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Appendix A

Ichnobase

Supplementary data of chapter 2.1

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Appendix B

A history of ideas in ichnology

Chapter 1

A History of Ideas in Ichnology

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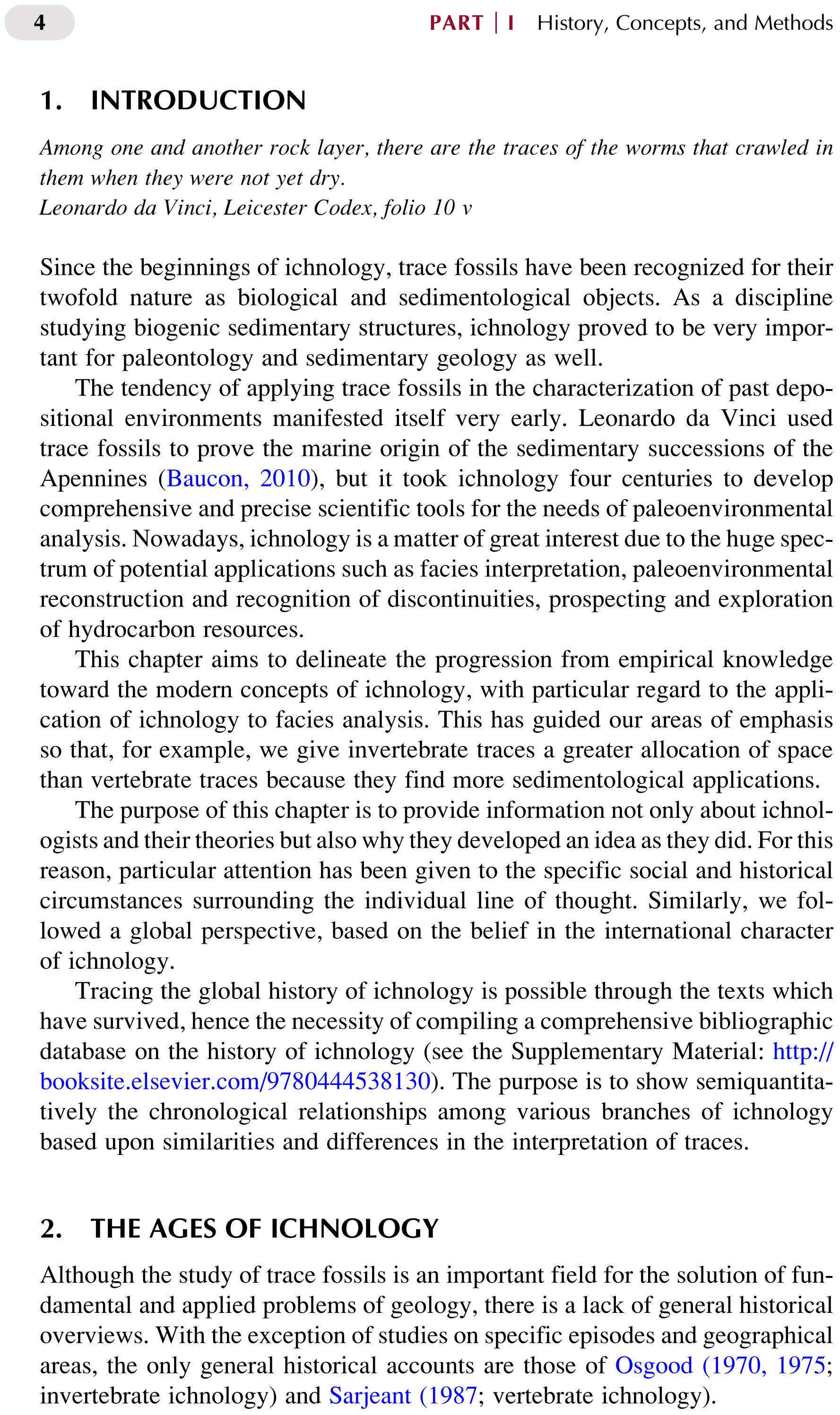


1. INTRODUCTION

> *Among one and another rock layer, there are the traces of the worms that crawled in them when they were not yet dry.*
> *Leonardo da Vinci, Leicester Codex, folio 10 v*

Since the beginnings of ichnology, trace fossils have been recognized for their twofold nature as biological and sedimentological objects. As a discipline studying biogenic sedimentary structures, ichnology proved to be very important for paleontology and sedimentary geology as well.

The tendency of applying trace fossils in the characterization of past depositional environments manifested itself very early. Leonardo da Vinci used trace fossils to prove the marine origin of the sedimentary successions of the Apennines (Baucon, 2010), but it took ichnology four centuries to develop comprehensive and precise scientific tools for the needs of paleoenvironmental analysis. Nowadays, ichnology is a matter of great interest due to the huge spectrum of potential applications such as facies interpretation, paleoenvironmental reconstruction and recognition of discontinuities, prospecting and exploration of hydrocarbon resources.

This chapter aims to delineate the progression from empirical knowledge toward the modern concepts of ichnology, with particular regard to the application of ichnology to facies analysis. This has guided our areas of emphasis so that, for example, we give invertebrate traces a greater allocation of space than vertebrate traces because they find more sedimentological applications.

The purpose of this chapter is to provide information not only about ichnologists and their theories but also why they developed an idea as they did. For this reason, particular attention has been given to the specific social and historical circumstances surrounding the individual line of thought. Similarly, we followed a global perspective, based on the belief in the international character of ichnology.

Tracing the global history of ichnology is possible through the texts which have survived, hence the necessity of compiling a comprehensive bibliographic database on the history of ichnology (see the Supplementary Material: http://booksite.elsevier.com/9780444538130). The purpose is to show semiquantitatively the chronological relationships among various branches of ichnology based upon similarities and differences in the interpretation of traces.

2. THE AGES OF ICHNOLOGY

Although the study of trace fossils is an important field for the solution of fundamental and applied problems of geology, there is a lack of general historical overviews. With the exception of studies on specific episodes and geographical areas, the only general historical accounts are those of Osgood (1970, 1975; invertebrate ichnology) and Sarjeant (1987; vertebrate ichnology).

Osgood (1975) attempted to subdivide the history of ichnology on the basis of periods of time with relatively stable characteristics:

1. *Age of Fucoids* (*1823–1881*): This stage started with Brongniart (1823), who considered invertebrate trace fossils as *fucoids*, or seaweed. During this historical stage, the botanical interpretation dominated the scientific view of trace fossils.
2. *Period of Reaction* (*or Age of Controversy*) (*1881–1925*): Based on analogies with modern traces, Nathorst (1881) argued that many *fucoids* were trace fossils. This aroused a consistent debate, with prominent scientists like Lebesconte and de Saporta supporting the botanical interpretation.
3. *Development of the Modern Approach* (*1925–1953*): This stage started with the establishment of the Senckenberg Laboratory, a marine institute devoted to neoichnology (Cadée and Goldring, 2007). The geologists of the period agreed about the ichnological nature of trace fossils, opening the avenues to the decisive steps toward modern ichnology.

In more recent times, two historical stages were added to Osgood's classical periods: Pemberton et al. (2007) recognized a *Modern Era of Ichnology*, extending from 1953 to the present day. This period saw the foundation of the central concepts of modern ichnology, starting with Seilacher's (1953) seminal publication on the methods of ichnology. Recently, Baucon (2010) established the *Age of Naturalists*, spanning roughly the fifteenth to the seventeenth centuries. During this stage, several Renaissance intellectuals depicted and studied trace fossils, although ichnology existed as disconnected ideas about traces. Holding these stages as a chronological reference, this chapter will explore the evolution in the study of trace fossils, from Paleolithic times to the present.

3. FROM PALEOLITHIC TIMES TO GRECO-ROMAN ANTIQUITY

Archeological evidence indicates that humans have recognized trace fossils since Paleolithic times. Bioeroded Miocene mollusks are commonly found within the cultural layers of Pavlov and Dolní Věstonice (Czech Republic, Late Paleolithic, 29,000–24,000 years ago; Fig. 1A). Statistical data from the primary collection sites indicate that humans selectively collected mollusks with bioerosional trace fossils (*Oichnus*) in order to use them as items of personal adornment (i.e., segments of collars; Jarošová et al., 2004 in Supplementary Material: http://booksite.elsevier.com/9780444538130).

Such archeological evidence shows that trace fossils were a subject of ancient interest for humans, although it gives no information about their interpretation in past hunter/gatherer societies. In this regard, anthropological analogy with modern indigenous populations represents a valuable tool of analysis. As one of the oldest continuous cultures in the world, Australian Aborigines provide an exceptional insight in the anthropology of biogenic traces (Lowe, 2002). Native

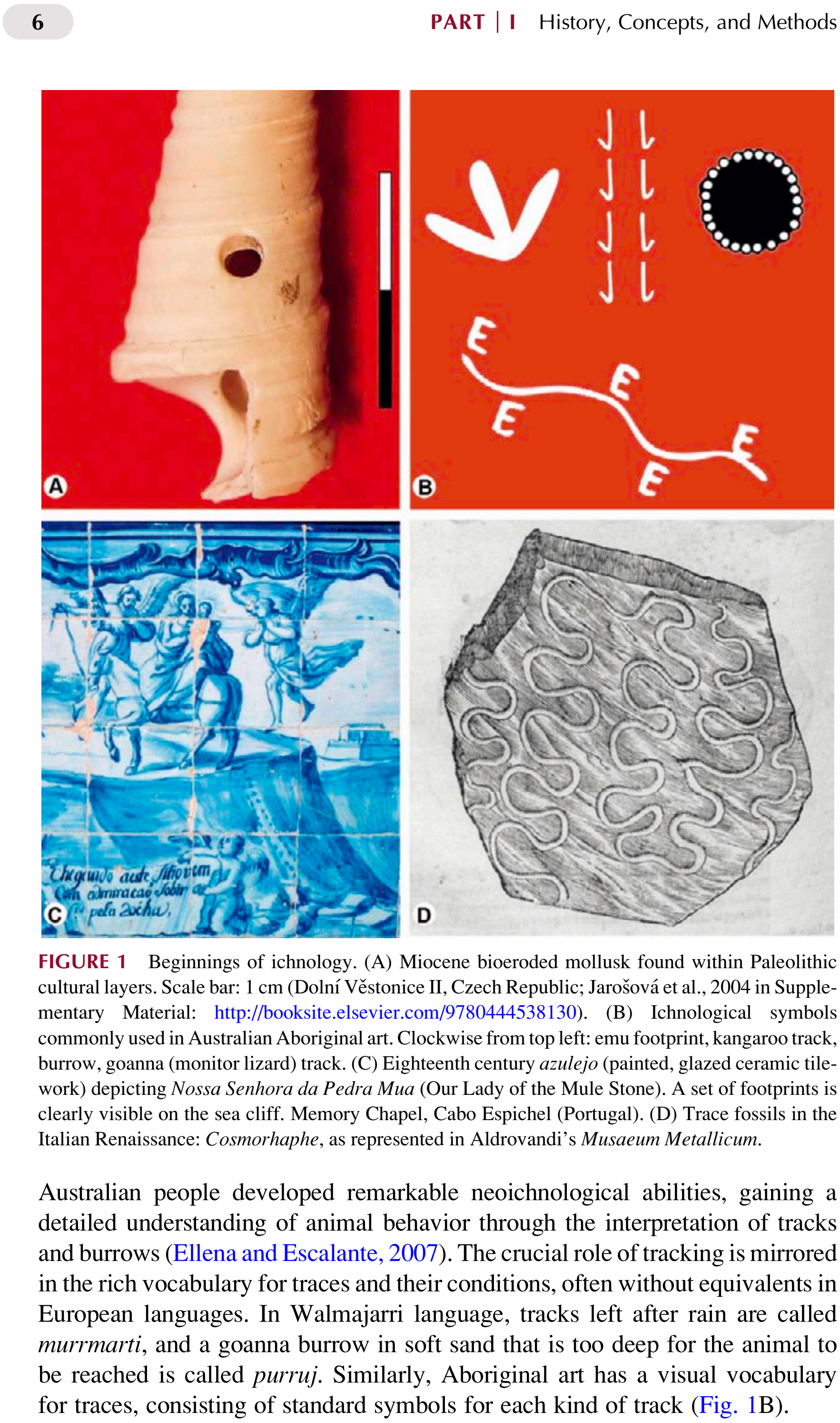


FIGURE 1 Beginnings of ichnology. (A) Miocene bioeroded mollusk found within Paleolithic cultural layers. Scale bar: 1 cm (Dolní Věstonice II, Czech Republic; Jarošová et al., 2004 in Supplementary Material: http://booksite.elsevier.com/9780444538130). (B) Ichnological symbols commonly used in Australian Aboriginal art. Clockwise from top left: emu footprint, kangaroo track, burrow, goanna (monitor lizard) track. (C) Eighteenth century *azulejo* (painted, glazed ceramic tilework) depicting *Nossa Senhora da Pedra Mua* (Our Lady of the Mule Stone). A set of footprints is clearly visible on the sea cliff. Memory Chapel, Cabo Espichel (Portugal). (D) Trace fossils in the Italian Renaissance: *Cosmorhaphe*, as represented in Aldrovandi's *Musaeum Metallicum*.

Australian people developed remarkable neoichnological abilities, gaining a detailed understanding of animal behavior through the interpretation of tracks and burrows (Ellena and Escalante, 2007). The crucial role of tracking is mirrored in the rich vocabulary for traces and their conditions, often without equivalents in European languages. In Walmajarri language, tracks left after rain are called *murrmarti*, and a goanna burrow in soft sand that is too deep for the animal to be reached is called *purruj*. Similarly, Aboriginal art has a visual vocabulary for traces, consisting of standard symbols for each kind of track (Fig. 1B).

Trace fossils are also an object of interest for Australian Aborigines. Dinosaur tracks are part of the *Ngarrangkarni* (or "Dreamtime"), a mythical past when giant ancestor beings left traces of their exploits, shaping the landscape to its present form. Native people attribute theropod tracks to an enormous feathered "Emu-man", *Marrala* (also spelled *Marella*; Mayor and Sarjeant, 2001). Marrala's footprints represent ichnohierophanies (*sensu* Baucon et al., 2008), which are supposed traces of supernatural entities in objects that are an integral part of our natural world (i.e., rocks). Ichnohierophanical accounts are reported from cultures all over the world and include both vertebrate and invertebrate trace fossils (Baucon et al., 2008).

One of the best examples are the sauropod trackways and the trace fossil *Rhizocorallium* of Cape Espichel (Portugal), object of curiosity and devotion since the thirteenth century. Fishermen from the region of Sesimbra interpreted such trace fossils as the footprints of a giant mule that carried the Virgin Mary (Lockley et al., 1994). During the eighteenth century, a sanctuary was erected and "Nossa Senhora da Pedra Mua" (Our Lady of the Mule Stone) became an object of national worship (Fig. 1C).

Ichnohierophanic interpretations were common in the Greco-Roman world, as exemplified by Lucianus of Samostata (approx. AD 125–after AD 180), who satirized the frequent claims of "footprints in rock" (Mayor and Sarjeant, 2001). The figure of Heracles often provided a mythological explanation for fossil footprints. For instance, Pseudo-Aristotle reported that "near Pandosia in Iapygia (present-day Heraclea, Italy), the footprints of Heracles are shown and no one is allowed to step on them". First attributed to Pleistocene mammal tracks (Mayor and Sarjeant, 2001), Heracles' footprints are most probably dinosaur footprints, as evidenced by the abundant dinosaur tracksites in the same area of Pandosia.

Although only a minor part of the texts of natural philosophers survived to us, neoichnological observations are found in Aristotle's (384–322 BC) *History of Animals* and Theophrastus' (approx. 371–287 BC) *On Fish* (Sharples, 1995). Trace fossils were apparently ignored by early natural philosophers, with the exception of Pliny the Elder (23–79 AD). In his *Naturalis Historia*, the Roman author described *phycites* as an "alga-like stone", possibly some kind of branched trace fossil. In fact, the term "phycites" or "ficite" was successively used to indicate *Chondrites* (i.e., Targioni-Tozzetti, 1777).

4. THE AGE OF NATURALISTS

Despite these early interpretations, the move toward a rational understanding of trace fossils began in the European Renaissance. This cultural movement flourished in Italy during the fourteenth century and rapidly spread across Europe, bringing the start of a revolution in the way to investigate nature.

In Renaissance times, the inquiry into the natural world took place both in science and art, which were connected by a coherent line of continuity. This phenomenon can be clearly seen in the work of Leonardo da Vinci, the founding father of ichnology (Baucon, 2010). Indeed Leonardo not only sketched

Paleodictyon, but he also examined the subject of trace fossils when dealing with the origin of body fossils or, with Leonardo's words, *nichi petrificati* (petrified seashells). While his contemporaries supported an inorganic origin for body fossils, Leonardo referred to bioeroded specimens to disprove this idea. Similarly, da Vinci used bioturbational traces (*andamenti delli lombrici* or "traces of worms") as a paleoenvironmental tool to demonstrate the marine origin of the sedimentary layers. Da Vinci's accurate analysis shows that, from the beginnings of ichnology, trace fossils have been an indispensable tool for facies analysis and paleobiology. However, Leonardo did not have influence on his contemporaries because he wrote in mirror-image Italian, at a time when Latin was the idiom of erudition. Despite his revolutionary conclusions, Leonardo remained an isolated voice, not participating in the academic discussion. In contrast, Ulisse Aldrovandi, the first professor of natural sciences at the University of Bologna, left a considerable legacy, including the word *geology* (Vai and Cavazza, 2003). The *Musaeum Metallicum*, his most extensive work in geology and paleontology, contains several trace fossils, frequently described in detail and with magnificent illustrations. Aldrovandi described *Cosmorhaphe* as a snake-like structure, possibly suggesting an inorganic origin, but he accurately interpreted bioerosional structures as produced by bioeroding mollusks (Baucon, 2009).

Known for his vast cabinet of curiosities, Aldrovandi exchanged specimens and ideas with another prominent naturalist of the Renaissance, the Swiss Conrad Gesner. *De omni rerum fossilium genere*, Gesner's (1565) geological treatise, exemplifies a common trait of the Renaissance pioneers of ichnology: a non-exclusive interest in traces. In fact, Gesner, as many other contemporaries, investigated any aspect of the natural world that aroused his interest, from trace fossils to gemstones. Though younger than Gesner, Johann Bauhin was the main pupil of the influential naturalist. He published a tourist guide in which he described a branched trace fossil (*Phymatoderma*). The accompanying illustration shows intricate angelic figures, but Bauhin commented, "The human figures have been mistakenly added either by the painter or the wood cutter" (Seilacher, 2007).

A chondritid was also reported by Legati (1677) when describing Ferdinando Cospi's *Wunderkammer*, placed next to the Aldrovandi's Museum. Legati followed the interpretation of Aldrovandi, who previously studied the same specimen, and indicated it as "Wooded-stone" ("Alberina", "Dendrite", "Pietra Imboscata"; Legati, 1677; Fig. 2A). The "Alberina stone" was commonly excavated in the surroundings of Bologna and used as a building material after calcination. For this reason, Ovidio Montalbani proposed *Chondrites* as the symbol of stone masonry, accompanied by the Latin motto, *Silex medio cremium sibi viscere sculpsit*, *an cupit in calcem versa parare domos?* ("Hard stone has carved out its bowels into brushwood, perhaps does it want to build houses after becoming lime?"; Legati, 1677: 174). Bioerosional traces were also present in the Cospi collection and compared to petrified ant burrows (Legati, 1677: 175).

FIGURE 2 Interpretation of trace fossils through time. (A) Legati's *Pietra Alberina* (Tree stone) exemplifies the fact that chondritids have been compared to plants since the seventeenth century or earlier. (B) William Buckland, pioneer of the study of fossil feces, owned a table made with sectioned coprolites from Carboniferous deposits (Duffin, 2009). (C) Fanciful representation of a funnel-weaving spider, placed by Eberhard Werner Happel among *vermes lapidum*, or rock-boring organisms (Happel, 1707, published posthumously).

These naturalists pioneered the study of ichnology and added many descriptions of trace fossils to their natural histories. Their work demonstrates that ichnology has its roots firmly anchored in Renaissance times, although it existed as disconnected ideas about traces.

5. SEVENTEENTH TO EIGHTEENTH CENTURY: A PERIOD OF TRANSITION

For many years after Osgood's (1970, 1975) work, it was argued that ichnology was born in the nineteenth century, Age of Fucoids—a not implausible suggestion, given the difficulty to find ichnological studies from prior to the 1800s. However, recent works not only highlight the Renaissance roots of ichnology (Section 4; Fig. 2A) but also evidence some ichnological observations dating back to the 1700s (i.e., Duffin, 2009). As a consequence, one question might arise: what historical phenomena connected the Age of Naturalists to the Age of Fucoids?

By the late 1600s, the emphasis on reason in the intellectual life of Europe started to become pervasive. The early Enlightment in Europe went hand in hand with an expansion of scientific societies which, by the start of the eighteenth century, had transformed the organization of scientific research (Gohau, 1991). This aspect affected also the study of trace fossils, as evidenced by the central role of the Royal Society of London in the study of coprolites. Indeed, John Woodward, fellow of the Royal Society, provided one of the first explanations for their origin by comparing Mesozoic specimens to "Iuli" or cones of larch trees (Woodward, 1729). However, he was not the only researcher to describe coprolites. Indeed another fellow of the Royal Society, Lhwyd (1760), figured a spiral coprolite, and Mylius (1709) previously illustrated some Permian specimens. The botanical interpretation of coprolites has been predominant since the time when Buckland (1822), an influential fellow of the Royal Society, recognized them as fossil feces (Duffin, 2009; Fig. 2B). Bioerosional structures also received attention during the eighteenth century. Intellectuals such as Lorentz Spengler and Gottfried Sellius focused on modern bioeroding bivalves (Supplementary Material: http://booksite.elsevier.com/9780444538130). Bioeroding organisms, collectively named as *vermes lapidum*, were attributed by some authors to funnel-weaving spiders (Happel, 1707; Lémery, 1716; Fig. 2C). By the late 1700s, the attention given to bioturbational structures gradually rose. This phenomenon emerged from the same cultural areas—the Italian and the German-speaking regions—which dominated the Age of Naturalists.

From the eighteenth to the early nineteenth century, the term *fucite* was widely adopted by Italian scholars to indicate bioturbated rocks; the term may refer to Pliny's *phycites*, or alga-like stone. In his travel reports from Tuscany, Targioni-Tozzetti (1777) accurately described *fuciti*: "they are similar to the Worm-Stones (Pietre Lombricarie), and when they are split-off . . . they reveal impressions of algae (Fuci)". Despite the alga-like appearance, Tozzetti questioned the vegetal nature of *fuciti*, of which the origin "botanical or animal, is not known" (Targioni-Tozzetti, 1777). To solve this issue, he collaborated with the abbot Alberto Fortis, who had previously described *elmintoliti* (*Helminthoida*) from Istria and Dalmatia (Fortis, 1774; Surić et al., 2007). Adolphe Brongniart, the initiator of the Age of Fucoids, studied *Fucoides* (=*Chondrites*) *targionii* from the collections of the Italian scientist, proving Targioni-Tozzetti's far-reaching influence (Brongniart, 1828: 56–57). After the 1830s, the term *fucite* fell into disuse, being quickly replaced by the etymologically analogous *fucoid*.

In Germany, interest for natural history became popular in Thuringia, Saxony, and Bavaria, giving particular attention to Permian and Triassic units, among which the trace-fossil-rich Muschelkalk. In naming rocks, researchers came up with specific descriptors, often based on those aspects of the texture resulting from bioturbation. Among these early contributors, Schütte (1761) used a Renaissance term, *osteocolla*, for describing bone-like rocks characterized by *Protovirgularia* and *Planolites*. However, the best example of this tendency is Batsch (1802), who meticulously described *Zungenkalkstein* ("tongue limestone", for its *Rhizocorallium*-dominated ichnofabric), *Loecherkalkstein* ("holey limestone", for the abundant *Balanoglossites*), and *Wurmkalkstein* ("worm limestone", for the prominent presence of *Planolites* and *Protovirgularia*).

The botanical interpretation, successively prominent in the Age of Fucoids, was followed by a German student of Couvier and friend of Alexander von Humboldt, namely, Johann Gotthelf Fischer von Waldheim, who reported *Umbellularia logimna* (now *Zoophycos*) from the Ural Mountains (Supplementary Material: http://booksite.elsevier.com/9780444538130). Invertebrate trace fossils were also noticed by the explorer Hinrich Lichtenstein during his travel in South Africa (Master, 2010 in Supplementary Material: http://booksite.elsevier.com/9780444538130).

While in continental Europe, the major part of the ichnological observations appeared in treatises; in Britain, they regularly appeared in periodic journals published by scientific societies. Together with the Philosophical Transactions of the Royal Society, the Transactions of the Geological Society of London were a major channel for disseminating ichnological research. For instance, McCulloch (1814) published a description of the pipe rock of north-western Scotland, suggesting similarity to sabellid marine worm-burrows. Other influential contributors include Buckland, who described "paramoudras" from the Chalk of Northern Ireland, and Webster, who figured *Thalassinoides* and *Ophiomorpha* as zoophytes (plant-like animals, e.g., alcyonarian cnidarians; Supplementary Material: http://booksite.elsevier.com/9780444538130).

In conclusion, the voyage from the Age of Naturalists to the Age of Fucoids was tortuous (Fig. 3A and B), and the corresponding transitional period incorporated concepts and media from both cultural stages.

6. THE AGE OF FUCOIDS

6.1 Emergence of the Paleobotanical Interpretation

The end of the French Revolution, the expansion of colonial empires, and the Industrial Revolution were conditions that made the nineteenth century a period of profound social and economic change (Frey and Frey, 2004). This milieu served as the background to the French botanist Adolphe Brongniart, defined as the "typical child of the best of the French revolution" (Stafleu, 1966; Fig. 3B). Adolphe held a name with status: he was the grandson of Napoleon's architect and the son of the eminent geologist Alexandre Brongniart. In 1817, Adolphe joined his father in a geological *grand tour* through the Swiss and

FIGURE 3 Pioneers in the study of trace fossils. (A) Leonardo da Vinci. (B) Adolphe Brongniart. (C) Alfred Nathorst.

Italian Alps, where he observed abundant trace fossils from the Apennines foredeep basin (Brongniart, 1828: 45).

A new stage in the history of ichnology began in the year 1823, when Brongniart published his *Observations sur les fucoides et sur quelques autres plantes marines fossiles* (Brongniart, 1823; Osgood, 1970, 1975). By his attitude toward comparative anatomy, Brongniart associated some branching forms of trace fossils (e.g., *Chondrites*) to modern algae, and according to the resemblance to the brown alga *Fucus*, he used the term *fucoid* to indicate such fossils. Although other researchers previously supported the botanical origin of trace fossils (i.e., von Schlotheim, 1822), none of these reached the influence of the French botanist. One reason may be found in the scientific authority of Brongniart, who was recognized as the founding father of paleobotany even during his lifetime (Stafleu, 1966). Second, Brongniart provided the scientific community with relevant tools: the first classification of all known fossil plants (including fucoids) and its biostratigraphical application (Brongniart, 1828). Finally, French was one of the most used international languages in Europe, being the language of diplomacy from the seventeenth to mid-twentieth centuries (Chew, 2009).

The French School and the rising discipline of paleobotany offered convincing arguments in support to the fucoid hypothesis (e.g., de Saporta, 1873), which was readily accepted by the international scientific community. For instance, the German paleontologist Bronn (1837) described and figured numerous *Fucoiditen*, an interpretation that was also provided for *Asterosoma* (von Otto, 1854). Much of the fucoid research originated from the flysch in the Swiss Alps, where Fischer-Ooster followed Brongniart in using "fucoids" for stratigraphical correlation (Supplementary Material: http://booksite.elsevier.com/9780444538130). Among the various works that have dealt with fucoids, *Flora Fossilis Helvetiae* (Heer, 1876/1877) stands preeminent for the detail of the descriptions.

The champions of the fucoid hypothesis came from the most disparate parts of Europe. Specifically, the Portuguese paleontologist Joaquim Nery Delgado had a central role in supporting the botanical origin of trace fossils, although he successively interpreted *Nereites* and *Skolithos* as trace fossils (e.g., Delgado, 1903). Similarly, the Bohemian geologist Sternberg (1833–1838), one of the founding fathers of paleobotany, was one of the most prominent authors of the Age of Fucoids for his numerous descriptions of *Chondrites*.

The term *fucoid* soon became part of the international geological lexicon, from Spain (De Prado, 1864) to Poland (Pusch, 1837), and from Britain (Buckland, 1836) to Italy (Savi and Meneghini, 1851). The important legacy of the fucoid approach included not only substantial advances in descriptive knowledge but also the establishment of still valid ichnogenera such as *Rhizocorallium*, *Scolicia*, *Daedalus*, *Paleodictyon*, *Spirophyton*, *Diplocraterion*, and *Zoophycos* (Häntzschel, 1975). Particularly noteworthy is the case of *Cruziana*, described as a body fossil by the French naturalist Alcide d'Orbigny during a mission for the Paris Museum. He established the (ichno)-genus *Cruziana* after the Bolivian president Mariscal Santa Cruz, who had sponsored his visit to South America (Seilacher, 2007). The significance of his work resides in the definition of a taxon that was subsequently reinterpreted as a trace fossil, gaining immense popularity worldwide.

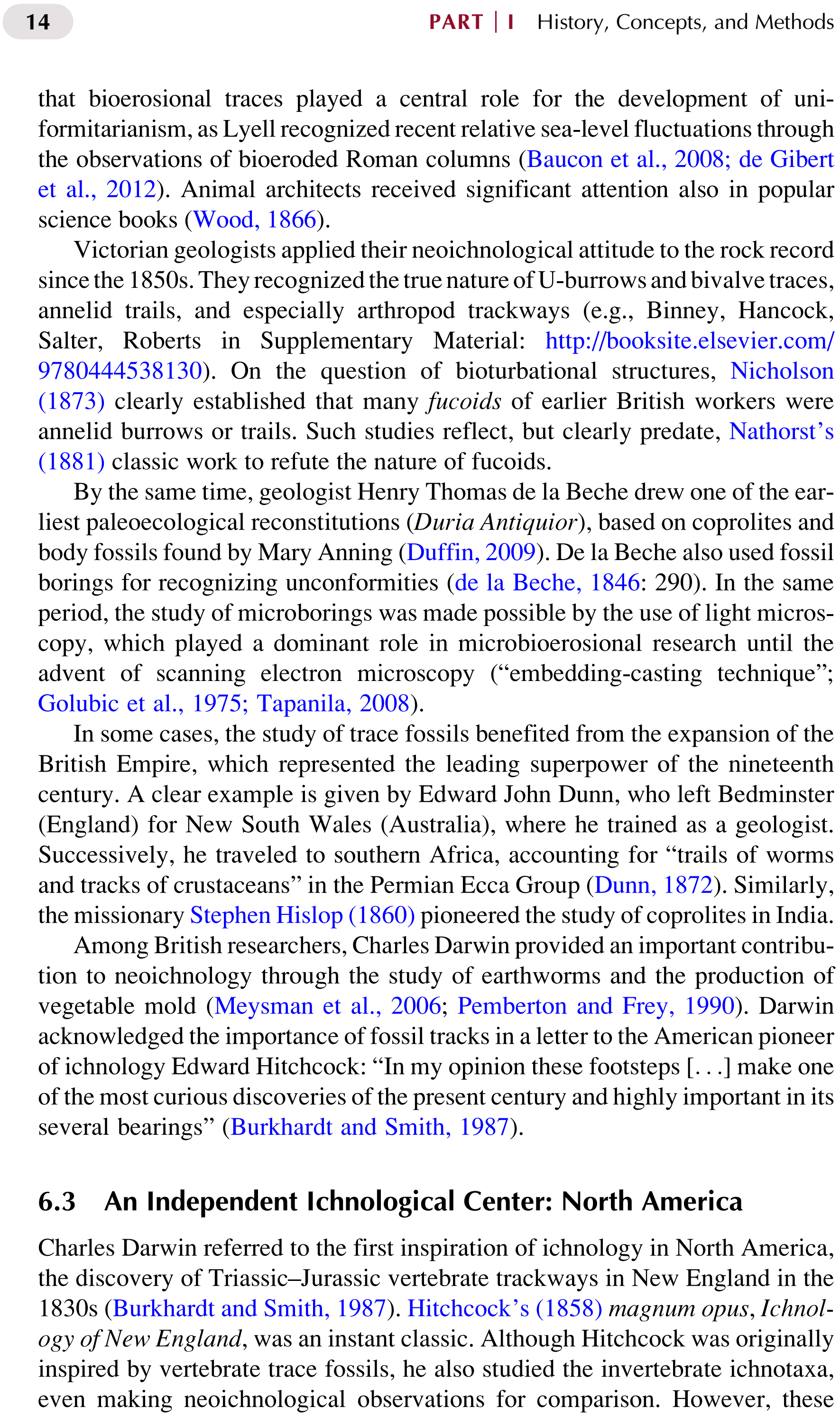
6.2 Zoophytes and other Popular Interpretations

Together with the dominant botanical hypothesis, the interpretation of trace fossils followed three other themes, namely, as zoophytes (plant-like animals); as worm-like body fossils; and as true invertebrate burrows, tracks, and trails.

The plant-like aspect of branched burrows suggested the zoophyte interpretation, which appeared even before Brongniart's (1823) seminal paper. Indeed, Webster (1814) appears to have been the first to interpret *Thalassinoides paradoxica* and *Ophiomorpha* as alcyonarian cnidarians. The "zoophyte" interpretation was usually applied to such burrows as *Oldhamia* (Forbes, 1848). The zoophyte interpretation had a particular success in eastern Europe. For instance, Zaręczny (1878) described *Spongia sudolica* from the Cretaceous marls near Cracow. As the etymology may suggest, the trace fossil was considered a sponge, being later included in *Spongeliomorpha* (Raciborski, 1890). Alongside to the description of several fucoids from Russia, Estonia, and Ukraine, Eichwald (1860–1968) presented *Paleodictyon* (his *Cephalites maximus*) as a sponge. A less conspicuous number of trace fossils were described as body fossils of annelids. This is the case for *Nereites* MacLeay (1839) and "*Nemertilites*" (now *Scolicia*) *strozzii* (Savi and Meneghini, 1851), both interpreted as marine worms.

In the same years, a minor part of scholars suggested the ichnological nature of some trace fossils, but their morphological diversity was a particularly challenging subject. It is therefore not surprising that ichnological interpretations often coexisted with other explanations. For instance, Savi and Meneghini (1851) interpreted "*Nemertilites*" (now *Scolicia*) *strozzii* as a "giant marine worm" and *Chondrites* as seaweed, and in the same work, they admitted the ichnological origin of "*Nemertilites meandrites*" (possibly *Scolicia*). Specifically, they argued, "as it is impossible to see any animal remains, at least it is necessary to recognize the action of an animal, that is, a physiological imprint (*impronta fisiologica*)". This term is strongly reminiscent of d'Orbigny's "*emprintes physiologiques*" (d'Orbigny, 1849: 27–29). Another example is given by the paleobotanist Heer, who not only recognized several species of *Zoophycos*, *Chondrites*, and *Gyrophyllites* as fucoids, but also described *Wurmsteine* (*Helminthoiden*) as sediment-filled burrows of marine worms (Heer, 1876/1877; Supplementary Material: http://booksite.elsevier.com/9780444538130).

Britain was a very fertile ground for the fucoid hypothesis (i.e., Buckland, 1836), but Victorian geologists were also familiar with animal traces on modern tidal flats. For instance, Charles Lyell devoted some space in his *Principles of Geology* to explain burrowing mollusks (Lyell, 1833: 288). It should also be noted



that bioerosional traces played a central role for the development of uniformitarianism, as Lyell recognized recent relative sea-level fluctuations through the observations of bioeroded Roman columns (Baucon et al., 2008; de Gibert et al., 2012). Animal architects received significant attention also in popular science books (Wood, 1866).

Victorian geologists applied their neoichnological attitude to the rock record since the 1850s. They recognized the true nature of U-burrows and bivalve traces, annelid trails, and especially arthropod trackways (e.g., Binney, Hancock, Salter, Roberts in Supplementary Material: http://booksite.elsevier.com/9780444538130). On the question of bioturbational structures, Nicholson (1873) clearly established that many *fucoids* of earlier British workers were annelid burrows or trails. Such studies reflect, but clearly predate, Nathorst's (1881) classic work to refute the nature of fucoids.

By the same time, geologist Henry Thomas de la Beche drew one of the earliest paleoecological reconstitutions (*Duria Antiquior*), based on coprolites and body fossils found by Mary Anning (Duffin, 2009). De la Beche also used fossil borings for recognizing unconformities (de la Beche, 1846: 290). In the same period, the study of microborings was made possible by the use of light microscopy, which played a dominant role in microbioerosional research until the advent of scanning electron microscopy ("embedding-casting technique"; Golubic et al., 1975; Tapanila, 2008).

In some cases, the study of trace fossils benefited from the expansion of the British Empire, which represented the leading superpower of the nineteenth century. A clear example is given by Edward John Dunn, who left Bedminster (England) for New South Wales (Australia), where he trained as a geologist. Successively, he traveled to southern Africa, accounting for "trails of worms and tracks of crustaceans" in the Permian Ecca Group (Dunn, 1872). Similarly, the missionary Stephen Hislop (1860) pioneered the study of coprolites in India.

Among British researchers, Charles Darwin provided an important contribution to neoichnology through the study of earthworms and the production of vegetable mold (Meysman et al., 2006; Pemberton and Frey, 1990). Darwin acknowledged the importance of fossil tracks in a letter to the American pioneer of ichnology Edward Hitchcock: "In my opinion these footsteps [. . .] make one of the most curious discoveries of the present century and highly important in its several bearings" (Burkhardt and Smith, 1987).

6.3 An Independent Ichnological Center: North America

Charles Darwin referred to the first inspiration of ichnology in North America, the discovery of Triassic–Jurassic vertebrate trackways in New England in the 1830s (Burkhardt and Smith, 1987). Hitchcock's (1858) *magnum opus*, *Ichnology of New England*, was an instant classic. Although Hitchcock was originally inspired by vertebrate trace fossils, he also studied the invertebrate ichnotaxa, even making neoichnological observations for comparison. However, these terrestrial trace fossils were difficult to compare with the Paleozoic examples found by later generations of geologists and, until continental ichnology emerged as a field of research, Hitchcock's work on invertebrate traces lay fallow.

Other early workers on invertebrate trace fossils, for example, James Hall, Elkanah Billings, and Léo Lesquereux (Supplementary Material: http://booksite.elsevier.com/9780444538130) usually ascribed them to fucoids. The first trace fossil to be named in North America was *Fucoides* (*Cladorytes*, now *Arthrophycus*) *alleghaniensis* (Rindsberg and Martin, 2003) from the Silurian of Pennsylvania, but it was set within the realm of botany, not ichnology. James Hall, who had firsthand experience of the New England coast, did figure a few Paleozoic "molluscan" trails. Hall taught many North American geologists, and they followed his interpretation of *fucoids*.

Accordingly, the development of ichnology in North America radiated from two independent centers: a Canadian School of professional geologists centered at the Geological Survey of Canada, and a partly New York-inspired Cincinnati School consisting of self-taught paleontologists (Pemberton et al., 2007). Both schools had impact and worked somewhat in isolation from active European researchers. This isolation not only had its negative aspects but also allowed American workers to explain these obscure structures in novel ways.

The Canadian geoscientists William Logan and J. William Dawson, who were well acquainted with the seashore, were quick to dismiss the fucoid origin and ready to consider other options. This resulted in insightful observations such as Dawson's interpretation of *Rusophycus*, *Arthrophycus*, and *Nereites* as products of burrowing trilobites. The interpretation of *Rusophycus* as a trilobite trace predated the first European to come to the same conclusion by almost 15 years (Pemberton et al., 2007). Although these views were widely disseminated, for the most part Europeans did not agree, having already set their minds. However, when Logan similarly interpreted traces unknown in Europe, *Climactichnites* and *Protichnites* as locomotion traces, there was no disagreement that they were made by animals.

The Cincinnati School started work in a landscape as rich in fossils as to demand attention from amateurs, some of whom became authors. Samuel Almond Miller, C. B. Dyer, Uriah P. James, and others contributed to the roster of fucoids before Joseph F. James, a nephew of U. P. James, ushered in the Period of Reaction (Supplementary Material: http://booksite.elsevier.com/9780444538130).

6.4 The Rise of Vertebrate Ichnology

For its influence, Edward Hitchcock subsequently became known as the father of vertebrate ichnology. Nevertheless, he was not the first to study vertebrate tracks. The first scientific studies on vertebrate traces, which appeared in a series of short newspapers, magazines, and journal articles between 1828 and 1831, referred to tracks found in Permian sandstones in Scotland. First interpreted as turtle tracks, and therefore named *Chelichnus*, they attracted much attention and stimulated William Buckland, the first professor of Geology at Oxford, to conduct experiments with modern turtles walking in pastry dough. We now know these tracks to be those of mammal-like reptiles (synapsids) that inhabited ancient dune fields (Supplementary Material: http://booksite.elsevier.com/9780444538130). According to Häntzschel (1975: W2), Buckland's legacy includes the term "ichnology" itself.

In 1835, the famous "hand-shaped" track *Chirotherium* was reported from the Triassic of Germany before any equivalent skeletal remains were known. This gave rise to many fanciful interpretations, and it was not until the 1930s that it was convincingly attributed to an archosaur (Seilacher, 2007). Likewise, in 1836, Edward Hitchcock described the first vertebrate tracks known from North America, before the concept of dinosaurs was established in 1842. Famously, he named large, emu- to moa-sized Jurassic tracks from the Connecticut valley region as *Ornithoichnites*, implying that they were made by giant birds (Hitchcock, 1836). In naming tracks, he established the tradition of vertebrate ichnotaxonomy (naming tracks rather than body fossils) and his seminal work is frequently cited to this day.

During his scientific career, Hitchcock assembled a vast ichnological collection, housed at the Appleton Cabinet at Amherst. Hitchcock's ichnological cabinet served as a reference collection and attracted scientists from all over the world. Among others, these include the Italian geologist Capellini (1867) and the Austrian paleontologist Abel (1926), who studied the famous Upper Triassic vertebrate track sites of Connecticut and Massachusetts.

7. PERIOD OF REACTION

7.1 Fucoids *versus* Traces

What did begin to emerge in the late Age of Fucoids was an increased interest in invertebrate trace fossils as biogenic sedimentary structures. However, yet even where the fucoid hypothesis was rejected or modified, the ichnological interpretation was still not persuasive. Of crucial importance to the history of ichnology are the publications by Nathorst (Supplementary Material: http://booksite.elsevier.com/9780444538130; Fig. 3C). Indeed, his 1881 work is seen as a major watershed in the history of ichnology in that it generated a broad acceptance for a trace-fossil origin of various structures that at the time were considered remains of plants or animal body fossils (Osgood, 1970).

Nathorst conducted systematic neoichnological experiments by introducing various animals into dishes with plaster of paris and observing their traces. Nathorst pointed out the correspondence between modern invertebrate traces and fucoids, challenging traditional ideas about how trace fossils formed. Among Nathorst's arguments was also the common preservation along bedding planes and in such pronounced relief that he found an algal origin impossible. He also remarked on the absence of any organic material.

