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A Generic Review of the Family Ardeidae (Aves)

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INTRODUCTION

It is of paramount importance to keep systematics in accord with the recent advances in knowledge of the principles of evolution, phylogeny, and related fields. Yet revisions of many groups lag far behind, so that today our classification is based largely on the knowledge and ideas of earlier years.

This is the case with the herons. The supraspecific relationships in the family Ardeidae have received very little attention from systematists during the past half-century, a period in which the concepts of classification have changed radically. Almost all taxonomic studies of herons during this period have dealt with the geographic variation within a species, the relationships among the species of a single genus, or at best of a small group of related genera. Except the large general works on the classification of birds, such as Sharpe (1898) and Peters (1931), there has not been a single study concerned with the classification of the entire family since Reichenow's study (1877), now almost 80 years old. The general works, by their very nature, have too wide a scope to treat with careful detail all aspects of the problems in any one group and usually follow earlier works or cite but little evidence for any changes. Sharpe believed in a monotypic species concept; hence his classification contains many more species and genera than would be recognized today, though it is entirely consistent within itself. Since the publication of Sharpe's work (1898), the concept of the species has changed from a monotypic one to

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a polytypic one, and today many of Sharpe's genera are considered as species and the included species as subspecies. While many of Sharpe's species were reduced to subspecies of a polytypic species, the corresponding changes in the limits of the genera did not keep pace. Peters, although he did bring together some related genera, kept most of Sharpe's genera and at the same time employed a modern species concept. In the resulting classification, based partly on modern ideas and partly on outdated ones, the genus and species were no longer always in accordance with one another.

For the present paper, the relationships within the Ardeidae were studied mainly with the use of those characters that can be observed on museum skins. The research was done at the American Museum of Natural History, in the collections of which are contained all recognized species of herons and generally specimens showing all the different plumages of each species. Thus I have been able to examine specimens of all the living species of herons and, except for the noted exceptions, all the important plumages. Most of the life history data used in this study were taken from the literature.

The primary objective of this paper is to present a classification of the Ardeidae in the hope of bringing the generic limits into agreement with the present-day species concept.

A secondary objective is concerned with the practical necessity of a proper linear arrangement of the groups. A survey of both Sharpe's and Peters' list of genera will reveal an almost complete lack of order. Closely related genera are often widely separated, and there is no hint of any logical arrangement. While it is generally agreed that a phylogeny of a group cannot be represented in a linear order, some rules can be followed that will at least result in a consistent system. In the scheme presented here, the groups at each level are arranged from the one considered the most primitive to the most specialized.

I am deeply indebted to Dr. Dean Amadon for suggesting the problem and for the encouragement and help offered during the course of study. Mr. Robert Risebrough read and criticized the many drafts of this paper, offering many helpful suggestions and giving much encouragement. Drs. Ernst Mayr, Dean Amadon, Charles Sibley, and Ernest Williams, and Mr. Andrew Meyerriecks have read the manuscript and have given excellent comments and advice. Mr. Andrew Meyerriecks also offered many suggestions and ideas from his studies on the courtship behavior of the herons. Miss Helen Hays translated Salomonsen's revision of the genus *Ardeola* from the French into English. Mr. James Greenway kindly lent the series of *Gorsachius magnificus* under his care at the Museum of

Comparative Zoölogy. I am also indebted to Mr. J. D. MacDonald of the British Museum (Natural History) and Dr. H. Friedmann of the United States National Museum who kindly checked certain specimens of herons in their respective museums. Dr. Friedmann also lent me two specimens of *Zebrilus undulatus*, which first showed me the immature plumage of this species and for which I am extremely grateful. The officials of the American Museum of Natural History kindly placed the collections and facilities of the museum at my disposal during the summer of 1953 and later periods, for which I am deeply indebted. My mother typed the several drafts of the paper. Lastly I must thank my many friends in the American Museum of Natural History and at Cornell University with whom I discussed the problem and who offered much help and advice.

It is important in a taxonomic study to state briefly the ideas and principles on which the conclusions are based. The following remarks are limited to supraspecific groups and mainly to a discussion of the concepts of the genus. The basic ideas that I have followed come mainly from the papers of Mayr (1942), Delacour and Mayr (1945), Simpson (1945, 1953), and Amadon (1943).

The species is the only taxonomic category for which both a workable and objective definition can be given (i.e., reproductive isolation; see Mayr, 1942, p. 120) and serves as the basis on which both supraspecific and infraspecific classification can be built. The ranks of the taxonomic hierarchy above the species can be given, at best, a subjective definition which is open to many different interpretations. While the boundaries of the highest ranks (phylum, class, and sometimes order) are usually quite distinct, those of the lower ranks (family and genus) tend to be less distinct and are often subject to much disagreement. The evolutionary basis for this decrease in objectivity of a group as one proceeds down to the genus is well explained by Simpson (1953). If a rank is to be meaningful, it should not be allowed to infringe on the category above it or below it, and all the groups of that rank in at least the next higher category (for example, all the genera in a family) should show approximately the same amount of diversity (see Simpson, 1945, pp. 12-24; and Amadon, 1943, pp. 1-3, for a more detailed discussion). As mentioned above, the generic concept applying to the herons did not keep pace with the changing species concept, which resulted in a lopsided classification. This situation was and is still common to many groups. In his revision of the starlings, Amadon (1943, p. 1) summarizes the problem: "It has not been sufficiently realized that the modern broadening of the species concept must be accompanied by a compensatory adjust-

ment in the genus concept if the genus is to retain its importance." Another problem concerns the size of the genus. A broad generic concept is adhered to in the present study. The arguments in favor of this viewpoint are well summarized by Mayr, Linsley, and Usinger (1953, p. 48): "The specific trivial name signifies singularity and distinctness; the generic name calls attention to the existence of a group of similar or related species—it relieves the memory."

CHARACTERS USED

In taxonomy groups of organisms and the organism as a whole, rather than separate characters, should be the primary object of investigation. Once established, however, the groups must be set off from related groups by some combination of diagnostic characters (see Mayr, Linsley, and Usinger, 1953, pp. 49–51). To understand the significance and taxonomic value of the characters used in the analysis of a group, the worker must study their variation in the whole of the next highest category, their function, and the possible functional relationships of groups of characters that form character complexes and that must be studied as single units. Only then is the worker able to study the probable evolution of the groups and characters.

The major characters used in classifying the Ardeidae are discussed and attention is given to their variation, function, possible evolutionary development, and value in showing the relationships of herons.

POWDER DOWN PATCHES

Powder down consists of continually growing feathers found in many groups of birds, either scattered over all or part of the body, or in dense patches or tracts as in the herons. The major work on the powder down of birds is that of Schüz (1927). Other works, dealing mainly with the structure and function of the patches in the herons, are those of Miller (1924, p. 328), Percy (1951, pp. 36–39, pls. 31–49), Wetmore (1920), and Hindwood (1933, pp. 97–102).

The number of powder down patches is one of the major characters used in the separation of families and subfamilies of herons. The number varies from two pairs in the bitterns and three in most herons to four in *Cochlearius* and some tiger herons. There has been much debate over the number of patches found in *Cochlearius*. Gadow (1893, p. 139) and Beddard (1898, p. 429) report three pairs of patches, while Ridgway (1878, p. 220) and Miller (1924, p. 328) give four pairs for this species. All specimens of the Boat-Bill Heron that I have examined had the three pairs found in the Ardeinae and, in addition, a small tuft located

at the caudal end of the scapular feather tract. *Tigrisoma mexicanum* and *T. salmoni* have a fourth pair of patches running up the center of the back, as first pointed out by Miller (1924, p. 328).

The patches are:

1. BREAST: Found in all herons and generally the largest patch. Sometimes two distinct patches are present, but more often they are fused into a single bilobed patch. This difference may be partly due to the way the specimen has been prepared. The patch lies in the space just caudal to the division of the ventral feather tract.

2. RUMP: Found in all herons and usually the second largest patch. It lies just lateral to the femoral feather tract, often curving down and about the rear of the leg to approach and sometimes meet the inguinal tract.

3. INGUINAL: Present in the Ardeinae where they form the smallest pair of patches. All species of the Botaurinae lack the inguinal patches. This patch lies in the inguinal region next to the ventral feather tract, between it and the leg. It often curves up and about the rear of the leg to meet the descending rump patch.

4. BACK PATCHES: Used to refer to the miscellaneous patches found in *Cochlearius* and some species of *Tigrisoma*. The term is employed for convenience only and not to imply homology, for the patch in *Cochlearius* may have been secondarily acquired.

The powder down patches are closely associated with and usually lie next to a feather tract. The rump and inguinal patch may be connected, or they may approach each other in varying degrees. This condition follows no set pattern in the family, and there may be much individual variation within a species with respect to the degree these patches come together. The breast and inguinal patches in some *Tigrisoma* are connected, as first pointed out by Miller (1924, p. 328). From the variation shown in the family, it seems very possible that the primitive condition was a continuous tract from the upper breast (the two sides may or may not have been connected), down along the ventral feather tract, about the rear of the leg, and finally up along the spinal feather tract to about the region of the upper back. Evolutionary development may have consisted of a process of reduction and breaking up this continuous tract into a smaller number of patches at definite locations. If this is true, stabilization must have occurred early in the evolution of the Ardeidae, for most of the present-day variation is about the pattern of three patches: breast, rump, and inguinal. The bitterns would then exhibit the greatest reduction; the inguinal patch was most likely lost after the stage when three definite patches were formed. The extra patch

and continuous ventral patch in some *Tigrisoma* are considered as remnants of the primitive condition. It is not definite whether the small tuft found in *Cochlearius* is a remnant of the primitive condition or has been secondarily acquired. A second hypothesis for the evolution of the powder down patches would be an increase in the number of patches, perhaps through a condensation of down scattered over the body. The first explanation also involves the formation of a continuous tract which probably evolved by a condensation of the powder down into this tract. The important difference between the two hypotheses concerns the formation of a continuous tract and then reduction to the present number of patches, rather than a direct condensation of down into the definite patches present today. The connection between patches and extra patches, especially in the group considered the most primitive, and the very constant number of patches in most species lend support to the theory of reduction of a continuous tract rather than to other possibilities.

Lord Percy (1951, pp. 36-39, pls 33-49) has given the best explanation of the function of powder down. Other workers (Hindwood, 1953, pp. 97-102; and Wetmore, 1920) agree to the extent that the powder is used in the upkeep of the plumage, but conclude that the powder down serves as a waterproofing device in somewhat the same manner as the oil from the uropygial gland. Percy has shown, with an excellent series of pictures, that the powder is used to remove fish slime and oil (also natural oil) from the feathers. The bird (the observations were made mostly on the European Bittern and partly on the Gray Heron) first rubs the powder down over the feathers, remains quiet for a time during which interval the oil and slime are probably taken up by the powder, combs the powder down out of the feathers, using the pectinated claw of the middle toe, and then oil from the oil gland is rubbed into the feathers. The above authors, as well as the present writer, have observed herons nibbling at powder down patches, then drawing feathers, such as the flight feathers, through the bill and thus rubbing the powder down on these feathers. More work is needed in order to show the exact way the powder down removes oil from the surface of the feathers, or if it in some way dresses the feathers, as suggested by Wetmore.

If the powder down is of importance in the upkeep of the plumage, the total amount of powder down and location of the patches would be selected for and the mere number of patches would be of little importance. The amount of slime, etc., that gets on the plumage would determine the selection pressure for the size of the patches and also the rate of growth of the down feathers, and larger patches would result in some species. No satisfactory way of measuring the observed variation or of

determining how much of the variation is individual or seasonal is known, so that the differences in relative sizes of the powder down patches in the different species cannot be compared.

Powder down patches are a taxonomically valuable character, as the number of patches probably has little selective value. The number of patches is quite constant over a large number of species, the major expression of variation being at the subfamily level. Caution, however, must be used when one deals with the extra patches in *Cochlearius* and *Tigrisoma*. The problem in each genus is discussed under the respective generic headings.

