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Phylogeny of the avian family Corvidae

Hope, Sylvia, Ph.D.

City University of New York, 1989

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PHYLOGENY OF THE AVIAN FAMILY CORVIDAE

by

Sylvia Hope

A dissertation submitted to the
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in partial fulfillment of the requirements
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12/12/88
date

Leslie A. Marcus
Chairman of Examining Committee
Dr. Leslie A. Marcus, Queens College

12/12/88
date

Executive Officer
Dr. Peter C. Chabora

Dr. Michael Novacek, American Museum of Natural History

Dr. Max K. Hecht, Queens College

Dr. Wesley E. Lanyon, American Museum of Natural History

Dr. Stanley Salthe, Brooklyn College

Dr. Richard Zusi, National Museum of Natural History

Supervisory Committee

The City University of New York

Abstract

PHYLOGENY OF THE AVIAN FAMILY CORVIDAE

by

Sylvia Hope

Advisor: Dr. Wesley E. Lanyon

Phylogeny of Corvidae is reconstructed here from osteology. Treepies, *Dendrocitta* and *Crypsirina*, the piapiac, *Ptilostomus*, and Southeast Asian magpies, *Cissa* and *Urocissa*, appear to be paraphyletic early lineages of Corvidae, with the remaining corvids a monophyletic group. American jays appear to be sister taxon to the large assemblage of primarily holarctic corvids. *Cyanolyca* appears to be sister taxon to other American jays. It retains many primitive corvid characters, in accord with other evidence for long isolation of the American jays. North American jays *Aphelocoma*, *Cyanocitta*, and *Gymnorhinus* are a monophyletic group, with *Gymnorhinus* probably sister taxon to *Aphelocoma ultramarina*. The holarctic corvids include northern magpies, *Pica* and *Cyanopica*; Eurasian and boreal jays, *Garrulus* and *Perisoreus*; and the crow-like birds, including crows, nutcrackers, ground jays, and choughs, *Corvus*, *Nucifraga*, *Podoces*, and *Pyrrhocorax*. *Garrulus* and *Perisoreus* are similar but possibly not monophyletic. *Pica* retains many primitive corvid characters but its skeleton is also crow-like. The crow-like birds are a monophyletic assemblage within which *Pica* may also be included but its relationship to that group is not fully clarified. Podoces and Pyrrhocorax appear to be sister taxa. Phylogeny and geography suggest Corvidae originated in the western Malaysian region. Early corvids probably were sedentary woodland birds. The northern radiations entail several different adaptive radiations. Specialization on acorn crops involves different mechanisms for opening nuts in Eurasian and American jays. Pica and crow-like birds have moved into less forested environments and concommitantly are more mobile than primitive corvids. Among American jays migratory Cyanocitta and nomadic Gymnorhinus are also exceptionally mobile. Platylophus may be a member of the sister group of the Corvidae. Pseudopodoces is a distantly related oscine.

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INTRODUCTION

Birds of the family Corvidae include the crows, choughs, nutcrackers, a variety of forms called jays and magpies, and the treepies. The one hundred five nominal species in twenty six genera have radiated worldwide into many different regions and habitats. They are much more widespread than any of their closest relatives in the order Passeriformes. Nevertheless many corvids, including most jays and magpies, are more sedentary than many birds, including most passerines, and the patterns of their geographic history may be easier to trace.

The diversity and complexity of corvids and have stimulated many studies. A phylogenetic analysis of the group based on morphology may help to interpret evolution of corvid behavior and ecology.

The term "jay" refers to any of the smaller corvids with only a moderately long tail and jaylike behavior - noisy and gregarious. Jays of some sort are found almost worldwide except in the high arctic and Antarctica, Australia and New Guinea, southern Africa, extreme southern South American, and oceanic islands. The term "magpie" refers to any of several genera of larger jaylike birds; usually they have a long tail and gaudy markings. Magpies are very diverse in India and Southeast Asia. The "common" magpie (Pica) belongs to a less elaborate holarctic genus. The treepies or tree magpies of India and Southeast Asia are small jay-like corvids with a very long tail and a very short, heavy bill. The nutcrackers, crows, and choughs are large, strong flyers with somber plumage, very heavily constructed bills, and more sedate behavior. Nutcrackers are holarctic high mountain birds and choughs are palearctic alpine and inland cliff-dwelling birds. Crows have spread worldwide even to remote Pacific islands, but not to Central and South America.

The traditional view of corvid history is that the group originated in the Old World tropics, where the magpies are most diverse, and where other members of the corvoid assemblage are found. In this view the corvids then spread later to the Palearctic and the Americas. According to Sibley and Ahlquist (1986) the ancestor of corvids came from Australia, the group then radiated extensively in Eurasia, and crows then invaded Australia secondarily. Also, the American corvids immigrated recently. A date of -4 Mya was loosely assigned to an American invasion.

Like most other Passeriformes, corvids have been difficult to diagnose. Amadon (1944) provided the following description:

> "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 [= Corvidae] 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 predatory feeding habits; bold and inquisitive nature.

No unique diagnostic anatomical characters for Corvidae have been identified from a comprehensive comparative study.

This study began with the object of clarifying relationships among the species of American jays. In order to do that it was necessary to look more widely first at all corvids and also at other passerines. The original objective was broadened to include defining the limits of the avian family Corvidae and the intergeneric relationships within corvids.

SYNOPSIS OF THE GENERA

Goodwin (1986) gives a comprehensive review of ecology, behavior, and systematics of the birds of the family Corvidae. Turcek and Kelso (1968) compiled an extensive bibliography and summary emphasizing feeding ecology.

The order of discussion of taxa here reflects approximately the systematic relationships suggested by this study. Generic and specific names are as in Peters' Checklist of the Birds of the World (Volume 15, 1962).

Platylophus (crested jay or shrike jay)

Platylophus galericulatus is a chunky, dark, jaylike bird of tropical forests in Malaysia including Borneo, Java, and Sumatra. *Platylophus* resembles the smaller American jays in size and shape, with its only moderately long tail, plushy short frontal crest, and long, spatulate occipital crest. Like many American jays of the genus *Cyanocorax*, *Platylophus* has white supraciliary and subocular spots. The bird is poorly known from field observations but is said to behave like a jay. It is omnivorous, usually travels in pairs or groups, and seems unafraid of humans. Like most or all corvids it has a varied vocal repertoire including the distinctive rattle call.

Platysmurus (black jay)

Platysmurus leucopterus occurs on the Malay penninsula and the islands of Sumatra and Borneo but not Java. This is a robustly built but not extremely large bird, with bristly frontal crest and a short spatulate occipital crest, tail shorter than in treepies and plumage all black except for large white wing patches (mainland form) or all black (Borneo). It feeds omnivorously, is mostly arboreal, and its behavior and voice are jay like.

Dendrocitta, Crypsirina, and Temnurus (treepies)

The nine species of treepies of the genera Crypsirina, Dendrocitta, and Temnurus, range through India, south China, Formosa, and Malaysia including the islands west but not east of Wallace's line. These are small, primarily arboreal corvids with relatively plain plumage in white, rufous, grey, and black, irridescent in the diminutive Crypsirina. The bill is short, deep, and heavily decurved. The tail is very long and in several species is raqueted at the tip; in Temnurus it is elaborately notched. Like most corvids the treepies are more or less omnivorous and opportunistic, but they apparently do not to eat large hard items. They go about frequently in small parties, following each other in jay-like fashion. Like most jays and magpies they use a variety of loud or musical calls, including a rattle call.

Ptilostomus (piapiac)

The piapiac is an isolated West African form. It is a medium size, all black bird with a substantial bill superficially resembling that of crows, but it has a long graduated tail like a magpie. It frequents woods and open fields.

Cissa (green magpies)

The green magpies are large, robust, short-tailed, short-winged birds with bright green plumage, heavy red bills, red legs, a black mask, and red wattles about the eyes. They range through India and southern China and Malaysia including Borneo and Sumatra, inhabiting forest and woodlands but occurring also in adjacent open areas. They are omnivorous and take many large food items including small vertebrates. Like jays they travel in small parties or pairs, and they hide food in typical corvid manner. The vocal repertory is large.

Urocissa (blue magpies)

The five species of Urocissa are large, long-tailed, heavy billed birds, some with bright red bills and one with wattled eyes as in Cissa. They are rather diverse. Most but not all have blue prominent in the plumage; some have a short occipital crest. The species ornata is endemic to Sri Lanka; it has distinctive silky caerulean and bright roufous plumage. The species whiteheadi from South China has very plain bicolored plumage and a shorter tail than others. The species caerulea is a very large blue and black bird endemic to Taiwan. Urocissa erythrorhyncha and flavirostris are spectacularly long-tailed magpies, very similar, ranging through the Himalayas into China and east to the Pacific, inhabiting jungle, scrub, and forest, with flavirostris typically at higher altitudes. An account of behavior of Urocissa on Taiwan (L. Severinghaus 1986, 1987) found it is much like the American jays though evidently more aggressive.

Cyanolyca, Cissilopha, Calocitta, Psilorhinus, Cyanocorax, Aphelocoma, Cyanocitta, Gymnorhinus (American jays)

The American jays share similarities in plumage, vocalizations (Hardy 1969a), and pterylosis (Clench 1985). Pitelka (1951d) noted their apparent long isolation in the Americas. Many neotropical jays live and breed in cooperative groups.

The six species of Cyanolyca are small Central and South American jays of humid middle elevation and especially highland cloud forest, occurring from southern Mexican highlands through the Panamanian isthmus and south through the Andes to northern Bolivia. Several very similar Central American and Mexican species have small disjunct ranges in high altitude cloud forest. The species viridicyana is differentiated into numerous well-defined subspecies in the Andes. Relatively little is known of the behavior or ecology of Cyanolyca.

The genus Cyanocorax is very diverse. Three species are very similar, relatively small jays, with long spiked frontal crests and bright facial markings in a widespread Cyanocorax pattern consisting of supraocular, subocular, and malar pale spots on a black face and throat. These are the green jay, Cyanocorax yncas, which inhabits mesic woods and thickets with a trans-Andean and Carribean slope distribution from the Rio Grande to Bolivia; the species mystacalis in drier woodlands of Ecuador and Peru; and dickeyi with a restricted range in pine woods and barrancas of Sonora. The species chrysops is similar but larger, with the long bristly frontal crest extending over the entire head, and the facial pattern very bright. Its range extends through drier woodlands of southern Brazil and northern Argentina.

Except in yncas which is green the ground plumage color in all these jays is dark blackish blue. The seven other species of Cyanocorax, all east of the Andes, are very large, with plainer or more obscure facial patterns, and deep dark blue to purplish-lavender or brownish plumage. The frontal crests are shorter and more lax, or curly (cristatellus). The species affinis north of the Andes in Colombia, Venezuela, and Carribean Central America is most like this group. Within Cyanocorax apparently only heilprini is a bird of true rain forest. Most inhabit campo cerrado, open woods or edge habitats (Hardy 1969b; Haffer 1978, 1987; Cracraft 1985). The very large brown jays, genus Psilorhinus (one species, morio) range from southern Texas to Costa Rica on the Caribbean slope, inhabiting open woods and farmlands. The very large, long tailed, gaudily marked magpie jays of the genus Calocitta occur in dry, open woodlands on the western margin of the drier parts of Central America and Mexico. The brown jay and the magpie jay are nearly in contact over the Isthmus of Tehuantepec. The distinctive jays of the genus *Cissilopha* have dark, silky caerulean body plumage and all black hoods. Most inhabit humid lowland and middle altitude edge forests and plantations in Central American and southern Mexico and drier woodlands in Sonora. *Cissilopha melanocyanea* ranges into higher elevations.

Of the jays of the genus *Aphelocoma* two species, *coerulescens* and *ultramarina*, inhabit dry oak woodlands in western North America from inland Oregon south throughout the drier mountainous regions to central Mexico. The species *coerulescens* also extends into drier scrubby areas in the southwestern United States and in patchy disjunct areas in Florida. The species *unicolor*, largest and southernmost member, inhabits a restricted area of higher elevation humid forest in central Mexico (P. Escalante, pers. comm.). The jays of the genus *Cyanocitta* inhabit denser North American forests: *stelleri* in western North American conifer and mixed lowland forest from southern Alaska to Guatemala, *cristata* in eastern deciduous forests in Canada and the United States south to Florida. *Gymnorhinus cyanocephalus*, the pinyon jay, is associated with dry pinyon pine forests in the Great Basin of western North America. All of these North American jays harvest pine nuts or acorns and accumulate stores, most notably *Gymnorhinus*.

Garrulus (Eurasian jays)

Three species of Garrulus occur in Eurasia mostly north of the Himalayas. Garrulus jays are moderately large (except lanceolatus) pinkish or blue and dull roufous birds. The small species lanceolatus is more ornate than others, with a crest and markings resembling those of the blue jay Cyanocitta cristata of North America. The lanceolated jay has a restricted range in western Asia. Garrulus lidthi is the largest member of the genus, restricted to the Ryu-Kyu Islands. In color, form, and size it resembles Urocissa ornata. Garrulus glandarius is widespread throughout Eurasia. It is extremely varied over its range, with the race from northern India much plainer than others. This form is often likened to Perisoreus jays. Garrulus glandarius is omnivorous like all corvids but also depends more than most on acorns.

Perisoreus (boreal jays: Canada jay, Siberian jay, Szechuan jay)

Jays of the genus Perisoreus inhabit holarctic boreal forests in Siberia, Tibet, and North America. They are small, small-billed, plain colored birds. The three species are very similar. Food storage in trees enables the Canada jay to overwinter far north (Dow 1965).

Cyanopica (azure-winged magpie)

Cyanopica cayana is a relatively gracile, pale blue, long tailed bird that is not obviously related to any other particular corvid. It occurs in eastern Asian and in Spain. The two widely separate populations are very similar.

Goodwin (1986) suggested that Spanish birds may be descended from cage-birds introduced by early traders. The azure winged magpie lives in groups in patchy woodlands and also occurs in more open areas.

Pica (common magpie, yellow-billed magpie)

Pica magpies inhabit relatively open fields and nearby groves. The common magpie inhabits suitable areas throughout the holarctic except in Eastern North America. The yellow-billed magpie is endemic to the inland valleys of California. Like all corvids these magpies are omnivorous and store food but Pica depends heavily on grains and such other food as can be secured in open fields. Pica apparently is expanding into the increasingly cultivated areas in Asia (Goodwin 1987) and its range in Asia may now be much larger than it was in the recent past. Pica has only recently reached Taiwan (L. Severinghaus, pers. comm.). Domed nests protect magpies against predation and may be important in allowing expansion into the same habitats as their larger and more aggressive and clever relatives the crows.

Podoces (ground jays, running jays)

The four species of Podoces are small to medium sized corvids inhabiting steppes in Asia. They are unusual among corvids in being primarily terrestrial. Otherwise reports of their behavior indicate typically corvid aspects. Narrow, sickle-shaped bills enable them to probe crevices in rocks for prey. Plumage is grey or pale pink, markings are simple, and wings and tail are short; legs are long.

Zavatarriornis

Zavatarriornis stressemanni is an isolated and poorly known corvid found only in desert foothills and thorn scrub of Ethiopia. It is a small, short-tailed bird with plumage pearly grey, bare blue skin about the eyes, and simple markings; overall it resembles the Clark's nutcracker of North America. The bill is also however relatively delicate and sickle shaped.

Nucifraga (nutcrackers)

The two species of Nucifraga have a distribution corresponding to high elevation and high latitude conifer forest throughout Eurasia and western North America south to the Sierra San Pedro Martir. Nutcrackers are implicated in co-evolution and spread with certain pines (Tomback 1977; Turcek and Kelso 1968). The birds depend very heavily on a restricted variety of pines. They harvest and bury the pinenuts often at great distances from the parent trees in concentrated stores. They are irruptive and may wander far. In North America nutcrackers inhabit principally subalpine forests above the ponderosa belt.

Pyrrhocorax (choughs)

The two species of choughs range through Eurasia, nesting in caverns and foraging in neighboring fields and meadows. They use their long, sickle shaped bills to probe in crevices. Choughs are large, strong flying birds. They have short tails and all black plumage. The alpine chough is smaller and has a much shorter bill than the red-billed or common chough.

Corvus (crows, ravens, rook, jackdaws)

Of the thirty nine species of *Corvus* many are all black but others are black and white, sharing a plumage pattern basic to many magpies and jays, consisting of black wings and tail, black head, and pale nape and body plumage. Like choughs and nutcrackers, crows are large, long-winged, short-tailed, strong flying birds. Crows are noteworthy for the long distances they may cover in routine daily activities. The range of the genus includes all suitable parts of Eurasia and Africa, North America, Australia, and islands of the western Pacific including Hawaii. Thus *Corvus* is distinguished by being nearly worldwide and the most cosmopolitan genus of the family. The wide spread of the crows seems to be a function of far ranging habits, omnivory, and opportunism. These characters are not entirely novel in corvids but are best developed in crows. Thus the nominate genus for the family Corvidae is not at all typical.

The two species of jackdaws (*monedula* in Europe, *dauuricus* in Asia) are distinctive, only moderately large birds with a smaller bill than in typical crows. The "typical" crows, e.g. all other species, have a conspicuously elongated bill. "Raven" is a term for any of the larger typical crows. All members of the genus are omnivorous and opportunistic. Most species inhabit open woodlands and utilize fields for foraging. Some populations of the northern raven, *Corvus corax* and the jungle crow, *C. macrorhynchos*, occur in deeper forest. Several have adopted unique foraging habits, e.g. the northwestern crow *C. caurinus*, which feeds on clams. Many crows use tidelands part of the time.

Pseudopodoces

Pseudopodoces humilis, the dwarf ground jay of Asian steppe, is classified with Corvidae because of its resemblance to the *Podoces* jays of the same regions. *Pseudopodoces* nests in holes in the ground, and in other ways, according to field observers, it does not give the impression of corvid behavior.

HISTORY OF SYSTEMATIC STUDY

Corvidae are a family of the suborder Oscines (songbirds) in the avian order Passeriformes (so-called perching birds, although many other birds also perch). Oscines are a monophyletic group characterized primarily by complex, unique structure of the syrinx. "Suboscines" are a paraphyletic assemblage of non-oscine Passeriformes. Evidence for these arrangements amd history of systematic study were reviewed recently by Raikow (1982) and Sibley (1970). Anatomical differences among the families of oscines are slight and relationships among the families are poorly understood. The position of the corvids within oscine passerines remains unclear despite a long history of investigation.

The corvoid assemblage

Birds included in Corvidae have been associated together since earliest classifications, because many aspects of corvid behavior are conspicuous and characteristic of all. Sibley (op.cit.) reviewed the history of the earlier studies. From these works a concept of a "corvoid assemblage" appeared, to include possibly the families Corvidae, Paradisaeidae (birds of paradise), Cracticidae (curawong, bell magpie, butcher birds), Oriolidae (Old World orioles), Dicruridae (drongos), Corcoracidae (white winged chough, apostle bird), Grallinidae (mud nesters) and Calleidae (New Zealand wattlebirds). Mayr and Amadon (1951) added the Ptilonorhynchidae, bower birds, but they suggested that not all these families were necessarily related to each other. Amadon (1957) and Wetmore (1960) suggested that Sturnidae, starlings, may belong in the assemblage. Olson et al. (1983) proposed that the New Zealand "thrush," Turnagra, is not a thrush but is related to the birds of paradise and bower birds. Both Stonor (1937) and Bock (1963) recognized the many differences between bower birds, Ptilonorhynchidae, and Paradisaeidae, but did not explicitly exclude Ptilonorhynchidae as relatives of corvoid birds.

Based on limb myology Borecky (1977) found limited evidence to support a closest cladistic relationship of the Corvidae to the Grallinidae and Corcoracidae. Based on DNA hybridization Sibley and Ahlquist (1985) and Sibley, Ahlquist, and Munroe (1988) proposed a closest relationship of the traditional family Corvidae to a sister group composed of Oriolidae, Paradisaeidae, Cracticidae, Artamidae (wood swallows), and Campephagidae.

Relationship of corvoids to other oscines

Wetmore (1957) listed the corvoid families near the beginning of the oscine passerines. This position expressed the concept that corvoids represent a primitive type of oscine based on their more primitive humerus and lesser reduction in the number of primary feathers compared to most of the smaller common songbirds of the northern hemisphere. On the other hand, Mayr and Amadon (1951) listed the corvoids at the end of the passerines (and at the end of all the birds) based on their complex behavior. Each position of Corvidae expressed a different view of the relative recency of derivation of corvoids. Sibley and Ahlquist (1985) advocated a greatly enlarged family Corvidae to include not only most of the corvoid assemblage as previously understood but also many other primarily Australasian passerines. The traditional Corvidae and its closest relatives were made a subfamily "Corvinae" of a greatly enlarged "Corvidae." *Corcorax*, *Struthidea*, and *Grallina* were placed in "Corvidae" close to the "Corvinae" but in separate subfamilies with other birds that have not previously been called corvoids. The bower birds, Ptilonorhynchidae, and the starlings, Sturnidae, were removed far from the vicinity of corvoids. In a surprising departure from previous opinion bower birds, Ptilonorhynchidae, were removed and united with the lyre birds, Menuridae, long considered to be the sole remnants of an archaic lineage not closely related to other oscines.

The novelty in the DNA phylogeny is its inclusion of many taxa previously not regarded as close to the corvoid birds, as part of an Australasian passerine radiation. Apart from the Ptilonorhynchidae, Grallinidae, and Corcoracidae, the traditional corvoid assemblage is intact in the DNA phylogeny (Figure 1).

The branches at the base of Sibley and Ahlquist's Corvinae are very short and the error of measurement is not used to put a confidence limit on the nodes in the phylogeny. The procedures of DNA hybridization and its statistical analysis need reevaluation (Houde 1987). The measure of distance used is questioned, as well as the linearity and constancy of the the rate of evolution of DNA. Recently the integrity of the DNA data and analysis have been pointedly challenged (reviewed by Lewin 1988).

Generic limits within Corvidae

There is consensus about the generic limits of *Pica*, *Garrulus*, *Perisoreus*, *Nucifraga*, *Podoces*, *Pyrrhocorax*, and *Corvus*. The monotypic genera *Platylophus*, *Ptilostomus*, and *Platysmurus* have not been synonymized to other genera. There is some disparity in treatments of Southeast Asian magpies and the treepies. Amadon (1944) included all the treepies in *Crypsirina*, and all the southern magpies in *Kitta* (= *Cissa*). Vaurie (1962) maintained the three genera *Dendrocitta*, *Crypsirina*, and *Temnurus* for treepies and two genera for Southeast Asian magpies, *Urocissa* and the resurrected name *Cissa* Boie for the green magpies.

Within the American jays generic limits have been harder to define. The American jays have been associated together in systematic treatments at least since the early review by Sharpe (1877). Although Shufeldt (1888) and Ashley (1963) pointed out similarities in the humerus of the Canada jay to that of the American jays, *Perisoreus* has been excluded in recent systematic treatments. Often the pinyon jay, *Gymnorhinus* has been excluded. *Gymnorhinus* has been associated instead with crows and nutcrackers because of sharing strong flight and because of walking rather than hopping, and with nutcrackers because of similar bill form and foraging habits. Based on a comprehensive study of osteology Shufeldt (op. cit.) thought the pinyon jay was intermediate to crows and jays. Ashley (op. cit.) found its humerus to be like that of American jays. Pitelka (1951) considered provisionally that it was an American jay. Ligon and White (1974) found that pterylosis of the pinyon jay is like that of American jays. Ligon (1974) reviewed the systematics of *Gymnorhinus* and pointed out resemblances in plumage to the Mexican jay, *Apheiocoma ultramarina*. From a study of the jaw articulation Zusi (1987) found compelling evidence for monophyly of the American jays including *Gymnorhinus* and excluding *Perisoreus*.

Early classifications by Sharpe (1877), Ridgway (1904), and Hellmayr (1934) recognized many genera of American jays.

Ridgway thought that *Cyanolyca*, *Aphelocoma*, and *Cyanocitta* were closely related. Amadon (1944) advocated combining genera to retain only four: *Cyanocitta* (including *Cyanolyca* and *Aphelocoma*), *Gymnorhinus*, *Psilorhinus*, and *Cyanocorax*. Pitelka (op. cit.) agreed that *Cyanocitta*, *Cyanolyca*, and *Aphelocoma* are closely related but withheld judgment on generic limits until neotropical jays were better studied. Blake (1962) maintained *Aphelocoma* separate from *Cyanocitta*. He also retained five genera of neotropical jays.

Hardy (1969a) proposed that there were two or possibly three lineages of the American jays, an "ornate" group, including all the lowland neotropical jays, e.g. *Cyanocorax*, *Psilorhinus*, *Cissilopha*, *Calocitta*, and possibly also the North American genus *Cyanocitta*; and an "inornate" group composed of the North American genus *Aphelocoma* and the neotropical montane genus *Cyanolyca*.

The occurrence of a natural hybrid between *Calocitta* and *Psilorhinus* (Pitelka et al. 1956) has led to some speculation that *Psilorhinus* and *Calocitta* are closely related and possibly representatives of an east-west disjuction across Central America, in spite of their extremely different plumages. The sixth edition of the AOU Checklist of North American Birds of (1983) has included both *Cissilopha* and *Psilorhinus* in *Cyanocorax*, but not *Calocitta*. Both Amadon and Hardy recognized several sections in *Cyanocorax*. Hardy proposed that within the ornate lineage of *Cyanocorax* the more boldly patterned members were primitive and that melanism had obscured patterns separately several times.

Cyanolyca has only rudimentary development of the unique features of jaw articulation that unite the American jays. Zusi (op.cit.) therefore suggested that Cyanolyca may be the earliest lineage of American jays.

Some species-level questions in the American jays

Pitelka (1951a, 1951b, 1951c) reviewed nomenclature and subspecies status of Mexican and Central American members of Cyanolyca. The distinctive Andean form Cyanolyca viridicyana turcosa may be a separate species; the status of separate populations in southern Ecuador is not clear. Selander (1959) subsumed both the morphs of the brown jay, Psilorhinus in the species morio. The recent revision of the American Ornithologist's Union Checklist of North American Birds (1983) has split Calocitta into two species, but studies of the contact zone between northern and southern populations are not cited. In the Cissilopha jays the species sanblasiana frequently is split into a western species, sanblasiana, and an eastern species, yucatanica, based on extreme differences in the juvenile plumages. In the Cyanocorax jays the form cyanopogon has sometimes been included in chrysops, based on a single suposedly intermediate specimen.

The close relationship of the two species of Cyanocitta in eastern and western North American respectively, has not been challenged. Most ornithologists assume these are one of many examples of species pairs separated by the Great

Plains. The occurrence of natural hybrids of the blue jay and the Steller's jay near Boulder, Colorado (Williams and Wheat 1971) has reinforced that idea. Nevertheless these two have marked differences in habitat preference and vocal repertoire.

The close relationship of the widely separated eastern and western populations of the scrub jay, *Aphelocoma coerulescens*, also is not questioned. It seems likely that they were in contact in relatively recent times and the eastern population is restricted to remnants of suitable habitat left in the Southeastern United States.

Relationships among the genera of Corvidae

In previous classifications of the Corvidae there has been some implicit recognition of the importance of identifying primitive corvid characters. For example, a basic divergence of opinion has been expressed sometimes as difference concerning the status of the crows, whether they represent an early radiation and retain many primitive corvid characters or alternatively are a recently derived holarctic radiation. The reason for considering crows primitive was that they are large black and white birds with heavy bills, and in other ways resemble some of their presumed relatives among passerines. This is perhaps a circular prophecy since many candidates for the corvoid assemblage were identified partly by their particular resemblance to crows. Amadon (1944) recognized the greater similarity of jays to other oscines and thought jays were a primitive type of corvid.

Relationships among the remaining genera of corvids have remained unclear. Amadon suggested that Platysmurus is related to treepies. He made treepies an offshoot of the Southeast Asian magpies in his tree (represented here in Figure 1). The DNA analyses placed the genus Dendrocitta as most distant taxon from Corvus, but in a radical difference from Amadon placed Platysmurus near to Nucifraga and Corvus. Neither of the Southeast Asian magpies Cissa and Urocissa was included in DNA studies.

Shufeldt (1888) found that osteologically Pica "is a Crow, pure and simple." Amadon placed Cyanopica and Pica with the Southeast Asian magpies and treepies and also placed Ptilostomus tentatively with this larger magpie group. Goodwin (1986) followed Amadon.

All authors have agreed on the early isolation of American jays. Blake and Vaurie in their joint treatment of the Corvidae in Peters' checklist (1962) judged the American jays primitive and listed them near the start of the Corvidae. The DNA hybridization analyses placed the American jays close together and far from Corvus but not all at the same distance. If they are monophyletic under the premises of the analysis they should have appeared at the same distance.

The Garrulus jays have usually been linked to the Urocissa magpies on the one hand or the Perisoreus jays on the other, as suggested by the extremes in the genus Garrulus. Amadon grouped all the Eurasian and boreal jays with American jays in his tree. Goodwin put the Eurasian jays and boreal jays with the southern magpies and treepies. Amadon and Goodwin both placed Podoces near Nucifraga, Pyrrhocorax, and Corvus. Sibley and Ahlquist placed Nucifraga next to Corvus but did not analyze Podoces and Pyrrhocorax. On the basis of pterylosis Clench (1985) thought that Podoces is not a corvid.

For three genera the validity of their placement in the Corvidae has often been questioned: Platylophus, Zavattariornis, and Pseudopodoces. None of these is known well from museum or field studies. Ripley (1955) provided line drawings of skull and palate of Zavatarriornis which are consistent with his suggestion that it might be closely related to the nutcrackers. Borecky (1977) and Clench (1985) have both produced strong evidence that Pseudopodoces is not a corvid. Amadon placed Platylophus at the start of the Corvidae to express uncertainty about its position, and he thought that it might be primitive in Corvidae. Goodwin (1986) questioned its inclusion in Corvidae. Sibley and Ahlquist placed it as the second branch of the Corvidae in a step diagram as DNA distance from Corvus. On the basis of pterylosis Clench (1985) excluded Platylophus from Corvidae.

On the basis of displays Verbeek (1972) concluded that Garrulus is more like Corvus than Pica is. His table indicates Pica is more like the North American jays. His survey was exhaustive but information was lacking for many species including Pyrrhocorax and Southeast Asian magpies. Goodwin (1986) cites studies of displays of Pyrrhocorax,

Figure 1. Previous phylogenies of the Corvidae compared to phylogeny found in the present study.

<u>Abbreviations for taxa</u>

AJ	American jays
Aph	*Aphelocoma*
Cal	*Calocitta*
Crp	*Crypsirina*
Crc	*Cracticus*
Csa	*Cissa*
Cslo	*Cissilopha*
Cv	*Corvus*
Cyly	*Cyanocyca*
Cypi	*Cyanopica*
Cycit	*Cyanocitta*
Cycor	*Cyanocorax*
Dn	*Dendrocitta*
Gar	*Garrulus*
Mn	*Manucodia*
Nuc	*Nucifraga*
Or	*Oriolus*
Per	*Perisoreus*
Pt	*Ptilostomus*
Pa	*Paradisea*
Pi	*Pica*
Pl	*Platylophus*
Plt	*Platysmurus*
Pod	*Podoces*
Ps	*Psilorhinus*
Psd	*Pseudopodoces*
Py	*Pyrrhocorax*
Zav	*Zavatarriornis*

After Amadon 1944:

```
Pa  Dn   Pi Csa Pt   AJ Gar Per Pl  Po Zav Nuc  Py Cv
¦   Crp Cypi ¦   ¦   ¦   ¦   ¦  ¦   ¦   ¦   ¦   ¦   ¦
¦   Plts ¦   ¦   ¦   ¦   \---/  ¦   ¦   ¦   ¦   \---/
¦    \---/   ¦   ¦   \-----/    ¦   ¦   ¦   \-----/
¦      \---------/      \-------/   \---------/
¦          ¦                ¦              ¦     Cal
¦          ¦                ¦              ¦      ¦    Ps Gy
¦          \----------------/              ¦    Cycor  ¦  ¦
¦                   ¦                      ¦      \----/  ¦
¦                   \----------------------/       Cycit  ¦
\------------------------------/                     \----/
```

After Goodwin 1986:

```
Pt Zav Pl  Dn Plts Csa Gar Per  Pi   other Gy  Po  Nuc Py Cv
¦   ?  ¦   Crp ¦    ¦   ¦   ¦   Cypi   AJ  ¦   ¦   ¦   ¦   ¦
\---/  ¦    ¦   ¦   ¦   \---/    ¦     \---/   ¦   ¦   \---/
  ¦    ¦    \---/   ¦     ¦      ¦       ¦     ¦   \-----/
  ¦    ¦      \-----------/      ¦       ¦     \-----/
  ¦    ¦          \--------------/       ¦        ¦
  ¦    ¦                  \-----------------------/
  ?    ?                            ¦
  \---------------------------------/
```

After Sibley and Ahlquist 1985 (DNA distance from *Corvus*):

```
Crc Or Pa Cn Pl Cycor  Aph Cycit Per Pi Plts Nuc Cv
\---/  ¦  ¦   ¦   ¦     ¦    ¦   ¦  ¦   ¦    \---/
  \----/  ¦   ¦   ¦     ¦    ¦   ¦  ¦   \------/
     ¦    ¦   ¦   ¦     ¦    ¦   ¦  \------/
     ¦    ¦   ¦   ¦     ¦    ¦   \----/
     ¦    ¦   ¦   ¦     ¦    \-----/
     ¦    ¦   ¦   ¦     \-------/
     ¦    ¦   ¦   \----------/
     ¦    ¦   \---------/
     ¦    \---------/
     \--------/
```

Present study:

```
Crc Or Pa Pl Dn  Pt Csa Uroc AJ Pi Cypi Per Gar Pyr Nuc Cv
¦   ¦  ¦  ¦  Crp ¦   ¦     ¦    ¦   ¦   ¦    ¦  Po    ¦  ¦
\---/  \--/  ¦   ¦   ¦     ¦    ¦   ¦   ¦    ¦   \---/  ¦
  ¦      ¦   ¦   ¦   ¦     ¦    ¦   ¦   ¦    ¦     \----/
  ¦      ¦   ¦   ¦   ¦     ¦    ¦   ¦   ¦    \--------/
  ¦      ¦   ¦   ¦   ¦     ¦    ¦   ¦   \--------/
  ¦      ¦   ¦   ¦   ¦     ¦    ¦   \--------/
  ¦      ¦   ¦   ¦   ¦     ¦    \--------/    alternate:
  ?      ¦   ¦   ¦   ¦     \--------/
  ¦      ¦   ¦   ¦   \---------/              Pyr Pi Nuc Cv
  \------/   ¦   \---------/                  Po  ¦  ¦   ¦
     ¦       \-------/                        \---/  \---/
     \-----------/                              \------/
```

which indicate both magpie and crow-like elements. Trees produced by Amadon, Goodwin, and Sibley and Ahlquist are redrawn here for comparison to the results of this study (Figure 1).

APPROACH TO THE STUDY

Choice and treatment of characters

Such features as dimensions of wing and leg are often said to be purely adaptive. Adaptive features are then discounted for phylogenetic reconstruction. However instead of making prior judgments of adaptedness of a particular character, variation alone may be considered. Then the search is simply for characters that vary sufficiently within the taxon studied that groupings may be made. The value of any particular character must be judged within the taxon studied according to its variation there. Adaptedness is not the issue. As a corrollary a classification based on supposedly adaptive characters is not automatically suspect. Like any other classification it merely requires corroboration. Adaptively very plastic features may be useful if they show an appropriate range of variation.

Current methods of phylogenetic analysis that treat large numbers of characters do not deal with the intercorrelation of change in characters due to functional or developmental constraints. Such constraints may vary in complex ways with different biological systems. Although I recognize that some characters may be more "important" than others, differential character weighting is not attempted here. In this section it is argued that the complex interactions among characters preclude any rational system for weighting without detailed studies of character transformation - heritablity, epigenetic effects, and functional constraints.

Design or qualitative characters

There is much difference among birds in the way the jaws are used, but in all they are intricate devices for manipulation. Corresponding to the varied uses, the jaw articulation is possibly the most adaptively plastic skeletal feature. Nevertheless the range of variation seems suitable for intergeneric analysis in the Corvidae. The kinetic jaw mechanism of birds includes more broadly the upper jaw and its hinges, the palate, and the quadrate articulations. Among postcranial elements the humerus, particular its complex proximal end, and the tarsometatarsus and toes show discreet variation sufficient to help define larger taxonomic groups.

Attempts here to assess differences in the axial skeleton as discrete characters were frustrated by the variability of design details within a similar frame of shape. In the rib cage and synsacrum the typical species shape is achieved with a great latitude for variation in the number of modules from which each section is built. Thus in the synsacrum the number of vertebrae may have a species mode of seven but individuals may vary in having between six and eight vertebrae. The situation is further complicated because the structural role of component vertebrae varies individually. Special structural roles in the synsacrum are participation in the dorsal section of the ventral acetabular strut. Vertebrae that form part of the dorsal section have a very heavy though short ventral costal process. Typically there are four vertebrae in the dorsal section in corvids but frequently the first vertebra of the sacral section is also involved, often unilaterally. Vertebrae that form an acetabular strut also retain a ventral costal process but it is long and attenuated. Typically this is the third vertebra of the sacral section but frequently it is the second or fourth, or more than one. Trends toward changes in these conditions appear to characterize some taxa but individual variation is so great as to preclude specifying a typical condition for a taxon. Yet the species-typical shape of synsacrum is recognizable.

Assessing shape

Cladistic phylogenetic analysis has neglected intergrading shapes for lack of appropriate ways of treating such continuously varying data. Continuously varying features may be difficult to specify as discrete coded characters. Nevertheless for a variety of organisms, shape seems to have multiple genetic determinants and it may be a powerful systematic indicator.

Differences in lengths of long bones are well known to be adaptively plastic, nevertheless plasticity at lower levels does not obscure trends at higher taxonomic levels within the corvoids.

Quantification and coding of shape

In this study some shape features of cranium, jaws, and long bones were assessed by qualitative descriptors using exemplars of states. A small set of measurements was also made and a few shape features were assessed from those.

It is important to measure shape as distances between homologous landmarks (Bookstein *et al.* 1985). Diameters measured without discreet landmarks are not homologous measures. Comparisons of measurements of width and depth of skull for example, may not refer to comparable distances because of the lack of landmarks for specifying the dorsal limit of the cranium, and the widest points of the cranium may represent expansion of different cranial areas in different taxa. It is just such features lacking landmarks that have been most subject to assessment by measurement. The reason is precisely that discrete design features are not obvious. In passerine birds for example the cranial sutures are almost entirely fused and imperceptible. The cranium is a smoothly rounded dome. The most widely used standard measures in ornithology (Robins and Schnell 1971) are subject to this criticism. It is not necessarily easy to find homologous landmark measurement points.

Use of measured size in phylogenetic analysis requires techniques for coding quantitative differences into qualitative categories. Archie (1985) reviewed the relevant techniques and developed a method of coding by setting interval sizes according to the extent of intra-taxon variation.

Method of analysis

The methods of cladistic phylogenetic analysis are now widely used and understood. However differences remain in details of practice and there are many practical problems in application. Usually the procedure is stated as combining taxa on the basis of shared derived characters. Combining taxa by shared characters, resemblance, without regard to polarity, or primitive state, can be justified only if rates of evolution are equal in all lineages (Farris 1972). Otherwise taxa sharing a large proportion of primitive states will be combined. Also essential to the cladistic method is the idea of parsimony, in which the least elaborate reconstruction of evolutionary change is preferred.

In most current practice, whether or not a character is derived or primitive is determined from character distribution in relatives of the taxon under study. The state that is commonest in related taxa is assumed primitive for the ingroup if it also occurs in the ingroup. Developmental information may be used to indicate the primitive condition, assuming the ontogenetic transformation recapitulates to some extent the sequence of derivation of adult states. Ontogeny may be more useful in study of homology. The philosophy and methods of phylogenetic analysis are discussed by Hennig (1966), Eldredge and Cracraft (1980), and Wiley (1981).

Homology and phylogenetic reconstruction

Recognition of a lineage depends on identifying homologous characters. Homology refers to similar morphology derived by common descent from the same ancestor. Then patterns of shared homologous features are used to infer patterns of descent.

In the enthusiasm for the logical elegance and explicit prescriptions of cladistic analysis, there have been frequent categorical statements that a character is either primitive or derived. Thus levels of homology are not distinguished. Bock (1974) suggested that statements of homology should give the taxonomic level at which homology is inferred, and the nature of the structure compared. Thus the forelimb is homologous among birds <u>as</u> a wing, but confusion arises if one tries to say that the forelimb of tetrapods is homologous <u>to</u> the wings of birds. The latter statement mixes levels of comparison and implies that forelimbs of all tetrapods are homologous to wings of birds.

Viewed in a framework of homology, shared derived character states are homologous at lower taxonomic levels, primitive character states are homologous at higher levels. Thus homologies are nested into increasingly general sets.

The primary criterion for homology should be detailed morphological comparison of the character evaluated. Homology is recognized by corresondence in form, composition, and location of parts (Remane 1956). Recently there has been an emphasis instead on taxonomic pattern to identify or confirm homology. Thus if a character transformation is conflict with the phylogeny, it is assumed homoplastic. But reliance on taxonomic distributional evidence simply displaces the burden of recognizing homology onto other characters.

<u>Character conflict</u>

It is not always possible to distinguish homology from similarity due to parallel or convergent evolution, particularly in closely related forms (Bock 1963), or with characters for which there are only a few alternative states, such as DNA bases (Felsenstein 1982), or if characters are very simple, as Hecht and Edwards (1976) suggested. The result of misidentified homology is character conflict.

With a highly homoplastic data set, the reconstruction of both ancestral and derived states can be ambiguous, since several interpretations of character evolution may be equally or almost equally parsimonious, as Felsenstein (1978) showed, and then parsimonious reconstruction of phylogeny is just as likely to be wrong as right. He showed that parsimonious methods depend on the assumption of equal or very slow rates of change in characters. If rates are very slow the chances of a parallel change are lessened. (However if rates are equal parsimony methods must be identical with similarity methods.) Felsenstein's arguments seem particularly pertinent in the case of large data sets composed of many relatively simple characters for which homology cannot be adequately assessed. This is not the sort of data envisioned in Hennig's early discussions, but it certainly is the sort much used now. Parsimony is likely to be straightforward only if the data set consists of a few complex, carefully analyzed characters.

Assumptions of the parsimony model of analysis

Parsimony may be seen as a model of evolutionary process incorporating only the general idea that simpler explanations are preferred. In the face of much homoplasy there is no simple explanation, there are many equally complicated ones. The noise obscures the message. It is difficult to see how complex constraints resulting from epigenetic and functional interactions among characters could be built into a phylogenetic analysis without further experimental evidence for how the constraints operate. In the present state of knowledge about character transformation, simple parsimonious analysis may be best. Parsimonious analysis may in fact reveal sequence of change in functionally correlated characters simply because the more inclusive or general aspects of a feature (pleisiomorphous states; higher level homologies) must evolve earlier and encompass more taxa than the more specific.

In spite of progress in automated analysis of large data sets, the result should be seen in the light of the assumptions of the methods and limitations of the analytic procedure. The analysis may assist in summarizing patterns but it is not necessarily correct. The data set is the product of the observer and the automated analysis is the product of the computer-driven algorithm.

Evaluation of trees - stability and corroboration

A common result with homoplastic or conflicting data is a set of equally short trees and instability of tree form when new characters or taxa are added. In other cases there are many trees almost as short as the shortest and there is little reason to prefer the very shortest tree.

Some approaches have been made to putting confidence limits on phylogenies by repeatedly resampling and analyzing subsets of the data to determine which parts of a tree are stable. Efron (1979) and Diaconis and Efron (1983) give introductions to bootstrap and jackknife methods. The more exhaustive bootstrap method resamples the data randomly with replacement before each draw, and does a large number of repeated analyses of random samples of the data. The jackknife resamples by successively removing one taxon at a time. Both methods produce psuedoreplicate data sets from which dispersal statistics may be calculated for the quantity that the analysis estimates. These methods are useful when constructing a new sample is not feasible. For phylogenetic analysis the quantity estimated is the branching pattern. Analysis of the resampled sets gives an estimate of the stability of that pattern, which may be expressed as the extent of concordance of the subset analyses.

In reference to phylogenetic data the term "pseudoreplicate" seems inappropriate because of constraints among characters that usually will exist in a complete data set. In drawing a new sample, one may remove or otherwise alter the pattern of constraints. Thus the resampled sets cannot be considered equivalent for the purpose of producing confidence statistics indicating the probable correctness of a phylogeny. Felsenstein (1985) recognized this problem. Nevertheless he justified resampling of characters, stating interdependence may exist typically perhaps only among a third of characters in a data set and corrections may be applied. Interdependence of characters may be more common and complex than Felsenstein estimates. Certainly characters of the jaw articulation in birds, which form a large part of the data set used for corvids in this analysis, are highly interdependent functionally and must impose interacting constraints on change. In turn they affect the shape of the cranium. Similarly characters of fore- and hindlimbs are interdependent. The assumption of independence of characters may simply mask ignorance of their operation in biological systems. Parsimonious analysis may actually succeed in reconstructing the sequences of change as nested subsets of homology, or synapomorphy, but not if higher level changes are deleted at random. Interdependence of characters is of course a serious problem with implications for the analytic method itself, not just the resampling procedure, as discussed earlier. Thus it seems best to avoid resampling characters because the limits of interdependence are not understood.

In an analysis of the avian family Tyrannidae, S. Lanyon (1987) resampled taxa instead of characters, to find out "what subsets of the results are worthy of further discussion." He produced a consensus tree. Resampling taxa simulates altered historical events; for example, removal of taxa could be thought of as a simulation for the effects of differential extinction. When taxa instead of characters are resampled the removal of one may change the tree. Resampling taxa also alters interacting constraints, but in this case constraints are among taxa, and are homoplasy and homology. When taxa are resampled the discrete units involved are understood better.

It turns out that instability affects most the branches of a tree that are very short and close to one another. Thus resampling taxa may reveal the taxonomic loci of homoplasy and the less reliable parts of the tree. Thus although resampling may show which clades are well supported, it seems inappropriate to calculate confidence statistics for the reliability of trees by this means, based on any assumption of random sampling and independence of units sampled.

Corroboration

Thus a tree may be preferred because it is stable in such successive analyses. But a distinction should be made between stability and corroboration. Corroboration refers to independent evidence for correctness of a result. There is some connection between stability and corroboration since a clade will be robust to altered taxonomic context if there is evidence for it from many characters, so that branches are long. But for short branches a result may be stable even though not well corroborated. This can happen simply because there is little contradictory evidence for a particular taxonomic arrangement.

In common phylogenetic practice "well corroborated" refers to a branch of a tree that is supported by many characters in the analysis, but if these characters happen all to be from a single functional complex or if they are developmentally related, that branch is not necessarily well supported. Paradoxically even if the characters are from several complexes, this may not indicate strong support. Isolated simple changes in several different complexes may be suspected of being homoplastic. However when two taxa share very many derived character states of several complexes - when there is detailed resemblance in more than one complex - a long course of common descent is indicated. Thus the nature of characters supporting a clade ought to be evaluated in concert.

External corroboration

It is a common practice in bird studies to include a few odd behavioral characters, into an otherwise "pristine" collection of morphologic characters or vice versa, simply because the author conceives that the extraneous characters are well documented and understood. Most often such extraneous characters are incompletely known. They may be poorly analyzed for homology and polarity. By restricting an analysis to a limited kind of data rather than a heterogeneous mix of characters, results from one set of characters may more intelligibly be compared to another.

METHODS

Taxonomic coverage

Material from as many species of corvids as could be obtained was studied. Skeletal material from all genera was seen except *Zavatarriornis* and *Temnurus*. Material from all species of American jays was seen except *Cyanolyca pulchra*, *Cyanocorax heilprini*, and *C. cyanopogon*. Birds formerly or now thought to be part of the corvoid group were also studied in detail, including the members of the families Corcoraciidae, Grallinidae, Oriolidae, Cracticidae, Artamidae, Paradisaeidae, Campephagidae, and Ptilonorhynchidae. A wide range of other passerines and non-passerines was examined for comparison, with emphasis on the non-passerine orders Coraciiformes, Piciformes, and Cuculiformes. Specimens examined in the Corvidae and the corvoid assemblage are listed in Appendix I.

Variation within the large genus *Corvus* is not considered here in detail. *Corvus* genera used in the analysis of intergeneric relationships were *monedula* representing jackdaws, and *brachyrhynchos* which is representative for all others. Variation within the genera *Dendrocitta*, *Cissa*, and *Urocissa* and several other Malaysian genera could not be adequately studied because specimens are scarce.

Terminology

Names for taxa are those of Peters' Checklist of Birds of the World (1934 - 1987). In general, anatomical terminology is follows Baumel et al. (1979) with some additions from Zusi (1987). I have introduced the following terms: lateral zygomatic crest, subzygomatic sulcus, suprameatic crest and ventral suprameatic crest, jugal brace, palatal flange of the ventral bar of the jaw, and lateral prominence of the lateral cotyla of the mandible.

Selection and coding of characters

Skeletal material from a wide taxonomic range of corvids was examined to find characters that vary qualitatively among species. A protocol was developed for cataloging character states. A wider range of species and specimens was then categorized according to the protocol. Primitive characters of the oscines were assessed from review of specimens of selected oscines, suboscines, and non-passerines, and from a review of literature, using the most parsimonious reconstruction. Primitive characters of corvoids were assessed by comparison with the primitive oscine. Primitive characters for corvids in turn were assessed by comparison with other members of the corvoid assemblage. Complete list of characters coded and the data set for Corvidae are given in Appendices II and III.

Qualitatively varying characters and some shapes were coded in a multi-state scheme according to apparent morphoclines. When more than one morphological transformation series appeared for a character it was either reevaluated as two characters or treated as "unordered" in the analysis (indicated in Appendix II, and see "Analysis" below). The unordered option allows a character to change with equal ease between any two states, but it also weakens the power of the character in the analysis.

Variability within species was treated partly by defining character states in terms that recognize variation. Characters were rejected from the analysis if variation was so great that within many species more than two of the coded states occurred. If more than two states occurred in only a few species, the character was retained and coded as missing data for the extremely variable taxa. For dimorphic characters, if each state was about equally frequent in a species, the character was also coded as missing. In these closely related taxa studied here, the character states coded were often intergrading and variable so that more rigid standards are not possible.

The following measurements were made using a reference series of specimens:

(1) Cranium width at caudal border of the temporal fossa

(2) Cranium depth, basicranium just lateral to the occipital condyle in a line parallel to the posterior wall of the orbit to the roof of the skull

(3) Cranium length, optic foramen to caudal limit of the cerebellar prominence

(4) Rostrum length, optic foramen to the incisure ventral to the ectethmoid at the interorbital septum

(5) Upper jaw depth from the craniofacial hinge to the jugal bar, projected vertically

(6) Upper jaw symphysis, total length

(7) Lower jaw length, from angle of the jaw to caudal limit of the symphysis

(8) Lower jaw length, from caudal limit of the symphysis to the tip

(9) Lower jaw width, dorsal rim at the angle of the jaw

(10) Femur length, intertrochanteric incisure to distal intercondylar incisure

(11) Humerus length, head to distal intercondylar incisure

(12) Humerus head width, dorsal tubercle to ventral tubercle

(13) Tarsometatarsus length, dorsal rim of the medial cotyla to medial intertrochlear incisure

Analysis of measures

Raw measurements were used as input to principal components analysis using the SAS statistical analysis package (SAS Institute 1988). Principal components were extracted from the correlation matrix. All measures contributed heavily to Principal Component-I (jaw measures least, femur most) and it was used as an indicator of size. Linear regression of postcranial measures except femur against PC-I was done and residuals for each measure were coded into discrete values for input to cladistic analysis. PC-I itself was also coded.

