Comparative Osteology of Harris's Flightless Cormorant (Nannopterum harrisi).

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When Sharpe created the new genus Nannopterum to contain Harris's Flightless Cormorant of Narborough Island, of the Galapagos Group, he referred to it as "Phalacrocorax alis brevissimis, quibus minime volare potest avis inepta."* This appeared in 1899, and three years after we were given the admirable paper in the Novitates Zoologica by Dr. Hans Gadow on "The Wings and the Skeleton of Phalacrocorax harrisi" (vol. ix., 1902, pp. 169-176, Pls. XIV., XV.) In this classical contribution Dr. Gadow makes some extensive comparisons among Cormorants, including Harris's, in the number of primary and secondary feathers in the wings—a matter that does not fall within the scope of the present paper to discuss.

With respect to the skelcton, Dr. Gadow gives an excellent series of tables, in which all the principal bones of the same have been compared by accurate measurements (millimeters) with the corresponding ones in skeletons of P. melanoleucus, P. bicristatus, P. novæ-hollandiæ, P. carbo, P. carboides, P. varius, and P.

cristatus.+

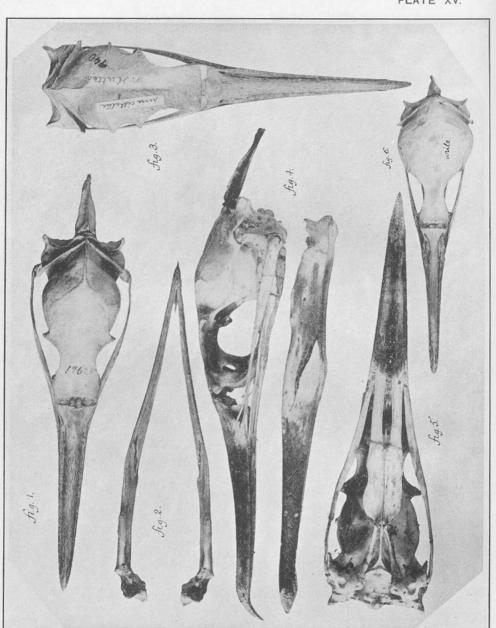
There is, however, very little comparative descriptive osteology in Dr. Gadow's contribution to the study of the skeleton of Nannopterum harrisi, while his instructive figures of the bones of that Cormorant, on the two plates, are diagrammatic rather than actually representative of what they are called. Such parts of the skeleton as the skull, the vertebral column, pelvis, and pelvic limbs are not figured at all. On the other hand, his discussion of the effects upon the skeleton of the pectoral limb, and the primary and secondary feathers of the wings, due to an abrogation of the power of flight, is most interesting.

In regard to this he says, with respect to the skeleton of the arm, that "Change in the power of flight is above all correlated with increased length or shortening of the forearm. Next, the hand is affected, last of all the humerus. A much degenerated hand-skeleton is a sign of extreme reduction" (loc. cit., p. 172).

Other points discussed by Dr. Gadow will be taken up here in connection with the various parts of the skeleton to which they

^{*}Sharpe, R. B., "Hand-list of Birds," vol. i., p. 235. In this place he also invites attention to the following literature:—Phalacrocorax, Rothsch., Bull. B.O.C., vii., p. lii., 1897; Ogilvie Grant, "Cat. Birds," xxvi., p. 655, 1898; also Rothsch., loc. cit., p. 655, for N. harrisi.

[†] In Sharpe's "Hand-list," vol. i., pp. 232-234, I fail to find of this list P. novæ-hollandiæ (Plotus novæ-hollandiæ?), P. carboides, or P. cristatus; the remaining four species are well-known forms. Skeletons of other species, not included in his tables, were before him, as P. albiventer, P. graculus, P. flamentosus, P. lucidus, P. capensis, P. gaimardi, and one he calls P. brasiliensis.



refer. As he in no way refers to the skull of Nannopterum in his article on its osteology, I shall dispose of that important part of

the skeleton before so doing.

During the past thirty years I have published a number of papers on the osteology of the Phalacrocoracidae, the most formal one being a memoir on the subject, entitled "The Osteology of the Steganopodes" (Mem. Carnegie Museum, No. 3), in which a very full account is given, illustrated with numerous plates of the skeletons of quite a number of existing and extinct Cormorants from various parts of the world. Since that memoir was published, however, the number of Phalacrocoracine skeletons in the collections of the United States National Museum has been substautially increased, and there are now to be found, among other valuable additions, no fewer than five more or less complete skeletons of Nannopterum. These, with others of the Phalacrocoracidae, have been placed at my disposal by that institution for the purposes of description. For this courtesy I am much indebted, and in connection therewith I have to thank Dr. Charles W. Richmond and Mr. J. H. Riley, of the Division of Birds of the Museum, for their kindness in transmitting me this valuable material.

1 find, in addition to the five skeletons of Harris's Cormorant referred to above, those of P. carbo, P. punctatus, P. auritus, P. urile, P. magellanicus, P. penicillatus, P. vigua, P. albiventris, P.

pelagicus, P. perspicillatus, and others.

The Skull (see figures on Plate XV.)—All the skeletons at hand of this Cormorant belonged to fully adult individuals, but unfortunately the sex of no one of them is recorded. Their Museum numbers run—19,628, 19,719, 19,720, 19,721, and 19,722, which last is without a skull.

Measured in a straight line from the apex of the superior mandible to the most posterior point on the occipital condyle, the skull numbered 19,719 has a length of 162 millimeters; 19,720, of 160 mm.; 19,721, of 164 mm.: while the one numbered 19,628, which certainly belonged to an old bird, measures in length but 147 mm. Disregarding this last skull, the average length of the skull of this Cormorant, based on the measurements of the first three, would be 162 millimeters.

Apart from these less important, though longer, transverse cranial diameters, and selecting the one of the brain-case at its widest part for comparison, skull No. 19,719 has a maximum width, through the broadest part of the parietal region, of 32 millimeters; 19,720, of 32 mm.; 19,721, of 32.5 mm.; while 19,628 measures but 30 mm. In the frontal region, superiorly, the shortest distance between the orbital peripheries in the first three skulls measures 18 mm., while in No. 19,628 the same transverse diameter measures but 13.5 mm. (See fig. 1, Plate XV.)

Unless there be a sexual difference bere, this is a remarkable case of individual variation in the matter of size, especially when skull No. 19,628 belonged to a very old bird, and one with an

unusually large "occipital style," and with great rigidity of the cranio-facial hinge. I have no explanation at hand for this discrepancy. It has almost the appearance of having belonged to some other species; and had I at hand nothing beyond the four above-mentioned skulls to represent Nannoplerum harrisi—that is, the ones numbered 19,719, 19,720, and these being in such close agreement in all particulars—this one (No. 19,628), being so much smaller, and exhibiting, as it does, some other slight differences, I certainly would have been justified in taking it to be the skull of some other species of Nannoplerum.

Other species of Cormorants, bowever, exhibit the same differences in size, where the skulls all appear to have belonged to fully adult individuals; for example, in the case of *P. penicillatus*, one skull at hand (No. 940, Coll. U.S. Nat. Mus.) has a length of 143 millimeters, while another (No. 18,535, Coll. U.S. Nat. Mus.) measures but 126 mm. in length, and with all other measurements and diameters proportionately less. The same thing is also found to obtain in *P. urile*, one skull at hand having a length of 117 mm., and another, from an adult, but 113 mm.—the first being No. 12,502 and the latter No. 12,505 of the collections of the U.S. National Museum.

Up to the present time, classifiers of the Cormorants seem to have held-and still hold-very diverse opinions as to the generic and sub-generic divisious of the family. Ridgway retained in the genus *Phalacrocorax* all the known species of North America, and if he considered the genus composed of two or more subgenera, he has not designated them by name in his "Manual." Coues, on the other hand, recognized no fewer than six sub-genera for the genus Phalacrocorax, taking into consideration the North American forms alone ("Key," 5th ed.) Of the world's Cormorants, Sharpe, in his "Hand-list," places 41 species of these birds in the genus Phalacrocorax without any sub-generic distinctions, including among them Phalacrocorax perspicillatus, which he claims to be "extinct"; then, with this form, and this form alone, creates for it the genus Pallasicarbo, giving us Pallasicarbo perspicillatus! Here, then, the same species is placed in two different genera in the same work. We also have here Nannopterum harrisi and the fossil genus Actionnis with one species—A. anglicus. There are also some ten fossil species in Phalacrocorax in the "Hand-list."

Turning next to the A.O.U. "Check-list" for 1910, we have *Phalacrocorax* divided into *three* sub-genera—viz., *Phalacrocorax*, *Compsohalieus*, and *Urile*, while Pallas's Cormorant (*Phalacrocorax perspicillatus*) occurs nowhere in the volume, not even in the index, among birds living or extinct.

These facts are set forth here with the view of economy in the matter of making comparisons of the skull of Nannopterum with other Cormorants, for the skulls of the species belonging to the Phalacrocorax series of the A.O.U. "Check-list" differ very markedly from those of the Urile series, holding apparently a

middle place between them, though evidently very near the firstnamed group generally, if separated from it at all. In fact, a skull of P. penicillatus (No. 940, Coll. U.S. Nat. Mus.) agrees very closely in all of its essential characters with the skull of Nannopterum harrisi-at least, with the one belonging to the collections of the U.S. National Museum numbered 19,628; and, character for character, this agreement is nearer than it is in the case of the aforesaid skull of Nannopterum harrisi and that of Phalacrocorax carbo (No. 18,851, Coll. U.S. Nat. Mus.) Dr. Gadow claims, in his article in the Novitates Zoologicae, that P. carbo is the "nearest ally" of Nannopterum harrisi (p. 169). I must believe that he did not have before him at the time a skeleton of P. penicillatus, though he did have a skin of that species (loc. cit., p. 170).

