THE CONDOR

VOLUME 65 NOVEMBER-DECEMBER, 1963 NUMBER 6

VARIATIONS IN THE NUMBER OF PRIMARIES

By ERWIN STRESEMANN

Modern birds have at least nine and, at the most, eleven functional primaries, a fact long ago disclosed by that great pioneer in the study of pterylosis, Christian Ludwig Nitzsch (1840). He found eleven primaries to be the normal number in grebes (*Podiceps*), the storks (*Ciconia, Ibis, Mycteria, Anastomus*), and flamingos (*Phoenicopterus*), while all other birds were said by him to have no more than ten primaries. The wing of passerines according to Nitzsch normally has 10 primaries, the most distal of which is always considerably shortened, and in certain species even completely aborted. How the primaries were attached to the bones of the wing was soon afterward described in great detail by Prechtl (1846).

When comparative morphology became exposed to the influence of the theory of descent, some ornithologists began to focus their interest on the evolution of the bird's wing. Jeffries (1881) was the first scientist who tried to reconstruct its original state. In birds of several orders endowed, according to Nitzsch, with ten primaries, he discovered a small feather in front of the outermost functional primary, fixed at the distal end of the second phalanx of the second, or index, digit. This little feather he interpreted as an aborted first primary, thereby relating it to the condition in the wing of songbirds (Oscines) where the gradual reduction of the distal (tenth) primary can still be traced. He therefore ascribed (p. 163) eleven primaries to the families "Alcedinidae, Falconidae, Plotidae, Ciconiidae, Phoenicopteridae, Anatidae, Charadriidae, Scolopacidae, Par-[r]idae [Jacanidae], Colymbidae, Alcidae, and probably most of the other lower birds."

Soon afterward, the same little feather was detected in England by Wray (1887: 344), who had been unaware of Jeffries' article. He, too, interpreted it as representing an originally functional primary and named it "remicle." He argued that: "its relations . . . show that it is as much a primary as the so-called 'spurious tenth' of many Passerines."

Gadow (1888), an ardent evolutionist, jumped to this view at once. He studied the attachment of the primaries in all families of birds, with the following result: 7 primaries are attached at the metacarpus in *Podiceps, Phoenicopterus,* and in the Ciconiidae, while there are only 6 metacarpal primaries in all other birds (with the exception of *Struthio, Rhea* and *Apteryx*). By including the remicle of the non-Passerines in the number of primaries, he formulated his theory (pp. 656–657) as follows:

"The most important result is evidence of the gradual reduction in the number of functional quills. . . . the reduction from 12 [Podicipidae, many Pelargi and *Rhea*] to 11 is due to the reduction from 7 to 6 of the metacarpal quills . . . . In all cases the reduction from 11 to 10 primaries is brought about by the reduction at the terminal end of the wing." This point of view has been emphatically supported by Degen (1894).

In Heilmann's well-known book on the "Origin of Birds" (1926) there is a figure (22,III) demonstrating the author's, or rather Gadow's, view on the attachment of the primaries in *Archaeopteryx*. It shows a wing with 12 primaries, of which numbers 1 to 7 are fixed at the metacarpus, number 8 at the basic phalanx of the third digit, numbers

