INTERGENERIC RELATIONSHIPS OF THE NEW WORLD JAYS INFERRED FROM CYTOCHROME b GENE SEQUENCES[1]

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Abstract. The six genera of corvids endemic to the Americas (i.e., *Aphelocoma, Calocitta, Cyanocitta, Cyanocorax, Cyanolyca,* and *Gymnorhinus*) form the assemblage that most ornithologists call the New World jays. The intergeneric relationships among these six genera are explored using complete sequences from the cytochrome *b* gene (1,143 bp) along with 29 morphological characters. A consistent phylogenetic hypothesis was obtained when the data sets were analyzed independently or in a total evidence approach. The phylogeny presented in this paper does not corroborate the existence of two evolutionary lineages as previously proposed by Hardy (1961, 1969). The most basal genus of the New World jays is *Cyanolyca,* which also is supported by independent evidence on cranial anatomy. The remainder of the genera are embedded within two major clades. The most derived is formed by *Cyanocitta, Aphelocoma,* and *Gymnorhinus,* being *Cyanocitta* the most basal genus within this clade. *Calocitta* and *Cyanocorax* constitute the other clade. A very close relationship between these two genera is supported by bootstrap values and branch support analysis. These results corroborate the hypothesis that the Piñon Jay (*Gymnorhinus cyanocephalus*) is a true New World jay, and a putative relationship with nutcrackers is not supported. The phylogeny obtained is used to infer a biogeographic scenario, as well to explain the evolution of a very derived jaw articulation present only in the New World jays. The biogeographic scenario agrees with a relatively recent arrival of a corvine ancestor via Beringia, and a very rapid dispersal and radiation into the Americas.

Key words: New World jays, Corvidae, cytochrome b gene, total evidence analysis, phylogenetic analysis, biogeography.

INTRODUCTION

Corvids (crows, jays and allies) are one of the most successful groups of passerine birds. The family has a world-wide distribution and exhibits a high species diversity. The corvids encompass a total of 25 genera and 113 species, which are found in numerous kinds of habitats (Goodwin 1976, Madge and Burn 1994). Six genera of corvids (i.e., *Aphelocoma, Calocitta, Cyanocitta, Cyanocorax, Cyanolyca,* and *Gymnorhinus*, sensu AOU 1983) are endemic to the Americas and have successfully radiated within tropical, subtropical, and mild temperate environments. Some morphological characters, like a buttress complex (Zusi 1987), shared by these taxa seem to support their monophyly, and for most ornithologists these six genera comprise the so-called New World jays. In contrast, others have argued that *Gymnorhinus* (the Piñon Jay) should be excluded from this assemblage. For instance, Hardy (1961) postulated that the Piñon Jay was most closely related to Old World corv-

ids, particularly to the genus *Nucifraga,* based on the fact that *Gymnorhinus* walks and runs instead of hops as do all the New World jays. Hardy argued that the walking behavior must be correlated with a rather different neuromuscular control system. Other workers have accepted the idea that the Piñon Jay is related to the other jays, but they have usually postulated that *Gymnorhinus* is basal and should be considered as the sister-group to the New World jays (Ashley 1941, Pitelka 1951, Goodwin 1976).

Not only has the position of the Piñon Jay been challenged, but the entire phylogenetic arrangement of the New World jays has been constantly questioned. Earlier workers have attempted to resolve corvid intergeneric relationships based on morphological characters (e.g., Ridgway 1904, Amadon 1944, Hardy 1961, 1969). Despite this attention, the phylogenetic conclusions of these studies show little congruence. Moreover, the methods used to establish monophyly of the New World jays in those analyses were weak, because they were based on poorly defined similarities and without evidence for polarity of the characters.

Using external morphological and behavioral

characters, Amadon (1944) postulated that all New World jays formed a monophyletic group, and he placed them as the sister-group to *Gymnorhinus cyanocephalus* (Piñon Jay). He considered *Gymnorhinus* to be a specialized jay that resembles nutcrackers (*Nucifraga* spp.) because of similarities in feeding habits. Amadon's classification divided the New World jays into four genera, instead of the nine previously proposed by Ridgway (1904). The genera recognized by Amadon were: *Cyanocitta* (which included *Aphelocoma, Cyanolyca* and *Cissilopha*), *Psilorhinus, Cyanocorax,* and *Calocitta* (Fig. 1a).

Hardy (1961) suggested that two main evolutionary lineages of New World jays could be identified using both behavioral and morphological evidence. He distinguished an "Inornate line" (tribe Aphelocomini) containing only the members of the genus *Aphelocoma,* and an "Ornate line" (tribe Cyanocorini) which encompassed five of the remaining seven genera (*Calocitta, Cissilopha, Cyanocitta, Cyanocorax,* and *Psilorhinus*). The genus *Cyanolyca* was omitted from either line because the species in this genus were considered to be so poorly known behaviorally that their affinities could not be assessed (Fig. 1b). Hardy (1969) later reviewed his previous classification and maintained the hypothesis of two evolutionary lineages inside the New World jays, but this time only recognized three genera. The ornate lineage consisted of *Cyanocitta,* as well as the largely Neotropical *Cyanocorax* within which *Calocitta, Cissilopha,* and *Psilorhinus* were ranked as subgenera. The inornate lineage contained the third genus, *Aphelocoma,* which also included the species formerly placed in *Cyanolyca.* A major problem with both of Hardy's classification schemes is that the inornate clade was defined mainly on the absence of ornate plumage which seems to be a plesiomorphic condition among corvids.

Goodwin (1976) concurred with previous authors' opinions that there was an early isolation of the New World jays within the corvid radiation. Although his classification followed Amadon's hypothesis and placed the New World jays as the sister-group of *Gymnorhinus,* relationships within the New World jays were completely unresolved (Fig. 1c).

Using a cladistic approach, Hope (1989) analyzed the phylogenetic interrelationships within the family Corvidae employing a set of 80 osteological characters. Although the analyses

within the group showed highly unstable topologies, her results supported the monophyly of the New World jays on the basis of four derived characters: (a) a very high rostral crest of the lateral cotyla of the mandible, (b) a rostral articulation of the lower jaw, (c) the presence of a medial basal ridge on the quadrate, and (d) an extensive fusion of the prepalatine bar to the ventral bar of the jaw. Hope (1989) presented three different phylogenetic hypotheses for relationships within the New World jays. In all of them, however, the genera *Aphelocoma* and *Cyanocorax* were postulated to be paraphyletic. Another constant result was the emergence of *Cyanolyca* as the most basal taxon. A strict consensus tree of the three solutions highlights the unresolved relationships among the New World jays (Fig. 1d).

