Phylogeny, Diet, and Cranial Integration in Australodelphian Marsupials

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Studies of morphological integration provide valuable information on the correlated evolution of traits and its relationship to long-term patterns of morphological evolution. Thus far, studies of morphological integration in mammals have focused on placentals and have demonstrated that similarity in integration is broadly correlated with phylogenetic distance and dietary similarity. Detailed studies have also demonstrated a significant correlation between developmental relationships among structures and adult morphological integration. However, these studies have not yet been applied to marsupial taxa, which differ greatly from placentals in reproductive strategy and cranial development and could provide the diversity necessary to assess the relationships among phylogeny, ecology, development, and cranial integration. This study presents analyses of morphological integration in 20 species of australodelphian marsupials, and shows that phylogeny is significantly correlated with similarity of morphological integration in most clades. Size-related correlations have a significant affect on results, particularly in Peramelia, which shows a striking decrease in similarity of integration among species when size is removed. Diet is not significantly correlated with similarity of integration in any marsupial clade. These results show that marsupials differ markedly from placentals in the relationships of cranial integration, phylogeny, and diet, which may be related to the accelerated development of the masticatory apparatus in marsupials.

INTRODUCTION

The correlated evolution of traits is a fundamental issue in evolutionary biology, with great importance for understanding morphological evolution and the generation of morphological diversity [1–3]. Morphological integration is the study of trait associations, measured through statistical analysis of patterns of trait covariation or correlation. Integration of functionally or developmentally-related traits can influence morphological evolution in many ways, from constraining the variability of individual traits to facilitating transformations of functional sets [1–10]. Yet, despite this importance to morphological evolution, cranial integration has been overlooked in most morphological analyses.

Most studies of morphological integration focus on microevolutionary hypotheses, documenting the relationships among development, genetics and phenotypic integration, usually in single species [for recent reviews see 2,3,10,11]. The few comparative studies conducted have focused on placentals and monotremes, as well as placentals, and has shown a high degree of conservation of cranial integration across therian mammals [10]. However, differences in patterns of trait integration do exist among therian taxa, and these differences may be ascribed to several factors. Phylogeny and ecology are of particular interest, as they have been correlated with similarity of cranial integration in the placental clades Primates [13,15,16] and Carnivora [11].

Because placentals and marsupials differ greatly in the timing of cranial bone ossification [18–22], and because developmental timing has often been considered to be a major influence on integration [14,23–29], examination of integration in marsupials will provide an important comparison to the extensive studies of placental mammals. In this paper, I assess the relationship between evolutionary history, ecology, and cranial integration in australodelphian marsupials. Specifically, I test the hypothesis that similarity in cranial integration in marsupials is correlated with phylogeny and dietary similarity.

A plausible null hypothesis is that evolutionary history (phylogeny) is correlated with similarity in patterns of morphological integration. Of the placental clades studied, however, only a few support this hypothesis [11,12]. Other clades display only a weak correlation between phylogeny and cranial integration [15,16,30], while some clades show stronger correlations between diet and morphological integration [11,16]. Diet strongly influences tooth size and shape and jaw musculature, and thus overall skull morphology. Skulls must accommodate the functional demands of juvenile and adult food processing, and, if masticatory traits are functionally integrated, then similarities in diet may be reflected in similarity in morphological integration.

These results from previous studies demonstrate that a complex relationship exists between phylogenetic relatedness, integration, and ecology across placental mammals. In addition, as suggested...
by Steppan [31], disparate microevolutionary and macroevolutionary processes may manipulate morphological integration. While it is clear that evolutionary history is related to morphological integration to some extent, it is not understood how general this relationship is, nor how significant patterns of integration are in morphological evolution.

As noted above, examination of morphological integration in marsupials is particularly important, because of the striking differences in the timing of cranial bone development between marsupials and placentals. Ossification of the anterior masticatory apparatus (premaxilla, maxilla, and dentary) is accelerated in marsupials relative to placentals. This heterochronic shift is related to the unique marsupial reproductive pattern in which neonates are birthed after a short gestation period and complete their early development attached to the teat [22]. If this early ossification and use of the masticatory apparatus influences the developmental integration of those bones, it may also affect potential functional integration related to adult diet. Therefore, this study of morphological integration in marsupials will provide the data to assess, in comparison with placental mammals, how heterochrony may be influencing morphological integration. Comparisons among marsupial and placental mammalian clades thus provides an opportunity to isolate three of the factors (phylogeny, ecology, and development) that have often been invoked as influences on morphological integration and morphological evolution.

