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Morphological Variability in Paleoanthropology: New Approaches, New Issues?

La variabilité morphologique en paléanthropologie : de nouvelles approches, de nouveaux enjeux ?

G. Daver · A. Balzeau · G. Berillon · F. Guy

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Since Darwin's seminal works, variability—from which selection acts—is considered as being specific to populations. Variability or the propensity to vary differs from variation, which represents 'the actually realised differences between individuals' in a population/sample, or between species in a clade [1, p. 967]. Hence, variability is more complex to quantify than variation, and in general, biological anthropologists focus their efforts primarily on variation *sensu stricto*. In human and non-human primates, as in all other living organisms, the potential causes of morphological variation have multiple sources. However, two main types can be identified: genetic and environmental. Genetic sources of variation are produced via mutations, sexual reproduction, epigenetics or gene flow. Environmental sources include, for instance, the prenatal environment, nutrition, quality of life and health care, culture and climate. Other sources of variation are more specifically considered in evolutionary anthropology as exemplified by diachronic or phylogenetic variations. For example, over the last decade, palaeoanthropology has yielded several new hominin taxa/groups based on morphological and genetic data (e.g. Denisova hominins [2], *Homo gautengensis* [3], *Australopithecus sediba* [4], new early representatives of the genus *Homo* [5], *Homo naledi* [6] and *Australopithecus deyiremeda* [7]).

Taken as a whole, the above-mentioned sources of variation illustrate the need to take variations of a distinctive nature (genotypic, phenotypic) into account at varying scales of organisation (from a simple anatomical structure to an integrated system), within and among clades (i.e. extant and extinct taxa).

Despite this increasingly well-documented variation and numerous conceptual and methodological developments, anthropologists seem to be inevitably confronted with the difficulty of interpreting, and even compiling, such very large amounts of data. This is why we wanted to explore this topic in a special session of the 1843rd SAP meeting, held in Poitiers, at the Espace Mendès-France, from 24 to 26 January 2018. Our guest speaker, Prof M. Bastir, introduced the special session and 21 papers were given, including 17 podium presentations and four poster displays. The six articles published in this issue of the BMSAP illustrate the diversity of the topics addressed during this session [8-13].

Five podium presentations and one poster display considered variation/variability in complex biological systems as a whole in terms of their different levels of organisation: introducing the session, Prof Bastir explored Neanderthal craniofacial morphology from the hierarchical and organism perspectives by integrating masticatory and respiratory biomechanics, ontogenetics and evolutionary morphological interactions between the central nervous system and the respiratory system, showing that integrative approaches yield a further understanding of the biological significance of specific features in hominin skeletal morphology [14]. For obvious reasons, such covariation analyses are still frequently applied to extant humans. For example, Albessard et al. highlighted similar spatial patterns of asymmetry between neurocrania and associated endocasts of 39 *Homo sapiens*, suggesting a close link between neurocranium asymmetry and brain

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development [15]. Le Maître and Mazurier emphasised the importance for bony labyrinth growth of the spatial constraints due to the shape of the petrosal bones in the cranium, a crucial point in any attempt to interpret the variation of such a structure from an ecological perspective [16]. In an attempt to better understand the correspondence between genotype and phenotype, Romeyer-Dherbey et al. compared the impacts of coronal nonsyndromic craniosynostosis on cranial shape in children, which made it possible to draw up a severity gradient and to consider setting up such analyses in new medical protocols [17]. By extension, the need to compare human variation/variability patterns with other patterns in non-human taxa is inherent to evolutionary studies and therefore to palaeoanthropology. Neaux et al. showed how morphological integration impacts shape disparity but not rates of phenotypic evolution, by demonstrating that the basicranium and face in primates are significantly integrated structures that can nevertheless also be considered as distinct modules, since both could evolve at different rates in response to different adaptive pressures [18]. From the postcranial perspective, Domalain et al. presented a realistic biomechanical simulation of hand force capability in fossil hominins and, as an example, demonstrated that the carpometacarpal joint of the fifth digit in *Australopithecus* could have been a factor limiting their ability to maintain Lomekwian-like tools [19].

The second set of presentations (four podium presentations, one poster display) focused on unravelling the form–function relationships of specific bone structures in connection with ecological functions, in order to propose potential applications to the fossil record. The impact of locomotion was the object of particular attention in this respect. Colombo et al. presented a new method for quantifying the morphological signal associated with the acquisition of bipedalism in the trabecular architecture of the radii in children from 0 to 3 years of age [20]. Druelle et al. demonstrated that, during growth, morphological variations in the body segments of olive baboons from 0 to 8 years of age conform to a general pattern typical of catarrhine primates, but they also showed that some inertial segment properties change with the varying locomotor repertoire [21]. Apart from locomotion, masticatory functions were also discussed. Investigating relationships between the distribution of enamel thickness and diets of extant primates, Thiery et al. showed, for instance, that various morphological and behavioural strategies might have been selected in primates that consume stress-limited food [22]. Martin-Moya et al. tested the influence of environmental and cultural behaviour patterns on craniomandibular morphology, using early settlement of the Americas a framework [23]. They identified a high correlation between cranial and mandibular shapes, but also highlighted the impact of cultural diets on variation in mandibular shape. Like locomotion and diet, the functional foundations of childbirth are also of prime ecological interest.

