

Feathered Dragons: Studies on the Transition from Dinosaurs to Birds

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Reviews

EDITED BY R. TODD ENGSTROM

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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The Howard and Moore Complete Checklist of the Birds of the World, 3rd edition.—Edward C. Dickinson, Ed. 2003. Princeton University Press, Princeton, New Jersey. 1,039 pp. ISBN 0-691-11701-2. Cloth, \$69.50.—In the past half-century, ornithologists have revolutionized taxonomy and systematics, created several new species concepts, and recognized dozens of new species-level avian taxa. Yet the ornithological community has been without a scholarly and functional standard classification and checklist of the world's birds since the 15-volume Peters checklist was finished in 1974 (with half the volumes now more than 45 years old). As global communication rises exponentially, scientists and globetrotting birdwatchers have been in dire need of a standard classification to serve as the *lingua franca* of ornithology.

With publication of *The Howard and Moore Complete Checklist of the Birds of the World*, edited by E. C. Dickinson, we now have a thorough and useful book that gives a modern classification of all the world's birds, down to the subspecific level, in a single volume. Checklists produced in the interlude between Peters and Dickinson fell short for a number of reasons, including out-of-date classifications, lack of subspecific treatment, overly novel classification schemes, and partial to complete lack of references. Justifications for taxonomic treatments have been all but absent in those volumes, especially at levels other than species. Dickinson does not suffer from those drawbacks and should serve as a standard reference for bird classification for the next little while. This volume arrived at an opportune time for our work at the Florida

Museum of Natural History, as we are using a recent move into an enlarged space to install our collections in a more modern sequence. I therefore had a golden opportunity to use and review this volume.

The introduction outlines three objectives. The first is to provide a comprehensive list, which necessitated including all newly described species, whether recognized or in synonymy. Regional consultants (E. C. Dickinson for Asia, D. Pearson for Africa, J. V. Remsen, Jr., for the Americas, K. Roselaar for the Palearctic, and R. Schodde for Australasia) helped to ensure completeness. Those subregional editors have worked within or closely with continent-wide committees on avian classification (e.g. Remsen in the AOU Committee on Classification and Nomenclature and the South American Classification Committee). The second objective is to present a conservative list. Using the Peters Checklist as a foundation, the consultants accepted changes only when there had been "persuasive published reasons." The third objective is a high standard of nomenclatural accuracy. Curiously, stability was not included as an objective, though the three stated objectives all work toward that goal. The introduction also gives explanations of list sequence, species concepts, taxon recognition, scientific names, English names (thankfully not a main focus of revisions), list of references, and cut-off date for incorporation of new material (31 December 2000).

A separate introductory chapter, written by J. Cracraft, F. K. Barker, and A. Cibois from the American Museum of Natural History, gives a quick overview of higher-level phylogenetics

(above the rank of family) and the rationale for some of the novel treatments in this volume, especially the sequence of families and the non-use of taxa above family (see below).

A list of families follows. The list sequence of families generally follows some of the more recent advancements in avian higher-level systematics, while retaining some similarity to more classical schemes. Some of the changes to traditional sequences have become widely accepted in recent years (e.g. beginning the sequence within the Neoaves with Galliformes and Anseriformes), whereas others may be more difficult to get used to, and may or may not gain future acceptance. Some of the changes seem premature and out of step with the conservative objectives of the book. In their brief synopses of ordinal- and family-level systematics, Cracraft et al. provide details on the placement of more controversial taxa (e.g. Cathartidae, Phoenicopteridae) but usually do not provide justifications for sequences within orders. For example, the first family listed for the traditional Falconiformes is the Falconidae (usually placed last within that order), and Bucconidae and Galbulidae are listed after other families in the Piciformes (usually placed before). Justification for the sequence in the Falconiformes is not given, and because the order does not have a clear close relative to serve as an outgroup, establishing the basal branching pattern is highly speculative. A more conservative approach would have been to keep the traditional sequence. In their explanation of the taxonomy of the Pici (Piciformes and relatives), Cracraft et al. state that there are two clear taxa (toucan plus barbets and honeyguides plus picids) and that Galbulidae may be more closely related to the Coraciiformes. The Bucconidae are not mentioned in their synopsis. A conservative sequence would thus be similar to traditional sequences (Galbulidae, Bucconidae, Ramphastidae, Indicatoridae, Picidae), but the family sequence they present (Ramphastidae, Indicatoridae, Picidae, Galbulidae, Bucconidae) appears to lack support and has little hope of long-term stability. A more egregious veering away from the traditional sequence makes little sense: the New World suboscine passerines consist of two related groups of families, the furnariid group (roughly Furnariidae–Dendrocolaptidae–Thamnophilidae–Formicariidae–Rhinocryptidae–Conopophagidae) and the tyrannid

