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Median-based resistant methods in the current framework of Geometric Morphometrics

Métodos resistentes basados en la mediana en el marco actual de la Morfometría Geométrica contemporánea

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Abstract: Landmark-based geometric morphometric (GM) methods have become a standard in shape analysis. Superimposition of landmark constellations, referenced to the mean, is performed using the least squares criterion under the consensus framework of Generalized Procrustes Analysis (GPA). While effective, especially when combined with multivariate statistics, this approach also has limitations. Specifically, if there is localized variation (if a few landmarks are significantly displaced in relation to the others), the method homogenizes variation to perform an optimal fit that can spread variation randomly, yielding unrealistic results. This limitation has long been recognized and discussed in the literature—especially palaeontological—proposing methods based on repeated medians that help checking for such localized variation in landmark constellations. However, the broad establishment of GPA has led to their neglect, potentially compromising interpretations in studies of allometry, integration, and modularity. Two real life examples, one biological (spiders) and one palaeobiological (pterosaur skulls), are used to illustrate what "localized variation" means and the effect it can have on the structure of Procrustes shape data, and consequently, on further statistical analyses. The intended message is that median-based resistant methods for landmark superimposition should be re-implemented in the field, at least to verify variation of landmark data analyzed under GPA.

Resumen: Los métodos morfométricos geométricos (GM) basados en landmarks (puntos de referencia) se han convertido en un método estándar en el análisis de la forma. La superposición de las constelaciones de landmarks, referenciada a la media, se realiza utilizando el criterio de mínimos cuadrados bajo el marco consensuado del Análisis de Procrustes Generalizado (GPA). Aunque el método es muy eficaz, especialmente cuando se combina con estadística multivariada, también tiene limitaciones. Específicamente, si hay variación localizada (si algunos puntos de referencia están significativamente desplazados en relación con los demás), el método homogeneiza la variación para realizar un ajuste óptimo que puede distribuir la variación de manera aleatoria, produciendo resultados poco realistas. Esta limitación ha sido reconocida y discutida durante mucho tiempo en la literatura—especialmente paleontológica—pero el establecimiento del método GPA lo han dejado de lado, comprometiendo potencialmente los resultados, muchas veces sin saberlo, en estudios de alometría, integración y modularidad. Se utilizan dos ejemplos reales y sencillos, uno biológico (arañas) y uno paleobiológico (cráneos de pterosaurios), para ilustrar lo que significa "variación localizada" y el efecto que puede tener en la estructura de los datos Procrustes, y, consecuentemente, en los análisis estadísticos posteriores. El mensaje de estas demostraciones es que la superposición resistente debería ser re-implementada, al menos para verificar la naturaleza de los datos antes de estudiarse únicamente mediante GPA.

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INTRODUCTION

The arrival of Geometric Morphometrics (**GM**) based on the comparison of Cartesian coordinates (landmarks; Bookstein, 1982), was received as a revolution in biological and palaeontological sciences (Rohlf & Marcus, 1993). Procrustes methods together with Kendall's Theory of Shape (Dryden & Mardia, 2016) opened a prospect to study biological form (and evolution), combining an expressive visual component of comparisons (*e.g.*, Thompson, 1917), with mathematical rigor and the robustness of multivariate statistics. GM is increasingly used in a wide range of fields where form can be abstracted to landmarks —*i.e.*, Cartesian coordinates— such as archaeology, astronomy, cartography, manufacturing, geology,

and geophysics (Goodall, 1991) and has gradually established itself as a computer assisted standard for studying shape change in biological evolutionary research (Adams *et al.*, 2004; Mitteroecker & Schaefer, 2022).

