



Citation for published version:

Brinkworth, A, Wills, M & Sansom, R 2019, 'Phylogenetic incongruence and homoplasy in the appendages and bodies of arthropods: Why broad character sampling is best' *Zoological Journal of the Linnean Society*, vol. 187, no. 1, pp. 100-116. <https://doi.org/10.1093/zoolinnean/zlz024>

DOI:

[10.1093/zoolinnean/zlz024](https://doi.org/10.1093/zoolinnean/zlz024)

Publication date:

2019

Document Version

Peer reviewed version

[Link to publication](#)

This is a pre-copyedited, author-produced version of an article accepted for publication in *Zoological Journal of the Linnean Society* following peer review. The version of record Andrew R Brinkworth, Robert Sansom, Matthew A Wills, Phylogenetic incongruence and homoplasy in the appendages and bodies of arthropods: why broad character sampling is best, *Zoological Journal of the Linnean Society*, Volume 187, Issue 1, September 2019, Pages 100–116, is available online at: <https://doi.org/10.1093/zoolinnean/zlz024>

University of Bath

General rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

Take down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

1 **Phylogenetic incongruence and homoplasy in the appendages and bodies of**
2 **arthropods: Why broad character sampling is best**

3
4 Andrew Brinkworth¹, Robert Sansom² & Matthew A. Wills*¹

5
6 **Author Affiliations:** *¹The Milner Centre for Evolution, Department of Biology and*
7 *Biochemistry, The University of Bath, The Avenue, Claverton Down,*
8 *Bath BA2 7AY, UK*

9 *²School of Earth and Environmental Science, The University of*
10 *Manchester, Oxford Road, Manchester, M13 9PL, UK.*

11
12
13 ***Correspondence:**

Matthew A. Wills
Department of Biology and Biochemistry
The University of Bath
The Avenue
Claverton Down
Bath BA2 7AY
United Kingdom

20
21 Telephone: 01225 383504
22 Fax: 01225 386779
23 E-mail: m.a.wills@bath.ac.uk

24
25
26
27

28 **Phylogenetic incongruence and homoplasy in the appendages and bodies of**
29 **arthropods: Why broad character sampling is best**

30

31 Andrew Brinkworth*, Robert Sansom, Matthew Wills*

32

33 **Corresponding author*

34

35 **Abstract**

36 Notwithstanding the rapidly increasing sampling density of molecular sequence data, morphological
37 characters still make an important contribution to our understanding of the evolutionary relationships
38 of arthropod groups. In many clades, characters relating to the number and morphological
39 specialisation of appendages are ascribed particular phylogenetic significance, and may be
40 preferentially sampled. However, previous studies have shown that partitions of morphological
41 character matrices often imply significantly different phylogenies. Here, we ask whether a similar
42 incongruence is observed in the appendage and non-appendage characters of arthropods. We apply
43 tree length (incongruence length difference: ILD) and tree distance (incongruence relationship
44 difference: IRD) tests to these partitions in an empirical sample of 52 published neontological data
45 sets for arthropods. We find significant incongruence about one time in five: more often than
46 expected, but markedly less often than in previous partition studies. We also find similar levels of
47 homoplasy within limb and non-limb characters, both in terms of internal consistency and consistency
48 relative to molecular trees. Taken together, these findings imply that sampled limb and non-limb
49 characters are of similar phylogenetic utility and quality, and that a total evidence approach to their
50 analysis is preferable.

51

52

53 Introduction

54 Despite the increasing ease and economy of obtaining ever larger volumes of molecular phylogenetic
55 data – coupled with progressively more sophisticated models for their analysis – morphological
56 characters can still contribute significantly to resolving the phylogeny of many clades (Wiens, 2004;
57 O’Leary & Gatesy, 2008; Gainett et al., 2014; also see discussion in Lopardo & Hormiga, 2015).
58 Morphological and molecular data are often reciprocally illuminating (e.g. Houde, 1994; Nicolalde-
59 Morejón et al., 2009), and can reveal hidden support when combined in a single total evidence
60 analysis (Kluge, 1989; Gatesy et al., 1999; Gatesy & Arctander, 2000; Wahlberg et al., 2005;
61 Damgaard, 2008; O’Leary & Gatesy, 2008; Padial et al., 2010; Mounce et al., 2016). For fossil
62 species, morphology is typically the only source of phylogenetic data, despite impressive strides in
63 obtaining sub-fossil DNA (e.g. Dabney et al., 2013; reviewed in Shapiro & Hofreiter, 2014; Orlando
64 et al., 2015) and the value of stratigraphic time series in a few special cases (Wills et al., 2008; Wills
65 *et al.* 2009; O’Connor & Wills, 2016). Unlike molecular sequence data, there are no widely
66 implemented standard frameworks for coding and archiving morphological data (but see O’Leary &
67 Kaufman, 2011; Davies *et al.*, 2017). Partly as a result of this, there is little systematic knowledge
68 concerning rates of evolution and levels of homoplasy in morphological characters from different
69 anatomical regions in different clades. Similarly, there is no consensus on the types of morphological
70 characters that are likely to be informative for cladogeneses of different geological ages. Despite this,
71 trees are often inferred from relatively restricted morphological character sets (Sanchez-Villagra &
72 Williams, 1998; Arratia, 2009; Song & Bucheli, 2010; Mounce et al., 2016) (a practice that may be
73 analogous to early molecular phylogenies that used small numbers of loci that may not always have
74 evolved at appropriate rates; Bateman, 1999). For fossil taxa, this may reflect various preservation
75 biases (Sansom et al., 2010, 2017; Sansom & Wills, 2013; Pattinson et al., 2014). For example,
76 molluscs typically lack all soft-part data (Castelin et al., 2017), while ostracods are almost exclusively
77 known from their sculpted, bivalved carapaces (Briggs *et al.*, 1993; Whatley *et al.*, 1993).

78

79 Character sampling in arthropods

80 Biased character sampling may be a particular problem in arthropods, where there is growing
81 evidence that overall levels of homoplasy are greater than in many other higher taxa (Engel, 2015).
82 Examples include the genital morphology of acarine mites (Klimov *et al.*, 2017) and insects (Bennik
83 *et al.*, 2016; Yoshizawa *et al.*, 2016), the wing morphology of lepidopterans (Finkbeiner *et al.*, 2017),
84 the limbs of amphipod crustaceans (Verheye *et al.*, 2016), and the overall morphology of cave-
85 dwelling Diplopoda (Liu *et al.*, 2017) and Collembola (Christiansen, 1960). Moreover, historically,
86 even the deep phylogeny of arthropods has been addressed with restricted character sets, and with a
87 striking diversity of results (e.g. Wheeler *et al.*, 1993; Giribet *et al.*, 2001; Boore *et al.*, 2005; Regier
88 *et al.*, 2005).

89 Characters pertaining to the number and morphological adaptations of limbs are particularly important
90 for arthropod systematics and phylogenetics (Størmer, 1939; Schulz, 2007; Gainett *et al.*, 2014).
91 Unfortunately, such characters are often poorly recorded in fossil arthropods, and several major
92 groups – notably trilobites (Størmer, 1939; Hughes, 2003) and ostracods (Smith, 2000) – preserve
93 limbs only under the most exceptional circumstances. Here, we address two questions in a sample of
94 38 arthropod data matrices comprising predominantly extant taxa, and coding a broad sample of
95 characters from both the limbs/mouthparts/antennae (appendages) and the rest of the body. Firstly we
96 ask whether levels of homoplasy differ between appendages on one hand, and body and carapace
97 characters on the other, such that the quality of data in either partition might be deemed superior (see
98 Pettigrew, 1991; Sanchez-Villagra & Williams, 1998; Williams, 2007; Song & Bucheli, 2010; Parker,
99 2016). Secondly we ask whether the hierarchical signals conveyed by appendage and body characters
100 imply different phylogenies (see Mounce *et al.* 2016; Sansom & Wills 2017; Sansom *et al.* 2017).

101

102

103 **Why examine morphological character partitions in arthropods?**

104 The rationale for this partitioning is twofold. Firstly, suites of characters can evolve in functionally or
105 developmentally integrated modules (Clarke & Middleton, 2008; Klingenberg, 2008; Lü *et al.*, 2010).
106 These can be subject to different selection pressures and evolve at different speeds (Maynard Smith,
107 1993; Lü *et al.*, 2010; Parker, 2016), thereby exhausting their character spaces at different rates

108 (Wagner, 1995,1997; Oyston et al., 2015; Oyston et al., 2016) and containing different levels of
109 homoplasy as a result. For example, Sánchez-Villagra & Williams (1998) demonstrated that strong
110 functional selection for feeding and locomotion increases the evolutionary lability of dental and
111 postcranial characters relative to cranial characters in the skeletons of mammals, while Sansom *et al.*
112 (2017) showed that mammalian dental data exhibit relatively poor congruence with independent
113 molecular phylogenies. Similarly, the mouthparts of insects (Angelini & Kaufman, 2005) and other
114 arthropods (Řezáč *et al.*, 2008; Baiocco *et al.*, 2017) are highly labile and are extensively modified in
115 lineage specific ways, reflecting the trophic resources that they exploit. The same is true of other
116 appendages, which are highly conserved in their underlying structure, but which possess a great
117 diversity of form and function across taxa of all ranks (Angelini & Kaufman, 2005). Relatively high
118 levels of homoplasy can also be found in arthropod body characters. For example, the classification of
119 ostracod crustaceans is heavily contingent on characters of the carapace (Tinn & Oakley, 2008),
120 despite marked and misleading convergence in form. Characters of the copulatory limbs, by contrast,
121 are much more conserved and less homoplastic (Park *et al.*, 2000; Cohen & Morin, 2003).
122 Secondly, much of the arthropod (particularly insect) fossil record is concentrated within a relatively
123 small number of Konservat-Lägerstätten (Sepkoski, 1981; Martinez-Delclòs *et al.*, 2004; Baalbergen
124 & Donovan, 2013). Outside of these exceptional localities, there are usually conspicuous biases in the
125 suites of characters or anatomical regions preserved. For example, Baalbergen & Donovan (2013)
126 found only the chelae of decapod crustaceans preserved (despite unusually good preservation of other
127 arthropod groups at the same site), while Stempien (2005) reported that the chelipeds and carapaces of
128 Brachyura were more likely to fossilize than their walking legs. Similarly, tough, sclerotized
129 structures such as the elytrae (Martinez-Delclòs *et al.*, 2004; Baalbergen & Donovan, 2013) of insects
130 are more frequently preserved than many other body parts. The calcite carapaces of ostracods
131 frequently preserve highly homoplastic and functionally constrained details of sculpture and
132 ornamentation, whereas limbs are only rarely fossilised (Smith, 2000). Among fossil Arachnomorpha,
133 the taxonomically diagnostic chelicerae are rarely reserved, obfuscating the systematic placement of
134 many specimens (Dunlop, 1997). Hence, body characters such as differentiation of the opisthosoma
135 and segmentation of the post-abdomen are more useful in fossil chelicerate systematics (Dunlop,

136 1997). Such anatomical biases on character sampling could mislead attempts to infer the relationships
137 of fossil arthropods, particularly if homoplasy is concentrated within the more readily preserved
138 characters.

139

140 **Materials & Methods**

141 **Datasets**

142 The character matrices utilised in this study were obtained from peer-reviewed papers published
143 between 2000 and 2017. We sought to sample all major living arthropod groups (Chelicerata,
144 Pancrustacea (Crustacea and Hexapoda), Myriapoda), including matrices of varying dimensions and
145 clades of both lower and higher ranks (genera through classes). Wherever possible, more recent and
146 more inclusive matrices were used. We utilised Graeme Lloyd's online compilation of matrices
147 (Lloyd,) and searches of Web of Science using higher taxon names plus the root keywords "phylog* +
148 morphol*". The resulting sample of 52 matrices contained representatives of 21 orders in 7 classes
149 (see Tables 1, 2). 38 matrices were collected for the incongruence tests and internal consistency tests
150 and 15 crustacean matrices were collected for the molecular consistency tests (see below).