The development of molecular protocols has allowed the integration of biochemical data into phylogenetic analysis. Sibley and Ahlquist (1985) employed DNA-DNA hybridization distances to explore the phylogenetic affinities among corvids. Their analysis included three genera of New World jays (*Cyanocitta, Aphelocoma,* and *Cyanocorax*). Their results show the New World jays as a paraphyletic group inside the tribe Corvini (sensu Sibley and Ahlquist), which also includes crows, magpies, nutcrackers and coughs. It should be noted, however, that the resolving power of DNA hybridization data, as well as the methodology used to analyze them, have been questioned (Cracraft 1987, Houde 1987, Harshman 1994).

Several other molecular studies have addressed the phylogenetic relationships within the corvine assemblage (Sibley and Ahlquist 1990, Helm-Bychowski and Cracraft 1993). However, none of these studies has confronted relationships within the New World jays in detail. The goal of the present study is to clarify the generic interrelationships of these taxa by generating a new data set, namely sequences from the mitochondrial cytochrome *b* gene.

To avoid further confusion, we will use the noun "jays" when referring to the seven genera of corvids used in this study, and the noun "New World jays" for the six genera endemic to the Americas (*Aphelocoma, Calocitta, Cyanocitta, Cyanocorax, Cyanolyca,* and *Gymnorhinus*).

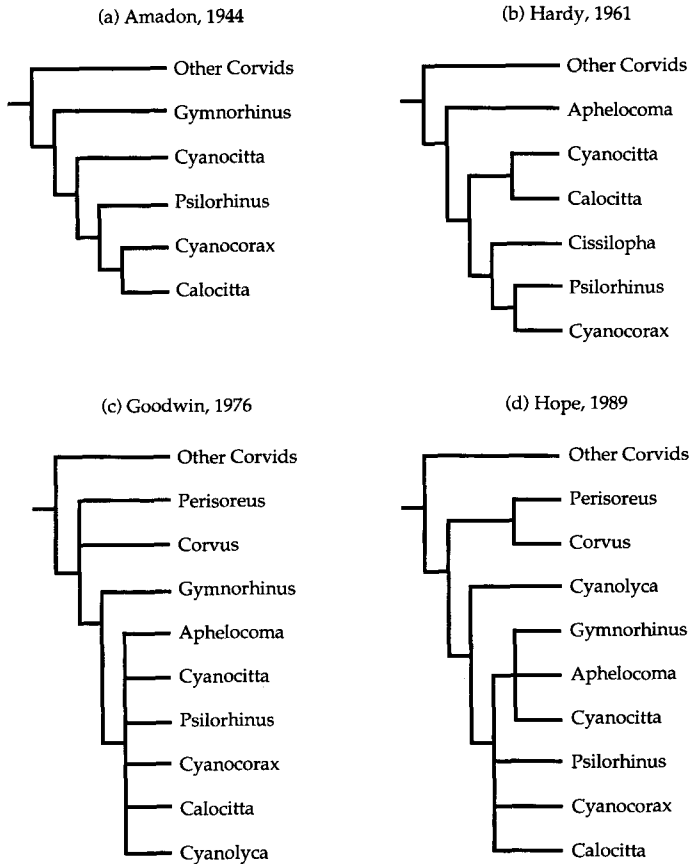FIGURE 1.   Some phylogenetic hypotheses previously proposed for the intergeneric relationships of New World jays.

METHODS

TAXA EXAMINED

Complete cytochrome *b* gene sequences (1,143 bp) were determined for six species of jays (Table 1), each representing a different genus within the lineage. Four sequences belong to what conventionally has been recognized as the core New World jays: the Scrub Jay (*Aphelocoma coerulescens*), Magpie Jay (*Calocitta formosa*), Plush-capped Jay (*Cyanocorax chrysops*), and White-collared Jay (*Cyanolyca viridicyana*). The fifth sequence corresponds to the Piñon Jay (*Gymnorhinus cyanocephalus*) which for some ornithologists should be considered as a close relative to New World jays, but not as part of this assemblage. Finally, the last sequence belongs to the Gray Jay (*Perisoreus canadensis*).

The rest of the sequences used for this analysis were taken from Helm-Bychowski and Cra-

craft (1993). The Blue Jay (*Cyanocitta cristata*) complemented the sequences of the New World jays presented here. Four species of birds-of-paradise (*Manucodia keraudrenii, Epimachus fastuosus, Ptiloris paradiseus,* and *Cicinnurus magnificus*) and two bowerbirds (*Ailuroedus melanotus* and *Ptilonorhynchus violaceus*) were used as representatives of closely related lineages within the corvine assemblage. Finally, the Hermit Thrush (*Catharus guttatus*), a non-corvine passerine, was employed as an outgroup to root the tree.

DNA EXTRACTION AND SEQUENCING

Frozen tissue (muscle, liver and heart) of selected taxa was obtained from the Museum of Natural Science, Louisiana State University, and the Museo de Zoologia Facultad de Ciencias, Universidad Nacional Autonoma de Mexico. To-

TABLE 1. Jay specimens sequenced.

