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REVIEW

PALEOGNATHOUS BIRDS FROM THE EARLY TERTIARY OF THE NORTHERN HEMISPHERE, by Peter W. Houde, 1988. Nuttall Ornithological Club, Cambridge. viii + 148 pp., 27 tables, 40 figs. \$25.00.

Among the thornier problems in the evolution of birds is the puzzle of the palaeognaths. Living palaeognaths include ratites (ostriches, cassowaries, etc.) and tinamous. The relationships of ratites, tinamous, and other living birds (Neognathae) have been a matter of debate for over a century. These three groups form a monophyletic taxon, Neornithes. Within Neornithes, however, the monophyly of Ratitae, Palaeognathae, and even Neognathae has been challenged (see Olson, 1985, for an excellent review). In particular, ratites, with their unique constellation of characters, appear to stand so far apart from other birds that some early authors even argued for their separate origin (see discussion by Witmer, in press). Thus, it is with great anticipation that we turn to Peter Houde's recent study of archaic neornithine birds in hopes that new light will be shed on this old problem. Houde's authoritative treatise indeed sheds much light, but a solution to this perhaps intractable problem is probably an unreasonable expectation.

Houde's monograph centers on an analysis of the osteology, functional morphology, and systematics of a group of predominantly late Paleocene to early Eocene birds. Houde groups these superficially tinamou-like birds into the Order Lithornithiformes, which comprises one family, three genera (*Lithornis*, *Pseudocrypturus*, and *Paracathartes*), and eight species; the order, family, one genus, and four species are new taxa. The North American material derives mostly from calcareous nodules collected from the Fort Union Formation of Montana and the Willwood Formation of Wyoming. The fossils that come out of these nodules are truly spectacular in being generally complete and uncrushed. Although similar nodules had been collected previously, Houde deserves a great deal of credit for his careful collection and painstaking acid preparation of these fossils. Because of the high quality of the material and the large number of new taxa (avian and otherwise), these fossils are clearly very important and record a portion of the fauna that was previously poorly known. The European material is mostly from England and was collected as long ago as the mid-nineteenth century. Much of this material is fragmentary and had been assigned to many different modern families. The discovery of the relatively complete North American material has allowed Houde to identify the true affinities of many enigmatic European fos-

sils. Thus, the long lists of synonymies in this monograph will be especially useful to paleornithologists overseas.

In many respects, this volume represents the long-awaited elaboration and extension of two earlier papers (Houde and Olson, 1981; Houde, 1986). Houde's descriptions and measurements are very precise, clearly presented, and should satisfy those looking for details of the morphology of these important birds. One of the great strengths of this paper is that the high quality of the fossils is faithfully reproduced in the many well-executed photographs, some of which are stereopairs. However, many of the figures are completely unlabeled, thus the reader is expected to have a considerable knowledge of avian anatomy. Furthermore, all but a few of the tables and figures are grouped in one 60-page section rather than interspersed throughout the text, a format that becomes tiresome during careful reading. Although the specimen photographs are excellent, it was disappointing to find almost no reconstructions of the skeletal elements. In fact, the only detailed reconstructions of the skull and skeleton are found in Houde and Olson (1981)—and these are composites of two genera.

Houde's monograph also includes insightful discussions of the paleoecology and functional morphology of these birds. He characterizes them as looking generally like tinamous but differing from them in some functionally important ways. Their jaw apparatus was similar to that of kiwis and other sensitive-billed birds that probe leaf litter for prey. Interestingly, the flight apparatus of at least *Lithornis* and *Pseudocrypturus* shows that they were capable of sustained flight, including periods of gliding; this is quite different from tinamous, which generally fly powerfully but for only short periods. Lithornithids were not especially cursorial, and their feet indicate that perching in trees was possible. Houde's functional analyses are generally sound, and he draws attention to some important features that often are overlooked. However, the discussion could have benefited from more formal biomechanical analysis and more reference to other works on avian functional morphology. Furthermore, Houde rarely puts his functional arguments for adaptation in a phylogenetic context, and thus it is difficult to tease out the constraints (functional, historical, architectural, etc.) acting on lithornithid features.

