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Abstract

Modern fish are able to produce a plethora of different traces (both bioturbation and bioerosion structures) according to several behaviours, yet only five ichnotaxa have been interpreted as produced by the activity of fish in the fossil record. Many taphonomic factors may favour the non-fossilization of many of these traces and, even fossilized, they could have been misinterpreted. In this contribution, shallow and bilobed traces produced by the feeding activity of the perciform fish _Diplodus vulgaris_ (Sparidae) in the estuary of the Piedras

River (Lepe, Huelva, SW Spain) are described. Neoichnological study and comparison of these bioturbation structures with the fossil record allow associating them as *Cruziana-* and *Rusophycus-*like traces, i.e. traces with features very similar to those of such ichnogenera. Since these ichnotaxa have been commonly interpreted as the result of the locomotion and resting of different kinds of invertebrates, in order to get a better understanding of the marine and continental fossil record, we also propose taking into account fish as potential producers of these kind of traces in future paleoichnological studies.

1. Introduction

Fish behaviour, besides different modes of swimming (Sfakiotakis et al., 1999), also includes such activities as feeding, hunting, walking, flying, gliding or burrowing. Most of these behaviours have the potential to leave different types of bioerosion and/or bioturbation structures on a given substrate. Some members of the family Scaridae (parrotfish) or of the superorder Selachimorpha (sharks) are major bioeroders, either feeding on corals or leaving bitemarks on the bones of their prey, respectively (Warme, 1975; Muñiz et al., 2009). But it is as burrowers when their activity is noteworthy since, among vertebrates (especially at present), fish show one of the highest diversities with respect to number of different bioturbation strategies that they are able to carry out.

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There are many studies about modern fish bioturbation. For example: cichlid fishes, such as tilapia (Cichlidae), excavate circular nests and large burrows in lakes of southeastern Africa (Ribbink et al., 1981); male pufferfishes (Tetraodontidae) construct complex large geometric circular structures on the seabed probably to court females (Kawase et al., 2013); Atlantic sturgeon (Acipenseridae) leave feeding traces with the mouth and trails with the fins (Pearson et al., 2007); rays (Batoidea) excavate feeding depressions or pits by jetting water or by flapping their wings (Howard et al., 1977; Gregory et al., 1979; Martinell et al., 2001); male mudskippers (Oxudercinae) dig complex underwater burrows with air-filled egg chambers (Ishimatsu and Graham, 2011) and vertical shafts with turret-shaped openings (Takeda et al., 2011); gobiid fish (Gobiidae) may construct U-, W- and amphora-shaped burrows or branched burrow systems for dwelling and hiding (Atkinson et al., 1998; Gonzales et al., 2008; Minh Dinh et al., 2014) as well as large mounds of coral-rubble and sand over their burrows (Clark et al., 2000); tilefishes (Malacanthidae) excavate shafts and trenchs (Able et al., 1982; 1987); red band-fishes (Cepolidae) dig vertical shafts with funnel-shaped apertures and occasional branching (Atkinson and Pullin, 1996); weeverfishes (Trachinidae) usually leave resting traces on the seafloor (Seilacher, 2007); male warmouths and bluegills (Centrarchidae) excavate semi-bowl-like depressions used as nests (Martin, 2013); sea lampreys (Petromyzontidae) build nesting structures by gathering pebbles into a circle or semicircle, and scooping out a central depression (Chamberlain, 1975); sticklebacks (Gasterosteidae) create shallow depressions filled with vegetation glued with bodily secretions for nesting (Hansell, 1984); among others. In

summary, modern fish produce a plethora of different types of epi- or endogenic bioturbation structures in both fresh and marine waters at a variety of depths.

However, this great diversity of modern traces is not reflected in the fossil record. Despite the fact that some ichnogenera are very common and have a wide stratigraphic range (e.g. *Undichna*), trace fossils interpreted as produced by fish are scarce. In part, this may be because many of these traces have a very low preservation potential (mainly the epigenic ones), or because they have been misidentified and attributed to the activity of other organisms.

In the present paper, feeding traces produced by perciform fish *Diplodus vulgaris* (Geoffroy Saint-Hilaire, 1817) (Family Sparidae) in the estuary of the Piedras River (municipalities of Lepe and Cartaya, Huelva, SW Spain) are presented and compared with bilobate trace fossils. The main objectives of this study are: 1) to describe the morphology of these traces and to explain them from an ethological point of view and in relation to the ontogenetic stages of *D. vulgaris* and 2) to establish their implications in the fossil record from a comparison (ichnotaxonomic discussion) with similar ichnogenera interpreted as the result of fish activity or not.

2. Geographical and sedimentological setting of the Piedras Estuary

The Huelva Coast is located in the southwest of the Iberian Peninsula, specifically in the north sector of the Golfo de Cádiz (Gulf of Cádiz), and bounded to the west by the Guadiana River and to the east by the Guadalquivir River (Fig. 1A). This is a sandy, low relief coast with extensive beaches and littoral spits over 145 km in length, which is interrupted by important estuaries

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(those from Guadiana, Piedras, Odiel-Tinto and Guadalquivir rivers) in an advanced stage of sediment infilling (Borrego et al., 1995; Morales et al., 2001). This is a mesotidal coast with high tides around 3.37 m and low tides around 0.75 m (Borrego and Pendón, 1989; Delgado et al., 2005; Morales et al., 2010). The coast is framed by a Mediterranean climate with oceanic influence (Capel Molina, 1981), with an average annual temperature of 18.2 ºC and an average annual rainfall of 583 mm.

The Piedras Estuary (located between the municipalities of Lepe and Cartaya) constitutes a lagoon (Fig. 1B) with a progradational trend as a response to the progressive reduction of the tidal prism, which is caused by the advanced stage of sediment infilling of the estuary (Morales et al., 2001). The marine side of this estuary is characterized by a long, sandy spit (locally known as Flecha de Nueva Umbría or Flecha del Rompido) with an area of 534.7 ha, 12 km in length and 300-700 m in width. This spit runs parallel to the coast, developed from the union of several barrier islands and affected by rapid apical accretion (West-East) of wave bars (Delgado et al., 2005). Its origin and evolution results from a combination of the effect of tides, waves, longshore currents, and fluvial sediment input (Dabrio, 1982; Zazo et al., 1994; Borrego et al., 1995; Morales et al., 2001, 2010; Delgado et al., 2005; Gibert et al., 2013).

2.1. Study site

The study of the traces was carried out both in the inner coast of the spit (along the intertidal plain; Fig. 1B, C) as well as in a secondary channel located inside the salt marsh (Fig. 1B, D), both areas are influenced by flood and ebb

tidal currents. All observations were recorded during low tides, in March-April, 2009.

Sediments in the intertidal area consist of sandy mud to muddy sand, with a decreasing sand content toward the estuarine channel. During low tides the exposed intertidal area was around 20 m wide, with an upper boundary characterized by a dense accumulation of cockle shells *Cerastoderma edule* (Linnaeus, 1758). Main epi- and infaunal organisms inhabiting this area are the crustaceans *Uca tangeri* (Eydoux, 1835), *Pestarella tyrrhena* (Petagna, 1792), and *Carcinus maenas* (Linnaeus, 1758); bivalves such as the tellinoid *Scrobicularia plana* (Da Costa, 1778) and the cardiid *C. edule*; and onuphid polychaetes (Mayoral et al., 1994, Gibert et al., 2013).

