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*** START OF THE PROJECT GUTENBERG EBOOK PHYLOGENY OF THE WAXWINGS AND ALLIED BIRDS ***

Transcriber's Notes

The text herein presented was derived from scans of the original report which were OCRed and proofread. Minor typographical errors (genus name initial not italicized, missing parenthesis, missing or superfluous commas, etc.) were made but are not noted here. With the exception of those corrections and those noted below, it is the same text.

One additional note, many of the figures list notation such as "× 1/2" to denote that the image is shown at half the actual size. The images reproduced herein most likely will not match the original printed scale due to the display resolution used by the viewer.

Typographical Corrections

Page 480 : [Luis Potosí](#) => [Luís Potosi](#)

Page 481 : [Luis Potosí](#) => [Luís Potosi](#)

Page 481 : [Measureemnts](#) => [Measurements](#)

Page 486 : [cedorum](#) => [cedrorum](#)

Page 496 : [Luis](#) => [Luís](#)

Page 516 : [Gatrocnemius](#) => [Gastrocnemius](#)

[Cover]

Phylogeny of the Waxwings and Allied Birds

BY
M. DALE ARVEY

University of Kansas Publications
Museum of Natural History

Volume 3, No. 3, pp. 473-530, 49 figures in text, 13 tables

October 10, 1951

University of Kansas
LAWRENCE
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INTRODUCTION

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A small family of passerine birds, the Bombycillidae, has been selected for analysis in the present paper. By comparative study of coloration, nesting, food habits, skeleton and soft parts,

an attempt is made to determine which of the differences and similarities between species are the result of habits within relatively recent geological time, and which differences are the result of inheritance from ancient ancestral stocks, which were in the distant past morphologically different. On the basis of this information, an attempt is made to ascertain the natural relationships of these birds. Previous workers have assigned waxwings alone to the family Bombycillidae, and a question to be determined in the present study is whether or not additional kinds of birds should be included in the family.

It has generally been assumed that the nomadic waxwings originated under boreal conditions, in their present breeding range, and that they did not undergo much adaptive radiation but remained genetically homogeneous. Also it is assumed that the species were wide ranging and thus did not become isolated geographically to the extent that, say, the Fringillidae did. The assumption that waxwings originated in the northern part of North America or Eurasia may be correct, but it is more probable that the origin was more southerly, perhaps, in northern Mexico, of North America (see p. 519.) Subsequent to the differentiation of this stock in the south, there was a northerly movement, while certain populations remained behind and underwent an evolution different from the northern group. Since the fossil record does not permit us to say when in geological time the family originated, we must rely on anatomical evidence and the distributional evidence of present-day species to estimate when the family stock had diverged from some unknown group sufficiently to merit the status of a separate family.

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It is with pleasure that I acknowledge the guidance received in this study from Professor E. Raymond Hall of the University of Kansas. I am indebted also to Dr. Herbert Friedmann of the United States National Museum for the loan of certain skins, skeletons, and alcoholic material; to Mr. Alexander Skutch, for notes on certain Central American birds; and to Dr. Henry W. Setzer, Mr. George H. Lowery, Jr., Mr. Victor E. Jones, Mr. Victor Housholder, Mr. Alvaro Wille-Trejos, and Mr. Morton F. Davis, for gifts of specimens that have been used in this work. Suggestions and critical comments from Professors Worthie H. Horr, Charles G. Sibley and Edward H. Taylor are gratefully acknowledged. I wish also to thank Mrs. Virginia Unruh for the preparation of the drawings used in this work.

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NOMENCLATURAL HISTORY

The oldest name available for any species of the waxwings is *Lanius garrulus* Linnaeus (1758). *Lanius garrulus* and *Lanius garrulus* variety *B. carolinensis* were described as conspecific. The description has been associated with the first of the two names. The latter name is a *nomen nudum* since it was not accompanied by a separate description. The generic name *Lanius* was originally applied to both shrikes and waxwings by Linnaeus. Since that name is applied to the shrikes only, the next available generic name that may be applied to the generically different waxwings must be used. This is *Bombycilla*, a name originally proposed by Brisson (1760) for the Cedar Waxwing. In the 12th Edition of the *Systemae Naturae* (1766) Gmelin proposed the generic name *Ampelis* for the Bohemian Waxwing, and combined it with the specific name *garrulus*, the Cedar Waxwing being termed variety *B.* Vieillot (1807) proposed the generic name *Bombycilla* and combined it with a new specific name, *cedrorum*, for the Cedar Waxwing. Vieillot has been cited as the author of *Bombycilla* since that time, although Brisson used *Bombycilla* 33 years before. Oberholser (1917) did not cite Brisson's work in his discussion of the proper generic name for the waxwings, and *Bombycilla* should be ascribed to Brisson and not Vieillot, since Opinion 37, rendered by the International Zoölogical Committee on Nomenclature, states that generic names used by Brisson (1760) are valid under the Code. In consequence, the specific name available for the Cedar Waxwing, since Brisson is ruled not to be a binomialist, is *Bombycilla cedrorum* Vieillot (1807).

Most workers prior to 1900 utilized the family name Ampelidae to include waxwings, silky flycatchers, and palm-chats. Ridgway (1904:113) elevated the silky flycatchers to family rank under the name Ptilogonatidae, and assigned the palm-chats to a separate family, the Dulidae.

MATERIALS

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The following specimens, numbering 238, and representing each currently recognized species and subspecies, were used in the study, and were supplemented by observation in 1947 on specimens in the United States National Museum.

SPECIES OR SUBSPECIES

Skin

Skeleton

Alcoholic

<i>Phainoptila melanoxantha melanoxantha</i>	8	1	2
<i>Phainoptila melanoxantha minor</i>	2		
<i>Ptilogonys cinereus cinereus</i>	13	3	4
<i>Ptilogonys cinereus molybdophanes</i>	6		
<i>Ptilogonys caudatus</i>	16	3	4
<i>Phainopepla nitens nitens</i>		1	5
<i>Phainopepla nitens lepida</i>	12	5	4
<i>Bombycilla cedrorum</i>	53	27	8
<i>Bombycilla garrula garrula</i>	4	3	
<i>Bombycilla garrula centralasiae</i>	9	2	
<i>Bombycilla garrula pallidiceps</i>	7	3	2
<i>Bombycilla japonica</i>	10		
<i>Dulus dominicus dominicus</i>	9	5	2
<i>Dulus dominicus oviedo</i>	4	1	
Totals	153	54	31

DIAGNOSES

Family Bombycillidae

Diagnosis.—Bill short, flat, somewhat obtuse, minutely notched near tip of each maxilla, flared at base; gape wide and deeply cleft; culmen convex; nasal fossa broad, exposed, or filled with short, erect or antrorse, close-set velvety feathers; nostril narrowly elliptical; rictal vibrissae long, short, or absent; lacrimal bone free, articulating at two points; wings long and pointed, or short and rounded; primaries ten, tenth reduced in some species; tail short, narrow, even, two thirds or less length of wing, or much longer and forked or rounded; feet weak (except in *Dulus* and *Phainoptila*); tarsus generally shorter than middle toe and claw, distinctly scutellate with five or six divisions, the lateral plate subdivided (except in *Phainoptila*); lateral toes of nearly equal length; hallux approximately as long as inner lateral toe, or shorter; basal phalanx of middle toe more or less united to that of outer and inner toes; body stout; head generally conspicuously crested; plumage soft, smooth and silky (except in *Dulus*); eggs spotted; nest in trees; three subfamilies, five genera, eight species.

Subfamily Ptilogonatinae

Diagnosis.—Rictus with conspicuous bristles; nasal fossa almost entirely exposed; tail long and rounded, graduated, or square; caudal muscles and pygostyle well developed; wings rounded and short, first primary a half to a third as long as second; second primary shorter than third; humerus long, with small external condyle; plumage soft and silky, less so in *Phainoptila*; sexes dissimilar, young like adult female; three genera, four species.

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Genus *Phainoptila* Salvin

Phainoptila Salvin, Proc. Zoöl. Soc. London, 1877:367, April 17, 1877. Type
Phainoptila melanoxantha Salvin.

Diagnosis.—Without crest; tarsus longer than middle toe and claw, and booted or very slightly reticulate; tail shorter than wing, rounded; nostril exposed, ovate; rictal bristles distinct; first primary well developed; plumage normal, bill flared slightly at base.

Range.—Costa Rica and Panamá.

Phainoptila melanoxantha melanoxantha Salvin

Phainoptila

Phainoptila melanoxantha melanoxantha Salvin, Proc. Zoöl. Soc. London, 1877:367;
April 17, 1877.

Diagnosis.—Coloration of adult males: Pileum, hindneck, back, scapulars, and upper tail

coverts Black (capitalized color terms after Ridgway, Color Standards and Color Nomenclature, Washington, D. C., 1912), with Bluish Gray-Green gloss; rump Lemon Yellow tinged with Olive; lower breast and abdomen Gull Gray or Slate Gray; sides and flanks clear Lemon Yellow; lower chest, upper breast, and under tail coverts Yellowish Olive-Green, extending to patch on sides and flanks of same color; bill and feet Black or Blackish Brown. Coloration of adult females: Most of upper parts Olive-Green, with Yellowish Olive on rump; thighs Olive-Gray, as are sides of head; rest of coloration as in male. Coloration of young: As in adult female, but duller throughout.

Measurements.—Wing 99.0, tail 88.5, culmen 15.2, tarsus 28.4.

Range.—Highlands of Costa Rica and extreme western Panamá (Volcán de Chiriquí).

Phainoptila melanoxantha minor Griscom

Phainoptila

Phainoptila melanoxantha minor Griscom, Amer. Mus. Novitates, 141:7, 1924.

Diagnosis.—Coloration as in *P. m. melanoxantha*, but female with hindneck more extensively gray and of slightly darker shade; rump, upper tail coverts, and edgings to tail feathers slightly greener, less yellow; average size smaller than in *P. m. melanoxantha*.

Range.—Highlands of western Panamá (Cerro Flores and eastern Chiriquí).

Genus **Ptilogonys** Swainson

Ptilogonys Swainson, Cat. Bullock's Mex. Mus., App. 4, 1824. Type *Ptilogonys cinereus* Swainson.

Diagnosis.—Tail much longer than wing, even or graduated; head with bushy crest; nostril large, rounded and fully exposed, bordered by membrane; rictal bristles well developed; tarsus shorter than middle toe with claw; plumage soft, blended.

Range.—Southwestern United States to Costa Rica.

Ptilogonys cinereus cinereus Swainson

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Ashy Ptilogonys

Ptilogonys cinereus cinereus Swainson, Cat. Bullock's Mex. Mus., App. 4, 1824.

Diagnosis.—Coloration of adult male: Frontals, supralorals, malars, and chin White; orbital ring White; auriculars and nape grayish brown; rest of head smoke gray; back, scapulars, wing coverts, rump, and upper tail coverts plain Bluish Black; rectrices (except middle pair) with large patch of White midway between base and tip, rest plain Bluish Black; chest, breast, and anterior parts of sides plain Bluish Gray-Green, much lighter than back, and fading into paler Gray on throat; abdomen and thighs White; flanks and posterior part of sides Olive-Yellow or Yellowish Olive; under tail coverts Lemon Yellow; bill, legs and feet Black. Coloration of adult females: Head plain Smoke Gray, passing into White on frontals, malars, and chin; back, scapulars, wing coverts, and rump Hair Brown; upper tail coverts Dark Gull Gray; remiges and rectrices Black with faint Dusky Green gloss, edged with Gull Gray; chest Dark Grayish Brown lightening to Wood Brown on sides and flanks; abdomen White; under tail coverts Yellow Ocher. Coloration of young: As in adult female, but paler throughout.

Measurements.—In adult male, wing 94.0, and tail 104.2; in adult female, wing 93.3, and tail 94.8; both sexes, culmen 11.1, and tarsus 18.7.

Range.—Mountainous districts of central and southern Mexico, in states of Durango, Zacatecas, Hidalgo, México, Oaxaca, Colima, Morelos, Veracruz, San [Luís Potosí](#), Guerrero and Michoacán.

Ptilogonys cinereus molybdophanes Ridgway

Ashy Ptilogonys

Ptilogonys cinereus molybdophanes Ridgway, Man. N. American Birds, 464 (footnote), 1887.

Diagnosis.—Coloration of adult male: Upper parts darker bluish than in *P. c. cinereus*; venter paler; flanks Olive-Green rather than Olive as in *P. c. cinereus*. Coloration of adult female: Like female of *P. c. cinereus* but colors darker throughout; dorsum more olivaceous.

Measurements.—In adult male, wing 89.4, and tail 97.1; in adult female, wing 89.4, and tail 93.3; both sexes, culmen 11.7, and tarsus 17.3.

Range.—Western Guatemala, in subtropical and temperate zones.

Ptilogonys caudatus Cabanis

Costa Rican Ptilogonys

Ptilogonys caudatus Cabanis, Jour. für Orn., 1866:402, Nov. 1866.

Diagnosis.—Coloration of adult male: Forehead and crown Pale Grayish Blue, slightly paler anteriorly; orbital ring Lemon Yellow; rest of head and neck, including crest, Olive-Yellow; throat paler and tinged with Light Gull Gray; back, scapulars, rump, upper tail coverts and wing coverts uniform Bluish Slate-Black; chest and breast similar but paler; sides and flanks Yellowish Olive-Green; thighs, lower abdomen, and under tail coverts Lemon Yellow; remiges, primary coverts, and tail Black, glossed with Bluish Black and edged with Gull Gray; inner webs of rectrices (except two middle pair) with large middle patch of White; bill, legs, and feet Black. Coloration of adult female: Forehead and crown Pale Gull Gray, becoming paler anteriorly; rest of head, together with neck, back, scapulars, rump, and wing coverts plain Yellowish Olive Green; chest and breast similar but more grayish; lower abdomen and flanks White tinged with Yellowish Olive; under tail coverts Olive-Gray; remiges, primary coverts, and rectrices Black with Gull Gray edges. Coloration of young: Dorsum plain Light Grayish Olive; upper tail coverts Brownish Olive; underparts Grayish Olive anteriorly, becoming more Yellowish Olive on abdomen; under tail coverts pale Yellowish Olive with Grayish Olive base; bill and feet Brownish Drab.

