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TRACHEAL ELONGATION IN BIRDS-OF-PARADISE

MARY H. CLENCH

Although elongated tracheae are relatively well known in certain groups of non-passerines such as swans, cranes, cracids, and guineafowl (e.g., Portmann 1950), study of their occurrence in passerines has been neglected. In this paper I shall review what is known about elongated tracheae in birds-of-paradise (mostly from the 19th century literature), and report on additional specimens that extend our understanding of the morphology of the phenomenon. In the hope of stimulating further study, I shall also offer some speculations on the function of what is a highly interesting, perhaps even spectacular, anatomical specialization.

MORPHOLOGY

The only passerine genera known to exhibit elongated tracheae are *Phonygammus* and *Manucodia,* closely related birds-of-paradise (Paradisaeidae). In both, the elongation is superficial, with the looped trachea lying on the ventral body surface between the skin and the body musculature, and held in place by connective tissue.

PHONYGAMMUS

An elongated trachea in passerines was first recorded in 1826 in the original description of the Trumpet Bird (*Phonygammus keraudrenii*) by Lesson (cited in Pavesi 1874). Lesson's figure and Pavesi's later studies (1874, 1876) on nine more specimens show that in this monotypic genus the trachea typically extends down the neck and then coils in a loop to the right, regularly or irregularly, over the pectoral muscles. In some specimens the trachea is so long that the coils extend down over the abdominal muscles as well, to cover virtually the entire ventral surface of the body. In most individuals the coils form a flat spiral, but occasionally one coil may lie on top of another. Very long and tightly coiled tracheae seem to be found only in adult males (seven specimens). In females (two specimens) the looped trachea is shorter, and merely bends laterally across the pectoral muscles, without forming a coil. Pavesi (1876) also noted that in females the trachea lies in a groove in the pectoral muscles, presumably to facilitate brooding. His specimens may have shown this condition through an artifact of preservation: no later authors have mentioned a groove.

In 1882 Forbes reported on six more specimens of *P. keraudrenii*: two males with tightly coiled tracheae; one female with a single curved loop (like Pavesi's specimens); another female in which the trachea apparently was coiled but less so than in males (Forbes's wording is ambiguous); a third female with an unelongated trachea (an adult with a mature egg in the oviduct); and a male, "probably young," with an unelongated trachea.

Since Forbes, several additional specimens have been reported (e.g., Rüppell 1933), but with few details. Recently I examined the following specimens in alcohol at the American Museum of Natural History: three whole adult males (Fig. 1), one fledgling, and four unnumbered "carcasses" from study skins collected by E. T. Gilliard (Fig. 2). In addition, three study skins in the AMNH collection have dried tracheae tied to them, and one has a label notation describing the tracheal configuration.

Although no one has had a long series in which to study the precise effects of age and sex on tracheal length, the present limited information (approximately 30 specimens) will support the hypothesis that young birds of both sexes of *Phonygammus* have simple, straight (unelongated) tracheae, and that as the birds age, males develop the extremely coiled condition whereas females develop fewer coils—and probably develop them more slowly. As a practical matter, the tracheal development of this species could be studied easily in captive birds. The skin is thin and, as the tracheal coils lie primarily under the ventral apterium, they are readily visible and can be measured without doing injury to the bird.

MANUCODIA

In this genus the elongated trachea forms a single loop that extends a variable distance down the ventral body surface, but does not coil. The tracheal lengths of even fewer specimens of this genus have been recorded, but it appears that length may differ in the four species of *Manucodia.* According to both Forbes and D'Alberti (Forbes 1882), the Glossy-mantled Manucode (*M. ater*) has only a short loop in the male. The Green-breasted Manucode (*M. chalybatus*) was reported by Pavesi and by Salvadori (Pavesi 1876) to be

