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A baraminological analysis of the landfowl (Aves: Galliformes)

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A Baraminological Analysis of the Landfowl (Aves: Galliformes)

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Abstract

We performed a baraminological analysis on 60 extant landfowl taxa (Aves: Galliformes) using 102 morphological characters. Both baraminic distance correlation analysis and multidimensional scaling suggest the possibility of four holobaramins within the landfowl order: Megapodiidae, Cracidae, Numididae, and the remaining Phasianoidea. Hybridization, however, connects three of these holobaramins (six of the currently recognized families). Considering both sets of evidence, we conclude that the landfowl are composed of two holobaramins: Megapodiidae and [Phasianoidea + Cracidae]. The five currently recognized families in the superfamily Phasianoidea have, until recently, been considered subfamilies in a more broadly conceived family Phasianidae, so it should not be surprising that they are members of the same holobaramin. Perhaps the most surprising result of this study then, is the inclusion of the Cracidae in the phasianoid holobaramin. A closer inspection of our data along with more recent phylogenetic analyses of the landfowl, however, suggest that that the Cracidae are more closely related to the Phasianoidea than once assumed. This study emphasizes the continued value of hybridization data in baraminological research, illustrates the importance of using multiple lines of evidence when delimiting holobaramins, and is suggestive of the potential uses and limitations of statistical baraminology.

Introduction

The Order Galliformes (landfowl, gamebirds, chicken-like birds, gallinaceous birds) is a cosmopolitan group of birds (Class Aves) composed of approximately 281 extant species in 81 genera (Sibley and Monroe, 1990; del Hoyo et al., 1994; Hockey et al., 2005) and seven families (Sibley and Ahlquist, 1985, 1990; del Hoyo et al, 1994). The seven families in this order are the: Megapodiidae (mound-builders, scrub-fowl, and brush-turkeys), Cracidae (guans, chacalacas, and curassows), Numididae (guineafowl), Meleagrididae (turkeys), Tetraonidae (grouse), Odontophoridae (New World quail), and Phasianidae (Old World quail, peafowl, tragopans, pheasants, partridges, and allies). These are further classified (Wetmore, 1960; Sibley and Ahlquist, 1990; del Hoyo et al., 1994) into the superfamilies (sometimes suborders or orders) Cracoidea (Cracidae and Megapodiidae) and Phasianoidea (remaining five families). This arrangement is suggestive of the traditional view that the megapodes and cracids are sister groups. The landfowl are thought to be an osteologically uniform group and have consistently been grouped together since the inception of avian taxonomy (see Dyke et al., 2003). From a baraminological perspective then, they form a distinct cognitum and quite possibly an apobaramin (Sanders and Wise, 2003).

Baraminology is the study of God's created kinds or baramins (see Wise, 1990, 2002; Frair, 2000; Wood et al., 2003; Wood and Murray, 2003). The goal of baraminology is to identify holobaramins (groups of known organisms that share continuity and are bounded by discontinuity) by building up monobaramins (groups of known organisms that share continuity) and dividing apobaramins (groups of known organisms bounded by discontinuity). Following this method of successive approximation, we present the first baraminological analysis of the Order Galliformes using hybridization data and statistical baraminology techniques.
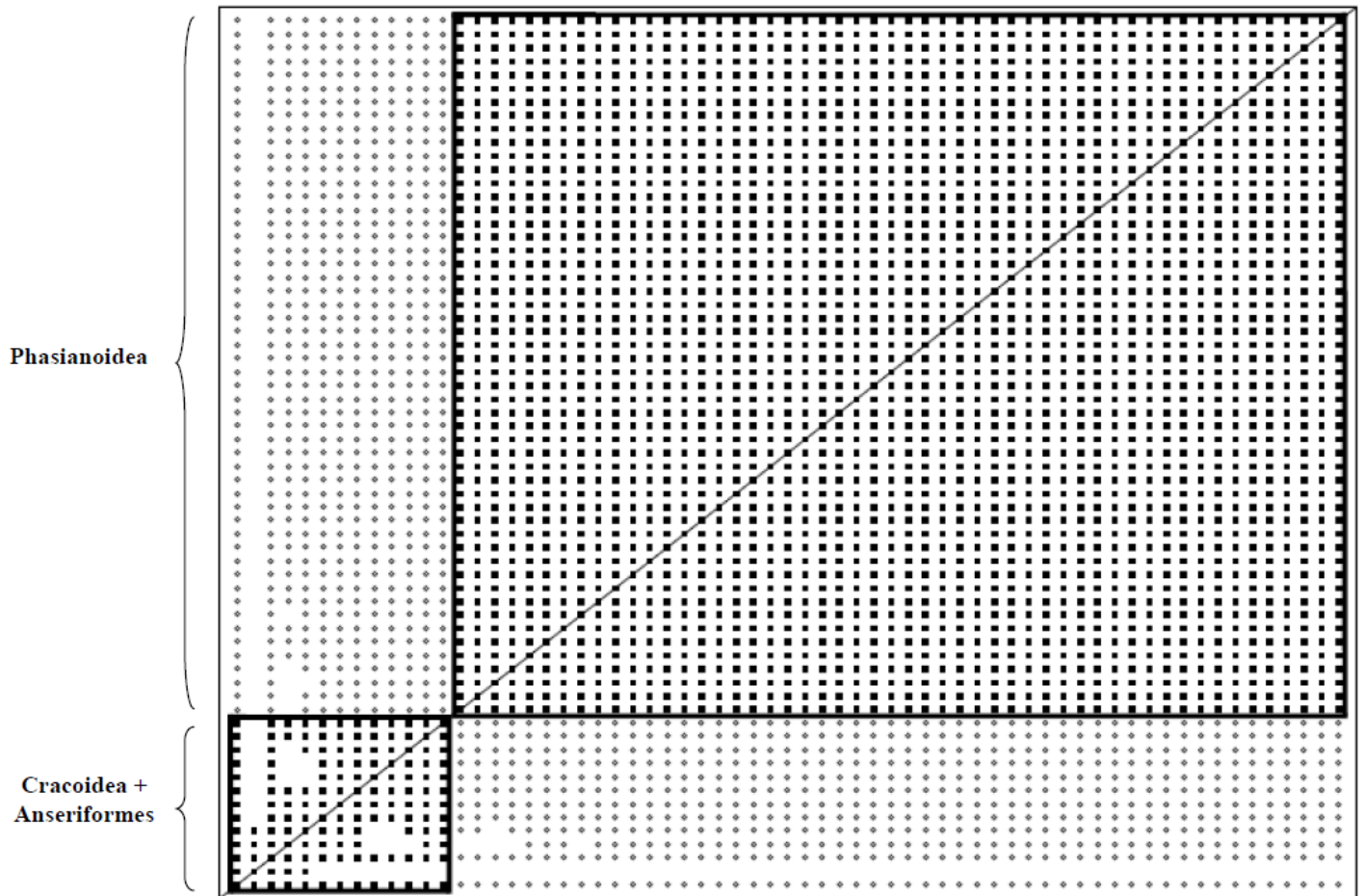
Figure 1. Baraminic distance correlation for the complete Dyke et al. (2003) dataset , using a relevance cutoff value of 0.95. Taxa with significant ($p<0.05$) positive correlation are indicated as filled squares. Taxa with significant ($p<0.05$) negative correlation are indicated as open circles. 98 of the original 102 characters are used to calculate baraminic distances.

