

Trivers's theory of parent-offspring conflict has shed relatively little empirical light on siblicide in birds will undoubtedly provoke some raised eyebrows. But Mock's perspectives are so clearly articulated and thoughtfully explained that even readers with dissenting views will be unlikely to object strenuously.

I highly recommend this book to anyone interested in the evolutionary biology of family conflict. It will be especially useful to ornithologists working on such topics as hatching asynchrony, siblicide, brood reduction, and parental care. And for anyone wanting to know how to write a scholarly biological book that will appeal to a general audience, *More Than Kin and Less Than Kind* should be essential reading.—RONALD L. MUMME, *Department of Biology, Allegheny College, 520 North Main Street, Meadville, Pennsylvania 16335, USA. E-mail: rmumme@allegheny.edu*

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Magnificent Mihirungs. The Colossal Flightless Birds of the Australian Dreamtime.—Peter F. Murray and Patricia Vickers-Rich. 2004. Indiana University Press, Bloomington, Indiana. vii + 410 pp. ISBN 0253342821. Quarter cloth and boards, \$75.00.—This is an exhaustive, superbly illustrated treatment of the Dromornithidae, a family of large to very large flightless birds known from fossils from Australia and Tasmania. The fossils range in age from a rather equivocal early Eocene partial footprint to the late Pleistocene *Genyornis newtoni*, which died out about 50,000–30,000 years ago, presumably as a result of human predation and habitat modification by fire.

The book is divided into four major sections: "Discovery," a short chapter on the history of fossil finds and their discoverers; "Systematics and Morphology," the longest section, containing paleontology, descriptive osteology, systematics and phylogeny, and evolutionary origins; "Paleobiology," consisting of functional morphology, biomechanics, weight estimates, and so forth; and "Paleoecology," which treats

associated fauna and flora, biotic history of Australia, possible feeding habits, and the like. The book's concept, organization, and visual presentation are brilliant, but the execution has some serious flaws.

The first known species, *Dromornis australis*, was described in 1874 by Richard Owen, and for almost a century and a quarter the dromornithids were associated with paleognathous ratites such as emus and cassowaries. The name "mihirung" was originally adopted for these birds by Rich (1979) from Aboriginal traditions of giant emus (*mihirung paringmal*) believed possibly to apply to *Genyornis*. It was not until the seminal paper of Murray and Megirian (1998), based on newly collected Miocene skull material, that the anseriform relationships of the Dromornithidae were revealed. Six years later, Murray and Vickers-Rich glibly and rather misleadingly refer to these birds as gigantic geese and imply that their nonratite nature should have been apparent earlier.

E. C. Stirling and A. H. C. Zietz, who were director and assistant director, respectively, of the South Australian Museum, excavated and published impressive monographs on extensive fossil material of *G. newtoni* from 1896 to 1913. According to Murray and Vickers-Rich,

Stirling and Zietz's comparisons and discussion of *Genyornis* morphology and relationships are so intently focused on ratite osteology that as each structural incongruity is realized they dutifully note it, adjust their spectacles, and move on as though there were no alternatives. (p. 59)

Furthermore, the skull "contains ample evidence to have placed the *Genyornis* [*sic*] among the Neognathae even at the time Stirling described it" (p. 60). The penetrating clarity of Vickers-Rich's hindsight is a scientific marvel, for in her own monographic treatment of the Dromornithidae (Rich 1979) they were ratites from start to finish.

For the record, the first person in the history of the Dromornithidae to insist that these birds could not be ratites was unlovable old cladist-baiting *moi* (Olson 1985). This seemingly significant fact, acknowledged by Murray and Megirian (1998), was omitted by Murray and Vickers-Rich. Although the reference can be found in the bibliography, it is not cited in the text.

Although I was pleased to learn of the evidence that the dromornithids were derived from Anseriformes, one might now fairly ask "Derived how many times?" Nowhere here or in Rich (1979) is there a clearly articulated argument or character analysis demonstrating that the Dromornithidae constitute a monophyletic group. The skull and foot structure of the clade that includes *Genyornis* are very different from the skull and foot, when known, of the other members of the family. If all these birds are large flightless derivatives of Anseriformes, why might not the *Genyornis* clade have evolved large size and flightlessness independently within the Anseriformes? In fact, because details of the skull of *Genyornis* are poorly known (owing to the incomplete, crushed nature of the available specimens), the evidence that the relationships of this group lie with the Anseriformes is less satisfactory than in older taxa for which better skulls are known. For example, the large, blade-like retro-articular process shown for *Genyornis*, one of the most characteristic features of the Anseriformes, appears to be an almost entirely hypothetical construct (fig. 107, p. 127). Monophyly of the Dromornithidae is, therefore, an issue that still needs to be addressed.

