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34 **Abstract**

35 Despite the increasing importance of molecular sequence data, morphology still makes an important

36 contribution to resolving the phylogeny of many groups, and is the only source of data for most

37 fossils. Most systematists sample morphological characters as broadly as possible on the principle of

38 total evidence. However, it is not uncommon for sampling to be focussed on particular aspects of

39 anatomy, either because characters therein are believed to be more informative, or because

40 preservation biases restrict what is available. Empirically, the optimal trees from partitions of

41 morphological data sets often represent significantly different hypotheses of relationships. Previous

42 work on hard-part versus soft-part characters across animal phyla revealed significant differences in

43 about a half of sampled studies. Similarly, studies of the craniodental versus postcranial characters

44 of vertebrates revealed significantly different trees in about one third of cases, with the highest

45 rates observed in non-avian dinosaurs. We test whether this is a generality here with a much larger

46 sample of 81 published data matrices across all major dinosaur groups. Using the incongruence

47 length difference (ILD) test and two variants of the incongruence relationship difference (IRD) test,

48 we found significant incongruence in about 50% of cases. Incongruence is not uniformly distributed

49 across major dinosaur clades, being highest (63%) in Theropoda and lowest (25%) in Thyreophora.

50 Our partition tests are not sensitive to the size of the tree, to differences in partition size, to the

51 amount of missing data in the matrix, difference in the amount of missing data between partitions or

52 the difference in levels of homoplasy between partitions. Incongruence must therefore reflect

53 differences in *patterns* of homoplasy between partitions, which may itself be a function of

54   modularity and mosaic evolution. Finally, we implement new tests to determine which partition

55   yields trees most similar to those from the entire matrix. Despite no bias across dinosaurs overall,

56   there are striking differences between major groups, with the craniodental characters of

57   Ornithischia and the postcranial characters of Saurischia yielding trees most similar to the 'total

58   evidence' trees derived from the entire matrix.

59   **Introduction**

60   The fossil record is notoriously incomplete, not only in terms of diversity and species richness

61   (Verriere et al., 2016; Davies et al., 2017; Tutin and Butler, 2017), but also with respect to

62   stratigraphy (Maxwell and Benton, 1990; Dunhill et al., 2012; Brocklehurst and Froebisch, 2014;

63   O'Connor and Wills, 2016b; Verriere et al., 2016) palaeobiogeography (Lieberman, 2002; Ksepka and

64   Boyd, 2012; Davies et al., 2017), palaeoecology (Stanley et al., 1989; Jablonski, 2005) and behaviour

65   (Hsiang et al., 2015; Daley and Drage, 2016; Fan et al., 2017). However, it is organismal

66   incompleteness – the selective preservation of tissues and body regions – that impinges most

67   directly on attempts to infer phylogeny (Kearney and Clark, 2003; Cobbett et al., 2007; Sansom,

68   2015). The fossil record of non-avian dinosaurs mostly comprises bones and other hard parts (Wills

69   et al., 2008a; Mannion and Upchurch, 2010), but there are further biases towards the preservation

70   of more heavily mineralised and massive elements (e.g., limb bones) at the expense of more

71   frangible and delicate structures (e.g., skulls). Inferred relationships may differ substantially

72   depending upon which subsets of characters are used, but palaeontologists may nonetheless wish to

73   infer the relationships of dinosaurs described from partial skeletal material.

74   We therefore address four related questions using a sample of 81 cladistic taxon-character matrices

75   published between 2011 and 2017, each comprising both craniodental and postcranial characters.

76   Firstly we determine whether levels of homoplasy differ between characters of the skull and

77   dentition on one hand and characters pertaining to the body on the other. Any such difference

78   might be used to argue for the superiority of one body region over the other for phylogenetic

79 inference (Pettigrew, 1991; Sanchez-Villagra and Williams, 1998; Williams, 2007; Song and Bucheli,

80 2010; Mounce et al., 2016; Parker, 2016). Secondly we use established (incongruence length

81 difference, ILD; Farris et al., 1994) and more recent (Mounce et al., 2016; Sansom et al., 2017) tests

82 to determine whether the most parsimonious trees inferred from craniodental and postcranial

83 character partitions are significantly different (Mounce et al., 2016; Sansom et al., 2017). Thirdly, we

84 ask whether there are differences in the incidence of significant craniodental/postcranial

85 incongruence across major taxonomic groups. Fourthly, we present a novel test to determine

86 whether the tree(s) inferred from craniodental characters or the tree(s) derived from

87 postcraniodental characters are more similar to those derived from the entire matrix, with the latter

88 being used as a proxy for the 'true' phylogeny. We do this by resampling from the partitions and the

89 entire matrix in order to control for differences in the number of characters in each partition.

90

91 **What is the rationale for comparing the signals within partitions of characters?**

92 Suites of morphological characters are often functionally and developmentally integrated into

93 modules (Clarke and Middleton, 2008; Klingenberg, 2008; Lue et al., 2010) that can be subject to

94 different selection pressures and consequently evolve at different speeds (J, 1993; Lue et al., 2010;

95 Parker, 2016). This has consequences for the rate at which new character states are utilised and the

96 subsequent exhaustion of character space (Wagner, 1995; Wagner, 1997; Oyston et al., 2015;

97 Oyston et al., 2016), resulting in different levels of homoplasy. For example, it has been shown that

98 the dental characters of mammals are particularly labile and prone to convergence/reversal

99 (Sanchez-Villagra and Williams, 1998; Sansom et al., 2017), which is explicable in terms of the strong

100 functional and biomechanical constraints upon the form and arrangement of teeth. This particular

101 bias is unfortunate given the predominance of teeth in the mammal fossil record. More generally,

102 the craniodental and postcranial characters of vertebrates have been shown to contain significantly

103 incongruent signals about one time in three (Mounce et al., 2016). Moreover, it is possible that

104   incongruence is partly a function of the extent to which the skull and the rest of the body are

105   biomechanically decoupled (Ji, Q. et al. 1999). Fishes (lacking a functional neck) typically show

106   integration, while the most striking incongruence has been observed in some of the long-necked

107   dinosaur groups.

108   As a prerequisite for combining data in early, multi-gene molecular analyses, systematists commonly

109   checked for homogeneity of signal across loci using a variety of partition tests (Templeton, 1983;

110   Rodrigo et al., 1993; Farris et al., 1994). This practice is rarely implemented nowadays, and for

111   principally three reasons (Cunningham, 1997). Firstly, as analyses of increasingly large numbers of

112   genes graded into phylogenomic studies, the concept of the contingent inclusion of individual genes

113   became largely obsolete. Secondly, more advanced analytical methods were developed that allow

114   heterogeneous rates across sites and branches to be modelled rigorously (Damgaard, J. 2012).

115   Thirdly, a consensus emerged amongst systematists in favour of the simultaneous analysis of all

116   available character data, on the principle of 'total evidence' (Kluge, 1989), not least because of

117   'hidden support'. This is the phenomenon whereby signals that are weak within particular partitions

118   of the data may be common to many (or all) such partitions, such that they become the dominant

119   signal when all partitions are analysed together (Kluge, 1989; Gatesy et al., 1999; Gatesy and

120   Arctander, 2000; Wahlberg et al., 2005; O'Leary and Gatesy, 2008; Padial et al., 2010; Damgaard,

121   2012; Mounce et al., 2016).

122   Despite the ascendance of molecular phylogenetics, morphological character data can still

123   contribute to our understanding of the relationships of many groups (Houde, 1994; Wiens, 2004;

124   O'Leary and Gatesy, 2008; Nicolalde-Morejon et al., 2009; Gainett et al., 2014; Lopardo and

125   Hormiga, 2015). Moreover, for extinct and particularly for fossil groups, morphology is usually the

126   only direct source of phylogenetic data, notwithstanding exceptional cases utilising sub-fossil DNA

127   (Dabney et al., 2013; Shapiro and Hofreiter, 2014; Orlando et al., 2015).

128

Materials & Methods

Datasets

The character matrices utilised here were obtained from peer-reviewed papers published between

2000 and 2017. We utilised Graeme Lloyd's online compilation of matrices (Lloyd, 2018) and

searches of Web of Science using the keywords phylog* and evolution* in combination with any

higher taxonomic name of non-avian dinosaurs. We sought to sample all major dinosaur groups,

including matrices of varying dimensions sampled at different taxonomic levels. We initially included

104 matrices, but these were further checked for overlap since systematists often repurpose data or

otherwise add modest numbers of novel taxa and sometimes characters to existing studies. In order

to remove any such pseudoreplication from our sample, each data set was compared with every

other, and for each pair the number of matrix cells in common (replicated taxa and characters) was

expressed as a percentage of the total number of cells in the smaller of the two matrices. For pairs

with 20% or more overlap, the least inclusive (or otherwise the oldest) was removed from

consideration, reducing our sample to 81 data sets (See Supplementary Materials 1 for the

percentage of character and species overlap between all pairs). Character lists were then used to

define partitions. The "craniodental" partition included all characters pertaining to the skull and

dentition. The "postcranial" partition encompassed all characters of the vertebral column, girdles

and limbs.

Poorly known taxa, or those that are otherwise scored for only a small number of characters, can be

highly mobile within parsimony trees. This, in turn, can result in large numbers of MPTs, prohibitively

extending search times, and yielding poorly resolved consensus trees (Wilkinson, 1995; Mounce et

al., 2016). Where such complications were found in our analyses, the matrix was edited by removing

taxa with more than 40% of characters scored as missing ("?") or non-applicable ("-") in either

partition. Any characters rendered uninformative or invariant by this process were also deleted

(Wiens, 1998). On average, 20 taxa and 18 characters were removed from each dataset in this way,

154   equating to 33% of taxa and 7% of characters. For a list of characters and taxa discounted, see

155   Supplemenary Materials 2. Matrices were manipulated using Mesquite Version 3.04 (build 725) for

156   Macintosh. The resulting sample of 81 matrices contained an average of 26 taxa scored for a mean

157   of 115 craniodental and 133 postcranial characters.

