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Investigating the primate fossil record using diffeomorphic deformation: what have we learnt?

Explorer le registre fossile des primates à travers la déformation par difféomorphisme : qu'avons-nous appris ?

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Abstract – One of the most challenging tasks in palaeontology is to identify the nature of the morphological variation observed in the fossil record. Accurately and quantitatively investigating morphological variation in fossil assemblages requires appropriate analytical methods. Through the use of imaging techniques, 3D digital twins of existing objects have opened up the possibility of developing innovative protocols for *in silico* analyses of variation patterns in fossil primate bones and teeth. Landmark-based geometric morphometrics initiated a critical methodological shift in the discipline, leading to significant discoveries in palaeontology. However, in some cases (e.g., smooth and complex structures, discrete traits) landmark-based geometric morphometrics fail to fully capture differences in shape. One possible alternative is a landmark-free diffeomorphic deformation approach based on correspondences between surfaces. Since the first application of diffeomorphic deformation in biological anthropology a decade ago, this method has successfully revealed previously unknown details of the skeletal anatomy of fossil primates, opening up promising avenues for further investigation.

Keywords – morphological variation, shape differences, diffeomorphism, surface-based comparison, primate evolution

Résumé – L'une des tâches les plus difficiles en paléontologie consiste à identifier la nature de la variation morphologique observée dans le registre fossile. En effet, explorer de façon exacte et quantitative la variation morphologique au sein des assemblages fossiles nécessite des méthodes analytiques appropriées. À travers l'utilisation des techniques d'imagerie, la construction de jumeaux numériques 3D à partir d'objets réels a ouvert la possibilité de développer des protocoles innovants pour l'analyse *in silico* des patrons de variations des os et dents des primates fossiles. En particulier, la morphométrie géométrique par points repères est à l'origine d'un changement méthodologique radical dans la discipline et de découvertes majeures. Cependant, dans certains cas (par ex. structures complexes et lisses, caractères discrets), la morphométrie géométrique par points repères n'est pas capable de saisir l'ensemble des différences morphologiques. Une alternative possible est la déformation par difféomorphisme basée sur les correspondances entre surfaces. Depuis sa première utilisation en anthropologie biologique il y a plus de 10 ans, cette méthode a révélé des détails jusqu'alors inconnus de l'anatomie du squelette des primates fossiles et ouvert des perspectives prometteuses pour la discipline.

Mots clés – variation morphologique, différences morphologiques, difféomorphisme, comparaison de surfaces, évolution des primates

Why quantify morphological variation?

In the absence of soft tissues and molecular data, the only reliable approach to disentangle the evolutionary history of primates has been to assess patterns of shape variation through comparative anatomical studies of fossil teeth and bones. Variation is the substrate upon which natural selection acts (Darwin, 1859), so that patterns of morphological variation detected in the fossil record are likely to reflect the selective pressures that have shaped the evolution of both extinct and extant lineages (e.g., Vrba, 1993; Potts, 1998). This being so, one of the most challenging tasks in palaeontology is to identify the nature of observed morphological variations, i.e., discriminating inter- from intra-specific variation. Because of their intrinsic properties, inter- and intra-species patterns of variation document different aspects of the biology and evolution of an extinct population (e.g., sexual dimorphism, time-averaging, biogeography, ontogeny; rev. Beaudet, 2022; 2023). On the one hand, inter-specific

variation plays a key role in the search for diagnostic criteria and testing for the presence of more than one species in a sample (i.e., taxonomic diversity). On the other hand, a vast array of factors is responsible for intra-specific variation at the population level, such as the presence of females and males (sexual dimorphism), immature and mature individuals (ontogeny), pathologies, geographical variants, and, in the case of fossil samples, diachronic changes (temporal depth). As such, morphological variation, when accurately quantified, is an invaluable source of evidence for understanding both the palaeobiodiversity and the palaeobiology of primate taxa and investigating micro- and macro-evolutionary processes.

