

Variations in skull base morphology during phylogenesis and different hypotheses

F. de Brondeau

University Lecturer - Hospital Specialist Practitioner – University of Bordeaux

ABSTRACT

The relationships between the craniofacial structures at the base of the skull are modified during ontogenesis and phylogenesis. The scientific community is in agreement regarding the major role that the skull base has in the hominization and the etiopathology of maxillofacial dysmorphia.

Comparing ancient fossils to current populations, the origin and interpretations of the various skull base morphologies, more specifically the sphenoidal angle, are complicated. Therefore, different hypotheses are advanced. Most compare them to the larger characteristics of human evolution. In this article, they are presented as to how each author developed their respective hypotheses.

The knowledge of these hypotheses helps in the comprehension of the evolutionary mechanisms of basal craniofacial configurations of modern man.

KEY WORDS

Skull base, phylogenesis, variation

INTRODUCTION

The skull base figure is the major element in the context of hominization. During ontogeny and phylogeny, basal craniofacial relations are modified. In modern humans, the origin of these changes, both at the skull base and facial levels, remain unclear. The scientific community agrees on the major role of the skull base in hominization, and on the etiopathogenesis of maxillofacial dysmorphia.

The skull base reflects determinism (it is derived from endochordal precursors whose shapes are known to be dependent on

genetic factors); it constitutes the first part of the skeleton to reach maturity (Moore and Lavelle⁴⁶) and it finally plays an important role in shaping the face. Lieberman et al.⁴¹ demonstrate the existence of multiple, complex interactions between the skull base, the brain, and the face, and emphasize the difficulty of knowing the ontogenetic mechanisms that govern skull base flexion and its relationship to the face. Penin et al.⁵², Jeferry³³, Bastir et al.⁵ stress the importance of the rhythm and timing of growth in different parts of the skull base and its connection

Address for correspondence:

François de Brondeau – UFR des sciences odontologiques
Université de Bordeaux – 16 cours de la Marne
33082 Bordeaux Cedex
E-mail: fdb33@aol.com

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arrangements with the face. Thus, facial growth is dependent on genetic, epigenetic, and functional factors.

The interactions that lead to the current concept of the role of the skull base on facial morphology remain subject to much controversy.

Because of its embryogenesis and ontogenesis, the skull base appears as a true “pivot” (Hoyte³²) on which the sphenoid bone occupies a central position. The latter, in various craniometric and cephalometric studies, presents correlations with the anteroposterior facial skeletal discrepancy.

In anthropology, these mechanisms between skull base and facial morphology, as well as the implementation method of a specific architecture for each population, remain subject to numerous hypotheses.

Therefore, the interpretation of variations in skull base morphology, and more particularly in the sphenoidal angle, is difficult. Most studies not only involve major characteristics of human evolution, such as brain development, postural changes, facial

verticalization, but also morphogenetic factors, such as genome mutation or the influence of soft tissues, with the fundamental role of masticatory forces.

Yet most often, these hypotheses overlap and are difficult to classify.

For analysis purposes, we will present them according to the primary factor that they each highlight chronologically, according to the authors, along with their differences.

As such, for Strait⁶⁷, most hypotheses are so-called “structural” in nature, meaning that any change of the skull base skeleton during evolution is the result of an alteration in another anatomical region.

Other hypotheses are “functional,” connecting all morphological variation of the skull base to a change in behavior or function. But at present, most authors agree on an interactive role among the different structural and functional factors. Indeed, skull base characteristics can be correlated with one or more structural or functional phenomena (Strait⁶⁷).

VARIATIONS IN THE EVOLUTION OF BASAL CRANIOFACIAL RELATION: PHYLOGENETIC HYPOTHESES

Brain development hypotheses

- Hypotheses correlating the skull base shape to brain size are among the oldest. Papillaut⁵¹, Bolk⁹, Anthony², Beauvieux⁷, Ashton, and Zuckerman³ had argued that the development of the frontal and parietal lobes caused development of the skull in the three dimensions of space, followed by the rise of the skull, frontal remodeling, and its backward and downward development. This posterior coiling, whose center is located in the sella turcica region, could be the origin of the stop of the rear portion of the cerebral mass against the occipital bone and the clivus, causing the skull base flexion.
- Beauvieux⁷ already stressed the “hinge” role of the spheno-occipital synchondrosis, which enables the

lowering of the basal occipital portion relative to the basal sphenoid portion.