group (Tyrannidae–Pipridae–Cotingidae). With a two-taxon statement, it does not matter which group is first; thus, the traditional sequence with the furnariid group first could have been preserved. Instead, Cracraft et al. begin with the tyrannid group of families.

The main list follows. The author and date are given for each genus, species, and subspecies. I loudly applaud the inclusion of full citations for all taxa described since the Peters Checklist; these are given in the list of references. Each genus includes its gender, which should help describers of new taxa. Each species has an English name, and, if monotypic, its distribution is given. If a species has multiple subspecies, distributions are described briefly. All stated distributions are highly abbreviated, and almost always are given in political units. For large units (e.g. Mexico, California) the distributions are excessively abbreviated; for example, the distributions of four subspecies of *Melospiza melodia* are “coastal [entral] California,” but there was ample space to put, for example, “N San Francisco Bay.” Nevertheless, abbreviation pays off in having everything fit into a tight volume. Between 25 and 45 terminal taxa (subspecies and monotypic species) are included per page. The copious comments are footnoted (up to 22 per page), which include standard author and date citations. Full citations (2,739 of them) are in the list of references at the end of the list. Taxonomic names are completely indexed, so that genus and species are given for each sub-specific name.

I found the decision not to include taxa above family level a major disappointment in the checklist. Thus, you will not find mention of such well-established higher taxa as Passeriformes, Anseriformes, Galliformes, Falconiformes, Strigiformes, and Procellariiformes. The families that compose these and most other orders are well known, though the relations among orders are still far from clear. Cracraft et al. explain in the introductory chapter on the subject that higher-level relationships among birds “are still clouded with uncertainties.” However, what taxonomic level is not clouded by such uncertainties? Though Cracraft et al. spell out many of the better-documented higher-level relationships in their introductory chapter, the checklist should have used an ordinal-level classification.

With such a large, data-rich volume, it is not hard to find minor problems and quibbles with

the text; I will mention just a few. Distribution errors are especially numerous. For example, the distributions for the monarchids *Neolalage banksiana* and *Clytorhynchus pachycephaloides griseus* are both given as the Banks Islands, within Vanuatu, when in fact both taxa are distributed throughout the Vanuatu archipelago. In the distribution of the fantail *Rhipidura rufifrons*, the large islands of Chousieul and Santa Ysabel (= Isabel) in the Solomon Islands are missing; they are inhabited by *R. r. commoda*. Dickinson follows the ridiculous lumping of the flightless rail *Nesoclopeus woodfordi* of the Solomon Islands into the equally flightless *N. poecilopterus* of Fiji, though thousands of kilometers and several very deep ocean trenches separate the two taxa. In splitting up what was the world's most geographically variable species (*Pachycephala pectoralis*), one of the eight resulting species (citing personal communication from R. Schodde, but not keeping to the goal of "persuasive published reasons") is given the English name New Caledonian Whistler, even though it also occurs in Vanuatu. Dickinson neglects to cite T. A. Parker (1982, *Wilson Bulletin* 94:484) for discovering that the recently described antbird *Percnostola macrolopha* Berlioz, 1966, was actually the female of *P. lophotes*. Dickinson does not provide justification for retaining North American parids in *Parus* instead of placing them in *Poecile* (chickadees) or *Baeolophus* (titmice). In general, Dickinson closely follows the classification presented in the seventh edition of the AOU *Check-list of North American Birds*, which recognized *Poecile* and *Baeolophus*.