Raw measures of cranium and jaw shape showed patterns among taxa that seemed intractable to interpretation. Thus indices of concerted change in shape were sought through separate principal component analyses of these measures. In order to restrict heterogeneity in the data the four measures of cranium shape and five of jaw shape were analyzed separately. Restricting anatomical regions in each analysis makes interpretation of components more straightforward. Again PC-I in each analysis indicated size. Excluding PC-I for these analyses, components were retained that contributed more than 0.025 of the variance, two for cranium shape and three for jaw. Taxa were scored on each component using the scoring procedure of the SAS package and scores were coded into discrete values for input to analysis. Table 1 and Figures 16 through 20 illustrate the procedure.

Coding residuals and principal component scores

In most cases residuals and scores intergraded among taxa so that gap coding into discreet values was not possible. Since the measurements had been done on a reference series no statistics on variation were available that would allow homogeneous subset coding on the basis of intraspecific variation. Therefore coding was designed around intrageneric variation. The most typical (modal) range of variation within genera was determined and that range was assigned two code categories. Extremes in the distribution, e.g. far outliers including five to six percent of the taxa were assigned upper and lower code values and the rest of the range was divided into segments of size equal to half the typical within-genus range.

Since characters assessed from measurement showed extreme variation in the comparison groups the primitive corvid state was estimated by comparison among the Manucodia, Platylophus, and the southern magpies and treepies, which are assessed here later, on the basis of other characters, as earliest lineages of Corvidae. For certain measured characters, however, the Corvidae differed from the comparison groups and were apparently closer to the more primitive oscine condition as inferred from direct observation; in these cases a value most representative (modal) for southern magpies and treepies was used as primitive for Corvidae.

Data Analysis

Data were analyzed initially using the computer program PAUP, "Phylogenetic Analysis Using Parsimony," version 2.4 (Swofford 1985). This program searches for the shortest tree based on distances of taxa from an hypothesized ancestor or outgroup, using the distance Wagner algorithm as described by Farris (1972). Initially the program calculates distances among taxa, then it searches for the shortest unrooted tree connecting taxa. Next the tree is rooted by the specified outgroup or ancestor, along the branch between the two nodes closest to the root taxon. Finally, the character state changes over the tree are reconstructed in such a way that the minimum number of changes is required. Several options allow flexibility in the treatment of characters and in the assumptions used to reconstruct changes. The program will provide tree length, lists of character state changes, synapomorphies of clades, indices of consistency and homoplasy, distance and homoplasy matrices, and a list of branch lengths and branch length ranges possible under alternative reconstructions.

Alternatively a user may construct a tree topology and the program will draw and evaluate the tree statistics.

The consistency index used is that of Kluge and Farris (1969), which is the sum over all characters of the ratio between the path length computed for that character alone and the tree length computed using all characters. The index of homoplasy used is the f-value of Farris (1972) which is the total over all taxa of the difference between intertaxon distance and path length distance. The f-value is normalized by dividing by the total of pairwise intertaxon distances, and the resulting f(norm) then is comparable among trees and indicates to what extent the path lengths on the tree as a whole differ from the taxonomic distances.

The tree form is not affected by the option used for reconstructing character state changes, but branch lengths are affected. I used the DELTRAN option routinely, which is conservative in its assignment of character state changes to early branches of a phylogeny (minimizing interpretation of character changes as parallelism). I also evaluated by inspection all changes assigned by the program and ammended appropriately, since the program at times assigned changes to higher level nodes, and then that character was extremely homoplastic at lower levels, even using the DELTRAN option. Thus in the discussion changes are not cited as support for combining taxa if those characters are very homoplastic within the taxon concerned. To discuss such changes would not illuminate major outlines of the phylogeny.

When a value is missing the analysis ignores that case in computing the intertaxon difference matrix and the unrooted tree.

The reconstructed corvid ancestral states were used to root the tree for analysis of corvid genera. The entire taxonomic set was analyzed and taxonomic subsets were then analyzed bu eliminating one genus or group of genera one at a time. Sixteen total subsets of genera were analyzed. For this analysis only one species of each genus of American jays was included. Additional subset analyses of the American jays, employing all species, were done separately. Results of subset analyses were used to determine which clades were consistently supported in altered taxonomic context and which were disrupted. The taxa affected by altered context are suspected of showing homoplastic changes, as discussed in "Approach." The alternative arrangements that resulted were used to construct alternative tree topologies and were submitted to PAUP to determine tree length, consistency index, and f-normalized.

COMPARATIVE OSTEOLOGY

1. Characters Used and Primitive Oscine States

This section is a general description of the characters used in the analysis and a summary of the primitive states inferred for oscines. Discussions of avian osteology that were useful were those of deBeer (1937), Jollie (1957, 1958), Bellairs and Jenkins (1960), Bock (1964, 1974), Beecher (1953, 1962), Bühler (1981), Baumel et al. (1979), Raikow (1982, 1985), and Zusi (1967, 1984), and a series of papers in a special issue on the noisy scrubbird, Atrichornis clamosus, summarized in the issue by Bock and Clench (1985). Feduccia and Olson (1982) give a series of useful comparisons among Coraciiformes and some perhaps archaic passerines. Cracraft (1968) provided a comparison of the antorbital plate (= lacrimal-ectethmoid complex) in many families of birds. Otherwise conclusions here are based on my survey of skeletal features in passerines and other birds.

If a character state is universal in suboscines and occurs also in oscines this taxonomic distribution is evidence that the state may be primitive to oscines. Comparisons external to passerines are harder to evaluate because there is no agreement about which other birds are the closest relatives of passerines. Interpretations are a parsimonious reconstruction based on occurrence in selected non-passerines particularly in the families Cuculiformes, Coraciiformes, and Piciformes, in suboscines, and in a variety of oscines. Whatever the phylogenetic relationships of these orders the many resemblances may represent shared features primitive to all. Primitive states suggested by this analysis might be subject to revision with a more complete study but nevertheless this survey is presumed to yield better estimates than the idea that the common passerine state is primitive to corvids.

Many of the original bony units of the bird skeleton are obscured by fusion or else by development of new articulations or zones of flexion within preexisting bones. The differences among modern birds can be understood better by recognizing the new units. Figures 2 through 15 illustrate some of the features discussed. Some general preliminary description is necessary.

Skull

In passerines the dermal bones of the roof and sides of the skull are entirely fused to each other and to the chondrocranial elements. The cranium of oscines is relatively large, but unusual enlargement probably is a further derived feature within oscines at the level observed. Proportions of the cranium expressed as length, width, and depth are too varied to allow generalizations.

Primitively the upper jaw probably had a moderately decurved dorsal margin, and its ventral margin was slightly inflected with respect to the jugal arch (about 160-170°). The jaw may have been about as long as the cranium, the tip slightly decurved but not strongly hooked. Extent of ossification of the symphysis and palate are too variable in passerines for forming hypotheses as to the primitive state. The lower jaw was probably rather narrow at the angle of the jaw and may have been about one quarter as wide as long, and the symphysis about one quarter to one third the total length of the jaw. The dorsal margin of the lower jaw flared slightly at the angle of the jaw and in lateral view the lower jaw was slightly inflected at nearly the same angle as the upper jaw. In dorsal view the lateral margin was concave (tapered) beyond the angle of the jaw. The ventral margin of the tip (bony gonys) was slightly convex.

Many aspects of shape of the jaws are nearly universal in passerines but estimates of primitive states for some other shape characters of the jaws are very tentative because of the great variability. In particular the small, weak jaws of various taxa presumed archaic in passerines (Menura, Atrichornis, some suboscines) casts uncertainty on the size of the jaws and on the extent of palatal ossification.

The very large orbits are perforated by numerous foramina for cranial nerves and blood vessels. There are usually large bilateral orbital fontanelles through the postorbital wall and a large fontanelle in the interorbital septum; primitively these fontanelles seem to have been very large. The supraorbital shelf is made up of the fused frontals. The interorbital septum is made up largely of the rostral part of the parasphenoid and a plate from the ethmoid. The ethmoid forms an expanded complex bone beneath the craniofacial hinge. The interorbital septum extends a short way into the nasal capsule but there is a hiatus below the craniofacial hinge to allow bending of the upper jaw on the cranium. There is usually a well developed bony antorbital plate made up of lateral wings of the ethmoid (ectethmoids) and of the prefrontal (lacrimal of most authors). Primitively the ectethmoid did not extend far laterally and did not contact the frontal. The prefrontal was evidently larger than in most contemporary oscines and its plate-like dorsal lobe was situated more dorsally, at the lateral border of the orbit.

Upper jaw

The upper jaw is made up of the premaxillae, the nasals, the maxillae, and the palatines. The fused premaxillae form the rostral part of the jaw. Their paired dorsal nasal processes extend caudally all the way to the frontals. In nestlings they extend even farther, separating the frontals in the midline. Paired lateral processes of the premaxilla form most of the ventral bar of the jaw. The premaxilla also extends more or less onto the palate. The nasals extend from the frontals laterally and form the dorsal and posterior borders of the nostrils. Thus the dorsal nasal bar is constructed from the premaxillae dorsally and the nasals laterally.

In passerines the craniofacial hinge is situated at the juncture of the frontals with the nasals and the nasal processes of the premaxillae. Conspicuousness of the hinge varies greatly. The long suture between the nasal processes of the premaxillae and nasals is usually not fused. The suture between the frontals and the upper jaw may be conspicuous, nearly approaching a true articulation, or may be a simple flexible area of the bone, or may take many intermediate conditions.

In hatchlings the craniofacial hinge is much more prominent, its elements entirely unfused and evidently extremely flexible throughout. Thus a conspicuous hinge in adults is unlike that of juveniles in passerines. In most oscines the craniofacial hinge is rather inconspicuous but evidently alteration toward a more conspicuous hinge has occurred repeatedly or vice versa. Similarly the hinge varies in non-passerines. Primitive states cannot be assessed.

The nostril in oscines is usually oval, rarely more round. The nostril in many suboscines and non-passerines of the primary comparison groups is more caudally elongated. The nostril in oscines primitively was probably oval and less elongated caudally than in most suboscines; more rounded nostrils probably are further derived in oscines. An elongated nostril and flexible nasal bars imply more bending within these structures (Zusi 1984). Rounding of the nostrils and discreet localization of the craniofacial hinge would seem to make the upper jaw of oscines relatively rigid. The hinge itself may nevertheless be a site of great mobility.

Laterally the maxilla is barely or not at all visible, being much reduced from the primitive tetrapod condition. It forms at most a tiny wedge in the suture between the lateral nasal bar and the ventral bar of the jaw, less than in most other birds. Further reduction is derived within in oscines. The maxilla is fused to the jugal arch caudally. This site of fusion is flattened and very flexible. These two bending zones, the craniofacial hinge and the bending zone of the jugal arch, form the primary sites for flexion of the upper jaw on the cranium, but several other rodlike bones in the upper jaw are also more or less flexible in their entirety (Zusi, 1984).

Palate (Figure 8)

The rostral section of the palate is made up largely of a palatal extension of the premaxilla. The extent of its ossification varies greatly. The prepalatine bars of the palatines extend to the premaxilla and fuse with it. In all birds compared, except some corvoids, the prepalatine bars lie close together at their rostral ends and do not lie close to the ventral bar of the jaw. The maxilla evidently forms two structures in the palate. Together with the premaxilla it probably forms part of a palatal flange of the ventral bar of the jaw. This palatal flange contacts the prepalatine bar laterally in a long suture. The two lie in about the same plane in a wide variety of passerines. No comparable structure occurs in comparison groups of non-passerines. The maxilla also extends its maxillopalatine process caudomedially to end just below the tip of the vomer. Details of shape of the maxillopalatines are extremely variable; in a variety of oscines they are inflated at the tips. The huge maxillary sinuses of many birds (e.g. Coraciiformes) are difficult to compare to the tiny maxillopalatines in Passeriformes.

There is frequently a palatine process of the premaxilla between the prepalatine bar and the palatal flange of the ventral bar. This process always is present and large in hatchlings, but is variously reduced and modified in adults. Although a large process is an early developmental stage its presence in adults is not necessarily a primitive condition. The large size in hatchlings suggests a functional role that is lost in adults. Bock (1960) could find no systematic significance for the structure. Differences among adults, including presence of a large process, are evidently secondary and apomorphic at the level observed.

The nasal floor and septum usually are not ossified and probably lack ossification in primitive oscines. The caudolateral lamellae of the palatines lying below the nasal floor are broad plates that serve as attachment surfaces for the pterygoideus musculature. This muscle complex is important in lowering the upper jaw but the jaw muscles in birds have complex coordinated roles in both lowering and raising the jaws (Bock 1964; Buhler 1981; Zusi 1967). In passerines the ventral palatine surface is marked by a usually very shallow sulcus. In all passerines but elsewhere only in hoopoes and woodhoopoes the palatines are provided with transpalatine processes extending from the caudolateral tips of the palatines. The transpalatine processes are usually rather delicate. The transpalatines are very late to ossify in maturing birds. Heavy processes may be assumed derived in oscines.

The vomer is broadened rostrally in passerines. It appears that the broadening is achieved by co-ossification with accessory elements and that the contribution of the true vomer to this structure is a long pointed bone as in other birds. The rostral accessory ossifications form a broadly cupped shovel that seems designed to abut and push the floor of the upper jaw, if one can judge by the conformation in species in which all these structures are well ossified (e.g. Manucodia, Dendrocitta). The vomer is fused to the palatines caudally under the keel of interorbital septum. More caudally the palatines meet the pterygoids in an only partly open suture. This suture is the intrapterygoid hinge developed in post-fledging birds. In hatchlings the (probably) true pterygoid-palatine articulation is more rostral (Jollie 1958). This pterygoid-palatine-vomer chain of bones slides along the ventral keel of the interorbital septum when the quadrate pushes it forward.

Temporal fossa (Figure 8)

The temporal fossa is a prominent lateral depression on the cranium, smaller than in most Coraciiformes and suboscines, bounded by the postorbital process rostrodorsally and the zygomatic process rostroventrally. The postorbital process forms the cranial attachment surface for the postorbital ligament. The zygomatic process is an attachment surface for mandibular adductors. In the probable primitive condition the postorbital process descends from the postorbital wall rostral to it and free of it. The zygomatic process is not very heavy. There is a lateral zygomatic crest that in the primitive condition apparently was elevated above the ventral border of the process. There is a short subzygomatic sulcus that may extend very slightly onto the temporal fossa, rarely farther. The homologies of other crests in the temporal fossa are not traceable throughout oscines without knowing their correspondence to overlying muscles.

Lower jaw articulation (Figure 10)

The quadrate articulates with the skull below the temporal fossa via its dorsal otic process. The otic process bears a medial (otic) condyle that articulates with the periotic and a lateral or squamosal condyle. At the articulation there is often a rudimentary meatic process of the quadrate extending laterally from the quadrate, and a slightly outset suprameatic process of the squamosal.

The ventral articulations of the quadrate are exceedingly complex. The lateral and medial condyles of the quadrate articulate with corresponding cotylas of the mandible. The medial cotyla is a rounded cup with a rostral trough. The lateral cotyla is a raised lateral rim. The lateral cotyla is expanded laterally near the lateral process of the mandible; this expanded area may be called the "lateral prominence of the lateral cotyla of the mandible." The lateral condyle of the quadrate has a corresponding ventral articular surface. The lateral condyle also bears a moderately large abutment against the jugal arch. The abutment on the quadrate lies just dorsal and lateral to the mandibular articular surface of the lateral condyle. This abutment may be called the "jugal brace." The brace is widespread in birds and in most passerines. There is a small caudal condyle and cotyla; their surfaces are continuous with those of the lateral condyle and cotyla.

The lateral process of the mandible is the attachment site for the postorbital ligament descending from the cranium. Also the internal articular ligament of the jaw originates on the lateral process. It traverses the rim of the lower jaw in a well marked groove and attaches on the caudal rim of the mandible. There is usually a sesamoid in this strong ligament. The mandible sometimes produces a keel (retroarticular process) below this groove. The jugal arch articulates on the lateral surface of the lateral condyle of the quadrate. The rodlike pterygoid articulates with the quadrate medially below the orbital process of the quadrate. When the ventral part of the quadrate is pulled forward it slides along the medial and lateral cotylas of the mandible and pushes on the pterygoid. The pterygoid pushes on the palatine and vomer, and these in turn lift the upper jaw. The quadrate may also transmit some lifting force via the jugal arch but this is such a delicate structure that it seems more likely the jugal arch is involved in delicate adjustments of the attitude of the upper jaw rather than heavy pushing.

Primitively the caudal condyle and cotyla probably were very small, and the lateral cotyla a nearly flat, continuous articular surface extending rostrally slightly beyond the lateral process of the mandible. The caudal cotyla probably tilted moderately with respect to the lateral cotyla, to orient rostrodorsally, but the cotyla was not twisted medially. The medial cotyla was probably not extremely elongated and the caudal wall of the mandible was very low or absent. The lateral condyle of the quadrate was about as wide as the otic process or wider, and the jugal arch articulated directly laterally on it. There was a large jugal brace. There was no enlarged retroarticular process.

The basicranium is composed of the exoccipital and the fused basisphenoid and parasphenoid. Its complex foramina for cranial nerves and blood vessels are similar in all passerines.

The ear region (Figure 10 shows some detail) is intimately associated with the jaw articulation. In many oscines, but perhaps not in all, the tympanic membrane attaches to the caudal border of the quadrate, the ventral rim of the squamosal, and the exoccipital. Ventrally it is bounded by the siphonium tube connecting the extensive air spaces of the interior of the cranium and ear region to the interior of the lower jaw. The quadrate, as noted, articulates partly on the periotic. The bulla is made up of the exoccipital and the basioccipital plus a large membranous component. There is little variation in oscines in this basic arrangement, that can be appreciated from a surface view. Some differences simply accomodate changes in the jaw articulation. In the ear region primitively there may have been moderate but not extreme inflation of the squamosal and exoccipital areas. Slightly greater inflation may be derived in oscines, and extreme inflation may be derived within suboscines. The rounded bulla probably extended a short distance along the rather short suprameatic crest.

Postcranial Elements

Humerus (Figure 13)

The complexity of the humerus in birds is related to the great development of flight muscles. Comparison among oscines, suboscines, and non-passerines indicates the proximal humerus was less expanded primitively than in most present oscines. This estimate of a primitive condition of the humerus was incorporated in Wetmore's (1957) arrangement of the passerines. The dorsal and ventral tubercles were relatively close together and there was no ascending sulcus for the dorsal head of the m. humerotriceps. Bock (1962) described the very enlarged sulcus in many oscines, the second pneumatic fossa of the humerus. This is a derived condition in oscines. Sibley, Ahlquist, and Munroe (1988) note that the second pneumatic fossa characterizes their non-corvoid oscines. In oscines the pectoral crest primitively probably was close to the articular head and only moderately wide at its distal end. The biceps crest was angular and its distal margin deeply concave. Distally the sulcus for m. humerotriceps was perhaps broader than in most suboscines but not so wide as the shaft of the humerus. The epicondyles were broader than in most birds but possibly narrower than in most present-day oscines.

Synsacrum

The synsacrum is made up of a variable number of verbebrae fused to each other and to the fused ilium, ischium, and pubes. There are two distinct sections, a narrower "dorsal" section and a broad "sacral" section. The ischia form the lateral walls of the sacral section including the acetabulum for the head of the femur. Coraciiformes, suboscines, and many oscines have three vertebrae in the dorsal section. The number of vertebrae in the sacral section is more variable. Most oscines have eight in the sacral section but exceptions are common.

Tarsometatarsus and toes (Figure 15)

Compared to most other birds the tarsometatarsus in passerines is long and slender. The hypotarsus is uniquely displaced far laterad and the plantar sulcus is shallow and poorly defined. The lateral crest of the tarsometatarsus usually forms a prominent shin on the dorsal surface. The medial crest is recessed far plantarward and is very indistinct. Compared to suboscines and many Coraciiformes, in oscines the first metatarsal articulates slightly more on the medial surface of the shaft. Metatarsal trochlea I does not lie at the dorsal surface of the foot. Except in Menura and some Rhinocryptidae the trochlea for toe II is notched ventrally to accomodate the trochlea of metatarsal I.

Primitively in oscines trochlea II therefore probably was broad and distinctly trochleate in shape and articulated partly on the plantar and partly on the medial surface of metatarsal I.

In a condition described by Feduccia and Olson (1982) for some Rhinocryptidae and Menura, but also in my comparisons found to be common to a wide variety of oscines including among those I examined Cinclosoma, Turdus, Gracula, Corcorax, and all Corvidae, toes III and IV articulate with each other by a substantial epicondyle on toe III and notch on toe IV. Where this condition occurs, usually also the first phalanx of toe IV is one-half to two-thirds the length of the first phalanx of toe III. Where the notch is absent toe IV is longer. The occurrence of this complex character in a diverse array of passerines including some suboscines indicates the character is primitive for oscines. Woodhoopoes (Coraciiformes) have a similar conditon.

COMPARATIVE OSTEOLOGY

2. Comparison Groups of Corvoid Birds

Corvoid birds most similar to corvids are described here, with notes on others. Throughout, discussions of shape and size may be clarified by reference to Figures 16 through 20 (but see interpretation of principal componenets in "Review of Osteology"). Features described are illustrated in Figures 2 through 15. Descriptions here focus on characters important to this study.

Parker (1872) described development in the crow's skull. Shufeldt (1888) described osteology of North American corvids and compared them to Icteridae. His 1890 study of the myology of the raven and 1925 description of the osteology of *Grallina* are also relevant. Stonor (1937) and Bock (1963) gave detailed descriptions of the skull and jaws of birds of paradise and bower birds. Ashley (1941) provided a key to North American corvids based on the proximal humerus. Two studies of limb myology give information that helps in the interpretation differences in postcranial osteology (Hudson and Lanzilotti 1955; Borecky 1977).

Platylophus (crested jay or shrike jay)

The nominal corvid *Platylophus galericulatus* is described here as a basis for comparisons between corvids and other corvoids. Osteologically *Platylophus* greatly resembles the manucodes among the birds of paradise and yet its jaylike behavior and external appearance have resulted in its current, though questioned, systematic placement in the Corvidae. The juxtaposition of features has suggested describing this poorly known bird as a standard for initial comparisons. This description is based on only two specimens that were available.

Skull and jaw shape (Figure 2): The cranium of *Platylophus* is deep and dorsolaterally more expanded than in most oscines. The skull is robust in appearance but is more highly pneumatized than is usual in oscines. The bulla extends far rostrally along the suprameatic crest, almost to the quadrate articulation. The middle ear region is similar to that of most oscines but fenestration of the periotic is more extensive, concommitant with greater pneumatization of the entire skull. The basicranium is similar to that of other oscines. The orbits are approximately as deep as long. The postorbital and interorbital fontanelles are slightly smaller than in most oscines. The numerous formina within the orbit for cranial nerves and blood vessels are typically passerine. Deep sulci on the caudal wall of the orbit and the interorbital septum mark the origins for jaw muscles. The supraorbital shelf is moderately wide.

The upper jaw is deep at the base and highly inflated. The dorsal profile of the upper jaw is nearly straight. The nostril is shorter than in most oscines but is ovate, not round. It is partly covered by superficial ossified membranes of the external nares. The upper jaw is less inflected ventrally at the angle of the jaw than in most oscines. The ventral margin of the upper jaw is almost straight.

The ramus of the mandible is moderately deep. The dorsal rim of the mandible flares laterally at the angle of the jaw much more than in most passerines. As in most oscines and suboscines, in dorsal view the tip of the lower jaw is slightly tapered. In lateral view the tip of the lower jaw (bony gonys) is deeply convex. In frontal view the tip is deeply cupped. The symphysis of the lower jaw is longer than in most passerines.

Craniofacial hinge: The craniofacial hinge is moderately conspicuous but does not form a true articulation. The frontals are slightly inflated at the hinge. The nasal processes of the premaxilla are unusually wide and heavy, forming a slight boss just in front of the craniofacial hinge.

Maxilla: The lateral nasal bar is broad and inflated and obscures the maxillopalatines from lateral view. The sutures of the maxilla are entirely fused and obscured.

Nasal capsule: The nasal septum is heavily ossified. The nasal capsule is short. The ectethmoid is wide, reaching and fusing to the frontal. Its dorsal lobe is moderately inflated. Ventrally it forms a wide, rounded lateral flange. No prefrontal is apparent. In some other birds of this assemblage that are most similar to *Platylophus* vestiges of an ossified margin indicate a prefrontal is present but not ossified.

Palate (Figure 9): The premaxilla is extensively but not densely ossified in the rostral part of the palate, and ossification extends caudally between the prepalatine bars and slightly below the nasal capsule, but the ossification does not meet ventrally in the midline. The prepalatine bars are relatively broad and flat. The lateral rim of the prepalatine bar contacts extensively the narrow palatine flange of the ventral bar of the jaw. The rostral end of the prepalatine bar is in a slightly more lateral position than in most oscines. The palatine process of the premaxilla is not visible.

In an unusual condition for oscines the lateral border of the palatine is straight as it extends back to form the transpalatine. The transpalatine is stout. The ventral palatine fossa for attachment of retractor muscles is very deep, slightly undercutting the preprepalatine bar and extending far forward along it. The caudal border of the palatine is moderately decurrent from the parasphenoid rostrum its margin extending diagonally toward more rostral the transpalatine. This is the common passerine configuration. The tip of the maxillopalatine is stubby and not broadly inflated.

The vomer is long. Its shaft is very narrow and the tip flares widely. The prominent rostral accessory ossifications appear to be designed to fit around the caudal end of the ossified palate when the vomer is pushed forward. The pterygoid-palatine hinge and the pterygoids resemble those of most passerines.

<u>Temporal</u> <u>fossa</u> (Figure 10): In most respects the lower jaw articulation is not distinctively different from that of many oscines and resembles the form nearly universal in suboscines. The squamosal, exoccipital, and periotic are more highly pneumatized than in most oscines but less so than in suboscines. The postorbital process descends rostral to the caudal wall of the orbit. The caudal wall of the orbit is inclined rostrodorsally from the jaw articulation. The suprameatic crest is moderately wide but narrows rostrally and is not outset laterally at the

quadrate articulation. The zygomatic process is short and broad and moderately elevated above the quadrate-squamosal articulation. The subzygomatic sulcus is poorly defined but evidently extends caudally only slightly past the articulation.

Quadrate articulations (Figure 12): The dorsal quadrate articulation is as in the hypothetical primitive oscine. The otic process of the quadrate is very slender and moderately tall. The mandibular articulation shows no unusual features but the cotylas for the quadrate are moderately deep. There is a large jugal brace. The rostral trough of the medial cotyla of the mandible is short. The jugal arch articulation is elevated and displaced caudally on the lateral condyle. There is a low caudal wall of the mandible. The lateral cotyla of the mandible is oriented approximately dorsally and there is a smooth transition from its surface to the dorsal rim of the ramus of the mandible.

Humerus (Figure 13): The head of the humerus between dorsal and ventral tubercles is wider than in suboscines but not so wide as in many oscines. This moderate widening seems to be related to the slight expansion of the dorsal head of m. humerotriceps, as indicated by the small sulcus ascending dorsal to the triceps fossa toward the head of the humerus and slightly undercutting it. The triceps fossa is fenestrated. The head of the humerus is rather small and the pectoral crest is only slightly recessed distally from it. The pectoral crest is short and widely outset from the shaft of the humerus distally, but the crest is not large. Just distal to the triceps fossa there is a very large, deep, rounded depression, in diameter about equal to the triceps fossa. This seems to be the attachment site for the m. scapulohumeralis cranialis; it is extremely large. The distal end of the humerus is broad. The sulcus for the distal end of m. humerotriceps is moderately wide, about as wide as the shaft. The crest separating this sulcus from the sulcus for m. scapulotriceps is only moderately distinct. The sulcus for m. scapulotriceps is half as wide as that for m. humerotriceps. The dorsal supracondylar process is not elongated. The ventral epicondyle is wide and is slightly rotated toward the cranial surface. The flexor process is short, not extending much past the distal end of the ventral condyle. The fossa for m. brachialis is deep.

Synsacrum: The dorsal surface of the synsacrum from the acetabulum to the tip of the caudolateral process of the ilium is a little longer than broad. There are four vertebrae fused into the dorsal section and seven vertebrae making up the sacral section of the synsacrum (eleven total in the synsacrum).

Tarsometatarsus and toes: The tarsometatarsus is much shorter and broader than in most other oscines. The medial crest is very wide. There is a deep plantar sulcus and a very well defined extensor sulcus. The first metatarsal articulates more on the medial surface of the shaft of the tarsometatarsus than in most oscines. The shaft forms a conspicuous bulge on its dorsal surface, surrounding the first metatarsal articulation. The distal trochlea of the first metatarsal lies approximately in the same dorsoventral plane as the trochleae for the other digits (in the articulated specimen ANSP 38106), thus lying much farther dorsal than is typical for oscines. This position is probably natural for intact specimens, as indicated by the conformations of the trochleae for digits I and II and the heavy cartilage pads intercalated among the metatarsals and toes. The trochlea of metatarsal II is less notched than in most oscines.

Paradisaeidae (birds of paradise)

Among the Paradisaeidae the cnemophilines stand out as being different (*Cnemophilus*, *Loria*, *Loboparadisaea*). Bock (1963) noted their differences from the other birds of paradise and implied that they had many primitive features. They are so distinct in morphology, (and also in behavior, M. LeCroy, pers. comm.), that I have not used them in comparisons for this study. *Lyccocorax* is also very distinctive but is much more similar to the typical birds of paradise. Remaining genera of Paradisaeidae are readily compared to each other, although they are diverse. Among these, the manucodes most resemble *Platylophus*, and *Paradisaea* is representative of the typical birds of paradise. This description focuses on comparison to *Platylophus*.

Skull and jaw shape (Figure 2): Compared to *Platylophus*, *Manucodia* is larger and the bill is longer, but otherwise *Manucodia* greatly resembles *Platylophus*. In *Paradisaea* the jaws are narrower, longer, sickle shaped, attenuated at the tip, elongated, and sharply inflected downward with respect to the cranium. In both, the cranium is elongated. Both resemble *Platylophus* in the pronounced lateral flare of the dorsal rim of the mandible. The cranium is less pneumatized in *Paradisaea*. The nostril is less elongated, approaching being round, in *Paradisaea*.

Craniofacial hinge: The craniofacial hinge is even more conspicuous than in *Platylophus* and the nasal processes of the premaxilla are very wide. In *Paradisaea* the hinge is very conspicuous and may approach being a true articulation.

Nasal capsule: The nasal septum and floor are heavily ossified but the ossification in the floor is not complete. The ectethmoid is hugely inflated. In *Manucodia* and *Paradisaea* the prefrontal is rudimentary or lacking as in *Platylophus*, but some other members of the Paradisaeidae have a moderately large, markedly bilobed prefrontal lying rostral to the ectethmoid along the lateral border and partially expanded into the nasal capsule dorsally, much as in most passerines.

Palate (Figure 9): In *Manucodia* the rostral palate is very similar to that of *Platylophus* but is ossified slightly farther caudally. In *Paradisaea* the palate is more densely but less extensively ossified. In both, the palatine process of the premaxilla is adnate but not entirely fused to the prepalatine bar; sutures are visible. The prepalatine bars are more medial than in *Platylophus*. Otherwise the structure of the palate, including vomer, palatines, and maxillopalatines, is similar to that of *Platylophus*.

Temporal fossa: The subzygomatic sulcus is long, extending nearly to the bulla in *Manucodia* and past it in *Paradisaea*. The suprameatic crest is outset at the quadrate-squamosal articulation forming a narrow shelf. The shelf does not articulate with a meatic process of the quadrate. Otherwise *Manucodia* and *Paradisaea* resemble *Platylophus*.

Quadrate articulations: The quadrate articulations are similar in *Manucodia* and *Platylophus*. In *Paradisaea* the lateral prominence of the lateral cotyla of the mandible is tilted slightly caudolaterally.

Humerus: The shape of the shaft and proximal end of the humerus in *Manucodia* and *Paradisaea* is as in *Platylophus* but the humerus in Paradisaeidae is much longer. The sulcus for origin of m. scapulohumeralis cranialis is very large but not huge, as in *Platylophus*. *Synsacrum*: Typically there are twelve synsacral vertebrae, eight in the sacral region.

Tarsometatarsus and toes: Paradisaeidae share the peculiar configuration of the tarsometarsus and toes seen in *Platylophus*. The plantar sulcus is similarly wide and deep but the dorsal extensor sulcus is shallower.

Oriolidae (Old World orioles)

The genus Oriolus is representative of the Oriolidae. Skull and jaw shape: In overall shape the skull is rounded, not unusally elongated, and less robust than in Platylophus and Paradisaeidae. The cranium is less pneumatized. The jaws are long and narrow and only moderately deep. The dorsal profile is moderately decurved but the ventral border is approximately straight. The upper jaw is inflected less than in most oscines with respect to the cranium. The craniofacial hinge is conspicuous and nasal processes of the premaxilla are wide. The nostril is ovate or nearly round. The lower jaw tapers distally and the dorsal rim of the ramus flares widely at the angle of the jaw but not quite so much as in Platylophus and Paradisaeidae.

Nasal capsule: The nasal septum is heavily ossified. The ectethmoids are highly inflated. The prefrontal is displaced into the nasal capsule and is poorly ossified.

Palate: The rostral ossified palate is long but ossification is not dense. There is a wide palatal flange of the maxilla contacting the lateral rim of the prepalatine bars. The bars are far medial in a more typically oscine position than in Platylophus. They lie in the same plane as the ventral bar of the jaw. The palatine process of the premaxilla is adnate but not entirely fused to the prepalatine bar. The palatines and prepalatine bars are lightly built, and the transpalatines flare laterally slightly and are attenuated into a short delicate tip. The ventral fossa of the palatine is not well marked. Although the symphysis of the upper jaw is long, the palatal ossification extends only slightly below the floor of the nasal capsule. The floor of the nasal capsule is not ossified and the septum is only lightly ossified. The tip of the maxillopalatine is broad but not expanded. The shaft of the vomer is broader and more rounded than in *Platylophus* and very long and widely flared rostrally. The nasal capsule is long and the vomer does not approach the ossified rostral palate in the retracted upper jaw, as it does in *Platylophus*. Evidently elongation of the jaw in Oriolidae occurred at least partly in the region of the nasal capsule, and not entirely rostral to the angle of the jaw.

Temporal fossa and lower jaw articulation (Figure 12): The postorbital process descends rostral to the orbital wall as in *Platylophus*, but it is longer. The caudal wall of the orbit is inclined rostro-dorsally. The zygomatic process is short. The lateral zygomatic crest is slightly elevated but is continuous with an outset suprameatic crest. The subzygomatic sulcus is confined to the zygomatic process. The cranium is more than usually inflated around the ear region but less so than in *Platylophus*. The mandibular articular cotylas for the quadrate are shallower than in *Platylophus*. Otherwise the jaw articulation is similar.

Humerus, synsacrum, tarsometatarsus, and toes resemble those of Paradisaeidae.

Cracticidae (currawong, bell magpie, butcher bird)

All three monotypic genera of Cracticidae are very much alike but the smallest, *Cracticus*, is most like other corvoids and is described here.

Skull and jaw shape and nasal capsule: The cranium is most similar in shape to that of *Oriolus*, except that jaws are extremely long and are very deep at the base, and the entire nasal capsule is very heavily ossified, including not only the midline septum but also the nasal conchae. There is much peripheral superficial ossification about the nostrils. The skull is not unusually pneumatized but the jaw and ossified membranes of the nasal capsule as well as the lateral nasal bars are highly inflated. The craniofacial hinge is only moderately conspicuous. Nasal processes of the premaxilla are wide and heavy, forming a very conspicuous boss just rostral to the craniofacial hinge. As in *Platylophus* and *Manucodia* the dorsal and ventral profiles of the upper jaw are approximately straight, and the jaw is not much inflected with respect to the cranium.

Palate: As in *Oriolus* but even more extreme, both rostral and nasal segments of the palate are very long. The nasal floor is entirely ossified but is separated from the rostral palate by a gap. Thus the premaxilla is not co-ossified with the nasal floor. There is no palatal flange of the ventral bar of the jaw. The prepalatine bars are close together. The palatine process of the premaxilla is not visible. The tip of the maxillopalatine is very broad and flat but not expanded. The shaft is co-ossified with the nasal floor. The shaft of the vomer is stout, rounded, and very long but not unusually broad rostrally. The tip of the maxillopalatine appears be lightly fused to the vomer.

The transpalatines are very long and attenuated beyond the palatines. The lateral rim does not form a heavy bar. The ventral palatine fossa is short and shallow. The caudal border is deeply decurrent.

Temporal fossa and jaw articulation: The temporal fossa is most like that of Oriolus but there is a double zygomatic process. The new process lies medial to the first. The lateral zygomatic crest is continuous with the suprameatic crest. The suprameatic crest is directly over the ear region and is widely outset and well defined as in Oriolus. The bones around the inner ear are not excessively inflated. The squamosal wall descends ventral to the suprameatic crest and meets the caudal face of the quadrate. The lateral prominence of the lateral cotyla of the mandible faces medially and the caudal cotyla is steeply tilted to face rostrodorsally and slightly medial. The medial cotyla is shallow and short. There is a large jugal brace.

Humerus: The humerus is very long, more even than in Paradisaea and Manucodia. The proximal end is much as in Paradisaeidae.

Synsacrum: The synsacrum typically has only eleven vertebrae, seven in the sacral section.

Tarsometatarsus and toes are similar to those of Oriolidae and Paradisaeidae.

Other corvoid birds

The Artamidae (wood swallows) share the unusual structure of the zygomatic process seen in *Cracticus* and the skull and palate are otherwise similar in design elements although very different in shape. Pycraft (1907) was evidently the first to associated these two families. Howell (1982) reported osteologic evidence for their affinities. Sibley and Ahlquist (1985) also placed them with the cracticids.

Campephagidae (cuckoo shrikes) have not always been included in the corvoid assemblage but Sibley and Ahlquist place them as part of the sister group of corvids. I found Campephagidae are diverse osteologically and thus full description is not attempted here. *Pteropodoces* is similar to *Oriolus*. *Coracina* has a very large broad jaw and associated with that many apomorphic conditions. The palate and skull are similar to those of *Oriolus*. These campephagid genera share the unusual structure of the tarsometatarsus and toes described for *Platylophus*. In *Pteropodoces* the palate is much as in the hypothetical primitive oscine and the tarsometatarsus is not unusually broad or short. Toes III and IV do not interlock and toe IV is relatively long.

Although they are very different superficially, *Corcocax* and *Struthidea* nevertheless seem to be correctly associated. These two genera have a relatively inconspicuous craniofacial hinge. In *Struthidea* the upper jaw is deep, short, and strongly decurved and hooked, and the nasal capsule is heavily ossified. In *Corcorax* the upper jaw is narrow, elongated, and sickle shaped. In both, the palate is very heavily ossified rostrally and the prepalatine bars are far medial. The palatine process of the premaxilla is large and not entirely fused to the lateral rim of the prepalatine bar. The palatal flange of the ventral bar of the jaw is conspicuous only in the wider-jawed *Struthidea*. In both, there is an elongated ventral palatine sulcus, as in *Platylophus*. The jaw articulations of these genera are very similar. The rather long tarsometatarsus is much as in the hypothetical primitive oscine but metatarsal I articulates a little more medially on the shaft of the tarsometatarsus. Toes III and IV interlock. The suprameatic crest is elevated above the quadrate articulation and continuous with the wide, sharply defined lateral zygomatic crest. The squamosal forms a vertical lamina below the suprameatic crest. The lamina meets the otic process of the quadrate on its caudal face.

In *Grallina* the wide, conspicuous craniofacial hinge that appears to be a true articulation that traverses the entire distance across the hinge. Uniquely the dorsal profile of the upper jaw is concave. The jaws are very shallow. The temporal crests are similar to those of *Struthidea* and *Corcorax* except for a prominent crest running from the elevated suprameatic crest to the quadrate articulation. The tarsometatarsus is as in Corcoracidae but is very long and the first metatarsal is farther plantar.

The lateral and medial crests of the tarsometatarsus are well defined but not wide and there is no conspicuous plantar or extensor sulcus. The tarsometatarsus is long. The hind toe is slightly more medial and plantar than in many oscines but not so much so as in Platylophus. The third and fourth toes have a conspicuous interlocking articulation at the base.

The Ptilonorhynchidae retain a variety of primitive oscine characters lost in most other oscines. Several resemblances to Menura may be primitive oscine features, including wide supraorbital shelf, large, plate-like, dorsally situated prefrontal, small caudal cotyla of the quadrate, very large cranial fontanelles, and a narrow proximal and distal humerus. Osteologic evidence thus suggests separation of the bower birds from the corvoid assemblage, but wider comparisons would be needed to infer relationship of Ptilonorhynchidae to Menuridae or any other oscines.

COMPARATIVE OSTEOLOGY

3. Corvidae - Treepies, Piapiac, Green Magpies, Blue Magpies, Black Jay

Dendrocitta, Crypsirina, Temnurus (treepies)

The six species of Dendrocitta are similar externally. Skeletal material was available only for the species formosae and vagabunda. Of the two externally very similar species of Crypsirina only temia was available. Crypsirina is osteologically similar to Dendrocitta, except for smaller size and slight differences as noted below. Skeletal material for the genus Temnurus was not available for examination. X-rays of skulls in skin specimens were done but revealed little detail. As far as could be determined Temnurus resembles the other treepies.

Skull and Jaw Shape (Figure 2): The cranium in Dendrocitta is more expanded dorsolaterally than that of Platylophus and not quite so deep. The skull is similarly extensively pneumatized. Despite the pneumatization the skull is robust. The jaw is very deep, wide, short, and markedly decurved, and the ventral border of the upper jaw is strongly hooked at the tip. The upper jaw is moderately inflected ventrally at the angle of the jaw. Crypsirina is similar but is smaller and more delicately built. The nostril is ovate or nearly round in Dendrocitta, more than in Platylophus, and is entirely round in Crypsirina. The upper jaw is highly pneumatized. The ramus of the mandible is deep. Its dorsal rim does not flare unusually, as it does in Platylophus. The tip is broad and in dorsal view the lateral margin is only slightly incised. The tip is moderately cupped.

Craniofacial hinge: The craniofacial hinge is similar to that of Platylophus. The frontal boss is conspicuous.

Lateral nasal bar: The lateral nasal bar is highly pneumatized and sutures to the maxilla and ventral bar of the jaw are completely fused, as in Platylophus. In Crypsirina the symphysis of the lower jaw extends far caudally between the rami of the mandible.

Nasal capsule: The nasal capsule is short. The ectethmoid reaches and fuses with the frontal and is slightly inflated dorsally in *Dendrocitta* but not in *Crypsirina*. The prefrontal is vestigial, absent, or unossified. In some specimens there are small ossified remnants of a separate prefrontal, so it does not appear to have disappeared by fusion with the ectethmoid. The nasal septum is ossified.

Palate (Figure 9): The rostral part of the palate is relatively long but ossification does not extend between the prepalatine bars. The nasal floor is elevated far above the rostral part of the palate and is ossified and co-ossified with the shaft of the maxillopalatine. The tip of the maxillopalatine is not expanded. The vomer tip flares broadly, as in *Platylophus*, but the vomer shaft is somewhat wider and much shorter. The tip abuts directly the ossified nasal floor. The prepalatine bars, transpalatines, and palatine plate are as in *Platylophus* except that the prepalatine bars contact the ventral bar of the jaw at their rostral ends. The palatine process of the premaxilla is not visible.

Temporal fossa and lower jaw articulation (Figure 10): The lower jaw articulation differs from that of *Platylophus* in several ways. The postorbital process descends farther caudally, along the lateral rim of the orbital wall. The zygomatic process is very heavy and is wedge shaped in lateral view. In *Dendrocitta* but not in *Crypsirina* a large subzygomatic sulcus emerges and extends far caudally onto the temporal fossa. In *Crypsirina* the suprameatic crest is slightly elevated above the quadrate articulation. In both, the suprameatic crest is short and the bulla extends forward along it. The suprameatic crest is outset laterally more than in Platylophus and contacts a small meatic process of the quadrate. The quadrate-mandibular articulation resembles that of Platylophus except that the lateral prominence of the lateral cotyla of the mandible is tilted so that the articular surface faces caudodorsally. In Dendrocitta, particularly in the one specimen of D. formosae seen, the lateral prominence is strongly tilted and greatly enlarged so that it is almost a separate articular facet. In lateral view the caudal cotyla of the mandible is less tilted than in most oscines, its surface oriented more dorsally.

Humerus (Figure 13): The humerus resembles that of Platylophus. There is a deep, round depression for the attachment of the m. scapulohumeralis cranialis distal to the triceps fossa, comparable to the large depression in paradisaeids but not so deep as in Platylophus.

Synsacrum: The synsacrum typically incorporates eleven vertebrae. Its dorsal surface is rounded and about as wide between dorsolateral iliac crests as it is long (acetabulum to caudolateral process). The iliac crests converge caudally and the distance between the caudolateral processes is typically about half to two thirds the distance between the iliac crests more rostrally.

Tarsometatarsus and toes: The tarsometatarsus is short, as in Platylophus. However, there are no enlarged plantar or extensor sulci. The shaft is moderately tapered as in most oscines. Metatarsal I articulates partly on the plantar and partly on the medial surface of the shaft, but it is not in such a far dorsal position as it is in Platylophus. There is a very slight bulge around the base of metatarsal I, suggesting the much more pronounced condition in Platylophus. The distal trochlea of metatarsal I lies farther toward the dorsal surface than in the hypothesized primitive oscine condition but not nearly so far plantar as in Platylophus. The trochlea for toe II is slightly notched by the trochlea for the hallux. Toes III and IV interlock at the base.

Ptilostomus (black magpie or piapiac)

The monotypic genus Ptilostomus is distinctive among corvids but is osteologically most similar to the treepies.

Skull and jaw shape (Figure 2): The cranium lacks the extensive pneumatization seen in Platylophus and treepies. The frontal boss is not so heavy as in Dendrocitta and Crypsirina, and the craniofacial hinge is less distinct. The dorsal and lateral nasal bars are inflated and the nostrils are round as in treepies.

The upper jaw is extremely inflated rostrally as in treepies but instead of being very short is greatly elongated. This combination gives Ptilostomus a profile that has led to comparisons with Corvus but the two are entirely different in structural detail and design. The jaws in Ptilostomus are elongated by extension rostral to the nasal capsule. The nasal capsule is short. The jaws of Ptilostomus are very narrow and the quadrates articulate far medially under the cranium.

The symphysis of the lower jaw is very short. The upper jaw is not hooked at the tip as in treepies. The ramus of the mandible is moderately deep along its entire length but is not heavily constructed. The tip of the lower jaw is deeply cupped. In dorsal view the jaw is not incised laterally.

Craniofacial hinge: The craniofacial hinge is less conspicuous than in Dendrocitta or Platylophus and the nasal processes of the premaxilla are not so wide.

Lateral nasal bar: The lateral nasal bar is inflated and sutures to the maxilla are entirely obscured by fusion.

Nasal capsule: The nasal septum is moderately ossified. The antorbital plate is much as in Dendrocitta. The nasal capsule is very short.

Palate: The palate is similar to that of Dendrocitta. The rostral ossification of the premaxilla is similar in form and the nasal floor is similarly ossified, but the floor of the nasal capsule is even more extremely elevated. The palatine bars lie much farther lateral than in Dendrocitta, but they are reduced to thin rods. The palatine process of the premaxilla is not visible. The transpalatines are long and delicately attenuated. The ventral fossa of the palatine is elongated as in Platylophus and Dendrocitta but it is shallow. The vomer is long and the shaft is moderately broad. It is pointed rostrally because the co-ossified accessory parts are recessed caudolaterally, thus the vomer is very atypical among passerines. The tips of the maxillopalatines are not ossified. Noting the lack of ossification of the prefrontal, but the occasional presence of vestiges of it, lack of ossification of the maxillopalatines, and lack of ossification of the rostral accessory parts of the vomer, it seems likely that all these structures associated with the nasal capsule are present but not ossified.

Temporal fossa and lower jaw articulation: The postorbital process is as in _Dendrocitta_. The zygomatic process is rather small and is oriented more nearly vertically than in other corvoids. Evidently the mandibular adductors attach close to the quadrate-mandibular articulation. There is no subzygomatic sulcus. The very short suprameatic crest is projected as a ventrolateral shelf. Rostrally it meets the quadrate rather low and ventrolaterally on the otic process, otherwise the dorsal quadrate articulation is as in _Dendrocitta_. The quadrate is slender, as in _Platylophus_ and _Dendrocitta_, but is taller. In lateral view, the caudal cotyla of the mandible is strongly tilted to orient rostrodorsally. The lateral and medial cotylas are much as in _Platylophus_.

Humerus: The humerus is very short. The fossa for attachment of m. scapulohumeralis cranialis is smaller and more nearly distal to the ventral tubercle than in the treepies or Platylophus. The pectoral crest is moderately long, continuing distally down the shaft beyond the attachment site for m. pectoralis. The distal end of the humerus is much as as in treepies but the dorsal supracondylar process extends a little farther proximally along the shaft.

Hindlimb: The synsacrum and tarsometatarsus are similar to those of Dendrocitta but the tarsometatarsus is very long. The toes are unique among corvids. They are very long and slender, except that the phalanges of the fourth toe are all extremely short and broad. Toes III and IV interlock (as in all corvids).

Cissa (green magpies)

Of the two species of Cissa only chinensis was examined. Externally the species are very similar. Specimens of chinensis differed substantially in details of the suprameatic crest. Specimens were too few to determine if the differences were characteristic of populations.

Skull and jaw shape (Figure 4): Cissa is much larger than the treepies. The skull is very robust but the cranium is shaped much like that of Dendrocitta. The supraorbital shelf is broad and the frontals are inflated rostrally. The jaw is longer, very heavy, and less pneumatized than in Dendrocitta. The upper jaw is deep and strongly decurved and hooked at the tip but this decurvature is much less extreme than in Dendrocitta. The nostrils are ovate. The symphyses of upper and lower jaws are both long. The jaws are very broad. The ramus of the mandible is deep and the tip is deeply cupped. In dorsal view the lower jaw is not incised laterally.

Craniofacial hinge: The craniofacial hinge is relatively inconspicuous. The nasal processes of the premaxilla are very narrow.

Nasal Capsule: Ossification of the nasal septum is moderate. The prefrontal is ossified and is moderately expanded into the nasal capsule. The ectethmoid is as in Dendrocitta.

Lateral nasal bar: The lateral nasal bar is not unusually inflated and the maxilla is visible in the suture between the lateral nasal bar and the venral bar of the jaw. It is conspicuous laterally.

