John H. Ostrom
(1928–2005)

We remember John H. Ostrom as the most influential dinosaur paleontologist of the second half of the 20th century. In his lengthy and distinguished career, John proved a worthy successor to O.C. Marsh, who founded the Peabody Museum of Natural History in 1867. John was an undergraduate geology major at Union College in Upstate New York. There, he was inspired by the writing of George Gaylord Simpson, one of Yale's greatest, and when the time came he went to Columbia University graduate school with the idea of studying with Simpson. John achieved his goal of becoming a paleontologist and evolutionary biologist but, despite Simpson's notable hospitality, John elected instead to study with the distinguished dinosaur paleontologist E. H. Colbert, whose temperament was perhaps a better match for John's. John's dissertation topic was a challenging one, a detailed anatomy of both skeletal and soft tissues (muscles, brain, and peripheral nerves) of the skulls of hadrosaurian dinosaurs. This project was a logical outgrowth of another major Yale project, "The hadrosaurian dinosaurs of North America" published two decades earlier (Lull and Wright, 1942). John left Columbia for a teaching position at Beloit College in Wisconsin before completing his Ph.D. In 1961, he defended his dissertation and joined the Yale faculty, where he remained for 31 years until his retirement in 1992.

John's first major publication, "The cranial morphology of the hadrosaurian dinosaurs of North America," a 1961 Bulletin of the American Museum of Natural History, set standards which few subsequent scholars have attained. The lavishly illustrated monograph has a timeless quality, and is still widely cited today. For the next 15 years, one paper after another revolutionized our understanding of dinosaurs and their relationships to animals living today. When John began his career, dinosaur paleontology was a sleepy field, scarcely legitimate as a recognized sub-discipline within

paleontology. By the time he ceased his labors, dinosaur paleontology was a flourishing discipline across the globe, and occupies some of the finest minds in science. The vigor and health of the discipline represent the best tribute to his scholarship. John became curator of a great legacy of dinosaur fossils that resulted from Marsh's activities during the latter decades of the 19th century. He wrote a seminal paper on the paleoecology of hadrosaurs for the American Journal of Science in 1964, and then turned his attention to the skulls of *Triceratops* and other horned dinosaurs, writing for *Postilla* and then for *Evolution*.

The great world traveler and fossil collector Barnum Brown (1873-1963) cast a long shadow at the American Museum of Natural History. As a student, John was constrained from studying materials that the elderly Brown had collected and *might* someday study. Once the constraint was removed, John seized the opportunity and acted quickly. He will never be remembered as a field paleontologist, but the results of John's first major field project were long-lasting and far-reaching. Up to that time, dinosaurs were well known primarily from the Late Jurassic and the Late Cretaceous, both in North America and worldwide. There was a dearth of fossils of Early Cretaceous (Aptian-Albian) age, most of what we knew coming from the *Iguanodon* fauna of the British Wealden. John undertook a major exploration of the Cloverly Formation of the Bighorn Basin of Wyoming and Montana, an area that Barnum Brown had explored and collected in the 1930s but had never published. He organized a series of six Yale Peabody Museum expeditions from 1962 to 1967. The Yale crews, which included many undergraduates, including Robert Bakker, a brilliant Ostrom protégé, met with great success. John published a monograph as a Peabody Museum Bulletin in 1970, introducing several components of an entirely new Early Cretaceous fauna. These included a large and still enigmatic ornithopod dinosaur, *Tenontosaurus tilletti;* an important nodosaurid ankylosaur, *Sauropelta edwardsi;* and a small theropod, *Microvenator celer,* described as a coelurosaur but now regarded as a possible oviraptorosaur. Since then, *Tenontosaurus* has been found in Utah, Oklahoma and Texas. *Tenontosaurus* continues to generate interest (Forster, 1990; Winkler, and others, 1997; Schachner, 2005). In recent years, research by James Kirkland, Ken Carpenter and others has revealed a distinctive Cloverly-correlative fauna in Utah (Dodson, 2005).

