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EVOLUTION

The earliest evidence of deep-sea vertebrates

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Vertebrate macroevolution has been punctuated by fundamental habitat transitions from shallow marine origins to terrestrial, freshwater, and aerial environments. Invasion of the deep sea is a less well-known ecological shift because of low fossilization potential and continual loss of abyssal fossil record by ocean floor subduction. Therefore, there has been a lack of convincing evidence of bottom-living vertebrates from pre-Paleogene deep seas. Here, we describe trace fossils from abyssal plain turbidites of the Tethys Ocean, which, combined with nannofossil dating, indicate that fishes have occupied the deep seafloor since at least the Early Cretaceous (Hauterivian–Barremian). These structures are identical to those produced by modern demersal fishes that feed by either scratching the substrate or expose their prey by water flow generated by suction or jetting. The trace fossils suggest activity of at least three fish species exploiting a productive abyssal invertebrate sediment fauna. These observations are consistent with Early Cretaceous vertebrate transition to the deep sea triggered by the availability of new food sources. Our results anticipate the appearance of deep-seafloor fishes in the fossil record by over 80 My while reassessing the mode of vertebrate colonization of the deep sea.

palaeontology | evolution | Cretaceous | deep sea

Significance

Vertebrates are a prominent component of modern deep-sea ecosystems. However, there has been no fossil evidence of deep-seafloor vertebrates older than 50 My. Here, we report fish-feeding traces from Lower Cretaceous (130 Mya) deep-sea deposits of NW Italy. These fossils represent the earliest direct evidence of bottom-living vertebrates from the deep sea. Our findings reveal that the Early Cretaceous abyssal plains were already characterized by a modern-type deep-sea ecosystem characterized by multispecies aggregations of fishes. The studied fossils represent at least the last point of deep-sea vertebrate reorganization, if not the earliest.

Vertebrates are an ecologically successful group of animals that originated in shallow seas and now occupy a wide range of habitats ranging from the stratosphere (1) to hadal depths (2). This broad distribution is the result of evolutionary steps of colonization by which vertebrates invaded novel environments thanks to the development of specific morphological and physiological adaptations. The fossil record is crucial for understanding the mode and tempo of these ecological transitions. Body fossils of sarcopterygians (*Tiktaalik*), basal pterosaurs (*Preondactylus*), and winged dinosaurs (*Archaeopteryx*) have provided crucial insights into the Devonian transition from water to land (3) and the Triassic–Jurassic colonization of the air (4, 5). Biogenic sedimentary structures (trace fossils) are remarkable for our knowledge of ecological transitions because of their high preservation potential, providing the earliest evidence for land colonization by vertebrates (6) and recording the invasion of the marine realm by mammals (7).

By contrast, an exceptionally poor fossil record hampers our understanding of the vertebrate colonization of the deep sea, which is defined as beginning at the shelf break (~200 m depth) and extending to hadal trenches (~10,000 m depth) (8). Although marine vertebrates are known from the early Cambrian (9), the earliest unambiguous body fossils of deep-sea vertebrates date back to the Late Cretaceous (10). The Bonarelli Level (Cretaceous: Cenomanian/Turonian, Italy) preserves aulopiforms and tselfatiiforms, which are interpreted as pelagic, open-water fishes by modern analogy (11). Body fossils of myctophiforms and halosaurs have been reported from Cretaceous chalk (12, 13), which was however deposited on the shelf (14) and not in the deep sea. Swimming, resting, feeding, and courtship fish trace fossils are reported since the Silurian and the Devonian (15–18), although only from shallow-marine deposits. While bottom-living (demersal) fishes are a conspicuous component of modern deep-sea fauna (19), there is no fossil record of pre-Paleogene deep-sea demersal fishes.

Because of this lack of Mesozoic deep-sea demersal fishes, the colonization of the deep sea remains one of the largest gaps in vertebrate evolution. Here, we describe exceptionally well-preserved vertebrate trace fossils from the abyssal plain deposits of W Tethys (Ligure-Piemontese Ocean, Palombini Shale Formation, Italy; Early Cretaceous) (20, 21) (Figs. 1–3). Calcareous nannofossils provide precise biostratigraphic age constraints (late Hauterivian-early Barremian) for the trace-fossil assemblages (21) (see *SI Appendix* for detailed biostratigraphy data). The material consists of biogenic sedimentary structures, formed during the interaction of organisms (fishes) with the seafloor. Because of their nature, the studied material has not been subject to transport or reworking and can be unambiguously attributed to fish activities on the deep seafloor. These trace fossils represent

