



Sampling diverse characters improves phylogenies: Craniodental and postcranial characters of vertebrates often imply different trees

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Morphological cladograms of vertebrates are often inferred from greater numbers of characters describing the skull and teeth than from postcranial characters. This is either because the skull is believed to yield characters with a stronger phylogenetic signal (i.e., contain less homoplasy), because morphological variation therein is more readily atomized, or because craniodental material is more widely available (particularly in the palaeontological case). An analysis of 85 vertebrate datasets published between 2000 and 2013 confirms that craniodental characters are significantly more numerous than postcranial characters, but finds no evidence that levels of homoplasy differ in the two partitions. However, a new partition test, based on tree-to-tree distances (as measured by the Robinson Foulds metric) rather than tree length, reveals that relationships inferred from the partitions are significantly different about one time in three, much more often than expected. Such differences may reflect divergent selective pressures in different body regions, resulting in different localized patterns of homoplasy. Most systematists attempt to sample characters broadly across body regions, but this is not always possible. We conclude that trees inferred largely from either craniodental or postcranial characters in isolation may differ significantly from those that would result from a more holistic approach. We urge the latter.

KEY WORDS: Fossils, macroevolution, morphological evolution, paleobiology, phylogenetics.

Despite the increasing importance of molecular and genomic data over the last two decades, morphology still makes an invaluable contribution to vertebrate phylogenetics, and is the only suitable source of data for palaeontological phylogenies (Hillis and Wiens 2000; Asher and Müller 2012). Levels of morphological homoplasy in vertebrate groups are generally lower than those among their invertebrate counterparts (Hoyal Cuthill et al. 2010), suggesting that the signal quality for vertebrates is relatively high. Morphological systematists usually seek to code as many valid characters from as wide a selection of organs and body regions as possible, and to analyze these simultaneously, typically citing

the principle of total evidence (Kluge 1989). Heterogeneity in the performance of characters is often quantified in retrospect, and can also be utilized formally to increase stability in various weighting schemes (Farris 1969; Goloboff et al. 2008a; Goloboff 2014). However, coded matrices are usually analyzed holistically rather than in partitions defined a priori. This is not least because hidden support (the presence of weak signals within putative partitions that become reciprocally reinforcing, and therefore the dominant signal when all characters are considered) is most readily identified in this way (Gatesy et al. 1999; Gatesy and Arctander 2000). It is therefore conceded that different body regions can be

subject to different levels and patterns of homoplasy (Gaubert et al. 2005), such that anatomical subsets of characters can yield significantly different trees. This is especially true when there is strong functional selection in particular organ systems, leading to convergence (Ji et al. 1999; Tseng et al. 2011; Kivell et al. 2013).

Few cladistic studies have analyzed the performance of morphological characters within partitions explicitly (e.g., Sánchez-Villagra and Williams 1998; Rae 1999; Gould 2001; Song and Bucheli 2010). Although analyses may concentrate upon characters of particular types or from particular organ systems, it is still rare that trees are inferred explicitly from subsets of these data (but see Rae 1999; Vermeij and Carlson 2000; O'Leary et al. 2003; Poyato-Ariza 2003; Diogo 2004; Young 2005; Clarke and Middleton 2008; Smith 2010; Farke et al. 2011). Notable exceptions are taphonomic studies that investigate the effects of omitting volatile, soft-part characters with a low fossilization potential (Sansom et al. 2010, 2011; Sansom and Wills 2013; Pattinson et al. 2014; Sansom 2015).

Where levels of homoplasy across morphological character partitions are considered at all, these are usually investigated by comparing distributions of the consistency index (CI: Kluge and Farris 1969; Fig. 1). The CI is given simply as the minimum possible number of state changes (states minus characters) divided by the most parsimonious tree (MPT) length. More appropriate functions underpin most weighting schemes (Goloboff et al. 2008a; Goloboff 2014). In the case of insects, Song and Bucheli (2010) found male genital characters to be less homoplastic than characters coding other aspects of form. In brachiopods, Leighton and Maples (2002) revealed that shell characters are significantly more homoplastic than those describing internal anatomy (a disconcerting finding in a group whose fossil record consists largely of hard parts, and in which phylogeny is inferred almost exclusively with recourse to such characters). Similarly, in hedgehogs, Gould (2001) reported significantly higher consistency indices for dental characters compared with those describing other aspects of anatomy. However, she also noted that the optimal trees inferred from the dental characters alone were seriously at odds with those inferred from the other characters. Kangas et al. (2004) noted that many morphological characters of mammalian teeth have exceptionally strong developmental interdependence, all being under the correlated control of a small number of genes. Most ambitiously, Sánchez-Villagra and Williams (1998) compared the consistency indices between dental, cranial, and postcranial character partitions of eight mammalian datasets, but reported no significant differences. We note that the relative performance of particular characters and character partitions may be contingent, especially with respect to the taxonomic hierarchical level of study. Hence, characters entailing little or no homoplasy for shallow branches may exhibit greater homoplasy when considered at deeper lev-

els. Goloboff et al. (2010) have proposed analytical approaches that take account of this variability in the evolutionary lability of characters along branches.

The dominant practice of total evidence analysis for morphology contrasts with the more qualified approach that was sometimes adopted with molecular data (Felsenstein 1988; Pamilo and Nei 1988; Bull et al. 1993; Maddison 1997; Nichols 2001; Degen and Rosenberg 2009). Molecular systematists have debated the relative merits of partitioned versus combined analyses, although the consensus has emerged in favor of the latter (Gatesy et al. 1999; Gatesy and Baker 2005; Kjer and Honeycutt 2007; Thompson et al. 2012). Historically, the issue of morphological versus molecular incongruence has been more to the fore (Gatesy and Arctander 2000), motivated by striking examples of conflict between molecular and morphological cladograms in some groups (Mickevich and Farris 1981; Bledsoe and Raikow 1990; Bremer 1996; Poe 1996; Baker et al., 1998; Hillis and Wiens 2000; Wiens and Hollingsworth 2000; Jenner 2004; Draper et al. 2007; Pisani et al. 2007; Springer et al. 2007; Mayr 2011), although see Lee and Camens (2009).

WHY EXAMINE THE CONGRUENCE OF CRANIODENTAL AND POSTCRANIAL PARTITIONS?

Some systematists hold that craniodental and postcranial characters convey signals of differing quality (Ward 1997; Collard et al. 2001; Naylor and Adams 2001; Finarelli and Clyde 2004). However, the evidence for this is piecemeal and largely anecdotal. Many practitioners take a more holistic approach (Sánchez-Villagra and Williams 1998), sampling densely from as many anatomical regions as possible. However, even where potential characters are reasonably homogeneously distributed throughout the body, “certain body regions and organs still hold a considerable mystique for taxonomists as classificatory tools, while others are neglected” (Sokal and Sneath 1963; p. 85). Arratia (2009) noted that actinopterygian systematists focus on cranial characters, despite rich seams of underexploited data within the fin rays and fulcra. Murray and Vickers-Rich (2004) suggested that the crania and mandibles of birds often provide the most informative characters because of their structural complexity. Similarly, Cardini and Elton (2008) demonstrated that characters of the chondrocranium were most informative in studies of *Cercopithecus* monkeys, and suggested that this might apply across primates and perhaps across all mammals. Lastly, Ruta and Bolt (2008) found that characters of the lower jaws of temnospondyls recovered many of the same relationships as those inferred from a more holistic dataset.

Studies of extinct organisms *necessarily* focus on those characters capable of fossilization (typically shells and bones). In vertebrates, disproportionate numbers of characters are often coded from the most recalcitrant skeletal elements, notably teeth in

