UNIVERSITÀ DEGLI STUDI DI MILANO
SCUOLA DI DOTTORATO
TERRA, AMBIENTE E BIODIVERSITÀ

Dottorato di Ricerca in Scienze della Terra
Ciclo XXVI

Network theory in ichnology: from behavioural topology to the depositional environment

Ph.D. Thesis

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Anno Accademico
2012-2013

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Chapter 1

Introduction

Although the concept of ichnology as a single coherent field arose in the 19th century, the endeavour of understanding traces is old as civilization and involved cultural areas worldwide. In fact, fossil and recent traces were recognized since prehistoric times and their study emerged from the European Renaissance. This progression, from empirical knowledge towards the modern concepts of ichnology, formed a major research field which developed on a global scale.

Since the beginnings of ichnology, traces have been recognized for their twofold nature as biological and sedimentologic objects. As a discipline studying biogenic sedimentary structures, ichnology proved to be very important for paleontology and sedimentary geology as well. In this context, the tendency of applying traces in the characterization of depositional environments manifested itself very early and is the focus of the present study. In particular, this study aims to (1) develop quantitative approaches for the study of ichnological systems; (2) model, for the first time, ichnosites as networks; (3) analyze the response of ichnological systems to global dynamics, with particular regard to Late Paleozoic fluvial-influenced settings.

This study is organized in chapters, which are optionally subdivided in sections (i.e. section 3.1 is referred to chapter 3). Each section is article-based, that is, it is intended for publication in an academic journal. For this reason and for enhancing readability, numbering of figures, tables, videos and section structure restart at the beginning of each section. For the same reasons, figures, captions and tables are listed after the text of each section.

Analogies from history can serve as a guide or inspiration for future insights and, consequently, this study starts from a historical analysis of ichnology – from Palaeolithic to present day (chapter 2). With regard to the trace-environment relationship, historical analysis shows that yet Leonardo da Vinci used trace fossils as a palaeoenvironmental tool, but, at the present day, there is a lack of quantitative studies on modern and fossil traces. This historical aspect guides one of the major goals of this project - developing and applying quantitative methods for studying the relationship between traces and the environment.

For this purpose, modern environments present the advantage of manifesting environmental processes, therefore they represent the ideal ground for developing, applying and testing quantitative methods for the study of the trace-environment relationship. This approach is supported by the historical development of ichnology, according to which 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. For these reasons, the peritidal environments of the Grado lagoon (Italy, Adriatic Sea) have been selected for developing, applying and testing a new framework for ichnological analysis: the IchnoGIS method (chapter 3).

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? These questions are tackled by the IchnoGIS method, providing a framework to analyze the spatial distribution of traces and study their association relationships. More specifically, this approach is based on the integration of spatial, geostatistical techniques with network theory, aiming to characterize the environmental significance of recent traces.

While geostatistics is very efficient for the study of modern systems, its application in the fossil record is difficult because it requires optimal outcrops with wide bedding planes. In contrast, network theory is a practical and accurate tool for studying the structure of fossil ichnological systems because it focuses on relational data, i.e. presence/absence data along a stratigraphical section. More specifically, an ichnological network (ichnonetwork) maps which ichnotaxa are associated to each other, and the strength of each association relationship.

According to the ethologic approach to ichnology, traces are environmentally-controlled evidences of behaviour, therefore ichnonetwork topology derives from the environmental structure. Consequently, ichnonetwork analysis – presented for the first time in this study – has a significant potential for palaeoenvironmental reconstitution and, for this reason, it is the major focus of this work. The network approach is applied to the study of trace fossils (chapter 4) and, specifically, for reconstituting the palaeoenvironment of the Nurra sequence (Permian-Triassic; Italy) and the Pramollo ichnolagerstätte (Carboniferous-Permian; Italy-Austria).

Further perspectives of study are discussed, tackling the question of how ichnodiversity is structured at a global scale (chapter 5). In this regard, network theory finds application in analyzing the major bioturbation patterns of the Phanerozoic, suggesting a new perspective on the widely applied ichnofacies model.

Chapter 2

History of Ichnology

Historical awareness is important because analogies from history can serve as a guide or inspiration for future insights. For this reason, this research starts from a historical study of ichnology – from Paleolithic times to present day – delineating the progression from empirical knowledge towards the modern concepts of ichnology. More specifically, the focus is on the application of ichnology for characterizing depositional environments, which is the major focus of this research project.

The purpose of this chapter is not only to provide information 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, a global perspective has been followed, based on the belief in the international character of ichnology. In addition, a comprehensive bibliographic database on the history of ichnology has been developed and analyzed with the purpose to show semi-quantitatively the chronological relationships among various branches of ichnology.