The Procrustes superimposition shows shape differences by aligning landmark configurations to a common reference by translating, rotating, and thereafter rescaling them to minimize differences between corresponding landmarks. In the morphometric jargon, "shape" is the mismatch between landmark configurations after such optimal fit, and the consensus is to be obtained by minimizing the sum of squared distances between all the landmarks (inspired in Boas, 1905); this is what is normally referred to as the General Least Squares superimposition (**GLS**). Gower (1975) generalized this criterion as the Generalized Procrustes Analysis (**GPA**) to the study of multiple configurations of Cartesian coordinates using the mean as the consensus reference system in psychometrics; Rohlf and Slice (1990) extended its use of landmarks (Benson, 1967; see below), which is what is extensively used today (and used as synonymous with GM). In the meantime, however, concerns—particularly in the field of palaeontology—were raised about the use of the least squares criterion, with especial emphasis in its susceptibility to large differences at one or a few landmarks within a portion of the configuration (Benson, 1967; Siegel & Benson, 1982). This was later termed the "Pinocchio Effect" (**PE**) (Chapman, 1990), metaphorically alluding to change in the nose of this tale character as localized variation in face of a lie.

Because capturing shape differences using coordinate-based methods heavily relies on alignments (Richstmeier *et al.*, 2002), the central issue has always revolved around the criterion used to align landmark configurations (Webster & Sheets, 2010). In order to optimally align the configurations (goodness of fit), the least squares method assumes equal or nearly equal variance at all landmarks, implying that variation is circularly (randomly) distributed at each landmark (Zelditch *et al.*, 2012). When localized variation exists—if one or a few landmarks are significantly displaced relative to the others—such inhomogeneity is masked by the Procrustes least squares methods, which distributes local differences across all landmarks to minimize overall difference; namely, the least squares method inevitably spreads such local variation randomly, out over all the landmarks of the configuration (Slice, 2005). The Resistant Fit Theta Rho Analysis (**RFTRA** or Resistant-Fit superimposition) was proposed as an alternative method to be applied in this situation (Benson *et al.*, 1982; Siegel & Benson, 1982; Chapman, 1990; Rohlf & Slice, 1990; Torcida *et al.*, 2014, 2016; Palci & Lee, 2019).

RFTRA emerged as a refinement of the original Theta-Rho analysis, originally proposed as a coordinate-graphical tool to assess the fit of outlines (Benson, 1967), by introducing together the use of landmarks as reference points, and as a more resistant (robust) statistical method that relies on the repeated use of medians as the primary statistic to optimally superimpose landmarks (because medians are 'resistant' to outliers; Dryden & Mardia, 2016). An important departure from GPA is that the repeated medians approach solely focuses on rotations to minimize orientation differences between configurations. Thus, in methods such as that of Rohlf and Slice (1990), the initial step involves conducting a GPA to ascertain the accurate estimation of rotation angles by subsequently iteratively superimposing each configuration onto the median configuration (see alternatives in Torcida *et al.*, 2014; Dryden & Mardia, 2016).

The most significant praise of GPA has been its theoretical sophistication for the application of multivariate statistics (Slice, 2005). Accordingly, the recommendation has always been to us RFTRA as a means to verify that data lacks localized variation that can affect GPA (see *e.g.*, Zelditch *et al.*, 2004, 2012; Slice, 2005; Webster & Sheets, 2010), but such recommendation has gradually fallen into oblivion, or considered insignificant (Klingenberg, 2021). Consequently, GPA has become commonplace in biological research and in many other disciplines of inquiry in which localized variation can be present, but practitioners clearly overlook that localized variation can affect superposition and distort results. For instance, allometry yields straightforward examples of localized change; in a complex structure such as the skull of a tetrapod whose face grows at a different rate than the neurocranium, GPA can yield different results (Siegel & Benson, 1982; Torcida *et al.*, 2014). Bird beaks are a striking example of this situation (Klingenberg & Marugán-Lobón, 2013). Other biological examples are those that imply growth dynamics (Salazar-Ciudad & Jernvall, 2010), which were used by Chapman (1990) to demonstrate the Pinocchio effect. Beyond Biology, the wide (and growing) multidisciplinary research utilizing GM includes instances where objects might encompass localized variation. For instance, in Archeology objects are hand-made, and things are stitched or manually deformed within the object which would unquestionably entail local variation in such parts without change in others.

