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Just a different place to graze? An unusual occurrence of the echinoid feeding trace *Gnathichnus pentax* on a marine vertebrate coprolite (Miocene, Italy) and its palaeoethological implications

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Abstract: Faeces produced by marine vertebrates and macro-invertebrates contain sufficient organic matter to represent a usable food source for a wide array of macroscopic animals. In some extant marine environments, coprophagy even represents a crucial trophic interaction in food webs. In ancient ecosystems, coprophagy by macroscopic animals is occasionally exemplified by coprolites that exhibit biting traces or burrows. Here, we report *Gnathichnus pentax* on an exquisitely preserved vertebrate-bitten vertebrate coprolite from the marine calcareous deposits of the Pietra leccese (Miocene, southern Italy). This unusual occurrence is interpreted as evidence of the feeding activity of a regular echinoid; in particular, it may represent either exploratory coprophagy or the browsing of an algal (microbial) film that locally developed on the exterior of the faeces. Strengthening the former interpretation, the development of microbial communities on submerged faeces often leads to their destruction; furthermore, some extant Antarctic echinoderms are well known to ordinarily feed on vertebrate faeces, and coprophagy is believed to be fairly widespread among sea urchins. Supporting the algal browsing hypothesis, in turn, only a limited area of the external surface of the faeces was subject to grazing, and the resulting trace is neatly defined, which suggest that the feeding sea urchin targeted a precise location on the dung's exterior when the latter was already rather firm. To our knowledge, the *G. pentax* specimen studied here represents the first published record of this ichnotaxon on a coprolite.

Keywords:

- bromalite;
- coprophagy;
- Echinodermata;
- palaeoichnology;
- Pascichnia;
- Pietra leccese;
- sea urchin;
- Vertebrata

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Résumé : ***Juste un endroit différent pour brouter ? Une occurrence inhabituelle de la trace d'alimentation d'un échinoïde* Gnathichnus pentax *sur un coprolithe de vertébrés marins (Miocène, Italie) et ses implications paléoéthologiques.*-** Les matières fécales produites par les vertébrés et les macro-invertébrés marins contiennent une quantité suffisante de matière organique pour représenter une source de nourriture utilisable pour un large éventail d'animaux macroscopiques. Dans certains environnements marins modernes, la coprophagie représente une interaction trophique cruciale dans les réseaux trophiques. Dans les écosystèmes anciens, la coprophagie par des animaux macroscopiques est parfois illustrée par des coprolithes qui présentent des traces de morsure ou des terriers. Ici, nous rapportons un spécimen de *Gnathichnus pentax* présent sur un coprolithe de vertébré, parfaitement préservé et lui-même mordu par des vertébrés, provenant des dépôts calcaires marins de la Pietra leccese (Miocène, sud de l'Italie). Cette occurrence inhabituelle est interprété comme une preuve de l'activité alimentaire d'un échinoïde régulier; en particulier, il peut résulter soit d'une coprophagie exploratoire, soit du broutage d'un film algal (microbien) qui s'était développé localement à l'extérieur des fèces. Renforçant la première interprétation, le développement de communautés microbiennes sur les matières fécales submergées conduit souvent à leur destruction ; en outre, certains échinodermes vivants antarctiques sont bien connus pour se nourrir habituellement d'excréments de vertébrés et la coprophagie semble être assez répandue chez les oursins. D'autre part, à l'appui de l'hypothèse du broutage algal, seule une zone limitée de la surface externe des fèces était sujette au pâturage, et la trace résultante est bien définie, ce qui suggère que l'oursin en train de se nourrir visait un endroit précis à l'extérieur de l'excrément alors que le dernier était déjà assez raide. À notre connaissance, le spécimen de *G. pentax* étudié ici représente le premier enregistrement publié de cet ichnotaxon sur un coprolithe.

