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Parallel Evolution in
the Small Species of *Indicator*
(Aves)

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One of the aspects of avian taxonomy that inevitably has to wait on the gradual amassing of considerable material is the appreciation, and the consequent elucidation, of sympatric sibling species. Until sufficient numbers of specimens become available, the investigator can only treat the minor differences that he may notice as inconsistent, but apparently individual, variations in a not completely homogeneous taxon.

The genus *Indicator* presents an unusual array of sympatric, closely similar species distinguished primarily by size. In the Acacia grasslands of much of eastern Africa there are three similar species (in descending order of size): *minor*, *meliphilus*, and *narokensis*. In the forests of western and central Africa there are *conirostris* (a race of *minor*), *exilis*, *willcocksii*, and *pumilio*. Not only are the species of the two groups similar in appearance, but their habits vary but slightly. Chapin (1962) found *pumilio* and *exilis* (*pachyrhynchus*) together at Tshibati and saw no difference in their behavior. We can infer that *minor* and *meliphilus* also must be extremely similar in their actions and vocalisms, or variances would have been recorded by the numerous observers who

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have written about them. Some collectors were not aware that there were two species involved until they studied the dried specimens after their field experience.

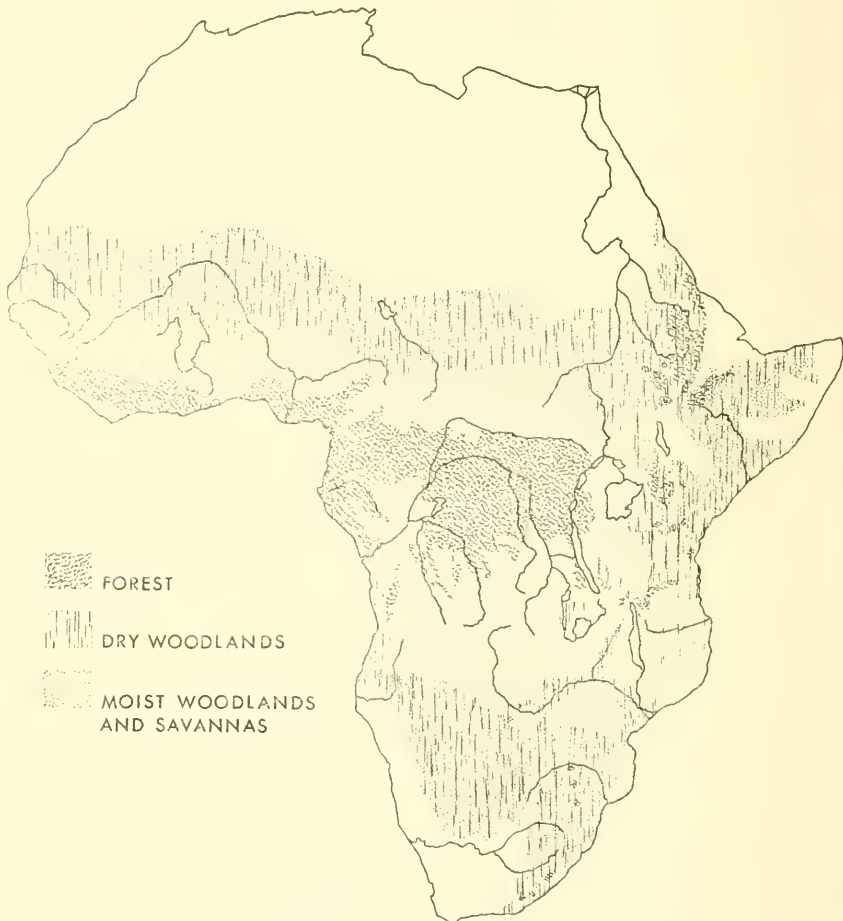


FIGURE 1.—Simplified vegetation map of Africa. The large equatorial forest area is the home of the following honeyguides discussed in this paper: *maculatus*, *conirostris*, *exilis*, *willcocksii*, and, at its eastern end, chiefly at higher altitudes, of *pumilio*. The woodlands and savannas are the home of *variegatus*, *minor*, *meliphilus*, and *narokensis*.