Here, two instances of natural localized variation are tested. First, the dynamical change of the opisthosoma of female spiders, which was demonstrated to mask previously undetected prosomal male dimorphism (Fernández-Montraveta & Marugán-Lobón, 2017), is used to illustrate a clearcut example of the effect of PE in spider body superimposition. Subsequently, the notable allometric facial variation in pterosaurs (Mesozoic flying reptiles) is further used to illustrate the meaning and profound impact that localized variation can yield different statistical analyses, much as it does with bird beaks. The aim of comparing these data through the lenses of GPA and resistant methods is to demonstrate, visually and analytically, not only what

localized variation means and how it looks, but also to show the undesirable effect that it can have on the interpretation of Procrustes results, and in statistics. Ultimately, the goal is to show that it is important to consider the presence of localized variation in order to prevent the results of GPA from being misled.

MATERIALS AND METHODS

Two samples of landmark data are utilized to compare GPA and RFTRA methods. One consists of a published sample of 178 spiders photographed dorsally in 2D and encompassing 35 landmarks and semilandmarks (listed in Fig. 1 caption), the latter outlining the opistosoma (Fernández-Montraveta & Marugán-Lobón, 2017). The second source of data is a small collection of 24 pterosaur skulls in lateral view and in 2D. To capture as much facial morphological diversity as possible, skulls were scanned from the reconstructions offered in Wellnhofer (1991), a large database of skull reconstructions. A reconstruction of *Zeihyangopterus* was scanned from Unwin (2003) to include azdharcoids in the sample. Most of the main clades were represented in the sample except for the anurognathids and *Darwinopterus* specimens, and most accessible species (*Pterodactylus*, *Rhamphorhynchus*, and *Anhanguera*) are repeated to further test consistency of the methods (*i.e.*, same genera should group together). Skull geometry was captured with a series of 8 landmarks evenly denoting major features of the whole facial skeleton (including the beak) and the neurocranium (shown on a scheme of *Dimorphodon*; Fig. 2).

For simplicity, median-based resistant methods will be referred across the whole text as RFTRA. The GPA and RAFTRA superimposition equations are deployed in Rohlf and Slice (1990), Zelditch *et al.* (2004). A fine-tuned robust superimposition method for faster computations in Torcida *et al.* (2014), implemented in RPS software and R (not used here). The spider landmark data were RFTRA superimposed and visualized in IMP Coordgen8 (Sheets, 2014). Pterosaur RFTRA residuals were also computed with Coordgen and thereafter submitted to Past (Hammer *et al.*, 2001) to perform a PCA and an **MDS** (Multidimensional Scaling; the ordination method based on distances to compare shapes statistically, suggested by; Torcida *et al.*, 2014). MDS is often preferred to PCA because median-based methods can yield discontinuities in shape space instead of smooth, continuous variation. However, because the obtained PCA ordination was nearly identical to that of the MDS, the latter PCA was used here for comparative consistency when comparing with the PCA ordering for the GPA data. Using PAST, a Minimum Spanning Tree (**MST**)—a graph that connects all the points (projected onto the principal component space) with the shortest possible total distance between them, ensuring no loops and minimal connectivity (see *e.g.*, Costa *et al.*, 2007)— was also computed and plotted in each ordination to have a better visual sense of the phenetic distances between specimens (*i.e.,* pairwise similitude) in the ordinations.