Secondary channels, constituted by muddy sediments, have widths ranging from 0.5 to 2 m and maximum depths of 1.5 m. Channel sections show an open U-shaped morphology, with abundant *U. tangeri* burrows (Gibert et al., 2013). Both the intertidal areas as well as the walls of the secondary channels are intermittantly covered by algal mats, mainly composed of the genera *Chaetomorpha* Kützing, 1845 and *Ulva* (*Enteromorpha*) Linnaeus, 1753.

3. Methodology

During the period between high and low tides (approx. 6 hours), preliminary observations of the traces of interest and their producers were carried out in different locations of the estuary. After the traces were totally exposed by low tide, their maximum width was measured *in situ* (*n*=210). All

measurements were performed at random, both in the intertidal area of the main channel and in secondary channels.

Additionally, the feeding behaviour of *D. vulgaris* was simulated in experiments that were conducted in the laboratory with 19 carcasses and flat pieces of sculpting clay. Since it is a species highly commercialized in Spain, all specimens were obtained from local fish markets. In these experiments, marks were produced by scraping the flat surface of clay pieces with the upper incisor-like teeth of each specimen. The angle of attack ranged from 40⁰ to 50⁰, and pressure was kept constant. The body length of the fish (i.e. from the tip of the snout to the distal part of the spinal column) was measured, as well as the maximum width of the experimentally produced traces. All measurements (those obtained in the field and in the laboratory) were carried out with a vernier caliper with a precision of +/− 0.05 mm.

4. Ecology of *Diplodus vulgaris*

Familiy Sparidae comprises 33 genera and approximately 115 species (Chiba et al., 2009) and, as well as many families inside the Order Peciformes, its stratigraphic record ranges from the Eocene until today (Petterson, 1993). In general, its geographical distribution is quite wide, occupying shallow marine habitats ranging from tropical to temperate waters with some brackish-water tolerant species (Nelson, 1994). This diversity has been attributed to the great variety of different feeding strategies within the group (Day, 2002).

In particular, the species *Diplodus vulgaris* (Fig. 2) studied herein, is abundant in the Atlantic Ocean and the Mediterranean Sea, being of high

commercial value in southern Europe (FAO, 2004). This species is commonly known as 'mojarras' in Spanish, as 'safia' in Portuguese, and as 'two-banded sea bream' in English.

Diplodus vulgaris is considered a demersal species, inhabiting rocky and muddy seafloors and seagrasses in a bathymetric range from 0 to 150 m, usually exhibiting a gregarious behaviour (Lorenzo et al., 2002). Family Sparidae exhibits a non-selective omnivorous diet with some trophic variation during ontogeny, which is related to the development of teeth (Karpouzi and Stergiou, 2003). *Diplodus vulgaris* feeds mainly on polychaetes, small crustaceans (e.g. isopods) and bivalves (Osman and Mahmoud, 2009). During searching for food, individuals plow the sea floor with their upper incisor-like teeth leaving significant grooves on the sediment, which are the focus of this paper.

During the first ontogenetic stage (alevin), *D. vulgaris* preferentially inhabits protected areas like coastal lagoons and estuaries; this has been interpreted as a defense strategy against predators (Abecasis et al., 2009). Alevin stage ranges from the hatching to the first year (from 2.6 to 92.9 mm in average length; Gonçalvez et al., 2003). Thereafter, the juvenile stage ranges from years 1-4, reaching an approximate length of 120 mm (Gonçalvez et al., 2003). Sexual maturity is reached around 2 years old, and at this time the length is not significantly different between two sexes, ranging from 16 cm for males to 18 cm for females (Gonçalvez and Erzini, 2000). Adult stage is reached at 4 years, with a maximum life span around 12 years (Gonçalvez et al., 2003; Abecasis et al., 2009). During this period individuals may exceptionally reach 450 mm in length, although the most common lengths

range from 200 to 250 mm (Bauchot and Hureau, 1986). Abecasis et al. (2009) showed that specimens larger than 120 mm belonging to the species *D. vulgaris* and *D. sargus* leave the protection of the Ría Formosa coastal lagoon (Portugal; area very close to the Piedras Estuary), which is used as a nursery area during juvenile stages, and occupy the adjacent coastal areas during the winter.

5. Neoichnology: Feeding traces of *D. vulgaris*

Study of the traces allows differentiating two morphotypes:

- *Morphotype A* (Figs. 3A; 4A-D): a shallow, horizontal and longitudinally elongated, bilobed depression with a slightly concave cross-section (16-120 mm length; 5-15 mm width; up to 4 mm deep). The bilobation is characterized by two parallel grooves separated by a raised central ridge that is oriented lengthwise (≤ 1 mm width) and occasionally sinuous (Fig. 4B, C). At the base of these grooves and parallel to the main ridge, much less prominent longitudinal ridges or striations may occur (Fig. 4A).

  This morphotype is densely distributed along the muddy walls of the secondary channels, and these traces frequently overlap each other (Fig. 3B). In the intertidal plain of the main channel, preservation of the described features is poorer, since it is controlled by a coarser grain size (sands). In this area, traces may be oriented with their major axis parallel-subparallel to the channel axis, may be isolated or may be contiguous and exhibiting a zig-zag arrangement (Fig. 3A).

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- *Morphotype B* (Fig. 5A-D): two short, horizontally-elongated, parallel
  grooves (13 mm of maximum length; 6-11 mm width) separated by a
  raised central ridge, similar to that of 'morphotype A', however
  'morphotype B' exhibits a more penetrating or deep distal part (10 mm
  maximum depth) characterized by a U-shaped termination. The 'U'
  shape is open toward the proximal part, and the bend of the 'U' is
  commonly partially covered by a small mound of sediment (Fig. 5A, B,
  D). Additionally, its proximal part commonly presents a V-shaped
  morphology (Fig. 5B).

  Usually, distribution of this morphotype is limited to the edges of
  secondary channels (i.e. where the slope is steeper), where it is very
  abundant and overlaps with 'morphotype A' traces (Fig. 3B).

6. Discussion

6.1. Ethological implications of D. vulgaris *traces*

The traces described here are the direct result of the activity of *D. vulgaris* while grazing and feeding on the bottom of the Piedras River estuary. Resulting morphotypes are constrained by the movements that individuals perform to obtain food from the mud.

In the bilobed traces constituting 'morphotypes A and B', each lobe corresponds to the groove left by upper flattened (incisor-like) teeth located on each of the two premaxillae (Fig. 6B). The central ridge separating these two lobes corresponds to sediment flowing through the diastema present between

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the two biggest incisor-like teeth, which are located closer to the symphysis existing between the premaxillae, i.e. the two teeth located just in the mesial plane (Fig. 2B). Longitudinal striations if present are located parallel to the main central ridge (Figs. 4A; 5D), and are formed due to the slightly depressed areas existing between each of the other incisor-like teeth (Fig. 2B).

'Morphotype A' is the result of a front-to-back raking movement during which the sediment is gathered and accumulated in the lingual area of the upper incisor-like teeth, and finally picked up, sucked and ingested (Gállego and Mitjans, 1985) by closing the lower jaw (Fig. 6B, C).