158   **Measuring homoplasy**

159   The ensemble Consistency Index (CI)(Kluge and Farris, 1969) is a commonly used and well-

160   characterised index of homoplasy, and was calculated here to compare levels of homoplasy across

161   partitions. However, the CI suffers from well-documented drawbacks, notably its correlation with

162   the number of characters and taxa in the dataset (Archie, 1989; Mounce et al., 2016). We remove

163   these biases empirically here, using the residuals from regression analyses of CI on both matrix

164   dimensions. In addition, we report the ensemble Retention Index (RI)(Kluge and Farris, 1969) as a

165   measure of retained synapomorphy. All indices were calculated in PAUP* 4.0a.154 for Macintosh

166   (Swofford, 2017).

167   **Statistical tests for congruence**

168   The Incongruence Length Difference (ILD) test (Mickevich and Farris, 1981; Farris et al., 1995) is a

169   widely implemented partition homogeneity test based upon the difference in most parsimonious

170   tree length for a matrix when analysed as a whole, and the sum of MPT lengths for the partitions of

171   the matrix analysed in isolation (MPTs) (Norman et al.) More formally, the ILD for a bipartitioned

172   matrix is given by $L_{AB} - (L_A + L_B)/L_{AB}$, where L_{AB} is the optimal tree length (in steps) from the analysis of

173   the entire matrix (the total evidence analysis), and L_A and L_B are the optimal tree lengths for

174   partitions A and B analyzed independently (Figure 1). This ILD is compared with a distribution of ILD

175   values (here, 999) for random bipartitions of the matrix in the same proportions as the original, and

176   a p value is derived from the fraction of these as large or larger than the original. The ILD test has

177   been criticized on philosophical grounds, and because it has a high Type I error rate(Dolphin et al.,

178   2000; Barker and Lutzoni, 2002; Ramirez, 2006; Sansom et al., 2017). However, it remains very

179   widely applied (Mounce et al., 2016) and is used here as a measure of matrix partition incongruence

180   rather than as a criterion for combining those partitions.

181   In addition to the ILD test, we also implemented the incongruence relationship difference (IRD) test

182   of Ruta & Wills (2016) and Mounce et al. (2016). This is analogous to the ILD test in that a measure

183   of incongruence for the original data partition is compared with a distribution of incongruence

184   values for a large number of random partitions. However, whereas for the ILD incongruence is

185   measured in terms of additional tree length, a tree-to-tree distance metric is used for the IRD. Many

186   such metrics are available, but here we used the symmetrical-difference (RF) distance

187   (IRD_{RF})(Robinson and Foulds, 1981) and matching (MD) distance ($IRD_{Matching}$) (Lin et al, 2012). The RF

188   distance is well characterised and widely applied but prone to saturation, while the matching

189   distance has a particularly favourable distribution and other theoretically desirable properties. It is

190   unusual for a single most parsimonious tree (Norman et al.) to result from a parsimony search, and

191   we therefore followed Mounce *et al.* (2016) in calculating the mean nearest neighbour distance

192   (NND) between each tree resulting from one partition and the most similar tree in the other

193   partition. In addition, we calculated the distances between strict, semi-strict and 50% majority rule

194   (plus compatible groupings) trees for the two partitions, although we caution that these offer poor

195   or summaries of the differences between sets of trees (Mounce et al., 2016). IRD tests were initially

196   based upon 99 random partitions of the data (c.f. 999 for the computationally much faster ILD).

197   However, in those cases where p≤0.10, we re-ran the test for that matrix using 499 random

198   partitions).

199   All parsimony searches were implemented using 25 random additions of taxa, followed by tree

200   bisection and reconnection branch swapping, and retaining 10 trees at each step. We also

201   condensed the resulting most parsimonious trees by collapsing branches with a minimum length of

202   zero (Goloboff's 'amb-') and removing all but one of any consequently identical trees. To expedite

203   the searches, we limited the number of trees stored in memory to 100,000, and for the IRD tests we

204   calculated nearest neighbour tree-to-tree distances based upon no more than 1,000 most

205   parsimonious trees (MPTs) from each partition (1,999,000 tree-to-tree distances calculated for each

206   metric in order to find the minima). We further checked that fewer than 1,000 MPTs were found

207   from the analysis of the original partitions, and from no more than 5% of the randomised partitions.

208   Consensus trees were calculated from all MPTs, up to the 100,000 limit. All analyses were carried

209   out in PAUP* 4.0a.154 for Macintosh (Swofford, 2017), and with the use of scripts (see ESM) that

210   produced batch files for PAUP* and summarised it's logged output.

211

212   **Determining whether craniodental or postcraniodental characters yield trees more similar to**

213   **those from the entire data matrix**

214   In cases where the tree(s) inferred from craniodental and postcranial characters differ (and

215   especially where these differences are significant), it is reasonable to ask which tree is likely to be

216   most accurate. Unfortunately, there are no objective tests of phylogenetic accuracy, except in those

217   exceptional cases where phylogeny is known (e.g., laboratory cultures or simulated data sets). One

218   approach for extant taxa (Sansom et al., 2017) is to determine the congruence of suites of

219   morphological characters with a robustly supported molecular tree for the same taxa (an

220   independent data source). However, this assumes that the molecular tree is likely to offer the best

221   approximation of the truth: a standpoint defended in many quarters (Scotland et al., 2003; Olmstead

222   and Scotland, 2005; Wortley and Scotland, 2006; Zou and Zhang, 2016). For fossil taxa, stratigraphic

223   congruence may be used as an ancillary criterion for choosing between alternative trees (Wills,

224   1998; Wills et al., 2009; O'Connor and Zhou, 2013; O'Connor and Wills, 2016a), but this is only

225   defensible where the fossil record is relatively complete, or at least where the order of first

226   occurrences for lineages is preserved with reasonable fidelity (Wills et al., 2008b; Wills et al., 2009).

227   Here, we ask whether trees from the craniodental or postcranial data partition are most similar to

228   those derived from the entire data matrix, with the underlying assumption that the total evidence

229   tree is likely to be the most accurate (Kluge, 1989; Gatesy et al., 1999; Gatesy and Arctander, 2000).

230   A straightforward approach would be to calculate mean nearest neighbour tree-to-tree distance

231   metrics for the craniodental to entire tree sets versus the postcranial to entire tree sets. However,

232   *all other things being equal*, a larger partition contributes more characters to the entire matrix than

233   a smaller one. In cases where the optimal trees for the two partitions differed, the larger partition

234   might therefore be expected to yield trees more similar to those from the entire data set. The

235   difference in character numbers in the partitions could be overcome by differential weighting of

236   characters, but the tree-to-tree distance metrics utilised here are sensitive to the reductions in

237   resolution that are likely as the character:taxon ratio declines (and this is not overcome by

238   weighting). We therefore adopted a resampling approach, repeatedly jack-knifing characters at the

239   sample size of the smallest partition (n) from both the larger partition and the entire matrix. For the

240   entire matrix, we randomly jack-knifed the same number of characters ($n/2$) from both the

241   craniodental and postcranial partition, such that neither was favoured with a larger sample size.

242   Where n was an uneven number, we alternately sampled the 'additional' character from either

243   partition. For each of 100 resamplings, we then calculated the mean nearest neighbour distance

244   between craniodental and entire trees, and the mean nearest neighbour distance between

245   postcranial and entire trees. We report the median of these 100 comparisons (which partition is

246   closest to the entire), as well as Mann-Whitney test results to approximate a p value at which to

247   reject the null that the medians of these distances are the same.

248   **Results**

249   **1. Craniodental and postcranial characters contain similar levels of homoplasy and retain similar**

250   **amounts of synapomorphy**

251   Statistics and test results for all data sets are given in Table 1, and we distil these further in Table 2

252   and Figure 2. We found no significant difference in the level of craniodental/postcranial ensemble

253   consistency index (CI) across all 81 data sets (Wilcoxon test paired V = 3453, p = 0.5645). Despite

254 remarkably similar medians (100 and 97) and overall distributions, the median number of

255 craniodental and postcranial characters differed non-significantly (V = 3112.5, p = 0.5747). We

256 therefore compared the residual CI values from a linear regression of CI on the log of the number of

257 characters and the log of the number of taxa, plus their interaction. This model was significant

258 overall (p < 2.2e-16), but none of the individual slope terms was significant (p > 0.1 in all cases).

259 Residuals from this model likewise showed no significant difference between partitions (paired t =

260 0.38211, p = 0.7032). Likewise, we found no significant difference in the level of

261 craniodental/postcranial ensemble retention index (RI) across all 81 data sets (V = 3717.5, p-value =

262 0.1437). Similarly, the residuals from the regression of RI onto the number of taxa, number of

263 characters and their interaction (p = 3.668e-12 overall, but with no significant slopes for individual

264 terms) also showed no difference between partitions. Neither partition of the data can be deemed

265 superior on the basis of these ensemble indices of internal consistency.