- If the authors agree on the fundamental constraint of the brain on the shape of the skull base, the debate remains open regarding the mechanisms involved, notably the impact of brain development on the anterior portion of the skull base.

For some, it is the development of the anterior part of the frontal lobe that impacts ethmoidal evolution.

- In 1965, Olivier⁵⁰ already highlighted one of the essential elements of contradiction in this encephalic hypothesis for skull base flexion. Indeed, the posterior development of the brain exists already in primates and the sphenoid angle opens, whereas in humans it is subject to ontogenetic closure.
- For Gould³¹, in 1966, the combination of increase in the brain's relative size and the decreased length of the skull base (*spatial-packing hypothesis*) would be the most important factor of skull base flexion in modern humans.
- However, Ross and Ravosa⁵⁸ and Spoor⁶⁵ only sustain this hypothesis for nonhuman primates.
- For Moss⁴⁷, Dean¹², and Strait⁶⁶, according to the aforementioned so-called *spatial-packing hypothesis*, a more flexed skull base is a way to increase the volume of the cerebral lodging for a given skull base length.
- The works of Ross and Henneberg⁵⁶ have demonstrated that in modern man, skull base flexion and brain size relative to skull base length are not significantly correlated, but are rather related to the orientation of the face.
- For Spoor⁶⁵, humanization results in skull base flexing associated with increased brain size. However, if the

brain is to influence skull base morphology, the initial stage will affect skull base flexion by accentuating it.

- For Lieberman et al.⁴¹, the impact of cerebral development in modern man would occur on its width which, on a narrow skull base, would result in projection of the posterior occipital bone. In his opinion, the main factor is the greatest width of the skull base (which affects the entire neural skull base complex), which would be accompanied by narrower, longer faces in the anteroposterior dimension.
- Strait⁶⁶ considers that, if skull base flexion could be an adaptation to accommodate the relative size of the brain to the length of the skull base, the reason for this adaptive phenomenon is not related to the reduction of the skull base length. In his study, Strait⁶⁶ shows that the latter is inversely proportional to the development of the diencephalon, mesencephalon, and myelencephalon. He concludes that the development of these brain components could be responsible for the development of the skull base flexion.
- McCarthy⁴⁵ was interested in these cephalic hypotheses, which were based on two studies (Ross and Henneberg⁵⁶, Spoor⁶⁵). Both studies agreed on the fact that the skull base flexion degree is linked to the relative volume of the brain and the length of the skull base.
- Thus, Spoor⁶⁵ contradicts the arguments of Ross and Henneberg⁵⁶ using different references: the cephalization index reflects the ethmoidal lamina cribrosa. The results show that among *Homo sapiens*, the skull base is no less flexed than expected for a primate with respect to the relative size of the brain.

McCarthy⁴⁵ insists on the difference in the hypotheses of Ross and Henneberg⁵⁶ and Spoor⁶⁵, whose interest is to raise the question of the origin of the highest skull base flexion in modern humans: is it related exclusively to a large brain or does it result from other factors such as posture or pharyngeal morphology?

The results of the study by McCarthy⁴⁵ indicate that the posterior part of the skull base and sphenoidal plane are significantly shorter in *Homo sapiens* than in apes, as a result of a greater cephalic index.

Therefore, measurements of the skull base flexion and the relative size of the brain allow quantifying skull base architecture in *Homo sapiens* and apes.

- Jeffery³³, in a comparative study of intrauterine skull base growth in nonhuman primates, questions the spatial-packing hypothesis.
- The work of Ross et al.⁵⁷ emphasizes that skull base flexion may be the consequence of the relative increase of brain size, but other factors might influence flexion during postnatal growth as suggested by Jeffery and Spoor³⁵.

