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The ichnofacies concept in vertebrate ichnology

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SUMMARY - *The ichnofacies concept in vertebrate ichnology* - Nowadays, it is well clear that two different opinions exist on the concept of land-vertebrate ichnofacies. Consistently, different definitions and formalizations of this term have been suggested. After a short historical review, we analyzed the applicability and the effectiveness of both interpretations. We believe that the two existing opinions are inadequate for different reasons. Furthermore the ichnofacies concept itself should be considered with caution, difficult to apply, frequently useless and, perhaps dangerous, tending to diminish the information content of the analytical studies.

RIASSUNTO - *Il concetto di icnofacies nell'icnologia dei vertebrati* - Oggi esistono in letteratura due differenti opinioni sul concetto di icnofacies per i tetrapodi continentali e, in accordo con queste, sono state stilate due differenti liste di icnofacies a tetrapodi continentali di cui si è verificata l'applicabilità e utilità. Entrambe le definizioni risultano tuttavia inadeguate per differenti motivi. Il concetto stesso di *land-vertebrate-ichnofacies* deve, inoltre, essere considerato con estrema prudenza, poiché sembra di difficile applicazione, spesso inutile e forse pericoloso, dato che tende a diminuire il contenuto informativo ricavato da studi analitici.

Key words: ichnofacies, land-vertebrate ichnology
Parole chiave: icnofacies, icnologia a tetrapodi continentali

1. INTRODUCTION

In recent years, vertebrate ichnology has been taking an ever increasing importance in stratigraphy, basin analysis and palaeogeography. This is largely due to the reliability that land-vertebrate traces have reached, throughout some fundamental steps, namely: the introduction of fossil traces into the Codex of Nomenclature (ICZN 1999), the understanding of the importance of extramorphologies and/or "phantom taxa" concept (Voigt & Haubold 2000; Swanson & Carlson 2002), the reduction, in some cases dramatic, of a plethoric nomenclature (Haubold 1996). Moreover, along with a modern approach to the land-environment ichnology, new study methods have been proposed (e.g. the establishment of land-vertebrate ichnofacies by Lockley *et al.* 1994) as well as new opportunities have been revealed (i.e. the establishment of land-invertebrate ichnofacies by Lockley 2007).

Some important points are still debated (e.g. the actual value of the track-trackmaker relationship, as well as to what degree a fossil trace can be considered as a proxy for zoological taxon). At the end of the '90 an intriguing question, concerning the applicability and the effectiveness of the ichnofacies concept to land-vertebrate ichnology, was posed. This question, still controversial, as already indicated by Lockley (2007) and worth of some close investigations, is the subject of this paper.

2. HISTORICAL BACKGROUND

An almost complete and good historical review of the evolution of the ichnofacies concept is reported in Hunt & Lucas (2007) and it is here shortly summarized. The term ichnofacies could be easily parallelized to the better known biofacies. In its original meaning (Gressly 1838), the biofacies concept was closely related to the lithofacies one. The latter records a depositional environment, the former the fossilized organisms that had the more favorable life conditions in such environment.

The further step was the application of this concept to invertebrate traces, throughout a series of well established definition and classification; Seilacher (1964) defined the first four types of facies (*Skolithos*, *Cruziana*, *Zoophycos* and *Nereites* facies) as "general traces associations or type of ichnocoenoses representing certain facies with a long geological range" (Seilacher 1964: 303). Subsequently two further facies were recognized (*Scoyenia* and *Glossifungites* facies) rising to six their number (Seilacher 1967). In establishing this succession of trace fossil facies, Seilacher underlined their importance as "useful tools in palaeobathymetry" and he constantly used the term ichnocoenosys stressing that the key of their usefulness is the association of different traces to sediments (Seilacher 1967: 417). In these studies the term "ichnofacies" was applied for the first time.

After these seminal works, for long time, the ichnofa-

cies concept kept more or less the Seilacher's model so that they were defined as "seilacherians" (Bromley 1996) or "archetypal" (Frey & Pemberton 1987). Nevertheless, as underlined by Bromley & Asgaard (1991), some ichnofacies, subsequently introduced, changed in different way the original meaning, so that these authors concluded that the unitarian philosophical bases of the concept were lost. Nevertheless, they stated that "although non-uniformitarian, although not bathymetrically controlled, and although not homogeneous, the ichnofacies remain the most important means of classifying trace fossil assemblages" (Bromley & Asgaard 1991: 161).

