# THE AUK

A QUARTERLY JOURNAL OF

ORNITHOLOGY

VOL. 76 JULY, 1959 NO. 3

## THE STATUS OF AVIAN SYSTEMATICS AND ITS UNSOLVED PROBLEMS*

BY ERWIN STRESEMANN

BIOLOGISTS all over the world have devoted the year 1958 to the memories of Darwin and Wallace. We ornithologists also should call to our attention the powerful impetus which we have received from the intellectual work of these great men, to whom we owe a better understanding of the origin of the great diversity among birds. Two factors are responsible, according to Darwin's theory, for the ever greater perfection of the living world: variation and selection. I suggest that these same factors are of major importance in the interplay of ideas and concepts. Permanent advances in our scientific understanding we owe likewise to variation and selection.

Variation is the consequence of the individuality of those who work on the same topic. Zoologists differ in their philosophical background, in the extent of their knowledge, in their thoroughness, and in their gift of combination. This variability is certainly displayed to a high degree by the avian systematists. What Max Fürbringer has written about them, will forever remain true: "At various times a few fortunate individuals have existed who were gifted with such an acute insight that it revealed to them intuitively, one might almost say instinctively, this or that systematic relation among related forms without the necessity of laborious investigation." At the other extreme there have been some poor devils who did wrong whatever they did and who were completely lost without methodology.

Survival of the fittest will decide which of the many competing theories will prevail. Only one can finally survive. Each revisor attempts to shorten the struggle by acting as a selective factor. When

* This paper was delivered in essence at the Seventy-fifth Anniversary Meeting of the American Ornithologists' Union on October 16, 1958, in New York, during the Symposium on Contemporary Problems in Ornithology. Participation of Dr. Stresemann was made possible by a grant from the National Science Foundation, which the American Ornithologists' Union gratefully acknowledges.

he has to synthesize a modern system of birds he is forced to choose a single one among many conflicting theories, often without having the opportunity of examining thoroughly the arguments of the different authors. I myself have painfully experienced the feelings of a taxonomic compiler, for I developed (1934) an eclectic system of bird classification some 25 years ago. While doing so, I made a few mistakes, as I now realize. Has not the experience of others been the same? On the whole all the avian systems presented in the standard works in this century are similar to each other, since they are all based on Fürbringer and Gadow. My system of 1934 does not differ in essence from those which Wetmore (1951) and Mayr and Amadon (1951) have recommended.

The most obvious differences between the several recent classifications are in the delimitation of the higher categories. Wetmore arranges them in 27 orders, Mayr and Amadon in 28 orders, while I recognized 49 orders (1933–34: 738–853). In other words: I preferred to leave the question of phylogenetic relationship open in many more cases than the authors of the other two systems. Today I would recognize 51 orders (see Appendix).

An answer has tentatively been given now to some of the questions of relationship which I had considered as unsolved; others which seemed to be solved at that time have meanwhile been reopened for discussion. The outsider who reads some of the recent critical discussions may easily get the impression that our conventional system is full of errors. It seems to me, however, that one must apply to many of the newer proposals the same evaluation which was made by Alfred Newton in 1893, who wrote: "Some of the later attempts to systematic arrangement are in my opinion among the most fallacious, and a good deal worse than those they are intented to supersede."

A considerable part of these objections are due to efforts to create an avian system which specifies with great precision the degree of phylogenetic relationship of all groups. The construction of phylogenetic trees has opened the door to a wave of uninhibited speculation. Everybody may form his own opinion on the phylogeny of the higher categories of birds, because, as far as birds are concerned, there is virtually no paleontological documentation which has revealed such important information on the phylogeny as has been the case with the other classes of vertebrates. The investigator of avian phylogeny must rely on indirect clues, which are nearly always ambiguous. It is for this reason that Seebohm (1890) recommended to the systematists to ignore phylogenetic endeavors by the following sentence: "The classification of existing birds is the study of a horizontal section of

the great bird mass of the world, and ought to form a different and distinct system confined to the horizon of the present time." To be honest, we must admit that we mix the horizontal and the vertical system to this very day. It is a concession to the "horizontal section" if, for instance, in a much used contemporary system the "true birds" are divided into two superorders—the Impennes or Penguins and the Neognathae or Typical birds—because the author has surely not doubted the close relationship between penguins and Procellariiformes and has surely known Simpson's (1946) important conclusions. Yet, in the same system, an attempt is made to group the "Typical birds" according to the vertical principle; that is, not according to their apparent similarity or difference but according to their presumable phylogenetic relationship. For this reason the author follows McDowell (1948) by dropping the former distinction between Palaeognathae and Neognathae.