Given that the dromornithids, or at least some of them, belong in the Anseriformes, where do their relationships lie within the order? This question gets more consideration than that of monophyly, but its treatment is badly distorted by prejudices and by another, more serious, omission of pertinent literature.

The authors are dismissive, even derisive, of the suggestion of Olson and Feduccia (1980) that screamers (Anhimidae) might be secondarily derived macrofeeders that evolved from a filter-feeding ancestor. They conclude that macrofeeders such as screamers and the Magpie Goose (*Anseranas semipalmata*) represent the primitive condition in Anseriformes and that filter feeding is derived. They also state that the Anseranatidae have no fossil record. Did they simply overlook the early Eocene *Anatalavis oxfordi* (Olson 1999)? That species was published in one of the quadrennial proceedings of the Society of Avian Paleontology and Evolution, each of which has become a primary source in avian paleontology and ought to be familiar to everyone in the field. *Anatalavis oxfordi* was based on an excellent associated skeleton,

lacking the hindlimbs, from the London Clay and was referred to the Anseranatidae on the basis of highly distinctive derived characters of the pectoral girdle. The bill morphology indicates very clearly that it was a filter-feeder. The type species of *Anatalavis* from marine deposits in New Jersey is either late Cretaceous or earliest Paleocene. Thus, the earliest certain member of the Anseriformes, which is also the earliest member of the Anseranatidae, was a filter-feeder. This strongly suggests that the macro-feeding Magpie Goose is secondarily derived from a filter-feeder. Screamers, too, may thus be so derived.

Unfortunately, the two known early Eocene taxa of Anhimidae, from Wyoming and England, have never been described. Those were not filter-feeders and lacked many of the autapomorphic characters of modern screamers, such as great skeletal pneumaticity and the double-spurred carpometacarpus. Murray and Vickers-Rich make a weak case for dromornithids being screamer-like, on the basis of the supposed lack of uncinat processes and the presence of a knob at the distal end of the pectoral crest of the humerus. Eocene screamers lack that knob, however. Furthermore, the authors show a rib of *D. stirtoni* (fig. 60) with a large, very distinct facet for an uncinat process. Such a facet would seem to indicate a synovial joint, and I doubt that such would form were there not a bony uncinat process to articulate with it.

In the end, no good case is made for the relationships of the Dromornithidae within the Anseriformes, even at the level of family. Although the authors favor a closer relationship with either the Anhimidae or Anseranatidae, it would seem that even the Anatidae, through a terrestrial goose-like form such as *Cereopsis*, cannot be ruled out.

The generic-level systematics used in this book is a complete mess. To begin with, the type species of *Dromornis*, Owen's *D. australis*, is known only from a single femur and remains practically the only Pliocene fossil of the family. The paucity of Pliocene material makes it uncertain that the late Miocene *D. stirtoni* is correctly referred to *Dromornis*. The close relationship between the middle Miocene *Bullockornis planei* and the larger *D. stirtoni* that succeeds it is emphasized repeatedly. At first implicitly (p. 273), and then more explicitly (p. 330), it is

suggested that this is an ancestral–descendent relationship. Why, then, are the two species maintained in separate genera?

Then we have the species that was originally described by Rich (1979) as *Ilbandornis? lawsoni*. The only change in status for this species in 25 years is that quotation marks were added around the genus, so that everywhere it appears as “*Ilbandornis?*” *lawsoni*. Do the quotation marks make the identity even more uncertain than before, or make us more certain of the uncertainty, or what? The illustrations and descriptions make it very clear that this late Miocene species has nothing to do with *Ilbandornis* but shares distinctive characters with *Genyornis*. It would have been far preferable to have simply called it *G. lawsoni* rather than carry it through the entire book, befogged in punctuation, in a genus to which it patently does not belong. Another taxon is referred to throughout as “*Bullockornis?*” sp. Does the fact that the question mark comes before the genus here, rather than after, have any significance? The quotation-mark fetish reaches its apogee with “*Dromornis?*” *australis* (p. 304). Because *australis* is the type-species of *Dromornis*, it belongs in *Dromornis* by definition, and the quotation marks add nothing but confusion.

