

FRAGMENTATION AND BIOEROSION AS TAPHONOMIC RECORDS OF BIOTIC INTERACTIONS: A CASE STUDY OF EXTANT BRACHIOPODS (BOUCHARDIIDAE) FROM BRAZIL

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Here we document that two of the main destructive biostratinomic processes (fragmentation and bioerosion) operating in the taphonomically active zone of the shallow water marine settings can provide crucial taphonomic records of biotic interactions, offering us important paleoecological data applicable to the fossil record.

Shells and shell fragments (~2mm) of *Bouchardia rosea* are abundant in late Holocene death assemblages (median age 695.7 years) found in nearshore settings (depth range: 0-30 m) of the general area of Ubatuba Bay (23° 26'S and 45° 02'W), northern coast of São Paulo State, Brazil, SW Atlantic. *B. rosea*, an endemic, sessile epifaunal, freely living brachiopod of the Brazilian platform is the unique extant member of the Family Bouchardiidae, a group with a fossil record going back to the K/T boundary. *B. rosea* has a small, smooth, punctuated, low Mg-calcite shell, with a thin primary layer, a thick fibrous fabric secondary layer, and no tertiary shell layer.

Bulk samples included a total of 1616 valves of *B. rosea* collected from 14 nearshore localities. The samples were wet-sieved with fresh water through 8-mm and 2-mm mesh, and air-dried. The examined taphonomic variables are: 1- articulation, 2- valve type, 3- fragmentation, 4- abrasion, 5- edge modification, 6- color alteration, 7- dissolution, 8- bioerosion, 9- encrustation, and 10- predation traces. Among these taphonomic variables fragmentation and bioerosion provided interesting (paleo)biological data. For example, out of 1616 brachiopod shells examined, 292 displayed worm traces represented by a more or less straight U-shaped tube. The sides of the tubes are deeper than their middle parts, resulting in a typical central elongated ridge (thus, in the cross-section, tube morphology looks like a broad-centered "8"). Both tube openings communicate with the outside of the shells, not reaching the internal soft parts of the brachiopod shells. In many cases, the tube may run along the whole brachiopod shell (up to 15 mm). Typically, more than one tube may be present on a single *B. rosea* shell. No other worm traces were found on the examined shells. Additionally, internal blisters or other tumor-like structures were not observed. Interestingly, the surfaces of shells containing tubes are, in general, free of encrustation, whereas the surfaces of shells without tubes are commonly covered by serpulid, bryozoan, bivalve mollusk and other skeletal remnants of encrusting organisms. Finally, to check for occurrences of similar traces in the fossil record of bouchardiids, a collection containing 154 valves of *B. zitteli*, *B. patagonica* and *B. transplatina* from the Miocene of Argentina and Uruguay was also examined. Monographs and other papers (over 50 references) dealing with Cenozoic bouchardiids of the Antarctica, New Zealand, Australia, Argentina and Uruguay complemented our data.

For pooled data (292 infested shells), the infestation frequency (IF) of the present-day material is 18%, with the greatest IF values (26%) occurring in assemblages found at 25 meters of depth (Station UBA 4). When shells were grouped according to their size into three categories (8mm, 6mm, and 2mm) the corresponding IF values were 28%, 20%, and 12%, respectively. Higher rates of infestation were observed for dorsal valves (n=110, 74%). This may reflect the bias toward dorsal valves, a common phenomenon in the studied material. However, for those samples where the proportion of dorsal to ventral valves approximated a 50/50 ratio (Station UBA 4, 25 meters, n= 113, 30 infested shells), 51% of dorsal valves were infested. Notably, none of 2536 co-occurring bivalve specimens [42 genera, infaunal (n=865), semi-infaunal (n=163), epifaunal (n=364) and unidentifiable shells (n=1144)] were infested with the same worm or worm trace. Also, none of the examined bouchardiid fossil shells yield similar bioerosional traces.

It is noteworthy that in some sites, such as UBA 4 (25m of depth), shell fragments of *B. rosea* are very common. These fragments were clearly the result of the shell breakage along the surface defined by worm tubes, especially when localized along the maximum convexity plane of the shell.

During the sampling program, in addition to the 1616 dead *B. rosea* shells, ten specimens were recovered alive all were infested by living worms allowing us to identify the culprit and document

directly their physical association with the traces left on *Bouchardia* shells. The infested specimens exhibit worms with long and coiled structures (presumably peristomial palps) stretching out of the tube. Worms produce a more or less straight U-shaped tube similar to that of the ichonogenus *Caulostrepsis*. In many cases, the tube can extend across the entire length of the brachiopod shell (up to 15 mm). The worm and trace morphologies both are similar to those typically attributed to the Spionidae polychaetes (Martin and Britayev 1998). Because no other trace of commensalisms/parasitism was recorded in *B. rosea* shells, the documented interaction may represent a strictly “monoxenous association” (requiring only one host in the life cycle), but further studies are needed to prove this. The similar rates of infestation for dorsal/ventral valves noted here may reflect the free-lying mode of life of *B. rosea* (the shells are not attached to the bottom). However, the high rate of IF observed is in accordance with the fact that members of Spionidae (a boring family) are common and abundant in the research area (Petti 1997). Also, the IF reported above may be underestimated, since the recognition of Spionidae traces is difficult in fresh (unaltered) shells. In these shells only the tube openings, with their characteristic “figure 8” morphology, can be readily observed. Well exposed traces (outer tube surface destroyed) exhibiting its typical central ridge structure are easily identifiable only in heavily abraded and/or corroded shells. Also related to, and facilitating the identification of those tubes are high rates of fragmentation. In the case of Station UBA 4 (25 meters of depth) the shells are heavily infested, corroded and/or abraded. In these shells, the fracture plane runs along the tube wall making these particular shells more prone to fragmentation (a biologically facilitated fragmentation) and the resulting fragments have distinctive, biotic source-dependent breakage patterns that can be easily recognized.

In conclusions, our data have multiple paleoecological implications. First, bioeroders (trace producers) may strongly inhibit encrusters (perhaps by changing the shell micro-relief). Second, the data confirm that *Caulostrepsis*-like traces can be in fact produced by Spionidae polychaetes. This is one of the first contributions where the parasite/commensal (and their traces) was directly observed in association with brachiopod shells (see Baumiller and Gahn 2002 for a recent review of the fossil record of parasitic interactions), adding a new group of rhynchonelliform brachiopods (Bouchardiidae) to the hosts infested by Spionidae. Third, whereas it is difficult to determine whether this was a truly parasitic or commensal relationship, the absence of clear evidence of endo-parasitism (e.g., blisters or tumor-like structures) and the fact that the tubes open only to the exterior, both suggest that this may be a commensal relationship. Finally, the fact that fossil bouchardiids are not infested by such traces (even in those sequences where *Caulostrepsis* are common on bivalve shells and/or other carbonate substrates; S. Martinez, and M. Verde pers. comm., 2005) may indicate that the Spionidae – *Bouchardia* association is either geologically young or that the bouchardiid commensal/parasite fossil record is temporally biased and/or insufficiently studied.

References

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