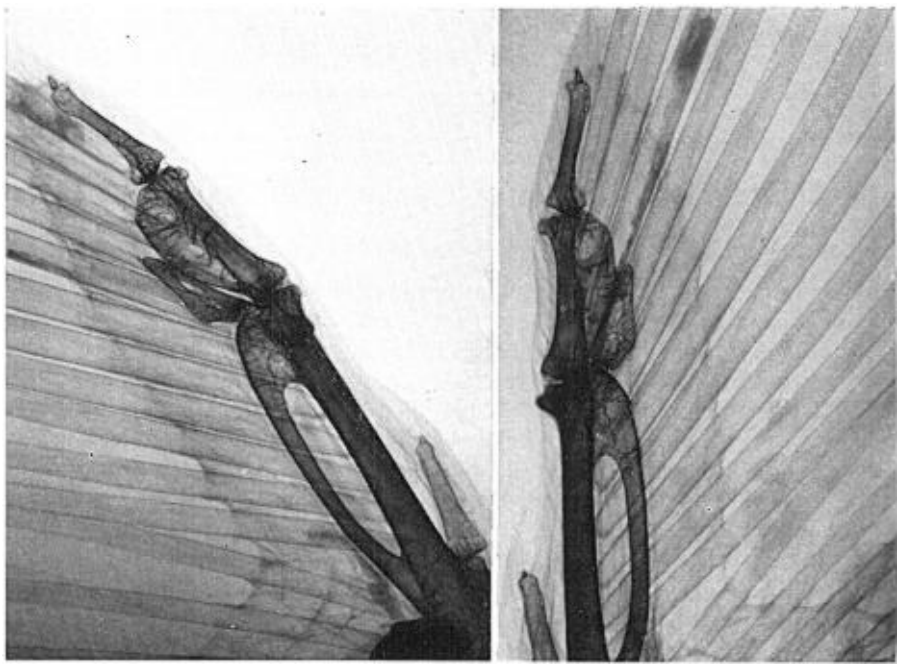

Fig. 1. *Anhima cornuta,* AMNH no. 469872, ventral view showing (left) 11 primaries on right wing and (right) 10 primaries on left wing. Third phalanx of second digit clearly visible.

9 and 10 at the first phalanx of the second digit, and numbers 11 and 12 at the second phalanx of the second digit. The twelfth primary (the remicle) is drawn in the shape of a strong functional flight feather, exactly as postulated by the theory of Jeffries and Gadow. Heilmann's figures 20 to 22, intended to give an idea of the wings of *Archaeopteryx,* are beautifully drawn. However, when filling out the many important details which do not appear in the slabs of the Berlin specimen, the author has been guided by his own preconceived notions, and one has therefore to be cautious when consulting these special drawings.

The hypothesis of Jeffries and Gadow has quite recently been further developed by Stegmann (1962). Being, like his predecessors, convinced that the original number of primaries has been reduced in the course of phylogeny, and that such reduction could only take place at the terminal end of the wing and not within the succession of primaries, Stegmann evolves an hypothesis which supplements that of Gadow. His views seem to have been influenced by those of Degen (1894), who reproduced them in his imaginary figure B on plate I.

According to Stegmann, the decrease from 11 functional primaries (still existent in *Podiceps, Ciconia, Phoenicopterus*) to 10 must have begun with the loss of the 11th. By losing the distal one of its three primaries the second digit was for some time left with two primaries only. Its previous number of three became re-established by a process of primary migration, the most distal of the metacarpal quills (no. 7) migrating across the joint to the third digit, thereby forcing the former addigital primary to migrate to the first phalanx of the second digit, thus becoming a mid-digital primary (in the terminology of Wray, 1887), and so forth. The result of this outward move-