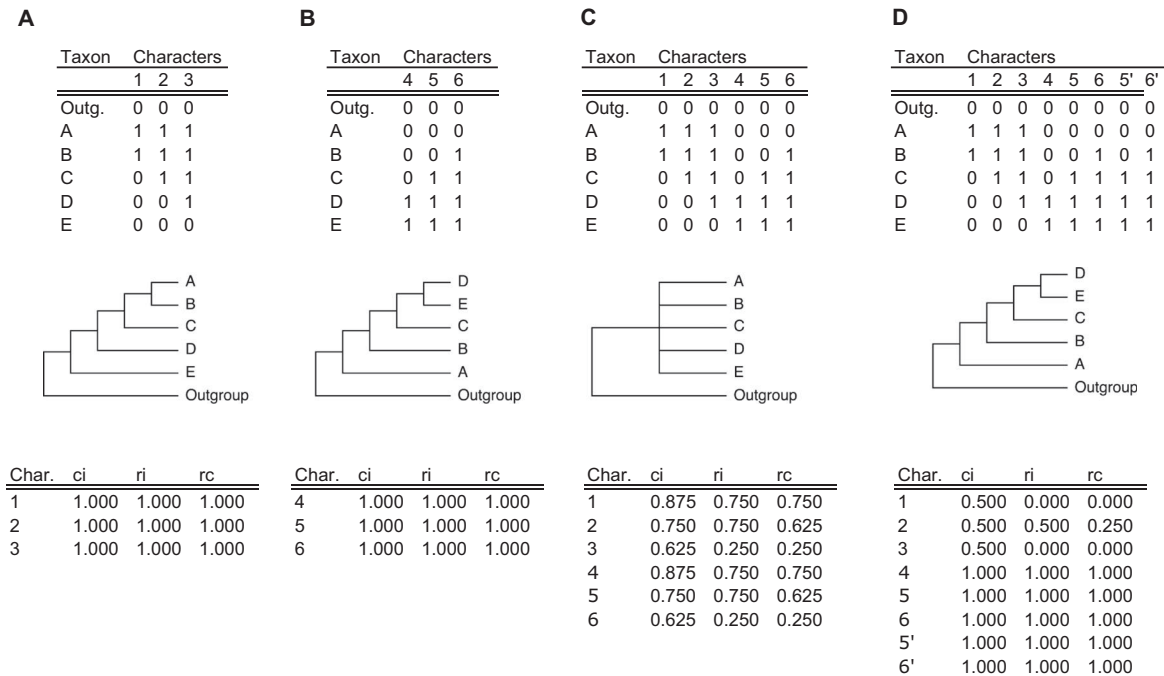


Figure 1. (A and B) Characters sampled from different anatomical regions can yield radically different MPTs when analyzed in isolation. In both cases, there is no homoplasy *within* either region (characters 1–3 or characters 4–6), and a single MPT results in each case. (C) Combining the data from both partitions (characters 1–6) yields four MPTs, the strict consensus of which (illustrated) is entirely unresolved. Character statistics have been averaged over the four trees. (D) Two additional characters (5' and 6') are sampled from the same region as "b," and these have the same distribution as 5 and 6, respectively. Analysis of all characters now reveals a single MPT with relationships identical to those in "b" (characters 4–6). Characters 4–6, 5' and 6' contain no homoplasy: all conflicts are resolved with a cost to characters 1–3. In this case, the MPT is identical to the result that would be obtained by a clique analysis (sensu Le Quesne 1969).

mammals (Billet 2011; Alejandra Abello 2013). More generally, there is a tendency for soft part characters to resolve as more derived apomorphies than those characters with a higher preservation potential. Removal of soft characters therefore results in preferential "stemward slippage" across animal groups (Sansom et al. 2010, 2011; Sansom and Wills 2013); the phenomenon whereby taxa resolve closer to the root of the tree than they otherwise would.

In this study, we apply a variety of methods to explore differences in the strength and nature of phylogenetic signals in craniodental and postcranial partitions of 85 published vertebrate datasets. We address the following questions: (1) Do levels of homoplasy in craniodental character partitions differ from those in postcranial character partitions (Sanchez-Villagra and Williams 1998), and are any observed differences more than simply a function of differing numbers of characters within these partitions? We quantify this using conventional indices of homoplasy (Kluge and Farris 1969; Archie 1996) modeled with respect to dataset parameters. (2) Is there more conflict between craniodental and postcranial characters than we would expect for random partitions, and do craniodental and postcranial characters support significantly different trees as a result? We investigate this using the

incongruence length difference (ILD) test (Mickevich and Farris 1981; Farris et al. 1995a,b) and a new partition homogeneity test based upon tree distance metrics rather than differences in tree lengths.

Materials and Methods

THE DATASETS

Phylogenetic datasets published between 2000 and 2013 were sourced from the literature. Matrices were also garnered from Brian O'Meara's TreeBASE mirror (O'Meara 2009), Graeme Lloyd's collection of dinosaur matrices (Lloyd, 2009), and MorphoBank (O'Leary and Kaufman 2011). We restricted our focus to discrete character morphological matrices composed entirely of vertebrate taxa, and analyzed using equal weights maximum parsimony. Although morphological data can be analyzed with model-based likelihood (Lewis 2000; Lee and Worthy 2012) and Bayesian (Nylander et al. 2003; Pollitt et al. 2005; Clarke and Middleton 2008; Tsuj and Mueller 2009; Bouchard-Cote et al. 2012) methods, the considerable majority of published morphological trees are generated utilizing maximum parsimony. We excluded matrices with fewer than eight taxa or partitions with

fewer than eight parsimony-informative characters (for reasons of statistical power). We interpret craniodental characters here as those pertaining to the skull (cranium plus mandible and dentition).

Our resulting sample comprised 85 matrices, spanning all major vertebrate groups. A small number of these datasets contained characters that were not strictly morphological (e.g., character 618 relating to habitat choice in the matrix of Spaulding et al. 2009). These were removed prior to any further analysis. We also removed phylogenetically uninformative taxa within partitions using the principles of safe taxonomic reduction (Wilkinson 1995). We additionally removed taxa with large amounts of missing data that were demonstrated empirically to obfuscate resolution within partitions, usually because they inflated search times and numbers of optimal trees to impractical levels. The number and percentage of craniodental and postcranial characters in each matrix were recorded, as well as the fraction of missing entries within these partitions. Wilcoxon signed-rank tests were used to assess the significance of differences between these medians in different groups.

Simply recording percentages of missing cells has limitations, as these can be distributed randomly (usually less problematic analytically) or can be concentrated within particular taxa. Such concentrations are often observed in real datasets, and particularly in matrices including fossil taxa (Cobbett et al. 2007). Our pruning of taxa removed the worst of these effects. Simulations have demonstrated that it is the signal within the characters that are coded that is critical in determining the placement of particular taxa (Wiens 2003a,b) rather than numbers of missing cells per se.

All phylogenetic analyses were performed using *TNT* (Tree Analysis Using New Technology; Goloboff et al. 2008b), using equally weighted parsimony. We also reproduced any assumptions regarding character order, polarity, and rooting. Empirically, we determined that comprehensive searches involving 200 parsimony ratchet iterations (Nixon 1999) and 100 drift iterations per replication, with 10 rounds of tree fusion (Goloboff 1999) were effective at recovering the set of MPTs reported by the original authors in each case. These settings were used throughout.

TESTING WHETHER CRANIODENTAL AND POSTCRANIAL CHARACTERS EXHIBIT DIFFERENT LEVELS OF HOMOPLASY

Consistency and retention indices

There are two intuitive ways to calculate differences in mean/median CIs (Kluge and Farris 1969) and retention indices (RIs; Farris 1989) for characters in partitions of a dataset (*ci* and *ri* in lower case pertain to individual characters). The usual approach is to find the optimal tree or trees for all characters analyzed simultaneously (the global MPT(s)) and to take mean values

for characters reconstructed on this/these (Sánchez-Villagra and Williams 1998; Song and Bucheli 2010). However, there are theoretical partition size effects, even in the absence of differences in the levels of character conflict *within* partitions. All other things being equal, the characters within the larger partition are likely to have higher *ci* values on average (Fig. 1). The other approach is to report metrics for characters within each partition analyzed independently. However, the ensemble CI and ensemble RI (and therefore *ci* and *ri* for individual characters) are influenced by dataset dimensions (Archie 1989; Sanderson and Donoghue 1989; Faith and Cranston 1991; Klassen et al. 1991): there is a strong, negative correlation between CI and the number of taxa and a weaker, negative relationship between CI and the number of characters (Archie 1989, 1996; Archie and Felsenstein 1993).

There are two ways in which differences between indices can be tested. For individual data matrices, Mann–Whitney or *t*-tests can be applied to character *ci* and *ri* values, with the null that these have the same median or mean in the two partitions. For the more general comparison across all 85 matrices simultaneously, Wilcoxon-signed ranks or paired *t*-tests can be used to test the nulls that the median/mean CI or RI in craniodental and postcranial partitions are similar.

Homoplasy excess ratio (HER)

The HER (Archie and Felsenstein 1993) was proposed as an adjunct to the ensemble CI, and argued to be relatively immune to its worst shortcomings. HER is given by $(\text{MEANNS} - L)/(\text{MEANNS} - \text{MINL})$, where MEANNS is the mean length of the MPTs resulting from a large sample of matrices (here 999) in which the state assignments within each character have been randomized. *L* is then the optimal length of the original dataset, and MINL is the minimum possible length of the dataset (number of states minus number of characters). HER was calculated for craniodental and postcranial partitions in isolation, and we then tested for differences in partitions across all 85 datasets using the Wilcoxon signed ranks test.