Materials and Methods

Statistical Baraminology. We obtained a published morphological (primarily osteological) dataset consisting of 102 characters from 60 extant landfowl taxa (Order Galliformes) and five extant waterfowl (Order Anseriformes) taxa (Dyke et al., 2003). The landfowl taxa include three mound builder genera (Megapodiidae), five cracid genera (Cracidae), four guineafowl genera (Numididae), seven New World quail genera (Odontophoridae), two turkey genera (Meleagrididae), six grouse genera (Tetraonidae), and 33 phasianid taxa (including Old World quails, peafowl, tragopans, pheasants, partridges, and allies). The waterfowl outgroup taxa include two screamer genera (Anhimidae), the magpie-goose (Anseranatidae), and two true duck genera (Anatidae).

We performed a baraminic distance correlation analysis (BDC) on the complete dataset described above using BDISTMDS, v. 1.0 (Robinson and Cavanaugh, 1998; Wood, 2002, 2005b, 2006a). First, character relevance (a) was calculated, which for each character is the percentage of taxa for which a character state is known. Robinson and Cavanaugh (1998) recommended that a

≥ 0.95 for all characters used in calculating baraminic distances. We eliminated all characters from the dataset for which $a < 0.95$. Second, baraminic distances were calculated for all possible pairs of taxa in the dataset. The baraminic distance between two taxa is the percentage of characters for which the two taxa differ in their character states. This distance is used to identify both significant similarity (implying baraminic relationship) and significant difference (implying discontinuity) between taxa. Third, using the matrix of baraminic distances, the Pearson product-moment correlation coefficient (r) was calculated for all possible pairs of taxa. Fourth, these correlation coefficients were converted into Student's t statistics, from which probabilities were estimated using a standard t-test (df = n-2). If a set of points are randomly distributed in two-dimensional space, then points that are close together will be similarly distant from other points whereas points that are very far apart will be inversely distant from other points. Robinson and Cavanaugh (1998) suggested that significant positive correlation indicates that two taxa are continuous (i.e. members of the same monobaramin) and significant negative correlation indicates that two taxa are discontinuous (i.e. members of different apobaramins). Finally, a square matrix was generated
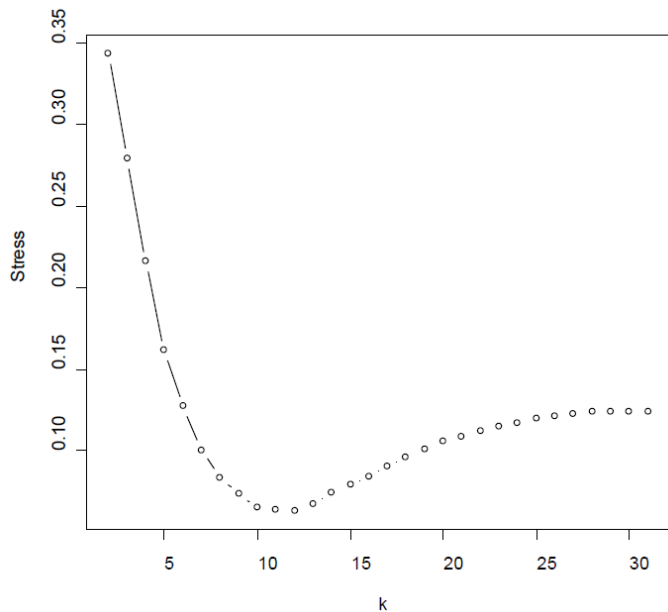
Figure 2. Stress of k-dimensional MDS on uncorrected baraminic distance matrix, calculated from complete Dyke et al. (2003) dataset, plotted as a function of the number of dimensions (k).

that summarizes both correlation and significance between taxa. Each cell in the matrix corresponds to a comparison between taxa and contains one of the following symbols: 1) open circles = significant (p < 0.05) negative correlation; 2) closed squares = significant (p < 0.05) positive correlation; and 3) blank space = non-significant correlation.