266

267 **2.** **Half of craniodental and postcranial data partitions yield significantly different trees**

268 Previous work on a broad sample of tetrapod matrices revealed significant incongruence between

269 craniodental and postcranial character partitions about one time in three, as measured by both the

270 incongruence relationship difference (IRD) test of Ruta & Wills (2016) and the incongruence length

271 difference (ILD) test (Mickevich and Farris, 1981; Farris et al., 1995). Here, we report that 50% of

272 dinosaur matrices yielded significantly (p<0.05) incongruent trees according to the IRD test for

273 nearest neighbours using matching distances ($IRD_{NND+matching}$) and 54% for the IRD test using the RF

274 distances (Robinson and Foulds, 1981) (IRD_{NND+RF}). Moreover, the $IRD_{NND+matching}$ and IRD_{NND+RF} values

275 were closely correlated (r_s = 0.649, p = 8.999e-14). We note that analyses of partitions reached the

276 limit of 1,000 trees for nearest neighbour (NND) computations in 47% of runs (see Supplementary

277 Materials 3). We therefore also report the results of IRD tests using majority rule consensus trees

278 derived from up to 10,000 optimal source trees. Inevitably, consensus trees cannot reflect accurately

279   the diversity of relationships within a set of source trees (Mounce et al., 2016) but they do permit

280   tests that incorporate all source trees more readily. The consensus results were closely similar to

281   those for the nearest neighbour tests: 63% of matrices were significantly incongruent using

282    $IRD_{MR+matching}$ and 60% were incongruent using IRD_{MR+RF}). Moreover, the consensus results were

283   strongly and significantly correlated with the NND results for both the $IRD_{MR+matching}$ (r_s = 0.688, p =

284   7.31e-16) and IRD_{MR+RF} (r_s = 0.560, p = 6.412e-10). The rate of significance (33% at p < 0.05) for the

285   ILD test was lower than that for variants of the IRD, and similar to that observed for tetrapods

286   overall (Mounce et al., 2016). Nevertheless, we found significant correlation between the ILD p value

287   and the p values for both the $IRD_{matching}$ (r_s = 0.308, p = 0.001) and the IRD_{RF} (r_s = 0.297, p = 0.002)

288   using NNDs.

289   Mounce *et al*. (2016) tested empirically whether the rate of null rejection was influenced by several

290   data matrix parameters. Here we used logistic regression to determine the outcome of each of our

291   five partition homogeneity tests (significant or not with p < 0.05) as a function of the overall number

292   of taxa, overall number of characters (both partitions), the interaction between characters and taxa,

293   the difference in partition size (scaled relative to the total number of characters), total amount of

294   missing data, the difference in the percentage of missing data between partitions and the higher

295   taxonomic group. Results are summarised in the supplementary materials. For IRD_{NND+RF}, only the

296   total number of characters and total number of taxa were retained in a minimum adequate model

297   (McDonald et al., 2012) selected using the AIC. For IRD_{MR+RF}, these parameters plus their interaction

298   and the difference in partition size (number of characters) was retained in the MAM. Hence, as

299   reported by Mounce *et al.* (2016), tests based upon symmetrical differences (Robinson and Foulds,

300   1981) are influenced, at least in part, by data matrix dimensions. By contrast, for the $IRD_{NND+matching}$

301   (based upon nearest neighbour matching distances), no matrix parameters were retained in the

302   MAM, but higher taxonomic group was highly significant. Similarly, taxonomic group was highly

303   significant for the $IRD_{MR+matching}$ (based upon majority rule matching distances), and the difference in

304   partition size was also retained by the AIC (although p>0.05).

305

3. Levels of incongruence vary significantly across major dinosaur groups

307 Of our 46 saurischian matrices, 31 (67%) showed significant (p < 0.05) incongruence using

308 $IRD_{NND+matching}$, compared with 9 from 35 (26%) ornithischian matrices: a significant difference in the

309 rate of null rejection (G = 20.1841, p = 0.00046). A similarly significant difference was observed for

310 the $IRD_{MR+matching}$ (G = 19.3857, p = 0.00066). For the IRD using Robinson Foulds distances, by

311 contrast, differences across saurischian and ornithischian matrices were non-significant (IRD_{NND+RF} G

312 = 6.7962, p = 0.14706: IRD_{MR+RF} G = 5.4241, p = 0.24648). At a finer taxonomic level (specifically

313 assigning trees to Theropda (e.g., Fig. 2), Sauropodomorpha (e.g., Fig. 3), Cerapoda, Ornithopoda,

314 and Thyreophora) there were highly significant differences in the rate of null rejection using the

315 matching distance (p = 0.00046 for the $IRD_{NND+matching}$: p = 0.00066 for $IRD_{MR+matching}$) no difference

316 using the symmetrical difference (RF) variants of the tests (Table 2) (Fig. 4). This difference between

317 'RF' and 'Matching' variants of the IRD test is consistent with that observed for the modelling of

318 outcomes above (i.e., taxonomic group was significant in determining the binary outcome of

319 $IRD_{matching}$ variants, but not for the IRD_{RF}). Rates of partition incongruence are relatively high in the

320 Sauropoda (53% for the $IRD_{NND+matching}$), Theropoda (66%) and Ceropoda (43%) compared with the

321 Ornithopoda (20%) and Thyreophora (14%). A similar hierarchy of outcomes pertained for the other

322 tests.

323

4. Craniodental and postcranial characters produce trees equally similar to the entire data set, but

with strong biases across major groups

326 Our second set of tests sought to determine whether the most parsimonious trees from the entire

327 matrix were more similar to those from the craniodental or postcranial partitions. The results from

328 these were in strong agreement. Considering the NNDs for matching distances across all 81 matrices,

329   42 were closer (using the matching distances for nearest neighbours: NND+matching) to the

330   postcranial partition, while 39 were closer to the craniodental partition (a non-significant bias:

331   binomial test p = 0.8243). Within Saurischia and Ornithischia, however, the biases were highly

332   significant, but in opposite directions (G = 6.42421, p = 0.01126). For Saurischia, trees from the

333   entire data set were most often more similar to those from the postcranial partition 29 cases) than

334   to those from the cranium (17 cases) (binomial p = 0.1038). For Ornithischia, by contrast, trees from

335   the whole data set were more often most to those from the craniodental partition (22 cases) than to

336   those from the postcranium (13 cases) (p = 0.1755). When partitioned into five groups as above,

337   there was also a significant difference in which partition was most similar to the entire matrix across

338   groups (G = 8.7347, p = 0.006209), with the bias for Sauropoda (13 postcranial verus 4 craniodental)

339   being the most striking. Similar findings were made for the other three tests (Tables 1 and 2).

340   These biases were much less marked if comparisons were restricted to only those data sets

341   for which there was a significant difference (p < 0.05) between the distributions of distances (entire

342   to craniodental versus entire to postcraniodental) according to the Mann-Whitney U test.

343   Considering NND+matching distances, 31 data sets favoured the craniodental partition and 33 the

344   postcranial partition (binomial p = 0.9007). Moreover, there was no longer a significant bias in favour

345   of postcranial characters for the Saurischia (23 out of 33: p = 0.0308) or in favour of craniodental

346   characters for the Ornithischia (17 out of 31: p = 0.7201) (overall G = 3.98451, p = 0.04592).

347   However, for the partition into Theropda, Sauropodomorpha, Cerapoda, Ornithopoda and

348   Thyreophora, we still marginally rejected the null that groups behave identically (G = 9.29294, p =

349   0.05418027). Similar findings for the other three tests are summarised in Table 2.

350

351

352

353   **Discussion**

354   **Implications for dinosaur phylogeny**

355   Our analyses of 81 published matrices demonstrate empirically that the relationships of dinosaurs

356   inferred from craniodental or postcranial characters in isolation differ significantly ($p < 0.05$) from

357   each other about half of the time. This is much more often than similar partitions for tetrapods in

358   general (about 1 in 3:(Mounce et al., 2016). At the same time, we find similar levels of homoplasy (as

359   measured by the ensemble consistency index: CI) and retained synapomophy (RI) in craniodental

360   and postcranial character partitions across all dinosaurs. Similarly, when character sample sizes are

361   controlled, the relationships inferred from either partition are equally congruent with those from

362   the entire matrix. Hence, there is no reason to prefer characters sampled from one partition versus

363   another across dinosaurs as a whole, and we concur with general recommendations to sample

364   characters widely from all anatomical regions in accordance with the principle of total evidence

365   (Kluge, 1989; Gatesy et al., 1999; Gatesy and Arctander, 2000; Mounce et al., 2016). However, we

366   also observe marked differences in levels of incongruence across major dinosaur groups, being

367   significantly higher in Ornithischia than Saurischia.

368   Homoplasy is always a problem for phylogenetic inference, but is least troublesome when

369   homoplastic states approximate to a random distribution across taxa (in which case it largely

370   contributes noise). Homoplasy is more problematic when it is correlated across complexes of

371   characters, especially when this occurs at higher frequencies. The morphological phylogeny of

372   mammals appears to have been subject to such problems. Phylogenomic trees (Dolphin, K. et al.

373   2000,) overturned many of the groups (e.g., Ungulata and Insectivora) that had emerged from nearly

374   all previous analyses of morphological characters over the preceding decades. Most problematic of

375   all are cases where correlated homoplasy is concentrated within a particular region of the body, and

376   especially where available data are limited to such regions. The teeth of mammals appear to be

377   subject to such convergence (Goswami A et al. 2011), with many aspects of their form changing in

378   concert and being controlled by a relatively small number of genes (Castelin et al., 2017). This is

379   singularly unfortunate for those studying mammalian evolution, since the high preservation

380   potential of teeth means that they dominate the fossil record. The fossil record of dinosaurs is also

381   biased, with sauropodomorphs and theropods being known predominantly from their postcranial

382   remains (skulls are often fragmentary or not recovered), and ceratopsians being more often

383   described from their much more massive skulls (Evans, D.C. and Ryan, M.J. 2015,). Our sample of

384   matrices suggest that the number of coded characters strongly reflects these differences. However,

385   it remains unclear whether this is solely a function of the available material, or whether systematists

386   preferentially code or more finely atomise characters from these regions. Whatever the case, we do

387   not find a higher concentration of homoplasy in either partition, whether across all dinosaurs or

388   within major clades. Moreover, although craniodental and postcranial characters often yield

389   significantly conflicting trees, we find no evidence that one partition is more likely to be congruent

390   with the "total evidence" tree than the other.