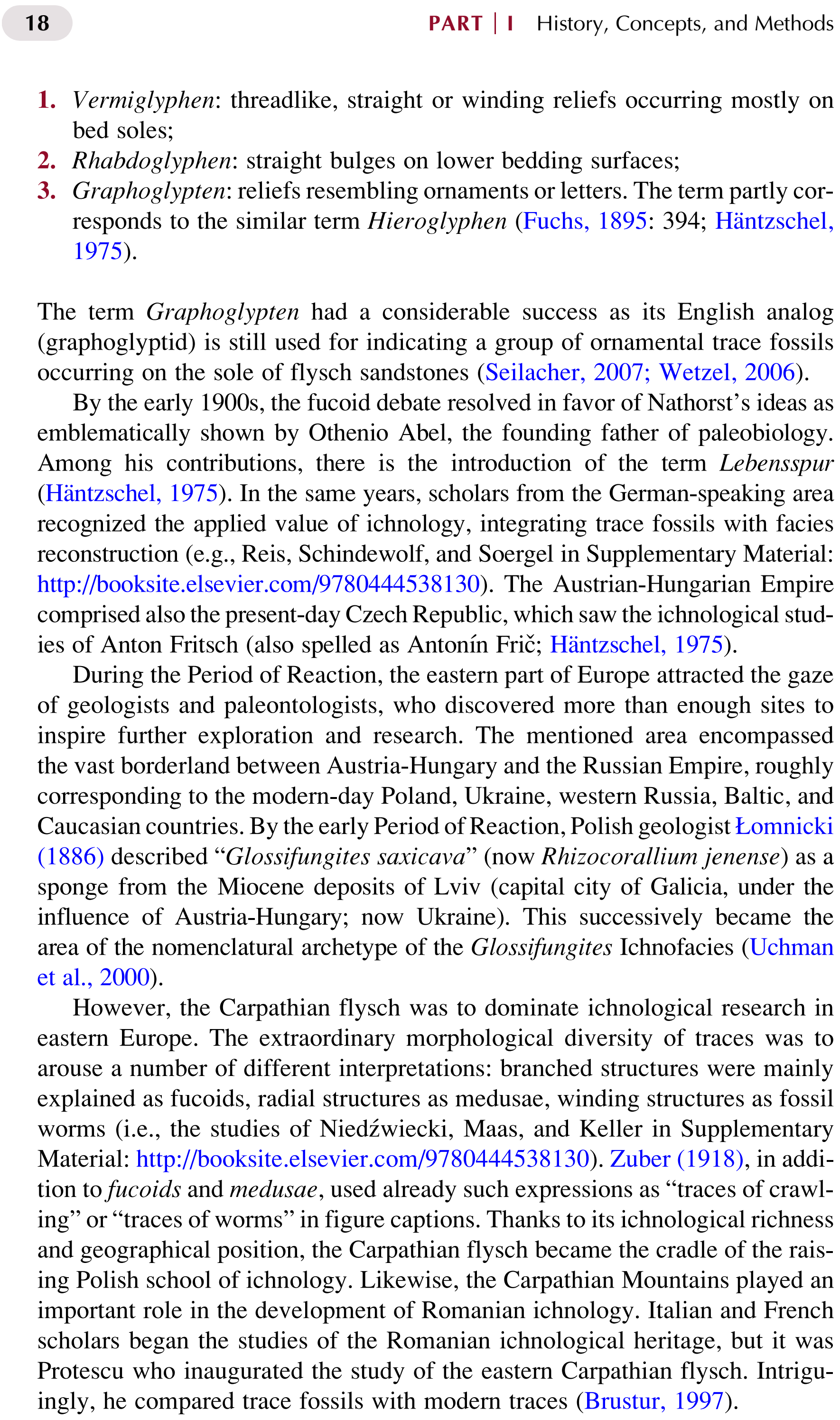
Thanks to the extended summary in French that accompanied his work, Nathorst provided the impetus for the development of paleoichnology. Throughout this historical stage, discussion and argument over the nature of fucoids took on increasing prominence among scientists. In fact, by the late nineteenth century, French scholars began to mount a sustained attack on the rising paleoichnology and published voluminous descriptive and taxonomic works (e.g., de Saporta, 1882; Lebesconte, 1883). Only in 1886 did Nathorst take part in the discussion (Cadée and Goldring, 2007). In holding his opinion against such authorities as Lebesconte and de Saporta, Nathorst showed his sturdy independence of judgment.

7.2 The Period of Reaction: a Worldwide Phenomenon

The Period of Reaction was a worldwide phenomenon, although not all of the elements of debate appeared everywhere in the same order and with the same strength. For instance, the reaction against the fucoid interpretation had much less impact in Britain than on the continent where the extensive fucoid monographs of Brongniart, Heer, and de Saporta had been published. Nathorst's invertebrate interpretation was readily accepted by several workers, such as Keeping (flysch traces), Taylor, Smith, Bather (worm trails and burrows), and Beasley, Smith (arthropod tracks; Supplementary Material: booksite.elsevier.com/9780444538130).

Conversely, the Iberian Peninsula saw one of the strongest advocates of the fucoid interpretation, the Portuguese geologist Joaquim Nery Delgado. However, by the early 1900s, Delgado interpreted *Cruziana* as "crustacean trails"; *Nereites* as "annelid trails"; and *Skolithos* as "worm burrows" (Supplementary Material: http://booksite.elsevier.com/9780444538130). Spanish workers maintained vague interpretations, due mostly to the controversial explanations that characterized the Period of Reaction (e.g., Palacios, 1918). Within a recently unified Italy, Federico Sacco published his *Notes on Italian Palaeoichnology* (Sacco, 1888), but geological literature often referred to fucoids. Other influential studies were performed by Peruzzi, Gabelli, Stoppani, and Gortani (Supplementary Material: http://booksite.elsevier.com/9780444538130).

During most of the Period of Reaction, the geopolitical scenario of central-eastern Europe was dominated by the Austrian-Hungarian Empire. Despite its multinational nature and the contentious questions concerning language, the Austrian-Hungarian Empire contributed to spread the use of German, which rapidly became one of the most important languages of science and scholarship (Ammon, 1998). As Chew (2009) argued, in many disciplines, knowledge of German became a basic requirement up to 1945. In this context, Austrian geologist Theodor Fuchs added valid arguments in deciphering the true nature of *fucoids* as burrows, although this view was controversial for a long time (Supplementary Material: http://booksite.elsevier.com/9780444538130). Fuchs (1895) introduced also the first classification of trace fossils, based on flysch trace fossils. He distinguished three family groups:



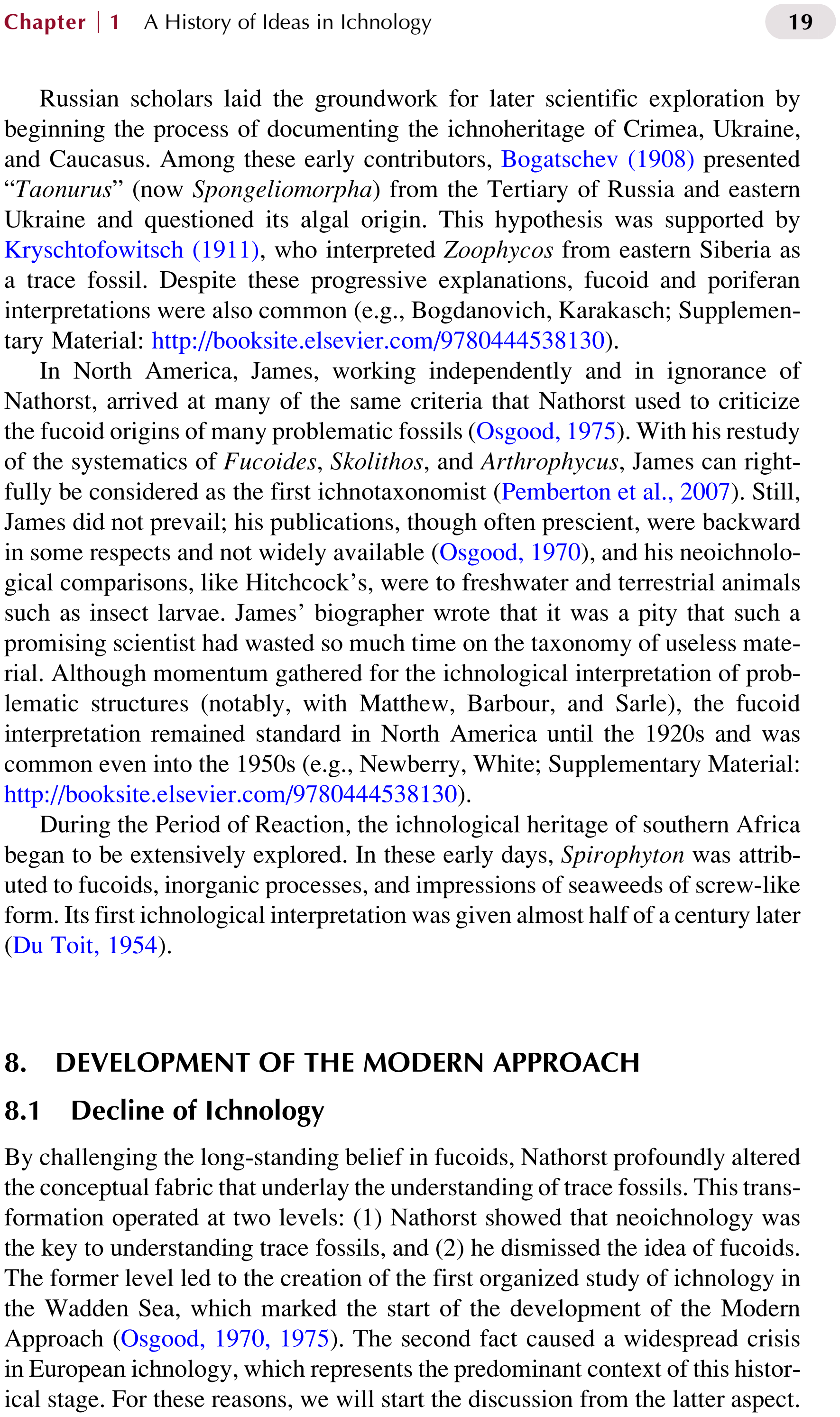
1. *Vermiglyphen*: threadlike, straight or winding reliefs occurring mostly on bed soles;
2. *Rhabdoglyphen*: straight bulges on lower bedding surfaces;
3. *Graphoglypten*: reliefs resembling ornaments or letters. The term partly corresponds to the similar term *Hieroglyphen* (Fuchs, 1895: 394; Häntzschel, 1975).

The term *Graphoglypten* had a considerable success as its English analog (graphoglyptid) is still used for indicating a group of ornamental trace fossils occurring on the sole of flysch sandstones (Seilacher, 2007; Wetzel, 2006).

By the early 1900s, the fucoid debate resolved in favor of Nathorst's ideas as emblematically shown by Othenio Abel, the founding father of paleobiology. Among his contributions, there is the introduction of the term *Lebensspur* (Häntzschel, 1975). In the same years, scholars from the German-speaking area recognized the applied value of ichnology, integrating trace fossils with facies reconstruction (e.g., Reis, Schindewolf, and Soergel in Supplementary Material: http://booksite.elsevier.com/9780444538130). The Austrian-Hungarian Empire comprised also the present-day Czech Republic, which saw the ichnological studies of Anton Fritsch (also spelled as Antonín Frič; Häntzschel, 1975).

During the Period of Reaction, the eastern part of Europe attracted the gaze of geologists and paleontologists, who discovered more than enough sites to inspire further exploration and research. The mentioned area encompassed the vast borderland between Austria-Hungary and the Russian Empire, roughly corresponding to the modern-day Poland, Ukraine, western Russia, Baltic, and Caucasian countries. By the early Period of Reaction, Polish geologist Łomnicki (1886) described "*Glossifungites saxicava*" (now *Rhizocorallium jenense*) as a sponge from the Miocene deposits of Lviv (capital city of Galicia, under the influence of Austria-Hungary; now Ukraine). This successively became the area of the nomenclatural archetype of the *Glossifungites* Ichnofacies (Uchman et al., 2000).

However, the Carpathian flysch was to dominate ichnological research in eastern Europe. The extraordinary morphological diversity of traces was to arouse a number of different interpretations: branched structures were mainly explained as fucoids, radial structures as medusae, winding structures as fossil worms (i.e., the studies of Niedźwiecki, Maas, and Keller in Supplementary Material: http://booksite.elsevier.com/9780444538130). Zuber (1918), in addition to *fucoids* and *medusae*, used already such expressions as "traces of crawling" or "traces of worms" in figure captions. Thanks to its ichnological richness and geographical position, the Carpathian flysch became the cradle of the raising Polish school of ichnology. Likewise, the Carpathian Mountains played an important role in the development of Romanian ichnology. Italian and French scholars began the studies of the Romanian ichnological heritage, but it was Protescu who inaugurated the study of the eastern Carpathian flysch. Intriguingly, he compared trace fossils with modern traces (Brustur, 1997).



Russian scholars laid the groundwork for later scientific exploration by beginning the process of documenting the ichnoheritage of Crimea, Ukraine, and Caucasus. Among these early contributors, Bogatschev (1908) presented "*Taonurus*" (now *Spongeliomorpha*) from the Tertiary of Russia and eastern Ukraine and questioned its algal origin. This hypothesis was supported by Kryschtofowitsch (1911), who interpreted *Zoophycos* from eastern Siberia as a trace fossil. Despite these progressive explanations, fucoid and poriferan interpretations were also common (e.g., Bogdanovich, Karakasch; Supplementary Material: http://booksite.elsevier.com/9780444538130).

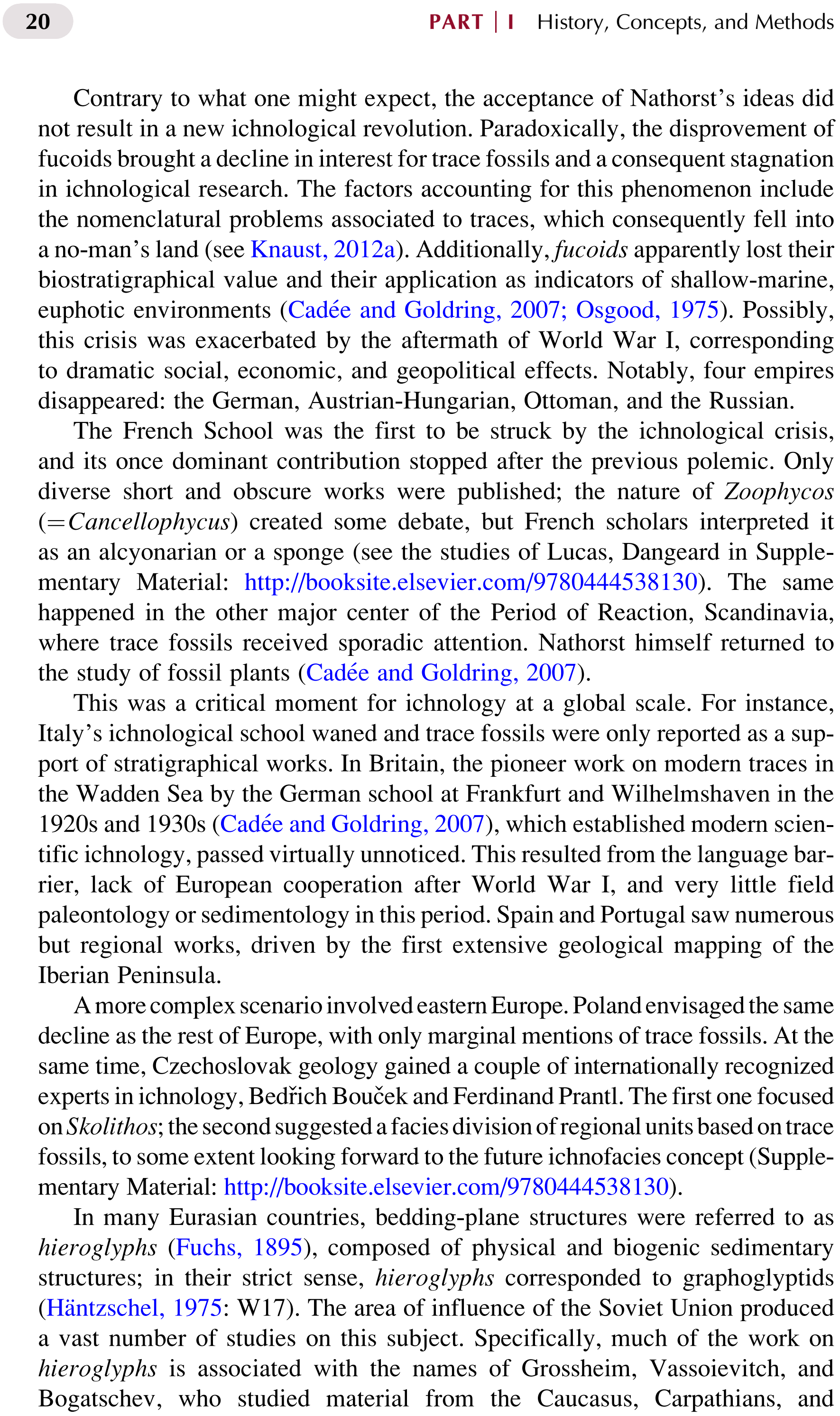
In North America, James, working independently and in ignorance of Nathorst, arrived at many of the same criteria that Nathorst used to criticize the fucoid origins of many problematic fossils (Osgood, 1975). With his restudy of the systematics of *Fucoides*, *Skolithos*, and *Arthrophycus*, James can rightfully be considered as the first ichnotaxonomist (Pemberton et al., 2007). Still, James did not prevail; his publications, though often prescient, were backward in some respects and not widely available (Osgood, 1970), and his neoichnological comparisons, like Hitchcock's, were to freshwater and terrestrial animals such as insect larvae. James' biographer wrote that it was a pity that such a promising scientist had wasted so much time on the taxonomy of useless material. Although momentum gathered for the ichnological interpretation of problematic structures (notably, with Matthew, Barbour, and Sarle), the fucoid interpretation remained standard in North America until the 1920s and was common even into the 1950s (e.g., Newberry, White; Supplementary Material: http://booksite.elsevier.com/9780444538130).

During the Period of Reaction, the ichnological heritage of southern Africa began to be extensively explored. In these early days, *Spirophyton* was attributed to fucoids, inorganic processes, and impressions of seaweeds of screw-like form. Its first ichnological interpretation was given almost half of a century later (Du Toit, 1954).

8. DEVELOPMENT OF THE MODERN APPROACH

8.1 Decline of Ichnology

By challenging the long-standing belief in fucoids, Nathorst profoundly altered the conceptual fabric that underlay the understanding of trace fossils. This transformation operated at two levels: (1) Nathorst showed that neoichnology was the key to understanding trace fossils, and (2) he dismissed the idea of fucoids. The former level led to the creation of the first organized study of ichnology in the Wadden Sea, which marked the start of the development of the Modern Approach (Osgood, 1970, 1975). The second fact caused a widespread crisis in European ichnology, which represents the predominant context of this historical stage. For these reasons, we will start the discussion from the latter aspect.



20 **PART | I** History, Concepts, and Methods

Contrary to what one might expect, the acceptance of Nathorst's ideas did not result in a new ichnological revolution. Paradoxically, the disprovement of fucoids brought a decline in interest for trace fossils and a consequent stagnation in ichnological research. The factors accounting for this phenomenon include the nomenclatural problems associated to traces, which consequently fell into a no-man's land (see Knaust, 2012a). Additionally, *fucoids* apparently lost their biostratigraphical value and their application as indicators of shallow-marine, euphotic environments (Cadée and Goldring, 2007; Osgood, 1975). Possibly, this crisis was exacerbated by the aftermath of World War I, corresponding to dramatic social, economic, and geopolitical effects. Notably, four empires disappeared: the German, Austrian-Hungarian, Ottoman, and the Russian.

The French School was the first to be struck by the ichnological crisis, and its once dominant contribution stopped after the previous polemic. Only diverse short and obscure works were published; the nature of *Zoophycos* (=*Cancellophycus*) created some debate, but French scholars interpreted it as an alcyonarian or a sponge (see the studies of Lucas, Dangeard in Supplementary Material: http://booksite.elsevier.com/9780444538130). The same happened in the other major center of the Period of Reaction, Scandinavia, where trace fossils received sporadic attention. Nathorst himself returned to the study of fossil plants (Cadée and Goldring, 2007).

This was a critical moment for ichnology at a global scale. For instance, Italy's ichnological school waned and trace fossils were only reported as a support of stratigraphical works. In Britain, the pioneer work on modern traces in the Wadden Sea by the German school at Frankfurt and Wilhelmshaven in the 1920s and 1930s (Cadée and Goldring, 2007), which established modern scientific ichnology, passed virtually unnoticed. This resulted from the language barrier, lack of European cooperation after World War I, and very little field paleontology or sedimentology in this period. Spain and Portugal saw numerous but regional works, driven by the first extensive geological mapping of the Iberian Peninsula.

A more complex scenario involved eastern Europe. Poland envisaged the same decline as the rest of Europe, with only marginal mentions of trace fossils. At the same time, Czechoslovak geology gained a couple of internationally recognized experts in ichnology, Bedřich Bouček and Ferdinand Prantl. The first one focused on *Skolithos*; the second suggested a facies division of regional units based on trace fossils, to some extent looking forward to the future ichnofacies concept (Supplementary Material: http://booksite.elsevier.com/9780444538130).

In many Eurasian countries, bedding-plane structures were referred to as *hieroglyphs* (Fuchs, 1895), composed of physical and biogenic sedimentary structures; in their strict sense, *hieroglyphs* corresponded to graphoglyptids (Häntzschel, 1975: W17). The area of influence of the Soviet Union produced a vast number of studies on this subject. Specifically, much of the work on *hieroglyphs* is associated with the names of Grossheim, Vassoievitch, and Bogatschev, who studied material from the Caucasus, Carpathians, and

Dagestan. Such studies started in the 1930s and significantly deepened the knowledge of trace fossils, although their exact nature was not always clear. For instance, Grossheim (1946) noted traces of crawling worms but considered *Paleodictyon* as a cast of mudcracks. Thanks to their abundance within the Carpathian flysch, *hieroglyphs* were also commonly reported in the Romanian geological literature. For instance, Mrazec compared *hieroglyphs* to modern insect and gastropod traces, pioneering neoichnological studies in Romania. Interestingly, Filipescu described *Paleodictyon* as a "burrow system" (Brustur, 1997). Despite these insightful interpretations, throughout the first half of the twentieth century, the major part of Romanian geologists used the term *fucoid* to indicate trace fossils.

A period of stagnation was experienced also on the other side of the world. In North America, ichnology was viewed as a minor branch of paleontology, and minor progress was made. Carroll Lane Fenton and his wife Mildred Adams Fenton were paleontologists who turned their careers to popular science writing—and who, like Dawson and Logan, had seashore experience that enabled them to propose plausible makers of Paleozoic trace fossils by use of actualistic reasoning. For example, they showed that phoronids could make *Skolithos linearis* (Supplementary Material: http://booksite.elsevier.com/9780444538130). Other influential studies included those of the Cincinnati-based Kenneth Caster (Devonian limuloid trackways), Lionel Brady (Permian arthropod trackways), and Benjamin F. Howell (*Skolithos* and other early Paleozoic burrows) (Supplementary Material: http://booksite.elsevier.com/9780444538130). The piecemeal nature of this work made progress slow; few attempts were made outside Europe to systematize ichnology at this time. However, the stage was set as the value of actualistic marine research, especially in Germany, France, and England, became more broadly appreciated.

In the same period, ichnology started blooming in South America and Asia. It should be emphasized, however, that these ichnological schools had a different development under different circumstances than European and North American ichnology. For this reason, Osgood's (1970, 1975) periodization serves here only as a chronological reference. South American ichnology went through a slow start. Trace fossils were only occasionally mentioned, almost invariably within the context of regional studies. The Uruguayan school teacher Lucas Rosselli represents an exception, as he accurately documented insect trace fossils from Paleogene paleosols in Uruguay (Roselli, 1938). These deposits host the world's most diverse paleosol ichnofauna, and Rosselli's studies are at the foundation of the present-day school of insect paleoichnology in Argentina and Uruguay. Likewise, Asian ichnological schools followed a gradual development. In India, few studies characterized the development of Modern Approach and the earliest years of the Modern Era. In these early years, Davitashili (1945) coined the term ichnocoenosis to indicate the traces of a biological community (biocoenosis); the term was also independently proposed by Lessertisseur (1956).

In the early stages of ichnological study in Japan, trace fossils were simply referred to as sand pipes or problematica. *Archaeozostera*, a trace fossil occurring in Cretaceous turbidites, has a place of relevance in the ichnological history of Japan. In Japanese folklore, this structure is referred to as *Shobu-ishi*, which relates to plants. Koriba and Miki (1931) assigned the name *Archaeozostera* and considered it a plant fossil of an ancestor of marine seagrass. Nevertheless, the most accepted hypothesis interprets *Archaeozostera* as a trace fossil (e.g., Seilacher, 2008). Ichnology in China started with the report of vertebrate footprints (Young, 1929) and *Cruziana* (Yin, 1932). During this stage, Chinese scholars had only a rudimentary knowledge of trace fossils and provided prevalently morphological descriptions.

8.2 The Senckenberg Marine Institute

The pictured scenario reveals a widespread crisis in almost all Europe and a slow development in the rest of the world. Nevertheless, this historical period is synchronously marked by major advances related to the Senckenberg Laboratory, the first marine institute devoted to the comparison of modern and fossil depositional environments. Founded by Rudolf Richter in 1928 at Wilhelmshaven (Wadden Sea), it is regarded as the birthplace of modern ichnology (Cadée and Goldring, 2007).

What prompted this change in the way of studying traces was a combination of factors. Translations and reviews of Lyell's *Principles of Geology* were published, especially in France and Germany, from the late 1830s onward (Vaccari, 1998). German geoscientists were particularly receptive to modern environments, as shown by the influential work of Johannes Walther (Middleton, 2003). Of further significance for neoichnology, Nathorst's work promptly penetrated the German-speaking area, as recognized by Fuchs (1895).

In this scientific context, Rudolf Richter developed a strong interest for tidal areas as open-air laboratories where one may see geology at work. For instance, he spent several weeks on a *Wohnbake* (a tidal palafitte-like observation post) with his wife Emma (Cadée and Goldring, 2007). It was probably during that and similar fieldwork that he sought a permanent facility for the study of modern environments. Richter fulfilled this idea in 1928, when he founded the "Senckenberg am Meer" Institute in Wilhelmshaven (Germany). From the very beginning of the institute, ichnology occupied a central place. Soon, the Senckenberg Marine Institute became renowned as a center for ichnology and a magnet for biologists and paleontologists alike.

As a result of his actualistic research, Richter coined the terms *Aktuopaläontologie* (Richter, 1928) and *bioturbate Textur* (Richter, 1952). The Senckenberg Marine Institute had profound and far-reaching effects on the history of ichnology, being a source of inspiration for generations of ichnologists. Richter's articles on modern analogs of *Skolithos* were influential for his contemporaries, such as the Fentons (Cadée and Goldring, 2007). In this regard, numerous

English reviews contributed to disseminate Richter's work outside from Germany (Cadée and Goldring, 2007).

When Richter was designated director of the Senckenberg Museum, Walter Häntzschel became his successor at Wilhelmshaven. Walter Häntzschel, who first worked on trace fossils from the Createceous of Saxony, led the Senckenberg Institution from 1934–1938 before he continued his ichnological work in Dresden (see Cadée and Goldring, 2007). In the same period, an important contribution originated far from Senckenberg: it was Othenio Abel's *Vorzeitliche Lebenspuren*, which became the standard reference book over the next 20 years (Abel, 1935; Osgood, 1975).

In 1938, Wilhelm Schäfer succeeded Häntzschel at Wilhelmshaven. Schäfer continued to develop the *Aktuopaläontologie* as an important branch of geosciences, with special focus on facies relationships. Unfortunately, the world was entering a tumultuous period, which culminated in the dramatic events of World War II. Ichnology suffered heavily from these years: Richter tried to reduce Nazi influence in Senckenberg, Häntzschel was drafted in a Russian prison camp, Schäfer was in military service, and *Senckenberg am Meer* was almost destroyed.

After the war, Häntzschel worked as a librarian in Hamburg, becoming an expert in ichnological literature (Cadée and Goldring, 2007). This opened the doors for his most influential contribution, the ichnological section of the Treatise of Invertebrate Paleontology (Häntzschel, 1975). In 1947, Schäfer started to rebuild the Marine Institute and its research facilities. Though never part of the Wilhelmshaven group, Adolf Seilacher had proficient contacts with Schäfer and Häntzschel (Seilacher, 2007). This cultural exchange, together with the studies on the Wadden Sea, formed the base for Seilacher's seminal papers, which initiated the Modern Era of Ichnology (Cadée and Goldring, 2007).

9. MODERN ERA

9.1 The Ethological Revolution

The Seilacherian approach of the early 1950s reshaped ichnology by opening up new pursuits unexpected in the classical approaches of the previous stages. Adolf Seilacher (Fig. 4A) significantly contributed to the conceptual framework of modern ichnology, establishing trace fossils as facies indicators. A considerable part of the conceptual innovations introduced by Seilacher evolved around one concept, *viz*. that trace fossils are a manifestation of behavior. On this side, Seilacher (1953) developed an ethological classification, consisting of basic categories named for the prevailing behavioral pattern. For instance, cubichnia correspond to resting traces. As Cadée and Goldring (2007) argued, Seilacher's ethological classification was possibly influenced

FIGURE 4 Important personalities of the Modern Era. (A) Adolf Seilacher. (B) James Howard. (C) Marian Książkiewicz.

by earlier taxonomical categorizations such as those by Richter and Krejci-Graf (see also Häntzschel, 1975: W17).

During the same years, ichnologists started to pay attention to the spatial arrangement of trace fossils. Seilacher (1953, 1964) and Martinsson (1965) developed two different toponomical classifications, both based on the spatial relationship between a trace fossil and its casting medium (see Bromley, 1996 and Rindsberg, 2012, for a detailed treatment of both classifications). The set of terms introduced by Seilacher and Martinsson were rapidly adapted as a powerful and easy-to-use descriptive tool.

In his forward-looking article, Häntzschel (1955) recognized the value of the *Spuren-Vergesellschaftung* (trace-fossil association) for the characterization of sedimentary environments and *Ichno-Fazies*. These principles were emphasized by Seilacher's ethological approach, stating that trace fossils reveal fossil behavior and, as such, can be modified by the environment. Seilacher discerned the divergence between shallow-marine and deep-sea trace-fossil assemblages at a global scale and throughout the Phanerozoic (Pemberton et al., 2001; Seilacher, 2007). These propositions were the cornerstone for the ichnofacies concept, originally consisting of six sets of traces named for a characteristic ichnotaxon and related to a bathymetric gradient (Seilacher, 1967). Ichnofacies are distinctive, recurring ethological groupings of traces with specific environmental significance. Initially, paleobathymetry was the principal controlling factor, but more environmental implications underlie the modern concept (i.e., substrate consistency, hydrodynamics, turbidity, food resources; MacEachern et al., 2007, 2012).

Seilacher built the archetypal ichnofacies on a great deal of empirical observations (Seilacher, 2007: 205). Indeed, the ichnofacies concept was chronologically preceded by contacts with Schäfer and Häntzschel at the Senckenberg

Institute in Wilhelmshaven, examination of flysch ichnocoenoses in Italy, and an expedition to the Salt Range in Pakistan (Seilacher, 2007: VII). Later, Seilacher has put much effort in the use of trace fossils for paleoecological reconstructions; recognition of depositional environments; trace-fossil evolution; and ichnostratigraphy, ideas, and results which are manifested in his book on *Trace Fossil Analysis* (Seilacher, 2007).

It is important to point out that, in the same period, the school of researchers of the Senckenberg Marine Institute continued to achieve significant results, among which are the works of Häntzschel, Schäfer, Reineck, Dörjes, and Hertweck (Supplementary Material). In particular, Reineck (1963) established a classification of bioturbation from the North Sea as the basis of the modern bioturbation index scheme (Knaust, 2012b). Based on neoichnological studies in the North Sea and on Sapelo Island (Georgia, USA), Günther Hertweck developed methods for the analysis of ichnocoenoses in the light of their sedimentological context, environmental significance, and facies zonation (Hertweck, 1970, 1972). This approach was later developed into the study of ichnofabrics, a concept widely used today (Ekdale et al., 2012). An important milestone in the history of ichnology is the *Trace Fossils and Problematica* volume by Häntzschel. Its second edition (Häntzschel, 1975), chronologically corresponding with other seminal contributions about trace fossils (Basan, 1978; Crimes and Harper, 1970; Frey, 1975) and the history of ichnology (Osgood, 1975; Sarjeant, 1974), broadly defines the limit of the early Modern Era.

9.2 Early Modern Era: A New Impetus for the Study of Traces

Ichnology owes an immense debt to Seilacher, not only for the development of clear goals and methods (Osgood, 1975), but also for giving new impetus to the study of trace fossils. Indeed, in many regions, the resurgence of interest in trace fossils was largely due to the work of Seilacher. Seilacher had frequent contacts with Jacques Lessertisseur in France; Roland Goldring in Britain; and Richard Osgood, among others, in the United States. Osgood (1975) pointed out that, as early as 1956, Lessertisseur authored *Traces fossiles d'activité animale et leur signification paléobiologique*, which gave an excellent panorama of the discipline and reviewed the German work of Seilacher in French. This important volume initiated the Modern Era in France although, despite the recognized importance of trace fossils, ichnology was not considered as a major discipline of the earth sciences.

Goldring et al. (2000) indicated that the development of modern ichnology in Britain emerged from three main phases:

1. The pioneer work of Scott Simpson, who was familiar with the pre-World War II work of Richter's Frankfurt School. From 1955 to 1956, Simpson was the Ph.D. supervisor of Roland Goldring, who met many of the leaders

of the Senckenberg School of researchers, including Richter, Häntzschel, Schäfer, Seilacher, and Reineck (Pollard, 2007).

2. Seilacher's visit in 1962 and subsequent publication of his work in English. During the 1960s, Roland Goldring, George Farrow, Peter Crimes, James Harper, Richard Bromley, and J. I. Chisholm gave a new impulse to ichnology, applying trace fossils to sedimentology, facies analysis, stratigraphical correlation, study of hardgrounds, and core analysis (Supplementary Material: http://booksite.elsevier.com/9780444538130).
3. The First International Trace Fossil Meeting (Liverpool, 1970), which resulted in the volume *Trace Fossils* (Crimes and Harper, 1970), provided a great stimulus to British ichnologists.

The seminal publications of Adolf Seilacher in Germany and Jacques Lessertisseur in France during the 1950s did not have as immediate an impact in North America as they did in Europe, though Ager, Goldring, Simpson, and others were inspired by it in England. When the new ideas were presented in English, geologists in North America began to pay attention. It was Seilacher's demonstration that trace fossils could be used as bathymetric indicators, presented at the Annual Meeting of the Geological Society of America in Cincinnati in 1962, that seized the attention of American researchers. This was a seminal talk indeed, for Seilacher inspired Richard Osgood to begin his innovative dissertation, published in 1970 as *Trace Fossils of the Cincinnati Area*. This work emphasized the relationship of formal ichnotaxa to behavior as opposed to morphology and still ranks as one of the most influential ichnological studies ever performed.

Geologists of the Humble Petroleum Company (later Exxon) invited Seilacher to return to the United States for a summer to explore trace fossils in critical outcrops and core. Graduate student James D. Howard accompanied him and was inspired to conduct his own research in ichnology; and he inspired C. Kent Chamberlain. Seilacher's report was proprietary, but similar work was published (e.g., Seilacher, 1964: fig. 7). To place the significance of the bathymetric use of trace fossils in context, one must recall that until the work of Kuenen and Bouma, flysch was thought by many geologists to be of intertidal origin. Seilacher's research, along with that of micropaleontologists, sedimentologists, and structural geologists, allowed the discovery of vast resources of petroleum.

9.3 The Golden Age of North American Ichnology

The 1970s were a golden age for ichnology, and Robert W. Frey stands out as the most important ichnologist in North America, for he inspired a generation of researchers (Pemberton, 1992). Frey ascribed his initial inspiration in trace fossils to reading Derek Ager's *Principles of Paleoecology* (Rindsberg, 1999). Frey began his research in the Cretaceous chalk of the Western Interior Basin. Realizing that he needed experience with modern processes, he took a course in 1965 at the marine station at Beaufort, North Carolina, where he heard of James Howard

(Fig. 4B), a chance that eventually led to Frey's being hired by the University of Georgia. Several happy years of ichnological research followed at the University of Georgia Marine Institute on Sapelo Island, where the two joined forces and began to publish works that attracted a long series of graduate students. The petroleum-savvy James Howard invited Hans-Erich Reineck and other researchers from the Senckenberg Institute, resulting in two thematic volumes of *Senckenbergiana Maritima* and establishing Sapelo Island as a touchstone for neoichnology. Marginal-marine environments were extensively studied, leading to the discovery of stratigraphic traps in the Western Interior Basin and elsewhere, notably by Robert Weimer and his students at the Colorado School of Mines.

Howard established the *Ichnology Newsletter* in 1968 as a means to share recent findings, and this "gray" periodical, the first devoted to ichnology, has continued episodically to the present day. Frey corresponded with ichnologists throughout the world to put the basics of the science, especially its terminology, on a firm basis. He organized and edited the first summation of ichnology, *The Study of Trace Fossils* (Frey, 1975), the publication of which galvanized many students to enter the field. About the same time, the *Society of Economic Paleontologists and Mineralogists (now: Society for Sedimentary Research*, *SEPM)* established its *Trace Fossil Research Group*, which was influential during the crucial 1970s, when surges in the price of oil encouraged new methods of exploration. The recognized importance of ichnology in the petroleum industry fostered the study of trace fossils in core. Among the first to bring this approach in practice, C. Kent Chamberlain studied the core appearance of several ichnogenera (Bromley, 1996: 261) and made important achievements in the fields of ichnotaxonomy and paleoethology (Seilacher, 2007: 105).

Although this section deals with the early Modern Era, it is important to note that this golden age laid the basis of present-day North American ichnology, acting by direct transmission of knowledge. An intricate set of connections departs from John E. Warme, who focused on deep-sea ichnology and on bioerosion during the 1970s and 1980s. He taught Allan "Tony" A. Ekdale and others at Rice University before joining the faculty of the Colorado School of Mines, where he taught Andrew K. Rindsberg before moving onto sedimentological topics. Ekdale went on to the University of Utah and developed the ichnofabric approach together with long-term collaborator Richard Bromley. Together with J. F. Bockelie, the pair founded the long-lasting series of *International Ichnofabric Workshops* (see Ekdale et al., 2012); Bromley (1990) successively authored the influential textbook *Trace Fossils*: *Biology and Taphonomy*. Notably, the book was translated into German, Japanese, and Chinese (Bromley, personal communication). Another example is represented by Frey and Pemberton, who established a fruitful collaboration in the 1980s. Among other accomplishments, they taught one of the first courses in ichnology in North America and founded the first standard journal in the field, *Ichnos* (1990). Pemberton went on to the University of Alberta, teaching many of the most active researchers in petroleum ichnology and leading numerous workshops for petroleum companies around the world.

David Bottjer taught the first ichnological course in North America at the University of Southern California. He is probably best known for developing the tiering concept along with William Ausich, among many other accomplishments (Supplementary Material: http://booksite.elsevier.com/9780444538130). His students include many of today's most active ichnologists. The loose association of researchers connected with the Gerace Research Station on San Salvador (Bahamas) should be mentioned as well. Centered on H. Allen Curran of the Smith College, they include many accomplished researchers. Notably, Curran (1985) edited the first ichnological book treating all major depositional environments. Space does not allow a complete listing of every North American ichnologist here; our intent is to make clear that many of the most influential were inspired and trained by other ichnologists, and many indeed at a few centers.

9.4 The Eastern Bloc During the Early Modern Era

The social and political consequences of World War II influenced the development of ichnology. The rise of English and the decline of German as the international language of science created new channels for disseminating research at a global scale. On the geopolitical side, the Soviet Union and the United States emerged as rival superpowers after the end of the war. The so-called Eastern Bloc, under direct influence of the Soviet Union, developed an independent but complementary school of ichnology.

East German paleontologist Arno Herman Müller worked, based on his foundations of biostratinomy, on many ichnological issues from the Carboniferous, Permian, Triassic, and Cretaceous of Germany. In his classic textbook *Lehrbuch der Paläozoologie*, he dedicated a long appendix on the ichnology of invertebrates with focus on facies reconstruction (Müller, 1989, and references therein).

The Polish geologist Marian Książkiewicz (Fig. 4C) occupies a prominent place in the fields of ichnology and sedimentary geology. At the early beginnings of the Modern Era, Książkiewicz (1954) distinguished between pre- and post-depositional trace fossils; this fundamental idea was developed and popularized in the successive decade by Seilacher (see Seilacher, 2007: 206). Książkiewicz had also a profound impact in ichnotaxonomy; his numerous contributions were summarized in two classical works (Książkiewicz, 1970, 1977), in which trace fossils are classified in nine morphological groups. During his career, Książkiewicz formed one of the largest ichnological collections in the world, which has been studied by later workers, such as Kern and Uchman (Supplementary Material: http://booksite.elsevier.com/9780444538130). Książkiewicz also worked on paleoecology, stratigraphy, taphonomy, and paleoenvironmental significance of flysch trace fossils, trying to calibrate bathymetry of trace fossils on the basis of benthic Foraminifera (Supplementary Material: http://booksite.elsevier.com/9780444538130).

In the same period, an active group of researchers assembled in Warsaw. Centered on Radwański, Karaszewski, Orłowski, and Roniewicz, they focused particularly on early Paleozoic and Jurassic units from the Holy Cross Mountains. Notably, Radwański and Roniewicz developed the ichnocoenosis concept (Häntzschel, 1975: W2). Radwański pioneered the application of borings for defining paleoshorelines, although he did not follow the parataxonomical system in naming trace fossils (Häntzschel, 1975). Among other Polish contributions may be noted those by Nowak, Birkenmajer, Ślączka on ichnotaxonomy and ethological analysis of flysch trace fossils (Häntzschel, 1975).

As concerns the Russian academic scenario, the Modern Era saw many of the main characters of the previous stage. For instance, Vassoievich (1953) supported the ichnological nature of "fucoids" by analyzing several traces from the Caucasus and the Carpathians. Grossheim gave some correct interpretations but withdrew his opinion (Grossheim, 1946) about a mudcrack origin of *Paleodictyon* and placed it among biogenics (Imprints of snail eggs or imprints of algae). Similarly, he regarded *Ubinia wassoevitschi* as seaweed and interpreted some star-shaped trace fossils (*Lorenzinia*, *Atollites)* as imprints of ammonite shells (Supplementary Material: http://booksite.elsevier.com/9780444538130).

Within the middle to late twentieth century, ichnologists came to see Russia and central Asia as a place of interest for field investigation. This period of intense ichnological traveling was inaugurated between 1930 and 1960 by Hecker and Vialov, who described many invertebrate and vertebrate ichnotaxa from Russia, Ukraine, and central Asia (Häntzschel, 1975). Vialov also proposed a new classification of trace fossils (Häntzschel, 1975: W23–W24). However, his definition of trace fossils was broad, unfitting to the mainstream opinion (i.e., Bertling et al., 2006; Knaust, 2012a). Nevertheless, Vialov's ideas are still vivid in many Russian scientific institutions, partly because of his influential textbook (Mikuláš and Dronov, 2006; Vialov, 1966).

Between the late 1950s and 1970s, Romanian paleontology saw significant achievements in the field of vertebrate ichnology, for which reason Brustur (1997) distinguished a Stage of Vertebrate Footprints in Romanian Ichnology. An important figure of this stage is the academician Gheorghe Murgeanu, who promoted several sedimentological investigations, while Nicolae Panin gave a great impulse to paleoichnological studies. In the same period, Miroslav Plička, Ilja Pek, and Ivo Chlupáč contributed to Czech ichnology by ichnotaxonomical proposals, descriptions of trace fossils in unusual substrates and settings, and ethological interpretations (Supplementary Material: http://booksite.elsevier.com/9780444538130).

