Evolution of vanga pedal morphology and its relation to ecology

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ABSTRACT

Adaptive radiations are clades that exhibit exceptional diversification in response to ecological opportunity. Studying them is a great way to develop an understanding of the evolution of morphology in response to environmental pressures. In bird adaptive radiations, bills are the most commonly studied anatomical trait. Hindlimbs, like bills, have strong associations with ecological functions, and studying them allows us to capture a different ecomorphological aspect of this adaptive radiation that may not be visible from just studying bills. To do this, we studied the hindlimb morphology of the family Vangidae. We found that bone length varies based on expected patterns of locomotion, with longer tarsometatarsi and shorter halluxes and penultimate phalanges for walking birds, and vice-versa for more arboreal birds. There was more bone length variation within Malagasy vangas than non-Malagasy vangas, supporting how locomotory diversification supported an adaptive radiation that included two extreme taxa. Only one phalanx significantly differed in length based on foraging strategy, showing that hindlimbs capture a different aspect of ecology than bills, where a significant difference has been previously found.

1. INTRODUCTION

Adaptive radiations are diversifications of single lineages that evolve to occupy many different niches given sufficient ecological opportunity. They often evolve on islands, where abundant resources and less competition allow diverse niches to be quickly colonized by a single clade (Wellborn and Langerhans 2014; Stroud and Losos 2016). Well-known examples include the Galápagos finches (Geospizinae) and Hawaiian honeycreepers (Carduelinae).

A useful way to study adaptive radiations is to investigate the effects of environmental niches on anatomical traits (Gavrilets and Losos 2009). In avian adaptive radiations, bills are the most researched trait: because they are closely related to diet and foraging niches (Cooney et al. 2017), they are one of the most obviously variable and ecologically relevant traits across species. However, other anatomical regions also play a role in determining the range and efficacy of a bird's foraging ecology (Martin and Karr 1990). For example, even subtle differences in tarsal and wing length can play a role in resource partitioning (Zeffer et al. 2003; Baumgart et al. 2021).

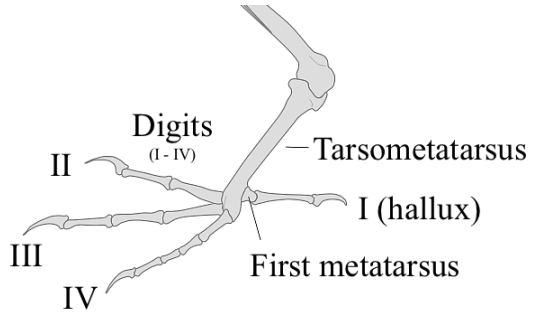


Figure 1. Labeled digits of an anisodactyl foot (Wikimedia Commons).

Despite its importance, avian pedal morphology is understudied. Feet interact directly with habitat substrate and play a crucial role in locomotion and foraging strategies (Zinoviev and Dzerzhinsky 2000; Abourachid et al. 2012; Abourachid et al. 2017). The length of certain phalanges can be used to make locomotory predictions: both the hallux and penultimate phalanges can indicate a bird's degree of terrestriality, with the hallux shortened and penultimate phalanges lengthened in walking species, and the hallux lengthened in perching and climbing species (Figure 1) (Hopson 2001;

Kavanagh et al. 2013; Abourachid et al. 2017; Falk et al. 2020). However, these data are collected from a small number of species widely arrayed across the phylogenetic tree (Zeffer et al. 2003), and do not examine morphological patterns in single diverse clades. Other research explores specific taxonomic groups with highly specialized morphology, such as raptors (Einoder and Richardson 2007) and parrots (Ksepka and Clarke 2011). These studies often focus on structure and mechanics. There still exists a need for research that closely examines morphological variation and patterns of diversification. Hindlimbs, like bills, are an important trait to study in adaptive radiations. Studying hindlimbs allows us to look at additional dimensions of ecomorphology that studying bills alone may not capture. To complement a study that looks at bills, we studied the evolution of hindlimb morphology in an adaptive radiation of birds: the vangas.

Vangas (Vangidae) are a primarily insectivorous family of passerines found throughout central and southern Africa, and south and southeast Asia. The Malagasy vangas (Vanginae) are an adaptive radiation of vangas endemic to Madagascar; this subfamily contains about half of the total species in Vangidae. Despite both groups of birds containing a similar number of species, Malagasy vangas have diversified substantially more than their non-Malagasy counterparts (Reddy et al. 2012). The main source of Vanginae morphological diversity is likely a result of their differing foraging strategies, which has led to vangas evolving a variety of shapes, sizes, and behaviors (Yamagishi and Eguchi 1996; Reddy et al. 2012).

Like most birds, vangas are anisodactyl, with one backward pointing digit (digit I or the hallux), and three forward-pointing digits (digits II, III, and IV). They are primarily perching birds. Their foraging strategies can be divided into three main categories: gleaning, probing, and sallying (Reddy et al. 2012). Pedal morphology plays a critical role in accessing foraging substrates: vangas may use their feet for perching, walking, and climbing.

In this study, we asked how foot morphology evolved in Malagasy vangas, compared to non-Malagasy vangas. We looked at patterns of bone length within all hindlimbs to determine which bones were the most likely to vary. We studied how this variation related to different aspects of locomotion and foraging. Finally, we compared the bones' rates of evolution between Malagasy and non-Malagasy vangas.