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Chapter 2

2.1 A history of ideas in ichnology

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Supplementary material in Appendix A

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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 palaeontology and sedimentary geology as well.

The tendency of applying trace fossils in the characterization of past depositional environments manifested itself very early. Yet 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 palaeoenvironmental analysis. Nowadays, ichnology is a matter of great interest due to the huge spectrum of potential applications such as facies interpretation, palaeoenvironmental reconstitution, recognition of discontinuities, prospecting and exploration of hydrocarbon resources.

This chapter aims to delineate the progression from empirical knowledge towards 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 ones because they find more sedimentological applications.

The purpose of this chapter is not only to provide information 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: ICHNOBASE (2011). It is maintained as a web application that showcases bibliographic lists developed as a part of the present research. The purpose is to show semi-quantitatively 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 periodize the history of ichnology on the basis of periods of time with relatively stable characteristics:

- Age of Fucoids (1823-1881). This stage initiated 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.

- 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 arose a consistent debate, with prominent scientists like Lebesconte and de Saporta supporting the botanical interpretation.

- 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 towards modern ichnology.

In more recent times, two historical stages were added to Osgood's classical ones. Pemberton et al. (2007a) 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 15th to the 17th 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 paper will explore the evolution in the study of trace fossils, from Palaeolithic times to present day.

3. From Palaeolithic times to Greco-Roman Antiquity

Archaeological evidence indicates that humans have recognized trace fossils since Palaeolithic times. Bioeroded Miocene mollusks are commonly found within the cultural layers of Pavlov and Dolní Věstonice (Czech Republic, Late Palaeolithic, 29,000 to 24,000 years ago; Fig. 1A). Statistical data from the primary collection sites indicates 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).

Such archaeological 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 Australian people developed remarkable neoichnological abilities, gaining a detailed understanding of animal behaviour 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 Aborigenes. 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), that 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 from 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 18th 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 (ca. A.D. 125 - after A.D. 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' (ca. 371 - ca. 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 towards a rational understanding of trace fossils began in the European Renaissance. This cultural movement flourished in Italy during the 14th 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 palaeoenvironmental 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 palaeobiology. 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 palaeontology, contains several trace fossils, frequently described in detail and with magnificent illustrations. Aldrovandi described *Cosmorhaphe* as a snake-like structure (Fig. 1D), 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 Lorenzo Legati (1677) when describing Ferdinando Cospi's *wunderkammer*, placed next to the Aldrovandi's Museum. Legati followed the interpretation of Aldrovandi, which previously studied the same specimen, and indicated it as "Wooded-stone" ("Alberina", "Dendrite", "Pietra Imboscata"; Legati, 1677; Fig. 2A). The "Alberina stone" was commonly caved 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).

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 into the Renaissance times, although it existed as disconnected ideas about traces.

5. 17th-18th century: a Period of Transition

For many years after Osgood's (1970, 1975) work, it was argued that ichnology was born in the 19th century Age of Fucoids – a not implausible suggestion given the difficulty to find ichnological studies prior to the 1800s. However, recent works highlighted not only the Renaissance roots of ichnology (previous section), but also evidenced 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 in hand with an expansion of scientific societies which, by the start of the 18th 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 member of the Royal Society, Edward Lhwyd (1760), figured a spiral coprolite and Gottlieb Friedrich Mylius (1709) previously illustrated some Permian specimens. The botanical interpretation of coprolites has been predominant since when William Buckland (1822), an influential fellow of the Royal Society, recognized them as fossil faeces (Duffin, 2009; Fig. 2B).

Bioerosional structures also received attention during the 18th century. Intellectuals such as Lorentz Spengler and Gottfried Sellius focused on modern bioeroding bivalves, namely the genera *Pholas* and *Teredo* (Wilson, 2008). Knowledge of bioeroding organisms, collectively named as *vermes lapidum*, has led some authors to classify as such funnel-weaving spiders (Happel, 1707; Lémery, 1719; Fig. 2C).

Fossil borings were understudied respect to recent ones, but John Woodward accurately interpreted a bioeroded fossil shell: "[…] there is in one of the Valves of this Shell a round Hole of that Sort that is commonly made by the Purpura in the Shells of living Fishes" (Woodward, 1729: p.12).

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 area – which dominated the Age of Naturalists.

From the 18th to the early 19th 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, Giovanni 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: p.56-57). After the 1830s, the term *fucite* fell into disuse, being quickly replaced by the etymologically analogous *fucoid*.

In Germany, several natural histories originated 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* ("Hole-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 (ICHNOBASE, 2011). Invertebrate trace fossils were also noticed by the explorer Hinrich Lichtenstein during his travel in South Africa (Master, 2010).