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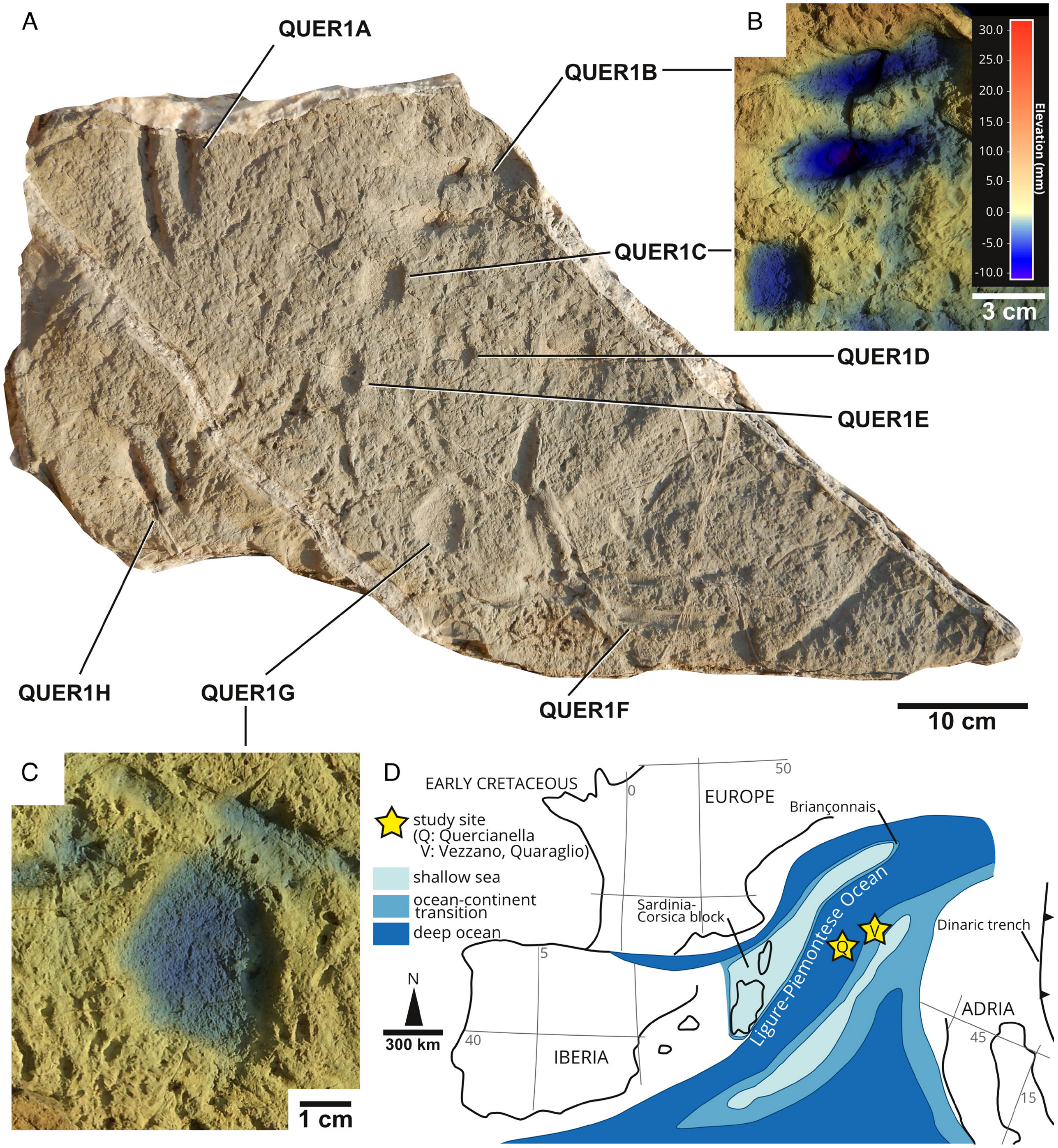

Fig. 1. Morphology of the fish-feeding trace fossils. (*A*) Slab containing fish-feeding trails (QUER1A, B, and H) and pits (QUER1C, D, E, and G). (*B*) False-color height map of the feeding trail QUER1B and the feeding pit QUER1C. (*C*) False-color height map of the feeding pit QUER1G. The color scale is the same as in Fig. 1*B*. (*D*) Palaeogeographical location of the studied fossil sites.

the earliest and most robust evidence for demersal fish feeding on the substrates and hence the colonization of the deep seafloor by vertebrates.

Results

Fish-Feeding Pits. The material comprises shallow discoidal sedimentary structures, oriented concave upward in a horizontal plane (NHMP 359, QUER1C to E, QUER1G, QUER7, and VEZ1; Figs. 1 *A*–*C*, 2, and 3*A*). The outline is circular and ranges from 12 to 41 mm (average: 31 mm) in diameter. The specimens are referrable to the ichnogenus *Piscichnus* (22) based on the following features: dish- or bowl-shaped morphology, circular outline, and concavity upward.

