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THE preceding article (Skutch, 1962) calls attention to a species meriting further behavioral and anatomic study. Field experience with *Rhodinocichla* in Panama aroused interest in its taxonomic status, and, as I expressed to Dr. Skutch an opinion very different from his, he generously suggested that I publish my comments. The resemblances to the Mimidae seem to me convergent adaptations to a similar habitat niche. On the available evidence *Rhodinocichla* may properly be kept in the Thraupidae, where Hellmayr (1936) and most subsequent writers placed it.

Relationship with the Mimidae

The taxonomic value of the nine-primaried condition. Mimidae are characterized, inter alia, by a rather long, well-developed tenth (outermost) primary wing quill. Rhodinocichla, like other nine-primaried birds, has the tenth primary represented by a tiny vestige, completely concealed by the primary coverts. The nine-primaried condition is certainly not conclusive of relationships; but it serves as a convenient "key" character because it is usually associated with a complex of other characters found in allied groups. There is an evident evolutionary trend toward reduction in the number of flight feathers. Many more "primitive" bird orders have 11 or more primaries; most non-passerines have 10 (Indicatoridae nine). In the order Passeriformes non-oscines generally have 10 (in a few genera 11 primaries); in the song-bird suborder Passeres (Oscines), the primaries are 10 or nine. Most oscine families have 10 primaries; some seem to be in a transitional stage (e.g., Dicaeidae, Ploceidae, Vireonidae); only a few are definitely nine-primaried. This condition probably evolved independently several times, for it prevails in the Hirundinidae, Motacillidae, and Zosteropidae, families which seem quite distinct from the structurally intergrading group of families often called the "American nine-primaried assemblage." Modern systematists generally agree that this large, anatomically similar aggregation, comprising at least the tanagers, cardinal grosbeaks, American sparrows, buntings, wood warblers, honeycreepers, and icterids, is probably of common ancestry. There is, however, much dispute as to family divisions within the assemblage, and as to whether the cardueline finches, the vireos, and a few anatomically aberrant genera should be included (cf. Wetmore, 1951, 1960; Mayr and Amadon, 1951; Beecher, 1953; Tordoff, 1954; Mayr and Greenway, 1956; Amadon, 1957; Delacour and Vaurie, 1957; Bock, 1960; Storer, in Marshall, 1960: 88-89; George, 1962: 23).

The Mimidae, all systematists agree, belong in a different aggregation,

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including the thrushes, wrens, Old World flycatchers, and similar groups, which intergrade structurally. Some authors (Mayr and Amadon, 1951) treat the mockingbird-thrasher group as a subfamily of the "primitive insect eaters," Muscicapidae *sensu latu* (with the thrushes, wrens, Old World warblers as other subfamilies). Even the majority, who preserve family rank for the Mimidae, classify them in a different group of oscinines from the American nine-primaried assemblage.

CHARACTERS OF *RHODINOCICHLA* NOT FOUND IN MIMIDAE BUT PRESENT IN MANY THRAUPIDAE

- 1. Only nine visible primaries—the tenth vestigial and wholly concealed by primary coverts (cf. Ridgway, 1902: 769; 1907: 180).
- 2. Middle toe adherent to inner toe for about half of basal phalanx (cf. Ridgway, 1902: 769; 1907: 180).
- 3. Lateral toes of equal length (cf. Ridgway, 1902: 769; 1907: 180-181). (Among Mimidae only *Donacobius* shows this, but it has otherwise a different toe arrangement; cf. Ridgway, 1907.)
- Bill rather stout and moderately compressed; not terete (cf. Ridgway, 1902: 769; 1907: 180).
- 5. Rictal bristles obsolete, though present (cf. Ridgway, 1902: 769; 1907: 180).
- 6. Feathers of lores and frontal antiae with bristly points, erect and harsh (*Rhodino-cichla* personally examined; cf. Ridgway, 1907: 180).
- 7. Bony palate "typically tanagrine" (Clark, 1913).
- 8. Sternum "typically tanagrine" (Clark, 1913).
- 9. Hyoidean structures unlike Mimidae and typical of tanagers and other members of American "nine-primaried assemblage" (George, 1962: 8, 17, 23).
- 10. Jaw musculature unlike Mimidae, agreeing with tanagers (*fide* W. J. Beecher, orally).
- 11. Rose-red color (presumably carotenoid pigment) in male plumage.
- 12. Sexes distinctly different in color.

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13. Mouth lining of nestling red (cf. Skutch, 1954: 260; 1962, supra).

Morphology and anatomy. As appears from the attached list, Rhodinocichla shows none of the structural features by which the Mimidae are distinguished. In these characters it agrees with the Thraupidae, and also with some of the other members of the nine-primaried assemblage that intergrade structurally with the tanagers (see below). Comment on some of these characters seems in order.