While in continental Europe the major part of the ichnological observations appeared in treatises, in Britain they regularly appeared on 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 on its pages the description of the pipe rock of Northwest Scotland, suggesting similarity to sabellid marine worm burrows. Other influential contributors include Buckland, who described 'paramoudras' from the Chalk of Northen Ireland, and Webster, who figured *Thalassinoides* and *Ophiomorpha* as zoophytes (plant-like animals, e.g. alcyonarian; ICHNOBASE, 2010).

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

6. The Age of Fucoids

6.1. Emergence of the palaeobotanical interpretation

The end of the French Revolution, the expansion of colonial empires, and the Industrial Revolution were conditions that made the 19th 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 Switzerland, the Alps and Italy, where he probably observed abundant trace fossils from the Apennines foredeep (Brongniart, 1828: p. 45).

A new stage in the history of ichnology may be said to date from 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 towards 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. 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 the founding father of palaeobotany even during his lifetime (Stafleu, 1966). Secondly, 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 17th to mid-20th centuries (Chew, 2009).

The French School and the rising discipline of palaeobotany 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 palaeontologist 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 (ICHNOBASE, 2011). Among the various works that have dealt with fucoids, *Flora Fossilis Helvetiae* (Heer, 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 palaeontologist 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 Kaspar Maria von Sternberg (1833-1838), one of the founding fathers of palaeobotany, 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), 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: just to cite some, *Rhizocorallium*, *Scolicia*, *Daedalus*, *Paleodictyon*, *Spirophyton*, *Diplocraterion*, *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 other three themes, namely as zoophytes (plant-like animals), as worm-like body fossils or 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 (1817) 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 anellids. 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 (1850) interpreted *Nemertilites* (now *Scolicia*) *strozzii* as a 'giant marine worm', *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*)”. The term is strongly reminiscent of d’Orbigny’s “*emprintes physiologiques*” (d’Orbigny, 1849: p.27-29). Another example is given by the palaeobotanist Heer, who recognized several species of *Zoophycos*, *Chondrites* and *Gyrophyllites* as fucoids, but also described *Wurmsteine* (*Helminthoiden*) as sediment-filled burrows of marine worms (Heer, 1877; ICHNOBASE, 2011).

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: p. 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; Gibert et al., 2012, this volume). 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 ICHNOBASE, 2011). 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 palaeoecological 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: p. 290; Wilson, 2008). 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, 2007; Wisshak, 2012, this volume).

In some cases the study of trace fossils benefited from the expansion of the British Empire, which represented the leading superpower of the 19th 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 mould (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 centre: 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). Edward 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 Palaeozoic examples found by later generations of geologists, and until continental ichnology emerged as a field Hitchcock’s research on invertebrate traces lay fallow.

Other early workers on invertebrate trace fossils, e.g., James Hall, Elkanah Billings, and Léo Lesquereux (ICHNOBASE□□□□□) 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 Palaeozoic “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 centres: a Canadian School of professional geologists centred around the Geological Survey of Canada, and a partly New York-inspired Cincinnati School consisting of self-taught palaeontologists (Pemberton et al., 2007). Both schools had impact and worked somewhat in isolation from active European centres. This isolation had its negative aspects, but also freed 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 fifteen 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 so 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 (ICHNOBASE, 2011).

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 newspaper, magazine 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 (ICHNOBASE, 2011). 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. Hitchock's ichnological cabinet served as a reference collection and attracted scientists from all over the world. Among others, these include the Italian geologist Giovanni Cappellini (1867) and the Austrian palaeontologist Othenio 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 papers of Nathorst (ICHNOBASE, 2011; Fig. 3C). Indeed, his 1881 paper has been seen as a major water-shed 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 were 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 palaeoichnology. Throughout this historical stage, discussion and argument over the nature of fucoids took on increasing prominence among scientists. In fact, by the late 19th century, French scholars began to mount a sustained attack on the rising palaeoichnology, and published voluminous descriptive and taxonomic works (e.g. Saporta, 1882; Lebesconte, 1883). Only in 1886 did Nathorst take part to the discussion (Cadée and Goldring, 2007). In holding his opinion against such authorities as Lebesconte and Saporta, Nathorst showed his sturdy independence of judgement.

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 British palaeontology than on the continent where the extensive fucoid monographs of Brongniart, Heer and 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), Beasley, Smith (arthropod tracks; ICHNOBASE, 2011).

Conversely, the Iberian Peninsula saw one of the strongest proponents 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" (ICHNOBASE, 2011). 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 (ICHNOBASE, 2011).

