

THE COLOR PATTERNS OF DOWNY YOUNG RATITES AND TINAMOUS

JOSEPH R. JEHL, JR.

ABSTRACT.—Plumage patterns of downy young ratites indicate that the Casuariidae and Dromiceidae are closely related, and they suggest that the Struthioniformes and Casuariiformes may be more closely related to each other than either is to any other living ratite taxon. Relationships of the Rheiformes and Apterygiformes are not clarified. The Tinamidae fall into two distinct groups of genera: 1) *Tinamus*, *Nothocercus*, and *Crypturellus*, and 2) *Rhynchotus*, *Nothura*, *Nothoprocta*, and *Tinamotis*; chicks of *Taoniscus* were not examined. Chick plumages provide no evidence for close relationship between tinamous and any ratite taxon.

The ratites are large, flightless, running birds with an unkeeled sternum which, with one minor exception, are now restricted to the southern hemisphere. They include the extant families Struthionidae, Rheidae, Casuariidae, Dromiceidae, and Apterygidae, and the extinct Opisthodactylidae, Dromornithidae, Emeidae, Eleutherornithidae, and Aepyornithidae (Brodkorb, 1963). Interrelationships among these families have long been among the most controversial problems in avian systematics (Bock, 1963), as has the question of whether these flightless birds share a common ancestor. (References to much of the relevant literature are contained in Bock, 1963, de Beer, 1956, 1964, and Parkes and Clark, 1966). Some recent authors (e.g., Bock, 1963; Parkes and Clark, 1966) have argued that the ratites are probably monophyletic, but ornithologists have yet to reach a consensus on this point.

The tinamous (Tinamidae) are ground-dwelling, chicken-like birds of the Neotropics. Their possible close relationship to the ratites, and particularly to the rheas, has received much attention, but relationships within the Tinamidae have been largely ignored.

Because chick color patterns have been used to elucidate relationships within certain other taxa (e.g., Podicipedidae: Storer, 1967; Anatidae: Delacour and Mayr, 1945; Tetraoninae: Short, 1967; Charadrii: Jehl, 1968) their importance in suggesting relationships within the ratites and tinamous was investigated. The results provide limited evidence in support of relationships that have been suggested among ratites, and they clarify the subdivisions of the tinamous.

In this study I was able to examine specimens or descriptions of most ratite species, as well as living chicks of *Struthio camelus*, *Dromiceius novaehollandiae* and *Crypturellus soui* in the San Diego Zoo. Most tinamou genera were also available, but many species were not. Studies in other groups have shown that an index to color pattern within a genus can usually be obtained from a few representative species. Thus, the general conclusions reached here are unlikely to be affected by the limited material. Nevertheless, further collecting is desirable, particularly of species in the genera *Nothoprocta*, *Crypturellus*, and *Taoniscus*.

In the following section the major color patterns are described for each taxon. For each species the number of specimens examined is given in parentheses. Species for which I have examined only a description in the literature are denoted by an asterisk. In view of the limited material, no attempt has been made to provide descriptions adequate for species identification.

RATITES

STRUTHIONIFORMES: STRUTHIONIDAE

Struthio: camelus (2)

Ostrich chicks (Fig. 1A) are covered on the back with a thick mat of tan and blackish down feathers. Several barbs on each of these feathers are prolonged, flattened, and



Figure 1. Downy young ratites in dorsal and ventral view: (A): *Struthio camelus* (B) *Pterocnemio pennata*, (C) *Dromiceius novaehollandiae*, (D) *Casuarius bennetti*.

twisted, and intertwine with those from adjacent feathers. The resulting appearance is that of a pile of straw and I cannot determine whether any underlying color pattern is present.

There is a definite though variable striped pattern on the neck. Because several of the stripes are discontinuous, the configuration of this pattern is not as evident in flattened study skins as it is in living chicks (see photos by Sauer and Sauer, 1966: Fig. 31, 32). It consists (Fig. 2) of a mid-dorsal stripe (A) and one dorso-lateral (B) stripe on each side of the neck; an interrupted stripe (C) on each side of the neck; an interrupted stripe (D) on the ventro-lateral surface of the neck that starts near the base of the bill and continues to the upper chest, and (E) a short interrupted stripe in the throat region. On the head a stripe extends from the base of the upper mandible, dorsal to the eye, to the ear region; facial markings are variable but usually include a dark spot posterior to the eye and a short line from the rictus that passes dorsally anterior to the ear.