Postural hypotheses

- Weidenreich⁷¹, Schultz⁵⁹, Dubrul²⁷ have already demonstrated over the first half of the 20th century the role of posture on skull base configuration. In fact, the skull base, because of its continuity with the vertebral column, is the site of its union with the cephalic skeleton. Thus, the transition to the standing position is accompanied by a ventral "rotation" of the posterior region of the skull base.

- Delattre and Fenart¹⁹ took up the study of mechanical factors (especially standing upright) that changed skull base morphology. They have attempted to link the changes in shape observed in terms of the forces acting on the cephalic region.

For them, the anterior region of the skull base, during body remodeling, either remains fixed or is subject to proportional development. Posture verticalization thus acts only upon the posterior region, causing the displacement of the sphenoid clivus and therefore of the posterior portion of the base toward the front, thereby increasing skull base flexion in the sella turcica area.

This flexion of the skull base allows the development of the brain. As Beauvieux⁷, Delattre and Fenart¹⁹ were able to demonstrate by using the vestibular referential, the essential basis of postural hypothesis is not the plane fixity in relation to the clivus displaced by the standing position, but the skull base flexion that allows the secondary development of the brain.

Although several paleontologists agree with this design showing that the standing position appears before cephalization, discussion of this hypothesis remains valid.

- Bolk⁹, since 1926, supports a postural hypothesis regarding the central development, but does not describe it in the same way. He opposes the theory presented above by showing that at the ontogenic level, skull base flexion exists in the fetuses of primates and all mammals, and therefore cannot be caused by the standing posture.

The standing position is not the cause but instead the consequence of the sphenoid angulation, or more precisely, of the persistence of this angle. The foramen magnum's anterior position is not related to standing position, because it precedes the latter. The vertical remodeling would not be the cause, but rather the consequence, and would prevent the foramen from receding.

It is interesting to note that, to support this notion, Bolk⁹ advances embryological data: the persistence of fetal characters and the slow development of human fetuses. Thus, during ontogenesis in primates, a common position of the foramen magnum is observed in the fetus, but it is displaced backward, in contrast to what is observed in humans.

- Ashton and Zuckerman³, Adams and Moore¹, and Dean and Wood¹⁴ agree with the previous concept. For them, the skull base flexion is an adaptation to the foramen magnum's anterior rotation, which reorients itself ventrally, so as to place the occipital condyles below the head's center of gravity.
- Leroi-Gourhan³⁹ suggests that the change in posture is probably the main factor responsible for the morphogenetic development of the craniofacial skeleton, but also emphasizes the importance of the forces developed by mastication, which would play a vital role in the balance of the cephalic pole.
- The work of Ross and Ravosa⁵⁸ supports the postural hypothesis, by showing that standing primates feature more flexed skull bases than other primates. However, since then, Strait and Ross⁶⁸ have shown

that the study by Ross and Ravosa was missing data and did not enable such a conclusion. In contrast, Strait and Ross⁶⁸ assumed as hypothesis basis that, in order to move from a quadruped primate species to a bipedal species, it was necessary to the field of vision, which secondarily leads to skull base flexion.

The study Strait and Ross is important because it shows that, if the postural hypothesis is confirmed, the postures of the head and neck are not the primary determining factors of flexion.

- According to Spoor⁶⁵, who favors the brain development hypothesis, the postural hypothesis can be retained to understand skull base flexion in hominids. In fact, he was able to find more flexed bases in some species, which should not have led to the relative size of their brains.
- More recently, the study of McCarthy⁴⁵ has taken up the steps of the spatial-packing hypothesis. However, the results lead to support the influence of bipedal posture and pharyngeal dimensions on skull base morphology.

Indeed, one of the most interesting findings of McCarthy⁴⁵ is that the posterior part of the skull base and the sphenoid plane are significantly shorter in *Homo sapiens* than in apes. This ties to the hypotheses by Dean¹², whereby the vertical remodeling and biped posture of *Homo sapiens* require a shorter posterior portion of the skull base and a smaller pre-pituitary region of the sphenoid bone than in other apes.

