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THE LIGHT OF RECENT PUBLICATIONS

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While my study of the parasitic weaverbirds (1960) was in press, an important paper by Steiner (1960) appeared. Although his attention was centered largely upon the waxbills and their allies (the spermestids of his paper; estrildids of mine), he briefly discussed the systematic position of the Viduinae and their relationships with the waxbills and came to conclusions different from my own. Inasmuch as Steiner's experience and thinking concerning the waxbills were both prolonged and extensive, it is necessary to consider his comments carefully and objectively, even though I am still of the opinion that to accept them poses more difficulties than it solves.

The various recommendations made by Steiner and others prior to 1959 were reviewed in my account (1960, pp. 3-9), where a consideration of their not altogether harmonious contents led me to conclude that it was more nearly correct and acceptable to keep the waxbills and their allies in the Ploceidae than to erect a separate family for them. It was recognized that there were substantial arguments for recognizing a separate family for the estrildines, but there were equally suggestive ones for keeping them as a subfamily of the Ploceidae. One could not lightly overlook the conclusion that they constitute a distinct family arrived at by two of their most careful investigators, Steiner and Nicolai, under conditions of aviculture. On the other hand, Chapin's very extensive field acquaintance with many of the included genera and species and his interest in the classification of the whole assemblage caused him to consider them as one family. In his last extensive treatment of a good portion of the whole weaverbird complex, Chapin (1954, pp. 286-287) has this to say:

The three most highly specialized subfamilies are believed to be the Passerinae, Ploceinae, and Estrildinae. The most primitive group of all is the Bupalornithinae, which at one time I believed should be treated as a distinct family. In 1925 Peter Sushkin convinced me that the Plocepasserinae are distinctly intermediate between the buffalo-weavers and the sparrows, and he

regarded *Sporopipes* as fairly close to the ancestral line of both Ploceinae and Estrildinae.

I still find it difficult to visualize a possible common ancestor for these two subfamilies. Suslikin considered the *Vidua* group to be fairly close to the Estrildinae, yet showing some rather primitive characters in their anatomy. I have always felt that the Viduinae, now commonly raised to subfamily rank, are closely allied to the Estrildinae, of which they appear to be always nest parasites. They share the curious mouth markings and gape wattles of nestlings, and these were not acquired independently, in my opinion, by the Viduinae through mimicry.

None of the characters that have been cited for the recognition of the Estrildidae is completely trenchant, and none is wholly constant. While it is true that the estrildines show no seasonal plumage dimorphism, which many of the ploceids do have, there are numbers of the latter group that agree in this respect with the waxbills. Among such examples may be cited such genera as *Amblyospiza*, *Bubalornis*, *Dinemellia*, *Histurgops*, *Malimbus*, *Passer*, *Petronia*, *Philetairus*, *Phormoptectes*, *Plocepasser*, *Ploceus* (many species, especially of the subgenera *Heterophantes*, *Hyphanturgus*, *Icteropsis*, *Melanoploceus*, *Melanopteryx*, *Otyphantes*, and *Xanthoploceus*, although many other species have marked seasonal plumages in the adult males), *Sorella*, *Sporopipes*, and *Symplectes*. As shown in my 1960 summary, the presumed behavioral differences are also not constant and therefore they cannot be looked upon as trenchant systematic criteria. It may seem that the point at issue is a very minor one—whether we have two closely related families or two subfamilies of one family—but the difference in the status of the two is supposed to reflect something of the closeness or remoteness of their relationship, and this is important.

The recognition of a separate family Estrildidae, based on admittedly "average," nontrenchant characters, would result in either of two unfortunate situations. If the viduines were to be included as a specialized subfamily of the waxbills, the supposed criteria of the family would break down completely. If the viduines were not included, but were left as a subfamily of the Ploceidae, they would then be separated systematically from the birds to which they seem most closely allied. The closeness of their affinity to the waxbills appears to be agreed upon by most students of the viduines—Chapin, Delacour, Friedmann, Sushkin, and others. For that matter, Steiner, who places them as a subfamily of the Ploceidae and recognizes a separate family for the waxbills and their relatives, admits that the widowbirds developed reflection globules and buccal patterns essen-

tially similar to their estrildine hosts, “. . . auf Grund wirklicher Verwandtschaft . . .,” and he considers the Viduinae as the section of Ploceidae nearest to the Estrildidae.

