Reviews

Edited by Rebecca L. Holberton

The following critiques express the opinions of the individual evaluators regarding the strengths, weaknesses, and value of the books they review. As such, the appraisals are subjective assessments and do not necessarily reflect the opinions of the editors or any official policy of the American Ornithologists' Union.

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Anatomy and Systematics of the Confuciusornithidae (Theropoda: Aves) from the Late Mesozoic of Northeastern China.—L. M. Chiappe, S. Ji, Q. Ji, and M. A. Norell. 1999. Bulletin of the American Museum of Natural History, Volume 242. 89 pp. ISSN 0003-0090. Paper, $8.60.—Only a few years ago, the fossil record for the earliest known period in the evolution of birds was depressingly meager. From the late Jurassic *Archaeopteryx* to the late Cretaceous *Hesperornis* and *Ichthyornis*, only scrappy avian remains were known. This changed dramatically with the discovery of birds in early Cretaceous lake deposits in Spain and particularly in northeastern China's Liaoning Province, where thousands of fossils have been recovered, including several different kinds of birds. Incredible as it once would have seemed, one of these early Cretaceous birds, *Confuciusornis sanctus*, is now known from hundreds of specimens.

The work reviewed here has the superficial appearance of a monographic treatment of *Confuciusornis* and its relatives. Unfortunately, it is not. The authors, steeped in cladistic fundamentalism, have been among the more insistent proponents of the origin of birds from theropod dinosaurs, with its attendant corollaries, such as the origin of flight from the ground up. The present work appears to be but an attempt to put a dinosaurian "spin" on the still-emerging interpretations of the significance of *Confuciusornis.*

Most of the specimens from the Liaoning deposits were collected, and to some extent prepared, not by scientists, but by those intent on selling the specimens, so that the possibility of artificial "enhancement" of fossils is rather high. Indeed, Chiappe et al. (p. 68, figures 60 to 63) note several specimens of *Confuciusornis* with parts glued on from other individuals or with structures that have been sculpted out of matrix with a binder. It has also been suggested that the otherwise inexplicable proximal humeral foramen of *Confuciusornis* is an artifact. Although Chiappe et al. deny this, information in their paper may be interpreted to the contrary, so to this reviewer the issue remains unresolved.

Most of this publication consists of descriptive anatomy, which had been treated in at least eight shorter papers on *Confuciusornis* by other authors. Instead of summarizing this literature, however, Chiappe et al. have selectively chosen from it various points of which to be critical, even when the view in question may not be the most current. Such selectivity, apart from being disingenuous, detracts from the usefulness of the work as a whole, which cannot be relied upon to supercede the earlier literature. For example, Hou et al. (1999) are cited only to say that Chiappe et al. were "unable to examine the recently described *Confuciusornis dui.*" Yet, nowhere is it mentioned that the main importance of this specimen is that it preserves the horny rhamphotheca. Likewise, Chiappe et al. spare nothing to reproduce and criticize an outdated reconstruction by Hou et al. (1996), made when only a few incomplete specimens of *Confuciusornis* existed, but they never allude to the preposterous reconstruction on the cover of *Scientific American* that accompanied an article by Padian and Chiappe (1998) in which *Confuciusornis* is depicted like some medieval rendition of a dyspeptic phoenix that had just dismounted from a horse.

It had previously been determined that the skull of *Confuciusornis* exhibits the primitive diapsid condition and, in a separate section on kinesis (pp. 72–75), Chiappe et al. argue that the skull was akinetic. Food processing by a toothless bird with an akinetic skull would be highly problematic, so a more detailed study of the wealth of specimens potentially available will more likely show that the skull was in fact kinetic.

