AN ADDITIONAL CHARACTER LINKING RATITES AND TINAMOUS, AND AN INTERPRETATION OF THEIR MONOPHYLY

KENNETH C. PARKES and GEORGE A. CLARK, JR.

For more than a century there has been a debate as to whether the so-called ratites—the ostriches, rheas, emus, cassowaries, and kiwis, plus the extinct moas and elephant birds—were of common ancestry, or had evolved convergently from unrelated stocks. Superimposed on this argument was a debate as to whether these flightless birds had ever had flying ancestors, or had evolved directly from preflying ancestral forms. The latter school of thought has been largely discredited, but has had a few persistent advocates (see Verheyen, 1961, and papers cited therein). The debate as to monophyletic versus polyphyletic origin of the ratites, however, has continued, with outspoken adherents to either position. The volant tinamous were thought long ago by various authors to have some kind of affiliation with the flightless ratites, but their relationships could not be clarified until the "preflying ancestor" theory of ratite origins was disposed of.

Much of the history of these debates, together with useful bibliographies, can be found in recent publications by Bock (1963), Meise (1963), and de Beer (1956, 1964), and details need not be recapitulated here. It is oversimplifying to state that the monophyletic and polyphyletic schools of thought have alternated in popularity, as at any one time adherents to both could probably be found. We suspect that some of the early classifiers might have admitted that the ratites could have arisen independently from unrelated flying ancestors, but that these birds were placed together in avian classifications merely for lack of any evidence as to what such ancestors may have been.

McDowell (1948) concluded that the palaeognathous arrangement of the bones of the palate, long considered one of the major characters held in common by the ratites, was a heterogeneous composite. His work gave strong impetus to the polyphyletic school, which gave rise to some widely quoted papers (see Mayr and Amadon, 1951:3, and Stresemann, 1959:275), and reached its zenith in the dogmatic statement of the late Rene Verheyen (1960:293), part of which reads ". . . it is already firmly established that close relationship between the orders of *Ratitae* is pure fiction . . . ." Some of the recent synthetic and secondary literature has reflected this viewpoint. For example, Lagler *et al.* (1962:412) state, in a section entitled "Parallel evolution or convergence" in an ichthyology text: "The distribution of the large, flightless birds, the Ratites . . . is a classic example. Once thought to be intimately related and hence all placed in a single group, these birds are now *known* [italics ours] to have sprung from divergent ancestors . . . ." See also, in this connection, Mayr *et al.* (1953:42–43). As various kinds of evidence are reexamined and new data forthcoming, however, students of the ratites are returning to the theory that the similarities among these birds are, indeed, to be attributed to common ancestry (Sibley, 1960; Bock, 1963; Meise, 1963).

There are obvious difficulties inherent in making comparisons between external features of adult birds as large as most ratites. During a study of natal downs, we handled and compared downy young of several ratites and tinamous, and we were struck by the constancy of a character of the bill, visible on adults but seen to much better advantage on small young. We believe this to be an additional piece of evidence favoring the theory of monophyletic origin of ratites and tinamous, and one

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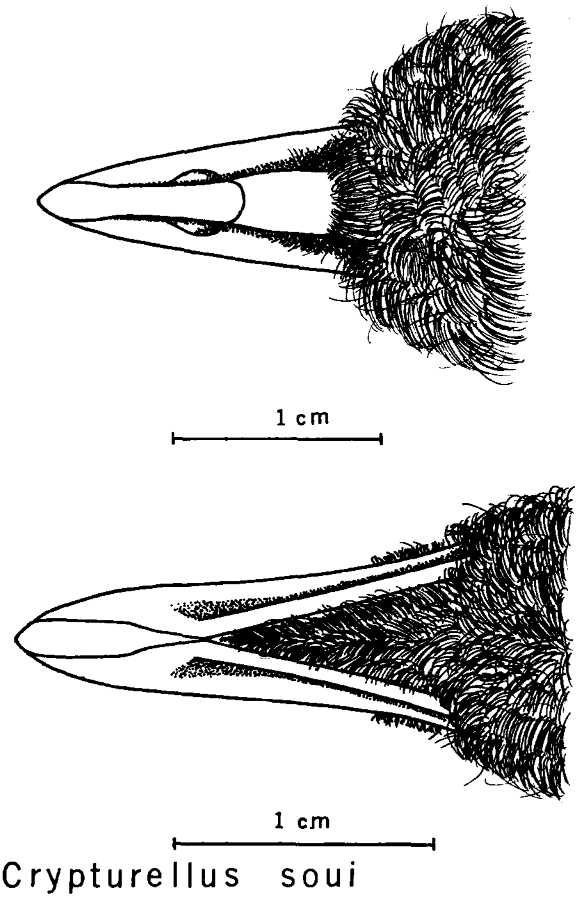

