

THE TAXONOMY OF PIGEONS

By RICHARD F. JOHNSTON

The arboreal pigeons of the genus *Columba* have received considerable taxonomic attention in the past two decades. Such attention probably reflects doubt concerning the validity of the genus, either as a monophyletic unit or as a useful, subjective taxon designed only to show presumed present relationships within the subfamily. Some doubt had long existed (for example, see Ridgway, 1916), but it was reinforced by the work of the Wisconsin geneticists on the serological relationships of 11 species of pigeons from the eastern and western hemispheres (see, for example, Cumley and Irwin, 1944). This work showed that "Old World" pigeons could be considered a group distinct from "New World" pigeons and that the relationships varied considerably within each of these geographically-defined units. Parenthetically, Sibley's (1960) data from electrophoresis of egg-white proteins shows parallel differentiation but, regrettably, for only four species.

Modern treatment of the taxonomy of pigeons has fluctuated between the use of one genus, *Columba* (Salvadori, 1893; Peters, 1937; von Boetticher, 1954; Goodwin, 1959), and the use of 11 genera (Verheyen, 1957). It is perhaps significant that taxonomists who employ chiefly feather and other external characters tend toward use of one genus, whereas those who use skeletal and micromorphological characters mostly use several genera. It is true that Cumley and Cole (1942) used plumage patterns to separate "Old World" from "New World" pigeons, but they proposed no new nomenclatural treatment. It is noteworthy in this connection that Goodwin's singularly perceptive studies of patterns of plumage in *Columba* have, in part, led him to the use of the inclusive genus; Goodwin had the advantage of examining skins of every species in the genus.

Verheyen's study (1957) of characters of columbiform birds was the most complete yet undertaken of the skeleton, but he examined only 20 species of pigeons, 13 of which were from the western hemisphere. Considering the variability evident in some of the skeletal features he studied, the inclusive genus shows remarkable homogeneity. Nevertheless, it is possible to find osteometric differences between geographically-restricted groups of pigeons, and Verheyen (*op cit.*:33) has pointed out the most important of these in separating "Old World" from "New World" pigeons. However, further separation of both American and Afro-Eurasian pigeons into a total of 11 genera is clearly beyond what most of the evidence indicates, and I agree with Goodwin (1959:3) in that I cannot accept Verheyen's taxonomy without a great deal of additional evidence.

The present study has been organized chiefly around the work of Cumley and Cole (1942), Verheyen (1957), and Goodwin (1959). Most of the present work has necessarily been on plumage and on skeletal morphology. Skins and skulls of all, and skeletons of most, species of pigeons have been examined. I am indebted to authorities at the American Museum of Natural History, the United States National Museum, and the Museum of Vertebrate Zoology for use of specimens in their care and for their courtesies and help to me when I visited their collections. Financial assistance was received from the National Science Foundation (G 10043), the National Academy of Sciences-National Research Council (S-59-9), and the General Research Fund of The University of Kansas.

Two heretofore unremarked characters have proved useful in the present work. These are first, the condition of the tenth remex, whether or not equipped with a trailing fringe (fig. 1), and second, the angle on the skull at the frontal hinge, whether more or

