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VARIATIONS IN THE STRUCTURE OF THE AFTERSHAFT AND THEIR TAXONOMIC VALUE[1]

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If a feather from the body of a pigeon is compared with one from a grouse or pheasant a notable difference in their structure will be observed. The pigeon's feather consists of a single shaft bearing a bilaterally symmetrical vane or web, and thus conforms to the common notion of a feather. The feather of the gallinaceous bird, on the contrary, is double. Lying closely apprest against the under or ventral side of the feather is a secondary plume, which, when undisturbed, so blends in appearance with the main feather that on casual examination it may easily be overlooked. When raised, however, it is conspicuous, and has the appearance of a smaller and more downy feather joining the main shaft at its base, that is, at the junction of the rachis with the short calamus, which is inserted in the skin.

This secondary feather is known as the aftershaft or hypoptilum, and its presence or absence constitutes the most important structural difference in the feathers of existing birds. It usually varies comparatively little in size on feathers from different parts of the body. In a few instances a fairly developed aftershaft is found on the feathers of one or more tracts, while others may entirely lack one. The rectrices and the full-sized remiges are never furnished with this supplementary feather, but a well-marked vestige of it may be found on the small inner secondaries or tertials.

The presence of the aftershaft is unquestionably a primitive character, and its reduction or loss is therefore a sign of specialization.

In the majority of orders this appendage is present in a greater or less degree of development, but rarely so large and perfect as in the gallinaceous birds. In these it is certainly not a vestige, but in many groups, as, for instance, the Passeres and the Anseres, it is truly vestigial.

The pigeons furnish the best example of a large group in which the aftershaft is entirely wanting. It is also absent in the Steganopodes, the hornbills and hoopoes, the cuckoos, owls, puff-birds and the Clamatores or at least the Tracheophones.

[1]Presented before the American Ornithologists' Union at Chicago, Illinois, October 25, 1922.

While the aftershaft has long been used as a taxonomic character, it has been employed only in a very general way, as, for instance, its mere presence or absence or whether large or small. The term "vestigial" as applied to it has been used very loosely. In the general works there is scarcely any reference to the variations in its form or structure and, if any special papers on the subject have appeared, they have escaped me.

Soon after beginning to give attention to this subject I realized that it was not sufficient to record merely the length of the aftershaft relative to that of the main feather in order to indicate its degree of development. In songbirds, toucans, and barbets the appendage may practically equal the feather in length, being fully as long as in gallinaceous birds. In structure, however, it is entirely different from the latter, consisting of a tuft of long delicate filaments with no common shaft. It is therefore important to record the length of the rachis of the aftershaft as well as that of the hypoptilum itself.

While it is impossible, on account of numerous transitional stages, to classify the variations in the form of the aftershaft so that they will fall into sharply defined groups, yet, owing to the several well-marked variations, it is highly desirable that some such arrangement be attempted.

It appears to me at present that feathers may best be classified in seven groups according to the degree of development and structure of the aftershaft.

The first group consists only of the ratite order, Casuarii, comprising the cassowaries and emus. In these birds the feathers are very long, narrow, lax, and loose-webbed. The aftershaft is very similar to the main feather, equalling it in length and differing only in the slightly more slender rachis (Fig. 1).

The second group includes most of the higher gallinaceous birds, such as pheasants, grouse, and quail; also certain tinamous. In these the aftershaft is narrowly oblong and the shaft runs nearly to the tip. The relatively short barbs are closely set at right angles to the rachis and are furnished with unusually long barbules (Fig. 2).

The next group is a large and heterogeneous one, comprising such diverse forms as the diurnal birds of prey, herons, turacos, parrots, trogons, and sandpipers. The aftershaft is well developed, with a moderately long shaft, but lacks the peculiar form and structure of the gallinaceous type (Figs. 3 and 4). This class, by degeneration of the aftershaft, gradually passes into the next, which is typified by the songbirds, and includes also the toucans, barbets, and woodpeckers. Here the after-

shaft may sometimes equal the main feather in length, but its shaft is extremely short and fine, so that the whole is virtually only a tuft of delicate filaments. In the picine birds enumerated the shaft is better developed than in the Oscines (Fig. 5).

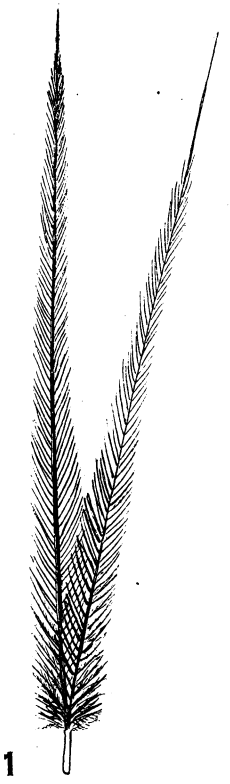
The fifth type is shown by the curassows and the hoatzin. The shaft of the hypoptilum is entirely basal, the barbs springing only from its tip (Fig. 6).