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Measurements.—In adult male, wing 96.2, and tail 135.7; in adult female, wing 93.9, and tail 113.7; both sexes, culmen 12.6, and tarsus 19.1.

Range.—Highlands of Costa Rica and extreme western Panamá.

Genus **Phainopepla** Sclater

Phainopepla Sclater, Proc. Zoöl. Soc. London, 26:543, 1858. Type *Phainopepla nitens* (Swainson).

Diagnosis.—Tail almost as long as wing; head with pointed crest of narrow, separated feathers; rectrices without white; bill narrow, compressed terminally; conspicuous white patch under wing; nostril small, exposed; rictal bristles distinct; tail slightly rounded.

Phainopepla nitens nitens (Swainson)

Phainopepla

Phainopepla nitens nitens (Swainson), Anim. in Menag., 1838:285, Dec. 31, 1837.

Diagnosis.—Coloration of adult male: Uniform glossy Bluish Black; inner webs of primaries except innermost pair with middle portion White; bill, legs, and feet Black. Coloration of adult female: Plain Olivaceous Black, longer feathers of crest Black, edged with Gull Gray; remiges and rectrices Dusky Drab to Black; rectrices and coverts margined by White; bill and feet Brownish Drab to Dusky Brown. Coloration of young: Like adult female but more Brownish Drab.

Measurements.—No specimens examined; larger than *P. n. lepida* (Van Tyne, 1925).

Range.—Central and southern Mexico, in states of Coahuila, San [Luís Potosí](#), Durango, Guanajuato, México, Puebla, and Veracruz.

Phainopepla nitens lepida Van Tyne

Phainopepla

Phainopepla nitens lepida Van Tyne, Occ. Pap. Bost. Soc. Nat. Hist., 5:149, 1925.

Diagnosis.—Coloration same as *P. n. nitens*; separated by smaller size.

Measurements.—Wing 91.0, tail 90.3, culmen 11.5, tarsus 17.6.

Range.—Southwestern United States, from central California, southern Utah, and central western Texas southward to Cape San Lucas in Baja California, and into northwestern Mexico (Sonora and Chihuahua).

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Subfamily **Bombycillinae**

Diagnosis.—Wings long and pointed, reaching almost to tip of tail; first primary spurious; second primary longest; tail short and even; rectal vibrissae few and short; secondaries generally, and sometimes also rectrices, tipped with red, corneous appendages; nasal fossa partly filled with short, antrorse, close-set velvety feathers; plumage soft, silky; tail tipped with yellow band (red in *B. japonica*); sexes alike; humerus short with large external condyle; caudal muscles and pygostyle not well developed; bill flared widely at base; one genus, three species.

Range of subfamily.—Holarctic breeding area; wanders nomadically south in winter to Central America and West Indies, southern Europe and Asia.

Genus **Bombycilla** Brisson

Bombycilla Brisson, Orn. ii, 1760:337. Type *Bombycilla garrula* (Linnaeus).

Diagnosis.—As described for the subfamily.

Bombycilla cedrorum Vieillot

Cedar Waxwing

Bombycilla cedrorum Vieillot, Hist. Nat. Amer., 1:88, Sept. 1, 1807

Diagnosis.—Coloration of adults: Shading from Saccardo's Umber on dorsum to Bister on top of head; upper tail coverts and proximal rectrices Gull Gray; underparts shade through pale Lemon Yellow wash on belly into White on under tail coverts; forehead, lores, and eye-stripe Black; chin same, soon shading into Blackish Mouse Gray and into color of breast; side of under jaw with sharp White line; narrow line bordering forehead, and lores, White; lower eyelid White; quills of remiges Dark Mouse Gray, darkening at tips; inner quills tipped with red horny wax appendages; tail feathers like primaries, but tipped with Lemon Yellow, and occasionally showing also red horny wax appendages; bill and feet Black. Coloration of young: Dorsum as in adult, but lightly streaked with White; head concolor with dorsum; forehead White; lores Black; eye stripe Black anterior to eye and White posterior to eye; throat Light Buff; belly with alternate streaks of Dresden Brown and light Ochraceous Buff but posteriorly White; tail tipped with Lemon Yellow bar; bill black at tip, shading to Sepia at base.

Measurements.—Wing 92.9, tail 55.5, culmen 10.9, tarsus 16.8.

Range.—Breeds from central British Columbia, central Alberta and Manitoba, northern Ontario, southern Quebec and Cape Breton Island south to northwestern California, northern New Mexico, Kansas, northern Arkansas, North Carolina, and northern Georgia. Winters south to Louisiana, Mississippi, Texas, Arizona, Colorado, Florida, Honduras, Costa Rica, Jamaica, Little Cayman Island, Haiti, and Panamá.

Bombycilla garrula (Linnaeus)

Bohemian Waxwing

Bombycilla garrula (Linnaeus), Syst. Nat., 10th Ed., 1758:55.

Diagnosis.—Coloration of adults: General color Olive-Brown, shading insensibly from clear Smoke Gray of upper tail coverts and rump to Cinnamon-Drab anteriorly, heightening on head and forehead to Hazel; narrow frontal line, lores, broader mask through eye, chin, and upper throat, Sooty Black; under tail-coverts Cinnamon-Brown; tail Smoke Gray, deepening to Blackish Mouse Gray distally, and tipped with Lemon Yellow; wings Blackish Mouse Gray; primaries tipped with sharp spaces of Lemon Yellow or White, or both; secondaries with White spaces at ends of outer web, shafts usually ending with enlarged, horny red appendages; primary coverts tipped with White; bill Blackish Slate and paler at base; feet Black. Coloration of young: Much like adult, but general color duller; some streaking on venter and back; chin, throat, and malar region dull White. Three subspecies.

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Bombycilla garrula garrula (Linnaeus)

Bohemian Waxwing

Bombycilla garrula garrula (Linnaeus), Syst. Nat., 10th Ed., 1758:55.

Diagnosis.—Coloration: As described for the species, but darkest of the three subspecies; tending to be more Vinaceous dorsally than either *pallidiceps* or *centralasiae*.

Measurements.—Wing 113.5, tail 63.1, culmen 12.5, tarsus 20.7.

Range.—Europe; breeds north to northern Russia and Norway, south to about 65° N latitude; winters south to England and Ireland, southern France, northern Italy, and Turkey.

***Bombycilla garrula centralasiae* Poljakov**

Bohemian Waxwing

Bombycilla garrula centralasiae Poljakov, *Mess. Orn.* vi:137, 1915.

Diagnosis.—Coloration: As described for the subspecies *garrula*, but less Vinaceous dorsally, and more Cinnamon; venter lighter gray than *garrula*, and much paler than *pallidiceps*.

Measurements.—Wing 114.7, tail 63.0, culmen 12.2, tarsus 21.0.

Range.—Asia; breeds northern Siberia south to Vladivostok; winters to Turkestan and central eastern China and Japan.

***Bombycilla garrula pallidiceps* Reichenow**

Bohemian Waxwing

Bombycilla garrula pallidiceps Reichenow, *Orn. Monats.* 16:191, 1908.

Diagnosis.—Coloration: As described for the species, but more grayish above and below than *B. g. garrula*; darker gray than in *centralasiae*.

Measurements.—Wing 115.1, tail 71.7, culmen 12.6, tarsus 21.1.

Range.—Breeds from western Alaska to northern Mackenzie and northwestern Manitoba south to southern British Columbia, southern Alberta, northern Idaho, and possibly Colorado (Bergtold 1924) and Montana (Burleigh 1929); winters east to Nova Scotia and irregularly over much of Canada, and south irregularly to Pennsylvania, Ohio, Michigan, Indiana, Kansas, Colorado, California, Arizona, and Texas.

***Bombycilla japonica* (Siebold)**

Japanese Waxwing

Bombycilla japonica (Siebold), *Nat. Hist. Jap.*, St. No. 2:87, 1824.

Diagnosis.—Coloration: Dorsum generally Brownish Drab shading to Light Brownish Drab on lower back, rump, and upper tail coverts; secondary and tertiary coverts Pale Brownish Drab, washed on outer web with Carmine; primary coverts Blackish Slate, with White edging; tail feathers Slate-Gray, broadly tipped with Carmine, bordered anteriorly by subterminal Black bar; head crested, forehead Chestnut; lores, frontals, and stripe extending around eye and nape, Black; throat Black, narrowing on lower throat; breast, sides of flanks Light Drab; venter pale Sulphur Yellow; thighs Brownish Drab; under tail coverts Carmine; bill, legs, and feet Black.

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Measurements.—Wing 108.3, tail 53.6, culmen 11.2, tarsus 19.4.

Range.—Breeds eastern Siberia, northern China; winters south in China, and to Japan (Hokkaido, Kyushu), Taiwan, and Korea.

Subfamily *Dulinae*

Diagnosis.—Bill deep and compressed, culmen strongly depressed; nostrils circular, wholly exposed; tail even, and shorter than wing; tenth primary less than half length of ninth; under parts streaked; plumage hard and harsh; rictal bristles minute; wing rounded; humerus long and with small external condyle; pygostyle and caudal muscles not well developed; one genus, one species.

Range of subfamily.—Islands of Haiti and Gonave, Greater Antilles.

Genus *Dulus* Vieillot

Dulus Vieillot, *Analyse*, 1816:42.

Diagnosis.—Like the subfamily.

Dulus dominicus dominicus (Linnaeus)

Palm-chat

Dulus dominicus dominicus (Linnaeus), Syst. Nat., 12th Ed., 1766:316.

Diagnosis.—Coloration: Dorsum Olive, back, scapulars, and wing coverts more Brownish Olive; lower rump and upper tail coverts Olive-Green; pileum and hindneck with indistinct streaks of Brownish Olive; tail Brownish Drab, edged with Light Olive Gray; lores, suborbital region, and auricular regions Dusky Brown; malars Dusky Brown and streaked with Sooty Black, streaks narrower on abdomen, broader and paler on under tail coverts, bill Light Brownish Drab; legs and feet Brownish Drab.

Measurements.—Wing 85.0, tail 68.8, culmen 15.0, tarsus 24.7.

Range.—Island of Haiti, Greater Antilles.

Dulus dominicus oviedo Wetmore

Palm-chat

Dulus dominicus oviedo Wetmore, Proc. Biol. Soc. Wash., 42:117, 1929.

Diagnosis.—Coloration: Like *D. d. dominicus*, but averaging more Grayish Olive; rump and tail coverts with less greenish wash.

Measurements.—Wing 90.1, tail 71.3, culmen 16.2, tarsus 25.1.

Range.—Gonave Island, off Haiti, Greater Antilles.

COLORATION

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The general coloration of waxwings is cryptic, that is to say, concealing or blending. The lighter color of the venter, especially of the belly, contrasts with the duller, darker vinaceous color of the dorsum. Several ruptive marks tend to obliterate the outline of the body. The crest of the head, when elevated, tends to elongate the body, making the outline less like that of a normal bird. The facial mask effectively breaks up the outline of the head, and conceals the bright eye, which would otherwise be strikingly distinct. The white spots on the distal ends of the secondaries of *B. garrula* and the yellow color on the distal ends of the rectrices (red in *B. japonica*) are also ruptive. These ruptive marks on an otherwise blending type of plumage might be important to waxwings, and probably are more effective when the birds remain motionless in either a well-lighted area or in one that is partly in shadow, rather than in one that is wholly in shadow.

The red wax tips on the secondaries of the flight feathers, and sometimes found on the ends of the rectrices in *Bombycilla*, are puzzling and no wholly convincing reason has been suggested for their occurrence. Two instances are known of yellow instead of red-colored wax tips in *B. cedrorum* (Farley, 1924). It is well known that many individuals, especially of *B. cedrorum*, do not possess these tips; they are absent in a smaller proportion of individuals of *B. garrula*. Of the 53 skins of *B. cedrorum* available in the University of Kansas Museum of Natural History, which might be taken as a sampling at random of the general population of this species, only 17 possess wax tips. A few specimens are unilateral, and the tips are of varying sizes in different individuals. Of these 17 birds, 6 are female and 7 male, the others being unsexed at the time of skinning. This proportion is, roughly, half and half. Of the seven skins of *B. garrula pallidiceps* in the same Museum, five possess the tips, and two that are females have no trace of the red tips at all. Of the five which do have the tips, two are males, two are females, and one is unsexed. In a series of 13 specimens of the three subspecies of *B. garrula*, loaned by the United States National Museum, all but two individuals possess the tips on the secondaries, and, in addition, four specimens, equally divided between the two sexes, have color on the rachis of some rectrices, and small appendages of pigment extend beyond the feathers. Stevenson (1882) found that among 144 specimens of *B. garrula garrula* killed by storms in England in the winter of 1866-67, 69 individuals had wax tips. Of these, 41 were males and 27 were females; the remaining one was of uncertain sex. Among 38 definitely sexed *B. garrula pallidiceps* in the California Museum of Vertebrate Zoölogy, Swarth (1922:276) lists tips in 22 males and 16 females. These data indicate that the proportion of birds with the wax tips is higher in *B. garrula* than in *B. cedrorum*. The potentiality for wax tips is possibly inherited according to Mendelian ratio.

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Bombycilla japonica is of interest in that the adults, at least, seldom have the waxy appendages. Nevertheless, in the specimens observed, the entire distal ends of the feathers normally possessing the tips in other species are suffused with red color. This may be the original

condition of all waxwings, or perhaps, instead, this species is in a transitional stage in the development of the tips. Swarth (1922:277) says concerning the probable derivation of the wax tips in *B. garrula* (and in *B. cedrorum*): "the ornamentation, in fact, may well have begun with the coloring of the shaft, spreading later over adjoining feather barbs. The last stage would have been the coalescing of the barbs, forming the waxlike scale as is now seen. Various steps of this hypothetical development are supplied in the wing and tail feathers of different birds of this series." *Bombycilla japonica* thus may be close to the ancestral condition in the waxwing stock in the development of the waxy appendage.

