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BARAMINOLOGICAL ANALYSIS OF JURASSIC AND CRETACEOUS AVIALAE

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KEYWORDS: Avialae, Dromaeosauridae, Troodontidae, baraminic distance, multidimensional scaling, baraminology, discontinuity

ABSTRACT

The baraminic status of Jurassic and Cretaceous Avialae was evaluated using statistical baraminology. Baraminic distance correlation (BDC) and three dimensional multidimensional scaling (MDS) was applied to six previously published character matrices. The results reveal discontinuities between most Avialae and the Deinonychosauria (Troodontidae + Dromaeosauridae) and little evidence of continuity between modern birds and dinosaurs, suggesting that recent claims that statistical baraminology supports the evolution of birds from dinosaurs are misplaced. Nevertheless, we did find positive BDC and MDS clustering of some Avialae and deinonychosaurians in four of our analyses, suggesting that at least some Jurassic and Cretaceous Avialae may be clustered with dinosaurs. This observation raises the interesting philosophical question: what is a bird?

INTRODUCTION

In 1868, “Darwin’s bulldog” Thomas Henry Huxley suggested that reptiles and birds shared anatomical affinities that could indicate an evolutionary relationship. He based this idea on the close resemblance between the newly discovered *Archaeopteryx* and the coelurosaurian dinosaur *Compsognathus*, both from the Upper Jurassic Solnhofen Limestone of Bavaria. Ever since, there has been general agreement in the evolutionary community about the affinities of birds and reptiles, although the identity of the specific group of reptiles that gave rise to birds has been a matter of considerable debate. Following Huxley’s lead, a link with dinosaurs was supported by Marsh (1877), Gegenbaur (1878), Williston (1879), Parker (1882), Baur (1883; 1884; 1885; 1886), Boas (1930), Lowe (1935; 1944) and Holmgren (1955). However, other proposed ancestors included lacertilians (Vogt, 1879; Wiedersheim, 1884; 1885; Petronievics, 1921; 1927; 1950) and pterosaurs (Owen, 1875; Seeley, 1881; Wiedersheim, 1883; 1886). In 1888, Fürbringer argued that the similarities between birds and dinosaurs were the result of convergent evolution and that both groups had arisen from a less specialized “thecodontian” archosaur. This “common ancestor” theory was adopted by Osborn (1900) and Broom (1908; 1913) and became widely accepted when it was popularized by Heilmann (1926) in his influential book, *The Origin of Birds*. Coelurosaurian dinosaurs were explicitly rejected by Heilmann as avian ancestors since none was known to have possessed clavicles, regarded as the evolutionary precursors of the furcula or wishbone. For the next fifty years the general consensus favoured the “thecodont” hypothesis.

However, with the description of *Deinonychus* in 1969 (Ostrom, 1969), the dinosaurian hypothesis of bird origins was resurrected. Ostrom (1973; 1975a; 1975b) noted that dromaeosaurs such as *Deinonychus* shared many skeletal features with *Archaeopteryx*, including long forelimbs, three-fingered hands with recurved claws, and a semilunate carpal that facilitated great flexibility of the wrist. Dromaeosaurs were able to fold their hands in a manner similar to that of modern birds and their predatory grasping action was found to closely resemble the avian flight stroke. Today, rotating wrists are known to have been possessed by several coelurosaurian groups including the dromaeosaurs, troodontids, therizinosaurs and oviraptors, collectively known as the maniraptorans (“hand snatchers”). Ostrom (1991; 1994) noted other striking morphological similarities between *Archaeopteryx* and various coelurosaurs in the foot and hindlimb, the pectoral arch, the vertebral column, the cranium and the mandible. He also emphasised the obligate bipedality of theropods, something that was shared with birds but not with “thecodontians”. Significantly, the absence of clavicles from coelurosaurs that had been a crucial part of Heilmann’s (1926) case against the theropod hypothesis turned out to be incorrect. Clavicles are now known to be present in a wide range of coelurosaurian taxa (Padian and Chiappe 1998).

Support for the theropod hypothesis came also from the developing field of cladistics (Gauthier and Padian, 1985; Gauthier, 1986) and the growing awareness that the “Thecodontia” constitutes an ill defined, paraphyletic grouping. A small minority of palaeontologists and ornithologists has continued to maintain that the ancestry of birds should be sought among reptiles other than the dinosaurs, including the crocodylomorphs (Walker, 1972; Martin, 1983; 1991), basal archosaurs (Tarsitano and Hecht, 1980; Hecht and Tarsitano, 1982; Tarsitano, 1991) and non-archosaurian diapsids such as *Longisquama* and *Megalancosaurus* (Tarsitano, 1991; Feduccia and Wild, 1993). Nevertheless, despite these expressions of dissent, most evolutionary scientists now accept the dinosaurian ancestry of birds, especially after recent discoveries of theropods with feathers and feather-like integumentary structures (Norell and Xu, 2005). Among the most remarkable of these discoveries are the taxa described from the Lower Cretaceous Yixian Formation of Liaoning Province, northeastern China, including *Protarchaeopteryx* (Ji and Ji, 1997), *Caudipteryx* (Ji *et al.*, 1998), *Sinosauropteryx* (Chen *et al.*, 1998), *Beipaiosaurus* (Xu *et al.*, 1999a), *Sinornithosaurus* (Xu *et al.*, 1999b; Xu *et al.*, 2001) and *Dilong* (Xu *et al.*, 2004). The integumentary structures associated with these coelurosaurian dinosaurs are morphologically diverse, ranging from simple or compound filaments to plumaceous or pennaceous feathers. Though some authors have claimed that the filamentous structures are degraded collagen fibres and thus preservational artefacts (Feduccia *et al.*, 2005; Lingham-Soliar *et al.*, 2007), the pennaceous feathers observed in several of these non-avian dinosaurs cannot be explained in this way (Prum, 2003). Another stunning discovery was *Microraptor* from the Lower Cretaceous Jiofutang Formation of Liaoning Province, a “four-winged dinosaur” with pennaceous feathers on the forelimbs, hindlimbs and tail (Xu *et al.*, 2003). At least one member of the enigmatic maniraptoran family Alvarezsauridae, *Shuvuuia* from the Upper Cretaceous of Mongolia, also seems to have possessed feathers or feather-like structures (Schweitzer *et al.*, 1999). In 2007, Turner *et al.* even reported the presence of quill knobs in *Velociraptor*. Although feathers themselves were not preserved, the six regularly spaced bumps on the ulna are features seen only in feathered organisms. The spacing indicated the presence of 14 secondary feathers, comparable to the 12 known in *Archaeopteryx*.

