FUNCTIONAL MORPHOLOGY AND EVOLUTION

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dedicated to

JOHN H. OSTROM

in appreciation of his first 25 years

as Editor of the American Journal of Science

PETER DODSON AND PHILIP GINGERICH

EDITORS

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FUNCTIONAL MORPHOLOGY AND EVOLUTION: A SPECIAL VOLUME OF THE AMERICAN JOURNAL OF SCIENCE

EDITORIAL INTRODUCTION

John Ostrom was born in New York City in 1928, received his bachelor’s degree (B.S.) from Union College in 1951, and his Ph.D. from Columbia University in 1960. As John tells it, he was invited to visit Columbia by George Gaylord Simpson who impressed the young recruit with his hospitality. That summer, 1951, before starting graduate school, John and David Kitts worked with George Whitaker as Simpson’s field assistants in the San Juan Basin of New Mexico. John was later influenced by Edwin H. Colbert at the American Museum of Natural History and wound up studying dinosaurs for his dissertation. Dinosaurs have been central to his research ever since.

John taught for one year at Brooklyn College, then left New York in 1956 to assume duties first as a lecturer then as an assistant professor in geology at Beloit College in Wisconsin. He was called to Yale in 1961, where he was appointed assistant professor of geology and geophysics and assistant curator of vertebrate paleontology at the Peabody Museum. John thus came to occupy the position established for O.C. Marsh and subsequently occupied by Richard Swann Lull. Five years later he was promoted to the level of associate in both capacities, and five years after that to full professor and curator.

John’s first two papers were published in the American Journal of Science in 1951 and 1952. One was on an occurrence of the mineral chrysoberyl at Greenfield, New York (with R. H. Navias) and the other was on a Pleistocene caribou from New York State (with D. W. Fisher). John’s first dinosaurian paper was on the dinosaur stapes (with E. H. Colbert in 1958), which followed from his discovery of an exquisitely preserved stapes in the middle ear of Corythosaurus casuarius. John described his first new species in 1961, a small-crested version of the magnificent trumpet-crested duckbill Parasauroplophus, which he named Parasauroplophus cyrtocristatus. He elaborated the description in 1963.

Functional morphology has been a recurring theme in John’s research. His dissertation was a comparative functional morphological study of the cranial anatomy of hadrosaurs (duck-billed dinosaurs), which was beautifully illustrated by John himself—a brilliant graduate of the Margaret Colbert school of scientific illustration. Now a classic monograph, John’s study was originally published as a Bulletin of the American Museum in 1961 when it sold for $2.50 a copy! John has probably published more profusely-illustrated monographs of dinosaur osteology than any paleontologist active today, and he has set standards of descriptive morphology that few have followed—as Gaffney (1991) tartly observed.

In 1964 John published an important paper (again in American Journal of Science) on the paleoecology of his beloved hadrosaurs. In this
he moved hadrosaurs out of the water and established them firmly on dry ground, a position that most scientists and artists have accepted ever since.

At Yale John assumed curatorship of a magnificent collection of skulls of horned dinosaurs that had been the subject of two important monographs, one a classic that endures today (Hatcher, Marsh, and Lull, 1907), the second (Lull, 1933) somewhat disappointing in terms of standards set by the earlier study. It was natural that John’s attention would turn to the horned dinosaurs and that he would bring his unique perspective of functional morphology to the evolution of this group (which had also been considered earlier by his mentor; Colbert, 1948). The papers that resulted were published in Postilla in 1964 and in Evolution in 1966. As with the paper on hadrosaur paleoecology, these papers defined attributes of the paleobiology of horned dinosaurs that have been canonical ever since, for instance that the unusual jaw apparatus indicated a diet of tough fibrous plants such as palms and cycads.

Two projects launched at Yale during the 1960’s have had an enormous influence on our understanding of dinosaur evolution: the first was a field project in the Lower Cretaceous (Aptian-Albian) Cloverly Formation of the Bighorn Basin in Wyoming and Montana, and the second was a critique of dinosaurs as paleoclimatological indicators. In doing the Cloverly work, carried out between 1962 and 1967 with support from the National Science Foundation, John had the rare privilege of describing an entirely new dinosaurian fauna from an interval of time previously poorly represented in the geological record. Two monographs resulted, as well as a number of shorter papers. In these he introduced a completely new lexicon of dinosaurs into our vocabulary. The most important discovery was that of Deinonychus antirrhopus (etymologically the “counterbalancing terrible-claw”), a new small theropod whose skeleton with menacing claws was found on a rusty hillside in Montana in 1964. John described and monographed Deinonychus in two separate publications in 1969. Deinonychus, the terrible claw, figured prominently in both of John’s influential projects. The little terror also has become one of the most famous dinosaurs of all time.

In 1967 the Yale Peabody Museum centennial celebration included a symposium on Evolution and Environment. J. E. Heath contributed a paper on the origins of thermoregulation in which he proposed that a shift to upright posture in therapsids (mammal-like reptiles leading to mammals) provided heat, even at rest, because of the mandatory activity of muscles required to maintain this posture. Heath did not discuss dinosaurs, but John was stimulated to consider the role posture might have played for heat production in dinosaurs.