Among the more interesting propositions in the book is that lithornithids had a mating system characteristic of many living palaeognaths—sequential polyandry and simultaneous polygyny, whereby several females mate with and lay their eggs in the nest of a single male who then tends the huge clutch and rears the chicks by himself. The basis for this claim is the often large accumulations of eggshell fragments in the nodules. Houde does not regard the accumulations as nests, and many will probably view his inferences about reproductive behavior as speculative until the taphonomy of the nodules is better known.

Although lithornithids are fascinating in their own right, one of the major interests ornithologists and paleontologists will have in this monograph is the phylogenetic conclusions and their implications for the evolution of birds. Houde's rather eclectic cladistic analysis is, by his own admission, the "weakest aspect of this paper." Although he recognizes the importance of derived characters and provides character polarities and cladograms, his methodology and philosophy are unusual. Claims that phylogenetic hypotheses are not falsifiable will raise the eyebrows of many readers. Houde forthrightly asserts the naturalness of paraphyletic groups, but does not cite or discuss the vast literature associated with this controversial statement. This is a relevant criticism in that Houde regards the Lithornithiformes, the subject of the monograph, as a paraphyletic assemblage, with *Pseudocrypturus*, *Lithornis*, and *Paracathartes* being successively closer to ratites.

Houde describes these birds as being generally primitive, and they certainly occupy a position near the base of the neornithine radiation. He characterizes them as "paleognathous," literally meaning "ancient jawed." There has been much debate as to whether the "paleognathous palate" is primitive or derived in birds; Houde supports the former. Indeed, lithornithids possess many palatal features that have been considered plesiomorphic (e.g., Witmer and Martin, 1987), and I agree that the palate of the basal neornithine probably was similar to that of known palaeognaths. Houde denies the presence of any derived characters uniting a monophyletic Palaeognathae. In fact, he proposes that Palaeognathae is paraphyletic, with tinamous and Neognathae (both of which are monophyletic) being sister-groups. This conclusion is controversial (but may well be correct) and represents one of the more important findings of his research. Although too recent to appear in Houde's monograph, it is interesting to note that the molecular data of Sibley et al. (1988) suggest that Palaeognathae is monophyletic and Neognathae is paraphyletic—which is the reverse of what Houde's paleontological data indicate.

As a paraphyletic group, lithornithids cannot be diagnosed by a unique suite of derived characters. Lithornithids and ratites are united by only a few synapomorphies, and these characters exhibit massive ingroup homoplasy. Most of his synapomorphies at the ratite node are features associated with flightlessness, despite stating here and elsewhere (Houde, 1986) that he regarded the ancestor of kiwis as having flown to New Zealand. Monophyly of the ratites remains a problem. An important input to Houde's phylogenetic scheme is the Eocene Messel bird *Palaeotis*, which Houde (1986) and Houde and Haubold (1987) considered to be not only a ratite but an ostrich (Struthionidae). Peters (1988) takes issue with Houde's characters, but nevertheless, *Palaeotis* has features of ratites, tinamous, and lithornithids, and deserves more attention.

Houde effectively dovetails his work on these early neornithine birds with his research on DNA-DNA hybridization (Houde, 1987). The molecular clock of Sibley and Ahlquist (1983) is calibrated by the timing of the tectonic breakup of Gondwanaland with the presumed separation of the rhea and ostrich clades. This calibration is based on the assumptions of uniform rates of molecular evolution and that flightlessness evolved only once in ratites. Houde has offered data here and elsewhere (Houde, 1987) that challenge both these suppositions.

In summary, Houde's monograph unquestionably belongs on the shelf of paleontologists and ornithologists who are interested in the early history of the clade that includes all 9,000 species of modern birds. The price of \$25.00 for a small-format book of 148 pages may be difficult for some to justify, but the volume is hard-cover and well bound. It constitutes a clear presentation of the current controversies, and includes a wealth of data on a group of birds that was virtually unknown previously. In general, firm phylogenetic conclusions are elusive at the origin of any major group, and this case is no exception. Nevertheless, Houde takes important steps in this direction, and provides the critical data for the rigorous phylogenetic analysis that is necessary to unravel the base of the modern avian radiation.

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