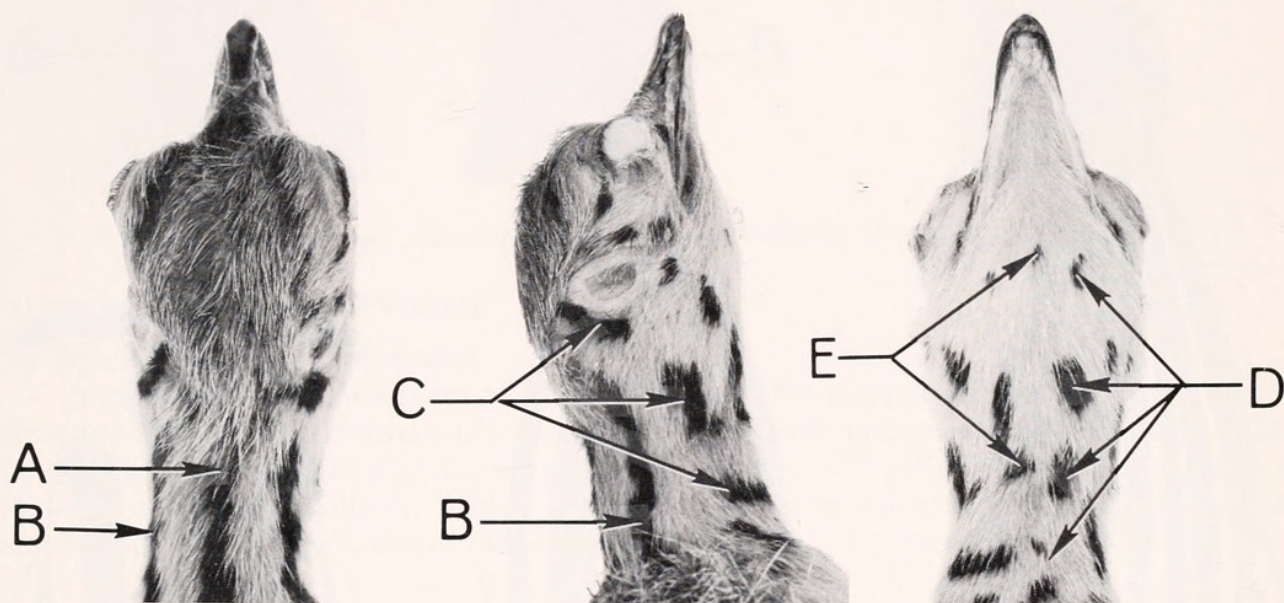


Figure 2. The interrupted pattern of head and neck striping in *Struthio camelus*. The major stripes are indicated.

RHEIFORMES: RHEIDAE

Rhea: americana (6). *Pterocnemia: pennata* (4)

Color patterns of *Pterocnemia* (Figs. 1B, 3C) and *Rhea* chicks are identical. A dark central stripe extends from the crown to the rump, but broadens to a diamond-shaped figure on the mid-back and sends branches along the dorsal surface of the wing. Lateral stripes extend from the rump to the mid-back, where they turn ventrally. When the chick's wings are folded, the wing and lateral stripes appear to form a continuous stripe along the entire length of the body. The chin and belly are whitish; the neck is dusky gray and this coloration extends onto the chest as a thin central line.

The ground color of *Pterocnemia* chicks is whitish and the patterned areas are chocolate brown; minor pattern variations occur in the width of the striping. In *Rhea* the ground color is tan, the patterning dark brown. *Rhea* chicks hatched in captivity show considerably more color variation than wild chicks. This presumably results from inbreeding and selection for albinistic birds.

CASUARIIFORMES: CASUARIIDAE, DROMICEIIDAE

Casuaris: casuaris (3), *unappendiculatus*, *bennetti* (2)

Species limits in the cassowaries are not well known. Peters (1931) lists six species,

but Rand and Gilliard (1967) recognize only three.

