sections are circular. At the onset of the zigzag burrow shown on Fig. 2c (right part), the burrow wall is eroded thus permitting us to observe a very distinct peletoidal infill. The inner diameter is 1.0-1.5 mm, whereas outer width is 1.2-3.5 mm. The maximum observed length for this part of the trace is 24.7 cm. Segments are preserved as hollow full reliefs.

3.3. U-shaped burrow (Fig. 2i)

Complex, unlined U-shaped vertical burrow. The two shafts (which roughly keep parallel to each other along their paths) are perpendicular to the substrate at their openings, but then they deviate from the vertical and start meandering. Thus a curved first order path and a slightly sinuous second order path can be observed on both shafts. Shaft diameter is 1.5-1.9 mm. Maximum observed depth is approximately 2 cm. Preserved as full relief.
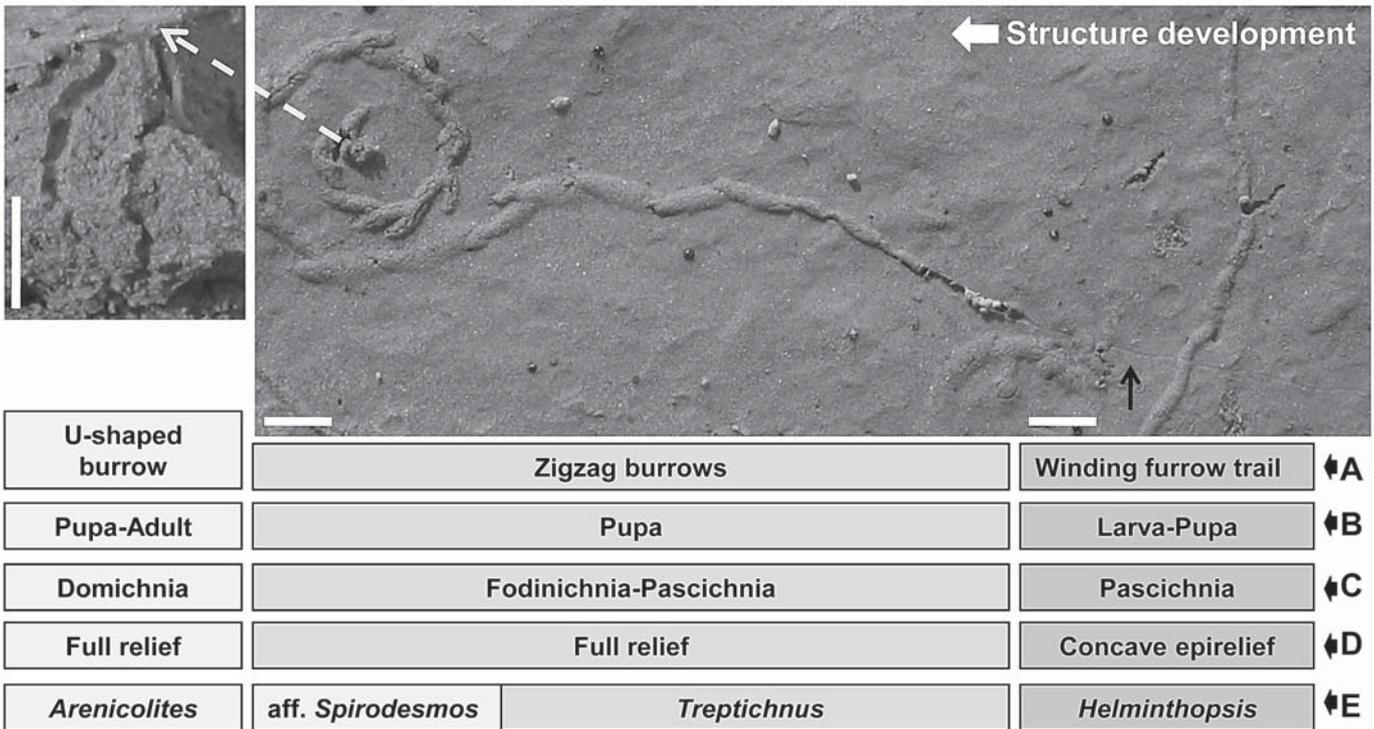
4. DISCUSSION

