

VARIATION IN THE TRACHEA OF  
THE CRACIDAE (GALLIFORMES)  
IN RELATION TO THEIR CLASSIFICATION

by

Dean Amadon<sup>1</sup>

In memory of my friend Herbert G. Deignan, who, in his volume on the types of birds in the U.S. National Museum, contributed to the classification of the Cracidae.

In a few birds, often of distantly related groups, the trachea or windpipe is greatly lengthened. Among them are the Whooping Crane (*Grus americana*), the Trumpeter Swan (*Cygnus buccinator*), and certain members of the family Cracidae, such as the chachalacas (genus *Ortalis*). Most birds with such modifications are noted either for the loudness or for the low pitch of their vocalizations, as reflected in such designations as "Whooping" Crane. It is usually assumed that the tracheal modification amplifies or modifies the voice. Thus Dickey and Van Rossem (1938, p. 142) write of the White-breasted Chachalaca (*O. leucogastra*): "The long, extraordinary trachea, the loop of which reaches nearly to the end of the sternum, produces a volume and power which remind one of the bugling of a crane, and a full-voiced male can be heard a mile away." A long tube will have the effect of impeding higher frequencies, and of decreasing the range of frequencies transmitted (C.L. Harris, letter).

As described later, the trachea of some curassows is flattened and expanded for part of its length. Furthermore, the skin above the tracheal area is swollen or distended with blood vessels, at least during the season of booming. This condition exists in certain other birds that produce booming sounds, e.g. the North American Bittern (*Botaurus lentiginosus*). In some such birds, the "booming," or other

---

1) Department of Ornithology, American Museum of Natural History, Central Park West at 79th. Street, New York.



sound is believed to be produced by the expulsion of air from air sacs not connected with the trachea. Whether this is true of curassows, and the function of the flattened section, remains to be determined. The primary intention of this paper is only to consider the bearing of tracheal modification upon the classification of various races, species and genera of Cracidae.

The chachalacas (*Ortalis*) appear in general to be the least specialized members of the family. In the eight or ten species of this genus, the male (only) has a long loop in the trachea (Pl. XX, fig. 1.). This loop is "superficial" (as in all cracids in which one occurs), that is, it lies just beneath the skin and not coiled up in a dilated and hollowed pocket in the keel of the sternum as in some cranes and swans.

One species only, the Gray-headed Chachalaca (*Ortalis cinereiceps*) of Central America, does not utter loud, resounding "chachalaca" cries (Davis, 1965; Skutch, 1963). Nevertheless, the male of this form has a tracheal loop like that of the other members of the genus (Wetmore, 1965, p. 306). The form *garrula* to the southeast in Colombia does possess the usual strident chachalaca song (J. Haffer, letter). This is one reason why we (Delacour and Amadon, *ms*) follow Wetmore in regarding *cinereiceps* and *garrula* as distinct species. Nevertheless, as noted, *cinereiceps* seems to have "lost its voice" so recently that no change in the male's trachea has taken place. Though lacking the stentorian "chachalaca" outcry, it is still a noisy bird.

The next genus, *Penelope*, or "typical" guans, is the largest in the family, containing 13 species according to Vaurie (1968), or 15, as Delacour and I see them. As regards the trachea, one finds a tremendous variation from species to species. Thus, the Crested Guan (*purpurascens*) has no loop (Schaefer, 1953, and others), both North and South American races examined, the Marail Guan (*marail*) a small loop (Pl. XX, fig. 2.), and Spix's Guan a large loop like that of a male *Ortalis*. As compared with *Ortalis* and with the curassows (the only other Cracidae in which the trachea is sometimes specialized), *Penelope* has this significant distinction: the tracheal loop when present is found in both sexes, though slightly, but only slightly, smaller in relation to overall size in the female. This difference, along with the



absence of a wing drumming flight display in *Ortalis*, among other distinctions, convinces me that *Ortalis* is not as close to *Penelope* and other guans as one might conclude from some published statements.

