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THE CLASSIFICATION OF THE FAMILY DENDRO-COLAPTIDÆ.

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PLATES XI-XII.

In a paper just published in the 'Revista do Museu Paulista,' Vol. IX, 1914, I was able to show that the life histories of the birds composing the several subfamilies of Dendrocolaptidæ exhibit important differences well calculated to aid in the proper systematic arrangement of the various genera. More recently I have studied the craniological characters of the different genera and it is the purpose of the present paper to set forth the results of these studies.

I have already shown that biological conditions in the family Tyrannidæ furnished excellent indications of the proper systematic arrangement of the genera, and lately I have been able to complete my former work especially with regard to the genera *Onychorhynchus* and *Myiobius*. My investigations inspire my admiration for the accuracy of the systematic arrangement proposed by R. Ridgway who on morphological characters has already divided the genus *Myiobius* exactly in the same manner as my observations on the nidification of the species demand.

I am of the opinion that the family Dendrocolaptidæ of Sclater is also in need of further study and in this connection biological THE AUK, VOL. XXXII.



observations furnish valuable hints on the systematic arrangement of the genera. According to their manner of life these birds form three natural groups. Those allied to *Furnarius* are inhabitants of the open country and low lands. They construct their nests in the ground with subterranean burrows leading to them, sometimes of considerable length. The custom of the Ovenbirds of constructing their nests in trees is evidently a secondary adaptation and the material employed in their construction — mud indicates that their ancestors nested in the ground.

The second group contains the genus *Synallaxis* and related forms. They live like many other small birds upon trees and bushes and construct big dome-shaped nests, either of grass, moss and other soft materials or of sticks.

The birds of the last section comprising the Dendrocolaptinæ, and part of the Philydorinæ, live in the forest like the woodpeckers and nest in holes in trees.

The eggs of all the members of the family are white or whitish green except in a few genera of Synallaxinæ in which they assume a uniform blue-green coloration.

If we compare the above facts with the classification given by Sclater in the 'Catalogue of Birds of the British Museum' we find a general correspondence and are inclined to adopt his subfamilies with some modification. The removal of the genus *Anumbius* from the Synallaxinæ cannot be approved. The Philydorinæ with the exception of a few genera approach the Dendrocolaptinæ but are easily distinguished by morphological characters.

Radically opposed to our views, however, is the classification adopted by Ridgway in his admirable work 'The Birds of North and Middle America,' Vol. V, where the birds under consideration are distributed in two distinct families,— Furnariidæ and Dendrocolaptidæ. The reason for distinguishing two families is stated to rest chiefly on differences in the structure of the skull. I have studied the skulls of a great number of genera and shall explain the results of my researches.

In accordance with Garrod, Beddard and other authors, Ridgway places the genera with a holorhinal skull in the family Dendrocolaptidæ, and those with a schizorhinal skull in the Furnariidæ. In the latter group the osseous nostril reaches the posterior end of the premaxilla or passes above it, but does not extend to this point in the holorhinal skull. It must however be observed that the term schizorhinal cannot properly be applied to the members of the Furnariidæ because the posterior end of the nostril does not end in a gap but has always a rounded extremity. For this very reason Fürbringer rejects the term schizorhinal in this connection, substituting for it the new term pseudo-schizorhinal, and adds that both terms probably only refer to different modifications of the same anatomical condition.

We shall see this opinion amply confirmed by my studies.

The Synallaxinæ are without exception schizorhinal as are also the Furnariinæ, although *Geobates* has the nasal foramen somewhat shortened, its posterior end being situated somewhat before that of the intermaxillary.

Pronounced holorhiny is found only among the Dendrocolaptinæ of which, however, some genera — Sittasomus, Dendrocincla and probably others — are typically schizorhinal.

The Philydorinæ (*Philydor, Xenicopsis, Xenops, etc.*) form a transition group leading up to the Dendrocolaptinæ and the species are schizorhinal with the exception of *Automolus* and *Anabazenops* which have the nasal foramen shortened.

