choose to ignore the chapters dealing with vadoids. Still, by incorporating discussions of these various grains into a single volume, Peryt has provided a basis for solving some of the potential terminological and conceptual problems in dealing with coated grains. For that alone he is to be congratulated.

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## **Primate Morphometrics**

The Order of Man. A Biomathematical Anatomy of the Primates. CHARLES E. OXNARD. Yale University Press, New Haven, Conn., 1984. xiv, 366 pp., illus. \$30.

The past several decades of research in biological anthropology and primatology have witnessed a proliferation of complex new investigative and analytical techniques. Perhaps the leading advocate and practitioner of this growing "high-tech" science of biological form is Charles Oxnard, whose career has spanned more than 30 years. In The Order of Man, Oxnard has summarized the results of his many studies of extant and fossil primate morphology. This most recent book is the third in a series (the first two being Form and Pattern in Human Evolution, 1973, and Diversity and Uniqueness in Human Evolution, 1975, both from the University of Chicago Press); although it focuses in detail on studies of nonhuman primates, the author's interpretations of recent discoveries and developments in paleoanthropology are also presented.

Oxnard's book is unusual in that it attempts to bring the results of some rather complex research to the general reader as well as to the professional primate biologist-the goal professed on the dust cover is "animals, anatomies and algebras without tears." The book is handsomely illustrated and contains many background discussions that the nonspecialist will undoubtedly find useful. Anatomists and anthropologists familiar with Oxnard's work will discover little new here-indeed, they may recognize entire pages and passages from earlier publications. The book might have more appropriately been entitled "Oxnard on Primates," as it is largely a compendium of results of the multivariate statistical analyses carried out by Oxnard, his collaborators in Birmingham, Paris, and Hong Kong, and several of his former students. Thus in spite of the title this book is not an attempt to

provide a broad summary of our knowledge of primate biology and history.

The volume opens with two chapters discussing new developments in paleoanthropology and recent approaches to the study of primate morphology and evolution. The next two chapters, entitled "Mathematical 'dissection' of anatomies" and "Biological 'meaning' of structures," lay out the methodological and theoretical foundations of Oxnard's approach to understanding animal form. The discussions of multivariate morphometrics here are lucid, although it is unclear exactly what links many of the new techniques reviewed (ranging from optical Fourier transforms to bio-orthogonal grids to Moiré fringes to central axis functions), except for their esoteric nature. It remains to be seen whether Oxnard's pleas for the wider use of such techniques foreshadow productive application of techniques utilized in engineering, physics, and medicine to biological investigations or whether they merely reflect an overemphasis on quantification and an emulation of the "hard" sciences.

Oxnard also (chapter 4) clearly outlines how morphometric studies relate to other approaches in the investigation of animal form and function, such as direct experimental studies of muscle function or bone strain and observational "experimental" field studies that examine morphology and functional behavior in two or more groups selected for certain contrasts and comparisons (for example, arboreal versus terrestrial). The general reader should find this discussion most helpful. Although Oxnard notes the functional significance of many of the primary variables chosen for the multivariate analyses, additional consideration of this topic would have been desirable. How one goes about selecting primary dimensions (or angles or ratios), perhaps the most important step in any morphometric study, is not at all straightforward. Had Oxnard dealt with the issue more fully, he would have informed the general reader and increased the likelihood of productive communication with those (too) many primatologists who are distrustful of multivariate statistical approaches and uncomfortable with the thought of "doughnuts," "dumb-bells," "hyper-sausages," and "signet rings" in *n*-dimensional space.

The bulk of the book (chapters 5 through 9) summarizes results of the studies of Oxnard and his collaborators on primate morphometrics. Three chapters consider structure-function associations in primate forelimbs, primate hind limbs, and the limbs of catarrhine quad-

rupeds. Here we most clearly see the potential insights obtainable by the multivariate morphometric approach. These statistical analyses constitute "morphological fishing expeditions," as Oxnard calls them, that may elucidate structurefunction relationships and lead to testable hypotheses. A particularly nice example is provided in Oxnard's morphometric study of the hip and thigh in prosimians, which indicated the existence of several distinctive structural configurations in leaping forms. This finding predicts biomechanically different leaping behavior in certain animalsa hypothesis that can be tested by additional field and laboratory investigations. What we know so far appears to support the original morphometric distinctions. Other statistical associations reflecting functional similarities link the arboreal and suspensory gibbons, siamangs, orangutans, spider monkeys, and woolly spider monkeys in the forelimb analyses and the terrestrial vervets, patas monkeys, and baboons in the hind-limb studies.

The major weaknesses of The Order of Man emerge when Oxnard attempts to derive systematic and phylogenetic information directly from his multivariate morphometric results. This attempt is made in spite of a long and rather confusing discussion of the reasons why the notion of primitive and derived features is either misleading or simply not applicable to the sorts of data that enter into his multivariate studies. Oxnard bases this argument on the claim that behavioral-adaptive reversals (for example, arboreal to terrestrial to arboreal) may have been quite common in primate lineages; he further argues that particular quantitative measures of bone shape (or ratio, angular, or log transforms) do not define features or character states in the sense traditionally required by cladistic methodology.

