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Description of the Modifications of certain Organs

which seem to be Illustrations of the Inheritance of Acquired Characters in Mammals and Birds.

By

Hans Gadow, Ph. D., M. A.,
Strickland-Curator and Lecturer on advanced Morphology of Vertebrata in the University of Cambridge.

With 2 Plates.

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„I may give another instance of a structure which apparently owes its origin exclusively to use or habit."

Charles Darwin, Origin of Species.

The eagerness with which the question of the inheritance of acquired characters has been discussed within the last few years, and the hitherto apparently unsuccessful attempts to bring forward cases which can be used for a settlement of this question, has induced me to collect a few instances which possibly may help to throw some light upon this problem.

As Professor Lankester has recently stated (Nature, March 6th 1890) the cases should be such „in which the transmission of acquired characters is directly demonstrated", or „in which it seems impossible to explain a given structure except on the assumption of the truth of Lamarck's second law" [1]). Moreover „we want well ascertained facts and straightforward reasoning from facts."

1) It will be convenient to repeat here the original wording of Lamarck's second law: Tout ce que la nature a fait acquérir ou perdre aux individus par l'influence des circonstances où leur race se trouve depuis longtemps exposé, et par conséquent par l'influence de l'emploi prédominant de tel organe, ou par celle d'un défaut constant d'usage de telle partie, elle le conserve par la génération aux nouveaux

Teratological cases, like repeatedly occurring supernumerary toes, should be excluded, because we are unable to explain how they were acquired. Cases of mutilation are not likely to be inherited unless the whole organism has been affected through correlation of a series of changes, which have been necessitated by the regaining of the equilibrium upset by the primary cause or insult. I have therefore tried to select such cases in which the obviously primary modification seems to have brought about changes in other organs; in other words cases, in which the whole organism seems to have become imbued with the subsequent effects of the original „eingreifende" Modification. Lastly, if these modifications are referable to mechanical strain, they enhance our chances of an explanation, and are less likely to be looked upon as gratuitous variations.

I do not flatter myself that the explanations of the primary causes of the six or seven cases, which I propose to discuss in the following pages, are absolutely binding, on the contrary, I have sometimes suggested opposite solutions and have had to content myself with pointing out which of the two seems to be the more probable. These attempts occasionally necessitated the discussion of, at first sight, rather remote analogies. At any rate the facts are well ascertained; the original specimens figured in the accompanying plates are with few exceptions in the Cambridge Museum of Zoology and Comparative Anatomy.

The following organs are treated in this essay:

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3. The tracheal labyrinth of the Ducks, p. 635.
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1. The beak of the Crossbills.

The peculiar formation of the beak of the Crossbills is well known and has attracted the attention of several zoologists [1]). The

individus qui en proviennent, pourvu que les changements acquis soient communs aux deux sexes ou à ceux qui ont produit ces nouveaux individus.

1) R. Townson „Tracts and Observations in Natural History and Physiology", London 1799, p. 116—123.

examination of a considerable number of specimens in the Collection of the University of Cambridge, together with the observations made by TOWNSON and YARRELL, yields the following results.

Both, the upper and lower halves of the beak are drawn out into ong, pointed and curved hooks and cross each other, the mandible being curved upwards, the premaxilla downwards. This crossing occurs in all the species of the Genus *Loxia*; this genus has a wide distribution, Crossbills inhabiting the pineforests of North-America, the Northern half of the palaearctic region, and the Himalayas.

The mode of crossing varies individually in every species, i. e. the mandible is turned either to the right or to the left, no predilection for one side being shown. Out of 36 specimens, belonging to six species examined, 20 had the mandible turned towards the right, 16 to the left side. Of the 19 males 12 were rightbilled and 7 leftbilled, whilst of the 13 females 6 were right and 7 leftbilled. Of the remaining 4 young birds the sex was undetermined.

The amount of curvature exhibited by the upper and lower beak varies considerably. (See figures 1—3). As a rule the lateral distortion is more marked in the mandible, but in fully adult birds nearly the whole of the upper beak is also laterally distorted. Where the cutting edge of the left mandible meets the right edge of the premaxilla, or vice versa, these edges are turned inwards to a varying extent, but are not filed away, so as to enable the beak to be closed; sometimes however a gap remains.

As YARRELL [1]) has shown, this distortion and the peculiar mode of feeding of the Crossbills produces an asymmetrical arrangement of the whole masticatory apparatus. The temporal and pyramidal muscles on that side of the head to which the lower jaw is inclined, are considerably larger than those of the other side, and indicate the great lateral power these birds are capable of exerting. Moreover not only the muscles but also the bones of the same side are affected. In rightbilled specimens the right quadrate is much stronger, and the right half of the occipito-squamosal region is larger than the corresponding left parts. The quadrate possesses a large spherical condyle, which fits into a corresponding hollow circular cup of the mandible, this arrangement admitting therefore the universal motion of a ball

1) W. YARRELL, „On the structure of the beak and its muscles in the Crossbill (*Loxia curvirostris*)", in: Zoological Journal, vol. 4, 1829, p. 459—465, pl. XIV.

and socket joint, specially in a lateral direction, in opposition to the chiefly vertical motion of the mandibles of most other birds.