During the most of the Period of Reaction, the geopolitical scenario of Central-Eastern Europe was dominated by the Austria-Hungarian empire. Despite its multinational nature and the contentious questions concerning language, the Austria-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 (ICHNOBASE, 2011). Fuchs (1895) introduced also the first classification of trace fossils, based on flysch trace fossils. He distinguished three family-groups:

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

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

By the early 1900s, the fucoid debate resolved in favour of Nathorst's ideas as emblematically shown by Othenio Abel, the founding father of palaeobiology. 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, Soergel in ICHNOBASE, 2011). The Austria-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 palaeontologists, 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 Caucasus countries. By the early Period of Reaction, Polish geologist Łomnicki described *Glossifungites saxicava* 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, Keller in ICHNOBASE, 2011). Zuber (1918), beside ‘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, Vladimir Vladimirovich 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, Karasch; ICHNOBASE, 2011).

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; ICHNOBASE, 2011).

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: (a) Nathorst showed that neoichnology was the key for understanding trace fossils, (b) 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 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.

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, this volume). Additionally, 'fucoids' apparently lost their biostratigraphical value and their application as indicators of shallow marine, euphotic environments (Osgood, 1975; Cadée and Goldring, 2007). Possibly, this crisis was exacerbated by the aftermath of the World War I, corresponding to dramatic social, economic and geopolitical effects. Notably, four empires disappeared: the German, Austro-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*) aroused some debate, but French scholars interpreted it as an alcyonarian or a sponge (i.e. studies of Lucas, Dangeard in ICHNOBASE, 2011). The same happened in the other major centre 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 of the Wadden Sea by the German school at Frankfurt and Wilhelmshaven in 1920s and 1930s (Cadee 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 palaeontology 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 of 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 (ICHNOBASE, 2011).

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 to 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 20th 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 palaeontology, and minor progress was made. Carroll Lane Fenton and his wife Mildred Adams Fenton were palaeontologists 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 Palaeozoic trace fossils by use of actualistic reasoning. For example, they showed that phoronids could make *Skolithos linearis* (ICHNOBASE, 2011). 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 lower Palaeozoic burrows) (ICHNOBASE, 2011). 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 Asia and South America. It should be emphasized, however, that these ichnological schools had a different development under different circumstances with respect to 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 Palaeogene palaeosols in Uruguay (Rosselli, 1938). These deposits host the world's most diverse palaeosol ichnofauna and Rosselli's studies are at the foundation of the present-day school of insect palaeoichnology 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, Davitashvili (1945) coined the term ichnocoenose to indicate the traces of a biological community (biocoenose); the term was also independently proposed by Lessertisseur (1955).

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 marked by synchronous 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), 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 onwards (Vaccari, 1988). 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 in 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 beginnings of the institute, ichnology occupied a central place at Wilhelmshaven. After little time, the Senckenberg marine institute became renowned as a centre for ichnology and a magnet for biologists and palaeontologists alike.

As a result of his actualistic research, Richter coined the terms *Aktuopaläontologie* (Richter 1928) and *bioturbateTextur* (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 analogues 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 to an important branch of geosciences, with special focus on facies relationship. Unfortunately, the world was entering a tumultuous period, which culminated in the dramatic events of the Second World War. 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, *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 Ichnology (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 revolved around one concept, that trace fossils are a manifestation of behaviour. On this side, Seilacher (1953) developed an ethological classification, consisting of basic categories named for the prevailing behavioural pattern.

For instance, cubichnia correspond to resting traces. As Cadée and Goldring (2007) argued, Seilacher's ethological classification was possibly influenced by earlier taxonomical categorizations such as those by Richter and Krejci-Graf (see also Häntzschel, 1975: W17).

By the same years, ichnologists started to pay attention to the spatial arrangement of trace fossils. Seilacher himself (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 for a detailed treatment of both classifications). The set of terms introduced by Seilacher and Martinsson rapidly entered in use 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 are fossil behaviour and, as a such, they can be modified by the environment. Seilacher discerned the divergence between shallow-marine and deep-sea ichnoassemblages 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 palaeobathymetry was the principal controlling mechanism, but more environmental implications underlie the modern concept (i.e. substrate consistency, hydrodynamics, turbidity, food resources; MacEachern et al., 2007).

Seilacher built the archetypal ichnofacies on a great deal of empirical observations (Seilacher, 2007: p. 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, an expedition to the Salt Range in Pakistan (Seilacher, 2007: VI). Under a sociological perspective, the theoretical innovation of Seilacher may be seen in the light of Rudwick's (1996) hypothesis about the role of geological travel on scientific creativity. In fact the ichnofacies concept can be seen as a product of trained experience and the perceptual impact of new and exotic features (liminality). With the words of Rudwick (1996): "It is liminality that, as it were, takes both the geologist's previous experience and his experience of the new features, and lifts them out of the plane of ordinary life, giving them a heightened significance that makes the development of a new insight possible". Geological travel played also an important role in the development of *Cruziana* ichnostratigraphy, influenced by fieldwork in Spain (Seilacher, 2007: VI).