From what has been set forth above, then, it is clear, in comparing the skull of Nannopterum harrisi with the skulls of other Cormorants, that we may pay but scant attention to those of the Urile series, while the direct comparisons should be made with the skulls of the typical representatives of the Phalacrocorax series, especially with those of P. penicillatus, P. carbo, P. perspicillatus, P. auritus, and their immediate allies. The reason for this will at once be apparent after comparing the skulls shown on Plate 1. of the present paper and those on Plate XXIV, of my "Osteology of the Steganopodes," where views of this part of the skeleton of some five other species of Cormorants are presented, while still others occur in the text (pp. 184, 186).

There appear to be four principal types of skulls met with in the Phalacrocoracidæ. The first of these may be designated as the Urile type, wherein the skull is smaller than in the others, of a lighter and more delicate structure. The superior mandible is rather lengthy, and the cranium compressed from above downward. The occipital line and crest is somewhat reduced, and the occipital style small. Over the parietal region, in the midlongitudinal line, the surface is smooth and the crest absent. its mesial inlerior angle the lacrymal is connected with mesethmoid by a slender, bent bar of bone, which is larger and stronger in the remaining three types. (In P. urile, No. 12,502, Coll. U.S. Nat. Mus., there is a long, free, very slender vomer present.) The foramen magnum is very large in proportion to the size of the skull. The occipital line and crest meet in the middle line at the site where the occipital style articulates.

lu the second type, which may be designated as the penicillatus type, the skull is stronger and less delicately fashioned; the superior mandible is long and somewhat acute; the cranium is not nearly so much compressed from above downward. occipital line and crest are conspicuously developed, and the interparietal crest is also present as a sharp, raised line, running from the facet for the occipital style forwards to a point over the centre of the cerebral casket, where it bifurcates and continues forward and laterally either way to the apex of either squamosal process. The occipital line and crest do not meet at the facet for the articulation of the occipital style. The occipital lines meet each other in the middle line, several millimeters anterior to this facet, in the interparietal crest. There may be a rudimentary pars plana present on either side, and the maxillo-palatines considerably developed. Transverse frontal area on superior aspect of cranium, between the orbits, broad. This is the group or type to which Nannopterum harrisi belongs.

Passing to the third group, which may be designated the carbo type, we find the superior mandible to be much shorter. The cranium is large and strong, exhibiting no vertical compression, nor is it especially broad. The foramen magnum is much smaller, both actually and relatively, than it is in the two foregoing types, and the cranio-facial hinge is more or less inflexible.

Lastly, we have the *perspicillatus* type, in which the cranium is compressed from above, downward to some degree, very broad and thick. *Pars plana* is better developed; the great vacuity in the anterior wall of the brain-case, present in all the other types, is bere vertically divided in the middle line by a slender bar of bone. The cranio-facial hinge is more mobile, and, as in the types two and three, the squamosal and post-frontal processes are developed, especially the latter. These are practically absent in the *Urile* type of skull. The occipital crest and occipital line are more separated, as in the *penicillatus* and *carbo* types.

Lucas, in his description of P, perspicillatus, states, and I reproduced the statement in my "Osteology of the Steganopodes," p. 168, that "the absence of external narial openings is also a secondary character, for the young Cormorant possesses perfectly open nostrils, while the cranium is almost as schizorhinal as that of a Gull. As growth proceeds the narial openings become more and more restricted, until, about the time (the exact time is uncertain) that the young birds take to the water, not only the external openings, but those of the cranium, have become com-

pletely filled."*

While the nostrils are obliterated in all adult Cormorants, in so far as the superior mandibular theca is concerned, I very much question that they are entirely obliterated in the osseous mandible of the skull; they certainly are not in any of the skulls now before me—that is, if the more or less conspicuous foramen at the posterior ending of the nasal groove passing down the lateral aspect of the superior mandible on either side does not represent what remains of these openings. In some skulls I find a second and smaller foramen at some little distance in advance of the one here referred to. It also lies in the track of the nasal groove, and, as in the case of the large one, leads directly backward into the rhinal chamber, just as the narial passage would do were it present. Moreover, the larger and more posterior of the two foramina, when two are present, is always situated at the anterior margin of the nasal bone where the avian nostril commonly

^{*}Lucas, F. A., Proc. U.S. Nat. Mus., 1889, pp. 88-94.

terminates, and where it does terminate in a young Cormorant. They are double in Nannopterum, and usually rather small. This species may even have three such foramina on either side (No. 19,721, Coll. U.S. Nat. Mns.) They are large in Pallas's Cormorant (No. 19,417, Coll. U.S. Nat. Mus.), and nearly as big in P. carbo. Although I have not dissected a Cormorant lately, I would not be surprised to find that these several foramina transmitted both nerves and vessels to the structures of the superior mandible beneath its theca; but, even if this be so, it would not disprove what has just been set forth as to their being at the same time the remains of the narial apertures, and I must believe that they are.

The plate of the mesethmoid in Nannopterum exhibits near its centre quite a sizable vacuity. This opening, in the same locality, is also present in the skulls of P. urile (where it is very large), P. auritus, and P. penicillatus, but is never found in Pallas's Cormorant or in P. carbo—that is, in the crania of adult

birds

In all Cormorants the presphenoid exists as a conspicuous keel, co-ossified in the middle line on the ventral aspect of the braincase, extending from the basitemporal to a point above the pterygo-palatine articulation, from which point, as a straight, narrow bar, it bounds the immense interorbital vacuity below, till it merges, anteriorly, with the mesethmoid, projecting in front of the latter as a prominent, sharp spinelet. Sometimes the floor of the cranial casket, upon one side or the other of this sphenoidal keel, may be so thinned as to have, as a result, a vacuity of some size remain in it. This is the case in the skull of one of the specimens of Harris's Cormorant (No. 19,628), also in P. penicillatus (No. 940), where it is much smaller. In P. carbo the floor of the brain-case in this locality is very much thicker than it is in the two Cormorants just mentioned, and no such foramen is ever left there after cranial ossification is complete in the adult. In all Cormorants the basitemporal area is small and concaved. These birds have the osseous chamber of the ear much exposed, and a free, bony siphonium leads into it upon either side.

The massive quadrates, the big pterygoids with their sharpened superior borders, and the large, posteriorly-fused palatines, are all so well seen in fig. 5 of Plate 1. of this paper that it would be superfluous to give any detailed description of these parts.

With respect to the mandible in Nannopterum (figs. 2 and 4, Plate XV.), the bone presents the same general pattern we find it to possess in Cormorants at large, and this has been quite fully described in my "Osteology of the Steganopodes" (p. 169).

In P. carbo the distal symphysial part of the mandible is conspicuously bent down (No. 18,851, Coll. U.S. Nat. Mus.), which is not the case in any other Cormorant before me at this time, including Harrie's

including Harris's.

In my description of the skull of Anhinga anhinga (loc. cit., pp. 151, 152, figs. 3, 4, sr. m.), I gave a short description of a bone found articulating with the distal extremity of the maxillary,

on either side, and there called the *supramaxillary*. This bone has probably been lost from the skulls of *Nannopterum*, but I find it present and well developed in the skull of a specimen of *P. auritus* (" *P. dilophus*," No. 19,262, Coll. U.S. Nat. Mus.), where it agrees with what we find in *Anhinga*. It will undoubtedly be found to be present in other Cormorants, especially in *P. carbo*, which species has a skull very much like that of *P. auritus*—that is, the one referred to above.

Nannopterum presents nothing peculiar in the sclerotals of the eyes; the platelets, with their rounded angles, number in either circlet from 15 to 18 pieces. They overlap in the usual manner, and the anterior ones are smaller somewhat than the posterior one, the gradation from before, backward, being gradual. (No. 19,628. — Antero-posterior diameter of inner circle equals 11 millimeters and the outer 16 mm.) They agree in P. auritus,

but the eye is smaller than it is in Harris's Cormorant.

Cormorants have the osseous elements of the tongue much reduced; some of its parts never ossify, as is the case with the glosso-hyal, the uro-hyal, and the epi-branchials. The basi-hyal has a length of only 6 millimeters, it being wedge-shaped anteriorly, and its sides prominently concaved with a midlongitudinal keel on its ventral aspect. In front it supports the cartilaginous glosso-hyal, while posteriorly the long cerato-branchials articulate with it by their enlarged, laterally compressed anterior extremities, side by side. There is no uro-hyal. Either of these cerato-branchials is a somewhat stoutish rodlet with a length of 48 millimeters. In form they are somewhat cylindrical and very slightly curved upward, their distal tips being in cartilage, which latter may represent the epi-hyal elements.

In P. auritus the osseous parts of the hyoidean apparatus are slenderer than they are in Nannopterum, the basi-hyal being much pressed from side to side in its continuity, while the cerato-branchials are very much more curved from before, backwards; otherwise they agree, anatomically, with what has been described above for Harris's Cormorant, and very probably other members of the

Phalacrocoracidæ.

THE SKELETON OF THE TRUNK.

As stated above, Dr. Gadow, in his paper on Harris's Cormorant in the Novitates Zoologicæ, recorded many measurements he made of the bones of Cormorants. Among them ("Table A," p. 171) he gives the length of the trunk skeleton in Nannopterum harrisi as 240 millimeters. This must have been a much larger bird than any of those I now have before me; for in the case of the two largest ones, this part of the skeleton, measuring from the most anterior point on the 19th cervical vertebra to the most posterior one on the last uro-sacral vertebra—or the last one fused with the sacrum—I find the length to be, in both cases, but 199 millimeters.

Fearing that I might have made some error with respect to the

vertebræ, although I do not think I did, I determined to test it with some rigid long bone of the skeleton, and selected for the purpose the humerus. Dr. Gadow found this bone in his skeleton of Nannopterum harrisi to have a length of 101 millimeters (loc. cil., Tab. A, p. 171).

The humerus in the skeleton of No. 19,720 of the U.S. National Museum collection, a large specimen of Harris's Cormorant, measures in total length fully III millimeters; in the one numbered 19,719, III millimeters; and the same bone in No. 19,721, only 98.5 millimeters; so that the lengths of the three humeri would give us an average of 106.8 mm., or over 5 millimeters longer than

the big male harrisi that Dr. Gadow had before him.