Mots-clefs :

- bromalithe ;
- coprophagie ;
- Echinodermata ;
- paléoichnologie ;
- Pascichnia ;
- Pietra leccese ;
- oursin ;
- Vertébrés

1. Introduction

It is well known that the faeces produced by marine vertebrates and macro-invertebrates contain sufficient organic matter to represent a usable food source for a wide array of macroscopic animals (NEWELL, 1965; FRANKENBERG & SMITH, 1967; FRANKENBERG *et al.*, 1967; ROBERTSON, 1982; PARRISH, 1989; SAZIMA *et al.*, 2003). In some extant marine environments, including coral reefs, the consumption of faeces (*i.e.*, coprophagy) is so important that it is sometimes a crucial kind of trophic interaction in food webs (BAILEY & ROBERTSON, 1982; FULLER & PARSONS, 2019). In ancient ecosystems, coprophagy by macroscopic animals is occasionally envisaged on the basis of fossilised faeces (*i.e.*, coprolites) that display feeding-related modifications like tooth marks (*e.g.*, GODFREY & SMITH, 2010; GODFREY & PALMER, 2015; GODFREY & FRANDSEN, 2016; DENTZIEN-DIAS *et al.*, 2018, 2021; FRANDSEN & GODFREY, 2019; CUEILLE *et al.*, 2020; GODFREY *et al.*, 2020; ROZADA *et al.*, 2021; RUMMY *et al.*, 2021) and burrows (BRADLEY, 1946; CHIN & GILL, 1996; CHIN, 2007; MILÀN *et al.*, 2012; GODFREY *et al.*, 2022; GODFREY & COLLARETA, 2022). Overall, the fossil record demonstrates that faecal matter has been an important source of nutrition in the marine realm since the Cambrian (KIMMIG & PRATT, 2018; HUNT *et al.*, 2021).

With the aim of contributing to the short but growing list of coprolites with associated feeding traces, COLLARETA *et al.* (2019) described fossilised vertebrate (shark?) dung from the Miocene of southern Italy featuring tooth marks referred to both cartilaginous and bony fishes. The recent reappraisal of this coprolite led to the identification of an additional trace originating from the grazing activity of a macro-invertebrate, namely, a sea urchin. Here, we characterize and describe this echinoid feeding trace from this remarkable coprolite.

2. Material and methods

The studied coprolite is currently housed in the Museo di Storia Naturale dell'Università di Pisa (=MSNUP, Calci, Pisa Province, Italy) with accession number MSNUP I-17604. Photographs and microphotographs of MSNUP I-17604 were taken using a Nikon D5200 digital camera equipped with a Sigma 50 mm F2.8 macro lens and a Sony a6000 digital camera equipped with a Sony 50 mm F1.8 lens. A 3D model of the specimen was created by aligning 133 photos through the photogrammetric software Agisoft Metashape v1.70. The 3D model is freely available via *figshare* at the following internet address: https://doi.org/10.6084/m9.figshare.17161235.

MSNUP I-17604 (Fig. 1) is an oval, spiral, heteropolar coprolite (*sensu* HÄNTZSCHEL *et al.*, 1968, and HUNT & LUCAS, 2012). It is almost complete, only lacking some fragments (likely because of post-burial breakage) at one end. It measures 79 mm in maximum length (estimated total length if missing parts are included ~85 mm), 58 mm in width, and 54 mm in thickness. Hand-held energy dispersive X-ray fluorescence analyses demonstrated that MSNUP I-17604 is very rich in calcium (ca. 36 wt%) and phosphorous (ca. 14 wt%) (COLLARETA *et al.*, 2019). A number of different traces occur on the surface of MSNUP I-17604, mostly consisting of tooth incisions from indeterminate bony fishes and sharks (COLLARETA *et al.*, 2019).

