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Article

Trace fossils on a trace fossil: a vertebrate-bitten vertebrate coprolite from the Miocene of Italy

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With 3 figures and 1 table

Abstract: Despite their long history of discoveries and research, of all the vertebrate coprolites currently known worldwide, only a very few have been explicitly recognised as exhibiting bite marks by other vertebrates. These rare specimens represent "compound ichnofossils", i.e., trace fossils (the lithified faeces) on which other trace fossils (the tooth incisions) are present. Here we report on an unusual large-sized coprolite from the Miocene "Pietra leccese" formation of southern Italy that displays several superficial bite marks. This specimen is described, figured, and chemically characterised by means of hand-held energy dispersive X-ray fluorescence – the first application of this method to the analysis of a vertebrate coprolite. Based on its size, morphology, structure, and major-element composition, the Pietra leccese coprolite is here identified as the fossilised excreta of a large carnivorous vertebrate, possibly a shark, whereas the tooth incisions are attributed to the biting action of indeterminate fish, likely including both bony and cartilaginous fish. Biting seemingly occurred prior to the eventual deposition of the scat at the seafloor (i.e., when it was still in the water column) and probably reflects unintentional snagging or aborted exploratory coprophagy aimed at testing the palatability of the faeces. In conclusion, the highly idiosyncratic specimen described in this paper represents a significant addition to the overly scanty record of vertebrate-bitten vertebrate coprolites and provides an unusual window on the ecological interactions between marine vertebrates in the Miocene central Mediterranean ecosystems witnessed by the remarkable fossil assemblage of the Pietra leccese.

Key words: Bite marks, bromalite, compound ichnofossil, Digestichnia, HHXRF, Mediterranean, palaeoecology, Pietra leccese, vertebrate ichnology, shark.

1. Introduction

Vertebrate coprolites were recognised as fossilised faeces very early in the study of vertebrate fossils, i.e., in the earliest XIX century, by the Reverend William Buckland (Hunt et al. 2012). Even before Buckland's pioneering works, however, vertebrate coprolites had been collected and described without being correctly identified (Duffin 2012). In spite of this long history of discoveries and scientific research, of all the vertebrate coprolites currently known worldwide, only a very few have been explicitly recognised as exhibiting bite marks by other vertebrates (Godfrey & Smith 2010; Godfrey & Palmer 2015; Godfrey & Frandsen 2016; Dentzien-Dias et al. 2018; Frandsen & Godfrey 2019). Each of these very rare specimens represents a "compound ichnofossil" (*sensu* Godfrey & Palmer 2015), i.e., a trace fossil (the coprolite) on which other trace fossils (the tooth incisions) are present.

In the present paper, we report on another unusual coprolite from the Miocene "Pietra leccese" formation of southern Italy that displays a plethora of superficial bite marks. This specimen is described, fig-

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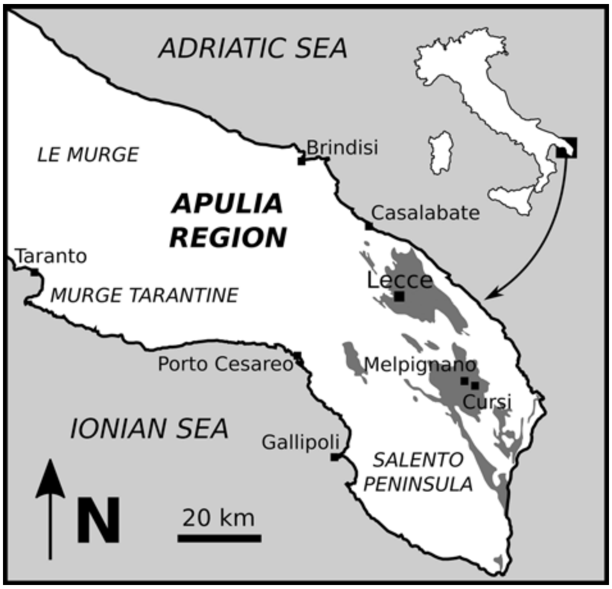

Fig. 1. Schematic geological map of the Salento peninsula (Apulia, southern Italy). Grey-shaded areas indicate the exposures of the Pietra leccese, the Miocene calcarenite limestone from which the fossil specimen MSNUP I-17604 originates. Modified from Peri et al. (2019), after the original illustration by Calia et al. (2014).

ured, and chemically characterised by means of handheld energy dispersive X-ray fluorescence. The coprolite itself is interpreted as having been produced by a large carnivorous vertebrate, possibly a shark, whereas the tooth incisions are referred to indeterminate fish, likely including both chondrichthyans and osteichthyans. The processes that led to the formation of this unusual fossil specimen are also briefly discussed.