The immediate problem of uppermost concern to me was, and still is, how to interpret most cautiously and most accurately the parasitic breeding habit of the viduines, and it was obvious that to do so entailed an appreciation of the degree of their phylogenetic affinity to their chief hosts, the waxbills forming the estrildine group.

If the two groups, Viduinae and Estrildinae, were considered as closely related and as stemming from a common ancestral stock, the striking similarity in the mouth markings and reflection globules of their nestlings could be interpreted readily as something retained by both from the stock from which the two groups bifurcated. If, however, the two groups were looked upon as not so closely related and as not derived from a common ancestry, this important feature of their young would have to be treated as a parallel development, and quite probably as an adaptive one on the part of the parasitic Viduinae. This is, in fact, what Steiner concludes when he writes (translation mine) that “in the viduines, as a specialized small sub-family of the ploceines, we have nothing else but a case of true mimicry, which, in the imitation of the mouth markings, is not more astonishing than are other known examples in insects, snakes, and other creatures, and which have developed in the viduines in place of the complicated reflex behavior of nestlings of other brood parasites . . .,” such as the evicting behavior of young cuckoos of some species, and the deliberate and usually lethal attacks by newly hatched Indicators on their nest mates. Steiner expressly calls the mouth markings a “spermestid character” in the viduines, and he considers that in any evaluation of them a decisive role would have to be assigned to the thought that the viduines obtained or developed “through true relationship, in their 6 or 7 species, various distinct mouth-markings similar to those of their similarly distinguishable host species—*Pytilias*, *Granatinas*, *Lagonostictas*, and *Estrildas*. This would presume that each of their species had developed with its coordinated host species from a primitive form, which, in retrospect, must be assumed to have had a disclosed value for each presumed parasite-host pair of species.” As I pointed out in my account, this point of view has also been stated by Southern (1954), who accepted the opinion that the viduines were extremely specialized brood parasites, each species being practically an obligate parasite of a single species of estrildine host to which it was thought to be permanently

attached by virtue of a "very complicated form of mimicry. . . ."

The great difficulty in accepting this appraisal of the host-parasite situation lies in the fact that the several species of *Vidua* are not each rigidly restricted to single species of hosts. Of some of these birds our knowledge is still very scanty (or even wanting), but of others, such as *V. macroura* with 18 recorded kinds of hosts, *V. regia* with 7, *V. chalybeata* with 2, and *Steganura* with 9, the available data certainly contradict any postulated rigid host specificity. To account for the development of nestling mouth markings similar to those of the host species would necessitate, as Steiner himself outlined, a strictly limited host-parasite specificity, and this we do not find to be the case. It is true that each of the species of viduines does appear to have a single most-favored host, but the percentage of deviates from it is too great to ignore. Thus, of the best known species, *Vidua macroura*, I was able to assemble data on 77 records with 18 species of hosts, and of these more than three-quarters were of 10 species of waxbills of the genus *Estrilda* and more than half were of the races of a single species, *Estrilda astrild*. However, the different species of waxbills differ as much in their mouth markings among themselves as do the species of *Vidua*. If, as Steiner implies, the mimetic similarity of buccal patterns of each species of parasite and its normal host can only be looked upon as having an importantly selective survival value, we would expect a considerably higher adherence to the specific host relationship it is supposed to serve.

It might be considered that there may have been such a rigid host selection originally and that subsequently the parasites broadened their range of fosterers, but this would imply a subsequent denial of an original, and ostensibly a continuing, selective force. In view of the inconstant nature of the differences tabulated in support of familial rank for the waxbills, and in view of the great difficulties such an arrangement would make in interpreting the breeding biology of the widowbirds, I still think it better to keep them all in one systematic family group.

It has occurred to me that the above argument may make it seem that the conclusions arrived at may imply something akin to a manipulation of classification to simplify or to eliminate what would otherwise be a perplexing problem, rather than to maintain a systematic arrangement based purely on traditional characters, and to let the tangential problem continue to perplex us if need be. This is not the case, as the characters advanced by the proponents of familial rank for the waxbills are not constant, on the one hand, and the mouth

markings of the nestlings are also valid morphological characters in themselves. The fact that these buccal patterns may be functional as well as morphological, and hence to some extent possibly subject to the pressure of natural selection, need not rule out the possibility, the probability even, that they are also phylogenetically stable characters, useful as indicators of relationship. This idea is by no means novel at this point, nor was it in my 1960 discussion, where (p. 24) I pointed out that Morris (1957, p. 199) concluded that these mouth markings were conservative taxonomic characters and as such were useful aids to understanding the evolution of the birds that have them.