The Liaoning sediments have also yielded many fossil avialans. The Avialae comprises the Aves together with the Scansoriopterygidae (*Scansoriopteryx* and *Epidexipteryx*) (Zhang *et al.*, 2008). Among the Liaoning avialans are *Confuciusornis* (Hou *et al.*, 1995) and

Changchengornis (Ji *et al.*, 1999). Lower Cretaceous avialans have also been discovered at Las Hoyas, Cuenca Province, east central Spain, including *Iberomesornis* (Sanz *et al.*, 1988), *Concornis* (Sanz and Buscalioni, 1992) and *Eoalulavis* (Sanz *et al.*, 1996). The Archaeopterygidae of the Jurassic (including *Archaeopteryx*) are usually included within the Avialae, although the taxonomic status of *Archaeopteryx* has been questioned following recent cladistic studies (Xu *et al.*, 2011; Lee and Worthy, 2011).

Since the Bible claims that birds had a separate origin from land animals (Genesis 1:20-25, 31), *contra* evolutionary theory, creationists have predicted that birds will be separated from dinosaurs by phylogenetic (and perhaps morphological) discontinuity. This prediction can be tested using the methods of statistical baraminology, which enables us to detect and evaluate morphological discontinuity between taxa. However, Senter (2010) recently argued that even creationists should accept the evolutionary relationship of birds and dinosaurs based on the application of statistical baraminology. Specifically, Senter used classical multidimensional scaling (MDS), a technique commonly applied in statistical baraminology, to demonstrate a morphological continuum between coelurosaurian dinosaurs and Mesozoic birds. Senter argued that this continuum supported the grouping of coelurosaurs and birds in the same 'created kind,' a conclusion that would be strongly disputed by most creationists. Wood (2011) responded by evaluating other sets of taxa with more characters and found evidence of discontinuity between Avialae and Deinonychosauria and between Avialae and Oviraptorosauria, thus lessening the impact of Senter's more limited study. Here, we examine six additional avialan character matrices from Chiappe (2001), Clarke and Norell (2002), Zhou *et al.* (2008), O'Connor *et al.* (2009), Xu *et al.* (2011) and Senter (2011) using baraminic distance correlation (BDC) and three dimensional MDS.

METHODS

BDISTMDS version 2.0 was used to carry out a BDC analysis on the datasets (Wood, 2008). Baraminic distance is the percentage of character states that two organisms have in common (Robinson and Cavanaugh, 1998). The BDC correlates the distances between taxa using linear regression to derive a statistical significance of the similarity of two organisms. Ideally, baraminologists hope to identify well-defined groups of taxa that are united by significant, positive correlation (interpreted as evidence of continuity) and separated from the outgroup taxa by significant, negative correlation (interpreted as evidence of discontinuity). For baraminic distance calculations, characters are omitted that do not meet a minimum criterion of character relevance (the percentage of taxa for which a character state is known). In the present analysis, we used a character relevance cutoff of 75%. Our baraminic distance correlations were supplemented with the application of classical MDS, as described by Wood (2005). MDS converts a matrix of Euclidean distances between objects into a set of k -dimensional coordinates of the objects, where k is a predetermined dimensionality. One major advantage of MDS is the introduction of the concept of *stress*, a measure of how the observed baraminic distances are distorted by the reduction in dimensionality. The smaller the stress, the better the fit between the baraminic distances and the distances inferred from the classical MDS.

Chiappe's (2001) matrix consisted of 24 taxa and 169 characters. The taxa focus on Jurassic and Cretaceous Avialae with a composite Dromaeosauridae as an outgroup. For our calculations, we used 13 taxa with >40% character states known. After filtering at 0.75 character relevance cutoff, we used 76 characters to calculate baraminic distances.

Clarke and Norell's (2002) matrix consisted of 19 taxa and 202 characters. As with Chiappe's matrix, Clarke and Norell focused on Avialae with a composite Dromaeosauridae as the outgroup. For our calculations, three taxa with taxic relevance <0.4 (*Concornis*, *Neuquenornis*, and *Vorona*) were eliminated from the matrix. After filtering at 0.75 character relevance cutoff, we used 139 characters to calculate baraminic distances.

Zhou *et al.*'s (2008) matrix consisted of 205 characters and 29 taxa. As with the previous character matrices, Zhou *et al.* include a composite Dromaeosauridae as the outgroup to a much larger selection of Avialae. For our calculations, we used 23 taxa with $>40\%$ character states known and 107 characters (character relevance cutoff: 0.75).

O'Connor *et al.*'s (2009) matrix consisted of 242 characters and 28 Avialae taxa and one Dromaeosauridae outgroup taxon. We used 22 taxa with $>40\%$ of their character states known. After filtering at a character relevance cutoff of 0.75, we used 87 characters to calculate baraminic distances.

Senter's (2011) revised matrix contained 391 characters scored for 102 taxa. As per Wood's (2011) analysis, we limited the taxa to just 24 Paraves taxa with taxic relevance >0.4 . We omitted 17 other Paraves taxa with taxic relevance between 0.066 and 0.361. The 24 Paraves taxa consisted of nine dromaeosaurids, six troodontids, and nine Avialae. At a character relevance cutoff of 0.75, we retained 158 characters for baraminic distance calculations.

Xu *et al.*'s (2011) data contained 374 characters and 89 taxa. As with Senter's matrix, we examined only the 21 Paraves taxa with at least 40% of their character states known (14 other Paraves taxa were omitted from the analysis). The 21 Paraves taxa consisted of seven dromaeosaurids, six troodontids, and eight Avialae (We follow Lee and Worthy [2011] in classifying *Xiaotingia* as a troodontid and *Archaeopteryx* and *Wellnhoferia* as Avialae). At a character relevance cutoff of 0.75, we used 132 characters for calculating baraminic distances.

RESULTS

The baraminic distance correlation results for Chiappe's (2001) matrix are summarized in Figure 1. We found negative BDC between the alvarezsaurids and the Avialae. Positive BDC was limited to three groups of avialans: Ornithuromorpha (*Patagopteryx*, *Ichthyornis*, and *Anas*, but not *Hesperornis*), Euenantiornithes (*Sinornis* and *Concornis*), and other Avialae (*Archaeopteryx*, *Rahonavis*, *Changchengornis*, and *Confuciusornis*). *Hesperornis* was not positively or negatively correlated with any other taxa. As expected, the 3D MDS results (Figure 2) revealed little clustering (3D stress 0.090, minimum stress of 0.037 at five dimensions). The alvarezsaurids were slightly offset from the diffuse cloud of Avialae taxa.

The baraminic distance correlation results for Clarke and Norell's (2002) matrix are summarized in Figure 3. We found two well-defined groups of taxa corresponding to the Ornithurae and the remaining taxa. Within each group, most taxon pairs have significant, positive BDC, and between the groups, taxon pairs have significant, negative BDC. *Patagopteryx* is neither positively nor negatively correlated with any other taxa. In the 3D MDS results (Figure 4), the Ornithurae appear as a tight cluster with a more diffuse set of taxa surrounding them (3D stress 0.080, minimum stress 0.038 at five dimensions). *Archaeopteryx* appears closely allied to Dromaeosauridae, and *Patagopteryx* is offset both from the main Ornithurae cluster and from any other taxa.