TESTING INCONGRUENCE BETWEEN CRANIODENTAL AND POSTCRANIAL CHARACTER PARTITIONS

ILD test

To assess the significance of congruence between whole character partitions as measured by optimal tree length, the ILD test (Mickevich and Farris 1981; Farris et al. 1995a,b; Barker and Lutzoni 2002) was applied to the matrices in *TNT* using 999 replicates (Allard et al. 1999a,b). The ILD score is given by $L_{AB} - (L_A + L_B)/L_{AB}$, where L_{AB} is the optimal tree length (in steps) of the simultaneous analysis of both partitions together (the total evidence analysis), and L_A and L_B are the optimal tree lengths for partitions A and B analyzed independently. To determine the significance of the observed ILD score, random partitions of the

same size (number of characters) as the specified partitions are also generated to yield a distribution of randomized ILD scores. Given the nature of phylogenetic data, the suitability of this test has been questioned on a variety of grounds (Dolphin et al. 2000; Hipp et al. 2004; Planet 2005, 2006; Ramirez 2006). Despite this, the ILD test remains commonly used to compare the congruence of data partitions. We did not apply the arcsine transformation of Quicke et al. (2007) because they justified their correction on the basis of empirical and simulated *molecular* data (morphological data have different statistical properties).

TESTING WHETHER PARTITIONS SUPPORT DIFFERENT TREES

The incongruence relationship difference (IRD) test: A new test of the congruence of relationships

Much like the ILD test, this is a randomization-based test. However, partitions are compared via the distances between the optimal trees that result from them, rather than via tree length (ILD) or a matrix-representation of topology (TILD; Wheeler 1999). There are many possible tree-to-tree distance measures including symmetric difference (RF; Bourque 1978; Robinson and Foulds 1981; Pattengale et al. 2007) quartets distance (QD; Estabrook et al. 1985), nearest neighbor interchange distance (NNID; Waterman and Smith 1978), nodal distance (Bluis and Shin 2003), maximum agreement subtree distance (Goddard et al. 1994; de Vienne et al. 2007), transposition distance (Rossello and Valiente 2006), subtree prune and regraft distance (SPR; 2008), and path-length difference (PLD; Zaretskii 1965; Williams and Clifford 1971). For reasons of familiarity (it is among the most well characterized; e.g., Steel and Penny 1993) and ease of computation, we chose to use the symmetric difference or Robinson and Foulds distance (RF; Fig. 2) as our measure of tree-to-tree distance. We note that all other implementations are possible. We illustrate the approach for two examples: first, the theropod data of Ezcurra and Cuny (2007; Fig. 3A) and second the mammalian data of Beck et al. (2008; Fig. 3B). The results from each partition are illustrated as 50% majority rule consensus trees for ease of visualization. The left-hand tree in both cases is that derived from the analysis of craniodental characters alone, while the right-hand tree is inferred from just the postcranial characters. The open circles indicate nodes present in one partition tree that are absent from the other, and the total number of such nodes gives the measure of RF between the trees. This value corresponds to the IRD_{MR} (in the case of the majority rule trees illustrated).

All MPTs from the analysis of each partition were saved and then compared to each other in two different ways. (1) "Nearest neighbors" (IRD_{NND}) for up to 10,000 trees in each partition: the mean of the minimum distance between each tree in one set, compared with the trees in the other (and vice versa; Cobbett et al. 2007). (2) The distance between the 50% majority-rule con-

sensus trees (from up to 10,000 fundamentals) for each partition (IRD_{MR} ; Figs. 3 and 4). We then generated random partitions of the original data in the original proportions, and repeated the above exercises to yield a distribution of randomized partition tree-to-tree distances. Distances for the original partitions were deemed significantly different from this distribution when they lay in its 5% tail. Our *P* values were derived from 999 replicates. All but three (98%) of our 170 partitions yielded less than 10,000 trees; the imposition of a 10,000 bound for the remainder was a necessary limitation to restrict prohibitively long searches in poorly resolved partitions.

Tests not implemented

The topological incongruence length difference (TILD) test (Wheeler 1999) is analogous to the ILD test, but is applied to a matrix representation (GIC; Farris 1973; also known as MRP coding, Baum 1992; Ragan 1992) of the branching structure of a consensus of the optimal trees from the data partitions. The test appears to have limited discriminatory power and high type I error rate (Wills et al. 2009).

Rodrigo et al. (1993) proposed three interrelated tests to investigate differences in relationships directly. The first of these determines whether the symmetrical difference distance (RF; Robinson and Foulds 1981) between sets of MPTs from independent analyses of the two dataset partitions is distinguishable from the distribution of RF distances between a large sample of pairs of random trees. Only weak congruence between partitions is needed to pass this test. The second test of Rodrigo et al. (1993) compares the partitions directly, and determines if there is any overlap between the MPTs derived from the two partitions upon bootstrap resampling. This is problematic because the probability of encountering common trees changes with the bootstrap parameters (Lutzoni 1997), especially the number of replicates (Page 1996). The third test compares RF distances between partitions with those between trees bootstrapped from within partitions. Although a useful test, it may have limitations, particularly where the partitions of the dataset are of very different sizes, and especially where the number of characters in the smaller partition is also small relative to the number of terminals. In such cases, bootstraps of the smaller partition may consistently yield poor resolution and low RF distances between trees *within* this partition (Page 1996). The IRD_{NND} test proposed above controls this partition size difference.

Results

HOMOPLASY IN CRANIODENTAL AND POSTCRANIAL DATA PARTITIONS

Across our sample of 85 datasets, craniodental partitions had more characters (median = 58) than postcranial partitions (median =

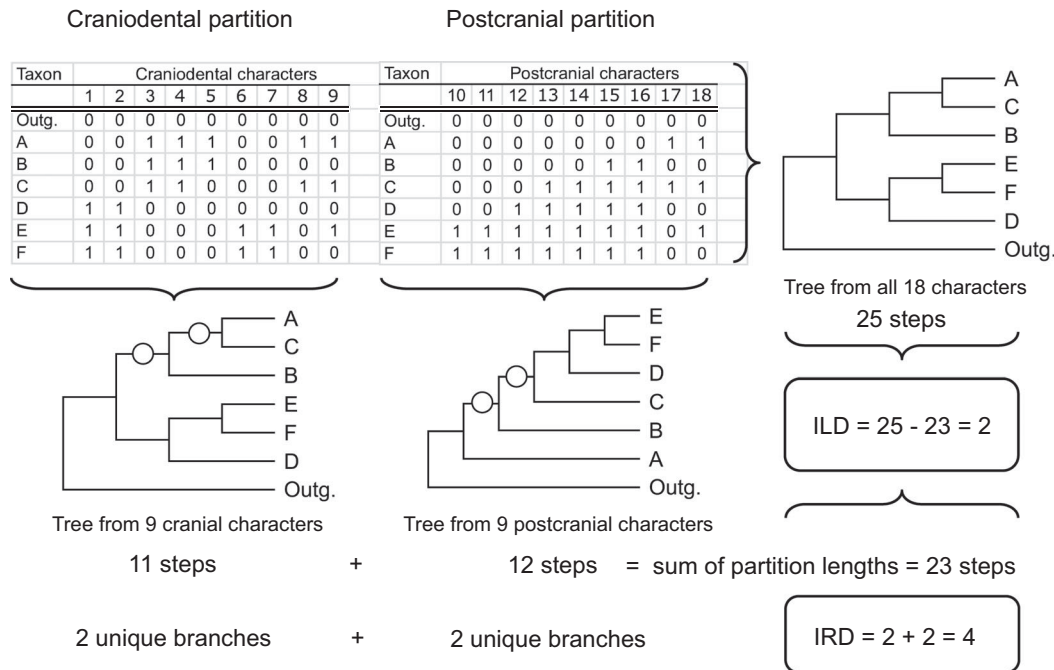


Figure 2. Calculation of two partition inhomogeneity metrics for “craniodental” and “postcranial” partitions of a hypothetical dataset. In this example there are equal numbers of craniodental (1–9) and postcranial (10–18) characters, but this need not be the case. For the ILD measure, MPTs are inferred from the craniodental and postcranial partitions of the data *independently*. The summed lengths of these trees (11 steps + 12 steps) is the sum of partition lengths (23 steps). In parallel with this, an MPT is inferred from both partitions analyzed *simultaneously*. This tree is longer (25 steps) than the sum of partition lengths (23 steps), and the difference between them is the ILD (25 – 23 = 2). The ILD represents the reduction in homoplasy afforded by the isolation of the two partitions (two extra steps are needed when the partitions are combined). For the IRD measure, the branching structure of the craniodental and postcranial partition MPTs are compared (rather than their lengths) using one of several possible tree-to-tree distance metrics. Here, we illustrate the symmetric difference distance (RF) of Robinson and Foulds (1981). Open circles mark branches in either the craniodental or postcranial MPT that are absent from the other. The tally of these unique branches on both trees is the RF (2 + 2 = 4). Some background level of ILD or IRD is anticipated wherever a dataset contains homoplasy. To interpret these observed metrics, therefore, we need to know what values would be expected for partitions of similar datasets in similar proportions. Random character partitions are used to generate null distributions for both the ILD and IRD, and observed values deemed significantly different from the null if they lie in some specified fraction of the tails.

