

Anatomy and Systematics of the Confuciusornithidae (Theropoda: Aves) from the Late Mesozoic of Northeastern China

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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 stillemerging 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 Cre-

taceous 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).

Downloaded From: https://bioone.org/journals/The-Auk on 26 Aug 2024 Terms of Use: https://bioone.org/terms-of-use 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 papera 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 extraor-dinarily 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.*

LITERATURE CITED

- BURKE, A. C., AND A. FEDUCCIA. 1997. Developmental patterns and the identification of homologies in the avian hand. Science 278:666–668.
- CLARK, J. M, M. A. NORELL, AND L. M. CHIAPPE. 1999. An oviraptorid skeleton from the Late Cretaceous of Ukhaa Tolgod, Mongolia, preserved in an avianlike brooding position over an oviraptorid nest. American Museum Novitates 3265:1–36.
- FEDUCCIA, A. 1999. The origin and evolution of birds, 2nd. ed. Yale University Press, New Haven, Connecticut.
- HINCHLIFFE, J. R. 1985. "One, two, three" or "two, three, four": An embryologist's view of the homologies of the digits and carpus of modern birds. Pages 141–147 *in* The beginnings of birds

(M. K. Hecht et al., Eds.). Freunde des Jura-Museum, Eichstätt, Germany.

- HOLMGREN, N. 1955. Studies on the phylogeny of birds. Acta Zoologica 36:243-328.
- HOU, L.-H., L. D. MARTIN, Z. ZHOU, AND A. FEDUC-CIA. 1996. Early adaptive radiation of birds: Evidence from fossils from northeastern China. Science 274:1164–1167.
- HOU, L.-H., L. D. MARTIN, Z. ZHOU, A. FEDUCCIA, AND F. ZHANG. 1999. A diapsid skull in a new species of the primitive bird *Confuciusornis*. Nature 399:679–682.
- JI, Q., L. M. CHIAPPE, AND S.-A. JI. 1999. A new late Mesozoic confuciusornithid bird from China. Journal of Vertebtrate Paleontology 19:1-7.
- OSTROM, J. H. 1976. Some hypothetical anatomical stages in the evolution of avian flight. Smithsonian Contributions to Paleobiology 27:1–21.
- PADIAN, K., AND L. M. CHIAPPE. 1998. On the origin of birds and their flight. Scientific American 278(2):38-47.
- SANZ, J. L, L. M. CHIAPPE, B. P. PÉREZ-MORENO, A. D. BUSCALIONI, J. J. MORATALLA, F. ORTEGA, AND F. J. POYATO-ARIZA. 1996. An early Cretaceous bird from Spain and its implications for the evolution of avian flight. Nature 382:442-445.
- VAZQUEZ, J. R. 1992. Functional osteology of the avian wrist and the evolution of flapping flight. Journal of Morphology 21:259–268.
- WAGNER, G. P., AND J. A. GAUTHIER. 1999. 1,2,3 = 2,3,4: A solution to the problem of the homology of the digits of the avian hand. Proceedings of the National Academy of Sciences USA 96:5111–5116.

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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

who do not have the background with which to understand some of the sophisticated approaches employed in this book. Although this book should be present on the shelves of every academic library, it is unlikely to appeal to all but the most enthusiastic students of avian egg/embryo biology.

This book focuses on patterns of development throughout the altricial-precocial spectrum. In this regard, comparative biologists who use the development of the chicken embryo to represent patterns of development in all birds might be in for a surprise. The contributions of the editors, who are authors on 9 of the 17 chapters, present many of the freshest ideas and novel analyses that most represent significant advances over previous volumes. Their chapters cover embryonic growth and development, structural variants and invariants in avian development, comparative analyses of and internal constraints on growth, developmental plasticity, models of avian development, and the evolution of avian developmental modes, as well as patterns of development throughout the altricial-precocial spectrum. New approaches found in these chapters include the development of a new measurement (lean body mass of hatchlings) used in classifying various taxonomic groups along the altricial/precocial spectrum, and the construction of various predictive models. Readers must be armed, however, with a thorough knowledge of statistics and principal components analysis to understand these chapters fully.

