Phylogenetic evolutionary aspects of the vertebrate skull - an approach for teaching

Aspectos filogenéticos evolucionários do crânio de vertebrados – uma abordagem para o ensino

Tales Alexandre Aversi-Ferreira[1]*, Pietra Bruna Barbosa Bento[1], Kassandra Kenia Andrade Nogueira[1], Wellika Dorta[1], Kaynara Trevisan[1]

ABSTRACT

In this work, the fundamental data will be placed as logically as possible within a simple, but not simplistic philosophy, therefore, the objective was to indicate the basic ontogenetic and phylogenetic data in terms of the evolutionary history of the vertebrate skull starting from the initial, often idealized, structures that formed the framework of the primitive vertebrate skull. Therefore, the methodology used was a literature review, in order to refine the information. From this methodology, the expected result was to reduce the excess or oversimplification of information that could fail in the teaching processes, to avoid the danger of errors of the interpretation. An overview with basic data, but well ordered in terms of substitutions and phylogenetic history is essential to prepare future scientists in the areas of morphology, taxonomy, evolution, comparative anatomy, paleontology, forensic anatomy; therefore, this text was builded objectively as possible to be consulted for the teaching/learning of the cranium comparative anatomy.
Key words: Skull, Phylogenetic, Comparative anatomy, Vertebrate.

RESUMO

Neste trabalho, os dados fundamentais serão colocados o mais logicamente possível dentro de uma filosofia simples, mas não simplista, portanto, o objetivo foi indicar os dados ontogenéticos e filogenéticos básicos em termos da história evolutiva do crânio dos vertebrados a partir das estruturas iniciais, muitas vezes idealizadas, que formaram a estrutura do crânio dos vertebrados primitivos. A metodologia utilizada foi uma revisão de literatura a fim de refinar as informações. A partir dessa metodologia, o resultado esperado é o de reduzir o excesso ou uma simplificação excessiva de informações que poderão prejudicar o processo de ensino, com o perigo de gerar erros de interpretação. Um panorama com dados básicos, mas bem ordenados em termos de substituições e história filogenética é essencial para preparar futuros cientistas nas áreas de morfologia, taxonomia, evolução, anatomia comparada, paleontologia, anatomia forense; portanto, esse texto foi feito o mais objetivamente com o intuito de ser consulta para o ensino/aprendizado da anatomia comparativa de crânio.

Palavras-chave: Crânio, Filogenética, Anatomia comparativa, Vertebrados.

[1] Federal University of Alfenas, Alfenas, Brazil
*e-mail: tales.ferreira@unifal-mg.edu.br

INTRODUÇÃO

The study of the skeleton is a fundamental basis for the other topics of anatomy teaching because the names of muscles, vessels and nerves are derived from their relationships to the components of the skeleton (TORREY, 1978).

Bones and calcified pieces of cartilage are the best-preserved fossil structures (MATA; MATA; AVERSI-FERREIRA, 2010; TERRAY *et al*., 2022), and from a single bone it is often possible to reconstruct the general characteristics of a specimen (O'RAHILLY, 1983]. In a limb bone, one can have an idea of the locomotion mode, weight and muscular organization of an individual; for example, the human femur, in general indicates about 40% of the size of the individual and its thickness is proportional to the weight when alive (STANDRING *et al*., 2008).

Bones have tended to fuse over phylogenetic time and the human skull anatomy is the simplest in the evolutionary history (TORREY, 1978; HIDELBRAND; GOSLOW, 2006), but for scholars in basic areas, a more complete knowledge is desired to base researches and comparative studies.

The skull is the most studied and documented part of the vertebrate skeleton, perhaps because of its relationship to the encephalon. In fact, data derived from the skull indicate the volume of the encephalon and the encephalization index of a species allowing to verify the cognitive evolution of the species, especially primates (TORREY, 1978; MADDIN *et al*., 2020; ABREU *et al*., 2021).

Due to the many data on the bones, mainly the skull, two situations can occur: the excess of information that should be the scope of the specialists, or an oversimplification that will fail in the teaching processes with the danger of generating errors of interpretation (HIDELBRAND; GOSLOW, 2006; MONSON, 2020).

In this work, the fundamental data will be placed in the most logical way possible within a simple but not simplistic way; therefore, the objective is to indicate the basic ontogenetic and phylogenetic data in terms of the evolutionary history of the vertebrate skull starting from structures, often idealized, that formed the vertebrate skull framework.

The skull, without much rigor, can be conceptualized as a more or less rigid tissue envelope that, in animals of the clade Craniata, surrounds the brain, the organs of sense and serves as a support for the external organs of the respiratory and digestive apparatus,

and defines the animal sense of movement (TORREY, 1978; HIDELBRAND; GOSLOW, 2006; TERRAY *et al*., 2022).

Bone and cartilaginous structures form the skull with the same name in fish are the homologs in mammals and maintain more or less constant relationships with the neural system (STORER *et al*., 1986; MADDIN *et al*., 2020).