There is a general consensus (22–25) that *Piscichnus* represents the excavations produced by demersal fishes on the seafloor. Observations of modern fishes (24–26) provide unambiguous further evidence of piscine origin of such traces (Fig. 4 *A* and *B*; see *SI Appendix* for the morphology of modern fish-feeding pits).

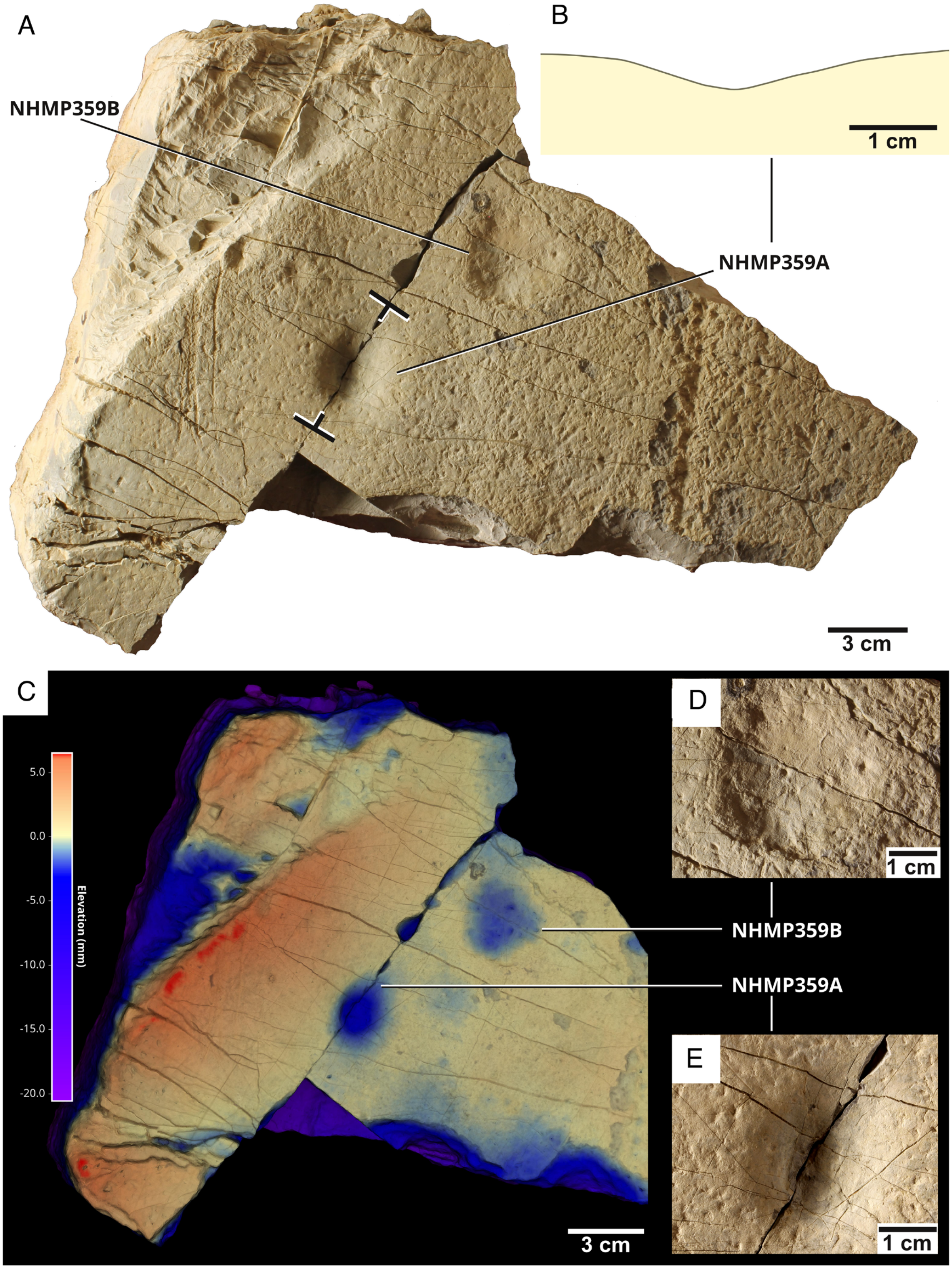

Fig. 2. Morphology of the fossil fish-feeding pits. (*A*) Fish-feeding pits. The T-shaped icons represent the vertices of the cross-section in Fig. 2*B*. (*B*) Cross-section of the feeding pit NHMP359A. (*C*) False-color height map of NHMP359. (*D*) Specimen NHMP359B displaying dish-shaped morphology. (*E*) Specimen NHMP359A displaying bowl-shaped morphology.