Cassowary chicks are pale brown with well-marked longitudinal stripes on the back. The head is chestnut or tan, and may be unmarked or dotted irregularly with dark brown markings (Figs. 1D, 3B). On the back three major dark brown stripes extend from the shoulder region to the rump; within each of these stripes a light central stripe of varying prominence is formed by the chestnut tips of the feathers. A dark stripe on the side is paralleled ventrally by an indistinct stripe that appears to be continuous with the leg stripe. The belly and chin range from light tan to light brown and are unmarked. The neck and chest are irregularly flecked with gray-brown markings; in most specimens the neck coloration continues on to the chest as a thin central line, similar to that found in the Rheidae (cf. Figs. 1B, D).

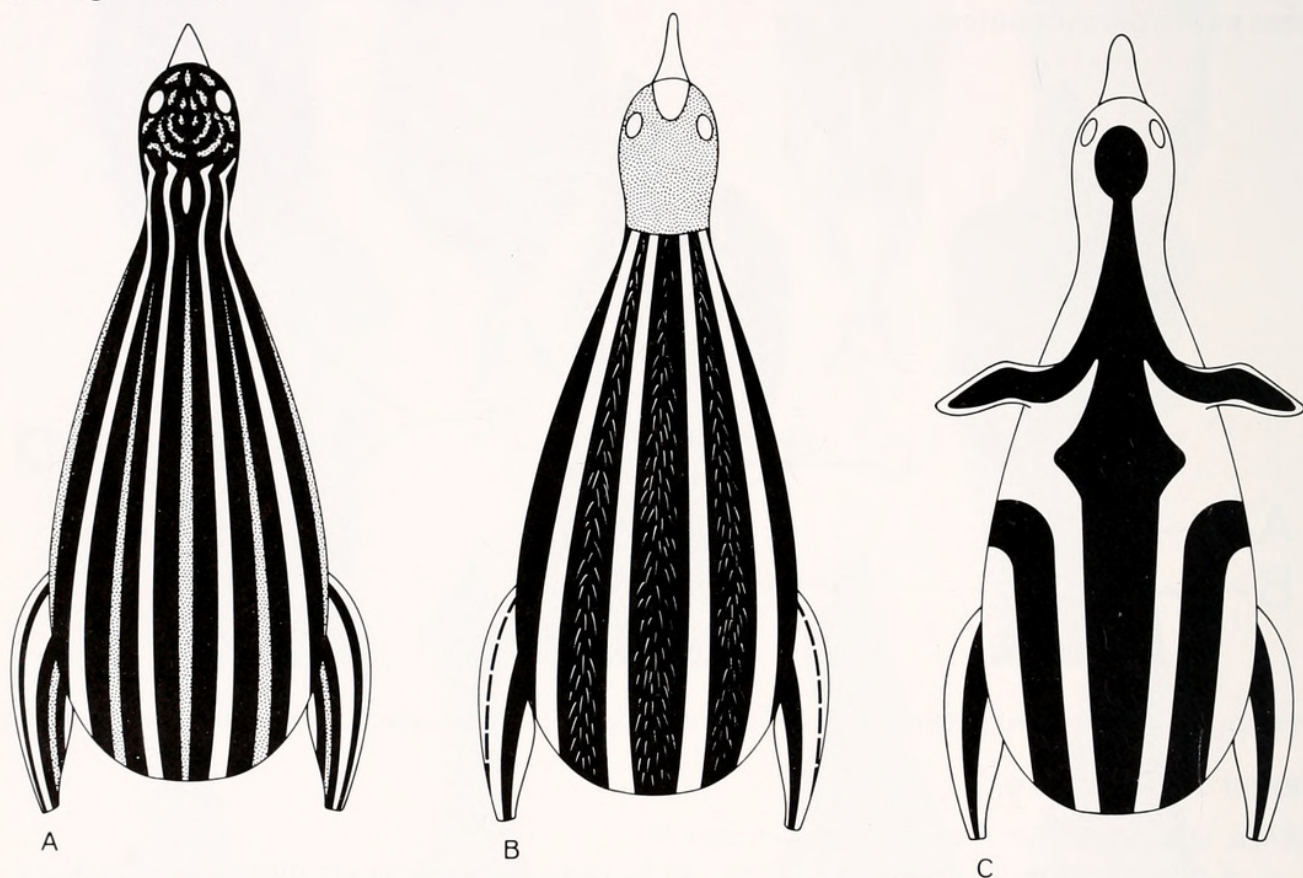


Figure 3. Diagrammatic color patterns of: (A) *Dromiceius novaehollandiae*, (B) *Casuarius casuarius*, and (C) *Pterocnemia pennata*.

