

2. On some Points in the Morphology of the Wings of Birds.
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by Professor FLOWER, P.Z.S.)

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(Plates XXIX.-XXXII.)

Since the publication of Sundevall's paper "On the Wings of Birds" in 1843 but little advance seems to have been made in our knowledge of the disposition and modification of the feathers of the bird's wing, although his original Swedish paper was twice translated into German. In fact the paper, though forty years old, contains much information not to be found in modern descriptions, a great deal of it having apparently been overlooked. I have had occasion to go into the subject somewhat fully in preparing specimens to illustrate the structure of the bird's wing in the Index Museum of the British Museum (Natural History). While doing this I found the ordinary descriptions unsatisfactory, and at times could not reconcile what I saw with them. This occasioned me to examine a great many birds' wings of different groups, and led to the results described in the following paper. The wings were all examined with a view to make out the mode of insertion of the feathers, their relations one to another and to the bones, and dried skins were used only when fresh specimens were unavailable. Through the kindness of Professor Flower I had great facilities afforded me in the way of obtaining specimens, and I take this opportunity of expressing my great thanks to him for his encouragement and assistance throughout the work.

While Sundevall's paper gives the correct relations of the parts, especially of the coverts, yet many points with regard to the remiges and greater coverts he seems to have overlooked, and of others his interpretation is erroneous. The relation of the remiges to the bones of the manus is not fully described nor accurately figured. That the primaries form two groups, metacarpals and digitals, is recognized, but the absolute constancy of the most proximal digital resting upon the phalanx of digit III. has never been insisted upon; Sundevall's figure shows it as having no connection with the phalanx. The presence of one or two more dorsal greater coverts than remiges on examination turns out to be erroneous, since every one may be accounted for. The presence of a small accessory remex (remicle) which I have made out renders the interpretation of the relations of the coverts to the remiges more intelligible. These and some other important points are discussed in the present paper. References to Sundevall's paper are to the English translation which appeared in 'The Ibis'¹ for October 1886, and are indicated thus (S. p. 396).

The nomenclature adopted is founded upon that most in use

¹ "On the Wings of Birds," by C. J. Sundevall. Translated from the original Swedish of the 'Kongl. Vetensk.-Akad. Handlingar,' 1843, by W. S. Dallas, F.L.S. (Ibis, 1886, p. 389.)

at present, and has this advantage that it is applicable to both sides of the wing, and reduces the terms used to a minimum. Professor Flower and Dr. Selater have done me the kindness of revising the nomenclature¹ for the remiges. The term "tertials" or "tertiaries" has been abandoned, "cubitals" always including them when present, because there is no way of absolutely distinguishing any definite number of remiges as belonging to this special category. There is certainly a distinction to be founded upon the arrangement of the little muscular slips and tendons attached to the cubital remiges; but it would not be of much use in practice, owing to the difficulties in the way of determining it with regard to many birds.

The main points of interest brought to light by the examination of a considerable number of birds, some of almost every large group, will be treated of, the wing of the Wild Duck, which is an extremely good type, being first described in detail. The preparations in the Natural-History Museum fully illustrate this paper, and most of the accompanying drawings are taken from these preparations or from essentially similar ones.

The Wild-Duck's Wing.

When the wing is extended for flight, the surfaces and borders correspond to those of the primitive vertebrate limb, the preaxial border being directed forwards, the postaxial backwards, and the dorsal and ventral surfaces upwards and downwards respectively. It is in this position the wing is best studied; and when plucked of feathers posteriorly it presents a fold of skin from the elbow to the tip in which the flight-feathers and their principal coverts are embedded; these and their position are first described.

When the wing is prepared as shown in the drawing (Plate XXIX.) two main groups of quill-feathers are seen:—the SECONDARIES or CUBITALS attached to the ulna, and the PRIMARIES or METACARPO-DIGITALS attached to the manus. Of the latter, six, the *Metacarpals* (1–6), are attached to the metacarpus, and five, the *Digitals* (7–11), attached one (*addigital*, 7) to phalanx 1 of digit III., two (*middigitals*, 8, 9) to phalanx 1 of digit II., and two (*predigitals*, 10, 11) to phalanx 2 of digit II. The distal predigital (11) is always small, and is designated the *remicle*; its relations, described in detail later, show that it is as much a primary as the so-called "spurious tenth" of many Passerines. The quill-feathers on the cubitus stand out more or less at a right angle to the bone; those on the manus form a gradually increasing obtuse angle, till the last feather lies parallel with the phalanx to which it is attached.

The remiges are best numbered from the wrist-joint, proximally for the cubitals and distally for the metacarpo-digitals; because with scarcely any exception reduction in number takes place at the distal end of the manus and the proximal end of the cubitus.

¹ A somewhat similar nomenclature was proposed by Dr. Alix, 'Journal de la Société philomatique,' 1874, p. 10. "Sur les plumes ou rémiges des ailes des oiseaux."

The remaining feathers of the wing are the coverts; they are best understood if described from the posterior margin of the wing.

On the dorsal side the row of feathers (Plate XXX. fig. *a*, *a*) lying next the remiges are the *tectrices majores*, being quite definitely related to the remigeal quills, and lying close pressed upon their bases. Each remex is serial with the covert proximal to it, the cubital coverts crossing over the bases of the remiges, the metacarpal coverts lying parallel and pressed upon two contiguous remiges (cf. Plate XXXI. figs. *b* and *c*). There is a well-developed covert to every metacarpal except the first, which possesses only a very small and vestigial one, 1', which is completely hidden by a median covert, 1'' (Plate XXXII. fig. 8), which in many birds functionally replaces it, the *t. major* disappearing.

