THE FUNCTION OF THE OESOPHAGUS IN THE BITTERN'S BOOMING.

BY JAMES P. CHAPIN.

Plate VI

ON May 4 1921 the American Museum received from West Nyack, N. Y., an adult male American Bittern which immediately aroused our interest, because of the unusual thickening of the skin of its neck. This exhibited a flabby, oedematous condition like that commonly met with in the "brood-spot" on the breast of an incubating bird. The looseness and great width of this skin, thanks to the sparseness of the feathers on the back of the neck, are well shown in Pl. I, Fig. 2, from a photograph of the dead bird. I was at once reminded of the condition I had observed in the male of an African Rail, *Sarothrura elegans*, which seemed beyond a doubt to inflate its oesophagus with air to use it as a resonating organ for its remarkable voice.

Thus we sought to inflate the neck of the Bittern, blowing through a glass tube. By inserting this in the glottis it was a simple matter to expand the air-sacs of the body, especially the abdominal ones, but also a pair just behind and below the wings, and the "cervical" sacs between the clavicles. Yet there was clearly no connection here with any air-sac in the neck proper, and indeed the Hornbills are almost the only birds known to possess such a connection in the pneumatic system. A number of other birds, however, the best type of which is the Marabou Stork (*Leptoptilos*), do have so-called "cervico-cephalic" sacs that extend down the neck from the head, and receive air from the nares, whence it passes through the space beneath the eye-ball.

Our Bittern was tested for such sacs in the neck by blowing strongly into the internal nares. A slight bulging of the sub-ocular region resulted, but this did not extend to any air-cavity in the neck; nor could we obtain any better result by blowing directly into the air-space under the eye through a large hypodermic needle. Cervico-cephalic air-sacs were entirely wanting.

This left only one organ in the neck that might be filled with air: the oesophagus itself. Blowing straight into the gullet it was easy to distend the neck throughout its whole length, until it

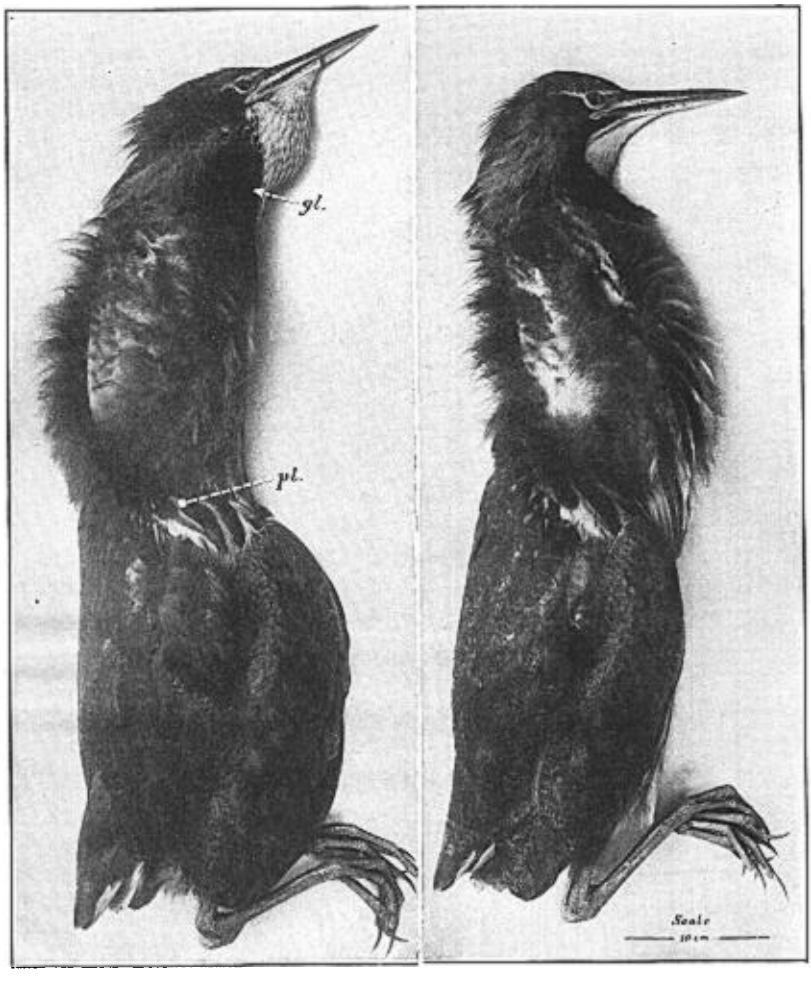

Fig. 1. Adult male American Bittern in breeding season when oesophagus is blowm up with air; *gl.* indicates the position of the glottis at this time: *pl.* marks the point where the white plumes are inserted in the skin. Inasmuch as the air-sacs of the body are also expanded, it will be evident that none of them is concerned with elevating the white feathers, here scarcely visible.