The other chapters deal with topics that have been frequently reviewed in the past (ontogeny of thermoregulation, energy metabolism and gas exchange, endocrinology) or with new topics that have not been addressed in the avian egg/embryo forum before (immunology and development of locomotion). However, even in the chapters that cover familiar ground, particularly those by Carol Vleck and Terry Bucher on metabolism, gas exchange, and ventilation, the authors find new issues to cover.

Even without its other contributions, the thorough coverage of the literature, complete list of citations, and plethora of tables make the book a valuable reference. It is an outstanding contribution to the literature on growth and development and will serve as a standard in its field for years to come.—CYNTHIA CAREY, Department of Environmental, Population and Organismic Biology, University of Colorado, Boulder, Colorado 80309, USA.

LITERATURE CITED

- CAREY, C. (Ed.). 1980. Physiology of the avian egg. American Zoologist 20:1-484.
- DEEMING, D. C., AND M. W. J. FERGUSON (Eds.). 1991. Egg incubation: Its effects on embryonic development in birds and reptiles. Cambridge University Press, Cambridge, United Kingdom.
- METCALFE, J., M. K. STOCK AND R. L. INGERMANN

(Eds.). 1987. Development of the avian embryo. Journal of Experimental Zoology (Supplement) 1:1-376.

SEYMOUR, R. (Ed.). 1984. Respiration and metabolism of embryonic vertebrates. Dr. W. Junk Publishers, Dordrecht, The Netherlands.

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Rails: A Guide to the Rails, Crakes, Gallinules and Coots of the World.—Barry Taylor. 1998. Yale University Press, New Haven, Connecticut. 600 pp., 43 color plates, 15 text figures. ISBN 0-300-07758-0. Cloth, \$49.95.—Among the many family-level bird books that appeared in the 1990s, this is one of the best. Barry Taylor's encyclopedic knowledge of rails leaps from every page of this carefully researched book. Whatever criticisms I put forth here do little to dampen my overall enthusiasm for *Rails*, a book with small but legible print that packs more good information than any mortal could ever absorb.

With clarity, conciseness, and fairness, the introductory section covers the topics of phylogeny, classification, morphology, flightlessness, habitat, feeding, voice, behavior, breeding, movements, conservation, and extinction. Taylor presents the information objectively, unafraid of controversy where it exists, such as in the classification of rails. The new book is much more thorough than the rail chapter that Taylor wrote for the Handbook of the Birds of the World, vol. 3 (del Hoyo et al. 1996). Previous to Taylor's efforts, the last time that all rails were treated in book form was in the lavish, large-format Rails of the World by S. Dillon Ripley (1977). Except for Storrs Olson's chapter on fossil rails (which is now obsolete in parts but still very useful) and certain of the color plates by J. Fenwick Lansdowne, little need now exists for ornithologists to reach for Ripley's Rails.

The species accounts follow a standard format, furnishing 145 species of rails (133 extant, 12 extinct) with a distribution map and a text with sections on taxonomy and nomenclature, identification, voice, description, measurements, geographic variation, molt, distribution and status, movements, habitat, food and feeding, habits, social organization, social and sexual behavior, and breeding and survival. These accounts serve as a proxy for how much we know about some species (13 pages worth for *Porphyrio porphyrio* and 12 for *Gallinula chloropus*, for example) and how little we know about others, such as less than one page for the historically extinct *Porzana monasa* or for the extant *Rallina leucospila*.

The distribution maps are very useful but would be even more so with the addition of place names. This is especially true for the widespread oceanic species *Gallirallus philippensis, Porzana tabuensis,* and *P. porphyrio.* Most of the maps are fairly accurate, although for *P. porphyrio,* southern Tonga (Tongatapu, 'Eua) and nearly all of the Solomon Islands are erroneously excluded from the range. The map for *Porzana tabuensis* also has inaccuracies. I would add, however, that Taylor's accounts of these three difficult species are outstanding and by far the most useful ever written.

