A systems-model for the morphological analysis of integration and modularity in human craniofacial evolution

Markus Bastir

Paleoanthropology Group, Department of Paleobiology, Museo Nacional de Ciencias Naturales, CSIC; c/ Jose Gutiérrez Abascal 2, 28006 Madrid, Spain
e-mail: mbastir@mncn.csic.es

Summary - *In spite of a long history of research in craniofacial biology the extent to which developmental cascades between the brain, the cranial base, and the face influences the evolution, development and variation of the skull, is not clear. This paper discusses aspects of these problems in terms a "systems-model" of morphological integration and modularity of human craniofacial morphology. This model proposes analysing morphological variation and evolution of the human skull by considering ontogenetic and evolutionary modifications of modules by local (cranial) as well as general (non-cranial) factors, which implies an organismal view on human skull evolution. For example, the size and shape of brain lobes have local effects on skull shape, moulding lateral basicranial morphology. These effects, which are relatively independent from midline cranial base variation, interact with the position and morphology of the mandible and the postero-superior limit of the ethmo-maxillary complex. Another local factor within the face includes changes of the size and shape of nasal cavity. However, this cranial module is functionally integrated with a more general body system, such as respiratory apparatus and functionally linked with non-cranial factors such as body energetics, size and allometry. This paper suggests that a joint consideration of local and general factors likely improves the development of holistic hypotheses about human craniofacial evolution.*
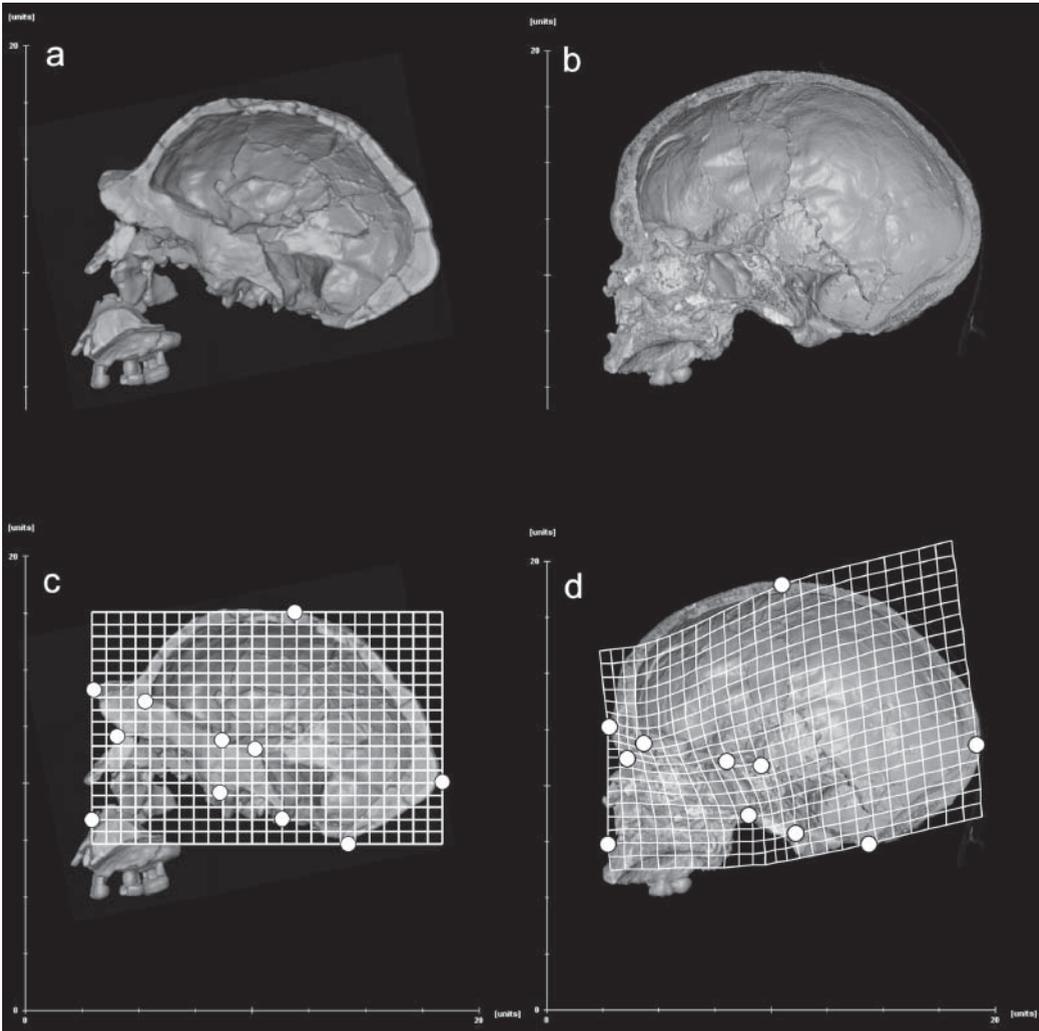
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Introduction

The evolution of modern human craniofacial morphology is characterized by three major morphological features: an enlarged, globular braincase, a reduced face and an increased basicranial flexure (Fig. 1) (Stringer & Andrews, 1988; Stringer, 2001; Lieberman *et al.*, 2002). Despite a long history of research in evolutionary craniofacial biology (Biegert, 1957; Moss & Young, 1960; Hofer, 1965; Enlow, 1968; Ross & Ravosa, 1993), the extent to which developmental cascades between the brain, the cranial base, and the face are responsible for the generation of the modern human craniofacial pattern is far from clear and their exact morphological relationships are still discussed (Lieberman, 1998; Strait, 1999; Spoor *et al.*, 1999; Lieberman *et al.*, 2000a, b; Bruner, 2007; Bastir *et al.*, 2008).

At the core of these observations are the following two framing questions: Can facial reduction be explained as a structural consequence of encephalisation and/or basicranial modification? Or is facial reduction a simultaneous but independent trend in human evolution? The aim of this paper is to address these questions in the light of developmental integration and modularity and the way they play together in human craniofacial biology.

Fig. 1 - Midsagittal sections of early human, KNM-ER 3733 (a), modern human, Lautsch 1 (b), and thin plate spline transformation of the midline geometry of the early (c) into modern human (d). The thin plate spline transformation illustrates central trends in modern human evolution: overall facial reduction, neurocranial globularisation and basicranial flexion.