Accordingly, modern *Piscichnus* are feeding pits produced by fishes using their jaws and water flow (jetting or suction) generated by the buccal pump to remove sediment and expose their infaunal prey (Fig. 3*B*). We infer a similar origin for the studied biogenic sedimentary structures. This is further supported by the association with small vertical burrows, which are less dense within *Piscichnus* (e.g., 1 burrow/cm^2 in NHMP359B) than in the surrounding sediment (5 burrows/cm^2).

Fish-Feeding Trails. Fish-feeding pits are often associated with bilobed sedimentary structures (QUER1A, QUER1B, QUER1F, and QUER1H), which are also documented as isolated occurrences

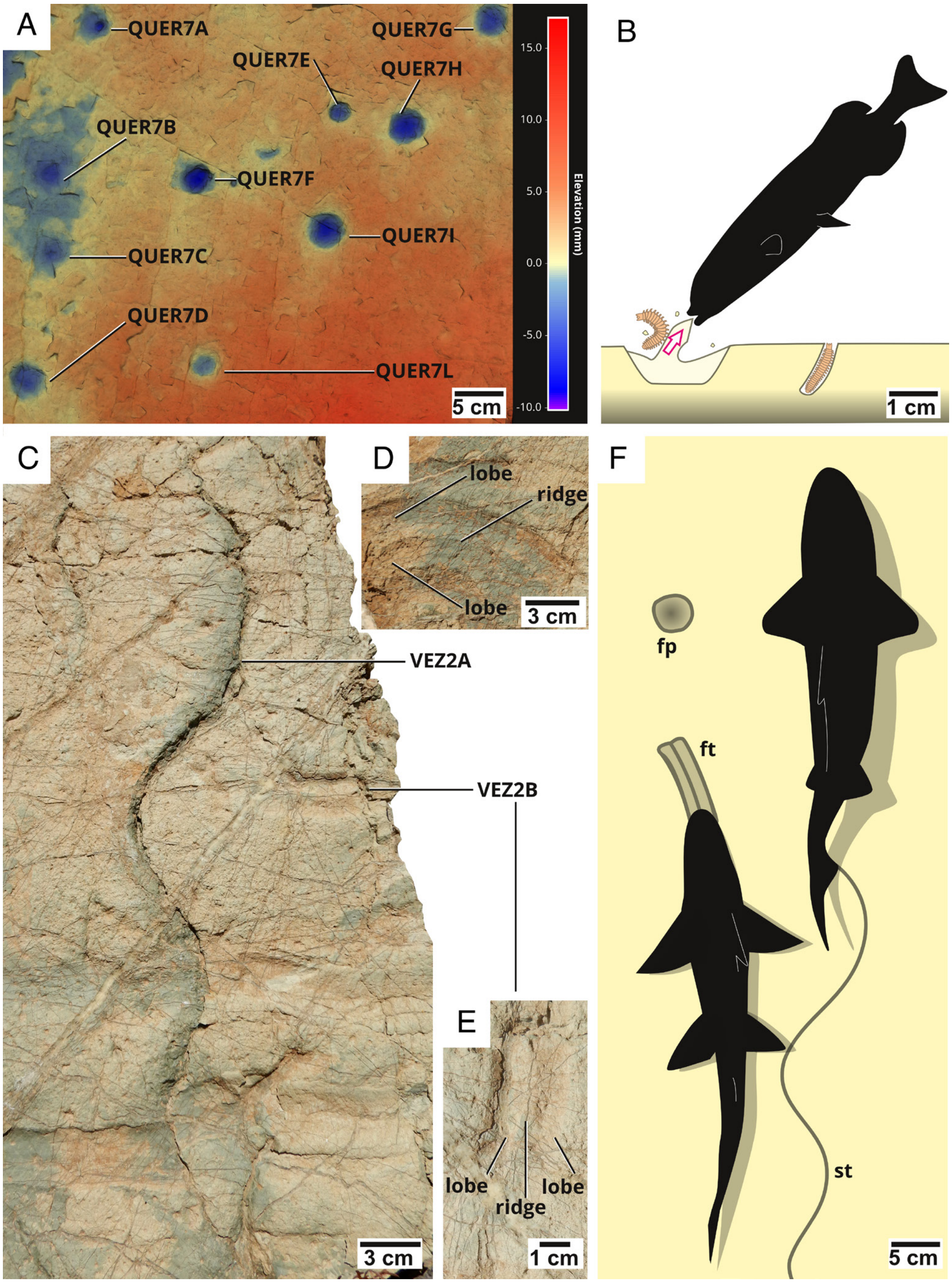

Fig. 3. Fish trace fossils and reconstruction of their production mechanism. (*A*) Feeding pits (false-color height map). (*B*) Reconstructed production mechanism of the feeding pits, according to which a fish exposes its prey by water flow. (*C*) Swimming trail (VEZ2A) associated with feeding trails (VEZ2B and VEZ2C). (*D*) Feeding trail (VEZ2C). (*E*) Feeding trail (VEZ2B). (*F*) Reconstruction of the production mechanism of swimming and feeding trails (st: swimming trail; ft: feeding trail; fp: feeding pit).