No one had detected uncinate processes on the ribs in any of the specimens of *Confuciusornis* hitherto examined. Nor do these processes occur in *Archaeopteryx* or other very early birds. Supposed uncinate processes have recently been reported in late Cretaceous theropods, however (Clark et al. 1999). If they are invariably absent in late Jurassic and early Cretaceous birds, it would suggest to any reasonable person that the structures are unlikely to be homologous between birds and dinosaurs. Therefore, for advocates of the theropod origin of birds, it would be desirable to find uncinate processes in early birds or to wish their absence away. Chiappe et al. do both. They illustrate (figure 34) what they claim to be uncinate processes articulating with six ribs in only a single specimen of *Confuciusornis,* from which they go on to speculate "that their absence in other basal birds . . . may be due to preservational factors or ontogenetic development" (pp. 32–33). This goes beyond special pleading, because the authors could not possibly believe that this would explain the absence of uncinate processes in all of the specimens of *Archaeopteryx* or in any of the hundreds of other specimens of *Confuciusornis.*

As shown (fig. 34), the so-called uncinate processes originate only on the posterior six ribs, whereas at least two strong ribs anterior to these do not have processes, which would be unlike any known bird. Also, "the uncinate processes are long and extend over nearly two subsequent ribs" (p. 32), an utterly unheard of condition. And judging from the illustration, some of the ribs must have had two uncinate processes, which is even more implausible. Clearly, these cannot be uncinate processes and are probably displaced gastralia or ribs that have been misrepresented to serve a larger purpose.

The furcula of *Confuciusornis* is large and robust and the scapula and coracoid are fused; "consequently, the acrocoracoid process is not developed" (p. 29). Therefore, the shoulder girdle is more like that of *Archaeopteryx* than that of modern birds. The sternum is a large ossified plate but lacks an ossified carina. From this osteological evidence, it is clear that the supracoracoideus muscle was not functioning as a dorsal elevator in *Confuciusornis.* The lack of an acrocoracoid process and other adaptations for the supracoracoideus to function as a dorsal elevator were among the main evidence used by Ostrom (1976) and others to argue that *Archaeopteryx* was at best a poor flier or even a "pre-flight" stage in the evolution of avian flight. Chiappe et al. do not mention any of this in connection with *Confuciusornis,* however.

The humerus is robust, with a very large pectoral crest. It is slightly longer than the radius and ulna, and the hand is much longer than either the forearm or the humerus. Chiappe et al. (p. 33) consider this to be "clearly primitive" but do not explain their reasoning.

The hand consists of three digits, the outer and inner of which bear large, recurved claws with large flexor tubercles. The ungual phalanx of the major (middle) digit is reduced and is not clawlike in form. Although the authors make no interpretation of this condition, it is likely that it reflects the increasing importance of the major digit as the site of attachment of the outermost primary feathers. Regrettably, in none of their photographs are all of the elements of the hand of *Confuciusornis* clearly displayed, and there is no interpretive diagram of the hand.

Vazquez (1992) identified a number of specializations of the wrist in all modern birds that he considered to be necessary for flapping flight. He suggested that the wrist in *Archaeopteryx* "was probably incapable of executing the kinematics of modern avian powered flight." Because this has been seized upon as supporting the "ground up" theory of the origin of flight, what bearing does the morphology of the wrist of *Confuciusornis* have on this question? Chiappe et al. do not cite Vazquez and do not address this issue. They describe the ulnare (which nowhere is labeled in their illustrations) as much smaller than the radiale, a condition unlike modern birds. Another important difference is that the alular metacarpal is not fused to the major metacarpal, and the major and minor metacarpals are not fused distally. Therefore, it seems safe to say that *Confuciusornis* did not have all of the adaptations of the modern avian wrist.

One aspect of its wrist must have been as well developed as in modern birds, however, as inadvertently demonstrated in figure 70, which shows a reconstructed skeleton of *Confuciusornis* with the shaded outline of the body and wings. Here the hand is shown extending down at an angle of about 45° from the horizontal. In this position, had the bird been terrestrial, as the authors would prefer, its long primaries would have been pressed down and bent against the surface of the ground. Instead, the primaries are shown projecting straight back, horizontally, as though they were coming off the ulna perhaps. Thus, it can be seen that with its very long wing, whether it came to rest on the ground or on a tree limb, *Confuciusornis* had to be able to flex the wrist to the same degree as in modern birds to keep its primaries clear of the substrate.