151

152 **Definition of character partitions**

153 The "appendage" character partition included those pertaining to the legs and leg-derived appendages.
154 This encompassed all podomeres of the walking legs and modified legs such as brooding limbs (e.g.,
155 Jenner *et al.*, 2009) and the spinnerets of spiders (Selden *et al.*, 2008). Also included were characters
156 pertaining to the mouthparts, including mandibles, maxillae, and the labium (Angelini & Kaufman,
157 2005), as well as the palps, chelicerae and glossae. The labrum, hypopharynx and epipharynx were
158 also included in the "appendage" partition as they are closely functionally associated with the other
159 mouthparts and in some groups form a feeding apparatus for sucking or piercing in conjunction with
160 these other elements (Angelini & Kaufman, 2005). As such, we suspect that they are subject to similar
161 selective pressures (Klingenberg, 2008). Antennae were also included (Angelini & Kaufman, 2005),
162 as were genital structures derived from legs or fused coxae such as the hypandria. Characters

163 pertaining to setation or other elaborations of leg, mouthpart or appendage podomeres were also
164 included, as were characters referring to limb musculature.
165 The “body” character partition was defined, by default, as all those characters not encompassed
166 above. This included the wings and elytrae of insects, since we consider these to be derived from the
167 carapace of the thorax rather than from pre-existing limb structures (Clark-Hatchel & Tomoyasu,
168 2016). The “body” partition also included all characters encoding genital structures that were not
169 derived from appendages, such as those pertaining to the vulva, genital pore, spermatheca and
170 ovipositor. Characters pertaining to elaborations and ornamentations of body segments were included
171 with the “body” partition, as were characters of the eyes and internal organs. Behavioural, molecular,
172 developmental and sperm characters were removed from each matrix (these accounted for just 3% of
173 those analysed).

174

175 **Missing and inapplicable codes**

176 Poorly known taxa (or those that were otherwise scored for only a small number of characters) can be
177 highly mobile in sets of optimal trees; particularly those inferred using maximum parsimony. This
178 can, in turn, result in large numbers of MPTs, prohibitively long search times and poor resolution of
179 consensus trees (Wilkinson, 1995; Mounce et al., 2016). Where data matrices were found to be
180 subject to these issues empirically, we edited them (using Mesquite Version 3.40: Maddison &
181 Maddison 2018) by removing taxa with more than 75% of characters scored as missing (“?”) or
182 inapplicable (“-”) in either partition (50% for the data set of Schulz, 2007). We also removed taxa
183 found to be taxonomically equivalent to others (*sensu* Wilkinson, 1995). Any characters rendered
184 uninformative or invariant by this process were also deleted. A mean of just 0.47 taxa (~2.2%) and
185 3.34 characters (~3.6%) were removed from each dataset in this manner (for a list of the precise taxa
186 and characters deleted, see Appendix 1).

187 We did not set out to analyse matrices of fossils, since our intention was to compare signals in limb
188 and non-limb characters. Fossil taxa often tend to contain larger proportions of missing codings
189 (Wilkinson, 1995; Wiens, 1998; Mounce et al., 2016), and these missing codes tend to be
190 concentrated in characters pertaining to regions of anatomy with lower preservation potential. In

191 particular, fossils tend to lack data for limbs and other appendages. However, fossils are often
192 informative in phylogenetic analyses of arthropods (Legg et al., 2013) and other taxa (Cobbett *et al.*
193 2007), so fossil taxa within matrices of predominantly extant taxa (e.g. Schulz, 2007; Olesen, 2009;
194 Liu et al., 2012) were not discounted *a priori*, but only as a consequence of obfuscating analyses as
195 described above.

196

197 **Measuring homoplasy**

198 We took two approaches to measuring homoplasy: internal consistency of morphological characters
199 relative to the most parsimonious trees derived from those same morphological characters, and
200 molecular consistency of morphological characters when optimised onto independent molecular trees
201 (e.g. Sansom *et al.* 2017, Sansom and Wills 2017). With both approaches, we used the ensemble
202 Consistency Index (CI; Kluge & Farris, 1969) and ensemble Retention Index (RI; Farris, 1989). CI is
203 a commonly used and well-characterised index of homoplasy. However, it is subject to known biases,
204 notably a correlation with the number of characters and taxa in the dataset (Archie, 1989; Mounce *et*
205 *al.* 2016). For the internal CI, we removed these biases empirically by comparing the residuals from
206 regression analyses of CI on both matrix dimensions. For comparisons of the CI of morphological
207 character partitions optimised into molecular trees, however, there are no such biases because the
208 (molecular) trees are not inferred from the (morphological) data. For molecular consistency tests, we
209 sought independent molecular trees (Sansom and Wills 2017, Sansom *et al.* 2017). Taxa were pruned
210 (typically from the morphological data set) such that both morphological and molecular trees had the
211 same residual leaf set. This had the potential to render some morphological characters uninformative,
212 and these were subsequently removed from the matrix. Internal consistency measures were derived
213 using *PAUP* 4.0a.154* (Swofford, 2017) whilst molecular consistency measures were derived using
214 *TNT* (Goloboff, 2008) and *Mesquite* (Maddison & Maddison, 2018).

215

216 **Statistical tests for incongruence**

217 The Incongruence Length Difference (ILD) test (Mikevich & Farris, 1981; Farris *et al.*, 1995a; Farris
218 *et al.*, 1995b) is a widely implemented partition homogeneity test based upon the difference in most

219 parsimonious tree (MPT) length for a matrix when analysed as a whole, and the sum of MPT lengths
220 for the partitions of the matrix analysed in isolation (MPTs). More formally, the ILD for a bi-
221 partitioned matrix is given by $L_{AB} - (L_A + L_B)/L_{AB}$, where L_{AB} is the optimal tree length (in steps) from
222 the analysis of the entire matrix (the total evidence analysis), and L_A and L_B are the optimal tree
223 lengths for partitions A and B analyzed independently. This ILD is compared with a distribution of
224 ILD values (here, 999) for random bipartitions of the matrix in the same proportions as the original,
225 and a p value is derived from the fraction of these as large or larger than the original. The ILD test has
226 been criticized on philosophical grounds, and because it has a high Type I error rate (Dolphin *et al.*,
227 2000; Barker & Lutzoni, 2002; Ramirez, 2006; Sansom *et al.* 2017). However, it remains very widely
228 applied (Mounce *et al.*, 2016), and is used here as a measure of matrix partition incongruence rather
229 than as a criterion for combining those partitions (Figure 1).

230 In addition to the ILD test, we also implemented the incongruence relationship difference
231 (IRD) test of Ruta & Wills (2016) and Mounce *et al.* (2016). This is analogous to the ILD test in that a
232 measure of incongruence for the original data partition is compared with a distribution of
233 incongruence values for a large number of random partitions. However, whereas for the ILD
234 incongruence is measured in terms of additional tree length, a tree-to-tree distance metric is used for
235 the IRD. Many such metrics are available, but here we use two tests based upon the symmetrical-
236 difference (RF) distance (IRD_{RF} ; Robinson & Foulds, 1981) and maximum agreement subtree
237 (MAST) distance (IRD_{DI} ; Goddard *et al.*, 1994; de Vienne *et al.*, 2007). We acknowledge that other
238 metrics may have more desirable properties, but the RF distance in particular well characterised and
239 widely applied. It is unusual for a single most parsimonious tree (MPT) to result from a parsimony
240 search, and we therefore followed Mounce *et al.* (2016) in calculating the mean nearest neighbour
241 distance (NND) between each tree resulting from one partition and the most similar tree in the other
242 partition. In addition, we calculated the distances between strict, semi-strict and 50% majority rule
243 (plus compatible groupings) trees for the two partitions, although we caution that these offer poor or
244 positively misleading summaries of the differences between sets of trees (Mounce *et al.* 2016). We
245 illustrate this latter approach for the eumalacostracan data of Jenner *et al.* (2009) and Wills *et al.*
246 (2009) (Figure 2), and for the myriapod data of Blanke and Wesener (2014) (Figure 3). IRD tests were

247 initially based upon 99 random partitions of the data (c.f. 999 for the computationally much faster
248 ILD). However, in those cases where $p \leq 0.10$, we re-ran the test for that data set using 499 random
249 partitions (Figure 1).

250 All parsimony searches were implemented using 25 random additions of taxa, followed by
251 tree bisection and reconnection branch swapping, and retaining 10 trees at each step. To expedite the
252 searches, we limited the number of trees stored in memory to 100,000, and for the IRD tests we
253 calculated nearest neighbour tree-to-tree distances based upon no more than 1,000 trees from each
254 partition (2,000 trees in total and 1,999,000 tree-to-tree distances calculated for each metric in order to
255 find the minima). Consensus trees were calculated from all MPTs, up to the 100,000 buffer. We also
256 condensed the resulting most parsimonious trees by collapsing branches with a minimum length of
257 zero (Goloboff's 'amb-') and removing all but one of any consequently identical trees. All analyses
258 were implemented in PAUP* 4.0a.154 for Macintosh (Swofford, 2017), using scripts (by MAW) that
259 produced batch files for PAUP* and summarised the log files that it produced (see Supplementary
260 Materials).

261

262 **Results**

263 **There is no difference in levels of homoplasy (CI) or retained synapomorphy (RI) for limb and** 264 **body characters**

265 There were no significant differences in mean levels of internal homoplasy (as measured by the
266 ensemble Consistency Index, CI) between limb and body partitions, either for the 38 datasets in
267 combination, or for subphyla considered in isolation ($p > 0.05$ in all cases) (Fig. 5). To account for the
268 known biases in CI, residuals from regression analyses of internal CI on both the log of the number of
269 characters and the log of the number of taxa were also compared across partitions. The results differed
270 little from those for raw CI (Figure 4), and no significant differences were detected. A similar set of
271 analyses for retained synapomorphy (as measured by the Retention Index: RI) also revealed no
272 differences between limb and body partitions, either overall or within subphyla. Our findings were
273 similar for the 15 crustacean data sets for which we had independent molecular trees: there were no

274 differences between the CI or the RI of limb versus body character partitions when optimised onto
275 those molecular trees ($p < 0.05$ for paired t tests) (Fig. 5).

276

277 **Limb and body partitions imply significantly different trees one time in five**

278 Both the ILD test and the IRD_{RF} test for nearest neighbours reported significant ($p < 0.05$)
279 incongruence between the trees inferred from limb and body character partitions in about one in five
280 cases (8/38 and 7/38 respectively). The IRD_{D1} test for nearest neighbours reported significant ($p < 0.05$)
281 incongruence slightly less often (5/38). We note that the different tests assess different aspects of
282 incongruence, and the p values for ILD, IRD_{RF} and IRD_{D1} do not precisely coincide. Hence, a
283 significant p-value ($p < 0.05$) is obtained for both IRD_{RF} and IRD_{D1} in 3 datasets, and for all three tests
284 (including the ILD) in only 2 cases. Rates of significant incongruence are summarised in Table 2. For
285 the ILD test, our finding that 8 from 38 data sets were incongruent with $p \leq 0.05$ means that
286 incongruence is significantly more common than expected by chance (two would be anticipated:
287 binomial test $p = 0.0005$). The IRD_{RF} test also detected significant incongruence significantly more
288 often than expected ($p = 0.0025$). Whilst reporting significant incongruence at the lowest rate, the
289 IRD_{D1} test also detected a significantly higher rate of incongruence than would be expected ($p =$
290 0.03973 , binomial test).