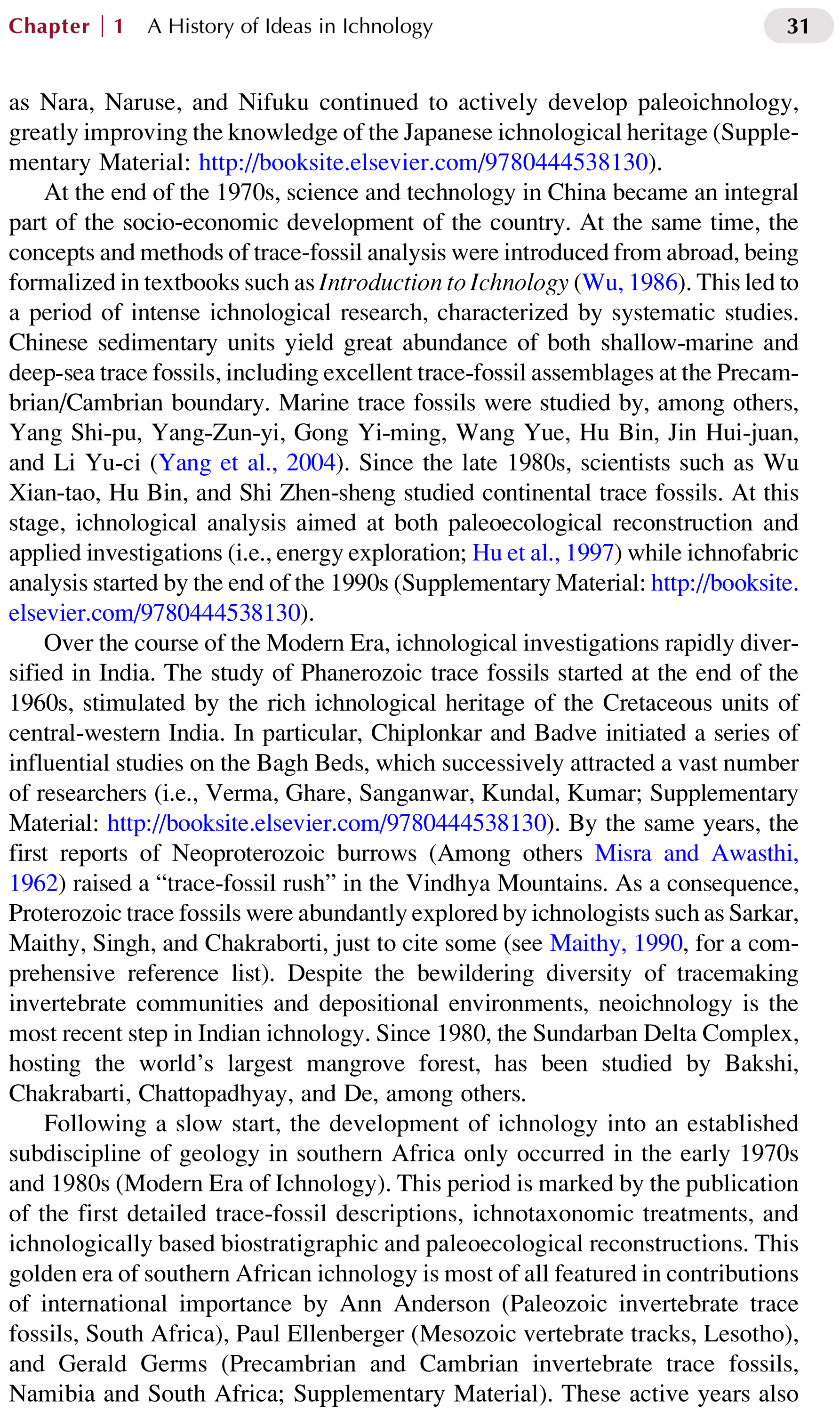
9.5 Global Ichnology

The fruitful advancements made at the European and North American schools were accompanied by a global momentum guiding the development of ichnology at a large scale. Nevertheless, mode and tempo of this expansion were slightly different in Asia, South America, and Australia with respect to the other areas.

Between 1950 and 1965, Rodolfo Casamiquela and the Italian-Argentinean Joaquin Frenguelli opened the avenues for the development of modern South American ichnology. While previous studies mostly mentioned trace fossils as accessory components, their works were entirely devoted to ichnology (Supplementary Material). The birth of South American Ichnology took place between the 1960s and the 1980s and is illustrated by the work of researchers in Argentina, Venezuela, and Brazil. Although the scope of some of these studies is still mostly regional, trace fossils moved from the margins to the core. This tendency undoubtedly reflected global developments in the discipline, most likely the influential work of Adolf Seilacher, who was personally connected with some of the classic figures of this age during his frequent trips to South America. At the same time that Borrello undertook his research in Argentina, Macsotay (1967) dealt with Cenozoic turbidite trace fossils from Venezuela. Macsotay's work gave a strong impulse to the use of trace fossils in paleoenvironmental reconstructions, particularly oriented to the flourishing oil industry in Venezuela, an applied side of ichnology that was subsequently explored by another Venezuelan ichnologist, Nicolas Muñoz. In the same period, Rodolfo Casamiquela and the Italian-Brazilian priest Giuseppe Leonardi investigated vertebrate ichnology (see Fernandes et al., 2002, for a comprehensive bibliographic review).

The next phase of studies within this age took place in the 1970s and 1980s, particularly with the work by Florencio Aceñolaza and his research associates in the Precambrian and early Paleozoic units of north-western Argentina. In the same years, there was a rapid development of Brazilian invertebrate ichnology, as shown by multiple contributions of Gerardo Muñiz and Antonio Fernandes (Fernandes et al., 2002). In Brazil, new studies were undertaken during the 1980s by Henrique Godoy Ciguel in Paleozoic units and Ismar de Souza Carvalho, mostly on vertebrate ichnology (Fernandes et al., 2002). Among other Argentinean contributions may be noted those by Ricardo Alonso on vertebrate ichnology, Jose Laza on ant trace fossils, Poiré on the sedimentological application of trace fossils, and Luis Buatois and Gabriela Mángano whose multifaceted work is summarized in a textbook (Supplementary Material: http://booksite.elsevier.com/9780444538130).

On the other side of the ocean, Asian ichnology followed a composite development, to some extent comparable to the recent history of South American ichnology. In Japan, trace fossils have received vague interpretations ("sand pipes", "problematica") since the 1960s, when the description and taxonomy of some Japanese trace fossils were carried out by Katto, Shuto, and Shiraishi (Supplementary Material: http://booksite.elsevier.com/9780444538130). During the early 1970s and 1980s, there was an increased interest in trace fossils as environmental indicators. For example, Kikuchi (1972) suggested the use of "white vermiform trace fossils" (successively identified as *Macaronichnus segregatis*) for recognizing beach environments. Studies on paleoethology and tracemaking mechanisms began in the 1980s with Kotake, famed for his model of *Zoophycos* (Kotake, 1989). In the following years, scientists such



as Nara, Naruse, and Nifuku continued to actively develop paleoichnology, greatly improving the knowledge of the Japanese ichnological heritage (Supplementary Material: http://booksite.elsevier.com/9780444538130).

At the end of the 1970s, science and technology in China became an integral part of the socio-economic development of the country. At the same time, the concepts and methods of trace-fossil analysis were introduced from abroad, being formalized in textbooks such as *Introduction to Ichnology* (Wu, 1986). This led to a period of intense ichnological research, characterized by systematic studies. Chinese sedimentary units yield great abundance of both shallow-marine and deep-sea trace fossils, including excellent trace-fossil assemblages at the Precambrian/Cambrian boundary. Marine trace fossils were studied by, among others, Yang Shi-pu, Yang-Zun-yi, Gong Yi-ming, Wang Yue, Hu Bin, Jin Hui-juan, and Li Yu-ci (Yang et al., 2004). Since the late 1980s, scientists such as Wu Xian-tao, Hu Bin, and Shi Zhen-sheng studied continental trace fossils. At this stage, ichnological analysis aimed at both paleoecological reconstruction and applied investigations (i.e., energy exploration; Hu et al., 1997) while ichnofabric analysis started by the end of the 1990s (Supplementary Material: http://booksite.elsevier.com/9780444538130).

Over the course of the Modern Era, ichnological investigations rapidly diversified in India. The study of Phanerozoic trace fossils started at the end of the 1960s, stimulated by the rich ichnological heritage of the Cretaceous units of central-western India. In particular, Chiplonkar and Badve initiated a series of influential studies on the Bagh Beds, which successively attracted a vast number of researchers (i.e., Verma, Ghare, Sanganwar, Kundal, Kumar; Supplementary Material: http://booksite.elsevier.com/9780444538130). By the same years, the first reports of Neoproterozoic burrows (Among others Misra and Awasthi, 1962) raised a “trace-fossil rush” in the Vindhya Mountains. As a consequence, Proterozoic trace fossils were abundantly explored by ichnologists such as Sarkar, Maithy, Singh, and Chakraborti, just to cite some (see Maithy, 1990, for a comprehensive reference list). Despite the bewildering diversity of tracemaking invertebrate communities and depositional environments, neoichnology is the most recent step in Indian ichnology. Since 1980, the Sundarban Delta Complex, hosting the world’s largest mangrove forest, has been studied by Bakshi, Chakrabarti, Chattopadhyay, and De, among others.

Following a slow start, the development of ichnology into an established subdiscipline of geology in southern Africa only occurred in the early 1970s and 1980s (Modern Era of Ichnology). This period is marked by the publication of the first detailed trace-fossil descriptions, ichnotaxonomic treatments, and ichnologically based biostratigraphic and paleoecological reconstructions. This golden era of southern African ichnology is most of all featured in contributions of international importance by Ann Anderson (Paleozoic invertebrate trace fossils, South Africa), Paul Ellenberger (Mesozoic vertebrate tracks, Lesotho), and Gerald Germs (Precambrian and Cambrian invertebrate trace fossils, Namibia and South Africa; Supplementary Material). These active years also led to pioneering application of trace fossils to sedimentary facies interpretation and incorporation of neoichnological studies in trace-fossil interpretations (see works by Hobday, Mason, Shone, Smith, Stanistreet, Rust, and Turner; Supplementary Material: http://booksite.elsevier.com/9780444538130).

10. CONCLUSIONS AND DISCUSSION

10.1 Evolution of the Interpretation of Trace Fossils

The collection of numerous bibliographic resources allows building a database (Supplementary Material: http://booksite.elsevier.com/9780444538130), graphically resulting in a semiquantitative evolutionary tree of ichnology (Fig. 5). This "tree of ichnology" supports the reliability of the current periodization of the history of ichnology and shows very well the phases of ferment and stasis in

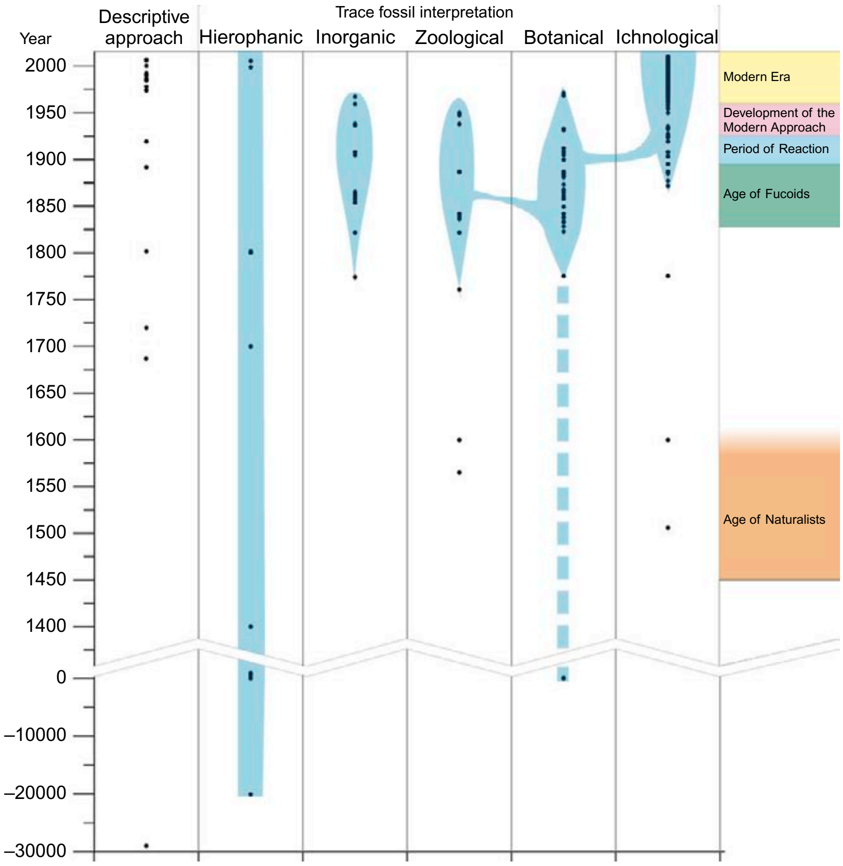


FIGURE 5 Tree of ichnology, showing the evolution in the interpretation of trace fossils. Dots correspond to bibliographic data in the Supplementary Material: http://booksite.elsevier.com/9780444538130.

ichnological research, that is, the crisis that followed the dismissal of fucoids (Fig. 5). Accordingly, the history of ichnology is paced by discontinuities and dominant interpretations; although at a narrower temporal scale, the development of ichnological concepts has an incremental (conservative) evolution.

10.2 Modern Centers of Ichnological Research

A great part of modern-day ichnological schools is best seen in the light of past historical events. The recent history of ichnology pictures a decline in working invertebrate ichnologists in many cultural areas, such as Italy, France, and Britain. While this critical situation is a recent phenomenon in Britain, the Italian and French decline is a direct by-product of the Age of Reaction. However, fields such as the ethology of trace fossils, facies analysis, and the study of arthropod trackways still remain active in these cultural areas. In contrast, new centers have arisen in Europe, South America, and Asia (e.g., Spain, Brazil, and China) as a direct consequence of the global impetus of the early modern era. Likewise, direct transmission of knowledge played an important role in the development of many ichnological schools, that is, the major part of active North American researchers was trained by other ichnologists during the golden age of the 1970s.

10.3 Modern Trends in Ichnology as a Legacy from the Past

Isaac Newton's famous admonition about standing on the shoulders of giants fits well with present-day ichnology. In fact, modern ichnology expanded substantially on the achievements of prior stages, which were influencing and guiding its contemporary trends. For instance, the ethological revolution of the 1950s established trace fossils as representing fossil behavior, and for this reason, they are nowadays crucial ingredients of both evolutionary paleoecology and paleobiology. The mentioned assumptions are valid even for those concepts explained by the impact of individual researchers, such as ichnofacies. Obviously, the ichnofacies concept primarily derived from the brilliant intuitions of Adolf Seilacher, although it would not exist in the present form without a set of antecedents such as Nathorst and the Wilhelmshaven school.

However, the ichnofacies approach is based on the interpretation of individual morphologies, and for this reason, it is difficult to apply to well cores (Seilacher, 2007: 201). Consequently, since the 1980s, some workers have encouraged consideration of those aspects of the texture that result from bioturbation and bioerosion: ichnofabrics (Bromley and Ekdale, 1986; Ekdale et al., 2012). The ichnofabric paradigm appeared to be an excellent methodology for paleoenvironmental reconstruction, complementary to the ichnofacies approach. It found particular application in the study of coalfields (i.e., Pollard, 1988) and hydrocarbon reservoirs (Knaust, 2012b; Taylor and Goldring, 1993).

Not only does the importance of historical awareness regard the question of memory, but also analogs from history can serve as a guide or inspiration for future insights. For instance, history reminds us of the cultural value of trace fossils. Already in the seventeenth century, Bauhin included invertebrate trace fossils in his tourist guide of Bad Boll, Germany (Seilacher, 2007) and Jacinto Pedro Gomes pioneered geoconservation of dinosaur tracksites in the nineteenth century (Supplementary Material: http://booksite.elsevier.com/9780444538130). Vertebrate tracksites play a major role in ichnological geotourism, although invertebrate geosites are also under development, providing new economic activities and additional sources of income, especially in rural regions (i.e., the Ichnological Park of Penha Garcia, Portugal; Neto de Carvalho et al., 2009).

As concerns scientific research, history shows us that almost every major idea in ichnology has depended on neoichnological observations; it is a pervasive influence. As Gingras et al. (2011) argued, the models we have for animal/sediment relations are largely based on neoichnological studies of the 1950s, 1960s, and 1970s. History warns us that for higher-resolution models, new studies on modern environments are required.

10.4 Disciplinary and Interdisciplinary Aspects in Ichnology

Owing to its nature, ichnology is a system of knowledge with a very well-defined nucleus (traditional ichnology) but with poorly defined borders. “Traditional ichnology” is often based on a geological background, but it blurs in a vast gray area shared with other disciplines. A typical example is given by recent traces, the study of which is often referred to biology, archeology, or forensic science, avoiding mention to ichnology (Baucon et al., 2008; Bromley, 1996: xi). This tendency can be traced back to the nineteenth century (i.e., Wood, 1866), and it is still influencing the study of traces. For instance, significant overlap exists between neoichnology and tracking, a discipline practiced by hunting guides, biologists, search-and-rescue teams, soldiers in war, and forensic investigators (Cunningham, 2004; Liebenberg et al., 2010). According to Liebenberg et al. (2010), tracking involves each and every indication of an animal’s presence. It typically includes not only traces (i.e., footprints, feces, burrows) but also other structures (i.e., eggs, auditory signs, etc.).

The present organization of scientific knowledge is a product of historical phenomena, and the study of traces makes no exception. While earth sciences had a prevalent role in the evolution of traditional ichnology, the development of modern tracking has been guided by military, zoological, and forensic specialties since the early nineteenth century. Despite of the commonality of subject matters and internal logic, ichnology is poorly connected to tracking, although recent cases of mutual recognition are recorded (i.e., Eiseman et al., 2010: ix; Lockley and Meyer, 2000: 1).

This scenario fits a long-standing trend in science: the uncommunicative piling-up of similar fields of research (Campbell, 1969). Such clustering of specialties results in lack of communication (i.e., unshared knowledge between ichnologists and biologists) and duplication of effort (i.e., ichnology and tracking embody their own separate terminology, nomenclature, and community). Additionally, this phenomenon produces knowledge gaps between or at the edges of disciplinary clusters. This is the case of root-related structures, which fall in a land of convergence between body and trace fossils, therefore posing a semantic problem in their categorization (Gregory et al., 2004). Although Sarjeant (1975) clearly recognized root systems as trace fossils, they still remain an understudied field. Yet, the assessment of plant trace fossils is typically limited to identifying such structures as “root traces” (Gregory et al., 2004).

Besides the aforementioned semantic issues, the interplay of interpretative, cultural, and historical factors explains the present state of plant ichnology. In fact, plant trace fossils offer significant interpretative challenges, while most of the active ichnologists have a prevailing zoological training (Gregory et al., 2004). Additionally, two distinct historical phenomena played a crucial role. First, Nathorst’s neoichnological experiments involved crustaceans, annelids, and bivalves (Cadée and Goldring, 2007), thus suggesting animals as the main actors in ichnology. Second, and of equal importance, the path between the Period of Reaction and the Modern Era was mediated by the Senckenberg Institute. Being a marine research center, it focused on marine invertebrates, consolidating the leaning toward animal tracemakers.

10.5 Ichnology as a Historical Product

An important point, for our understanding of ichnological innovation, is that the historical background plays a parallel role in respect to the scientific one. Paraphrasing Spencer (1896), ichnologists are the products of their societies, and their actions would be impossible without the conditions built before their lifetime. This question does not only involve catastrophic geopolitical events (e.g., the French Revolution), but also relies on the whole social and cultural scenario. For instance, success of an ichnological concept depends as much on the idea itself as on its recognition by the scientific community. A clear example comes from the roots of ichnology: the innovative ideas of Leonardo da Vinci did not influence the course of ichnology because he compiled handwritten manuscripts in mirror-image Italian, at a time when scientific communication rested on Latin treatises. It is therefore evident that the question of language and scientific communication plays a crucial role. Dominant schools of thought often coincide with the *lingua franca* of the moment: just coincidence or factual interrelation?

Technology has been a driving force both in the field of scientific communication and in the design of analytic tools. For instance, the invention of movable-type printing spreads the results of the Scientific Revolution and allowed the establishment of periodical reports such as the *Philosophical Transactions of the Royal Society*, one of the oldest scientific journals disseminating ichnological ideas. This historical aspect is clearly seen in the radical changes introduced by the advent of digital media. The impact of digital technologies such as internet, email, and PDF, brought the ability to easily move ichnological information between media and to access or distribute it remotely. Similarly, they implied a greater interconnectedness between researchers and encouraged social research. Nowadays, the *Skolithos* forum and the *Ichnology Newsletter* are digital-based media widely used for informal communications. However, in contrast with other scientific disciplines, ichnology is lacking a database of ichnological data. With increased accessibility to and elaboration upon advanced analytical techniques, new methods and perspectives in the study of trace fossils are recently emerging. These include molecular paleontology methods, 3-D visualization, and computer modeling of trace fossils, topoichnology, theoretical foraging (i.e., the studies by Gong, Hu, Si, Plotnick in Supplementary Material: http://booksite.elsevier.com/9780444538130 see Knaust, 2012b). It is desirable that these innovations should bring the same stimuli of the techniques designed and improved by the Senckenberg am Meer scientists (e.g., box cores, sediment peels, resin casts; Cadée and Goldring, 2007).

In conclusion, this historical synthesis shows that innovation in ichnology is fueled by a complex interplay of factors: not only scientific but also geopolitical, social, and technological. Historical knowledge of such factors will inspire new directions in further investigations and define the place of ichnology in our culture.

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Appendix C

Neoichnology of a barrier-island system: the Mula di Muggia (Grado lagoon, Italy)

Palaeogeography, Palaeoclimatology, Palaeoecology 375 (2013) 112–124

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Neoichnology of a barrier-island system: The Mula di Muggia (Grado lagoon, Italy)

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ABSTRACT

Barrier-islands are common landforms and biodiverse habitats, yet they received scarce neoichnological attention. This gap is tackled by studying the Mula di Muggia barrier-island system (Grado lagoon, Italy), focusing on morphology, ecology and ethology of individual traces. The following incipient ichnotaxa are identified: *Archaeonassa*, *Arenicolites*, *Bergaueria*, 'diverging shafts', *Helminthoidichnites*, *Lockeia*, *Macanopsis*, *Monocraterion*, *Nereites*, *Parmaichnus*, *Polykladichnus*, *Skolithos*, *Thalassinoides* and 'squat burrows'. Vertebrate (*Avipeda*-/*Ardeipeda*-like, *Canipeda*) and invertebrate tracks ('parallel furrows') are also described.
For each ichnotaxon, tracemaker and behavior are discussed, together with their position with respect to sediment barriers. Results suggest that sediment barriers impose a sharp contrast in terms of ichnological composition. Back-barrier is dominated by branched burrows (i.e. *Thalassinoides*, *Parmaichnus*), while the fore-barrier presents vertical and U-shaped burrows (*Arenicolites*, *Skolithos*). The environmental conditions of the back-barrier show that low-oxygen substrates favor intense bioturbation, provided that the water column is sufficiently oxygenated.

1. Introduction

Barrier-islands are elongate accumulations of unconsolidated sediment that separate the open sea from a landward restricted basin (Schwartz, 2005; Nichols, 2009). At present day, they are important coastal landforms, lining the 10% of the world's shoreline length (Stutz and Pilkey, 2011). Barrier-island systems are also well-represented in the rock record, being documented from the Mesoproterozoic onwards (Köykkä and Lamminen, 2011).

This conspicuous record is not the only reason of importance. In fact, barrier-islands are normally delimiting coastal lagoons, which play a major ecological role. In fact, they commonly provide a collection of habitat types for many species, housing high biodiversity levels and considerable biomass (Pérez-Ruzafa et al., 2011). Historically, barrier-island ecosystems supported numerous human communities, which often posed a threat to these fragile environments (Pérez-Ruzafa et al., 2011). At this regard, barrier-islands are also very sensitive to sea-level rise and storm patterns, thus providing clues to process changes through time (Mallinson et al., 2010).

Despite their inferred importance, barrier-island neoichnology is relatively understudied. In fact, in contrast to the large number of ecological and sedimentological studies, comparatively few barrier-island systems received neoichnological attention: the Wadden Sea (e.g. Cadée and Goldring, 2007; Hertweck et al., 2007), the Georgia Coast (e.g. Howard and Frey, 1985; Martin, 2013) and the New Brunswick Coast (Hauck et al., 2009).

There is therefore a need for neoichnological records of barrier-island systems, in terms of either autecology or synecology of bioturbation. This goes in parallel with another *tenet* of neoichnology, the need of studying tidal depositional systems, which received less ichnological study than wave-dominated environments (Buatois and Mángano, 2011).

The Grado-Marano lagoon (Italy) satisfies both requirements, presenting a vast complex of barrier-islands within a low-energy, tide-influenced regime. Within the Grado lagoon, the area of the Mula di Muggia provides optimal study conditions, given its particularly integer environment. More specifically, the goal of this study is to provide information on morphology, ecology and ethology of individual traces. Knowledge of these aspects is essential for the understanding of the ichnological system as a whole, which will be discussed quantitatively in Baucon and Felletti (2013–this issue).

2. Study area

The Grado-Marano lagoon, located along the Adriatic coast in Northern Italy, is composed of two communicating shallow basins known as the Grado and Marano lagoons. The lagoonal complex started to develop during the transgression that followed the end of the last glacial maximum. The Marano basin is older (5000 years BP), while the Grado lagoon formed in post-Roman times as the result of the diversion of the Isonzo River (Gatto and Marocco, 1992; Triches et al., 2011).

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At present day, the Grado-Marano lagoon extends between the Isonzo and Tagliamento rivers, stretching out for about 160 km^2. The lagoon is connected to the sea through inlets which subdivide barrier islands into six segments (Blasutto et al., 2005; Triches et al., 2011). The tidal magnitude is unusual for the Mediterranean Sea, with semidiurnal mean and spring tidal ranges of 65 and 105 cm respectively (Sconfietti et al., 2003; Covelli et al., 2008). Climate is temperate, influenced by ENE (Bora) and SE (Scirocco) winds (Fontolan et al., 2007).

Although the Grado-Marano system has been subject to significant anthropogenic pressure over the past centuries (Covelli et al., 2008), it remains one of the more pristine wetlands in the Northern Adriatic and Mediterranean Sea as well. In fact the lagoon of Grado and Marano is an important ecological system, both for the habitats of numerous vegetal and animal species (Sconfietti et al., 2003; Ferrarin et al., 2010; Barbone et al., 2011). In particular, the area of the Mula di Muggia Bank (Fig. 1) is recognized for its outstanding biodiversity, for which reason it is receiving environmental protection (i.e. Ramsar Convention, EU Natura 2000 Network; Barbone et al., 2011). Here, a shallow lagoon is fronted by sediment barriers (Fig. 2), which are significantly moderating the effects of waves and currents (Fig. 1). Two geomorphological domains are distinguished on the basis of position with respect to the sediment barriers:

1. the back-barrier (Fig. 3A) is dominated by muddy sand, commonly covered by dense seaweed meadows (Video 1). Laminated and filamentous microbial mats develop on intertidal flats.
2. the fore-barrier (Fig. 3B) present higher-energy conditions and rippled sand. Shell debris is locally abundant (Video 2).

In light of these geological and ecological features, the area of the Mula di Muggia is recognized as an ideal study site for the neoichnology of barrier-island systems.

3. Materials and methods

The study area was inspected between 2009 and 2010; subtidal areas were explored with a kayak. Major geomorphological features were traced with a GPS unit, which was also used to georeference selected photographic and video documentation (Fig. 1). Burrow architecture was analyzed by resin casting and manual excavation, further refining the morphological description of Baucon (2008).

4. Marginal marine ichnology

This section presents the morphological, biological and ethological features of the major ichnotaxa. 16 incipient ichnotaxa were recognized and divided into morphotypes on the basis of burrow morphology and size, after which they are named. A descriptive classification scheme, partly based on Książkiewicz (1977), is adopted to organize the ichnotaxa, to be considered as incipient in conformity with Bromley (1996, p. 164). Trace distribution is qualitatively described in Table 1.

4.1. Branched structures

4.1.1. Thalassinoides form XL (very large)

Description: Burrow networks with multiple openings, one of which presents a large sediment mound (diameter: 15–25 cm). Tunnel

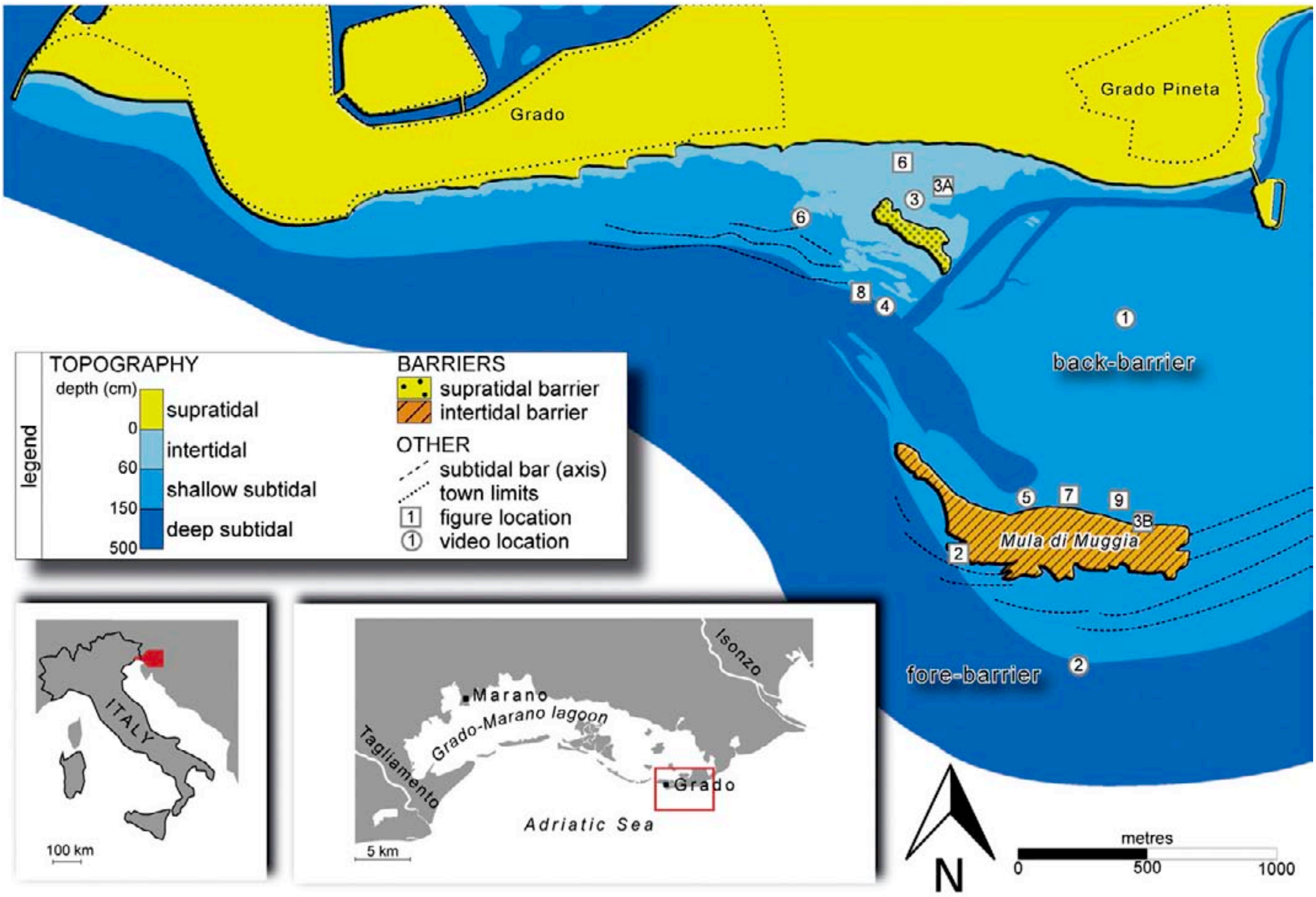

Fig. 1. Geographical and geological setting.

Fig. 2. The Mula di Muggia separates the back-barrier from the open sea. Photo location in Fig. 1.

section cylindrical to elliptical (diameter: 1.5–2 cm); vertical extension usually exceeding 40 cm. This morphotype is confidently assignable to the ichnogenus *Thalassinoides*, consisting of three-dimensional burrow networks connected to surface by vertical shafts (after Häntzschel, 1975).

Tracemaker: *Pestarella candida* (Crustacea: Decapoda).

Ethology: Presence of sediment mounds is indicative of sediment processing, suggesting deposit-feeding (Video 3). This interpretation is supported by different functional classifications of thalassinidean burrows (Griffis and Suchanek, 1991; Nickell and Atkinson, 1995).

4.1.2. *Thalassinoides form L (large)*

Description: Burrow networks characterized by funnel-like openings and chambers characteristically filled by seagrass. Burrow section circular (diameter: 1 cm); vertical extension ranging between 20 and 40 cm. Mounds are small (diameter: 5–10 cm), commonly absent. At a nearby site (Grado Punta Spin), Dworschak et al. (2005) realized complete resin casts of similar forms, revealing spiral shafts from which

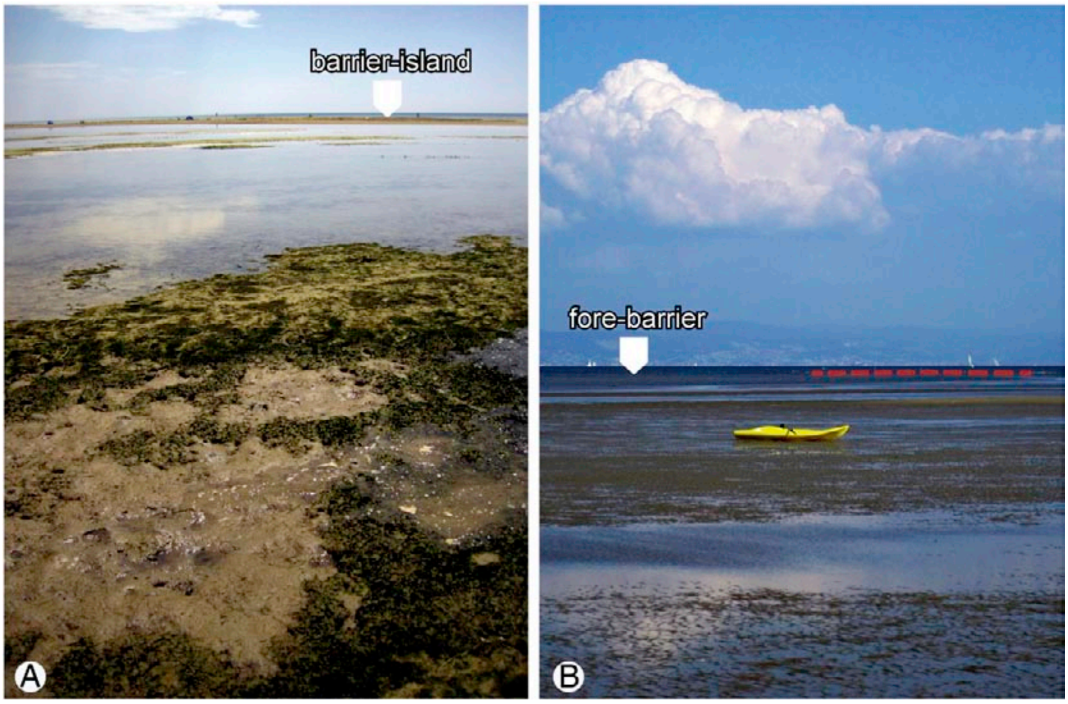

Fig. 3. Main geomorphological domains. (A) The sheltered back-barrier is characterized by muddy sands and biomats. (B) The fore-barrier is characterized by higher hydrodynamics and by numerous subtidal bars, one of which is evidenced by the dashed line. Photo location in Fig. 1.

Table 1
Qualitative abundance of ichnotaxa with respect to geomorphological domains: *** = very common, ** = common and * = occasional presence.

Morphological class	Ichnotaxon	Geomorphological domain	
		Fore-barrier	Back-barrier
Branched structures	*Thalassinoides* XL		***
	Thalassinoides *L*	*	*
	Parmaichnus	*	**
	Polykladichnus		***
U-burrows	*Arenicolites XL*	**	
	Arenicolites L	***	*
	Arenicolites S	*	**
Chambered burrows	'*Squat burrow*'		**
	Macanopsis		**
Plug-shaped burrows	*Bergaueria*	*	
Winding structures	*Helminthoidichnites*		*
Simple burrows	*Skolithos L*	**	
	Skolithos M	**	
	Skolithos S	**	*
	Skolithos XS	*	*
	Monocraterion	**	
Tracks and footprints	*Avipeda-/Ardeipeda*-like	*	*
	Canipeda	*	*
	Parallel furrows	*	*
Trails	*Archaeonassa*	**	**
	Nereites biserialis	**	
	Nereites uniserialis	**	
Miscellaneous group	'Diverging shafts'	**	**
	Lockeia S	**	**
	Lockeia XS	*	**
	Mottling		**

several debris-filled chambers branched off. Based on the general morphology, these structures are assignable to the ichnogenus *Thalassinoides*.

Tracemaker: *Pestarella tyrrhena* (Crustacea: Decapoda).

Ethology: According to Dworschak et al. (2005), *Pestarella tyrrhena* pulls seagrass debris into the burrow from the funnel-like openings, where it passively accumulates during low tide, for enriching the sediment around the burrow. Indeed, the tracemaker is mainly a sediment feeder (Dworschak et al., 2005).

4.1.3. *Parmaichnus*

Description: Y-shaped burrows consisting of an upper U-shaped section and a lower I-shaped part, both presenting short branches (Fig. 4A). Swellings are present at the base of the U-shaped sections. Tunnels circular in cross section. The same morphology was described by Dworschak (1987a) in adjacent study sites. Although the morphology may be reminiscent of *Psilonichnus*, the presence of swellings at the base of the U-shaped section is diagnostic of *Parmaichnus* (Pervesler and Uchman, 2009).

Tracemaker: *Upogebia pusilla* (Crustacea: Decapoda).

Ethology: Funnel-shaped openings, Y shape and circular tunnel cross section are consistent with current generation and suspension-feeding (Nickell and Atkinson, 1995). Such interpretation is corroborated by the classification scheme of Griffis and Suchanek (1991). Dworschak (1987a) shown that the main feeding activity of *Upogebia pusilla* occurs in one of the swellings (turning chambers), where the animal intercepts suspended matter with the setae of the pereiopods, acting as a basket. Although filter feeding is considered as the primary mechanism of obtaining food, the tracemaker shows also evidences of deposit-feeding and gardening (Dworschak, 1987a; Griffis and Suchanek, 1991). Pervesler and Hohenegger (2006) demonstrated that burrow segments connecting the steep entrance shafts in *Upogebia* are shoreline indicators, being oriented almost parallel to the shoreline.

4.1.4. *Polykladichnus*

Description: I- or U-shaped burrows with Y-shaped bifurcations connecting to the bedding surface (Fig. 4B). This morphology is consistent with the ichnogenus *Polykladichnus*, described by Schlirf and Uchman (2005) as vertical to steeply oblique tubes with single or multiple Y- or U-shaped bifurcation.

Tracemaker: *Nereis* (= *Hediste*) *diversicolor* (Polychaeta: Nereididae).

Ethology: *Polykladichnus* may have multiple functions, as the tracemaker *Nereis diversicolor* (Fig. 4C) uses a wide spectrum of feeding strategies: a) deposit-feeding on the sediment surface and around the burrow; b) suspension-feeding, through the release of a mucus net in the gallery; c) herbivory; and d) carnivory (Fidalgo e Costa et al., 2006; Engelsen et al., 2010).

4.2. U-burrows

4.2.1. *Arenicolites form XL (very large)*

Description: Vertical U-burrow without spreite. One opening is funnel-shaped, the other is simple and commonly presents a single pile of sediment casts. Tunnel diameter 0.8 cm, burrow penetration 20–40 cm. The morphotype is confidently assigned to the ichnogenus *Arenicolites*, consisting of vertical U-burrows without spreite (Häntzschel, 1975).

Tracemaker: *Sipunculus nudus* (Sipuncula: Sipunculidae).

Ethology: The presence of sediment casts suggest deposit-feeding, which is the typical mode of life of most Sipuncula (Cutler, 1994).

4.2.2. *Arenicolites form L (large)*

Description: Vertical U-burrow without spreite. Simple or funnel-like openings surrounded by radially disposed fecal casts (Fig. 5A). Tunnel diameter 0.5 cm, burrow penetration 20–40 cm. General morphology and the absence of a spreite are consistent with the ichnogenus *Arenicolites* (Häntzschel, 1975).

Tracemaker: *Sipunculus nudus* (Sipuncula: Sipunculidae).

Ethology: According to the presence of sediment casts and to the biology of the tracemaker (Cutler, 1994), these structures are permanent burrows related to deposit-feeding.

4.2.3. *Arenicolites form S (small)*

Description: Simple vertical U-burrow; tunnel diameter 1 mm, limb spacing 1–2 cm (Fig. 5B). Research from other study areas revealed the presence of a spreite between the limbs of similar U-burrows (Bromley, 1996: p.43); apparently, the structures from Grado do not present this feature. Consequently, the described burrow displays all the diagnostic features of the ichnogenus *Arenicolites* (see Häntzschel, 1975).

Tracemaker: *Corophium volutator* (Crustacea: Amphipoda).

Ethology: The tracemaker is predominantly an unselective deposit-feeder, although suspension-feeding and epipsammic browsing may also occur. In particular, diatoms form a consistent part of its diet (Gerdol and Hughes, 1994; Smith et al., 1996). *Corophium* is also known for producing several kinds of trails (Uchman and Pervesler, 2006).

