

Morphometric Analysis and Classification of Isolated Pedal Phalanges of Eocene Antarctic Penguins

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1. INTRODUCTION

Penguins (Sphenisciformes) are highly specialized seabirds that exhibit a range of morphological and physiological adaptations. Within their skeletal structure, the pedal phalanges (bones of the toes) are among the elements heavily involved in both aquatic and terrestrial locomotion. As components of the feet, they enable penguins to navigate marine environments, acting functionally like the distal portion of a rudder, while also facilitating walking and tobogganing on land and ice (Williams 1995). In the fossil record of Eocene Antarctic penguins, these bones are common yet typically disarticulated, posing challenges for both taxonomic and functional interpretation (Jadwiszczak 2006). This study examines pure-shape variation in such isolated phalanges using geometric morphometrics and ordination techniques to evaluate whether consistent patterns linked to anatomical identity can be detected. By establishing a morphological baseline for early Antarctic penguins, this work contributes to understanding long-term anatomical responses to polar environmental change, offering a historical perspective relevant to current transformations in high-latitude ecosystems.

2. MATERIALS AND METHODS

The study includes 49 penguin phalanges from the Eocene (56.0–33.9 Ma) La Meseta and Submeseta formations (Seymour Island, Antarctic Peninsula), preliminarily classified based on qualitative anatomical assessment, and seven reference specimens assignable to an extant Gentoo penguin (*Pygoscelis papua*). All bones are housed at the University of Białystok. They were 3D scanned with a structured-light scanner and post-processed in the Revo Scan 5 application. Mesh models were exported to 3D Slicer software. Each left-sided phalanx model was mirrored. All phalanges were landmarked using five open curves comprising 23 points (Fig. 1a). Landmark coordinates were analyzed in R using the *geomorph* and *uwot* packages, as well as base R *prcomp* function. The data were normalized for position, orientation, and scale using Generalized Procrustes Analysis. Allometric effects were accounted for by incorporating the log of

centroid size into a size-shape PCA (Mitteroecker et al. 2013). To explore nonlinear shape variation, Uniform Manifold Approximation and Projection (UMAP; McInnes et al. 2018) was performed on 13 size-adjusted PCs, covering >90% of shape variance.

3. RESULTS

The size-shape PCA (Fig. 1b), representing a linear approach, predictably revealed that PC1 was driven by size, explaining 90.4% of total variance. The consecutive five (shape-related) principal components explained an additional 6.4%. The PC2–PC3 plane revealed well-separated clusters for phalanges II-1, IV-1, and III-3, while overlaps occurred among III-1, III-2, IV-3, and II-2. The most intriguing outlier was the sole extant III-1 specimen, far removed from its fossil counterparts. The non-linear 2D UMAP analysis (Fig. 2) revealed only two essentially

