

## **Insect trace fossils, their diversity, classification and scientific importance**

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Abstract. The meaning, contents, and nomenclature of insect taphonomy is briefly reviewed. A combinatory system is proposed for the classification for insect trace fossils.

Key words: insect ichnofossils, classification, combinatory system.

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Animal traces, taken in the broad sense, can be defined as any signs of an animal activity that does not constitute a part of the organism itself. This definition covers any marks produced by an animal on or inside other material objects as well as the external manifestations of its vital functions including excreta, cocoons, webs, domicile cases and other items. Fossil traces, or ichnofossils, are widespread and often rather abundant. Moreover, they may occur even in deposits lacking any other fossils. They provide a valuable source of information on biology, ecology, distribution and behaviour of extinct animals.

Insect, myriapod and arachnid ichnofossils also are diverse and common. They represent diverse types of insect activities including resting, jumping, crawling (MORRISON 1987; MÁNGANO et al. 1997), wood boring (LABANDEIRA et al. 1997), feeding on fungi and various plants (SCOTT et al. 1992), nesting in varied substrates (LAZA 1982, 1997; BRUES 1936), oviposition (GALL & GRAUVOGEL 1966), digging, pupation in chambers, building of protective shelters (GENISE & BOWN 1994b), and so on. Nevertheless, insect traces largely have been neglected for a long time. Paleontologists interested in ichnofossils principally as indicators of paleoenvironments have focused on marine trace assemblages. Entomologists were, and often still are, skeptical regarding the importance of ichnofossils. Unfortunately, exceptionally risky conclusions based on ichnofossils have supported this skepticism. There are papers, including some recently published, wherein Carboniferous traces have been attributed to polyphagan beetles (FEDCHENKO & TATOLI 1983), or Triassic and Jurassic ichnofossils to wasps, bees, termites, and ants (HASIOTIS & DEMKO 1996a,b; HASIOTIS et al. 1995; KAY et al., 1997; GENISE & BOWN 1994a). Such records are so evidently controversial with the body fossil record that specialists consider these reports dubious at best.

As a result of this long-time underappreciation, insect traces often are simply ignored by collectors. Even after detection and recognition, most trace fossils are only briefly mentioned in publica-

tions without reference to descriptions or figures. Some occasional records are scattered in paleontological and geological literature but are often published in arcane sources and are difficult to find. There are no modern reviews or catalogues; in two editions of the "Treatise" (HÄNTZSCHEL 1962, 1975) even named insect ichnofossils are often overlooked. Insect ichnofossil nomenclature is in a chaotic state. Many insect traces, including those described in detail, remain unnamed. Others are assigned to certain genera of the natural system linked to body fossils, which is in my view an unfortunate and potentially misleading practice. We can tentatively ascribe some characteristic ichnofossils to certain insect families or even genera; but we know so little about the present-day insect traces that we never can be sure that similar nests or leaf galls are not produced by some other genera as well. In this context a number of insect ichnofossils have been misinterpreted and described as plant seeds, reptile eggs (JOHNSTON et al. 1996), phytoparasitic fungi and other non-insect fossils. Probably, many of such assignments still remain unrecognized. Finally, most of the named insect traces have never been subsequently revised later, and many names are likely synonyms.

Recent studies on some selected trace fossils demonstrate clearly the great potential importance of ichnological investigation for palaeoentomology. In particular, first of all the works by I. SUKACHEVA on the caddis cases and evolution of larval caddisfly behaviour should be mentioned (SUKATSHEVA 1985), the papers by J. GENISE on insect nests (GENISE 1995, 1999; GENISE & HAZELDINE, 1995, 1998a, b), and the most interesting studies of plant damage by C. LABANDEIRA (1996, 1998a, 1998b, 2002). However, I doubt that any important progress is possible in this field without accurate and formal descriptions and the classification of insect ichnofossils. The present-day state of their nomenclature is unacceptable.

One of the key tenets of modern ichnology is that similar traces can be made by taxonomically different, and sometimes even unrelated, organisms while the same individual can produce a variety of distractive traces (BROMLEY 1990). It immediately follows that ichnology needs its own classification and nomenclature, different from the common taxonomic ones based on body fossils. Fortunately, the last edition of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature 1999) has returned the ichnotaxa back under the power of general rules of zoological nomenclature, with some reasonable and exclusive articles. In particular, ichnotaxa do not compete with any natural taxa with respect to priority. Hence major problems have been resolved for formal description of ichnospecies and ichnogenera independent from natural taxa. However, suprageneric ichnotaxic classification still provides a number of unresolved questions.