4.3. Chambered burrows

4.3.1. *'Squat burrow'*

Description: unbranched burrow with a squat morphology, formally defined by the low depth/diameter ratio (ratio: 1–2.5). Burrow

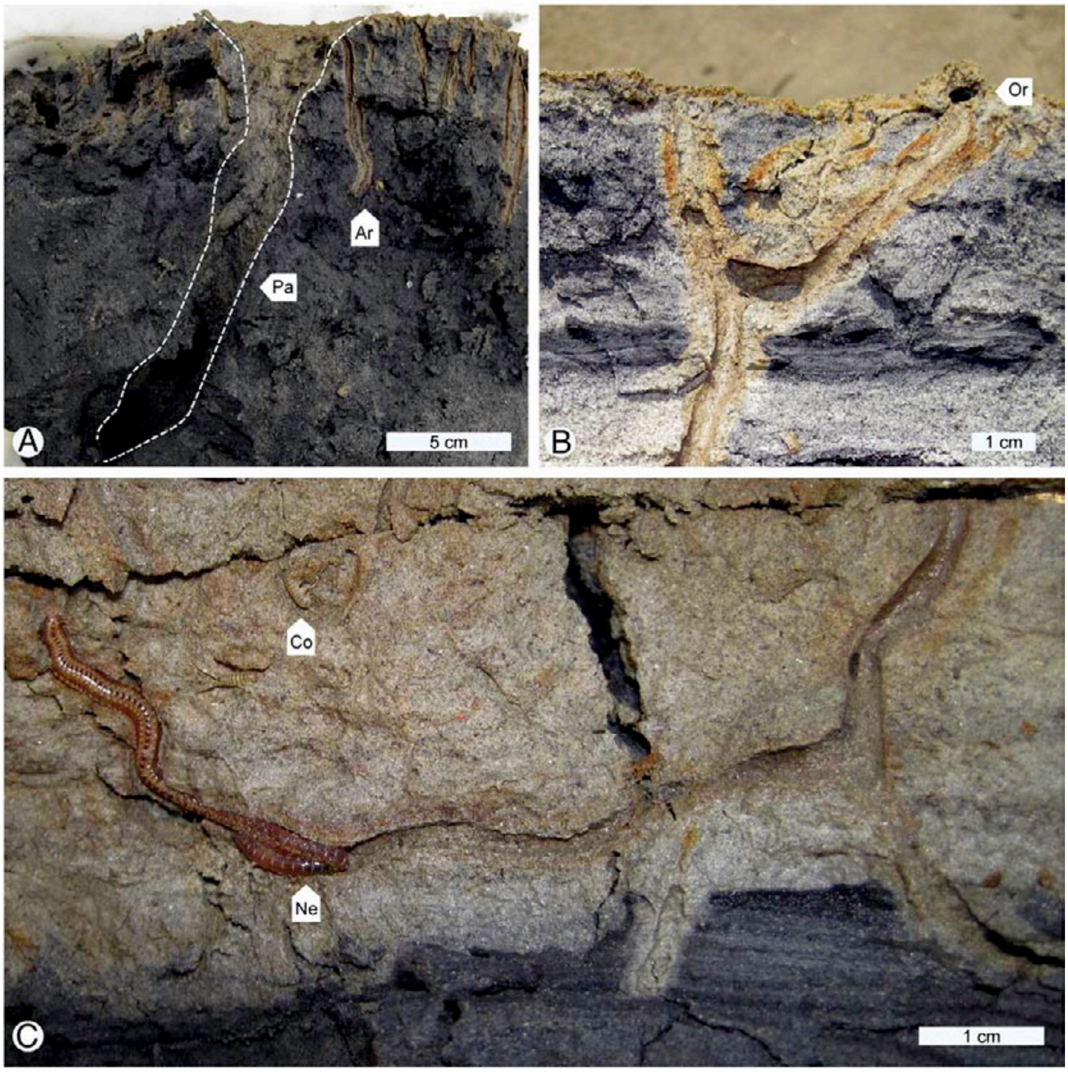

Fig. 4. Branched structures. (A) Muddy sands with *Parmaichnus* (Pa) and *Arenicolites* (Ar). Profile view. (B) *Polykladichnus* burrow within a laminated microbial mat. The burrow system changes from vertical to horizontal in correspondence of the organic-rich horizon (Or) of the biomat. (C) *Polykladichnus* with its tracemaker, the polychaete *Nereites* (Ne). Note also the amphipod *Corophium* (Co) within a U-burrow. Profile view.

architecture grades from straight (plug- or I-shaped) to variously bending morphologies (L-, J-, U- or banana-shaped). Usually, the lower part of the burrow is occupied by a disc-shaped chamber oriented obliquely or in parallel with respect to the sediment surface. Burrow section sub-circular (diameter: 5–8 cm), with irregular, rounded margins. Piles of loose sediment with crab tracks are commonly present at the burrow entrance.

The broad range of morphological variation poses ichnotaxonomical problems:

a) Plug-shaped burrows resemble the ichnogenus *Cheiichnus*, a bowl-shaped trace with scratch marks (Muñiz et al., 2010). Nevertheless, the Grado specimens do not preserve bioglyphs because of the geotechnical properties of the sediment.
b) The banana-shaped forms closely resembles *Macanopsis plataniformis*, an unbranched J-shaped burrow attributed to brachyurans (Muñiz and Mayoral, 2001).
c) The larger J- and U-shaped shaped forms reveal similarities to *Psilonichnus*, which comprises simple Y-, J- and U-burrows (Nesbitt and Campbell, 2006). However, it should be noted that the Grado specimens are significantly squatter than the typical occurrences of the ichnogenus.

In conclusion, open nomenclature ('squat burrows') is to be preferred for indicating the broad morphospace that includes these burrows. Similar problems were pointed out by De (2005) for ocypodid crab burrows of the Bengal coast.

Tracemaker: *Carcinus maenas* (Crustacea: Decapoda).

Ethology: In the study area, this burrow is commonly occupied by a crab male holding a female during precopulatory mate guarding. During breeding season, the male of *Carcinus maenas* guards the female several days before mating, defending her against predators and other male competitors (Hardege and Terschak, 2011). For this reason, 'squat burrows' are likely to be mating burrows.

4.3.2. *Macanopsis*

Description: unbranched burrows with a characteristic lower clavate chamber and a convolute, tapered neck (Fig. 6A). Conical piles of sediment (0.5–0.8 cm in diameter) are present in correspondence of the burrow entrance, which is usually concealed. Burrow penetration ranging between 2 and 7 cm.

The presence of a rounded base apparently recalls the ichnofamily Celliformidae (Genise, 2004), but the Grado structures are less

Fig. 5. U-shaped structures. (A) Openings of *Arenicolites* L. Most of the fecal casts have been washed out by waves, but the radial geometry is still manifest. Top view. (B) *Arenicolites* S with its tracemaker (Tr), the amphipod *Corophium*. Sediment-water interface (Sw) colonized by filamentous algae. Profile view.

regular in shape, present tunnels ('necks'), and do not show spiral closures (Genise, pers. com.). The observed structures are more fitting with the ichnogenus *Macanopsis*, consisting of a straight or slightly bent burrow enlarging to hemispherical hollow (Häntzschel, 1975).

Tracemaker: *Heterocerus flexuosus* (Insecta: Coleoptera).

Ethology: These burrows are linked with the life cycle of heterocerid beetles, as puparia, pupae and adults are commonly found within the burrows (Baucon, 2008). Laminated microbial mats are a source of food, as beetles feed on algae, zooplankton and organic debris (Evans and Hogue, 2006).

4.4. Plug-shaped structures

4.4.1. Bergaueria

Description: rounded plug-shaped depressions. Diameter 3–5 cm. General morphoplogy is consistent with the ichnogenus *Bergaueria*, consisting of cylindrical or baglike burrows with rounded ends (Häntzschel, 1975).

Tracemaker: sea anemones, including *Cereus* (Cnidaria: Sagartiidae), *Condylactis* and *Anemonia* (Cnidaria: Actiniidae).

Ethology: In the study area, *Bergaueria* is a domichnial structure produced by anemones (Fig. 7). The tracemakers are opportunistic omnivorous suspension feeders (Chintiroglou and Koukouras, 1996).

4.5. Winding structures

4.5.1. Helminthoidichnites

Description: unbranched horizontal, curved burrows with circular cross-section (diameter: 1 mm). Burrows develop in parallel respect to lamination and maintain a predominantly constant depth. Openings usually concealed, loops very rare. These features are characteristic of the ichnogenus *Helminthoidichnites* (i.e., Uchman et al., 2005).

Tracemaker: Dipteran larvae (Insecta: Diptera).

Ethology: These traces accurately follow the interface between the organic-rich and the mineral-rich layer of microbial mats (Fig. 6B). Consequently, it is likely to assume an undermat mining behavior, typical of Precambrian to recent microbial mats (Seilacher, 1999; Gerdes, 2003).

4.6. Simple burrows

4.6.1. Skolithos form L (large)

Description: Open, vertical burrow composed by (1) an upper, short shaft presenting an 8-shaped cross-section and (2) a longer lowermost part, elliptical in section, usually extending for more than 15 cm. Similar bivalve-produced structures include *Siphonichnus* (Gingras et al., 2010) and *Teichichnus* (Bromley, 1996, p. 69), although predominant morphological features are more compatible with the ichnogenus *Skolithos*. In fact the structure is straight, mostly of uniform diameter and do not display evidence of spreite.

Tracemaker: *Solen marginatus*, *Ensis ensis*, *Ensis minor* (Mollusca: Bivalvia).

Ethology: The tracemakers of *Skolithos* L are suspension-feeders, capable of rapid burrowing when threatened (Little, 2000).

4.6.2. Skolithos form M (medium)

Description: Straight vertical burrow with constructional lining made of mucus-bound sand grains. Burrow section circular, penetration depth 10–15 cm. General morphology is fully consistent with the ichnogenus *Skolithos* (Häntzschel, 1975).

Tracemaker: *Megalomma* sp. (Annelida: Polychaeta).

Ethology: The tracemaker *Megalomma* possesses specialized feeding structures, consisting of ciliated tentacles (radioles) for capturing suspended particles (Dame et al., 2001; Fig. 8). Several compound eyes are present at the tips of the ciliated radioles and serve as a

Fig. 6. Simple and chambered structures. (A) *Macanopsis* (Ma) is commonly associated with intertidal microbial mats, constituted by an upper, organic rich layer (Or) and a lower, mineral rich one. Note the tracemaker of *Macanopsis*, an heterocerid coleopteran (Co). Profile view. (B) *Helminthoidichnites* is produced by dipteran lavae (He) while feeding beneath the organic-rich layer (Or) of intertidal biomats. Profile view.

photosensitive alarm. In fact the tracemaker responds to shadows by rapidly retreating inside its domichnial burrow (Video 4).

4.6.3. *Skolithos form S (small)*

Description: simple, vertical burrows with very low diameter/height ratio. Usually, vertical extension ranges between 3 and 7 cm, while burrow diameter is less than 1 mm. General form is strongly reminiscent of the ichnogenus *Trichichnus*, but the studied burrow lacks of the diagnostic walls described by Häntzschel (1975). Consequently, the structure is attributed to the ichnogenus *Skolithos*, although its characteristically small diameter approaches the boundary of the realm of cryptobioturbation.

Tracemaker: worm-like organisms, possibly annelids and nematodes.

Ethology: Vertical burrows are commonly associated to suspension-feeding, but they are produced also by carnivores, deposit and detritus feeders (Bromley, 1996: p. 200).

4.6.4. *Skolithos form XS (very small)*

Description: vertical, unlined cylindrical burrow penetrating for 1–5 cm. Burrow diameter 1 mm. According to the straight, vertical geometry, this trace belongs to the ichnogenus *Skolithos*.

Tracemaker: *Talitrus saltator* (Crustacea: Amphipoda).

Ethology: During the day the tracemaker inhabits its burrow, emerging at night for feeding on stranded macroalgal detritus (Williams, 1983). Therefore, the burrow may be interpreted as a shelter against desiccation.

4.6.5. *Monocraterion*

Description: vertical, cylindrical tunnels with a funnel-shaped opening at the top of the burrow. Burrow diameter 0.5–1 cm, vertical extension up to 10 cm. These morphological features are diagnostic of the ichnogenus *Monocraterion* (Häntzschel, 1975). It should be noted that this ichnogenus can be potentially confused with the vertical shafts of *Thalassinoides* L, also presenting a characteristic funnel-like opening.

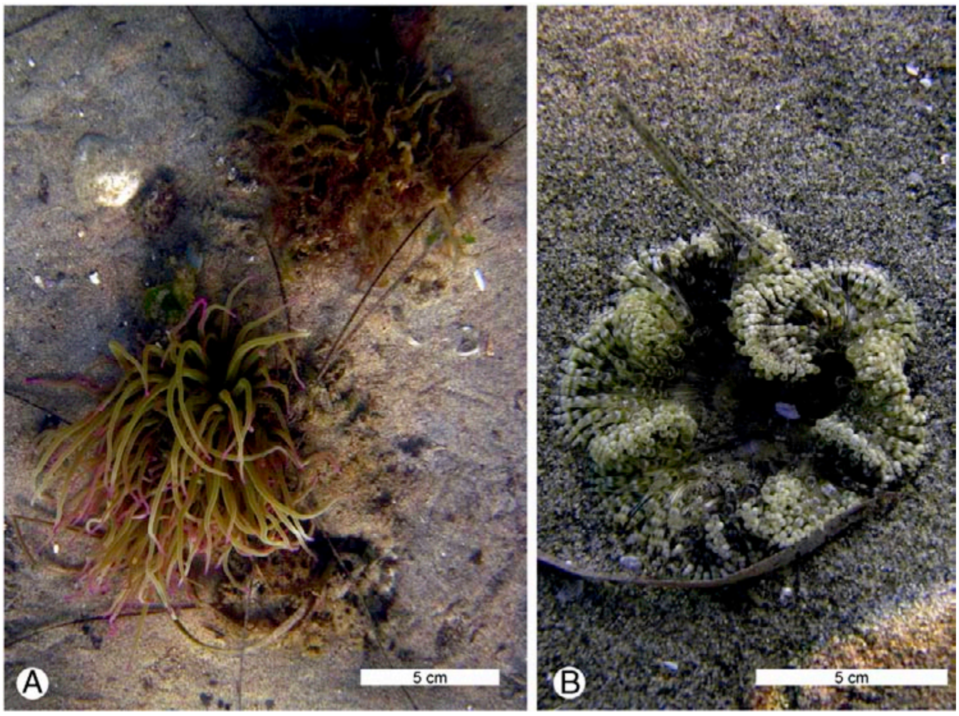

Fig. 7. Plug-shaped structures. (A) Top view of an actinian anemone, producer of *Bergaueria*. (B) *Cereus* is among the commonest producers of *Bergaueria*. Top view; photo location in Fig. 1.

Tracemaker: undetermined annelid.

Ethology: Most probably, this trace is a domiciliary burrow of a suspension-feeder. Nevertheless, it should be noted that vertical morphology is consistent with several trophic functions, including suspension, deposit, detritus and carnivore feeding (Bromley, 1996: p. 200).

4.7. Tracks and footprints

4.7.1. Avipeda-/Ardeipeda-like footprints

Description: broad morphospace including footprints with three digits directed forward; additional features include claw marks, hallux and webbing imprints. Trace width: 5–13 cm. Morphological features resemble known avian ichnotaxa, primarily *Avipeda* and *Ardeipeda*. Nevertheless, avian ichnotaxonomy is still in flux (Lockley et al., 2007), therefore open nomenclature is used.

Fig. 8. *Skolitos* M. The suspension-feeding polychaete *Megalomma* produces vertical burrows, corresponding to the ichnogenus *Skolithos*. Photo location in Fig. 1.

Tracemaker: *Ardea cinerea*, *Egretta garzetta* (Aves: Ardeidae), *Laurus michahellis* (Aves: Laridae).

Ethology: These structures are produced during locomotion.

4.7.2. Canipeda

Description: tetradactyl footprints with a distinctive heel pad. Trace width: 5–13 cm.

Tracemaker: *Canis lupus familiaris* (Mammalia: Canidae).

Ethology: These structures are produced during dog locomotion.

4.7.3. 'Parallel furrows'

Description: sets of parallel, elongated furrows. Furrow width: 1–3 mm; trace width: 3–5 cm.

Tracemaker: *Carcinus maenas* (Decapoda: Brachyura).

Ethology: These traces are produced by green crabs during sideward locomotion (Video 5).

4.8. Trails

4.8.1. Archaeonassa

Description: horizontal trail consisting of a median furrow flanked by two lateral ridges (Fig. 9A). Trace width: 2–3 cm. Based on general morphology, these structures are assigned to the ichnogenus *Archaeonassa* (Häntzschel, 1975).

Tracemaker: *Bolinus brandaris* and *Hexaplex trunculus* (Gastropoda: Muricoidea) are the most conspicuous producers of *Archaeonassa*. Other known tracemakers are *Cerithium vulgatum* (Gastropoda:

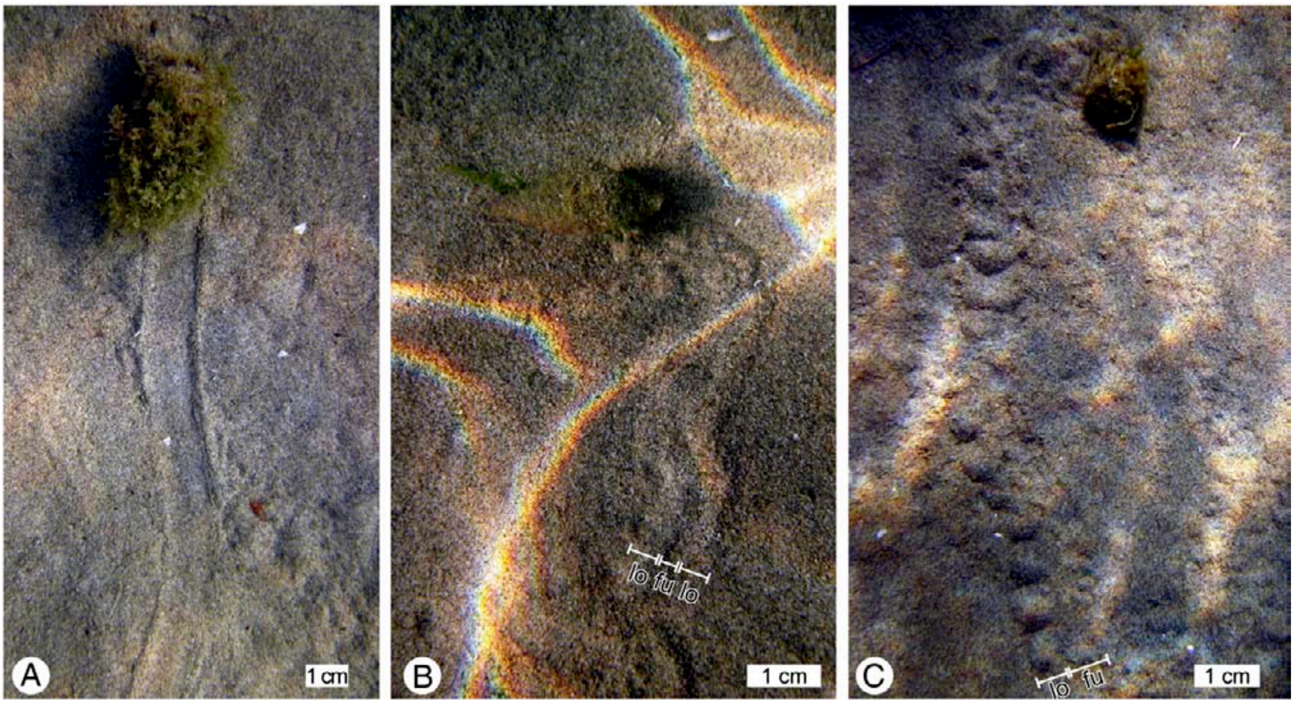

Fig. 9. Trails. (A) An algae-covered gastropod producing *Archaeonassa*. (B)*Nereites biserialis* produced by hermit crab with oblate shell (*Cerithium*). Furrows (f) and lobed ridges (l) highlighted. (C) Hermit crab with globose shell producing *Nereites uniserialis*. Furrows (f) and lobed ridge (l) highlighted. Photo location in Fig. 1.

Cerithiidae), *Pirenella conica* (Gastropoda: Potamididae), *Sphaeronassa mutabilis* and *Nassarius nitidus* (Gastropoda: Nassariidae).

Ethology: In the study site, *Archaeonassa* is related to locomotion behavior of gastropods, independently of their feeding strategy (Video 6). However, the most representative tracemakers are carnivorous muricids.

4.8.2. Nereites biserialis

Description: winding trails constituted by a furrow flanked on both sides by lobes (Fig. 9B). Trail width: 1–3 cm. The presence of a central furrow and lateral reworked zones is characteristic of nereitids (Seilacher, 2007). More specifically, the arrangement of lobes coincides with the ichnospecies *Nereites* (=*Neonereites*) *biserialis* (Mángano et al., 2002; Seilacher, 2007).

Tracemaker: hermit crabs, probably *Pagurus* (Decapoda: Paguridae), inhabiting oblong shells.

Ethology: Traditionally, two models have been proposed for *Nereites*:

1. in the 'worm model', *Nereites* is a feeding burrow produced by worm-like organisms, probing and backfilling laterally (Seilacher, 2007)
2. in the 'arthropod model', the characteristic lobes are pressure-release structures made by arthropod legs. According to this interpretation, *Nereites* is a locomotion trail (Martin and Rindsberg, 2007).

In the study site, tracemaker identity and behavior fits with the 'arthropod model'.

Furthermore, there is a strong relationship between lobe arrangement and shell shape. In fact, biseriate *Nereites* are produced by hermit crabs occupying oblong shells (i.e. *Cerithium*). In contrast to *Nereites biserialis*, the uniseriate form (*Nereites uniserialis*) is related to crabs inhabiting trochiform shells, such as the top shaped *Gibbula* (Section 4.8.3). This aspect shows that hermit crab locomotion is affected by shell shape.

4.8.3. Nereites uniserialis

Description: winding trails consisting of a furrow flanked by a single row of lobes (Fig. 9C). Trail width: 0.8–3 cm. General morphology is consistent with nereitids, while the single row of lobes is diagnostic of *Nereites* (=*Neonereites*) *uniserialis* (Mángano et al., 2002; Seilacher, 2007).

Tracemaker: hermit crabs, probably *Pagurus* (Decapoda: Paguridae), inhabiting trochiform shells.

Ethology: The here studied *Nereites uniserialis* is the locomotion trace of a hermit crab, matching the 'arthropod model' described by Martin and Rindsberg (2007). In contrast to the roughly symmetric *Nereites biserialis*, *Nereites uniserialis* is produced by hermit crabs occupying trochiform shells. As discussed in Section 4.8.2, this ichnological evidence reflects how the locomotion of hermit crabs is affected by shell shape.

4.9. Miscellaneous group

4.9.1. 'Diverging shafts'

Description: vertical V-shaped tunnels with circular cross-section. Tunnels diverge from a larger structure, usually represented by a curved cylindrical burrow (Fig. 10A). In this case, burrow morphology and tracemaker coincides with *Solecurtus* burrows (Dworschak, 1987b), which are commonly accompanied by *Teichichnus*-like structures (Bromley, 1996). In other cases, tunnels diverge from an almond-shaped burrow, corresponding to the ichnogenus *Lockeia* (Sections 4.9.2 and 4.9.3; Fig. 10B).

These V-shaped traces are reminiscent of the ichnogenus *Siphonichus*, consisting of vertical tubes cutting backfilled laminae (Carmona et al., 2009). Nevertheless, backfilled laminae have never been discerned unequivocally in the study site, therefore open nomenclature is preferred.

Tracemaker: *Abra alba*, *Donax trunculus*, *Solecurtus* sp., *Venus* sp. (Bivalvia: Veneroida).

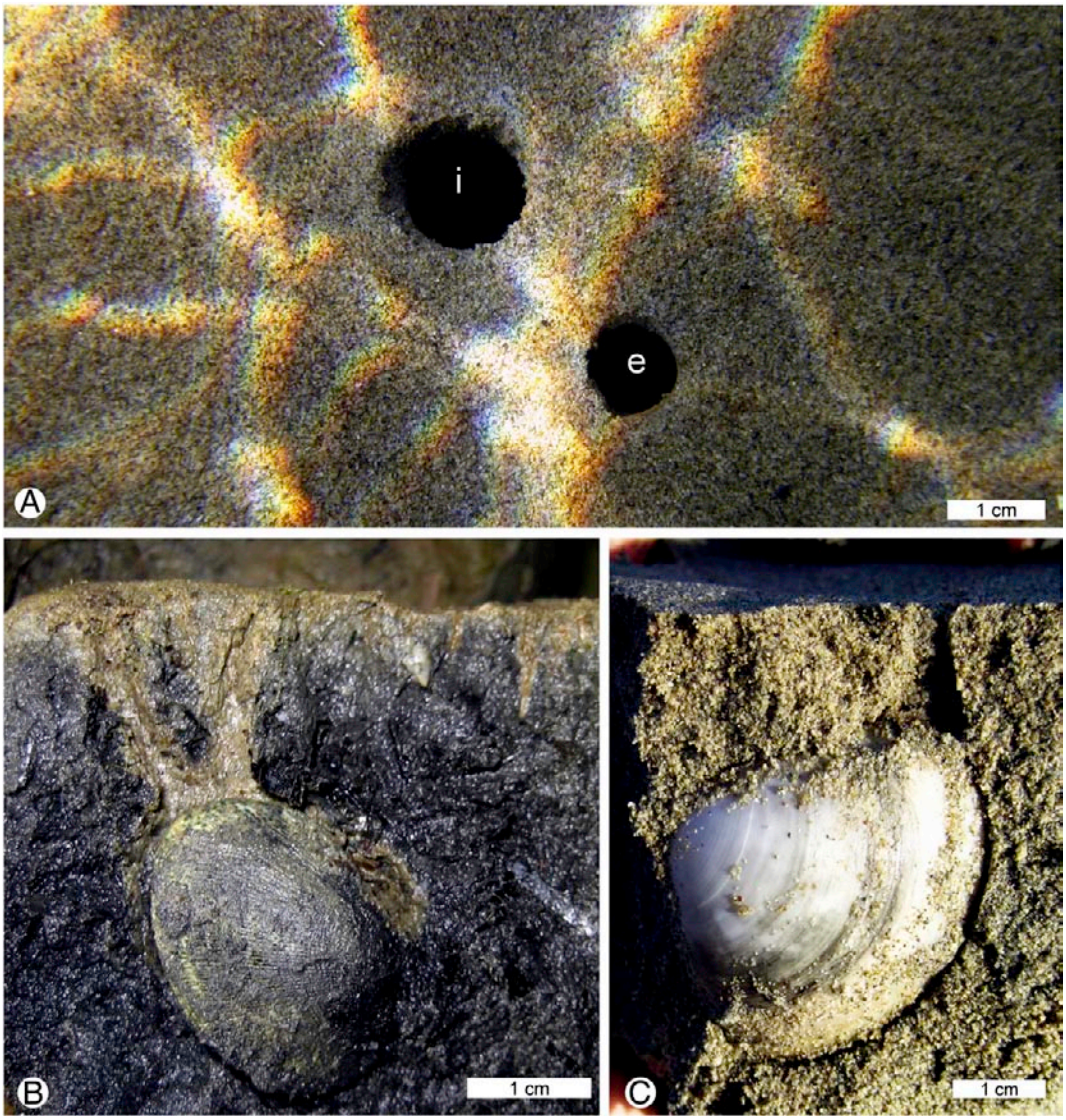

Fig. 10. Bivalve traces. (A) Openings of the *Solecurtus* burrow. Following Dworschak (1987a), the larger opening correspond to the inhalant siphon (i), the smaller one to the exhalant siphon (e). Top view. (B) The bivalve *Mactra* produces an almond shaped-burrow (*Lockeia*) connected to the surface by a single shaft. Profile view. (C) The bivalve *Venerupsis* produces *Lockeia* and two 'diverging shafts'. Profile view.

Ethology: these structures represent siphon traces of suspension-feeding bivalves.

4.9.2. Lockeia form S (small)

Description: almond-shaped burrow with smooth, rounded margins. Burrow depth usually ranging between 3 and 5 cm. The almond-shaped part is commonly connected to the surface by a single tapered shaft (diameter: 0.3–0.7 cm) or by two thin arcuate branches (diameter: 1–2 mm; Fig. 10B, C). According to Schlirf et al. (2001), the almond-shaped part closely resembles the ichnogenus *Lockeia*. The connections to the surface are reminiscent of the ichnogenus *Siphonichnus*, as illustrated in Gingras et al. (2010, their Figure 5).

Tracemakers: *Mactra corallina*, *Venus* sp., *Venerupsis philippinarum* (Bivalvia: Veneroida).

Ethology: The observed *Lockeia* are resting traces produced by suspension-feeding bivalves, while the *Siphonichnus*-like structures are produced by the siphons of the tracemakers (Section 4.9.1).

4.9.3. Lockeia form XS (very small)

Description: almond-shaped burrow connected to the surface by two elongate segments. Branches irregular, very thin (<1 mm) and poorly defined. Burrow depth usually less than 3 cm. The almond-shaped structure is consistent with the ichnogenus *Lockeia*, while the branched segments resemble *Siphonichnus* (Schlirf et al., 2001; Gingras et al., 2010).

Tracemaker: *Abra alba*, *Donax trunculus* (Bivalvia: Veneroida).

Ethology: *Lockeia* is the resting trace of suspension-feeding bivalves, whose siphons leave the *Siphonichnus*-like structures (Section 4.9.1).

4.9.4. Mottling

Description: intense, indistinct bioturbation resulting in a massive lumpy texture, occasionally intersected by convolute patches of varying color. Physical sedimentary structures not discernible.

Tracemaker: marine phanerogams, primarily *Zostera marina*, *Zostera noltii* and *Cymodocea nodosa* (Magnoliophyta: Najadales), followed by

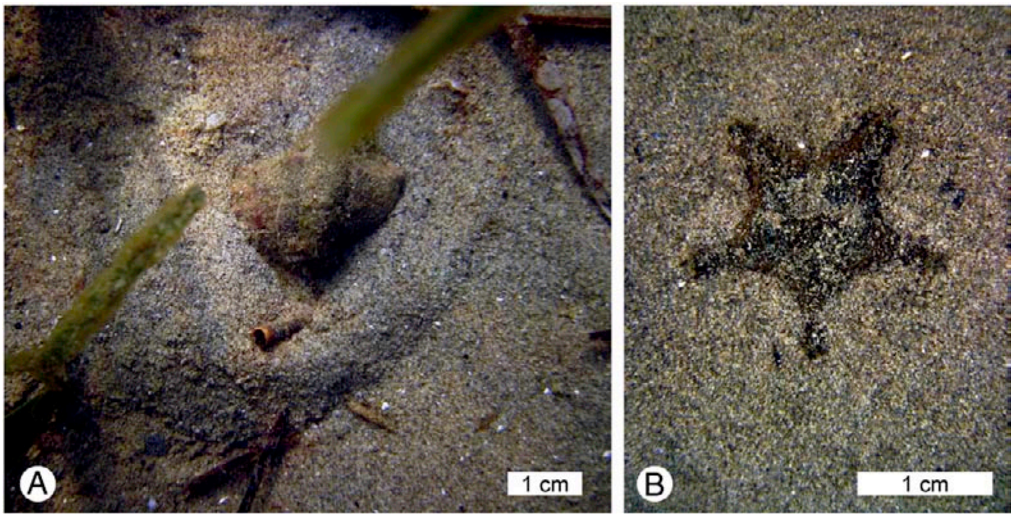

Fig. 11. Sediment disturbance structures. (A) Bioturbating gastropod. (B) A sea star, probably *Asterina gibbosa*, partially buried into the sand.

Posidonia oceanica in the shallow subtidal. *Nereis diversicolor* (Anellida: Polychaeta), *Echinocardium cordatum* (Echinodermata: Spatangoida), *Asterina gibbosa* (Echinodermata: Asteroidea), *Bolinus brandaris*, *Hexaplex trunculus* (Gastropoda: Muricoidea) and other animal tracemakers may significantly contribute to the amount of biogenic reworking (Fig. 11).

Ethology: general sediment disruption is produced by roots of marine phanerogams, accompanied by polychaetes passing through water-saturated sediments. Polychaete-related mottling resembles the ‘mantle and swirl’ traces described by Lobza and Schieber (1999).

5. Discussion

Overall, the studied ichnofauna is characterized by dominance of boxworks, vertical and U-shaped burrows (i.e. *Thalassinoides*, *Skolithos*, *Arenicolites*). Horizontal trails (*Archaeonassa*, *Nereites*) and chambered burrows (*Macanopsis*) are locally abundant, while ichnodiversity is moderate. These features are consistent with the *Skolithos* and *Cruziana* ichnofacies, and similar characteristics have been recognized in other tidal (i.e. Garrison et al., 2007) and barrier-island systems (i.e. Hauck et al., 2009).

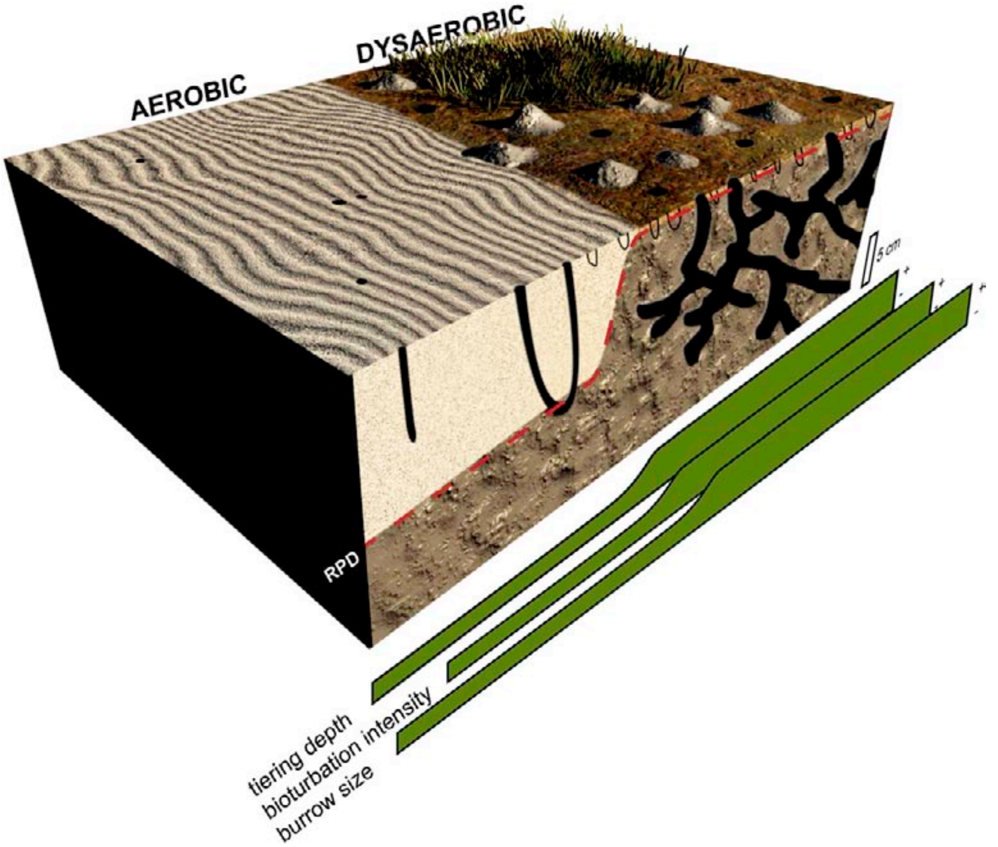

Fig. 12. Inverse relationship between oxygenation and bioturbation. Maximum tiering depth, bioturbation intensity, burrow size expressed as relative values. Redox potential discontinuity depth (RPD) is shown by the dashed line.

Although this study is at a qualitative stage, data suggest that characteristic patterns emerge at finer scales of observation. In fact, sediment barriers impose a sharp contrast in terms of environmental variables, feeding strategies and ichnological composition. The sheltered back-barrier is characterized by low-energy conditions, high bioturbation intensity, large deep-tier boxworks (i.e. *Thalassinoides*). Deposit-feeding is the dominant trophic strategy. On the other hand, the fore-barrier exhibit inverse characteristics: higher energy, lower bioturbation intensity, smaller and shallower burrows.

Notably, sediment texture and depth of the redox potential discontinuity show lower oxygen conditions in the fore-barrier. This evidence is contrasting with the majority of the oxygenation models, which suggest that higher oxygen levels support higher bioturbation, larger burrows and deeper tiering (see the reviews in Martin, 2004; Buatois and Mángano, 2011).

The Mula di Muggia paradox (Fig. 12) is explained by a complex relationship involving hydrodynamics, interstitial oxygen and nutrient availability. Interstitial oxygenation is controlled by sediment permeability, which affects the depth of the redox potential discontinuity. Therefore, interstitial oxygenation depends from grain size which, in turn, is controlled by hydrodynamics (see Raffaelli and Hawkins, 1996: p. 20–23). Sheltered, fine substrates, with their reduced permeability and hence dominating anaerobic chemistry, are optimal for many tracemakers because of their quiet hydrodynamics. Indeed, such low-energy settings offer abundant organic matter and low mechanical stress. Not surprisingly, the major groups of intertidal tracemakers are adapted to dysoxic, sulfide-rich environments: *Corophium* (author of *Arenicolites* S), thalassinidean shrimps (tracemakers of *Thalassinoides* and *Parmaichnus*) and *Nereis diversicolor* (responsible for *Polykladichnus*) (Gamble, 1971; Kristensen, 1983; Johns et al., 1997).

The example from Grado evidences that, if the water column is sufficiently oxygenated, low-oxygen settings favor intense bioturbation with large and deep burrows. This conclusion supports the model of Ekdale and Mason (1988) which considers the relationship between water column and pore-water oxygenation.

In light of these observations, the ichnological contrast between fore- and back-barrier can be considered a signature of barrier-island systems, because it reflects environmental, ecological and sedimentological features proper of these depositional environments. In fact, following Otvos (2012), the essential feature of sediment barriers is their protective function, which impose a shore-parallel boundary between inshore and open marine conditions.

6. Conclusions

This study portrayed the ethological complexity of a barrier-island system through the description of individual ichnotaxa. Consequently, the importance of this research relies in the autecology of bioturbation within a neoichnologically understudied environment. This approach provides a rich source of information for interpreting trace fossils and paleoenvironments.

In this regard, the studied ichnotaxa allow ‘geological analogies’, such that a fossil evidence can be compared to phenomena already known (Baker, in press). This philosophy is exemplified by the brachyuran-related *Nereites*, serving “not much to provide definitive explanations as to provide a source for hypotheses that move geological research into productive lines of inquiry” (Baker, in press). The same perspective can be applied to other findings of this research, such as the fore-/back-barrier dichotomy and the inverse relation between oxygenation and bioturbation intensity.

Nevertheless, many questions remain unanswered. How are traces distributed in space? What are the mutual relationships between ichnotaxa? What are the environmental mechanisms regulating ichnoassociation patterns?

For these reasons, there is a need for synecological records from the Mula di Muggia system, which will be quantitatively tackled in future studies (i.e. Baucon and Felletti, 2013–this issue). To this end, the present autecological perspective is both the prerequisite and the complementary step for understanding the ichnological system as a whole.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.palaeo.2013.02.011.

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Appendix D

The IchnoGIS method: Network science and geostatistics in ichnology. Theory and application (Grado lagoon, Italy)

Palaeogeography, Palaeoclimatology, Palaeoecology 375 (2013) 83–111

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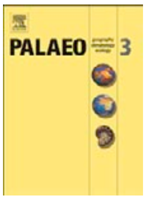

The IchnoGIS method: Network science and geostatistics in ichnology. Theory and application (Grado lagoon, Italy)

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ABSTRACT

A new method is proposed for capturing, managing, analyzing, and displaying geographically referenced ichnological data: IchnoGIS. This approach is based on the integration of spatial, geostatistical techniques with network theory, aiming to characterize the environmental significance of recent traces. The efficiency of the IchnoGIS method is tested against a case-study: the Grado lagoon (Italy). The studied site, located within the epeiric Northern Adriatic Sea, consists of a complex mosaic of peritidal environments in a barrier-island context. Here, a diverse ichnofauna includes the following incipient ichnotaxa: *Arenicolites*, *Helminthoidichnites*, *Lockeia*, *Macanopsis*, *Monocraterion*, *Parmaichnus*, *Polykladichnus*, *Skolithos*, *Thalassinoides* and ‘squat burrows’. Ichnofaunal distribution is described by the spatial and geostatistical tools proper of the IchnoGIS approach. Additionally, the application of network theory documents the emergence of organized structures (ichnoassociations) from interactions driven by environmental factors. Our results elucidate the role that environmental processes play in producing the complex ichnological patterns of the Grado site. In particular, emersion time, hydrodynamics, substrate firmness and microbial binding are the major control factors determining the structure and distribution of trace associations. These structuring factors are used to define a predictive model of ichnoassociation composition, providing an immediate tool for future palaeoenvironmental reconstitutions.

1. Introduction

> “[a certain species of mollusk] does not swim, but makes a furrow in the sand and proceeds along the furrow's edges”– Leonardo da Vinci, Leicester Code, folio 8v

Since its earliest roots in Renaissance times, trace fossil analysis has relied on actualistic experiences for inspiring and testing theories and models. In fact, each of the major watersheds in the history of ichnology was initiated by advances in neoichnological knowledge (Baucon et al., 2012): the palaeoichnological knowledge of Leonardo da Vinci was inspired by modern burrowing and boring organisms (Baucon, 2010), the experiments of Nathorst disproved the botanical interpretation of trace fossils, the Senckenberg Laboratory marked the development of the modern approach in ichnology (Osgood, 1975). In more recent times, Adolf Seilacher's ethological approach benefited from his studies on modern tidal flats (Cadée and Goldring, 2007), while Robert Frey and the Georgia coast school outlined the palaeoenvironmental significance of trace fossils through the observation of modern ones (Frey and Seilacher, 1980).

Despite these notable landmarks, neoichnology came to a standstill throughout the 1980s and 1990s (Gingras et al., 2011b). With the words of Frey and Seilacher (1980), “the present has been studied considerably less than its importance would dictate”. This scenario is currently exacerbated by the poor integration between marine biology and ichnology, each one with their own nomenclature and literature. As a result, our present models for palaeoenvironmental interpretation still rely on the neoichnological studies of the 1950s, 1960s and 1970s (Gingras et al., 2011b).

With the Internet and GPS among the faster-growing technologies of the decade, the previous historical considerations addresses traditional questions with novel approaches: How are traces distributed in space? What are the association patterns (‘links’) between ichnotaxa? What is the relationship between traces and their environment?

This paper aims to answer to these questions by developing a neoichnological method based on geostatistics and network theory, through which delineate an ichnological model of a mesotidal barrier-island system: the Grado lagoon (Italy) (Fig. 1).

2. Study area

This study is conducted in the region of the Grado–Marano lagoon, a large transitional system located along the Adriatic coast (Northern

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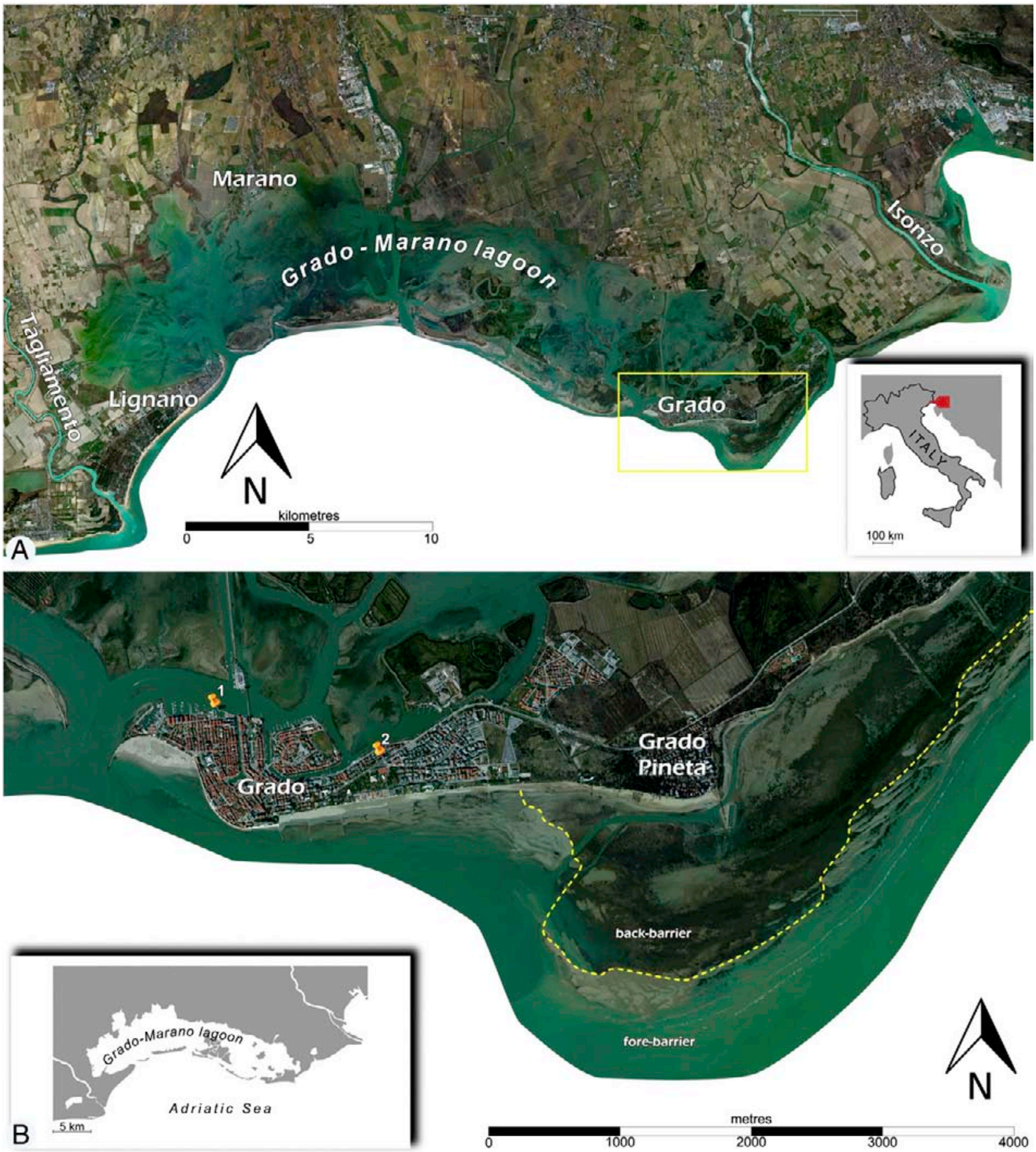


Fig. 1. Geographical setting. (A) Grado lagoon. (B) The study area is comprised between Grado and Grado Pineta towns. Location markers refer to the ISPRA mareograph (1) and the OSMER metereological station (2). Images courtesy of Digital Globe.