Max Fürbringer, with his incomparable practical experience, has frankly admitted that the decision in questions of relationship is very often based on rather subjective considerations. Some of the more recent revisors do not display a similarly wise modesty. Verheyen (1958b) makes the proud assertion: "in contradistinction to the conventional classifications we will introduce rational classification," which is based on the totality of as many individual characters as possible. This total sum of characters Verheyen calls the "morphological potential." After equating the morphological potential for a given group of birds with 100, he compares it with the morphological potential of other groups of birds, then calculates the percentage of agreement, and draws from this his phylogenetic conclusions. In this method arithmetic replaces the role of intuition and of a judgment trained in functional interpretation. Elsewhere Verheyen (1955) states: "A clear, precise and phylogenetically sound classification must be based on characters that are practically invariable and which are essentially immune to the adaptation and modification imposed by the habitat." To this I answer: Taxonomy would be indeed a simple matter if such "practically invariable characters" existed. However, the relentless modifying power of evolution does not spare a single structural element; any change of the well integrated morphological total results either at once or gradually in correlated changes from which neither the skeleton, nor the muscles, nor the external features, nor the behavior remain excepted. Let me give one example: the loss of the power of flight causes not only extensive changes of muscles and bones of the anterior limb and of the shoulder girdle, but it also has effects on the pelvis and the posterior limb, and even on the

feathers of the entire body, which become greatly simplified as shown by the struthious birds, by *Apteryx,* by the Dodo, and by some of the flightless rails.

Verheyen is not an isolated example. Other recent students have believed they have found invariable characters that would show them the way through the labyrinth of avian diversity. Lowe relied on the structure of the skull in his studies of the Charadriiformes, but got badly off the track (Bock, 1958). Beecher (1953) based a new classification of the song birds largely on the jaw muscles. His methods and paradoxical conclusions have likewise received well-merited criticism (Mayr, 1955).

The easiest solution was tried by certain authors who compared the accepted system of birds with the system of their parasites, and who in all cases of conflict considered the parasitological evidence as more decisive than the findings of comparative anatomy. This was done by Timmermann (1957). On the basis of their Mallophaga, he concludes that Rostratula does not belong to the Limicolae (Charadrii) but with the rails, *Phaethon* not to the Steganopodes (Pelecaniformes) but with the Laro-Limicolae (Charadriiformes), and so forth. Such an exaggerated evaluation of the parasitological evidence has had the effect that ornithologists will utilize parasitological information only with the greatest caution. In this conclusion I am in entire agreement with Ernst Mayr (1957). For instance, the fact that the flamingos (*Phoenicopterus*) are parasitized by two genera of Mallophaga which otherwise occur only on Anatidae can by no means be considered as proof for an origin of the flamingos from the Anatidae rather than from the Ciconiiformes. It appears by far more probable, that the Mallophaga have been transferred rather recently from the waterfowl to the flamingos. This is not only the view of the ornithologist Mayr (1957), but also of the mallophagan specialist, Dr. von Kéler (1957). May I refer to still another case. Some taxonomists have recently considered it possible that *Struthio* and *Rhea* might form a phylogenetic group because a genus of bird-lice, *Struthiolipeurus,* has been found on both. Von Kéler, however, informs me that close relationship of the mallophagan species found on *Rhea* with that found on *Struthio* has not yet been proved, for their anatomical investigation is still lacking. He is inclined to believe that the superficial similarity between Mallophaga on these birds is due to convergence caused by the similarity of feather structure.

To give you an idea of the kind of "reforms" of our system which have been proposed for anatomical reasons during the past twenty years

(some even earlier), I shall list only a few, making comparison with the classification of Wetmore.

Miss Cottam (1957) has concluded from a detailed study of the skull of *Balaeniceps* that the Whale-headed Stork belongs to the Pelecaniformes and not to the Ciconiiformes. Some 19th century authors suspected, or claimed, relationship between *Sagittarius* and *Cariama*. In the current systems one finds *Sagittarius* with the hawks, *Cariama* with the cranes and their relatives. Verheyen (1957) has again combined these two genera in a special order Cariamiformes, basing his conclusions on their "morphological potential," which includes the relative length of limb bones.