2. Stratigraphic and palaeontological background

The Pietra leccese is an informally named Miocene calcareous formation cropping out in the Salento peninsula (Apulia, southern Italy) (Fig. 1). This sedimentary unit is mostly comprised of foraminiferal biomicrites and biosparites, ranging chronostratigraphically between the Burdigalian and the Messinian (e.g., Foresi et al. 2002; Bossio et al. 2005; Bossio et al. 2006; Mazzei et al. 2009). Surprisingly, despite its modest thickness (a few tens of metres; Foresi et al. 2002), the Pietra leccese records an 11-million-year-long history of sedimentation (Bossio et al. 2006); this might be explained by the occurrence of several depositional hiatuses, attributed to the erosional action of marine currents, which are marked by glauconite-rich intervals (Bossio et al. 2005). Based on observations on the Pietra leccese microfossils (e.g., Bossio et al. 2006) and macrofossils (e.g., Carnevale et al. 2002), the depositional environment of this limestone has been interpreted as located in the deepest portion of the outer neritic zone.

Body fossils of marine vertebrates from the Pietra leccese have been known to the scientific community since the mid-XIX century and have been thoroughly investigated since; they include turtles, crocodiles, bony and cartilaginous fishes, sirenians, and cetaceans (both toothed and baleen-bearing whales) (Costa 1853; Costa 1856; Costa 1865; Capellini 1878; Vigliarolo 1891; Misuri 1910; Bassani 1911; Bassani 1915; Moncharmont Zei 1950; Moncharmont Zei 1956; Menesini & Tavani 1968; Menesini 1969; Bianucci et al. 1992; Bianucci et al. 1994a; Bianucci et al. 1994b; Bianucci 2001; Bianucci & Landini 2002; Carnevale et al. 2002; Delfino et al. 2003; Bianucci et al. 2004; Bisconti & Varola 2006; Bianucci & Landini 2006; Chesi et al. 2007; Bianucci et al. 2016; Peri et al. 2019). The presence of vertebrate Digestichnia (i.e., trace fossils originating from the digestive processes of animals, such as coprolites, regurgitalites, and gastroliths; Vallon 2012) in the Pietra leccese has been proposed by Tavani (1973) based on the occurrence of centimetre- to decimetre-sized metamorphic and calcareous clasts, possibly interpretable as gastroliths of large-sized cetaceans or fish.

As many other vertebrate fossils from the Pietra leccese, the bitten coprolite here described was collected by one of the authors (A.V.), in the late XX century, in the framework of the activities of "Gruppo Naturalisti Salentini". This specimen is currently housed in the Museo di Storia Naturale dell'Università di Pisa (= MSNUP, Calci, Pisa Province, Italy) with accession number MSNUP I-17604. Although the provenance of MSNUP I-17604 from the Pietra leccese strata is ascertained, the exact stratigraphic position of this specimen is unfortunately uncertain.

3. Methods

Measurements of MSNUP I-17604 were taken using a standard analog caliper. Photographs and microphotographs of MSNUP I-17604 were taken using a Nikon D5200 digital camera and a Canon EOS 60D digital camera mounted on a Zeiss Stemi 2000-C optical stereomicroscope, respectively.