Dromiceius: novaehollandiae (5)

Emu chicks are boldly patterned (Figs. 1C, 3A, 4). The head markings show no consistent arrangement but the neck and back markings are distinctive. Dorsally, a central (A) and two lateral (B) stripes extend from the occiput to the rump; a stripe from the auricular region broadens at the shoulder, where it acquires a buffy central stripe, and continues to the flank; a buff-centered stripe on the lateral surface of the thigh is bordered by a thin (sometimes interrupted) black stripe on the antero-lateral surface. On the ventral surface of the neck stripes run from the base of the bill to the sides of the chest (D); a short central stripe (E) is present in the throat region. Pattern details are variable. In some birds parts of stripes are interrupted or missing, and in the bird shown in Figure 4 the posterior part of the central stripe has fused with a lateral stripe.

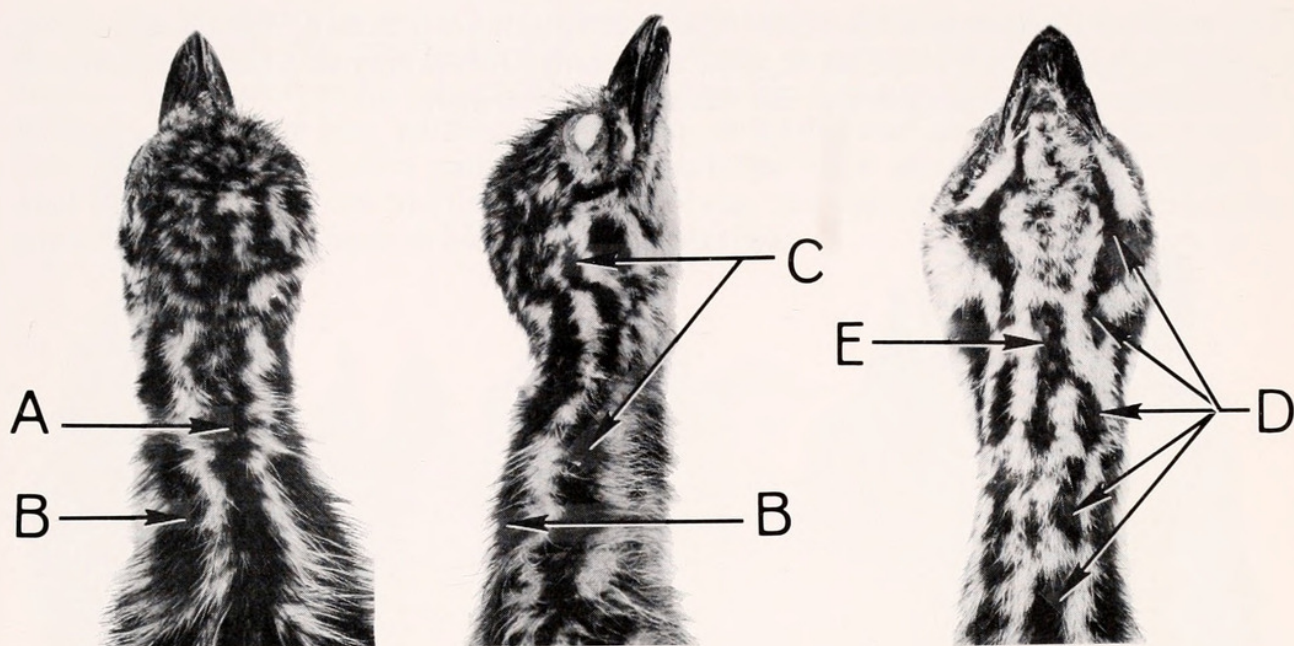


Figure 4. Head and neck pattern of *Dromiceius novaehollandiae*. The major stripes are indicated.

APTERYGIFORMES: APTERYGIDAE

*Apteryx: australis**, *oweni*, *haasti*

Newly-hatched Kiwis seem to be unpatterned. No trace of a color pattern could be detected in a well-developed embryo of *Apteryx australis* preserved in alcohol at the Carnegie Museum (Mary H. Clench, pers. comm.). Oliver (1957: 48) described the nestling of *Apteryx australis* as follows: "Upper surface black streaked with brown mainly on the shafts and bases of the feathers. On the head, breast and abdomen it is greyer."