„When holding the head of this bird in my fingers, I found I could bring the point of the under mandible in a line underneath and touching the point of the upper, but not beyond it towards the left side, while on its own side the point passed with ease to the distance of $^3/_8$ of an inch" (YARRELL).

The principal food of the Crossbills consists of seeds of Conifers, but other seeds like those of apples are likewise taken. Their mode of feeding is this: „They fix themselves across the pinecone, then bring the points of the maxillae from their crossed or lateral position, to be inmediately over each other. In this reduced compass, they insinuate their beaks between the scales, and then opening them, not in the usual manner, but by drawing the inferior maxilla sideways (and by energetically turning their heads) force open the scales or squamae" (TOWNSON). Thereupon, whilst the points of the beak press the shell from the body of the cone, they insert the scooped end of their tongue underneath the seed, and the food thus dislodged is transmitted to the mouth (YARRELL).

I have examined a nestling of *Loxia curvirostris*. Not yet fledged it had not been able to leave the nest; its stomach contained the unhusked seeds of some species of Conifer. These seeds must have been collected by the parents and brought in their crops to the young. The beak of the young bird (Fig. 4) is still somewhat soft, the horny sheath of the jaws is not yet protruded into curved points, the cutting edges are still straight, not bent inwards. Whilst the upper beak is still quite symmetrical, the lower jaw is, when viewed from in front, seen to be slightly turned to the right, so that its tip deviates not more than one millimeter from the middle line. The cranium and the quadrato-mandibular apparatus do not show any asymmetry in size and shape.

Consequently the distortion of the beak increases with the age of the bird to such an extent that it even affects a considerable portion of the skull in a secondary way, and it is produced by the frequent oblique pressure upon the tips of the beak during the operation of opening the pinecones.

This distortion which would have to be called pathological, if it did not happen to turn out useful, begins to show itself, although late, but still at a time when the young bird has not yet any necessity of submitting its soft jaws to any deforming strain. It can hardly be doubted that the ancestors of the Genus *Loxia* had straight beaks like the other *Fringillidae*, e. g. like the Genus *Pinicola*. The latter have a thick stout beak, which they can use like a powerful pair of forceps. To the Loxias a pointed and more slender beak has the advantage of being able to be insinuated between the scales. This elongation may have arisen as a gratuitous variation, subjected to and intensified by natural selection, but the subsequent distortion seems to have been produced mechanically, by the bird itself. If it had turned out to be harmful, natural selection would not permit it to be transferred indefinitely, on the other hand the same factors will elevate it to a permanent feature.

Of course the side to which the first *Loxia* dislocated its under jaw must have been almost, or probably quite, accidental, as the equal number of right and leftbilled specimens still indicates.

In connexion with this is a point which requires to be considered. If the distortion of the beak is inheritable, then its equally common right and leftsided occurrence amongst the parents must tend to abolish or to diminish its repetition in the offspring. The young bird produced by a leftbilled male and a rightbilled female would, as we should suppose, have a straight bill, and would have to acquire the deflexion anew, unless it follows that parent whose organisation has been most strongly affected by the distortion of the beak, be this due to age or to this same parent's being the descendant of a series of leftbilled birds. It is only fair to assume that generations of solely leftbilled Crosbills will accumulate and intensify the same tendency in their offspring. However we do not know if the difference in the crossing of the beak is deemed by the Crossbills an obstacle to pairing. The behaviour of birds in captivity would not settle this question, and observations concerning the pedigree of nestling crossbills have not come to my knowledge.

2. The bill of the Wry-billed Plover.

The wry-billed Plover, *Anarhynchus frontalis*, is restricted to New Zealand. In all the specimens hitherto known, the slender and sharply pointed bill is invariably turned towards the right side. The right edges of the premaxilla and of the mandible are thin and strongly turned inwards so that the right and left sides are very non-symmetrical in section. The left nostril and the groove, which is continued from it towards the terminal third of the bill, remain in their original position, but the right nostril, and still more the groove, are perceptibly slanting towards the right, as can be ascertained, when viewed from the dorsal side. Near the end of the left nasal groove, or about the region whence the bill turns towards the right side, the horny sheath is slightly thickened.

This bird lives on the seashore or in half dry riverbeds, where it pokes under pebbles and larger stones to extract small worms, insects and crustacea from their hiding places. It seems to use its longish bill somewhat like a lever and probe combined. That its bill is subjected to mechanical strain is clearly indicated by the edges which are turned inwards and by the apparent absence of tactile corpuscles in the uniformly smooth and entirely horny rhamphotheca.

As Professor Newton has shown (Proc. Zool. Soc. 1870, p. 673) the very young birds show already the curve of the bill in a marked degree. The specimen figured, was hardly more than three days old, the cutting edges of the right side are not yet turned inwards, but the position of the nostrils and their grooves is already asymmetrical.