The ichnological system generally accepted now is based on the so-called ethological principle proposed by SEILACHER (1953). It suggests that the traces are arranged in accordance with the type of the producer's activity such as traces of feeding, locomotion, breeding, and other behaviors. This is not the best basis for classification, in my view. The fossil traces can be observed directly but their origin is a matter of interpretation, which is not always unequivocal. For example, the tunnels in wood are not necessarily feeding traces of xylophagous insects. They may represent the workings of borers never feeding on wood as in some burrowing mayfly nymphs (THENIUS 1979) or carpenter bees. Hence they should be distributed between three major ethological groups: feeding traces, or Fodinichnia (GRAUVOGEL-STAMM & KELBER 1996; CREPET 1974) (Fig. 1); dwelling traces, or Domichnia (TILLEY et al. 1997) (Fig. 2-3); and breeding traces, or Calichnia (Fig. 4-5). Moreover, borings of wood-nesting termites should be allocated to all three groups simultaneously. This co-occurrence is why a special group, Xylichnia, has been established to include all types of wood borings (GUO 1991; LINCK 1949). This is a very utilitarian group because one can observe whether a trace belongs to Xylichnia or not. However, the unit is not ethologically grounded, and its introduction into the SEILACHER's system is evidently illogical. If we recognized Xylichnia as a separate group, we should add to it traces in sediments, paleosols, leaves, bones, and others as distinct ichnotaxa. There were attempts to propose alternatives to the SEILACHER's system based on trace morphology or combining both ethological and morphological approaches (MÜLLER 1981; VIALOV 1966, 1968). However, these systems were either less sophisticated or less universal, and they have not become widely accepted.



Fig. 1. Insect feeding traces. Fodinichnia / Phagophytichnia / Caulophagichnia / Oedemichnia, *Ramoecidium lesquereuxi* (COCKERELL), Oligocene, Colorado, USA (after COCKERELL 1917).

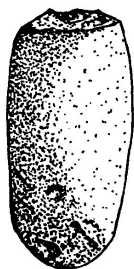


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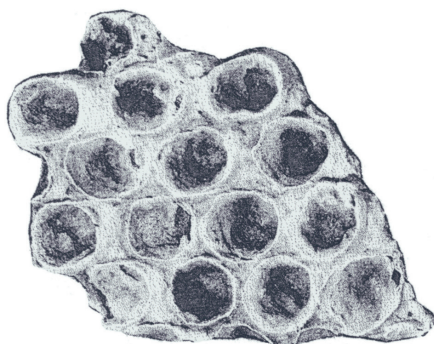


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Figs 2-3. Insect dwelling traces. Domichnia: 2 – Bioendoplyphia / Bentichnia / Tripichnia, *Diplocraterion* ichnosp. Quaternary, Moscow Region, Russia; 3 – Bioexoglyphia / Bentichnia / Indusichnia, *Indusia tubulata* Brongniart, Oligocene, France.



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Figs 4-5. Insect breeding traces. Calichnia: 4 – Bioexoglyphia / Synemichnia: *Desertiana mira* NESOV, Cretaceous, Uzbekistan (after NESOV 1997); 5 – Bioendoglyphia / Synemichniad / Edaphichnia / Trypichnia, *Celliforma arvernensis* DUCREUX et al., Eocene, France (after DUCREUX et al. 1988).

I would like to propose here a simple and radical solution of this difficult problem. The ichnological system is both a formal and an artificial one. In particular, it does not reflect phylogenetic relationships among the ichnotaxa. Given this, it is unnecessary to extend the common and formal system of taxonomical classification to the higher ichnotaxa.

In my opinion, ichnotaxic classification should be combinatory, and not hierarchical. In the systems of the combinatorial type, linearly arranged lists of taxa based on different selected characters are combined together in a table as lines and columns. Thus, one can combine the ethological units of the SEILACHER's system (SEILACHER 1953), for example with the units based on the position of traces on the substrate surface or within the structure, as was proposed by VIALOV (1968). The internal traces are called Bioendoglyphia, and the external ones Bioexoglyphia (Table I). Almost all main ethological units except for the equilibrium traces include each both external and internal traces. Correspondingly, the chewing marks on leaves should be classified as external feeding traces, or Fodinichnia Bioexoglyphia, and leaf mines as Fodichnia Bioendoglyphia. Wasp nests on plants or stones belong to the external breeding traces, or Calichnia Bioexoglyphia (Fig. 5), and the soil nests of solitary bees and sphecoid wasps are assigned to Calichnia Bioendoglyphia.

Table I

General ichnological classification, used on SEILACHER 1953, VIALOV 1966, and BROMLEY 1996, modified. + insect, myriapod and/or arachnid traces known; ? attribution of known traces to insects, myriapods, or arachnids may be doubted; - no insect, myriapod or arachnid traces of this type

Ethology	Substrate relations:	
	External traces (Bioexoglyphia)	Internal traces (Bioendoglyphia)
Equilibrium traces (Equilibrichnia)	–	
Locomotion traces (Repichnia, incl. Fugichnia)	+	+
Resting traces (Cubichnia)	+	–
Feeding traces (Fodinichnia, incl. Pascichnia, Praedichnia and Xylichnia)	+	+
Dwelling traces (Domichnia)	+	+
Gardening and trapping traces (Agrichnia)	+	?
Breeding places (Calichnia)	+	+

This morphological classification is more flexible because there is nothing morphologically in common between, say, wasp nests and feeding traces on leaves. However, this universal classification can be favorably combined with more particular ones. For instance, locomotion traces (TREWIN 1995) can be subdivided into body traces, or Apodichnia, and the tracks of appendage impressions, or Podichnia (Table II), as was proposed also by VIALOV (1968). These special types may be easily combined with universal ones based on the subaquatic or subaerial environments, as well as with the above-mentioned groups based on substrate relations.

