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THE BIOLOGY OF THE TYRANNIDÆ WITH
RESPECT TO THEIR SYSTEMATIC
ARRANGEMENT.

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THE systematic arrangement of animals is usually based on morphological characters only, but biological observations may often give us precious hints which may help us to settle difficult questions in this respect. Considering that the present systematic arrangement of the genera belonging to the great family of Tyrannidæ is far from being a satisfactory one, I have thought it useful to study in a comparative way the biology of the members of this family.

Of the four subfamilies accepted according to the classification of Mr. Sclater, at least one seems to be unnatural as well as regards morphological as biological characters; that is to say, the *Platyrrhynchinæ*.

In my paper on eggs and nests of Brazilian birds (*Revista do Museu Paulista*, IV, 1899, p. 226) I described the nest and eggs of *Platyrrhynchus mystaceus* and expressed my surprise at their great difference when compared with the nests and eggs of the allied genera. Having obtained this year an authentic nest of this species I am able to state that as regards the first described nest there was a mistake. The nest of the above mentioned species of *Platyrrhynchus*, which will be fully described in Vol. V of the

'Revista do Museu Paulista,' is purse-shaped and suspended at the extremity of a branch. It has a round opening in the middle protected by a shelter above. I have quite similar nests of *Todirostrum cinereum*, *Orchilus auricularis*, *Hemitriccus diops*, and of different species of *Euscarthmus*. The same form of nest is, therefore, common to the genera *Platyrhynchus*, *Todirostrum*, *Euscarthmus* and *Orchilus*. Moreover, the eggs of the members of all these genera are yellowish white or brownish with very fine points on the larger end.

On the other hand the nests of *Serphophaga* are placed among the diverging boughs of a branch and are cup-shaped, while the eggs are of a uniform yellowish white. Of the same type are the nests and eggs of *Anæretes* and *Hapalocercus*. The nest of *Phylloscartes ventralis*, however, as Mr. Krone assured me, has one wall of the nest elongated above and recurved, forming a somewhat globular, domed structure.

A form of nest like that of *Serphophaga* is found in the genera *Elainea* and *Phyllomyias*, and in other Elaineinæ, among which, however, occurs also a second form of nest. This form is illustrated by the nest of *Ornithion obsoletum* which I have recently examined. It is of a pear-shaped form, similar to that of *Euscarthmus*, but not suspended from the top of a twig but fixed at different points on the branches.

Euler has described the nest of this species differently, but the nest observed by him, which was much hidden between masses of *Tillandsia*, was not probably of a normal form. Besides, *O. obsoletum* does not occur in Rio de Janeiro and Bahia, where the species is represented by *O. cinerascens* (Wied), which, in opposition to Mr. Allen, I do not doubt is identical with *O. imberbe* Scl. A similar nest is built by *Mionectes rufiventris* (Licht.), as has been observed by Mr. Krone.

The nest of *Ornithion* forms the transition between that of *Serphophaga* and that of *Euscarthmus*. We may be justified to assume that such an artificial and wonderful construction as the nest of *Euscarthmus* is not the work of free invention but is to be considered as the result of development from a previous form of nest. We have but to suppose the nest of *Ornithion*, instead of being fixed on various branches successively, to be placed on one

branch only and we have the suspended nest of *Euscarthmus*. A very remarkable form of suspended nest among the Tyrannidæ occurs in the genus *Rhynchocyclus*, but I believe it to be nothing more than an extreme modification of the Euscarthmine nest type. In this respect it is remarkable that the much bristled and flattened bill of *Rhynchocyclus* is very like that of *Platyrhynchus*, and quite different from that of the typical *Elainææ*.

Although the predominant form of nest among the Tyrannidæ is certainly the cup-shaped one, we meet also with very different structures in this family. Covered nests occur in the genera *Phylloscartes*, *Arundinicola*, *Pitangus*, and *Myiozetetes*, leading us on to the nest of *Ornithion* above described, and to the suspended nests of *Euscarthmus* and *Rhynchocyclus*. According to Euler *Myiobius barbatus* has a suspended, purse-shaped nest, while the nest of *Myiobius nævius* is cup-shaped, but is fixed suspended within the fork of two diverging branches in the manner typical of the nests of *Thamnophilus* and other Formicariidæ. On the other hand we find nests of very slight structure made of a small number of slender sticks and roots in the genera *Tyrannus*, *Empidonomus*, *Myiodynastes*, *Megarhynchus*, and others. These nests are extremely flat and apparently not well suited to retain the eggs in safety.