The sheer volume of molecular systematics papers nowadays is rocking the boat of avian classification and will, no doubt, cast asunder much of current taxonomy and classification in the future. Workable classifications and checklists will have to be able to adapt to new arrangements as published evidence becomes available, but also will have to retain some stability to be useful. The only way to do this is to be thorough, be conservative in changes, and provide justification and citations for taxonomic treatments. Dickinson has set a high standard for how checklists should be written. I hope to see future editions in a similar style.—ANDREW W. KRATTER. *Florida Museum of Natural History, P.O. Box 117800, University of Florida, Gainesville, Florida, 32611, USA. E-mail: kratter@flmnh.ufl.edu*

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Feathered Dragons: Studies on the Transition from Dinosaurs to Birds.—Philip J. Currie, Eva B. Koppelhus, Martin A. Shugar, and Joanna L. Wright, Eds. 2004. Indiana University Press, Bloomington. xiii + 361 pp. ISBN 0-253-34373-9. Cloth, \$49.95.—The discovery in 1993, in Upper Cretaceous sediments in Montana, of a remarkably complete skeleton of a subadult birdlike dinosaur, *Bambiraptor feinbergi* (Burnham et al. 1997, 2000), prompted Martin Shugar to organize the Florida Symposium on Dinosaur–Bird Evolution, an international event held on 7 and 8 April 2000 in Fort Lauderdale. The guest of honor was John Ostrom, the Yale paleontologist whose work initiated the current resurgence—now in its fourth decade—of interest in the origin of birds. *Bambiraptor feinbergi* was on display at the meeting, along with some new fossils from China. Most of the papers in this volume were presented orally at that meeting.

The book has a section of fanciful color plates of drawings of dinosaurs that suit the book's flamboyant title, but the text has a serious scientific intent. Even so, nearly every chapter repeats the mantra of the birds-are-dinosaurs movement, and the foreword assures the reader that, because the "level of controversy over bird origins has waned" (p. xii), attention can now turn to other issues, such as the evolution of feathers and flight. In general, the book reflects the heady enthusiasm of the many paleontologists and systematists in the 1990s who were interpreting the wonderful new fossil discoveries in Early Cretaceous deposits in China and elsewhere as increasing support for the view that birds evolved from certain maniraptoran theropod dinosaurs (troodontids and dromaeosaurs).

After an introductory tribute by Robert Bakker to Edward Hitchcock's mid-19th-century studies of dinosaur footprints found in the Connecticut Valley redbeds, the 14 chapters that report original work are organized into three sections: two on the setting; six on osteology and ichnology (tracks); and six on

eggs, nests, feathers, and flight. Dale Russell compares dinosaur assemblages of central Asia and North America, emphasizing the importance of the many specimens of well-preserved small birdlike dinosaurs found in the dune fields of Mongolia, a region that was isolated in the Late Cretaceous period. Most relevant for the subject of this book are the oviraptorosaurs (*Oviraptor*), troodontids (*Saurornithoides*), and dromaeosaurs (*Velociraptor*), plus two primitive “theropod-mimic” birds (*Mononykus* and *Shuvuuia*). Russell reminds readers that we do not know the biogeographic origin of birds, or theropods, or dinosaurs. In Chapter 2, Gregory Retallack argues that large-scale acidification was the most direct cause of the selective extinctions of animals and plants that occurred 65 million years ago, after the now-famous meteorite impact that marked the transition from the Cretaceous to the Tertiary period, taking with it all the dinosaurs, the enantiornithine birds, and many other taxa.

The section on osteology and ichnology begins with David Burnham’s formal description of the virtually complete skull and postcranium of the holotype of *Bambiraptor feinbergi*, based on the individual bones; the description is supplemented with photographs of the skull and drawings of most of the bones. Additional study has suggested that this dromaeosaurid is less velociraptorine than stated here (Senter et al. 2004). The forelimb is very similar to that of *Archaeopteryx*, but there is no discussion of whether *Bambiraptor* may indeed have been a bird.