Italy; Fig. 1A). In particular, the main target are the intertidal flats of the external margin of the Grado lagoon, located — from west to east — between Grado and Grado Pineta town (Fig. 1B). This area is characterized by significant biodiversity and an integer environment. Indeed it borders several protected areas recognized by the EU Natura 2000 Network (both habitat and birds directive sites) and the international Ramsar wetland convention (Barbone et al., 2011). The study area is markedly influenced by tides, which are unusually high for the Mediterranean Sea, while the climate is temperate (Baucon and Felletti, 2013; Fig. 2).

The sampling area was selected after a preliminary study (Baucon and Felletti, 2013) because it represents widely differing environmental situations, with shoals separating an intertidal back-barrier lagoon from a fore-barrier area (Fig. 1B). Sediments in the back-barrier are dominated by microbial mats and muddy sands, commonly covered by marine phanerogams. Conversely, the fore-barrier shows a dominance of sands and paucity of phanerogams. This configuration, characterized by sediment barriers separating the open sea from a lagoon, makes the area an ideal model for modern and ancient barrier-island systems.

3. The IchnoGIS method

A novel method for neoichnological analysis has been designed for investigating the study area (Fig. 3). Similarly to a geographic information system (GIS), the proposed approach integrates hardware, software, and data for capturing, managing, analyzing, and displaying

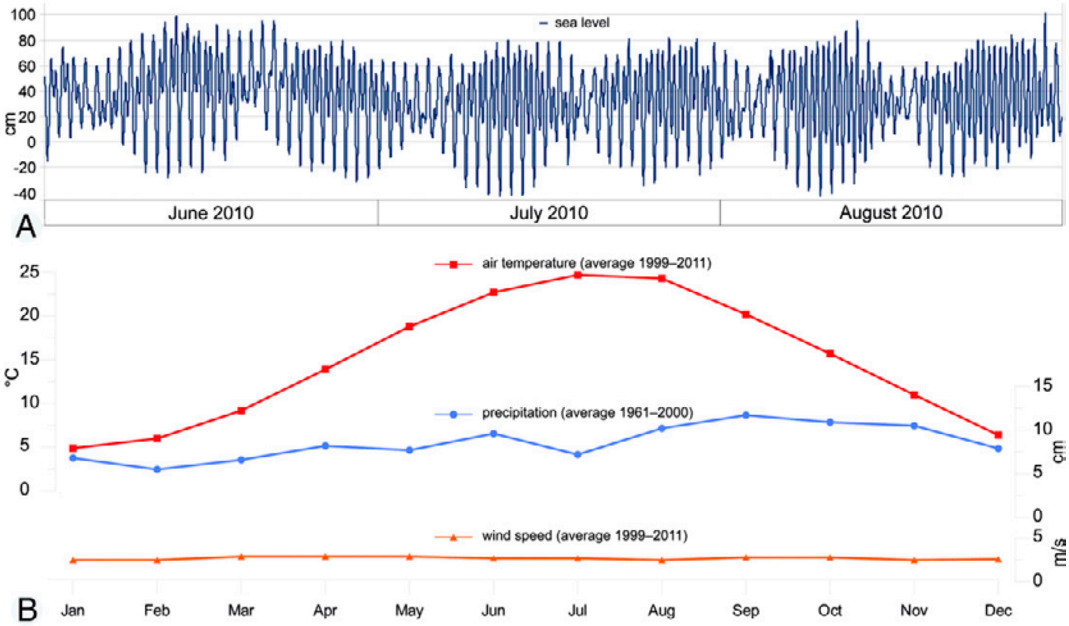
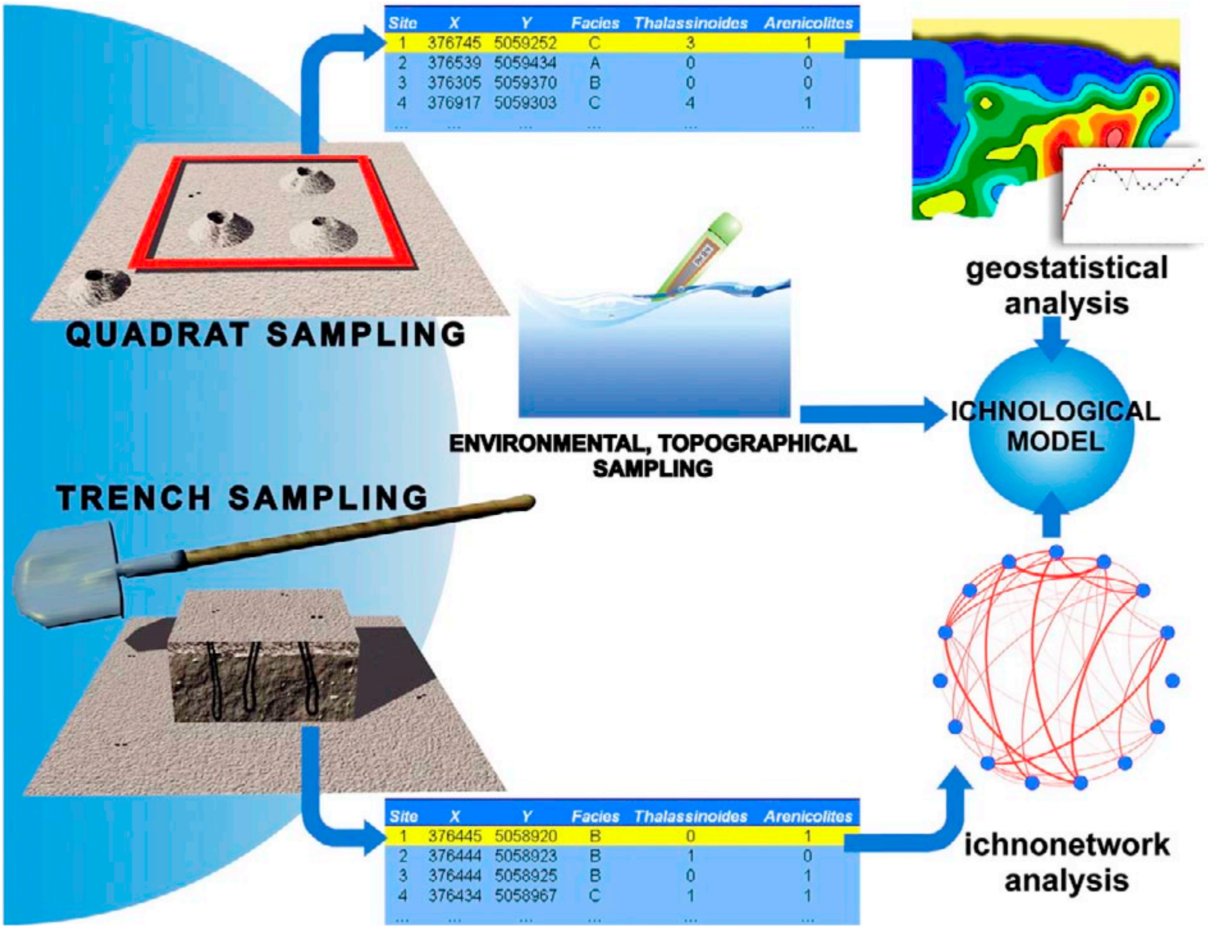


Fig. 2. Climatological setting. (A) Sea level, measured during the sampling period. Data from ISPRA mareograph (see Fig. 1 for location). (B) Climatic features of the studied area: average of the average daily temperature, precipitation and wind. Data from OSMER metereological station (see Fig. 1 for location).

geographically referenced ichnological data. For this reason, the method has been named ‘IchnoGIS’. Its development derived from previous work on the application of GPS and GIS techniques to neoichnology (Baucon, 2008). The present section describes materials and procedures of the IchnoGIS approach through its application to the Grado case study.



Site	X	Y	Facies	Thalassinoides	Arenicolites
1	376745	5059252	C	3	1
2	376539	5059434	A	0	0
3	376305	5059370	B	0	0
4	376917	5059303	C	4	1
...	...	...	...	...	...

Site	X	Y	Facies	Thalassinoides	Arenicolites
1	376445	5058920	B	0	1
2	376444	5058923	B	1	0
3	376444	5058925	B	0	1
4	376434	5058967	C	1	1
...	...	...	...	...	...

Fig. 3. The IchnoGIS method.

3.1. Survey design

The initial step for this study required the definition of the biogenic structures of interest and their correspondence with existing ichnogenera (Table 1). Dominant sedimentary facies were recognized on the basis of texture, colour and sedimentary structures, further refining the classification scheme presented in Baucon (2008) (Table 2). According to practical and logistical considerations, different sampling schemes were adopted for quadrat, trench, environmental and topographical sampling (Table 1).

3.2. Ichnological and sedimentological sampling

- Quadrat sampling: trace abundance is crucial to know how ichnotaxa are distributed in a particular habitat; however, it is usually impossible to count each and every trace present. For this reason, one of the core steps of IchnoGIS is based on quadrat sampling, a method widely used in the interpretation of large ecological data sets with environmental gradients (McIntyre and Eleftheriou, 2005). At each sampling site, a frame of a set size (0.25 m^2) was placed on the substrate to determine sedimentological and ichnological attributes occurring within it. In particular, facies type and abundance of each structure of interest (i.e. number of *Arenicolites*) were recorded in conjunction to the spatial coordinates of the sampling site, determined by a GPS unit (Fig. 3). Practical and logistical considerations were unfavourable for adopting a regular sample distribution, therefore nearest neighbour analysis (Borradaile, 2003) was iteratively used to test sampling randomness (Section 3.4). A total of 2622 samples were analyzed between June and September 2010 (Table 1).
- Trench sampling: quadrat sampling emphasizes the recognition of distinct structures on the sediment surface, being unsuitable for burrows with poorly visible openings. Consequently, quadrat sampling was complemented by the study of vertical trenches, realized at regularly spaced sites (spacing: 5 m). 13 transects perpendicular to the coast were conducted to obtain sufficient material for analysis (619 sampling sites). Spatial coordinates of each sampling site were recorded, in conjunction with facies type and presence/absence of studied traces (Fig. 3).

3.3. Environmental and topographical sampling

- Environmental sampling: representative sampling sites were selected for estimating water and sediment proprieties. Measured parameters include: pH, Reduction Potential (Eh), nutrients (nitrite, nitrate, phosphate) and salinity. These measurements were conducted both for the water column and interstitial water (Table 1). Sediment proprieties include depth of the Redox Potential Discontinuity Layer (Fenchel and Riedl, 1970) and substrate firmness, measured with the modified Brinell method (Gingras and Pemberton, 2000). Emersion time was measured by monitoring 19 sites during a complete tidal cycle.
- Topographical sampling: major topographic features were mapped by GPS unit. Bathymetry of 237 sites was obtained by subtracting the tidal influence from the water depth, measured with a metrestick. Tidal influence was derived from the mareograph of ISPRA Venice (recording frequency: 10 min).
- Significance test: nearest neighbour analysis was used to test assess the quality of quadrat sampling. This method compares the average site separation with the average separation of randomly distributed sites (Borradaile, 2003). As concerns sampling scheme, nearest neighbour analysis revealed a significant tendency to randomness (nearest neighbour index: 0.78), sufficient for a coherent data analysis.

3.4. Data visualization and analysis

In order to explore the relationship between traces and their environment, a defined set of mathematical and graphical techniques were applied for visualizing and analyzing the data collected. This section presents the mentioned techniques, organized according to their target of investigation:

- Spatial organization: point maps were selected for visualizing trench sampling data. As concerns quadrat sampling, a geostatistical approach based on kriging estimation (Matheron, 1962) was applied for interpolating the number of traces at unsampled positions. Among the major interpolation techniques, kriging is well-suited for irregularly distributed sampling sites (Conolly and Lake, 2006; dell'Arciprete et al., 2012) such as our data. This technique uses a

Table 1
Sampling features.

Object of interest	Notes	Number of samples	Sample unit	Sampling scheme	Type of survey
Surface sediment mound	Corresponding to *Thalassinoides* XL	2622	0.25 m^2	Random	Quadrat sampling
Simple opening	Corresponding to *Thalassinoides* and *Parmaichnus*				
Paired openings with single fecal cast	Corresponding to *Arenicolites* XL				
Paired openings with radial fecal casts	Corresponding to *Arenicolites* L				
Large opening	Corresponding to 'squat burrow'				
Facies					
Thalassinoides Parmaichnus Arenicolites Polykladichnus Macanopsis Monocraterion Skolithos mottling	Different morphotypes were distinguished when sampling	621	3 trenches within a 0.25 m^2 area	Systematic sample traverse	Trench sampling
Facies					
pH	SERA art .04310 FT11	10	0.25 m^2	Selected sites	Environmental sampling
NO_2	Askoll nitrite test	10			
NO_3	Askoll nitrate test	10			
PO_4	Askoll phosphate test	10			
Salinity	D&D Seawater Refractometer	10			
Redox Potential	HANNA	10			
Redox Potential Boundary Layer depth		7			
Modified Brinell test		14 × 3 measures			
Emersion time		19			
Facies boundaries		5856	0.25 m^2	Geomorphologically controlled site distribution	Topographical sampling
Bathymetry		237		Selected sites	

Table 2
Facies and depositional environments.

Facies	Description	Environment
A — laminated sand	Tabular sand with parallel lamination, occasionally grading to homogeneous shelly sand with faint lamination. Small ripple patches may be found. Shell fragments often common.	Upper intertidal flats
B — rippled sand	Medium- to fine-grained sand with subordinate contributions of silt. Diagnostic presence of wave ripples with straight to sinuous crests.	Moderate-energy intertidal and subtidal
C — muddy sand	Grey-coloured sand with significant contributions of mud and vegetal debris. Sparse shelly bioclasts.	Protected lagoonal environment, intertidal to subtidal
D — filamentous mat	Muddy sand to sandy mud pervasively colonized by filamentous algae. Dispersed bioclasts.	Low-energy intertidal flats
E — laminated mat	Microbial mat represented by laminated sediments with an upper, organic-rich layer and a lower mineral-rich one. Very common structures related to growth (stabilized surfaces, biostabilized and levelled ripples), physical mat destruction (chips, erosional fringed edges, upcurled shrinkage cracks); presence of features linked with the metabolic activity (green and dark horizons).	Intertidal microbial mats
F — sandy firmground	Sandy firmgrounds with occasionally abundant bioclasts. Such deposits are often organized in decimetric layers.	Exhumation of dewatered sediments
G — gravel	Pebble-sized gravels with well-rounded clasts. Variable contribution of sands.	Exhumation of fluvial deposits; anthropic deposits

variable to weight the contribution of known values on a given location, based on the assumption that more distant observations have decreasing influence on its estimate (Matheron, 1962; Borradaile, 2003; Conolly and Lake, 2006; Felletti et al., 2006). For this reason, kriging is preceded by an analysis of the spatial structure of the data (variogram analysis; Fig. 4), which is integrated into the weighting procedure (Wackernagel, 2003). More precisely, it is required to define a model variogram (i.e. theoretical variogram) to fit the empirical variogram (i.e. experimental variogram). The variogram analysis of studied variables (i.e. the number of traces per sampling unit) quantifies the lateral correlation length of each sample separated by a distance *h* (usually called the *lag* distance). Variograms are usually described using two parameters: (a) the *range* is the lag distance at which all successive values are independent from each other; (b) the *sill* is the variogram value corresponding to the range. These parameters constitute one of the strongest constraints in the geostatistical analysis and, depending on their behaviour, they can reveal several spatial characteristics such as continuity, anisotropy, zone of influence, and the trends. Therefore variogram analysis was used as a descriptive tool for discerning the following spatial features (Fig. 4A):

1. Small scale variability: a sudden jump at the origin, termed nugget effect, usually mean that the studied variable (i.e. *Arenicolites* density) is characterized by small-scale fluctuations (Matheron, 1962; Caers, 2011).
2. Spatial correlation: the presence of a nugget effect does not necessarily correspond to erratic behaviour at all scales. In fact, the rate of increase of the variogram indicates how quickly the influence of a sample drops off with distance (Matheron, 1962; Armstrong, 1998).
3. Zone of influence: the mentioned increase could flatten off at a given separation distance, marking the range of the variogram (Matheron, 1962; Caers, 2011). When the variogram stabilizes on a ‘plateau’ (sill), there is no longer influence (correlation) between samples. Consequently, the range determines the maximum distance of sample-to-sample influence (Zuur et al., 2007).
4. Structure: a variogram can be characterized by other features, such as a bump (corresponding to a hole in the covariance), a ‘peaks-and-valleys’ shape (diagnostic of periodicity) and nested structures (significant of variations at different scales; Matheron, 1962; Sarma, 2009).

— Ichnoassociation composition: network theory (Réka and Barbási, 2002) was used to discern and explore patterns of association. This emerging scientific area, considered as “the new flag of the complexity sciences” (Bascompte, 2007), focuses on systems constituted by interconnected entities. In particular, network theory was applied to ichnoassociation analysis, based on the assumption that ichnotaxa assemble in complex weblike structures (‘ichnological networks’). Despite its vast employ in information science and ecology (May, 2006; Montoya et al., 2006; Bascompte, 2007) network analysis is a new field of application in ichnology and palaeontology as well. For this reason, theory and application of ichnological networks are more thoroughly discussed in Section 6.

- Ichnoassociation–environment relationship: one of the crucial goals is to describe the influence of the environment on the numbers and types of traces. In analogy with Legendre (2005), this aim was achieved by finding the ecological requirements common to most or all members of an ichnoassociation. In order to reach this aim, regularities were searched in the environmental parameters coupled to each ichnoassociation, typifying the most recurrent properties. The results were used to define a predictive model based on the major structuring processes of ichnoassociation composition and distribution.

4. Facies and environment

Within the study area, 7 sedimentary facies were recognized and mapped (Fig. 5). These were defined on the basis of texture, colour and primary physical sedimentary structures (Fig. 6). Each facies represents various combinations of environmental parameters that correspond to specific depositional environments. The descriptions of facies and their significance, based on field observations, are summarized in Table 2.

5. Spatial organization

This section presents the spatial distribution of ichnotaxa, as derived from quadrat and trench sampling. Spatial distribution is outlined with a descriptive approach, based on the geomorphological units distinguished in Figs. 1 and 5. Ichnotaxonomy is summarized in Table 3 and follows Baucon and Felletti (2013), to which the reader is addressed for a complete description of traces and their ethology. Ichnotaxa, to be considered as incipient (Bromley, 1996: p. 164), are presented with respect to a descriptive classification scheme, partly based on Książkiewicz (1977).

5.1. Branched structures

5.1.1. Thalassinoides form XL (very large)

Extensive burrow networks, assigned to the ichnogenus *Thalassinoides*, are commonly produced by the decapod shrimp *Pestarella candida* (Table 3). Sediment mounds, diagnostic of the studied structure, are restricted in environmental and sedimentological range (Figs. 7, 8). In fact, they are more abundant in the back-barrier zone,

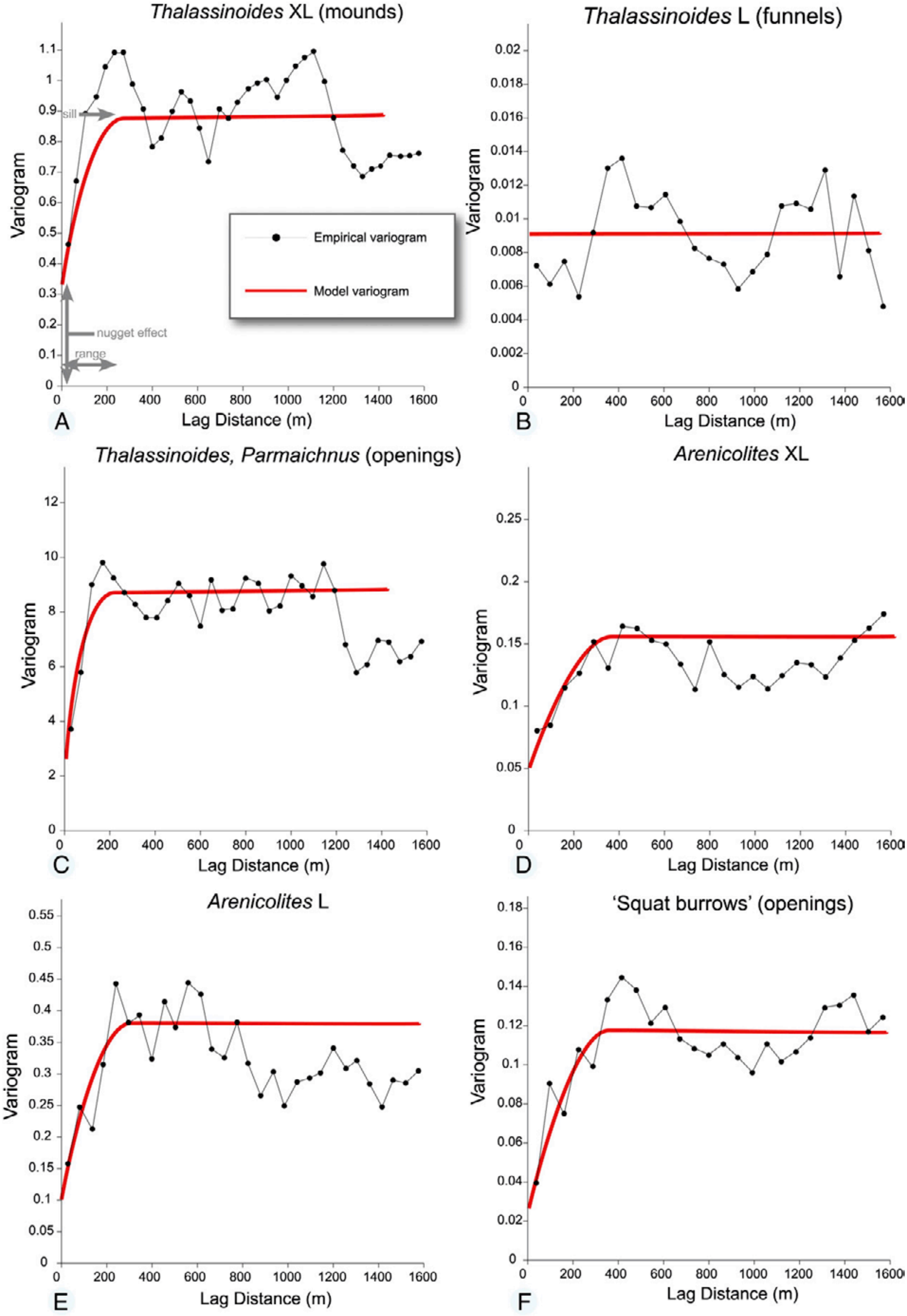


Fig. 4. Variogram analysis. (A) Nomenclature used in variogram analysis, superimposed to the variogram of *Thalassinoides* XL. (B) Variogram of *Thalassinoides* L (openings). (C) Variogram of *Thalassinoides*, *Parmaichnus* (openings). (D) Variogram of *Arenicolites* XL. (E) Variogram of *Arenicolites* L. (F) Variogram of the 'squat burrows'.

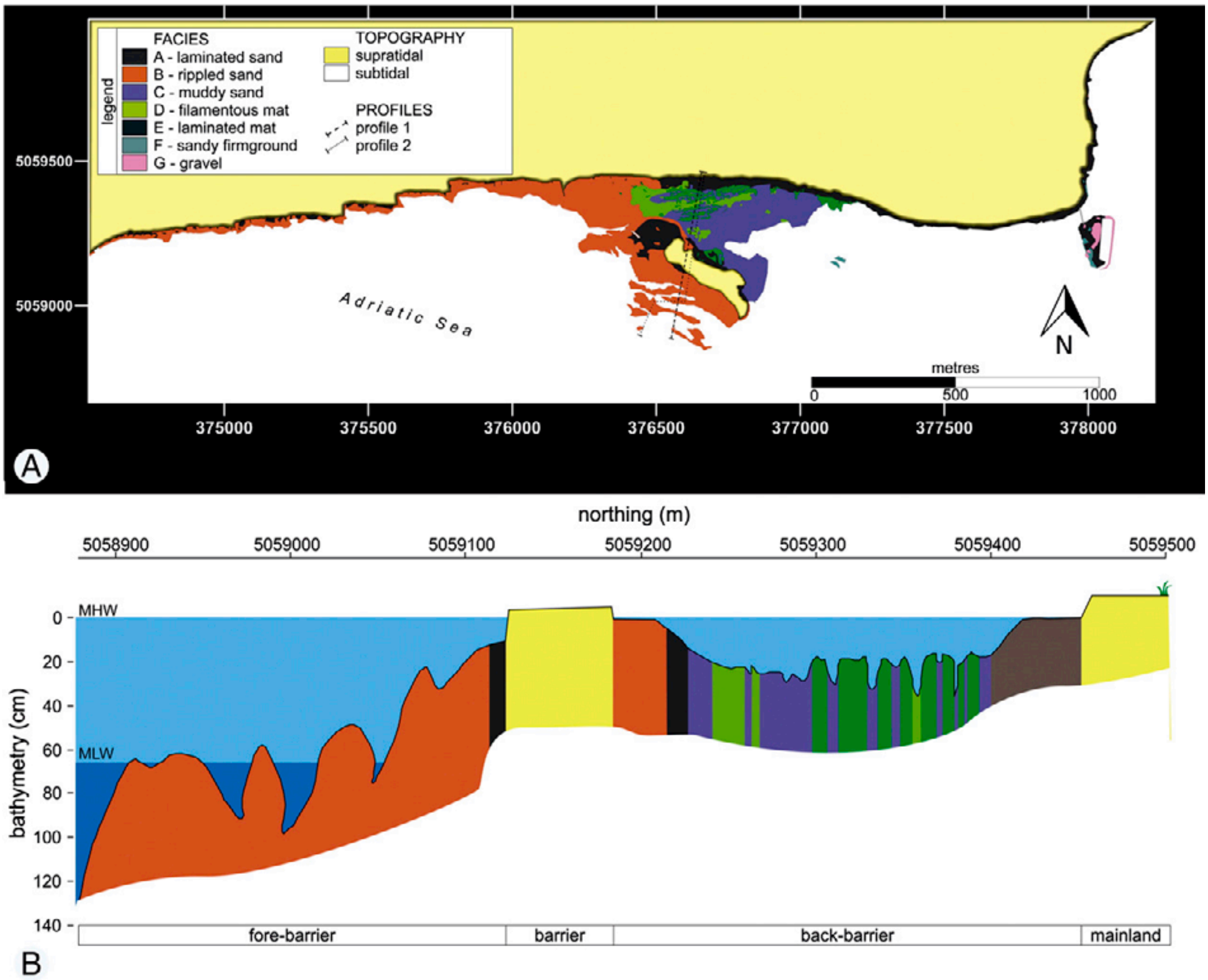


Fig. 5. Geological setting. (A) Facies map, drawn after quadrat, trench and topographical sampling. Coordinates indicate eastern and northing, referred to the UTM zone 33; the same convention is adopted throughout the paper. (B) Profile 1: cross-section of the barrier-island system showing facies distribution (colour codes in A). Sea-floor morphology based on 109 bathymetric measurements.

which is associated to protected conditions and disposability of organic material (Fig. 8). This spatial distribution is well represented by the variogram (Fig. 4A). In fact, the relative low value of the correlation range (~220 m) approximates the average lateral distribution of *Thalassinoides* XL, showing a produced correlation periodicity (a 'peaks-and-valleys' shape). The relative high value of the nugget effect (~50% of the sill), indicates a high discontinuity of the variable at short distance (close to the sampling points). The observed distribution

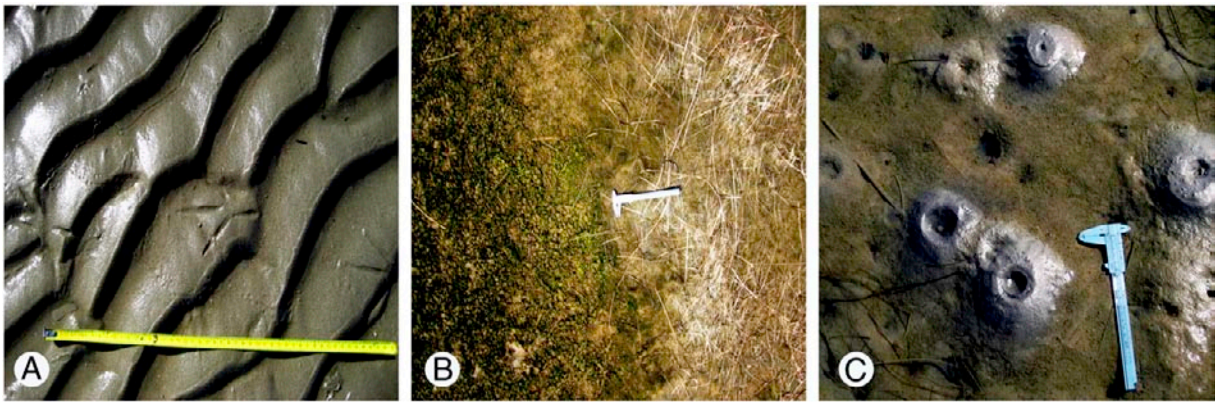


Fig. 6. Sedimentary facies. (A) Rippled sands (facies B). (B) Mat-related facies: algal mat (left, facies D) and microbial mat (right, facies E). (C) Muddy sands (facies C).

Table 3
Morphological, ethological and taxonomical features of the here studied ichnotaxa. Based on Baucon and Felletti (2013).

	Ichnotaxon	Amended description	Tiering depth	Dominant behaviour	Tracemaker
Branched structures	*Thalassinoides* XL	Burrow network with multiple openings	40 cm	Deposit feeding	*Pestarella candida* (Crustacea: Decapoda)
	Thalassinoides L	Burrow network with chambers filled by seagrass	20–40 cm	Deposit feeding	*Pestarella tyrrhena* (Crustacea: Decapoda)
	Parmaichnus	Y-shaped burrow with swellings	20–40 cm	Suspension feeding, ?deposit feeding	*Upogebia pusilla* (Crustacea: Decapoda)
	Polykladichnus	I- or U-shaped burrow with Y-shaped bifurcations	5–10 cm	Deposit feeding, suspension feeding	*Nereis diversicolor* (Annellida: Polychaeta)
U-burrows	*Arenicolites* XL	U-burrow	20–40 cm	Deposit feeding	*Sipunculus nudus* (Sipuncula: Sipunculidae)
	Arenicolites L	U-burrow	20–40 cm	Deposit feeding	*Sipunculus nudus* (Sipuncula: Sipunculidae)
	Arenicolites S	U burrow	3–10 cm	Deposit feeding, suspension feeding	*Corophium volutator* (Crustacea: Amphipoda)
Chambered burrows	‘Squat burrow’	Squat burrow with terminal disc.-shaped chamber	5–15 cm	Mating	*Carcinus maenas* (Crustacea: Decapoda)
	Macanopsis	Clavate burrow	2–7 cm	Feeding, sheltering, reproducing	*Heterocerus flexuosus* (Insecta: Coleoptera)
Winding structures	*Helminthoidichnites*	Unbranched horizontal burrow	<1 mm	Undermat mining	Dipteran larvae (Insecta: Diptera)
Simple structures	*Skolithos* L	Vertical burrow with 8-shaped opening	>15 cm	Suspension feeding	*Solen marginatus*, *Ensis ensis*, *Ensis minor* (Mollusca: Bivalvia)
	Skolithos M	Vertical burrow with constructional lining	10–15 cm	Suspension feeding	*Megalomma sp.* (Annelida: Polychaeta)
	Skolithos S	Vertical burrow	3–7 cm	?Suspension feeding	Worm-like organisms
	Skolithos XS	Vertical unlined burrow	1–5 cm	Sheltering	*Talitrus saltator* (Crustacea: Amphipoda)
	Monocraterion	Vertical burrow with funnel-shaped opening	10 cm	?Suspension feeding	Worm-like organisms
Miscellaneous group	*Lockeia* S	Almond-shaped burrow	3–5 cm	Suspension feeding	*Mactra coralline*, *Venus* sp. (Bivalvia: Venroida)
	Lockeia XS	Almond-shaped burrow	<3 cm	Suspension feeding	*Abra alba*, *Donax trunculus* (Bivalvia: Veneroida)
	Mottling	Indistinct bioturbation	1–40 cm	Rooting locomotion	*Zostera marina*, *Zostera noltii*, *Cymodocea nodosa* (Magnoliophyta: Najadales), *Nereis diversicolor* (Annellida: Polychaeta)

is in line with the distribution of the tracemaker, occurring in muddier and more proximal sediments respect to other thalassinidean shrimps (*Pestarella tyrrhena* and *Upogebia pusilla*, authors of *Thalassinoides* L and *Parmaichnus*, respectively; Ngoc-ho, 2003).

Despite its abundance in the middle intertidal, *Thalassinoides* XL is absent in the upper (landward) intertidal (Figs. 7, 9), probably in relation to prolonged subaerial exposure during low tide, which is a stressful condition for the producer.

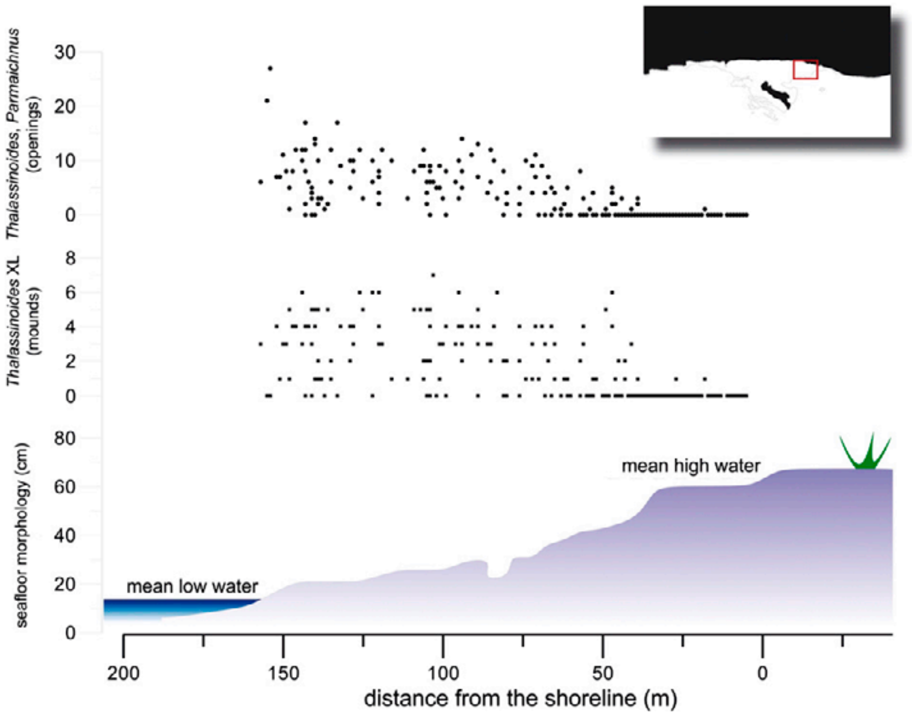


Fig. 7. Burrow density and geomorphological gradient. Scatterplots show the number of mounds (*Thalassinoides* XL) and openings (*Thalassinoides*, *Parmaichnus*) against their distance from the coastline. Source area in the inframe, centered on the barrier-island.

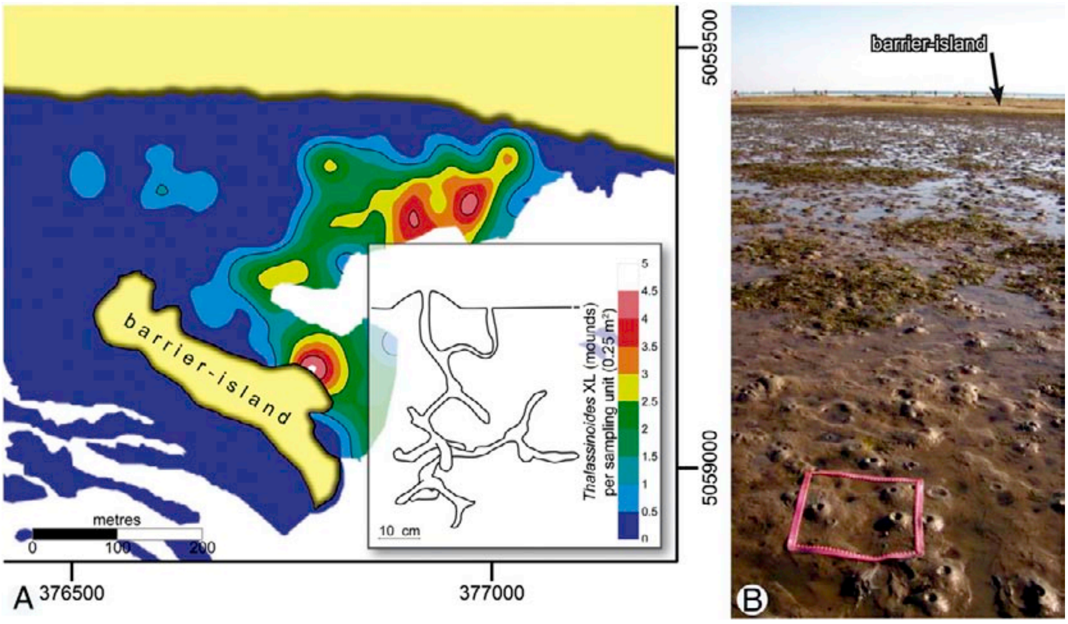


Fig. 8. *Thalassinoides* XL, as manifested by sediment mounds. (A) Density map of *Thalassinoides* XL (mounds). Burrow morphology based on Dworschak (2002). (B) A barrier-island (arrowed) separates the turbulent fore-barrier from the quieter back-barrier. Numerous sediment mounds characterize the back-barrier, here photographed at low tide. Quadrat for scale.

5.1.2. *Thalassinoides form L (large)*

Burrow networks with funnel-like openings and chambers filled with seagrass (*Thalassinoides* L; Table 3) are particularly abundant in the middle and lower intertidal of the fore-barrier. Similarly to *Thalassinoides* XL, this ichnotaxon is virtually absent from the upper tidal flat, probably because of low-tolerance to desiccation (Fig. 7). This interpretation is consistent with the physiology of the tracemaker, the decapod shrimp *Pestarella tyrrhena*. Variographic analysis indicates complete absence of spatial correlation (*pure nugget effect*), suggesting a highly discontinuous presence of this ichnotaxon or sampling error (*Thalassinoides* L is easily mistaken for *Monocraterion*; Fig. 4B).

5.1.3. *Parmaichnus*

Y-shaped burrows with swellings, assigned to the ichnogenus *Parmaichnus*, are produced by Upogebiid shrimps (Table 3). In the study area, *Parmaichnus* is absent from the landward part of the tidal flat (Fig. 7, 9). More in detail, *Parmaichnus* is related to back-barrier environments with abundant organic debris, corresponding to muddy sand facies (C). The environmental distribution of *Parmaichnus* overlaps with that of *Thalassinoides* XL, although the latter prefers more proximal environments. This observation corroborates the distribution of the respective tracemakers, summarized in Ngoc-ho (2003). *Parmaichnus* is also associated to firmgrounds, which are characterized by dense monoichnospecific assemblages (since a maximum of 25

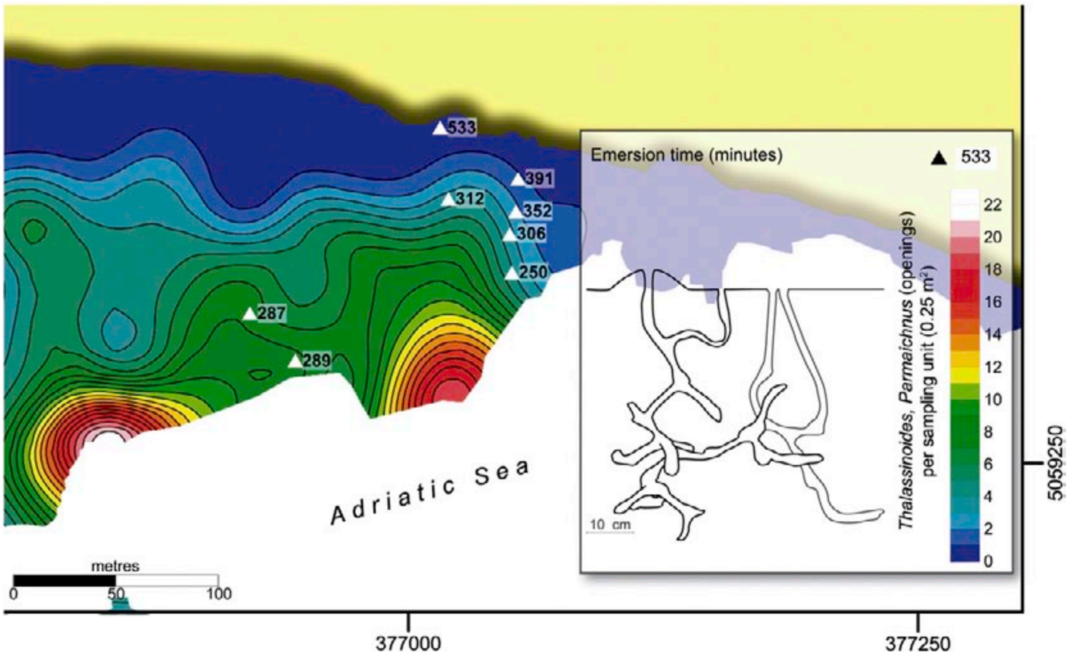


Fig. 9. Emersion time and density map of decapod burrows (*Thalassinoides*, *Parmaichnus*). A clear trend is evidenced: the longer the emersion time, the lower the burrow density. Burrow morphology based on Dworschak (1987, 2002).

openings of *Parmaichnus* per sampling unit). This observation is in line with the fossil record of *Parmaichnus* (Pleistocene firmground muds: Pervesler and Uchman, 2009) and with some recent occurrences of Upogebiid burrows (Asgaard et al., 1997; Gingras et al., 2001).