Palate: The rostral part of the palate forms a long ossified symphysis of the upper jaw, with the ossification extending back slightly between the prepalatine bars and below the nasal capsule. The palate is less pneumatized than in Platylophus and Dendrocitta. The palatal flange of the maxilla is sharply inflected to meet the lateral edge of the prepalatine bar, which lies more ventral and lateral than in treepies and non-corvids. The palatine process of the premaxilla is not visible. The transpalatines are expanded laterally and their surface is excavated or notched laterally, apparently for muscle attachment surface. The medial border of each transpalatine is well defined but does not extend rostrally along the medial border of the prepalatine bar; instead it traverses the palatine plate diagonally. The caudal border of the palatine is less decurrent than in treepies. The vomer is short and broad the the tip flares broadly. The tip of the maxillopalatine is not ossified.

Temporal fossa, lower jaw articulation (Figures 10, 11 12): The suprameatic crest is very heavy and at its juncture with the quadrate it extends laterally as a wide suprameatic process which articulates with a meatic process of the quadrate. Viewed ventrally the suprameatic crest is very wide, in some specimens tapering toward the quadrate and in others widening toward the quadrate, both medially and laterally. None of the available specimens were wild caught or carried information about locality of information so that it was not possible to determine if difference have systematic significance. The quadrate is shorter than in Dendrocitta but the otic process is similarly slender. The lateral prominence of the lateral cotyla of the mandible is enlarged and widely outset and strongly tilted; the form is similar to that of Dendrocitta but less extreme.

Humerus: The humerus is very short. The pectoral crest is moderately long, its dorsal crest continuing down the shaft of the humerus well past the attachment area for m. pectoralis. The area of attachment for m. scapulohumeralis cranialis is not deep or unusually large. The distal sulcus for m. humerotriceps is narrow. The epicondyles are small and not very broad.

Synsacrum (Figure 14): The sacral section of the synsacrum is rather long, and typically the synsacrum includes twelve vertebrae rather than eleven as in many corvids.

Tarsometatarsus and toes: The tarsometatarsus resembles that of *Dendrocitta* and *Ptilostomus* but is intermediate in length. The feet are very stoutly made and the interlocking articulation of toes 3 and 4 is very well developed.

Urocissa (blue magpies)

Urocissa is most like *Cissa*. *Urocissa* magpies are very large. Osteologically the species *erythrorhyncha* and *flavirostris* are very similar. The species *caerulea* is larger, with a more robust skull. The species *ornata* and *whiteheadii* were not available for study.

Skull and jaw shape: The skull and jaws are large and heavily built. The cranium and jaws are deep and otherwise similar in form to *Cissa* but the jaws are more elongated, the upper jaw is less decurved and hooked, the nostril is longer, and the supraorbital shelf is slightly narrower. The frontals are less inflated at the craniofacial hinge but the craniofacial hinge is similarly very narrow.

The lateral nasal bar is similar in *Cissa* and *Urocissa*.

Palate: Compared to *Cissa* the rostral palatal ossification is similar but slightly more dense. The maxillopalatine tips are ossified and slightly expanded in some specimens. Otherwise the palate is as in *Cissa*.

Temporal fossa and lower jaw articulation: The temporal fossa and dorsal articulations of the quadrate are as in *Cissa* but the ventral view of the suprameatic crest does not show quite such a heavy development as in some specimens of Cissa. The body of the quadrate is as in Cissa. The mandibular facets for the quadrate are shallower than in Cissa and the lateral prominence of the lateral cotyla is not tilted. The caudal cotyla is only slightly tilted.

Humerus: The humerus is relatively longer than in Cissa but still shorter than in the treepies. The distal sulcus for m. humerotriceps is wide. The flexor process is short, extending only slightly beyond the condyles.

Synsacrum: The synsacrum is long and typically has twelve vertebrae as in Cissa. The tarsometatarsus and toes are also similar.

COMPARATIVE OSTEOLOGY

4. Corvidae - American Jays

In the succeeding descriptions, comparisons are primarily to Southeast Asian magpies and treepies. Throughout, this account follows Zusi's (1987) description of the rostral articulation and suprameatic process but adds details I observed on the suprameatic crests. Description here incorporates my own view of the homology of the suprameatic crests.

Cyanolyca (neotropical montane jays)

The species of Cyanolyca are more diverse osteologically than their external features suggest. All are relatively small, but some are the smallest corvids, approached only by the diminutive representatives of the scrub jay, Aphelocoma coerulescens, from the Florida Keys.

Cyanolyca cucullata and *C. viridicyana* are largest in the genus; smaller species are *pulchra*, *mirabilis*, *argentigula*, *nana*, and *pumilo*. The species *pulchra* was not available for study. R. Zusi examined the jaw articulation by opening a skin from the collection at USNM and found it had a well developed rostral crest of the lateral cotyla of the mandible, as in the species *cucullata* and *viridicyana* described here.

Cranium and jaw shape (Figure 4): The cranium in larger *Cyanolyca* species is deep and the orbit is short. In *Cyanolyca cucullata mitrata* the cranium is robustly made. The supraorbital shelf and the cranium are wide and are extensively pneumatized. In *C. c. cucullata*, a smaller subspecies from Costa Rica, the cranium and suprorbital shelf are slightly narrower and less inflated. In the other species the cranium is more gracile, less inflated, and appears to be narrower. Measurements are ambiguous as reflected in the principal components coded (discussed in "Review of Characters").

The upper jaw is moderately deep, long, moderately decurved dorsally, and hooked at the tip, except that in *nana* the jaws are shallow. The jaws are widest and deepest in *cucullata*. The quadrate is at least slightly inset medially in all, but is more obviously inset in *viridicyana* than in *cucullata* and is deeply inset in the smaller species, articulating well under the skull. The jaws are correspondingly much narrowed in the smaller species. The lower jaw is deeply cupped at the tip and the bony gonys is convex (*nana* not checked).

Craniofacial hinge: In *cucullata* and *viridicyana* the craniofacial hinge is similar to that of the southern magpies but in the smaller species the nasal processes of the premaxilla are slightly wider. There is a moderate frontal boss in *cucullata* but not in the other species.

Nasal capsule: In *C. c. mitrata* there is diffuse ossification about the border of the nostril and moderate ossification of the interorbital septum but in others the nostril is entirely open and the nasal septum is only lightly or not at all ossified. The nostril is oval. The prefrontal is variable, being not much inflated or else unossified in some specimens of *cucullata*, only moderately inflated in *viridicyana* and lying along the lateral border of the ectethmoid, but moderately expanded and inflated into the nasal capsule in the smaller species.

Lateral nasal bar: In *cucullata* the lateral exposure of the maxilla at the base of the nasal bar is very similar to the condition in *Cissa* and *Urocissa* except that the ascending process of the maxilla is very large. In other species the maxilla is less or not at all exposed laterally. *Palate*: In all, the symphysis of the upper jaw is very long but not densely ossified. At its rostral end the prepalatine bar meets the ventral bar of the jaw but does not fuse with it except in *cucullata*. The palatal flange of the ventral bar of the jaw is inflected and meets the prepalatine bar not on its lateral edge but instead on its dorsal surface. The palatine process of the premaxilla is not visible. The transpalatines are much as in _Cissa_ and _Urocissa_. The tip of the maxillopalatine is expanded in most specimens, but is distinctly inflated only in the smaller species. The vomer is moderately long and only moderately broad. Rostral accessory ossifications are less prominent than in treepies.

Temporal fossa and lower jaw articulation (Figures 10, 11, 12):

The zygomatic process is moderately long in _cucullata_ and _nana_ but is shorter in other species. The suprameatic crest is reduced in width and slightly to moderately elevated above the quadrate-squamosal articulation, least in _cucullata_. The suprameatic crest is only faintly visible except in _viridicyana_. The lateral zygomatic crest is confluent with the suprameatic crest just caudodorsal to the squamosal-quadrate articulation and there is often a ridge present defining the caudal boundary of the subzygomatic sulcus, descending to the quadrate articulation. The ridge is most distinct in _viridicyana_.

The squamosal forms a ventral wall below the elevated suprameatic crest. The ventral wall of the squamosal meets the quadrate caudally or caudolaterally. The ventral border of the ventral wall of the squamosal may be called the "ventral suprameatic crest". In most specimens the ventral suprameatic crest is slightly enlarged where it meets the quadrate, forming a small suprameatic process. This enlargement evidently is not homologous as a rostral expansion of the more dorsal suprameatic crest to the suprameatic process in *Urocissa* and *Cissa*. Nevertheless this suprameatic process of the ventral suprameatic crest articulates with a meatic process of the quadrate that is indistinguishable in all.

In ventral view the ventral suprameatic crest is much narrower than the crest bounding the ear region in southern magpies and treepies. In *Cyanolyca* the medial rim of the crest, to which the tympanic membrane attaches, is straighter, extending for most of its length approximately parallel to the lateral rim. In *cucullata* the crest is widest in *cucullata*. The squamosal cotyla of the otic articulation is narrowed by a small process of the squamosal, which projects onto the cotyla, forming a small abutment. In overall form the quadrate is relatively tall and delicately built, not much different from that of *Cissa* or *Urocissa* except in scale. As in those genera there is a large jugal brace and the lateral condyle is wide. However, the medial condyle is unusually long. In some species the articular surface of the lateral condyle shows a medial expansion apparently for articulation with the high rostral slope of the lateral cotyla of the mandible. In some specimens of *cucullata* and *viridicyana* there is also a more medial crest on the base of the quadrate.

There is a well defined rostral crest on the rostral slope of the lateral cotyla of the mandible. The rostral slope is long. The crest is highest in the species *nana*, *cucullata*, and *viridicyana*. In *cucullata* there is sometimes an accessory ossification situated on the dorsal rim of the crest. This small ossification resembles in position and caudolateral orientation of its face the larger rostral cotyla of the mandible of other American jays (described by Zusi 1987). The ossification in cucullata appears to be homologous as a rudimentary rostral cotyla of the mandible to the larger cotyla of other American jays.

In the species viridicyana the rostral trough of the medial cotyla of the mandible is elongated and undercuts the median eminence. The elongated medial condyle of the quadrate has an enlarged lateral surface that slides through this undercut channel of the medial cotyla.

Humerus: The humerus is very short in all species (nana not measured) except in pumilo, but is not relatively shorter than in Cissa. As in Cissa, in some species of Cyanolyca the pectoral crest continues distally down the shaft. The head of the humerus and the pectoral crest are not enlarged. The depression for attachment of m. scapulohumeralis cranialis is large but slightly smaller than in treepies. The distal sulcus for m. humerotriceps is narrow. The epicondyles are only moderately wide and the flexor process is rather long. The depression for origin of m. brachialis is variable in depth.

Synsacrum: The synsacrum incorporates eleven vertebrae in the species cucullata and argentigula but only ten (six in the sacral region) in specimens seen of viridicyana, pumilo, and nana.

Tarsometatarsus and toes: The medial crest of the tarsometatarsus is a thin, sharply defined ridge, recessed less toward the plantar surface than in other corvids so far considered. In most specimens the crest is abruptly tilted toward the dorsal surface of the shaft near the proximal end. Toes III and IV interlock.

Cyanocorax (neotropical lowland jays, in part)

Based on osteology species of Cyanocorax may be grouped for discussion as follows:

(1) the violaceus group including species violaceus, cyanomelas, and caeruleus

(2) the affinis group including species affinis, cristatellus, cayanus, and chrysops

(3) mystacalis and dickeyi

(4) yncas.

Specimens of heilprini and cyanopogon were not available.

Cranium and jaw shape (Figures 5, 6): Jays in the nominal genus Cyanocorax usually have a short, deep orbit (shallower and longer in the species cyanomelas) and a deep and wide cranium and jaws. The cranium is not unusually pneumatized. The interorbital and postorbital fontanelles are smaller than in Cyanolyca, Urocissa, or Cissa. The violaceus group are very large jays, with a massive skull; the shape is most nearly like that of Urocissa. The orbit and cranium are deep. The other Cyanocorax jays all are smaller, many with a slightly narrower cranium and jaws. The species yncas is smallest.

The supraorbital shelf is about as in Urocissa in the larger species but is narrower in the smaller species. The dorsal profile of the jaw is moderately decurved and the tip is moderately hooked. The bony gonys is convex and the tip is moderately cupped. The symphysis of the lower jaw is moderately long, by extension caudally between the rami, not by rostral elongation.

Craniofacial hinge: The craniofacial hinge is very inconspicuous, with narrow nasal processes of the premaxilla, recessed slightly between the frontals.

Nasal capsule: The nasal septum is moderately ossified in large to medium size species but lightly or not at all ossified in smaller species. The ectethmoid is similar to that of most corvids. The prefrontal is ossified but not expanded into the nasal capsule, lying along the lateral rim. In individual specimens the prefrontal is often vestigial.

Lateral nasal bar: The maxilla is excluded from the lateral surface of the jaw at the base of the lateral nasal bar. In the violaceus group the ascending process of the maxilla is rather large.

Palate: The rostral palatal ossification is dense. The symphysis of the upper jaw is long in the violaceus group, slightly shorter in the affinis group, and in mystacalis and dickeyi, and is very short and very densely ossified in yncas. The nasal floor is not ossified, except peripherally in the violaceus group. The tip of the maxillopalatine is ossified and partly inflated. It is squarish in shape. The vomer is moderately wide and only moderately broadened rostrally.

The prepalatine bars are very far apart and the rostral ends are fused extensively to the ventral surface of the ventral bar of the jaw, nearly as far as the maxillopalatine. The palatal flange of the ventral bar of the jaw is present only as an inconpicuous vertical lamina or rounded bulge descending to meet the prepalatine bar on its dorsal surface. The palatines are heavy and similar to those of Urocissa. The transpalatines usually have a pit on the tip. The caudal margins of the palatines are irregular but not steeply decurrent from the parasphenoid rostrum.

Temporal fossa and lower jaw articulation (Figures 10, 11, 12): Several new features of the jaw articulation occur in Cyanocorax. Details of differences in the jaw articulation appear in a mosaic fashion among the included species and there is much intraspecific variation.

The temporal fossa is moderately large and is well defined. The zygomatic process is shorter than in Urocissa. In the species mystacalis and dickeyi it is very short. The lateral zygomatic crest is faint in most specimens and variable in location. A crest may be present in the temporal fossa but it is always faint and its location is inconsistent, except in yncas, where although faint the crest is usually present and similar in form and location to that of Cyanolyca viridicyana. Thus except in yncas the identity of the crest bounding the bulla cannot be directly confirmed. There is a strong presumption that this is the homolog of the ventral suprameatic crest in Cyanolyca, but this identification depends on evidence for the monophyly of Cyanocorax. The ventral suprameatic crest is more widely set out laterally than in Cyanolyca. When two crests are present the dorsal and ventral crests are confluent near the bulla. The ventral crest is variable in width and lateral definition both within and among species. In ventral view the suprameatic crest is wide. In the violaceus group it narrows rostrally, as in Urocissa. In all other species it widens rostrally. In yncas it also narrows in midsection. In all except the violaceus group the squamosal produces an abutment against the otic process of the quadrate as in Cyanolyca cucullata. In all, compared to southern magpies and treepies the ventral crest is narrower at the bulla and straighter. There is a large suprameatic process probably of the ventral squamosal crest but as explained above the homology of the suprameatic crest forming the process is unclear. The suprameatic process articulates with an enlarged meatic process of the quadrate lateral to the squamosal cotyla of the otic articulation.

The otic process of the quadrate is widened and appears short. The body of the quadrate is shortened. The medial condyle of the quadrate is moderately long but shorter than in Cyanolyca. The lateral condyle is narrower.

There is a large rostral condyle (c.f. Zusi 1987) of the quadrate, smallest in the violaceus group, intermediate and variable in the affinis group, and large in the others. The rostral condyle is situated on the base of the quadrate just medial and slightly dorsal to the lateral cotyla. Its articular surface is continuous or nearly so with that of the lateral condyle. The jugal brace is small in the *violaceus* group and is very small, variable in size, and often absent in the others. In *violaceus* and *cyanomelas* there is usually a well defined crest on the quadrate medial to the rostral articulation, similar in appearance to the medial crest in *Cyanolyca*. The rostral condyle of the quadrate is designed to oppose a rostral cotyla of the mandible when the quadrate is pulled forward. The medial cotyla of the mandible is deep and its rostral trough is short. In caudal view the caudal cotyla of the mandible is often tilted far medially but this surface is individually variable. In lateral view the caudal cotyla of the mandible faces slightly rostrodorsally.

All species have a conspicuous rostral cotyla of the mandible. This new articular surface appears on the dorsal rim of the rostral crest of the lateral cotyla. In all, the rostral condyle and cotyla are larger than in *Cyanolyca* but are relatively small and variable in size in the *violaceus* group. The rostral condyle and cotyla are larger and farther caudal in some specimens in the *affinis* group but these features are variable individually in this group. The condyle and cotyla are consistently large in *chrysops*, *yncas*, *mystacalis*, and *dickeyi*, and the cotyla is situated more caudally so that the rostral slope of the lateral cotyla is shortened, and the lateral cotyla is narrowed (for fuller description see Zusi op.cit.).

Humerus: The humerus has a relatively long pectoral crest extending down the shaft, and in general appearance it is much as in Urocissa, but the distal sulcus for m. humerotriceps is narrow. In the species caeruleus the humerus is very long. The head and pectoral crest are not widened unusually. The epicondyles are wide. The flexor process is short.

Synsacrum: The synsacrum is relatively long, incorporating twelve vertebrae (eight in the sacral section) in most species, but only has eleven vertebrae in chrysops and yncas.

Tarsometatarsus and toes: The medial crest of the tarsometatarsus is only moderately recessed. The tarsometatarsus is slightly tapered distally. The toes are typically corvid.

Psilorhinus

The monotypic Psilorhinus (morio) is the largest jay. Osteologically it is much like the violaceus group of Cyanocorax. It has a slightly narrower cranium and slightly greater rostral enlargement of the suprameatic process.

Calocitta

The northern subspecies C. formosa colliei, is much larger than the nominate and other more southern subspecies. Details of suprameatic and rostral crests differed among specimens but specimen localities were scattered so that I could not tell if differences were characteristic of localities or individuals.

Calocitta is most like the affinis group of Cyanocorax but differs distinctively from that group in osteology as much as in plumage. The jaws are very long and narrow though remaining deep and otherwise shaped as in Cyanocorax. The rostral articulation of the jaw is moderately well developed and the cotyla is moderately tall but uniquely narrow. The suprameatic process is well developed but variable in size.

The synsacrum is shorter than in most Cyanocorax, typically with eleven vertebrae. The tarsometatarsus is very short. Otherwise Calocitta is like Cyanocorax.

Cissilopha (neotropical lowland jays, in part - Central American lowland blue jays)

The three species of Cissilopha and particularly the species melanocyanea are most similar osteologically to Cyanocorax mystacalis and dickeyi. Descriptions here of Cissilopha sanblasiana refer to the eastern subspecies C. s. yucatanica since no specimens for the nominate subspecies were obtained. These two forms have often been separated as species. All statements made about the osteology of Cyanocorax species mystacalis and dickeyi apply also to Cissilopha melanocyanea except the synsacrum in Cissilopha incorporates only eleven vertebrae. In sanblasiana and beecheii the cranium is narrowed and it is shallower and appears longer, and the jaw is long. In the species sanblasiana the lateral zygomatic crest height and zygomatic process length are extremely variable among specimens, even from the same locality. There is some correspondence to size of the specimen. The species *beecheii* is much larger than the other two and its jaw is very long.

Aphelocoma, *Cyanocitta*, *and* *Gymnorhinus* (North American jays)

The genera of North American jays are much alike osteologically and differ distinctively from other Aemrican jays. These are small to medium sized jays. The smaller species resemble *Cyanocorax* *yncas* in design details of osteology. *Aphelocoma* *unicolor* is largest of the group and has cranium proportions and details somewhat more like those of the larger *Cyanocorax* jays.

Skull and jaw shape (Figure 5): The skull is more gracile than in *Cyanocorax* but is densely ossified. In all except *Aphelocoma* *unicolor* and *Cyanocitta* *cristata* the cranium is wider and shallower; in *Aphelocoma* *ultramarina* and *Gymnorhinus* the cranium is very broad and shallow. The orbit is elongated, particularly in *Cyanocitta* and *Aphelocoma* *ultramarina*, and it is extremely long in *Gymnorhinus*. The jaws are narrowed and in most species they are slightly to moderately elongated (not in *Cyanocitta* *cristata* and Florida populations of *Aphelocoma* *coerulescens*, moderately in *Aphelocoma* *unicolor*, *A*. *ultramarina*, western populations of *A*. *coerulescens*, *Cyanocitta* *stelleri*, most in *Gymnorhinus*). The upper jaw is shallower than in *Cyanocorax* and has a straight dorsal profile. The tip is less decurved. The ventral profile of the lower jaw is less convex. In *A*. *ultramarina* and more extremely in *Gymnorhinus* the ventral border of the lower jaw is straight. In all, the to[pf tje lower jaw is less cupped than in other American jays, and it is very p[em in *A. ultramarina* and *Gymnorhinus*. The symphysis of the upper jaw is short and very densely ossified, particularly in the last two species. The tip is blunt and rounded in *Gymnorhinus*.

Craniofacial hinge: The nasal processes of the premaxilla are wider than in *Cyanocorax* and are very wide in *Aphelocoma ultramarina* and often in *Gymnorhinus*. The nasal processes of the premaxilla are sometimes recessed between the frontals but this is not consistent.

Nasal capsule: The nasal septum is not ossified. The ventral lobe of the prefrontal is more expanded than in *Cyanocorax*. The ectethmoid is as in most other corvids except that it is slightly tilted in the forms with an elongated orbit.

Lateral nasal bar: The maxilla is excluded from the suture at the base of the lateral nasal bar and its ascending process is small.

Palate: The rostral palate is very densely ossified and does not extend below the nasal capsule. The prepalatine bars are as in *Cyanocorax* but are more distinct rostral to the maxillopalatine partly because of lack of ossification between them in this area. The maxillopalatines are well inflated and elongated to a caudal point; they are narrower than in *Cyanocorax*. The vomer is similar to that of *Cyanocorax* but narrower.

There is a large pit on the ventral surface of the transpalatine; its size and shape varies individually. The caudal margin of the palatine is irregular and only slightly decurrent. The ventral fossa is as in Cyanocorax. Temporal fossa and lower jaw articulation (Figure 10, 11, 12): The postorbital process is recessed along the lateral wall of the cranium. In ventral view the ventral suprameatic crest is wide at the squamosal-quadrate articulation but is somewhat narrowed in midsection (not narrow in Gymnorhinus). The suprameatic precess is very large. The squamosal abutment against the otic process of the quadrate is conspicuous, particularly in Gymnorhinus and Aphelocoma ultramarina. The appearance of the temporal fossa including crests is very similar to that of Cyanolyca viridicyana and Cyanocorax yncas. The dorsal suprameatic crest is slightly visible in some specimens of all species of North Americn jays but is most conspicuous in Gymnorhinus and in Aphelocoma ultramarina. In these species it is well separated from the ventral crest for its entire length; the bulla extends dorsally to meet the dorsal suprameatic crest separate from the ventral crest.

In Aphelocoma coerulescens, Cyanocitta stelleri, and to an extreme extent in A. ultramarina and in Gymnorhinus the ventral suprameatic crest is elongated caudally, notching the bulla. The zygomatic process is very short in all except Gymnorhinus. The caudal boundary of the subzygomatic sulcus forms a distinct crest in many specimens and particularly in the latter two species. In Gymnorhinus and sometimes slightly in other species the ventral end of this crest is enlarged, forming a dorsomedial lobe of the very large suprameatic process (Figure 10).

The quadrate is stout in all, but especially in *Gymnorhinus*. The meatic process is large. The rostral articulation of the jaw is large and is like that of *Cyanocorax yncas*. The jugal brace is rudimentary or absent. In lateral view the caudal cotyla of the mandible is nearly flat. In caudal view it is twisted so that the articular surface is oriented medially in *Aphelocoma* and in some specimens of *Cyanocitta*. It is twisted to face far medially in *Gymnorhinus*. In *Gymnorhinus* there is a large retroarticular process projecting beyond the caudal cotyla of the mandible, lateral and ventral to the groove for the internal articular ligament of the jaw.

Humerus: The pectoral crest does not extend as a ridge down the shaft of the humerus beyond the prominent attachment site for m. pectoralis, except in *Gymnorhinus*. The head of the humerus is very wide in *Cyanocitta cristata*, *Aphelocoma ultramarina*, and *Gymnorhinus*. The distal sulcus for m. humerotriceps is widened, particularly in these later species.

Synsacrum, tarsometatarsus, and toes: The synsacrum typically incorporates eleven vertebrae but sometimes has twelve in *Aphelocoma ultramarina*; the synsacrum is rather broad in all. The tarsometatarsus is much as in other American jays but more slender, and the medial crest is usually well defined. The toes are as in most corvids.

COMPARATIVE OSTEOLOGY

5. Corvidae - Northern Magpies, Eurasian Jays, Boreal Jays, Crows, Nutcrackers, Choughs, Ground Jays

Garrulus (Eurasian jays)

Although Garrulus is moderately diverse in external features, nevertheless species are similar osteologically. Within the genus the species lidthi is most like Urocissa.

Skull and jaw shape (Figure 3): Compared to Urocissa the cranium is much the same shape but the jaws are very short. The frontals are more narrowed over the orbit. The dorsal nasal bar is not unusually heavy and the nostrils are oval. The upper jaw is deep except in lanceolatus, with both dorsal profile and ventral border straight, without a hooked tip. The lower jaw is very wide. The tip of the lower jaw is deeply cupped and the bony gonys is strongly convex. The symphyses of both lower and upper jaws are very short.

Craniofacial hinge: The nasal processes of the premaxilla are wide. The hinge is not unusually conspicuous and there is no frontal boss.

Lateral nasal bar: The maxilla is recessed entirely within the nasal cavity.

Nasal capsule: The nasal septum is not ossified. The antorbital plate is similar in Garrulus and Urocissa.

Palate (Figure 9): The rostral palatal ossifications are very dense and are confined to the area rostral to the prepalatine bars. The palatal flange of the ventral bar of the jaw is very narrow or absent. The prepalatine bar is fused to the ventral bar of the jaw all the way to the maxillopalatine. At the maxillopalatine its lateral rim lies along the medial border of the ventral bar of the jaw. The prepalatine bars are very far apart. The maxillopalatine is inflated at the tip and elongated with a rounded caudal toe and lateral and rostral flaring wings. The lateral crest of the palatine is not heavy and the transpalatines are only slightly flared laterally. The ventral fossa is shallow. There is a tiny ventral pit on the transpalatine in some specimens. The caudal border of the palatine is straight and extends directly laterally from the midline.

Temporal fossa (Figure 10): The postorbital process is as in *Urocissa*. The zygomatic process is wedge shaped as in *Urocissa* but longer. The lateral zygomatic crest is not elevated. The suprameatic crest is elevated well above the quadrate articulation. The crest is only faint rostrally but is wide caudally and continuous with the bulla. The wall of the squamosal ventral to the crest meets the quadrate on its caudal surface. There is no expanded suprameatic process. In the species *lidthi* the lateral zygomatic crest and suprameatic crest are at separate levels. In the species *lanceolatus* the subzygomatic sulcus shows a distinct boundary a little caudal to the quadrate articulation. Juvenile specimens of the species *glandarius* are like this, but in adults the two crests are continuous without indication of the caudal border of the subzygomatic sulcus. Thus the crests are comparable in position and contacts with those of *Cyanolyca viridicyana* though differing slightly in form. The bulla extends above the caudal limit of ventral rim of the squamosal wall (= ventral suprameatic crest).

Quadrate articulations (Figure 12): The dorsal articulations are as in Urocissa. The quadrate is slightly stouter than in Urocissa but otherwise similar. There is a large jugal brace. The lateral prominence of the medial cotyla of the mandible is tilted so that the articular surface of the cotyla orients mediodorsally. The very wide apart quadrate articulations seem to be designed so that the lateral condyles of the quadrate are confined by these medially tilted surfaces. The rostral channel of the medial cotyla of the mandible is a little longer than in Urocissa and is very long in glandarius.

Humerus: The humerus is short in the species lidthi but is long in glandarius. The pectoral crest is moderately long but does not extend down the shaft. The proximal sulcus for the dorsal head of m. humerotriceps is only moderately large except in lanceolatus where it extends to the head of the humerus and undercuts it slightly. Distally the humerus in G. lidthi is much as in Urocissa but in G. glandarius and in G. lanceolatus it is wide. In glandarius the flexor process is strongly rotated toward the ventral surface.

Synsacrum: The synsacrum typically includes eleven vertebrae. It is very wide betweem the dorsolateral iliac crests.

Tarsometatarsus and toes: Compared to *Urocissa* the tarsometatarsus is similar in form but is slightly shorter. The toes are typically corvid.

Perisoreus (boreal jays)

The two species of *Perisoreus* examined are very similar externally and osteologically. No osteologic specimens were available for *P. internigrans*.

Skull and jaw shape (Figure 8): A remarkable feature of the small *Perisoreus* jays is their very large cranium. Otherwise in overall shape of skull and jaws *Perisoreus* resembles *Garrulus*. The skull in *Perisoreus* is less heavily constructed than in *Garrulus*. The supraorbital shelf is narrow. The upper jaw is shallow at the base. The dorsal profile is straight and the ventral border of the upper jaw is nearly straight. The lower jaw is cupped distally and the bony gonys is shrongly convex. As in *Garrulus* the symphysis of the upper and lower jaw is very short and the jaws are short.

Craniofacial hinge: The craniofacial hinge resembles that of *Garrulus*.

Nasal Capsule: The nasal septum is not ossified. The prefrontal is not much expanded, lying mostly along the rostrolateral rim of the ectethmoid. The ectethmoid is typically corvid.

Lateral nasal bar: The maxilla is excluded from the lateral surface of the jaw.

Nasal capsule: The nasal septum is not ossified.

Palate: The symphysis of the upper jaw is very short and densely ossified. The prepalatine bars are far apart and lie ventromedial to the ventral bar of the jaw but are not so extensively fused to it as in Garrulus. The palatal flange of the ventral bar of the jaw is present but is obscured by the underlying prepalatine bar. The maxillopalatine tip is expanded but not much inflated and is square in shape with the inflation on the medial side. The vomer is short, flaring moderately at the tip. The lateral crest of the palatine flares widely at the transpalatine process but there is no lateral excavation for pterygoideus musculature, nor is there a terminal pit. The caudal border is straight or irregular and extends almost directly lateral from the midline.

Temporal fossa (Figure 10): The temporal fossa is similar to that of Garrulus but the suprameatic crest is not heavy and the zygomatic process is smaller. The ventral suprameatic crest is elongated caudally, notching the bulla.

Quadrate articulations (Figure 12): The quadrate is much as in Garrulus but not so robust. There is a large jugal brace. The suprameatic crest meets the quadrate on its caudal face as in most specimens of Garrulus. There is no suprameatic process. The articulations are similar to those of Garrulus but the lateral prominence of the lateral cotyla is not tilted medially.

Humerus: The humerus is similar to that of Garrulus and as in G. lanceolatus there is a relatively large sulcus for the dorsal head of the humerotriceps. The flexor process is not strongly rotated.

Synsacrum: The synsacrum is as in Garrulus but in some specimens there are twelve vertebrae included. It is very wide between the dorsal iliac crests.

Tarsometatarsus and toes: The tarsometatarsus is tapered slightly as in Garrulus but the medial crest is only very slightly recessed from the dorsal surface and the crest is well defined. Some specimens of Perisoreus have a very large medial epicondyle of the first phalanx of digit 2. Otherwise the toes are as in most other corvids.

Cyanopica (azure-winged magpie)

The two widely separated populations of Cyanopica cayana from Spain and eastern Asia differ little either externally or osteologically.

Skull and jaw shape (Figure 8): Cyanopica is small, comparing in size to Perisoreus, and shares many of the features of Perisoreus and Garrulus in which they all differ from the Southeast Asian magpies Cissa and Urocissa, but Cyanopica and Perisoreus are rather different from each other. In Cyanopica the cranium is relatively longer and shallower than in Perisoreus. The orbit is elongated. The supraortital shelf is narrow. The jaws are relatively longer and narrower than in Perisoreus. The dorsal and ventral margins of the upper jaw are nearly straight. The tip of the lower jaw is less deeply cupped.

Craniofacial hinge: The dorsal nasal bar is not heavy and the nasal processes of the premaxilla are moderately wide.

Nasal capsule: The nasal capsule and antorbital flange are as in *Perisoreus*.

Lateral nasal bar: The maxilla is prominent in the suture at the base of the lateral nasal bar and is visible at the lateral surface.

Palate: The maxillopalatines are as in *Perisoreus* . The transpalatines are expanded and notched laterally but are not pitted. The caudal border of the palatine is often irregular but never deeply decurrent.

Temporal fossa and jaw articulation (Figure 10): The temporal fossa is smaller and less well defined than in *Garrulus* and *Perisoreus*. The zygomatic process and crest and suprameatic crest are much as in *Perisoreus*. As in *Perisoreus* the ventral suprameatic crest is long and notches the bulla. The quadrate is only moderately heavy and is shaped much as in *Perisoreus*. There is a large jugal brace. The ventral suprameatic crest is usually projected ventrolaterally and often is enlarged rostrally to form a very small suprameatic process of the ventral crest. The medial cotyla of the mandible is long. There is an elevated rostral crest of the lateral cotyla that is never so high as in its greatest development in *Cyanolyca*, although the appearance of the crest is similar.

Humerus: The humerus is similar to that of *Garrulus*. It is wide distally and the ventral epicondyle is slightly rotated toward the dorsal surface.

Synsacrum: The synsacrum is moderately wide but less than in *Garrulus* and *Perisoreus*. Typically it incorporates only eleven vertebrae, seven in the sacral section.

Tarsometatarsus and toes: The medial crest of the tarsometatarsus is at the dorsal surface. It is well defined so that there is a shallow extensor sulcus. The shaft is not at all attenuated distally. The toes are typically corvid.

Pica (common magpie, yellow-billed magpie)

Aside from differences in size the widespread holarctic magpie *Pica pica* is similar osteologically throughout its range and very similar to the yellow-billed magpie of California (*P. nuttalli*).

Skull and jaw shape (Figure 3): The cranium in *Pica* is shaped much as in *Garrulus*. The jaw is long, narrow, shallow at the base, and inflated rostrally. Its dorsal profile is moderately decurved and the ventral profile is slightly decurved at the tip. The symphysis of the lower jaw is very short. The quadrates are slightly inset medially.

Craniofacial hinge: The craniofacial hinge is usually only moderately conspicuous and the nasal process of the premaxilla moderately wide. There is no frontal boss.

Nasal capsule, antorbital flange: The nasal septum is not ossified. The antorbital flange is as in *Garrulus*.

Lateral nasal bar: The maxilla forms a wedge in the suture at the base of the lateral nasal bar but is sometimes not exposed laterally because it is covered by the lateral process of the premaxilla.

Palate: The rostral palate is much as in *Urocissa* but less caudally extended. The ossification is only moderately dense. The prepalatine bars are farther lateral than in *Urocissa* but less extensively fused to the ventral bar of the jaw than in *Cyanopica*. The palatal flange of the ventral bar of the jaw is obscured by the underlying prepalatine bar but it is inflected and meets the prepalatine bar on its dorsal surface. The transpalatines are expanded laterally by a moderately large pit on the ventral surface. The medial border of the transpalatine runs diagonally across the palatine plate and is well defined. The caudal border is irregular but not deeply decurrent. The maxillopalatines are as in *Garrulus*.

Temporal fossa and jaw articulation (Figure 12): The temporal fossa is very small and is recessed in conjunction with the medially inset quadrate. The suprameatic crest is very high but not conspicuous; it is only a rough ridge. There is a hiatus between the lateral zygomatic crest and the suprameatic crest. The zygomatic process is smaller than in *Garrulus*. Many specimens have a small suprameatic process of the ventral suprameatic crest of the quadrate and its articulations are much as in *Cyanopica*. There is usually a rostral crest of the lateral cotyla of the mandible. Samples of *Pica* were large enough to suggest that presence and height of the crest is varies among populations.

Humerus (Figure 13): The humerus is moderately long and the pectoral crest is very long, extending distally down the shaft beyond the m. pectoralis attachment site. The proximal crests, fossas, and tubercles and the head of the humerus are much as in *Urocissa*. The distal epicondyles are broad and the ventral epicondyle is slightly rotated dorsally. The dorsal supracondylar process is moderately elongated. The distal fossa for m. humerotriceps is narrer than in *Urocissa*.

Synsacrum: The synsacrum typically includes eleven vertebrae. It is only moderately broadened compared to *Urocissa*.

Tarsometatarsus and toes: The tarsometatarsus is shaped as in *Cyanopica* but it is slightly shorter. The toe articulations and proximal phalanges are typically corvid and are stout, as in *Urocissa*.

Corvus (crows, ravens, rook, jackdaws)

Of the thirty nine species of *Corvus* only jackdaws, *C. monedula* and *C. dauuricus*, are distinctively different osteologically from the rest. Unusual forms of the bill in the African ravens do not reflect very great differences in the design of the jaws. The ravens and typical crows, including such varied forms as the rook, *C. frugilegus*, the small Pacific island species *C. kubaryi*, and the Sinaloa crow, *C. sinaloae*, although differing in size and proportions are osteologically very similar. They would not be well distinguished by an analysis of discreet osteologic characters. The species *monedula* and *brachyrhynchos* will be described.

Skull and jaw shape (Figure 3, *Corvus monedula* and Figure 7, *C. ossifragus* are illustrated): *Corvus* includes the largest corvids but *monedula* is only moderately large. The cranium is heavily built and large, and is relatively wide and shallow. The supraorbital shelf of the frontals is relatively wide. The antorbital plate is tilted so that the orbit is lengthened dorsally. The jaws are greatly elongated rostrally in typical crows but not in the jackdaws. The upper jaw is slightly shallower than in *Urocissa* and its dorsal profile is only moderately decurved. The ventral profile of the upper jaw is only slightly decurved at the tip. The nostril is oval. The dorsal bar of the upper jaw is not unusually heavy. The symphysis of the lower jaw is short.

Craniofacial hinge: The nasal processes of the premaxilla are very wide at the craniofacial hinge. The hinge is only moderately distinct. There is a very slight frontal boss in *monedula*.

Nasal capsule, antorbital flange: The nasal septum is not ossified. The prefrontal is confined to the anterolateral border of the ectethmoid and is not much inflated.

Lateral nasal bar: In *monedula* the maxilla is visible laterally in the suture at the base of the nasal bar but does not form a large wedge. In *brachyrhynchos* the maxilla is entirely within the nasal capsule.

Palate: In brachyrhynchos the ossification in the rostral part of the palate and the configuration of the prepalatine bars are similar to that in Pica. In monedula the rostral palate is densely ossified and is restricted to the area rostral to the nasal capsule. In both, the maxillopalatine is expanded but broadly open laterally. The palatines in brachyrhynchos resemble those of Pica. The transpalatines in monedula are very broad and wedge shaped. In both, there is a large transpalatine pit.

Temporal fossa, lower jaw articulation (Figures 10. 11, 12): The suprameatic crest is very heavy and in brachyrhynchos it is well elevated but in monedula it is only slightly elevated. In brachyrhynchos the ventral suprameatic crest is as in Pica. Among populations and species of Corvus as within populations of Pica pica there is much variation in position of contact of the ventral suprameatic crest to the quadrate and presence of lack of a small suprameatic process. The mandibular articulations are also similar in Pica and C. brachyrhynchos including the presence of a prominent rostral crest of the lateal cotyla. In Corvus brachyrhynchos the caudal cotyla is flatter than in Pica, in lateral view, its articular surface in about the same plane as the lateral cotyla. In C. monedula there is no extension of the lateral wall of the squamosal ventral to the suprameatic crest, and there is no rostral crest of the lateral cotyla of the mandible. Humerus: The humerus is greatly elongated and widened proximally widened in Corvus. The articular head is enlarged, more in brachyrhynchos than in monedula. Enlargement of the head of the humerus makes it appear that the pectoral crest is slightly recessed from the head. In monedula the pectoral crest is wide and rounded but in brachyrhynchos it is straight and moderately long. The biceps crest is more rounded than in other corvids because of slight displacement of the protruding scar for m. scapulohumeralis caudalis from the rim into the triceps fossa. Distally the biceps crest attenuates more gradually, e.g. it is elongated, down the shaft of the humerus. These features give the proximal muscle attachment area of the humerus an elongated appearance. The dorsal tubercle is set out ventrally from the shaft of the humerus, more in brachyrhynchos than in monedula. The dorsal supracondylar process is elongated along the shaft and is close to it. The site for origin of m. brachialis is deep. The distal sulcus for m. humerotriceps is narrow.

Synsacrum (Figure 14): The synsacrum is very broad, as in Garrulus. Typically eleven vertebrae are incorporated.

Tarsometatarsus and toes: The tarsometatarsus is even shorter than in Pica but its shape is similar. The toes are typically corvid.

Nucifraga (nutcrackers)

The Eurasian and American species of Nucifraga, although so different in plumage and so far separated in range, are nevertheless extremely similar osteologically, differing primarily in size.

Skull and jaw shape (Figure 6): The cranium is slightly deeper and wider than in Pica. The antorbital plate is tilted forward so that the orbit is longer. The cranium in Nucifraga as well as in Corvus appears overall somewhat larger than in Pica or Garrulus. The supraorbital shelf is a little narrower than in Corvus. The jaws are heavy but the upper jaw is a little shallower than in Corvus. The nostril is shortened and is almost round. The dorsal profile of the jaw is only very slightly decurved and the ventral profile is very slightly and continuously decurved. The jaw is sickle shaped; it is slightly longer than in Corvus monedula. The upper jaw is not at all inflated rostrally but instead is attenuated toward the tip, but densely ossified and not delicately constructed. The ventral profile of the lower jaw is straight. The lower jaw is attenuated toward the tip. The tip of the lower jaw is narrow and shallow. The symphysis of the lower jaw is very long, primarily by caudal extension of the symphysis broadly between the rami, but possily also by slight rostral extension. The jaw is broad at the angle.

Craniofacial hinge: The nasal processes are wide at the craniofacial hinge, as in Corvus and a variety of other holarctic corvids. There is no frontal boss.

Nasal capsule, antorbital flange: The nasal septum is not ossified. The ectethmoid and prefrontal are much as in Garrulus.

Lateral nasal bar: The maxilla forms a prominent wedge in the suture at the base of the lateral nasal bar and is exposed on the lateral surface.

Palate: The rostral part of the palate is short and very densely ossified. It does not extend below the nasal floor. The prepalatine bars are far apart and are extensively fused to the ventral bar of the jaw almost as far as in Garrulus, obscuring the palatal flange of the ventral bar of the jaw, which is however present as a rudiment dorsal to the prepalatine bar. The tip of the maxillopalatine is as in Garrulus and Pica except that it lacks the flaring extensions. The palatines are much as in Corvus brachyrhynchos. The transpalatine pit is extremely large, making the transpalatines very long.

Temporal fossa: The temporal fossa is much as in Corvus brachyrhynchos. The suprameatic crest is well elevated. As in Garrulus there is a large, wedge-shaped zygomatic process.

Quadrate articulations: The ventral suprameatic crest is not widened. It resembles the crest in Garrulus. It meets the quadrate on its caudal face, extending very slightly down the shaft and not forming a distinct process. The quadrate articulations are much as in Corvus monedula.

Humerus: Surprisingly for such a strong flying, high altitude bird, the humerus is not long. The proximal expanded area of the humerus is much as in Pica, but the pectoral crest is not so long. The ventral epicondyle is moderately broad and slightly rotated toward the ventral surface. The dorsal supracondylar process is narrow and slightly elongated. The distal sulcus for m. humerotriceps is narrow. The depression for m. brachialis is moderately deep.

Synsacrum: The synsacrum is broad, as in *Garrulus*, with eleven vertebrae.

Tarsometatarsus and toes: The shaft of the tarsometatarsus is as in *Corvus*, *Pica*, and *Cyanopica* except that the medial crest is less well defined. Thus the extensor sulcus is less distinct. The tarsometatarsus is extremely short. The toe articulations are typically corvid.

Podoces (ground jays)

The two species of *Podoces* that were examined (*hendersoni*, *panderi*) represent the two parts of the genus, as Goodwin (1986) divided its four species based on external characters. The two seen are similar osteologically but with some differences in the lower jaw articulation and large differences in the size of the jaws.

Skull and jaw shape: The cranium is deeper and narrower than in *Pica* and the orbit is very long. The skull is gracile but densely ossified. The jaw is shallow and narrow at the base and is moderately long and slightly sickle shaped. In *Podoces biddulphi*, which was not seen, the upper jaw is very long, approaching the size and shape of *Pyrrhocorax*. The nostril is shortened.

Craniofacial hinge: The nasal processes of the premaxilla are broad and there is a slight frontal boss.

Nasal capsule, antorbital flange: The nasal capsule lacks ossification. The prefrontal lies along the rostrolateral border of the ectethmoid and is not much inflated. It is deeply incised between dorsal and ventral lobes and is somewhat inset into the nasal capsule. The ectethmoid is typically corvid, but tilted in conjunction with the longer orbit.

Lateral nasal bar: The maxilla is not exposed laterally in the suture at the base of the lateral nasal bar.

Palate: The rostral ossification of the palate is dense and does not extend caudally between the prepalatine bars. The prepalatine bars are extensively fused to the ventral bar of the jaw, obscuring the palatal flange of the ventral bar. Its vestige meets the prepalatine bar on the dorsal surface of the prepalatine bar. The tip of the maxillopalatine is inflated and shaped much as in *Nucifraga*.

The transpalatine bears a large but shallow pit and the lateral border is moderately flared by this structure. The caudal border of the palatine is not ducurrent.

Temporal fossa: The temporal fossa is much as in *Pica* but even smaller. The postorbital process thus is very low. The ventral suprameatic crest is elongated caudally.

Quadrate articulations (Figure 12): The quadrate articulation with the cranium is slightly inset medially. The quadrate is very short. There is a large jugal brace. In *hendersoni* the ventral wall of the squamosal is long. It meets the otic process on its caudal face and extends rather far down it, not as a distinct process but as a part of a general enlargement of the sulcus ventral to the suprameatic crest. There is a small abutment from the quadrate against the *medial* side of the crest. In *panderi* the ventral wall of the squamosal is outset ventrolaterally and articulates with a very delicate, widely outset meatic process of the quadrate. The squamosal and periotic articulations are not unusual. The mandibular articulations are very shallow. There is a large jugal brace. The rostral channel of the medial cotyla of the mandible is very wide, shallow, and short. The lateral cotyla is widened and its surface is more or less flat, e.g. the lateral prominence is not tilted and there is no separate rostral facet. The lateral cotyla is continuous with the rostral slope, which extends rather far forward along the ramus of the mandible. In one specimen of _Podoces_ _hendersoni_ a heavy ossified accretion built up at the limit of the rostral slope, is in a far lateral position and is not similar to the rostral cotyla in American jays. The caudal cotyla is approximately in the same plane as the lateral cotyla and is very narrow.

Humerus: The head of the humerus is not enlarged but the dorsal tubercle protrudes ventrally from the shaft slightly, as in _Corvus_, though less. The pectoral crest is small. In _Podoces_ _panderi_ there is slight enlargement of the sulcus for the ascending head of the dorsal portion of m. humerotriceps. The sulcus for the distal end of m. humerotriceps is slightly widened and the dorsal epicondyle is narrow. The ventral epicondyle is moderately widened and is strongly rotated. The depression for m. brachialis is shallow.

Synsacrum: The synsacrum is narrow. Typically eleven vertebrae are incorporated.

Tarsometatarsus and toes: The shaft of the tarsometatarsus is shaped as in Nucifraga. The first metatarsal articulates rather high on the shaft and on the plantar surface rather than laterally. The tarsometatarsus is very long in panderi (hendersoni not measured). The toes are typically corvid.

Pyrrhocorax

The two species of Pyrrhocorax differ in size and differ greatly in overall shape and size of the jaw but share the same unique design features of the palate. The smaller alpine chough, P. graculus, departs less from the form of other corvids.

Skull and jaw shape (Figure 7): The common chough, P. pyrrhocorax, is very large, the alpine chough, P. graculus, not particularly large for a corvid. The cranium in choughs is very large but not so robustly built as in the nutcrackers and crows. In general form the skull of Pyrrhocorax greatly resembles that of Podoces. The quadrate is more deeply inset medially, particularly in the larger species, pyrrhocorax, and the lower jaw is consequently very narrow. The jaw is sickle shaped and elongated by rostral extension evidently, since the lower jaw symphysis does not extend caudally very far between the rami of the mandibles. The jaw is only slightly elongated in graculus but is extremely long in pyrrhocorax. The nostril is oval in graculus but is shortened in pyrrhocorax. In the species pyrrhocorax there is heavy ossification of superficial membranes around the external nares.

Craniofacial hinge: The craniofacial hinge is as in Podoces.

Nasal capsule: The nasal septum is not ossified. The antorbital flange is much as in Podoces.

Lateral nasal bar: The maxilla is not exposed on the lateral surface of the jaw.

Palate: The ossified rostral part of the palate is not fused in the midline. The ossification is dense but does not extend below the nasal capsule. The design of the palate differs radically from that of any other corvid. In the species pyrrhocorax the prepalatine bars lie far medial. The palatal flange of the ventral bar of the jaw is very broad and meets the prepalatine bar at its lateral rim, without ventral inflection. The palatine process of the premaxilla is moderately large, adnate to the prepalatine bar but not entirely fused to it. The transpalatines are only very slightly flared. There is sometimes a tiny terminal pit. The caudal margin of the palatine is straight and extends approximately laterally from the midline.

The species graculus differs only in that the palatal flange of the ventral bar of the jaw meets the prepalatine bar on its dorsal surface and there is no terminal transpalatine pit. The tip of the maxillopalatine is inflated and similar in form to that of Podoces and Nucifraga.

Temporal fossa and quadrate articulations are very similar to those of Podoces. In Pyrrhocorax graculus the ventral suprameatic crest is as in Podoces panderi, resembling the form common to several other holarctic corvids, but in Pyrrhocorax pyrrhocorax the crest has the same unusual form as in Podoces hendersoni.

The quadrate is very short and stout, with an elevated lateral condyle in the species pyrrhocorax. The jugal brace is large. In the species pyrrhocorax the jugal articulation is elevated and displaced caudally. Also the ventral rim of the caudal wall of the mandible is deeply notched medially and there is a short, blunt retroarticular process. In both species the mandibular articulations are as in Podoces.

Humerus (Figure 13): In both species but particularly in graculus the pectoral crest is reflected far dorsally. The crest is only moderately long. The dorsal tubercle is strongly outset from the shaft in the species pyrrhocorax. The articular head is enlarged more in pyrrhocorax than in graculus. The distal margin of the biceps crest is elongated and the biceps crest is smoothly rounded rather than angular, resembling Corvus. At the distal end the ventral epicondyle is moderately wide and slightly rotated in graculus but is narrower and unrotated in pyrrhocorax. The sulcus for m. humerotriceps is narrow. The dorsal supracondylar process is lengthened along the shaft and the epicondyle is narrow. The flexor process is long in the species pyrrhocorax.

