1 Charles Oxnard: an appreciation

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In an extraordinary scientific career extending across the whole second half of the twentieth century and into the twenty-first, Charles Oxnard has placed his unique stamp on nearly every aspect of biological anthropology. He has profoundly influenced the growth and direction of our discipline all around the world, beginning in Europe and moving westward through North America to Asia and Australia. His research accomplishments have been almost as global as his residence patterns. When we think of his work as a whole, we tend to think first of his morphometric work – his lifelong quest for finding reliable ways of taking huge numbers of data or complicated shapes, and crunching them into simpler functions that reveal a small number of underlying patterns reflecting diet, or locomotor behavior, or phylogeny. And most of us think mainly of the works in which Oxnard has applied these approaches to the study of primate and human evolution. But a glance at Oxnard's long bibliography shows an amazingly diverse span of other work, from classical comparative studies of primate anatomy down through studies of growth and development, bone biology, and vitamin B12 metabolism in primates, to the patterns and causes of sexual dimorphism, lower back pain, and osteoporosis in aging. In this introductory chapter, I intend only to sketch briefly the story of what I take to be the central theme in Charles Oxnard's career as a scientist – namely, primate biometrics and its implications for human evolution.

To appreciate the importance of Oxnard's work in this field, we need to look back across the historical landscape of paleoanthropology to 1958, when Oxnard was beginning his graduate studies at the University of Birmingham under Solly Zuckerman. Zuckerman had come to Birmingham in 1945 from Oxford, where he had worked under Le Gros Clark. The two men had quarreled (Oxnard, 1997), and Zuckerman had taken the job at Birmingham to start a program that would strike out in new directions to remedy what he thought of as the unscientific character of primate biology.

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When Oxnard began his graduate work, Birmingham was in many ways an exciting place to be. Zuckerman and his colleagues were innovative and intellectually lively. They were out on the forefront of the methodological revolution in biometry that the digital computer was beginning to make possible. But they were also manning an embattled outpost of an increasingly unpopular school of thought about human phylogeny – namely, the idea, stemming ultimately from Henry Fairfield Osborn, that the human lineage had been separate from all other mammals throughout most of the Cenozoic. Zuckerman believed that "it was reasonable to infer from the available evidence that man . . . had begun his independent evolution as far back as the Oligocene" (Zuckerman, 1954, p. 349). Throughout his career, Zuckerman was convinced that none of the australopithecines could possibly be a human ancestor. In fact, he thought that *Australopithecus* was more likely to be ancestral to modern gorillas and chimpanzees (p. 396).

All this had seemed more plausible back in the 1930s, when Zuckerman had first begun publishing on human evolution. Most experts then thought that both the cercopithecoid and gibbon lineages were represented in the Fayum Oligocene. It was not much of a stretch to think that the hominid lineage might have been around at the same time. And up to the end of the Second World War, *Australopithecus* was generally dismissed as an aberrant ape that showed a few interesting convergences with real hominids like *Eoanthropus*, *Pithecanthropus*, and *Homo* (Gregory, 1949).

But by the time Oxnard arrived at Birmingham, the *Zeitgeist* had started leaning in the other direction. The postcranial fossils from South Africa that had come to light over the preceding decade had shown that *Australopithecus* was distinctively human-like in some respects, especially in the lower limb. By the early 1950s, many of the other leading experts in this field had identified *Australopithecus* as something very close to the long-sought missing link between man and his simian ancestors (Dart, 1940, 1948, 1949; Le Gros Clark, 1947, 1952; Gregory, 1949; Broom *et al.*, 1950; Washburn, 1951). Zuckerman and his colleagues set to work to refute this thesis, and immediately got into trouble.

A 1950 paper by Ashton and Zuckerman compared australopithecine teeth with those of *Homo* and living apes, and concluded that "in their metrical attributes, [they] are more ape-like than human." But the paper contained a mathematical error; and when this was pointed out and corrected (Yates and Healey, 1951; Ashton and Zuckerman, 1951), the australopithecines looked far less ape-like. Undaunted, Zuckerman argued in 1954 that the sagittal crest seen in some *Paranthropus* skulls proved that this form must have had a flaring, gorilla-like nuchal crest. "The implication," he wrote, "is thus clear that *Paranthropus* carried its head on its vertebral column far more in the manner of a gorilla than of a man" (Zuckerman, 1954, p. 390). And Zuckerman spoke with some contempt of the ignorance of those who could possibly think otherwise.