Taxon	Locality	Collection	Reference number
Aphelocoma coerulescens	USA; California	LSUMZ[a]	B-15539
Calocitta formosa	MEXICO; Oaxaca	MZUNAM[b]	OMVP-168
Cyanocorax chrysops	BOLIVIA; Santa Cruz	LSUMZ[a]	B-18785
Cyanolyca viridicyana	PERU; Huanuco	LSUMZ[a]	B-3501
Gymnorhinus cyanocephala	USA; California	LSUMZ[a]	B-14328
Perisoreus canadensis	USA; New Mexico	LSUMZ[a]	B-10198

[a] Collection of Frozen Tissues, Louisiana State University Museum of Natural Science.
[b] Museo de Zoologia Facultad de Ciencias, Universidad Nacional Autonama de Mexico.

tal genomic DNA was extracted using Chelex 5% following the protocol suggested by Singer-Sam et al. (1989). The cytochrome *b* gene (1,143 bp) was amplified by the use of conventional PCR techniques (Kocher et al. 1989). A total of 14 oligonucleotide primers were used for amplification and sequencing (primer sequences documented in Helm-Bychowski and Cracraft 1993). Single-stranded template for sequencing was produced by asymmetric PCR using unbalanced primer ratios (Gyllensten and Erlich 1988). DNA sequencing was performed using T7 DNA polymerase (Sequenase version 2.0, United States Biochemical) following standard dideoxy chain-termination protocols (Sanger et al. 1977). Finally, sequencing reactions were subjected to denaturing gel electrophoresis and autoradiography. Sequences were easily aligned by eye with the aid of the ESEE editor program, version 1.07 (Cabot and Beckenbach 1989).

MORPHOLOGICAL DATA

Hope (1989) undertook an analysis of corvid phylogeny using osteological characters. To complement the present study, we employed a total of 28 characters from her analysis that were phylogenetically informative for the jays. The remainder character (Character 1) was suggested by Peterson. In our analysis all character-states

were considered as unordered, and their polarization was determined by the use of outgroup comparison. The Gray Jay was employed as the outgroup for this part of the analysis. A character-state matrix for all these data is presented in Table 2. A detailed list of the characters as well as a description of the character-states can be consulted in Appendix 1.

DATA ANALYSIS

Independent cladistic analyses of each data set (i.e., molecules and morphology), as well as a data set that combined both morphological and molecular characters, were performed. Phylogenetic analyses were undertaken with the computer program Phylogenetic Analysis Using Parsimony (PAUP version 3.1.1; Swofford 1993). To insure the discovery of the most parsimonious solution, exhaustive searches were executed. Nucleotide transformations were considered unordered during all analyses.

Many methodologies have been suggested to evaluate cladistic signal in sequence data (Swofford and Olsen 1990, Cracraft and Helm-Bychowski 1991, Hillis 1991). We adopted the following approach: (a) only most parsimonious trees were used, (b) in those cases in which the solution included more than a single most parsimonious tree, the signal was identified using

TABLE 2. Character-state matrix for 29 morphological characters for the seven genera of jay.

Taxon	Characters[a]																												
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Cyanolyca	0	2	2	1	1	0	0	0	0	0	0	0	1	2	1	1	2	1	0	0	1	1	0	1	0	1	0	0	1
Cyanocorax	0	1	0	0	1	1	1	1	1	1	0	0	1	1	2	1	1	3	0	0	0	0	1	1	1	0	0	1	0
Calocitta	0	1	2	0	1	1	1	1	1	0	0	0	1	0	1	1	1	2	0	0	0	0	1	1	0	1	1	0	0
Cyanocitta	1	1	2	1	0	2	0	1	1	1	1	1	0	0	1	1	1	3	1	1	1	1	2	1	2	1	0	1	0
Aphelocoma	1	1	0	1	0	2	0	1	1	1	1	1	0	0	1	1	1	3	2	1	1	1	2	1	2	1	0	1	0
Gymnorhinus	0	0	0	2	0	2	0	1	2	1	1	1	0	0	2	1	0	3	2	2	1	2	3	1	2	0	1	1	0
Perisoreus	0	3	1	2	0	0	0	0	2	1	0	0	2	2	0	0	2	0	1	0	2	2	0	0	1	2	0	2	2

[a] Characters and character-state descriptions are presented in Appendix 1.

strict consensus trees, (c) branch lengths of most-parsimonious trees were optimized by the DELTRAN option in PAUP, and (d) relative strength of signal was examined by the bootstrap test (1,000 replications), as well as by branch support (Bremer 1988, 1994).

RESULTS

SEQUENCES AND SEQUENCE COMPARISONS

Complete sequences of the cytochrome *b* gene for *Aphelocoma, Calocitta, Cyanocorax, Cyanolyca, Gymnorhinus,* and *Perisoreus* were obtained for this study. These sequences have been deposited in GenBank to allow an easier access to these data. The accession number for the sequences are: U77331 (*Perisoreus canadensis*), U77332 (*Gymnorhinus cyanocephalus*), U77333 (*Cyanolyca viridicyana*), U77334 (*Cyanocorax chrysops*), U77335 (*Aphelocoma coerulescens*), and U77336 (*Calocitta formosa*). Sequences for the remainder taxa and their accession numbers can be found in Helm-Bychowski and Cracraft (1993).

No deletions or insertions in the 381 codons in the cytochrome *b* gene were detected among these birds. The termination codon for the six sequences was TAA as commonly found in the chicken mitochondrial protein-coding genes (Desjardins and Morais, 1990). Recently, several studies have reported nuclear copies of mitochondrial genes especially cytochrome *b* (Quinn 1992, Smith et al. 1992, Kornegay et al. 1993). These nuclear copies are characterized by frameshifts and nonsense codons, neither of which were apparent in the sequences that we obtained. Furthermore, based on the fact that the complete cytochrome *b* gene was isolated initially as a single fragment, we assume that these sequences are of mitochondrial origin only. Therefore, they do not represent pseudogenous or translocated fragments that might be located elsewhere in the jays' genome.

The nucleotide ratio among the different taxa is typical for the avian cytochrome *b* gene. The average relative frequencies of each kind of nucleotide for the DNA sequences was: 31.87% cytosine, 25.84% thymine, 29.22% adenine, and 13.08% guanine. Third positions showed an average divergence of 35.6%, followed by first positions with 8.28%, and finally second positions with 2.84%.

The complete data set (14 taxa), contained a total of 332 phylogenetic informative characters, from which 150 sites represent transversion substitutions. Within the jays, the cytochrome *b* gene had a total of 177 phylogenetic informative characters, and 43 when just transversions were considered. The mean number of base substitutions was 153 (13.4%), a relatively high value when compared to the paradisaeinines which had an average divergence of 111 (9.7%). The transversion analysis showed an average divergence of 47 substitutions (4.08%). The maximum number of transversion differences among the corvids was found between *Perisoreus* and *Calocitta* at 76, and the minimum number was 25 between *Gymnorhinus* and *Cyanocitta*. Table 3 summarizes the relative nucleotide divergence among the jays.