On the ventral surface of the wing is a row of feathers (Plate XXX. fig. *b*, *a*), bearing the same relations to the remiges as those just described; these are the *tectrices majores* of the lower surface (cf. Plate XXX. fig. *b*, and Plate XXXI. fig. *b*). If fig. *b*, Plate XXXII., be examined, which shows the relations of the above feathers in section, starting at the tip of the wing the remicle, or predigital 2 (R'), is seen to have proximal to it a dorsal and ventral covert, forming a group of three. The next remex is similar, and so to the 1st metacarpal, whose dorsal covert is very small and rudimentary. These relations show that the remicle is a small metacarpo-digital which has probably not been differentiated into a flight-feather. The cubitals show the same arrangement except the fifth group, where there are a pair of coverts, but no remex; this condition is termed *aquincubital*, and is later described more fully.

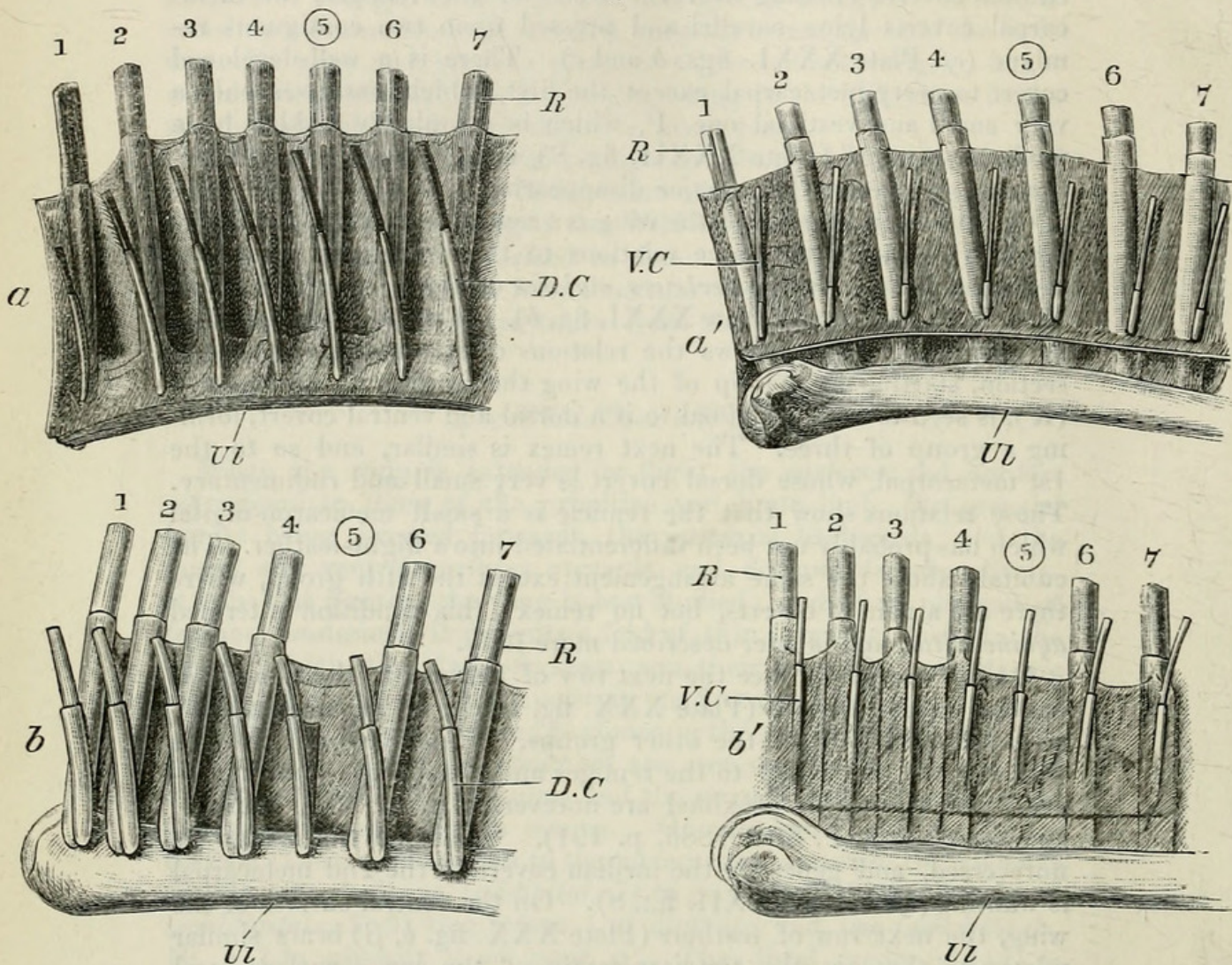
On the dorsal surface the next row of feathers to the *t. majores* are the median coverts (Plate XXX. fig. *a*, β), or *tectrices mediae*, arranged serially with the other groups. On the cubitus they lie with a reversed overlap to the remiges and *t. majores*; those, however, which lie most proximal are unreversed (S. p. 415, footnote, and Goodchild, P. Z. S. 1886, p. 191). Those on the manus lie unreversed, and generally the median covert of the 2nd metacarpal is wanting (cf. Plate XXXII. fig. 8). On the ventral surface of the wing, the next row of feathers (Plate XXX. fig. *b*, β) bears similar relations; they are the *tectrices mediae* of the lower surface, and always lie with reversed overlap to the remiges and *t. majores* (S. p. 491). The distal four or five are generally deficient on the manus in the Duck (Plate XXXI. fig. *b*). In many birds they are nearly all suppressed on the manus.