A systemic view on explanations in morphology

Morphological features have been traditionally interpreted either from a rather functional perspective or from a structural point of view (Alberch, 1990). Sometimes these different perspectives can lead to apparently conflictive interpretations, for example, the Neanderthal face (Rak, 1986; Trinkaus, 1987, Spencer & Demes, 1993). While functional approaches have aimed to explain the Neanderthal facial morphology as adaptation to biomechanical stress caused by mastication, paramasticatory

activity and torsions due to facial loading (Rak, 1986; Spencer & Demes, 1993), structural models have recurred to basicranial architecture and the combination of primitive retentions of prognathism and structural reconfigurations of facial elements ("zygomatic retreat" model) (Trinkaus, 1987).

Methodological reductionism of explanations in biological sciences (including morphology) disregards a consideration of the biology of the organism. As recently reviewed (Drack *et al.,* 2007) this problem has been recognized often, together with a need for "exhaustive" explanations in biology and has led to systems approaches in biology (Bertalanffy, 1953, 1956; Lorenz, 1973; Riedl, 1975; Moss, 1981; Riedl, 1981; Alberch, 1990; Ahl & Allen, 1996; Moss, 1997c,d; Laubichler & Wagner, 2000; Bastir, 2004; Laubichler, 2005; Lidicker, 2008).
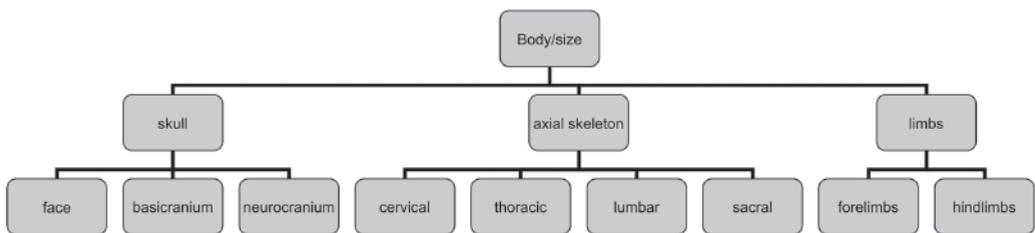
A system can be seen as a three-dimensional fraction of the universe over a time period, the boundaries of which are arbitrary, but most usefully matched to natural discontinuities of matter or energy (Lidicker, 2008). It contains parts that interact with each other and the whole system (holon) possesses features not contained in its constituent components. In this sense, systems theory is closely connected with hierarchy theory (Ahl & Allen, 1996). Many biologists have adopted an organization hierarchy, in which a *holon* is seen as composed of nested and interacting subsystems, which are themselves systems (*holons*), but at lower scales of complexity (Riedl, 1975; Ahl &

Allen, 1996). In such a context the parts determine what is possible in principle, and the context limits which of these possibilities can in fact be realized although it is important to note that the levels are defined arbitrarily. This can be considered a disadvantage, because the boundaries need not necessarily correspond to real life's organisation (Lidicker, 2008). On the other hand, as epistemological fundament such theoretical partitioning of life into systems permits modelling that can be compared with reality, which is advantageous because this serves as potentially powerful heuristic tool in holistic biological research.

"Exhaustive" in a systems context means that an explanation (or a hypothesis) is built on "necessary and sufficient" arguments but it is obviously difficult to translate these terms rationally into a morphological research program.

One possibility to approach exhaustive modes of explanations is thus provided by a systems- and hierarchical view on morphological structures (Riedl, 1975; Moss, 1981; Riedl, 1981; Wagner, 1996; Wagner & Altenberg, 1996; Chernoff & Magwene, 1999; Bastir, 2004; Bastir & Rosas, 2005). Thus, a systems model of craniofacial evolution favours an organismal view on evolutionary morphological change and potentially reconciles theoretically contradicting positions of externalism and internalism, or functionalism and structuralism by viewing them complementarily, (systemically) (Riedl, 1975,1977; Alberch, 1990).

A systemic representation of an organism is shown in Figure 2, in which different functional

Fig. 2 - Integrative scales of an organism as a modular system. The size of an organism (on the top of the diagram) can be considered a general (large-scale) integrative factor. Morphological co-variation of structures with the size of the organism (allometry) is considered more general than morphological co-variation among modules at lower organismal scales (e.g. among skull components) (Modified after Chernoff & Magwene, 1999).
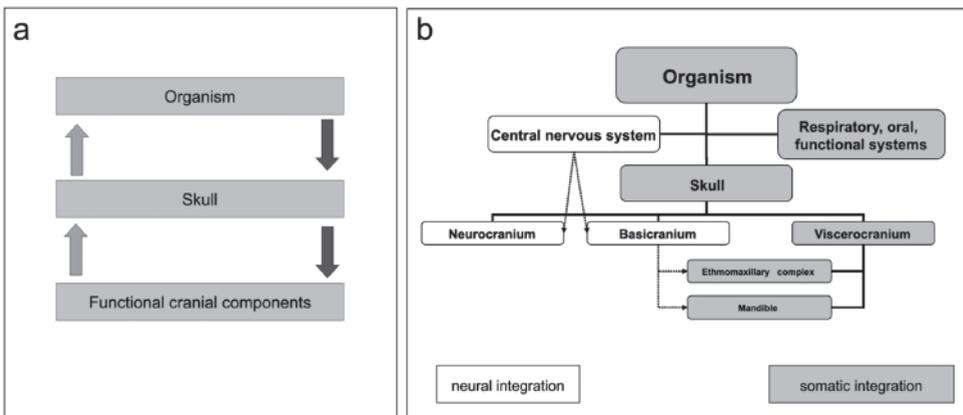
and developmental parts are integrated to form a unified complex, the organism as a whole. An organismal view on morphology (following the systems concept as described above) contemplates interdependent relations between different components of the organism, which follow different regularities. Some of these regularities are local and affect only a specific region of structures. Others are more general, that is, regionally more extended and can be detected in different parts of the body (Bastir, 2004).

Following ideas of Nikolai Hartmann, Paul Weiss, and Ludwig von Bertalanffy, the Viennese morphologist and evolutionary biologist Rupert Riedl (1975, 1981; Wagner & Laubichler, 2004) has developed a stratified model of biological complexity, which can be modified to a standard model for explanations in craniofacial biology and morphology. Riedl suggested that any biological observation is embedded within higher and lower complexity levels (Fig. 3a).

The lower complexity level contains necessary, but insufficient causative information regarding the next higher level. This is because novelty, that is, appearance of new features, "emerges" as new level-specific properties that are not contained at lower levels (Riedl, 1975; 1981; Müller & Wagner, 1991, 1996). "Low-complexity level explanations" are often characterised by a materialistic connotation and refer to principles of physics, chemistry and molecular biology. For example, Moss (1997c) criticized exclusively genetic explanations of higher order biological structures such as bone configurations giving rise to craniofacial morphology. Such kind of explanations can be seen as bottom-up, or up-stream explanations, because their line of reasoning is directed from a lower complexity level towards a higher one, or more generally, from the detail to the whole.