Fig. 2. Bittern in the breeding season, to show the width of the neck here completely deflated. (Photos supplied by the American Museum of Natural History).

measured 10 centimeters in diameter; and when the bill was held closed, this air escaped only very slowly, even though no effort was made to close the nostrils. To make the photograph shown in Pl. VI, Fig. 1, it was necessary to place a small rubber band round the bill, and a small piece of damp cotton in the mouth. The glottis seemed unusually free from the hyoid arch or base of the tongue, and lay relatively far back in the throat. When the neck was moderately distended with air, the glottis was situated six centimeters behind the posterior angle of the gape, while the tip of the long slender tongue still reached just to the angle of the gonys, quite well out in the beak.

One unusual feature of this Bittern's mouth still remains to be mentioned. When the tongue came up it passed between or below two curious elongated pads placed on the inside of the mandibular rami, and nearly touching in the center. These we had never noticed before in any member of the Heron family, and it may well be that they have something to do with keeping the air in the gullet, especially since their internal structure resembles that of the thickened skin of the neck, and they are apparently only enlarged temporarily. When the bill is closed these pads lie well in front of the internal nares as may be seen in Figure 2, so they cannot serve to block the nostrils, but rather to close the mouth itself more tightly.

Supposing then that the Bittern does swell its oesophagus with air, how does this proceed? It might conceivably swallow one gulp of air through the action of the tongue and hyoids, but I do not think it could engulf a second mouthful while still retaining the first. As for sucking air into the lower oesophagus, there is no adequate mechanism available. Far more likely I should consider it, that the air is forced into the oesophagus through the trachea, by closing the beak and driving the breath from the air-sacs of the body. The distance to which the glottis can be retracted into the throat renders this more probable.

Thus far my statements may seem highly hypothetical, and I confess that I have never seen a Bittern dilate its neck. I simply believed that it might do so from analogy with other birds like the Pectoral Sandpiper, in which the practice is well known.[1] But fortunately there is an excellent and detailed account, in Brad-

[1] Cf. Nelson, Auk, 1884, pp. 218–221.

