Convergent Evolution of Locomotory Modes in Euarchontoglires

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The research of phenotypic convergence is of increasing importance in adaptive evolution. Locomotory modes play important roles in the adaptive evolution of species in the Euarchontoglires, however, the investigation of convergent evolution of the locomotory modes across diverse Euarchontoglires orders is incomplete. We collected measurements of three phalangeal indices of manual digit III, including metacarpal of digit III (MC3), manus proximal phalanx of digit III (MPP3), and manus intermediate phalanx of digit III (MIP3), from 203 individuals of 122 Euarchontoglires species representing arboreal (orders Scandentia, Rodentia, and Primates), terrestrial (orders Scandentia and Rodentia), and gliding (orders Dermoptera and Rodentia) locomotory modes. This data can be separated into seven groups defined by order and locomotory mode. Based on combination of the three phalangeal indices, the Principle component analyses (PCA), phylomorphospace plot, and C-metrics analyses clustered the arboreal species of Scandentia, Rodentia, and Primates together and the terrestrial species of Scandentia and Rodentia together, showing the convergent signal in evolution of the arboreal (C1 = 0.424, P < 0.05) and terrestrial (C1 = 0.560, P < 0.05) locomotory modes in Euarchontoglires. Although the gliding species from Dermoptera and Rodentia did not cluster together, they also showed the convergent signal (C1 = 0.563, P < 0.05). Our work provides insight into the convergent evolution of locomotory modes in Euarchontoglires, and reveals that these three indices contribute valuable information to identify convergent evolution in Euarchontoglires.

Keywords: convergent evolution, Euarchontoglires, metacarpal, manus proximal phalanx, manus intermediate phalanx, locomotory modes

INTRODUCTION

The relationship between morphology, locomotory modes and habitat has been receiving greater attention in evolutionary studies of phenotypic variation (Losos and Sinervo, 1989; Losos, 1990; Bonine and Garland, 1999; Vanhooydonck and Van Damme, 1999; Thorington and Santana, 2007; Goodman et al., 2008; Irschick et al., 2008; Pfaff et al., 2015; Kawashima et al., 2018). It has
been observed that differences in habitat trigger divergence in the evolution of the morphology of locomotory systems across many different taxonomic taxa (Losos, 1990; Runestad and Ruff, 1995; Irschick et al., 2005; Calsbeek and Irschick, 2007; Sargis et al., 2007; Samuel and Van Valkenburgh, 2008; Schmidt, 2008), and that convergent evolution of locomotory modes for the same habitat niche adaptation in phylogenetically unrelated taxa can lead to similar morphological traits (Lemelin and Grafton, 1998; Kingsolver and Huey, 2003; Samuel and Van Valkenburgh, 2008; Gleiss et al., 2011; Losos, 2011; Edwards et al., 2012; Chen and Wilson, 2015; Morris et al., 2018; Grossnickle et al., 2019, 2020). The morphological convergence provides clues to better understanding functional adaptation and how distantly related species evolved in a similar way.

The mammalian superorder Euarchontoglires is comprised of five orders and includes Lagomorpha (rabbit, pika, and hare), Rodentia (mouse, rat, squirrel, and beaver), Dermoptera (flying lemur), Scandentia (tree shrew), and Primates (human, monkey, and ape) (Murphy et al., 2001; Kriegs et al., 2006; Vander Linden et al., 2019). A great diversity in locomotory modes is observed among and within the Euarchontoglires orders, including fossorial, ricochetal, arboreal, terrestrial, and gliding (MacPhee, 1993). Interestingly, the same locomotory modes are found in different orders of Euarchontoglires, including the arboreal mode in Scandentia, Rodentia, and Primates, the terrestrial mode in Scandentia and Rodentia, and the gliding mode in Dermoptera and Rodentia (Kirk et al., 2008; Meng et al., 2017; Vander Linden et al., 2019; Grossnickle et al., 2020; Figure 1). The sharing of locomotory modes among orders makes Euarchontoglires an intriguing group for the investigation of morphological convergence with locomotory modes. Previous studies with Euarchontoglires have focused on the convergence of forelimb evolution with several locomotory modes, but these studies only examined species within Rodentia (Samuel and Van Valkenburgh, 2008) or on skeletal convergence with the gliding mode in Dermoptera and Rodentia (Grossnickle et al., 2020).