The color plates by Ber van Perlo are generally accurate and artistically gratifying. Multiple depictions for most species cover much of the variation due to age, sex, or geography. Some of the birds are too pale; the colors should be more saturated in, for example, various species of *Gallirallus* and *Porzana* (plates 14 and 28). A few other plates are too red. The soft-part colors are inaccurate for some poorly known species, such as for both species of *Nesoclopeus* (plate 11).

Extinction is no small topic when discussing rails; if not for anthropogenic extinction, more species of rails would be alive today than of any other family of birds. Taylor discusses extinction of island rails thoroughly, reviewing even some of the massive amount of extinction that took place prehistorically on oceanic islands. This sets his book apart from most modern treatments of avian biogeography, which ignore human-caused extinctions that occurred before 1600.

Because of their secretive habits, many species of rails are difficult to detect and therefore difficult to survey. Large-scale population estimates are simply unavailable and unrealistic to attempt for most species. Thus, the conservation status is highly speculative for many, perhaps most, species of rails. On average, Taylor does a much better job than many conservationists in not crying wolf about species whose status is, in fact, either poorly known or simply not qualified for the subjective classification "endangered." An exception would be Nesoclopeus woodfordi, which he calls "globally ENDANGERED and possibly close to extinction" (p. 230) in spite of being "locally common" (p. 231) on the large island of Isabel. During my field work on Isabel in 1997, N. woodfordi was common in riverine forest and was well known to local people. It is not close to extinction.

To continue with *Nesoclopeus*, I was disappointed to see that Taylor repeated the oft-made but illogical claim that *N. woodfordi* of the Solomon Islands and *N. poecilopterus* of Fiji form a "superspecies" and may even be conspecific. These two flightless species are distinct from each other morphologically, and they live on islands that are separated by 2,200 km of deep ocean. Just as untenable is suggesting superspecies status for *P. monasa* and *P. atra* (p. 422), two flightless species that are isolated by 6,000 km of deep ocean and hundreds of intervening islands.

Among my minor quibbles, unavoidable in a work

as extensive as Taylor's, are using "eruptive" rather than "irruptive" (p. 37), "classed" rather than "classified" (p. 349), and various misspelled island names (p. 361). Pettiness aside, *Rails* is a book that will never be far from my reach. Barry Taylor has set a very high standard for future family-level bird books.—DAVID W. STEADMAN, *Florida Museum of Natural History, Uni*versity of Florida, Gainesville, Florida 32611, USA.

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The Directory of Australian Birds. Passeriformes: A Taxonomic and Zoogeographic Atlas of the Biodiversity of Birds in Australia and its Territories.-R. Schodde and I. J. Mason. 1999. CSIRO Publishing, Canberra, Australia. x + 851 pp., numerous text figures. ISBN 0-643-06457-7. Cloth, AUS \$180.00 (available from <sales@publish,csiro.an>).—Assessment of the species-level taxa of Australian birds has been a major problem ever since the publication in the early part of this century of the many volumes of The Birds of Australia by G. M. Mathews, A predominant difficulty has been the location of the largest collections of Australian birds, including most of the type specimens, in European and North American museums. For several decades, Richard Schodde and Ian Mason have built up the largest current Australian collection of Australian birds with excellent label data at CSIRO-Wildlife in Canberra. They have used this material as the foundation for a review of the species taxa of this avifauna. In addition, Schodde has examined the important collections of Australian birds in overseas museums, paying particular attention to the type specimens in to clarify the nomenclature of these birds. The results of this enormous labor on the passerines of Australia are presented in this volume.

