A STUDY OF THE PTERYLOSIS AND PNEUMATICITY OF THE SCREAMER

WITH THREE ILLUSTRATIONS

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The South American screamers (family Anhimidae) are best known, perhaps, for their unusually extensive system of air sacs, their almost continuous feathering, and their many archaic structures. Numerous references to these peculiarities may be found in the literature, but few articles include more than a brief mention of them. Garrod (1876) reports that the pterylosis of *Palamedea cornuta* and *Chauna cristata* (but not *C. chavaria*) was described by Nitzsch in 1840. He also states that the plumage of *C. chavaria* does not differ greatly from that of *C. cristata,* except that there is no bare ring around the neck. Apparently no detailed study of the air sacs of any of these species has been made.

The present study is based on the examination and dissection of a single formalin specimen of *C. chavaria,* the viscera of which had previously been removed. The specimen came from the aviaries of W. J. Sheffler. Lack of comparative material has, unfortunately, made some of the observations tentative rather than definite. I gratefully acknowledge the valuable suggestions and criticism of Dr. Loye H. Miller, of the University of California at Los Angeles, under whom this work was done.

PTERYLOSIS

Among the Recent birds, only a few (the penguins, the ostriches and other ratite birds, and the screamers) are considered to be continuously feathered (without apteria). The plumage of these birds also seems to be unusual, for the feathers of the penguins are scalelike and those of the ratite birds do not possess hooklets. The feathers of the screamers are soft, rounded, and loosely arranged, especially on the back. In the cervical region they are small and stand out all around, giving the neck a fuzzy appearance.

The method here used in the study of the feather tracts follows that suggested by Burt (1929). Feathers on the right side of the body of this specimen were clipped off close to their bases, whereas those on the left side were used for comparison and checking.

Capital tract.—A small crest in the frontal region continues over the head to the occipital region, where the largest feathers reach a length of 2½ inches. The superciliary, ocular, and loral regions are bare.

Ventral tract.—The interramal region is not feathered, but short feathers at the corners of the bill stand out horizontally to the sides. The neck is continuously feathered, with the feathers more widely spaced on the ventral surface. The sternal region is covered evenly, with the slightly larger feathers on each side forming fairly definite tracts along the edges of the axillar region and posteriorly toward the legs. The axillar region is covered only with scattered down feathers, and a very few contour feathers near the posterior proximal edge of the wing. Plumage of the outer abdominal region is smaller than that of the breast.

Spinal tract.—Feathers of the interscapular, dorsal, and pelvic regions are also smaller than those on the breast; they cover the back continuously.

Crural tract.—The feathering all around the legs is small, dense, and without apteria; the distal third of the tibiotarsus is bare.

Caudal tract.—This specimen has 8 upper tail coverts (four pairs) and 11 rectrices, 6 on the right and 5 on the left. (I find no follicle for a sixth feather. Garrod, 1876, Mitchell, 1895, Beddard and Mitchell, 1894, and others, state that there are 12 rectrices in *Chauna* and 14 in *Palamedea.*) These and two others are the only contour feathers on the dorsal side of the tail of this specimen. The uropygial gland is surrounded by small down feathers.

Humeral tract.—These are by far the largest of the contour feathers, some of them reaching a length of 9½ inches. They are arranged in about seven rows of five or more feathers each, increasing in size posteriorly.

Alar tract.—There are 10 primaries, about equal in size except the most distal, which is slightly smaller than the rest. The 17 secondaries vary in size, the two on the elbow being much the smallest. The tertiaries, 8 in number, are still smaller. All of the coverts appear in more definite rows than any other feathers on the body. I find 10 greater primary coverts, each slightly distal to its primary,