MATERIALS AND METHODS

Data collection

Cranial landmarks were captured using an Immersion Microscribe G2×3-D digitizer. Fifty-seven landmarks were collected across the skull, emphasizing points of certain homology across taxa, such as tripartite sutures. In addition, landmarks corresponding to those in earlier studies also were used, to permit direct comparison with previous results. Landmarks are listed in Table 1 and illustrated in Figure 1 (symmetrical landmarks are displayed on one side only).

Twenty species of australodelphian marsupials were included in this analysis, spanning Dasyuromorpha, Peramelia, and Diprotodontia (Appendix S1). Taxa were chosen due to their morphological convergence with placental groups in which cranial integration has been studied (Phalangeridae on Primates; Dasyuromorpha on Carnivora), their relationship to fossil taxa, not morphological integration and morphological evolution.

| Symbol Landmark |
|-----------------|
| PMv Premaxilla–Maxilla ventral suture |
| PM Premaxilla–Maxilla anterior suture |
| Nant Nasal–anterior extreme |
| NP Nasal–Premaxilla–anterior suture |
| CI Canine–lateral extreme |
| Cm Canine–mesial extreme |
| M1 Anterior lateral M1 |
| MRL Posterior lateral M2 |
| M1m Anterior mesial M1 |
| PalM Palatine–Maxilla ventral suture |
| JMc Jugal–Maxilla ventral suture |
| JMd Jugal–Maxilla dorsal suture |
| NF Nasal–Frontal suture |
| JML Jugal–Maxilla–Lacrimal suture |
| LFM Lacrimal–Frontal–Maxilla suture |
| PB Postorbital process of the frontal |
| Ba Bulla–anterior extreme |
| Pt Pterygoid–posterior extreme |
| PFL Palatine–Frontal–Lacrimal suture |
| OAF Orbitosphenoid–Alisphenoid–Frontal suture |
| BP Basisphenoid–Presphenoid suture |
| PP Presphenoid–Palatine suture |
| JSv Jugal–Squamosal ventral suture |
| Jsd Jugal–Squamosal dorsal suture |
| Bp Bulla–posterior extreme |
| P0c Paroccipital process |
| OC Occipital condyle–lateral extreme |
| BBB Basioccipital–Basisphenoid–Bulla suture |
| PF Parietal–Frontal suture |
| PO Parietal–Occipital suture |
| PSA Parietal–Squamosal–Alisphenoid suture |
| PFA Parietal–Frontal–Alisphenoid suture |

Shown in Figure 1. Midline traits are marked in bold. doi:10.1371/journal.pone.0000995.t001

reduce the significance of results, rather than to create false similarity and increase significances. This methodology is thus more conservative and would impact all analyses for phylogeny and diet equally.

Data analysis

Analytical methods follow previous studies [10,11], and a brief review of methodology is provided here. Only landmarks from the midline (6) and right side of the skull (26) were used in analyses. Specimens were aligned with Procrustes analysis, using an algorithm written in Mathematia 5.0 (Wolfram Research Inc., Champaign, IL). Scaling, a common Procrustes procedure, was not applied to specimens, to reduce the effect of inducing covariances through Procrustes fitting. Pearson product–moment dot covariances were calculated for individual species in Mathematia 5.0. For some analyses, the first eigenvector, which mainly reflects size, was removed from the covariance matrix prior to matrix correlation analysis. Comparisons among results
Phylogeny

To test the relationship between MSI and phylogenetic relatedness, multiple phylogenetic similarity matrices were constructed for all of the taxa examined, using recently published phylogenetic hypotheses [33–43]. Recent phylogenetic hypotheses incorporating the taxa examined in this study differed in the relative placements of the three orders examined in this study. Some studies placed Dasyuromorphia as basal to Peramelia+Diprotodontia [35,36], some placed Peramelia as basal to Dasyuromorphia+Diprotodontia [37], and still others placed Dasyuromorphia and Peramelia as sister groups relative to Diprotodontia [38,39]. There is also a lack of consensus on the relationships within Peramelia. Groves and Flannery [41] recognised two families, Peramelidae (Perameles, Isoodon, and Macrotris) and Peroryctidae (Peroryctes, Microperoryctes, and Echymipera). Szalay [40] placed Macrotris as the nearest outgroup to the rest of the peramelians included in this study, while Westerman et al. [42] also placed Peroryctes outside the remaining peramelians in this study. Each of these competing phylogenetic hypotheses for Marsupialia and for Peramelia was analysed separately to test the relationship between phylogeny and similarity of morphological integration (Fig 2).