Therefore, knowledge on the convergent evolution of locomotory modes across Euarchontoglires orders is very limited and it remains unclear whether the underlying skeletal morphology of terrestrial and arboreal species from the different Euarchontoglires orders have converged.

In the present study, we collected three phalangeal indices of manual digit III from 203 individuals of 122 Euarchontoglires species that represent the arboreal (orders Scandentia, Rodentia, and Primates), terrestrial (orders Scandentia and Rodentia), and gliding (orders Dermoptera and Rodentia) locomotory modes to investigate the convergent evolution of locomotory modes across these Euarchontoglires orders. The three phalanges include metacarpal of digit III (MC3), manus proximal phalanx of digit III (MPP3), and manus intermediate phalanx of digit III (MIP3), which represent the inherent properties of the manus (Corruccini, 1995; Hamrick, 2001; Bloch et al., 2007; Kirk et al., 2008) and have been used to illustrate the locomotory modes of mammals (Lemelin, 1999; Hamrick, 2001; Meng et al., 2006, 2017; Bloch et al., 2007; Kirk et al., 2008; Samuel and Van Valkenburgh, 2008; Venkataraman et al., 2013; Zheng et al., 2013; Chen and Wilson, 2015; Grossnickle et al., 2020; Young and Chadwell, 2020). Our morphometric analyses based on quantitative methods provide insights into the convergent evolution of locomotory modes in Euarchontoglires, and moreover, evaluate the potential of these indices for studies on the convergent evolution of locomotory modes in Euarchontoglires.

### MATERIALS AND METHODS

#### Data Collection

Publicly available data for the three phalangeal indices of manual digit III, including MC3, MPP3, and MIP3, from a total of 152 individuals from 122 Euarchontoglires species belonging to the orders Scandentia, Rodentia, Dermoptera, and Primates were collected from published sources (Kirk et al., 2008; Samuel and Van Valkenburgh, 2008; Chen and Wilson, 2015; Meng et al., 2017). These species represent arboreal (99 individuals from 83 species of Scandentia, Rodentia, and Primates), terrestrial (33 individuals from 28 species of Scandentia and Rodentia), and gliding (20 individuals from 11 species of Dermoptera and Rodentia) locomotory modes. In addition, three phalangeal indices of manual digit III were measured from 51 individuals of the gliding complex-toothed flying squirrel (Rodentia, Trogopterus xanthipes) that were bred in the Runxing Planting and Breeding Cooperative, Liqueun County, Xi’an, Shaanxi Province in the present study and were added to the relatively limited data available to represent the gliding locomotory mode. The three phalangeal indices measured using the electronic digital indicator for Trogopterus xanthipes were shown in Supplementary Figure S1. Chordal nodes for each bone element were measured from the nearest to the farthest end, and from the parallel to the midline of the axis on the sagittal plane based on the methods of Kirk et al. (2008). In total, three phalangeal indices from 203 individuals of 122 species were collected for the present study (Supplementary Table S1).

Individuals were divided into seven groups for analyses according to their taxonomic order and their locomotory mode. The groups are: Rodentia Gliding (RG; 64 individuals of 9 species), Dermoptera Gliding (DG; 7 individuals of 2 species), Scandentia Terrestrial (ST; 8 individuals of 3 species), Rodentia Terrestrial (RT; 25 individuals of 25 species), Scandentia Arboreal (SA; 6 individuals of 4 species), Rodentia Arboreal (RA; 34 individuals of 27 species), and Primate Arboreal (PA; 59 individuals of 52 species). For the present analysis, the MC3, MPP3, and MIP3 indices used were the percentage of the length of each indices of the total combined length for these three elements, i.e., MC3(p), MPP3(p), and MIP3(p), as previously used (Corruccini, 1995; Elissamburu and Vizcaino, 2004). Statistical differences within the 3 indices among the different groups were detected using the Wilcoxon test.