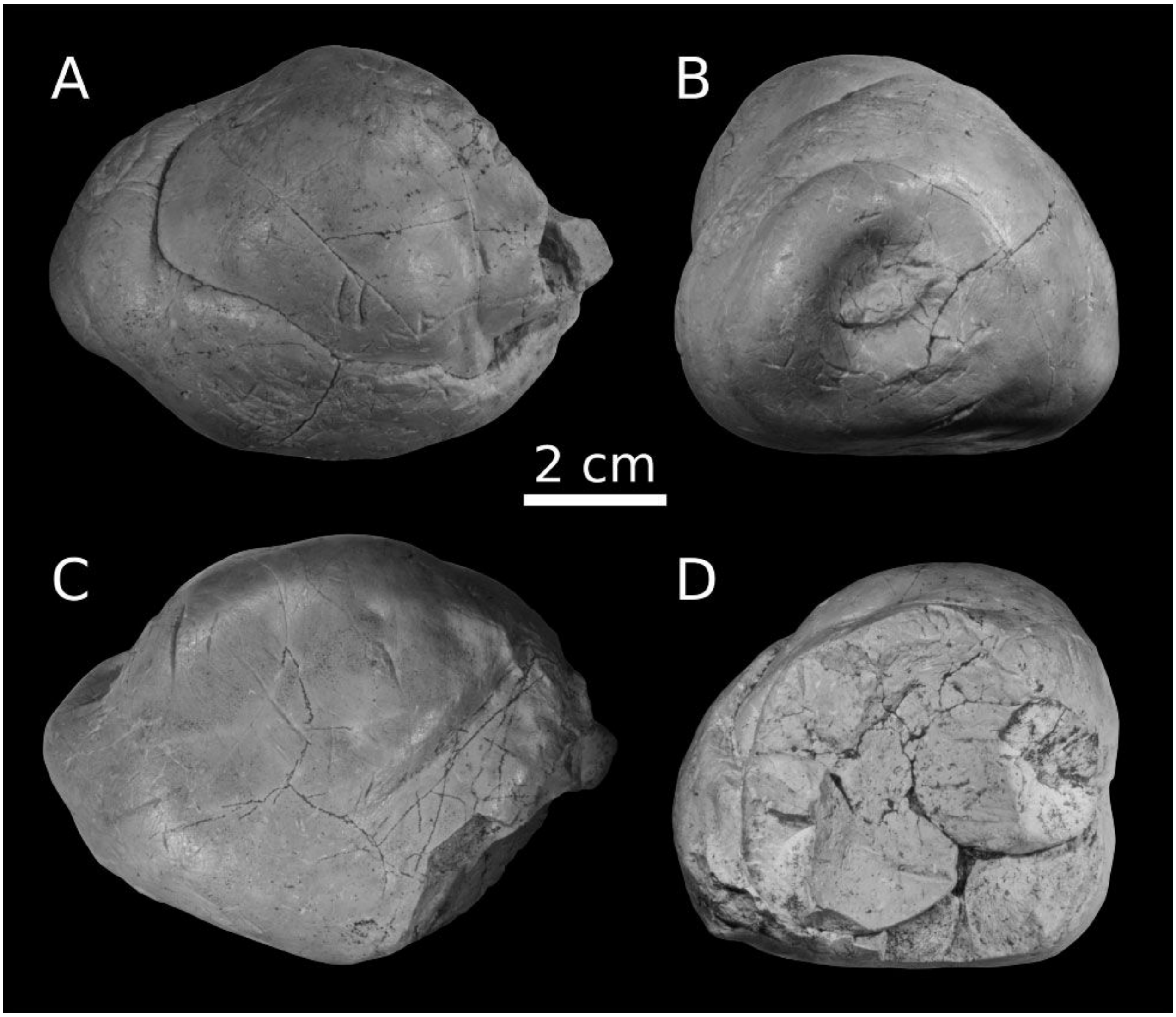
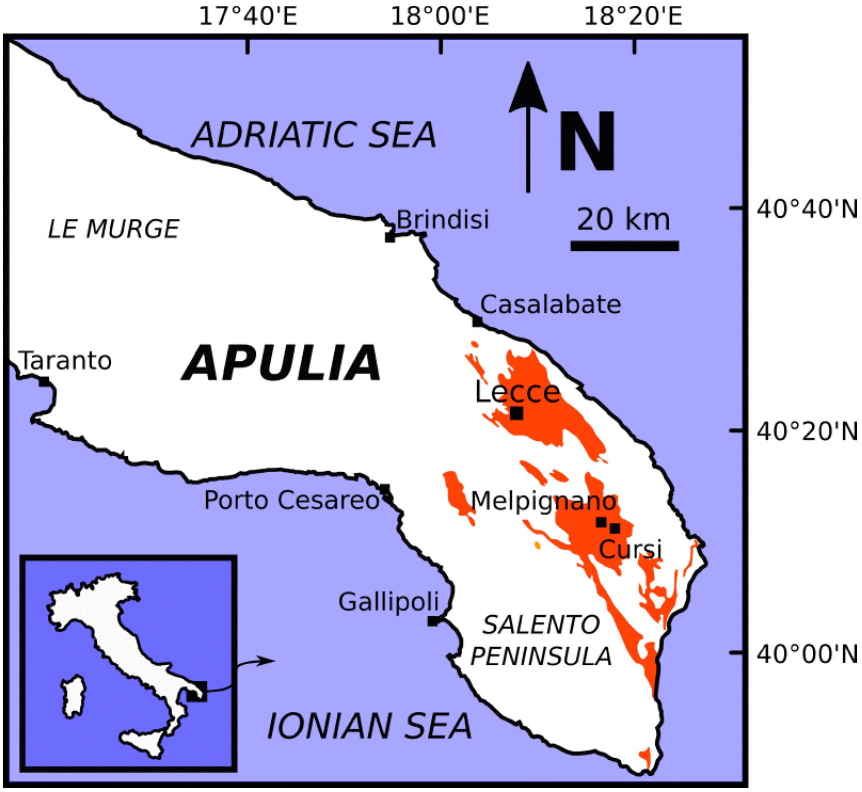