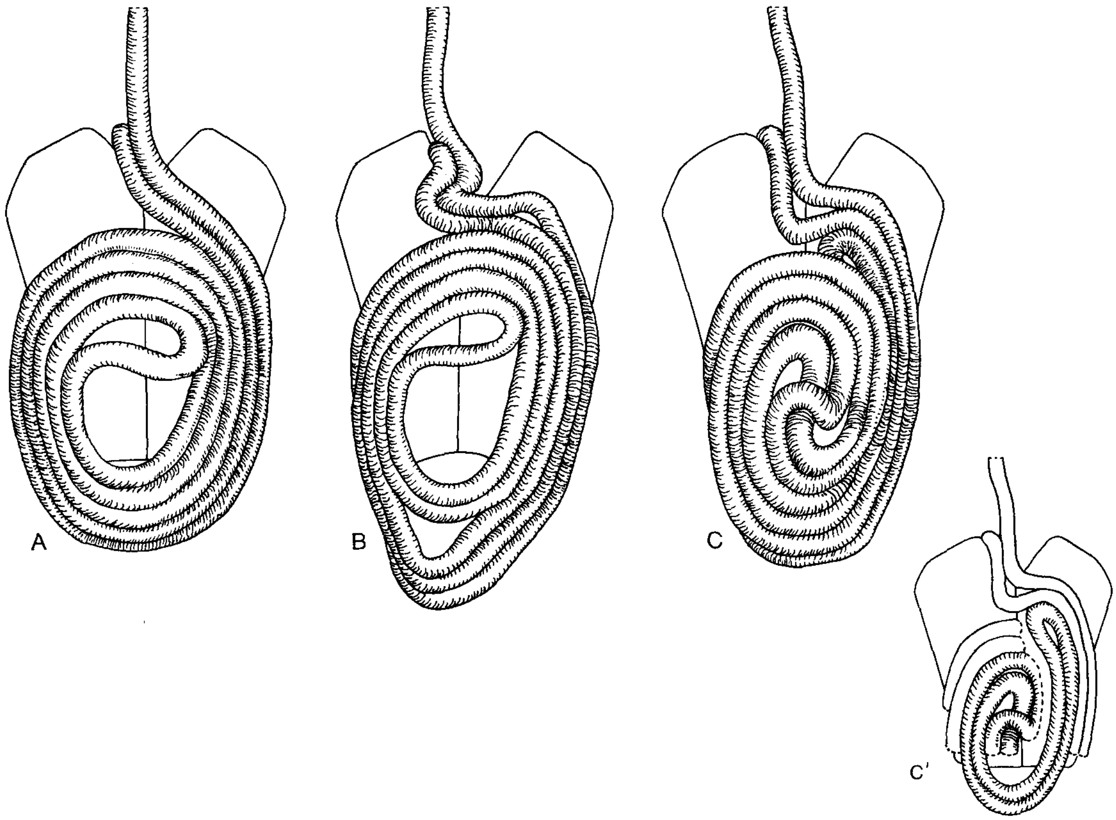

FIGURE 1. *Phonygammus keraudrenii* (probably *jamesii*, cf. Crandall 1935); AMNH Alc. Coll. nos. 17, 19, 18, all *ex* N.Y. Zool. Park. AMNH 18 (C, C′) was at least 13 years old when it died, its trachea is overlapped in two places, and is approximately 750 mm long.

similar to the Jobi Manucode (*M. jobiensis*): both have single-looped tracheae that extend about ⅔ the length of the thorax. Salvadori added that in *chalybatus* the elongation occurs only in males, that older males have longer tracheae than do young males, and that in very young males the tracheae are not elongated. In the Curl-crested Manucode (*M. comrii*) the trachea is even longer. Beddard (1891) figured a specimen in which it extends the full length of the ventral body surface before doubling back on itself to ascend to the furcular region.