The very early repetition of the peculiarity of this bill in young birds, most probably already beginning in the embryo, and the fact that only rightsided deviation is known, seem to indicate that this has become a very settled feature. This unique anomalous formation of the bill is combined with a most striking asymmetry of the coloration of the bird. Whilst young specimens, and the adult in winter plumage, possess only a grey patch on each side of the neck, the rest of the neck and underparts being white, the adult in breeding plumage have a black collar, (so common amongst *Charadriidae*) but the breadth of the black collar is nearly double on the left side to what it is on the right. This point has been noticed by various ornithologists (although the sides have been mixed, and in Seebohm's „Charadriidae" the woodcut has through inadvertence of the artist reversed the picture) and has by some been referred to natural selection. The broader half of the band is on the side which is exposed to view, when the bird puts its bill under a stone, which of course must be on the right side of the bird owing to the curvature of the bill. If the stone is big, the right side of the bird is hidden, and therefore need not be ornamented or be protected by a conspicuously black patch. What would be the use of such a mark unless the same be seen? On the other hand, assuming this patch to be merely ornamental, and therefore occasionally a source of danger and not protective, it might be argued that this bird, which spends a considerable time of its life in an oblique and lopsided position whilst examining the stony ground in search of food, thereby turns the left side of its head and neck towards the ground, and thus hides the conspicuous spot, whilst the right side is exposed to the view of enemies and consequently cannot by natural selection be permitted to develop so fully. However I do not feel inclined to favour this latter view, and have given it only as a possible suggestion. The bird whilst sleeping will by the very configuration of its bill put the latter over its right shoulder, and will then fully expose the broad portion of the collar; hence I conclude that the patch is ornamental as well as protective, in other words that it is meant to be seen.

At any rate it seems reasonable to consider the asymmetry of the bill to stand in correlation with that of the plumage, that the former is the primary and the latter the secondary modification. The interdependence between two so widely different characters, as shape of bill and colour of plumage, indicates again the very old and ancient nature of this abnormally shaped bill, and explains its early repetition in the young birds, long before they would be able to bend their bills invariably to the right side.

3. The tracheal labyrinth of the Ducks.

The following communication refers to an observation made by Wunderlich [1]) on the well known bullae or labyrinthic swellings of the syrinx of the male Ducks. He examined the embryos of more than 30 Ducks and found that the future labyrinth (leftsided in the common drake) was already indicated, in embryos from 3—20 days of incubation, by a swelling on the left side, and was on about the 10th day formed by 4 rings which were thicker and broader than the rest. This dilatation persists in the males but in the females it undergoes, from about the 27th day of incubation, a retrogressive metamorphosis, and disappears before the bird is hatched.

Owing to want of material I have not been able to examine this point myself, but to judge from the painstaking way in which Wunderlich's paper is written and illustrated, we have no reason to doubt the accuracy of his observation, especially as he was fully aware of its importance.

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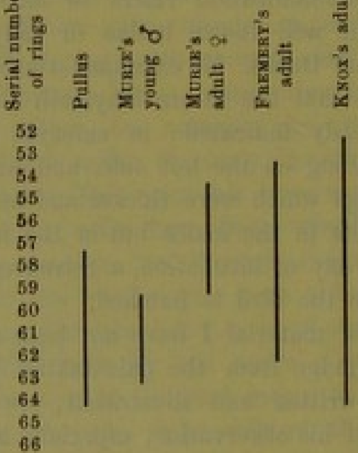
1) L. Wunderlich, Beiträge zur vergleichenden Anatomie des unteren Kehlkopfes der Vögel, in: Nov. Act. Kaiserl. Leop.-Carol. Deutsche Akademie der Naturforscher, Bd. 43, 1884.

We have here an instance of the inheritance of an organ by the embryos of both sexes, which in the adult persists only in the male. We cannot well assume that the ancestral *Anatinae* were possessed of such swellings in both sexes, although they are now almost universal in this group of birds. These swellings are, without exception, restricted to the males; they occur on both sides, or on one side only, and in the former case the swelling on the left side is generally the larger.

4. The tracheal pouch of the Emu.

The adult Emus of both sexes possess a large pouch on the ventral side of the trachea; its lumen communicates with that of the trachea through a longitudinal slit which is produced by a variable number of the cartilaginous tracheal rings being deficient in the medio-ventral line. The total, and also the serial, number of these split rings varies individually, as the following table will show, within considerably wide limits. As many as 14 and as few as 5 rings are known to be thus affected. Their position is at about the beginning of the lower third or fourth of the whole trachea.



The deficient tracheal rings are rounded off and stand asunder to the extent of 0,5—1,0 cm. The tracheal pouch is lined with the same mucosa as the inside of the trachea itself, and its lining passes without a break over the ends of the split rings. The outer lining of the pouch is continuous with the elastic and common connective tissue, which envelopes the tracheal rings, and it receives numerous fibres from the broad although thin muscular bands, which accompany the trachea as Mm. tracheales longi and then, below the pouch leave the trachea, to be inserted into the sternal apparatus as Mm. tracheo-sternales. Outside the pouch follows of course the thinned out common skin of the neck, the fibres of the M. constrictor colli forming a thin network over the lateral and ventral sides.

The whole organ is highly elastic, and, when blown out by the bird at will, is capable of assuming large dimensions. In Murie's adult specimen the length of the slit was about 7 cm; the length of the sac about 38 and its width 7—10 cm. In an adult specimen in the Cambridge Museum the length of the slit is 4,5 cm, the width of the slit 0,6 cm; width of trachea 3,4 cm, depth of trachea 1,5 cm.

Although the Emus possess no syringeal muscles, they have on each bronchus an internal tympaniform membrane, and are capable of emitting a deep, hollow and grunting sound. The pouch seems to act as a sort of resounding organ, and is most frequently dilated during the breeding season.