The next three papers describe new details of specimens from Canada and Mongolia. Then Fernando Novas, without suggesting that *Unenlagia* might be a bird, argues that its ilium is even more birdlike than that of dromaeosaurids, and Joanna Wright reviews information about the birdlike features of dinosaur footprints. Overall, this section adds new information about the birdlike osteology of various maniraptorans.

Section 3 begins with an important paper by Gerald Grellet-Tinner and Luis Chiappe that compares the microstructures of eggs and the nesting behaviors of turtles, crocodylians, dinosaurs, and birds. Like birds, troodontids and oviraptorids laid eggs at daily intervals in open nests (not covered by substrate). Like birds, they had asymmetrical eggs with

at least two eggshell layers separated by an aprismatic delimitation. David Varricchio and Frankie Jackson add details to information about *Troodon* and argue that, because delayed incubation and brooding behavior must have synchronized the hatching of eggs, the body temperature of the adult must have at least temporarily surpassed that of the environment. The argument by Thomas Hopp and Mark Orsen in Chapter 11 that brooding behavior selected for the evolution of long flight feathers is supported only by some drawings of birds in unnatural poses. Contrary to Ostrom, Sankar Chatterjee and R. J. Templin consider the cursorial model for the origin of flight to be biomechanically untenable. They construct a thesis that involves the theropod origin of birds and the arboreal origin of flight and support it by putting the new Chinese fossils in an order that fits that scenario.

The most ornithological paper in the book is the detailed analysis of the plumage of *Archaeopteryx* by Peter Wellnhofer, confirming that *Archaeopteryx* was a true bird. It had an especially avian ulnar abduction in the wrist, was adapted for powered and active flight, and—except for the feathered tail—had modern avian plumage in every detail. *Caudipteryx*, with its short forelimb and modern feathers, living at least 25 million years after *Archaeopteryx*, is more controversial. It has been called a dinosaur, but it has many characteristics of a flightless bird. Wellnhofer remarks that the “protofeathers” of several other fossil taxa from China are also present in pterosaurs and “it could be that these filamentous structures of the integument have nothing to do with protofeathers at all” (p. 294). Note also that ichthyosaur integumental fibers conform to dromaeosaur protofeathers (Lingham-Soliar 2003). The final chapter by Robert Bakker and Gary Bir is not ornithological. It attempts to characterize the predatory behavior of three genera of large predaceous dinosaurs from the distribution of their shed teeth at Como Bluff, Wyoming.

Most authors in this book have taken the birds-are-dinosaurs paradigm as a given, dismissing alternatives in Kuhnian fashion, but ornithologists should be more cautious. They know that 35 families of modern birds include taxa that are flightless, and that flightless birds can get very large. At least one group of

“dinosaurs,” the oviraptorosaurs, is now recognized as flightless birds (Lü 2000, Maryanska et al. 2002). No wonder they have birdlike eggshells and brooding behavior! If several different groups of early birds evolved flightlessness, deciphering the origin of birds from the fossil evidence is going to require more ornithological expertise and skepticism than is apparent in this book or several other recent books on this subject. Some of the papers here are not relevant to ornithology. Others may be more relevant to ornithology than their authors thought.—FRANCES C. JAMES AND JOHN A. POURTLESS IV, *Department of Biological Science, Florida State University, Tallahassee, Florida, 32306, USA. E-mail: james@bio.fsu.edu.*

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A Concise History of Ornithology.—Michael Walters. 2003. Yale University Press, New Haven, Connecticut. 255 pp., numerous black-and-white illustrations. ISBN 0-300-09073-0. Cloth, \$32.50.—Although the dust jacket describes this book as a history of ornithology from the ancient Chinese, Greeks, and Romans to the present, the book falls a little short of the present—much like every history class I ever had. To some extent, this is understandable. So many aspects of our understanding of history come only after a proper period of “digestion”; it is often premature to place the contributions of living individuals into the context of history; and ornithology, like so many sciences, has grown tremendously in the past century. With what I sense as a bit of frustration, Walters capitulated (p. 10): “The volume of ornithological literature has become overwhelming, and the number of individuals working on the subject has increased to the extent that a comprehensive survey of the subject in the 20th century is beyond the scope of this book.”