John was studying Deinonychus at this time and knew from the functional morphology of its limbs, that it must have had an upright position and from claws on its hands and feet that it must have been an active agile predator. Coupling these interpretations with Heath’s idea concerning heat production of postural muscles led John to question the
generally-held assumption that dinosaurs were cold-blooded and therefore reliable climatic indicators. Ectotherms such as amphibians, turtles, lizards, and crocodilians living today are dependent on, and thus limited by, the ambient temperatures of their environment. Birds and mammals, on the other hand, are endotherms that produce heat internally and live with greater independence from external environmental temperature. If dinosaurs had a metabolic physiology like that of birds and mammals, then dinosaurs were suspect as climatic indicators. John discussed this in a seminal paper on “Terrestrial vertebrates as indicators of Mesozoic climates” presented at the first North American Paleontological Convention in Chicago in 1969 and published the following year (Ostrom, 1970).

The idea that dinosaurs may have been warm-blooded was not entirely new. When Richard Owen (1842) first conceived of the “Dinosauria,” he compared them to “heavy pachydermal mammals” and speculated on their hearts, circulatory systems, and lungs. Adrian Desmond (1979) has reviewed this bit of history and considers Owen’s brilliant idea of dinosaurs as reptiles-of-mammalian-grade to exceed by far the limited evidence available at the time. Owen’s comparison was motivated instead by his interest in showing reptiles to have outlived the zenith of their physiological organization. In a bigger picture this was an argument against inexorable evolutionary progress, and Owen took it as evidence against evolution of any kind. The idea of warm-blooded dinosaurs came up again in this century with tentative suggestions by Wieland (1942) and Russell (1965).

Robert Bakker was an undergraduate at Yale from 1963 to 1967 and worked as a field assistant on John’s Cloverly project in Wyoming and Montana. In 1968 Bob published a paper on “The superiority of the dinosaurs” in the Yale Peabody Museum’s popular magazine, Discovery, and he contributed both a skeletal reconstruction and a fleshed-out restoration to John’s 1969 Deinonychus monograph. Bob’s restoration quickly became the icon of the “new” warm-blooded dinosaur. Where John was cautious, Bob was evangelical. Each deserves considerable credit for revolutionizing our concept of dinosaurs. This happened quickly, and investigation of warm-blooded dinosaurs became an agenda for paleontological research for the following decade, culminating in publication of a symposium of the American Association for the Advancement of Science (Thomas and Olson, 1980).

Deinonychus is important for another reason. In 1970 John was in Europe studying Jurassic pterosaurs from Solnhofen, the source one of Yale’s paleontological treasures acquired many years earlier by O. C. Marsh. Thorough knowledge of osteology meant John was able to recognize a pterosaur that wasn’t: the Haarlem specimen of Archaeopteryx, which had been described as Pterodactylus crassipes by von Meyer in 1859 and subsequently largely forgotten. The first Archaeopteryx skeleton came from Solnhofen in 1861, and this “feathered reptile” was a sensational new evolutionary intermediate, discovered at a time when evolution and Darwin’s theory of natural selection were at the fore in every educated
mind. This specimen, known as the London specimen, was obtained by the British Museum (Natural History) in 1863. A second skeleton (the Berlin specimen) was found in 1877, and patriotic fervor meant it remained in Germany. John recently documented how the Berlin specimen was offered for sale to Marsh at an early date (Ostrom, 1985) and might have come to Yale had Marsh not balked at a purchase price of $10,000 (which, John pointed out, was the equivalent of 3 to 5 million dollars today!).

The Haarlem skeleton of *Archaeopteryx* that John reidentified in 1970 was not only a new specimen of this important and extremely rare taxon, but John also recognized that osteologically it was very similar to *Deinonychus* and other small carnivorous dinosaurs. He brought the Haarlem specimen triumphantly back to Yale at the beginning of term in 1970 and announced the find in *Science* before the close of the year. In a series of papers that followed over the next half-dozen years, John effectively revolutionized prevailing concepts of the relationship of birds to reptiles. Without the benefit of cladistic jargon, he effectively and almost completely convinced the paleontological and biological communities that birds are descended from dinosaurs. Today’s generation of systematists (those of the ubiquitous, and some say diabolical, forked diagrams) insist that birds therefore are dinosaurs (for example, Gauthier, 1986; Sullivan, 1991). In any case, acceptance of a phylogenetic link between birds and dinosaurs reinforces the idea that small carnivorous dinosaurs had high, bird-like metabolic rates.

John remains interested in small theropods, in his old love, ceratopsians, and, as ever, in travel to Germany, where the company is excellent and the ski slopes beckon! In 1978 he produced a beautiful monograph on the exquisite Solnhofen specimen of *Compsognathus longipes*, in 1981 he wrote an important paper on the enigmatic *Procompsognathus triassicus*, and in 1986 he revisited his old friend *Triceratops*, which he redescribed with Peter Wellnhofer. Together they described the beautiful skull of *Triceratops brevicornus* that flew from New Haven to Munich early in John’s tenure.

