On the Origin of Feathers.

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In the ,,Dictionary of Birds",[1]) article ,,Feathers" I stated that: The Teleoptiles [the feathers of adult birds] whether contour feathers, or downs, are each originally preceded by a Neossoptile [first, or nestling plumes], the base of which is in direct continuity with the tips of the rami of its succeeding final feather; but owing to a shortened process of development or caenogenetic conditions many, or even all Neossoptiles may occasionally be suppressed, to that the tips of the first feathers which appear, are actually those of the second generation."

When, in the autumn of 1908 I had the pleasure of delivering a course of lectures ,,on the coloration of Birds" at the Lowell Institute, Boston, Mass., I was not aware of Dr. Lynd Jones[2]) paper on the development of nestling feathers, nor of Oscar Riddle's[3]) papers, because I had just returned from a six months tour through Mexico. At Boston I elaborated the above condensed statement and explained that the now well known structural continuity of the neossoptile with the teleoptile was all-important for our understanding of the moult or succession of feathers, and of their phylogeny itself. Often, most completely in Ducks and their allies, the Neossoptile of first down forms a complete, typical spool which in time is lifted out of the skin, whilst it may still be enclored by remnants of its sheath; then the base of the spool splits and its constituent shreds reveal themselves as the direct continutions of the tips of the rami or barbs of the next following feather or first teleoptile. In such a case therefore the first and second generation are still continuous in structure and in time, although the transition is sharply marked by the formation of a spool. This process finds a fair analogy in the ,,year-rings" of the horns of cattle.

The moult of feathers is therefore the periodical interruption of an originally ever-growing feather. The interruption in structure and in time between any two successive teleoptiles has become

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1) A. Dictionary of Birds. Alfred Newton assisted by Hans Gadow. London 1893—1896.

2) Laboratory Bulletin No. 13, Oberlin College; Oberlin, Ohio 1907.

3) The cause of the production of Down and other Downlike structures in the plumages of birds. Biological Bulletin, vol. XIV, Februar 1908.
The Genesis of fault-bars in feathers and the cause of alternation of light and dark fundamental bars. Biol. Bulletin, May 1908.

complete, and therefore these feathers represent typical, individual generations.

The connexion with the Neossoptile is therefore a truly palingenetic feature. In many birds this first feather degenerates, sometimes with a mere vestige of a shaft, or the whole is reduced to a few filaments attached to the rami of the first teleoptile, or it may be suppressed altogether.

Unfortunately Dr. Jones, after quoting my passage cited above, did not rise to the broader view. He says „Though a continuity between the nestling down „neossoptile" and the definitive feather „teleoptile" has been recognised, the former has been regarded as a relatively complete and distinct feather. I shall attempt to show that the neossoptile is only a more or less differentiated part of the first teleoptile." In the summary of his paper, which is full of interesting detail and is amply illustrated, he states the following conclusions.

3. „The first down has no shaft. The barbvanes [rami] which compose the first down, are continuous and separate through the entire length of the down." So they are in many birds, but in many others the nestling downs have a shaft, for instance Rhea, Dromaeus, Casuarius, Anseriformes; cf. Gadow, Bronn's Thier-Reich, p. 534

4. „The first down has no quill." In order to be able to make such a statement he describes the quill or spool, where such occurs, as „a more or less homogeneous horny cylinder which can be split along the lines continuous with the barb-vanes by pressing or rubbing the so-called „quill" between two hard surfaces"! We may wonder what would be his definition of a quill or feather-spool. Distally it passes imperceptibly into the shaft with its vanes, and proximally it comes to on apparenty sudden termination only in the teleoptiles. The interesting fact is that in some neossoptiles this spool is still in an incipient, archaic, condition.

5. „No shaft is formed at the extreme distal end of the first definitive feather. The rudiments of a shaft begin to appear several millimeters proximal to the distal end of the feather by the coalescing of two or more barb-vane ridges." One fails to see the importance of this statement. Did he expect the shaft alone to pass upwards into the spool of the neossoptile? How could this happen if, as he asserts, the first down has neither shaft nor quill? Moreover there are many teleoptile downs which have no shaft. If any thing, his remark could be taken to mean that there is a difference between the neossoptile and the first teleoptile, a conclusion which he rejects.

