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ORIGINAL PAPER

Cranial shape and size variation in human evolution: structural and functional perspectives

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Abstract
A glimpse into modern paleoanthropology In the last decades, paleoanthropology has been deeply modified, changing from a descriptive and historical science to a more quantitative and analytical discipline. The covariation of multiple traits is investigated to study the evolutionary changes of the underlying anatomical models, mostly through the introduction of digital biomedical imaging procedures and of computed geometrical analyses supported by multivariate statistics.
Functional craniology The evolution of the human cranium is consequently considered in terms of functional and structural relationships between its components, largely influenced by the allometric variations associated with the increase in the relative cranial capacity. In the human genus, the changes in the face, base, and neurocranium are characterised by a mosaic variation, in which adaptations, secondary consequences, and stochastic factors concur to generate a set of anatomical possibilities and constraints.
Systemic perspectives to the evolution of the human cranial morphology Concepts like morphological modularity, anatomical integration, and heterochrony represent key issues in the development of the current human evolutionary studies.

Keywords Functional craniology · Paleoanthropology · Morphology · Hominid evolution

A glimpse into modern paleoanthropology

Human paleontology has a relatively recent historical origin, officially becoming a debated subject in the second half of the nineteenth century. In 1856, the first Neandertal vault was recovered in Germany, although some human fossils had already been discovered (but not recognised as such) before. The Feldhofer Neandertal calotte, interpreted in turn as a modern human ancestor, an independent and extinct human form or a pathologic modern individual, originated the debate on human evolution. In 1891, the first *Homo erectus* cranial remain was recovered in the Javanese fossil record, and in 1924, the first australopithecus was described in South Africa. Since then, anatomists, morphologists, statisticians, and anthropologists have attempted to quantify and qualify the biological diversity expressed by extinct hominid forms.

If humans evolved, paleoanthropology has likewise shown marked changes over 150 years and more of scientific and social development. Although the media too often tend to provide a conservative view of this discipline, human paleontology has undergone (especially in the last 20 years) a definite reorganisation of its targets, perspectives, and tools.

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The phenotypic variability is perceived in a different way in comparison with its perception in the early historical stages. Firstly, the analysis of single traits has been substituted by the analysis of multiple traits, moving from a merely descriptive approach to a more proper analytical approach. Secondly, the analysis of simple diameters has been changed into the analysis of the spatial relationships between different structures. Thirdly, the analysis of the variation of the characters has changed into the study of the covariation of anatomical and morphological traits through the integration of univariate/bivariate statistics and multivariate approaches. These three conceptual and methodological transformations represent a single epistemological revolution, in which the phenotype is no longer intended as sum of features, but is instead viewed as an integrate model of functional and structural systems. Such changes can clearly be intended as historical consequences of a more complex framework, which largely depends upon technology. In the last decades, this refers in particular to the development of digital tools.

The first major advance in paleoanthropology was the application of biomedical imaging to the analysis of fossil remains [39, 40, 55, 80, 93, 96] (Fig. 1). Computed tomography is currently used to reconstruct fragmented specimens [95], to analyse inner anatomical structures like the paranasal sinuses [52, 70] or the vestibular system of the inner ear [79], to consider the preservation of the fossil remains [16], and to produce stereolithographic models useful for museology and didactics [29]. The study of the cortical brain morphology of extinct species through the reconstruction of the endocranial casts (*paleoneurology*) [24, 30, 32] has been particularly facilitated by the application of such digital tools [13, 69, 88].

The second revolution was represented by the development of geometric morphometrics and other landmark-based approaches in the late 1980s [9, 56, 63, 78]. Geometric morphometrics relies upon the multivariate analysis of geometric two- or three-dimensional models representing anatomical structures [57, 92]. Systems of coordinates from different specimens are registered and normalised by using superimposition procedures involving translation, rotation, and scaling of the geometrical models. The residuals of such transformation (that is, the remaining spatial differences between individuals) are used in multivariate ordination techniques, aimed at revealing the patterns of covariance between the different anatomical components (Fig. 2). Such approach is able to quantify the morphological differences and to describe the functional and structural relationships underlying the observed anatomical variation. Clearly, such patterns of covariation between structures are consequences of the biological network organising the morphogenesis, involving the interaction of growing tissues, tendons, and organs.