In the next group the shaft has been entirely lost and we find only a fringe of barbs or filaments crossing the base of the shaft. In the ducks transitions from a true, though very vestigial, aftershaft to this fringe type can be clearly traced, so that there is no doubt that the latter represents the aftershaft, though it can scarcely be called by this name. The owls, very constantly, the Anseres, the American vultures and *Steatornis* exhibit this style (Fig. 7).

The seventh and last group is characterized by the entire absence of the aftershaft. As already stated this is the case in all pigeons (Fig. 8), in the hornbills and hoopoes, the Steganopodes, and in nearly all Clamatores including all of the Tracheophones (a very characteristic Neotropical group comprising the antbirds, woodhewers, and several other families). In a few of the pelican tribe there is a transition to the preceding group.

My particular interest in studying these variations has been to determine their bearing on the classification of the birds. While nothing very surprising has been discovered, the style of the aftershaft has proven helpful in characterizing certain groups. For example, I have never seen it mentioned as a differentiating feature of the Oscines, yet of the fifty or more families of songbirds examined, the aftershaft has been, with one or two exceptions, notably the swallows, invariably present except in a few genera of three or four families. On the other hand there is never more than a trace of it in any of the fifteen families of Clamatores or songless perching birds. A curious partial exception is found in *Acanthisitta*, one of the three genera of the New Zealand family Xenicidæ, in which some of the dorsal feathers only bear a rather short and very slender aftershaft. In several families, for instance the tinamous and the Icteridæ, there is more than the usual amount of variation in the aftershaft, and I believe that this will prove an important aid in classifying these groups.

How useful this feature may sometimes be for the systematist, by whom it is commonly neglected though it is an easily determined external character, is shown by the recent case of *Rhamphocænus*. This small,



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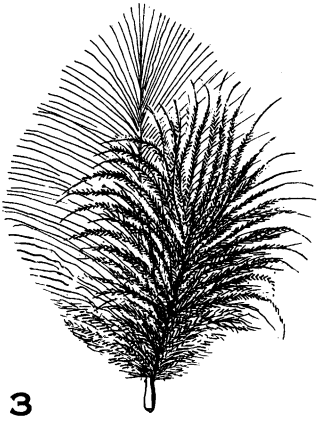

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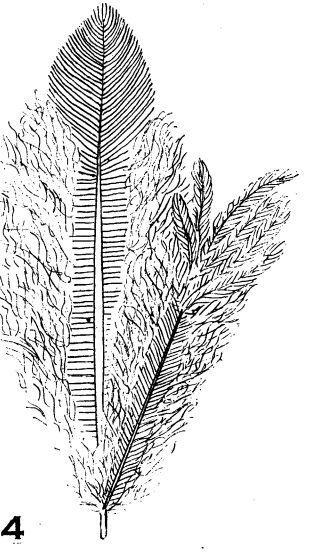

