

Organism-substrate interactions and astrobiology: Potential, models and methods



Andrea Baucon^{a,b,*}, Carlos Neto de Carvalho^b, Roberto Barbieri^c, Federico Bernardini^{d,e},
Barbara Cavalazzi^{c,f}, Antonio Celani^g, Fabrizio Felletti^h, Annalisa Ferretti^a,
Hans Peter Schönlaubⁱ, Antonio Todaro^j, Claudio Tuniz^{d,e,k}

^a Department of Chemical and Geological Sciences, University of Modena, Via Campi 103, 41125 Modena, Italy

^b Geology and Palaeontology Office, Geopark Naturtejo da Meseta Meridional – UNESCO Global Geopark. Municipality of Idanha-a-Nova – Centro Cultural Raiano, Av. Joaquim Morão, 6060-101 Idanha-a-Nova, Portugal

^c Department of Biological, Geological and Environmental Sciences, University of Bologna, Via Zamboni 67, Bologna, Italy

^d Centro Fermi, Museo Storico della Fisica e Centro di Studi e Ricerche "Enrico Fermi", Piazza del Viminale 1, 00184 Roma, Italy

^e Multidisciplinary Laboratory, The "Abdus Salam" International Centre for Theoretical Physics, Strada Costiera 11, 34014 Trieste, Italy

^f Department of Geology, University of Johannesburg, Auckland Park Kingsway (APK) campus, Johannesburg, South Africa

^g The "Abdus Salam" International Centre for Theoretical Physics, Strada Costiera, 11 I, 34151 Trieste, Italy

^h Department of Earth Sciences "Ardito Desio", University of Milan, Via Mangiagalli 34, 20133 Milano (MI), Italy

ⁱ Austrian Academy of Sciences, Commission for Geosciences, Dr. Ignaz Seipel-Platz 2, 1010 Vienna, Austria

^j Department of Life Sciences, University of Modena, via G. Campi 213/D, 41125 Modena, Italy

^k Centre for Archaeological Science, University of Wollongong, Northfields Ave, Wollongong, NSW 2522, Australia

ARTICLE INFO

Keywords:
Ichnology
Astrobiology
Geology

ABSTRACT

Organism-substrate interactions and their products – biogenic structures – are important biosignatures on Earth. This study discusses the application of ichnology – the study of organism-substrate interactions – to the search for present and past life beyond Earth. Three main questions are addressed: (1) Why to look for biogenic structures (i.e. traces and ichnofabrics) beyond Earth? (2) What biogenic structures to expect on other planets, moons and asteroids? (3) How to study extraterrestrial biogenic structures?

Review of terrestrial evidence highlights a set of properties that make traces and ichnofabrics important for the search of potential extraterrestrial life: trace fossils preserve the activity of soft-bodied organisms; biogenic structures are resilient to processes that obliterate other biosignatures (i.e. mechanical and chemical degradation, diagenesis, tectonism and metamorphism); traces are very visible biosignatures; traces indicate environment and behaviour; traces can be universal biosignatures, i.e., biosignatures ideally suited for detecting any type of life.

A model of organism-substrate interactions beyond Earth is here proposed. Expected extraterrestrial traces are those that manifest behaviours that allow to maintain homeostasis: excavations, meandering traces and biodeposition structures.

Most of the existing rovers and orbiters provide basic instruments for searching these traces. It is here suggested that the search for extraterrestrial biogenic structures by rovers would also benefit from artificial adjustable lighting, GPR, LiDAR, and drilling equipment with optical televiewer.

In this study, open-access databases of rover and orbiter imagery have been searched for traces and ichnofabrics, but no unquestionable evidence of biogenic structures beyond Earth has been found besides those produced by humans. This sounds along the lines of the famous Fermi Paradox: if the universe is teeming with aliens, where are their traces?

Results of this search show that habitable environments are not the only place to look for biogenic structures; non-habitable environments such as moons without atmosphere can favour the preservation of shallow-tier traces. The better preservation potential of traces compared to other biosignatures greatly widens the issue of planetary protection, including the interaction between astronauts or vehicles and the substrate may produce disturbances.

Although this study highlights a new direction of study with the tools and concepts of ichnology, dialogue

* Corresponding author at: Department of Chemical and Geological Sciences, University of Modena, Via Campi 103, 41125 Modena, Italy.
E-mail address: andrea@tracemaker.com (A. Baucon).

between the astrobiological and ichnological communities is needed to use its full potential and possibly answer one of the major questions of science: Does life exist beyond Earth?

1. Introduction

“Does life exist beyond Earth?” is one of the major questions of astrobiology (Ćirković, 2006; Cockell, 2002; Des Marais et al., 2008; Des Marais and Walter, 1999). This question is tackled by searching for biosignatures, namely remnants of processes and structures of biological origin (Des Marais et al., 2008; Des Marais and Walter, 1999; Gargaud, 2011). Biosignatures of critical importance include for example anomalous sulphur and carbon isotope ratios, hopanoids or magnetite chains (Chela-Flores et al., 2015; Des Marais et al., 2008; Ohmoto et al., 2008; Slater, 2009; Bell et al., 2015).

Organism-substrate interactions and their products – biogenic structures (e.g., traces and ichnofabrics) – are important biosignatures on Earth as they represent direct evidence of biological behaviour (Bromley, 1996; Buatois and Mángano, 2011; Plotnick, 2012; Seilacher, 2007) (Table 1, Fig. 1). It was also the recovery of trace fossils that has revealed biological activities in the early history of life on the Earth, e.g., Archean stromatolites and microborings or Proterozoic burrows (McLoughlin et al., 2007; Nutman et al., 2016; Ohmoto et al., 2008; Jensen et al., 2005). In spite of their relevance as biosignatures, however, the study of organism-substrate interactions (ichnology) (Buatois and Mángano, 2011) received relatively little attention in the search for life beyond Earth.

Iconic traces such as burrows, footprints and coprolites have widely been ignored in the field of astrobiology, with only a few exceptions (Baucon et al., 2015; Hasiotis et al., 2002, 2006). Although biogenic sediment fabrics are regularly listed among the major categories of biosignatures (e.g., Des Marais and Walter, 1999; Sephton, 2004; Westall et al., 2015), sediment mixing by organisms (bioturbation; Bromley, 1996) has received little attention in the astrobiological literature. The only products of organism-substrate interactions that captured some astrobiological attention are microbially induced sedimentary structures (e.g., Brake and Hasiotis, 2008; Noffke, 2015; Noffke et al., 2013) and microbioerosional structures (e.g., Buijs et al., 2004; Fisk et al., 2006; Friedmann and Weed, 1987; Slater, 2009; Sugawara et al., 2014; White et al., 2014).

Even from a methodological perspective, information on the astrobiological application of ichnology are scanty and lack case histories framed in a proper geoenvironmental context (Baucon et al., 2015; Hasiotis et al., 2002, 2006). This is surprising, as astrobiology is inherently a multidisciplinary field of knowledge (Des Marais et al., 2008). Unshared knowledge between different disciplines is likely to produce gaps in knowledge (Campbell, 2005), therefore the lack of communication between the astrobiological and the ichnological community is likely to have produced vast gaps in the search for life beyond Earth.

The goal of this study is to discuss the application of ichnology to the search for present and past life beyond Earth. To do this, three questions arise:

1. Why to look for biogenic structures (i.e., traces and ichnofabrics) beyond Earth?
2. What biogenic structures to expect on other planets, moons and asteroids?
3. How to study extraterrestrial biogenic structures?

The aims of this study are to provide answers to these questions and to document ichnodiversity beyond Earth. For this reason, this paper is organized in three major sections, each of which refers to a specific question, followed by a discussion on ichnodiversity beyond Earth.

2. Methods

Three classes of data sources are used in this study:

1. Unpublished data. Several ichnosites (Table 2) were explored in the field for finding the peculiarities of biogenic structures with astrobiological potential and to provide first-hand figured examples. They were selected to encompass different environmental and chronological ranges (continental to marine; Cambrian to present day).
2. Published data sources. Rover, lander and orbiter imagery of astronomical objects beyond Earth was analyzed to document extra-terrestrial ichnodiversity (Table 2). It was not possible to inspect each and every available image of the Solar System, hence a set of criteria has been used to select the astronomical objects to be inspected in more detail: (a) presence of suitable substrates for the preservation of traces (e.g., the Moon fits with this criterion, Jupiter not); (b) availability of images with at least 10 cm of resolution (e.g., Mars fits with this criterion, Uranus not); (c) occurrence of broad conditions required for life (thermodynamic disequilibrium and temperatures consistent with stable chemical bonding; Benner et al., 2004) in the present or in the past (e.g., Mars fits with this criterion, the Sun not). The analysis of published data sources is based on photo inspections with image analysis software on a 23" monitor.
3. Previous studies. Previous ichnological studies were analyzed to support the field-based data (Table 2; other ichnological studies are cited in-text).

Definition of ichnological and astrobiological concepts is based on previous literature from both disciplines (Bromley, 1996; Buatois and Mángano, 2011; Doyle, 2014; Frey and Pemberton, 1985; Gargaud, 2011; Seilacher, 2007; Slater, 2009) and summarized in Tables 3 and 4, respectively.

Table 1

Processes and products studied by ichnology. Processes and products based on previous literature (Buatois and Mángano, 2011; Pemberton et al., 2001). Examples of agents (tracemakers) from previous literature (Baucon et al., 2014; Baucon and Felletti, 2013a, 2013b; Bromley, 1996; Chen et al., 2012; Farlow and Holtz, 2002; Garcia-Guinea et al., 2014; Reid et al., 2000; Rhoads and Stanley, 1965).

Process	Product	Agent (example)	
Organism-substrate interactions	Bioturbation	Biogenic structures	Trilobite
		Burrows	Gastropod
		Trails	Dinosaur
		Tracks	Foraminifera
	Biostratification	Bioturbated sediment	
		Biogenic graded bedding	Polychaete
		Byssal mats	Bivalve
		Stromatolites	Cyanobacteria
	Biodeposition	Feces	Cow
		Fecal pellets	Shrimp
		Pseudofeces	Bivalve
	Bioerosion	Borings	Fungus
Gnawings		Dinosaur	
Scrapings		Polyplacophoran	
Bitings		Dinosaur	

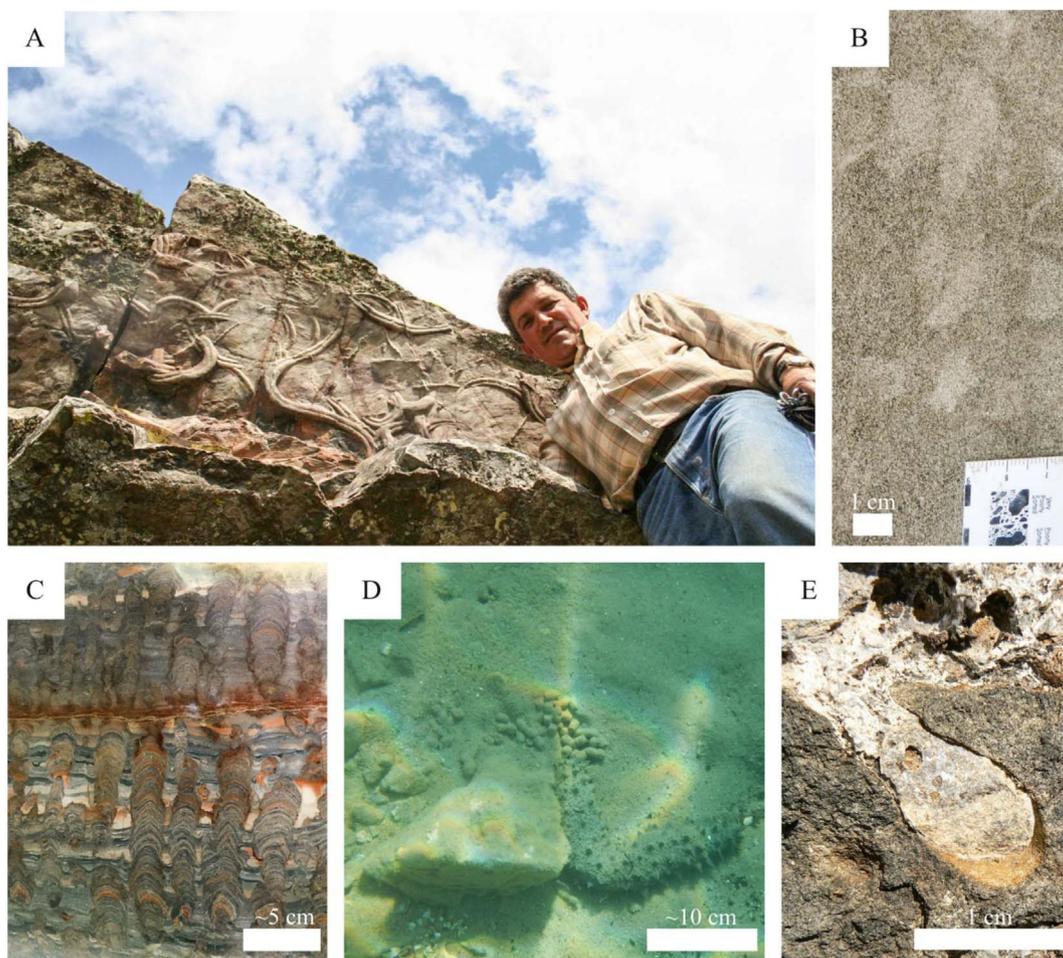


Fig. 1. Biogenic structures, the products of organism-sediment interactions. A. Bioturbation structure: the trilobite burrow *Cruziana* at the base of a quartzite bed. Ordovician, Penha Garcia (Portugal). B. Ichnofabric: the overall texture of the sediment results from bioturbation; individual burrows are hardly discernible. Vertical section. Plio-Pleistocene, Arda river (Italy). C. Biostratification structure: columnar stromatolites. Proterozoic (2 Ga), Songshan (Henan, China; Museum of the Songshan Geopark). Vertical section. D. Biodeposition structures: fecal pellets and their producer, a holothurian. Recent, Adriatic Sea, ca. 3 m of depth. E. Bioerosion structure: lateral view of the bivalve boring *Gastrochaenolites* from the Middle Miocene of Porto Santo Island (Portugal). The specimen is coming from the ichnosite described in Santos et al. (2011).

3. Why to look for biogenic structures beyond Earth?

Organisms (and their body fossil record) evidently represent a more direct evidence of life than traces (and trace fossils). For instance, a dinosaur or a trilobite appears a more direct evidence than their traces, namely footprints and burrows. Chemical and isotopic biosignatures are seemingly more robust evidence for life than ichnofabrics. Therefore, a question might arise: Why looking for extra-terrestrial biogenic structures (i.e., traces and ichnofabrics) beyond Earth? This section aims to answer this question by providing a set of properties, deduced from terrestrial evidence, which can be extended to potential extra-terrestrial environments.

3.1. Trace fossils preserve the activity of soft-bodied organisms

The fossil record on Earth is incomplete, because organisms that live on land or that do not possess hard parts are less likely to be preserved than than marine animals with hard parts (Doyle, 2014). Soft-bodied and lightly mineralized organisms are rarely preserved as body fossils other than under circumstances such as low oxygen and high sedimentation rate (Crimes and Droser, 1992; Doyle, 2014; McIlroy, 2004).

Such “loss of information by nonpreservation” (Lawrence, 1968) has noteworthy astrobiological implications because it limits the application of body fossil biosignatures for describing past biodiversity. At least on Earth, this loss of information is quantitatively important as soft-bodied organisms represent the largest part of the benthic biota in

modern (Benton, 2009; Benton et al., 2011; Lawrence, 1968; Paul, 1998) and fossil (McIlroy, 2004; von Bitter et al., 2007) ecosystems. This non-preservation of soft-bodied organisms may eliminate from 40 to 70% or more of a given community (Lawrence, 1968; Paul, 1998; von Bitter et al., 2007; Benton, 2009; Benton et al., 2011). The aforementioned percentages will be increased when considering the first three billion years of Earth history, during which life was mostly soft-bodied (Cohen et al., 2011; Porter, 2011).

In contrast, biogenic structures such as burrows, borings and stromatolites (Tables 1, 3) record accurately the activity of soft-bodied organisms – from microscopic prokaryotes to annelids (Buatois and Mángano, 2011; Crimes and Droser, 1992; McIlroy, 2004). The reason for this depends on the nature of biogenic structures, that are both sedimentological and biological objects (Baucon et al., 2012; Bromley, 1996; Seilacher, 2007). Bioturbational structures are indeed sedimentary structures (Seilacher, 1967a) and, as such, they record very well the activity of organisms that burrow within the sediments (Buatois and Mángano, 2011). For instance, fossil burrows (*Skolithos*, *Monocraterion*) record the activity of worm-like organisms during the early phase of the Phanerozoic diversification, as evidenced by the Cambrian and Lower Ordovician ‘pipe rocks’ (Desjardins et al., 2010; Droser, 1991; McIlroy and Garton, 2009) (Fig. 2). Burrowers tend to reduce the skeleton because their burrow duplicates the advantages provided by the skeleton itself (e.g., physical protection; anti-predator sheltering; protection against desiccation; Bromley, 1996) and because hard parts can be detrimental to infaunal life (Buatois and Mángano, 2011).

Table 2

Astronomical objects searched for biogenic structures. Data freshness indicates newly developed data (a), interpretation of published data sources (b) and previous studies (c).

System	Astronomical object	Data source	Type of data source	Data freshness	Number of images	Reference
Mercury	Mercury	Mariner 10	Orbiter	b	5	(“JPL Photojournal,” 2015)
	Mercury	Messenger	Orbiter	b	11	(“JPL Photojournal,” 2015)
Venus	Venus	Galileo	Orbiter	b	3	(“JPL Photojournal,” 2015)
	Venus	Magellan	Orbiter	b	13	(“JPL Photojournal,” 2015)
	Venus	Messenger	Orbiter	b	2	(“JPL Photojournal,” 2015)
	Venus	Venera 9	Lander	b	1	(“NSSDCA Photo Gallery,” 2015)
	Venus	Venera 10	Lander	b	1	(“NSSDCA Photo Gallery,” 2015)
	Venus	Venera 13	Lander	b	3	(“NSSDCA Photo Gallery,” 2015)
	Venus	Venera 14	Lander	b	1	(“NSSDCA Photo Gallery,” 2015)
Earth-Moon	Earth, Grado lagoon (Recent, Italy)	Fieldwork	Fieldwork	a, c	–	(Baucon, 2008; Baucon and Felletti, 2013a, 2013b)
	Earth, Northern Apennines (Cretaceous-Oligocene, Italy)	Fieldwork	Fieldwork	a	–	
	Earth, Penha Garcia (Ordovician, Portugal)	Fieldwork	Fieldwork	a, c	–	(Neto de Carvalho, 2006; Neto de Carvalho and Baucon, 2016)
	Moon	Chandrayaan1	Orbiter	b	1	(“JPL Photojournal,” 2015)
Mars-moons	Moon	Lunar Reconnaissance Orbiter	Orbiter	b	25	(“LROC website,” 2015)
	Deimos	Mars Reconnaissance Orbiter	Orbiter	b	1	(“JPL Photojournal,” 2015)
	Mars	Opportunity rover	Lander (rover)	b	117	(“Mars Exploration Rover Mission: Multimedia,” 2016)
	Mars	Phoenix	Lander	b	18	(“JPL Photojournal,” 2015)
	Mars	Spirit rover	Lander (rover)	b	113	(“Mars Exploration Rover Mission: Multimedia,” 2016)
	Mars	Viking 1	Lander	b	6	(“NSSDCA Photo Gallery,” 2015)
	Mars	Viking 2	Lander	b	6	(“NSSDCA Photo Gallery,” 2015)
	Mars	Curiosity rover	Lander (rover)	b	340	(“Raw Images - Mars Science Laboratory,” 2016)
	Mars	Mariner 9	Orbiter	b	1	
	Mars	Mars Global Surveyor	Orbiter	b	1	(“JPL Photojournal,” 2015)
	Mars	Mars Reconnaissance Orbiter	Orbiter	b	16	(“JPL Photojournal,” 2015)
	Phobos	Mars Reconnaissance Orbiter	Orbiter	b	3	(“JPL Photojournal,” 2015)
	Ceres	Phobos	Mars Global Surveyor	Orbiter	b	5
Ceres		Dawn	Orbiter	b	5	(“JPL Photojournal,” 2015)
Jupiter-moons	Amalthea	Galileo	Orbiter	b	3	(“JPL Photojournal,” 2015)
	Callisto	Galileo	Orbiter	b	7	(“JPL Photojournal,” 2015)
	Europa	Galileo	Orbiter	b	19	(“JPL Photojournal,” 2015)
	Ganymede	Galileo	Orbiter	b	19	(“JPL Photojournal,” 2015)
	Jupiter	Cassini-Huygens	Orbiter	b	3	(“JPL Photojournal,” 2015)
Saturn-moons	Thebe	Galileo	Orbiter	b	1	(“JPL Photojournal,” 2015)
	Calypso	Cassini-Huygens	Orbiter	b	1	(“JPL Photojournal,” 2015)
	Dione	Voyager 1	Orbiter	b	3	(“JPL Photojournal,” 2015)
	Dione	Voyager 2	Orbiter	b	1	(“JPL Photojournal,” 2015)
	Dione	Cassini-Huygens	Orbiter	b	9	(“JPL Photojournal,” 2015)
	Enceladus	Cassini-Huygens	Orbiter	b	26	(“JPL Photojournal,” 2015)
	Epimetheus	Cassini-Huygens	Orbiter	b	1	(“JPL Photojournal,” 2015)
	Helene	Cassini-Huygens	Orbiter	b	4	(“JPL Photojournal,” 2015)
	Hyperion	Cassini-Huygens	Orbiter	b	7	(“JPL Photojournal,” 2015)
	Iapetus	Cassini-Huygens	Orbiter	b	8	(“JPL Photojournal,” 2015)
	Io	Galileo	Orbiter	b	21	(“JPL Photojournal,” 2015)
	Janus	Cassini-Huygens	Orbiter	b	3	(“JPL Photojournal,” 2015)
	Mimas	Cassini-Huygens	Orbiter	b	7	(“JPL Photojournal,” 2015)
	Phoebe	Cassini-Huygens	Orbiter	b	6	(“JPL Photojournal,” 2015)
	Prometheus	Cassini-Huygens	Orbiter	b	3	(“JPL Photojournal,” 2015)
	Rhea	Cassini-Huygens	Orbiter	b	14	(“JPL Photojournal,” 2015)
	Saturn	Cassini-Huygens	Orbiter	b	11	(“JPL Photojournal,” 2015)
	Telesto	Cassini-Huygens	Orbiter	b	3	(“JPL Photojournal,” 2015)
	Tethys	Cassini-Huygens	Orbiter	b	9	(“JPL Photojournal,” 2015)
	Titan	Huygens	Lander	b	2	(“JPL Photojournal,” 2015, “NSSDCA Photo Gallery,” 2015)
Titan	Titan	Cassini-Huygens	Orbiter	b	11	(“JPL Photojournal,” 2015)
	Ariel	Voyager	Orbiter	b	1	(“JPL Photojournal,” 2015)
Uranus-moons	Uranus	Voyager 2	Orbiter	b	1	(“JPL Photojournal,” 2015)
Pluto-moons	Pluto	New Horizons	Orbiter	b	9	(“JPL Photojournal,” 2015)

Consequently, burrowers are predominantly soft-bodied or lightly mineralized organisms (Bromley, 1996). In parallel to burrows in soft substrates, borings in hard substrates provide similarly significant advantages to their producers, for which reason many soft-bodied groups

excavate and maintain borings (Staudigel et al., 2008; Taylor and Wilson, 2003). Borings produced by soft-bodied organisms are preserved in the same way as the hard substrates in which they are excavated (Frey, 1975), and, for this reason, they have a far better

Table 3
Ichnological terms.

