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A stroll in the forest of the fucoids: Status of *Melatercichnus burkei* Miller, 1991, the doctrine of ichnotaxonomic conservatism and the behavioral ecology of trace fossil variation

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ABSTRACT

The ichnogenus *Melatercichnus* was described in 1991 from Cretaceous deep-ocean turbidte beds at Trinidad Bay, northern California. The type (and only) ichnospecies, *Melatercichnus burkei*, features all the primary characters (ichnotaxobases) of *Phymatoderma*, and is here reassigned to this ichnogenus. In so doing, *Phymatoderma* now consists of two palmate forms (*P. penicillum* and *P. alcicorne*), two digitate forms (*P. melvillensis* and *P. granulata*), and the reassigned ichnospecies (*P. burkei*) representing a kind of intermediate form. Reassignment follows the doctrine of ichnotaxonomic conservatism, by employing a limited number of primary characters and abandoning a superfluous ichnotaxon. All of the ichnospecies now included within *Phymatoderma*–as seems to be true of many of the so-called fucoids and certain other groups of trace fossils–are extremely variable in terms of morphology, although basic structure (in this case bunches of outward branching, unlined tunnels stuffed with fecal pellets) is consistent. This aspect of trace fossils needs more attention, both from an ichnotaxonomic and a biologic point of view. At the Trinidad Bay collecting site, the 'perfect' examples of *P. burkei* featuring all the characters of the ichnospecies grade into specimens that would be identified with *P. granulata* or possibly *Alcyonidiopsis* isp. if preserved in isolation or if the 'perfect' specimens had never been observed. These variants are difficult to accommodate in traditional ichnotaxonomy, pointing to a need for special categories in open nomenclature (e.g., identification of some of the 'imperfect' specimens as '*Phymatoderma* forma variabilis' or possibly '*Phymatoderma* f. v. *P. burkei*–*P. granulata*'—to reflect the kind and degree of variation). In terms of behavioral ecology, *P. burkei* appears to be a fancy cesspit: the producer either fed at a different level and simultaneously deposited fecal pellets at depth (polychaete, echiuran?), or fed at or near the seafloor then dove into the turbidite sand blanket to discharge the pellets (sipunculan?). Variations in the structure could have resulted from the producer encountering different conditions in the substrate at different times and places (e.g., owing to dewatering), interruptions in the typical pattern caused by encounters with other organisms, limited time available to construct the usual pellet-filled structure, avoidance of other conspecific burrowers, or simply the inability of some individuals to execute precisely the construction plan.

1. Introduction

Most ichnologists base new ichnospecies on the 'best' or 'most typical' specimens selected from a series of specimens that often includes significant variants. Some studies include discussion of morphologic or structural variation, but the specimens selected as types or for illustrations may not reveal the full range of this variation. This seems to be especially true for the structures traditionally referred to as fucoids— burrow systems resembling plants or algae with branching stems or thalli. In some cases, ichnospecies from the same formation or collecting site feature practically all the conceivable intermediate versions between two or more nominal end-members (i.e., ichnotaxa of undoubted identity—the specimens that actually 'look like something' as opposed to nondescript structures and 'hybrids'). Some of this variation is certainly the result of differences in preservation from place to place, but some must reflect irregularities in trace-producer behavior (reactions to variations in physical properties of substrates, switching behavioral routines in response to changing stimuli—such as chemical signals related to availability of food, insertion vs. withdrawal from burrowing sites, avoidance of adjacent burrowers, recycling the contents of previous burrows, etc.). The impact of trace fossil variation on ichnotaxonomy, and how these patterns might inform interpretation of behavioral ecology and possible identification of the trace producers are issues that need to be more

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fully explored. The practical problems are obvious: in a highly variable ichnospecies, when should application of a specific name be avoided and identification of specimens simply to ichnogenus be employed? In terms of description of new ichnotaxa, how much variation should be encompassed in the hypodigm of a new ichnospecies? What do the morphologic variants indicate about the full range of activities and reactions of the producer? Could the variations be used to identify the organisms that produced the burrow systems (by referring to observations of modern trace producers)?

This paper has two related goals: taxonomic revision of an unusual Cretaceous deep-marine trace fossil described from a single locality in northern California (Miller, 1991), and evaluation of some problems inherent in the taxonomy and biologic interpretation of morphologically variable ichnotaxa. The revision will be used to highlight the associated issues of nomenclature, identifying and judging the status of key characters (ichnotaxobases), causes and consequences of morphologic variability, and the relationship of ichnotaxa to biologic taxa.

As a starting place, I should make clear that I support the proposals to stabilize and standardize ichnotaxonomic methodology advocated by Bertling and colleagues (Bertling et al., 2006; Bertling, 2007). These contributions extend earlier efforts to develop a generally acceptable, consistent methodology for the application of trace fossil names (Magwood, 1992; Pickerill, 1994; Bromley, 1996). I will demonstrate, however, that a few practical issues involving the classification and identification of ichnotaxa remain unsettled. And I will use as primary guide to the fucoids and related trace fossils the important overview by Fu (1991), which serves both as an authority for reassignment of *Melatercichnus burkei* and as a good example of what we might call the *doctrine of ichnotaxonomic conservatism* (which includes the principle of nomenclatorial austerity of Seilacher, 1992)—recognition and application of the fewest practically useful names based on a few recurrent key characters. Although the temptation to coin new names based on slight variations and limited material can be irresistible, most ichnologists probably would favor some version of the doctrine. But when it comes to the identification of morphologically variable ichnotaxa, some new ideas are needed.