'Morphotype B' is the consequence of a thrust into the surface sediments (bulldozing) combined with a forward raking movement of the upper incisor-like teeth (Fig. 6D). Additionally, the U-shaped morphology of the distal part of 'morphotype B' is similar to the semicircular section of the upper lip of *D. vulgaris*. By contrast, V-shaped morphology of the proximal part, whose apex is aligned with the main ridge, is equivalent to the angle existing between the two premaxillae.

Additional supports for these interpretations were obtained from simulations of the feeding behaviour of *D. vulgaris* conducted with 19 of their carcasses. In particular, traces very similar to those studied in the estuary were obtained by scraping the flat surface of clay pieces with the upper incisor-like teeth of each carcass (Fig. 7C, D). Width of the resulting traces (ranging from 3 to 8 mm) was compared with the body length (ranging from 100 mm to 190 mm) of the specimen used in each case (Fig. 7A).

Compared with the data obtained in the laboratory, the distribution of the 210 widths measured *in situ* during the field survey (average of 7.96 mm;

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ranging from 5 mm to 15 mm) shows that all of their producers would correspond with adult specimens (up to 4 years) according to the studies of Gonçalvez et al. (2003) (Fig. 7A, B).

6.2. Implications for the fossil record (Ichnotaxonomy)

Although the oldest known vertebrate burrow (Devonian) has been attributed to the activity of a lungfish (Romer and Olson, 1954), the ichnodiversity of trace fossils identified as fish bioturbation is low. In fact, only five ichnogenera have been described. These may be linked to two main fish behaviours (Fig. 8):

a) Swimming traces: *Undichna* Anderson, 1976 comprises trace fossils with a single horizontal wave, or set of horizontal waves (paired and parallel, or unpaired) of common wavelength and direction of travel (Minter and Braddy, 2006); *Parundichna* Simon et al., 2003 consists of swimming traces in which undulation of scratches is not induced by the trail fin, but by an active gait of paired fins with protruding fin rays (Simon et al., 2003); and *Broomichnium* (Kuhn, 1958), a small, bilaterally symmetrical trace composed of two pairs of thin linear or curvilinear imprints (Benner et al., 2008).

b) Feeding traces: *Piscichnus* Feibel, 1987, a steep-sided, cylindrical or plug-like to shallow, circular, dish-shaped structure of moderate to large size oriented concave upward, more or less vertical to bedding (Gregory, 1991); and *Osculichnus* Demírcan and Uchman, 2010, hypichnial, bilobate mounds, generally elliptical or crescentic in outline, having a

smaller and a larger, lip-like lobe separated by an undulate furrow (Demírcan and Uchman, 2010). Despite the fact that *Piscichnus* is commonly related to a feeding behaviour, this ichnogenus has been also interpreted as a nesting trace (e.g. Feibel, 1987).

Morphological features of trace fossils attributed to swimming fish are totally different from the modern Sparidae traces studied herein. With respect to feeding ichnogenera, *Piscichnus* (typified by *P. brownie* Feibel, 1987) clearly lacks the typical bilobed morphology of such traces. If ichnogenus *Osculichnus* (typified by *O. labialis* Demírcan and Uchman, 2010) is considered as a concave epirelief (equivalent expression to the hypichnial, bilobate mounds described in its diagnosis), then this trace would be constituted by two crescentic grooves separated by an undulate ridge; which in any case, is still far from 'morphotypes A and B'.

With respect to other trace fossils attributed to vertebrates with swimming behaviours, Thomson and Lovelace (2014) and Boyd and Loope (1984) described several Triassic reptile footmarks with longitudinal striations which could be comparable to the Sparidae traces examined in this study; although most of these footmarks lack their characteristic bilobed cross-section, the most evident difference is the common orientation of these swim traces against a lack of orientation in the Sparidae feeding traces.

So, following the proposal 'in the final analysis, it is the morphology of the trace fossils as an expression of animal behaviour that is the basis of the name' (Bromley,1996), if feeding traces produced by *D. vulgaris* were to become part of the fossil record, they could be assigned to a bilobed ichnotaxon based on their preservation as convex hyporelief (Fig. 6A).

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Several bilobed and/or bilateral trace fossils have been described in the fossil record, mainly attributed to the burrowing activity of invertebrate organisms. Ichnogenera *Cardioichnus* (typified by *C. planus* Smith and Crimes, 1983) and *Lockeia* James, 1879, interpreted as resting traces produced by irregular echinoids and burrowing bivalves respectively, have some comparable characters, mainly to 'morphotype B'. However, the oblique scratches and the ovoid-to-subquadrate outline of *Cardioichnus* as well as the non-bilobed, almond-shaped morphology of *Lockeia* differ much from this morphotype.

Conversely, overall morphology of ichnogenera *Cruziana* D'Orbigny, 1842, *Rusophycus* Hall, 1852 and *Didymaulichnus* Young, 1972 are which have more diagnostic features in common with both morphotypes. Among them, the two elongate ichnotaxa interpreted as locomotion traces, i.e. *Cruziana* and *Didymaulichnus*, share more similarities with 'morphotype A' and the bilateral resting trace *Rusophycus* with 'morphotype B'.

Despite *Didymaulichnus* is a bilobate furrow-like trail, the smooth surface (without any kind of bioglyphs) of its lobes and the possible presence of thin marginal ridges or bevels (Young, 1972; Pickerill et al., 1984) are quite different to the diagnostic features of 'morphotype A'.

Overall morphology of ichnogenus *Cruziana* shares many similarities with 'morphotype A'. The main difference lies in the arrangement of bioglyphs along the lobes; scratches are oblique with respect to the central ridge in *Cruziana* but the longitudinal striations in modern Sparidae traces are parallel. However, in the particular case of ichnospecies *C. acacensis eleongata* and *C. ac. acacensis* (see Seilacher, 2007: Plate 15), similarities increase because their scratches, though not longitudinal, are parallel or sub-parallel with respect to the

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central ridge as occur in 'morphotype A'. For these reasons, shorter specimens of 'morphotype A' and those belonging to 'morphotype B' are quite similar to certain *Rusophycus*-like structures.

The two feeding traces ('morphotypes A and B') produced by *D. vulgaris*, could be designated as 'cruzianaeform' or 'rusophyciform' traces which are informal groups proposed by Seilacher (2007). Nevertheless, biting/grazing/feeding ('morphotypes A and B'), plowing (cruzianaeform) and resting (rusophyciform) are very distinct burrowing behaviours , made in very different ways and resulting in very different structures (scratch marks versus burrows); we prefer to designate these modern Sparidae traces as *Cruziana*- or *Rusophycus*-like structures.

In the hypothetical case that future evidences demonstrate their presence in the geological record, the erection of new *Cruziana* or *Rusophycus* ichnospecies to define ichnotaxa related to fish feeding have to be considered. As knowledge about modern tracemakers increases, capability to interpret trace fossils also improves. New neoichnological data may reveal that previous identifications and interpretations of trace fossils may be incomplete or non-appropriate (e.g. Martinell et al., 2001).