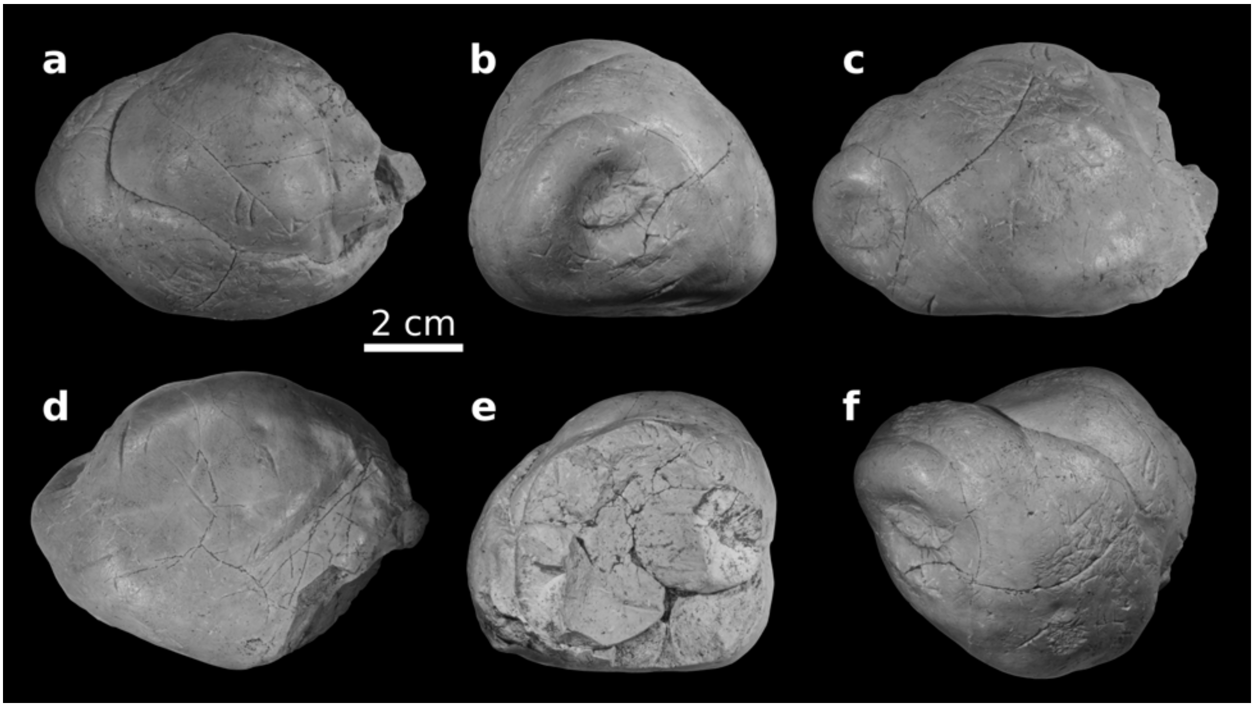

Fig. 2. MSNUP I-17604, vertebrate-bitten vertebrate coprolite from the Miocene Pietra leccese of southern Italy, in (a) upper; (b, e) terminal; (c) lateral; (d) lower; and (f) oblique views (photographs).

Concern for the integrity of MSNUP I-17604 precluded removing any part of it for destructive chemical analyses. Therefore, in order to obtain a major-element compositional characterisation of this fossil specimen, we analysed it by means of hand-held energy dispersive X-ray fluorescence (HHXRF), a non-destructive and non-invasive analytical technique (e.g., Piorek 1997). Analyses were performed at Dipartimento di Scienze della Terra dell'Università di Pisa (Italy) with a NITON XL3t GOLDD+ hand-held spectrometer (see Gemelli et al. 2017 for performances and accuracies). Three spot analyses were performed on different areas of the external surface of the coprolite. The beam spot diameter was 8 mm. Measurement time was 150 s for each replicate. To our knowledge, this was the very first application of HHXRF to the study of vertebrate coprolites.

4. Results

Similar to many vertebrate body fossils from the Pietra leccese, MSNUP I-17604 (Fig. 2) exhibits a pinkish-yellowish colouration. No unambiguous inclusions are visible on its external surface. Similar to another vertebrate-bitten vertebrate coprolite described by Godfrey & Palmer (2015), the external surface of MSNUP I-17604 displays a somewhat reective patina.

MSNUP I-17604 appears as almost complete, only lacking some fragments (likely because of post-burial breakage) at one termination; it measures 79 mm in maximum preserved length (estimated total length around 85 mm), 58 mm in maximum width, and 54 mm in maximum thickness. The morphology of MSNUP I-17604 could be described as oval (*sensu* Häntzschel et al. 1968: fig. 1) (Fig. 2a, c, d). Moreover, following the terminology proposed by Hunt & Lucas (2012), it might be further characterised as spiral (i.e., it appears to be formed by three rather thick coils of faecal material wrapped around the long axis) and heteropolar (i.e., these coils appear to accumulate at one end of the coprolite) (Fig. 2b, e, f). Reflecting the heteropolar arrangement of the coils, one end of MSNUP I-17604 is convex (Fig. 2b) whereas the other termination (i.e., the slightly incomplete one) is concave (Fig. 2e). One side of MSNUP I-17604 is distinctly flattened and displays a few roughly circular, poorly defined, shallow depressions that do not exceed six millimetres in diameter (Fig. 2d).