Class	Term	Definition of the term	Reference	
Concepts	Ichnology	The study of structures produced by organisms on or within a substrate. Divisions include palaeoichnology for fossil biogenic structures, and neoichnology for recent ones.	(Buatois and Mángano, 2011; Frey and Pemberton, 1985)	
	Tiering, ecological stratification, storey structure	Vertical partitioning of a community	(Bromley, 1996)	
Processes	Bioturbation, sediment mixing, sediment reworking	Process by which the primary consistency and structure of a sediment are modified by the activities of organisms living within it	(Bromley, 1996; Pemberton et al., 2001)	
	Biostratification	Process by which stratification features are imparted by biological activity	(Pemberton et al., 2001)	
	Biodeposition	Production or concentration of sediments by the activities of an organism	(Pemberton et al., 2001)	
Products	Bioerosion	Mechanical or biochemical excavation of a rigid substrate	(Pemberton et al., 2001)	
	Biogenic structure	Any tangible evidence of organism activity other than the production of body parts	(Frey and Pemberton, 1985; Pemberton et al., 2001)	
	Trace, lebensspur	An individually distinctive biogenic structure	(Pemberton et al., 2001)	
	Trace fossil, ichnofossil	A fossil trace	(Bromley, 1996; Doyle, 2014)	
	Burrow	An excavation made within unconsolidated sediment; space within sediment occupied and maintained by an organism	(Bromley, 1996; Pemberton et al., 2001)	
	Boring	An excavation made into a hard substrate	(Pemberton et al., 2001)	
	Track	An impression left in underlying sediment by an individual foot or podium; footprint is a similar term	(Pemberton et al., 2001)	
	Trackway	A succession of tracks reflecting a single excursion or trip	(Pemberton et al., 2001)	
	Trail	A continuous groove produced during locomotion by an animal having part of its body in contact with the substrate surface, or a continuous subsurface trace made by an animal travelling from one point to another	(Frey and Pemberton, 1985)	
	Ichnofabric, bioturbated texture	All aspects of the texture and internal structure of a substrate that result from organism-substrate interactions at all scales	(Bromley, 1996; Frey and Pemberton, 1985)	
	Agents	Tracemaker, producer	The organism responsible for the trace (fossil)	(Bromley, 1996)
	Methods	Ichnofacies method	Approach that uses ethological groupings based on temporally and spatially recurring trace-fossil suites to determine palaeoenvironments	(Gingras et al., 2011; McIlroy, 2008)
		Ichnofabric method	Approach that focuses on the aspects of the texture of a substrate that result from organism-substrate interactions (ichnofabric) to determine palaeoenvironments	(Gingras et al., 2011; McIlroy, 2008; Taylor et al., 2003)
	Other ichnology-related terms	Pseudo-trace, pseudotrace, pseudo-lebensspur	Trace-like structure that owe its origin to physical processes.	(Frey and Pemberton, 1985; Seilacher, 2007)
Body fossil		Fossils that preserve the original body of an organism	(Doyle, 2014)	
Ichnotaxon		A taxonomic unit (taxon) based on the fossilized work of an organism	(ICZN, 1999)	
Ichnogenus		Genus-group name formally assigned to trace	(Bromley, 1996)	
Ichnosite		Trace-bearing locality		
Fill		Material that fills a burrow	(Bromley, 1996)	
Lining		Material applied to the burrow wall by the occupant	(Bromley, 1996)	
Ichnodiversity	Number of ichnotaxa present	(Bromley, 1996; Buatois and Mángano, 2011)		

Table 4
Astrobiological terms.

Class	Term	Definition of the term	Reference	
Concepts	Astrobiology	The study of the origin, evolution, distribution, and the future of life in the Universe	(Gargaud, 2011)	
	Habitable	A location that has the necessary conditions for at least one known organism to be active	(Cockell, 2014)	
	Analogue site	Specific location on Earth that is similar in some important respects to extraterrestrial locales	(Preston and Dartnell, 2014)	
	Extreme environment	An environment that is characterized by conditions that are hard to survive for most known life forms	(Gross, 1996)	
	Extremophile	An organism that not only survives, but thrives under extreme conditions	(Cavicchioli, 2002; Rothschild and Mancinelli, 2001)	
	Planetary protection	The process of preventing contamination of planetary environments by living organisms from other planets	(Gargaud, 2011)	
Processes	Life	A consensus about the definition of life is yet to emerge	(Machery, 2012)	
	Products	Biosignature, marker of life, biomarker (some authors use the term to indicate specific classes of biosignatures), trace of life, biondex, index of life	Chemical, morphological, sedimentary or isotopic process or structure that is biogenic and could be detected to infer the past or present presence of life	(Gargaud, 2011; Slater, 2009)
		Abiosignature	A signature derived from an abiotic (i.e., chemical or physical) process	(Slater, 2009)
Agents	Organism	A consensus about the definition of life, and therefore organism, is yet to emerge	(Machery, 2012)	
Methods	Direct imaging	Direct imaging of planets refers to the effort to detect and study exoplanets from the light emitted or scattered by the planets themselves	(Gargaud, 2011)	
Other astrobiology-related terms	Exoplanet, extrasolar planet	A planet in orbit around a star other than the Sun	(Gargaud, 2011)	

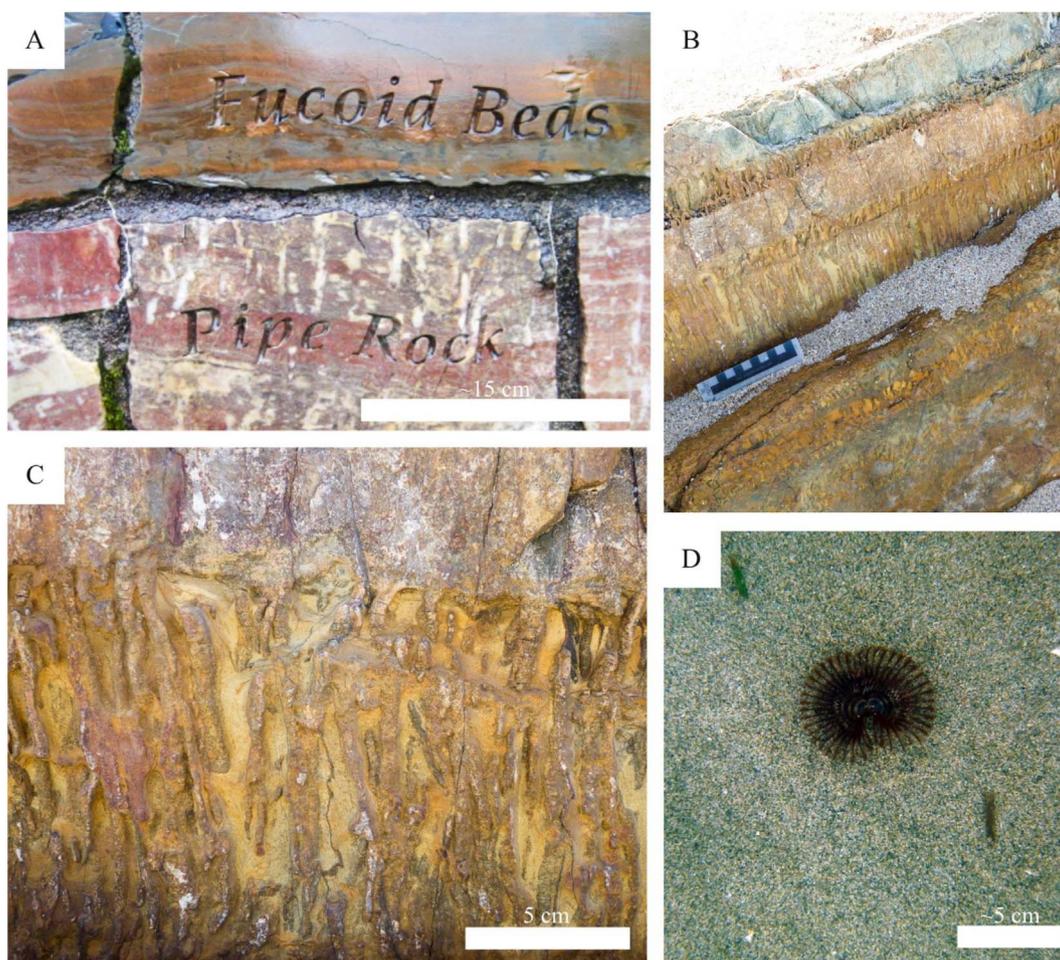


Fig. 2. Trace fossils preserve the activity of soft-bodied organisms. A. *Skolithos* pipe-rock from an artificial outcrop. Vertical section. Cambro-Ordovician, Knockan Crag (Scotland). B. *Skolithos* pipe rock from the Lower Ordovician Armorican Quartzite Formation. Apulia Beach (Portugal). Scale ticks are 1 cm. C. Close-up of C, showing numerous vertical burrows (*Skolithos*). D. A polychaete expanding from its burrow, that is the modern equivalent of *Skolithos*. Top view. Recent, Adriatic Sea.

preservation potential than their tracemakers. Similarly, stromatolites, as well as other microbialites, are primarily composed of trapped particles and chemical cements, and are therefore likely to have a higher preservation potential than their soft-bodied microbial tracemakers (Della Porta, 2015; Shapiro, 2007). The low preservation potential of soft-bodied organisms can be extended to potential counterparts beyond Earth. In fact, soft-bodied organisms are by nature more delicate and difficult to preserve than mineralized ones. Consequently, as observed on Earth (Buatois and Mángano, 2011; Crimes and Droser, 1992; McIlroy, 2004), biogenic structures are important for detecting potential soft-bodied life beyond Earth.

3.2. Biogenic structures are resilient to processes that obliterate other biosignatures

One of the peculiarities of biogenic structures is that they are the only macroscopic biosignatures in many rock units on Earth (Bromley, 1996; Buatois and Mángano, 2011; Pemberton et al., 2001) (Fig. 3).

For instance, the thick succession (> 400 m) of weakly metamorphosed rocks (quartzites) outcropping at Penha Garcia (Portugal) has been studied since the late 19th century (Delgado, 1886; Neto de Carvalho, 2006) (Table 2); several bioturbated horizons and > 5000 individual trace fossils have been discovered (Fig. 1A, Fig. 2B, Fig. 3C), whereas only 2 fragmentary macroscopic body fossils have been found since then (Neto de Carvalho, 2011). Similarly, whereas no vertebrate body fossils have been reported from the Cretaceous Botucatu Formation (Brazil) across an area of > 1,500,000 km², dinosaur, mammal and

arthropod footprints have been extensively documented (Francischini et al., 2015; Scherer and Goldberg, 2007). These examples are not fully explained by the previously discussed principle, that is, “trace fossils preserve the activity of soft-bodied organisms” (Section 3.1). In fact, the fossil record of the two above examples includes traces produced by organisms with mineralized parts (e.g., trilobites, bivalves, mammals and dinosaurs), but the corresponding body fossils are not found, if not in rare cases. For these reasons, the excellent preservation of biogenic structures is to be explained by their resilience with respect to the processes that commonly obliterate other biosignatures:

1. Mechanical and chemical degradation prevents the preservation of organic matter (Prothero, 2013), however, this does not apply to biogenic structures (Savrda, 2007). Hence, they depict more accurately the “hidden biodiversity” (Smith et al., 2008) represented by biosignatures with low preservation potential (Fig. 3A).
2. Diagenesis usually alters or obliterates body fossils, but it can often enhance trace fossils (Buatois and Mángano, 2011; Dodd and Stanton, 1990; Frey, 1975). Activities of burrowing organisms are among the most important factors controlling the diagenesis of organic matter in sediments (Kristensen, 2000). Burrowers may change the local chemistry of the sediment and therefore burrows may be selectively cemented, chertified, silicified, dolomitized or pyritized (de Gibert and Goldring, 2008; Dodd and Stanton, 1990) (Fig. 3B). In addition, diagenetic mineralization may emphasize borings (Savrda, 2007) and coprolites (Brachanec et al., 2015; Shen et al., 2014).

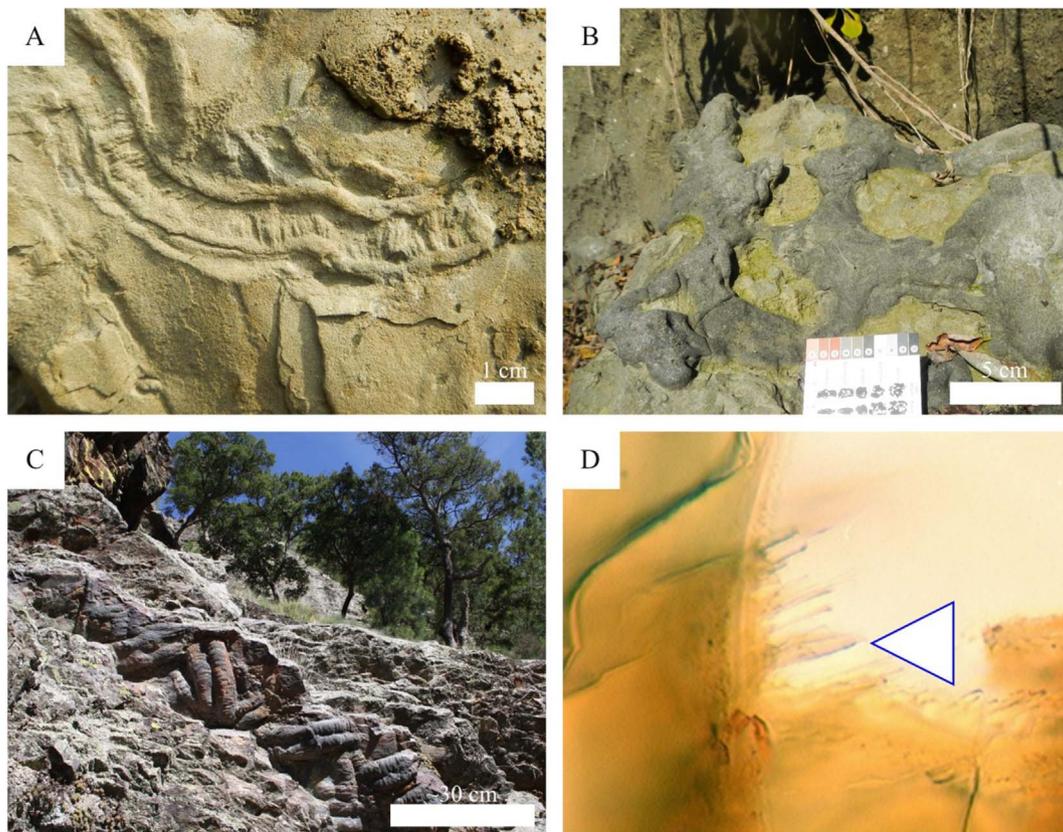


Fig. 3. Biogenic structures are resilient to processes that obliterate other biosignatures. A. Bedding plane with a specimen of *Scolicia*. Mechanical and chemical degradation prevented the preservation of the tracemaker, an irregular urchin. Eocene-Oligocene deep-sea deposits of the Northern Apennines (Italy). B. Diagenetically-enhanced *Thalassinoides*. Although the *Thalassinoides*-bearing unit has a rich body fossil record, the tracemaker (a ghost shrimp) is rarely preserved. Stirone river (Italy), Plio-Pleistocene. C. Metamorphic rocks with trilobite burrows. Only few fragmentary macroscopic body fossils have been found in the ichnosite, that is extremely rich in well-preserved trace fossils. Ordovician, Penha Garcia (Portugal). D. Microboring-like structures from the meteorite Nakhla. The structures have been transported from Mars to Earth by meteorite impact. The longest structures are about 10 μm long. Thin section. These structures have been described by Fisk et al. (2006).

3. Biogenic structures can survive tectonism and metamorphism that would obliterate body fossils (MacNaughton, 2011), as well as chemical and isotopic biosignatures (Bernard et al., 2007; Gargaud, 2011). For instance, recrystallized microbial trace fossils have been documented from metamorphosed Permian basalts (Sugawara et al., 2014). Decimetre-scale fossil burrows are described from low-metamorphic Ordovician phyllites (Hollocher, 2014). Ordovician burrows are reported from quartzites (Neto de Carvalho, 2006) (Fig. 3C). Stromatolites have also been found in highly metamorphosed Precambrian marble (Hollocher, 2014). Titanite preservation of microborings can withstand metamorphic overprinting up to lower amphibolite facies (Izawa et al., 2010). Microboring-like structures of Martian origin have been reported from several meteorites, suggesting that eventual microborings may survive transport from one planet to another by meteorite impact (Fisk et al., 2006; Izawa et al., 2010; White et al., 2014) (Fig. 3D).

The mentioned physical processes, that are mechanical and chemical degradation, diagenesis, tectonism, metamorphism and meteorite impact, are not Earth-specific, but they have been recognized on other objects of the Solar System (Basilevsky et al., 2014; Grotzinger et al., 2011; Knoll et al., 2005; McLennan et al., 2005; Orofino et al., 2010; Watters and Schultz, 2010) and they are likely to characterize Earth-like exoplanets (Foley et al., 2012; Noack and Breuer, 2014; Van Heck and Tackley, 2011). The documented resilience of the ichnological record can consequently be generalized to other astronomical objects. For this reason, trace fossils are important for detecting and describing past biodiversity beyond Earth.

3.3. Traces are very visible biosignatures

Colour, motion, orientation and size are all supported as guiding attributes of human visual attention (Wolfe and Horowitz, 2004); therefore, they provide a framework to evaluate visibility sensu Savrda (2007) by considering the contrast between biogenic structures and the substrate. First, the colour of recent and fossil traces tends to be different from the colour of the host sediment. During tracemaking, bioturbating organisms can change the optical properties of the sediments by compaction or by exposing deeper, differently coloured layers. For example, on the Moon, astronaut tracks appear darker or brighter than unbioturbated areas at some light angles (Kaydash et al., 2011; Mitchell et al., 1972) (Fig. 4A).

Similar phenomena are likely to occur on other astronomical objects, as evidenced by the effect of non-biological disturbances on Mars. Dark surface structures are caused by passing whirlwinds (dust devils) that lift dust from the surface of Mars (Reiss et al., 2014) (Fig. 4B) and by rover wheels that excavates dark sediments buried beneath a thin mantle of bright dust (Geissler et al., 2010) (Fig. 4C). Colour contrast is also associated to actively filled or lined burrows, e.g., fossil and incipient *Macaronichnus* (Clifton and Thompson, 1978).

Biogenic activities change the colour of the substrate not only by the physical effects of tracemaking, but also by changing the biochemistry of the substrate (Fig. 4D) (Aller, 1988; Bromley, 1996; Gingras et al., 2014). Commonly, burrows and borings are differently coloured than the host substrate (Aller, 1988; Bromley, 1996; Gingras et al., 2014; Bromley et al., 1990; Herringshaw et al., 2010; Baucon and Felletti, 2013a, 2013b; Gingras et al., 2014). Similarly, biodeposition structures imply sediment processing by the producer, for which reason their

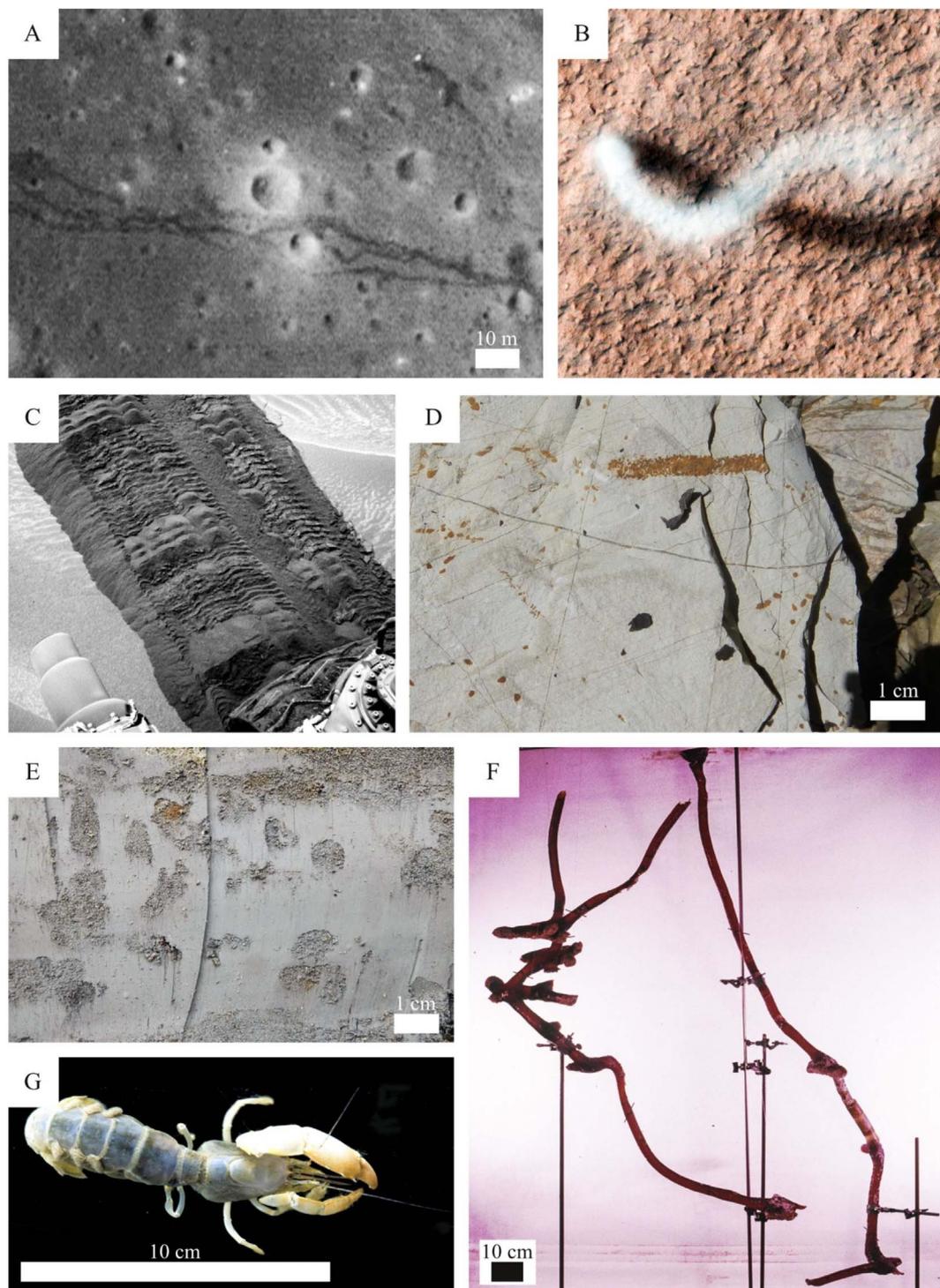


Fig. 4. Traces are very visible biosignatures. A. Astronaut trackways imaged from Lunar Reconnaissance Orbiter. They are sharply contrasting in colour with the unbioturbated regolith. Recent, Moon (Apollo 14 Landing Site). Image credit: NASA. B. Dust devil with shadow. Picture imaged by the High Resolution Imaging Science Experiment (HiRISE) camera on Mars Reconnaissance Orbiter. The plume is about 30 m in diameter. Recent, Mars (Amazonis Planitia). Image credit: NASA/JPL-Caltech/Univ. of Arizona. C. Curiosity rover tracks on Sol 709. Image from the Navigation Camera on the Curiosity Mars rover. Recent, Mars. Image credit: NASA/JPL-Caltech. D. *Chondrites* burrows contrasting in colour with the host rock. Cretaceous-Paleocene, surroundings of Osera (Italy). E. Ichnofabric characterized by sand-filled burrows. The burrows have been passively filled by event deposition (hyperpycnal flow). Vertical section. Plio-Pleistocene, Arda river (Italy). F. Resin cast of a *Glypturus acanthochirus* burrow in side view. The producer, much smaller than the burrow itself, is figured in G. Recent, Twin Cays (Belize). The burrow cast appeared in previous literature (Dworschak, 2002; Dworschak and Ott, 1993). G. The decapod crustacean *Glypturus acanthochirus* produces burrows that are much larger than it, i.e., the burrows in F. Specimen from Dworschak and Ott (1993).

colour may differ from the host sediment. Modern biostratification structures also tend to contrast in colour with non-biostratified sediments because of the tracemaker ecology; e.g., dull-green or blue-green coloration of some microbial mats is dictated by the pigment phycocyanin that has a light-capturing function (Gerdes et al., 1985; Vincent

et al., 1993; Vincent and Quesada, 2012). Preservation processes may result in contrasting colours as well. The remobilization and redeposition of sediment accumulated relatively slowly (event deposition) frequently generate sharp boundaries of contrasting lithologies by filling open burrows (Einsele, 1996; Jensen et al., 2005) (Fig. 4E).

deposition is not limited to Earth, as evidenced by flood deposits and subaqueously resedimented evaporites on Mars (Rodríguez et al., 2014; Wezel and Baioni, 2010).

Traces tend to be enhanced by diagenesis because they are delimited by conspicuous physical and biochemical breaks in the fabric of the substrate in which they are emplaced (Bromley, 1996; Dafoe et al., 2008; Frey, 1975; Pemberton and Frey, 1982; Savrda, 2007). Diagenetic enhancement is usually more intense for biogenic sedimentary structures (Fig. 3B) than for bioerosion structures (Frey, 1975), although prominent exceptions are the phosphatization of boring fills (Žitt and Mikuláš, 2006) and the sealing of microborings by authigenic mineral precipitation (Staudigel et al., 2008). Phosphatization of coprolites is a common phenomenon that is attributed to the decomposition of organic material and the consequent formation of a specific, phosphate-rich microenvironment (Brachaniec et al., 2015; Shen et al., 2014). The biochemical, preservational, diagenetic processes can result in differential weathering of traces and enhanced visibility (Savrda, 2007).