2. METHODS

A. *Bone length comparisons*

We measured the hindlimb bones of 51 specimens from 30 species in the family Vangidae. 16 species were Malagasy vangas, and 14 species were non-Malagasy vangas. We used a mix of skeletal, round skin, and fluid-preserved specimens acquired from The Field Museum of Natural History, the American Museum of Natural History, the Natural History Museum London, and the Yale Peabody Museum (SI Appendix 2AI). We CT scanned each specimen, and then cleaned the scan slices to make the hindlimb bones clearly visible.

We used the software 3D Slicer to measure the length of each bone from one foot per specimen. We chose whichever foot was in a better position for measuring, as left and right feet are assumed to be symmetrical at the scale of between-species comparisons. We measured twelve bones from each specimen: the tarsometatarsus (tmt), metatarsus (m1), hallux (d1p1), and proximal to penultimate phalanges of each digit (d2p1, d2p2, d3p1, d3p2, d3p3, d4p1, d4p2, d4p3, and d4p4). We did not measure the ungual phalanges (claws), as they were

not consistently present across specimens; in addition, the less-dense keratin of the claws required a different visualization in Slicer. We viewed and measured each bone, except m1, from the dorsal aspect in the 3D view, using the Line Markup tool in Slicer (SI Appendix 2AII). We measured the tmt from the center of the ridge just below the eminentia intercondylaris, to the distal-most point on the trochlea metatarsus III (Baumel et al. 1993, p. 132). We measured m1 from the proximal-most point where it was fused to the tmt, to the center of the area intercondylaris. We measured d1p1 using the highest points of the ridges below and above the proximal and distal eminentia intercondylaris, in specimens where these ridges were present. Some specimens lacked a distinct ridge; in these cases, we placed the points at equivalent places where ridges were present in other species. In most cases, we digitally separated the hallux bone from the rest of the hindlimb to place these points. We measured d2p1 from the apex of the proximal crest to the center of the divot at the distal end of the bone. We measured all other digits from the center of their proximal- and distal-most points as viewed from the dorsal aspect of the bone. If these points were obscured by digit configuration, we used the slice view to place the points.

We performed all further analyses in R. We size corrected each specimen's data using the geometric mean of that specimen's measurements. Following this, we log-transformed the data to standardize the variance between phalanges, and then averaged the measurements for species represented by multiple specimens.

We calculated the variance for each bone and the strength of correlation between each bone in the dataset. We then performed a principal component analysis (PCA) to assess overall patterns of shape variation and correlated shape change, as well as to determine which bones accounted for the most variation in the dataset. To see whether patterns of shape variation were different when we accounted for covariance due to phylogenetic relatedness, we conducted a phylogenetic PCA using a UCE phylogeny of all vangas (Reddy et al. in prep) using the phyl.pca function in phytools (Revell 2009, Revell 2012).

B. ***Ecomorphological correlations***

We tested for a relationship between phalanx length and foraging strategy (as classified in Reddy et al. 2012) using ANOVAs. We used a Tukey test to determine which foraging strategies had a significant effect on phalange length. To identify how much of bone length variation could be accounted for by phylogenetic relatedness, we performed a phylogenetic ANOVA using the phylANOVA function in phytools (Revell 2012).

C. ***Rates of evolution***

Next, to visualize patterns of trait evolution across the phylogeny, we used just the geomean- but not log-corrected data to perform an ancestral state reconstruction on each bone using the ace function in ape (Pagel 1994, Paradis and Schliep 2019). We determined and compared the net rate of shape evolution of individual bones between Malagasy and non-Malagasy vangas using the compare.evol.rates function in geomorph (Adams 2014, Baken et al. 2021, Adams et al. 2022).

We then returned to the geomean- and log-corrected data to calculate overall phylogenetic signal using the physignal function in geomorph (Blomberg et al. 2003; Adams 2014) to determine whether the evolution of Malagasy and non-Malagasy vanga hindlimbs showed significant phylogenetic signal.

3. RESULTS

A. *Bone length comparisons*

When processing our data, we tested two methods of size correction—using the geometric mean, and using bird species mass. In our analyses, we focused on the geomean-corrected data, as it was more specific to the actual measurements taken, and better separated out species, showing variation more widely spread across different PC axes.

After size correction, all individual bones had relatively small variance (Figure 2). The tmt, d1p1, d2p1, and d4p4 had the most variation between measurements.

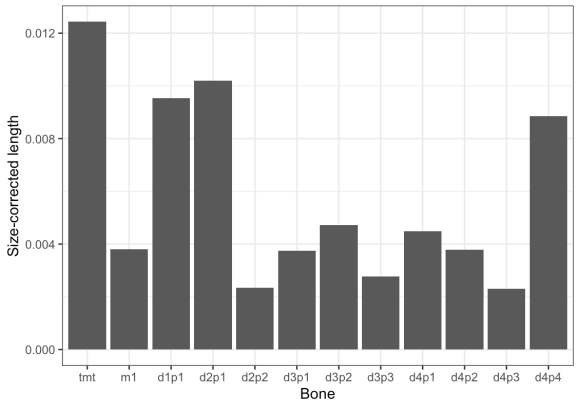


Figure 2. The variation of each phalanx's measurements.