In a similar albeit contrary sense, consideration of the upper complexity level alone provides necessary but insufficient explanatory content. "High complexity level explanations" sometimes show a finalistic connotation and also extremely adaptationist explanations of morphology belong to this way of causative argumentation. The associated "directionality" of explanation could be considered top-down, or downstream, from higher to lower complexity levels, or from the whole to the detail.

Fig. 3 - (a) Hierarchical relations of morphological observations according to the systems model. Morphological variation of the skull needs to consider both, general causative factors related to the organism (non-cranial factors) and factors related to local (cranial) functional components. (b) The same hierarchical scheme in modular representation. The morphology of the brain is integrated with the neurocranium and the basicranium (cranial factors). The viscerocranium is integrated with functional systems related to the properties of the body. The respiratory function integrates nasal cavity and thorax. Also the lower face (oral system) shares functional relationships with the size and energetic demands of the body (non-cranial factors).

In the light of a systems-approach only both points of view together provide "exhaustive" (that is: sufficient and necessary) modes of explanation in morphological sciences (Riedl, 1975, 1977, 1981; Moss, 1981, 1997d). Any condition for the morphology of a given structure is interdependently embedded within its upper and lower complexity levels. Figure 3a aims to visualize this principle representing the skull as composed of functional cranial components at lower complexity levels and as part of an organism at a higher complexity level. It aims to represent morphologically relevant aspects and there are certainly other, more complete, stratification representations of biological complexity (Wagner & Mueller, 1996; Strait, 2001). It is this kind of interdependent hierarchies, in which modularity and morphological integration acquire a key importance for an organism-related view on morphology (Bastir, 2004; Bastir & Rosas, 2005).

Any biological structure can be seen as an encaptive (Laubichler, 2005), nested, integrated and modular system. With respect to the human body the head is a module that is integrated with the rest of the organism, while the head itself is an integrated unit which consists of its functional craniofacial components (Fig. 3b). An attractive aim of the paleoanthropologist is therefore to analyse mutual developmental and evolutionary relationships between the whole and its parts.

Morphological integration and modularity

What are integration and modularity and why are they important in the study of the evolution of the human skull?

Morphological integration (Olson & Miller, 1958; Zelditch, 1987; Chernoff & Magwene, 1999) has been defined in various ways, but a particularly useful definition implies that evolutionary change in one element is reflected by changes in another element (Smith, 1996). Thus morphological integration comprises a set of mechanisms that connect (integrate) these elements. In accordance with such a definition,

in paleoanthropology it has been classically assumed that evolutionary increase of the brain (encephalisation) is reflected by changes in other elements, such as the basicranium and the face (Dabelow, 1931; Weidenreich, 1941; Hofer, 1952), for review Bastir (2004).

It has been outlined on several occasions that different levels of morphological integration should be distinguished: individual-specific levels of integration (developmental, functional) and population-specific levels (genetic, evolutionary) (Cheverud, 1995, 1996, Strait, 2001; Klingenberg, 2005). Integration patterns at one level (genetic) can be different from integration patterns at other levels. This difference of integration and lack of correspondence across different complexity scales has - particularly regarding the "genotype - phenotype map" - also been termed "representation problem" (Wagner & Altenberg, 1996). A possible link between different categories of integration is that functional, developmental integration at the individual level leads to genetic and evolutionary integration, when selected for (Cheverud, 1996). Alternatively integration can be achieved by linkage disequilibrium or pleiotropy (Cheverud, 1996). In mice the relationship between the genetic, developmental and morphological level has been addressed looking at quantitative trait loci (Cheverud *et al.,* 1997; Leamy *et al.,* 1999; Klingenberg *et al.,* 2004). In human evolution the study of morphological integration in the framework of growth and development permits the development of hypotheses (or speculations) about possible evolutionary modifications of these ontogenetic processes. Such evo-devo hypotheses about integration can then be assessed with respect to the human fossil record (Ross & Henneberg, 1995; Lieberman, 1998; Strait, 2001; Jeffery & Spoor, 2002; Bastir & Rosas, 2005; Bastir *et al.,* 2008).

Modularity is highly important in this evolutionary context because it allows for evolvability (Wagner & Altenberg, 1996; Winther, 2001; Klingenberg, 2005). Klingenberg and colleagues described modules as units that "are made internally coherent by manifold and strong interactions among their component parts, but […]

relatively independent from other modules and have relatively weak or few connections with other parts of a system" (Klingenberg *et al.*, 2003) (p. 522). At a morphological level, a recent study has indicated that the semi-independence of modules is not only characterized by their proper spatial aspects but also by its own temporal onto-genetic structure (Bastir *et al.*, 2006).

The relative independence among compo-nents of morphological structures -associated with modularity and integration- is an impor-tant precondition of mosaic evolutionary change because modifications in one functional system should not impinge on the functional or struc-tural integrity of others (Riedl, 1975; Raff, 1996). If integration were homogeneously per-vasive, then morphological evolution would not occur (Smith, 1996). All parts of a system would be affected in the same way by a modification of one specific component, and this is unlikely to produce viable biological results (Riedl, 1975, 1977; Wagner & Altenberg, 1996).

In order to develop hypotheses about the mechanisms of morphological integration it is previously essential to identify and delimit mod-ules (Klingenberg *et al.*, 2003). Once identified, these modules can be traced during their evolu-tion in terms of mutual changes in size, shape, relative position or variability. A coherent picture of identified modules in development and evolu-tion can help to establish hypotheses about the morphological units of change, which is interest-ing for example in the search for morphological characters or traits (Lieberman, 1999; Laubichler & Wagner, 2000). This is why the study of mod-ularity and integration is important in paleoan-thropology, a science that is essentially based on the morphological study of fossils.

Morphological integration and modularity are related concepts because within a hierarchi-cal, and nested system (Fig. 3), both ideas dif-fer only with respect to the complexity level at which an observation is carried out. What at a given complexity level appears as a single module (morphologically integrated unit), in fact repre-sents multiple modules seen from the next lower complexity level (Fig. 3a). This complexity-level

relativity of units is expressed in the hierarchical nature of morphological integration and modu-larity (Strait, 2001; Bastir & Rosas, 2005).

With respect to the evolution of the modern human skull a theoretical fundament such as the systems-approach to craniofacial variation is as important as a biological one, such as craniofacial biology. To bring both fields together can provide a framework for improved hypothesis-generation in the study of human craniofacial evolution.