Facial bone development hypotheses

These hypotheses are among the oldest, and rest upon ontogenic data: in the fetus, the face is smaller and the sphenoidal angle is closed; thereafter, the face develops, resulting in the opening of the sphenoidal angle followed by the projection of foramen magnum toward the rear or ascension of the sphenoidal plane.

Looking at growth in humans, the morphogenesis data is confirmed, as there is a decrease in the sphenoid angle up to the prepubertal period, and eventually increase again along with the development of the face.

In primates, a correlation between the facial angle and the sphenoid angle is found among the different species, resulting in an opening of the skull base angle with closing of the facial angle. It is the development of the face that causes such phenomenon.

- Another factor advanced by advocates of these hypotheses is that the face and skull base share several ossification centers. Thus, an alteration in the architecture of the face may be followed by skull base change.

But as Strait⁶⁷ points out, although many studies have examined the relationship of the face and skull base flexion (Dabelow¹¹; Scott⁶⁰; Enlow^{29,30}; RossetRavosa⁵⁸), the ensuing facial rotation hypotheses remain questionable.

The measurement method described in these studies is in itself a major problem. In fact, the orientation of the face is most often appraised by studying the angle between the palatal plane and the skull base. It is therefore normal

to find correlations between skull base characteristics and facial orientation. For Strait⁶⁷, it is necessary to measure the facial prognathism using a referential that involves no connection with certain features of the skull base.

- Dean and Wood¹³, in inquiring about the similarity in the width and length of the skull base morphology in *Australopithecus robustus* and *Homo sapiens sapiens*, have shown that different facial mechanisms entail the same transformations at the skull base. Their study shows that the rotation of the face below the wide neurocranium in modern man, and the orthognathic face with wide jaws of *Australopithecus robustus*, would have the same implications at the skull base level: a reduction in the sphenoid body and angle.
- Lieberman⁴⁰, in an assay of human fossil radiographs, has shown that the skull base flexion angle is greater on average by 15° in the archaic *Homo sapiens* lineage than in hominids from the Pleistocene and in modern man.

He concludes that this difference, which results in the closure of the sphenoid angle in modern humans, is related to facial retraction and other factors such as the smaller pharynx behind the palate.

Functional or muscle hypotheses

The influence of masticatory forces

- Papillaut⁵¹ already evoked the influence of masticatory forces, and more particularly, of the pterygoid strap on skull base flexion. For him, important masticatory forces, or more exactly the stress generated

by the pterygoid strap, entail sphenoid angle closure.

- Sicher⁶¹, Dubrul²⁸, and Spencer⁶⁴ have identified numerous masticatory variables that may influence skull base characteristics. It would appear from Strait⁶⁷ that the most significant area is the glenoid fossa, whose relative position to the occlusal plane can change the amplitude of occlusal forces and the effectiveness of the masticatory muscles. In contrast, for Ross and Ravosa⁵⁸, the deeper, more pronounced glenoid fossa in anatomically modern man, with a less developed posterior apophysis, would be the consequence of skull base flexion.

The question is whether it is the masticatory forces which, in leading to skull base closure, have changed the configuration of the glenoid fossa, if the cause–effect action is reversed. For Radinsky⁵³ and Demes^{20,21}, skull base flexion can play a role in resisting the constraints imposed by mastication.

Varrela⁶⁹, in a comparative study between a population with a solid-based diet to a population with a more liquid-based diet shows no significant differences in the sphenoid angle.

Influence of ventilation and language

- Scott⁶⁰ hypothesized a connection between the skull base and regression of cones during development, itself linked to better skin temperature regulation.

Thus, would the “remote cause” of skull base flexion be linked to an adaptation of the skin?

- Laitman et al.^{36,37}, in a study of fossil hominids showed that the skull base could be an indicator of their

respiratory system, noting the existence of relations between the exocranial orientation of the skull base and the position of upper respiratory structures. Thus, the effect produced by the descent of the tongue and larynx can be one of the factors responsible for the change in inclination of basal occipital position and the flexion, by changing the inserts of the constrictor muscle system of the pharynx.