Figure 1. Bill of downy young tinamou (*Crypturellus soui*), dorsal and ventral aspects. Carnegie Museum no. 36271.

which must certainly be taken into account by anyone attempting a definitive classification of these birds.

The earliest mention we have found of similarities in the rhamphothecal structure of ratites is that of Lesson (1844:col. 1045); in describing the bill of the kiwi, Lesson wrote: "Ce bec présente une autre anomalie, c'est d'être muni à sa base d'une cire échancrée en avant, cire qui n'est pas sans analogie avec celle des nandus ou autruches d'Amérique." Parker (1862:206) noted the close resemblance of the rhamphothecal structure of *Tinamus* to that of the ostrich and kiwi. He, however, considered the segmentation of the rhamphotheca of *Chionis* and of the Procellariiformes to be "struthious" as well; our reasons for believing otherwise will be mentioned below. Resemblances among bills of ratites were noted by several subsequent authors (see Newton and Gadow, 1896:33, and Pycraft, 1900), but no real attempt was made to invoke this character in assessing relationships throughout the group. Lönnberg (1904) and von Boetticher (1928) dwelt at some length on the epidermal covering of bird bills, and depicted some of the patterns to be discussed in the present

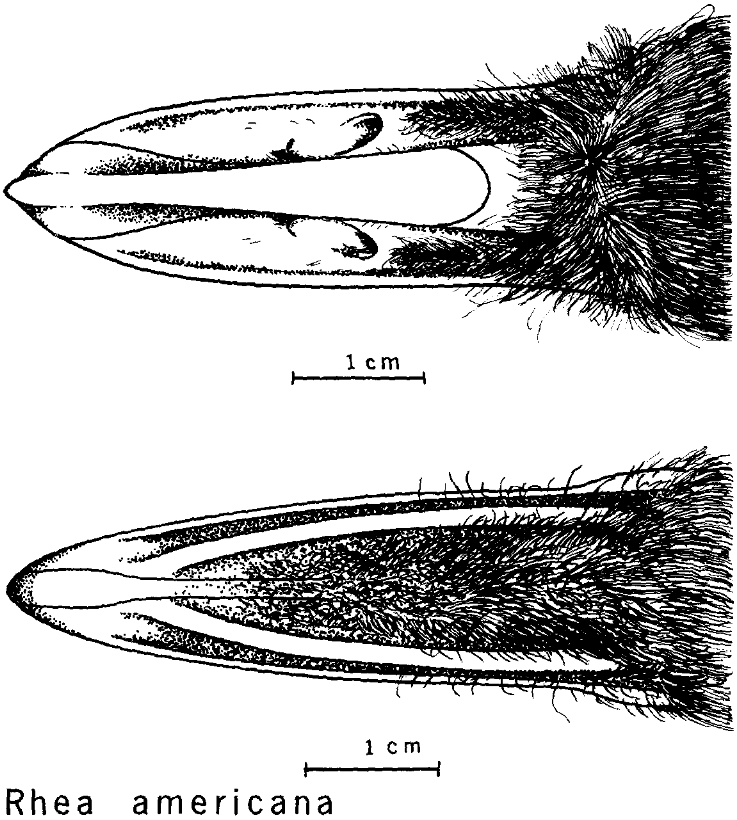

Figure 2. Bill of downy young rhea (*Rhea americana*), dorsal and ventral aspects. Carnegie Museum no. 94648.

paper. The primary preoccupation of these authors, however, was an attempt to homologize the parts of the rhamphotheca with the scales of reptiles, going so far as to give names to the various segments of avian rhamphothecae based on the nomenclature of reptilian scales. Although both of these authors noted certain similarities among the bill patterns of ratites and tinamous, they did not attribute this phenomenon to monophyletic origin. On the contrary, they believed that these, supposedly the most "primitive" of living birds, retained these bill patterns independently from their reptilian ancestry. Lönnberg went so far as to attribute the terminal position of the nostrils of the kiwi to a retention from reptilian ancestry, as he believed that the nostrils would be a nuisance at the tip of the bill during feeding, not knowing of the importance of the sense of smell to kiwis. As Bock (1963:53) has reemphasized, the ratites do not appear to be particularly "primitive" among birds, and the Lönnberg/von Boetticher theory of bill-segment homology must be regarded as highly dubious at the very best.