The exterior of MSNUP I-17604 displays several different surface textures and features. Some of them seemingly testify to the deformation of the faeces during excretion or the subsequent alteration of their su-

Table 1. Results of the HHXRF analyses, detailing the major-element chemical composition of MSNUP I-17604. Element concentrations (wt%) are the average of three spot analyses performed on different areas of the external surface of the studied coprolite. “Bal” stands for “balance”; it includes all elements lighter than magnesium that cannot be detected by means of HHXRF analyses.

Element	**Ca**	**P**	**Si**	**Al**	**S**	**Fe**	**K**	**Sr**	**Sc**	**Ba**	**Cl**	**Ma**	**Bal**
Concentration	36.2	14.0	2.0	1.6	0.8	0.5	0.2	0.1	0.1	0.1	≪0.1	≪0.1	44.4

perficial properties and aspect during exposure to seawater. For example, a few parallel folds are observed close to the convex end of the coprolite (Fig. 3), and the external surface of MSNUP I-17604 locally exhibits a somewhat wrinkled aspect due to the presence of several very shallow, subparallel, and closely spaced creases (e.g., Fig. 3b). In turn, other typologies of surface features that are observed on MSNUP I-17604 evoke the bioerosional action of organisms other than the producer of the faeces. A few centimetre-sized patches of short, shallow, closely spaced, often overlapping, subrectilinear to slightly wavy striations locally ornament the external surface of the coprolite with a rough aspect (e.g., Fig. 3c). Similar short, very shallow, sometimes isolated scars are almost ubiquitous all over the specimen. More prominent traces include a pair of close, parallel, weakly curved incisions, having a length of about 7 mm and one termination shaped as a ca. 2-mm-deep conical cavity (Figs. 2a, 3d). Roughly a dozen of the scars observed on MSNUP I-17604 can be attributed to this kind of morphology. Simpler, substraight to weakly sigmoidal gouges, ranging between a few millimetres and 13 mm in length and reaching their maximum depth and width at about mid-length, are also present (e.g., Figs. 2d, 3e). Several traces of this kind are rather evenly distributed over the external surface of MSNUP I-17604 (Fig. 2); those that occur on the flat side of the coprolite, however, appear as somewhat planate, which makes their identification and characterisation difficult in some cases. Locally, where the outer aspect of MSNUP I-17604 is not affected by the aforementioned bioerosional scars, it appears as substantially smooth, although some fracture lines (sometimes lined by inconspicuous oxide coats) are present here and there (e.g., Fig. 3c, d, f).

The application of HHXRF to the major-element chemical characterisation of MSNUP I-17604 proved successful. The results of the HHXRF analysis are reported in Table 1. Notably for the purposes of our study, MSNUP I-17604 appears as very rich in phosphorous (ca. 14 wt%) and calcium (ca. 36 wt%).

5. Discussion and conclusions

What kind of organism is responsible for producing MSNUP I-17604? The large size of this specimen excludes any possible derivation from an invertebrate organism; indeed, invertebrate faecal pellets are usually less than 5 mm long (Häntzschel et al. 1968). Spirally coiled coprolites are generally referred to non-teleost fish having a spiral valve within their lower intestine; in particular, of all the spiral coprolites, those exhibiting a heteropolar arrangement of the coils are generally referred to sharks (e.g., Williams 1972; McAllister 1985; Hunt et al. 1994; Stringer & King 2012). In the light of these considerations, the Miocene coprolite described in the present paper might be best interpreted as produced by a shark; corroborating this interpretation, the high abundances of phosphorus and calcium recovered in MSNUP I-17604 (Table 1) compare very well with the chemical characteristics of other coprolites from carnivorous vertebrates, including sharks (e.g., Chin 2002; Godfrey & Smith 2010; Stringer & King 2012; Schwimmer et al. 2015). Indeed, remarkable concentrations of phosphorus and calcium in a coprolite suggest that the diet of the producer of the faeces was rich in biogenic calcium phosphate, which is provided by bones, teeth and scales of the prey. This also favours the preservation of the scat as fossil by providing an autochthonous source of the chemical elements that are involved in phosphatisation (e.g., Bradley 1946; Chin 2002) and, possibly, nucleation sites in form of crystallites of undigested hydroxyapatite, similar to what has recently been proposed for the phosphatisation of poorly calcified “soft tissues” such as baleen (Gioncada et al. 2016).