On the evolutionary scale the skull of the most derived beings shows the least amount of bones (JOLLIE, 1984; BASTIR *et al*., 2010). Bone fusions occur; however, other possibilities such as the disappearance of bone pieces and/or the primordial cartilage, or in some rare cases, a new bone which has developed and does not present a homology with the others if the latter is of dermal origin and the other located in a nearby place is of endochondral origin, are other possibilities [NOERDEN, 1987; MADDIN *et al*., 2020).

In descriptive terms of morphogenesis, one can divide the skull in physiological terms, into neurocranium and splancnocranium (HIDELBRAND; GOSLOW, 2006).

The neurocranium is related to the parts of the skeleton of dermal or cartilaginous origin that surround the sense organs and the encephalon (figure 1) (NODEN; TRAINOR, 2005; BASTIR *et al*., 2010). The splancnocranium is the skeleton, also with the two origins mentioned above, that forms the structure of the maxilla, the mandible and the support of the mouth (HIDELBRAND; GOSLOW, 2006) (figure 1).

Figure 1 - General structure of the skull of a simple vertebrate. The parts that have been designated with regions form the neurocranium. Around the neurocranium below the branchial arches is the dermatocranium.
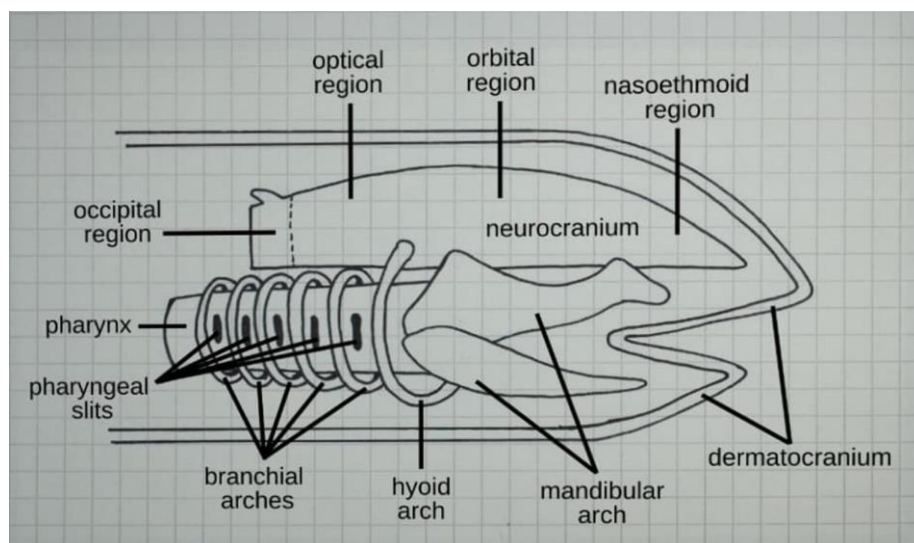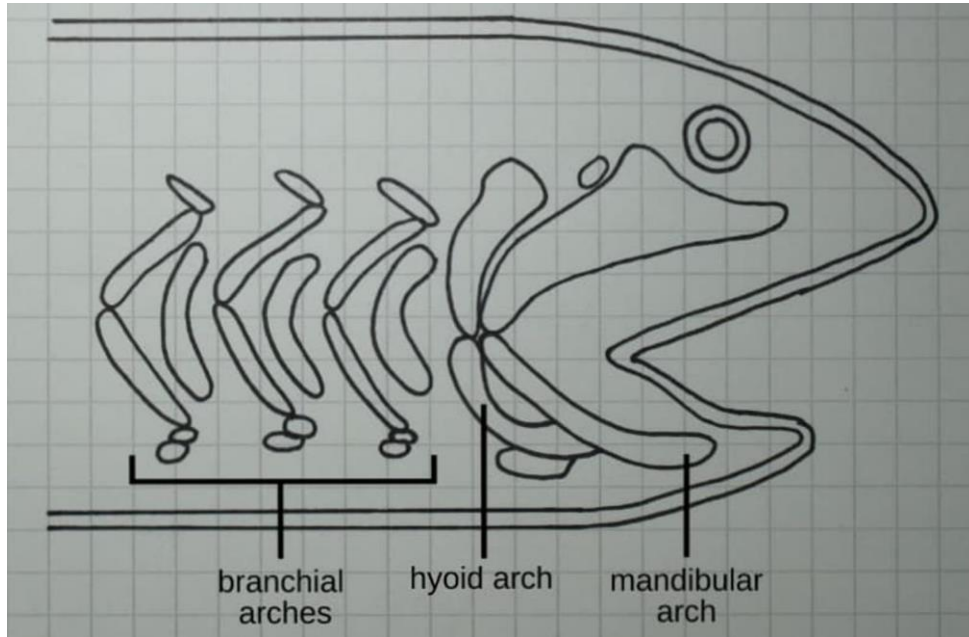

Fonte: Bento & Nogueira (2022)

The two functional divisions of the skull can be represented, in relation to the embryonic development, in the endocranium that is internal and derived from cartilaginous parts that will be replaced by bones, except for the species that have a cartilaginous skeleton; and the dermatocranium that is superficial and is formed by membranous or dermal bones. These dermal bones had a probable phylogenetic origin from the exoskeleton of primitive fish, and their ontogenetic origin from the branchial arches (THOMSON, 1971; HIDELBRAND; GOSLOW, 2006; MOORE; PERSAUD; TORCHIA, 2015).