In fact, in Neogene (upper Miocene) sediments located near Lepe, Muñiz et al. (2010) identified a unique specimen of bilobed trace as *Rusophycus* cf. *tugiensis* and they attributed it to crustacean activity. Despite the fact that this trace shows a much more rounded perimeter that 'morphotypes A and B', they share many similarities (Figs. 4; 5; 7C-E). Additionally, this ichnofossil was located in sedimentary rocks identified as deposits of a marginal bay or estuary that existed in the western sector of the Guadalquivir Basin (i.e. an environment

very similar to that of the Piedras estuary; see Gibert et al., 2013). Hence, a much more detailed study of this area and the discovery of new specimens will be needed to conclude if these trace fossils were produced by fish.

7. Conclusions

Based on the study of feeding traces produced by Recent *D. vulgaris* in the estuary of the Piedras River (Lepe, Huelva, Spain)*,* two morphotypes corresponding to two different feeding behaviours have been identified. Morphological features allow identifying them as *Cruziana-* and *Rusophycus-* like traces. In the fossil record, this kind of traces has been commonly attributed to the activity of different groups of invertebrates; thus, a new potential producer is proposed within pisces.

Comparisons between anatomical dimensions of modern *D. vulgaris* specimens and those of their traces could be very useful to infer the dimensions of possible counterparts in the fossil record.

This contribution highlights neoichnology as a very powerful tool to interpret and to better understand the trace fossil record.

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References

Abecasis, D., Bentes, L., Erzini, K., 2009. Home range, residency and
movements of *Diplodus sargus* and *Diplodus vulgaris* in a coastal lagoon:
Connectivity between nursery and adult habitats. Estuarine, Coastal and
Shelf Science 85, 525–529.

Able, K.W., Grimes, C.B., Cooper, R.A., Uzmann, J.R., 1982. Burrow
construction and behavior of tilefish, *Lopholatilus chamaeleonticeps*, in
Hudson submarine canyon. Environmental Biology of Fishes 7, 199–205.

Able, K.W., Twichell, D.C., Grimes, C.B., Jones, R.S., 1987. Tilefishes of the
genus *Caulolatilus* construct burrows in the sea floor. Bulletin of Marine
Science 40, 1–10.

Anderson, A., 1976. Fish trails from the Early Permian of South Africa.
Palaeontology 19, 397–409.

Atkinson, R.J.A., Pullin, R.S.V., 1996. Observations on the burrows and
burrowing behaviour of the red band-fish, *Cepola rubescens* L. P.S.Z.N. I
(Pubblicazioni della Stazione Zoologica di Napoli I): Marine Ecology 17,
23–40.

Atkinson, R.J.A., Froglia, C., Arneri, E., Antolini, B., 1998. Observations on the
burrows and burrowing behaviour of *Brachynotus gemmellari* and on the
burrows of several other species occurring on Squilla grounds off
Ancona, Central Adriatic. Scientia Marina 62, 91–100.

Bauchot, M., Hureau, J., 1986. Sparidae. In: Whitehead, P., Beauchot, M., Hureau, J., Nielsen, J., Tortose, E. (Eds.), Fishes of the North-eastern Atlantic and the Mediterranean, II. Unesco, Paris, pp. 883–907.

Benner, J.S., Ridge, J.C., Taft, N.K., 2008. Late Pleistocene freshwater fish (Cottidae) trackways from New England (USA) glacial lakes and a reinterpretation of the ichnogenus *Broomichnium* Kuhn. Palaeogeography, Palaeoclimatology, Palaeoecology 260, 375–388.

Borrego, J., Pendón, J.G., 1989. Caracterización del ciclo mareal en la desembocadura del Río Piedras (Huelva). *XII Congreso Nacional de Sedimentología*, pp. 97–100.

Borrego, J., Morales, J.A., Pendón, J.G., 1995. Holocene estuarine facies along the mesotidal coast of Huelva, southwestern Spain. In: Flemming, B.W., Bartholomä, A. (Eds.), Tidal Signatures in Modern and Ancient Sediments. Special Publications of the International Association of Sedimentologists 24, 151–170.

Boyd, D.W., Loope, D.B., 1984, Probable vertebrate origin for certain sole marks in Triassic red beds of Wyoming. Journal of Paleontology 58, 467–476.

Bromley, R.G., 1996. Trace Fossils. Biology, Taphonomy and Applications. Second Edition, Chapman & Hall, London, 361 pp.

Capel Molina, J.J., 1981. Los climas de España. Oikos-Tau, Barcelona, 429 pp.

Chamberlain, C.K., 1975. Recent lebensspuren in nonmarine aquatic environments. In: Frey, R.W. (Ed.), The study of trace fossils. A synthesis of principles, problems and procedures in ichnology. Springer-Verlag, New York, pp. 431–458.

Chiba, S.N., Iwatsuki, Y., Yoshino, T., Hanzawa, N., 2009. Comprehensive phylogeny of the family Sparidae (Perciformes: Teleostei) inferred from mitochondrial gene analyses. Genes & Genetic Systems 84, 153–170.

Clark, E., Stoll, M.J., Alburn, T.K., Petzold, R., 2000. Mound-building and feeding behavior of the twostripe goby, *Valenciennea helsdingenii*, in the south Red Sea. Environmental Biology of Fishes 57, 131–141.

Dabrio, C.J., 1982. Sedimentary structures generated on the foreshore by migrating ridge and runnel systems on microtidal and mesotidal coast on S Spain. Sedimentary Geology 32, 141–151.

Da Costa, E. M., 1778. Historia Naturalis Testaceorum Britanniae, or the British Conchology. Millan, B. White, Elmsley & Robson, London, xiv + 254 + viii p., 16 pls.

Day, J.J., 2002. Phylogenetic relationships of the Sparidae (Teleostei: Percoidei) and implications for convergent trophic evolution. Biological Journal of the Linnean Society 76, 269–301.

Delgado, I., Morales, J.A., Gutiérrez Mas, J.M., 2005. Dinámica de formas de fondo en la desembocadura del estuario del Río Piedras (Huelva). Geogaceta 38, 143–146.

Demírcan, H., Uchman, A., 2010. Kiss of death of a hunting fish: trace fossil *Osculichnus labialis* igen. et isp. nov. from late Eocene - early Oligocene prodelta sediments of the Mezardere Formation, Thrace Basin, NW Turkey. Acta Geologica Polonica 60, 29–38.

D'Orbigny, A.C.V., 1842. Voyage dans l'Amérique Méridionale, Tome Troisième, 4. Partie, Paléontologie. Paris and Strasbourg: Pitois-Levrault et Levrault, 188 pp.

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Eydoux, F., 1835. Nouvelle espèce de Gélasime. Magasin de Zoologie 5, 1–4.

FAO (Food and Agriculture Organization of the United Nations), 2004. State of World Fisheries and Aquaculture. Fisheries and Aquaculture Department, Rome, Italy, 153 pp.

Feibel, C.S., 1987. Fossil fish nests from the Koobi Fora Formation (Plio-Pleistocene) of northern Kenya. Journal of Paleontology 61, 130–134.

Gállego, L., Mitjans, G., 1985. La diversificación de los Sparidae (Pisces) basada en las fórmulas dentarias. Trazos, Trabajos Zoológicos 3, 2–26.

Geoffroy Saint-Hilaire, E., 1817. Poissons de la Mer Rouge et de la Méditerranée *In: Description de l'Égypte*... Paris, Planches Histoire Naturelle, 1, Poissons, pl. 18–27.