In a young male, dissected by Murie [1]), about one third of the adult size, the pouch was still very small (Fig. 8), it did hardly cover the flattened trachea in width and its length extended only over a few inches beyond the slit.

In a very young specimen, probably only three or four days old (Fig. 9), I found no indication of a pouch, but as many as 8 rings deficient in the middle line; the 56th and 65th rings being complete.

The pouch is consequently a hernia of the tracheal walls, rendered possible by a medioventral deficiency of some cartilaginous rings, produced by the wilful action of the bird through the pressure of the air within the respiratory tract, and increasing in size from youth to age. That such a hernia is effected through mechanical strain cannot be doubted, but the question is how the deficiency in the rings arose. It either began as an accidental defect in the thickness of the cartilage, and the bulging out of the membrane was a subsequent feature, or the frequent distention of the trachea was the primary agent and produced the thinning and ultimate rupture of

1) J. Murie, On the tracheal pouch of the Emu (Dromaeus Novae Hollandiae), in: Proc. Zool. Soc., 1867, p. 405—415.

the rings. In any case the tracheal rings will give way at their weakest point.

The first of these two assumptions seems to be the less acceptable, because of the following reasons. In birds the cartilaginous rings begin, according to WUNDERLICH (Sparrow and Duck) on the lateral sides of the trachea, according to RATHKE on the ventral side, and grow towards the median line; they always meet latest on the dorsal side, and it is here that some of them, when at all, remain open; they agreeing in this respect with Mammalian conditions. The ossification of the rings begins always on the ventral side and proceeds dorsalwards.

The males of certain Ducks e. g. *Metopiana*, possess a globular but flattened swelling at the beginning of the last third of the trachea; this swellings is composed of about 15 broadened and widened rings which ossify and almost completely fuse with eachother into an osseous bulla, but on the dorsal side a longitudinal space of from 2—3 mm in width remains, where the cartilaginous rings remain unossified.

In various Passerine birds, which like many *Cotinginae*, e. g. *Chasmorhynchus*, and *Tracheophonae*, e. g. *Grallaria* and *Hylactes*, have a very loud voice, and which cause their tracheae to swell up considerably, many of the rings in the vibrating membranes are extremely thin and often deficient. They have all the appearance of having been stretched out and ultimately rent asunder.

Dromaeus affords the only instance amongst all birds known of a ventral deficiency in otherwise well developed cartilaginous rings. The bulging out could not well proceed towards the dorsal side, because there the trachea lies upon the oesophagus and the muscles of the neck, whilst on the ventral side only the skin offers any additional resistance.

The tracheal pouch may therefore be looked upon as a ventral hernia of the trachea, acquired by the birds themselves, and inherited by their offspring to at least a preliminary extent. It has obvious, although distant analogies in the laryngeal and pharyngeal sacs of various Mammals, and how these can shape, and exert a lasting influence upon neighbouring skeletal structures, we shall be able to see in the next chapter.

1) I have found recently that J. BLAND SUTTON has also described and figured the „tracheal cyst" of *Dromaeus*, and regards it as a hernia. On the origin of certain cysts, in: J. Anat. and Phys., vol. 20 (1886), p. 432 f.

5. The larynx and the manubrium sterni of Howling Monkeys.

ALBRECHT[1]) has drawn attention to the cleft manubrium of the Howling Monkeys as „the first positive proof of DARWIN's theory of adaptation and inheritance".

He sums up the results of his investigations as follows.

There are Monkeys, belonging to the Genus *Mycetes*, 1) which possess an unpaired manubrium sterni like all other Mammals; 2) in which the premanubrium is cleft whilst the postmanubrium (equal to the copulae between the first and second sternal ribs) is still unpaired or united; 3) in which the whole manubrium is cleft into a right and a left half. The second case is by far more frequent than the others, and now represents the normal or actual condition. Since obviously the Howling Monkeys are descendants of Monkeys without a cleft manubrium, the first case is, concerning *Mycetes*, atavistic, the third case (complete fissure) „epigonistic".

According to ALBRECHT the fissure can be explained only in this way, that the two halves of the manubrium have been prevented from joining each other in the middle line by the colossal development of the basihyal and the thyreoid cartilages, which is known to occur already in the 7th week of embryonic life. Again, such an enlargement of the howling apparatus cannot have been acquired by the embryos, but must have been transferred to them by their ancestors, which developed it through excessive use. The fissure, originally teratological, has become normal, and there will probably come the time, when all the species of *Mycetes* will possess a complete fissura or „sternoschisis manubrii". The enormous enlargement of the basihyal bone and of the thyreoid cartilage occurs in both sexes, although in the female to a smaller extent. So far ALBRECHT.

But there exists a difficulty concerning the relative position of the laryngeal apparatus and the manubrium sterni. In the adult the thyreoid cartilage lies from 1 to 2 cm in front of or headwards from the manubrium, and not inside of, or between, the two halves of the manubrium and the first sternal ribs. The mere size of the larynx cannot therefore interfere with the framework of the chest, at least not when the animal is at rest. But when the Monkey, whilst howling, inflates the laryngeal sacs and distends

1) P. ALBRECHT, Sur les éléments morphologiques du manubrium sterni, Bruxelles 1884.

the whole throat, the recoil will cause the cricoid and the upper portion of the trachea to press upon the inside of the manubrium, and tend to strain its two horns with the clavicles and the first ribs asunder, in fact to produce an exaggerated „incisura jugularis manubrii".

