

THE GENERA OF AMERICAN GROUND DOVES

RICHARD F. JOHNSTON

THE several species of small American columbids generally termed ground doves comprise a relatively homogeneous assemblage. Nevertheless, the species have received varying treatment generically. Salvadori (1893) recognized eight genera and 17 species, Peters (1937) seven genera and 17 species, Hellmayr and Conover (1942) 10 genera and 16 species, and Goodwin (1959) five genera and 17 species. Hellmayr and Conover emphasized differences among the species and consequently recognized many genera, whereas Salvadori (for his time), Peters, and Goodwin emphasized similarities among the species and consequently recognized few genera.

The immediate purpose of the following account is to assess the validity of the genus *Scardafella* Bonaparte and the genus *Columbina* Spix, *sensu* Goodwin (1959). The genera *Claravis* and *Metriopelia* are not here treated; Peters and Goodwin do not differ in their taxonomic views of the two genera, and I have nothing of importance to add to their remarks.

Specimens examined in the course of my study are housed at the Museum of Natural History, The University of Kansas; the Museum of Vertebrate Zoology, Berkeley; the Museum of Zoology, The University of Michigan, Ann Arbor; the United States National Museum, Washington, D.C.; The American Museum of Natural History, New York. Observations on some of the species in the field were made in Arizona, New Mexico, Texas, Sonora, Nayarit, Veracruz, Oaxaca, and Chiapas. Live doves of most of the species mentioned here were observed in the Bronx Zoo, New York; the Brookfield Zoo, Chicago; San Francisco Zoological Gardens; the San Antonio Zoo, San Antonio. Financial assistance was received from the American Academy of Arts and Sciences, the NAS-NRC Committee on Research in Problems of Sex, The National Science Foundation, and the General Research Fund of The University of Kansas. Permission to take specimens in México was received from the Dirección General de Caza of the Secretary of Agriculture, through the courtesy of Sr. Luis Macias Arellano.

Goodwin (1959: 512) has proposed that the genera *Eupelia* and *Columbigallina* be placed in the genus *Columbina*. The argument for such treatment emphasizes similarities of the species involved, rather than differences; this argument is persuasive and probably correct. Yet, the fact that there are differences among the species is important to bear in mind. Recognition of such differences is not so much

to emphasize heterogeneity as it is to admit that some exists, and this is useful in gauging degrees of relationship obtaining in the inclusive genus.

Columbigallina, as treated by Peters, included the species *passerina*, *minuta*, *cruziana*, *buckleyi*, and *talpacoti*. *C. passerina* and *C. minuta* are morphologically the closest of the five, although they are by no means close enough to be considered sibling species, and the other three species are well removed from any hypothetical common ancestor. The five species share in common a short tail lacking white marks, rounded wings having dark or iridescent signal markings on the coverts, and some kind of emargination on the trailing edge of primary feather 7 (Johnston, 1960: Figure 1). The only species showing any aberrancy in these characters is *cruziana*, the lobe on primary 7 (the lobe is there, contrary to Todd, 1913: 512) being simple and lacking the recurved edge characteristic of the other species. Beyond this there are a few external divergences; *cruziana*, *buckleyi*, and *talpacoti* have broad, blade-shaped 10th primaries that lack subterminal extension of barbs forming a fringe, and *talpacoti* and *buckleyi* have a row of small feathers on each side of the tarsus. Todd (*loc. cit.*) and Hellmayr and Conover (1942) treated *cruziana* as of another genus (*Eupelia*), but I see no reason to remove *cruziana* from the group of five species mentioned above, unless the genus *Columbigallina* is to be split into at least three genera.

According to all authors, *Scardafella* is composed of the allopatric species *inca* and *squammata*, although Hellmayr and Conover considered the two kinds to be one polytypic species. Species of *Scardafella* lack signal markings on the wings and have long, white-marked tails, but otherwise resemble *Columbigallina*. The long tails of these birds caused Goodwin to exclude *Scardafella* from his inclusive genus *Columbina*. Tails of these species are used in the species-specific aspect of epigamic display; observations on comparative behavior suggest that the species-specific aspect of columbine courtship is an isolating mechanism (see below for details). If so, tails and behavior associated with their use are more sensitive in an evolutionary sense than structures lacking such significance. Therefore, tails should be considered less reliable indicators of phylogenetic relationships than are more conservative structures.

Columbina (sensu stricto) is monotypic. The tail of *C. picui* resembles that of *Scardafella*, and the signal markings on the wings resemble some of those in *Columbigallina*. *C. picui* in certain other respects is intermediate between *Columbigallina* and *Scardafella*, and it would be

difficult to include *C. picui* in either of those genera as presently constituted.

