REVIEWS

Animal Colonies: Development and Function Through Time; edited by RICHARD S. BOARDMAN, ALAN H. CHEETHAM, and WILLIAM A. OLIVER, JR. P. 603. Stroudsburg, Pa., 1973 (Dowden, Hutchinson and Ross, Inc., $35.00).—This book is an anthology based for the most part on presentations given in a symposium sponsored by the Paleontological Society and held in Washington, D.C. at the November 1971 Annual Meeting of the Geological Society of America. The book is divided taxonomically into four major categories: Coelenterates (seven full-length papers), Bryozoans (ten papers), Graptolites (four papers), and Sponges (two papers); its conceptual conformity, as revealed in an introductory passage by the editors, is stated most simply as: What is a colony? Where, when, and how does the individual begin to lose its physiological and functional freedom and become an integrated member of a colonial organism? The reader is advised that even to begin to gain some elemental understanding of coloniality, we must begin with the fundamentals, that is, detailed morphological, physiological, and behavioral studies. A life habit characteristic believed to make these studies especially revealing is that of asexual reproduction. By assuming a common parentage for all individuals in a particular colony, that is, genetic constancy, the phenotypic manifestations of microenvironmental effects can be considered apart from those of astogeny and ontogeny. Although I believe this to be a reasonable assumption, we as yet know little of the genetic degree of physiological connections within colonial organisms. Obviously 23 papers, averaging over 25 pages per paper, cannot be reviewed to the satisfaction of each of the individual contributors, nor, in fact, of the reviewer, hence I mention only some of the highlights from each of the four sections which I have found personally intriguing, pausing to reflect that most of the papers offer some new data and/or interesting interpretations.

Coates and Oliver *(Coloniality in Zoantharian Corals)* remark that increased levels of coloniality in corals appear associated with the development of large reef structures; phaceloid and cerioid corals dominate the Paleozoic whereas much higher levels of colonial integration, as expressed by the coenosteoid and meandroid corals, are common in the Mesozoic and Cenozoic. It is not that the latter were missing from the Paleozoic seas, in fact there was a brief fling at the coenosteid-type of colonial organization in the early Paleozoic, but it seems not to have survived the Middle Devonian. Meandroid colonies, extremely rare in the Paleozoic, with their characteristically massive corallum and "valley streams" are believed by Hubbard *(Sediment-Shifting: A Guide to Functional Behavior in Colonial Corals)* to represent a morphologically significant step toward increased efficiency in particle movement over the surface of the corallum. Hubbard's contribution can be most profitably read, however, by referring to a more lengthy discussion of models of calical shapes and functional morphology of the polyps by her and Yvonne Pocock in *Geologische Rundschau* (1972, B. 61). An earlier paper

by Oliver *(Jour. Paleontology,* 1968, v. 42) is also a valuable supplement. Although functional integration seems to increase throughout geological time, polymorphism continues to be very limited; initial and later polyps show little change in calical elements and presumably in the basic functional aspects of the coral calyx as a supporting cup. Hubbard would like to measure the angle of intersection of these elements and then determine the direction of tension that may be applied by the polypal muscle tissue which should offer a means of interpreting the degree of stabilization of active polyps. Unfortunately it appears most difficult to determine this angle of intersection in fossil materials unless one is willing to resort to a detailed study of the, hopefully preserved, trabecular structure.

In Bayer's *(Colonial Organization in Octocorals)* review of life habits, functional integration and distribution of the octocorals, it is interesting to note that among octocorals some of the largest forms are not associated with zooxanthellae or with the reef habitat, yet it has been speculated that it was the development of the symbiotic relationship with zooxanthellae that enabled the zooantharian corals to reach sufficient size to produce reefs of considerable size and geographic extent. The octocorals, as the zooantharian corals, display a wide and continuous range of colonial organization, culminating in the octocorals in the formation of highly specialized zooids arranged in intricate geometric patterns and functioning together as a unit. Herein a strong case is made for colonial as opposed to individual zooid selection, because each zooid appears situated with respect to the others in a manner that permits the most efficient distribution of food to the colony. The most geometrically complicated forms, showing regular clockwise or counterclockwise branches with numerous associated bifurcations or branchlets, appear to be most common in the deep sea.

