



MICROMORPHOLOGY OF MARINE INVERTEBRATE TRACE FOSSILS AND THEIR ETHOLOGICAL AND ICHNOTAXONOMIC IMPLICATIONS

Diana E. Fernández^{1,2*}; Carolina Gutiérrez^{1,2}; Gabriel A. Arambarri¹; Marcos Comerio³; José I. Cuitiño⁴; Luciana M. Giachetti⁴; Colin W. Taylor⁵; Pablo J. Pazos^{1,2}

¹Universidad de Buenos Aires, Facultad de Ciencias Exactas y Naturales, Departamento de Ciencias Geológicas, Ciudad Autónoma de Buenos Aires, Argentina. *elizabeth@gl.fcen.uba.ar; cgutierrez@gl.fcen.uba.ar; garambarri@gl.fcen.uba.ar; pazos@gl.fcen.uba.ar

²CONICET - Universidad de Buenos Aires (UBA), Instituto de Estudios Andinos Don Pablo Groeber (IDEAN), Ciudad Universitaria – Pab. II, Ciudad Autónoma de Buenos Aires, Argentina.

³YPF-Tecnología (Y-TEC– CONICET), Berisso, Buenos Aires, Argentina. marcos.a.comerio@yypftecnologia.com

⁴Instituto Patagónico de Geología y Paleontología, Centro Nacional Patagónico (IPGP, CENPAT-CONICET), Puerto Madryn, Chubut, Argentina. jcuitino@cenpat-conicet.gob.ar; giachetti.luciana@gmail.com

⁵University of Aberdeen, School of Geosciences, Aberdeen, Scotland. c.w.taylor@abdn.ac.uk

It is common for proposed paleobiological models for specific ichnotaxa to blend or associate concepts related to trace fossil production, basic feeding strategy, and biological affinities of the producers. These models persist in the literature as a whole, hindering the separation of partial interpretations (e.g., detailed interpretation of only the feeding strategy, or only the potential tracemaker) achievable through microscale studies of exceptionally preserved samples. Additionally, analyzing numerous specimens of the same ichnotaxon at different scales allows discussion of established ichnotaxobases due to the morphological variety involved, with the intention that morphologically based diagnoses present inferences about the tracemaker [1]. Micromorphological studies on current and fossil insect traces have yielded excellent results regarding producer behavior and biological affinity, along with ichnotaxonomic implications [2]. However, micromorphological studies on trace fossils produced by marine invertebrates with this scope are much scarcer, and include techniques such as petrography, scanning electron microscopy (SEM), X-ray microcomputed tomography, etc. [3-10]. These studies provide insights into the trace fossil production mode, potential tracemakers, substrate modification, and their consequences. For instance, in the case of *Nereites* MacLeay, some microscale features of analyzed specimens supported a construction differing from the typical worm-like organism model, aligning with other previous ideas, and also suggested an interpretation of an arthropod as tracemaker, a concept explored in previous neoichnological studies [6]. In the case of *Bolonia* Meunier, backfilling structures were interpreted as produced by the aboral and lateral spines of irregular echinoids, which worked together to compact the sediment anteroposteriorly and moved alternatively [10]. Here we present new results from the same line of research, describing and discussing the internal structure of examples of two other iconic ichnotaxa: *Ophiomorpha* Lundgren and *Dictyodora* Weiss. Exceptionally preserved examples of *Ophiomorpha* from Patagonian units (the Lower Cretaceous Agrio Formation and the Miocene Gaiman and Puerto Madryn formations), and of *Dictyodora* from the Silurian Gala Group (Scotland), were serially thin-sectioned. Transverse (vertical) and parallel (horizontal) to the bedding plane, or longitudinal and transverse to the main axis (depending on the ichnotaxon) sections were analyzed following previously used methods [3,6,10].

Ophiomorpha is one of the most globally recognized ichnogenera in marine deposits of various depths and age. Its ichnospecies are primarily classified based on pellet morphology. *Ophiomorpha irregulaire* Frey et al. exhibits conical or outwardly acute pellets with non-uniform sizes. The validity of this pellet morphology as diagnostic for *O. irregulaire* has been debated due to the possibility that these pellets are filled with sand-sized grains, enveloped by a layer of mud and organic material, and the conical appearance may result from an incomplete muddy rim [4,11].