To this information I can add notes on several specimens at the AMNH and on one from the British Museum (Natural History). None of the few female alcoholic specimens of any species of *Manucodia* I have examined has an elongated trachea, and none of the female study skins in the AMNH have tracheal notations on the label. The single additional alcoholic specimen of an adult male *M. ater* consists solely of an excised trachea (AMNH, unnumbered). This trachea is approximately 75 mm long from the posterior end of the glottis to the beginning of the bronchi, and forms a short loop of approximately 34 mm. It agrees well with the specimen of *ater* figured by Forbes (1882). The carcass of an adult male *M. chalybatus* collected by Gilliard has a much longer trachea, with the loop extending just beyond the posterior border of the sternum (Fig. 3). Gilliard remarked in his field notes that when this specimen was prepared "It had the trachea so greatly enlarged that the native skinner took fright, thinking it was a giant worm." A description of this trachea appears in Gilliard and LeCroy (1967). A sketch on the skin label of another male *chalybatus* (AMNH 427595) shows a similar tracheal configuration to that of Gilliard's specimen—a simple loop extending just posterior to the sternal border.

Five additional specimens of *M. comrii* demonstrate the much greater elongation of the trachea in this species. One AMNH carcass has a relatively short trachea that curves to the right at the posterior border of the sternum (Fig. 4a). Another (Fig. 4b) is longer, with the curve well down over the abdomen and the end of the loop also extending up as far as the furculum. In both a third

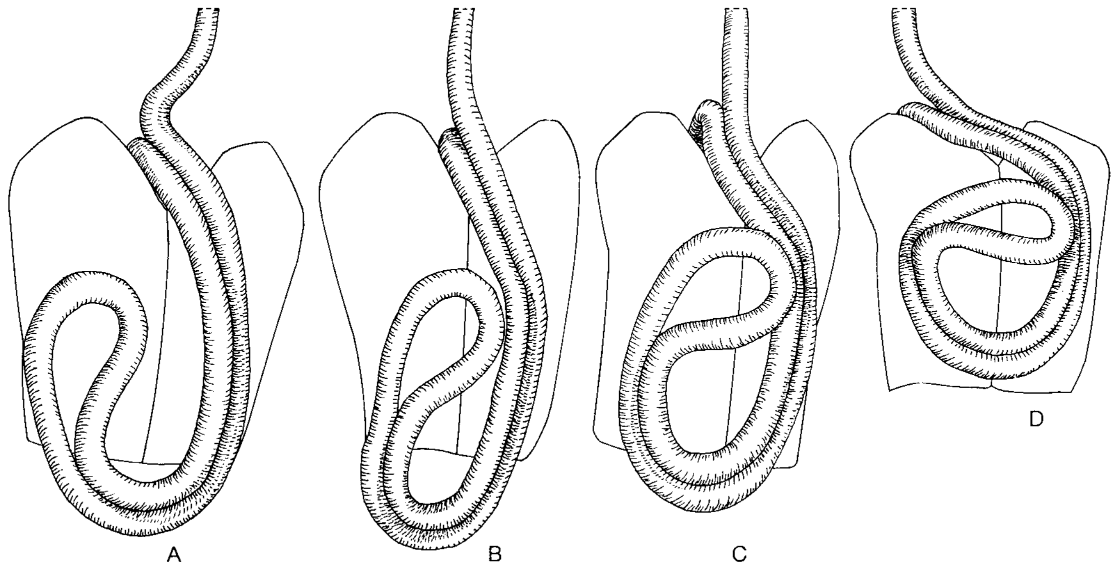

FIGURE 2. *Phonygammus keraudrenii adelberti.* This series suggests the manner in which an elongating trachea begins to coil. Carcasses from AMNH Alc. Coll., all males with enlarged testes; coll. E. T. Gilliard.

carcass from the AMNH and a whole specimen from the BM (1905.9.18.9) (Fig. 4c) the trachea descends on the left side of the body, then curves slightly to the right of the cloaca and along the right side of the tail musculature. It then makes a loop back to the ventral side of the body and extends anteriad approximately ⅔ the length of the right side of the body before making a wide loop to double back to the cloaca. From the cloaca it extends anteriad, packed closely between the ascending and descending loop on the right side of the body and the original descending loop on the left, and enters the body cavity on the right side. Its visible length is 627 mm.