Accurately and quantitatively investigating morphological variation with appropriate analytical methods is therefore key to the study of fossil samples. Since the 1990s, the field of palaeontology has gradually incorporated advanced 3D imaging and modelling techniques, starting with the use of X-rays for non-invasive access to details of the internal anatomy of fossil specimens (e.g., Conroy et al., 1990). Thanks to the digitisation process, 3D models of fossil specimens and virtual repositories documenting the diversity of morphologies within living species can be generated and made available to the scientific community (e.g., Skinner et al., 2013; Adams et al., 2015). 3D digital twins of existing objects have opened up the possibility of developing innovative protocols for *in silico* analyses of variation patterns in bones and teeth, such as geometric morphometrics (GM) (Rohlf, 1990; Bookstein, 1991; O'Higgins, 2000; Slice 2007). Instead of investigating variation in linear distances, angles or distance ratios as in traditional morphometric approaches, landmark-based geometric morphometric methods rely on the relative positions of predefined homologous points (landmarks) on biological objects (Bookstein, 1991). Generalised Procrustes analyses are applied to the Cartesian coordinates of landmarks as a superimposition method, with the aim of eliminating variations in landmark configurations not related to shape. Variations in shape configurations are then captured and investigated through multivariate analyses. Geometric morphometric methods are highly popular in palaeontology and regularly applied to produce comparative descriptions and characterisations of newly discovered specimens and taxa (e.g., Détroit et al., 2019) and to investigate patterns of variation within primate taxa (e.g., Harvati et al., 2004).

Although alternative landmark-based methods have been explored (e.g., sliding and surface semi-landmarks, Gunz and Mitteroecker, 2013), as well as algorithms for computing distances and correspondences between pairs (Boyer et al., 2011; Pomidor et al., 2016), in some cases, traditional GM analyses fail to fully capture differences in shape. For instance, smooth and complex structures (e.g., brain endocasts) are challenging to study through landmark-based GM since the number of identified and reliable landmarks is very small (Neubauer, 2014). Other anatomical structures, such as the articular facets of primate joints or the buccal aspects of primate molars, vary locally in terms of degrees of concavity/convexity or flare, and such subtle variations cannot easily be rendered by 3D landmark configurations (e.g., Singleton, 2003). Similarly, quantitatively documenting the presence or absence of discrete traits through 3D landmark-based GM can be of interest but is often difficult to carry out in practice (e.g., Skinner et al., 2008: Braga et al., 2019). Lastly, because of the complex organisation of anatomical structures, involving modularity and morphological integration, examining inter-individual (i.e., global) and intra-individual (i.e., local) shape differences is a prerequisite to produce a comprehensive overview of evolutionary changes. In short, alternative methods need to be explored.

Diffeomorphic deformation

One possible alternative to landmark-based GM is the landmark-free diffeomorphic deformation (DD) approach. This method is also referred to in the literature as "deformation-based models" (e.g., Beaudet et al., 2016a; 2016b), "diffeomorphic surface matching" (e.g., Braga et al., 2019; Pan et al., 2020; Zanolli et al., 2023) or "deformation-based 3D geometric morphometric analysis" (Urciuoli et al., 2020). In the interests of clarity, we recommend the term "diffeomorphic deformation", as it is under this name that the method was first introduced in biological anthropology (e.g., Durrleman et al., 2012). Instead of analysing the coordinates of predefined landmarks, DD investigates the geometric characteristics of surfaces by determining point correspondences over a 3D surface. Contrary to traditional landmark-based geometric morphometric approaches, DD is based on correspondences between surfaces (not on predefined homologous points) and statistics are computed for deformations (not for individual landmark coordinates) (Durrleman et al., 2012). 3D surfaces are embedded in a 3D space (i.e., grid of control points) and shape differences are quantified as the magnitude of the deformation of the 3D space required to warp one surface to another (Grenander, 1994). Deformations are mathematically modelled as diffeormorphism (i.e., smooth and invertible 3D deformations). This procedure relies on the metrics of currents, which involve integrating information (including local orientation) from all of the data points available on the surface, without assuming a point-to-point correspondence between surfaces, and estimating an optimal non-linear deformation (Durrleman et al., 2012). The deformation process is defined by a number of parameters, such as the deformation kernel widths, which depend on shape size and have to be carefully defined so that differences in the relative position of meshes are captured and local and global variations are integrated (Durrleman et al., 2014).