#### Morphometric Analyses

To avoid the possible bias of morphological variations resulted from the unbalanced individual numbers for each species, we calculated the average values per species to perform the morphometric analyses based on species level.
First, a principle component analyses (PCA) was conducted using the FactoMineR and factoextra packages in R (Version 3.6.2) to visualize the overall distribution of the groups in the morphospace.

Then, taking into the phylogenetic effect, the principal components of the Procrustes coordinates were projected in the phylomorphospace plot by using the phytools package in R (Version 3.6.2). A well-accepted mammalian species tree of 122 species in our study from TimeTree database1 was used as the input tree (Figure 1). This plot could detect the convergence based on the length and direction of branches in relation to their ancestral states (Feijó et al., 2020).

To statistically quantify the magnitude of convergence for the three locomotory modes from different orders, i.e., the gliding

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1http://www.timetree.org/
(RG and DG), arboreal (RA, PA, and SA) and terrestrial (ST and RT) modes, the distance-based metric (C1–C4) were calculated (Stayton, 2015) by using the “convrat” function from convevol package in R (Version 3.6.2). C1 is the distance between the convergent tips of the taxa of interest (Dtip) divided by the maximum distance between any ancestral nodes (Dmax), which represents the proportion of the maximum distance between two lineages. This change of this value from 0 to 1 means the degree of convergence signal from non-convergence to convergence. C2 is obtained by Dtip minus Dmax and represent the magnitude of convergent change. C3 and C4 are the standardized value of C2 which were calculated by dividing C2 by the total morphological branch length of convergent taxa of interest (C3) and the total amount of branch length in the entire clade (C4) (Stayton, 2015), respectively. The significance of the metrics was assessed by the “convratsig” function of the same package with 1000 iterations.

RESULTS AND DISCUSSION

The three indices, i.e., MC3(p), MPP3(p), and MIP3(p), used for the seven groups, including Rodentia Gliding (RG), Dermoptera Gliding (DG), Scandentia Terrestrial (ST), Rodentia Terrestrial (RT), Scandentia Arboreal (SA), Rodentia Arboreal (RA), and Primate Arboreal (PA) are listed in Supplementary Table S1. Statistical tests for the three indices among the different groups revealed significant differences \((p < 0.05)\) between most groups, with the exception of MIP3(p) for the same locomotory modes, including MIP3(p) between ST and RT \((p = 0.4774)\), SA and RA \((p = 0.3449)\), SA and PA \((p = 0.7868)\), and RA and PA \((p = 0.089)\), and MPP3(p) between RA and RG \((p = 0.5345)\) (Supplementary Table S2).

A PCA of the three indices \([MC3(p) + MPP3(p) + MIP3(p)]\) showed that PC1 explained 73.6% of variation and separated the terrestrial species of Scandentia and Rodentia (ST and RT groups) from the arboreal and gliding species (RA, PA, SA, RG, and DG groups) \((p < 0.05)\). PC2 explained 26.4% of variation and separated the gliding species of Dermoptera (DG group) from the other species examined \((p < 0.05)\) (Figure 2).

As seen from the phylomorphospace plot, the terrestrial species from Scandentia (ST group) and Rodentia (RT group) clustered together, suggesting that their similar phalangeal morphology may contribute to adapt to the same ground habitat. Likewise, the arboreal species from Scandentia (SA group), Rodentia (RA group), and Primate (PA group) clustered together, suggesting that their similar phalangeal morphology help them adapt to their grasping behavior. These results indicate the similarity of these morphological traits in the terrestrial and arboreal locomotory modes in Euarchontoglires. Interestingly, we found that the gliding species from Rodentia (RG group) were located between the arboreal species (RA, PA, and SA groups) and the gliding species from Dermoptera (DG group), consistent with the observation that the RG group species have evolved their morphological characteristics by not only adapting to tree-dwelling and branch-grasping life, but also to the gliding movement (Samuels and Van Valkenburgh, 2008; Grossnickle et al., 2020). The gliding species from Dermoptera are most distantly separated from the other species. Although the gliding species of Dermoptera (DG group) did not cluster with those from Rodentia (RG group) in the phylomorphospace plot (Figure 2), these two groups possess the same gliding locomotory mode and show a trend of closer proximity.