In another whole adult male of *comrii* (AMNH Alc. Coll. no. 12, Fig. 5) the tracheal configuration on the ventral surface is almost identical to that figured by Beddard (1891). The trachea does not, however, turn to double back at the posterior end of the body. It continues to extend around the body, passing to the right of the cloaca and up along the right side of the synsacrum for approximately 50 mm. At the level of the right acetabulum it loops tightly back on itself, returns to the ventral body surface and then follows the original descending loop to enter the body cavity on the right side. The total visible length is 511 mm.

Thus, in *Manucodia comrii*, when a growing trachea reaches the end of the body, further growth does not result in a ventral spiral as in *Phonygammus*. The extension may lie in part along the dorsolateral plane, and (as in the only available specimen with a truly long trachea) may then return to the ventral surface, forming folds parallel to the original course of the trachea.

DEVELOPMENT

For the mechanism by which these tracheae achieve their remarkable length, we have no information from studies of living birds. Instead, we can only try to reconstruct the process from the limited series of dead specimens that is available.

All known young individuals of both genera have simple, straight tracheae. The stub-tailed fledgling *Phonygammus* (AMNH Alc. Coll. no. 20) has such an unelongated trachea, approximately 47 mm long, with some 73 tracheal rings visible without dissection. The outside diameter of this young trachea varies from 4 to 5 mm, with the rings narrow (0.5 to 1 mm wide) and strongly compressed and packed together. The internal lumen diameter of the trachea is 2.5 to 3 mm. In contrast, an adult *Phonygammus* (AMNH Alc. Coll. no. 19, Fig. 1b) has a trachea that is 828 mm long, and contains approximately 150 rings. Most of this bird's rings are 5 to 7 mm wide, but some are as much as 22 mm, primarily where the trachea is acutely curved. As with all the spirit specimens I examined, the trachea is hard, but the degree to which this hardness is a result of preservation is unknown—the tracheae of some specimens are slightly more elastic than others. The preserved coil is a surprisingly rigid structure (Pavesi called it

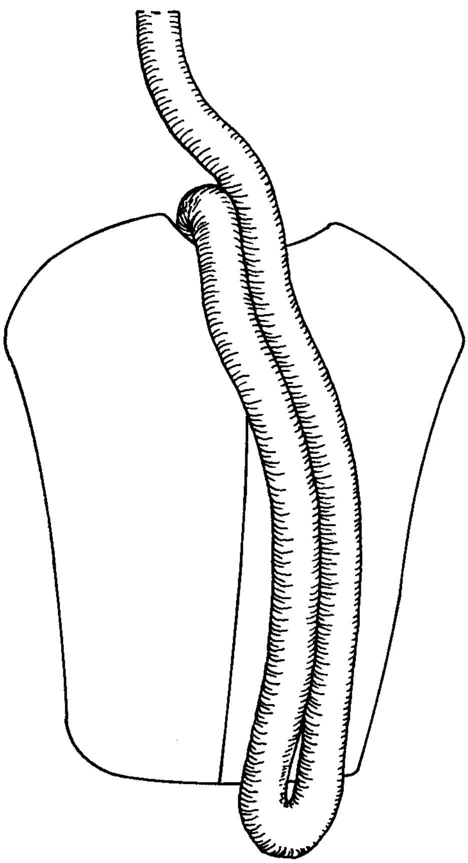

FIGURE 3. *Manucodia chalybatus.* Male, cf. Gilliard and LeCroy 1967.

a "shield"), with little connective tissue between the closely apposed segments. I was able to make approximate measurements on two of the *Phonygammus* carcasses with relatively short and uncoiled tracheae: 90 rings total 315 mm in length (Fig. 2c) and 100 rings total 300 mm (Fig. 2d). The outside tracheal diameter of all seven AMNH adults in alcohol averages about 3.5 mm, but the lumen is 2.5 to 3 mm: the same as in the juvenile. Hence it may be reasonable to assume that as a bird ages, the trachea lengthens both by differential longitudinal growth (widening) of the rings already present, and by the formation of additional rings. During this process, although the walls of the tracheal rings become thinner as the ring widens, the diameter of the lumen seems to remain constant at 2.5 to 3 mm.