291

292 **The outcome of the ILD and IRD tests is not significantly influenced by data set parameters or** 293 **by taxonomic group**

294 We sought to determine whether various data set dimensions and imbalances might determine the
295 outcome of our incongruence tests ($p \leq 0.05$ or $p > 0.05$). In addition to data matrix dimensions,
296 previous studies (e.g., Mounce et al., 2016; Sansom *et al.* 2013, 2017.) have accounted for (or
297 variously controlled) amounts of missing data within partitions or regions. In general, we found that
298 there was no significant difference in the median percentage of cells scored as missing/inapplicable
299 for limb and body partitions across the entire data set (Mann-Whitney $U = 36.9636$, $p = 0.4242$).
300 Neither were there significant differences in the mean or variances of percentages of
301 missing/inapplicable codings for limb and body partitions within individual sub-phyla: myriapods

302 (paired $t = -0.3868$, $p = 0.7148$), crustaceans (paired $t = -0.5852$, $p = 0.5768$), chelicerates (paired $t = -$
303 0.7982 , $p = 0.4510$), hexapods (paired $t = -0.4896$, $p = 0.6315$) (Fig. 6). For each data set, however,
304 we also took account of the difference in percentage of missing data between partitions (this was a
305 marginally significant factor in the study of Mounce *et al.*, 2016). However, a logistic regression
306 model (see Appendix 2) showed that the outcome of the ILD was not significantly influenced by the
307 log of the percentage of missing data across both partitions ($p=0.6127$), the difference in the
308 percentage of missing data between partitions ($p=0.1551$), the difference between partition sizes
309 ($p=0.1564$), the log of the number of taxa ($p=0.0606$), log of the number of characters ($p=0.0667$) or
310 the interaction between these last two variables ($p=0.0619$). The model also showed that higher
311 taxonomic group (i.e., Chelicerata, Crustacea, Hexapoda, Myriapoda) had no effect on ILD outcome.
312 Similarly, a log-likelihood ratio test (G-test) revealed no difference in the frequencies of significant or
313 non-significant outcomes across these higher taxa ($G = 4.0863$, $p = 0.2523$). We found similar results
314 from logistic modelling of the outcome of the IRD_{RF} and IRD_{DI} tests, with no significant effect for
315 overall percentage of missing data ($p=0.511$ and $p=0.396$), the difference in percentage of missing
316 data between partitions ($p=0.330$ and $p=0.987$), the log of the number of taxa ($p=0.838$ and $p=0.379$),
317 log of the number of characters ($p=0.692$ and $p=0.417$), or the interaction between characters and taxa
318 ($p=0.727$ and $p=0.381$). Higher taxonomic group also had no effect for either test, and G-tests also
319 revealed no difference in the frequency of significant outcomes for the four groups (IRD_{RF} , $G =$
320 2.7948 , $p = 0.4244$; IRD_{DI} , $G = 1.4049$, $p = 0.7044$).

321

322 **Limb and body character sampling**

323 Overall there was no significant difference in the log of number of characters sampled from each
324 partition of the datasets in Table 1 ($t = -0.3461$, $p = 0.7312$, paired t-test of logs). Furthermore, no
325 significant difference was observed in chelicerates ($t = -0.5679$, $p = 0.5907$, paired t-test) or
326 myriapods ($t = 2.1830$, $p = 0.0808$, paired t-test). However, differences were observed within
327 crustaceans ($t = 2.7658$, $p = 0.0279$, paired t-test of logs) and hexapods ($t = -4.4382$, $p = 0.0005$,
328 paired t-test of logs). Crustacean datasets contained significantly more limb characters than those
329 from the body, while the opposite tendency pertained in hexapod datasets. We do not assume that

330 these differences reflect a bias of sampling from the hypothetical universe of possible leg and body
331 characters, since there is no reason to suppose that the two partitions should yield identical character
332 numbers (a naïve null hypothesis). Rather, we merely report that the numbers do, in fact, differ in the
333 case of crustaceans and hexapods.

334

335 Discussion and Conclusions

336 1. Levels of incongruence

337 Rates of significant ($p < 0.05$) incongruence between limb and body partitions across our sample of
338 arthropod matrices were significantly higher than expected for all of our tests. We found 8 from 38
339 significant with $p \leq 0.05$ for the ILD (one in five) and 7 from 38 for the IRD_{RF} , whereas two (one in
340 twenty) would be expected by chance (binomial test $p = 0.0005$). The only previous, systematic studies
341 of partition homogeneity using similar approaches to those deployed here concerned the craniodental
342 and postcranial characters of vertebrates (Mounce *et al.*, 2016), the dental and osteological characters
343 of mammals (Sansom *et al.*, 2017) and hard and soft part characters across a diversity of animal
344 clades (Sansom & Wills, 2017). Higher rates of significant ($p < 0.05$) incongruence were reported in
345 those earlier studies: about 1 in 3 (ILD and IRD) for craniodental/body characters and hard/soft
346 characters, and up to 1 in 2 (ILD) for dental/osteological characters (compared with 1 in 5 for the ILD
347 and IRD across our arthropods). There is no reason to expect limb versus body partitions for
348 arthropods to yield similar rates of null rejection to functionally and anatomically different partitions
349 in other groups. However, levels of limb to body incongruence for our sample of arthropods are not
350 especially high, and this is good news for those attempting to infer the relationships of fossil
351 arthropods that lack details of appendage morphology, provided there is enough character data
352 overall.

353 Lack of partition homogeneity can result from a variety of factors other than conflict between
354 the phylogenetic signals inherent in partitions (Mounce *et al.*, 2016; Dolphin *et al.*, 2000; Planet,
355 2006). However, we demonstrate that there are no significant ($p < 0.05$) differences in overall levels
356 of either internal or molecular consistency between the partitions of our data sets (CI and RI, Figures

357 4, 5), and neither are there differences in amounts of missing data. Although the levels of homoplasy
358 contained within each partition may be comparable, the quality of this noise often misinforms the
359 inference of phylogenies in different ways, thereby resulting in incongruence.

360

361 **2. Implications of incongruence**

362 Whatever the cause of the incongruence between partitions, it is still observed more often than we
363 would expect, with several implications. Focussing on restricted suites of characters to the exclusion
364 of others is questionable practice, unless it has been demonstrated *a priori* (e.g., in a large empirical
365 sample: Sansom *et al.*, 2017; Sansom and Wills, 2017) that some classes of characters are intrinsically
366 more informative and less prone to homoplasy than others. This is not the case for the appendage and
367 body characters of arthropods. Nevertheless, uneven character sampling is commonplace in arthropod
368 systematics (Clarke, 2011), and we find these biases in some higher taxa here. Such biases probably
369 reflect previous expectations that certain characters are of more value or contain a stronger
370 phylogenetic signal than others (see Sanchez-Villagra & Williams, 1998; Williams, 2007; Song &
371 Bucheli, 2010; Parker, 2016; Mounce *et al.*, 2016; Sansom *et al.*, 2017). For example, Gainett *et al.*
372 (2014) focused upon appendicular characters in their phylogeny of harvestmen, while Dunlop (1997)
373 found that characters of body segmentation and segment differentiation were particularly helpful in
374 determining the higher-level relationships of chelicerates (Dunlop, 1997). Our sample of data sets
375 does not support this idea for limb and body characters across arthropods.

376 Such biases are most acute (and often unavoidable) in many fossil groups, where the more
377 heavily mineralized or sclerotized cuticle of the carapace and tergites typically preserve more readily
378 than that of the limbs. Hence, many fossil arthropod taxa lack details of the appendages, and focus,
379 out of necessity, on ‘body’ characters of segmentation and ornamentation. In ostracods, for example,
380 body characters are the most readily available (Tinn & Oakley, 2008), despite suggestions that
381 appendicular characters are of much greater utility (Park *et al.*, 2002; Cohen & Moren, 2003).
382 Notwithstanding, many arthropod studies uncover hidden support and hidden branch support (Gatesy
383 *et al.*, 1999) from combined suites of morphological characters (Clarke, 2011) and from the
384 combination of morphological and molecular data (e.g. Damgaard, 2008; Wahlberg *et al.*, 2005). We

385 therefore advocate holistic character sampling (Song & Bucheli, 2010) and principles of total
386 evidence (Kluge, 1989; Gatesy & Springer, 2014; Mounce *et al.*, 2016; see also Gatesy & Arctander,
387 2000) in arthropod phylogenetics.

388 There are other systematic problems that may occur when trees are inferred from non-random
389 character samples, although these are usually framed in terms of the effects of missing data. In this
390 regard, it is not the number of missing entries in a matrix so much as the amount of data that *are*
391 present that influences the resolution of trees and the stability of taxa within them (Wiens, 2003ab;
392 Cobbett *et al.*, 2007). Non-random blocks of missing data – such as those that typically result from
393 the concatenation of molecular data sets with different taxon samples (Chernomor *et al.*, 2016;
394 Dillman *et al.*, 2016; Dobrin *et al.*, 2018) or morphological data sets containing a mix of fossil and
395 extant taxa (Pattinson *et al.*, 2015; Sansom, 2015) – bring their own particular set of problems. The
396 processes of decay prior to fossilisation obliterate soft part character data, but a recent and surprising
397 finding is that such characters tend to optimize along branches further from the root of the tree than
398 their more fossilizable counterparts. The simulated removal of soft part data from species within real
399 neontological data sets therefore tends to result in the disproportionate ‘stemward slippage’ of
400 lineages towards the root of the tree (Sansom & Wills, 2013; Sansom, 2015). It is therefore likely that
401 many fossils appear more plesiomorphic and erroneously resolve closer to the roots of phylogenies as
402 a function of taphonomic filters (Sansom *et al.*, 2017). This needs to be explored on greater detail
403 across the phylogeny of arthropods.

404

405

406 References

407 **Adamowicz SJ, Purvis A. 2006.** From more to fewer? Testing an allegedly pervasive trend in the
408 evolution of morphological structure. *Evolution* **60**: 1402-1416.

409 **Angelini DR, Kaufman TC. 2005.** Insect appendages and comparative ontogenetics. *Developmental*
410 *Biology* **286**: 57-77.

411 **Archie JW. 1989.** Homoplasy excess ratios: New indices for measuring levels of homoplasy in
412 phylogenetic systematics and a critique of the consistency index. *Systematic Biology* **38(3)**:
413 253-269.

414 **Arratia G. 2009.** Identifying patterns of diversity of the actinopterygian fulcra. *Acta Zoologica* **90(1)**:
415 220-235.

416 **Baalbergen E, Donovan SK. 2013.** Terrestrial arthropods from the Late Pleistocene of Jamaica:
417 systematics, palaeoecology and taphonomy. *Geological Journal* **48**: 628-645.

418 **Baiocco M, Bonato L, Cardini A, Fusco G. 2017.** Shape variation of prey-catching structures in
419 geophilomorph centipedes: A preliminary investigation using geometric morphometrics.
420 *Zoologischer Anzeiger* **268**: 11-18.

421 **Banks JC, Paterson AM. 2004.** A penguin-chewing louse (Insecta: Phthiraptera) phylogeny derived
422 from morphology. *Invertebrate Systematics* **18**: 89-100.

423 **Barker FK, Lutzoni FM. 2002.** The utility of the Incongruence Length Difference test. *Systematic*
424 *Biology* **51(4)**: 625-637.

425 **Bateman RM. 1999.** Integrating molecular and morphological evidence of evolutionary radiations.
426 In: Hollingsworth PM, Bateman RM, Gornall RJ editors. *Molecular Systematics and Plant*
427 *Evolution*, p. 432-471.

428 **Bennik RM, Buckley TR, Hoare RJB, Holwell GI. 2016.** Molecular phylogeny reveals the repeated
429 evolution of male genital traits in the New Zealand moth genus *Izatha* (Lepidoptera:
430 Xyloryctidae). *Systematic Entomology* **41**: 309-322.

431 **Blagoderov V, Hippa H, Sevcik J. 2009.** *Asiorrhina*, a new Oriental genus of Lygistorrhinidae
432 (Diptera: Sciaroidea) and its phylogenetic position. *Zootaxa* **2295**: 31-45.