7. „The first down and its succeeding definitive feather are produced by one continuous growth, and therefore cannot be regarded as two distinct feathers. The first down is the plumulaceous tip of the first definitive feather."

My detailed explanation of the phyletic and morphological meaning of the succession of feathers has hitherto been oral only. Quite recently it has recieved an unexpectedly complete support, amounting to proof, through the discovery by Frieda Bornstein[1]) of the „Federleiste", the ectodermal germinal ridge or strand which forms the feathers, and through which the germs of all the generations of any particular feather are continuous, from the neossoptile to the first, and from this to the last member of an apparertly inexhaustible series of teleoptiles!

The „Federleiste" behaves much like the dental ridge of Mammals, but in stead of producing germbuds which are packed side by side and then lose connexion which each other, the feathergerm ridge behaves rather like the growth of a perennial bulbous plant, for instance a Scilla, which, as is well known, thereby sinks from year to year deeper into the ground. Further, instead of several, only one germ for a future feather is laid down at the time. The papilla of the first teleoptile is already forming whilst the neossoptile is still growing!

This continuity between two successive generations of feathers is absolute until the present feather has finished its growth. The pulp is reduced, or shrunk down to the base and there closes the socalled lower navel of the quill. During the following prolonged period of rest there is probably no live connexion, authough if a perfectly adult, old feather be pulled out, its navel will always be found to be soft and torn, whilst if this quill is moulted, it leaves the pocket with a hardened and finished navel base.

This long-protracted continuity may throw light upon a still very obscure point. It makes it reasonable to assume that a modification of the growing feather, induced by external, environmental, conditions, may also similarly affect the next generation, although to a lesser extent. Lesion of the pulp, within the bloodquill, sometimes causes abnormal growth or coloration in the successor. It is not excluded that some enthusiasts may take such a case as one of an inherited acquired character.

Frl. Bornstein's observations are not quite perfect in so far as she does not mention the continuity of the barbs of the nestling down with those of the following feather. The conditions represented in her Fig. 12 would indeed seem to make such a continuity impossible, but this difficulty is apparent only, not real. We must remember that it is always the basal portion of the papilla which produces the featherbuilding cells, whilst the apical portion is inactive. This must be so, since the top of the pulpa proper, covered only by the basal membrane, projects out through the upper navel. This circumstance may further help to explain

[1]) Über Regeneration der Federn und Beziehungen zwischen Federn und Schuppen. Archiv f. Naturgeschichte. 77. Bd. 1. 4 Supplement. 1911.

the real meaning of Jones' point 5 of his summary. The necessary continuity of the nestling barbs with those of the first teleoptile have to be looked for in that dark strand of cells which border the right side of the central white gap in Bornstein's Fig. 12.

Until her discovery it was thought that portion of the whole circumference of the papilla was reserved for, and remained dormant until, the growth of the next feather.

The behaviour of the ,,Federleiste" and the growing into it of a new pulpa, enables us further to correct the perverse notion hitherto entertained about the homologies of feathers with reptilian scales.

,,Regelmäßig angeordnete Erhebungen der Lederhaut, von der Epidermis überkleidet, bilden die erste embryonale Anlage, welche von den bei Reptilien bestehenden Einrichtungen nicht wesentlich sich unterscheidet. Diese Papillen gewinnen aber eine bedeutende Länge . . . Von den Schuppen sind sie durch bedeutendere Länge verschieden." (Gegenbaur. Vergl. Anat. d. Wirbeltiere, I, p. 134.)

The usual statement that feathers are modified reptilian scales requires several restrictions. The difference between reptilian scales and feathers is that the bulk of the reptilian organ is composed of connective tissue, mesoderm, with a thin horny coat, the share of the epiderm. The feather is an entirely ectodermal product and its pulp is an extremly vascular apparatus which is with drawn and vanishes without contributing any cell-material to the feather. The feather is therefore homologous only with the ectodermal portion of a scale or ,,Schuppe".

It has been customary to homologise the pulpa of the feather with the whole of the ,,Schuppenkoerper" or mesodermal portion of the scale. Bornstein, by further elaborating Ghigi's view, has shown that the feather represents only a small portion of the epidermal scale. Sagaciously she has examined those structures which alone can be expected still to represent more or less intermediate ancestral conditions, to wit the feather-producing scutes of the feet.