The branchial arches are structures that have a metameric organization in simpler vertebrates and in the embryos of all the vertebrates and give rise to the structures associated with the head and the neck (HIDELBRAND; GOSLOW, 2006; MOORE; PERSAUD; TORCHIA, 2015). They are also associated with the gill or pharyngeal clefts and are present in six pairs in humans. Their origin from the embryonic leaflets is uncertain, but they are believed to derive from neural crest cells (BURT, 1995; CARROLL, 1990).

The branchial or visceral arches (figures 1, 2 and 3) are designated by numbers in the craniocaudal direction. The 1st branchial arch, also called the mandibular arch, forms the maxillary and the mandibular process, the middle ear ossicles in mammals (anvil and hammer) and the hyoid-mandibular bone in agnates. The 2nd branchial arch, called the hyoid forms part of the hyoid bone and the middle ear stapes in mammals. In mammals, the 3rd arch forms the lower part of the hyoid bone and the cartilages of the larynx derive from the 4th to the 6th arches (THOMSON, 1971; MOORE; PERSAUD; TORCHIA, 2015).
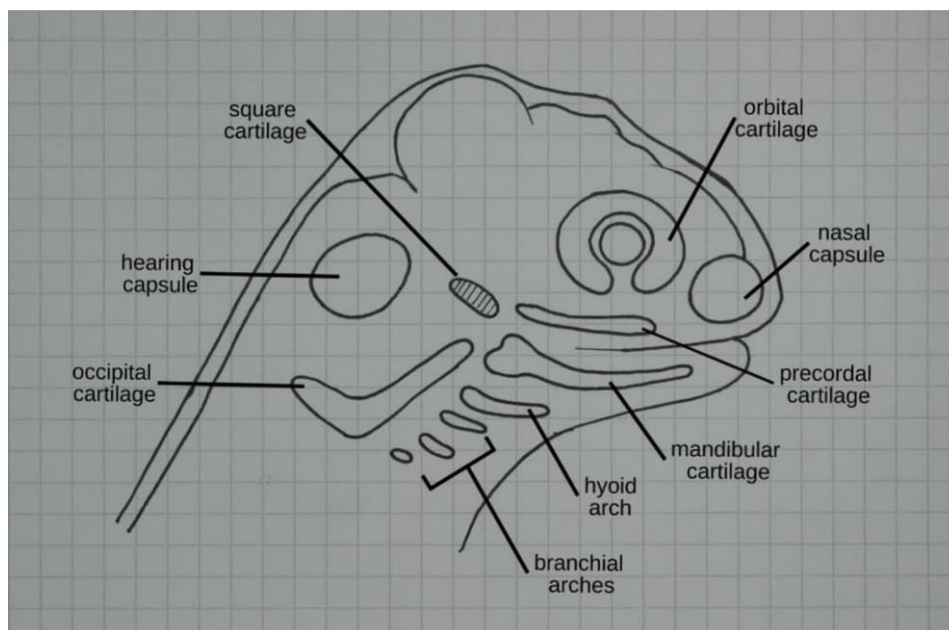
Figure 2 - Branchial arches of a gnathostome.

Fonte: Bento & Nogueira (2022)

The formation of the neurocranium occurs by six isolated even groups of cartilages; the para-chordal, pre-chordal, occipital, orbital cartilages, and the auditory and nasal capsules (figure 3) (TORREY, 1978; MADDIN *et al*., 2020).

**Figure 3** - Primitive structures of the vertebrate embryo skull.

Fonte: Bento & Nogueira (2022)

The positions of the cartilage formation and their associations are depicted in the scheme in figure 3. The occipital cartilage is similar to a cervical vertebra, so some authors argue that the occipital bone possibly includes some vertebrae of the metameric skeleton (STANDRING, 2008; MATA; MATA; AVERSI-FERREIRA, 2010).

The splancnocranium is formed by the isolated cartilage centers and mesodermal centers of the branchial arches. The mandibular arch is represented by the squared and the mandibular (Meckel's) cartilages (DE BEER, 1985).

The fusions of the original cartilages then form the neurocranium and the splancnocranium. In the formation of the neurocranium, these fusions generate other derived structures, the so-called regions and basal plate. The regions formed by the original cartilages and capsules are: the occipital region, the ethmoid, the sphenoid orbito, the auditory, and the basal plate (figures 4 and 5) (HIDELBRAND; GOSLOW, 2006; STANDRING, 2008).