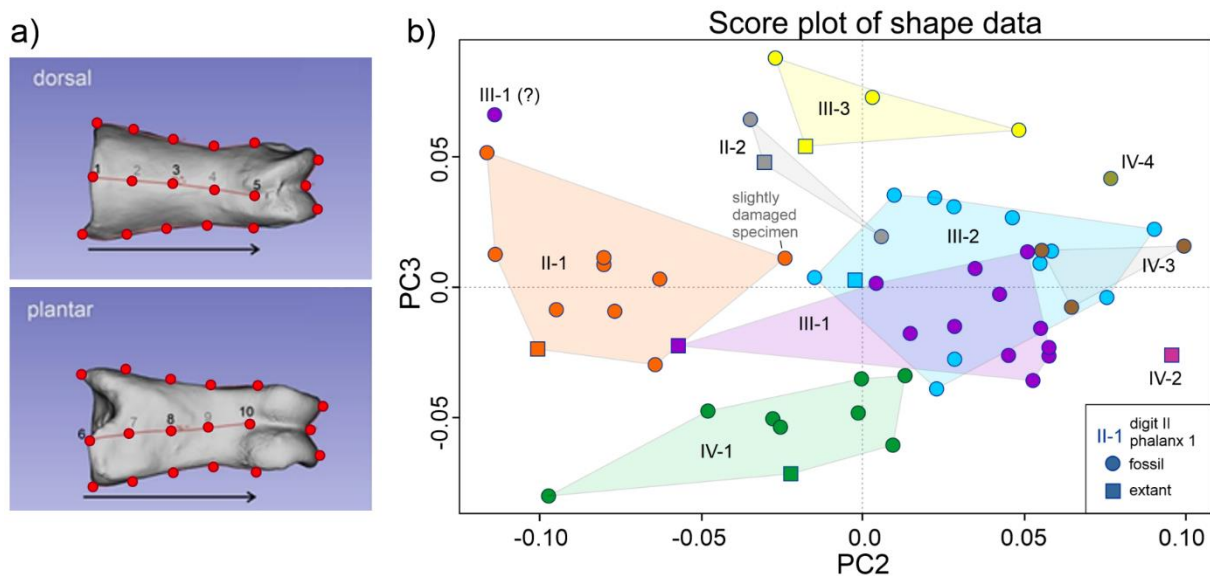


Fig. 1. Landmarking scheme (a) and score plot of shape data for PC2 and PC3 (first two size-independent components) from size-shape PCA (b). PC2–3 explained 32.3% and 13.5% of variance remaining after (size-dominated) PC1 was rooted out.

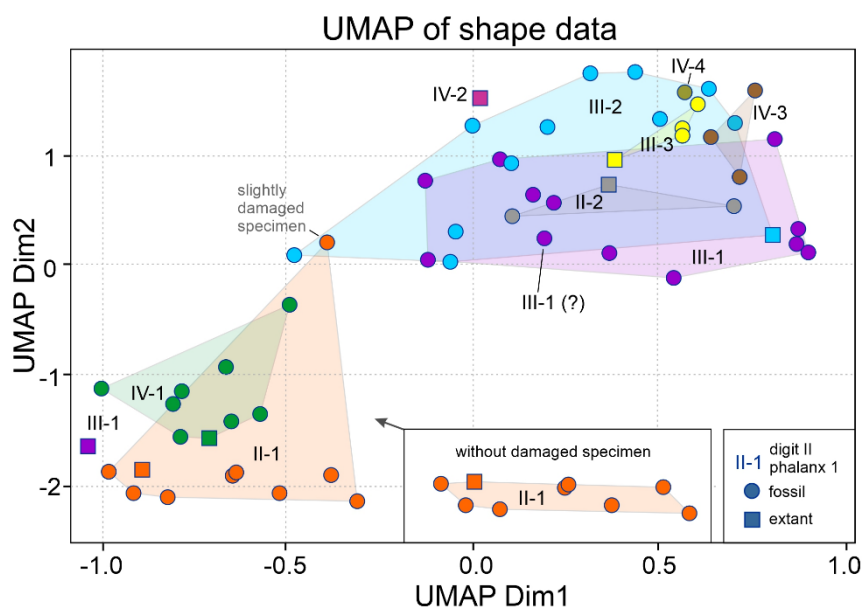


Fig. 2. Score plot of shape data (PC2–14 from size-shape PCA) projected onto the UMAP dimensions.

distinctive clusters, formed by phalanges II-1 and IV-1, and confirmed distinctiveness of modern III-1 and IV-2 observed in PCA. The 3D UMAP projection made the separation between clusters II-1 and IV-1 even more profound.

4. DATA INTERPRETATION

Results show that multivariate ordination methods can (to some degree) differentiate phalanges by anatomical position, particularly for basal-and-peripheral elements (II-1, IV-1). Apparently, these bones may undergo stronger functional constraints due to their articulation with the tarsometatarsus and their role in stabilizing the foot. Conversely, phalanges III-1 and III-2 were consistently overlapping across methods, reflecting morphological similarity likely due to their axial adjacency and position along the central axis of the foot skeleton. Such a congruity can be a by-product of the more uniform distribution of stress along this axis. Notably, the sole modern III-1 specimen was morphologically distinct, though showing a clear affinity to the II-1 cluster. The reasons for this remain unclear; however, it is likely that an evolutionary factor is involved. Since this is only a single specimen, far-reaching conclusions are not justified.

5. CONCLUSION

Multivariate shape analysis reveals that certain pedal phalanges, particularly proximal bones of digits II and IV, exhibit distinct morphological patterns amenable to classification. Central phalanges show less differentiation, likely constrained by their functional and positional homogeneity. These findings highlight the potential of landmark-based morphometrics for identifying isolated penguin phalanges and contributing to interpretations of foot function and evolutionary adaptation in early Sphenisciformes. In the context of contemporary climate-driven tipping points in polar regions, such fossil-based analyses help elucidate past adaptive pathways in Antarctic vertebrates, offering comparative insights into potential biological responses under current and future environmental stressors.

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