4.1. Implications for ichnotaxonomy

Fossil representatives of this biogenic structure would be assigned to different ichnotaxa depending on the portion of the trace preserved. The winding furrow shows affinities with *Helminthopsis*, the zigzag burrows with *Treptichnus*, the spiral portion with *Spirophycus* and *Spirodesmos*, and the U-shaped burrows with *Arenicolites*. In terms of a Seilacherian ethological classification, the winding furrow trails (incipient *Helminthopsis*) belong to pascichnia, the zigzag burrow system and the spiral burrow (incipient *Treptichnus*, *Spirophycus* and *Spirodesmos*) to fodinichnia, and the U-shaped burrow (*Arenicolites*) to domichnia (Fig. 4).

The observed structures are best understood as compound traces, which result from the changing behaviour of a single producer during its ontogeny (Pickerill, 1994; Pickerill & Narbonne, 1995). In the most common situation, such as the one documented in this study, the tracemaker behaves in distinct ways in chronological order, comprising intergradations of one ichnotaxon into another. This has been well documented in the fossil record, as illustrated by the transition between locomotion and resting traces, such as *Cruziana* and *Rusophycus* in the case of trilobites (Crimes, 1970; Mángano *et al*., 1996), and *Protovirgularia* and *Lockeia* in the case of bivalves (Mángano *et al*., 1998). However, other ethologic categories may be involved, as shown by the transition between the echinoid grazing trace *Scolicia* and its resting counterpart *Cardioichnus* (Smith & Crimes, 1983). In other cases, transitions may occur within an ethologic category, such as the more typical cases of the crustacean dwelling burrows *Ophiomorpha*, *Thalassinoides* and *Gyrolithes* (Bromley & Frey, 1974; Muñiz *et al*., 1995).

Although these chronological intergradations are well known from the fossil record, they are usually interpreted as behavioural changes mostly linked to the daily activities of the tracemakers. Our study documents for the first time that these intergradations may actually reflect an ontogenetic trajectory, opening a research line for the recognition of this phenomenon in the fossil record. Incidentally, these compound traces provide further information that sheds light on ichnotaxonomic debates. Our view fully agrees with that of Bromley's (1996, p. 166) perspective that "*in the final analysis, it is the morphology of the trace as an expression of animal behaviour that is the basis of the name*". Ichnology is forced to use a dual nomenclature, two separate names for biotaxa and ichnotaxa. Almost invariably, behavioural convergence rules out establishing a one-to-one relationship between a producer and a trace fossil. Inclusion of factors other than the morphologic expression of behaviour, such as identity of the tracemaker and depositional environment or age of the rocks, would be methodologically and conceptually flawed, because it would invariably lead to circular reasoning (see discussion in Buatois *et al*., 1997, and Buatois & Mángano, 2011).

This situation is clearly illustrated by some of the zigzag burrows observed at Lepe (Figs 5a-b). These burrows are morphologically identical to *Treptichnus pedum* (Fig. 5c), an ichnospecies whose first appearance indicates the Ediacaran-Cambrian boundary in shallow- to marginal-marine environments (Narbonne *et al*., 1987; Brasier *et al*., 1994; Buatois *et al*., 2013). *T. pedum* are most likely produced by priapulids (Vannier *et al*., 2010). The fact that zigzag burrows are present in strata of highly variable age, depositional environments and spectrum of fabricators is no ground for assigning such fossils to different ichnotaxonomic names (*contra* Dzik, 2005).