Gibert, J.M. de, Muñiz, F., Belaústegui, Z., Hyžný, M., 2013. Fossil and modern fiddler crabs (*Uca tangeri:* Ocypodidae) and their burrows from SW Spain: ichnologic and biogeographic implications. Journal of Crustacean Biology 33, 537–551.

Gonçalvez, J.M.S., Erzini, K., 2000. The reproductive biology of the two-banded sea bream (*Diplodus vulgaris*) from the southwest coast of Portugal. Journal of Applied Ichthyology 16, 110–116.

Gonçalves, J.M.S., Bentes, L., Coelho, R., Correia, C., Lino, P.G., Monteiro, C.C., Ribeiro, J., Erzini, K., 2003. Age and growth, maturity, mortality and yield-per-recruit for two banded bream (*Diplodus vulgaris* Geoffr.) from the south coast of Portugal. Fisheries Research 62, 349–359.

Gonzales, T.T., Katoh, M., Ishimatsu, A., 2008. Intertidal burrows of the air-breathing eel goby, *Odontamblyopus lacepedii* (Gobiidae: Amblyopinae). Ichthyological Research 55, 303–306.

Gregory, M.R., 1991. New trace fossils from the Miocene of Northland, New Zealand: *Rorschachichnus amoeba* and *Piscichnus waitemata*. Ichnos 1, 195–205.

Gregory, M.R., Mallance, P.F., Graham, W.G., Ayling, A.M., 1979. On how some rays (Elasmobranchia) excavate feeding depressions by jetting water. Journal of Sedimentary Petrology 49, 1125–1130.

Hall, J., 1852. Palaeontology of New York, Volume II. Containing descriptions of the organic remains of the Lower Division of the New York System (equivalent in part to the Middle Silurian rocks of Europe). C. van Benthuysen, Albany, 362 pp.

Hansell, M.H., 1984. Animal architecture and building behavior. Longman Group, New York, 324 pp.

Howard, J.D., Mayou, T.V., Heard, R.W., 1977. Biogenic sedimentary structures formed by rays. Journal of Sedimentary Petrology 47, 339–346.

Ishimatsu, A., Graham, J.B., 2011. Roles of environmental cues for embryonic incubation and hatching in mudskippers. Integrative and Comparative Biology 51, 38–48.

James, U.P., 1879. Description of new species of fossils and remarks on some others, from the Lower and Upper Silurian rocks of Ohio. The Paleontologist 3, 17–24.

Karpouzi, V.S., Stergiou, K.I., 2003. The relationships between mouth size and shape and body length for 18 species of marine fishes and their trophic implications. Journal of Fish Biology 62, 1353–1365.

Kawase, H., Okata, Y., Ito, K., 2013. Role of huge geometric circular structures in the reproduction of a marine pufferfish. Scientific Reports 3, 2106; DOI: 10.1038/srep02106.

Kuhn, O., 1958. Die Fährten der vorzeitlichen Amphibien und Reptilien. Bamberg, Meisenbach KG, Hamburg, 64 pp.

Kützing, F.T., 1845. *Phycologia germanica*, d. i. Deutschlands Algen in bündigen Beschreibungen. Nebst einer Anleitung zum Untersuchen und Bestimmen dieser Gewächse für Anfänger. pp. i-x, pp. 1–340. Nordhausen: W. Köhne.

Linnaeus, C. 1753. Species plantarum, Tomus II. Holmiae, Stockholm, pp. 561–1200.

Linnaeus, C., 1758. Systema Naturae per Regna Triae Naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. 10th edition, vol. 1. Holmiae (Stockholm), L. Salvii (824 pp.).

Lorenzo, J.M., Pajuelo, J.G., Méndez-Villamil, M., Coca, J., Ramos, A.G., 2002. Age, growth, reproduction and mortality of the striped seabream, *Lithognathus mormyrus* (Pisces, Sparidae), off the Canary Islands (Central-east Atlantic). Journal of Applied Ichthyology 18, 204–209.

Martin, A.J., 2013. Life traces of the Georgia coast. Revealing the unseen lives of plants and animals. Indiana University Press, Indiana, USA 670 pp.

Martinell, J., Gibert, J.M. de, Domènech, R., Ekdale, A.A., Steen, P.P., 2001. Cretaceous ray traces?: an alternative interpretation for the alleged dinosaur tracks of La Posa, Isona, NE Spain. Palaios 16, 409–416.

Mayoral, M. A., López-Serrano, L., Vieitez. J.M., 1994. Macrofauna bentónica intermareal de tres playas de la desembocadura del río Piedras (Huelva, España). Boletín de la Real Sociedad Española de Historia Natural. Sección Biológica 91, 231–240.

Minh Dinh, Q., Qin, J.G., Dittmann, S., Tran, D.D., 2014. Burrow morphology and utilization of the goby (*Parapocryptes serperaster*) in the Mekong Delta, Vietnam. Ichthyological Research 61, 332–340.

Minter, N.J., Braddy, S.J., 2006. The fish and amphibian swimming traces *Undichna* and *Lunichnium*, with examples from the Lower Permian of New Mexico, USA. Palaeontology 49, 1123–1142.

Morales, J.A., Borrego, J., Jiménez, I., Monterde, J.R., Gil, N., 2001. Morphostratigraphy of an ebb-tidal delta system associated with a large spit in the Piedras Estuary mouth (Huelva Coast, Southwestern Spain). Marine Geology 172, 225–241.

Morales, J.A., Delgado, I., Borrego, J., Cantano, M., Rodríguez Ramírez, A., 2010. Nueva Umbría spit: a guide for a physiographic and dynamic understanding. In: Muñiz, F., Gibert, J.M. de, Mayoral, E., Belaústegui, Z. (Eds.), Fieldtrip Guidebook, Workshop on Crustacean Bioturbation Fossil and recent. Huelva, Universidad de Huelva, pp. 29–36.

Muñiz, F., Toscano, A., Bromley, R.G., Esperante, R., 2009. Excepcional caso de interacción trófica entre tiburones hexanchiformes y una ballena Balaenoptera en el Plioceno Inferior de Huelva (SO de España). In: Palmqvist, P., Pérez-Claros, J.A. (Coords.), Comunicaciones de las XXV Jornadas de la Sociedad Española de Paleontología, Universidad de Málaga, pp. 242–244.

Muñiz, F., Gibert, J.M. de, Mayoral, E., Belaústegui, Z., 2010. Fieldtrip Guidebook, Workshop on Crustacean Bioturbation - Fossil and recent. University of Huelva, Huelva, Spain, 46 pp.

Nelson, J.S., 1994. Fishes of the World. Wiley, New York, NY, 600 pp.

Osman, A.M., Mahmoud, H.H., 2009. Feeding biology of *Diplodus sargus* and *Diplodus vulgaris* (Teleostei, Sparidae) in Egyptian Mediterranean waters. World Journal of Fish and Marine Sciences 1, 290–296.

Pearson, N.J., Gingras, M.K., Armitage, I.A., Pemberton, S.G., 2007. Significance of Atlantic sturgeon feeding excavations, Mary's Point, Bay of Fundy, New Brunswick, Canada. Palaios 22, 457–464.

Petagna, V., 1792. Institutiones Entomologicae. Naples, 718 pp.