391   **Interpreting incongruence**

392   The inference of significantly different trees from craniodental and postcranial character partitions

393   can be understood in terms of divergent selective pressures operating on different regions of the

394   body (Gould and Gould, 1977; J, 1993; Kemp and Kemp, 2005; Lue et al., 2010). This results in

395   different rates and patterns of character evolution (Mitteroecker and Bookstein, 2007; Klingenberg,

396   2008), in addition to distinct patterns of homoplasy. Anatomical modules are commonly recognised

397   in studying the evolution of form (Mitteroecker and Bookstein, 2007; Cardini and Elton, 2008;

398   Klingenberg, 2008; Lue et al., 2010; Goswami et al., 2011; Hopkins and Lidgard, 2012; Cardini and

399   Polly, 2013; Goswami et al., 2015), and it is reasonable to suppose that such modules will contain

400   phylogenetic characters that are more congruent with one another than with characters from other

401   modules (Clarke and Middleton, 2008)

402   The tetrapod skull is variously decoupled from the skeleton of the body, both biomechanically and in

403   terms of the selective pressures operating upon it (Ji et al., 1999; Koski, 2007; Mitteroecker and

404   Bookstein, 2007). However, this decoupling is particularly marked in the non-avian dinosaurs

405   (Mounce et al., 2016). The long necks of sauropodomorphs effect the greatest biomechanical

406   decoupling between the skull and the body, and sauropods unsurprisingly have one of the highest

407   levels of significant incongruence. Ornithischia, by contrast, show much lower levels of incongruence

408   overall: especially low (14%) in the thyreophorans.

409   Anatomical modules are typically envisaged as comprising physically proximate sets of characters or

410   aspects of form. However, particular selective pressures might result in the coordinated evolution of

411   suites of characters widely distributed across the body (Gardiner et al., 2011; Abourachid and

412   Hoefling, 2012; Godefroit et al., 2013). For example, a mode of predation or scavenging favoured by

413   many theropods entailed bracing a carcass with a back leg whilst ripping with powerful jaws and a

414   strong neck (Rayfield, 2004). This manner of feeding evolved in at least three large theropod clades,

415   and entailed coordinated changes in the limbs and skull (Snively et al., 2006; Snively and Russell,

416   2007a; Snively and Russell, 2007b; Hone and Rauhut, 2010). Similarly, the massive skulls of many

417   ceratopsians were braced into the body and pectoral girdle consistent with their ability to face and

418   ward off predators, and this may have effected other coordinated changes in the vertebral column

419   and back limbs.

420   In the infancy of molecular phylogenetics, trees were often inferred from single genes (Gatesy, J. and

421   Arctander, P. 2000), and it was not uncommon for the trees derived from different genes to be

422   strikingly at odds (Gatesy, J. and Arctander, P. 2000). In addition, molecular trees often differed

423   markedly from those inferred from morphology. A more cautious, combinatorial approach initially

424   evolved, therefore, along with partition tests designed to ensure homogeneity of signal (Mounce,

425   R.C.P. et al. 2016). This agglomerative approach may have been a function of the manner in which

426   data originally became available, with systematists exploring incongruent signals at a fine level of

427 granularity. The ascendance of phylogenomic analyses has brought its own bioinformatic challenges,

428 but all approaches seek to derive trees from increasingly inclusive data sets. More philosophically, a

429 consensus has emerged in favour of the principle of total evidence (Kluge, 1989): the procedure by

430 which all available character data are combined into a single matrix and analysis. One reason for this

431 is the phenomenon of 'hidden support' (Gatesy et al., 1999; Gatesy and Arctander, 2000), whereby

432 signals that are weak and therefore hidden within individual character partitions become dominant

433 when all data are analysed together. Various tests for partition homogeneity (Farris et al., 1994,

434 1995; Dolphin et al., 2000) will tend to return significant results in precisely those circumstances in

435 which support is hidden, and such tests are therefore no longer commonly used to preclude the

436 combination of data sources in this manner (Kluge, 1989; Gatesy et al., 1999; Gatesy and Arctander,

437 2000; Wahlberg et al., 2005; O'Leary and Gatesy, 2008; Padial et al., 2010; Damgaard, 2012; Mounce

438 et al., 2016). However, while molecular systematics has retained and elaborated the notion that

439 different suites of characters within large molecular matrices might be most effectively modelled

440 with different rate parameters (e.g., different sets of genes, and different codon positions),

441 morphological data are rarely treated in this manner. Moreover, there is relatively little quantitative

442 empirical data on the sorts of morphological characters that might be most useful for resolving

443 relationships at different hierarchical levels within a phylogeny, or for radiations of different ages.

444 This is partly because morphology is less likely to be constrained to evolve in a clock-like manner

445 throughout a tree (or to change it's rate in a manner amenable to modelling), and partly because

446 there are no standard repositories for morphological characters that enable data to be archived,

447 retrieved, coded and compared in a uniform manner. Despite this, trees are often inferred from

448 relatively restricted character sets (Sanchez-Villagra and Williams, 1998; Arratia, 2009; Song and

449 Bucheli, 2010; Mounce et al., 2016). In fossil taxa, this may reflect preservational biases, particularly

450 those favouring hard part preservation (Sansom et al., 2010; Sansom and Wills, 2013; Pattinson et

451 al., 2015; Sansom et al., 2017).

452

Conclusions

1. Across our sample of 81 data sets, practitioners have abstracted slightly fewer characters from the skull (mean 115, median 100) than the rest of the skeleton (mean 132 and median 97) overall. However, this masks particular biases in major dinosaur groups: markedly and significantly ($p < 0.02$ in all cases) in favor of postcranial characters in Sauropodomorpha and Theropoda and in favor of postcranial characters in Ornithopoda, Thyreophora and Cerapoda.

2. The overall frequency of significant ($p < 0.05$) incongruence between dinosaur trees inferred from craniodental and postcranial characters was about 50% for variants of the Incongruence Relationship Difference (IRD) test (Ruta and Wills, 2016); (Mounce et al., 2016). This was substantially higher than that previously reported (30%) for tetrapod clades in general. The Incongruence Length Difference Test (ILD) reported significant incongruence in 33% of cases: comparable to the level seen across tetrapods hitherto (Mounce et al., 2016).

3. Despite the high frequency of incongruence overall, rates of significance were heterogeneously distributed across major dinosaur groups, being highest (a mean of 48% for variants of the IRD) in Theropoda and lowest (25%) in Thyreophora. A number of factors have been purported to influence the outcome of the IRD test, notably the data matrix dimensions, relative partition sizes and the amount and distribution of missing entries (Mounce et al., 2016). We nevertheless found similar heterogeneity in rates of significant incongruence across groups when these variables were modelled out.

4. Tests to determine which partition (craniodental or postcranial) were most congruent with trees inferred from the entire character set were equivocal overall: equal numbers favoured the two partitions once differences in sample size were controlled for. However, there were significant asymmetries in many groups, with the bias for Sauropoda (13 postcranial verus 4 craniodental) being the most striking.

477   5. We show that our partition tests are not sensitive to the size of the tree (number of terminals), to

478   differences in partition size (differences in the number of characters), to the overall amount of

479   missing data in the matrix, the difference in the amount of missing data between partitions or the

480   difference in levels of homoplasy or retained synapomorphy between partitions. We also

481   demonstrate that there are similar levels of homoplasy and retained synapomorphy between

482   partitions overall. Incongruence therefore reflects differences in *patterns* of homoplasy between

483   partitions, which may itself be a function of modularity and mosaic evolution. We note that

484   incongruence is greatest in those groups (Sauropodomorpha and Theropoda) in which the

485   biomechanical decoupling between head and body is greatest.

486   6. Our results demonstrate clearly that phylogenies of dinosaurs inferred from craniodental and

487   postcranial characters differ significantly much more often than expected. We therefore make the

488   straightforward recommendation that characters should be sampled as broadly as possible from

489   across all body regions. This accords with the theoretical principle of total evidence (Kluge, 1989;

490   Gatesy et al., 1999; Gatesy and Arctander, 2000), as well as our empirical findings for tetrapods in

491   general (Mounce et al., 2016) and mammals in particular (Sansom and Wills, 2017).

492

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922 **Table 1. Summary of all tests and statistics for all 81 partitioned data sets**