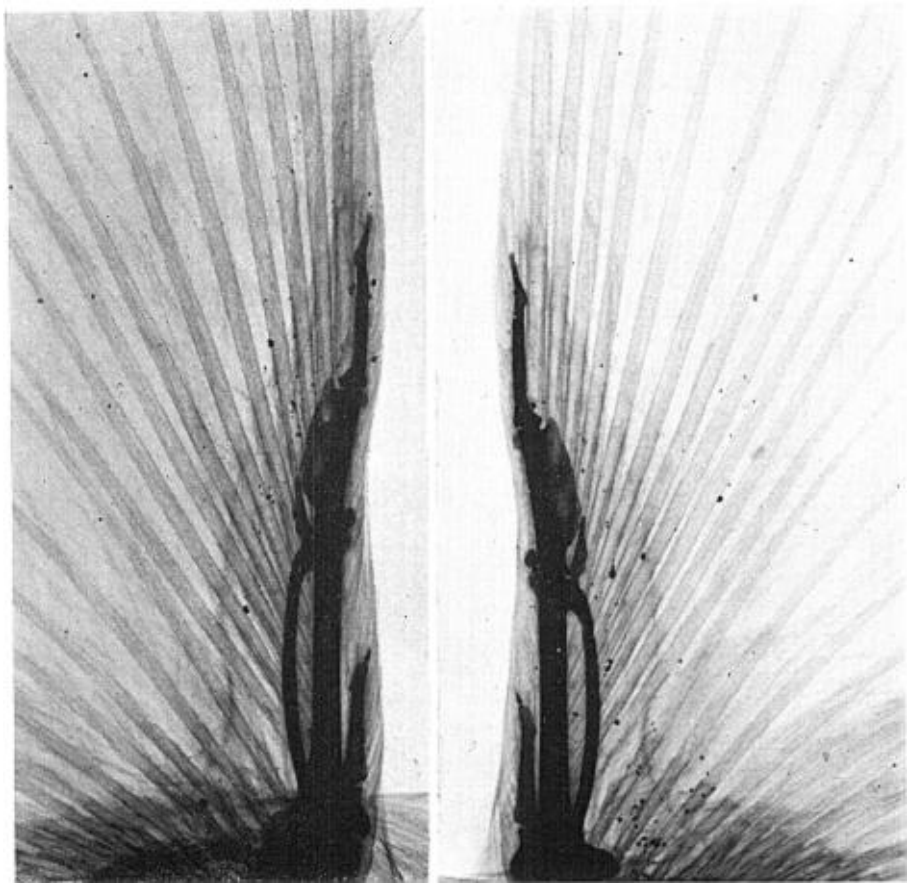

Fig. 2. *Ptychoramphus aleuticus,* AMNH no. 39547, dorsal view showing (left) 10 primaries on left wing and (right) 11 primaries on right wing. Third phalanx of second digit well developed.

ment was as follows: 6 (no longer 7) metacarpals and 4 digitals (3 on the second digit), a condition now found in all birds except the "primitive" eleven-primaried ones, and the nine-primaried groups.

THE ELEVENTH FUNCTIONAL PRIMARY

So far no author seems to have questioned the validity of the tenet that the number of primaries could only have decreased, but not increased, in the course of evolution. This appears all the more surprising since some published facts point in the opposite direction.

Bates (1918:542) collected a specimen of *Glaucidium sjöstedti* with "twelve remiges, eleven large ones and the remicle .... The abnormal number of manual remiges and corresponding coverts in the specimen of *Glaucidium* is one of several like instances found among birds of different orders."

W. DeW. Miller (1924:316) recorded the following cases of this abnormality: "*Necrosyrtes pileatus* [*monachus*], ten functional primaries in one wing, eleven in the other (the remicle also present in each wing). *Ixobrychus exilis,* ten large primaries in