PLUMES

Specialized feathers or plumes are found in all herons, from the slightly developed crown plumes of the tiger herons to the extremely specialized plumes of the egrets and *Agamia*. Differences in plumes, without regard for their function, were often the major or only basis of separation of many genera of the Ardeidae. Much use of the variation of the plumes is made in this paper, but in considering the plumes from a functional viewpoint and with the intention of showing relationships between species, not differences. Plumes, like many other characters because of their function (discussed below), are not constant within a genus; indeed it is the rule rather than the exception for the plumes to break down as a diagnostic generic character in a genus containing more than one biogeographic species.¹ Therefore retaining "*Nyctanassa*" or the several genera of egrets, which are based mainly on a difference in plumes, is not justified when the many similarities are considered.

With few exceptions and intermediate conditions, the plumes can be separated into three major types. To designate these types I have used the names most commonly found in the literature. These descriptions are only brief and somewhat crude, and still much exact work must be done before the detailed structure and variation of the plumes can be completely understood.

1. LANCEOLATE: Characterized by the scapular plumes of *Butorides*. The feathers are long and narrow (strap-like), with the short barbs firmly held together. Occasionally the plume is wider at the base and tapering towards the tip, or it may be very broad as in the crown plumes of *Cochlearius* or *Agamia*. The barbs are commonly freed at the edges of the feather as in the scapular plumes of *Nycticorax violaceus*.

¹ Biogeographic species include all species and superspecies except those species that are members of a superspecies. The term logically follows the use of superspecies when species are compared biogeographically and an inclusive term is needed.

2. FILAMENTOUS: Best shown by the scapular plumes of *Ardeola* or *Hydranassa rufescens*. The feather is long and hair-like. The barbicels have degenerated, and in the most specialized extreme the barbules have also degenerated, leaving the barbs free. As in the aigrette, the barbs are long.

3. AIGRETTE: Found only in the genus *Egretta*. The barbicels have degenerated, leaving the elongated barbs free, and resulting in a loose fine feather.

Most herons have crown (also called head or occipital) plumes consisting of a tuft of elongated feathers extending caudad. Frequently there are several longer feathers, which are often different from the plumes composing the shorter tuft and are usually of the lanceolate type (e.g., in *Nycticorax* and *Ardeola*). In many of the more primitive herons only the crown plumes are present; their loss in such forms as *Egretta alba* and *E. intermedia* is secondary. The feathers of the scapular region are often modified as plumes that cover the back and often reach beyond the tail. Scapular plumes (also called back plumes) are considered the most specialized for they are found only in the Ardeini and a few species of the Nycticoracini. The feathers of the upper breast and lower neck have developed into plumes in most herons. In the bitterns and less-specialized herons these feathers are hardly more than elongated contour feathers, but they are more specialized in the typical herons. Occasionally the entire neck and side of the face bear plumes, as in *Agamia* and *Hydranassa rufescens*.

The most primitive of the fully developed plumes is the lanceolate type. Evolution from the contour feather to the lanceolate plume would involve an elongation, narrowing, and strengthening of the contour feather, as partly shown by the crown plumes of tiger herons and to a lesser degree by the peculiar sickle plumes found on the neck of *Agamia*. The other plume types were derived from the lanceolate type. This is nicely shown in the *Hydranassa* series (*tricolor* and *rufescens*) in which all stages from the lanceolate to the filamentous plume may be found or in *Egretta* (*sacra* and *eulophotes*) in which the steps from the lanceolate plume to the aigrette can still be seen.

Plumes have always been of the greatest importance to the heron systematist but were generally used to separate genera without consideration for the role they play in the life of the birds. Therefore if we are to make intelligent use of the plumes in classifying herons, we must first investigate their function and the selective forces that have been important in the evolution of the present observed variation. It is hoped that the following discussion will show that the plumes with the associated

displays serve as isolating mechanisms and that much of the diversity in plume types, which was formerly considered of generic value, is in reality significant only at the specific level.

Plumes are found in both sexes and are usually present only in the breeding season. They function in "courtship" and other displays associated with the formation and maintenance of the pair bond. As the plumes are closely related to the displays involving them, this is the best place to mention the present state of knowledge of the "courtship" behavior of herons. Up to now only a few species of herons have been well studied, notably *Nycticorax nycticorax* (Lorenz, 1934; Noble, Wurm, and Schmidt, 1938; Noble and Wurm, 1942; and Allen and Mangels, 1940) and *Ardea cinerea* (Verwey, 1929, 1930), but studies are now being made of other species (Koenig, 1953; and Meyerriecks, personal communication). While it is too soon to make use of these displays in determining relationships in the Ardeidae, the above cited works and others, especially the recent studies of the Anatidae (Delacour and Mayr, 1945; Lorenz, 1941; and Sibley, MS) are very useful in an interpretation of the plumes of herons.

Lorenz (1941; see, for example, pp. 284–287, on the correlation between the "sail" and false preen of *Aix galericulata*) has shown that various displays are enhanced by morphological modifications. In the herons, the plumes are so located that they enhance the displays; one example would be the head plumes and the greeting display of *Nycticorax nycticorax* (Noble and Wurm, 1942). Sibley (MS) discusses the function of the epigamic displays in the genus *Anas* of the Anatidae. In this group of closely related, sympatric, interfertile species, the "courtship" displays of the males and correct responses of the females serve as isolating mechanisms to prevent "mixed" (interspecific) pair formation and hybridization. Sibley points out that there is a positive correlation between the number of closely related species in a given area and the diversity of the ritualized "courtship" movements and associated structures that function as isolating mechanisms.

The Ardeidae would form an excellent group for a similar study once the "courtship" patterns are well known, but here only a few facts and crude generalizations are given in order to give a firmer foundation for an understanding of the variation of the plumes between the different species and genera of herons. Many herons nest in large mixed colonies, with as many as eight species breeding together in the same colony or at least in the same locality as along the coast of the Gulf of Mexico. The species of the Ardeini and Nycticoracini, which are colonial, have more highly developed plumes than the solitary nesting species of the Botaurinae and

Tigriornithini. With few exceptions (*Egretta alba* and *E. intermedia*, *E. gularis* and the *E. garzetta-dimorpha* complex, and possibly some species in *Ardea*) all sympatric species have a different combination of plumes. More study is needed, especially in the case of the above-cited exceptions, to determine if differences in displays and time of nesting exist between sympatric species of herons. Thus it can be easily seen why the plumes vary in a genus containing two or more sympatric species, for if these species are to breed in the same place, some mechanism to prevent mixed pair formation must evolve. In the Ardeidae, a difference in plumes helps to fulfill this function. Sibley (MS) shows that the selection pressure for the complex of display and associated structural modification results only from the interrelation among the species found in one place at the time of pair formation. He then concludes that reënforcement of isolating mechanisms will come to an end only when the interacting species in a community are responding to one another as if the others did not exist, that is, in regard to pair formation. Consequently, in the Ardeidae, once the plumes and displays are functioning successfully to prevent interspecific pair formation there is no reason to expect the plumes to undergo any further change, because there is no longer any effective selection pressure for such changes.

Within the framework of the above ideas, the plumes, although very variable, can serve as valuable characters at all levels in the family, but are most useful at the specific and generic levels.

PROPORTIONS

In the past the use of fine differences in proportions, expressed as ratios between parts of the body, as generic characters was carried to a ridiculous extreme. It was common practice to give as generic characters bill longer than tarsus, or tarsus longer than tibia, etc., and at the same time to make no attempt to compare the same ratio in closely related genera, or to discover the adaptive function of the character. The value of these ratios is even harder to determine when the great amount of individual variation in size shown by the herons is considered. I have taken a number of measurements on a small series of all species of herons but am not presenting the results because they are of no help in the clarification of relationships.

Nevertheless, the use of general proportions, such as the contrast between short-legged, chunky-bodied birds and long-legged, slim-bodied birds provides a good basis for showing relationships and is widely used in this paper. Its great value lies in the fact that the general build of different animals is compared, and in this way the different adaptations, which are closely related to general build, are contrasted. Great care

must be taken when animals are compared on the basis of measurements, for measurements often obscure much detail and thus make it much more difficult for convergence to be detected.

COLOR AND COLOR PATTERN

Color by itself is one of the poorest characters on which to base generic or higher groups. This is especially true when a solidly colored bird is compared to a bird of another color or to an all-white bird. In herons the problem is further increased by the common occurrence of color phases, especially a white one. In some species there may be several different phases, for example, dark, mottled or partly white, and white. Some species, especially in *Egretta*, often have a few dark feathers in the white phase. Based on the sharp divisions between the phases, a simple genetic mechanism may be postulated. This is in agreement with the color phases in mammals which are known to have usually a simple genetic basis (Castle, 1940, for example, see chap. 4).

Herons of the tribe Ardeini, in which the white phase occurs most commonly, have little need for concealment. They are large birds, feed in open marshes, and nest in large noisy colonies. A dark color would not have a greater selective value, and being white may be advantageous for the bird is more conspicuous to other individuals of the same species. The best explanation for the pattern of occurrence of the white phase in the Ardeidae is that it evolved independently several times and the dark phase has been lost in the all-white species.

Color pattern is more conservative than color alone and is useful in grouping species of herons at the generic level, as in *Ardea* and *Ardeola*, and sometimes at the tribal level, as in the Tigriornithini. In general, the more complex a color pattern, the less chance there is of convergence. Yet a complex color pattern may be selected for in one particular environment and thus be found in unrelated genera, as in the case of the meadow-larks of the New World (*Sturnella*, Icteridae) and a genus of African pipits (*Maxronyx*, Motacillidae), both of which inhabit open, grassy fields (Friedmann, 1946, p. 395). Other examples could be easily cited. There is no evidence that this has happened in the Ardeidae, and color pattern is used as one of the important indices of relationship, at least to the generic level.

BILL

The heron bill varies from the long thin bill of *Agamia* to the short rail-like bill of *Zebritus*, but with one exception, *Cochlearius*, it is a pointed spear-like structure. The primary feeding adaption of the Ar-

deidae is spear-fishing, the prey being caught by a rapid thrust of the bill. The bill does not pierce the prey; rather the prey is grasped between the mandibles. The anatomy of the neck is modified for this rapid forward thrust. The facets of the zygapophyses shift backward to a more vertical position between the sixth and seventh cervical vertebrae. The vertebrae in front of this point have the zygapophyses in a more horizontal position; those beyond this point are in the vertical position. This point also serves as the origin or insertion of many cervical muscles and thus acts as a hinge (personal observations, and Boas, 1929, which should be consulted for further details, especially pls. 2, 11, 15, and 20).

Cochlearius has a broad, scoop-like bill, which cannot be called flattened as it is about the same depth as the bill of *Nycticorax*, its nearest relative. Based on the current theories of evolution, the only conclusion that can be drawn is that *Cochlearius* feeds in a manner different from that of the other herons. It may use its bill as a scoop or feed on smaller prey, capturing its food with a rapid thrust of the bill. If the latter possibility is correct, the expanded bill would better enable the Boat-Bill to capture its food, as is the case with swallows and flycatchers. It should be noted that the shift in position of the zygapophyses starting at the sixth cervical vertebra of *Cochlearius* is identical with that of *Nycticorax*, so that, as far as is known, *Cochlearius* still possesses the adaptation necessary for a rapid thrust of the bill. I have, however, been unable to find a description of the feeding method of *Cochlearius*, and this gap in our knowledge must be filled before the evolution of the Boat-Bill's remarkable bill can be fully understood.

The bill is of little help in showing relationships owing to the great similarity over a wide range of species, although it is of some use in the separation of the night herons (shorter, heavier bill) and *Cochlearius* (expanded bill) from the rest of the Ardeidae.

TOES AND CLAWS

The two subfamilies of the Ardeidae can be distinguished by the condition of the inner and outer toes, the bitterns having the outer toe shorter than the inner, and the opposite being true for the Ardeinae. This difference in length varies from an easily observed one to the condition in which the toes are almost equal and must be measured in order that a difference can be shown to exist. I have been unable to discover an advantage of having either type and at present can conclude only that each has the same selective value. Characters for which the alternatives have no selective advantage over one another are often the most valuable in taxonomy, which I feel may be true in this case.