Reference	Craniodental Number	Postcranial Number	Taxa	Taxa removed	ILD test	IRD RF NN	IRD RF M	IRD Match NND	IRD Match MR	p-value	Craniodental missing %	Postcranial missing %	Craniodental CI	Craniodental RI	Postcranial CI	Postcranial RI
Allain_etal_2012a-Bc	74	94	20	9	0.140	0.11	0.04	0.07	0.04	4.19E-09	16.22	19.47	0.5172	0.6667	0.585	0.7615
Araujo_etal_2013a-Bc	159	187	22	42	0.011	0.01	0.01	0.03	0.03	3.12E-02	30.16	26.15	0.5064	0.6025	0.5899	0.729
Brusatte_et_Benson_2013a-Bc	200	107	18	16	0.164	0.01	0.01	0.02	0.05	2.20E-16	23.67	34.53	0.6809	0.8353	0.6648	0.846
Brusatte_etal_2014a-Bc	368	473	56	95	0.054	0.01	0.01	0.01	0.01	0.1693	49.53	39.33	0.4584	0.7616	0.4219	0.5781
Canale_etal_2015a-Bc	100	55	16	1	0.610	0.01	0.21	0.05	0.07	2.20E-16	35.8	39.27	0.6667	0.7617	0.6239	0.6583
Cau_etal_2012a-Bc	338	443	29	8	0.031	0.03	0.03	0.02	0.01	3.18E-08	38.32	45.39	0.3934	0.4944	0.4329	0.5189
Choiniere_etal_2014ba-Bc	216	290	58	56	0.001	0.01	0.01	0.01	0.01	0.0001219	48.83	46.83	0.2892	0.5817	0.3029	0.6013
Evers_etal_2015a-Bc	152	192	42	22	0.106	0.01	0.01	0.01	0.01	0.5229	46.2	43.42	0.434	0.6721	0.4636	0.7163
Eddy_et_Clarke_2011a-Bc	95	66	19	3	0.032	0.18	0.23	0.11	0.11	0.002423	26.93	35.35	0.6294	0.6702	0.7048	0.7304
Fanti_etal_2012a-Bc	109	69	17	2	0.001	0.01	0.02	0.03	0.03	2.20E-16	31.41	37	0.75	0.8442	0.5548	0.5988
Farke_et_Sertich_2013a-Bc	81	106	18	12	0.998	0.02	0.01	0.01	0.01	0.01551	46.52	43.64	0.7328	0.8558	0.5867	0.6773
Foth_etal_2014a-Bc	177	357	53	89	0.001	0.01	0.01	0.01	0.08	0.2493	39.2	35.9	0.4114	0.7684	0.392	0.7412
Godefroit_etal_2013b-Bc	373	614	27	28	0.001	0.01	0.01	0.01	0.01	8.94E-01	41.22	47.8	0.4647	0.5216	0.5207	0.5776
Hu_etal_2015a-Bc	41	171	27	35	0.231	0.63	0.76	0.02	0.02	5.02E-02	57.18	33.1	0.6761	0.783	0.4815	0.6337
Lamanna_etal_2014a-Bc	130	86	22	19	0.001	0.04	0.01	0.03	0.02	3.36E-16	34.44	45.4	0.6441	0.7711	0.5312	0.5909
Lee_etal_2014b-Bc	42	181	20	45	0.165	0.35	0.68	0.38	0.75	3.58E-11	37.5	33.5	0.6901	0.8211	0.6144	0.7315
LiZ_etal_2014a-Bc	45	162	16	20	0.372	0.84	0.85	0.67	0.7	0.003983	30.42	16.51	0.5446	0.6085	0.4641	0.5339
Loewen_etal_2013a-Bc	297	196	40	0	0.122	0.08	0.06	0.05	0.12	5.72E-07	29.69	29.96	0.4093	0.7603	0.4239	0.7713
Longrich_etal_2011a-Bc	46	163	26	20	0.002	0.01	0.01	0.01	0.03	2.58E-02	42.5	21.53	0.8154	0.9084	0.6353	0.7913
Lu_etal_2014b-Bc	203	107	20	5	0.233	0.01	0.01	0.01	0.01	2.20E-16	25.15	38.78	0.663	0.8345	0.6536	0.8438
Novas_etal_2013aa-Bc	91	188	21	24	0.475	0.03	0.05	0.01	0.09	0.03884	21.4	30.37	0.4823	0.6528	0.514	0.6661
Parsons_et_Parsons_2015a-Bc	254	188	28	90	0.016	0.01	0.01	0.03	0.02	3.49E-02	24.41	23.74	0.5523	0.7823	0.6348	0.8331
Porfiri_etal_2014a-Bc	122	159	31	14	0.374	0.04	0.04	0.38	0.31	0.1477	37.49	39.49	0.3989	0.6326	0.4371	0.6698
Sanchez-Hernandez_et_Benton_2014a-Bc	68	78	17	4	1.000	0.01	0.05	0.01	0.01	3.28E-08	45.16	44.34	0.7553	0.8655	0.6296	0.6875
Senter_etal_2012b-Bc	153	229	79	31	0.021	0.04	0.06	0.01	0.01	2.20E-16	20.73	17.83	0.6583	0.8601	0.6196	0.8179
Tortosa_etal_2014a-Bc	118	177	16	24	0.017	0.01	0.01	0.01	0.01	6.80E-11	44.6	34.03	0.7822	0.8327	0.6022	0.6613
Wang_etal_2015b-Bc	40	185	17	41	0.018	0.18	0.51	0.17	0.13	3.83E-04	43.38	30.84	0.7121	0.7841	0.6546	0.7103
Zanno_et_Makovicky_2013a-Bc	148	190	36	26	0.080	0.05	0.23	0.05	0.04	3.44E-15	42.59	33.81	0.4474	0.6555	0.4725	0.7113
Zhou_etal_2014a-Bc	46	94	15	18	0.001	0.02	0.02	0.03	0.12	5.59E-02	26.96	15.84	0.7746	0.8571	0.7462	0.8107
DEmic_2013a-Ba	15	96	13	12	0.018	0.05	0.06	0.03	0.08	6.40E-05	23.6	18.2	0.7273	0.8065	0.7769	0.8585
Gorscak_etal_2014a-Ba	100	145	22	13	0.074	0.02	0.02	0.02	0.01	6.10E-09	40.09	31.57	0.6687	0.7611	0.6681	0.7557
Santucci_et_Arruda-Campos_2011a-Ba	76	152	27	11	0.010	0.01	0.01	0.01	0.03	7.63E-15	32.2	21.36	0.7391	0.7778	0.7054	0.7692
Tschopp_et_Mateus_2013a-Ba	66	96	14	0	0.131	0.12	0.29	0.04	0.32	1.06E-07	47.29	30.73	0.6964	0.6634	0.5824	0.6181
Wilson_et_Allain_2015a-Ba	66	80	13	0	0.263	0.01	0.01	0.01	0.01	2.20E-16	31.47	15.38	0.8675	0.9106	0.6641	0.7676
Carballido_&_Sander-Bb	99	223	22	52	0.002	0.10	0.09	0.17	0.16	8.80E-13	33.47	29.03	0.6628	0.7852	0.5704	0.6525
Carballido_etal_2015a-Bb	95	231	18	55	0.041	0.05	0.03	0.04	0.05	6.60E-02	29.07	20.06	0.6467	0.7204	0.5859	0.5983
Fanti_etal_2015a-Bb	72	126	20	0	0.466	0.01	0.01	0.16	0.11	2.88E-10	41.32	27.18	0.7105	0.8187	0.5153	0.6333
Lacovara_etal_2014a-Bb	100	226	22	53	0.009	0.03	0.03	0.01	0.01	0.2951	34.4	27.82	0.6667	0.7765	0.5744	0.6679
LiL_etal_2014-c	99	220	21	50	0.020	0.34	0.24	0.26	0.28	2.05E-08	32.13	26.02	0.6686	0.7778	0.5752	0.6555
Mannion_etal_2013a-Bb	53	222	18	33	0.129	0.06	0.20	0.03	0.03	1.32E-01	39.41	22.87	0.5758	0.6693	0.4018	0.5108
McPhee_etal_2015a-Bb	117	233	32	22	0.496	0.04	0.20	0.16	0.15	2.20E-16	30.9	20.53	0.4227	0.6924	0.3894	0.6524
Rauhut_etal_2015a-Bb	102	216	29	43	0.677	0.01	0.01	0.01	0.01	2.20E-16	47.63	26.48	0.6031	0.7475	0.476	0.7051
Rubilar-Rogers_etal_2012a-Bb	68	150	22	8	0.080	0.01	0.01	0.01	0.01	2.20E-16	46.35	24.94	0.7064	0.7867	0.6614	0.8009
Xing_etal_2015b-Bb	101	237	28	17	0.096	0.01	0.01	0.01	0.01	2.20E-16	26.22	22.6	0.3269	0.5566	0.7135	0.6628
Pol_etal_2011a-Bb	102	160	38	12	0.120	0.52	0.58	0.37	0.29	7.14E-03	37.59	36.12	0.625	0.7931	0.6667	0.7978
Saegusa_et_Ikeda_2014a-Bb	15	99	13	16	0.025	0.06	0.04	0.01	0.03	0.001353	23.6	18.41	0.7273	0.8065	0.7803	0.8585
Evans-Aa	51	48	24	1	0.078	0.04	0.03	0.01	0.01	2.20E-16	29.17	43.66	0.6471	0.8266	0.7639	0.844
Farke_etal_2011-A	48	22	16	2	0.796	0.10	0.71	0.04	0.47	0.07588	16.5	31.1	0.7391	0.7857	0.8519	0.8519
Farke_etal_2014ba-Aa	103	43	14	19	0.082	0.04	0.22	0.03	0.01	5.04E-08	20.94	20.59	0.75	0.8413	0.746	0.8367
Han_etal_2015a-Aa	162	47	18	19	0.207	0.02	0.62	0.22	0.93	5.45E-03	17.18	20.8	0.5938	0.7784	0.68	0.831
Longrich_2011aa-Aa	90	23	19	3	1.000	0.47	0.45	0.43	0.41	4.79E-07	17	27	0.7983	0.8983	1	1
Longrich_2014a-Aa	159	32	16	19	0.727	0.05	0.09	0.02	0.31	8.64E-04	17.33	33.98	0.7449	0.8098	1	1
Boyd_2015a-Ab	128	99	34	65	0.814	0.85	0.74	0.59	0.6	4.24E-05	40.72	31.7	0.37	0.6056	0.4206	0.6477
Boyd_et_Pagnac_2015a-Ab	90	41	28	40	0.028	0.07	0.01	0.02	0.01	2.53E-12	25	27.44	0.5714	0.7894	0.5481	0.7991
Brown_etal_2011a-Ab	76	53	20	3	0.181	0.39	0.46	0.21	0.38	0.7277	27.43	23.11	0.5189	0.6877	0.5034	0.654
Evans_etal_2013a-Ab	28	10	12	6	0.993	0.01	0.07	0.07	0.37	0.2078	15.18	46.7	0.6792	0.7302	0.9167	0.9091
Godefroit_etal_2012b-Ab	100	46	19	2	0.108	0.02	0.01	0.02	0.02	2.20E-16	18.84	30.32	0.6875	0.7766	0.6782	0.7667
He_etal_2015a-Ab	191	144	34	27	0.007	0.68	0.49	0.83	0.71	0.1416	22.16	24.04	0.4275	0.6648	0.4595	0.6855
McDonald_etal_2012a-Ab	91	41	42	25	0.285	0.04	0.03	0.13	0.15	1.60E-09	21.89	24	0.5955	0.7977	0.596	0.8113
McGarrity_etal_2013a-Ab	102	46	20	2	0.202	0.01	0.01	0.01	0.01	2.20E-16	19.12	33.8	0.6759	0.7727	0.6782	0.7667
Norman_2015a-Ab	68	37	23	4	0.772	0.97	0.98	0.97	0.96	0.6486	10.29	17.63	0.594	0.781	0.6542	0.8405
Norman_etal_2011a-Ab	66	57	13	1	0.090	0.12	0.23	0.11	0.15	0.03156	12.82	18.89	0.5659	0.5591	0.6311	0.6481
Prieto-Marquez_2014b-Ab	155	67	19	15	0.088	0.34	0.83	0.12	0.37	2.20E-01	21.59	16.1	0.7233	0.7751	0.6013	0.7067
Prieto-Marquez_et_Wagner_2013a-Ab	194	91	34	17	0.303	0.69	0.68	0.39	0.32	0.02466	27	20.49	0.5737	0.8063	0.4843	0.7587
Prieto-Marquez_etal_2013a-Ab	143	66	26	8	0.475	0.01	0.03	0.14	0.43	0.0001373	27.65	29.37	0.5971	0.78	0.5577	0.6849
Shibata_etal_2015a-Ab	68	37	23	28	0.760	0.95	1.00	0.96	1	0.0393	10.29	17.62	0.5914	0.781	0.6542	0.8405
Xing_etal_2014a+Ab	233	111	32	30	0.645	0.16	0.60	0.06	0.21	9.42E-08	14.06	11.09	0.6359	0.8806	0.5991	0.8791
Arbour_et_Currie_2013c-Ac	70	56	17	1	0.436	0.11	0.73	0.58	0.83	0.04001	20.84	29.05	0.5692	0.72	0.7093	0.7642
Arbour_etal_2014b-Ac	57	66	19	1	0.460	0.14	0.31	0.11	0.08	7.00E-07	22.3	44.82	0.5455	0.7207	0.6729	0.7569
Barrett_etal_2014a-Ac	130	94	36	19	0.240	0.06	0.05	0.09	0.25	0.02561	22.54	29.28	0.4531	0.6841	0.5194	0.7324
Burns_et_Currie_2014-A	45	33	23	0	0.761	0.01	0.01	0.05	0.09	4.97E-05	16.14	45.85	0.4522	0.6957	0.6479	0.7312
Burns_et_Currie_2014-B	26	23	16	0	0.002	0.21	0.08	0.09	0.06	2.20E-16	13.94	32.07	0.6522	0.8261	0.6818	0.7407
Burns_etal_2011a-Ac	45	16	23	0	0.426	0.29	0.75	0.24	0.61	0.05312	12.8	36.76	0.5484	0.7103	0.7143	0.7838
Butler_etal_2011b-Ac	124	93	31	20	0.234	0.03	0.04	0.51	0.69	0.000465	22.11	23.93	0.4964	0.6745	0.5381	0.7217
Coria_etal_2013a-Ac	130	97	28	24	0.022	0.03	0.15	0.17	0.22	3.14E-02	19.86	20.95	0.5199	0.6787	0.5567	0.7463
Godefroit_etal_2014a-Ac	130	94	31	24	0.041	0.02	0.02	0.38	0.48	0.01808	19.35	21.17	0.4814	0.6585	0.512	0.6973
Han_etal_2012a-Ac	127	94	38	24	0.137	0.07	0.04	0.24	0.12	1.79E-01	18.06	18.56	0.5112	0.6881	0.5323	0.7134
Osi_etal_2012b-Ac	132	97	40	18	0.313	0.03	0.03	0.01	0.02	4.78E-02	18.56	18	0.4354	0.6708	0.5094	0.707
Pol_etal_2011b-Ac	129	97	42	9	0.020	0.01	0.03	0.01	0.11	0.01531	19.92	26.08	0.5238	0.6692	0.5567	0.7362
Ruiz-Omenaca_etal_2012a-Ac	130	94	35	18	0.641	0.04	0.01	0.23	0.05	6.85E-13	20.68	30.67	0.4545	0.6872	0.5347	0.7307
Thompson_etal_2012a-Ac	88	75	39	12	0.294	0.09	0.13	0.02	0.11	6.95E-09	24.45	35.8	0.445	0.729	0.4536	0.6753