The 1970 monograph was not comprehensive, for it lacked one faunal member, to which John dedicated an entire monograph in 1969, following his announcement in a February 25 *Postilla* paper the same year. All of this follows from one of those electrifying discoveries that alter the course of science. In late August 1964, following a long and grueling season, John and Grant Meyer were prospecting on the side of a colorful conical hill ("Clovely tit") near Bridger, Montana when they chanced upon a set of exquisitely preserved crescentic claws weathering out of the hillside. As much as we love all dinosaurs, paleontologists are particularly transported by the remains of theropods (meat-eaters), and the twosome recognized instantly what they had. Feverish excavation revealed complete forelimbs, and subsequent excavation over the next three years resulted in the recovery of the remains of three individuals of one of the most remarkable dinosaurs known to that time. John named the animal *Deinonychus antirrhopus,* the "counterbalancing terrible claw." *Deinonychus* is characterized as a large-brained, agile, highly active, sickle-clawed killing machine. John recognized the similarity of *Deinonychus* to *Dromaeosaurus* from Alberta and the Mongolian predators *Velociraptor* and *Saurornithoides*. He presciently observed in his monograph: "it seems probable that other examples will be discovered from other strata and other continents." Bob Bakker sketched *Deinonychus* for the monograph, and his drawing of the fiercely intelligent, swiftly running predator became virtually overnight the icon of the New Dinosaur, built for high, possibly even avian, levels of activity. John cautiously suggested the *possibility* that theropods might have been warm-blooded, and thus not

sensitive candidates as climate indicators. Bakker took this idea and developed it with a vengeance. The idea of hot-blooded dinosaurs, launched by *Deinonychus,* became the paleontological *cause célèbre* of the 1970s, and dinosaur paleontology as an academic discipline was revitalized. Artists and authors seized on hot-blooded dinosaurs, and the sedate Mesozoic world visualized by Rudolf Zallinger and Charles R. Knight has vanished, replaced by the terrors of Michael Crichton's *Jurassic Park* (in which *Deinonychus*—mistakenly called *Velociraptor*—was the major player).

John had had enough of hot, dry Montana summers, so he spent the summer of 1970 in Europe, tracking down pterosaurs, an entirely new direction of research for him. He focused on pterosaur specimens from the Solnhofen Limestone of Bavaria, many of which had been collected during the 19th century. Relentless in his pursuit, no matter how obscure the fossil, John found himself in late August at the venerable Tyler Museum in Haarlem, the Netherlands. The quarry here was *Pterodactylus crassipes,* a fragmentary fossil described by Meyer in 1857 and all but forgotten thereafter. As he examined the specimen in the attenuated light within the museum, John was puzzled at what he was looking at. Whatever it was, it was no pterosaur. Could it be? He carried the specimen over to a window, where the directional rays of the late afternoon sun threw the contours of the fossil surface into relief, and was rewarded with the sight of feather impressions—this was indeed a specimen of the famous *Urvogel,* the dinosaur-bird, *Archaeopteryx* (originally described by Meyer in 1861), only the third one recognized, and the first since 1877 (Marsh attempted to purchase the 1877 'Berlin' specimen for the Peabody Museum, but balked at the very substantial asking price of 10,000 marks!). For the second time in his gifted career, John was struck by lightning, and he responded with characteristic alacrity and perspicacity to his serendipitous find.

These were heady times for paleontology at Yale. Elwyn Simons was working his magic with fossil primates in the Fayum of Egypt, and David Pilbeam likewise in the Siwaliks of India and Pakistan. Keith Thomson was mastering the mysteries of coelacanths and rhipidistian fishes. Farish Jenkins had completed his dissertation on therapsids, and was not far away; Ian Tatersall was completing his dazzling graduate career; Richard Kay was in the middle of his graduate studies. Ken Rose, John Fleagle and Paul Olsen were outstanding undergraduates, each showing his precocious promise of a superb career to come. This was the time that we too arrived at Yale to begin our graduate careers. Within days of our walking through the front doors of the Kline Geology Laboratories, John burst on the scene clutching his precious bundle from Haarlem, generously loaned for study. John published a preliminary paper in *Science* before the end of October, then spent the next six years deep in study. He published a series of superbly detailed papers (Ostrom, 1973, 1974, 1975, 1976) that literally changed the world of paleontology, specifically our understanding of the relationship of birds to dinosaurs.

Thomas Henry Huxley (a.k.a. "Darwin's bulldog") had drawn attention to the similarity between birds and dinosaurs as early as 1868. The wisdom that prevailed for at least half a century prior to John's discovery was that, while there were indeed similarities between the two groups, the ancestor of birds was more primitive than dinosaurs, and was to be found among the "thecodonts," the presumed ancestors of dinosaurs. Fresh from his study of *Deinonychus,* John looked at *Archaeopteryx* with fresh eyes and saw things that had never been seen before. He saw numerous similarities between theropods and *Archaeopteryx* that convinced him that the ancestry of birds was not remote but was from theropods little different from *Archaeopteryx.* For example, *Deinonychus* had a specialized bone in the wrist, a moon-shaped bone called a semi-lunate radial carpal. *Archaeopteryx* had just such a wrist-bone, and so do birds. John recognized whole suites of such characters shared by certain small theropods and

birds, and laid out a detailed case for a direct relationship with birds. In a *Nature* paper in 1973, he enumerated 21 similarities between theropods and birds that excluded "thecodonts." His papers culminated in 91-page masterpiece in the Biological Journal of the Linnean Society in 1976.

