The Wing in the Archaeornithes.[1]

By

BIRGER BOHLIN.

(Halmstad.)

Could the Archaeornithes fly? None of the authors who have dealt with the problem have assumed that these primitive birdlike animals were good flyers. ABEL (1912) speaks of "Flatterflug und primitiver Drachenflug" comparing the Archaeornithes with the Hoatzin. HEILMANN (1926, p. 39 *et seq.*) gives a vivid description of how *Archaeornis*, launching itself from the top of a tree-fern sails gently through the air to catch a dragonfly; how missing its aim it glides by before it is able to stop, how it succeeds in turning and flops its small wings trying to rise a little higher, how the attempt ends with the bird flopping down to the roots of a cykad trunk from where it rapidly climbs to the top. The kind of flight he describes is chiefly passive, the attempts made by the bird to counteract gravitation on the whole being futile. LOWE (1935, p. 408, referring to an earlier paper; also 1944) points out "that it would have been impossible for *Archaeopteryx* to have flown in the avian sense, without breaking its fore-limbs."

Facts could not be interpreted otherwise. Not only are the arm-bones weak, there are also no (ossified) breast-bone and whatever cartilaginous breastbone there was it can not have been very large as there is very little space for one in front of the ventral ribs (HEILMANN, *op. cit.* p. 16).

According to earlier authors there were only 6 primaries (metacarpodigitales; *cf.* ABEL 1912, p. 342). HEILMANN counted 12, two of the additional six plainly visible distally to the ones known before and four others vaguely seen as imprints covered by the barbs of the primaries lying on the surface of slab. These imprints which are plainly visible in HEILMANN's photograph of the wing of *Archaeornis* (*op. cit.* fig. 20) might be interpreted as made by the rather heavy shafts of the 3rd, 5th, 7th and 9th primaries before the wing came into its definite position on the slab (*cf.* ABEL 1912, p. 96 *et seq.*: "Der Kalkschlamm war von so zäher Beschaffenheit, dass uns der erste Abdruck des mit dem Tode kämpfenden Tieres

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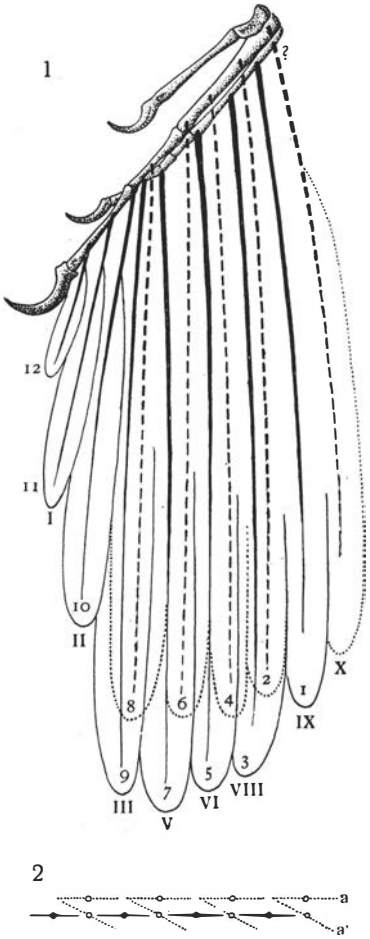

Fig. 1. Diagrammatical reconstruction of the primaries in the wing of Archaeornis and their relation to the skeleton of the hand (after HEILMANN). I—III, V, VI, VIII—X = numbering of the primaries according to HEINROTH; 1—12 according to HEILMANN. About $^2/_3$ nat. size.

Fig. 2. Diagrammatical section through some of the primaries. *a* arrangement as presumed in the present paper; *a'* according to HEILMANN. Not to scale.

auf der Platte erhalten blieb" — in this case it was a small lizard that had been caught on the sticky surface). I do not believe this to be the case as the imprints discovered by HEILMANN (a suggestion of their presence in the right wing is found in HEINROTH's paper of 1923, p. 279 and Plate 5) are quite distinct. Something more substantial than a groove in the mud must have caused them, or else they would probably have been smoothed out by the barbs of the covering vanes, and thus their outlines would have been more diffuse. Further the distances between these imprints and the

nearest shaft distally to them is not equal: 2 and 3, 4 and 5 are approximately equally far apart, but the distance between 6 and 7, 8 and 9 is another, and the shafts in these groups of two are not parallel as they probably (though maybe not necessarily) would have been if they were made by the same feather. HEILMANN also points out that the imprints of the 1st and the 5th primaries to some extent have the same character as the imprints discovered by him (p. 30).