The history of the origin of feathers may now be told as follows.

The initiation is taken by proliferation of a much restricted portion of the epiderm at the apex, or at the imbricating edge of a scale. It is immaterial whether the resulting cornified thickening is single or multiple. It need not at once have formed a prominant cone, on the contrary it is advantageous to liken it to a wart with its characteristic inward growing tendency. Feathers, hairs, nails, scales, in short most growths due to ectodermal proliferation show the tendency of sinking- in with their base and this often leads to a more or less pocket like arrangement, which with the additional necessity of a pulpa terminates in the well-known in- and evaginated follicle. It was E. B. Poulton who first pointed out that the feather follicle itself is merely a mechanism whereby a better ,,nutrition and support" of the feather is attained.[1])

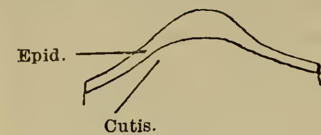

Fig. 1.

Fig. 2.

Fig. 3.

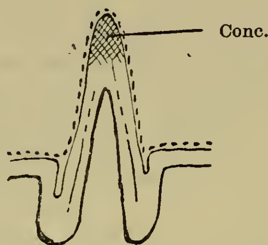

Fig. 4.

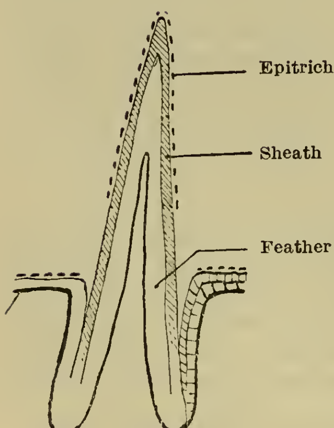

Fig. 5.

Fig. 6.

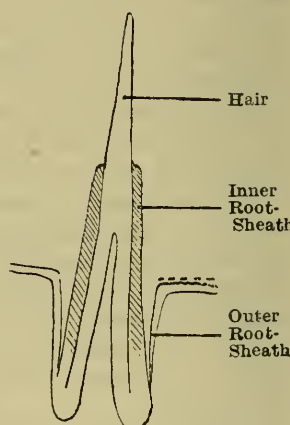

Fig. 7.

Schemes illustrating the origin of Feathers.

1. A scale with epidermal thickening at the apex.
2. Thickening with incipient pulpa.
3. Papilla ,,rising" above the surface level of the original scales area, the scale having last its ,,body" excepting so far as this is represented by the pulpa.

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[1]) This sentence is quoted from O. Riddle, ,,Genesis of Fault-bars . . . "who refers to Professor Poulton's Structure of the bill and hair of Ornithorhynchus, Q. J. M. S. June 1894.

This is the stage which is the first to appear in the ontogeny of Neossoptiles on the typical scale-less skin of the bird's body.

4. Papilla „sinking in", with the formation of a follicular pocket. Epitrichium still complete. The solid horny cone is further down supplanted by the hollow sheath and the Neossoptile rami.
5. Neossoptile and Teleoptile or first final feather. Epitrichium severed by the growth of the Teleoptile.
6. Three branches of a Neossoptile combining as a spool*, which in turn splits again and is continued as two branches of the final feather.
7. A Hair for comparison. Epitrichium apparently no longer repeated; Sheath severed or pierced by the growth of the hair.

It can not be emphasised enough that the whole pulp is not the homologue of the core or body of a scale, except in so far as it represents some of the latters blood-vessels. It is nothing but vascular, a much developed artery and vein with much lymphatic meshwork, developed as a consequence of the activity of the cluster of epidermal cells. The outer, environmen tal effect upon there cells, their reaction upon pressure, insults, „need of protection", is the primary cause; the pulp or swelling of the mesodermal parts is a result; and the suppression, not conversion, of the respective portion of the original core is a further result.

If this proliferation takes place periodically, with intervening stages of lesser activity there will result feathers much resembling those which are represented in Fig. 18, Pl. II of Bornstein's paper; and if the pulp grows much in length, the archaic solid epidermal cone (cf. Fig. 18) will, in one of the next generations be replaced ly a longer, partly hollow, cone. Such a thing, a cylinder, closed at the top, is the horny transparent sheath, which encases every growing feather, from Neosso- to Teleoptile. It represents the second stage of the feather's genesis. The wart-like excrescence, the solid cone, and the Neossoptile are still covered the by epitrichium. This archaic, outmost product of the epiderm is, for obvious reasons no longer regenerated from the first Teleoptile onwards.