The DD approach relies on the construction of an atlas (figure 1). An atlas includes a template (i.e., a 3D surface), a set of initial control points (grid) and momenta that parameterise the deformation from the template to each specimen (deformation fields) (Durrleman et al., 2014). The position of the control points is automatically adjusted

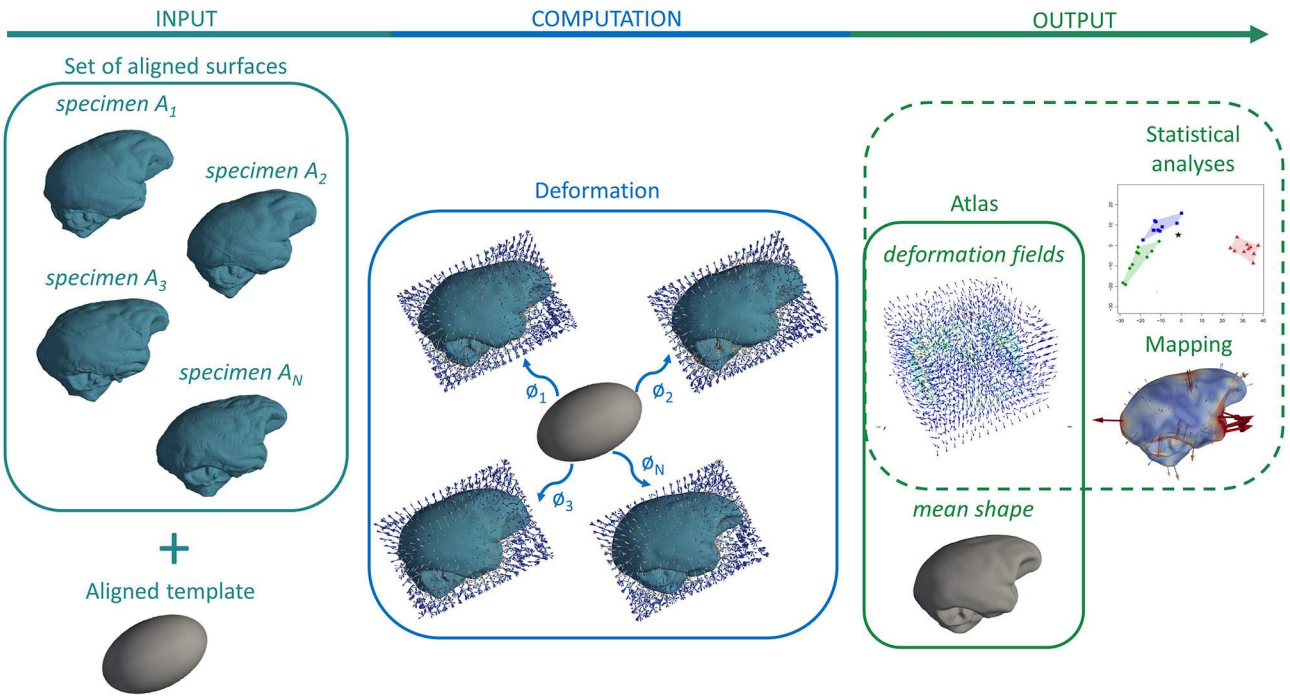

Figure 1. Protocole showing the successive steps of the landmark-free surface-based comparison approach using Deformetrica / *Protocole illustrant les étapes successives de l'approche par comparaison de surfaces sans points repères en utilisant Deformetrica*

to the most variable parts of the template (Durrleman et al., 2014). A template can be a geometrical shape (e.g., ellipsoid, sphere) or an actual specimen heavily smoothed to be as geometrically neutral as possible. The set of specimens is represented by 3D surfaces that are first rigidly aligned in position, orientation and scale with respect to a reference surface. A mean shape is computed by deforming the template to the set of aligned surfaces using an iterative optimisation algorithm (Durrleman, 2010). This process generates deformation fields (i.e., parameters of non-linear deformations) that are distributed in the 3D space deformation embedding the specimens. The magnitude and orientation of the deformations can be rendered by 3D colour maps and vectors (i.e., local maxima of deformations) that illustrate the topographical distribution of shape differences. Additionally, deformation fields integrating the local orientation and magnitudes of individual deformations can be statistically analysed (e.g., by principal component analyses). This approach considers the overall surface, effectively eliminating the inter-observer errors typically associated with landmark-based methods. Furthermore, previous studies comparing landmark-based GM and DD analyses of primate teeth and inner ears have demonstrated that the landmark-free approach not only preserves information on the variation of homologous structures but also captures variations in discrete features, enhancing their effectiveness in group discrimination (Beaudet, 2015; Zanolli et al., 2018; Braga et al., 2019; Urciuoli et al., 2020).

