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ICHNOTAXOBASES FOR BIOEROSION TRACE FOSSILS IN BONES

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ABSTRACT-Bioerosion trace fossils in bones are defined as biogenic structures that cut or destroy hard bone tissue as the result of mechanical and/or chemical processes. Under the premise that their paleoecological potential can completely be realized only through correct taxonomic assignment, this work focuses on the methodology for naming these biogenic structures. Thus, we propose the following ichnotaxobases in order to assist in naming trace fossils in bones: general morphology, bioglyphs, filling, branching, pattern of occurrence, and site of emplacement. The most common general morphologies are: pits and holes (borings); chambers; trails; tubes; channels (canals); grooves; striae; and furrows. The main types of bioglyphs are grooves and scratches, which may display different arrangements, such as parallel and opposing, or arcuate paired. The nature of the fill may help recognition of the origin, composition, and relationship with the surrounding sediment, as well as processes of destruction or consumption of bony tissue. The structure and layout of the filling, such as meniscate backfill or pelleted filling, offer information about the bioeroding processes. Branching structures on cortical bone are present in canals and furrows. Where the trace penetrates spongy bone, branching structures are forming tunnels that may connect internal chambers. The common patterns of occurrence are individual, paired, grouped, overlapping, lined, and arcuate. The site of emplacement may be in cortical bone, spongy bone, articular surfaces, internal bone microstructures, and external bone anatomical structures. The use of substrate as an ichnotaxobase is problematic, but as biological substrate, bone itself is a valuable source of information for paleoecologic and ethologic inferences. Given the paleontological importance of bioerosion trace fossils in bones, we underscore interactions between ichnology and other sciences, such as forensic entomology, archaeology, paleoecology, and taphonomy.

INTRODUCTION

URING RECENT years, bioerosion trace fossils in bones have been mostly used as tools to decipher aspects of the identity and paleoecology of their producers (Cruickshank, 1986; Currie and Jacobsen, 1995; Martin and West, 1995; Jacobsen, 1998; Tanke and Currie, 2000; Rogers et al., 2003; Hone and Rauhut, 2010; Xing et al., 2012). Many authors have recognized their importance in reconstructing the taphonomic processes involved, particularly during the first stages of decay, and the implications of bioerosion in bone preservation (Behrensmeyer, 1978; Behrensmeyer et al., 2000; Laudet and Antoine, 2004; Bader et al., 2009; Huchet et al., 2011; Backwell et al., 2012). However, with the exception of a few studies (Jacobsen and Bromley, 2009; Backwell et al., 2012), little has been published on the methodology for naming bioerosion trace fossils in bones. An ichnotaxobase is a distinctive morphologic feature of a trace fossil that displays significant and readily detectable variability and, therefore, is commonly used in ichnotaxonomic classifications (Bromley, 1996; Buatois and Mángano, 2011). Given the growing literature on trace fossils in bones, we consider that their potential can only be realized through correct taxonomic assignment and ethologic interpretation. Therefore, the aims of this work are to: 1) define what is considered a bioerosion trace in a bony substrate, 2) define ichnotaxobases for bioerosion trace fossils in bones, and 3) discuss a set of criteria that may help distinguish these structures from other kinds of non-biogenic marks commonly present on bone surfaces. In addressing these problems, we discuss the controversies surrounding the use of substrate as an ichnotaxobase. Abbreviations used in this paper are RTMP (Royal Tyrrell Museum of Palaeontology), MPM-Pv (Museo Padre Molina Paleontología de Vertebrados, Río Gallegos, Santa Cruz), and IANIGLA-Icn (Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales, Colección de Icnología, Mendoza, Argentina).

DEFINING BIOEROSION TRACE FOSSILS IN BONES

Bioerosion was defined as every form of biologic penetration into hard substrates (Neumann, 1966). When traces are related to bones, it is important to determine whether the trace fossil represents a true bioerosion structure rather than a bioturbation structure in contact with the bone surface or in the associated substrate. In this paper, bioerosion trace fossils in bones are defined as biogenic structures that cut or destroy hard osseous tissue structures as the result of mechanical and/or chemical processes (Fig. 1). On the other hand, bioturbation structures produced in the sandy substrate attached to the bone surface may be misidentified as bioerosion structures. Analysis of thinsection shows examples of trace fossils preserved in full relief, in host sediment, but not eroding the bone surface.