Although it is not possible to exactly correlate the coprolite size and the total body size in extinct selachians (Schwimmer et al. 2015), given the large size of MSNUP I-17604, the producing shark should also have been large. Large-sized shark species from the Pietra leccese that might account for the production of the studied coprolite include the extinct lamniforms

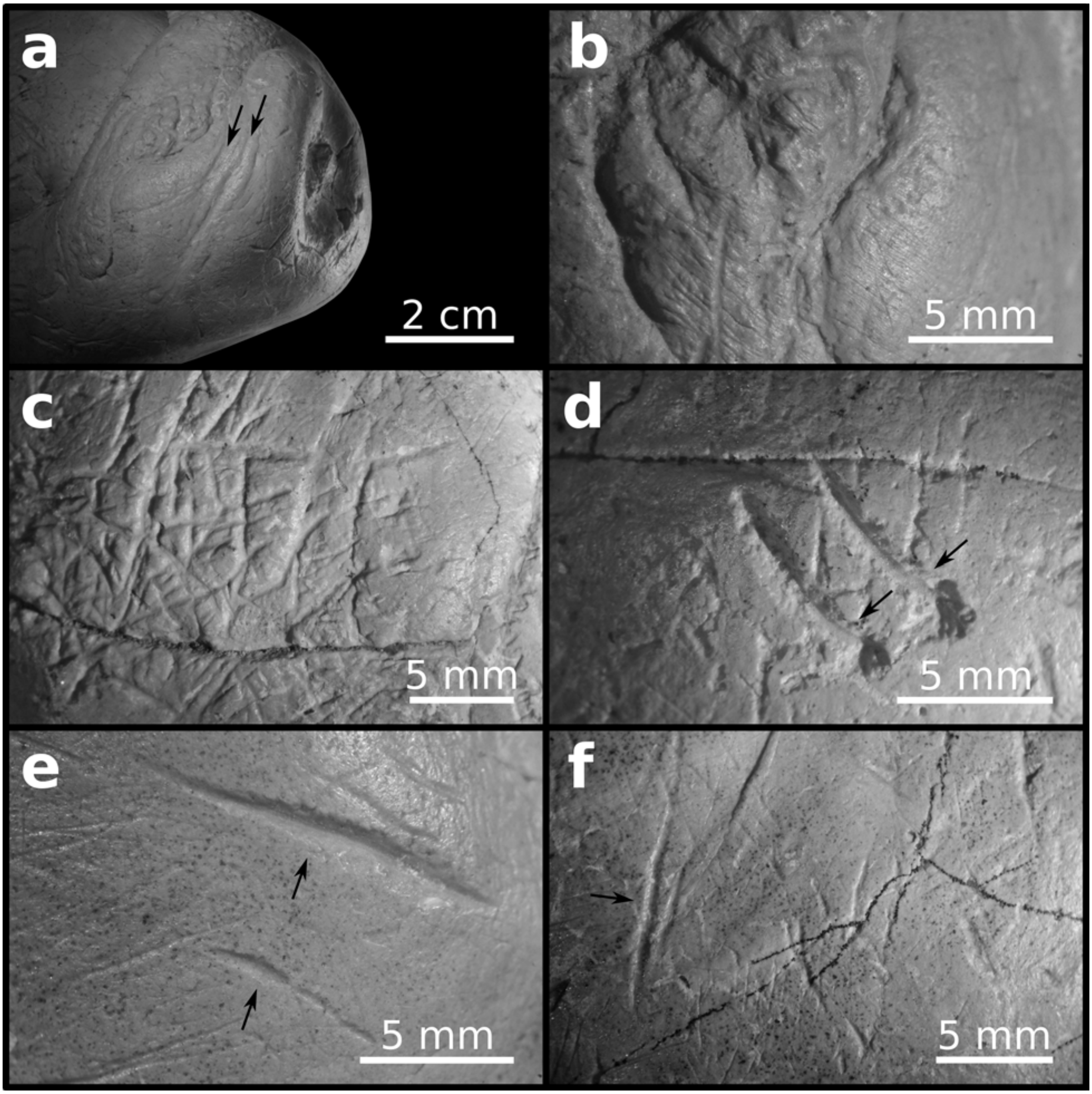

Fig. 3. Details of the surface textures and features of MSNUP I-17604, vertebrate-bitten vertebrate coprolite from the Miocene Pietra leccese of southern Italy. (a) Parallel folds (black arrows) taking place close to the convex ending of the coprolite (photograph); (b) very shallow, subparallel, and closely spaced creases (microphotograph); (c) patch of short, shallow, closely spaced, often overlapping, subrectilinear to slightly wavy striations, ornamenting the external surface of the coprolite with a rough aspect (microphotograph); (d) pair of close, parallel, weakly curved incisions (black arrows), having one end shaped as a conical impression (microphotograph); (e) long, substraight to weakly sigmoidal gouges (black arrows), reaching their maximum depth and width at about mid-length (microphotograph); (f) planate scar (black arrow), recalling those figured in the previous panel, found on the flat (i.e., lower) side of the coprolite (microphotograph).

Carcharocles megalodon, *Cosmopolitodus hastalis*, *Isurus retroflexus* (= *Anotodus agassizii*), and *Parotodus benedeni* (Menesini 1969; Sorce 2009).

Following de Figuereido Souto (2010), Lewis (2011), Milàn (2012), and Pesquero et al. (2011), the slightly incomplete concave ending that characterises one termination of MSNUP I-17604 might be interpreted as resulting from muscular contraction (i.e., peristalsis), as well as a further confirmation of the organic nature of this specimen. Furthermore, following Hunt et al. (1994) and Godfrey & Smith (2010), we interpret the flattened side of MSNUP I-17604 (Figs. 2d, 3f) as the surface upon which the scat came to rest on the substrate (i.e., its lower surface). In