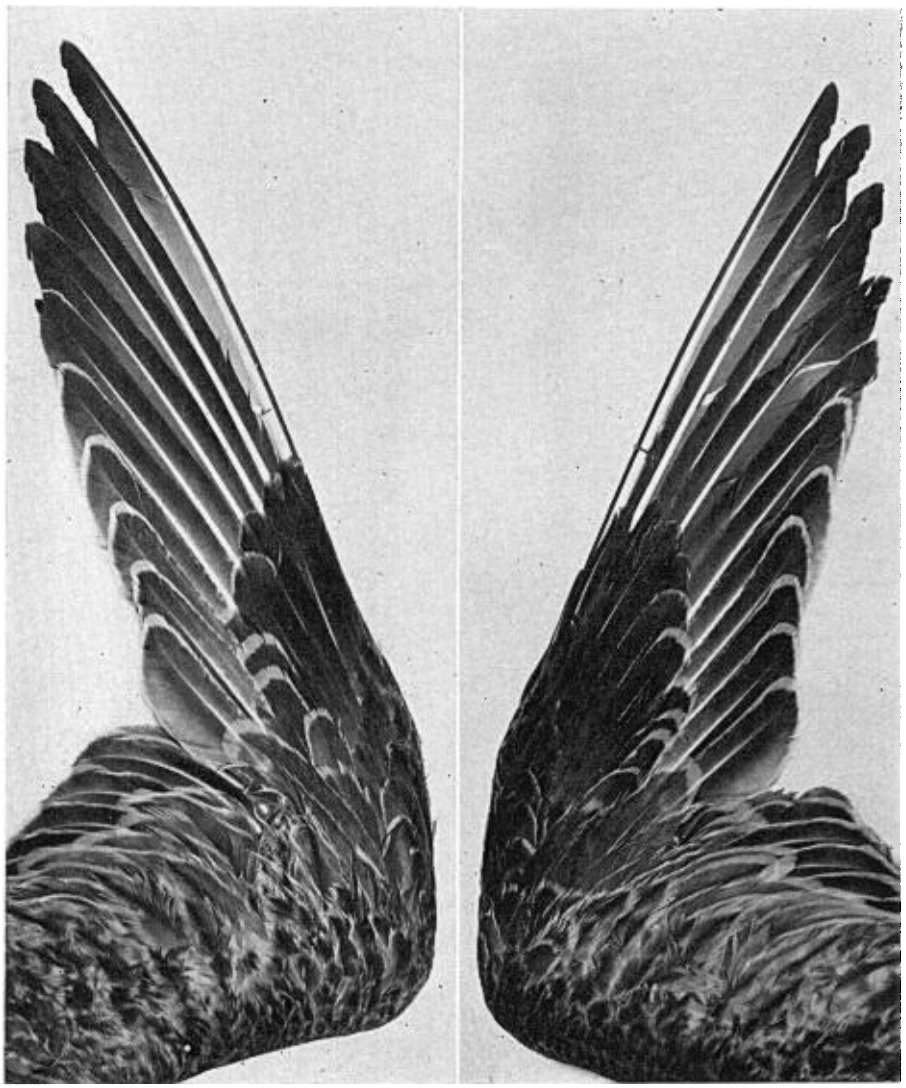

Fig. 3. *Limosa lapponica baueri,* AMNH no. 738545, dorsal view showing (left) 10 primaries on left wing and (right) 11 primaries on right wing.

the left wing, eleven in the right (minute remicle apparently present in each wing). *Philohela minor,* ten large primaries in the left wing, eleven in the right (three outer quills in each wing shortened and greatly narrowed as usual in this species; the remicle, normally present, was not determined with certainty) . . . . Of the three fresh specimens of *G.* [*Gavia*] *immer* examined, no two had the same number of primaries. Excluding the remicle, which was always present, the numbers were: ten in each wing; eleven in each wing; eleven in one wing, twelve in the other."

When examining the wings of a great many birds in the American Museum of Natural History in order to study their molt, we (Mrs. Vesta Stresemann and the

author) found four specimens to have 11 functional primaries instead of the normal number of 10:

Anhima cornuta, western Colombia, January 14, 1894, AMNH no. 469872; ten primaries in the left, eleven in the right wing.

Ptychoramphus aleuticus, Pacific Grove, California, January 28, 1914, AMNH no. 359471, ten primaries in the left, eleven in the right wing.

Limosa lapponica baueri, Lord Howe Island, October 31, 1913, AMNH no. 738545, ten primaries in the left, eleven in the right wing.

Plegadis falcinellus, Lenkoran (USSR), April 25, 1883, AMNH no. 531263, eleven primaries in both wings.

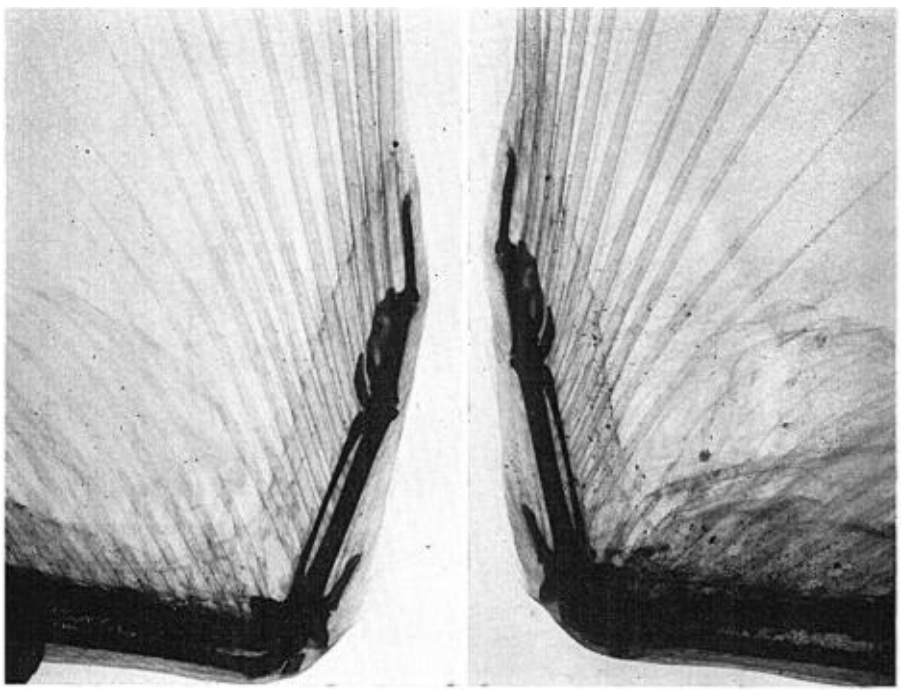

Fig. 4. *Limosa lapponica baueri,* AMNH no. 738545, ventral view showing (left) 11 primaries on right wing and (right) 10 primaries on left wing.