Two claw types are present in the herons; the first is a short and strongly curved claw and the second type is long and only slightly curved. Those species with long claws also have relatively longer toes, while the short-clawed species have shorter toes. This condition was once used as a distinction between the Botaurinae (long, slightly curved) and the Ardeinae (short, strongly curved), but *Ardeola* and *Ardea purpurea* have long, slightly curved claws and some species of *Ixobrychus*, especially *flavicollis*, have short, strongly curved claws. This character is correlated with the habitat in which the heron spends most of its time or, better, the habitat in which it nests and roosts. Those species nesting in trees have short, strongly curved claws, while the claws of marsh-nesting herons are long and slightly curved. Lord Percy (1951, p. 24) has nicely shown that the long claws have a definite advantage in gathering together many sedges which gives the bird more support as it proceeds through the marsh. Short claws may be advantageous to a bird perching on branches, but I cannot demonstrate any good reason why there may be an advantage, other than pointing out that most perching birds have short, strongly curved claws. Long claws have evolved independently several times, and the difference in the condition of the claws is no help in showing relationships at the subfamily level and is usually of little use at the generic level.

CALL

The call of the Ardeini herons and some species of the Nycticoracini is usually described as a harsh "croak" or "quok." Although the calls of these species of herons may be distinguished, the differences are slight, and the calls are basically the same. Colonial herons, although noisy when they are in the nesting colony, are quiet feeders and generally call only when disturbed. In addition to the harsh call note, the colonial herons may have special notes used with various displays, such as the hiss and click in the snap-hiss ceremony of the black-crowned night heron (Noble, Wurm, and Schmidt, 1938, p. 25). *Nycticorax sibilator* has a most unique call, a high-pitched, whistling note (see Friedmann and Smith, 1950, p. 434, for description).

A second type of call given by the bitterns of the genus *Botaurus*, the tiger herons (Bannerman, 1930, pp. 81-82; Dickey and van Rossem, 1938, p. 82; Gurney, 1928), and *Gorsachius goisagi* and *G. melanolophus* (Hachisuka, 1926, p. 591) is generally described as a booming note. The similarities among the calls may be due partly to the crudeness of the descriptions. The call of the small bitterns, *Ixobrychus*, is a series of low soft notes. These species are solitary, and the call may serve to bring the

sexes together in the breeding season and also may serve as a territorial note. In *Botaurus* the male gives the booming note, which is given only in the spring (Bent, 1926, pp. 80–81; Witherby *et al.*, 1943, p. 157). The esophagus is enlarged during the breeding season for this function (Chapin, 1922). In at least some species of *Ixobrychus* (Bent, 1926, p. 90; Witherby *et al.*, 1943, p. 153), only the male has a "spring call," but it is not known if this is true of all species. The calls of the tiger herons and *Gorsachius* are even less known. Dickey and van Rossem (1938, p. 82) report that *Tigrisoma mexicanum* calls throughout the year, but little else is known about the calls of these species.

The call is not utilized in this paper for the determination of relationships but is discussed mainly to indicate that the booming note is one of the characteristics of the solitary nesting herons and does not necessarily imply close relationship between bitterns and tiger herons, as is so frequently believed.

NESTING HABITS

The Ardeinae are tree-nesting birds, the bitterns ground or marsh nesters. Where trees are lacking, or rarely when trees are present, members of the Ardeinae may nest on the ground or in marshes (see Bent, 1926, and commonly reported in other sources). *Ardea purpurea* has secondarily taken to nesting in large colonies in marshes (Witherby *et al.*, 1943, p. 134). Nests of the least bitterns are sometimes found in bushes or low trees, this being a common occurrence in some species (Ticehurst, 1923, pp. 274–275; Chapin, 1932, p. 447; Witherby *et al.*, 1943, p. 153). While these exceptions are noted, the general difference in the location of the nest is a good basis of separation between the two subfamilies of herons.

Colonial versus solitary nesting is the second major difference in nesting habits in the Ardeidae. Solitary nesting is characteristic of the bitterns, tiger herons, and *Gorsachius*, and is the more primitive condition. Colonial nesting, the more specialized condition, is found in the rest of the family.

The most primitive nesting habit is solitary tree-nesting as shown by the tiger herons (*Zebrilus*, unknown) and *Gorsachius*. The bitterns have taken to nesting in the marsh but have retained the habit of solitary nesting. The Ardeini, *Nycticorax*, and *Cochlearius* have for the most part remained tree nesters but have become highly colonial. Nests are commonly placed close to one another, and the colonies are often very large and usually contain several species of herons and other waders.

The nest is a simple structure. In trees it is a loose platform of sticks;

in marshes a platform of rushes is built; and sometimes the nest may be built of twigs and rushes when placed in a low bush in the marsh.

Solitary nesters are silent about the nest and are cryptically colored birds. These features are of special advantage to ground nesters. The selection pressure for cryptic coloration in colonial herons was removed after they started to nest in large, noisy colonies, and the selection pressure for the more highly developed and necessary plumes and displays was free to act. When the Ardeinae herons nest on the ground, their large size and compact colony serve as protection against predators.

Many characteristics of herons, such as the display and plumes, coloration, call, and structure of the toes and claws, are strongly correlated with the nesting habits, which thus serve as the key to an understanding of the pattern of variation found in these structures. While many facts are still unknown, it is quite safe to conclude that the evolution of nesting habits has been of great importance in the evolution within the family, and it is therefore a major clue in an understanding of the relationships and evolution of the major subdivisions of the Ardeidae.

ANATOMY

Comparative anatomy is one of the best foundations for systematic work on the generic and suprageneric levels. Unfortunately, besides the scattered information obtainable from the large works on avian anatomy such as Gadow and Selenka (1891–1893) and Beddard (1898), little can be found concerning comparative anatomy within the Ardeidae. Shufeldt (1889, 1901) studied the osteology of the North American species of Ardeinae, which include only part of the Nycticoracini and Ardeini, and thus his conclusions are not so useful as they might be, owing to the lack of knowledge of the other groups of herons. For completeness only, some of the anatomical features of the subfamilies are given here, but no evaluation of the significance of the characters or whether they are found in all members of the respective groups or not can be given at the present time.

FAMILY ARDEIDAE

HERONS AND BITTERNS

No attempt is made to give a description of the family Ardeidae or to delimit it from the rest of the order, for these lie outside the scope of the present paper. An adequate description can be found in any of the note that the family is clearly delimited and that there is no doubt, with standard works (e.g., Beddard, 1898, p. 429). It is of importance only to

the possible exception of one or two aberrant genera such as *Scopus* and *Balaeniceps* which some persons may regard as subfamilies of the Ardeidae, whether a species is a member of the Ardeidae. *Scopus* and *Balaeniceps* have been considered, for the present study, as not belonging to the Ardeidae and thus were not carefully examined, but will be included in my future studies on the anatomy of the group. Even if future work indicates that one or both of these genera should be included in the Ardeidae, they would most probably be placed in a different subfamily than the group studied in this paper, or, to put it in another way, the members embraced by this study are probably more closely related to one another than to any other genus of the order. It should be mentioned in passing that the order and included families are quite old, and little is known of a possible phyletic history of the order. Therefore it is impossible at this time to determine the primitive nature of any of the studied characters by an examination of their condition in the other families in the order.

The following arrangement of species and genera is based on a comparative study of the characters just described. The sequence, as far as possible, is from the more primitive forms to the most specialized in each group. It is well realized that this goal has been far from attained in the complex genera, such as *Ardea*, *Egretta*, and *Ixobrychus*, and that the sequence in these genera is partly arbitrary. Superspecies (for definition, see Mayr, 1942, pp. 169–172) are bracketed, and one doubtful form, *occidentalis*, is enclosed in parentheses. Whenever a species has been transferred to a new genus, the old generic name (Peters' arrangement of 1931 is used as the basis of comparison) follows in parentheses.

The recognized subfamilies have been retained, and in addition the Ardeinae were divided into three tribes. While there is much difference of opinion over the use of tribes in avian classification (see Wetmore, 1951, pp. 12–13; Delacour and Mayr, 1945; and Mayr and Amadon, 1951), more use of this category is presently being made, and it has proved valuable in the discussions in this paper. The use of tribes in the Ardeinae is only tentatively advanced until their reality has been more definitely shown through further study and their usefulness has been established.

Figure 1 shows the postulated relationships between the genera of the Ardeidae.

CLASSIFICATION OF THE ARDEIDAE

Family Ardeidae, Bitterns and Herons

Subfamily Botaurinae, Bitterns

Genus *Botaurus*

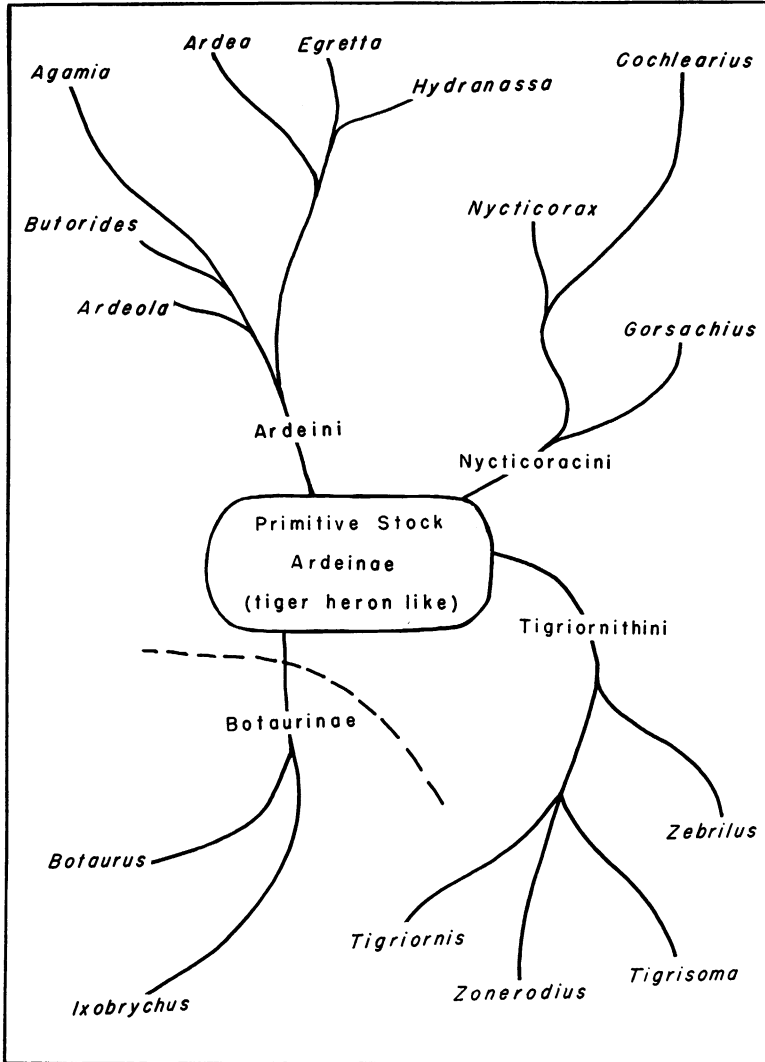


FIG. 1. Dendrogram showing relationships within the Ardeidae. The diagram involves only a single time level, the present, and should be thought of as the top view of a "family tree" rather than the more standard side view. The primitive stock which is considered as belonging to the Ardeinae (and further to the Tigriornithini) has given rise to four lines; one of these, having diverged much more than the others, is given subfamily rank (Botaurinae). The dashed line separates the two subfamilies.

