THE GENERA OF CORVIDAE AND THEIR RELATIONSHIPS

By DEAN AMADON

This paper summarizes a study of the genera of Old World Corvidae undertaken while arranging the collection of the American Museum of Natural History. For completeness the few exclusively New World genera are included. There has been no comprehensive survey of this family since Sharpe's (1909), and many important modern regional lists such as that of Hellmayr (1934) are uncritical in their treatment of genera. Ridgway's (1904) work on the North American genera, while eminently sound, entailed a degree of genus splitting which often obscures relationships. The only species not available to me were Cyanocitta ("Cyanolyca") nana and mirabilis, Cyanocorax dickeyi, and Zavattariornis strenmanni; the latter is the only genus not examined. My field experience is limited to the genera Crastes, Cyanocitta, "Aphelocoma," Gymnorhinus, Pica, Nucifraga, and Corvus.

The plan of this paper is similar to that of a preceding one on the Sturnidae (1943, Amer. Mus. Novitates, no. 1247) in which I gave my reasons for favoring the present trend towards a broad genus concept. Some might prefer the use of subgenera for certain of the lesser groups. Since subgeneric names are indistinguishable in form from generic ones, use of the former, as Dunn (in Bogert, et al., 1943, p. 131) recently pointed out, seems to tempt later authors to elevate them to generic status. Accordingly, formal use of subgenera has here been avoided, but where a section of a genus has commonly been referred to under a generic name the latter is used in the discussion, but in quotation marks to indicate that it is not considered to be a valid genus. In other cases, sections of genera are referred to under the name of the included species that was first described. Type species of generic names are given in parentheses after the name of the author. Generic synonyms given include only those with different type species.

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LIMITS OF THE FAMILY CORVIDAE

Although some vertebrate zoologists have thought that the Passeriformes could all be united in a single family, ornithologists have divided this order into 50 or more families. Even so, many aberrant genera have been included in various families at the risk of making them polyphyletic (cf. Mayr, 1943). A compromise involving reduction of some of the present families to subfamilies and their subsequent combination into larger families will probably be the best eventual solution. A beginning was made by Hartert (1910) when he reduced the babblers, thrushes, Old World flycatchers, and Old World warblers to the status of subfamilies of the Muscicapidae. Another group of closely allied subfamilies can similarly be gathered in the Corvidae. It is beyond the scope of this paper to decide which groups will be included in such an enlarged family Corvidae. They will be essentially what Sharpe (1877, p. 4) called Group Coliormorphae: Corvidae, Paradisaeidae, Oriolidae, Dicuridae, Prionopidae. The Prionopidae probably do not belong here, while the Cracticidae and
perhaps others are to be added. Accordingly, the Corvidae as generally understood is here considered to be a subfamily, Corvinae. It is true that this group has been divided by some ornithologists into two subfamilies, the Corvinae and Gar- 

rulinae, chiefly on the extremely variable and trivial character of tail/wing proportions. Ridgway (1904, p. 204, footnote) although accepting this division, expressed doubt as to whether these groups are actually of subfamily rank. The jays, magpies, nutcrackers, and crows are closely related and agree in all important morphological characters and even in many minor ones, as well as in characteristic behavior patterns.

Hartert (1910, p. 1) and Ridgway (1904, pp. 252–254) give definitions of the Corvidae (Corvinae) which may be con- sulted by those interested. In general the group is characterized by large size of the included species; nasal bristles; large, strongly scutellated tarsi, booted behind; large tenth (outer) primary; and by a few prevailing types of coloration. The behavior of the Corvinae is equally diagnostic. The following traits are usually present: long-continued courtship feeding; nest building and feeding of young by both male and female; incubation and brooding by female only; burying or hiding of food; breaking of food with the bill while the food is held in the feet; loud and usually harsh notes; omnivorous and more or less preda- 

tory feeding habits; bold and inquisitive nature.

Of the genera here included in the Cor- viniae, the only ones concerning whose allo- 
cation there can be any serious doubt are Platyplophus and possibly Pilostomus and Zavattariornis. Life history rather than anatomical studies may well furnish con- 

clusive evidence as to the affinities of these genera.

Stonor (1942) has shown that the New Zealand genera Callaeas, Heteralocha, and Philesturnus, which have sometimes been considered members of the Corvidae, are best considered a separate family, the Callaeidae. It will perhaps prove possible to consider this a subfamily of the Corvidae in the broad sense, for I doubt if the special relationship formerly postulated between Heteralocha and Philesturnus and the Sturnidae exists.

Two anomalous Australian genera, Struthidea and Corcorax, may be allied to the Callaeidae, as several authors have suggested. At any rate they are probably members of the Corvidae in the broad sense, but almost certainly do not belong to the typical Corvinae as here understood. Even if their resemblance to the Callaeidae does not prove to be significant, they are probably more closely related to other sub- 

families of the Corvidae occurring in the Australian region than to the Corvinae.

Struthidea and Corcorax are sometimes placed in different families, but their similarity in habits (Gould, 1865, pp. 470–473) and in the more conservative features of external morphology leaves little doubt in my mind that they are related and may be placed in a single subfamily, Corcora- cinae. The differences between Struthidea and Corcorax parallel those between Cal- laes and Heteralocha to some extent but are less striking.

Since Corcorax, like the chough (Pyrr- 

hcorax), is large, black, and has a curved bill it received the common name of white- 

winged chough. Shufeldt (1923) com- 

pared skeletons of the two genera and concluded that they are closely related. I am convinced that he was mistaken. Since reliable osteological characters useful in taxonomy are scarce among closely related birds such as comprise the entire order Passeriformes, Shufeldt concen- 

trated upon plastic, adaptive “habitus” characters such as the shape of the bill and associated parts of the skull. Paral- 

lelism in such characters was often erroneously considered by Shufeldt to indicate true relationship. He concluded that Corcorax is allied to Pyrrhocorax; that Cyanoccephalus is a link between the jays and such icterids as Sturnella, and that since Struthidea has a heavy bill it is profitable to compare it with the neotropi- cal finch Saltator. The extreme improb- 

ability that the semi-terrestrial Corcorax of the Australian bush should have as its closest ally the strong-flying Pyrrhocorax of the alpine regions of Eurasia was ignored
by Shufeldt, as were many differences in the morphology and habits of the two genera.

The curious West African genus *Pica-thartes*, which contains two geographically representative species of so-called bald crows, certainly does not belong in the Corvinae and doubtfully in the Corvidae. Elsewhere (1943) I have given reasons opposing Lowe's (1938) suggestion that *Pica-thartes* is a starling. The habits of the bald crows suggest to me that they may be a very aberrant offshoot of the thrush-babbler assemblage (Walker, 1939).

Although behavior is useful in delimiting the Corvinae as a group from structurally similar subfamilies such as the birds of paradise, great caution must be used in interpreting differences in behavior among members of the Corvinae. A few examples will make this apparent. The Florida race of *Cyanocitta* ("Aphelocoma") *coeruleus* is as bold and confiding as a Canada Jay (*Cacicus*), while the Great Basin race *woodhousei* is furtive and shy. The three species of "Aphelocoma" as usually understood, *coeruleus*, *sordida*, and, *unicolor*, are morphologically very similar, except for variation in wing/tail proportions. Yet *coeruleus* lays spotted eggs, most of its notes are harsh, and it is only moderately gregarious, while *C. sordida* is very gregarious, has a peculiar finch-like call, and lays blue, unsotted eggs. Less is known of the third species, *unicolor*, but it inhabits humid cloud forests (Dickey and Van Rossem, 1938, p. 409), while the other two live in subarid regions. There is also considerable variation in the behavior of some species of the genus *Corvus*. The jackdaw, *C. monedula*, unlike the others, nests usually in hollows of trees or of buildings and lays an egg rather unlike that usual in this genus. *C. typicus* of Celebes was found by Heinrich to be so unlike most crows in voice and habits that Stresemann (1940, p. 16) suggested leaving it in a monotypic genus, but it is so closely related to various other species of *Corvus* of the East Indian region that this procedure is hardly acceptable. *Podoces humilis* nests in rodent burrows and lays white eggs while its congeners build nests in bushes and lay spotted eggs, though some of them occasionally nest in burrows.