To confirm/investigate the results of the BDC, we performed classical multidimensional scaling (MDS) on the uncorrected baraminic distance matrix using BDISTMDS, v. 1.0 (Robinson and Cavanaugh, 1998; Wood, 2005b, 2006a). We also made the baraminic distance matrix metric by adding the maximum distance in the matrix, which was 0.673 between *Anhima* and *Dendragapus*. Multidimensional scaling converts distance data for a given set of points into a set of k-dimensional coordinates, where k is a predetermined dimensionality. Next, the minimal stress and the stress at three dimensions were calculated for these procedures. Stress is a measure of the "goodness of fit" between the scaled data and the baraminic distances. Finally, all three-dimensional scaling results were converted into Kinemages for display using Mage (http://kinemage.biochem.duke.edu/software/mage.php), so that clustering patterns could be visually inspected for clues to potential baraminic classification.

Since the taxic clustering revealed by the 3D MDS of the baraminic distance matrix revealed a number of clusters that did not correspond to the groups implied by the distance correlation results, we performed baraminic distance correlation analyses for various subsets of the taxa in the complete dataset (using methods described above). Correlation calculations on subsets of the full dataset can be justified because the geometry of taxic patterns can adversely influence baraminic distance correlation results (e.g. by revealing significant negative distance correlation without

discontinuity, see Cavanaugh et al., 2003). Removal of taxa that dominate correlation calculations might reveal significant negative or positive correlation patterns undetectable in the full dataset (Wood, 2005a).

Hybridization. An analysis of interspecific hybridization was also conducted for the landfowl. No direct hybridization experiments were performed in this study, but numerous hybrids have been described in this group since they are raised worldwide for meat and decorative plumage (Klemm, 1993). Our primary data source for this analysis was Eugene McCarthy's (2006) *Handbook of Avian Hybrids of the World*. This source was verified and, in a few cases, supplemented by Rutgers and Norris (1970), Delacour (1977), and Johnsgard (1983, 1999). Since some of these sources used Gray (1958) as a starting point for their compilations, we did not directly compile the data in Gray (1958). We compiled, assessed, and summarized the data from these newer sources in the form of hybridograms (Wood, 2002).

Results and Discussion

Statistical Baraminology. With a character relevance cutoff of 0.95, 98 characters were included in the BDC of the complete dataset. Immediately apparent from these results are two different groups of birds (Figure 1). The first major group includes the anseriform outgroup taxa along with the mound builders and cracids (superfamily Cracoidea + Anseriformes). With a few notable exceptions among the cracids, this group is connected by significant positive correlation and bounded by significant negative correlation. The second major group recovered from this analysis includes the rest of the galliform taxa (superfamily Phasianoidea). Each of these shows significant positive correlation with all others from this group, and with the exception of the cracids discussed below, significant negative correlation with all taxa from the first major group.

The genus *Ortalis* (Cracidae) lacks significant positive correlation with all the anseriform and mound builder taxa, and
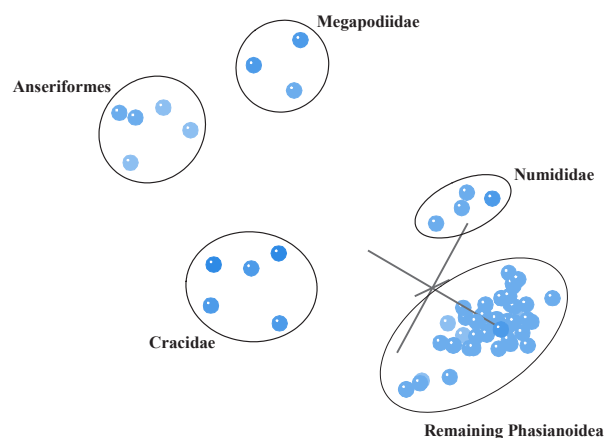