TINAMOUS

TINAMIFORMES: TINAMIDAE

Tinamus: tao, *solitarius**, *osgoodi*, *major* (5), *guttatus*

De Schauensee's (1966) classification of tinamou is followed in this paper.

The head pattern in *T. major* is complex (Figs. 5, 6); a grayish patch extends from the base of the bill onto the forehead; posteriorly, a brown crown patch extends over the occiput and onto the neck; a gray-brown postorbital stripe runs from above and behind the eye to the side of the neck; a brownish line of variable prominence extends from the base of the bill to the anterior corner of the eye and continues posteriorly as a broad band through the auriculars; the cheeks and throat are grayish, except for a short, dark malar stripe. Feathers on the nape of the upper back are brown, lightly barred with gray, whereas those on the midback appear uniformly brown. A broad, light brown or golden band on the lower back extends to the rump and is bordered laterally by a thin line of dark feathers (Fig. 5). The color pattern of *T. solitarius* is similar (Salvadori, 1895: 502).

Nothocercus: bonapartei (1), *julius* (1), *nigricapillus*

The coloration of the two species of *Nothocercus* at hand differs slightly, but there are no important differences in color pattern. In *N. bonapartei* (Figs. 5, 6) a light grayish patch from the base of the bill extends onto the forehead, where it blends with a dark gray crown that extends onto the occiput; the face and cheeks, including a broad supraorbital stripe, are grayish, and an obscure dark line runs from the base of the bill to the anterior corner

of the eye; the throat is grayish-white. The back is uniformly brown, individual feathers being thinly barred with black. In *N. julius* the crown patch is grayish-white and is sharply bordered laterally by a dark stripe; the facial area is orangish.



Figure 5. Downy young tinamous. Left to right: *Tinamus major*, *Crypturellus boucardi*, *Crypturellus undulatus*, *Crypturellus soui*, *Nothocercus bonapartei*.

Crypturellus: *cinereus*, *soui* (2), *ptaritepui*, *obsoletus*, *undulatus* (1), *brevirostris*, *bartletti*, *variegatus* (2), *atrocapillus*, *noctivagus*, *duidae*, *cinnamomeus* (1), *transfasciatus*, *strigulosus*, *casiaquiare*, *boucardi* (2), *saltuarius*, *kerriae*, *parvirostris*, *tataupa* (2)

Color patterns in this large genus are variable (Figs. 5, 6). In *C. boucardi*, *variegatus*, *cinnamomeus*, *tataupa* and *undulatus*, the head pattern is similar to that of *Tinamus* except that a light brown narrow median stripe is enclosed in the posterior part of the crown



Figure 6. Head patterns of tinamou chicks. Left to right: *Tinamus major* (2), *Crypturellus undulatus*, *Crypturellus soui*, *Nothocercus bonapartei*.

patch, and the auricular stripe is narrower and much less prominent (Fig. 6); in *variegatus* (see Beebe, 1925; Fig. 22) the borders between the prominent head patches are less distinct; in *soui* the auricular patch is absent and the head patches blend into each other, as in *Nothocercus*. The back patterns of *boucardi*, *variegatus* and *cinnamomeus* are similar to that of *Tinamus* but lack a pale patch on the lower back; in *undulatus* and *tataupa* the back is uniformly brown and lightly barred; in *soui* the feathers appear uniformly brownish but are finely barred with black, as in *Nothocercus*.



Figure 7. Downy young tinamous. Left to right: *Rhynchotus rufescens*, *Nothura maculosa*, *Nothoprocta curvirostris*, *Nothoprocta pentlandii*, *Nothoprocta perdicaria*, *Eudromia elegans*.

Rhynchotus: rufescens (2)

The color pattern of *Rhynchotus* chicks (Figs. 7, 8) is unlike that of the preceding genera. The back appears to be longitudinally streaked with dark and light feathers in no ob-



Figure 8. Head patterns of tinamou chicks. Left to right: *Rhynchotus rufescens*, *Nothura maculosa*, *Nothoprocta curvirostris*, *Nothoprocta perdicaria*, *Eudromia elegans*.

vious pattern and to be overlain by a thin coat of stiff bristles. This streaked pattern reflects the structure of the dorsal down feather, which consists of a rachidial main feather and a prominent aftershaft of almost equal size. The rachis of the main feather bears dark-colored barbs for about two-thirds of its length, then forks to form a pair of stiff bristles; the aftershaft bears light colored barbs for almost its entire length. A similar down structure is present in *Nothura*, *Nothoprocta*, and *Eudromia*. In down feathers of *Tinamus*, *Nothocercus* and *Crypturellus*, a rachis is poorly developed and aftershafts seem to be lacking or rudimentary.