The first organic discussion on land-vertebrate ichnofacies has to be credited to Lockley *et al.* (1994) even if, according to Hunt & Lucas (2007), already Baird (1965) noticed some differences among the ichnoassociations of Permian red beds in the western United States. Lockley *et al.* (1994), adapting to vertebrate traces the original concept of ichnofacies (*sensu* Seilacher 1964), defined vertebrate ichnofacies as "recurrent ichnocoenoses that are associated with particular ancient environments (preserved as distinctive lithofacies)" (Lockley *et al.* 1994: 244). As for the invertebrate ichnofacies, a distinctive ichnogenus was chosen to name each ichnofacies. In Lockley *et al*. (1994) some groups of traces/environment associations were distinguished, sometimes defined as ichnofacies and sometimes as ichnocoenoses (Tab. 1).

Subsequently Lockley & Meyer (2000), coming back

Tab. 1 - Land-vertebrate ichnofacies subdivision according to Lockley *et al.* (1994).
Tab. 1 - Suddivisione delle icnofacies a vertebrati continentali secondo Lockley et al. *(1994).*

TETRAPOD ICHNOFACIES	CONSTITUENT ICHNOCOENOSES	INFERRED ENVIRONMENT
Laoporus (Upper Palaeozoic)	(1) *Laoporus* dominant, with invertebrate traces (*Paleohelcura-Octopodichnus*) (2) Fluvial and plains with abundance of *Limnopus* and *Antichnium* (in Europe considered a separated ichnofacies)	Desertic, fluvial and plains
Mesozoic vertebrate (Upper Trias)	*Brachychirotherium* and other tracks. Two ichnofacies: (A with great prints - i.e. *Brachychirotherium* - and B with small prints - i.e. *Rhynchosauroides*)	Not indicative of particular environment
Brasilichnium (Lower Jurassic)	Similar the *Laoporus* ichnofacies (Coconino) and the associated ichnofacies of the eolian facies of the Navajos Sandstone (Lower Jurassic) at *Brasilichnium* ichnocoenosys- dominant	Eolian
Mesozoic vertebrate (Lower Jurassic)	Other Lower Jurassic ichnocoenoses and ichnofacies - *Eubrontes* s.l. and *Otozoum* (playa)	More or less arid environments
Brontopodus (Upper Mesozoic)	(1) Ichnoassociation dominated by sauropods, abundant theropods with robust size, small theropods and ornithopods (2) Lagoons, carbonate platforms. In Europe (Portugal and Switzerland) *Brontopodus* is associated to *Rhyzocorallum*, *Thalassinoides* or *Cruziana*	Carbonate platform (carbonate and evaporitic facies), lakes with alkali-carbonates, lagoon
Caririchnium (Upper Mesozoic)	*Caririchnium*- dominant. With invertebrate traces (*Skolithos)* association linked to energy rather than depth	Siliciclastic environments
Upper Mesozoic	Other ornithopod-dominat ichnofauna – Ceratopsid, ornithopod and theropod tracks (Laramie Formation).	Lacustrine shoreline, lake, molasse
Shore birds (and *Jindongornis*) ichnofacies Late Mesozoic and Cenozoic	(1) Lacustrine shoreline, lake (Cretaceous-Tertiary) recurrent ichnoassociations of bird prints and invertebrate traces. (2) Lacustrine shoreline (Cretaceous of the Jindon Formation). The *Jindongornis* ichnofacies is a rare example of birds and dinosaurs association	

Tab. 2 - A scheme of land-vertebrate ichnofacies subdivision after Lockley (2007).
Tab. 2 - Schema della suddivisione delle icnofacies a vertebrati continentali di Lockley (2007).

TETRAPOD ICHNOFACIES	MAIN CHARACTERISTICS
Batrachichnus (*Limnopus-Antichnium* association)	Low and more humid lands. The new ichnofacies "label" is due to the taxonomic changes recorded for these taxa.
Chelichnus	Arid continental deposits in eolic dune environments of the Permian until to the Lower Jurassic. The original *Laoporus* ichnofacies was renamed as *Chelichnus* ichnofacies, minding the ichnotaxonomic revision of McKeever & Haubold (1986).
Grallator-Brachychirotherium-Rhynchosauroides	It is in association with *Scoyenia* and *Diplichnites*. *Grallator-Brachychirotherium* and *Rhynchosauroides*, the ichnofacies is representative of a large spectrum of the Late Triassic ecosystems linked to the humid climatic conditions. It has also a stratigraphic meaning.
Brasilichnium	Lower Jurassic. Similar to the *Chelichnus* or *Laoporus* ichnofacies but differing for the different age.
Chelonichnium	Based on recurrent turtle tracks in lithographic limestone (carbonate platform lagoon) Upper Jurassic of France.
Brontopodus	Ichnofacies from Upper Jurassic carbonate platform deposits. Also present in low latitude carbonate platform deposits and in the Lower Cretaceous.
Pteraichnus	Two ichnofacies: one dominant in the basal Upper Jurassic clastic environments of the N. America and rarely in carbonates. The second from the carbonate platform deposits of the uppermost Jurassic of France.
Caririchnium	It does not differ from its original definition.
Ornithopod ichnofacies	Unchanged from its original definition.
Shore-bird ichnofacies	Unchanged from its original definition.