Among the Tæniopterinæ, inhabitants of the open plains, there are species which breed in holes in banks, as is said to be the case in Argentina with *Tænioptera nengeta* by Mr. Hudson, while in Brazil this species builds its nest on trees. The species of *Copurus* and *Machetornis* breed in holes of trees, as also does *Tænioptera irupero*. The last-named species likes to appropriate the large covered mud-nests of *Furnarius*, and *Machetornis* prefers the large thorny nests of *Anumbius*. Thus we see among the Tyrannidæ the most different forms of nest structures represented.

In general the nests of species that inhabit the woods are well built, and covered carefully with dry plant material in order to be well hidden. Some of them, such as that of *Elainea*, are true masterpieces of art, being generally ornamented externally with pieces of lichen carefully fixed on by spiders' webs. On the other hand, the Tæniopterinæ and Tyrannidæ, inhabitants of the pampas and campos, contrary to what would be expected, take little

care to hide their nests. Everyone would suppose that these birds should prefer to build their nests under cover of the grass and form simple structures of dried grass, as do the species of *Sycalis*, *Ammodromus*, *Embernagra*, *Emberizoides* and other Fringillidæ of the campos. Except, however, in the genus *Alectrurus*, I do not know any other example among the Tyrannidæ of this form of nesting. In general these birds are not very careful to hide their nests. On the contrary the large species of Tyranninæ, and the species of the allied genera *Myiozetetes* and *Pitangus*, seem to prefer to place their nests on isolated trees, as much exposed as possible. This custom corresponds well with the bold characters of these birds.

Taking a general view of the eggs of Tyrannidæ, we find a uniformity in coloration which is in strong contrast to the variety of forms of their nests. The eggs in this family, as a rule, are white or cream-white with reddish brown spots at the larger end. These spots are small and pointed in the Euscarthminæ, while they are obsolete in the buff eggs of the Serphophaginæ. The occurrence of pure white eggs is limited to the genera *Copurus*, *Arundinicola*, and a few others. In the genus *Muscivora* the ground color is somewhat dark brownish. The eggs of the genus *Myiarchus* are remarkable for the elongated form of the numerous red-brown spots.

If we compare the color of the eggs with the mode of construction of the nests no pronounced correlation is to be found. Uniformly white or cream-colored eggs exist in the genera *Copurus* and *Arundinicola*, which are deposited in covered nests, while the similar eggs of the Serphophaginæ are laid in open nests. The eggs of the Euscarthminæ, though deposited in closed nests are adorned with numerous red spots, while those of *Myiozetetes* and *Pitangus*, which are laid in closed and domed-shaped nests, have the same large, reddish brown spots as those of the genera *Tyrannus*, *Mitvulus*, and others, the nests of which are wholly open. Similar cases prevail in the eggs of other South American birds. In this respect the example of the American Gallinæ is instructive, for while as regards the careless construction of the nest no difference is noticeable, the eggs of the Brazilian representatives of the Gallinæ are white, while those of the Crypturi are distin-

guished by the most brilliant colors of brown, red, blue, and green. It is true that the Pici, Psittaci, and other birds that lay their eggs in hollow trees, all have white eggs, but eggs of the same color are found also in the open nests of the Trochilidæ and of the Columbæ. Returning to the Tyrannidæ we find the egg of *Machetornis rixosa* wholly different from those of the true Tæniopterina, and resembling in its numerous, large, somewhat elongated brownish spots the eggs of the genera *Empidonomus* and *Myiarchus*, especially those of the latter. These facts throw doubt on the correctness of the generally accepted systematic position of *Machetornis*. So far as regards the egg of *Tyrannus aurantioatrontatus* Lafr. & D'Orb., it belongs to the genus *Tyrannus* and not to *Empidonomus*.

These differences, therefore, cannot be explained by the so-called law of 'natural selection,' but bear relations to the genetic affinities and the inner movements which, independently of the supposed 'natural selection,' determined the individual variation as well as the phylogenetic development of the organisms.

After what I have stated it is evident that the systematic arrangement of the Tyrannidæ in its present form can only be considered as provisional, and it may be well altered when a general anatomical study of the whole group has been made. At present the systematic sections are only based on a restricted number of external characters, principally on the form of the tarsi, feet and bills. These characters are in intimate connection with the manner of life. In this way we are exposed to the danger of confounding essential typical characters with adaptive ones. I think that such a mistake took place on the occasion of the formation of the subfamily Tæniopterina. This section embraces forms with strong feet, strong and elongated tarsi, and slender elongated bills, characters which seem to result from the life on the ground on the pampas and campos, which these birds inhabit.