Figure 1: MSNUP I-17604, trace-bearing vertebrate coprolite from the Miocene Pietra leccese of southern Italy, in (A-D) four different views, including (B,D) two terminal views.

3. Geological and palaeontological background

All that is known about the geographic and stratigraphic origin of MSNUP I-17604 is its provenance from the Miocene Pietra leccese formation (Collareta *et al.*, 2019), which crops out in the Salento peninsula (Apulia Region, southern Italy; Fig. 2). This informal lithostratigraphic unit consists mostly of foraminiferal biomicrites and biosparites that were deposited between the late Burdigalian and the early Messinian (Foresi *et al.*, 2002; Bossio *et al.*, 2005, 2006; Mazzei *et al.*, 2009; Margiotta, 2015). A few major depositional hiatuses occur within the Pietra leccese, being often marked by glauconite-rich horizons (Balenzano *et al.*, 2002; Foresi *et al.*, 2002; Mazzei *et al.*, 2009). The depositional environment is considered to be the deepest part of the continental shelf (Bossio *et al.*, 2005, 2006).

The Pietra leccese is home to an impressive marine vertebrate fossil assemblage. Most of the collected fossils belong to cetaceans, with both toothed and baleen whales well represented (Moncharmont Zei, 1950, 1956; Bianucci *et al.*, 1992, 1994, 2016; Bianucci & Varola, 1994; Bianucci, 2001; Bianucci & Landini, 2006; Bisconti & Varola, 2006; Peri *et al.*, 2019, 2020, 2021, 2022). Sirenians and marine reptiles (turtles and crocodilians) are also present (Costa, 1853, 1856; Aldinio, 1896; Bianucci *et al.*, 2003; Chesi *et al.*, 2007). Fishes are represented by elasmobranchs (sharks and rays) and teleosts (bony fishes; Menesini, 1969; Vigliarolo, 1891; Carnevale *et al.*, 2002; Collareta *et al.*, 2021). Finally, but not the least of which, Digestichnia of marine vertebrates have also been reported, including putative gastroliths as well as the coprolite studied herein (Tavani, 1973; Collareta *et al.*, 2019).



◄ **Figure 2:** Schematic geological map of the Salento peninsula (Apulia, southern Italy). Orange-shaded areas indicate the exposures of the Pietra leccese, the Miocene limestone from which the fossil specimen MSNUP I-17604 originates. Redrawn and modified after the original illustration by CALIA *et al.* (2014).

4. Systematics

***Gnathichnus* BROMLEY, 1975**

Remarks. The monotypic ichnogenus *Gnathichnus* is a grazing structure (Pascichnia) that usually occurs on calcareous invertebrate shells and hardgrounds (*e.g.*, BROMLEY, 1975; FÜRSICH & WENDT, 1977; MARTINELL, 1982; BROMLEY & ASGAARD, 1993a, 1993b; GIBERT *et al.*, 2007; WILSON, 2007; BELAÚSTEGUI *et al.*, 2017; ANGSEESING, 2021) but has also been described from consolidated sediments such as burrow walls (MAYORAL & MUÑIZ, 1996) and, rarely, vertebrate bones (TWITCHETT, 1994; MEYER, 2011; REOLID *et al.*, 2015; JAGT *et al.*, 2020).