433 **Blanco-Bercial L, Bradford-Grieve JM, Bucklin A. 2011.** Molecular phylogeny of the Calanoida
434 (Crustacea: Copepoda). *Molecular Phylogenetics and Evolution* **59**: 103-113.

435 **Bochkov AV, Klimov PB, Wauthy G. 2011.** Phylogeny and coevolutionary associations of
436 makialgine mites (Acari, Psoroptidae, Makialginae) provide insight into evolutionary history of
437 their hosts, strepsirrhine primates. *Zoological Journal of the Linnean Society* **162**: 1–14.

438 **Boore JL, Collins TM, Stanton D, Daehler LL, Brown WM. 1995.** Deducing the pattern of
439 arthropod phylogeny from mitochondrial DNA rearrangements. *Nature* **376**: 163-165.

440 **Botero-Trujillo R, Ott R, Carvalho LS. 2017.** Systematic revision and phylogeny of the South
441 American sun-spider genus *Gaucha* Mello-Leitão (Solifugae: Mummuciidae), with description
442 of four new species and two new generic synonymies. *Arthropod Systematics & Phylogeny*
443 **75(1)**: 3-44.

444 **Bracken-Grissom HD, Ah Yong ST, Wilkinson RD, Feldmann RM, Schweitzer CE, Breinholt**
445 **JW, Bendall M, Palero F, Chan T-Y, Felder DL, Robles R, Chu K-H, Tsang L-M, Kim D,**
446 **Martin JW, Crandall KA. 2014.** The emergence of lobsters: Phylogenetic relationships,
447 morphological evolution and divergence time comparisons of an ancient group (Decapoda:
448 Achelata, Astacidea, Glypheidea, Polychelida). *Systematic Biology* **63**:457-479.

449 **Bradford-Grieve JM, Blanco-Bercial L, Boxshall GA. 2017.** Revision of the family Megacalanidae
450 (Copepoda: Calanoida). *Zootaxa* **4229**: 1-183.

451 **Bradford-Grieve JM, Boxshall GA, Ah Yong ST, Ohtsuka S. 2010.** Cladistic analysis of the
452 calanoid Copepoda. *Invertebrate Systematics* **24**: 291-321.

453 **Calor AR, Holzenthal RW. 2008.** Phylogeny of Grumichellini Morse, 1981 (Trichoptera:
454 Leptoceridae) with the description of a new genus from southeastern Peru. *Aquatic Insects*
455 **30(4)**: 245-259.

456 **Castelin M, Williams ST, Buge B, Maestrati P, Lambourdiere J, Ozawa T, Utge J, Couloux A,**
457 **Alf A, Samadi S. 2017.** Untangling species identity in gastropods with polymorphic shells in
458 the genus *Bolma* Risso, 1826 (Mollusca, Vetigastropoda). *European Journal of Taxonomy* **288**:
459 1-21.

460 **Chamorro ML, Konstantinov AS. 2011.** Cachiporrini, a remarkable new tribe of Lamprosomatinae
461 (Coleoptera, Chrysomelidae) from South America. *ZooKeys* **78**: 43-59.

462 **Chan TY, Ho KC, Li CP, Chu KH. 2009.** Origin and diversification of the clawed lobster genus
463 *Metanephrops* (Crustacea: Decapoda: Nephropidae). *Molecular Phylogenetics and Evolution*
464 **50**: 411-422.

465 **Chang S, Tshudy D, Sornhannus U, Ahyong ST, Chan T. 2016.** Evolution of the
466 thaumastocheliform lobsters (Crustacea, Decapoda, Nephropidae). *Zoologica Scripta* **46**: 373-
467 387.

468 **Chernomor O, von Haeseler A, Bui Quang M. 2016.** Terrace aware data structure for
469 phylogenomic inference from supermatrices. *Systematic Biology*, **65**:997-1008.

470 **Christiansen K. 1960.** Convergence and Parallelism in Cave Entomobryinae. *Evolution* **15**: 288-301.

471 **Clarke DJ. 2011.** Testing the phylogenetic utility of morphological character systems, with a revision
472 of *Creophilus* Leach (Coleoptera: Staphylinidae). *Zoological Journal of the Linnean Society*
473 **163**: 723-812.

474 **Clarke JA, Middleton KM. 2008.** Mosaicism, modules, and the evolution of birds: Results from a
475 Bayesian approach to the study of morphological evolution using discrete character data.
476 *Systematic Biology* **57(2)**: 185-201.

477 **Clark-Hatchel CM, Tomoyasu Y. 2016.** Exploring the origin of insect wings from an evo-devo
478 perspective. *Current Opinion in Insect Science* **13**: 77-85.

479 **Cobbett A, Wilkinson M, Wills MA. 2007** Fossils impact as hard as living taxa in parsimony
480 analyses of morphology. *Systematic Biology* **56(5)**: 753-766.

481 **Cohen AC, Morin JG. 2003.** Sexual morphology, reproduction and the evolution of bioluminescence
482 in Ostracoda. *The Paleontological Society Papers* **9**: 37-70.

483 **Dabney J, Knapp M, Glocke I, Gansauge M-T, Weihmann A, Nickel B, Valdiosera C, García N,**
484 **Pääbo S, Arsuaga J-L, Meyer M. 2013.** Complete mitochondrial genome sequence of a
485 Middle Pleistocene cave bear reconstructed from ultrashort DNA fragments. *Proceedings of the*
486 *National Academy of Sciences of the United States* **110(39)**: 15758-15763.

487 **Damgaard J. 2008.** Phylogeny of the semiaquatic bugs (Hemiptera-Heteroptera, Gerromorpha).
488 *Insect Systematics & Evolution* **39**: 431-460.

489 **Davies TG, Rahman IA, Lautenschlager S, Cunningham JA, Asher RJ, Barrett PM, Bates KT,**
490 **Bengston S, Benson RBJ, Boyer DM, Braga J, Bright JA, Claessens LPAM, Cox PG, Don**
491 **X-P, Evans AR, Falkingham PL, Friedman M, Garwood RJ, Goswami A, Hutchinson JR,**
492 **Jeffery S, Johanson Z, Lebrun R, Martínez-Pérez C, Marúgan-Lobón J, O'Higgins PM,**

493 **Metscher B, Orliac M, Rowe TB, Rücklin M, Sánchez-Villagra MR, Shubin NH, Smith**
494 **SY, Starck JM, Stringer C, Summers AP, Sutton MD, Walsh ST, Weisbecker V, Witmer**
495 **LM, Wroe S, Yin Z, Rayfield EJ, Donoghue PCJ. 2017.** Open data and digital morphology.
496 *Proceedings of the Royal Society B* **284**: 20170194.

497 **Del Rio MG, Malvardi AE, Lanteri A. 2012.** Systematics and cladistics of a new Naupactini genus
498 (Coleoptera: Curculionidae: Entiminae) from the Andes of Colombia and Ecuador. *Zoological*
499 *Journal of the Linnean Society* **166**: 54-71.

500 **de Vienne DM, Giraud T, Martin OC. 2007.** A congruence index for testing topological similarity
501 between trees. *Bioinformatics* **23**: 3119-3124.

502 **di Giulio A, Fattorini S, Kaupp A, Taglianti AV, Nagel P. 2003.** Review of competing hypotheses
503 of phylogenetic relationships of Paussinae (Coleoptera: Carabidae) based on larval characters.
504 *Systematic Entomology* **28**: 509-537.

505 **Dillman CB, Sidlauskas BL, Vari RP. 2016.** A morphological supermatrix-based phylogeny for the
506 neotropical fish superfamily Anostomoidea (Ostariophysi: Characiformes): phylogeny, missing
507 data and homoplasy. *Cladistics*, **32**:276-296.

508 **Dobrin BH, Zwickl DJ, Sanderson MJ. 2018.** The prevalence of terraced treescapes in analyses of
509 phylogenetic data sets. *BMC Evolutionary Biology*, **18**.

510 **Dolphin K, Belshaw R, Orme CDL, Quicke DLJ. 2000.** Noise and incongruence: Interpreting
511 results of the Incongruence Length Difference test. *Molecular Phylogenetics and Evolution*
512 **17(3)**: 401-406.

513 **Dreyer H, Wägele JW. 2001.** Parasites of crustaceans (Isopoda: Bopyridae) evolved from fish
514 parasites: Molecular and morphological evidence. *Zoology* **103**: 157-178.

515 **Dunlop JA. 1997.** Palaeozoic arachnids and their significance for arachnid phylogeny. *Proceedings of*
516 *the 16th European Colloquium of Arachnology* 65-82.

517 **Edgecombe GD, Barrow L. 2007.** A new genus of scutigrid centipedes (Chilopoda) from Western
518 Australia, with new characters for morphological phylogenetics of Scutigromorpha. *Zootaxa*
519 **1409**: 23-50.

520 **Engel MS. 2015.** Insect Evolution. *Current Biology Magazine* **25**: 868-872.

521 **Farris JS, Kallersjo M, Kluge AG, Bult C. 1995a.** Constructing a significance test for
522 incongruence. *Systematic Biology* **44(4)**: 570-572.

523 **Farris JS, Kallersjo M, Kluge AG, Bult C. 1995b.** Testing significance of incongruence. *Cladistics*
524 **10**: 315-31.

525 **Finkbeiner SD, Briscoe AD, Mullen SP. 2017.** Complex dynamics underlie the evolution of
526 imperfect wing pattern convergence in butterflies. *Evolution* **71(4)**: 949-959.

527 **Gainett G, Sharma PP, Pinto-da-rocha R, Giribet G, Willemart RH. 2014.** Walk it off: predictive
528 power of appendicular characters toward inference of higher-level relationships in Laniatores
529 (Arachnida: Opiliones). *Cladistics* **30**: 120-138.

530 **Gatesy J, O'Grady P, Baker RH. 1999.** Corroboration among data sets in simultaneous analysis:
531 Hidden support for phylogenetic relationships among higher level artiodactyl taxa. *Cladistics*
532 **15**: 271-313.

533 **Gatesy J, Arctander P. 2000.** Hidden morphological support for the phylogenetic placement of
534 *Pseudoryx nghetinhensis* with bovine bovids: A combined analysis of gross anatomical
535 evidence and DNA sequences from five genes. *Systematic Biology* **49(3)**: 515-538.

536 **Gatesy J, Springer MS. 2014.** Phylogenetic analysis at deep timescales: Unreliable gene trees,
537 bypassed hidden support, and the coalescence/concatalescence conundrum. *Molecular*
538 *Phylogenetics and Evolution* **80**: 231-266.

539 **George KH. 2017.** Phylogeny of the taxon Paralaophontodes Lang (Copepoda, Harpacticoida,
540 Laophontodinae), including species descriptions, chorological remarks, and a key to species.
541 *Zoosystematics and Evolution* **93(2)**: 211-241.

542 **Gerstmeier R, Eberle J. 2011.** Definition and revision of the Orthrius-group of genera (Coleoptera,
543 Cleridae, Clerinae). *ZooKeys* **92**: 35-60.

544 **Giribet G, Edgecombe GD, Wheeler WC. 2001.** Arthropod phylogeny based on eight molecular
545 loci and phylogeny. *Nature* **413**: 157-161.

546 **Goloboff PA, Farris JS, Nixon KC. 2008.** TNT, a free program for phylogenetic analysis. *Cladistics*
547 **24**:774-786.

548 **Goddard W, Kubicka E, Kubicki G, McMorris FR. 1994.** The agreement metric for labelled
549 binary trees. *Mathematical Biosciences* **123(2)**: 215-226.

550 **Grebennikov VV, Newton AF. 2009.** Good-bye Scydmaenidae, or why the ant-like stone beetles
551 should become megadiverse Staphylinidae sensu latissimo (Coleoptera). *European Journal of*
552 *Entomology* **106**: 275-301.