Wetmore places the Screamers (*Palamedea*) as a suborder of the Anseriformes, with which, according to Verheyen (1953), they have nothing to do. Wetmore has *Opisthocomus* in the order Galliformes, *Musophaga* in the order Cuculiformes. Verheyen (1956) on the other hand combines *Opisthocomus* with the Musophagidae in the order Musiphagiformes. Barnikol (1953) considers *Opisthocomus* a very isolated species, which can be placed neither with the Galli nor with the Musophagidae and represents a separate order Opisthocomae.

Wetmore and all previous authors have placed the Dodo, *Raphus,* together with *Pezophaps,* in a highly specialized family of the Columbiformes. Verheyen (1957a), on the contrary, includes both, together with *Goura* and *Caloenas,* in the Caloenadidae, another family of the pigeons. Quite recently Lüttschwager (1958) has contended that *Raphus* and *Pezophaps* do not belong to the pigeons at all, but rather to the rails, or to a special order related to the rails.

Fürbringer's category of Gruiformes, which Wetmore had accepted essentially without change, has been severely attacked by Verheyen (1957b). He removes from the Gruiformes the Sunbittern (*Eurypyga*) and the Kagu (*Rhynochetos*) and combines them with the Jacanidae in the order Jacaniformes. Wetmore placed the Jacanidae in the Charadriiformes, but Lowe (1931) declared the Jacanidae to be Gruiform. *Thinocorys* has been placed by Verheyen (1958a) as a family with the Pterocletes (sandgrouse). The Pterocletes, combined with the buttonquails (Turnices) and the Mesoenatidae, form Verheyen's new order Turniciformes. According to Lowe (1923, 1924), however, *Thinocorys* is "undoubtedly charadriiform," while the Mesoenatidae represent an entirely isolated group of birds with gruiform similarities, and the Turnices, together with the sandgrouse, belong near the pigeons. The swifts (Apodes) are according to Verheyen (1956a) near to the Caprimulgi, while according to Lowe (1939) they are not at all related

to them. These examples indicate how utterly different the taxonomic conclusions of these two authors are.

Even though this is only a small selection from recent proposals, I fear that the readers are already confused. But they need not feel ashamed of their discomfort. In my opinion only few, if any, of these taxonomic variants will survive the struggle for existence. Most of them will be forgotten within a few years, even though they have been to a large part the result of laborious and conscientious investigations. They have however contributed to one important realization. They have made it apparent that the relationship of certain species or groups of species is far less unequivocably established than one would conclude from a study of currently adopted systems, the authors of which attempt to present a simplified phylogenetic tree of birds. This "attempt to reduce the number of the branches of the phylogenetic tree, to make the ornithic tree simpler, more a noble tree with fewer but more generous branches," as Friedmann (1955) has put it, may have didactic advantages, but does not give a realistic representation of the actual pattern of development. Fürbringer's (1888) attempt at phylogenetic tree construction conveys a more realistic view of actuality. It shows a tall trunk which after sending out a few side branches (the ratites or protocarinates), splits up completely into a dense bush of individual branches. These branches either diverge widely from each other, or else remain closely parallel for longer or shorter stretches. The main branches correspond to the 73 families or family groups accepted by Fürbringer. He attempted to combine these into Gentes, Subordines, Ordines and Subclasses, but emphasized that the difficulties and uncertainties grow with each higher category. Let me quote his own words: "At the present time only very little is completely certain, some is highly probable, the majority of the groupings are however probable only to a medium degree."

The degree of uncertainty has decreased remarkably little since the time when the great anatomist wrote these words—in spite of all the efforts of subsequent authors. The currently adopted systems have eliminated with good reason many of Fürbringer's hypothetical groupings, particularly his Subordines and Ordines, and retained only the Gentes of his system, for which they use the name orders. Wetmore has not been entirely consistent in this, because his orders correspond sometimes to Fürbringer's Subordines, sometimes to his Gentes, which leads to unharmonious results. No doubt Wetmore has been guided by didactic considerations—an endeavor to propose a system that would be convenient for teaching purposes. Lowe (1939) seemed to have had the same objective when he was loath to place the Apodes and

