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Incidentally-adjoined growth together

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ABSTRACT

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A stromatoporoid colony developed on the conchs of adult cerithiid gastropods from the Cenomanian of Sinai (Egypt) and Tunisia. Morphological analysis suggests that the gastropod conchs were in motion, propelled either by the mollusc or by a hermit crab, while encrustation and colony growth proceeded. Examples of encrustation upon mobile substrates are discussed. These examples refer to an incidentally-formed intimate partnership, in which the conch of the live organism, or its inhabited exoskeleton, was the only available substrate for the larva of the encrusting organism. This ecologically-induced, nonparasitic life partnership later became, in some cases, disastrous to the host. Hence, instead of the term commensalism, this mode of life partnership should be regarded as incidental growth together.

INTRODUCTION

Moore et al. (1952, p. 19) defined the term commensalism as the "growth together of different species in a manner helpful to one without hurt to its host", in contrast to parasitism where the host is despoiled and consequently hurt. Commensal and parasitic life associations develop in nature through long evolutionary processes into well-established, recurring partnerships. However, there are cases of incidental partnership which do not occur systematically in the biological system and thus have unpredicted consequences. These, for example, are caused by the desperate need of larvae of marine-cemented organisms to settle on a suitable substrate before metamorphosis. When the local oceanographic setting lacks a suitable substrate, any available rigid object will be colonized.

The cemented surface of epizoans encrusting an invertebrate skeleton copies that sculpture as an imprint. The unattached part of the epizoan grows under the effect of this sculpture and responds to it by reflecting that shape in varying intensity and accuracy (xenomorphic sculpture; see Lewy, 1972). The imprint and xenomorphic sculpture made by calcitic epizoans preserves the record of diagenetically dissolved aragonitic conchs such as those of the biostratigraphically significant ammonites (Lewy, 1972). Another contribution of encrusting epizoans to paleontology results from the preferred orientation, in which the larvae of marine epizoans attach themselves to a substrate as a function of currents, illumination, and substrate morphology to obtain optimal living conditions. Accordingly, the orientation of attached epizoans enables one to reconstruct the position of the substrate (e.g., Schmid, 1949; Seilacher, 1960). Detailed analysis of epizoan orientation upon cephalopod conchs suggests that some were encrusted while the mollusc was alive. Therefore the mode of life of these encrusted invertebrates can be evaluated, as well as their growth rate (Lange, 1932; Schindewolf, 1934; Seilacher, 1960;

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Heptonstall, 1970). Further study of epizoans upon ammonites has demonstrated in several cases that encrustation started when the adult mollusc was alive, and that the accumulating weight on the conch caused it to sink to the bottom. The restricted mobility of the ammonite resulted in its ultimate death, as well as the death of those epizoans that became buried under the reclining conch. Palmer and Hancock (1973) demonstrated that the external surface of Upper Bathonian trochacean gastropods was encrusted by bryozoans (the ectoproct *Berenicea*) while the molluscs were alive. At that stage, the conical conch was carried by the foot above the sediment, enabling the bryozoan zoaria to extend over the raised lower surface of the conch close to the aperture. Abrasion and truncation of the zoarial layers at this lower (apertural) surface of these gastropods suggest that after the death of the mollusc, the empty conchs were occupied by hermit crabs, which dragged the conch over the sediment. Further growth of the bryozoan colony was restricted to those parts of the conch that were not in contact with the sediment. It is possible that the death of the molluscs may have been caused by the accumulated weight of the bryozoan colony, which slowed down locomotion and feeding.