The pelvis has the avian retropubic construction, but with the primitive condition of having the pubes fused distally. The tarsometatarsus is short and squat, much shorter than the tibiotarsus or femur, which is very unlike any truly terrestrially adapted birds and militates against any interpretation of this bird being at all cursorial.

Perhaps the most spectacular aspects of *Confuciusornis* are revealed by the preservation of feathers with the skeleton. These indicate that the wing was extremely long and pointed, with the primaries having very asymmetrical vanes. There was, however, no alula on the outer digit, whereas the alula has been argued as being necessary for avian flight at low speed with high maneuverability (Sanz et al. 1996).

Some individuals of *Confuciusornis* (Chiappe et al. do not indicate what proportion; Feduccia [1999] says 5 to 10%) have two extraordinarily long central tail feathers with expanded tips that appear to be nearly 2.5 times the length of the body (fig. 48).

Chiappe et al. maintain that all the other rectrices of *Confuciusornis* are decomposed and hidden among the feathers of the rump. Yet, Hou et al. (1996) show a specimen with apparently normally developed rectrices, which would certainly accord better with the well-developed pygostyle. So what are we to believe? Regardless of what the facts may prove to be, this point alone should be sufficient to demonstrate that Chiappe et al. have not dealt adequately either with the existing specimens or the literature.

The only other member of the Confuciusornithidae recognized by Chiappe et al., *Changchengornis hengdaoziensis,* is from the same deposits as *Confuciusornis.* This new genus and species was described by Ji et al. in March 1999. In November 1999 it was completely redescribed in the present work, which repeats all six illustrations from the previous paper—a rather egregious case of "double-dipping." That *Changchengornis* is a valid genus is highly doubtful. The only known specimen is the holotype, which by the authors' own admission (p. 50) "has been compressed and deformed . . . and it does not provide much information." What is apparent is that it has the same wing shape, the same two elongated rectrices, the same distinctive shape of the humerus, and the same overall proportions of the wing and leg as *Confuciusornis.*

At one point (p. 67), Chiappe et al. say of *Changchengornis* that "the phalangeal formula of the foot is typical of theropod dinosaurs: 2-3-4-5-x . . . ." Who do they expect to impress with this choice tidbit? It happens to be true, but it is also true that the same phalangeal formula is found in *Confuciusornis* (p. 47) and is the typical and primitive condition found in almost all birds. Such gratuitous statements are characteristic of the propagandizing that the theropod proponents of avian origin seem to think is necessary to bolster their hypothesis. In the same vein, Chiappe et al. refer to the digits of the hand in the Confuciusornithidae with the theropodan formula of I, II, III, whereas it has been repeatedly shown (Holmgren 1955, Hinchliffe 1985, Burke and Feduccia, 1997) and conceded (Wagner and Gauthier 1999) that the digits of the hand in birds are II, III, IV. Because this is such compelling evidence against the theropod origin of birds, it is hardly any wonder that Chiappe et al. cannot bring themselves to use the correct formula.

One line of evidence suggesting that *Changchengornis hengdaoziensis* is at least a valid species is that it appears to be smaller than *Confuciusornis sanctus.* This can be ascertained only by referring to the authors' meager tables of measurements, because nothing about its size is discussed. Size is something that the authors all but ignore. Tremendous size variation exists in *Confuciusornis*—note the dramatic difference in the two individuals illustrated in the same slab in figure 62—but despite the fact that hundreds of individuals exist, Chiappe et al. provide only a few measurements for four specimens (Tables 1 and 2). The measurements of the humeri and femora of these are repeated in Table 4 (we can take comfort that they are the same in both places), along with those of nine other specimens. There is no analysis to determine whether size variation is a continuum or bimodal or has some other distribution. Are the ones with long tail feathers at the upper end of variation, the lower, or throughout the range? Chiappe et al. (p. 4) note that "the high number of extraordinarily preserved specimens affords an unprecedented opportunity to investigate intraspecific variation, allometric growth, and sexual dimorphism in one of the earliest and most primitive lineages of birds," but their own study does nothing of the kind.