50; Wilcoxon-signed ranks; $V = 2288.5$, $P = 0.044$; Table 1). The percentage of missing data cells was comparable in craniodental (median = 12.8%) and postcranial (median = 16.9%) partitions, although this difference was significant (paired Wilcoxon; $V = 868.5$, $P = 0.006$). The mean ensemble CIs for craniodental and postcranial characters across all 85 datasets were not significantly different (paired $t = 1.184$, $P = 0.240$), with postcranial partitions ($\bar{x} = 0.564$) having slightly higher values than craniodental partitions ($\bar{x} = 0.550$). Using the mean partition (per character) ci index across all matrices (characters optimized onto the globally optimal tree(s) for the entire matrix) revealed a nonsignificant difference ($\bar{x} = 0.632$ and 0.627 for craniodental and postcranial partitions, respectively; paired $t = 0.450$, $P = 0.654$). Mann–Whitney tests of craniodental and postcranial ci values *within* the 85 datasets yielded 40 significant ($P < 0.05$) results (four or five might be expected). Twenty-one of these 40 had higher means (less homo-

plasy) for cranial characters, despite their larger partition size. A simple linear model was used to express partition ensemble CI in terms of the log of the number of taxa, the log of the number of characters, and the log of the percentage of missing data (+1) across all 170 partitions. The term for missing data was not significant, but both the log of the number of taxa ($P < 0.001$) and the log of the number of characters ($P < 0.014$) were highly so (multiple $R^2 = 0.458$, $P < 0.001$). A subsequent paired t -test of the residual CI values from this model revealed no significant difference ($t = 0.917$, $P = 0.362$) between craniodental and postcranial partitions. We note that other variables have been demonstrated empirically to influence CI (Donoghue and Ree 2000; Hoyal Cuthill et al. 2010).

HER values (Archie 1989, 1996; Archie and Felsenstein 1993) were similar in the craniodental ($\bar{x} = 0.582$) and postcranial skeleton ($\bar{x} = 0.571$; paired $t = 0.621$, $P = 0.537$). A linear model

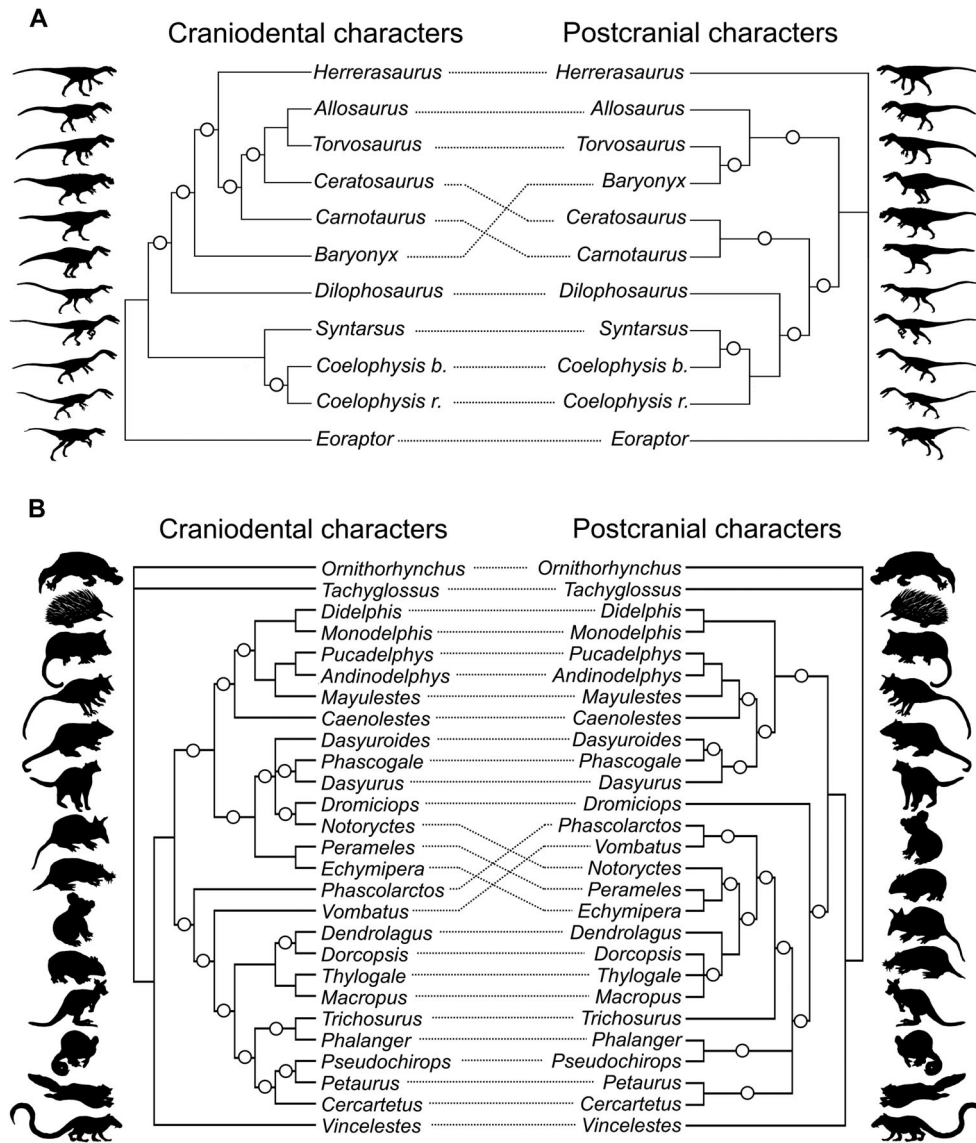


Figure 3. Most parsimonious trees derived from craniodental and postcranial partitions can be significantly more different than we would expect. Tanglegrams computed using Dendroscope (Huson and Scornavacca 2012). (A) The theropod data of Ezcurra and Cuny (2007) yielded one most parsimonious tree from the craniodental partition and six from the postcranial partition, the latter summarized as a majority rule tree merely for ease of visualization (we advocate the use of tests based upon mean nearest neighbors within sets of most parsimonious trees). Branches labeled with circles are unique to one or other tree (those unlabeled are common to both). The RF distance between the two is simply the sum of unique branches ($6 + 6 = 12$). Although the ILD test returned a highly significant result ($P = 0.011$), our new IRD_{NND} test using RF did not ($P = 0.791$). (B) Six craniodental and four postcranial trees in the mammalian data of Beck et al. (2008), again summarized as majority rule consensus trees for visualization. In this case, the ILD test for partition homogeneity returned a highly significant result ($P = 0.004$), whereas our IRD_{NND} test did not ($P = 0.259$). Indicative images are, from top to bottom on right hand side: *Ornithorhynchus*, *Tachyglossus*, *Didelphis*, *Monodelphis*, *Caenolestes*, *Dasyurus*, *Phascolarctos*, *Vombatus*, *Perameles*, *Echymipera*, *Macropus*, *Phalanger*, *Petaurus*, *Vincelestes*. Image of *Tachyglossus* courtesy of Alan Dale of echidnasclub.com. See text for further explanation.

of HER in terms of the logs of numbers of characters and taxa and the percentage of missing data (+1) revealed no significant independent variables. Finally, ensemble RIs were significantly higher for postcranial than craniodental partitions when measured across all characters in a partition (RI; paired $t = 2.654$, $P = 0.009$) but

not as the average of per character values within a partition (ri; paired $t = 1.538$, $P = 0.128$). Linear modeling of the partition RI in terms of the logs of numbers of characters and taxa and the percentage of missing data (+1) revealed no significant independent variables.