The humerus of the specimen of *P. carbo* Dr. Gadow had had a length of 165 millimeters, and that bone of an individual of the same species in the Coll. U.S. Nat. Mus. (No. 18,851) has identically the same length; so I am inclined to think that the long bones in the pectoral limbs of these birds exhibit, when adult, but a very slight amount of variation. Further on I shall have something more to say about these measurements: the question was only introduced here in order to demonstrate such value as they possess in the matter of the total length of the trunk skeleton in *Nannopterum harrisi*.

Harris's Cormorant stands among the largest of the *Phalacrocoracidæ* in the world's avifauna, and the fact of its having lost its power of flight has, pari passu with the atrophy of its pectoral limbs and certain parts of its sternum and shouldergirdle, resulted in an augmentation in size and strength of most of the bones in the remaining parts of its skeleton. In this category the vertebral column and pelvis hold a prominent place, while the skeleton of a pelvic limb is, actually as well as relatively, better developed than that of any other Cormorant at present known to me.

In the cervical section of the spinal column the first 18 vertebræ are without free ribs. The 19th vertebra is free, and supports a pair of long, slender ribs. These have elongate, well-developed epipleural appendages upon them; but the ribs themselves are not articulated with the sternum through costal rihs. In this Cormorant the 20th and 21st vertebræ fuse solidly together to form one piece, the ribs on the 20th being longer and stouter than the pair on the 19th, though they still fail to connect with the sternum by means of costal ribs. It is interesting to note that in both pairs of these ribs their lower free extremities are knobbed, just as though the usual provision had been made for articulation with costal ribs; but the latter, as I say, are non est, neither are the vestiges of facets to he seen on the costal borders of the sternum for them, indicating that these two pairs of ribs, in the ancestors of this Cormorant, did so articulate with the sternum through the intervention of such costal ribs.

As stated above, the 21st vertebra is completely fused with the 20th, even the large quadrate neural spines being included in the

fusion, while the hæmal spine of the 21st vertebra—also a long, stout one—plays its part in forming the contour below of this united bone (fig. 16, Plate XVII.)

Between the vertebral element formed by the fused 20th and 21st vertebræ there are two others in the dorsal region of the spine and the pelvis. These are the 22nd and 23rd vertebræ of the column, and they are entirely free. Their ribs meet the sternum through elongate, stout costal ribs, as do the first pair of ribs coming from beneath the ilia of the pelvis and the pair on the 21st vertebra. All of these ribs are large, highly developed in every way, and support big epipleural appendages. The last pair of the series, however, or the second pair which articulate with the pelvic section of the column beneath the ilia, do not possess "uncinate processes," nor do their flattened and very long hæmapophyses reach the costal border of the sternum on either side. There is also a pair of "floating" costal ribs, each of considerable length, and they articulate with the posterior border, on either side, of the just-mentioned pair which precedes them.

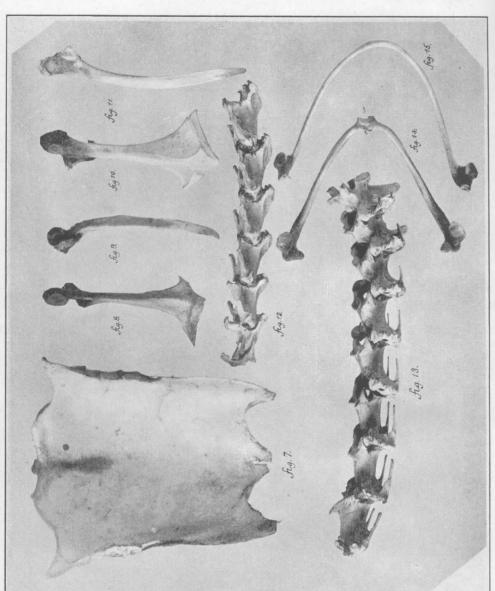
This arrangement of the *ribs* also obtains in \hat{P} . *urile*, but all the bones are slenderer and rather longer, and, all to the last pair, their unciform processes are very large and elongate, while those on the leading free pair of rihs of the series are conspicuously expanded. As in the case of *Nannopterum*, the free, lower ends of the rihs on the 19th and 20th vertehræ are "knobbed," while the posterior borders of the third, fourth, and to some extent the fifth pairs of ribs are sharpened, the lower part of which edge in the case of the fourth pair being perceptibly extended. In Harris's

Cormorant these borders of the ribs are rounded.

In P. vigua, P. auritus, P. carbo, and doubtless other species, this arrangement is essentially the same as we find it in Harris's Cormorant, while slight differences may obtain in other species, as, for instance, in P. punctatus the last pair of ribs—that is, the second pair coming from beneath the ilia—have well-developed epipleural appendages upon them, and this is the only Cormorant I have met with that does have them on that pair of the series. But then Phalacrocorax punctatus of New Zealand presents a number of other peculiarities in its skeleton, which will be touched

upon further on in this paper.

Returning to the cervical vertebræ of Nannopterum, we are to observe, in the case of the atlas, that its neural arch is a flat, smooth platelet of bone, broad and deep and nearly square in outline. Its postero-external angles are produced backwards and outwards as conspicuous apophyses, while the neural canal is large and transversely elliptical. The cup for the occipital condyle has a circular perforation at its base, and the hæmal spine is large, somewhat inclined backward, has sharpened borders and minute lateral processes above. These characters, with slight variations, are repeated in the atlases of other Cormorants, though in P. auritus the lateral apophyses on the hæmal spine are unusually well-produced.



Passing to the axis of N. harrisi, we find a bone having many striking characters. Its cylindrical neural canal is not more than half the size of that tube as it exists in the atlas, and the centrum projects far heyond its anterior opening. Distally, this supports the rather large, sessile odontoid process, below which the body of the bone is enlarged and concaved on its anterior aspect. Mesially, and below this, we find a deep pitlet, and posterior to this, on either side, a prominent little process. Above this, laterally, there passes, in life, the vertebral artery in a shallow groove there found.

The neural arch is much expanded, posteriorly, and produced backward far heyond the centrum. Its free borders are thickened, and its spine is represented by a low, median ridge or line. On the other hand, the hæmal spine is large and triangular, having an anterior sharpened border with its apex supporting an

elliptical lamina of bone.

The postzygapophysial facets are flush with the surface of the nether side of the neural arch, one on either side of the entrance of the spinal canal. This is the position they likewise occupy in the third cervical vertebra, while the prezygapophysial ones, on the dorsal aspect of the bone—each elliptical in outline—are placed one on either side, above the large canal for the vertebral The pleurapophyses commence on this vertebra rather short, stout processes, and the hæmal-still of considerable size—is sharp in front and bifurcated below. On the dorsal aspect, the neural arch, still broad behind, inclines to curl forward, its outer angles being produced in that direction as minute spinelike processes, while mesfally, at the same time posteriorly, a low neural spine develops. Fig. 12 of Plate XV1. shows these vertebræ -the leading seven cervicals—but their dorsal surfaces are toward the lower border of the plate, whereas they should be in the same position as the cervicals shown in fig. 13 of the same plate.

To include the *eighth* cervical they all exhibit, on the ventral aspect of the centrum, just posterior to the articulation, a notable concavity, which disappears in the succeeding vertebræ. The hæmal spines likewise disappear. There is but little change in the neural spine from what we found it to be in the third cervical, and the pleurapophyses do not change in any marked degree. The vertebral canals increase somewhat in size, and the vertebrae

themselves gradually become larger and broader.

This eighth cervical vertebra of Harris's Cormorant is the leading one shown in fig. 13 of Plate XVI., and it will be noted there that the character of its neural spine has changed, it being well developed, and triangular, with its apex directed forwards. The post-zygapophyses in this vertebra are more individualized and forking.

In my "Osteology of the Steganopodes," cited above, I have given a full account of the peculiarities of the seventh, eighth, and ninth cervical vertebræ in various Cormorants, as well as in Anhinga and the Bitterns. This account is so complete that it is

quite unnecessary to enter, to any great extent, upon the subject here.

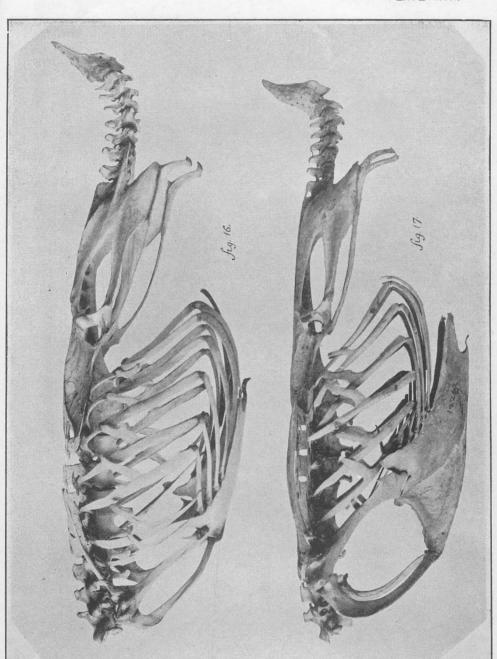
Nannopterum presents the same modifications of the three cervicals in question, only better marked than we find them in P. urile or P. carbo and others. In this eighth vertebra of Harris's Cormorant the rudimentary beginning of the carotid canal is in evidence; it is large and completely formed in ninth to the fourteenth inclusive, but in none is it quite closed in the median line below. In the 15th cervical its place is taken by a long, straight hæmal spine. A similar spine is found in all the rest of the vertebræ of the pelvis, and even here the character still obtains, though the process is shorter, while it becomes shorter and shorter in the next two following pelvic (dorso-lumbar) vertebræ, to be lost entirely on the next succeeding one (27th). There is a stumpy little neural spine on the 14th cervical; it is double the size on the 15th, and increases in size thereafter to the 19th vertebra, where it assumes the big quadrate form it has throughout the dorsal vertebræ.

The pleurapophyses of the 8th to the 11th inclusive are long and moderately slender, the longest pair being on the ninth cervical. Ventrally, the centra of the 16th to the 18th cervical inclusive are very broad and flat, while they promptly change in the dorsal series to become markedly compressed from side to side.