The application of these techniques to the study of fossil records lead to consider human evolution not merely as a process of changing features but rather as a process of changing biological models.

Functional craniology

In 1960, the term *functional craniology* was proposed to indicate an approach to the study of the human skull based

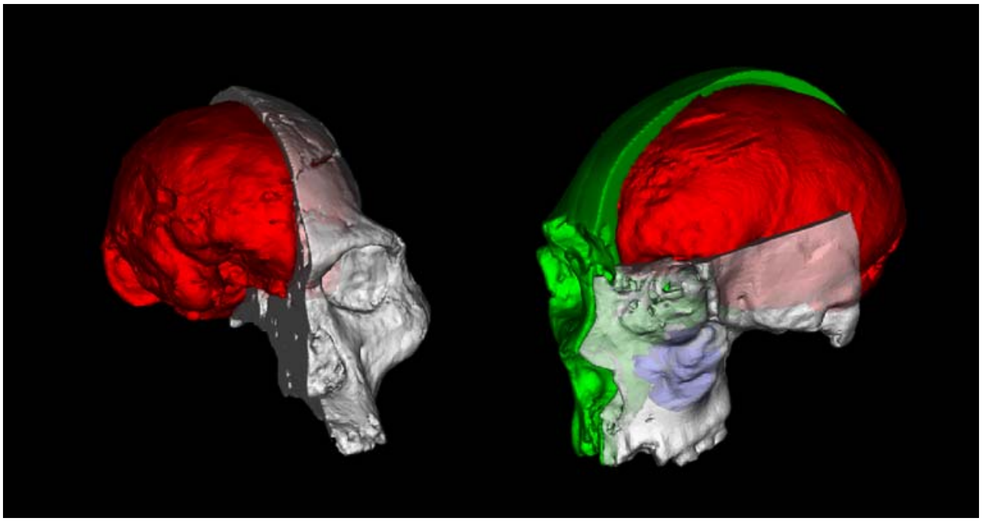

Fig. 1 Computed tomography represented one of the major advances in current paleoanthropology, improving the reconstruction of fragmented specimens and allowing the anatomical and morphological analysis of the inner structures (endocranium, paranasal sinuses, semicircular canals, tooth, diploe, etc.). Here, the endocasts and other features are shown on the digital replicas of an australopithecus (*left*) and of an early Neandertals (*right*)

