SPECIAL REVIEW

John Ostrom's Studies on *Archaeopteryx*, The Origin of Birds, and the Evolution of Avian Flight

Archaeopteryx lithographica is the most significant fossil species in the class Aves. Studies on *Archaeopteryx* have formed the basis for 3 generally accepted ideas about avian evolutionary history: (1) birds have their origins in reptiles, specifically within the pseudosuchian Thecodontia, (2) birds evolved their adaptive way of life—flight—from bipedal, arboreal ancestors, and (3) the origins of more modern avian taxa were post-Jurassic in time, *Archaeopteryx* being considered on the "main-line" of avian evolution or "close to it." *Archaeopteryx* has held this central position because it is the oldest fossil with obvious avian affinites and is represented by a number of well-preserved specimens. It is not surprising therefore that in addition to considerable work on the morphology of *Archaeopteryx*, many workers have attempted to reconstruct from that morphology much about the ecology and behavior of this species; and by inference these findings have been assumed to represent the avian ancestral condition. This controversial literature leads one to the important question of just how far historical analysis, which is highly inferential, can depart from the available evidence and yet remain "respectable" science, or alternatively to what extent can historical narrative explanation be regarded as "good" science? Indeed, this is one of the critical questions of paleontological methodology and I will return to it later.

The recent discovery of additional specimens of *Archaeopteryx* has created new interest in this species and in the larger problems mentioned above. Dr. John Ostrom of Yale University, a leading student of dinosaurs, was studying pterosaurs in 1970 and discovered that one specimen was actually referable to *Archaeopteryx*. His study of the other known specimens resulted in a series of papers (1970, 1972, 1973, 1974, 1975a, 1975b, 1976a) culminating in a large descriptive review (1976b). Ostrom's work focuses on two problems, the origin of birds and the origin of flight, and I believe that his solutions to these problems will almost certainly change contemporary viewpoints about *Archaeopteryx* and early avian evolution. I find most of his arguments persuasive, not in the sense that they are necessarily *true*, but that they "explain" far more than previous hypotheses. This is an important distinction, because arguments against Ostrom's viewpoints have not focused so much on his analysis of morphology and the hypotheses derived *directly* from it, but rather on alternative hypotheses that appear to have little evidentiary support.

Ostrom (1976b) presents a detailed comparative anatomical discussion, either refuting or calling into serious question many previous ideas about the morphology of *Archaeopteryx*. For example: (1) the pubis was probably not directed sharply backward as the Berlin specimen seems to indicate; (2) the hand and forelimb skeletons are not especially birdlike, and on the basis of comparisons with reptiles, Ostrom argues that the digits are numbers I, II, III; by implication this would be true for modern birds as well and thus contradicts the conclusions of some embryologists who have identified the digits as II, III, and IV; (3) x-ray studies indicate that there was proximal fusion of the metatarsals, and two proximal tarsal elements were co-ossified with the tibia and fibula, and at least two distal tarsals were fused to the metatarsus; (4) Ostrom believes that elements previously considered parts of the sternum are misidentified, and he concludes that an ossified sternum was not present.

Ostrom has made other notable discoveries about the morphology of *Archaeopteryx*

that have significance when comparisons are made to modern birds and fossil reptiles. It is here that ornithologists owe Ostrom a particular debt, for it is doubtful whether any avian morphologist or paleontologist has as complete understanding of reptilian morphology as he does. This special knowledge has permitted him to undertake a broad comparative investigation, far surpassing efforts by previous authors. Which brings us to his two major conclusions, first about the relationships of *Archaeopteryx* and birds to reptilian taxa, and second, about the origin of flight.