The *tectrices majores* and *mediae* on the ventral surface have at first sight an anomalous position. Being on the ventral side of the adult wing, one would expect the backs of the feathers to look ventralwards, whereas they look dorsalwards just as do the remiges. This is pointed out by Sundevall (S. p. 419), who, however, gives an erroneous explanation, saying they are aftershafts developed at the expense of the true feather-shaft; a more probable explanation is discussed later.

The feathers so far described are seated in the wing-membrane,

the next rows being in the skin covering the muscular portion of the wing and in the patagium. On the dorsal surface five rows of feathers (Plate XXX. fig. *a*, γ) follow the *t. mediæ*, lying with the same overlap, and on the manus being scantily represented; they

Fig. 1.



a, *a'*. Drawings of preparations of the distal cubital remiges, with their attached tectrices majores, of the Pheasant.

a, Dorsal view; *a'*, ventral view. (This shows the "quincubital" condition.)

b, *b'*. Drawings of preparations of the distal cubital remiges, with their attached tectrices majores, of the Golden Eagle. "Aquincubital."

b, Dorsal view; *b'*, ventral view; 1, 2, 3, &c. the remiges (*R*), numbered from the wrist-joint; *D.C.*, dorsal tectrix major; *V.C.*, ventral tectrix major; *Ul*, ulna.

are the *tectrices minores*. They extend on to the arm, and on the dorsal surface of the humerus a row of 6 feathers becomes elongated, forming an apparent continuation of the remiges of the forearm, the feathers of the next row taking the form of coverts; they

form the humerals (*pennæ humerales*), the "parapteron" of Nitzsch (Plate XXX. fig. *a, h*). On the ventral surface next the median coverts are three row of feathers (Plate XXX. fig. *b, γ*), the *tectrices minores* of the lower surface, which are but scantily represented on the manus.

A fairly well-marked space¹ running the whole length of the cubitus separates these from two to three rows of feathers which run from the wrist to the elbow; and then are continued on the arm, where they become largely developed, 6 to 8 feathers (Plate XXXI. fig. *b, ax*) forming the axillaries (hypopteron of Nitzsch). This row may be termed, when distinct as here, an axillary row, though really forming part of the minores; in some birds there is no space separating them, and then they are confluent. The t. minores of the upper and lower surface generally correspond, both producing special developments, the "humerals" and "axillars."

The next group of feathers (Plates XXX. & XXXI., μ) grow along the posterior border of the wing, extending from the proximal end of the patagium to the end of the manus. On the dorsal surface they soon approach the minores and become confluent with them, though distinguishable in fresh undisturbed plumages by difference of overlap. On the ventral surface the patagial space is large, and separates them well from the minores. The feathers growing from the edge of the patagium are sufficiently elongated to cover this deficiency. At the wrist they become confluent with the other series and are continued on the hand. This group of feathers is common to both surfaces of the wing, insomuch as they form on the anterior border a shelving series, giving a clean finishing edge to the anterior margin of the wing. They are best termed marginals (*tectrices marginales*). The feathers of the pollex, *plumæ pollicis* ("alula," "ala spuria"), are partly of this series and of the minores; and by specialization produce four small quill-feathers with coverts, which lie closely embracing the dorsal part of the anterior border of the manus, and hiding many of its lesser coverts.

The table at the end of this paper (p. 355) shows the relation of the nomenclature adopted above with that of Sundevall, and the ordinary nomenclature such as that found in Coues's Key to N. A. Birds. All birds' wings (except the Penguins) are directly referable to the type just described. It contains all the elements which occur in the wing, and it is by the specialization and suppression of these parts that the different wing-forms have been derived, at any rate among Carinates, the Ratite wing being more primitive in structure.

Some Modifications of the Wing.

The remiges of the manus show a remarkable constancy both in number and position, for (with the sole exception of the Penguins) the first *digital* always lies upon the phalanx of digit III., its end resting upon the metacarpo-phalangeal articulation; the *middigitals* are always constant in position, so are the *predigitals*. On the metacarpus are six feathers always except in Flamingoes, Grebes, and

¹ This is especially well seen in the Grebes.

Storks, where seven occur. The *predigitals* are the only other remiges of the manus which show modifications of any interest. In the typical condition (*cf.* Plate XXXI. fig. *a*) we have the large predigital 2 (α) and the small remicle (β), with their dorsal and ventral coverts all intimately attached to the phalanx. This arrangement is probably generally present in the Pygopodes, Gaviæ, Tubinares, many Limicolæ, *Pterocles*, Odontoglossæ, Herodiones, Anseres, Pelicans, Striges, and Accipitres. Among other birds it is probably not generally present, but it may be found in many of the lower forms of Passeres, and in some Picariæ, probably never in Gallinæ.

The remicle disappears in these forms, but its dorsal covert remains well developed, especially well seen in the Gallinæ, and its ventral covert may also remain, but often disappears. All trace of the group may disappear, as in the nine-primaried Passerines, where predigital 2 is reduced to a mere rudiment, but can generally be detected; its covert is always well marked. The so-called pencil-feather of the Woodcock is the dorsal covert of the remicle group.