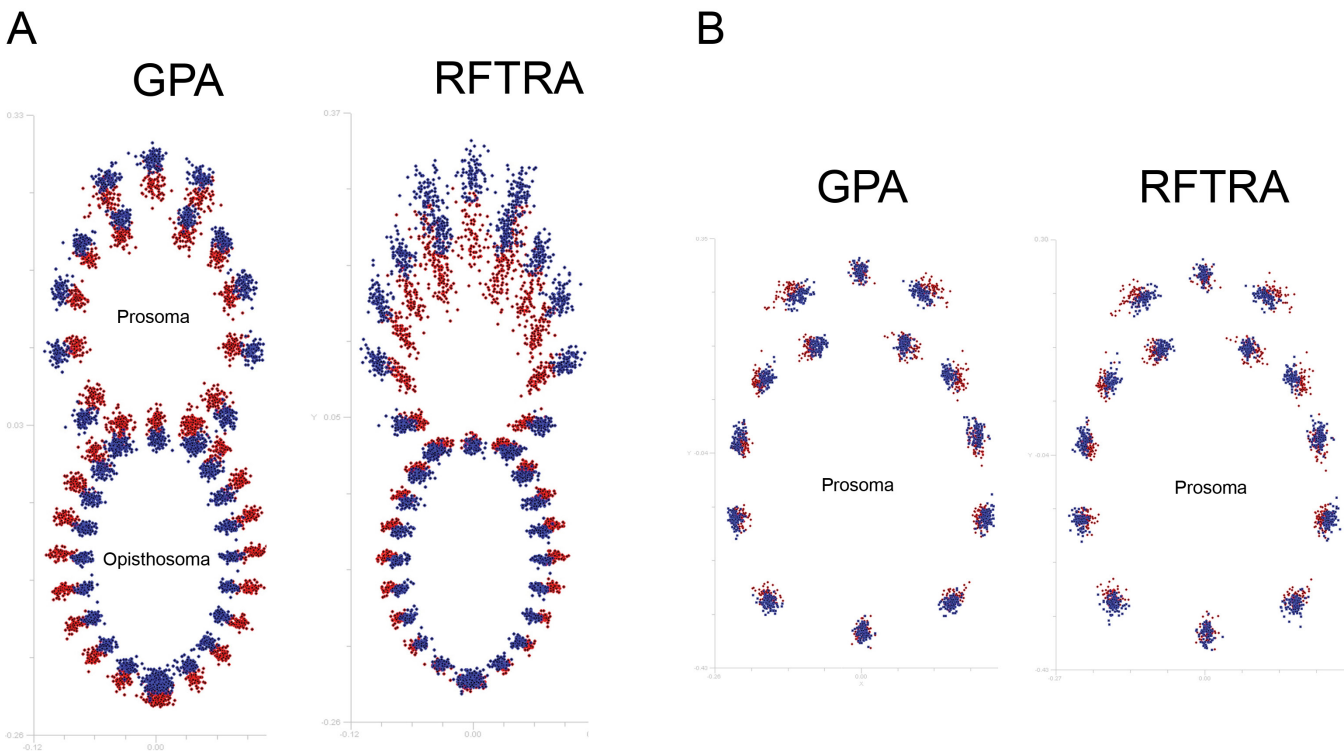

Figure 1. GPA and RFTRA superimpositions of spider landmark data. **A,** Full body; **B,** prosoma only. Red=females, Blue=males. The prosoma's carapace landmarks are the places at which legs, pedipalps or chelicerae insert at the carapace (*i.e.*, Type I), and opistosoma is denoted by semilandmarks.

RESULTS

The Procrustes fits of the spider and of the pterosaur landmark data differ notably depending on the criterion of superimposition used (GPA and RFTRA). In spider bodies, both methods clearly indicate a sound sexual shape dimorphism (Fig. 1), as previously reported (Fernández-Montraveta & Marugán-Lobón, 2017). However, GPA shows these differences evenly distributed across the entire body, as the dispersion of landmarks around the mean is very similar across the whole configuration, including both the prosoma and opisthosoma (Fig. 1A). Namely, the landmark clusters fit evenly around the mean of each landmark, indicating that differences between prosoma and opisthosoma shape are evenly distributed. In contrast, RFTRA shows that shape differences in the opisthosoma are minimal, highlighting that the largest differences concentrate in the prosoma, with superimposed landmark residuals clearly encompassing a longer axis (*i.e.*, no near circularity around the mean). Importantly, when comparing the prosoma only (*i.e.*, excluding the opisthosoma), GPA and RFTRA yield nearly identical alignments, again expressing sexual dimorphism, as expected (see Fernández-Montraveta