Since its discovery in 1861, nearly all authorities have recognized the avian affinities of *Archaeopteryx*, yet its morphology was recognized as basically reptilian. Ostrom identifies two features as clearly indicating a relationship to birds: the possession of feathers and the fusion of the clavicles into a furcula. He also mentions other "birdlike" features, but does not make a strong attempt to use them as evidence of relationship. For example, the fusion of metatarsal elements and the fusion of tarsal elements with the tibia-fibula and metatarsals are characters shared with birds, though the theropod *Syntarsus* exhibits similar conditions. The tibia and fibula have become slender in *Archaeopteryx*, and especially in later birds, and both bones are elongated relative to the femur. Furthermore, Ostrom considers the orientation of the pubis to be intermediate between theropods and birds. All these features would seem to corroborate a phyletic relationship between birds and *Archaeopteryx* that excludes other vertebrates (but see comments below on *Syntarsus*).

Although not expressed entirely in Hennigian terminology, Ostrom's analysis very much follows the principles of phylogenetic systematics. He recognizes that "proof" of homology is not possible, therefore "the only reasonable working hypothesis remaining is that . . . resemblances are homologous in the absence of contrary evidence" (1976b:100). Contrary evidence would be, of course, support for a phylogenetic hypothesis requiring convergence in the characters under consideration. Ostrom also supports the notion that only derived character-states can be used to indicate relationships, shared primitive character-states lacking such information. For the most part, I believe Ostrom's conclusions and statements about systematics are well-founded and expressed in a logically consistent framework of phylogenetic reasoning. Unfortunately, we are all captives of our past—intellectually and psychologically—and Ostrom is no exception. When examined closely some of his statements lack clear meaning, but it must be said that all previous persons writing about *Archaeopteryx* fell into the same trap. As an example, consider the old argument about whether *Archaeopteryx* is (1) an aberrant form off the "main-line" of avian evolution, (2) on the "main-line" of avian evolution, or (3) the "direct ancestor" of birds (the second and third arguments are sometimes interchangeable). I doubt that there is a more pointless issue in the study of avian evolution than this. Ostrom (1975b:521) believes that considering *Archaeopteryx* as a "main-line" (never defined by him) transitional form is fundamental to his arguments about avian-*Archaeopteryx* affinities to theropods. Nothing could be further from the truth, because the conclusion to be drawn from his studies is that birds + *Archaeopteryx* are more closely related to theropod dinosaurs (and perhaps only a few genera of theropods) than to other reptiles; this conclusion can be reached whether *Archaeopteryx* is "main-line" or not. Thus, Ostrom has not yet escaped from some unnecessary doctrine of his paleontological training: "I personally believe *Archaeopteryx* lies very close to bird origins and probably is directly ancestral to all later birds" (1975a:61). It is questionable whether "very close" has any precise semantic or biological meaning as used here or whether "probability levels" are at issue. Nowhere does Ostrom (nor do paleontologists in general) present ways in which hypotheses of

ancestral-descendant relationships can be tested. One necessary condition for an ancestor is that the ancestral species (only species can be ancestors) must have *all* primitive character-states relative to its descendants. Indeed, Ostrom considers the greatly shortened ischium as a unique (derived) feature of *Archaeopteryx*. If *A. lithographica* were the direct ancestor of birds it would be necessary to postulate reversals in the avian lineage for each derived character-state of *A. lithographica*, and this is less parsimonious than assuming that these derived states were evolved *after* the speciation event giving rise to birds on the one hand and *Archaeopteryx* on the other. But to repeat, I fail to see that these types of arguments have a fundamental bearing on Ostrom's major conclusions.

Following the discovery of *Archaeopteryx* in 1861 many morphologists and paleontologists wrote about the similarities of *Archaeopteryx* to different reptilian taxa. Many of these workers identified various dinosaur groups as the possible ancestors of *Archaeopteryx* and birds, and this view gained some acceptance. Later R. Broom and G. Heilman argued that dinosaurs and the *Archaeopteryx*-avian lineage were both derived from the same common ancestor, the pseudosuchian thecodonts. With few exceptions (particularly P. Lowe and N. Holmgren) this viewpoint of avian origins has been accepted dogma for over 50 years, and Ostrom's historical analysis (1976b:168–173) adds yet another example within avian systematics where a particular idea about relationships is maintained on the basis of authority rather than documented evidence.