Out of 132 correlation tests between phalanges, 23 were statistically significant (Table 1). D1p1 and d2p1 had the strongest correlation at -0.8806 ($P < 0.001$). There were strong positive correlations between the penultimate forward-facing phalanges (d2p2, d3p3, and d4p4). In addition, the tmt correlated negatively to all penultimate phalanges. Phalanges within d4 were generally negatively correlated with each other. M1, by comparison, showed only a few weak negative correlations. Figure 3 shows a visualization of these relationships.

		cor	R^2	*P*
d1p1	d2p1	-0.8806	0.7674	< 0.001
d3p3	d4p4	0.7717	0.5810	< 0.001
d4p2	d4p4	-0.7375	0.5275	< 0.001
d3p3	d4p2	-0.6134	0.3540	< 0.001
d4p1	d4p2	0.5729	0.3043	< 0.001
tmt	d4p4	-0.5564	0.2849	0.001
tmt	d1p1	-0.5109	0.2346	0.004
tmt	d3p3	-0.5044	0.2278	0.004
d2p2	d4p4	0.5046	0.2280	0.004
d2p1	d4p4	-0.4852	0.2081	0.007
d2p2	d3p3	0.4840	0.2069	0.007
tmt	d2p1	0.4792	0.2022	0.007
d2p2	d4p1	-0.4660	0.1892	0.009
d1p1	d4p4	0.4573	0.1809	0.011
d3p1	d4p4	-0.4391	0.1640	0.015
d4p1	d4p4	-0.4223	0.1490	0.020
d2p1	d3p1	0.4196	0.1466	0.021
d2p2	d3p2	-0.4090	0.1375	0.025
d3p1	d3p3	-0.4085	0.1371	0.025
m1	d4p3	-0.4063	0.1352	0.026
tmt	d2p2	-0.3977	0.1281	0.030
m1	d2p1	-0.3968	0.1274	0.030
d2p2	d4p2	-0.3734	0.1087	0.042

Table 1. The correlation, R^2, and *P*-value of significantly correlated phalanges.

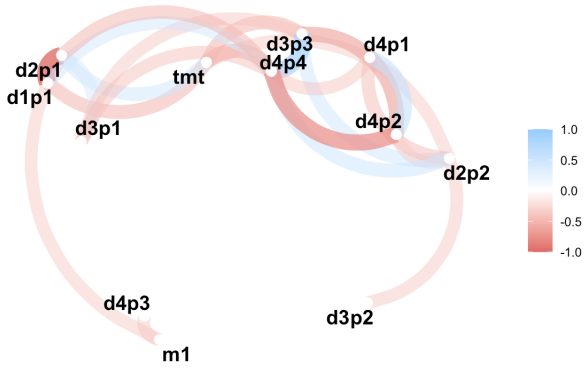
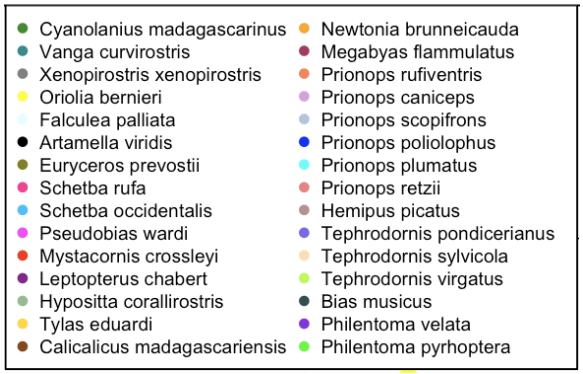


Figure 3. A network plot of the measured bones, with red indicating significant negative correlation and blue indicating positive correlation, and the darkness of the color indicating strength of the correlation.

A principal component analysis (PCA) showed that the first four PC axes accounted for over 80 percent of variation. PC1 (43.60 percent) was composed mostly of variation in the tmt, as well as d2p1, d1p1, d4p4, and d3p3: all bones which are the most strongly correlated to the tmt. PC2 (19.18 percent) was composed mostly of variation in d4p4 and d4p1, again showing correlation between the phalanges in d4. The tmt loaded the most on PC3 (14.47 percent), and d3p2 loaded the most on PC4 (6.379 percent). Plotting PC axes allowed us to visualize general patterns of morphological diversity across species (Figure 4).