In a pair of Spix's Guans (Pl. XXI) dissected in the field in 1968, I described the tracheal loops as follows: "In two, brought in together, perhaps a pair, the male had a very large loop in the trachea, which extended about 15 centimeters down over the pectoral muscle to within 3 centimeters of the end of the sternum, to which it was attached by a strip of muscle. In the female the loop was, considering her smaller size, a little, but only a little, less developed; it was about 12 centimeters in length and reached to within 5 centimeters of the end of the sternum." Perhaps the muscle observed is that referred to by **Beddard** (1898, p. 294): "Where the trachea is convoluted it sometimes happens that the extrinsic muscles are quite abnormal in their attachments; thus in the males of *Penelope pileata* and *Ortalis albiventris* [= *O. motmot araucuan*] the muscles in question do not enter the thoracic cavity, but pass close to the carina sterni and are inserted at the very end of the sternum."

Though *purpurascens* and *jacquacu* resemble each other closely, and have even been regarded as conspecific (**Vuilleumier**, 1965), the contrast in their tracheas suggests that the similarity may be superficial. At any rate, I would not place them together in a superspecies, much less the same species.

We turn now to another similar form, the Cauca Guan, *perspicax*. It has been regarded as a race of *purpurascens* by some authorities (**Hellmayr** and **Conover**, 1942, p. 137), while **Vaurie** (1966) makes it a race of *jacquacu*. *Perspicax*, now nearly extinct, is chiefly confined to the upper Cauca Valley of Colombia. It is primarily a subtropical (lower montane) species, while *purpurascens* and *jacquacu* are essentially lowland, tropical birds. The range of *perspicax* is almost or quite cut off from that of *jacquacu* by two southern prongs of that of *purpurascens*. For these and other reasons, I considered discretion to be the better part of valor, and called *perspicax* a species. This was before looking into the matter of the trachea. In view of the unexpected difference in those of *purpurascens* and *jacquacu*, the



situation in *perspicax* became of great interest. In reply to an inquiry, my friend Carlos Lehmann writes that he examined a *perspicax* (I assume a zoo bird, the trachea is easily felt through the skin) and that, like *purpurascens*, it has no tracheal loop! To me, this is sufficient evidence that *perspicax* cannot be a race of *jacquacu*, and is probably an offshoot of *purpurascens*, as seems more likely on geographical grounds, too. But it probably has reached species level.

It is true that a fourth species, the Dusky-legged Guan, *Penelope obscura*, which resembles the three just described, proves intermediate as regards the trachea. Professor Gunnar Hoy of Salta, Argentina, sends me a photo of the skinned carcass of one showing a small loop, about like that of *Penelope marail*. However, *obscura* is in no sense intermediate geographically between the others, but instead occurs south of *jacquacu* in Brazil, Uruguay, and Argentina. It may be related to *jacquacu*, though its tracheal loop is much smaller than in that species. The two are not conspecific, as Vaurie (1966: 12, 13) has convincingly demonstrated.

In the more specialized guans the trachea is, so far as known, always of normal configuration; there is no loop. At least this is true of the Piping Guan, *Aburria (Pipile) pipile* (all races or species), and the Wattled Guan, *Aburria aburri* and, apparently, of the Highland Guan (= "Black Chachalaca"), *Penelopina nigra*, as well as the two species of *Chamaepetes*, the Black and the Sickle-winged Guans. Some of these, notably the Piping, Wattled, and Highland Guans, have a whistled "song," which, at least in the Wattled Guan, is quite loud. Nevertheless, the trachea is simple. Referring back to *Penelope*: Spix's Guan emits a tremendously loud, discordant "crowing," not matched by the Crested Guan, which lacks a tracheal loop. Apparently the trend in guans is towards loss of the tracheal elongation, and (perhaps) loss of certain types of discordant outcries which are possibly homologous with those of chachalacas. It is tempting to go further and suggest that such outcries are being replaced by "instrumental" music—namely wing-drumming. The evidence does not support such a conclusion. All species of *Penelope*, so far as known, including Spix's Guan and others with a tracheal loop, are



PLATE XX.