The rectrices of all three species of waxwings seldom possess the wax tips, unless the secondaries have the maximum number of tips. In these individuals, the pigment seems to "spill over" onto the tail feathers. Eight is the maximum number of tips found on the secondaries. Rectrices with wax tips are more frequently found in *B. garrula*, and only occasionally in *B. cedrorum*. The pigment in the tip of the tail of *B. japonica* is red rather than yellow as it is in the other two species, and some individuals of the Japanese Waxwing show a slight amount of coalescence of wax in the tail feathers as well as in the secondaries.

If the tips were present in all members of the two species, it could be postulated, in line with recent investigational work by Tinbergen (1947), that the tips are in the nature of species "releasers," facilitating species recognition. Such recognition is now regarded as of prime importance in the formation of species. It is improbable that sex recognition may be aided, as there is no evidence to indicate that the tips are found predominantly in either sex.

The wax tips are not limited to the adult birds in the species *B. garrula*. Swarth (*op. cit.*) mentions the capture of several young Bohemian Waxwings, and describes them as "possessing all the distinctive markings of the most highly developed adult." This includes wax appendages, and several citations are given (Wolley 1857, Gould 1862) to indicate that this is the rule rather than the exception, not only for the American subspecies *pallidiceps*, but at least for the European subspecies *garrula* as well. On the other hand, the young of *B. cedrorum* lack the wax tips, at least as far as available data show.

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Some characteristics of living animals are of the "relict" type; that is to say, they were developed in ancient times when some unknown ecological factor was operative which is no longer demonstrable, and the characteristic is now neutral or at least not detrimental, although of no positive value to the organism. Possibly the wax tips of waxwings are thus to be explained. I am more inclined to the opinion that the wax tips are adaptations to present-day ecological conditions for the birds.

The wax tips are raptive in effect, since the birds, especially in winter, are habitués of bushes and trees that have berries, and the tips, on the otherwise dull body, suggest berries. The red tips tend further to disrupt the body outline at the midline, or slightly posterior to this. Perhaps the wax tips on the rectrices emphasize the end of the tail, the region of the body that is the least vital and that may be expendable in times of pursuit by an enemy.

Any characteristic is of survival value to an organism if in any way the characteristic enhances the chances of survival up to the time when the organism can successfully raise even a few young to maturity. If that character, as for example, the red wax tips on the secondaries, helps to maintain the individual until it can raise to independence a greater number than merely a few young, such a character can be said to be of greater survival value. The character may be effective for a brief period of time and may be uncommon; it might be effective for a split second in time, and only at a particular stage in the life history.

The winter period probably is the most hazardous for waxwings, in that they then depend at times upon long flights to find food. The food is vegetable, and thus is comparatively low in food value; the birds must ingest large quantities of berries or dried fruits to maintain themselves. In winter, in northern latitudes at least, predators are more apt to prey upon those species which, like waxwings, do not migrate south. The winter months are those in which waxwings frequent berry bushes, and it may well be that in these months, the wax tips that appear like berries, are especially valuable to the birds, and operate selectively.

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It is suggested, therefore, that the wax tips are of positive value to waxwings, rather than being relict characters. Coalescence of pigment has taken place in the formation of the wax tips. *B. japonica* is closer to the ancestral stock insofar as wax tips are concerned, and generally lacks the tips. *B. cedrorum* has the tips in approximately half of the adults, and not at all in the young. *B. garrula* has the tips in almost all the adults, and in a like proportion of the young, and probably has evolved further in the development and retention of the wax tips than has either of the other two species.

The streaked plumage of *Dulus* is decidedly generalized, and is probably more nearly like the color of the ancestral stock. In this connection it is notable that young Cedar Waxwings are streaked, and young Bohemian Waxwings are streaked to a lesser degree. This streaking is apparently a recapitulation of the feather color of the stock. Perhaps the color of *Dulus* has not changed, as the streaking would not be a disadvantage to the birds in their environment of light and shadow. In joining together in groups and in the construction of large communal nests, *Dulus* has evidently gained sufficient protection against predators; other birds solve this problem by modifying their coloration.

Ptilogonys is raptively colored, but in a different fashion than *Bombycilla*. The tail markings,

the distinct yellow on the under tail coverts, the sharply marked pileum, are all examples of raptive coloration. The generally lighter venter (especially under tail coverts), the crest that may be elevated, and the generally drab bluish dorsum, are cryptic and serve to hide the animal insofar as is possible considering its habits. The very conspicuous coloration of the male, in contrast to the more drab color of the female, however, would lead one to believe that in *Ptilogonys*, following the pattern of many passerine birds, the male leads a predator from the nest, leaving the drab female to incubate the eggs, and thus preserve the young.

It is difficult to suggest reasons for the brilliant coloration of the male *Phainopepla*, unless it is for decoying predators away from the nest. Possibly some birds survive not because of, but in spite of, their coloration, and *Phainopepla* may be a case of this sort. Anyone who has observed *Phainopepla* in life will agree, certainly, that the male makes no attempt at concealment, and flaunts his color to all comers.

The coloration of *Phainoptila*, in contrast to *Phainopepla*, is much more plain, and is suited to its habits of brush dwelling; in a brush habitat the drab coloration is difficult to detect. The Yellowish Olive under tail-coverts and the Olivaceous dorsum are all evidences of cryptic coloration, and undoubtedly, this bird depends upon hiding for escape from its enemies, since it is a bird of the dense forest cover.

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Coloration, which varies relatively rapidly in response to differing ecological conditions, has become more different in the species of Bombycillidae than is true in many other families of passerine birds. The explanation lies in early geographical isolation of the three subfamilies, with consequent radiation in three directions. Waxwings have become adapted by possessing a thick protective layer of feathers and drab coloration broken by raptive marks. They still retain the streaked plumage, which is probably ancestral, in the juveniles; this is lost at the first molt in the fall. In its evolution, *Dulus* has developed large feet, heavy decurved beak, and the large communal nest that affords protection from enemies; as a consequence, perhaps *Dulus* did not need a plumage different from the primitive and streaked one. The survival of *Dulus* may not have depended on either raptive marks or on brilliant and outstanding plumage. The large feet and large bill seem to be responses to particular ecological requirements, as will be shown later.

The Ptilogonatinae, with habits paralleling those of the flycatchers, probably are considerably modified from the ancestral stock; the coloration probably is more brilliant and conspicuous. Perhaps this type of coloration and the habit of capturing insects from a perch are correlated. Some amount of territoriality is characteristic of this subfamily and dimorphism in color—the plumage of the male is outstandingly conspicuous—possibly is of selective value to the race. In a tropical forest community, a duller pattern possibly would be more visible and thus would be selectively disadvantageous.

COURTSHIP

Waxwings are gregarious birds and individuals establish no well-defined territories as do many birds. The nest itself is the only defended territory, and as Crouch (1936) has shown, the Cedar Waxwing will nest in close proximity to others of the same species. Swarth (1932:275) mentions that the Bohemian Waxwing is tolerant of the nests of other pairs near by. The extreme condition is that found in *Dulus*, in which the territory is not limited even to the nest, but to the individual compartment of the community nest. *Phainopepla*, a less gregarious bird than *Dulus* and waxwings, has a much more definite territory, although individuals of *Phainopepla* are tolerant of others of the same species; no feeding territory is established, and small flocks of birds feed together at any time of the year.

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In birds whose territories lack well-defined boundaries, it would be expected that elaborate song would not have evolved, and that most of the recognition of kind and sex would be dependent upon the behavior of the birds. This is the fact; song, as such, is lacking in the three subfamilies Bombycillinae, Ptilogonatinae, and Dulinae. Waxwings utter (1) notes that serve to keep the flock together, (2) calls used by the young in begging for food, and (3) some low notes that Crouch (*op. cit.*:2) considered as possibly concerned with courtship. *Phainopepla* has various call notes, and in addition, a succession of notes which are run together. *Ptilogonys* utters a note which Skutch (MS) characterizes as a loud, not unmusical "tu-whip" that is used as the birds "fly in straggling parties which keep in contact by their constant chatter." *Dulus* is described by Wetmore and Swales (1931:349) as having only a variety of rather harsh chattering notes in chorus.

The most notable behavior pattern associated with courtship in Waxwings, in the absence of song, is the so-called "mating dance" described by Crouch (1936), and observed by me in Lawrence, Kansas, in the spring of 1948. This consists of one bird of a pair (presumably the male) hopping along a branch toward the other bird (the female), then away again, repeating the procedure for some little time. The female remains motionless until, as the male approaches, mutual fondling of the head and neck feathers takes place, or the birds may peck at each other's bill. A berry may be passed from bill to bill, although generally the berry is not utilized for food, and this can be interpreted as a nervous reaction of the birds. It may be an instance of "false feeding" as is seen in many birds, in which the female begs for food, as a nestling would beg, as a

preliminary to the sexual act. I am of the opinion that these reactions are in the nature of behavioristic patterns that bring the birds into the emotional balance for copulation, as copulation follows the "dance." Sometimes, however, copulation is preceded by a "nuptial flight" around the nesting area, at which time the birds utter loud calls. Armstrong (1924:183) is of the same opinion, citing numerous instances in which nuptial flights and elaborate displays have evolved for just this purpose. The birds are then in the proper physiological balance to initiate the complicated sequence of copulation, nesting, incubation, feeding, and brooding of the young.

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It would be valuable to know more concerning the life histories of the other birds considered in this paper, since behavior is inherent, and probably can be cited as evidence of close relationship or the opposite. All that I have been able to learn is that *Phainopepla* has a nuptial flight in which the male chases the female, and that *Dulus* (Wetmore and Swales, 1931:347) seeks the company of others of its kind at all times, and that two birds, presumably paired, will sidle up to one another when they are perched.

NEST BUILDING

There are numerous papers concerning the nesting of waxwings. *B. garrula*, owing to its nesting in the far north, where observers are few, has received less attention than *B. cedrorum*. There is, on the other hand, no literature that deals with the nesting habits of the majority of the Ptilogonatinæ, with the exception of *Phainopepla*, on which there is considerable literature (Merriam, 1896; Myers, 1907, 1908). No detailed study of the nesting of *Dulus* has been reported, although Wetmore and Swales (1931) have described carefully the large communal nest of this genus.

In *Bombycilla*, both members of a pair apparently aid in the construction of the nest (Crouch, 1936; Swarth, 1932). Although the sexes are alike in plumage and general appearance, most students of the nesting of waxwings agree that one bird, assumed to be the female, does most of the arranging of the material, and does the shaping of the nest, whereas both birds carry materials to the nest site. As is characteristic of many passerine birds, both members of the pair gather materials and fly back to the nest site, where the female takes the more active part in the construction of the nest itself.

Both species of American waxwings build bulky nests, with the base or platform composed of a large amount of twigs and sticks, from which there often trails a mass of sticks and moss or string. Softer materials such as moss, plant fibers, and string, are placed inside the platform; moss is readily available to, and preferred by, *B. garrula* according to Swarth (*op. cit.*:271), and various plant fibers and string are used by *B. cedrorum*. The inner lining consists of soft plant fibers or down, dry grasses, and feathers. The nest is usually unconcealed in a tree either adjacent to a trunk or on a main side branch, but sometimes in a fork. Nest building by both Cedar and Bohemian waxwings is rapid, taking from three to five days, and is followed immediately by egg laying.

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Nesting by waxwings is late in the season; June is the month in which the nest is usually started. This is readily explainable in Bohemian Waxwings, since adverse weather would prohibit earlier nesting in the area in which they spend the summer. Crouch (*op. cit.*:1) remarks that *B. cedrorum* possibly evolved in the far north where it was impossible for it to start nesting earlier, and that the habit has been retained. Perhaps, on the other hand, nesting is delayed until the berry crop is ripe, to insure sufficient food for the young.

Desertion of the nest is not uncommon in waxwings, despite the tolerance to other animals that is shown by the birds. A new nest may suddenly be begun before the first one is finished, and all the materials from the first nest may be removed, or the nest may be abandoned before it is completed. The eggs may be left at any time up to hatching, and the young may be deserted, especially in the earlier stages of development.

The very large and bulky communal nest of *Dulus* is not radically different from the nest of waxwings. In the absence of sufficient nesting sites, a pair of gregarious birds such as *Dulus* could combine their nest with those of other pairs, retaining for their own territory only the nest cavity, and in this way communal nests might have evolved. The nest of *Dulus* is communal probably because of the lack of suitable trees for nesting sites, and only incidentally does this type of nest afford better protection from natural marauders. Large numbers of Palm-chats work together in the construction of the nest platform, and both sexes probably take part in the work.

In *Phainopepla* the nest is built mostly by the male (Merriam, 1896; Myers, 1908), although the female does some of the work, especially in the shaping and lining of the nest. In this genus, the nest is usually a compact structure, but exceptional nests are of considerable bulk. The nest is commonly placed in a fork near the main trunk of a tree, in a conspicuous location, and generally is 10 to 20 feet from the ground. In shape and location, the nest closely corresponds to that of *Bombycilla*, but the materials used for a base are stems of annual plants, whereas *Bombycilla* uses more woody twigs. The finer materials used by *Phainopepla* are more readily obtainable in the ecological association inhabited by *Phainopepla* than would be heavier twigs such as *Bombycilla* uses.

FOOD

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Waxwings are typically frugivorous; berries are the staple food. The birds are known to catch insects, especially in the spring and summer, and their insect gathering technique has been likened to that of Tyrannid flycatchers. Nice (1941) experimented with a young captive Cedar Waxwing and found that it had a decided preference for red or blue berries, and that meal worms were utilized as food only when the birds became educated by other captive birds of other species as to the food value of the worms. Post (1916) indicates that the food given to the nestlings of Cedar Waxwings is entirely animal for the first three days, and that a mixed diet of berries and insects is subsequently offered.

In feeding of the young, regurgitation of partly digested food does not take place, according to Wheelock (1905). Rather, the adults "store" food in the form of berries in the expanded esophagus or crop, feeding them whole to the young. Digestion is an unusually rapid process, involving merely minutes for the passage of berries and cherries. This is correlated with a short intestinal tract, which is unusual for a frugivorous bird. Nice's (1940) experiments with Cedar Waxwings revealed that cherries would pass through the digestive tract in 20 minutes, blueberries in 28 minutes, and chokecherries in 40 minutes. Heinroth (1924) states that berries pass through the digestive tract of Bohemian Waxwings in the space of a "few minutes." This rapid digestion is obviously adaptive, since the value of the food is slight and therefore large quantities of it must be ingested; the large seeds would hamper further ingestion until they were eliminated, since they seem not to be regurgitated.