NAMING BIOEROSION TRACE FOSSILS IN BONES

Although many studies have described trace fossils in bones, only a few provide a taxonomic treatment (Cruickshank, 1986; Thenius, 1988; Mikuláš et al., 2006; Roberts et al., 2007; Jacobsen and Bromley, 2009; Muñiz et al., 2010) (Fig. 2). Regardless of its pitfalls, the ichnotaxonomic classification provides the best common ground on which to base more theoretical elaborations and practical applications (Bromley, 1996; Buatois and Mángano, 2011). As stated by Bromley (1996, p. 166), "in the final analysis, it is the morphology of the trace as an expression of animal behavior that is the basis of the name." In practice, it is difficult to adopt a strictly descriptive procedure for naming ichnotaxa because while morphology is



Figure *I*—The concept of bioerosion for trace fossils in bones; *I*, schematic representation of different bone tissues (cortical and spongy) and the associated trace fossils; a-c indicate bioerosion trace fossils affecting bone tissues at different levels (cortical and spongy bone) whereas *d* shows a bioturbation trace fossil associated with the bone surface but not eroding the bone tissue; *2*, close-up of a polished surface showing a transversal view of a bioerosion trace fossil in dinosaur cortical bone tissue; IANIGLA-Icn 11, Río Neuquén Subgroup, late Turonian–late Coniacian, Mendoza Province, Argentina.

observed, behavior is inferred (Mángano et al., 2002; Buatois and Mángano, 2011).

In any case, a number of characteristics are frequently used for naming ichnotaxa (Bromley, 1996). Pickerill (1994) noted that the relative importance of some taxonomic characteristics varies widely among different types of ichnofossils. This is based on the fact that one characteristic that is used to define an ichnogenus, may be in other instances used at ichnospecific level, or not used at all.

Bioerosion structures in bones show some marked departures with respect to some of the most common bioturbation structures and even to the most typical bioerosion structures in other substrates. The first issue to address is why it is necessary to propose specific characters that should be considered in the description and taxonomic classification of bioerosion trace fossils in bones. In the field of bioerosion, there is presently no ichnotaxonomy specifically designed to accommodate trace fossils in bones. Therefore, we propose ichnotaxobases for describing bioerosion trace fossils in bones. These ichnotaxobases are not that different from the original ones proposed for trace fossils in general (Bromley, 1996), but they focus on some relevant aspects directly related to development and mechanisms of bioerosion. These ichnotaxobases are thought to be applied to both vertebrate and invertebrate trace fossils.

ICHNOTAXOBASES FOR BIOEROSION TRACES IN BONES

The following ichnotaxobases are proposed in order to assist in naming traces in bones: 1) general morphology; 2) bioglyphs; 3) filling; 4) branching; 5) pattern of occurrence; and 6) site of emplacement (Fig. 3).

General morphology.-Jacobsen and Bromley (2009) noted

that "application of ichnotaxa to trace fossils is a procedure that must vary according to the group of trace fossils under study." They differentiated a group of trace fossils that display relatively constant morphology, such as invertebrate burrows (e.g., Uchman, 1999) and insect nests (e.g., Genise, 2004), from another group of structures that tend to show extreme variation in morphology, such as tracks of tetrapods (e.g., Manning, 2004; Milán and Bromley, 2006), due to preservational or behavioral differences or because of variations in substrate consistency (e.g., Bromley, 2001; Fornós et al., 2002).

Britt et al. (2008) proposed morphotypes and some general morphological categories to group trace fossils in bones attributed to insects in continental settings. Roberts et al. (2007) proposed to group the most commonly recorded trace-fossil morphologies into five general categories: ovoid chambers (e.g., *Cubiculum* isp.); shallow circular to elliptical pits; star-shaped pit traces; surface trails (e.g., *Osteocallis* isp.); and tunnels and subcortical cavities. The recognition of a pattern based on the shape of the biogenic structure could be very useful for interpreting the ethology and to identify an ichnotaxon (Fig. 4). This approach follows the view of morphology as an expression of behavior, as recommended by Bromley (1996). In addition, traces produced by predation of vertebrates (e.g., tooth traces) are usually described by comparing size and disposition of carnivorous fossil mandibles (Mikuláš et al., 2006; Noriega et al., 2007; Jacobsen and Bromley, 2009).