Clark's (1913) anatomical study (concluding that *Rhodinocichla* was a tanager), although supported by features of external morphology, admittedly was limited in scope and in the amount of available comparative material. For example, he was unable to examine the Hispaniolan Chat-Tanager (*Calyptophilus frugivorus*), which in bill shape, and apparently in feeding habits, resembles *Rhodinocichla* more closely than does any other tanager (see Bond, 1936: 375–376), and which Bond (1956: 168) considers related.

Recently Dr. William George has made an elaborate study of the hyoidean structures (bones and muscles controlling the tongue) in oscinine birds. He found (1962: 7, 8, 23-24) that in the undoubted members of the American nine-primaried assemblage (tanagers, cardinals, American sparrows, buntings, wood-warblers, and their allies) these structures are visibly different from those in the Mimidae and other members of the "primitive insect-eater" aggregation. The hyoidean apparatus of *Rhodinocichla* is typical of the nine-primaried assemblage.

Dr. William J. Beecher, who very recently dissected the jaw musculature of a specimen of *Rhodinocichla*, found that it agreed with that noted in tanagers, was very distinct from that in Mimidae, and also differed from that in the many genera of Icteridae and Parulidae he has dissected (oral comm.).

Further, strongly negating alliance with the Mimidae is the fact that Rhodinocichla is sexually dimorphic and that the male is largely rose-red below. In the Mimidae (as in their allies the Troglodytidae) the sexes are invariably alike, and there is no red (nor even orange or yellow) in the plumage. The absence of carotenoid plumage pigment in Mimidae and its conspicuous presence in Rhodinocichla and in many tanagers (and other members of the American nine-primaried assemblage) seems particularly significant. Rhodinocichla is a skulking species, keeping to the dark undergrowth in shady woodland, which, as Skutch observes, uses loud and persistent vocalizations to maintain contact between the sexes. Yet it preserves the sexual dimorphism and rich red color (modified to magentarose) to be expected in a bird using visual signal characters. To me this suggests that Rhodinocichla, although it has evolved a slender shape and superficially thrushlike bill, suitable to its dense undergrowth niche and insectivorous feeding, still betrays in its color pattern the fact that its ancestors lived in trees or fairly open niches-as do most tanagers and their allies.

Indications of a similar, less-advanced evolution are apparent in two undergrowth tanagers of the genus *Habia*, studied in British Honduras by Willis (1960a, 1960b). Both ant-tanagers are sexually dimorphic and the males preserve red plumage, although the color is noticeably dulled and darkened. Like *Rhodinocichla*, these ant-tanagers live in the dark, low vegetation, are largely insectivorous, probably remain paired through all or most of the year, and have loud, melodious songs. Moreover the species that feeds nearer the ground keeps concealed when singing and tends to sing for a longer period during the day (Willis, 1960a: 76–78, 80). Although less terrestrial than *Rhodinocichla*, both ant-tanagers occasionally do leaf tossing to find a fallen arthropod (Willis, 1960b).

The Chat-Tanager (Calyptophilus frugivorus) of Hispaniola suggests

evolution in bill shape. Like *Rhodinocichla* it is chiefly terrestrial, lives in thickets, has a largely arthropod diet, and utters loud, musical notes, said to be reminiscent of the North American Cardinal (*Richmondena cardinalis*) (Bond, 1936; Wetmore, 425–428). Its apparent allies, the Hispaniolan Palm Tanagers (*Phaenicophilus*), are much more arboreal, much less vocal, and have heavier bills (presumably reflecting a more frugivorous diet).

Calyptophilus, originally described as a tanager, was removed by Ridgway (1907: 180, 278) to the Mimidae (with a question mark) in the erroneous belief that it had a very long tenth primary. Actually, as pointed out by W. deW. Miller (1918), Calyptophilus has the usual invisible, vestigial tenth primary of a tanager; since then systematists have placed it in the Thraupidae between Rhodinocichla and Phaeni-cophilus (Hellmayr, 1936: 357-359).

Nestlings. The nestlings of *Rhodinocichla* have red mouth linings. This, so far as known, is true of all tanagers (Skutch, 1954), as well as some of their allies, but not of any Mimidae.

Juvenal plumage. Although this plumage is not mentioned by Skutch, I checked specimens in the American Museum of Natural History to see what clue to relationship, if any, they might provide. While I am unable to draw any positive conclusions, perhaps because the comparative material for other genera was inadequate, it seems worthwhile to describe the young *Rhodinocichla*, as I have read no good description; Ridgway (1902: 771) had not personally seen a juvenal.