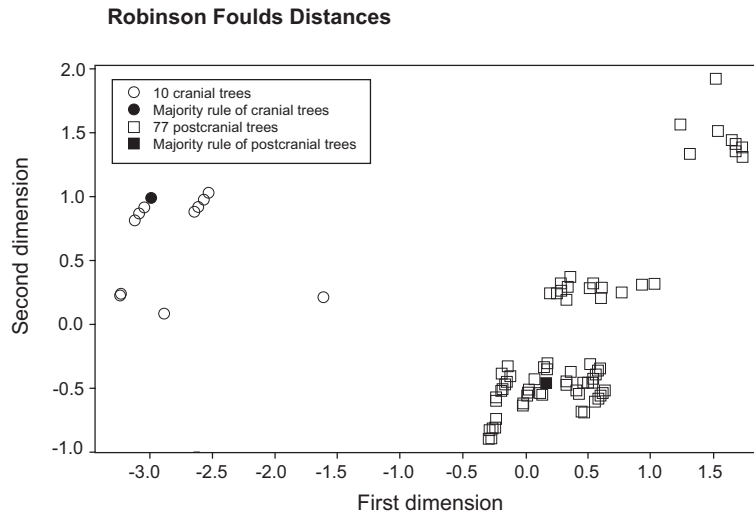


Figure 4. Summarizing sets of most parsimonious trees (MPTs) for partitions prior to calculating tree-to-tree distances is computationally much faster than calculating distances between all nearest neighbors. However, majority rule trees present modal or most frequent relationships, and may therefore plot eccentrically in tree space. This is an undesirable property when attempting to summarize distances between sets of trees. Figure shows Robinson Foulds tree-to-tree distances for craniodental and postcranial partitions of the mammalian data of Pujos et al. (2007). Distance matrices have been plotted in two dimensions using nonmetric multidimensional scaling (NMDS), and rotated using principal components analysis (PCA). Circles indicate craniodental trees and squares indicate postcranial trees. Open symbols denote original MPTs, filled symbols (black) denote majority rule trees.

CONGRUENCE BETWEEN CRANIODENTAL AND POSTCRANIAL SIGNALS (ILD TESTS)

When originally described, the ILD test was used with a standard significance level of 5% (0.05). At this level, 31 of our 85 dataset partitions had significant character incongruence (Table 1). Some have advocated more stringent levels (e.g., Cunningham 1997): with $P < 0.010$, we still rejected the null for 23 of our datasets. We note that the correlation between ILD P values and the percentage of missing data within a dataset was not significant ($\tau = -0.115$, $P = 0.125$), although there was a significant correlation between ILD P values and the *difference* in the percentage of missing data cells in the two partitions ($\tau = -0.161$, $P = 0.031$). When culling our matrices to those with a difference of just 5% or less in the fraction of missing cells in the two partitions ($n = 40$), we still observed 11 datasets with an ILD significant at $P < 0.050$ (a similar rate of rejection: $G = 2.653$, $P = 0.103$).

Logistic regression was used to model the binary outcome of the ILD test (significant or not at $P < 0.05$) as a function of log of the number of taxa, log of the number of characters, the imbalance in number of characters between partitions (as a percentage of the total number), the percentage of missing entries in the dataset, and the log of the imbalance in the percentage of missing entries between partitions. Terms for the number of characters ($P < 0.001$) and the imbalance in character numbers ($P = 0.021$) were retained in the minimum adequate model selected by the progressive deletion of nonsignificant terms ($P > 0.05$).

THE SIMILARITY OF RELATIONSHIPS IMPLIED BY PARTITIONS

Across all 85 datasets, 27 had significantly incongruent relationships (IRD_{NND}) at $P < 0.05$, of which 14 were also significant at $P < 0.01$ (Table 1). Correlation between P values and the difference in the percentage of missing data between partitions was not significant ($\tau = -0.012$, $P = 0.876$). Moreover, the rate of rejection of the null at $P < 0.05$ was similar for the culled ($n = 40$) dataset and those matrices ($n = 45$) with more than 5% difference in missing data between partitions (11 and 16 significant results respectively; $G = 0.637$, $P = 0.425$). Logistic regression of the binary outcome of the IRD_{NND} test ($P < 0.05$ or otherwise) as above yielded no significant terms in the minimum adequate model.

The correlation between P values for the nearest neighbor and majority rule variants of the IRD test was highly significant ($P < 0.001$) but not particularly tight ($\tau = 0.387$). The latter offers a very imprecise proxy for the distances measured by nearest neighbors, and we do not advocate its use.

HIGHER TAXONOMIC DIFFERENCES IN CONGRUENCE

Partitioning datasets into six broad and inclusive taxonomic groups (Aves, other Ornithodira, Synapsida, other reptiles, amphibians [including early tetrapods], and fishes) revealed some significant differences (Fig. 5). In particular, synapsids and amphibians were less likely to have congruent partitions according to the ILD test than other groups ($G = 11.808$, $P = 0.038$;

Table 1. Summary statistics for the 85 vertebrate morphological datasets analyzed herein.

Author(s)	Year	Clade	Taxa	Cran. chars.	Post. chars.	Cran. miss %	Post. miss %	ILD	IRD _{NND}	Cran. CI	Post. CI	Cran. ci	Post. ci	Cran. HER	Post. HER
Bourdon et al.	2009	Palaeognathae	17	35	94	4.0	8.0	1.000	0.979	0.956	0.855	0.971	0.908	0.975	0.921
Clarke and Middleton	2008	Avialae	20	45	141	38.7	22.7	0.001	0.127	0.740	0.643	0.774	0.732	0.734	0.703
de Pietri et al.	2011	Charadriiformes	12	15	25	0.6	2.3	0.158	0.685	0.667	0.758	0.567	0.756	0.383	0.442
Hospitalache et al.	2007	Sphenisciformes	19	20	23	5.5	14.6	0.290	0.600	0.479	0.509	0.539	0.617	0.502	0.367
Manegold and Toepfer	2013	Picidae	27	20	47	1.7	0.4	0.485	0.005	0.710	0.458	0.816	0.647	0.904	0.761
Maurício et al.	2012	Rhynocriptidae	38	40	46	1.1	1.1	0.043	0.048	0.480	0.517	0.646	0.654	0.721	0.710
Mayr et al.	2010	Basal Psittaciformes	32	25	68	3.9	3.3	0.466	0.180	0.456	0.341	0.541	0.456	0.400	0.355
Mayr	2010	Caprimulgiformes	10	18	51	1.7	2.4	0.572	0.374	0.692	0.643	0.735	0.735	0.604	0.522
Mayr	2011	Pelagornithidae	25	19	39	21.3	8.1	0.002	0.071	0.431	0.388	0.569	0.419	0.494	0.426
Nesbitt et al.	2011	Strisores	20	36	61	13.6	23.1	0.002	0.002	0.656	0.447	0.756	0.566	0.753	0.379
O'Connor et al.	2009	Enantiornithines	19	40	152	43.7	29.7	0.067	0.557	0.712	0.578	0.760	0.699	0.608	0.565
Smith	2010	Pelecaniformes	53	94	370	5.3	2.7	0.845	0.865	0.493	0.441	0.622	0.581	0.804	0.799
Smith	2011	Mancallinae	54	51	163	3.5	6.7	0.063	0.175	0.214	0.212	0.313	0.331	0.511	0.581
Allain and Aquesbi	2008	Sauropods	18	62	150	31.1	21.5	0.006	0.009	0.683	0.686	0.756	0.790	0.662	0.682
Allain et al.	2012	Spinosaurids	23	75	94	19.5	24.7	0.044	0.025	0.514	0.579	0.649	0.675	0.516	0.656
Andres et al.	2010	Basal Pterosaurs	18	44	31	18.2	17.7	0.054	0.556	0.667	0.574	0.718	0.649	0.658	0.537
Burns et al.	2011	Ankylosaurs	17	45	15	12.8	36.9	0.365	0.024	0.548	0.704	0.661	0.661	0.527	0.439
Butler et al.	2008	Ornithischia	29	124	88	19.8	25.0	0.367	0.134	0.502	0.521	0.666	0.693	0.574	0.604
Carrano and Sampson	2008	Ceratosauria	12	66	76	36.3	31.9	0.304	0.451	0.863	0.769	0.924	0.846	0.854	0.690
Ezcurra and Cuneo	2007	Coelophysoidea	11	63	73	12.8	15.3	0.011	0.791	0.610	0.731	0.678	0.768	0.617	0.668
Gates and Sampson	2007	Hadrosaurinae	13	59	14	14.5	20.3	0.276	0.024	0.607	0.667	0.679	0.674	0.499	0.390
Godefroit et al.	2008	Hadrosauridae	15	30	7	9.3	8.5	1.000	0.003	0.918	1.000	0.958	0.956	0.927	1.000
Lü et al.	2010	Pterosauria	37	59	55	8.5	21.0	0.002	0.066	0.561	0.457	0.695	0.572	0.698	0.624
Lü et al.	2013	Oviraptoridae	17	108	69	31.1	33.2	0.002	0.001	0.756	0.516	0.837	0.581	0.760	0.315
Martinez and Alcobcer	2009	Dinosauria	12	28	70	33.6	27.7	0.067	0.779	0.732	0.560	0.780	0.677	0.544	0.251
Nesbitt et al.	2009	Early Dinosaurs	35	113	194	32.2	30.8	0.001	0.003	0.413	0.469	0.540	0.603	0.429	0.653
Nesbitt	2011	Archosaurs	55	166	223	23.1	28.2	0.001	0.030	0.402	0.413	0.576	0.562	0.592	0.706

(Continued)

Table 1. Continued.