Petterson C. 1993. Vertebrates, Osteichthyes: Teleostei. In: Benton M.J. (Ed.), The Fossil Record 2. London, Chapman & Hall, pp. 621–657.

Pickerill, R.K., Romano, M., Melendez, B., 1984. Arenig trace fossils from the Salamanca area, western Spain. Geological Journal 9, 249–263.

Ribbink, A.J., Marsh, A.C., Marsh, B.A., 1981. Nest-building and communal care of young by *Tilapia rendalli* Dumeril (Pisces, Cichlidae) in Lake Malawi. Environmental Biology of Fishes 6, 219–222.

Romer, A.S., Olson, E.C., 1954. Aestivation by Permian lungfish. Brevoria 30, 1–8.

Seilacher, A., 2007. Trace Fossil Analysis. Springer-Verlag, Berlin Heidelberg, New York, 226 pp.

Sfakiotakis, M., Lane, D.M., Davies, J.B.C., 1999. Review of fish swimming modes for aquatic locomotion. IEEE (Institute of Electrical and Electronics Engineers) Journal of Oceanic Engineering 24, 237–252.

Simon T., Hagdorn H., Hagdorn M.K., Seilacher A., 2003. Swimming trace of Coelacanth fish from the Lower Keuper of South-West Germany. Palaeontology 46, 911–926.

Smith, A.B., Crimes, T.P., 1983. Trace fossils formed by heart urchins - a study of *Scolicia* and related traces. Lethaia 16, 79–92.

Takeda, T., Hayashi, M., Toba, A., Soyano, K., Ishimatsu, A., 2011. Ecology of the Australian mudskipper *Periophthalmus minutus*, an amphibious fish inhabiting a mudflat in the highest intertidal zone. Australian Journal of Zoology 59, 312–320.

Thomson, T.J., Lovelace, D.M., 2014. Swim track morphotypes and new track localities from the Moenkopi and Red Peak Formations (Lower-Middle Triassic) with preliminary interpretations of aquatic behaviors. In: Lockley, M.G., Lucas, S.G. (Eds.), Fossil footprints of western North America, NMMNHS (New Mexico Museum of Natural History and Science) Bulletin 62, pp. 103–128.

Warme, J.E., 1975. Borings as trace fossils, and the processes of marine bioerosion. In: Frey, R.W. (Ed.), The study of trace fossils. A synthesis of principles, problems and procedures in ichnology. Springer-Verlag, New York, pp. 181–227.

Young, F.G., 1972. Early Cambrian and older trace fossils from the Southern Cordillera of Canada. Canadian Journal of Earth Sciences 9, 1–17.

Zazo, C., Goy, J.L., Somoza, L., Dabrio, C.J., Belluomini, G., Improta, S., Lario, J., Bardaji, T., Silva, P.G., 1994. Holocene sequence of sea-level fluctuation in relation to climatic trends in the Atlantic-Mediterranean linkage coast. Journal of Coastal Research 10, 933–945.

Figure captions

Fig.1. Geographical and geological map, and location of the areas studied herein, indicated by the black and white stars.

Fig. 2. *Diplodus vulgaris*. A. Side view. B. Ventral view of the two premaxillae (upper jaw).

Fig. 3. Feeding traces of *Diplodus vulgaris* in the estuary of the Piedras River. A. Traces located in the intertidal plain of the main channel (mainly 'Morphotype A'). B. Traces located in the edges of secondary channels (both morphotypes).

Fig. 4. 'Morphotype A'. A to D. Different specimens of straight (A and D) or sinuous (B and C) bilobed traces. Note specimen showing less prominent ridges parallel to the main ridge in A. Scale bar: 5 mm.

Fig. 5. 'Morphotype B'. A to D. Different specimens showing the deep and U-shaped distal part that characterizes this morphotype. Note specimen showing the common V-shaped proximal part in B; and specimen showing less prominent ridges parallel to the main ridge in D. Scale bar: 5 mm.

Fig. 6. Ethological and constructional interpretation of the feeding traces of *Diplodus vulgaris*. A. Mode of preservation. B and C. Behaviour of *D. vulgaris* producing 'morphotype A', i.e. a front-to-back ranking movement during which the sediment is gathered in the lingual area of the upper incisor-like teeth, and

finally picked up by closing the lower jaw. D. Movement of *D. vulgaris* producing 'morphotype B', i.e. a thrust of the surface sediments (bulldozing) combined with a forward raking.

Fig. 7. A. Graphic illustrating the relation between the width of the traces (those experimentally produced) versus the body length of 19 specimens of *Diplodus vulgaris*, and the relation with its ontogenetic stages (white circles). B. Line joining the black circles shows the width distribution of the 210 traces measured in the field. White star show the average width of field measurements (7.96 mm). C and D. Experimental traces (epireliefs) very similar to 'morphotypes A and B' respectively. E. Bilobed trace preliminary identified as *Rusophycus* cf. *tugiensis* (hyporelief) by Muñiz et al. (2010) in Miocene deposits of Lepe. Scale bar: 5 mm.

Fig. 8. Main ichnogenera related to feeding and swimming activity of fish, and a representation of their likely tracemakers. Drawings: *Undichna* and *Parundichna* from Seilacher (2007); *Broomichnium* from Benner et al. (2008); *Piscichnus* after Gregory et al. (1979); *Osculichnus* from Demírcan and Uchman (2010).
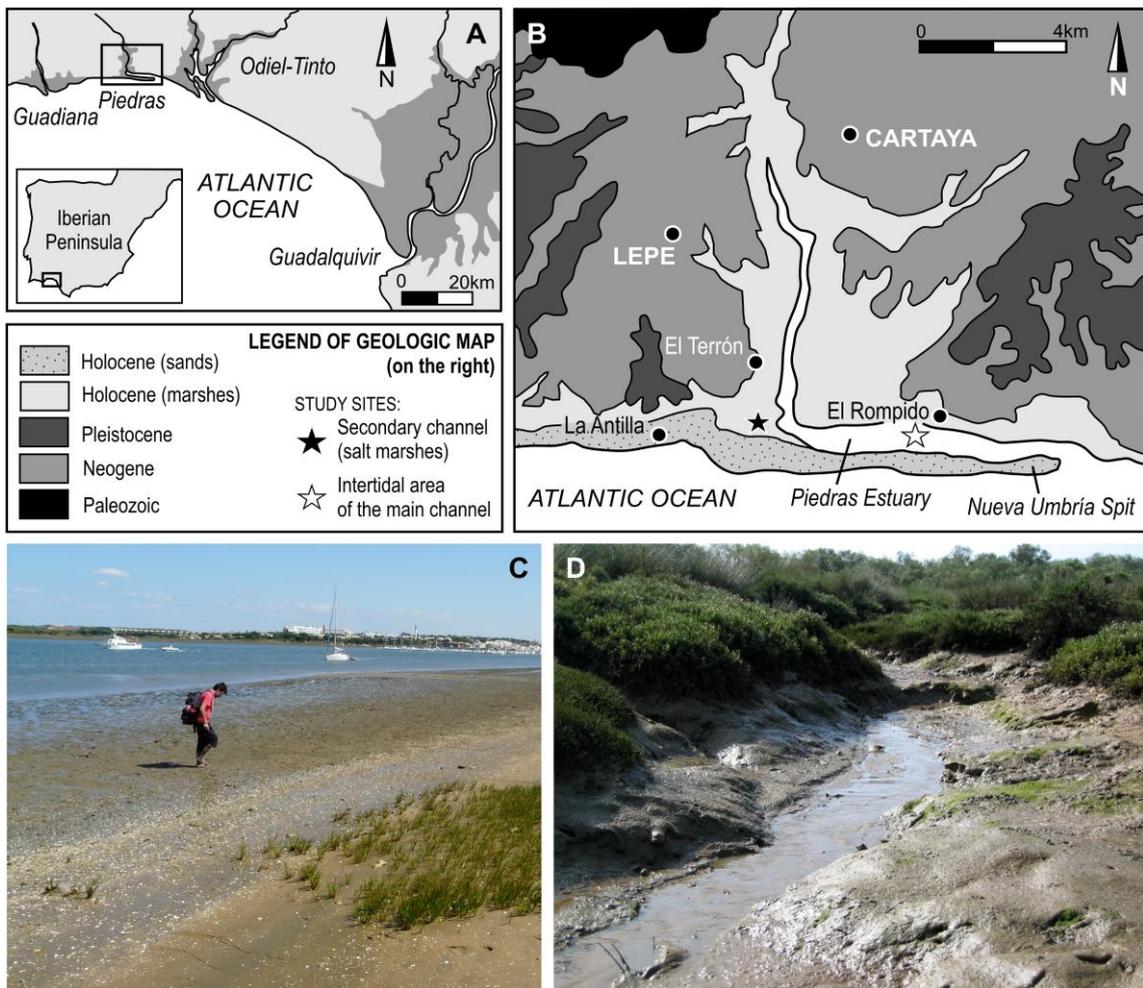
Figure 1