The considerable force, which a strained larynx can exhibit, needs no further comment than reference to a braying ass or a gurgling and bellowing camel.

However, since the howling apparatus begins to show itself already in the embryo whilst the two halves of the sternum are still separated, and whilst the organs between head and chest are still much crowded together owing to the bent up position of the embryo, it is not impossible that the fissure of the manubrium has already originally been acquired by the embryo itself, and has not been inherited. At any rate the fissure is the secondary, the enlargement of the voice organs the primary feature. An examination of the enormous bulla formed by the basihyal bone and by the likewise extremely enlarged thyreoid cartilage, can only be explained as resulting from the distention into these parts of the blown out laryngeal sacs and similar recessus so common in the Mammalia.

The various sacs of ***Mycetes*** have been described by Sir R. OWEN in his Anatomy of Vertebrates, vol. 3, p. 598. „From the forepart of the space between the upper and lower vocal cords the pair of sacculi are developed, which line or occupy the thyreoid bulla. Between the glottis and the arytaenoid cartilages are the orifices of a pair of pouches, continued rather from the pharyngeal than the laryngeal membrane, which extend forward and upward on each side of the epiglottis. From the upper part of the thyreoid sacculi are continued a pair of pyramidal oval sacculi, which occupy the sides of the interspace between the epiglottis and the hyoid; and from the forepart of the thyreoid sac is continued the neck of the large infundibular sac, which expands to occupy and line the huge bulla or bony case formed by the basihyal." Similar laryngeal pouches occur in the Great Apes and in other Oldworld Monkeys. According to VROLIK [1]) they are larger in the males than in the females; they grow with the age of the animal and are consequently the largest in the most aged; they are dilatations of the ventriculi Morgagni in the Chimpanzee and in the Orang-Utan, and sometimes reach far down on the neck,

1) VROLIK, Article Quadrumana, in: TODD's Cyclopaedia of Anatomy and Physiology.

outside the larynx. A median sac is formed by a second dilatation of the left large sac, and is partly covered by the somewhat hollowed out basihyal bone. In other Catarrhinae an unpaired pouch is in direct communication with the larynx through an aperture at the base of the epiglottis, and is received by a corresponding cavity of the basihyal, which however never assumes anything like such an excessive inflation as in *Mycetes*. Not all these laryngeal sacs are therefore strictly homologuous formations, and they seem to have been developed independently by various groups of Monkeys.

6. The stomach of the Ostrich.

The peculiar and almost unique shape and position of the stomach of the African Ostrich has been described by various anatomists, notably by Meckel [1]), Macalister [2]), and myself [3]).

While in the typical position of the avine stomach the gizzard follows lower down upon the proventriculus, and is frequently separated from it by a glandless space or „Zwischenschlund" of oesophageal structure, the proventriculus of the Ostrich is enormously dilated and situated dorsally from the gizzard. The glandular area, not rarely, e. g. in *Rhea*, restricted to a circumscript region in the dorsal wall of the oesophagus, is somewhat dumb-bell shaped, and contains about 300 orifices of compound glands, which, instead of being placed closely together, are rather separated from each other, and occupy only about the dorsal quarter of the proventricular wall. The portion, which corresponds with the „Zwischenschlund" of other birds, is drawn out into a thin-walled bag, the blind end of which reaches considerably to the tailward from the gizzard. The opening into the gizzard looks tailwards instead of towards the heart. The gizzard itself is small but extremely muscular; one tendinous speculum, that of the pyloric or right side, looks towards the heart and right side, but is situated above the pylorus instead of below it; the morphologically left speculum looks ventrally, and likewise somewhat towards the right side. The strong furrow, which in all birds with a strongly muscular gizzard marks the line of junction of its two lateral muscles, and partly projects into the lumen of the gizzard, looks obliquely headwards instead

1) J. F. Meckel, System der vergleichenden Anatomie, 1829.

2) A. Macalister, in: Proceed. Roy. Irish Acad., vol. 9, 1869.

3) H. Gadow, in: Jenaische Zeitschrift f. Naturwiss., Bd. 13, 1879; and Bronn's Klassen und Ordnungen des Thierreichs, Vögel.

of tailwards. The pyloric portion of the duodenum makes a peculiar curve upwards (see Fig. 5). Compared with that of other birds, the gizzard of the Ostrich is turned over, round its transverse axis, to the extent of about 150°, pulled upon by the dilatation of the proventriculus. The latter has slided tailwards, past the dorsal and left side of the gizzard, and has drawn the orifice of the gizzard with it.

The cause of this enlargement and of the subsequent dislocation of the stomach is obviously the amount of stones, which Ostriches swallow during their life time. Most birds with a strong gizzard assist trituration of the vegetable food by small stones, preferably sharp edged pebbles of quartz. They are however sparingly used, because they seldom pass through the alimentary canal, and they are not disgorged, so far as I am aware. Only the Ostrich, and to a certain extent the Nandu, take up stones in excess. The Ostrich has a regular idiosyncrasy for almost any absolutely indigestible matter. GARROD found in the stomach of an adult male more than half a gallon of stones (about 7 lbs. in weight); „most of them were about the size of cobnuts or peas; they fully dilated the organ and pulled it down abnormally". I found in another specimen about 4 lbs. of gravel, the sandy detritus mixed with pebbles and being located in the blindsac of the proventriculus. The food rests on the top, and the finest detritus sinks down lowest. Comparatively few stones, mostly sharp, and hardly any sand occur in the gizzard, where alone they can assist the grinding process.