Walters has produced a very readable, fascinating glimpse of ornithological history that follows the timeline of discovery and the threads of guesswork, scientific endeavor, and controversy that have led to our current understanding of bird classification. I was initially disappointed that the book does not begin with depictions of birds in cave art or the uses of birds by early man, that it does not mention the importance of the writings of Xenophon (5th century B.C.) in documenting the presence of ostriches in Asia Minor and the use of incubators by early Egyptians. But this is not a history of birds, nor even a history of our knowledge or use of birds. It is a history of the practice of the science of ornithological classification, with a few other things ornithological incidentally woven in. Perhaps the major focus on classification should have been included in the title. In 10 chapters, following both chronological and geographic sequences, Walters details the growth of our understanding of the interrelationships among birds and our efforts to find meaning in

the diversity of birds through various schemes of classification. The reading is considerably spiced by tidbits of personal lives: personalities, professional feuds, triumphs, and tragedies. For example, we learn (p. 67) that George Montagu (1751–1815) devoted his life to natural history after he left his wife, moved in with an already married woman, and was court-martialed and forced from the military. Far from detracting from the “facts,” such trivia show the human side of ornithological endeavor.

Walters’ opinions of the contributions of ornithologists are often strong and sometimes at variance with those held by others. In contrast to the favorable treatment given John Gould (1804–1881) by Stresemann (1975), Walters is ruthless in belittling Gould’s efforts. He suggests (p. 130) that Gould “probably lacked the ability to understand the significance of speciation” and that those species described by Gould that “proved valid were probably arrived at fortuitously rather than [through] perspicacity on his part.” Noting that Gould’s collector, John Gilbert, was murdered by aborigines in Australia, Walters comments (p. 131): “Callous and calculating as ever, Gould saw Gilbert’s death merely as a loss of a source of material and revenue.” This latter sentiment was shared by Mearns and Mearns (1998), and Tree (1991) supports Walters’ assessment of Gould’s use and abuse of others in satisfying his ambitions.

We also learn (p. 152) that American ornithologist Elliott Coues (1842–1899) “was outspoken and many found him antagonizing.” Mearns and Mearns (1988) also mentioned these traits. Walters speculates that this is probably why Coues “never obtained from [Spencer Fullerton] Baird the official position at the Smithsonian which he had coveted.”

Language used to describe favored personalities also contributes life to this history. Richard Bowdler Sharpe (1847–1909) is said (p. 156) to have “moved the collections [of the British Museum] from a fusty basement, to which no sane ornithologist would wish to go, into a temple where it was, if not exactly a pleasure, at least bearable to work.” We are also told that Sharpe had ten daughters.

The fabric of this history is frayed toward the end, stopping short of the 20th century with discussion of the early rejection of trinomials, their slow acceptance in Europe, and a strong American influence in their acceptance. In a

deviation from matters of classification, Walters adds a bit of commentary on the history of bird banding and lack of knowledge of the causes of migration. As somewhat of a “patch” and bridge to the future, a concluding chapter by John Coulson, “Ornithology and Ornithologists in the Twentieth Century,” identifies some ornithologists and elements pivotal in the growth of ornithology in the past century.

Thirty numbered appendices present 29 classifications of the birds of the world presented by “ornithologists” ranging chronologically from Walter Charleton (1668) to Hans Gadow (1892). Much of the focus of the text concerning these individuals is elaboration of characteristics and influences associated with these classifications, but annotation of the classifications in the appendices is limited. Two lettered appendices provide (without explanation) a list of birds from Emperor Rudolph II’s collection and a list of birds described by “Quoy & Gaimard on Freycinet’s Voyage 1817–1820.”

Although this “concise history” chronicles the development of our understanding of the interrelationships among birds, the threads of other ornithological matters are sparse and broken. No doubt, this is a combined function of the past focal points of scientific interest, available information, and the inclination of the weaver.