The rhamphothecal features held in common by ratites and tinamous may be described as follows. The culmen is an elevated, flattened ridge which usually widens (except in kiwis) near the tip of the bill. At the base of the culmen is a cere-like

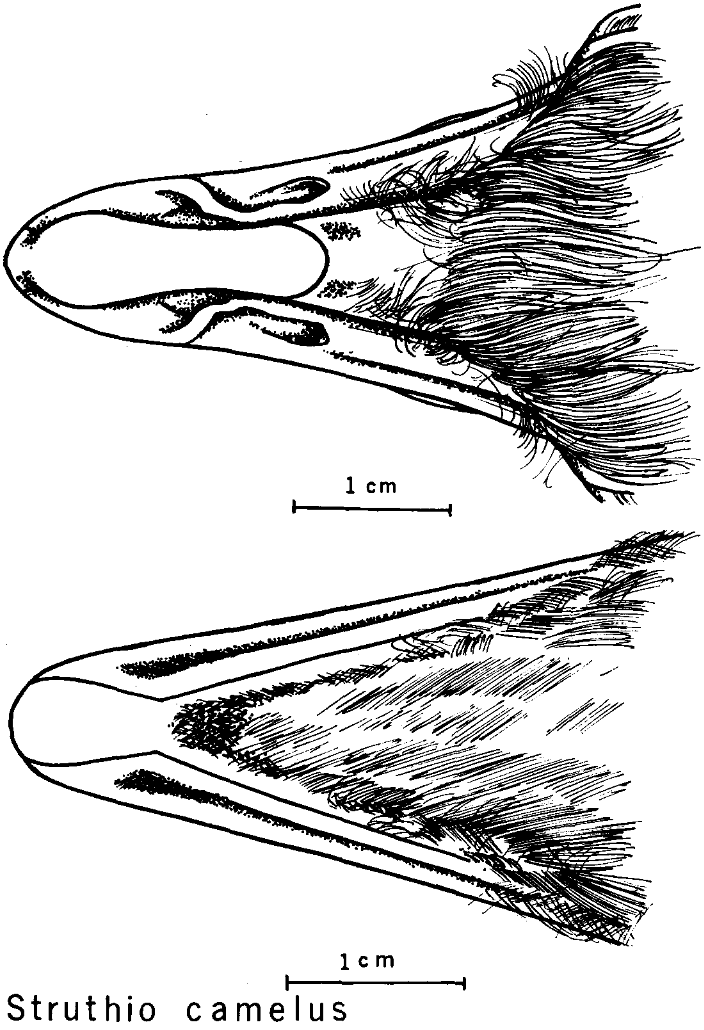

Figure 3. Bill of downy young ostrich (*Struthio camelus*), dorsal and ventral aspects. Carnegie Museum no. 140038.

structure, the anterior margin of which is U- or V-shaped, with the point toward the forehead. The lateral margins of this structure extend as distinct grooves, passing dorsad of the nostrils, to the anterior end of the bill. These grooves may be relatively straight, as in the kiwi (fig. 6), or flare apart just posterior to the bill tip (most noticeably in the rhea, fig. 2). On the lower mandible, the rhamphotheca appears tripartite. A central, more-or-less wedge-shaped piece extends from the tip of the bill to the gonydeal angle. In most species this gonydeal piece is decidedly narrower than the lateral pieces, but in the elongated bill of the kiwi, the lateral pieces taper rather sharply, anterior to the gonydeal angle, and continue as narrow lateral ridges.

