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# COMPARATIVE ANATOMICAL ANALYSIS OF THE VISCERAL AND CEREBRAL PARTS OF THE SKULL IN TERMS OF ONTOGENESIS AND PHYLOGENESIS

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***Annotation.*** The article is a literature review devoted to the comparative anatomy of the cerebral (neurocranium) and visceral (splanchnocranium, viscerocranium) parts of the human skull in ontogenesis and phylogenesis. The embryonic sources of both parts (neural crest, paraxial mesoderm), the types of ossification, the chondrocranium–dermatocranium–splanchnocranium concept, postnatal growth patterns, and evolutionary trends from fishes to Homo sapiens are discussed. Special attention is given to the reduction of the facial skeleton, the expansion of the brain case, the flexion of the cranial base and the repositioning of the foramen magnum as consequences of encephalization and bipedalism, and to congenital anomalies which can be interpreted from the point of view of development and evolution. The review is based on published data and contains no original clinical observations.

***Keywords:*** skull, neurocranium, viscerocranium, splanchnocranium, ontogenesis, phylogenesis, neural crest, craniofacial development, evolution.

# СРАВНИТЕЛЬНО-АНАТОМИЧЕСКИЙ АНАЛИЗ ВИСЦЕРАЛЬНОГО И МОЗГОВОГО ОТДЕЛОВ ЧЕРЕПА В АСПЕКТЕ ОНТОГЕНЕЗА И ФИЛОГЕНЕЗА

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***Аннотация.*** Статья представляет собой обзор литературы, посвящённый сравнительной анатомии мозгового (нейрокраниум) и висцерального (спланхнокраниум, лицевой отдел) отделов черепа человека в онто- и филогенезе. Рассмотрены эмбриональные источники обоих отделов (нервный

гребень, парааксиальная мезодерма), типы окостенения, концепция хондрокраниума, дермато- и спланхнокраниума, закономерности постнатального роста и эволюционные тенденции от рыб до Homo sapiens. Особое внимание уделено редукции лицевого скелета, расширению мозговой коробки, флексии основания черепа и смещению большого затылочного отверстия как следствиям энцефализации и прямохождения, а также врождённым аномалиям, которые могут быть истолкованы с позиций развития и эволюции. Обзор основан на опубликованных данных и не содержит собственных клинических наблюдений.

***Ключевые слова:*** череп, мозговой череп, лицевой череп, спланхнокраниум, онтогенез, филогенез, нервный гребень, краниофациальное развитие, эволюция.

## Introduction

The human skull is traditionally divided into two parts: the cerebral skull (neurocranium), which encloses the brain and the organs of hearing and balance, and the visceral skull (viscerocranium, or facial skeleton), which forms the skeletal support of the initial parts of the digestive and respiratory tracts, the orbits and the nasal cavity. This division, introduced in classical anatomy, reflects functional differences, but it also corresponds to differences in the origin of the bones and to the sequence of their evolutionary transformations.

Ontogenesis and phylogenesis are linked in the skull in a particularly clear way. The bones of the human skull can be traced back to the skeletal elements of the head of the first vertebrates, and many details of the adult morphology—sutures, foramina, bony processes, anomalies—find their explanation only when the embryonic development and the evolutionary history of the structure are considered together.

## Relevance

Craniofacial malformations (clefts, craniosynostoses, hypoplasia of the mandible and maxilla, syndromes of the first and second pharyngeal arches) are among the most frequent congenital defects. Understanding of the developmental origin of the neurocranium and the viscerocranium allows to explain why some defects affect the face and spare the brain case, and vice versa. In addition, modern orthodontics, maxillofacial surgery and paediatric neurosurgery require knowledge of the age-related dynamics of the skull and of the growth zones (sutures, synchondroses, periosteal surfaces).

From the educational point of view, a comparative analysis of the two parts of the skull makes it possible to integrate the data of embryology, comparative anatomy and

clinical anatomy and to demonstrate the biological logic of the skull structure. Such a review is particularly useful for students, since textbooks usually describe the ontogenetic and phylogenetic aspects separately.

## Aim

The aim of the review is to analyse and compare the cerebral and visceral parts of the skull in the aspects of ontogenesis and phylogenesis on the basis of published data and to identify the general regularities of their development and transformation.

## Main part

### Embryonic sources and types of ossification

The skull develops from the mesenchyme of the head, which has a double origin: cranial neural crest cells and the cephalic paraxial mesoderm. Experimental studies of vertebrate embryos, in particular lineage tracing in the mouse and in birds, have shown that the cranial neural crest forms most of the facial skeleton, the anterior part of the cranial base and the frontal bone, while the paraxial mesoderm gives rise to the occipital region of the base and the parietal bone; the boundary between the two sources lies in the area of the coronal suture in the mouse. The sphenoid and temporal bones are of mixed origin. This dual origin is usually regarded as one of the factors of regional vulnerability of the skull to various syndromes.