For each topology, the patristic distance between each pair of species was calculated. Because a similarity matrix is required for comparison, each patristic distance was subtracted from the maximum value among species (those related only as australodelphian marsupials)+1, such that the most distantly-related species have a value of one and sister taxa have the maximum value. Matrix correlation analysis was used to test the correlation of various phylogenetic distance matrices with MSI. Mantel’s test is used to determine the significance of the matrix correlation. Mantel’s test randomly reorders the rows and columns of one of the two correlation matrices being compared and recalculates the matrix correlation between the two matrices [44]. This operation was repeated 10,000 times, providing a random distribution of matrix correlations with which to assess the significance of the observed matrix correlation.

An alternative analysis of phylogenetic relationship also was employed. Pairwise similarity of morphological-integration values were averaged for taxa related at various taxonomic levels (single pairs analysis [32]). For example, the matrix correlations between all pairs of species that are related at the genus level are averaged, versus all pairs that are related at the family level but not at the genus level, etc. This analysis was conducted among all species and within individual orders for four taxonomic levels of relationship: infraclass, order, family, and genus. If phylogenetic relatedness is correlated with similarity in morphological integration, average pairwise MSI values should decrease from the generic to the infraclass level. Analysis of variance (ANOVA) was conducted to determine if there are significant differences in similarity of morphological integration across taxonomic ranks.

Diet

To test the correlation between MSI and similarity in diet, a dietary similarity matrix was constructed among all taxa, based

Figure 2. One phylogenetic hypothesis for taxa included in this study [37,42]. Alternative phylogenies, with Peramelia basal and with different topologies within Peramelia, were also tested.

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on the proportion of shared diet between species. This analysis followed the methodology of Marroig and Cheverud [16] for quantifying similarity in diet based on the proportion of shared dietary types. Each species was categorised by the approximate percentage of vertebrates, invertebrates/insects, fruits, and leaves in its diet (Appendix S1). Dietary information was taken from existing literature, using approximated contributions of each category to a species’ total diet [45,46].

Dietary similarity between two species was calculated as a sum across the four categories, where each category had a value comprised of the square root of the product of each species’ percentage for that particular dietary type [see 11]. This process was repeated for each pair of taxa, resulting in a matrix of dietary similarity. The dietary similarity matrix (hereafter DSM) was then compared to MSI using matrix correlation analysis with Mantel’s test for significance.

Phylogenetic relatedness has the potential to complicate the analysis of diet, due to the possibility that more closely-related taxa are more similar in diet because of common ancestry alone. To test for the possible influence of phylogeny, the dietary-similarity matrix was compared to the phylogenetic-distance matrix, using matrix correlation analysis with a Mantel’s test for significance.

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RESULTS

Phylogeny

Across all australodelphian marsupials, there was a significant correlation with phylogeny using all topologies (Fig. 3, Table 2). This correlation was statistically robust to the inclusion or exclusion of size. Across the smaller clades examined in this study, however, only Dasyuromorphia and Dasyuridae showed a significant correlation with phylogeny. Peramelia showed a marginally significant correlation with phylogeny in all three topologies when size was included, but in none when size was removed. Diproctodonta, represented by Vombatidae and Phalangeridae, did not show a significant correlation with phylogeny in the analyses with or without size.