The youngest *Rhodinocichla* available, a female with wings and tail not full grown, was taken at Esquintla, Sinaloa, Mexico, 20 October 1904, and represents the paler race, *R. rosea schistacea*. The generally brownish slate color above and below is relieved by a white superciliary stripe (not extending above the lores), and by a light tawny throat; a tawny tinge appears on the malars (suggesting an indistinct stripe) and on the upper breast; the feathers of the lower breast and abdomen are more or less broadly marked, subterminally or terminally, with pale gray or whitish, producing a rather mottled effect. Specimens from Costa Rica and Panama, *R. rosea eximia*, although older and well advanced into the postjuvenal (first basic) plumage, indicate that the juvenal, while darker, would have a pattern similar to *schistacea*.

I was able to examine juvenals of most genera of Mimidae, but of only about one third of the genera of Thraupidae and their allies in tropical America. Juvenals of all Mimidae examined (except *Melanotis* and *Dumetella*) were streaked below (including *Mimus* with unstreaked adults). Juvenals of all tanagers having unstreaked adults were unstreaked below (except *Piranga* and *Spindalis*, the latter with streaked female in one form). Among American Oscines in which the juvenal is ventrally mainly slaty and somewhat mottled with paler slate, I noted *Melanotis hypoleuca* (Mimidae), *Setophaga* [Myioborus?] picta (Parulidae), Tangara johannae and T. inornata (Thraupidae). In all of these, as in *Rhodinocichla*, much of the ventral surface in adults is differently colored from that in the juvenal plumage. I have not seen a juvenal of *Calyptophilus* or of *Donacobius*.

Voice. As I have heard it in Panama, the voice of *Rhodinocichla* seems to me to lack the elaborate phrasing of thrashers (*Toxostoma*), mockingbirds (*Mimus*), or catbirds (*Dumetella*). To my ear *Rhodinocichla* shouts a loud, clear, repeated phrase, wheeoo-cheéo, chwee, varied to cho-ho, choweé, or cheéa-wo, chowéh. The notes are highly musical, but rather monotonous, and in their ringing repetitiveness somewhat suggest the calls of tropical wrens of the genus *Thryothorus*. *Rhodinocichla* also gives a distinctive alarm call, which I can characterize only as a fluttering or whirring chatter, and when foraging often utters a low whistle, syllabized by Major Chapelle as *fueeooo* (probably the same as Skutch's chio). On 18 April 1961 I saw a captive adult male singing a rather soft, squeaky, but somewhat musical, tew-kadéw-ka, tew-kadéw-ka, tew-kadéw---totally different in quality from the usual ringing notes.

Singing by females occurs in species of many families, including the nine-primaried assemblage. Antiphonal singing by both members of a pair is characteristic of certain tropical birds (notably the wrens), which skulk in the undergrowth and remain paired for all or most of the year. Such duetting regularly occurs in the North American Cardinal, *Richmondena cardinalis* (Gould, 1961: 247), and in the tropical Buff-throated Saltator, *Saltator maximus* (Skutch, 1954: 64), formerly allocated to the tanagers but currently included in the cardinal grosbeak subfamily—which many ornithologists regard as belonging in the same family as the tanagers (Mayr and Amadon, 1951; Beecher, 1953; Tordoff, 1954; Delacour and Vaurie, 1957).

Nesting. The nest of Rhodinocichla illustrated in P. Schwartz's fine photograph (in Gilliard, 1958: pl. 174), with its coarse twig foundation, certainly is very thrasherlike. But, discounting the difference in habitat, it seems to me similar structurally to the nest of the arboreal Western Tanager (Piranga ludoviciana) illustrated in the same work (Gilliard, 1958: pl. 200). According to Schwartz (in Gilliard, 1958: 378), Rhodinocichla eggs usually closely resemble those of the Grayish Saltator (Saltator coerulescens) and sometimes those of the Silver-beaked Tanager (Ramphocelus carbo). Incubation by the male, recorded for Rhodinocichla, is rare in oscinine birds. Among the Mimidae it has been reported only for thrashers. In the nine-primaried assemblage it is regular in the Rosebreasted and Black-headed grosbeaks (Pheucticus ludoviciana and P. melanocephalus) of the cardinal grosbeak group, and has been reported, although perhaps mistakenly (see Skutch, 1954: 120), in the Summer Tanager (Piranga rubra) and a few tropical Calliste (= Tangara) species. It should be noted that we have detailed published incubation data only for about 20 species and some 10 genera of tanagers, out of more than 200 species of more than 60 genera of the family listed by Hellmayr (1936).

Foraging behavior. While "leaf-tossing" occurs in some Mimidae, it is by no means restricted to that family. It prevails in a variety of unrelated ground-feeding birds. Hallinan (1924: 325) reports finding "hard shrub seeds" in the stomachs of two *Rhodinocichla* taken in Panama. Doubtless arthropods are also eaten. Major (now Colonel) F. O. Chapelle wrote me from Panama that the leaf tossing of *Rhodinocichla* reminded him of the Rufous-sided Towhee (*Pipilo erythropthalmus*)—another member of the nine-primaried assemblage. The description of foraging by *Calyptophilus*, although not fully detailed, suggests similar behavior (Bond, 1936).