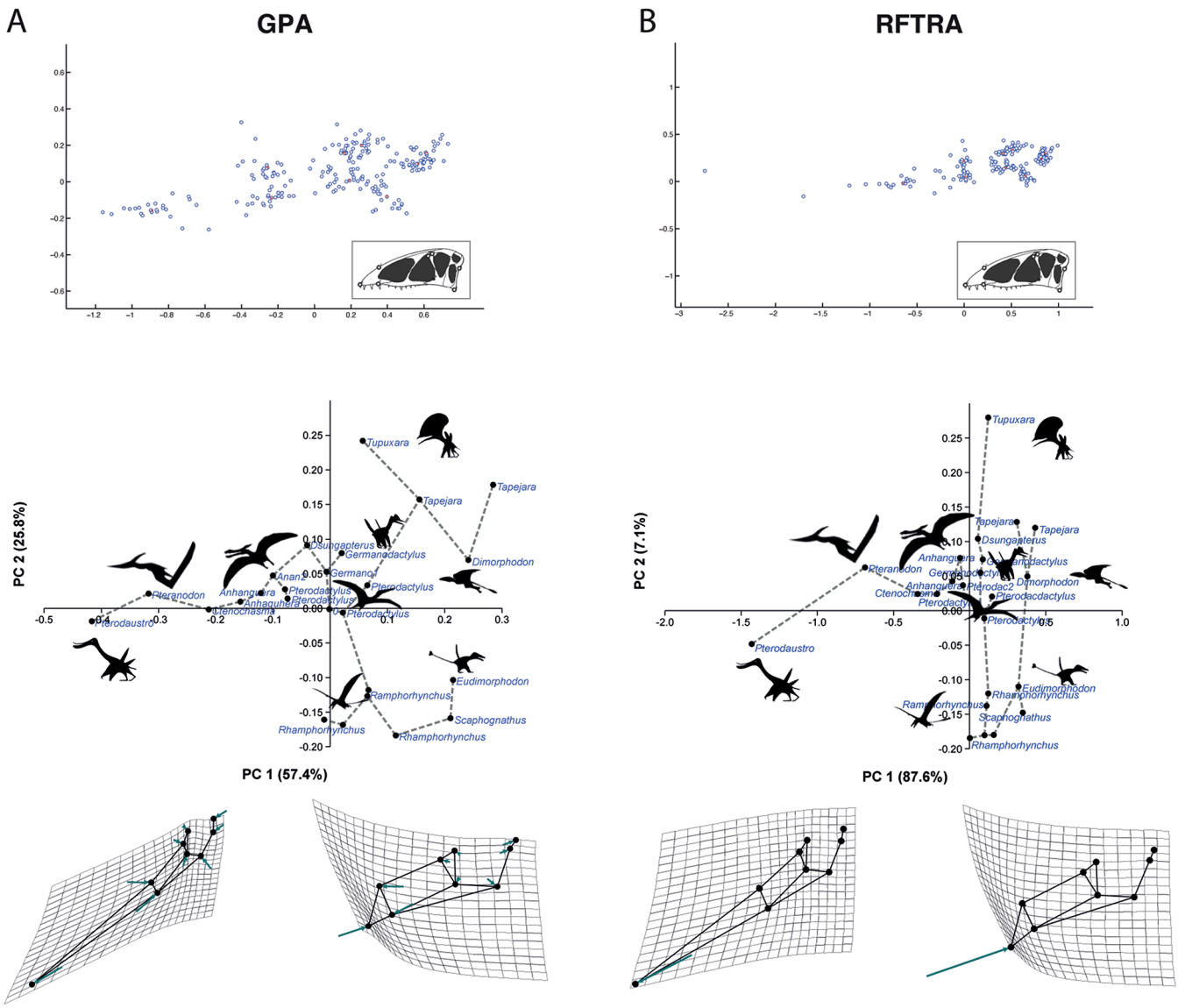

Figure 2. A, Pterosaur skull shape data after GPA superimpositions and **B,** RFTRA superimpositions. Below each superimposition there is a corresponding PCA ordinations and, below each of these, there are two deformation grids displaying shape differences accounted by PC1 at positive and negative scores. Landmark vector displacements are implemented to the deformation grids to ease interpretation of shape variation. Notice the contrast between superimpositions in A and B, which are unambiguously caused the notable lengthening of the beak, thus forcing a Pinocchio effect. This is much more obvious on the PCAs that summarize the variation. Also notable is the fact that although the PCA dispersions look alike, the Minimum Spanning Trees capture notable differences, showing a large dichotomy in PC2 under GPA separating short-faced pterosaurs into two groups that is not shown under RFTRA. Landmarks are shown on a sketch of *Dimorphodon* and are; the tip of the premaxilla, the projection of the anterior margin of the nares to the maxillary and nasal margins, the most caudo-dorsal and caudo-ventral margins of the antorbital fenestra, the ventral articulation f the quadrate and the quadrato-squamosal suture. Silhouettes from PhyloPic.

& Marugán-Lobón, 2017) (Fig. 1B). These convergent superimpositions of different methods on the prosoma data clearly underscore that the inflation of the opisthosoma, known to be related to the presence of gravid—egg bearing—females, is a case of localized variation, and key to the superimposition differences between the methods.

In the pterosaur skulls (Fig. 2), both superimpositions denote notable craniofacial differences. However, much as it happened with the residuals in the superimposed landmarks of spider bodies, differences in pterosaur skulls are shown evenly distributed under GPA. In contrast, RFTRA highlights that skull differences between pterosaurs are significantly concentrated in the anterior portion of the face (the beak) and not evenly across the whole cranium. A Multi-Dimensional Scaling analysis (MDS) on RFTRA data yields an ordination that is fully congruent with that of PCA (not shown), the