The next stage is characterised by the formation of a cylinder within the first, by a repetition of the process of proliferation from deeper strata of the Malpighian cells which meanwhile have increased their number of layers. But this second cylinder, owing to irregular apical growth, is frayed out like a brush; this lowest of Neossoptiles however still recapitulates its ancestral condition by repeating with its basal portion a solid mantle, the incipient or first spool.

It stands to reason that the fraying-out process began at the tip of the whole projecting structure and worked downwards, and further that repeated splitting of the primary branches of rami has produced the radii and ultimately the cilia and hooklets.

We had satisfied ourselves in the first part of this paper that there is, or was, absolute continuity between the successive generations of feathers. The formation of a spool may therefore be looked upon as originally the result of a periodic arrest of splitting proliferation.

Further stages concern only the perfecting of this still primitive brush-like neossoptile into a typical feather; the arranging of at first equivalent rami onto a shaft and the consolidation of the spool with its incidental advantages.

The first solid cornified cone, the first hollow cone and the sheath of each succeeding feather are continuous, products of the same outer layer (itself composed of several layers, or thicknesses of cells) of the proliferating papilla, and as such they are homologous with the periodically cast off skin of the Snakes, or the congrowing ,,Tortoiseshell" of Chelonians. But whilst in Reptiles the basal membrane is soon abolished through the establishment of an intermediate layer, due to immigration of ectodermal elements into the corium, in the birds' feather-follicle the basal membran remains intact; and in correlation with the elaborate follicular pocket with papilla, it has become possible for an inner, deeper mass or layer of cells to produce a second cornified cone within the first, and at the same time. As explained before, periodic growth of this second, inner layer, produces the Neossoptile and its continuation the Teleoptile. Lastly, with an innermost layer we arrive at the basal membrane, which transforms itself into the feather-soul, and this may well be looked upon as the representative of still another structure, a kind of future feather, at least potentially if there were any need of troubling about super-feathers.

When considered from an unbiassed point of view it is not difficult to homologise the feather-sheath with the ,,inner root sheath" (innere Wurzelscheide, composed of Henle's and Huxley's layer) of the Mammalian hair, just as much as the hair is homologous with the feather. There is however this difference that the sheath of the hair now appears reduced in comparison with the sheath of the feather and that its cells do not form a solid cornified mantle. In some respects the hair is precocious, it pierces its sheath at an early stage; in others it appears simpler (more primitive ?) than a feather, as it is never branched and remains at the solid cone stage with only a very short pulp. Even this difference disappears when the hair assumes the dimensions of a spine with the starshaped constrictions, or expansions of its elongated pulp. It may as well be mentioned that the ,,Oberhäutchen" of the hair is not the same as the epitrichium.

The notorious attempt to derive the Mammalian hairs from some hind of pre-reptilian sensory apparatus, analogous to the perl-organs of fishes, could be paralleled by the assumption that the peculiar sensory pits in the scales of crocodiles and snakes are the forerunners of feathers, especially since the latter are now known to be not the whole scale but a small highly modified part only.

Küster has introduced the idea of the ,,Tastfeder". The occurrence of sensory elements near the base of a feather does not necessarily turn this into an organ of touch, although it is quite conceivable that the brisles of a Nightjar or of a Flycatcher do not merely add to the gape for catching purposes. Probably they are also used as organs of touch, just like the whishers of a Cat, but this is no reason for assuming that such feathers or hairs owe their origin to this function. These sensory elements are there primarily for the benefit of the respection epidermal organs and not vice versa; and incidentally it may have proved advantageous for the nerves to become more intimately correlated with them. Tortoises have organs of touch beneath their large horny shields; are the later therefore ,,Tastschilder"?

The hypothesis of the origin of hairs, mentioned above, seems to be still alive, and I regret having disappointed its adherents by failing to observe nerve-endings in the mysterious filaments of Trichobatrachus. Superior method applied by Professor Kükenthal has revealed their presence.