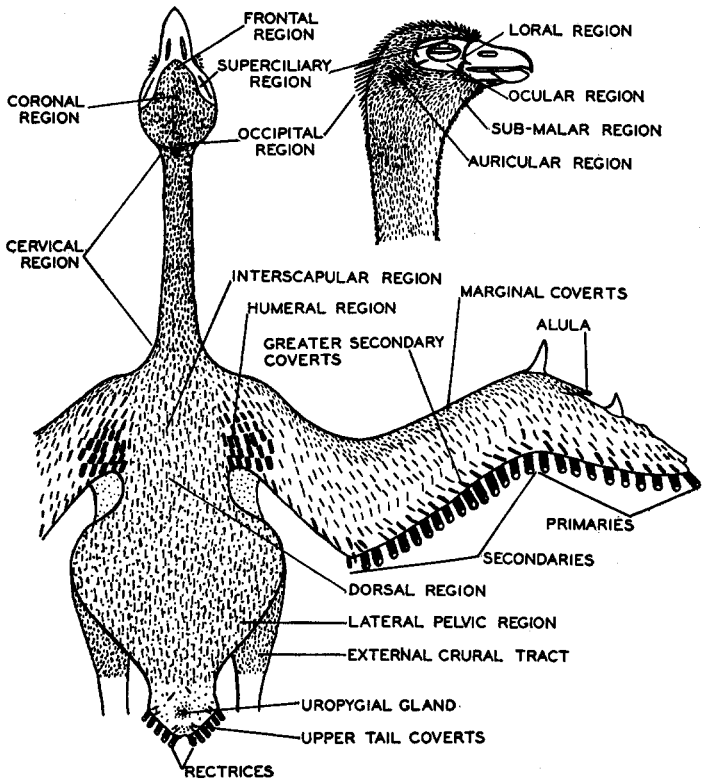

Fig. 31. Feather tracts of the screamer. Dorsal view, x⅛; lateral view of head, x¼.

and lying at an angle over it. There appear to be 13 middle primary coverts, 17 greater secondary coverts (with a gap above the 14th secondary), and 17 middle secondary coverts (with a gap over the 12th). The alula bears 4 remiges and 5 coverts, the remex on the tip being the largest. Of the undercoverts, there are 11 greater and 6 middle primary coverts; and 18 greater, 17 middle, and 16 lesser secondary coverts. A narrow strip along the under side of the ulna and part of the humerus is completely bare.

Down feathers.—As Garrod (1876) and Nitzsch (1840) state, the down feathers are scattered among the contour feathers all over the body, legs, and wings.

PNEUMATICITY

Subcutaneous air cells.—In the screamers the subcutaneous air mattress is unusually extensive, and reaches a depth of about one-fourth inch on many parts of the body (Garrod, 1876; Knowlton, 1909), particularly on the breast and back. It is deepest between the clavicles, filling the space from the skin to the surface of the interclavicular sac, and extending ventrally into a small, irregular air chamber just anterior to the curved carina and between the sternal ends of the coracoids. The finely divided layer of air cells is thinner on the back of the neck, on the head, in the axillae, under the wings, on the outer side and distal third of the tibiae, and on the feet (Beddard, 1898; Beddard and Mitchell, 1894; Garrod, 1876; Mitchell, 1895).

Along the anterior and medial surfaces of the furculum these cells seem to be continuous with those in the anterior part of the thorax; in the axilla and around the medial side of the femur and knee the air cells appear to be continuous with the greatly subdivided intermuscular diverticula in these regions. Whether there actually are passages for air from the internal sacs to the subcutaneous air mattress in these areas I was unable to determine.

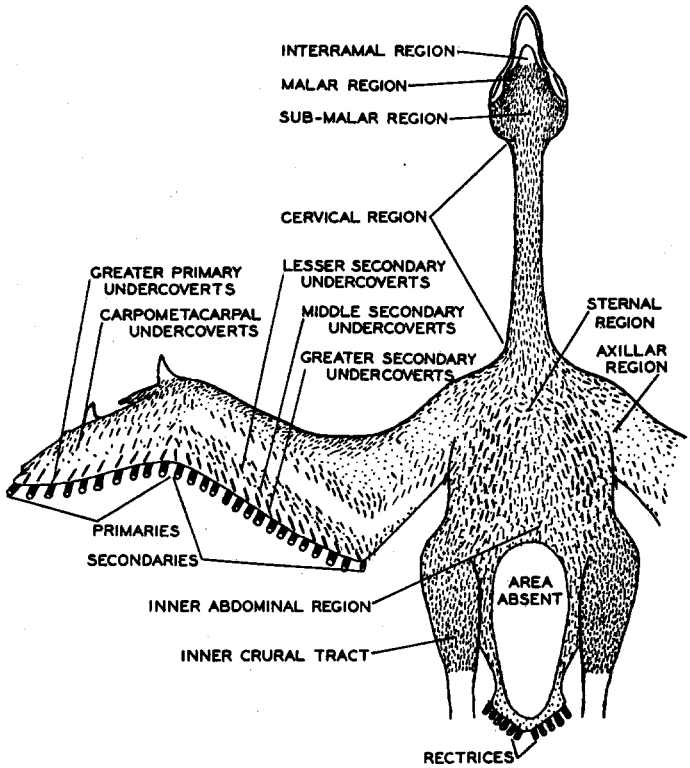

Fig. 32. Ventral view of feather tracts, x ⅙.

As Garrod (1876) and Beddard (1898) state, the feathers do not penetrate the subcutaneous air cells, "but cause the skin to be indented where they are situated."