Ostrom resurrects the theory of dinosaurian origins and convincingly demonstrates that the morphology of *Archaeopteryx* is extremely similar to that of theropod dinosaurs and very different from other reptilian groups, including pseudosuchians—on such comprehensive work are new dogmas born and sustained! Basically, Ostrom's argument is that theropods and *Archaeopteryx* share many derived character-states within reptiles and therefore his hypothesis of common ancestry seems well supported. Ostrom appears to have done a masterful job in this analysis, although it will take a specialist familiar with reptilian anatomy to be the final arbiter. Hecht (1976:357–360) criticizes Ostrom's list of shared derived characters because he believes they are "adaptive" or "fusion-reduction" characters and therefore of "low weight." Hecht's contentions are straws in the wind, for all significant taxonomic characters are "adaptive," and derived characters are either the result of common ancestry or independent origin (convergence). The only way to distinguish between these alternatives is by reference to a particular phylogenetic hypothesis. At best, all that Hecht offers is support for Bock (1965), who at that time accepted a pseudosuchian ancestry.

It is impossible here to summarize all the similarities between *Archaeopteryx* and theropods, but they are so substantial that without feathers *Archaeopteryx* would have been classified as a theropod. The similarities are strongest in the morphology of the forelimb, pectoral girdle, vertebral column, and skull. Of particular interest is the possibility, not discussed by Ostrom, that *Archaeoptryx* may be related to only one or a few genera of theropods rather than the entire group. For example, *Syntarsus* and *Archaeoptryx* appear to share some specializations absent in other theropods. This problem deserves further attention because it has obvious relevance for the analysis of avian origins and higher taxa in general.

As Ostrom correctly points out, the morphology of theropods and *Archaeopteryx* is the key to understanding the origin of birds and their flight mechanism, and his inferences from that morphology have led him to an unconventional, and controversial, hypothesis for the origin of avian flight. The literature on the origin of flight is an amalgam of good science and speculations bordering on science fiction. The latter are sometimes passed off as scientific because it is "historical narrative explanation," but the essential

problem remains how to "describe" (one somehow hesitates to call this "explanation") the events of an admittedly interesting historical occurrence and yet not succumb to making inferences that exceed the available evidence.

The main outline of the different theories on avian flight extends back to 19th century workers. Basically there are two: flight originated from terrestrial, cursorial bipeds or from arboreal bipeds that passed through a gliding phase. The latter has been generally accepted by contemporary biologists and has had its clearest exposition by Bock (1965, 1969). Ostrom (1974, 1976a) resurrects the theory of terrestrial origin, but with a new twist. He argues as follows: (1) morphologically *Archaeopteryx* is a theropod, thus functional inferences should be based on that morphology with little emphasis given comparisons with modern birds; (2) *Archaeopteryx* was an active biped, and the hindlimb provides no indication of special adaptations for an arboreal habit; (3) the forelimb of *Archaeopteryx*, like that of closely related theropods, was a grasping appendage with strong powers of adduction and was adapted for predation and not climbing; (4) feathers evolved along with high metabolic activity and as a thermoregulatory control mechanism; (5) contour feathers of the forelimb were modified to aid in capturing prey and only later evolved flight functions.