Craniofacial biology

Modern craniofacial biology is by defini-tion a multidisciplinary field (Carlson, 1985, 2005). Several fields of research can be synthe-sized into a theoretical framework of human craniofacial development and evolution: com-parative anatomy and embryology (Dabelow, 1929, 1931; Kummer, 1952a, b; Starck, 1952; Starck & Kummer, 1962), experimental anat-omy (Moss, 1958; Moore, 1959; Moss & Young, 1960; Moss, 1962), primatology (Hofer, 1952; Biegert, 1957; Hofer, 1957, 1960; Biegert, 1963; Hofer & Spatz, 1963; Hofer & Tigges, 1963), evolutionary biology (Riedl, 1975; Gould, 1977; Riedl, 1977; Alberch, 1985, Cheverud, 1982; Shea, 1985; Müller, 2007), orthodontics and clinics (Björk, 1951; Enlow, 1966; Enlow, 1968; Enlow *et al.*, 1969; Moss & Salentijn, 1969a, b, 1971; Björk, 1972; Richtsmeier *et al.*, 2006), theoretical (Riedl, 1975, 1981; Wagner, 1996) and methodological (morphometric) improve-ments (Rohlf & Slice, 1990; Bookstein, 1991, 1996; O'Higgins & Jones, 1998; O'Higgins, 2000; Mitteroecker & Bookstein, 2007). This intellectual fusion has recently been overviewed and schematized (Bastir, 2004).

In the centre of many of these, particularly anatomically oriented sciences has been the inter-est for the morphology of the human basicra-nium, particularly the basicranial flexure and the way how flexure relates to the morphology of the brain and the face. It has always been assumed that brain increase is most relevant for under-standing variation of basicranial flexure [recent
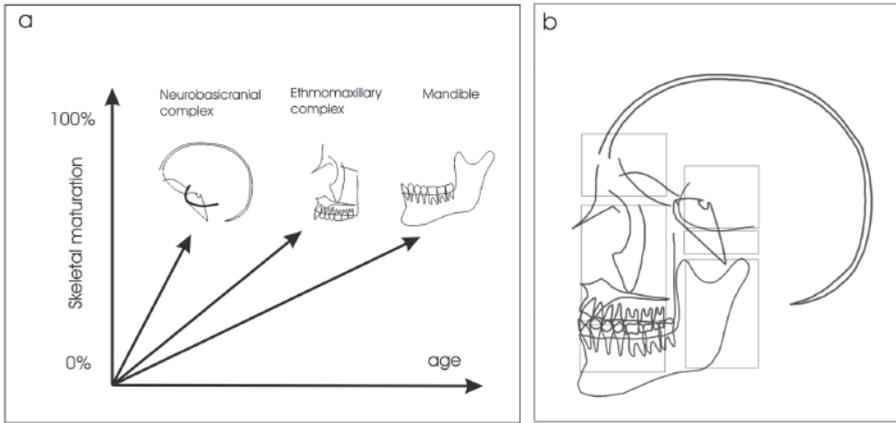
review in Lieberman *et al.,* (2000b)] although the mechanisms of this effect are still under investigation (Ross & Henneberg, 1995; Strait, 1999; Jeffery & Spoor, 2002; Jeffery, 2003; Ross *et al.*, 2004; Jeffery, 2005). While from an evolutionary point of view relative brain size is integrated with basicranial flexure (Lieberman at el., 2000b), ontogenetic studies have shown that the underlying process is not the same (Jeffery & Spoor, 2002). This is a clear example illustrating the key importance of distinguishing between different levels of integration discussed before.

However, as a matter of fact, human basicranial flexure between the anterior and the posterior cranial base approximates spatially the facial skeleton and the cranial base in a way that the face comes to lie below the anterior cranial base. Thus, whatever factors cause the cranial base to flex, play also a role in the size, shape and position of the facial skeleton. This spatial re-arrangement has led to recognition of "the plan of the human face", the rationale of Enlows school of craniofacial biology (Enlow, 1968, 1990; Enlow & Hans, 1996), increasingly referred to in modern paleoanthropology (Shea, 1985; Bromage, 1992; Ross & Ravosa, 1993; Ross & Henneberg, 1995; Lieberman, 1998; McCollum, 1999; Lieberman *et al.,* 2000a; Lieberman *et al.,* 2000b; McCarthy, 2001; Rosas, 2001; Strait, 2001; Bastir & Rosas, 2004b; Bastir *et al.*, 2004; Lieberman *et al.*, 2004; Bastir & Rosas, 2005, 2006; Bastir *et al.*, 2007c, 2008). This increasing attractiveness derives from the fact that Enlow has designed a very intuitive picture of human craniofacial growth and development which is based on structural regularities. These regularities relate ontogenetic development with adult variation and evolution and can thus be used to address morphological problems in human evolution. In addition, they provide an interesting basis for the assessment of different levels of integration at the individual and population levels.

Enlows counterpart principles (Enlow *et al.,* 1969) assume a structural framework, in which each of Moss functional matrices (functional spaces, volumes, eye, ear and nasal capsules) (Moss & Young, 1960; Moss, 1962, 1997c, d) are integrated and arranged spatially, to give

rise to a morphological whole, the skull (holon). According to Enlows counterpart principles, the cranial base sets structural limits for the spatial - and thus morphological - development of facial elements. Enlow assumes that the morphology of the basicranium is moulded importantly by the development and evolution of the brain lobes. A developmental sequence of morphological maturation implies that relatively early, once the brain and the basicranium have ceased growth, a structural (i.e. spatial) basis is set up, on which facial structures are suspended during their remaining development (Fig. 4a). And because the brain and the basicranium mature morphologically before the facial skeleton, the development of the face is "constrained" structurally by the spatial conditions of the basicranium (Cheverud, 1996). Such a constraint has a "causal" connotation as it determines (causes morphologically) to some degree the morphological development of the attached structures (but see Alberch, 1985). Ontogenetic and evolutionary changes of the brain and the basicranium are assumed to cause indirectly changes in facial morphology because of morphological integration in the sense of Smith (1996).