The facets for the ribs arc extensive, considerably elevated, and each pair is strictly confined to the vertebra to which it belongs; in other words, there are no demifacets as we find in some of the vertebrata elsewhere. On the under side of a transverse process, extended hetween the facet on the centrum of the same vertebra to the facet at the outer end of the transverse process, there is a very prominent raised ridge, so that, when the rib is duly articulated there, this ridge practically comes in contact with the entire dorsal surface of its neck, and thus greatly increases the solidarity of its articulation with the ventral side of the transverse process on either side. Two such similar ridges are provided for the two pairs of ribs that articulate beneath the ilia of the pelvis.

Nineteenth and twentieth vertebræ fuse together in *P. auritus*, as they do in Harris's Cormorant, but not so in *P. urile* or in *P. carbo*. They also remain distinct in *P. pelagicus*, but not in *P. punctatus*. To a certain extent, for any particular species, age would have something to do with this, and it is possible that in old, or very old, Cormorants of any species we might find those two vertebræ firmly fused into one bone.

Dr. Gadow points out in his paper (loc. cit., p. 174) that the three specimens of Harris's Cormorant examined by him "possess, like other Cormorants, 18 cervical and 2 cervico-dorsal vertebræ, and the 29th forms the last preacetabular buttress"; and further on, on the same page, he states:—"The two sacral vertebræ of P. harrisi seem to be the



32nd and 33rd, so that this region of the whole sacrum contains one more vertebra than other Cormorants. The following post-sacral, caudal, and pygostyle vertebræ exhibit no more than, or rather as much, individual variation in numbers and connections as other species. The pygostyle hegins with the 48th vertebra—in one specimen apparently with the 49th—but it is, unfortunately, not possible to determine how many vertebræ have been fused into the pygostyle. It is possible that the additional vertebra contained in the presacral complex of the sacrum, and thus lengthening the whole pelvic region, accounts for the unsatisfactory results which we arrive at by comparing the proportions of length of pelvis to the bones of the hind limbs of *P. harrisi* with other Cormorants."

As stated above, I have at this time five pelves of Harris's Cormorant at hand, and they present similar differences, due to individual variation, that Dr. Gadow found to obtain in his three

specimens.

In all five of the skeletons belonging to the collections of the. U.S. National Museum (Nos. 19,628, 19,719, 19,720, 19,721, and 19,722) it is the 24th vertebra that is the first of the spinal column which fuses with the ilia in the formation of the pelvis. It is the anterior one of the series that forms the pre-acetabular vertebral part of the pelvis, which terminates at the anterior peripheres of the acetabulæ. These are easily counted, for their transverse processes, abutting against the ventral surfaces of the

ilia, are in plain sight.

Dr. Gadow, as just stated, found the 29th vertebra to form "the last pre-acetabular buttress," and so it does in Nos. 19,628, 19,721, and 19,722 of the specimens here being considered; while in Nos. 19,719 and 19,720 it is the 30th vertebra that does so, instead of the 29th. Then follow two inore, in which the transverse processes have been almost entirely aborted. These two vertebræ are directly between the acetabulæ; their centra are large, and the spinal canal, as it passes through them, is at its maximum calibre for this part of its continuity. In No. 19,719 and 19,720 these two vertebræ are the 31st and 32nd, while in the other specimens they are the 30th and 3rst. Next follow two vertebræ which are the true sacral vertebræ. In Nos. 19,719 and 19,720 these are the 33rd and the 34th, while in the remaining three specimens they are the 32nd and 33rd.

If we reckon the last uro-sacral vertebra to be the last one that fuses with the pelvis, then in No. 19,719 this vertebra is the 42nd; in No. 19,720 it is the 43rd; in 19,628 it is the 40th; while in Nos.

19,721 and 19,722 it is the 41st.

This is rather a remarkable variation, and I could scarcely believe it until I had made the count with the greatest possible care several times over.

No. 19,719 has 7 vertebræ plus the pygostyle in the skeleton of its tail (43rd-49th + P.); No. 19,720 has 44th-48th + P.; but I am inclined to believe that the last caudal vertebra has been lost

in this skeleton, for the reason that that vertebra always has shorter transverse processes than the one next preceding it. In No. 19,721 the caudal vertebræ include the 42nd to 48th, being 7 in all, to which the pygostyle is to be added; in 19,722 the skeleton of the tail is probably in the skin of this specimen, which was preserved, and so the count cannot be made.

Finally, we have No. 19,628, in which, differing from all the rest, although it has seven vertebræ and the pygostyle in its tail, these

vertebræ are the 41st to the 47th inclusive.

As to the number of vertebræ in the pygostyle, I should say that there were about seven, although there can be no certainty about it until they have been correctly counted in many young Cormorants at different ages and proper stages of development. There is no difficulty in making out the leading five vertebræ in the pygostyle of a Cormorant, and the posterior pointed looks as

though it might contain two more.

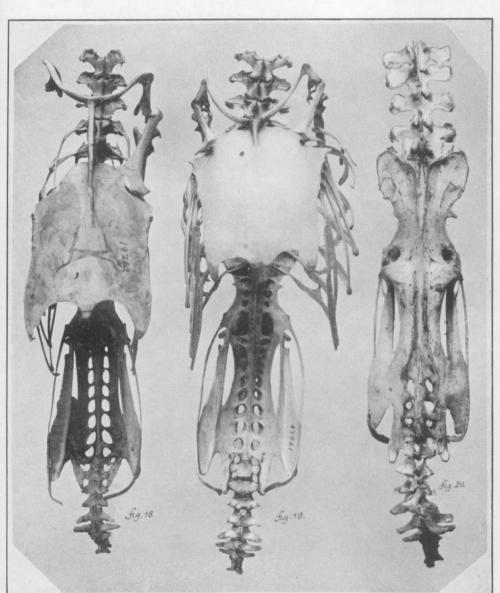
Harris's Cormorant has the caudal vertebræ and pygostyle of great size—in fact, of comparatively massive proportions, with all the main processes well developed. This is not the case with many other species, where, although they are fairly well developed, the caudal vertebræ rarely exceed six in number, and the added pygostyle may be small in comparison. This is the case, to some extent, in P. albiventris, while P. punctatus possesses seven caudals and a good-sized pygostyle. Doubtless there is an individual variation in the number throughout the family, while in general terms it may be said that Nannopterum usually has seven caudals and a pygostyle, and most all other Cormorants but six and a pygostyle.

Good views of the *pelvis* of *Nannopterum harrisi* are presented in figs. 16, 19, and 20 of the plates accompanying this paper. This part of the skeleton is also liable to vary in different individuals, while in old birds of the species it is always a big, strong, and massive bone. As a whole, it assumes the narrow, elongate form

seen among water-birds of the Cormorant class.

Viewed from above, it will be observed that the pre-acetabular part of the bone is very considerably less than the post-acetabular, and that its spreading anterior portion is horizontally disposed, the surface rapidly becoming sub-vertical as we pass backward to the acetabulæ. In front the surface is roughened and lined for muscular insertion, and is often perforated here and there by small vascular foramina. Either antero-lateral angle is rounded off; the anterior border exhibits a raised and definite emarginate finish, with generally some small, blunt processes extending directly forwards. We also find occasionally one or more conspicuous apophyses outstanding from the lateral borders of this pre-acetabular portion of the pelvis, and one of these is shown in fig. 20 of Plate XVIII., the left-hand side one having been broken off.

Anteriorly, there is a re-entering angle between the ilia, far into which projects the neural spine of the first "pelvic vertebra,"



Mesially, the ilia form a solid crista the entire length of the bone, which, in the pre-acetabular region, is finished off with a horizontally spreading lamina having an average width of some 4.5 millimeters. This disappears at a point in advance of the acetabulæ, and the ilia and "crista" fuse in the same plane. As we pass posteriorly, however, the latter again comes more and more in evidence with its thickened border, until it reaches its maximum height, at its posterior termination, where it is as high as the neural spines of the caudal vertebræ. In the post-acetabular region the mesial margins of the ilia gradually curve away from the sacral crest, which curvature terminates at the place where the mesial margins of the ilia articulate with the transverse processes of the uro-sacral vertebræ (fig. 20).

There are large interdiapophysial foramina among the last three uro-sacral vertebræ; but anterior to these such openings hecome, as a rule, very small. A little way back of either anti-trochanter, on the dorsal aspect of the pelvis, there is a big, rough elevation for muscular insertion. P. carbo and P. urile possess similar tuberosities on their pelves, while in a number of other kinds of Cormorants they are present, but not especially notice-

Regarding the pelvis of Nannopterum on side view, it is to be observed that a rudimentary prepubic spine is a character constantly present, and that the cotyloid ring or acetabulum is very large, as is the massive antitrochanter. As a matter of fact, all this part of the pelvis in Harris's Cormorant is of the most substantial sort, as, indeed, is the entire pelvic structure.

The ischiac foramen is a very large, elliptical vacuity, and, being so large, tends to lighten greatly the pelvis as a whole. So, too, we find the obturator foramen of good size and almost continuous with the obturator space, which latter is a vacuity nearly as large as the ischiac foramen. Posterior to it there is a broad, flat area of bone, formed about equally of the ischium and ilium, the free, moderately sharp border of the former being deeply convex outward. The pubic element or style articulates here, broadening as we follow it backward, then thickening turning very abruptly toward the mesial plane, and terminating with an expanded tip.

Where this pubic element bounds the obturator space below, however, it is a very slender and long rod of bone—in fact, slightly slenderer than the quadrato-jugal arch of the skull, and no stronger than the lower part of the fibula in the leg.

A very deep, triangular notch indents the posterior border of the pelvis, it being the ilio-ischiac notch, and is characteristic of the pelves in the *Phalacrocoracidæ* generally. It results in converting the hindermost extension of the ilium into a long, strong, backward-directed, straight process, which, with the aid of the corresponding process of the other side, furnishes great protection to the leading caudal vertebræ. (See figs. 18, 19, and 20 of Plate XVIII.)