The species taxa recognized in this treatment are based on the biological species concept, and this volume includes a discussion of the advantages of this species concept and the species taxa based on it. However, because this treatment of Australian passerines is also intended for use by general biologists, conservation managers, bird watchers, and interested lay persons, the authors felt that a general term for the basic units of Australian avian biodiversity was needed. This need is not well served by the phylogenetic species concept that would result in species taxa with widely different properties. Hence, the concept of the ultrataxon-a neutral grouping-was proposed to delimit the geographic units, generally subspecies, within species-level taxa. Use of the term "ultrataxon" is equivalent to the legal definition of "species" in some laws such as the U.S. Endangered Species Act, and it avoids all of the problems and shortcomings associated with species taxa under the phylogenetic species concept.

The area covered is Australia and its territories (e.g. Norfolk and Lord Howe Islands), and extends to Christmas, Cocos, Macquarie, and Heard islands, as well as the Australian Antarctic Territories. Accepted vagrants are treated briefly in a supplementary list covering only the Australian region.

Each species taxon description begins on a new page and, for each, the ultrataxa (subspecies) are presented with a brief description of each with a standard map showing its breeding range and zones of intergradation, if any. Species taxa, whether monotypic or polytypic, are not described. Synonymies for species-group names are not given. Other discussion is brief and often includes taxonomic (including comments on the genus, the species, and ultrataxa) and nomenclature circumscriptions. Because of an ingenious scheme for subdividing Australia into geographic regions and subregions, and using acronyms for habitats (see p. 9), the included information for each species and the ultrataxa is immense. When combined with the detailed citations, this organization provides the reader with full information of the biodiversity and distribution of Australia's passerines. A number of new subspecies is described: these are clearly noted in the text and are listed in Chapter 4 with all other taxonomic changes proposed in this work. Families are introduced on a blue background that makes the start of each family easy to spot simply by looking at the edge of the volume. Each family is delimited and the genera rather briefly discussed. Authors and dates for generic names are not given, nor are generic-group synonymies included.

The same map of Australia, with state boundaries, cities, river systems, mountain ranges, and deserts, is presented on the front and back end pages. Additional maps (fig. 1, p. 9) showing geographic regions and subregions, and historic geographic barriers (fig. 2, p. 787), together with acronyms of habitat types, are provided. Extensive glossaries (27 pp.) for geographic, taxonomic, biological, etc., terms are provided, as is a large bibliography (23 pp.) as well as complete indices of scientific and common names (16 pp.). Although information about the diversity and distribution of Australian birds in this volume is terse, every effort was made by the authors to insure that users can find it.

The scheme followed in this volume allows the presentation of each ultrataxon in a clear and unambiguous way regardless of different opinions on the taxonomic status of the taxon. Hence, the endangered Black-eared Miner, often considered a separate species, is included here as the ultrataxon *Manorina flavigula melanotis* (p. 270), with a full discussion of the evidence supporting or refuting the advocated taxonomic position. In a similar manner, the Varied Sittella (*Daphoenositta chrysoptera*; p. 428) is treated as a complex of five ultrataxa in a single species rather than five separate species, again with a full discussion of the evidence, in this case, supporting the decision. In this way, the 720 ultrataxa of Australian perching birds are clearly and consistently arranged in 340 species taxa corresponding to the biological species concept such that the information is available and useful to a diversity of ornithologists from the pure systematist to the practical conservation manager.

This initial volume of The Directory of Australian Birds is one of the most important works to be published in a number of decades on the diversity and distribution of a continental avifauna. It is certainly the most important such work to appear for Australian birds. Although an outstanding significant reference work for anyone with the slightest interest in the Australian avifauna, I can recommend it to everyone from bird watchers and conservation specialists to scientific ornithologists in all fields as the baseline for the systematics and distribution of Australian passerines. Richard Schodde and Ian Mason are to be congratulated for their several decades of hard work collecting the data needed to write this volume and for producing such an outstanding work. All ornithologists can look forward with anticipation and pleasure to the appearance of the promised two additional books in this series.-WAL-TER J. BOCK, Department of Biological Sciences, Columbia University, 1200 Amsterdam Avenue, New York, New York 10027, USA.