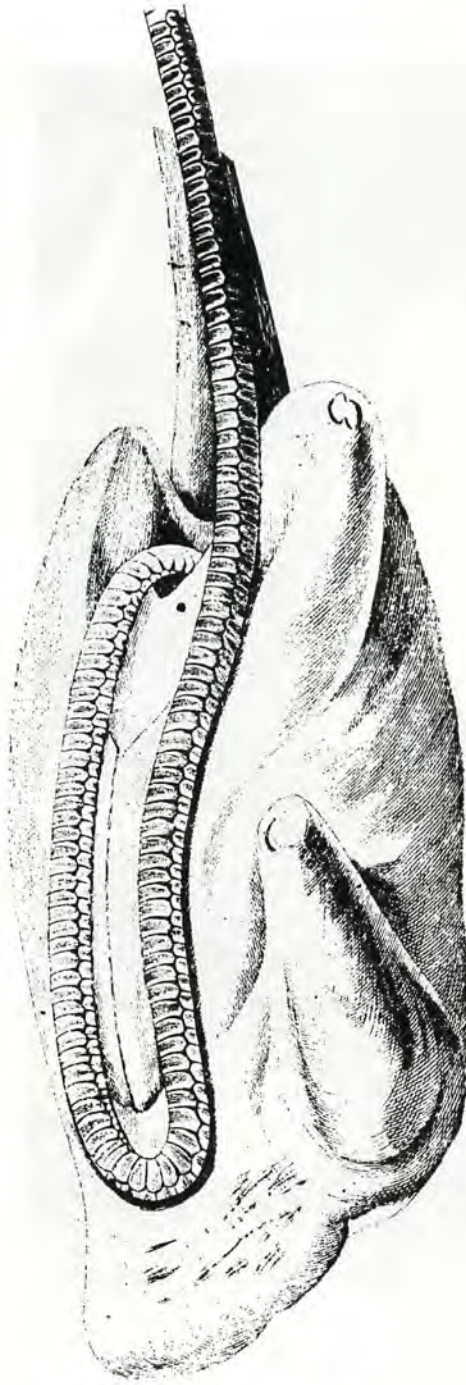


Figure 1. Trachea of a male chachalaca (*Ortalis motmot*), after Temminck.

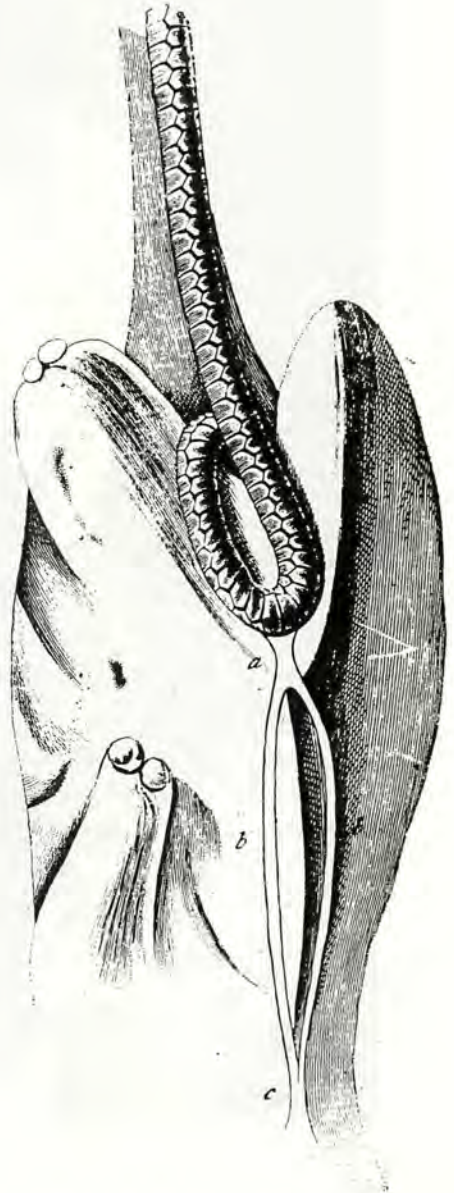


Figure 2. Trachea of a Marail Guan (*Penelope marail*), after Temminck.