Figure 3. Three-dimensional classical MDS applied to uncorrected baraminic distance matrix calculated from complete Dyke et al. (2003) dataset.
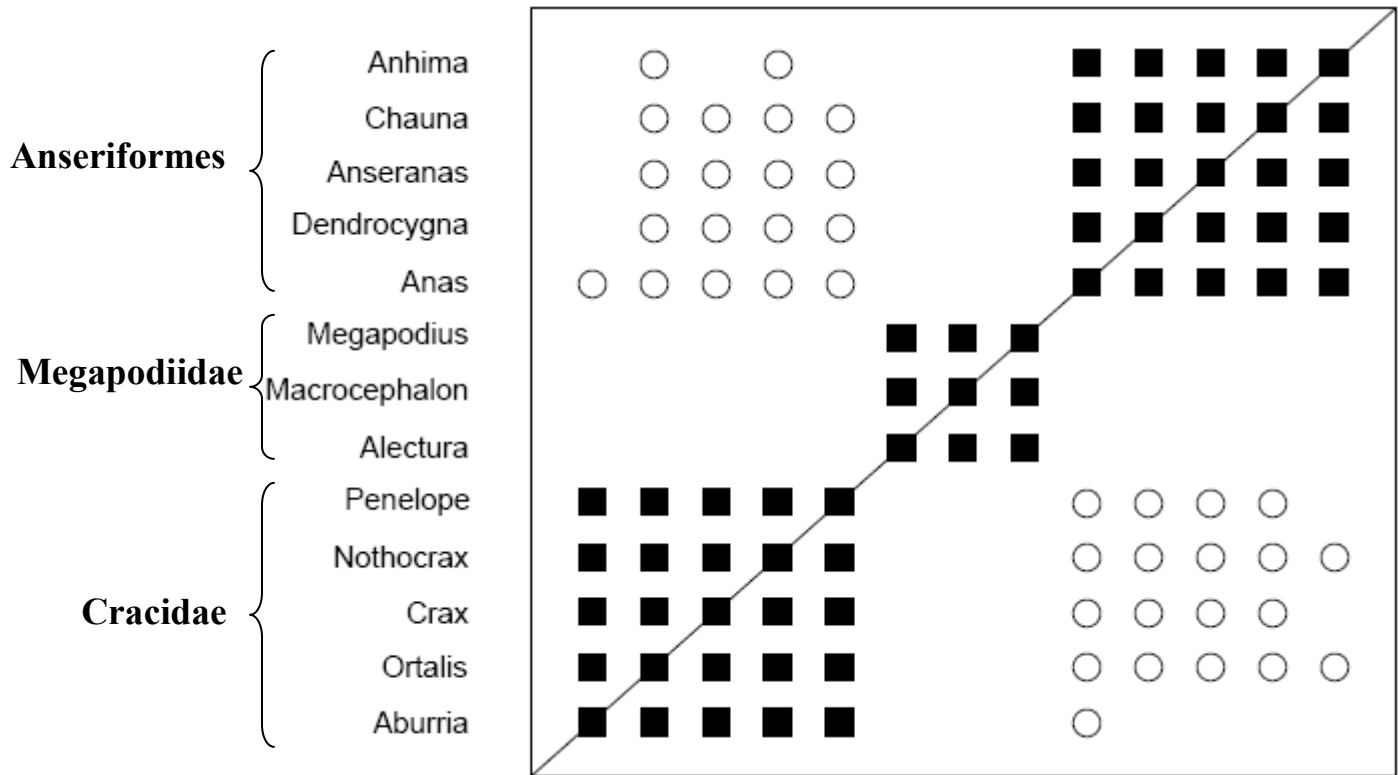
Figure 4. Baraminic distance correlation for a subset (Cracoidea and Anseriformes) of the Dyke et al. (2003) dataset, using a relevance cutoff value of 0.95. Taxa with significant ($p<0.05$) positive correlation are indicated as filled squares. Taxa with significant ($p<0.05$) negative correlation are indicated as open circles. 99 of the original 102 characters are used to calculate baraminic distances.

significant negative correlation with all taxa from the second major group in this analysis. The genera *Nothocrax* and *Penelope* (Cracidae) also lack significant positive correlation with several of the anseriform taxa, and significant negative correlation with several of the guineafowl (Numididae) and argus (Phasianidae) taxa from the phasianoid group (second major group) in this analysis.

For the MDS analysis, the minimal stress for the uncorrected matrix was 0.063 at 12 dimensions, and the stress at three dimensions was 0.279 (Figure 2). MDS on the corrected distance matrix yielded a minimal stress of ≤ 0.287 at ≥ 31 dimensions (not calculated exactly by BDISTMDS) and a 3D stress of 0.587. Because of the substantially lower stress, we describe the 3D MDS for the uncorrected distance matrix only.

The taxic clustering in the 3D MDS of the baraminic distance matrix reveals a number of clusters that do not correspond to the groups implied by the baraminic distance correlation analysis (Figure 3). Instead of forming a single group, the anseriforms, mound builders, and cracids are clearly distant from each other and the rest of the galliform taxa. The guineafowl (Numididae), instead of being a part of the second major group, form a distinct cluster from the remainder of the phasianoid taxa (New World quail, turkeys, grouse, and phasianids).

The baraminic distance correlation results alone suggest the existence of two holobaramins, but the 3D MDS (Figure 3) seems to show five different clusters that could potentially be separated by discontinuity: 1) five outgroup genera from the Order Anseriformes; 2) three mound builder genera (Megapodiidae); 3) five cracid genera (Cracidae); 4) four guineafowl genera (Numididae); and 5) the remaining phasianoid taxa (superfamily Phasianoidea minus the guineafowl). To test this possibility, we calculated baraminic distance correlations for subsets of the taxa in the complete dataset

The first subset (Cracoidea + Anseriformes from original BDC) consists of the anseriform outgroup taxa, mound builders, and cracids. The correlation results (99 characters utilized) reveal significant positive correlation within each of these groups, and significant negative correlation between most of the anseriform outgroup taxa and the cracids. There is no significant negative correlation, however, between the mound builders and the other two groups (Figure 4). To investigate this even further, we reduced the dataset again to include just the mound builders with each of the other two groups separately. When the mound builders are analyzed with just the anseriform taxa (99 characters utilized), significant negative correlation occurs between most of the taxa in these two groups (Figure 5). Similarly, when the mound builders and cracids are analyzed alone (101 characters utilized), significant negative correlation exists between most of the members of these two groups as well (Figure 6).