The following example epitomizes the addled systematics used in this book:

The genera [*sic* = species] *Ilbandornis woodburnei* and “*Bullockornis?*” sp. have slightly more derived morphological states and share no definite synapomorphic states with *Genyornis* or “*Ilbandornis?*” *lawsoni*. They retain several plesiomorphic states but also share some derived states with *Bullockornis planei* and *Dromornis stirtoni*. Despite the current retention of distinct generic names, they probably represent species of a single genus, among which were structurally suitable ancestors for *Bullockornis planei* and ultimately *Dromornis stirtoni*. “*Bullockornis?*” sp. represents a species close to the ancestry of *Ilbandornis woodburnei*. Cranial fragments are known for “*Bullockornis?*” sp. and *Ilbandornis woodburnei*, indicating a close relationship. (p. 329)

It is a great pity that a competent systematist was not enlisted to sort out this horrendous

farrago of indecision before such an important book was published. Still, because of the superior nature of the illustrations, it is possible for an intelligent reader to make some sense of part of the evolutionary history of these birds, in spite of the disastrous nomenclature.

A lengthy chapter on body mass estimates goes into great detail to document three different methods of estimating mass and rather diffidently concludes that *D. stirtoni* may have been the heaviest bird that ever lived. Here, as elsewhere throughout the book, there is much additional information and speculation on other large flightless “ground birds” such as *Diatryma*, moas, and phorusrhacids, so that the volume should become an essential reference for anyone studying those birds.

Sections on appearance and posture, locomotion, and feeding apparatus are replete with beautiful anatomical reconstructions. As with any group of organisms known only from fossils, one must rely to a greater or lesser extent on conjecture, and there will doubtless be more than one interpretation of the structure of dromornithids. But I have never known any two functional anatomists to agree on anything, even concerning living birds, so this should not be regarded as a detraction.

Complementing the functional anatomical discussions are chapters on paleoecology and the fauna and flora associated with dromornithids through the Cenozoic. What emerges is a most useful overview of the evolution of terrestrial biotas on the Australian continent that should be particularly useful for those outside Australia who are unfamiliar with this history. These sections are not without a good measure of advocacy, conjecture, and redundancy, but the overall conclusions seem quite reasonable and believable to me.

In a nutshell, the dromornithids are presented as large, browsing herbivores that evolved in open-canopy scleromorphic forests. They were capable of moving over considerable distances with reasonable celerity, and the taxa at any given period are believed probably to have been widespread on the continent. The authors repeatedly argue that most of Australia was not a wet, closed-canopy rainforest as apparently has often been asserted. From the middle Miocene onward, dromornithid diversity declined, as did overall body size; in contrast, diprotodontids and other large herbivorous

marsupials show overall increases in size over the same interval. Those animals are believed to have been better adapted than dromornithids to the decreasing quality of browse as climatic conditions became drier and plants responded accordingly.

Following the main text is an idiosyncratic appendix entitled "Basic Avian Skeletal Anatomy," which emphasizes comparisons between taxa thought relevant to understanding the osteology of dromornithids, namely emu, magpie goose, and megapode. Terminology is supposed to be based on Howard (1929) rather than adopting "the strictly formal Latin *nomina anatomica*" (p. 337), as though that were a medieval incunabulum rather than a citable reference (Baumel 1993). The reader is unlikely to be much enlightened by the tedious descriptive text, but the section is salvaged by the excellent illustrations. Discrepancies in anatomical nomenclature are evident: e.g. "furculum" (fig. A1) vs. the correct "furcula" (fig. A12) or "pygidium" (fig. A12) vs. the correct "pygostyle" (fig. A1). I suspect that there are even more serious errors to be found here, especially among the details of the cranium.

Because many of the legends are long and complex, one wishes that more labeling had been included directly on the figures. Nevertheless, the quality of the copious illustrations is uniformly excellent. The stunning life-reconstruction of a pair of *Bullockornis planei* by Peter Trusler that adorns the dust jacket is one of the most arresting of its kind that I have ever seen. Because many librarians discard dust jackets, it is fortunate that this painting is reproduced in color on the half-title and title pages. The two-page black-and-white reproduction that appears later in the text is washed-out and completely ineffectual.

The Glossary may have been an afterthought, perhaps at the insistence of an editor, in which a selection of words were randomly picked from the text and crude definitions supplied. This makes for entertaining reading, as there are some real howlers. Definitions may be completely wrong ("Alpha taxonomy: A classification of organisms based on overall similarity of morphology") or misleading or unhelpful ("Dorsal: The top side"; "Lacrimal: A bone of the skull"). Mandibles are defined as "lower jaws," though the term "upper mandible" is used throughout the book. "Endocranial fossa"

is defined only as "the space occupied by the brain," which called to my mind the jar of alcohol in which Einstein's brain now floats. Is that an endocranial fossa? We can only imagine the perplexity of the nonscientist who, fifteen lines down, finds that "fossa" is "a slender cat-like carnivorous mammal from Madagascar."