The summary of the systematics of the Confuciusornithidae (pp. 68–72) deals mainly with synonymizing two other species of *Confuciusornis* described by Hou. There is some discussion of why previous authors were "wrong" in the overall placement of the Confuciusornithidae, and then the authors present their cladogram in which the family is shown as more derived than *Archaeopteryx* but the sister-group to all other known birds. No cladistic analysis is presented to justify the cladogram, however, and the legend refers to an unpublished book. Thus, no justification is provided in this putative "monograph" regarding the most important systematic conclusion that one would care to know about the family. The two additional cladograms in figure 68 are not discussed in the text, and the legend again refers only to the same unpublished book. These cladograms have no bearing on the systematic position of *Confuciusornis* and have been inserted only to further another hidden agendum that is irrelevant to the present review.

The short terminal section on "Life-style of the Confuciusornithidae" reveals the true weakness of theory-laden analyses. The original describers envisioned *Confuciusornis* not only as an arboreal but a climbing bird. On the other hand, even though millions of years had elapsed since the time of *Archaeopteryx,* the theropodists still seem to want all birds in the early Cretaceous to be terrestrial, as though this would somehow add strength to their requisite "ground-up" theory of avian flight. Based on some rather tedious and unconvincing evidence on proportions and structure of bones of the toes, Chiappe et al. argue not so much that *Confuciusornis* was terrestrial, but that it was not arboreal, as though a terrestrial life-style were the only alternative. This leaves them with the problem that *Confuciusornis* obviously could fly, yet (and they do not make this point) some aspects of its morphology are the same as those used to suggest that *Archaeopteryx* could not fly, or at least not fly well. Consequently, they are forced into the assumption that *Confuciusornis* was "able to lift off after a short take off run" (p. 79). Lift off any time it pleased would be more like it, because it is obvious that *Confuciusornis* was neither terrestrial nor arboreal in the sense of clambering around in trees. The very long pointed wings and highly asymmetrical vanes of the remiges are those of an aerially adapted bird such as a tropicbird, tern, falcon, nightjar, or swallow. The two extremely long central rectrices of some individuals make sense only if used in aerial display, as are the long rectrices of tropicbirds and some nightjars, or in arboreal displays as in some birds-of-paradise.

As Chiappe et al. note (p. 79), the presence of many individuals in a single layer over a small area of lake deposit suggests colonial (or at least flocking) behavior and a catastrophic dieoff, perhaps associated with volcanic activity. I would suggest that the reason *Confuciusornis* is the most abundant bird in the deposit is because flocks of them were flying over the lake when disaster struck. There can be little doubt that the principal means of locomotion of *Confuciusornis* was flight. This is a most important fact because it was flying with a primitive, fused scapulocoracoid without an enlarged acrocoracoid process, it was flying without a keeled sternum, it was flying without an alula, and it apparently was flying without a fully modern avian wrist. *Confuciusornis* shows us, therefore, that we should not posit the highly refined aspects of modern birds as being requisite for active flapping flight. It also removes virtually all of the objections to *Archaeopteryx* being capable of active flight.

Thus, if Chiappe et al. actually understand the true significance of *Confuciusornis*, then they have done their best to prevent it from being revealed. Their paper will stand as an exemplar of manipulation of information to conform to preconceived ideas, but it is otherwise insufficiently credible or comprehensive to constitute a lasting addition to knowledge.—STORRS L. OLSON, *Division of Birds, MRC 116, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, USA.*

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Avian Growth and Development: Evolution within the Altricial-Precocial Spectrum.— Edited by J. Matthias Starck and R. E. Ricklefs. 1998. Oxford University Press, Oxford. v + 441 pp., 177 figures. ISBN 0-19-510608-3. Cloth, $70.00.—This book is the latest in the long and rich history of seminal articles, symposia, and authoritative reviews on the subject of avian eggs and growth and development of avian embryos. The pioneering work of Portmunn, Nice, Hamburger, Romanoff, and other more recent treatments (Carey 1980, Seymour 1984, Metcalfe et al. 1987, Deeming and Ferguson 1991) published on this subject may serve as a useful background for understanding the foundation on which this book was written. Reading these other books first may be a necessary prerequisite for beginning graduate students or ornithologists/developmental biologists