In general this subfamily may be considered a very natural one. The predominant colors of the species are gray, white, and black. These colors are not common in the family Tyrannidæ as a whole, and they are evidently to be considered as being acquired characters and not of a phylogenetic value. This is proved by

the fact that in the species of *Cnipolegus*, *Lichenops*, and others in which the males are wholly black, the females and young are of a brownish color or have a spotted plumage. Among the more or less similar members usually placed in this subfamily two monotypic genera are completely different in their coloration, namely, *Sisopygis* and *Machetornis*, which in my opinion do not belong to this subfamily, but to the Elaineinæ. *Machetornis* seems to me to be allied to *Pitangus*, and *Sisopygis* to *Mionectes*, *Capsiempis*, and similar genera. While *Machetornis*, at least in its mode of life, resembles the Tæniopterinæ, *Sisopygis* inhabits the woods like the Elaineinæ.

That the Platyrhynchinæ really consist of two different subfamilies, Euscarthminæ and Serphophaginæ, we have shown above. With the biological differences correspond such important morphological ones, principally those of the form of the bill, that the separation here proposed will probably be accepted as being naturally founded.

In order to obtain a natural classification of the Tyrannidæ it is necessary to get an idea of the phylogenetic development of the family. In this respect the Tyranninæ, judging from their large dimensions and their large, somewhat depressed bills, do not represent the original form, but, as I think, an extreme branch of the family. Other specialized branches are found in the Euscarthminæ and Tæniopterinæ. The latter offer not only a coloring somewhat uncommon in this family, but also cases of decided sexual dimorphism, which evidently represents a specialization acquired within the subfamily.

Excluding from the Elaineinæ the Pitanginæ — large birds with strong bills that biologically much approximate to true Tyranninæ — the Elaineinæ evidently represent the group most nearly allied to the ancestors of the Tyrannidæ. These forms are also those which have the nearest relations with the Pipridæ. Strongly developed syndactylism, which is one of the characters distinguishing the latter, is also very remarkable in many genera of the Elaineinæ, as for example in the genus *Tyranniscus*.

Among the Pipridæ the same fact is observable as in the Tyrannidæ, namely, that sexual dimorphism in coloration exists only in the more highly organized forms. In the subfamily of Piprinæ

the very striking and beautiful coloration is found only in the adult males, while the females and young males retain uniform olive colors, and it is also only among the adult males that we meet with such abnormal characters as enlarged stems of the primaries and secondaries, erect frontal feathers, and elongated tail-feathers, while the Ptilochlorinæ resemble the Elaineinæ not only in coloration, but also in the rather small and bristled bill. These facts induce us to conclude that the Pipridæ and Tyrannidæ have descended from a common ancestral form, the nearest relatives of which are the Elaineinæ among the Tyrannidæ with the Ptilochlorinæ among the Pipridæ. The common ancestors must have been birds of small size, with pronounced syndactylism of the outer toes, with rather small, somewhat compressed and bristled bill, and of uniform olive color. The frequent occurrence of a yellow coronal patch among the Pipridæ as well as the Tyrannidæ leads us to suppose that this ornament may have been transferred from the common ancestors, which were inhabitants of the woods. From the Elaineine branch of the Tyrannidæ originated, besides the Euscarthminæ and Serphophaginæ, whose biological conditions are nearly the same, two great sections of inhabitants of the campos, mostly large-sized birds, the Tæniopterinæ and the Pitangine-Tyranninæ.

With these general results the geographical distribution accords. As is generally the case with the wood-inhabiting birds, the distribution of the Elaineinæ of Brazil is a somewhat restricted one. While a number of species are distributed through the forest region of Brasil, only a few range through Guiana and Central America to Mexico. The Euscarthminæ in this respect also do not diverge much from the Elaineinæ, but the Serphophaginae, preferring open plains and river banks, do occur not only in the campos but the majority of them is restricted to the Andine Region. These two groups of campos inhabiting Tyrannidæ are wholly different not only in their way of life but also in their geographical distribution.

The habits of the Tæniopterinæ are terrestrial. They run on the ground and have in relation therewith elongated tarsi and strong ambulatorial feet, seeking their insect food on the ground. They inhabit the pampas and the campos of central Brazil, being

represented in the littoral zone by but few species. On the other hand, many species and genera are adapted to live in the Andes, where they occur from Patagonia to Colombia, but no species of these Andine forms passes into Mexico and Texas. For this reason I think it to be right to separate the genus *Sayornis* from the Tæniopterinae, and to unite it to the Tyranninae, in the society of which it is found in North America and from which it does not differ regarding its biology.