Minor errors of every description are disturbingly frequent: typographical, spelling, grammatical, word-choice, factual, bibliographic. These start on the first page of text (Acknowledgments: p. vii), where Brad Livezey appears as "Brad Linezen," and continue throughout the book to the last page of the bibliography, where we find the following reference: "Zeitz, A. C. 1894. *Nature* 50:184-208." The name should be spelled "Zietz," not "Zeitz," and the article was not authored by Zietz anyway, but by Stirling. The title should not have been omitted, and the actual pagination is 184-188, 206-211. Out of curiosity, I checked each of the other 10 references on that less than half a page and found 11 additional errors, including completely erroneous pagination for another reference.

What is termed at one point the "Magnificent Teratorn" (p. 255) is later called "Great Teratorn" (p. 275) but is never identified by its scientific name (*Argentavis magnificens*). Then, *Teratornis* is erroneously stated to have been "the largest flying bird known" (p. 319), when that honor actually goes to *Argentavis*. And so on.

Don't get me wrong. This is still a highly meritorious and impressive book. Anyone with an interest in morphology, paleontology, and evolution of birds; in the evolution of terrestrial ecosystems; or simply in exquisite scientific illustration, will find much to learn and enjoy in these pages. In concluding, the authors note some recent discoveries and remark that "after a decade of digging, preparing, comparing, measuring, and hypothesizing, our effort remains a work in progress" (p. 335). My sincere hope is that, in another decade, knowledge of dromornithids will have advanced so far as to merit a reissue of this work in which the new information can be incorporated and all the flaws of the present edition corrected. This might then become one of the great classics in both ornithology and paleontology.—STORRS L. OLSON, *Division of Birds, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, USA. E-mail: olsons@si.edu*

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Speciation.—Jerry A. Coyne and H. Allen Orr. 2004. Sinauer Associates, Sunderland, Massachusetts. xiii + 545 pp. ISBN 0-87893-091-4. Cloth, \$89.95. ISBN 0-87893-089-2. Paper, \$54.95.—This is an important book, perhaps the most important work on the subject of speciation in decades. The species problem—explaining the origin of discrete groups living together in nature—is undoubtedly one of the greatest questions in all of biology. I found the book's logic extremely compelling. The authors first establish the existence of the phenomena under

study—in this case, the reality of species. They unapologetically justify the biological species concept as an appropriate framework for studying the origin of species. And they are explicit about what they consider to be the central conceptual theme in speciation research: the origin and evolution of reproductive isolating barriers. Coyne and Orr do not dabble in semantics or philosophy, and the book cuts quickly to the process of species formation, relegating the traditional debate (or quagmire) over species concepts to a carefully worded appendix.

The remainder of the book is a tour and status review of the most significant facets of the speciation process: the geography of speciation, the nature of isolating barriers, the genetics of reproductive isolation, speciation by reinforcement, polyploidy, speciation by hybridization, the relative importance of natural selection and genetic drift, and macroevolutionary considerations. Each chapter follows a predictable format: the authors examine theoretical and experimental evidence, as well as evidence from nature. They critically revisit the literature (including their own work) and provide their own conclusions and synthesis. Through it all, the authors demand testable hypotheses and insist on examples from nature wherever possible. Such hard-nosed empiricism, from two scientists who clearly understand the theory, is very refreshing.

Some readers may find Coyne and Orr to be overly critical—perhaps downright negative—in their assessment of previous research. They hold all studies to a hard standard, and it occasionally seems difficult to do anything properly in their world. But they are at least consistent, and they clearly indicate what needs to be done in future studies. Their extensive discussion of sympatric speciation (Chapter 4) is a good example of this. To satisfy sympatric speciation, they hold a long list of potential cases to extreme scrutiny and a standard of evidence that is difficult to obtain. They conclude that, although several promising cases exist, sympatric speciation appears to receive far more attention than it warrants. One may disagree with their dismissal of some putative cases of sympatric speciation, or with their null hypothesis of allopatry—that speciation is allopatric until proven sympatric. But in the end, the lack of evidence for sympatric speciation when it should be detected (e.g. among species on small oceanic islands or among host-specific