I thoroughly enjoyed reading *A Concise History of Ornithology*, but was also frustrated. The index includes only the names of people mentioned, and I found myself creating my own subject index for future reference. Even the index of names is incomplete. For example, although much of the information on Mark Catesby (1683–1749) is in chapter 2 (“The Renaissance of Ornithology”), he is also discussed (but not indexed) in chapter 7 (“The Beginnings of American Ornithology”). The book is profusely illustrated with portraits of ornithologists, but sources of portraits are not provided, a loss for future historians and a loss of credit for those who provided them. Indeed, there are no acknowledgments of source materials or assistance in the book. Citations of references are generally absent from the text, though the bibliography of sources used in writing the book includes nearly 500 references—including an amazing assemblage of centuries-old titles. Within the bibliography, however, publishers of books are rarely given, and volume numbers of journal articles are often missing.

Because of its lack of text citations, the book may be useful mainly as a source of general knowledge of ornithological history and as fodder for comparison with other interpreters of that history. Perhaps that was Walters' goal. *A Concise History of Ornithology* led me to seek more knowledge of those who shaped our science; it gave me new insight and appreciation of where we have been; it made me think of the future. What more could an author hope for?

A Concise History of Ornithology represents a mammoth, scholarly effort—and should facilitate the daunting task of preparing a more comprehensive history. Perhaps the best approach for that task would be to follow Walters' lead by drawing out single threads—the efforts to understand bird anatomy, physiology, behavior, ecology, domestication, conservation, and so on—before attempting to assemble the tapestry of what our science has become. Certainly this is an important book for those interested in ornithology and the history of science and a must for university and other major libraries.—JEROME A. JACKSON, *Whitaker Center, Florida Gulf Coast University, 10501 FGCU Boulevard South, Ft. Myers, Florida 33965, USA. E-mail: jjackson@fgcu.edu*

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- TREE, I. 1991. *The Ruling Passion of John Gould*. Barrie and Jenkins, London.
- ISBN 0198548443. Paper, \$164.50.—This 10th *Oxford Bird Families of the World* volume treats the 20 species of bowerbirds endemic to Australia and New Guinea. The unique and fascinating behavior of building and decorating bowers has brought much attention to this family, for which there has been no serious book-length treatment since Gilliard's 1969 classic. The first of the two parts of this book addresses general topics, including an introduction to the bowerbirds, biogeography, foraging and ecological cycles, morphology, demography, relationships among species, breeding biology, and parental care. Three additional chapters discuss issues specific to bowerbirds, such as bower site, bower structure, courtship display, and the evolution of bowers and the bowerbird mating system. Part two presents species accounts organized by the eight bowerbird genera. Between the two parts are pictures of bowerbird males at bowers and females at nests and a set of excellent illustrations of each species by Eustace Barnes.
- Frith and Frith present a detailed review of the bowerbird literature, including many obscure references and personal communications. This is supplemented by numerous helpful tables, figures, and maps that provide information on morphometrics, bower dimensions, numbers of decorations, nest characteristics, egg dimensions, biogeography, and other aspects of bowerbird natural history. The authors discuss the phylogenetic placement of the bowerbirds in relation to other families, and the relationships of bowerbird genera and species, using morphological, behavioral, and limited molecular information. Classification at the species level is little changed from recent descriptions, with the exception that the two morphologically distinct Flame Bowerbird subspecies are now separated as the Masked Bowerbird (*Sericulus aureus*) and the Flame Bowerbird (*S. ardens*).
- The authors' informal and qualitative analysis of species' relationships is biased toward morphological characters, including plumage, but they do not explicitly consider behaviorally based traits such as bowers and decorations. They fail to use modern phylogenetic techniques, and this may contribute to their inability to resolve problematic issues associated with species' relationships. The robust Kusmierski et al. (1997) mitochondrial-DNA bowerbird phylogeny is not shown or used in any systematic attempt to resolve relationships among

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The Bowerbirds: *Ptilonorhynchidae*.—Clifford B. Frith and Dawn W. Frith. 2004. Oxford University Press, Oxford. xxiii + 508 pp.

bowerbird species. Significantly, that phylogeny suggests a major change in the relationships of the bowerbirds: the Streaked Bowerbird (*Amblyornis subalaris*) is a sister group to the clade including *Prionodura*, *Archboldia*, and the remaining *Amblyornis*, which suggests that those taxa form a single genus. And although they suggest that those taxa are tightly linked, Frith and Frith offer no clear evidence supporting that claim.