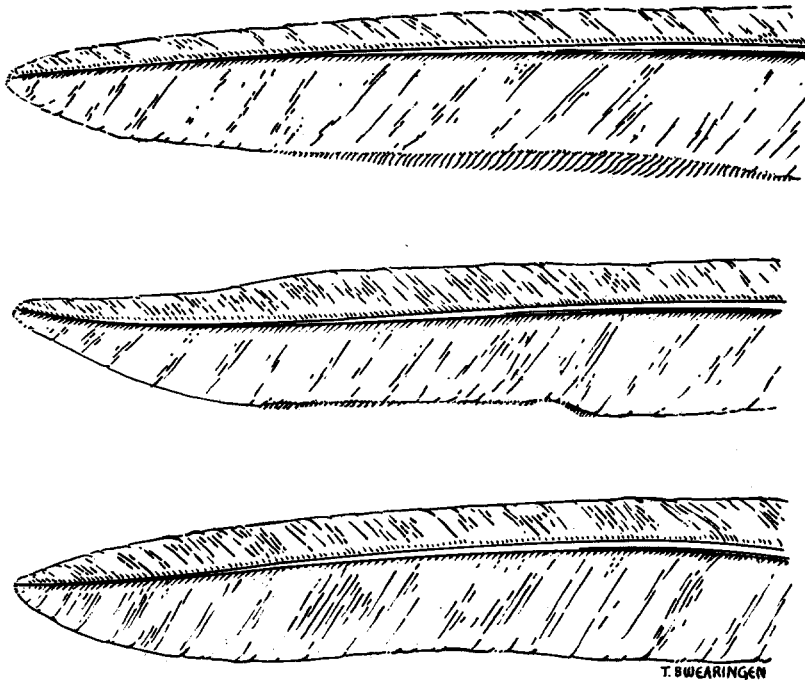


Fig. 1. Semi-diagrammatic drawings of underside of tenth (outermost) remiges from right wing of pigeons, to show presence and absence of the trailing fringe. Upper, *Columba fasciata* ($\times 1$) in worn condition, typical of most members of the genus *Columba*; middle, *Columba eversmanni* ($\times 1\frac{1}{4}$) in worn condition, typical of members of the subgroup *oenas*; bottom, *Patagioenas flavirostris* ($\times 1$) in worn condition, typical of members of the genera *Patagioenas* and *Oenoenas*.

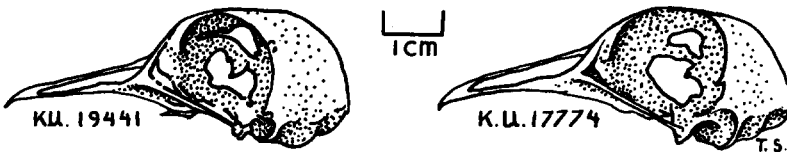


Fig. 2. Skulls of pigeons, to illustrate extremes of angles at the frontal hinge as seen in profile. Left, *Columba livia*; right, *Columba fasciata*.

less abrupt (fig. 2). With the addition of these characters to those already in use, groups and subgroups of pigeons can be arranged approximately as Goodwin did except that most pigeons from eastern and western hemispheres are clearly separated. Following is a listing of characters and the 47 species of pigeons arranged in three genera; the division is nearly complete at the time-honored level of "Old World" versus "New World" species, but the American superspecies *C. fasciata* is placed with "Old World" pigeons, and the remainder of the American species requires use of two genera in order best to show degrees of relationship. The useful convention of infrageneric groups suggested by Cain (1954) and followed by Goodwin (1959) is here employed; this hierarchy is as follows:

Genus
 Subgenus
 Species-group
 Subgroup
 Superspecies (denoted by brackets)
 Species
 Subspecies

THE GENERA AND SPECIES OF PIGEONS

GENUS COLUMBA LINNAEUS

Columba Linnaeus, Syst. Nat., ed. 10, 1, 1758, p. 162. Type, by subsequent designation, *Columba oenas* Linnaeus (Vigors, 1825).

These birds are small to large pigeons, chiefly of Old World distribution. The trailing edge of the tenth remex is fringed with extensions of barbs, evident in fresh feathers in all species, which may wear off in the course of a year's use. Display plumage on the neck is usually well developed, and the wings of many species have conspicuous signal markings.

SUBGENUS COLUMBA

These are generally large pigeons of Old World distribution, but one superspecies occurs in the Americas. Most species have a relatively abrupt angle at the frontal hinge of from 140° to 150°.

SPECIES-GROUP *palumbus*

These are large or medium-large pigeons of chiefly arboreal habits. The display plumage on the hindnecks is well developed and usually restricted to hindnecks only. The trailing fringe on the tenth remex is robust and clearly evident even in worn feathers.

Subgroup *palumbus*.—These are large pigeons, the tails of which have pale subterminal bands. The distribution is Eurasian; three species are isolated on islands.

- C. palumbus* Linnaeus, 1758
- C. trocaz* Heineken, 1829
- C. bollii* Godwin, 1872
- C. junoniae* Hartert, 1916
- C. uncinata* Cassin, 1859

Subgroup *fasciata*.—These are medium-large pigeons, the tails of which have pale terminal bands. The distribution is montane American. The frontal angle is 150° or more.

- { *C. fasciata* Say, 1823
- { *C. araucana* Lesson, 1827
- { *C. caribaea* Jaquin, 1784

SPECIES-GROUP *elphingstonii*

These are medium-sized to medium-large pigeons, usually with relatively broad areas of display plumage on necks. The distribution is Afro-Asian and insular Pacific. The trailing fringe on the tenth remex is well developed, but it does not persist on many worn feathers.