923

924 IRD tests are based either upon the mean tree-to-tree distances between nearest neighbours (NND)
925 or the distance between majority rule (plus compatible grouping) trees (MR). The tree-to-tree
926 distance metric used is either the Robinson Foulds (symmetrical difference) distance (RF) or the
927 Matching distance (Match). Sources: (Brown et al., 2011; Burns et al., 2011; Butler et al., 2011;
928 Carballido et al., 2011; Eddy and Clarke, 2011; Farke et al., 2011; Longrich, 2011; Pol et al., 2011a;
929 Pol et al., 2011b; Santucci and De Arruda-Campos, 2011; Allain et al., 2012; Fanti et al., 2012; Han et
930 al., 2012; Ignacio Ruiz-Omenaca et al., 2012; McDonald, 2012; Osi et al., 2012; Rubilar-Rogers et al.,
931 2012; Senter et al., 2012a; Senter et al., 2012b; Thompson et al., 2012; Araujo et al., 2013; Arbour
932 and Currie, 2013; Brusatte and Benson, 2013; Cau et al., 2013; Coria et al., 2013; D'Emic, 2013; Farke
933 and Sertich, 2013; Godefroit et al., 2013; Loewen et al., 2013; Mannion et al., 2013; McGarrity et al.,
934 2013; Novas et al., 2013; Prieto-Marquez et al., 2013; Prieto-Marquez and Wagner, 2013; Tschopp
935 and Mateus, 2013; Zanno and Makovicky, 2013; Arbour et al., 2014; Barrett et al., 2014; Brusatte et
936 al., 2014; Burns and Currie, 2014; Carballido and Sander, 2014; Choiniere et al., 2014; Evans et al.,
937 2014; Farke et al., 2014; Foth et al., 2014; Gorscak et al., 2014; Lacovara, 2014; Lamanna et al., 2014;
938 Lee et al., 2014; Li et al., 2014; Longrich, 2014; Lu et al., 2014; Porfiri et al., 2014; Saegusa and Ikeda,
939 2014; Sanchez-Hernandez and Benton, 2014; Tortosa et al., 2014; Xing et al., 2014; Zhou et al., 2014;
940 Boyd, 2015; Boyd and Pagnac, 2015; Carballido et al., 2015; Evans and Ryan, 2015; Evers et al., 2015;

941   Fanti et al., 2015; Hu et al., 2015; Ignacio Canale et al., 2015; McPhee et al., 2015; Norman, 2015;

942   Parsons and Parsons, 2015; Rauhut et al., 2015; Shibata et al., 2015; Wang et al., 2015a; Wang et al.,

943   2015b; Wilson and Allain, 2015; Xing et al., 2015; He et al., 2016)

944

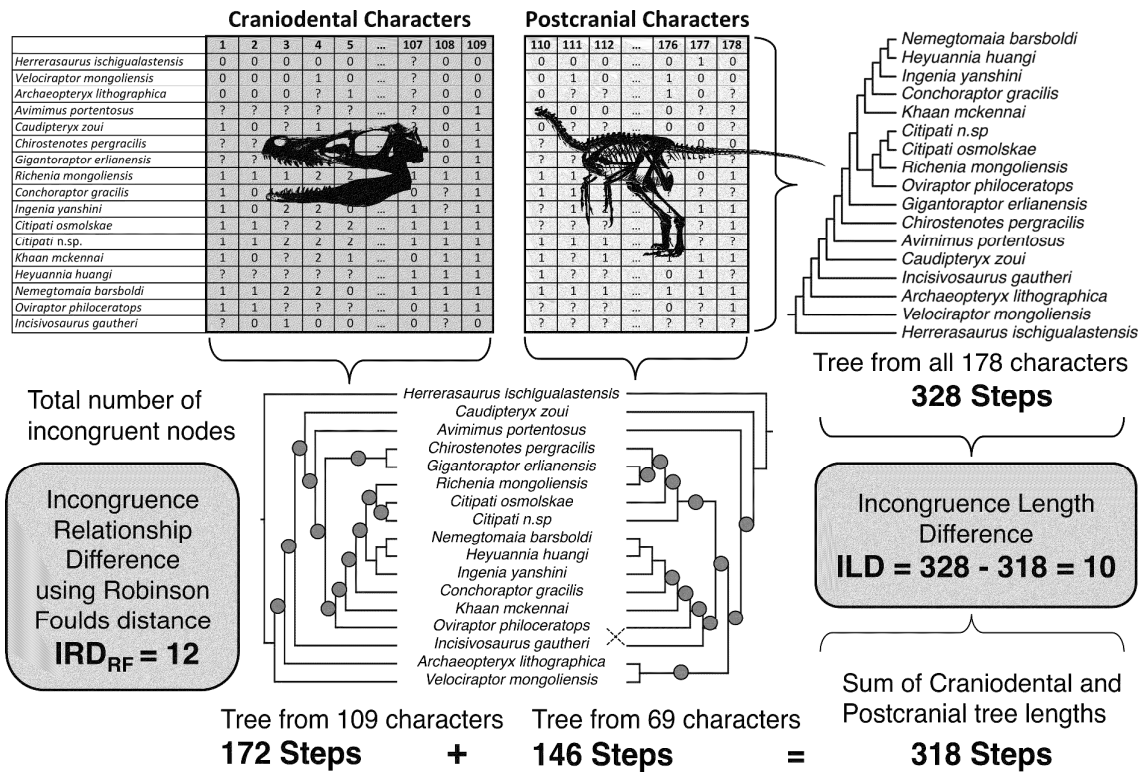945   **Table 2. Summary of matrix partitions and results of tests**