on this topic, repeated the same concept as "distinctive sedimentary deposit representing a particular ancient habitat in which the same tracks and traces recur repeatedly" (Lockley & Meyer 2000: 16), once again stressing the close relationships between deposition environment and the "same" recurrent biocoenoses.

As it is well clear in the list of table 1, the distinction in the first draft has been limited to large group of associated lithologies and tracks (not still all formally grouped as ichnofacies), but it has been also based on a stratigraphic base. This mix of different concepts seems to found its ultimate realization in a following paper (Lockley 2007). In this paper land-vertebrate ichnofacies were better defined and resulted slightly different from the originally described ones (Tab. 2).

In the Lockley's last subdivision, the above quoted conceptual mixing is more apparent. Although the ichnofacies have been defined for ichnocoenoses with long or short stratigraphical range, when an evolutionary substitution was recognized, deposits ascribed to the same deposition environment have been subdivided into different ichnofacies. At a first glance, this scheme seems to underline once again an unambiguous link between deposition environment and a type of association but, at the same time, the short-ranging ichnofacies assume also a stratigraphical meaning. Linking the rock bodies to a chronologically characterized biological content, the ichnofacies lose in part their role of tools for unitary environment interpretation and are moved toward the zones of the classical biostratigraphy.

In practice, the concept of vertebrate ichnofacies met only a partial achievement among vertebrate ichnologists, so that the keynote lecture of Lockley at the 32nd IGC held in Florence (Italy) in 2004 was entitled "Vertebrate ichnofacies: do we take them seriously?" (Lucas 2005).

The following step is represented by a new interpretation of the ichnofacies concept by Hunt & Lucas (2006, 2007). The opinion of these authors, anticipated in the 2004

Tab. 3 - Land-vertebrate ichnofacies subdivision (after Hunt & Lucas 2007, mod.).
Tab. 3 - Suddivisione delle icnofacies a vertebrati continentali (Hunt & Lucas 2007, mod.).

TETRAPOD ICHNOFACIES	ICHNOCOENOSES	INFERRED ENVIRONMENT
Chelichnus	*Chelichnus* (=*Laoporus*) (Early Permian); *Brasilichnium* (Late Triassic-Early Jurassic)	Eolian crossbeds
Batrachichnus	*Batrachichnus* (Early Carboniferous-Early Permian): separable into sub-ichnocoenoses: (1) inland/distal alluvial fan settings characterized by the presence of *Ichniotherium* and a paucity of *Dimetropus*; (2) alluvial plan settings characterized by the presence of *Amphisauropus* and (3) coastal/tidal flat settings characterized by the relative abundance of *Batrachichnus* and *Dimetropus*	Tidal flat-fluvial plain
Brontopodus	Coastal plain *Ceratopsipes* (Late Cretaceous); ornithopod (Early-Late Cretaceous). Clastic marine shoreline *Carichnium* (Early Cretaceous). Carbonate marine shoreline *Chelonichnium* (Late Jurassic); *Brontopodus* (Early Cretaceous)	Costal plain, clastic or carbonate marine shoreline
Grallator	*Avipeda* (=shore-bird ichnofacies-Tertiary); *Eubrontes* (Early Jurassic); *Jindongornipes-Koreanornis* (Early Cretaceous)	Lacustrine margin
Characichnus	Unnamed (St. George, Utah Early Jurassic,); *Characichnus* (Middle Jurassic); *Hatcherichnus* (Late Jurassic)	Shallow lacustrine

32nd IGC at Florence (see Lucas 2005), is fully explained in two sister papers. In the first (Hunt & Lucas 2006), the authors presented a scheme of their ichnofacies, quoting as the main source an existing paper, at that time submitted but unfortunately only subsequently printed (Hunt & Lucas 2007). We believe correct to re-establish the original chronological sequence, reflecting the evolution of their ideas: thus we refer here the origin of the new ichnofacies concept (*sensu* Hunt & Lucas) to the 2007 paper.