PLATE XXI.



Figure 3. **Antonio**, collector and taxidermist at the Rancho Grande Station, Venezuela, bringing in a male and female Spix's Guan (*Penelope jaquacu orienticola*). Caño La Urbana, a tributary of Caura River, Venezuela.



PLATE XXII.

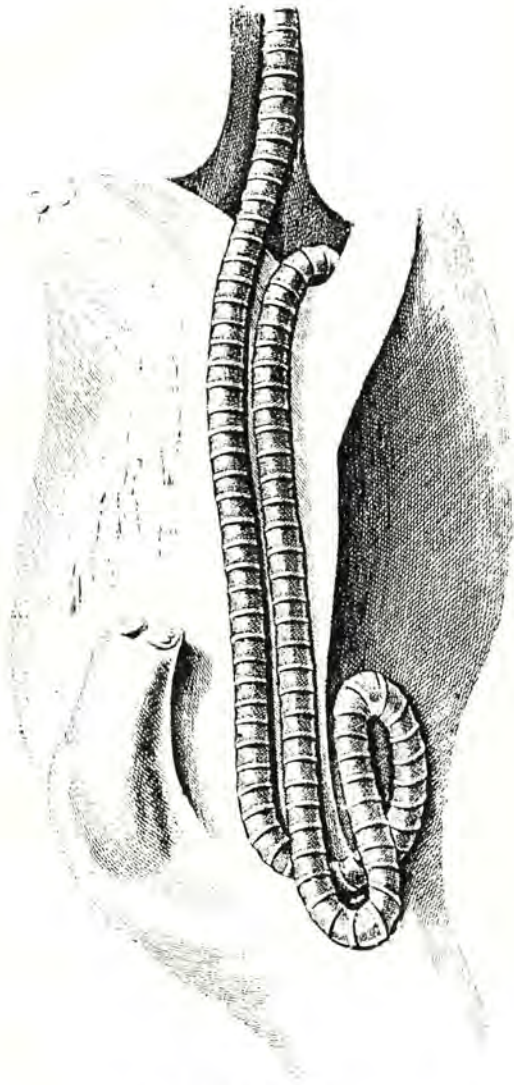


Figure 4. Trachea of a male Helmeted Curassow (*Crax pauxi*), after Temminck.