U-shaped burrow	Zigzag burrows		Winding furrow trail	A
Pupa-Adult	Pupa		Larva-Pupa	B
Domichnia	Fodinichnia-Pascichnia		Pascichnia	C
Full relief	Full relief		Concave epirelief	D
Arenicolites	aff. *Spirodesmos*	*Treptichnus*	*Helminthopsis*	E

A: morphology; B: ontogenetic stages of the producer; C: ethology; D: stratinomy; E: equivalent trace fossil

Figure 4. Summary diagram with empirical and interpretative data for a particular trace made by a larva and pupa of the genus *Symplecta*. Scale bars, 1 cm.

4.2. Tracemaker, ontogeny and ethology

Most tipulomorphs place their eggs in soils that are relatively humid or dry, and associated with a stagnant water body nearby. In the present case, the eggs were placed in a sandy substrate where humidity is constant due to artificial irrigation. *Symplecta* (see Fig. 2j) has a complete metamorphosic life cycle consisting of four ontogenetic stages and a larval stage consisting of four instars. Information on the European species, *S. hybrida* and *S. stricta*, indicates that the larva hatches from the egg between 26 and 45 days.

From a functional point of view, the structure is highly variable throughout construction, reflecting a series of behavioural changes of *Symplecta* that eventually are revealed by the production of a compound trace. These behaviours may have been influenced by the interplay of intrinsic factors such as ontogenetic stages and extrinsic constraints, such as substrate type. The winding furrow trail corresponds to the larval stages, that displays a progressive increase in trail width (Figs 2a-c, 6). The observed morphology suggests horizontal exploitation of the organic particles on the substrate (detritus feeding). In a subsequent phase, the organism constructs a complex infaunal burrow (zigzag burrow system), which may have been controlled jointly by sediment grain size and the size of the larvae. *Symplecta* may use blood pressure (through

volumetric changes in hemolymph) as an excavation tool. With increased burrowing capability, the pupa is able to burrow into the sediment. Indeed, trace width doubles at the shift from a winding furrow trail to a zigzag burrow (Figs 2a-d, 6). An alternative explanation to the construction of an infaunal structure is protection from predators. At the distal end of the zigzag burrow, another sharp change is detected in shape (associated to trace width decrease) where the pupa tends to form a spiral that either is dextral or sinistral. This change in pattern suggests feeding optimization through maximum exploitation of the substrate and minimum energy costs as a likely strategy for food acquisition (deposit feeding). This transition occurs before entering in an immobile phase near the end of the pupal stage, eventually producing the adult stage within the U-shaped burrow. The width of the spiral progressively decreases until the structure disappears into the substrate (Figs 2c, e, g, h, 6).

4.3. Environmental implications and the trace-fossil record

The genus *Symplecta* (familia Limoniidae) has a worldwide distribution, and inhabits riparian and marginal lacustrine environments. In the fossil record, this compound trace of *Symplecta* potentially may occur in lake-margin, fluvio-
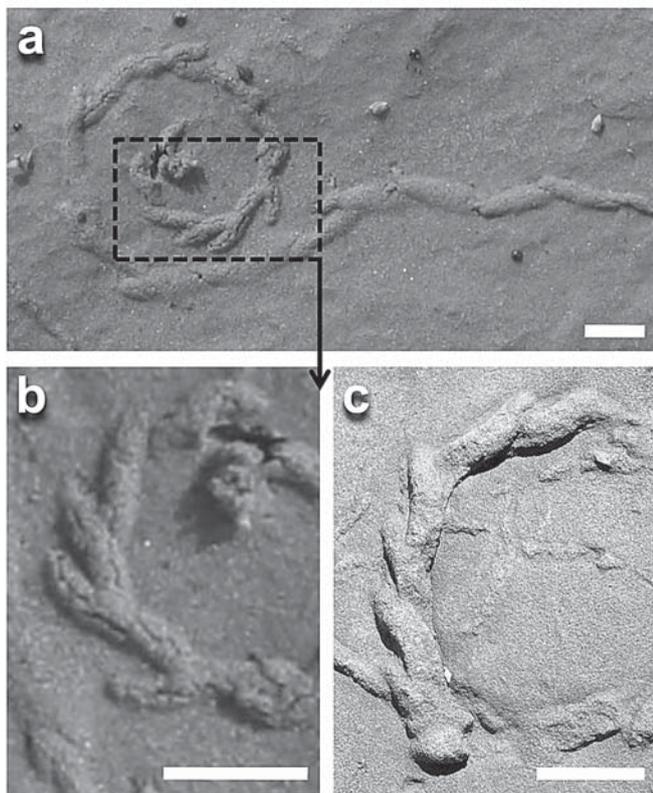
Figure 5. Similarities between the modern fly pupal zigzag burrows of Lepe (Huelva, SW Spain) and the Fortunian ichnospecies *Treptichnus pedum*. **a)** General view of a fly pupal zigzag burrow. **b)** Close-up of the burrow segment framed in "a" (rotated 90° clockwise), identical to *T. pedum*. **c)** Specimen of *T. pedum* from the Fortunian, Klipbak Formation, Vanrhynsdorp Group (South Africa). Scale bars, 1 cm.