Throughout his career at Yale John has had curatorial responsibility for one of the most important collections of vertebrate fossils in the world. He is, surprisingly, the only research specialist on dinosaurs to hold curatorial rank at a major natural history museum in the United States. John’s work on older parts of the Yale collection and his discovery of new fossils in museums and in the field illustrate the value of museums and museum collections for progress in paleontology. The renaissance of dinosaurs owes much to the discovery of *Deinonychus antirrhopus* in the field and subsequently to research inspired by Yale’s nineteenth-century Solnhofen pterosaur.

Old collections are important in documenting published reports, but they also provide material for new investigations and sometimes stimulate completely new lines of research. New finds fill gaps in knowledge, making biological, geological, and paleontological hypotheses about un-
known times and places testable. New finds, even in old collections, are a stimulus for new ideas and new avenues of research, as John's career so amply testifies. In a record with as many gaps as the history of life, it is vitally important that all leads be investigated!

John has served science well. He was acting director of the Peabody Museum in 1975–1976. He served as president of the Society of Vertebrate Paleontology in 1969–1970 and edited the news bulletin of the society from 1963 to 1973. He has received many awards. These include a John Simon Guggenheim fellowship in 1966–1967 and a U.S. Senior Scientist Award from the Alexander von Humboldt Stiftung in Germany in 1976–1977 (and again in 1985). In 1986 he succeeded Stephen Jay Gould as recipient of the prestigious Hayden Memorial Geological Award presented by the Academy of Natural Sciences of Philadelphia. Good sport that he is, he overlooked the fact that the medal had been awarded many years earlier to Yale's arch rival, Edward Drinker Cope (it was also awarded to Eli's favorite son, George Gaylord Simpson). The citation for this award reads as follows:

The Hayden Medal is given for excellent work in geology that stimulates active discussion in the scientific community. John Ostrom's work on the osteology of Archaeopteryx provided new information needed for studies of the relationships of dinosaurs and birds, and his analysis and suggestions evoked many new studies of the capabilities of Archaeopteryx for climbing, running, and flying. The numerous debates resulted in convening of the International Archaeopteryx Conference in Eichstatt in 1984. His monograph on the small carnivorous dinosaur Deinonychus similarly served to fuel arguments focused on activity levels in dinosaurs.

Throughout his career he has approached a variety of important problems with a new and insightful point of view. His work on ceratopsian functional jaw morphology and the cranial anatomy of hadrosaurids are classics of the paleontological literature. His study of the paleoecology of hadrosaurids resulted in a new interpretation of their habits. Using modern techniques in studies of trackways, he offered exciting deductions on the social behavior of carnivorous dinosaurs. Ostrom's important revision of the osteology and relationships of the little dinosaur Compsognathus also includes a delightful identification of the lizard that formed Compsognathus' last meal. His field study of the stratigraphy and sedimentology of the Cloverly Formation's dinosaurs helped to fill a gap in our knowledge of the North American faunas. He continues his studies of dinosaurs, most recently on Triceratops.

John Ostrom exemplifies the traditional paleontologist as teacher to his students, the scientific community, and to the general public. His papers are so well written that they are accessible to workers from other disciplines, and he has been tireless in his work with artists, bringing skeletons to life for everyone. It is a pleasure to present Dr. John Ostrom as the 1986 recipient of the Hayden Medal.

Hayden Prize Committee

Twenty years ago we were graduate students at Yale privileged to share the heady excitement of John’s discoveries. We appreciated him then but, like many students, have come to appreciate our professor even more since leaving. He has brought dinosaur paleontology into the mainstream of thought in evolutionary biology, and he did this initially through insight gained interpreting morphology functionally. He has
long been interested in functional morphology and in evolution, and these are fitting themes for a volume celebrating his work, affectionately offered here by many of his friends, colleagues, and students.

Peter Dodson
Philip Gingerich

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xiv—left: fishing in the mountains of New York State (photo courtesy of Mrs. John (Nan) Ostrom)
right: graduate student at Columbia University (photo courtesy of American Museum of Natural History, New York City)
lower: with Cathy Skinner and Preston Cloud—October 1990 when the Cloud volume, John Ostrom Editor, was presented to P. Cloud. (photo courtesy of Mrs. John (Nan) Ostrom)

xv—left: graduate student at Columbia University (photo courtesy of Mrs. John (Nan) Ostrom)
right: with Peter Wellnhofer (photo courtesy of Dr. Peter Wellnhofer)
lower: 4 generations of paleontologists—John Ostrom with his advisor, Edwin Colbert, his student, Peter Dodson, and Peter’s student, David Weishampel, summer 1987 at the Royal Tyrrell Museum of Palaeontology, Alberta, Canada (photo courtesy of Professor Peter Dodson)

xvi—top: with Edwin Colbert in 1984—Archaeopteryx field trip at Eichstätt (photo courtesy of Professor Peter Dodson)
bottom: recipient of Hayden Geological Memorial Award presented by the Academy of Natural Sciences, Philadelphia (photo courtesy of Academy of Natural Sciences)