In this line of reasoning, Enlow (1990) suggested that the frontal lobes and olfactory bulbs of the brain correspond to the anterior cranial fossa, which sets the limit for the ethmo-maxillary complex (containing capsules such as the eyes, and the nasal cavity) and the mandibular corpus (part of the oral functional space). These growth counterparts are integrated within what could be called "anterior craniofacial column". In turn, the temporal lobes mould the lateral parts, the middle cranial fossa (posterior cranial base), which correspond spatially to the length of the pharyngeal structures (spaces) and the breadth of the mandibular ramus, called here "posterior craniofacial column". The anterior and the posterior craniofacial columns are delimited by a structural boundary, the posterior maxillary (PM-) plane, defined mainly by the anterior limit of the middle cranial fossae (sphenoethmoid (SE)-point) and the back of the maxillary tuberosity (Enlow *et al.,* 1969; Enlow, 1990; McCarthy & Lieberman, 2001). The spatial relationships of these modules (growth counterparts)

Fig. 4 - a) Temporal sequence of skeletal maturation suggested by Enlow (1990). The neurocranium matures morphologically together with the maturing brain. This is also true for the midline cranial base. The face matures later, together with the somatic systems. Therefore it has been suggested that the brain-driven cranial base morphology constrains the spatial development of the attached face. b) Details of spatial correspondence of the counterpart principles. Anterior and posterior craniofacial columns are separated by the posterior maxillary (PM-) plane. These columns were suggested to comprise and organize spatially the arrangement of growth counterparts (modules; indicated as grey boxes). The spatial dimensions of growth counterparts correspond among each other.

are depicted in Figure 4b. The underlying ideas have been used extensively to explain facial variations in human populations as well as in clinics (Enlow *et al.,* 1969; Enlow *et al.*, 1971; Enlow & McNamara, 1973; Enlow *et al.*, 1982; Bhat & Enlow, 1985). However, they have also led to some problems in research of craniofacial development and evolution, which are intimately related to modularity and integration (Lieberman *et al.,* 2000a; Bookstein *et al.*, 2003; Bastir & Rosas, 2004a; Bastir *et al.,* 2007c) and will be reviewed in the following section of the text.

Morphological integration and modularity in the human face

Studies on facial integration were among the first that have been undertaken (Cheverud, 1982; Richtsmeier *et al.*, 1993; Richtsmeier & Walker, 1993; Cheverud, 1995; Ackermann, 2002, 2005; O'Higgins *et al.*, 2006; Polanski & Franciscus, 2006). However, most of research on facial integration has concentrated on non-human primates.

Less work has been done investigating integration in the hominin face (Cheverud *et al.,* 1992; McCollum, 1999; Rosas, 2001; Bastir & Rosas, 2004a, b; Ackermann, 2005; Bastir *et al.*, 2005).

One interesting and important feature of morphological integration concerns the relationship between maxilla and mandible within what Enlow had called "head form" patterns. What are head form patterns?

Anthropology has a long history of "classifying" craniofacial morphology into categories such as dolichocephalics (narrow skulls), and brachycephalics (rounded skulls). However, clinical observations led Enlow and collaborators to add an interesting developmental dimension to old-fashioned typology and classifications in anthropology (Enlow & McNamara, 1973; Enlow *et al.,* 1982). On the basis of the counterpart principles an integrated suite of craniofacial characters has been associated with head form patterns. Rounded braincases, strongly flexed cranial bases, broad faces with highly angled mandibles with vertically short anterior facial heights were suggested to form a suite of brachycephalic,

and -facial morphological features. These features are opposed to the dolichocephalic suite of elongated, narrow braincases, weakly flexed cranial bases, narrow faces with open angled mandibles and increased anterior facial heights.

However, empirical studies, which addressed these hypotheses in terms of integration detected integration of many, but not all of the mentioned features (Lieberman *et al.,* 2000a; Bastir *et al.*, 2002; Rosas *et al.*, 2002; Zollikofer & Ponce de León, 2002; Bookstein *et al.,* 2003; Bastir & Rosas, 2004a). Importantly, basicranial flexure did not correlate with facial patterns (Lieberman *et al.,* 2000a). In fact, basicranial flexure showed even the opposite pattern, being highly flexed in the long face patterns and weakly flexed in the short face patterns (Bookstein *et al.,* 2003; Bastir & Rosas, 2004a, 2006). In turn, the mandible and the maxilla showed high integration where longer anterior upper and midfaces were associated with open angled mandibles with higher symphyses (Bastir & Rosas, 2004a; Bastir *et al.,* 2005). Interestingly, these features were identified as cranial, locally delimited integrative features, because they are independent on allometric growth changes that affect other features of craniofacial (and post-cranial body) variation (Bastir & Rosas, 2004). These local integration effects were detected not only in lateral, but also in medio-lateral dimensions of the skull. A recent study addressed these questions combining lateral and frontal radiographs and found that increased nasal breadth and maxillary dental arcades are correlated strongly with increased mandibular dental arcade width (Bastir *et al.,* 2007c). These integration patterns were not surprising and are well compatible with Enlows head form patterns. Yet, it was found that not all long faces were narrow and not all short faces broad, while whenever basion was in an anterior position increased facial breadth was observed. In addition, very little variation was found in basicranial flexure. This suggests that not basicranial flexure, but rather overall basicranial orientation is important in the context of Enlows head form patterns (Kuroe *et al.*, 2004). In fact, Enlow (1968) mostly referred to basicranial orientation within its craniofacial context.

However, apparently the basicranial angle is such a straightforward, well implemented and classical measurement in anthropology (Lieberman & McCarthy, 1999; Bastir, 2004) that little attention has been paid to a careful distinction between basicranial flexure and basicranial overall orientation (Rosas *et al.*, 2008a). This is also compatible with Lieberman *et al.*'s (2000a) findings that reported a lack of correlations between facial patterns and basicranial flexure. Also, while Enlows gross concept suggested that these patterns are generally independent from sexual dimorphism, a recent study found -at least- in a Japanese population a clear sexual dimorphic signal in these integrative patterns (Bastir *et al.,* 2007c).

Given the broad range of potential consequences for skull variability, it is not surprising that head form patterns are increasingly appreciated for the understanding of variation in the human fossil record (Rosas *et al.,* 2002; Bastir *et al.,* 2005; Gunz & Harvati, 2006; Rosas *et al.*, 2006b, 2008b). What is more surprising is the fact that the underlying developmental causes are still far from being clear. Facial morphology associated with head form patterns has been related to several factors such as climatic (Nicholson & Harvati, 2007), geographic-genetic (Rosas *et al.*, 2006b) and intra-population aspects (Bastir & Rosas, 2004). This may suggest that several and different (!) causes may lead to similar, possibly developmentally canalized, variation patterns (Bastir *et al.*, 2005; Mitteroecker & Bookstein, 2008). Clearly, more research is necessary to understand facial integration and its complex relations with sexual dimorphism, and head form variations. Also investigation on 3D data covering more spatial aspects of geographic variation and covariation between endocranial and exocranial data is necessary.