The chief, most interesting, and most puzzling modification of the cubital feathers is that in a great many birds the fifth remex is always undeveloped, its coverts being normally developed and present. This occurs probably in all birds except *Phœnicopterus*, Gallinæ, Passeres, and a few Picariæ. Up to the present I have never met with a trace of this feather in a vestigial condition. If the figures of the preparation of the distal part of the cubitus of the Golden Eagle be compared with those of the Pheasant (see p. 346), the exact nature of this modification is at once apparent. In the Pheasant (*a, a'*) the fifth remex is present with its coverts, showing all normal relations; in the Golden Eagle (*b, b'*) the coverts are present but no remex. The former condition may be termed *quincubital*, the latter *aquincubital*. Such is the constancy of one or the other condition in each natural group, that I have as yet met with no exceptions anywhere, except among the so-called Picariæ, many of which are, and most of which probably will turn out to be, *quincubital*. The Goatsuckers are *aquincubital*, while the Swifts are *quincubital*. *Pterocles* is *aquincubital*; *Goura* is *aquincubital*. Of course exceptions may turn up, seeing that of the whole number of birds but a comparatively few have as yet been tested for this point.

In the Gallinæ the first cubital feather is shortened; this is possibly due to mechanical requirements in the folding of the wing, as the metacarpal remiges are inserted so near the actual joint as to leave but little room. Nitzsch states that sometimes the last feather on the manus undergoes shortening. I have not met with this condition.

In the description of the Duck's wing it was pointed out that the upper major covert to the first metacarpal remex is very small and rudimentary. When the feathers are all plucked off except the remiges, major and median coverts, the appearance at the wrist-joint is that represented in the figs. 6-9 (Plate XXXII.), where the remiges are red, the major coverts yellow, and the median blue. The diagram above each of the figures shows the real homologies of these

feathers, in their undisturbed primitive conditions. Sundevall mentions that there are generally one or two extra major coverts connected with the cubital series, of which the feather *l* in his figures (the median covert here under consideration) is one. The other he does not mention (S. p. 414, par. 2). Really there are no extra coverts at all, unless the fifth cubital coverts in the aquincubital condition of the wing are so considered. In the Duck (Plate XXXII. fig. 8) it is seen that the larger feather (1''), which at first sight appears to represent the major covert, is really the median covert in front of the remex in the undisturbed quincunx series; the little feather (1') underneath being the real major covert. In this wing the two feathers have not become so closely attached to the first metacarpal as is the case in some other birds, example the Golden Eagle, Barn-Owl, &c. (Plate XXXII. fig. 6). Here the relations are more apparent; the major covert is small and rudimentary, but bears the same relation the other major coverts do. The median covert is a fairly large feather, which crosses the metacarpals at a considerable angle. In the Duck the median covert of metacarpal 2 is suppressed, in the Eagle it is present (2'', fig. 6). The Grebe, with seven metacarpals, shows similar modifications at the wrist-joint (Plate XXXII. fig. 7). In many birds (*e.g.* Passerines) the major covert altogether disappears, the median covert is large, and takes its place, lying across the metacarpals at a considerable angle, and causing the suppression of the next one or two mediæ (Plate XXXII. fig. 9).

The remaining feather-tracts undergo modifications in different groups, which are generally of more or less minor importance. The axillars and humerals vary in their development in different groups, in the Passerines disappearing almost absolutely, in all probability in connection with the relative shortness of the humerus. The marginals in many birds of this group are much elongated on the ventral side and cover the patagium.

When the wing is folded these feathers (often with the last two or three major cubital coverts) present much the appearance of the axillars in some birds. They have often been erroneously so described, whereas they have nothing whatever to do with them, the true axillars being represented by but a few semiplumes at most.

The modifications of the overlap of the dorsal cubital median and minor coverts have recently been very fully worked out by Goodchild (P. Z. S. 1886, pp. 184-203). These feathers are termed by Goodchild the "median cubital coverts;" but it is much better to confine the term "median coverts" to the row following the majores, and call the others "minor coverts." Goodchild's terms "supplementary row of median coverts" or "upper wing-coverts" and "posterior row of median coverts" are unnatural, because part of his supplementary row in the majority of cases belongs to the t. mediæ, and the greater and proximal part of his posterior row to the same, whereas the distal part belongs to the first row of minores (*cf.* his fig. 1, p. 186, P. Z. S. *loc. cit.*). His supplementary row generally means the distal t. mediæ proper, and sometimes includes some of the feathers of the next two or three rows on the wrist,

which appear, as a consequence of folding superficially, to form a series with them; it is simply accommodation, and is only very striking when the wing is examined in the folded condition, as most of his were. Grouping the feathers according to their insertion, and remembering the conditions of folding which must occur at the wrist, the observations of Goodchild give the most complete view of this subject we have. The Passerine birds possess only the single row, *t. mediæ*, the minores being completely absent (S. p. 415, *cf.*); this is characteristic of them, and goes along with a very scantily feathered ventral surface.

The median and minor coverts of the lower surface¹ show a great variety of modification, which if systematically worked out would I believe furnish valuable characters. But practically ornithologists take no account of the lower surface of the wing, and but little can be made out from ordinary skins. For skins to be of much value for studying wing-characters, some of them ought to be prepared with one wing in the extended position. Fresh wings are much the most valuable, but they are not always available. According to Sundevall the median coverts often show a tendency to disappear, which I have noticed, often they are very small. In the Passeres the row of *t. majores* disappears; this is recognizable by difference of overlap.