Leaving aside this argument and such relevant issues as parsimony, testable hypotheses, and Oxnard's notion that primitive and derived characters must be "uninfluenced by function or anything else," where do his phylogenetic analyses actually lead? Two examples will suffice.

Oxnard's studies of the enigmatic prosimian aye-aye (*Daubentonia*) indicate substantial distance between this genus and other lemurs in morphometric space. On this basis, he argues that "we are bound to infer a much older and more divergent phylogenetic placement [for *Daubentonia*] than generally believed in recent years" (he cites the possibility of a separate lineage since the Paleocene). But this inference flies in the face of a body of morphological evidence (presumed synapomorphies or shared derived traits) linking the aye-aye with other lemurs. As Ian Tattersall has pointed out elsewhere in regard to Oxnard's assessment of Daubentonia, the presence of specialized features (autapomorphies) developed in a particular lineage subsequent to an event of evolutionary divergence is irrelevant in reconstructing its relationship to other taxa stemming from that divergence. Oxnard's multivariate studies may inform us in a general way about morphological distinctions and functional specializations, but they cannot be used in the way he uses them to determine phylogenetic relationships (that is, unless positions along multidimensional axes can be reliably translated into symplesiomorphies, synapomorphies, autapomorphies, and parallelisms, a possibility that he himself rejects).

The second example involves Oxnard's controversial interpretations of Australopithecus. Again on the basis of morphometric divergence, Oxnard has concluded that Australopithecus could not have been ancestral to Homo (although he notes that he cannot rule out A. afarensis as a possible ancestor, since he has not examined these most recently discovered fossils). While Oxnard views Homo habilis as a direct progenitor of later hominids, he removes the Olduvai specimens traditionally assigned to this genus by most paleoanthropologists (notably the OH 8 foot and the OH 7 hand, skull, and mandibular fragments). This is because his morphometric analyses indicate that the postcranial fossils from Olduvai and South Africa are "uniquely different" when compared with the differences observed between African apes and humans. But again, because we cannot meaningfully translate such morphometric distances and differences into phylogenetic characters, the removal of such groups from direct human ancestry is unwarranted. Oxnard's task, using all the morphological information currently available, is to demonstrate that the features distinguishing his australopithecines from Homo are truly autapomorphic in the former, that is, that they were not present in the common ancestor of Homo and the australopithecines (whether or not we'd call that common ancestor an australopithecine). This he has not done.

It is particularly ironic that Oxnard's assessment of australopithecines as "uniquely different" is relative to a comparison of the African apes and Homo, because his own work has been of fundamental importance in establishing certain orangutan and early hominids (though he takes this to reflect functional convergence rather than genetic affinity, just the reverse of the logic he uses to exclude Australopithecus as ancestral to Homo). In fact, it is likely that additional fossil evidence may show that certain postcranial features shared by the orangutan, Australopithecus, and early Homo are primitive, that many postcranial differences between Australopithecus and later Homo are the result of post-divergence specializations in Homo, and that many of the postcranial dissimilarities between the African apes and Homo plus Australopithecus result from recent specializations in the knuckle-walking chimpanzees and gorillas. Thus, a consideration of australopithecine morphology relative to an orangutan-Homo axis. with the African apes seen as divergent and particularly specialized, might have led Oxnard to different conclusions.

morphological similarities between the

Whatever the difficulties with Oxnard's phylogenetic assessment of Australopithecus, his conclusions regarding morphology and behavior have been prophetic. His and his collaborators' claims that Australopithecus engaged in a form of locomotion quite different from that of modern Homo were ignored or ridiculed by many for years, but they have recently gained support from various analyses. Much of this new evidence is summarized by Oxnard in an appended nota bene to the concluding discussion on human fossils (chapter 10). Oxnard would be justified in gloating much more than he does in this discussion. The ability of his morphometric investigations to provide functional insights is nowhere better demonstrated. His persistent arguments about the associations of structure, function, and behavior in early hominids have encouraged others to rethink and reanalyze traditional assumptions.

But what is the precise relationship between the investigative techniques and statistical methodologies favored by Oxnard and the biological conclusions reached? One cannot conclude that Oxnard's significant insights into early hominid morphology and function could have been made only by using these "new" approaches. Indeed, different workers using more traditional methods of comparative anatomy (Tuttle and Stern and Susman), as well as other techniques (Prost), have all to some degree converged upon the view presented by Oxnard that australopithecines were more proficient in the trees and more different from modern Homo in their form of bipedalism than was previously

believed. These advances, like most others in the scientific endeavor, result from asking appropriate and important questions that are indeed answerable. It is Oxnard's excellence as a scientist in this respect, rather than his use of particular methods, that underlies his significant contributions to primatology. This is the most important lesson in Oxnard's work for both the general reader and the professional primatologist.

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## **Books Received**

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