Later, Seilacher has put much effort in the use of trace fossils for palaeoecological 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 the work of Häntzschel, Schäfer, Reineck, Dörjes and Hertweck (ICHNOBASE, 2011). In particular, Reineck (1963) established a classification of bioturbation from the North Sea as the basic of the modern bioturbation index scheme (Knaust, 2012b, this volume). 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. 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 (Crimes and Harper, 1970; Frey, 1975; Basan, 1978) and the history of ichnology (Sarjeant, 1974; Osgood, 1975), broadly defines the limit of the early Modern Era.

9.2. Early Modern Era: a new impetus for the study of traces

Ichnology owes 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) points out that, as early as 1955, 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 Earth Sciences.

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

(A) 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 PhD 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).

(B) 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 (ICHNOBASE, 2011).

(C) The First International Trace Fossil Meeting in Liverpool in 1970, which resulted in the volume *Trace Fossils* (Crimes and Harper, 1970) and 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 paper emphasized the relationship of formal ichnotaxa to behaviour as opposed to morphology, and still ranks as one of the most influential ichnological papers ever written.

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 students James D. Howard and C. Kent Chamberlain accompanied him and, again, were inspired to conduct their own research in ichnology. 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 micropalaeontologists, 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, in 1965 he took a course 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 papers 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 theme 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 "grey" 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), publication of which galvanized many students to enter the field. About the same time, the Society of Economic Paleontologists and Mineralogists 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, Charles K. Chamberlain studied the core appearance of several ichnogenera (Bromley, 1996: p. 261) and made important achievements in the fields of ichnotaxonomy and palaeoethology (Seilacher, 2007: p. 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 on to 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;* Bromley (1990) successively authored the influential text-book *Trace Fossils, Bioloogy and Taphonomy.* Notably, the book was translated into German and Japanese (Bromley, pers. com.). 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*, in 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 (ICHNOBASE, 2010). His students have included 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 around H. Allen Curran of Smith College, they include many accomplished researchers. Notably, Curran edited the first ichnological book treating all major depositional environments (Curran, 1985).

Space does not allow a complete listing of every North American ichnologist here; our intent has been to establish that many of the most influential were inspired and trained by other ichnologists, and many indeed at a few centres.

9.4. The Eastern Bloc during the Early Modern Era

The social and political consequences of the 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.

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: p.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 (ICHNOBASE, 2011).

Książkiewicz also worked on palaeoecology, stratigraphy, taphonomy and palaeoenvironmental significance of flysch trace fossils, trying to calibrate bathymetry of trace fossils on the basis of benthic Foraminifera (ICHNOBASE, 2011).

In the same period, an active group of researchers assembled in Warsaw. Centred around Radwański, Karaszewski, Orłowski and Roniewicz, it focused particularly on lower Palaeozoic 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 palaeoshorelines, although he did not follow the parataxonomical system in naming trace fossils (Häntzschel,1975). Among other Polish contributions may be noted 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, Vassoievitch (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 mudcrack origin of *Paleodictyon* and placed it among biogenics (?imprint of snail eggs, ?imprint of algae). Similarly, he regarded *Ubinia wassoevitschi* as seaweed and interpreted some star-shaped trace fossils (*Lorenzinia, Atollites)* as imprints of ammonite shells (ICHNOBASE, 2011).

Within the mid- to late-20th century, ichnologists came to see Russia and Central Asia as a place of interest for field investigation. This period of intense ichnological travelling 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 fossil was broad, unfitting to the mainstream opinion (i.e. Bertling et al., 2006). Nevertheless, Vialov's ideas are still vivid in many Russian scientific institutions, partly because of his influential text-book (Mikuláš and Dronov 2006; Vialov, 1966).

Between the late 1950s and 1970 Romanian palaeontology 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 palaeoichnological 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 by ethological interpretations (ICHNOBASE, 2011).

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

(ICHNOBASE, 2011). The birth of South American Ichnology took place since the sixties to the eighties, 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 into 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, Oliver Macsotay (1967) dealt with Cenozoic turbidite trace fossils from Venezuela. Macsotay's work gave strong impulse to the use of trace fossils in palaeoenvironmental reconstitutions, 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 researched on vertebrate ichnology (see Fernandes et al., 2002 for a comprehensive bibliographic review).

The next phase of studies within this age took place in the seventies and eighties, particularly with the work by Florencio Aceñolaza and his research associates in the Precambrian and lower Palaeozoic units of northwest Argentina. In the same years, there was a rapid development of Brazilian invertebrate ichnology, as shown by the 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 Palaeozoic units and Ismar de Souza Carvalho, mostly on vertebrate ichnology (Fernandes et al., 2002). Among other Argentinean contributions may be noted Ricardo Alonso on vertebrate ichnology, Jose Laza on ant trace fossils and Poiré on the sedimentological application of trace fossils (ICHNOBASE, 2011).