This condition is not abnormal, and is not the cause of death of Ostriches kept in captivity. All Ostriches hitherto examined, exhibited the same features. Moreover the examination of a number of embryonic and of very young Ostriches, collected by Mr. SEDGWICK at Ostrich-farms at the Cape, assisted by a grant from the Royal Society, show that the dilatation of the proventriculus, and the reversion of the gizzard are already present long before the stomach contains anything but foodyolk.

Fig. 18 represents an Ostrich embryo with the intestines in situ, after removal of the sternum, the right wall of the trunk and the liver. The heart has been affected in its position by the turning of the gizzard. Nearly the whole of the intestinal canal is shoved towards the right and dorsal side; the same is the case in the adult, and in such birds in which, e. g. Cormorant, Heron, the thinwalled and very elastic stomach is so large that its fundus reaches into the neighbourhood of the anus.

Fig. 16—17 represent the stomach of an Ostrich chick, about 3—4 days old, in its natural position and shape. It contained already some grass and a few small sharp edged pebbles in the proventriculus and in the gizzard, none larger than half a pea. The glandular area was still oval and only slightly elongated or stretched; the blindsac of the proventriculus looked tailwards, as does its opening into the gizzard. The specula of the latter were already distorted out of their normal position, but to a smaller extent than in the adult. The course of the gastric branches of the N. vagus likewise indicated a torsion.

The following measurements will show that, taking the breadth of the gizzard as the standard for comparison of increase in growth, in the chick as well as in the adult the increase of *ef* is smallest, whilst the length *cd*, i. e. the elongation of the proventricular sac increases most with age.

	Embryo	Chick	Adult
	mm	mm	mm
ab	14	28	140
ef	28	38	180
cd	34	50	400

or, the lengths in the Embryo taken as 1:

	Embryo	Chick	Adult
	mm	mm	mm
ab	1	2,0	10
ef	1	1,4	7
cd	1	1,5	12

In order to show that the amount and the nature of the food, together with other material, influences the shape of the stomach, reference to a few other birds is necessary.

Cormorants and Herons swallow their food, consisting of fishes, wholesale; the stomach is thinwalled and highly elastic; the two triturating muscles, so typical of the avine stomach, are very weak, but the two tendinous specula are still present. The stomach attains a great size, taking up the greater portion of the body cavity. — We cannot assume that such an arrangement existed in the ancestral Steganopodes and Herodii, because, although descendants of fisheating birds themselves, there exist other Steganopodes, like *Pelecanus*, with small and more normally avine stomachs, whilst the fish are stored up in the enlarged gullet; moreover the stomachs of young Cormorants and Herons do not yet show the excessive enlargement. Their fishdiet distends the yielding stomach, and this, like an overstrained elastic bag, does ultimately retain the originally only temporary shape.

The gizzard of the American Ostrich or *Rhea* is by far less muscular than that of the African Ostrich. The gizzard of young birds exhibits the usual furrow on its great curvature, but in the adult this furrow and projection into the stomach has disappeared and has given place to a round bag, produced by the weight of the pebbles which the Nandu takes up, although in a much smaller quantity than the Ostrich. These pebbles naturally bulge out the walls of the stomach, were the latter is weakest.

The measurements of the stomachs of a young and an adult *Rhea americana* are:

$\alpha\beta$ in young 34 mm, in adult 70, i. e. increase about 2 fold.
$\gamma\delta$ „ „ 33 „ „ „ 120 „ „ „ „ 4 „

The extraordinary strength of the gizzard of the Ostrich does not permit of a bulging out of any part of itself, and the excessive amount of stones, in aggregate bulk several times larger than the whole gizzard, drags down the yielding proventricular wall and rotates the gizzard.

Considering the dead weight of about 5—7 lbs. which the adult Ostrich carries about without any apparent use, almost its whole organisation must be affected to meet the greater expenditure of muscular power which is necessitated by this ballast.

7. The stomach of Tubinares.

The gizzard of most Petrels is small, roundish, flattened down on the right and left side. It is strongly muscular in *Procellaria* and *Ossifraga*, softer and comparatively larger in *Diomedea*. The proventriculus is many times more roomy than the gizzard, and is very dilatable. In those species, which possess a strong gizzard, the portion between the glandular area of the proventriculus and the gizzard forms a sac which, like in the Ostrich, extends dorsal- and analwards from the gizzard. The latter is completely turned over in a direction opposite to that in the Ostrich, the originally left speculum looking directly ventral, the right one towards the proventriculus or the neck. The course of the pyloric portion of the duodenum indicates the way in which the gizzard has been turned.

Fig. 25 shows these organs in situ in an advanced embryo of the English small Petrel, collected by Prof. Newton at St. Kilda. Fig. 26 shows the same in the adult. The reversion is already repeated in the young bird, although the necklike connexion between gizzard and proventricular sac is still less marked, and the rotation of the duodenal portion is less advanced.

The mechanical causes of this reversion of the stomach are similar to those of the Ostrich. The place of the gravel is taken by Cephalopods and other marine animals, swallowed wholesale by the Tubinares, as is indicated by the wide cropless gullet and by the frequent occurrence of the chitinous beaks of Cephalopods in this proventricular sac.