The head pattern is well defined. A narrow blackish crown patch which extends from above the eye to the occiput is bordered by a thin buffy stripe that begins at the base of the bill but forks on the forehead to encircle the crown patch; the buffy stripes, in turn, are bordered by a dark stripe that extends from the base of the bill to the nape. The face is generally buffy, but with interrupted dark stripes in the post-orbital and auricular regions; there is a thin malar stripe (Fig. 8).

Nothoprocta: *taczanowskii*, *kalinowski*, *ornata* (1); *perdicaria* (1), *cinerascens*, *pentlandii* (2), *curvirostris* (3)

Chicks of *Nothoprocta* (Figs. 7, 8), like those of *Rhynchotus* have a streaked pattern. In *Nothoprocta*, however, the bristle-like tips of the main feather are much less prominent and usually are flanked by one or more additional barbs. The chick of *N. perdicaria*, in addition to being streaked dorsally, has a slightly barred appearance, because the dark feathers are buffy at both the base and tip.

The head markings in *perdicaria* and *ornata* are similar to those of *Rhynchotus*, except that the boundaries between the major stripes are less pronounced. In *curvirostris* and *pentlandii* the head is dotted irregularly with black, brown, and white, but the pattern is a variation of that found in *perdicaria*.

Nothura: *boraquira*, *minor*, *darwinii*, *maculosa* (1), *chacoensis*

The chick of *Nothura maculosa* (Figs. 7, 8) also has a streaked pattern and is extremely similar to that of *Rhynchotus*; the hairlike bristles of the dark back feathers, however, are less strongly developed than in that genus. The head pattern is like that of *Rhynchotus*, except that the borders between the major stripes are less clearly defined. *Nothura* lacks a post-orbital stripe; auricular and malar stripes, though present, are inconspicuous.

Taoniscus: *nanus*

I have seen neither a chick nor a description of the downy plumage of this species.

Eudromia: *elegans* (5), *formosa*

The dorsal color pattern of *Eudromia* (Fig. 7) is similar to that of the other streaked genera, although light-colored feathers are less abundant than in *Rhynchotus*, *Nothoprocta* and *Nothura*. The darker feathers are subterminally barred with blackish brown, so that the chick, like that of *Nothoprocta perdicaria*, appears slightly barred. The bare tips of these feathers are much shorter than in the genera listed above.

The dorsal surface of the head and neck is flecked with gray and brown; from each side of the bill an indistinct whitish line extends across the crown to the occiput; the face and throat are generally buffy-white, but the lores are dark; posterior to the eye a brown stripe extends through the auriculars to the side of the neck; there is prominent malar stripe (Fig. 8).

Tinamotis: *pentlandii* (3), *ingoufi*

So little down remains on the three half-grown chicks of *T. pentlandii* that I have ex-

amined that no assessment of the body pattern is possible. The head, however, is boldly striped. Two broad dark stripes, one on each side of the bill, pass dorsal to the eyes and around the periphery of the crown to the nape; a small white-centered patch on the occiput extends onto the nape as a thin median line; a stripe from the lores passes through the eye to the auricular region; and a malar stripe extends from the gape through the cheeks and onto the side of the neck. At first glance the head markings of *Tinamotis* seem unique but the pattern is clearly a variant of those found in genera with streaked chick plumages and closely resembles that of *Nothoprocta perdicaria*.

DISCUSSION

RATITES.—In the following discussion I assume that similarities in complex patterns and the potential for easy transformation of one pattern to another are evidence for close relationship. The sequence of pattern transformation cannot be determined in the absence of information regarding the ancestral downy pattern. However, if one assumes that the ratites are monophyletic, it is reasonable to infer that a striped pattern of some sort may have been primitive, inasmuch as a striped pattern or presumed remnant thereof is present in four of the five extant ratite families and is lacking only in the Kiwis, whose burrow-nesting habits are unusual in that group.