Integration and modularity in the posterior craniofacial column

In the latest review on basicranial interactions with facial morphology Lieberman, Ross and Ravosa have asked: "What are the actual

units in the cranial base and skull […] (p.160) (Lieberman *et al.,* 2000b)? It seems that Enlows counterpart model, translated into a 3D perspective, gives some potential answers. In a series of papers we followed the principle of: 1) identifying modules (Bastir *et al.,* 2004); 2) testing for modularity (Bastir & Rosas, 2005); 3) tracing the size, shape, position and variability of these modules during development (Bastir *et al.,* 2006) and 4) evolution (Bastir *et al.*, 2007b; Bastir & Rosas, 2008; Bastir *et al.,* 2008). In these studies it could be shown that midline basicranial elements show different variability patterns than lateral ones. This basicranial modularity is interesting in several respects: 1) the discussion about constraints on basicranial flexure; 2) the relationship between encephalization and mandibular morphology; and 3) the relationship between encephalization and facial position.

During a series of papers Ross and collaborators have addressed the evolution of the cranial base and its relationship to facial orientation (Ross & Ravosa, 1993; Ross & Henneberg, 1995; Ross *et al.,* 2004). As a particularly interesting result was the speculation about possible constraints on basicranial flexure (Ross & Henneberg, 1995), which was grounded on the observation that basicranial flexure between the pre-sphenoid plane and the spheno-occipital clivus was never observed below 90 degrees. In addition, humans had less flexed basicrania than predicted on the basis of their relative endocranial capacity (a proxy for brain size). The authors referred to functional arguments that possible constraints on flexure could avoid a problem of airway obstruction. In follow up studies it was disputed whether or not basicranial flexure is constrained (Spoor, 1997; Strait, 1999; McCarthy, 2001) until finally it has been concluded that "currently it cannot be determined whether or not basicranial flexure is constrained" (Ross *et al.,* 2004). Still, this latest analysis using a very broad comparative and ontogenetic dataset supports the well established idea that basicranial flexure is highly correlated evolutionarily with increase of brain size relative to basicranial length and that variation in flexure below 90 degrees has not been observed so far.

Now an interesting observation is that modern humans show values for basicranial flexures already present in other hominids, Australopithecines (Sts 5), *H. erectus* (Sambungmacan 4), *H. heidelbergensis* (Bodo) (Conroy *et al.*, 1978; Ross & Henneberg, 1995; Baba *et al.*, 2003) yet modern humans are quite more encephalized than these fossils (Kappelman, 1996; Ruff *et al.*, 1997; Rightmire, 2004). How must the cranial base then become modified morphologically for such encephalization to occur? Potential answers have been provided early in anthropology, although not in the context of integration and modularity. Dabelow (1931) and Biegert (1957) suggested downward deflection of the orbits and of the lateral base, but how is this compatible with the observed stabilized (if not constrained) evolution of the midline basicranial flexure? This question was addressed looking at the modularity of the lateral base and posterior face (Bastir *et al.,* 2004; Bastir & Rosas, 2005). If the basicranial angle is constant since the australopithecines, then alternative developmental mechanisms should be available for orbital or lateral base deflection as suggested by Dabelow (1931), and Biegert (1957) in order to further accommodating volumetric increase in brain lobes. One possible mechanism could be a dissociation of midline and lateral basicranial elements, which was detected looking at factors that influence mandibular ramus breadth (Bastir *et al,.* 2004). These authors observed that variation in the orientation of the petrosals from postero-superior to antero-inferior relative to the PM-plane was associated with variation in mandibular ramus breadth, while variation in midline basicranial structures was much smaller and apparently unrelated. This observation suggested that some midline basicranial elements might be characterized by different variation patterns as lateral basicranial parts, a hypothesis which has been confirmed in modern humans (Bastir & Rosas, 2005). This conclusion is compatible with a very recent analysis of Bruner and Ripani (2008) who suggest low levels of integration among basicranial elements.

Addressing potential developmental underpinnings of these dissociations, in a following step the developmental maturation patterns of midline and lateral basicranial elements were addressed testing Enlows (1990) hypothesis of craniofacial levels, that is, the delayed development of facial versus basicranial structures (Buschang *et al.*, 1983; Bastir *et al.,* 2006). In particular it was shown that indeed there is a maturation gap of four years between the midline cranial base, which attains maturity in shape around 8 years and the lateral base, which attains shape maturity around 12 years (Bastir *et al.,* 2006) (Fig. 5a). This suggests that modules are characterized by their own spatio-temporal ontogenetic structure. However, whether this dissociation is unique for the genus *Homo* needs to be tested. While preliminary analysis (unpublished data) on limited samples in chimpanzees and gorillas cannot reject the hypothesis of developmental dissociation between midline and lateral basicranial elements, this does not contradict a hypothesis of basicranial dissociation midline-lateral basicranial elements in hominids. Future study and more data on fossils may clarify these issues.
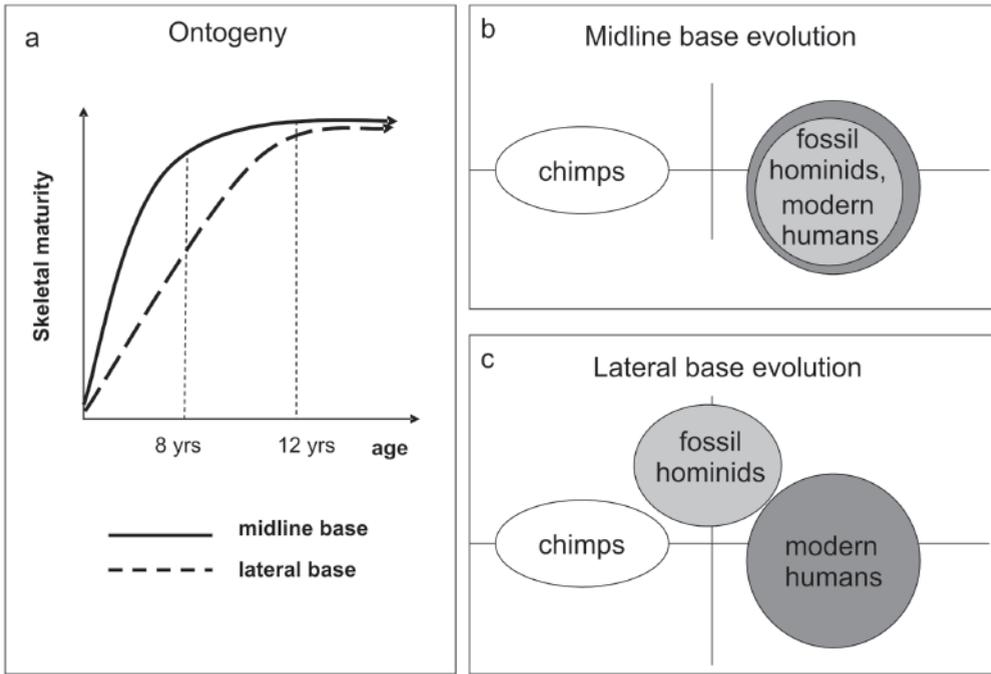
Finally, and consistently with the suggested sequence of analysis, identifying and delimiting modules, and studying their development and evolution, the question of independent basicranial evolution of midline and lateral elements has been addressed. The data suggest that while morphological evolution of midline basicranial morphology is very subtle (Bastir & Rosas, 2008) (Fig. 5b) evolutionary shape differences at the lateral base are much more pronounced (Fig. 5c) (Bastir *et al.,* 2008). In particular, it could be shown that the anterior poles of the lateral middle cranial fossae (MCF) of modern humans are uniquely projecting forwards, with respect to central parts of the MCF. Possible factors could be either specific expansion of parietal lobes (Bruner *et al.*, 2003; Bruner, 2004) acting on the temporal lobe position, or of the temporal lobes themselves (Semendeferi & Damasio, 2000; Rilling & Seligman, 2002; Rilling, 2006). It can be speculated that this forward expansion might have led to basicranial "invasion" of areas