In terms of ossification the skull consists of three components. The chondrocranium forms as a cartilaginous base and capsules of the sensory organs, and it is replaced by bone endochondrally; in the adult human, the occipital (except the upper part of the squama), the sphenoid (except part of the pterygoid processes), the petrous part of the temporal bone and the ethmoid have this origin. The dermatocranium (the cranial vault, the facial bones) ossifies directly in membrane, without a cartilaginous precursor: the frontal, parietal, squamous part of the temporal bone, the upper occipital squama, the maxilla, zygomatic, nasal, lacrimal, palatine bones, the vomer and the mandible. The splanchnocranium, or the skeleton of the pharyngeal arches, is represented by cartilages of the first arch (Meckel cartilage; malleus and incus), second arch (Reichert cartilage; stapes, styloid process, lesser horn of the hyoid), and the lower arches (hyoid and laryngeal cartilages).

### Ontogenesis of the cerebral skull

The neurocranium of the newborn comprises a relatively large vault with unossified intervals: the anterior and posterior fontanelles and, in addition, the sphenoid (anterolateral) and mastoid (posterolateral) fontanelles. They permit the deformation

of the head during labour and subsequent growth of the brain. The posterior fontanelle usually closes during the first months of life, the sphenoid and mastoid fontanelles during the first year or somewhat later, and the anterior fontanelle at the end of the second year, although the individual variability is considerable.

The growth of the vault follows the growth of the brain, which is the most rapid in early childhood; as a result, the neurocranium reaches a large proportion of its final size earlier than the face. The vault grows by apposition of bone at the sutures and by remodelling of the outer and inner surfaces. Premature closure of one or several sutures (craniosynostosis) changes the shape of the head in a predictable way, in accordance with the rule that growth is restricted perpendicular to the fused suture and compensatory growth occurs in the other directions; this gives, for example, scaphocephaly in the case of the sagittal suture and brachycephaly in the case of bilateral coronal synostosis.

The cranial base grows differently, mostly at synchondroses (the spheno-occipital, intersphenoidal, spheno-ethmoidal and others), which are growth plates analogous to those of long bones. The spheno-occipital synchondrosis continues to function until late adolescence and is used in forensic and clinical practice as one of the indicators of skeletal maturity. The cranial base also passes through remodelling in connection with the development of the temporal bone, in which the tympanic ring, the petrous part and the squama merge during the first years of life.

**Ontogenesis of the visceral skull**

The facial skeleton develops in connection with five facial prominences (frontonasal, paired maxillary and mandibular) that surround the stomodeum during the fourth–eighth weeks of embryonic life. The maxillary prominences give the maxilla, zygomatic bone and the palatine processes; the mandibular prominences form the mandible by intramembranous ossification around the Meckel cartilage, which itself largely regresses. Failure of fusion of the prominences leads to the typical clefts of the lip and palate, which illustrate the strictly defined time windows of development of the face.

In the newborn the face is small in comparison with the brain case, the paranasal sinuses are rudimentary, the mandible consists of two halves joined by a fibrous symphysis, and the alveolar processes are not yet developed. The postnatal development of the viscerocranium is connected to the eruption of teeth, the development of mastication, nasal breathing and speech; the maxillary sinus enlarges, the ramus of the mandible increases in height, the gonial angle decreases, and the face

grows downward and forward. The visceral skull has a longer growth period than the neurocranium and, in comparison with the latter, is more plastic in response to functional load, and therefore it is more influenced by environmental factors (feeding consistency, habitual breathing, orthodontic treatment).

In old age the alveolar processes undergo resorption after tooth loss, the mandibular angle becomes more obtuse, and the chin appears to protrude; in the neurocranium, the diploë becomes thinner and some sutures synostose. These changes complete the age-related cycle and provide the basis for the use of skull morphology in age estimation.

**Phylogenesis of the skull in vertebrates**

In primitive jawless vertebrates the head skeleton was represented by a cartilaginous neurocranium and by branchial arches that supported gills. The emergence of the jaws from the first pair of the arches in gnathostomes was a key step, since it altered feeding and, thus, the whole evolutionary trajectory of vertebrates. In bony fishes the skull consists of a complex mosaic of dermal bones overlying the chondrocranium, with a series of opercular and branchial structures.