The internal air sacs.—Müller (1908) has given an excellent description of the air sacs of the pigeon, with several very helpful diagrams showing their extent and relationship to each other. There are nine large sacs which lie within the body cavity: (1) the interclavicular sac, which is unpaired in most birds but develops from two rudiments on each side (Goodrich, 1930); (2 and 3) the paired cervical sacs; (4 and 5) the anterior thoracics; (6 and 7) the posterior thoracics; (8 and 9) the abdominal sacs. All of these except the anterior and posterior thoracic sacs have diverticula extending between the muscles into the cavities of the bones.

The basic arrangement of the sacs was found to be the same in the screamer as it is in the pigeon and most other birds, but, as we have already noted, the sacs are much more extensive in this species.

The interclavicular sac.—The interclavicular sac is irregular in shape, and extensive in this bird. The anterior part of the sac occupies the space between the heart and clavicles, and between the sternum and coracoids and the oesophagus. The trachea and numerous arteries and veins pass through it, and on either side of the thorax a cylindrical muscle extends from the trachea to a point near the anteroventral surface of the lungs. This part of the sac does not seem to be subdivided, but there are numerous septa anteriorly, posteriorly, and in the diverticula. As Beddard (1886) states, it is difficult to determine the boundary between the interclavicular and cervical sacs because the septa are so numerous in this region.

A prolongation of this sac extends posteriorly along the dorsal surface of the sternum on either

side of the mid-line as far as the posterior edge of the sternum. From the median septum just above the carina, it extends laterad to the costal edge of the sternum. It is bordered dorsally in the thorax by the pericardial sac, and in the abdominal cavity by the liver and stomach. The posterior part of this prolongation is only slightly subdivided, but in the thoracic region there are numerous partitions and many small pneumatic foramina leading into the sternum.

The axillary diverticulum communicates with this sac by several openings which lie behind and dorsal to the coracoid and the axillary nerves and blood vessels, and just anterior to the lungs. It extends laterally between the humerus and scapular muscles and around the head of the humerus just under the skin (as the suprahumeral diverticulum). Medially, it lies between the pectoralis major and the sternum, extending from the clavicle to the posterior edge of the muscle, and from a short distance lateral of the carina across the ventral surface of the sternum to the axilla. As Beddard (1886) states, the air space is subdivided into smaller cells, especially in the axilla and anteriorly and ventrally between the pectoralis major and pectoralis minor.

The subscapular diverticulum extends beyond the axillary diverticulum under the scapula, separating it from the ribs and intercostal muscles. It is subdivided into tiny cells.

The interclavicular sac communicates with the lungs by a passage on either side of the heart, above the sternal ends of the coracoids. These passages are the first to leave the mesobronchus after it enters the lungs (as noted by Richardson, 1939, in the pelican, and by Goodrich, 1930, and Juillet, 1911*b*).

The cervical sacs.—The cervical sacs, in the inferior part of the neck, lie dorsal to the interclavicular sac, slightly anterior to it on either side of the trachea and oesophagus and just anterior to the lungs. They appear to be separated from the interclavicular sac just dorsal to the coracoid. There are so many subdivisions in these sacs (as noted by Beddard, 1886) that they appear to merge into the subcutaneous air cells.

The cervical sacs arise from the first entobronchus with the interclavicular sac, but the passages separate just before leaving the lungs.

The anterior thoracic sacs.—The anterior thoracic sacs lie immediately behind the lungs on either side of the thorax. They are bordered laterally by the ribs and intercostal muscles, and posterodorsally

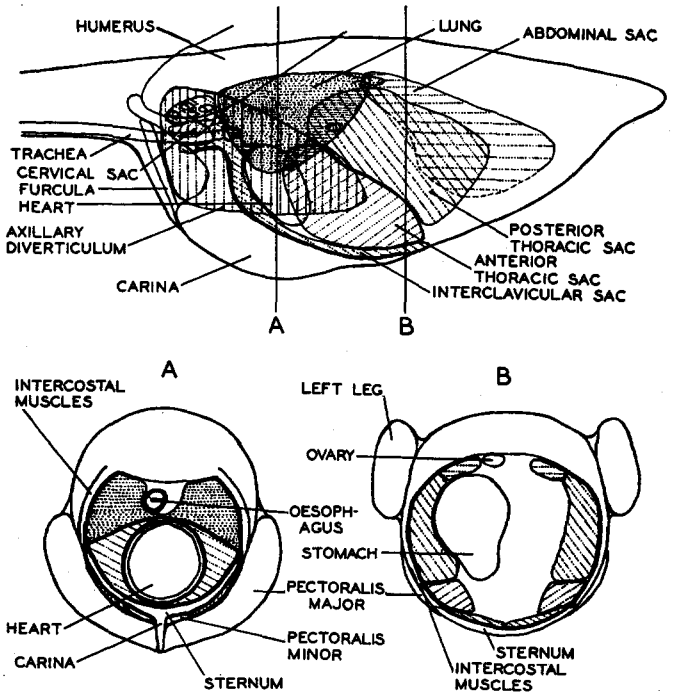

Fig. 33. Diagrams of the air sacs of the screamer, x ¼. Lower figures represent cross sections of body at levels indicated in upper figure.