The Duckling's Wing.

If the wing of a Duckling be examined when it is a mere downy appendage, of no use for flight, it will be found to be an exact foreshadowing of the flying wing. The fifth cubital remex is absent, not even a vestige of it can be found; so we may conclude that this modification is a very ancient and deep-seated one. The plumules (down) clothing the wing are more feather-like than the adult down. In fact a Duckling's wing forms an interesting comparison with an Ostrich's or Rhea's, these wings probably never having got beyond a stage parallel to this. The way the plumules of the Duckling are shed is very interesting; at the base of the plumule the new pennaceous feather forms, grows, and begins to force its way out from the skin. The plumule remaining attached by its base to the tip of the new feather is carried out away from the skin about $\frac{1}{2}$ to $\frac{3}{4}$ inch, then the connection becomes very slight, and soon the plumule is lost. This forms an analogous parallel to the shedding of milk-teeth, the plumule being retained till the new feather can functionally take its place.

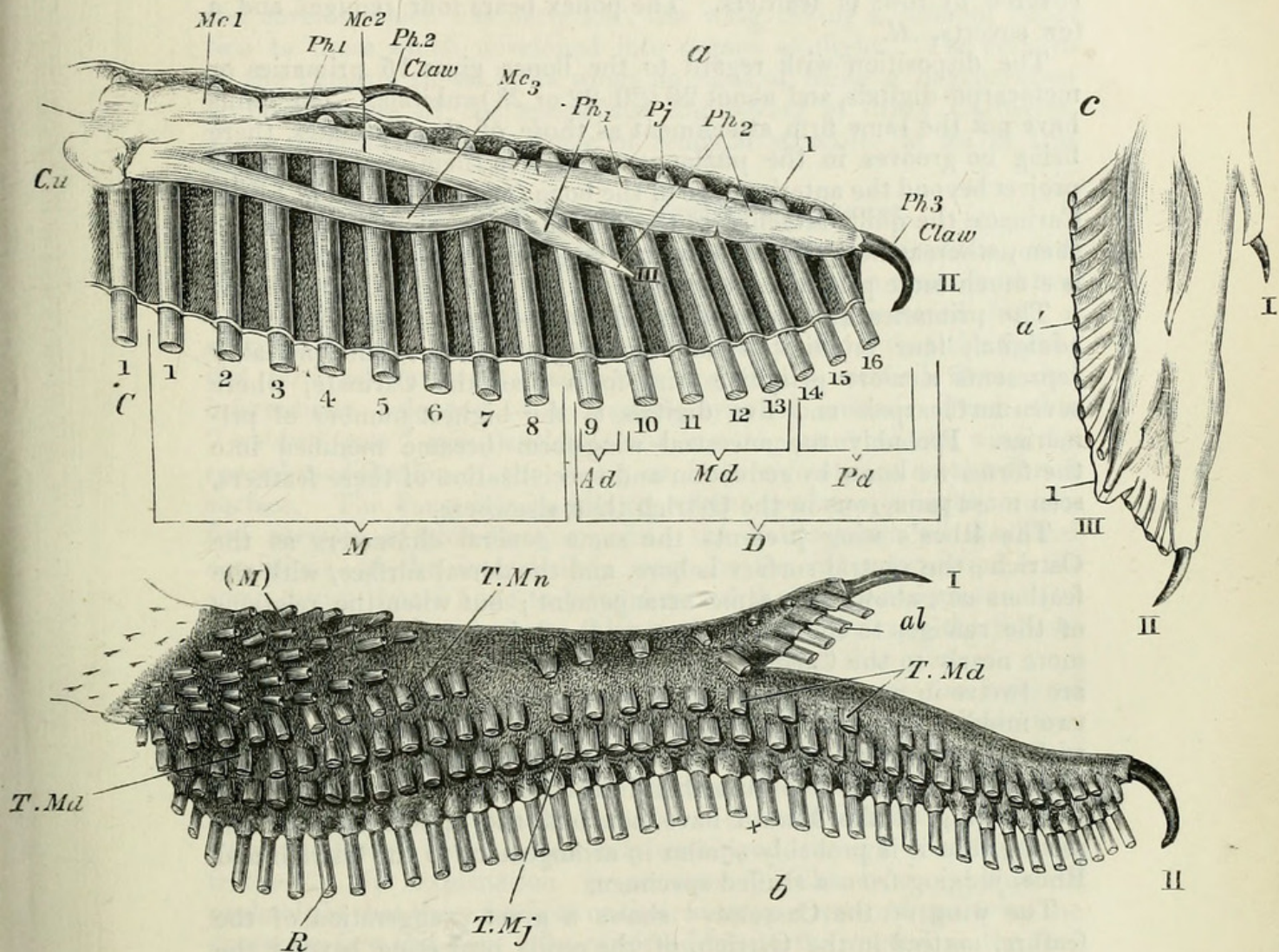
The Wings of the Ratitæ.

The wings of the Ratitæ conform to the same general plan as those of the Carinatae, presenting a modification of a more generalized type, which correlates with their bony structure.

In the unplucked Ostrich wing, little beyond a confused mass of feathers can be made out. The ventral surface is totally devoid of

¹ There are some very good figures of the lower surface of the wing of certain Hawks in the 'Zoologist,' 1880, p. 273, pls. 2 and 3.

Fig. 2.



a. Preparation of the manus of the Ostrich, showing the primaries and the manner of their attachment to the bones.

b. Dorsal view of the antibrachium and manus of the wing of the Ostrich.

c. Ventral view of the manus of an embryo Ostrich.