In this paper, we encourage the use of morphology in the diagnosis of bone bioerosion ichnotaxa, and we recommend differentiating between morphologic description and ethologic interpretation wherever possible. The latter is vital to illuminate our understanding on the genesis of the structure, but it is not advisable to include this in the description of an ichnotaxon. The most common morphologic types to be considered are: pits and holes (borings); chambers; trails; tubes; channels (canals); grooves; striae; and furrows. Each of these may present different orientation with respect to the substrate surface.

Bioglyphs.—As mentioned by Mikuláš (1998) and Ekdale and Gibert (2010), morphologic features interpreted as bioglyphs have been used as valid ichnotaxobases for bioerosion in bones (e.g., Hasiotis et al., 1999; Tapanila et al., 2004; Roberts et al., 2007; West and Hasiotis, 2007; Bader et al., 2009) and bioerosion in other substrates (Kelly and Bromley, 1984; Gibert and Ekdale, 2010; Donovan, 2002, 2011). They provide evidence of how the trace fossil was produced. They also can provide information about substrate characteristics. Ekdale and Gibert (2010) proposed revising the term bioglyph "to encompass only carvings or engravings that are inscribed into the wall of a burrow or boring." We follow their definition in our study.

Because of the characteristics of bone as hard substrate and as a result of animal activity, bioglyphs represent the clue to understanding specific methods and strategies of bioerosion in bones. They also can supply detailed information for interpreting anatomy and identify the producer. For these reasons, they constitute an important ichnotaxobase. Despite the importance of bioglyphs as a distinctive character in ichnotaxonomy, few ichnotaxa have been erected using them as ichnotaxobase. *Cubiculum ornatus* and *Osteocallis mandibulus* Roberts et al. 2007 are notable exceptions. In both cases, bioglyphs were interpreted as the result of insect mandibles scratching or gnawing.

The under-utilization of bioglyphs as an ichnotaxobase is probably due to difficulties in their recognition, especially in the case of tunnels that penetrate into bone. Part of the problem lies in the physical structure of certain types of bone tissues, such as trabecular and cortical. Trabecular bone is a light, porous material enclosing numerous large spaces that give a spongy appearance. The bone matrix is organized into a three-dimensional network of

Ichnotaxa	Schematic Illustration	lchnotaxa	Schematic Illustration
Asthenopodichnium ossibiontum Thenius, 1988		<i>Machichnus multilineatus</i> ^{Mikuláš et al.,2006}	
<i>Brutalichnus brutalis</i> Mikuláš et al.,2006		<i>Machichnus regularis</i> Mikuláš et al., 2006	
<i>Cubiculum</i> <i>ornatus</i> Roberts et al., 2007		<i>Mandaodonites coxi</i> Cruickshank, 1986	000000000000000000000000000000000000000
Knethichnus parallelum Jacobsen and Bromley, 2009		<i>Nihilichnus nihilicus</i> Mikuláš et al., 2006	
<i>Linichnus</i> <i>serratus</i> Jacobsen and Bromley, 2009		<i>Osteocallis mandibulus</i> Roberts et al.,2007	HALL HALL
<i>Machichnus bohemicus</i> Mikuláš et al., 2006		<i>Trypanites ionasi</i> Muñiz et al., 2010	

Figure 2-List of ichnotaxa defined for bioerosion traces in bones and schematic representation of their general morphology. Trace fossils appear in black, bone-substrate in gray.



Figure 3-Diagram illustrating the most common attributes of ichnotaxobases for bioerosion trace fossils in bones and their terminology.

trabeculae (plates and rods). Spaces between are commonly filled with marrow (soft tissue). In contrast to cortical bone, at a microarchitectural scale, trabecular bone does not have a plain hard surface that allows recording of the pattern of bioglyphs resulting from macrobioerosion. Examples discussed in this paper, such as *Cubiculum ornatus*, are all emplaced in cortical bone, which can be eroded in such a way that bioglyphs are recorded and commonly recognized. Modern technologies, such as SEM studies (e.g., Britt et al., 2008, fig. 1, p. 63), are proving useful in assisting recognition of bioglyphs. The main types of bioglyphs on the walls of bioerosion trace fossils on bones are grooves and scratches. These bioglyphs may present different arrangements, such as parallel and opposing or arcuately paired.