estuarine and overbank deposits, such as those associated with levees, crevasse splays and ponds. Accordingly, such traces would form part of the *Scoyenia* or the *Mermia* ichnofacies. Unsurprisingly, similar structures to those described in this study have been recorded as common elements of freshwater ichnofaunas since the Devonian, particularly involving winding trails and zigzag burrows.

In particular, examples of the ichnogenus *Treptichnus* in fluvio-lacustrine and fluvio-estuarine settings are known from the Devonian of Wales (Morrissey & Braddy, 2004; Marriott *et al*., 2009); Carboniferous of Argentina (Buatois & Mángano, 1993a, b, 2003; Pazos 2000; Buatois *et al*., 2006, 2010; Pazos *et al*., 2007; Desjardins *et al*., 2010), Brazil (Netto *et al*., 2009), the United States (Archer & Maples, 1984; Maples & Archer, 1987; Buatois *et al*., 1997, 1998; Mángano *et al*., 2001; Lucas *et al*., 2004; Mángano & Buatois, 2004; Lucas & Lerner, 2005; Rindsberg & Kopaska-Merkel, 2005) and Canada (Keighley & Pickerill, 1997; Falcon-Lang *et al*., 2006); Permian of Antarctica (Miller & Isbell, 2010) and the United States (Haubold &

Lucas, 2001, 2003; Minter *et al*., 2007; Minter & Braddy, 2009); Triassic of the United States (Metz, 1995, 1996); Jurassic of the United States (Metz, 1992); Cretaceous of the United States (Buatois *et al*., 2000); Oligocene of Switzerland (Uchman *et al*., 2004); and the Pleistocene of England (Gibbard & Stuart, 1974) and Canada (Gibbard & Dreimanis, 1978).

4.4. Evolutionary history of diptera

The Diptera, or true flies, represents an old lineage of holometabolous insects (Grimaldi & Engel, 2005; Labandeira, 2005; Blagoderov *et al*., 2007). The mecopteroid precursors of the Diptera, as recorded by isolated wings or whole specimens with four wings, are known from upper Permian deposits (Willmann, 1989; Shcherbakov *et al*., 1995) and extend to the Late Pennsylvanian (Nel *et al*., 2007). The oldest true (i.e., two-winged) diptera have been recovered from Lower Triassic strata (Blagoderov *et al*., 2007). Recent molecular analysis (Bertone *et al*., 2008) placed the origin of crown group Diptera at approximately 267 Ma (middle Permian), marking the split between Deuterophlebiidae and all remaining Diptera. Accordingly, molecular-clock data point to a slightly earlier appearance for the crown group than the body-fossil record. Molecular data also indicate that further diversifications took place during the Mesozoic and that by the end of the Cretaceous (65 Ma) all major groups of extant lower (nematocerous) Diptera were already present (Bertone *et al*., 2008). Attribution of Palaeozoic freshwater *Treptichnus* to the Diptera remains speculative at this stage, and the most parsimonious interpretation is that the oldest freshwater zigzag structures likely were produced by other insects, reflecting behavioural convergence similar to the early Cambrian marine *Treptichnus*, produced by priapulids.