Second, modern and fossil traces do not move because they are embedded in the substrate. Hence, locomoting organisms are easier to detect.

Third, orientation of modern and fossil traces is variable, although there are well-documented case studies in which multiple traces share the same orientation in response to an oriented environmental gradient: parallel vertebrate trackways (Pleistocene) (Fornós et al., 2002), rheotactic, shore-perpendicular *Macaronichnus* (Holocene) (Bromley et al., 2009), preferentially oriented crustacean burrows (modern) (Pervesler and Hohenegger, 2006).

Fourth, the size of a trace has to be different from the size of the grains of the substrate in order to allow interaction with the substrate itself. For instance, bioturbation involves the displacement of sediment grains, therefore bioturbation structures are always larger than the individual sediment grains where they are produced. Similarly, bioerosion is always smaller than the solid where it is produced. On Earth, traces encompass a wide range of dimensional scales, from dinosaur tracks to borings produced by bacteria, but they are frequently bigger, and therefore more visible, than their tracemakers. In particular, burrows, trackways, trails, and stromatolites are bigger than their tracemakers, and this should be valid also for traces beyond Earth. In fact, burrows consist of the space within sediment occupied and maintained by an organism (Bromley, 1996), thus they are at least as large as their tracemaker. Traces that reflect non-stationary burrowing are regularly far larger than their tracemaker (Fig. 4F–G). For example, the modern ghost shrimps *Pestarella candida*, *Glypturus acantochiurus*, *Callianassa louisianensis* are typically < 15 cm long but produce *Thalassinoides*-like burrows with a vertical extension of about 60 cm, 150 cm and 250 cm, respectively (Dworschak, 2002; Dworschak and Ott, 1993; Griffis and Suchanek, 1991). Another example is represented by modern ant nests, some of which are up to 4 m deep (Tschinkel, 2003). Similar trace fossils (*Thalassinoides*, *Daimoniobarax*) have also been reported from the fossil record (Baucon and Avanzini, 2008; Cherns et al., 2006; Ekdale and Bromley, 2003; Jin et al., 2012; Neto de Carvalho et al., 2010; Smith et al., 2011). For the same reason, trackways and trails are commonly longer than their tracemaker. For instance, the centimeter-sized crab *Ocypode* produces the Earth's longest invertebrate trackways ever recorded (about 100 m long) (De, 2014). Biostratification structures are the product of a large number of organisms (e.g., stromatolites) and, therefore, they are larger than their producers. Traces are not only larger than their tracemakers, but they are regularly far more abundant than them because the same organism can produce numberless traces of the same type. This is shown, for instance, by the abundance and visibility of biodeposition structures: fecal stains are so visible to be used to map penguin colonies from satellite (Fretwell and Trathan, 2009). In addition, the same organism can produce different biogenic structures corresponding to different behaviours (Seilacher, 1967a; Bromley, 1996). For instance, the green crab *Carcinus maenas*

produces long trails when locomoting, squat burrows for sheltering and mating, indistinct bioturbation when avoiding potential predators and bioerosional traces on mollusc shells when predated (Baucon, 2008; Baucon and Felletti, 2013a, 2013b). For these reasons, biogenic structures can potentially provide abundant biosignatures even on low-biomass planets or moons.

In sum, both modern and fossil traces frequently contrast with the host substrate in terms of colour and size, being therefore very visible biosignatures. This attribute can be extended because the processes responsible for this contrast are either found beyond Earth (change of optical properties of sediments; event bedding) (Kaydash et al., 2011; Mitchell et al., 1972; Rodríguez et al., 2014; Wezel and Baioni, 2010) or can be plausibly extended beyond Earth (diagenesis; ratio trace/tracemaker size). In addition, several traces are by nature larger and more abundant than their tracemakers. Because of their good visibility, trace fossils are important for the search of life beyond Earth.

3.4. Traces indicate environment and behaviour

Chemical and isotopic biosignatures are robust evidence for life, but they are not well suited to answer three major astrobiological questions (Brasier and Wacey, 2012):

1. “What did remote life look like?”
2. “Where did it live?”
3. “How did it feed and behave?”

Morphological biosignatures are the optimal class of biosignatures to answer these questions (Brasier and Wacey, 2012). First, body fossils preserve morphological information, therefore they are potentially the best biosignatures to understand what did remote life look like. In contrast, biogenic structures seldom provide accurate morphological information about the identity of the tracemaker (Seilacher, 1967a). Footprints are one of the rare classes of biogenic structures that allow to establish a direct relationship between the trace and the tracemaker (Plotnick, 2012) (Fig. 4A).

Second, trace fossils are rarely transported, therefore they can provide direct information about where tracemakers actually lived, that is, the depositional environment in which traces were emplaced (Buatois and Mángano, 2011). The information provided by biogenic structures concerns not only the biological setting, but also the physico-chemical properties of the ecosystem in which they have been produced: hydrodynamics, substrate, oxygenation, salinity, sedimentation rate, water turbidity, climate, level of the water table, among others (Buatois and Mángano, 2011; Pemberton, 1992; Taylor et al., 2003). This is the reason why trace fossils are useful tools for reconstructing sedimentary environments through time, and the concept of ichnofacies is so widely applied (Frey and Pemberton, 1985; Frey and Seilacher, 1980; Pemberton et al., 2001; Seilacher, 1953, 1954, 1967a).

Third, trace fossils allow to understand “how did life feed and behave?”, because they are primary evidence of biological behaviour (Seilacher, 1967a). For instance, a vast set of behavioural patterns is revealed by the ichnological record of non-avian dinosaurs: terrestrial locomotion is shown by trackways, swimming by well-imprinted scratch marks, resting behaviour by tracks with body impressions (*Anomoepus scambus*, *Sauropus barrattii*), resting and feeding by a crater-like marking in front of the footprints (*Moyenisauropus natator*), predated by tooth marks, digestion behaviour by coprolites, courtship behaviour by impressions with scratch marks, parental care by burrows with dinosaur body fossils and reproduction by nests (Bromley, 1996; Brusatte et al., 2010; Ezquerro et al., 2007; Farlow and Holtz, 2002; Ghosh, 2003; Lockley et al., 2016; Thulborn, 2012; Varricchio et al., 1999, 2007).

The Ordovician deposits of Penha Garcia (Table 2) show excellent examples of fossil behaviours attributable to invertebrates. For example, the long bilobate burrows (*Cruziana*) made by trilobites indicate

constant digging and feeding behaviour while moving forward (Fig. 1A); they may locally intergrade with smaller burrows (*Rusophycus*), corresponding to digging and feeding in one place (Neto de Carvalho, 2006). Any trace is a record of behaviour, and other prominent examples of the behavioural significance of trace fossils are Miocene and Cretaceous brooding traces (*Coprinisphaera*, *Celliforma*, *Cellicalichnus chubutensis*) (Genise, 2000; Genise et al., 2002; Genise and Bown, 1994; Laza, 2006) (Fig. 5A), Ordovician dwelling burrows (*Diplocraterion*) (Fig. 5B), Pleistocene locomotion tracks (Fig. 5C), Permian aestivation burrows (*Torridorefugium*) (Hembree et al., 2005), feeding burrows (*Lophoctenium*) (Fig. 5D), or Proterozoic grazing traces (*Radulichnus*) on a biomat (Seilacher, 2007).

Since the environmental and behavioural significance of trace fossils is proper of the concept of trace itself, it follows the potential relevance of traces for understanding ecology and ethology of ecosystems beyond Earth.

3.5. Traces can be universal biosignatures

Life on Earth is the only known example of life (Hoehler et al., 2007), it is, therefore, the single reference for biosignatures. Since life beyond Earth might differ from the terrestrial one it might be not detectable through Earth-type biosignatures (Davies et al., 2009; Hoehler

et al., 2007; Schulze-Makuch and Irwin, 2006). Since that extra-terrestrial life may differ significantly from the one on Earth in morphology and size, its recognition through body fossils may be difficult. Similarly, the detection of life beyond Earth through chemical or isotopic biosignatures may also be difficult. In fact, despite some contrasting views (Flores Martinez, 2015; Pace, 2001), Earth-type biochemistry could not be the only plausible one (Benner et al., 2004; Hoehler et al., 2007; Schulze-Makuch and Irwin, 2006). For these reasons, a biosignature ideally capable of detecting any type of life (herein named ‘universal biosignature’) should be independent from morphology, size and biochemistry of the life form it documents.

As a document of biological behaviour, most traces approach the concept of universal biosignature: morphologically different organisms can produce the same trace (independence from morphology); organisms of different sizes can author similar trace patterns (independence from size); behaviour, not biochemistry, is the primary driver of trace shape (independence from biochemistry) (Ekdale and Lamond, 2003; Seilacher, 2007; Buatois and Mángano, 2011).

This observation points to an explanation in terms of basic principles and paves the way for the mathematical modeling of behaviour. For instance, meandering traces document a foraging behaviour and they are produced by organisms of different morphologies and sizes: from microscopic fungi to macroscopic animals (e.g., gastropods,

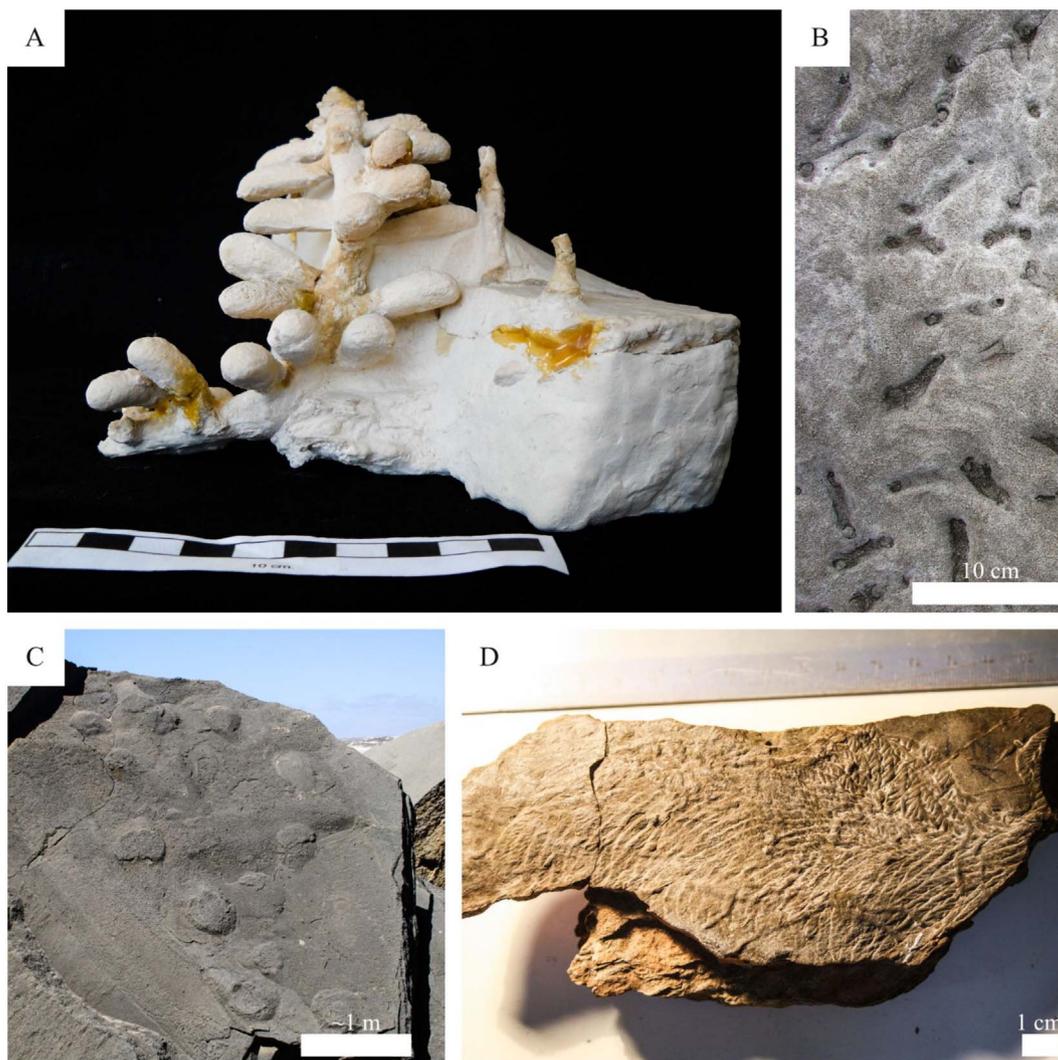


Fig. 5. Traces indicate environment and behaviour. A. The brooding trace *Cellicalichnus chubutensis* from the Cretaceous of Patagonia. The trace is attributed to bees. The specimen has been discussed in Genise (2000). B. The dwelling trace *Diplocraterion*. Late Jurassic, Lourinhã (Portugal). C. Proboscidean locomotion tracks attributed to the ichnospecies *Proboscipeda panfamilia*. The tracks have been probably produced by the straight-tusked elephant *Elephas antiquus*. Upper Pleistocene, Malhão beach (Portugal). D. The feeding trace *Lophoctenium*. Lower Carboniferous, South Portuguese Zone (Portugal). Specimen from the collections of the Museu Geológico (Lisbon).

insects, enteropneusts, polychaetes, echinoderms) (Garcia-Guinea et al., 2014; Santos et al., 2015; Seilacher, 2007) (Fig. 4). Meandering traces are not a signature of a specific biochemistry, but a record of an efficient strategy to forage. Computer simulations show that meandering is an advantageous foraging strategy as it allows to cover a nutritious surface without retracing already explored areas (Hammer, 1998; Plotnick, 2012; Raup and Seilacher, 1969; Seilacher, 2007).

This conclusion is qualitatively supported by the resemblance between many fossil trails and self-avoiding random walks in mathematics (Sims et al., 2014). A similar information is provided by the morphology of the iconic meandering trace *Nereites irregularis* (formerly *Helminthoida labyrinthica*), the fractal dimension of which shows that it tends to completely fill space (Baucon, 2010a). The universal character of meandering traces is evidenced by their long stratigraphic range, from the Proterozoic to present day (Häntzschel, 1975; Jenkins, 1995; Seilacher, 2007), suggesting that completely different organisms follow the same behaviour pattern (behavioural convergence) (Buatois and Mángano, 2011). The large majority of trace fossils displays similar long stratigraphical ranges, and therefore behavioural convergence (Buatois and Mángano, 2011). For the above reasons, traces can be envisaged as universal biosignatures able to document life, independent from morphology, size and biochemistry of the tracemakers. This property is very important for the search of life beyond Earth because it allows detecting life that differs from known life.

4. What biogenic structures to expect on extra-terrestrial bodies?

A predictive model that answers the question of what biogenic structures are expected to be present in the Universe is important either for theoretical or applied reasons, as it allows to envisage what and where to look for and what technological tools would be best suited for ichnological research beyond Earth.

The development of a predictive model for organism-substrate interactions on other astronomical objects is a significant challenge because data are still insufficient, and life on Earth is still the only documented example through which to build a model of life beyond Earth (Benner et al., 2004; Catling et al., 2005; Hoehler et al., 2007).

A possible approach for building a predictive model is to generalize the characteristics of Earth tracemakers by considering biological convergence, constraints on the range of forms that could evolve and biological history (Chela-Flores, 2012; Morris, 1999). This argument would predict extraterrestrial microbial prokaryotes (and their traces) because they are found in terrestrial environments which are assumed analogues to those for other planetary bodies, in particular Mars, they are within the constraints on the range of forms that could evolve and they dominated the Earth's biosphere during the first 2 Ga of its history (e.g., Horneck, 2000; Knoll et al., 2005; Westall, 2013). However, these arguments are weak to predict organism-substrate interactions beyond Earth because of statistical, ichnological and ecological reasons.

From a statistical perspective, Earth is the only documented example of life, and reference to this single documented example of life may lead to a very specific model of life (Hoehler et al., 2007) which, therefore, produces a biased model for tracemakers and traces. From an ichnological perspective, since traces do reflect behaviours rather than tracemakers, the mentioned arguments appear unreliable for developing a model of organism-substrate interactions. Instead, the ecological perspective is multifaceted, and rather considers both Earth-alike and Earth-like ecosystems. Extraterrestrial ecosystems may be very different for environmental conditions, biochemistry and evolutionary history from the Earth's ecosystems (e.g., Benner et al., 2004; McKay, 2010). For this reason, even stromatolites and microbioerosions – collectively the commonest traces in space and time on Earth – might be not significantly represented on a given extraterrestrial planet. Even in the case of an Earth-like planet (such as Mars) it would be difficult to make any robust prediction. There is in fact no consensus about the extent to which the origin and evolution of life on Earth were directed

(deterministic) processes or were more random (driven by contingency) (Des Marais et al., 2002), which makes predictions even more difficult. In addition, evolution is a historical product, and the history of any inhabited astronomical object should be unique (Morris, 1999). Environmental events can spur evolution via the mechanism of directional selection leading to diversification or to the extinction of certain life forms (Schulze-Makuch et al., 2013). For instance, although the physical and chemical surface properties of early Earth and Mars were very similar (Horneck, 2000; Kargel, 2004), the environmental history of early Earth and Mars is necessarily different, and there can not be a perfect analogy between the two planets during their early history (Hipkin et al., 2013). A different timing of evolutionary processes should be taken into account; e.g., an unanswered question is if a strongly protracted interval of microbial evolution equivalent to the Earth's Archean and most of the Proterozoic can be considered plausible also for other planets (Morris, 1999). In addition, the knowledge of Archean ecosystems is at present still very limited because few rock units have survived from the Archean to the present, and a large amount of Archean deposits have been deeply metamorphosed (e.g., Schopf et al., 2007). Hypothetically, there could have been dinosaur-like organisms in the Archean, but not a single preserved fossil evidence around which to build a model for extraterrestrial organism-substrate interactions.

For the above reasons, the here proposed model of organism-substrate interactions beyond Earth is built on a behavioural approach. Specifically, the expected biogenic structures are determined by finding the behaviours that are required by organisms for maintaining homeostasis; expected biogenic structures are those that manifest such behaviours.

4.1. Dwelling: excavations

The substrate surface of any astronomical object presents difficult conditions for the maintenance of homeostasis such as high flux of UVs and cosmic rays, physical disturbance (e.g., currents in marine and fluvial settings, winds in aeolian environments), or rapid fluctuations in temperature. Since the substrate subsurface has less harsh conditions than those at the surface (Bromley, 1996), infaunal modes of life may have a better chance of being present beyond Earth. This may be suggested by considering that subsurface-habitability zones are wider and include many more planets than conventional surface-based habitable zones (McMahon et al., 2013). In this perspective, also the subsurface of Mars has been recognized as “the most obvious region to search for potential habitats” (Fernández-Remolar et al., 2008). If the interactions between organism and substrate can be common, the same can be true for their typical products, i.e., bioturbation and bioerosion structures. The substrate surface is not solely characterized by stressful conditions. Rather, it can provide energy coming from the central star of a planetary system (McKay, 2014) and, in case of sediment transport in aquatic environment, it can be characterized by a rapid recycling of matter. For these reasons, although organisms require to be protected from the surficial environmental stressors, they need access to the surficial resources (energy and food). Dwelling is an efficient behaviour for being protected from the stressors of the substrate surface and keeping access to its resources. It is manifested by excavations such as burrows and borings (Figs. 3A and 5A). For these reasons, excavations are common biogenic structures and could also exist beyond Earth. The ichnofauna of the Rio Tinto, a reliable analogue site for Martian environments, supports this hypothesis because it includes burrows produced by earthworms and coleopterans (Fernández-Remolar et al., 2008). Mars is considered to have a good potential for near-surface microborings even in continental environments as candidate microbial ichnofossils have been reported from continental basaltic tuffs that represent an analogue site for Mars (Nikitczuk et al., 2016a, 2016b).

A possible exception to the dual need of being protected from the surface and having access to its resources is represented by

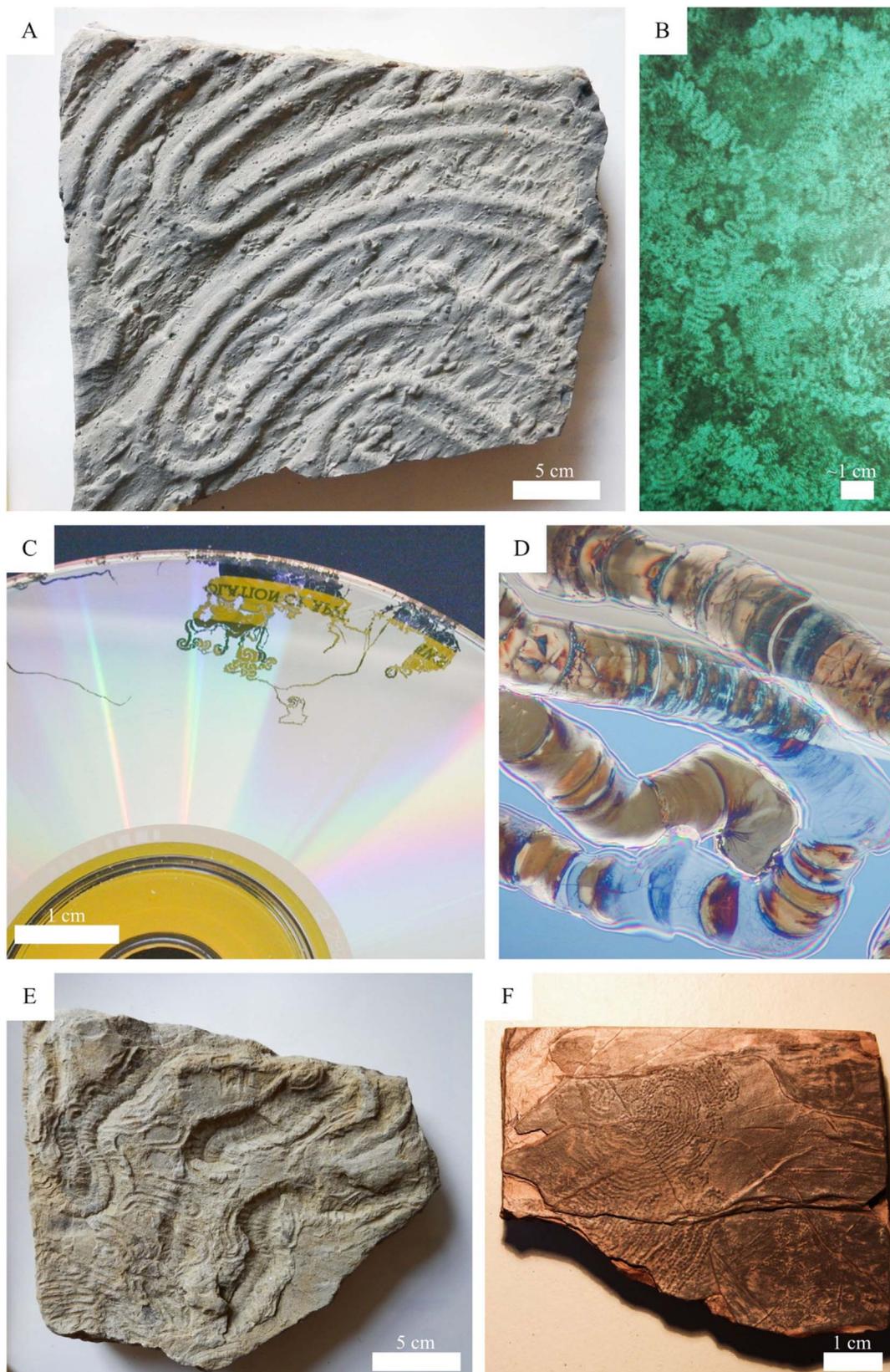


Fig. 6. Traces can be universal biosignatures. A. Meandering trace fossil (*Scolicia*) from deep-sea deposits. The tracemaker is likely to have been an irregular echinoid. Cretaceous-Eocene, near Rio Ribà (Italy). B. Meandering trail left by a foraging gastropod on an algae-covered panel. Recent, Italy. C. Meandering boring of a CD-eating fungus, previously discussed in Garcia-Guinea et al. (2014). Recent, Belize. D. Close-up of the bioerosion trace in C. E. Meanders from deep-sea deposits. Smaller meanders are attributed to the meandering trace *Nereites* (= *Helminthoida*) *irregularis*, produced by a worm-like organism. The larger ones are identified as *Scolicia*, a burrow produced by irregular echinoids. Specimen of possible Cretaceous-Paleogene age, Northern Apennines (Italy). F. *Nereites* from the Baixo Alentejo Flysch Group (Mértola Fm., Carboniferous). The tracemaker is a worm-like organism.

chemosynthetic tracemakers, such as those hosted in the Earth's deep biosphere.

