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Abstract:	<p>Despite increased use of genomic data in phylogenetics, morphological information remains vital for resolving evolutionary relationships, particularly for fossil taxa. The properties and models of evolution of molecular sequence data are well characterized and mature relative to those of morphological data. In particular, heterogeneity, integration and relative homoplasy of empirical morphological data could prove problematic for phylogenetic reconstruction. Here we compare osteological and non-osteological characters of 28 morphological datasets of extant saurians in terms of their homoplasy relative to molecular trees. Analysis of individual avian datasets finds osteological characters to be significantly more consistent with molecular data than soft characters. Significant differences between morphological partitions were also observed in the age at which characters resolved on molecular trees; osteological character changes occur relatively earlier in deep branches whilst soft-tissue character transitions are more recent in shallow branches. The combined results demonstrate differences in evolutionary dynamics between morphological partitions. This may reflect evolutionary constraints acting on osteological characters, compared with the relative lability of soft characters. Furthermore, it provides some support to phylogenetic interpretations of fossil data, including dinosaurs, which are predominately osteological. Recent advances in amphibian and mammal phylogenetics may make these patterns possible to test for all tetrapods.</p>

Osteological characters of birds and reptiles show greater congruence with molecular phylogenies than soft characters:

hHomoplasy of morphological partitions

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Abstract:

-Despite increased use of genomic data in phylogenetics, morphological information remains vital for resolving evolutionary relationships, particularly for fossil taxa. The properties and models of evolution of molecular sequence data are well characterized and mature relative to those of morphological data. In particular, heterogeneity, integration and relative homoplasy of empirical morphological data could prove problematic for phylogenetic reconstruction. Here we compare osteological and non-osteological characters of 28 morphological datasets of extant saurians in terms of their homoplasy relative to molecular trees. Analysis of individual avian datasets finds osteological characters to be significantly more consistent with molecular data than soft characters. Significant differences between morphological partitions were also observed in the age at which characters resolved on molecular trees. O-osteological character changes occur relatively earlier in deep branches, whilst soft-tissue character transitions are more recent in shallow branches. The combined results demonstrate differences in evolutionary dynamics between morphological partitions. This may reflect evolutionary constraints acting on osteological characters, compared with the relative lability of soft characters. Furthermore, it provides some support to phylogenetic interpretations of fossil data, including dinosaurs, which are predominately osteological. Recent advances in amphibian and mammal phylogenetics may make these patterns possible to test for all tetrapods.

1. Introduction

Phylogenetics, the reconstruction of the evolutionary relationships between taxa, underpins evolutionary biology. It is necessary for resolving morphological and molecular evolution, since well-resolved, topologically accurate phylogenies allow us to track evolutionary changes through time. In the age of

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3 phylogenomics, morphology remains a vital source of phylogenetic information
4 (Wiens, 2004; Lee & Palci, 2015; Wanninger, 2015) despite challenges such as
5 the convergence and non-independence of characters. This is principally because
6 morphological information is usually the only kind available from fossil taxa, and
7 morphological data are therefore essential for their phylogenetic placement. An
8 additional consideration is that morphological data provide an independent
9 source of information with which to corroborate molecular data, with such
10 consistency potentially strengthening hypotheses of evolutionary history,
11 although simultaneous analyses of molecular and morphological data make the
12 future role of morphology for consistency uncertain.

13
14 Underlying these considerations is the widespread distribution of homoplasy in
15 morphological data i.e. convergence of phenotypic characters in distantly related
16 species, often due to the action of similar selective regimes. Morphological
17 homoplasy has been demonstrated to confound phylogenetic reconstruction (e.g.
18 Torres & Van Tuinen, 2013; Reeder *et al.*, 2015). In order to best use
19 morphological data, we need to understand and estimate the distribution of
20 homoplasy as this could potentially aid in the building of more effective models
21 for probabilistic inference methods. While convergence has also been observed
22 in molecular data (Castoe *et al.*, 2009; Foote *et al.*, 2015; Zou & Zhang, 2016), it is
23 nevertheless necessary to address these questions with regard to morphological
24 data using molecular sequence data as an independent benchmark.

25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 *1.1. Morphological partitioning and congruence*