previously occupied in space by posterior parts of the ethmo-maxillary complex. If true then this factor was likely involved in facial reduction at the posterior part of the face. In modern humans there is no doubt that this position of the anterior poles of the middle cranial fossae sets the posterior limit of the ethmo-maxillary complex.

It remains to be tested in fossils whether lateral basicranial modifications are responsible for known differences in mandibular ramus shape caused by changes within the petroso-mandibular unit (Bastir *et al.,* 2004). If so, then encephalisation of the temporal lobes and their effects on middle cranial fossa size, shape and position could have influence on both, anterior and posterior facial morphology in development and evolution. For example, such a mechanism could be involved in evolutionary changes of mandibular ramus morphology and the trend towards ramus breadth reduction (Rosas, 1997; Rosas & Bermudez de Castro, 1998; Rosas, 2001; Bastir *et al.,* 2002, 2004, 2007a).

However, two "directions" of morphological influence have been discussed, that is: from the base towards the face and from the face towards the base. On the one hand it is well known that that during embryogenesis brain tissue differentiates into basicranial cartilages which ossify into the bony basicranium (Sperber, 1989). Also it has been shown that ontogenetic maturation is oriented basically in a top-down morphological gradient (Buschang *et al.,* 1998; Bastir *et al.,* 2006). During evolution early differentiation of larger brain masses might have modified the lateral basicranium and in consequence led to a lower petrosal and a narrower mandibular ramus morphology (Bastir *et al.,* 2004, Rosas *et al.* 2006b).

On the other hand, it has been suggested in a more functional context that the interaction may be likewise driven by the mandible. Strong functional selection on the masticatory system might have effects acting on basicranial and neural structures (Bruner, 2007; Bruner, pers comm.). Not only at the evolutionary level, but also from an ontogenetic point of view such effects are possible. Skeletal maturation at the lateral floor does not terminate before puberty (Bastir *et al.,*

Fig. 5 - Development and evolution of the midline and lateral base. a) temporal dissociation of midline and lateral development. Midline base achieves adult shape at 8 years, lateral base around 12 years (Bastir et al., 2006). B) schematic representation of shape evolution of the midline base (Bastir & Rosas, 2008). Humans and hominids overlap and plot separately from chimpanzees. C) lateral base shows a different evolutionary pattern. Humans plot differently from hominids and chimpanzees (Bastir et al., 2008).

2006), which implies potential for mutual morphological adjustments between the base and the face. While both models might apply, it is a clear case, in which a systems approach can contribute to order different scopes of analysis (top-down versus bottom-up) (Fig. 3). This discussion also highlights the importance of clear distinction between different levels of developmental and evolutionary integration as mentioned earlier (Cheverud, 1996; Strait, 2001).

Research on the evolution and development of the posterior base and face in modern humans provides an exciting example in which the analysis of modularity and integration sheds light on evolutionary principles related to encephalisation and emergence of modern skull morphology. In the light of the systems model such basicranial changes would represent clearly local (cranial) factors in the evolution of modern human craniofacial morphology.

Integration and modularity in the anterior craniofacial column

Enlows counterparts suggest that the morphology of the anterior cranial fossa and the frontal lobes set the spatial limits of the anterior face (maxilla, mandibular corpus). Additionally, Enlow and Azuma (1975) suggested further stable (invariant) angular relations between some facial planes: the PM-plane with the orbits and the cribriform plate with the anterior facial plane. In non-human primates and some hominid

fossils these and other angular relations have been addressed by several researchers (Bromage, 1992; Ravosa & Shea, 1994; Lieberman *et al.,* 2000b; McCarthy & Lieberman, 2001) but only some suggested angular constraints have been supported (see Ravosa & Shea, 1994).

McCarthy and Lieberman (2001) have coined the term "facial block" to express a highly constant 90º angular relation between the PM-plane and orbital orientation in anthropoids. Since these angles are constant the morphological structures they describe have been interpreted as highly integrated. Because the roof of the orbits is the floor of the anterior cranial fossa (ACF), any modification of ACF morphology is expected to have impact on facial morphology. In human evolution the facial block was used to explain changes in facial projection. It has been suggested that upward rotation of the facial block with respect to the posterior base would increase facial projection, while downward rotation would decrease it (Lieberman *et al.,* 2000b; McCarthy, 2001). This perspective supports Biegerts (1957) suggestion of orbital deflections. However, one problem remains: facial rotation seems not sufficient, because it would imply upwards- or downwards rotation of the orbits, which in humans are likely in a fixed, physiologically meaningful, horizontal position [termed "neutral orbital axis" (Ross & Ravosa, 1993)]. In addition, it has been convincingly argued that there is no "rotation" of anterior and posterior basicranial elements (McCarthy, 2001). Also geometric morphometrics of the basicranium indicate that rotation is likely an intellectual artefact, derived from the use of angular measurements. Rather, the spatial position of basicranial elements varies in different ways, involving also -but not only- changes of their angular relations (Bookstein *et al.,* 2003; Bastir *et al., 2004, 2006*). In a similar way it is likely that angular and other spatial modifications (e.g. shifts) lead to repositioning of the facial block. In hominids it seems reasonable to assume a relatively stable facial position with horizontally orientated eyes and a vertically orientated PM-plane (Enlow, 1968; Enlow & Azuma, 1975; Enlow, 1990). Posterior to the

facial block, spatial modifications occur at the cranial base and they likely involve angular and other, complex, spatial modifications (see later).

One such mechanism was suggested by Lieberman (1998). Evolutionary changes of the anterior sphenoid length were thought to influence facial projection in human evolution. His suggestion was based on comparative ontogenetic data in humans and chimpanzees, in which increase in sphenoid length was accompanied by increase in facial projection (Lieberman, 1998). It would have been a strong example for integration of purely cranial factors *sensu* Smith (1996) but a follow up study on CT data, which permitted better identification of anatomical structures than using lateral radiographs did not support that mechanism (Spoor *et al.,* 1999). What factors could then account for evolution of facial projection or facial reduction?