The baraminic distance correlation results for Zhou *et al.*'s (2008) matrix are summarized in Figure 5. We found positive BDC within two groups corresponding to the Ornithurae (except *Patagopteryx*) and the remaining Avialae plus the Dromaeosauridae outgroup. Negative BDC was observed between the two groups, except for positive BDC between *Archaeorhynchus* and three Ornithurae taxa, *Yixianornis*, *Yanornis*, and *Hongshanornis*. Despite the evident separation in the BDC results, 3D MDS analysis of the same distances revealed a diffuse cloud (Figure 6), with a loose cluster of Ornithurae taxa on one side of the cloud and the remaining taxa loosely clustered on the other side of the cloud (3D stress 0.115, minimal stress 0.058 at five dimensions). Again, *Archaeopteryx* is closely allied with the composite Dromaeosauridae taxon.

The baraminic distance correlation results for O'Connor *et al.*'s (2009) matrix are summarized in Figure 7. We found three groups of taxa corresponding to the Enantiornithes, Ornithuromorpha, and Avialae plus the Dromaeosauridae outgroup. Within each group, only positive BDC was observed, and negative BDC was observed between Ornithuromorpha and Enantiornithes and between Ornithuromorpha and other Avialae. Between Enantiornithes and other Avialae, we found no negative BDC and one instance of positive BDC (between *Sapeornis* and DNHM D2522). These three groups are also evident in the 3D MDS results (Figure 8) (3D stress 0.178, minimal stress 0.081 at seven dimensions). Again, *Archaeopteryx* clusters close to the composite Dromaeosauridae outgroup.

The baraminic distance correlation results for Senter's (2011) matrix are summarized in Figure 9. BDC results imply the presence of as many as three groups. The first group consists of the troodontids *Troodon*, *Saurornithoides*, *Sinornithoides*, and *Mei*. The second and third groups consist of dromaeosaurids and avialans respectively. The troodontids *Anchiornis* and *Sinovenator* and the dromaeosaurid *Buitreraptor* are positively correlated with dromaeosaurids and troodontids but not with any avialans. Avialan taxa are only negatively correlated with dromaeosaurid and troodontid taxa. Despite the apparent separation evident in the BDC results, 3D MDS revealed a very tightly clustered cloud of taxa (Figure 10), with Avialae on one side and the Deinonychosauria on the other (3D stress 0.155, minimal stress 0.092 at five dimensions).

The baraminic distance correlation results for Xu *et al.*'s (2011) matrix are summarized in Figure 11. BDC results reveal two clear clusters. One cluster consists of six Avialae: *Epidexipteryx*, *Epidendrosaurus*, *Yanornis*, *Sapeornis*, *Jeholornis*, and *Confuciusornis*. The remaining Avialae (*Archaeopteryx* and *Wellnhoferia*) appear in a cluster with the Dromaeosauridae and Troodontidae. Of the 90 taxon comparisons between the groups, 51 exhibit significant, negative BDC, but only eight have bootstrap values >90%. Within each group, only significant, positive BDC is observed. The 3D MDS results (Figure 12) (3D stress 0.177, minimal stress 0.074 at seven dimensions) generally support the BDC results, with the same two clusters.

DISCUSSION

These results add to Wood's (2011) suggestion of discontinuity between some Avialae and dinosaurs by suggesting additional discontinuities within the Avialae. Minimally, we find little evidence of continuity between modern birds and dinosaurs. Our analysis of O'Connor *et al.*'s (2009) data matrix suggests the presence of three apobaramins: (1) Ornithuromorpha, (2) Enantiornithes, and (3) other Avialae plus Dromaeosauridae. Chiappe's (2001) data

matrix does not support a conclusion of discontinuity within the Avialae (due to a lack of negative BDC), but it does not contradict it either (due to a lack of positive BDC). Further, even with the larger datasets of Xu *et al.* (2011) and Senter (2011), we still find discontinuity between most Avialae and the Deinonychosauria (Troodontidae + Dromaeosauridae). These results suggest that Senter's (2010) confidence that statistical baraminology supports the evolution of birds from dinosaurs is misplaced.

Despite this robust evidence of discontinuity, we also found positive BDC and MDS clustering of some Avialae and deinonychosaurians in four of our analyses. Analysis of the Clarke and Norell (2002) dataset revealed that the composite dromaeosaurid taxon was positively correlated with *Archaeopteryx* and *Confuciusornis*. Our analysis of Zhou *et al.* (2008) revealed three instances of positive BDC between Ornithurae and the remaining taxa that are otherwise separated by significant, negative BDC. With O'Connor *et al.*'s (2009) dataset, we found positive BDC between the composite dromaeosaurid taxon and three Avialae. Finally, with Xu *et al.*'s (2011) character matrix, *Archaeopteryx* and *Wellnhoferia* clustered with the Deinonychosauria rather than the Avialae. These results appear to corroborate the idea that at least some Jurassic and Cretaceous Avialae can be clustered with dinosaurs. Alternatively, though we have chosen to classify *Archaeopteryx* and *Wellnhoferia* within Avialae, it is at least possible that *Archaeopteryx* and *Wellnhoferia* actually are dromaeosaurs, as argued by Xu *et al.* (2011). This observation itself raises the interesting philosophical question: what is a bird? A bird is not a unique species nor a created kind. *Bird* is at least a higher category containing multiple created kinds, as is *dinosaur*. Since these organisms represent the descendants of God's original creation, these higher categories of kinds give us a glimpse into the original design pattern. Whereas parts of that created pattern appear to show an affinity between certain Avialae and dinosaurs, a closer examination reveals robust evidence of discontinuity.

However, a cautionary note must also be raised. In our analyses, *Archaeopteryx* correlates positively with the Dromaeosauridae only when the latter is included as a composite "taxon" (Clarke and Norell, 2002; Zhou *et al.*, 2008; O'Connor *et al.*, 2009). When there are no dromaeosaurs in the dataset (Chiappe, 2001), or when the dromaeosaurs are represented by actual taxa (Senter, 2011; Xu *et al.*, 2011), *Archaeopteryx* correlates positively with other avialans. Furthermore, in all three cases in which *Archaeopteryx* correlates positively with the Dromaeosauridae, the Dromaeosauridae is the only composite "taxon" and all the other taxa are represented by genera. This suggests the possibility that using a composite "taxon" within the ingroup may have skewed our results, at least in the case of *Archaeopteryx*.

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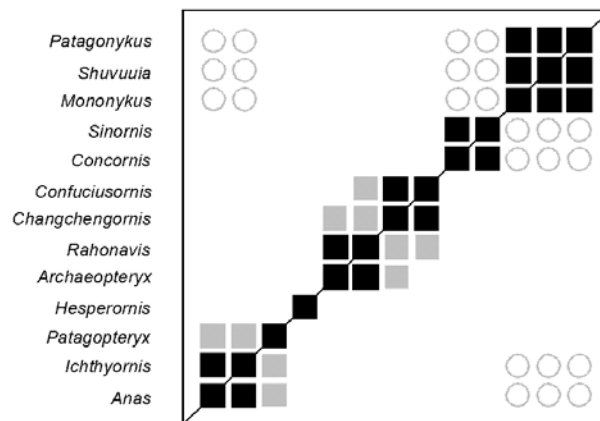


Figure 1. BDC results for Chiappe's (2001) matrix, as calculated by BDISTMDS (relevance cutoff 0.75). Closed squares indicate significant, positive BDC; open circles indicate significant, negative BDC. Black symbols indicate bootstrap values >90%; grey symbols represent bootstrap values <90%.