Author(s)	Year	Clade	Taxa	Cran. chars.	Post. chars.	Cran. miss %	Post. miss %	ILD	IRD _{NND}	Cran. CI	Post. CI	Cran. ci	Post. ci	Cran. HER	Post. HER
Osi and Makadi	2009	Ankylosauria	15	43	14	20.3	32.9	0.117	0.216	0.537	0.643	0.626	0.598	0.502	0.827
Sereno	2008	Carcharodontosaurids	9	37	23	31.8	29.5	0.485	0.327	0.848	0.639	0.899	0.692	0.950	0.201
Smith and Pol	2007	Plateosauria	26	115	232	23.2	17.9	0.250	0.414	0.461	0.362	0.550	0.533	0.563	0.581
Sues and Averianov	2009	Iguanodontidae	25	100	38	11.9	24.4	0.265	0.014	0.650	0.672	0.280	0.305	0.838	0.827
Zanno et al.	2009	Therizinosauria	21	80	191	29.3	25.1	0.054	0.380	0.528	0.524	0.617	0.609	0.460	0.540
Asher et al.	2005	Lagomorpha	29	157	58	7.1	1.8	0.001	0.048	0.373	0.331	0.460	0.403	0.501	0.429
Asher and Hofreiter	2006	Afrotheria	20	90	22	9.0	4.4	0.795	0.617	0.406	0.441	0.487	0.445	0.404	0.325
Asher	2007	Eutheria	46	121	75	6.4	5.2	0.001	0.040	0.223	0.275	0.305	0.406	0.286	0.384
Beard et al.	2009	Amphipithecidae	22	216	55	17.0	37.6	0.004	0.478	0.305	0.569	0.503	0.555	0.426	0.427
Beck et al.	2008	Marsupiala	27	101	139	10.7	9.1	0.004	0.259	0.432	0.400	0.532	0.517	0.543	0.477
Bloch et al.	2007	Plesiadapiforms	12	98	61	3.2	17.3	0.001	0.062	0.401	0.627	0.531	0.702	0.337	0.295
Gaubert et al.	2005	Feliformia	39	229	100	1.1	3.1	0.001	0.500	0.356	0.335	0.266	0.219	0.497	0.519
Gaudin et al.	2009	Pholidota	16	298	90	14.8	23.3	0.528	0.155	0.339	0.325	0.598	0.658	0.522	0.532
Lister et al.	2005	Cervidae	10	21	41	0.5	1.7	0.729	0.410	0.750	0.623	0.778	0.659	0.418	0.261
Martinelli and Rougier	2007	Ictidosauria	16	65	17	10.9	31.3	0.088	0.001	0.674	0.770	0.790	0.778	0.646	0.837
Phillips et al.	2009	Monotremes	55	325	126	25.3	21.0	0.004	0.002	0.337	0.503	0.543	0.625	0.682	0.811
Pine et al.	2012	Oryzomyini	36	55	34	3.1	16.5	0.033	0.207	0.271	0.384	0.371	0.388	0.248	0.304
Pujos et al.	2007	Folivora	18	25	17	7.8	21.6	0.066	0.441	0.455	0.628	0.503	0.610	0.382	0.457
Sanchez-Villagra et al.	2006	Talpidae	17	73	83	4.7	4.3	0.003	0.010	0.495	0.549	0.587	0.652	0.445	0.609
Sigurdson et al.	2012	Bauroidea	20	95	20	8.3	35.8	0.507	0.049	0.520	0.706	0.638	0.725	0.588	0.597
Simmons and Conway	2001	Mormoopidae	16	103	106	16.0	14.0	1.000	0.974	0.650	0.659	0.539	0.586	0.679	0.685
Simmons et al.	2008	Chiroptera	25	48	154	16.9	21.7	0.201	0.559	0.445	0.419	0.524	0.521	0.525	0.459
Spaulding et al.	2009	Artiodactyla	37	353	137	17.6	21.0	0.018	0.711	0.235	0.307	0.326	0.444	0.288	0.444
Brochu et al.	2010	Crocodyloidea	24	57	23	7.3	14.1	0.032	0.030	0.598	0.540	0.703	0.530	0.658	0.464
Cheng et al.	2012	Sauroptrygia	35	69	70	10.7	14.0	0.463	0.830	0.401	0.405	0.503	0.471	0.471	0.586

(Continued)

Table 1. Continued.

Author(s)	Year	Clade	Taxa	Cran. chars.	Post. chars.	Cran. miss %	Post. miss %	ILD	IRD _{NND}	Cran. CI	Post. CI	Cran. ci	Post. ci	Cran. HER	Post. HER
Gaffney et al.	2009	Bothremyridae	23	100	50	18.0	27.1	0.001	0.186	0.686	0.727	0.789	0.800	0.733	0.729
Hill	2005	Amniota	19	124	150	1.4	4.6	0.457	0.616	0.550	0.620	0.655	0.729	0.664	0.737
Ji et al.	2013	Ichthyosauria	23	42	56	27.4	16.9	0.024	0.001	0.620	0.716	0.655	0.808	0.653	0.822
Lee and Scanlon	2002	Serpentes	21	204	53	9.9	4.3	0.882	0.209	0.505	0.522	0.627	0.569	0.548	0.472
Li et al.	2007	Squamata	23	212	97	8.1	15.1	0.099	0.389	0.536	0.511	0.644	0.614	0.591	0.447
Lyson and Joyce	2009	Baenidae	10	31	17	11.2	14.7	0.960	0.155	0.672	0.708	0.753	0.755	0.503	0.571
Matsumoto et al.	2009	Choristodera	14	49	29	14.6	13.3	0.002	0.728	0.647	0.571	0.704	0.558	0.611	0.424
Muller and Reisz	2006	Eureptiles	24	58	19	12.3	16.3	0.171	0.028	0.418	0.468	0.479	0.309	0.347	0.399
Palci et al.	2013	Serpentes	26	181	29	15.4	13.4	0.613	0.945	0.468	0.595	0.594	0.639	0.570	0.662
Parilla-Bel et al.	2013	Metriorhynchoidea	29	139	59	25.0	38.3	0.191	0.005	0.582	0.862	0.692	0.883	0.743	0.918
Sues & Reisz	2008	Parareptilia	12	34	9	10.3	38.8	0.034	0.004	0.731	0.750	0.797	0.657	0.738	0.631
Tsuji & Mueller	2013	Pareiasauria	21	64	50	22.3	36.3	0.118	0.066	0.755	0.793	0.811	0.847	0.772	0.795
Vieira et al.	2005	Corytophanidae	12	40	28	0.8	0.3	0.485	0.625	0.788	0.673	0.829	0.745	0.819	0.597
Anderson et al.	2008	Batrachia	52	143	76	18.4	29.3	0.001	0.911	0.254	0.285	0.347	0.367	0.407	0.379
Holland and Long	2009	Tetrapodomorpha	12	54	41	8.5	21.3	0.009	0.093	0.800	0.710	0.843	0.774	0.777	0.655
Ruta and Coates	2007	Lissamphibia	46	189	104	20.9	15.7	0.001	0.196	0.320	0.314	0.466	0.470	0.460	0.463
Skutchas and Gubin	2012	Salamanders	21	16	40	18.5	34.2	0.067	0.015	0.565	0.491	0.512	0.558	0.283	0.276

(Continued)

Table 1. Continued.