Subgroup *arquatrix*.—Display plumage on necks is of lanceolate-shaped feathers. Wing coverts and/or underparts are spotted with white. The distribution is Afro-Asian.

- { *C. arquatrix* Temminck, 1809
- { *C. hodgsonii* Schlegel, 1866
- { *C. albinucha* Sassi, 1911

Subgroup *elphingstonii*.—These are medium-sized pigeons having unpatterned tails; the display plumage on the hindnecks is of black feathers tipped with paler color. The distribution is in south-central Asia, from Tibet to Ceylon.

- { *C. pulchricollis* Blyth, 1845
- { *C. elphingstonii* (Sykes, 1832)
- { *C. torringtoni* Bonaparte, 1854

Subgroup *punicea*.—These birds lack well-differentiated display plumage on hindnecks. They

occur in southeast Asia and adjacent islands.

C. punicea Blyth, 1842

C. argentina Bonaparte, 1855

Subgroup *palumboides*.—The head and neck are silver-gray.

C. palumboides (Hume, 1873)

SPECIES-GROUP *janthina*

These are medium-large pigeons of insular distribution in the western and southwestern Pacific area. Their plumages tend toward dark grays and iridescent black and lack signal markings on wings and tails.

- { *C. janthina* Temminck, 1830
- { *C. vitiensis* Quoy and Gaimard, 1830
- { *C. norfolciensis* Latham, 1801
- { *C. versicolor* Kittlitz
- { *C. jouyi* Stejneger, 1887
- { *C. pallidiceps* (Ramsay, 1877)

SPECIES-GROUP *oenas*

These are small to medium-sized pigeons of African and Eurasian distribution. All have black signal markings on wing coverts. The trailing fringe on the tenth remex is reduced and in worn feathers is completely gone.

C. oenas Linnaeus, 1758

- { *C. evermanni* Bonaparte, 1856
- { *C. oliviae* Stephenson Clarke, 1918
- { *C. livia* Gmelin, 1789
- { *C. rupestris* Pallas, 1811
- { *C. leuconota* Vigors, 1831
- { *C. albitorques* Rüppell, 1837

SUBGENUS *TURTUROENA*

These are small, African pigeons. All possess a well-developed fringe of barbs on the trailing edge of the tenth remex. The angle at the frontal hinge is about 140°. The birds are markedly sexually dimorphic in plumage (reduced in *C. malherbii*).

- { *C. delagorguei* Delagorgue, 1847
- { *C. iriditorques* Cassin, 1856
- { *C. malherbii* Verreaux and Verreaux, 1851

GENUS *PATAGIOENAS* REICHENBACH

Patagioenas Reichenbach, Av. Syst. Nat., 1852, p. 25. Type, *Columba leucocephala* Linnaeus.

These are small to medium-sized pigeons of Central and South America. The display plumage of the hindnecks is generally well developed (see subgroup *cayennensis*). All possess a smooth trailing edge on the tenth remex. Most have an angle of 150° or more at the frontal hinge.

Subgroup *leucocephala*.—These are medium-sized pigeons of the Caribbean region. The display plumage is broadly spread on the hindnecks, with soft, robust feathers on napes. The plumages are of dark colors, with no marks on tails.

P. leucocephala (Linnaeus, 1758)

P. squamosa (Bonnaterre, 1792)

Subgroup *speciosa*.—The size is medium-small; the feathers are generally edged marginally with dark pigment, giving a scaly appearance; the dorsum is of purple-chestnut or brown, and the tail is unmarked.

P. speciosa (Gmelin, 1789)

Subgroup *picauro*.—These are medium-sized pigeons of South American distribution. They have well-defined display plumage on the hindnecks; the outer wing coverts are edged with white, and tails have an obsolete, dark terminal band.

- { *P. picauro* (Temminck, 1813)
- { *P. corensis* (Jaquin, 1784)

P. maculosa (Temminck, 1813)

Subgroup *cayennensis*.—These are small or medium-sized pigeons of extensive American distribution. Their plumages are mostly vinous-purple, with rufous wing coverts; they show no display plumage on the hindnecks, except for *P. cayennensis*, in which the head and neck are iridescent.