HÖPNER and BERTLING (2017) argued that since the nutrition of grazers is nonselective regarding the substrate, the nature of the latter is not a valuable ichnotaxobase for naming grazing traces. Such a statement would imply that all grazing traces do originate from feeding upon organisms that encrust or bore into the substrate, and not upon the substrate itself and/or remains of the associated tissues. As discussed below, this premise is controversial, but identifying cases of deliberate targeting of specific substrates by ancient grazers often leads to questionable conclusions, hence our assignment of the gnathichnian trace that occurs on MSNUP I-17604 to the ichnogenus *Gnathichnus*.

Gnathichnus almost invariably occurs in multiples of several overlapping grooves intersecting at angles of ~72° as a result of the star-shaped arrangement of the five calcium-carbonate teeth that comprise the "ARISTOTLE's lantern", *i.e.*, the chewing organ of most sea urchins (BROMLEY, 1975).

In spite of its low preservation potential, *Gnathichnus* even gives its name to an archetypal marine ichnofacies (*e.g.*, BROMLEY & ASGAARD, 1993a, 1993b; GIBERT *et al.*, 2007; MACEACHERN *et al.*, 2007).

***Gnathichnus pentax* BROMLEY, 1975**

(Fig. 3)

Referred material. A single cluster of grooves preserved on the surface of MSNUP I-17604, a marine vertebrate coprolite.

Occurrence. MSNUP I-17604 originates from the Pietra leccese, a Miocene (upper Burdigalian to lower Messinian) calcareous formation of southern Italy (Apulia Region, Salento peninsula) (see above for more details).

Description. This *Gnathichnus pentax* trace consists of a cluster of sub-linear, partly overlapping grooves that are a few millimetres long and meet each other at angles of ~72° (after BROMLEY, 1975; Fig. 3). The individual grooves have submillimetric transverse widths, and their distal terminations are often acuminate. The whole trace fossil appears as a densely sculptured area measuring ~10 mm × 8 mm. The *G. pentax* trace seemingly obliterates a pre-existing shark tooth mark (ichnospecies *Linichnus bromleyi*; see MUÑIZ *et al.*, 2020, and GODFREY & LOWRY, 2021).

Remarks. The Pietra leccese preserves remains of regular echinoids (cidaroids and temnopleuroids; RAGAINI, 1994) that may account for the production of the gnathichnian trace observed on MSNUP I-17604. Because the morphological quality of the latter is as high as in similar representatives of *G. pentax* from hard substrates such as oyster valves (*e.g.*, WILSON, 2007: Fig. 20.10), the dung was likely firm when grazing took place.

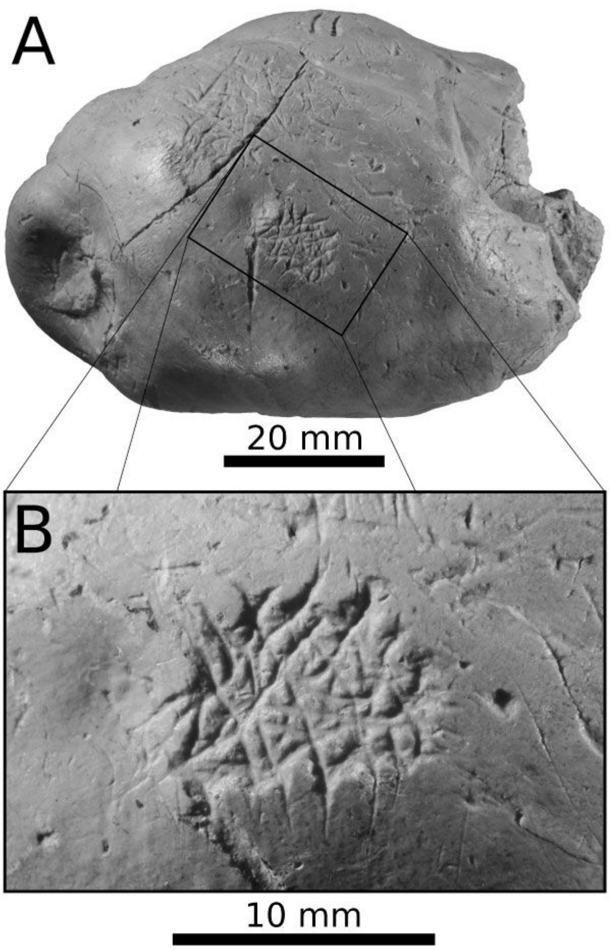


Figure 3: MSNUP I-17604, trace-bearing vertebrate coprolite from the Miocene Pietra leccese of southern Italy. (A) Lateral view of the coprolite, featuring the occurrence of the echinoid feeding trace *Gnathichnus pentax* (black rectangle); (B) close-up of the *G. pentax* specimen.