Figure 2
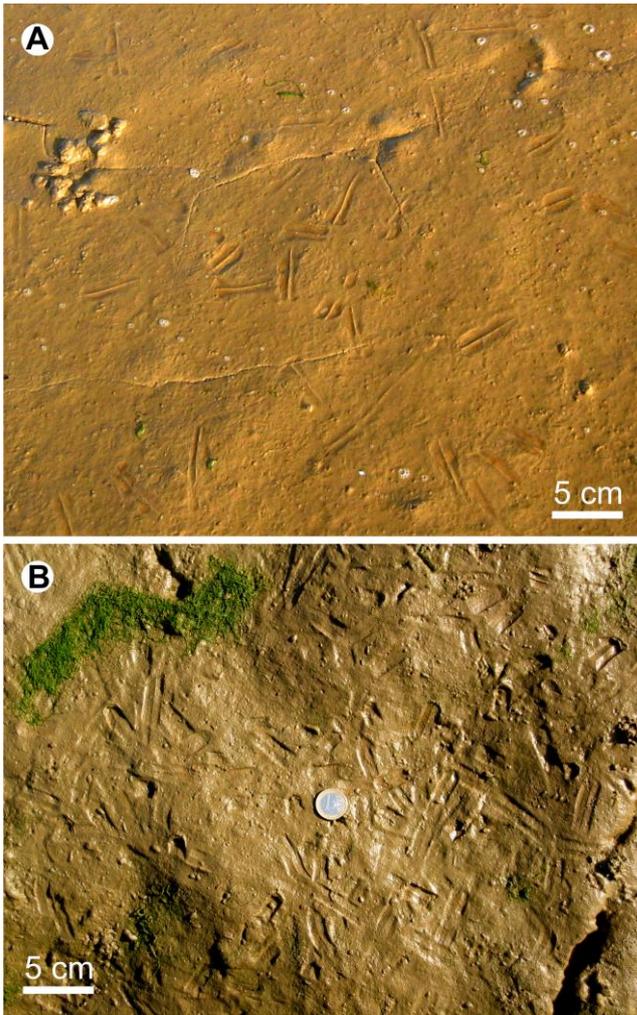
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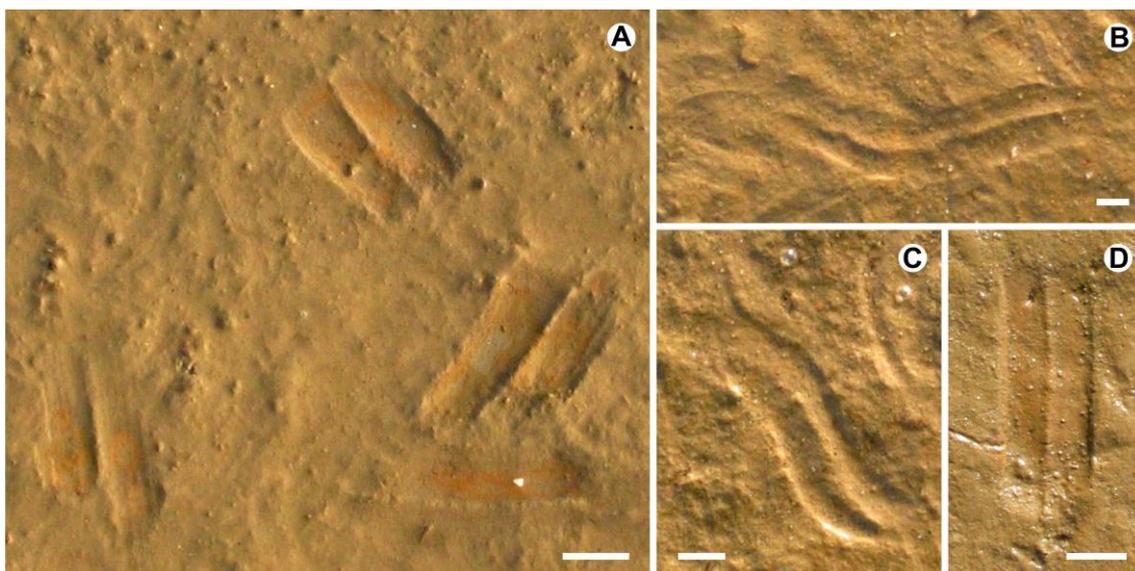
Figure 4
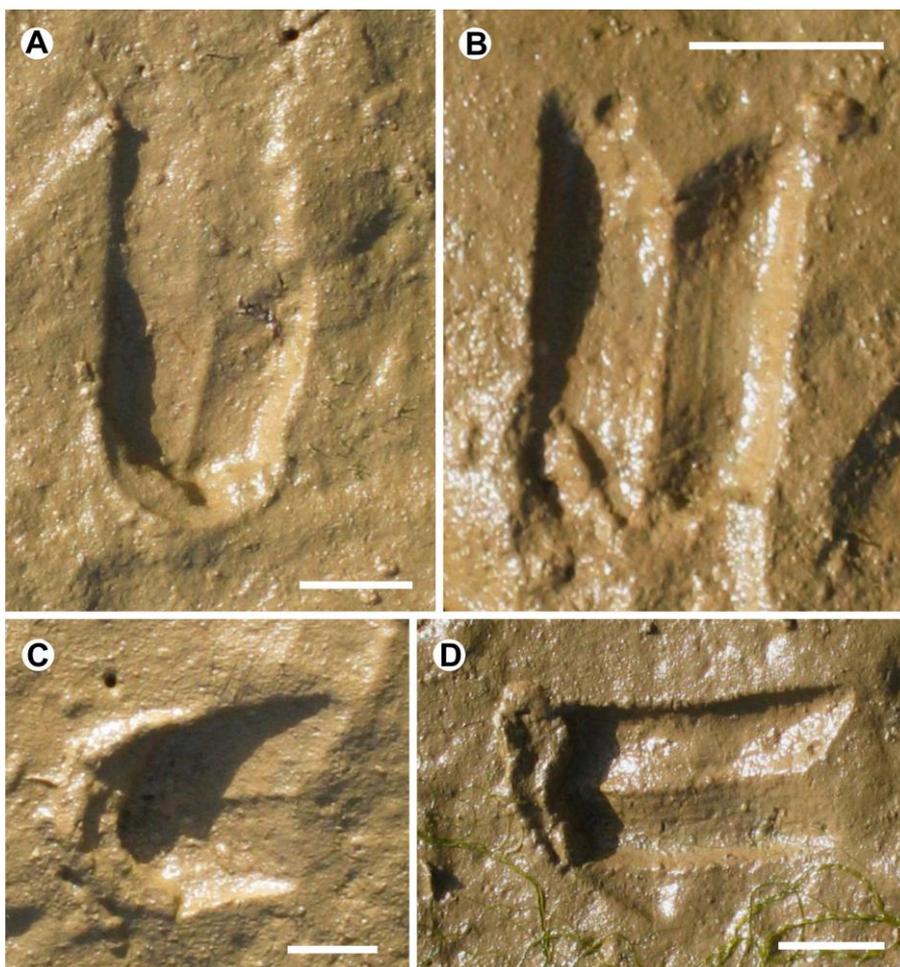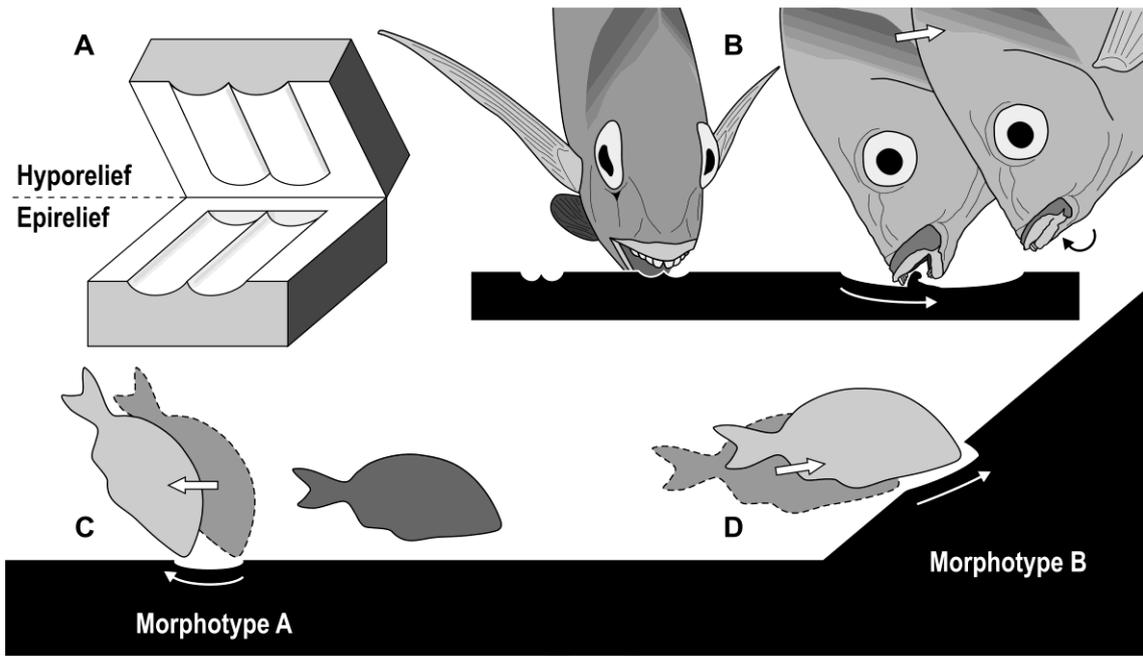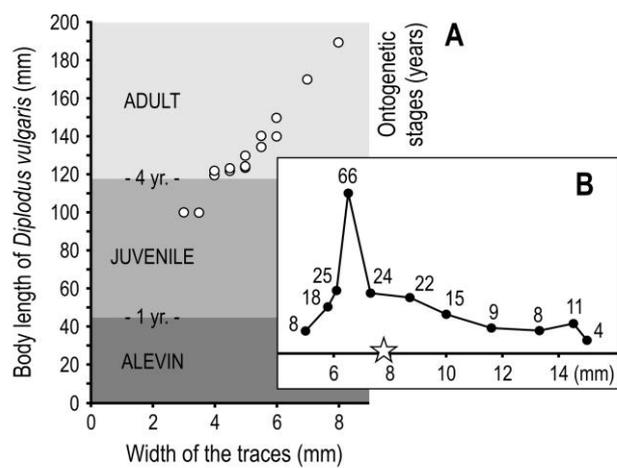
Figure 5