- For Lieberman et al.⁴³ and Dean and Wood¹⁴, skull base flexion increase can be linked to a shift in the basal occipital position and attachment of different ligaments and suprahyoid muscles.
- Laitman et al.³⁶ have suggested that significant decreases in the size of the nasopharynx and oropharynx and the oral cavity lead to the skull base flexion.

According to Lieberman et al.⁴³, the combination of an anteroposteriorly short oral cavity and oropharynx, and a situation of low pharynx, enabled the expression of speech.

- Washburn⁷⁰ stressed the role of brain functions, and in particular the acquisition of language, in the expansion of the brain and the cephalic evolution of man.
- Strait⁶⁷ stresses that it is difficult, at present, to test the hypotheses linking the shape of the skull base and speech (Lieberman et al.⁴³; Reidenberg and Laitman⁵⁴), because of the methodological difficulty in evaluating speech.
- Jeffery³⁴, following an ontogenetic study of human fetuses, questions the hypothetical link between the

formation of the upper airways and skull base flexion phenomena during intrauterine life.

Multifactorial hypotheses

Integration hypothesis

Based on the fact that many variables influence the skull base and considering the key role of the latter in craniofacial architecture as a whole, Lieberman et al.⁴² speculate that these so-called variables can affect other aspects of the cranial shape via the skull base structure.

Therefore, they raise the issue of the role of the skull base in craniofacial development and evolution through its integration.

This notion of craniofacial integration was defined by Smith⁶³ as “the combination of elements through the play or regrouping of mechanisms, explaining that any change in one element is accompanied by changes in the other.”

But for Cheverud¹⁰, integration is defined as “a process referring to the connections and interactions between morphological elements.”

The skull base is described as acting directly through the development and function with variations affecting the skeleton, muscles, neurosensory complex, and particularly the brain, the orbits, the ethmoidal complex, and the cervical spine. All these units have direct or indirect actions on other potential units such as the oropharynx and the nasopharynx, the mandible, and the dental arches (Lieberman⁴⁰).

But does the skull base play an active or passive role in the integration of the cranial shape among these units, and how?

Lieberman⁴⁰ suggests that the skull base may partially play an “intermediary role” during growth between the brain and the face and between the craniofacial complex and the neck. It relies on anatomic and physiological considerations, because skull base appears to be the common boundary of different regions. However, a question remains: given the complexity of the relational mechanism, what are the current units in the skull base and facial skeleton that interact, and what are their regulatory mechanisms?

- For Moss⁴⁸, this integration phenomenon can occur through direct induction or mechanical interactions of the neighboring bone tissue. In fact, the side effects of growth cause changes in the management of relations between the bones in different anatomical regions. According to Moss⁴⁸, it is either the action of a single gene that would affect multiple regions, or the coordination of several genes by pleiotropy. The genetic hypothesis is advanced herein. Deshayes²⁶ evokes the Hox system genes as the mechanism underlying the flexion of the skull base.
- This integration concept was echoed by Lieberman et al.⁴² in a study of the skull base in primate showing strong relationship percentages between skull base shape variations and factors such as brain volume, skull base length, facial angle, and posture. In humans, the skull base angle is related to the length, width, and brain size.

The results indicate a “*pattern*” by which multiple combined factors influence the flexion angle, so that a variability in the angle itself may play multiple roles in modulating the interactions among the various cranial regions.

But this, as highlighted by these authors, remains to be tested more accurately. This is also why the same authors are currently seeking to identify a cellular determinism through histological examinations for explaining the interaction mechanisms to better understand the integration.