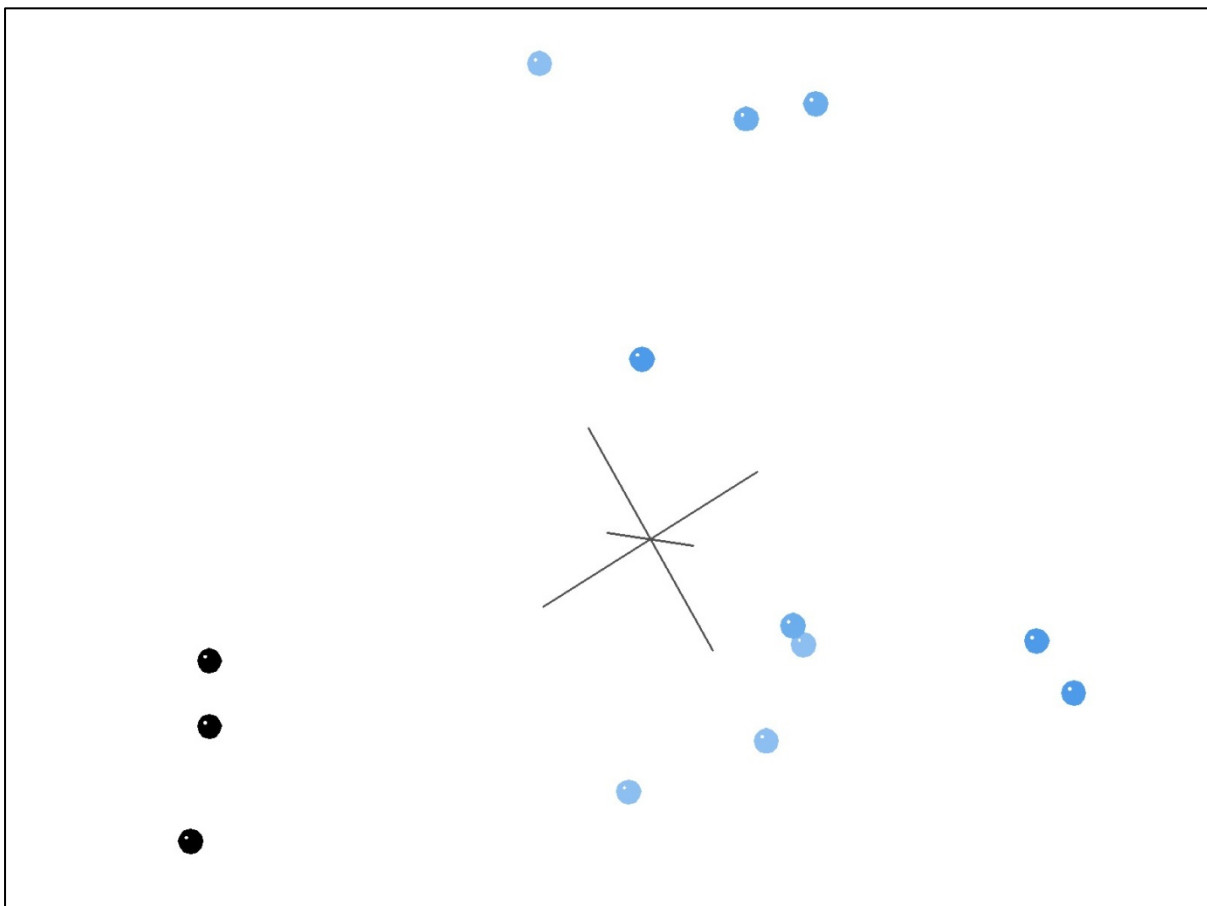


Figure 2. Three dimensional MDS applied to Chiappe's (2001) matrix. Members of Alvarezsauridae are shown in black and Avialae in blue.

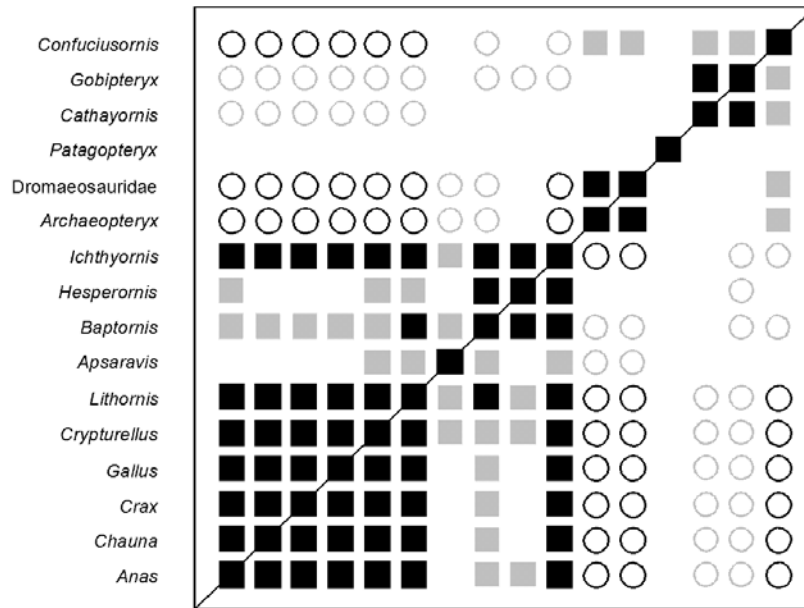


Figure 3. BDC results for Clarke and Norell's (2002) matrix, as calculated by BDISTMDS (relevance cutoff 0.75). Closed squares indicate significant, positive BDC; open circles indicate significant, negative BDC. Black symbols indicate bootstrap values >90%; grey symbols represent bootstrap values <90%.