The description above is a generalization, to which a few modifications may be

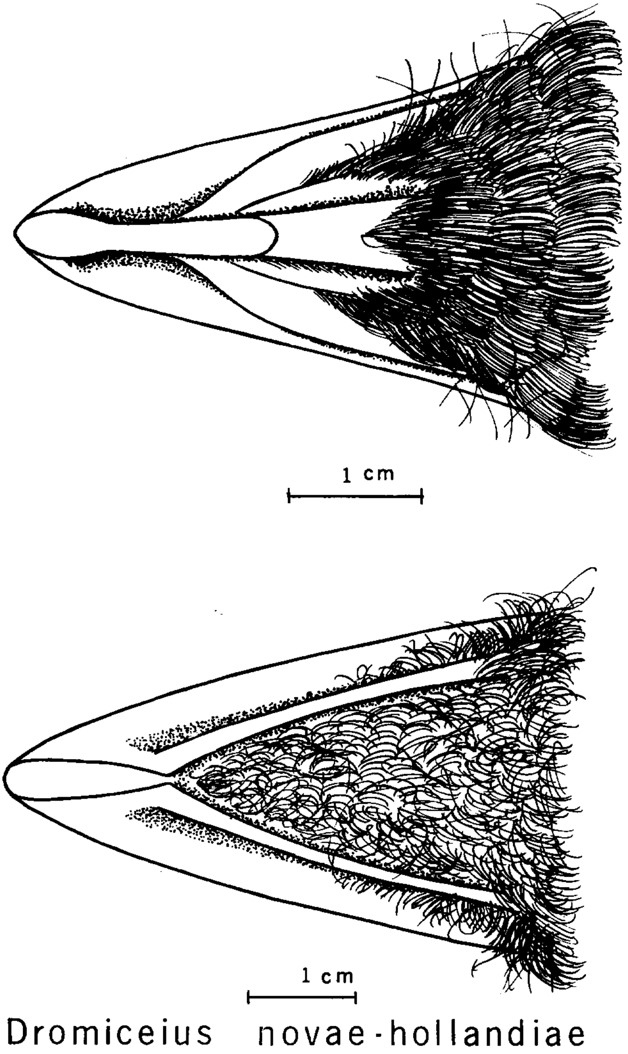

Figure 4. Bill of downy young emu (*Dromiceius novaehollandiae*), dorsal and ventral aspects. American Museum of Natural History no. 156544.

mentioned. The grooves delimiting the pieces of the rhamphotheca are seen to best advantage in young birds; in older individuals they are sometimes obscured by wear, and in the case of *Casuarius,* distorted and masked by the growth of the casque. In all but two of the genera of tinamous, the general description applies. In *Rhynchotus* the anterior portion of the grooves of the upper mandible has become obsolete, and the division of the lower mandible has almost completely disappeared, being faintly visible in some individuals. The genus *Nothoprocta* is transitional toward the *Rhynchotus* condition. *N. perdicaria* has both dorsal and ventral grooves well developed, as typical of other tinamou genera. In other species of *Nothoprocta*, however, the