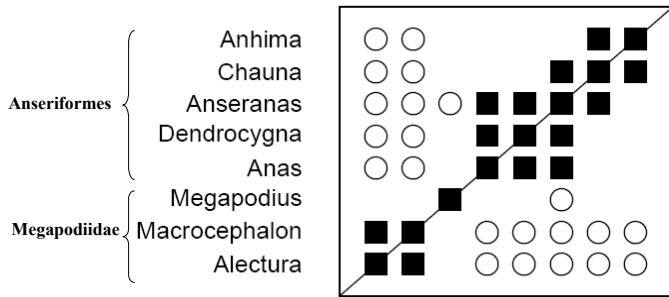The second subset (Phasianoidea from original BDC) consists

Figure 5. Baraminic distance correlation for a subset (Megapodiidae and Anseriformes) of the Dyke et al. (2003) dataset, using a relevance cutoff value of 0.95. Taxa with significant (p<0.05) positive correlation are indicated as filled squares. Taxa with significant (p<0.05) negative correlation are indicated as open circles. 99 of the original 102 characters are used to calculate baraminic distances.

of members of the superfamily Phasianoidea (guineafowl, New World quails, turkeys, grouse, and phasianids). The BDC of this subset (100 characters utilized) reveals the possibility of two holobaramins (Figure 7). First, the guineafowl (family Numididae) seem to be separate from the remaining phasianoid taxa. Their is significant positive correlation between all guineafowl, and significant negative correlation between the guineafowl and many of the remaining phasianoid taxa. To investigate this further, and to see whether the predominance of non-guineafowl taxa was masking the true level of discontinuity between the guineafowl and others, the dataset was further reduced by eliminating every other non-guineafowl taxa. This analysis (101 characters utilized) confirms the high level of discontinuity between the guineafowl and the remaining phasianoid taxa in this analysis (Figure 8). Second, the phasianoid taxa seemed to form one large and diffuse holobaramin. Even after the guineafowl were eliminated from the dataset, there was no clear pattern that allowed for this group to be broken into more than one holobaramin.

On the basis of the statistical analyses alone (Figures 1-8), we probably would have concluded that the landfowl comprise four holobaramins: Megapodiidae, Cracidae, Numididae, and the remaining Phasianoidea. An analysis of hybridization within this order, however, leads to a slightly modified conclusion.

Hybridization. There are no reliable hybridization records that connect the landfowl to any other group of birds (Klemm, 1993; McCarthy, 2006). Even though hybridization should only be used as an additive criterion in baraminology, this lack of hybridization helps to confirm the apobaraminic status of this order. There are several records of interspecific hybridization within the Family Megapodiidae (Figure 9). These represent six unique interspecific crosses. None of these, however, are intergeneric or interfamilial. Seven species in the genus *Megapodius* are connected by hybridization, and therefore form a moderately sized monobaramin. Similarly, three species in the genus *Talegalla* form a small monobaramin. Klemm (1993) concluded that the entire Family Megapodiidae forms a single basic type (≈ monobaramin),

even though he discovered no records of hybridization within the family. He makes this conclusion based on their unique nesting habits and the possession of a unique combination of molecules in their uropygial gland secretions. Even though none of our sources connect the several genera in the Family Megapodiidae via hybridization, we also conclude that the entire family probably represents a single monobaramin.

All of the remaining landfowl families (Cracidae, Numididae, Meleagrididae, Tetraonidae, Odontophoridae, and Phasianidae) are connected, directly or indirectly, by numerous records of intergeneric hybridization (Figure 10). These represent 90 unique intergeneric crosses, many of which are also interfamilial.

In response to these observations, McCarthy (2006, p. 41) created a new category (non-taxonomic) which he called the "Upland Game Birds" and noted that "Five families are listed here together under the heading Upland Game Birds because reports of hybridization connect them." Even though several hybridization records connect the Odontophoridae to this group of five families, McCarthy (2006) did not include them in his "Upland Game Birds." Two species (genera or families in this case) belong to the same monobaramin if they can successfully interbreed or if they can each successfully interbreed with the same third species (Remine, 1990; Wise, 1990; Scherer, 1993). Based on this criterion, these six landfowl families form one large monobaramin.

Klemm (1993) considered five of these families (Numididae, Meleagrididae, Tetraonidae, Odontophoridae, and Phasianidae) to be part of the same basic type. In contrast to our study, however, he concluded that the Family Cracidae formed its own separate basic type. Klemm (1993) dismisses the five hybrids between Cracidae and Phasianidae, as reported by Gray (1958), because of a lack of documentation. Similarly, Johnsgard (1999) comments that "all of the interfamilial combinations [between Cracidae and Phasianidae] are sufficiently vague and unsupported as to
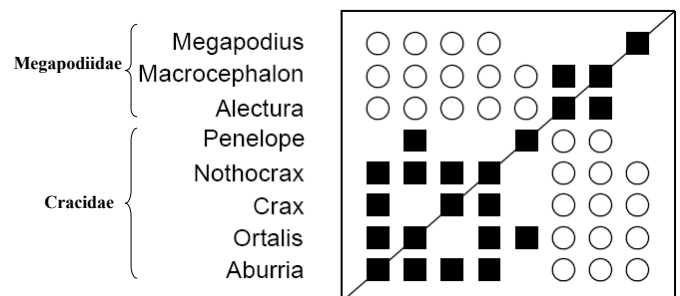