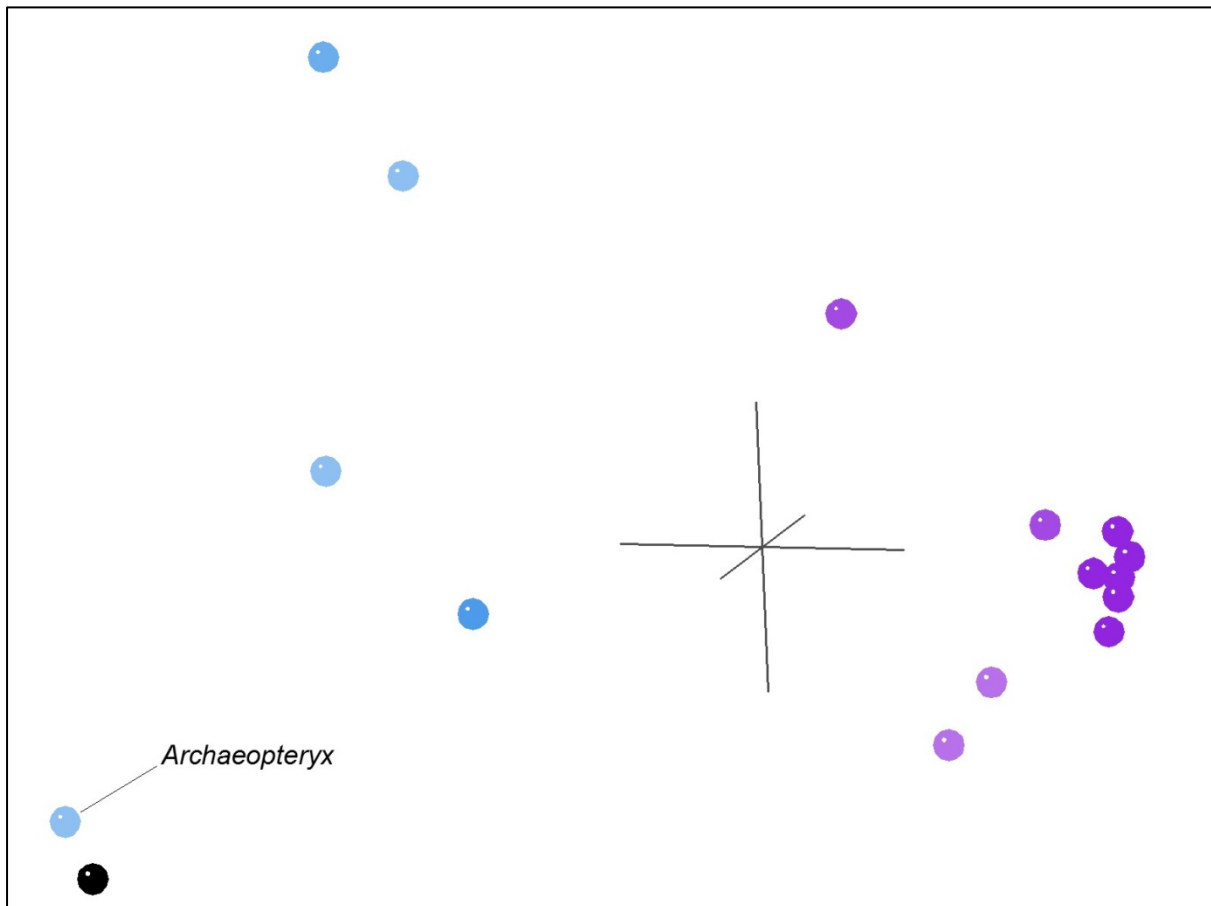


Figure 4. Three dimensional MDS applied to Clarke and Norell's (2002) matrix. Members of Dromaeosauridae are shown in black, basal Avialae in blue and Ornithurae in purple.

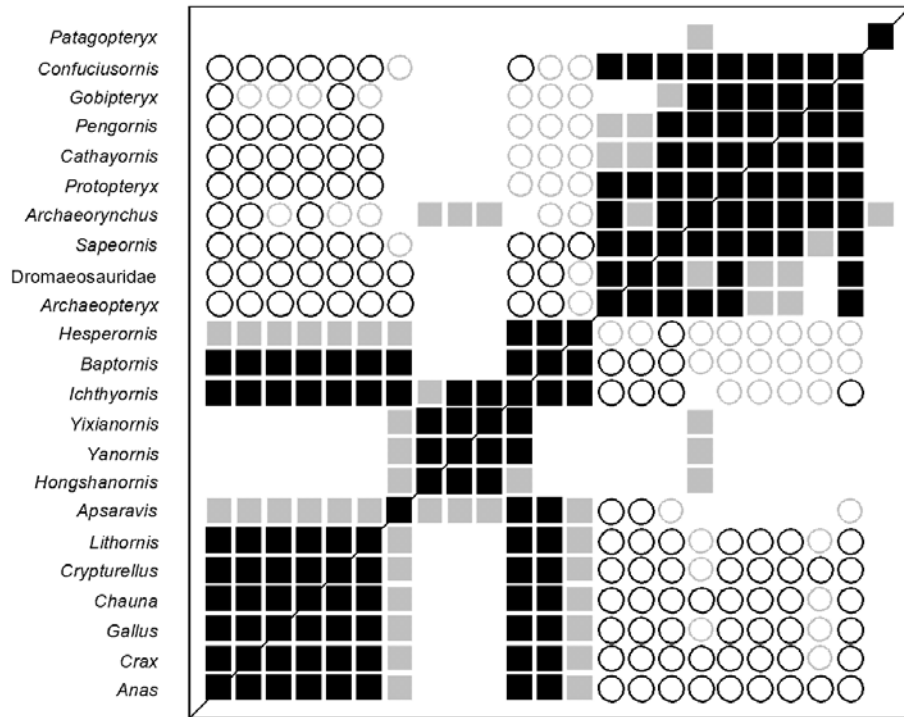


Figure 5. BDC results for Zhou *et al.*'s (2008) matrix, as calculated by BDISTMDS (relevance cutoff 0.75). Closed squares indicate significant, positive BDC; open circles indicate significant, negative BDC. Black symbols indicate bootstrap values >90%; grey symbols represent bootstrap values <90%.