553 **Grebennikov VV. 2010.** First *Alaocybites* weevil (Insecta: Coleoptera: Curculionoidea) from the
554 Eastern Palaearctic: a new microphthalmic species and generic relationships. *Arthropod*
555 *Systematics & Phylogeny* **68(3)**: 331-365.

556 **Hermoso-Salazar M, Wicksten M, Morrone JJ. 2008.** Phylogenetic analysis of the Paulsoni species
557 group (Decapoda: Alpheidae) from the American Pacific, with implications for the
558 phylogenetic classification of the genus *Synalpheus*. *Zootaxa* **1744**: 19-30.

559 **Houde P. 1994.** Evolution of Heliornithidae: Reciprocal illumination by morphology, biogeography
560 and DNA hybridization (Aves: Gruiformes). *Cladistics* **10**: 1-19.

561 **Hultgren KM, Hurt C, Anker A. 2014.** Phylogenetic relationships within the snapping shrimp genus
562 *Synalpheus* (Decapoda: Alpheidae). *Molecular Phylogenetics and Evolution* **77**: 116-125.

563 **Hughes NC. 2003.** Trilobite Tagmosis and body patterning from morphological and developmental
564 perspectives. *Integrative and Comparative Biology* **43(1)**: 185-206

565 **Jenner RA, Ní Dhubhghaill CN, Ferla MP, Wills MA. 2009.** Eumalacostran phylogeny and total
566 evidence: limitations of the usual suspects. *BMC Evolutionary Biology* **9**:21.

567 **Karasawa H, Schweitzer CE, Feldmann RM. 2013.** Phylogeny and systematics of extant and
568 extinct lobsters. *Journal of Crustacean Biology* **33**: 78-123.

569 **Klimov PB, Mironov SV, OConnor B.M. 2017.** Convergent and unidirectional evolution of
570 extremely long aedeagi in the largest feather mite genus, *Proctophyllodes* (Acari:
571 *Proctophyllodidae*): Evidence from comparative molecular and morphological phylogenetics.
572 *Molecular Phylogenetics and Evolution* **114**: 212-224.

573 **Klingenberg CP. 2008.** Morphological integration and developmental modularity. *Annual Review of*
574 *Ecology, Evolution and Systematics* **39**: 115-132.

575 **Klompen H, Amin M, Gerdeman BS. 2013.** A revision of the genus *Afroheterozercon* (Acari:
576 *Heterozerconidae*). *Zootaxa* **3626(3)**: 301–325.

577 **Kluge AG, Farris JS. 1969.** Quantitative Phyletics and the Evolution of Anurans. *Systematic Zoology*
578 **18(1)**: 1-32.

579 **Kluge AG. 1989.** A concern for evidence and a phylogenetic hypothesis of relationships among
580 *Epicrates* (Boidae, Serpentes). *Systematic Zoology* **38(1)**: 7-25.

581 **Koch M, Parschke S, Edgecombe GD. 2009.** Phylogenetic implications of gizzard morphology in
582 scolopendromorph centipedes (Chilopoda). *Zoologica Scripta* **38(3)**: 269-288.

583 **Legg DA, Sutton MD, Edgecombe GD. 2013.** Arthropod fossil data increase congruence of
584 morphological and molecular phylogenies. *Nature Communication* **4**: 2485.

585 **Liu W, Golovatch S, Wesener T, Tian M. 2017.** Convergent Evolution of Unique Morphological
586 Adaptations to a Subterranean Environment in Cave Millipedes (Diplopoda). *PLoS ONE* **12(2)**:
587 e0170717.

588 **Liu X, Wang Y, Shih C, Ren D, Yang D. 2012.** Early evolution and historical biogeography of
589 fishflies (Megaloptera: Chauliodinae): Implications from a phylogeny combining fossil and
590 extant taxa. *PLoS ONE* **9(9)**: e40345.

591 **Lopardo L, Hormiga G. 2015.** Out of the twilight zone: phylogeny and evolutionary morphology of
592 the orb-weaving spider family Mysmenidae, with a focus on spinneret spigot morphology in
593 symphytognathoids (Araneae, Araneoidea). *Zoological Journal of the Linnean Society* **173**:
594 527–786.

595 **Lörz AN, Brandt A. 2004.** Phylogeny of Antarctic Epimeria (Epimeriidae: Amphipoda). *Journal of*
596 *the Marine Biological Association of the United Kingdom* **84**: 179-190.

597 **Lörz AN, Held C. 2004.** A preliminary molecular and morphological phylogeny of the Antarctic
598 Epimeriidae and Iphimediidae (Crustacea, Amphipoda). *Molecular Phylogenetics and*
599 *Evolution* **31**: 4-15.

600 **Lü J, Unwin DM, Jin X, Liu Y, Ji Q. 2010.** Evidence for modular evolution in a long-tailed
601 pterosaur with a pterodactyloid skull. *Proceedings of the Royal Society B* **277**: 383-389.

602 **Ma KY, Chan TY, Chu KH. 2009.** Phylogeny of penaeoid shrimps (Decapoda: Penaeoidea) inferred
603 from nuclear protein-coding genes. *Molecular Phylogenetics and Evolution* **53**: 45-55.

604 **Maddison WP, Maddison DR. 2018.** *Mesquite*: a modular system for evolutionary analysis. Version
605 3.51. <http://www.mesquiteproject.org>

606 **Martinez-Delclòs X, Briggs DEG, Peñalver E. 2004.** Taphonomy of insects in carbonates and
607 amber. *Palaeogeography, Palaeoclimatology, Paleoecology* **203**: 19-64.

608 **Maynard Smith J. 1993.** The Theory of Evolution. Cambridge University Press: Cambridge.

609 **McLaughlin PA, Lemaitre R, Sorhannus U. 2007.** Hermit crab phylogeny: a reappraisal and its
610 “fall-out”. *Journal of Crustacean Biology* **27(1)**: 97-115.

611 **Meland K, Willasen E. 2004.** Molecular phylogeny and biogeography of the genus *Pseudomma*
612 (Peracarida: Mysida). *Journal of Crustacean Biology* **24**: 541-557.

613 **Mendes AC. 2011.** Phylogeny and taxonomic revision of Heteropachylinae (Opiliones: Laniatores:
614 Gonyleptidae). *Zoological Journal of the Linnean Society* **163**: 437–483.

615 **Michel-Salzat A, Cameron SA, Oliveira ML. 2004.** Phylogeny of the orchid bees (Hymenoptera:
616 Apinae: Euglossini): DNA and morphology yield equivalent patterns. *Molecular Phylogenetics
617 and Evolution* **32**: 309-323.

618 **Mickevich MF, Farris JS. 1981.** The implications of congruence in Menidia. *Systematic Zoology* **30**:
619 351-370.

620 **Mounce RCP, Sansom R, Wills MA. 2016.** Sampling diverse characters improves phylogenies:
621 Craniodental and postcranial characters of vertebrates often imply different trees. *Evolution*
622 **70(3)**: 666-686.

623 **Nicolalde-Morejó F, Vergara-Silva F, Vovides AP, de los Monteros AE. 2009.** Reciprocal
624 illumination of morphological characters upon a molecular hypothesis supports proposal of a
625 new species of cycad from Mexico. *Systematics and Biodiversity* **7(1)**: 73-79.

626 **Oakley TH, Wolfe JM, Lindgren AR, Zaharoff AK. 2012.** Phylotranscriptomics to bring the
627 understudied into the fold: Monophyletic Ostracoda, fossil placement, and pancrustacean
628 phylogeny. *Molecular Biology and Evolution* **30**: 215-233.

629 **O'Connor A, Wills MA. 2016.** Measuring stratigraphic congruence across trees, higher taxa and
630 time. *Systematic Biology* **65(5)**: 792-811.

631 **O'Leary MA, Gatesy J. 2008.** Impact of increased character sampling on the phylogeny of
632 Cetartiodactyla (Mammalia): combined analysis including fossils. *Cladistics* **24**: 397-442.

633 **O'Leary MA, Kaufman S. 2011.** *MorphoBank*: phylophenomics in the 'cloud'. *Cladistics*. **27**:1-9.

634 **Olesen J. 2009.** Phylogeny of Branchiopoda (Crustacea) – Character evolution and contribution of
635 uniquely preserved fossils. *Arthropod Systematics & Phylogeny* **67(1)**: 3-39.

636 **Orlando L, Gilbert MTP, Willerslev E. 2015.** Reconstructing ancient genomes and epigenomes.
637 *Nature Reviews Genetics* **16**: 395-408.

638 **Oyston JW, Hughes M, Wagner PJ, Gerber S, Wills MA. 2015.** What limits the morphological
639 disparity of clades? *Interface Focus* **5**: 20150042.

640 **Oyston JW, Hughes M, Gerber S, Wills MA. 2016.** Why should we investigate the morphological
641 disparity of plant clades? *Annals of Botany* **117(5)**: 859-879.

642 **Packer L, Litman J, Praz CJ. 2017.** Phylogenetic position of a remarkable new fideleine bee from
643 northern Chile (Hymenoptera: Megachilidae). *Systematic Entomology* **42**: 473-488.

644 **Padial JM, Miralles A, De la Riva I, Vences M. 2010.** The integrative future of taxonomy.
645 *Frontiers in Zoology* **7**: 16.

646 **Park LE, Martens K, Cohen AS. 2002.** Phylogenetic relationships of *Gomphocythere* (Ostracoda) in
647 Lake Tanganyika, East Africa. *Journal of Crustacean Biology* **22(1)**: 15-27.

648 **Parker WG, 2016.** Revised phylogenetic analysis of the Aetosauria (Archosauria: Pseudosuchia);
649 assessing the effects of incongruent morphological characters sets. *PeerJ* **4**, e1583.

650 **Pattinson DJ, Thompson RS, Piotrowski AK, Asher RJ. 2014.** Phylogeny, paleontology, and
651 primates: Do incomplete fossils bias the Tree of Life? *Systematic Biology* **64(2)**: 169-186.

652 **Pena-Barbosa JPP, Sierwald P, Brescovit AD. 2013.** On the largest chelodesmid millipedes:
653 taxonomic review and cladistic analysis of the genus *Odontopeltis* Pocock, 1894 (Diplopoda;
654 Polydesmida; Chelodesmidae). *Zoological Journal of the Linnean Society* **169**: 737-764.

655 **Pettigrew JD. 1991.** Wings or brain? Convergent evolution in the origins of bats. *Systematic Zoology*,
656 **40(2)**: 199-216.

657 **Planet, P. 2006.** Tree disagreement: measuring and testing incongruence in phylogenies. *Journal of*
658 *Biomedical Informatics*, **39**: 86-102.

659 **Prendini L, Esposito LA. 2010.** A reanalysis of Parabuthus (Scorpiones: Buthidae) phylogeny with
660 descriptions of two new Parabuthus species endemic to the Central Namib gravel plains,
661 Namibia. *Zoological Journal of the Linnean Society* **159**: 673–71.

662 **Ramirez MJ. 2006.** Further problems with the incongruence length difference test:
663 “hypercongruence” effect and multiple comparisons. *Cladistics* **22**:289-295.

664 **Regier JC, Schultz JW, Kambic RE. 2005.** Pancrustacean phylogeny: hexapods are terrestrial
665 crustaceans and maxillopods are not monophyletic. *Proceedings of the Royal Society B* **272**:
666 395-401.

667 **Řezáč M, Pekár S, Lubin Y. 2008.** How oniscophagous spiders overcame woodlouse armour.
668 *Journal of Zoology* **275**: 64-71.

669 **Richter S, Scholtz G. 2001.** Phylogenetic analysis of the Malacostraca (Crustacea). *Journal of*
670 *Zoological Systematics and Evolutionary Research* **39**: 113-136.