Figure 6. Baraminic distance correlation for a subset (Cracoidea only) of the Dyke et al. (2003) dataset, using a relevance cutoff value of 0.95. Taxa with significant (p<0.05) positive correlation are indicated as filled squares. Taxa with significant (p<0.05) negative correlation are indicated as open circles. 101 of the original 102 characters are used to calculate baraminic distances.
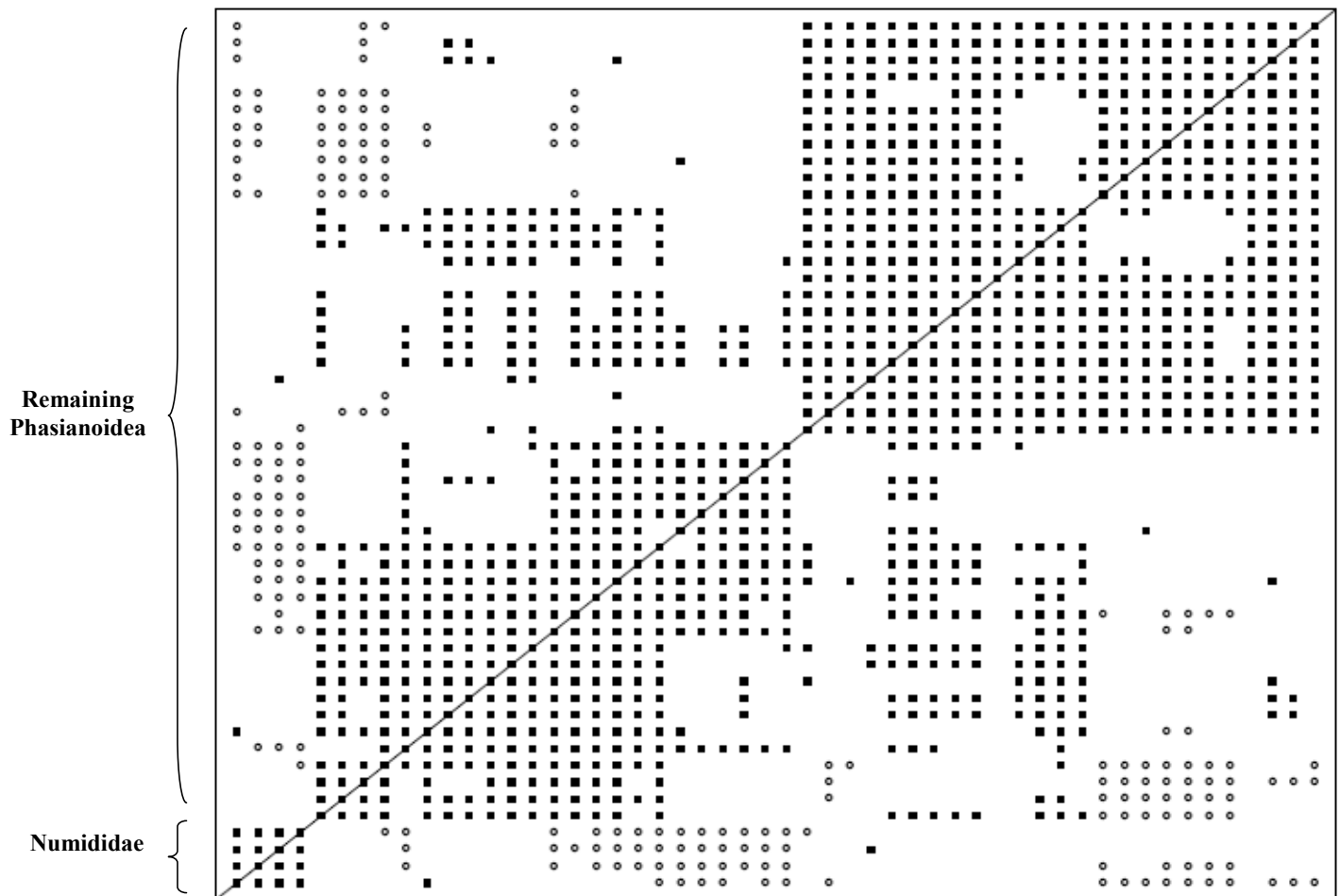
Figure 7. Baraminic distance correlation for a subset (Phasianoidea only) of the Dyke et al. (2003) dataset, using a relevance cutoff value of 0.95. Taxa with significant (p<0.05) positive correlation are indicated as filled squares. Taxa with significant (p<0.05) negative correlation are indicated as open circles. 100 of the original 102 characters are used to calculate baraminic distances.

probably be discounted." Johnsgard (1999), like Klemm (1993), only considered the records given by Gray (1958).

Our newer sources (Gunski et al., 2001; McCarthy, 2006) provide several records that were not considered by either Klemm (1993) or Johnsgard (1999). According to McCarthy (2006), both Ruschi and Amadon (1959) and Esteban (1963) provide reliable hybridization records that connect the Cracidae to the Numididae. In addition, McCarthy (2006) also claims that Ruschi and Amadon (1959) supply reliable hybridization records that connect the Cracidae to the Phasianidae. Ahlquist and Lightner (2019) provide a fascinating and worthwhile historical account of the twists and turns surrounding these putative hybrids but, in the end, conclude that "the numerous and persistent reports of cracid X phasianid hybrids... suggest that such probably exist" (p.99).