MOLECULAR PHYLOGENETICS

Examination of the eight basic types of nucleotide substitutions among jays and the outgroup taxa (i.e., *Catharus, Ailuroedus* and *Ptilonorhynchus*) reveals a clear saturation in third position transitions (Fig. 2). Therefore, to avoid the effect of excessive homoplasy in third positions, transversions at this position were up-weighted ten times over transitions (i.e., transitions weight = 0.1) when estimating phylogenetic trees. All other kinds of substitutions were considered with equal weight, assigning to them the same weight as third position transversions (i.e., weight = 1). We determined this weighting scheme via successive approximations decreasing the weight of third position transitions until the phylogenetic analysis yielded a consistent tree.

The result produced two equally most parsimonious trees of 428 steps in length with a consistency index of 0.607 and a retention index of 0.466. The only disagreement between the two topologies was the position of *Cyanocitta* as the sister taxon to the clade *Aphelocoma-Gymnorhinus* or to the clade *Calocitta-Cyanocorax*. The signal contained in these trees was condensed by a strict consensus tree and the result is shown in Figure 3.

Using the Hermit Thrush to root the network, three monophyletic groups were resolved: the jays (Corvidae), birds-of-paradise (Paradisaeidae), and bowerbirds (Ptilonorhynchidae). In all the analyses that we performed, the sister-group to Corvidae was the birds-of-paradise. This was a constant result even when the taxa within the

TABLE 3. Pairwise comparison of relative nucleotide divergence among the jays. TOT = Total; TS = Transitions; TV = Transversions; 1st, 2nd and 3rd = first, second and third position; 1ts, 2ts and 3ts = first, second and third position transitions; 1tv, 2tv and 3tv = first, second and third position transversions; K2 = Kimura's two-parameter model.

Taxa		TOT %	TS %	TV %	1st %	2nd %	3rd %	1ts %	1tv %	2ts %	2tv %	3ts %	3tv %	K2 %
Gymnorhinus	Perisoreus	14.4	10.1	4.3	5.5	1.3	36.5	4.5	1.0	1.0	0.3	24.9	11.5	16.3
Cyanolyca	Perisoreus	13.8	9.2	4.6	5.8	2.1	33.6	4.2	1.6	1.3	0.8	22.0	11.5	15.5
Cyanolyca	Gymnorhinus	13.2	9.7	3.5	5.8	1.8	32.0	4.7	1.0	1.3	0.5	23.1	8.9	14.8
Cyanolyca	Cyanocorax	14.3	9.8	4.5	7.3	3.4	32.0	6.0	1.3	2.1	1.3	21.3	10.8	16.1
Cyanolyca	Cyanocitta	12.9	9.7	3.2	8.4	1.6	28.9	7.1	1.3	1.0	0.5	21.0	7.9	14.5
Cyanolyca	Calocitta	14.9	9.8	5.1	8.7	4.5	31.5	6.6	2.1	3.1	1.3	19.7	11.8	16.8
Cyanolyca	Aphelocoma	13.6	10.0	3.7	8.1	2.6	30.2	6.3	1.8	1.6	1.0	22.0	8.1	15.4
Cyanocorax	Perisoreus	15.8	9.4	6.5	7.1	2.9	37.5	5.2	1.8	1.8	1.0	21.0	16.5	18.0
Cyanocorax	Gymnorhinus	12.3	8.6	3.8	5.8	1.6	29.7	4.5	1.3	0.8	0.8	20.5	9.2	13.7
Cyanocorax	Cyanocitta	12.6	8.9	3.7	6.6	1.8	29.4	5.0	1.6	1.0	0.8	20.7	8.7	14.0
Cyanocorax	Calocitta	10.8	7.7	3.1	5.5	2.6	24.1	3.7	1.8	1.6	1.0	17.8	6.3	11.8
Cyanocorax	Aphelocoma	13.6	9.6	3.9	8.4	2.9	29.4	6.8	1.6	1.6	1.3	20.5	8.9	15.2
Cyanocitta	Perisoreus	14.3	9.5	4.7	5.8	1.6	35.4	5.0	0.8	1.3	0.3	22.3	13.1	16.1
Cyanocitta	Gymnorhinus	10.7	8.5	2.2	5.0	0.3	26.8	4.2	0.8	0.3	0.0	21.0	5.8	11.8
Cyanocitta	Aphelocoma	12.3	9.6	2.7	7.6	1.6	27.8	6.0	1.6	1.0	0.5	21.8	6.0	13.8
Calocitta	Perisoreus	15.7	9.1	6.6	6.8	3.9	36.2	4.2	2.6	2.9	1.0	20.2	16.0	17.7
Calocitta	Gymnorhinus	13.7	9.7	4.0	5.8	2.6	32.8	3.7	2.1	1.8	0.8	23.6	9.2	15.5
Calocitta	Cyanocitta	13.0	8.9	4.1	7.3	2.9	28.9	5.0	2.4	2.1	0.8	19.7	9.2	14.5
Calocitta	Aphelocoma	14.3	10.1	4.2	7.9	3.4	31.8	5.5	2.4	2.1	1.3	22.8	8.9	16.2
Aphelocoma	Perisoreus	14.6	9.8	4.8	6.6	2.1	35.2	4.7	1.8	1.8	0.3	22.8	12.3	16.5
Aphelocoma	Gymnorhinus	11.6	9.2	2.4	6.6	1.3	27.0	5.2	1.3	0.8	0.5	21.5	5.5	12.9
Average divergence		13.4	9.4	4.1	6.8	2.3	31.3	5.2	1.6	1.5	0.8	21.4	9.8	15.1

ingroup were changed and alternative taxa were used as an outgroup. Although the consensus tree depicts the phylogenetic relationships within the New World jays as incompletely resolved, the Gray Jay (*Perisoreus*) always appears as the sister taxon to the New World jays.
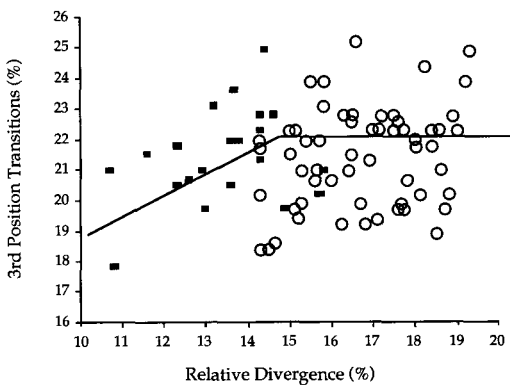

FIGURE 2. Saturation curve third-position transitions plotted against relative sequence divergence. Squares represent pairwise comparisons among the genera of jays; circles represent pairwise comparisons between the jays and the outgroup. Growing transitions differences leads to a plateau indicating a saturation in third positions (line was adjusted by eye).