the Trochili into two separate orders. This, he said, "is an easy way of getting out of a difficult situation, but it tells us nothing of their affinities. In effect, it merely tells us that the swifts are swifts and the hummingbirds are hummingbirdlike birds." For this reason Lowe decided to redefine the order Passeriformes and include in it as suborders the Passeres, Cypseli, Trochili and Pici. However this is a rather hypothetical grouping, which has not fully pleased anyone. Personally I prefer a system that is as realistic as possible, a system in which no room is given to phylogenetic speculations, and in which the gaps in our knowledge are frankly admitted. If one follows these guiding principles one is forced to recognize a greater number of the highest categories, that is orders, than accepted by Wetmore—indeed even more than I admitted in 1934. Combining swifts and hummingbirds in the order Macrochires and turacos and cuckoos in the order Cuculi, as I had done following Fürbringer, was insufficiently supported by the evidence and has since been heavily attacked. The new attacks against Wetmore's system are particularly directed against those places where the author adopted as an "order" one of Fürbringer's Subordines, that is a category of "medium probability" and gave it the same rank as one of Fürbringer's Gentes, that is a category of "high probability." It seems to me that the critics would have done a more useful job if they had been satisfied to leave isolated, as groups "incertae sedis," those elements from Wetmore's structure which they removed as incongruous. However, like Lowe, they thought that that would "tell us nothing of their affinities," and thus they have inserted these building stones in a different place, where they fit even less.

To strike a more positive note, I should like to mention some successful attempts to improve the avian system. Many authors have recently studied the question of the evolution of the so-called Ratitae. This was done through ontogenetical investigations by Lutz (1942), McDowell (1948), de Beer (1956), and Charlotte Lang (1956) and through comparative studies of the bony palate by Hofer (1945). All agree in considering, as did Fürbringer, the Ratitae to have originated not from flightless Procarinatae but from flying Protocarinatae. However, while Hofer postulates for all Palaeognathae a common origin from a type not unlike the Tinamids, this is not the case according to McDowell. This author considers the palaeognathic palate to have developed from the neognathic palate, and therefore not to represent a group character of any taxonomic value. He thinks that *Rhea* might have descended from the Tinamids and have acquired by neoteny a simplified palate. The close affinity of *Dinornis* to *Apteryx* on the

other hand, and their great phylogenetic distance from the other ostrich-like birds, has recently been confirmed by Starck (1955) and Charlotte Lang (1956), who studied the endocranium. In most other cases the result of successful attempts has been a clarification on the level of the lower categories of the rank of family, subfamily, or genus. Owing to convergent evolution, similarities may develop between unrelated lines which can deceive sytematists into assuming a phylogenetic relationship. Such errors can only be uncovered by thorough anatomical investigation. By this method it has been shown by Stolpe (1935) that the similarity between grebes and loons is due to convergence, a similarity which had been interpreted by Fürbringer as a manifestation of phylogenetic relationship. Amadon (1951) succeeded, through a study of the syrinx, in unmasking the Madagascar genus *Neodrepanis* (in spite of its sunbird-like features) as a relative of *Philepitta*—that is a Mesomyodian passerine. By the same reliable technique it has been shown by Wetmore (1943:306) that the wren-like South American genus *Ramphocaenus* is an Oscinine bird and not a Mesomyodian, as had been believed formerly for zoogeographic reasons. Mayr (1931) showed that the Pitta-like Papuan genus *Melampitta* does not have an oligomyodian but a polymyodian syrinx and that it therefore does not belong to the Pittidae. Syrinx structure is unfortunately of no help in the task of a subdivision of the Oscines with their immensely great number of species which have entered the most diverse ecological niches. In order to separate within this great mass of forms those which are related from those which have become similar through convergence, one must search for combinations of novel clues, including such as revealed by ethological studies. A combination of characters has quite recently been used by Deignan (1958) for clarifying the relationship of the curious genus *Apalopteron* from the Bonin Islands, hitherto regarded as an aberrant Pycnonotid or Timaliid. He found not only that the tongue of *Apalopteron* suited the general type of the Meliphagidae, but also other structures, like the *nares perviae,* and he refers besides to the type of nest, which supports the morphological arguments. Beecher (1951) has, on the basis of the conformation of the jaw muscles, broken up the family Coerebidae and assigned its genera to the Thraupidae and the Parulidae. His conclusions appear to be valid. However, it has become apparent that the taxonomic usefulness of this structural character, utilized by Beecher, is in general rather questionable. In many cases the systematist who wants to place an aberrant species of song bird is essentially forced to rely on intuition and courage. I am amazed at the courage which is apparent in some of the most recent attempts to

classify the Oscines, for I am one of those timid souls in whose vocabulary the word "perhaps" occurs very frequently. My own system contains therefore many monotypic genera and monotypic families of Oscines.