Through the cooperation of the American Museum of Natural History, the Field Museum, and the National Museums of Rhodesia, together with the now considerable holdings of the Los Angeles County Museum of Natural History, plus earlier study of the specimens in the Royal Museum of Natural History in Brussels, the British Museum (Natural History), the Musée d'Histoire Naturelle of La Chaux-de-Fonds, Switzerland, and the United States National Museum, I have

been able to study in depth the morphology and distribution of the smaller *Indicator* species. Some of the specimens were collected under National Science Foundation Grant GB-5107.

The *exilis-willcocksii* Relationship

The small west African forest honey-guides, *exilis* and *willcocksii*, were considered conspecific prior to Chapin's 1962 study when, for the first time, the specific identity of the latter sibling form was elucidated. Until then *willcocksii* had been treated as a western race (Ghana and Togoland) of *exilis*; the fact that *willcocksii*-like individuals occurred here and there throughout the range of nominate *exilis* was, if anything, looked upon as evidence that the latter race provided the variational trends that had become "solidified" in *willcocksii*.

A good number of specimens of *willcocksii* collected in 1966 and 1967, along with those of *exilis* (*pachyrhynchus*) in extreme western Uganda (Kibale and Impenetrable Forests), clearly upholds Chapin's conclusions in regard to the distinctness of the two sympatric species. When series are laid out, the differences between the species is more marked than that suggested by single examples.

Chapin's attention was brought to bear on the *exilis-willcocksii* situation as a result of his discovery and description of the still smaller, partly sympatric *pumilio*. While the validity of *pumilio* as a species distinct from its sympatric congeners is clear as has been universally accepted by all students of African birds, Chapin (1958, p. 47) did not pursue the question of its relation to the paler, small *Indicator* species of the open country of eastern Africa beyond commenting that the very small beak of *pumilio* caused him to think at first that it might be conspecific with *meliphilus*. The striking difference in coloration of the two species persuaded him to name *pumilio* binomially, but he felt constrained to add that he was still of the opinion that "its small beak may well indicate relationship with *meliphilus*"

The *meliphilus-narokensis* Relationship

Just as *willcocksii* had been looked upon as a part of the variational limits of *exilis* until sufficient series of specimens became available for study, *meliphilus* too has been assumed to comprise within its extremes, the species *appellator* Vincent (1933) and *narokensis* Jackson (1906). Ever since Chapin's discovery of *pumilio* in the Kivu forests I have wondered whether or not *meliphilus*, like *willcocksii*, might also have a smaller, sympatric sibling form. The description and dimensions of *appellator*, described from Zobué on the border of Mozambique and Malawi, were too close to those of *meliphilus* to

cause any concern, but *narokensis* was described as much smaller than the average *meliphilus* as *pumilio* was than the average *exilis* (or *wilcocksii*). As long as *narokensis*, however, was known from only one or two odd specimens, to decide if it was a taxon in its own right or merely the smallest specimens of *meliphilus* was impossible. Accordingly, in three different publications (1954, 1955, 1958) I could treat it only as a probable synonym of *meliphilus*, which, until 1958, was still considered to be an eastern, pale, gray-breasted race of *exilis*.

As long ago as 1938 Grant and Mackworth-Praed (pp. 143-144) examined van Someren's pair of *narokensis* from Mt. Moroto and found that the two specimens agreed with Jackson's type from Mt. Doinyo Narok and with Granvik's specimen from Kacheliba. Grant and Mackworth-Praed concluded that comparison with examples of *meliphilus* "clearly show that *I. narokensis* is a distinct species having a smaller bill and a smaller wing measurement It is a very remarkable fact that there are two birds so very similar in coloration . . . and, although they both occur in the same general area in Kenya Colony, it may be found that they inhabit different types of country, as Granvik records *I. narokensis* in tall acacias in dry open country, and Moreau records *I. e. meliphilus* in the vestiges of coastal forest"

I now feel certain that only lack of critical specimens in most of the large museums caused Grant's and Mackworth-Praed's conclusion to be overlooked. In the absence of such material, it had been impossible to test it. At the time of their report, their conclusion seemed too remarkable to be likely, and I left *narokensis* in the unverified synonymy of *meliphilus*. White (1965) does not even mention *narokensis*, either as a valid taxon or as a synonym—an indication that he was content to go along with current disbelief in it. The remarkable, and hence unlikely aspect of a distinct species, *narokensis*, being sympatric with *meliphilus* has, of course, been changed completely by Chapin's findings of three sympatric sibling *Indicator* species in the Congo. In the light of his results, it is not surprising that a comparable situation should exist among the small *Indicator* species of eastern Africa.