(NHMP356, NHMP357, and QUER2 to 6; Figs. 1 *A* and *B* and 3 *C*–*E*). Each bilobed structure consists of two parallel grooves that are separated by a narrow ridge (e.g., QUER5; Figs. 3*D* and 4*C*) or by undisturbed sediment (e.g., QUER1A; Fig. 1*B*). The total widths of the trails range from 12 to 48 mm (average: 28 mm), and their preserved length is from 21 to 171 mm (average: 86 mm).

Recent neoichnological observations (27) demonstrate that such bilobed biogenic sedimentary structures correspond to feeding trails produced by fishes that scratch the seafloor with their teeth in search for food. Further evidence for the piscine origin of the trace fossils is shown by the similarity with experimental feeding trails of Holocephali (Fig. 4*D*) and is supported by new observations on sparid feeding trails (Fig. 4*E*; see *SI Appendix* for additional information about modern fish trails). Accordingly, each lobe of the fossil trail corresponds to the groove produced by the upper incisor-like teeth located on each of the two premaxillae; the central separation between lobes corresponds to sediment flowing through the diastema between the two biggest incisor-like teeth. Modern feeding trails are produced by a front-to-back raking movement during which the sediment is gathered (27). The bilobed structures studied herein show notably similar characteristics (horizontal orientation, lack of branching, bilobed nature, presence of a central ridge, and centimetric size), and thus, we infer that they have been produced in the same way (Fig. 3*F*). QUER4 shows delicate longitudinal striations, which have also been documented in modern fish-feeding trails (27). In NHMP286, NHMP287, and QUER3,