**VARIABLE CHARACTERS**

The Corvinae, though by no means so plastic as their relatives, the birds of paradise, are a variable group. The relative lengths of wing and tail are especially variable, often even in closely related species, as will be apparent from examination of table 1. Since wing and tail lengths often vary independently, the ratio of tail/body and wing/body is given in addition to the usual tail/wing ratios to permit variation in wing and tail to be studied separately. Body length as used here was obtained by subtracting the tail length from the total length, the latter taken from skins, and serves to give a very rough index to general size. The measurements of North American species are from Ridgway (1904), of *Cyanocorax dickeyi* from Moore (1935), of *Zavattariornis* from Moltoni (1938), and of the others from specimens in the American Museum.

One or two examples of variability illustrated in the table may be mentioned. *Kitta chinensis* and *thalassina*, while specifically distinct, are so similar that Chasen (1935, p. 310) called them subspecies of each other. Yet the relative tail length differs greatly. *Cyanocitta coeruleus* has a relatively much shorter wing than the otherwise morphologically similar *sordida* and *unicolor*.

The crest is also extremely variable in the Corvinae. For example, in the *beecheii* superspecies of *Cyanocitta* ("Cissolopha"), *san-blasiana* has a prominent frontal crest absent in the other three species of the group. The remarkable range of structure in the crest exhibited by various species of the genus *Cyanocorax* is described in the discussion of that genus below.

Of the 19 genera here recognized no
**American Museum Novitates**

**SPECIES**

<table>
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<th>Species</th>
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<th>Tail/Body</th>
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Table 1. Proportions and body lengths of some species of the Corvidae. The body length is given to supply a rough index to general size.

Fewer than eight are monotypic. Three of the eight monotypic genera are so distinct and aberrant that there is some question whether they belong to the Corvidae (Platylophus, Zavattariornis, Ptilostomus). Despite the large percentage of monotypic genera, the average of about five species per genus is fairly satisfactory.

**Corvidae**

**Crows, Birds of Paradise, Old World Orioles, Etc.**

**Corvidae**

**Crows, Magpies, Jays, Nutcrackers, Etc.**

**Platylophus Swainson (Galericulatus)**  
Shrike Jay

**Species:** 1, galericulatus.

**Range:** Malay Peninsula, Sumatra, Java, Borneo.

**Diagnosis:** Plumage brown or black with white crescents on the sides of the neck; a few of the occipital feathers greatly elongated and broadened near their tips, thus forming a large crest; nasal bristles sparse and short; rictal bristles exceptionally long; tip of mandible more hooked than in other jays; bill otherwise like that of Garrulus.

**Remarks:** Platylophus has usually been considered a member of the Laniidae, but this is evidently incorrect. Bartels and Stresemann (1929, p. 136) place it in the Corvidae and state that its habits and nidification are jay-like but give no details. More evidence is needed.

Of the three Old World genera of jays, one is boreal, one temperate, and the present one tropical, in distribution. I do not consider this an argument against allocation of Platylophus to the jays, as the New World jays are concentrated in the tropics. Probably other jays once existed in the
tropics of Asia but have been displaced by the more specialized magpies. *Platylophus*, though in some respects aberrant, may be primitive. Partly to express this and partly because knowledge of *Platylophus* is still insufficient, it is placed at the beginning of the Corvidae.

**CRACTES Billberg (PERISOREUS auct.) (INFAUSTUS)**

**CANADA JAY, ETC.**

**SYNONYMS:** Boanerges Thayer and Bangs (internigrans).

**SPECIES:** 1, *internigrans*; 2, *infaustus* (including *canadensis* and *obscurus*, considered by some to be specifically distinct).

**RANGE:** Boreal regions of Northern Hemisphere, south in the mountains to western China and California.

**DIAGNOSIS:** Color varying from black to grayish white, sometimes rufous; plumage soft and fluffy; bill rather short and somewhat depressed.

**REMARKS:** The interesting *internigrans* of the mountains of western China suggests *Garrulus lanceolatus* of the Himalayas in its bill and black head. Though it is larger and has relatively stronger bill and legs than *infaustus*, it is unnecessary to recognize *Boanerges*, as Stegmann and others have already concluded. The un-specialized appearance of *Cractes* may be in part secondary adaptation to its boreal habitat, but the genus is rather primitive. The resemblance of *internigrans* to *Garrulus* and the occurrence of both species of *Cractes* in Asia leave little doubt that it is an Old World genus which reached America recently, later than the other American jays.

**GARRULUS Brisson (GLANDARIUS)**

**EUROPEAN JAY, ETC.**

**SYNONYMS:** Laletris Reichenow (*lanceolatus*); Lalocitta Reichenow (*lidthi*).

**SPECIES:** 1, *glandarius*; 2, *lanceolatus*; 3, *lidthi*.

**RANGE:** Palaeartic region and Amanio-Oshima and Tokunoshima Islands, Ryu Kyu Group, south of Japan (*lidthi*).

**DIAGNOSIS:** Alula and sometimes remiges and rectrices blue barred with black; body plumage reddish or vinaceous; wings and tail bluish black; size large for jays.

**REMARKS:** As compared with *glandarius*, *lidthi* is specialized in the following respects: size larger; bill coarser, less upturned; coloration brighter; remiges and rectrices tipped with white; throat feathers lanceolate; tail relatively longer (table 1). The third species, *lanceolatus* of the Himalayas, is intermediate in almost every respect. The specialization of *lidthi* is, it would seem, to be attributed to its isolation on two small tropical islands. The three species obviously comprise a natural group comparable with other genera of jays; this is concealed and nothing gained by placing each of the three in a monotypic genus. That *lidthi* is more specialized and magpie-like than *glandarius* seems to me self-evident. Sushkin (1927), however, reached the surprising conclusion that *lidthi* is a primitive species representing stock ancestral to both the New and Old World jays and surviving on segments of a former intercontinental land bridge which he called Behringia. This suggestion seems to have been based upon theories concerning land bridges rather than upon the actual characters of *lidthi*.

Jahn (1942, pp. 79-82) found *lidthi* to be essentially like *glandarius* in habits, except that it nests in holes in trees. A substantial nest is built, and one or two nests have been found in the open in thick cover—indications that the hole nesting of *lidthi* is of recent origin. The number of eggs laid is less than in *glandarius*; this may represent the reduction usual in tropical species rather than an adjustment to lack of enemies as Jahn suggests. The eggs of *lidthi*, unlike those of *glandarius*, are unspotted and blue. This variation in egg color is similar to that existing between *Cyanocitta sordida* and other species of *Cyanocitta*.

The colored map of the distribution of the various forms of *Garrulus* which forms the frontispiece of Wallace’s “Island life” (1881) is still of interest. Since then some of the forms have been subdivided into minor subspecies; it has been learned that the true home of *lidthi* is the Ryu Kyu Islands, not southern Japan, and that the only member of the genus which overlaps
the range of others without hybridizing is the distinct species lanceolatus. Wallace (op. cit., p. 23) thought that because Garrulus occurs from the British Isles to Japan and Formosa and yet is absent from many apparently suitable districts and is nowhere abundant, it is a "decaying" genus. This accords with the belief that the jays are in general a primitive group in process of displacement by more specialized corvids, but I am by no means sure that the facts mentioned by Wallace are reliable indications that Garrulus is a decadent genus.

THE AMERICAN JAYS

The approximately 32 species of American jays are, with the possible exception of Gymnorhinus, a closely related monophyletic group. The facts would be better expressed by placing them all in one genus than by splitting them into nine as was done by Ridgway (1904). An intermediate course is here followed, and four genera are recognized. These I believe are natural and monophyletic, but their characters are very trivial, intergrading, and variable, and later opinion may dictate further reduction. The assemblage may, by relying on a combination of characters, be split into two large genera, Cyanocitta and Cyanocorax, the latter slightly more specialized. Two additional genera, Psilorhinus and Calocitta, containing but a species or two each, must then also be upheld to retain a semblance of consistency in evaluating the characters of the group.