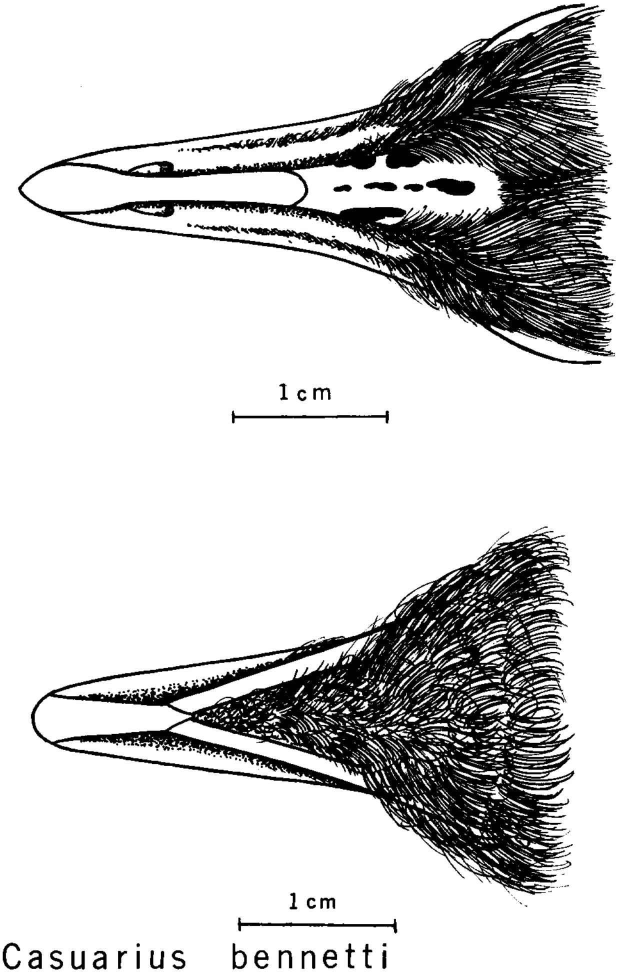

Figure 5. Bill of downy young cassowary (*Casuarius bennetti*), dorsal and ventral aspects. American Museum of Natural History no. 266664.

grooves separating the gonydeal from the lateral pieces of the lower mandible do not quite reach the end of the bill, and there is also a tendency for the anterior portion of the dorsal grooves to disappear, as in *Rhynchotus*. Even within a single species of *Nothoprocta* there is much individual variation in the development of these grooves.

All of the genera of living ratites have been examined, both as adults and as downy young, except that the smallest available *Apteryx* specimens appear to be about half grown (fig. 6). Figures 1 through 5 were drawn from downy young.

The relationship of the extinct moas to the living kiwis, emus, and cassowaries has generally been accepted (Oliver, 1949:182 ff.). Figure 7 has been redrawn from a lithograph (Owen, 1883:pl. 59) of the mummified head, complete with integument, of *Megalapteryx didinus* (Owen), one of the smaller moas. It will be seen that the

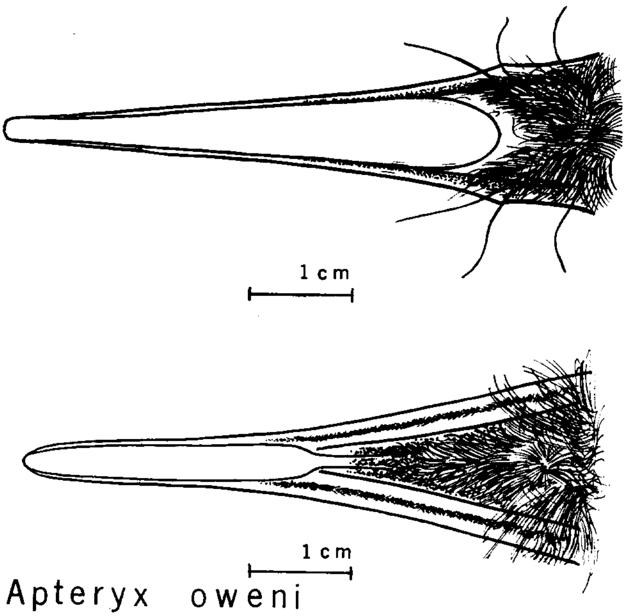

Figure 6. Bill of juvenile kiwi (*Apteryx oweni*), dorsal and ventral aspects. Carnegie Museum no. 24216.

conformation of the rhinotheca agrees with that of other ratites; no ventral view of the head of this bird was published. We know of no comparable mummified specimens of any species of Aepyornithidae.

We have thus shown the presence of a remarkably consistent pattern of rhamphothecal structure among the ratites and tinamous. The question then arises as to whether this same pattern is present in any other birds. In this connection we have examined bills of all orders and most families of living birds. Although segmentation of the rhamphotheca is typical of birds of several orders, notably the Procellariiformes and Pelecaniformes, we have not found any other birds conforming precisely to the ratite–tinamou pattern as described above. Although there is a superficial similarity between certain of the patterns of rhamphothecal segmentation in all of these orders, it is doubtful that they can be truly homologized as attempted by Lönnberg and von Boetticher. And even within single families, patterns may be less consistent than among the ratite–tinamou group as a whole. Striking pattern differences among albatrosses (Diomedeidae) are shown in figures 2, 3, and 4 of von Boetticher (1928). An important difference between the rhamphothecal segmentation of the ratite–tinamou group and that of other birds, in our opinion, is the fact that in the former the sutures appear more distinctly in downy young individuals than in adults, whereas in the Procellariiformes and Pelecaniformes, the reverse is true, with much of the segmentation barely if at all visible in young birds (see fig. 11 of von Boetticher [1928], comparing adult and chicks of *Phalacrocorax carbo*).