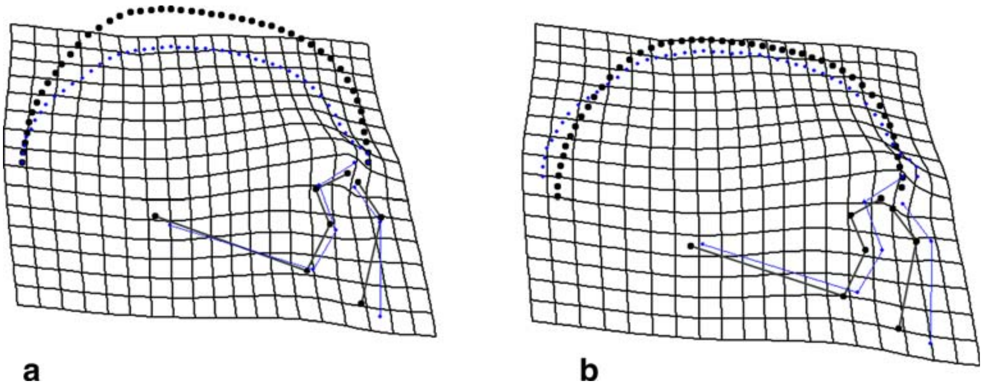

Fig. 2 Shape analysis and morphometrics have been deeply improved by the development of geometric computed approaches (landmark-based techniques and geometric morphometrics). Coordinates from different specimens can be superimposed according to iterative and standardised criterions, and the resulting differences can be analysed by using multivariate statistics. The patterns of covariance among and within structures are therefore described and quantified, revealing the underlying biological model (morphogenesis, functional relationships, etc.). Here, a bi-dimensional cranial configuration in right lateral view is compared in one modern human (*black*) and one Neandertal specimen (*blue*) through baseline superimposition according to the maximum neurocranial length (**a**) and least-square superimposition (Generalised Procrustes Superimposition) to minimise the shape differences (**b**). The spatial deformation from the modern to the Neandertal configuration is visualised by using the *thin-plate spline* interpolant function

on the structural and functional relationships between the different cranial components [48]. The skull is an object formed by anatomical structures arranged into a physical network, in which the final result of the morphogenesis (both in ontogeny and phylogeny) depends upon the interaction of forces and constraints among the different parts involved. The morphogenetic process is based on changes in size (*growth*) and changes in shape (*development*) of the anatomical structures. These two components can be split conceptually and thus analysed separately, primarily to understand the degree of their reciprocal dependence. In terms of physical interaction, cranial morphology is the result of pressures and tensions associated with expanding organs (such as the brain), binding connectives (such as the *falx cerebri* or the *tentorium cerebelli*), contacting sutures, bone displacements, and muscular influences. Each cranial district interacts directly with its neighbouring structures according to the counterpart principle [23], thereby generating a complex system in which the whole organisation is not the mere sum of each single process. Such interaction occurs at different levels, within genes, tissues, bones, and organs. For example, cranial growth patterns at the sutures are influenced by the strains associated with the brain pressure, perhaps by means of angiogenetic processes or of dura connective layers [28]. It is therefore clear that minor random or selective changes in one of the components of such network (distribution of the intracranial pressure, composition of the dura layers, strains distribution, bone response) will involve major evolutionary changes in the neurocranial morphology.

Clearly, this network, based on forces and constraints, relies upon a genetic program, in which patterns of deposition and reabsorption of tissue (*growth fields*) are the result of species-specific evolutionary pathways [22]. It is worth noting that such growth fields can also be found on fossil surfaces by recognising the traces left by osteoblasts and osteoclasts. This is the basic principle of *paleohistology* [44].

Interestingly, beyond the information made available from the bones themselves, the vascular structures also leave their imprints on the endocranial walls, providing support for hypotheses regarding physiological processes [20, 34].

The approach of functional craniology can be also used in an experimental setting, studying the influence of the physical/physiological environment or the genetic components in animal models. Interestingly, because of the impossibility of using a similar experimental approach on the human cranial matrix, relevant evidence comes from the artificial cranial deformations deriving from cultural and ethnic practices or from the craniosynostotic individuals [4, 5, 33, 47, 49]. This is particularly true when dealing with the relationship between brain and braincase [3, 58].

A general framework on encephalisation and human evolution

As soon as the evolutionary process was acknowledged for the human lineage, it was described as linear, gradual, and progressive. Namely, evolution was supposed to move from more imperfect to more efficient species through continuous and directional changes. The current interpretation of human evolution is quite different, describing a “bush” of species, representing alternatives of similar models, evolving sometimes more gradually and other times more