It is hard to read anything written about bowerbirds and not be captivated by their amazing natural history, but serious errors and omissions greatly detract from this volume. Figure 1.1 is meant to show the distribution of bowerbirds but omits the distribution of Satin and Regent bowerbirds along the Australian east coast. In Table 4.1, values given in the third row in each cell do not show male–female differences as stated. In numerous instances, work of other researchers is inaccurately represented. Frith and Frith (p. 123) mistakenly report that Borgia et al. (1987) found that blue items were common in the habitat, when actually we showed the opposite; and they report that only one later paper quantitatively assessed likely decorations in the habitat, when our paper had used the same methods. Too often, Frith and Frith cite papers without mentioning that they are about nonbowerbird species and have dubious relevance to bowerbirds; for example, it is unclear how Mulder and Magrath's (1994) finding that fairy wrens use the timing of prenuptial molt to assess male quality is useful in understanding bowerbird mate assessment, which occurs at bowers when all males have completed their molt.

The authors' views are commonly offered without support or with explanations that are less than compelling. They reject others' observations that males trim leaves over bower platforms to increase light falling on the bower platform (p. 103), even though (1) they have observed males trimming leaves, (2) they argue that light on platforms likely critically affects display, and (3) it is clear that removing leaves that block light just above the bower platform would change its illumination. They recognize that divergence in female preferences between Vogelkop (*Amblyornis inornatus*) populations leading to dramatic differences in bower shape and decoration "supports the speciation by sexual selection hypothesis" (p. 29) but, without explanation, conclude that those populations

have not attained species or even subspecies status (Table 2.4). Frith and Frith uncritically report the claim that local similarities in bower decoration are attributable to cultural transmission, even though there has been no attempt to measure cultural transmission and likely alternative hypotheses were not effectively eliminated.

The discussion of the evolution of bowers and bower decorations (Chapter 7) deserves special attention, because these are the signature traits of the bowerbirds. Frith and Frith support our (Borgia et al. 1985) marker hypothesis, which suggests that bowers and decorations serve as indicators of male genetic quality. But that hypothesis requires a pre-existing array of bowers with differences related to genetic male quality, so another hypothesis is needed to explain bower origins. Frith and Frith propose as "plausible" the hypothesis that bowers evolved to hide the female during courtship from interfering males. That hypothesis receives little behavioral support from species of the two major clades of bower-building species. In the maypole-building clade, maypole or courts without bowers almost fully expose the female and, in the two independently evolved hut-building species, the courting male hides in the hut while the female stands outside. Avenue bowers expose females from the front, rear, and above, the directions of likely approach by interfering males; and females of several species often do not move completely into the bower avenue, apparently not concerned with hiding. Frith and Frith suggest that overhanging bushes hide the female from above, but that is rarely complete, and therefore does not prevent intruding males from determining whether a female is in the bower. Also, if bushes typically completely hide the female, that would eliminate the need for bowers rather than favor their evolution.

Frith and Frith dislike my hypothesis that bowers originated to increase female comfort when visiting display courts in response to the threat of forced copulation by the courting male (I call this the "female protection from forced copulation" (FPFC) hypothesis, but Frith and Frith incorrectly label it the "rape hypothesis"). They question how males can benefit from building a structure that prevents their own forced copulation, ignoring my suggestions that bower-building males benefit from (1) increased female visitation by less-threatened females and (2), for the best males, less-threatened females

who are able better to attend to and choose their high-quality displays. I suggested that males initially courted from behind trees, thus enhancing the female's opportunity to escape male attempts at forced copulation. Males then evolved to embellish those obstacles with sticks (to form true bowers), allowing improved functional design of bowers over naturally available barriers. Supporting the FPFC hypothesis is (1) strong evidence that females are under threat of forced copulation, (2) evidence that the hypothesis is functionally consistent with existing bower types (in all bower-building species, males must run around the bower wall or maypole to mount the female, thus giving her time to escape unwanted copulations), and (3) the requirement to deal with the threat of forced copulation in court-clearing bowerbirds that do not build bowers. In the non-bower-building Archbold's Bowerbird (*Archboldia papuensis*), the unique male groveling courtship behavior is consistent with reducing threat of forced copulation but is not predicted by the hiding-from-the-female hypothesis that Frith and Frith prefer. In Toothbilled Bowerbirds (*Scenopoetes dentirostris*), there also is no bower; and after very short displays, males typically capture visiting females by their nape in violent copulations that are similar to forced copulations.