Higher-level relationships in this phylogenetic hypothesis are consistent with the findings of other studies (Sibley and Ahlquist 1985, 1990, Helm-Bychowski and Cracraft 1993). However, a branch support analysis showed that three of the five nodes in the jay clade collapse only one step away from the most parsimonious tree. In addition, the low bootstrap values registered within the jays can be considered as another indicator of clade instability. One explanation for spurious topologies is the presence of relatively small internodal distances compared to the lengths of terminal branches. Smith (1994) suggested that this imbalance between internodal distances and terminal branches can increase the probability of rooting the network in the wrong position.

An important factor that affects tree topologies is the use of outgroups that are too distantly related to the ingroup (Maddison et al. 1984, Wheeler 1990, Smith 1994). To investigate this, *Catharus* and the bowerbirds were eliminated from the analysis and the birds-of-paradise were chosen as the outgroup to root the jay phylogeny. Removing these taxa apparently eliminates the observed saturation in third position transi-
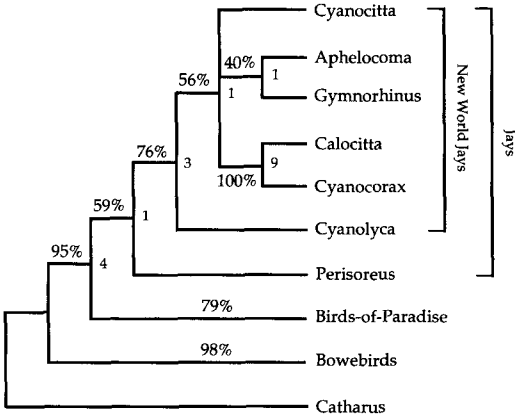
FIGURE 3.   Strict consensus tree of two equally parsimonious trees (length: 428 steps; CI: 0.607; RI: 0.466). Third position transitions were down-weighted ten times with respect to transversions. Percentages are bootstrap values obtained for 1,000 replications; numbers represent the branch support for the specified node. Outgroup branches have been collapsed, for details on species used refer to Taxa Examined under Methods.

tions; therefore, for this and the subsequent analyses all characters were considered as equally weighted. Once this was done, a single most parsimonious tree of 935 steps in length was found (Fig. 4). This topology is consistent with the result obtained in the previous analysis, and the polytomy inside the jay clade is resolved. In this tree, *Cyanocitta* is the sister taxon to the clade *Aphelocoma-Gymnorhinus*, the sister-group to them is the clade *Calocitta-Cyanocorax*, and the most basal genus of the New World jays is *Cyanolyca*. Finally, the sister-group to the New World jays is the Gray Jay (*Perisoreus canadensis*). A bootstrap test was computed for this phylogeny and only the clade formed by *Calocitta-Cyanocorax* had a substantially high value (98%). Although the rest of the nodes show low bootstrap values, an increase in the branch support for each node suggests that the phylogeny has gained stability.

Finally, if the interrelationships of the jays are examined using *Perisoreus* as the root of the tree, a single tree with a length of 582 steps, consistency index of 0.729, and retention index of 0.325 is found. This result yields an identical pattern of relationships to that of the previous analysis. Although no changes are registered for the relationships among the genera, no improvement in bootstrap or branch support is observed.

A constant result in all these phylogenies was the high support for the clade *Calocitta-Cyanocorax*. In the last analysis, the bootstrap value for that clade was 99%, and to break apart this clade it was necessary to incur an additional 13 steps from the most parsimonious solution.

CLADISTIC ANALYSIS OF MORPHOLOGICAL CHARACTERS

A cladistic analysis of the morphological data (Table 2; Appendix 1), which included only the New World jay genera and *Perisoreus*, resulted in two equally parsimonious trees of 62 steps each. Using *Perisoreus* as the root, the relationships depicted in these trees are consistent with the results obtained using the molecular data alone. One of the trees shows exactly the same topology as the one obtained for the molecular data set. The alternative tree differs in the position of *Gymnorhinus* which is placed as the sister taxon to the clade *Aphelocoma-Cyanocitta*. Thus, the strict consensus of these two trees presents an unresolved node for these three taxa. In this analysis, two nodes received significant values from the bootstrap test and branch support. The clade formed by *Aphelocoma-Cyanocitta-Gymnorhinus* was represented in 82% of the bootstrap replicates, and had a branch support value of three. The clade *Calocitta-Cyano-*
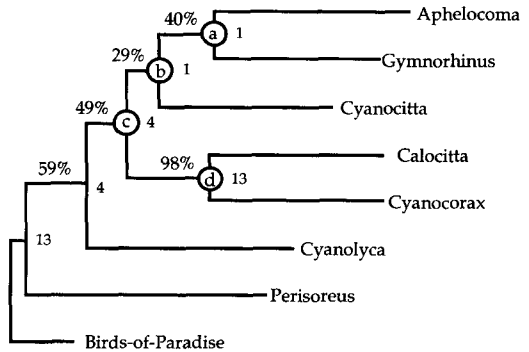

FIGURE 4.   Single most parsimonious tree for the jays using birds-of-paradise as the outgroup (length: 935 steps; CI: 0.588; RI: 0.388). Using this outgroup, no evident saturation is observed in the data, therefore in this analysis all characters were considered with the same weight. Percentages are bootstrap values; numbers represent the branch support for the specified node. When the birds-of-paradise were deleted and *Perisoreus* was used to root the phylogeny the same topology was obtained using molecular, morphological, and total evidence analysis. Letters are the reference name for each node as used in Table 4.

TABLE 4. Descriptive values for the analyses using the Gray Jay as outgroup, and statistics for each node as indicated in Figure 4.