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Restoring North America's Wild Birds: Lessons from Landscape Ecology.—Robert A. Askins. 1999. Yale University Press, New Haven, Connecticut. ISBN 0-300-07967-2. Paper, \$30.00.—Anyone questioning why wild birds are "flagships for conservation" will find their answers in this wonderful book. Robert Askins' eyes-wide-open approach to the task set forth in the title is utterly engaging, and, although clearly for people with avian affinities, it is especially relevant for conservation biologists from all walks of life.

Reading Askins' book was like being a student in a field course! In the first nine chapters (of a total of 10), I romped through the major biomes and habitats of North America, looking at each through the eyes of an experienced and impassioned naturalist-ornithologist. In each chapter, Askins focuses on a region's bird species and communities that are declining, at risk of decline or extinction, or are already extinct. Then, he sys-

tematically employs foreshadowing to prepare readers for the central lesson that "Conservation of birds depends on a clear understanding of both their habitat requirements and how their habitats are sustained." To convey the complexities of this truth, Askins builds each focal ecosystem step by step, attending to historical generative processes (biotic and abiotic), presettlement distributions and species composition of the vegetation, as well as key requirements of the bird species at risk. Then, using copious scientific results woven into a pleasing format, Askins explains what features of the system are needed to maintain species at risk, and, in turn, how these features are generated and maintained. Chapter conclusions extend understanding of processes that maintain the habitat in the condition and at the scale needed by the species at risk, to what it will take to protect those processes.

For me, two aspects of Restoring North America's Wild Birds were especially valuable. First, the book destroys certain myths that hinder intelligent bird conservation. The media hype that Neotropical migrants (e.g. wood-warblers) are the only North American songbirds at risk has clouded our professional recognition of other systems in need of scientific study and crisis management, such as grasslands and eastern shrublands. For example, many of us uncritically accept the common perception that the current decline of birds that are characteristic of eastern thickets (e.g. Yellow-breasted Chat [Icteria virens], Brown Thrasher [Toxostoma rufum], Painted Bunting [Passerina ciris]) is not a crisis. If we assume that the eastern seaboard was once a seamless blanket of deciduous forest, we might not opt to manage habitats for those species that enjoyed ephemeral old fields. But Askins lucidly explains how shrublands must have been extensive along the hurricane-battered coasts and oft-flooded riverine corridors in coastal lowlands before European settlement. He points out that coastal and river margins in the East were densely settled before we began accounting for the distributions of shrublands we destroyed, thus challenging the dogma that shrubland birds don't belong in the East owing to their lack of historic existence there.

Second, Askins examines without bias modern human influences on ecosystems and species, therefore encouraging the intellectual means to understand where and how we can fit into a continental scheme of conservation. For example, now that coastal and riverine shrublands are scant in the East, inland oldfield communities and some suburban ecosystems serve as refugia for the displaced thicket birds. Askins argues that these habitats should be recognized in regional conservation planning for their ecological roles. Furthermore, the question has been raised as to whether livestock grazing is good or bad for grassland birds. Askins explains how grazing can be both, depending on the nature and history of the ecosystem and the likelihood of its conversion to more de-

structive land uses. Birds of short-, mixed-, and tallgrass prairie (e.g. Mountain Plover [Charadrius montanus]. Dickcissel [Spiza americana]. longspurs [Calcarius spp.]) historically coexisted with large-bodied grazers, and they currently exhibit adaptations that facilitate coexistence with cattle. Vast areas of grazing lands, therefore, can help maintain some of the continental grassland bird assemblage. Conversely, bird species of the drier deserts, semidesert grasslands, and wooded streamsides cannot tolerate cattle grazing because cattle destroy the habitat itself. Askins argues that, although not a perfect mimic of native herbivory, contemporary cattle grazing represents a tolerable alternative to crop conversion or human settlement for many grassland areas. This means that rural livelihoods can be appropriately fostered in large-scale conservation planning that can cope with regional differences in ecology.