I, therefore, agree with HEILMANN that there were more than six primaries (at least 12; see below). The original count gave a wing that must have been very inefficient also as a parachute. The wing looks tight enough as it lies spread on the slab but in reality the soft brims of the vanes would have yielded to the pressure of the air as they did not have much support from the adjoining feathers. We may only imagine a bird's wing in which every second primary were pulled out. The same reflection occured to HEINROTH who suggests that there were a number of "Mauserlücken" in the *Archaeornis* wing, and he has "die Empfindung eines regelrechten Vogelflügels mit 10 Handschwingen" (*op. cit.*, p. 279). Thus HEINROTH's and HEILMANN's discovery of a set of primaries which would fill the gaps is very important. The point is, however, if the reconstruction made by HEILMANN is correct (*op. cit.* figs. 33 and 35). HEILMANN is surprised to find "the very high number of 12 primaries" in "the most primitive bird we know," but yet he does not hesitate to arrange them in the same way as in the wing of a recent bird — thus constructing a wing which is perfect as far as the plumage is concerned, but with a skeleton not fit to stand the mechanical strain of true flight (LOWE 1944, p. 549. "If we went back as far as the Jurassic it would seem highly improbable that we should find that the primary remiges were confined solely to the second metacarpal and its digits.")

From Heilmann's excellent photograph it can be plainly seen that the vanes of the primaries 1, 3, 5, 7, 9, 10 and 11 are beautifully preserved, the barbs not being ruffled at all. The bird evidently dropped dead on the exposed silt, its wings were spread and after that no violence was done to it. The entire skeleton presents evidence of the same. But how could then the primaries 2, 4, 6 and 8 have slipped out of their original position and come to lie on the top of (or below) the others. I have tried to derange the primaries of a wing of a hen and found it almost impossible — at least it cannot be done leaving the vanes in such good condition as in the primaries of *Archaeornis*. And it is not only so, that the feathers in *Archaeornis* were undamaged before the imbedding took place, nature would also have managed to perform the shifting so deftly that primaries with odd numbers and such with even numbers now alternate in a regular way. Such a thing did hardly occur! It is true that the primaries in *Archaeornis* were probably

not so firmly attached to the bones of the arm and the hand as they are in a recent bird (*cf.* ABEL 1912, p. 343) but yet the attachment would have offered some resistance to deranging forces. In the London specimen the primaries are in disorder, but that individual was evidently imbedded in a state of advanced decay.

Neither can the present arrangement of the primaries be explained by supposing that some feathers were pushed in under others and that therefore only their shafts are visible. Take, for instance, the 8th primary which lies only a little closer to the 9th than to the 7th. We should expect to see the posterior web of the 8th and not almost the entire anterior web of the 7th (in the distal portion of this feather). We do not get away from this difficulty by assuming that the feathers were originally much broader than they look on the slab (HEILMANN *op. cit.*, p. 30).

If *Archaeornis* was moulting — a process which, of course, must have taken place also in the earliest birds — the primaries with even numbers might not yet have developed the vanes. But the shaft of the 8th primary can be traced to a point level with the tip of the 10th primary (HEILMANN fig. 20), the shafts of the 6th, 4th, and 2nd primaries are also rather long, and it is highly improbable that the feathers should have grown to such length before the vanes began to spread. Furthermore, the shaft of the 8th primary has a structure at its proximal end which suggests that the shaft belonged to a fully developed feather.

I am convinced that what we see on the slab is a very nearly perfect impression of one of the surfaces of the wing (*cf.* below) with the feathers arranged so as they were in life, and the only possible interpretation seems to be that the primaries (Nos. 2, 4, 6 and 8) discovered by HEILMANN belong to another series than those observed by earlier authors, the two series probably belonging to different rays of the hand skeleton (*cf.* LOWE 1944, p. 540).

HEILMANN states (p. 31) that most of the primaries in recent birds are connected with the second finger (*cf.* his figures): "The first 7 quills, as a rule, are attached to the united metacarpals 2 and 3, the next primary (in this case No. 8) is always borne by the first phalanx of the third digit, while Nos. 9 and 10 are attached to the first phalanx of the second digit, its second phalanx bearing Nos. 11 and 12." I have tried to see this on several wings but failed. It is of no importance as a proof of the theory put forth here how the primaries are arranged in recent birds and therefore I have not thought it necessary to enter on that problem. But after I had made an attempt to bring HEILMANN's reconstruction in agreement with the arrangement of the primaries seen in the fossil, the passage quoted hinted at a possible way of solving the problem of the *Archaeornis* wing.

If the surface of the wing that left the imprint on the slab is the lower

one, the primaries Nos. 2, 4, 6, and 8 lay dorsally to Nos. 1, 3, 5, 7 and 9. The two series were in all probability not attached to the same finger; therefore those with odd numbers would have belonged to the third finger, those with even numbers to the second. Nos. 10—12 cannot well belong to the same series as Nos. 2, 4, 6 and 8 as the posterior web of the 10th primary is seen in the photograph covering the anterior web of the 9th (*cf.* below). Thus no less than 8 primaries out of the 12 would have been connected with the comparatively weak third finger, whereas the strong second finger would have carried only 4. Such an arrangement is very unlikely also for the reason that the prolongation of the 12th and evidently also of the 11th primary cuts the claw of the third finger. Further if the distal portion of the third finger carried any primaries at all, its position in relation to the second finger would probably have been fixed, but instead the two distal phalanges of the third finger are on both sides bent in quite the same way, crossing the second finger at the articulation between its first and second phalanges. Therefore the two distal phalanges of the third finger were probably free.