Figure 4 - Top view of a scheme of the base of the human chondrocranium with the cartilaginous fusion regions identified.
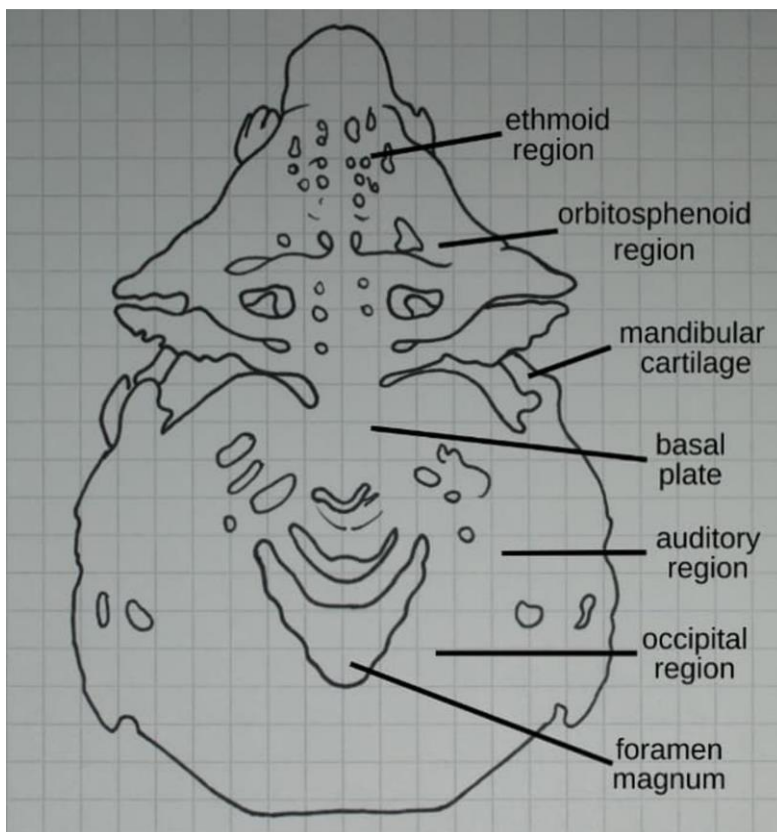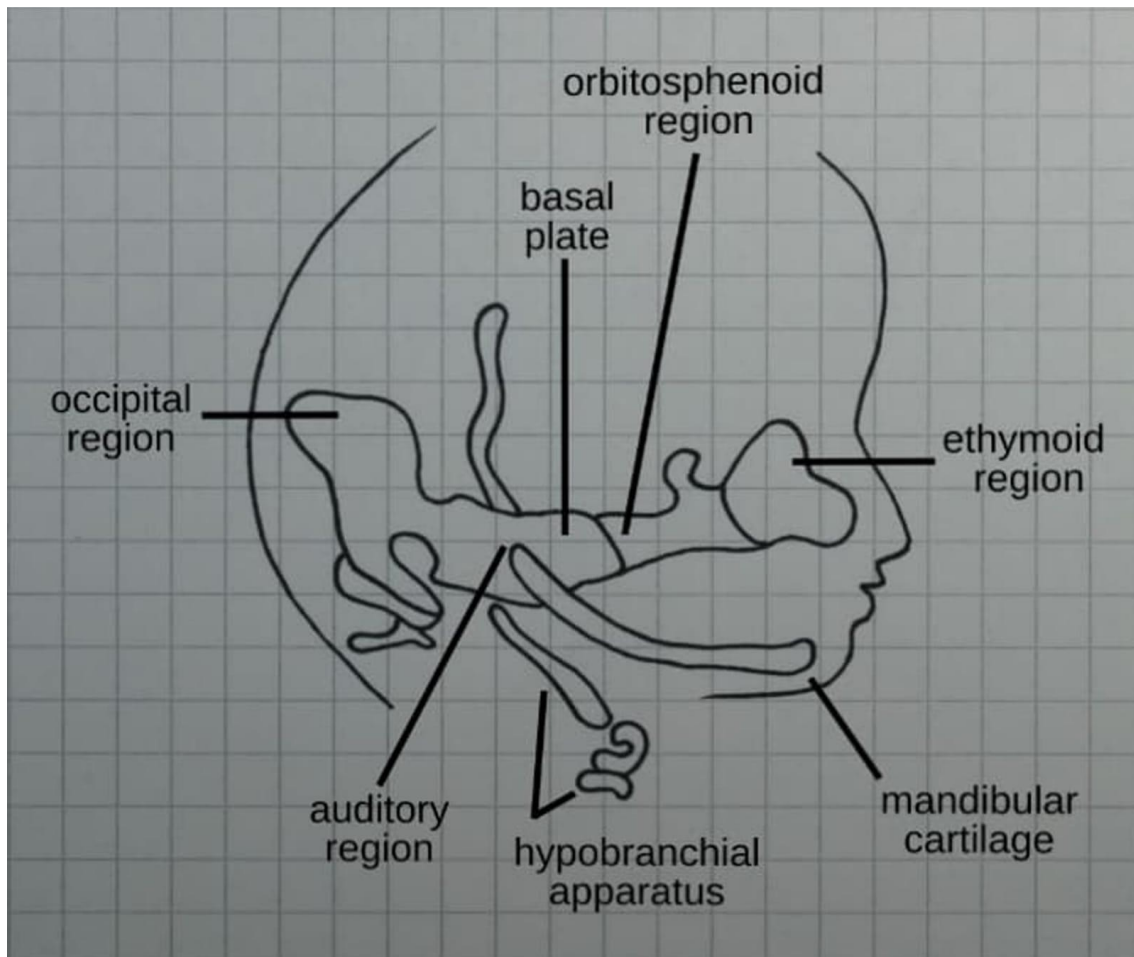

Fonte: Bento & Nogueira (2022)

The basal plate is formed by joining the para-chordal cartilages and fuses in the rostral portion of the embryo with the ethmoid region that is formed by the fusion of the prechordal cartilages and the nasal capsules (TORREY, 1978).