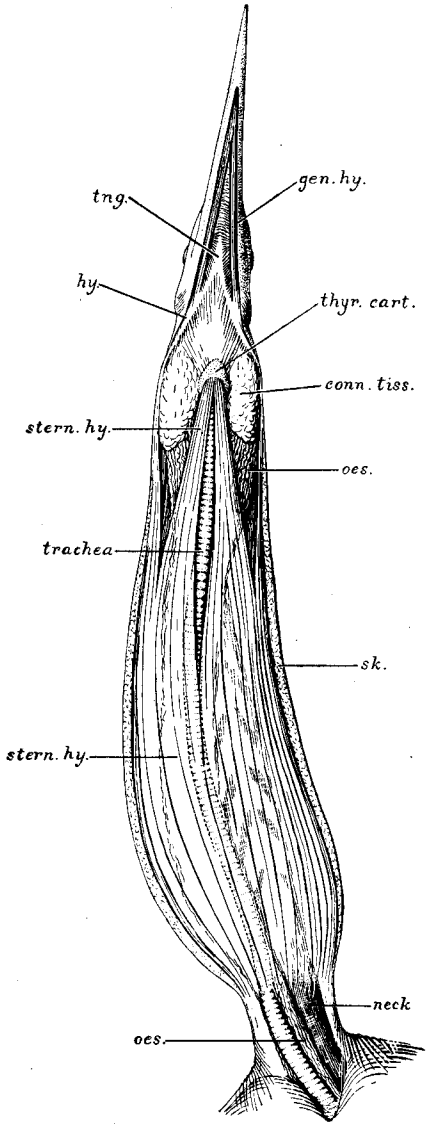

Fig. 1

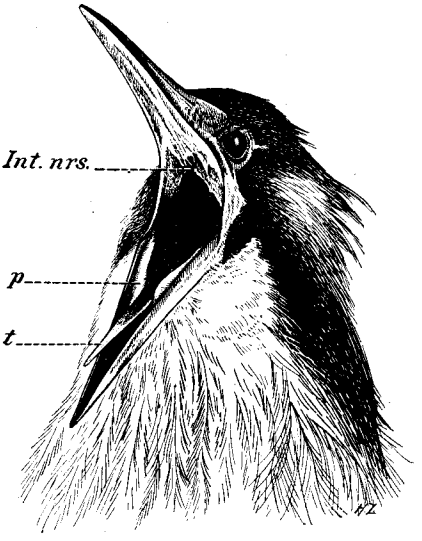

Fig. 2

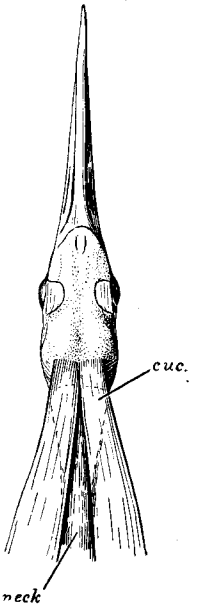

Fig. 3

ford Torrey's 'Everyday Birds' (1901) pp. 69–81, of the actions of several Bitterns as seen during their spring "pumping" in a Massachusetts marsh. On taking up this charming little book, after many years' neglect, I was surprised to find how closely my hypothesis tallied with Torrey's conclusions after watching the live bird. I cannot do better than to quote him directly:

"The Bittern has been standing motionless . . . . ."

"Suddenly he lowers his head, and instantly raises it again and throws it forward with a quick, convulsive jerk. This movement is attended by an opening and shutting of the bill, which in turn is accompanied by a sound which has been well compared to a violent hiccough. The hiccough—with which, I think, the click of the big mandibles may sometimes be heard—is repeated a few times, each time a little louder than before; and then succeed the real pumping or stake-driving noises.

"These are in sets of three syllables each, of which the first syllable is the longest, and somewhat separated from the others . . . .

"But the looker-on is likely to quite as much impressed by what he sees as by what he hears. During the whole performance, but especially during the latter part of it, the bird is engaged in the most violent contortions, suggestive of nothing but a patient suffering from uncontrollable nausea. Moreover, as soon as the preliminary hiccoughs begin, the lower throat or breast is seen to be swelling; the dilatation grows larger and larger till the pumping is well under way; and so far as my companion and I could detect, does not subside in the least until the noises have ceased altogether.

Explanation of figures on p. 198.

Fig. 1. Neck of the Bittern, partly dissected, skin removed from lower side, leaving superficial muscles intact. Oesophagus not inflated; *conn. tiss.*, mass of swollen connective tissue at sides of throat; *gen. hy.*, genio-hyoid muscle; *hy.*, hyoid arch; *oes.*, oesophagus; *sk.*, thickened skin, seen in section; *stern. hy.*, sterno-hyoid muscle, ensheathing the neck below. *thyr. cart.*, thyroid cartilage, lying beneath glottis; *tng.*, base of tongue, as seen through floor of mouth. One-third natural size.

Fig. 2. Open mouth of male Bittern in Spring; *int. nrs.*, the opening of the internal nares; *p.*, one of the pads on the inside of the mandible, between which the tongue, *t*, protrudes. (From photo supplied by the American Museum of Natural History.)

Fig. 3. Skinned head of Bittern, from above, showing the occipital portion of the cucullaris muscle, *cuc.*, attached to back of skull. One-third natural size.

"How are the unique, outlandish notes produced? I cannot profess to know. Our opinion was that the bird swallowed air into his gullet, gulping it down with each snap of the beak. To all appearance it was necessary for him to inflate the crop in this way before he could pump, or boom. . . .

"I made some experiments afterwards, by way of imitating the noises, and these experiments, together with the fact that the grand booming seemed to be really nothing more than a development of the preliminary hiccoughs, and the further fact that the swelling of the breast did not go down gradually during the course of the performance, but suddenly at the close,—all these incline me to believe that the notes are mainly if not entirely caused by the inhalation or swallowing of the air . . . "

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The only point on which I cannot agree with Torrey is the "swallowing" of the air, which is mechanically so difficult to explain. I believe rather that it comes from the trachea through the glottis.

To examine further the structure of the accessory vocal organs, since it would seem still as though the sound must originate in the syrinx, I made a thorough examination of the neck and its covering, Rolling up the skin of the neck from below, I found the walls of the oseophagus as thin as usual, and extensible as they always are in a Heron's or Bittern's neck. There was no trace of true air-sacs, all dilation must involve the oesophagus alone. But the skin of the neck, down to a point close to the shoulders, was very much thickened all the way round save for the mid-dorsal line, where it remained as thin as normally. The thickening was due mainly to the bloated condition of the connective tissue forming the deeper layer of this skin, now five millimeters thick over a large part of the neck. Besides an infiltration of lymph, a very rich supply of small blood-vessels was also noticeable in this tissue, which extended from near the base of the neck up to a point close to the back of the skull. Just behind the head, more deeply placed, and close to the horns of the hyoid, there was a loose mass of similar lymphoid tissue on each side of the throat; and as already stated, the elongate pads inside the lower jaws were filled with the same tissue, all of which would undoubtedly subside if not com-

pletely disappear after the breeding season.