At the anterior extremity of this pelvis of Nannopterum there will be observed the marked downward extension of the first three vertebræ beneath the ilia. The transverse compression of them is very great, and all of the three hæmal spines sent down by them are much in evidence, forming, as they do, a very striking feature of the pelvis, not only in this flightless Cormorant, hut in the pelves of most of its relatives in the genus Phalacrocorax.

The posterior articular facet on the centrum of the 21st vertehra, or the hinder one of the two together-fused vertebræ of the dorsal region of the column, is elongo-elliptical in outline, with the major axis vertical, and the whole markedly concave. This accounts for an ellipsoidal, convex facet on the anterior face of the centrum of the 22nd vertebra, which, in the duly articulated skeleton, fits accurately into the concave one previously described. This kind of articulation with facets of similar size and form—an opisthocœlous one—also obtains in the ease of the last dorsal vertebra, and further accounts for the large, hemi-ellipsoidal facet on the leading vertebra consolidated with the pelvis beneath the ilia.

Ventrad, in the deep and ample pelvic basin, in the case of Nannopterum, there is an unusual variation to be noted with respect to the diapophysial braces thrown out on the part of the two sacral vertebræ that brace the pelvic walls directly opposite the antitrochanters. Sometimes these are both perfect and strong (No. 19,628); again, the anterior one on the right side may be absent (Nos. 19,719, 19,720, and 19,721, \mathfrak{P}); or the anterior ones may be stout and the posterior pair slender (No. 19,722). This, however, is a peculiarity that holds in the case of other, or at least some other, Cormorants.

In *P. punctatus* the pelvis is long and narrow, reminding one of the bone in some of the Loons or Grebes, notwithstanding the fact that all of its essential characters are strictly phalacrocoracine. In it, however, the obturator space is very long and narrow, with the pubic element bounding it below very slender, the distal, thickened part of which makes a very close articulation with the lower border of the ischium, which latter, at its postero-external angle, is produced to mould itself upon it, and passing which, the free extremity of the pubis is curved directly downwards and in no degree backwards.

inwards, and in no degree backwards.

In nearly all Cormorants of the genus *Phalacrocorax* the interdiapophysial foramina in the post-acetabular region, dorsad, are large, and most often occur as far forward as the antitrochanters. In them, too, the backward-extending process of the ilium, on either side, forming the mesial houndary of the "ilio-ischiac notch," is short—much shorter in proportion than we find it in *Nannopterum*.

The Sternum.—Harris's Cormorant has this bone fashioned along the lines of the typical "raft" pattern, as will ever be the case with any hird wherein the power of flight has, for many

generations, been entirely lost, and the wings have become reduced to mere secondary aids to locomotion under water.*

At this writing, there are five practically perfect sterna of this flightless Cormorant before me; and, while they all offer essentially the same characters, there are, nevertheless, some very interesting differences to be seen among them upon comparison.

To be explained in one way or another, these sterna may, in the first place, differ markedly in size. For example, in all of them the costal processes are large, drawn out into a somewhat acute triangular form, and tipped off with a little bony nib. These nibs are good points from which to measure the extreme transverse width of the bone, and this width in No. 19,721 equals 84 millimeters, while in No. 19,628 it but equals 74 millimeters, and in No. 19,722 rather more, or 78 mm. Again, No. 19,721 has an extreme mid-longitudinal length of 89 mm.; in 19,628 this is again much less in comparison, equalling but 72 millimeters, and so on for the rest. In other words, whatever may he the actual size of the sternum, with respect to width and length, the fact remains that in its form it is nearly square in outline. It is also much flattened out from above, downwards, the general concavity of its ventral side not being as profound as in most all other Cormorants, as in, for example, P. auritus, P. urile, and P. carbo.

I find no exception to there being four large facets on either costal border whereon the hæmapophyses or "costal ribs" articulate. There are no pneumatic foramina among these—that is, in the oblong concavities separating them, or in the triangular one anterior to the leading facet or behind the last one; in fact, the sternnm of Nannopterum harrisi is a non-pneumatic hone, like nearly all, if not all, of the rest of its skeleton. Some of the species in the genus Phalacrocorax have a pneumatic sternum, but not every one of them. It enjoys that condition in P. auritus, but not in P. urile, and so on.

The keel or carina of the sternum in Harris's Cormorant has become reduced to a mere rudiment of what that part of the bone is in those species of the *Phalacrocoracidæ* that fully possess the power of flight (see fig. 7, Plate XVII.; fig. 16, Plate XVII.: and fig. 19, Plate XVIII.) Anteriorly, the "carinal angle" is still preserved and enlarged for its articulation with the os furcula, while but a remnant of the keel itself remains. This last is coneaved upon either side, and in some specimens this concaving is so profound

^{*} Dr. Gadow, in a few forceful words, refers to what the skeleton of Nannopterum should teach us when he says that "An important and stern lesson, taught by this flightless Cormorant, a first-rate swimmer, is, of course, its analogy with Hesperornis, which, in spite of all that has been said about its structure and affinities by Furbringer and myself, occasionally still figures as a member of the Ratilæ. He has no keel, therefore he is a Ratite, Fial justitia, pereat common-sense!" (loc. cit., p. 173). It occurs to me that there were still others who very materially assisted in eradicating the erroneous notion that Hesperornis was some sort of a "swimming Ostrich"—Professor D'Arcy W. Thompson, for instance.

that the bone is very thin at the bases—so thin, indeed, that in some sterna the light can be readily perceived through it when the bone is properly held up to the sun or a flame (No. 19,720).

After quitting the hæmapophysial facets and their indentations, the lateral borders of the bone become sharp and thin, remaining

so to their terminations.

Posteriorly, the xiphoidal border of the bone, in all Cormorants' sterna examined by me, present a somewhat broad, mesially notched, middle projection; at either postero-external angle a somewhat longer and narrower prolongation, while the so-called "notches"—one on either side—between them are moderately profound only, and sub-circular in outline (fig. 7, Plate XVI.)

In some specimens of Harris's Cormorant this pattern of its

In some specimens of Harris's Cormorant this pattern of its xiphoidal horder exhibits some indications of absorption, as a shallowing of the "notches," and a disappearance of a part of

the median prolongation.

All Cormorants have the dorsal aspect of the sternum very smooth, while a raised, rounded ridge passes backward from either costal border to meet, and merge completely, in the median plane posteriorly (P. auritus, P. urile, &c.) This is also found in Nannopterum, but is far more feebly marked; and in this bird, where the xiphoidal part of the bone begins to exhibit evidences of disappearance, this ridge behind has already disappeared. This is the case in all specimens now at hand.

Ventrally, the sternum of Harris's Cormorant is likewise smooth, its areas for muscular insertion having been reduced to a limited triangular area, bounded by a raised ridge on either side of the rudimentary carina. These concavities vary in different specimens with respect to their distinctness or depth. They do not show well in fig. 19, for example, for they are to some extent shallow in the sternum of that individual—in fact, the sternum of that hird has its "body" very thin in some places—so thin, indeed, that in one place a vacuity is formed, as may be noted in the round spot in the figure.*

One of the most interesting features to be noticed with respect to the sternum of Harris's Cormorant is its anterior border. Here, the middle and above this is occupied by a rather deep, broad, and uniformly concave notch, with its concavity directed upward. This occurs just above the thick and shallow remains of the anterior border of the rudimentary keel, which is fashioned after the articulatory support of the os furcula. Far apart, and on either side, is found a deep, well-marked coracoidal groove, these being quite as much in evidence as they are on the sterna

^{*} The foramen in question might be taken for a shot-hole, but it is not, for its edges are sharp, clean, and unbroken. Two of the sterna of this Cormorant at hand have shot-holes in them—that is, No. 19,721, which received four, and No. 19,719, which has one. These all show the unmistakable diagnostic evidences or signs of gunshot perforations through an osseous plate, and are very different from such openings as are due to deficient ossification.

in most of the species of the genus Phalacrocorax. In no Corinorant, however, possessing the full power of flight are they so far apart, though we find a certain degree of separation in some species, as in P. urile and P. pelagicus (No. 19,655, Coll. U.S. Nat. Mus.), while in others a slight decussation is to be observed, as in P. auritus. Finally, in other species the mesial, inferior angles of the coracoids are simply in contact when duly articulated in their sternal grooves as in life (P. magellanicus).

The Shoulder-Girdle (Plate XVI., figs. 8-11, 14, and 15).—In most of the skeletons of Nannopterum at hand the os furcula is a broad, U-shaped one, possessing most of the characters of the bone as seen in Cormorants generally. The breadth of the U varies in different specimens; for example, in No. 19,721 the clavicular heads are 67 mm. apart, while in No. 19,628 they are but 54 mm., and in No. 19,719, a large bird, they are 74 mm. apart. Probably these figures represent the extremes in this matter. Either clavicular head is enlarged in the same way as it is in all true Cormorants, there being a short scapular process above, which, by the way, does not reach the scapula in the articulated skeleton, and an abutment bearing on its posterior aspect a flat, articular facet of sub-circular outline for the head of the corresponding coracoid.

The main arc of the os furcula exhibits some, though not a great deal of, reduction, and this likewise varies, being less in some individuals than in others. Some Cormorants have the clavicular arc of the os furcula donbly as stout as it is in any specimen of Harris's, as, for instance, P. auritus (No. 19,262, Coll. U.S. Nat. Mus.), where, likewise, it seems to be, to a certain extent, pneumatic. Every vestige of a hypocleidium in the os furcula of Nannopterum has disappeared; in the articulated skeleton, as in life, the bone simply rests against the smooth surface on the anterior face of the rudimentary keel of the sternum, being held in position by binding ligaments in the living bird. All other Cormorants, in so far as I have examined them, possess some sort of a hypocleidium wherewith to meet the carinal angle of the sternum in articulation (fig. 14, Plate XVI.)

A coracoid of this flightless Cormorant has a length, generally, of about 66 millimeters, though it may be much shorter, as it is in No. 19,628, where it is but 58 mm. long. Measuring its inferior angles from apex to apex, it may be broader transverselyeverything else being equal-than is the coracoid in some other Cormorants. For example, the distance just mentioned measures 32.5 mm. in No. 19,721 of the series of Harris's Cormorant, while in an adult skeleton of P. auritus (No. 19,262) the same line equals 30 mm.