Filling.—Recognition of the presence of filling and distinguishing passive from active filling constitutes an important tool for reconstructing taphonomic histories and ethologic significance of biogenic structures. As active filling represents the result of animal handling of the substrate, it usually contrasts with the surrounding sediment and possesses a typical structure (Bromley, 1996). Because of its highest significance, this ichnotaxobase has been used in the diagnosis of many bioturbation ichnotaxa (Clifton and Thompson, 1978; Pemberton and Frey, 1982).

Actively filled traces, eroded into bone substrate, involve a set of complex processes that imply destruction of superficial and internal bone structures, consumption of organic matter, processing of waste material, and locally mixing with surrounding soft sediment, especially when part of the fill resembles the host sediment or part of bone structure is drawn out into the sediment (Paik, 2000). Therefore, analysis of the nature of the fill may help recognition of the origin, composition, and relationship with the surrounding sediment, as well as processes of destruction or consumption of bony tissue. On the other hand, the structure and layout of the filling, such as meniscate backfill or pelleted filling, offer much information about the bioeroding processes, commonly related to insect and microfauna feeding behavior. In bioerosion traces in bones, meniscate backfill could result from the alternation of organic matter (derived from the bone) and sediment ingestion and backfilling by the producer (Fig. 5). Bone fragments have been reported as part of the composition of filling (Paik, 2000). The presence of bone fragments in the filling, a recognizable pattern of their distribution, as well as bone fragment shape, could be also considered an ichnotaxobase, if these characteristics are interpreted as the result of a specific and recurrent behavior, namely selection or destruction of bone based



Figure 4 – Bioerosion trace fossils displaying ovoid chamber morphology eroded on cortical bone; IANIGLA-Icn 1, Río Neuquén Subgroup, late Turonian–late Coniacian, Mendoza Province, Argentina); 1, general view; 2, close view of 1.

on specific size, shape, and the subsequent arrangement in the filling. Although the presence of bone chips associated with bioerosion traces on bones has been reported in the fossil record (Paik, 2000), we are unaware of modern examples of the manipulation of bone fragments. Passive filling is of no taxonomic importance, but analysis of content, origin, relationship with surrounding sediment, and composition can be very useful in the reconstruction of pre and post-burial taphonomic processes, especially when recognizing diagenesis or changes in the sediment type.

Branching.-According to Bromley and Frey (1974) and D'Alessandro and Bromley (1987), four styles of branching can be identified: primary successive, produced by successive probing activity from an unbranched structure resulting in a cumulative structure; simultaneous, consisting of a network of passages simultaneously opened; secondary successive, resulting when the producer enters and follows along an earlier fill; and false branching, caused by accidental intersection and incomplete preservation. The presence and type of branching (including order, angle values, and size relations) provide valuable information about the producer's behavior. At present, no bone bioerosion ichnotaxa have been introduced that are specifically based on the presence of branching, although branching itself has been recorded and interpreted as produced by termites constructing galleries on the cortical bone and into the inner tissue (Huchet et al., 2011). In addition, superficial and shallow structures on the surface of bones commonly display branching as a result of feeding behavior. Some of these trace fossils have been interpreted as "probing" traces (Britt et al., 2008), but have not been described in detail yet. In both cases, and as highlighted by Bromley (1996), even in the cases in which the branched form does not directly reflect the shape of the original structure, it certainly reflects the producer behavior. In bioerosion traces in bones, identifying the arrangement of branching is a fundamental tool for recognizing feeding strategies, presence of different scavengers, and even stages of decomposition. Branching as an ichnotaxobase for bioerosion traces in bones is intimately related to the type of bone tissue eroded. On cortical bone, branching structures are present in canals and furrows. Where the trace penetrates spongy bone, branching structures are forming tunnels that may connect internal chambers (Fig. 6).