Dwelling traces, or domichnia, are widely known from the fossil record and are represented by ichnogenera such as the well-known *Skolithos*, *Arenicolites*, *Thalassinoides* and *Ophiomorpha* (Bromley, 1996; Buatois and Mángano, 2011; Rindsberg, 2012) (Fig. 7A). Their behavioural function is not just restricted to dwelling, rather, it is often mixed with farming and feeding (Pemberton et al., 2001). This aspect can be seen by the perspective of the extended organism, according to which domichnia such as *Arenicolites*, *Thalassinoides*, and termite nests are adaptive structures which promote homeostasis of the organism and its local environment by channelling or tapping into surficial energy sources for doing physiological work (Turner, 2003).

4.2. Foraging: meandering traces

Foraging is the set of processes by which organisms acquire energy and nutrients (Kramer, 2001) necessary for homeostasis and for carrying out the metabolic processes (Des Marais and Walter, 1999; Ruiz-Mirazo et al., 2004; Schulze-Makuch et al., 2002). The ichnological heritage of Earth preserves an abundant record of foraging traces, among which grazing traces on the surface of the sediment (pascichnia) and feeding traces within the substrate (fodinichnia) (Rindsberg, 2012).

According to the optimal foraging theory, if natural selection has favoured the evolution of decision rules that maximize foraging success, the observed foraging patterns should be those that ensure the greatest

foraging success (Kramer, 2001). Meandering traces seem to be an example of this type of foraging pattern because they cover a given surface with a continuous, self-avoiding path (Seilacher, 2007), and are therefore expected to be a common component of extraterrestrial habitats (Fig. 7B). This observation is supported by the evolutionary success of meandering traces, as also observed above, that have a long stratigraphic range, going from the Proterozoic to today (Häntzschel, 1975; Jenkins, 1995; Seilacher, 2007), and a wide environmental range, going from deep-sea muddy floors to the surface of a CD (García-Guinea et al., 2014; Seilacher, 2007) (Fig. 6). A nature so ubiquitous for this foraging pattern could ultimately represent a convincing point in favour of its eventual discovery elsewhere beyond the Earth.

4.3. Digestion and excretion: Biodeposition structures

The maintenance of homeostasis is ruled by thermodynamics, hence digestion and excretion are major physiological processes. Digestion and excretion behaviour are primarily manifested by biodeposition structures (Fig. 7C), that reflect the biological production or concentration of sediment (Frey and Pemberton, 1985). Biodeposition structures should therefore represent traces potentially present in a broader perspective of the Earth itself.

Biodeposition structures on Earth are abundant in space and time. Digestichnia, the traces that are made by digestive processes (Vallon et al., 2015) are known at least since the Cambrian (Shen et al., 2014). They can shape the environment at the landscape scale, as shown from



Fig. 7. The main types of biogenic structures to be expected beyond Earth. A. Excavation traces: the dwelling trace *Ophiomorpha* from shallow marine deposits. Plio-Pleistocene, Arda river (Italy). B. Meandering traces: the foraging burrow *Nereites* (= *Helminthoida*) *irregularis*. Lower Ordovician, Barrancos (Portugal). Specimen from the collections of the Museu Geológico (Lisbon). C. Biodeposition traces: the crustacean microcoprolite *Palaxius mendozaensis*. Cretaceous, Mendoza (Argentina). The specimen has been discussed and figured in Kietzmann and Palma (2010).

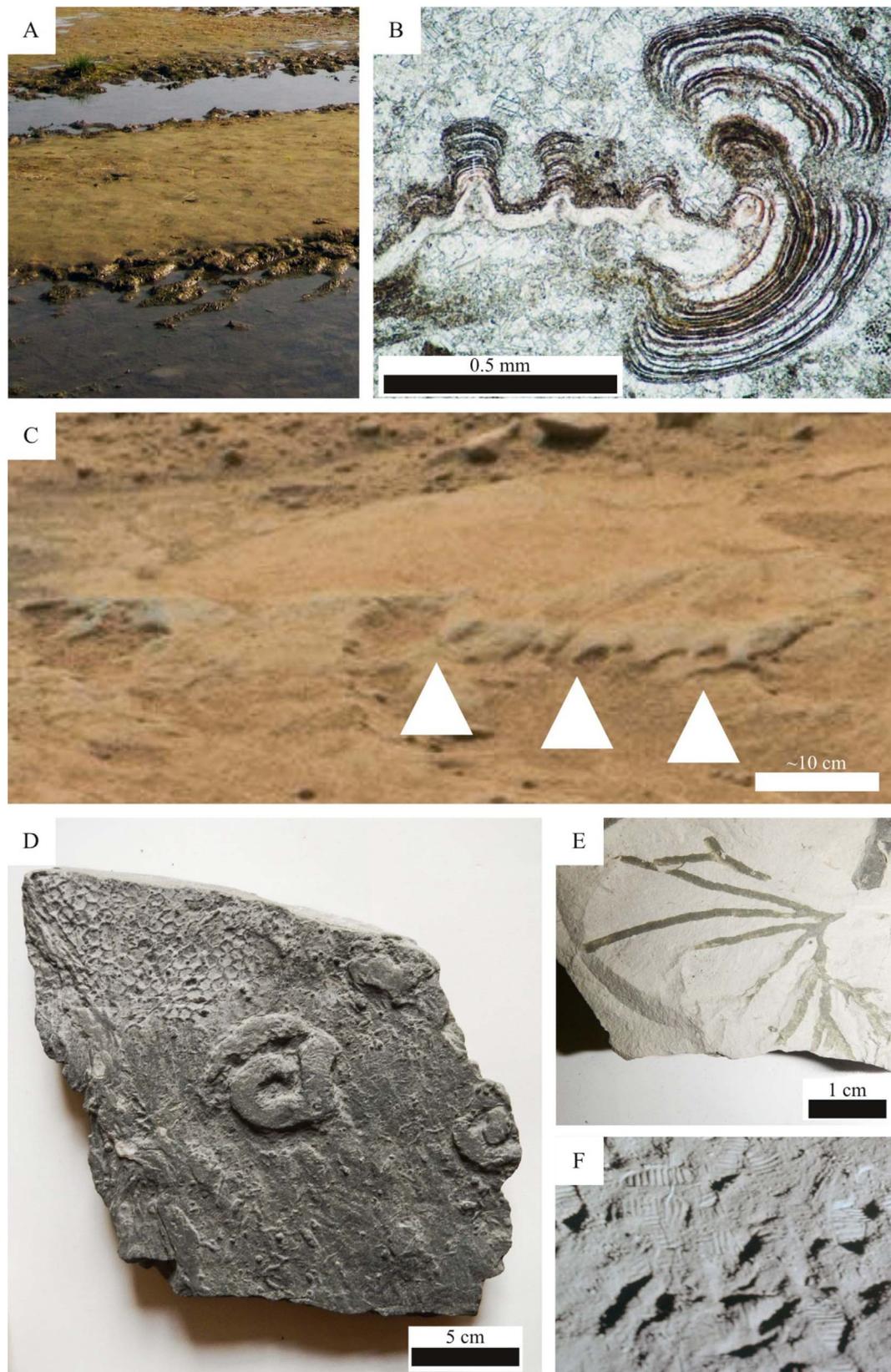


Fig. 8. Other types of biogenic structures to be expected beyond Earth. A. Microbial mat. Recent, Grado lagoon (Italy). B. Microstromatolite from the Silurian of the Carnic Alps (Austria). The specimen is analogous to those figured by [Ferretti \(2005\)](#) and [Ferretti et al. \(2012\)](#). C. Elevated structure from Mars resembling a fossil microbial mat, i.e., compare its morphology with [Fig. 8A](#). Arrows indicate the edges of the structure. The structure has been discussed by [Noffke \(2015\)](#). If the structure is biogenic, its age is < 3.7 Ga. Mars. D. Agrichnia. The honeycomb-like trace fossil *Paleodictyon* represents an example of agrichnion. Note also a specimen of *Spirophyucus*. Specimen of possible Cretaceous-Paleogene age, Northern Apennines (Italy). E. Chemichnia, *Chondrites*-dominated ichnofabric from the Cretaceous of the Northern Apennines (Italy). F. Space explorer ichnofabric. Trampled moon regolith pictured during the Apollo 11 mission. Recent, Moon. Image credit: NASA.

fecal pellets, that have been demonstrated to constitute at least 80% of the top 5 mm of the surface of a modern intertidal mudflat (Andersen and Pejrup, 2011). Another example is a mass movement deposit, having a volume of 600 m³, originated as a guano mudflow in a cave environment (Dykes, 2007). Waste products may include gases or liquids, although ichnological evidences in this case are rare or hardly recognized. Biogenic sedimentary structures produced by liquid urine have been reported for modern elephants, but fossil examples (urolites) have been described for dinosaurs only (Platt and Hasiotis, 2014).

4.4. Other biogenic structures

The previously discussed traces may potentially be present also beyond Earth. Other ichnological features, although plausibly expected, are supported by weaker arguments because of their tight link with Earth-type ecology. They include:

1. Biostratification structures. Similarly to dwelling, biostratification can be also seen as an efficient behaviour for being protected from the stressors of the substrate surface and have access to its resources (Wynn-Williams and Edwards, 2002) (Fig. 8A). For instance, cyanobacteria of microbial mats can migrate within the substrate to cope with the daily fluctuations in irradiance over the mat surface (Garcia-Pichel et al., 1994). Biostratification structures can also be found at the microscale, suggesting the opportunity to look for extraterrestrial traces from the micro- to the macroscale (Fig. 8B). With some caution, since their morphologies are strictly linked with their Earth-type (and possibly specific) biochemistry, biostratification structures such as microbial mats and stromatolites (Frey and Pemberton, 1985) can therefore be expected as biogenic structures beyond Earth. They are among the few trace fossils that occupy a prominent place in the astrobiological literature (Noffke, 2015; Westall et al., 2015) (Fig. 8C) and are the most abundant macrofossil in the Precambrian rock record (Allwood et al., 2007; Gargaud, 2011). They also provide the oldest macrofossil evidence of life (Gargaud, 2011), being reported from the Archean, some 3.5 Ga ago (Schopf et al., 2007). Recent studies expanded this record by describing ~ 3700-Myr-old stromatolites representing the evidence for oldest life remains (Nutman et al., 2016).
2. Deep-biosphere biogenic structures. Dwelling traces and biostratification structures have been suggested to be potential extraterrestrial traces because they allow tracemakers to be protected from the harsh conditions at the surface and at the same time to access its resources. The organisms that inhabit the rocky habitats at depths of up to several km in the Earth's crust, constituting the so-called 'deep biosphere', demonstrate that access to surface resources is not the only possible strategy (McMahon et al., 2013). Some organisms of the deep biosphere are indeed independent from surface conditions, being chemolithoautotrophs (McMahon et al., 2013). Intriguingly, the deep biosphere is not only the realm of single-cell organisms, as evidenced by nematodes from 0.9–3.6-km-deep fracture water (Borgonie et al., 2011). Fossil biogenic structures from the Earth's deep biosphere (Staudigel et al., 2015) combined with the chance of finding extraterrestrial deep biospheres (Hofmann, 2008; McMahon et al., 2013) makes plausible their discovery also outside our planet. Ichnology of the deep biosphere is still poorly known, therefore further studies are required on Earth to model the distribution of hypothetical traces in such environments. Furthermore, their study, based on deep drilling, would represent a major challenge on other planets, as it is on Earth.
3. Calichnia (Fig. 5A). Life characteristically self-replicates (Des Marais and Walter, 1999), hence brooding traces (calichnia) might be expected beyond Earth. Because the morphology of calichnia is often tracemaker-dependent and – at least on Earth – restricted to a very limited set of organisms, further studies are required to properly evaluate calichnia in an astrobiological perspective.
4. Root traces. Light is among the commonest sources of energy for life (McKay, 2014), therefore “light harvesting organisms” (Seager et al., 2005), similar to vegetation, might be a possible type of extraterrestrial life. Some types of vegetation on Earth interact with the substrate through roots, and the corresponding trace fossils – rhizoliths – are common in the fossil record (Baucon et al., 2014; Klappa, 1980; Rodríguez-Aranda and Calvo, 1998). For this reason, root traces, or functionally homologous structures, might represent a component of extraterrestrial ecosystems. However, caution is needed because they are inferred by analogy with Earth-type life.
5. Agrichnia and chemichnia. Chemical energy is an alternative source of energy with respect to light. On Earth, chemosynthetic modes of life are manifested by farming traces (agrichnia) (Fig. 8D) and chemosymbiotic traces (chemichnia) (Fig. 8E) (Vallon et al., 2015). Agrichnia include putative microbial gardens (graphoglyptids) that are well-known from Mesozoic and Cenozoic deep marine turbidites (Bromley, 1996; Cummings and Hodgson, 2011; Lehane and Ekdale, 2014). Chemichnia are also well-known from different environments, and there is robust evidence of modern chemichnia traces. For instance, modern thyasirid bivalves produce sulphide wells to provide energy required by endosymbiotic bacteria (Bromley, 1996); the corresponding trace fossil, *Chondrites*, is known at least since the Ordovician (Häntzschel, 1975). The macroscopic trace fossil *Trichichnus* has been interpreted as a bioelectrochemical system produced by biomat-forming bacteria (Kędzierski et al., 2015). Similarly to previously mentioned traces, agrichnia and chemichnia might be considered in an astrobiological perspective, however, caution is needed because they are inferred by analogy to Earth-type chemosynthetic ecosystems.
6. Ichnofabrics by doomed pioneers. It has been suggested that life may naturally travel throughout space; e.g., microorganisms can be transferred by meteorites from one planet to another (Burchell, 2004). This process, known as Panspermia (Burchell, 2004; Wickramasinghe, 2010), can bring tracemakers from one astronomical object to another, possibly presenting hostile conditions for the transported organisms. The doomed pioneer concept (Föllmi and Grimm, 1990) allows to predict the ichnofabric produced by tracemakers that are transported to hostile environments. Doomed pioneers are tracemakers that colonize hostile environments after being transported by event deposition; although the original concept focuses on thalassinidean shrimps transported by gravity flows to anoxic environments, it can be plausibly extended to other hostile environments and transport processes, including those involved by Panspermia. On the basis of previous considerations on the concept of doomed pioneer (Pemberton et al., 2001), Panspermia is expected to develop the following characteristics when transporting organisms in hostile environments: (a) organism-substrate interactions take place only within event strata and in directly subjacent sediments; (b) biogenically disrupted intervals are sharply overlain by sediments with no traces; (c) tiering is absent. Since at present the process of Panspermia can not unequivocally be proven or not (Burchell, 2004), further studies are required to evaluate the possibility of related ichnofabrics.
7. Space-explorer ichnofabrics (Fig. 8F). The ichnological record of the Moon, including several footprints of human space explorers, represents a possible analogue. In other words, the Earth is a typical member of the planetary set (Ćirković and Bradbury, 2006) and for this reason, space explorers from other planets are likely to have left their biogenic traces on other astronomical objects. This argument is based on the principle of mediocrity (Dick, 2013), but, paraphrasing the Fermi paradox, in the form stated by Webb (2002), the question is: if the universe is teeming with aliens, where are their traces?

4.5. Pseudo-traces

The aim of finding biogenic structures beyond Earth requires to

predict not only the traces most likely to be found, but also the major types of pseudo-traces, and the criteria to distinguish them from genuine traces. Several examples of pseudo-traces are provided by the geological record on the Earth and other astronomical bodies. They are here grouped according to a genetic classification built around the classification of pseudo-traces by Seilacher (2007):

1. Tool marks. Tool marks are grooves made by an object impelled by an abiotic transporting agent (Allen, 1982; Seilacher, 2007). The protracted contact between the transported objects and the sediment often results in a trail-like structures (drag marks sensu Allen, 1982), such as those produced by drifting and grounding icebergs, rocks sliding across the playas, debris transported by turbidity currents (Allen, 1982; Norris et al., 2014). Because tool marks are flow-parallel structures (Allen, 1982), drag-marks can be distinguished from trails by their dominantly rectilinear, parallel to each-other trajectories. In other cases, the contact between the transported objects and the sediment surface can be brief (Allen, 1982) (e.g., meteorite impact structures) (Grotzinger et al., 2011) and resemble individual tracks. Such pseudo-traces can be distinguished by the periodic nature of trackways (Fig. 9A). Tool marks may also be periodic when they derive from brief and periodic contact between the transported object and the sediment surface, such as in the case

of tumbling or saltating objects (Allen, 1982). The geological record of the Moon shows several examples of tumbling marks produced by boulders (“boulder tracks”) (Hovland and Mitchell, 1973) (Fig. 9B). Similarly to drag marks, these tool marks display dominantly rectilinear, parallel-to-each-other trajectories because of their flow-parallel orientation, being therefore distinguishable from tracks.

2. Erosional structures. Flute casts hold a burrow-like morphology, although they can be distinguished from traces because of their tendency to be parallel to each other, evenly spaced and unidirectionally oriented (Allen, 1982). In addition to the tracks of rovers (Fig. 9C), Mars orbiters have frequently pictured the track-like structures left by dust devils (Fig. 9D), that are convective vortices formed from unstable, near-surface warm air (Balme et al., 2003). Mesoscale linear streaks, likely caused by the entrainment and deposition of dust from wind transport, have been observed on Mars (Thomas et al., 2003). These abiogenic structures resemble biogenic tracks and trails, especially when imaged from orbiters, such as the astronaut tracks on the Moon (Fig. 9). They differ from biogenic tracks and trails in being parallel to each other (Balme et al., 2003; Drake et al., 2006). However, it should be noted that parallel dinosaur tracks were described on Earth (Vila et al., 2008) and less typical curvilinear and nonparallel dust devils tracks produced by light winds have been reported from Mars (Drake et al.,

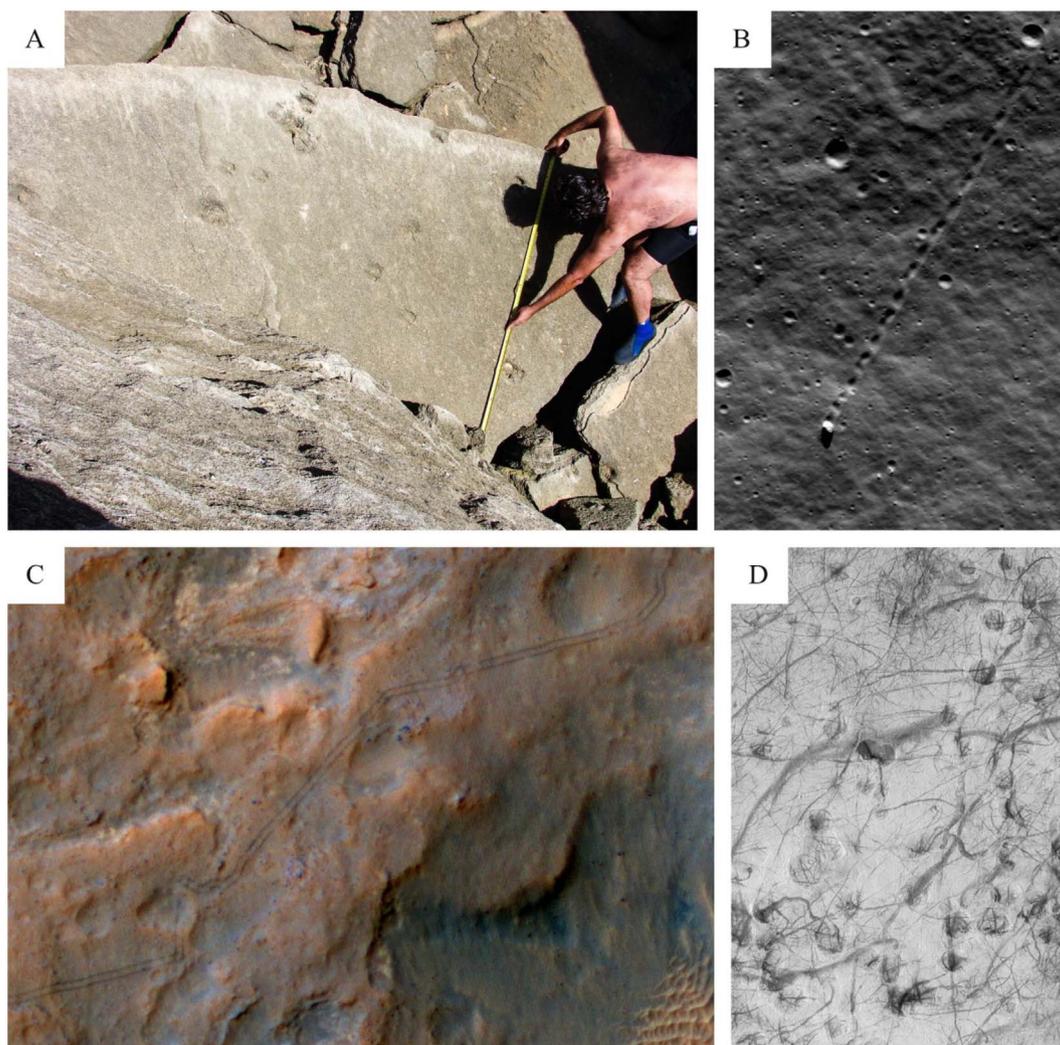


Fig. 9. Traces and pseudotraces. A. Fossil trackway, corresponding to the ichnogenus *Bifidipes*, attributable to a cervid tracemaker. Pleistocene, Praia do Malhão (Portugal). The trackway has been described in Neto de Carvalho (2011). B. Boulder track. Recent, Moon. The boulder track has been described by the Moon Zoo project (Bugiolacchi et al., 2016). C. Curiosity rover ‘track’ imaged from orbiter. Recent, Mars. Image credit: NASA/JPL-Caltech/Univ. of Arizona. D. Dust devil ‘tracks’. Recent, Mars. The field of view is about 3 km wide. Image credit: NASA/JPL-Caltech/Malin Space Science Systems.

- 2006).
- Soft-sediment deformation and water escape structures. Layered heterolithic sediments are often affected by early deformation, which may develop when the sediments are still unconsolidated or partly cohesive. Deformation of sediments generally occurs on the exposed surface or in the immediate subsurface in subaerial/subaqueous conditions and in the presence of low-permeability beds capping water-saturated sediments. The triggering factors which control the deformation of soft or partly-consolidated sediment (ductile and brittle deformation structures) can be ascribed to slope instability, to loading of sediments and escape of water or to shaking of sediment due to seismic activity. These different factors can often produce large variety of similar trace-like structures, with complex geometries and morphologies (Berra and Felletti, 2011).
 - Desiccation structures. They originate as shrinkage cracks formed by the evaporation of water from the surface of sediment. Arrays of trace-like polygonal cracks resulting from this process (Middleton, 2003) are commonly seen on dried-out surfaces in puddles and slurry pits, around the margins of lakes, reservoirs and playas, and on tidal mudflats.
 - Diagenetic structures. Diagenesis can result in a variety of trace-like structures with different processes and products (e.g., Seilacher, 2007).
 - Tectograms. Trace-like structures, named tectograms or tectographs, are produced by the movement of rock layers relative to each other (Seilacher, 2007; Seilacher et al., 2000). A prominent example is the meniscate structure named “*Vermiforma antiqua*”, that has been interpreted as one of the oldest (Precambrian) records of metazoans (Seilacher, 2007). The following characteristics allowed the re-interpretation of the structure as a tectogram: (a) nearly identical

structures are preserved on the same bedding plane; (b) individuals may vary in proportion, but not in orientation; (c) the overlying bed bears the counterparts of the structures as inverted images (the counterparts of body and trace fossils are mirror images) (Seilacher, 2007).

- Abiotic dissolution structures. Both biotic and abiotic processes can produce microtunnels that are collectively termed ‘tubular microcavities’ (McLoughlin et al., 2010). There are abundant features (e.g., timing of formation, morphology, infilling mineralogy, host matrix, distribution, mechanical abrasion and dissolution) that can be used to confidently distinguish biotic from abiotic tubular microcavities (McLoughlin et al., 2010).

It should also be noted that trace-like structures can be produced by biologically-related processes. They include tool marks produced by transported organisms (e.g., ammonites, corals, aggregates of microbial mats) and structures related to the microbial binding of sediments, such as elephant-skin structures, “*Kinneya*”, “*Protospiralichnus*”, “*Astropolithon*” and “*Manchuriophycus*” (Mariotti et al., 2016; Seilacher, 2007). However, “*Kinneya*” and other structures that mimic microbially induced sedimentary structures (pseudo-MISS) can also develop without microbial mats (Davies et al., 2016).