the light of this assumption, the small depressions that are present on this side of the coprolite can be explained via partial draping of substrate asperities by the faecal matter. Therefore, MSNUP I-17604 does not represent the *in situ* content of a chondrichthyan spiral valve (i.e., it is not an enterospira), but it was rather expelled from the producer's digestive tract. This is also supported by the observation of parallel folds close to the convex ending of the coprolite (Fig. 3a), which might indicate intra-coil plastic deformation during evacuation of the faeces (see also Dentzien-Dias et al. 2018 in this regard). If this interpretation is correct, biting of MSNUP I-17604 should have occurred after its excretion, otherwise the tooth marks would have been obliterated during the passage of the plastic faeces through the anus. At the same time, as the tooth incisions are regularly present also on the flattened surface of this coprolite (Fig. 3f.), biting should have occurred prior to the eventual deposition of the excreta at the seafloor (i.e., when the scat was still in the water column).

The tooth incisions observed on the exterior of MSNUP I-17604 are rather shallow, not exceeding 2 mm in maximum depth, thus indicating that the faeces were firm enough at the time it was bitten to inhibit tooth penetration. Moreover, as observed in another recently described vertebrate-bitten vertebrate coprolite from the Eastern U.S.A. (Godfrey & Frandsen 2016), the edges of some tooth incisions preserved on MSNUP I-17604 appear as somewhat "ragged", thus suggesting that the external surface of the excreta did not yield compliantly as it was raked by the teeth. Furthermore, some portions of MSNUP I-17604 display closely spaced, very shallow creases that locally confer a wrinkled aspect to the external surface of the coprolite (Fig. 3b). Although these creases resemble the structures interpreted by Williams (1972) as impressions of mucosal folds, we concur with Dentzien-Dias et al. (2012) that they are better interpretable as reflecting incipient decomposition of the faeces.