671 **Riehl T, Wilson GDF, Malyutina MV. 2014.** Urstylidae – a new family of abyssal isopods
672 (Crustacea: Asellota) and its phylogenetic implications. *Zoological Journal of the Linnean*
673 *Society* **170**: 245-296.

674 **Robalino J, Wilkins B, Bracken-Grissom HD, Chan TY, O’Leary M. 2016.** The origin of large-
675 bodied shrimp that dominate modern global aquaculture. *PLoS One* **11**:e0158840.

676 **Robinson DR, Foulds LR. 1981.** Comparison of phylogenetic trees. *Mathematical Biosciences* **53**:
677 131-147.

678 **Ruta M, Wills MA. 2016.** Comparable disparity in the appendicular skeleton across the fish-tetrapod
679 transition, and the morphological gap between fish and tetrapod postcrania. *Palaeontology* **59**:
680 249-267.

681 **Sánchez-Villagra MR, Williams BA. 1998.** Levels of homoplasy in the evolution of the mammalian
682 skeleton. *Journal of Mammalian Evolution* **5(2)**: 113-126.

683 **Sansom RS. 2015.** Bias and sensitivity in the placement of fossil taxa resulting from interpretations of
684 missing data. *Systematic Biology* **64(2)**: 256-266.

685 **Sansom RS, Gabbott SE, Purnell MA. 2010.** Non-random decay of chordate characters causes bias
686 in fossil interpretation. *Nature* **463**: 797-800.

687 **Sansom RS, Wills MA. 2013.** Fossilization causes organisms to appear erroneously primitive by
688 distorting evolutionary trees. *Scientific Reports* **3**: 2545.

689 **Sansom RS, Wills MA. 2017.** Differences between hard and soft phylogenetic data. *Proceedings of*
690 *the Royal Society B* **284**: 20172150.

691 **Sansom RS, Wills MA, Williams T. 2017.** Dental data perform relatively poorly in reconstructing
692 mammal phylogenies: Morphological patterns evaluated with molecular benchmarks.
693 *Systematic Biology* **66(5)**: 813-822.

694 **Schulz JW. 2007.** A phylogenetic analysis of the arachnid orders based on morphology. *Zoological*
695 *Journal of the Linnean Society* **150**: 221-265.

696 **Schnabel KE, Ah Yong ST, Maas EW. 2011.** Galatheaidea are not monophyletic – Molecular and
697 morphological phylogeny of the squat lobsters (Decapoda: Anomura) with recognition of a new
698 superfamily. *Molecular Phylogenetics and Evolution* **58**: 157-168.

699 **Selden PA, Shear WA, Sutton MD. 2008.** Fossil evidence for the origin of spider spinnerets, and a
700 proposed arachnid order. *Proceedings of the National Academy of Sciences of the USA* **105(52)**:
701 20781-20785.

702 **Sepkoski JJ. 1981.** A factor analytic description of the Phanerozoic marine fossil record.
703 *Paleobiology* **7(1)**: 36-53.

704 **Shapiro B, Hofreiter M. 2014.** A Paleogenomic Perspective on Evolution and Gene Function: New
705 Insights from Ancient DNA. *Science* **343(6169)**: 1236573.

706 **Smith RJ. 2000.** Morphology and ontogeny of Cretaceous ostracods with preserved appendages from
707 Brazil. *Palaeontology* **43(1)**: 63-98.

708 **Song H, Bucheli SR, 2010.** Comparison of phylogenetic signal between male genitalia and non-
709 genital characters in insect systematics. *Cladistics* **26**: 23-35.

710 **Stempien JA. 2005.** Brachyuran taphonomy in a modern tidal-flat environment: preservation
711 potential and anatomical bias. *Palaios* **20**: 400-410.

712 **Størmer L. 1939.** Studies on trilobite morphology: Part I. The thoracic appendages and their
713 phylogenetic significance. *Norsk Geologisk Tidsskrift* **19**: 143-273

714 **Swofford DL. 2017.** PAUP*: Phylogenetic Analysis Using Parsimony, Version 4.0a.154.

715 **Tinn O, Oakley TH. 2008.** Erratic rates of molecular evolution and incongruence of fossil and
716 molecular divergence time estimates in Ostracoda (Crustacea). *Molecular Phylogenetics and*
717 *Evolution* **48**: 157-167.

718 **Tshudy D, Chan TY, Sornhannus U. 2007.** Morphology based cladistics analysis of Metanephrops:
719 The most diverse extant genus of clawed lobster (Nephropidae). *Journal of Crustacean Biology*
720 **27**: 463-476.

721 **Vereshchaka AL, Lunina AA. 2015.** Phylogeny and taxonomy of the enigmatic genus *Petalidium*
722 (Decapoda, Sergestidae), with biological remarks. *Zoological Journal of the Linnean Society*
723 **174**: 459-472.

724 **Vereshchaka AL, Olesen J, Lunina AA, 2016.** A phylogeny-based revision of the family
725 Luciferidae (Crustacea: Decapoda). *Zoological Journal of the Linnean Society* **178**: 15-32.

726 **Verheye ML, Martin P, Backeljau T, d'Udekem d'Acoz C. 2016.** DNA analyses reveal abundant
727 homoplasy in taxonomically important morphological characters of Eusiroidea (Crustacea,
728 Amphipoda). *Zoologica Scripta* **45(3)**: 300-321.

729 **Wahlberg N, Braby MF, Brower AVZ, de Jong R, Lee M-M, Nylin S, Pierce NE, Sperling FAH,**
730 **Vila R, Warren AD, Zakharov E. 2005.** Synergistic effects of combining morphological and
731 molecular data in resolving the phylogeny of butterflies and skippers. *Proceedings of the Royal*
732 *Society B* **272**: 1577-1586.

733 **Wagner PJ. 1995.** Testing evolutionary constraint hypotheses with early Paleozoic gastropods.
734 *Paleobiology* **21(3)**: 248-272

735 **Wagner PJ. 1997.** Patterns of morphologic diversification among the Rostroconchia. *Paleobiology*
736 **23(1)**: 115-150

737 **Wesener T, VandenSpiegel D. 2009.** A first phylogenetic analysis of Giant Pill-Millipedes
738 (Diplopoda: Sphaerotheriida), a new model Gondwanan taxon, with special emphasis on island
739 gigantism. *Cladistics*, **25**: 545-573.

740 **Whatley RC, Siveter DJ, Boomer ID. 1993.** Arthropoda (Crustacea: Ostracoda). In: Benton MJ
741 editor. The Fossil Record 2. London, Chapman & Hall, p. 343-356.

742 **Wheeler WC, Cartwright P, Hayashi CY. 1993.** Arthropod phylogeny: A combined approach.
743 *Cladistics* **9**: 1-39.

744 **Wiens JJ. 1998.** Does adding characters with missing data increase or decrease phylogenetic
745 accuracy? *Systematic Biology* **47(4)**: 625-640.

746 **Wiens JJ. 2003a.** Missing data, incomplete taxa, and phylogenetic accuracy. *Systematic Biology*
747 **52**:528-538.

748 **Wiens JJ. 2003b.** Incomplete taxa, incomplete characters, and phylogenetic accuracy: Is there a
749 missing data problem? *Journal of Vertebrate Paleontology*, **23**:297-310.

750 **Wiens JJ. 2004.** The role of morphological data in phylogeny reconstruction. *Systematic Biology*
751 **53(4)**: 653-661.

752 **Wilkinson M. 1995.** Coping with abundant missing data in phylogenetic inference using parsimony.
753 *Systematic Biology* **44(4)**: 501-514

754 **Williams BA. 2007.** Comparing levels of homoplasy in the primate skeleton. *Journal of Human*
755 *Evolution* **52(5)**: 480–489.

756 **Wills MA, Barrett PM, Heathcote JF. 2008.** The modified Gap Excess Ratio (GER*) and the
757 stratigraphic congruence of dinosaur phylogenies. *Systematic Biology* **57(6)**: 891-904.

758 **Wills MA, Jenner RA, Ní Dhubhghaill CN. 2009.** Eumalacostracan evolution: Conflict between
759 three sources of data. *Arthropod Systematics and Phylogeny* **67**: 71-90.

760 **Wilson GDF. 2009.** The phylogenetic position of the Isopoda in the Peracarida (Crustacea:
761 Malacostraca). *Arthropod Systematics and Phylogeny* **67**: 159-198.

762 **Wipfler B, Machida R, Müller B, Beutel RG. 2011.** On the head morphology of Grylloblattodea
763 (Insecta) and the systematic position of the order, with a new nomenclature for the head
764 muscles of Dicondylia. *Systematic Entomology* **36**: 241-266.

765 **Wood HM, Griswold CE, Gillespie RG. 2012.** Phylogenetic placement of pelican spiders
766 (Archaeidae, Araneae), with insight into evolution of the “neck” and predatory behaviours of
767 the superfamily Palpimanoidea. *Cladistics* **28**: 598–626

- 768 **Wyngaard GA, Holyńska M, Schulte JA. 2010.** Phylogeny of the freshwater copepod *Mesocyclops*
769 (Crustacea: Cyclopidae) based on combined molecular and morphological data, with notes on
770 biogeography. *Molecular Phylogenetics and Evolution* **55**: 753-764.
- 771 **Yoshizawa K. 2004.** Molecular phylogeny of major lineages of *Trichadenotecnum* and a review of
772 diagnostic morphological characters (Psocoptera: Psocidae). *Systematic Entomology* **29**: 383-
773 394.
- 774 **Yoshizawa K, Lienhard C. 2010.** In search of the sister group of the true lice: A systematic review
775 of booklice and their relatives, with an updated checklist of Liposcelididae (Insecta: Psocodea).
776 *Arthropod Systematics & Phylogeny* **68(2)**: 181-195.
- 777 **Yoshizawa K, Yao I, Lienhard C. 2016.** Molecular phylogeny reveals genital convergences and
778 reversals in the barklouse genus *Trichadenotecnum* (Insecta: Psocodea: 'Psocoptera':
779 Psocidae). *Molecular Phylogenetics and Evolution* **94**: 358-364

<u>Author, Year</u>	<u>Clade</u>	<u>Taxa</u>	<u>Limb chrs</u>	<u>Body chrs</u>	<u>% missing limb</u>	<u>% missing body</u>	<u>IRD_{RF}</u>	<u>IRD_{DI}</u>	<u>ILD</u>	<u>CI limb</u>	<u>CI body</u>	<u>RI limb</u>	<u>RI body</u>
Chelicerata													
Bochkov et al., 2010	Acari: Psoroptidae: Makialginae	11	27	23	1.01	5.93	0.084	0.142	0.751	0.70	0.79	0.77	0.81
Botero-Trujillo et al., 2017	Solifugae: Mummuciidae	15	14	6	2.38	9.33	0.072	0.152	1.000	1.00	0.90	1.00	0.75
Klumpen et al., 2013	Acari: Heterozetidae	10	23	6	3.04	1.67	0.56	0.81	0.202	0.60	0.75	0.58	0.80
Kuntner, 2005	Araneae: Nephilidae: Nephilinae	28	69	88	13.35	13.46	0.182	0.019	0.002	0.52	0.42	0.72	0.73
Mendes, 2011	Opiliones: Laniatores: Gonyleptidae	21	46	56	11.49	13.10	0.029	0.499	0.061	0.56	0.44	0.71	0.63
Prendini & Esposito, 2010	Scorpiones: Buthidae	29	28	38	0.37	1.72	0.182	0.020	0.097	0.55	0.48	0.81	0.77
Schulz, 2007	Arachnida	44	77	86	7.76	10.31	0.72	0.86	0.014	0.61	0.56	0.88	0.84
Wood et al., 2012	Araneae: Archaeidae	37	75	51	28.43	21.67	0.75	0.56	0.010	0.48	0.48	0.78	0.79
Crustacea													
George, 2017	Copepoda: Laophontodinae	9	32	18	4.17	0.62	0.022	0.019	0.033	0.49	0.44	0.64	0.66
Jenner et al., 2009	Eumalacostraca	24	99	63	9.60	19.44	0.016	0.159	0.008	0.49	0.44	0.64	0.66
McLaughlin et al., 2007	Anomura: Paguroidea	20	34	45	1.18	0.22	0.229	0.387	0.507	0.56	0.47	0.66	0.59
Olesen, 2009	Branchiopoda	15	44	28	30.45	29.76	0.631	0.459	0.122	0.84	0.85	0.75	0.84
Richter & Scholz, 2001	Malacostraca	19	34	41	10.22	22.21	0.098	0.461	0.161	0.59	0.58	0.68	0.65
Riehl et al., 2014	Isopoda: Asellota: Urstylidae	28	283	124	15.57	26.64	0.294	0.950	0.002	0.52	0.56	0.76	0.70