On the other side of the ocean, Asian ichnology followed a composite development, to some extents 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 have been carried out by Katto, Shuto and Shiraishi (ICHNOBASE, 2011). 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 palaeoethology and trace-making 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 palaeoichnology, greatly improving the knowledge of the Japanese ichnological heritage (ICHNOBASE, 2011).

From 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 ichnoassemblages at the Precambrian-Cambrian boundary. Marine trace fossils were studied, among others, by 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. In this stage, ichnological analysis aimed both to palaeoecologic reconstitution and applied investigations (i.e. energy exploration; Hu et al., 1997) while ichnofabric analysis started by the end of the 1990s (ICHNOBASE, 2011).

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 inaugurated a series of influential studies on the Bagh Beds, which successively attracted a vast number of researchers (i.e. Verma, Ghare, Sanganwar, Kundal, Kumar; ICHNOBASE, 2011).

By the same years, the first reports of Neoproterozoic burrows (i.e. 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 trace-making 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 palaeoecological reconstructions. This golden era of southern African ichnology is most of all featured in contributions of international importance by Ann Anderson (Palaeozoic invertebrate trace fossils, South Africa), Paul Ellenberger (Mesozoic vertebrate tracks, Lesotho), and Gerald Germs (Precambrian and Cambrian invertebrate trace fossils, Namibia and South Africa; ICHNOBASE, 2010). 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; ICHNOBASE, 2011).

10. Conclusions and discussion

10.1. Evolution of the interpretation of trace fossils

The collection of numerous bibliographic resources has allowed to build a database (ICHNOBASE, 2011), graphically resulting in a semi-quantitative 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 ichnological research, i.e. the crisis that followed the dismissal of fucoids. According to it, 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 centres 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 centres 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 for the development of many ichnological schools, i.e. 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 are influencing and guiding its contemporary trends.

For instance, the ethological revolution of the 1950s established trace fossils as fossil behaviour, and for this reason they are nowadays crucial ingredients of both evolutionary palaeoecology and palaeobiology. 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: p.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). The ichnofabric paradigm resulted as an excellent methodology for palaeoenvironmental reconstitution, complementary to the ichnofacies approach. It found particular application in the study of coalfields (i.e. Pollard, 1988) and hydrocarbon reservoirs (Taylor and Goldring, 1993; Knaust, 2012b, this volume).

The importance of historical awareness does not regard only the question of memory, but analogies from history can serve as a guide or inspiration for future insights. For instance, history reminds us of the cultural value of trace fossils. Yet in the 17th 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 19th century (ICHNOBASE, 2011). 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 grey area shared with other disciplines. A typical example is given by recent traces, whose study is often referred to biology, archaeology or forensic science, avoiding mention to ichnology (Bromley, 1996: p. xi; Baucon et al., 2008).

This tendency can be traced back to the 19th century (i.e. Wood, 1886) and it is still influencing the study of traces. For instance, significant overlapping exists between neoichnology and tracking, a discipline practised by hunting guides, biologists, search-and-rescue teams, soldiers in war and forensic investigators (Liebenberg, 2010; Cunningham, 2004). According to Liebenberg (2010), tracking involves each and every indication of an animal's presence. It typically includes traces (i.e. footprints, faeces, burrows) but also other structures (i.e. eggs, auditory signs).

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 19th 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: p. ix; Lockley and Meyer, 2000: p. 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 the most of 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), therefore suggesting animals as the main actors in ichnology. Secondly, 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 centre, it focused on marine invertebrates, consolidating the leaning towards 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 Herbert 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. French Revolution), but 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 da Vinci did not influence the course of ichnology because he compiled hand-written 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 inter-relation?

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 spread 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; the ICHNOBASE (2011) project, developed as part of this contribution, is aimed to fill this gap. 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 palaeontology methods, 3D visualization and computer modelling of trace fossils, topoichnology, theoretical foraging (i.e. studies by Gong, Hu, Si, Plotnick in ICHNOBASE, 2011; Knaust, 2012b, this volume). 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 fuelled by a complex interplay of factors: 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.

Acknowledgements

Andrea Baucon sincerely thanks Richard G. Bromley and Dirk Knaust for the invitation to compile this contribution. The manuscript greatly benefited from the constructive reviews of Richard Bromley and Günther Hertweck. This chapter directly benefited from helpful correspondences with Leonardo Ambasciano, Heracli Astudillo, Matteo Belvedere, David Bressan, Mathias Heckroth, Scott Linklater, Duncan McIlroy, Fabio Massimo Petti, Serena Privitera and Maša Surić.