	All matrices	Theropoda	Sauropoda	Cerapoda	Ornithopoda	Thyreophora	W or G	p
No. Matrices	81	29	17	6	15	14	-	-
Median Number Craniodental/Postcranial Characters	100/97	122/177	95/160	96.5/37.5	100/53	125.5/93.5	-	-
Median Craniodental/Postcranial CI	0.5971/0.5867	0.6294/0.585	0.6686/0.5824	0.742/0.8079	0.5914/0.5991	0.5038/0.5474	-	-
Median Craniodental/Postcranial RI	0.7711/0.7307	0.7684/0.7103	0.7778/0.6679	0.8182/0.84795	0.7766/0.7667	0.68765/0.7318	-	-
*Craniodental/Postcranial most similar to entire (NND+Matching)	39/42	13/16	4/13	5/1	10/5	7/7		
f p<0.05 ILD	27	14	7	0	2	4	11.3810	0.0226
f p<0.05 IRD NND+RF	45	21	9	3	5	7	6.7962	0.1471
f p<0.05 IRD MR+RF	39	17	9	1	5	7	5.4241	0.2465
f p<0.05 IRD NND+Matching	40	19	12	4	3	2	20.1841	**0.0005**
f p<0.05 IRD MR+Matching	35	19	9	3	3	1	19.3857	**0.0007**

946

947   *Craniodental/Postcranial most similar to entire (NND+Matching). Both partitions and the entire

948   matrix were repeatedly (x100) resampled at the sample size (number of characters) of the smaller

949   partition, and most parsimonious trees were inferred from all three samples of characters. For each

950   resampling, the mean matching distance between nearest neighbours was used to determine which

951   partitioned tree(s) (craniodental or postcranial) were most similar to the tree(s) from the

952   subsampled entire matrix. The mean of these distances across all random re-samplings was then

953   used to determine which partition (craniodental or postcranial) yielded trees mot similar to that

954   from the entire matrix overall. The last five rows of the table indicate the frequency with which

955   partitions yield trees that are significantly different (with p < 0.05) for the ILD and variants of the IRD

956   test. IRD tests are based either upon the mean tree-to-tree distances between nearest neighbours

957   (NND) or the distance between majority rule (plus compatible grouping) trees (MR). The tree-to-tree

958   distance metric used is either the Robinson Foulds (symmetrical difference) distance (RF) or the

959   Matching distance.

960

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Craniodental Characters

	1	2	3	4	5	...	107	108	109
Herrerasaurus ischigualastensis	0	0	0	0	0	...	?	0	0
Velociraptor mongoliensis	0	0	0	1	0	...	?	0	0
Archaeopteryx lithographica	0	0	0	?	1	...	?	0	0
Avimimus portentosus	?	?	?	?	?	...	?	0	1
Caudipteryx zoui	1	0	?	1		...		0	1
Chirostenotes pergracilis	?	?				...		0	1
Gigantoraptor erlianensis	?	?				...		0	1
Richenia mongoliensis	1	1	1	2	2	...	1	1	1
Conchoraptor gracilis	1	0				...	0	?	1
Ingenia yanshini	1	0	2	2	0	...	1	?	1
Citipati osmolskae	1	1	?	2	2	...	1	1	1
Citipati n.sp.	1	1	2	2	2	...	1	1	1
Khan mckennai	1	0	?	2	1	...	0	1	1
Heyuannia huangi	?	?	?	?	?	...	1	1	1
Nemegtomaia barsboldi	1	1	2	2	0	...	1	1	1
Oviraptor philoceratops	1	1	?	?	?	...	0	1	1
Incisivosaurus gautheri	?	0	1	0	0	...	0	?	0

Postcranial Characters

110	111	112	...	176	177	178
0	0	0	...	0	1	0
0	1	0	...	1	0	0
0	?	?	...	1	0	?
0	0	0	...	0	0	?
0	?	?	...	0	0	?
?			...	0	0	0
?	?	?	...	0	0	?
1	1		...	0	1	1
1	1		...	?	?	?
?	1		...	1	1	1
?	?	?	...	1	1	?
1	1	1	...	1	1	1
1	?	?	...	1	1	1
1	?	?	...	0	1	?
1	1	1	...	1	1	1
?	?	?	...	0	1	1
?	?	?	...	?	?	?

Nemegtomaia barsboldi
Heyuannia huangi
Ingenia yanshini
Conchoraptor gracilis
Khaan mckennai
Citipati n.sp
Citipati osmolskae
Richenia mongoliensis
Oviraptor philoceratops
Gigantoraptor erlianensis
Chirostenotes pergracilis
Avimimus portentosus
Caudipteryx zoui
Incisivosaurus gautheri
Archaeopteryx lithographica
Velociraptor mongoliensis
Herrerasaurus ischigualastensis

Tree from all 178 characters
328 Steps

Total number of incongruent nodes

Incongruence Relationship Difference using Robinson Foulds distance
IRD$_{RF}$ = 12

Herrerasaurus Ischigualastensis
Caudipteryx zoui
Avimimus portentosus
Chirostenotes pergracilis
Gigantoraptor erlianonsis
Richenia mongoliensis
Citipati osmolskae
Citipati n.sp
Nemegtomaia barsboldi
Heyuannia huangi
Ingenia yanshini
Conchoraptor gracilis
Khaan mckennai
Oviraptor philoceratops
Incisivosaurus gautheri
Archaeopteryx lithographica
Velociraptor mongoliensis