In the transition to land, the relationship of the elements of the splanchnocranium changed. The hyomandibular bone, which originally connected the jaw to the neurocranium in fishes, became the stapes in tetrapods; later, in the mammalian lineage, the articular and quadrate bones of the primary jaw joint moved into the middle ear as the malleus and incus, and the dentary became the only bone of the lower jaw, joining the squamosal in a new (temporomandibular) joint. This transformation, which is documented by fossil intermediates and recapitulated during embryonic development, is a classical example of how the same skeletal element can change its function while maintaining its identity.

Among the mammals the number of skull bones decreased as a result of fusion (oligomerization), and the cranial vault became thin and large. The ratio between the neurocranium and the viscerocranium varies according to feeding habits and the development of the olfactory apparatus: carnivores and ungulates have a long facial part, whereas primates have a shortened muzzle, forward-directed orbits and a more spherical brain case.

**Hominin evolution of the skull: encephalization and facial reduction**

The evolution of the hominin skull can be summarized as an increase in the size of the neurocranium and a decrease in the relative size of the viscerocranium. Early hominins retained a relatively small brain case and a large face with a prominent jaw apparatus, in some forms associated with powerful masticatory muscles and sagittal crests. In the

genus Homo, brain volume increased several times over the course of the Pleistocene, while the tooth size and masticatory apparatus gradually decreased; the use of tools and food processing, including cooking, is among the factors that are hypothesized to have relaxed the selection for a robust jaw.

In Homo sapiens, the face is relatively small and tucked beneath the frontal lobes, the brow ridges are reduced, the forehead is high, the chin is a distinct bony protrusion, and the brain case is globular. Recent studies using geometric morphometrics suggest that the globular shape appears during the development of the species by changes in the growth trajectory of the neurocranium after birth, and that the facial retraction and the globularity of the brain case are partly connected through the cranial base. The cranial base is more flexed in modern humans than in the great apes, which is related both to the large brain and to the vertical orientation of the head on the spine.

Bipedalism was accompanied by a shift of the foramen magnum forward and downward, so that the head is balanced on the vertebral column. This feature is used in palaeoanthropology as an indicator of the habitual posture in fossil forms. Together, the encephalization, the basicranial flexion and the reduction of the face may be regarded as a closely interrelated set of changes rather than as independent events—the so-called craniofacial integration.

**Developmental and evolutionary interpretation of anomalies**

Several variants and anomalies of the skull become understandable in the light of the above. The persistent metopic suture, the interparietal (Inca) bone, Wormian bones and the paramastoid processes are interpreted as results of the variability of ossification centres and are common at the population level. The third occipital condyle, the occipitalization of the atlas and the basilar impression reflect disorders of the occipital sclerotome and the craniovertebral junction. Hypoplasia of the mandible in Treacher Collins syndrome, Pierre Robin sequence and hemifacial microsomia is related to disturbances of the neural crest migration and of the first and second pharyngeal arches; syndromic craniosynostoses (Apert, Crouzon, Pfeiffer) are associated with mutations of genes of the fibroblast growth factor receptor family and thus with the regulation of osteogenic differentiation in the sutures.

## Discussion

The data reviewed show that the division of the skull into cerebral and visceral parts is not only anatomical but also developmental and phylogenetic. The neurocranium is predominantly connected with the evolution of the brain and the sensory organs, grows earlier and is relatively more conservative, whereas the viscerocranium is related to the

feeding and respiratory apparatus, grows for a longer period and responds more flexibly to functional and environmental influences. At the same time, the two parts cannot be considered separately: the cranial base is a common structural and developmental platform for them, and its changes are reflected both in the shape of the face and in the shape of the brain case.

The classical statement that ontogenesis repeats phylogenesis should be applied to the skull with care. The development of the skull shows certain stages which recall ancestral conditions (for example, the Meckel cartilage and the primary jaw joint in the embryo), but the details of growth are subject to their own regularities, and the evolution of the skull often occurs by changes in the timing and rate of development (heterochrony), not by simple addition of stages. In this connection, the reduction of the face in modern humans is often discussed as a paedomorphic trait, although this interpretation is still debated among researchers. Another limitation of the present review is that molecular mechanisms are mentioned only briefly, and the fossil data are subject to the incompleteness of the record.

## Conclusion

The cerebral and visceral parts of the skull differ in embryonic origin, in type of ossification, in time and mode of growth, and in the direction of evolutionary transformation: the neurocranium expanded together with the brain, while the viscerocranium was reduced and became more compact, with the cranial base as the connecting element. Knowledge of these regularities helps to explain normal variants and congenital malformations and is important for clinical disciplines dealing with the head and face. Further integration of embryological, comparative and imaging data, including local population data, is desirable for educational and clinical purposes.

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