Pattern of occurrence.—This ichnotaxobase applies to those trace fossils that can be analyzed at a larger scale and that present a distinctive arrangement, so a recurrent mode of occurrence can be identified. Examples of this ichnotaxobase are "bite traces" of vertebrates or series of perforations interpreted as pupal chambers. Almost all tooth traces and biting traces have been described on the basis of a comparison of the position of traces on the bone surface and teeth in jaws (Cruickshank, 1986; Jacobsen, 1998; Rogers et al., 2003; Mikuláš et al., 2006). Jacobsen and Bromley (2009) illustrated this point by underscoring the morphology of specific theropod bitings. They also encouraged further observation, studies of distribution, and use of similar ichnologic terminology for all tooth and biting traces. Previous



Figure 5—Transversal view of three different trace fossils filling section with bone chips in. *1*, *2*, trace fossils displaying a concentric pattern of distribution, bone chips are similar in size and shape; IANIGLA-Icn 14, Río Colorado Subgroup, Santonian–early Campanian, Mendoza Province, Argentina; *3*, trace fossil filling consisting of randomly distributed bone chips of different size and shape; MPMPv3457 *Orkoraptor burkei* Novas et al., 2008, Pari Aike Formation, Maastrichtian, Santa Cruz Province, Argentina.



Figure 6—Trace fossils displaying false branching (i.e., trace-fossil overlap). *1*, general view; *2*, closer view of the same traces. Black arrows point traces displaying on bone surface; IANIGLA-Icn 16, Río Colorado Subgroup, Santonian–early Campanian, Mendoza Province, Argentina.

works recognized the importance of identifying different types and categories of biting traces, as in the case of theropod bites (Tanke and Currie, 2000; Rogers et al., 2003) or other groups of vertebrates (Delaney-Rivera et al., 2009; Longrich and Ryan, 2010). As suggested by Jacobsen and Bromley (2009), we consider of paramount importance the recognition of a recurrent pattern that offers accurate information, in order to reach paleoecological conclusions (Fig. 7). However, this criterion should be applied only when a distinct pattern can be identified. Many random biting traces, pits, or holes on varying bone substrates offer a wealth of structures, despite the fact they do not display any consistent pattern of occurrence. To summarize, common patterns reported for trace fossils in bones are individual, paired, grouped, overlapping, lined, and arcuate.

Site of emplacement.—This ichnotaxobase refers to the place where traces are constructed on the bone. It not only refers to the orientation of the trace (parallel or perpendicular to the bonetissue layers), but to its relationship to internal and external bony structures, such as channels, spongy bone, compact bone, collagen fibers, extracellular matrix, and articular surface. Distinguishing the site of emplacement can help us understand bioerosion processes and the types of nutrients that were being consumed. Internal and cortical bones do not have the same structure, neither the same elasticity nor resistance to fractures and destruction. Thus, it is expected that bioerosion processes needed for destroying the bone will be different depending on the bone area (type of bone tissue) eroded. Identifying the site of



Figure 7—The trace fossil *Knethichnus parallelum* displaying parallel arcuate grooves pattern on bone surface; RTMP88.36.39, Dinosaur Park Formation, Campanian, Alberta, Canada.

emplacement can also constitute a clue for understanding the ethological meaning of the trace (Fig. 8). Many trace fossils in bones have been interpreted considering which part of the bone has been destroyed or consumed. *Brutalichnus brutalis* Mikuláš et al. 2006 is interpreted as a feeding trace on bones. This ichnotaxon consists of straight to arcuate lines on bones, recording breaking of the cortical bone and penetration into the internal part of the organic-rich trabecular bone (Mikuláš et al., 2006). Similar interpretations have been made for insect (Roberts et al., 2007; Britt et al., 2008; Hauchet et al., 2011) and vertebrate (Mikuláš et al., 2006; Jacobsen and Bromley, 2009) trace fossils, especially bite and gnawing traces. Thus, bioerosion trace fossils in bones may occur in cortical bone, spongy bone, articular surfaces, internal bone microstructures, and external bone anatomical structures.

DISCUSSION

Different ichnotaxobases have been used for describing bioerosion traces in bones. One of the most controversial ichnotaxobases is substrate. Mikuláš et al. (2006) proposed considering bones (as substrate) as a potentially useful ichnotaxobase. Muñiz et al. (2010) placed within Trypanites, a typical bioerosion ichnotaxon of hardgrounds, the ichnospecies T. ionasi, produced in whale bones. Bertling et al. (2006) underscored the importance of substrate as an ichnotaxobase if it implies a different behavior by the producer. Although these authors considered that trace fossils found in different substrates should "be kept separate regardless of morphologic similarity," they did not consider substrate as a high-rank ichnotaxobase, and emphasized the importance of detailed studies of morphology and other restrained differences. Carmona et al. (2007) argued against the use of substrate as an ichnotaxobase if similar morphologies in different substrates are produced by the same mechanism (i.e., some organisms such as lithophagid bivalves, which are able to both bore and burrow without essentially changing their basic behavior).