In 1957 Mackworth-Praed and Grant (p. 745) again treated *narokensis* as a species, smaller and generally paler in color than *meliphilus*, and listed a number of specimen-based locality records: Mt. Moroto in eastern Uganda; Kacheliba in Turkanaland, northwestern Kenya; Mt. Doinyo Narok, Sokoke Forest, and Malindi, all in southern Kenya; and Lushoto, in northeastern Tanzania. Subsequently, I have seen other records that have reported the species from Shimba Hills, near Kwale, and southern Guaso Njero, in southern Kenya, and from Sigor, West Pokot, western Kenya. With these

last three examples, it became obvious that there were indeed two very similar species living side by side in eastern equatorial Africa. This caused me to assemble as complete a series as possible in order to review the situation again and to seek new conclusions.

Although very similar to each other, *narokensis* and *meliphilus* should be treated as specifically distinct. In *narokensis*, the wing length varies from 65 to 70 mm in four females, 67 and 69 mm in two males; in *meliphilus*, 18 females have wing lengths from 69 to 78.5 mm, 18 males, from 73.5 to 85.5 mm. The bill is "stubbier" to the eye in *narokensis*, more so than actual measurements reveal; length from distal end of nostril to tip of culmen is 4.2 to 4.8 mm (4.7 to 5.9 mm in *meliphilus*), the exposed culmen is 5.7 to 7 mm (7.1 to 8.5 mm in *meliphilus*). Actually, the bills of *narokensis* are very similar to those of *pumilio*. This supports Chapin's comment, cited above, that *pumilio* may be related not merely, as he put it, to *meliphilus*, but even more closely to that part of *meliphilus* (*olim*) now separated as *narokensis*.

In my 1958 paper I explored the question of the status of the western race of *meliphilus*, which Monard (1934, p. 55) had designated *angolensis* as a subspecies of *minor*! I still believe that there are two recognizable races of *meliphilus*, although they are based on average differences and not on more trenchant characters; *angolensis* is usually paler gray, especially on the throat, breast, and upper abdomen than nominate *meliphilus*. Chapin (1954, p. 633; 1962, p. 44) considered *angolensis* indistinguishable from *meliphilus*, but he also put *narokensis* in this category. More recently, Traylor (1963, p. 108) has supported the belief that *angolensis* is the southwestern race of *meliphilus*, and I may add that the additional specimens I have seen since my 1958 paper also have supported this division. The removal of *narokensis* from *meliphilus* increases the average duskiness of the residual nominate *meliphilus* since the palest members of that taxon, as formerly treated, are all *narokensis*.

The *narokensis-pumilio* Relationship

The relationship of *narokensis* and *pumilio* parallels very closely that of *meliphilus* and *exilis* and that of *minor* and *conirostris*. Inasmuch as *meliphilus* and *exilis* have been found to overlap sympatrically in the Mwinilunga district, Zambia, and in the Upemba Park, in the Congo (Verheyen, 1953, pp. 406-407), their specific distinctness has to be granted. The situation between *minor* and *conirostris*, however does not include this convenient sympatry, and they usually are still considered to be races of one species. While *conirostris* is a dark-colored forest-inhabiting form with a discontinuous range from western Kenya (Kakamega and Kapenguria) west to southern

Cameroon and Gabon, typical *minor* is the bird of the open country of southern and eastern Africa, west and south of the Congo forest to Angola. It now seems that *pumilio* is the dark forest counterpart (from the eastern Congo, discontinuously to Kakamega, in western Kenya) of the pale *narokensis*, which is now known to occur from Turkanaland south to northeastern Tanzania and west to the Upemba Park in the Congo.