CYANOCITTA STRICKLAND (CRISTATA)

BLUE JAY, etc.

SYNONYMS: Aphelocoma Cabanis (californica, a race of coerulescens); Cissolophia Bonaparte (san-blasiana); Cyanolyca Cabanis (armillatus, a race of viridi-cyana); Garrulina Gray (unicolor); Lophocorax Kaup (diademata, a race of stelleri); Sieberocitta Coues (arizonae, a race of sordida).

Species: 1. cristata; 2. stelleri; 3. coerulescens; 4. sordida; 5. unicolor; 6. pumilio; 7. nana (not seen); 8. mirabilis (not seen); 9. argenticula; 10. viridi-cyana; 11. turcosa; 12. pulchra; 13. melanocyanea; 14. yucatanica; 15. sanblasiana; 16. beechei.

RANGE: Alaska and southeastern Canada to western South America as far as Peru and Bolivia.

DIAGNOSIS: As compared with Garrulus, Cyanocitta differs as follows: no reddish or vinaceous in plumage; instead prevalently blue or blue and black; usually without black bars on remiges and rectrices, when present they do not occur on the alula as in Garrulus; mandible less upturned, or not at all so; size usually smaller, body slenderer. Cyanocitta is much more closely related to the other American jays than to Garrulus, but is in general less specialized (see below).

The genus Cyanocitta, as thus delimited, contains the following sections:

1. Cyanocitta in the restricted sense contains two species, cristata of eastern, and stelleri of western North America. Unlike other members of the genus, they have occipital crests and black bars on the wings and tail. It is perhaps justifiable to consider the two as forming a super-species, but cristata is somewhat more specialized than stelleri in color pattern.

2. "Aphelocoma," which contains the single species coerulescens (unless californica and insularis are considered specifically distinct), lacks the crest and black wing and tail bars of the preceding group. The wing is relatively shorter. It occurs in Florida, the southwestern United States, and Mexico.

3. "Sieberocitta" (including "Garrulina") includes two species, sordida and unicolor, which are usually referred to "Aphelocoma." They have a relatively longer wing than coerulescens or even cristata. C. sordida is more gregarious than coerulescens, has a finch-like note, and lays unspotted blue eggs. Less is known of unicolor, but unlike either of the other species mentioned it occurs in cloud forests, not semi-arid regions. In proportions it is similar to sordida. This group ranges from Arizona to Central America.

4. The "Cyanolyca" group contains species 6–12, which occur from southern Mexico to western South America as far as Peru and Bolivia. They are much like the preceding two sections but have the black
eye stripe expanded into a mask. Often there is a light area on the nape and a crescentic mark across the breast like that of *C. cristata*. The frontal feathers are usually bristly or velvety.

5. "*Cissolopha*" contains the four species 13–16, which are closely related and evidently comprise a single superspecies. They have a heavier and more magpie-like bill, and the entire head and at least the anterior half of the underside are black. The group occurs from northern Mexico to Central America.

It is significant that four of the five groups are represented in Central America by forms that are primitive and similar to one another. These are *stelleri* (southern races), *unicolor*, *pumilio* (and *nana*), and *melanoceyanea*. Furthermore, "*Cissolopha*" *pulchra*, which also occurs in Central America, is a link between "*Cyanolyca*" and "*Cissolopha*." It has the pattern of the former, but the heavy bill and to some extent the backish head region of the latter. *C. pumilio* and *nana* similarly connect the "*Apheoloma*"-"*Sieberocitta*" groups with "*Cyanolyca*." As Ridgway (1904, p. 324) pointed out they are structurally the same, while the color difference is much less than would be inferred from Ridgway's remarks. In fact Salvin and Godman (1879–1904, pp. 407–414) placed *nana* in "*Apheoloma*" and considered "*Cissolopha*" a synonym of "*Cyanolyca*." *C. cristata* and *stelleri* are essentially similar to "*Apheoloma*" in habits, and they should not be separated generically on such an extremely trivial basis as the presence or absence of a crest. The similar variation in the crest in "*Cissolopha*" among forms which Hellmayr (1934, p. 37) has even suggested may be subspecies (though I do not agree) was noticed above.

To summarize, although it is possible to subdivide the enlarged genus *Cyanocitta* into five sections, most of these contain but a single species or superspecies, and all of them are characterized by extremely variable and intergrading characters. All twelve of the species are similar in most respects, so it seems preferable to unite them in one genus.

**Gymnorhinus Wied (Cyanoccephalus)**

**Piñon Jay**

Brodkorb (1936, p. 1) is evidently correct in stating that *Gymnorhinsus* Wied is not a homonym of *Gymnorhinsus* Gray and hence must be used for the piñon jay rather than *Cyanoccephalus* Bonaparte.

**Species:** 1, *cyanocephalus*.

**Range:** Southwestern United States and northern Lower California.

**Diagnosis:** As compared with *Cyanocitta*: color nearly the same as in *C. sordida*; tail shorter; wing more pointed; flight stronger; bill longer and almost straight, slightly depressed towards its tip; nasal bristles lacking.

**Remarks:** Though much like *C. sordida*, *Gymnorhinsus* resembles *Nucifraga* also, as regards bill shape and proportions (although the tail is not quite so short). It has generally been placed with the crows and nutcrackers, not with the jays. I am inclined to consider the piñon jay a specialized American jay which parallels *Nucifraga columbiana* somewhat because of similarity in feeding habits. Both species feed on piñon cones, and I have seen them feeding together in the same woods in large numbers. A jay thus specialized for feeding on the cones of a tree which fruits irregularly and is discontinuous in distribution would require strong flight. The difference in relative wing length between *Cyanocitta coerulescens* and *sordida* is as great as that in tail length between the latter and *Gymnorhinsus*. The absence of rictal bristles in the piñon jay is not surprising if it is an American jay, in which they are absent in some other genera, but is remarkable if it is a relative of the boreal nutcrackers. Nor is the blue color of *Gymnorhinsus* suggestive of either species of *Nucifraga*, though it might, it is true, be a reversion to the coloration of the Old World jays ancestral to *Nucifraga*. The fact that the latter has its most specialized representative in the Old World suggests that it, like all the other more specialized corvine genera, is of Old World origin. There is a slight possibility, however, that *Nucifraga* is of New World origin and
that Gymnorhinus is a true link between it and the more primitive Cyanocitta.

As regards habits, Cyanopephalus does not share the very early nesting season of Nucifraga, though the eggs of the two are rather similar. However, egg color varies greatly in Cyanocitta. Some jays of the genus Cyanocorax lay eggs similar to those of Nucifraga. The shrill note of the piñon jay suggests that of the Arizona jay, but certain notes of the former have been likened to those of crows or nutcrackers.

Comparison of a skull of Gymnorhinus with those of Nucifraga, Garrulus, Cyanocitta, and Corvus reveals that Gymnorhinus shares with Nucifraga a narrowing of the anterior part of the skull, correlated with the chisel-shaped bill. This is probably entirely adaptive. Gymnorhinus agrees with Cyanocitta and Garrulus in having the post-frontal and the squamosal process less prominent than in Nucifraga or Corvus, but this may be correlated with their smaller size. The skulls of all these species are very similar. Shufeldt's (1888) study of the skeletons of American Corvidae unfortunately did not include Nucifraga. Though he states in his conclusions that osteologically Gymnorhinus is a link between Cyanocitta and Corvus, in the actual comparisons of skeletal elements, wherever a difference exists between the two, he found Gymnorhinus to agree with Cyanocitta (pp. 330, 333, 341, 343).

While I believe that a preponderance of evidence indicates relationship of Gymnorhinus to Cyanocitta rather than to Nucifraga, it must be remembered that Nucifraga itself is only a specialized offshoot of the (Old World) jays.