Synsacrum: The synsacrum is very broad and typically includes only eleven vertebrae.

Tarsometatarsus and toes: The tarsometatarsus is shaped as in Nucifraga and Podoces. It is long in graculus and short in pyrrhocorax. Toes III and IV interlock and toe III is short, as is typical of corvids.

Zavatarriornis

No skeletal specimen of Zavatarriornis could be located. X-rays of the skull in museum skins are not very revealing but so far as can be determined are consistent with this genus being related to Podoces or possibly Nucifraga, as Ripley's (1955) drawings and discussion suggest.

Pseudopodoces (dwarf ground jay)

Pseudopodoces humilis, the dwarf ground jay of central Asian steppe, is very atypical for corvids, not only in size and behavior, but also in osteology. Nevertheless there are some striking resemblances to Podoces. This brief description gives only points of interest.

Skull and jaw shape (Figure 8): Pseudopodoces is a much smaller bird than any corvid. The cranium is very large. The cranium is rounded rather than dorsolaterally expanded as in Podoces (and corvids generally) but the orbit and cranium are similarly proportioned otherwise. The orbital fontanelles are very large. The upper jaw is shallow and sickle shaped. The nostril is rounded.

Craniofacial hinge: The craniofacial hinge has a well developed articulation traversing all or most of its distance (varies among specimens).

Nasal capsule: The nasal septum is not ossified. The flexion zone in the rostral part of the jugal bar appears to be a syndesmotic bending zone (c.f. Bühler 1981).

Palate: The rostral part of the palate is constricted, not gradually attenuated, and densely ossified. The prepalatine bars are far medial and contact the ventral bar of the jaw directly in a long suture. There is no palatal flange.

Temporal fossa: The zygomatic process is very high and broad. The subzygomatic sulcus is a large, rounded fossa. The suprameatic crest is elongated caudally, and the bulla is notched deeply.

Quadrate articulations: The very thin ventral border of the squamosal wall is broadly outset ventrolaterally. Otherwise the dorsal articulations of the quadrate are typical of oscines. The mandibular articulations resemble those of *Podoces* but the lateral prominence of the lateral cotyla of the mandible is tilted to face caudally.

Humerus: The humerus has a well-developed second pneumatic fossa.

Tarsometatarsus and toes: Metatarsal I articulates entirely on the plantar surface. Its trochlea is entirely plantar to the other trochleae. There is no interlock between toes III and IV and toe IV is about three fourths the length of toe III, longer than in any corvid.

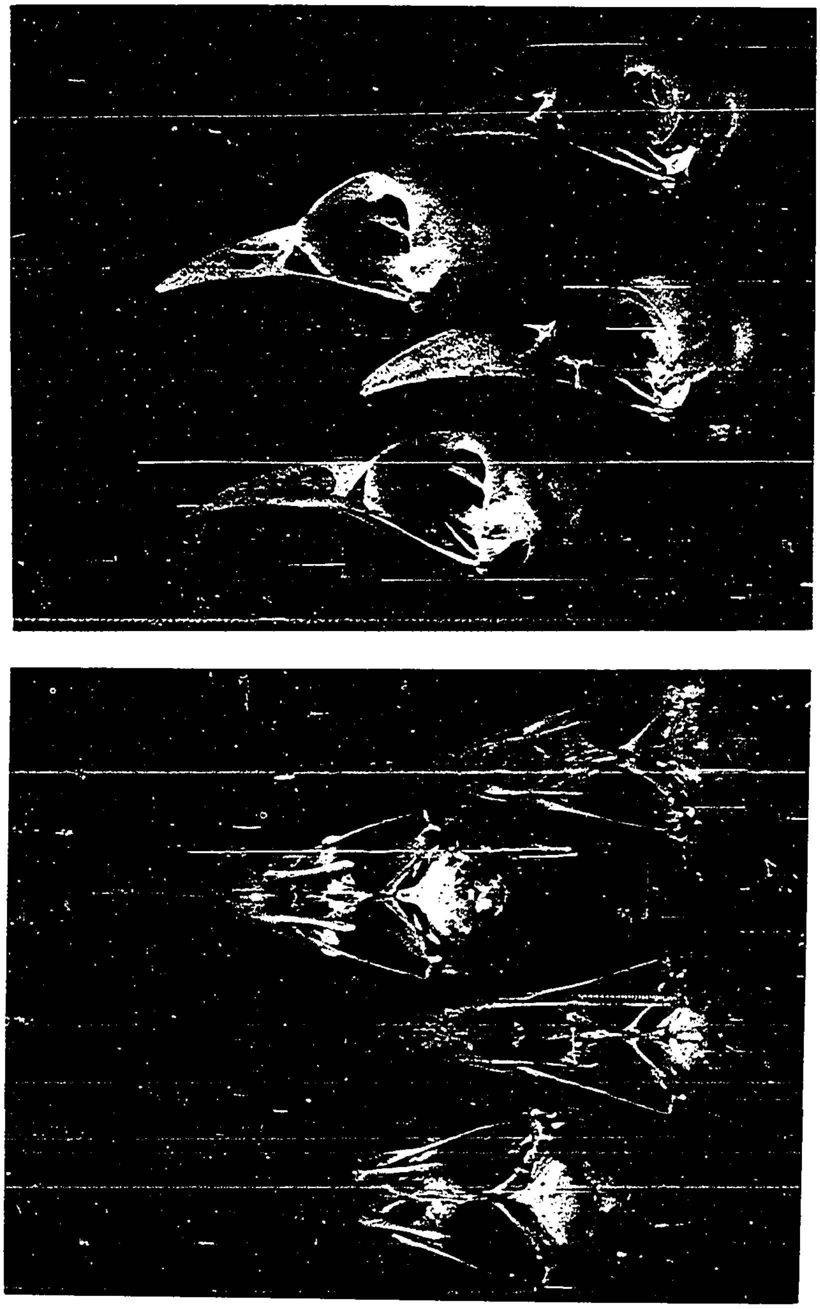

Figure 2. Skull and palate (top to bottom) of *Dendrocitta vagabunda*, *Platylophus galericulatus* *Ptilostomus afer* and *Manucodia ater*. Approximately natural size.

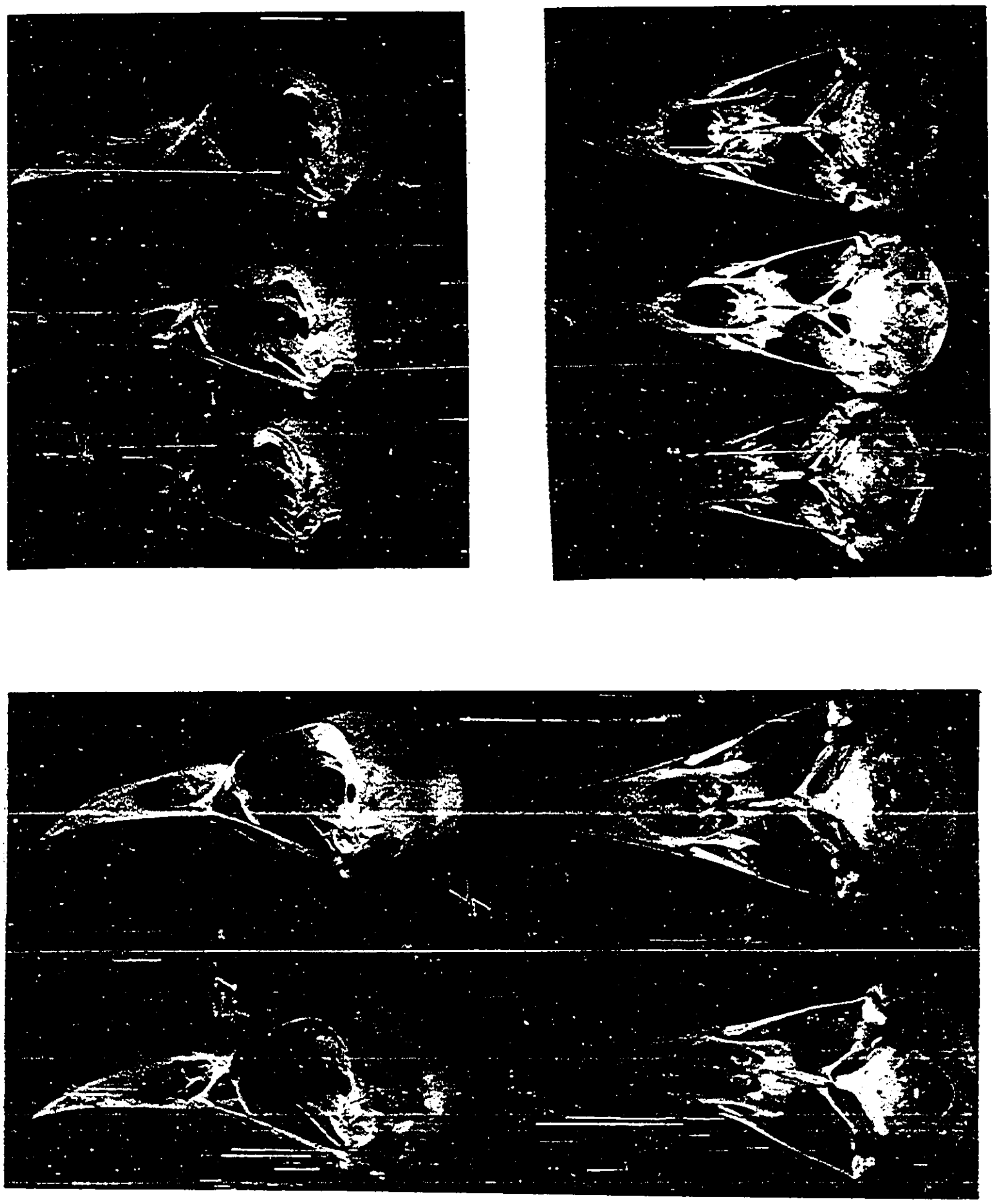

Figure 3. Skull, left, and palate, right, of (top to bottom) *Cyanolyca cucullata*, *Cyanolyca viridicyana*, *Cyanolyca argentigula*, *Cyanocorax chrysops*, *Cyanocorax mystacalis*. Natural size.

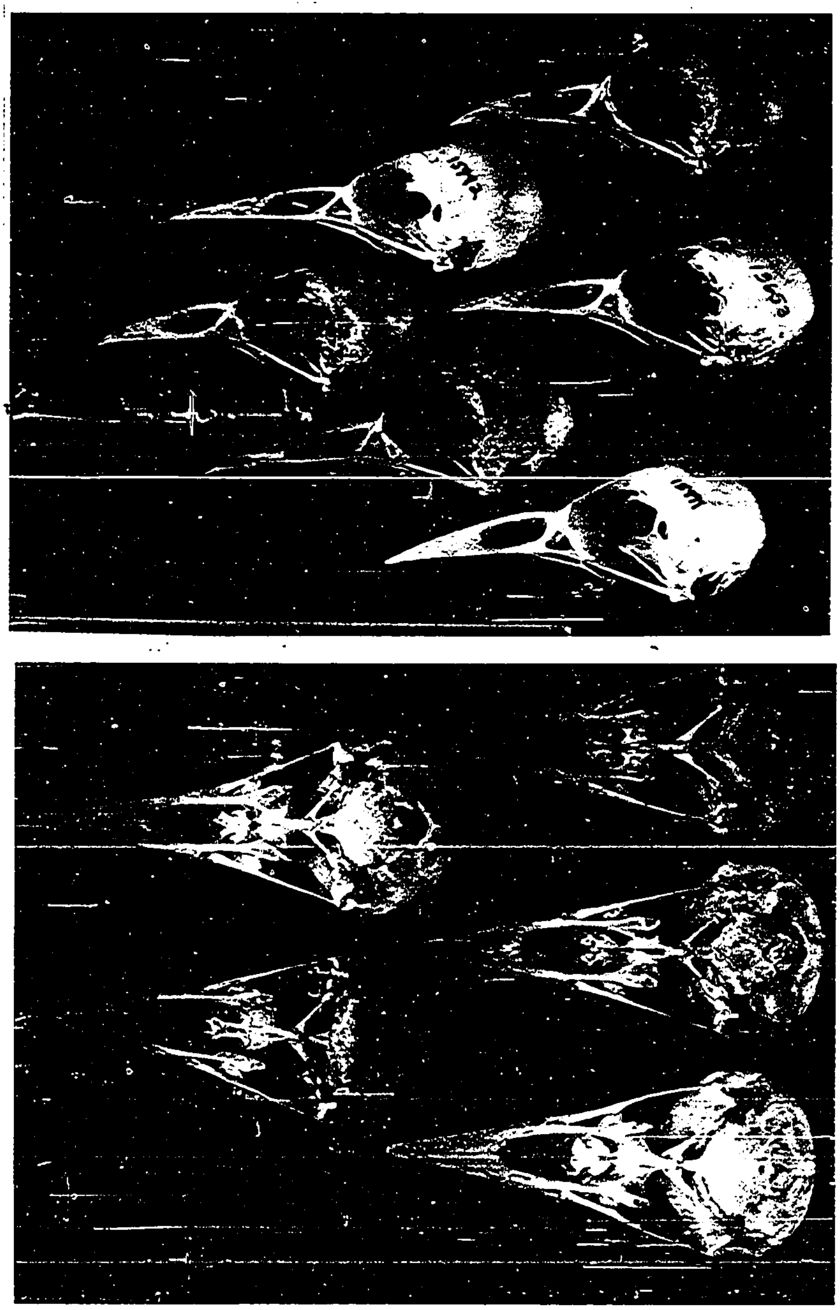

Figure 4. Skull and palate (top to bottom) of *Cyanocorax yncas*, *Cyanocitta stelleri*, *Aphelocoma coerulescens*, *Aphelocoma ultramarina*, *Gymnorhinus cyanocephalus*. Approximately natural size.

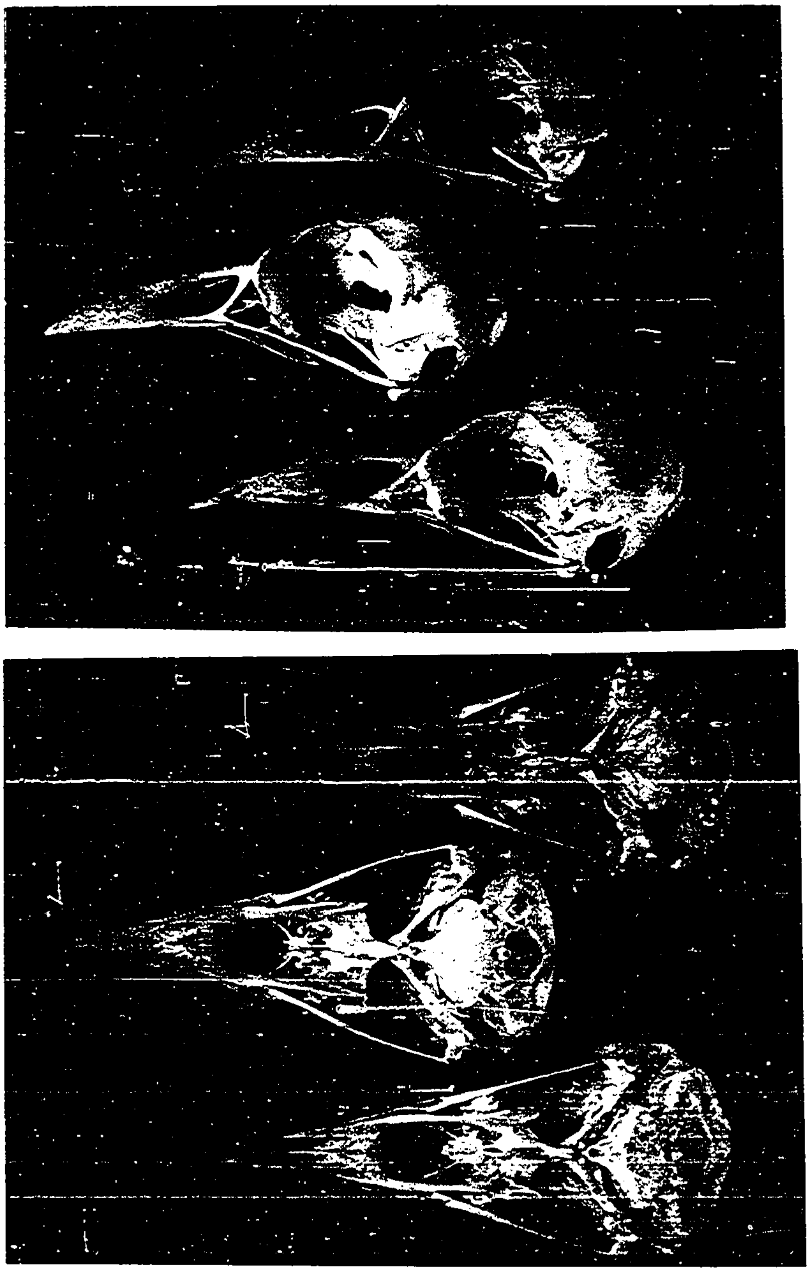

Figure 5. Skull and palate (top to bottom) of *Corvus monedula*, *Garrulus lidthi*, *Pica pica*. Approximately natural size.

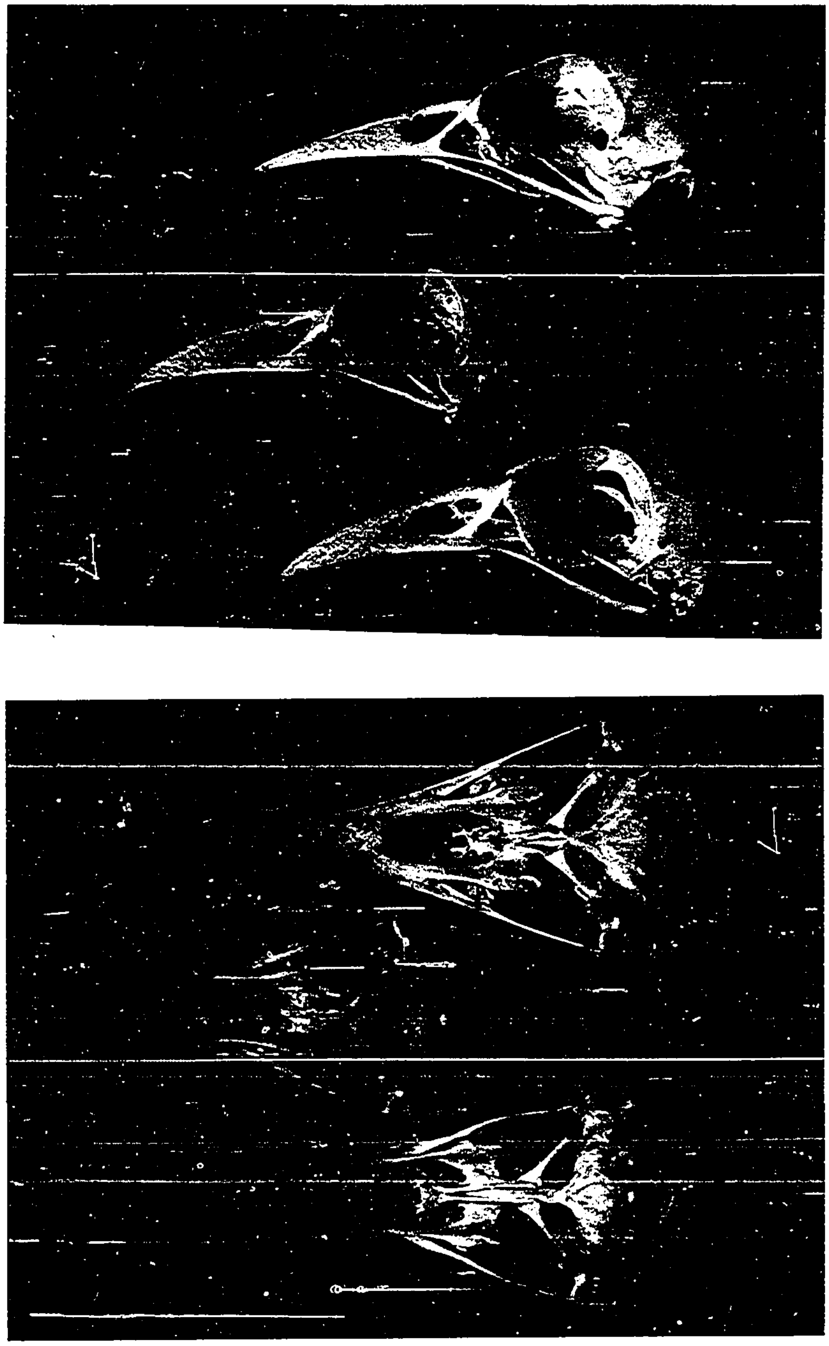

Figure 6. Skull and palate (top to bottom) of *Nucifraga caryocatactes*, *Cissa chinensis*, *Urocissa erythrorhyncha*. Approximately natural size.

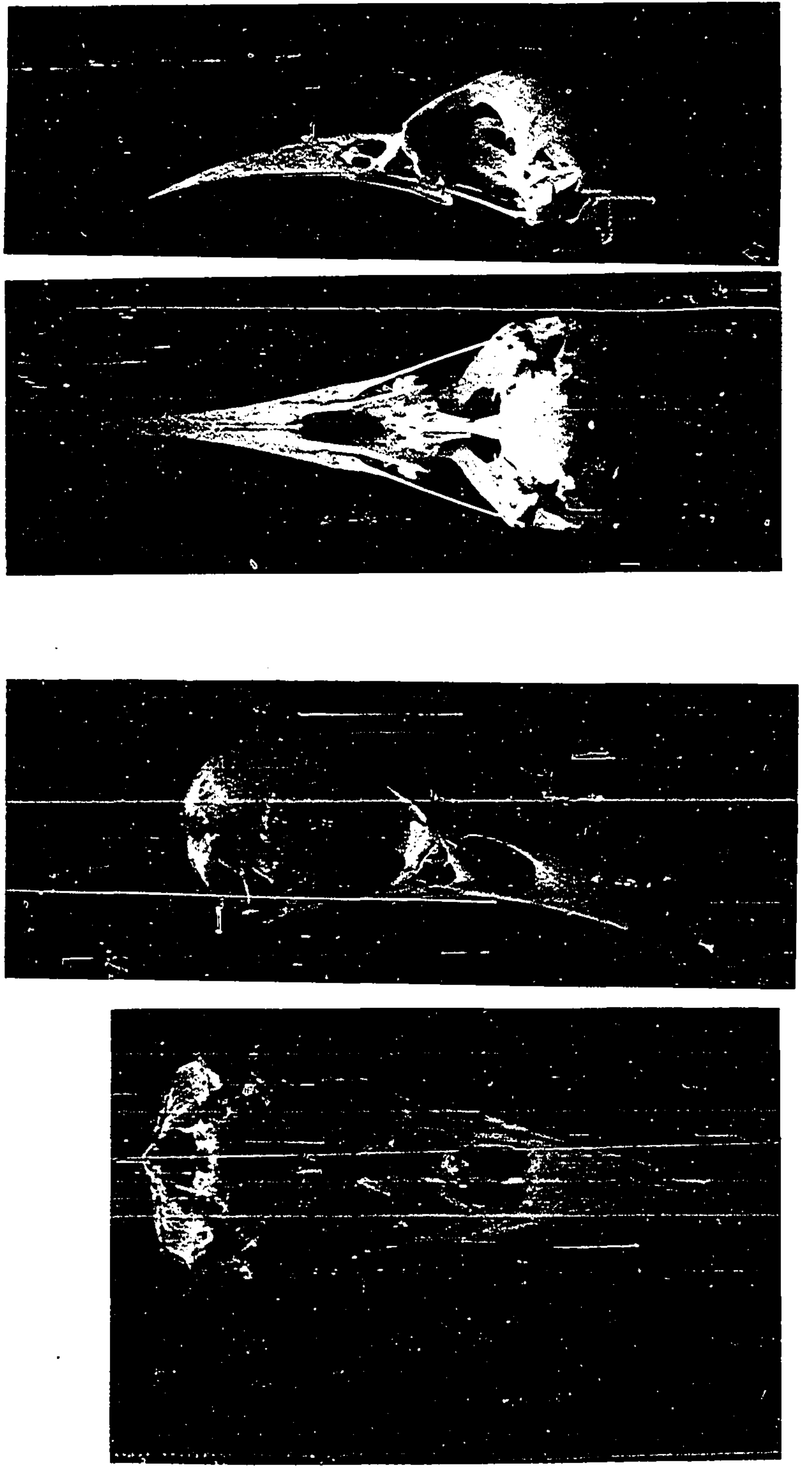

Figure 7. Skull and palate (top to bottom) of *Pyrrhocorax pyrrhocorax*, *Corvus brachyrhynchos*. Approximately natural size.

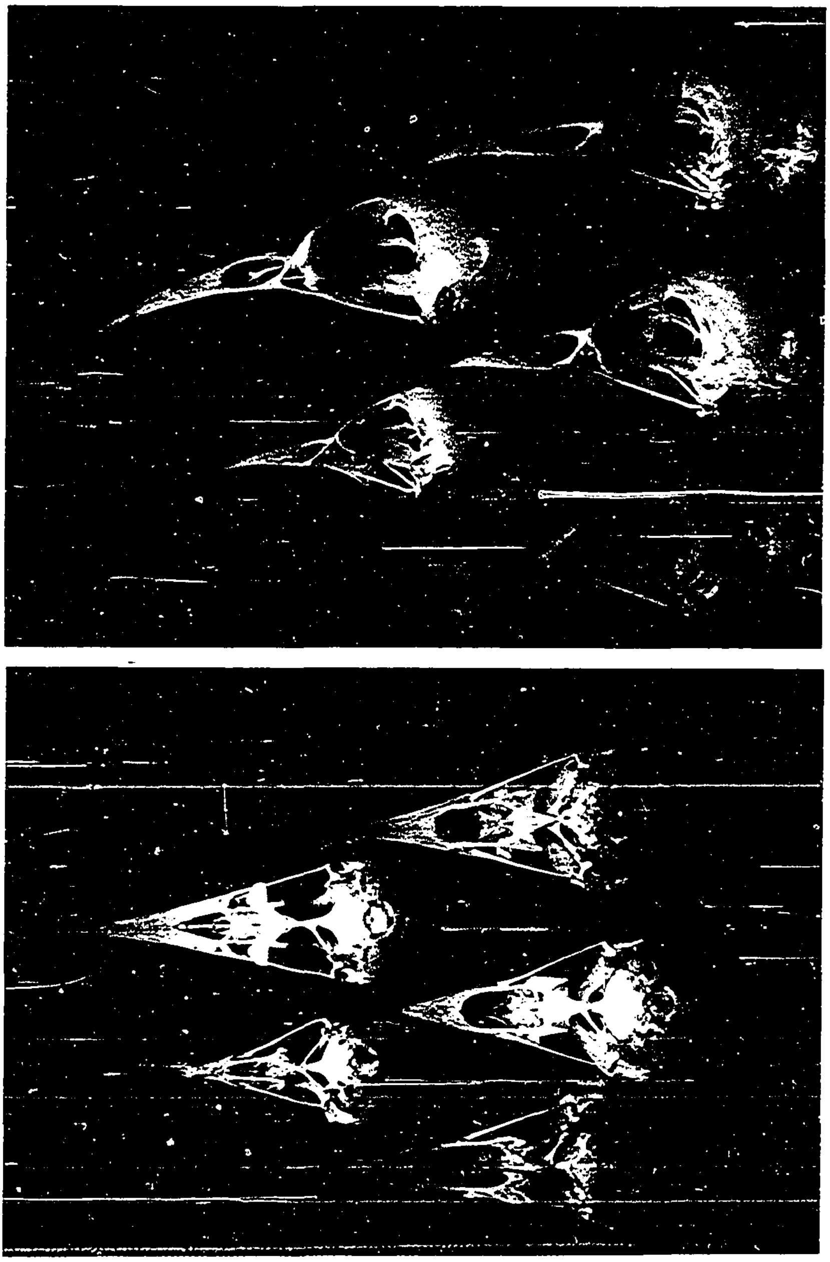

Figure 8. Skull and palate of Podoces panderi, Oriolus trailli, Perisoreus canaaensis, Pseudopodoces humilis, Cyanopica cayana. Approximately natural size.

Figure 9a. Palate to show detail: top Platylophus galericulatus, bottom Dendrocitta vagabunda (10X).

Figure 9b. Palate to show detail (10X). Top, Garrulus glandarius, bottom Gymnorhinus cyanocephalus

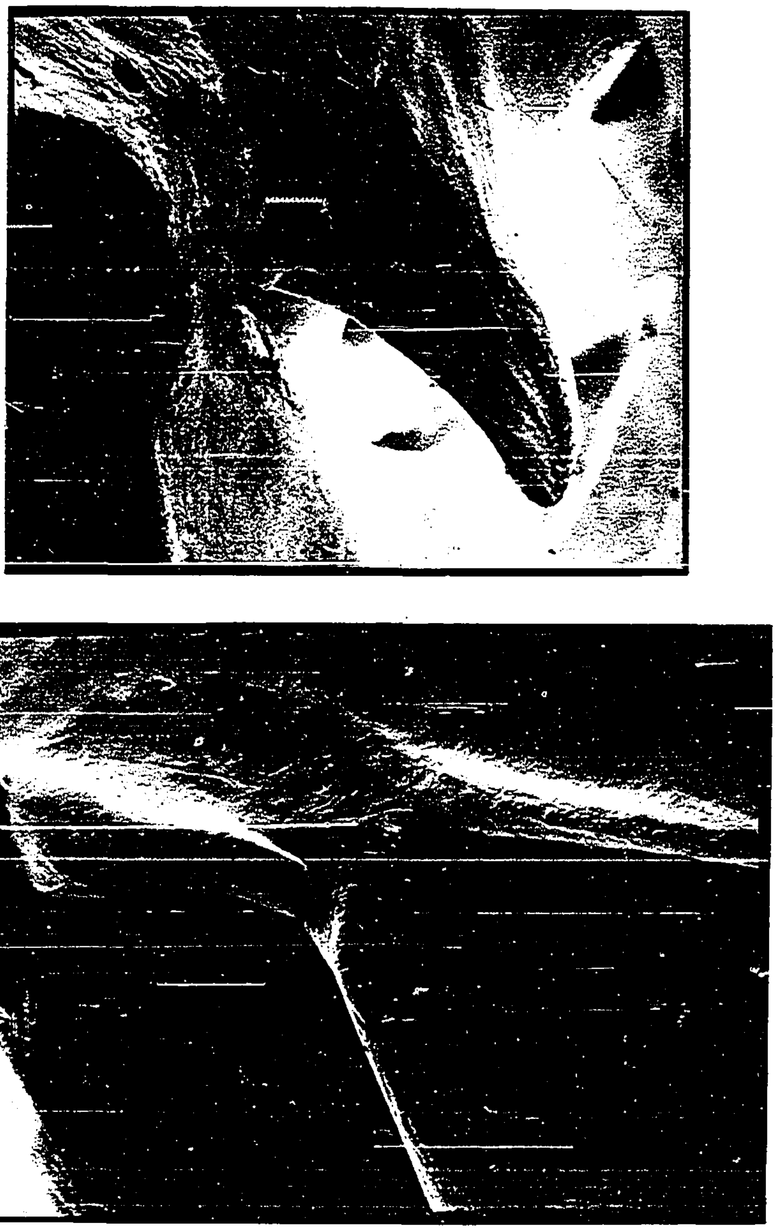

Figure 10a. Detail of crests over the ear region, right lateral view. Top, Platylophus galericulatus, quadrate-squamosal articulation showing, 20X. Bottom, suprameatic crest, Dendrocitta vagabunda, 10X. Note (1) large subzygomatic sulcus in Dendrocitta is continuous rostrally with the ventral surface of the zygomatic process. The corresponding sulcus in Perisoreus and Garrulus is shorter. (2) Separation of suprameatic crests in Perisoreus and Garrulus. The ventral suprameatic crest in Perisoreus and Garrulus corresponds to the large suprameatic crest in Dendrocitta.

Figure 10b. Detail of crests over the ear region, right size. Top, Perisoreus canadensis, bottom Garrulus glandarius (10X).

Figure 11a. Suprameatic crests in top, Cyanopica cayana, and bottom, Cyanolyca viridicyana. Left side, 10X.

Figure 11b. Suprameatic crests in top, Aphelocoma coerulescens, and bottom, Gymnorhinus cyanocephalus. Right side, 10X

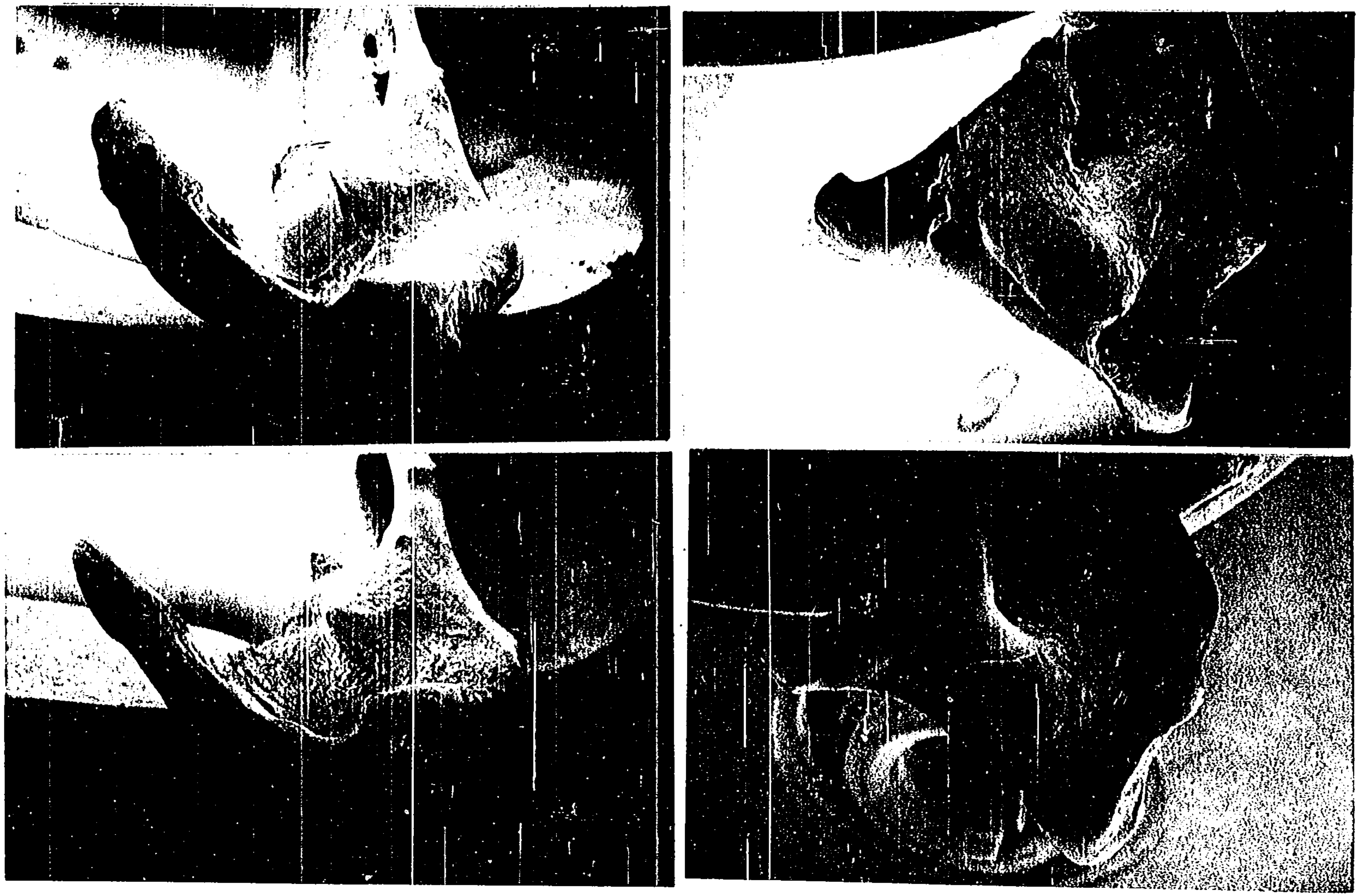

Figure 12a. Mandible, articular area of right ramus, left, caudal view; on right, dorsal view, 10X. Top, *Oriolus trailli*, bottom, *Platylophus galericulatus*.

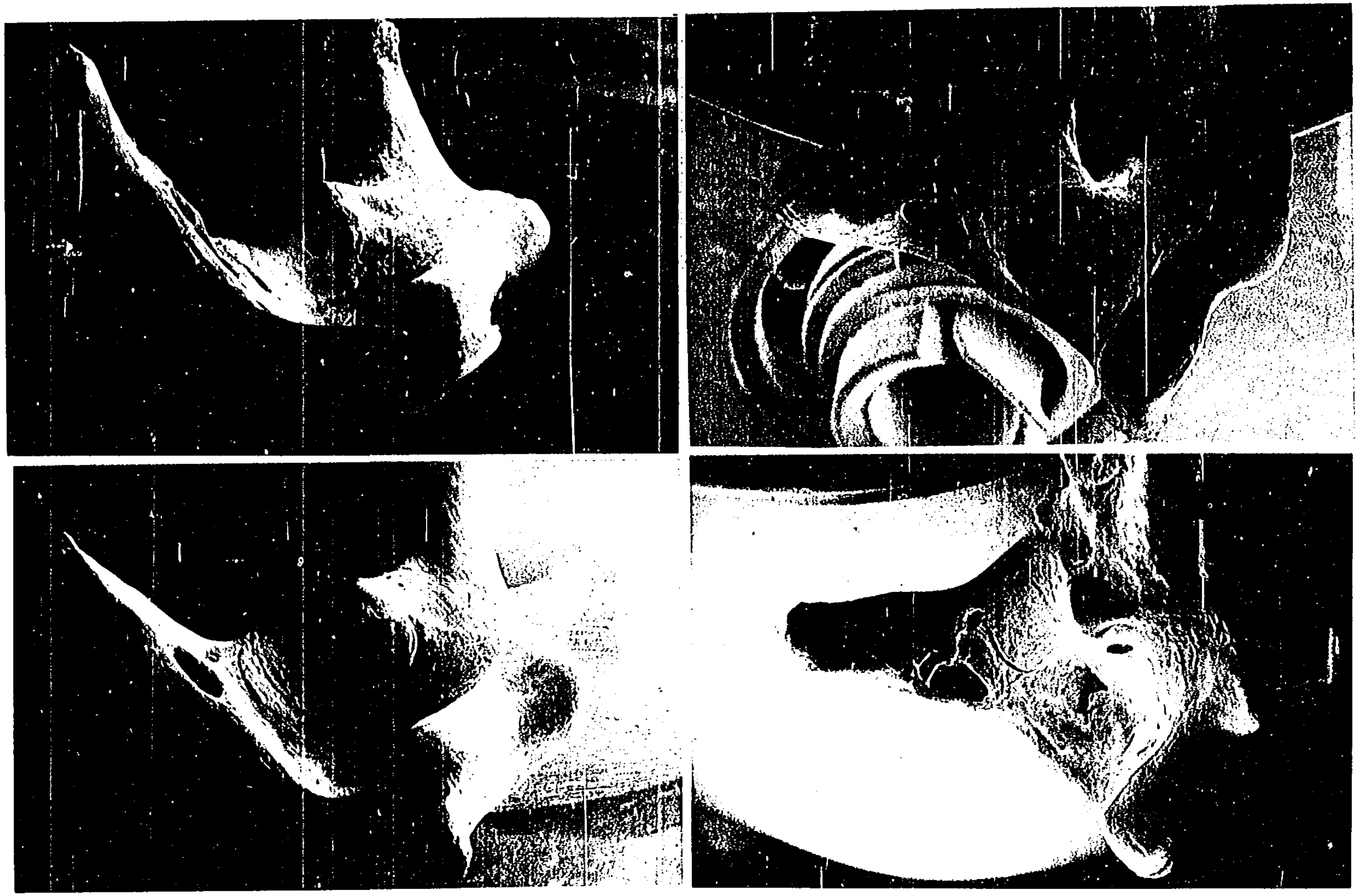

Figure 12b. Mandible, articular area of right ramus, on left caudal view, on right dorsal view (10X). Top, *Cissa chinensis*, bottom, *Dendrocitta vagabunda*.

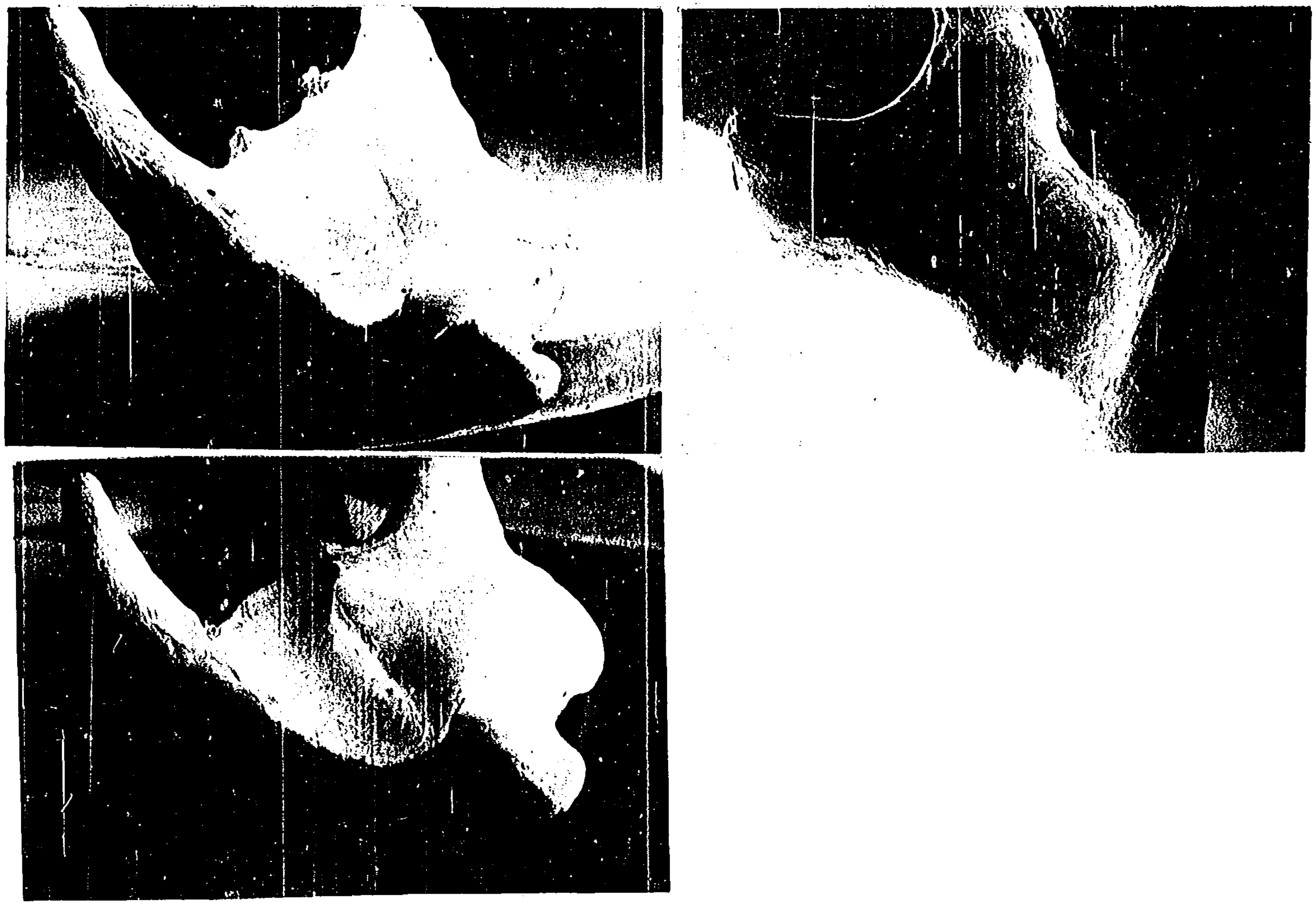

Figure 12c. Mandible, articular area of right ramus, on left caudal view, on right dorsal view (10X). Top, Nucifraga columbiana, bottom, Pica pica.

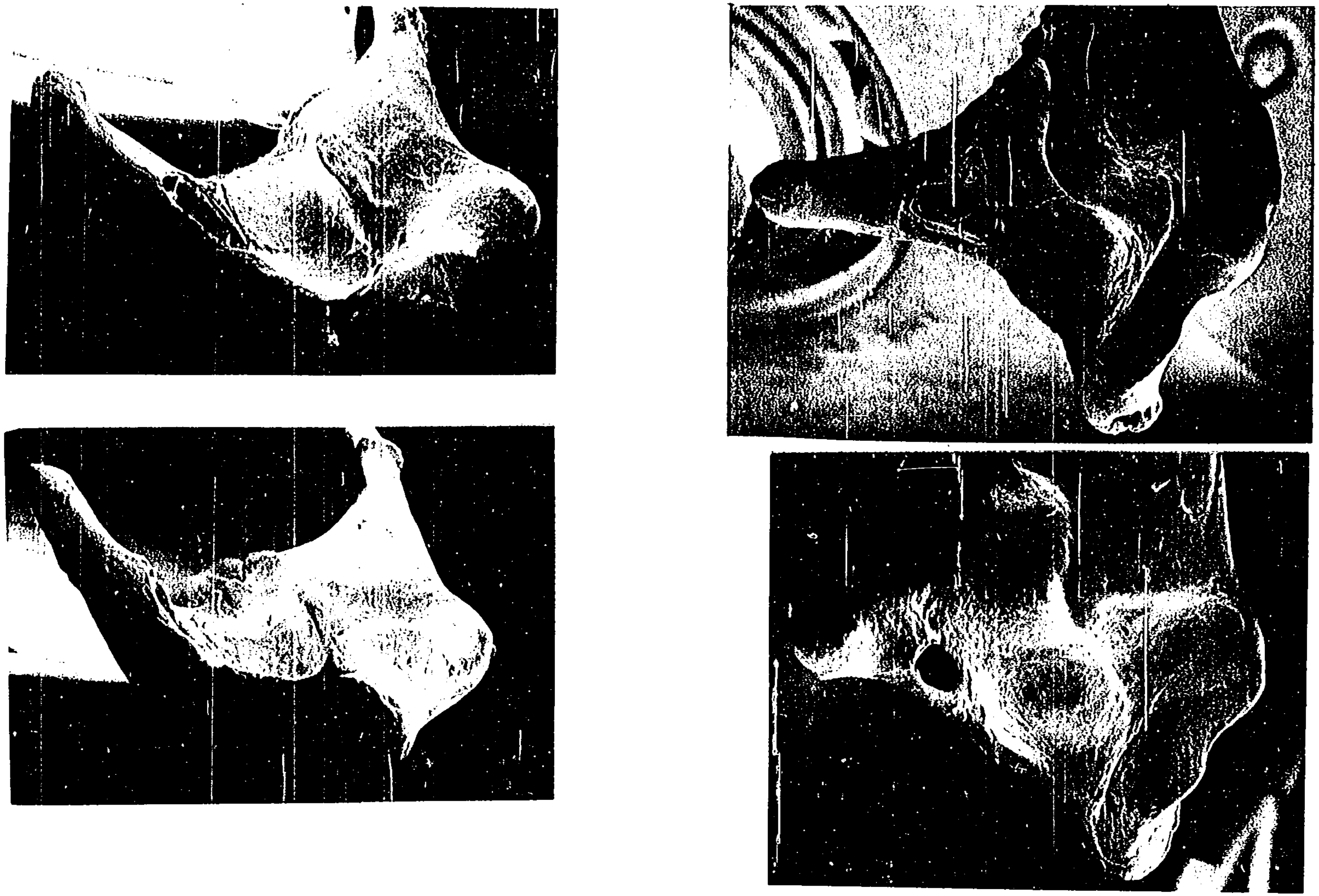

Figure 12d. Mandible, articular area of right ramus, on left caudal view, on right dorsal view (10X). Top, Perisoreus canadensis, bottom Garrulus glandarius.

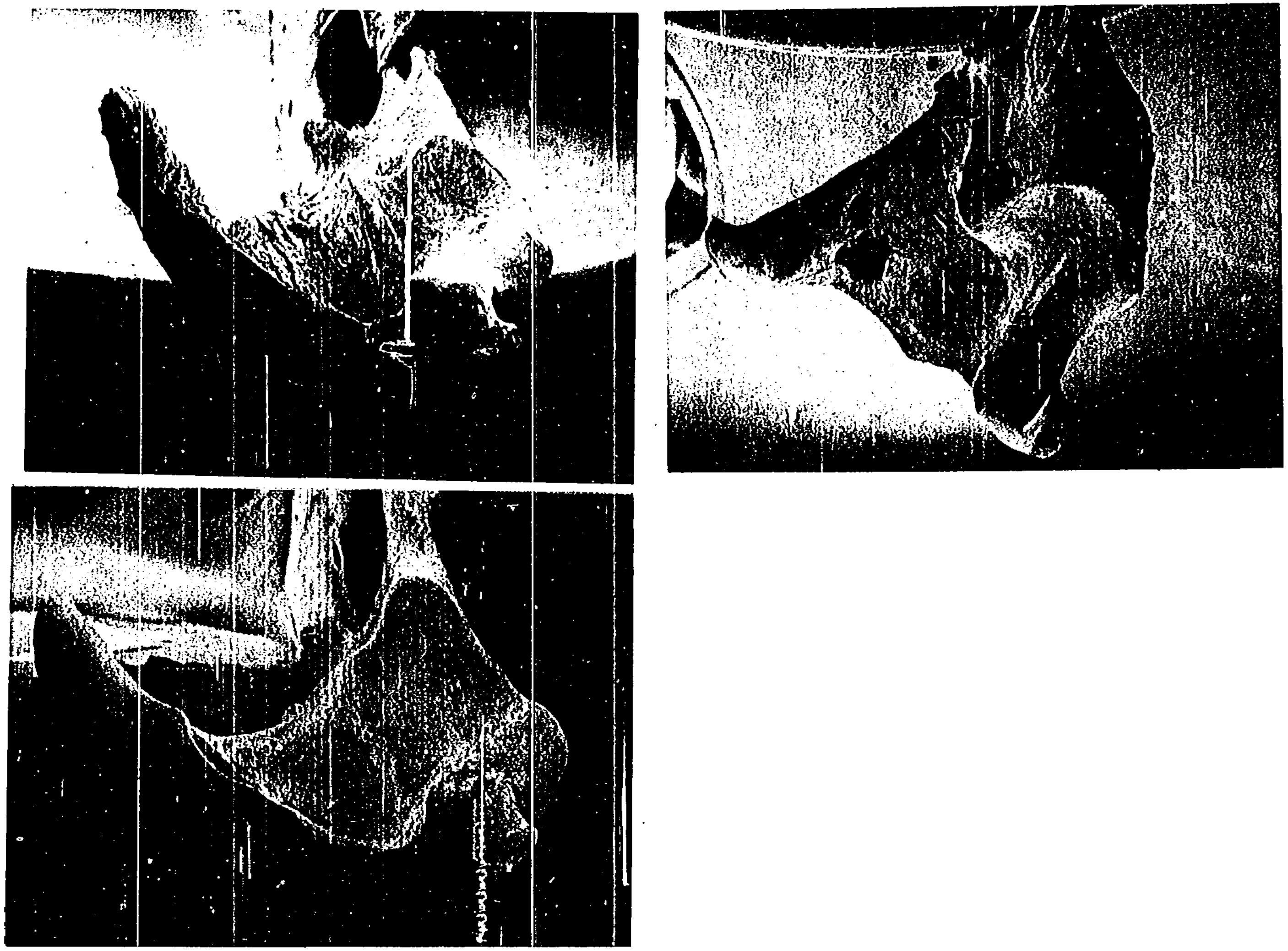

Figure 12e. Mandible, articular area of right ramus, on left caudal view, on right dorsal view (10X). Top, *Cyanolyca viridicyana*, bottom *Cyanocorax cyanomelas*.