2. *Melatercichnus burkei* is really a kind of *Phymatoderma*

The ichnogenus *Phymatoderma* has had a long and complicated history, involving periods of utilization and intervals of ‘submergence’. When *Melatercichnus burkei* was discovered in Cretaceous turbidite beds in northwestern California in the late 1980s (Figs. 1, 2; Miller, 1991), *Phymatoderma* was in a period of retirement, the ichnospecies once assigned to it having been either placed in synonymy with other ichnospecies or reassigned to other ichnogenera—in particular *Zonarites* and *Chondrites* (see Fu, 1991 for an outline of the history of this interesting and complex shift in the use of nomenclature). At that time the major source for identification (Häntzschel, 1975) did not recognize *Phymatoderma*, and the key revision of the fucoids (Fu, 1991) had not yet been published. The specimens that were collected did not seem to fit very well into any of the recognized ichnogenera, although there were obvious similarities to *Chondrites* and *Lophoctenium* considering branching pattern of tunnels, and to *Alcyonidiopsis* based on abundance of fecal pellets filling the tunnels (Miller, 1991, p. 163). *Phymatoderma* seemed to be unavailable and matches with recognized ichnogenera were difficult to support, so the name *Melatercichnus* was coined. It is now clear that the type (and only) ichnospecies, *M. burkei*, is really a kind of *Phymatoderma*, as resurrected and revised by Fu (1991), and applied subsequently in the naming of new ichnospecies by Uchman (1999) and Uchman and Gaździcki (2010). But the ichnospecies still appears to be valid: it does not resemble closely any of the currently recognized forms of *Phymatoderma*.

3. Ichnotaxonomy

I will first make the necessary reassignment of *Melatercichnus burkei* to *Phymatoderma*, which results in the ichnogenus consisting of five distinctive ichnospecies including: *P. granulata* (von Schlotheim, 1822); *P. alcicorne* (von Fischer-Ooster, 1858); *P. penicillum* Uchman, 1999; *P. melvillensis* Uchman and Gaździcki, 2010; and now *P. burkei* (Fig. 3). After completing this formality, I will evaluate the biologic significance of trace fossil variation and suggest some forms of open nomenclature that could be applied in the identification of variants.

3.1. Ichnogenus Phymatoderma Brongniart, 1849

3.1.1. Synonymy

For a review of the history of the ichnogenus and entry place to the older literature concerning the fucoids, see Fu (1991). Because the type ichnospecies is morphologically and structurally allied to the previously established ichnospecies of *Phymatoderma*, *Melatercichnus* Miller, 1991 must be considered a junior synonym. (And in doing so, the doctrine of ichnotaxonomic conservatism is followed.)

3.1.2. Diagnosis

Endobenthic burrow systems consisting of sets of branching, unlined tunnels oriented horizontally to subhorizontally; tunnels lack sharply defined edges and usually occur in bunched sets, either directed outward in one dominant direction (quadrant) from an area of initiation or in a semi-radial or radial pattern arising from a central area. Branching tunnels filled with fecal pellets often arranged crossways with respect to long axis of the tunnels; pellets in many cases have a different color/composition compared to the surrounding sediment (amended diagnosis based on Fu, 1991, p. 25).

3.1.3. Remarks

All five ichnospecies of *Phymatoderma*, as it is presently defined, are burrow systems constructed by deposit feeders that excavated and processed food, and backfilled their tunnels, in localized zones in a more or less horizontal orientation (conforming generally to sedimentary layering) (Seilacher, 2007; Uchman and Gaździcki, 2010). Because fecal pellet composition is often different compared to the surrounding sediment, the structures probably represent feeding at the sediment surface or at a different zone within the substrate (Miller and Vokes, 1998). Some of the ichnospecies appear to have a main shaft that came from below the level of the branches (Fu, 1991; Seilacher, 2007), while others consist of branching sets of tunnels initiated from above (Miller, 1991; Miller and Aalto, 1998; Miller and Vokes, 1998). Whether or not the direction of the main shaft is a diagnostic or variable feature of the ichnospecies of *Phymatoderma* (e.g., *P. alcicorne*) remains to be convincingly demonstrated.

In Fu's (1991)revision the arrangement of fecal pellets is given central importance as a diagnostic feature, along with branching pattern and irregular tunnel margins. Seilacher (2007, p. 144) remarked that in the case of burrow systems such as these, “…the overall shape of the burrow should be given less taxonomic weight than structure, because it resulted from general rules of space utilization…True biologic relationships are probably better reflected in modes of backfilling and pattern execution.”

In addition, the *range* of shapes and structural variations ought to be informative when it comes to interpretation of behavioral ecology of the trace producer.

Fig. 3 shows the five ichnospecies included now within *Phymatoderma* differentiated mostly based on the arrangement and density or crowding of the tunnels, features of secondary importance within the ichnogenus. In cases where more than one ichnospecies is present and a large number of specimens are available for study, it is likely that