Based on 131 extant dyads, Frémondrière and Marchal supported that rotational birth likely have occurred with the emergence of the genus *Homo*, and suggest that such a physiological process may have been accompanied by the onset of a secondary altriciality and obstetrical assistance [24].

Finally, seven podium presentations and two poster displays proposed a reappraisal of morphological variation in extinct species based on new specimens and/or new approaches. Most concerned the difficulties of working out the perimeter of morphological variation in early hominins. Beaudet explained how new methodological developments (3D modelling) show that the endocast of *Australopithecus africanus* departs from the ancestral morphotype and pointed to unexpected degrees of variation in the spatial organisation of the frontal lobes of later hominins such as *Homo erectus-ergaster* and *Homo heidelbergensis* [25]. Daver et al. described three new limb bones (i.e. phalanx, proximal radius and second metatarsal) assigned to *Paranthropus boisei* (2.12 Ma, Shungura Formation). Evidence of habitual bipedalism and a propensity for climbing supported by these remains has helped to gain a better understanding of morphofunctional variations in an as yet poorly documented hominin [26]. Cazenave presented a reappraisal of isolated postcranial bones from various South African sites classically assigned to *Paranthropus robustus*, where high-resolution computed tomography and 3D analyses identified contrasting signals between the external and inner morphology of some of these remains (e.g. patella, distal humerus) and close affinities with extant humans for others (femur) [27]. Souron and Boisserie addressed the question of the taxonomic status of the early African and Georgian representatives of the genus *Homo* [28]. Considering dentognathic remains from two populations of African bush pigs and their fossil relatives, they showed that extinct morphospecies might represent complexes of several biological species. Based on quantitative measurements of various traits of both taxonomic and adaptive interests (dental tissue proportions, topographic distribution of enamel thickness, enamel–dentine junction), Zanolli identified different morphological trends that distinguish Southeast Asian specimens (Java) from continental Middle Pleistocene humans [29]. In their exhaustive comparative analysis, Condemi et al. found that the 19 Neanderthal teeth identified at Vergisson II, like those from other Burgundian sites, share closer affinities with specimens from the Mediterranean basin and even from Northern and Western Europe than with specimens from the ‘Near East’ [30].

Two presentations focused on the recently created species *Homo naledi*, which provides a unique opportunity to assess morphological variation in a fossil human species, thanks to its exceptionally rich hypodigm. Based on a reappraisal of the endocrania and of some of their reconstructions, Balzeau and de Bruicker underlined the close morphological affinities of the species with early representatives of the genus

Homo and *Homo erectus* [31]. Voisin et al. analysed the numerous remains of clavicles and scapulae from the cave chambers of Dinaledi and Lesedi and pointed to the intriguing combination of arboreal and bipedal behaviour suggested by the shoulder architecture and lower limb morphology in this geologically recent species [32]. In their study of the footprints from Rozel (Late Pleistocene, Manche, France), Dubeau et al. presented an actualistic approach that involved recording 24 humans moving barefoot at various speeds on Rozel-like substrates: the authors demonstrated that different individuals (1–1.70 m in height) could have walked on the same surface of occupation [33]. Coutinho Nogueira et al. brought new insights into variations in Near Eastern Late Pleistocene humans through a reappraisal of age at death, developmental abnormalities and descriptions of the inner structures of the craniofacial remains of the Qafzeh 9 individual [34].

To summarise, this session showed that biological anthropologists have to deal with numerous sources of variation/variability (phylogeny, development/ontogeny/growth, genetics, behaviour, ecology, environment, sexual dimorphism, geography, idiosyncratic variation) to which many different fields are contributing, including palaeontology, primatology, palaeopathology, ontogeny and biomechanics. Whatever the sources, variations in complex biological systems occur at different levels of organisation (from individual organisms, species or populations to the ecological or community level), but the transmission of variation from one level to the next is neither straightforward nor intuitive [35]. This is why any source of variation in a biological system should be investigated further from an integrative or transdisciplinary perspective. There is now, more than ever, a need for such a holistic approach, and the many fascinating presentations we heard during this SAP meeting at Poitiers testify to the vitality of current research on this topic.

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