- Strait⁶⁷, in order to explain the functional and structural relationships of the skull base characters, offers a hypothesis according which phylogenetic independence cannot be demonstrated, because these characters are presumed integrated and bundled in a complex. But his study shows that the concept of integration can only be used in a phylogenetic analysis if the integration hypotheses can be tested properly.
- Penin et al.⁵², using Procrustes superimpositions comparing growth paths in modern humans and chimpanzees, argue that the human brain is the result of a simple change in growth allometry by gene regulation. For these authors, the structural features such as the skull base flexion and the face of modern man are more closely related to masticatory, respiratory, and locomotive phenomena.
- Bastir and Roses⁴, based on a sample of modern men (n = 144), suggest the hypothesis of a “petromandibular” unit which would be the consequence of changes in the phylogenetic skull base configuration and in posterior face during hominization. Their study shows that in modern man, this morphological integration is organized hierarchically.
- Simonis-Sweat⁶², through the work on geometric morphometrics on craniofacial variability in a sample of 290 current and fossil subjects,

shows that skull base flexion results from allometric relationships as well as static growth. His analysis shows that the face, the vault, and the skull base function as three semiautonomous modules. According to the authors, the integrated structure of the skull would result from allometric and geometric constraints.

In contrast, cranial configuration variations are interpreted by interactions over the effect of muscle growth on bone structures.

Delaire Hypothesis 15-18

According to Delaire, skull base development is essentially under the influence of three fundamental factors: head formation, mastication, and brain expansion.

- He highlights the key role of soft tissue in cephalic skeletal changes during phylogeny. Muscles and viscera would act first on the pre-skeletal mesenchyme, then on skeletal parts derived therefrom. To support this hypothesis, he analyzed the different factors of cephalic morphogenesis and their action mechanisms (Delaire¹⁶).

Thus, over phylogeny, head and neck muscles, especially the posterolateral cervical muscles (mainly responsible for head remodeling during ontogeny) played the main role in the rotation of the back of the skull, in skull base flexion, and in the changes in the remainder of the cranial vault. Moreover, relying on the work of Björk⁸, Riolo et al.⁵⁵, he points out that after the acquisition of the upright posture, the angle of the skull base of children and adolescents changes in normal physiological conditions, while the head continues

to grow. The closure of the sphenoid angle would therefore depend more on brain development than on head remodeling.

He also recalled that in hominids, the adoption of the upright posture and “cephalic humanization” preceded the growth of the brain.

- The action of the superficial and deep facial muscles in the human phylogenetic lineage is mainly effective at the level of facial morphology. In ensuring the lower position of the hyoid bone and the tongue in *Homo sapiens sapiens*, deeper-seat dampers allow the release of the oral cavity and facilitate the retraction of the maxilla and the mandibular body. This is followed by the modification of facial relief (accentuation of the nose and chin) under the control of superficial facial muscles.
- Mastication has contributed to the development of the temporomandibular joint (TMJ) but also the evolution of all elements of the craniofacial skeleton, especially in apes and hominids (Delaire¹⁶).

In addition, the effects on the mandible and dentition because of the type of diet and the development of the masticatory muscles, through the change in occlusal forces, has determined the development and expansion of intraosseous pillar insertion ridges for maxillary reinforcement, which run from the vault and skull base (Delaire¹⁶). The impact of the masticatory muscles through occlusal forces had already been demonstrated by Leroi-Gourhan³⁹.

In addition to this muscular action, Delaire also emphasizes the role of the brain in cephalic humanization. In fact, it has not only followed the expansion

of the cranial vault triggered by head remodeling; it would also have strongly contribute through its own growth linked to the development of brain function. The latter was determined by cultural changes, language, imagination, and writing (Lieberman et al.⁴³).

Conclusion: we see in this theory the complexity and interaction of several determining factors.

Thus, between the upright posture, increased brain capacity, and brain development, there are direct correlations whose effects have gradually led to *Homo sapiens sapiens*.

Deshayes Hypothesis²²⁻²⁶

This hypothesis is based on a concept of “craniofacial biodynamics,” resulting in a craniofacial skeleton arrangement as part of a “three-dimensional facial contraction process resulting in the ontogenetic phenomenon of skull base flexion” (Deshayes²⁶).

The Deshayes thesis is complex. To explain it, the author recalls the concept of integration that we mentioned previously in this chapter.