We believe that this consistent bill pattern among ratites and tinamous is additional evidence for a phylogenetic rather than a convergent relationship among these birds. We cannot conceive of an adaptive bill character which would appear in both

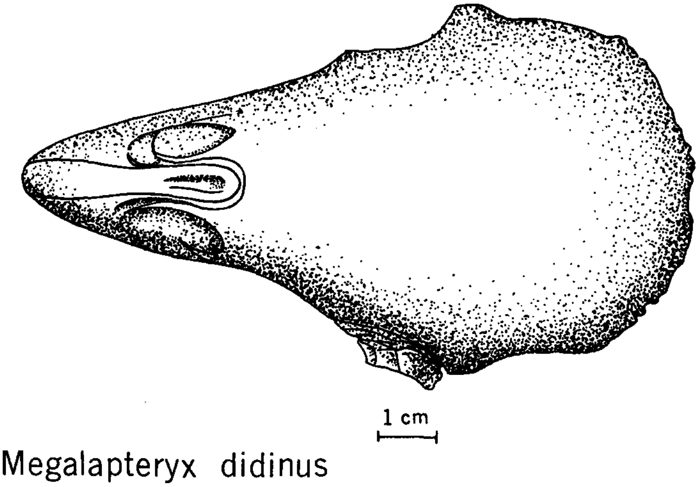

Figure 7. Head of mummified moa (*Megalapteryx didinus*), dorsal aspect. Redrawn from Owen, 1883.

tinamous and kiwis, and not, for example, in the similar-feeding Galliformes and snipes. This rhamphothecal character, of course, proves nothing, but we believe that it must be taken into consideration by anyone attempting a definitive classification of the ratites, especially those continuing to hypothesize a polyphyletic, convergent origin of these birds.

Assuming, then, a monophyletic relationship to exist among the ratites and tinamous, we turn next to some conjectures as to their distributional history. A survey of the literature on ratite phylogeny, much of which was written by anatomists (especially the early papers), shows that the zoogeographical aspects of the problem have generally been omitted or given but the briefest treatment. The ideas presented below are intended to be heuristic; we have not seen quite this sort of conjecturing before, and we hope it may stimulate productive discussion among those who know more about ratites than we do.

Even if ratites and tinamous be monophyletic, the many studies made of their anatomy together with the limited fossil record all suggest that the living (and recently extinct) forms have been long separated phylogenetically. The only fossil believed to represent an intermediate stage in ratite evolution is *Eleutherornis helveticus* Schaub, of the Lower Middle Eocene of Switzerland. This is assigned to its own family within the Struthioniformes by Wetmore, who agrees with Schaub that *Eleutherornis*, although ostrich-like, shows indications of carinate affinities (Wetmore, 1951:55). Another possible intermediate form is *Opisthodactylus patagonicus* Ameghino, of the Lower Eocene of southern Patagonia. Originally placed in the Phororhacoidea, this species and its monotypic family were allocated to the Rheidae by Patterson and Kraglievich (1960:11) with no explanation, but with a citation to an unpublished manuscript by Patterson. As pointed out by Brodkorb (1963:200, footnote), certain characters of *Opisthodactylus* as originally described "preclude its reference to the Rheidae as currently understood." The presence of a hind toe suggests that *Opisthodactylus*, if correctly assigned to the Rheiformes, may occupy a transitional position in the ancestry of the three-toed rheas. It is the oldest fossil listed among the ratites by Brodkorb (1963).

In discussing the phylogeny of the ratites, we inevitably encounter the question, as elucidated by Simpson (1961:120 ff.), of the definition of monophyly. Superimposing on this question that of the origin of present distribution, one possible interpretation of their monophyly would demand that the ratites arrived at their present geographic ranges *as ratites,* with the living species thus representing relicts of a formerly almost cosmopolitan group. "Missing links" would presumably once have connected the surviving forms, with all having descended from a common ratite ancestor in some one part of the world.