	Trees		
	Molecular	Morphology	Combined
Statistics			
Length[a]	582 (1)	62 (2)	644 (1)
C.I[b]	0.729	0.823	0.738
R.I.[c]	0.325	0.676	0.369
Length next tree[a]	583 (1)	63 (2)	652 (2)
Bootstrap Node			
a	43%	44%	84%
b	34%	82%	87%
c	57%	60%	90%
d	99%	90%	100%
Branch Support Node			
a	1	0	8
b	2	3	8
c	1	1.	10
d	13	3	18

[a] The number in parentheses indicates the number of trees with that particular length.
[b] Consistency index.
[c] Retention index.

corax had a bootstrap value of 90% and a branch support of three. The remaining node collapsed one step from the shortest tree.

COMBINED ANALYSIS

The morphological and molecular data sets were combined in a total evidence approach. The search yielded a single most parsimonious tree of 644 steps, a consistency index of 0.738 and a retention index of 0.369. The total evidence tree corroborated the results obtained with the other two data sets. In this analysis all the nodes have bootstrap values over 80% and branch support of at least eight. Bull et al. (1993) suggested that combining different data sets in which results are not significantly different from one another will result in a strongly corroborated phylogenetic hypothesis. When the data sets were analyzed independently, alternative trees were only one step away from the most parsimonious tree, but in the combined analysis the nearest trees were eight steps longer than the most parsimonious solution. A comparison among the three analyses and a detailed list of statistics is presented in Table 4.

DISCUSSION
COMPARISONS WITH PREVIOUS PHYLOGENIES

The molecular phylogeny obtained for the complete set of taxa (Fig. 3) coincides in several general points with other higher-level hypotheses proposed for passerine interrelationships. Our phylogenetic analysis (hypothesis) was able to identify as monophyletic the three main groups of birds represented (i.e., Corvidae, Paradisaeidae and Ptilonorhynchidae). The relationships depicted here among jays, birds-of-paradise and bowerbirds are consistent with previous reviews of corvid phylogeny (Sibley and Ahlquist 1985, 1990, Edwards et al. 1991, Helm-Bychowski and Cracraft 1993). With respect to the New World jays, this phylogeny agrees with the proposal that these birds are a monophyletic group. There are disagreements, however, when our hypothesis is contrasted to other phylogenies at finer levels.

For instance, one of the hypotheses about the history of the New World jays (hereafter referred to as Hardy's hypothesis) proposes a separation into two distinct lineages, the so called "ornate" and "inornate" lines (Hardy 1961, 1969). The phylogenetic hypothesis proposed by us (Fig. 4), does not support Hardy's hypothesis. Incongruences arise with the position of *Cyanolyca*. Based on external morphology and behavior, Hardy's hypothesis sustains the idea that the species in the genus *Cyanolyca* are the most primitive of the New World jays, which is consistent with our phylogeny. However, Hardy's hypothesis also postulates that *Cyanolyca* should be placed inside the inornate lineage along with the genus *Aphelocoma*. Hardy's hypothesis arose mainly because some species of *Cyanolyca* produce a relatively simple call very similar to those of *Aphelocoma*. Indeed, *Cyanolyca* was discarded as a generic name, and its species were included within *Aphelocoma*. Our phylogeny suggests that these two genera are not each other's closest relatives: *Cyanolyca* appears as the most basal clade within the New World jays, whereas *Aphelocoma* is the sister taxon to *Gymnorhinus* comprising one of the most derived clades. One of the major problems in Hardy's systematic study is that the so-called inornate lineage was established using plesiomorphic characters (e.g., no crests, uniform bluish above, gray below, simple calls), therefore this lineage can not be accepted as a cladistic entity.

Hardy's hypothesis recognized the remainder of the genera as the ornate line, and lumped them as a subgenus within *Cyanocorax* (Hardy 1969). Proposed evolutionary trends showed by the ornate line included: (a) shortening of crest,

(b) increase in melanin leading to a darker and simpler pattern of plumage, and (c) a reduction of song repertoire. Based on these tendencies the subgenera *Calocitta* and *Cyanocitta* were considered to be close to each other and to be the sister-group to *Cyanocorax*. This conclusion contradicted a previous observation made by Pitelka et al. (1956) when describing a hybrid between *Calocitta formosa* and *Cyanocorax morio*. The hybrid led Pitelka et al. to suggest that these two species of jays were not very divergent and probably should not be considered two separate genera.

Our phylogenetic hypothesis, in contrast, does not recognize the ornate line as a monophyletic group, and in all analyses *Cyanocorax* was the sister taxon of *Calocitta*. Therefore, we do not accept the hypothesis that two evolutionary assemblages exist within the New World jays such as proposed by Hardy (1961, 1969).

Finally, Peterson (in Edwards and Naeem 1993) proposed a phylogenetic hypothesis for the New World jays based on electrophoretic data. The phylogeny shows an unresolved clade formed by *Aphelocoma, Cyanocitta,* and *Gymnorhinus*, which is the sister-group to an unresolved clade consisting of *Calocitta, Cyanocorax, Psilorhinus,* and *Cissilopha*; the sister-taxon to these clades was the genus *Cyanolyca*. Although the tree is not resolved, Peterson's results are consistent with the hypothesis presented here.

ON THE POSITION OF THE PIÑON JAY

A key question investigated by those interested in the evolutionary history of New World corvids has been the phylogenetic position of the Piñon Jay (*Gymnorhinus cyanocephalus*). The results presented here agree with the hypothesis that *Gymnorhinus* belongs to the New World jay assemblage, and they also support the placement of this genus as the sister-taxon to *Aphelocoma*, well inside the New World jay assemblage. Thus, another question can be raised: Why are there so many similarities in morphology and behavior between the Piñon Jay and Clark's Nutcracker (*Nucifraga columbiana*)? Although this analysis did not include any representative of the genus *Nucifraga*, alternative morphological evidence supports the hypothesis that nutcrackers are not members of the New World jay lineage. Zusi (1987) described a structural configuration of the jaw articulation called the buttress com-

