

volume of the *Treatise on Invertebrate Paleontology* in 1959. The treatment assumes a working knowledge of paleontology in general and trilobites in particular.

The abundance of trilobites, particularly in Cambrian faunas, is exaggerated by the fact that they moulted periodically, with the result that many if not most of the remains found are those of moults rather than of living animals. Whittington notes that the existence of moults permitted workers such as Barrande, a French civil engineer exiled to Prague, to describe growth series for trilobites as early as 1852. Growth stages of several species are illustrated in this book, which has 120 excellent plates accompanied by detailed explanations that are a very useful feature of the book.

Questions often asked by students and non-paleontologists are How did trilobites live and What did they eat? Whittington notes that the early larval stages were probably soft-bodied and presumably planktonic, as with many modern marine invertebrates, but that in later life most trilobites probably lived on the sea floor as predators of smaller animals, scavengers, and sediment feeders. Others may have burrowed in the mud. Whittington suggests that some may have been swimmers, perhaps by sudden enrollment that produced quick, spasmodic movements. Other groups, particularly those that are small and have thin shells, may have been planktonic. Even though trilobites have the earliest known visual organs, some groups were blind and may have been adapted to deeper, darker waters.

Drawing in part on specimens found in the famous Middle Cambrian Burgess Shale of British Columbia, Whittington discusses the anatomy and functional morphology of trilobites in some detail. In this as in other parts of the book the subject matter is put into historical context. For example, Whittington describes the techniques used by early workers in dealing with features such as trilobite limbs. The amount of painstaking work undertaken by workers such as Størmer, who serial-sectioned enrolled specimens in order to look at the appendages inside, must have been enormous. More or less as a postscript to the section on anatomy and trilobite activity Whittington discusses traces supposedly left by trilobites. He suggests that of *Rusophycus* and *Cruziana*, two trace fossils generally accepted as having been formed by trilobite activity, only *Rusophycus* is likely to be due to trilobites. However, he does not offer an explanation for the formation of *Cruziana*.

Discussing the relationships between depositional environment, depth of water, substrate, and types of trilobites, Whittington points out the use of Lower Paleozoic trilobite faunal provinces in providing both positive and negative evidence regarding plate tectonics and continental drift, concepts that many Northern Hemisphere geologists accepted

long after their southern colleagues. It is curious that in this section of the book the only diagram showing depth relationships of different trilobite groups, and the only one showing former continental distributions, shows post-Cambrian situations.

As Whittington notes, the morphological complexity of the earliest trilobites from near (but not at) the base of the Cambrian suggests a long Precambrian history of soft-bodied trilobites. He also points out that only one new family of trilobites, the Phillipsidae, originated after the early Ordovician. Whittington notes that despite many years of endeavor, there is no single widely accepted classification of trilobites; he stresses the need for more detailed knowledge of trilobite morphology and development. One topic not covered in any detail is the use of trilobites in biostratigraphy, which is the most practical application of paleontology. In these days of increasing difficulty in getting financial support for paleontological research, it would seem necessary to stress the more utilitarian aspects of the subject.

In summary, this is an excellent, readable book packed with detailed information on how trilobites lived, functioned, evolved, and eventually became extinct.

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Dolphin Echolocation

The Sonar of Dolphins. WHITLOW W. L. AU.
Springer-Verlag, New York, 1993. xii, 277 pp.,
illus. \$79.

I attended an animal sonar conference in 1979 and remember feeling a little smug about what I perceived to be a superior understanding of echolocation on the part of the bat researchers over those working with dolphins. Dolphin studies seemed mired in the difficulties of working with mammals whose popularity with the public prevented the neurophysiological experiments that, at least to me, seemed essential. Au's new book demonstrates that these restrictions may have been blessings in disguise. The noninvasive methods (for example, x-ray cinematography, signal detection theory) that have been used to probe the mechanisms of sonar production and processing in dolphins have provided an understanding of these animals' perceptive abilities that may have out-

stripped what we know of bats.

Au's book is not for the timid. It assumes a thorough understanding of acoustics and no small measure of mathematical facility. Filled with informative illustrations, it provides an exhaustive chronology of the studies of dolphin auditory and vocal mechanisms and target detection and discrimination and ends with a comparison of dolphins and bats and some suggestions for future work. In addition to describing the many experiments that have been performed on dolphins, Au analyzes their strengths and weaknesses, with a view to establishing the extent and limits of our knowledge of dolphin sonar.

The answers to many of the basic questions are still elusive. How do dolphins hear? Apparently not through their ear canals, but how exactly constitutes a fascinating detective story that gradually unfolds. It seems that a route through the fatty tissues of the lower jaw is most plausible. Where do dolphins produce their sounds? This is another persistent puzzle, with researchers now favoring the nose over the larynx. Although Au summarizes the information currently available, he never totally dismisses any of the theories and thus preserves the excitement that these questions evoke. In fact, to the book's credit, I was left with more questions than answers about dolphin sonar. Why don't the peak frequencies of dolphin echolocation clicks match the frequencies of their maximum auditory sensitivity? What is the trade-off between echolocation and social vocalizations in the design of their ears? As we ponder explanations offered by laboratory studies, Au reminds us that dolphins live in a real world and face problems (such as the remarkable din created by snapping shrimp in the bays of Hawaii) not encountered in soundproof chambers.

Cetacean sonar presents a wonderful opportunity for comparative studies, and the book could have benefited from a more evolutionary perspective. For example, Au reviews the work done to test whether dolphins manipulate the pitch of their clicks, as do insectivorous bats. An evolutionary approach would suggest that since most echolocating animals (for example, swiftlets, oilbirds, fruit bats) do not frequency-manipulate, there is little reason to expect this ability in dolphins. An understanding of the phylogenetic occurrence of echolocation may help steer the future course of dolphin research.

Au's book is an excellent synthesis of the mountain of work on dolphin sonar and serves as a reminder of the experiments yet to be performed on the other echolocators. It should be required reading for young (and occasionally smug) scientists about to start off in this line of research.

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