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THE EVOLUTION AND USE OF THE AFTERSHAFT IN BIRDS.

BY HUBERT LYMAN CLARK, PITTSBURGH, PA.

THE presence of an aftershaft on the contour-feathers of the body has long been recognized as a taxonomic character of some value in the classification of birds, but little, if anything, has been published regarding its history or use. Admitting that every part of the body either has some function, the exercise of which has tended to preserve and strengthen it, or else that, if functionless, it is gradually being atrophied, it is necessary, before the evolution of any organ can be followed through all its stages, to first discover if it has any function, and, if so, what it is. The probable history of the aftershaft can best be traced in this way, and so the first point to be settled is the question of its use. The primary function of feathers is the retaining of heat, and, while forming a non-conducting covering, it is still essential that the weight be as little as possible. As the feathers differentiated other functions, some becoming long and stiff for flight and steering and some taking on new shapes and colors simply for ornament, every change which made the coat of contour-feathers more compact was a distinct gain to the bird. If any feather with a well-developed aftershaft be examined, it will be seen that the smaller shaft lies exactly underneath the larger and its vanes are closely appressed to those of the main feather, thus practically doubling its thickness and increasing its heat-retaining power with the least possible loss of compactness. Now, on the other hand, if a feather is examined which has only a very small aftershaft, the latter is not closely appressed to the main shaft and adds almost nothing to its thickness or warmth. Exceptions will, of course, be easily found to these rules, but the fact remains that where the aftershaft is vigorous it gives plain evidence of adding warmth to the plumage, while it is clear that it can have no secondary function of ornament or locomotion. Another reason for believing that the aftershaft is functionally of no importance, except when an assistance to greater warmth, is found by examining the list of birds which lack it. They are as follows:—

1. Some Ratitæ (Ostriches, Rheas, Apteryx?).
2. Diomedinæ (Albatrosses).
3. Steganopodes (Gannets, Pelicans, Cormorants, etc.).
4. Lamellirostres (Ducks, Swans, Geese), except Flamingoes and some Ducks.
5. Columbæ (Pigeons).
6. Cathartidæ (American Vultures).
7. Striges (Owls).
8. Pandionidæ (Ospreys).
9. Cuculidæ (Cuckoos).
10. Alcedinidæ (Kingfishers).

Since there are known to science to day about ten thousand species of birds, only one-tenth of which are included in the above list, the absence of an aftershaft may certainly be considered exceptional. If it is functionally of any importance, why should it be wanting in the albatross, though present in the petrel? Or

wanting in many ducks and present in others? And indeed to assign it any function common to all birds except to those in the above list, while wanting in all of them, will be readily found impossible. That it may be the cause of greater warmth receives a proof of negative value from our knowledge that, while very large in all the other Ratitæ, it is totally wanting in those species which inhabit the open plains and deserts of the tropics, where it is not desirable to retain too much heat. Still further evidence appears in the facts that all of the birds which lack an aftershaft (except owls and pigeons) are supplied with a thick coat of down beneath the contour-feathers, and all of the groups except Striges, Lamellirostres, and a few Steganopodes are most largely represented in the tropics and warmer temperate countries. While much of this evidence is very general, some of it purely negative, it seems undoubtedly true that the aftershaft, when not serving as an additional heat-retainer, is wholly functionless.

The conclusion is now unavoidable that the aftershaft, if functionless, must, according to our original proposition, be undergoing a process of gradual atrophy. That such is the case admits of little doubt. It must, however, be kept in mind that its possible function as a heat-retainer is admitted, and in cases where this function has been sufficiently exercised, atrophy, if ever begun, has been stopped. Illustrations of this may be found all through the class, but two will be sufficient to show the point. In the Casuaridæ (Cassowaries) the aftershaft is of equal size with the main shaft, and its function is undoubtedly the same. It is practically a second feather, and, since compactness of plumage is of no advantage to non-flying birds, it has continued to exercise its function, and atrophy has never begun. In the Gallinæ, one of the oldest and most generalized groups, where compactness of plumage is very desirable, not only because it creates less friction in flight, but also because, being essentially ground birds, they are greatly exposed to cold and damp, the aftershaft is large and thick, but entirely different from the Cassowary's. Increasing compactness of the plumage has greatly modified it, but atrophy has not occurred because it still exercises to an important degree its function as a heat-retainer. In the Passeres, on the other hand, the condition of the aftershaft shows evident loss of function and consequent atrophy, being very small and weak. Perhaps in no better way can the degeneration of the aftershaft consequent on its loss of function be proven than by an examination of the feathers of the wing. As is well known, the chief function of the primaries and secondaries is no longer heat-retaining but locomotive, and they entirely lack an aftershaft in all flying birds. But this change of function has undoubtedly been brought about gradually, and on the elbow of the wing are several feathers, very slightly different from the contour-feathers, which grade by almost imperceptible differences into the fully-developed secondaries. If these feathers are examined in any bird with aftershafted plumage, as, for example, the ruffed grouse (*Bonasa umbellus*), a very evident aftershaft will be found on the smallest ones, but decreasing rapidly in size as the main shafts become flight-feathers, until, on the true secondaries, they are either wholly wanting or represented only by a slight meeting of the vanes.

It will be noticed that throughout the preceding argument, the assumption has been made that the aftershaft is a degenerated and not a recently evolved part of the feather. That is, that it was originally characteristic of feathers in general and its condition as known to us is worse than formerly, rather than that it is an acquired character, which never occurred where it is now wanting. The truth of this assumption must now be proven, or the foregoing statements are meaningless. The first reason to be offered for believing it to be a primitive part of the feather is found in the facts of its occurrence and development in the different orders of birds. In the Casuaridæ, which is admitted to be one of the very oldest families of modern birds, we find a very large aftershaft, indeed, as already said, it is practically one-half of the feather. In the other Ratitæ, in which it is wholly wanting, local causes, such as excessive heat, have destroyed its usefulness, and its loss is easily explained. Large aftershafts are also found in *Opisthocomus*, the Gallinæ, and the Penguins, all old and little specialized groups; while, on the other hand, in the