- { *stellaris*, European Bittern
- { *poiciloptilus*, Australian Bittern
- { *lentiginosus*, American Bittern
- { *pinnatus*, South American Bittern

Genus *Ixobrychus*

- { *exilis*, Least Bittern
- { *minutus*, Little Bittern
- { *sinensis*, Yellow Bittern
- involucris*, Streaked Bittern
- eurhythmus*, Schrenck's Bittern
- cinnamomeus*, Cinnamon Bittern
- sturmii*, African Dwarf Bittern
- flavicollis* ("Dupetor"), Black or Mangrove Bittern

Subfamily Ardeinae, Herons

Tribe Tigrionithini, Tiger Herons

Genus *Zonerodius*

- heliosylus*, New Guinea Tiger Heron

Genus *Tigriornis*

- leucolophus*, White-crested Tiger Heron

Genus *Tigrisoma*

- lineatum*, Lined Tiger Heron
- salmoni*, Salmon's Tiger Heron
- mexicanum* ("Heterocnus"), Mexican Tiger Heron

Genus *Zebrilus*

- undulatus*, Zigzag Heron

Tribe Nycticoracini, Night Herons

Genus *Gorsachius*

- goisagi*, Japanese Heron
- melanolophus*, Malay Heron
- magnificus* ("Oroanassa"), Magnificent Night Heron
- leuconotus* ("Calherodius"), White-backed Night Heron

Genus *Nycticorax*

- { *nycticorax*, Black-crowned Night Heron
- { *caledonicus*, Nankeen Night Heron
- { *pileatus* ("Pilherodius"), Pileated Night Heron
- { *violaceus* ("Nyctanassa"), Yellow-crowned Night Heron
- { *sibilator* ("Syrigma"), Whistling Heron

Genus *Cochlearius*

- cochlearius*, Boat-billed Heron

Tribe Ardeini, Typical or Day Herons

Genus *Ardeola*

- { *ralloides*, Squacco Heron
- { *idae*, Madagascar Squacco Heron
- { *grayii*, India Pond or Paddy Heron
- { *bacchus*, Chinese Pond Heron
- { *speciosa*, Javanese Pond Heron
- { *rufiventris* ("Erythocnus"), Rufous-bellied Heron
- { *ibis* ("Bubulcus"), Cattle Egret

Genus *Butorides*, Green Herons

- virescens*, Little Green Heron
- sundevalli*, Galapagos Green Heron
- striatus*, Green-backed Heron

Genus *Hydranassa*

- picata* ("Notophoxyx"), Pied Heron
- ardesiaca* ("Melanophoxyx"), Black Heron
- caerulea* ("Florida"), Little Blue Heron
- tricolor*, Louisiana Heron
- rufescens* ("Dichromanassa"), Reddish Egret

Genus *Egretta*, Egrets

- sacra* ("Demigretta"), Reef Heron
- eulophotes*, Swinhoe's Egret
- thula* ("Leucophoxyx"), Snowy Egret
- gularis* ("Demigretta"), African Reef Heron
- dimorpha*, Dimorphic or Madagascar Egret
- garzetta*, Little Egret
- intermedia* ("Mesophoxyx"), Intermediate Egret
- alba* ("Casmerodius"), Greater Egret

Genus *Ardea*

- purpurea*, Purple Heron
- novaeollandiae* ("Notophoxyx"), White-faced Heron
- pacifica*, White-necked Heron
- cinerea*, Gray Heron
- herodias*, Great Blue Heron
- (occidentalis)*, Great White Heron
- cocoi*, Cocoi Heron
- melanocephala*, Black-headed Heron
- humbloti*, Madagascar Heron
- goliath*, Goliath Heron
- imperialis*, Imperial Heron
- sumatrana*, Sumatra Heron

Genus *Agamia*

- agami*, Agami or Chestnut-bellied Heron

Totals

- Number of genera, 15
- Number of species, 64
- Number of biogeographic species, 46 (for definition, see p. 7)

Genera recognized by Peters and synonymized here are:

- Bubulcus* = *Ardeola*
- Calherodius* = *Gorsachius*
- Casmerodius* = *Egretta*
- Demigretta* = *Egretta*
- Dichromanassa* = *Hydranassa*
- Dupetor* = *Ixobrychus*
- Erythocnus* = *Ardeola*

Florida = *Hydranassa*
Heterocnus = *Tigrisoma*
Leucophoyx = *Egretta*
Melanophoyx = *Hydranassa*
Mesophoyx = *Egretta*
Notophoyx novaehollandiae = *Ardea*
Notophoyx picata = *Hydranassa*
Nyctanassa = *Nycticorax*
Oroanassa = *Gorsachius*
Pilherodius = *Nycticorax*
Syrigma = *Nycticorax*

The following species, accepted by Peters, have been synonymized for various reasons (see under the respective genera) :

Butorides rogersi = *B. striatus rogersi*
Demigretta asha = synonym of *Egretta gularis schistacea*
Demigretta (gularis?) schistacea (usually known as *D. schistacea*) = *E. gularis schistacea*
Heterocnus cabanisi = *Tigrisoma mexicanum*
Melanophoyx vinaceigula = color phase of *Hydranassa ardesiaca*
Tigrisoma (lineatum?) bolivianum = *T. lineatum bolivianum* (according to Hellmayr and Conover, 1948, p. 222, this is inseparable from *T. l. marmoratum*)
Tigrisoma (lineatum?) fasciatum = *T. lineatum fasciatum*

In the generic headings that follow, the generic name is followed by the describer's name, then the type species follows in parentheses, and finally the year in which the genus was described. The included species are listed, and a brief generic synonymy is given. For a complete synonymy of the American species, see Hellmayer and Conover (1948). A recent synonymy for the other species is not available in a single source; Sharpe (1898) is the latest. The ranges given in the discussion of each genus are taken chiefly from Peters (1931).

SUBFAMILY BOTAURINAE

BITTERNS

The bitterns are sufficiently different from the other herons, in both structure and behavior, to be given subfamily rank. They are short-legged, stocky-bodied, marshland birds with solitary and secretive habits. It should be noted that the term "marsh" means more exactly cattail or any other high sedge or grass marsh. The Ardeinae herons are rarely seen in this type of marsh and generally feed in open places along the banks of streams, in shallow water, and on dry land. When alarmed bitterns usually resort to the concealing pose (also called protective pose; for description, see Witherby *et al.*, 1943, p. 157; Bent, 1926, pp. 79-80;

and commonly described in other sources) rather than to escape by flight. Bitterns are solitary nesters; the nest is usually placed in the reeds. Species of the genus *Ixobrychus* sometimes nest in bushes or trees. The inner toe is longer than the outer; vinculum absent between the deep plantar tendons (Beddard, 1898, p. 431); only two pairs of powder down patches: the breast and rump patch; tail feathers vary from eight to 10 (see also Beddard, 1898, p. 430; and Miller, 1924, p. 319, who note exceptions). Beddard (1898, p. 431) reports only one carotid artery for this subfamily. However, Glenn (1945, 1953) describes much variation in the condition of the carotid arteries in the family. The bicarotid and conjugate carotid conditions may occur in both subfamilies and even in the same genus or species and are thus of no help as diagnostic characters of the subfamilies of herons. The plumes are only slightly developed and consist of the crown plumes, a pair of white scapular tufts in *Botaurus*, and possibly the feathers along the side of the neck in *Ixobrychus*.

Botaurus Stephens (*stellaris*), 1819

INCLUDED SPECIES: *stellaris*, *poiciloptilus*, *lentiginosus*, and *pinnatus*.

DIAGNOSIS: Large bitterns having the plumage brown or buff, with many dark streaks; sexes alike and the young similar to the adult. Plumes are only slightly developed; a tuft of crown plumes and a pair of white tufts in the scapular region (see Brewster, 1911, for description and display) are present. They are strictly birds of the marsh and are only extremely rarely seen perching in trees. Males have a loud booming call in the breeding season, the esophagus being modified for this function (Chapin, 1922).

RANGE: World-wide, found on all continents and even reaching New Zealand; mainly in the temperate zones.

REMARKS: The four allopatric species of *Botaurus* are very similar, forming a superspecies. Perhaps future study will show that they are best considered as conspecific.

Ixobrychus Billberg (*minutus*), 1828

INCLUDED SPECIES: *exilis*, *minutus*, *sinensis*, *involucris*, *eurhythmus*, *cinnamomeus*, *sturmi*, and *flavicollis*.

SYNONYMS: *Ardetta* Gray, 1842 (*minuta*); *Nannocnus* Stejneger, 1887 (*eurhythmus*); *Dupetor* Heine and Reichenow, 1890 (*flavicollis*); *Erythrophox* Sharpe, 1894 (*woodfordi* = *flavicollis*); *Ardeirallea* Sharpe, 1895 (*sturmi*).

DIAGNOSIS: Small bitterns; *flavicollis* is from one-third to one-fourth larger than its congeners. Three different color patterns are found in the

genus. They are: dark back and light wing patches, *exilis*, *minutus*, *sinensis* (male only), and *eurhythmus*; heavily streaked on back, *involucris sinensis* (female only) and *cinnamomeus* (female?); and solidly colored back and wings, *cinnamomeus* (male only), *sturmi*, and *flavicollis*. In some, *exilis*, *minutus*, *sinensis*, *cinnamomeus*, and *flavicollis*, the sexes are dissimilar in color; the female is lighter, duller, and generally more heavily streaked or spotted and thus is more like the immature. This occurrence of sexual dimorphism is unique in the Ardeidae. The immature is unlike the adult and is heavily streaked; perhaps *involucris* has retained the streaked immature plumage as the adult plumage. The plumes are more developed than in *Botaurus*; crown plumes are developed in all species, and the feathers of the lower neck are especially long and swept back about the neck and may serve as plumes. This condition is most specialized in *flavicollis*. Although the least bitterns are usually found in marshes, they perch and nest in bushes and trees more often than do the large bitterns. Males have a low call in the breeding season, not a booming note.

RANGE: World-wide, found in all continents and also New Zealand; in temperate and tropical regions.

REMARKS: The Mangrove Bittern, *flavicollis*, differs from the other species of *Ixobrychus* only by being larger, but agrees with them in all other respects. Size alone is a poor generic character, and for this reason *flavicollis* has been included in *Ixobrychus*.

Ixobrychus exilis has a melanistic, eurythematic color phase, the "Cory's Least Bittern." *Ixobrychus flavicollis* has several color phases besides the "normal" one: a partly white phase, which always contains many dark feathers; a melanistic one, which is all black; and a rufescent phase. Most or all of these phases may be found in the same population (Mayr, 1945, p. 45).

SUBFAMILY ARDEINAE

HERONS

The true herons range from short-legged, stocky-bodied species to long-legged, thin-bodied forms. The more primitive species are solitary feeders and nesters, but social feeding and colonial nesting is the typical and more advanced condition, the flocks and colonies often containing several species. The nest is usually placed in a tree, whenever it is available, except for that of *purpurea*, which is placed on the ground. The outer toe is longer than the inner; a slender vinculum is present between the deep plantar tendons (Beddard, 1898, p. 431); carotids

variable (see above under the Botaurinae); always more than two pairs of powder down patches, the typical number being three: breast, rump, and inguinal patches; tail feathers 12, with a single exception, *Zebrilus*, in which there are 10. The plumes vary from slightly developed in the tiger herons, about the same as in the bitterns, to the peak of their development in such genera as *Egretta*, *Hydranassa*, and *Agamia*.

TRIBE TIGRIORNITHINI

TIGER HERONS

The tiger herons are the most primitive group in the Ardeidae and probably closest to the stock from which the rest of the family evolved.

The three genera containing the larger species, *Zonerodius*, *Tigriornis*, and *Tigrisoma*, form a well-characterized group and are collectively known as tiger herons, the term "tiger herons" being preferred over "tiger bitterns" for they are herons, not bitterns. *Zebrilus* differs from these forms in several respects, mainly its small size and coloration, and at first may appear too distinct to fit in with the Tigriornithini. If the variation in the three tribes is compared and if also the relict nature of the Tigriornithini is considered, the gap between *Zebrilus* and the larger tiger herons can be seen to be the result of a lack of intermediate genera and not of a greater difference in structure.

The dorsal plumage is generally dark brown or black, with lighter-colored bars or fine vermiculations; the under parts, especially the neck, may be streaked. The immature plumage is dorsally light reddish brown, with coarse, dark bars producing a barred or sometimes a spotted effect. The major difference between the immature and adult is the relative widths of the black and brown bars in the feathers; the narrow black bars of the immature become wider in the adult and almost obscure the lighter brown bars. The gross change between the immature and adult plumage is thus from a reddish brown bird with coarse black bars to a dark brown or black bird with narrow light brown bars. The under parts of the immature are generally a dirty white or light brown in color, sometimes with faint streakings. Plumes are little developed, consisting of a tuft of crown plumes. The shape of the bill and scutellation of the tarsus vary greatly among the genera and are described under each genus. All species have at least three pairs of powder down patches, but *Tigrisoma salmoni* and *T. mexicanum* have an extra pair. A small projection is found on the jugal bar where the lacrimal bone attaches. This structure is not found in the other groups of the Ardeidae, although in some, notably *Ardea*, the lacrimal bone is large and firmly fastened to the jugal

bar. Because no skeletons of *Zebrilus* have been available for study, the condition of the jugal bar in this species is unknown.