latter which is left for comparative congruence with the way in which shape data variance is summarized for GPA data. The presence of localized variation in the beak results in notable differences in the PCA ordinations of pterosaur skull data, particularly in the shape differences accounted for and, consequently, in the amount of explained variance for each vector (PC1 and PC2 % explained variance being 57.4 and 25.8, and 87.6 and 7.1, respectively). Moreover, although the dispersions appear somewhat equivalent, the minimum spanning trees within the ordinations (morphospaces) clearly underscore different taxonomic pairings, indicating a varying assessment of phenetic similarity between pairs, regardless of their proximity within morphospace. For instance, in the GPA ordination, *Eudimorphodon* and *Rhamphorhynchus* are paired, forming a grouping located in the lower-right corner of the ordination. In the RFTRA ordination, this same grouping also includes *Dimorphodon*, positioned in the upper corner alongside the Tapejarids. Although the GPA tree linkages might initially seem more phylogenetically reasonable, neither case is congruent with actual phylogeny.

DISCUSSION

Geometric Morphometrics based on a least squares criterion is used in research contexts where localized variation may arise as a problem in the fit. However, current literature tends to overlook the potential issues introduced by such localized variation, making practitioners, particularly new ones, unaware of the issue. The examples provided here illustrate two normal scenarios in biology and palaeobiology, in spiders and pterosaurs, respectively, that demonstrably lead to discrepancies between GPA and RFTRA outcomes. Localized variation in the two examples stem either from the dynamic expansion of the opisthosoma in female spiders, due to egg carrying, and significant interspecies facial (beak) shapes in pterosaurs attributable to evolutionary allometry. The discrepancy in the obtained superpositions in both cases comes from the fact that GPA compensates for localized variation, distributing it evenly across all the landmarks, encompassing, by definition, what Chapman (1990) labelled as the “Pinocchio effect”.