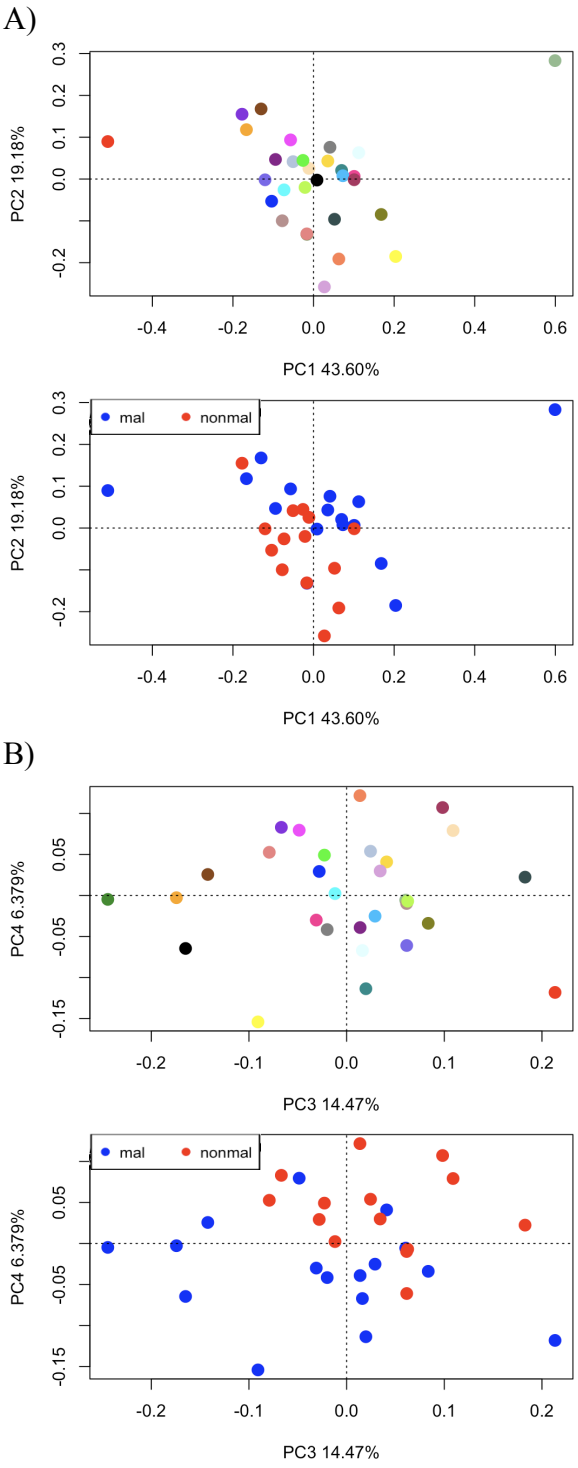


Figure 4. Morphospace of tmt and phalange length comparing species (legend above), and Malagasy (blue) versus non-Malagasy vangas (red), plotting PC1 against PC2 (A) and PC3 against PC4 (B).

Along PC1, *Mystacornis crossleyi* and *Hypositta corallirostris* were strong outliers on opposite sides of the axis. *H. corallirostris* was a slight outlier along PC2, but otherwise did not stand out as much in PC2, PC3, or PC4. The Malagasy and non-Malagasy groups separated out to generally occupy distinct, though slightly overlapping, regions of morphospace. The overlap was smaller along PC 2, 3, and 4.

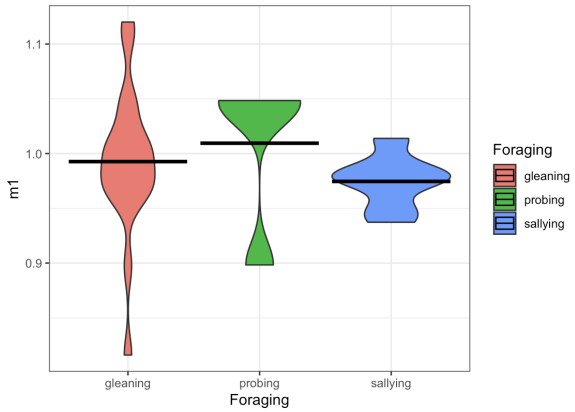
A phylogenetic PCA showed how different the morphology was when accounting for phylogenetic relatedness. The scores and loadings of the phyloPCA were similar to that of the PCA (SI Appendix 3A), so we focused on the PCA for our analysis.

B. *Ecomorphological correlations*

Finally, we tested to see if the size of the bones were different depending on species' foraging strategy. Only m1 and d3p1 varied significantly with foraging strategies. For m1, a Tukey test determined that there was significant bone length difference between probing and gleaning birds ($P = 0.007$), and probing and sallying birds ($P = 0.001$). For d3p1, there was a significant bone length difference between gleaning and probing birds ($P = 0.002$), and gleaning and sallying birds ($P = 0.006$) (Figure 5).

A phylogenetic ANOVA determined that, after accounting for phylogenetic relatedness, only d3p1 significantly differed in length between gleaning and probing birds ($P = 0.045$) and gleaning and sallying birds ($P = 0.039$).

A) m1



B) d3p1

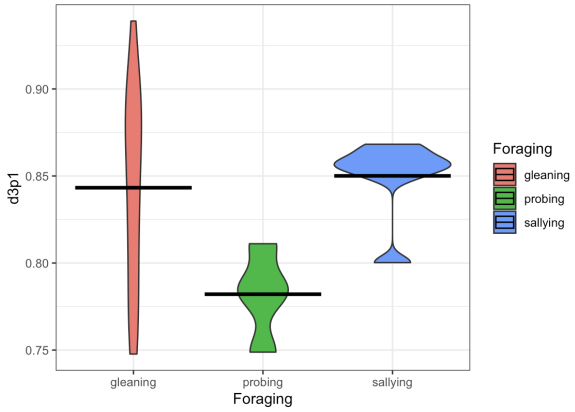


Figure 5. Violin plots showing the range of measurements for m1 (A) and d3p1 (B) length. Species are grouped based on foraging strategy, with their mean included.

C. *Rates of evolution*

We performed an ancestral state reconstruction on the tmt, d2p1, d1p1, m1, and d3p1 (Figure 6). The tmt, d2p1, and d1p1 showed strong correlations and stood out as having high loadings on PC1 in the PCA. M1 was the only bone that evolved significantly faster in Malagasy than in non-Malagasy vangas. D3p1 was the only bone which significantly differed in length based on vanga species' foraging strategies.