Although many workers will be skeptical at first exposure to Ostrom's ideas—after all, the wings look like those of modern birds—once one confronts the totality of the evidence, his ideas become more and more acceptable *compared to the alternatives that have been suggested.* Ostrom is willing to construct hypotheses about the origin of avian flight only on the evidence presented by *Archaeopteryx.* Previous hypotheses—particularly the arboreal theory of flight—have been biased by expectations that *Archaeopteryx* should function as a bird. *But Archaeopteryx was a theropod dinosaur with feathers.* Personal prejudicies against the use of wings as capture devices should *not* be based on one's experiences with living birds—where the wing is clearly flight adapted—but on what might be expected of a feathered theropod. If non-feathered theropods were using forelimbs for predation, then might not *Archaeopteryx* have done likewise? In one of his most interesting papers, Ostrom (1976a) suggests that in *Archaeopteryx* the pectoralis minor (supracoracoideus) was a depressor of the arm, not an elevator as in birds, that the trunk skeleton was flexible, that the pectoral girdle was not rigidly fixed, that the sternum was probably cartilaginous, and that the forelimb skeleton exhibited no specializations usually attributed to avian flight. *Archaeopteryx* apparently could not elevate the humerus above shoulder level nor could the hand be folded back against the forearm. On the other hand, Ostrom claims that forelimb functions included rapid extension of the manus, powerful anteroventral flexion of the forearm toward the midline, and the capacity for extreme hyperextension of the wrist—all adaptations expected in a predator.

It seems to me that *Archaeopteryx* cannot be used to support an arboreal origin of avian flight. *Archaeopteryx* does not appear to have arboreal adaptations, and one wonders whether a species previously adapted for cursorial locomotion could move into the trees without such adaptations. Moreover, *Archaeopteryx* does not appear to possess a morphology indicating flight or even parachuting-gliding ability. If workers insist on building hypotheses based only on what we presently know, then we may be compelled to accept a terrestrial origin of avian flight. To invoke additional, unknown proto-avian stages is tantamount to the erection of *ad hoc* hypotheses. Nowhere does Ostrom deny the possibility of an arboreal origin (nor would I), but such a conclusion must await further discoveries. Surely there must have been a radiation of feathered coelurosaurs, and perhaps some of these were arboreal— but *Archaeopteryx* was not.

Historical narrative explanation typically does not involve direct deduction of historical events from natural laws, hence some philosophers of science claim that historical narration is not explanation, but merely description. Be that as it may, systematic hypotheses can be evaluated on the basis of how well they account for the available data and how consistent they are with known properties of organisms (physiology, genetics, etc.). In the case of the origin of avian flight, *Archaeopteryx* is about the only real evidence we have; to his credit, Ostrom is unwilling to extend himself much beyond that evidence.

I am not trying to create a bandwagon over Ostrom's papers, but they are exciting. Some of his findings may eventually be refuted, but there is no doubt that much of his meticulous work will last and that our ideas on avian evolution will be significantly influenced by his results. Ornithologists owe this non-ornithologist a great deal for this contribution.—JOEL CRACRAFT.

LITERATURE CITED

BOCK, W. J. 1965. The role of adaptive mechanisms in the evolution of higher levels of organization. Syst. Zool. 14:272–287.

———. 1969. The origin and radiation of birds. Ann. New York Acad. Sci. 167:147–155.

HECHT, M. K. 1976. Phylogenetic inference and methodology as applied to the vertebrate record. Evol. Biol. 9:335–363.

OSTROM, J. H. 1970. *Archaeopteryx*: Notice of a "new" specimen. Science 170:537–538.

———. 1972. Description of the *Archaeopteryx* specimen in the Teyler Museum, Haarlem. Koninkl. Nederl. Akad. van Wettenschappen, ser. B, 75:289–305.

———. 1973. The ancestry of birds. Nature 242:5393.

———. 1974. *Archaeopteryx* and the origin of flight. Quart. Rev. Biol. 49:27–47.

———. 1975a. The origin of birds. Ann. Rev. Earth Planet. Sci. 3:55–77.

———. 1975b. On the origin of *Archaeopteryx* and the ancestry of birds. Proc. Centre Nat. Rech. Sci. Collog. Int. 218 Problèmes Actuels de Paléontologie-Evolution des Vertébrés, pp. 519–532.

———. 1976a. Some hypothetical anatomical stages in the evolution of avian flight. Smithson. Contrib. Paleobiol. 27:1–21.

———. 1976b. *Archaeopteryx* and the origin of birds. Biol. J. Linn. Soc. 8:91–182.