Jull *(Ontogeny and Hystero-Ontogeny in the Middle Devonian Rugose Coral Hexagonaria anna)* studied a specific instance of ontogeny and septal insertion and in the process has altered at least some of my preconceived notions regarding septal insertion. Detailed examination of serial sections emphasized that septa are not inserted in an orderly fashion in the cardinal and alar fossulae according to "typical" patterns of rugose insertion, but rather both major and minor septa are inserted in groups where space is available around the corallite and are both the same length during early development. Concluding the section on coelentrates, Phillips *(Evolution of Holopelagic Cnidaria: Colonial and Noncolonial Strategies)* provides us with one of the most provocative papers when he attempts to relate the evolution of the holopelagic Cnidaria to tectonic cyclicity. Scant notice is given to defining what is meant by tectonic activity or how one recognizes its growth and decay; yet Phillips believes those times of intensification provide a most effective selection device that allowed only those Cnidaria that could survive and reproduce completely within the water column to escape extinction. The implication of his ideas seems to be that the shelf benthos becomes

intermittently inhospitable to those organisms that must have recourse to a sessile polypoid stage to complete their life cycle. The model is a trellis work of assumptions, one has little feeling that it is testable, and there is an almost pathological adherance to the allopatric speciation model which eventually requires Phillips to postulate extinction at the geographic centers of oceanic populations. Need I add that this is a strange model indeed, perhaps better an exemplar of procrustean striving.

A lengthy review (100 pages, the longest paper in the volume) of Bryozoa coloniality by Boardman and Cheetham *(Degrees of Colony Dominance in Stenolaemate and Gymnolaemate Bryozoa)* leads off the second section and rather nicely expands, in part, on the earlier studies of Borg. Astogenetic and ontogenetic changes in colony growth are interpreted to be expressions of underlying similar genetic control within a colony, hence providing a method of filtering out microenvironmental variability and deciphering non-genetically based polymorphisms. Boardman constructs a detailed analogy between the mode of growth and soft anatomy of modern cyclostomes to the three Paleozoic orders of Stenolaemates. The non-specialist reader must enter this discussion with some background in basic bryozoan morphology, and I have found the rereading of previous contributions by Boardman and Cheetham *(Jour. Paleontology*, 1969, v. 43) and/or Boardman, Cheetham, and Cook *(North Am. Paleont. Convention Proc.*, 1970) very useful. Unfortunately, as Boardman so well expresses, the Paleozoic stenolaemate genera are so poorly known that data on the degree of integrative morphology will only be available after a thorough restudy of many specimens [examples of this type of restudy are provided in this volume by Utgaard, *Mode of Colony Growth, Autozooids, and Polymorphism in the Bryozoan Order Cystoporata,* and Blake, *Coloniality and Polymorphism in Bryozoa of the Families Rhabdomesidae and Hyphasmoporidae (Order Rhabdomesonata)*]. Presumably both single and double-walled Stenolaemata, a reflection of, respectively, a low and a high level of functional integration, have been in existence since the beginning of the fossil record of the Bryozoa, and some single and double-walled species may well be considered congeneric. Conversely, Cheetham notes that the cheilostomes (Gymnolaemata), although appearing not to have evolved progressively toward more highly integrated structures, initiate their preserved record expressing the lowest levels of colonial dominance. Thus it seems as if selection has not acted on all aspects of colonial integration in concert, and the attainment of maximum levels of integration in different character states may be representative of more than one adaptive trend. Advances in structural integration apparently led to rigidly erect or free-living forms, whereas the encrusting genera, stocks that appear early in the fossil record, seem to show a wide range of relatively low levels of functional and structural integration. Abbott *(Intra- and Intercolony Variation in Populations of Hippoporina)* provides a carefully thought out study of intercolony variation and astogenetic framework in recent species of the genus *Hippoporina,* forms that construct some colonies

characterized by continuous growth from the ancestrula but others whose growth is interrupted and renewed. Her conclusions suffer if only because there have been few such studies undertaken, but this one nicely compliments the theoretics of Boardman and Cheetham.