Members of the subfamily Ptilogonatinae are both insectivorous and frugivorous insofar as available data show, although again there is relatively little information available concerning them. Skutch (MS) has found that the Guatemalan *Ptilogonys cinereus* catches insects by repeated sallies into the air from a perch, after the manner of flycatchers. He notes also that the birds feed on berries of *Eurya theoides* and *Monnina xalapensis*. It is well known that *Phainopepla* catches insects when these are available, and its liking for berries is so apparent that in parts of its range, it is known as the "pepper bird," since it frequents pepper trees (*Schinus molle*) and feeds on the small red berries. The preserved specimens of *Ptilogonys* and *Phainoptila* available for this study contain only berries in the digestive tract. *Dulus* feeds mostly, if not wholly, on plant food. According to Wetmore and Swales (1931:349), berries, fruits, and parts of flowers are eaten.

SKELETON

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A critical analysis of the skeletons provides evidence that aids the student in estimating which differences are merely the result of habits developed in relatively recent geological time as opposed to those which owe their existence to more ancient heritage. Stresses caused by the action of different sets of muscles can apparently stimulate changes in bones to meet new needs, and the evidence from genetics is that such mutations in wild birds are minute and cumulative, rather than of large degree and of sudden appearance. Once adaptive mutations have occurred, if genetic isolation from one source or another accompanies it, a new population different from the parental stock may become established. Study of the skeleton of any species of living bird may indicate those characters identifiable as modifications fitting it to a particular environment. If no distinguishing characters are discovered that may be attributed to environmental factors, such a species can be spoken of as generalized; the inference then is that such a species is not modified for a single, particular ecological niche.

Some parts of the skeleton, obviously, are more adaptable or plastic than others. The beak seems to be the most adaptable part. Probably this results from its frequent use; it is the part of the bird to capture the food. The long bones, meeting the environment as legs which serve as landing mechanisms or as locomotory appendages, and as wings which provide considerable locomotion for most birds, probably come next in order as regards plasticity. In these parts, then, one may look for the most change in birds, which, within relatively recent geologic times, have been modified to fit a particular set of conditions. From the beak and long bones of a species in which habits are unknown, one can infer the habits and habitat from a comparison with the skeletal features of species of known habits.

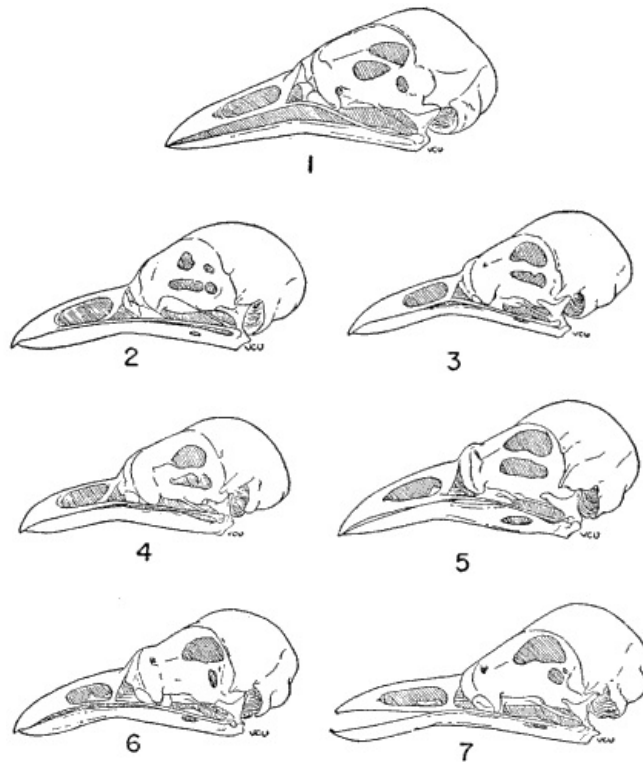
Skull.—The skulls in all three subfamilies have essentially the same general appearance and structure, the most marked differences being, as would be expected, in the bills and associated bones.

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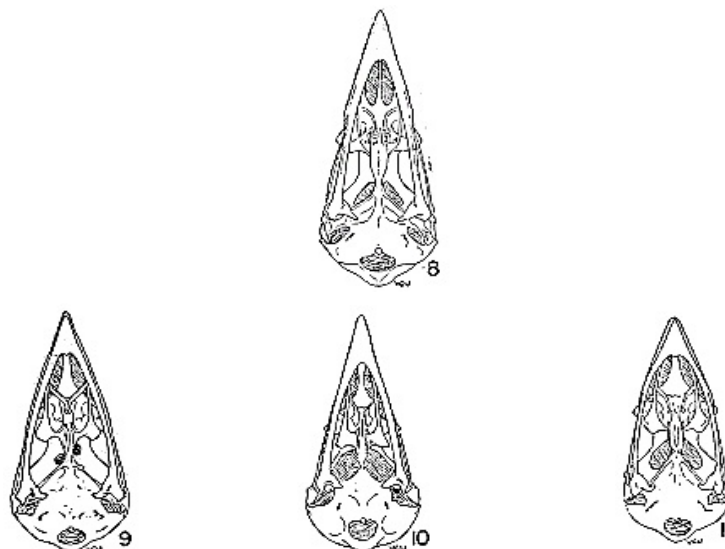
The most specialized bill is to be found in *Dulus*; its bill is decurved, and the associated bones are correspondingly changed for support of the bill. For example, the palatines and "vomer" are much wider, the palatines are more concave from below and have longer posterior processes than the corresponding bones in *Bombycilla*. Moreover, the "vomer" in *Dulus* and in *Phainoptila* is larger and heavier than in *Bombycilla*, and the quadrate and pterygoid bones are relatively

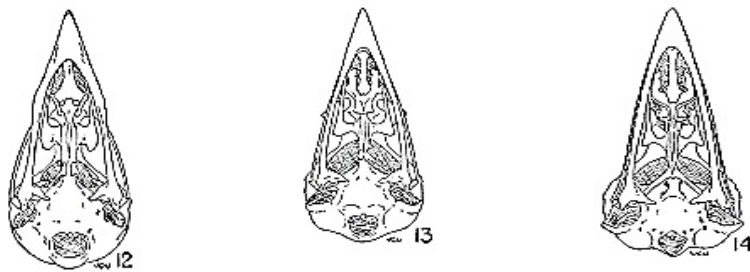
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large for support of the beak. The palatines, however, are weak in *Phainoptila*. In the Ptiligonatinae, with the exception of *Phainoptila*, the wings of the palatines flare more than in *Bombycilla*, but not to the extent that they do in *Dulus*, nor does the palatine bone present a concave appearance in the Ptiligonatinae. The premaxilla is a relatively weak bone in *Bombycilla* and *Phainopepla*, stronger in *Ptilogonys*, and is notably heavy in *Phainoptila* and *Dulus*, and in these latter two genera shows a sharply-ridged tomium. The maxillae connect to somewhat widened nasal and naso-lateral processes in all the genera, and the premaxillae narrow abruptly from this point forward. In the family, *Phainopepla* and *Phainoptila* show the least flaring in this region.



FIGS. 1-7. Skulls in lateral view of five genera of Bombycillidae. Natural size.
 1. *Phainoptila m. melanoxantha*, sex?, MNH no. 26493, 15 mi. SE Cartago, Costa Rica.
 2. *Ptilogonys caudatus*, male, MNH no. 24492, 15 mi. SE Cartago, Costa Rica.
 3. *Phainopepla nitens*, male, MNH no. 24752, Pima Co., Arizona.
 4. *Ptilogonys cinereus*, female, Louisiana State University no. 297, Xilitla Region, San Luis Potosi, Mexico.
 5. *Dulus dominicus*, female, USNM no. 292652, Don Don, Haiti.
 6. *Bombycilla cedrorum*, male, MNH no. 15331, Bexar Co., Texas.
 7. *Bombycilla garrula*, sex?, USNM no. 223895, Bozeman, Montana.

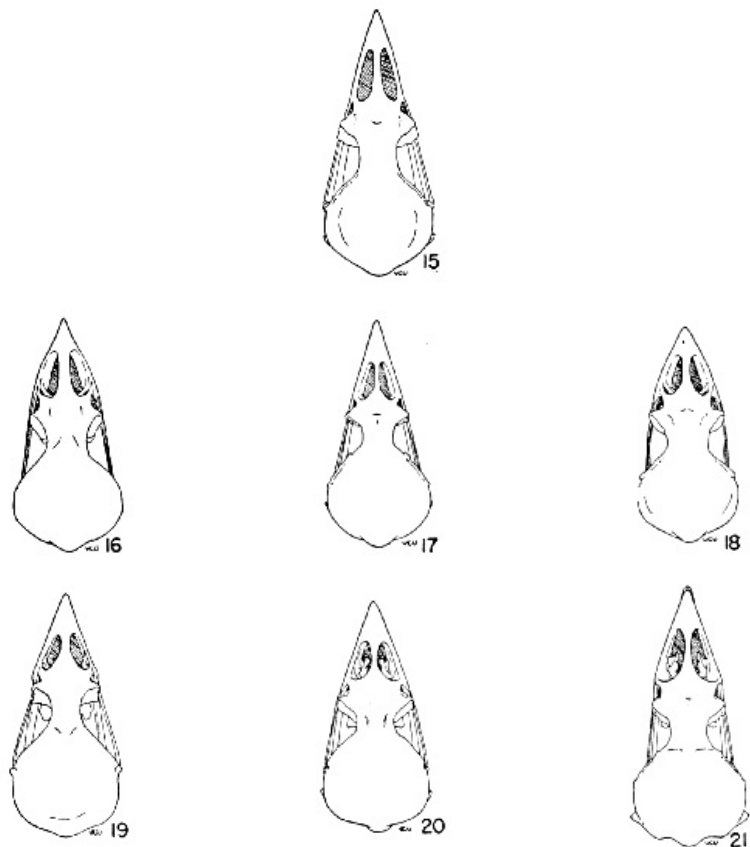




FIGS. 8-14. Skulls in ventral view of five genera of Bombycillidae. Natural size.

8. *Phainoptila m. melanoxantha*, sex?, MNH no. 26492, 15 mi. SE Cartago, Costa Rica.
9. *Ptilogonys caudatus*, male, MNH no. 24492, 15 mi. SE Cartago, Costa Rica.
10. *Phainopepla nitens*, male, MNH no. 24754, Pima Co., Arizona.
11. *Ptilogonys cinereus*, female, Louisiana State University no 297, Xilitla Region, San [Luís](#) Potosi, Mexico.
12. *Dulus dominicus*, female, USNM no. 292652, Don Don, Haiti.
13. *Bombycilla cedrorum*, male, MNH no. 15331, Bexar Co., Texas.
14. *Bombycilla garrula*, sex?, USNM no. 223895, Bozeman, Montana.

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FIGS. 15-21. Skulls in dorsal view of five genera of Bombycillidae. Natural size.

15. *Phainoptila m. melanoxantha*, sex?, MNH no. 26493, 15 mi. SE Cartago, Costa Rica.
16. *Ptilogonys caudatus*, male, MNH no. 24492, 15 mi. SE Cartago, Costa Rica.
17. *Phainopepla nitens*, male, MNH no. 24752, Pima Co., Arizona.
18. *Ptilogonys cinereus*, female, Louisiana State University no. 297, Xilitla Region, San Luís Potosi, Mexico.
19. *Dulus dominions*, female, USNM no. 292642, Don Don, Haiti.
20. *Bombycilla cedrorum*, male, MNH no. 15331, Bexar Co., Texas.
21. *Bombycilla garrula*, sex?, USNM no. 223895, Bozeman, Montana.

This flaring, immediately lateral to the antorbital plate, is common to all Bombycillids and constitutes a major skeletal characteristic useful for recognition of the members of the family, since the swelling is easily discernible both externally and on the cleaned skulls. In *Phainopepla* there is much variability in this character; some specimens have a narrower antorbital bridge than others. Only one skeleton of *Phainopepla n. nitens* was available. The flaring in the skull of this specimen is identical with that in *Ptilogonys*. Among the skulls of *P. n. lepida* in the University of Kansas Museum of Natural History, is No. 19228, a juvenile, taken 5 miles south of Tucson, Arizona. In this specimen, the flaring in the antorbital region is clearly evident and equal in amount to that in skulls of *P. n. nitens*, but the bird had not attained full skeletal growth. However, the flaring of the antorbital region appears to be common in the nestlings of many species of passerine birds. Other specimens of the subspecies *lepida* show a varying amount of flaring, the least (in the series available) being in No. 24754, MNH, in which the proportion of the skull (length divided by width) closely corresponds to that in *Phainoptila*; the skull of No. 24754 is long and thin, and the base of the bill is only slightly swollen. The skull of *Phainopepla nitens lepida* is more generalized than that of *Phainopepla n. nitens*, having a longer and narrower bill like the generalized *Phainoptila*. In *Phainopepla n. nitens* and in members of the genus *Ptilogonys*, more flaring occurs in the antorbital region.

Phainoptila, as noted above, has no great amount of flaring in the antorbital region. When more specimens of *Phainoptila* are examined, the base of the bill probably will be found to flare more in some individuals than in others; this would be expected if we may judge by the data on *Phainopepla*. The premaxilla and maxilla of *Phainoptila* are similar to the same bones in *Dulus*, and there is a well-marked ridge on the tomium (possibly for cutting flower parts). In *Phainoptila*, the palatines are narrower than in any other genus of the family and abut the lacrimals. The entire skull appears to be modified along different lines from those of the skull of *Dulus*; the skull of *Phainoptila* seems to be modified for a frugivorous rather than an insectivorous diet. The skull of *Phainoptila* probably is more nearly similar to the ancestral skull than is that of any other living species in the family. The wide gape characteristic of some members of the family is undoubtedly a modification for aiding in the capture of insects, and *Phainoptila* has progressed less in this direction than have other species in the family.