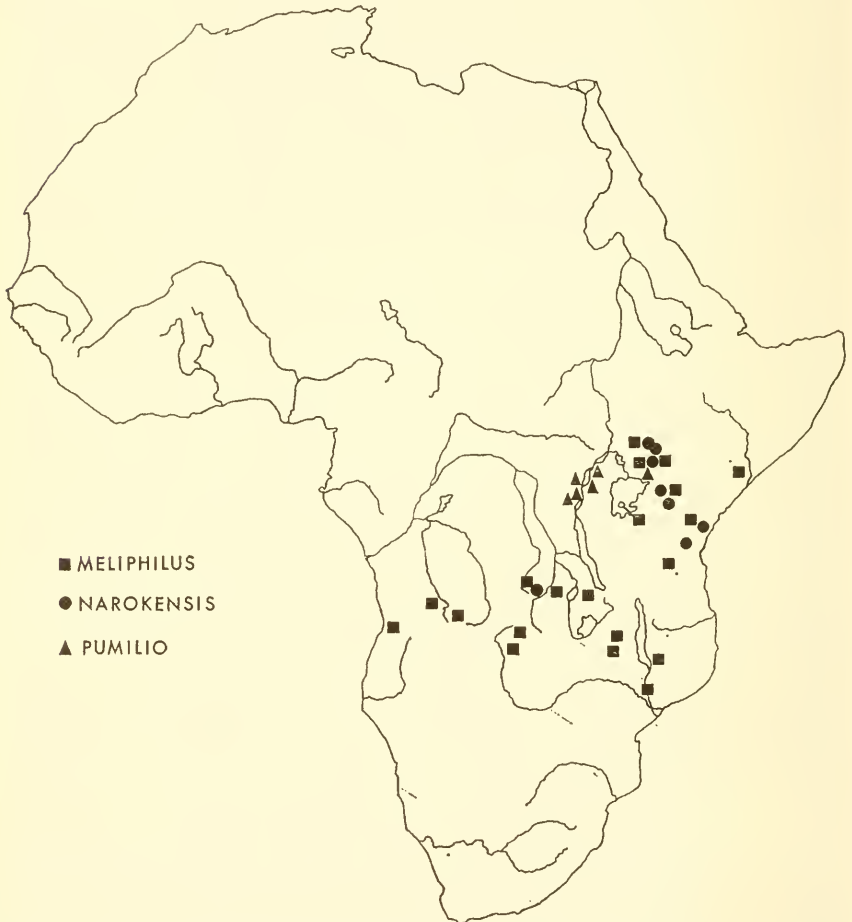


FIGURE 2.—Specimen records of the three small species of *Indicator* whose relationships are reinterpreted in this paper.

The subspecies *conirostris* is not wholly constant in its color characters; in fact, in parts of western Africa, especially in Upper Guinea, it and its geographic replacement *riggenbachi* frequently show some intergradation toward the adjacent, paler forms of *minor*—*alexanderi*,

ussheri, and *pallidus*, some of which are such intermediates as to be doubtfully recognizable as racial entities. Similarly, *pumilio* has been found to be geographically variable. Its data are much less extensive, being based merely on the fact that its easternmost example (Kakamega Forest, western Kenya) is different from Kivu topotypes, a difference that was sufficient to cause Williams and Friedmann (1965) to raise the possibility of the Kakamega bird being racially separable from the eastern Congo population. We found the single Kakamega specimen to be slightly larger (wing 70 mm), to have more uniformly grayish underparts without the streaks that are present in the birds from the Kivu and the Impenetrable Forest, southwestern Uganda, and to have the top and sides of the head less greenish, more grayish. If additional material from Kakamega should agree in these color characters, which are in the direction of a more grayish and paler shade—or, to an extremely slight, almost incipient degree, in the direction of the very much paler and grayer *narokensis*—there would be a situation faintly resembling that existing in *conirostris* and *riggerbachii* in Upper Guinea and other races of *minor* in the open country north of the forest belt. Kakamega, where *pumilio* occurs, and Sigor, West Pokot, where *narokensis* has been taken, are barely 75 miles apart.