Traces in biologic tissue (bone) are the result of specific ecologic niche selection by specialist necrophagous borers, as reported in studies of forensic entomology. Although the selection of substrate reflects obligate behavior by organisms having specific feeding requirements and that specific biologic tissue (bone) is used as a source for those nutrients, adopting substrate as an ichnotaxobase is controversial. Most traces found in bones are the result of scavengers and necrophagous activity produced during different stages of decay, as observed in modern studies (Behrensmeyer et al., 1978; Haynes, 1983;



Figure 8—Trace fossil eroding different bone tissues. *1*, trace fossil (arrow) erodes surface of cranial bone, penetrates throughout cortical tissue, spongy bone, and continuous into the substrate; MPM-Pv 3457 *Orkoraptor burkei* Novas et al., 2008, Pari Aike Formation, Maastrichtian, Santa Cruz Province, Argentina; *2*, graphic representation of bioerosion trace fossil and the different bone tissues eroded.

Benecke, 2004). Due to its mineralogical composition, the bone remains hard during decomposition and, sometimes, may even get increasingly harder after this process (Trueman et al., 2004, 2008). However, during these stages, physical (strength) and chemical (mineral composition) properties of bone tissue do not remain constant (Korsakov and Savostin, 1975). These properties are widely influenced by environmental conditions, as analyzed in many actualistic studies (Behrensmeyer et al., 1978, 2000, and references therein). In paleontological studies, it is difficult to access the information concerning the changes of mechanical properties of the bone tissue since the time of death and along the process of decay. Finally, if we consider environmental influence on the process of decay, diversity of scavengers (trace-producers), and taphonomy, then the marine and continental environments display quite different ecological and physical pressures on bone decay processes. Because of the unstable condition of bone as substrate, we avoid its use as an ichnotaxobase. However, as a biological substrate, we consider bone as a valuable source of information for establishing paleoecological and ethological inferences. Haynes (1983) conducted several experiments in order to recognize patterns of occurrence and selectivity of bone pieces by different predators and scavengers. The results offer a view of bone selection and utilization as a source of food by actual scavengers and carnivores. Examples of species from Africa as well as North America show how biological agents can create and modify bone assemblages in numerous ways (Haynes, 1983, 1985; 1988; Cutler et al., 1999).

Modern ecologic studies highlighted the significance of detritus quality in the ecology of food webs (Moore et al., 2004), and outlined the importance of scavengers into food-web theory, noting that they represent the most effective way of transferring energy, even surpassing predators (Wilson and Wolkovich, 2011). From this perspective, the study of trace fossils in bones may provide more refined and detailed information about paleoecosystem dynamics.

The role of ichnology as a bridge between life and earth sciences is relatively well understood. However, in the field of bioerosion trace fossils in bones there are still some frontiers to cross. Interactions with other disciplines, such as forensic entomology, pathology, medicine, physiology, and taphonomy, remain poorly explored and may provide invaluable information for understanding the complex processes that affect the production and preservation of trace fossils in bones. On the other hand, some disciplines have already made some attempts to apply ichnology in their field. Recent work on ichnoarchaeology (Mikuláš, 2001; Hladilová and Mikuláš, 2005; Cílek et al., 2007; Baucon et al., 2008) applies ichnological concepts to the study of ancient civilizations, offering additional information for a better comprehension of past times.

CONCLUSIONS

Bioerosion trace fossils in bones are biogenic structures that cut or destroy hard osseous tissue structures as the result of mechanical and/or chemical processes. The value of these structures as direct evidence of species interactions in the fossil record is underscored. The information potential of traces in bones can only be explored through a correct taxonomic assignment and ethologic interpretation. The following ichnotaxobases are proposed in order to assist in naming traces in bones: general morphology, bioglyphs, filling, branching, pattern of occurrence, and site of emplacement. The unstable mineral and physical condition of bone during the process of decay makes the use of substrate not advisable as an ichnotaxobase. However, as a biological substrate, bone itself is a valuable source of information for paleoecological and ethological inferences. Interactions between ichnology and other sciences (e.g., forensic entomology, archaeology) are highlighted.

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