5. How to study extraterrestrial biogenic structures?

The study of modern and fossil traces on Earth, and partly on the Moon and on Mars, is based on the direct observation of the geological record. Extrasolar planets (exoplanets; Table 4), however, are particularly challenging when considering that because (a) their direct imaging is difficult (Brown and Burrows, 1990; Marois et al., 2008; Peters

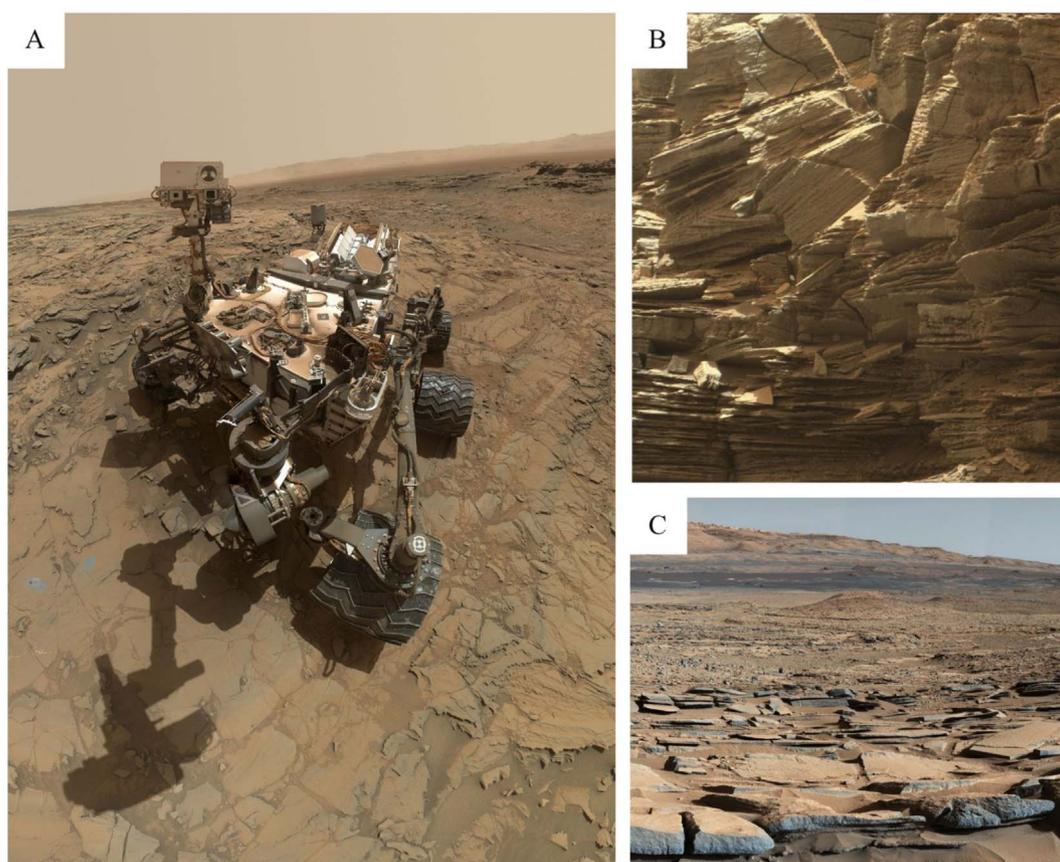


Fig. 10. Data acquisition from rovers. A. Self-portrait of the Curiosity rover on Mars. The picture consists of several images taken during the 1126 Sol by the Mars Hand Lens Imager (MAHLI) camera of the Mars Curiosity rover. The rover wheels are 50 cm in diameter and about 40 cm wide. Image credit: NASA/JPL-Caltech/MSSS. B. Cross-bedded aeolian deposits from Mars, The image has been pictured by the Curiosity rover on the 1454 Sol. Mars. Image credit: NASA/JPL-Caltech/MSSS. C. Strata imaged by the Curiosity rover on Mars (base of the Mount Sharp). The image has been pictured by the Mast Camera (Mastcam) of the Curiosity rover on the 580 Sol. Image credit: NASA/JPL-Caltech.

and Turner, 2013), (b) resolution of direct images of exoplanets is very coarse (Traub and Oppenheimer, 2010), (c) cloud cover and liquid bodies may hide both the substrate and the potential products of organism-substrate interactions, if any. For these reasons, the search for biogenic structures beyond Earth is – at present – limited to the Solar System. Sample return and manned missions are under consideration (or already planned) for exploration of extraterrestrial planets and moons of the Solar System, especially Mars (Falkner et al., 2007) (Falkner et al., 2007; McLennan et al., 2012).

5.1. Data acquisition from rovers

Ground-level extra-terrestrial acquisition of geologic, palaeohydrologic, palaeoclimatic, and possible astrobiologic information is largely performed through landers and rovers (Fink et al., 2005) (Fig. 10). Therefore a fundamental question is how to record ichnological data when no specifically designed instrumentation for this type of investigation is existing on rovers and landers. Another key question is what ichnological tools are best suited for future lander and rover missions. These questions can be answered by considering what ichnological tools fit with the recommended properties of lander/rover devices (Brown et al., 2004; Falkner et al., 2007; Jorge-Villar and Edwards, 2004): lightweight, rugged, multi-purpose portable instruments that use minimal power, require no sample preparation, and provide suitably diagnostic information to an Earth-based exploration team.

Record of ichnological data can be efficiently achieved by photography (Martin, 2013). Cameras fit with the recommended properties of rover/lander instruments and they are commonly included on landers and rovers as multi-purpose tools (Anderson and Bell, 2013). A major difference exists, however, between the ichnological application of photography on Earth and beyond it: on Earth, photography is mainly used for documenting biogenic structures that have been previously detected by field observations; beyond Earth, photography provides data for both the search and the documentation of ichnological data.

There are some camera specifications that are particularly favourable for the search of trace fossils. Because the size range of macroscopic traces on Earth is relatively wide, an ideal camera for detecting macroscopic traces beyond Earth should focus at least between 0.1 cm to infinity. Photography of millimetre-size traces and cryptobioturbation (i.e., sediment reworking by meiofauna or infauna; Frey and Pemberton, 1985; Pemberton et al., 2001, 2008) requires a maximum resolving power of at least 0.5 mm. In fact, as evidenced by other authors (Pemberton et al., 2001, fig. 147), what appears as an unburrowed laminated sandstone could get progressively cryptobioturbated the closer is examined. Visualization of microbioerosional structures requires sample preparation techniques (thin-sectioning, epoxy cast-embedding) and high resolving power (tunnel diameters are commonly less than a hundred microns) (Wisshak, 2012), making difficult the development of a lander- or rover-based photographing system for microbioerosion. There is, however, a strong increase in camera resolution capability. On the ExoMars rover, for example, scheduled for launch in 2020, high-resolution close-up images will be obtained by a specific instrument with the aim to allow work on the ground as a field geologist does with his hand lens (Josset et al., 2012).

The first step for acquiring palaeoichnological data through photography is to facilitate the observation of the outcrop. To this aim, a motorized brush – similar to the Rock Abrasion Tool of the Mars Exploration Rovers (Thomson et al., 2014) – provides an efficient solution for removing dust particles deposited on outcrops.

Correct lighting is an essential aspect for detecting and photographing modern and fossil traces (Green, 2001; Przeslawski et al., 2012). Low-angle light generally enhances the relief of trace fossils, for which reason observation of outcrops during the morning or the evening is recommended (Green, 2001). Consequently, natural light conditions are important variables to take into account when planning

rover-based searches for traces. Visibility of traces can be enhanced with artificial light sources; best results are given by low angle light or low contrast, non-directional light (Farrow, 1975; Green, 2001; Hammer et al., 2002; Noffke, 2010). An artificial source of light with adjustable angle would therefore be a useful tool for the search of biogenic structures beyond Earth, also because it fits with the recommended properties of rover instruments. The search for traces with adjustable light sources could be particularly effective during the night because the lack of light from the central star would provide full control on the illumination properties.

Polynomial texture mapping (PTM), a technique for imaging surface relief using a digital camera and multiple light sources, offers an opportunity to enhance relief of traces (Hammer et al., 2002). It is practical to use a “flash dome” with computer-controlled light sources in fixed positions, although polynomial texture mapping images can be acquired by a single light source that is repositioned after each exposure (Hammer et al., 2002). The flash dome typically requires 50 light sources (Hammer et al., 2002), therefore it does not fit with the minimal power recommendation for rover instruments. A single light source that is repositioned after each exposure may represent a more efficient solution for polynomial texture mapping beyond Earth.

This approach could also benefit from of imaging spectroscopy. Originally as remote measurement technique, high-resolution imaging spectrometers are now widely used in the investigation of planetary surfaces (down to microns spatial resolution) by inserting miniaturized instruments in the payload of planetary rovers (Greenberger et al., 2015).

In addition to visible light photography, infrared and ultraviolet photography finds application in the imaging of trace fossils. Infrared photography and fluorescing in ultraviolet have shown to enhance the visibility of traces (Bromley, 1981; Frey and Pemberton, 1985). These techniques need specific hardware (photographic filter, UV light) that fits with the recommended properties of the instruments for lander/rover missions (Brown et al., 2004; Falkner et al., 2007; Jorge-Villar and Edwards, 2004). Infrared photography and fluorescence in ultraviolet light have the advantage to be multi-purpose techniques, e.g., the rover of the Mars Science Laboratory includes UV illumination in order to search for fluorescent materials (Grotzinger et al., 2012) (Fig. 7B).

Visibility of trace fossils can be also significantly enhanced by sample preparation techniques, among which staining, sandblasting and brushing oil onto smoothed surfaces (modified Bushinsky technique) (Bromley, 1981; Farrow, 1975; Frey and Pemberton, 1985; Knaust, 2012). Because the mentioned techniques require a considerable amount of material (stain, sand, oil) for sample processing, they are not recommended for landers and rovers (Brown et al., 2004).

Enhancement of visibility can be also performed after data acquisition with digital tools (see below).

Geometrically precise 3D digital models of physical exposures are an increasingly important source of geological (Hartzell et al., 2014) and ichnological information (Bates et al., 2008). They can be obtained with the application of photogrammetry to traditional images or with specific hardware (i.e., laser scanner, including LiDAR). Both methods have been shown to be successful for modeling of either modern or fossil traces, from the centimeter scale to the metric one (Bates et al., 2008; Breithaupt et al., 2004; Genchi et al., 2015; Platt et al., 2010).

Cameras and laser scanners (including LiDAR) fit with the recommended properties of rover instruments and have already been tested on the field. In particular, the photogrammetric processing of imagery from Mars rovers (Di et al., 2008) demonstrates the feasibility of this approach for obtaining 3D digital models of physical exposures; similarly, outcrops at Mars analogue sites have been modelled by a LiDAR equipped on a rover (Barfoot et al., 2011).

Modern and fossil traces are not always exposed on the surface, therefore a major problem is extracting data from rocks and sediments (Cunningham et al., 2014; Seike et al., 2012). At the hand sample scale, non destructive methods for extracting ichnological data include X-ray,

X-ray computed tomography (CT) and magnetic resonance imaging (MRI) (Gingras et al., 2002). Micro-CT is particularly advantageous for the study of microborings because it allows to characterize sediment-filled borings otherwise inaccessible for vacuum cast-embedding technique, a traditional sample preparation method for the study of microborings (Wisshak, 2012). The object to be imaged with micro-CT has to be positioned between the source and the detector, requiring, therefore, sample preparation, especially in case of a sample larger than the micro-CT instrument. Unfortunately, micro-CT systems that can be used in situ are not yet available. The analyses could be done in a laboratory (including a synchrotron radiation beamline) in case of a sample return mission.

Subsurface ichnological information can be studied by casting techniques such as resin casting (Fig. 4H) and relief casting (Atkinson et al., 1997; Hertweck et al., 2007; Knaust, 2012). Both techniques require sample preparation (e.g., excavation of the cast) and a considerable quantity of casting material; resin casting is based on the knowledge of the position of burrow openings. For these reasons, casting techniques are not recommended for landers and rovers.

Drilling represents an efficient solution for extracting geological data from rocks and sediments. On Earth, ichnological analysis by drilling is generally achieved by core recovery (Heard et al., 2014), which is an energy-costly activity. For this reason, in situ imaging of drilled rocks and sediments is an alternative to be considered for the search of extraterrestrial biogenic structures. Images of the drilled substrate can be recorded by a camera contained in the drill and protected by a transparent window, similarly to the spectrometer of the ExoMars rover (De Sanctis et al., 2012; De Angelis et al., 2014). A wider field of view is provided by an optical televiewer housed in the drill, resulting in continuous and oriented 360° views of the borehole wall. Optical televiewers use a ring of lights to illuminate the borehole, a camera, and a conical or hyperbolic reflector housed in a transparent cylindrical window; the most powerful approach is the combined application of acoustic and optical televiewer imaging with integrated interpretation (Williams and Johnson, 2004). If trace fossils are large enough and filled with material that has resistivity of sufficient contrast to that of the host rock, they may also appear in borehole resistivity images (Gingras et al., 2015). Drilling tools are not lightweight, not portable and they require significant power; consequently, they do not fully fit with the recommended properties of rover tools. Nevertheless, the quality of the information they provide justifies their equipment on rovers. This approach is supported by the set-up of the next-generation rovers, such as the one planned by the ExoMars mission, that include drilling tools (De Sanctis et al., 2012; Ellery, 2016).

Shallow geophysics is another approach for extracting data from rocks and sediments, although it usually provides data at a coarser resolution than photography. Ground penetrating radar (GPR) is among

the most popular geophysical techniques for imaging and interpreting subsurface sedimentary architecture (Woodward et al., 2003). It finds also application for imaging the 3D morphology of burrows, among which centimeter-scale burrows (Kinlaw and Grasmueck, 2012). GPR fits with the recommended properties of rover instruments and it has been already considered as an instrument to be included in rovers (Barfoot et al., 2011).

In sum, most of the existing rovers provide basic instruments for ichnological analysis (cameras, motorized brush, artificial lighting). It is here suggested that the search for extraterrestrial biogenic structures by rovers would also benefit from artificial adjustable lighting (including instruments for fluorescence in ultraviolet light), GPR, LiDAR, drilling equipment with optical televiewer. This set up can eventually be realized in the near future because the mentioned technologies are already available.

This research is still expanding thanks to the progress in the miniaturisation of mass spectrometers and other instruments suitable for the in-situ characterisation of extra-terrestrial materials of interest (Chela-Flores et al., 2015). Short wave, visible-near and thermal infrared spectroscopy may be used to distinguish stromatolites from dolomitization and silification, as demonstrated by a Mars analogue study (Kose et al., 2016).

The above-mentioned instrument set up is mainly focused on the exploration of continental environments, while marine ecosystems on Earth provide a compelling example of possible life within liquid bodies beyond Earth (McKay, 2014). Underwater exploratory robots such as autonomous underwater vehicles (AUV) and remotely operated vehicles (ROV) are expected to play an important role in the astrobiological study of liquid bodies beyond Earth (Forrest et al., 2010). Together with towed cameras, they are among the most important tools for studying benthic ecology and ichnology of marine environments on Earth (Przeslawski et al., 2012). For these reasons, these systems could play an important role in the astrobiological exploration of aquatic environments. Their major limitation, however, is to provide mainly images of the seafloor. Therefore, sediment profile imagery (Wilson et al., 2009) could be an important complementary technique to be used for the search of biogenic structures in liquid bodies beyond Earth.

The ichnological exploration of liquid planets cannot be realized in a very near future because most of the liquid bodies of the Solar System are concealed beyond ice, such in the case of the ocean of Enceladus, or rock, such as in the case of the water layer of Ceres (Hussmann et al., 2006; Küppers et al., 2014; Ruesch et al., 2016; Postberg et al., 2009; Roberts and Nimmo, 2008).

5.2. Data acquisition from orbiters

The excellent visibility of traces on Earth opens the avenues for the

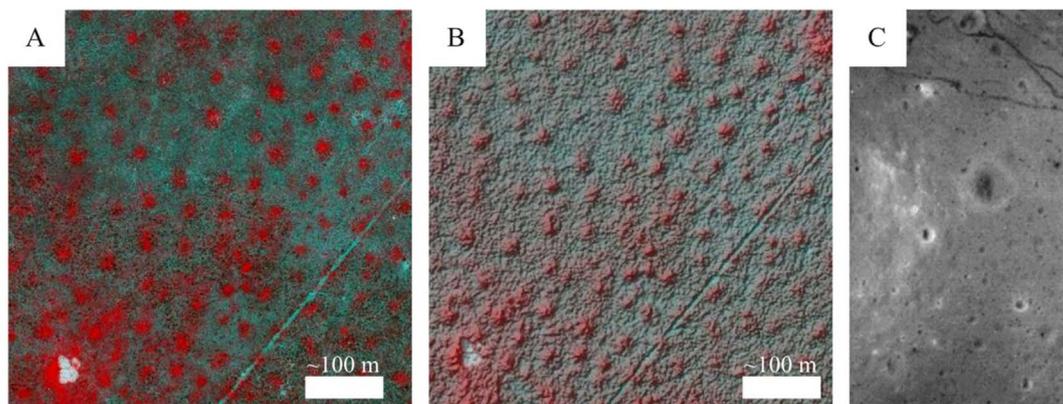


Fig. 11. Data acquisition from orbiters. A. False-colour infrared Quickbird satellite image of termite mounds. Recent, Kenya. The spatial pattern of the mounds is discussed in previous studies (Bonachela et al., 2015; Pringle et al., 2010). B. Shaded relief image of termite mounds from the same study area of Fig. 12A. C. Astronaut tracks of the Apollo 12 Mission detected by the Lunar Reconnaissance Orbiter. Image credit: NASA. Recent, Moon.

aerial imaging of traces beyond Earth. In parallel to the previous section, a fundamental question is how to record ichnological data with existing non-ichnological instruments on orbiters. Another question is what ichnological tools are best suited for future orbiter missions.

Few studies searched satellite imagery of Earth for modern and fossil biogenic structures. Wombat burrows (*Lasiurhinus latifrons*) have been detected from satellite (LANDSAT) multispectral imagery (Löffler and Margules, 1980). Multispectral Quickbird satellite image (2.4 m resolution) shows even spacing of termite mounds (Bonachela et al., 2015; Pringle et al., 2010) (Fig. 11A, B). The precise location of emperor penguin colonies in Antarctica have been detected from Landsat imagery by identifying the fecal stains produced on the sea ice by birds; specifically, visible blue light has been subtracted from visible red light (Fretwell and Trathan, 2009). Despite the few but successful neoichnological application of orbiters, there are no peer-reviewed studies on the application of satellite imagery to the search for fossil biogenic structures. However, verifiable web sources show that dinosaur tracks are visible from satellite data, including USGS, Google, Bing, and TNIRIS imagery (Butler, 2015). These examples not only show that biogenic structures can be imaged by orbiters, but they also suggest that multispectral cameras are important instruments to be carried on orbiters for the search of modern biogenic structures.

The Lunar Reconnaissance Orbiter detected the tracks produced by astronauts and rovers on the surface of the Moon (Fig. 11C). Such ichnological information served to characterize the physical properties

of the lunar regolith (Kaydash et al., 2011) and therefore demonstrates the feasibility of orbiter-based ichnology beyond Earth.

The images from Mars rovers show that the rovers themselves mix the uppermost layer of Martian regolith (Grotzinger et al., 2005, Fig. 2). Intriguingly, the tracks produced by the Opportunity rover (wheel width: 40 cm; track width: 2.7 m) have been detected by the High Resolution Imaging Science Experiment (HiRISE) camera on the Mars Reconnaissance Orbiter (Fig. 9C). Biogenic tracks of similar size could therefore be spotted by the HiRISE camera or by similar instruments.

The aforementioned data show that no specific technique is required for recording ichnological data with existing non-ichnological instruments on orbiters. Orbiter imagery from Earth and beyond show that multispectral cameras with a decimetre-scaled resolution are best suited for the search of biogenic structures beyond Earth.

The aforementioned examples show that decimetric traces can be already detected from orbiter imagery. This is especially true for the Moon and Mars, while the resolution of other astronomical objects, including planets of astrobiological interest (e.g., Titan), is too coarse for the detection of eventual decimetre-sized traces. Consequently, the search for ichnological data from orbiters can be realized, but more detailed imagery is required for most of the astronomical objects of the Solar System.

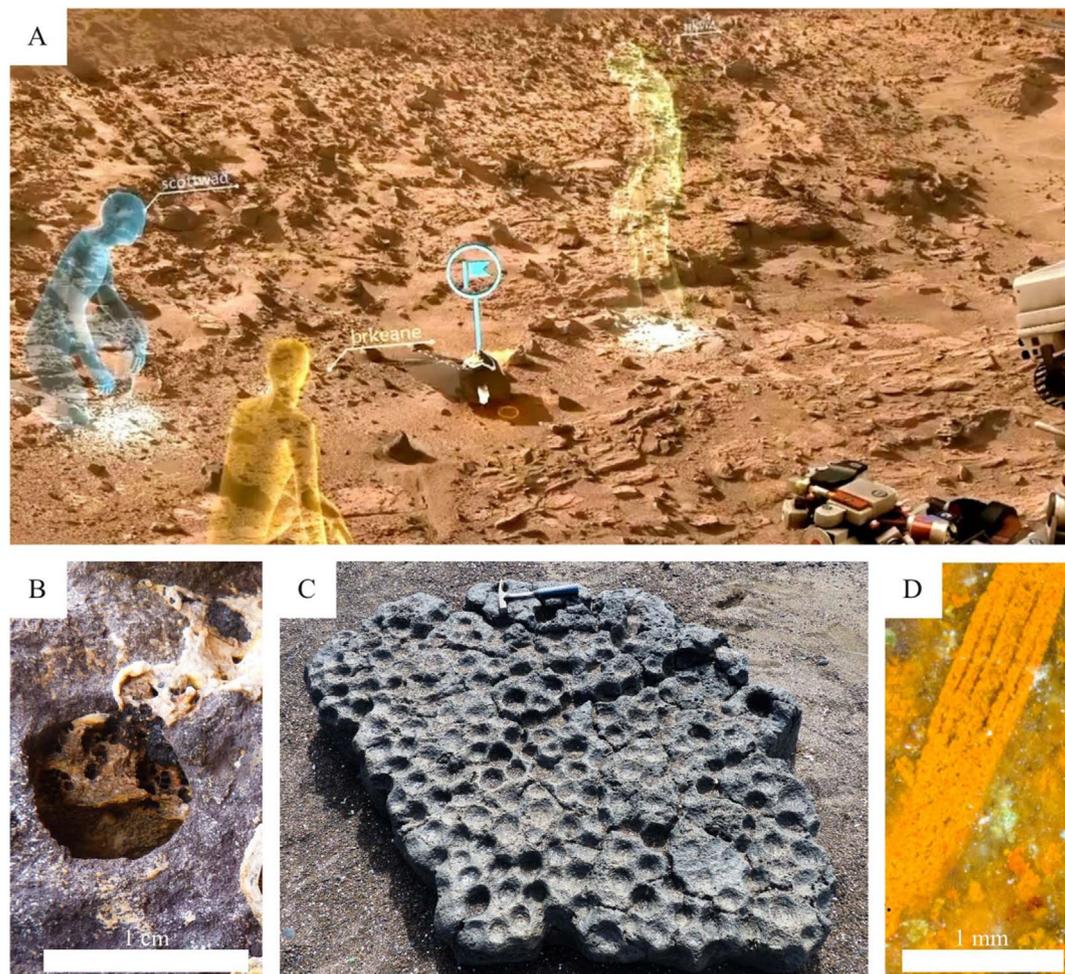


Fig. 12. Data processing and Earth-based methods. A. A screen view from OnSight, a software tool, developed by NASA and Microsoft, allowing scientists to work virtually on Mars. Image credit: NASA/JPL-Caltech (“JPL news,” 2015). B. The boring *Gastrochaenolites* in basalt. Middle Miocene of Porto Santo Island, Portugal. The ichnofauna and the study area are described in previous studies (Santos et al., 2012); see also Johnson et al. (2014). C. Echinoid borings (*Circolites*) from the Holocene of Sal Island (Cape Verde). Hammer for scale. Specimen discussed in Santos et al. (2015). D. Hydrothermally altered coprolite *Favreina belandoi* in interpillow limestone. Cretaceous, Hungary. The specimen is discussed and figured in Jäger et al. (2012).

5.3. Data processing

With increasing availability of open-access high-resolution imagery from rovers, landers, and orbiters, the photographic search for past and modern traces is possible for several astronomical bodies such as the Earth's moon, Jupiter and its satellites, Mars, Venus, Titan and Mercury. Open-access databases of extraterrestrial imagery are available for the Moon ("LROC website," 2015), Mars ("Mars Exploration Rovers website," 2015) and the Solar System ("JPL Photojournal," 2015, "NSSDCA Photo Gallery," 2015, "PDS Imaging Node," 2015).