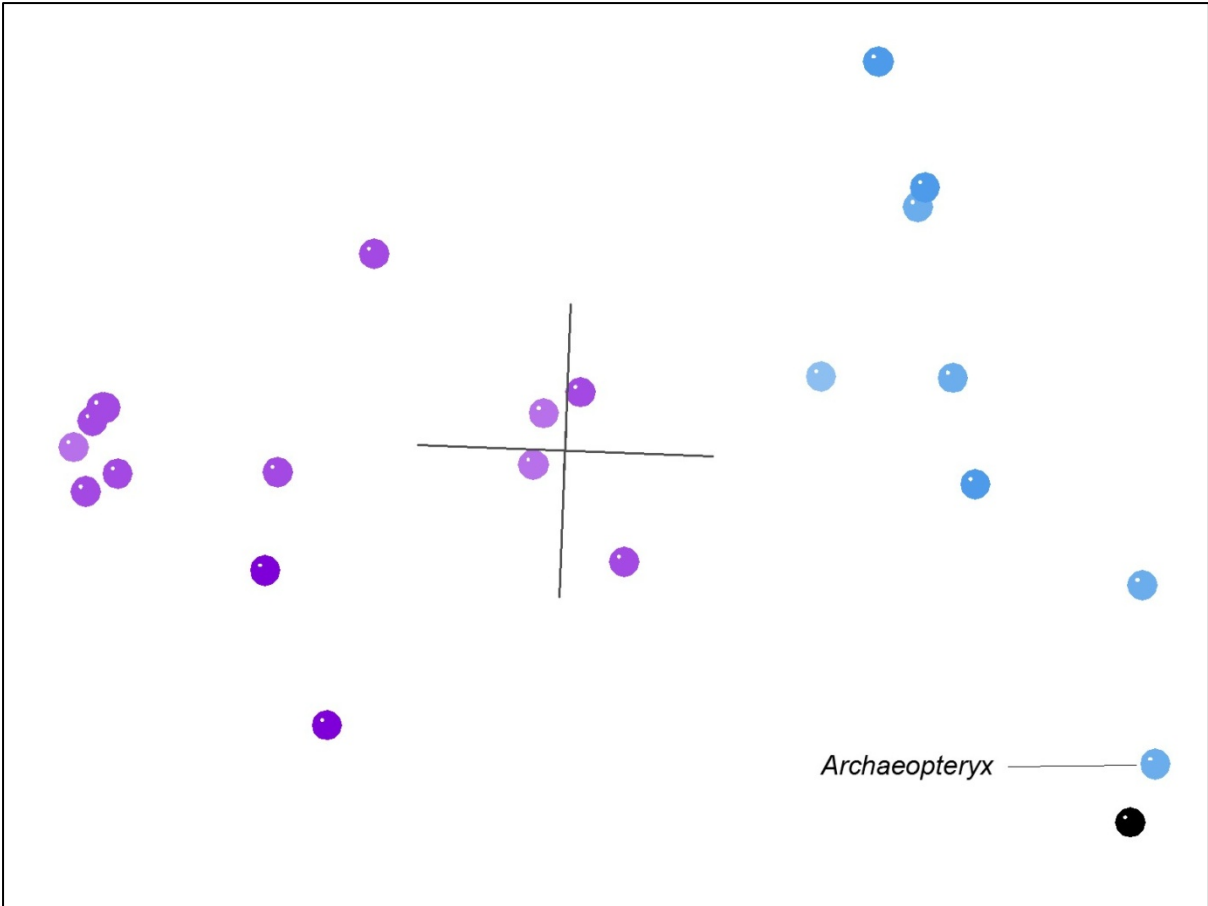


Figure 6. Three dimensional MDS applied to Zhou *et al.*'s (2008) matrix. Members of Dromaeosauridae are shown in black, basal Avialae in blue and Ornithurae in purple.

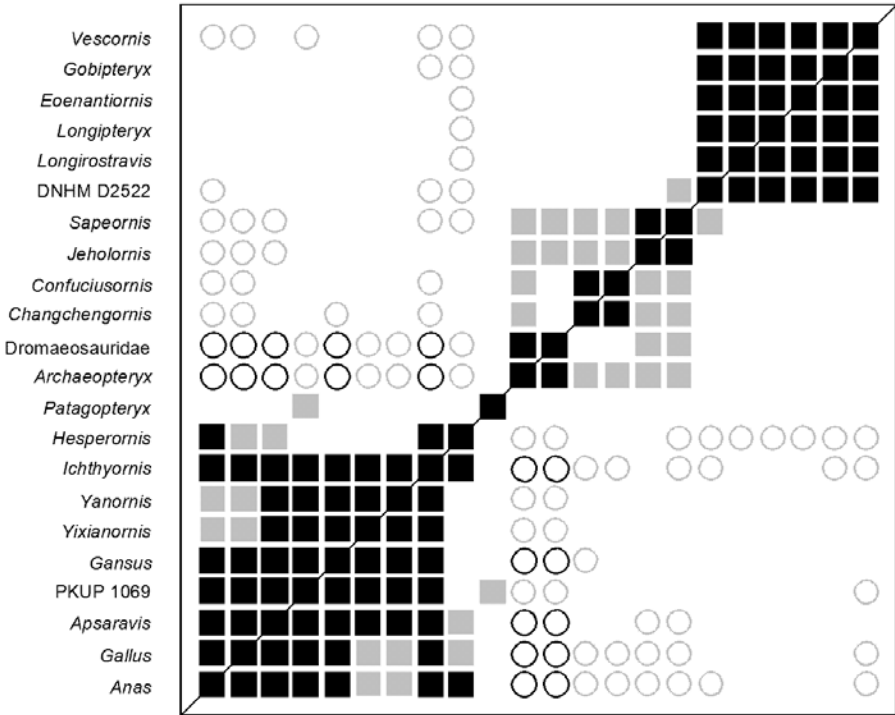


Figure 7. BDC results for O'Connor *et al.*'s (2009) matrix, as calculated by BDISTMDS (relevance cutoff 0.75). Closed squares indicate significant, positive BDC; open circles

indicate significant, negative BDC. Black symbols indicate bootstrap values >90%; grey symbols represent bootstrap values <90%.