In every instance the outline of the wing appeared perfectly normal, despite the existence of an extra primary. At first sight it was by no means apparent in which place the additional primary might have been inserted. We had therefore to enlist the help of Mr. R. E. Logan, chief of the photographic division at the American Museum, who very kindly supplied us with excellent X-ray photographs of the expanded wings.

These X-ray photographs prove the supernumerary primary to be inserted, in all cases, on the metacarpus and not on one of the digits. Thus the normal number of metacarpals has been augmented from 6 to 7 by intercalation, which probably took place at the proximal or distal side of the sixth primary. The calamus of this additional primary does not differ in its dimensions nor in any other respect from that of all other metacarpals which slightly, but almost unnoticeably, became pressed against each other. In *Anhima,* and apparently also in the two other instances of unilateral increase in the number of primaries, the length of the fissura metacarpi is exactly the same in both

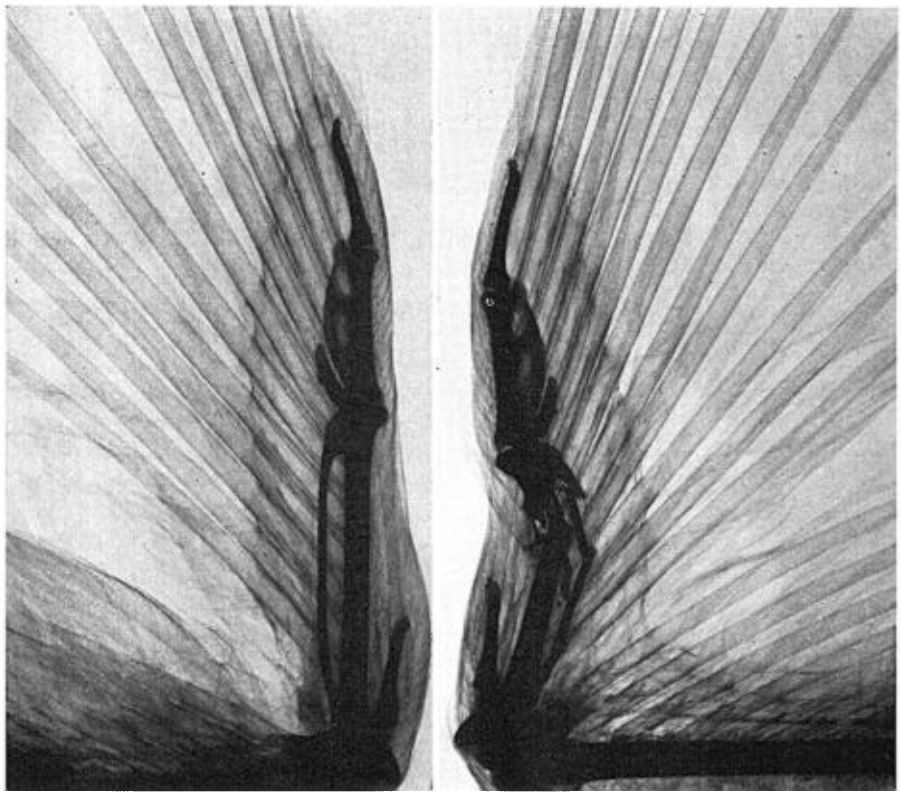

Fig. 5. *Plegadis falcinellus,* AMNH no. 531263, ventral view showing (left) 11 primaries on right wing and (right) 11 primaries on left wing, metacarpus broken.

wings. We did not pay attention in every case to the problem of supernumerary coverts. In *Limosa* we found the additional remex to have its own upper major covert.

In the abnormal specimen of *Anhima* we measured the length of each primary in both wings, taking the distance from the attachment of the under covert to the feather tip. Unfortunately the tips of primaries 6 to 10 are much abraded.

TABLE 1

Anhima, AMNH no. 469872, LENGTH OF PRIMARIES

	Left wing	Right wing
1	31.3	30.8
2	33.2	32.5
3	36.3	35.0
4	40.0	38.0
5	41.7	41.5
5a	.....	43
6	37.5+	37.5+
7	39.0+	38.0+
8	38.4+	37.5+
9	37.8+	36.8+
10	28.4+	29.7+

These figures show that the supernumerary primary is not an exact recapitulation of one of its two neighbors. By being harmoniously inserted in the graduated wing it gives the impression of having obtained its place in a general coordinating design. It looks almost as if the length of primaries 1 to 5 on the right had stayed behind the length of their representatives on the left to enable the supernumerary primary 5a to fit into the graduated wing.