When we seek to explain the phylogenetic developments here set forth, it is evident that the forms which present the greatest modification are the Dendrocolaptinæ, which are completely adapted for climbing after the manner of the Woodpeckers. The extraordinarily lengthened exterior rectrices and the protruding shaft points are peculiarities which characterize them as terminal members of a developmental series issuing from the Philydorinæ.

We are able to distinguish among the Dendrocolaptinæ two groups of genera. One of these, beginning with the schizorhinal genera, Sittasomus and Dendrocincla leads by way of Dendroplex, to Dendrocolaptes and Xiphocolaptes the most powerful forms of the family with the heaviest beaks. The other group beginning with Picolaptes leads to forms with extremely long, curved beaks such as Nasica and Campylorhynchus. Xiphocolaptes as well as Drymornis, Nasica, etc., are extremely modified members of the family, of considerable size, and their peculiarities can be easily explained by comparison with the structure of the smaller, less specialized, forms. Corresponding with the two groups above indicated we find modifications in the structure of the skull. In both series the strongly modified forms have the frontal bone exceedingly large and the nasal foramen relatively small — the extreme reduction being reached in *Campylorhynchus* and allied genera. By this means the basal bridge between the nostril and frontal bone becomes extraordinarily large and strong, an adaptation corresponding to the increased demand in these birds for strength and resistance at the base of the beak. While the precursors of *Picolaptes* seem to be extinct the line of evolution originating from *Sittasomus* is nearly uninterrupted. The skull of *Sittasomus* differs but little from that of *Automolus* and to this the skull of *Sclerurus*, seems closely related.

With regard to skull structure the Synallaxinæ may be considered as a more or less uniform group in which the genera *Thripophaga* and *Phacellodomus* are somewhat differentiated by the strongly convex base of the beak, prolonged posteriorly in two divergent ridges, surrounding a deep pit.

A peculiarity of the species of Synallaxis and Septornis is the large, deep median furrow of the frontal bone with a corresponding projecting ridge on the inner side of the skull. There is also a deep pit at the posterior end of the intermaxillary near the anterior end of the frontal. We meet with the same conformation in Lochmias nematura where the lateral parts of the frontal bone are extraordinarily convex and separated by a deep median furrow. Cinclodes presents the same condition while Upucerthia differs somewhat in the more projecting nasals which surround the posterior part of the intermaxillary. The skull of Upucerthia resembles that of Thripophaga and Phacellodomus while Lochmias agrees with Synallaxis.

Of the subfamilies of the Dendrocolaptidæ proposed by Sclater the least natural one seems to be the Furnariinæ.

There are in general no great differences between the skulls of *Furnarius* and *Synallaxis*. In the former, however, the frontal fontanelle, so well marked in *Synallaxis* is absent, while the frontal bone in *Synallaxis* and allied genera is much narrower than in *Furnarius*. Anumbius agrees in cranial characters with *Synallaxis*; and *Pseudoseisura* with *Phacellodomus*. If, therefore, we place *Lochmias* in the Synallaxinæ on the basis of skull structure





we should be able to find other characters to support our action and these, I believe, exist.

The true Furnariinæ have the tail truncated while in the genera Lochmias, Upucerthia and other Cinclodinæ the exterior rectrices are successively shortened. If we consider that this latter condition prevails in general throughout the Dendrocolaptidæ we must realize that the tail structure in the true Furnariinæ is quite a remarkable peculiarity.

The Furnariinæ have probably originated through localization in the vast prairies of the La Plata states and the adjacent parts of Brazil and Bolivia, while the origin of the Cinclodinæ has been in Patagonia and the Andes.

It is not easy to trace the lines of dispersal which have brought about the present distribution of the South American Dendrocolaptidæ but some light is thrown upon the matter by the study of ornithological literature. Of special interest in this connection is the history of *Furnarius*, the Ovenbird, one of the characteristic species of the central Brazilian and Argentine fauna which seems to be still extending its range. When Natterer in the years 1818– 1823 explored the state of São Paulo, he did not meet with it although at the present time it is common in the valley of the Parahyba river and appeared some fifteen years ago at Campinas where it nests.