In the light of the systems model, a different kind of answers could be sought, which require changing from cranial to non-cranial points of view. For example, the size of the nasal cavity is physiologically related to the size of the body (Hall, 2005) and the lungs (Chinn *et al.*, 2006). Nasal cavity and lungs are functionally integrated into the respiratory system, which is represented cranially by the proportions of the nasal cavity, but non-cranially by the size and shape of the lungs and thorax (Churchill, 2006). It has been suggested that for metabolic reasons, facial sexual dimorphism is attributable largely to sexual differences in airway proportions (Enlow & Hans, 1996). Males of the same overall size as females have relatively larger nasal cavities, which has been identified as a clearly discernible feature of craniofacial sexual dimorphism (Rosas & Bastir, 2002). In addition, it was shown that relative nasal expansion in males was also accompanied by morphological features related to muscle insertions. This coincidence of features was interpreted as morphological reflection of the fact that in humans the whole metabolic system is functionally, sexually dimorphic. Sex-differences in body composition (higher proportions of skeletal muscle mass versus fat in males) require higher oxygen intake and thus relatively more airway space. Physiological

studies support this morphological interpretation (Hall, 2005; Chinn *et al.,* 2006).

Following the systems approach, it can be expected that facial changes in human evolution are probably also influenced by similar factors (Bastir, 2004; Rosas *et al.*, 2006a, Churchill, 2006). Semi-autonomy (modularity) of the anterior face implies that changes in facial size and shape (upper- or midfacial projection) need not be driven exclusively by anterior basicranial factors (Enlow, 1990; Lieberman, 1998; Spoor *et al.,* 1999). Instead, in addition to the possible influence of frontal lobe and anterior cranial base morphology implied by the counterpart principles, forward projection of the upper and midface may be importantly ruled by non-cranial factors. From a non-explicative but descriptive point of view, scaling studies that show stronger correlations between facial elements and body size than between body size and basi- or neurocranial elements can be interpreted in these terms as well (Biegert, 1957; Emerson, 1993; Strait, 1999; Bastir, 2004; Rosas *et al.,* 2006a).

In a similar context it is interesting to see how variation in facial size and allometric scaling relates to species-specific differences in facial morphology between Neanderthals and modern humans (Bastir *et al.,* 2007a). It has been shown that the mandibular part anterior and superior to the mandibular nerve displays allometric shape variation, which is absent in the basal part of the mandible (Rosas & Bastir, 2004). These authors have shown that shape variation implies potential for the formation of a retromolar space (Franciscus & Trinkaus, 1995) in great apes and several hominid species. It is also known that facial size differs in Neanderthals and modern humans (Trinkaus, 2003). So if facial size is linked to differences in body mass then it is possible that non-cranial factors related to body size find their expression in facial/mandibular morphological characters via scaling effects.

Another, non-cranial factor of craniofacial variation might be related to bone thickness. Lieberman (1996) has convincingly shown on experimental data of physically active versus inactive pigs that for systemic (hormonal) reasons (Vogl *et al.*, 1993), activity patterns influence morphological features such as cranial vault thickness. Visual inspection of axial cranial sections in hominids suggests that the thickness of the basicranial bones at the greater sphenoid wings may not be unimportant for craniofacial morphology because thick cranial vaults shift any face of a given size into a more anterior position. This hypothesis requires more research but it is particularly interesting to see how evolution of activity and energetic patterns would link hormonal factors with energetic ones, both clearly allocated by the systems model to non-cranial and potentially highly important factors for the understanding of the evolution and development of the human craniofacial system.

Closing remarks and perspectives

At the beginning of this review two questions have been asked: Can facial reduction be explained as a structural consequence of encephalisation and/or basicranial modification? Or is facial reduction a simultaneous but independent trend in human evolution?

This paper has aimed to address these questions in the light of a theoretical systems model of craniofacial evolution and development. It has provided much support for the view that both questions are not mutually exclusive, but rather complementary in order to draw a realistic picture of trends in human evolution.

The human skull is highly modular. Some modules are integrated by local cranial factors such as purely spatial proximity, or by other factors such as the functional matrix principles linking aspects of brain and basicranial morphology (Enlow, 1990; Moss, 1997a, b; Lieberman *et al.,* 2000a; Bruner, 2004; Richtsmeier *et al.,* 2006). Human cranial sphericity (Lieberman *et al.,* 2000a; Zollikofer & Ponce de León, 2002) is probably influenced by such interactions and some features like mandibular ramus breadth (Bastir *et al.,* 2004), facial heights (Bastir & Rosas, 2004a) and widths (Bastir *et al.,* 2007c) are integrated parts of these local factors. The lateral basicranium is also

important for local cranial integration because the spatial relations of anterior and middle cranial fossae set also the posterior and superior limit of the face (Bastir *et al.,* 2008).

However, evidence suggests that particularly with respect to the evolution of the ethmo-maxillary complex and the mandible possibly additional, non-cranial factors need to be considered as well. One possible example of such factors could be the evolution and development of the nasal cavity as a functionally integrated -cranial- part of the respiratory system (Hall, 2005; Chinn *et al.,* 2006; Weinstein, 2008). Coordinated evolution of the respiratory system (Churchill, 2006) and body size is likely a factor that interferes with facial evolution (Biegert, 1957). Another factor -not unrelated to evolution of the respiratory system- regards energetics, activity patterns and their effects of the skeletal system as a whole (Vogl *et al.,* 1993; Lieberman, 1996; Churchill, 2006). Such factors likely find their metric reflection in the positive facial scaling trend with respect to body size.

This implies that craniofacial trends the evolution of modern humans should be not exclusively be restricted *a priori* to basicranial factors and the brain, but underlines that the evolution of size and shape, and energetics of the biology of the entire body is equally important. A systems approach highlights the need for consideration of the human organism in order to advance in problems of human craniofacial evolution. This could be considered a major conclusion of this review. Future research should expand on these principles.

Acknowledgements

Info on the web

http://www.rupertriedl.at/
   Rupert Riedl, and his research in evolution, morphology, and theory

http://www.bertalanffy.org/
   The founder of systems theory

http://www.univie.ac.at/theoretical/research4.html
   A leading group in research in development and evolution

http://www.mncn.csic.es/investigacion.php?cat=4
   Department of Paleobiology, Museo Nacional de Ciencias Naturales

http://www.evan.at/Members/mbastir
   Markus Bastir's home page

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