How did the ornithological and paleontological communities receive his groundbreaking thesis? Remarkably well! Within the short time, the bird-dinosaur link became the new orthodoxy. John's careful presentation of the evidence and tightly reasoned logic were completely convincing to an overwhelming majority in the scientific community. Within a 15-year period from 1961 to 1976, John's scientific efforts had transformed paleontology and had defined the research agenda for the rest of the century. *Archaeopteryx* has become a growth industry (the tenth specimen was just announced in December 2005! Mayr and others, 2005), as has the study of small, birdlike theropods, known today as maniraptorans, or "raptors" for short. In the 1980s, a paradigm shift was ushered into paleontology, as phylogenetic systematics or cladistics made its impact felt. Within the new paradigm, the theropod-bird link is stronger than ever—in fact, birds are now known to the *cognoscenti* as "avian theropods," and the old dinosaurs that John spent his career studying are now a dreaded "paraphyletic group" (a severe put-down in the *patois* of cladistics) to be known henceforth as "non-avian dinosaurs." John was never comfortable with this newspeak.

John was very impressed with the running capabilities of *Archaeopteryx,* and he developed a model for the origin of flight from the ground up, rather than from the trees down as in the classical model for flight articulated by Walter Bock. He visualized the proto-wing as a "fly-swatter" for a swiftly-running, insect-chasing theropod. His idea was much discussed during the 1980s, but it would be an overstatement to say that he convinced the scientific community on this aspect of the biology of *Archaeopteryx.* In 1986, John re-visited an old friend, *Triceratops,* under the most agreeable of circumstances. Early in his career, he had traded one of the many Yale specimens of *Triceratops* to Munich. At the invitation of his close friend in Munich, Peter Wellnhofer, John and Peter published a description of the Munich specimen, known as *Triceratops brevicornus* (Ostrom and Wellnhofer, 1986). (This incidentally was John's first co-authored paper since he was junior author to Ned Colbert in 1958!) The specimen had been named by Marsh but was previously undescribed. Revising the genus *Triceratops,* the pair concluded that there was but a single valid species, *Triceratops horridus,* despite an accumulation over the years of 13 species.

John "retired" (whatever that means for an academic these days) from the active faculty at Yale in 1992, after a truly distinguished career spanning 31 years. Though no longer active in fossil bird research, he received one of the greatest thrills in his career in 1996, when Chen Peiji from the Nanjing Institute of Paleontology brought to the American Museum of Natural History photographs of a small theropod from Liaoning, in northeastern China, that appeared to show a body-covering reminiscent of "protofeathers," seemingly documenting a primitive stage in the evolution of feathers. The exquisite little animal, which was decidedly non-volant, was named *Sinosauropteryx* ("Chinese reptile wing") by Ji and Ji. John was invited to join a "dream team" of ornithologists and paleontologists to visit China in March 1997 to examine the fossils first hand. There he witnessed the beginning of what has become a deluge of superb fossils from Liaoning that seemingly document every state of the transition from feathered dinosaurs to fully modern birds, all of Early Cretaceous age. He returned home with the euphoric feeling that all of his predictions had been borne out by the fossil record.

John received many honors during his career. He received a Guggenheim Fellowship, the Hayden Medal of the Academy of Natural Sciences (1986), the Romer-Simpson medal of the Society of Vertebrate Paleontology (1994), and the

Addison Emery Verrill medal of the Yale Peabody Museum in 1999. On his 65th birthday, the American Journal of Science honored him with a special volume of the AJS that he had edited so diligently for 25 years. The 478-page volume is entitled *Functional Morphology and Evolution* (Dodson and Gingerich, 1993), epitomizing the twin themes of his distinguished career. His work was held in especially high regard at the Academy of Natural Sciences. This venerable Philadelphia museum was the first to exhibit skeletons of *Deinonychus,* and in 1987, dedicated a larger-than-life outdoor bronze sculpture of a pair of *Deinonychus.* John was very proud of this honor. In 1999, the Peabody Museum organized a wonderful symposium in John's honor, *New Perspectives on the Origin and Evolution of Birds* (Gauthier and Gall, 2001), bringing together for the occasion a stunning exhibit of breath-taking Chinese fossils as well as specimens of *Archaeopteryx.*