Variographic analysis indicates a correlation range of ~180 m that reflects the smaller lateral continuity of *Parmaichnus* rather than that found in the *Thalassinoides XL* (Fig. 4C). The relative high value of the nugget effect (~50% of the sill), indicates small-scale fluctuations of the variable at short distance (close to the sampling points).

5.1.4. *Polykladichnus*

The ichnogenus *Polykladichnus*, consisting of I- or U-shaped burrows with Y-shaped bifurcations (Table 3), is restricted to the back-barrier area, with high densities associated to algal and microbial facies (facies D and E; Fig. 10). The highest densities correspond to the central area of the tidal flat, which is characterized by high organic content and dysoxic conditions. This phenomenon could be explained by the high sulphide detoxification in the tracemaker *Nereis diversicolor*, which allows it to stay in sulphide-rich patches (Vismann, 1990). Accordingly, Engelsen et al. (2010) provided experimental support that *Nereis diversicolor* can tolerate periods of oxygen depletion and feed on macroalgal mats.

5.2. U-burrows

5.2.1. *Arenicolites form XL (very large)*

In the study area, sipunculan worms inhabit deep U-shaped burrows, corresponding to the ichnogenus *Arenicolites* (Table 3). The largest morphotype, presenting a single pile of sediment casts, is almost exclusively associated to the sandy sediments of the fore-barrier, being particularly abundant on longshore bars at the intertidal–subtidal limit (Fig. 11). The observed pattern is in accordance with the typical distribution of the tracemaker, common in sandy, unvegetated tidal flats with high and stable salinity. Low emersion times, moderately reducing conditions and moderate hydrodynamics are also typical environmental conditions associated to peanut worms (Ha et al., 2007). In particular, grain size seems to be an important control factor on distribution of Sipuncula, with a preference for sandy sediments (Cutler, 1994; Ferrero-Vicente et al., 2011). Within this depositional environment, *Arenicolites* XL shows a very good lateral continuity (Fig. 4D). This spatial distribution is well represented by the relative high value of the variogram range (~400 m), even though the value of the nugget effect (~30% of the sill) indicates a discontinuity of the variable at short distance (close to the sampling points).

5.2.2. *Arenicolites form L (large)*

Large U-shaped burrows surrounded by sediment casts, radially arranged, are produced by deposit-feeding sipunculan worms (Table 3). Quadrat sampling indicates that this form, corresponding to the ichnogenus *Arenicolites*, is particularly abundant in the fore-barrier, whereas it is patchily distributed in the back-barrier (Fig. 12). Maximum densities (24–36 burrows per m^2) are reached at about 80 m from the shoreline (high tide line). The observed pattern is in line with the environmental requirements of the tracemaker, a sipunculan worm (Cutler, 1994; Ha et al., 2007; Ferrero-Vicente et al., 2011). Variographic analysis indicates a correlation range of ~200 m that reflects the smaller lateral continuity of *Arenicolites* L. rather than that found in the *Arenicolites* XL (Fig. 4D–E). The relative low value of the nugget effect (~25% of the sill), indicates a good lateral continuity of the variable at short distance (close to the sampling points).

5.2.3. *Arenicolites form S (small)*

The amphipod *Corophium* inhabits small U-shaped burrows, which are distributed either in the fore- or in the back-barrier. More specifically, these structures are corresponding to the ichnogenus *Arenicolites* (Table 3). They are restricted within a belt extending between 40 and 250 m from the shoreline (Fig. 10). The observed

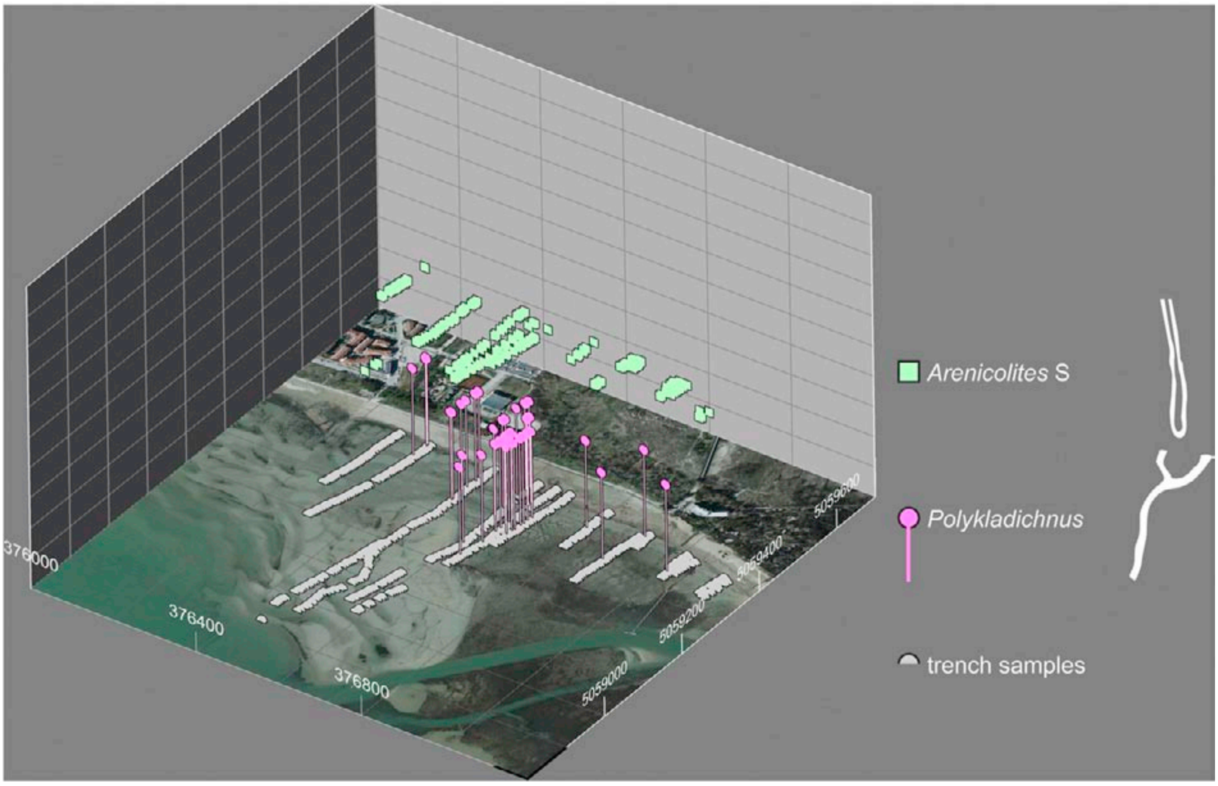


Fig. 10. Occurrences of *Polykladichnus* and *Arenicolites* S within trench sampling. Both traces are abundant in the back-barrier, usually associated to algal turfs and microbial mats. Coordinates in metres. For graphical clarity, vertical drop lines have not been traced for *Arenicolites* S.

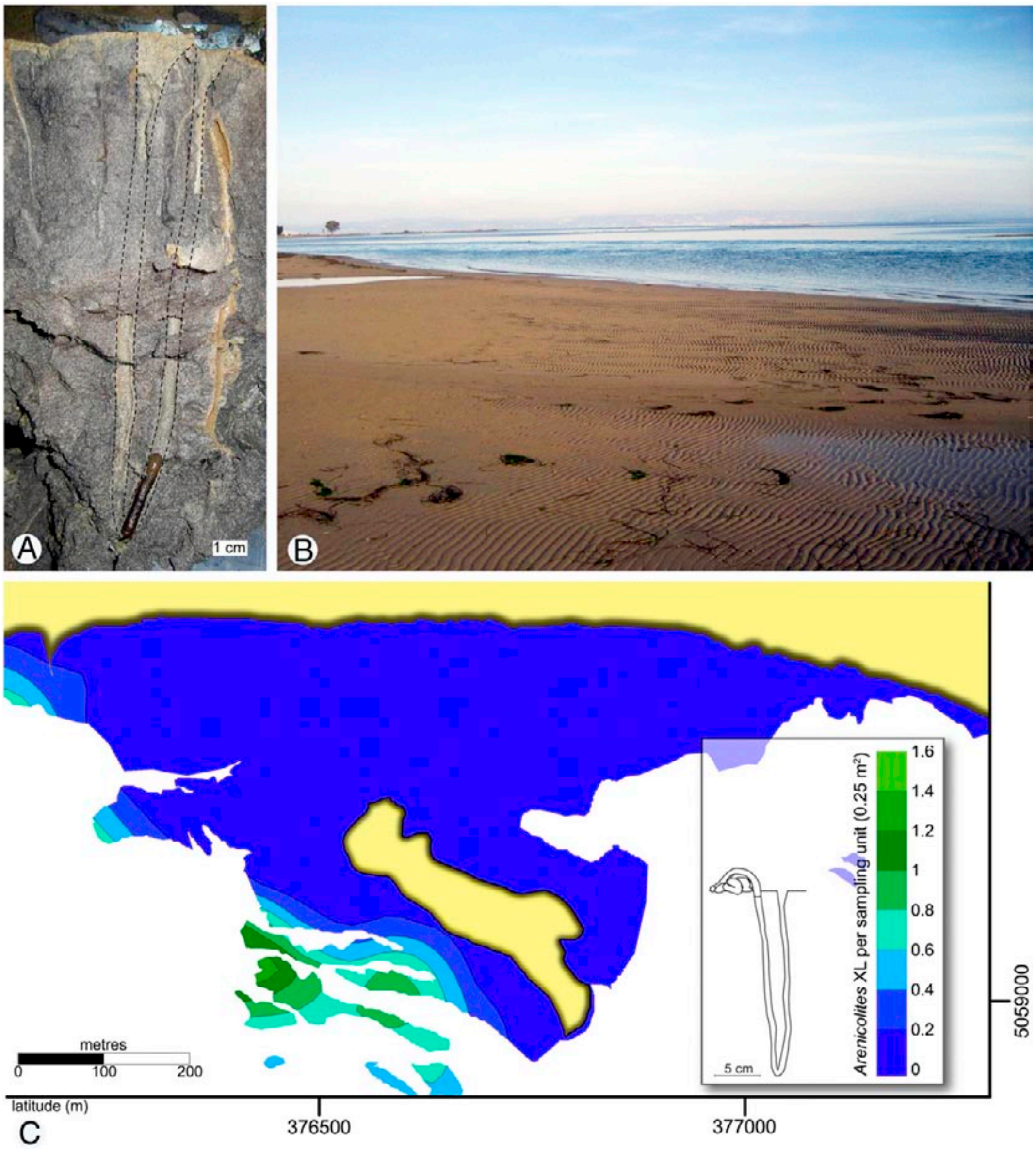


Fig. 11. *Arenicolites* XL. (A) *Arenicolites* XL with its tracemaker, a sipunculan worm. Burrow outlined with dashed line.(B) The typical environment of *Arenicolites* XL: fore-barrier with rippled sands. (C) *Arenicolites* XL, density map.

pattern is in line with literature data on the distribution of the tracemaker *Corophium* (Beukema and Flach, 1995).

Within the study area, the highest densities of *Arenicolites* S are concentrated in the middle-upper part of the aforementioned belt, largely but not exclusively dominated by biomats (Fig. 10). This distribution reflects the environmental niche of the tracemaker *Corophium volutator*, which prefers muddy dysoxic sediments respect to well-oxygenated sands (Gamble, 1971). On North Sea tidal flats, microbial mats and other microphytobenthos-rich environments are characteristically associated to U-burrows produced by *C. volutator* and *Corophium arenarium*, which feed on diatoms and bacteria (Gerdes et al., 1985; Gerdes, 2003; Andersen et al., 2010).

5.3. Chambered burrows

5.3.1. 'Squat burrow'

During mating season, green crabs (*Carcinus maenas*) build burrows with a low depth/diameter ratio, commonly presenting a terminal disc-shaped chamber (Table 3). These structures, interpreted as mating burrows (Baucon and Felletti, 2013), occur only in the back-barrier, being almost exclusively associated to filamentous algal mats (facies D; Fig. 13). This pattern is clearly shown by quadrat sampling, which reveals maximum densities (5 openings per sampling unit, 0.25 m^2) in the eastward filamentous mats. Moksnes (2002) evidenced the importance of filamentous algal mats for *Carcinus maenas* by showing the habitat selectivity of its megalopae. Possibly, these results confirm the hypothesis that *Carcinus maenas* prefers structured, nutrient-rich habitats during delicate periods of its lifecycle. Indeed filamentous mats provide shelter, nutrients and easy-to-burrow substrates. 'Squat burrows' could also trigger a positive feedback in the filamentous mats by influencing the nitrogen cycle (Vopel and Hancock, 2005). It should be noted that, serving as a mating burrow, 'squat burrows' are produced only during the breeding season. For this reason, trench sampling — conducted after quadrat sampling — did not reveal specimens of 'squat burrows'.

Within this depositional environment, this ichnotaxon shows a very good lateral continuity (Fig. 4F). The spatial distribution is well portrayed by the relative high value of the variogram range (~400 m).

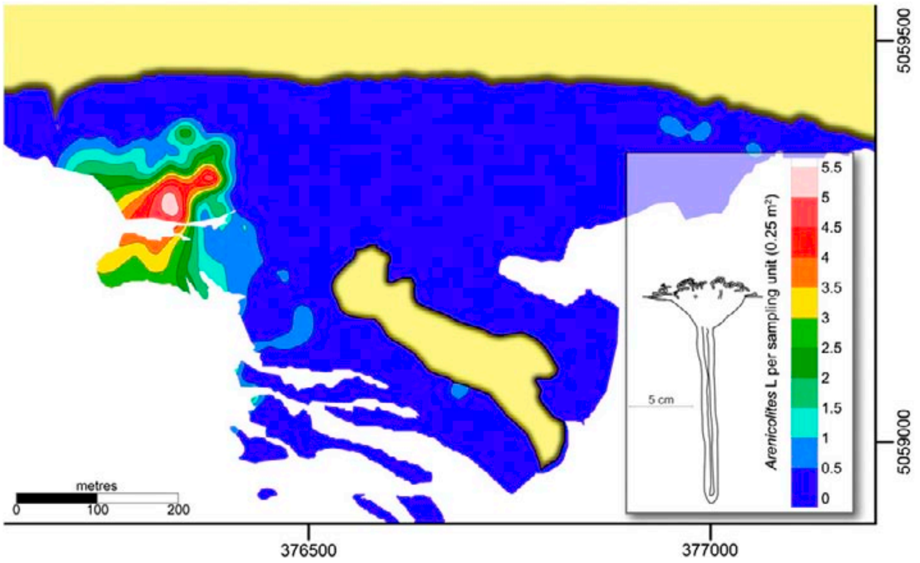


Fig. 12. *Arenicolites* L, density map.

Moreover, the low value of the nugget effect (~25% of the sill) point to a good lateral continuity of the variable at short distance (close to the sampling points).

5.3.2. Macanopsis

The biomats of the study area are commonly burrowed by heterocerid beetles, which produce clavate chambers with convolute necks. The distribution of these structures, corresponding to the ichnogenus *Macanopsis* (Table 3), is strongly controlled by biomats (Figs. 14, 15). In fact, 97% of the samples with *Macanopsis* were recovered from laminated mats (facies E). The geotechnical proprieties of the microbial mat provide an explanation for this strict trace distribution pattern, as the biofilm isolates immature forms from predators and physical stress. At the same time, the microbial mat itself constitutes a source of nutrients, readily available to both adults and juveniles (see Evans and Hogue, 2006). Synecological factors are equally important; being submerged during high tide, microbial mats offer a secure protection from terrestrial vertebrates. Few marine invertebrates can compete for space with insects, as the laminated microbial mats are characterized by reducing conditions, noxious phosphate content and moderate to high exposure time (see also Baucon, 2008: p. 198).

These observations support the idea of insect burrows as indicators of biomat-dominated environments (see Gerdes, 2003). In fact, chambered burrows produced by insects are reported from microbial mats of both temperate and arid conditions (Farmer, 1992; Gerdes, 2003). In particular, Gerdes et al. (1985) described heterocerid and staphilinid burrows as typical traces of the Mellum island tidal flats. Finally, insect traces are also associated to lacustrine microbial mats (Scott et al., 2009).

5.4. Winding structures

5.4.1. Helminthoidichnites

In the study area, unbranched horizontal burrows, consistent with the ichnogenus *Helminthoidichnites*, are strictly related to biofilms (Table 3; Figs. 14, 15). These structures are produced by dipteran larvae, following the interface between the organic-rich and the mineral-rich layer of the microbial mats. More than the 92% of the occurrences are associated to laminated microbial mats, suggesting an undermat mining behaviour *sensu* Seilacher (1999). This strict distribution pattern is explained by the abundant nutrients associated to the microbial mat. Furthermore, the microbial mat offers a significant protection from predators and physical stress. These observations are in line with previous data on dipteran tracemakers (Scott, pers. com.; Seilacher, 1999; Gingras et al., 2011a).

5.5. Simple burrows

5.5.1. Skolithos form L (large)

Razor clams produce deep vertical burrows with 8-shaped openings, resembling the ichnogenus *Skolithos* (Table 3). Trench sampling revealed the presence of the studied morphotype within the fore-barrier, mostly on sandbars at the intertidal–subtidal limit (Fig. 16). This observation is in line with the suspension-feeding behaviour of razor clams, requiring sufficient turbulence for suspending nutrients. The spatial pattern of *Skolithos* L is also supported by the typical distribution of the tracemakers, which are generally associated to oxygenated sandy bottoms, moderate degree of wave exposure and upper intertidal to lower subtidal conditions (Holme, 1954; Ruppert and Fox, 1988).

5.5.2. Skolithos form M (medium)

In the study area, sabellid worms inhabit straight vertical burrows with constructional lining, which are consistent with the ichnogenus *Skolithos* (Fig. 17; Table 3). Trench sampling shows clear evidence of the importance of physical factors in the distribution of this morphotype. In fact, *Skolithos* M is absent in the upper and middle intertidal, while it becomes abundant towards the lower intertidal of the fore-barrier (Fig. 16). Semiquantitative observations recorded its presence in shallow subtidal bottoms, at a maximum depth of 1.5 m.

The observed distribution suggests a positive correlation with turbulence, which is needed for suspending the nutrients for sabellid feeding (Dame et al., 2001). Such pattern confirms the classical distribution of sabellid worm aggregations, generally found on sandy intertidal and near subtidal zones (Dame et al., 2001).

5.5.3. Skolithos form S (small)

Small vertical burrows, resembling the ichnogenus *Skolithos*, are widely distributed on the tidal flat, with the exception of the lowermost intertidal (Table 3). Highest densities are reported from the middle sector of the fore-barrier.

5.5.4. Skolithos form XS (very small)

Talitrid amphipods excavate shallow vertical burrows, corresponding to the ichnogenus *Skolithos* (Table 3). In particular, this morphotype marks very precisely the supratidal–intertidal limit (Fig. 16). This zonation is explained by the physiology of its tracemaker, which needs

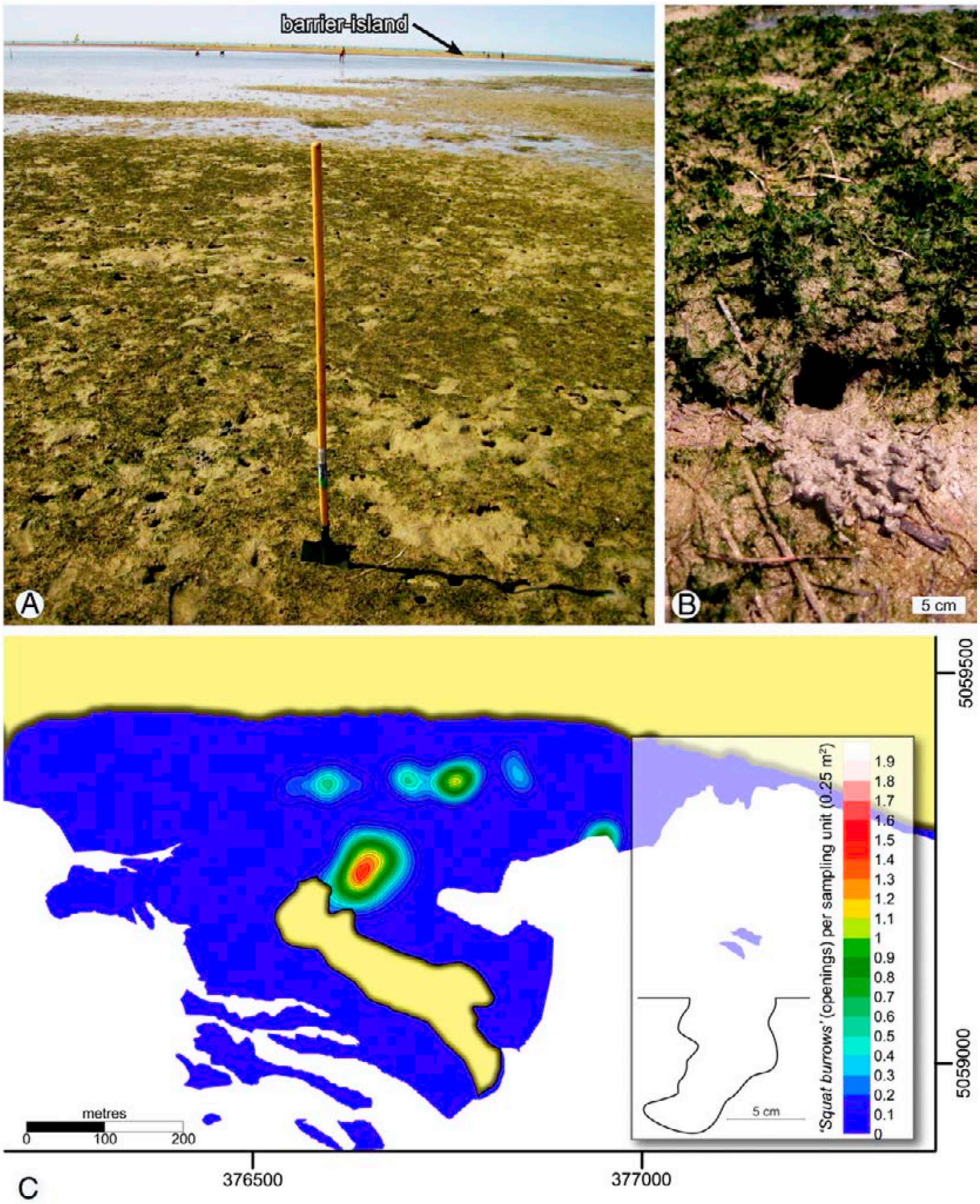


Fig. 13. 'Squat burrows'. (A) Filamentous algal mat with numerous openings of 'squat burrows' produced by crabs. (B) Close-up of a filamentous mat with the opening of a 'squat burrow'. (C) Density map.

sufficient moisture but suffers from abrupt inundation (Williams, 1983, 1995). Trophic strategy is an additional element of explanation, as stranded algae tend to concentrate in the extreme upper intertidal zone.

For these reasons this morphotype is potentially a very precise environmental indicator, confirmed by similar zonation patterns reported by Williams (1983) and Little (2000). Nevertheless, these burrows present low fossilization potential, although Williams (1983) described deeper talitrid burrows (up to 100 cm) and some fossil examples are known from Cornwall (Scourse, 1996).

5.5.5. *Monocraterion*

Vertical burrows with a funnel-shaped opening (*Monocraterion*; Table 3) are limited to the middle to distal fore-barrier. These structures are easily confused with the vertical shafts of *Thalassinoides* L, also presenting a funnel-like opening.

5.6. Miscellaneous group

5.6.1. *Lockeia* form S (small)

Bivalves, among which *Mactra corallina* and *Venus* sp., are responsible for almond-shaped burrows resembling the ichnogenus *Lockeia* (Table 3). Trench sampling evidenced high densities of *Lockeia* S on the longshore bars that characterize the fore-barrier sector. Nevertheless, a previous study (Baucon, 2008) reported large specimens from muddier, more protected sectors of the study area. Gingras et al. (2012) interpret *Siphonichnus* as a typical component of tidal deposits.

5.6.2. *Lockeia* form XS (very small)

Small specimens of *Lockeia* are found either in the back-barrier or in the fore-barrier. Nevertheless, higher densities are usually related to the back-barrier lagoon in mat-dominated areas.

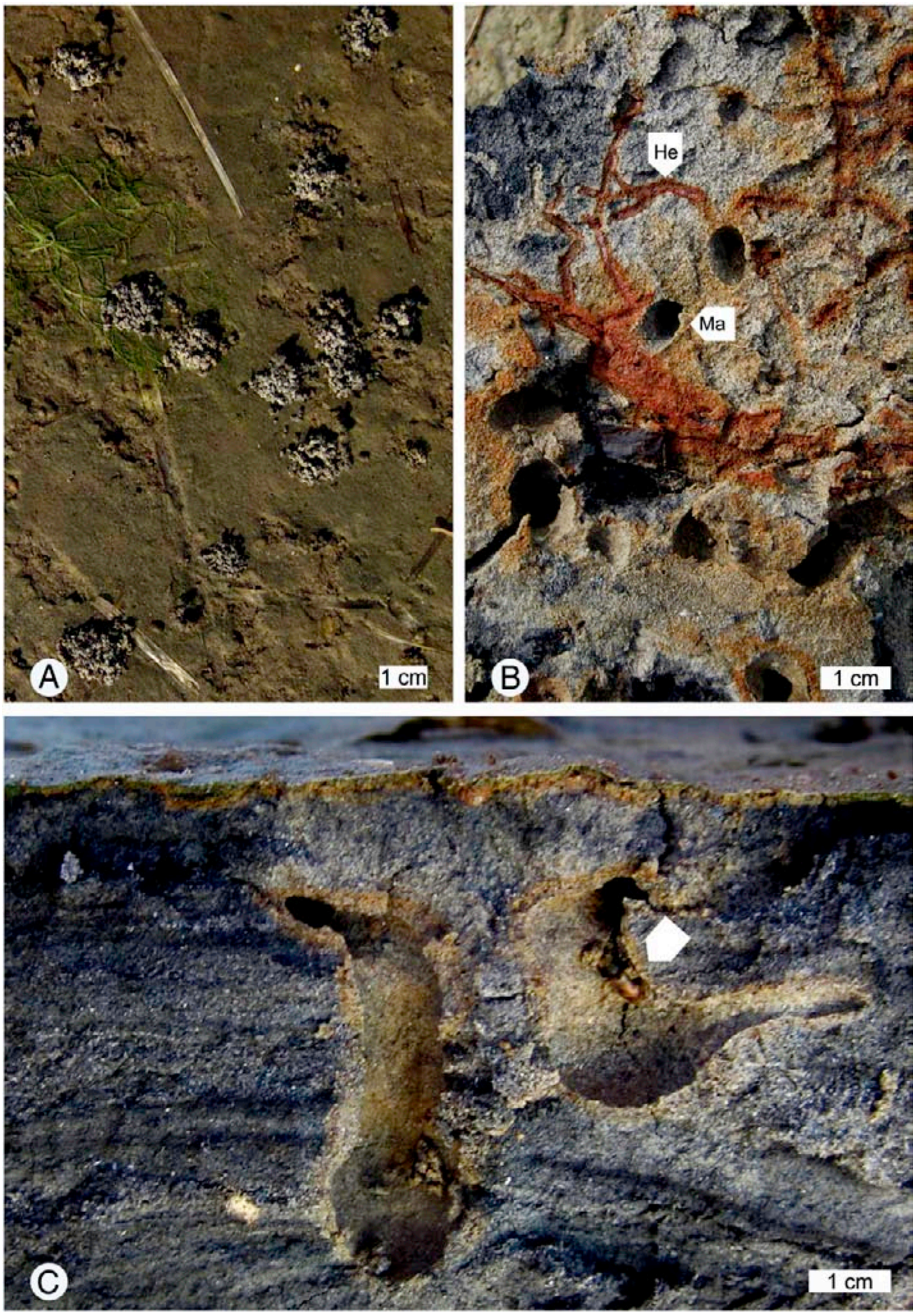


Fig. 14. Insect traces. (A) Top view of the microbial mat with numerous sediment piles, deriving from the burrowing activity of heterocerid coleopterans. The correspondent burrow is *Macanopsis*. (B) After peeling off the topmost horizons of the microbial mat, numerous insect burrows are visible: *Helminthoidichnites* (He) and *Macanopsis* (Ma). (C) Profile view of two specimens of *Macanopsis*, produced by heterocerid coleopterans (arrowed).

5.6.3. Mottling

The roots of marine phanerogams are among the major bioturbating agents of the studied site, as they are responsible for intense reworking of the sediment. The resulting mottling is restricted to the back-barrier, where it is usually associated to the middle and lower intertidal. This distribution pattern is explained by the environmental requirements of the major group of tracemakers, marine phanerogams, which suffer severely from desiccation. Indeed, according to recent studies (Koch, 2001; Boese et al., 2003), emersion time and the resulting desiccation stress is the most important factor setting the upper limit of seagrasses. In particular, Koch (2001) defined the minimum depth of seagrass distribution as half the tidal amplitude.

As concerns the association with protected settings, it is difficult to provide a 'cause-and-effect' explanation. Indeed seagrasses are ecosystem engineers which attenuate current speed and wave energy, producing a positive feedback on their own growth (Koch, 2001). For instance, currents in seagrass beds can be 2–10 times slower than in adjacent unvegetated areas, while wave attenuation in *Zostera* meadows can reach the 43% (Koch, 2001). According to this interpretation, marine phanerogams are both the cause and the effect of low-energy settings.

In some cases, mottling can be ascribed to the burrowing activity of polychaetes in water-saturated substrates. In such conditions, distinct tunnels cannot be produced, while polychaetes leave convolute

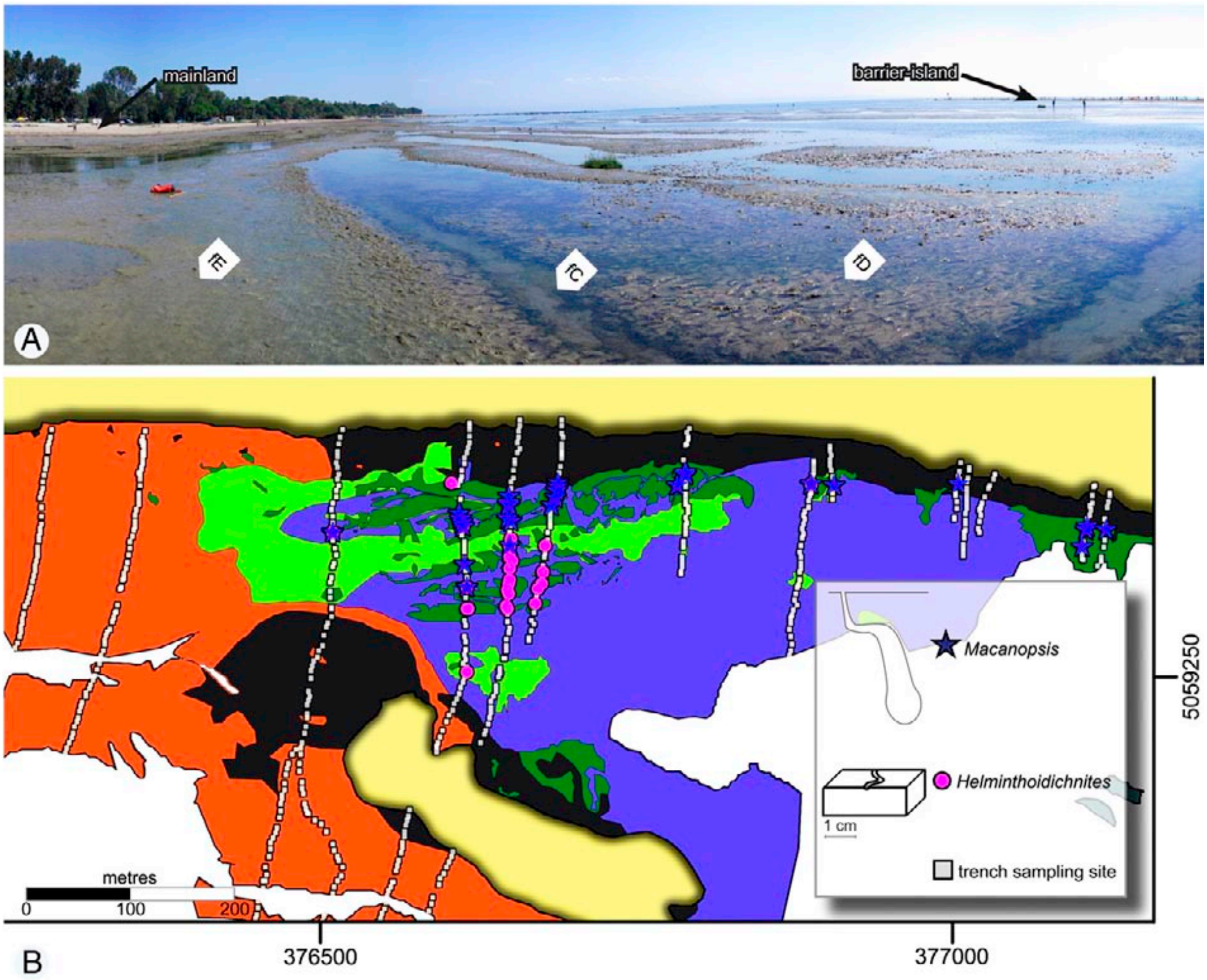


Fig. 15. Microbial mats and their ichnofauna. (A) Stitched panorama of the tidal flat during lowering tide. Laminated microbial mats (fE: facies E) constitute topographical highs with respect to filamentous mats (fD: facies D) and muddy sands (fC: facies C). (B) *Macanopsis* colonizes the laminated microbial mats of the high intertidal, while *Helminthoidichnites* is more distal.

structures similar to the 'mantle and swirl' traces described by Lobza and Schieber (1999).

6. Ichnological networks

6.1. Quantification of the degree of association

After breaking down the Grado ichnological system into single elements (ichnotaxa), the next logical step is to reassemble them and analyze how they work together. This is a typical task of complexity science, although some aspects have already been introduced in ecology and palaeoecology. For instance, the search for taxa associations is one of the classical problems of community ecology as they provide a conceptual framework to synthesize environmental and ecological characteristics (Legendre, 2005). This philosophy proves to be extremely useful in ichnology, where ichnoassociations are the major building-blocks of (palaeo)environmental analysis. Consequently, a question might arise: what are the recurrent groups of traces in the studied ichnosite?

Life sciences provide several statistical methods for finding associations of taxa, but their major limitation is to assume, for each taxon, within-taxon randomness of the spatial distribution patterns (Roxburgh and Chesson, 1998). On the contrary, the studied trace distribution is characterized by patchy patterns. In fact variogram analysis evidenced that the Grado dataset is characterized by positive spatial autocorrelation, therefore violating the principle of within-taxon randomness.

For overcoming this problem, a method based on probability analysis was followed. In fact ichnoassociation analysis can be approached by measuring the degree to which different ichnotaxa are associated in nature. For instance, a measure of association between *Macanopsis* and *Polykladichnus* is the number of samples presenting both of these ichnogenera (associated occurrences).

Nevertheless, this number of associated occurrences does not provide an immediate description of the likely co-occurrence of two ichnotaxa. This issue is solved by considering the proportion between the number of associated occurrences and the samples with one ichnotaxon (A) or the other (B):

$J_{A,B} =$ Number of samples with A and B/number of samples with A or B.

This measure of association corresponds to the Jaccard similarity for absence-presence data, a robust index which is widely used in numerical ecology (Wheater et al., 2011) and palaeontology (Hammer and Harper, 2006). It can be seen as a probabilistic measure of association, answering to questions such as: what is the probability of finding both ichnogenera if at least one of them is present in the sample?

By calculating the Jaccard index for each pair of ichnotaxa, an association matrix is obtained, where each cell measures the probability of association between two ichnotaxa. This association matrix is

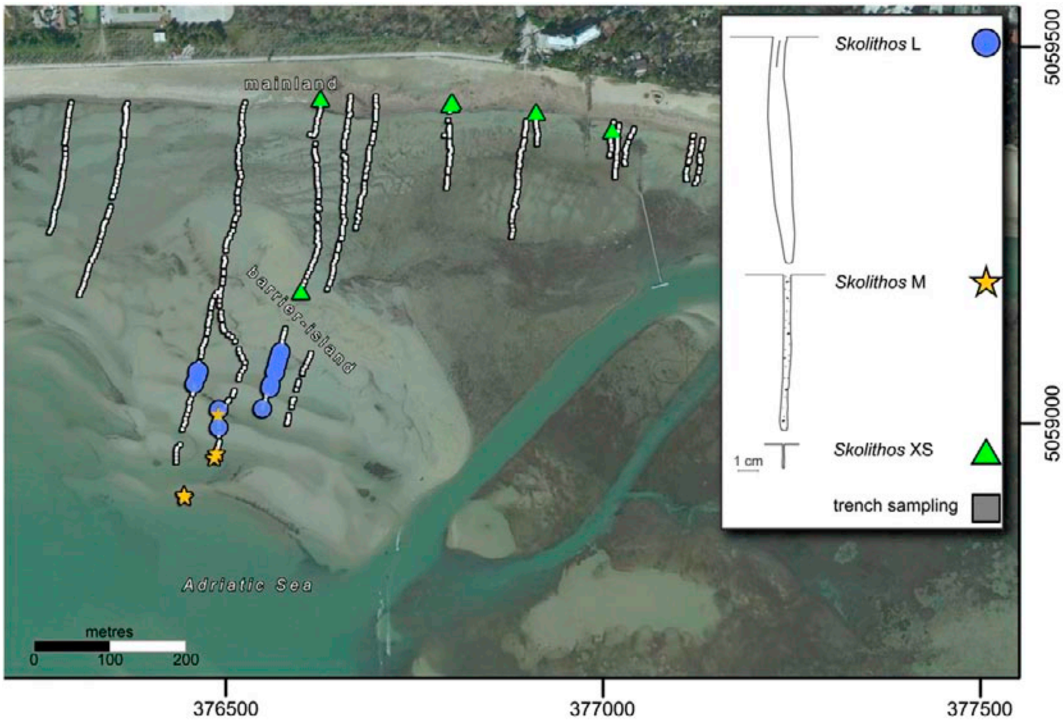


Fig. 16. Distribution of the major morphotypes of *Skolithos* according to trench sampling. Base map from Fig. 1B.

conveniently visualized by a heat map, which represents each value in the matrix as a colour (Fig. 18).

6.2. Ichnonetwork analysis

6.2.1. Ichnological systems are networks

Although the association matrix displays coherently the relationships between ichnotaxa and their strength, patterns are difficultly perceived. This problem emerges from the complex structure of ichnological systems, comparable to webs of mutually associated ichnotaxa. This conceptual image offers an immediate analogy with information networks, typically constituted by blocks of information (nodes) linked by connections (edges) (Brandes and Erlebach, 2005). Typical examples include food webs, neural networks and the Internet (Buchanan, 2003). Similarly, ichnological systems have their nodes (ichnotaxa), some of which are connected to form ichnoassociations. In a network perspective, the association matrix of Fig. 18 can be seen as an adjacency matrix, defining which nodes (ichnotaxa) are connected (associated) to which other nodes (Junker and Schreiber, 2008).

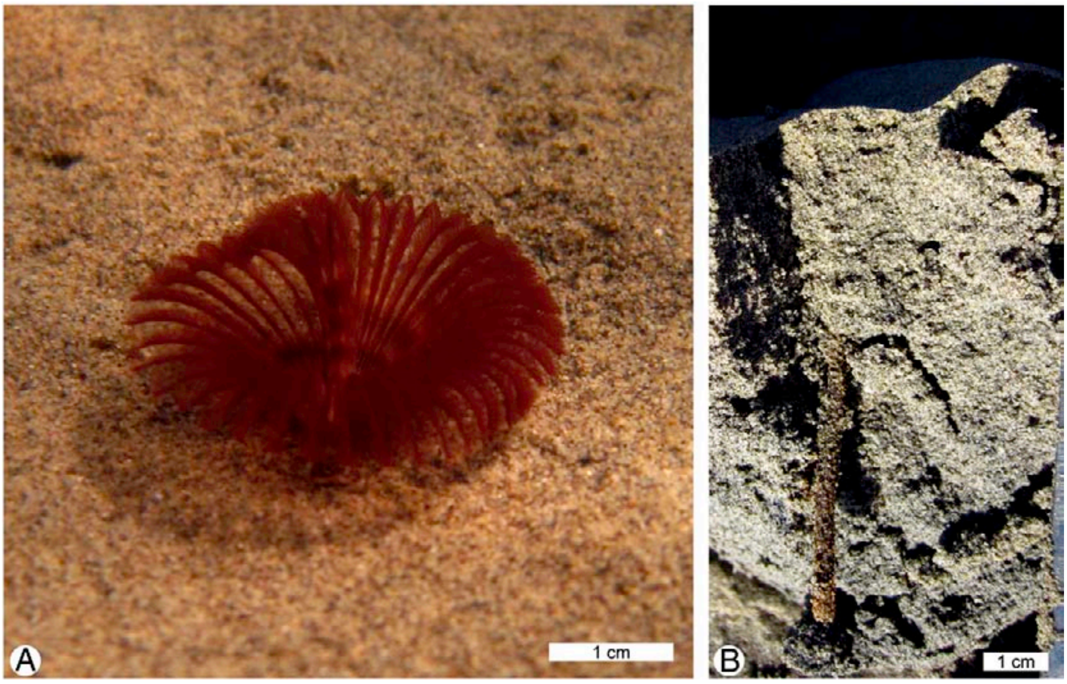


Fig. 17. *Skolithos* M. (A) The polychaete *Megalomma*, emerging from its burrow (*Skolithos* M) for suspension-feeding. (B) *Skolithos* M, profile view. Note the constructional lining.

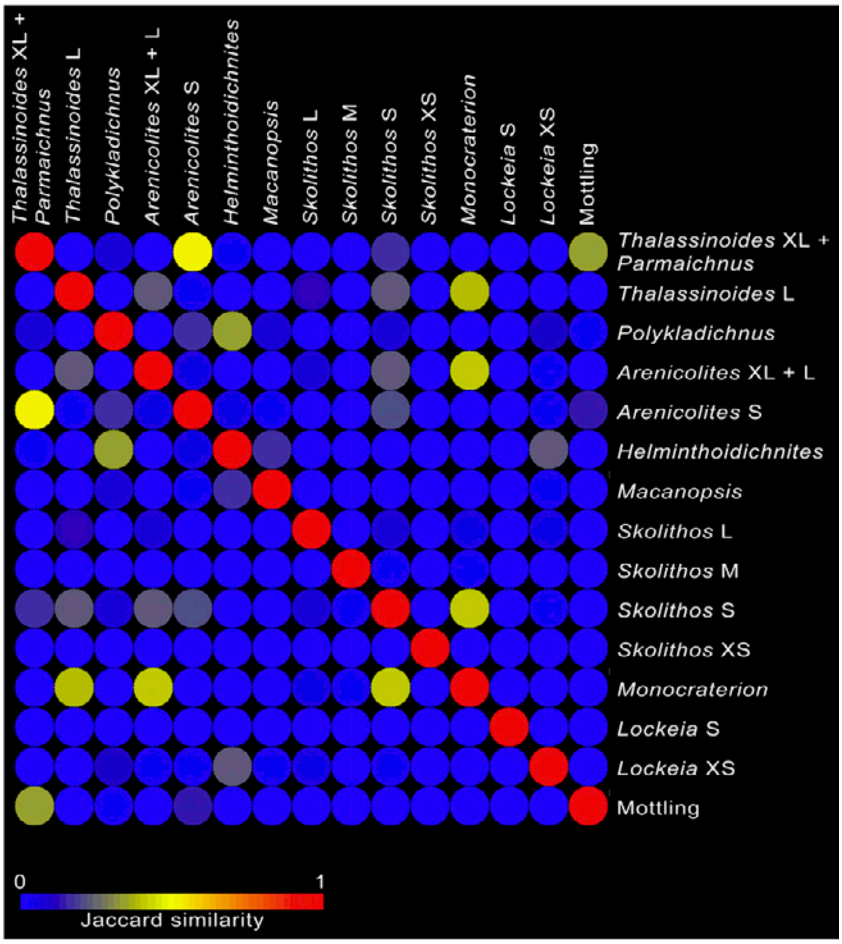


Fig. 18. Association matrix. Each cell measures the probability of co-occurrence of two ichnotaxa, as expressed by the Jaccard similarity.