The search for cases in which systematists have so far been deceived by convergence will surely produce further surprising discoveries. We can therefore look forward to much useful activity by those who plan to devote their energy to the field of bird anatomy. I recommend that he confine his comparative studies to representatives of the same order, family, or genus, the close relationship of which facilitates separation of relatively recent *functional* modifications from the more stable and taxonomically more important structures. He will be fascinated by this topic, for every true naturalist has been uplifted by the discovery of interrelations between form and function. In this field he is sure to move on firm ground and does not need to bridge the gaps in our knowledge by flimsy speculations.

Professional zoologists tended in former days to look down at occupation with systematic categories below the level orders. They found a greater challenge to their ingenuity in the search for the major lines of evolution. Within recent decades however there has been a complete revaluation of the scientific significance of the systematics of the lower categories. It is now recognized that it is as important as is a knowledge of histology and cytology for an understanding of the integral structure of the body.

But as far as the problem of the relationship of the orders of birds is concerned, so many distinguished investigators have labored in this field in vain, that little hope is left for spectacular break-throughs. Only lucky discoveries of fossils can help us, but the chances of making such finds are very small. Simpson (1946) has recently pointed out that the evolution of birds has made virtually no progress since early Tertiary times, quite in contrast to the situation among the mammals. The separation of the existing orders of birds from each other had already taken place in the Cretaceous, if not even in the Jurassic. It is therefore not surprising, that no light has been shed on avian phylogeny by the few well preserved fossil remains from the upper Cretaceous. *Hesperornis* as well as *Ichthyornis* were already highly specialized and entirely different from each other, at least as much as are today a penguin and a gull.

The bird life of the Tertiary was richer in different types than the avifauna of today. Many branches of the avian tree died before or during the Pleistocene.

In view of the continuing absence of trustworthy information on the

relationship of the highest categories of birds to each other it becomes strictly a matter of convention how to group them into orders. Science ends where comparative morphology, comparative physiology, comparative ethology have failed us after neary 200 years of efforts. The rest is silence.

## APPENDIX

### SUGGESTED AVIAN ORDERS

In parentheses are indicated the corresponding taxa and nomenclature of the Wetmore (1951) classification (names ending in -formes representing orders). Colymbiformes of that (1951) classification was changed to Podicipediformes in the A.O.U. Check-list (1957).

| | |
|---|---|
| Struthiones | (Struthioniformes) |
| Rheae | (Rheiformes) |
| Casuarii | (Casuariiformes) |
| Aepyornithes | (Aepyornithiformes) |
| Apteryges | (Dinornithiformes + Apterygiformes) |
| Crypturi | (Tinamiformes) |
| Galli | (Galliformes) |
| Opisthocomi | (Suborder of Galliformes) |
| Turnices | (Suborder of Gruiformes) |
| Columbae | (Suborder of Columbiformes) |
| Pterocletes | (Suborder of Columbiformes) |
| Ralli | (Superfamily Ralloidea of Suborder Grues of Gruiformes) |
| Heliornithes | (Suborder of Gruiformes) |
| Mesoenades | (Suborder of Gruiformes) |
| Jacanae | (Superfamily Jacanoidea of Suborder Charadrii of Charadriiformes) |
| Thinocori | (Superfamily Thinocoroidea of Suborder Charadrii of Charadriiformes) |
| Rhynocheti | (Suborder of Gruiformes) |
| Eurypygae | (Suborder of Gruiformes) |
| Cariamae | (Suborder of Gruiformes) |
| Psophiae | (Fam. Psophiidae of Superfamily Gruoidea of Suborder Grues of Gruiformes) |
| Grues | (Fam. Gruidae + Aramidae of Superfamily Gruoidea of Suborder Grues of Gruiformes) |
| Otides | (Suborder of Gruiformes) |
| Laro-Limicolae | (Suborders Charadrii + Lari of Charadriiformes) |
| Alcae | (Suborder of Charadriiformes) |
| Gaviae | (Gaviiformes) |
| Podicipedes | (Colymbiformes, now Podicipediformes) |
| Sphenisci | (Spheniscifomes) |
| Tubinares | (Procellariiformes) |
| Anseres | (Suborder of Anseriformes) |
| Anhimae | (Suborder of Anseriformes) |
| Steganopodes | (Pelecaniformes) |
| Phoenicopteri | (Suborder of Ciconiiformes) |
| Gressores | (Suborders Ardeae + Balaenicipites + Ciconiae of Ciconiiformes) |
| Accipitres | (Falconiformes) |
| Musophagae | (Suborder of Cuculiformes) |
| Cuculi | (Suborder of Cuculiformes) |
| Psittaci | (Psittaciformes) |
| Striges | (Strigiformes) |
| Caprimulgi | (Caprimulgiformes) |
| Coraciae | (Families Coraciidae + Leptosomatidae + Brachypteraciidae of Suborder Coracii of Coraciiformes) |
| Halcyones | (Superfamily Alcedinoidea of Suborder Alcedines of Coraciiformes) |
| Meropes | (Suborder of Coraciiformes) |
| Momoti | (Superfamily Momotoidea of Suborder Alcedines of Coraciiformes) |