M, metacarpals; *D*, digitals; *Ad*, addigitals; *Md*, middigitals; *Pd*, predigitals; *Cu*, cuneiforme; *Mc* 1, 2, 3, metacarpals 1, 2, 3; *Ph* 1, 2, 3, phalanges 1, 2, 3; *I*, *II*, *III*, digits *I*, *II*, *III*; *T.Mj*, tectrices majores; *T.Md*, tectrices mediae; *T.Mn*, tectrices minores; *M*, marginals; *Al*, pennæ pollicis (alula); *1*, beneath this fold are the two ventral t. majores mentioned in the text; *a'*, tectrices majores inferior.

feathers except for one row, the t. majores of the lower surface. If the feathers be cut short, so that only the base of the quill is left in the skin, their arrangement can then be satisfactorily studied (cf. fig. 2). On looking at the figure (2, a), the remiges, *R*, are seen in their natural position, next a row of t. majores, *T.Mj*, then the

t. mediæ, *T.Md*, but scantily represented on the manus. There is part of a row, *T.Mn*, representing the minores, and a few rows of marginals, *M*. The dorsal surface of the humerus is uniformly covered by rows of feathers. The pollex bears four remiges and a few coverts, *Al*.

The disposition with regard to the bones gives 16 primaries or metacarpo-digitals, and about 20 (20-22 or 23) cubitals. The quills have not the same firm attachment as those of the Carinates, there being no grooves in the phalanges to receive them, and their bases project beyond the anterior edge of the bone (*cf.* fig. 2, p. 351). In the Carinatae the quills attached to the phalanges lie almost parallel to them, whereas here the angle is little larger than a right angle. This is a much more primitive condition.

The primaries are disposed as follows:—Eight metacarpals, one addigital, four middigitals, and three predigitals. This probably represents a more primitive wing-form than the Carinate, where seven metacarpals and five digitals is the highest number of primaries. Probably the ancestral wing-form became modified into the forms we know by reduction and specialization of these feathers, seen more numerous in the Ostrich than elsewhere.

The Rhea's wing presents the same general characters as the Ostrich; the ventral surface is bare, and the dorsal surface, with the feathers cut, shows the same arrangement; but when the relations of the remiges to the bones are considered, it is seen to approach more nearly to the Carinate type in some respects. The primaries are twelve in number, there being seven metacarpals, one addigital, two middigitals, and two predigitals. This reduction is correlated with shortening and reduction of the manus. The angle of insertion of the digitals is more obtuse than in the Ostrich.

The wing of the Emu I have not had the opportunity of dissecting, but it is probably similar in arrangement to the Ostrich and Rhea, judging from a stuffed specimen.

The wing of the Cassowary¹ shows a great exaggeration of the feature, noticed in the Ostrich, of the quills projecting beyond the bones, its quill-spines being the sole remains of the cubital remiges.

The Apteryx shows, as was first pointed out by Prof. Flower (*Roy. Instit. Lect.* 1886), a few true cubital remiges, indicated by their long quills.

The Penguin's Wing.

This departs the most of all wings from the general plan. The paddle form of the wing and its scale-like feathers are familiar, and there is little or no differentiation apparent beyond the passage from mere scales anteriorly to feathers posteriorly. On the ventral side

¹ In the wing of a Cassowary dissected since writing the above there are to be seen structures representing, in all probability, the "primaries," which appear at first sight to be entirely wanting in these forms. I hope to describe this specimen, together with some other interesting Ratite wings, in a future paper.

this is all. On the dorsal the first four rows of feathers show a certain amount of differentiation, being somewhat elongated, and showing what might be looked upon as a tendency to form remiges and coverts, which was early lost, the wing taking a different function to those which developed into organs of flight. The embryo of the Penguin shows in its wings no signs of being a degeneration or modification of the specialized flight-wing of other Carinates. There appears to be no trace of remigial structure at all in this wing.

Origin of Wing and General Conclusions.

The study of the wings of living birds leads to the conclusion that the power of flight was gradually acquired, and also tends to throw some light upon the way wings were originally evolved from a reptilian manus. Recent researches¹ seem to show that the ancestral form of the avian manus was probably a webbed form, and inferentially belonged to an aquatic type of animal. From this "webbed paw" was developed the starting-point of the wing, by special modification of the scales or feather foretypes on the dorsal surface. The Penguin's paddle represents, perhaps, a highly modified survival of this starting-point; the Ratite wings are modified conditions of the intermediate stage in the wing-formation. At some future time I hope to bring forward the evidence in favour (or otherwise) of this view more fully worked out; however, the following are some of the points which tend to support that view.