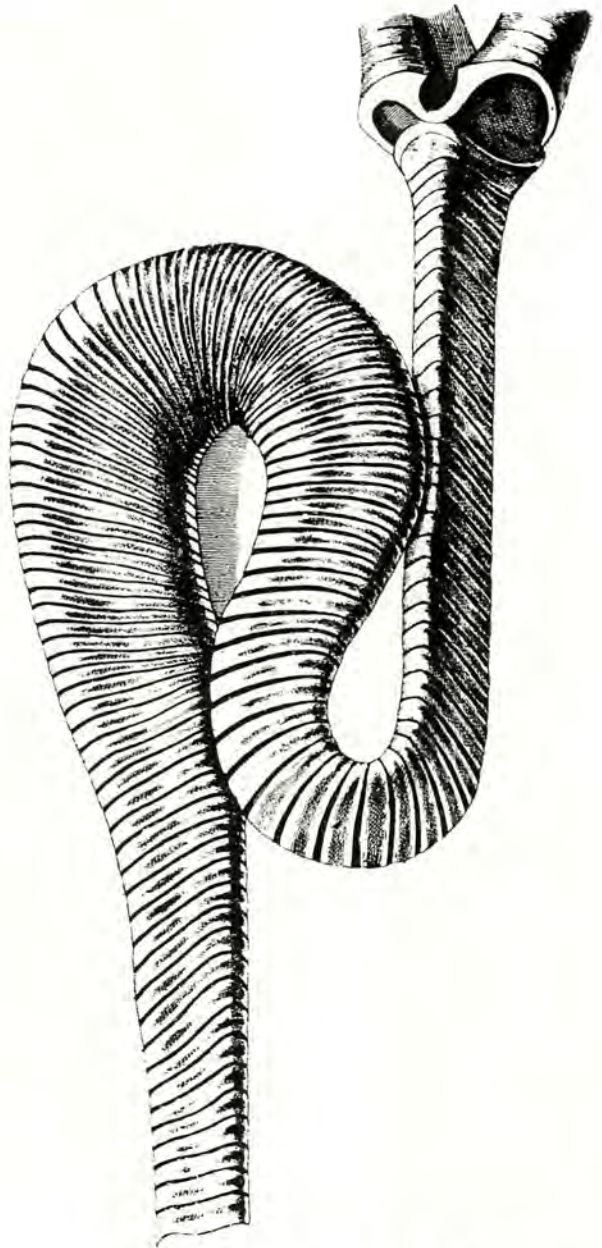


Figure 5. Trachea of a male Black Curassow (*Crax alector*), after Temminck.







confirmed wing drummers. On the other hand, although the tips of the primary quills are more incised in the Wattled Guan than in any *Penelope*, Schwartz found that it drums rather sparingly (at a season when it was in full song). This may be because it inhabits cloud forest where visibility is often poor. Its lowland relative, the Piping Guan, drums frequently; its sharply incised quill-tips producing a much sharper sound than the 'thump-thump-thump' of the *Penelope* guans.

The Horned Guan (*Oreophaps*) is so specialized that it is in a class by itself, but closer to the guans than to the curassows. It is said to utter a low-pitched "mooing," which suggests the "booming" of curassows and the possibility that it does, like them, have a tracheal loop. However, a male sent to G.E. Hudson by M. Alvarez del Toro does not have a tracheal loop (Hudson, in litt.), though it is thought the bird may be sub-adult.

### CURASSOWS

In curassows, tracheal modifications, where present, are again restricted to the male, as in chachalacas. Delacour and I classify the curassows as follows:

Genus *Nothocrax*: One species, *urumutum*, the so-called Nocturnal Curassow, better named the Urumutum.

Genus *Crax* (synonyms: *Mitu*, *Pauxi*)

(a) superspecies *Crax* [*mitu*]—the Razor-billed Curassow (*mitu*) and two allied species, *salvini* and *tomentosa*.

(b) superspecies *Crax* [*pauxi*]—the Helmeted Curassow (*pauxi*) and its Bolivian relative (*unicornis*), the latter perhaps only a subspecies.

(c) superspecies *Crax* [*rubra*]—the "typical curassows", or *Crax*, *sensu stricto*, with seven allospecies, ranging as a group from Mexico to Argentina.

The Helmeted Curassow, *Crax pauxi*, has a very long tracheal loop which, as will be seen (Pl. XXII. fig. 1.) extends even beyond the end of the pectoral muscle. That of the Razor-billed Curassow seems



to be the same. Its relatives, Salvin's and the Crestless (*tomentosa*) Curassows, also have long tracheal loops, but a photograph of that of the latter sent to me by Paul Schwartz suggests that it is not quite as long but about like that of a chachalaca (possibly the bird was not fully adult). Alexander Wetmore has kindly sent me a description of the trachea of a *Nothocrax*. The loop was well developed and had a special feature: at the place near the end of the sternum where it turned back, the diameter narrowed suddenly to about one-half of what it had been and so continued back and into the pectoral cavity.

In the "typical" curassows, *Crax [rubra]*, the situation is very different. None of the seven species has a long tracheal loop. Rather, the loop is short, as figured for the Black Curassow, *Crax alector*, and the trachea itself is flattened in the peculiar way shown (Pl. XXII. fig 2.). The anatomist Forbes (1875) referred to this very figure as follows: "The flattening of the trachea in male Cracinae, excellently depicted in Temminck's figure of *alector*, is lateral or from side to side, so that the well known notching of the rings of the trachea is on the thin edge of the flattened tube."

Most male curassows, including the Urumutum, the Helmeted, and the three species of the razor-billed group, have a very low-pitched song variously referred to as "booming," "droning," or "moaning." Five of the seven species of "typical" curassows, super-species *Crax [rubra]*, are "boomers," and probably all have a short tracheal loop and flattened trachea like that of *alector*. In addition to that species, the other four are the Great Curassow (*rubra*), the Blue-billed or Albert's (*alberti*), the Bare-faced or Sclater's (*fasciolata*), and the Red-billed or Blumenbach's (*blumenbachii*).