| | |
|---|---|
| Todi | (Superfamily Todoidea of Suborder Alcedines of Coraciiformes) |
| Upupae | (Families Upupidae + Phoeniculidae of Suborder Coracii + Suborder Bucerotes of Coraciiformes) |
| Trogones | (Trogoniformes) |
| Colii | (Coliiformes) |
| Apodes | (Suborder of Apodiformes) |
| Trochili | (Suborder of Apodiformes) |
| Pici | (Piciformes) |
| Passeres | (Passeriformes) |

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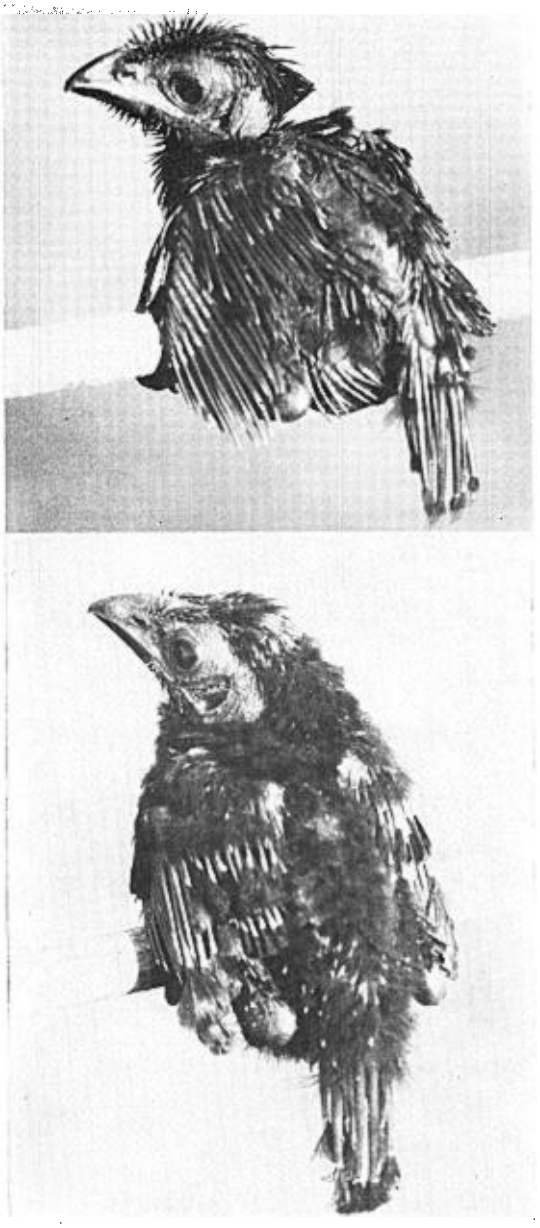
*Berlin-Charlottenburg, Wandalenallee 38, Germany.*



*(Above)* Nestling Groove-billed Ani about six days old, its feathers just beginning to unsheath. Near Tela, Honduras, August 15, 1930. *(Below)* The same nestling 24 hours later, showing rapid advance in feathering. Near Tela, Honduras, August 16, 1930. (Photos. by A. F. Skutch.)