In the reconstruction (HEINROTH, Tafel 5, Gr. 1), six or seven primaries are attached to the third finger and two or three to the distal phalanges of the second finger. Of these No. 10 lies proximally to HEILMANN's No. 1, Nos. 9, 8, 6, 5, 3, 2 and 1 (Fig. 1) are the same as Heilmann's Nos. 1, 3, 5, 7, 9, 10 and 11. Distally to No. 1, HEINROTH has drawn the outline of a small feather that is the same as HEILMANN's No. 12. Thus of the primaries recognized by HEILMANN five (Nos. 1, 3, 5, 7 and 9) would belong to the third finger and three (10—12) to the second. HEILMANN's Nos. 2, 4, 6 and 8, which undoubtedly formed a separate series might have been attached to the second finger as well. If the imprint seen on the slab is of the dorsal surface of the wing the main series would belong entirely to the second finger and the "accessory" primaries to the third. HEINROTH is more concerned with the number of primaries than with their relation to the skeleton, but the arrangement proposed by him might be correct in so far as a series of primaries attached to the third finger were continued distally by a few feathers belonging to the second.

It may be that HEINROTH and HEILMANN were mistaken and that the surface of the wing seen on the slab is really the upper one. The evidence brought forth is, however, in favour of their interpretation. "Die etwas wirren Deckfedern, die ganz den Eindruck von Unterflügeldecken machen, sprechen dafür, und die Tatsache, dass die Innenfahnen der Schwungfedern meist auf den Aussenfahnen liegen bestärkt uns in unserer Auffassung. Bei genauestem Zusehen finden wir an verschiedenen Federshäften je einen Längskiel, also den Abdruck einer Rille, 5. Tafel 4, 6 b und die ist bei allen gegenwärtig lebenden Vögeln nur an der Unterseite der Federn

vorhanden." (HEINROTH, p. 278.) The last point is perhaps the least convincing. If a feather were imbedded with the lower side downwards the grove would be filled with silt. If after imbedding it were exposed to pressure the rather porous shaft would collapse but the silt gathered in the groove would offer some resistance and there would be a marked ridge also in the dorsal aspect.

A detailed study of the specimen, with the problem discussed above in view, might give a clue to how the apparently contradictory results shall be reconciled. It is also possible that on closer examination still some feathers, large enough to be counted as primaries, will be discovered. So it seems as if on HEILMANN's photograph there were a small remainder of a shaft close to the 5th primary 6 or 7 millimeters below the "5." The shaft of the 7th primary seems to be double in the same way for some distance below the "7."

An attempt at a reconstruction is made in Fig. 1. A wing with alternating rows of feathers combined to produce an air tight parachute is quite in accordance with the primitive quincuncial arrangement of the feathers in the pterylia. LOWE (1944, p. 519) points out that the vanes on either side of the central rachis of the feathers were very narrow and of equal width. This observation made on the London specimen is probably more convincing than a similar statement based on the Berlin specimen. In this one the primaries look symmetrical but their undisturbed position in the wing may always justify the suggestion that part of the vanes were covered by adjoining primaries. Alternating rows of feathers go very well with a symmetrical development of the barbs, whereas the unsymmetrical primaries in recent birds must be an adaptation correlated with a uniserial disposition.

In a recent paper (1946, p. 95) SIMPSON is evidently inclined to assume that *Archaeopteryx* and *Archaeornis* were really ancestral to later birds. "The logical bearing of the evidence would still be that birds arose as feathered fliers, even if this development occurred (contrary to probability and without known evidence) in more than one line and if *Archaeopteryx* and *Archaeornis* were not in the successful particular line that did give rise to the later Aves as a whole." The development of feathers is of course such a complicated process that it can hardly have occurred in more than one group [the feathers in *Archaeornis* are so similar to the feathers in living birds that even if there were minor differences (*cf.* LOWE 1944, p. 539) — and not all living birds display the same microstructure of their feathers! — the presence of feathers forms a sufficient reason to refer the Archaeornithes to the same well defined group as the still unknown true ancestors of birds] but there is no logical reason to assume that this group of feathered reptilians represented only one single evolutionary trend: All lines did not needs develop flyers because there is no logical reason

why in all feathered forms a number of feathers should be enlarged; and the lines in which this took place did not needs all of them tend to develop the same type of flying apparatus. There exists, in my opinion, no doubt that the wing in *Archaeornis* was fundamentally different in its structure from the wing of later birds: impermeable to air also when the wing was raised, rather fit as a parachute than as a wing (the tail was certainly widely inferior as a rudder to the fan-shaped tail in recent birds). Thus even if the skeleton does not display any specializations leading away from the pedigree of the later Avians, the arrangement of the primaries definitely remove the Archaeornithes from the ancestral line.

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