Vereshchaka et al., 2016	Decapoda: Luciferidae	29	119	48	33.20	24.31	0.390	0.330	0.213	0.72	0.74	0.85	0.91
Vereshchaka & Lunina, 2015	Decapoda: Sergestidae	23	100	48	24.40	19.02	0.51	0.22	0.223	0.72	0.78	0.72	0.83
Hexapoda													
Banks & Paterson, 2004	Phthiraptera: Philopteridae	16	14	41	1.79	7.47	0.59	0.29	0.624	0.85	0.58	0.94	0.74
Blagoderov et al., 2009	Diptera: Sciaroidea: Lygistorrhinidae	18	25	35	10.47	7.14	0.81	0.920	0.121	0.55	0.45	0.67	0.60
Calor & Holzenthall, 2008	Trichoptera: Leptoceridae	11	10	21	9.09	12.99	0.099	0.269	0.411	0.86	0.74	0.93	0.82
Chamorro & Konstantinov, 2011	Coleoptera: Chrysomelidae: Lamprosomatinae	13	5	21	12.30	3.66	0.042	0.011	0.103	1.00	0.81	1.00	0.85
Clarke, 2011	Coleoptera: Staphylinidae	24	26	104	2.16	1.64	0.32	0.190	0.616	0.68	0.55	0.86	0.77
Del Rio et al., 2012	Coleoptera: Curculionidae: Entiminae	11	9	40	0.00	5.23	0.45	0.35	0.691	0.68	0.58	0.58	0.55
Di Giulio et al., 2003	Coleoptera: Carabidae	9	26	30	0.85	16.30	0.46	0.57	0.703	0.76	0.75	0.76	0.77
Gerstmeier & Eberle, 2011	Coleoptera: Cleridae: Clerinae	12	10	13	2.50	8.33	0.180	0.820	0.062	0.61	0.50	0.72	0.68
Grebennikov & Newton, 2009	Coleoptera: Scydmaenidae	38	106	105	3.80	5.66	0.57	0.51	0.042	0.34	0.30	0.70	0.66
Grebennikov, 2010	Coleoptera: Curculionoidea	16	10	13	6.25	7.21	0.220	0.210	0.014	0.84	0.96	0.82	0.94
Liu et al., 2012	Megaloptera: Chauliodinae	24	17	24	18.38	6.08	0.450	0.044	0.921	0.85	0.54	0.95	0.81
Michel-Salzat	Hymenoptera:	23	19	18	4.58	0.00	0.089	0.056	0.191	0.79	0.76	0.95	0.95

<i>et al., 2004</i>	Apinae: Euglossini												
Packer et al., 2017	Hymenoptera: Megachilidae	27	87	127	1.53	6.27	0.23	0.79	0.362	0.41	0.36	0.68	0.65
Wipfler et al., 2010	Grylloblattodea	18	49	55	6.24	8.83	0.33	0.61	0.924	0.64	0.67	0.67	0.72
Yoshizawa, 2004	Psocoptera: Psocidae	14	11	22	7.79	2.92	0.27	0.26	0.390	0.75	0.81	0.84	0.90
Yoshizawa & Leinhard, 2010	Psocoptera: Liposcelididae	14	9	16	0.00	8.93	0.32	0.32	0.845	0.71	0.93	0.81	0.83
Myriapoda													
Blanke & Wesener, 2014	Diplopoda	16	23	33	2.99	5.11	0.015	0.027	0.094	0.87	0.74	0.94	0.86
Edgecombe & Barrow, 2007	Chilopoda: Scutigromorpha	21	41	14	10.57	17.35	0.53	0.99	0.407	0.91	0.79	0.97	0.92
Koch et al., 2009	Chilopoda: Scolopendromorpha	30	46	34	2.54	19.31	0.030	0.520	0.089	0.60	0.60	0.85	0.86
Pena-Barbosa et al., 2009	Diplopoda: Polydesmida: Chelodesmidae	15	31	16	17.20	8.33	0.457	0.904	0.689	0.61	0.62	0.76	0.80
Pitz & Sierwald, 2010	Diplopoda: Helminthomorpha	33	34	20	7.75	0.00	0.98	0.24	0.800	0.46	0.63	0.74	0.78
Wesener & Vanden-Spiegel, 2009	Diplopoda: Sphaerotheriida	38	48	41	1.15	1.16	0.110	0.240	0.053	0.55	0.60	0.83	0.83

780

781 **Table 1** – Summary of the 38 published morphological datasets across all arthropod groups utilised in this study, and the results of all tests. IRD test results

782 based upon 999 randomisations (where quoted to 3 decimal places) or 99 randomisations (where quoted to 2 decimal places, and were $p < 0.20$).

783

784

<u>Morphology</u> <u>Author, Year</u>	<u>Molecular</u> <u>Author, Year</u>	<u>Clade</u>	<u>Taxa</u>	<u>Limb</u> <u>chrs</u>	<u>Body</u> <u>chrs</u>	<u>CI</u> <u>limb</u>	<u>CI</u> <u>body</u>	<u>RI</u> <u>limb</u>	<u>RI</u> <u>body</u>
Crustacea									
Admowicz & Purvis 2006	Meland & Willassen 2004	Pseudomma	18	26	5	0.31	0.28	0.30	0.23
Bradford-Grieve et al., 2010.	Blanco-Bercial et al., 2011	Calanoida	29	93	7	0.29	0.53	0.58	0.75
Bradford-Grieve et al., 2017	Bradford-Grieve et al., 2017	Megacalanidae	12	37	5	0.29	0.53	0.58	0.75
Chang et al. 2016	Chang et al. 2016	Nephropidae	13	23	28	0.62	0.65	0.75	0.75
Dreyer & Wägele 2001	Dreyer & Wägele 2001	Bopyridae	21	37	13	0.50	0.65	0.66	0.73
Hermoso-Salazar et al., 2008	Hultgren et al., 2014	Synalpheus	13	22	12	0.45	0.44	0.40	0.17
Karasawa et al., 2013	Bracken-Grissom et al., 2014	Pleocyemata	19	22	43	0.87	0.51	0.95	0.72
Lörz & Brandt	Lörz & Held 2004	Epimeriidae	16	41	49	0.45	0.46	0.67	0.54
Oakley et al., 2012	Tinn & Oakley 2008	Ostracoda	34	22	12	0.77	0.75	0.92	0.93
Robalino et al., 2016	Ma et al., 2009	Penaeidae	37	103	94	0.34	0.27	0.63	0.54
Schnabel et al., 2011	Schnabel et al., 2011	Anomura	64	58	61	0.32	0.35	0.76	0.76
Tshudy et al., 2007	Chan et al., 2009	Metanephrops	10	8	14	0.47	0.54	0.44	0.64
Wills et al., 2009	Jenner et al., 2009	Eumalacostraca	14	59	54	0.35	0.39	0.23	0.32
Wilson 2009	Wilson 2009	Peracarida	75	124	55	0.29	0.27	0.69	0.68
Wyngaard et al., 2010	Wyngaard et al., 2010	Mesocyclops	15	41	9	0.62	0.40	0.67	0.40

786

787 **Table 2** – Summary of the 15 published crustacean morphological and molecular datasets used for
788 molecular consistency tests

789

790

791

792

793

794 **Figure 1** – Calculation of p values associated with the Incongruence Length Difference (ILD) test
795 (Mikevich & Farris, 1981; Farris *et al.*, 1995a; Farris *et al.*, 1995b) and the Incongruence Relationship
796 Difference (IRD) test (Ruta & Wills 2016; Mounce *et al.*, 2016) using the Robinson Foulds (RF)
797 distance (IRD_{RF}). **A.** A hypothetical data set is partitioned into ‘limb’ characters (left hand) and ‘non-
798 limb’ or body characters (right hand). For illustrative purposes, limb and non-limb character numbers
799 are both contiguous, and both partitions are the same size. This need not be the case. Each matrix
800 partition is then analysed independently using PAUP*, and a single most parsimonious tree (MPT) is
801 inferred from each. The lengths of these are summed (marked *). The incongruence length difference
802 (ILD) is not shown here, but would be equivalent to the difference between this summed length and
803 the length of the MPT(s) resulting from the analysis of both partitions simultaneously). The number of
804 nodes unique to one or both trees is also tallied as the Robinson Foulds (RF) distance (\dagger). **B.**
805 Characters are partitioned at random to yield null distributions of sums of lengths and RF distances.
806 Random partitions contain the same number of characters as the original partitions, and the procedure
807 is repeated a large number of times (999 in this example). **C.** The randomised partitions in ‘B’ yield
808 empirical distributions of sums of tree lengths (left hand histogram, ILD) and RF distances (right hand
809 histogram, IRD_{RF}). The ILD p-value is calculated as the fraction of the random partitions (plus the
810 original partition) for which the sum of MPT tree lengths is less than or equal to that for the original
811 partition ($p = 126/1000 = 0.126$). Random partitions with sums of lengths less than the original are
812 those in which the internal consistency of each partition (‘leg’ or ‘body’) is greater than that in the
813 original. The IRD_{RF} p-value is calculated as the fraction of the random partitions (plus the original
814 partition) for which the sum of MPT tree lengths is greater than or equal to that for the original
815 partition ($p = 384/1000 = 0.384$).