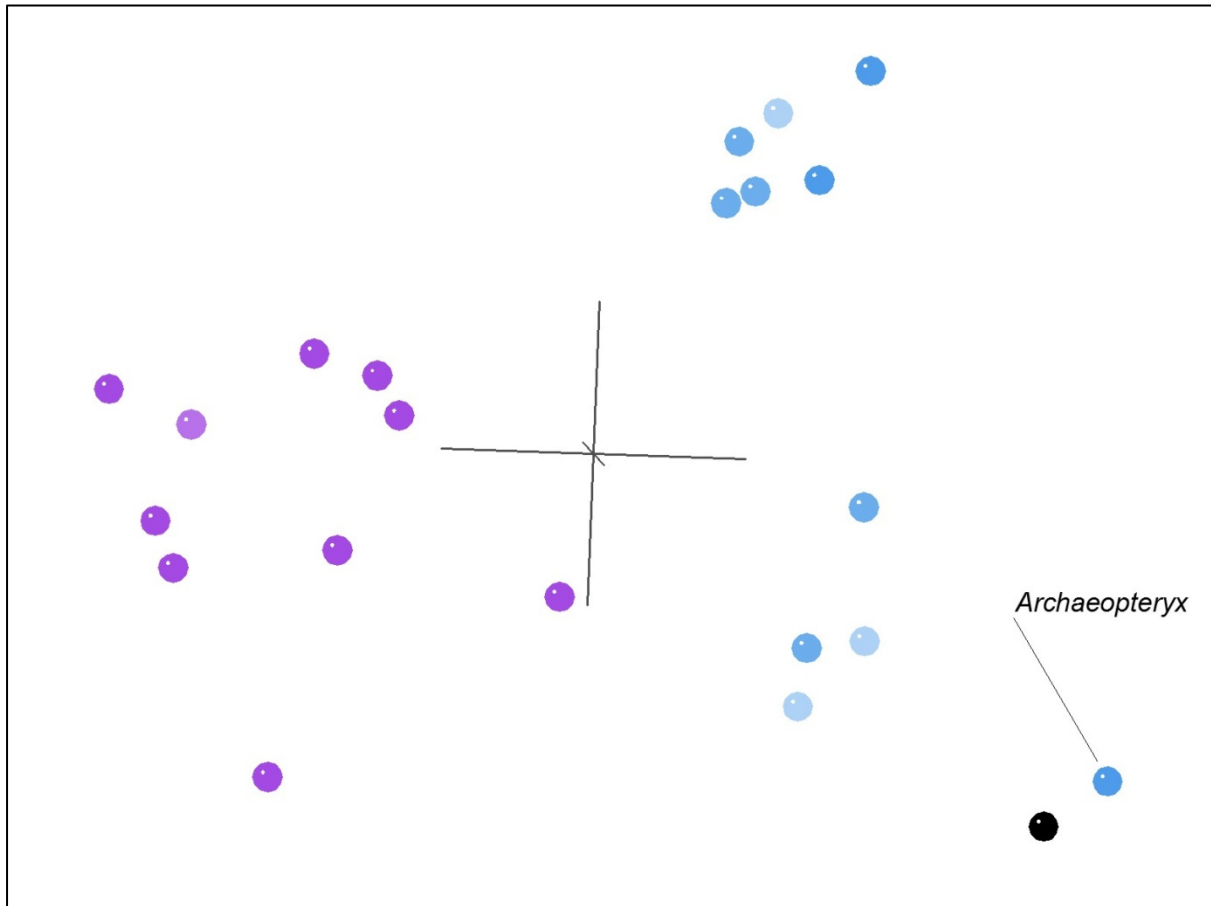


Figure 8. Three dimensional MDS applied to O'Connor *et al.*'s (2009) matrix. Members of Dromaeosauridae are shown in black, basal Avialae in blue and Ornithuromorpha in purple.

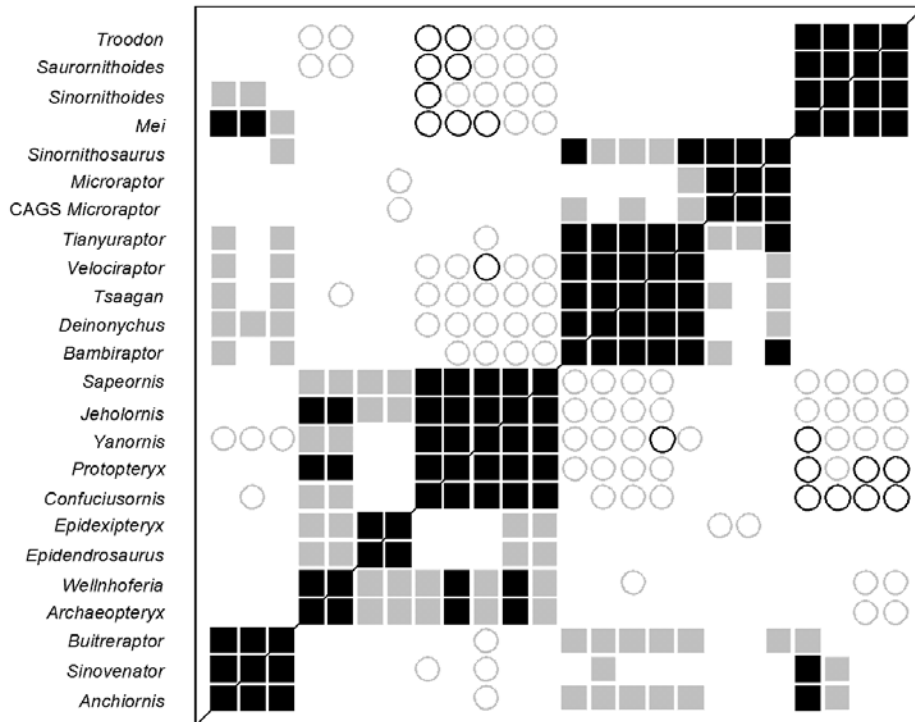


Figure 9. BDC results for Senter's (2011) matrix, as calculated by BDISTMDS (relevance cutoff 0.75). Closed squares indicate significant, positive BDC; open circles indicate significant, negative BDC. Black symbols indicate bootstrap values >90%; grey symbols represent bootstrap values <90%.

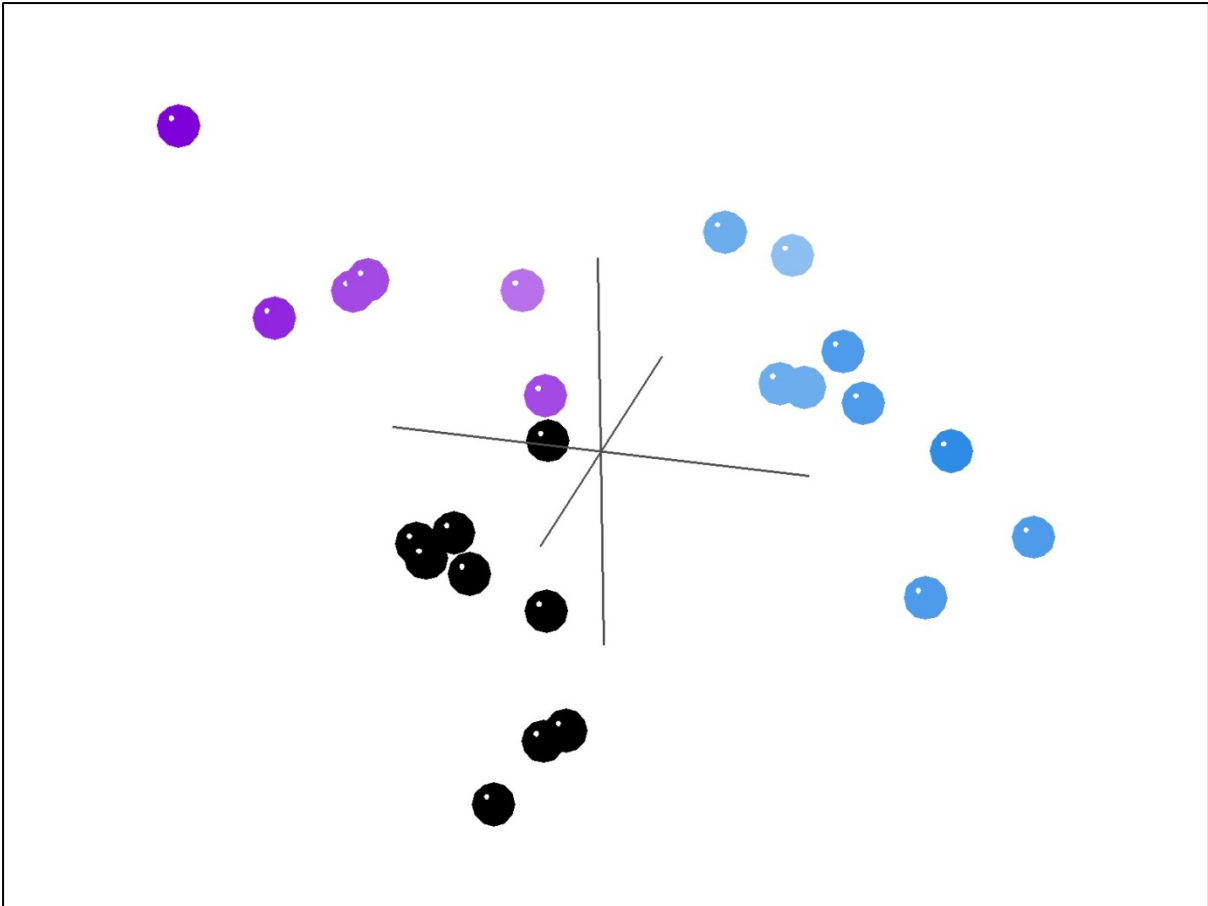


Figure 10. Three dimensional MDS applied to Senter's (2011) matrix. Members of Dromaeosauridae are shown in black, Troodontidae in purple and Avialae in blue.