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46 While there has been a focus in recent literature on the use of different models
47 for morphological phylogenetic data (Wright & Hillis, 2014; O'Reilly *et al.*, 2016;
48 Puttick *et al.*, 2017), somewhat less attention has been paid to the characters
49 themselves (but see Song & Bucheli, 2010; Mounce *et al.*, 2016; Sansom *et al.*,
50 2017). This is an important problem because there are several reasons to expect
51 that different partitions of morphological data may give rise to different
52 estimates of evolutionary history, such as selective regimes giving rise to
53 convergence (e.g. Kivell *et al.*, 2013), evolutionary lability leading to rapid and
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3 superimposed changes (Omland & Lanyon, 2000; Wiens, 2009), modularity and
4 mosaicism (Clarke & Middleton, 2008) and stochastic noise (e.g. Gaubert *et al.*,
5 2005). Differences have been shown in the phylogenetic signal conveyed by
6 dental and osteological character partitions in mammals (Sansom *et al.*, 2017),
7 hard and soft character partitions in various animals (Sansom & Wills, 2017) and
8 craniodental and postcranial partitions in vertebrates (Mounce *et al.*, 2016).
9
10 The results of these and other studies (e.g. Sadleir & Makovicky, 2008; Goswami
11 & Polly, 2010b) demonstrate that different groups of morphological characters
12 evolve with different dynamics, rates and trends. Some characters evolve under
13 strong confounding selection, while others retain phylogenetic signal which is
14 recoverable when compared to a good estimate of the true underlying
15 phylogeny. Characters evolving under selection can often be convergent (e.g.
16 Sadleir & Makovicky, 2008), leading to suites of characters which, while
17 compatible with each other, are incompatible with the underlying phylogeny
18 (Holland *et al.*, 2010). In this case, genomic data can in theory help reveal which
19 of these characters convey signal consistent with underlying evolutionary
20 history, while acknowledging that the true phylogeny is unknowable. This
21 approach, i.e. evaluating the performance of subsets of morphological characters,
22 has an important role to play in phylogenetics, as it demonstrates that the
23 indiscriminate use of morphological characters without regard to convergence
24 may be harmful to morphological phylogenetics, as is the same approach to
25 molecular phylogenetics (e.g. Reddy *et al.*, 2017).
26
27 Assessing the consistency of morphological data with independent molecular
28 trees and vice versa is useful because it reveals where data types are most
29 consilient, and such consilience has the potential to strengthen or call into
30 question existing hypotheses of phylogenetic history (Field *et al.*, 2014;
31 McInerney, O'Connell, & Pisani, 2014; Reddy *et al.*, 2017). It can also provide
32 potential insight into the modes of evolution of those characters which are not
33 congruent with the molecular trees, for example convergence and modularity.
34
35 Examining consistency and tracing morphological evolution on molecular trees
36 provides insight into the basis of evolutionary change and allows us to interpret
37 phenotypic traits in the context of evolutionary history. Although congruence has
38 been tested for and discussed in previous literature, this study builds upon
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3 previous research by testing a wider group of datasets spanning birds and
4 reptiles.
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7 8 9 10 *1.2. Rationale and Approach* 11

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13 Here, we use morphological data and molecular trees from birds and squamates,
14 the two largest groups within the Sauropsida, to test hypotheses of the
15 correspondence of morphological characters with molecular trees. Specifically,
16 we test whether osteological characters differ from soft tissue characters in their
17 consistency with molecular phylogenies. Previous studies have shown
18 differences in the phylogenetic signal conveyed between hard and soft
19 characters (Sansom & Wills, 2017). Within the osteological partition, we test
20 whether the postcranial and cranial subpartitions differ, and within the soft
21 tissue partition we test whether plumage and integument and myology
22 subpartitions differ. We may expect these partitions and subpartitions of
23 morphological data to contain different levels of homoplasy due to differences in
24 the action of sexual selection, directional selection, and ecological and
25 developmental constraint on different character subsets. Furthermore,
26 characters might be expected to be informative at different taxonomic ranks
27 reflecting varying levels of evolutionary constraint and lability. There are *a priori*
28 reasons to expect different amounts of homoplasy in these different
29 morphological regions; specifically, we hypothesize that soft characters such as
30 plumage may be expected to contain more apparent homoplasy than osteological
31 characters due to higher evolutionary lability and convergence (Omland &
32 Lanyon, 2000; Price, Friedman, & Omland, 2007). Additionally, different
33 topologies are inferred from cranial and postcranial characters (Mounce *et al.*,
34 2016), and retention of only dental data in particular results in loss of
35 phylogenetic signal (Sansom *et al.*, 2017), and we therefore hypothesize that
36 there may be greater homoplasy in this region.
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39 It is particularly important to apply these analyses to osteological data, as this is
40 usually the only data available when assessing the phylogenetic position of fossil
41 species. We additionally indirectly test whether soft characters are more
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3 evolutionarily labile and therefore likely to resolve at different taxonomic levels
4 by performing a simple, parsimony-based ancestral state reconstruction for each
5 character, and then assigning each character state change an age based on the
6 node ages of the molecular tree. We expect more labile traits to have more recent
7 ages due to higher frequency of change, and potentially be more informative at
8 lower taxonomic levels. We additionally directly test the relationship between
9 retention index and character transition age, to determine whether any
10 difference in transition age between partitions can be primarily explained by
11 homoplasy.
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22 **2. Material and methods**