Enough has been said to warrant raising the question whether or not *pumilio* is a true species or an unusually distinct race of *narokensis*. To be wholly consistent, I would have to treat the two as conspecific forms by the same standards that I use when considering *conirostris* and *minor* in this matter. The real question is whether they are representative races or whether they have differentiated to the point where they are specifically distinct. Unfortunately, this question could be answered only by bringing them into contact under natural conditions, which cannot be done. I, therefore, favor considering the two as races of a single species merely to point out their mutually representative nature and to suggest their closer relationship in the not too distant past. That they are closely allied is intimated by analogy with *minor* and *conirostris*, and while this is certainly no proof, it may yet reveal a pattern or trend in these small species of *Indicator*.

Without pressing the point beyond its realistic implications, I add the suggestion that *maculatus* (with *stictithorax* as a race) is no more than a west African forest representative of *variegatus* of eastern and southern Africa. It is a comparable case.

Morphological Overlap and Sympatry in Sibling Species

While I conclude that *narokensis* is a species distinct from *meliphilus*, I realize that other observers may have the experience of finding specimens that are difficult to place in either species. It would be

comforting to find reliable and rigid key characters by which to separate *narokensis* from small *meliphilus*, but this is not always feasible.

A similar state of affairs occurs, however, with such generally accepted species as *exilis* (*pachyrhynchus*) and *minor*. Small individuals of the latter often are difficult to distinguish from examples of the former, but this does not cause serious doubts as to their specific distinctness. In these birds, not only is there a serial gradation in size among sympatric species, but also the very limits of the species are at times difficult to distinguish. The resulting situation makes one wish for more observational data regarding the critical isolating mechanisms involved. In the case of *pumilio* and *exilis* (*pachyrhynchus*), I was able to find skeletal characters that corroborated their external specific distinctness, but these differences are not necessarily isolating mechanisms (1963). Benson and Irwin (1964, p. 110) write that *meliphilus* has a thinner, softer skin than *exilis* and other local species of *Indicator*. They even suggest that, in this respect, *meliphilus* is more like *Prodotiscus* than like other species of *Indicator*. So far, however, no pertinent observations on the feeding habits of *meliphilus* have been brought forth that indicate whether or not it is more or less given to feeding on small insects generally than are other species of *Indicator*. It is known that it does feed on bee comb like its congeners and unlike *Prodotiscus*.

Sympatry and Parallelism in Sibling Species

Considering the fact that sibling species, or even species of only approximately similar external characters, usually are related fairly closely, and considering the further fact that the origin and establishment of the discontinuities between such species ordinarily involve allopatry of some duration, it is noteworthy how quickly and how extensively some of these small *Indicator* species once more have become sympatric. This fact argues for effective, but as yet unrecognized, isolating mechanisms. The number of instances of two or more of these morphologically similar honey-guides occurring together is very impressive—Kabompo District, Zambia: *exilis* (*pachyrhynchus*) and *meliphilus* (Benson and Irwin, 1965, p. 4); Tshibati, Kivu District, Congo: *pumilio* and *exilis* (*pachyrhynchus*) (Chapin, 1958, p. 48); Doinyo Narok, Kenya: *meliphilus* (specimen in American Museum of Natural History, collected by Jackson) and *narokensis* (Jackson, 1906, p. 20); Kibale Forest, west Uganda: *exilis*, *willcocksii*, *conirostris*; Impenetrable Forest, west Uganda: *willcocksii*, *exilis pumilio*; Sigor, West Pokot, western Kenya: *narokensis*, *meliphilus*; Mt. Moroto: *minor*, *narokensis*; Victoria, British Cameroons: *minor* (*conirostris*), *exilis*, *willcocksii* (Serle, 1965, p. 77).

Here, then, is a series of remarkably parallel situations of similarly colored, sympatric species, each with a paler, grayer form in the open grasslands of eastern Africa and each with a darker, greener representative in the forests of central and western Africa. In some, the representatives are clearly conspecific; in others, they have achieved specific distinction—*minor* and *conirostris*; *meliphilus*, *willcocksii*, and *exilis*; *narokensis* and *pumilio*; *variegatus* and *maculatus*.