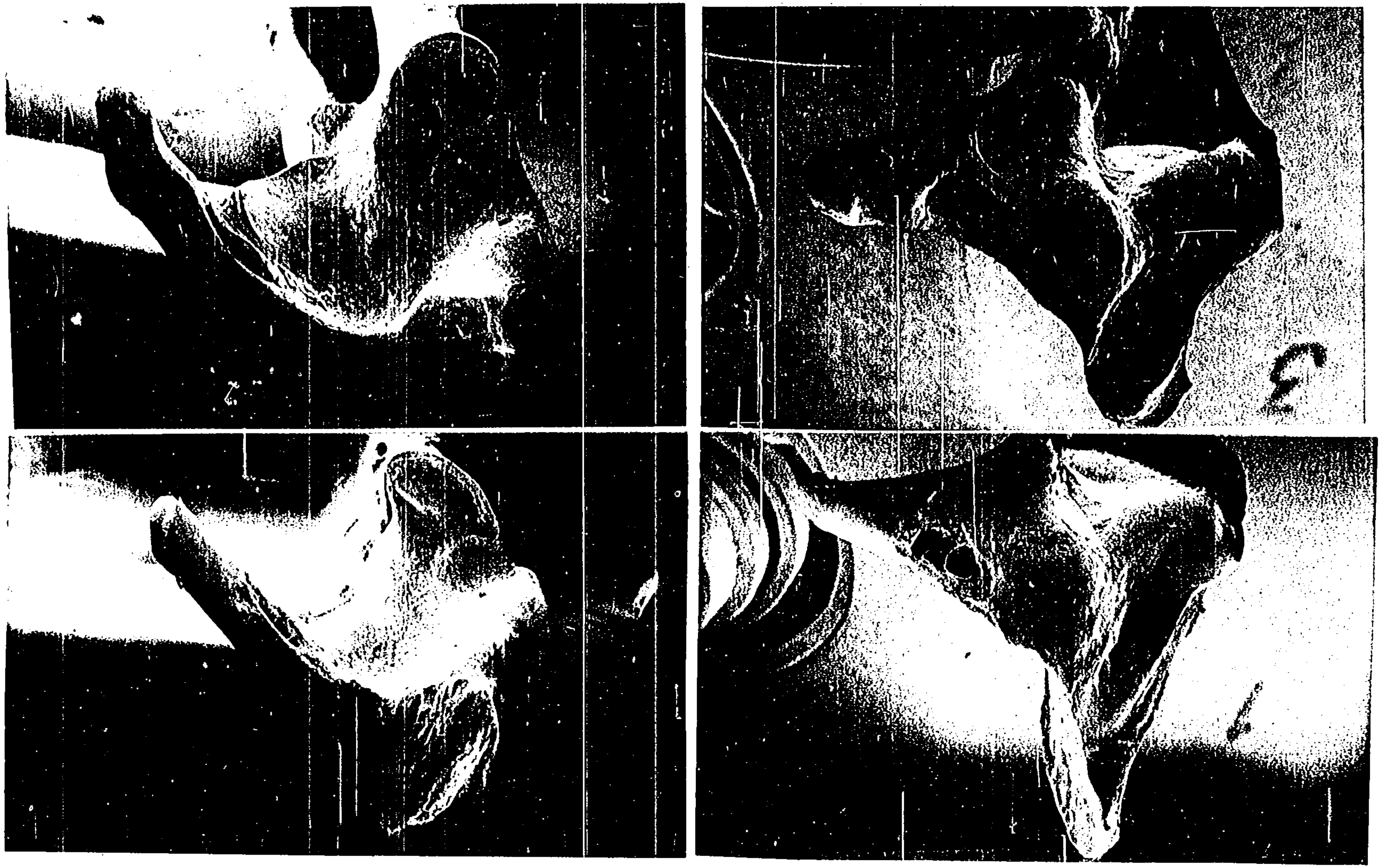

Figure 12f. Mandible, articular area of right ramus, on left caudal view, on right dorsal view (10X). Top, *Aphelocoma coerulescens*, bottom *Gymnorhinus cyanocephalus*.

Figure 13. Humerus, caudal view. Left to right: Platylophus galericulatus, Dendrocitta vagabunda, Pica pica, Pyrrhocorax pyrrhocorax. Natural size.

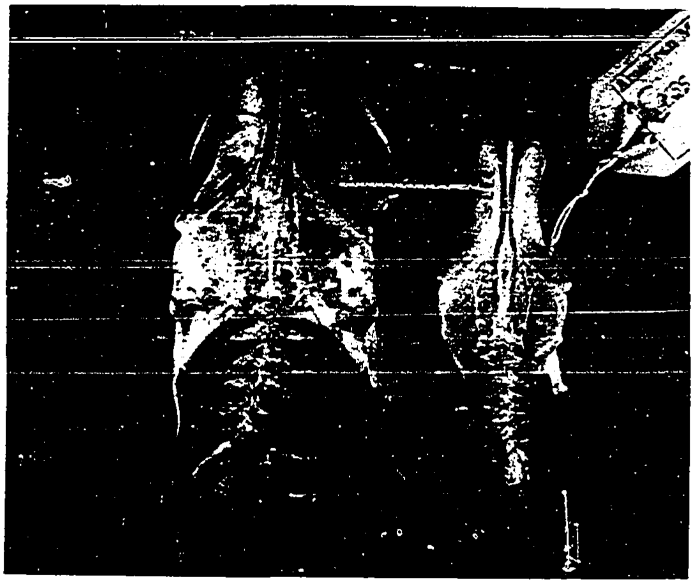

Figure 14. Synsacrum, dorsal view. Left, Cissa chinensis, right, Corvus ossifragus.

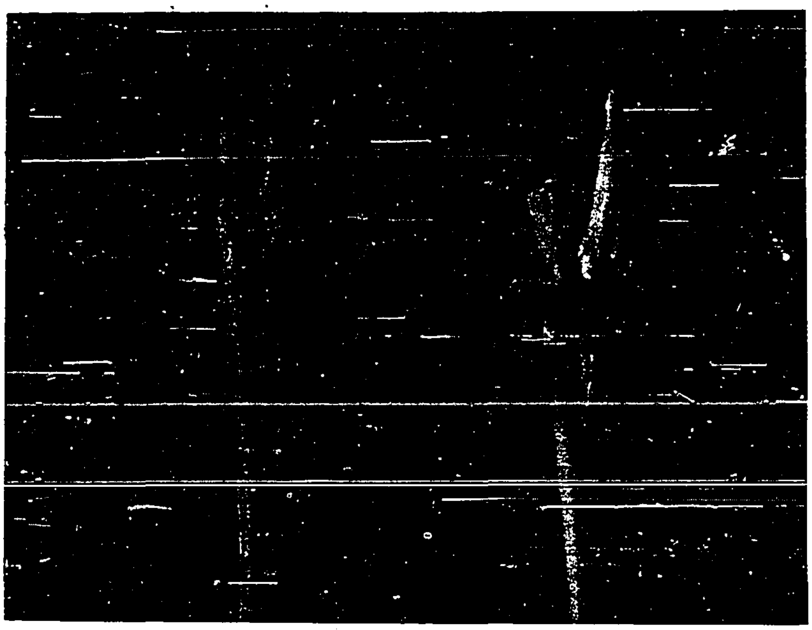

Figure 15. Distal tarsometatarsus and toes, dorsal view, left, a corvid, right a manucode (Paradisaeidae), diagrammatic, not to scale. Hallux removed.

REVIEW OF CHARACTERS

Certain characters that give conflicting phylogenetic information at higher taxonomic levels are reviewed here to clarify homology. This review includes some details of form that were not coded for analysis. Also in this section the principal components extracted from measurements are interpreted. Arguments for homology are based primarily on morphology or development of structures compared, in accordance with the discussion in the "Approach" section. Arguments based on taxonomic distribution of other characters are used only secondarily and arguments based on hypotheses of adaptive plasticity are avoided. The monophyly of American jays except for Cyanolyca is assumed initially in these discussions since there is adequate evidence for this in advance of the formal phylogenetic analysis. The evidence for monophyly of Cyanolyca with other American jays is examined. This review is used to develop alternate hypotheses of phylogeny in the succeeding section. Abbreviations for taxa used in this section are given in Appendix IV.

Cranium size - Appears generally large in all corvids; very large in Per, Cv, Nuc, Po, Py, Gy, one species of Aph.

The cranium appears larger than in other oscines in all corvids, and particularly large in crows, choughs, Perisoreus jays, nutcrackers, and in the Mexican and pinyon jays. Portman (1946) found a higher encephalization for Corvus than for Pica and both were much higher than the many other passerines studied, but he did not measure other corvids. However assessment of cranium size by measures used in this study was complicated by changes in shape and apparently also by allometry and perhaps by non-homology of measurements as discussed in the "Approach" section and beyond. Attempts to quantify size of cranium were not successful and will not be discussed here.

Orbit shape - Deep, e.g. approximately as deep as long in southern magpies, treepies, and many other corvids; slightly longer in Per, Gar, Pi, some Cyly, many AJ; very long in Cypi, Cv, Nuc; longest in Po, Py, one Cycor of the *violaceus* group, some Aph, Gy.

The measured length of the orbit contributes most of the variance assigned to Principal Component-II from the cranial dimensions (Table 1 and Figure 16). The dimension measured gives a low value when the antorbital plate is tilted, lengthening the dorsal dimension of the orbit but shortening its ventral dimension (compare *Cyanocorax* and *Aphelocoma*, Figures 5 and 6). The interpretation of PC-II is perhaps complicated by the low negative loading on cranium length. Other measures contribute very little. In the smallest *Cyanolyca* jays a low score on PC-II may be due to smaller overall size and relatively greater size of the cranium, since it appeared in the course of attempts to estimate cranium size that smaller birds do have relatively larger crania. In other taxa direct observation confirmed that a low score on PC-II clearly indicates a distinctly longer orbit. Thus the low scores may not be due to comparable changes throughout Corvidae. Within closely related taxa similar scores occur for similar shapes.

Table 1. Principal component patterns from measures. Printed values for the components have multiplied by 100 and rounded to the nearest integer. Values greater than 0.497438 have been flagged by an '*'. Initial factor method principal components.

a. Eigenvalues of the correlation matrix and factor pattern for measures of the orbit and cranium.

Eigenvalues of the Correlation Matrix:

	1	2	3	4
Eigenvalue	3.508220	0.331919	0.102578	0.057283
Difference	3.176301	0.229341	0.045294	
Proportion	0.8771	0.0830	0.0256	0.0143
Cumulative	0.8771	0.9600	0.9857	1.0000

Pattern of Principal Components:

	PC - I	PC - II	PC - III
ORBIT LENGTH	87 *	50	5
CRANIUM LENGTH	94 *	-26	20
CRANIUM DEPTH	96 *	-11	-25
CRANIUM WIDTH	98 *	-9	1

b. Eigenvalues of the correlation matrix and factor pattern for measures of the jaws.

Eigenvalues of the Correlation Matrix:

	1	2	3	4	5
Eigenvalue	3.396776	1.042160	0.249435	0.212638	0.098992
Difference	2.354616	0.792725	0.036797	0.113646	
Proportion	0.6794	0.2084	0.0499	0.0425	0.0198
Cumulative	0.6794	0.8878	0.9377	0.9802	1.0000

Factor pattern:

	PC - I	PC - II	PC - III	PC - IV
RAMUS WIDTH	74 *	58 *	-27	21
JAW LENGTH	89 *	-32	-20	-15
L.JAW SYMPH	74 *	-58 *	14	30
U.JAW SYMPH	94 *	-12	1	-23
U.JAW DEPTH	79 *	51 *	34	-4

Figure 16. PC-II from cranial measures and coded scores. Mnemonics for taxa explained in Appendix IV.

```
-----------------------------------------------------------------------------------------
PC-score:         3          -2          -1            0           1           2
Coded score:                  0           1            2           3           4
-----------------------------------------------------------------------------------------
Cracticus torquatus                  ¦          ¦          ¦           ¦   A
Oriolus trailli                      ¦          ¦          ¦           ¦           A
Paradisaea apoda                     ¦          ¦          ¦       A   ¦
Manucodia ater                       ¦          ¦          ¦        A  ¦
Platylophus galericulatus            ¦          ¦ A        ¦           ¦
Dn vagabunda                         ¦          ¦          ¦     A     ¦
Crp temia                            ¦          ¦      A   ¦           ¦
Csa chinensis                        ¦          ¦          ¦   A       ¦
Pt afer                              ¦          ¦          ¦A          ¦
Uroc caerulea                        ¦          ¦          ¦       A   ¦
Uroc erythrorhyncha                  ¦          ¦          ¦    A      ¦
Cyly pumilo                          ¦          ¦     A    ¦           ¦
Cyly mirabilis                       ¦          ¦ A        ¦           ¦
Cyly v. viridicyan                   ¦          ¦          ¦A          ¦
Cyly v. turcosa                      ¦          ¦          ¦   A       ¦
Cyly c. cucullata                    ¦          ¦          ¦       A   ¦
Cyly c. mitrata                      ¦          ¦          ¦      A    ¦
```

(continued)

Figure 16, continued

```
----------------------------------------------------------------------------------------
PC-score:         3          -2          -1           0           1           2
Coded score:                  0           1           2           3           4
----------------------------------------------------------------------------------------
Ps morio                             ¦          ¦          ¦ A         ¦
Cycor caeruleus                      ¦       A  ¦          ¦           ¦
Cycor cyanomelas                     ¦          ¦     A    ¦           ¦
Cycor violaceus                      ¦ A        ¦          ¦           ¦
Cycor cristatellus                   ¦          ¦          ¦         A ¦
Cycor affinis                        ¦          ¦        A ¦           ¦
Cycor chrysops                       ¦          ¦         A¦           ¦
Cycor mystacalis                     ¦          ¦         A¦           ¦
Cycor dickeyi                        ¦          ¦    A     ¦           ¦
Cycor yncas                          ¦          ¦          ¦ A         ¦
Cal f. formosa                       ¦          ¦          ¦   A       ¦
Cal f. colliei                       ¦          ¦          ¦   A       ¦
Cslo beecheii                        ¦          ¦          ¦   A       ¦
Cslo melanocyanea                    ¦        A ¦          ¦           ¦
Cslo sanblasiana yucatanica          ¦          ¦        A ¦           ¦
Aph unicolor                         ¦          ¦    A     ¦           ¦
Cycit cristata                       ¦   A      ¦          ¦           ¦
Cycit stelleri                       ¦    A     ¦          ¦           ¦
Aph c.coerulescens                   ¦          ¦        A ¦           ¦
Aph c. californica                   ¦          ¦     A    ¦           ¦
Aph ultramarina                      ¦      A   ¦          ¦           ¦
Gy cyanocephalus              A      ¦          ¦          ¦           ¦
```

(continued)

Figure 16, continued

```
----------------------------------------------------------------------------------------
PC-score:         3         -2          -1            0           1           2
Coded score:                 0           1            2           3           4
----------------------------------------------------------------------------------------
Gar glandarius                       ¦          ¦     A    ¦           ¦
Gar lidthi                           ¦          ¦          ¦   A       ¦
Per canadensis                       ¦          ¦ A        ¦           ¦
Per infaustus                        ¦       A  ¦          ¦           ¦
Cypi cayana                          ¦  A       ¦          ¦           ¦
Pi pica                              ¦          ¦     A    ¦           ¦
Nuc columbiana                       ¦    A     ¦          ¦           ¦
Nuc caryocatactes                    ¦          ¦ A        ¦           ¦
Po panderi                         A ¦          ¦          ¦           ¦
Pseudopodoces hum.             A     ¦          ¦          ¦           ¦
Py pyrrhocorax      A                ¦          ¦          ¦           ¦
Py graculus                        A ¦          ¦          ¦           ¦
Cv monedula                          ¦          ¦ A        ¦           ¦
Cv brachyrhynchos                    ¦        A ¦          ¦           ¦
```

Figure 17. PC-III from cranial measures and coded scores. Mnemonics for taxa in Appendix IV.

```
----------------------------------------------------------------------------------------
PC-Score:          -4        -3        -2        -1         0         1         2
Coded score:                            0         1         2         3         4
----------------------------------------------------------------------------------------
Cracticus torquatus                         !          !    A     !         !
Oriolus trailli                             !          !      A   !         !
Paradisaea apoda                            !          !          !      A  !
Manucodia ater                              !          !        A !         !
Platylophus galericulatus                   !          ! A        !         !
Dn vagabunda                                !         A!          !         !
Crp temia                                   !          !          !A        !
Csa chinensis                               !          !  A       !         !
Pt afer                                     !          !          !  A      !
Uroc caerulea                               !          !         A!         !
Uroc erythrorhyncha                         !          !      A   !         !
Cyly pumilo                  A              !          !          !         !
Cyly mirabilis                              !  A       !          !         !
Cyly v. viridicyana                         !          !A         !         !
Cyly v. turcosa                             !          !   A      !         !
Cyly c. cucullata                           !          !       A  !         !
Cyly c. mitrata                             !          !        A !         !
```

(continued)

Figure 17, continued

```
----------------------------------------------------------------------------------------
PC-Score:          -4        -3        -2        -1         0         1         2
Coded score:                            0         1         2         3         4
-----------------------------------------------------------------------------------------
Ps morio                                    |        A |          |         |
Cycor caeruleus                             |   A      |          |         |
Cycor cyanomelas                            |          |A         |         |
Cycor violaceus                A            |          |          |         |
Cycor cristatellus                          |          |          |A        |
Cycor affinis                               |  A       |          |         |
Cycor chrysops                              |          |   A      |         |
Cycor mystacalis                            |          |  A       |         |
Cycor dickeyi                               |  A       |          |         |
Cycor yncas                                 |          |          |  A      |
Cal f. formosa                              |          |       A  |         |
Cal f. colliei                              |    A     |          |         |
Cslo beecheii                               |          |          |     A   |
Cslo melanocyanea                           |        A |          |         |
Cslo sanblasiana yucatanica                 |          |          | A       |
Aph unicolor                                |          |  A       |         |
Cycit cristata                              |          |    A     |         |
Cycit stelleri                              |   A      |          |         |
Aph c. coerulescens                         |          |          |A        |
Aph c. californica                          |          |      A   |         |
Aph ultramarina                             |          |          |   A     |
Gy cyanocephalus                            |          |          |         |    A
```

(continued)

Figure 17, continued

```
----------------------------------------------------------------------------------------
PC-Score:          -4        -3        -2        -1         0         1         2
Coded score:                            0         1         2         3         4
----------------------------------------------------------------------------------------
Gar glandarius                              ¦          ¦       A  ¦         ¦
Gar lidthi                                  ¦          ¦         A¦         ¦
Per canadensis                              ¦          ¦        A ¦         ¦
Per infaustus                               ¦          ¦          ¦ A       ¦
Cypi cayana                                 ¦          ¦       A  ¦         ¦
Pi pica                                     ¦          ¦         A¦         ¦
Nuc columbiana                              ¦          ¦         A¦         ¦
Nuc caryocatactes                           ¦    A     ¦          ¦         ¦
Po panderi                                  ¦          ¦A         ¦         ¦
Pseudopodoces humilis                       ¦          ¦      A   ¦         ¦
Py pyrrhocorax                              ¦          ¦          ¦         ¦     A
Py graculus                                 ¦          ¦  A       ¦         ¦
Cv monedula                                 ¦          ¦          ¦    A    ¦
Cv brachyrhynchos                           ¦         A¦          ¦         ¦
----------------------------------------------------------------------------------------
```

Figure 18. Scores on principal component-II from jaw measures. Mnemonics for taxa as in Appendix IV.

```
----------------------------------------------------------------------------------------
PC-score:          -4       -3        -2       | -1   |     0|     |   1  |      2
Coded score:                            0      |  1   |   2  |  3  |   4  |    5
----------------------------------------------------------------------------------------
Cracticus torquatus                            |      |  A   |     |      |
Oriolus trailli                                |     A|      |     |      |
Paradisaea apoda                               |     A|      |     |      |
Manucodia ater                                 |      |      |     |  A   |
Platylophus galericulatus                      |      |      |     |A     |
Dn vagabunda                                   |      |      |     |A     |
Crp temia                                      |A     |      |     |      |
Csa chinensis                                  |      |      |   A |      |
Pt afer                                        |      | A    |     |      |
Uroc caerulea                                  |      |      |     |    A |
Uroc erythrorhyncha                            |      |      |   A |      |
Cyly pumilo                                    |      |      |     |      |
Cyly mirabilis                                 |      |      |     |      |
Cyly v. viridicyan                             |      |      |  A  |      |
Cyly v. turcosa                                |      |      |     | A    |
Cyly c. cucullata                              |      |      |    A|      |
Cyly c. mitrata                                |      |      |     |A     |
```

(continued)

Figure 18, continued

```
-----------------------------------------------------------------------------------------
PC-score:          -4        -3        -2      ¦ -1    ¦    0¦     ¦   1  ¦      2
Coded score:                            0      ¦  1    ¦  2  ¦  3  ¦   4  ¦    5
-----------------------------------------------------------------------------------------
Ps morio                                       ¦       ¦     ¦     ¦      ¦
Cycor caeruleus                                ¦       ¦     ¦     ¦A     ¦
Cycor cyanomelas                               ¦       ¦     ¦     ¦  A   ¦
Cycor violaceus                                ¦       ¦     ¦     ¦      ¦
Cycor cristatellus                             ¦       ¦     ¦     ¦ A    ¦
Cycor affinis                                  ¦       ¦     ¦  A  ¦      ¦
Cycor chrysops                                 ¦       ¦     ¦   A ¦      ¦
Cycor mystacalis                               ¦       ¦    A¦     ¦      ¦
Cycor dickeyi                                  ¦       ¦     ¦     ¦      ¦
Cycor yncas                                    ¦       ¦     ¦    A¦      ¦
Cal f. formosa                                 ¦       ¦   A ¦     ¦      ¦
Cal f. colliei                                 ¦       ¦     ¦   A ¦      ¦
Cslo beecheii                                  ¦  A    ¦     ¦     ¦      ¦
Cslo melanocyanea                              ¦       ¦     ¦     ¦      ¦
Cslo sanblasiana yucatanica                    ¦       ¦     ¦A    ¦      ¦
Aph unicolor                                   ¦       ¦     ¦     ¦      ¦
Cycit cristata                                 ¦       ¦     ¦ A   ¦      ¦
Cycit stelleri                                 ¦       ¦  A  ¦     ¦      ¦
Aph c. coerulescens                            ¦       ¦ A   ¦     ¦      ¦
Aph c. californica                             ¦       ¦ A   ¦     ¦      ¦
Aph ultramarina                                ¦     A ¦     ¦     ¦      ¦
Gy cyanocephalus                               ¦  A    ¦     ¦     ¦      ¦
```

(continued)

Figure 18, continued

```
----------------------------------------------------------------------------------------
PC-score:          -4        -3        -2      ¦ -1   ¦     0¦     ¦   1  ¦      2
Coded score:                            0      ¦  1   ¦   2  ¦  3  ¦   4  ¦    5
----------------------------------------------------------------------------------------
Gar glandarius                                 ¦      ¦      ¦     ¦A     ¦
Gar lidthi                                     ¦      ¦      ¦     ¦     A¦
Per canadensis                                 ¦      ¦      ¦     ¦   A  ¦
Per infaustus                                  ¦      ¦      ¦     ¦      ¦
Cypi cayana                                    ¦      ¦   A  ¦     ¦      ¦
Pi pica                                        ¦      ¦     A¦     ¦      ¦
Nuc columbiana                                 ¦  A   ¦      ¦     ¦      ¦
Nuc caryocatactes                              ¦      ¦   A  ¦     ¦      ¦
Po panderi                                     ¦ A    ¦      ¦     ¦      ¦
Pseudopodoces humilis                          ¦ A    ¦      ¦     ¦      ¦
Py pyrrhocorax          A                      ¦      ¦      ¦     ¦      ¦
Py graculus                                    ¦      ¦ A    ¦     ¦      ¦
Cv monedula                                    ¦      ¦      ¦    A¦      ¦
Cv brachyrhynchos                              ¦      ¦      ¦     ¦      ¦         A
----------------------------------------------------------------------------------------
```

Figure 19. Scores on principal component-III from jaw measures. Mnemonics for taxa in Appendix IV.

```
-----------------------------------------------------------------------------------------
PC-score:          -2  |        -1 |           |0         |   1       |     2           3
Coded score:       0   |    1      |     2     |    3     |     4     |     5
-----------------------------------------------------------------------------------------
Cracticus torquatus    |           |           |          |           |           A
Oriolus trailli        |           |           |A         |           |
Paradisaea apoda       |           |  A        |          |           |
Manucodia ater       A |           |           |          |           |
Platylophus galer.     |           |           |      A   |           |
Dn vagabunda           |           |           |          |          A|
Crp temia              |           |           |          |         A |
Csa chinensis          |           |           |          |      A    |
Pt afer                |           |           |   A      |           |
Uroc caerulea          |    A      |           |          |           |
Uroc erythrorhyncha    |           | A         |          |           |
Cyly pumilo            |           |           |          |           |
Cyly mirabilis         |           |           |          |           |
Cyly v. viridicyana    |           |           |       A  |           |
Cyly v. turcosa        |           |           |      A   |           |
Cyly c. cucullata      |           |           |    A     |           |
Cyly c. mitrata        |           |         A |          |           |
```

(continued)

Figure 19, continued

```
-----------------------------------------------------------------------------------------
PC-score:         -2   ¦        -1 ¦           ¦0         ¦   1       ¦     2           3
Coded score:       0   ¦     1     ¦     2     ¦    3     ¦     4     ¦     5
-----------------------------------------------------------------------------------------
Ps morio               ¦           ¦           ¦          ¦           ¦
Cycor caeruleus        ¦           ¦        A  ¦          ¦           ¦
Cycor cyanomelas       ¦    A      ¦           ¦          ¦           ¦
Cycor violaceus        ¦           ¦           ¦          ¦           ¦
Cycor cristatellus     ¦           ¦           ¦          ¦A          ¦
Cycor affinis          ¦           ¦    A      ¦          ¦           ¦
Cycor chrysops         ¦           ¦           ¦       A  ¦           ¦
Cycor mystacalis       ¦           ¦           ¦          ¦    A      ¦
Cycor dickeyi          ¦           ¦           ¦          ¦           ¦
Cycor yncas            ¦           ¦          A¦          ¦           ¦
Cal f. formosa         ¦           ¦    A      ¦          ¦           ¦
Cal f. colliei         ¦     A     ¦           ¦          ¦           ¦
Cslo beecheii          ¦           ¦           ¦ A        ¦           ¦
Cslo melanocyanea      ¦           ¦           ¦          ¦           ¦
Cslo sanblasiana yucatanica        ¦     A     ¦          ¦           ¦
Aph unicolor           ¦           ¦           ¦          ¦           ¦
Cycit cristata         ¦           ¦   A       ¦          ¦           ¦
Cycit stelleri         ¦           ¦          A¦          ¦           ¦
Aph c. coerulescens    ¦           ¦       A   ¦          ¦           ¦
Aph c. californica     ¦           ¦           ¦          ¦A          ¦
Aph ultramarina        ¦           ¦         A ¦          ¦           ¦
Gy cyanocephalus       ¦           ¦           ¦  A       ¦           ¦
```

(continued)

Figure 19, continued

```
------------------------------------------------------------------------------------------
PC-score:         -2   ¦        -1 ¦           ¦0         ¦   1       ¦     2           3
Coded score:       0   ¦     1     ¦     2     ¦    3     ¦     4     ¦     5
------------------------------------------------------------------------------------------
Gar glandarius         ¦           ¦    A      ¦          ¦           ¦
Gar lidthi             ¦        A  ¦           ¦          ¦           ¦
Per canadensis         ¦           ¦           ¦ A        ¦           ¦
Per infaustus          ¦           ¦           ¦          ¦           ¦
Cypi cayana            ¦           ¦   A       ¦          ¦           ¦
Pi pica                ¦     A     ¦           ¦          ¦           ¦
Nuc columbiana         ¦           ¦           ¦ A        ¦           ¦
Nuc caryocatactes      ¦           ¦           ¦       A  ¦           ¦
Po panderi             ¦           ¦           ¦          ¦   A       ¦
Pseudopodoces humilis  ¦           ¦           ¦A         ¦           ¦
Py pyrrhocorax         ¦A          ¦           ¦          ¦           ¦
Py graculus            ¦           ¦        A  ¦          ¦           ¦
Cv monedula            ¦           ¦ A         ¦          ¦           ¦
Cv brachyrhynchos      ¦           ¦           ¦          ¦           ¦                 A
------------------------------------------------------------------------------------------
```

Figure 20. Scores on principal component-IV from jaw measures. Mnemonics for taxa in Appendix IV.

```
------------------------------------------------------------------------------------
PC-score:          -4             -2     ¦    ¦   0¦   ¦   ¦      2               4
Coded score:                       0     ¦ 1  ¦ 2  ¦ 3 ¦ 4 ¦      5
------------------------------------------------------------------------------------
Cracticus torquatus                      ¦    ¦   A¦   ¦   ¦
Oriolus trailli                          ¦    ¦    ¦   ¦  A¦
Paradisaea apoda                         ¦    ¦    ¦  A¦   ¦
Manucodia ater                           ¦    ¦    ¦A  ¦   ¦
Platylophus galericulatus                ¦    ¦    ¦ A ¦   ¦
Dn vagabunda                             ¦    ¦A   ¦   ¦   ¦
Crp temia                                ¦    ¦    ¦   ¦   ¦      A
Csa chinensis                            ¦   A¦    ¦   ¦   ¦
Pt afer               A                  ¦    ¦    ¦   ¦   ¦
Uroc caerulea                            ¦    ¦  A ¦   ¦   ¦
Uroc erythrorhyncha                      ¦   A¦    ¦   ¦   ¦
Cyly pumilo                              ¦    ¦    ¦   ¦   ¦
Cyly mirabilis                           ¦    ¦    ¦   ¦   ¦
Cyly v. viridicyana                      ¦   A¦    ¦   ¦   ¦
Cyly v. turcosa                          ¦    ¦    ¦ A ¦   ¦
Cyly c. cucullata                        ¦    ¦   A¦   ¦   ¦
Cyly c. mitrata                          ¦    ¦    ¦   ¦A  ¦
```

(continued)

Figure 20, .continued

```
------------------------------------------------------------------------------------
PC-score:          -4             -2      |    |   0|   |   |      2               4
Coded score:                        0     | 1  | 2  | 3 | 4 |      5
------------------------------------------------------------------------------------
Ps morio                                  |    |    |   |   |
Cycor caeruleus                           |    |    |   |  A|
Cycor cyanomelas                          |    |    |   | A |
Cycor violaceus                           |    |    |   |   |
Cycor cristatellus                        |    |    |  A|   |
Cycor affinis                             |    |    |   |A  |
Cycor chrysops                            |    |    |A  |   |
Cycor mystacalis                          |    |    |   |  A|
Cycor dickeyi                             |    |    |   |   |
Cycor yncas                               |    |   A|   |   |
Cal f. formosa                            |   A|    |   |   |
Cal f. colliei                            |    |    |A  |   |
Cslo beecheii                             |    |    |A  |   |
Cslo melanocyanea                         |    |    |   |   |
Cslo sanblasiana yucatanica               |    |   A|   |   |
Aph unicolor                              |    |    |   |   |
Cycit cristata                            |    |   A|   |   |
Cycit stelleri                            |    |   A|   |   |
Aph c. coerulescens                       |    |  A |   |   |
Aph c. californica                        |    |    | A |   |
Aph ultramarina                           |    | A  |   |   |
Gy cyanocephalus                          |   A|    |   |   |
```

(continued)

Figure 20, continued

```
-----------------------------------------------------------------------------------
PC-score:          -4             -2     |    |   0|   |   |      2               4
Coded score:                       0     | 1  | 2  | 3 | 4 |      5
-----------------------------------------------------------------------------------
Gar glandarius                           |    |    |   | A |
Gar lidthi                               |    |  A |   |   |
Per canadensis                           |    |  A |   |   |
Per infaustus                            |    |    |   |   |
Cypi cayana                              |    |  A |   |   |
Pi pica                               A  |    |    |   |   |
Nuc columbiana                           |    |    |   |   |    A
Nuc caryocatactes                        |    |    |   |   |          A
Po panderi                               |  A |    |   |   |
Pseudopodoces humilis                    |   A|    |   |   |
Py pyrrhocorax                           |   A|    |   |   |
Py graculus                           A  |    |    |   |   |
Cv monedula                              |    |    |   |A  |
Cv brachyrhynchos                     A  |    |    |   |   |
----------------------------------------------------------------------------------------
```

Concerted change in shape of the cranium is assessed by PC-III from the cranial dimensions, which has a moderate negative loading on cranium depth and a moderate positive loading on length (Table 1 and Figure 17). Thus Cranium PC-III scores as a continuum from a short, deep cranium to long and shallow.

Comparing the scoring on Cranium PC-III as shown in Figure 17 to shape of the skulls by direct inspection, it appears that this component is indicating similar relative depth and length throughout. In some cases Cranium PC-III appears to give erratic results, for example in the genus *Cyanocorax*. Some inadequacy in this component may be due to unreliability of the measure of cranial depth. There is no homologous landmark for the highest point of the cranium.

Shape of the jaws - Wide in most corvids; narrower in Pi, some Cyly, many other AJ; very narrow in Pt, Po, Py. Very long and expanded distally in Pt, Cv, Pi; tapered and sickle shaped in Po, Py, Nuc; slightly tapered in Dn, Crp. Symphysis of the lower jaw greatly elongated in Crp, Po, Py, Nuc. Length, depth, and profile of the jaws extremely varied.

Narrow jaws in *Pica*, *Pyrrhocorax*, and *Podoces* are accompanied by medial inset of the quadrate, which is extreme in the latter two. There is no morphologic grounds for rejecting the homology of these conditions. Width of jaws varies in *Cyanolyca* but where it is narrowest the quadrate is deeply inset. Thus these conditions are similar. In the North American jays instead narrowing of the jaws occurs in the distal part at the angle and beyond, without medial inset of the quadrate. The latter condition does not appear to be homologous to that in *Cyanolyca*.

Quadrate inset is extreme in Ptilostomus. The very narrow jaw is however otherwise so different from that of any other corvid that homology of the inset quadrate condition among all appears unlikely but the determination thus rests on extrinsic evidence indicating non-monophyly. Quadrate inset thus appears to be separately derived at least twice and probably three times in Corvidae.

Elongated, distally inflated jaws in Pica and Corvus occur in a context of design differences from Ptilostomus. These differences cannot be appreciated from external appearance. Corvus and Pica lack caudal incursion of the inflated bony rostrum onto the nostril, as seen in Ptilostomus. The rostral palate structure is extremely different in Ptilostomus from that of Corvus and Pica, which are very much alike. The structure of the palate shows some of these differences (Figures 2, 3, 7).

In Podoces and Pyrrhocorax the symphysis of the lower jaw is elongated rostrally, in Nucifraga, Crypsirina, and slightly in Cyanocorax, caudally, as shown by a shortened distance between angle of the mandible and caudal border of the symphysis. Tapering of the tip of the jaws is associated with very narrowed and long jaws in Pyrrhocorax but with simple lateral incisure in Nucifraga. These differences cast doubt on homology of the elongated symphysis and tapering in Nucifraga to that of Pyrrhocorax and Podoces. The homology of the long symphyses in Nucifraga, Crypsirina, and Cyanocorax and tapering in the two former is counterindicated by other very great differences in the shape of the jaws, but in any case the point is moot since there is no question of the monophyly of these three.

Concerted change in shape of the jaws was assessed by PC-II, III, and IV from five jaw measurements (Table 1 and Figures 18 through 20). Jaw PC-II has a high positive loading on jaw width and depth and a high negative loading on lower jaw symphysis length. It performs very well in polarizing taxa with a shallow, narrow jaw and long lower jaw symphysis against those with a deep and wide jaw and a short jaw and short lower jaw symphysis, e.g. Nucifraga, Podoces, Pyrrhocorax, vs. Garrulus and Perisoreus. It also distinguishes this contrast in Cyanocorax compared to North American jays. It distinguishes the relatively deep-jawed Corvus from Pyrrhocorax species very well. The uniqueness of Crypsirina, Ptilostomus, and the boreal jays is indicated. It is apparent though that similar scores do not always indicate homologous conditions (c.f. Ptilostomus, Garrulus). Nevertheless the distinctions are finer and more objective than could have been achieved by observation and coding from exemplar.

Jaw PC-III has a high negative loading for width and a high positive loading for depth, also a lesser negative loading on length and lesser positive loading on lower jaw symphysis length. Jaw PC-III should be contrasting primarily a wide, shallow jaw to a narrow, deep jaw. Complexity of the factor loading makes interpretation difficult at higher taxonomic levels and homology of the underlying shapes highly uncertain. Again, although the scoring usually corresponds to direction observations, on this component some taxa with differently shaped jaws receive the same score, for example Nucifraga columbiana and Garrulus lidthi.

Jaw PC-IV has a high negative loading on length of the upper jaw symphysis, high positive loading on length of the lower jaw symphysis, and moderate positive and negative loadings respectively on width and length of the jaw. Thus this component score should be polarizing primarily on length of the symphyses and contrasting taxa with a long upper and short lower jaw symphysis to those with the reverse situation. That such a reciprocal relationship exists is rather interesting from a functional point of view. The short upper jaw symphysis and long lower symphysis co-occur with wide, short jaws. Within American jays highest values are in largest Cyanocorax jays and values decrease gradually to the North American jays. Within Cyanolyca values decrease from high in cucullata to lower in viridicyana. For jaw PC-IV most corvids are close to the middle value; only a few taxa are very distinctive, thus this component accounts for only a very small proportion of the variance. Nevertheless it is informative. For example Jaw Principal Component-IV distinguishes the caudally elongated symphysis of the lower jaw in Nucifraga from the rostrally elongated symphysis in Podoces and

Pyrrhocorax. The high values in large _Cyanocorax_ jays probably reflect a slight caudal elongation of the lower jaw symphysis as well as widening, that is apparent to the eye but cannot be evaluated by categorization. The decreasing values in the smaller American jays reflect the progressively shorter upper and longer lower jaw symphysis, plus narrowing and lenthening, which is greatest in _Gymnorhinus_. This component appears to reflect shapes correctly.

Position of contact of the palatal flange of the ventral bar of the jaw - Far medial in primitive oscine, Py; moderately far lateral in Dn, Crp; far lateral in all other corvids.

The far lateral position of the prepalatine bars is essentially similar in all corvids showing the condition except that the extent of fusion with the ventral bar of the jaw varies, as does the shape of the palatal flange of the maxilla.

There is no intrinsic evidence to show that the far medial position of the prepalatine bars in _Pyrrhocorax_ is not the primitive oscine condition. In this case other evidence (which is extensive) of the monophyly of _Pyrrhocorax_ and its membership in the Corvidae is required to demonstrate non-homology.

In the species _graculus_ the palatal flange of the maxilla contacts the prepalatine bar on its dorsal surface, a condition derived within corvids as analyzed beyond, but in the species _pyrrhocorax_ the palatal flange is flat and contacts the lateral rim of the prepalatine bar, as in the primitive oscine. The two conditions appear to be a morphocline in which graculus is less aberrant from other corvids.

Transpalatine pit - No ventral pit on the transpalatines in primitive oscine, southern magpies and treepies, Pt, Cypi, Per, Cyly; pit absent or small in Gar, Py; usually present but small and variable in size in Cslo, Ps, Cal, Cycor; moderately large in Aph, Cycit, Gy; very large in Pi, Nuc, Cv; large but shallow in Po.

The shape of the transpalatine pit is very similar in Pica, Corvus, Nucifraga, and Podoces. The unflared transpalatines and very small pit in Garrulus and Pyrrhocorax suggest a transitional condition between lack of the pit its presence. The conditions of the caudolateral lamellae and transpalatines in these two genera are strikingly similar despite the very different contacts of the prepalatine bars. Thus there is no direct evidence to reject the hypothesis that the rudimentary pits in these genera are homologous as an intermediate development of a transpalatine pit. In Perisoreus the lateral border of the palatine flares, but there is only a broad, spade shaped transpalatine with no pit. The appearance is not similar to that in any other taxon.

Suprameatic crests

Suprameatic crests were discussed with osteology of American jays. In reprise, the homology of crests and processes in larger neotropical jays cannot be demonstrated directly. Interpretation of the conspicuous crest in larger neotropical jays (Cyanocorax, Cissilopha, Calocitta, Psilorhinus) as indicated in the data set (Appendix III) assumes homology of the ventral suprameatic crest and process to that of _Cyanocorax_ _yncas_ in which homology can be demonstrated because two crests are visible and similarly located to crests in _Cyanolyca_, North American jays, and holarctic corvids (Figure 10). Homology of the crests among American jays and holarctic corvids is also demonstrated by developmental information (not available for _Cyanocorax_). The single conspicuous suprameatic crest of treepies, piapiac, and southern magpies appears to correspond to the more elevated crest traversing the temporal fossa in holarctic corvids and in those American jays in which it can be distinguished, but this interpretation needs support from study of jaw muscles. The ventral border of the squamosal wall below the dorsal suprameatic crest is homologous among holarctic genera and possibly all American jays as a ventral suprameatic crest. Correspondingly the suprameatic processes of treepies and southern magpies are _not_ homologous as rostral enlargements of the ventral suprameatic crest to the suprameatic processes of some holarctic corvids and many (?) all American jays.

Size _of_ _the_ _temporal_ _fossa_ - Moderately large and well defined in most corvids; very small in Pi, Po, Py, Gy.

The very small temporal fossa in the named genera has a poorly defined caudal border. The fossa is smallest in _Podoces, Pyrrhocorax, and Gymnorhinus_. The dorsal suprameatic crest is only moderately conspicuous. Among the holarctic genera named there is no intrinsic evidence to argue against homology. The reduction in the temporal crest in these but not in Gymnorhinus is associated with medial inset of the quadrate and a short, blunt zygomatic process with little or no elevation of the lateral zygomatic crest.

Rostral slope of the lateral cotyla of the mandible - Gradual slope to dorsal rim of ramus in primitive oscine and many corvids, distinct rostral crest in Cyly, Pi, some Cv; rostral crest very high in most Cyly, other AJ.

The very similar appearance of the lateral cotyla of the mandible in Cyanopica and Cyanolyca suggests homology of the elevated rostral crest of the lateral cotyla of the mandible in American jays and several holarctic genera but that it is separately modified from this condition in various lineages. This character is discussed at length with the comparative osteology of Cyanolyca, Cyanopica, and Pica.

Humerus shape - External tubercle confluent with the shaft and the head (most Corvidae); set out slightly ventrally from the shaft (Corvus monedula, Po, Nuc); set out strongly (Corvus brachyrhynchos, Py). Head of the humerus not large, biceps crest angular, humerus short to moderately long (most Corvidae); head of the humerus enlarged, biceps crest elongated, humerus greatly elongated (Cv, Py). Dorsal supracondylar process short and wide (most Corvidae); narrow and extending farther proximally along the shaft (moderately in Nuc, Po; extremely in Cv, Py).

Moderate extension of the dorsal supracondylar process proximally along the shaft occurs in all the crow-like genera except Podoces. At least minimal outset of the ventral tubercle occurs in all. Similar configuration of the head of the humerus occurs uniquely in Corvus and Pyrrhocorax. These conditions shared by several of the crow-like genera occur among them in a mosaic distribution. Although there is no intrinsic reason to suggest non-homology the relative simplicity of each change suggests the possibility of parallelism as the explanation of the mosaicism.

Number of synsacral vertebrae; shape of the synsacrum - vertebrae 12 in primitive oscine, some corvids; 11 in Pi, Cypi, Gar, Per, Cv, Nuc, Py, Cyly, NAJ. Synsacrum narrow in many corvids; broader in Cypi, Pi, NAJ; very broad in Gar, Per, Cv, Py, Po.

The form of the individual vertebrae in the synsacrum is extremely variable individually in corvids. Thus the identity of component vertebrae is difficult to verify so that one cannot see if it is the same vertebra lost in all cases. Nevertheless differences in shape of the synsacrum are some evidence. A reduction in the number of synsacral vertebrae from the typical and probably primitive oscine number, twelve, seems to be associated with small overall size in Cyanolyca since the largest species has eleven, the smaller species, uniquely among corvids, have only ten. Holarctic corvids in contrast have a reduced number in conjunction with a short, wide synsacrum. The reduction in number of component vertebrae thus appears to be part of a different overall design in each case, and probably non-homologous.

Summary

Two characters that seem to unite Cyanolyca to some or all holarctic genera are probably not homologous among these taxa: few synsacral vertebrae and short orbit. Other characters examined appear to be homologous among a large group including not only Cyanolyca and holarctic corvids but also American jays: elevation of the suprameatic crest, presence of a rostral crest of the lateral cotyla of the mandible. Similar narrowed jaws in *Pica* and some *Cyanolyca* do suggest homology. However the rudimentary rostral articulation of the jaw in *Cyanolyca* clearly seems to be homologous to the well developed articulation in other American jays as discussed in the section "Comparative Osteology" and elsewhere (Zusi 1987). This character remains the strongest evidence for affinities of *Cyanolyca*, with the American jays.

The homology of suprameatic crests in larger species of *Cyanocorax* is uncertain. Reduction in size of the temporal fossa, associated with inset quadrate and narrowing of the jaws, may be homologous among *Pica*, *Pyrrhocorax*, and *Podoces*. Far lateral position of the prepalatine bars is probably homologous among all corvids showing the condition. The medial position in *Pyrrhocorax* is not homologous to the more medial condition common to most oscines. The long symphysis and tapering of the lower jaw is evidently not homologous in *Nucifraga* to that of *Pyrrhocorax* or *Podoces*.

Unusual characters of the humerus that occur in the crow-like birds (*Corvus*, *Nucifraga*, *Pyrrhocorax*, *and Podoces*) are present in a mosaic pattern among them but there is no intrinsic evidence for non-homology. Thus these characters provide equivocal evidence for uniting any of these taxa.

Several coded characters included in the data set are especially ambiguous at higher taxonomic levels: taper of the jaw and PC-III from jaw measures, PC-III from cranium measures, number of synsacral vertebrae, and transpalatine pit shape. The assessment of shape by principal components analysis thus shows mixed success.

Many other characters occur in similar form both in some American jays and some holarctic corvids. These characters include dense ossification of the rostral palate and extensive fusion of prepalatine and ventral bar of the jaw (greatest in some North American jays and in Eurasian jays and nutcrackers), large size of transpalatine pits (some North American jays, Pica, Corvus, and Nucifraga), widening of nasal processes of the premaxilla (all holarctic corvids, North American jays), lengthening of the orbit (crow-like birds, some Cissilopha, some Cyanocorax, North American jays), and reduction in cranial and/or interorbital fontanelles (many American jays, some crow-like birds, Garrulus. For these features, homology among American jays and holarctic corvids is rejected on the basis of other characters strongly indicating monophyly of the American jays. Additionally the appearance of these characters is often in such a mosaic pattern within the holarctic corvids that few of them appear to have arisen only once even within that group.

PHYLOGENETIC ANALYSIS

1. Limits and definition of the Corvidae

Review of osteology indicates that the bower birds, Ptilonorhynchidae, and cnemophiline birds of paradise (in the sense of Bock 1963b), do not share most of the diagnostic osteologic characters common to other corvoid birds. This finding needs review in the context of other oscines.

Characters of the corvoid assemblage

Some changes from the hypothetical primitive oscine are shared by corvoids with a wider group of oscines. In the antorbital plate the prefrontal is more rostral and ventral, lying partly within the nasal capsule. The ectethmoid is expanded laterally and fused with the frontal. The humerus is broader proximally, associated with a slight extension of the sulcus for the dorsal head of the m. humerotriceps toward the head of the humerus. In some corvoids this sulcus ascends far enough to undercut the head of the humerus slightly.

An additional set of changes from the primitive oscine characterize most or all members of a limited group of corvoids including Oriolidae, Cracticidae, Paradisaeidae except cnemophilines, Platylophus, and some of the Corvidae, particularly the (genera Dendrocitta, Crypsirina, Ptilostomus, and Cissa and Urocissa). Some of these changes probably are characteristic of a larger group that includes at least the Artamidae, Dicruridae, and some Campephagidae, but the limits of such a group have not been explored here. Some heterogeneity in Campephagidae precludes much comment on that group. Corcoracidae and Grallina share some but not all of these changes (node 1 Figure 21). Numbers in parentheses refer to the character number from the data set,

Appendix III, uniting nodes in Figure 21. Descriptions of characters are in Appendix II, ordered within character complexes.

The orbit and cranium are relatively deep (about as deep as wide) and the orbit is not elongated. The primitive oscine condition for these shapes could not be evaluated. Node 2 is united by (9, 10) moderate reduction in size of the interorbital and postorbital fontanelles. (28) The craniofacial hinge is conspicuously developed and (16) the nasal processes of the premaxilla are wide. They are almost completely fused to the nasals laterally. The dorsal nasal bar is heavy, and (7) the nostrils are ovate, approaching round, that is, they are less elongated than in most oscines and much less elongated than in suboscines.

The rostral ossification of the palate extends between the prepalatine bars, making a long upper jaw symphysis, but as noted earlier this may be a primitive oscine feature. The nasal floor is partly or completely ossified, but ossifications of the floor clearly are not all homologous among the groups and taxa concerned. (31) The transpalatines are well defined by a long, deep, rostral extension of the sulcus on the medial plate of the palatine (not in Oriolidae). (30) The lateral rim of the palatine and transpalatine is straight, in these groups forming a heavy bar (also in Struthidea, Dicrurus, not in Oriolus) and the transpalatines are not flared laterally. (10) The tip of the maxillopalatine is bluntly truncated, not expanded. The temporal fossa and quadrate articulations are much as in the primitive oscine.

(73) The tarsometatarsus is very short (also in Dicruridae). (76) The first metatarsal is moved slightly to articulate less on the plantar surface and more on the medial surface of the shaft of the tarsometatarsus. Its trochlea articulates with the hind toe slightly more dorsally (also in Corcoraciidae, extreme in Dicruridae).