**Psilorhinus Rüppell (MEXICANUS)**

**Brown Jays**

**Species:** 1, mexicanus; 2, morio. The two species occur together and are very similar. They may prove to be representatives of a single species, but this is unlikely (cf. Wetmore, 1943, p. 297).

**Diagnosis:** Similar to the larger, coarser species of Cyanocitta (“Cissolopha” group) but structurally coarser; nasal bristles sparse; plumage dull brownish or dirty white. Psilorhinus has a crop-like furcular sac formed by a diverticulum of the clavicular air sac and used in producing a snapping sound (Sutton and Gilbert, 1942, p. 165).

**Remarks:** Psilorhinus seems to be secondarily coarsened in structure and simplified in coloration until it is difficult to tell if it is more nearly related to the larger species of Cyanocitta such as beecheii or to Cyanocorax as Salvin and Godman thought. Accordingly it is here placed between them, as the only logical alternative would be to unite the three genera. The furcular sac may be the best generic character of Psilorhinus as Sutton and Gilbert (tom. cit.) intimate.

**Cyanocorax Boie (CHRYSOPS)**

**Green Jay, etc.**

**Synonyms:** Coronides Cabanis (violaceus); Uroleuca Bonaparte (cristatella); Xanthoura Bonaparte (yncae).

**Species:** 1, caerules; 2, cyanomelas; 3, violaceus; 4, cristatella; 5, heilprini; 6, cayanus; 7, affinis; 8, cyanopogon; 9, chrysops; 10, mystacalis; 11, dickeyi; 12, yncas.

**Range:** Southern Texas to Argentina.

**Diagnosis:** Like Cyanocitta but in general more specialized; crest usually present but extremely variable; throat, breast, and usually large areas on sides and top of head black; the black breast more sharply demarked from the remainder of the underside than in any species of Cyanocitta; lower breast and abdomen and large areas in the tail characteristically white or yellow but sometimes blue or purple; size averaging larger and body form, legs, and feet more robust than in Cyanocitta.

**Remarks:** Cyanocorax can be subdivided into the following sections:

A. The “Coronides” group contains species 1–3, which occur in eastern South America. They are characterized by robust form and by a simple color pattern in which the abdomen and tail lack white and the head is entirely black. This group, although most like the more primitive Cyanocitta in coloration, is atypical by reason of its robust form, and in view of its distribution may be a side branch of the genus. “Coronides” has not usually been recognized.
B. "Uroleuca" is usually treated as a monotypic genus characterized by the recurved crest of the single species cristatella. This species combines the robust form and black head of the "Coronides" group with the white abdomen and white-tipped rectrices of the restricted Cyanocorax section. It occurs on the Brazilian tableland, suggesting relationship with the "Coronides" group.

C. The restricted Cyanocorax section contains species 6-11, which occur in southern Sinaloa and from Central America to western South America as far as Peru. In this group the body is slenderer and the tail relatively longer; the abdomen and end of the tail are white or yellowish, and there is a characteristic head pattern of blue or white marks above and below the eyes, the lower one extending over the malar region. The rare C. heilprini of the Brazil-Venezuela borderland is so nearly intermediate between this and the "Coronides" group that it cannot be included in either. It has the purple under parts of the "Coronides" section, but the abdomen is whitish posteriorly, and there are narrow white tips on the rectrices; the head pattern is only partly developed, and the form is slender.

D. "Xanthoura" is another monotypic group; the sole species, yncas, ranges from southern Texas to Peru. It is even more slender in appearance, perhaps because its tail is relatively longer (see table 1 for proportions of this and other species of the genus). The under parts and lateral rectrices of yncas are bright yellow; the upper parts and central rectrices are green, washed with blue in some races; the frontal crest, as well as the usual marks on the face, is blue; the size is small.

The commonest type of crest in Cyanocorax is composed of bristly, narrow feathers which are short in cyanomelas but longer in heilprini and others. In some species such as yncas the crest is essentially similar but the feathers somewhat softer. In cristatella the feathers of the crest are much longer and curved back over the crown. C. cyanopogon has a frontal crest of the usual type, and in addition the occipital feathers are lengthened and broadened to form a short, full crest which overhangs the white nape. As an example of the frequent parallelism which suggests that all genera of the Corvidae are rather closely allied, it may be mentioned that the Malaysian magpie, Platysmurus, has two similar crests. The type species chrysops is unique in that the feathers of the entire top of the head are bristly or velvety and not merely the frontal feathers. In dickeyi the crest is said to include the crown but not the occiput as in chrysops. Moore (1935, p. 275, pl.) described the crest of dickeyi as a "straight, stiff and erect crest, which tends to segregate at the apex into numerous tufts of stiff, narrow and unusually elongated feathers...." In chrysops the form of the crest varies considerably among the subspecies.

Cyanocorax dickeyi, which I know only from the published plate and photographs, is a member of the restricted Cyanocorax group. It resembles mystacalis of Ecuador by having the head pattern white, the back blue (though not of exactly the same shade), and the tail extensively white. In dickeyi, however, even the lateral rectrices have dark bases, while in mystacalis they are entirely white. Presumably one must admit dickeyi to be closer to mystacalis than to any other species of the genus despite the more than 3000 miles which separate their ranges. Captain Delacour tells me he would consider them representatives of a single species or superspecies, but, aside from the geographical improbability of this, the striking differences in general size and in the crest are almost certainly of specific importance. I think it is possible that, in this assemblage of closely related species in which a few common characters occur in different combinations, this may be another instance of parallelism. At any rate, it seems misleading when Moore (1935, p. 277) states that dickeyi is furthest in characters from the geographically nearest species, affinis, which ranges north to Costa Rica. C. dickeyi may be as nearly related to affinis as to any other living species except (probably) mystacalis, and is, in my opinion, closer to affinis than to heilprini or volaceous, species which Moore mentions as
resembling dickeyi in some respects. He might also have pointed out when emphasizing the territorial gap between dickeyi in Sinaloa and its congeners in Central and South America that the intervening area is occupied by "Xanthoura," which is obviously a Cyanocorax in essential characters, and by Calocitta and Psilorhinus, both of which are apparently offshoots of Cyanocorax. The American jays are concentrated in Middle America. Presumably competition is thereby increased, and it is possible that the small, isolated range of dickeyi is somehow correlated with this fact.

From the above discussion it will be apparent that Cyanocorax, as here understood, can be subdivided only by resorting to extremely variable characters. "Coronideus" with its simple coloration and robust form is perfectly united with the more typical members of the genus by cristatella and heilprini. The crest is so extremely variable in this group that it is inconsistent to maintain "Uroleuca" on this basis. Nor does the green back, yellow abdomen (the latter shared by the type species, chrysops), and long tail of yncas conceal the fact that it is a close ally of chrysops. The problem for one who would like generic characters to be more stable and substantial than specific characters is not whether to unite the above species in Cyanocorax, but how to keep Cyanocorax separate from Psilorhinus, Calocitta and, for that matter, Cyanocitta.

**Calocitta Gray (Formosa)**

**Magpie-Jays**

**SPECIES:** 1, formosa. The form colliei is considered specifically distinct by some authors.

**RANGE:** Mexico and Central America.

**DIAGNOSIS:** Essentially like Cyanocorax, but tail very long and graduated; some of the crown feathers much elongated and somewhat spatulate, forming a conspicuous crest; size large.

**REMARKS:** In view of the great variability in proportions and crests existing in the genus Cyanocorax, it is doubtful whether Calocitta should be kept separate. In Calocitta f. colliei we find the following unmistakable signs of close affinity with Cyanocorax: black throat and breast; white abdomen; similar head pattern and white in the lateral rectrices. In C. f. formosa the black throat and breast are absent except for a black bib similar to, and homologous with, that of Cyanocitta cristata and some other species of Cyanocitta. As noted above in discussing Cyanocorax, Calocitta has perhaps replaced more primitive earlier Mexican species of the former.

**The True Magpies**

Although the New World jays have given rise to some magpie-like types, notably Calocitta, the intergradation with the jays is so complete that no line can be drawn. In the Old World magpies there is a more definite gap separating them from the jays. Garrulus lidthi, however, has acquired some magpie-like characters and is quite similar to Kitta, especially Kitta ornata.