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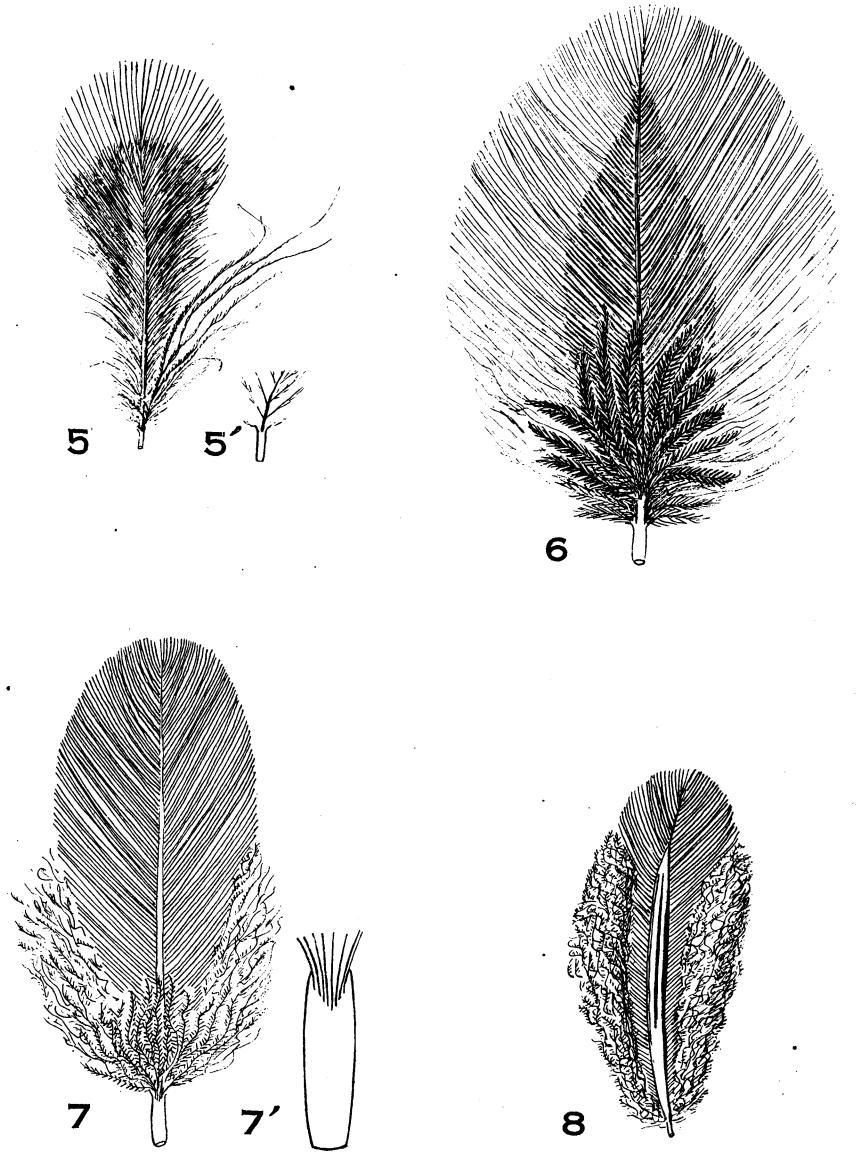

Figs. 1 to 8.—Body feathers (ventral aspect), about $\frac{4}{5}$ natural size, to illustrate variations in aftershaft.

1, Cassowary (*Casuarius*); 2, Pheasant (*Phasianus*); 3, Ibis (*Carphibis*); 4, Trogon (*Pharomachrus*); 5, Jay *Xanthoura*); 5′, Its base enlarged; 6, Hoatzin (*Opisthocomus*); 7, Goose (*Anser*); 7′, Its base enlarged; 8, Pigeon (*Columba*).

long-billed Neotropical bird had been universally referred to the Formicariidæ. The discovery that its feathers have a long aftershaft led to further investigation and its removal to the Oscines. A similar case is the flat-billed vireo (*Lawrencia*) of Haiti which could not have passed as a tyrant flycatcher for thirty years after its discovery had its oscine aftershaft been used to determine its position.

An important feature of the taxonomic value of the aftershaft is the fact that it is not an adaptive character. As is well known, most characters are subject to adaptive changes which obscure their systematic value.

The extremely divergent groups in which the aftershaft persists show at once that its mere presence at least is not affected by increase or reduction in size of the bird or its individual feathers, by habitat, climate, power of flight, food or any other known environmental factor, nor by presence or absence of down on the body. As examples, may be cited the cassowary, penguins, hummingbirds, petrels, grebes, herons, birds of prey, snipe, parrots, nightjars, trogons, woodpeckers and songbirds. In all of these groups the aftershaft has been retained.

The families that have lost it are also very diverse. Compare, for instance, the ostrich or the pelicans and their allies with the hornbills, pigeons, and songless perching birds.

It is possible that there is to a certain degree a correlation between temperature and the development of the aftershaft. The tinamous, gallinaceous birds, Accipitres and Passeres furnish some evidence that the aftershaft is often better developed in birds of colder regions than in those of the tropics. Further study of the subject is required, however, before this can be considered as more than a suggestion.

The constancy of the aftershaft throughout large groups is striking. Thus, it is present in every species of parrot examined, including almost every genus from the pigmy *Nasiterna* up to the great macaws and cockatoos. In the very diverse but natural assemblage of lariform birds, including the gulls, auks, and snipe, and in the allied families of cranes and bustards, there is so far as known not a single exception to the presence of the aftershaft.

In the picarian group comprising the barbets and toucans, the honey guides and the woodpeckers, it is, although degenerate in structure, invariably developed. It is even more reduced in structure in the Oscines, yet in the extensive group of nine-primaried families including the finches, tanagers, wood-warblers and honey-creepers it occurs with equal constancy.

In the allied family of troupials or Icteridæ, however, the aftershaft has been eliminated in some of the large oropendolas and related forms. This is only one of several reasons for placing the Icteridæ, and the giant Oropendola *Gymnostinops* in particular, at the top of the avian tree.