23 *2.1. Data cCollection*

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26 Morphological data matrices for extant birds and squamates were compiled from
27 three sources; a) Google Scholar (using the search terms “Phylogeny” and
28 “Morphology” with each taxonomic order), b) Graeme Lloyd’s collection of
29 matrices (Lloyd, 2009), specifically the Cenozoic bird collection, and c) the
30 reference list of the supertree study of Davis & Page (2014).
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33 Matrices were categorized and scored according to their taxonomic coverage,
34 taxonomic level of terminals, number of taxa, number of characters, types of
35 characters and source of data. We excluded datasets with fewer than twenty
36 characters and 10 taxa. Characters were split into osteological and non-
37 osteological partitions, and then further split into subpartitions (cranial,
38 postcranial, integumentary and myological). Non-osteological morphological
39 data in these datasets include mainly plumage, integument and myological data.
40 It was necessary to exclude datasets for which the original data were either
41 unavailable or unreadable. In many cases, matrices have been modified by
42 various authors over time (e.g. Strauch, 1978), in which case the most recent
43 version (e.g. Chu, 1995) was used to minimize pseudoreplication. We also
44 identified non-independence of matrices due to taxonomic overlap and excluded
45 some from analyses accordingly. Additionally, some matrices were removed
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3 from analyses due to the unavailability of character descriptions or of the
4 matrices themselves. A total of 18 avian and ~~eight~~8 squamate matrices were
5 ultimately included, in addition to two large datasets with broad taxonomic
6 coverage, one avian (Livezey & Zusi, 2007) and one squamate (Reeder *et al.*,
7 2015). Analysed edited datasets are available in the supplementary materials.
8
9 Molecular trees for Aves were extracted from Jetz *et al.*'s (2012) companion
10 website (birdtree.org) for comparison with avian morphological data. Trees
11 based on either of the two phylogenies used as backbone constraints by Jetz *et*
12 *al.*; (2012) are available to download, with the option to include all species of
13 interest, or just those species with sequence data available.

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21 Of the two separate backbone phylogenies used by Jetz *et al.*; (2012), the one
22 using the Hackett *et al.*; (2008) topology as a constraint was used due to the
23 larger amount of data used to build this phylogeny. It should be noted that the
24 Hackett *et al.*; (2008) tree uses β -fibrinogen, a gene which has been flagged as
25 potentially problematic in recovering higher-level branching patterns (Mayr,
26 2011; Jetz *et al.*, 2012). However, since our analysis primarily uses small avian
27 datasets (apart from one dataset) with narrow taxonomic spread, this should not
28 affect this study. We additionally performed analyses on an alternative
29 Galloanserae supertree (Eo, Bininda-Emonds, & Carroll, 2009) for one of our
30 datasets (Livezey, 1991), to test whether these results are robust to different
31 estimates of evolutionary history.

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Molecular trees were only extracted with taxa for which sequence data are
available. The morphological data matrices were modified accordingly, by
removing any taxa lacking molecular data. Additionally, some avian taxon names
were altered in the morphological matrices to reflect alternative nomenclature
used by Jetz *et al.*, (2012). Avibase (Lepage, 2003), a database of bird taxonomy,
was used to establish synonymy. Invalid taxa of any other kind (i.e. extinct taxa
or taxa for which no synonymy in Jetz *et al.*, 2012 could be established) were also
deleted from the final morphological matrices. For each avian morphological
matrix, 1,000 trees were sampled from the Jetz *et al.*, (2012) posterior
distribution.

For squamates, the molecular supermatrix tree of Zheng & Wiens (2016) was
used. The maximum likelihood tree includes around half of all squamates (4162

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3 species) and 52 total mitochondrial and nuclear genes (12 genes for 4161
4 species and 44 genes for 161 species).

5
6 Some changes were made to matrices as necessary before analysis. For example,
7 as the molecular data of Jetz *et al.*, (2012) includes taxa only at species level, any
8 taxa in morphological matrices at the level of subspecies were changed to reflect
9 this. For example, character coding for some subspecies were combined, some
10 taxa were removed that overlapped between datasets to ensure independence,
11 and taxa without corresponding molecular data were removed. In all cases,
12 original character ordering and outgroup taxa were retained.
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20 21 22 *2.2. Homoplasy and transition ages*

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26 The congruence of morphological characters relative to molecular trees was
27 derived by calculating the retention indices of individual characters and, in the
28 case of birds, averaging them over the 1000 trees for each dataset in TNT
29 (Goloboff, Farris, & Nixon, 2008). The retention index of a cladistic character is a
30 measure of its homoplasy, and is defined as the difference between the
31 maximum number of steps on the tree and the number of state changes on that
32 tree, divided by the difference between maximum number of steps on the tree
33 and the number of state changes in the data. Values range from 0--1, with 1
34 indicating no homoplasy. Additionally, the ensemble retention index, the
35 retention index for a group of characters rather than individual characters, was
36 calculated for partitions (osteological and non-osteological data) and
37 subpartitions (cranial and postcranial osteological data and integumentary and
38 myological data).
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42 The difference in homoplasy between partitions was assessed by comparing
43 mixed linear effects models in the R package nlme, with character retention
44 index as the response variable and dataset treated as a random effect. Models
45 compared were a null model, partition as a fixed effect and partition + clade as
46 fixed effects. Heteroskedasticity was first accounted for by fitting different
47 models of heteroskedasticity to the data and using the preferred model in all
48 further analyses.
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3 To test whether morphological partitions resolve on a phylogeny at different
4 times and are informative at different taxonomic levels, the average ages of
5 transition for osteological and non-osteological characters were compared. Each
6 informative, binary morphological character was applied to 100 trees from the
7 posterior distribution of Jetz *et al.*, (2012) to estimate unambiguous character
8 transitions in a parsimony framework (ACCTRAN) using the `ancPropStateMat`
9 function in the R package `Paleotree` (Bapst, 2012). This gives an estimate of the
10 node or nodes at which a character transitions. To estimate the age of transition,
11 a random age between the age of the node of transition and its immediate
12 ancestor was derived 100 times for each tree. The average of these ages was then
13 taken as the transition age of a character on that tree. For characters
14 transitioning multiple times on a tree, an average was taken of the ages for each
15 of the branches along which the character transitions. The transition ages on
16 each tree were then averaged to obtain the final transition age for each character
17 (R script available in supplementary information). Note that this approach is
18 likely to overestimate absolute transition ages due to the use of the ACCTRAN
19 algorithm and averaging ages along the branch preceding the transition.
20 However, this does not affect our interpretation of the results since in this case
21 we are testing for relative differences of character transition ages between
22 partitions.
23