T. J. M. Schopf *(Ergonomics of Polymorphism . . .)* presents a stimulating discussion of latitudinal differences in modern cheilostome polymorphisms; working from an extensive bibliography, and, in fact, incorporating his data in the form of an appendix, he sets out to demonstrate that levels of polymorphism can be interpreted as expressions of the level of environmental stability and/or rigor and shows that among species that exhibit polymorphisms, interzooecial (or vicarious to use Schopf's terminology) polymorphs occur in 26 percent of the tropical species, but only about 6 percent of the Arctic fauna; leaving 74 and 94 percent respectively for adventitous polymorphs, that is, those that occupy space on the autozooids. Schopf concludes that the interzooecial polymorphs as opposed to the adventitous defensive polymorphs require a "more persuasive selection" for their origin and are therefore more specialized. The crux of the argument is that the higher percentage of *true* (=interzooecial) polymorphs occur in the tropics, and this is principally due to the *lack* of environmental braking effects in such a uniform and predictable regime. Although discounting previous suggestions that evolutionary rates are higher in the tropics—hence the fauna averages geologically younger—in favor of a local ecological control of polymorphism, Schopf's reasoning can be contrasted to that of Banta *(Evolution of Avicularia in Cheilostome Bryozoa)* who develops an admittedly speculative evolutionary model for the development of defensive polymorph avicularia in the cheilostomes. Herein interzooecial avicularia are the first to appear, and they later give rise to the adventitous avicularia. Using the data from the previous appendices of Schopf, I note that there is a higher percentage of Banta's more evolutionarily advanced adventitous avicularia in the Arctic regions; this could give rise to further speculation that the Arctic fauna may be older than that in the tropics, the latter evolving more rapidly and exhibiting a greater percentage of the supposedly more youthful interzooecial avicularia. These ideas can be tested, of course, if the Tertiary fossil record is reasonably faithful, and some careful developmental biology is carried out on a number of modern cheilostome species. It is perhaps worthwhile reflecting upon the earlier contributions of Bayer, in which the deep-sea, presumably an environmentally stable regime, exhibited an octocoral fauna of a quite high and intricately integrated polymorphic condition. An isolated point, perhaps, but one that may be in Schopf's favor.

In the third section on the graptolites, Urbanek *(Organization and Evolution of Graptolite Colonies)* outlines in some detail the evolution of the graptoloids emphasizing that the understanding of astogeny is equally as important in the study of graptoloids as it is in the bryozoans. Thecal modifications are ingeniously related to potential enzymatic functions of the sicula, deduced to be the site of physiological control for

the rhabdosome. This is the most imaginative paper in this collection and one that concludes with some rather highly speculative notions concerning the genetics of graptoloid colonies, but who would have expected the study of these long-extinct organisms to progress to a state where such speculation was even possible?

The volume concludes with a good general summary of the morphology and function of modern sponges by Simpson *(Coloniality Among the Porifera),* in which is stressed the development of a theme that sponges are individual organisms and not colonies. This is elaborated upon by Hartman and Reiswig *(The Individuality of Sponges)* who discuss interpretations of the organization of the Porifera on morphological, developmental, and physiological grounds and conclude that individuality is recognizable at only two levels, that of the single cells and of the entire specimen; therefore they find themselves unable to substantiate some prior claims for the existence of intermediate units of subindividuality.

It is apparent that I have found this compilation of papers to be a valuable contribution to our understanding of the evolution of animal colonies. Most of the papers are rewarding either for their new data or speculative insights into both small and large scale evolutionary events. The contributions by Coates and Oliver, Boardman and Cheetham, and Urbanek dominate the volume but not to the extent that a diversity of opinion does not exist. I highly recommend the volume to all those interested in animal colonies and the evolution of coloniality.

PETER BRETSKY

Les Rongeurs du Miocène de l'Afrique Orientale; by RENÉ LAVOCAT. V. 1, p. 5, 284; v. 2, 44 pls. (Mém. Trav. Inst. Montpellier, no. 1) Montpellier, 1974, (Ecole Pratique des Hautes Etudes, Inst. Montpellier, Place Eugène Battaillon, 34060 Montpellier, France, 1900 French francs).—Students of fossil rodents have long known that large collections have been made in the later Cenozoic (early Miocene to early Holocene) of East Africa, mostly by Louis and Mary Leakey. It was also evident that publication of these materials would be important not only to those specialists but also to paleontologists in general, evolutionists, systematists, and biogeographers. Now at last a thorough work on both the richest and most important of those collections, those from the early Miocene (Burdigalian), has been published after years of study by René Lavocat, one of the ablest and most experienced students of rodents.

This extensive memoir is published in two volumes in quarto format, the first text, with two maps and twenty text figures, the second a folding cover containing 44 unbound plates. The drawings in the text figures are careful and attractive, but some have lost detail in the photolithographic reproduction. The plates are prints from photographic negatives (not printing plates) and are truly remarkable. All are stereo pairs, and since no plate has fewer than four pairs and most have more,