Tiger herons are solitary, secretive birds usually found along wooded streams, but may be found in marshes or along the sea coast (Dickey and van Rossem, 1938, pp. 82–83; Chapin, 1932, pp. 423–424; Bannerman, 1930, pp. 81–82). The last two are especially true of *Tigrisoma* (Wetmore, 1926, p. 59; 1946, p. 22). The solitary nest is placed in a tree near water and sometimes on rock cliffs (*mexicanum*) (Dickey and van Rossem, 1938, p. 83; Wetmore, 1946, p. 22). All have a loud booming note, not unlike that of the large bitterns (Gurney, 1928, and the above-cited works). They often resort to the concealing pose when alarmed, even when in the open or when perched in a tree (Naumburg, 1930, p. 94; Friedmann and Smith, 1950, p. 435). The habits of *Zebrilus* are unknown.

The distribution of the tribe is justly called relict. The different genera are each found in a small area and usually in a different part of the world: *Zonerodius* in New Guinea, *Tigriornis* in central Africa, *Tigrisoma* in Middle America and South America, and *Zebrilus* in northern South America.

A survey of the characters and a consideration of the distribution of the Tigriornithini lead to the conclusion that the tiger herons are close to the ancestral stock of the Ardeidae. Many characteristics, such as general habits, nesting habits, plumes, and powder down patches, are found in the most primitive condition in this group and become increasingly specialized in the rest of the family. The relict distribution suggests an earlier, more widespread distribution and subsequent replacement by later groups of herons. This is not to imply that the recent species are the ancestors, but that the ancestral stock is close to the group to which the recent species belong. There is no question that the tiger herons are members of the Ardeinae, for they possess all the typical Ardeinae characters. They share, however, many characters with the bitterns, such as solitary habits, cryptic coloration, loud booming note, and frequent use of the protective pose. It is important to note that these characters are also shared with the less-specialized members of the Nycticoracini and, to a lesser extent, the Ardeini.

Zonerodius Salvadori (*heliosylus*), 1882

INCLUDED SPECIES: *heliosylus*.

DIAGNOSIS: Dorsally black, with narrow, light tan bands crossing the feathers, producing a barred plumage. The breast is like the back, the

chin is white, and the belly is white suffused with tan. The immature plumage is much lighter in color; the back and breast feathers appear brown, with narrow black bars, and the belly is white in color. The bill is short and heavy, like that of *Nycticorax*. The scutes are continuous across the front of the tarsus. The powder down patches are all separate from one another, and the powder down is white in color. A crest of short black plumes is present.

RANGE: New Guinea and adjacent islands.

Tigriornis Sharpe (*leucolophus*), 1895

INCLUDED SPECIES: *leucolophus*.

DIAGNOSIS: The dorsal surface and neck are dark reddish brown in color and crossed by narrow bars of dark tan. Breast and belly are about the same color as the back, but with whitish streaks. The immature plumage is lighter in color, but is more like that of the adult than in the other genera in respect to the relative widths of the dark and lighter bands of color of the back and neck feathers. The bill is long and slender, unlike the shorter, heavier bill of the other genera of tiger herons. The scutes across the front of the tarsus are subdivided and are hexagonal in shape. Three pairs of powder down patches are present; the powder down is gray, not white, in color. A small crest of white feathers extends caudad from the center of the crown.

RANGE: Forests of central Africa (Congo).

Tigrisoma Swainson (*lineatum*), 1828

INCLUDED SPECIES: *lineatum*, *salmoni*, and *mexicanum*.

SYNONYMS: *Heterocnus* Sharpe, 1895 (*mexicanus*); *Tigribaphe* Reichenow, 1912 (*leucolaema* = *salmoni*).

DIAGNOSIS: Color of the back and wings is brown-gray, with fine light-colored vermiculations, and the under parts are reddish brown, with white streakings on the fore neck. Immature plumage is much lighter in color than the adult plumage and is composed of a ground color of light reddish tan, with narrow black bars producing a pattern of many light-colored spots, rather than a barred plumage as in the other genera of tiger herons. The throat is bare (*mexicanum*) or covered with short feathers. Bill is short and heavy as in *Zonerodius*. The scutes across the front of the tarsus are subdivided and hexagonal in shape as in *Tigriornis*. Three (*lineatum*) or four (*mexicanum* and *salmoni*) pairs of powder down patches; the patches on the ventral surface of *mexicanum*

and *salmoni* are connected. A crest of black feathers, similar to that of *Zonerodius*, is present.

RANGE: Middle America and South America; from northern Mexico south to Argentina.

REMARKS: The Mexican Tiger Heron is not distinct enough from *lineatum* and *salmoni* to warrant its being placed in a separate genus, *Heterocnus*. It agrees closely with its congeners in all respects except in the feathering of the throat, and here the difference is a matter of degree; *mexicanum* has a bare throat, while *salmoni* and *lineatum* have the throat more or less covered with short feathers.

Peters (1931) lists *mexicanum* as *Heterocnus cabanisi*. Subsequently van Rossem (1942) showed that *Tigrisoma mexicana* Swainson, 1834, had priority over *Heterocnus cabanisi* Heine, 1854, and gives the correct name for the Mexican Tiger Heron as *Heterocnus mexicanus*.

Peters (1931) lists *T. (lineatum?) bolivicanum* and *T. (lineatum?) fasciatum* as doubtful species. Hellmayr and Conover (1948, pp. 222, 224) give *fasciatum* as a subspecies of *lineatum* and state that *bolivianum* is inseparable from *marmoratum*, another subspecies of *lineatum*. I have seen only a few specimens of *bolivianum* and none of *fasciatum* (which I know only from descriptions) and can only agree that they are not separable specifically from *lineatum*.

Zebrilus Bonaparte (*undulatus*), 1855

INCLUDED SPECIES: *undulatus*.

DIAGNOSIS: A very small heron, about the size of the small species of *Ixobrychus*, and is the smallest member of the Ardeinae. The adult is very dark in color; black dorsally with narrow whitish bands crossing the feathers and producing a vermiculated effect. The pattern of the under parts is hard to describe because of its complexity. The breast and belly feathers are white, with irregular black bars crossing them. The feathers of the fore neck and upper breast are generally like those of the back, but some are similar to the feathers of the belly. The pattern is further complicated by a varying amount of grayness of the ground color of these feathers. There was much variation in the color of the under parts in the small series of birds available to me. Some birds were much lighter in color, and the complex pattern of the under parts was less developed. It seems most probable that the increase in darkness of the under parts is correlated with age; lightness may be a sign of immaturity, perhaps of second year birds. The adult also has a crest of short black feathers. The immature is lighter in color than the adult and has much reddishness

suffused throughout the entire plumage. Dorsally the young bird is black; the bands running across the feathers are only slightly wider than in the adult but are reddish brown in color, not whitish as in the adult. The head, especially the side of the face and neck, is heavily colored with red. The under parts are a light red-brown, with a black longitudinal streak along the shaft of a few feathers. There is none of the characteristic design found in the adult. The bill is short and moderately heavy. Tail feathers are 10 in number, as in the bitterns.

RANGE: Northern South America.

REMARKS: Peters, following Sharpe, places this species in the Botaurinae. However, neither author cites any reason for doing so or a paper showing why it should be considered a bittern. Ridgway (1878, pp. 223, 225) noted that *Zebrilus* has three pairs of powder down patches and that the outer toe was longer than the inner, concluding that it should be included in the Ardeinae, even though it has only 10 tail feathers. Another character allying it to the Ardeinae is the coloration of the plumage. Its barred back and peculiarly streaked under parts make it unlike any bittern, but rather cause it to agree closely with the other tiger herons and with *Gorsachius goisagi* and *G. melanolophus*. The internal anatomy of *Zebrilus* is unknown. There is no reason to retain this genus in the Botaurinae, and it has been placed in the Ardeinae, where it probably belongs unless new evidence indicates otherwise.

TRIBE NYCTICORACINI

NIGHT HERONS

The night herons consist of two separate lines: an Old World group, *Gorsachius*, and an essentially New World group, *Nycticorax* and *Cochlearius*.

The better-known species feed at night, yet it is still unknown if some, such as *N. sibilator* and *N. pileatus*, do so. Night herons have a stocky body, short legs, and a short stout bill. In *Cochlearius* the bill is broad, but from the side it appears very much like the bill of *Nycticorax*. Head plumes are well developed, but scapular plumes are present in only a few species. Night herons are either solitary (*Gorsachius*), or gregarious (*Nycticorax* and *Cochlearius*) in habits. The nest is usually placed in a tree. The call of the different species is very variable and may be a booming, a high-pitched, or a harsh croaking note.

Gorsachius Bonaparte (*goisagi*), 1855

INCLUDED SPECIES: *goisagi*, *melanolophus*, *magnificus*, and *leuconotus*.

SYNONYMS: *Calherodius* Bonaparte, 1855 (*leuconotus*); *Oroanassa* Peters, 1930 (*magnifica*).

DIAGNOSIS: Night herons with a crest of only slightly elongated, black, lanceolate feathers (reddish in *goisagi*), which closely resemble the short black feathers of the *Nycticorax* crest. The dorsal surface is usually brown, while the under parts are white with irregular streaks of brown or black. The immature plumage is either brown (*magnificus* and *leuconotus*) or gray (*goisagi* and *melanolophus*), but it always has some scattered round whitish spots on the back and wings and a short crest with a narrow white streak along the shaft of the otherwise dark feather. They are solitary birds at all seasons of the year and inhabit wooded streams (Hachisuka, 1926, pp. 588-589; Chapin, 1932, pp. 421-422; Bannerman, 1930, p. 80).

The species of *Gorsachius* fall into two subgroups, the first consisting of *goisagi* and *melanolophus* and the second of *magnificus* and *leuconotus*. The dorsal surface of the wing of the adults of the first group is brown, with many fine vermiculations of a darker brown. The under parts are slightly more heavily streaked with buff than those of the second group. The immature is dark gray, slightly spotted with white, and with a pronounced vermiculation on the wings. It also has a tuft of black feathers with broad elongate white markings on the shaft. Bill is short and rail-like. The species of the second group are more specialized, *leuconotus* being the most advanced member of the genus, for it has the most specialized plumes and is the least like the tiger herons. The color pattern is similar to that of the first group, but without the vermiculations on the wings, and in *leuconotus* the ventral streakings are reduced. The white lanceolate scapular plumes of *leuconotus* form a conspicuous white patch on the back. The immature plumage is much like the adult plumage but has scattered round white spots on the back and wings and has a short crest of dark feathers, with a narrow white streak along the shaft.

RANGE: Restricted to the Old World; *leuconotus* is found in central Africa, and the other species are found in southeastern Asia.

REMARKS: Evolution in *Gorsachius* has presumably proceeded from *goisagi* to *leuconotus*. The specialization of the crest and scapular plumes, reduction of the ventral streaks, and change in bill shape have changed more or less together and in a seemingly linear sequence.

Peters (1930, p. 275) placed *leuconotus* and *magnificus* in separate subgenera of "*Caltherodius*" and correctly pointed out the differences between "*Caltherodius*" and *Nycticorax*. In his "Check-list" these subgenera were elevated to generic rank. However, the characters used to distinguish them, only slight differences of the scapular plumes and bill shape, do not justify generic separation.

Gorsachius has long been considered distinct from "*Oroanassa*" and

"*Caltherodius*," but its two species agree with *magnificus* and *leuconotus* in many respects, such as plumes, coloration, and habits, and *magnificus* is often intermediate in those characters in which *leuconotus* differs markedly from *goisagi* and *melanolophus*. While the species included in this genus are admittedly quite dissimilar, there is no sharp gap between the four species. If one considers that it is more important to use the genus to show relationships between species rather than differences, it would seem wiser to include all four species in one genus than to divide them among two genera "*Caltherodius*" and *Gorsachius*. With little doubt, *Gorsachius* is the most primitive genus in both the Nycticoracini and the Ardeini, as it shares many characters with the tiger herons (see above, p. 24) which the other genera do not. It could perhaps be thought of as a transitional group between the tiger herons and the night herons, but it very definitely tends towards the other night herons in many characters and lacks some important tiger-heron characteristics, such as the immature plumage and the projection on the jugal bar, and thus it is included in the Nycticoracini.