816 **Figure 2** – Tanglegram of the 50% majority rule consensus (plus compatible groupings) trees inferred
817 from the “limbs” (left) and “body” (right) partitions of the eumalacostracan data of Jenner et al.
818 (2009) and Wills et al. (2009). The IRD_{RF} test revealed the partitions to be significantly incongruent
819 ($p=0.016$). Nodes unique to each tree are marked with black dots: only two nodes are shared by the
820 trees inferred from the “limb” and “body” partitions. Majority rule trees are figured for illustrative

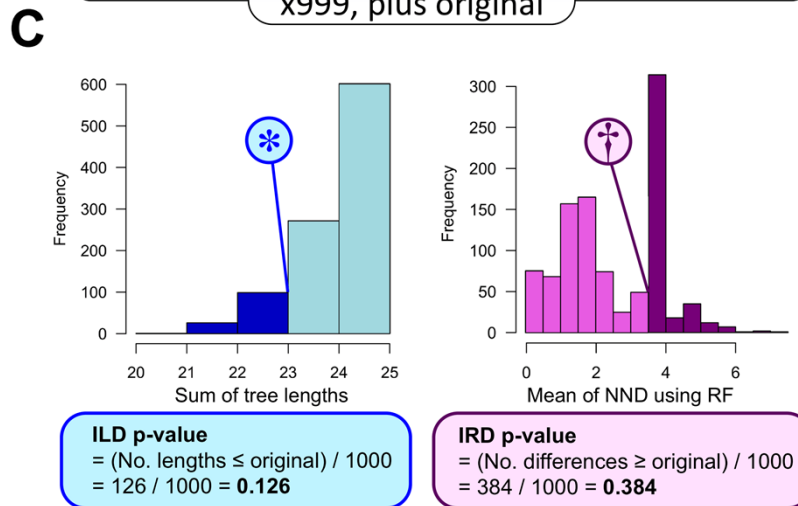
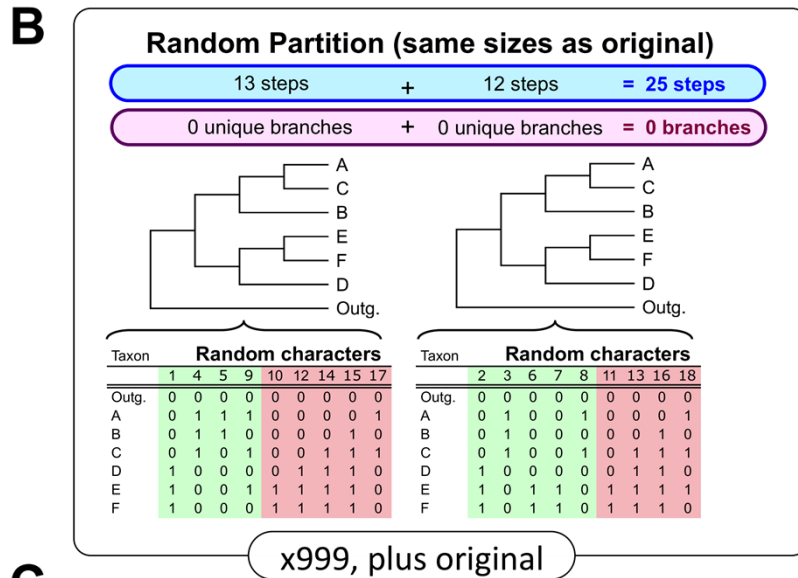
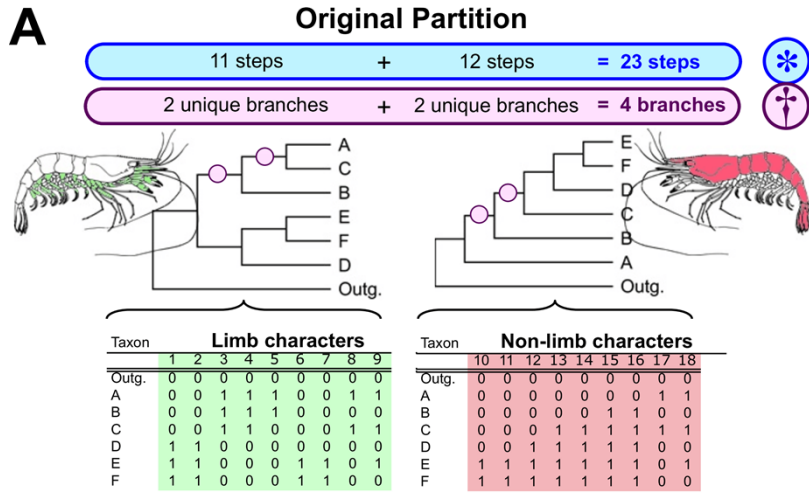
821 purposes. We advocate measures based upon the mean distance between nearest neighbours in the two
822 partitions.

823 **Figure 3** – Tanglegram of majority consensus trees implied by a “limbs” (left) and “body” (right)
824 partition of the diplopod data of Blanke & Wesener (2014), shown to be significantly incongruent by
825 IRD_{RF} ($p=0.015$) and IRD_{D1} ($p=0.025$). Unique nodes in each phylogeny are indicated by black dots.
826 In this case, the tree inferred from the “limbs” partition contains all of the same nodes as the strict
827 consensus tree derived from the entire data set by Blanke & Wesener (2014).

828 **Figure 4 – A.B.** Box and whisker plots of the distribution of ensemble CI (A) and RI (B) values
829 obtained for limb and non-limb partitions of 38 datasets across all arthropod groups (summarised in
830 Table 1). There were no significant differences in CI or RI between partitions overall, or in any
831 individual taxonomic grouping. **C.D.** Boxplots comparing residual CI (C) and RI (D) values for the
832 same sample of datasets, modelling out the effects of data matrix dimensions (number of characters
833 and number of taxa). There were no significant differences between the partitions, either overall or in
834 any individual taxonomic grouping.

835 **Figure 5** – Box and whisker plots of the distribution of ensemble CI and RI (B) values obtained for
836 limb and non-limb partitions of 15 morphological datasets of crustaceans. Characters have been
837 optimised onto corresponding but independently derived molecular trees for the same leaf set
838 (summarised in Table 2). There were no significant differences in CI or RI between partitions.

839

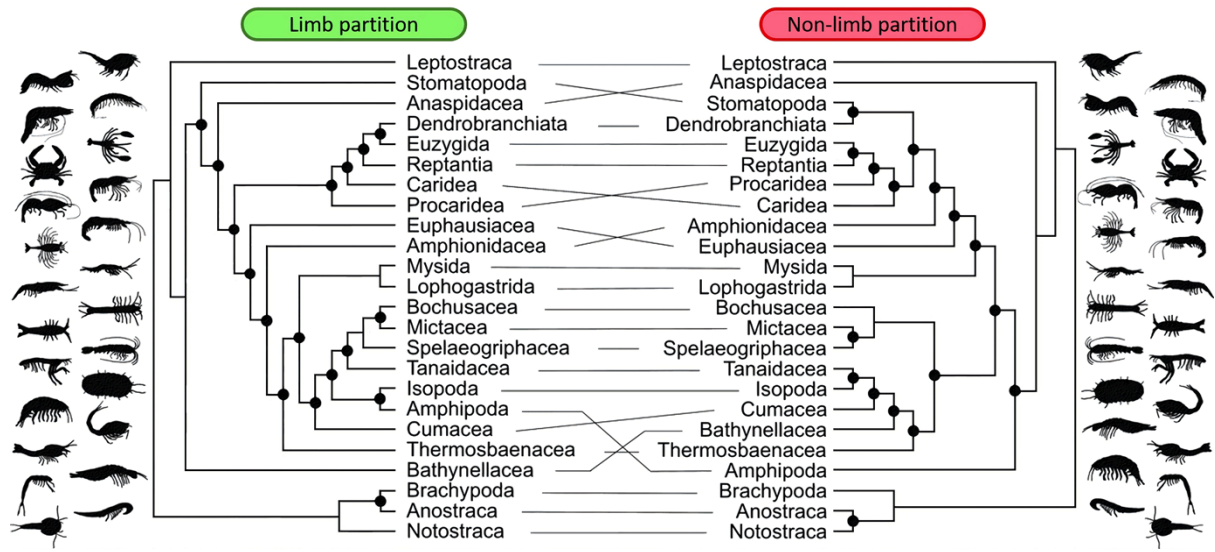


840

841

842 **Figure 1.**

843

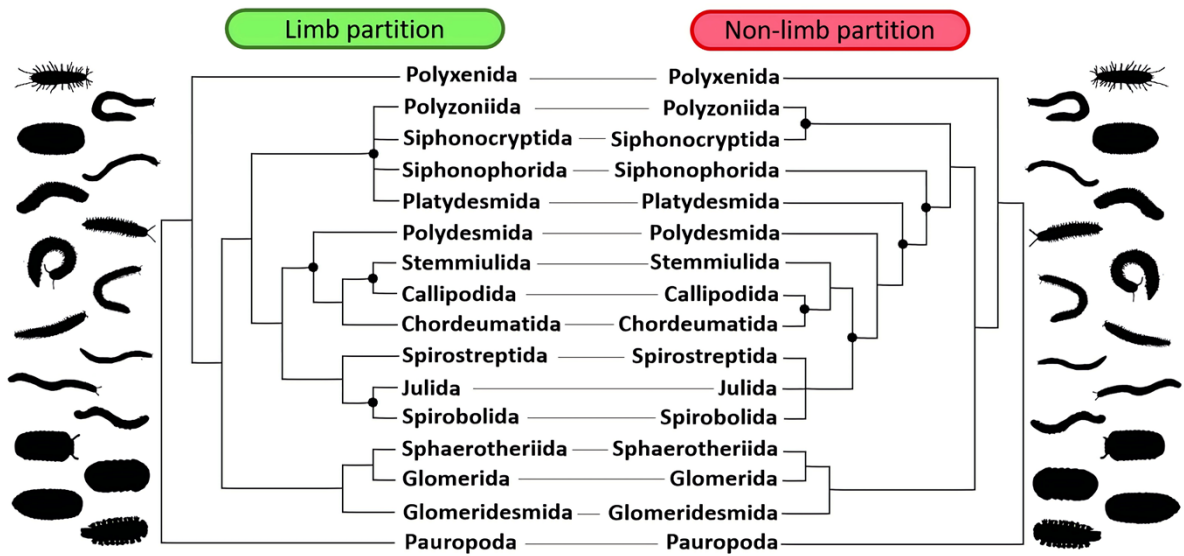


845

846 **Figure 2.**

847

848



850

851

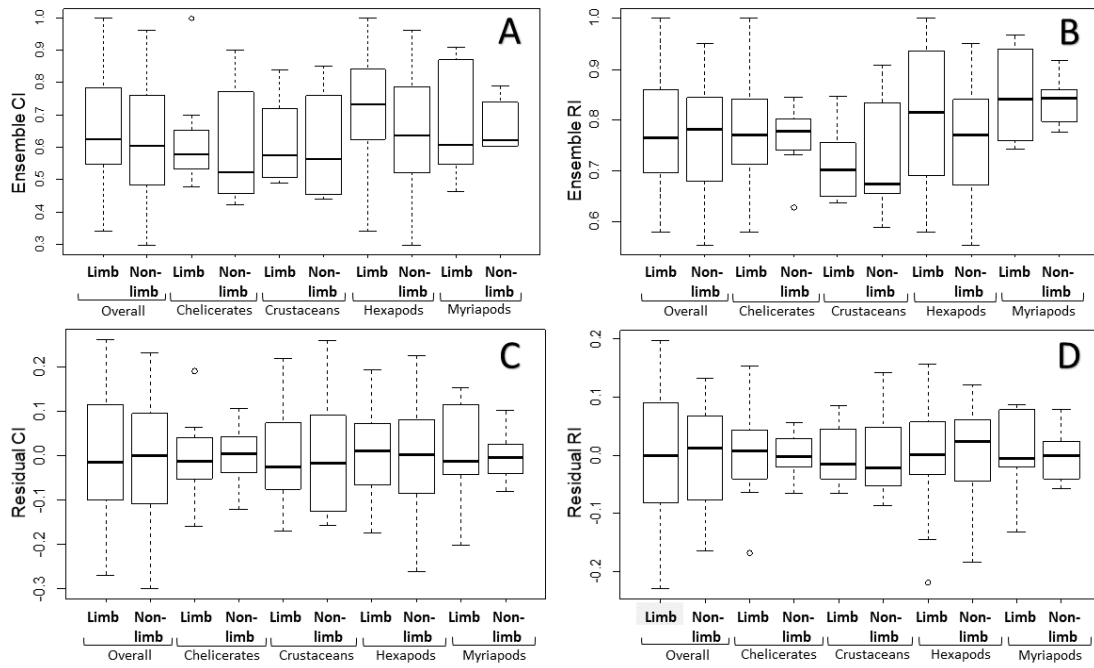
852 **Figure 3.**

853

854

855

856

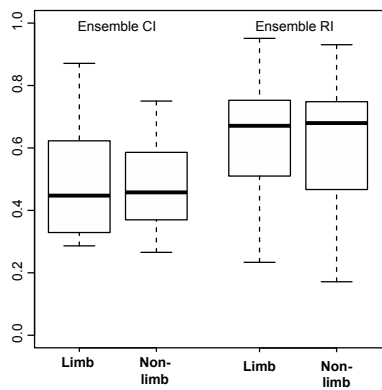


857

858

859 **Figure 4**

860



861

862 **Figure 5**

863