by the posterior thoracic sacs. Medially the left sac is contiguous with the oesophagus and the anterior part of the stomach; the right sac is bordered medially by the liver. Ventrally they are bounded by the posterior extension of the interclavicular sac, and anterodorsally by the lungs.

A large ostium is situated in the anterodorsal apex of the sac, and there is a smaller opening a short distance ventrolateral to the large one. The passage to the mesobronchus is very short, opening close to its point of entrance into the lungs.

The posterior thoracic sacs.—The posterior thoracic sacs are separated from the anterior thoracic sacs by a membrane which extends diagonally upward and forward from the posterior edge of the sternum to a point anterior to the stomach, where the posterior sacs reach the lungs. They lie lateral to the abdominal sacs, extending along the thoracic and abdominal walls. The stomach indents the left sac anteromedially. In this region, the wall of the sac contains a thin, fan-shaped muscle, and is fastened to the stomach by connective tissue.

There is a large ostium in the lateral wall near the anterior end of the left posterior thoracic, and several smaller openings in the corresponding position in the right sac. From these openings, the air passages to the mesobronchus run along the posteromedial surface of the lungs for a short distance before entering them.

The abdominal sacs.—Although both abdominal sacs were badly torn in my specimen, something of their extent anteriorly could be determined. These sacs occupy the space between the intestines and the wall of the abdominal cavity. Anteriorly they lie medial to the posterior thoracic sacs, and extend along the lateral edges of the kidneys and ovary on the dorsal body wall. The left sac is indented anteroventrally by the stomach; the right is larger, extending forward between the lateral lobe of the liver and the stomach.

From the dorsolateral wall of the sac near its anterior end a large passageway extends dorsal to the posterior thoracic to reach the lungs. All along the posterolateral edge of the lungs, small openings lead from this passageway into the lung tissue to the mesobronchus (which becomes progressively smaller and more branched after the entobronchi to the anterior air sacs are given off). The main passage from the abdominal sac continues along the outer side of the lung, soon branching out into it.

There are two large openings in the posterior part of the dorsal body wall in the abdominal cavity (just anterior to the tail) which probably lead to the suprarenal extensions of these sacs. They pass anteriorly, dorsal to the kidneys, and enter the spaces between the sacrum and the transverse processes of the sacral vertebrae. Since the end of the mesobronchus apparently does not enter the anterior end of the abdominal sac directly or by a large orifice, as may be the case in some other species of birds (Gilbert, 1939; Goodrich, 1930; Müller, 1908), and since there are at least three large canals leading from the anterior end of the mesobronchus across the posterior surface of the lungs to this region dorsal to the kidneys, it seems possible that this passage may serve to connect the abdominal sacs with the lungs rather directly.

There is an air passage on either side of the posterior tip of the ovary which leads to the femoral diverticulum, entering opposite the proximal third of the femur, and opening between the crureus and sartorius muscles, lateral to the gluteus medius. The diverticulum is large, extending more than half the length of the femur along its anterior side. It is bordered medially by the posterior ribs and intercostal muscles, and laterally by the subcutaneous air cells. The diverticulum continues over the knee, curves around the insertion of the sartorius muscle, and fills the spaces between the muscles on the medial and posterior sides of the knee. It even extends beneath the tendon of the crureus muscle, filling the space around the bones of the knee joint. From a point just distal to the proximal end of the femur, the much divided diverticulum passes medial to the origin of the gluteus medius muscle and the pelvic bones, and enters the pneumatic foramen of the femur.

Miscellaneous air cells.—On the anteroventral side of the stomach, surrounding the junction with the oesophagus, is an irregular patch of air cells, which lie between the stomach and the walls of the anterior thoracic, posterior thoracic, and abdominal sacs (also mentioned by Beddard, 1886, and Beddard and Mitchell, 1894). These are connected with the lungs by a small opening just dorsal to the upper ostium of the anterior thoracic sac.