**Kitta Temminck (Chinensis)**

**Green Magpies, etc.**

**SYNONYMS:** Cissopica Delacour (whiteheadi); Uroicissa Cabanis (erythroryncha).

**SPECIES:** 1, thalassina (and geographical representatives); 2, chinensis; 3, whiteheadi; 4, ornata; 5, flavirostris; 6, erythroryncha; 7, caerulea.

**RANGE:** India and Ceylon to China and Formosa south through the Malay Peninsula and Greater Sunda Islands.

**DIAGNOSIS:** As compared with Garrulus: structure coarser; size usually larger; tail more graduated and usually longer; bill, legs, and feet heavier and red or yellow in color (legs blackish in whiteheadi); nostrils exposed; nasal bristles sparse or absent. Differs from other magpies by the coarser, heavier bill, by having the bill red, and in other respects noted later.

**REMARKS:** This genus divides naturally into four sections:

A. Kitta proper contains two species, thalassina and chinensis, distinguished by small size; greenish or yellowish coloration which fades rapidly after death; coronal feathers lengthened, forming a crest; a black eye stripe which extends back beneath the crest; eyelids wattled and
brightly colored. These species occur in
dense mountain jungle in southeastern
Asia and adjacent islands. As Delacour
(1929, p. 3) indicated in his key to this
group there are two natural divisions:
(1) those in which the tertials are white-
tipped and have a subterminal black
spot, and the tail is relatively longer
(chinensis), and (2) those lacking the e
characters (superspecies thalassina).
Whether the forms of group (2), all of
which are geographically representative,
are considered subspecies, or, in the more
differentiated forms, species, is a matter of
opinion. The members of group (2) from
south (Java) to north (Hainan) are:
thalassina, jefferyi, hypoleuca, chauleti,
concolor, jini, and katsumatae. Peters
(1940, p. 203) has already pointed out that
Chasen (1935, p. 310) was in error in con-
sidering jefferyi and thalassina races of
chinensis.
B. K. ornata of Ceylon has the eyelids
wattled like the preceding group to which
it has usually been referred, but it is closer
to the following group, “Urocissa,” with
which it has in common concolorous head
and breast, longer tail and coloration
which lacks the evanescent qualities of
that of the Kitta group. K. ornata differs
from both Kitta and “Urocissa” by hav-
ing the head, breast, and remiges bright
rufous.
C. “Urocissa” includes flavirostris, ery-
thrornithyrhyncha, and caerulea. This section
differs from ornata by lacking the wattled
eyelids; the tail is even longer and the
head, breast, and remiges are black or blue.
The first two species are similar; caerulea
of Formosa is probably a representative
of one of them, but it is difficult to say
which. K. caerulea is much bluer than
either of the mainland forms and has a
heavier bill.
D. “Cissopica,” which contains only
whiteheadi, was characterized by Delacour
(1927, p. 164) as follows: “Differs from
Urocissa in having a much coarser and more
powerful bill and legs and a shorter tail...,
General plumage grey, black and pale
yellow, never blue. I chose the name of
this new genus to show the affinity of these
birds to the Cissa [group A above] which
they exactly resemble in their voices and
actions.” Captain Delacour informs me
that he now considers it preferable to in-
clude whiteheadi in Kitta, though it forms a
distinct subgroup. K. whiteheadi is coars-
ened and simplified in coloration just as is
Psilorhinus in the New World. The black
breast and lighter abdomen of the “Uro-
cissa” group are suggested in whiteheadi,
and it also agrees with this group in its
large size and coarse structure. However,
it resembles the restricted Kitta group in
some details as well as in habits and may
be a link between it and “Urocissa.”
The enlarged genus Kitta contains a
natural assemblage of only seven species.
The immediate common ancestry of all
these species is obscured if they are placed
in three or four genera.

**Cyanopica Bonaparte (Cyans)**

**Azure-winged Magpie**

**Species:** 1, cyanus.

**Range:** Iberian Peninsula and eastern
temperate Asia north to Japan and
Siberia. (For a map of this remarkable
instance of discontinuous distribution see
*Ibis*, 1928, vol. 25, opp. p. 532.)

**Diagnosis:** Coloration blue and white
and rectrices white-tipped as in some
species of Kitta; bill black and shaped as in
Pica; nasal bristles well developed as in
Pica; form slenderer, size smaller, legs
weaker, plumage silkier than in either
Kitta or Pica; nest open as in Kitta; pri-
marily arboreal. Cyanopica connects Kitta
and Pica in some respects, but is too dis-
tinctive to be united with either.

**Pica Brisson (Pica)**

**Common Magpie**

**Species:** 1, pica.

The yellow-billed magpie, nuttalli, of
California is considered by many distinct
enough to warrant specific status in the
same superspecies as pica. Some of the
Old World races at times build their nests
at considerable heights in tall trees as does
nuttalli. Yellow-billed individuals have
occurred as sports in some of the Old World
races. Coues’ (1894, p. 421) statement that
nuttalli is a “perpetuated accident” of *P.*
p. hudsonica is in keeping with present opinion as to the frequent fixation of non-adaptive characters in isolated populations.

Range: Palaeartic region and western North America.

Diagnosis: Outer primary falcate; a distinctive color pattern of white and metallic bluish or greenish black; throat feathers lanceolate; nest domed, often with two entrances, with an interior cup of mud; feeds much on the ground, where it progresses mostly by walking. Pica is nearest to Cyanopica with which it shares characters mentioned in diagnosing that genus and also some details of coloration. It is less closely related to Cryptsirina (including “Dendrocitta”). Pica is obviously an Old World genus that has reached North America relatively recently. Probably it will eventually adjust itself to conditions in eastern North America, since in the Old World it occurs both in semi-arid and in humid regions.

Cryptsirina Vieillot (Temna)

Racquet-tailed and Tree Magpies

Synonyms: Dendrocitta Gould (leucogaster); Temnura Temminck (temnura); Vagabunda Kaup (vagabunda).

Species: 1, vagabunda; 2, frontalis; 3, leucogaster; 4, occipitale; 5, formosa; 6, bayleyi; 7, temnia; 8, cucullata; 9, temnura.

Range: India, southern China, and Formosa south through the Greater Sunda Islands to Bali.

Diagnosis: Bill black, short, heavy, strongly arched, nasal bristles short but dense; color variegated brown, white, gray, or black but not blue, sometimes wholly black; frontal feathers short and velvety, especially in temnia and cucullata; legs black and relatively smaller than in Kitta or Pica; proportions about as in Pica; nest open; primarily arboreal, hopping when on the ground.

Remarks: This genus has the following three easily separated sections:

A. “Dendrocitta” contains species 1–6. Its characters are as for the genus; the rectrices are normal.

B. Cryptsirina proper contains temnia and cucullata characterized by smaller size; spatulate central rectrices; velvety frontal plumes and silky plumage. C. cucullata has a pattern much like members of the preceding group, but temnia is entirely black.

C. “Temnura” contains only temnura, which has a restricted range in part of Indo-China. This species has rectrices that are incised along their edges and truncated at their tips as though bites had been taken from them. C. temnura is entirely black like temnia, but the plumage is not so soft.

In various species of “Dendrocitta” the rectrices increase in width distally, thus foreshadowing the spatulate condition. This is especially true of bayleyi of the Andaman Islands, a species whose small size also suggests temnia and cucullata. The increase in width of the central tail feathers distally in bayleyi is as follows in four specimens:

Width of feather near center: 19, 20, 20, 22 mm. Width of feather near tip (specimens in same order): 23, 29, 29, 26 mm.