What kinds of organisms and activities are responsible for producing the bioerosional scars observed all over the external surface of MSNUP I-17604? The origin of the very small, often clustered incisions (Fig. 2c) remains unknown. Given their high abundance and frequent clustering, following Godfrey & Palmer (2015), these traces are here interpreted as likely reflecting coprophagy by indeterminate invertebrates. By contrast, in terms of both size and morphology, the larger incisions exemplified in Fig. 3e cannot easily match any bioerosional feature originating from the activity of an invertebrate; in turn, they are perfectly consistent with the well-known bite marks left on bones by sharks provided with relatively large, blade-like tooth crowns having unserrated cutting edges (e.g., several species of Lamniformes, including *Anotodus agassizi*, *Cosmopolitodus hastalis*, and *Parotodus benedeni*, which are known from the Pietra leccese strata) (e.g., Bianucci et al. 2010; Govender 2015; Bianucci et al. 2018). In the light of the classification scheme of shark bite marks proposed by Cigala Fulgosi (1990) and subsequently amended by Bianucci et al. (2010) and Collareta et al. (2017), these scars are here identified as due to type I (i.e., the cutting edge of the tooth impacted the surface of the faeces from above downward, thus producing a subrectilinear or weakly curved mark) or type II (i.e., the tooth edge dragged in parallel with the dental axis, thus producing a more or less elongated incision) biting actions. Furthermore, as already observed, a few tooth marks preserved on the surface of MSNUP I-17604 (Fig. 3d) are close, parallel to each other, and have one end shaped as a conical impression, likely reflecting their origin from the impact of two adjoining teeth of a bony fish, as proposed by Godfrey & Palmer (2015) and Dentzien-Dias et al. (2018) for similar features found on other bitten vertebrate coprolites. Indeed, the proximate conical terminations of these furrows seemingly preserve the shape of the pointed apexes of conical tooth cusps and indicate the direction of dragging of the teeth over the surface of the faeces.

Therefore, at least two different vertebrates – one shark and, most likely, one bony fish – had their teeth interacting with the faeces now represented by the coprolite specimen MSNUP I-17604. Since the neontological literature dealing with coprophagy by marine vertebrates is rather scanty, the motivations behind such a behaviour can be only tentatively reconstructed. As pointed out by Godfrey & Smith (2010), extant sharks are known to test the palatability of possible prey or scavenging items via tentative biting (Klimley 1994; Collier et al. 1996; Ritter & Levine 2004). As regards the bony fish, several lineages of osteichthyans have been observed or hypothesised to engage in coprophagy, at least for exploratory purposes (Robertson 1982; Cherry et al. 1989; Parrish 1989; Dentzien-Dias et al. 2018). Given these premises, we argue that the bite marks found on MSNUP I-17604 are the product of aborted exploratory coprophagy or unintentional snagging, as already hypothesised by Godfrey & Smith (2010), Godfrey & Palmer (2015), Godfrey & Frandsen (2016), and Dentzien-Dias et al. (2018) for explaining the presence of tooth marks on other bitten coprolite specimens. Possibly supporting the hypothesis of unintentional snagging, none of the tooth marks observed on MSNUP I-17604 is deep enough to be consistent with a high level of intent, and the same can be said for the absence of coupled series of furrows that might indicate an origin from opposing teeth in the upper and lower jaws of the biting fish. On the other hand, the abundance of tooth marks recovered all over the surface of MSNUP I-17604 is a strong argument supporting a not completely fortuitous interaction between the biting fish and the bitten excreta. As suggested by Godfrey & Palmer (2015) for a remarkable gar-bitten coprolite from South Carolina, USA, the faeces might have been momentarily mistaken as prey or snagged unintentionally as the biting organisms were snapping at nearby, genuine food items.

In conclusion, MSNUP I-17604 represents a significant addition to the overly scanty record of vertebrate-bitten vertebrate coprolites, being indeed the first fossilised vertebrate scat from the Euromediterranean region to be formally recognised as preserving tooth impressions. The highly idiosyncratic specimen described in the present paper can thus be regarded as a trace-bearing trace fossil, i.e., a true compound ichnofossil that provides an unusual window on the ecological interactions between marine vertebrates in the Miocene central Mediterranean ecosystems witnessed by the remarkable fossil assemblage of the Pietra leccese. Therefore, our findings should encourage the recovery of marine vertebrate fossils in this well-known fossiliferous limestone by demonstrating that, after more than one and a half centuries of palaeontological research, the study of the Miocene fossil record of Apulia can still yield significant novelties. Last but not least, HHXRF proved successful in providing a major-element chemical characterisation of MSNUP I-17604, thus suggesting that this non-destructive, non-invasive, rapid, and relatively inexpensive analytical method might be extensively (or even routinely) applied to the study of vertebrate coprolites.

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