P. cayennensis (Bonnaterre, 1790)

- { *P. flavirostris* (Wagler, 1831)
- { *P. oenops* (Salvin, 1895)
- { *P. inornata* (Vigors, 1827)

GENUS OENOENAS SALVADORI

Oenoenas Salvadori, Cat. Birds Brit. Mus., 21, 1893, p. 248, in text (as subgenus). Type, *Columba nigrirostris* Sclater.

These are small pigeons of Central America and South America. Their plumages tend to be uniformly colored, showing chiefly dark browns, grayish purple, and reddish purple. The display plumage on the hindnecks is obsolete (almost wholly absent); they have no markings on wings and tails. The trailing edge of the tenth remex is smooth. The angle at the frontal hinge is 145° to 150°.

O. subvinacea (Lawrence, 1868)

O. plumbea (Vieillot, 1818)

- { *O. nigrirostris* (Sclater, 1859)
- { *O. goodsoni* (Hartert, 1902)

REMARKS

Columba palumbus, *C. bollii*, *C. trocaz*, *C. junoniae*.—Peters (1937) considered *C. bollii* to be a subspecies of *C. trocaz*. The populations are allopatric, but the degree of morphological differentiation between the two is at the species level. Both species seem to be derivatives of *C. palumbus*, that is, from *palumbus*-stock that colonized the Canary Islands at different times in the past. It is noteworthy that *C. palumbus* has colonized the Canaries at least three times; the population that resulted from the third colonization is recognized at the subspecies level (*C. p. maderensis*). If the Laurel Pigeon (*C. junoniae*) is also a derivative of *C. palumbus*, there have been at least four distinct colonizations of the Canaries by Wood Pigeon stock.

Columba fasciata.—Included with the North American Band-tailed Pigeon is the South American representative, as the subspecies *C. f. albilinea*.

Columba caribaea.—The Jamaican band-tailed pigeon has received the most inconsistent taxonomic treatment of any American pigeon. The species is clearly a band-tailed type, as Goodwin (1959) recently pointed out; von Boetticher erred in placing *C. caribaea* in a subgenus different from that for the other band-tailed pigeons, and Verheyen erred even more in placing *C. caribaea* in one genus and the other band-tails in another. The plumage of *C. caribaea* is paler than that of other band-tails, and the display plumage is greatly reduced, but the plumage is nevertheless that of a band-tailed pigeon. The fringe on the tenth remex likewise is typical of band-tailed pigeons.

Columba arquatrix.—I consider "*C. thomensis*" and "*C. polleni*" to be subspecies of *C. arquatrix*, in accord with the suggestions of Goodwin (1959:13–14). *C. hodgsonii*, on the other hand, deserves full specific status; it is closely related to, but not conspecific with, *C. arquatrix* (see Verheyen, 1957:37, who treats *hodgsonii* as a subspecies of *arquatrix*).

Species-group *janthina*.—The arrangement here of members of this group is identical with that of Goodwin. Verheyen separated the six species into three genera, but such treatment seems unnecessary for birds that, in my opinion, compose a relatively distinct group.

Patagioenas cayennensis.—The affinities of this pigeon, while clearly with those of

the subgroup *cayennensis*, are not chiefly with *P. oenops* (see Verheyen, 1957:37). *P. cayennensis* in fact stands somewhat apart from *P. oenops*, *P. inornata*, and *P. flavirostris*, which three share a relatively recent common ancestor and comprise a clear-cut superspecies.

Oenoenas subvinacea.—“*O. purpureotincta*” is here considered to represent a subspecies of *O. subvinacea*. “*O. chiriquensis*,” known only from the unique type described in 1915, is clearly an aberrant individual of *O. subvinacea* and cannot be maintained even at the level of the subspecies.

The genera *Columba*, *Patagioenas*, and *Oenoenas* should obviously be thought of as closely related. There is little question that these evolutionary lines arose directly from a common ancestor; this is strongly indicated by part of the serological evidence (Cumley and Irwin, 1944) and by much of the external and gross morphological evidence (see especially, Goodwin, 1959). It is considered here, however, that dividing the 47 species between three genera best indicates present relationships.

SUMMARY

The arboreal pigeons, frequently regarded as a unit (*Columba*), can be subdivided realistically into “New World” and “Old World” pigeons. The division is not, however, so simple as some taxonomists have proposed. Most of the American species comprise the two genera, *Patagioenas* and *Oenoenas*, but the superspecies of American band-tailed pigeons made up of *C. fasciata*, *C. araucana*, and *C. caribaea* belong in the large, Afro-Eurasian genus *Columba*.

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