A small postcardial sac, subdivided by septa, occupies the space just posterodorsal to the heart, and medial to the anterior thoracic sac. It is roughly cone-shaped, base upward. By a small passage at the anterodorsal end of the sac, it communicates with a smaller, more rounded air cell dorsal to it and just ventral to the oesophagus. From this cell a small passage runs dorsal to the heart to enter the lungs near the upper ostium of the anterior thoracic sac.

The membranous walls of the sacs bordering the abdominal cavity are fibrous, and seem quite heavy in comparison with those of the pigeon, duck and chicken.

As noted by many authors, the bones are exceedingly pneumatic, even to the ends of the digits of both limbs.

SUMMARY AND CONCLUSIONS

The plumage of the screamers is almost uninterrupted (Garrod, 1876), as in the penguins and ratite birds (Allen, 1925). Although this is not necessarily a mark of antiquity (Beddard, 1898), there are many other anatomical structures in the screamers which substantiate the belief that these are the most archaic of living carinate birds (Gadow, 1893; Shufeldt, 1901). It is believed that they may represent a group which branched off from the ancestral stock of the goose-like and stork-like birds before these orders became distinct, but they are classified with the Anseriformes (Gadow, 1893; Knowlton, 1909). The plumage of the anserines is close and compact, with relatively few bare spaces (Knowlton, 1909).

In the screamer, the only spaces without contour feathers are the axillary regions (Nitzsch, 1867), and the dorsal side of the tail, which are covered almost exclusively with down feathers; and the superciliary, ocular, loral, and interramal regions, and a narrow strip along the ventral side of the ulna and humerus, which are bare.

The presence of down feathers among the contour feathers all over the body of this bird is thought to be an archaic character (Beddard, 1898).

Pterylae may be distinguished in certain regions by differences in the size of the feathers. The humeral feathers are much larger than any other contour feathers (as noted by Garrod, 1876), thus forming definite tracts. This is apparently quite unusual, for examination of several anserines, stork-like birds, and pigeons has not disclosed any similar modification in size, nor has any been noted in other species by Beddard (1898). In the femoral and lateral sternal regions, the feathers are slightly larger than the surrounding plumage, forming rather indefinite pterylae.

The high degree of pneumaticity of the screamers indicates that, although the living birds are archaic in some respects, they are not the ancestral type. They are much more specialized in this character than either the geese and ducks or the storks and flamingos (Gadow, 1893).

The emphysematous layer is found almost everywhere under the skin, but reaches its greatest depth on the breast and back. These subcutaneous air cells are not found in the anserines (Beddard, 1898), but are present in the pelicans and most other plunging birds. They differ, however, in structure and function in these species (see Richardson, 1939).

In comparison with the air sacs of the pigeon, the interclavicular sac and its diverticula are especially extensive, and the diverticula are, in addition, subdivided by numerous septa. The cervical sacs are also composed of many small cells, and thus resemble those of the storks and flamingos rather than the anserines, in which the cervical sacs are undivided (Beddard, 1886, 1898). The thoracic and abdominal sacs are relatively larger than those of the pigeon, and the femoral diverticula are definitely more extensive. The emphysematous patch on the stomach and the small postcardial sac seem to be unique.

The connection of the interclavicular sac with the lungs is of the anserine type (as described by Juillet, 1911*b*), opening from the first entobronchus. There are two openings to each anterior thoracic sac, and one to each cervical and posterior thoracic sac. The mesobronchus does not terminate in a single direct passage to the abdominal sac, as described in the domestic fowl, gallinule, pigeon, duck, and other birds by Juillet (1911*a*, 1911*b*), in the pelican by Richardson (1939), and in birds in general by Goodrich (1930) and Gilbert (1939). It branches out through the tissues of the lung, as is generally the case in the pigeon, according to Müller (1908). The opening from the abdominal sac directly into the lung also branches and joins the smaller air tubules. Since there are at least three large passages leading directly from the anterior end of

each mesobronchus across the posterior surface of the lungs to a suprarenal air space on either side of the vertebral column, it seems possible that this may serve as a connection between the lungs and the abdominal sacs. However, I have found no similar statement in the literature on the subject.

The function of this unusually great pneumacity in the screamers is not known, but it has been suggested (Crisp, 1864) that it may aid the birds in soaring or in wading and swimming. The air sacs may also serve as resonators to increase the volume of the birds' call notes, so that they can be heard for great distances. The screamers are swamp dwellers, and their pneumaticity undoubtedly gives them great buoyancy in the water, as is the case with the pelicans. However, as Richardson (1939) states, it apparently does not serve as a cushion, for the screamers are not plunging birds.

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