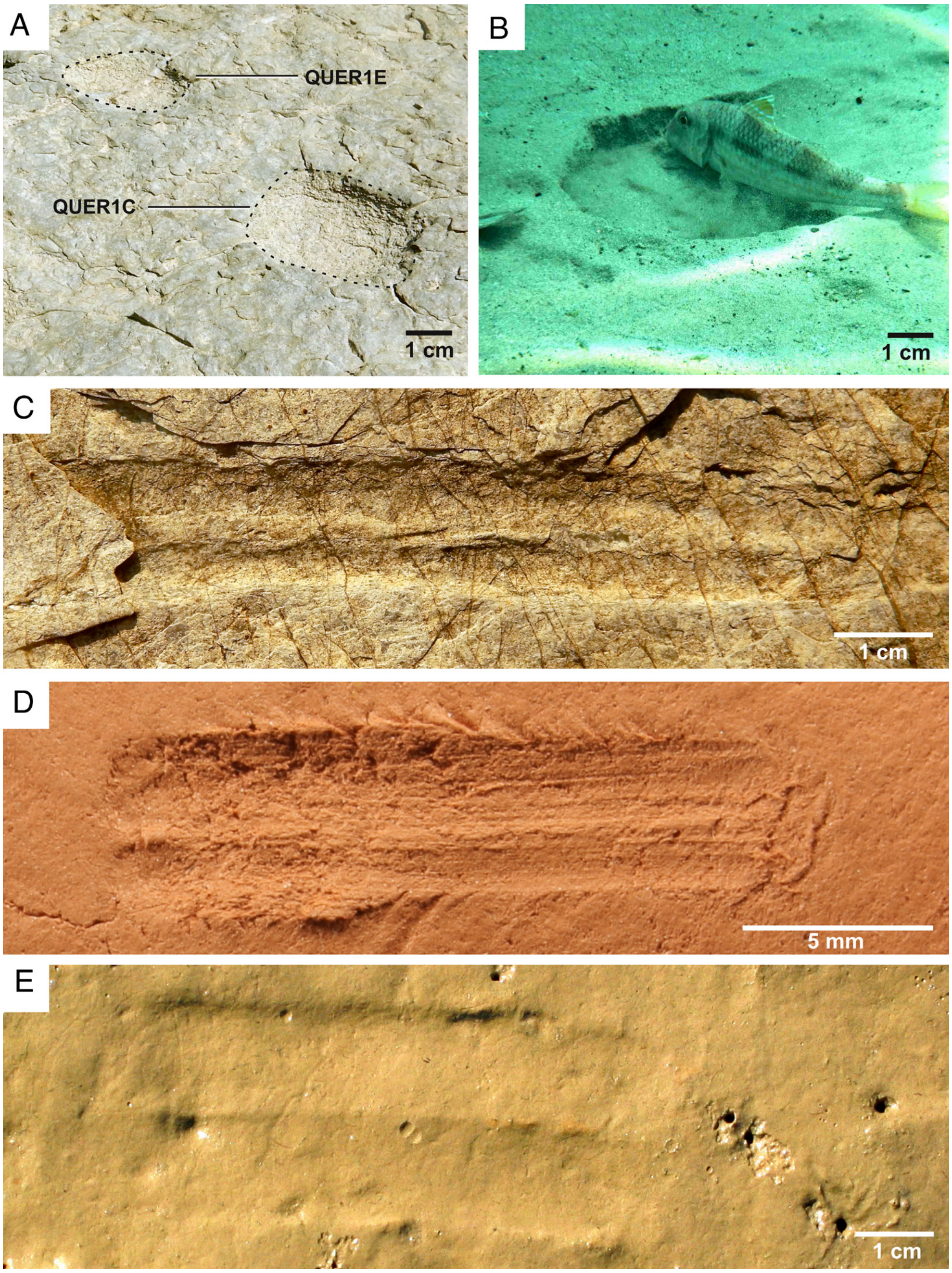

Fig. 4. Comparison among fossil, experimental, and modern piscine traces. (*A*) Fossil fish-feeding pits (QUER1C and QUER1E). (*B*) Modern feeding pit with its producer (*Mullus surmuletus*; Paraggi, Italy). (*C*) Fossil feeding trail (QUER5). (*D*) Experimental feeding trail referred to *Hydrolagus bemisi*. (*E*) Modern feeding trail produced by a sparid fish in the Piedras Estuary, Spain.

one end of the trace is more penetrating, resulting in a V-shaped outline. NHMP286 is also ornamented by a set of delicate ribs. Modern fishes are known to produce similar V-shaped, ornamented feeding trails by a thrust of the surface sediments (bulldozing) combined with forward raking (27).

Fish-Swimming Trail. The material comprises a horizontal groove with the shape of a damped sinusoidal wave (VEZ2A; Fig. 3*C*). The wavelength tends to be constant along the trace length and ranges from 135 to 176 mm (average: 156 mm). The wave amplitude is 7 to 24 mm (average: 18 mm). The groove is sharply incised and is associated with fish-feeding trails. The sinusoidal trail is referrable to the ichnogenus *Undichna* Anderson, 1976 based on the horizontal configuration, sinusoidal shape, constant wavelength, and sharp trace margins (28, 29). The studied material shares its major features with *Undichna unisulca* de Gibert et al., formed by one unpaired sinusoidal wave (30). There is general agreement (28, 29, 31) that *Undichna* is formed by the fins or the spines of a swimming fish, incising the substrate surface. Specifically, the presence of a single wave indicates that the trail was produced by dragging the caudal or anal fin (31) (Fig. 3*F*). For the same reason, the caudal fin was large enough to reach the seafloor without the anal fin doing so, or vice versa (30).

Discussion

The completely preserved traces of piscine activity in the Palombini Shale Formation of W Tethys provide a crucial documentation of the deep seafloor colonization by vertebrates, as well as information about the behavior and evolution of abyssal fishes. Specifically, the piscine traces indicate that the deep seafloor was inhabited by vertebrates at least since the Early Cretaceous, as confirmed by calcareous nannofossils. The piscine traces are preserved within distal turbidites that represent waning sediment fluxes in the abyssal plain of the Ligure-Piemontese Ocean (20, 21, 32). Sedimentation occurred below the carbonate compensation depth, as indicated by the lack of carbonatic hemipelagites, the poor preservation of calcareous nannofossils, and the dominance of dissolution-resistant nannofossil taxa.

Observations on modern environments show that identical structures are produced by modern fishes (24, 27), with no evidence supporting invertebrate producers. The piscine origin is reinforced also by new actualistic and experimental observations (Fig. 4 and *SI Appendix*), as well as the associated occurrence of fossil pits and trails. Such structures co-occur also in modern environments because the excavation of feeding pits by water-jetting fishes attracts sediment-scratching fishes (33). Such behavior has been documented in shallow seas, depressions in the deep-sea floor have been interpreted as feeding craters of fishes (34), and sharks have been observed at depths >1,300 m plunging their mouths into the sediment to feed (35).

The ethological analysis of the trace fossils demonstrates that the earliest abyssal vertebrates employed at least two sets of feeding behaviors, i.e., water flow and sediment scratching. The presence of incisor-like teeth in the upper jaw is required for sediment scratching (27), whereas their absence is an adaptation enabling water flow techniques (36). The burrow density is lower within the feeding pits than in the surrounding sediment, indicating the successful removal of infaunal prey by the excavators of the pits.