In temnia the spatulate rectrices measure about 17 mm. across at the center and 39 mm. at the tip. The difference in feather shape involved is only a matter of degree and, other things being equal, would be of no more than subspecific value. C. temnia is also specialized slightly by reason of its small size, silky black plumage, and especially the velvety frontal feathers which cover the nostrils and take the place of nasal bristles. However, cucullata, which agrees with temnia in size, presence of spatulate rectrices, and has always been placed in the same genus, is intermediate as regards coloration and nasal bristles between the restricted Cryptsirina and “Dendrocitta” groups. In view of the close relationship and minor distinctions of these two groups, it seems that the facts will be best expressed by considering Dendrocitta a synonym of Cryptsirina. It is unfortunate that the latter name has priority over the better-known Dendrocitta. But for this, the two would probably have been united before now.

The little-known species temnura is a member of the Cryptsirina group in the broad sense. The tail is variable in this genus, so it seems justifiable to include
“Temnura” in Crypsirina. Moreover, temnura links Crypsirina and “Dendrocitta” in some respects, just as bayleyi does in others. C. temnura has the black coloration of temia, but the coarser plumage and nasal bristles of “Dendrocitta.” Its size is intermediate as shown by the following sample wing lengths of the species most important in defining the limits of Crypsirina: temia, 118; bayleyi, 121; temnura, 137; leucogaster, 148 mm.

**Platysmurus** Reichenbach *(Leucopterus)*

**White-winged Magpie**

Species: 1, leucopterus.

Range: Malay Peninsula, Sumatra, Borneo.

Diagnosis: Differs from Crypsirina thus: frontal feathers bristly and elongated, forming an erect crest; feathers of occiput elongated and broadened, forming a short, full crest distinct from the frontal one; rictal bristles long; rectrices not spatulate; tail relatively shorter and less graduated; form more robust; plumage black with the exception of a white streak on the wing.

*Platysmurus* is a close ally of Crypsirina as shown by the similarity in bill form and other details. It resembles *C. temnura* especially. Presumably the long rictal bristles of *Platysmurus*, like those of its Malaysian associate *Platylaphus*, are correlated with its jungle habitat.

With the genus *Platysmurus* we conclude the treatment of the true magpies.

**Ptilostomus** Swainson *(Afer)*

Piapiac

Species: 1, afer.

Range: Northern Africa south of the Palaearctic fringe.

Diagnosis: Rectrices pointed, only ten present; form magpie-like; legs and feet very large; nasal bristles dense and short, meeting above the culmen; bill stout and arched; plumage black; lacrimals absent; vomer tending to be pointed anteriorly rather than truncate as in other Corvineae.

Remarks: This is an aberrant genus whose allocation to the Corvineae has been questioned. It possesses the external characteristics of this family, such as nasal bristles, large, strongly scutellated legs, large tenth primary, and others, and I see little reason to doubt that it is an aberrant member of the group. Jackson (1938, p. 1268) wrote that *Ptilostomus* is a gregarious, noisy bird whose notes are a “shril and squeaky pipe” and a chattering. It feeds on palms and also on the ground where it often attends livestock. Around camp it is very tame, and Jackson thought it would make a good pet; its nidification is crow-like. These habits suggest a corvine bird. Lowe (1938, p. 261) called attention to the skull characters mentioned in the above diagnosis. I have compared the skull with that of various genera of Corvineae, and in most respects they are similar. The loss of the lacrimals and the slight distinction in the shape of the vomer, like the reduction in the number of rectrices, attest that this is an aberrant genus, but do not, in my opinion, bar inclusion in the Corvineae. Lacrimals may also be wanting in *Podoces* which is certainly a member of the Corvineae, as Lowe *(loc. cit.*) could find none in two examined specimens.

I have placed *Ptilostomus* near the end of the magpies, but its very strong legs and black coloration suggest it may be an early offshoot of the *Corvus* group. The latter has had a long history in the Ethiopian region, as witnessed by the presence there of such distinct endemic species as *C. crassirostris*, while the magpies are not represented in the Ethiopian region unless by *Ptilostomus*.

**Podoces** Fischer *(Panderi)*

Ground or Running Jays

Synonyms: *Eu podoces* Sarudny and Loudon *(biddilphi)*; *Pseudopodoces* Sarudny and Loudon *(humilis)*.

Species: 1, hendersoni; 2, biddilphi; 3, pleskei; 4, panderi; 5, humilis.

Range: High, semiarid plateaus of central Asia.

Diagnosis: Derivatives of Old World jays, but highly specialized. As compared with *Garrulus*: bill attenuated and decurved; wing and tail relatively shorter and legs longer; plumage sand-colored but with wings and tail mostly bluish black as in
**Garrulus** and sometimes with a dark malar area as in *Garrulus*; largely terrestrial and cursorial.

**Remarks:** Hartert did not recognize either of the generic synonyms listed. “*Eupodoces*” *bidulphi*, as the generic name implies, is a true *Podoces* which resembles *panderi* so closely that it is unfortunate that a generic name was applied to it. “*Pseudopodoces*” *humilis* is much more distinct, but hardly enough so to require a monotypic genus. This little bird is not larger than a bluebird (*Sialia*). It has almost lost the darker markings, but the malar region and central pair of rectrices are dull blackish. As usual in genera whose species vary considerably in size, the tenth primary is relatively shorter than in the larger species of the genus. *P. humilis* nests in rodent burrows or crevices in walls. Its eggs have become white as in many cavity-nesting species. Some of the other species of *Podoces* exceptionally nest in subterranean holes, but usually build more or less jay-like nests in bushes and lay spotted eggs. *P. humilis* looks like a lark and represents the extreme of de-differentiation and loss of corvine characters.

**Nucifraga** Brisson (Caryocatactes) **Nutcrackers**

**Synonym:** Picocorvus Bonaparte (*columbiana*).

**Species:** 1, *columbiana*; 2, *caryocatactes*.

**Range:** Mountains of Eurasia and western North America.

**Diagnosis:** As compared with *Podoces*: bill similarly long but stouter, less decurved, and with the mandible somewhat upturned; wings and tail mostly bluish black as in *Podoces* but with some white in tail; wing relatively much longer; legs shorter; body plumage ashy or brown speckled with white.

**Remarks:** *Podoces* and *Nucifraga* both seem to be descendants of Old World jay stock but whether they resemble each other sufficiently to indicate a period of common ancestry after diverging from the jays, as suggested by Menzbier and others, is a moot question. *Garrulus*, *Podoces*, and *Nucifraga* are very distinct from one another.

The two species of *Nucifraga* are rather different; *caryocatactes* is a larger bird with much heavier bill, longer nasal bristles, and more uniform coloration than *columbiana*. Nevertheless, their similar habits and habitats and essential morphological similarity stamp them both as nutcrackers, and there is little reason to question the current practice of assigning both to *Nucifraga*. Stegmann (1934) gives reasons for considering *caryocatactes* more specialized than *columbiana* of North America; everything in their external appearance supports this conclusion. The common situation in which a primitive form survives in a peripheral area where it has escaped being overrun by successively more advanced types arising near the center of the origin of the group apparently exists in *Nucifraga*. It is, however, barely possible that the genus is of North American origin and related to *Gymnorhina* as mentioned in discussing the latter genus.

**Pyrrhocorax** Tunstall (Pyrrhocorax) **Coughs**

**Synonym:** Graculus Koch (*graculus*).

**Species:** 1, *graculus*; 2, *pyrrhocorax*.

**Range:** Palaearctic region in rocky or mountainous districts.

**Diagnosis:** Plumage glossy black; nasal bristles dense; bill and feet yellow or red; tarsus booted; bill slender and decurved; wing long; tail short; flight powerful; habits terrestrial.

**Remarks:** A very distinct genus. If *Corvus* is considered to be derived from *Nucifraga*-like stock, *Pyrrhocorax* in many respects forms a link between the two. If those who consider *Corvus* to be a relative of the magpies are correct, it is difficult to judge whether *Pyrrhocorax* is correctly placed near *Corvus* or near *Nucifraga*.

In 1760 an anonymous author published a perhaps rather fanciful account of a “little bird” supposed to inhabit the Islet de Met, near Rodriguez. It is commonly supposed that he was alluding to the extinct starling, *Necropsar leguati*, of which one specimen exists. Hachisuka (1937) somehow convinced himself that this description must refer to an extinct, turtle-
eating chough, and even went so far as to name this hallucination!