At present no case of hereditary transfer of such an anomaly seems to be known. There is, however, no reason for excluding such a possibility. A mutation resulting in an increase of the number of primaries by one would in time spread over the entire population if coupled with some selective advantage even if it were a very slight one.

The Podicipedidae, Ciconiidae, and Phoenicopteridae are gifted with 7 metacarpal primaries. According to the author's view these three groups are derived from ancestors with only 6 metacarpals. If this assumption is accepted, then certain deductions of Gadow (1893) and W. DeW. Miller (1915) can no longer be considered valid. They both considered the fact that storks and flamingos had seven metacarpals as being an indication of affinity. For the same reason I disagree with Stegmann (1962) who declared (translation from German text): "Plainly, the storks diverged long since from the herons and ibises, since the former have eleven and the two latter ten primaries." This conclusion is in conflict with the unanimous opinion of morphologists who have shown the ibises to be close relatives of the storks and to be only distantly related to the herons. If, however, one supposes the storks and ibises to have sprung from one and the same ten-primaried stock, and the eleventh primary to be a secondary acquisition by the ancestry of the storks, all difficulties disappear.

Instead of an increase of primary-number from 10 to 11, abnormal individuals may show a decrease from 10 to 9. "In two cases, an ibis, *Carphibis spinicollis* and a parrot, *Alisterus cyanopygius,* there were in each wing only nine large primaries, with no evidence of loss by molt or accident" (W. DeW. Miller, 1924:316). Referring to *Lophortyx californicus,* Williams (1959:210) stated: "A captive bird has been found with *eleven* primaries and a few wild quail from one locality with an apparent full complement of *nine.*" While searching for molting birds we handled a small number of specimens, belonging to different orders, which seemed to have 9 primaries only, but owing to lack of time we did not pursue the matter through X-ray photography.

After concluding this article, we found that the grebe *Centropelma micropterum* has only ten primaries, in contrast to all other members of the family Podicipedidae. X-ray photographs show that the reduction of the original number by one took place in the metacarpal region and not at the tip of the wing. Thus *Podiceps* has 7 metacarpal primaries while *Centropelma* has 6. The latter, which is restricted to Lake Titicaca, is the only species of this family that does not fly at all. Consequently, the wing skeleton became greatly reduced in length; and while the number and arrangement of the digital primaries stayed unaffected, one of the metacarpal primaries and about seven secondaries became suppressed owing to lack of space. *Podiceps grisegena,* equaling *Centropelma* in size of body, has 20 secondaries whereas *Centropelma* has 13.

THE REMICLE

Jeffries' (1881) and Wray's (1887) interpretation of the remicle as representing an aborted eleventh primary was never questioned in the English literature. Instead it became a highly respected dogma. Reichling (1915:145–147) is the only author who dared to oppose the general view; but nobody paid any attention to his heterodox remarks (translated) about "the so-called eleventh primary" which he considered to be, and to have always been, a covert.

The presence or absence of the "vestigial eleventh primary" and, if present, the degree of its development has been carefully studied by W. DeW. Miller (1915, 1924) in all orders of birds. He found it to be sometimes accompanied by an eleventh lower covert but never by an upper covert. It is always left to the tenth major upper covert to shelter this little feather from above (Stegmann, 1962:59).

The remicle is fairly well developed in the Anseres. Humphrey and Clark (1961: 367), when dealing with *Anas platyrhynchos,* described it as follows: "The most distal primary (the remicle) is very much reduced and markedly different in shape from the ten, more proximal primaries. This eleventh primary is a stiff, lanceolate feather with narrow vanes. It is not superficially visible on either the dorsal or the ventral surface of the wing, being covered dorsally by the tenth greater upper primary covert and ventrally by the tenth and eleventh greater under primary coverts."

The position of the remicle at the distal end of the second phalanx of the index digit is shown on a plate (XXIX) included in Wray's famous article. In this figure, accurately copied by Van Tyne and Berger (1959), one notices a short, unfeathered third phalanx of the second digit, not mentioned in the text. Practically the same figure, drawn "after Wray, 1887," has been included in the article of Humphrey and Clark (*op. cit.*:368), but here the remicle has been shifted from the second to the third phalanx, probably by some error of the artist.