But in 1959, the *Zinjanthropus* find proved that an australopithecine could in fact have a high sagittal crest without having a gorilla-like nuchal shelf (Leakey, 1959; cf. Holloway, 1962; Tobias, 1967, pp. 23–25). Zuckerman and his ideas were again discredited, and they grew increasingly peripheral to the mainstream of paleoanthropology. As Zuckerman put it sarcastically in 1966 (p. 92), "the anatomical findings which my colleagues and I have reported have been consistently out-of-step . . . in the context of generally accepted views about the australopithecines . . . It is something of a record for an active team of research workers whose strength has seldom been below four, never to have produced an acceptable finding in some 15 years of assiduous study!"

Zuckerman had his own fixed ideas about human evolution. But I think that he was correct in saying that the conventional wisdom of the time rested on some intellectual fashions that had no empirical basis. In the 1960s, it was regarded as enlightened and virtuous to obliterate taxonomic distinctions. Splitting was out of style and lumping was in, and there was a general effort to interpret fossil taxa as direct ancestors of living ones. During this period, Neanderthals joined the human species, *Pithecanthropus* and *Sinanthropus* joined the human genus, and *Australopithecus* and *Ramapithecus* were welcomed into the family of man. As Zuckerman insisted, the leading lights of paleoanthropology in the 1960s (e.g., Mayr, 1951; Simons, 1961, 1963; Simpson, 1963; Brace, 1964; Simons and Pilbeam, 1965; Buettner-Janusch, 1966) shared a general wish to draw simple lines of descent through as many fossils as possible, especially where hominids were concerned; and this agenda was blinding them to some unwelcome facts about the australopithecines.

Oxnard received his Ph.D. in 1962 and went on working at Birmingham, collaborating with Ashton on a series of classic studies on comparative morphometrics and locomotor adaptations in the primate forelimb. After joining the University of Chicago faculty in 1966, Charles set to work painstakingly and systematically to uncover those unwelcome facts about the australopithecines, using innovative methods borrowed in part from other fields of science.

In 1968, he demonstrated that the fragmentary Sterkfontein scapula showed clear signs of having a glenoid and a spine that were markedly cranial in orientation, like those of apes but unlike those of human beings. Oxnard concluded that "the fragment was almost as well adapted for suspension of the body by the limbs as is the corresponding part of the present-day gibbon" (Oxnard, 1968a, p. 215).

That same year, Oxnard (1968b) reported on the supposed *Homo habilis* clavicle from Olduvai, and inferred from its ape-like axial twist that this fossil as well must have had a cranially directed glenoid. In two 1969 papers, Oxnard put together these two girdle fragments and compared them with extant primates in a canonical analysis. He found that the composite form was specifically orangutan-like (Oxnard, 1969a, 1969b), and suggested that "the presumed common ancestor of man and the African apes may well have been an animal that lived in trees and which used its shoulder in a manner reminiscent of that of the orangutan" (Oxnard, 1969b, p. 94).

In 1972, Oxnard published a generalized distance analysis of the fossil hominid tali from Olduvai and Kromdraai, which showed them to be *sui generis*, differing both from later species of *Homo* and from the African apes. He further suggested that *Homo habilis* was probably not generically different from *Australopithecus* (Oxnard, 1972, p. 8).

In his book *Form and Pattern in Human Evolution*, Oxnard (1973a) showed using experimental stress analysis that the phalanges of the Olduvai hand functioned best in a suspensory posture, while those of *Homo* and *Pan* did not. He concluded that the Olduvai hand was orang-like in function. In a paper that same year with Zuckerman and three Birmingham co-authors, Oxnard concluded that the pelvis of *Australopithecus* was human-like in its weight-bearing features, but ape-like in muscle vectors. It was probably a biped, but not a human-like biped (Zuckerman *et al*., 1973). Perhaps most tellingly, Oxnard (1973b) noted that in all known australopithecines, the hind-limb articular surfaces were much smaller than those of the forelimb.