The upper extremity of the bone, which articulates with both the os furcula and the scapula, presents the characters found there among Cormorants at large, there baving been no change beyond a certain amount of shrinkage (Plate XVI., figs. 8 and 10). The shaft of this coracoid, however, has become, through a uniform

and general reduction in calibre, much slenderer, and this has given prominence to the muscular line passing down its anterior

aspect, especially at the lower part of its course.

The U.S. National Museum specimens do not support all that Dr. Gadow says of the coracoid of Nannopterum in his abovecited paper (loc. cit., p. 172), for he states, in regard to this bone, that "The coracoids are much reduced in length and strength. Their feet have remained as broad as they were originally, but they have crept asunder to the extent of 18 mm., and the shafts have been diminished at their median sides." That they have become reduced in "strength" there can be no doubt, and, perhaps to a slight degree, in "length," while it would not appear that their "feet" have remained as broad as they were originally, although the anterior and posterior facets on them, for the coracoidal grooves of the sternum, have increased in depth.

In support of this, I would invite attention to the coracoid of an adult specimen of P. urile (No. 18,982). It was about as big a bird as was the Harris's Cormorant numbered 19,628 of the collections of the U.S. National Musenm. Now, in that specimen of P. urile the full width of the foot of the coracoid—or that part of the sternal end of the bone which articulates with the coracoidal groove of the sternum—from angle to angle measures 24 mm., the same distance on the coracoid of the Harris's Cormorant measuring but 18 mm. The length of this coracoid of P. urile equals 72 mm., while in the specimen of Harris's it is but 58 mm. long. That the reduction in the calibre of the shaft did not take place exclusively on its "median side," as Dr. Gadow states, is evidenced in the coracoids of the skeletons at hand. I am compelled to believe that there was a general reduction of the bone, for the reason that in all Cormorants, including our P. urile, the process at the infero-external angle of the coracoid is very inconspicuous, while in Nannopterum it may attain a length of not less than nine millimeters. It has, beyond doubt, acquired this length by remaining almost its original size, while the shaft of the bonc, on its own side, bas shrunk away from it in the course of the diminution of its calibre as a whole. That this was the case is clearly evidenced in all the coracoids of this Cormorant now before me—that is, five pairs of them.

Everyone will agree with Dr. Gadow in his statement that "the reduction of the scapulæ is extreme" in Nannopterum harrisi (loc. cit., p. 172), for not only has the head of the bone suffered much reduction, but likewise in the length of its shaft, the width or calibre of it not having changed to any appreciable degree. This is very clearly shown in figs. 9 and 11 of Plate XVI. of the present paper, where such excellent representations of these bones are given that any further description of them becomes

quite unnecessary.

When articulated, as in life, the scapulo-coracoidal angle equals about 90° in *Nannopterum harrisi*, whereas in ordinary Cormorants this angle ranges between 63° and 70°. Again, when

thus articulated the shafts of the coracoids, in the case of Harris's Cormorant, come within a few degrees of being parallel to each other (Nos. 19,628 and 19,722). This degree of parallelism varies for different individuals, hut it can be estimated; for example, if we draw a transverse line through the "feet" of the coracoids when they are normally articulated, then extend the lines of their longitudinal axes until they meet below the sternum, we will find that, from their point of meeting to the middle of the line drawn between the coracoidal feet, they have a length of some 73 millimeters. A corresponding line, in the case of P. urile (No. 19,655, Coll. U.S. Nat. Mus.), measures but 45 millimeters the intersection of the extended imaginary lines, prolonging the longitudinal axes of the coracoids of this species, being opposite the posterior termination of the keel of the sternum on that bone. This goes to how that the angle formed by the extended longitudinal axes of the coracoids in Nannopterum harrisi is much more acute than it is in such a Cormorant as P. urile, and, consequently, the approach to parallelism is just so much the nearer in the former hird. They are, however, never absolutely parallel any more than are the articulated scapulæ, for when we extend, by imaginary lines, the long axes of the blades of the latter, when those bones are normally articulated in the skeleton, the point of intersection of those lines is posterior to them at a point about opposite the second caudal vertebra.

THE APPENDICULAR SKELETON.

The Pectoral Limb (fig. 25, Plate XIX.)—Harris's Cormorant has the skeleton of its wing quite as perfectly formed, and has in it just as many of the bones as has any other Corinorant known to me; it simply has suffered great reduction in size. Dr. Gadow has demonstrated that it has been "reduced to less than one-half of its normal size" (p. 171). As a matter of fact, the skeleton of this wing has all the appearance of one that might easily, without any alteration whatever, helong to some small species of Cormorant about the size of a Hooded Merganser (Lophodytes cucultatus). This has nothing to do with the characters the bones present, for the wing of Nannopterum is wholly Cormorant in particular and steganopodine in general. It is completely nonpneumatic, as is the case of the wing-skeleton in most all ordinary Cormorants. The humerus in P. auritus is an exception, for it is certainly pneumatic in that species (No. 19,262, Coll. U.S. Nat. Mus.), while it is never so in P. urile, but may be in P. carbo.

The pneumatic fossa of the humerus belonging to the skeleton of Harris's Cormorant (No. 19,628) is shallow and elongate, extending down the ulnar side of shaft for a distance of 20 mm., narrowing all the time until it merges upon the same at a point opposite where the *radial crest* terminates on the other side of the bone.

On the palmar aspect of this humerus, just within the proximal part of the radial crest, there exists a considerable concavity, which is likewise large and deep in the same location on the humerus of *P. urile*, and, to a greater or less degree, seems to be present in the case of all Cormorants. In Harris's the shaft presents the same amount of sigmoid curve as it does in other species, and we also find the peculiar, in-turned extension of the ulnar trochlea of the distal extremity of the bone.

In length, this humerus differs considerably in different individuals, it being 101 mm. according to Gadow, while in No. 19,628 of the specimens here being examined it is 90 mm. In No. 19,719 it is 102 mm., being the same in No. 19,720, and so on.

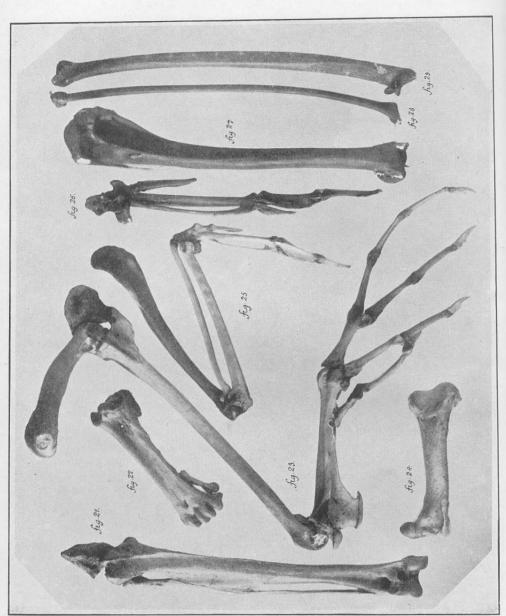
As Gadow has already pointed out in his memoir, the greatest amount of reduction in the skeleton of the wing of this bird is to be seen in the bones of the antibrachium, for, while the ulna and radius are about of equal length, they are each very much shorter than the humerus. Moreover, it is to be noted here that the radius has lost the most of that peculiar double curve its continuity presents in other Cormorants, and so well exemplified in the radius of P. urile. Here, as in other Cormorants, when normally articulated, its distal moiety, or rather less, is parallel and close to the ulna, while the proximal half of the bone, from head to mid-shaft, curves away from its companion in the forearm, and thus creates, in that locality, a large "interosseous space."

With a gently curved shaft, which has double the calibre of that of the radius, the ulna of Nannopterum has lost much of that conspicuous process seen in other Cormorants, which curves about the head of radius and supports the facet of the lesser sigmoid cavity. Proximal fourth of this shaft, on its palmar aspect, is scooped out longitudinally to an extent both actually and relatively greater than we see it in other Cormorants, while the insertional points for the quill-butts of the secondary feathers are shallow pitlets rather than papillæ, as they are in P. carbo and its congeners. In P. urile these papillæ are paired, thus creating a double row down the shaft in this and probably in

other species of these birds.

Radiale and ulnare of the carpal joint are rather large in proportion, as compared with the bones with which they articulate; but this is so slight that it would hardly be safe to say that their reduction had not proceeded quite so far, relatively, as the other bones with which they are in contact, although, judging by the eye alone, this appears to have been the case. If it be so, it is very slight. However, the trausverse diameter of the ulnare enters into the length of the ulna's shaft in P. carbo eighteen times, while the corresponding diameter of the ulnare in Nannopterum enters into the length of the shaft of its ulna less than ten times.

Apparently there does not seem to have been the same amount of shrinkage, in proportion, in the case of the bones of *manus* as there has been with respect to the humerus and the radius and ulna of the forearm. The clawless terminal joints of the thumb and two fingers are all present, having been retained in



proportion with the carpometacarpus and proximal phalanx of index digit. As a matter of fact, were this wing of Nannopterum harrisi the wing of a bird the size of a Partridge, and possessed of the same muscles, ligaments, vessels, nerves, and other structures that it has in the Cormorant, that Partridge would surely enjoy the power of flight in a high degree. In other words, in its reduction this wing has so well sustained its proportions and factors necessary to its function that, while it is useless to this big Cormorant, except as an adjunct in swimming, it would be a most powerful structure for aerial locomotion, in the case of a bird of the proper size, to use it effectively.

The Pelvic Limb.—Compensation for the reduction in size of the bones of the pectoral limb is seen in the increased size and power of those of the posterior extremity here to be considered. This is especially the case with respect to the tibio-tarsus, though it is equally evident in all of the others composing this limb. From femur to ungual joints inclusive they are big, strong bones, and would well serve a Cormorant fully one-fourth larger than

Harris's.

All the bones of the pelvic limb of this Cormorant are well shown in Plate X1X. (figs. 21-24), some of them on two different views.