24 The average age of transition was compared between partitions for all datasets
25 using a linear mixed model using the R package `nlme`, accounting for
26 heteroskedasticity. A model treating partition (osteology and non-osteology) as
27 fixed effect, and a model treating partition and clade (bird and reptile) as fixed
28 effects were compared against a null. In all analyses, dataset was treated as a
29 random effect. Additionally, to test for the effect of homoplasy on apparent
30 transition age, a null model with age as response variable was compared with a
31 model treating individual character retention indices as a fixed effect and models
32 treating both retention index and partition as fixed effects, both with and
33 without interaction terms.
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56 57 58 59 **3. Results** 60

3.1. Homoplasy

Osteological characters in morphological data are significantly more consistent with the molecular trees than soft tissue characters for avian and squamate datasets (paired t of ensemble retention indices, $n = 28$, $p = 0.0004$ (Figure 1), linear mixed effect model, likelihood ratio = 98.18, $p = <.0001$, least square mean for osteology = 0.666, non-osteology = 0.555). However, there is no significant difference between cranial and postcranial partitions, possibly due to the relative paucity of adequate data when splitting the osteological partition (paired t, $n = 19$, $p = 0.5174$). The relative homology between myology and integument could not be compared between all datasets due to the small number of characters in each subpartition. There is no significant difference between myological and integumentary or plumage characters in any individual dataset out of the three tested (Mann-Whitney U , Table 1). The addition of subpartition as a fixed effect does not significantly improve the explanatory power of linear models, although postcranial data had the highest least square mean retention index (0.682), compared with cranial (0.631), integument (0.525) and myology (0.673).

The single large morphological dataset covering all birds (Livezey & Zusi, 2007) was analysed separately due to possible differences in properties between it and smaller datasets, and found significantly higher retention indices in soft characters with the underlying molecular phylogeny, as well as significantly higher consistency of cranial characters versus postcranial characters (Table 1). For squamates, the single large morphological dataset (Reeder *et al.*, 2015) shows significantly higher consistency of osteological and cranial characters (Table 1, $p <.0001$).

Table 1 at End of Document

Table 1. Showing number of taxa, number of informative characters per partition, ensemble retention indices for partitions for each dataset and results of Mann-Whitney U comparing the

mean retention index between partitions, where the null hypothesis is that the two sets of retention indices are drawn from the same distribution. Due to differences in taxonomic level, avian datasets are categorised by superorder or order, while squamate datasets are categorised by sub- or infraorder or superfamily.

Figure 1. Ensemble retention index between osteological and non-osteological partitions for birds and squamates. Osteological data has higher consistency in datasets falling below the $x=y$ line. Colour corresponds to clade and dot size is proportional to dataset size (in number of total characters).

Figure 2. Ensemble retention index between cranial and postcranial partitions for birds and squamates. Cranial data has higher consistency in datasets falling below the $x=y$ line. Colour corresponds to clade and dot size is proportional to dataset size (in number of total osteological characters).

A highly significant correlation (Pearson correlation coefficient, $\rho = 0.83$, $n = 27$, $p < .0001$) between the ensemble retention indices between osteological versus soft character partitions across all datasets suggests that properties of the individual study or taxa are an important determinant of how well both sets of characters fit the molecular phylogeny, perhaps indicating that the age of datasets, coding practices of particular authors or underlying properties of the morphology are important factors determining character consistency.

There are more characters in osteological compared with non-osteological partitions (paired t test, $t = 2.081$, $df = 27$, $p = 0.047$). However, there is no correlation between the number of characters and the ensemble retention index within either osteological (linear regression, $F = 0.2282$, $df = 27$, $p = 0.637$) or soft tissue partitions (linear regression, $F = 0.3596$, $df = 27$, $p = 0.554$) suggesting that the marginally significant difference in the number of characters between partitions likely does not explain the observed relationship between retention index and data type.

Additionally, we find similar results on the alternative topology for Livezey, (1991), with an ensemble retention index of 0.82 for osteological data and 0.70 for non-osteological data, suggesting that our overall results are robust to different topologies.

3.2. Relative transition ages

Average character transition ages are significantly older for osteological characters relative to non-osteological characters (Figure 3; Supplementary Figure 2). The best linear mixed effect model was that including both partition and clade as fixed effects (one-way anova, Table 2), indicating older ages for transitions in osteological data, and older ages for transitions in squamate data. Transition age data was highly heteroskedastic, with variability around the mean increasing with age. In all analyses, dataset was treated as a random effect.