Incongruence Length Difference
ILD = 328 - 318 = 10

Sum of Craniodental and Postcranial tree lengths
318 Steps

Tree from 109 characters   Tree from 69 characters
172 Steps   +   146 Steps   =

Figure 1. Calculation of the Incongruence Length Difference (ILD) and the Incongruence Relationship Difference (IRD) for the cranial and postcranial character partitions in the data of Fanti et al., 2012. Parsimony analysis of all 178 characters together yields a single most parsimonious tree (MPT) of 328 steps. Analysis of 109 craniodental characters alone yields an MPT length of 172 steps, while 69 postcranial characters alone yield an MPT length of 146 steps. The sum of these partitioned lengths (172+146 = 318) is less than the length of the global MPT by 10 steps (328-318 = 10). This discrepancy is the incongruence length difference (ILD = 10). The partitioned trees imply different relationships, and the magnitude of this difference can be measured using a diversity of tree-to-tree distance metrics. The Robinson Foulds (RF) or symmetrical difference distance (Robinson and Foulds, 1981) is among the most widely applied, and is calculated as the sum of the number of internal tree nodes that are present in one tree but not the other. The IRD$_{RF}$ is therefore the incongruence relationship difference measured using the RF distance. The RF distance has the disadvantage that it can saturate quickly. Numerous other tree-to-tree distance metrics are available, and we also implement the matching distance here (MD) (Lin et al, 2012), to yield the IRD$_{Matching}$. The ILD, IRD$_{RF}$ and IRD$_{Matching}$ each enables a test of incongruence, implemented by randomly partitioning the data set into character sets of the same size as the original (here, 109 and 69) and recalculating the metric. This is repeated a large number of times to yield a null distribution for randomised metric values, and the value for the original partition is compared with this in order to yield an empirical p value. Because the ILD, IRD$_{RF}$ and IRD$_{MD}$ all measure different things (tree length versus different aspects of tree shape and relationships), the results of these tests do not invariably coincide.
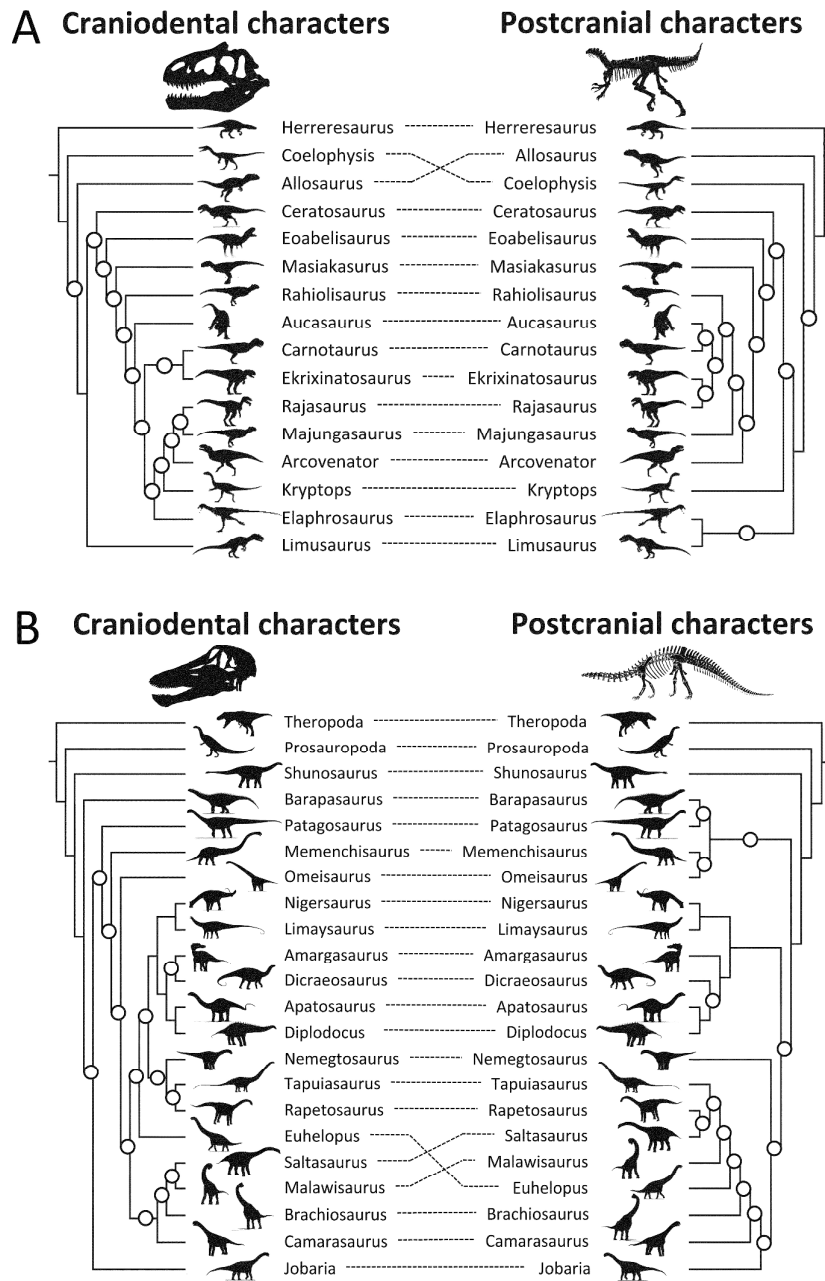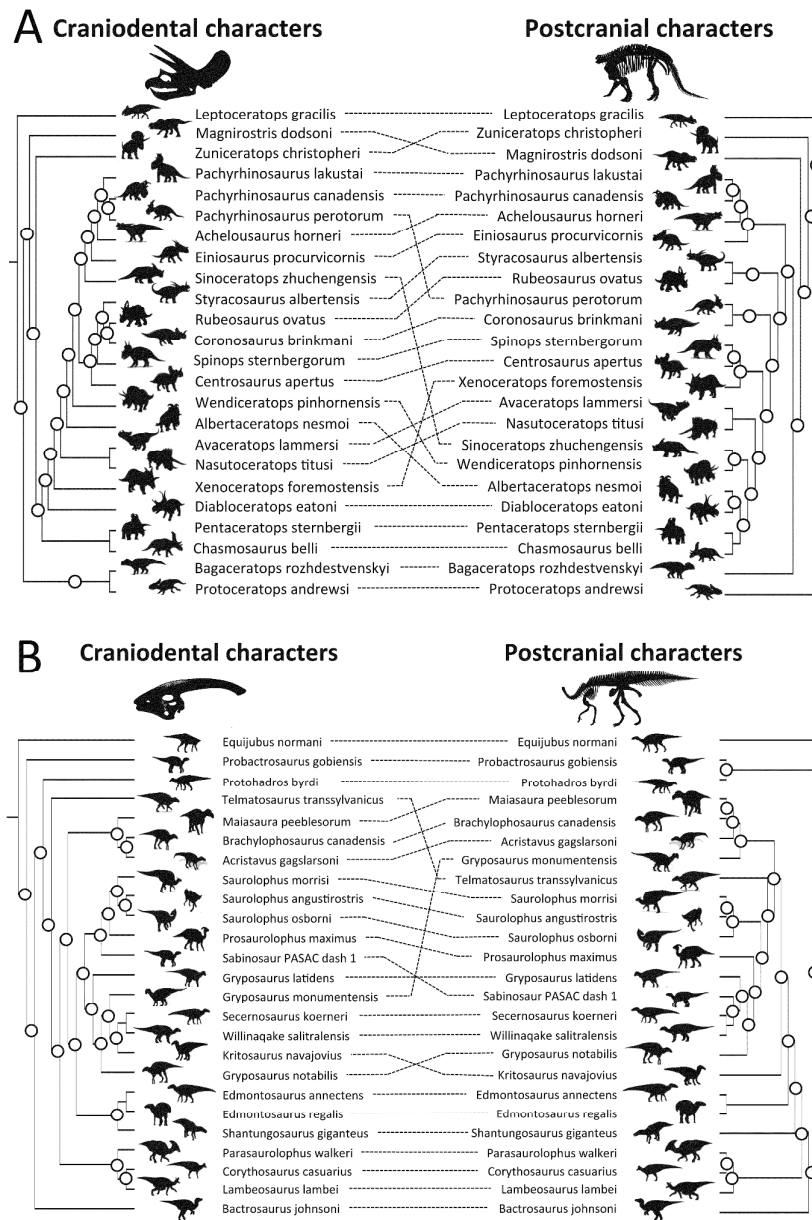
Figure 2. Exemplary tanglegrams for two groups of Saurischia. All trees are majority rule trees, plus compatible groupings. We do not necessarily recommend the use of majority rule trees in calculating IRD statistics (although we summarise these IRD_{MR} calculations in Tables 1 and 2), because they can be far from the centroid of tree space (Mounce et al., 2016). Rather, we advocate the use of mean distances between nearest neighbours in the two sets of trees for comparison. The left hand tree in each panel is derived from craniodental characters, while the right hand tree is derived from postcranial characters. Circled internal nodes are those present in one tree but not the other, and are tallied to give the Robinson Foulds (RF) or symmetrical difference distance (Robinson and Foulds, 1981). **A.** Tanglegram for Theropoda using data from Tortosa et al., (2014). (ILD p=0.017; IRD_{NND+RF} p=0.01; $IRD_{NND+Matching}$ p=0.01; IRD_{MR+RF} p=0.01; $IRD_{MR+Matching}$ p=0.01). **B.** Tanglegram for Sauropoda using data from Gorscak et al., 2014. (ILD p=0.074; IRD_{NND+RF} p=0.02; $IRD_{NND+Matching}$ p=0.02; IRD_{MR+RF} p=0.02; $IRD_{MR+Matching}$ p=0.01).

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Figure 3. Exemplary tanglegrams for two groups of Ornithischia. All trees are majority rule trees, plus compatible groupings. We do not necessarily recommend the use of majority rule trees in calculating IRD statistics (although we summarise these IRD$_{MR}$ calculations in Tables 1 and 2), because they can be far from the centroid of tree space (Mounce et al., 2016). Rather, we advocate the use of mean distances between nearest neighbours in the two sets of trees for comparison. The left hand tree in each panel is derived from craniodental characters, while the right hand tree is derived from postcranial characters. Circled internal nodes are those present in one tree but not the other, and are tallied to give the Robinson Foulds (RF) or symmetrical difference distance (Robinson and Foulds, 1981). **A.** Tanglegram for Ceratopsia using data from Evans and Ryan,(2015). (ILD p=0.078; IRD$_{NND+RF}$ p=0.04; IRD$_{NND+Matching}$ p=0.01; IRD$_{MR+RF}$ p=0.03; IRD$_{MR+Matching}$ p=0.01). **B.** Tanglegram for Hadrosaurida using data from Prieto and Marquez, 2014. (ILD p=0.088; IRD$_{NND+RF}$ p=0.34; IRD$_{NND+Matching}$ p=0.12; IRD$_{MR+RF}$ p=0.83; IRD$_{MR+Matching}$ p=0.37).

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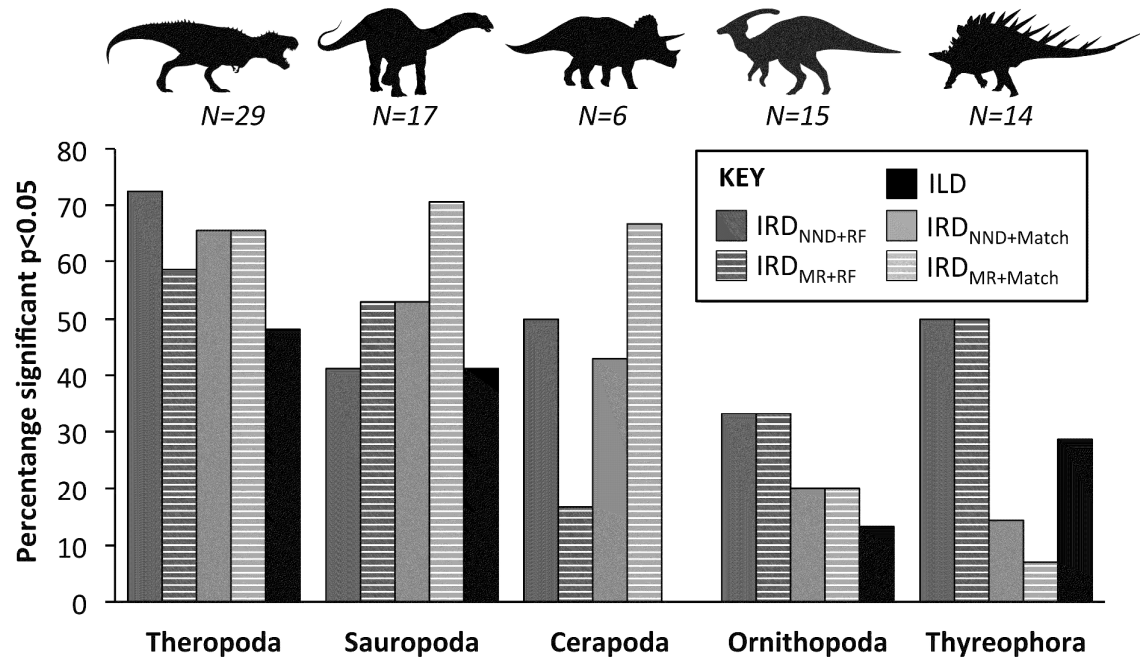
Figure 4. Summary of results of Incongruence Length Difference (ILD) and variants of the Incongruence Relationship Difference (IRD) tests, partitioned by major taxonomic group. Bars denote the percentage of data sets for which $p<0.05$. 'RF' in the subscript denotes IRD tests utilising the symmetrical-difference distance of Robinson and Foulds (1981), while 'Match' in the subscript denotes tests utilising the Matching distance of Linn et al. (2012). Comparisons are either made using majority rule consensus trees (MR), or the mean nearest neighbour distance between each tree in one set and its nearest neighbour in the other.

```
Data file(s):
Nexus files and partition data
Basic script for performing IRD tests in conjunction with
PAUP*
PARTRELAT is a Basic script for determining which of two
character matrix partitions (e.g., craniodental or post-
cranial) yields trees most similar to those derived from the
entire matrix.
Supplemenatry Materials 1 – Table of overlap between
matrices
```

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