In the posterior portion, the basal plate fuses with the occipital region, formed by the fusion of the occipital cartilages with the para-chordal cartilages. In the posterolateral region, the occipital region and the basal plate fuse with the auditory region, formed by the auditory capsules, and the orbito-sphenoid region. The nasal cartilages fuse with the precordal cartilages to form the ethmoid region (DE BEER, 1985, BIBI; TYLER, 2022).

Figure 5 - Lateral view of a scheme of the human chondrocranium with the regions of cartilaginous fusion highlighted.
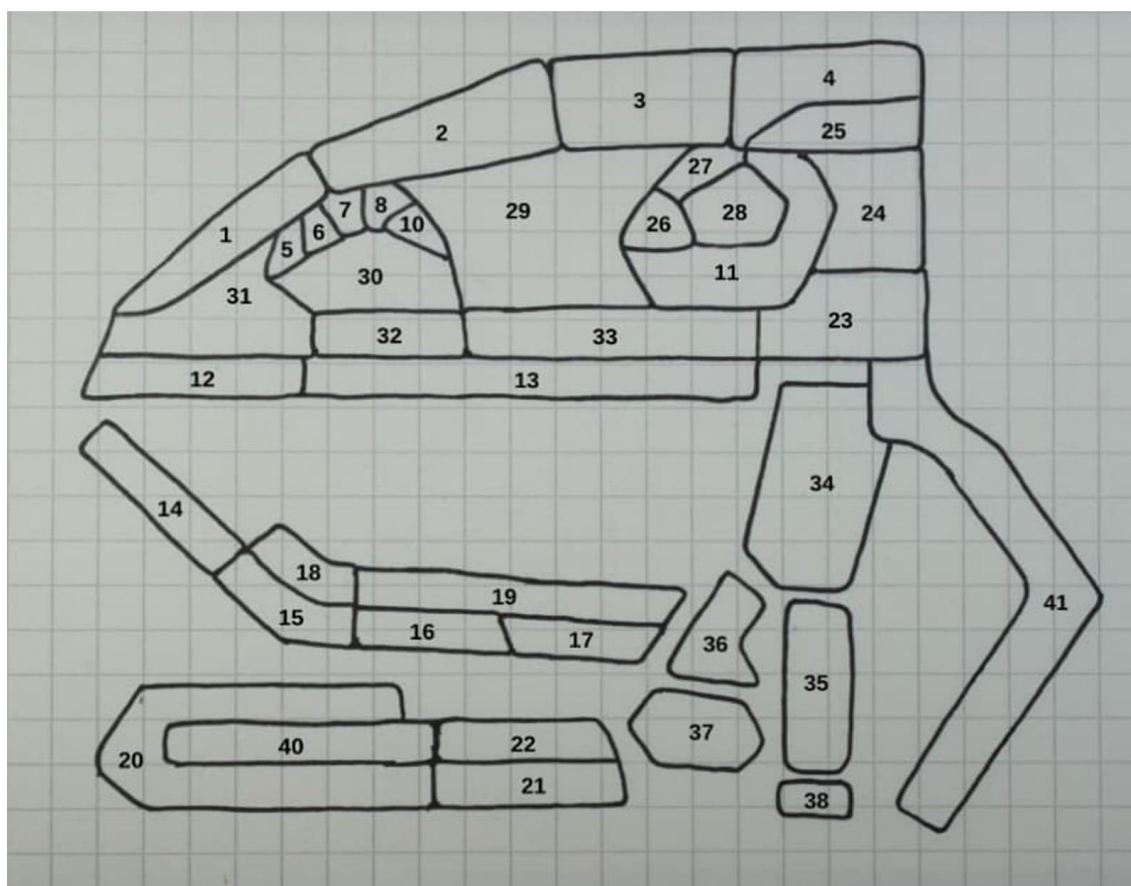

Fonte: Bento & Nogueira (2022)

These fusions form a cartilaginous neurocranium that configures the base of the encephalon, the so-called chondrocranium. The mandibular cartilages fuse with the neurocranium from the auditory region (TORREY, 1978; MADDIN *et al*., 2020).

The next event in the phylogenetic cranial construction is the replacement of the cartilaginous and the membranous regions by a bone tissue. In the simplest vertebrates there are more bones and they are the basis of observation and study, because their general structure will indicate the formation, by homology, of the skulls of derivative vertebrates (DE BEER, 1985; STORER *et al*., 1986; ORR, 2000; HIDELBRAND; GOSLOW, 2006).

However, it is possible to organize the bones into an ideal primitive skull to serve as a basis for later correlations (TORREY, 1978; HIDELBRAND; GOSLOW, 2006). Figure 6 depicts the major bones that form the skull of an ideal primitive vertebrate (Figure 6).

Figure 6 - Scheme of an ideal vertebrate skull with its primitive bones. The numbers 1 to 22 represent the bones of dermal origin colored gray, and those 23 to 41 of cartilaginous origin in white.