Fixed Effects	df	AIC	Log Likelihood	Likelihood Ratio	P value
None	23	11355.15	-5654.58		
Partition	24	11326.53	-5639.26	30.62	<.0001
Partition + Clade	25	11314.8	-5632.39	13.73	<.0001

Table 2. Table comparing fit of three different linear mixed effect models to examine the effect of partition (osteological or non-osteological) on character transition age. Models compared include a null model, a model including partition as a fixed effect, and a model including both partition and clade (birds or reptiles) as fixed effects. Dataset is treated as a random effect in all models. AICs, likelihood ratios and p values all prefer the most complex model, suggesting that partition and clade both have strong explanatory power. Transitions in osteological characters are significantly older, as are transitions in squamate characters.

For individual datasets, five out of 16 avian datasets and three out of six squamate datasets show significant differences in age of transition between individual osteological and non-osteological characters (Mann-Whitney *U* tests; Table 3).

Subpartitions (cranial vs postcranial and myology versus plumage) for all datasets were harder to assess statistically due to paucity of data. There is no significant difference in cranial versus postcranial character transition ages between datasets for birds and squamates together (paired *t*, $t = -0.36538$, $df =$

14, $p = 0.7203$). Out of 15 assessed datasets, only three are significantly different between cranial and postcranial partitions, and one out of two datasets show a significant difference between myology and integument (Mann-Whitney U tests; Table 3).

Figure 3. Showing differences in pooled character transition ages in millions of years between partitions in all bird and squamate datasets. Dashed lines indicate mean ages of osteological (older) and non-osteological (younger) characters. Data is coloured by partition, with osteological data in purple and non-osteological data in green.

There is a significant correlation between transition age and retention index (linear regression, $F = 15.38$, $df = 955$, $p < .0001$) in the Livezey and Zusi (2006) dataset, showing a direct association between the age of a character change and homoplasy. Additionally, there is a negative correlation between difference in the ensemble retention index between osteological characters and non-osteological characters, and the root age of the dataset in birds (linear regression, $F = 6.038$, $df = 18$, $p = 0.025$; Supplementary Fig. 3), indicating that osteological characters become relatively less congruent with molecular trees compared to soft characters further back in time. Given that both retention index and transition age differ between partitions, and retention index and transition ages are correlated (Supplementary Fig. 1), further linear mixed effect models were compared in order to further examine the relationship between homoplasy, transition age and partition. Retention index had significant explanatory power for transition age. Explanatory power was further improved with the addition of partition as a fixed effect, with an interaction term between retention index and partition, indicating that the difference in homoplasy between partitions explains the difference in transition ages between partitions (Table 3).

Fixed			Log	Likelihood	
Effects	df	AIC	Likelihood	Ratio	P value

None	23	11355.15	-5654.575		
RI	24	11310.02	-5631.01	47.13005	<.0001
RI +					
Partition	25	11315.48	-5632.739	3.45623	0.063
RI *					
Partition	26	11297.53	-5622.767	19.94243	<.0001

Table 3. Table comparing fit of four different linear mixed effect models to examine the effect of homoplasy (as measured by the retention index) on apparent transition ages. Models compared include a null model, a model including retention index as a fixed effect, and models including both retention index and partition (osteology and non-osteology) as fixed effects. Character transition age is the response variable and dataset is treated as a random effect in all models. AICs, likelihood ratios and *p* values all prefer the most complex model, suggesting that retention index has strong explanatory power on transition age. Homoplasy is significantly stronger in younger characters, explaining the difference in transition age between osteological and soft characters.

4. Discussion

The results of this analysis of saurian datasets demonstrate that non-osteological characters exhibit greater levels of homoplasy relative to molecular trees than osteological characters do, and that this homoplasy explains a difference in average character transition ages between these morphological regions. This is consistent with previous studies showing differences in phylogenetic properties between hard and soft morphological data (Sansom & Wills, 2017). Interestingly, however, soft characters have a higher consistency with molecular data than osteological characters in the single, larger (Livezey & Zusi, 2007) dataset. This may be due to the coding style of the individual authors rather than a reflection of the properties of the morphological data themselves. Additionally, as this is a very large dataset, it may be affected by issues such as the non-independence of characters to a greater extent than the smaller datasets analyzed here. Alternatively, different classes of characters may be phylogenetically informative at different taxonomic levels, and this discrepancy is therefore explained by the difference in taxonomic breadth between the single broad dataset spanning all

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3 birds, and the datasets of smaller clades. This is supported by the fact that
4 between individual avian datasets, the difference in congruence between
5 osteological and soft characters decreases and appears to even reverse deeper in
6 time. It is also possible that spurious higher-level relationships in the molecular
7 topology have affected the results. Future analyses would benefit from
8 comparisons between several molecular phylogenies, ~~however~~ but this was not
9 possible here as currently available molecular phylogenies for birds are limited
10 in taxonomic coverage.
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21 *4.1. Evolutionary constraint and selection*