The few other *Phonygammus* specimens whose tracheal lengths have been reported have all been adult males: three specimens have tracheae ranging from about 450 to 550 mm long, and containing from about 100 to 120 rings. (My uncertainty here results both from Pavesi's measurements being in *pollici*, which I have been assured by several people fluent in Italian is the equivalent of the English inch, and from having to resort to counting the number of rings visible in Pavesi's apparently meticulously drawn illustrations, as he gave few ring counts in his text.) None of these measurements has been from an individual with an extremely long trachea, but what is more significant is the same lumen diameter reported in a 500 mm-long trachea: 2.5 to 3 mm (Rüppell 1933). Unfortunately most of the other measurements available in the literature seem to have been published for their astonishment value (e.g., Ogilvie-Grant 1904)— perhaps understandable in view of the incredible lengths involved. For example, the 828 mm trachea of the adult *Phonygammus* noted above is almost as long as the normal trachea of an Ostrich (*Struthio camelus*, 910 mm; Hinds and Calder 1971), while *Phonygammus* has approximately the body size of a Common Flicker (*Colaptes auratus*, which has a tracheal length of about 38 mm).

DISCUSSION

In 1971 Hinds and Calder published a study of the tracheal dead air space in the respiration of birds. They were particularly concerned with the increased length of the avian trachea, compared to that of mammals of equivalent body weight, and the consequent increase in mechanical resistance of air flow within the longer cylinder in long-necked animals. They showed that, in general, birds compensate for the added resistance by having a greater tracheal diameter (lumen width) and hence greater air volume in that trachea (4½ times that of mammals of equal body mass), in turn partially compensated for by a lower respiratory rate. Non-passerine birds with elongated tracheae, however, have much greater tracheal volumes for their body mass than do those with straight tracheae: Whistling Swan (*Olor columbianus*) 2.4 times greater; Trumpeter Swan (*O. buccinator*) 3.8×; and Sandhill Crane (*Grus canadensis*) 3.2× in the male, 2.4× in the female—compensating for the increased tracheal length by an increased width of the lumen.

Hinds and Calder did not measure a bird-of-paradise, although they were aware of the condition: "The trumpter manucode and the whooping crane have also inherited a respiratory inexpedience of similar or greater severity [than the Trumpter Swan]" (1971:438). Hinds and Calder were using (usually) fresh specimens, measuring the length of the tra-