The mandibles vary somewhat in the shape and proportionate size of the bones. The mandible is proportionately, as well as actually, highest in *Dulus*. The medial condyle varies to some extent, being slightly flattened medially in *Bombycilla*, and less so in the other genera. The mandible of *Bombycilla* narrows to the symphysis much more gradually than it does in the other genera.

[Pg 499]

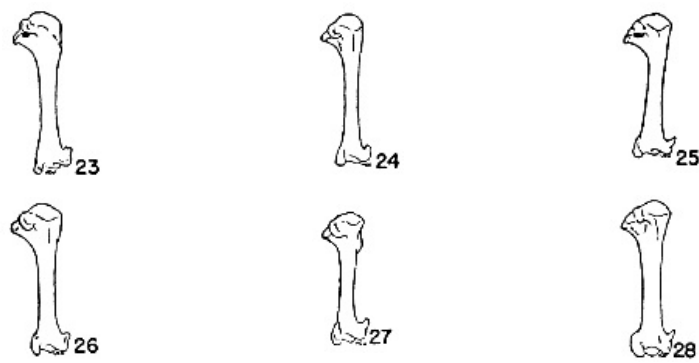
The antorbital plate is large and divides the orbital chamber from the nasal chamber. The small lacrimal bone anterior to the plate articulates with the maxilla and the premaxilla. Shufeldt (1889) states that the free lacrimal ossicle might be of some taxonomic importance in the passerines, since it is found in the generalized Corvids and in nestling Turdids. I find it well developed and identical, with a double articulation and free ends, in all the Bombycillids. There is no significant variability in the family, and this is more evidence of close taxonomic relationship between the members of the family.

The size of the crania is somewhat variable, although the differences seem to be primarily those of proportion. Ptilogonatinae have long crania, whereas the crania of the Bombycillinae and Dulinae are shorter but deeper. I regard the longer cranium as primitive, and it is longest in *Phainoptila*. In order of decreasing relative length of the cranium, *Phainoptila* is followed by *Ptilogonys caudatus*, *P. cinereus*, and *Phainopepla*. *Bombycilla garrula* has the deepest cranium in the family.

The measurements of the lengths and widths of the skulls are given in [Table 9](#). The relative length of the bill and relative width of the skull are given in [Table 10](#). These relative measurements are calculated by using the actual measurements in Table 9 as numerators, the length of the skull from the lacrimal bone to the posteriormost end of the skull being used as the denominator. The data indicate that *Phainoptila* has a slightly narrower cranium.

Humerus.—Certain families of passerine birds have a noticeable variation in the characteristics of the humerus; the bone varies in length, in diameter, and in the complexity of the processes at either end. In the Bombycillids, however, the amount of variation is relatively small, and the diaphysis of the bone is somewhat twisted, especially so in *Dulus*. The deltoid tuberosity is variable, being shorter but more elevated in *Bombycilla* than it is in the Ptilogonatinae and in the Dulinae. The tendon from the pectoralis major muscle, which inserts on this process, probably finds better insertion on a higher process than on a lower but longer one.

[\[↑ TOC\]](#)



FIGS. 22-28. Humeri of five genera of Bombycillidae. Natural size.

22. *Phainoptila m. melanoxantha*, sex?, MNH no. 26493, 15 mi. SE Cartago, Costa Rica.
 23. *Ptilogonys caudatus*, male, MNH no. 24492, 15 mi. SE Cartago, Costa Rica.
 24. *Phainopepla nitens*, male, MNH no. 24754, Pima Co., Arizona.
 25. *Ptilogonys cinereus*, female, Louisiana State University no. 297, Xilitla Region, San Luís Potosi, Mexico.
 26. *Dulus dominicus*, female, USNM no. 292652, Don Don, Haiti.
 27. *Bombycilla cedrorum*, male, MNH no. 15331, Bexar Co., Texas.
 28. *Bombycilla garrula*, sex?, USNM no. 223895, Bozeman, Montana.

Distally, the two major condyles and the intercondylar groove or olecranon fossa that make efficient articulation with the ulnar process, are not variable. The external condyle, however, is significantly variable in the family. This condyle is longest and most pronounced in birds in which the humerus is short in relation to the trunk, as for example in *Tachycineta*. In the Bombycillidae the condyle is smallest in *Phainoptila*, where it is a mere suggestion of a process. In the remainder of the Ptilogonatinae, the condyle is larger but rounded, and shows a double process in *Ptilogonys caudatus*, and a slightly pointed process in *P. cinereus*. The external condyle in *Dulus* is not specialized, being low and rounded, but in *Bombycilla*, it is noticeably elongated, indicating a better attachment distally for the deltoid muscle. (No measurements are tabulated for this condyle, as the percentage of error in measuring this small structure is great.) [Table 1](#) gives lengths of humeri, and [Table 2](#) gives lengths of the humeri expressed as percentages of the length of the trunk, a standard measurement.

[Pg 501]

The area of insertion of the deltoid muscle is elongated in those birds with shortened humeri; these birds have also greater flight power than do birds with longer humeri and therefore a shorter external condyle.

TABLE 1. Lengths of Arm Bones in cm.

Species	Humerus	Radius	Ulna	Manus
<i>Ptilogonys caudatus</i>	2.39	2.57	2.79	2.25
<i>Ptilogonys cinereus</i>	2.24	2.48	2.78	2.38
<i>Phainopepla nitens</i>	2.21	2.59	2.82	2.39
<i>Phainoptila melanoxantha</i>	2.40	2.51	2.70	2.25
<i>Dulus dominicus</i>	2.23	2.38	2.63	2.31
<i>Bombycilla garrula</i>	2.35	2.58	2.88	2.67
<i>Bombycilla cedrorum</i>	2.06	2.34	2.60	2.38

TABLE 2. Arm-trunk Ratios (in percent)

Species	Humerus	Radius	Ulna	Manus	Total
<i>Ptilogonys caudatus</i>	85	92	93	80	2.58
<i>Ptilogonys cinereus</i>	84	90	103	89	2.76
<i>Phainopepla nitens</i>	84	98	107	91	2.82
<i>Phainoptila melanoxantha</i>	73	77	82	69	2.31
<i>Dulus dominicus</i>	78	83	92	81	2.51
<i>Bombycilla garrula</i>	69	75	87	78	2.34
<i>Bombycilla cedrorum</i>	67	76	85	77	2.29

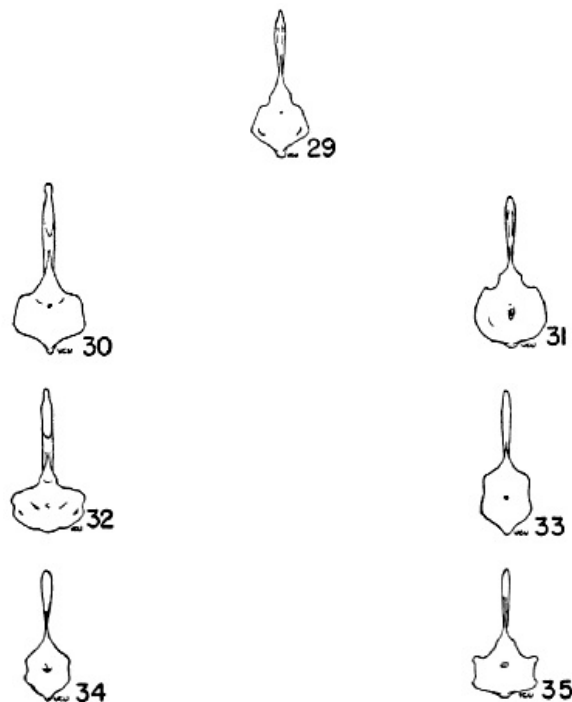
TABLE 3. Arm-trunk Ratios (in percent)

SPECIES	Humerus	Radius	Ulna	Manus	Total
<i>Corvus brachyrhynchos</i>	90	101	111	106	307
<i>Dendroica audubonii</i>	68	82	90	77	237
<i>Setophaga ruticilla</i>	69	82	91	75	235
<i>Myadestes townsendi</i>	71	84	96	81	248
<i>Sialia sialis</i>	72	84	98	86	256
<i>Hylocichla mustelina</i>	75	81	92	80	247
<i>Parus atricapillus</i>	85	90	106	81	272
<i>Tachycineta thalassina</i>	71	95	107	128	306
<i>Myiarchus crinitus</i>	83	105	115	92	290
<i>Dumetella carolinensis</i>	76	75	89	78	243
<i>Polioptila caerulea</i>	85	93	105	71	261
<i>Eremophila alpestris</i>	91	99	110	95	296
<i>Muscivora forficata</i>	85	111	120	108	313

Pygostyle.—This part of the skeletal system is variable in the species dealt with, not so much in size as in complexity. It reflects, of course, the character of the caudal muscles and their size, as well as the length of the rectrices and the corresponding force necessary to hold these feathers upright and in a useful position. Firm attachment is important even in flight, because the tail is used as a rudder, and in the Ptiligonatinae as a brake. The pygostyle is most modified in this subfamily.

[1 TOC]

In lateral aspect, the pygostyles of the species of the Ptiligonatinae are similar. The crest of the bone is flattened dorsally, and has a broad anterior surface that is thin and bladelike. This is widest in *Ptilogonys caudatus*, and narrowest in *Phainoptila*, in which genus, however, the entire bone is of small size. The centrum is widest in *Ptilogonys caudatus*, and is progressively narrower in *P. cinereus*, *Phainopepla*, and *Phainoptila*. Greater width provides a larger area of attachment for the larger rectrices and also more area for insertion of the lateralis caudae muscle, the size of which varies more than that of the other caudal muscles in the different species of the Bombycillidae.



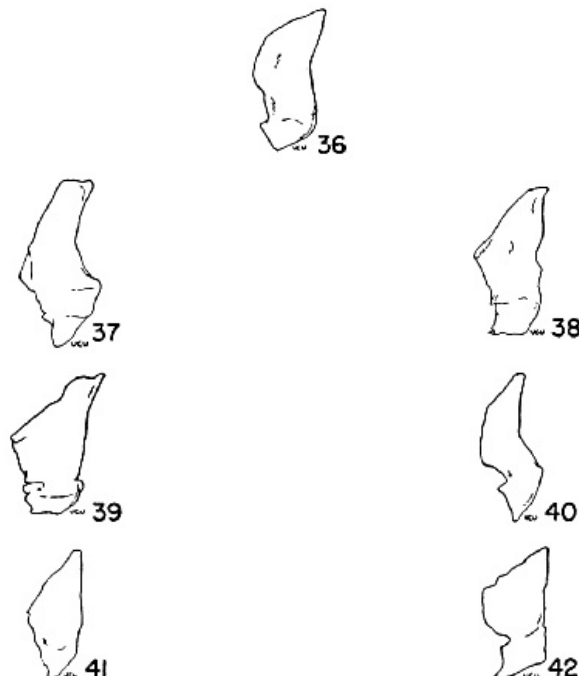
- FIGS. 29-35. Pygostyles in posterior view of five genera of Bombycillidae. × 2.
29. *Phainoptila m. melanoxantha*, sex?, MNH no. 26493, 15 mi. SE Cartago, Costa Rica.
 30. *Ptilogonys caudatus*, male, MNH no. 24492, 15 mi. SE Cartago, Costa Rica.
 31. *Phainopepla nitens*, male, MNH no. 24754, Pima Co., Arizona.
 32. *Ptilogonys cinereus*, female, Louisiana State University no. 297, Xilitla Region, San Luís Potosi, Mexico.
 33. *Dulus dominicus*, female, USNM no. 292652, Don Don, Haiti.
 34. *Bombycilla cedrorum*, male, MNH no. 15331, Bexar Co., Texas.
 35. *Bombycilla garrula*, sex?, USNM no. 223895, Bozeman, Montana.

In proportionate size (see [Table 7](#)), the pygostyle of *Bombycilla* is the smallest in the family. The dorsal spinous portion is acutely pointed instead of flattened as in the Ptilogonatinae. In *Dulus*, the spinous portion is extremely thin, and shows a decided curve dorsad from the centrum, and there is no flattened area anterior to the spinous portion as is seen in *Ptilogonys*.

The centrum in cross section varies considerably. In *Bombycilla* the walls are indented, with definite terminal knobs; both knobs and indentations are more pronounced in *B. garrula* than in *cedrorum*, however. The spinous portion is enlarged in both species, and the rest of the neck region is constricted ([Figs. 29-35](#)).

The centrum of *Dulus* in posterior aspect presents the appearance of a simple shield; little of the indentation seen in *Bombycilla* is present. The spinous portion is plain, with no constriction nor terminal enlargement in the neck. The centrum in *Phainopepla* is similar to that in *Dulus*, but has a small expansion at the base of the spine, the entire centrum being wider in proportion to its over-all size than in any of the other species mentioned previously. The centrum in *Ptilogonys* shows great width, and the spine is in a large expanded tip as in *Bombycilla*. The lateral edges of the centrum in *P. cinereus* are "winged" and in two separate halves; whereas the centrum of *P. caudatus* is fairly plain, its specialization being reflected primarily in breadth and flatness. In cross section of the centrum, *Phainoptila* is similar to *Phainopepla*, although, in the former, the bone is smaller in proportion to the size of the animal, and the lateral wings are more angular than in *Phainopepla*.

[Pg 504]



- FIGS. 36-42. Pygostyles in lateral view of five genera of Bombycillidae. × 2.
36. *Phainoptila m. melanoxantha*, sex?, MNH no. 26493, 15 mi. SE Cartago, Costa Rica.
 37. *Ptilogonys caudatus*, male, MNH no. 24492, 15 mi. SE Cartago, Costa Rica.
 38. *Phainoptila nitens*, male, MNH no. 24754, Pima Co., Arizona.
 39. *Ptilogonys cinereus*, female, Louisiana State University no. 297, Xilitla Region, San Luís Potosi, Mexico.
 40. *Dulus dominicus*, female, USNM no. 292652, Don Don, Haiti.
 41. *Bombycilla cedrorum*, male, MNH no. 15331, Bexar Co., Texas.

In specialization for muscle attachment, the centra of the pygostyles of the Ptilogonatinae have more area for muscle attachment than do the centra in the Bombycillinae and Dulinae; the centrum is wide, the spinous portion is long, and the bone is flattened anteriorly. The most generalized pygostyle is in *Phainoptila*, and that of *Dulus* differs only slightly. In *Bombycilla* the pygostyle is proportionately small, but is complex in shape; there is seemingly not the need for greatly expanded areas since the caudal muscles are less specialized in this genus.