Description of the Plates.

Fig. 1 e 2. The beaks of two right-billed males of the Crossbill, *Loxia curvirostris*; nat. size.

Fig. 3. Beak of a right-billed male of the Parrot-Crossbill, *L. pityopsittacus*; nat. size.

Fig. 4. Beak of a nestling of *L. curvirostris*; nat. size.

Fig. 5 a 6. Dorsal view of the bills of an adult and a very young specimen of the Wry billed Plover, *Anarhynchus frontalis*; nat. size.

Fig. 7. Transverse diagramatic section through the trachea and pouch of an adult *Dromaeus*; reduced, from a specimen in the Cambridge Museum.

Fig. 8. Ventral view of the trachea and pouch of an immature male of *Dromaeus*; reduced; after Murie.

Fig. 9. Ventral view of the trachea of a very young chick of *Dromaeus*; nat. size.

Fig. 10. Sagittal section through head and laryngeal apparatus, with reference to the position of the trachea to the manubrium sterni, of an adult *Mycetes sp.* nat. size, from a specimen in the Cambridge Museum.

Fig. 11, 12, 13. The manubrium sterni of various species of adult *Mycetes*, after Parker, Mivart and Albrecht. The manubrial parts are toned grey.

Fig. 14. Outlines of an Ostrich, with the position, size and shape of the stomach drawn in.

Fig. 15. Shape and position of the stomach of a nearly adult Ostrich, when nearly empty. $^1/_6$ nat. size.

Fig. 16, 17. Shape and position of the stomach of an Ostrich chick, about 3 days old; viewed from the right and from the left side; nat. size.

Fig. 18. The embryo of an Ostrich, of 25 days, after removal of the liver, sternum and ventral wall of the body. All the parts are drawn strictly in situ and in nat. size.

Fig. 19. The stomach of an Ostrich, 2 years old, viewed from the right side; drawn to a scale of one half nat. size. The distance *ab* measured 14 cm, *cd* 40 cm, *ef* 18 cm.

Fig. 20. Right view of the stomach of a 4 months old specimen of *Rhea americana*.

Fig. 21. Right view of the stomach of an adult specimen of *Rhea americana*.

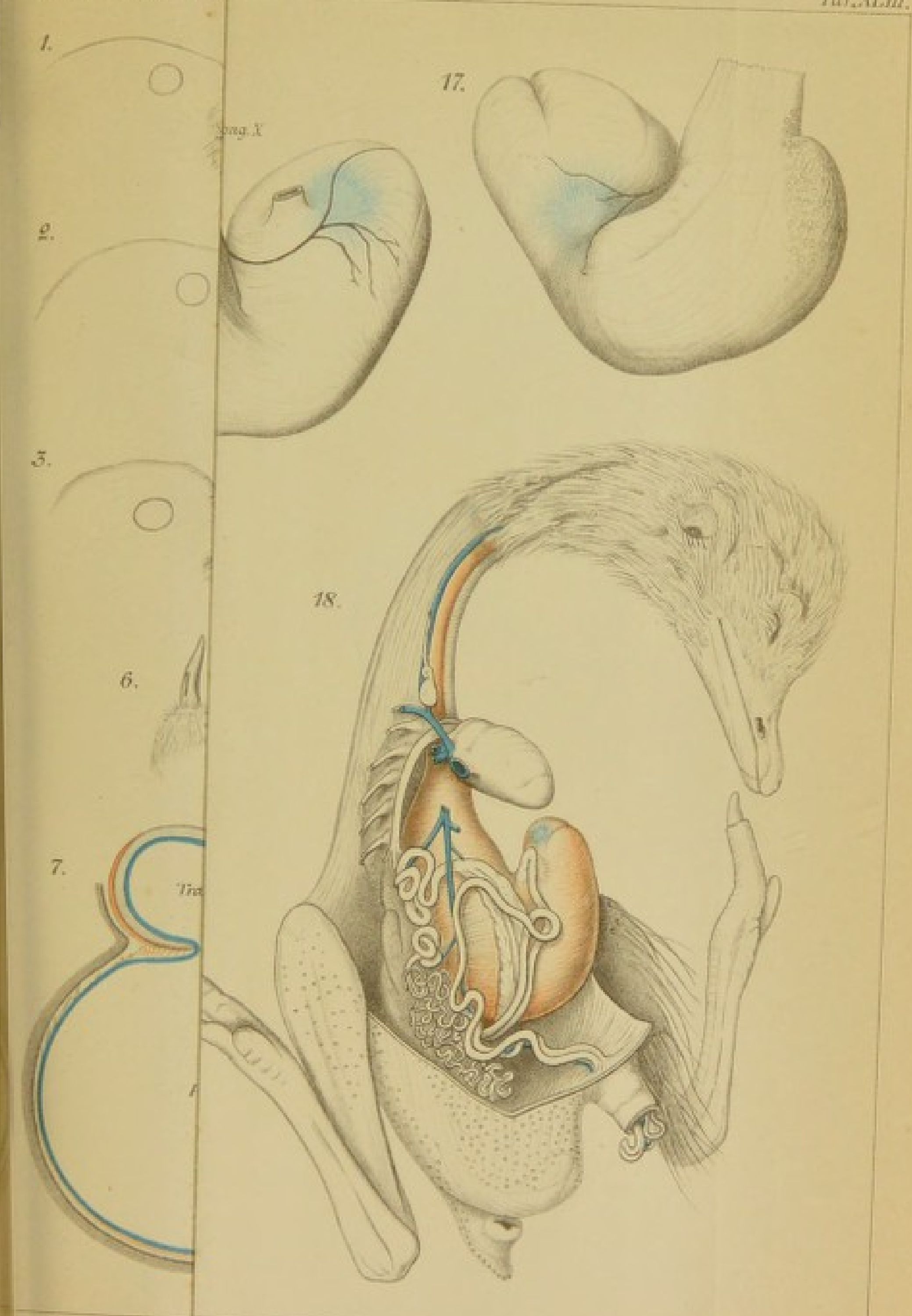
Fig. 22. Right view of stomach and proventriculus of ***Diomedea sp.*** Reduced.