To this rigid interpretation of monophyly, we prefer the more flexible definition of Simpson (1961:124), which permits us to speak of *levels* of monophyly. We doubt that the living forms all descended from an ancestral *species* recognizable as a ratite. We think it quite likely, on the other hand, that all of the birds in question (including the tinamous) have been derived from a single stock, perhaps at the family level. In Simpson's terms, the ratite–tinamou assemblage would thus be considered monophyletic at the family level, but polyphyletic at lower (generic, specific) levels. Simpson's discussion (1961:125 ff.) of Huxley's term *grade* is also appropriate here. The "ratite" stage of evolution (large running birds with reduced number of toes, loss of flight, lack of carina on sterna, etc.) may be considered a *grade,* which we believe to have been independently attained several times within the same general group. As Simpson points out (1961:128), "The concept of a grade has little meaning unless it is applied to related animals only . . . . At a minimum, grades must be based on parallelism, not convergence, and their use certainly cannot eliminate a phylogenetic basis." Thus the tinamous, although considered to be related to the ratites in a phylogenetic sense, represent a different grade. This attainment of the "ratite grade" by some but not all members of a monophyletic group would resemble, for example, the independent evolution of flightlessness in several parts of the world among the confamilial but nevertheless fairly diverse rails, crakes, and gallinules.

As the only living flying members of this assemblage are the tinamous, one is tempted to believe that they most nearly represent the general ancestral family, which we may thus for convenience call the proto-tinamous. Although living tinamous resemble their ancestors in having retained the power of flight, they may well have diverged in other characteristics almost as far as have the "ratite grade" descendants. The antiquity of the group as a whole is such that it is likely that the proto-tinamous included adaptive types not represented among the living Tinamidae.

At its peak, the family of proto-tinamous was widely distributed, and probably of Old World origin. There appear to be three fairly obvious phyletic lines among the living or recently extinct Old World descendants of the proto-tinamous: the ostriches, the elephant birds, and the Australia–New Guinea–New Zealand radiation, including the emus, cassowaries, kiwis, and moas. The latter all show so many resemblances that they possibly represent descent from a single line of early proto-tinamous (perhaps thus monophyletic at a subfamilial or even generic level). For a discussion of the evolution of this group, see Oliver, 1949:182 ff. Sibley's evidence (1960:230) from egg-white protein patterns suggests that the ostrich is closely related to this last assemblage, and we believe that it is, in the sense that it is an Old World descendant of the proto-tinamou stock. Nevertheless, the anatomical and zoogeographical evidence strongly supports the idea that the Australia–New Zealand group is more closely interrelated than any of its members is to the ostrich.

The situation in the New World is particularly interesting. It appears reasonable to assume that the rheas, of all of the large flightless birds, have attained the "ratite grade" most recently. Their wings are the least reduced, and they show many resemblances to tinamous, leading McDowell (1948) to combine the Rheidae and Tinamidae into a single order. It seems to us to be probable that the rheas evolved flightlessness in South America, possibly from ancestors appreciably nearer the tinamou than the proto-tinamou level. Thus they retain ancestral characteristics common to the whole group (cf. the rhamphothecal structure), but share certain special characteristics with the only other New World group, the tinamous.