Two examples illustrate these distinctions. The ichnogenus *Paleohelcura* from the Permian eo-lian Coconino Sandstone of the southwestern United States belongs to external locomotion traces with appendage impressions produced in a subaerial paleoenvironment, classified as Repichnia Bioexoglyphia /Podichnia /Edaphichnia. *Siskemia* tracks from the fluvial Old Red Sandstone of Great Britain belong to the same higher units except for occurring subaquatic setting or Benthichnia (Fig. 7).

Table II

General classification of locomotion traces. Repichnia. + insect, myriapod and/or arachnid traces known:

Environment	Morphology	
	Body traces (Apodichnia)	Appendage traces (Podichnia)
Subaquatic traces (Benthichnia)	+	+
Subaerial traces (Edaphichnia)	+	+

The feeding traces, or Fodinichia, can be subdivided accordingly to the nature of consumed food. For example, the Fodinichia on plant fossils may be attributed to Phagophytichnia, traces within wood to Xylichnia (GUO 1991; LINCK 1949), those found in fossil fungi to Mycophagichnia (Fig. 6), and features on plant leaves Phyllophagichnia (Figs 7-10). Phagophytichnia can be further classified based on their occurrence on certain plant organs, or, alternatively on the type of damage morphology (Table III). Thus one can distinguish between the chewing marks, galls, and mines on leaves as constituting morphologically different feeding traces on the same organ, as well as a different distinction between the mined leaves and bored strobili as being morphologically similar damages on different organs. Additionally, borings in fungi can be placed within the group Trypichnia, which together with tunnels in leaves, strobili and wood should be assigned to Mycetophagichnia (Fig. 6). Moreover, we can use the same name, Trypichnia, for the dwelling traces as well, namely to the nests occurring on bottom sediment substrates (Fig. 2).

Table III

General classification of feeding traces on plants. Phagophytichnia (excl. Xyl-ichnia). + insect, myriapod and/or arachnid traces known; ? insect, myriapod and/or arachnid traces recorded but attribution may be doubted; (+) insect, myriapod and/or arachnid traces unrecorded but probably occur as fossils; - no insect, myriapod and/or arachnid traces known. (\* supplemented by C. LABANDEIRA)

Localisation Morphology	Flower and inflorescence damage (Antho- phagichnia)	Fructification and seed damage (Carpo- phagichnia)	Leaf and petiole damage (Phyllo- phagichnia)	Stem and shoot damage (Caulo- phagichnia)	Root damage (Rhizo- phagichnia)
Chewing marks (Trogichnia)	(+)	+	+	(+)	(+)
Piercing marks (Nygmichnia)	(+)	+	+	+	(+)
Rolled organs (Ellichnia)	-	-	(+)	-	-
Tunnels and holes (Trypichnia)	+	+	+	+	+
Malformations (Teratichnia)	(+)	+	+	+	(+)
Neoplasms (Oedemichnia)	(+)	+	+	+	(+)

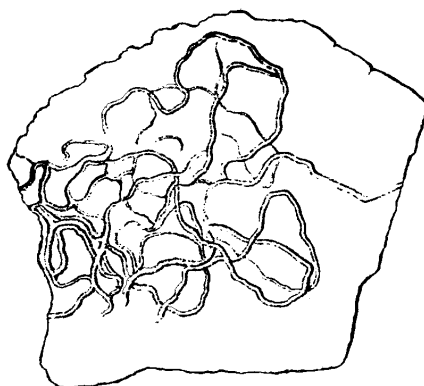


Fig. 6. Insect feeding traces. Fodinichnia / Bioexoglyphia / Mycophagichnia / Trypichnia. *Mycophagichnus heydeni*, ichnogen. et ichnosp. nov. Oligocene, Rott Formation, Germany (after HEYDEN 1863).



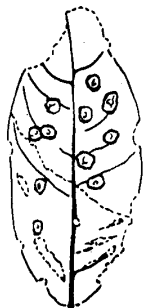
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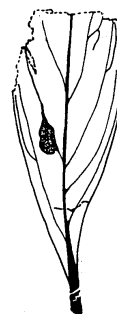
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Figs 7-10. Insect feeding traces. Fodinichia / Phagophytichnia / Phyllophagichnia: 7 – Trogichnia, *Phagophytichnus feistmanteli*, ichnosp. nov. Permian, India (after FEISTMANTEL 1881); 8 – 10. Cretaceous, USA (after SCOTT et al. 1992): 8 – Oedemichnia, unnamed, 9 – Trypichnia, unnamed; 10 – Nygmichnia, unnamed ichnogenus Mattoon Formation (Carboniferous, Illinois, USA (after LABANDEIRA & PHILLIPS 1996).



I believe that the introduction of the combinatory system to ichnology will be useful for practical classification, formal description and identification of trace fossils.

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