Fonte: Bento & Nogueira (2022)

The structure of the neurocranium is represented in figure 6 by the numbers 23 to 33. What will be called bone should be considered to be derived from a cartilage of the same name.

In the posterior portion, the occipital region is formed by three bones: (23) basooccipital, single and middle; (24) exooccipital, a lateral pair; (25) supraoccipital, single superior (TORREY, 1978; GANS; NORTHCUTT, 1983).

The auditory capsule also has three bones: (26) prootic, anterior; (28) opisthotic, posterior; (27) epiotic, superior (TORREY, 1978; GANS; NORTHCUTT, 1983).

At the base of the skull, the basal plate is formed by the bones (33) basosphenoid, posterior, and (32) presphenoid, anterior. The cranial box has as lateral walls the bones (29) aliessphenoid, posterior, and (30) orbito-sphenoid, anterior (TORREY, 1978; GANS; NORTHCUTT, 1983).

The ethmoid region is complex and highly variable. It consists of the ethmoid complex (31) (TORREY, 1978; GANS; NORTHCUTT, 1983). The cartilaginous splancnocranium is formed by the bones numbered 34 to 41 (TORREY, 1978). The maxilla is formed by the square bone (36), the mandible formed by the articular (37) and the mandible (40) (TORREY, 1978).

The hyobranchial apparatus is formed by the bones (34) hyomandibular, superior; (35) ceratohial, middle; (38) basihial, inferior, which will form the hyoid bone itself (TORREY, 1978).

The cartilage number (41) represents the branchial arches that will form the lower portion of the hyoid bone and the tracheal cartilages (GANS; NORTHCUTT, 1983). The bones of the chondrocranium described above are represented in Table 1.

The structures derived from the dermatocranium are represented by the numbers 1 to 22 and their names are shown in table 2.

Other dermal bones were not shown, such as the opercular bones, present only in fish, and the temporal bones, situated on each side, in a middle position between the parietal and squamous bones (TORREY, 1978).

Comparative Analysis

The analysis of the skull will be carried out in a general way with an emphasis on the main modifications, considered here as those that will appear in the more specialized classes and having the man as the end of this analysis.

Regarding the dimensions of the skull, major changes have occurred in its surface shape, and according to their dimensions, they can be called dolichocephalic, when the length is greater than the width; brachycephalic, when the length is less than the width; mesocephalic when it has intermediate dimensions (HALL, 1985; ORR, 2000; HIDELBRAND; GOSLOW, 2006; STANDRING, 2008).

In the interspecies context, from fish that are dolichocephalic, to man (mesocephalic), the variations are expressive, as the anterior portion of the skull grows extensively in reptiles, birds and herbivorous mammals with a lateral enlargement of the cranial vault which can be seen clearly in zoology studies (STORER *et al*., 1986; ORR, 2000).

Present day fish have skulls with the largest amount of bones and the largest proportional orbit of vertebrates. The endocranium is cartilaginous and dermal plates surround almost the entire adult skull, but fossils show ossified endocranial components (STORER *et al*., 1986; ORR, 2000).

Another item to consider during the evolution is about the joints of the maxilla with the neurocranium. (1) Amphistyletic hinge joints are those in which both the palate-square and the hyomandibular articulate with the neurocranium and occur in some cartilaginous fish; (2) iostyletic hinge joints are those in which only the hyomandibular articulates with the neurocranium and occur in most bony fishes; (3) autostyle hinge joints are those in which the neurocranium and the splancnocranium tend to fuse as in most tetrapods (TORREY, 1978; HIDELBRAND; GOSLOW, 2006).

Table 1 - Skull bones of vertebrates from the basic cartilaginous regions.

Cranial Region	Numbers	Derived bones name
Occipital	23	Basooccipital
	24	Exooccipital
	25	Supraoccipital
Auditory	26	Pre-optical
	27	Supra-optical
	28	Post-optical
Orbital	29	Aliessphenoid
	30	Orbitoesphenoid
Anterior or ethmoid	31	Ethmoid complex

| Basal plate	32	Presphenoid
	33	Basosphenoid

In mammals, the maxillomandibular joint forms from the dental and scale of the temporal bone (STORER *et al*., 1986). In reptiles and mammals, the choanae moved to the posterior part of the oral cavity for the formation of the secondary palate, a bony septum that separates the airways from the digestive tract. In birds, the secondary palate tends to disappear, probably due to the lack of teeth and then existence of the beak formed by the incisor bone in the upper portion (ORR, 2000; HIDELBRAND; GOSLOW, 2006).

From now on, the basic denominations of the ideal skull will be considered and from them, modifications, fusions and new bones will be indicated.

For fish, only the skull of those with a bony skeleton will be considered. The bones of the bony fish were the basis for the construction of the idealized skull in this work, and the main modifications were the transfer of the jugal bone to the orbital region, the existence of coronoid and opercular bones that surround the gills, besides even pterygoid and ectopterygoid bones parallel to the parasphenoid (LAUDER; LIEM, 1983). The basooccipital fuses with the spine by two fixed joints and therefore the fish cannot move its neck (LAUDER; LIEM, 1983; HIDELBRAND; GOSLOW, 2006).