Behavioral considerations. Behavior associated with wings is especially well developed in doves. Throughout the family, wings are used (aside from flight) as weapons, to signal anxiety, and to give the prime solicitation signal in courtship feeding. Few species have highly elaborated signal markings on the wings, but most have some sort of modification in shape of some of the feathers, apparently associated with production of sound. The particular features vary from one group of species to another (rather than from one species to another), and as such they are more useful as taxonomic characters than any other morpho-behavioral feature associated with wings.

All eight species here considered have posteriorly emarginated 7th primaries, and two of the eight have such emarginations on the 6th primary; the function of such shapes is thought to be the production of sounds used in communication of individuals in groups. The sounds are of the same functional order as vocal flight calls of other kinds of birds (and none of these doves has a flight call). No other species of dove from North or South America has such emarginations on the feathers mentioned. The similar emarginations present on primaries 6, 7, 8, and 9 of species of *Claravis* are best considered independent acquisitions.

Four of the eight species also have an extension of barbs subterminally on the 10th primary, forming a faint fringe on the trailing edge; the fringe may be a vestige of an extension of barbs resembling the extension found on the 7th primary. The fact that *passerina*, *minuta*, *inca*, and *squammata* all have fringes is to me the strongest evidence available that the four species are closely related.

The several morphologic features mentioned above are listed in Table 1, together with their distribution among the eight species of doves.

A few more nearly strictly behavioral patterns have some bearing on estimates of relationships among the eight species here treated. But it should be emphasized that the entire realm of ritual behavior concerned with relationships between the sexes is of minor significance in estimating relationships of doves. Heretofore, too much emphasis has been placed on the configuration of courtship sequences as an aid in indicating relationships.

In most pigeons and doves epigamic behavior consists of four distinct, serially oriented rituals: head bobbing, heteropreening, bow-coo, and courtship feeding. In pair formation, these appear in each season of

TABLE 1
DISTRIBUTION OF CERTAIN MORPHOLOGICAL CHARACTERS
IN EIGHT SPECIES OF AMERICAN GROUND DOVES

	<i>Species</i>							
	<i>passerina</i>	<i>minuta</i>	<i>cruziana</i>	<i>buckleyi</i>	<i>talpacoti</i>	<i>inca</i>	<i>squamimata</i>	<i>picui</i>
Emargination on primary 6	o ¹	o	o	o	o	x	x	o
Emargination on primary 7	x	x	x	x	x	x	x	x
Iridescent or dark spots on wings	x	x	x	x	x	o	o	x
Narrow primary 10, subterminal incision	x	x	o	o	o	x	x	x
Extension of barbs on primary 10	x	x	o	o	o	x	x	o
Short tail with no white marks	x	x	x	x	x	o	o	o
Nude tarsus (no rows of feathers)	x	x	x	o	o	x	x	x

¹ Presence of character indicated by "x," absence by "o."

breeding in about the order just listed, and they are used serially, subsequent to pair formation, in the preliminaries of any attempt at copulation. Two exceptions can be noted: first, courtship feeding is not essential to pair formation, but is necessary before copulation can occur, and second, the bow-coo is occasionally left out of the precopulatory sequence. Even so, the bow-coo is easily the most important ritual in pair formation because the bow-coo is the only one of the series of acts that is species-specific (for example, the vertical tail fanning of *S. inca*, *Geopelia* spp., *Leucosarcia*, *Zenaida asiatica*, etc., the strut and coo of *Columbia* spp., and the "classical" bow-coo of *Streptopelia* spp.). As the only species-specific element in sexual behavior of doves, the bow-coo can be expected to become subject to intense selection to form an effective isolating mechanism. That the bow-coo is a behavioral isolating mechanism is clearly shown in *Streptopelia*, where female parental individuals of *S. decaocto* and *S. risoria* do not even respond to the bow-coo of (experimentally produced) male F₁ hybrids (Konrad Lorenz, personal communication). This isolating mechanism is sex linked,

and males are much less discriminating than females, but it is markedly effective in *Streptopelia*. Such selection pressure in the past would explain how the bow-coo today can be expressed with such variation, even in species that are otherwise seemingly closely related. I can conclude only that the bow-coo cannot be used as evidence for or against close relationship in doves, especially at the generic level.

Likewise, the remainder of the epigamic *Gestalt* is of little use in tracing relationships at a level below that of subfamily; all species that I have seen in the field, in captivity, or have read about, seem to have nearly identical bobbing, heteropreening, and courtship feeding routines.

Information of some relevance on additional behavioral features may be treated summarily: *picui* (Hudson, 1920: 159), *inca*, and *talpacoti* form flocks in winter, but *passerina* does not; none of the species seems to clap the wings in flight; *cruziana* (Marchant, 1960: 356), *picui* (Friedmann, 1927: 171), *talpacoti*, *inca*, and *passerina* pay no attention to sanitation at the nest and frequently use the reinforced nests more than once in one season of nesting (Johnston, 1960: 14).