Oxnard summarized all these studies in his 1975 book, *Uniqueness and Diversity in Human Evolution* (Oxnard, 1975a). In a review article of the same year in *Nature*, he concluded:

> the fossils have ankle, hand, and shoulder bones patterned somewhat after those of the orang-utan . . . we can only surmise that perhaps, as the orang-utan, the fossils had ankles, hands, and shoulders adapted for climbing. Because they have pelves that have articular relationships parallel to those of man, we may guess that . . . they stood and moved upright with a vertical load distribution. But . . . the muscular features of the pelvis are positioned in a way more like those of the great apes . . . [and] they have relatively small articular surfaces in the hindlimb as compared with the forelimb . . . They may have been bipedal in a way that is no longer seen, but have retained abilities for climbing, and perhaps minor arboreal acrobatics such as might be found in an intermediately sized ape-like creature.
> (Oxnard, 1975b, p. 394)

These words from over 25 years ago sound extraordinarily fresh and up to date. Essentially similar conclusions about the persistent arboreal habits and nonhuman bipedality of *Australopithecus* have since been urged upon us by studies of later finds from East Africa and the Transvaal (Stern and Susman, 1983; Susman *et al*., 1984; Clarke and Tobias, 1995; McHenry and Berger, 1998). There is now increasing doubt about the inclusion of *habilis* and *rudolfensis* in the genus *Homo* (Wood and Collard, 1999; cf. Wolpoff, 1996, p. 387), and increasing evidence for the antiquity of the *erectus/ergaster* lineage alongside those of the better-known australopithecines (Larick and Ciochon, 1996; Kimbel *et al*., 1996; Gabunia *et al*., 2000).

All these issues are of course still debated. But on every one of these points, the current consensus has largely shifted to Oxnard's view of things. Just as Oxnard predicted in his 1984 magnum opus *The Order of Man* (pp. 331–332), new fossils and new investigations have borne out the results of his biometric work. Most of the rest of us are just now catching up with the positions that Charles Oxnard established over 25 years ago. That fact has not been sufficiently appreciated, and this seems like the right place to point it out.

I have touched only on one sector of Oxnard's research, and I have said nothing whatever about other facets of his extraordinary career: his work as an editor, or the long list of honors and awards that he has received, or his 22-year service to three Universities as a chair, a dean, and a mentor of students and faculty. But because I had the good luck to be Charles's first American graduate student, I want to say something about him as a teacher. I learned a lot of things from Charles during my years at Chicago. I learned the importance of anatomical detail, and the rigors and constraints of anatomical description. I learned to doubt my measurements, and I learned how to remove those doubts. I learned the ideals of scientific methodology that Charles had absorbed at Birmingham. All these things were valuable. But I could have learned them from other people, or elsewhere. What I gained uniquely from Charles, and could not have gained from anyone else, was an attitude.

More than any other scientist I have ever known, Charles Oxnard positively fizzes with what I can only call boyish enthusiasm for everything he does. Ever since I have known him, Charles has radiated love for his work and his knowledge and his profession. He gives you the feeling that doing research is such sheer, unadulterated fun that it's something of a scandal that the government pays people to do it. I never miss an opportunity to hear Charles give a paper, even on some point where I think he is wrong, because the infectious energy and enthusiasm that he communicates is a more precious gift than empirical certainty.

Through his life in science, Charles Oxnard has given us some rich and valuable presents: his methodologies, his research findings, his prescient analyses, his example as a rigorous investigator, his service as a member of our discipline and our university communities. But he has given us nothing so rich and valuable as the example he has set us of a lasting, unshakable, disinterested joy in trying to figure out how the world works. The contributors to this volume, whose work and careers have all been guided and encouraged by Charles's science and mentorship and example, hope that we can return some partial reflection of that joy to him in this celebratory anthology.