Visibility of traces from digital images can be enhanced digitally. For instance, modifications to image features such as contrast, brightness, vibrance, saturation, exposure, lightness, and colour balance using graphic editing software has given good results with cores, in some cases revealing traces not detected previously (Dorador and Rodríguez-Tovar, 2013). Image analysis methods allow to isolate biogenic sedimentary structures from the host sediment, while gray-level co-occurrence matrices allow to characterize ichnofabrics and structure of traces (Honeycutt and Plotnick, 2008). Edge-detection filters are a promising tool for enhancing biostratification structures (Li et al., 2012).

The elevation data of 3D models of physical exposures can be amplified or surface normals.

estimated for the purpose of specular enhancement or diffuse gain (Hammer et al., 2002).

Image-based search for traces beyond Earth is a time-consuming approach. For this reason, in parallel to the search for intelligence beyond Earth (Davies and Wagner, 2013), the search for life beyond Earth could benefit from automated recognition of biogenic structures. Automatic detection of stromatolites from images has been demonstrated (Li et al., 2012), encouraging similar approaches to the detection of other biogenic structures.

The promising results of the Moon Zoo project, a citizen science project focusing on Moon craters (Bugiolacchi et al., 2016), encourage similar initiatives in the field of ichnology in order to complement expert and automated surveys of extraterrestrial biogenic structures.

In parallel to the data processing of images, data processing of 3D models includes enhancement of visibility and automatic detection of traces. As a result of processing different data provided by the Structure-from-motion approach, that is, colour and spatial coordinates data, it has been possible to detect bioerosional structures and to characterize their geometry (Genchi et al., 2015).

At present, the search for traces on extraterrestrial objects is mainly performed by examining images on screens. The search for extraterrestrial traces may benefit from mixed reality frameworks, such as Microsoft's and NASA's OnSight, a technology that will enable scientists to work virtually on Mars using wearable technology called HoloLens ("JPL news," 2015) (Fig. 12A).

Most of the proposed approaches for data processing have been tested for years on Earth data, therefore they can be applied also to the search of extraterrestrial traces. Exceptions are the automatic detection of trace fossils, for which algorithms are available (Li et al., 2012) but more training datasets and more case studies are needed, and the mixed reality frameworks, the application of which is currently in progress.

5.4. Earth-based methods

The aforementioned in-situ observations of astronomical bodies are a very direct way of searching for biogenic structures. However, the Earth provides important data sources for the search of biogenic structures beyond Earth, i.e., meteorites as extraterrestrial substrates, and modern and fossil ichnosites as analogue sites. Meteorites that have come to the Earth by impact events on other planets are a source of information about possible ancient life (McKay et al., 1996). Being substrates of extraterrestrial planets, these meteorites may potentially preserve trace fossils, among which microbioerosional traces (White et al., 2014). Meteorites are a particularly interesting source of

information because, if bioerosional structures exist in silicate rocks in Mars, they may be better preserved than on Earth because water has been mostly lost from the surface in the early history of Mars (Fisk et al., 2006).

In addition to meteorites, astrobiology and the search for life beyond Earth are remarkably informed by the study of ecosystems on Earth. Terrestrial environmental analogues of extraterrestrial sites may inform on the habitability of certain astronomical objects, on the potential for the long-term preservation of biogenic structures, and on how to search for biogenic structures beyond Earth (e.g., Preston and Dartnell, 2014). Analogue sites are commonly extreme environments, especially when considering that the only terrestrial environments where life forms are totally excluded are those with an extremely high temperature or insufficient water (Marion et al., 2003). Because extreme environments constrain the range of what might be considered a habitable environment beyond Earth (Preston and Dartnell, 2014), the study of the ichnofaunas of extreme environments is particularly informative. For instance, ichnological analysis reveals the presence of biogenic structures produced by the activity of the earthworm *Lumbricus terrestris* and the coleopteran *Platystethus* from a Mars analogue, the Tinto River area (Fernández-Remolar et al., 2008). Similarly to the study of extreme environments, the study of extremophiles plays a major role in the field of astrobiology (Cavicchioli, 2002). Other examples of traces from extreme environments are borings from volcanically active palaeoshores with hydrothermal activity (Macaronesia) (Santos et al., 2012) (Fig. 12B, C) and crustacean coprolites from hydrothermally-influenced Cretaceous marine environments (Jäger et al., 2012) (Fig. 12D).

The ichnological study of individual extremophile tracemakers is important for understanding behaviours that allow to thrive under extreme conditions. For similar reasons, the ichnological study of mass extinctions (Baucon et al., 2014; Twitchett and Wignall, 1996; Zonneveld et al., 2010) could be astrobiologically informative.

It is now fully recognized that life must rely on a source of energy, including light and chemical energy (McKay, 2014). Several habitable environments of the Solar System are characterized by the lack of sunlight, thus chemosynthetic tracemakers and related ichnosites could provide insight on potential chemosynthetic habitats beyond Earth. For instance, the apparent lack of photosynthetic life on the surface of Mars indicates that any organisms must also rely on chemical forms of energy and, for this reason, investigation of chemosynthetic ecosystems on Earth could provide further insight on potential Mars life (Schulte et al., 2006). Similarly, deep sea environments and chemosymbiotic traces (chemichnia) (Fig. 5C) such as *Chondrites*, *Solemyatuba* and *Trichichnus* (Vallon et al., 2015) could help be particularly informative for the search of life.

Although ecosystems on Earth provide a rich source of ichnological data for generating hypotheses and making predictions about organism-substrate interactions beyond Earth, it should be noted that reference to life on Earth may lead to a very specific model of life that does not necessarily fit with extraterrestrial life (Hoehler et al., 2007). Generalization is therefore an important step to consider in the development of models of organism-substrate interactions beyond Earth.

With regard to the feasibility of the Earth-based methods, the long tradition of ichnological research indicates that technologies and know-how are already available, therefore encouraging the development of more astrobiology-related ichnological studies.

5.5. Conceptual tools

Ichnology provides a vast set of conceptual tools for the study of modern and fossil traces. Among the methods with astrobiological applications, the ichnofacies model (Seilacher, 2007, 1967b, 1954) provides a conceptual framework for analyzing the distribution of trace fossils and thus the distribution of behaviour (Crimes and Droser, 1992). Because the ichnofacies model relies on the availability of

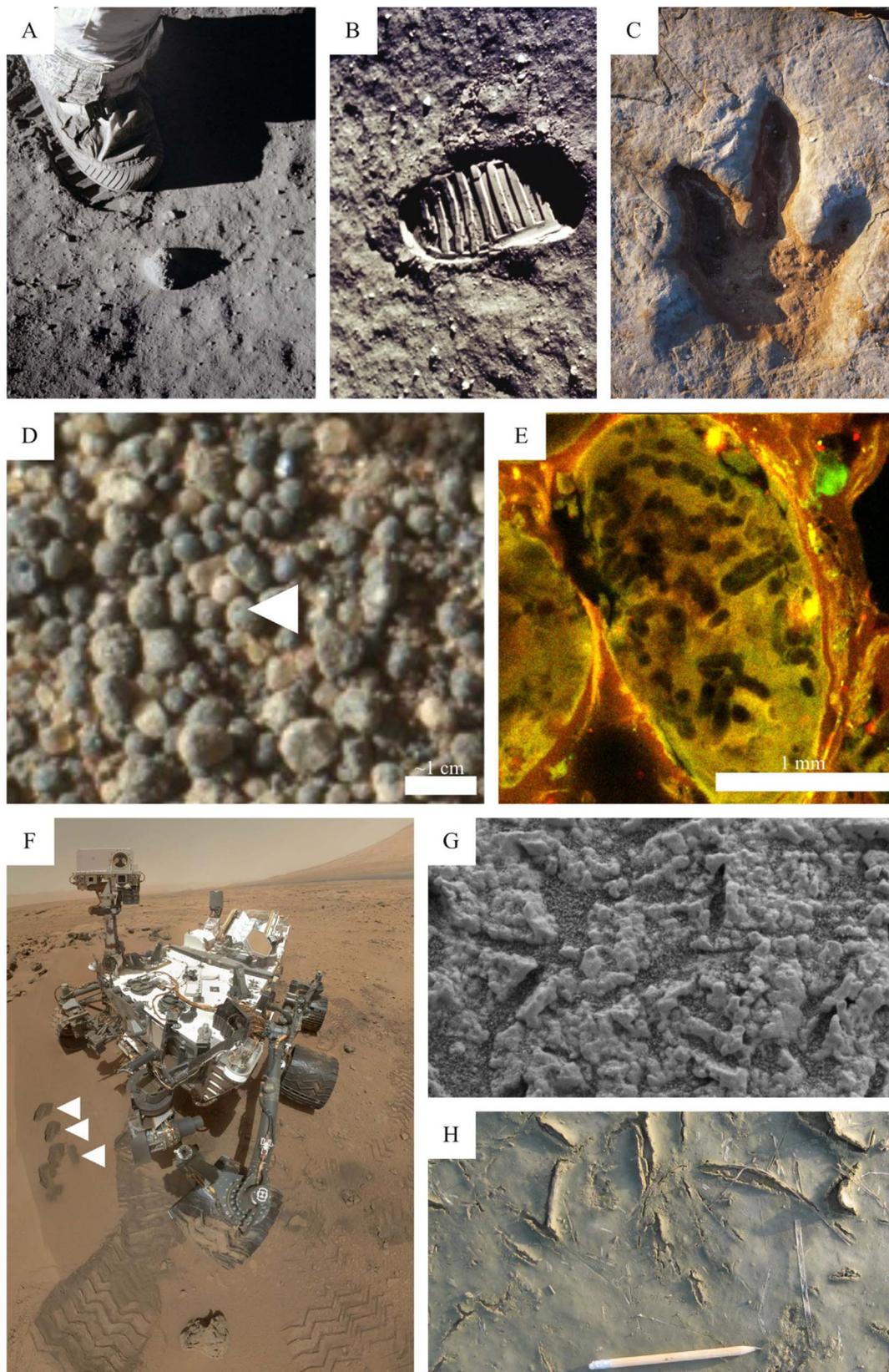


Fig. 13. Circular and elliptical structures. A. Bootprint of human astronaut. Recent, Moon. Image from NASA Image and Video Library. B. Bootprint of human astronaut. Recent, Moon. Image from NASA Image and Video Library. C. Theropod dinosaur footprint. Footprint length is approximately 50 cm. Jurassic, Portugal. Middle Jurassic, Vale de Meios ichnosite (Portugal). D. Round pit on a hematite spherule (arrowed) from Mars. The image has been pictured by the rover Curiosity on Sol 1182. Image credit: NASA/JPL-Caltech/MSSS. E. Bioeroded ooid from a modern subtidal stromatolite. The specimen has been discussed in [Petrisor and Decho \(2004\)](#). F. Trenches (arrowed) produced by the Curiosity rover. Note also the conspicuous disturbance of the regolith. Rover wheels are 50 cm wide. Recent, Mars. Image credit: NASA/JPL-Caltech/Malin Space Science Systems. G. Concave prismatic structures (vugs) from Mars. The background texture consists of sand-sized grains ([Squyres et al., 2004](#)). The image has been pictured by the Microscopic Imager of the Opportunity Rover on Sol 27. Vugs are approximately 1 cm long. Image Credit: NASA/JPL/US Geological Survey. H. Shrinkage cracks on a modern microbial mat. Pencil for scale. Recent, Grado (Italy).

nutrients, that ultimately depends on hydrodynamics ('food resource paradigm') (Pemberton et al., 2001), the environmental distribution of extraterrestrial ichnofacies is likely to differ from the archetypal ichnofacies.

Whereas the ichnofacies model emphasizes the observation of distinct traces (Pemberton, 1992; Seilacher, 1967b, 2007), the ichnofabric analysis method (Ekdale and Bromley, 1983; McIlroy, 2008; Taylor et al., 2003) focuses on the products of biogenic sediment mixing and, for this reason, it is particularly well-suited to analyze cores and vertical sections (Bromley, 1996). The aforementioned ichnological resilience makes ichnofabric analysis a robust method for the analysis of both fossil and modern biogenic structures. For example, Desjardins et al. (2010) have described early Cambrian ichnofabrics; microbioerosional ichnofabrics have been proposed to be preserved in the form of titanite textures in Paleoproterozoic metamorphosed volcanic glass (Staudigel et al., 2015); the oldest stromatolites are 3700 million years old (Nutman et al., 2016). As a comparison, molecular biosignatures have been reported in Precambrian rocks, but unaltered biomolecules are rarely reported from sediments older than Paleogene (Marynowski et al., 2007). The oldest isotopic biosignatures are from 3800 to 3700 million year-old metamorphosed sedimentary rocks and minerals, but their biogenicity is debated (Nutman et al., 2016).

The mentioned conceptual tools can be used in a very near future, although they may require to be adjusted in order to encompass the observational limitations proper of extraterrestrial objects.

6. Results

Based on the theoretical framework developed in the previous sections, 904 images from open-access databases have been searched for biogenic structures. This section presents the trace-like structures found in this search and reviews putative biogenic structures reported in previous studies. Trace-like structures are organized in morphological classes based on previous classifications of trace fossils (Książkiewicz, 1977; Uchman, 1995). The following aspects are discussed for each structure: (a) morphology, toponomy and size ('description'), (b) the primary sources on which the description is based ('material'; specific Mars images are referred to their Sol, that is the date of the image expressed in Martian days), (c) the astronomical object where the trace-like structure formed ('astronomical object'), (d) the age of formation of the structure ('age'), (e) the type of substrate where the structure has been emplaced ('substrate'), (f) interpretation of the structure, with special emphasis on its biogenicity ('remarks').

6.1. Circular and elliptical structures

6.1.1. Bootprints (Figs. 5C and 13A, B)

Description: Plantigrade, elongate concave epireliefs with transverse ornamentation and no digits. The structures are elliptical, decimetric in length and organized in trackways.

Material: Imagery captured by astronauts' cameras and imagery from orbiter (Lunar Reconnaissance Orbiter).

Astronomical object: Moon.

Age: Recent.

Substrate: Softground (regolith) (Kaydash et al., 2011; Mitchell et al., 1972).

Remarks: The structures are bioturbation structures produced by human astronauts. They have the same behavioural significance of other footprints (Fig. 13C), that is, locomotion. They have been used to understand the properties of the Moon regolith (Kaydash et al., 2011; Mitchell et al., 1972).

6.1.2. Round pits (Fig. 13D)

Description: Circular, round pits on hematite spherules (Lin, 2016). The structures are < 1 mm wide; they seem wider than deeper.

Material: The pits have been reported by several authors (Lin, 2016;

Rizzo and Cantasano, 2009) from imagery of the Gale Crater, e.g., Mars Hand Lens Imager of the Curiosity Rover on Sol 1182.

Astronomical object: Mars (Gale Crater).

Age: The pits are necessarily younger than the hematite spherules in which they are found. Depending on the interpretation of the spherules, the maximum age of the pits goes from few years (Misra et al., 2014) to billions of years (Squyres et al., 2004).

Substrate: Hardground, represented by hematite spherules, also known as 'blueberries' (Misra et al., 2014).

Remarks: The round pits have been interpreted as bioerosion structures by comparison with microborings in ooids (Lin, 2016). However, the structures are wider than deeper, differing in morphology from typical ooid borings on Earth (Fig. 13E). The most parsimonious explanation is that the structures have been produced by abiotic processes, such as the mechanical impact between spherules during their transport. It should be noted that each spherule typically bears one pit, possibly suggesting that the pits could be also related to dissolution at contact points.

6.1.3. Trenches (Fig. 13F)

Description: Unlined, unbranched trenches; walls indistinct, although bioglyphs may be present at the base of the structure; the structures are centimetric in width.

Material: Imagery captured by astronauts' cameras and discussed by other authors (Allton, 1989). Curiosity rover imagery Mastcam on Sol 61.

Astronomical object: Moon, Mars.

Age: Recent.

Substrate: Softground (regolith).

Remarks: The structures have been produced on the Moon by a variety of geological sampling tools for sampling the lunar regolith. They include scoop-like tools (e.g., Contingency Soil Sampler, Scoop, Lunar Rover Soil Sampler), spade-like tools (e.g., Trenching Tool), rake-like tools (e.g., Lunar Soil Rake, Tongs) (Allton, 1989). On Mars, similar structures are produced by Mars rovers for sampling the Martian regolith.

6.1.4. Vugs (Fig. 13G)

Description: Tabular concave prismatic structures that cut across lamination. They are thickest in the middle and taper towards both ends. They are randomly oriented. Typical width is 1–2 mm and length is approximately 1 cm (Squyres et al., 2004).

Material: The structures have been documented by the Pancam of the Opportunity Rover on Sol 27 and by the Microscopic Imager of the Opportunity Rover on Sol 29 (Squyres et al., 2004). Similar structures have been imaged by the Curiosity Mars Hand Land Lens Imager on Sol 809.

Astronomical object: Mars.

Age: Vugs are present on rocks that are likely to be as much as several billion years old and are crosscut by spherules, the age and origin of which is controversial (Misra et al., 2014; Squyres et al., 2004). Vugs are therefore younger than the deposits in which they are found and older than the spherules.

Substrate: The substrate deposited as a softground, but the interpretation of the vugs requires a certain degree of cohesiveness during their formation. For this reason, the substrate is regarded as a softground to hardground. The substrate texture is clumpy.

Remarks: The morphology of the vugs is reminiscent of shrinkage cracks, that on Earth are associated to cohesive substrates including microbial mats (Baucon, 2008; Gerdes et al., 2000) (Fig. 13H), and the clumpy texture of the substrate may also recall the texture of microbial-bound sediments. However, vugs are smaller than typical shrinkage cracks on Earth, and are apparently of very constant size. For this reason, the most parsimonious interpretation is abiotic. Structures are interpreted as depressions formed by the chemical dissolution of a relatively soluble mineral phase, likely sulphates (Benison, 2006; Squyres

et al., 2004). Alternatively, the vugs are interpreted as a consequence of ice crystal formation followed by thaw and desiccation (Wdowiak, 2007).

6.2. Simple structures

6.2.1. Curved microtunnels (Fig. 14A)

Description: Curved or S-shaped, undulating microtunnels that may contain areas of enhanced carbon abundance; large ($\geq 0.5 \mu\text{m}$ in width)

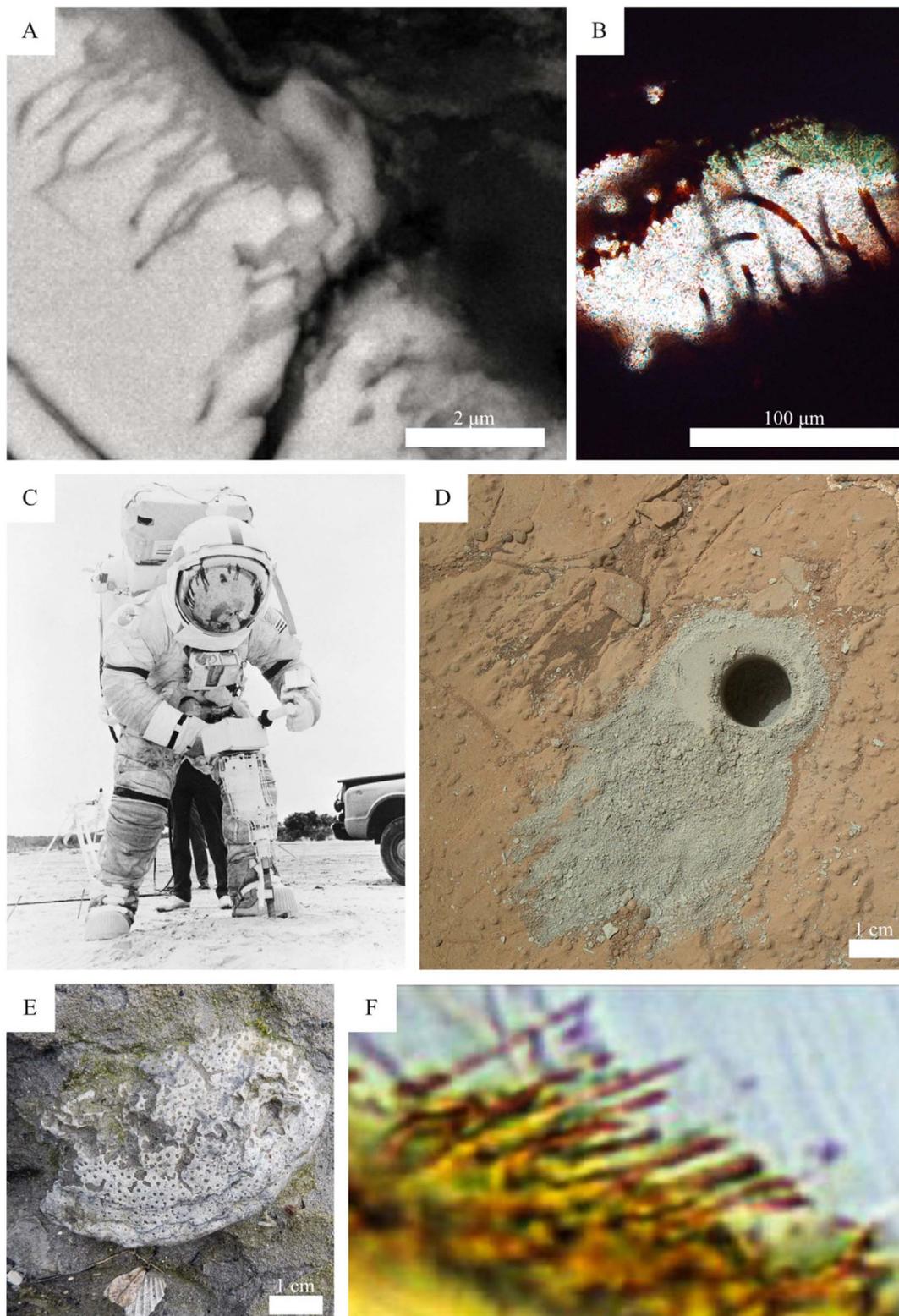


Fig. 14. Simple structures. A. Curved microtunnels from the Martian meteorite Yamato 000593. Specimen discussed in White et al. (2014). B. Microboring in trilobite shell. Silurian, Valentintörl (Austria). Specimen discussed in Ferretti et al. (2012). C. Astronaut producing a cylindrical drill using the lunar drill during a simulation on Earth. D. Detail of a cylindrical drill produced by the Curiosity rover. Recent, Mars. Image credit: NASA/JPL-Caltech/MSSS. E. Mollusc with the bioerosional trace *Entobia*. Plio-Pleistocene, Arda river (Italy). F. Straight microtunnels from the Martian meteorite Nakhla. The longest microtunnels are about $10 \mu\text{m}$ long. Specimen discussed in Fisk et al. (2006).

and tens of microns in length) (Fisk et al., 2006; White et al., 2014) and small (~100 to 200 nm in width and 1 to 4 μm in length) structures are reported (White et al., 2014). Microtunnels emanate from iddingsite veins and may be filled with iddingsite (White et al., 2014).

Material: The structures have been described by Fisk et al. (2006) from a thin-section of the Martian meteorite Nakhla. White et al. (2014) described similar structures from a thin-section of the Martian meteorite Yamato 000593. Because of their morphological similarity, also noted by previous authors (White et al., 2014), these structures are here discussed together.

Astronomical object: Mars. The provenance of the meteorites has been determined by direct.

comparison with Martian materials (e.g., composition of Martian atmosphere) and on consistency with inferences about Mars (Treiman et al., 2000).

Age: The microtunnel-bearing meteorites Nakhla and Yamato 000593 have different alteration histories on Earth, indicating that the microtunnels are not the result of contamination on Earth (White et al., 2014). Consequently, the microtunnels have been produced between crystallization on Mars and ejection from Mars, that is, approximately between 1.3 and 0.1 Ga. More in particular, Yamato 000593 has a crystallization age of 1367 ± 7 Ma (Park et al., 2009) and an ejection age of 11.2 ± 1.2 Ma (Christen et al., 2005), Nakhla has a crystallization age of 1357 ± 11 Ma (Park et al., 2009) and an ejection age of 11.6 ± 1.8 Ma (Eugster et al., 1997). According to White et al. (2014), the microtunnels of Yamato 000593 formed prior to or contemporaneously with iddingsite, a secondary mineral assemblage of iron oxides and clays (Fisk et al., 2006). The iddingsite of Yamato 000593 may have the same age as the iddingsite of Nakhla, therefore the curved microtunnels formed about 600 million years ago (White et al., 2014). However, the discussion on the timing of the aqueous alteration on Mars is still open (Fisk et al., 2006).

This would also exclude that the microtunnels have been produced during the transit from Mars to Earth.