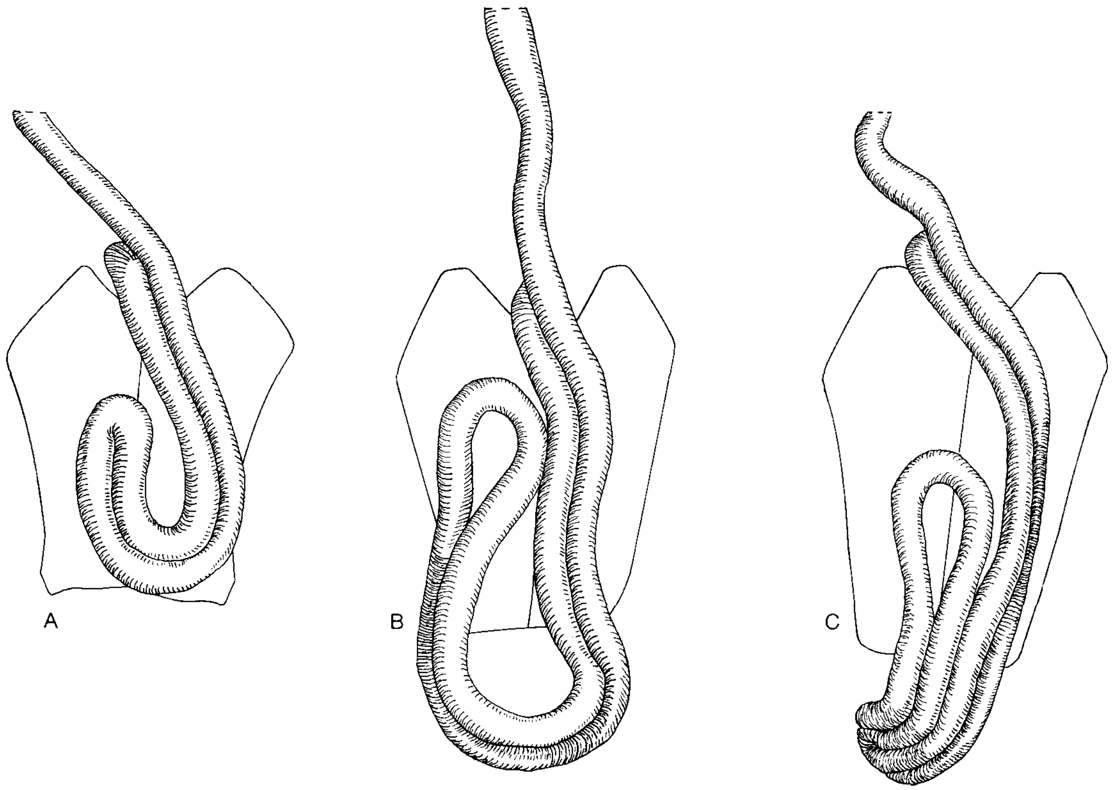

FIGURE 4. *Manucodia comrii.* A, B: carcasses from AMNH Alc. Coll.; C: BM 1905.9.18.9.

chea from the glottis to the syrinx, and comparing tracheal data with body weights. For the paradisaeids, I have seen only preserved specimens of unknown fresh weights, and a few weights of other individuals recorded on the labels of study skins. To avoid damage to rare, perhaps irreplaceable specimens, my measurements of tracheal length have been limited to the visible portion of the trachea: from the glottis in carcasses or from near the glottis in whole but skinned alcoholics, to the furcular region where the trachea enters the body cavity. Hence calculations exactly comparable to those of Hinds and Calder cannot be made. I can, however, suggest that tracheal (lumen) diameters of 2.5 to 3 mm in preserved *Phonygammus keraudrenii* and 4 to 6 mm in *Manucodia comrii* do not sufficiently compensate for the elongated tracheae in these birds, compared to other passerines. I make this suggestion from the following data: single fresh specimens of Black-billed Magpie (*Pica pica*) and (presumably) Great-tailed Grackle ("*Cassidix mexicanus*") measured by Hinds and Calder both had 3 mm lumen diameters. These species have a body size comparable to that of *Phonygammus*. The weight of the magpie used by Hinds and Calder was 156.2 g; that of the grackle, 159 g. The mean weight of 12 specimens of *P. keraudrenii* (males only, three subspecies pooled) is 166.2 g, range 130–190 g. Unfortunately I have been unable to locate any weights for *M. comrii. M. ater* males average 219.4 g (n = 7), *M. chalybatus*, 236 g (n = 6), and a single *M. jobiensis*, 232 g; but *M. comrii is* considerably larger than the other three species in this genus (male *comrii* wing measurements range from 219 to 248 mm, compared to 159 to 208 for the others [Gilliard 1969]). Hinds and Calder reported the tracheal length of a preserved Whistling Swan as 876 mm (vs. a visible length of 828 in the *Phonygammus*), yet its tracheal diameter was 10.8 mm (vs. 2.5 to 3 mm in *Phonygammus*). The same measurements in preserved Trumpeter Swans were 1210–1350/12.2–12.3 and in preserved Sandhill Cranes, 605–691/8.1–9.0. As Hinds and Calder showed, preservation reduces tracheal dimensions slightly, hence these swan and crane figures as well as those from the birds-of-paradise above represent minima for living birds. It is therefore clear that *Phonygammus* and *Manucodia* have approximately the same tracheal lumen measurements as "normal" passerines of similar body weight, and much smaller lumens than non-passerines with elongated tracheae.