Note. Salvadori erroneously set aside the genera *Geopelia*, *Scardafella*, and *Gymnopelia* in a distinct subfamily, the Geopeliinae. Although no one today believes that subfamily to be valid, there has been sporadic belief that *Scardafella* and *Geopelia* are closely related in some way, owing to the remarkable resemblance in plumage and behavior between *S. inca* and *G. striata*. Point for point comparison of 12 morphologic and behavioral characters has shown that the resemblance between *S. inca* and *G. striata* is really an instance of convergence (Johnston, MS). Moreover, if modalities of morphology and behavior found in *Geopelia* (considering the most divergent species, *G. humeralis* and *G. cuneata*, as well as *G. striata*) are compared with those of *S. inca* and *S. squammata*, the grounds for any relationship at the level of subfamily are eliminated. Once such grounds are eliminated, a puzzling "problem" in biogeography is also eliminated: the Australasian *Geopelia* is an Old World autochthon, probably allied to *Streptopelia*, and the Neotropical *Scardafella* is a New World autochthon, clearly allied to other doves of that region.

As one last point, it will have been noticed that the affinities of *Oxytelia cyanopsis*, included by Goodwin in his genus *Columbina*, have not been discussed here. Practically nothing is known about *O. cyanopsis*, but to judge by external morphology alone the species is best considered to lack close contemporary relatives. At all events, *O. cyanopsis* cannot be considered a congener of any ground dove discussed here.

CONCLUSION

The evidence presented here, plus that discussed by Goodwin (1959), shows the eight species to be alike in many features. Moreover, the

differences amongst them are so unevenly distributed (Table 1) that no useful line can be drawn to separate any one species from the remainder at the generic level, and the reference of the species to two or more genera will continue to obscure relationships. Therefore, the genus *Scardafella* Bonaparte (1855) should be placed in the synonymy of *Columbina*. The genus *Columbina* Spix and included species should stand as listed below.

Genus **COLUMBINA** Spix

Columbina Spix, Av. Bras., 2, 1825, p. 57, 58. Type, by subsequent designation, *Columbina strepitans* Spix. (G. R. Gray List Gen. Bds., ed. 2, 1841, p. 75.)

Columbigallina Boie, Isis von Oken, 1826, col. 977. Type, by monotypy, *Columba passerina* Linnaeus.

Scardafella Bonaparte, Compt. Rend. Acad. Sci. Paris, 40, 1855, p. 24. Type, by original designation *Columba squamosa* Temminck (not of Bonnaterre) = *Columba squammata* Lesson.

Eupelia Todd, Ann. Carnegie Mus., 8, 1913, p. 512. Type, by original designation, *Columba cruziana* Prévost and Knip (= Prévost).

Columbina passerina (Linnaeus): Common Ground Dove

Columbina minuta (Linnaeus): Minute Ground Dove

Columbina cruziana (Prévost): D'Orbigny Ground Dove

Columbina buckleyi (Sclater and Salvin): Buckley Ground Dove

Columbina talpacoti (Temminck): Ruddy Ground Dove

Columbina squammata (Lesson): Scaled Dove

Columbina inca (Lesson): Inca Dove

Columbina picui (Temminck): Picui Ground Dove

LITERATURE CITED

- FRIEDMANN, H. 1927. Notes on some Argentine birds. Bull. Mus. Comp. Zool., **47** (4): 139-236.
- GOODWIN, D. 1959. Taxonomic notes on the American ground doves. Auk, **76**: 510-515.
- HELLMAYR, C. E., and B. CONOVER. 1942. Catalog of birds of the Americas. Field Mus. Nat. Hist., Zool. Ser., 13, Pt. 1, No. 1: vi + 1-636.
- HUDSON, W. H. 1920. Birds of La Plata. Vol. 2. London and Toronto, J. M. Dent and Sons. ix + 240 pp.
- JOHNSTON, R. F. 1960. Behavior of the Inca Dove. Condor, **62**: 7-24.
- MARCHANT, S. 1960. The breeding of some S. W. Ecuadorian birds. Ibis, **102**: 349-382.
- PETERS, J. L. 1937. Check-list of birds of the world. Vol. 3. Harvard University Press, Cambridge. xiii + 311 pp.

- SALVADORI, T. 1893. Catalogue of the birds in the British Museum. Vol. 21.
The British Museum, London. xvii + 676 pp.
- TODD, W. E. C. 1913. A revision of the genus *Chaemepelia*. Ann. Carnegie
Mus., **8**: 507-603.

*Museum of Natural History, The University of Kansas, Lawrence,
Kansas.*