Substrate: Hardground. Yamato 000593 and Nakhla are igneous rocks (White et al., 2014).

Remarks: The morphology of the curved microtunnels is consistent with biogenic traces on Earth, including microbioerosion traces observed in basaltic glasses (Fisk et al., 2006; McLoughlin et al., 2007; White et al., 2014). The morphology of the curved microtunnels is also resembling the microbioerosions reported by Ferretti et al. (2012), although the size is different (Fig. 14B). The here discussed microtunnels are associated to other biogenic-like structures, that are morphologically different types of microtunnels in Nakhla (Gibson et al., 2006; McKay et al., 2006) and nanometer- to micrometer-sized spherules, similar in size and shape to known fossilized microbes, in Nakhla and Yamato 000593 (White et al., 2014).

However, most authors agree with the need of further studies to claim that the curved microtunnels are biogenic (Fisk et al., 2006; McLoughlin et al., 2007; White et al., 2014). The curved microtunnels are likely to have been produced in the Mars subsurface under low oxygen conditions (Fisk et al., 2006).

6.2.2. Cylindrical drills (Fig. 14C, D)

Description: Vertical, straight, cylindrical depressions with sharp wall; diameter ranges between 1 and 10 cm, vertical extension ranges from < 1 cm to 100 cm.

Material: Imagery captured by astronauts' cameras (Allton, 1989). Curiosity rover imagery from Sol 31, 35, 182.

Astronomical object: Moon, Mars.

Age: Recent.

Substrate: Softground (regolith) or hardground (bedrock).

Remarks: On the Moon, cylindrical drills have been produced by a variety of tools, either manually operated (e.g., core tubes) or powered (e.g., Apollo Lunar Surface Drill) (Allton, 1989). On Mars they are produced by the Curiosity rover with the Rock Abrasion Tool. From an

ichnologic point of view, the structures are bioerosional traces similarly to *Gastrochaenolites* (Figs. 1E and 12B), *Circolites* (Fig. 12C) or *Entobia* (Fig. 14E).

6.2.3. Straight microtunnels (Figs. 3D and 14F)

Description: Straight, pointed microtunnels. Structures emanate from a zone of alteration that contains iddingsite. Structures are 1 μm in diameter and 10 μm long (Fisk et al., 2006).

Material: the structures have been described by Fisk et al. (2006) from a thin-section of the Martian meteorite Nakhla.

Astronomical object: Mars. The provenance of the meteorite with straight microtunnels has been determined by direct comparison with Martian materials (e.g., composition of Martian atmosphere) and on consistency with inferences about Mars (Treiman et al., 2000).

Age: The structures are likely to have been produced between the crystallization and ejection from Mars, that is between 1357 ± 11 Ma (Park et al., 2009) and an ejection age of 11.6 ± 1.8 Ma (Eugster et al., 1997). Specifically, structures appear to be contemporary with the hydrous alteration on Mars < 1300 million years ago (Fisk et al., 2006). Based on the age of iddingsite in Nakhla reported by White et al. (2014), straight microtunnels formed about 600 million years ago. However, the mode and tempo of the alteration is debated.

Substrate: Hardground. Nakhla is an igneous rock (White et al., 2014).

Remarks: The straight microtunnels are similar in size, shape and distribution to those found in terrestrial rocks, that are likely to be of biotic origin (Fisk et al., 2006). Similar morphologies are not known to be produced by abiotic processes (Fisk et al., 2006). However, there is insufficient evidence to claim the biogenicity of the structures, the origin of which remains an open question (Fisk et al., 2006).

The structures have been produced in the Martian subsurface (Fisk et al., 2006).

6.3. Branched structures

6.3.1. Dendritic microtunnels

Description: Carbon-bearing dendritic-like projections and tiny tubes (Gibson et al., 2006; McKay et al., 2006). Structures emanate from carbonaceous veins and are filled with the same material (McKay et al., 2006). Structures are < 10 μm long (McKay et al., 2006).

Material: The structures have been described in previous studies (Gibson et al., 2006; McKay et al., 2006) from thin-sections of the Martian meteorite Nakhla.

Astronomical object: Mars. The provenance of the meteorite Nakhla has been determined by direct.

comparison with Martian materials (e.g., composition of Martian atmosphere) and on consistency with inferences about Mars (Treiman et al., 2000).

Age: The structures are likely to have been produced between crystallization and ejection from Mars, that is, between 1357 ± 11 Ma (Park et al., 2009) and 11.6 ± 1.8 Ma (Eugster et al., 1997).

Substrate: Hardground. Like other nakhlite meteorites, Nakhla is a fragment of an ancient lava flow and contain a variety of minerals that formed in the presence of liquid water (Needham et al., 2013).

Remarks: Different processes have been proposed to explain the observed features (Gibson et al., 2006; McKay et al., 2006): (a) introduction of C by a carbonaceous-rich impactor on Mars; (b) biogenic-related processes in which organic acids from microbes produced the corrosion and the remains of the biofilm and the included microbes provide the carbonaceous fill. It should be noted that the structures should have been produced by boring organisms to be trace fossils, that are traces of life by definition.

Further studies are needed to confirm biogenicity (Gibson et al., 1999, 2001; McKay et al., 2006).

The meteorite with the here discussed structures also shows curved microtunnels (White et al., 2014) and circular blebs of nearly opaque

material (McKay et al., 2006).

6.3.2. Digitate protrusions (Fig. 15A)

Description: Irregular surfaces with digitate protrusions composed of opaline silica. Protrusions are usually upward-directed. Sub-centimetric scale (Ruff and Farmer, 2016; Ruff, 2015; Squyres et al., 2008).

Material: These structures have been described by previous authors (Ruff, 2015; Squyres et al., 2008; Ruff and Farmer, 2016) from Spirit rover imagery on Sol 1160 and Spirit Microscopic Imager on Sol 1157.

Astronomical object: Mars.

Substrate: Regolith composed of opaline silica in a hydrothermal setting (Ruff and Farmer, 2016).

Remarks: The structures have been compared to stromatolites (Fig. 15B), although at present there are no sufficient proofs about their biogenicity (Ruff, 2015; Ruff and Farmer, 2016). They are also very similar to weathered burrows, although abiotic processes may produce similar structures. They have been interpreted as the products of a hydrothermal system (Squyres et al., 2008) and there is evidence for a role of wind in shaping the silica-rich outcrops (Ruff et al., 2011).

6.4. Winding structures

6.4.1. Parallel trails (Figs. 13F and 16A)

Description: Horizontal structure consisting of a median undisrupted zone flanked by two lateral furrows; furrows may be ornamented and reach depth of several centimetres. Width is decimetric, length may range from few meters to kilometres.

Material: Imagery from the Lunar Reconnaissance Orbiter and the Mars Reconnaissance Orbiter.

Astronomical object: Moon, Mars.

Age: Recent.

Substrate: Softground (regolith).

Remarks: Parallel trails have been produced by manned (e.g., ‘moon buggy’) and unmanned (e.g., Mars rover) vehicles. The structures recall the ichnogenus *Archaeonassa* (Fig. 16B, C) but they are characterized by parallel furrows instead of parallel ridges.

6.5. Other structures

6.5.1. Hematite spherules (Fig. 17A, B)

Description: Hematite spherules with no observed internal structure (Bell et al., 2004; Squyres et al., 2004). The typical diameter is 4 mm and all structures are < 6.2 mm in diameter (Misra et al., 2014). They generally do not disturb surrounding lamination. The spherules are colloquially termed blueberries for their shape and colour (Squyres et al., 2004).

Doublets and triplets have also been observed (Misra et al., 2014).

Material: Spherules have been described by Squyres et al. (2004) from Curiosity rover imagery at Meridiani Planum, Mars.

Astronomical object: Mars.

Age: Hematite spherules are at least as old as the fluvial deposits in which they are embedded, but there is no consensus about the origin of the spherules, and different ages have been proposed. According to Misra et al. (2014) some of the spherules are only a few years old, while Squyres et al. (2004) suggest that spherules are embedded in rocks that could be as much as several billions years old.

Substrate: Softground.

Remarks: Hematite spherules have been interpreted as biostromatolite structures (ooids) on the basis of the morphological resemblance with ooids on Earth (Lin, 2016). However, broken spherules seem to lack the internal structure that typify ooids (Squyres et al., 2004), although they are not always visible in Earth material because of micritization (Petrisor and Decho, 2004). Enigmatic Triassic spheres, compared to MISS (Simpson et al., 2015), resemble Martian hematite spherules in shape and morphology but present an outer micritic layer and an inner sandy core, a structure that is lacking in hematite spherules from Mars. This morphological aspect resembles the layered structure of ‘newberries’, that are hollowed, non-hematitic spherules from Mars (Sols 3061, 3064, 3247) (Fig. 17C). However, ‘newberries’ are not flattened as the Triassic spheres from Earth, thus suggesting a different origin.

The most parsimonious hypothesis is therefore an abiotic origin of the hematite spherules. These structures have been interpreted as concretions, and several possible terrestrial analogues have been proposed (Clarke and Stoker, 2011). However, the observed Martian spherules are limited in size, suggesting that they may be not concretions but cosmic spherules formed by the ablation of meteorites (Misra et al., 2014). Spherules have been also explained by volcanic processes, meteorite impact, hydrothermal origin, alteration of basaltic tephra, among others (Gánti et al., 2005; Morris et al., 2005; Newsom et al., 2015).

Hematite spherules may be associated with spherules of similar size and morphology but different colour that have been named ‘yellow berries’ (Misra et al., 2014).

6.5.2. MISS-like structures (Figs. 8C and 17D, E)

Description: Sets of spatially associated structures, first described by Noffke (2015) as follows:

- Association 1) Elevated planar surface defined by a 3–5 cm high cliff (Fig. 17D); the edge of the cliff face displays triangle-shaped protrusions that point down and away from the platform. The structures

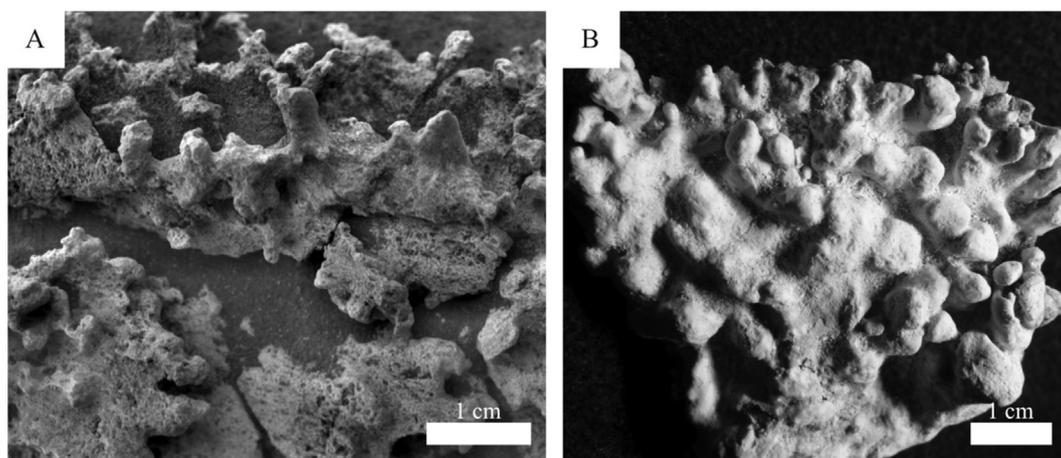


Fig. 15. Branched structures. A. Digitate protrusions from a silica outcrop on Mars. Structures discussed in Ruff and Farmer (2016). B. Silica structures at a hot spring discharge channel (El Tatio, Chile). Specimen discussed in Ruff and Farmer (2016).

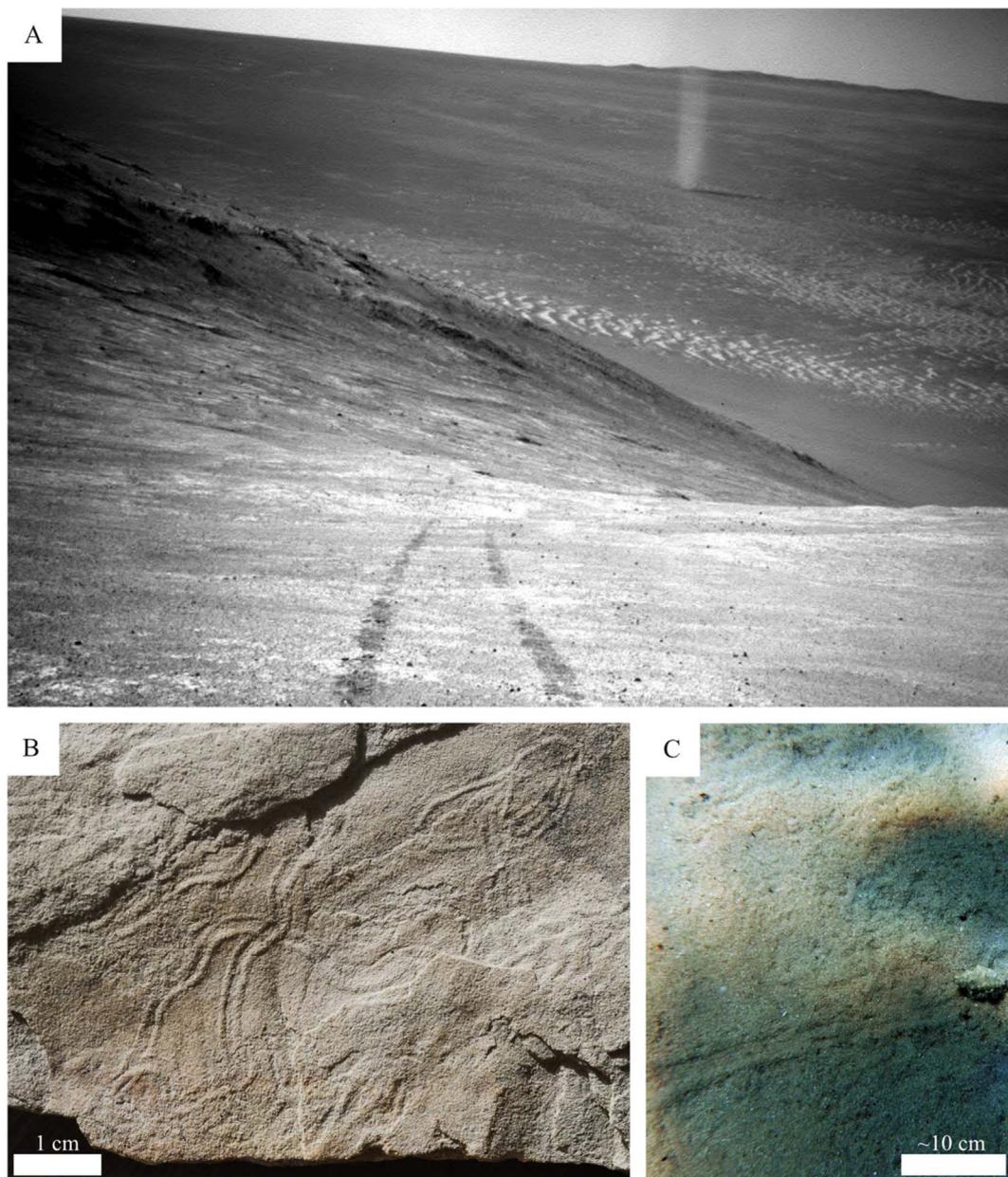


Fig. 16. Winding structures. A. Parallel trails produced by the Opportunity rover. A dust devil in the background. Recent, Mars. Image credit: NASA/JPL-Caltech. B. The trace fossil *Archaeonassa*. Neoproterozoic, White Sea. The specimen is figured and discussed in [Jensen \(2003\)](#). C. Incipient *Archaeonassa* and its producer. Approximate depth 3 m. Recent, Adriatic Sea.

are associated with round-shaped depressions, some of which are surrounded by a half-moon-shaped ridge; lineations, depressions, and small ridges in a seemingly random pattern; flat clasts and fragments.

- Association 2) Round- to oval-shaped depressions associated with triangular-shaped structures, small half-moon-shaped ridges, and flat clasts. It should be noted that these structures come from the same rock bed of the association 1.
- Association 3) Centimeter-scale pits of irregular but generally round to ellipsoidal shapes ([Fig. 17E](#)); centimeter-scale flat clasts with edgy corners and irregular shapes; irregular polygonal pattern of cracks.

Laminae are associated to triangular-shaped structures.

Material: Curiosity rover images (Curiosity Mastcam 100 camera on Sols 126 and 306).

Astronomical object: Mars (Gale Crater).

Age: The structure-bearing deposits are fluvio-lacustrine sandstones with a maximum age of 3.7 Ga (Gillespie Lake Member; Hesperian epoch) ([Noffke, 2015](#)).

Substrate: The substrate was a softground that, if microbially-bound ([Noffke, 2015](#)), become a stiffground.

Remarks: The here discussed structures have been compared to biostratification-related features, i.e., MISS ([Noffke, 2015](#)):

1. elevated and irregular rock surface morphologies (association 1) resemble erosional remnants ([Fig. 17F](#)), pockets, roll-ups, and chips of microbial mats;
2. oval-shaped depressions associated with ridges and clasts (association 2) resemble the fringes of microbial mats and mat chips;
3. pits, flat clasts, and cracks (association 3) resemble structures related to gas domes ([Fig. 17G](#)) and mat chips.

The lamination that has been observed in Mars imagery may also

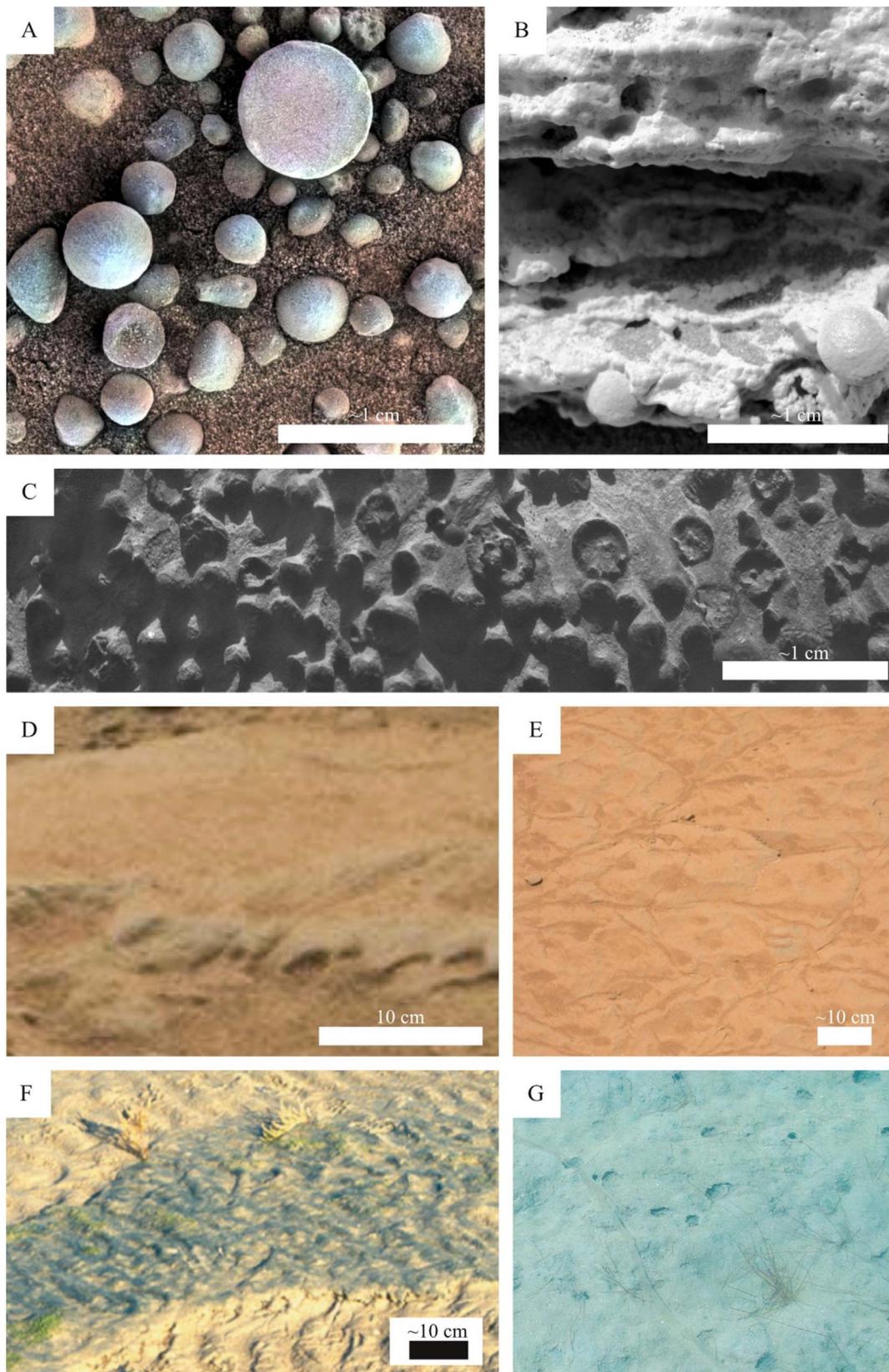


Fig. 17. Other structures. A. Hematite spherules. Image credit: NASA/JPL-Caltech/Cornell/USGS. B. Hematite spherules within laminated sediment. Image credit: NASA/JPL-Caltech/Cornell Univ./USGS. C. Newberries. D. Elevated planar surface from Mars. Detail of Fig. 8C. Specimen discussed in Noffke (2015). E. Pits, flat clasts and cracks association. Mars. Specimen discussed in Noffke (2015). F. Erosional remnant of a modern microbial mat in a nearshore environment. Recent, Earth. Specimen described in Noffke (2015). G. Hole pattern of a modern microbial mat in a nearshore environment. Recent, Earth. See Noffke (2015).

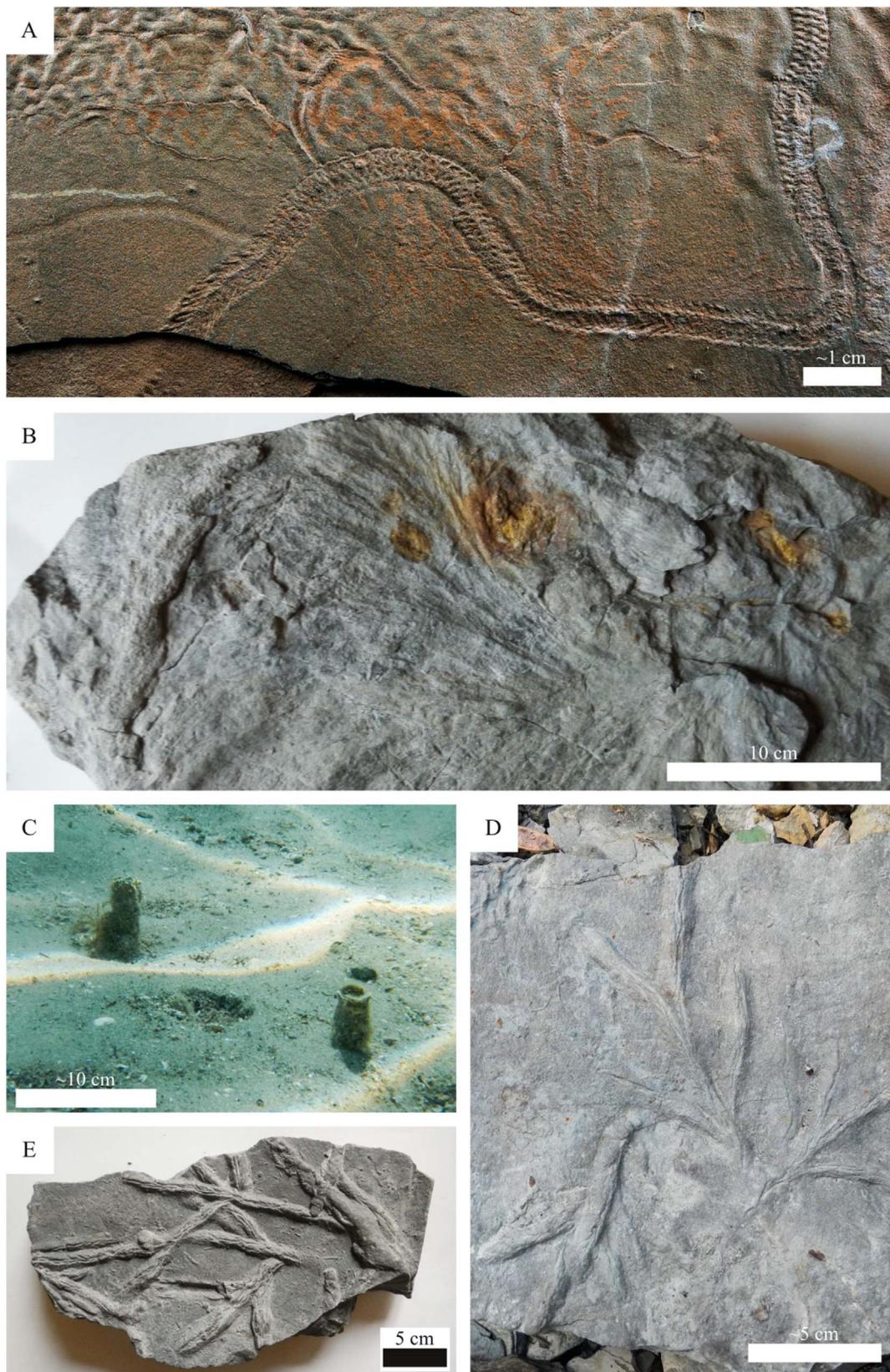


Fig. 18. Traces present the features according to which people actually identify examples of life. A. Structure. Patterned locomotion trail. Lower Ordovician, Barrancos (Portugal). Specimen from the collections of the Museu Geológico (Lisbon). B. Dynamic. *Zoophycos* has been produced by a process of dynamic maintenance. Paleogene-Oligocene, Northern Appennines (Italy). C. Dynamic. Chimneys of the burrow of the polychaete *Chaetopterus*, dynamically maintaining its burrow. The burrow is U-shaped and is an incipient *Arenicolites*. Approximate water depth of 1.5 m. Recent, Adriatic Sea. D. Groups. The trace fossil *Halopoa* is a recurring morphology. Eocene-Oligocene, Northern Appennines (Italy). E. Groups. Another specimen of *Halopoa*, demonstrating the tendency to occur in groups. Specimen of possible Cretaceous-Paleogene age, Northern Appennines (Italy).

derive from the process of biostratification (Noffke, 2015). An alternative interpretation of these structures is that they are abiotic erosion and weathering textures that postdate the deposition of the Martian sedimentary rocks (Davies et al., 2016).