plex that is a shared character of all genera of jays endemic to the New World, including *Gymnorhinus*, but which is absent from all Old World genera. This character supports the monophyly of New World jays to the exclusion of *Nucifraga* and *Perisoreus*. There is additional evidence supporting the hypothesis that *Gymnorhinus* is a specialized New World jay that is superficially similar to *Nucifraga*. Both species live in the same kind of coniferous forest under similar environmental conditions. The Piñon Jay and Clark's Nutcracker base their diet on pine seeds, and both use their beaks for stabbing into unripe cones, hammering on bark, and probing the ground (Marzluff and Balda 1992). Similarity in external morphology and behavior presumably have converged in the two. Only *Nucifraga* species possess a specialized structure (i.e., sublingual pouch) for carrying conifer seeds, whereas the Piñon Jay uses a distensible esophagus to resolve this problem. Thus, the presence of different morphological structures for carrying seeds suggest that these two genera independently acquired their specialized dependence on pine seeds (Ligon 1974). In addition, the Piñon Jay shares other features with the New World jays that are lacking in *Nucifraga*: (1) the Piñon Jay is completely blue as are many New World jays, (2) chicks of the Piñon Jay are naked at birth, whereas down is present in nutcrackers, crows and ravens, and (3) the presence of the buttress complex in *Gymnorhinus*.

ON THE EVOLUTION OF THE BUTTRESS COMPLEX

The development and complexity of the buttress complex varies among the different genera of New World jays. Specimens of *Cyanolyca* examined in the American Museum of Natural History collection showed a very poorly developed buttress complex. Within *Cyanocorax* the buttress is always present, but in some species the buttress is lower, less vertical, and more widely separated from the rostral condyle of the quadrate. In nestlings of *Aphelocoma*, the mandibular buttress is fully developed at the time of hatching, and the same seems to be true for *Cyanocitta* and *Gymnorhinus* (Zusi 1987).

The lack of a robust phylogeny for the New World jays has made an interpretation of the evolutionary history of this structure difficult. Zusi was unable to decide if the intermediate stages found in *Cyanocorax* represented the
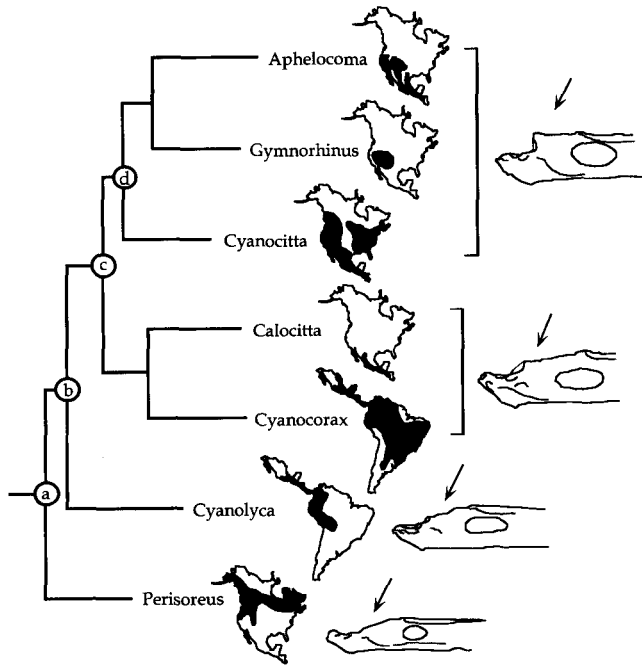
FIGURE 5. Biogeography of jays and scenario for the evolution of the buttress complex in the New World jays. Shaded areas are current distributions of each genus. Letters represent the most parsimonious explanation in the change of the buttress complex: (a) ancestral state, (b) origin of the complex in the New World jays' ancestor, (c) increment in complexity, and (d) maximum complexity reached.

starting point of a morphocline or if they were secondarily reduced. Furthermore, it was not possible to infer whether the buttress complex developed only once or multiple times within New World jays. Zusi's interpretation of the evolution of the group based on this character made him conclude that *Cyanolyca* should be the sister-group to the remaining genera of New World jays. Building on the ideas presented by Zusi, the descriptions of the jaw articulation for the jays can be interpreted within the context of the phylogeny proposed in this analysis (Fig. 5). The result is a gradual increase in complexity toward the most derived lineages. It is possible, moreover, to identify three general patterns in the development of the jaw articulation and each apparently evolved once. The rudimentary buttress complex of *Cyanolyca* probably resembles the condition that was present in the ancestor of the New World jays. An increase in complexity occurred in the ancestor of the rest of the genera and a similar form remains in *Cyanocorax* and *Calocitta*. Finally, the highest complexity was reached in the ancestor of *Aphelocoma, Cyanocitta,* and *Gymnorhinus.*

BIOGEOGRAPHIC SCENARIO

Although absolute dates of diversification cannot be obtained without reliable paleontological data, some studies have suggested that relative times can be estimated based on differences in transversion substitutions in mitochondrial DNA (Brown et al. 1982, DeSalle et al. 1987, Miyamoto and Boyle 1989, Irwin et al. 1991). This clock principle bases its assumptions on a uniform rate of molecular evolution within a clade. Peterson (1992) showed that some *Aphelocoma* jay populations present evolutionary rates three to four times greater than those of their sister taxa, making the assumption of a molecular clock for this group unreliable. Sibley and Ahlquist (1985) proposed that the origin of corvines can be traced to Australia. Between 20 to 30 million years ago the ancestor of crows and jays was able to disperse to Asia and the group radiated in Asia and Europe. More recently an invasion through Beringia resulted in the colonization of the New World by the corvids.

Figure 5 shows the distribution of each genus of jays along with their relative transversion divergence. The result is compatible with the sce-

nario presented by Sibley and Ahlquist for the recent invasion of the New World. The basal position of a genus with a clear Palaearctic affinity (*Perisoreus*) suggests that the origin of the New World jays was the result from a single dispersal event into the Americas. This event could have taken place around the early Miocene when the climatic conditions were dominated by warm temperatures and deciduous forest covered Alaska (Potts and Behrensmeyer 1992). A jay-like fossil from late Miocene sediment of Colorado (Brodkorb 1972) suggests that the ancestor of jays must have dispersed throughout the Americas rather rapidly. The available paleogeographic data suggest that the older genera (i.e., *Cyanolyca, Cyanocorax,* and *Calocitta*) might have entered and radiated in South America probably by the early Pliocene when the Isthmus of Panama emerged. More recently, a secondary radiation within North America took place and gave rise to *Cyanocitta, Gymnorhinus,* and *Aphelocoma.*

Along these analyses, we have followed the assumption that all the genera as defined are monophyletic. We acknowledge the need for detailed analyses at the species level, especially for the genus *Cyanocorax* in which former genera have been lumped (i.e., *Cissilopha, Psilorhinus* and *Xanthoura*). Another genus that certainly deserves attention is *Cyanolyca,* because the specific status of some of their populations have been debated for a long time. Therefore, until some of these problems are settled the overall intergeneric relationships among the New World jays presented here should be considered tentative.