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24 Due to evolutionary and developmental constraints on vertebrate body plan (Hu
25 *et al.*, 2017), it seems sensible to suggest that osteological characters may tend to
26 evolve more slowly than some soft characters. In birds, these constraints may
27 particularly pertain to flight, which requires a specific bauplan, largely conserved
28 across flighted birds (Sullivan *et al.*, 2017). While also extremely important for
29 flight, such constraints may not be shared by some types of plumage characters
30 which, by contrast, are considered relatively evolutionarily labile and therefore
31 highly convergent due to sexual selection in many avian taxa (Omland & Lanyon,
32 2000; Price *et al.*, 2007; Hofmann, Cronin, & Omland, 2007). In this case, the
33 relative paucity of integumentary characters in the large Livezey & Zusi (2007)
34 dataset (98 compared with 237 myological characters) may itself be a reflection
35 of the difficulty in finding homologous plumage characters across all birds due to
36 the faster evolutionary rates of these characters.
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47 It is therefore possible that superimposed changes in some plumage traits such
48 as colouration, where characters may change multiple times on a tree, could lead
49 to saturation and convergence of these characters, while only through deep time
50 and across a broad taxonomic range do osteological characters become
51 convergent. Labile and ecologically important traits may be expected to poorly
52 reflect evolutionary history (Price *et al.*, 2007; Kamilar & Muldoon, 2010),
53 possibly due to this overwritten phylogenetic signal in characters accruing
54 multiple changes. This cannot however explain why the same pattern is not
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3 observed in larger squamate datasets. Although reproductive success in
4 squamates is often determined by physical capability and behaviour (Shine,
5 Langkilde, & Mason, 2004; Swierk, Ridgway, & Langkilde, 2012), colouration is
6 also important in many species (Chen *et al.*, 2012).
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10 11 12 13 14 *4.2. Character transition ages* 15

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17 To test whether different classes of characters are informative at different
18 taxonomic levels, we compared the ages at which these different character types
19 transition. Our results show that soft characters generally change on a phylogeny
20 at younger ages than osteological characters for all datasets together, and that
21 levels of homoplasy are directly related to age of transition for a character. This
22 supports the hypothesis that different morphological regions may be
23 phylogenetically informative at different taxonomic levels. Evolutionarily labile
24 traits may contain the phylogenetic signal to resolve the relationships between
25 extremely young taxa, but may be subsequently overwritten over time, while
26 slower-evolving traits become overwritten only in deeper time. For example,
27 Benson & Choiniere (2013) suggest that although musculoskeletal evolution
28 during the dinosaur–bird transition may have driven early rapid speciation,
29 some of this potentially strong phylogenetic signal has been overwritten by
30 subsequent diversification. Plumage characters, by contrast, may be
31 phylogenetically useful within a genus, but are more likely to be homoplasious at
32 the level of family or order. These changes may become saturated over time, a
33 situation almost analogous to the long-branch attraction observed in molecular
34 systematics. By contrast, traits that evolve slowly may be phylogenetically
35 uninformative at lower taxonomic levels but may help to resolve relationships
36 where they vary between higher taxa. This idea is supported by the fact that soft
37 characters change more recently on phylogenies in both birds and squamates.
38 Since we performed ancestral state reconstructions under a parsimony
39 framework, evolutionary rates are not modelled, and therefore evolutionary
40 lability and overwritten signal are expected to manifest as younger ages on trees.
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3 The observed higher consistency of osteological characters in birds is consistent
4 with previous studies which have suggested that plumage contains weak
5 phylogenetic signal due to homoplasy (Price *et al.*, 2007). However, while the
6 non-osteological characters used in the meta-analysis have been split into the
7 sub-partitions of myology and plumage or integument, there was not enough
8 data from any of these partitions alone to compare with osteology. Given more
9 data, splitting the non-osteological characters into more subpartitions may help
10 to further resolve the distribution of support among character types by reducing
11 the potentially conflicting signal between the morphologically disparate
12 characters within the partition. This is because the non-osteological data are
13 derived from plumage, myology, integument and in some cases other categories
14 such as nervous tissue. As, these all have different developmental and
15 evolutionary origins, there is potential for conflicting signal between these data
16 types.

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18 An alternative explanation for the results presented here is that differences in
19 the consistency of different morphological partitions with a molecular phylogeny
20 may reflect differences in coding strategies in different subsets of morphological
21 data rather than any inherent difference in the ability of these areas of
22 morphology to elucidate evolutionary history *per se*. However, there is no
23 obvious *a priori* reason to suspect that plumage or other soft tissue characters
24 are more difficult to accurately code than osteological characters. It may be the
25 case that since osteological characters are more conserved across vertebrate
26 species they are better understood and therefore easier to code, which is
27 consistent with the idea that osteological characters contain more phylogenetic
28 signal than other areas of morphology.

5-Conclusion

29
30 Examining the consistency of different classes of morphological characters
31 against a molecular phylogeny provides a way of identifying consistency between
32 these different data types. Here, we have identified greater consistency of
33 osteological characters than soft tissue characters with molecular phylogenies,
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3 implying that hard characters may be more reliable in reconstructing
4 evolutionary history, while relatively more evolutionarily labile soft characters
5 such as plumage, which are affected to a greater extent by sexual and directional
6 selection, are less affected by evolutionary constraint. This is supported by their
7 more recent apparent transitions on phylogenetic trees.
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12 The higher consistency of osteological characters with an underlying molecular
13 tree is potentially good news for palaeontologists when placing fossil taxa, since
14 osteological data are often the only phylogenetic information available when
15 working with fossil species. However, caution must still be exercised since as the
16 Livezey & Zusi (2007) data show, this is not always the case, and osteological
17 data may become increasingly unreliable deeper in time.
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21 These findings may have implications for the use of morphological data in
22 phylogeny reconstruction. Future analyses, for example those using models of
23 morphological evolution in probabilistic frameworks, may benefit from
24 incorporating morphological partition schemes that reflect the shared
25 evolutionary properties of characters within partitions.
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30 Whether these patterns apply more broadly across vertebrate species can be
31 investigated with recent well-sampled molecular trees. This will be especially
32 useful for teasing out any difference between the different types of soft tissue
33 characters found in different vertebrates.
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For Review Only