**Zavattariornis Moltoni** (Stresemanni)

- **Species**: 1, stresemanni (described in 1938; no specimen seen).
- **Range**: Southern Abyssinia.

**Diagnosis**: Circumorbital area and lores unfeathered; bare skin blue in life; coloration, shape of bill, and nasal bristles about as in *Nucifraga columbiana*; size scarcely larger than in *Cyanocitta cristata*; proportions about as in the American jay, *Cyanocitta sordida*, i.e., wing rather long, tail moderate; nest large, domed, with an entrance tunnel on top.

**Remarks**: Elsewhere (1943) I have summarized reasons for considering Zavattariornis a true member of the Corvineae. It is, however, so distinct that it is difficult to decide from published drawings, photograph, and descriptions to what living genus it is nearest in characters. Moltoni (1938) compared it with *Podoces*. The bluish black wings and tail of Zavattariornis suggest that it, like *Podoces* and *Nucifraga*, is a highly modified offshoot of *Garrulus*-like ancestry. The unfeathered, pigmented circumorbital area and domed nest, on the other hand, suggest the possibility that this genus, like *Ptilostomus*, may be an aberrant African representative of the magpies.

**Corvus Linnaeus** (Corax)

**Crows, Ravens, Jackdaws**

**Synonyms**: *Amblycercus* Bonaparte (violaceus, a race or geographical representative of enca); *Anomalocercus* Fitz (splendens); *Coleus* Kaup (monedula); *Corone* Kaup (corone); *Corvultur* Lesson (albicollis); *Frugilegus* Selys Longchamps (frugilegus); *Gymnocorax* Lesson (tristis); *Heterocorax* Sharpe (capensis); *Microcorax* Sharpe (jamaicensis); *Macrocorax* Sharpe (fuscicapillus); *Nesocorax* Riley (typicus); *Physocorax* Bonaparte (monedulaeide); *Ptero-corax* Kaup (albus); *Rhincorax* Sharpe (rhipidurus).

- **Species**: 1; tristis; 2; fuscicapillus; 3; validus; 4; unicolor; 5; typicus; 6; monedulaeide; 7; woodfordi; 8; meeki; 9; kubaryi; 10; enca; 11; splendens; 12; frugilegus; 13; monedula; 14; brachyrhynchos; 15; leucognaphalus; 16; ossifragus; 17; jamaicensis; 18; caurinus; 19; hawtiensis; 20; coronoides; 21; orru; 22; bennetti; 23; macrorhynchos; 24; corone; 25; torquatus; 26; corax; 27; cryptoleucus; 28; albus; 29; capensis; 30; rhipidurus; 31; albicollis; 32; crassirostris.

**Range**: Almost cosmopolitan except in South America.

**Diagnosis**: Large, powerfully built birds; wing relatively long; tail relatively short; coloration mostly black, rarely grayish or brownish, not infrequently with some white areas in plumage; rictal bristles long; bill and feet usually large and strong.

**Remarks**: *Corvus* is the most advanced and successful genus of the Corvineae. Its large size and resilient, adaptable behavior have enabled it to exploit many secondary habitats produced by human activities. It has spread to many areas not otherwise inhabited by the group and as a result has split into almost three times as many species as any other genus of the subfamily.

Meinertzhagen (1926, pp. 57–58) has given reasons for combining all crows into one genus, though they were divided by Sharpe and others into about a dozen genera. The above arrangement is based partly on Meinertzhagen (1926) and I am also indebted to Dr. E. Mayr for assistance in the arrangement of this genus. In his opinion it is a mistake to combine the American crow (*brachyrhynchos*) specifically with *corone*, the two differing in voice and other respects. I have left the northwestern crow, *caurinus*, as a species, as it seems doubtful that it should be a race of the fish crow, *ossifragus*, of the east coast of North America.

Subgenera or other subgroups were not used by Meinertzhagen. Superficial similarity is so deceptive among the many species of this difficult genus, that the interrelationship of the species of the genus is a difficult task. A few natural subdivisions may be mentioned, however. Species 1–10 form a subgroup occupying southeastern Asia and the adjoining archipelagoes. *C. tristis* stands somewhat apart from the others by reason of partial loss of head feathers and dull coloration. *C. splendens* and *frugilegus* suggest one another in some respects, but this may be parallelism. The jackdaw, *C. monedula*, is rather distinct. In fact, Harttert left it in a monotypic genus, though most re-
cent authors have lumped *Coleus* with *Corvus*. The jackdaw is small, has a characteristic small bill, nests in cavities, and lays eggs which are rather atypical in color for the genus. The American and Hawaiian crows, species 14–19, are probably allied, as are most of the following eight species, 20–27. The African crows, species 28–32, form a natural group, with the exception of *albus* which may be an African representative of one of the Asiatic groups and perhaps should come near *torquatus*. The three last species are in some respects the most modified of the genus. *C. rhipidurus* has a short tail. Its peculiar fan-shaped rictal bristles, as Meinertzhagen (1926, p. 96) pointed out, as well as several other characters show it to be a close relative of the large-billed *albicollis* and *crassirostris* and a link between them and other members of *Corvus*. Moreover, the bill is considerably smaller in *albicollis* than in *crassirostris* and scarcely bigger or more arched than in some of the Asiatic crows. The recognition of "Corvultur" seems unnecessary.

The relationship of *Corvus* to other genera is discussed below.

**PHYLOGENY**

The conclusions reached in the present study as to the interrelationships of the genera of Corvinæ are represented in the accompanying diagram and summarized below. The jays are the most primitive subdivision. Most of the more specialized forms such as the magpies and nutcrackers seem to be variously modified jays. The jays are primitive not only morphologically but to some extent in habits, as indicated in the following quotation translated from the Heinroths (1924–1926, p. 235) based on study in the field and aviary of representatives of the genera *Garrulus*, *Nucifraga*, *Pica*, and *Corvus*: "We incline to the opinion that the jay [Garrulus] of all these genera has the Corvid characteristics least developed and in its behavior shows rather a certain similarity to bush-dwelling songbirds."

That the Corvinæ evolved in the Old World is scarcely open to question. The groups to which they are most closely related occur exclusively in the Old World, chiefly in the tropics. Furthermore, all the more specialized genera of the Corvinæ are primarily Old World, though a few of them, such as *Nucifraga*, *Pica*, and *Corvus*, have reached North America. This indicates a longer history for the subfamily in the Eastern Hemisphere, even admitting that the larger areas and perhaps more varied topography of the Old World might result in greater evolutionary advance. The primitive jay-group occurs both in the Old and New Worlds, but 32 of the approxi-

mately 38 species are American. This is evidently another instance of the type of distribution in which the primitive forms of a group have survived more abundantly in peripheral areas. In the Old World the jays have been almost eliminated by magpies, nutcrackers, and crows which are, after all, only transformed jays. In the New World there has been less competition, and the jays have undergone considerable adaptive radiation without losing their group characteristics. The very poor representation of the Corvinæ in South America is another indication that the subfamily is of Old World origin.

Although the Corvinæ are now well represented in both the Palaearctic and Oriental regions, the fact that closely related groups such as the birds of paradise are primarily tropical suggests that the group evolved in the Oriental region. Many forms occur in the Himalayan and Chinese mountains, which form the boundary between these regions, and it is quite possible that the Corvinæ evolved in this general area and later spread both north and south. The jays, since they are the most conservative group in the subfamily, might be expected to furnish evidence on this point. *Garrulus* and *Cractes* occur chiefly in temperate or boreal districts, but the former extends south well into the Oriental region, while *Cractes internigrans* is endemic in the mountains of Szechwan, China. The resemblance of this species to *Garrulus lanceolatus* of the
Fig. 1. Phylogeny of the Corvidae.
Himalayas is a point in favor of the suggested origin of the Corvinæ in the mid-Asian mountains, since the Old World jays seem to have evolved there. *Platylophus*, the third genus of Old World jays, is entirely tropical but is aberrant and may not be a jay.