ACKNOWLEDGMENTS

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APPENDIX 1

Morphological characters that are phylogenetically informative for the genera presented in this analysis. Character 1 was suggested by Peterson (pers. comm.). The rest of the characters were modified from Appendix II of Hope (1989 and pers. comm.).

CRANIAL CHARACTERS

(1) Bony lateral bar rimming one side of the sclerotic ring. 0 = Absent; 1 = Present.

(2) Fontanelles on the posterior walls of the orbit. 0 = Absent; 1 = Bilateral fontanelles, smaller than the optic foramen; 2 = Larger, up to two times the size of the optic foramen; 3 = Over two times the size of the optic foramen.

(3) Interorbital fontanelle. 0 = Round shape, small or similar to the diameter of the optic foramen; 1 = Larger, up to three times the diameter of the optic foramen; 2 = Irregular shape and very

large, over three times the diameter of the optic foramen.

(4) Nasal processes of the premaxilla at the craniofacial hinge. 0 = Narrow, less than one third the width of the hinge, incomplete fusion of the paired processes; 1 = Wider, nearly one third the width of the hinge; 2 = More than one third the width of the hinge, the paired processes completely fused.

(5) Lateral view of the upper jaw. 0 = Dorsal and ventral border straight; 1 = Dorsal and ventral border continuously decurved, the ventral border continuously decurved.

(6) Tip of the maxillopalatine. 0 = Not inflated; 1 = Inflated; 2 = Inflated, with one spur projected caudally.

(7) Median septum of nasal capsule. 0 = No Ossification; 1 = Ossification present.

(8) Pit on the ventral surface of the transpalatine. 0 = Absent; 1 = Present.

(9) Premaxilla in the palate. 0 = Light ossification; 1 = Ossification dense but the symphysis not fully fused on the ventral view; 2 = Ossification dense, symphysis completely fused on the ventral view.

(10) Fusion of the prepalatine bar to the ventral bar of the jaw. 0 = Partially fused; 1 = Entirely fused.

(11) Ventral lobe of the prefrontal. 0 = Inflated but small, lying mostly along the lateral border of the anteorbital plate; 1 = Highly inflated laterally and contracting the jugal arch extensively.

(12) Postorbital process. 0 = Located near to the caudal wall of the orbit; 1 = Located on a more caudal position, continues along the lateral wall of the cranium.

(13) Zygomatic process. 0 = Very small, looks like a small rostroventral projection from the orbital wall, the dorsal border abruptly curved; 1 = Slightly longer, the dorsal border forming a shallow curve at the junction with the dorsal border of the orbit; 2 = Long, wedge-shaped in lateral profile.

(14) Jugal brace on the quadrate. 0 = Absent; 1 = Present but small; 2 = Present, forming a big abutment against jugal bar.

(15) Otic process of the quadrate. 0 = Narrow with a crest on the lateral border; 1 = Wider, the lateral border rounded with a small shaft; 2 = Shaft very big.

(16) Rostral crest of the lateral cotyla of the mandible. 0 = Absent; 1 = Present.

(17) Rostral groove of the medial cotyla of the mandible. 0 = Very short; 1 = Longer, extending

rostrally about half way to the attachment process of the muscle pseudotemporalis superficialis; 2 = Longer, nearly all the way to the attachment process.

(18) Rostral cotyla of the mandible. 0 = Absent; 1 = Present, with a very small facet on the dorsal rim; 2 = Facet larger forming an articulation with a rostral condyle of the quadrate; 3 = High cotyla, as high as the dorsal rim of the ramus.

(19) Ventral suprameatic crest. 0 = Short, not elongated caudally; 1 = Long, the bulla notched at the suprameatic crest; 2 = Longer, the crest extended caudally.

(20) Dorsomedial lobe on the suprameatic process of the ventral suprameatic crest. 0 = Absent; 1 = Very small, sometimes inconspicuous; 2 = Large and conspicuous.

(21) Ventral suprameatic crest at the quadrate. 0 = Located close to the squamosal articulation; 1 = In ventrolateral position from the squamosal articulation, extended slightly as a shelf; 2 = Forming a wide ventrolateral shelf.

(22) Dorsal suprameatic crest at the bulla. 0 = Absent; 1 = Small, merges with the ventral suprameatic crest before joining the bulla; 2 = Well developed, dorsal to the ventral suprameatic crest at the quadrate and at the bulla.

(23) Abutment against the otic process of the quadrate just medial to the squamosal condyle. 0 = Absent; 1 = Present but small; 2 = Well developed abutment but not ossified; 3 = Well developed and heavily ossified.

(24) Ventral view of the suprameatic process at the quadrate. 0 = Narrow; 1 = Wide.

(25) Subzygomatic sulcus. 0 = Absent; 1 = Present, extended slightly caudally up to the quadrate-squamosal articulation; 2 = Extending beyond the quadrate-squamosal articulation.

POSTCRANIAL CHARACTERS

(26) Pectoral crest of the humerus. 0 = The distal margin forms a continuous ridge with the shaft; 1 = The distal margin slightly outset from the shaft; 2 = The distal margin widely outset from the shaft.

(27) Dorsal epicondyle of the humerus. 0 = Small; 1 = Longer, extending beyond the level of the proximal rim of the dorsal condyle.

(28) Sacral vertebrae. 0 = Six; 1 = Seven; 2 = Eight.

(29) Synsacrum. 0 = Rectangular shape, the width between the dorsolateral illiac crest is the same as the length from trochanter to caudal limit of the fused vertebrae; 1 = Slightly wider; 2 = Very wide.