The physical adaptations for pit excavation and sediment scratching are so distinctive that we hypothesize that the studied palaeo-seafloor was colonized by at least three different species of deep-sea fishes. The presence of a third species is suggested by the feeding trails with the central ridge, which indicates a narrower diastema with respect to the producer of the trails with a large separation between the lobes. The associated occurrence of feeding pits and trails indicates a plausible gregarious behaviour between the toothless waterflow excavator species and the toothed sediment scratching species. This fits well with observations in modern environments (33), where excavation of feeding pits by fishes attracts other, sediment-scratching fishes that cannot excavate by water flow. Consequently, the studied material indicates that the Early Cretaceous abyssal plains were already characterized by an ecologically complex vertebrate community, with multispecies aggregations of fishes.

The early vertebrates (e.g., *Haikouichthys*) were marine animals that originated in the Cambrian (9). It is therefore surprising that the earliest evidence for deep-seafloor vertebrates (i.e., living at depths > 200 m), represented by the studied fossils, postdate the appearance of vertebrates by ~400 My. By comparison, there are just ~150 My between *Haikouichthys* and the first vertebrate land invasion (3), which is separated by ~130 My from the colonization of the air by pterosaurs (4). Putative delayed colonization of the deep seafloor by vertebrates is remarkable even if the adaptations for deep-sea life (e.g., modified eye structures, low-density tissues, slow metabolism, and enzymes and proteins showing enhanced structural stability) (37, 38) are evolutionary innovations as significant as wings and tetrapod limbs. Consequently, a key question is what factors in the deep sea might have delayed vertebrate colonization, and which ones might have triggered it.

Prior to our findings, an important role has been attributed to the most recent (Late Cretaceous: Cenomanian-Turonian) oceanic anoxic event (OAE2). It has been suggested that ancient deep-sea fishes were extinguished by oceanic anoxic events so that the modern deep-sea fauna is the result of recolonization since the OAE2 (13, 19). It has also been argued that the OAE2 may have promoted allopatric speciation of demersal fishes in the deep sea by restricting isolated populations to disjunct hydrochemical refugia ("deep allopatry hypothesis") (39). Our findings have important implications for the debate over the causes of the vertebrate colonization of the deep sea because the studied trace fossils predate the OAE2. In other words, the late Hauterivian-early Barremian age of our material indicates that fishes colonized the deep sea before the OAE2, which implies that the OAE2 was not the initiating factor in the vertebrate colonization of the deep sea.

We propose that the delayed colonization of the deep sea was triggered by the remarkable input of organic matter that occurred between the Late Jurassic and the Early Cretaceous. We infer that the increased amount of organic matter in the deep seas favored the benthic invertebrate infauna, which, in turn, allowed bottom-living piscine predators to colonize the deep seafloor. Specifically, the Late Jurassic-Early Cretaceous oceans experienced a dramatic increase in productivity (40, 41), partially fueled by the radiation of angiosperms (40–42). This organic matter increase had dramatic effects on deep-sea life, as shown by the Late Jurassic-Early Cretaceous acceleration in the diversity of deep-sea burrows (40) and the onshore/offshore trend that is evident in most benthic marine invertebrate clades (43–45). In turn, the growing presence of deep-sea burrowers, such as the producers of the vertical burrows in NHMP286 and NHMP363, attracted fishes that used specific behavioral strategies to expose them. It should be noted that the organic matter hypothesis does not exclude the role of OAEs in structuring fish biodiversity, but it represents the necessary argument to explain the trigger of the vertebrate colonization of deep seafloors. An additional, although subordinate, role may have been played by the Mesozoic increase in dissolved oxygen in the seawater. Specifically, dissolved oxygen concentrations increased between the Jurassic and the Early Cretaceous (46). However, there was a comparable increase between the Devonian and the Carboniferous, while most of the Permian was characterized by dissolved oxygen levels higher than the Early Cretaceous ones (46). Nevertheless, there are no known fossils of Paleozoic deep-sea fishes; therefore, seawater oxygenation is not the primary trigger of the deep-sea colonization by vertebrates.