From proximal to distal extremity the femur exhibits a general as well as a considerable curvature to the front, this stout bone. upon that aspect, being convex longitudinally. Its summit, though convex from before, backward, is otherwise in one plane, and devoted to the large, smooth facet for the antitrochanter on the pelvis. Large and semiglobular, the caput femoris is sessile as to the shaft, and, instead of a pit for the ligamentum teres, presents an extensive roughened surface. A broad trochanter major projects only to the front, while its outer surface-and extending round to the back of the shaft above—has upon it a number of prominent elevations for muscular attachment; others of these occur at the usual sites on the shaft below and above the condyles posteriorly. There is no trochanter minor, and the "rotular channel" is shallow. For its middle third the shaft nearly cylindrical, and the condyles are very prominent posteriorly, where a deep pit is found between them in the middle line and above.

The usual sulcus for the head of fibula in the external condyle is deep and smooth.

Femora of Nannopterum range in length between 63 and 73 millimeters, being stout in proportion thereto.

From their general appearance, one would say that all the bones of this limb were non-pneumatic, while at the same time there are many minute foramina found in all the long bones, as well as in the patella, that need be accounted for. In the femur they occur about the head, and in the intercondylar fossa posteriorly. They are found about the proximal extremity of the tibio-tarsus and also of the tarso-metatarsus. If these be

"nutrient foramina," and not pneumatic ones, the boues of this

limb have an abundant vascular supply.

In P. urile the femur, as compared with the one just described, is relatively longer with respect to the average, and considerably smoother and slenderer. For the size of the species, this likewise applies to P. auritus. The bone is especially smooth in P. carbo (No. 18,851, Coll. U.S. Nat. Mus.) and in other species at hand. In P. punctatus it is shortened and much bowed, almost reminding us of the femur in some Grebes, though the femur exhibiting the greatest amount of curvature belongs to P. penicillatus (No. 18,535).

The patella is very large, trihedral in form, with an extensive, squarish hase, moulded to receive in articulation the larger share of the surfaces of the femoral condyles. Above its middle it has, passing transversely through it, a good-sized foramen, which, on the inner aspect, is at the base of a more or less circumscribed concavity there; while on the outer side it comes out about flush with the surface of the bone. This foraminal passage transmits the ambiens muscle, but I find it is not patulous in all Phalacrocoracida. Garrod, who studied it in P. carbo and in "P. lugubris," remarks that "Meckel did not find the ambiens in the Cormorant; it is peculiar, in that it runs through the substance of the large triangular patella, in a bony canal" (Coll. Sci. Mems., footnote, p. 198). Possibly Meckel may have had a Cormorant where the ambiens does not pass through the aforesaid bone; this is a matter I have not looked up.

Patellæ of Cormorants I have figured in a number of my published papers; one of these figures Coues used in his "Key" (5th ed., vol. ii., p. 961, fig. 675, P. bicristatus), stating in the text that, with respect to Cormorants, "There is a bulky free patella, co-existent with a short cnemial apophysis or rotular process of tibia, but perfectly distinct therefrom, as in Grebes." Now, at the present writing, after having compared and studied this big seasmoid in a good many Cormorants, I am convinced that this statement is entirely erroneous. As to the patellæ and the cnemial process of the tibio-tarsus in Loons and Grebes, it has been correctly described by numerous ornithotomists, including myself. Coues, in the volume just cited, gives, on page 1,052, a figure—one of my own, unacknowledged—of a tibiotarsus and patella of a Grebe. This is a correct drawing, and from it will be observed that the cnemial process of the tibio-tarsus (a) co-ossifies with and is a part of the latter, while the big, free patella is in close contact with its posterior surface. As I have pointed out in many places, the arrangement is quite different in the Loons.

^{*}Shufeldt, R. W., "Concerning the Taxonomy of the North American Pygopodes, Based Upon Their Osteology," Journ. Anat. and Phys., London, June, 1892, pp. 199-203. On page 202 it is stated, with respect to the Loons ("Urinatoroidea") that they possess "only a very small, flake-like sesamoid, which occurs in the tendon of the extensor femoris muscle at its

In Cormorants something entirely different from either the Grebes or the Loons obtains, and what I find to be the case I think will hold throughout the Phalacrocoracida. In this family, the upper or proximal half of the cnemial process of the tibio-tarsus has, in the young, become dissociated entirely, and in the adult, as a free segment, eventually completely co-ossifies with the big true patella forming the aforesaid sesamoid, which heretofore has always been described as the patella, irrespective of the fact that its entire anterior third is represented by the proximal moiety of the enemial process of the tibio-tarsus. In many birds the ambiens muscle has a groove for its accommodation on the anterior face of the patella, and this was probably the case in the ancestors of the Cormorants, prior to the time when, for some reason or other, the upper half of the cnemial process of the tibio-tarsus becomes dissociated and thoroughly fused with the true patella behind it. When this came about, the ambiens muscle originally passed in a groove on the anterior face of the patella, came to pass through a foramen, which foraminal passage was formed in the manner above pointed out.

In some Cormorants this foraminal passage is extremely minute, and I believe that in such species it will be found that the ambiens muscle is gradually disappearing. This is the case in a skeleton of *P urile* before me (No. 19,655, Coll. U.S. Nat. Mus.), where the line of union or fusion of the patella, and the dissociated upper half of the enemial apophysis of the tibio-tarsus can be most plainly discerned. All this is still more evident in the *patella* of *P. auritus* ("*P. dilophus*") (No. 19,262, Coll. U.S. Nat. Mus.), where the *ambiens* not only goes through the foraminal passage aloresaid, but the entire dissociated enemial apophysial portion can be made out. Indeed, the apex of the

latter is distinct from the apex of the patella.

In P. vigua this compound patella is comparatively small, and its compound nature, as described above, very distinct, the

passage for the ambiens being commodious.

In P. carbo (No. 18,851, Coll. U.S. Nat. Mus.) the foraminal passage for the ambiens is almost entirely absorbed in both patellæ, while the part of the enemial apophysis which has united with the patella, as in the other Cormorants above described, is most clearly to be made out.

The foraminal passage has entirely dsappeared in *P. penicillatus*, and the patella is wedge-shaped and longer longitudinally than in other Cormorants. The part of the tibio-tarsal enemial process, which has united with it to form the big, free sesamoid, is plainly

to be made out.

P. albiventris has the foraminal passage nearly gone—impervious in some individuals—and the bone clearly showing its composition.

msertion, and probably the true patella has co-ossified in the adult with the elongated enemial process of the tibio-tarsus." In this matter, then, as stated above, two groups of divers are, morphologically, quite dissimilar. In fact, while formed on the same general lines, this sesamoid, composed as described above, with and without a foraminal passage for the ambiens muscle, varies considerably (sometimes) in form throughout the family Phalacrocoracidæ generally.

Returning to the skeleton of Harris's Cormorant, we may say,

Returning to the skeleton of Harris's Cormorant, we may say, in regard to its tibio-tarsus (figs. 21, 23, Plate XIX.), that it is a very straight, stout bone, having an average length of some 140 millimeters. Such part of its chemial process as remained with the shaft rises well about the summit of the latter, and has well-developed ento- and ecto-chemial processes. They do not extend far down the front of the shaft, but very soon gradually emerge npon it. Chiefly posteriorly, the level summit extends considerably beyond the shaft, and presents on top extensive articular surfaces for the femoral condyles.

On the outer aspect of the straight, antero-posteriorly flattened shaft there is a very long and wide fibular ridge for the fibula, which latter closely articulates with its entire extent-some Anteriorly there is the usual groove in the 30 mm. or more. lower third for the passage of tendons, and this passes under a strong osseous bridge just above the condyles, as we find it in so many birds. Of the two massive condyles, the inner one is much lower on the shaft than the outer, and, combined, they present posteriorly an extensive articular surface for the tarso-metatarsus. A large, free sesamoid is found in the ligaments at the back of the inner condyle, and this is shown in fig. 23 of Plate XIX. I am inclined to think that such a sesamoid does not occur at the back of the outer condyle, as I do not find it in any of the other skeletons where the other is invariably present; most all, if not all, other Cormorants possess it (P. urile, &c.)

Some interesting variations are to be found in the tibio-tarsi of other species of this group of birds, as, for example, in the extinct Pallas's Cormorant, the unusually broad fibular crest has its anterior surface in the same plane with the anterior surface of the tibio-tarsal shaft, thus creating a broad, flat area of bone immediately below the enemial processes. The tendinal canal at the lower end of the shaft is remarkably deep at its lower part, and the osseous bridge spanning it looks, to an unusual degree, upward rather than forward. Throughout the family, however, the morphology of the bone is practically the same, though the study of its variations are highly important.

In all Cormorants the *fibula* is remarkably well developed, being long and stout, especially stout opposite the fibular ridge and above, while distally, in some old birds, Harris's Cormorant not excepted, it almost reaches down to the side of the outer condyle of the tibio-tarsus, the short interval being spanned by ligament.

While the type of them is the same, the tarso-metatarsi of Cormorants likewise exhibit a considerable amount of variation—more so, perhaps, everything else being equal, than do the tibiotarsi of those birds. In some it is stout and rather shortish; in

others it is longer and considerably more slender with respect to

its shaft, and so on through the family.

Nannopterum harrisi possesses a rather short, very stout, straight, broad, antero-posteriorly flattened tarso-metatarsus, with large, prominent, distal trochleæ, which lie nearly in the same plane, though the middle one is somewhat the lowest. The anterior aspect of the shaft is excavated above, which excavation imperceptibly merges on to the shaft as a shallow, longitudinal concavity, as far as the large, circular foramen below, which in life transmits the anterior tibial artery.

The outer side of the shaft is also longitudinally grooved for the passage of certain tendons to the toot. Posteriorly, the shaft is flatter, though a little less so internally, where, at its lower third, is attached by ligament the rather large first or accessory metatarsal, the enlarged distal end of which articulates with the

first joint of hallux.