The studied ichnological system is conveniently represented by a circular layout graph ('ichnonet graph'; Fig. 19), in which ichnotaxa are placed onto a circumference and each connection is drawn as a line. More in detail, the positive entries of the association matrix (Fig. 18) record the presence of a connection between node pairs, and its weight (Sporns, 2010). As a result, the ichnonet graph maps which ichnotaxon is associated to which other.

As stated above, the ichnonet graph displays not only the presence of a connection between ichnotaxa, but also records the intensity of each relation. For instance, an intense degree of association is found between *Arenicolites* S and *Thalassinoides* XL + *Parmaichnus* (Fig. 19). Although some weighted metrics exist for valued graphs, concepts, definitions and software are not as well developed as they are for graphs and directed graphs (Wassermann and Faust, 1994; Brede and Boschetti, 2009). For this reason, traditional metrics are adopted for describing the Grado ichnonet, while weights are taken into account when discerning ichnoassociations (Section 6.3).

6.2.2. Degree and network density

The most immediate feature of the network is that each ichnotaxon (node) has a varying number of connections (edges) with other ichnotaxa (Fig. 20A). This number, termed degree of connection (Scott, 2000), provide important information about the internal organization of the Grado ichnological system (Table 4):

1. Isolated nodes: *Skolithos* XS and *Lockeia* S have no edges incident to them. This property indicates that these ichnotaxa occur as monoichnospecific assemblages.
2. High-degree nodes: many edges meet *Skolithos* S, *Arenicolites* S, *Lockeia* XS, *Arenicolites* XL + L and *Thalassinoides* XL + *Parmaichnus*. Although these traces co-occur with many others, these nodes are not necessarily environment-crossing ichnogenera. In fact, node degree measures the number of ties only, while environment-crossing ichnogenera are usually appearing in multiple ichnological contexts.

Whereas degree refers to the number of connections incident with each node, it is possible also to consider the number of connections in the network as a whole (Wassermann and Faust, 1994). More in detail, it is useful to measure how close is our network to the full saturation of connections. In the Grado ichnonetwork, the 42.9% of all possible connections are present (network density: 0.429). This measure shows that the Grado ichnonetwork is not a highly-ordered regular graph, but heterogeneities are present.

6.2.3. Bridge ichnotaxa

Although an ichnotaxon might be associated to others (Fig. 20A), it could be central for a local group of ichnotaxa (Fig. 20B) or, alternatively, it could be central for the whole network (Fig. 20C). For this reason, it is important to take into account those ichnotaxa that act as a bridge between different groups of ichnotaxa, potentially connecting different ichnoassociations and/or subenvironments. In other words, the goal is to find those nodes that lie between many others.

This problem can be solved by considering node betweenness, a centrality measure that examines 'how between' a node is

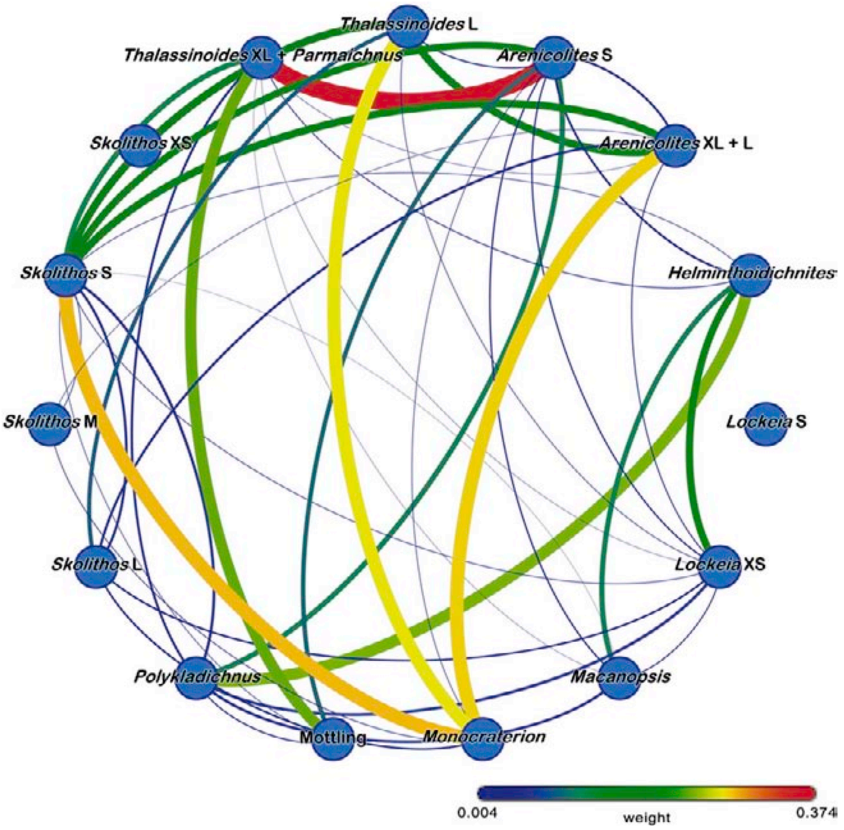


Fig. 19. The Ichnonetwork graph consists of a set of nodes (ichnotaxa) linked by a set of connections, each of which record the association between pairs of ichnotaxa. Edge colour and thickness proportional to the degree of association.

(Wassermann and Faust, 1994). More in detail, betweenness is quantified in terms of the number of shortest paths that run through a given node (Wuchty and Stadler, 2003).

Skolithos S, *Arenicolites* S, *Lockeia* XS are characterized by notable betweenness (Table 4; Fig. 20C), meaning that they connect distinct structural entities in the network. If bridge ichnotaxa are removed, parts of the ichnonetwork will be almost disconnected. Therefore bridge ichnotaxa are hubs connecting different structural units, being poor environmental indicators as they are likely to lie between multiple ichnoassociations.

The presence of bridges is an indicator of structure for the whole ichnonetwork: bridge ichnotaxa would not exist in an ichnological system with random co-occurrence patterns. As explained by Barbási (2002), a random system does not support connectors.

6.2.4. Distance and network diameter

Alongside to the centrality of nodes, it is important to look at the degrees of separation between them. This quality is formalized by the geodesic distance, which measures the shortest path of connection between two nodes (Wassermann and Faust, 1994). The Grado network is characterized by the following non-trivial extreme cases:

1. Distance = 1 corresponds to directly connected nodes (i.e. *Helminthoidichnites* and *Macanopsis*), which are separated by only one edge. This situation indicates that such ichnotaxa co-occur with a probability proportional to edge weight.
2. Distance = 2 corresponds to nodes with two degrees of separation. This is the case of nodes which are only indirectly connected by a common node (i.e. *Skolithos* M and *Thalassinoides* XL + *Parmaichnus*). This topology has an analogue in social networks: a friend shared between people who do not know each other. This configuration is diagnostic of two ichnotaxa with incompatible ecological requirements, which are yet suitable to a more plastic ichnogenus.

Intriguingly, the maximum distance between all pairs of nodes is equal to 2. This measure, known as network diameter (Wassermann and Faust, 1994), indicates a very compact system in which most nodes can be reached from every other by a small number of steps. This phenomenon is also supported by a small average distance (equal to 1.4).

6.2.5. Core ichnotaxa

After considering the distance between an ichnotaxon and a co-occurring one (*neighbour*), a question might arise: how an ichnotaxon is embedded in its neighbourhood? With an example, it is important to know if the ichnotaxa associated to *Macanopsis* are also associated to each other.

In order to solve this question, it is useful to count the number of connections between the ichnotaxa co-occurring with *Macanopsis*. This measure, divided by the maximum number of connections, is the clustering coefficient and quantifies the density of connections between the direct neighbours of a node (Bhadra et al., 2009). In the case of *Macanopsis*, the clustering coefficient is equal to 1 because all of its neighbours are connected to each other. The high degree of clustering, together with the low betweenness (Table 4), implies that *Macanopsis* lies at the core of a group of co-occurring traces.

This interpretation highlights that core ichnotaxa occupy central positions in ichnoassociations and have few connections towards other groups of traces (Fig. 20B). For this reason, core ichnotaxa are potentially the most environment-sensitive traces in a given ichnological system.

This aspect is very evident when comparing core ichnotaxa to bridge ichnotaxa. For instance, *Skolithos* S has a clustering coefficient of 0.5 because only some of its neighbours are connected (i.e. *Skolithos*

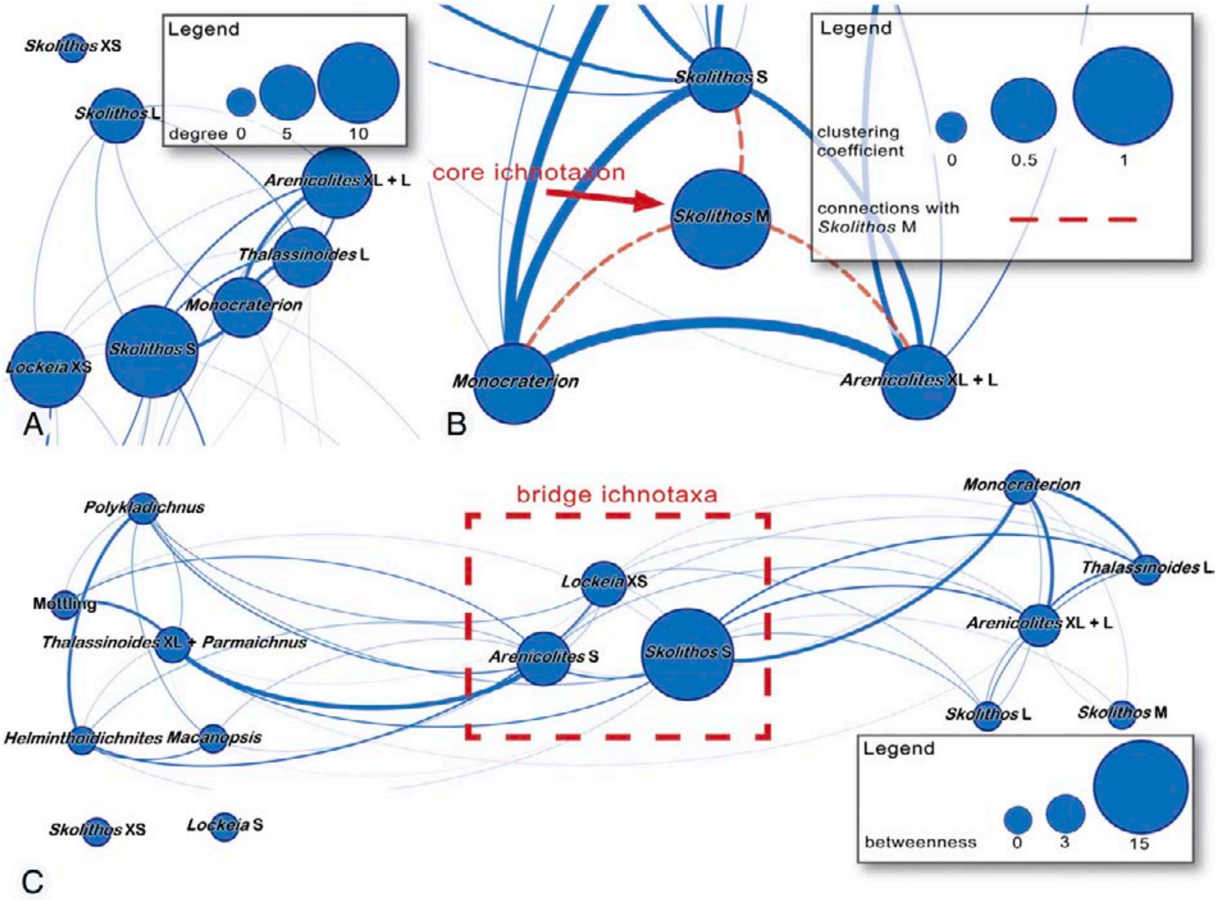


Fig. 20. Network topology. The illustrated graphs are fully equivalent to the ichnonetwork graph; layout has been adjusted to evidence topological patterns. (A) In the ichnonetwork context, node degree measures the number of ichnotaxa co-occurring with a given one. Detail of the network. (B) The ichnotaxa associated to a core ichnotaxon tend to be associated to each other. Detail of the network. (C) Bridge ichnotaxa tend to connect otherwise disconnected areas of the network.

S is associated either to *Macanopsis* or *Skolithos* M, but these ichnotaxa are never occurring together; Fig. 20C). If the traces co-occurring to *Skolithos* S are poorly associated, they are likely to pertain to different domains which are connected by bridge ichnotaxa such as *Skolithos* S itself. In fact clustering depends on the local connectivity pattern, while betweenness reflects the topological structure of the whole graph (Cabana et al., 2008).

Table 4
Metrics of the ichnonet graph.

Node	Degree	Betweenness Centrality	Clustering Coefficient
Skolithos S	12	15.150	0.5
Arenicolites S	10	6.117	0.6
Lockeia XS	9	4.033	0.667
Arenicolites XL + L	8	3.317	0.643
Thalassinoides XL + *Parmaichnus*	8	1.833	0.75
Polykladichnus	7	0.75	0.857
Helminthoidichnites	6	0	1
Macanopsis	6	0	1
Monocraterion	6	1.2	0.733
Thalassinoides L	6	0.4	0.867
Skolithos L	5	0.2	0.9
Mottling	4	0	1
Skolithos M	3	0	1
Lockeia S	0	0	0
Skolithos XS	0	0	0
Network average (with isolated nodes)	6	2.2	0.701
Network average (without isolated nodes)	6.923	2.54	0.809

6.2.6. The small-world effect

As seen for other local measures, the clustering coefficient can be averaged over the whole graph to determine the degree to which ichnotaxa tend to cluster together. The clustering coefficient of the Grado network is significant (0.701) and measures the probability that two ichnotaxa with a common neighbour are connected (Steuer and Zamora López, 2008). The measured clustering coefficient indicates that the network tend to form interconnected clusters of nodes, like a regular lattice; at the same time, the average distance of the Grado ichnonetwork (1.4) is similar to that of a correspondent random graph (1.6, calculated with the algorithm of McSweeney, 2008). These features suggest that the Grado ichnonetwork lies between regular and random networks or, in more formal terms, it represents a small-world network (Watts and Strogatz, 1998). This assumption is confirmed by measuring the small-worldness of the Grado ichnonet with the quantitative index S developed by Humphries and Gurney (2008). Indeed the small-worldness S of the studied network is equal to 1.736 (1.541 by ignoring isolated nodes).

The small-world property imply that network architecture and its substructures (i.e. ichnoassociations) do not emerge from random assemblage rules. Rather, a small-world is governed by underlying organizing principles (Réka and Barbási, 2002).

6.3. Ichnoassociations as network communities

Real-world networks usually display inhomogeneities, consisting of high concentrations of edges within special groups of nodes, and low concentrations between these groups (Fortunato, 2010). In the language of network science, these groups are named communities and their detection has important implications in understanding network organization. Indeed, communities represent "groups of vertices which probably share common properties and/or play similar roles within the graph" (Fortunato, 2010). Typical examples of communities include groups of web pages dealing with the same topic (in the World Wide Web network), groups of friends (in a social network), compartments (in a food web) (Porter et al., 2009; Fortunato, 2010).

In the context of the ichnonet graph (Fig. 19), communities correspond to groups of ichnotaxa which are highly associated to each other, but weakly associated to other groups of ichnotaxa. According to these assumptions, the communities of network science are ichnoassociations. In light of the neoichnological scenario, each ichnoassociation is likely to represent the work of a group of organisms living in the same space and time, or, an ichnocoenose (also known as ichnocommunity; Buatois and Mángano, 2011; Morin, 2011). Nevertheless, the more neutral term ichnoassociation is here preferred, in the sense of a group of commonly co-occurring traces.

The problem of finding ichnoassociations may be approached graphically, i.e. by looking for groups of strongly interconnected nodes. In the ichnonet graph of our case study (Fig. 19), *Helminthoidichnites–Lockeia XS–Macanopsis–Polykladichnus* form a well-defined group of nodes: an ichnoassociation, or, with the nomenclature of network theory, a community. Nevertheless, the ichnonet graph is too intricate for perceiving other ichnoassociations at first-sight and, consequently, a more analytical approach must be followed.

6.3.1. Infomap method

The Infomap method (Rosvall and Bergstrom, 2008) is one of the most accurate analytical approaches for revealing the organization patterns in networks (Fortunato, 2010). This algorithm is based on finding an efficient description of how information flows on the network under analysis. As expressed by its name, the Infomap method has significant analogies with a geographic map, in which dense clusters of streets are described as towns. Similarly, the Infomap method attempts to simplify the structure of a network by describing groups of well-connected nodes as single, well-connected modules (Rosvall and Bergstrom, 2008). According to this idea, ichnoassociation mining is equivalent to optimally describe the ichnonet graph by using less information than that encoded in the full similarity matrix (see Fortunato, 2010). In fact, paraphrasing Rosvall and Bergstrom (2008), an ichnoassociation can be regarded as a group of nodes among which information flows easily and, consequently, it can be efficiently represented as a single well-connected region.

The Infomap algorithm uses a random walk as a proxy for finding an optimal coarse-grained description of how information flows on the network; a thorough description of the algorithm is found in Rosvall and Bergstrom (2008). The application of Infomap revealed four ichnoassociations, named after the salient characteristics (Fig. 21A):

1. Low-bioturbation ichnoassociation: The presence of an isolated node (*Skolithos* XS) suggest the existence of a monoichnospecific ichnoassociation; due to its very sparse occurrences, *Lockeia* S has been not considered an ichnoassociation.
2. *Thalassinoides* ichnoassociation: *Thalassinoides* XL + *Parmaichnus*, *Arenicolites* S, Mottling.
3. *Arenicolites*/*Skolithos* ichnoassociation: *Arenicolites* XL + L, *Thalassinoides* L, *Monocraterion*, *Skolithos* S, M, L.
4. *Macanopsis* ichnoassociation: *Macanopsis*, *Helminthoidichnites*, *Polykladichnus*, *Lockeia* XS.

To ensure that the results of the ichnoassociation analysis were robust, they were tested against other popular methods for community mining.

6.3.2. Cluster analysis

Among the traditional techniques, cluster analysis has the advantage of not requiring a preliminary knowledge on the number and size of the communities (Fortunato, 2010). This technique groups the nodes (ichnotaxa) in a dendrogram with horizontal lines at the levels of similarity between clusters, based on a predefined similarity measure (Hammer and Harper, 2006; Wheater et al., 2011). Keeping with Hammer and Harper (2006), the average linkage algorithm was applied on the association matrix shown in Fig. 18.

The ichnoassociations defined by cluster analysis coincide with those of the Infomap method, with the only exception of *Skolithos* M (Fig. 21B). It is also interesting to note how *Macanopsis* is slightly separated from the rest of the cluster, reflecting the spatial distribution pattern discussed in Section 5.3.2.

6.3.3. Multidimensional scaling

Despite its widespread use, cluster analysis has been commonly criticized because it may recognize groups even when they are not present (Hammer and Harper, 2006). For this reason, the robustness of the recognized clusters was tested against another popular method of network analysis: non-metric multidimensional scaling. This technique aims to spatially represent the similarity between nodes on the basis of a similarity matrix (Wassermann and Faust, 1994). In our case, the target is to position the nodes (ichnotaxa) so that the higher the degree of association, the closer the distance between nodes, and vice versa (Fig. 21C). A stress value gives a measure of the ability to represent the relationships between the ichnotaxa (Hammer and Harper, 2006; Speight and Henderson, 2010). In order to fulfil the recommended stress value (less than 0.3; Wheater et al., 2011), poorly-represented ichnotaxa (*Skolithos* XS and *Lockeia* S) have not been displayed. A minimal spanning tree has been used to connect the nearest neighbours by respecting the original distances specified in the similarity matrix (Hammer and Harper, 2006).

With respect to Fig. 21, there are striking similarities in the results of multidimensional scaling, cluster analysis and Infomap method. Nevertheless, cluster analysis and multidimensional scaling tend to separate vertical traces from other clusters. This aspect suggest a hierarchical organization of the *Arenicolites*/*Skolithos* association, composed of a subunit dominated by vertical traces (*Skolithos* S, M, L) and a subunit with prevailing U-shaped burrows (*Arenicolites* XL + L, *Monocraterion*, *Thalassinoides* L).

7. Ichnoassociations and environment

The integration of ichnonetwork and spatial analysis allows an accurate definition of ichnoassociations, which are the fundamental building blocks of environmental analysis. Indeed, taxa associations are better environmental predictors than individual taxa because they are less subject to sampling error (Legendre, 2005). In line with this principle, this section discusses the results of geostatistical and ichnonetwork analysis, addressing the question of the environmental significance of the observed ichnoassociations through the search for regularities. More in detail, the idea is to find the average environmental conditions related to each ichnoassociation, e.g. the most common hydrodynamic setting of the *Thalassinoides* ichnoassociation. This approach is presented by describing the ichnological and the environmental characteristics of each ichnoassociation, as defined by the IchnoGIS method (Figs. 22, 23):

- The low-bioturbation ichnoassociation characterizes areas undergoing to prolonged emersion. Such conditions are commonly correlated to sandy sediments with well-developed lamination (facies A), which is a consequence of the low degree of biogenic reworking.
- The *Arenicolites*/*Skolithos* ichnoassociation develops in energetic, fore-barrier areas, where constant wave action produces widespread

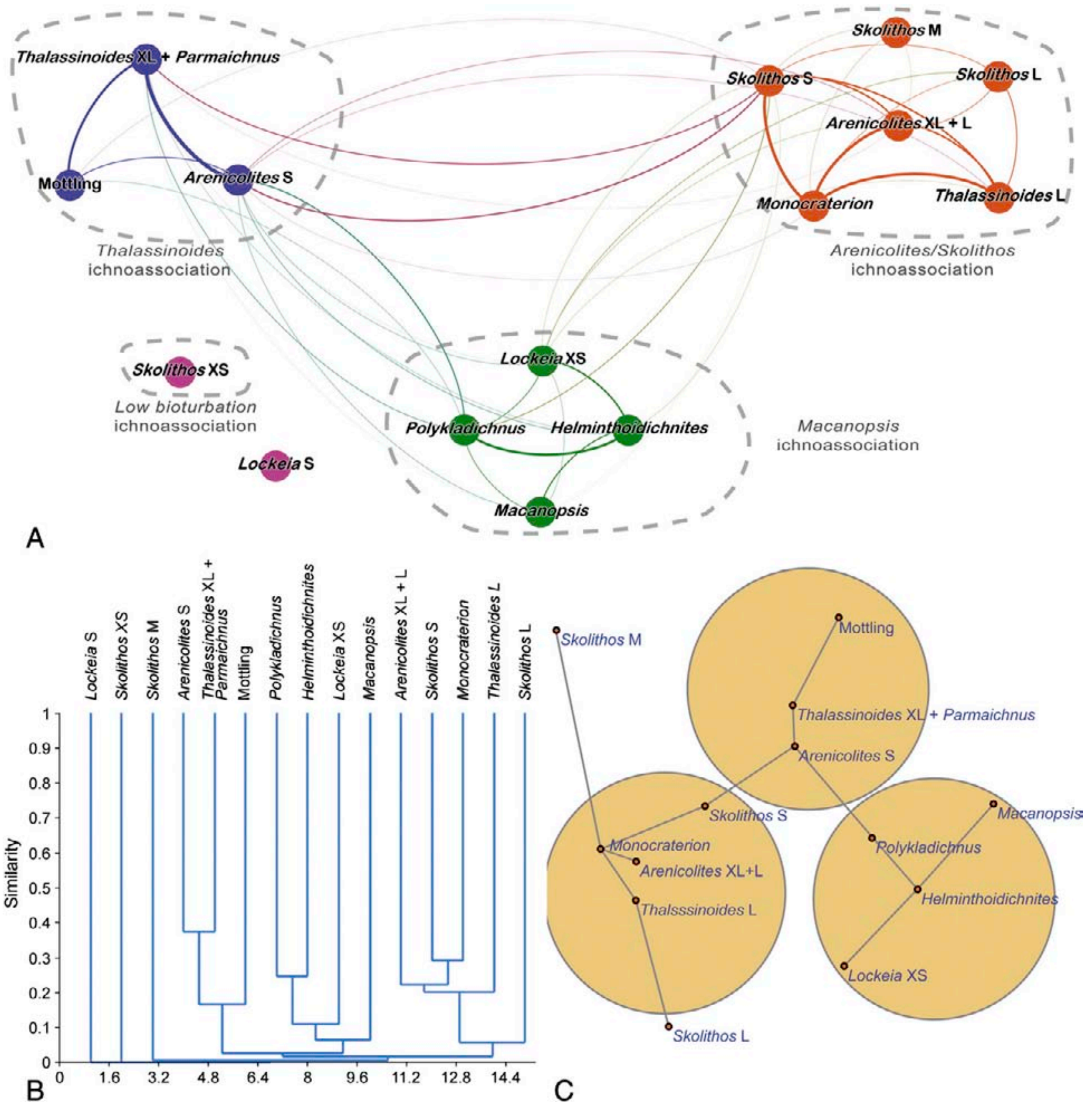


Fig. 21. Methods for ichnoassociation mining. (A) The Infomap algorithm finds ichnoassociations by mapping the information flow. (B) Cluster analysis groups ichnotaxa into sets based on their degree of association. Note the correspondence with the groups evidenced in A. (C) Multidimensional scaling positions the nodes so that more associated ichnotaxa are closer in space; edges are not represented for graphical clarity. Circles are used to highlight the proximity, while a minimum spanning tree connects nearest neighbours.

ripples (facies B; Fig. 22). In this environmental context, the *Skolithos* ichnoassociation is exposed to higher hydrodynamics, while quieter conditions favour the *Arenicolites* ichnoassociation (Fig. 24).

- The *Thalassinoides* ichnoassociation is largely concentrated on the sheltered flats of the back-barrier, with the exception of those areas with long emersion times (Figs. 9, 24).
- The *Macanopsis* ichnoassociation characterizes sheltered portions of the tidal flats colonized by cohesive microbial mats (Facies E). Significant emersion times and noxious phosphate levels are common (Figs. 22, 24).
- The '*Squat burrows*' ichnoassociation is established on the basis of quadrat sampling, because the dominant ichnogenus is produced during breeding season (Section 5.3.1). 'Squat burrows' may co-occur with *Thalassinoides* XL, *Parmaichnus*, *Polykladichnus* and *Arenicolites* S. This ichnoassociation characterizes filamentous algal mats, developed in low-energy intertidal flats (Fig. 23).
- The *Parmaichnus* ichnoassociation is established on the basis of quadrat sampling, because of the extreme cohesiveness of sandy firmgrounds. In fact, dense monoichnospecific assemblages of *Parmaichnus* are found in the distal parts of the tidal flat, with high concentrations of burrows within firm, exhumed substrates (Fig. 23).

8. Discussion

8.1. Ichnological modelling of the Grado system

The results of the IchnoGIS method had shown a marked habitat specificity in ichnoassociations, each of which occurs within a restricted range of environmental parameters. Making sense of such heterogeneity is a major goal for providing a predictive model with

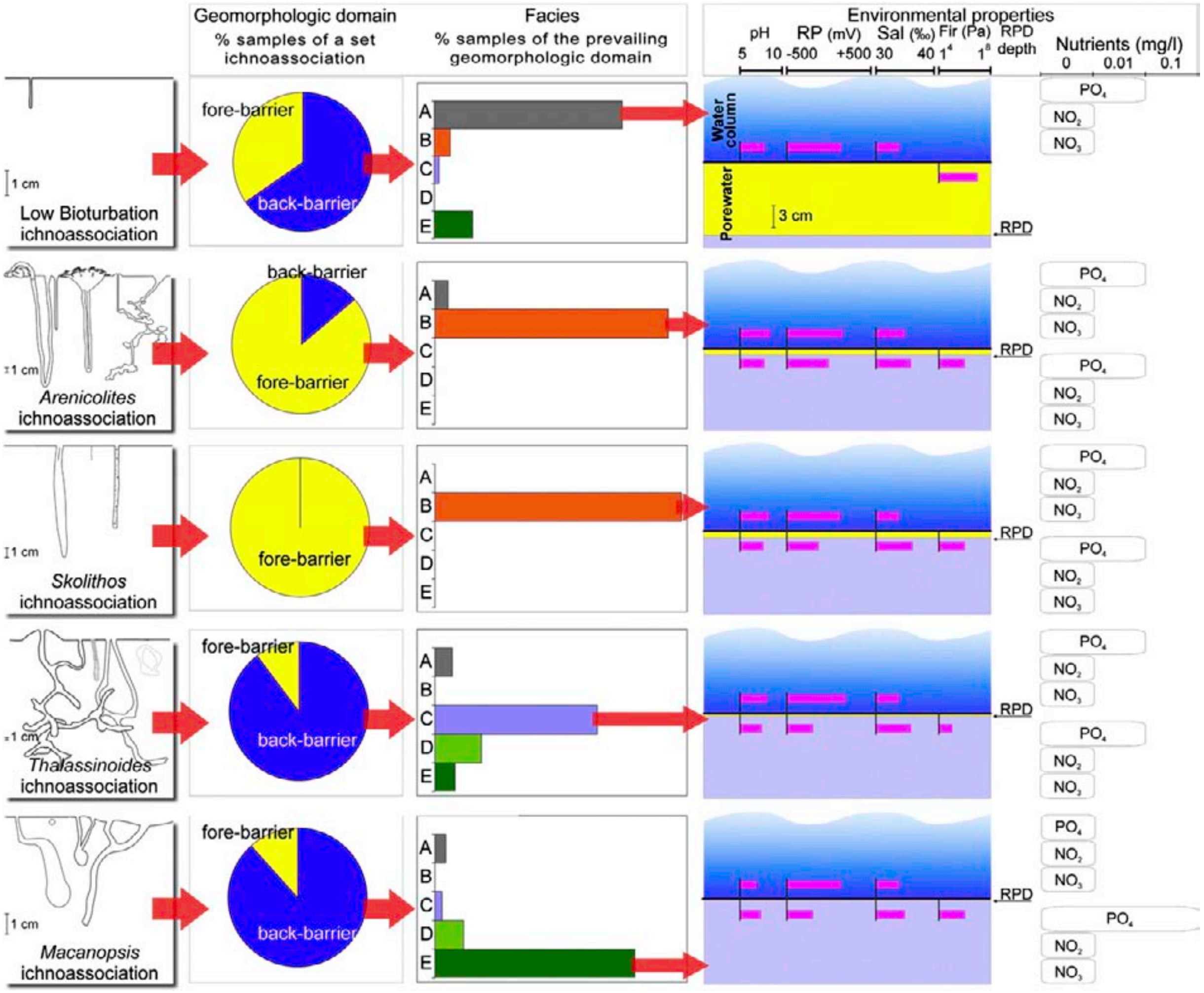


Fig. 22. Environmental setting of the ichnoassociations derived from ichnonetwork analysis.

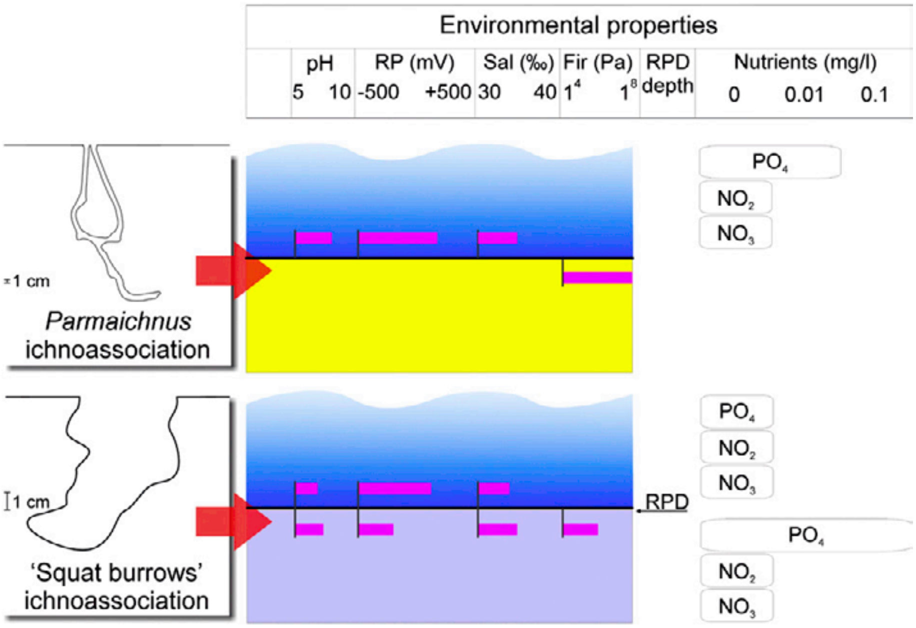


Fig. 23. Environmental setting of the ichnoassociations derived from quadrat sampling.

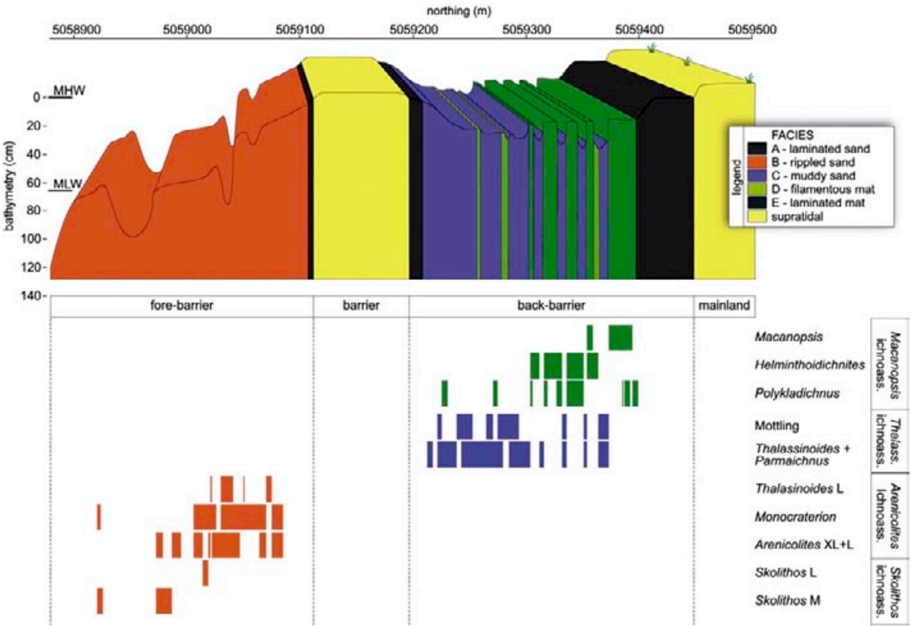


Fig. 24. Distribution of ichnoassociations along a land-sea transect. Bridge ichnotaxa not shown; transect corresponding to profile 2 in Fig. 1B.

immediate palaeontological application and, consequently, the definition of structuring forces is of primary importance.

It is widely accepted that organism behaviour can be influenced by a wide variety of environmental factors, including hydrodynamic energy, substrate, oxygenation, salinity, sedimentation rate, bathymetry, among others (Buatois and Mángano, 2011). In order to delineate a defined set of control factors which explain the observed ichnoassociations, two simple principles were followed:

a. Regularity exclusion. Factors exhibiting no significant variation across different ichnoassociations were excluded. For instance, salinity is a major control factor in coastal environments (Buatois and Mángano, 2011), but similar salinities characterize different ichnoassociations (Figs. 22, 23). Therefore salinity cannot explain the observed differences in ichnofaunal composition.
b. Parsimony. If different ichnoassociations exhibit different but correlated environmental parameters, the parameter which explains the other(s) is selected. For instance, the *Thalassinoides* ichnoassociation occurs in fine sediments and quiet environments. As grain size depends on hydrodynamics, the latter is to be considered the major structuring factor.

The application of these simple principles evidenced four major structuring factors (emersion time, hydrodynamics, firmness, microbial binding) synthesized in Fig. 25 and discussed below.

8.2. Emersion

Quadrat and trench sampling showed a sea-land gradient along which bioturbation intensity markedly decrease. The acme of this gradient corresponds to a shore-parallel belt within which only few, small sized ichnotaxa are found (low-bioturbation ichnoassociation).

The period of emersion (exposure or emersion time) is the most obvious aspect accounting for this gradient. In fact, more proximal sites generally experience longer period of emersion, which is a fundamental structuring process in intertidal environments (Raffaelli and Hawkins, 1996). This interpretation is proved not only by the low bioturbation index at high intertidal sites, but also by direct comparison of exposure time and burrow abundance (Figs. 7–9). This trend is confirmed for the vast majority of ichnotaxa, with the exception of burrows produced by organisms well-adapted to dry environments (i.e. *Macanopsis* and *Skolithos* XS).

The structuring power of exposure is explained by the numerous types of physical stressors associated to long period of emersion. In particular, desiccation plays a major role as it severely affects the vast majority of marine animals (Raffaelli and Hawkins, 1996). In particular, polychaetes are probably the most sensitive group of tracemakers, being virtually incapable of resisting desiccation (Glasby et al., 2000). Burrowing itself is a strategy to cope with long emersion times, as it allows to reach the water table during low tide. This is particularly true for thalassinidean tracemakers, which rely on water for gas exchange.

In addition, emersion time directly influences important trophic modes. For instance, filter feeders can only feed in water, therefore the time available for feeding dramatically increases towards the sea (Raffaelli and Hawkins, 1996). This phenomenon explains the distribution of the *Skolithos* ichnoassociation, largely dominated by suspension-feeding behaviours and found only at the intertidal–subtidal limit. Furthermore, prolonged emersion time negatively affects seaweed, whose photosynthetic tissues have a poor performance out of water (Raffaelli and Hawkins, 1996). According to Koch (2001) and Boese et al. (2003), exposure and the resulting desiccation stress are the most important factors setting the upper limit of seagrasses. Therefore, emersion time accounts for the distribution of rhizome-produced mottling, which is a core component of the *Thalassinoides* ichnoassociation. The absence of seagrasses triggers a negative feedback for deposit-feeders, which are favoured by the abundant organic matter deriving from the seagrass meadows. Finally, it should be noted that the areas undergoing to long emersion times are also subject to significant climatic stress. Indeed, air temperature is much more variable than water temperature, therefore proximal areas experience very extreme conditions (Raffaelli and Hawkins, 1996).

These results are supported by numerous ecological studies which recognize a sea-land gradient (or intertidal gradient), determined by emersion and its directly correlated variables. For instance, Salvat (1964) distinguished four ecological belts on the basis of sand moisture, which is largely a consequence of the shore position and therefore depends on emersion time. At this regard, McLachlan (1990) suggested that the zones of Salvat (1964) correlate with distinct faunal groups characterized by different desiccation tolerance. Salvat's (1964) zonation has a good correspondence with the faunal belts described by Dahl (1952) (Raffaelli and Hawkins, 1996). Furthermore, Swinbanks (1982) subdivided beaches on the basis of emersion time. In geological

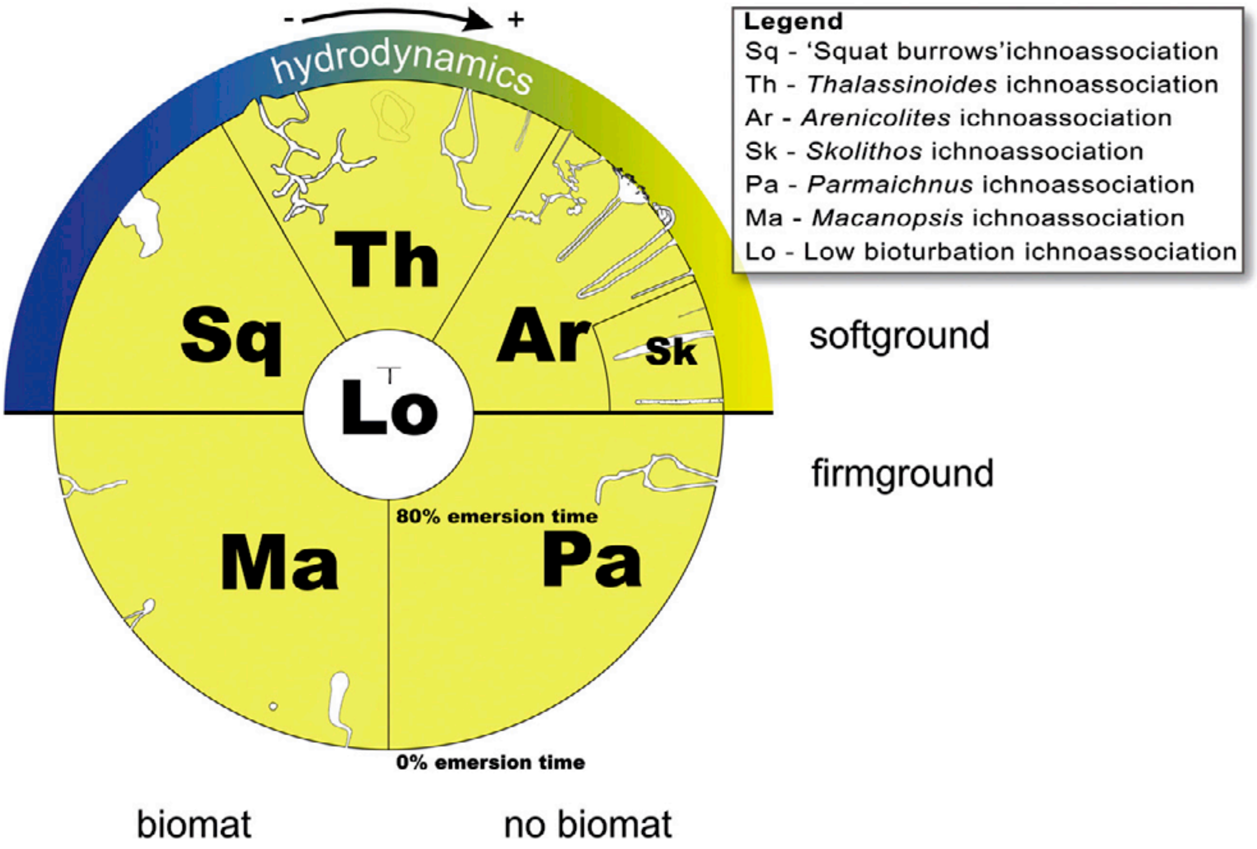


Fig. 25. The Grado ichnological model. Each ichnoassociation is explained by the combination of four environmental factors: emersion time, hydrodynamics, substrate firmness and microbial binding.

literature, the exposure index of Ginsburg et al. (1977) confirms the major role of emersion time in structuring habitats. According to these authors, emersion time define similar environments, each with distinct fauna, sedimentology and traces (Ginsburg et al., 1977; see also Rankey and Berkeley, 2012).

In conclusion, emersion time is one of the major structuring factors in intertidal systems, directly affecting bioturbation intensity. Fig. 25 models this phenomenon by mapping decreasing emersion times with the distance from the centre of the scheme.

8.3. Hydrodynamics

While the patterns found along the land-sea gradient are largely attributable to differences in emersion time, other structuring factors are acting in concert along this same gradient. For instance, *Thalassinoides* ichnoassociation and *Arenicolites* ichnoassociation are exposed to the same range of emersion times, but the differences in ichnofaunal composition are striking.