Figure 6

Figure 7

ICHNOGENUS	SCHEMATIC ILLUSTRATION OF TRACES	INTERPRETATIVE DRAWING FOR THE PRODUCTION
SWIMMING TRACES *Undichna* Anderson, 1976		
Parundichna Simon et al., 2003		
Broomichnium (Kuhn, 1958)		
FEEDING TRACES *Piscichnus* Feibel, 1987		
Osculichnus Demírcan & Uchman, 2010		
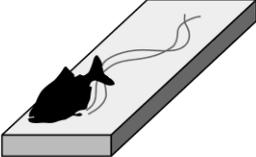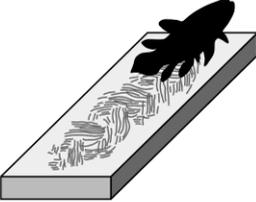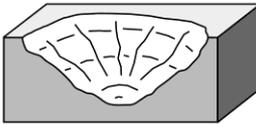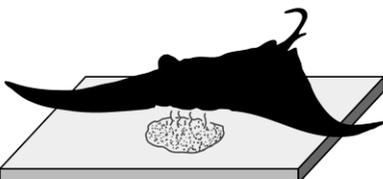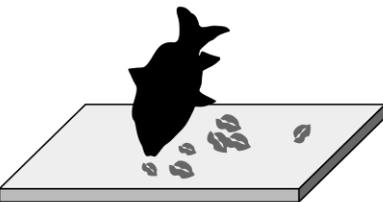
Figure 8

***Cruziana*- and *Rusophycus*-like traces of recent Sparidae fish in the estuary of the Piedras River (Lepe, Huelva, SW Spain)**

Fernando Muñiz, Zain Belaústegui, Carolina Cárcamo, Rosa Domènech, Jordi Martinell

Highlights

- Feeding traces of Sparidae fish are described in the Piedras Estuary (Lepe, Spain).

- Two morphotypes corresponding to two different feeding behaviours are identified.

- Morphological features allow identifying them as *Cruziana*- or *Rusophycus*- traces.

- *Cruziana* and *Rusophycus* are commonly attributed to fossil invertebrate activity.

- Neoichnology allows consider fish as possible producers of *Cruziana* and *Rusophycus*.