At the base of the excavation at the upper third of the bone in front there is to be observed the usual pair of foramina, placed closely side by side. They pierce the shaft as usual, their posterior exits being not far apart, one on either side of the large quadrate hypotarsus. This latter springs from the inner mesial aspect of the shaft above, being a large quadrate osseous lamina, finished off posteriorly by an expanded cap of bone, rounded above, and pointed below, flat behind, and with its margin protruding all round—this finishing-off piece itself being at right angles to the hypotarsal plate proper (Plate XIX., fig. 23). In Harris's Cormorant it extends below the latter; but this is not the case in all Cormorants—such species as Pallas's, P. urile, and many others being exceptions to it.

Then to the outer side of the hypotarsal plate in Nannopterum we find one large groove for tendons, and external to it one or two very shallow, and very indefinite others. There are no piereing foramina, while in Pallas's Cormorant, in P. punctatus, and doubtless in others, one very distinct foraminal, tendinal passage passes through the hypotarsus longitudinally. This is the case

also in P. urile and P. auritus.

The condylar cavities on the summit of the bone are, as we might suspect, extensive—the inner one being the larger as well as the deeper of the two, while a big, intercondylar tubercle stands between them in front. Postero-externally, the outer of these two articular areas is drawn out into a distinct apophysis, which is present in most other Cormorants.

In pes the joints are long and somewhat flattened from above, downwards, except in the case of the long, curved joint of hallux.

The ungual joints, though of fair size, are of a feeble pattern, as is the rule in the case of most swimmers among hirds (fig. 23, Plate XIX.) All the hasal joints of the anterior toes are nearly of a length, each averaging about 26 mm. from base to distal trochlea; this is more or less true of other Cormorants.

CONCLUSIONS.

Osteologically, Nannopterum harrisi presents all the characters, with the usual specific variations, found in the Phalacrocoracidæ generally. Its title to generic distinction rests entirely, in so far as its skeleton is concerned, upon those morphological changes which have taken place in its osseous and other systems, due to the gradual loss of the power of flight. In other respects it is a true Cormorant, and had it never become flightless, and the result not taken place in its structure, there would have been no occasion to remove it from the genus Phalacrocorax.

In that genus it sees its nearest relatives among the "long-faced," more or less compressed crania types, though not the extremes among them, as, for example, the *Urile* series. With respect to its skull as a whole, it agrees best with some individuals of *P. penicillatus*; while, upon the whole, in the remainder of its osteology, it is as near allied to *Phalacrocorax perspicillatus*—the extinct Pallas's Cormorant—as it is to any other form now existing

in the world's avifauna.

EXPLANATION OF PLATES.

(All the figures in the Plates, with the exception of Plates XVII. and XVIII. (where they are reduced about one-fourth), are of natural size.* being reproductions of photographs made direct from the specimens by the author.)

PLATE XV.

- Fig. 1.—Skull of adult Nannopterum harrisi. Direct superior view.

 Large occipital style in normal position. (No. 19,628, Coll. U.S. Nat. Mus.)
- Fig. 2.—Lower mandible of *N. harrisi*. Direct superior view. Belongs to the skull shown in fig. 1 above.
- Fig. 3.—Skull of Brandt's Cormorant (Phalacrocorax penicillatus), adult. Viewed directly from above. Mandible, quadrates, and occipital style removed. (No. 940, Coll. U.S. Nat. Mus.) The removal of the quadrates allow the zygomas to spring inward too near the mesial plane of the cranium.
- Fig. 4.—Skull of adult N. harrisi. Direct lett lateral view, with maudible detached and occipital style in position. (No. 19,720, Coll. U.S. Nat. Mus.)
- Fig. 5.—Skull of Harris's Cormorant (N. harrisi). Adult. Viewed from above. Mandible and occipital style removed. (No. 19,720, Coll. U.S. Nat. Mus.)
- Fig. 6.—Skull of an adult Red-faced Cormorant (*P. urile*). Viewed directly from above, with lower mandible removed. (No. 12,505, Coll. U.S. Nat. Mus.)

PLATE XVI.

- Fig. 7.—Dorsal view of the sternum of N. harrisi. (No. 19,720, Coll. U.S. Nat. Mus.) Skull belonging to this skeleton is shown in fig. 5, Plate XV., above:
 - * Dr. Shufeldt's plates were reduced by about one-third to fit the page.

- Fig. 8.—Left coracoid of N. harrisi; anterior view. (No. 19,720, Coil. U.S. Nat. Mus.) See fig. 5, Plate XV., and fig. 7 of this plate.
- Fig. 9.—Left scapula of N. harrisi, dorsal view. (No. 19,720, Coll. U.S. Nat. Mus.) See fig. 5, Plate XV., and figs. 7 and 8 of this plate.
- Fig. 10.—Right coracoid of P. carbo; direct anterior view. (No 18,851, Coll. U.S. Nat. Mus.)
- Fig. 11.—Right scapula of the Cormorant (P. carbo); dorsal view. (No. 18,851, Coll. U.S. Nat. Mus.) See fig. 10 above.
- Fig. 12.—First seven cervical vertebræ of N. harrisi. Direct left lateral view. Adult. (No. 19,628, Coll. U.S. Nat. Mus.) See figs. 1 and 2 of Plate XV. above.
- Fig. 13.—Cervical vertebræ (eighth to the fifteenth inclusive) of N-harrisi. Direct left lateral aspect. The leading seven are shown in fig. 12 of this plate.
- Fig. 14.—Os furcula of P. carbo. Direct posterior view. (No. 18,851, Coll. U.S. Nat. Mus.) From the same skeleton which furnished the scapula and coracoid shown above in figs. 10 and 11.
- Fig. 15.—Os furcula of N. harrisi. Direct posterior view. (No-19,720, Coll. U.S. Nat. Mus.) See figs. 7, 8, 9, and others in the plates.

PLATE XVII.

- Fig. 16.—Trunk skeleton of Harris's Cormorant (N. harrisi). Adult. Direct left lateral view. (No. 19,628, Coll. U.S. Nat. Mus.) See fig. 1, Plate XV., and figs. 12 and 13 of Plate XVI.
- Fig. 17.—Trunk sheleton of the Double-crested Cormorant (P. auritus).

 Adult. Direct left lateral view. (No. 19,262, Coll. U.S. Nat. Mus.)

PLATE XVIII.

- Fig. 18.—Trunk skeleton of P. auritus. Ventral view. Same as shown in fig. 17 of Plate XVII. above. (No. 19,262, Coll. U.S. Nat. Mus.) Right coracoid removed.
- Fig. 19. -Trunk skeleton of N. harrisi. Ventral view; adult. Same as shown in fig. 16 of Plate XVII. above. (No. 19,628, Coll. U.S. Nat. Mus.)
- Fig. 20.—Pelvis, four last dorsal vertebræ, and the skeleton of the tail of N. harrisi. Adult. Viewed on direct dorsal aspect. (No. 19,720, Coll. U.S. Nat. Mus.) See various figures in Plates XV., XVI., and XVII. for other parts of the skeleton of this individual. Prominent process on the external free border of the ilium (anterior to the acctabulum) on the left side broken off, and it would further appear that the seventh caudal vertebra is missing.

PLATE XIX.

Fig. 21.—Right tibio-tarsus, fibula, and patella of N. harrisi. Anterior view. Adult. (No. 10,628, Coll. U.S. Nat. Mns.) See fig. 16, Plate XVIII., and fig. 10, Plate XVIII.

- Fig 22.—Right tarso-metalarsus and accessory metalarsal of N. harrisi.

 Anterior view. From the same skeleton that furnished the bones seen in fig. 21.
- Fig. 23.—Left pelvic limb (complete) of N. harrisi. Internal or mesial aspect. From the same skeleton that furnished the trunk skeleton shown in figs. 16 and 19 and other bones in the plates. Note large sesamoid above the tarso-metatarsus.
- Fig. 21.—Right femur of N. harrisi. Anterior view. (No. 19,628, Coll. U.S. Nat. Mus.) Same skeleton as shown in part in figs. 16, 19, and other figures on the plate.
- Fig. 25.—Right pectoral limb of N. harrisi. Palmar aspect, and complete. (No 19,628, Coll. U.S. Nat. Mus.) From the same skeleton that furnished the pelvic limb figured on this plate.
- Fig. 26.—Skeleton of the left manus, including carpal bones, of P. carbo. Adult Palmar aspect. (No 18,851, Coll. U.S. Nat. Mus.) See figs. 10, 11, and 14 of Plate XVI., which are bones from the same skeleton.
- Fig. 27.—Left humerus of P. carbo. Anconal aspect. From same limb as the previous figure. (No. 18,851, Coll. U.S. Nat. Mus.)
- Fig. 28.—Left radius of the Cormorant (P. carbo). Supero-palmar surface. (No. 18,851, Coll. U.S. Nat. Mus.) See figs. 26, 27, and 29 of this plate; also figs. 10, 11, and 14 of Plate XVI.
- Fig 29.—Lelt ulna of P. carbo. Supero-anconal surface. (No. 18,851, Coll. U.S. Nat. Mus.) For other bones of this skeleton see references under previous figure.

Nesting of the Black Cormorant (Phalacrocorax carbo) in Tasmania.

By (Miss) J. A. Fletcher, R.A.O.U., Springfield (Tas.)

My sisters and I, some years ago, were spending the Michaelmas vacation at Bridport, which is the nearest seaport to Springfield. I had chosen this trip, being anxious to study the bird-life of the surrounding district, and also to see if Fairy Martins (Petrochelidon ariel), a species reported as breeding at Bridport in 1883, were present. In this I was disappointed, and also with regard to the district's bird-life, for, though much country was traversed, few interesting notes were made. Snakes, however, were numerous, and I found myself wondering what they lived upon.

I identified the Forty-spotted Pardalote (Pardalotus quadragintus) in some timber on the way down, and at Bridport found the haunt of a pair of Azure Kingfishers (Alcyone azurea). The presence of Black Cormorants (Phalacracorax carbo) attracted my attention, and I observed that, in the evening, they always flew in one direction. Watching them carefully, I came to the conclusion that the birds

remained in this locality for nesting.