In the spider example, GPA and RFTRA yield nearly identical outcomes when excluding the opisthosoma, indicating that differences related to sexual dimorphism primarily occur in the prosoma (Fernández-Montraveta & Marugán-Lobón, 2017). Importantly, however, the RFTRA superimposition effectively minimizes the contribution of localized variation in the opistosoma, emphasizing such dimorphic differences in the prosoma considering the entire spider body. As such, using RFTRA would make it unnecessary to demote the opistosoma (as the authors did in the original paper) to detect differences in the prosoma, because the method would detect it and perform an optimal fit of the portion with less variance. A notable fact arising from this situation in the spider body is that the uneven distribution of variance between the prosoma and the opisthosoma suggests that RFTRA could be effective in contexts involving modularity, allowing for more nuanced interpretations of shape variation.

The discrepancy between GPA and RFTRA driven by the pterosaur beak’s ‘Pinocchio effect’ is evident in the superimposition and in the PCA morphospace (Fig. 2). While the ordinations are somewhat consistent overall (*i.e.*, in how the taxa are spread and positioned within the morphospace), implying the same source of variation accounted by the PCs (*e.g.*, PC1 is beak elongation), the pairwise similarities between individuals vary according to the minimum spanning tree (MST). Such pterosaur pairing differences stem from discrepancies between GPA and RFTRA that inevitably lead to different biological, ecological, or evolutionary interpretations. Accordingly, the effect of localized variation can be significant and compromising if the analyses were carried out only based on GPA (Webster & Sheets, 2010; Zelditch *et al.*, 2004, 2012).

As shown, the Pinocchio Effect is not merely a perceptual or psychological matter related to landmark choice (see Klingenberg, 2021), but researchers might overlook it in their interpretation of analyses if they are unaware of the issue. The bias is concerning not only when attempting taxonomic classification but also when statistically forecasting evolutionary shape change. In the pterosaur example, interspecific beak variance was evenly distributed across the whole skull after applying the GPA criterion (*e.g.*, see magnitude of vector displacements in PC1 on GPA for pterosaurs; Fig. 2), inevitably leading to a statistical inference that would yield spurious correlations across landmarks affected by inflated variation. Specifically, studying the evolutionary allometry of a comparable interspecific sample of pterosaur skulls using Generalized Procrustes Analysis (GPA), without awareness of the Pinocchio Effect, would likely lead to a misinterpretation of the relationship between overall skull shape and size, which may be misleading. This

evaluation of the nature of the data and the degree of analytical convergence between GPA and RFTRA was historically recommended to mitigate such issues (Rohlf & Slice, 1990; Zelditch *et al.*, 2004; Webster & Sheets, 2010), and it is why it is brought back to the scene for that same sake.

Given all that has been shown empirically on the spiders and pterosaurs, it would be beneficial to persuade the community back on the importance of understanding and being aware of the Pinocchio Effect, and encourage future developers and programmers to incorporate both GPA and RFTRA algorithms into their software or scripts, as was done historically for that sake in old, and not so old mainstream programs such as GRFnd, IMP, RPS, and TPS Relw (all freely available at the SUNY-StonyBrook server). The prospect is further opened for mathematically inclined researchers to address the challenge of formalizing RFTRA for building a comprehensive Procrustes-based geometric morphometrics framework, fulfilling the long-standing objectives of pioneers in the study of biological shape and morphological evolution with these methods.

CONCLUSIONS

The present study aims at demonstrating with real biological examples (present and past, in invertebrate and vertebrate animals), that different superimpositions (GPA and Resistant methods, based on the least squares and repeated medians, respectively) can generate significantly different results if there is non-biologically subjective localized variation. The examples used are intended to demonstrate that the argument that these differences are due solely to perception (Klingenberg, 2021) is insufficient to refute the fact that the different superimpositions can be attributed to how the different methodologies are sensitive to variation in specific parts of animal morphology, which can also lead to significant problems. The question of how and whether landmarks truly represent real animal parts is a broader issue, philosophical in nature, beyond the scope of this demonstration. The resolution to the methodological discrepancies that best fits the nature of the problem is to combine both approaches, as has long been acknowledged.

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