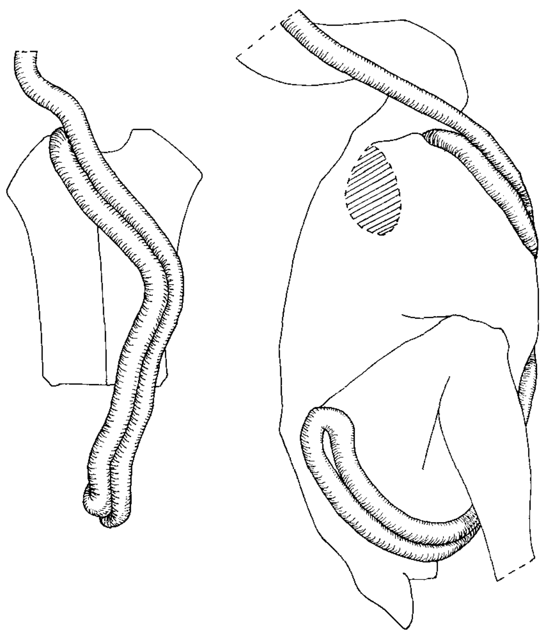

FIGURE 5. *Manucodia comrii.* AMNH Alc. Coll. no. 12; ventral and right lateral aspects.

There is also a serious discrepancy in comparative tracheal volumes. According to my rough estimates, the fledgling *Phonygammus* with a straight trachea had a minimum dead air volume of 0.33 cc in its trachea; the adult (AMNH Alc. Coll. no. 19) had a min. 5.85 cc. The *Manucodia* (AMNH Alc. Coll. no. 12) had a min. 10.03 cc. For comparison, Hinds and Calder reported a tracheal volume of 0.48–0.49 cc in the magpie and grackle and 80.25 cc in the Whistling Swan.

Phonygammus and *Manucodia* may have some additional form of compensation—physiological, behavioral, or morphological—to compensate for the high volume of dead air in their tracheae. I have searched for a connection between the ascending and descending portions of the tracheae, but have found no shunt mechanism that could act to bypass the elongated section. A compensating mechanism, if it exists, might be found through study of living birds.

It is also possible that a compensating mechanism does not exist. Hinds and Calder paid insufficient attention to the strong differences between avian and mammalian respiratory systems, especially the extensive air sac system in birds. Abbot S. Gaunt advises me (pers. comm.) that birds are much less susceptible to the problems of dead air space than are mammals. The expansile portions of the avian respiratory system are large and are not subject to the surface tension problems found in mammalian lungs. Hence the energy consumed in moving air across those surfaces is considerably less. In addition, the flow across the exchange surface is unidirectional, and the ability of birds to extract oxygen greatly exceeds that of mammals. Also, with the air sac system occupying as much as 25% of the volume of the body cavity, the potential tidal volume is enormous, especially in comparison with the dead air space in the trachea. Thus the amount of tracheal dead space is of comparatively less importance to birds than to mammals, except during periods of strenuous and prolonged activity when it could become critical. It may be that these birds-of-paradise can "afford" a greatly elongated trachea because they are sedentary (non-migratory) and, being relatively large forest birds, their daily flight distances are probably short and predators can be avoided by short dodging flights around foliage. All of these assumptions remain to be tested.

VOCALIZATIONS

One can also speculate on how this extreme tracheal elongation affects the vocalizations of the living birds. As with so many New Guinea and tropical Australian species, little is known of the habits of *Phonygammus* and *Manucodia.* Following the conclusions of Marion (1977) who studied the elongation of the trachea in maturing male Plain Chachalacas (*Ortalis vetula*), it is reasonable to assume that the tracheal elongations of birds-of-paradise also serve to lower the pitch of, and perhaps amplify, their vocalizations.

Concerning *Phonygammus*, Thorpe (quoted in Gilliard 1969:105) wrote "The males utter a very loud and deep guttural note, unlike that of any other bird I am acquainted with, and it astonished me that a comparatively small bird could make so much noise." Ralph Bulmer (field notes on file at the AMNH) remarked that *Phonygammus* is "a very noisy, obvious, tree-top feeding bird." Gilliard (1969) also characterized the species as having "powerful call notes."