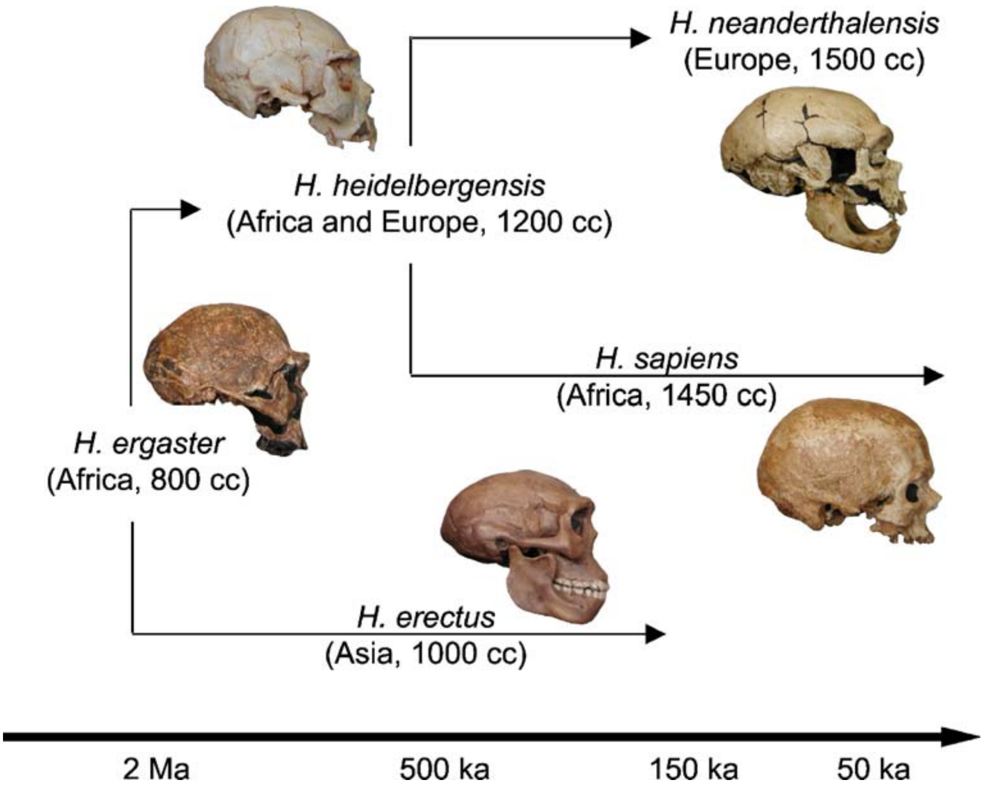

Fig. 3 The first recognised fossil record of the genus *Homo* can be found in East Africa, around 2 million years ago, and referred to as *H. ergaster*. Early humans soon moved to Asia, generating a variation presently described with the term *H. erectus*. A second dispersal is associated with a heterogeneous Afro-European group, called *H. heidelbergensis*, related to the following evolution of modern humans (in Africa) and Neandertals (in Europe). The relationship among these different evolutionary lineages are represented with their general chronology (*Ma* Million years ago; *ka* thousand years ago) and average cranial capacity (*cc* cubic centimeters)

abruptly, and not necessarily according to a directional criterion of change [90, 91]. Hominids are conventionally divided into two subfamilies, the Australopithecines (including the genera *Australopithecus* and *Paranthropus*, with about eight to ten species described) and the Hominines (including only the genus *Homo*, with five to six species described). The human genus is found in East Africa around 2 million years ago (Ma), and moves towards Asia after 1.7 Ma and to Europe at least about 1 Ma [42]. The first species to be fully recognised as representative of the human lineage was found in East Africa, and it is currently referred to as *H. ergaster*. The relationships between the subsequent African, European, and Asian morphs are still debated, with hypotheses suggesting a unique worldwide genetic population leading to modern humans or alternatively suggesting independent species that were finally replaced and substituted by the present human groups [86]. Nonetheless, the earliest populations of the three continents displayed geographical peculiarities, and this induces many authors to recognise at least three different derived human species: *H. sapiens* in Africa, *H. neanderthalensis* in Europe, and *H. erectus* in Asia (Fig. 3). Modern humans and Neandertals are related to a rather heterogeneous ancestral species named *H. heidelbergensis* [59, 60], which inhabited Europe and Africa in the Middle Pleistocene.

All these different lineages underwent a process of encephalisation, namely, a relative increase in the cranial capacity. The exact data are not available because cranial capacity should be considered as a relative figure with respect to other variables such as body size or metabolism that can only be hypothesised in fossil species. Nonetheless, the absolute endocranial volume increased from about 800 cc in the early humans to 1,000–1,200 cc in the species of Middle Pleistocene, and further to 1,500 cc and more in Neandertals and modern humans [32, 61].