In the adult flight-wing of the Carinates there are two rows of feathers situate on the ventral side of the wing, reversed in position, the *t. majores* and *mediæ*. Sundevall explains this by saying it is an aftershaft developed at the expense of the feather-shaft, and states (S. p. 419) that the aftershaft is entirely deficient; but in a Pheasant I have found it normally developed, though small in these feathers. His explanation is erroneous. The true explanation probably is that these feathers or their antetypes were originally on the dorsal surface and have been carried down to the ventral in the formation of the "*ala membrana*" by the excessive development of the remiges and *tectrices majores*. That is, that originally on the dorsal surface of the arm and manus there took place a special modification of the scales or feather foretypes by which rows of these were directed backwards in the "primitive embryonic" position of the limb. Next two or three rows began to be specialized and to become larger and more prominent than the others; then these, by their unequal growth, carried over a fold of skin and formed the wing-membrane, carrying some of the structures to the ventral side, which are now seen as the reversed feathers (*cf.* diagrams, Plate XXXII. figs. 1-5). In the embryo bird the feather-rudiments first appear on the dorsal surface, pointing to the fact that the modification here is very ancient and deep-seated; the remiges and greater coverts (superior) being the earliest to appear; quickly they begin to assume

¹ Prof. W. K. Parker's recent paper "On the Morphology of Birds," read at the Royal Society, Jan. 27, 1887.

larger proportions, and at the very earliest stages the remiges are distinguishable. At this stage the wing is quite rounded in section, there being no trace of the "ala membrana;" the next feathers to appear are the t. majores (inferior), closely followed by the other ventral coverts, the other dorsal coverts meanwhile having appeared. At this stage (*cf.* Plate XXXII. fig. 1) the inferior major and median coverts are distinctly more on the dorsal half of the rounded edge of the wing than its ventral, but very quickly they become quite ventral, owing to the rapid growth of the remiges. This stage is quickly passed over, but sufficient is visible to show that these feathers are carried distinctly to the lower surface by inequality of growth (*cf.* Plate XXXII. figs. 2-4). The feathers resulting from these are the plumules seen in the wing of the Duckling, and of no use for flight. The wing of a Duckling reproduces in a great measure, allowing for specialized differences, the adult Ostrich's wing or the Rhea's; and these wings are survivals of the transition state of the wing, probably never having been used for flight, but having undergone special modifications of their own from that point. It is pretty clear the remiges of the Ostrich and Duck's wing correspond, more so the Ostrich and Duckling's; in the Ostrich we have but one row of ventral coverts, and in the embryo we get them most distinctly on the dorsal side. The Ostrich embryo figured (fig. 2 c, p. 351) shows the manus from the ventral surface; digits I., II., and III. being well developed; digit III. at its tip projecting beyond the general fold of the wing; in fact there is a very complete webbed manus. The feathers seen (*a'*, fig. 2 c, p. 351) are the row of ventral coverts, and lying over digit III. on its dorsal surface are two of this row hidden from sight by it. In the adult, one of these feathers grows over the distal part of phalanx 1 of digit III., owing to elongation of its quills; here we have the dorsal position actually preserved in the adult. The wing of the Ostrich presents also a primitive condition especially in the cubital region, in that the "ala membrana" is not specialized as in the Carinatae, being in the intermediate condition of the Carinate embryo. Probably the feathers now representing the remiges and the principal coverts were more numerous in the primitive wing type, and have become restricted in number on the manus; thus the Ostrich has 16, the Grebes 12, while most birds have only 11 primaries.

Wing-Formula.

The main facts with regard to the feathers of a bird's wing may be expressed as a formula. Denoting the metacarpo-digitals by *Md*, the metacarpals by *m*, the digitals by *d*, and expressing the number of feathers in each group by a number placed after (thus, six metacarpals, *m* 6), the cubitals by *C*, "quincubital," "aquincubital" by *C*⁵, we formulate the remiges

$$Md\ 11\ m\ 6\ d\ 5\ C^5x^*.$$

The coverts are indicated by α , β , γ , for the t. majores, mediæ, and minores respectively; by placing a figure below the line, thus α_2 ,

* x = number of cubitals, which varies considerably in different groups.

TABLE OF NOMENCLATURE.

	THIS PAPER.	SUNDEVALL.	GENERAL.
Dorsal Coverts. Tectrices superiores.	Tectrices marginales.	Tectrices minimæ s. antecubitales.	Tectrices minores. (Parapteron (from Nitzsch) and humerals.)
	Tectrices minores. (Pennæ humerales.)	Tectrices minores cubiti vel manus. (Pennæ humerales.)	Tectrices medię. { Median primary coverts, { Median secondary coverts.
	Tectrices mediæ.	Tectrices secundæ seriei.	Tectrices majores. { Upper primary coverts. { Greater upper secondary coverts.
	Tectrices majores.	Tectrices majores.	Primaries.
	Primaries, or Metacarpodigitales.	Remiges primores.	Secondaries—Tertiaries.
	Secondaries, or Cubitales.	Remiges cubitales.	
	Tectrices majores.	Tectrices aversæ s. inferiores primæ.	Tectrices inferiores. (Under wing-coverts.)
	Tectrices mediæ.	Tectrices infrabrachiales s. plumæ infracubitales. (Plumæ infrahumerales.) (Axillars.)
	Tectrices minores. (Axillaries.)	Tectrices antecubitales inferiores or inframarginales.	
	Tectrices marginales.	Plumæ pollicis.	Alula or Ala spuria.
Ventral Coverts. Tectrices inferiores.	Alula or Plumæ pollicis.		

it indicates the number of rows, and placing these symbols above or below a line, thus $\frac{\alpha_1 \beta_1}{\alpha_1 \beta_1}$, their dorsal or ventral position; the marginals are expressed by μ , the humerals by h , the axillars by x , a number after the h or x denoting the number of specialized feathers forming the "parapteron" and "hypopteron." When any two rows are confluent it may be indicated thus, $\gamma \tilde{x}$, where the axillars and minores are indistinguishable as separate groups; Al expresses the quill-feathers of the pollex.