Remarkably, the remaining two species, the Yellow-knobbed (*daubentoni*) and the Wattled (*globulosa*), do not utter this low-pitched booming. Instead, their song is a peculiar high-pitched, leisurely whistle, "like air escaping from a bicycle tire" (P. Slud). This song is a "transferral;" such a whistle in sharper form is used by some other curassows, e.g., the Great, as a call of alarm or irritation. In fact, it is retained in this context, too, in the Yellow-knobbed and Wattled, but then uttered more emphatically. The whistle itself



seems to derive from shorter 'peet' alarm notes. Thus, a male Black Curassow, alarmed, uttered a 'peet peet peeer,' tending to trail off into a whistle like that of the other species.

It is certainly significant that the tracheal loop is less developed, or even sometimes lacking, in these two "whistlers." Schaefer said that in the breeding season, the old male of the Yellow-knobbed Curassow has the trachea swollen and slightly curved. This species is listed in some of the older literature as having a (small) loop, but there may have been an error as to the species. Or there may be individual variation, as seems to be the case in the Wattled Curassow.

I dissected an old male of the latter species, not in the best of condition, and saw no loop. G. Woolfenden more recently kindly dissected another for me and did find, if not a loop, at least a fold in the trachea. Since his description is the best we have, not only of this fold, but of the way in which the trachea in this group of curassows is flattened, I quote it. The loop in question lay within the interclavicular depression and did not extend out over the pectoral muscle.

"The total length of the trachea was about 390 mm. In the neck region, it measured 7 mm. in width, and in depth a little more, 10 mm. At about 170 mm. (from the glottis or throat end of the trachea) the depth (dorso-ventral) diameter of the trachea, already greater than its width as noted, began to increase and at about 240 mm. reached a maximum depth of 17 mm. (or more than twice its width). Before that point, however, between 180 and 240 mm. the trachea came to rest on its side with the right side uppermost. At about 240 mm. the trachea folds back on itself and continues in a forward direction for about 40 mm., after which it is abruptly curved back again. Shortly thereafter it narrows to about its original dorso-ventral diameter of 10 or 11 mm. and, passing through the interclavicular membrane, enters the thoracic cavity."



The two species of "whistlers" do not appear to be related to each other in any special way (the females are quite different) and their ranges are separated by that of the Black Curassow which has a booming song. It is possible, of course, that some "character displacement" is involved, i.e., that species recognition was easier once one of two inter-acting forms acquired a completely different song (as suggested to me by R. Banks). There are, however, instances in which two "booming" species must meet or nearly so, e.g., the Great Curassow and the Blue-billed (=Albert's). Further, we have ourselves listened to Black and Crestless Curassows droning away in the same woods. Their song differs in pattern, but in pitch and volume sounds similar. We had the impression that that of the Crestless Curassow, with its long tracheal loop, carried farther, but this requires confirmation. To be sure, these two belong to different superspecies.

What bearing do these modifications of the trachea in curassows have on classification? The fact that *Nothocrax* has a long tracheal loop like those of the razor-bill group, *Crax* [*mitu*], and the Helmeted Curassows, *Crax* [*pauxi*], suggests the special relationship shown by other resemblances. That we nonetheless keep *Nothocrax* apart, while putting the razor-bills and helmeted curassows in the genus *Crax* with the typical curassows, to which they may in the strict phylogenetic sense be less closely allied, merely shows that generic divisions must be based on an overall assessment of how divergent species, or groups of species, have become.

As to the bearing of the trachea on the general phylogeny of the curassows, it is with extreme trepidation that I come to the same conclusion as in the guans: namely, that they are in the process of losing a tracheal loop, not acquiring one. But surely one would not regard the Yellow-knobbed and Wattled Curassows as primitive? Rather, they seem to have lost the booming song of the others and in the process, to have nearly lost the tracheal loop, already reduced in the "typical" curassows. The latter, by and large, are more widely distributed and seem to be a more actively evolving group than the other curassows. To be sure, one cannot be certain of phylogeny by



analysing apparent trends in closely related contemporary living forms.