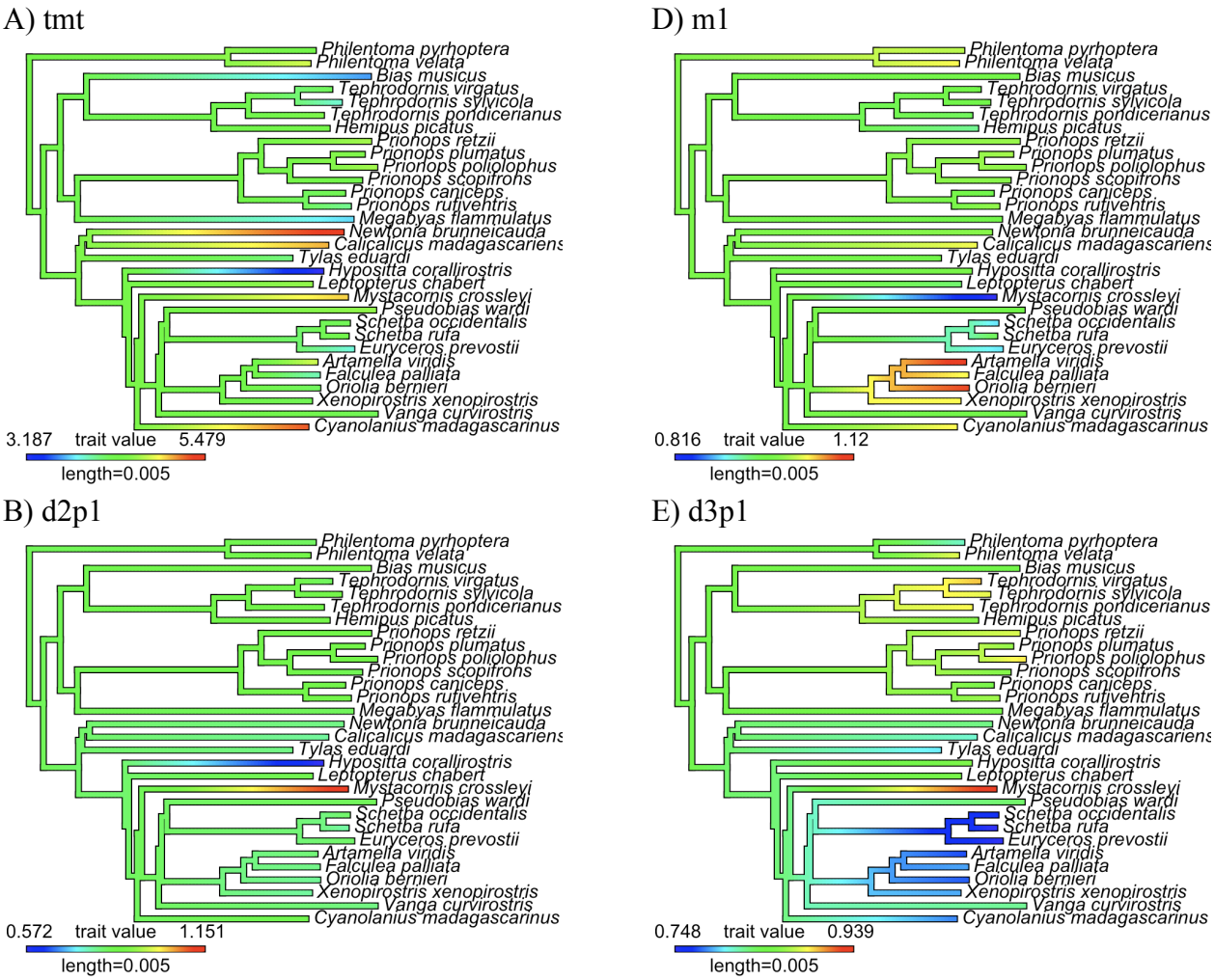


Figure 6. Ancestral state reconstructions, showing the length from shorter (blue) to longer (red) of the tmt (A), d2p1 (B), d1p1 (C), m1 (D), and d3p1 (E).

The ancestral state reconstructions showed that Malagasy vangas were more variable in their trait values than non-Malagasy vangas. Certain clades of vangas stood out as having more extreme values than other species in the reconstructions of m1 and d3p1. The trait values of *M. crossleyi* and *H. corallirostris* stood out particularly in the reconstructions of d2p1, where there wasn't much variation in other species. However, only m1 showed a significant difference in the overall rate of evolution, with Malagasy vangas evolving at a net rate 8.565 times faster than non-Malagasy vangas (P = 0.009). Two

other bones were close to being significant: d4p3 evolved at a rate 2.902 times faster in Malagasy than non-Malagasy vangas (P = 0.056), and the tmt evolved at a rate 2.682 times faster in Malagasy than non-Malagasy vangas (P = 0.077).

To determine whether Malagasy and non-Malagasy vangas were exhibiting significant phylogenetic signal, we calculated Blomberg's K. For all of Vangidae, K = 0.7139 and effect size = 4.093 (P = 0.001). Within Malagasy vangas, K = 0.8749 and effect size = 2.096 (P = 0.012), whereas within non-Malagasy vangas, K = 0.5930 and effect size = 3.357 (P = 0.002).

4. DISCUSSION

A. *Bone length comparisons*

After size correction, we found that the tmt, d1p1, d2p1, and d4p4 had the most variation among their measurements. This makes sense for the tmt and d1p1, which were the biggest bones. Penultimate forward-facing phalanges (d2p2, d3p3, and d4p4) were positively correlated, suggesting that there may be developmental or functional linkage between these phalanges regardless of locomotion, habitat, or foraging strategy. In addition, the penultimate phalanges were negatively correlated with the tmt and proximate phalanges. D3p2 did not have any strong correlations; digit III overall had some of the fewest significant correlations between phalanges. Its lack of correlations could be explained by its conservation; in a wide sample of birds, digit III was the least variable (Abourachid et al. 2017). Future research could look more into why this digit is so highly conserved.