Formula for the Duck:—

$$Md 11 \ m 6 \ d 5 \ \frac{\alpha_1 \beta_1 \gamma \mu}{\alpha_1 \beta_1 \gamma \mu} \ C 19 \ \frac{\alpha_1 \beta_1 \gamma_5 h 6 \mu}{\alpha_1 \beta_1 \gamma_3 x 7 (2-3) \mu} \ Al 4.$$

Typical Passerine formula:—

$$Md 10 \ m 6 \ d 4 \ \frac{\alpha_1 \beta_1 \gamma \mu}{\alpha_1 \beta_0 \gamma \mu} \ C 9 \ \frac{\alpha_1 \beta_1 \gamma_0 \mu}{\alpha_0 \beta_1 \gamma_2 \mu} \ Al 3.$$

Formula for Ostrich wing:—

$$Md 16 \ m 8 \ d 8 \ \frac{\alpha_1 \beta_1}{\alpha_1} \ C 20 \ \frac{\alpha_1 \beta_1 \gamma_1 \mu}{\alpha_1} \ Al 4.$$

These formulæ might prove of value to ornithologists by enabling them to briefly express the main characters of the wings of different groups of birds. The three given above at once express very great differences in the wings of these birds: thus it is seen at once how, in the Passerine, the upper minores, the axillars, and humerals are absent; and the whole of the lower coverts, except one row, in the Ostrich. These are here introduced to show the possibility of using a wing-formula expressing most of the characters.

DESCRIPTION OF THE PLATES.

PLATE XXIX.

Drawing of a preparation of the right wing of the Wild Duck, seen from below, showing the relation of the quill-feathers to the bones.

al. Plumæ pollicis (alula). *C.* Cubitals or secondary remiges. *Md.* Metacarpo-digitals or primary remiges. *M.* Metacarpals. *D.* Digitals. *Ad.* Addigital. *Md* 1 & 2. Middigitals 1 and 2. *Pd* 1. Predigital 1. *Pd* 2 or *R.* Predigital 2 or remicle. *H.* Humerus. *R.* Radius. *Ul.* Ulna. *Sc.* Scaphoid. *Cu.* Cuneiform. *Mc* 1, 2, 3. Metacarpals 1, 2, 3. *Ph* 1, 2, 3. Phalanges 1, 2, 3. *I., II., III.* Digits 1, 2, and 3.

PLATE XXX.

a. Plan of the arrangement of the feathers on the dorsal surface of the extended left wing of *Anas boschas*.

b. Plan of the arrangement of the feathers on the ventral surface of the extended right wing of *Anas boschas*.

C. Cubitals (grey). *Md.* Metacarpo-digitals (grey). *a.* Tectrices majores (pink). *β.* Tectrices mediæ (green). *γ.* Tectrices minores (brown). *μ.* Tectrices marginales (yellow). *Al.* Plumæ pollicis (red). *h.* Humerals. *x.* Axillars. *x'.* Axillary row of minores.

PLATE XXXI.

a. The distal phalanx of digit II. of the wing of the Barn-Owl, with the attached predigital and their coverts, showing the remicle and its relations.

1. Ventral view. 2. Dorsal view.
- a.* Predigital 1. *β.* Predigital 2 (remicle).
- a'*. Dorsal tectrix major to *a.*
- a''*. Ventral tectrix major to *a.*
- β'*. Dorsal tectrix major to remicle.
- β''*. Ventral tectrix major to remicle.
1. Phalanx 2 of digit II.
2. Fused phalanx 3 of digit II.

b and *c.* Diagrams of the ventral and dorsal surfaces of the wing of the Wild Duck, showing the points of insertion of the feathers of the different groups.

C. Cubitals. *M.* Metacarpo-digitals. *R.* Remicle. *r.* Remex.

- a.* Tectrices majores.
- β.* Tectrices mediæ.
- γ.* Tectrices minores.
- μ.* Tectrices marginales.
- x.* Axillars.
- h.* Humerals.
- Ax.* Axillary row.
- (5). Absent fifth cubital remex.
- Al.* Alula.

PLATE XXXII.

Figs. 1-5. Diagrams showing how the ventral tectrices majores and mediæ have been carried over from the dorsal side, and the "ala membrana" formed.

1. The earliest condition of the feather-rudiments.
- 2-4. Intermediate conditions.
5. The condition in the adult wing.

Remiges—red.
 Tectrices majores (superior)—yellow.
 Tectrices majores (inferior)—green.
 Tectrices mediæ (superior)—dark blue.
 Tectrices mediæ (inferior)—light blue.

These diagrams represent sections across the wing in the direction *x-y* (fig. 8).

Figs. 6-9. The remiges and upper principal coverts in the region of the wrist-joint in Barn-Owl (6), Grebe (7), Duck (8), and Lark (9).

- 1, 2, 3, 4. Metacarpal remiges (red).
- 1', 2', 3', 4'. The corresponding major covert (yellow).
- 1'', 2'', 3'', 4''. The corresponding median covert (blue).
- * Wrist-joint.

The plan of these feathers in section is shown above each, and represents the primitive unmodified relations.

a. Drawing of section through the large feathers of the wing just below the edge of the "ala membrana" of the Pheasant.

β. The same of the Duck. The proximal cubitals are not shown.

- R.* Remex (red).
- DC.* Dorsal covert, tectrix major (yellow).
- VC.* Ventral covert, tectrix major (green).
- R'*. Remicle.
- * The wrist-joint.
- Q.* Fifth cubital remex present.
- Aq.* Fifth cubital remex absent.



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