On the inside of this heavy skin of the neck, moreover, there was a thin layer of muscle, its fibers running in an antero-posterior direction, and lacking only on the median dorsal line. Posteriorly no attachment to the body was noticed, at most it was slight, and the muscle was closely united with the skin; but anteriorly there were two paired attachments. The upper ones were on the occipital region of the skull, and showed that the greater part of this muscular layer represents the longitudinal layer of the cucullaris muscle, present in very many birds. On the lower side of the neck, two muscular bands presumably representing the sterno-hyoid, inserted anteriorly on the thyroid cartilage, whence other muscular strands continued to the hyoid. (See Figures 1 and 3.)

The contraction of this sheet of dermal muscle would shorten the skin of the neck, and rather than to draw air into the oesophagus it would tend to expell it; so the explanation of the process is not to be found here. What we can say with certainty is that the American Bittern, in producing its well-known "pumping" notes, does distend the oesophagus with air, and that in connection with this habit there is developed in the breeding season a remarkable thickening of the skin of the neck, with perhaps a modification of parts of the lining of the mouth that serve to help in retaining the air. Another adult male Bittern, skinned by our taxidermist about a fortnight earlier, is stated by him to have had the neck in the same condition. Probably only the male birds exhibit these modifications, for they alone are known to pump or boom.

The use of the oesophagus in such a manner is by no means confined to the Bitterns. It is perhaps best known in the case of the Pectoral Sandpiper, though according to Pycraft[1] many of the Pigeons produce their incessant "cooing" in this way; and even the male Ostrich is said to fill his gullet with air, and then produce by its expulsion the loud sound known as "bromming."[2] A somewhat similar action has been observed in the case of an African Bustard, *Neotis cafra denhami*, which utters a loud bark like that of a Bushbuck,[3] yet has no pharyngeal sacs like those of

[1] 'A History of Birds,' 1910, pp. 148, 149.
[2] See Duerden, American Naturalist, LIV, 1920, p. 306.
[3] Forbes, Proc. Zool. Soc. London, 1880, p. 478.

Otis tarda; and an Australian member of the same family, *Eupodotis australis*,—Pycraft tells us— likewise employs its gullet as a vocal sac. Further, the male of an African Rail, *Sarothrura elegans*, which is responsible for a clear, long-drawn note recalling a tuning-fork, and heard usually at night, undoubtedly shares the habit of inflating the oesophagus, and has a thickening of the skin of the neck nearly comparable to that of the American Bittern. This I have examined personally in the Congo.

Finally, there are several passerine birds with patches of bare skin at the sides of the neck, for example the African *Camaroptera superciliaris* and *Bathmedonia rufa*, as well as the South American *Donacobius atricapillus*[1] in which something of the sort appears to take place.

A word may here be appended concerning the display of fluffy white plumes by many male American Bitterns in the mating season, to which attention was called by Mr. William Brewster some years ago.[2] These can be erected conspicuously at the sides of the upper back. The specimen we have been describing possessed such tufts of cream-colored feathers, arising from the anterior part of the pectoral tracts, a little in front of, and lateral to, the fore end of the large powder-downs. Mr. Brewster was not satisfied as to just how these plumes could be raised, though it had been suggested to him that the skin of this region might be inflated; but from what has already been said, it will be clear that no air-space exists beneath them. Instead the mechanism for elevating them was seen to consist of the superficial muscle commonly found at the base of the neck, the cervical portion of the cucullaris, which runs obliquely downward and backward from the mid-dorsal line at this point. Its lower edge, in this case, was found to be inserted in the skin about the bases of these white feathers, which are usually concealed by the dark streaked ones lying just in front. So the contraction of this muscle would suffice to elevate the plumes in exactly the way Mr. Brewster described it. Perhaps also the shortening of the longitudinal muscle strands beneath the skin of the neck would pull that of the base forward, and aid in the process.

American Museum of Natural History, New York, N. Y.

[1] See Fuertes, Bird-Lore, XV, 1913, p. 342.
[2] 'Auk,' 1911, pp. 90–100.