Author(s)	Year	Clade	Taxa	Cran. chars.	Post. chars.	Cran. miss %	Post. miss %	ILD	IRD _{NND}	Cran. CI	Post. CI	Cran. ci	Post. ci	Cran. HER	Post. HER
Vallin and Laurin	2004	Stegocephalia	47	99	60	15.8	26.7	0.002	0.028	0.355	0.417	0.435	0.538	0.584	0.544
Venczel	2008	Caudata	15	19	16	1.8	12.5	1.000	0.145	0.538	0.783	0.596	0.854	0.516	0.876
Choo	2011	Actinopterygii	27	51	26	12.4	16.4	0.635	0.460	0.424	0.448	0.550	0.600	0.464	0.451
Dutel et al.	2012	Actinistia	30	83	23	29.1	22.1	0.904	0.288	0.424	0.500	0.566	0.548	0.523	0.442
Friedman	2007	Actinistia	25	136	40	25.0	36.6	0.003	0.150	0.464	0.523	0.631	0.691	0.580	0.511
Friedman	2008	Pleuronectiformes	19	16	42	19.4	8.9	0.284	0.223	0.548	0.526	0.599	0.595	0.423	0.608
Hilton and Forey	2009	Acipenseriformes	18	31	17	6.5	6.5	0.661	0.010	0.634	0.724	0.751	0.740	0.670	0.739
Hurley et al.	2007	Actinopterygii	24	53	16	19.3	17.4	0.484	0.001	0.506	0.562	0.632	0.606	0.562	0.421
Inamura et al.	2005	Cottoidei	8	16	15	0.0	0.0	0.353	0.273	0.640	0.700	0.656	0.810	0.390	0.601
Lopez-Arbarello	2011	Ginglymodi	29	65	19	24.0	15.4	0.321	0.071	0.454	0.471	0.612	0.489	0.576	0.477
Parenti	2008	Adriamichthyidae	31	37	43	0.6	8.8	0.574	0.565	0.677	0.584	0.844	0.644	0.778	0.688
Shimada	2005	Lamniformes	16	40	15	12.7	1.3	0.214	0.284	0.525	0.810	0.552	0.769	0.551	0.860
Sparks	2008	Etoplinae	25	25	55	0.8	4.0	0.593	0.474	0.867	0.707	0.890	0.833	0.962	0.925
Swartz	2009	Actinopterygii	22	28	31	20.5	21.7	0.309	0.088	0.552	0.581	0.705	0.727	0.472	0.607
Wilson and Murray	2008	Osteoglossomorpha	24	50	37	17.6	23.2	0.769	0.820	0.522	0.571	0.614	0.603	0.593	0.591
Xu and Gao	2011	Scanilepiformes	22	45	27	21.3	16.5	0.210	0.110	0.509	0.604	0.680	0.716	0.470	0.587

Dataset dimensions (numbers of taxa [ntax] and informative characters [nchar]) refer to the pre-processed matrices after applying safe taxonomic deletion rules (see text for details). “Cran. chars.” and “Post. chars.” denote characters per partition. “Cran. miss %” and “Post. miss %” report the percentage of missing data cells for partitions. “ILD” column reports the P-value resulting from an ILD test with 999 random partitions. IRD columns report the P values resulting from IRD_{NND} tests with 999 random partitions. “IRD_{NND}” denotes the results of the IRD test using the RF tree-to-tree distance for nearest neighboring trees. ci columns give ensemble consistency indices for partitions of the dataset (craniodental or postcranial). Similarly, ci columns report the mean per character consistency indices for partitions of the dataset (craniodental or postcranial) when optimized onto the globally most parsimonious trees. HER gives the homoplasy excess ratio for partitions of the dataset (craniodental or postcranial) derived from 999 randomized matrices. An expanded version of this table containing additional statistics is provided within the Supporting Information.

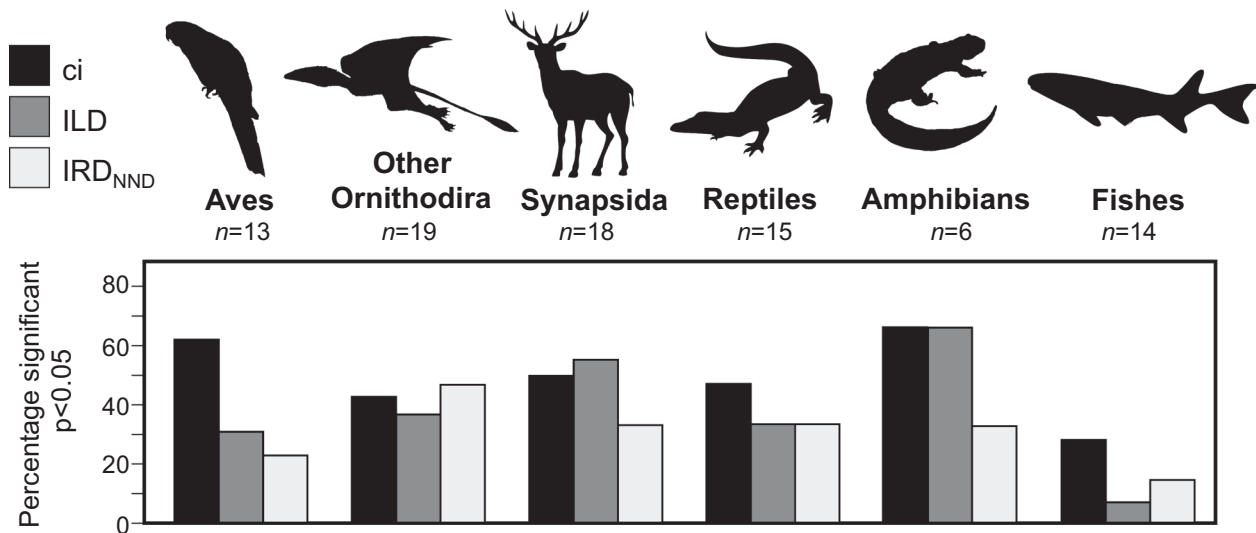


Figure 5. Summary of results from three partition homogeneity tests, subdivided by higher taxonomic group. Black bars denote significant ($P < 0.05$) differences in ci values between partitions (Mann–Whitney U -tests). Gray bars denote significant ILD results, while light gray bars indicate significant IRD_{NND} results. Images from phylopic.org (courtesy of M. Scroggie, O. Sanisidro, B. Kimmel, and S. Coombs). Salamander and pterosaur courtesy of M. Reinbold (modified by T. Michael Keesey) and M. Witton (<http://creativecommons.org/licenses/by-sa/3.0/>).

Table 2). However, there were significant differences in the log of the number of characters across groups ($F = 3.095$, $P = 0.013$), largely accounted for by the contrast between synapsids and fishes (Tukey HSD, $P = 0.003$). Taxonomic group was not significant as a factor in logistic regression models, and the residuals from models omitting taxonomic group membership retained no differences between groups (Kruskal–Wallis $\chi^2 = 2.976$, $P = 0.704$). A broadly similar taxonomic pattern was observed for the IRD_{NND} test, although differences in frequencies of null rejection across higher taxa were not significant ($G = 4.283$, $P = 0.510$).

Discussion

CRANIODENTAL AND POSTCRANIAL PARTITIONS CONTAIN SIMILAR LEVELS OF HOMOPLASY

It is well known that the CI is negatively correlated with the number of taxa in a matrix (Archie 1989; Sanderson and Donoghue 1989; Faith and Cranston 1991; Klassen et al. 1991), but it also has a weaker, negative relationship with the number of characters (Archie 1989, 1996; Archie and Felsenstein 1993). Despite the greater number of craniodental characters than postcranial characters across our sample of datasets, we found no significant difference in CI (paired $t = 1.184$, $P = 0.240$). Unsurprisingly, when modeling out both data matrix dimensions (numbers of taxa and characters) and the percentage of missing data (+1) across all 170 partitions, residual CI values were even more similar (for residuals: $t = 0.917$, $P = 0.362$). HER values were also similar in the craniodental ($\bar{x} = 0.582$) and postcranial skeleton ($\bar{x} = 0.571$; paired $t = 0.621$, $P = 0.537$).

We note that the absence of a clear difference between craniodental and postcranial levels of homoplasy does not necessarily imply that *additional* characters of equivalent phylogenetic informativeness can be garnered from the two partitions with comparable ease. One partition may have been exhausted with considerable care, the other not. Our conclusions therefore necessarily relate to the *coded* data. We also note that a high CI within a partition could be the result of a strong phylogenetic signal, or the developmental nonindependence of characters. Distinguishing between these causes requires detailed developmental and underpinning genetic knowledge, which are often unavailable.

PARTITIONS HAVE INCONGRUENT SIGNALS MORE OFTEN THAN WE EXPECT

Our ILD test results demonstrate that our partitions are incongruent about one time in three: 31 from 85 datasets. Assuming a significance level (false-positive rate) of 5%, we would expect four or five datasets to be significantly incongruent by chance. Significant incongruence is therefore detected across our sample of datasets (binomial test $P < 0.001$, assuming a 5% false-positive error rate), although this is partly accounted for by differences in partition parameters. We make no inferences concerning the overall quality of individual datasets on the strength of these results, and note that partitions were imposed by us in each case (rather than reflecting distinctions made by the original authors).

Table 2. Number of data matrices in higher taxonomic groups, with a tally of those with significant ($P < 0.05$) results for various partition homogeneity tests.

Taxonomic group	Aves	Other ornithodira	Synapsida	Other reptiles	Amphibians	Fishes	Log likelihood ratio (G)	P
No. datasets	13	19	18	15	6	14	–	–
ci sig. diff. $P < 0.05$	8	8	9	7	4	4	4.283	0.510
ILD, $P < 0.05$	4	7	10	5	4	1	11.808	0.038
IRD _{NND} , $P < 0.05$	3	9	6	5	2	2	4.801	0.441
IRD _{MR} , $P < 0.05$	1	7	5	3	0	1	9.522	0.090

G -test and P values quoted for the null that significant results are equally likely in the five higher taxonomic groups in each case.