				Osteological data		Non-Osteological Data		P (Wilcoxon)
Dataset	Superorder/Order	Focal Clade	Taxa	Ensemble character retention index	Informative Characters	Ensemble character retention index	Informative Characters	
Birds								
Chu, 1995	Charadriiformes	Various	70	0.84	62	0.76	5	0.1482
Smith, 2011	Charadriiformes	Pan-Alcidae	52	0.67	197	0.64	102	0.2762
Nesbitt, Ksepka, & Clarke, 2011	Cypselomorphae	Various	11	0.6	82	0.7	9	0.6089
Frank- Hoeflich <i>et</i> <i>al.</i> , 2007	Galloanserae	Cracidae	65	0.85	149	0.71	43	5.614e-05**
Livezey, 1991	Galloanserae	Anatini	49	0.79	28	0.67	115	0.1449
Livezey, 1996b	Galloanserae	Anserinae	25	0.85	31	0.71	51	0.0009672**
Livezey, 1996a	Galloanserae	Aythiini	12	0.75	7	0.59	38	0.4868

1 2 3 4 5 6 7	McCracken <i>et al.</i> , 1999	Galloanserae	Oxyurinae	11	0.65	25	0.54	28	0.1237
8 9 10	Livezey, 1998	Gruiformes	Rallidae	74	0.93	180	0.74	100	1.545e-11**
11 12 13	Birdsley, 2002	Passeriformes	Tyrannidae	31	0.58	27	0.46	12	0.9741
14 15 16 17 18	Irestedt, Fjeldså, & Ericson, 2004	Passeriformes	Dendrocolaptinae	38	0.79	9	0.66	21	0.08464
19 20 21 22	Maurício <i>et al.</i> , 2012	Passeriformes	Rhynocryptidae	34	0.76	80	0.7	8	0.6788
23 24 25	Patten & Fugate, 1998	Passeriformes	Emberizidae	27	0.47	6	0.4	24	0.8549
26 27 28	Prum, 1992	Passeriformes	Pipridae	30	0.69	29	0.49	10	0.04598*
29 30 31	Prum, 1993	Passeriformes	Eurylaimidae and Philepittidae	12	0.86	16	0.86	11	0.898
32 33 34	Winker & Pruett, 2006	Passeriformes	Catharus	17	0.41	11	0.26	29	0.1931
35 36 37 38 39 40 41 42 43 44 45 46	Clarke <i>et al.</i> , 2007	Sphenisciformes	Various	30	0.92	96	0.79	81	0.02412*

Bertelli, Chiappe, & Mayr, 2014	Tinamiformes	Tinamidae	17	0.72	85	0.88	39	3.86e-05**
Livezey & Zusi, 2007	Various	Various	139	0.6	1528	0.65	436	0.002469**
Squamates								
Daza & Bauer, 2012	Gekotta	Sphaerodactylidae	12	0.34	227	0.41	17	0.4753
Hitchmough, 1997	Gekotta	Diplodactylinae	12	0.83	10	0.84	9	1
Frost <i>et al.</i> , 2001a	Iguania	Polychrotidae	26	0.77	31	0.56	40	0.1222
Frost <i>et al.</i> , 2001b	Iguania	Tropiduridae	28	0.68	32	0.56	46	0.4259
Vieira, Colli, & Bao, 2005	Iguania	Corytophanidae	10	0.38	49	0.21	8	0.1132
Arnold, 1997	Lacertoidea	Takydromus	15	0.52	9	0.46	17	0.7854
Kearney, 2003	Lacertoidea	Amphisbaenia	36	0.74	118	0.72	16	0.3713
Yi & Norell, 2013	Lacertoidea	Various	25	0.62	209	0.67	25	0.09413

Reeder <i>et al.</i> , 2015	Various	Various	135	0.74	533	0.61	93	6.82e-05**
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Table 1. Showing number of taxa, number of informative characters per partition, ensemble retention indices for partitions for each dataset and results of Mann-Whitney U comparing the mean retention index between partitions, where the null hypothesis is that the two sets of retention indices are drawn from the same distribution. Due to differences in taxonomic level, avian datasets are categorised by superorder or order, while squamate datasets are categorised by sub- or infraorder or superfamily.