John Ostrom was a great man, and he had the humility of true greatness. He was motivated by the love of knowledge. He hadn't a shred of self-promotion about him, and disdained those who do. He detested hyperbole. He was a throwback, and like Joseph Leidy, the epitome of the gentleman scientist. He was a wonderful communicator, and loved talking about his discoveries and their significance, especially to young people destined to become the scientists of the future. The public found him graceful and approachable. It is a disappointment that he never left a personal memoir—because it would be interesting to know more of the circumstances of the discoveries he made, and what he himself thought of these. It remains for his friends and admirers to record the chapters of his life.

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References

Colbert, E. H., and Ostrom, J. H., 1958, Dinosaur stapes: American Museum Novitates 1900, p. 1–20.
Dodson, P., 2005, Utah!: American Paleontologist 13(1), p. 12–17.
Dodson, P., and Gingerich, P. D., editors, 1993, Functional Morphology and Evolution: American Journal of Science, v. 293A, p. 1–478.
Forster, C. A., 1990, The postcranial skeleton of the ornithopod dinosaur *Tenontosaurus tilletti:* Journal of Vertebrate Paleontology, v. 10, p. 273–294.
Gauthier, J., and Gall, L. F., editors, 2001, New Perspectives on the Origin and Early Evolution of Birds. Proceedings of an international symposium in honor of John Ostrom: New Haven, Connecticut, Yale University, Special Publication of the Peabody Museum of Natural History, 613 p.
Mayr, G., Pohl, B., and Peters, D. S., 2005. A well-preserved *Archaeopteryx* specimen with theropod features: Science , v. 310, p. 1483–1486.
Ostrom, J. H., 1961, Cranial morphology of the hadrosaurian dinosaurs of North America: Bulletin of the American Museum of Natural History, v. 122, p. 33–186.
——— 1964, A functional analysis of jaw mechanics in the dinosaur *Triceratops:* Postilla, v. 88, p. 1–35.
——— 1964, A reconsideration of the paleoecology of hadrosaurian dinosaurs: American Journal of Science, v. 262, p. 975–997.
——— 1966. Functional morphology and evolution of the ceratopsian dinosaurs: Evolution, v. 20, p. 290–308.
——— 1969, A new theropod dinosaur from the Lower Cretaceous of Montana: Postilla, v. 128, p. 1–17.
——— 1969, Osteology of *Deinonychus antirrhopus,* an unusual theropod from the Lower Cretaceous of Montana: Bulletin of the Peabody Museum of Natural History, v. 30, p. 1–165.
——— 1970, Stratigraphy and paleontology of the Cloverly Formation (Lower Cretaceous) of the Bighorn Basin area, Wyoming and Montana: Bulletin of the Peabody Museum of Natural History, v. 35, p. 1–234.
——— 1973, The ancestry of birds: Nature, v. 242, p. 136.
——— 1974, *Archaeopteryx* and the origin of flight: Quarterly Review of Biology, v. 49, p. 27–47.
——— 1975, The origin of birds: Annual Review of Earth and Planetary Sciences, v. 3, p. 55–77.
——— 1976, *Archaeopteryx* and the origin of birds: Biological Journal of the Linnean Society, v. 8, p. 91–182.
——— 1979, Bird flight: how did it begin?: American Scientist, v. 67, p. 46–56.
——— 1986, The cursorial origin of avian flight, *in* Padian, K., editor, The Origin of Birds and the Evolution of Flight: Memoir of the California Academy of Science, v. 8, p. 73–81.

Ostrom, J. H., and McIntosh, J. S., 1966. Marsh's Dinosaurs. The Collections from Como Bluff: New Haven, Connecticut, Yale University Press, 388 p. (reprinted 1999).
Ostrom, J. H., and Wellnhofer, P., 1986, The Munich specimen of *Triceratops* with a revision of the genus: Zitteliana, v. 14, p. 111–158.
Schachner, E. R., ms, 2005, Pectoral and forelimb musculature of the basal iguanodontid *Tenontosaurus tilletti* (Dinosauria: Ornithischia): Bristol, England, University of Bristol, Department of Earth Sciences, Unpublished M.S. thesis, 64 p.
Winkler, D. A., Murry, P. A., and Jacobs, L. L., 1997, A new species of *Tenontosaurus* (Dinosauria: Ornithopoda) from the Early Cretaceous of Texas: Journal of Vertebrate Paleontology, v. 17, p. 330–348.