Both "*Caltherodius*" and *Gorsachius* were described by Bonaparte in 1855 in volume 2 of his "Conspectus generum avium." As this is the first time the two genera have been proposed as being congeneric, one of these simultaneously published names must be selected by the first reviser. *Gorsachius* has been used for the longer time (*leuconotus* was generally included in *Nycticorax*) and is the better-known name; therefore *Gorsachius* is hereby designated as the proper name for this genus.

Nycticorax T. Forster (*nycticorax*), 1817

INCLUDED SPECIES: *nycticorax*, *caledonicus*, *pileatus*, *violaceus*, and *sibilator*.

SYNONYMS: *Pilherodius* Bonaparte, 1855 (*pileatus*); *Syrigma* Ridgway, 1878 (*sibilatrix*); *Nyctanassa* Stegner, 1887 (*violacea*).

DIAGNOSIS: Night herons with a crest of short black feathers and several (three to about 15) long lanceolate plumes. The adult plumage varies greatly, but the immature is brown, with elongated, not rounded, spots, and is unlike the adult. No immature specimens of *pileatus* or *sibilator* were available for study, nor do I know the location of any specimens or a description of the immature plumage of either of these two species, so that whether or not *pileatus* and *sibilator* agree with their congeners in respect to the immature plumage is unfortunately still unknown. The under parts are solidly colored, either white or gray. Scapular plumes are developed only in *violaceus* which has many lanceolate scapular plumes. The species of *Nycticorax* are somewhat gregarious while feed-

ing and nest in colonies. They feed in marshes or along the open shores of lakes, the ocean, and other bodies of water.

RANGE: World-wide, but essentially a New World group; *nycticorax* is world-wide, and *caledonicus* (same superspecies as *nycticorax*) is found in Australo-Papua, while *violaceus*, *pileatus*, and *sibilator* are found only in the New World.

REMARKS: The five species of *Nycticorax* combine characters in such a manner that it is impossible to separate them without using four genera as has been done previously. *Nycticorax pileatus* appears as a white night heron and differs mainly from *nycticorax* by being slimmer (for habits, see Friedmann and Smith, 1950, p. 431). The adult of *violaceus* is quite different from *nycticorax* in color pattern and plumes, which is to be expected as they are sympatric, but the immatures are almost identical, and the two species agree closely in general build and habits. The Whistling Heron, *sibilator*, appears as a slim *violaceus*, having similar head plumes and plumage coloration (for habits, see Wetmore, 1926, p. 57). Much must still be learned about the habits and immature plumage of *pileatus* and *sibilator* before we can be certain about their position. *Gorsachius leuconotus* was once placed in the genus *Nycticorax* and still is by some workers, but the two genera, although related, are quite distinct as can be easily seen by a comparison of their characteristics.

The *Nycticorax nycticorax*-*Nyctanassa* *volacea* problem was recently studied by Adams (1955), using the data from 47 measurements taken from a series of skeletons of each species. A good series of each species was measured, and the data were analyzed with the use of excellent statistical methods—the *t* test for differences between the two species and the coefficient of divergence to test sexual dimorphism. The important statistics are given for those measurements that differ significantly, thus offering an excellent basis for the identification of an unknown night heron bone.

Several comments should be made in order that Adams' conclusions can be judged more accurately and validly. Only the data for those measurements that differed significantly were given, while it is necessary to include also the data for those measurements in which the two species do not differ. No closely related species were studied. Here, no doubt, the fault lies in the lack of available material, but these species will also need to be studied. No mention was made of the functional adaptations of the characters studied or whether or not any groups of characters are functionally related to form character complexes. Only two species in the Ardeidae were reported on, and no statement was made on what is meant by a genus in the Ardeidae or how the differences between *nycticorax*

and *violaceus* compare with the differences between other pairs of herons.

Stating some of these difficulties, Adams, in the last paragraph of his summary, offers the tentative conclusion that the two genera should be maintained. It is to be expected that many of the measurements taken carefully on a series of skeletons of two sympatric species should differ significantly and thus by itself the fact that 38 of the 47 measurements differ significantly (t value 2.0 or greater) is of little importance in a determination of the taxonomic status of the two species. Until further study of a similar nature is done, the evidence presented by Adams cannot be considered as contradictory to placing both species in the same genus, a conclusion that I had reached before seeing Adams' paper and that I feel better expresses the relationships of the two species.

The course of evolution and the relationships within *Nycticorax* are still unknown. The largest gap is found between the *sibilator-violaceus* group and the *pileatus-nycticorax* group. The only other definite statement that can be made is that *nycticorax* and *caledonicus* form a super-species. There is little difference between these two allopatric species; the difference is mainly in the color of the dorsal surface. The only available evidence (Hoogerwerf, 1936, 1952) indicates that the two species may occasionally interbreed. Any further statement about the evolution within the genus would at this time be quite speculative.

Cochlearius Brisson (*cochlearius*), 1760

INCLUDED SPECIES: *cochlearius*.

SYNONYM: *Cancroma* Linnaeus, 1766 (*cochlearius*).

DIAGNOSIS: The outstanding feature of this genus is its broad, scoop-like bill. Adults are gray above, with the breast and belly reddish brown and the flanks black. The crest is composed of black, broad, lanceolate-like plumes. The immature has a brown unspotted back, crown black as in the adult, and is sometimes streaked ventrally. Besides the three normal pairs, the Boat-Bill has a small tuft of powder down in the scapular region. Habits so far as known are much the same as those of *Nycticorax nycticorax* (Dickey and van Rossem, 1938, pp. 84-85).

RANGE: Middle America and northern South America.

REMARKS: The curious Boat-Bill of the Neotropics has generally been placed in a monotypic family, the Cochleariidae (Peters, 1931; Wetmore, 1951, pp. 4-5). In their classification of the birds of the world, Mayr and Amadon (1951, p. 6) reduce it to subfamily level in the Ardeidae. At the start of my study, Mayr suggested that perhaps it deserves no more than generic distinction. After a careful survey of its characters and dis-

tribution and considering its possible evolution, I feel that the relationship of *Cochlearius* to the rest of the Ardeidae would best be expressed by assigning it generic rank and placing it in the Nycticoracini next to the genus *Nycticorax*. A further study of the anatomy and behavior of the herons may reveal that *Cochlearius* differs more from the night herons than the presently studied characters indicate. If so and if also the proposed use of tribes in the Ardeinae is accepted, it may be best to establish a separate tribe, the Cochleariini, for the Boat-Bill, but it is extremely doubtful that it is distinct enough to warrant its being given subfamily rank.

The major characters used in the separation of the family Cochleariidae from the Ardeidae were: (a) four pairs of powder down patches; (b) broad flat bill; (c) structure of the palate; and (d) shape of the lacrimal bone. Each character is discussed below, with particular attention given to its variation in the Ardeinae.

Ridgway (1878, p. 220) and Miller (1924, p. 328) correctly state that *Cochlearius* has four pairs of powder down patches. Earlier workers (Gadow, 1893, p. 139; and Beddard, 1898, p. 429) assigned three pairs of patches to this species. In all specimens of *Cochlearius* that I have examined, four pairs of patches were found, the fourth pair being a small tuft in the scapular region at the caudal end of the scapular feather tract which can be easily overlooked. The significance of this tuft is hard to evaluate owing to the manner in which the patches vary, especially in the genus *Tigrisoma*. If the presence of this tuft is partly indicative of family distinction, it could be similarly argued that *Tigrisoma salmoni* and *T. mexicanum* should be placed in a separate family or that the Botaurinae be elevated to family rank; either action would be ridiculous. Thus while the extra pair of powder down patches should be considered, it would be best not to place too much importance on this character.

The bill is much broader than the typical heron bill and is the most important distinction between *Cochlearius* and other herons. Ridgway (1878, p. 220) writes, "Bill greatly depressed and excessively dilated laterally, the lateral outlines much bowed; gonys excessively short, not longer than the width of the mandibular rami." These have been cited as separate characters, but all are part of the general development of the bill and constitute only a single character. The question is not whether or not the bill is different from that of other herons, for there is no doubt about this, but, rather, how much weight should be given to this character in view of the fact that in birds the bill is one of the most variable of all structures. I believe that much care and caution must be exercised in erecting a monotypic family, if a difference, even such a profound one,

in the structure of the bill is one of the few characters on which this monotypic family is based and especially if it is the only character that distinguishes such a group.

The palatines of *Cochlearius* flare out to the sides and are quite unlike the narrow palatines of the rest of the Ardeidae. I do not know the significance of this development but believe that it must be functionally correlated with the bill. The size and shape of the lacrimal bone are highly variable in the family, and in *Cochlearius* it is much smaller than the lacrimal in any other heron. Again the correlation between the lacrimal bone and the bill, in both *Cochlearius* and the other herons, is unknown. I strongly suspect that much of the anatomy of the skull of the Boat-Bill has changed in correlation with the enlargement of the bill, and the citing of a long list of these characters means no more than just saying that the bill has broadened and the skull is modified accordingly.

Thus the listed differences between *Cochlearius* and the other herons has been reduced to one major character—the broad bill and those features, including any unique feeding methods, directly associated with it.

The head plumes of *Cochlearius* are of the broad lanceolate type, very similar to those of *Agamia*. There are also differences in the color of the plumage, but these and the plumes show distinction only at the generic level.

Lorenz (1934, p. 217) states that the appeasing or greeting display is exactly the same in *Nycticorax* and *Cochlearius*, although the head plumes differ. He concludes that the two forms are related and that the greeting display existed before the two lines separated and the different head plumes evolved.

Before the evolution and taxonomic position of *Cochlearius* can be properly discussed, its method of feeding, as well as the niche it occupies, must be known. *Cochlearius* is found in lowland marshes, wooded swamps, and river bottoms (Dickey and van Rossem, 1938, pp. 84–85). While it is known that most of its feeding is done at night, I have been unable to discover the exact method by which it secures its food. If our arguments are based on the present theories of evolution, we must assume that *Cochlearius* feeds in a manner different from that of other herons. A broad bill may be used as a scoop or may enable the bird to feed on smaller animal life. On the label of one specimen in the American Museum of Natural History (A.M.N.H. No. 90929), the collector has written, "... feeds on small fish and shrimps." The latter is somewhat questionable, as the writing is not completely legible. This statement lends some support to the theory that the expanded bill of the Boat-Bill is an

adaption to feeding on smaller prey. This and all known modifications of the head and neck would support either possibility stated above but also would not remove the possibility of the ordinary heron method of feeding.

To summarize, we are dealing with a monotypic genus found in a small area of the world and common where found. It differs from its close relatives by a radical modification of the bill and associated structures. The manner of feeding, although unknown, is assumed to be different from that of the rest of the Ardeidae.

If one of the major criteria in the evolution of a new group is the successful filling of a new niche, and evolutionary change is to be expressed in classification, what is to be done with a group such as *Cochlearius*? The term "successful" is somewhat ambiguous, but I think the following discussion will make the meaning clear.

The spoonbills, Plataleinae, may serve as an analogous example. This group differs from the other threskiornithids mainly in the structure of the bill, which is flattened and broadened instead of thin and decurved, and a correspondingly different method of feeding. The spoonbill skims its bill sidewise through the water instead of picking its food up with the tips of its bill as do the other threskiornithids (Bent, 1926, p. 19). The spoonbills are world-wide in distribution, with six good species placed in three genera, the validity of which is questionable.

In the course of evolution of a group, one of the most important changes is the development of new feeding habits. Thus there should be, and are, groups that are very similar to the parent group except for one notable character that enables the animal to feed in a different way. The question is, When should family or other distinction be given and by what criteria? If the new type has spread world-wide, showing exploitation of the niche wherever available, or if it has given rise to an adaptive radiation in a more restricted area, I would consider this group as "successfully" evolved and that it should be given additional distinction in the classification, expressed by placing it in a higher category.