Amphibians have a skull with different dimensions compared to fish, it is flatter dorso-ventrally (figure 7). The bones of dermal origin become stabilized in number and maintain close relationships until the man (WAKE, 1966). The absence of the gills eliminates the opercular bones, which form the tympanic membrane in these animals, but it is not homologous to the mammalian tympanic membrane (NOBLE, 1931; HIDELBRAND; GOSLOW, 2006; WEAVEER; STRINGER, 2015).

Figure 7 - View of some bones in an amphibian (frog) skull.
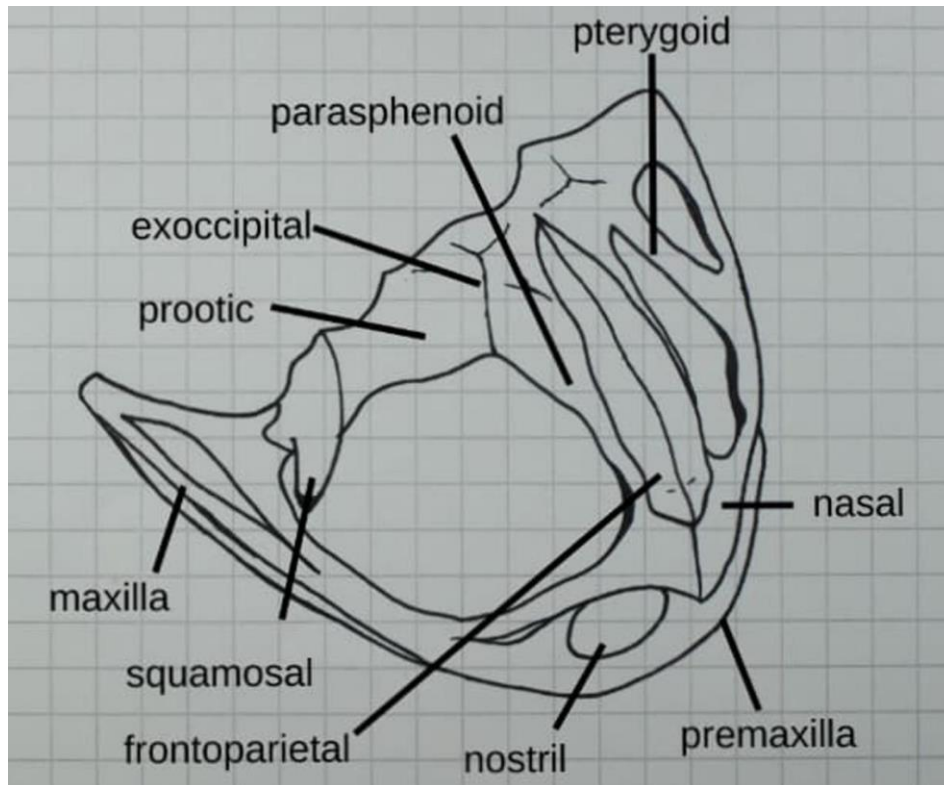
The anterior, nasal, frontal and parietal bones become more enlarged, as do the roof bones of the oral cavity, maxilla and dentary, and the temporal bones appear. The jugal bone becomes permanently associated with the orbital area and will form the zygomatic bone in mammals. The jugal-square bones fuse to the larger squamous bones. The square bone is attached to the maxilla and a new element, the epipterygoid bone, above the pterygoid bones. The parasphenoid bone fuses to the basooccipital (WAKE, 1966; TORREY, 1978; HIDELBRAND; GOSLOW, 2006).

Table 2 - Regions of the skull derived from the primitive dermatocranium.

Cranial Region	Numbers	Derived bones name
Upper anterior	1	Nasal
Upper middle	2	Frontal
	3	Parietal
Posterior-superior	4	Post-parietal
Orbital	5	Lacrimal
	6	Prefrontal
	7	Supraorbital
	8	Postfrontal

	10	Postorbital
Lateral area	11	Scaly
Maxillary	14	Pre-maxillary
	15	Maxillary
	16	Jugal
	17	Jugal square
Jaw	20	Dental
	21	Angular
	22	Suprangular
		Note: the splenic, pre-articular and coronoid bones are not shown
Palate	12	Paraesophenoid
	13	Veromer
	18	Palatine
	19	Pterygoid

The chondrocranium, in the adult, is firmly joined, without the membranes and the bony distances of bony fishes (TORREY, 1978; WEAVER; STRINGER, 2016).

The exooccipital bone has two condyles for the articulation with the spine in modern amphibians, and in primitive amphibians there was one condyle in the basooccipital bone (TORREY, 1978). In the auditory region, the supraoptic bone is no longer found in amphibians (STORER *et al*., 1986; ORR, 2000).

Importantly, the square bone is now part of the neurocranium and is fused to the articular that is part of the mandible (STANDRING, 2008). The ear of amphibians is in the position corresponding to the hyomandible which is homologous to the stapes that connects with the neural auditory region and is internal to the prootic bone (WAKE, 1966; TORREY, 1978).

It is interesting to note that the hyomandible becomes part of the amphibian ear and such a relationship continues down the evolutionary line.