Single pairs analysis was also conducted for each clade (Fig. 4). When size was included, average similarity of integration increased significantly (ANOVA, p<0.001) from species related only as australodelphian marsupials (0.77) to those in the same order (0.81), same family (0.86), and same genus (0.90). There were also significant increases in average similarity of integration with closer phylogenetic relationship within Dasyuromorphia (p<0.001), Peramelia (p<0.001), and Diprotodonta (p = 0.01). When size was removed, there was no significant relationship between taxonomic rank and similarity in integration across all australodelphian marsupials, although average similarity of integration slightly increased from infraclass (0.53), to order (0.55) to family (0.60), and to genus (0.61). Without size, Dasyuromorphia exhibited a significant similarity increase with phylogenetic relationship (p = .001), while Peramelia and Diprotodonta showed

| Group                              | Species | R with size | R without size |
|------------------------------------|---------|-------------|----------------|
| Marsupialla–Peramelia basal        | 20      | .55**       | .41**          |
| Marsupialla–Dasyuromorphia basal   | 20      | .45**       | .40*           |
| Marsupialla–Peramelia+Dasyuromorphia | 20 | .55**       | .42**          |
| Dasyuromorphia                     | 8       | .80**       | .90*           |
| Dasyuridae                         | 5       | .86**       | .90**          |
| Peramelia [41]                     | 7       | .73*        | .43            |
| Peramelia [40]                     | 7       | .71*        | .43            |
| Peramelia [42]                     | 7       | .71*        | .43            |
| Diprotodonta                       | 5       | .86         | .61            |

Results from matrix correlation analysis of phylogenetic distance matrix and matrix of similarity in morphological integration. Asterisks indicate significance at the p = 0.05 level (**) or the p = .1 level (*).
While size remains an important factor influencing trait variances and co-integration, size has little effect on the relationship between diet and cranial integration. Some subclades show significant correlations with phylogeny, whereas others do not. In both clades, size-related correlations significantly influence morphological variation. Differences in correlation values between analyses with and without size are greater in Peramelia than in other clades. Peramelia shows an intermediate pattern between Dasyuromorphia and Dasyuridae, with marginally significant correlations in matrix correlation analysis with size included, but not when size is removed. All three phylogenetic hypotheses for Peramelia produced similar results.

### DISCUSSION

Within placental mammals, morphological integration has been analysed comparatively in Primates [12–17,47,48] and Carnivora [11]. Within both of these placental clades, correlation with phylogeny and diet varies, with some subclades showing significant correlations with phylogeny, some with diet, and others with neither factor. In both clades, size-related correlations significantly affect the relationship between morphological integration and differences in evolutionary patterns. Size is an evolutionary factor, and size is often the dominant factor influencing trait variances and covariances [49]. While size remains an important factor influencing morphological integration in marsupials, the relationships among phylogeny, diet, and similarity of integration are quite different than those observed in placental mammals.

Matrix correlation analysis and single pairs analysis produced consistent results in most analyses. Both support a significant relationship between phylogeny and similarity of integration across australodelphian marsupials. These three orders are quite morphologically distinct and diverged 40–50 million years ago [38]; therefore, this correlation between phylogenetic relationship and similarity in morphological integration is perhaps expected. The three orders examined, however, display three different patterns with respect to phylogeny, size, and cranial integration. While Dasyuromorphia and Dasyuridae show significant correlations between phylogenetic distance and similarity of integration, both including and excluding size (Table 2), Dasyuridae only shows a correlation between phylogeny and integration in single pairs analysis, when size is included (Fig. 4). It should be noted that, because only phalangerids and a single vombatid were sampled, results for Diprotodontia may mainly reflect the lack of a phylogenetic signal within Phalangeridae, rather than in all diprotodontians.

Peramelia shows an intermediate pattern between Dasyuromorphia and Dasyuridae, with marginally significant correlations in matrix correlation analysis when size is included, but not when it is removed. All three phylogenetic hypotheses for Peramelia produced similar results. Interestingly, the differences in correlation values between analyses with and without size are greater in Peramelia than in other clades. Likewise, in single pairs analysis, Peramelia shows increased similarity of integration with phylogenetic relationship when size is included, but a negative correlation when size is removed. This result seems to be primarily influenced by a few taxa (e.g., *Peroryctes*) that show particularly low similarity of integration with other taxa, whether including or excluding size. However, *Perameles nasuta*, which shows comparatively high similarity of integration with other taxa, whether including or excluding size, shows a correlation between phylogeny and integration in single pairs analysis. Both support a significant correlation between phylogeny and similarity of integration across large clades. These analyses demonstrate that size and phylogeny are correlated with similarity in patterns of integration, but with strikingly disparate influences in the examined clades. If trait correlations significantly influence morphological variation, then these patterns provide the diversity necessary to isolate and test the evolutionary consequences of different patterns of morphological integration with empirical data from real species.