The Pitanginae and Tyranninae, on the contrary, are of very wide geographical distribution. Though preferring the campos, they avoid the treeless plains. They are not ground-walkers, but capture insects as they fly like Flycatchers. They are very active, courageous birds of large size and good flight, and their geographical distribution therefore, as a rule, is very wide, some of them occurring from Argentina to North America. Among the seventy-eight species of Tyrannidæ living in the State of S. Paulo forty-three belong to the Elaineinae and the allied groups of arboreal life, and of these ten, or 23 per cent, have a relatively wide geographical distribution. Among the six Pitanginae only the two species of *Conopias* and *Sirystes* are restricted to Brazil, while the species of *Legatus*, *Myiozetetes*, *Pitangus*, and *Myiodynastes* are represented even in the southern parts of North America by the same species or by little different local races. Among the sixteen Tyranninae of S. Paulo all have a very extensive geographical distribution except *Blacicus cinereus* (Spix) and *Tyrannus albigularis* Burm., so that more than 80 per cent of the Pitanginae and Tyranninae of S. Paulo have very wide geographical distribution.

These facts of geographical distribution show us that the only system of nomenclature well applicable to the discussion of zoogeographical problems is the trinomial.

The use of binomials as employed in the excellent Hand-list of Dr. Bowdler Sharpe may be more advantageous for collection purposes, but it combines in a very inconvenient manner well-defined species with local races. Such facts as the vast distribution of *Pitangus sulphuratus* (L.) and *Myiozetetes similis* (Spix) are completely hidden by the use of binomial nomenclature.

It is also among these birds that we meet true migratory forms,

so far as such exist among the Tyrannidæ. This fact is in intimate relation with the special biological conditions of the campos. No migratory birds at all exist among the wood-inhabiting Tyrannidæ, nor among the Pipridæ, Formicariidæ and other families of the forests.

True migratory birds are scarcely represented in South America and are essentially restricted to two families of insectivorous birds, the Hirundinidæ and the Tyrannidæ. In South Brazil, from Rio Grande to S. Paulo, I have observed migratory habits in the following species:—

Myiodynastes solitarius (Vieill.). *Tyrannus melancholicus* Vieill.
Pyrocephalus rubineus (Bodd.). *Muscivora tyrannus* (L.).

As I am preparing a paper on this subject to be published in 'Aquila' I will not discuss it in the present paper. It is evident, however, from the preceding deductions, that in biological respects the family of Tyrannidæ is one of the most interesting of the Neotropical Avifauna, strongly contrasting with the uniformity which in this regard prevails in most of the other characteristic families.

Although the object of this essay was only to refer to some general biological features and habits common to certain subfamilies I nevertheless think it useful to give briefly the results of my observations, as they may be of service to a subsequent worker who will undertake the necessary systematic revision of the family Tyrannidæ. They are as follows:

(1) The Tæniopterinæ represent a very natural systematic group but as usually arranged include some strange elements, such as *Sayornis*, *Sisopygis*, and probably *Machetornis*, which should be removed to other subfamilies.

(2) The Platyrhynchinæ of the systematic arrangement of Mr. Sclater contain two quite different sections, the Euscarthminæ and the Serphophaginæ.

(3) The Elaineinæ contain some aberrant forms which should be removed to other subfamilies. For example, the genus *Rhynchocyclus* should go to the Euscarthminæ, and the genera *Legatus*, *Myiozetetes*, *Conopias*, *Pitangus*, *Sirystes* and *Myiodynastes* should form a subfamily, Pitanginæ, a section which biologically is inti-

mately related to the Tyranninæ, while morphologically it is intermediate between the latter and the Elaineinæ.

(4) The Tyranninæ form a natural section with which perhaps the Pitanginæ should be united.

S. Paulo, Brazil, 9 Nov., 1903.

A DISCUSSION OF THE ORIGIN OF MIGRATION.

BY P. A. TAVERNER.

ONE of the first, if not the very first, phenomena of animate nature to be noticed by primeval man, must have been that of migration; and from that day to this it has been, to a greater or less extent, a subject of great interest to students. In the present day it has been approached from many different sides, and though many points have been pretty well cleared up, others are still enveloped in a haze through which the fundamental principles are but barely visible, while others still remain shrouded in a dense, impenetrable cloud of mystery.

The methods by which birds find their way to far distant points, the manner of their migrations, etc., lie without the scope of this paper, and will not be referred to here. Upon these points we all await the publication of the results of the investigations now in progress, when probably many obscure points will be cleared up.

Migration consists of two movements, one in the spring, away from the winter station; and the other in the fall, towards it again. The reason of the latter is self-evident. There is a lack of food. If they did not return in the fall they would perish of hunger, if not of cold. From general observations, it seems as if the former had a larger influence than the latter, and it is the northward movement that needs explanation. Why should a bird leave a warm land of plenty to journey to a country but half recovered from the frozen embraces of an arctic climate? It seems