The authors (p. 219) present two quotations from me suggesting contradictory claims about the role of the bower in preventing forced copulations, but the second was taken from the discussion of a different hypothesis suggesting that the bower protects females from aggressive physical attacks by males. They first deny (p. 219), then accept (p. 220) the occurrence of forced copulations, and then argue that females are not susceptible to forced copulation because they "turn onto their back to defend themselves" (p. 220). But our extensive video records show that females do not fight males and that birds on their back are typically intruding males attacked by the bower owner. Frith and Frith claim that forced copulations by marauding male Satin Bowerbirds (*Ptilonorhynchus violaceus*) are unimportant because they are carried out principally by sexually immature males, when in fact such copulations involve five-year-old and older juvenile-plumage males, which Marshall (1954) showed make viable sperm. Also, they never consider why those males carry out this risky behavior that may end in prolonged and

presumably costly fights with bower owners if there were no benefit. Frith and Frith point to the complex system of male and female signaling we found in Satin Bowerbirds as evidence against a threat of forced copulation, missing the point that top males can gain more by courting rather than forcing copulation, and that bower-building and courtship-signaling are similar in allowing males to reduce the threat to females to improve their chances for mating. Curiously, Frith and Frith seem to lose track of the hypothesis they are attempting to refute, confusing the role of the bower in protecting the female from forced copulation by the courting males with other, different hypotheses (i.e. protection from forced copulation by marauding males and protection from male aggression). In an attempt to refute the role of forced copulation in shaping bowerbird behavior, they ask why it is not important in other birds, not considering the obvious fact that female bowerbirds are unique in surveying decorated ground courts where they are more susceptible to forced copulation. Apart from discussing forced copulation, Frith and Frith fail to consider the other evidence offered to support the protection hypothesis.

The authors also reject the "threat reduction" hypothesis; they suggest that it was proposed as a general hypothesis for bower evolution, even though I developed it specifically to explain the unique bowers and high-intensity displays of some Spotted Bowerbirds (*Chlamydera maculata*). I suggested that males build a unique thin, see-through bower wall to filter out threatening aspects of their otherwise attractive high-intensity displays. Without having seen a bower in the population in question, Frith and Frith state, "Certainly a male spotted could burst through his wall to access the female" (p. 221). We have monitored on videotape more than 2,300 courtships in this population and have never seen males attempt to burst through the wall, and if they could, the delay associated with passing through the wall would likely allow females to escape. Frith and Frith do not mention our experiments in which we destroyed one bower wall and males courted predominantly from behind the remaining wall and lowered their display intensity when on the side without the wall, which supported the hypothesis that males use the wall to filter intense display elements. They propose that females may favor male aggressiveness because it is a signal that

they are better able to defend bowers and then pass on this trait to offspring. But that does not explain the unique behavior of displaying through specially modified bower walls and the adjustments that males make in our wall-destruction experiments.

The bowerbirds represent one of the high points of avian evolution and as such they deserve a book that fully captures the wonder of their fantastic natural history. In some ways, this book reflects many of the exciting aspects of bowerbird evolution. With its many references, maps, and tables, this is a useful tool for gaining access to the bowerbird literature. But what is most exciting about these birds is to understand how they came to have and use their unique adaptations—bowers and decorated courts. This book's quirky review of current thinking represents a missed opportunity to tell this exciting story, or at least what we know of it so far. This and the too-often inaccurate presentation of factual information suggest caution in using this book as a definitive source, particularly for issues related to bower evolution.—GERALD BORGIA, *Department of Biology, Biology-Psychology Building, University of Maryland, College Park, Maryland 20742, USA. E-mail: borgia@umail.umd.edu*

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