7. Discussion

7.1. Astrobiology and ichnology: the need for a dialogue

This study demonstrated that, despite its astrobiological potential, ichnological concepts have been widely ignored by astrobiology, supporting the idea that “Although astrobiology is a science midway between the life and physical sciences, it has surprisingly remained largely disconnected from recent trends in certain branches of both life and physical sciences” (Chela-Flores, 2012). This idea is reflected in the misleading use of the term “trace” in ichnology and astrobiology (Hasiotis et al., 2006). In ichnology, a “trace” denotes an individually distinctive biogenic structure (Pemberton et al., 2001), but in astrobiology a “trace of life” indicates any type of biosignature (Gargaud, 2011).

As evidenced by previous studies (Hasiotis et al., 2006), this creates unnecessary confusion between the astrobiological and the ichnological community. This scenario is complicated by the fact that “Even neoichnologists and ethologists do not speak the same language, let alone palaeoichnologists, but these scientists have much to tell each other” (Vallon et al., 2015, p. 1). For these reasons, and very similarly to “the path towards a paleobiology of behavior” (Plotnick, 2012), the landmarks for the path towards astroichnology – the astrobiological application of ichnology – are the following: (a) ichnologists should establish a discussion with the astrobiological community; (b) ichnologists should initiate research interactions with the community of behavioural biologists; (c) the astrobiological community should develop research interactions with the ichnological community.

7.2. Ichnology of the Earth as an extraterrestrial ichnology

Although a direct reference to Earth life could result in misleading predictions and interpretations in the analysis of potential extraterrestrial interactions between organism and substrate, the basic features of the terrestrial ichnological record may lead to useful predictions in an astrobiological perspective. The ichnology of the Earth might also be seen as an ‘alien’ one: What might we learn by assuming to remotely observe Earth’s (as a distant planet) ichnology? This question is clearly inspired from the perspective of observing the Earth as a distant planet (Vázquez et al., 2010).

Through the perspective of the ‘extraterrestrial ichnology of the Earth’, traces show a basic tenet of astrobiology, that is “life is shaped

by, and shapes, its host environment” (Hoehler et al., 2007). Traces are shaped by the host environment and this phenomenon goes from a planet’s scale to the one of an individual burrow. In fact, the distribution of trace types is not random but it is shaped by the environmental properties, as acknowledged by the ichnofacies model (Seilacher, 2007). The morphology of individual traces is as well shaped by the environmental properties. For instance, the trail morphology of the modern isopod *Chiridotea coeca* is shaped by the distribution of food (organic carbon) (Hauck et al., 2008); the morphology of fossil and modern crayfish burrows is linked to the depth of the water table (Hasiotis et al., 2007; Hasiotis and Honey, 2000). Conversely, traces shape their host environment. Organism-substrate interactions can result in landscape changes, developing “ichnolandscapes”, and influence resource availability for other species, that is a process known as ecosystem engineering (Buatois and Mángano, 2011; Fleming et al., 2014; Turner, 2003). For instance, mounded topographies produced by bioturbating shrimps, termites and mammals cover areas of hundred square meters to kilometres and may be detected by satellite (Buatois and Mángano, 2011; Löffler and Margules, 1980). Island topography may be modified by the deposition of guano, the thickness of which can reach almost 50 m on the Chincha islands (Hutchinson, 1960).

The perspective of an ‘extraterrestrial ichnology of the Earth’ shows the robustness of traces as biosignatures. Evolution is frequently cited as one of the key processes that characterize life (Bains, 2014; Benner et al., 2004; Cleland and Chyba, 2002; Machery, 2012), but there is a practical drawback to this approach, that is, demonstrating that a system is capable of Darwinian evolution requires a considerable amount of time (Cleland and Chyba, 2002). Some biogenic structures, e.g., meandering traces, do not answer to this drawback but are readily interpreted as the products of natural selection. In fact, natural selection is expected to favour the evolution of decision rules that maximize foraging success and, therefore – if natural selection shapes a given foraging pattern – the observed foraging patterns should be optimal by giving the greatest foraging success (Kramer, 2001). Meandering traces are mathematically optimal foraging patterns, thus they reflect the process of natural selection. A deeper knowledge of biological behaviour is likely to develop similar interpretations for other traces.

The perspective of the ‘extraterrestrial ichnology of the Earth’ indicates that traces are practical biosignatures. Traces present the features according to which people actually identify examples of life (Bains, 2014):

1. Structure (Fig. 18A): Traces have a structure that is highly improbable in its environment. For instance, there is no abiotic process that explains patterned trails (Fig. 18A) or the ornamental morphologies of graphoglyptids (Seilacher, 2007) such as *Paleodictyon* (Fig. 8D). This is also the reason for which traces have been

Table 5

Classification of the trace-like structures discussed in this paper. Classification system by McKay et al. (2003). See text for references about the trace-like structures.

Class (McKay et al., 2003)	Trace-like structure	Biogenic explanation	Abiogenic explanation	Astronomical object
Category I	Bootprints	Bioturbation	No abiogenic explanation	Moon
	Trenches	Bioturbation	No abiogenic explanation	Moon, Mars
	Cylindrical drills	Bioturbation, bioerosion	No abiogenic explanation	Moon, Mars
Category II	Parallel trails	Bioturbation	No abiogenic explanation	Moon, Mars
	Curved microtunnels	Bioerosion	Not known	Mars
Category III	Straight microtunnels	Bioerosion	Not known	Mars
	Dendritic microtunnels	Bioerosion	Fractures filled by C	Mars
	MISS-like structures	Biostratification	Erosion and weathering	Mars
Category IV	Digitate protrusions	Biostratification, bioturbation	Hydrothermalism, weathering	Mars
	Round pits	Bioerosion	Transport	Mars
	Hematite spherules	Biostratification	Concretions, ablation of meteorites, volcanism, meteorite impact, hydrothermal alteration	Mars
Other structures	Vugs	Biostratification	Dissolution, thaw and desiccation	Mars

- distinguished from the substrate since Leonardo da Vinci's time (Baucon, 2009, 2010a, 2010b; Baucon et al., 2012).
- Dynamic (Fig. 18B, C): The morphology of traces shows that they have been produced by a process of dynamical maintenance. For instance, the dynamic character of traces is well shown by the non-random meanders of *Nereites* (= *Helminthoidea irregularis* and *Scolicia* (Fig. 6A, E): “non-random, powered movement on any scale is a suggestion of life” (Bains, 2014). Dynamic maintenance is evident for burrows that are used to channel or tap into energy sources (i.e., traces as part of an ‘extended organism’) (Turner, 2003) such as *Zoophycos* (Fig. 18B), *Thalassinoides* (Fig. 3B) and *Arenicolites* (Fig. 18C).
 - Groups (Fig. 18D, E): Traces do not come in isolation, but there are always many of them that can be distinguished as a natural group. Traces are recurring morphologies from the scale of the outcrop to the global scale. For instance, the trace fossil *Zoophycos* is found at a global scale (Baucon and Avanzini, 2008), recurring morphologies of trace fossils are found (Fig. 18D, E), dinosaur tracks are made by individual footprints of similar morphology (Bates et al., 2008), and the pipe rock ichnofabric is made by simple but distinctive structures that co-occur within the same rock layer (McIlroy and Garton, 2009).
 - Substrate-independent. This property refers to the idea that living things can maintain their structure and their characteristic features in different environments; in this case the term ‘substrate’ is used to indicate food (Bains, 2014). Traces are substrate (food)-independent because they are not solely determined by their external environment, as shown by the typical facies-crossing ichnogenera *Planolites* and *Palaeophycus*.

7.3. The ichnological paradox

McKay et al. (2003) classified biogenic-like structures on the basis of their reliability, that is the probability of a structure to be biogenic, therefore providing a reference for the here discussed trace-like structures (Table 5):

- Category I biosignatures are nearly indisputable evidence for life and have characteristics which cannot be produced by any known non-biologic process in nature (McKay et al., 2003). Their reliability is higher than the 98% (McKay et al., 2003). In this study, reference was made to a few types of category I traces in extra-terrestrial environments (bootprints, trenches, cylindrical drills, parallel trails), all of them are attributable to human tracemakers or human-related vehicles. The reason for attributing these structures to category I is not only related to the distinctive, complex morphology of some of them, i.e., bootprints, but also to the fact that the anthropic tracemaking process has been directly observed (Kaydash et al., 2011; Mitchell et al., 1972).
 - Category II biosignatures are strong but not indisputable evidence for life that are less likely to be produced by known non-biologic processes (McKay et al., 2003). In other words, they are structures that are not known to be produced by abiotic processes (Fisk et al., 2006). Their reliability is 65%–98% (McKay et al., 2003). Fisk et al. (2006) suggested that curved and straight microtunnels are category II biosignatures (Fisk et al., 2006), but it should be noted that similar structures can be abiogenic (McLoughlin et al., 2010).
 - Category III biosignatures are known to be produced by life but they are also known to be produced by non-biologic processes (McKay et al., 2003). Their reliability is 50–65% (McKay et al., 2003). Although biofilms are considered category II biosignatures (McKay et al., 2003), MISS-like structures have been explained by both biotic (Noffke, 2015) and abiotic (Davies et al., 2016) processes, fitting with the definition of category III biosignatures. Similarly, the features of the dendritic microtunnels have been suggested to derive from a carbonaceous-rich impactor on Mars or biogenic corrosion (Gibson et al., 2006; McKay et al., 2006), for which reason they can be considered category III biosignatures. Fully abiotic processes are not ruled out for Martian digitate protrusions (Ruff and Farmer, 2016), thus they fit with the definition of category III biosignatures.
 - Category IV biosignatures are most likely formed by non-biologic properties (McKay et al., 2003). Their reliability is 2–50% (McKay et al., 2003). Round pits and hematite spherules are known to be produced by non-biologic processes, for which reason they are considered category IV biosignatures.
 - Other structures have not been studied enough to be classified. The biogenic hypothesis for vugs has not been comprehensively explored, consequently further studies are needed to place them in the mentioned classification. They are cautiously considered category III biosignatures.
- This shows that, until now, there is no unquestionable evidence of biogenic structures beyond Earth rather than those produced by humans. However, in spite of the wealth of biogenic structures that have been presented here, the absence of extraterrestrial structures potentially induced by biological activity – while we expect to find them – sounds along the lines of the famous Fermi Paradox. The solutions to the ichnological paradox are similar to some of those proposed for the Fermi Paradox (Webb, 2002 and references therein):
- There is no extraterrestrial life and, consequently, there are no extraterrestrial traces. As such, it is a version of the ‘rare Earth’ hypothesis, which emphasizes inherent uniqueness of our planet (Ćirković and Bradbury, 2006). The idea of a rare Earth is supported by arguments related to the Goldilocks principle, assuming that life occurs under such tight constraints that it is inevitably rare in the universe (Dick, 2013). The idea of a rare Earth is at the same time opposed by the principle of mediocrity, according to which Earth is a typical member of the planetary set, and by the fact that many exoplanets are reported to be parts of systems with stable circumstellar habitable zones (Ćirković and Bradbury, 2006). Extraterrestrial life, therefore, would appear to be probable.
 - Extraterrestrial traces exist somewhere, but they are too far away to be detected. The premise of this solution is that traces would not be present in the Solar System, but rather in other stellar systems. If this premise were plausible, traces would pass unnoticed because direct imaging of extrasolar astronomical objects is challenging and is still lacking of an adequate level of detail. Similarly, there would be no traces of interstellar travellers in the Solar System because they have not been in our star system because interstellar travel was not possible (Webb, 2002).
 - Extraterrestrial organisms of the Solar System do not interact with the substrate. This solution, as well as the following ones, narrows the focus of the ichnological paradox by hypothesizing extraterrestrial organisms that live or have lived in the Solar System. The hypothesized organisms, and their possible traces, would therefore be detectable by direct imaging. In this context, the here-discussed solution suggests that, if extraterrestrial organisms of the Solar System would not interact with the substrate, they would not leave traces. For instance, hypothetical floating organisms in the Jovian atmosphere (Sagan and Salpeter, 1976) obviously would not leave recognizable traces and, similarly, a hypothetical plankton in the ocean of the Saturn moon Enceladus.
 - Traces are not preserved. A related idea with the previous solution is that there would be no traces if their preservation potential is too low. For instance, footprints would have an extremely low preservation potential on present-day surface of Mars because of the strong winds. This is demonstrated by the preservation potential of rover ‘tracks’, that typically persist for only one Martian year because of the wind events and the associated seasonal dust storms

(Geissler et al., 2010). However, high-energy aeolian events could be also responsible for the preservation of tracks, such as in the case of track-bearing eolianites on Earth.

5. Traces are not detected. In this paper, traces are searched by analyzing images of astronomical objects of the Solar System. Low imaging resolution and coarse spatial sampling may explain the apparent absence of non-human extraterrestrial traces. This hypothesis could be supported by the detection of trace-like features only where lander images are available.
6. The search strategy is wrong. At present only images of the surface of extraterrestrial objects are available, but the subsurface has not been imaged yet, with few exceptions (e.g., the rock abrasion tool of Mars rovers explored the most superficial centimetres of the planet). Consequently, subsurface has not been observed yet. Similarly, the seafloors of the icy moons have never been observed, as well as their possible ichnological heritage.
7. Traces of extraterrestrial organisms have been encountered albeit unrecognized. This paper documented several trace-like structures whose morphology can be explained by abiotic processes. This raises a possibility: extraterrestrial traces have been already photographed, but they have been misunderstood. The human perception of Earth-type traces not necessarily implies the same ability for all possible types of extraterrestrial traces. In other words, extraterrestrial traces could be stranger than imagined.

The discussion on the ichnological paradox shows that there is not a unique reliable solution, but different and often contrasting solutions. The lack of non-human extraterrestrial traces could also stimulate the development of testable hypotheses by developing better technological tools for astroichnological research and extending the range of ichnological exploration. This might provide further directions of research in both astrobiology and ichnology.

7.4. Where to look for?

This paper has shown the great potential of ichnology in the search of extra-terrestrial life, however, the aforementioned ichnological paradox rises a further question: Where to look for biogenic structures if any?

Planets and moons of the Solar System that could have been habitable during their history represent the most obvious answer because of the technological limits in the imaging of exoplanets (Brown and Burrows, 1990; Des Marais et al., 2002; Marois et al., 2008; Peters and Turner, 2013; Traub and Oppenheimer, 2010). By assuming that the only absolute requirements for life are a thermodynamic disequilibrium and temperatures consistent with chemical bonding (Benner et al., 2004), life, and therefore tracemakers, might exist in a wide range of environments of the Solar System. Methane lakes of Titan, for example, are an object of a potential ichnological interest, although their biochemistry might not be based on water and carbon (Schulze-Makuch and Irwin, 2006). In a narrower sense, habitability is defined by the requirements of Earth-type life, that is the availability of energy, carbon, liquid water, and various other elements (N, P, S, Na, among others) (Des Marais et al., 2008; Fritz et al., 2014; McKay, 2014). This narrow definition of habitability indicates that Mars, some satellites of Jupiter (Europa, Ganymede, Callisto) and Saturn (Titan, Enceladus) have some potential to host present (or past) habitable environments (e.g., Des Marais et al., 2008) and, consequently, for the search of biogenic structures. Some of these astronomical objects (Europa, Enceladus, Mars, among others) are of high-value for the search of subaqueously microbioeroded basalts (Izawa et al., 2010) and even continental environments of Mars may preserve near-surface microborings (Nikitczuk et al., 2016a, 2016b). Exploration of these habitable astronomical objects is being considered (e.g., Titan, Enceladus, Europa) or planned (e.g., Mars) (Gowen et al., 2011; Izawa et al., 2010; Lorenz, 2015) and the predictive model for organism-substrate interactions

could find application in presenting possible ichnological scenarios. For instance, the model highlights a possible ichnological scenario at Oxia Planum, Mars, that is the landing site of the planned ExoMars 2020, based on the geological units described by Quantin et al. (2016):

1. The clay-rich formation outcropping at Oxia Planum deposited as softgrounds, therefore fossil burrows may be present. Slow sedimentation rates are likely to have characterized deposition of clay, favouring highly bioturbated ichnofabrics because organisms, if any, would have had the time to rework the sediment. Lower bioturbation intensities may characterize the fluvial channels at the top or embedded within the clay-rich formation.
2. At the top of the clay-rich formation, the deltaic deposits of Oxia Planum may also host bioturbated ichnofabrics. Bioturbation intensity is expected to decrease from the prodelta to the delta front because of the higher sedimentation rate. Lined trace fossils could be present at the delta front as a strategy to cope to mechanical stress and shifting substrates.
3. Substrate-controlled ichnoassemblages could be present in correspondence of non-deposition or erosion-surfaces, e.g., borings or burrows with bioglyphs.
4. The igneous hardgrounds that overly the mentioned formations could host borings. The microboring-like structures found in nakhlite meteorites, that once were igneous hardgrounds on Mars, are encouraging in this regard (Fisk et al., 2006).
5. Modern traces such as burrows and borings could be present at Oxia Planum, especially at the subsurface.

Oxia Planum has a high preservation potential for organics, but the resilience of trace fossils is an important aspect to consider for planning astrobiological exploration: they may be present within geological units even with low preservation potential for organics, such as the cross-bedded deposits at Meridiani Planum, Mars (Pullan et al., 2008).

Nevertheless, this study has not documented unquestionable biogenic structures – apart from those produced by humans – from the mentioned habitable astronomical objects. The evidence of recent bioturbation structures on the Moon (i.e., human footprints), a place that is not among the likely candidates for the persistence of life (Schulze-Makuch et al., 2005), suggests that non-habitable environments are also a place to look for biogenic structures. This is because the absence of autochthonous tracemakers, that otherwise would obliterate other biogenic structures, can favour the preservation of shallow-tier traces. The ichnological example of the Moon shows that astronomical bodies with no atmosphere may also favour trace preservation because the only major source of erosion and deposition comes from meteorite impacts, which occur at a very slow rate (Davies and Wagner, 2013; Spennemann, 2004). Traces on non-habitable astronomical bodies would be produced either by space travellers or by doomed pioneers.

7.5. From planetary protection to ichnological protection

Traces have a better preservation potential than other biosignatures, especially on astronomical objects with no atmosphere. This greatly widens the issue of planetary protection. In fact, the interaction between astronauts or vehicles and the substrate may produce disturbances that are not only an ecological threat to eventual extraterrestrial life forms, but they also could be a source of scientific misinterpretation by producing ambiguous sedimentary structures or by obliterating information.

The ecological threat of sediment mixing by rover wheels is significant. For example, vertical sediment mixing shaped the marine ecosystems of the Earth by favouring the transition from the Proterozoic biomat-dominated matgrounds to the Phanerozoic mixgrounds (Seilacher, 2007). This revolution, known as the Agronomic Revolution or the Cambrian Substrate Revolution, changed the ecology of the marine ecosystem at a global scale (Bottjer et al., 2000; Seilacher, 2007;

Seilacher and Pflüger, 1994) and therefore underlines the necessity of developing an ‘ichnological protection’ philosophy for exploring extraterrestrial astronomical objects.

‘Ichnological protection’ may also improve the quality of scientific information. Rovers are likely to produce sedimentary structures that are scientifically misleading: the rover ‘tracks’ could be interpreted as natural sedimentary structures; rover wheels may produce apparently natural ichnofabrics by mixing the sediment; similarly, sediment mixing may obliterate biogenic structures or physical sedimentary structures. A possible solution is to develop specific markings on the rover wheels, such in the case of the Mars rovers, in order to distinguish natural from artificial sedimentary structures. More in detail, the wheels of the Curiosity rover have a Morse code sculpture in order to leave a recognizable pattern on the sediments for visual odometry (Clavin, 2012); a similar pattern can also be used for determining the authorship of the pattern itself. This approach is not effective for deciphering the effects of sediment mixing because rover wheels do not produce distinct patterns. The solution is therefore an exact spatial knowledge of the rover path.

8. Conclusions

This study critically reviewed ichnological concepts and tools for the search for extraterrestrial life, highlighting a new direction of astrobiological research. Biogenic structures (i.e., traces and ichnofabrics) are important biosignatures for the search of past and present life beyond Earth because (1) they preserve the activity of soft-bodied organisms, (2) they are resilient to processes that obliterate other biosignatures, (3) they are visible biosignatures, (4) they indicate environment and behaviour, (5) they can be universal biosignatures, i.e., biosignatures ideally suited for detecting any type of life.

In addition to meandering traces, finding additional examples of extraterrestrial traces on Earth is an important scientific goal for the search of extraterrestrial life. To this aim, foraging theory represents a useful paradigm to test the universality of existing psychichnia and fodinichnia. Similarly, computational modeling of other types of traces (e.g., chemichnia) is likely to provide important insights.

Excavations, meandering traces and biodeposition structures are potential extraterrestrial biogenic structures because they manifest behaviours that allow to maintain homeostasis. This model of organism-substrate interactions could be refined by the systematic study of modern and fossil traces from extreme environments on Earth.

Basic instruments for searching traces are provided by existing rovers and orbiters, although rovers would also benefit from adjustable lighting, GPR, LiDAR, drilling equipment with optical televiewer. An interesting perspective of study would be to develop ichnological tools to be tested on analogue sites on Earth. Dialogue between the astrobiological and ichnological community is needed to use the full potential of this new approach.

Acknowledgments

Cristian Micheletti, André Strasser, Radek Mikuláš and an anonymous reviewer are thanked for improving the study by reviewing preliminary versions of the manuscript. Researchers of the Gruppo Mineralogico e Paleontologico Piacentino are thanked for their help in the study of the Northern Apennines trace fossils. Peter Dworschak, Javier Garcia-Guinea, Jorge Genise, Viktor Jáger, Sören Jensen, Diego Kietzmann, Eduardo Mayoral, Alexandru Petrisor, Robert Pringle and Ana Santos are thanked for providing photos of traces (Figs. 1E, 4F, G, 5A, 6C, D, 7C, 11A, B, 12B, C, D, and 13E). Martin Fisk, Radu Popa, Michael Storrie-Lombardi, Edward Vicenzi are thanked for providing images of microtunnels from Mars (Figs. 3D and 14F). Nora Noffke is thanked for providing images of microbial mat structures from Earth and microbial mat-like structures from Mars (Figs. 8C and 17D, E, F, G). Lauren White, Everett Gibson, Kathie Thomas-Keprta, Simon Clemett

are thanked for providing images of the tunnels from the Martian meteorite Yamato 000593 (Fig. 14A). Steve Ruff is thanked for providing images of microdigitate structures (Fig. 15; image source is licensed under a Creative Commons Attribution 4.0 International License). Lucia Angiolini and Gaia Crippa are thanked for indicating *Thalassinoides* of the Stirone river. Jorge Genise is also thanked for discussing the concept of frozen behaviour. This research was supported by the ROSAE project (<http://rosaeoproject.org/>).

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