B. *Ecomorphological comparisons*

Locomotion proved a challenge to categorize, as all vangas are considered to be in the same locomotory group—perching (Winkler et al. 2020)—except for *M. crossleyi*, which is as a terrestrial bird (Collar et al. 2020), and *H. corallirostris*, which is as a climbing bird (Yamagishi et al. 2020). These two species accordingly stood out on the PCA plot, where they occupied areas of discrete morphospace on opposite sides of the PC1 axis. In comparison, the remaining Malagasy vangas occupied similar regions of morphospace as non-Malagasy vangas. A sample size of one species per locomotory group meant we were unable to assess morphological differences between locomotory groups statistically, but we were able to situate observed differences in the context of prior work.

Both *M. crossleyi* and *H. corallirostris* stood out on the PC1 axis due to their more extreme measurements of the tmt and d1p1, as well as associated variance in correlated digits (Figure 3). *M. crossleyi* exhibited a long tmt and d2p1, and a short d1p1, d3p3, and d4p4; *H. corallirostris* followed the opposite pattern. This is likely due to their unique locomotion: *M. crossleyi* is almost entirely terrestrial, foraging mainly on the forest floor, where it probes for and chases down prey (Collar et al. 2020), while *H. corallirostris* clings to and ascends tree trunks while gleaning, similar to a nuthatch (Yamagishi et al. 2020). *O. bernieri*, which may also occasionally cling vertically to tree trunks (Yamagishi and Nakamura 2020), fell along the rightmost edge of the morphospace occupied by the majority of Vangidae on PC 1, and was the closest species to *H. corallirostris*. These species' differences in phalanx length are consistent with past conclusions that the hallux is lengthened in climbing species, and reduced in terrestrial ones (Abourachid et al. 2017; Falk et al. 2020). A long hallux provides robust support for climbing birds (Abourachid et al. 2017; Leblanc et al. 2023). On the other hand, a longer tmt could be beneficial for terrestrial species, as it

allows for greater stride length (Zeffer and Lindhe Norberg 2003), while a shorter tmt allows a climbing bird to hold their body closer to the substrate and lessens the muscle use required to maintain a vertical position (Winkler and Bock 1976). Our finding that tmt length was strongly positively correlated with d2p1 may suggest that much remains to be understood about the functional significance of variation in foot shape. These correlations suggest integrated variation in foot shape, and a useful future direction for this research would be to explicitly examine the functional significance of these patterns.

We also found that penultimate phalange length had significant negative correlation with the tmt, which suggests that as locomotion transitions from arboreal (which is associated with a short tmt) to terrestrial (which is associated with a long tmt), penultimate phalanges get shorter. In addition, 5 out of 9 possible correlations between proximate and distal phalanges (not including the hallux) were significantly negatively correlated (Table 1). This suggests that penultimate phalanges shorten as proximate phalanges lengthen, and vice versa, tending to conserve total digit length. This allows arboreal birds with short proximal phalanges—a morphology that reduces the amount of energy needed to perform grasping behaviors—to still be able to stably cling to substrates with a wide diameter (Kavanagh et al. 2013; Dickinson et al. 2023).

We also looked at how bone length relates to foraging. Foraging behaviors are the key way that Malagasy vangas diversified (Yamagishi and Eguchi 1996; Reddy et al. 2012). Locomotion is an important aspect of foraging behavior, as it allows multiple ways for a bird to access their foraging substrate, and we wanted to see if there was a relationship between this and hindlimb morphology. In vangas that exhibited multiple foraging techniques, we conducted our analyses using just the first listed—the more dominant—foraging technique (Reddy et al. 2012). Though we expected the tmt and d1p1 to vary with foraging behavior, once phylogeny was accounted for, only d3p1 significantly differed in length between gleaning and probing birds (P = 0.045) and gleaning and sallying birds (P = 0.039). It is important to note that this difference could have been caused by the large variation in d3p1 length in the gleaning category; by comparison, there was not much variation in the probing and sallying categories. When comparing means, there was not a large difference in the mean length of d3p1 between gleaning and sallying birds. This was interesting, as sallying birds may use their feet the least out of all three foraging strategies, considering they are mainly used for perching, while other foragers likely clamber around more. However, there was a large difference in the mean length of d3p1 between gleaning and probing birds (Figure 6). This finding was unexpected, as d3p1 did not stand out in previous research, our correlation tests, or our PCA.

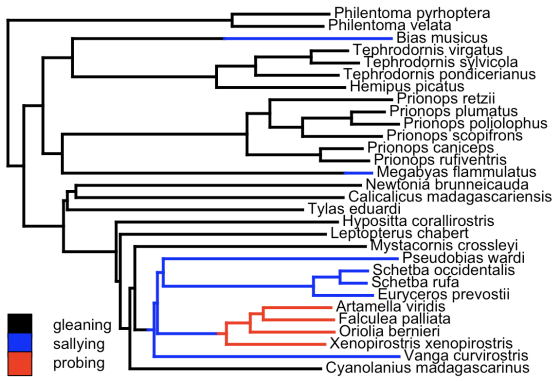


Figure 7. Taxonomy of Vangidae, showing dominant foraging behavior.