The downy young plumages provide limited evidence regarding relationships among ratite families. The long-accepted close affinity of cassowaries and emus is confirmed by the similar color patterns of their chicks. The transformation of a cassowary pattern to that of an emu requires only a change in head pattern (variable in cassowaries) and the introduction of a light central stripe to each of the major dorsal stripes. A hint of that line—the light chestnut tips to the central feathers of each stripe—is present in the cassowaries.

Ostrich chicks lack any discernible dorsal pattern, but the pattern of head and neck striping is closely similar to that of an emu (cf. Figs. 2, 4). This suggests, as Sibley (1960) and Glenny (1965) have indicated, that the Struthioniformes and Casuariiformes may be more closely related to each other than either is to any other living ratite order. If so, the neck pattern in ostriches might represent the remnant of a striped pattern that extended over much of the body. One could speculate that this pattern was replaced by a uniform pattern, and was complemented by a straw-like down structure, insuring crypticity in areas of sparse vegetation as proto-ostriches became adapted to desert habitats.

Downy plumage patterns do not suggest an alliance between rheas and other ratites. Although it would be possible to derive the striped rhea pattern from that of a cassowary, for example, no easy transformation is evident. Similar chest patterns in rheas and cassowaries are simple and could result from convergence. Thus, they provide no evidence for relationship.

Kiwis are thought to be most closely related to the extinct moas and to the living cassowaries and emus (Parkes and Clark, 1966). Young kiwis are unpatterned and their plumage offers no evidence on their possible relationship to other ratites. The lack of a distinct pattern may be a derived condition associated with the burrow-nesting habits of these birds.

TINAMOUS.—Downy young tinamous fall into two distinct groups of genera: 1) *Tinamus*, *Nothocercus*, and *Crypturellus*; 2) *Rhynchotus*, *Nothura*, *Nothoprocta*, *Eudromia*, and *Tinamotis*. Chicks of *Taoniscus* (not available) presumably fall into the second group. These groups correspond to the subfamilies Tinaminae and Nothurinae, respectively, of Miranda-Ribiero (1938). The downy young provide no evidence for von Boetticher's

(1934) subdivision of the Nothurinae into two subfamilies, Rhynchotinae (*Rhynchotus*, *Nothura*, *Nothoprocta*, *Taoniscus*) and Eudromiinae (*Eudromia*, *Tinamotis*).

Because the Tinaminae are forest dwellers whereas the Nothurinae are birds of the grasslands, pattern similarities within these groups might be attributable to convergence. This seems unlikely because patterns in the Tinaminae are complex, and the *Tinamus* pattern can be easily transformed into the more uniform pattern of *Nothocercus* through a small series of steps such as are represented in existing species of *Crypturellus* (Figs. 5, 6). Chicks of the Nothurinae are united by similarities in back pattern and feature structure; differences between color patterns of *Rhynchotus* and *Eudromia* are largely bridged by intermediate patterns within *Nothoprocta* (Figs. 7, 8).

Interrelationships of tinamou genera diagrammed by von Boetticher (1934; also reproduced in Ward, 1957: 336) are largely supported by Ward's study of mallophagan parasites on tinamous. Ward's suggestion that *Nothocercus* is more closely related to *Crypturellus* than to *Tinamus*, however, is also indicated by the similarity of chick color patterns. In addition, chick plumages suggest that *Nothoprocta* may be somewhat more closely allied to *Eudromia* (and *Taoniscus*) than von Boetticher postulated. In the species that I have examined there are no close similarities between patterns in the Tinaminae and Nothurinae.

The attempt to establish a phylogenetic link between the ratites and tinamous, and particularly between the rheas and tinamous, dates at least to the early 19th century, and the downy young have been used to give some support to that view. Salvadori (1895: 494) stated that newly hatched tinamous "... are covered with down, and more or less closely resemble the young of some of the Ratitae." While I agree with Salvadori's implicit thesis—that the downy plumages of birds may be of great taxonomic value—I differ with his conclusion. Nowhere among the tinamous that I have examined, nor in species whose chicks are described by Salvadori, are there patterns resembling those of rheas or any other ratite. This evidence, of course, cannot be used to refute the possibility that tinamous may be more closely related to rheas than to any other living taxon, but neither does it provide any support for that hypothesis. Whether analyses of other taxa with precocial young might suggest alternate relationships for the Tinamiformes (e.g., Galliformes, see Verheyen, 1960; Chandler, 1916) is problematical but worthy of investigation.

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San Diego Natural History Museum, P. O. Box 1390, San Diego, California 92112





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