In *Struthio, Casuarius, Dromiceius* and *Apteryx,* the second digit is always equipped with a third phalanx which carries a claw. A vestigial third phalanx, occasionally carrying a tiny claw, has also been found in some flying birds, as a group character or as an individual variation. Jeffries (1881, 1882) disclosed rudiments of a claw in the embryo of the domestic duck and some waterbirds and in a young *Buteo platypterus.* He also noticed the presence of a very minute claw in two adult ducks of the genus *Anas* and stated (1882:304), "Accordingly the ancestors of birds had a . . . three-jointed second finger, . . . provided with" a claw. A claw at the end of the second finger has also been found in a specimen of *Anhima* (Nitzsch, 1811) and in *Cathartes* and *Gymnogyps* (Shufeldt, 1881; Forbes, 1882), in embryos of *Chloephaga* and *Milvus* (Gadow, 1891: 503), and in some other birds.

The position of the remicle at the end of the second phalanx renders it probable that its function consisted in covering from above, or from above and within, the clawed and therefore movable third phalanx. After the atrophy of the claw, and in turn that of its phalanx, the remicle persisted in some groups of birds but tended more or less to degenerate.

THE WINGS OF ARCHAEOPTERYX

What is the number of remiges in *Archaeopteryx,* and how are they distributed in relation to the ulna, the metacarpus and the fingers? Various answers to these questions have been given. They all were considered in de Beer's (1954) important monograph on the British Museum specimen. The differences of opinion are, in part, due to the fact that some authors studied only the London slabs whereas others worked on those of Berlin.

According to de Beer (1954:36), the British Museum specimen shows "altogether . . . sixteen remiges on each wing, six primaries and ten secondaries." He continues: "By counting [in the Berlin specimen] as feathers impressions which appear 'double-struck', more recent authors (Heinroth, Heilmann, Bohlin) have raised the number of primaries (incorrectly, it is here believed) to a dozen." The London specimen appears to lack the digital primaries and therefore contributes but little to our problem.

Both wings are complete in the Berlin specimen; they have been studied most carefully by Heinroth (1923), who remarked: "When one is accustomed to examining many specimens one gets the knack of estimating the number of primaries; one notices a gap caused by molt even without counting, and one can judge how many feathers are lacking. A complete wing composed of only 7 or even 6 primaries would surprise the expert at once. This, however, is not the case with *Archaeopteryx*; at least I personally got the impression of a regular bird wing with 10 primaries. By counting the feather shafts one reaches the figures 8 or 9, but molt gaps are clearly apparent, and in the right wing undoubtedly a short growing feather is to be seen . . . . In my opinion the outermost primary is attached directly proximal to the claw of the second finger. Distal to this primary one sees a covert adhering to the claw-phalanx" (translation from the German text).

A figure on plate 5 of Heinroth's article illustrates the author's surmise in regard to the connection between remiges and wing bones, which is obliterated on both slabs by the overlying coverts. On this figure, the tenth (outermost) and the ninth primary have both been connected by broken lines with the second phalanx of the index finger. One notices, however, that Heinroth considered such details of his reconstruction to be of little importance, for he did not even mention them in the text. There is no objection to supposing that all ten primaries of *Archaeopteryx* were attached to the bones exactly as in modern birds. This presumption seems more probable than any other, since the disposition of the wing feathers of *Archaeopteryx* also agrees almost completely with modern birds in certain other details (Steiner, 1956).

The covert mentioned by Heinroth as being situated in *Archaeopteryx* "distal to the outermost primary and probably adhering to the claw-phalanx" and shown on his plate 5, figure "Gr.r.," is of special interest. I take it to represent the remicle. This little feather projects a bit beyond the terminal claw of the second finger and may be attached to the end of the second phalanx, not however, to "the claw-phalanx," as Heinroth had guessed.

ACKNOWLEDGMENTS

This study would never have been carried out had not the Committee of the Frank M. Chapman Memorial Fund very generously enabled us to work at the American Museum of Natural History. There we found the four birds with supernumerary primaries herein reported and were aided in many ways by Dean Amadon, Charles O'Brien, Robert E. Logan, and other members of the staff. My gratitude is also extended to Alden H. Miller who was very helpful in procuring literature and to S. H. Jerris Read who read, and amended, my English manuscript. Special credit is due to my wife, who always insisted on counting the primaries of a bird before examining its way of molting them and thereby discovered these significant anomalies. Her share in the final shaping of the article is likewise considerable.