It must also be kept in mind that the typical curassows, even if, as we guess, they are losing rather than acquiring a tracheal loop, do have a specialization of their own, the curious flattening. The change in diameter in the trachea of *Nothocrax* mentioned above might be a first step in this direction.

We thus arrange the curassows in the order given above with *Nothocrax* first, followed by the razor-bills, helmeted, and finally the "typical" curassows. To be consistent, one should probably place the two "whistlers," *daubentoni* and *globulosa*, at the end. The characters of the seven species of "typical" curassows, however, present a checkerboard pattern, as will be set forth at greater length in the book mentioned above. They seem to form a single superspecies. One can scarcely do more than throw up his hands and use a more or less geographical sequence which, from north to south, would read *rubra*, *alberti*, *daubentoni*, *alector*, *globulosa*, *fasciolata*, and *blumenbachii*.

In passing, it may be noted that the "voice box" or syrinx, including its vibrating membranes, is unusually well developed in the Cracidae. Glen Woolfenden wrote me as follows: "The syrinx of a male Wattled Curassow (*Crax globulosa*) is large; its lateral diameter immediately before entering into the two short bronchii is 25 millimeters; there are large external and internal tympaniform membranes. All cracids examined by me (curassows and guans) have a relatively larger syrinx than sample specimens I have dissected of other gallinaceous birds, including grouse, pheasants, turkeys and guinea-fowls." Paul Schwartz remarks on the large tympanic membranes of a Wattled Guan (*Aburria aburri*). The syrinx of that species is figured by Garrod (1879).



## REFERENCES CITED

- Beddard, F.E. 1898. Structure and classification of birds. London, Longmans, Green and Co.
- Davis, L.I. 1965. Acoustic evidence of relationship in *Ortalis* (Cracidae). Southwestern Nat., 10: 288-301.
- Delacour, J. and D. Amadon. MS. Curassows and related birds.
- Dickey, D.R. and A.J. van Rossem. 1938. Birds of El Salvador. Chicago, Field Mus.
- Forbes, W.A. 1882. On the convoluted trachea of two species of manucode (*Manucodia atra* and *Phonygama*); with remarks on similar structures in other birds. Proc. Zool. Soc. London: 347-353.
- Gadow, H. 1893-1896. In Newton A., A dictionary of birds. London, Adam and Charles Black.
- Garrod, A.H. 1879. ...Trachea in the ...Gallinae. Proc. Zool. Soc. London: 354-380.
- Hellmayr, C.E. and B. Conover. 1942. Catalogue of Birds of the Americas, pt. 1, no. 1. Chicago, Field Mus.
- Newton, A. 1893-1896. A dictionary of birds. London, Adam and Charles Black.
- Schäfer, E. 1953-1954. Estudio bio-ecológico comparativo sobre algunos Cracidae... Bol. Soc. Venezolana Cien. Nat., 15: 30-63.
- Skutch, A.F. 1963. Habits of the Chestnut-winged Chachalaca. Wilson Bull., 75: 262-269.
- Slud, P. 1964. Birds of Costa Rica. Bull. Amer. Mus. Nat. Hist., vol. 128.
- Temminck, C.J. 1815. Histoire naturelle des pigeons et des gallinacés, vol. 3. Amsterdam, J.C. Sepp et fils.
- Vaurie, C. 1966. Systematic notes on the bird family Cracidae, no. 5. Amer. Mus. Novitates, no. 2250.
- . 1968. Taxonomy of the Cracidae (Aves). Bull. Amer. Mus. Nat. Hist., vol. 138, art. 4.
- Vuilleumier, F. 1965. Relationships...within the Cracidae. Bull. Mus. Comp. Zool., vol. 134, no. 1.
- Wetmore, A. 1965. Birds of the Republic of Panama, pt. 1. Smithsonian Misc. Coll., vol. 150.