[Pg 505]

Sternum.—The sternum in Bombycillids is typically passerine in general shape and in having a long and deep carina or sternal crest. The caudal process of the bone is broad, with the terminal ends flattened, forming dorsally a graceful V-shaped outline, whereas the outline of the posterior end of the sternum is broad and convex.

[↑ TOC]

In lateral aspect, the carina is deeper in *Bombycilla* than in other genera of the family, and is deepest in *B. garrula*. In this species, the manubrium is more extended and comparatively larger than in the other species of the family. The anterior edge of the keel forms the sharpest angle in *B. cedrorum*. In *Dulus*, the keel is moderately deep, the manubrium short, and there is a distinct indented curve between the manubrium and the anterior angle of the keel.

In ventral aspect the lateral processes of the sternum tend to flare outwards in adult Ptilogonatines on almost the same plane as the rest of the bone, whereas in *Bombycilla* and *Dulus* the same process is closer to the body of the sternum. In *Bombycilla* the xiphoid process is more dorsal in position than in other species in the family, and in *Dulus* an upward curve is very noticeable. The process in these two genera is narrower than in the Ptilogonatinae, and lacks the heavy distal terminal enlargement which is apparent in *Ptilogonys*.

Relative Lengths of Bones.—In instances where the animals being compared are obviously different in over-all size, it is useful to express the size of a given part in relation to some other part of the same individual organism if the aim is to obtain clues as to differences in functions of the parts being compared. Differences in actual lengths of corresponding bones in two kinds of animals often, of course, reflect only the difference in over-all size of the animals. Consequently, the relative size of the part is expressed as a percentage in this paper. In computing a percentage it is well, of course, to select some relatively stable part of the animal to use as a denominator in the mathematical expression that yields the percentage. The thoracic region of the vertebral column is thought to be such a part. For example, the length of the humerus divided by the length of the thoracic region yields, in *Phainopepla* and *Ptilogonys*, respective percentages of .84 and .85. These are roughly the same, whereas the actual lengths of the humeri are 2.21 and 2.39 cm.

[↑ TOC]

[Pg 506]

TABLE 4. Lengths of Leg Bones in cm.

SPECIES	Femur	Tibiotarsus	Tarsometatarsus
<i>Ptilogonys caudatus</i>	2.04	3.10	1.94
<i>Ptilogonys cinereus</i>	1.89	2.90	1.77
<i>Phainopepla nitens</i>	1.76	2.78	1.72
<i>Phainoptila melanoxantha</i>	2.43	3.77	2.58
<i>Dulus dominicus</i>	2.09	3.34	2.09
<i>Bombycilla garrula</i>	2.32	3.46	1.99
<i>Bombycilla cedrorum</i>	1.92	2.95	1.64

TABLE 5. Leg-trunk Ratios (in percent)

SPECIES	Femur	Tibiotarsus	Tarsometatarsus	Total
<i>Ptilogonys caudatus</i>	73	110	69	252
<i>Ptilogonys cinereus</i>	71	109	66	246
<i>Phainopepla nitens</i>	69	106	65	240
<i>Phainoptila melanoxantha</i>	74	115	60	249
<i>Dulus dominicus</i>	73	119	73	265
<i>Bombycilla garrula</i>	68	101	59	228
<i>Bombycilla cedrorum</i>	63	96	53	212

TABLE 6. Leg-trunk Ratios (in percent)

[Pg 507]

SPECIES	Femur	Tibiotarsus	Tarsometatarsus	Total
<i>Corvus brachyrhynchos</i>	71	120	77	268
<i>Corvus corax</i>	73	139	78	290
<i>Dendroica audubonii</i>	62	109	81	252
<i>Setophaga ruticilla</i>	66	127	94	287
<i>Myadestes townsendi</i>	61	99	60	220
<i>Sialia sialis</i>	66	111	72	249
<i>Hylocichla mustelina</i>	75	133	97	305
<i>Parus atricapillus</i>	78	138	99	315
<i>Tachycineta thalassina</i>	61	97	56	214
<i>Myiarchus crinitus</i>	68	106	74	248
<i>Dumetella carolinensis</i>	73	136	94	303
<i>Polioptila caerulea</i>	75	144	113	332
<i>Eremophila alpestris</i>	73	113	115	301
<i>Muscivora forficata</i>	62	98	61	221

TABLE 7. Actual Length and Width in mm. of Pygostyle and Proportionate Length and Width of Pygostyle in percent of Lacrimal Length

SPECIES	Length	Width	Length, percent	Width, percent
<i>Ptilogonys caudatus</i>	9.8	3.9	45	18
<i>Ptilogonys cinereus</i>	8.8	4.1	41	19
<i>Phainopepla nitens</i>	8.4	3.9	41	19
<i>Phainoptila melanoxantha</i>	8.5	3.5	35	14
<i>Dulus dominicus</i>	8.5	2.9	38	13
<i>Bombycilla garrula</i>	7.0	3.5	31	15
<i>Bombycilla cedrorum</i>	7.1	2.9	35	14

TABLE 8. Length of Sternum and Depth of Carina expressed as percentages of the Length of the Trunk

[Pg 508]

SPECIES	Sternum	Carina
<i>Ptilogonys caudatus</i>	85	28
<i>Ptilogonys cinereus</i>	91	32
<i>Phainopepla nitens</i>	81	26
<i>Phainoptila melanoxantha</i>	76	25
<i>Dulus dominicus</i>	107	28
<i>Bombycilla garrula</i>	88	33
<i>Bombycilla cedrorum</i>	82	31

TABLE 9. Skull and Sternum, Length and Width in mm.

Species	Length of Skull	Width of Skull	Length of Sternum	Width of Sternum
<i>Ptilogonys caudatus</i>	34.9	15.6	23.9	7.8

Ptilogonys cinereus	33.4	14.7	24.3	8.5
Phainopepla nitens	33.3	15.1	21.3	6.9
Phainoptila melanoxantha	39.7	16.0	24.8	8.2
Dulus dominicus	36.4	16.6	30.5	8.0
Bombycilla garrula	37.0	16.8	30.0	11.2
Bombycilla cedrorum	34.0	15.5	25.3	9.6

The length of the trunk was taken as the distance from the anterior tip of the neural crest of the last cervical vertebra to the anterior edge of an acetabulum. The number of free thoracic vertebra was five in each specimen; consequently, there was no error from this source. In the cranium, a measurement was taken from the anterior edge of the lacrimal bone to the posteriormost end of the cranium, and the resultant figure was employed for a constant in cases in which small bones were compared.

TABLE 10. Relative Length and Width of Skull (in percent)

[Pg 509]

Species	Length of Skull	Width of Skull
Ptilogonys caudatus	160	72
Ptilogonys cinereus	158	69
Phainopepla nitens	162	73
Phainoptila melanoxantha	161	65
Dulus dominicus	164	75
Bombycilla garrula	164	74
Bombycilla cedrorum	162	74

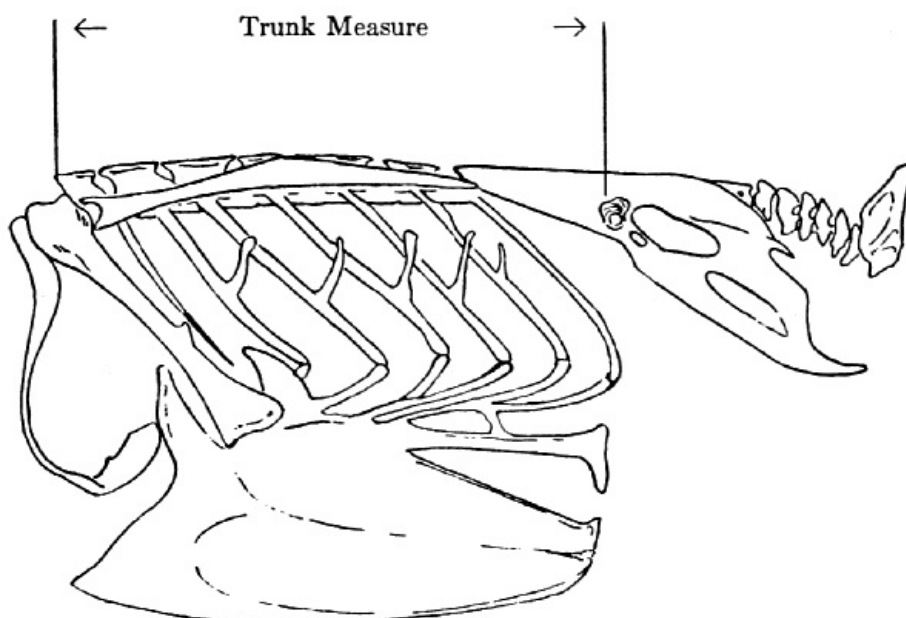


FIG. 43. Part of skeleton of *Bombycilla cedrorum* showing method of measuring the length of the trunk. Natural size.

Leg-trunk Percentages.—[Table 4](#) shows the relative lengths of the legs and of the separate bones in the legs of the different species of the Bombycillids. [Table 5](#) shows corresponding lengths for other passerine birds. The total length of the leg was computed by adding the figures obtained for the lengths of the femur, tibiotarsus and tarsometatarsus. The lengths of the toes were disregarded. Length of leg was recorded in this same way by Richardson (1942:333), who thought that only in swimming and running birds do the toes contribute to the functional length of the hind limb.

[↑ TOC]

[Pg 510]

[Table 4](#) shows that of the birds compared in this paper, *Dulus* has the longest legs. In order of decreasing length the others are the Ptilonogoninae, and finally the Bombycillinae, which have the shortest legs of all. In Waxwings the length of the legs, expressed as percentages of the body-lengths, are identical with those birds that are similar in habits, that is to say, birds which do not use the hind limb except in perching. It can be noted by reference to [Table 5](#) that *Tachycineta* and *Myadestes* fall into this category. This shortness of limb is obviously adaptive, and each of the segments of the limb has been correspondingly shortened, with no element reduced at the expense of the other two. The short leg can be more easily folded against the body while the bird is in flight, than can a long leg which is more unwieldy. It may be noted from tables 4 and 5 that birds which spend much time on the ground, or that hop a great deal in the underbrush, have longer legs than do birds which spend much time in flight. Two birds with noticeably long legs are *Hylocichla mustelina*, a typical ground dweller, and *Parus atricapillus*, which hops about in the trees and underbrush.

Insofar as the lengths of the legs show, *Dulus* and *Phainoptila* are the most generalized of the Bombycillidae, since the relative length of leg is approximately the same as that of more generalized birds such as warblers, crows and thrushes of similar locomotory habits. In other words, *Dulus* and *Phainoptila* have remained unspecialized, in contrast to the waxwings in which adaptive changes fitting them for a perching habit have taken place. *Ptilogonys* and *Phainopepla* are intermediate in length of leg between *Phainoptila* and *Bombycilla*, and *Ptilogonys* and *Phainopepla* have progressed from life on the ground toward the perching habit. *Bombycilla cedrorum* is more specialized than is *B. garrula* in shortness of leg, and the reduction is comparable, as is noted above, to that in the legs of *Tachycineta*.

In birds which have the legs much modified for walking or for hopping in the brush, such as *Polioptila* and *Eremophila*, it is noteworthy that the distal segment, the tarsometatarsus, is the longest, whereas in birds such as *Myiarchus* and *Tachycineta*, that do not utilize the limbs in this manner, the tibiotarsus, the middle segment, is the longest. Mammals much modified for walking or hopping likewise have the proximal segment, the femur, short, and the distal segment long (Howell, 1944). The waxwings have all of the segments short; these birds are modified for strong and sustained flight. Their hind limbs are used principally for landing devices and for perching. No one element of the leg has been shortened much, if any, more than any other.

[Pg 511]