What are the "Lessons from Landscape Ecology"? Each chapter communicates essential concepts of landscape ecology as part of the "story" of how each system works. For example, the importance of geomorphology and spatiotemporal disturbance regimes in guiding the historic development of ecosystems is featured in every chapter. Askins does not solve all of the mysteries of historic bird distributions, and he does not hold back his opinion when facts are insufficient. But logic is pervasive in his historical scenarios. The shifting mosaic of community structure is an obvious concept once we understand how grassland bird assemblages respond to fire and the spatial dynamics of prairie dog "grazing lawns." The enormity of spatial scales relevant to bird conservation and the nature of biological connectedness are inherent in our thinking once we understand where Phainopeplas (Phainopepla nitens) spend most of their time in a typical year. When we know the natural history of Red-cockaded Woodpeckers (Picoides borealis), crossbills (Loxia spp.), Brown-headed Cowbirds (Molothrus ater), and the intimacy between pinyon pine and Pinyon Jays (Gymnorhinus cyanocephalus), the evolutionary link between scale, process, and the birth and sustenance of wildlife-habitat relationships becomes tangible. Unlike a textbook, Restoring North America's Wild Birds educates the reader in much the same way as an elaborate and intensive field course in landscape ecology.

The title of the final chapter suggests that the pieces comprising the conceptual framework of landscape ecology, enchantingly explored in preceding chapters, would be riveted together here into more specific guidelines for protecting processes that sustain bird habitats. Instead, the concluding chapter was more general than I expected, beginning with another case study (the Ivory-billed Woodpecker's [*Campephilus principalis*] demise) to emphasize a basic principle: that the central cause of extinction is loss of large areas of functioning habitat. Arguably, we don't need a new discipline to understand this point! Askins moves on to general themes of restoration, leaving the reader with a practical vision of "cooperative management." The idea here is that if thinking based on landscape ecology is integrated with human dimensions (e.g. land use economics and policies), we can restore the complex weave of natural landscapes that comprise functioning ecosystems that support our (beloved) native species.

This book is appropriate for all readers with an interest in conservation and/or birds, but the conservation angle is emphasized as the main strength. Because birds are better known biologically than other organisms, a work with similar depth and breadth in community and landscape ecology could not have featured any other taxon. Conservationists dealing with planning at any spatial scale (local, regional, ecosystem management, national, etc.) will find here the kind of insights that spark good ideas for managing ecological communities to favor native species. Although the book is not a procedural manual for conservation, it is clearly more applicable than merely heuristic. I would use this book as recommended reading in undergraduate Landscape Ecology, Conservation Biology, Biogeography, and Wildlife Ecology courses, and as required reading in Avian Ecology and Conservation courses. I will extract parts of it for lectures in my own courses because of its extensive incorporation of scientific findings with relevance to conservation. The book would benefit from an index of concepts (there are taxonomic appendices, chapter notes, and references) to make it more useful in college courses. Ample visuals accentuate the readability; excellent line drawings by Julie Zickefoose and many good photographs enhance the text on most pages, and pithy quotes appear with each chapter heading. Restoring North America's Wild Birds should be available in every kind of library because its relevance to conservation crosses all societal boundaries.--KATHRYN E. SIEVING, Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, Florida 32611, USA.

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Wetland Birds: Habitat Resources and Conservation Implications.—Milton W. Weller. 1999. Cambridge University Press, New York. xv + 277 pp. ISBN 0-521-63326-5. Cloth, \$74.95. ISBN 0-521-63362-1. Paper, \$32.95.—They are hidden amid the Great Plains, and each spring they awaken from their winter slumber. Life of all forms flourishes within their still waters: stalks of *Typha* and *Scirpus* rise en masse to transform a sea of brown into a carpet of green; larval damselflies and dragonflies crawl to the

water's edge and cast off their shells to become creatures of the air. Predatory mink and giant waterbugs prowl above and below the water's surface. And each spring they are home to the great flocks of migratory birds, many of which will settle in to raise their families. They are, of course, the prairie wetlands, and they rank among the most productive habitats on the face of the earth.