We discovered an additional source that also connects the Cracidae to the Phasianidae via hybridization (Gunski et al., 2001). This study provides compelling evidence of hybridization (F1 and F2) between *Gallus domesticus* (i.e. chickens) and *Crax fasciolata*. F1 hybrids were viable and found to have a chromosome number (2n=83) between *G. domesticus* (2n=78) and *C. fasciolata* (2n = 88). In addition, Klemm (1993) does

not mention the cross between the Numididae and Cracidae that is provided by McCarthy (2006). The Numididae are known to interbreed with other members of the "Upland Game Birds" (acknowledged by Klemm), so this provides yet another link to the Cracidae. Coupling these additional hybridization records with the older ones reported in Gray (1958), we believe it is reasonable to conclude that the Family Cracidae forms a large monobaramin along with five other families (all except the Megapodiidae) in the Order Galliformes.

Combined Data. Based on the results of statistical baraminology and hybridization, we conclude that the landfowl comprise two holobaramins: Megapodiidae and [Phasianoidea + Cracidae]. Statistical baraminology alone suggests the possibility of four holobaramins within this order, but hybridization connects three of these. These seemingly contradictory results are instead complimentary. The hybridization data functions to join seemingly different morphological groups, whereas the statistical baraminology data is critical in establishing discontinuity between the two monobaramins suggested by hybridization. Statistical baraminology alone gives an inaccurate picture of the number of holobaramins, but hybridization alone is unable
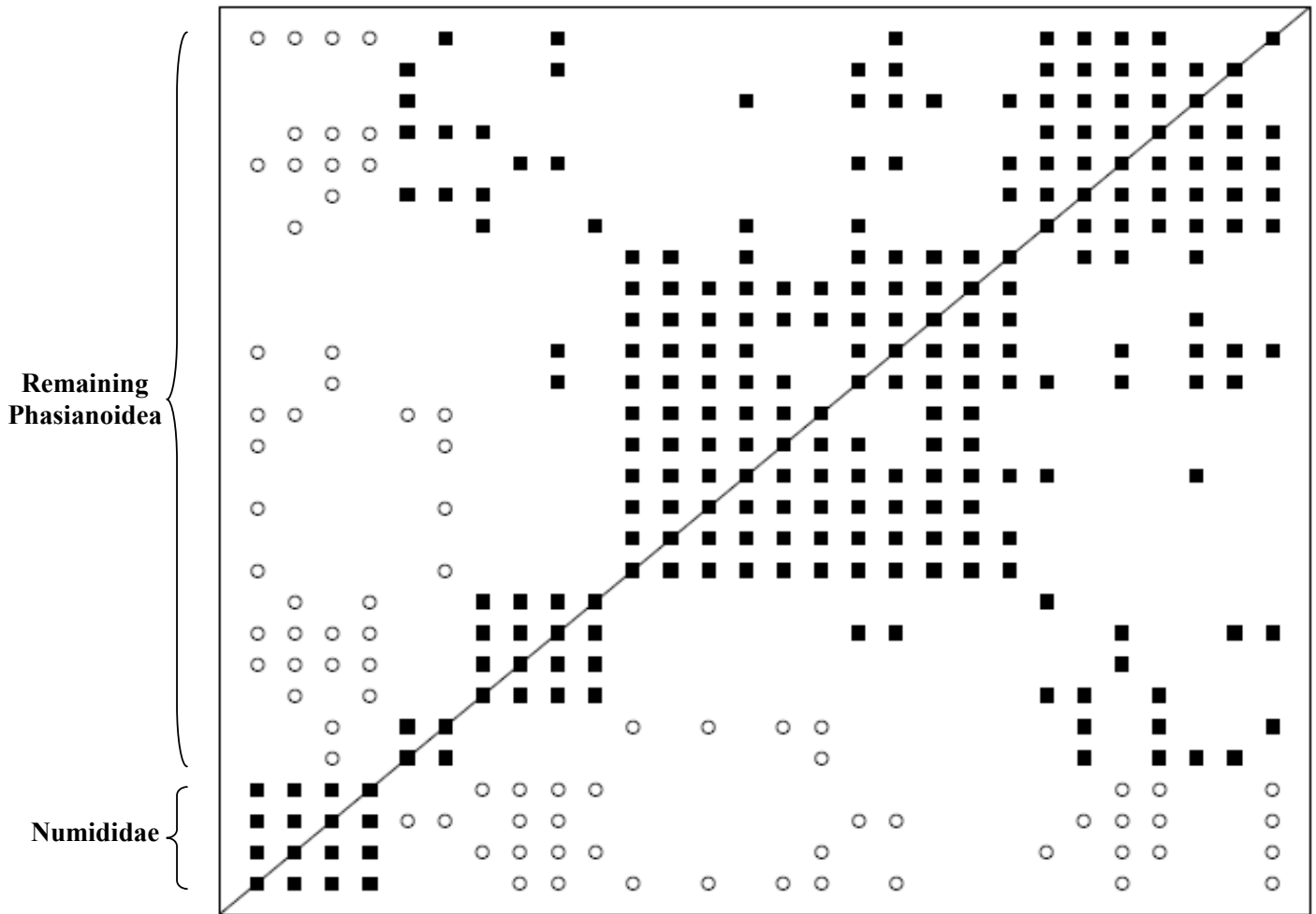
Figure 8. Baraminic distance correlation for a subset (Numididae and every other remaining phasianoid taxa) of the Dyke et al. (2003) dataset, using a relevance cutoff value of 0.95. Taxa with significant (p<0.05) positive correlation are indicated as filled squares. Taxa with significant (p<0.05) negative correlation are indicated as open circles. 101 of the original 102 characters are used to calculate baraminic distances.

to demonstrate discontinuity between groups and is therefore unable (by definition) to delineate holobaramins in this order. Our study emphasizes the continued value of hybridization data in baraminological research, illustrates the importance of using multiple lines of evidence when delimiting holobaramins, and is suggestive of the potential uses and limitations of statistical baraminology.