This is supported by our results from Lower Cretaceous *Ophiomorpha*, where walls with coating rich in clays and organic matter bear pellets that appear flame-like but under microscopic analysis show reoriented grains that allow to infer their original spherical shape (Fig. 1A). Also, two types of organic matter were detected within the wall: discrete, dense organic particles of terrigenous affinity (mostly phytoclasts), and amorphous organic matter, mixed with the inorganic matrix. The presence of fermentation chambers [11] in some sectors is not disregarded. Additionally, the Miocene *Ophiomorpha*-rich deposits, described as composed by *O. nodosa* Lundgren, are now thought to include *O. nodosa* and *O. borneensis* Keij in intergradation, with a dominance of the latter. This implies the tracemaker was able to produce both type of pellets. The characteristic bilobed morphology of the pellets and its regular distribution is confirmed by what is observed in cross-section (Fig. 1B): the semi-spherical reworking by the tracemaker continues inside the wall, reinforcing the idea that these are originally bilobed pellets and not a taphonomical artifact. This material allows to speculate that *O. borneensis* might be more common than it is currently represented in the literature.

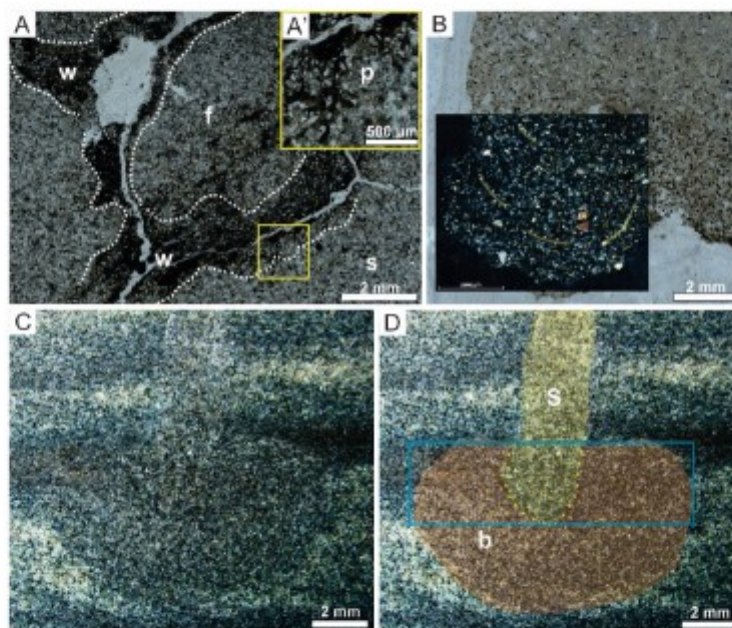


Fig. 1. A. Cross-section of main axis of *Ophiomorpha irregulaire* (CPBA 23328, UBA; Agrio Formation, Lower Cretaceous, Neuquén Basin) highlighting the wall in dotted white lines, and detail (yellow rectangle). A': Detail showing the original pellet morphology. B. Thin section of pelleted wall of *Ophiomorpha borneensis* (CNP-PIIC 1348, CENPAT; Gaiman Formation, Miocene). The section is parallel to the main axis of the burrow, showing bilobed pellet. One lobe of the pellet is shown with crossed nicols, and reoriented grains (transparent yellow lines) evidence that the semi-spherical reworking by the tracemaker continues inside the wall, reinforcing the idea that these are bilobed pellets. C. Vertical cross-section of *Dictyodora* (ABDUG Pal-10707, University of Aberdeen; Gala Group, Silurian, Scotland). D. Annotated version of C with the *spreite* (s) in yellow and the basal burrow (b) in orange. The dotted yellow line shows the area where they interconnect. The blue rectangle indicates the area that could explain the tripartite morphology seen in some samples, previously considered to be belong only to the basal burrow. Abbreviations: f = burrow fill; p = pellet; s = sandstone (bearing level); w = clay and organic matter-rich wall.

Dictyodora Weiss is a three-dimensional complex trace fossil characteristic of marine Paleozoic deposits recorded since the middle Cambrian. Its micromorphology under optical microscope has been illustrated [12,13] or very briefly described [14,15]; only one study illustrated part of the trace fossil under SEM [16]. Our preliminary results on Silurian samples include a thorough description of the internal structure of the area where the structures referred to as *spreite*



and basal burrow interconnect (Fig. 1C-D). In vertical cross-sections it is observed that the lowermost part of the *spreite* is surrounded by the uppermost and medial part of the basal burrow, in contrast with previous interpretations [17-19], allowing to discuss one of the possible interpretations of the *spreite*-producing structure as rigid [17]. The tripartite morphology of the basal burrow occasionally seen in samples [17,18] could be explained by this interconnection (Fig. 1D), supporting the necessity of a future diagnosis amendment [18].

More such studies are needed to challenge aspects of paleobiological/ethological models without necessarily completely discarding all ideas within them, and to discuss ichnotaxobases that do not depend but might rely on functional morphology.

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