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FIGURES

Figure 1 – Beginnings of ichnology. A – Ichnological symbols commonly used in Australian Aboriginal art. Clockwise from top left: emu footprint, kangaroo track, burrow, goanna (monitor lizard) track. B – Miocene bioeroded mollusk found within Palaeolithic cultural layers (Dolní Věstonice II, Czech Republic; Jarošová et al., 2004). C – 18th 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*.

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 17th century or earlier. B – William Buckland, pioneer of the study of fossil faeces, 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).

Figure 3 – Pioneers in the study of trace fossils: from the Age of Naturalists to the Period of Reaction. A – Leonardo da Vinci. B – Adolphe Brongniart. C – Alfred Nathorst.

Figure 4 – Important personalities of the Modern Era. A – Marian Książkiewicz. B – James Howard. C – Adolf Seilacher.

Figure 5 – Tree of ichnology, showing the evolution in the interpretation of trace fossils. Dots correspond to bibliographic data in ICHNOBASE (2011).

SUPPLEMENTARY MATERIAL

ICHNOBASE (2011) is listed in the appendix.

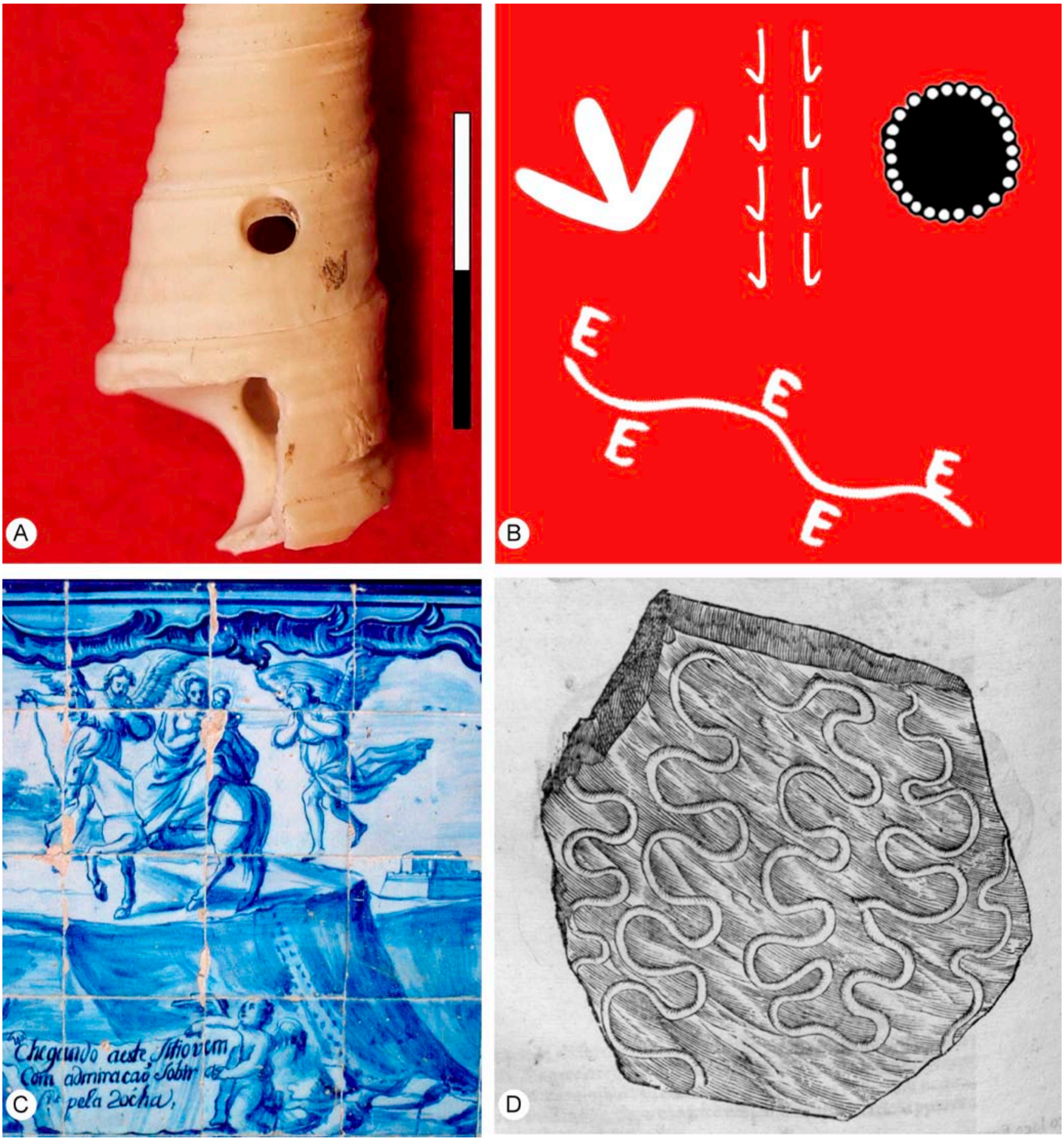
A
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Fig. 1.