Thus several characters unite Oriolidae, Cracticidae, and Paradisaeidae to the Corvidae. Some characters imply further a narrower sister group relationship of Corvidae to Paradisaeidae (Node 3). The manucodes among the birds of paradise particularly resemble the southern magpies and treepies of the Corvidae in the following characters, which may be interpreted as derived in oscines: (8) various parts of the skull (rostral palate and upper jaw, frontals, periotic and squamosal) are very highly pneumatized. The lateral nasal bar is inflated, its sutures to the maxilla obscured by complete fusion. (22, 24) The prefrontal is rudimentary or not ossified. If present its dorsal lobe is not exposed laterally. (25) The ossified palatal part of the premaxilla extends far caudally and partly below the nasal capsule. (28) The prepalatine bar is slightly farther ventrolateral, nearly touching the ventral bar of the jaw at its rostral end. The palatal flange of the ventral bar of the jaw is slightly inflected to meet the bar, but the flange continues to contact the prepalatine bar on its lateral rim. (not coded) The vomer is flared widely at the rostral end and has a very long, narrow, rodlike shaft. Even with the upper jaw not elevated, the vomer nearly reaches the ossifications in the floor of the nasal capsule or between the prepalatine bars. There is a wide suprameatic crest (not coded) which forms an outset suprameatic process at the quadrate. The process appears to be homologous among corvoids and southern magpies and treepies but probably is not homologous to a suprameatic process formed in some other corvids. (39) There is a subzygomatic sulcus that extends caudally onto the temporal fossa. (not coded) On the humerus there is an unusually large fossa for the origin of the m. scapulohumeralis cranialis.

Derived characters shared by Oriolidae, Cracticidae, Campephagidae, and Paradisaeidae (node 4) include (20) very heavy or extensive ossification of the nasal capsule (also in Struthidea, not in Oriolidae), and (28) a more conspicuous craniofacial hinge (also in Grallina). (23) Also the ectethmoids are very highly inflated. (74, 75) The tarsometatarsus is very short and broad and markedly tapered. There is a deep, wide plantar sulcus. (76, 77, 78) There is no interlocking articulation between toes III and IV or it is only represented by a low, rounded lateral epicondyle of toe III and a shallow medial facet of toe IV; the interlock is presumed lost. Toe IV is elongated. Metatarsal I articulates far dorsally with the first toe.

All characters of the tarsometatarsus and foot are also found in Dicruridae, in some but not all Campephagidae, and in Artamidae.

Thus the evidence is equivocal for which taxa form the sister group of Corvidae. First, there is the evidence from the tarsometatarsus implying a large sister group, to include not only Paradisaeidae, Oriolidae, and Cracticidae but also other taxa not formerly considered close relatives, e.g. the Dicruridae. Opposing this there is the evidence from the large number of characters drawn from other systems supporting narrower monophyly of Paradisaeidae and Corvidae.

It seems particularly unlikely that the complex and unusual conditions of the tarsometatarsus and foot, shared by all of this large assemblage except corvids, are primitive to corvoids and have been lost in Corvidae. On the contrary, the more dorsomedial articulation of the toes in Corvidae (shared with Corcoracidae) seems to be a minimal change toward the far plantar articulation, a characteristic component of the well-developed complex. Possibly the unusual conditions of the craniofacial hinge and palate shared by manucodes and southern magpies and treepies are primitive to the entire corvoid assemblage and have been lost in many.

These analyses circumscribe but do not completely define primitive corvid characters. The taxonomic composition of the sister group of Corvidae remains uncertain.

Platylophus

The black jay, Platylophus, shares many derived characters of the sister group, including detailed resemblance in the palate and upper jaw to that of manucodes among the birds of paradise, and in construction of the tarsometatarsus and toes. It therefore appears to be cladistically a member of that group. Nevertheless jaylike behavior of Platylophus indicates reservation in this conclusion.

Pseudopodoces

The dwarf ground jay, Pseudopodoces, is excluded from the Corvidae. Pseudopodoces lacks a diagnostic character of the corvoid groups, the reduction in size of orbital fontanelles, and it lacks the widened interpalatine distance characteristic of all corvids except Pyrrhocorax in which the state is secondarily derived (see beyond). Although Pseudopodoces resembles Podoces superficially in shape of jaws and cranium, Pseudopodoces shares with distantly related oscines a well developed second pneumatic fossa of the humerus and lack of the notched articulation between toes III and IV. Its distinctive upper jaw hinge is unlike that of any corvid but resembles that of certain birds of the families Sittidae and Paridae.

Characters of primitive Corvidae (node 5)

In Corvidae, the cranium is dorsolaterally more expanded than in other corvoids. The cranium appears larger but assessment of size and shape was complicated by allometry and inadequate measurement (discussed in the

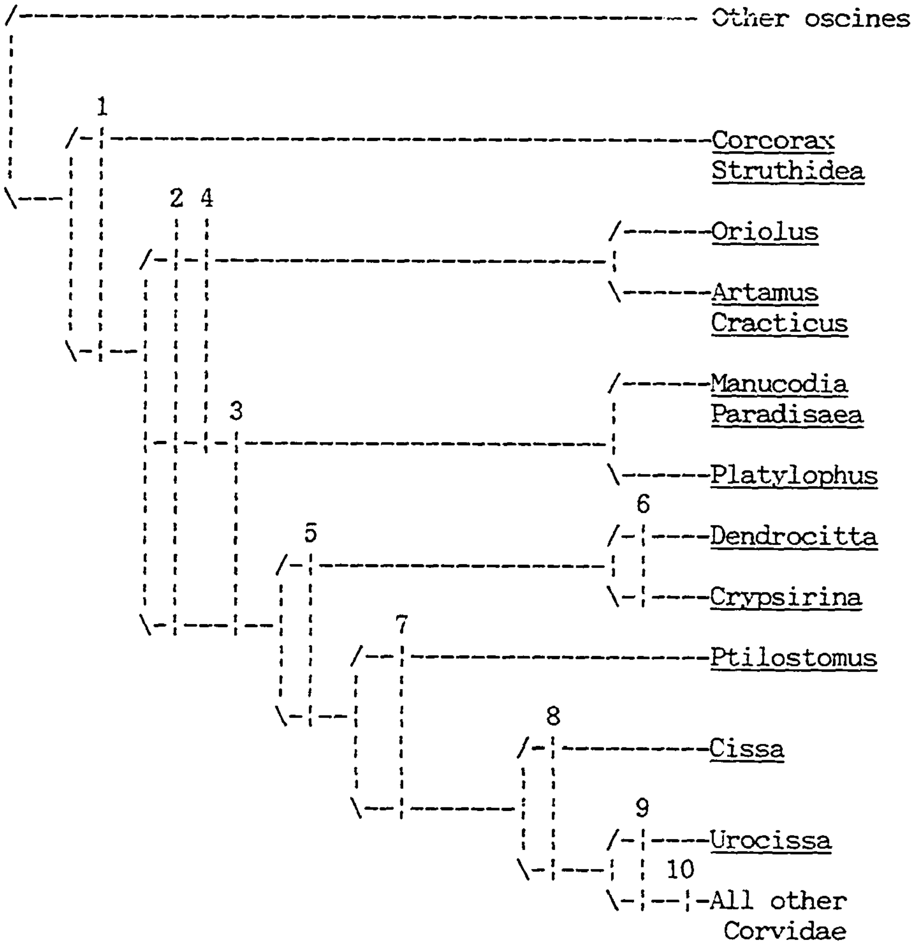

Figure 21. The major lineages of Corvidae and corvoid comparison groups.

"Approach" and "Methods", and "Review of Characters").

The many shared derived characters of manucodes and the southern magpies and treepies are assumed primitive for Corvidae. In addition most or all of the southern magpies and treepies additionally share the following changes: (11) The upper jaw is more inflected and decurved, and is hooked at the tip. (26, 27 28) The prepalatine bars are slightly farther lateral and the palatine process of the premaxilla is not visible. (21) The tip of the maxillopalatine is usually not ossified. (34) The postorbital process is recessed so that it descends along the caudal wall of the orbit or nearly so. It is often broadly notched in profile. (35) The caudal wall of the orbit is oriented more vertically. (5-5) The zygomatic process is heavy and wedge shaped in lateral view. (58) The caudal cotyla of the mandible lies at a flatter angle to the lateral cotyla (not in Ptilostomus). (51) The lateral prominence of the lateral cotyla of the mandible is tilted caudolaterally and enlarged.

PHYLOGENETIC ANALYSIS

2. The major lineages of Corvidae.

Based on the preceding assessments, treepies, Dendrocitta and Crypsirina, are included in Corvidae and placed as the most remote branch. Ptilostomus is the second branch, Cissa the third, Urocissa fourth and sister taxon to all remaining Corvidae (Figure 21). The same overall topology resulted from a separate analysis with characters not scaled to equal weights. When genera are eliminated one at a time there is only minor perturbation among these branches. When Ptilostomus is left out, Southeast Asian magpies Cissa and Urocissa are made monophyletic and when Cissa is left out Ptilostomus is made monophyletic with treepies. This repositioning is explained by a mosaic of character changes in Ptilostomus such that some may be interpreted as synapomorphic with the treepies, some with southern magpies.

Dendrocitta and Crypsirina (node 6)

The treepies Dendrocitta and Crypsirina consistently are placed monophyletically. They retain most of the primitive corvid characters but share with remaining Corvidae the minimal defining characters of the family as outlined above. Treepies uniquely have (4) a very short, deeply decurved and very strongly inflected and hooked upper jaw; the lower jaw is broad. The lateral profile remains very slightly incised. Ossification and (not coded) extreme elevation of the floor of the nasal capsule is shared with Ptilostomus. From examination of x-rays of skulls in skins Temnurus appears to belong with treepies.

Platysmurus

Preliminary examination of Platysmurus indicated similarity to the treepies but final assessment has not been done.

Ptilostomus

Ptilostomus shares with most remaining corvids (node 7) (8) a lesser inflation of the skull, (15) a less conspicuous craniofacial hinge, (14) no tapering of the lower jaw, (28) more lateral position of the prepalatine bars, (64) extension of the pectoral crest relatively far down the shaft of the humerus, (73) longer tarsometatarsus, and (75) less recession of the medial crest of the tarsometatarsus from the dorsal surface. Because the new characters Ptilostomus shares with remaining corvids are few and occur in context of a generally bizarre form, and because Ptilostomus shares some characters otherwise unique to treepies, it is hard to be sure which are homologous to changes in treepies and possibly primitive for Corvidae, possibly synapmorphic for treepies and Ptilostomus; which are homologous to changes in remaining corvids; and which are homoplastic or autoapomorphic. The cranium in Ptilostomus is less pneumatized but nevertheless occurs with a highly pneumatized jaw. The untapered lower jaw is extremely narrow and otherwise unique in form. The short nasal capsule is extremely elevated and the nasal floor is ossified and elevated as in treepies. The prepalatine bars are far apart as in most remaining corvids but uniquely are very thin and attenuated rods. In any reconstruction Ptilostomus is an isolated early lineage of Corvidae.

Cissa and Urocissa

Cissa and Urocissa share many changes with most or all of the remaining corvids (node 8). (not coded) The upper jaw is less pneumatized. (16) The craniofacial hinge is very inconspicuous, the nasal processes of the premaxilla are very narrow, and there is no frontal boss. (7) The nostrils are longer. (not coded) The lateral nasal bar is less inflated and the sutures to the maxilla are visible, not fused, the maxilla forming a rounded wedge visible laterally at the base of the bar. (24) The prefrontal is ossified and inflated into the nasal capsule. (22) Its dorsal lobe is exposed laterally. (25) The rostral palate ossification is slightly denser. (30) The transpalatines are flared laterally and the caudolateral margin is excavated, apparently as attachment surface for lateral pterygoideus musculature. (31) The ventral sulcus on the palatine plate is shorter and shallower, and (29) the caudal margin of the palatines is less decurrent rostrolaterally. (64) The pectoral crest is very long, extending distally well beyond the m. pectoralis attachment site. (not coded) The depression for m. scapulohumeralis cranialis is smaller.

Urocissa additionally shares with remaining corvids (node 9) character changes as follows: (6) the cranium between the orbits is slightly narrowed. (4) The upper jaw is slightly less deep. (27, 28) The prepalatine bar is farther ventrolateral and the palatal flange of the ventral bar of the jaw is very strongly inflected to meet the prepalatine bar on its lateral margin. (21) The tip of the maxillopalatine is ossified in some specimens. It is slightly expanded. Thus Urocissa shares more changes with remaining corvids than does *Cissa*.

Urocissa and *Cissa* may be interpreted either as paraphyletic taxa or as monophyletic. In the analysis of data the three coded taxa emerge as three paraphyletic lines or else two of them are in an unresolved trichotomy with remaining corvids. However the review of characters supported strongly the suggestion that *Urocissa* is sister taxon to all remaining corvids. Some characters that may appear as synapomorphies for *Cissa* and *Urocissa* are large size, narrow nasal processes, and long synsacrum. However large size is widespread in American jays and holarctic corvids. The narrowed nasals greatly resemble the condition in many American jays and may be synapomorphic for a large assemblage. A longer synsacrum (twelve vertebrae) is evidently primitive in oscines and occurs also in many American jays and be primitive in Corvidae even though shortened in treepies and others. When these characters are not considered synapmorphic for *Cissa* and *Urocissa*, support for their monophyly vanishes. Review of more specimens and species of these magpies is needed.

Summary

In the transition from earliest corvids, the ancestor of the holarctic corvids and the American jays became in certain respects more like other oscines, by the loss of some primitive corvoid characters that were nevertheless derived within corvoids (starred characters in the following). Summarizing, the common ancestor of remaining corvids may be characterized and compared to the primitive corvid as follows:

Skull shape: The cranium remained deep and moderately wide but was *less pneumatized. *The upper jaw was slightly less deep but the jaws were still wide, and they were wider distally (not incised laterally). *The lower jaw remained deeply cupped at the tip. *Dorsal and ventral profiles of the jaws retained their moderately convex profiles. *The upper jaw was less inflated.

Craniofacial hinge: The interorbit was slightly narrowed and the craniofacial hinge was much less conspicuous. The nasal processes of the premaxilla were very narrow.

Nasal-maxilla-premaxilla suture: *The maxilla formed a prominent wedge in the suture at the base of the lateral nasal bar. This is the primitive oscine condition, but in earlier corvids the maxilla was obscured by inflation of the lateral nasal bar and the sutures were obscured by fusion.

Antorbital plate: *The prefrontal was ossified. It lay along the rostrolateral border of the ectethmoid and was moderately inflated into the nasal capsule.

Palate: The rostral part of the palate was less extensively but slightly more densely ossified. The prepalatine bars were widely separated and slightly ventromedial to the ventral bar of the jaw. The palatal flange of the ventral bar of the upper jaw was sharply inflected to meet the prepalatine bar on its lateral rim. The tip of the maxillopalatine was ossified and slightly expanded.

Temporal fossa and quadrate articulations were much as in the primitive corvid but the caudal cotyla of the mandible was oriented more dorsally rather than angled and facing rostrodorsally.

Humerus: On the humerus *the huge depression for attachment of m. scapulohumeralis cranialis was reduced in size and moved to a position just distal to the medial bar of the ventral tubercle. The pectoral crest was very long, extending down the shaft well beyond the attachment for m. pectoralis. Synsacrum: The length of the synsacrum is equivocal but may have remained at the primitive oscine number, eight.

Tarsometatarsus and toes: *The tarsometatarsus was longer. *The medial crest of the tarsometatarsus was less recessed toward the plantar surface. The shaft remained slightly tapered. The toes remained as in the primitive corvid.

PHYLOGENETIC ANALYSIS

3. The Holarctic and American genera

The holarctic and American genera of Corvidae appear to be a monophyletic assemblage. In the loss of some primitive corvid characters the common ancestor of this group became in certain respects more like other oscines, displaying more of the probably primitive oscine characters, but the palate is unique. This conclusion of the monophyly and relatively late derivation of the northern groups is independent of any assumptions about the sister group of Corvidae. In separate analysis not shown here a similar topology for the Corvidae is found using only the hypothetical oscine ancestor without introducing any other corvoids.

The homology of some transformations that appear to unite the northern and American groups is ambiguous. However, the following additional changes appear to be homologous among all (Figure 21, node 10): (37, 38) In the temporal fossa the suprameatic crest was reduced in width at its rostral end and elevated above the quadrate articulation. The wall of the squamosal ventral to the suprameatic crest met the quadrate below and ventrolateral to the squamosal condyle of the otic articulation. Its ventral border formed a ventral suprameatic crest. (40) Rostrally the ventral suprameatic crest was slightly enlarged at the quadrate. (75) The medial crest of the tarsometatarsus was well defined and only slightly recessed from the dorsal surface.

More ambiguously, but possibly also synapomorhic for all, the northern magpies, many crows, and all American jays have (53) an elevated rostral slope of the lateral cotyla of the mandible with a conspicuous transverse rostral crest.

Relationships among the northern genera and American jays

Table 2 summarizes the analyses of the genera of Corvidae including the resampled subsets of taxa. The consistent results are

(1) The American jays of the genera *Gymnorhinus*, *Aphelocoma*, *Cyanocitta*, *Cissilopha*, *Cyanocorax*, *Psilorhinus*, and *Calocitta* are placed as a monophyletic group.

(2) The holarctic genera (including crows) are placed as a

Table 2. Results of the analysis of resampled subsets of taxa in the genera of Corvidae. Parentheses indicate phylogenetic nesting of taxa.

topology with all taxa present

```
Dn Pt Csa Uroc Cycit Cycor Cyly Pi Cypi Per Gar Cv Nuc Po Py
¦  ¦  ¦   ¦    \-----/     ¦    ¦  ¦    ¦   ¦   ¦  ¦   \--/
¦  ¦  ¦   ¦       ¦        ¦    ¦  ¦    ¦   ¦   ¦   \----/
¦  ¦  ¦   ¦       ¦        ¦    ¦  ¦    ¦   ¦   \------/
¦  ¦  ¦   ¦       ¦        ¦    ¦  ¦    ¦   \------/
¦  ¦  ¦   ¦       ¦        ¦    ¦  ¦    \------/
¦  ¦  ¦   ¦       ¦        ¦    ¦  \------/
¦  ¦  ¦   ¦       ¦        ¦    \----/
¦  ¦  ¦   ¦       ¦        \------/
¦  ¦  ¦   ¦       \----------/
¦  ¦  \-----------------/
¦  \-------------/
\--------/
```

taxon removed	changes resulting
All AJ	(Pi(Po,Py)(Cv,Nuc))
Csa & Uroc	no change
Dn, Crp	no change
Pt	no change
Csa	no change
Uroc	no change
Cycor	no change
Cycit	no change
Cyly	no change
Pi	(Gar(Per(Cv(Nuc(Po,Py)))
Cypi	(Cyly((AJ)(HAC))) and (Gar, Per)
Per	tree 1 no change, tree 2 (Nuc(Cv(Po,Py)))
Gar	((Pi(Po,Py))(Cv,Nuc))
Cv	no change
Nuc	((PiPo)(CvPy))
Po	(Nuc(Cv,Py))
Py	((PiPo)(CvNuc))

Summary of changes in topology and frequency of occurrence

freq.	change	freq.	change
9.5	none	.5	(Nuc(Cv(Po,Py)))
3	(Cv,Nuc)	1	(Per(Cv(Nuc(Po,Py))))
2	(Pi(Po,Py))	1	(Cv, Py)
2	(Pi(Po))	1	(Gar, Per)
1	(Cyly((AJ)(HAC)))	1	(Gar(Per
		1	(Nuc(Cv,Py))

monophyletic group (*Cyanopica*, *Pica*, *Perisoreus*, *Garrulus*, *Corvus*, *Nucifraga*, *Podoces*, and *Pyrrhocorax*).

Cyanolyca is placed as sister taxon to all group 2 except in the absence of *Cyanopica*, in which case *Cyanolyca* is made sister taxon to all holarctic corvids plus American jays.

Within the holarctic genera, most frequently *Corvus*, *Nucifraga*, *Pyrrhocorax*, and *Podoces* are made monophyletic, with *Corvus* sister taxon to the others and *Nucifraga* sister taxon to *Pyrrhocorax* plus *Podoces*. *Garrulus* then is made sister taxon to this assemblage of crow-like birds, *Perisoreus* to all of these, *Cyanopica* to all these, and *Pica* the sister taxon to all others.

Pica was very unstable, placed alternately as sister taxon to all others or as sister taxon to *Podoces* and/or *Pyrrhocorax*. In these topologies *Nucifraga* was usually made sister taxon to *Corvus*. Other instabilities were less frequent.

Cyanolyca

The analysis of stability usually showed *Cyanolyca* as sister taxon to holarctic corvids rather than American jays. Nevertheless in the presence of the complete set of American jay species *Cyanolyca* is made sister taxon to American jays (not figured). Osteologically *Cyanolyca* has many primitive features of the upper jaw compared to all other birds in this entire assemblage. Crania of the *Cyanolyca cucullata* and *C. viridicyana* are very much like those of the treepies and southern magpies. The *Cyanolyca* jays have relatively deep and decurved jaws as in the presumed ancestral corvid,

Table 3. Character complexes showing homologous conditions in groups of holarctic genera of Corvidae, from review of character homology. Abbreviations for taxa are as in Appendix IV.

	Cv Nuc Po Py Gar	Cv Nuc Po Py	Nuc Po Py	Po Py	Cv Nuc Po Py Pi	Pi Po Py	Cv Nuc	Gar Per	Cv Py
Cranium shape							X		
Orbit shape		X	X				X		
Lower jaw art.				X					
Jaw shape			X	X		X		X	
Craniofacial hinge	X								
Transpalatines					X-Py				
Quadrate-squamosal art.				X		X			
Humerus		X-Po							X
Tarsometatarsus					X		X		
Total	1	2	2	3	2	2	3	1	1

a relatively deep cup of the tip of the lower jaw, long symphysis of the upper jaw, and absence of fusion of the prepalatine bars to the ventral bars of the jaw, all primitive characters not seen in most other American jays and all holarctic corvids. Cyanolyca species do have a (minimally developed) rostral articulation of the jaw, an unambiguous character uniting other American jays. Also the ventral suprameatic crest (seen in ventral view), including the abutment to the quadrate in the species cucullata is similarly altered. Additionally they share an elongated medial condyle of the quadrate. These last two characters were not coded in the data set because of need to review specimens not available in the final preparation of the data set. On the other hand changes Cyanolyca shares with holarctic genera are extremely homoplastic, occurring also in some other American jays as well (unossified nasal capsule, smaller size, enlargement of the sulcus below the suprameatic crest, shorter synsacrum, longer medial cotyla of the mandible), and some of these were evaluated in the review section as probably non-homologous.

In view of plumage features that also argue rather convincingly for monophyly of all the American jays including Cyanolyca, further analyses of holarctic genera have been constrained by excluding Cyanolyca. The genera and species of American jays are analyzed beyond.

Holarctic genera

Strongest alternative phylogenetic hypotheses suggested by the analysis of stability and review of characters

Table 4. Statistical properties of alternative tree topologies for holarctic genera of Corvidae. Columns 1, 2, 3 with Perisoreus and Garrulus paraphyletic; columns 4, 5, 6 with Perisoreus and Garrulus monophyletic. Length = total path length, C.I. = consistency index of Kluge and Farris (1969), f(norm) = normalized total homoplasy (Farris 1972). Abbreviations for taxa are as in Appendix VI. Stars indicate results of interest. Parentheses indicate nesting of sets of taxa in monophyletic groups.

topology 1 (Cypi(Pi(Per(Gar(Cv(Nuc(Po,Py))))))
(Figure 22)

topology 2 (Cypi(Per(Gar(Pi(Cv(Nuc(Po,Py)))))))

topology 3 (Cypi(Per(Gar(Pi((Po,Py)(Nuc,Cv)))))

topology 4 (Cypi(Pi(Per(Gar((Pi(Po,Py))(Cv,Nuc)))))
(Figure 23)

topology 5 (Pi(Cypi(Gar((Po,Py)(Cv,Nuc)))))

topology 6 (((Cypi(Pi(Po,Py)))(Per(Gar(Cv,Nuc))

topology	length	CI	f(norm)	length	CI	f(norm)
	(Per(Gar			(Per,Gar)		
1	*194.317	0.376	0.412	not done		
2	*194.667	0.375	0.394	195.417	0.374	0.356
3	195.883	0.373	0.375	196.750	0.371	0.342
4	*193.800	0.377	0.375	195.380	0.374	0.331
5	195.683	0.373	0.381	197.117	0.370	0.348
6	196.917	0.371	*0.333	196.050	0.372	*0.325

```
/-------------------- Other Corvidae
|
|         /---------- Garrulus
|         |
|       /-|     /---- Pica
|       | |     |
|       | |   /5| /-- Podoces
|       | |   | \-|
|       | |   |   \-- Pyrrhocorax
|       | \-4-|
|   /---|     |   /-- Nucifraga
|   |   |     \-6-|
|   |   |         \-- Corvus
\---|   |
    |   \------------ Perisoreus
    |
    \---------------- Cyanopica
```

Figure 22. Shortest tree for the genera of holarctic Corvidae (topology 1, Table 4) when analysis is constrained by placing *Cyanolyca* with American jays. Taxa not included in the tree are discussed in the text.

```
/---------------------- Other Corvidae
|
|           /---------- Garrulus
|           |
|         /4|     /---- Nucifraga
|         | |     |
|         | |   /5| /-- Podoces
|         | |   | \6|
|     /-3-| \-5-|   \-- Pyrrhocorax
|     |   |     |
|     |   |     \--7--- Corvus
|   /2|   |
|   | |   \------------ Perisoreus
\-1-| |
    | \---------------- Cyanopica
    |
    \------------------ Pica
```

Figure 23. Alternate tree topology nearly as short as the shortest tree, for the holarctic genera of Corvidae (Table 4, topology 4).

(Tables 2, 3) were incorporated into tree topologies for the genera of holarctic corvids. These were submitted to PAUP to find tree length and other summary statistics (Table 4). Topology 1 corresponds to the shortest tree found from analysis of all taxa. Topologies 2, 3, 4 and 5 explore alternate positions for Pica, Corvus, and Nucifraga. Topology 4 was the most frequently suggested alternative in subset analyses and also is best supported in Table 2. Topology 6 challenges the monophyly of all the crow-like birds and is included for comparison because it corresponds to some external (behavior) similarities. None of these topologies explores the possibility of monophyly of Perisoreus and Garrulus nor of Corvus and Pyrrhocorax, nor the position of Cyanopica. These are discussed beyond.

When the analysis is thus constrained by removal of Cyanopica from the holarctic corvid group, the tree making Pica sister taxon to Podoces and Pyrrhocorax is the shortest tree. Others are slightly longer. The consistency index, showing how well overall the individual characters agree with the tree topology (range 0 to 1) is very close for all topologies. F-normalized, a high value indicating either high homoplasy or very disparate rates of evolution in lineages, is close in value among the shortest trees. It is interesting that topology 6 separating Corvus and Nucifraga completely from Podoces and Pyrrhocorax gave a much less homoplastic character reconstruction than the shortest trees. However trees that minimize homoplasy may be grouping taxa on the basis of shared primitive resemblances

(Farris 1972).

Since the primary assumption of parsimonious analysis is that the shortest tree is most likely to be correct, length should be the first criterion in choosing among trees. But tree 1 is only slightly longer than tree 4. Criteria are lacking for confidence in difference of a tree length. Confidence statistics based on stability of a result, from pseudoreplicate sets of resampled data, seem inappropriate to cope with the complex implications of homoplasy as discussed in "Approach."

Although resampled sets did not clearly suggest monophyly of Perisoreus and Garrulus some external data suggests that relationship. Alternative topologies tested with Perisoreus and Garrulus made monophyletic differed little in length from the original trees, and the direction of change was inconsistent. Alternative analyses placing Cyanopica in other positions (not illustrated) always increased length of the tree by three to four units.

Evidently homoplasy affecting Pica and several of the crow-like birds prevents further resolution of the tree from this data set.

Characters supporting cladistic relationshps among the holarctic genera (Cyanopica, Pica, Perisoreus, Garrulus, Corvus, Nucifraga, Podoces, Pyrrhocorax)

The term "holarctic" used here is a misnomer in view of the cosmopolitan range of crows but the holarctic distribution of other members makes that a convenient term. The characters unequivocally (e.g. not highly homoplastic) supporting the more stable clades are discussed here. Character numbers in this section cross reference nodes indicated on Figures 22 and 23, the favored alternative topologies.

Characters supporting monophyly of all holarctic genera (Figure 22, node 1)

In cranium and jaw shape (20) the nasal septum is only marginally or not at all ossified (also in some Cyanolyca, many other American jays). (11) The ventral margin of the upper jaw lacks abrupt decurvature at the tip (slightly decurved in Pica, Corvus; continuously decurved in Podoces, Pyrrhocorax; also much less decurved in North American jays). (3) The symphysis of the lower jaw is shortened by reduction from the proximal margin (lengthened in Nucifraga).

In the palate the symphysis of the upper jaw is shortened by reduction in the extent of ossification ventral to the nasal capsule (also in many American jays, shortest in North American jays). (27, 28) The prepalatine bars are partly fused to the ventral bar of the jaw and the palatal flange of the ventral bar of the jaw contacts the bar dorsally or is completely obliterated by fusion (not in Pyrrhocorax; also in most American jays but not in Cyanolyca). (21) The tip of the maxillopalatine is inflated (only slightly in Cyanopica; also in American jays except some Cyanolyca).

In the lower jaw articulation (47) the medial cotyla of the mandible is elongated (very short in Podoces, *Pyrrhocorax*; also long in *Cyanolyca*). (72) The synsacrum is slightly shorter, incorporating only seven vertebrae into the sacral section (also in *Cyanolyca* and many other American jays). (71) The dorsal surface of the synsacrum between the iliac crests is moderately widened (narrow in Po).

Characters supporting clades within the holarctic genera

Support for monophyly of *Garrulus* and *Perisoreus* is not strong. In alternate topologies monophyly of these two increased tree length slightly. They share derived characters as follows: (11) (3, in part) very short jaws, with a straight dorsal profile; very short symphysis of the lower jaw; (47) very long medial cotyla of the mandible, and (not coded) very wide distal humerus. This is meager evidence for uniting these genera. The medial cotyla is only slightly longer than in other holarctic genera and the distal humeri though wide are otherwise dissimilar in shape of epicondyles. Many other similarities of *Garrulus* and *Perisoreus* can be evaluated as primitive characters in holarctic corvids: magpie-like cranial proportions (Figures 1, 2, 16, 17), including large postorbital fontanelles, wide jaws, and a relatively deep cup of the tip of the mandible. *Garrulus* and *Perisoreus* are united to the crow-like birds (Figure 22, *nodes 3, 4*) by (71) wider synsacrum (only moderately wide in *Garrulus lidthi*, narrow in *Podoces*), (16) very wide nasal processes of the premaxilla, and (25) dense ossification of the rostral palate (lease in typical crows). Other characters producing the association are very homoplastic.

There is nothing to unite Cyanopica to Pica. These two genera show in common a different suite of pleisiomorphic characters from Garrulus and Perisoreus, including only moderately dense ossification of the rostral part of the palate, only moderately widened nasal processes of the premaxilla, and the synsacrum not consistently so wide as in other genera. Homoplasy affecting Pica prevents resolution of the posiiton of Cyanopica but it appears likely that Cyanopica is an early isolated lineage of holarctic corvids and possibly sister taxon to all others.

The retention of different suites of primitive characters by Pica and Cyanopica as contrasted to Perisoreus and Garrulus suggests the possibility of independent derivation of these two lineages from within southern magpies. The diversity of Urocissa and Cissa should be more fully investigated.

In Figure 22, the first alternative phylogeny, Corvus, Nucifraga, Podoces, and Pyrrhocorax are united (node 6) by (1) longer orbit. There are several changes shape of the head of the humerus. (65) The distal margin of the biceps crest is less angular, it is elongated and has a less concave outline (not in Podoces). (67) The dorsal tubercle is slightly outset ventrally from the shaft (not in Nucifraga. (68) The dorsal supracondylar process is elongated proximally and is narrow and close to the shaft (extreme in Pyrrhocorax, Corvus, least in Podoces). The mosaicism precluded confidence in this node.

Corvus (node 7) is further united by (80) very large size, and (6) widened supraorbital shelf. The evidence for monophyly of Corvus seems meager but more convincing evidence comes from the extreme similarity of skulls of an immature Corvus brachyrhynchos to an adult Corvus monedula, as described with the osteology. Skulls of immature nutcrackers would add valuable comparisons.

In Figure 22, Nucifraga, Podoces, and Pyrrhocorax are united (node 5) only by (2) further lengthening of the orbit, and (3) shallow, slightly elongated, sickle-shaped, and distally attenuated jaws.

Podoces and Pyrrhocorax (node 6) are united by (2) extremely long orbit, very narrow, more elongated and decurved jaws that (12) articulate with the quadrate far medially under the cranium, (17) reduction of inflation of the shaft of the maxillopalatine so that it is merely a flat bony sheet, (47, 48) a wide, short, shallow medial cotyla of the mandible and wide, shallow, lateral cotyla, and (not coded) deeply incised and medially displaced prefrontal.

In Figure 23, the second alternative, corresponding to topology 4, Pica and all the crow-like birds are united (node 4) by (2) slight elongation of the orbit, and (75) a far dorsally placed medial crest of the tarsometatarsus (also in Cyanopica). Pica, Podoces, and Pyrrhocorax would be united (node 5) by (5) narrowing of the jaws; shallow upper jaw, (12) moderate medial inset of the quadrate articulation under the cranium, (37) inconspicuous dorsal suprameatic crest, (18) very small, poorly defined temporal fossa, and (35) short zygomatic process with (39) no subzygomatic sulcus.

In Figure 23, node 6, Corvus and Nucifraga are united by a broadened, elongated cranium (not reflected in the analysis of measures), (2) further elongated orbit, (9) no postorbital fontanelle, and (73) very short tarsometatarsus. The characters of cranial shape, which would best support node 6, are not reflected well in codes developed from measures. The support for monophyly of Pica with the crow-like assemblage as a whole is good but the support for monophyly owith the more limited chough-ground jay clade comes entirely from a single limited region, the temporal fossa. The jaws are not similar except for proximal shallowness.

Zavatarriornis

X-rays of skulls in skin specimens as well as line drawings of the palate and skull, accompanying a discussion by Ripley (1955), and also plumage and external form of the bill, are all consistent with relationship of Zavatarriornis either to Podoces or Nucifraga.

PHYLOGENETIC ANALYSIS

4. The Genera and Species of American Jays

American jays are united (Figure 24b, node 1) by development of (28) a very high rostral crest of the lateral cotyla of the mandible and by (53) a rostral articulation of the jaw, (54) medial basal ridge of the quadrate and (57) more extensive fusion of the prepalatine bar to the ventral bar of the jaw (Figures 8, 9; Figure 24, *node 1*). None of these characters is present in all species nevertheless the taxonomic distribution taken together supports monophyly and suggests these were primitive conditons for the group.

Analyses of relationships within the group of American jays showed highly unstable topology. Results are summarized here. With regard to *Cyanolyca* the following were consistent:

(1) Monophyly

(2) Sister relationship of *cucullata* and *viridicyana*

(3) Sister relationship of *nana* to *cucullata* and *viridicyana*

(4) Sister relationship of *pumilo* to all other *Cyanolyca*

(5) Sister group relationship of *Cyanolyca* to all other American jays.
With regard to *Cyanocorax* the consistent results are

(6) Monophyly of *caeruleus*, *violaceus*, and *cyanomelas* (*violaceus* group)

(7) Monophyly of *mystacalis* and *dickeyi*.

The species *cayanus* and *affinis* consistently form paraphyletic branches outside the *violaceus* group but next to it. Separate analyses (not shown here) in which the species *cristatellus* was included show it belongs with the *affinis* cluster. The species *cayanus* is closest to *violaceus* and *affinis* is closest to *chrysops*. The species *yncas* and the *Cissilopha* jays usually appear as paraphyletic sister taxa to all *Cyanocorax* plus *Calocitta* and *Psilorhinus*.

With regard to Calocitta and Psilorhinus, although they appear monophyletically when together, within Cyanocorax, divergence in the separate placement of each in the absence of the other indicates that these forms are not monophyletic. In the absence of Calocitta, Psilorhinus groups with the violaceus group. In the absence of Psilorhinus, Calocitta is unstable, sometimes appearing with the affinis assemblage and sometimes as sister taxon to all Cyanocorax plus Cissilopha.

Consistent results for the North American jays are

(8) Monophyly of the group, composed of Aphelocoma, Cyanocitta, and Gymnorhinus

(9) Sister relationships of Aphelocoma unicolor to the rest

(10) Monophyly of Aphelocoma ultramarina and Gymnorhinus are monophyletic.

Characters producing the topology are a taxonomically mosaic changes of relatively slight, intergrading, and individually variable differences in the extent of development of the rostral articulation of the jaw, details of the temporal crests and processes, the jugal brace, and also a few details of palate form. Elimination of these probably homoplastic characters would simply reduce resolution of the phylogeny to a useless level. The usefulness of proportions in discriminating taxa at lower levels is apparent when closely related or similar taxa are compared (e.g. Cyanolyca), and more detailed and carefully considered measurements probably would be useful.

Two phylogenetic topologies for the American jays are shown in Figures 24 and 25. The first incorporates the most frequent topology for Cyanocorax and the North American jays. In 24b the positions of certain unstable taxa (starred) are altered as suggested by review of the analysis of stability. The second topology (Figure 25) incorporates an alternate rooting for Cyanocorax, suggested by the interpretation of the small rostral articulation in the violaceus group as a primitive condition rather than a derived loss. A major difference embodied in these two alternatives is that the second interprets the North American jays as a group derived from within Cyanocorax. Although this topology did not emerge from the formal analysis, there are biases in coding and analysis, that may have prevented emergence of this topology. This topology is supported also by trends in the shape of jaws and cranium, disappearance of the medial basal line on the quadrate, and widening of the suprameatic process.

The topology of the tree in Figure 24 implies that the rostral articulation of the jaw was well developed before the splitting of lineages of extant jays and that it has been reduced in many lowland neotropical jays. Since the program of analysis also did not recognize the greater similarity of Cyanolyca cucullata to Cyanocorax compared to the other species of Cyanocorax, these results counter observation and cannot be accepted uncritically. Nevertheless the resulting phylogeny (Figure 24) is consistent with some external evidence from plumage and

```
OTHER
CORVIDAE
 |       /------- Cyanolyca pumilo
 |   /---|
 |   |   |   /--- Cyanolyca nana
 |   |   \---|
 |   |       |/-- Cyanolyca viridicyana turcosa
 |   |       \|
 |   |        \----- Cyanolyca cucullata mitrata
 |   |
 |   |         /--- Cissilopha melanocyanea
 |   |         |
 |   |         |--Cissilopha sanblasiana yucatanica
 |   |      /--|
 |   |      |  |  /---- Cissilopha beecheii
 |   |      |  |  |
 |   |      |  |  |              /-- Cyanocorax caeruleus
 |   |      |  |  |             /|
 |   |      |  |  |         /---|\ Cyanocorax violaceus
 \---|      |  |  |         |   |
     |      |  |  |       /-|   \-- Cyanocorax cyanomelas
     |      |  |  |       | |
     |      |  \--|     /-| \---Cyanocorax cayanus
     |      |     |     | |
     |     /|     |     | |  /---- Calocitta formosa
     |     ||     |   /-| \--|
     |     ||     |   | |    \--- Psilorhinus morio
     |     ||     |   | |
     |     ||     | /-| \-- Cyanocorax affinis
     |     ||     | | |
     |     ||     | | |   / Cyanocorax mystacalis
     |     ||     \-| \---|
     |     ||       |     \-- Cyanocorax dickeyi
     \-----||       |
           ||       \-- Cyanocorax chrysops
           ||
           |\--- Cyanocorax yncas
           |
           |      /-- Cyanocitta cristata
           |      |
           |      |-- Cyanocitta stelleri
           |   /--|
           |   |  |  /- Aphelocoma coerulescens
           \---|  \--|
               |     |/-- Aphelocoma ultramarina
               |     \|
               |      \------- Gymnorhinus cyanocephalus
               |
               \----- Aphelocoma unicolor
```

Figure 24a. Phylogeny of American jays, produced when all taxa are present. See also Figure 24b.

```
OTHER CORVIDAE
     ¦
     ¦               /---- *Cyanolyca pumilo
     ¦             /-4   - - - mirabilis, argentigula
     ¦             ¦ \---- *Cyanolyca nana
     ¦           /-3
     ¦           ¦ \- *Cyanolyca viridicyana turcosa
     ¦   /---2---¦
     ¦   ¦       \----* Cyanolyca cucullata mitrata
     ¦   ¦               - - - pulchra
     ¦   ¦            /--- Cissilopha melanocyanea
     ¦   ¦            ¦
     ¦   ¦         /--¦   /-- *Cissilopha sanblasiana yucatanica
     ¦   ¦      /--¦  \---¦
     ¦   ¦      ¦  ¦      \--- Cissilopha beecheii
     ¦   ¦      ¦  ¦
     ¦   ¦      ¦  ¦                 /-- Cyanocorax caeruleus
     ¦   ¦      ¦  ¦                /¦
     ¦   ¦      ¦  ¦             /--¦\ Cyanocorax violaceus
     \-1-¦      ¦  ¦             ¦  ¦
         ¦      ¦  ¦          /--¦  \-- Cyanocorax cyanomelas
         ¦      ¦  ¦          ¦  ¦
         ¦      ¦  ¦        /-¦  \--- *Psilorhinus morio
         ¦      ¦  ¦        ¦ ¦   - - - heilprini
         ¦    /-¦  ¦        ¦ \---- Cyanocorax cayanus
         ¦    ¦ ¦  ¦      /-¦
         ¦    ¦ ¦  ¦      ¦ \-- Cyanocorax affinis
         ¦    ¦ ¦  ¦    /-¦- - - -cristatellus, cyanopogon
         ¦    ¦ ¦  ¦    ¦ \-- Cyanocorax chrysops
         ¦    ¦ ¦  ¦    ¦
         ¦    ¦ ¦  ¦    ¦  / Cyanocorax mystacalis
         ¦    ¦ ¦  \----¦--¦
         ¦    ¦ ¦       ¦  \ Cyanocorax dickeyi
         \--5-¦ ¦       ¦
              ¦ ¦       \-- *Calocitta formosa
              ¦ ¦
              ¦ \--- Cyanocorax yncas
              ¦
              ¦       /-- Cyanocitta cristata
              ¦       ¦
              ¦       ¦-- Cyanocitta stelleri
              ¦    /--¦
              ¦    ¦  ¦  /- Aphelocoma coerulescens
              \--6-¦  \7-¦
                   ¦     ¦/-- Aphelocoma ultramarina
                   ¦     \8
                   ¦      \------- Gymnorhinus cyanocephalus
                   ¦
                   \----- Aphelocoma unicolor
```

Figure 24b. Alternative topology for phylogeny of American jays. Within the same overall topology as in Figure 23, starred taxa here are in changed positions as suggested by the analysis of stability. Dotted lines indicate taxa not included in the coded data. Placements explained in text.

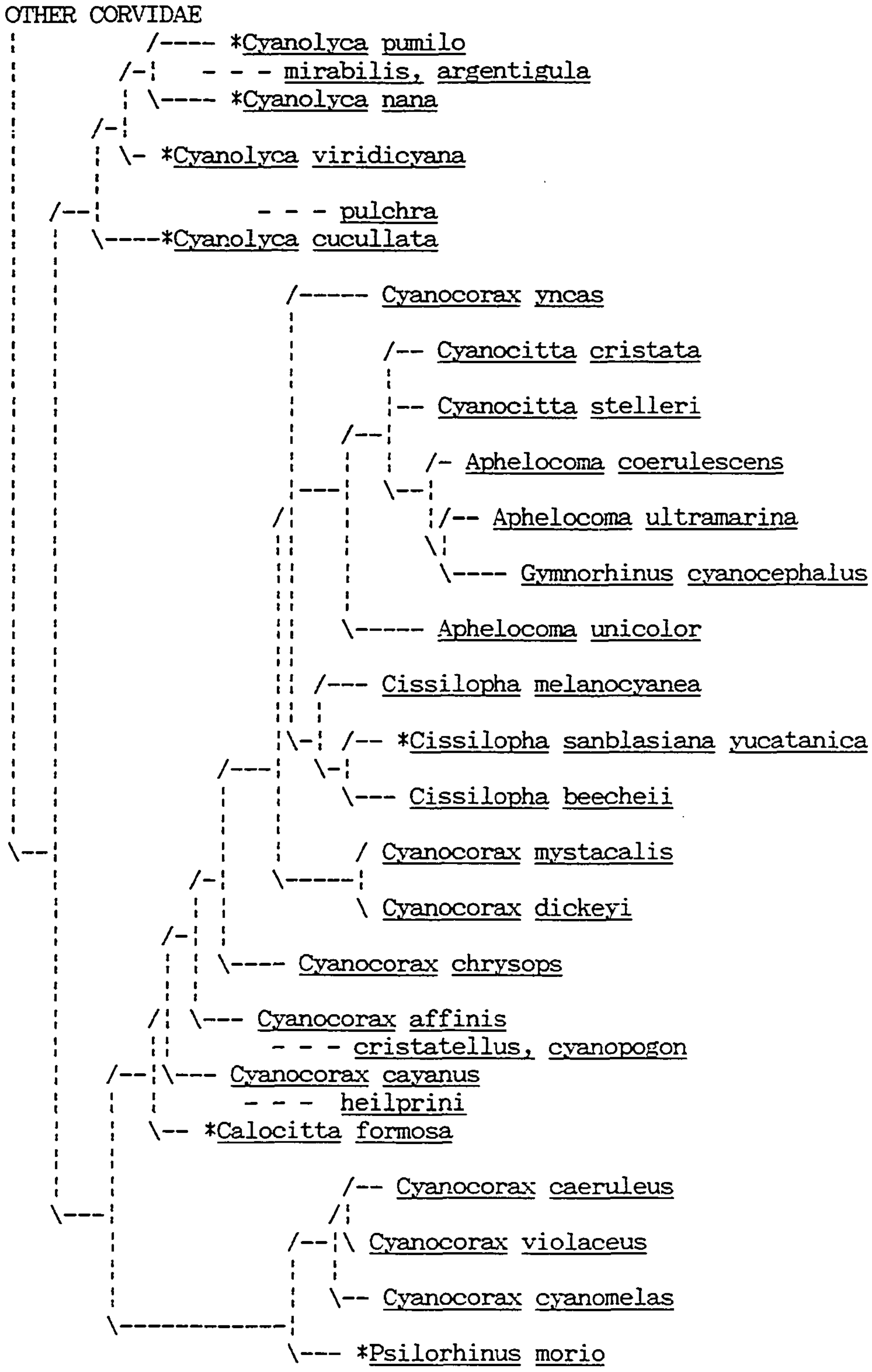

Figure 25. Alternative topology for phylogeny of American jays with position of rooting of Cyanocorax altered so that the violaceus group is made sister taxon other American jays. Starred taxa explained in Figure 24b.

geography.

In part the analysis depends on the interpretation of homology of the suprameatic crests, which was ambiguous in *Cyanocorax*. Alternative phylogenies will not be discussed further here since the resolution of this problem must depend on further information concerning character transformation.

Characters uniting taxa of American jays (Figure 24b)

Cyanolyca (*node 2*) is united by (12) slight medial inset of the quadrate-squamosal articulation, (47) elongated medial cotyla of the mandible, (not coded) undercutting the median eminence, (56) far rostral position of the mandibular attachment tubercle for the postorbital ligament, and (79) strongly tilted proximal end of medial crest of the tarsometatarsus toward the dorsal surface.

The computer analysis of the entire data set places the species *cucullata* as sister taxon only to *viridicyana*, but review of character transformations suggests *cucullata* is instead sister taxon to all other *Cyanolyca*. The species *cucullata*, and particularly the subspecies *mitrata*, from Mexico in the northern parts of the species range, greatly resembles *Cyanocorax*, and I suggest that many of its characters are primitive for the American jays and the resemblance to *Cyanocorax* is due to shared characters primitive for the American jays. Both resemble in many ways the hypothetical primitive corvid and the Southeast Asian magpies and treepies.

Compared to the species cucullata the other Cyanolyca species (Figure 24b, node 3) share (80, in part) more gracile form, (38) greater elevation of the dorsal suprameatic crest, (44) a very thin ventral suprameatic crest which extends further ventrolaterally or caudally on the quadrate, with enlargement of the sulcus above the ventral crest, (12) further inset of the quadrate, (28) the prepalatine bar not fused to the ventral bar of the jaw (a loss in this context), and (72) and extremely short synsacrum, typically incorporating only ten vertebrae.

The smaller species of Cyanolyca (argentigula, mirabilis, pumilo, nana) are united (node 4) by (57) complete lack of the rostral cotyla of the mandible, again, a loss in this context, (12) far medial inset of the quadrate articulation, (21) maxillopalatine tips expanded (also in all other American jays), (4) suprameatic crest meets the quadrate entirely caudally, (24) ventral lobe of the prefrontal expanded (also in North American jays), (80) size very small, (54) no medial basal crest on the quadrate, (2) changed proportions of the cranium so that it is deeper and shorter and the orbit appears to be relatively shorter (see discussion in "Review of Characters"). The species mirabilis and argentigula were not coded for analysis but their osteology has been partly assessed.

The species viridicyana and the smaller species of Cyanolyca share some similarities with holarctic corvids, particularly Cyanopica and Pica, but share other similarities with North American jays. These resemblances are interpreted as convergent based on the evidence for monophyly of Cyanolyca. Also the monophyly of smaller species of Cyanolyca with the North American jays is unlikely because of the many derived characters that unite these smaller species on the one hand and the North American genera with the Cyanocorax jays on the other hand. Nevertheless monophyly of Cyanolyca and North American jays was not definitively rejected since measurements and final observations were lacking or incomplete for the smaller species of Cyanolyca. In particular, the species nana is of interest because its jaw is much shallower than the jaw of other other Cyanolyca species, and is at least superficially similar to jaws of some North American jays. Since Cyanolyca has been considered closest relative of Aphelocoma by several previous workers (reviewed in "Introduction") these species should be examined further.

On the basis of an apparently well developed rostral crest and similar plumage, the species pulchra may be provisionally placed as sister taxon to cucullata. Costa Rican specimens resemble greatly, externally, the Ecuadorian species pulchra, and the two have been treated as conspecific by some authors (see Pitelka 1951b).

Other American jays

All the remaining American jays (Cyanocorax, Cissilopha, Psilorhinus, Calocitta, Aphelocoma, Cyanocitta, Gymnorhinus) (Figure 24b, node 5) are united by (9, 10) reduced size of the postorbital and interorbital fontanelles, (25) denser ossification of the rostral palate, (21) inflation of the maxillopalatines (also in some *Cyanolyca*), (1) a slight elongation of the orbit, (40) enlarged suprameatic process of the ventral suprameatic crest, with many associated features as in described in "Comparative Osteology" for the most highly developed conditions, as in *Cyanocorax yncas*, (49) reduction in size of the jugal brace, (57) enlargment of the rostral articulation of the jaw, (32) ventral pit usually present on the transpalatine.

Within *Cissilopha* and *Cyanocorax* stability and resolution are so poor that specification of synapomorphies of clades will not be attempted. The following discussion indicates the uncertainties. The clade composed of *Cyanocorax*, *Calocitta*, and *Psilorhinus* is united only by moderate narrowing of the cranium, which is not adequately reflected in the characters derived from measures. Other shared characters of members of this clade may be interpreted as primitive for the American jays (deep, strongly decurved jaw, deep orbit, narrow nasal processes). Within this clade character transformations will be discussed but not enumerated. All taxa except *yncas* are united by complete absence of the dorsal suprameatic crest, larger size, and a more massive ventral suprameatic crest (assuming homology is correctly identified).