I have been able to find few descriptions of the calls produced by *Manucodia.* The vocalizations of *M. ater* include whistles and a deep "chug" call (Rand 1938) and a "long-drawn-out plaintive whistle" either on one note (Mackay 1970:52) or tremulous (Anon. 1972). *M. jobiensis*, and possibly also *M. ater*, has a "long-drawn moaning cry" (Gilliard 1969). *M. chalybatus* has a staccato "tuk" call (Diamond 1972) and "a deep short 'whoo', like a pigeon or coucal, given after great swelling of the chest, rather like the Trumpet-bird" (Anon. 1972:5). Gilliard also remarked that, as *M. jobiensis* and *chalybatus* are sympatric over much of their range, and as their plumage is very similar, their isolating mechanisms must be "almost entirely behavioural (probably chiefly vocal)" (1969: 100). The vocalizations of *M. comrii* do not seem to have been reported. Information about them would be particularly useful, for this manucode exhibits the greatest elongation of the trachea.

In a description of captive "Manucode" (probably *Phonygammus*) vocalizations, Seth-Smith (1923:56) reported: "[the coiled trachea] doubtless accounts for the peculiar note of these birds, which, although, not loud, is penetrating and audible at a considerable distance. Before uttering this the bird raises its wings and extends the body, the note being emitted as the wings are lowered and the body contracted, the sound being, as it were, pumped out of the body through the specialized trachea." Both this description and that of *Manucodia chalybatus* (Anon. 1972) suggest that a call is produced only after a bird has taken an especially deep breath.

TAXONOMIC POSITION

Phonygammus and *Manucodia* were long considered generalized and crow-like primitive members of the Paradisaeidae (c.f. Stonor 1938). This was chiefly because they lack specialized courtship and breeding behavior; are not sexually dimorphic; and have relatively simple black plumage, although some of the feathers are structurally modified. In his study of the relationships of the birds-of-paradise and bowerbirds, Bock (1963) emphasized that, from skull characters, *Manucodia* and *Phonygammus* are not primitive but are as specialized as the ornately-plumed *Paradisaea.* He also speculated that the plain plumage and normal courtship and breeding habits are secondarily primitive, with the similarities to corvids being convergent. From the tracheal evidence (which Bock also mentioned) I agree that these two genera are, indeed, highly specialized. Unlike the rest of the family, however, these birds' specializations seem to lie primarily in their vocal structure and behavior—particularly in the quality, pitch, and volume of sound. If a greatly elongated trachea is a physiological liability, the vocalizations it produces must be sufficiently compensatory to the species to be adaptive.

SUMMARY

The morphology of the elongated tracheae in two genera of paradisaeids is described. In *Phonygammus* the trachea is unelongated in young birds but as they age, males develop a long spiraled tracheal coil on the ventral body surface beneath the skin; females develop a shorter loop or coil and probably develop it more slowly. In *Manucodia* the trachea lengthens as a loop rather than a coil. It has been found only in adult males and is probably species-specific, with minimum development in *M. ater* and maximum in *M. comrii.* The longest trachea recorded in *Phonygammus* is 828 mm; that in *Manucodia comrii* is 627 mm (both minimum measurements).

Speculations are offered on the physiological implications of this tracheal specialization. Both genera have approximately the same tracheal width (lumen diameter) as other passerines of similar body weight, and much smaller lumens than non-passerines with comparably elongated tracheae. The elongations may or may not be a serious physiological liability. Comments are also made on the possible effects of tracheal elongation on these birds' vocalizations.

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Abbot Gaunt generously shared his experience with avian respiratory systems. He also offered the suggestion that *Phonygammus* and *Manucodia* are not really birds, but clever wind-up toys: the supposed elongated trachea is actually a power spring that has been enclosed in a thin membrane to keep it waterproof. "Males" are simply the wound-up version, "females" the run-down version.

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