The method is implemented in the Deformetrica freeware package available at https://gitlab.com/icm-institute/aramislab/deformetrica. Additional tools have been developed for data pre- and post-processing (e.g., file conversion, statistical analyses with R, https://gitlab.com/jeandumoncel/tools-for-deformetrica).

Applications to the primate fossil record

Since the very first use of DD in biological anthropology (Durrleman et al., 2012), a number of studies have applied the method to palaeontological samples (e.g., enamel-dentine junctions, brain endocasts, inner ears, vertebrae). By assessing patterns of morphological variation in key primate taxa, they have provided previously unknown details of their biology, with significant taxonomic, evolutionary, phylogenetic and functional implications.

Under- or over-estimations of morphological variation could have a substantial impact on our understanding of palaeobiodiversity and, ultimately, of our reconstruction of the phylogenetic relationships between extinct and extant taxa. Consequently, DD offers a unique opportunity to quantitatively explore patterns of variation in fossil assemblages and thus clarify the number of species or genera that can be reliably identified. Taxonomic diversity in fossil primates has been intensively discussed and debated, partly because of the difficulty of identifying reliable diagnostic characters and metrics separating species and of estimating intra-specific variation in past populations (e.g., Plavcan and Cope, 2001). The morphology of the enamel-dentine junction (EDJ) in teeth, which is genetically controlled, is one of the most reliable sources of diagnostic traits in primates. DD applied to primate molar EDJs has yielded remarkable results, and has been proved to be more efficient in

discriminating between species than traditional landmark-based GM approaches (Braga et al., 2019). For instance, the quantitative analysis of intra- and inter-specific/generic variation of EDJs in southern African fossil cercopithecoids and European hominoids has brought the hypothesis of taxonomic diversity in the respective groups into question (Beaudet et al., 2016b; Zanolli et al., 2023). Similarly, the classification of hominin post-canine teeth using DD has successfully clarified uncertainties concerning the taxonomic assignment of dental specimens and the presence of *Homo* in hominin-bearing southern African and East Asian sites, as well as the origins of small-bodied *Homo* species in South East Asia and patterns of variation among Middle Stone Age humans in South Africa (Pan et al., 2020; 2022; Grine et al., 2021; Demeter et al., 2022; Zanolli et al., 2022a; 2022b). Apart from the enamel-dentine junction, external root shape in Middle Pleistocene hominins investigated by means of DD has been demonstrated as a taxonomically relevant indicator (Pan et al., 2019).

Morphological variation through time, as reflected by the differences and similarities identified between extinct and extant taxa, provides a window on the evolutionary processes that have shaped the history of a taxon. In particular, comparative analyses of fossil specimens and putative extant relatives may reveal significant morphological changes in key anatomical structures under selective pressure. In this regard, endocasts (i.e., replicas of the inner surface of the braincase used as proxies for brains) are the focus of much interest in palaeontology. However, because of the complexity of their shape and the lack of reliable anatomical landmarks, characterising patterns of brain morphological variation has been particularly challenging and has raised concerns as to the reliability of such studies (e.g., Bruner, 2017). Primate endocasts were the first objects to be characterised by DD in biological anthropology and revealed previously unknown details of endocranial ontogenies in extant hominids (Durrleman et al., 2012) as well as diachronic changes in cercopithecoids (Beaudet et al., 2016a). Furthermore, morphological differences between the endocasts of *Australopithecus*, *Paranthropus* and extant hominids have provided quantitative evidence that the *Australopithecus* brain was more derived than that of *Paranthropus* (Falk et al., 2000; Beaudet et al., 2018). At the same time, by directly comparing the endocasts of two specimens from eastern and southern Africa, DD highlighted local endocranial features specific to *Paranthropus* located in the parietal regions (e.g., Beaudet et al., 2021). Similarly, 3D mapping of the morphological differences and similarities between fossil *Homo* endocasts made it possible to reject the hypothesis of apparent stasis in the evolution of the frontal lobes within the genus *Homo* (Beaudet and Bruner, 2017). Last but not least, the shape of brains and endocasts of the same extant human individuals could be compared directly and quantitatively for the first time, to determine the degree to which information deriving from endocasts is reliable when reconstructing fossil brains (Dumoncel et al., 2021). As with endocasts, the shape of the canals in the primate vestibular apparatus, traditionally modelled by classic GM analyses as curves or series of landmarks, has been demonstrated by diffeomorphic deformation to vary throughout hominoid lineages and to be phylogenetically informative (Urciuoli et al., 2020). This has helped to clarify the nature of the phylogenetic relationships of Miocene dryopith great apes with *Hispanopithecus* and *Rudapithecus,* which were demonstrated to represent distinct Hominidae genera (Urciuoli et al., 2021). Additionally, the reconstruction of ancestral morphologies using this approach was key to identifying the plesiomorphic condition of hominines (Urciuoli et al., 2021).