The C-metrics analyses of all three locomotory modes showed statistically significant convergence [gliding (DG and RG), C1 = 0.563, \(p < 0.05\)], arboreal (RA, PA, and SA), C1 = 0.424, \(p < 0.05\) and terrestrial (ST and RT), C1 = 0.560, \(p < 0.05\)], which indicate that evolution has reduced the distances in the gliding species and terrestrial species by showing more than 50% similarity than expected by chance, and in the arboreal species by more than 40% (Table 1). In addition, we also explore

![Phylomorphospace plot of 122 Euarchontoglires species based on the scores of a principle component analysis (PCA) of three phalangeal indices of manual digit III. The yellow color represents the Scandentia Arboreal (SA) species; the gray color represents the Scandentia Terrestrial (ST) species; the red color represents the Dermoptera Gliding (DG) species; the green color represents the Primate Arboreal (PA) species; the purple color represents the Rodentia Arboreal (RT) species; the blue color represents the Rodentia Terrestrial (RT) species; the indigo color represents the Rodentia Gliding (RG) species.](https://www.frontiersin.org/articles/10.3389/fec.2020.615862/full#tab1)
has been demonstrated in arboreal Primates (Lemelin, 1999; them grasp branches while they are moving. This phenomenon

The numbers of species used in each locomotory modes were given in
parentheses. The **"** represents significant P-values among each locomotory
modes with P < 0.05 generated from 1,000 simulations.

Therefore, our morphometric analyses based on quantitative
methods provide insight into the convergent evolution of
terrestrial, arboreal, and gliding locomotory modes in
Euarchontoglires. In our analyses, the terrestrial species (ST and
RT groups) demonstrate a relatively long metacarpal (MC3) and
short phalange (MPP3 and MIP3) compared with the arboreal
and gliding species (P < 0.05) (**Figure 3**), which would help
increase their speed for hunting or feeding on the ground (Peng
et al., 1991; Kirk et al., 2008; Samuels and Van Valkenburgh, 2008;
Fuchs and Corbach-Söhle, 2010). In addition, previous studies
have reported the possible genetic mechanisms at the gene level
involving muscle contraction and skeletal morphogenesis for
locomotory adaptation of terrestrial in Scandentia group (Fan
et al., 2014). Our study not only confirmed the long metacarpal
and short phalange in the terrestrial species of both Scandentia
and Rodentia, but also demonstrated convergent evolution
with the terrestrial locomotory mode in these two orders of
Euarchontogliare.

In comparison, the arboreal species (RA, PA, and SA groups)
show an elongated phalange MPP3 and MIP3 compared with
terrestrial species (P < 0.05) (**Figure 3**), which would help
them grasp branches while they are moving. This phenomenon
has been demonstrated in arboreal Primates (Lemelin, 1999;
Hamrick, 2001; Bloch et al., 2007; Kirk et al., 2008; Young and
Chadwell, 2020) and Rodentia (Kirk et al., 2008; Samuels and
Van Valkenburgh, 2008). Our study not only observed this in
the arboreal species of Scandentia, Rodentia, and Primates, but also
demonstrated convergent evolution with the arboreal locomotory
mode in these three orders of Euarchontogliare.