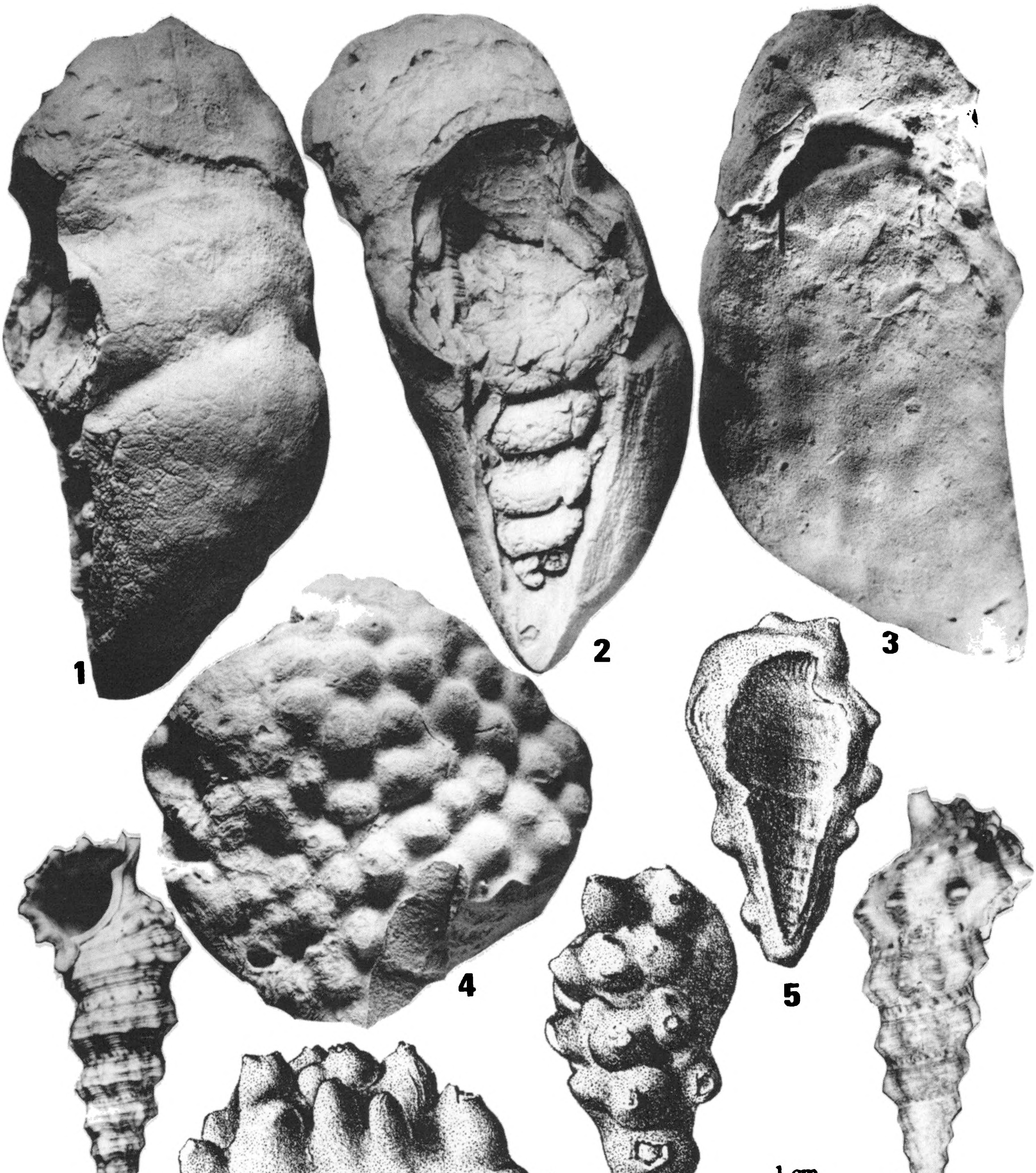
A stromatoporoid colony encrusting an adult cerithiid gastropod was found in the Cenomanian of southwestern Sinai, Egypt (Wadi Araba; Gebel Qabiliat). This specimen (Figs. 1–3; sample HU-37737, in the collections of the Hebrew University of Jerusalem, coll. Z. Lewy) shows remarkable similarity to the illustrations of a Tunisian Cenomanian smaller cerithiid (Peron, 1889–93; drawn by M.F. Gauthier) encrusted by a similar-looking stromatoporoid (refigured in Figs. 5–7) that was regarded as a bryozoan.

Both the Egyptian and Tunisian Cenomanian specimens show the same mode of controlled growth and orientation of the colony, suggesting a common history of growth together.

THE EGYPTIAN AND TUNISIAN ENCRUSTED CERITHIIDS

Both Tunisian and Egyptian Cenomanian cerithiid gastropods were encrusted by a stromatoporoid (*Actinostromaria*?) colony with a tuberculated surface structure (Figs. 3, 4, 6, 7; the Tunisian sample was referred to the bryozoan *Ceriopora letourneuxi* Thomas and Peron; Peron 1889–1893, pl. 30, figs. 16–18). These colonies developed to larger dimensions on the sediment of both Cenomanian sites. In both samples, the aragonitic shell of the gastropod was completely dissolved, leaving a clear imprint (Figs. 2, 5), as well as part of the internal cast in the Egyptian specimen (Fig. 2). Both imprints are of an adult *Cerithium* that has developed its modified gerontic aperture, as compared to the full-grown conch of the extant *Cerithium erthraeonense* Lamarck (Red Sea; Figs. 8, 9; private collection of the author). The stromatoporoid colony in both samples developed on the anti-apertural side of the conch, embracing ~1/2–2/3 of the conch circumference, except for the apertural side. The greatest thickness, hence weight, of the stromatoporoid colony overlies the conch axis. This thick development of the colony extends over the whole anti-apertural side, thinning out laterally on both flanks toward the apertural side. The absence of encrustation over this latter side indicates that the conch did not turn over, in spite of the gradually raised center of gravity due to the upward-growing colony. It seems that colonization on the apertural side was prevented because this surface was in contact with the sediment, in spite of the instability of this elongated, narrow, high structure. That means that the orientation of the encrusted gastropods was actively maintained and rapidly restored whenever the conch was incidentally tilted. A heavily encrusted empty conch would easily have been tilted and overturned. The fact that encrustation is so well balanced over the life orientation of these gastropods indicates that the live mollusc or a hermit crab kept it in position till death.