One reason for this is that some Vanginae foraging categories correspond closely with phylogeny: for example, most sallying birds (*L. chabert*, *P. wardi*, *S.*

occidentalis, *S. rufa*, *E. prevostii*, *V. curvirostris*, and *C. madagascarinus*) can be found in one clade. In addition, all probing birds (*A. viridis*, *F. palliata*, *O. bernieri*, and *X. xenopirostris*) are also contained in one clade, which is nested in the 'sallying' clade (Figure 7). This means we lack the ability to distinguish between morphological differences adapted to different foraging behaviors, and those due only to common descent. However, the strength of the correlation between morphology and phylogeny could support the idea that repeated shifts that allowed birds to develop new foraging behaviors promoted further diversification. This study has made clear that foraging strategies align better with bill shape than foot shape, and they cannot be a direct replacement for locomotory categories. Species placed in the same foraging group have very different methods of locomotion. For example, within the group of birds that glean or dominantly glean, *C. madagascarinus* often hangs upside down on leaf clusters at the end of twigs, using its feet to open dry leaves (Kirwan et al. 2022). *H. corallirostris* clings to and ascends tree trunks, gleaning from the bark's surface (Yamagishi et al. 2020), and *M. crossleyi* walks and runs along the ground, searching in leaf litter and occasionally probing in mosses and epiphytes (Collar et al. 2020)—which is also different from other probing vangas, which tend to chisel and strip bark, etc. (Reddy et al. 2012). Because of these vast differences in locomotion even within the same foraging category, it becomes obvious that these foraging groups do not necessarily closely relate to differences in locomotion. In the future, perhaps a better way to study the relationship between morphology and locomotion would be to study the relationship between morphology and habitat.

C. *Rates of evolution*

When we compared evolutionary rates of individual phalanges between Malagasy and non-Malagasy vangas, only m1 showed significant rate differences, evolving 8.565 times faster in Malagasy than non-Malagasy vangas ($P = 0.009$). D4p3 and the tmt were close to evolving significantly faster in Malagasy than non-Malagasy vangas ($P = 0.056$ and $P = 0.077$, respectively). For all other bones, the rate was nonsignificant ($P > 0.15$). M1 and d4p3 were significantly correlated, which could explain why d4p3, a bone that did not significantly stand out in the PCA or in most of the correlation tests, still had a higher net rate of evolution among Malagasy as compared to non-Malagasy vangas. Given that the length of the tmt is observed to be the most variable bone between species—particularly within Vanginae—it was surprising to find that its rate of evolution between Malagasy and non-Malagasy vangas was not significant. Overall, in fact, it was interesting that we did not see more bones having significantly different rates of evolution, as the ancestral state reconstruction plots showed that Malagasy vangas often showed more variable traits than non-Malagasy vangas, particularly with d3p1.

When we looked at Blomberg's K, we found that Vangidae exhibited significant phylogenetic signal, with K being closer to 1 for Malagasy as compared to non-Malagasy vangas. In both groups there was low phylogenetic signal and thus more within-clade diversity, meaning that closely related species were very different, which is consistent with diversifying selection. However, we were not able to test if phylogenetic signal deviated from what would be expected under Brownian motion; nor were we able to test whether the difference in phylogenetic signal between the two groups was significant. To do this in future research, would first require

simulating the evolution of multiple traits under a Brownian motion model.

Future research should look into these questions to determine whether Malagasy vangas exhibit lower phylogenetic signal than non-Malagasy vangas. Something that may affect this result is that non-Malagasy vangas have shorter branch lengths, due to having more species per genus than Malagasy vangas, a clade that consists of mostly monotypic genera. This may result in seemingly higher within-clade diversity for the non-Malagasy versus Malagasy vangas, which underwent rapid diversification about 20 MYA, with most recognized genera appearing around 15 MYA (Jønsson et al. 2012). This may be better accounted for when we are able to redo these analyses in the future with a time-calibrated phylogeny.

Future research could also look more into different evolutionary models and how rates of evolution may differ in the vanga adaptive radiation. Patterns of evolution may differ between Malagasy and non-Malagasy vangas, for example if there was an early burst of evolution within Vanginae and/or if rates of evolution are more variable within Vanginae, with significant rate shifts across the phylogeny. Another thing to test is whether rates of evolution for non-Malagasy vangas more closely match Brownian motion than Malagasy vangas. In addition, future research could test for correlated evolution between traits: especially bones that were identified to be strongly correlated in length.

5. CONCLUSIONS

In this study, we asked how foot morphology evolved in Malagasy vangas, compared to non-Malagasy vangas. We discovered that the length of the tmt and its correlated phalanges—d2p1, d1p1, d4p4, and d3p3—varied the most between species. The penultimate phalanges had strong positive correlations with one another, and negative correlations with proximate phalanges, suggesting that digit length is conserved, which benefits arboreal species. *M. crossleyi* and *H. corallirostris* exhibited these patterns in extreme and stood out as two outlier taxa, with their morphology demonstrating the anatomical differences between their different locomotory modes. Both Malagasy and non-Malagasy vangas exhibited significant phylogenetic signal. However, only m1 evolved more quickly in Malagasy compared to non-Malagasy vangas. Procedures in this research should be redone with a time-calibrated phylogeny. Finally, only d3p1 differed in length based on foraging strategy, perhaps because this particular way of defining foraging strategies is not a good way to differentiate species based on locomotion. Future directions could study the relationship between vanga morphology and other aspects of ecology, such as habitat, which may align better with hindlimb morphology than these foraging strategies. It is important to continue studying hindlimbs and other under-researched dimensions of morphological variation. As *M. crossleyi* and *H. corallirostris* showed, the species with the most divergent foot shapes were different from the vanga species with the most divergent bill shapes, illustrating how hindlimbs capture a different ecomorphological aspect of this adaptive radiation that may not be visible from just studying beaks.

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SUPPLEMENTARY INFORMATION

2AI. Complete list of specimens.