The gliding species (DG and RG groups) demonstrated an
evolution of the phalangeal MIP3 compared with arboreal
and terrestrial species (**Figure 3**), which is likely associated
with their unique attachment of the patagia to adapt the
gliding locomotory habitat (Macphee, 1993) or to their roosting
behavior (Grossnickle et al., 2020). Although they both possessed
patagium, but they are different in that the former shows
the patagium attachment by the styliform cartilages from the
wrist or elbow while the latter's patagium are attached to
the digits (Jackson, 2012). Further examination of the gliding
species from these two orders showed that the gliding species
from Rodentia have MPP3 lengths similar to those of arboreal
species and have elongated MIP3, while the gliding species from
Dermoptera have the shortest MIP3 and the most elongated
MIP3 compared with species of the other two locomotory
modes and the gliding species from Rodentia (**Supplementary
Table S1**). According to these above observations, we speculate
that the similarities and differences between these two orders
make them both distant from the other locomotory modes,
but prevent their clustering like that seen for the other two
locomotory modes, although they do show a trend of having
closer proximity in the phylomorphospace plot and do show the
significant convergence signal in C-metrics analyses. Besides the
phalangeal indices of manual digit III examined here, the gliding
mammals also developed other morphological modifications
for gliding adaptation, including the relatively elongated neck,
longer forearms, lumbar, and shorter thoracic vertebrae, hands,
feet bony as well as the more sensitivity of bony labyrinth
morphometry in the inner ear (Thorington and Santana, 2007;
Pfaff et al., 2015; Kawashima et al., 2018). So we hypothesized
that additional morphological traits, in addition to the three
indices used in the present study, are also necessary to address
the convergence in the gliding locomotory mode. Indeed, a
recent phylogenetic comparative analysis of 31 skeletal traits from

TABLE 1 | The C-metrics analyses of three locomotory modes (C1–C4 metrics).

| Locomotory modes | Groups | C1       | C2       | C3       | C4       |
|------------------|--------|----------|----------|----------|----------|
| Gliding (11)     | RG&DG  | 0.563*   | 0.082*   | 0.290*   | 0.008*   |
| Terrestrial (28) | ST&RT  | 0.560*   | 0.083*   | 0.290*   | 0.009*   |
| Arboreal (83)    | SA&RA&PA | 0.424*  | 0.054*   | 0.222*   | 0.006*   |

**Figure 3** | The distribution of the three indices among each locomotory mode. The abscissa represents the locomotory modes and the ordinate represents the ratios of the indices. MC3(p): The proportion of MC3 in the total combined length of the three elements; MPP3(p): The proportion of MPP3 in the total combined length of the three elements; MIP3(p): The proportion of MIP3 in the total combined length of the three elements; Terrestrial mode includes ST and RT groups; Arboreal mode includes SA, RA, and PA groups; Gliding mode includes DG and RG groups, Wilcoxon tests of the three indices among each locomotory mode all show significant P-values (P < 0.05).
the gliding mammals has observed convergence, including the gliding Dermoptera and Rodentia (Grossnickle et al., 2020).

CONCLUSION

In the present study, we used morphometric analyses based on quantitative methods to explore the convergence of locomotory modes across diverse Euarchontoglires orders. Our results showed that the phalangeal morphology of species with terrestrial, arboreal, and gliding locomotory modes from multiple Euarchontoglires orders is convergent, supporting the convergent evolution of these three locomotory modes. This study adds evidence of phenotypic convergent evolution of the locomotory modes in Euarchontoglires by extending the investigation into the terrestrial, arboreal, and gliding locomotory modes across four Euarchontoglires orders, which had previously only been studied for the gliding mode of Euarchontoglires or for the other modes only within Primates and Rodentia. With these findings we provide a framework for future work on convergence in mammals, and the application of the phalangeal indices used here to allow the inference and interpretation of locomotory modes of unknown or fossil species.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/Supplementary Material, further inquiries can be directed to the corresponding author/s.

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ETHICS STATEMENT

The animal study was reviewed and approved by the Committee on Animal Research and Ethics of Yunnan University.

AUTHOR CONTRIBUTIONS

LY designed the study. W-HG, L-FC, TZ, XW, and RL measured and collected the data. X-PW and W-HG performed the data analyses. LY, X-PW, and W-HG wrote the manuscript. CR and DI revised the manuscript. All authors read and approved the final manuscript.

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SUPPLEMENTARY MATERIAL

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