Thus the spoonbills, but not the monotypic *Cochlearius*, would be considered as having reached subfamily level. For reasons unknown to us, *Cochlearius* has not spread farther than Middle America and northern South America. Even though the Boat-Bill is in the first stage in the evolution of a new subfamily, we cannot be sure that it will ever reach this new level and to give it subfamily (or family) rank now would be to confer upon it a distinction that it has not yet attained.

For a more complete and detailed discussion of the above argument, see Simpson (1953, chap. 11) and Mayr, Linsley, and Usinger (1953,

pp. 48-51). This type of argument is, of course, invalid for such birds as the dodo (Raphidae) or kagu (Rhynochetidae), for these, though they have an extremely restricted range (island or small archipelago), are quite different morphologically from their nearest relatives and thus do not satisfy one of the basic requirements for the argument; that is, the group in question differs from its nearest relative mainly, or only, by having a different adaption, feeding or otherwise, involving both morphology and behavior.

The affinities of *Cochlearius* to *Nycticorax* are noted above, and once *Cochlearius* is reduced to generic level, there is no choice but to place it next to *Nycticorax*.

TRIBE ARDEINI

TYPICAL HERONS

This tribe consists of the day-feeding herons and includes the most advanced genera in the Ardeidae.

The body is slim, the legs and neck are longer than in the night herons, and the bill is long and slender. *Ardeola* and *Butorides* approach the night herons in these respects, being more stocky-bodied, with shorter legs and neck than the other genera of the Ardeini. Plumages are well developed in all genera and reach the peak of their development in the family in such genera as *Egretta* and *Agamia*. The true herons are generally gregarious when feeding and usually nest in mixed colonies; the colonies often include members of the Nycticoracini.

Ardeola Boie (*ralloides*), 1822

INCLUDED SPECIES: *ralloides*, *idae*, *grayii*, *bacchus*, *speciosa*, *rufiventris*, and *ibis*.

SYNONYMS: *Bubulcus* Bonaparte, 1855 (*ibis*); *Erythrocne* Sharpe, 1894 (*rufiventris*).

DIAGNOSIS: The squacco herons are small, stocky, short-legged herons with longer, less-curved claws than those of *Butorides*. The typical color pattern of the breeding plumage is a light-colored body with a darker color on the crown, breast, and back; the color of these areas may or may not be the same. This pattern is even found in the dark-bodied *rufiventris*, but in *idae*, an *Ardeola* in every other respect, the breeding plumage is pure white. This color pattern is due to the darker color of the plumes and is lost after the plumes are shed. The winter plumage is similar to the immature plumage which in most species consists of a brown back, brown and white streaked head, neck, and breast, and elongated crown feathers similar to the crest plumes of *ralloides*. In *ibis*, these

plumages are white, and in *rufiventris*, the winter and immature plumages are brown and somewhat like the immature plumage of *Butorides*. The plumes of the breast, scapular region, and sometimes the crest are filamentous. In addition, all species, except *ibis* and *rufiventris*, have several long lanceolate plumes extending back from the crown. They breed in small to large colonies (Ticehurst, 1923, p. 272; Jackson, 1938, pp. 54–55; and Witherby *et al.*, 1943, pp. 143, 145) and, except *ibis*, are quiet solitary feeders, feeding in marshes, wooded streams, salt mangrove swamps, and even mountain streams along the wider torrents (above citations, and also Whistler, 1928, pp. 397–398; and Deignan, 1945, p. 35). The Cattle Egret is an active feeder, accompanying large grazers in order to feed on the disturbed insects.

RANGE: Southern Europe, Africa, and southern Asia. *Ardeola ibis* has recently invaded Australia, South America, and then North America.

REMARKS: The little-known African species, *rufiventris*, had been placed in a monotypic genus, "*Erythocnus*," but it agrees with *Ardeola* in all respects except for the lack of the lanceolate crown plumes and, as noted above, this alone does not justify generic distinction. The immature plumage of this species differs from that of its congeners and is very similar to that of *Butorides*, possibly indicating relationship between the two genera.

Ardeola ibis, the Cattle Egret, has been shifted back and forth from *Ardeola* to "*Bubulcus*," with little agreement on its position. Those advocating placing it in "*Bubulcus*" point out its very distinctive habit of attending large hooved animals in order to feed on the disturbed insects. However, this feeding habit is not unique in the herons, for the Snowy Egret, *Egretta thula*, has been reported commonly associating with cattle in Florida in the same manner as the Cattle Egret and feeding on the disturbed insects (Rice, 1954). Except for its different feeding habit, the Cattle Egret agrees closely with its congeners and is best included in *Ardeola*.

Salmonsén (1929) studied the genus *Ardeola* and gave particular attention to the geographic variation in the *Ardeola ralloides* superspecies. He concluded that the five species should be considered as conspecific on the basis of the great similarity in the immature and winter plumage which he considers as being more important than the quite distinct breeding plumages. As he pointed out, much must still be learned about the interaction between the species in the areas of overlap, which are quite small in extent. Few or no definite hybrids are known, and thus more support is given to the idea that they are good species. It is most important to know how the forms react to one another in the breeding season.

The quite distinct breeding plumages may well serve to prevent mixed pair formation, which also indicates that these forms are good species. In *Egretta* and many other groups of birds, the species, or at least the males, have quite dissimilar breeding plumages and similar winter plumages. The best conclusion is that the similar immature and winter plumages show common descent and the dissimilar breeding plumages and lack of hybrids indicate that they are full species. They are allopatric, with only small areas of overlap, and thus form a superspecies.

Butorides Blyth (*striatus*), 1849

INCLUDED SPECIES: *virescens*, *sundevalli*, and *striatus*.

DIAGNOSIS: The green herons are small, stocky, short-legged herons, with shorter and more strongly curved claws than *Ardeola*. All species have a dark crest, streaked fore neck and breast, solidly colored side neck (gray or rufous), and greenish variegated back and wings. The scapular plumes are long lanceolate feathers reaching the tail, while the crest consists of short lanceolate plumes. The birds are found in marshlands, wooded swamps, and along the shores of wooded streams and lakes and are common on both fresh and salt water. In general, the green herons feed alone or in small diffuse groups, remaining motionless until their prey comes within striking range. They nest solitary or in small colonies (Bent, 1926, pp. 186-187; Hindwood, 1933, pp. 27-43).

RANGE: World-wide, except for Europe and most of temperate Asia. *Butorides striatus* and *virescens* have subspeciated greatly, there being about 20 subspecies of the former and eight of the latter.

REMARKS: *Butorides rogersi* were described by Mathews as a separate species, and so retained by Peters although he believed that it was probably a color phase of *B. striatus stagnatilis*. However, Mayr (1940, p. 5), in his revision of the green herons of the Australian region, concluded that *rogersi* is a well-marked subspecies of *striatus*.

Amadon (1953, p. 404) briefly discussed a possible history of the dispersal of the species of *Butorides* and concluded that *virescens* may have reached North America by way of Asia, that *striatus* most likely crossed the South Atlantic from Africa to South America, and that then the two forms spread until they met in Panama and other areas of overlap. The three species of *Butorides* constitute a superspecies and may be conspecific. The major difference between *virescens* and *striatus* is the color of the neck, rich rufous in the former and gray in the latter. I have briefly examined the series of green herons in the American Museum of Natural History and noted what appeared to be a trend

towards *striatus* in the neck color in the Central American populations of *virescens*. The only solution to this problem involves careful collecting of breeding herons in Panama and other possible areas of overlap, such as the Lesser Antilles. If these two forms are found to be only subspecies, *sundevalli*, a melanistic form of the Galapagos Islands, would be best regarded as a well-marked race of this species.

Hydranassa Baird (*tricolor*), 1858

INCLUDED SPECIES: *picata*, *ardesiaca*, *caerulea*, *tricolor*, and *rufescens*.

SYNONYMS: *Florida* Baird, 1858 (*caerulea*); *Dichromanassa* Ridgway, 1878 (*rufescens*); *Melanophoyx* Sharpe, 1894 (*ardesiaca*); *Tonophoyx* Mathews, 1913 (*picata*).

DIAGNOSIS: *Hydranassa* includes small- to medium-sized species, found on both fresh and salt water. The scapular plumes are lanceolate to filamentous. Any further description is hard to give because of the great diversity of the species; it is necessary to show how each species is related to the others in order to justify placing them in one genus.

Hydranassa tricolor and *rufescens* are closely related; their plumes, color pattern, and habits (Bent, 1926) are all very similar. The scapular plumes of each are almost identical—a mixture of lanceolate and filamentous feathers. There is a strong tendency in *tricolor* towards the neck plumes of *rufescens*, but the head plumes are different: a tuft of short white lanceolate plumes in *tricolor* and many short lanceolate feathers covering the entire head, including the face, in *rufescens*.

Hydranassa picata is similar to *ardesiaca* in plumes, both having a long heavy crest of lanceolate plumes and lanceolate scapular plumes, the latter being short in *picata*. The Pied Heron, *picata*, appears quite distinct on account of the striking contrast of the white neck and breast against the rest of the body, but this is not of importance. *Hydranassa ardesiaca* resembles *rufescens* in having a great development of plumes. However, the plumes are all lanceolate and not partly filamentous.

The Little Blue Heron, *caerulea*, is intermediate between the two groups, and it is difficult to determine whether it is closer to *tricolor* or to *ardesiaca*. It resembles *tricolor* in the color of the plumage and the nature of the small tuft of crest plumes. However, the scapular plumes of *caerulea* are similar to those of *ardesiaca*. There is a rare color phase of *ardesiaca*, formerly called *Melanophoyx vinaceigula*, in which the color of the neck and under parts is rufous maroon similar to the neck color of *caerulea* and indicating relationship between the two species.

RANGE: Temperate and tropical Americas, central and southern Africa, and the Australian region.

REMARKS: *Hydranassa rufescens* has three color phases: white, dark, and intermediate. The immature of *caerulea* is white, while the adult is blue.

Melanophoyx vinaceigula is known from two specimens collected in the Transvaal (Ayres, 1871, p. 264). Since then no more specimens have been collected in an ornithologically well-known area. From the description given in Ayres and in Sharpe's "Catalogue," the only difference between it and *ardesiaca* is the color of the neck and under parts, rufous maroon instead of black. For these reasons I consider *vinaceigula* a color phase of *ardesiaca*.

The lack of characters distinguishing *Hydranassa* from *Egretta* presents a major problem. Other than the difference in plumes, I have been unable to find any good character that separates the two genera. Both genera inhabit fresh and salt water, contain small, medium, and large species and active and slow-moving species. Up to five species of both genera are sympatric, as in the Gulf states, and breed in the same colony. It should be noted that a hybrid between *Hydranassa caerulea* and *Egretta thula* has been reported by Sprunt (1954). Much more detailed work is still needed before the relationships and ecological differences in the *Hydranassa-Egretta* complex are fully understood. Until these studies are carried out, it is best to maintain these two genera.

It is reasonable to assume that *Hydranassa* and *Egretta* evolved from a common ancestor. Among the living species, *Egretta sacra* seems closest to the possible ancestral form. In this egret the scapular plumes are a mixture of lanceolate and slightly specialized aigrettes, and the plumes found in all the other species of the two genera appear as specializations, beginning at this point.

Baird described both *Hydranassa* and "*Florida*" in the same volume (9, 1858) of the "Reports of the explorations and surveys for a railroad from the Mississippi River to the Pacific Ocean." As this is the first time the two genera have been considered as being congeneric, one of these simultaneously published names must be selected by the first reviser. There is no reason to select one name over the other, so *Hydranassa* is quite arbitrarily designated as the proper name for this genus.

Egretta T. Forster (*garzetta*), 1817

INCLUDED SPECIES: *sacra*, *eulophotes*, *thula*, *gularis*, *dimorpha*, *garzetta*, *intermedia*, and *alba*.

SYNONYMS: *Herodias* Boie, 1822 (*egretta* = *alba*); *Garzetta* Kaup, 1829 (*garzetta*); *Casmerodius* Gloger, 1842 (*albus*); *Demigretta* Blyth, 1846 (*sacra*); *Lep-terodius* Heine and Reichenow, 1890 (*gularis*); *Leucophoyx* Sharpe, 1894 (*thula*); *Mesophoyx* Sharpe, 1894 (*intermedia*); *Hemigarzetta* Mathews, 1914 (*eulophotes*).