Zoogeography. The Mimidae seem not to be a truly neotropical group; of the 13 genera usually recognized, none breeds in continental tropical America south of Honduras, except the widely distributed *Mimus* and the aberrant South American *Donacobius*, whose place in the Mimidae has been questioned. The distribution of *Rhodinocichla*, although interrupted, is certainly neotropical.

Conclusion. Inclusion in the Mimidae seems to be negated by the anatomical and morphological evidence, all of which points to the American nine-primaried assemblage. The available behavioral information is in no way inconsistent with this conclusion.

INCLUSION IN THE THRAUPIDAE

Much less clear is the question of family allocation within the nineprimaried assemblage. The family divisions in this group are to a considerable extent matters of convenience and tradition, rather than of clearly defined structural distinctions. When we examine the varied multitude of neotropical genera in this assemblage we find intergradation in all characters that have been proposed to separate the tanagers from the grosbeaks, emberzine finches, wood warblers, and honeycreepers. It is not surprising that almost all recent classifiers differ on family lines in this assemblage (see p. $640 \ supra$).

On known structural characters *Rhodinocichla* seems to fit best with the tanagers, which in this assemblage is the most varied group in bill and body shape. As Clark (1913), Hellmayr (1936), and subsequent systematists placed it in the Thraupidae, a justifiable conservatism suggests that it be kept there until definite evidence to the contrary is produced.

Behavioral similarities with *Saltator*, generally allocated to the cardinal grosbeak group, can hardly warrant a transfer, for that group is separated from the tanagers only by a heavy, conical bill, while *Rhodinocichla* is more slender billed than most tanagers.

The Chat-Tanager, *Calyptophilus*, which shows resemblances in bill and body shape, ties in to the thicker-bill type through *Phaenicophilus*. *Calyptophilus* also shows resemblances of pattern, although the rose is replaced below by white and on the supraloral and carpal regions by yellow. These similarities may be convergent.

Resemblances in red or rose-color pattern are apparent in two other groups. R. W. Storer (1958. Unpublished paper before American Ornithologists' Union) called attention to similarities of both sexes to *Granatellus*, a neotropical genus of small, thickbilled, arboreal birds, with a remarkably interrupted range. *Granatellus* is customarily placed in the Parulidae; it would fit about as well in the Thraupidae. To my eye two South American Icteridae, *Leistes militaris superciliaris* and *Pezites militaris*, show, in males, an even closer resemblance in color pattern—even to the extent of having red on the lesser wing coverts. These open grassland birds show the character by which Icteridae are separated from Thraupidae (unnotched, acute bill). Were *Rhodinocichla* transferred to Icteridae there would be no basis for distinguishing between the two families. The resemblances of pattern cannot be the result of adaptive convergence. They indicate, I believe, common descent from the stock that produced the nine-primaried assemblage and suggest that the ancestors of *Rhodinocichla* lived in a more open habitat.

Rhodinocichla does exhibit behavioral features adapted to its habitat niche, not reported of any of the relatively few tanagers that have been carefully studied. But, it should be noted, the Thraupidae are a very varied aggregation in habits, as well as in body form and bill shape. They represent the major radiation in the American tropics of the great nineprimaried assemblage. Some of the genera of the traditional Coerebidae, now often transferred to the Thraupidae as nectar-adapted tanagers, are certainly more unlike traditional tanagers in bill and body shape and behavior than is Rhodinocichla. The euphonia group of tanagers (Tanagra, Chlorophonia, Pyrrhuphonia) is more aberrant in internal anatomy, feeding habits, and nesting. Unless we are prepared to cut up the traditional tanager family into a number of families, there seems no over-all gain in erecting a separate monotypic family for Rhodinocichla-at least without anatomic basis. The hyphenated English group name "Thrush-Tanager," proposed by Clark (1913), adopted by Hellmayr (1936), and used as Rose-breasted Thrush-Tanager by most recent authors, seems adequately to suggest the taxonomic uncertainty and the appearance of the bird.

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SUMMARY

Rhodinocichla rosea, on the basis of all known structural characters, appears to be a member of the group called "American nine-primaried assem-

blage," which includes the tanagers, cardinal grosbeaks, American sparrows, buntings, wood warblers, icterids, and their allies.

The resemblances to Mimidae (negated by external and internal structural features) appear to be convergent adaptations to a similar habitat niche. The aberrant behavioral features occur also in certain other members of the American nine-primaried assemblage.

Inclusion in the varied family Thraupidae, first suggested by Clark's anatomical study, and adopted by Hellmayr and by most subsequent taxonomists, seems the most reasonable treatment on the basis of our present knowledge.

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