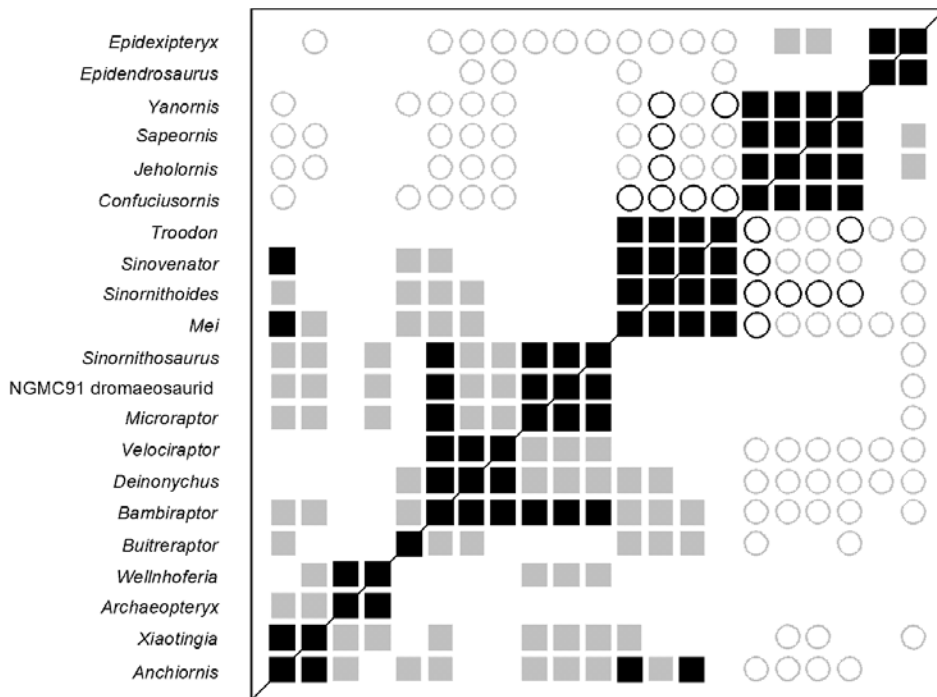


Figure 11. BDC results for Xu *et al.*'s (2011) matrix, as calculated by BDISTMDS (relevance cutoff 0.75). Closed squares indicate significant, positive BDC; open circles

indicate significant, negative BDC. Black symbols indicate bootstrap values >90%; grey symbols represent bootstrap values <90%.

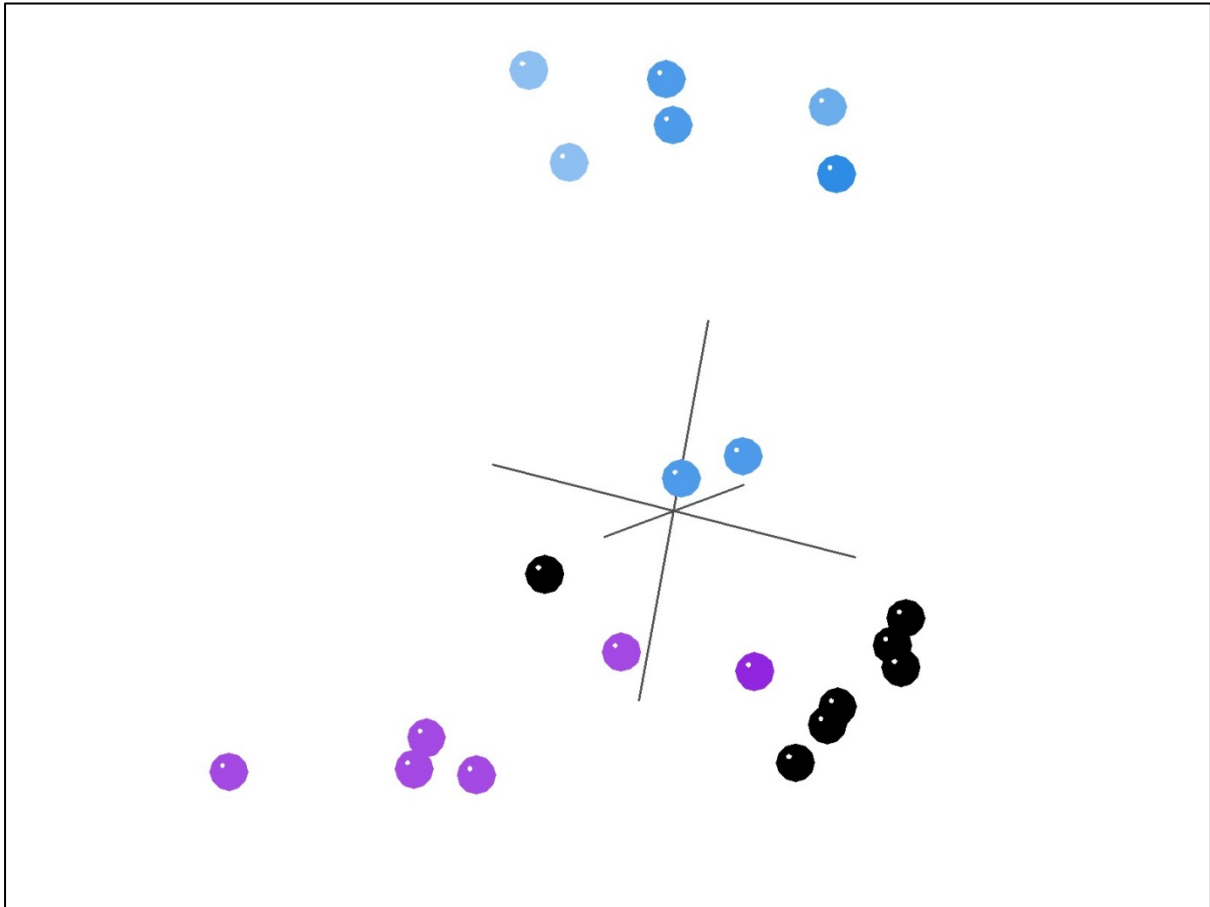


Figure 12. Three dimensional MDS applied to Xu *et al.*'s (2011) matrix. Members of Dromaeosauridae are shown in black, Troodontidae in purple and Avialae in blue.