Interpretation of characters synapomorphic for this clade is complicated by the great similarity of the species *yncas* to the North American jays. The arrangement placing the species *yncas*, with the most highly derived condition of the jaw articulation, as sister taxon to all others, is less than satisfactory. The topology in Figure 25 implies a reverse transformation in these characters.

Cissilopha probably is part of the *Cyanocorax* group. Splitting of *Cissilopha* species in the analysis (Figure 24a) is due to differences in proportions of skull and jaws among the included species of *Cissilopha* that cause differential associations with the very similar *Cyanocorax* species. *Cissilopha* is well defined by plumage characters. *Cissilopha melanocyanea* is much like *Cyanocorax mystacalis* and *C. dickeyi* in characters of the skull shape and jaw articulation, suggesting that these are primitive resemblances in the *Cissilopha* jays and that *Cissilopha yucatanica* and *beecheii* would be correctly associated together by shared changes in cranium and jaw shape (narrowing and elongation).

Cissilopha species share with *Cyanocorax dickeyi* and *mystacalis* and some specimens of *Calocitta* an extremely wide suprameatic shelf, (not coded) built out laterally and bowed outward in dorsal view so that the shelf is wider than the suprameatic process. In all these jays the suprameatic process is usually wider and more heavily constructed than in other American jays.

The species *mystacalis* and *dickeyi* are consistently united in all analyses but the few osteologic characters supporting this immediate sister association do not form a coherent complex (longer humerus, shorter zygomatic process, shallower origin for m. brachialis), or else they are ambiguous in polarity (longer synsacrum). It is clear in any case that they are very similar osteologically as well as in plumage.

The species chrysops has a well developed rostral articulation but the suprameatic process is less conspicuous than in the group just discussed. The ventral suprameatic crest is massive however. The species affinis, cristatellus (seen but not included in the formal analysis), and cayanus show variation in the development of the features associated with the rostral articulation and suprameatic crests and processes, in a mosaic of changes that in the topology of Figure 24 are interpretable as stages in reduction of the features associated with the rostral articulation and suprameatic crest are of the jaw. At the same time the suprameatic process is reduced the ventral suprameatic crest becomes more massive. Whether or not the direction of the trend is correctly interpreted, it seems clear that the affinis group of jays shows a mosaic of the characters associated with extent of development of the rostral articulation. Within this group it is best developed in affinis, least in cayanus. These jays are larger than chrysops but not so large as the violaceus group. On the basis of plumage the species cyanopogon (skeletal material not seen) would be included here. Also on the basis of plumage alone heilprini might be included here or with the violaceus group.

The extreme of small size of the rostral articulation and large body size occurs in the jays of the violaceus group. The cranium is shorter and deeper. The species violaceus and caeruleus are the largest.

Psilorhinus and Calocitta are probably not monophyletic. The placement of Calocitta in Figure 24b as indicates only uncertainty. Calocitta formosa colliei was examined but not included in the data set. This larger form is more distinct from nominal Cyanocorax than is C. f. formosa. The form compared here is more similar to the other American jays.

Although many characters suggest that Psilorhinus is part of the violaceus group, its external features are not wholly consistent with that placement. Psilorhinus is a more massive, much duller plumaged jay. It seems possible that both Calocitta and Psilorhinus are separate early radiations from the lineage that produced Cyanocorax.

Cyanocitta, Aphelocoma, and Gymnorhinus share changes in the squamosal-quadrate articulation and the associated temporal fossa crests as well as overall shape of cranium and jaws (Figure 24b, node 6). (3, in part: evident from observation but not adequately reflected for all in the coding derived from measures) The upper jaw is shallower, narrower, and elongated, and has a (11) straighter dorsal profile than in other American jays and the ventral profile of the upper jaw is also straighter. (6) The nasal process of the premaxilla are moderately widened. (24) The prefrontal is more inflated. (21) The maxillopalatines are elongated and well inflated. (34) The postorbital process is recessed caudally from the orbit. (44) The ventral suprameatic crest is set more ventrolaterally with respect to the quadrate (least in Cyanocitta cristata.) (35) The zygomatic process is very short (longer in Gymnorhinus). (64) The pectoral crest is shorter. Other characters are somewhat ambiguous since they are shared with Cyanocorax yncas. The rostral palate is short and (25) densely ossified. (Not coded) The ventral suprameatic crest is narrowed in midsection and (45) the squamosaal abutment to the otic process is relatively conspicuous. The conspicuousness of the abutment may be a consequence of narrowing of the ventral suprameatic crest.

Within the North American jays branch lengths are short. Aphelocoma unicolor emerged consistently as sister taxon to all in a separate resampling analysis of the species in this group. The North American jays exclusive of A. unicolor are united by (not well reflected in coding of character 3) a shallower jaw and (36) moderate elongation of the suprameatic crest so that the bulla is notched dorsally. These species are poorly resolved among each other except for the consistent grouping of Aphelocoma ultramarina and Gymnorhinus. The monophyly of Cyanocitta is not supported by any characters that do not also occur in Aphelocoma coerulescens. Aphelocoma coerulescens, A. ultramarina, and Gymnorhinus are united (node 7) by (2) very wide, shallow cranium, (wider in the Florida scrub jay), (10) very narrow jaw, (10) greater reduction in the interorbital fenestra, and (36) extreme elongation of the suprameatic crest.

Aphelocoma ultramarina is further united to *Gymnorhinus* (*node 8*) by (1) an extremely elongated orbit (also in *Cyanocitta*), (46) a very stout quadrate, (16) very wide nasal processes of the premaxilla, (3) further narrowing of the jaw and reduction in depth, with distal lengthening and a long symphysis of the lower jaw, (11) very straight margin of the distal tip of the upper jaw and ventral margin of the lower jaw, (41) usually large medial lobe of the suprameatic process, (38) enlargement of the sulcus below the dorsal suprameatic crest at the bulla, and (62) very wide head of the humerus. Details of the dorsal quadrate articulation in these two are extremely similar. Most conditions are more extreme in *Gymnorhinus*.

Overview

Figure 26 shows the most probable phylogeny of the genera of Corvidae and indicates the unresolved questions. According to the assessments of the analyses as discussed in this section, *Urocissa* and *Cissa* are made paraphyletic and *Cyanolyca* is considered to be sister taxon to other American jays. The position of *Pica* is not resolved, possibly because of homoplastic changes shared with the American jays and because *Pica* retains relatively many primitive corvid characters. *Pica* probably should be placed with the crow-like birds but more information is needed. Unresolved

```
/-------------------------- Other oscines
¦
¦ /-------------------------Corcorax       Australia
¦ ¦                         Struthidea
\-¦
  ¦                   /-----Oriolus        Eurasia,
  ¦ /-----------------¦                     N.W.Australia
  ¦ ¦                 ¦
  ¦ ¦                 ¦   /-Artamus        Asia,
  ¦ ¦                 \---¦                     Australia
  ¦ ¦                     \-Cracticus      Australia
  \-¦
    ¦                 /-----Manucodia      New Guinea,
    ¦                 ¦     Paradisaea      Australia
    ¦-----------------¦
    ¦                 \-----Platyiophus    Malay penn.,
    ¦                                         Borneo, Java
    ¦                                         Sumatra
    ¦
    ¦                 /-----Dendrocitta    S. E. Asia, Java,
    ¦ /---------------¦                     Borneo, Sumatra
    \-¦               \--?--Platysmurus    Sumatra, Borneo
      ¦
      ¦ /-------------------Ptilostomus    West Africa
      \-¦
        ¦ /-----------------Cissa          S. E. Asia,
        \-¦                                 Borneo, Sumatra
          ¦ /---------------Urocissa       Southeast Asia
          ¦ ¦
          ¦ ¦   /-----------Pica           Eurasia, N. Amer.
          ¦ ¦   ¦-----------Cyanopica      Spain, E. Asia
          \-¦   ¦-----------Garrulus       Eurasia
            ¦   ¦-----------Perisoreus     Holarctic boreal
            ¦ /-¦ /---------Corvus         Widespread, not
            ¦ ¦ ¦ ¦                         in S. America
            ¦ ¦ ¦ ¦---------Nucifraga      Holarctic montane
            ¦ ¦ \-¦-?-------Zavatarriornis Ethiopia
            ¦ ¦   ¦    /----Podoces        Asia, steppe
            \-¦   \----¦
              ¦        \----Pyrrhocorax    Eurasia, cliff,
              ¦                             montane
              ¦ /-----------Cyanolyca      Neotropic montane
              ¦ ¦
              ¦ ¦ /---------Cissilopha     Mesoamerica
              \-¦ ¦---------Cyanocorax     Neotropic lowland
                ¦ ¦---------Psilorhinus    Caribbean Mesoam.
                ¦ ¦---------Calocitta      Pacific Mesoamer.
                \-¦
                  ¦    /----Cyanocitta     North America
                  \----¦----Aphelocoma     North America
                       \----Gymnorhinus    North America:
                                            Great Basin
```

Figure 26. Phylogeny of Corvidae and corvoids suggested by this analysis.

nodes in the American jays are discussed elsewhere. Figure 26 also indicates geographic distribution.

BIOGEOGRAPHY

Although many families of corvoid birds are endemic to Australia and New Guinea, none of the early lineages of Corvidae sensu strictu occurs there (Figures 26, 27). The ranges of several species of southern magpies and treepies include the islands west but not east of Wallace's Line. The sedentary habits of these birds indicate that they spread to Java, Sumatra, and Borneo by overland dispersal, possibly when these islands but not those farther east were connected by broad savannah during times of low ocean levels during glacial advances (c.f. Morley and Flenley 1987). The corvids concerned are two or possibly three separate clades, the treepies, Cissa, and Platysmurus. Urocissa is also confined to Southeast Asia but does not occur on the islands. Thus these early lineages of corvids probably radiated on the mainland. The only corvids east of Borneo are the cosmopolitan crows. Since Corvus is evidently a later lineage it probably arrived only recently in Australia. This is somewhat different from the scenario of Sibley and Ahlquist (1986), who suggested the Corvidae had originated in Australia, arrived on the mainland early, and radiated there.

Sibley and Ahlquist (1983) suggested an Australian origin for the entire corvoid radiation. Platylophus' range in western Malaysia also extends east only just to Wallace's

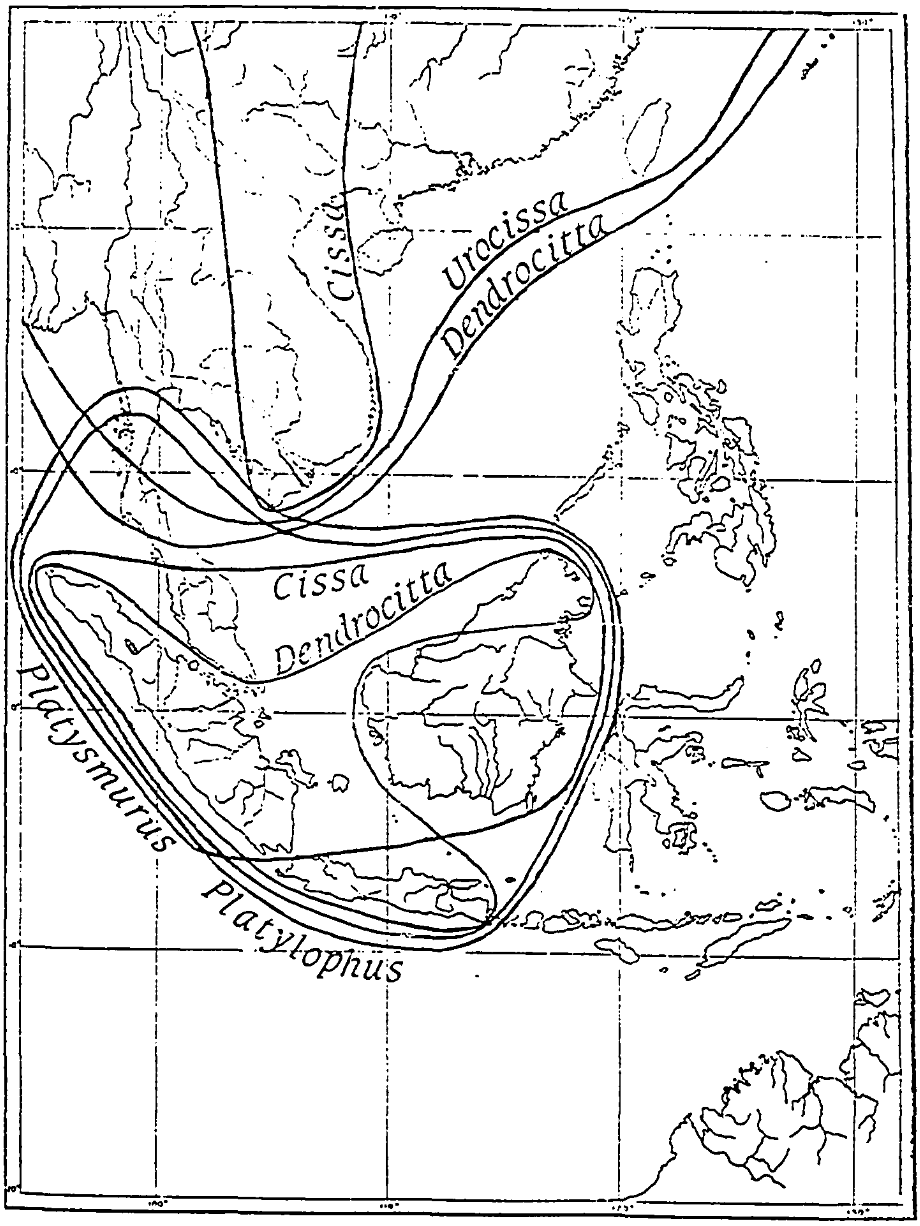

Figure 27. Distribution of Platylophus and corvids in Malaysia. Corvus, not shown, extends throughout.

Line. Although Paradisaeidae and Cracticidae are endemic to Australia and New Guinea, other birds in the apparent sister group of Corvidae occur not only in Australia but throughout Southeast Asia (Campephagidae, Oriolidae, Artamidae). Oriolidae only occur in northwestern Australia. The evidence is equally consistent with an origin elsewhere than in Australia for the entire sister group plus Corvidae, followed by invasion, isolation, and radiation in Australia by the Cracticidae and Paradisaeidae, and Corvus. The presence of Platylophus, an apparently early lineage of the sister group, on the mainland and in western Malaysia, is consistent with this interpretation (Figures 26, 27).

The immediate group of birds most closely related to Corvidae is just one of many clades in Sibley and Ahlquist's proposed Australian corvoid radiation. The biogeographic history of this particular isolated clade does not overturn the whole hypothesis of an Austraian passerine radiation. It is unfortunate that this clade is the name-bearer for the entire radiation.

The fossil record of neospecies of corvids is very abundant for the northern hemisphere, compared to other passerines, because of the large size of corvids. However the paleospecies as described are few and may need review. Several paleospecies of Corvus are described from Europe, the earliest being the late Miocene (Tortonian) Corvus larterti (Milne-Edwards 1871) described from abundant material. Forbes (1892) described a tiny crow, C. moriorium (= Palaeocorax), from the Quaternary of the Chatham

Islands, but the brief description without pictures suggests features not typical of contemporary crows. The earliest American records of Corvus are Pleistocene (Brodkorb 1978), from numerous localities.

Attempts to date an earlier arrival of corvids into the Americas are frustrated by the limited fossil record. A Miocene "jay" Miocitta galbreathi (Brodkorb 1972) described from a distal humerus from the late Miocene Pawnee Creek Formation, Colorado, appears to be a corvid but its identity as a jay seems questionable. The distal epicondyles are too narrow and the crest dividing sulci for triceps musculature is much too prominent. The sulcus for the distal end of the m. scapulotriceps is uniquely very wide. These features indicate a crow-like bird perhaps, but the sulci and crest are distinctive. Henocitta brodkorbi (Holman 1959) from the Pleistocene (Illinoian) of Williston, Florida is evidently a large jay but the specimen is too fragmentary for further diagnosis. Protocitta dixi (Brodkorb 1957) from the Pleistocene (Illinoian) at Reddick, Florida appears to be correctly identified as a large jay similar to Psilorhinus but that identification would also apply to several large Cyanocorax species. "Protocitta" ajax from the early Pleistocene, Palo Duro Falls, Texas, so assigned by Brodkorb (1972), was originally and probably correctly assigned to the genus Pica by Miller and Bowman (1956). My assessments except as noted are based only on the rather good illustrations.

Ecomorphology may illuminate the history and conditions in which the various corvids have spread. The Southeast Asian magpies and treepies are primarily rather sedentary woodland birds. The Eurasian and boreal jays and most neotropical jays, including the sister group of other American jays, _Cyanolyca_, share that habit. The early fossil record of corvids may be biased by poor preservation of woodland faunas, but it is unlikely that corvids were present in Europe in the early Tertiary. Early Oligocene faunas in France, which contained abundant fossils of small non-passerine perching birds representing several other orders of birds now found in woodlands, have not revealed any passerines (Mourer-Chauvire 1982).

Considering then the source point of entry for the American jays, it seems likely that the ancestors of this assemblage were woodland birds; furthermore that like birds of other early corvid lineages, typically they were sedentary. The blue jay _Cyanocitta_ _cristata_ is the only truly migratory corvid. Savannah, scrub, and cerrado jays seem to be recently derived (_Cyanocorax_ species south of the Amazon rain forest, _Aphelocoma_ _coerulescens_), and there is nothing to indicate a common derivation.

The late date of passerine and first corvid fossils in Europe and absence of jays in Australia argues against a North Atlantic (e.g. McKenna 1975) or South American route, leaving Beringia as the obvious choice. It is unlikely the ancestral American jays were boreally adapted. From all these considerations it seems probable that the earliest jays got to the Americas at a time when relatively moist, continuous, warm or cool temperate forest was more widespread in the North. By later Miocene the flora of southern Alaska had taken on a boreal character (Wolfe and Hopkins 1967).

Among the northern genera of Corvidae density of ossification of the palate and fusion of prepalatine bars to the ventral bar of the jaw are most developed in birds that depend heavily on nut crops. These are *Garrulus*, *Nucifraga*, North American jays, and apparently also *Cyanocorax yncas* (Goodwin's account of behavior, 1986; habits of most neotropical jays are less known.) Documentation for the importance of nut crops in the spread of nutcrackers and pinyon jays is extensive. The relationship is two-way: nutcrackers are implicated in co-evolution with certain pines (Turcek and Kelso 1968; VanderWall and Balda 1977; Tomback 1977).

The wide, short, heavy jaws in *Garrulus* are used to open nuts by crunching on them (Goodwin 1986), whereas the long, buttressed jaws in North American jays are used to open nuts by pounding with the lower jaw (Zusi 1987). To my knowledge there is no detailed description of the method nutcrackers use. The different morphologies in *Garrulus* and North American jays indicate independent radiations; the phylogenetic analysis suggests separate acquisition of specialization on nut crops but this does not preclude the use of nuts by a common ancestor.

All of the crow-like birds and also Pica use open habitats extensively. Pica and many of the typical crows are expanding rapidly to forage in cultivated fields. Choughs also use cultivated areas extensively, where they are available near their more constraining requirement for rocky cliffs. Even Nucifraga, the nutcrackers, travel over wide, open areas in search of irregular nut crops. In all except Podoces the humerus shows adaptation for strong flight; Podoces is a runner. Thus savannah corvids like mammals (Webb 1977) show adaptations for great mobility. The adaptation of the humerus in the crow-like birds is very different from that in the many strong-flying oscines that have developed a second pneumatic fossa for the enlarged dorsal head of m. humerotriceps. It seems also to be very different from the change seen in Platylophus and less prominently in Paradisaeidae and treepies, in which insttead the apparent attachment site for m. scapulohumeralis cranialis is enlarged as a fossa.

The osteologic similarity of the two widely separate nutcrackers may be due to the panmixia expected in highly mobile organisms. Nutcrackers travel over wide treeless expanses but not generally over oceans. It seems reasonable to suppose that the nutcrackers came across Beringia during the Pleistocene sea level lowering if not also during earlier regressions. Podoces and Pyrrhocorax have moved into novel habitats for the family. The choughs were probably much more widespread in Eurasia in the Pleistocene (Guillou 1981, Brodkorb 1978). The cliff-alpine, field, and steppe habitats of the contemporary choughs and ground jays suggest radiation in tree-barren deglaciated areas of Eurasia.

Although Podoces lacks powers of strong flight it is uniquely adapted for terrestriality, with its very long legs and relatively far plantar hind toe. Podoces and Pyrrhocorax share unusual bill morphology suited for probing crevices in rocky areas. All of the crow-like birds and also Pica and Cyanopica share a more prominent extensor sulcus of the tarsometatarsus and (minimally in Pica and Cyanopica) wider synsacrum, possibly related to greater terrestriality (more walking and foraging on open fields). However use of the feet in corvids is partly manipulative and this form cannot be ascribed to a particular role without careful study.

In view of the wide geographic range including remote Pacific islands the absence of crows from Central and South America is puzzling, especially since the genus is supposed to have been around since Miocene times. Early crows, however, may not have been wide ranging. It does not seem likely that a short over-water or forest barrier would have kept forms such as present day typical crows out of South America. The present distribution indicates that they were not present in the Americas during drier times as late as the most recent glacial advance, when there was a corridor of savannah across the Panama region, about 1.4 Mya (Marshall 1988). Thus the typical crows probably reached

North America only recently, as the fossil record indicates. Their present far-flying ability may be a relatively new evolutionary feature.

Within the American jays little geographic reconstruction can be offered without a better corroborated phylogeny. There are however several identifiable geographic radiations: the neotropical montane jays (*Cyanolyca*), the cis-Andean *Cyanocorax* jays, (*violaceus* and *affinis* groups, possibly including *chrysops*); the Central American *Cissilopha* jays, and the North American jays. Status of other species as geographic radiations of monophyletic assemblages is less clear. It is plausible that the species *mystacalis* and *dickeyi* are disjunct north and south representatives of a trans-Andean radiation, and that the Central American *Cissilopha* jays are a trans-Panamanian vicariant from this group of *Cyanocorax*. Except *yncas*, other *Cyanocorax* then would be a cis-Andean vicariant sister taxon to these. Within the cis-Andean group *chrysops* would be sister taxon to the *affinis* and *violaceus* groups. The present distribution of *chrysops* suggests it was more widespread in drier times and may have reached southern Brazil via a northern corridor. The intergrading characters of the *affinis* and *violaceus* groups are in accord with a "rasenkreis" scenario that Hardy presented in an informal seminar (1981, American Museum of Natural History). The interpretation would be reversed somewhat by the second alternative phylogeny suggested above (Figure 25). It is best to avoid comment about geographic history of *Calocitta* and *Psilorhinus* without a better established phylogeny. Hardy (1967, 1969b) has provided much original information on the habitat and ecological relationships of many of the neotropical lowland jays.

The North American jays may have expanded northward in the wake of glaciation, and their history of expansion may have involved several episodes. Most (excepting parts of *Aphelocoma coerulescens*) are closely associated with pine and oak forests and harvest nut crops to form large stores. Thus it has been suggested that the closest relatives of the *Aphelocoma* jays, among neotropical jays, may be the small *Cyanolyca* species, which inhabit high elevation conifer forests. However *Cyanocorax yncas* also inhabits oak and pine woods (drier lowland woods), and it uses acorns as part of its diet (Goodwin 1986).

For all the reasons given in the introductory paragraphs above about habitat and mobility of jays, it seems unlikely that the neotropical jays reached South America much if at all before the closure of the Panamanian isthmus. In this connection the sudden rather late appearance of oaks in South America (Van der Hammen and Cleff 1986) about 1 Mya is of interest, since the spread of oaks probably depends heavily on transport and burial by squirrels and jays. The present distribution patterns in neotropical jays seem to have some relationship to patterns of Quaternary climate change. During glacial times a broad savannah corridor across the Isthmus and also the Venezuelan

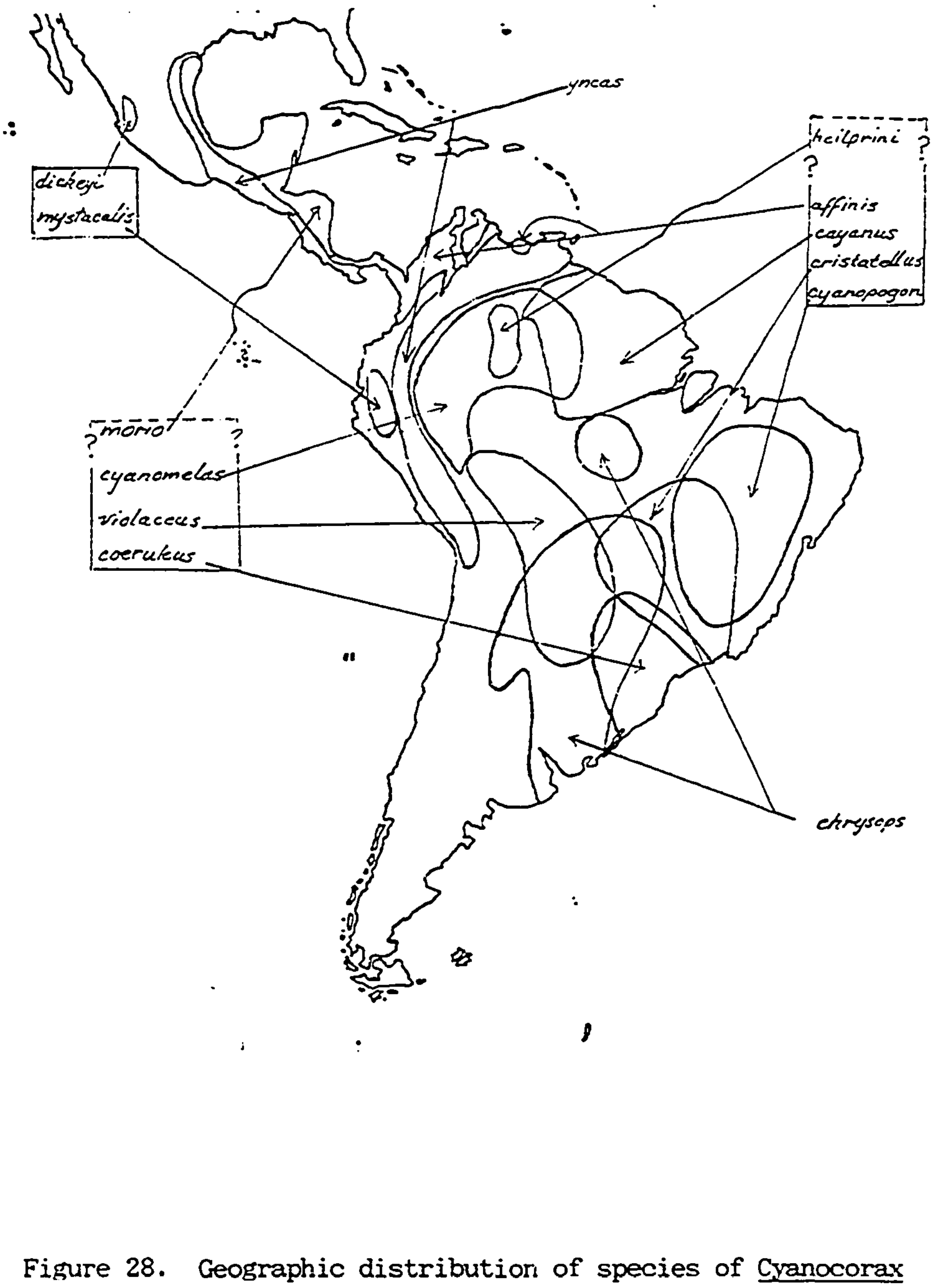

Figure 28. Geographic distribution of species of Cyanocorax (A) - affinis group, (V) - violaceus group. Ranges after Hardy (1969).

mountains (Haffer 1987) would have enabled easy spread of jays east of the Andes between Central and South America. In the past there has also apparently been a dry corridor across the northern Andes (Chapman 1926). The neotropical lowland jays do not show patterns of endemism related to rain forest refugia, except Cyanocorax heilprini. Instead, Cracraft (1975) includes several of the species in his lists covering endemism in drier neotropical areas. Neotropical montane jays, Cyanolyca, show patchy disjunct distributions in high altitude forests. Probably these were more continuous during cooler glacial times when cloud forest descended to lower altitudes. Thus range disjunctions in this group may be rather recent. The distribution of the green jays shows an interesting disjunction across Panama. Although the species is markedly dimorphic, the contact zone for the morphs of the green jay is not at the present range disjunction but instead is in Colombia. The present disjunction is explained by lack of suitable drier woodlands across Panama. The contact zone may correspond to a former range disjunction in Colombia caused by expansion of cloud forest, e.g. a reciprocal of the effect on Cyanolyca, cutting off drier low elevation woodlands to east from the west.

SUMMARY AND DISCUSSION

This analysis suggests the Oriolidae, Cracticidae, Artamidae, and Paradisaeidae, with cnemophiline birds of paradise excepted, are in a sister group of Corvidae. The limits of this sister group probably are larger but were not fully explored. Paradisaeidae are most similar to Corvidae, possibly because of sharing more primitive characters of the entire group. Grallinidae and Corcoraciidae would not be included in the sister group even though they share many of its derived osteologic characters.

Limits and osteologic definition of Corvidae

The primitive corvoid skull as reconstructed here was large for a passerine, heavily ossified in the orbit but with unusually extensive pneumatization elsewhere. This combination probably achieves lightness with robust build. The upper jaw was large, the nasal septum and possibly the floor ossified; the conspicuousness of the craniofacial hinge indicates the heavy jaw was nevertheless very mobile. The rostral palatal ossification was extensive, making a long symphysis of the upper jaw, that nearly reached the vomer. The vomer flared broadly rostrally. The heavy prepalatine bar and long, deep sulcus on the ventral surface of the palatine indicate heavy medial pterygoideus musculature possibly for moving the large upper jaw. The prefrontal was unossified. The tips of the maxillopalatines were bluntly truncated. A suprameatic crest was extended laterally as a shelf and not elevated above the quadrate articulation. Otherwise the temporal fossa and quadrate articulation apparently were much as in other oscines and many suboscines.

The head of the humerus was small, the pectoral crest short, the biceps crest was angular, and the proximal part of the shaft of the humerus was moderately expanded from the primitive oscine condition, but there was not an excavated second pneumatic fossa. The site of origin for m. scapulohumeralis cranialis was a very large fossa. Distally the sulcus for m. humerotriceps was not wider than the shaft. The epicondyles were moderately wide but not large. These characters of the humerus indicate design for improved flight compared to the probably primitive oscine condition.

In the hindlimb the first metatarsal articulated slightly more medially than in the primitive and common oscine condition, in which it is farther plantar. The first toe articulated in a slightly more dorsal position. The configuration of toes and intercalated cartilages suggests greater opposability of toes I and II. Between the bases of toes III and IV there was an interlocking articulation. Feduccia and Olson (1982) argued that this was a character linking certain primitive passerine families. Here it is analyzed as a primitive passerine character that persists in a variety of families. The form suggests design to facilitate rotation of the outer toe toward the plantar surface and perhaps to stabilize the outer toe during grasping. These conditions may be important in the use of the feet for holding objects, as corvids often do.

Compared to the primitive corvoid, primitive corvids are characterized by a more inflected upper jaw, hooked at the tip, and a lower jaw that was deeply cupped. There were minimal changes in the temporal fossa including a slight recess of the postorbital process to the orbital wall, and the zygomatic process was very large. The cranium probably was enlarged.

The sister group of Corvidae is characterized by more extreme enlargement of the upper jaw, very heavy ossification of the nasal capsule, and by an increase in prominence of the craniofacial hinge. The foot structure is unique. The tarsometatarsus is very short and broad, with a prominent plantar sulcus. The hind toe, though still reversed, is hardly hind since it articulates in the same plane as the others. It remains of course opposable to the second toe.

Platylophus galericulatus is tentatively excluded here from the Corvidae. This result is in accord with doubts about its membership expressed earlier (Amadon 1944; Goodwin 1986; Clench (1985), but does not agree with Sibley and Ahlquist (1985). Osteologically Platylophus seems to be a relatively undifferentiated representative of primitive corvoids and possibly cladistically a member of the Paradisaeidae. It most resembles the manucodes among the birds of paradise. Thus its jay-like behavior and appearance are of some interest to the reconstruction of evolution of behavior of corvoids as a whole, in which many spectacular courtship and social systems have evolved.

Pseudopodoces humilus is not a corvid. Its limb myology (Borecky 1977) and pterylosis (Clench op. cit.) are not corvid. Based on osteology this bird appears to be a non-corvoid oscine with some derived similarities to the Paridae and Sittidae, but the problem needs more study.

Treepies and magpies

The treepie genera *Dendrocitta* and *Crypsirina* retain many primitive corvoid characters. Their very short, sharply decurved and inflected upper jaw is unique. Skeletal material was not available for *Temnurus*, but external form and x-rays of skin specimens indicate the characters of a treepie. Based on preliminary observations *Platysmurus* appears to be similar to treepies.

Ptilostomus is a mosaic osteologically as it is externally, of treepie-like characters, unique characters, and a few magpie-like characters. *Ptilostomus* is an early lineage of Corvidae isolated in Africa, with uncertain cladistic affinities, either sister taxon of treepies or of all other Corvidae.

Although they are much alike there is little support for monophyly of *Cissa* and *Urocissa*. The Southeast Asian magpies *Cissa* and *Urocissa* probably are paraphyletic branches of the Corvidae, with *Urocissa* the sister taxon of all holarctic and American genera. Two distinctive species of *Urocissa* that were not examined, *whiteheadi* and *ornata*, would be of much interest and might change the present assessment of the relationships of Urocissa. In the transition from the corvid ancestor many unusual characters of the primitive corvids were lost making remaining corvids in some ways more like other oscines, but the palate is distinctive. Several of the birds in the assemblage of American jays and holarctic corvids are also called magpies: Pica, the holarctic magpie; Cyanopica, the azure-winged magpie; and Calocitta, the magpie jay. Thus "magpie" is a term applied to a polyphyletic assemblage of large, long billed, long tailed, gaudy and garrulous corvids. Usually the tail is graduated laterally and tipped with whate. Possibly all are like some ancient corvid.

The remaining corvids, which are the American jays and holarctic genera including the cosmopolitan crows, share many derived characters but the patterns of sharing indicate rampant homoplasy and few characters uniquely define the whole group. The retention of different suites of primitive characters in the holarctic and American genera suggests early separation and possibly separate even origins from within the assemblage of southern magpies and jaylike birds. The possibility has not been fully explored, for lack of necessary specimens of Southeast Asian species. On the basis of present evidence the holarctic and American genera are treated here as monophyletic.

In these later branches of the Corvidae further transformation generally produced only minor changes in the upper jaw but a great variety of modifications of the lower jaw. Large skulls are combined with denser ossification of jaw and cranium, but the jaws are shallower and there is a variety of designs for reinforcing parts of the skull, including fusion of prepalatine bar and ventral bar of the jaw, sometimes very extensive, a new rostral articulation of the jaw, dense ossification of the rostral part of the palate, heavier ossification of the orbit with closure of interorbital and postorbital fontanelles, heavy suprameatic crests, and large suprameatic and meatic processes.

Relationships among the holarctic and American jays, magpies, crows, nutcrackers, and choughs

Among holarctic corvids, osteologically Cyanopica greatly resembles the American jays of the genus Cyanolyca and may be the sister taxon of other holarctic genera. Garrulus and Perisoreus share many similar apparently primitive characters. Evidence for monophyly of Garrulus and Perisoreus is limited to great reduction in size of the jaw and is not wholly convincing. Pica is similar to Cyanopica but there is no evidence for monophyly. All of the crow-like birds probably are monophyletic including Corvus, Nucifraga, Pyrrhocorax, and also Podoces. Some but not all similarities in the humerus of Pyrrhocorax and Corvus probably are convergent. Similarities they share in the tarsometatarsus are shared also by all other crow-like birds and also Cyanopica and Pica. Cranium and jaws of Pyrrhocorax and Corvus are very divergent in shape and design. Pyrrhocorax seems instead to be sister taxon to Podoces. These two share detailed similarities in their very unusual jaw structure. Corvus may be sister taxon

Nucifraga, Podoces and Pyrrhocorax. There is some support for an alternate phylogeny in which Pica is sister taxon to Podoces and Pyrrhocorax and Corvus is then sister taxon to Nucifraga alone. External form and x-rays of the skull in skin specimens, as well as published line drawings (Ripley 1955) suggest that Zavatarriornis may be related to Podoces or Nucifraga.

American jays

Osteologically Cyanolyca has many primitive features of the upper jaw compared to all other American jays and appears to be their sister taxon. Crania of the larger species, cucullata and viridicyana, are very like those of southern magpies and treepies. These two Cyanolyca species as well as many Cyanocorax jays retain deep and decurved jaws and a deep orbit and cranium. In other ways their osteology is more magpie like than is that of any of the holarctic corvids or North American jays. Thus these American jays retain a set of primitive corvid characters not evident in the holarctic genera. Besides rudimentary development of the rostral articulation of the jaw as Zusi (1987) described, Cyanolyca is united to other American jays by other minor and less conspicuous but apparently derived features of the lower jaw articulation. Considering the plumage characters unique to the American jays the monophyly of all American jays nevertheless seems likely.

The genus Cyanolyca is united by reduction in the dorsal suprameatic crest, a far rostral attachment of the postorbital ligament, and a well-defined medial crest of the tarsometatarsus that tilts dorsally. Although some of the species share similarities of the temporal fossa with some holarctic corvids on the one hand and other similarities with North American jays, monophyly of *Cyanolyca* indicates these changes are convergent.

The species *cucullata* and *pulchra* probably are a sister lineage to *viridicyana* and all the smaller species. The *Cyanocorax*-like features are very pronounced in the northern (Mexican) populations of *cucullata*. Based on plumage the *cucullata* lineage appears to include the Ecuadorian species *pulchra*.

C. viridicyana and the smaller species of the genus probably are a monophyletic lineage characterized by greater separation of suprameatic crests, medial inset of the quadrate, unusually short synsacrum, and generally more gracile form. The species *argentigula*, *mirabilis*, *pumilo*, and *nana* are united by very small size and extremely inset quadrate and concommitant narrowing of the jaws. These species of *Cyanolyca* are high altitude birds in "cloud forest" with ranges fragmented probably by contraction of the habitat during interglacials.

The remaining American jays are united to each other by large size of the rostral articulation of the jaw and changes in associated structures of the jaw articulation. Some groupings of taxa can be made but species relationships within the group are not well resolved by the osteologic characters assessed here and the overall topology is also uncertain. Two alternative phylogenetic topologies are suggested. The first unites all Cyanocorax plus Cissilopha as sister taxon to the North American genera Aphelocoma, Cyanocitta, and Gymnorhinus. The second alternative places a violaceous group of Cyanocorax as sister taxon to all other members of the group, the North American jays thus constituting a derived clade within the assemblage of Cyanocorax jays. The uniqueness of Calocitta both in osteology and plumage prevents a satisfactory assignment within the larger Cyanocorax group although it most resembles the affinis group of Cyanocorax. Psilorhinus is most like the violaceus group of Cyanocorax jays and may be sister taxon to it or part of it. The distinctiveness of Calocitta and Psilorhinus suggests alternatively that they may each be relicts of earlier radiations of the neotropical jays. They probably are not monophyletic.

Within Cyanocorax, a violaceus group of species forms a monophyletic cis-Andean radiation in western Amazonia and northern Argentina. This includes the species violaceus, cyanomelas, and caeruleus. An affinis group of species forms a paraphyletic assemblage ranging from eastern Brazil, through northern Venezuela and eastern Central America. Within this group probably cayanus is closest to the violaceus group and affinis is closest to remaining Cyanocorax jays. This group also includes the species cristatellus and probably cyanopogon. Based on skins only, the species cyanopogon is assessed here as a member of the (admittedly poorly defined) *affinis* assemblage, not a subspecies of *chrysops*. Specimens were lacking for the species *heilprini* which is intermediate in plumage between the *violaceus* and *affinis* groups. The species *chrysops* in southern Brazil and northern Argentina may be sister taxon to all these. A group of trans-Andean species remains, including *mystacalis* and *dickeyi*, which are sister taxa and may be north and south relicts of a wider trans-Andean radiation. *Cissilopha* jays are most like this clade. The species *yncas* is either sister taxon to all other *Cyanocorax* and *Cissilopha* (first alternative) or else part of a clade that includes also *Cissilopha* and the North American jays (second alternative topology). The complex zoogeography of the species *yncas* may also reflect repeated range fragmentation by expansion of higher montane forest during glacial periods. The range of *yncas* thus appears to be a reciprocal of the range of *Cyanolyca viridicyana*. Thus it is not clear which is the earliest lineage of *Cyanocorax*. The species *yncas* is phenetically much like the North American jays and in the first topology is assessed as the sister taxon of all other *Cyanocorax*. *Cissilopha* is most like *Cyanocorax mystacalis* and *dickeyi* but uncertain polarity of transformations within *Cyanocorax* makes specification of their cladistic position impossible.

The North American jays, genera *Cyanocitta*, *Aphelocoma*, and *Gymnorhinus*, are a well defined monophyletic group. They share more gracile form and extreme similarity in many new details of cranium and jaw form and articulation. Among these jays, differences between Aphelocoma and Cyanocitta are trivial. Gymnorhinus appears to be sister taxon to Aphelocoma ultramarina.

This analysis differs from previous works of Amadon (1944) and Goodwin (1986) by placing the Southeast Asian magpies, the African piapiac, and the treepies as paraphyletic early lineages of Corvidae (Figure 1). In previous analyses the Eurasian and boreal jays have been placed either with the American jays or with the Southeast Asian magpies and treepies. Here the Eurasian and boreal jays are placed as early lineages in a larger assemblage that includes all the crow-like birds. This analysis agrees with previous phylogenies in grouping together all the American jays, and provides some limited additional evidence that Cyanolyca is a sister taxon to the others. The present study also agrees with previous studies in grouping together all the crow-like birds, including the nutcrackers, choughs, ground jays, and the crows themselves, but disagrees by not associating Corvus and Pyrrhocorax most closely. The northern magpies Pica and Cyanopica are associated here with the holarctic assemblage rather than with the Southeast Asian magpies.

DNA hybridization studies are harder to compare because many taxa are missing and because that analysis treats all taxa in terms of their distances from Corvus. Figure 1 shows both major differences and some close agreements between DNA analyses and this study. Particularly different are the placement of Platysmurus near to Corvus and the inclusion of Platylophus in Corvidae (= Corvini of Sibley and Ahlquist 1985).

Phylogeny and biogeography indicate that Corvidae originated on mainland Southeast Asia, not in Australia, and spread throughout Austral-Asia and elsewhere. Primitive corvids probably were sedentary woodland birds. Most American jays remain relatively sedentary; Cyanocitta is exceptional. American jays may have been isolated on this continent before late Miocene development of boreal floras in southern Alaska. Specialization on acorns by American and Eurasian jays entails different adaptations and was either independently acquired or independently elaborated in very different ways. Several of the more northern radiations of corvids have developed great mobility along with using relatively more open areas, fields and steppe. These are the pinyon jays, the magpie Pica, choughs, crows, and nutcrackers.

APPENDIX I. Specimens examined.

Abbreviations for museums:

AMNH	American Museum of Natural History
ANSP	Academy of Natural Sciences, Philadelphia
BMNH	British Museum (Natural History)
CAS	California Academy of Sciences
CNG	Carnegie Museum of Natural History, Pittsburg
FM	Field Museum of Natural History, Chicago
FSM	Florida State Museum, University of Florida
GW	Glenn Woolfenden
LSU	Louisiana State University
MCZ	Museum of Comparative Zoology, Harvard University
MLZ	Moore Laboratory of Zoology, Occidental College
MVZ	Museum of Vertebrate Zoology, University of California, Berkeley
ROM	Royal Ontario Museum
USNM	United States National Museum
UK	University of Kansas
UM	University of Michigan
YPM	Peabody Museum, Yale University
ZMK	Zoology Museum, University of Copenhagen
ZMU	Uppsala Universitets Zoologiska Museet

Part 1. Corvidae. Additional specimens of starred species were examined in collections at AMNH, CAS, MVZ or USNM.

Platylophus galericulatus ANSP 38106, FSM 14546

Platysmurus leucopterus USNM 14540 (humeri), ANSP 38142

*Gymnorhinus cyanocephalus MVZ 58047, FSM 105862, AMNH 15992

Cyanocitta cristata: **Midwestern U.S.** CAS 68537, FM 93268, USNM 499504, MVZ 80063 153952 45184 66697; **Northeastern U.S** AMNH 11576 10267 10266 12883 10480 10280 10058 4097 6396 *stelleri: **Coastal northwestern U.S.** CAS 68699 57315 57316, MVZ 79507 67580 60133; **Northern Rocky Mountains** CAS 57947, AMNH 4813 63103 73629 73631; **Southern Rocky Mts** AMNH 15988; **Sierra Nevada, California** AMNH 12449 70709 70710 70711 70712 70713; **Mesoamerica** CAS 72067, MVZ 121246 121250 121251

*Aphelocoma coerulescens: **Florida** AMNH 5548 5547, USNM 290001 499103 108884, MVZ 129170 129171; **Southwestern United States** USNM 555354, CAS 70108; **Calaveras County, California** MVZ 70895 70896; **Coastal and inland coast ranges, California** CAS 71347 57345 60951 70229, AMNH 13652 13653, CAS 70229, MVZ 67589 67590 *ultramarina: **Arizona, New Mexico** AMNH 13213 15991 13244 4770, MVZ 41422 59164 169324; **Texas** FM 105398; **Nuevo Leon** MVZ 84321; **Chiapas** MVZ 94872 unicolor: UM 209302 208300 209303 209301 209299, MVZ

121169 86129 121179 86134

Cyanolyca viridicyana quindiuna: USNM 428792 428794; *viridicyana turcosa*: LSU 81314; *viridicyana jolyae*: LSU 65043 114283 104428 90158, **aviary** GW 3537; *cucullata cucullata*: UM 209292 209293; *cucullata mitrata*: UM 133985 133984; *pumilo*: UM 209296 209295, MLZ S-265, USNM 343505, MVZ 86136 86138, MLZ S-983 S-746 S-111 S-251 S-265; *nana*: UM 209297 209298, MLZ S-873 S-674 S-1046 S-705; *mirabilis*: MVZ 121158, MLZ S-654; *argentigula*: USNM 429795 429796

Cissilopha melanocyanea: **Guatemala** UK34731 34733, AMNH 11729 11730, UK 34734; **Honduras** LSU 31964 31965; **Nicaragua** FM 103969; **El Salvador** MVZ 86142 86149 86143 *sanblasiana nelsoni*: UK 159172 40729, USNM 491877; *sanblasiana rivularis*: UK 40729 35161 40728, *sanblasiana yucatanica*: ROM 112885 113035, FM 104538, AMNH 3485, UK 40730, USNM 346442 85352 156593, UK 40730, USNM 347347; *beecheii*: UK 33171, AMNH 7885, USNM 7749, UM 210423, MVZ 78740 78741

Cyanocorax caeruleus: FM 105666 106296, USNM 558257, GW 2491 2057 ZMK 21.12.1949.4; *cyanomelas*: UM 202250 200890 202252 202252 222263 202253, AMNH 6721, LSU uncataloged 2 specimens (JVR 3167 3417), USNM 346080 227413; *violaceus*: UM 215037, FM 290512, USNM 490581 428845, LSU 65042, MCZ 6431, FM 106592, MVZ 141811; *cristatellus*: ZMK 9.3.1849.28, ZMK not numbered 1 specimen; *cayanus*: UM 208540 208541; *affinis*: UM 74679, AMNH 5155 5134, USNM 347126 430170, LSU 108792, FM 104996, MVZ 120754 94117 94116 94118; *chrysops*: UM200895 200894 200893 158872 158875 222262, AMNH 11711 11721 11718 11719 11722 10625 11717, YPM 6410, USNM 346079, LSU uncataloged 3 specimens (JVR 3475 3282 2892) MVZ 160622: *mystacalis*: AMNH 7197 7198, MCZ 6431, LSU 75634 81313 86683, USNM 347004; *dickeyi*: UM 159168 21503, MVZ 116505 116483 116488 116504 116506 153004, UM 210534; *yncas*: **Texas, Tamaulipas** YPM 10135 13049, UK 36118; **Mesoamerica** UK 24388 24391 40737 40738, CAS 72075, ROM 112878 115794 112817 118386 118388; **Western Colombia, Ecuador, Peru, Bolivia:** AMNH 5156, LSU 91185 90159 84088, AMNH 2190, MVZ 161292

Psilorhinus morio: MVZ 142150 142151 142152 142153 MVZ 142144 142145 142146 142148 142147 135178 84070 142149 157655, LSU 31963, YPM 4495 UK 24967

Calocitta formosa colliei: USNM 7750, UK 34525, AMNH 7901, MVZ 78742 78743 74792 123050 123051; *colliei formosa*: CAS 72068, UK 37772, AMNH 12652, MVZ 153953; *colliei azurea*: MVZ 129522 131539 131538; *colliei pompata*: LSU 48586, MVZ 86150 155770 86152

Garrulus glandarius: **Europe** UM 135694 119047, USNM 319098

334660 344657 319098 344660 224001, UM 119047 135694, ROM 114175; **East Asia:** USNM 289943 319162 319588, MVZ 130898 150933 120070; **aviary:** UM 119213, AMNH 1011 4793; _lanceolatus_: **aviary:** FM 106344, USNM 347001

Garrulus _lidthi_: **Aviary:** FM 104799, AMNH 4940 4941

*_Perisoreus_ §_canadensis_: CAS 57936, AMNH 13850 10080 5532; _infaustus_: **Western Europe:** BMNH 1899.11.21.2 ZMU S-751-22-NR3 S-751-22-V^{O}1

Urocissa _caerulea_: FM 104680, AMNH 405, USNM 490522 _flavirostris_: MCZ 1373: _erythrorhyncha_: UK 70492, AMNH 1418, YPM 9617 9616: **Aviary** AMNH 2191 3150 3752 2745, MCZ 7003

Cissa _chinensis_: **Aviary** AMNH 4075, UM 217755, AMNH 2205 3775, USNM 344668

Cyanopica _cyana_: **Spain:** UM 159703 159702 159704 156167; **Asia:** USNM 290315 290316 290317, UM 153030, MVZ 156103 123364 123393; **aviary:** CAS 61634, FM 104451, AMNH 402

Dendrocitta _vagabunda_: **Aviary:** UM 219857, FM 104643, AMNH 8779 404 _formosae_: **Aviary:** CNG S-874

Crypsirina _temia_: FM 104481, PB 1979, USNM 343292, AMNH 8749

*_Pica_ _pica_: CAS 42933 57560, AMNH 15993 15994 15995 8372; *_nuttali_: 151941

Podoces _hendersoni_: USNM 557519 557518, UM 220479, YPM 36482; _panderi_: USNM 291221

Pseudopodoces _humulis_: USNM 557979 557980 557978

Nucifraga _columbiana_: CAS 70047 61007 57235, USNM 17086, AMNH 9854 9855 9864; _caryocatactes_: MVZ 125498, USNM 319586 319585 319584

Pyrrhocorax _pyrrhocorax_: USNM 318365 319115 319399, YPM 26901A, MVZ 115964, USNM 319394 319115 AMNH 3458; _graculus_: UM 119048, YPM 16194A, USNM 321813 321814

Ptilostomus _afer_: AMNH 406 3963 3690 1964, USNM 291495 291458

Corvus _monedula_: USNM 555671, AMNH 3490; _dauuricus_: MVZ 132901: _splendens_: USNM 346860 YPM 27702 27701; _moneduloides_: UM 223755 223756 21855 223761; _enca_: USNM 224802; _kubaryi_: YPM 5218; _tristis_ AMNH 7419 7418 YPM 7038; _capensis_: USNM 431904; _frugilegus_: USNM 557543; _brachyrhynchos_: CAS 70199 70164 57780 57253, AMNH 10786; _caurinus_: CAS 60506 MVZ 68768; _sinaloae_: UK 38136 36550 28128; _imparatus_: UK 24397

ROM 115798; ossifragus: AMNH 14097 11082; palmarum: USNM 555843; jamaicensis: USNM 558928; nasicus: USNM 554292; leucognaphalus: GW 4206; corone: MVZ 123191 USNM 500773; macrorhynchos: AMNH 397 398; orru: USNM 559044; bennetti: AMNH 9320 9319; coronoides: AMNH 11466 11467 9607 9590; tasmanicus: USNM 204455; torquatus: USNM 289947; albus: USNM 558602, AMNH 1451; cryptoleucus: MVZ 68912; ruficollis: BMNH 1927.12.27.139; corax: CAS 60715 38756 42395, AMNH 2201; rhipidurus: YPM 5204 5205 5206 5207 5208, UK 707499; albicollis: AMNH 5237 5236 5238; crassirostris: AMNH 1352 3814

Part 2. Additional specimens of "corvoids" examined but not coded for analysis.