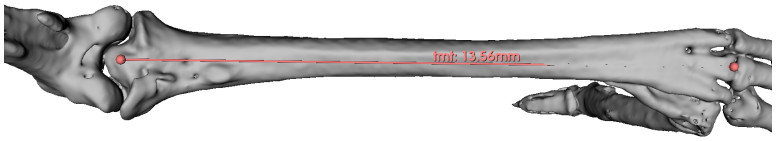
Cyanolanius madagascarinus	FMNH 356683
Cyanolanius madagascarinus	FMNH 384779
Vanga curvirostris	AMNH 412925
Vanga curvirostris	AMNH 412947
Vanga curvirostris	FMNH 431222
Xenopirostris xenopirostris	AMNH 412767
Xenopirostris xenopirostris	FMNH 356665
Oriolia bernieri	AMNH 202942
Oriolia bernieri	FMNH 356684
Falculea palliata	FMNH 356674
Artamella viridis	AMNH 412894
Euceryos prevostii	FMNH 43127
Euceryos prevostii	FMNH 356692
Schetba rufa rufa	AMNH 442991
Schetba rufa rufa	AMNH 664507
Schetba rufa occidentalis	AMNH 413002
Schetba rufa occidentalis	AMNH 413009
Pseudobias wardi	AMNH 196697
Pseudobias wardi	AMNH 411923
Mystacornis crossleyi	FMNH 384715
Mystacornis crossleyi	FMNH 393122
Leptopterus chabert	FMNH 434447
Hypositta corallirostris	FMNH 363833

Tylas eduardi	FMNH 356650
Calicalicus madagascariensis	AMNH 664517
Calicalicus madagascariensis	FMNH 352874
Calicalicus madagascariensis	FMNH 356653
Newtonia brunneicauda	FMNH 345884
Newtonia brunneicauda	FMNH 436522
Megabyas flammulatus	AMNH 159969
Prionops rufiventris	FMNH 122371
Prionops caniceps harteri	FMNH 95858
Prionops scopifrons scopifrons	FMNH 283278
Prionops scopifrons scopifrons	FMNH 283279
Prionops poliolophus	FMNH 32619
Prionops plumatus	AMNH 259735
Prionops plumatus	NHMUK 19684239
Prionops retzii	FMNH 86763
Prionops retzii	FMNH 86764
Hemipus picatus	FMNH 107601
Tephrodornis pondiceranius	AMNH 203554
Tephrodornis pondiceranius	AMNH 304735
Tephrodornis pondiceranius	FMNH 97175
Tephrodornis sylvicola	AMNH 801130
Tephrodornis virgatus	AMNH 655735
Tephrodornis virgatus	AMNH 655738
Bias musicus	AMNH 159965
Bias musicus	YPM 100619

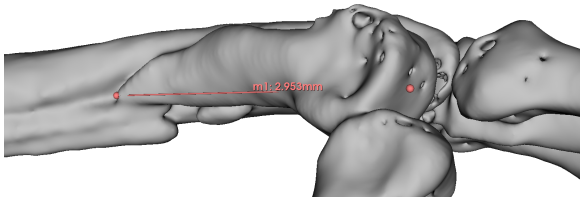
Philentoma velata	AMNH 652660
Philentoma pyrhoptera	AMNH 652687
Philentoma pyrhoptera	YPM 120422

2AII. Example markups of tmt (A) and phalanx (B, C, D, E, F) measurements taken in 3D Slicer of *Pseudobias wardi* (A, B, C, E), *Prionops caniceps* (D), and *Schetba rufa* (F). Markups are shown from the 3D view (A, B, C, D, E) or slice view (F) in 3D Slicer.

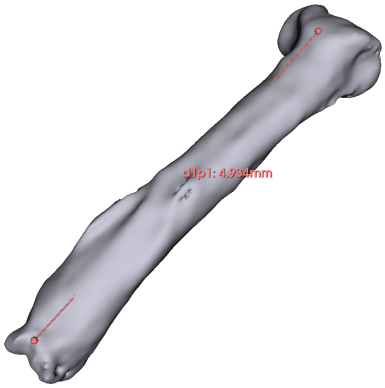
A) Dorsal view of a tmt markup.



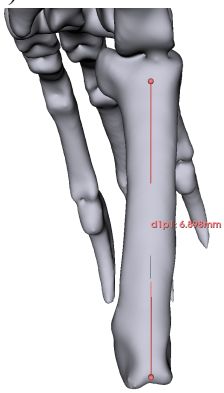
B) Angled side view of an m1 markup.



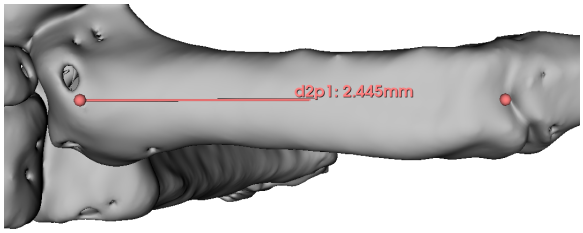
C) Angled view of a d1p1 markup.



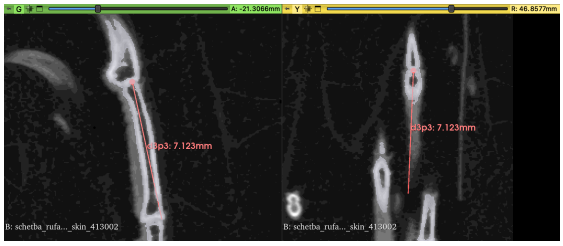
D) Dorsal view of a d1p1 markup.



E. Dorsal view of a d2p1 markup.



F. Slice view of a d3p3 markup.



3A. Phylogenetic PCA of PC1 and PC2, showing the morphospace of tmt and phalange length of Vangidae after accounting for phylogenetic relatedness.