CONCLUSION AND SUMMARY

Beginning with Jeffries' article (1881) the remicle has generally been considered homologous to a primary. Quite a tower of additional theories has been erected on this supposition which the present author believes to be erroneous.

The essence of this article may be explained by comparing it with the "classic" concept.

	Current view	Author's view
A. Number and distribution of functional primaries in the ancestry of modern birds:		
Total number of primaries	12	10
Metacarpal remiges	7	6
Predigital remiges	2	1
B. Function of remicle in the ancestral wing:	A primary	A covert to the terminal claw.

C. Evolutionary trend in the number of functional primaries:

Current view.—A decrease in all groups of flying birds (from 12 to 11 in Podicipedidae, Ciconiidae, Phoenicopteridae; from 12 to 10 in most other larger birds; from 12 to 9 in most Passeriformes, some Piciformes and some almost flightless rails).

Author's view.—No change in almost all groups of birds. Exceptions: increase in Podicipedidae, Ciconiidae, Phoenicopteridae, where the number of metacarpal primaries has been increased from 6 to 7 by intercalation, bringing the total number of primaries from 10 to 11; decrease from 10 to 9 by gradual reduction of the outermost primary in most Passeriformes and some almost flightless rails.

LITERATURE CITED

Bates, G. L.
1918. The reversed under wing-coverts of birds and their modifications, as exemplified in the birds of West Africa. Ibis, ser. 10, 6:529–583.

de Beer, G.
1954. *Archaeopteryx lithographica,* a study based upon the British Museum specimen (British Museum, London).

Degen, E.
1894. On some of the main features in the evolution of the bird's wing. Bull. Brit. Ornith. Club, 2:vii–xxxiii.

Forbes, W. A.
1882. The claw on the "index" finger of the Cathartidae. Amer. Nat., 16:141–142.

Gadow, H.
1888. Remarks on the numbers and on the phylogenetic development of the remiges of birds. Proc. Zool. Soc. London, 1888:655–667.
1891, 1893. Vögel. *In* Bronn's Klassen und Ordnungen des Thier-Reichs. I. Anatomischer Theil. II. Systematischer Theil (Leipzig).

Heilmann, G.
1926. The origin of birds (H. F. and G. Witherby, London).

Heinroth, O.
1923. Die Flügel von *Archaeopteryx.* Jour. f. Ornith., 71:277–283.

Humphrey, P. S., and Clark, G. A., Jr.
1961. Pterylosis of the mallard duck. Condor, 63:365–385.

Jeffries, J. A.
1881. On the number of primaries in birds. Bull. Nuttall Ornith. Club, 6:156–163.
1882. On the claws and spurs in birds' wings. Proc. Boston Soc. Nat. Hist., 21:301–306.

Miller, W. DeW.
1915. Notes on ptilosis, with special reference to the feathering of the wing. Bull. Amer. Mus. Nat. Hist., 34:129–140.
1924. Further notes on ptilosis. Bull. Amer. Mus. Nat. Hist., 50:305–331.

Nitzsch, C. L.
1811. Osteographische Beiträge zur Naturgeschichte der Vögel (Carl Heinrich Reclam, Leipzig).
1840. System der Pterylographie. Editor H. Burmeister (Eduard Anton, Halle).

Prechtl, J. J.
1846. Untersuchungen über den Flug der Vögel (C. Gerold, Wien).

Reichling, H.
1915. Die Flügelfederkennzeichen der nordwestdeutschen Vögel. Jour. f. Ornith., 63:229–267, 305–340, 513–548.

Shufeldt, R. W.
1881. The claw on the index digit of the Cathartidae. Amer. Nat., 15:906–908.

Stegmann, B.
1962. Die verkümmerte distale Handschwinge des Vogelflügels. Jour. f. Ornith., 103:50–85.

Steiner, H.
1956. Die taxonomische und phylogenetische Bedeutung der Diastataxie des Vogelflügels. Jour. f. Ornith., 97:1–20.

Van Tyne, J., and Berger, A. J.
1959. Fundamentals of ornithology (John Wiley and Sons, New York).

Williams, G. R.
1959. Aging, growth-rate and breeding season phenology of wild populations of California quail in New Zealand. Bird-Banding, 30:203–218.

Wray, R. S.
1887. On some points in the morphology of the wings of birds. Proc. Zool. Soc. London, 1887:343–357.

Berlin–Lichterfelde–West, Germany, March 24, 1963.