It is, of course, impossible to state with any certainty either that these similar species all originated as greenish forest birds that gave rise to paler, grayer races in the open country, or that all began as grayish denizens of the savannas and each evolved a darker, greenish representative form in the wooded areas. It is equally possible that some may have gone one way, and others, the opposite direction; but the end result, which is all we have for study, shows a remarkable parallelism. As Mayr (1963, p. 609) noted, true parallelism is due to the necessarily similar response of a common genetic heritage to similar selection pressures. Inasmuch as all of these species of honey-guides seem in every way to be closely related, and, hence, to have a basically similar genetic composition, their parallel evolutionary picture seems to be true parallelism rather than mere convergence, a situation wherein similar phenotypic developments have resulted as a response to similar environmental selection factors. The small species of *Indicator* have, at best, a very restricted phenotypic potential, much like some of the tyrant flycatchers of the genera *Empidonax* and *Elaenia*.

Literature Cited

- BENSON, C. W., and IRWIN, M. P. S.
 1964. Some additions and corrections to "A check list of birds of Northern Rhodesia." Occas. Pap. Nat. Mus. Southern Rhodesia, no. 27B, pp. 106-127.
 1965. Some birds from the north-western province, Zambia. *Arnoldia*, vol. 1, no. 29, pp. 1-11.
- CHAPIN, J. P.
 1954. The birds of the Belgian Congo, pt. 4. *American Mus. Nat. Hist. Bull.* 75B, 846 pp.
 1958. A new honey-guide from the Kivu District, Belgian Congo. *Bull. British Ornith. Club*, vol. 78, pp. 46-48.
 1962. Sibling species of small African honey-guides. *Ibis*, vol. 104, pp. 40-44.
- FRIEDMANN, H.
 1954. A revision of the classification of the honey-guides, Indicatoridae. *Ann. Mus. Congo, Tervuren, Zool.*, vol. 50, pp. 21-27.
 1955. The honey-guides. *U.S. Nat. Mus. Bull.* 208, 292 pp.
 1958. The status of the gray-breasted least honey-guides. *Proc. Biol. Soc. Washington*, vol. 71, pp. 65-68.
 1963. Morphological data on two sibling species of small honey-guides. *Los Angeles Co. Mus. Contr. Sci.*, no. 79, pp. 1-5.

- GRANT, C. H. B., and MACKWORTH-PRAED, C. W.
1938. On the status of *A. Melignotheres pachyrhynchus*, *B. Indicator pygmaeus*, *C. Melignotheres meliphilus*, *D. Indicator narokensis*, and *E. Indicator appellator*. Bull. British Ornith. Club, vol. 58, pp. 141-145.
- JACKSON, F. J.
1906. Description of new species of birds from equatorial Africa. Bull. British Ornith. Club, vol. 19, pp. 19-20.
- MACKWORTH-PRAED, C. W., and GRANT, C. H. B.
1957. Birds of eastern and northeastern Africa, vol. 1, ed. 2, 845 pp.
- MAYR, E.
1963. Animal species and evolution, 797 pp.
- MONARD, A.
1934. Ornithologie de l'Angola. Arq. Mus. Bocage, vol. 5, pp. 1-107.
- SERLE, W.
1965. A third contribution to the ornithology of the British Cameroons. Ibis, vol. 107, pp. 60-94.
- TRAYLOR, M. A.
1963. Check list of Angola birds. Mus. Dundo Publ. Cult., no. 61, 250 pp.
- VERHEYEN, R.
1953. Oiseaux. In Exploration du parc national de l'Upemba, Mission G. F. De Witte, fasc. 19, 687 pp.
- VINCENT, J.
1933. Descriptions of new species and subspecies of birds collected in Portuguese East Africa. Bull. British Ornith. Club, vol. 53, pp. 130-131.
- WHITE, C. M. N.
1965. A revised check list of African non-passerine birds, 299 pp.
- WILLIAMS, J. G., and FRIEDMANN, H.
1965. The pygmy honey-guide, *Indicator pumilio* Chapin, in East Africa. Bull. British Ornith. Club, vol. 85, pp. 21-22.