In contrast to the results for phylogeny, no clade in this analysis shows a significant correlation between similarity of integration and diet (Table 3). Among australodelphian marsupial orders, only Dasyuromorphia shows a marginally significant correlation between DSM and similarity of integration, and only when size is removed from analysis. Because this relationship is not observed when dietary similarity is regressed against phylogeny (DSRM), it

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### Table 3. Dietary similarity and cranial integration.

| Group                      | DSM with size | DSM without size | DSRM with size | DSRM without size |
|----------------------------|---------------|------------------|----------------|------------------|
| Marsupialia                | .25           | .24              | −.06           | .03              |
| Dasyuromorphia             | .61           | .60*             | .21            | .13              |
| Dasyuridae                 | .05           | .12              | .04            | .11              |
| Peramelia                  | .41           | .40              | .20            | .25              |
| Diprotodontia              | .42           | .28              | .11            | .09              |

Results of matrix correlation analysis of dietary similarity matrix (DSM), dietary similarity residual matrix (DSRM), and matrix of similarity in morphological integration (MSI). Asterisks indicate significance at the p = 0.05 level (*) or the p = .1 level (**).

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is probable that the marginally significant correlation between DSM and similarity of integration merely reflects the strong correlation between phylogeny and similarity of integration. While both phylogeny and diet are strongly correlated with similarity in integration in placental taxa, although often in different clades, this study suggests that only phylogeny plays a significant role in morphological integration in australodelphian marsupials.

Diet is expected to influence morphological integration by inducing the functional integration of traits required for mastication. The marsupial species examined in this study include a broad range of ecological and morphological diversity, including hypercarnivorous (Thylacinus), inverteivorous (Myrmecobius), and folivorous (Trichosurus, Vombatus) taxa, to species with a variety of mixed diets (Appendix S1). Therefore, this result does not simply reflect a lack of dietary diversity in sampled taxa, although marsupials are often considered to be less diverse in morphology and ecology than placentals. This lack of diversity has often been attributed to the observation that, in marsupials, the ossification of bones associated with feeding (premaxilla, maxilla, dentary) has been accelerated to accommodate the early birth and suckling of marsupials, relative to placentals [18–20,22,50]. If developmental timing or developmental integration is a major influence on morphological integration, then the early ossification of these bones that are typically associated with mastication may overshadow any diet-specific functional integration.

It is important to note that the relationship between morphological integration and morphological evolution are poorly understood [10]. A recent study of cranial shape in carnivorous marsupials [51], primarily dasyuromorphians, showed a strong correlation between diet and cranial shape. As discussed above, Dasyuromorpha was the only clade in this study to show a marginally significant correlation between cranial integration and diet, perhaps suggesting some relationship between morphological integration and cranial shape. While there are many hypotheses on the potential influence of character integration on morphological evolution, these have yet to be explicitly tested. Dasyuromorpha may well provide an ideal system for future studies of morphological integration’s evolutionary significance, as cranial shape, ecomorphology, and, with this study, cranial integration, are all well studied for this clade.

This comparative study of morphological integration in the australodelphian cranium demonstrates that a broad range of patterns exist in the relationships among phylogeny and similarity in integration, but that phylogeny is significantly correlated with similarity in integration in most clades. In contrast, while all examined placental orders exhibit some significant correlation between diet and similarity in integration, australodelphian marsupials do not show this relationship in any clade. These results support the finding of a previous study [11] that phylogeny is a primary factor influencing patterns of morphological integration in all large clades, while diet is a significant factor in only some clades. This study also suggests that the early ossification of the facial skeleton in marsupials may influence patterns of cranial integration and the relative importance of ecology in shaping morphological integration.

**SUPPORTING INFORMATION**

**Appendix S1** Species list, specimen numbers. Dietary categories used in construction of the dietary similarity matrix are invertivore (I), frugivore (F), folivore (F0), and carnivore (C). *The diet of Vombatus is primarily grasses and roots.

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**Appendix S2** Matrix of similarity of morphological integration. The lower triangle is the original MSI. The upper triangle is MSI without size.

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**Author Contributions**

Conceived and designed the experiments: AG. Performed the experiments: AG. Analyzed the data: AG. Contributed reagents/materials/analysis tools: AG. Wrote the paper: AG.

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