Nicolai (1961) has recently published in abbreviated form the results of a study of the vocalization of several species of *Vidua* under aviary conditions. He studied with a tape recording the sounds produced by *V. macroura*, *V. regia*, *V. chalybeata*, and *Steganura paradisaea* and reported that part of the notes of each was a fairly accurate copy of the song of their host species. He stated that the viduine sounds comprised a "weaverbird-like" series of notes, scarcely distinguishable in the four species, and a series of loud notes and songs of the respective host species (various species and races of *Estrilda*). Nicolai found in the ploceids and estrildids closest to the viduines all songs and notes to be consistently innate and nonvariable, and he concluded that probably the notes of the viduines were similarly somewhat "fixed." He went on to speculate that the young Viduinae probably acquired their vocabulary from their foster parents during their period of dependency in and out of the nest. Only in this way did he think the exclusive reproduction of the vocabulary of the particular host species could have been made possible. Furthermore, he pointed out that in the case of *V. macroura*, which is known to parasitize a number of species of *Estrilda*, each male had invariably only the notes of one host species. There were no cases of mixed songs, a fact which he considered in agreement with his premise as to how the imitative process could have taken place. On the other hand, Nicolai further contended that the "whispering nest notes" of the male, which appear in the vocalization of *V. regia* and *V. chalybeata*, were learned somewhat later, after the birds had become self-sufficient and no longer were in constant contact with their fosterers, when the latter began preparing to breed again and began nest building anew.

Nicolai further concluded that whereas, at the close of the period of parental dependency, the young of other, self-breeding, passerines

might go through what seemed like playing at nest building or playing at heterosexual pursuit, the young parasitic widowbirds were interested in watching the breeding preparations of their fosterers. The precise observations they made and the degree to which they seemed to incorporate these impressions were thought to become important later in their lives in helping to synchronize their reproductive cycles and activities with those of their hosts, and so to become significant in the breeding success of the widowbirds.

Inasmuch as Nicolai's work has not yet been published with sufficiently detailed documentation, it is somewhat difficult to appraise and to criticize his conclusions. The following comments must be read with this in mind, and some doubts that are raised here may prove to be baseless. I must stress that the observations, surprising as they seem to me, merit serious and respectful consideration. Their interpretation seems to be less certain.

For one thing, in a state of captivity birds may sometimes do things they would have little chance of doing or, as far as we know, do not do, in a wild state. I do not know whether Nicolai's birds had the presumed fosterers with them in the cage or in nearby cages where they could hear them. If they were not actually raised in captivity by these fosterers, one wonders how Nicolai could know which was the foster parent species in each instance, unless he assumed the most likely one from the total recorded literature (as was brought together in my book), or unless he assumed the identity of the host from the vocabulary of the parasite. The latter would be a matter of circular reasoning which would hardly be convincing, and which I cannot believe was done. Yet this was the way in which some of Neunzig's original (1929) conclusions seem to have been achieved.

I am wholly convinced that it is possible to learn many things, including vocalizations, from captive birds that it would be very difficult to learn in the free state, but I am still surprised that no one ever reported any constant and marked specific differences in the notes of the various species of *Vidua* in Africa. Although my own fieldwork is now many years past, and I do not pretend to remember accurately the songs and calls of these birds, I can find no mention in my journals of any marked differences between them, and I have found no published observations of others to this effect. This suggests that the differences noted in aviary birds are not sufficiently striking to be obvious in the field but require close-up observation for their discrimination. As a matter of fact, the vocali-

zations of the various host species of the genus *Estrilda*, as described in the literature, are all quite similar, or at least their specific patterns vary only slightly among themselves. This does not mean that the differences are less real, but I cannot dispell the thought that these portions of the songs resembling the notes of the presumed host species may have been due to the limiting conditions of the aviary, whereas the "weaverbird-like" notes common to all four species agree with what is known of their calls in the state of nature.