Hunt & Lucas (2007) made the attempt to change the vertebrate ichnofacies concept, coming back to its archetypal meaning and excluding the above described stratigraphical poisoning. The aim was to make the vertebrate ichnofacies comparable to invertebrate ichnofacies. We believe that, perhaps, they also perceived the intrinsic danger concealed in the close relationships between the ichnofacies concept and a too strong taxonomic, evolutionary and stratigraphical meaning, thus lowering their generalized environment application.

These authors made a correct analysis of the widespread divarication between the "two ichnologies" (Hunt & Lucas 2006). As a matter of facts, after recognizing that invertebrate ichnologists have an ethologic approach and privilege the organism/substrate relationships, while vertebratists show a more bio-taxonomic interest, privileging the track-trackmaker relationships, they defined the result of such widespread behavior, distinguishing between the "ethoichnofacies" for the invertebrates and the "biotaxoichnofacies" for vertebrates.

The authors suggested an use of the term "ichnocoenosys" restricted to its correct meaning of an association of traces that reflects the life-activity of organisms pertaining to a biocoenosys (a community of organism) (*sensu* Dvitashvili 1945, *fide* Hunt & Lucas 2006, 2007), thus made by coexistent animals.

In their interpretation, the Lockley's ichnofacies are thus considered only particular ichnocoenoses. With this meaning many ichnocoenoses of similar environment and different age were recognized, further grouped into ichnofacies, made free from stratigraphical constraints. In both Hunt & Lucas papers were listed the following ichnofacies: *Chelichnus* ichnofacies, *Batrachichnus* ichnofacies, *Brontopodus* ichnofacies, *Grallator* ichnofacies, *Characichnos* ichnofacies, each of them including 2 or more ichnocoenoses (Tab. 3); the *Chelonichnium* ichnocoenosys and the *Pteraichnius* ichnocoenosys were unassigned.

The vertebrate ichnofacies were simplified and generalized ("as traces of specific communities, that lack the

geographical, stratigraphical range" Hunt & Lucas 2007: 61) so that they could came back to play the role of "archetypal" ichnofacies.

3. TWO MEANINGS: A COMPARISON

Nowadays, for the above, we face two different meaning of the term "land-vertebrate ichnofacies" (*sensu* Lockley *et al.* 1994; Lockley 2007 and *sensu* Hunt & Lucas 2006, 2007). The former underlines the "dual influence of biologic evolution and facies relationships that gives ichnofacies their characteristic signature" (Lockley 2007: 50); the latter states that ichnofacies should be defined on morphological bases.

Both interpretations seem to not fit within the original Seilacher's concept and in both cases their use and usefulness seems at least questionable for several reasons.

Lockley (2007) tightly bonds its ichnofacies to their biological content, and emphasizes the influence of evolutionary substitution. It seems he simply recognizes that the more we approach to the trackmaker nature the more is difficult to apply seilacherian ichnofacies model. Including the animal behavior within the concept of extended phenotype, its definition could be accepted, but the so defined ichnofacies, inevitably with a strong biochronological meaning, have more or less the same meaning of the ichnofaunal units or ichnobiochrons. In this way a deep confusion originates and their use seems redundant.

Hunt & Lucas (2006, 2007) had the merit to formally recognize, in some way, the fundamental differences between the vertebrate and invertebrate ichnologies, well fixing the concepts of ethoichnofacies and biotaxoichnofacies. Nevertheless, probably on the wave of the growing tendency toward an improbable reunification (Bromley 1996; Conti *et al.* 1997; Lockley 2007), they made the attempt to parallelize the different approaches.

We believe that the authors failed in this attempt, noble *per se*, either assembling too extremely different environments (e.g. the *Pachypes* ichnocoenosys – riverine and alluvial plain – is associated to the *Brontopodus* ichnocoenosys – carbonate platform and lagoon within the *Brontopodus* ichnofacies) or interpreting similar morphologies as they were similar behaviors (avian and non-avian theropods are associated in the *Jindongornis* ichnofacies). Moreover, this way of thinking reflects completely the strong lumping approach to ichnotaxonomy so widespread in Lucas papers, that he calls "fusion method" (Lucas 2005: 159), and that predictably leads to collect different things in too huge boxes. In this way, the land-vertebrate ichnofacies (*sensu* Hunt & Lucas 2007) allow distinguishing only 4 deposition environments, as the land environment could be so simply subdivided. Among them, 3 mean simply "humid environment without vegetation cover", by-passing the complexity of the most diversified environment we known.