Additionally, the faeces would have had a fairly rigid consistency to facilitate the tube feet attachment (HENNEBERT *et al.*, 2012) to anchor the sea urchin to the curved surface of the dung so that its teeth could excavate the surface.

5. Discussion and conclusions

To our knowledge, the *Gnathichnus pentax* specimen studied here represents the first published record of this ichnotaxon on a coprolite, and this is quite remarkable in its own right. A cursory screening of the many marine vertebrate coprolites stored in the palaeontological collections of the Calvert Marine Museum (Solomons, Maryland, USA) revealed no specimens preserving gnathichnian traces (SJG, personal observation), though other kinds of traces (including bite marks) are present (*e.g.*, GODFREY & SMITH, 2010; GODFREY *et al.*, 2020, 2022). Thus, fossilised vertebrate faeces are a very rare substrate for the preservation of *G. pentax*.

What kind of behaviour is responsible for this unusual occurrence? Coprophagy certainly represents an intriguing explanation. Some extant Antarctic echinoderms, including the echinid sea urchin *Sterechinus neumayeri*, are known to feed on vertebrate faeces such as seal droppings (PEARSE & GIESE, 1966). Furthermore, according to MCCLINTOCK (1994), "[t]he ingestion of faecal material is not unique to Antarctic echinoderms, but to asteroids and echinoids in general." In light of these neontological observations, the *G. pentax* specimen observed on MSNUP I-17604 may be suggestive of coprophagy by a regular echinoid. As such, it would represent the first fossil evidence for faeces consumption by a sea urchin; in addition, it would demonstrate that coprophagy has been practiced by regular echinoids at least since the Miocene.

On the other hand, browsing of an algal (microbial) film that locally developed on the exterior of the faeces is also a possibility. Indeed, regardless of the nature of the substrate, gnathichnian traces have invariably been interpreted as evidence of the feeding activity of regular echinoids, and especially the grazing of epilithic (encrusting) and/or endolithic (boring) organisms (mostly algae) (BROMLEY, 1975; FÜRSICH & WENDT, 1977; BROMLEY & ASGAARD, 1993b; GIBERT *et al.*, 2007; WILSON, 2007; JAGT *et al.*, 2020; ANGSEESING, 2021), though feeding on residual organic matter associated with vertebrate and invertebrate hardparts or scavenging of bone tissues for phosphate has also been proposed (*e.g.*, BRETON *et al.*, 1992; REOLID *et al.*, 2015). Considering the trace that occurs on MSNUP I-17604, support for the algal browsing hypothesis may come from observing that only a limited area was subject to grazing, which suggests that the feeding echinoid targeted a precise location on the dung's exterior; furthermore, as mentioned, the faeces were likely firm when feeding took place. That said, even this scenario is not without concerns: indeed, the development of microbial communities on submerged faeces often leads to their destruction, whereas the exquisite state of preservation of MSNUP I-17604 evokes the rapid burial and early lithification of the dung (BRADLEY, 1946; THULBORN, 1991; DENTZIEN-DIAS *et al.*, 2012, 2018).

As detailed elsewhere (COLLARETA *et al.*, 2019), the studied coprolite also displays shark and bony fish tooth marks, which in turn suggests that for some reason it represented a target for exploratory consumption for a variety of marine organisms, including both vertebrate and invertebrate taxa. Thus, this new find further strengthens the notion that the analysis of coprolites is a powerful tool for investigating the feeding behaviours of ancient organisms, though sometimes in largely unexpected ways.

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As many other vertebrate fossils from the Pietra leccese, the coprolite MSNUP I-17604 was collected by the late and missed Angelo VAROLA in the framework of the scientific activities of the Gruppo Naturalisti Salentini.

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