As Darlington (1957:561) and others have pointed out, South America's fauna seems to have received far more contributions from the Old World than the reverse; Mayr (1946) emphasizes this phenomenon with reference to birds. In many groups there have been rather obvious secondary radiations into vacant niches (or niches occupied by competitively unsuccessful forms), descending from invading Old World ancestral forms. In some groups of animals, South America appears to have been a refuge for relatively primitive types, some of which have undergone these secondary radiations within the continent (notably marsupials and certain birds). There is an interesting parallel between the distributions of the living members of the ratite–tinamou group and the suboscine passerine birds. Among the latter, generally considered to be the more "primitive" group of passerines, South America is the metropolis. Here the suboscines have radiated into many adaptive types, comprising over one thousand species, divided into several families. This great assemblage, however, clearly represents only two major interrelated lines: the tyrant flycatcher–cotinga–manakin group, and the superfamily Furnarioidea, comprising the woodhewers, ovenbirds, ant-thrushes, etc. In the Old World, on the other hand, the suboscines consist of several highly specialized groups, with almost every family representing a separate line of obscure relationships, mostly of few species, and mostly of very limited distribution: Eurylaimidae (broadbills), Pittidae (pittas), Philepittidae (asities), Acanthisittidae (New Zealand wrens), Menuridae (lyrebirds), and Atrichornithidae (scrub-birds). Incidentally, this assemblage includes those passerines with the most limited powers of flight, such as the apparently wholly flightless Stephen Island Wren (*Xenicus lyalli*). Note the resemblance of this distributional picture to that of the ratite–tinamou assemblage. In South America there is a relatively large radiation of the most "primitive" (in this case, less specialized) of the living types, with 9 genera and about 40 species of tinamous, and two monotypic genera of rheas. In the Old World we have, again, a few highly specialized groups of limited distribution, limited ecological tolerance (within a given family), and no close relationships except probably, to some extent, within the Australia–New Zealand group. The radiation of suboscines in South America was more spectacular than that of the proto-tinamous, for fairly obvious reasons. The latter, when they reached South America, were probably well on the way to being primarily terrestrial running birds, yet capable of occupying almost any terrestrial habitat (as, indeed, they now do, with tinamous ranging in body size from that of a small quail to that of a half-grown turkey, and inhabiting everything from dark, wet tropical jungles to bleak Andean slopes). The smaller, fully volant ancestral suboscines undoubtedly arrived with a less specialized body form and found more available ecological opportunities, and could thus evolve into their present great diversification. No conclusions are drawn from this parallel, but it is nevertheless of some interest.

Thus, in summary, we believe that all presently available evidence, including the rhamphothecal character described in this paper, points to the tinamous and the living and recently extinct ratites as being phylogenetically related; resemblances are to be attributed to parallel evolution from a common stock (here postulated to be at the family level) rather than to convergence from unrelated stocks, and thus, employing Simpson's concepts, the group may be considered monophyletic. Bock (1963:53) refrained from making any decisions as to taxonomic ranks to be assigned to the ratites and their subgroups. Two other recent authors (Brodkorb, 1963; Meise, 1960) have proposed new classifications in harmony with a monophyletic origin for these birds, but quite different in taxonomic approach. Brodkorb emphasizes the "differentness" of the ratites and tinamous. He recognizes three subclasses of birds: Sauriurae for the Archaeopterygiformes, Odontotholcae for the Hesperornithiformes, and Ornithurae for all others. Within the latter subclass, Brodkorb proposes three infraclasses: Dromaeognathae for the Tinamiformes, Ratitae for six orders of ratites, and Carinatae for all others.

In Bock's discussion (1963:53) there is a strong implication, with which we agree, that the schism between ratites and other birds is not as fundamental as demanded by Brodkorb's classification. We prefer the approach of Meise (1960), who recognizes no division between carinates and ratites as such, at higher than the ordinal level. An order Crypturi is recognized for the tinamous, while all of the ratites are included in a single order Ratitae, divided into the families Rheidae, Struthionidae, Casuariidae (with three subfamilies), Aepyornithidae, Dinornithidae, and Apterygidae. We believe that such a classification (with minor modifications) probably best reflects the present state of our knowledge of the ratites and tinamous. In the system of ordinal nomenclature preferred by many ornithologists, Meise's two orders would become Tinamiformes and Struthioniformes, respectively. Some may prefer to combine these into a single order. The Aepyornithidae should probably be placed next to the Struthionidae (Bock, personal communication), and the moas may be divisible into subfamilies corresponding to the families recognized by Brodkorb and other authors. Further osteological studies (and, hopefully, additional fossil material as yet undiscovered) will indicate the best allocation of taxonomic rank to *Eleutherornis* and *Opisthodactylus*. In any case, we reiterate our belief that the ultimate classification of the ratites and tinamous should reflect (1) a monophyletic origin of these two groups, and (2) their general resemblances to, rather than differences from, the other post-*Archaeopteryx* birds.

SUMMARY

Examined ratites (ostriches, rheas, emus, cassowaries, kiwis, and moas) and tinamous share a conformation of the rhamphotheca not found in other birds. This is interpreted as an additional piece of evidence that resemblances among this group are to be attributed to monophyletic origin rather than to convergence. Their monophyly is thought to be at approximately the family level, with several lines of descent from a family of "proto-tinamous" having independently attained the "ratite grade." Classification of ratites and tinamous should reflect this relationship without exaggerating their differences from other birds.

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