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Part I
Craniofacial form and variation

The study of craniofacial form and variation has always been one of the most important areas for those interested in shaping primate evolution. Skulls were the most frequently collected specimens in museums. Skull parts, especially teeth, are most frequently found in the fossil record. Skulls and teeth are easily examined in the living. The bones of the face allow some estimation of how their owners appeared. Appearance and change in appearance as produced by medical and dental technologies have profound effects upon individual well-being. All these are good reasons why this is one of the most critical of anatomical regions.

At the same time, however, skulls, faces, jaws, and teeth are the most complex region of the body. More, perhaps, than in any other region, do a number of completely different functions have to be integrated in its structure. The genetics underlying cranium, face, jaw, and teeth are even now not well known and clearly far more complicated than the postcranium. The development and growth of the head depends upon complex mechanisms and processes, many of which have only been elucidated in the last two decades. In evolutionary terms, the "head problem" in chordates, reflecting at the same time both very ancient and very recent elements, has always been more difficult to understand than, say, the equivalent trunk problem or limb problem (which problems do not even rate quotation marks).

As a result, by far the best-known studies of this region have been carried out over the years by established workers. Beginning students, however, have also often been captivated by the range of these problems and frequently want to work on the skull. Most of the current students at the University of Western Australia are so challenged – and I am sure that it is also so in most other laboratories. There is an "alas, poor Yorick, I knew him well Horatio" influence upon us.

My own first investigations (for an Honors Bachelors degree) were in the same vein. I set out to study in one year (!) the comparative anatomy of the cranial nerves in mammals. This was reduced within the first week of reading to the cranial nerves in primates, and shortly after confined to the fifth cranial nerve. My first paper was limited to its maxillary division but concentrated upon its infraorbital and zygomatico-temporal branches in 21 specimens of seven species of Ceboidea!

Perhaps chastened by the complexities of the cranial nerves, my own doctoral studies, in contrast, were on the shoulder. I reasoned that the cranium, a region of such great complexity, should not be the entrée for a *novice, especially not a novice who was looking for a new way to gain a handle on functional adaptation. This was perhaps the best decision I ever made. Function in the shoulder was, relative to the skull, rather simple – there was a chance that I could understand it, even given the lack of functional knowledge and technology in those days. The form of the scapula was primarily two-dimensional, rather than the complex three-dimensional skull. The bone was almost totally suspended by muscle and so there was every chance that its form would mirror muscular activity and little else. Instead of being mired in a morass of complexity, it seemed possible that I might actually produce a modus operandi of my own for studying functional adaptation.*

However, it was my hope, even then, that if I could only work out a methodology for a relatively simple area, I might eventually work out how to tackle a complex one. And this has indeed occurred. But it has taken me 30 years to start studying the cranium, face, jaws and teeth, and the complexes of functional adaptations, and the developmental mechanisms and evolutionary relationships that underlie them. Most of my students and colleagues have beaten me to it and some of them have written the sections below. Thus, to me, the head came last. But in any book on shaping primate evolution, the head must come first.

Charles Oxnard

2 *The ontogeny of sexual dimorphism: the implications of longitudinal vs. cross-sectional data for studying heterochrony in mammals*

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Introduction

As the name suggests, studies of sexual dimorphism began with a focus on morphological differences between the sexes (Darwin 1871). Current use of the term "dimorphism" and current studies of sexual dimorphism have expanded to include ecological, behavioral, and physiological differences between the sexes (Harvey and Clutton-Brock, 1985). Charles Oxnard (1987) brought his unique quantitative perspective to the investigation of sexual dimorphism, showing that studies, particularly quantitative studies, of differences between the sexes in morphology are meaningful and not outdated. His work has provided inspiration for this chapter, which examines the role that data and analysis play in understanding evolution. As Oxnard identified multiple dimorphisms among taxa along morphological axes, this study examines heterochronic variation among taxa to show that different ontogenetic trajectories produced analogous multiple dimorphisms. Crucial to Oxnard's work, and to the results presented here, are matches among question, data, and method.

Studies of sexual dimorphism and growth

Most research addressing questions of growth and sexual dimorphism examines the ontogeny of that dimorphism, focusing on how growth produces adult differences (see German and Stewart, 2002 for review). A slight shift in focus

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