As Milton Weller outlines in *Wetland Birds*, the lifeblood of wetlands is water: it dictates seasonal plant growth and animal succession. Winter snows and spring rains fill ponds and recharge aquifers; small increases in summer temperatures accelerate evaporation, and temporary wetlands disappear while permanent ones shrink. Water control in the Florida everglades, for example, has transformed the annual cycle of seasonal flooding into semipermanent water with community-wide effects, highlighting an important problem: wetlands face the inexorable pressures of human intrusion. North America has lost half of its original wetlands to drainage, and much of the remainder is threatened; the figure is even higher in other regions of the world.

Another author writing about wetland birds might have chosen a more simplistic, taxonomic approach, but Weller, drawing upon a lifetime of experience, does not shrink from the challenge of doing justice to a complex topic. And he succeeds. The real subject of Wetland Birds is the intricate web of ecological factors that affect wetland dynamics; bird populations arise as an emergent property of these factors. Weller has done an admirable job of distilling mountains of material into easily digested chapters, 17 in all. Each is a short review of topics, including wetland types, habitat dynamics, foraging strategies, physiological adaptations, population biology, and management concerns. A reference list at the end of each chapter will allow readers access to a much larger underlying literature

The book is balanced geographically: North American work receives greater attention than other regions, but Weller draws examples from across the globe. And, as someone who has succeeded in working on wetland birds for two decades without studying ducks, the taxonomic balance in this book is welcome. Waterfowl biologists need not worry; they will have plenty to read, but unlike the philosophy of certain management agencies and conservation groups, there is more to life than anseriforms. The layout of the book is handsome, with crisp line drawings and black-and-white photographs, and in this era of upward-spiraling book costs, I would be remiss if I did not draw attention to its modest price. My criticisms of this volume are few. At the risk of being too trendy, I would have liked to see a bit more on the potential effects of global warming on wetlands. This minor item notwithstanding, I can unhesitatingly state that every wetland biologist should have a copy of Wetland Birds on his or her shelf. Were I to teach a course on wetland ecology, this book would be on the required reading list.—SCOTT FORBES, Department of Biology, University of Winnipeg, 515 Portage Avenue, Winnipeg, Manitoba R3B 2E9, Canada.

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A Birdfinder's Guide to the Rio Grande Valley.-Mark W. Lockwood, William B. McKinney, James N. Paton, and Barry R. Zimmer. 1999. American Birding Association, Colorado Springs, Colorado. viii + 280 pp., 43 maps, 5 drawings, 3 photographs. ISBN 1-878788-18-3. Paper, \$17.45.-In the 1950s and 1960s, Fisher and Peterson's Wild America and Pettingill's Bird Watcher's America stimulated us to dream about birding in exotic settings filled with unfamiliar species. Pettingill's Guide to Birdfinding East of the Mississippi, and its companion for the West, provided the information needed to undertake exploration of personal terrae incognitae, giving basic descriptions of the avifauna in each state and good birding sites around selected population centers. After Pettingill, a new era in birdfinding guides began with a series by James A. Lane that covered the nation's most popular birding destinations. The popular Lane Guides, together with refinements by Harold R. Holt (to whom the present volume is dedicated), were known for their level of detail, practicality of information, annotated lists of specialty species accompanied by advice for locating them, and occasional infusions of humor. Recently, the American Birding Association has been updating existing descendants of the Lane guides and developing new guides for additional regions. The present volume, in its third edition and relying on an entirely new cadre of authors, is a fine example of this genre.