In palaeontology, biological adaptations can be tracked through the identification of morphological changes affecting skeletal areas that play key functional roles. The search for locomotor adaptations in the axial and appendicular system has been intensified by the long-standing debates over the origins of hominin bipedalism (rev. in Stamos and Alemseged, 2023). For instance, subtle changes in the orientation and depth of articular facets, when captured, might be indicative of variation in the locomotor repertoire of fossil specimens. Besides craniodental material, the DD approach is also efficient in quantifying local and functionally-related shape variations in postcranial joints, as demonstrated by the study of the first cervical vertebra (atlas) in fossil hominins, for which the proportions of arboreal and terrestrial activities in the locomotor repertoire are partly unknown (Beaudet et al., 2020). Apart from locomotor adaptations detected in the postcranial skeleton, the morphology of internal cranial structures is a source of information about the ecological and geographical factors that influenced the evolution of a taxon. Recently, 3D deformation-based investigations of the nasal airway in modern humans have revealed that the correlation between the morphology of the nasal airways and environmental conditions is more complex than previously thought (Maréchal et al., 2023).

Prospects and conclusions

Because of the fragmentary nature of the paleontological record, missing data are inherently a major limitation when working with fossil specimens. There are two options when dealing with incomplete specimens: missing parts can be tentatively reconstructed (e.g., Gunz et al., 2009), or excluded from the analysis. DD opens up new prospects on both fronts. First, traditional methods for reconstructing partial specimens (e.g., assembling virtual fragments, mirroring of preserved areas, Gunz et al., 2009) can be applied in combination with the atlas construction and deformation process (e.g., Beaudet et al., 2022). Alternatively, missing parts can be identified and automatically removed from the rest of the sample. In this case, the same approach as described above is applied to the whole sample. From this process, non-common regions (i.e., regions not preserved in incomplete specimens) are automatically eliminated from the complete specimens (Dumoncel et al., 2016; Beaudet et al., 2018; 2020), so that only the intact

parts of the specimens are included in the analysis and the sample can accommodate partial specimens (Beaudet et al., 2018; 2020).

To conclude, since the methodological revolution that began with the introduction of geometric morphometrics into the study of fossil specimens, various approaches have been developed to overcome technical difficulties in the quantification of morphological variation. One of them is diffeomorphic deformation, which is a landmark-free deformation-based approach that has been proved to be relevant in addressing fundamental questions about taxonomy, evolutionary trends, phylogeny and functional adaptations in the fossil primate record, and to be applicable to anatomical structures that are notoriously difficult to investigate (endocast, inner ear, nasal airways) as well as to various categories of objects (e.g., volumes, curves, Dumoncel et al., 2021). Moreover, the computing resources required for such analyses are no longer a limiting factor since the capacity of computer clusters has dramatically increased over the last decade and the code, last updated 4 years ago, has been amended to be used with a GPU (Bône et al., 2018). However, although DD offers new prospects for the discipline, it is certainly not the solution to all the technical issues that may arise while studying fossil specimens, and it should be noted that the technical support currently available is limited. The investigative toolkit of palaeontologists is constantly being improved and enriched, and emerging technological innovations will probably bring the field of palaeontology into a new area of advanced analytical tools (e.g., AI, Fonta and Beaudet, 2024: data simulation and augmentation, Courtenay et al., 2023).

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