Fig. 2.

Fig. 3.

Fig. 4.

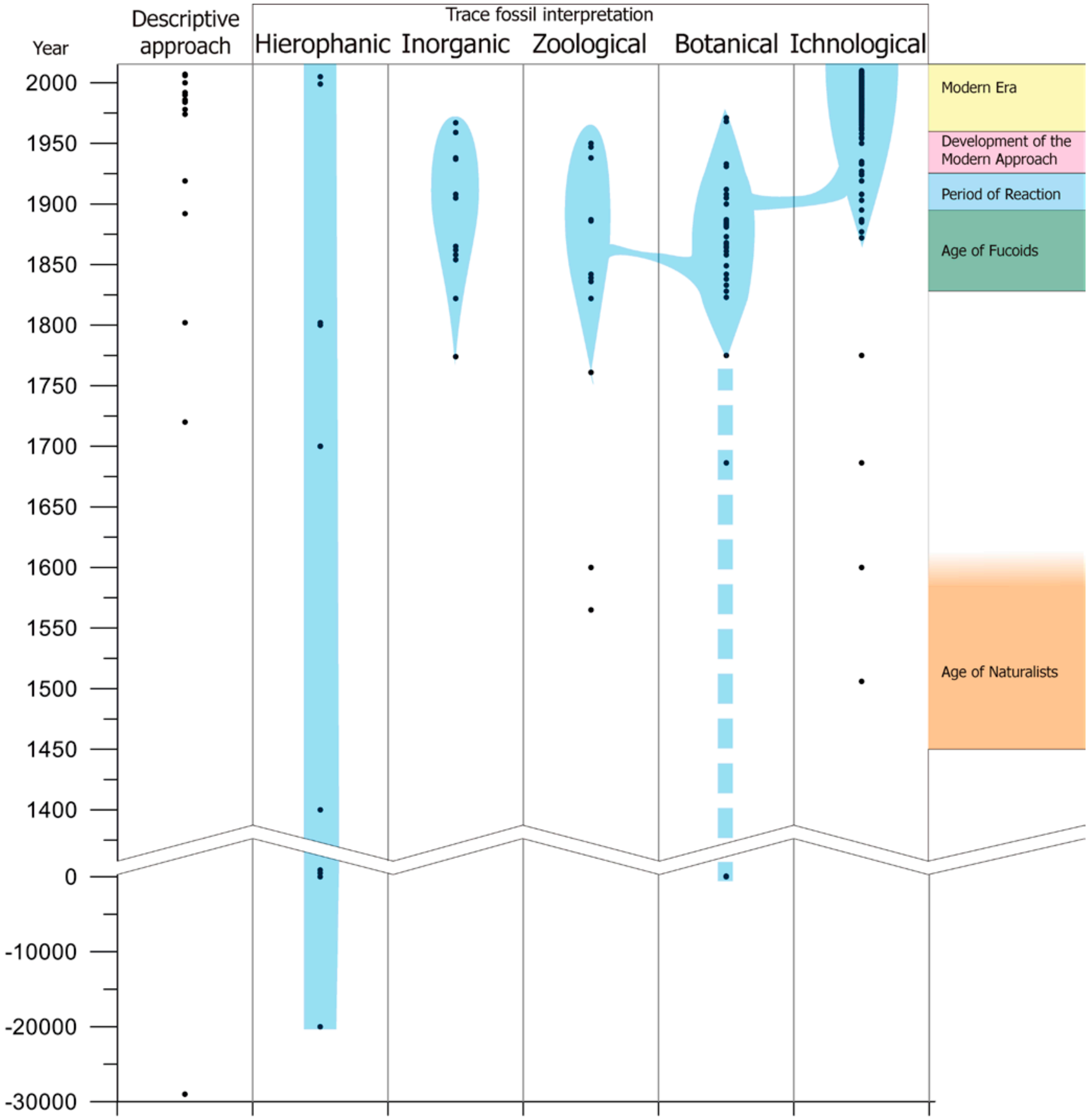
Year
Descriptive approach
Trace fossil interpretation
Hierophanic
Inorganic
Zoological
Botanical
Ichnological
2000
1950
1900
1850
1800
1750
1700
1650
1600
1550
1500
1450
1400
0
-10000
-20000
-30000
Modern Era
Development of the Modern Approach
Period of Reaction
Age of Fucoids
Age of Naturalists

Fig. 5.