It may seem unconventional to join the family Cracidae with the superfamily Phasianoidea to produce one large holobaramin, especially since previous creationist authors (Price, 1924, 1938; Woodmorappe, 1996; Jones, 2002; Wood 2006b) have suggested that the family-level grouping is a good approximation of the baramin. However, many of the current families within the superfamily Phasianoidea were, until recently, subfamilies in a more broadly conceived family Phasianidae. For example, both Johnsgard (1986, 1999) and Wolters (1975-1982) give the following taxonomic (or very similar) arrangement for the landfowl:

Order Galliformes

Family Megapodiidae
Family Cracidae
Family Phasianidae
    Subfamily Meleagridinae
    Subfamily Tetraoninae
    Subfamily Odontophorinae
    Subfamily Numidinae
    Subfamily Phasianinae

Some of the more recent phylogenetic studies of the landfowl are returning, at least in part, to this type of arrangement as well (e.g. Crowe et al., 2006). It is not surprising then, even from a creationist perspective, that all of the families in the superfamily Phasianoidea (Wetmore, 1960; del Hoyo et al., 1994) are members of the same holobaramin.

Perhaps the most surprising result of this study then, is the inclusion of the cracids in the phasianoid holobaramin. In our MDS analysis, the cracids form a distinct cluster in the 3D-MDS (Figure 3). It is worth noting, however, that among the non-phasianoid groups, the cracids are closest to the phasianoid

		1	2	3	4	5	6	7	8	9	10	11	12	13
Alectura l. lathami	1													
A. l. purpureicollis	2													
Megapodius affinis	3													
M. geelvinkianus	4													
M. reinwardt	5													
M. c. cumingii	6													
M. c. pusillus	7													
M. forstenii	8													
M. freycinet	9													
M. eremita	10													
Talegalla cuvieri	11													
T. fuscirostris	12													
T. jobiensis	13													

Figure 9. Interspecific hybridization within the family Megapodiidae. Black squares indicate successful interspecific hybridization. Gray squares indicate questionable reports.

clusters. At first glance, our BDC results also seem to suggest that the cracids form a unique group. They are part of the first major group in the initial BDC along with the megapodes and waterfowl (Figure 1). As mentioned previously, however, three of the five cracids in this analysis lack both significant positive correlation with several (if not all) of the moundbuilders/waterfowl and significant negative correlation with several (if not all) of the phasianoids. It is also worth noting, as would be expected from 3D-MDS clustering, that the phasianoids are closer to the cracids with respect to average baraminic distance in the complete dataset (0.44; 0.33-0.56) than they are to either the megapodes (0.52; 0.36-0.63) or anseriform outgroup (0.57; 0.44-0.67). All of this suggests that the cracids may not be as different morphologically from the phasianoids as they appear at first glance. And of course, as previously stated, the cracids are linked to the phasianoids by what appear to be several reliable hybridization records.

The cracids have traditionally been thought of as the sister group to the megapodes (Wetmore, 1960; Sibley and Ahlquist, 1990; del Hoyo et al., 1994). Several studies, however, have suggested that the Cracidae are more closely related to the Phasianoidea than was once assumed. Vuilleumier (1965) suggests that the

Figure 10. Intergeneric hybridization within and between the families Cracidae, Numididae, Tetraonidae, Meleagrididae, Phasianidae, and Odontophoridae. Black squares indicate successful intergeneric hybridization. Gray squares indicate questionable reports.

differences between the cracids and phasianoids are essentially due only to their nesting behavior. Cracids are well adapted to an arboreal lifestyle, which includes nesting in trees. They do share, however, several features and behaviors with various phasianoid taxa: nesting behavior with the Congo peacock and tragopans; clutch size with peacocks and pheasants; mode of tail molting with peacocks and pheasants. Instead of being a sister group to the megapodes, several phylogenetic studies have suggested that the cracids are sister to the phasianoids (Cracraft, 1981, 1988; Crowe, 1988; Brom and Dekker, 1992; Dyke et al., 2003; Crowe et al., 2006). The inclusion of the cracids within the phasianoid holobaramin should not be alarming then, because our data and several recent taxonomic studies suggest it is a plausible arrangement.

Conclusions

1. Both BDC and MDS suggest that the landfowl are composed of four holobaramins: Megapodiidae, Cracidae, Numididae, and the remaining Phasianoidea.

2. Interspecific hybridization, however, connects three of these holobaramins (six of the currently recognized families).

3. Based on both sets of evidence, we conclude that the landfowl are composed of two holobaramins: Megapodiidae and [Phasianoidea + Cracidae].

4. This arrangement, even from a creationist perspective, should not be surprising because several of these families were, until recently, considered to be subfamilies in a more broadly conceived family Phasianidae. In addition, recent evidence suggests that the Cracidae are more closely related to the Phasianoidea than once assumed.

5. This study, because it involves a group for which many hybridization records exist, provides an opportunity to test the potential uses and limits of statistical baraminology. Future studies should investigate the effects of character selection on resulting baraminic classifications.

Acknowledgments

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