Encrustation during the life of the molluscs cannot be totally excluded because most of the time the mollusc is enclosed in the conch, which reposes on the sediment along the whole anti-apertural side. Even when the mollusc is crawling, part of the anti-apertural side of this elongated conch is in touch with the foot, and its apical part being dragged over the sediment. The high and well-balanced stromatoporoid colony upon the elongated conchs demanded a strong carrier that maintained the orientation of the conch. This high colony may suggest that it continued to grow in this very orientation after the death of the host, being stuck in the sediment in the life position of the host. Because this position is with the aperture face down, the host must have been trapped in the conch as a result of the heavy load. It seems that a hermit crab is capable of tilting even such a heavy conch to escape from this trap, whereas a live mollusc will be slowed down by the overburden until becoming stuck in the sediment, unable to crawl further, gradually starving to death. The well-balanced structure of the colonies over the



Figs. 1–3. Threefold view of the stromatoporoid colony upon a cerithiid gastropod (HU-37737) from the Cenomanian of southwest Sinai, Egypt (Wadi Araba; Gebel Qabiliat). The tuberculate structure is better preserved on a colony (Fig. 4; HU-37737) grown on the sediment at the same site. Figs. 5–7. A Tunisian Cenomanian cerithiid encrusted by a similar-looking tuberculated stromatoporoid colony (refigured from Peron, 1889–1893, pl. 30, as the bryozoan *Ceriopora letourneuxi* Thomas and Peron). Figs. 8, 9. *Cerithium erythraeonense* Lamarck, showing the modified gerontic aperture for comparison with the Cenomanian cerithiid imprints.

elongated gastropods further suggests that stromatoporoid growth terminated shortly after the gastropod conch ceased moving. Colonies which developed on the sediment without any control on their growth direction attained much larger dimensions at the same sites (a Tunisian fragment: Peron, 1889–1893, pl. 30, fig. 14; part of the Egyptian sample in Fig. 4).

INCIDENTAL GROWTH TOGETHER

These examples of ammonites, and perhaps also of gastropods, which were overcome and killed by the accumulated weight of their encrusting partners, neither reflect a parasitic nor a commensal relationship (e.g., Meischner, 1968, in another nomenclature). The larvae of these attaching organisms merely happened to settle down on the gastropod and cephalopod conchs while seeking a suitably firm substrate. No such relationships have been evolutionarily established in nature, though exoskeletons of living invertebrates are commonly encrusted by sessile epizoans in the absence of suitable substrates (more examples illustrated in Peron, 1889–1893, pl. 30). This incidental partnership is caused by various ecological stresses (e.g., the limited time before metamorphosis, nature of available substrates), and the way it might develop cannot be predicted. In these cases the molluscs were hurt by the weight of the encrusting organism. Lewy (1995) tried to explain the successful nourishment of large individual rudists in Late Cretaceous deep sea settings by the probable presence of algae, sponges, and other sessile epibionts attached to the rudist conch. This is based on a model off the coast of Mauritania, where *Pinna* shells are heavily encrusted by algae, sponges, and alcyonarian corals, which together form restricted "reefal" settings that provide shelter and food to other marine organisms. The overall biogenic activity within such a reefal community which may have surrounded the individual rudists could have supplied them with much food. In this case, the incidental growth together is beneficial to all organisms involved.

CONCLUSION

Apart from commensalism and parasitism, there is a growth together partnership that is incidentally caused and, thus, its course in nature is not well established and its consequences are unpredictable. When lacking suitably firm substrates, larvae of attached organisms may settle on exoskeletons of living organisms. The encrusting organisms may affect the mobility and the balance of the host, resulting in its ultimate death. These fatal consequences of growth together were initially unintended, in contrast to parasitic relationships. This kind of ecologically induced life partnership neither relates to commensalism nor to parasitism; it may be regarded as incidental growth together.

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