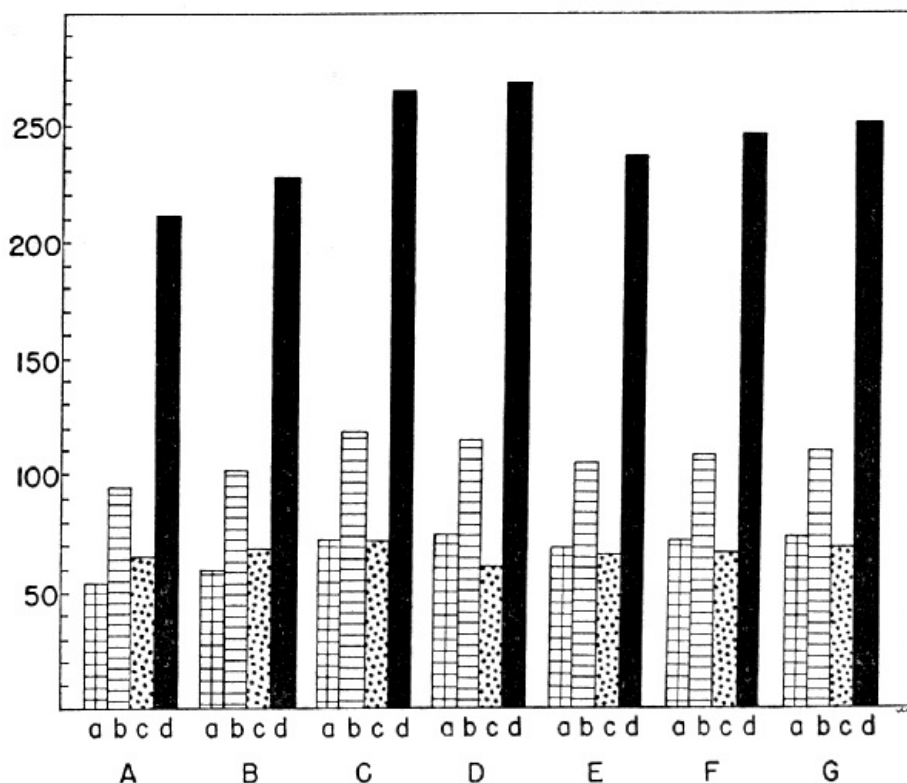


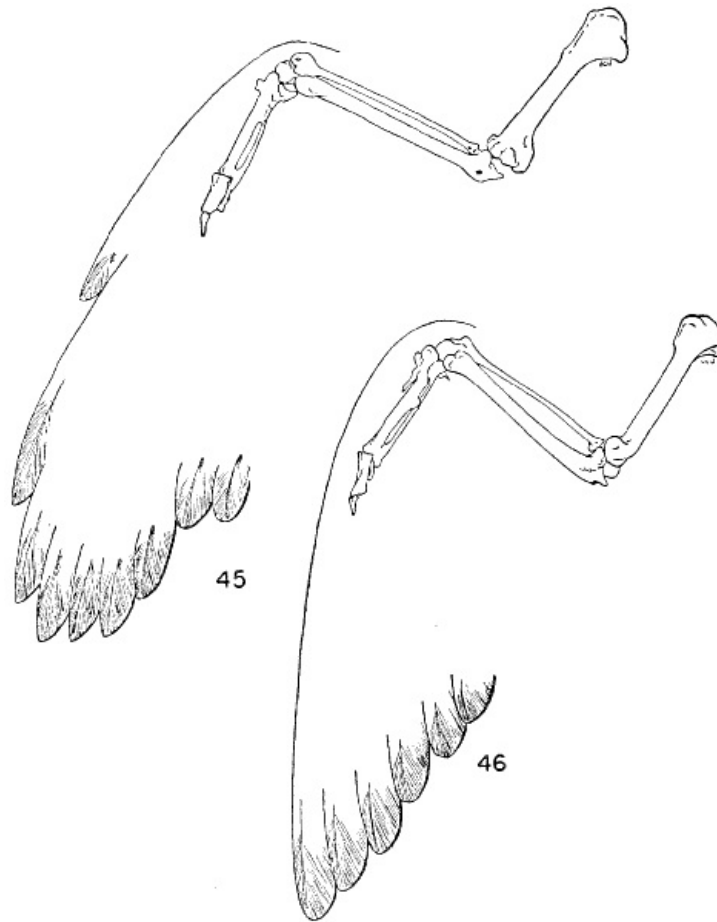
FIG. 44. Graph showing relative lengths of bones of the leg. The percentage values are shown on the axis of the ordinates.

A. *Bombycilla cedrorum*; B. *Bombycilla garrula*; C. *Dulus dominicus*; D. *Phainoptila melanoxantha*; E. *Phainopepla nitens*; F. *Ptilogonys cinereus*; G. *Ptilogonys caudatus*.
a. femur; b. tibiotarsus; c. tarsometatarsus; d. total.

Arm-trunk Percentages.—[Tables 1 and 2](#) show the total length of the arm, and lengths of the separate arm elements, relative to the trunk. [Table 3](#) gives the corresponding lengths for birds

[↑ TOC]

other than the Bombycillidae. Total length of arm was obtained by adding together the lengths of the humerus, ulna, and manus, and by dividing the figure thus obtained by the length of the trunk as was done for leg lengths in [tables 4 and 5](#). The method of adding together the component parts does not give the entire length of the wing, since the length of the feathers, which add effectively to the total length, as well as do the lengths of the small carpal elements, is lacking.



Figs. 45-46. Outlines of wings. $\times 1/2$

45. *Ptilogonys caudatus*, showing relation of outline of wing to bones of arm.

46. *Bombycilla cedrorum*, showing relation of outline of wing to bones of arm.

It may be noted that *Phainoptila* and *Bombycilla* have the shortest arm in the family Bombycillidae. The humerus, radius and ulna are comparable to the same elements in thrushes and the catbird, and it is only the extremely short manus in *Phainoptila* that affects the total. The manus in *Phainoptila* is comparatively smaller than in any other genus of the family Bombycillidae, and this indicates poor flight power. *Bombycilla* has a total length corresponding closely to that in warblers, but the lengths of the distal elements correspond closely to those in the catbird and thrushes. Of the three segments, the humerus is, relatively, the most shortened. Next in order of increasing length of arm is *Dulus*; measurements for it are roughly the same as those of *Myadestes*. The wing bones of the Ptilogonatinae, other than *Phainoptila*, are the longest in this series, and they most nearly resemble the same bones in flycatchers, Parids, and gnatcatchers.

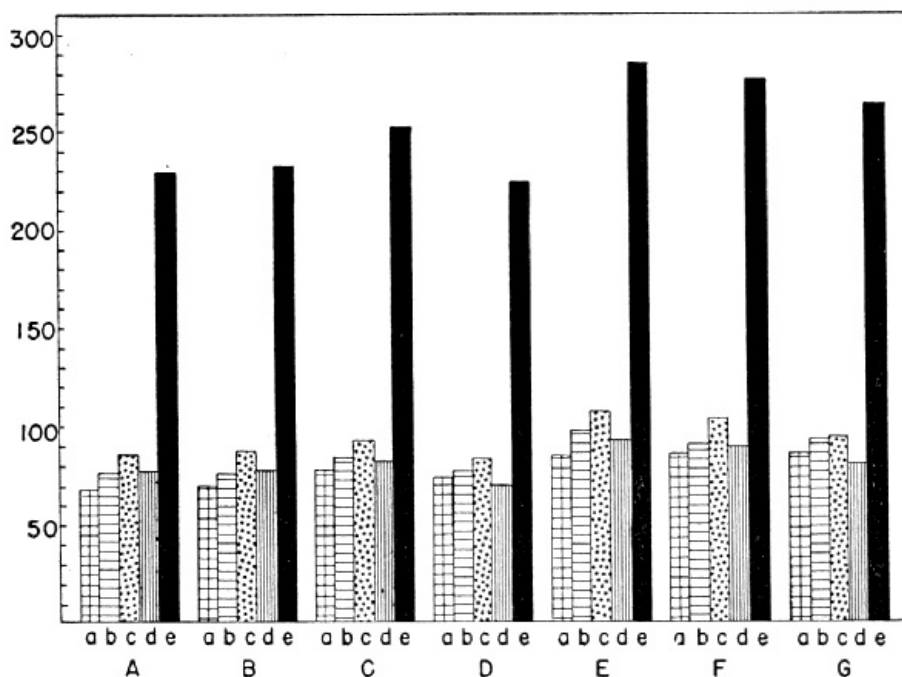


FIG. 47. Graph showing relative lengths of bones of the arm. The percentage values are shown on the axis of the ordinates.

A. *Bombycilla cedrorum*; B. *Bombycilla garrula*; C. *Dulus dominicus*; D. *Phainoptila melanoxantha*; E. *Phainopepla nitens*; F. *Ptilogonys cinereus*; G. *Ptilogonys caudatus*.
a. humerus; b. radius; c. ulna; d. manus; e. total.

It is notable that, in general, birds with long and narrow wings appear to have relatively the shortest humeri, with the distal bones, especially the manus, variable in length and seemingly correlated with the manner of feather attachment. Those birds with rounded and short wings have the longest humeri. In swallows, for example, the humerus is short, whereas the other arm bones are long, and the manus is unusually large and heavy. A short humerus gives better lever action in the flight stroke than a long humerus does.

MUSCULATURE

Dissections showed the same muscles to be present in all genera of the Bombycillidae. There are, nevertheless, differences in the size of the muscles in the various species, and these differences have been investigated primarily as a check on differences noted in the structure of the bones. Even slight differences in mass can be important functionally, but the difficulty in accurately measuring the mass prevents wholly reliable conclusions. The method first used in the attempt to determine the mass of a given muscle was that of immersing the muscle in a liquid-filled graduated tube, and then measuring the amount of liquid displaced. This method, although adequate for large muscles, was subject to a great amount of error in the case of small muscles, and consequently was abandoned. The technique eventually used was that previously employed by Richardson (1942). It consisted of dissecting out the muscle, placing it in embalming solution, leaving it there until a later period, and finally, weighing the muscle on scales, accurate to a milligram, after the muscle had been out of the liquid for a period of one minute. After being weighed, the muscle was measured by the displacement method in a graduated tube, as a check. The results indicate that, although the two methods give the same general results, weighing is accurate to one-hundredth of a gram, whereas the displacement method was accurate to only a tenth of a gram.

In determining the percentage of the weight of a muscle in relation to the total weight of the bird, the weight of the muscle was used as the numerator, and the weight of the preserved specimen was used as the denominator. Before weights were taken, all specimens were plucked in identical fashion.

Caudal Muscles.—The muscles of the caudal area that were used for comparison were the levator caudae and the lateralis caudae. These muscles are used by the living bird to maintain the position of the pygostyle and therefore the rectrices; these muscles are especially important to those birds that utilize the tail as a rudder in flight and as a brake. As may be seen by reference to [Table 11](#), the two muscles are largest in proportion to body weight in the Ptilogonatinae, in which subfamily the species have long rectrices and must have correspondingly well-developed

muscles in order to utilize the rectrices to best advantage in flight. The lateralis caudae differs more according to species than does the levator caudae, showing that rudder action of the tail is of primary importance in the adaptation for capturing insects. It will be remembered that the pygostyle in this subfamily has a flattened lateral surface for attachment of the levator caudae muscle, and it is therefore to be expected that this muscle will be larger in the Ptilogonatinae than it is in either the Bombycillinae or the Dulinae. The levator coccygis, together with the two muscles mentioned above, is responsible for elevation of the tail. The levator coccygis is less altered in different species of the family than is the lateralis caudae. It may be noted that the caudal muscles of *Dulus* and *Bombycilla* constitute a smaller percentage of the total weight of the bird than in any of the genera in the subfamily Ptilogonatinae.

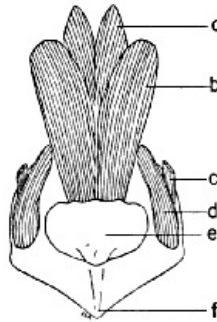


FIG. 48. Caudal musculature, of *Phainopepla nitens lepida*, in dorsal view. $\times 2$.
a. Levator coccygis; b. Levator caudae; c. Lateralis caudae;
d. Lateralis coccygis; e. oil gland; f. dorsal tip of pygostyle.

TABLE 11. Caudal Muscles (Actual and Relative Weights)

SPECIES	Levator	Lateralis
Ptilogonys caudatus	.145g. .092%	.022g. .045%
Ptilogonys cinereus	.030g. .076%	.010g. .026%
Phainopepla nitens	.025g. .096%	.008g. .029%
Phainoptila melanoxantha	.040g. .063%	.015g. .014%
Dulus dominicus	.028g. .063%	.006g. .014%
Bombycilla garrula	.034g. .048%	.010g. .014%
Bombycilla cedrorum	.026g. .050%	.008g. .014%

TABLE 12. Weights of Muscles (These percentages expressed in terms of weights of the body)

SPECIES	P. major	P. minor	Deltoid	Thigh	Peroneus	Gastrocnemius
Ptilogonys caudatus	2.42g. 4.94%	.29g. .59%	.55g. 1.12%	.43g. .88%	.15g. .31%	.96%
Ptilogonys cinereus	2.19g. 5.57%	.28g. .71%	.53g. 1.35%	.30g. .71%	.08g. .21%	1.02%
Phainopepla nitens	1.30g. 4.99%	.20g. .77%	.30g. 1.15%	.28g. 1.12%	.10g. .40%	1.42%
Phainoptila melanoxantha	3.93g. 6.18%	.44g. .69%	.92g. 1.45%	1.09g. 1.61%	.48g. .75%	2.97%
Dulus dominicus	2.09g.	.22g.	.50g.	.73g.	.18g.	

	4.81%	.50%	1.15%	1.68%	.41%	1.01%
<i>Bombycilla garrula</i>	3.85g.	.45g.	.55g.	.50g.	.15g.	
	5.31%	.62%	.76%	.69%	.18%	.59%
<i>Bombycilla cedrorum</i>	2.58g.	.35g.	.50g.	.37g.	.10g.	
	5.00%	.68%	.97%	.73%	.19%	.83%

[\[↑ TOC\]](#)

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Pectoral Muscles.—The pectoral set of muscles varies but little in the family; flight power is seemingly not dependent upon size of either the pectoralis major or pectoralis minor. The data indicate that the insertion on the humerus, with consequent changes in the relative length of that bone, is more significant in type of flight and over-all flight power than is the actual size of the muscle mass. The deltoid muscle, for example, is smaller in *Bombycilla* than in members of the other two subfamilies. The humerus in *Bombycilla* is shortened, and the muscle therefore does not need to be large to accomplish the same powerful stroke that would be accomplished by a longer humerus and a larger, more powerful deltoid muscle. In the case of the deltoid, the shortening of the humerus and the more complex arrangement of the points of insertion have obviated the necessity of enlarging the muscle.

Leg Musculature.—The muscles of the thigh are noticeably larger in birds that have long leg bones. (See [Table 12](#) for size of muscles.) On the tibiotarsus, the peroneus and gastrocnemius muscles were measured. When expressed as a percentage of the weight of the bird, the peroneus has much the same relative weight in all but one of the species, whereas the gastrocnemius varies much. The peroneus is proportionately large only in *Phainoptila*, in which genus all the leg muscles are well developed, but the gastrocnemius is larger in all the Ptilogonatinae and in *Dulus* than it is in the specialized *Bombycilla*, in which it has probably been reduced as the leg bones and other muscles have been reduced.

[\[↑ TOC\]](#)

The volume of the muscles of the hind limb changes more readily in response to saltation and running than do the muscles of the forelimb to flying.

DIGESTIVE TRACT

[\[↑ TOC\]](#)

The digestive tract is relatively uniform in all genera of the family; there are only slight differences between the species. The degree of compactness of the visceral mass varies, *Phainoptila* and *Ptilogonys caudatus* having the folds of the digestive tract loosely arranged, whereas *Ptilogonys cinereus* and *Phainopepla* have folds which adhere more tightly to the ventriculus and liver. In *Dulus* and *Bombycilla*, as compared with the Ptilogonatinae, the visceral mass (primarily liver and ventriculus) is situated more posteriorly in the body cavity, and is more compact, and the intestine is more tightly coiled.