Because of the structural relationships within an anatomical system (surface to volume ratios, biomechanical forces, and ontogenetic constraints), when size changes, shape must change accordingly. This is the basic assumption underlying *allometry*, namely, the changes in shape related to changes in size [25, 26, 35, 76]. During evolution, a selective pressure determining changes in one of these components (size or shape) involves secondary changes in the other. Such secondary changes are not necessarily adaptive but may be merely consequences of the adjustment within the structural system. It is clearly also possible for these secondary changes to uncover some interesting new functions. Finally, brand new allometric relationships can evolve from the actual reorganisation of the structural and functional networks, thus changing the biological model.

Back to the encephalisation process, if different lineages display similar size changes, a certain percentage of their similarities and differences will simply be a consequence of the allometric variation. One of the most important topics in human evolution is to investigate which anatomical and morphological traits are allometric differences and (more interestingly) which are not.

Some major cranial changes in the human genus

Since the early recovery of the first paleoanthropological remains, cranial variation has represented the main issue of investigation in this field, including studies on macro and micro anatomy, tissue organisation, metrics, and biomechanical models. In general, the cranial system is divided into three distinguished but related structural components: the vault, the face, and the base.

Neurocranial morphogenesis largely depends upon brain pressure for its size changes and upon endocranial connective tissues for its shape changes [23, 48]. Consequently, the morphological evolution of the braincase—and of the vault bones above all—is directly linked to the endocranial dynamics related to the ontogeny and phylogeny of the underlying soft tissues. It has been hypothesised that in the human genus the enlargement of the brain is associated with a relative widening of the frontal lobes and relative reduction in the parietal areas [14]. Neandertals show the maximum expression of this pattern, displaying also supernumerary ossicles at the parieto-occipital boundary on the ectocranial surface. This hypostotic feature was described as “morphological instability” [73–75] or as “ontogenetic stress” [41, 43], to hypothesise a lack of balance between size and shape variation during the morphogenesis, which would require additional centres of ossification. Modern humans depart from this allometric trajectory, displaying a marked development of the entire parietal volumes which involves a general convolution and globularisation of the brain [14, 18] and consequently of the braincase [19, 38]. Whether this change is primarily a structural adjustment or a cognitive adaptation has yet to be determined, recognising the role of the parietal cortex in visuo-spatial integration [21, 77], tool use [82], and possibly generation of an inner reality. Recently, single genes have been hypothesised to be responsible for the gyrification of large cortical areas, suggesting the possibility of discrete and rapid evolutionary changes in the endocranial organisation [54].

The allometric widening of the frontal lobes deserves further attention. A modern-like frontal morphology at the Broca’s area is recognised in fossils dated back to 2 Ma [31, 87]. After such early changes, no further differences have been described both with respect to the gross appearance of the Broca’s area and—at least in the last 500,000 years—with respect to the midsagittal shape of the anterior cranial fossa [10]. Nonetheless, within human evolution, bigger brains show relatively wider frontal lobes, with the frontal breadth at the Broca’s cap increasingly more comparable to the maximum (temporal) brain width. This allometric trend has been hypothesised to be the result of available lateral space with respect to the frontal area (because of the orbit frontation and reduction in the temporal muscle) and of constraints in the vertical dimension (because of the under-rotation of the underlying facial components and of the loading on the orbital roof) [14]. Although this positive allometric widening of the frontal lobes is rather confirmed, whether or not modern humans and Neandertals show a further frontal widening, beyond what expected for the *Homo* pattern, remains to be tested [15, 17]. A molecular difference in the myosin of the temporal muscle between modern humans and apes has been hypothesised to be involved in a decrease in lateral pressure with respect to the anterior braincase, thus allowing a further brain enlargement [81]. Although this hypothesis is rather debated [46], it is useful to consider and discuss the cranial morphogenesis in terms of its structural matrix. Clearly, where the morphological evolution of the frontal lobes may be said to be rather subtle and the volumetric enlargement only based on allometric variations [71, 72], the soft tissues nevertheless evidence some remarkable reorganisation associated with neural wiring and connectivity in modern humans [62].