CRANIODENTAL AND POSTCRANIAL PARTITIONS OFTEN IMPLY SIGNIFICANTLY DIFFERENT RELATIONSHIPS

Results from the incongruence relationship difference (IRD_{NND}) tests were broadly similar to those from the ILD test: 32% of datasets yielded significantly different trees from the two partitions. As with the ILD test, we would expect just three or four datasets (5%) to reject the null by chance (a highly significant difference: binomial test $P < 0.001$). Our empirical sample suggests that the IRD_{NND} test using the RF distance is less likely to yield a significant result than the ILD, and is less susceptible to differences in partition size and differences in levels of missing data. The IRD_{NND} therefore has certain advantages over the ILD, and also offers a more intuitive index of congruence (i.e., one based directly on differences in topological branching structure rather than differences in tree length). We note, however, that the IRD_{NND} is insensitive to differences in branch lengths. Many authors have identified difficulties with the ILD test (Dolphin et al. 2000; Hipp et al. 2004; Planet 2005, 2006; Ramirez 2006) and we do not repeat these here.

As with all similar metrics, the IRD is to some extent arbitrary (Wheeler 1999). Different indices of tree-to-tree distances will yield different distances and P values, and the IRD can be implemented with many such measures. For example, the RF distance penalizes distant and shallow branch transpositions much more strongly than close and shallow transpositions, whereas the maximum agreement subtree distance (Finden and Gordon 1985), for example, makes only a marginal distinction between these two cases. Similarly, the maximum agreement subtree distance is less sensitive to the depth of the transposition (Cobbett et al. 2007). Alternative metrics will have other, and perhaps more desirable, properties (Lin et al. 2011). Our choice of the RF distance here was partly pragmatic, as it is computationally less demanding than most alternatives.

WHAT DOES PARTITION INCONGRUENCE IMPLY?

In studying the evolution of form, it is now relatively common to recognize anatomical modules (Mitteroecker and Bookstein

2007, 2008; Cardini and Elton 2008; Klingenberg 2008; Lü et al. 2010; Goswami et al. 2011, 2015; Hopkins and Lidgard 2012; Cardini and Polly 2013). These are regions of the body (or suites of landmarks) within which morphological changes are strongly correlated through evolutionary time, but between which there is significantly less coordination. Different selective forces may operate on these modules or components of the mosaic (Gould 1977; Maynard Smith 1993; Kemp 2005; Lü et al. 2010), and they may therefore exhibit different evolutionary rates and trends (Mitteroecker and Bookstein 2007, 2008; Klingenberg 2008). In the context of phylogenetic characters, differing pressures on modules may favor particular patterns of convergence and homoplasy, and therefore suites of characters that imply different trees (Clarke and Middleton 2008). The skull of many tetrapod groups has often been regarded as biomechanically and functionally somewhat independent of the rest of the skeleton (Ji et al. 1999; Koski 2007; Mitteroecker and Bookstein 2008), hence the difficulty of making many inferences about the one from the other. We note that fishes have the lowest overall incongruence between partitions and the most similar levels of per character ci (Fig. 5). This may result from greater functional and biomechanical integration between the head and trunk in fishes compared with other vertebrate groups (i.e., fishes lack a functional neck; Klingenberg 2008; Larouche et al. 2015).

We note that while anatomical modules are usually envisaged as physically proximate suites of landmarks or characters, it is possible for characters to evolve in a coordinated manner across the body as the result of particular selective pressures (Kemp 2007). For example, adaptations for swimming, digging, or flying (Gardiner et al. 2011; Abourachid and Hofling 2012; Allen et al. 2013) might entail correlated suites of change across the body in a manner that would not be apparent from studying straightforward divisions into body regions (e.g., head, body, and limbs). Developmental regulatory processes may also entail counterintuitive suites of coordinated character change across the body (Chase et al. 2002; Kharlamova et al. 2007), but our objective was not to test for such suites of correlations here.

In the most general terms, character selection and coding clearly has an impact upon inferred phylogeny. Most straightforwardly, alternative datasets for identical sets of taxa can yield different trees (Freitas and Brown 2004; Munoz-Duran 2011; Penz et al. 2013), and this argues strongly for the synthesis of all characters. More generally, systematists rightly exercise their judgment in deciding which aspects of morphology to codify as putative homologies. Wings in birds, bats, and pterosaurs are not considered homologous as wings *a priori* (although they are as *limbs*) because the weight of evidence unambiguously rules this out (and in the absence of any formal analysis). In many cases, however, the decision is less straightforward, and the *a priori* omission of characters believed to be strongly homoplastic may unintentionally overlook useful signal at some level in the tree. Finally, it is often observed empirically that the tree(s) derived from a given matrix can alter markedly with the omission, reweighting, or ordering of characters (Wills 1998), such that even modest perturbations to the data yield large changes to the resulting trees.

In morphological phylogenetics, it is usual to combine all available data (Kluge et al. 1989). Our results therefore reinforce the importance of this approach. Although the patterns inferred from particular organ systems or suites of characters may be misleading (in the same way and for the same reasons that individual characters may merely introduce homoplasy and noise), combined analysis of all available characters often allows a globally strong phylogenetic signal to emerge from conflicting local homoplasy (Gatesy et al. 1999). We demonstrate that in vertebrate studies of this type, an exclusive focus upon characters of either the cranium or postcranium (at the expense of those of the other partition [e.g., Fitzgerald (2010; craniodental only) and Mayr and Mourer-Chauvire 2004 [postcranial only]]) will significantly influence the resultant optimal tree(s) about 30% of the time, irrespective of major group. We therefore strongly advocate garnering character data intensively from all anatomical regions whenever possible.

When analyzing fossils, it is usually impossible to sample across the same suite of characters that would ideally be coded for extant species (Wiens 2003a,b; Cobbett et al. 2007). For example, in fossil crocodyliforms, the vast majority of characters are coded from the skull (e.g., O'Connor et al. 2010; Turner and Sertich 2010; Cau and Fanti 2011; Hastings et al. 2011; Puertolas et al. 2011) and it is difficult to be confident that we are not merely inferring a “craniodental” tree. The only (and indirect) way to test this would be to conduct parallel analyses upon the closest living representatives of the clade. However, the (quite possibly limited) utility of this approach depends upon the phylogenetic proximity of the extant exemplars, the presumed constancy of selective pressures on putative modules through time and across clades (a big assumption: Hunt 2008; Frazzetta 2012), and the similarity of the available coded data. A related issue in the context of fossil vertebrates is the preferential preservation of hard part charac-

ters (bones rather than muscles or other more volatile tissues). An analogous concern, therefore, is whether skeletal and soft-part characters convey a consistent phylogenetic signal (Diogo 2004). If they do not, then this has implications for the manner in which fossil vertebrates are interpreted and analyzed (Sansom et al. 2010; Sansom and Wills 2013; Pattinson et al. 2014) and is an area particularly needing detailed future work.

Conclusions

1. Systematists typically abstract significantly more characters from the skull than the rest of the skeleton. However, tests for levels of homoplasy in the craniodental and postcranial partitions of our sample of 85 matrices revealed no significant differences, irrespective of how homoplasy was measured. Systematists appear to be coding characters of similar internal consistency from both regions of the body. It is unclear to what extent the bias toward coding craniodental characters reflects a real bias in their distribution, the availability of material, or arises from the preconceptions of systematists.
2. Craniodental and postcranial character partitions exhibited significant incongruence (ILD tests) in 31 of our 85 sample datasets. Likewise, our new IRD_{NND} test found significantly different relationships in 27 from 85 cases.
3. Although vertebrate systematists sometimes code morphological characters preferentially from particular anatomical regions (through necessity or by choice), received wisdom is that a broad and unbiased sampling is usually preferable when possible. Here, we provide empirical evidence for this view. Our results strongly support dense sampling of characters from across the vertebrate skeleton.
4. The IRD_{NND} test appears to be less sensitive to differences in numbers of characters or amounts of missing data between partitions than the ILD test. We advocate its use as an ancillary test for addressing differences in implied relationships between data partitions.
5. There were significant differences in the distribution of significant partition inhomogeneity across higher taxonomic groups, as measured by the ILD test. Synapsids and amphibians were less likely to have congruent craniodental and postcranial partitions than other groups. However, these differences were no longer significant when the imbalance in partition size was modeled out. Neither were the relationships inferred from craniodental and postcranial characters more likely to conflict significantly in some higher taxa than in others (IRD_{NND} test). Our findings therefore have some generality across vertebrates.

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