The very abbreviated form in which Nicolai's data were reported caused them to appear to imply further evidence for a definite host-parasite relationship, but this is not actually implicit in them. We are not informed how many individuals of each species of viduine were observed or under what conditions. Thorpe's (1958) work on the learning of song patterns by small passerine birds, especially the chaffinch, has indicated that the learned, as opposed to the innate, pattern of song is restricted to the "first 13 months of life and towards the end of this time there is a peak period of learning activity of a few weeks during which a young Chaffinch may learn, as a result of singing in a territory, the fine details of as many as six different songs." If Nicolai's assumption is correct, that the young parasitic widowbirds learn the utterances of their foster parents during the first two or three weeks of life, they are apparently more precocious than chaffinches in this respect. Furthermore, we may recall that in the case of parasitic cowbirds and cuckoos there is no sign whatever of the young learning any of the vocalisms of their fosterers. This cannot be looked upon as meaning that the same situation necessarily is true for the parasitic weavers, but judgment must be delayed until evidence is forthcoming. If eventual fuller publication of Nicolai's work should convince us that the viduines enhance their reproductive potential even very slightly by vocal mimicry of their common hosts, we would have to admit an unexpected uniqueness in these birds.

Another study that appeared too late for me to discuss in my account was Ziswiler's (1959) paper on features of the ontogenetic development of the waxbills. While presenting some data on the relative lack of sensitivity of later developmental stages to increasingly long interruptions of brooding, and also some data on the postembryonic (i.e., nestling) growth curves of several species, Ziswiler does not concern himself with the viduines at all; he does not even mention them. His paper therefore gives us no opinions to eval-

uate in the present connection. He does consider the waxbills a systematic family, but he gives no arguments or data either supporting or contradicting this treatment. The data he does present are not given as systematic criteria and show nothing peculiar to the "Spermestidae."

The problem as to which of the numerous described species or races of the combassous are really valid still awaits an answer based on much more extensive and more complete knowledge of them in the field. From my own field studies of many years ago and from much more recent examination of large numbers of museum specimens I arrived at the arrangement given in my 1960 publication. However, almost simultaneously, Wolters (1960) proposed a somewhat different treatment, based in part on observations of aviary birds. These differences are not particularly important, as no one has the data on which to formulate a completely convincing and wholly satisfying classification, but they do point out that until such information is assembled, all our judgments can have only limited validity. In our understanding of the combassous, as contrasted with the present knowledge of the long-tailed viduas, we are still confronted with the species of the systematists rather than the species of the naturalists. This is bound to continue until the living birds are studied much more thoroughly, as further examination of their preserved corpses will only lead to divergent and inconclusive arrangements.

Still more recently, Wolters (1961) has published an arrangement of the viduines in which the short-tailed species (subgenus "*Hypochera*") are placed at the top, whereas I put them at the base of the group. Wolters considers the absence of elongated rectrices in the breeding plumage of adult males to be a secondarily arrived at condition, and that the long-tailed species (subgenus *Vidua* proper) are to be looked upon as representing the original, ancestral character of the group. Also, he suggests that *Steganura* is the basic or primitive member of the viduines, whereas I placed it at the apex of the assemblage. While it is obvious that each of us came to our respective conclusions on the basis of all the evidence we could muster, it now becomes clear that, in the absence of any really conclusive data, these alternate, and, in fact, opposite, arrangements can only be looked upon as interpretations of the purely circumstantial evidence afforded by the appearance and the habits of the existing species. Actually the two classifications agree closely in the relative placement of the included species and genera, but differ in their overall orientation.

In defense of the arrangement proposed in my book I can only repeat here what I outlined there, namely, that inasmuch as rectricial elongation in male nuptial plumage is a character that has developed wholly independently in two of the main groups or sections of the family, it seems probable that within each of these groups the short-tailed species are nearer the stock from which they evolved than are their long-tailed relatives. There is nothing in the life histories of the short-tailed species to suggest that they are in any way more advanced than their congeners with elongated rectrices; in fact, the reverse is more in keeping with our still all too incomplete information. The courtship antics of the combassous are simpler, less involved, apparently more primitive than are those of the long-tailed species. All the viduines are quite similar in their vocalisms and, except for size (in *Steganura*), in the appearance of their eggs. It is perhaps a necessary commentary on so much of our present avian systematics to end this discussion with the observation that the one point of agreement in all these attempts is that we need to know more about the birds themselves.

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