Deshayes²⁶ summarizes the changes during humanization in a change in the cephalic pole toward sagittal shortening, broadening of the skull base, and an increase of vault height, resulting in the “plication” of the cranial base.

To understand the origin of this flexion phenomenon, Deshayes bases his hypothesis on the work of Moss et al.⁴⁹, which demonstrates the development of skull base flexion in primates because of the overlying neural tube.

Histological studies are guided toward the same concept, namely, that over the course of ontogeny, there is a succession of neural vesicle displacements that would imprint repositioning on the

underlying chondocranial units that would cause flexion.

For Deshayes, the synchondrosis of the skull base would limit the areas or functional units directly activated by the overlying neural vesicles. Deshayes evokes the establishment, since early neural development, of a biodynamic cell network that would organize itself from the microscopic level to the macroscopic level. This cell network would be able to integrate genetic and physiological–biochemical information. Thus, this design approaches the integration concept retaken by Lieberman⁴⁰.

Deshayes assumes the existence of a kinetic process within skeletal components, and raises the possibility of development to different morphologies through changes in the balance points of bone segments.

This supports his cranial biomechanics theory, according to which skull base flexion is a reflection of the kinetic forces acting on the occipital and sphenoid bones.

For Deshayes, “the study of the craniofacial contraction phenomenon must be analyzed independently of the biomechanical process that led to flexion.” It results in two different tables in terms of facial typology as defined in orthodontics.

The application of this cranial biomechanics theory in paleoanthropology is complex, but for Deshayes²⁶, if the flexion phenomenon is “a required phenomenon in primates, it is not exclusive of one biomechanical pattern.” Its origin would be a different biomechanics, with different sphenoidal–occipital kinetic modes.

For Deshayes, in fact, the question of what part initiates the cephalic

humanization phenomenon remains open. This cephalic kinetics would explain why the occipital rotational movement (the initiation of the cephalic hominization phenomenon for Delattre and Fénart¹⁹) is accompanied by sphenoid kinetics, playing a role somehow as second engine of flexion. For Deshayes, bipedalism would have strengthened the “occipital engine.” Deshayes^{25,26} offers a summary showing the interactions between phylogenetic and morphological factors.

On the basis of the impact of the environment on bipedalism, with the data by Beals⁶, for whom “climatic stress” is, on the phylogenetic level, the accelerator of the skull base flexion process, Deshayes develops his cranial biodynamics hypothesis. The craniofacial system must be ready to adapt and integrate the different factors of transformation.

The origin of this transformation is histological. The work of Lengelé³⁸ points to the existence of “a phylogeny in calcified tissues at both the morphological and topographical levels.” He notes that, as cartilaginous tissue may change phenotypic expression, it will invade part of the chondocranium. This tissue is the common denominator in all neurocranial developmental stages, prior to intrasphenoidal synchondrosis. It will therefore play a fundamental role in the organization of this region. On the other hand, according to Deshayes, following intrasphenoidal synchondrosis, the region that builds basioccipital bone, basal sphenoid bone, and the petrous pyramids will be dependent on Hox system genes, which constitute “the first primitive engine of flexion.”

Conclusion: the characteristic of the Deshayes hypothesis is to show

the need for the establishment of biodynamics that would behave as a true interface between the genome and the environment. Thus, as the skeletal pieces grow, they change

their relationship with each other, which results in a specific craniofacial configuration arrangement, which represents an integration of different factors.

CONCLUSION

This anthropological approach emphasizes the importance of the skull base and its consequences to the organization of the craniofacial complex. Knowledge of basal craniofacial development in phylogeny can help orthodontists and practitioners in understanding facial morphology, an area of care for which they are responsible.

On the basis of different hypotheses, it is currently difficult to know precisely what is the key factor or element responsible for craniofacial development.

The elements underlying the various theories are many, but one cannot help but accept their interactions as emphasized by Lieberman et al.^{41,42} and Strait⁶⁷. Soft tissues appear to play a key role.

For most authors, the skull base is still a better source of information than any other part of the skeleton at the phylogenetic level.

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