The evolution and development of the frontal bone cannot be merely interpreted as a function of brain influences. Because of the close contact between the anterior cranial fossa and the underlying facial structures, the browridge and the frontal squama are particularly interesting to analyse when considering the evolution of the relationship between splanchnocranium and neurocranium. For example, more archaic human morphs had the frontal lobes behind the orbital roofs, while later species had the frontal lobes lying on them [15, 70]. The browridge, which acts like a hinge between the face and the braincase [37], shows a very large variation within the human genus [10]. In more derived species the browridge shows greater continuity with respect to the frontal squama, while it is more separated in their ancestors [15]. Furthermore, archaic humans probably displayed small frontal sinuses [15], which were dramatically enlarged within the frontal squama in the Middle Pleistocene [52, 70] and again reduced in more derived species like modern humans and Neandertals. All these variations suggest that the relationship between face and braincase has evolved in

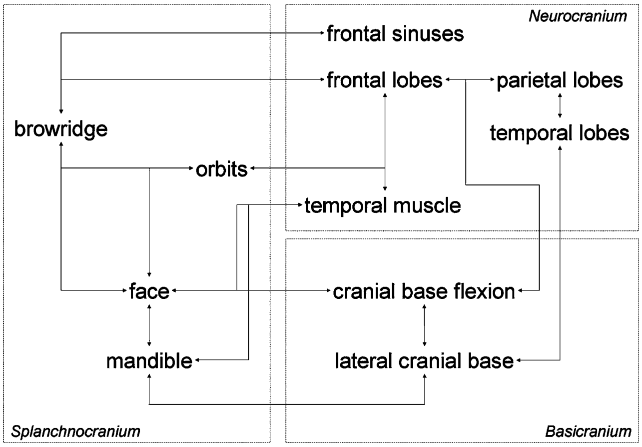

Fig. 4 The braincase, the cranial base, and the facial district, represent a structural network in which integration (the relationship within the whole system) and modularity (the partition of the whole system into sub-unities with high covariance, thus related in term of morphogenesis) must be carefully considered when analysing the evolutionary variation of single traits. Each single feature has its proper function, but in terms of structure, it is associated with the neighbour parts of the anatomical network. Therefore, the evolution of the whole system is constrained, characterised by adaptive pressures but also by structural and functional secondary consequences, as well as stochastic changes

a mosaic fashion within the human genus, under the potentialities and constraints of a complex structural network.

The facial morphology has also undergone some local morphological evolution and adaptations. The encephalisation process is associated with a general reduction in the splanchnocranial complex [11, 19, 38], extreme in modern humans. However, with respect to facial morphology, Neandertals represented the more specialised group, displaying a marked projection of the middle face, called midfacial prognathism, or oncognathism [53, 64; but see also 89]. This process involved changes in the face, mandible, teeth, and probably in the organisation of the lateral cranial base [7]. Evolutionary hypotheses regarding this feature are heterogeneous and not well-established, ranging from climatic adaptations, to the use of teeth as handling tools, or of stochastic changes. Nevertheless, it seems that the two more encephalised groups evolved in opposite directions: modern humans with a less-derived face but a derived neurocranial organisation, and Neandertals with derived faces but with a less-derived neurocranial arrangement [19, 85].

Finally, the role of the cranial base, linking the facial and neural components and representing the main determinant of the cranial architecture [66, 67], needs to be considered. The organisation of the cranial base is influenced by locomotion and posture, as well as diet and biomechanics of the mandibular structures [84]. By contrast, the skull architecture largely depends upon the regulation of the cranial base morphogenesis [23, 38], and structures such as the spheno-occipital synchondrosis probably acted as a major evolutionary source of variation, both in terms of genetics and of biomechanics. In primates, the more a species is encephalised, the more the cranial base is flexed to accommodate brain development [65]. Currently, whether or not the cranial base in humans is flexed as or more than expected based upon the pattern presented by non-human primates is debated [45]. Moreover, beyond the cortical components of the brain, the sub-cortical structures may also have had a role in generating constraints able to direct the evolution of the cranial base anatomy [83].