4. THE AIM OF AND THE PROBLEMS OF THE ICHNOFACIES CONCEPT

The term was originally coined in order to refer to marine deposits, largely extending in space and time, an environmental genetic signature (mostly the palaeobathymetry), previously recognized in case studies. They allowed paleoenvironmental analyses and helped in sequence stratigraphy in successions where other tools failed or lack at all. After an enormous amount of detailed analyses and after some changes in their original meaning they are still successfully used for the same purposes. Thus, the ichnofacies concept finds its meaning if it reflects a set of environmental conditions and helps in defining recurrent similar facies situations.

The application of this concept to continental facies in which land-vertebrates track and traces are uncovered, presents some problems. Among them four main problems can be easily evidenced, concerning respectively: 1) the differences between needs and behaviors of land-vertebrates and marine-invertebrates; 2) some intrinsic differences between marine and land environments; 3) the dramatic different rate of evolution and substitution between vertebrates and invertebrates; 4) the different taxonomic range at which tetrapod footprints are related to trackmakers.

The first observation is to be related to the differences that emerge when comparing the different needs and behavior of land vertebrates and invertebrates. The activity of invertebrate organisms at the sediment-water interface or within the sediments is usually restricted to movements in a small area and in sediments well characterized and related to their needs, in their turn controlling particular behavior. Thus the freedom degrees, for such organisms, are dramatically limited. In other terms, there is a very tight bond between the trackmaker behavior and the bottom characters. Consistently, an invertebrate palaeoichnocoenosys is closely connected to the type of sediment in which it is preserved (lithofacies) and thus to its deposition environment. On these bases the ichnofacies concept found its logical meaning.

On the contrary, a land-vertebrate usually needs to move on a different scale, displacing him on a larger area, almost surely and frequently crossing various subenvironments and quite different depositional environments. Indeed, some land-vertebrates live sheltered in vegetated area and feed in different spaces; some predators stay isolated in ambush while others continuously check their territory going in packs; almost all prepare concealed dens or nests far from feeding places. Thus not always footprints (and the related ichnoassociations) reflect the work and the behavior of a vertebrate on a type of substrate and only on that type.

Hunt & Lucas stated that "environmental restrictions of tetrapods, […] have been empirically demonstrated" (Hunt & Lucas 2007: 64). We believe this is a nude statement and it seems meaningless to consider the land-verte-

brate environmental restrictions at the scale of the facies analysis purposes. Moreover, if could be theoretically right that also land-vertebrates are environmentally constrained, this is not valid when the comparison is made to deposition environments that are the records we have.

In practice, all the above means that, in land-vertebrate ichnology, the basic and most informative paradigm of the ichnofacies concept, the "ichnocoenosys-sediment-environment relationship", falls down.

A second problem rises depending on the intrinsic differences between marine and land environments, so evident when comparing their principal physic characters. We can only hardly compare the small dimensions of the confined and fragmented areas in which footprints can be impressed and preserved (humid and dried, fine clastics, rate of sedimentation rapidly changing, no vegetal cover) in respect to the environmentally continuous wide areas which characterize marine bottoms. Furthermore the land environment is extremely variable and hard to define, due to the continuity and interfingering of the different subenvironment and due to they can change rapidly during a season. Already Bromley (1996), in agreement with Asgaard & Bromley (1983), considered impossible to classify in terms of ichnofacies the land environment due to their differences.

A third problem is linked to another apparent difference between vertebrates and invertebrates, that is the dramatically different rate of evolution and substitution. Thus the application of the character "long geological range" of seilacherian memory is made impossible by the relatively rapid turnover of land vertebrates. This was implicit in the definition of some ichnofacies and some ichnocoenoses in which the marker changes without changes in deposition environment (e.g. *Chelichnus* and *Brasilichnium*).

The fourth difference, deeply connected to the third, derives by the different fall-out, implicit in tetrapod footprint studies. Usually vertebrate ichnotaxonomic definition starts at the level in which the invertebrate trace studies end; thus the packing of strongly different taxonomic levels into large groups diminishes the information content.

5. CONCLUSIONS

In our opinion, for all the above, the use of ichnofacies concept in the practice of land-vertebrate track and trace studies meets the following problems:

- the basic concept of the equation "ichnocoenosys-sediment-environment relationship" is little supported and its theoretical fundaments are largely inconsistent;
- the term was established in order to supply and communicate useful information, but fails in this purpose, taking also the risk of diminish the information content or of making it confused;
- the concept is almost completely ignored by vertebrate specialists being largely considered useless. If the attempt of establish reference terms defining punctual concepts is highly appreciable, their introduction in the scientific nomenclature must pass the effectiveness test.

In conclusion, we have an almost completely negative feeling for the establishment and the use of the ichnofacies for land-vertebrate. In our opinion it is impossible to substitute more refined facies- and ichnotaxonomic-analyses with substantially meaningless terms.

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