The IchnoGIS analysis shows a well-defined relationship between ichnoassociations and hydrodynamic energy, as expressed by the position with respect to the geomorphological barriers (Fig. 24). In fact, the barrier-island which characterizes the Grado ichnosite acts as a protection against currents and waves, separating a low-energy zone (the back-barrier) from a higher-energy zone (the fore-barrier; Fig. 1). A positive feedback exists between low-energy settings and marine phanerogams, acting as true ecosystem engineers. Indeed seaweeds are favoured by sheltered environments and, at the same time, they induce low-energy environments by extracting momentum from the moving seawater (Koch, 2001).

The pictured scenario is mirrored by facies distribution, characterized by sandy sediments in the turbulent fore-barrier (i.e. facies B) and finer sediments in the sheltered back-barrier (i.e. facies C; Fig. 3A). Accordingly, fine organic material settles in the lower energy zone, favouring the deposit-feeders responsible of the *Thalassinoides* ichnoassociation. At the contrary, turbulence keep nutritious material in the water column, favouring suspension-feeding strategies (*Skolithos* ichnoassociation) in the fore-barrier. The observed ichnoassociations can be seen in light of the Seilacherian ichnofacies, with the *Skolithos* ichnofacies related to food particles suspended and the *Cruziana* ichnoassociation related to food particles deposited ("food resources paradigm" of Pemberton et al., 2001). It should be noted however that the *Skolithos* ichnofacies occurs seaward of the *Cruziana* ichnofacies, as the energy gradient of the Grado ichnosite is inverted with respect to wave-dominated environments; this aspect has been already highlighted by Mángano et al. (2002) and Buatois and Mángano (2011).

In contrast, food supply does not provide a complete explanation for the *Arenicolites* ichnoassociation, typically occurring within the fore-barrier (Figs. 22, 24). In fact, the dominant ichnotaxa (*Arenicolites* L and XL) are related to deposit-feeding sipunculans, although the fore-barrier provides less organic matter than the adjacent back-barrier. A basic explanation is given by the commonest environmental preferences of sipunculans, which coincide with the conditions of the fore-barrier. In addition, *Thalassinoides*-producing decapods are exploiting the same resource (detritus) of sipunculans, therefore they may compete and trigger spatial resource partitioning.

Although both of these assumptions may be partially true, a deeper level of explanation is required because *Arenicolites*-dominated ichnoassociations are well-documented in similar palaeoenvironments (Bromley and Asgaard, 1991; Bromley, 1996; Pemberton et al., 2001). In this regard, the extended organism perspective (Turner, 2003) have large implications for interpreting U-burrows, which can be regarded as external organs for channelling energy sources. Indeed, when water flows across a surface, its velocity gradient provides a potential source of work and therefore might be employed to induce burrow irrigation

(Vogel et al., 1973). U-shaped morphology is very efficient for exploiting such source of energy, which is required by both suspension- and deposit-feeders. In fact suspension-feeders depend on moving water for nutrition and, in some cases, for respiration. The latter aspect is particularly important for intertidal deposit-feeders, which rely on the organic-rich sediments below the redox potential discontinuity. These nutritious but anaerobic sediments can be explored only by ventilating the burrow with oxygenated water. Therefore, large concentrations of *Arenicolites* are explained by moderate hydrodynamic energy, which is channelled into the U-burrows. Quieter, more hypoxic environments can be inhabited only by very active ventilators such as mud shrimps, which irrigate their large and complex *Thalassinoides* burrows by pleopod beating (Atkinson and Taylor, 2005).

These examples evidence that the studied ichnosite is also affected by the availability of oxygen in the interstitial system. In general, availability of interstitial oxygen could derive (a) from the oxygen concentration in the water column (Weissberger et al., 2009) or (b) from the dynamics of the interstitial system itself (McLachlan and Brown, 2006). The latter hypothesis fits better with the Grado ichnosite because water column presents similar properties in different parts of the tidal flat (Figs. 22, 23). Previous studies (McLachlan and Brown, 2006; Fonseca et al., 2011) evidenced a strong relationship between oxygen availability and grain size, which is ultimately controlled by hydrodynamics. In fact, depth of the redox potential discontinuity reflects how rapidly oxygenating water passes through the sediment (Little, 2000). Therefore, sands deposited in turbulent waters (facies B) are more permeable and consequently are more oxygenated; muddy sediments settle in quiet environments and, being less permeable, display a shallower redox potential boundary. The relationship between hydrodynamics-grain size-interstitial oxygenation is coherently depicted in Raffaelli and Hawkins (1996: Fig. 1.14). The poor interstitial oxygenation of fine sediments is exacerbated by high demand of oxygen. Indeed, finer grain size means larger surface for bacterial attachment (see McLachlan and Brown, 2006).

Hydrodynamics also represents a source of mechanical stress which is promptly reflected in the ichnological record. For instance, organisms build burrows with constructional lining (*Skolithos* M) in order to face the turbulent waters of the outer fore-barrier, which is also characterized by a low bioturbation intensity (*Skolithos* ichnoassociation). On the other hand, low-energy settings do not favour filter feeders, because their delicate filtering structures may be damaged from an excess of fine particulate material.

In conclusion, data evidence that hydrodynamics influence both ichnofaunal composition and bioturbation intensity. The structuring effect of hydrodynamics is shown in Fig. 25 through a speedometer-like representation.

8.4. Biomat binding

Quadrat and trench sampling evidenced that matgrounds present very distinctive ichnoassociations (*Macanopsis* and 'Squat burrows' ichnoassociation), manifested by abrupt changes in ichnofaunal composition between biostabilized substrates and other facies. For instance, the mat-related *Macanopsis* ichnoassociation passes to the *Thalassinoides* ichnoassociation within few centimetres of space.

In light of these evidences, matgrounds exert an overarching control on ichnofauna, which is the effect of several factors linked to mat metabolism and growth. At this regard, sediment binding is the most obvious effect on substrate characteristics. In fact, the sediment particles of matgrounds are bound by algal filaments (facies D) and extracellular polymeric secretions (EPS; especially in facies E). The predominance of algal or EPS binding severely affects the geotechnical properties of the substrate. The most severe changes are imparted by extracellular polymeric secrections, which form a matrix embedding microbial cells such as diatoms, cyanobacteria and heterophic bacteria (Decho, 2000). EPS strongly characterizes laminated mats (facies E), which are consequently a modern analog of the firm, erosion-resistant biomats typical of Neoproterozoic sea bottoms (Seilacher, 1999; Gingras et al., 2011a). Spatial and ichnonetwork analysis revealed that insect burrows (*Helminthodichnites*, *Macanopsis*) are the most typical burrows within laminated mats (*Macanopsis* ichnoassociation). It may sound surprising that air-breathing insects are the most important tracemakers in periodically submersed environments, but the Grado ichnosite reflects a global trend. Indeed, insect burrows characterizes laminated mats worldwide (Seilacher, 1999; Reise, 2002; Gerdes, 2003). The presence of insects is explained by the geotechnical properties induced by the microbial mat, which seals the underlying sediment from seawater. Consequently, air-breathers may survive within the microbial mat during high tide, exploiting a rich trophic niche.

Both filamentous and laminated mats display a shallow redox boundary discontinuity and are commonly accompanied by considerable levels of interstitial phosphate (Fig. 22, 23), which is deleterious for marine invertebrates even at low concentrations (Blasiola, 2000). High concentrations of phosphate seems to be a common feature of both modern and fossil microbial mats in consequence of the metabolism of mat-forming organisms (Wilby et al., 1996; Rougerie et al., 1997). The effect of metabolic processes is exacerbated in laminated mats — less permeable than filamentous ones — because they seal upward-diffusing phosphorous (see Wilby et al., 1996).

The mentioned lower permeability is explained by tighter sediment binding in laminated mats. As a consequence, filamentous mats offer less cohesive and more humid substrates, providing more favourable conditions to marine organisms. In accordance with Österling and Pihl (2001), filamentous mats act as a refuge for predation, enhance food levels for detritivores but induce stressful conditions within the sediment (i.e. high phosphate, dysoxic conditions). For these reasons, filamentous mats are selectively burrowed by mating crabs ('squat burrows'), while *Thalassinoides* and *Arenicolites* are usually scarcer than in the correspondent non-microbial facies (muddy sands, facies C).

The role of biomat binding is modelled in Fig. 25, which displays matground-related ichnoassociations in the left hemisphere of the scheme.

8.5. Firmness

The previous section evidenced the role of substrate firmness in structuring the ichnoassociations of matgrounds, with the *Macanopsis* ichnoassociation occurring in firm, laminated mats and the 'squat burrows' ichnoassociation related to soft, filamentous mats. Firmness is crucial also for sediments without microbial binding, as witnessed by the specific relationships between ichnoassociations and the degree of consolidation. In fact, a large number of ichnoassociations are restricted to softgrounds, while the *Parmaichnus* ichnoassociation is commonly associated to firmgrounds (Figs. 22, 23).

In light of these examples, firm substrates structure ichnoassociations (a) by offering favourable geotechnical characteristics (i.e. pupation chambers require stable substrates) and (b) by excluding tracemakers unable to burrow firm substrates (i.e. the polychaete *Megalomma* is not provided with strong burrowing appendages). The latter aspect is well-evidenced by the nearly monospecific *Parmaichnus* ichnoassociation, dominated by Y-shaped upogebiid burrows. The importance of substrate firmness is traditionally well-recognized in ichnology, being a primary aspect in the ichnofacies concept (Bromley, 1996; Buatois and Mángano, 2011). At this regard, the *Parmaichnus* ichnoassociation fits very well to the *Glossifungites* ichnofacies.

Fig. 25 model the effect of firmness by displaying firmground-related ichnoassociations in the lower hemisphere of the scheme.

8.6. “Deep time on a tidal flat” or global model?

The above mentioned Grado model (Fig. 25) is consistent with previous ecological studies on tidal flats. Indeed numerous models of ecological zonation recognize a landward belt characterized by scarce biomass and talitrids (see Dahl, 1952; Jaramillo et al., 1993); there is full correspondence with the low bioturbation ichnoassociation, presenting *Skolithos* XS (authored by *Talitrus*) and a low intensity of bioturbation. According to most ecological zonations of temperate to tropical environments, decapod crustaceans start to dominate from the middle tidal flat (see the review in Raffaelli and Hawkins, 1996: pp. 52–61). This observation supports the *Thalassinoides* ichnoassociation. More turbulent, sandy environments commonly present bivalves or polychaetes inhabiting vertical burrows (see the review in Raffaelli and Hawkins, 1996: pp. 52–61). This is consistent with the *Arenicolites*/*Skolithos* ichnoassociation. These evidences support the global validity of the observed ichnological zonation, at least for similar environmental domains. Indeed, Jaramillo et al. (1993) demonstrated that reflective, intermediate and dissipative beaches display different zonation patterns.

These general features with global validity coexist with peculiar ichnological and environmental aspects. In fact, the Northern Adriatic Sea is an ideal model for past epeiric (epicontinental) seas, being a shallow (average depth: 35 m), semi-enclosed sea lying on continental crust (McKinney, 2003; McKinney, 2007; Zuschin and Stachowitsch, 2009). In addition, recent studies brought an additional analogy, suggesting that the benthic ecosystem of the Northeastern Adriatic Sea closely resembles Paleozoic-style ecology (McKinney, 2003, 2007; McKinney and Hageman, 2006). According to McKinney (2003), the Adriatic Paleozoic-style is characterized by low-nutrient water, low intensity of grazing predation, and relatively few endobenthic bioturbators. Although some objections were raised on the mentioned ecological aspects (Zuschin and Stachowitsch, 2009), the Northeastern Adriatic is unanimously considered one of the few modern epicontinental seas comparable to some Paleozoic–Mesozoic shelves (McKinney, 2003, 2007; McKinney and Hageman, 2006; Zuschin and Stachowitsch, 2009). Intriguingly, our results show pre-Jurassic styles of bioturbation which are coexisting with more modern, crustacean-dominated ones:

- Laminated microbial mats commonly display a low degree of bioturbation and common *Helminthoidichnites* (*Macanopsis* ichnoassociation). The observed *Helminthoidichnites* reflect the mining of the microbial mat from underneath: ‘undermat mining behaviour’ *sensu* Seilacher (1999). Similar behavioural strategies were particularly common within Proterozoic microbial mats, before of the Agronomic Revolution (Seilacher, 1999).
- The rippled sands of the fore-barrier are dominated by the *Arenicolites*/*Skolithos* ichnoassociation, consisting of simple, vertical or U-shaped burrows (*Skolithos*, *Arenicolites*) and rarer bivalve structures (*Lockeia*). With the exception of localized clusters with dense *Thalassinoides* L, crustacean burrows are absent. This ichnological expression closely resembles pre-Jurassic shallow marine ichnoassociations, before of the raise of crustacean bioturators (Buatois and Mángano, 2011).

These remarkable ichnological features, united to the peculiar physiographic and ecological context, make Grado an ideal analogue for past peritidal ichnological systems. Paraphrasing McKinney (2007), the Grado ichnosite allows to study “deep time on a tidal flat”.

This idea is only apparently contrasting with the global validity of the Grado model. Indeed, the background condition is that ancient bioturbation styles are modern equivalents and therefore they may develop nowadays under peculiar environmental conditions. For instance, undermat miners were common in Proterozoic matgrounds, but they are still present in extreme but recurrent conditions (i.e. Seilacher, 1999). Furthermore, ancient styles of bioturbation are relegated to specific areas of the studied tidal flat, where environmental conditions are unfavourable to decapods and preclude intense bioturbation (Fig. 24).

9. Conclusions

In this paper, a new method for ichnological analysis (IchnoGIS) is presented through its application on a modern case study. Results show that the IchnoGIS method provides unprecedented research opportunities for ichnologists, as it allows to determine accurately spatial distribution, association patterns and environmental significance of traces.

These outcomes encourage future applications of the IchnoGIS method, involving not only other modern environments but also their cross-comparison. In fact, network analysis proved to be particularly efficient in confronting even very different systems, such as wasp colonies and human classrooms (Bhadra et al., 2009), the Internet and food webs (Réka and Barbási, 2002), neural systems and power grids (Watts and Strogatz, 1998). At the same time, the geostatistical approach will facilitate spatial recognition of ichnologically-relevant patterns.

The IchnoGIS method also has much to contribute to future debates on palaeoichnology. In fact, the Grado model (Fig. 25) shows that the IchnoGIS method can be used to predict environmental properties from ichnoassociations, being a tool for palaeoenvironmental analysis. In addition, the IchnoGIS procedures are easily applicable to the analysis of the fossil record, thus representing a promising future direction in the study of fossil environments. In fact, this study demonstrates that the structure of an ichnological system can be described by an ichnonetwork, opening the avenues to the quantitative comparison of fossil and modern systems.

These desirable outcomes require usable tools to be provided to the ichnological community. At this regard, the first step has already been done. In fact, IchnoGIS is based on simple survey tasks relying on relatively low-cost tools, while the entire analytical process can be performed with free or open-source software (Table 5). A further step in this direction will be to develop a single software environment dedicated to IchnoGIS analysis.

In light of these assumptions, the IchnoGIS method provides a single template for understanding quantitatively the relationship between traces and their environment, thus giving prominent grounds for future research in the study of modern and fossil ichnological systems.

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Table 5
IchnoGIS analysis with free software: Libre Office (http://www.libreoffice.org/), PAST (http://folk.uio.no/ohammer/past/), Gephi (https://gephi.org/) and www.mapequation.org. Each step is the output for the successive one. This example assumes two spreadsheets with quadrat and trench sampling data; ichnotaxa and coordinates are stored in columns, sampling sites in rows.

	Step	Software	Operation	Command
Geostatistical analysis	1. Data preparation	Libre Office Calc PAST	Open the quadrat sampling file and copy data Paste data into PAST	[File > Open] [Edit > Copy] [Edit > Paste]
	2. Point map	PAST	Select three columns (X, Y and one ichnotaxon), then plot values	Shift-click on column label to select multiple columns, then [Plot > Bubble Plot]
	3. Variogram	PAST	Select three columns (X, Y and one ichnotaxon), then analyze them	Shift-click for multiple selection, then [Geomet > Gridding] and select [Kriging] and click [Semivariogram]
	4. Interpolation	PAST	Fit the variogram model and interopolate	Modify the values of the variogram dialog, then choose [Go!]
Network analysis	1. Data preparation	Libre Office Calc PAST	Open the quadrat sampling file and copy data Paste data into PAST	[File > Open] [Edit > Copy] [Edit > Paste]
	2. Create the association matrix	PAST	Transpose the data, then calculate the association matrix for ichnotaxa	[Edit > Transpose] Shift-click for multiple selection, then [Statistics > Similarity and distance indices > Index = Jaccard]
	3. Export the association matrix	PAST Libre Office Calc	Copy the association matrix Paste it into a Libre Office spreadsheet	Click on the rightmost icon of the dialog [Edit > Paste]
	4. Data setup	Libre Office Calc	Use first row and first column to store node names. Save as a semicolon-delimited csv file	[File > Save as…], then check the [Edit Filter Settings] box. Choose the semicolon as field delimiter. Make sure that the csv file uses full stop as the decimal separator
	5. Open data	Gephi	Open the previously saved file with Gephi.	[File > Open] and select the Undirected option
	6. Ichnonet Graph	Gephi	Use the Circular Layout	[Overview > Layout > Circular Layout] If Circular Layout is not available, download it: [Tools > Plugins > Available Plugins: Circular Layout] [Preview > Presets > Default Curved], then click on Refresh
	7. Network analysis	Gephi	Network analysis is accessed from the ranking panel, after running the statistics dialogs	
	8. Infomap	Gephi www.mapequation.org/	Save the network in pajek (net) format: Load the network and run the Infomap algorithm	[File > Export > Graph File] [Map Generator > Load Network > Open File (for undirected network)] [Calculate Clusters]
	9. NMDS	PAST	Perform non-metric multidimensional scaling	[Multivar > Non-Metric MDS: Jaccard]
	10. Cluster analysis	PAST	Perform cluster analysis	[Multivar > Cluster Analysis: Jaccard]

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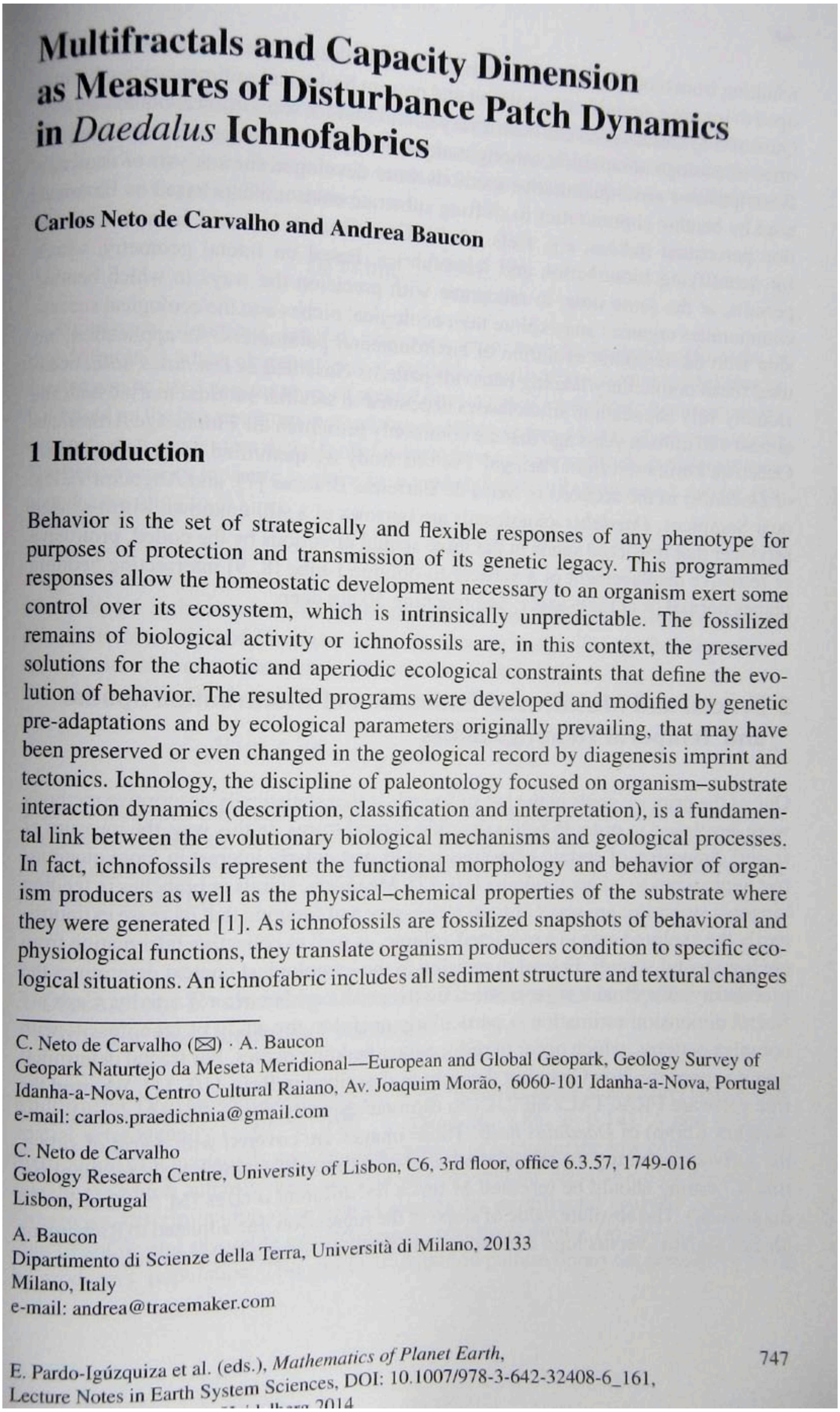
Appendix E

Multifractals and Capacity Dimension as measures of disturbance patch dynamics in *Daedalus* ichnofabrics



Multifractals and Capacity Dimension as Measures of Disturbance Patch Dynamics in *Daedalus* Ichnofabrics

Carlos Neto de Carvalho and Andrea Baucon

1 Introduction

Behavior is the set of strategically and flexible responses of any phenotype for purposes of protection and transmission of its genetic legacy. This programmed responses allow the homeostatic development necessary to an organism exert some control over its ecosystem, which is intrinsically unpredictable. The fossilized remains of biological activity or ichnofossils are, in this context, the preserved solutions for the chaotic and aperiodic ecological constraints that define the evolution of behavior. The resulted programs were developed and modified by genetic pre-adaptations and by ecological parameters originally prevailing, that may have been preserved or even changed in the geological record by diagenesis imprint and tectonics. Ichnology, the discipline of paleontology focused on organism–substrate interaction dynamics (description, classification and interpretation), is a fundamental link between the evolutionary biological mechanisms and geological processes. In fact, ichnofossils represent the functional morphology and behavior of organism producers as well as the physical–chemical properties of the substrate where they were generated [1]. As ichnofossils are fossilized snapshots of behavioral and physiological functions, they translate organism producers condition to specific ecological situations. An ichnofabric includes all sediment structure and textural changes

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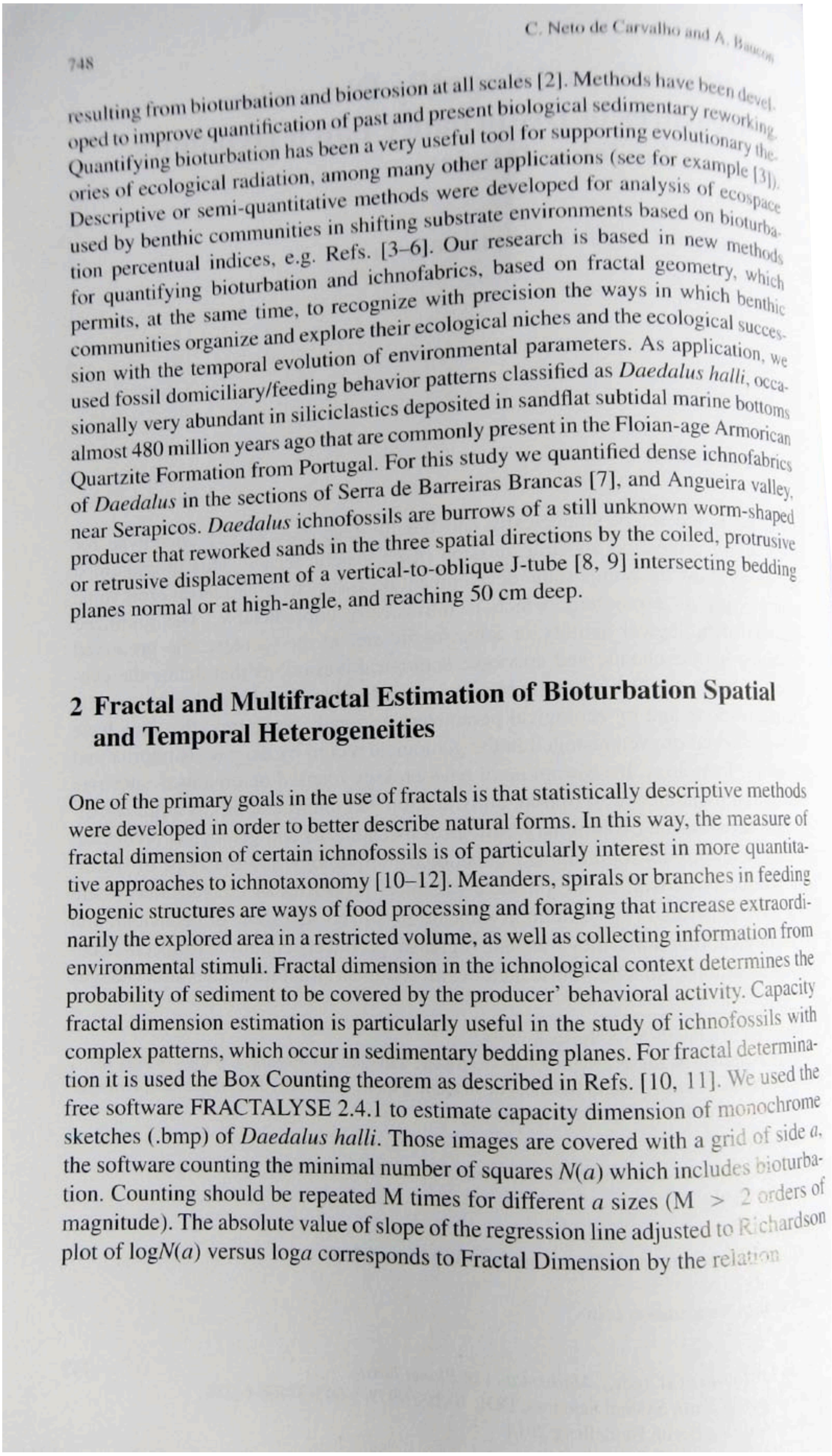
E. Pardo-Igúzquiza et al. (eds.), *Mathematics of Planet Earth*, Lecture Notes in Earth System Sciences, DOI: 10.1007/978-3-642-32408-6_161,



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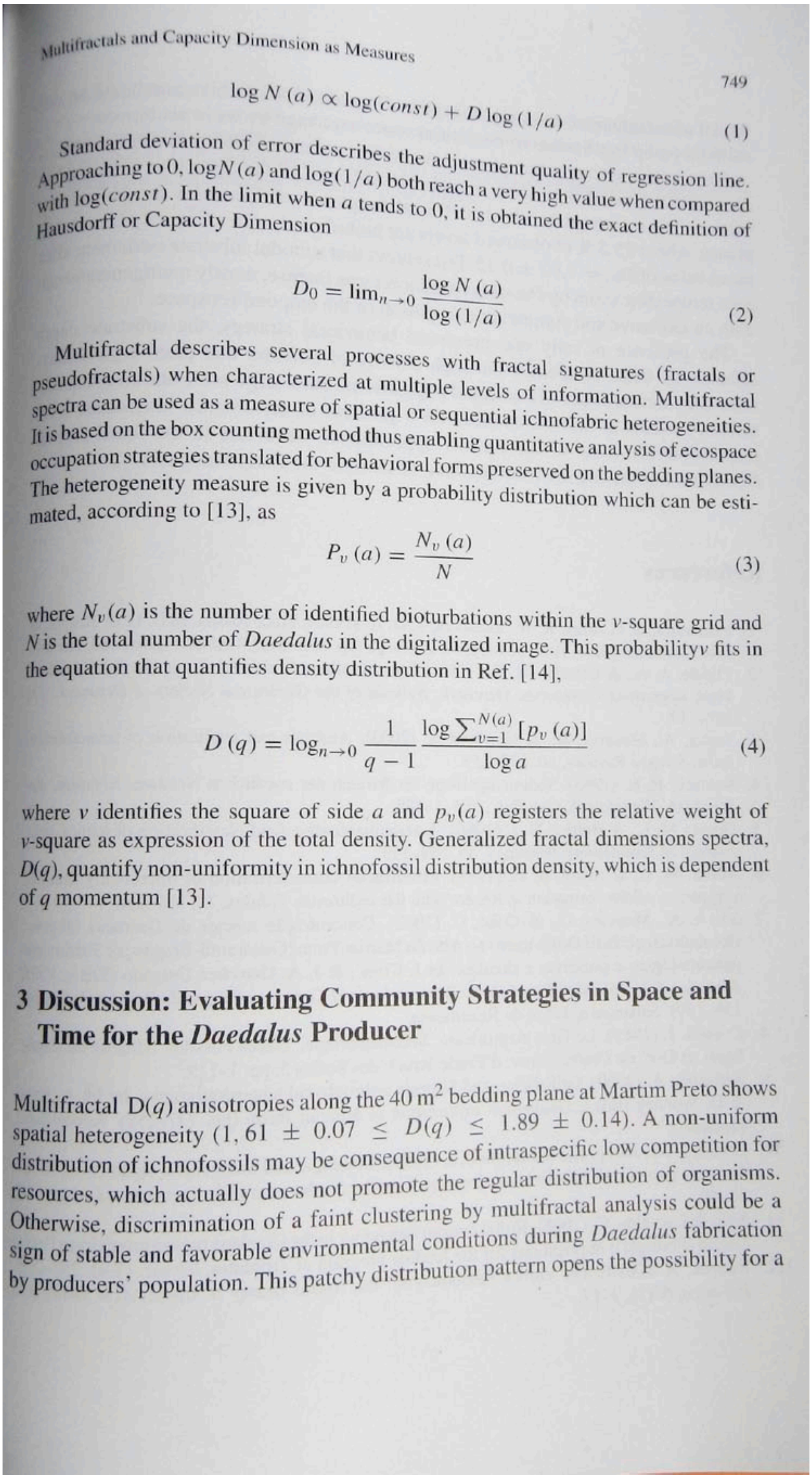
resulting from bioturbation and bioerosion at all scales [2]. Methods have been developed to improve quantification of past and present biological sedimentary reworking. Quantifying bioturbation has been a very useful tool for supporting evolutionary theories of ecological radiation, among many other applications (see for example [3]). Descriptive or semi-quantitative methods were developed for analysis of ecospace used by benthic communities in shifting substrate environments based on bioturbation percentual indices, e.g. Refs. [3–6]. Our research is based in new methods for quantifying bioturbation and ichnofabrics, based on fractal geometry, which permits, at the same time, to recognize with precision the ways in which benthic communities organize and explore their ecological niches and the ecological succession with the temporal evolution of environmental parameters. As application, we used fossil domiciliary/feeding behavior patterns classified as *Daedalus halli*, occasionally very abundant in siliciclastics deposited in sandflat subtidal marine bottoms almost 480 million years ago that are commonly present in the Floian-age Armorican Quartzite Formation from Portugal. For this study we quantified dense ichnofabrics of *Daedalus* in the sections of Serra de Barreiras Brancas [7], and Angueira valley, near Serapicos. *Daedalus* ichnofossils are burrows of a still unknown worm-shaped producer that reworked sands in the three spatial directions by the coiled, protrusive or retrusive displacement of a vertical-to-oblique J-tube [8, 9] intersecting bedding planes normal or at high-angle, and reaching 50 cm deep.

2 Fractal and Multifractal Estimation of Bioturbation Spatial and Temporal Heterogeneities

One of the primary goals in the use of fractals is that statistically descriptive methods were developed in order to better describe natural forms. In this way, the measure of fractal dimension of certain ichnofossils is of particularly interest in more quantitative approaches to ichnotaxonomy [10–12]. Meanders, spirals or branches in feeding biogenic structures are ways of food processing and foraging that increase extraordinarily the explored area in a restricted volume, as well as collecting information from environmental stimuli. Fractal dimension in the ichnological context determines the probability of sediment to be covered by the producer' behavioral activity. Capacity fractal dimension estimation is particularly useful in the study of ichnofossils with complex patterns, which occur in sedimentary bedding planes. For fractal determination it is used the Box Counting theorem as described in Refs. [10, 11]. We used the free software FRACTALYSE 2.4.1 to estimate capacity dimension of monochrome sketches (.bmp) of *Daedalus halli*. Those images are covered with a grid of side a, the software counting the minimal number of squares $N(a)$ which includes bioturbation. Counting should be repeated M times for different a sizes (M $>$ 2 orders of magnitude). The absolute value of slope of the regression line adjusted to Richardson plot of $\log N(a)$ versus $\log a$ corresponds to Fractal Dimension by the relation



$$\log N(a) \propto \log(const) + D \log(1/a) \tag{1}$$

Standard deviation of error describes the adjustment quality of regression line. Approaching to 0, $\log N(a)$ and $\log(1/a)$ both reach a very high value when compared with $\log(const)$. In the limit when a tends to 0, it is obtained the exact definition of Hausdorff or Capacity Dimension

$$D_0 = \lim_{n\to 0} \frac{\log N(a)}{\log(1/a)} \tag{2}$$

Multifractal describes several processes with fractal signatures (fractals or pseudofractals) when characterized at multiple levels of information. Multifractal spectra can be used as a measure of spatial or sequential ichnofabric heterogeneities. It is based on the box counting method thus enabling quantitative analysis of ecospace occupation strategies translated for behavioral forms preserved on the bedding planes. The heterogeneity measure is given by a probability distribution which can be estimated, according to [13], as

$$P_v(a) = \frac{N_v(a)}{N} \tag{3}$$

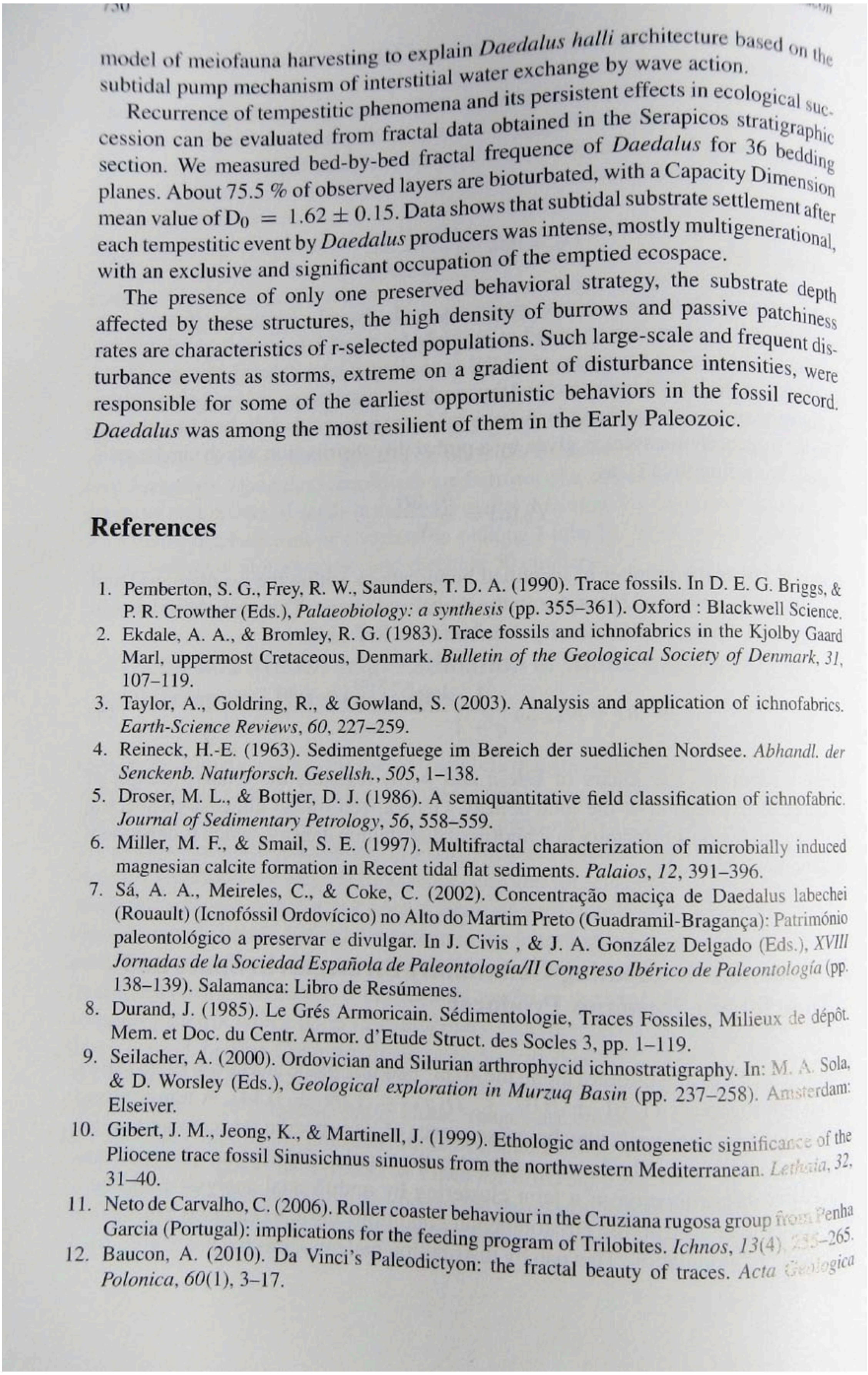
where $N_v(a)$ is the number of identified bioturbations within the v-square grid and N is the total number of *Daedalus* in the digitalized image. This probability$v$ fits in the equation that quantifies density distribution in Ref. [14],

$$D(q) = \log_{n\to 0} \frac{1}{q-1} \frac{\log \sum_{v=1}^{N(a)} [p_v(a)]}{\log a} \tag{4}$$

where v identifies the square of side a and $p_v(a)$ registers the relative weight of v-square as expression of the total density. Generalized fractal dimensions spectra, $D(q)$, quantify non-uniformity in ichnofossil distribution density, which is dependent of q momentum [13].

3 Discussion: Evaluating Community Strategies in Space and Time for the *Daedalus* Producer

Multifractal $D(q)$ anisotropies along the 40 m^2 bedding plane at Martim Preto shows spatial heterogeneity ($1,61 \pm 0.07 \le D(q) \le 1.89 \pm 0.14$). A non-uniform distribution of ichnofossils may be consequence of intraspecific low competition for resources, which actually does not promote the regular distribution of organisms. Otherwise, discrimination of a faint clustering by multifractal analysis could be a sign of stable and favorable environmental conditions during *Daedalus* fabrication by producers' population. This patchy distribution pattern opens the possibility for a



model of meiofauna harvesting to explain *Daedalus halli* architecture based on the subtidal pump mechanism of interstitial water exchange by wave action.

Recurrence of tempestitic phenomena and its persistent effects in ecological succession can be evaluated from fractal data obtained in the Serapicos stratigraphic section. We measured bed-by-bed fractal frequence of *Daedalus* for 36 bedding planes. About 75.5 % of observed layers are bioturbated, with a Capacity Dimension mean value of $D_0 = 1.62 \pm 0.15$. Data shows that subtidal substrate settlement after each tempestitic event by *Daedalus* producers was intense, mostly multigenerational, with an exclusive and significant occupation of the emptied ecospace.

The presence of only one preserved behavioral strategy, the substrate depth affected by these structures, the high density of burrows and passive patchiness rates are characteristics of r-selected populations. Such large-scale and frequent disturbance events as storms, extreme on a gradient of disturbance intensities, were responsible for some of the earliest opportunistic behaviors in the fossil record. *Daedalus* was among the most resilient of them in the Early Paleozoic.

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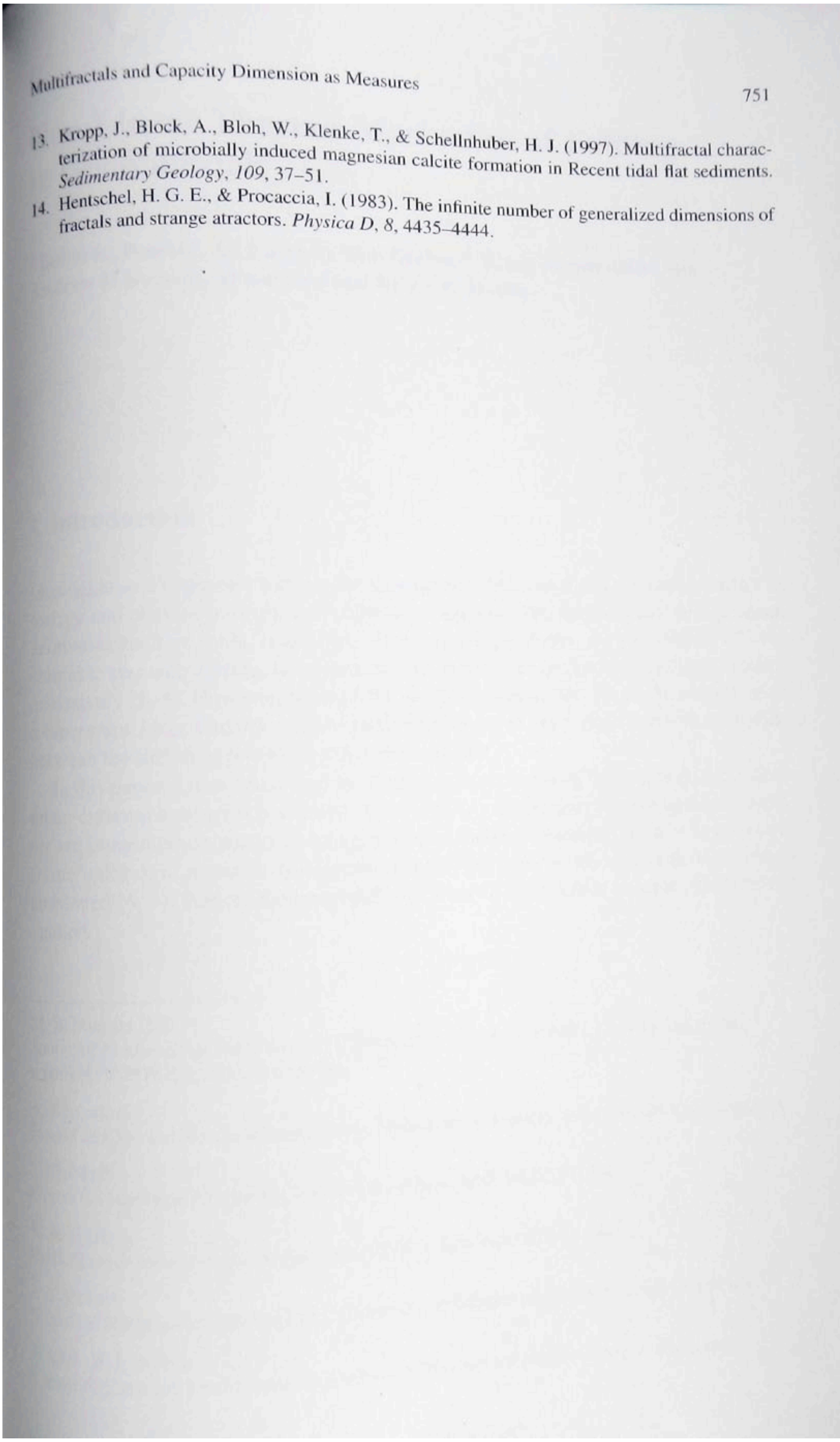

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