The variation within the four to five currently recognised species of the human genus is sometimes remarkable and other times subtle. Differences go beyond the main topics described in this synthetic review, ranging from the overall cranial architecture to a large number of very small and detailed anatomical features. Nonetheless, the important factor that remains noteworthy is the need to focus on the structural and functional relationships between the cranial components, evolving together as a single morphogenetic unit rather than on single traits (Fig. 4). This approach leads to the development of "organismic models" in human evolution [64].

Systemic perspectives to the evolution of the human cranial morphology

Cranial anatomy is the result of a functional and structural network formed by genetically determined growth fields, developmental and biomechanical interactions, and physical constraints, both in terms of morphogenesis and evolution. It therefore should be investigated as a system. Within the cranial matrix, the networks of causes and consequences are linked by feedbacks and loops that render any linear interpretation of the evolutionary or morphogenetic processes useless and misleading.

Two lines of investigation may help to approach the evolution of the cranial variation within this framework: heterochrony and modularity.

Heterochrony refers to evolutionary changes in the time or rate of the ontogenetic processes [25, 26, 35]. A given ontogenetic trajectory can be under-expressed (pedomorphosis) or over-expressed (peramorphosis), generating morphological variations on the basis of the actual allometric relationships. Growth and development are forced to covary within a fixed structural model, changing size and shape according to selective pressures. On the other hand, the allometric relationships may be altered, uncoupling size and shape variation (such as in *neoteny*, where only the rate of the shape changes is delayed). Heterochrony is known as one of the major determinants in evolutionary biology, accounting for morphological transformations (of the whole body, or of a part of it) based on different version of the same model through minor molecular and physiological changes [76].

Modularity refers to the localisation of given structural units more strongly constrained within the morphogenetic and evolutionary processes [36, 68]. "Modules" are anatomical regions within which the variation of each part is highly dependent upon the variation of the others because of structural or functional relationships. *Integration* is the opposite of modularity, thus a strong level of covariation within the whole structure. Such organisation represents both a constraint and a potentiality for the evolutionary processes. Cranial integration and modularity can be investigated both by comparing the patterns in different species [50] and by studying the patterns within the functional matrix of the modern human skull [6–8]. Such approach was successfully applied in studies considering the hominid craniofacial [1, 2] and basicranial [84] variation. A similar pattern of integration was described as responsible for the high vault and flattened occipital bones in modern humans with respect to the low vault and projecting occipital in Neandertals: different phenotypes resulting from a morphological continuum based on the same shared structural relationships [27]. Similarly, extinct species can be characterised not only in terms of morphological traits but also of developing models which take into accounts differences in the ontogenetic changes [51]. Once more, craniosynostosis are particularly relevant in the study of morphological integration and cranial evolution, mostly when considering the relationship between brain and braincase [3]. The analyses of craniosynostotic phenotypes suggest that, because of the structural and embryological influence between cranial bones, brain, and connective tissues, morphological changes can extend far from the areas directly and primarily involved in genetic or functional variations [58].

Considered together, heterochrony and modularity form the conceptual and analytical framework of the current *evolutionary developmental biology* (or "evo-devo"), as the functional and structural study of biological variations in terms of ontogeny and phylogeny [12, 94].

The evolution of the human cranial morphology is finally represented by a mosaic and complex process, in which similar heterochronic changes, allometric relationships, and modular organisation have been moulded by different selective forces in different human lineages. Some changes are strictly adaptive, others are mere consequences, which can eventually be reinvested in new functions. Finally, some may be simply related to casual variations associated with the small numbers of humans that it is often assumed to move in new territories (founder effect) or of residual populations after some marked climatic changes (bottlenecks).

In this framework, paleoanthropology may learn from the current biomedical knowledge how to interpret some of these variations and may in turn suggest how and why some of these variations may have become important to the current biomedical environment.

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