This guide covers a larger area than might be inferred by the title, resulting in one of few criticisms I have of this otherwise well-conceived volume. Information is presented for areas along the length of the Rio Grande from the Gulf of Mexico all the way to southern New Mexico, and also for sites as distant from the Rio Grande as the Edwards Plateau. Davis and Guadalupe mountains, and Carlsbad Caverns National Park. Many birders traveling to these areas may miss out on the resources in this book simply because they assume it to be confined to areas along the lower reaches of the Rio Grande. Given the large scope of this coverage, it would have been nice to have included a bit more information on birding opportunities in nearby portions of Mexico. Site accounts in A Birder's Guide are divided into three sections: Lower Rio Grande Valley (84 pp.), Trans-Pecos Texas (including Las Cruces and Carlsbad Caverns,

New Mexico; 62 pp.), and Edwards Plateau (22 pp.). The book gradually works the reader upstream. The site accounts are very informative and well written and contain an abundance of attractive maps. Details for finding particular birds at each site are well presented, and at times, finely detailed. For instance, precise directions are provided to a nest tree used by Common Black-Hawks (*Buteogallus anthracinus*) in the Davis Mountains. The authors provide interesting tangential details about other animal and plant species that might be seen, such as endemic fishes confined to individual ponds or springs, and about historical or cultural features.

In addition to the site accounts, the book contains a wealth of supplementary information. The guide begins with a collection of introductory material describing ecological regions of Texas, seasonality, accommodations, sources of information, birding organizations, and the potential for biting insects; it would have been useful to caution visitors more emphatically about the hazardous summer heat. The section summarizing nomenclatural changes in the region's bird species since 1973 is interesting to review in its own right. After the site accounts, the usual bar charts and annotated listing of specialty species have been replaced by a complete annotated list of all the region's birds (56 pp.). This, in itself, is worth the price of the book. Also included are helpful hints regarding identification of Tropical (Tyrannus melancholicus) and Couch's (T. couchii) kingbirds and Gray-crowned (Geothlypis poliocephala) and Common (G. trichas) yellowthroats; these provide details not available in standard field guides. Additional lists are provided by Jeffrey S. Pippin for butterflies of the region and by Alan H. Chaney for nonavian vertebrates (excluding fish), both with brief distributional notes. Following a list of selected references, a few pages describe the American Birding Association and its Code of Birding Ethics and provide instructions on how to submit reports of rarities to the review committees of Texas and New Mexico, with additional lists of species for which detailed information is requested. Finally, the index contains an interesting innovation by providing a 25-line Abbreviated Table of Contents on each page that should assist the reader in finding important sections without having to navigate the overall index.

In the interest of providing as well-rounded a review as possible, I feel compelled to point out the handful of deficiencies that I could identify. The text contains occasional grammatical errors. Terminology is occasionally confusing; the word *resaca*, referring to a small body of water, is used initially without introduction, and the use of the terms "Valley," "mid-Valley," and "Lower Valley" at times seems inconsistent. Sometimes species lists are redundant. Although the annotated bird list is a bonus, its depiction of seasonal variations in abundance and of arrival dates is less detailed than when presented as a bar chart. Indeed, in the site accounts, a few seasonally restricted species are listed in a way that implies they are permanent residents, potentially misleading readers. However, these blemishes are small compared with the overall value of the book, which constitutes a fine achievement.

In summary, A Birder's Guide is a valuable information source, geared to the birding hobbyist. Any bird enthusiast who explores the region would be remiss to arrive without this guide in hand, whether looking for an introduction to the area's avifauna or searching for specialty species. In addition, those not planning to visit the area but who are interested in bird distribution patterns will find the guide worth purchasing for its annotated list. Because the book will be of interest to lay birders as well as ornithologists, it would be a nice addition to both public and academic libraries. This volume undoubtedly will enrich the visit of any bird enthusiast to the Rio Grande region, one of the most popular birdwatching destinations in North America.—PETER H. YAU-KEY, Department of Geography, University of New Orleans, New Orleans, Louisiana 70148, USA.