Fig. 23. Ventral view of stomach and proventriculus of ***Diomedea sp.*** Reduced.

Fig. 24. Ventral view of stomach and proventriculus of ***Ossifraga gigantea***; nat. size.

Fig. 25. Shape and position of stomach and proventriculus of on Embryo of ***Procellaria leucorrhoa***; nat. size.

Fig. 26. The same of an adult specimen; nat. size.



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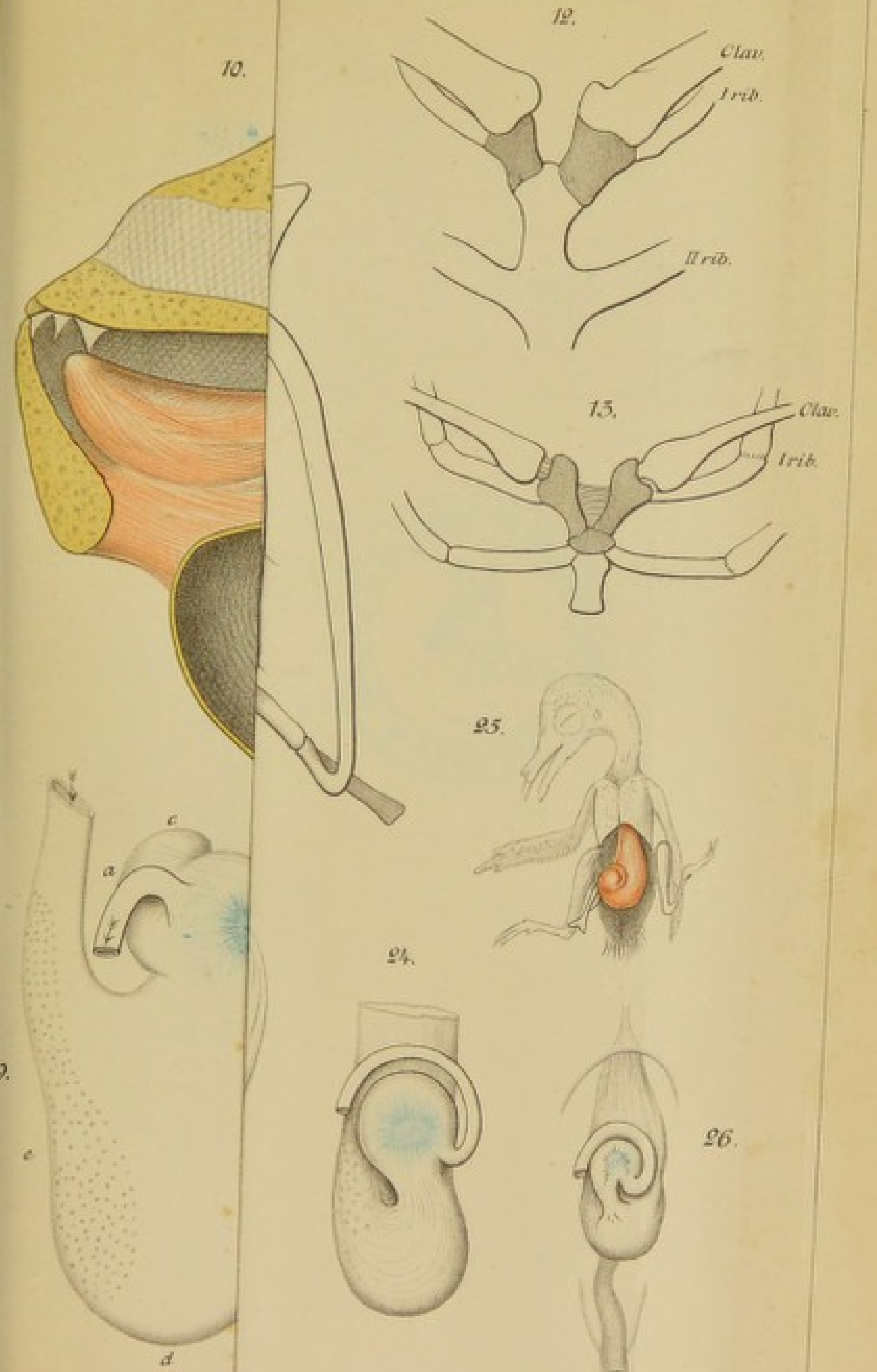

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