Molecular clock data indicate that most of the major lineages of deep-sea fishes originated in the Cretaceous, with a pulse of deep-sea colonization and speciation near the Jurassic–Cretaceous boundary (10). Specifically, present day deep-sea demersal ichthyofauna is dominated by members of the Neoteleostei which are estimated to have diverged from other Actinopterygii in the Late Jurassic about 175 Mya (47, 48) subsequently invading all aquatic habitats on Earth including the deep sea down to abyssal and hadal depths (>6,000 m). According to these studies, the Atelopodiformes and Aulopiformes (lizardfishes) emerged early in this diversification but other taxa with important deep-sea representation do not appear until the Cretaceous, such as the Gadiformes (100 Mya), Ophidiiformes (115 Mya) and Perciformes (60 Mya). The age of our material fits with the earliest origins of the swimbladder retia (130 to 140 Mya), which have been found among the Elopomorpha and Euteleostei using molecular data (49). The teleost retia represent a key adaptation for the colonization of the deep sea, being a central component of the O_2 secretion mechanism that removed the need to take in air at the surface for inflating the swim bladder (49). The present trace fossils therefore may represent a very early stage of diversification of Neoteleostei into the deep sea. A key feature of Neoteleostei is the highly developed suction feeding apparatus (50), which is compatible with the production of the studied feeding pits (ichnogenus *Piscichnus*). The delayed vertebrate colonization of the deep sea is a real macroevolutionary phenomenon and not the effect of a taphonomic bias.

Although Neoteleostei dominate the modern deep sea, there are earlier lineages of demersal fishes that inhabit modern deep-sea settings, e.g., the earliest stem holocephalan is from Upper Devonian shallow-sea deposits in Morocco (51). This opens the possibility that the deep sea has been colonized multiple times by fishes whenever conditions have been favorable, although there are no body or trace fossils that support this hypothesis. As such, the studied fossils represent at least the last point of major deep-sea ichtyofaunal reorganization, if not the earliest.

Materials and Methods

Trace Fossil Analysis. The new specimens are ichnofossil-bearing slabs housed in the Natural History Museum of Piacenza, Italy. The specimens come from the N Apennines (Emilia Romagna, Italy), from the Palombini Shale Formation, deposited during the Cretaceous (Hauterivian-Santonian) and widely suggested to have represented basin-plain turbidites (32). The geological setting is provided in *SI Appendix*, Fig. S1. The basin plain deposits correspond to white to gray–green limestones alternating with laminated black shales. We follow ref. 20 for palaeogeography of the Palombini Shale Formation and for the palaeogeographical base map of Fig. 1*D*. Specimens were recovered from Vezzano sul Crostolo (VEZ1, VEZ2, NHMP 356, NHMP357, and NHMP359), Quaraglio (NHMP286 and NHMP287), and Quercianella (QUER1 to QUER7). Each slab may contain more than one trace fossil, for which reason numerical suffixes are used (e.g., the slab NHMP357 includes the trace fossil specimens NHMP357A and NHMP357B). See *SI Appendix*, Figs. S2–S21, for photographs and false-color height maps of the studied material.

Trace fossils were compared with modern fish-feeding trails and pits observed in marginal-marine areas of the Mediterranean Sea (Paraggi, Italy; Spotorno, Italy; Grado, Italy; Piedras Estuary, Spain). A deep-sea site has been studied using video material recorded during a baited experiment carried out at a depth of 1,544 m (Kermadec Trench, Pacific Ocean). The Palombini Shale Formation trace fossils have been also compared with experimentally-simulated traces obtained by scraping the flat surface of clay pieces with the upper incisor-like teeth of Holocephali. Additional methodological information is provided in *SI Appendix*. See *SI Appendix*, Tables S4 and S6, for morphometric data of trace fossils and modern traces.

Biostratigraphy. Calcareous nannofossil analysis was performed on all the collected material in Vezzano sul Crostolo. Smear slide preparation and analyses were performed under crossed-polarized and transmitted light at 1,250 magnifications with a Zeiss Axioscope 40 optical microscope, scanning at least three transverses (ca. 600 fields of view). The Quercianella section is biostratigraphically well constrained (late Hauterivian-early Barremian) (21).

Photogrammetry. Using photogrammetry, we delivered photo-textured height maps for all the specimens housed at the Natural History Museum of Piacenza and for five field specimens (QUER1-4 and QUER7). Outdoor photo shooting was carried out using a Nikon W300 camera. Indoor photo shooting was taken using a DSLR camera (Canon EOS 1100D) equipped with a Canon Zoom lens 18/55 mm f 1:3.5-5.6 and a Sigma Macro lens 105 mm f 1:2.8. The photography setup included a Durst M301 stand with a micrometric slide, four 10W led lamps, and a cold light source (Starlight LED 3). Using this photographic setup, a minimum of 200 photos per sample was recorded for photogrammetric analysis. Photos were processed by the photogrammetric software 3DF Zephyr Lite to extract 3D information from the photos themselves. Using the software Cloud Compare, we delivered color-scaled height maps. Information about each specimen (i.e., ichnogenus, ichnospecies, author, collector, locality, stratigraphical unit, storage unit, and image) was entered in a Visual dBase-supported database. To date, the database records information about 500 specimens and 30 ichnogenera from the Piacenza territory. Every specimen is associated with a unique ID number (e.g., NHMP 357), to which we refer in this article.

Data, Materials, and Software Availability. All study data are included in the article and/or *SI Appendix*.

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