The coiling of the intestine, if its degree of compactness is disregarded, is nearly identical in the birds of the family; there are four major loops between the ventriculus and the anus. The length of this section of the tract is, however, somewhat variable, as can be seen by reference to [Table 13](#), in which the actual and relative lengths of the intestine are given. It may be seen that in *Bombycilla* and in *Phainopepla*, the tracts are much shortened. This is notable, since these are frugivorous birds, and in many frugivorous birds, the tract is lengthened for better extraction of edible portions of the food. Possibly the action of the digestive juices is correspondingly more rapid in *Bombycilla* and *Phainopepla*, thereby permitting the necessary nutriment to be extracted by a short digestive tract.

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In a migratory bird, or one that depends on flight power to find food and escape capture by predators, as in the case of the waxwings, the compacted and shortened visceral mass would seem to be advantageous, because of the consequent reduction in weight. I consider the longer intestine to be the ancestral condition, and that the intestine has become shorter to meet new environmental conditions.

TABLE 13. Digestive Tract: Actual Length, and Length Relative to Thoracic Length

SPECIES	Length in mm.	Relative length (in percent)
<i>Ptilogonys caudatus</i>	134	476.9
<i>Ptilogonys cinereus</i>	111	415.6
<i>Phainopepla nitens</i>	94	357.5
<i>Phainoptila melanoxantha</i>	150	457.1
<i>Dulus dominicus</i>	130	451.0

Beddard (1898:30) states that caecae in the tract may be highly variable in a single family of birds. The Bombycillidae is no exception in this regard. At the junction of the cloaca and the large intestine, there are two small caecae, the function of which is unknown to me. The caecae are largest in the Ptilonotinae, smaller in the Bombycillinae, and smallest in the Dulinae. There may be a correlation between large caecae and more insectivorous diet and small caecae and frugivorous diet; however, the data are not conclusive in this regard.

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ORIGIN OF THE SPECIES

[↑ TOC]

It is here postulated that the center of origin for the ancestral stock of the Bombycillidae was in a region of North America, which at the time concerned was temperate or possibly even semi-tropical in climate. Probably Northern Mexico was the place and probably the climate was temperate. It is reasonably certain, because of the distribution of the species of the family, that they originated in the Americas. In the absence of paleontological data (*Bombycilla* alone is reported, in essentially its modern form, from the late Pleistocene—Wetmore, 1940a), the place and time of origin cannot certainly be determined.

The distribution of the family is such that the more primitive groups are in the south. These are the Ptilonotinae in Central America and Mexico, and the isolated Dulinae in Haiti and the Dominican Republic. This distribution would support the view that the origin was in the south. However, the Holarctic Bombycillinae are so typically birds of northern latitudes that, were it not for such close relatives south of their range, it would appear logical to infer a northerly origin with a subsequent shifting of populations both southward and northward. The phyletic age of the family is probably great, however, as evidenced by the spotty distribution of the birds.

In the evolution of this family, population pressure possibly played the initial role in forcing members of the primitive, southern stock to seek habitable areas on the periphery of the range. Some birds also, being possessed of the "adventurous spirit", aided the northerly movement, thus effecting an extension of the breeding ranges to the north. So far as is now known, this family did not seek living space in South America. By extending its range, a species might find more abundant food and nesting sites. This process of extending the range probably would be costly to the species concerned, because only those individuals best able to adapt themselves to the new environmental conditions would be able to survive long enough to reproduce their kind.

The return flight to the south could, in time, be dispensed with, except in the coldest weather or when the local berry- and fruit-crop failed. Birds such as waxwings are, of course, able to subsist on dried fruits and berries in the critical winter season when strictly insectivorous birds, not so catholic in their food habits, must return south. It appears that waxwings are descendants of migratory birds that have adjusted themselves to a life in the north; and they are judged not to have evolved from year-round residents of the north.

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Even a short migratory journey in spring by part of a population of birds, while the other part remained in the original range, would quickly isolate one breeding population from the other, resulting in the formation of different genetic strains that lead to subspecies, species, and finally to genera and families. Any variation away from the ancestral, "sedentary" stock would become established more quickly because of such isolation at the breeding period. By the same token, the parental stock can, and no doubt does, become modified to suit its environment more perfectly, thus accelerating the tempo of this type of divergent evolution.

The original "split" of the Bombycillines is thought then to have been the result of migration on the part of some of the ancestral stock, with subsequent loss of regular migration because the need to return south was lost. Early in development, and before the migrational tendency was entirely lost, an isolated population, which later became sedentary, as it was an island population, diverged to give rise to the Dulinae. The Dulinae are a homogeneous group since on the islands now inhabited by the birds, they have not been isolated sufficiently long to produce even well-marked subspecies.

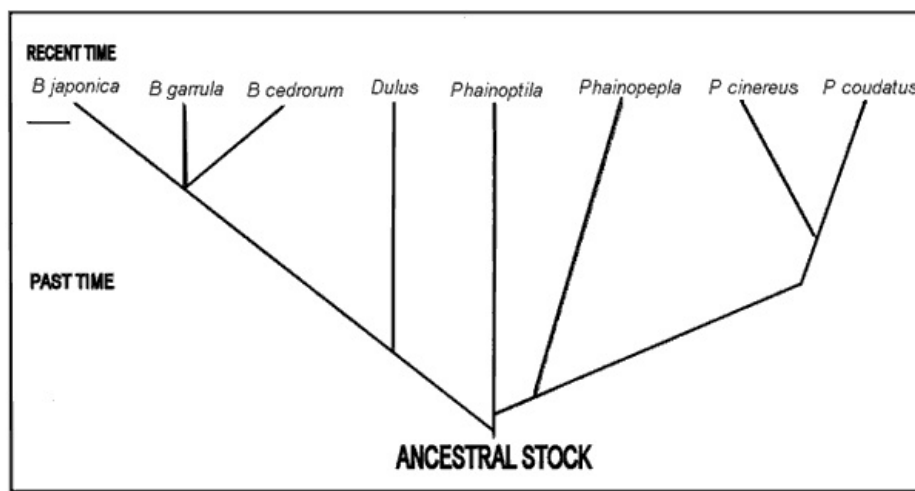


FIG. 49. Hypothetical family tree of the Bombycillidae.

The present day *Phainoptila* is most nearly like the ancestral group, and the remainder of the Ptiligonatinae have diverged to fit conditions similar to those to which the Tyrannid flycatchers, which parallel them, are also fitted.

[Pg 521]

In comparatively recent geological time, two basic lines developed from the Bombycilline stock, the future *B. garrula* and *B. cedrorum*. Possibly *garrula* originally was isolated in Europe and Asia, and later came into contact with *B. cedrorum*, following the time at which the two species were genetically well differentiated. It appears certain that *B. japonica* was an offshoot of the Bombycilline stock at an early time, since it has characteristics that seem relatively unspecialized. It possibly was isolated in the Orient.

Structural affinities of *Dulus* and *Bombycilla* are more pronounced than are those of *Dulus* and *Ptilogonys*, for example. Many of the structural features of *Dulus* parallel those of *Phainoptila*, and it seems likely that the Dulinae were separated early in the history of the family, perhaps as an isolated offshoot of the early migratory Bombycillinae.

CONCLUSIONS

[↑ TOC]

Nomenclature, as used by a taxonomist, should of course indicate affinities as well as apply a name, and the rank of the family should be applied to a structural unit based on common anatomical characters that are more fundamental than, in my opinion, are those used by Ridgway (1904) in proposing family status for the silky flycatchers and the palm-chats. The characters in the diagnosis ([page 478](#)) of the family Bombycillidae are common features regarded as warranting a single family unit for the waxwings, silky flycatchers, and palm-chats. The differences in morphology used by previous workers to characterize each of these groups: (1) the silky flycatchers; (2) waxwings and; (3) palm-chats are regarded as more properly characters of only subfamily rank.

The existing coloration of the species of the Bombycillidae appears to have been acquired relatively late, geologically speaking. The three subfamilies responded to ecological stimuli in three different ways, and the resulting color patterns are unlike in the three groups. Dulinae to this day have a color pattern that is most like the ancestral color pattern, and this is recapitulated in the juvenal plumage of the Bombycillinae before they attain their adult plumage.

Consideration of the geographic distribution of the species of the family indicates that the center of origin of the family Bombycillidae was south of the present range of the waxwings (subfamily Bombycillinae). Waxwings probably are the descendants of a migratory population that diverged from the primitive population at an early time in the history of the family. Owing to their adaptations to survive in the north, waxwings no longer return south in the autumn. Palm-chats (subfamily Dulinae) are descendants of an isolated population of the family stock that developed communal living habits as one specialization. Silky Flycatchers (subfamily Ptiligonatinae) became modified to catch insects, and have specializations that roughly parallel those of the Tyrannid flycatchers.

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Osteologically, the various species of the Bombycillidae are remarkably similar. Small variations do exist, but these are primarily differences in relative size. The modifications of the beak enable palm-chats to feed on parts of plants, and the beak of *Phainoptila* shows some similarity in this respect. Rounded wings, which cause a bird to fly by means of short, relatively weak strokes, are correlated with a comparatively long humerus, whereas long and pointed wings, which enable a bird to fly with more powerful strokes of the wing, are correlated with a

relatively short humerus. There is a positive correlation between a short humerus and a long external condyle, and between a long humerus and the absence or smallness of the external condyle.

In the Bombycillidae short bones of the leg are adaptive, and long bones of the leg are the generalized condition. Although all passerine birds were differentiated relatively late in geologic time, long hind limbs still could have been present in the immediate ancestors of passerine birds. As adaptive radiation took place in the class Aves, some birds, the Bombycillidae included, became more and more adapted for an arboreal, and eventually an aerial habitat, with consequent loss of saltatorial and running ability.

Birds, like mammals, have a short femur, the most proximal element in the leg, if the species is adapted to run fast. If the species is not adapted to run fast, birds, unlike mammals, have the tibiotarsus longer than any of the other elements; in mammals that are not adapted to run fast, the femur and tibia are approximately the same length. In non-running birds as compared with running birds, the leg element distal to the tibiotarsus, and the one proximal to it, are considerably shortened. In waxwings, all three elements of the hind limb are shortened, indicating that the reduction in length has been, evolutionarily speaking, a rapid process, in order to reduce the limbs to a convenient size as soon as possible.

The shape of the pygostyle varies in the Bombycillidae, but the simple shieldlike bone of *Phainoptila* is judged to resemble closely the ancestral type. In *Ptilogonys* there is a tall dorsal spine, coupled with a wide and heavy centrum and flattened lateral areas, for support of the long rectrices. In *Bombycilla* the bone is small with knobs on the centrum that have been developed for muscle attachment.

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The muscles were carefully dissected in each genus and in most of the species. The same homologous muscles are present in all species. Significant differences were found only in the relative size of certain muscles. No satisfactorily accurate method of measuring these differences was found. Consequently, less use was made of the results of the dissections than was originally planned.

The set of pectoral muscles varies but slightly in relative mass, and the variation is not considered significant. The deltoid muscle was selected for measurement since its point of insertion is unusually variable, while the mass of the muscle varies little. We can conclude that the extent of the area of insertion of the tendon of a muscle can determine that muscle's relative efficiency, while the muscle itself remains the same in bulk.

The muscles of the hind limb are notably larger in species that have long legs, and a good index of the hopping ability may be gained by study of certain of these muscles. In the Bombycillidae, and in those Ptilogonatinae that do not use the hind limbs for hopping, the bones are shortened, and the associated muscles are correspondingly smaller.

The gross anatomy of the digestive tract is practically identical in the members of the family. The variability noted is mainly in the degree of compactness of the visceral mass in *Bombycilla* and in *Phainopepla*. Also there is a tendency for the Bombycillinae and the Dulinae to have the mass situated more posteriorly than it is in the Ptilogonatinae. Moreover, *Bombycilla* has a shorter intestine than do the other genera. All of this indicates that the waxwings (Bombycillinae) have the center of gravity situated more advantageously for flight than do the birds of the two other subfamilies.

[\[↑ TOC\]](#)

SUMMARY

[Pg 524]

1. The silky flycatchers, waxwings, and palm-chats are included in the family Bombycillidae; the Ptilogonatidae and Dulidae are reduced to subfamily rank.
2. The coloration of the birds of each subfamily is different because the ecological needs are different.
3. Waxwings were at one time regularly migratory, but are now nomadic, since they are adapted to live in northern latitudes for the entire year.
4. The corresponding bones in different members of the family closely resemble one another, and the differences which do exist are the results of responses within relatively recent times to changes in habits.
5. In the Bombycillidae a rounded wing is judged to be the primitive condition. As the wing becomes more pointed, the humerus becomes shorter and its external condyle longer.
6. The hind limbs are short in birds that depend most on flight power, but are longer and the distal elements are disproportionately longer in birds that depend on saltation or on running.
7. The pygostyle varies in shape and size between genera and even between some species.
8. The pectoral muscles differ in size only slightly in the different members of the family, but the insertions are more extensive for these muscles in birds that fly a great deal.
9. The muscles of the hind limb vary in mass, but not in kind, in the members of the family

Bombycillidae.

10. In the Bombycillidae that depend on flight power, rather than on saltation or on running power, there is a tendency for the digestive tract to become shorter and for the whole visceral mass to become more compact.

[\[↑ TOC\]](#)

[Pg 525]

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Mention should be made here of an important paper by Jean Delacour and Dean Amadon (1949). The Relationships of *Hypocolius* (*Ibis*, 91:427-429, plates 19 and 20) which appeared after the present paper by Arvey was written. Delacour and Amadon stated that *Hypocolius*, a monotypic Persian genus, should be assigned to the Bombycillidae. Their conclusions (*op. cit.*:429) were as follows: "It might be advisable to set up three subfamilies in the Bombycillidae, one for *Bombycilla*, one for *Hypocolius*, and a third for the silky flycatchers, *Ptilogonys*, *Phainopepla* and *Phainoptila*. Further study may show that *Dulus* can be added as a fourth subfamily.

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"Previously the Bombycillidae appeared to be an American group of which one genus (*Bombycilla*) had reached the Old World. Inclusion of *Hypocolius* in the family makes this theory uncertain. Without obvious affinities to other families, and consisting of a small number of scattered and rather divergent genera, the Bombycillidae would seem to be a declining group whose origin cannot safely be deduced from the distribution of the few existing species."

—Eds.



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