We may also infer that the genus *Cinclodes* in eastern Brazil is a relatively recent immigrant, as also the few species of Pteroptochidæ, a family of Patagonian-Andean origin.

Of several genera of the Dendrocolaptidæ the skull is unknown to me, such as *Margarornis* and *Glyphorhynchus*, so that I cannot form an opinion upon their relationships from cranial characters. It is not, however, my intention to propose here a new system of classification for the family, my aim being rather to furnish new facts based upon biological and anatomical observations which may eventually be of value in the construction of such a system.

As in the Furnariinæ two lines of development have been demonstrated we can presume that the Dendrocolaptinæ sprang from two different groups of the Philydorinæ. Probably the case is more or less the same with respect to the somewhat aberrant genera Sclerurus, Glyphorhynchus and Margarornis. It follows therefore, as already suggested by Fürbringer (p. 1419), that the supposed difference between pseudoschizorhinal and holorhinal skulls in the Dendrocolaptidæ does not exist in fact, but that they are modifications of little importance which serve only in a limited degree in the characterization of genera, and not at all in the differentiation of families.

Most families which are related to the Dendrocolaptidæ have the skull holorhinal. We find in them, however, similar modifications to those existing in the Dendrocolaptidæ. For example in the Formicariidæ some species of Myrmotherula and Drymophila show prolongation of the narrow posterior portion of the nasal foramen almost up to the intermaxillary and it is probable that further studies based upon richer material will demonstrate that among the Formicariidæ too there are species with pseudoschizorhinal as well as holorhinal skulls. Of greater importance however is the modification in the bony nostril of the Formicariidæ. In Batara cinerea (Plate XII, figs. 3-4) it is closed for nearly its entire length (14 mm.) by a thin vertical osseous membrane, the anterior portion of which is perforated by a nostril 4 mm. in diameter, while the posterior part contains a second nostril communicating with the buccal cavity. I have found the same structure in Thamnophilus and Conopophaga lineata, the aspect of the several skulls being quite different but the structure essentially the same, except for the fact that the membrane of the nasal cavity remains soft in some and becomes ossified in others.

This style of skull structure in which instead of one large bony nostril we have two, a posterior and anterior one, I propose to call *amphirhinal*.

In the Dendrocolaptidæ, therefore, while the type of structure is always the same and there are no essential anatomical differences, the dimensions and proportions of the different bones and foramina vary to a degree rarely found in one family. The enormous variation in the form of the beak is seen in such genera as *Xenops*, *Synnallaxis*, *Philydor* and *Campylorhamphus*. In connection with the differences in form we find variation in the condition of the nostrils which are in some genera holorhinal, in others pseudoschizorhinal. The base of the beak is also differentiated variously, sometimes provided with an intermaxillary frontal fontanelle, sometimes not; while between the two parietal bones in some Vol. XXXII 1915

genera a profound median sulcus is developed. The configuration of the skull depends in a great measure upon the breadth of the interorbital part of the frontal bone and the proportion of this to the greatest breadth of the skull (considered as 100) varies from 16 to 50, the absolute measure being in *Synallaxis spixi* 2.4:14.3 mm. and in *Campylorhamphus trochilirostris* 8.8:17.2 mm. As already suggested by Fürbringer the study of the variations in the nostrils of the Dendrocolaptidæ has shown that this is a character of secondary value.

The importance which is given in ornithological literature to such terms as holorhinal and schizognathous represents an inheritance from the past century. When Huxley in 1867 published his classic treatise on the classification of birds it seemed as if the skull was to attain the same importance in the classification of birds as it had already reached in the mammalian system.

Six years later Garrod gave to the structure of the nostrils the same importance in avian classification as Huxley had given to the palate structure. And now we ask what is the situation to-day?