DIAGNOSIS: The herons of this genus are characterized by aigrettes, found in no other species of herons. All species are white or have a white color phase. Those (*sacra*, *gularis*, and *dimorpha*) with a white and dark phase also have a mottled or intermediate phase (see Mayr and Amadon, 1941, for a more extensive discussion of color phases in *Egretta*, especially *sacra*.) Three subgroups can be distinguished, based on the condition of the crest plumes. The first group (*sacra*, *eulophotes*, and *thula*) has a crest of short, aigrette-like plumes. The crest of the second group (*garzetta*, *dimorpha*, and *gularis*) is formed of a tuft of short, aigrette-like feathers and two long lanceolate plumes. The last group (*alba* and *intermedia*) has no crown plumes.

RANGE: World-wide, in temperate and tropical areas.

REMARKS: Peters (1931) placed the species of egrets in five genera and then separated the genera in his listing, which only obscured the close relationship between these species.

Egretta alba is much larger than its congeners and is sometimes believed to be related to *Ardea* (Parkes, 1955, p. 288). The slow, deliberate actions of *alba* are similar to those of the larger species of *Ardea*, but little is known of the behavior of the smaller species of *Ardea* (e. g., *novae-hollandiae* and *pacifica*) and of *Egretta intermedia*. However, in general larger birds tend to be less active than smaller species closely related to them. The shape of the ectethmoid bone (Adams, 1955, p. 60) is similar in *Ardea* and *Egretta alba*. I have briefly checked the variation in size and shape of this bone and noted what seemed to be a rough correlation between the size of the bill and size and shape of the ectethmoid bone. More careful study must still be done, but it is suggested that the similarities between *E. alba* and *Ardea* are due to the large size in both groups. As most of the differences between the small egrets and *alba* are probably the result of difference in size and as *intermedia* bridges this gap, *alba* is best included in *Egretta* unless new evidence indicates otherwise. The reef heron, *sacra*, has often been separated (sometimes with *gularis*) because of its heavy bill and short legs, but it is connected to *garzetta* through *gularis* and to *thula* through *eulophotes*. *Egretta gularis* is close to *sacra* in bill shape and leg length, but identical to *garzetta* with respect to the plumes. The development of the plumes in *eulophotes* is intermediate between that of *sacra* and that of *thula*. The Snowy Egret, *thula*, has often been considered (e. g., Parkes, 1955, p. 288) closely related to *garzetta* because of its long legs and thin black bill, but the two species have quite different plumes and appear not to be closely related.

The problem of the relationships to *Hydranassa* is discussed above under that genus.

The African egrets have long been a difficult systematic problem, and most papers have done little to solve it (Steinbacher, 1936; Grant and Mackworth-Praed, 1933, 1934, 1938, and 1943). Although brief, the best review of the *gularis-schistacea-asha* complex is that of Amadon (1953, pp. 405-406). He considers *gularis* and *schistacea* as conspecific and *asha* (as pointed out by Grant and Mackworth-Praed, 1933, pp. 194-195) synonymous with *schistacea*. *Egretta dimorpha* is very similar to *garzetta* and may be conspecific with it, but until this is definitely shown, the two species are considered distinct members of a super-species.

Ardea Linneaus (*cinerea*), 1758

INCLUDED SPECIES: *purpurea*, *novaehollandiae*, *pacifica*, *cinerea*, *herodias*, (*occidentalis*), *cocoi*, *melanocephala*, *humbloti*, *goliath*, *imperialis*, and *sumatrana*.

SYNONYMS: *Typhon* Reichenbach, 1852 (*goliath*); *Audubonia* Bonaparte, 1855 (*occidentalis*); *Pyrrherodia* Finsch and Hartlaub, 1870 (*purpurea*); *Phoyx* Stejneger, 1887 (*purpurea*); *Notophoyx* Sharpe, 1895 (*novaehollandiae*); *Myola* Mathews, 1913 (*pacifica*).

DIAGNOSIS: These are medium to large herons, including the largest of all herons. All have lanceolate plumes which are especially well developed in the first of the two subgroups. The genus is composed of two groups, which grade into one another, *humbloti* being the most nearly intermediate form. The first group is characterized by a slimmer bill, primaries darker than the rest of the wing, crest usually long (absent in *pacifica* and *novaehollandiae*), and long scapular plumes. Members of this group are *purpurea*, *novaehollandiae*, *pacifica*, *cinerea*, *herodias*, *occidentalis*, *cocoi*, and *melanocephala*. The species of the second group, composed of *sumatrana*, *imperialis*, and *goliath*, have a very deep bill, primaries the same color as the rest of the wing, short scapular plumes, and the crest short, with a few longer feathers, but these feathers are still shorter than those in the well-developed tuft of the first group.

RANGE: World-wide, in tropical and temperate zones.

REMARKS: There is no reason to retain "*Notophoyx*" for *novaehollandiae*. It is best described as a dwarf *Ardea*, and it closely resembles the other species, especially *pacifica*, in color pattern and plumes. *Ardea pacifica*, which was also once considered a member of "*Notophoyx*," is intermediate between *novaehollandiae* and such species as *cinerea*.

The Purple Heron, *purpurea*, is quite different from its congeners in being brightly colored and having different breeding habits and associated structures. It generally nests in large colonies in marshes, but sometimes the nest is placed in a tree (Witherby *et al.*, 1943, p. 134). Its "big-footedness" is due partly to its long, slightly curved claws, this being an adaption to walking and perching on reeds.

The species of the second subgroup (*goliath*, *sumatrana*, and *imperialis*) are all allopatric and similar to one another. They may be conspecific but are at present considered as species of a superspecies.

The species *cinerea*, *herodias*, and *cocoi* are also allopatric and very similar, but, until further work is done, it is best to retain them as distinct species forming a superspecies.

The status of the Great White Heron, *occidentalis*, remains unsolved even after much attention has been devoted to it. Bangs (1915, pp. 483–484) concluded that it is a color phase of *herodias*, pointing to the Reddish Egret and the Least Bittern (*exilis*) as analogous examples. Holt (1929) studied the bird in the field and museum and made a thorough review of the literature. He concluded that *occidentalis* is a distinct species which hybridizes with *herodias*, but his conclusions do not readily follow from his evidence. The most recent study of the problem is that of Mayr (1956), who reviews Holt's paper and the more recent evidence in the light of modern knowledge and suggests that *occidentalis* is a localized subspecies, in the Florida Keys, of *herodias*. His suggestion is in agreement with much of the evidence but still leaves many open questions. However, no paper to date has presented a fully convincing argument. The structural and behavioral characters of *occidentalis*, its distribution (Florida Keys, Greater Antilles, and Yucatan), and its interbreeding with *herodias* make the problem a complex one. Most statements about the status of *occidentalis* are only brief notes which do not consider all aspects of the problem. Several points should be made, as they have largely been overlooked in the past. No one has carefully considered the Antilles and Yucatan populations, but rather most of the work deals only with the Florida birds. These other populations must be studied before any conclusions are drawn. The much shortened crown and scapular plumes have often been discussed, but no one has pointed out that they resemble those of the *goliath* superspecies. This resemblance is probably the result of convergence, but it should be pointed out. The bill, however, is like that of the *cinerea* group. Much more work still needs to be done before the problem is solved and until then *occidentalis* should be considered as a form of unknown status.

Agamia Reichenbach (*agami*), 1852

INCLUDED SPECIES: *agami*.

SYNONYMS: *Doryphorus* Reichenow, 1877 (*agami*); *Doriponus* Heine and Reichenow, 1890 (*agami*).

DIAGNOSIS: This most peculiar heron has short legs, a very long neck, and a very long and slender bill. The crown and scapular plumes are broad lanceolate feathers. Along the side of the neck are unique sickle-shaped plumes, which are short, curved, lanceolate feathers. By examining the feathers of the entire neck, one can see all stages of development from the unspecialized feather to the most highly developed sickle plume. *Agamia* is the most richly and brilliantly colored of all herons; the under parts are bright chestnut, the back is blue, and the neck, crown, and scapular plumes are pale blue. The immature is brown dorsally, with dirty white or tan under parts. The fore neck and breast are streaked as are those of the immature of the green heron.

RANGE: Middle America and northern South America.

REMARKS: This heron is so aberrant that I have been unable to discover the true relationships. It may be related to the short-legged *Butorides*, as judged from its short legs and immature plumage, but this is little more than a guess.

"Notophoyx"

At the beginning of the present study, Mayr suggested that "*Notophoyx*" was not a valid genus, remarking that the only character that the two species shared was that they were both found in the Australian region. Subsequent study did not reveal a single character allying the species of this polyphyletic genus and at the same time excluding all other species of herons. The two members of "*Notophoyx*," *novaeollandiae* and *picata*, have been assigned to other genera (see *Ardea* and *Hydranassa*). As *novaeollandiae* is the type species of this genus, "*Notophoyx*" is placed in the synonymy of *Ardea*.

HISTORY AND FUTURE DISCOVERIES

In a family of large and conspicuous birds like the herons, it would be expected that all the species had been discovered long ago. This is exactly the case in the Ardeidae. A rough tabulation of the years in which the various species of herons were described reveals that only half a dozen new species have been discovered in the last 100 years, and only one (*Egretta dimorpha*, 1914, which may be a race of *garzetta*)

has been described in the last 50 years. In view of the small number of good species of birds described in the past two decades in spite of intensive field work in all parts of the world, it is quite safe to predict that no more species of herons remain to be discovered.

Except for purely taxonomic work, however, study of the family has been largely neglected. The present paper represents the first attempt to revise the family on the generic level since Reichenow's study in 1877, but it must still be considered a preliminary survey. Comparative and functional anatomy of the herons is still in its infancy, despite the fine work of the earlier anatomists, and most of the work in this field remains to be done. Adams has initiated a study of the comparative osteology of the herons and has already published one paper treating the night herons (Adams, 1955). I am continuing study of the relationships of the Ardeidae and have started an investigation of the comparative and functional anatomy of the herons. Except for the studies on *Ardea cinerea* (Verwey, 1929, 1930). *Nycticorax nycticorax* (Lorenz, 1934; Noble *et al.*, 1938, and 1942; and Allen and Mangels, 1940) and *Butorides virescens* (Meyerriecks, unpublished), almost nothing is known about the courtship of herons. Fortunately there is now a great deal of interest in this aspect of behavior, which must be fully known before we can understand the significance of the differences in the plumes and how so many closely related species can breed together in the same colony. Some other regions of inquiry that are still largely unexplored and that are important to the understanding of the evolution of the herons are their ecology; how several closely related species can exist in the same place; their migrations and movements in relation to the distribution of the family; and many problems of geographic variation, such as the *Butorides* complex and *Ardea herodias-occidentalis*.

Although the species of herons have long been described, knowledge of their biology is still very sparse, offering many opportunities for the interested student.

SUMMARY

A classification of the Ardeidae is proposed in which 64 species of herons are recognized and placed in 15 genera, as compared to the 70 species and 32 genera of Peters (1931). No new species or genera are proposed. The genera are arranged in the two recognized subfamilies, the Botaurinae and the Ardeinae, and in addition three tribes, the Tigriornithini, the Nycticoracini, and the Ardeini, are proposed in the Ardeinae. The family Cochleariidae has been dropped, and *Cochlearius* is

assigned to the Nycticoracini. A discussion of subspecies lies outside the scope of this study. A diagnostic description is given for each group except the Ardeidae with the use of the characters listed below.

The major characters used in this study are: powder down patches, plumes, proportions, color and color pattern, bill, toes and claws, call, and nesting habits. Each character is described, and the variation and evolution in the family and the value in the proposed classification are discussed. In addition, anatomy and life history data are used to a lesser degree. The extent of the knowledge of the behavior of the Ardeidae is mentioned.

Many of the important recent papers dealing with the systematics of herons, except subspecies, are briefly mentioned, and their conclusions commented upon.

A brief mention of the present state of our knowledge of the biology of the Ardeidae is presented, which indicates mainly that we are still in the beginning stages. There is at present much interest in the anatomy and behavior of the herons, and several studies of the anatomy (Adams, Bock) and of the behavior (Meyerriecks) of herons are now in process. Any speculations on the evolution of the herons should wait until these studies have been completed.

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