Since the Old World jays are few in number and may represent atypical forms which happen to have survived in the competition with magpies and other more advanced subgroups, the flourishing assemblage of American jays may be expected to give more reliable information as to whether the Corvinæ evolved in a tropical or in a temperate region. The American jays are very predominantly tropical or subtropical. Of 32 species only six range as far north as the United States. Three of these are southern species which only cross the border into the southern United States. Another, *Cyanocitta stelleri*, ranges from Alaska to Central America; the fifth, *Gymnorhinus*, extends slightly into Mexico. Only *Cyanocitta cristata* is not found south of the United States, but it is a geographical representative of the *stelleri* group and occurs in the subtropical portions of southern Florida. On the basis of all the evidence, it seems probable that the Corvinæ evolved in the tropics but that some members of the group early came adjusted to the colder climate of mountainous regions and were then able to colonize the Palearctic and Nearctic regions.

The zoogeographical history of the jays is an interesting problem, though in the absence of fossil evidence conclusions must be very tentative. Since the New World jays are mostly tropical and the Old World jays probably were originally so, the entrance of jays into the Americas presumably occurred at a time when tropical faunas extended farther north than at present and were able to cross from Asia to North America via a Bering land bridge. The large number of tropical families common to the New and Old Worlds supplies conclusive evidence that such conditions once existed. As in most such families, the Old and New World species of jays have become generically distinct.

Since there are jays in the temperate regions, the possibility cannot be eliminated that in this case the intercontinental transit was made by a northern jay (just as *Cractes* has done more recently) which later entered the American tropics and gave rise to the genera existing there now. The genera of jays which now have a northern distribution (*Garrulus* and *Cractes* of the Old World and the *Cyanocitta cristata* superspecies in the New) do not link the jays of the two hemispheres and hence offer no support to this theory. *Cyanocitta*, as Ridgway (1904, p. 346) emphasized, is related to the tropical American jays, not to *Garrulus*. The former relationship is so close that various tropical groups such as "*Cyanolyca,*" formerly considered genera, have been united with *Cyanocitta* in this paper. *C. stelleri* extends south in the mountains to Central America, suggesting that it represents tropical stock which first became adjusted to colder climates in the mountains and then ranged northward and spread over the North American continent. On the other hand it may have been a temperate-zone form which was forced south in the mountains by the Pleistocene glaciation and later returned northward.

It is significant that the American jays, though primarily tropical, are a distinctly North American group. South America has no endemic genera, though two of the North American genera, *Cyanocitta* and *Cyanocorax*, occur there. The considerable radiation of the American jays must have occurred in the tropics of North America before the re-establishment of the isthmial connection between the continents in the late Tertiary. The jays thus help to validate the belief recently expressed by Simpson (1943), following earlier work by Dunn, that the tropics of North and South America are more distinct faunally, as a result of the long period in which the two continents were unconnected by land, than is generally realized.

The magpies are an Old World group of genera which are essentially large, heavy-billed, long-tailed, short-winged, often
brightly colored jays. They are birds of weak flight, adapted to forested or brushy country. The New World jays also include magpie-like types, notably *Psilorhinus* and *Calocitta*, but here the relationship is so close that generic division is difficult. In the Old World, on the other hand, two natural groups, jays and magpies, may be recognized with a perceptible but not large gap between them. The gap is most nearly bridged by *Garrulus lidhti* and *Kitta ornata*, though the resemblance of these two species is doubtless partly parallelism.

Of the five genera of typical magpies, three, *Kitta*, *Crypsirina*, and *Platysmurus*, are Oriental in distribution. *Cyanopica* and *Pica* are primarily Palaearctic but extend into the northern parts of the Oriental region. They are offshoots of the more primitive tropical magpies.

In response to the peculiar conditions existing in the high, barren, or brushy plateaus of central Asia, the Old World jays have produced the peculiar genus *Podoces*. Its long legs, short wings and tail, decurved bill, sandy coloration, terrestrial, cursorial habits, and other distinctive characters make the gap between *Podoces* and *Garrulus* greater than that between *Garrulus* and the magpies. Nevertheless, *Podoces* has retained enough suggestion of the color pattern and other characteristics of jays to indicate beyond much question that it was derived from jays somewhat like the existing *Garrulus*.

*Nucifraga*, like *Podoces*, is a transformed Old World jay. It retains the bluish black wings and tail and a suggestion of the upturned bill of *Garrulus*. The tail is short, as in *Podoces*, but since *Nucifraga* is a bird of roving habits and inhabits mountainous country, its wings are long. *Podoces* and *Nucifraga* resemble each other in a few respects, and they may have had a period of common ancestry following their divergence from the jays. They are so distinct, however, that their few similarities may only reflect the fact that both were derived from the jays. The similarity in the nasal bristles is to be attributed to the cold climate of the regions inhabited by both genera. The possibility that *Nucifraga* is related to the American genus *Gymnorhinus* has been sufficiently considered in the remarks on that genus. *Nucifraga* reached North America long enough ago for the American species to become very distinct from the Palaearctic one.

The recently discovered Abyssinian genus *Zavattariornis* seems to resemble *Nucifraga columbiana* more than it does any other corvid; it has been compared also with *Podoces*. It is most surprising that a relative of either genus should exist in the brushy, hot country where *Zavattariornis* occurs. *Zavattariornis* has a bare pigmented area around the eye like *Pica*, and the nest is domed as in that genus. Possibly *Zavattariornis*, despite its short tail and long bill, is a magpie. The presence of a genus of the latter in Africa would be less remarkable in view of the occurrence there of *Ptilostomus* and of *Pica* in the Palaearctic fringe of northern Africa.

The choughs of the genus *Pyrrhocorax*, like *Nucifraga*, occur in the Palaearctic region and inhabit mountainous country. The two are similar in several details such as the nasal bristles, long bill, and proportions. It seems quite likely that *Pyrrhocorax* represents a further specialization of *Nucifraga*-like stock. *Pyrrhocorax* is very specialized by reason of its decurved red bill, very long wings, bootèd tarsi, and black coloration. *Corvus* has been considered to be related to *Pyrrhocorax*; the two are similar in proportions, color, and to some extent in habits. While this might be parallelism, it seems likely that *Corvus* evolves from the subgroup containing *Nucifraga* and *Pyrrhocorax*. The latter, despite its specializations, is intermediate between *Nucifraga* and *Corvus* in some respects. *Corvus* also resembles the magpies. Shufeldt (1888) considered the skeletons of *Pica* and *Corvus* almost identical, except in size, and concluded that the two genera are closely related. The skeletons of all the Corvinae are much alike except in purely adaptive details. If *Corvus* evolved from the magpies, it must have branched off rather early in the history of that group to acquire such different proportions. The fact that *Corvus* resembles one of the most
specialized of the magpies, Pica, much more than it does primitive magpies, such as Kitta, is strongly suggestive that this is a case of parallelism rather than of close relationship.

The rather generalized characters and almost cosmopolitan distribution of Corvus make it difficult to determine with finality to which other genera it is most nearly allied. If related to Pyrrhocorax and Nycti fringe it is, one would suppose, of Palaearctic origin. Yet the presence in Africa of perhaps the most specialized species of Corvus suggests the possibility that this genus evolved in Africa following the colonization of that continent by some nutcracker-like or perhaps magpie-like species. If Corvus is of African origin, Ptilostomus may well be an isolated side branch of the same stock. In any event the large size and adaptable and aggressive nature of the species of Corvus have made it the most successful and widespread genus of the subfamily. The Palaearctic, Oriental, and Ethiopian regions contain many distinct species of the genus, but North America and Australia have been colonized more recently. The presence in New Zealand of remains of an extinct "crow," Paleocorax, would seem to indicate that the Corvus group reached the Australian region at a rather remote period, but it is by no means certain that Paleocorax is not a member of the Cracticinae.

Corvus has also reached the Philippines, Polynesia, the West Indies, and other areas not otherwise occupied by the Corvinae. Its superior colonizing ability probably derives from a combination of powerful flight and unusual ability to survive under new or unfavorable conditions.

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