Grallinidae:

Grallina cyanoleuca: LSU 113190, AMNH 3826 9442, MVZ 143455

Corcoracidae:

Struthidea cinerea: LSU 113189, AMNH 9303 MVZ 154117

Corcorax melanorhamphos: LSU 103939, AMNH 9643 9390

Dicruridae:

Chaetorhynchus papuensis: AMNH 7583

Dicrurus hottentottus: AMNH 7557, LSU 101040, MVZ 149300,

Campephagidae:

Lalage leucomela: AMNH 9083; sueurii: MVZ 156702 AMNH 9606

Coracina montana: AMNH 6764; novaehollandiae: MVZ 11288 caerulogrisea: 6766

Pteropodoces maxima: AMNH 9378

Oriolidae:

Oriolus oriolus: LSU 28078; flavicinctus: AMNH 9097; chinensis: MVZ 136770, AMNH 2612; szalayi: AMNH 7409; trailli: AMNH 4936

Artamidae:

Artamus leucorhynchos: LSU 105076; cinereus: AMNH 9666 9638; leucorhynchus: MVZ 143479

Cracticidae:

Cracticus torquatus: LSU 105077, AMNH 9646; *quoyi*: LSU 101041; *nigrogularis*: CAS 61080

Gymnorhyna tibicien: LSU 95287 CAS 61667 71449, AMNH 11473

Strepera versicolor: LSU 105078; *graculina*: AMNH 11556

Ptilonorhynchidae:

Ptilonorhynchus violaceus: LSU 113188, AMNH 9309 11545

Ailuroides crassirostris: AMNH 2681 2309

Sericulus chrysocephalus: CAS 61079 61963

Amblyornis macgregoria: AMNH 6788

Paradisaeidae:

Loboparadisaea sericea: AMNH 6783

Lycocorax pyrrhopterus: AMNH 6464

Manucodia ater: AMNH 3967 3968 6785, MVZ 142665, LSU 101042; *chalybatus*: AMNH 6785

Phonygammus keraudrenii: AMNH 7690 7577

Paradisaea minor: AMNH 4927 7629; *apoda*: LSU 111780, MVZ 149307, AMNH 6787

Lophorhina superba: AMNH 6784

Diphyllodes magnificus: AMNH 6806 7630

Ptiloris paradiseus: CAS 61043 AMNH 7450

APPENDIX II. Characters coded for analysis.

Taxa in parentheses are exemplars for certain characters. * = assumed primitive oscine state (not assigned for all characters). Principal component scores are explained in "Methods." Character numbers are the number of the character in the data set (Appendix III), Characters are listed in the approximate order of discussion in the section "Comparative Osteology".

No.	Mnemonic	Character and States
Cranium and jaw shape		
15.	cran2	Coded Principal Component-II score for cranium measures
0 - 4		Defined in Table 1 and interpreted in "Review of Characters
73.	cran3	Coded Principal Component-III score for cranium measures.
0 - 4		Defined in Table 1 and interpreted in "Review of Characters
49.	jaw2	Coded Principal Component-II score for jaw measures.
0 - 5		Defined in Table 1 and interpreted in "Review of Characters
70.	jaw3	Coded Principal Component-III score for jaw measures.
0 - 5		Defined in Table 1 and interpreted in "Review of Characters
80.	jaw4	Coded Principal Component-IV score for jaw measures.
0 - 5		Defined in Table 1 and interpreted in "Review of Characters
29.	iow	Width of the supraorbital shelf
0		Narrow, less than the width of the craniofacial hinge, the margins over the orbits moderately concave
1		About the same width or wider than the hinge, the margins only slightly incised or approximately straight from the ectethmoid to the cranium

31. nosh	Shape of the nostril
0*	Oval
1	Ovate, nearly round
2	Round
66. infla	Inflation of the skull in the ear region
0*	Moderately pneumatized (*Cyanocitta*)
1	Very highly pneumatized (*Dendrocitta*)
6. pof	Size and shape of the fontanelles on the posterior walls of the orbit
0	No fontanelle
1	Small bilateral fontanelles, usually smaller than the optic foramen
2	Moderately large fontanelles, usually larger than the optic foramen to about twice its size, often with a narrow extension toward the roof of the orbit
3*	Fontanelles much larger
8. iof	Size and shape of the interorbital fontanelle
0	No fontanelle, the interorbital septum completely ossified
1	Small, less than twice the diameter of the optic foramen, round
2	Two to three times the diameter of the optic foramen, rounded, often confluent with the optic foramen
3	Larger, elongate or irregular in shape
4*	Huge, occupying most of the interorbital septum
51. ujtip	Lateral profile of the upper jaw at the tip
0	The dorsal border straight or only very slightly decurved, the ventral border straight or nearly so (*Garrulus*)
1*	The dorsal border continuously decurved, the ventral border continuously decurved or only slightly decurved at the tip (*Pyrrhocorax*, *Cyanocorax*)

2 The dorsal border strongly decurved, the ventral border strongly hooked (<u>Dendrocitta</u>)

13. sqin Medial inset of the quadrate-squamosal articulation

0* Not inset, near the lateral border of the cranium

1 Slightly inset, the otic process of the quadrate recessed slightly medially

2 Far inset, the otic process articulating about half way between the lateral border of the cranium and the foramen magnum

2. flare Lateral flare of the dorsal border of the mandible at the angle

0* Slight to moderate (<u>Cyanocitta</u>)

1 Extreme (<u>Paradisaea</u>)

28. bos Development of the craniofacial hinge

0* The hinge an area of thin bone laterally and medially, the frontals not inflated or only slightly inflated and not consistently so

1 The hinge conspicuous medially but not a true articulation, the frontals consistently slightly inflated over the hinge

2 The hinge well developed as an articulation or approaches that condition, the frontals highly inflated and forming a slight brow or boss over the hinge

27. nsw Width and shape of the nasal processes of the premaxilla at the craniofacial hinge

0 Very narrow, less than one third the width of the hinge, usually much less, the paired processes not entirely fused to each other

1* Wider, usuly approximately one third the width of the hinge

2 Very wide, always more than one third the width of the hinge, sometimes much wider, the paired processes always fused to each other

5. jms Configuration of the suture between lateral nasal bar, jugal arch, premaxilla, and maxilla

   0 Maxilla flat where it meets the ventral bar of the jaw, entirely in the nasal capsule, caudal border of the maxilla far rostral to the caudal border of the lateral nasal bar

   1 Maxilla slightly enlarged where it meets the ventral bar of the jaw, slightly more caudally placed, its caudal border between the rostral and the caudal borders of the lateral nasal bar

   2 Maxilla larger at the ventral bar of the jaw, more caudal than in state 1, the caudal border at the caudal border of the lateral nasal bar

   3* As in state 2 but the maxilla is wedged into the suture between the lateral nasal bar and the ventral bar of the jaw and the maxilla is visible on the lateral surface of the jaw

Nasal capsule:

58. nfos Ossification of the floor of the nasal capsule

    0* No ossification or ossification only slight and marginal

    1 The floor of the nasal capsule ossified extensively, extends caudally to vomer

74. membr Ossification of the nostril

    0 No ossification or ossification limited to borders or midline septum

    1 Most of the nostril covered by delicate ossification with small fenestrae over the surface

30. ncsp Ossification of the median septum of nasal capsule

    0 Ossification absent or slight

    1 Ossification moderate, inconsistent in form, usually incomplete, the septum thin

    2 Ossification consistently heavy

10. mpsh Shape of the tip of the maxillopalatine (conditions not ordered in the analysis)

0 Small and clublike, not inflated

1 Broader, not inflated

2 Broad and inflated medially

3 More inflated, one caudally projecting infrated spur

4 Two caudally projecting inflated spurs more or less confluent with each other, forming a rounded pocket

5 Not ossified

Antorbital plate:

48. lactp Position of the prefrontal and its role in formation of the anteorbital phlange

0 The prefrontal entirely displaced into the nasal capsule

1 The dorsal lobe of the prefrontal forming a small anterior wedge between the ectethmoid and the lateral nasal bar, the ventral lobe variably inflated

2* The dorsal lobe very large, platelike, forming most of the anteorbital phlange

60. ectsp Shape of the ectethmoid

0* The ectethmoid very small, does not reach the frontal (Ailuroides)

1 The ectethmoid forms most of the dorsal lobe of the anteorbital phlange, contacts and fuses with the frontal laterally

2 The ectethmoid forms all of the dorsal lobe and is moderately inflated (Platylophus)

3 As in state 2 but more inflated, the ventral lobe also much inflated (Paradisaea)

50. lacbs Size and shape of the ventral lobe of the prefrontal (conditions not ordered in the analysis)

0 Prefrontal absent, rudimentary, or unossified

1	Ventral lobe inflated but not large, lying mostly along the lateral border of the anteorbital plate
2	Ventral lobe highly inflated laterally and contacting the jugal arch extensively
3	Ventral lobe highly inflated into the nasal capsule

Palate:

57. apos	Density of ossification of the premaxilla in the palate
0	Ossification absent, the prepalatine bars extend rostrally to the ventral bar of the jaw near the tip
1	Ossification extensive but not dense, the palatine part of the premaxilla is moderately to highly pneumatized (<u>Pica</u>, <u>Dendrocitta</u>)
2	Ossification moderately dense but the symphysis not fully fused ventrally (<u>Corvus</u>)
3	Ossification very dense and the symphysis of the upper jaw fused ventrally across the midline usually for its entire length (<u>Nucifraga</u>)
4. pppm	Condition of the palatine process of the premaxilla
0*	Visible and free or adnate to the prepalatine bar but not fused to it
1	Not visible or occasionally visible as a slight trace, apparently fused to the lateral edge of the prepalatine bar
7. medph	Orientation of the medial phlange of the ventral bar of the upper jaw to the prepalatine bar
0*	The phlange lies lateral to the prepalatine bar and meets the lateral rim of the prepalatine bar in a long suture
1	The flange lies dorsolateral to the prepalatine bar and is slightly recurved to meet its lateral border

2 The flange lies dorsal to the prepalatine bar and its medial edge is strongly inflected to meet the dorsal surface of the prepalatine bar, or else the medial edge is reduced to a rounded rostral extension of the ventromedial crest of the jugal arch

9. pbedg Position of the prepalatine bar and extent of fusion to the ventral bar of the jaw

0 The prepalatine bar meets the premaxilla relatively far medial, does not contact the ventral bar of the jaw (Oriolus)

1 The prepalatine bar mees the premaxilla rostrally slightly farther lateral (Platylophus)

2 The rostral end of the prepalatine bar terminates at the ventral bar (Pica) and is sometimes fused to it for a short distance

3 The prepalatine bar meets the ventral bar of the jaw far caudally near the maxillopalatine (Garrulus) and is extensively fused to it

19. pwing Shape of the caudal border of the palatine

0 The caudal border extends approximately mediolaterally from the medial palatine crest to the transpalatine, its shape straight, slightly notched, or irregular

1* The caudal border very decurrent rostrolaterally from the medial palatine crest to the transpalatine

45. lbord Shape of the lateral crest of the palatine

0 Straight

1 Flaring laterally near the tip of the transpalatine process

46. mbord Shape of the medial border of the transpalatine process

0 Straight, the transpalatine heavy and well defined, set apart ventrally from the palatine plate by a long, distinct sulcus which is an extension of the fossa for attachment of palatine retractor muscles on the ventral surface of the palatine

1^* The medial border oriented at an angle to the lateral border so that the transpalatine is wedge shaped; the transpalatine is usually less distinctly defined

47. tpit Presence of a pit on the ventral surface of the transpalatine

0^* No pit

1 Small pit usually present

2 Large pit always present

Temporal fossa and lower jaw articulation:

18. tfsz Size of the temporal fossa

0^* Moderate (<u>Cyanocitta</u>)

1 Much smaller (<u>Podoces</u>, <u>Gymnorhinus</u>)

11. poor Position of the postorbital process

0 Descends slightly rostral to the caudal wall of the orbit, the muscle attachment surface oriented rostromedially

1^* At the caudal wall of the orbit

2 Recessed caudally, descends along the lateral wall of the cranium

12. zpln Length of the zygomatic process

0 Very short, extending only slightly rostroventrally from the orbital wall, the dorsal border abruptly curved (<u>Cyanocitta</u>)

1 Slightly longer, the dorsal border forming a shallow curve at the junction with the dorsal border of the orbit (<u>Calocitta</u>)

2 Moderately long, wedge shaped in lateral profile (<u>Garrulus</u>)

3 Very long, wedge shaped (<u>Nucifraga</u>)

53. smcln Length of the ventral suprameatic crest

0^* Short to moderate, the bulla with a phlange extending rostrally onto the suprameatic crest, shortening the crest, or without a phlange but the crest not elongated caudally

1	Long, the bulla notched at the suprameatic crest, the crest extended caudally
54. smcrl	Conspicuousness of the dorsal suprameatic crest
0*	Not outset, not visible
1	Crest a rough raised ridge only and not consistently visible in some (*Cyanocitta*, *Pica*)
2	Crest distinct and wide at the bulla but narrow over the quadrate (*Nucifraga*)
3	Crest heavy and wide for its full length (*Urocissa*)
69. stslc	Elevation of the dorsal suprameatic crest at the bulla
0*	Not elevated
1	Slightly to moderately elevated over the quadrate; merges with the ventral suprameatic crest before joining the bulla
2	Well dorsal to the ventral suprameatic crest at the quadrate and at the bulla suprameatic crest at the bulla, the bulla extending up to the midtemporal crest
76. zsulc	Length of the subzygomatic sulcus
0*	Short or none, if present extending from the ventral surface of the zygomatic process caudally only about as far as the quadrate-squamosal articulation or slightly farther
1	Extended slightly caudally
2	Extending well beyond the quadrate-squamosal articulation half or more the distance to the bulla
3	Extending far caudally, as far as the bulla or farther
55. smpwd	Width of the suprameatic process of the ventral suprameatic crest (lateral outset)
0*	No suprameatic process or the process very small and not usually present
1	Thickened rostral end of the ventral suprameatic crest, with slight widening (*Cyanocorax cyanomelas*)

2 Wide process consistently present (*Cyanocorax mystacalis*)

56. smpac Presence of a dorsomedial lobe on the suprameatic process of the ventral suprameatic crest, formed as an enlargment of the rostral end of the common border of the subzygomatic sulcus and the sulcus ventral to the dorsal suprameatic crest.

0* None present

1 Small lobe, not consistently present

2 Large lobe always present (*Gymnorhinus*)

75. smpww Shape of the suprameatic process at the quadrate, ventral view

0 Narrow

1 Moderately wide

2 Widened in a medial direction, slightly club-shaped (wider at its extremity than more proximally)

3 Consistently a very large meatic process (*Cyanocitta*)

61. mpmed Wall of the squamosal forms a long abutment against the caudal surface of the otic process of the quadrate, and there is a small process of the quadrate medial to the squamosal wall abutting it

0* Not as described

1 As described (*Pyrrhocorax*)

68. smclp Position of the ventral suprameatic crest at the quadrate

0* Near the squamosal articulation

1 Ventrolateral from the articulation, extended slightly as a shelf (not a finger-like projection down the otic process)

2 Forming a wide ventrolateral shelf

72. alter Periotic forming an abutment against the otic process of the quadrate just medial to the squamosal condyle

0 No abuttment

1 Small abutting surface present

2 Well developed and heavily ossified abuttment

20. qdwd Size of the otic process of the quadrate

0 Very slender, the lateral border a well defined crest (*Dendrocitta*)

1 The lateral border rounded, the shaft heavier (*Cyanocitta*)

2 Very heavy (*Gymnorhinus*)

23. mctxf Length of the medial cotyla of the mandible

0 Very short, the rostral groove shorter than broad

1 Moderately long, the groove extending rostrally about half way to the process for attachment of the *m. pseudotemporalis superficialis*

2 Longer, extending almost to the attachment process

24. mctdp Depth of the medial cotyla of the mandible

0 Shallow, the rostral groove not much differentiated from the caudal facet

1 Deep, the rostral groove saddle shaped and curving steeply into the deep caudal facet

17. jb Presence of a jugal brace on the quadrate

0 No brace or very small brace and not consistently present

1 Small brace usually present

2* The lateral condyle of the quadrate enlarged laterally just dorsal to the articular surface of the lateral condyle, the enlarged area forming a substantial abutment against jugal bar

50. rfdep	Depth of the rostral facet of the lateral cotyla of the mandible
0	Extended medially far toward the medial cotyla, the facet shallow (*Pica*)
1	Extended only slightly onto the medial cotyla
2	Deep, the rostral facet a trough leading into the medial cotyla (*Dendrocitta*)
22. tilt	Tilt of the lateral prominence of the lateral cotyla of the mandible
0*	The articular surface oriented dorsally, medially, or slightly mediodorsal and moderately but not extremely outset laterally
1	The articular surface oriented slightly caudodorsally (*Corvus*)
2	The articular surface enlarged, oriented distinctly caudodorsally, and abruptly outset laterally (*Dendrocitta*)
59. lwall	Cupping of the lateral prominence of the lateral cotyla of the mandible
0	The articular surface facing dorsally or caudodorsally
1	The articular surface oriented slightly medially, the lateral border of the prominence with a distinct crest, the polished articular surface of the lateral prominence extending onto the rostral slope without an abrupt transition in slope; in dorsal view the lateral prominence is not abruptly outset laterally and in caudal view there is little or no lip of the prominence extending caudally (*Garrulus*)
21. rsht	Height of the rostral crest of the lateral cotyla of the mandible
0*	No crest, the rostral slope extends without break to the dorsal rim of the ramus of the mandible
1	A crest walls the lateral margin of the rostral slope
2	A very distinct raised crest extends medially across the rostral slope of the lateral cotyla
3	The rostral slope high and the crest distinct

71. rline	Medial linear ridge on the rostral surface of the quadrate between the lateral condyle and the orbital process or if the rostral condyle is present medial to the rostral condyle
0	No linear ridge or surface
1	Ridge or surface present
25. rcrps	Position of the rostral crest of the lateral cotyla of the mandible
0	Other than as in condition 1
1	Near to the lateral cotyla and very broad laterally
79. lfwd	Position of the lateral process of the mandible
0	Close to the lateral prominence
1	Far rostral to the lateral prominence and distinctly outset (*Cyanolyca*)
26. rcht	Height of the rostral cotyla of the mandible
0*	No rostral cotyla
1	Very small facet on the dorsal rim of the rostral crest of the lateral cotyla, not consistently present
2	Larger facet forming a distinct small cotyla articulating with a rostral condyle of the quadrate when the quadrate is protracted
3	Very high cotyla, in lateral profile the rostral cotyla is as high as the dorsal rim of the ramus or nearly so
67. ccslp	Orientation of the caudal cotyla of the mandible
0	Dorsal or nearly so, the surface oriented in the same plane as the lateral cotyla
1	At a moderate angle (to about 145°) to the surface of the lateral cotyla
2*	Steeply angled to the lateral cotyla

14. qjart	Position of the articulation of the jugal arch on the quadrate, 1) caudal displacement
1*	The articulation is directly lateral on the lateral condyle of the quadrate
2	The articulation displaced far caudally from the lateral condyle
16. boot	Position of the articulation of the jugal arch on the quadrate, 2) dorsal elevation
0*	The articulation not elevated
1	The articulation elevated and separated from the ventral articular surface of the lateral condyle of the quadrate on a heel-like pedestal

Forelimb

63. humln	Humerus length from head to distal intercondylar incisure
0 - 8	Short to long, coded from measurements (described in "Methods")
65. humwd	Width of the head of the humerus from dorsal tubercle to ventral tubercle
0 - 7	Narrow to wide, coded from measurements
32. hh	Height of the head of the humerus
0*	Short to moderate, the articular head not much separated from the dorsal tubercle (*Cyanocitta*)
1	Long, the head a much more prominent structure proximal to the dorsal tubercle (*Corvus*)
41. pcrds	Shape of the distal margin of the pectoral crest of the humerus
0	Not outset, forms a continuous ridge distally down the shaft
1*	The distal margin slightly to moderately outset from the shaft
2	The distal margin widely outset from the shaft and the pectoral crest very short

42. bcrst	Shape of the biceps crest of the humerus
0*	Angular, the tubercle for the *m. scapulohumeralis caudalis* prominent on the rim, the distal margin short, abruptly curved at the shaft
1	Rounded, the tubercle usually entirely within the triceps fossa, the crest elongated down the shaft
43. tf2	Depth of the dorsal triceps fossa (fossa II)
0*	The fossa not apparent or very shallow
1	The fossa excavates the head of the humerus slightly
2	The fossa excavates the head of the humerus very deeply
44. xtub	Position and orientation of the dorsal tubercle of the humerus
0*	The ligament attachment surface is on the rim of the deltoid crest and orients mediodorsally
1	The ligament attachment surface orients slightly medioventrally and the tubercle is slightly outset ventrally from the shaft of the humerus
2	The dorsal tubercle is well outset ventrally from the shaft of the humerus
39. dspht	Size of the dorsal epicondyle of the humerus
0*	The body of the epicondyle small, not extending proximally beyond the level of the proximal rim of the dorsal condyle, or only slighly beyond it
1	The body of the epicondyle moderately elongated
2	The epicondyle larger, the attenuated tip of the supracondylar process very long
40. brcls	Depth and conspicuousness of the depression on the humerus for the origin of the *m.brachialis*
0	Very shallow
1	Moderately well marked
2	Very deep

Hindlimb

77. hips	Width of the synsacrum between the dorsolateral iliac crests
0	About the same width as length from trochanter to caudal limit of the fused vertebrae, the caudolateral spines close together (*Dendrocitta*)
1	Moderately widened (*Cyanopica*)
2	Very wide, the caudolateral spines far apart, the caudal border very broad (*Corvus*).
33. s7	Number of fused sacral vertebrae
0	Usually six
1	Usually seven
2*	Usually eight
64. tmtln	Tarsometatarsus length from medial tibial cotyla to medial intertrochlear incisure
0 - 6	Short to long, coded from measurements (see "Methods")
37. mdef	Definition of the medial crest of the tarsometarsus
0	Rounded
1	Distinct crest (*Pica*)
2	Wide proximally, well defined crest (*Cyanolyca*)
3	Very wide, well defined and heavy (*Platylophus*)
36. mrec	Position of the medial crest or margin of the tarsometarsus
0	At the dorsal surface or only slightly recessed toward the plantar surfac
1	Moderately recessed toward the plantar surface to about one third to one half the diameter of the shaft (viewed medially)
2*	Recessed as far as the plantar surface or nearly so
3	Projected plantarward, forming part of the border of a broad and deep plantar sulcus

38. mtblg		Position of articulation of the first metatarsal
	0^*	Entirely on the plantar surface of the tarsometatarsus, the articular facet deep; the distal trochlea of the first metatarsal lies entirely plantar to the other trochleae
	1	On both the plantar and the medial surfaces of the tarsometatarus, the distal trochleae of the metatarsal 1 lying farther dorsal and the lateral trochlea of metatarsal 2 slightly notched to accomodate metatarsal 2
	2	The articulation almost entirely on the medial surface, in a bulging prominence on the dorsal surface of the tarsometatarsus; the distal trochleae of metatarsal 1 as far dorsal as the trochleae of metatarsals 2-4 (all lie in about the same plane, seen in lateral or medial view)
34. d4ln		Length of the proximal phalanx of toe 4
	0	Very short, less than one half the length of the proximal phalanx of the toe 3
	1^*	Moderate, one half to two thirds the length of the proximal phalanx of toe 3
	2	Long, approximately three fourths the length of the proximal phalanx of toe 3
35. d4nch		Shape of the lateral epicondyle on the first phalanx of toe 3 and its articular facet on toe 4
	0	Epicondyle absent or only a rounded mound, very small, articular notch on toe 4 absent or only a shallow facet
	1^*	Epicondyle a large rounded ridge oriented proximoventrally to distodorsally, the articular notch deep
1. mtilt		Shape of the medial crest of the tarsometatarsus
	0	Straight
	1	Tilted dorsally near the proximal end about 15°
62. size		Overall size
	0 - 7	Small to large, coded from measurements

APPENDIX III. Data coded for analysis. Mnemonics for characters are in Appendix II, for genera in Appendix IV.

Character:		MTILT	FLARE	NULL	PPPM	JMS	POF	MEDPH	IOF	PBEDG	MPSH	POOR	ZPLN	SQIN	QJART	CRAN2
Char.	No:	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15
CORVIDO		0	0	0	1	?	3	0	3	2	5	1	2	0	1	3
Dn	vagabunda	0	0	0	1	?	3	?	1	2	0	1	3	0	1	3
Crp	temia	0	0	0	1	?	3	?	2	2	0	1	3	0	1	2
Pt	afer	0	0	0	1	?	3	?	3	2	5	1	2	2	1	3
Csa	chinensis	0	0	0	1	3	0	1	3	2	5	1	3	0	1	3
Uroc	erythror.	0	0	0	1	3	3	1	3	2	2	1	2	0	1	3
Uroc	caerulea	0	0	0	1	3	3	1	3	2	2	1	2	0	1	3
Cyly	pumilo	0	0	0	1	3	2	2	3	2	3	1	1	2	1	2
Cyly	nana	1	0	0	1	3	2	2	3	2	2	1	2	2	1	2
Cyly	viridicy.	1	0	0	1	3	2	2	3	2	1	1	1	1	1	3
Cyly	cucullata	1	0	0	1	3	2	2	3	3	1	1	2	1	1	3
Cslo	melanocy.	0	0	0	1	2	1	2	2	3	2	1	0	0	1	1
Cslo	sanblas.	0	0	0	1	2	1	2	2	3	2	1	1	0	1	2
Cslo	beecheii	0	0	0	1	2	0	2	2	3	?	1	1	0	1	3
Cycor	caeruleus	0	0	0	1	2	1	2	3	3	2	1	2	0	1	1
Cycor	cyanomel.	0	0	0	1	2	1	2	2	3	2	1	1	0	1	2
Cycor	violaceus	0	0	0	1	2	1	2	2	3	2	1	1	0	1	1
Cycor	cayanus	0	0	0	1	2	2	2	3	3	2	1	1	0	1	?
Cycor	affinis	0	0	0	1	2	1	2	2	3	2	1	1	0	1	2
Cycor	chrysops	0	0	0	1	2	1	2	1	3	2	1	1	0	1	2
Cycor	mystacal.	0	0	0	1	2	1	2	2	3	2	1	0	0	1	2
Cycor	dickeyi	0	0	0	1	2	1	2	3	3	2	1	0	0	1	?
Cycor	yncas	0	0	0	1	2	1	2	3	3	2	1	1	0	1	3
Cal	formosa	0	0	0	1	2	1	2	3	2	2	1	1	0	1	3
Ps	morio	0	0	0	1	2	2	2	2	3	2	1	2	0	1	3
Cycit	cristata	0	0	0	1	2	1	2	3	3	3	2	0	0	1	1
Cycit	stelleri	0	0	0	1	2	1	2	3	3	3	2	0	0	1	1
Aph	unicolor	0	0	0	1	2	2	2	2	3	3	2	0	0	1	2
Aph	coerules.	0	0	0	1	2	1	2	1	3	3	2	0	0	1	2
Aph	ultramar.	0	0	0	1	2	1	2	1	3	3	2	0	0	1	1
Gy	cyanocep.	0	0	0	1	2	0	2	1	3	3	2	0	0	1	0
Per	canadens.	0	0	0	1	2	3	2	2	3	1	1	2	0	1	2
Per	infaustu.	0	0	0	1	2	3	2	2	3	1	1	2	0	1	1
Gar	lidthi	0	0	0	1	2	3	2	1	3	4	1	2	0	1	3
Gar	glandari.	2	0	0	1	2	1	2	1	3	3	1	2	0	1	2
Cypi	cayana	1	0	0	1	3	3	2	3	3	1	1	1	0	1	1
Pica	pica	1	0	0	1	2	1	2	2	2	4	1	1	1	1	2
Cv	monedula	1	0	0	1	3	1	2	1	2	2	1	2	0	1	2
Cv	brachyrh.	0	0	0	1	2	0	2	2	2	2	1	2	0	1	1
Nuc	caryocat.	1	0	1	1	3	0	2	0	3	?	1	3	0	2	2
Nuc	columbia.	1	0	1	1	3	0	2	0	3	4	1	3	0	2	1
Po	panderi	1	0	1	1	2	1	2	1	3	4	1	2	0	2	1
Po	henderso.	2	0	1	1	2	0	2	1	3	4	1	1	1	2	?
Py	graculus	1	0	1	0	2	3	2	2	0	4	1	1	1	0	1
Py	pyrrhoco.	1	0	1	0	2	3	0	1	0	2	1	1	1	2	0

(continued)

Appendix III, continued

Character:		BOOT	JB	TFSZ	PWING	QDWD	RSHT	TILT	MCTXF	MCTDP	RCRPS	RCHT	NSW	BOS	IOW	NCSP
Char. No.:		16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Taxon																
CORVIDO		1	2	1	1	0	0	0	1	1	0	0	2	1	1	1
Dn	vagabunda	1	2	1	1	0	0	2	1	1	0	0	2	1	1	1
Crp	temia	1	2	1	1	0	0	2	1	1	0	0	2	1	1	1
Pt	afer	1	2	0	1	0	0	1	1	1	0	0	1	1	1	1
Csa	chinensis	0	2	1	0	0	0	2	0	1	0	0	0	1	1	1
Uroc	erythror.	0	2	1	0	1	0	0	1	1	0	0	0	0	1	1
Uroc	caerulea	0	2	1	0	1	0	1	1	1	0	0	0	0	1	1
Cyly	pumilo	0	2	1	0	?	2	1	2	1	0	0	1	0	0	0
Cyly	nana	0	2	1	0	?	3	1	2	1	0	0	1	0	0	0
Cyly	viridicy.	0	2	1	0	1	3	1	2	1	0	1	1	0	0	0
Cyly	cucullata	0	2	1	0	1	3	1	2	1	0	1	1	0	1	1
Cslo	melanocy.	0	0	1	0	1	3	1	1	1	0	3	1	0	0	0
Cslo	sanblas.	0	0	1	0	1	3	1	1	1	0	3	1	0	0	0
Cslo	beecheii	0	1	1	0	1	3	1	1	1	0	3	1	0	0	1
Cycor	caeruleus	0	0	1	0	2	3	1	1	1	0	2	1	0	0	1
Cycor	cyanomel.	0	1	1	0	1	3	1	1	1	0	2	1	0	0	1
Cycor	violaceus	0	1	1	0	1	3	1	1	1	0	2	1	0	0	1
Cycor	cayanus	0	1	1	0	1	3	1	1	1	0	3	0	0	0	1
Cycor	affinis	0	1	1	0	1	3	1	1	1	0	3	0	0	0	1
Cycor	chrysops	0	1	1	0	2	3	1	1	1	0	3	0	0	0	1
Cycor	mystacal.	0	0	1	0	1	3	1	1	1	0	3	0	0	0	1
Cycor	dickeyi	0	0	1	0	1	3	1	1	1	0	3	0	0	0	1
Cycor	yncas	0	0	1	0	1	3	1	1	1	0	3	0	0	0	0
Cal	formosa	0	0	1	0	1	3	1	1	1	0	2	0	0	0	1
Ps	morio	0	0	1	0	1	3	1	1	1	0	2	0	0	0	1
Cycit	cristata	0	0	1	0	1	3	1	1	1	0	3	1	0	0	0
Cycit	stelleri	0	0	1	0	1	3	1	1	1	0	3	1	0	0	0
Aph	unicolor	0	0	1	0	?	3	1	1	1	0	3	1	0	0	0
Aph	coerules.	0	0	1	0	1	3	1	1	1	0	3	1	0	0	0
Aph	ultramar.	0	0	1	0	2	3	1	1	1	0	3	2	0	0	0
Gy	cyanocep.	0	0	0	0	2	3	1	0	1	0	3	2	0	0	0
Per	canadens.	0	2	1	0	0	0	1	2	1	0	0	2	0	0	0
Per	infaustu.	0	2	1	0	0	0	1	2	1	0	0	2	0	0	0
Gar	lidthi	0	2	1	0	1	0	1	2	1	0	0	2	0	0	0
Gar	glandari.	0	2	1	0	1	0	0	2	1	0	0	2	0	0	0
Cypi	cayana	1	2	1	0	0	1	1	2	1	0	0	1	0	0	0
Pica	pica	0	2	0	0	0	1	1	2	1	1	0	1	0	0	0
Cv	monedula	0	2	1	0	1	0	1	2	1	0	0	2	0	1	0
Cv	brachyrh.	0	2	1	0	1	1	1	2	1	1	0	2	0	1	1
Nuc	caryocat.	1	2	1	0	1	0	1	2	1	0	0	2	0	0	0
Nuc	columbia.	1	2	1	0	1	0	1	2	1	0	0	2	0	0	0
Po	panderi	0	2	0	0	0	0	0	0	0	0	0	2	0	0	0
Po	henderso.	1	2	0	0	?	0	0	0	0	0	0	2	0	0	0
Py	graculus	1	2	0	0	1	0	0	0	0	0	0	2	0	0	0
Py	pyrrhoco.	1	2	0	0	2	0	1	0	0	0	0	2	0	0	0

(continued)

Appendix III, continued

Character:	NOSH	HH	S7	D4LN	D4NCH	MREC	MDEF	MTBLG	DSPHT	BRCLS	PCRDS	BCRST	TF2	XTUB	LBORD
Char. No.:	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
Taxon															
CORVIDO	1	0	1	1	1	2	0	1	0	1	1	0	0	0	0
Dn vagabunda	1	0	1	1	1	2	0	1	0	1	1	0	0	0	0
Crp temia	1	0	1	1	1	2	0	1	0	1	1	0	0	0	0
Pt afer	2	0	1	1	1	1	0	1	0	2	0	0	0	1	0
Csa chinensis	0	0	2	1	1	1	0	1	0	1	0	0	0	0	1
Uroc erythror.	0	0	2	1	1	1	0	1	0	1	1	?	0	0	1
Uroc caerulea	0	0	2	1	1	1	0	1	0	1	0	?	0	0	1
Cyly pumilo	0	0	0	1	1	1	0	1	0	0	0	0	0	0	1
Cyly nana	0	0	0	1	1	1	0	1	1	2	0	0	0	0	1
Cyly viridicy.	0	0	0	1	1	1	0	1	0	2	1	0	0	0	1
Cyly cucullata	0	0	1	1	1	1	0	1	0	1	0	0	0	0	1
Cslo melanocy.	0	0	1	1	1	1	0	1	0	1	0	0	0	0	1
Cslo sanblas.	0	0	1	1	1	1	0	1	0	2	0	0	0	0	1
Cslo beecheii	0	0	1	1	1	1	0	1	0	2	0	0	0	0	1
Cycor caeruleus	0	0	2	1	1	1	0	1	0	2	0	0	0	0	1
Cycor cyanomel.	0	0	2	1	1	1	0	1	0	2	0	0	0	0	1
Cycor violaceus	0	0	2	1	1	1	0	1	0	1	0	0	0	0	1
Cycor cayanus	0	0	2	1	1	1	0	1	0	2	0	0	0	0	1
Cycor affinis	0	0	2	1	1	1	0	1	0	2	0	0	0	0	1
Cycor chrysops	0	0	1	1	1	1	0	1	0	2	0	0	0	0	1
Cycor mystacal.	0	0	2	1	1	1	0	1	0	1	0	0	0	0	1
Cycor dickeyi	0	0	2	1	1	1	0	1	0	1	0	0	0	0	1
Cycor yncas	0	0	1	1	1	1	0	1	0	2	0	0	0	0	1
Cal formosa	0	0	1	1	1	1	0	1	1	2	0	0	0	0	1
Ps morio	0	0	2	1	1	1	0	1	0	2	0	0	0	0	1
Cycit cristata	0	0	1	1	1	1	0	1	0	?	1	0	0	0	1
Cycit stelleri	0	0	1	1	1	1	0	1	0	2	1	0	0	0	1
Aph unicolor	0	0	1	1	1	1	0	1	0	2	1	0	0	0	1
Aph coerules.	0	0	1	1	1	1	0	1	0	?	1	0	0	0	1
Aph ultramar.	0	0	2	1	1	1	0	1	0	2	1	0	0	0	1
Gy cyanocep.	0	0	1	1	1	1	0	1	1	0	0	0	0	0	1
Per canadens.	0	0	2	1	1	0	0	1	0	0	2	0	1	0	1
Per infaustu.	0	0	?	1	1	0	0	1	0	0	2	0	1	0	1
Gar lidthi	0	0	1	1	1	1	0	1	0	2	1	0	0	0	0
Gar glandari.	0	0	1	1	1	1	0	1	0	2	1	0	0	0	0
Cypi cayana	0	0	2	1	1	0	0	1	0	0	1	0	0	0	1
Pica pica	0	0	1	1	1	0	0	1	1	0	0	0	0	0	1
Cv monedula	0	1	1	1	1	0	0	1	2	2	1	1	0	1	1
Cv brachyrh.	0	1	1	1	1	0	0	1	2	2	1	1	0	2	1
Nuc caryocat.	1	0	1	1	1	0	0	1	1	1	1	1	0	0	1
Nuc columbia.	1	0	1	1	1	0	0	1	1	1	1	1	0	0	1
Po panderi	0	0	1	1	1	0	0	0	1	0	0	0	0	1	0
Po henderso.	1	0	1	1	1	0	0	0	1	0	0	0	0	1	0
Py graculus	0	1	1	1	1	0	0	1	2	2	1	1	0	2	0
Py pyrrhoco.	1	1	1	1	1	0	0	1	2	2	1	1	0	2	0

(continued)

Appendix III, continued

Character:		BORD	TPIT	LACTP	JAW2	LACBS	UJTIP	NULL	SMCLN	SMCR1	SMPWD	SMPAC	APOS	NFOS	LWALL	ECTOP
Char. No.		46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
Taxon																
CORVIDO		0	0	0	4	0	1	0	0	3	0	0	1	1	0	1
Dn	vagabunda	0	0	0	4	0	2	0	0	3	0	0	1	1	0	1
Crp	temia	0	0	0	1	0	2	0	0	3	0	0	1	1	0	1
Pt	afer	1	0	0	2	0	1	0	0	3	0	0	1	1	0	1
Csa	chinensis	1	0	1	3	2	1	0	0	3	0	0	2	0	0	1
Uroc	erythror.	1	0	1	3	2	1	1	0	3	0	0	2	0	0	1
Uroc	caerulea	1	0	1	4	1	1	1	0	3	0	0	2	0	0	1
Cyly	pumilo	1	0	1	?	2	1	0	0	1	0	0	?	0	0	1
Cyly	nana	1	0	1	?	2	1	?	0	1	1	0	?	0	0	1
Cyly	viridicy.	1	0	1	4	1	1	0	0	1	1	0	1	0	0	1
Cyly	cucullata	1	0	1	4	1	1	0	0	1	1	0	1	0	0	1
Cslo	melanocy.	1	1	1	?	1	1	0	0	0	2	0	2	0	0	1
Cslo	sanblas.	1	1	1	3	1	1	0	0	0	2	0	2	0	0	1
Cslo	beecheii	1	1	1	1	1	1	0	0	0	2	0	2	0	0	1
Cycor	caeruleus	1	1	1	4	1	1	0	0	0	1	0	2	0	0	1
Cycor	cyanomel.	1	1	1	4	1	1	0	0	0	1	0	2	0	0	1
Cycor	violaceus	1	1	1	?	1	1	?	0	0	1	0	2	0	0	1
Cycor	cayanus	1	1	1	?	1	1	?	0	0	1	0	2	0	0	1
Cycor	affinis	1	1	1	3	1	1	0	0	0	2	0	2	0	0	1
Cycor	chrysops	1	1	1	3	1	1	0	0	0	2	0	2	0	0	1
Cycor	mystacal.	1	1	1	2	1	1	0	0	0	2	0	2	0	0	1
Cycor	dickeyi	1	1	1	?	1	1	?	0	0	2	0	2	0	0	1
Cycor	yncas	1	1	1	3	1	1	1	0	1	2	0	2	0	0	1
Cal	formosa	1	1	1	2	1	1	1	0	?	?	0	2	0	0	1
Ps	morio	1	1	1	?	1	1	?	0	?	1	0	2	0	0	1
Cycit	cristata	1	1	1	3	2	0	1	1	1	2	1	2	0	0	1
Cycit	stelleri	1	1	1	2	2	0	0	1	1	2	1	2	0	0	1
Aph	unicolor	1	1	1	?	2	0	0	1	1	2	0	2	0	0	1
Aph	coerules.	1	1	1	2	2	0	0	2	1	2	1	2	0	0	1
Aph	ultramar.	1	1	1	1	2	0	1	2	1	2	1	2	0	0	1
Gy	cyanocep.	1	1	1	1	2	0	1	2	1	2	2	3	0	0	1
Per	canadens.	1	0	1	4	1	0	0	1	1	0	0	3	0	0	1
Per	infaustu.	1	0	1	?	1	0	0	1	1	0	0	3	0	0	1
Gar	lidthi	1	1	1	4	2	0	0	1	1	0	0	3	0	1	1
Gar	glandari.	1	1	1	4	2	0	0	2	2	0	0	3	0	1	1
Cypi	cayana	1	0	1	2	1	0	1	1	1	1	0	2	0	0	1
Pica	pica	1	2	1	2	2	1	0	0	1	1	0	2	0	0	1
Cv	monedula	1	2	1	3	1	1	0	2	2	0	0	3	0	0	1
Cv	brachyrh.	1	2	1	5	1	1	0	2	2	1	0	2	0	0	1
Nuc	caryocat.	1	2	1	2	2	0	0	2	2	0	0	3	0	0	1
Nuc	columbia.	1	2	1	1	2	0	0	2	2	0	0	3	0	0	1
Po	panderi	1	2	1	1	1	0	0	2	1	0	0	3	0	0	1
Po	henderso.	1	2	1	?	?	0	0	2	1	0	0	3	0	0	1
Py	graculus	0	0	1	2	1	0	0	1	1	0	0	?	0	1	1
Py	pyrrhoco.	0	0	1	0	1	0	0	0	1	0	0	?	0	0	1

(continued)

Appendix III, continued

Character:	MPMED	SIZE	HUMLN	TMTLN	HUMWD	INFLA	CCSLP	SMC1P	STSLC	JAW3	RLINE	ALTER	CRAN3	MEMBR	SMPWW
Char. No.:	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75
Taxon															
CORVIDO	0	2	3	0	2	1	1	0	0	?	0	0	3	0	0
Dn vagabunda	0	2	6	0	2	1	1	0	0	4	0	0	1	0	0
Crp temia	0	1	5	0	3	1	1	0	0	4	0	0	3	0	0
Pt afer	0	0	4	5	2	0	2	0	0	3	0	0	3	0	0
Csa chinensis	0	2	0	4	0	0	0	0	0	4	0	0	2	0	0
Uroc erythror.	0	3	4	3	3	0	0	0	0	2	0	0	2	0	0
Uroc caerulea	0	3	1	4	2	0	0	0	0	1	0	0	2	0	0
Cyly pumilo	0	0	6	3	2	0	1	1	1	?	0	0	0	0	1
Cyly nana	0	0	?	?	?	0	1	1	1	?	0	?	1	0	1
Cyly viridicy.	0	1	2	3	1	0	1	1	1	3	1	0	2	0	1
Cyly cucullata	0	1	1	2	1	1	1	1	1	3	1	1	2	1	1
Cslo melanocy.	0	1	4	2	3	0	1	0	0	?	0	0	1	0	1
Cslo sanblas.	0	2	4	4	2	0	1	0	0	2	0	1	3	0	1
Cslo beecheii	0	2	4	4	2	0	1	0	0	3	0	1	3	0	1
Cycor caeruleus	0	3	4	2	1	0	1	0	0	2	1	0	1	0	0
Cycor cyanomel.	0	2	7	3	3	0	1	0	0	1	1	0	2	0	0
Cycor violaceus	0	3	4	2	2	0	1	0	0	?	1	0	0	0	0
Cycor cayanus	0	?	?	?	?	0	1	0	0	?	1	?	?	0	1
Cycor affinis	0	3	3	3	2	0	1	0	0	2	0	1	1	0	1
Cycor chrysops	0	2	3	4	1	0	1	0	0	3	0	1	2	0	1
Cycor mystacal.	0	2	2	4	3	0	1	0	0	?	0	1	2	0	1
Cycor dickeyi	0	2	?	3	3	0	1	0	0	4	0	1	?	0	1
Cycor yncas	0	1	3	4	2	0	?	1	1	2	0	2	3	0	1
Cal formosa	0	3	4	1	2	0	1	0	0	2	0	0	2	0	1
Ps morio	0	3	5	2	3	?	1	0	0	?	0	0	1	0	1
Cycit cristata	0	1	6	2	3	0	1	1	1	2	0	2	2	0	1
Cycit stelleri	0	1	5	4	1	0	1	1	1	2	0	2	1	0	1
Aph unicolor	0	2	4	3	2	0	1	1	1	?	0	?	2	0	1
Aph coerules.	0	1	3	4	1	0	1	1	1	3	0	2	3	0	1
Aph ultramar.	0	2	7	3	3	0	1	1	1	2	0	3	3	0	1
Gy cyanocep.	0	1	4	2	4	0	1	1	2	3	0	3	4	0	1
Per canadens.	0	1	5	3	3	0	1	2	2	3	0	0	2	0	0
Per infaustu.	0	1	3	2	1	0	1	2	2	?	0	0	2	0	0
Gar lidthi	0	3	3	2	2	0	1	2	2	1	0	0	2	0	0
Gar glandari.	0	2	5	2	3	0	1	2	2	2	0	0	2	0	0
Cypi cayana	0	1	3	3	2	1	1	1	2	2	0	0	2	0	0
Pica pica	0	3	4	2	1	0	1	1	2	1	0	0	2	0	0
Cv monedula	0	3	7	1	4	0	0	0	0	2	0	0	3	0	0
Cv brachyrh.	0	4	8	1	4	1	0	1	1	5	0	0	1	0	0
Nuc caryocat.	0	?	?	?	?	0	0	2	2	3	0	0	1	0	0
Nuc columbia.	0	2	3	0	2	0	0	2	2	3	0	0	2	0	0
Po panderi	0	1	4	5	2	0	0	2	2	4	0	0	2	0	0
Po henderso.	1	?	3	1	?	0	0	2	2	?	0	0	?	0	0
Py graculus	0	2	4	3	5	0	1	2	2	2	0	0	2	0	0
Py pyrrhoco.	1	4	4	1	5	0	1	2	2	0	0	0	4	0	0

(continued)

Appendix III, continued

Character:		ZSULC	HIPS	RFDEP	LFWD	JAW4
Char. No:		76	77	78	79	80
Taxon						
CORVIDO		0	0	1	0	1
Dn	vagabunda	1	0	2	1	1
Crp	temia	0	0	2	1	5
Pt	afer	0	0	?	0	0
Csa	chinensis	0	0	2	0	1
Uroc	erythror.	0	0	0	0	1
Uroc	caerulea	0	0	0	0	2
Cyly	pumilo	0	0	1	1	?
Cyly	nana	0	0	1	1	?
Cyly	viridicy.	0	0	1	1	3
Cyly	cucullata	0	0	1	1	3
Cslo	melanocy.	1	0	1	0	?
Cslo	sanblas.	1	0	1	0	2
Cslo	beecheii	1	0	1	0	3
Cycor	caeruleus	0	0	1	0	4
Cycor	cyanomel.	0	0	1	0	4
Cycor	violaceus	0	0	1	0	?
Cycor	cayanus	1	0	1	0	?
Cycor	affinis	1	0	1	0	3
Cycor	chrysops	1	0	1	0	3
Cycor	mystacal.	1	0	1	0	4
Cycor	dickeyi	1	0	1	0	?
Cycor	yncas	1	0	1	0	2
Cal	formosa	1	0	1	0	1
Ps	morio	1	0	1	0	?
Cycit	cristata	2	0	1	0	2
Cycit	stelleri	2	0	1	0	2
Aph	unicolor	2	0	1	0	?
Aph	coerules.	2	0	1	0	3
Aph	ultramar.	2	0	1	0	2
Gy	cyanocep.	2	0	1	0	1
Per	canadens.	1	2	1	0	2
Per	infaustu.	1	2	1	0	?
Gar	lidthi	1	2	1	0	2
Gar	glandari.	1	2	1	0	2
Cypi	cayana	1	1	1	0	2
Pica	pica	0	1	0	0	0
Cv	monedula	0	2	0	0	3
Cv	brachyrh.	0	2	0	0	0
Nuc	caryocat.	0	2	?	0	5
Nuc	columbia.	0	2	1	0	5
Po	panderi	0	0	0	0	1
Po	henderso.	0	?	0	0	?
Py	graculus	0	2	0	0	0
Py	pyrrhoco.	0	2	0	0	1

APPENDIX IV. Mnemonics for taxa.

AJ	American jays
Aph	Aphelocoma
Cal	Calocitta
Crp	Crypsirina
Crc	Cracticus
Csa	Cissa
Cslo	Cissilopha
Cv	Corvus
Cyly	Cyanocyca
Cypi	Cyanopica
Cycit	Cyanocitta
Cycor	Cyanocorax
Dn	Dendrocitta
Gar	Garrulus
Mn	Manucodia
Nuc	Nucifraga
Or	Oriolus
Per	Perisoreus
Pt	Ptilostomus
Pa	Paradisea
Pi	Pica
Pl	Platylophus
Plt	Platysmurus
Pod	Podoces
Ps	Psilorhinus
Pyr	Pyrrhocorax
Zav	Zavatarriornis

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