The results set forth in this paper with reference to the schizorhiny of the Dendrocolaptidæ confirm the opinion of Fürbringer as stated above; who also (l. c. p. 1034) rejects Huxley's groups based on palate structure. Beddard (l. c. p. 140) also points out that the maxillo-palatine classification is not really satisfactory from a systematic point of view and adds that it is rendered harmless by the fact that the groups are really not as hard and fast as might be supposed from text books in general.

In this, however, I cannot agree with Beddard as generalizations of this sort, rejected by the most competent morphologists, often persist with tenacity in our systematic literature and in many instances hinder the zoölogist from following his own inclination. If in studying any family in the zoölogical system we take one anatomical character as a basis for the arrangement of the genera or species we construct a system which is entirely changed if we make use of some other character. Skull or pelvis, sternum or syrinx, pterylosis or muscles — in nearly every case we obtain a different arrangement.

The result of the exclusive application of certain anatomical characters is seen in Garrod's classification of the Psittaci, which has been accepted by Beddard, in which the South American Conurinæ are distributed in three different subfamilies, the Arainæ, Pyrrhurinæ and Platycercinæ!

The same process of development of a certain organ is repeated many times independently in different subfamilies and genera and therefore can be applied only to a limited extent in classification.

No single organ is of such importance that we can attribute to it absolute preference and it is never possible to determine à priori whether this or that character will be of most importance in systematic work. It happens sometimes that a relatively insignificant character will prove of great value, as for example the loss of a remex, which serves as a distinction between the large groups of quincubital and aquincubital birds. The quincubital condition is the archaic one and the loss of the fifth remex although representing a higher phylogenetic degree, must be considered as a process of degeneration, for which it would be stupid to make natural selection responsible.

What we learn from ornithological studies is that the wide range of variation which leads, or can lead to the origin of new groups, is on the definite lines of evolution which influence also the less important characters but which do not raise any question of survival since both the primitive and modified types succeed equally well in the struggle for existence.

In more than forty years of uninterrupted biological research I have been unable to discover any facts among free living animals which tend to prove the existence of natural selection, or even to elevate it to the rank of an indispensable or necessary factor in the origin of species. So long as we do not have at our disposal a complete series of morphological and paleontological observations, which would furnish a systematic arrangement of genera on the ground of actual phylogenetic experience, our classifications are more or less a question of our ability to accurately judge the importance of morphological characters for systematic use. Barriers erected by anatomists, however celebrated, during the past three decades should no longer be allowed to present difficulties in our ornithological work.

From the preceding discussion I reach the following conclusions.

1. The assumed difference between schizorhinal and holorhinal skulls does not exist in the Dendrocolaptidæ. The species in which

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the nasal foramen is prolonged posteriorly present only a modification of the common holorhinal type, and this condition should be named pseudoschizorhinal according to Fürbringer.

The variations in the palatine structure, moreover, are of no more importance than those of the nasal foramen.

2. The family Dendrocolaptidæ is an entirely uniform and natural one and there are no sufficient reasons for its subdivision into two families.

3. The morphological and biological characters to which I have alluded offer useful data for the systematic disposition of the subfamilies and genera of the Dendrocolaptidæ.

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EXPLANATION OF PLATES.

PLATE XI.

- FIG. 1. Sittasomus sylviellus (Temm.). $\times 2$.
- FIG. 2. Anabazenops fuscus Vieill. $\times 2$.
- FIG. 3. Dendroplex picus (Gm.). $\times 2$.
- FIG. 4. Synallaxis spixi Scl. Nat. size.

PLATE XII.

FIG. 1. Synallaxis spixi Scl. Nat. size.

FIG. 2. Picolaptes falcinellus (Cab. & Heine). $\times 2$.

FIGS. 3 & 4. Batara cinerea (Vieill.). Nat. size.

N = nostril, A = anterior, P = posterior.

F.F. = frontal fontanelle.

I.O. = interorbital part of frontal bone.