Cranial		Postcranial		P (Wilcoxon)	Plumage		Myology		P (Wilcoxon)
Ensemble character retention index	Informative Characters	Ensemble character retention index	Informative Characters		Ensemble character retention index	Informative Characters	Ensemble character retention index	Informative Characters	
0.91	23	0.8	39	0.02452*					
0.63	51	0.68	146	0.5143	0.572505	30	0.675355	72	0.493
0.64	35	0.59	47	0.5251					
0.84	79	0.86	70	0.173					

0.81	5	0.79	23	0.1494					
	4		27	NA					
	0		7	NA					
	0		25	NA					
0.9	36	0.93	144	0.01465*					
0.7	7	0.5	20	0.2419					
	9		0	NA					
0.75	39	0.76	41	0.1701					
	5		1	NA					
	0		29	NA					
	0		16	NA					
0.18	5	0.56	6	0.4015					
0.86	37	0.95	59	0.003018**					

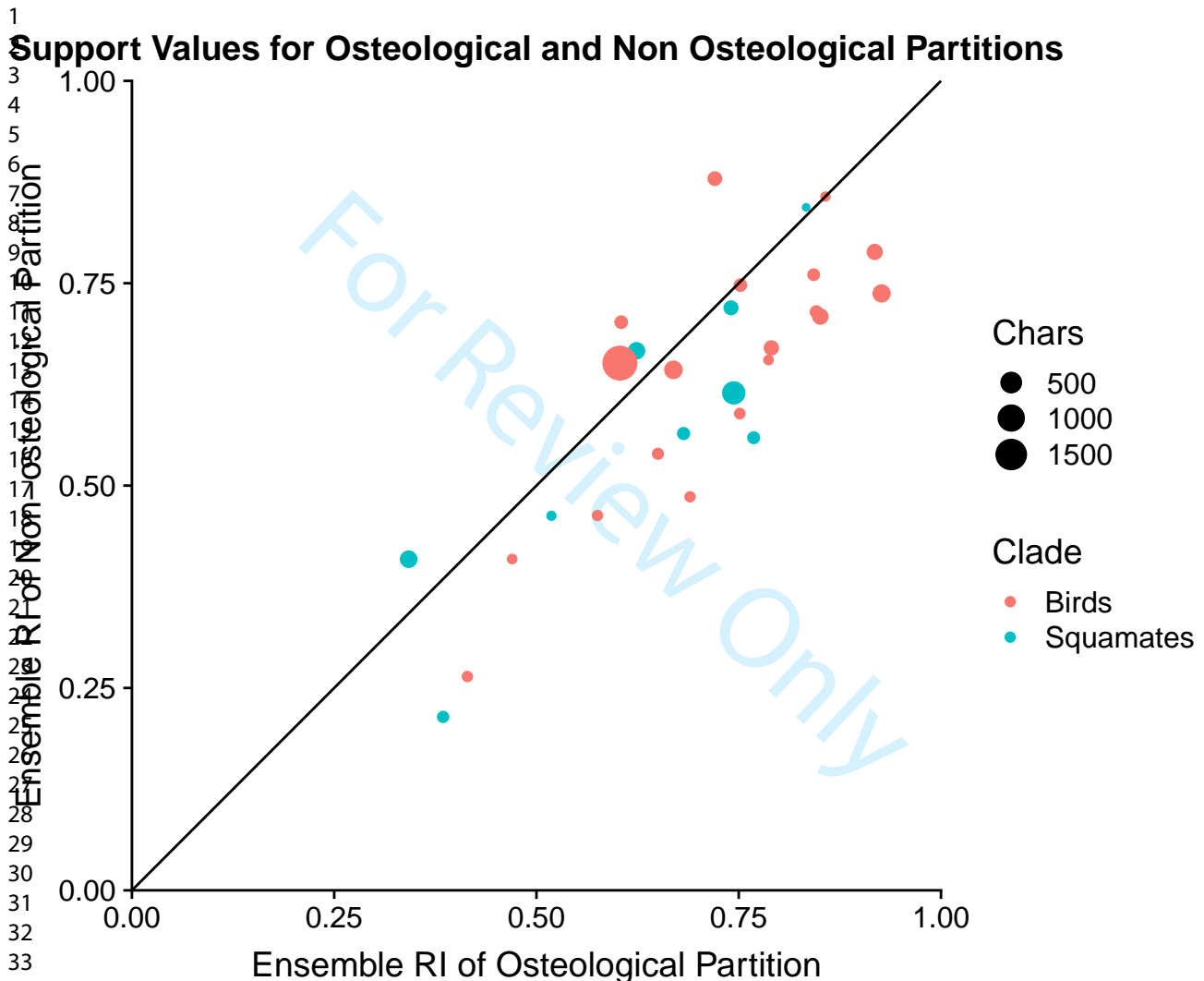
0.66	37	0.77	48	0.08348					
0.63	357	0.59	1171	0.0005366**	0.651811	98	0.623933	237	0.09542
0.33	152	0.36	75	0.7183					
	2		8	NA					
0.76	17	0.78	14	0.8555					
0.64	21	0.73	11	0.9351					
0.38	37	0.39	12	0.8625					
				NA					
0.75	88	0.7	30	0.6918					
0.62	169	0.65	40	0.2796	0.711538	10	0.608696	11	0.6851
0.76	411	0.67	122	0.000001994*					

Table 1. (cont.) Showing number of taxa, number of informative characters per partition, ensemble retention indices for partitions for each dataset and results of Mann-Whitney U comparing the mean retention index between partitions, where the null hypothesis is that the two sets of retention indices are drawn from the same

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distribution. Due to differences in taxonomic level, avian datasets are categorised by superorder or order, while squamate datasets are categorised by sub- or infraorder or superfamily.

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