5. CONCLUSIONS

Modern fly larvae and pupae belonging to the genus *Symplecta* (family Limoniidae) were observed producing distinctive traces that display: (1), a proximal part characterized by a winding furrow trail; (2), an intermediate section consisting of zigzag burrows; and (3), a distal part comprising an U-shaped burrow. The zigzag burrow may vary from irregularly sinuous and curved in its most proximal part to a spiraled form distally. This structure illustrates a compound trace representing multiple behaviours during the ontogenetic stages of the producer and, if partially preserved, would be assigned different ichnotaxonomic names. The winding furrow and the zigzag burrows are produced, respectively, by *Symplecta* larvae
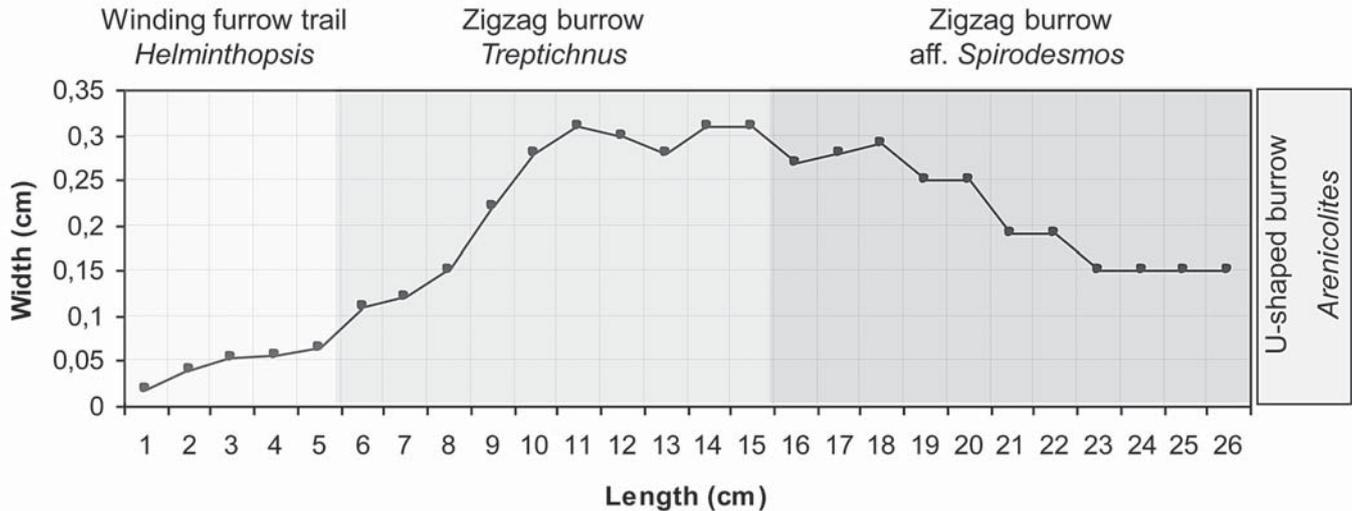
Figure 6. Length/width scatter diagram of the horizontal part of specimen illustrated in Figures 2a, c.

and pupae for feeding purposes, showing affinities with *Helminthopsis* and *Treptichnus*, respectively. By contrast, the U-shaped burrow is excavated during the end of the pupal stage for protection until adulthood, representing incipient *Arenicolites*. The spiral portion shows some similarities with *Spirophycus* and *Spirodesmos*. *Symplecta* presently inhabits riparian and marginal lacustrine environments. This is consistent with the trace-fossil record because segments of this compound trace are known in lake-margin, fluvio-estuarine transitions and overbank deposits, forming part of the *Scoyenia* or the *Mermia* ichnofacies since the Devonian. The body-fossil record and molecular-clock data place the origin of the Diptera around the Permian-Triassic boundary. Consequently, the occurrences of the oldest (pre-Permian) dipteran-like trace fossils may reflect behavioural convergence.

ACKNOWLEDGEMENTS

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