In reptiles (figure 8) some bones no longer exist compared to amphibians. The post-parietal bones, the elements of the orbital series, and the coronoids have joined the mandible (TORREY, 1966; COSSETE; GRASS; DEGUZMAN, 2021). Modern reptiles have two lateral openings on each side of the skull, except chelonians; however, mammals originated from one of the groups that had only one opening in the lateral portion of each side of the skull, the synapsids (ROMER, 1956; COSSETE; GRASS; DEGUZMAN,

2021). The skull of reptiles is elongated and the bones are rough. In crocodiles, the palatine, pterygoid and part of the maxilla bones form the secondary palate that separates the oral and nasal cavities (ROMER, 1956; STORER *et al*., 1986; ORR, 2000; HIDELBRAND; GOSLOW, 2006). An important aspect of reptiles is the association of the articular bone with the square that is part of the neurocranium. Except in snakes, the square bone is firmly associated with the scaly bone (TORREY, 1978; COSSETE; GRASS; DEGUZMAN, 2021).

**Figure 8** - Skull of a primitive reptile.
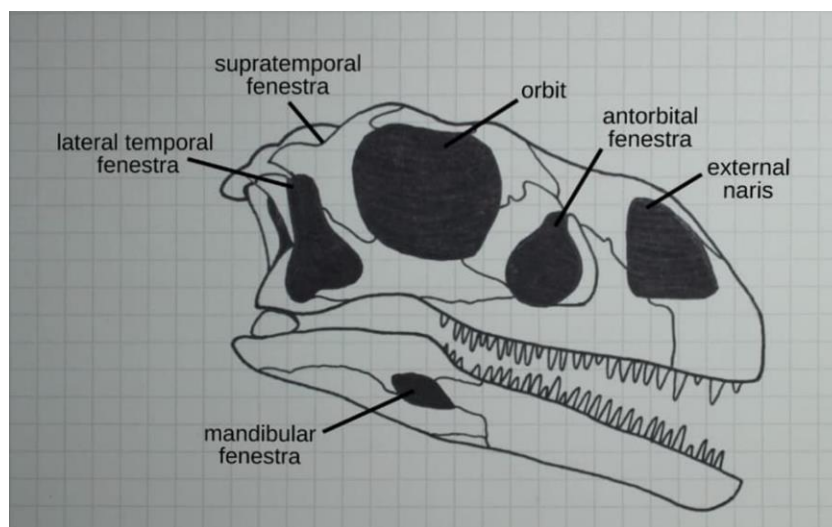
Fonte: Bento & Nogueira (2022)

The skull of birds (figure 9) is similar to that of reptiles, except that they have a single condyle at the junction with the vertebral column (TORREY, 1978).

The main differences are proportionally larger parietal and occipital bones to accommodate a proportionally larger cerebellum. There is an increase in bones with openings, the sinuses, to suit flight (a decreased specific weight of bones); the bones are more fused and ossified in the adult, the square bone is mobile at the juncture with the skull, and a joint also mobile, the naso-frontal with the maxilla is also mobile (FAMER; KING, 1972; TORREY, 1978; LEE; ESTEVE-ALTAVA; ABZHANOV, 2020).

Figure 9 - Skull of a bird.
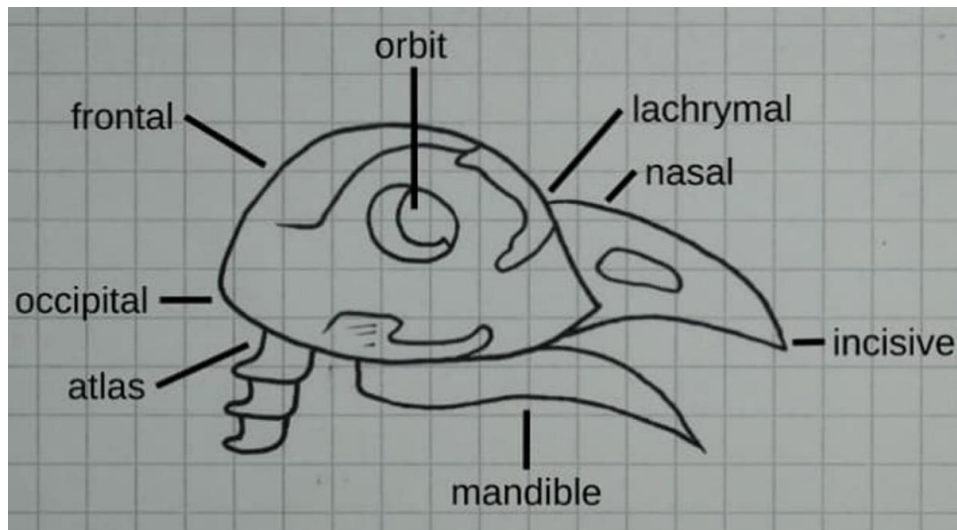
Mammals (figure 10) seem to be descendents of the primitive reptiles synapsids, one of the orders of which is the therapsids, which had a lateral orifice in the temporal region on each side of the head (TORREY, 1978). The main modifications occurred in the mammalian skull with several bone fusions and losses of elements (TORREY, 1978; HIDELBRAND; GOSLOW, 2006).

Figure 10 - Skull of a mammal.
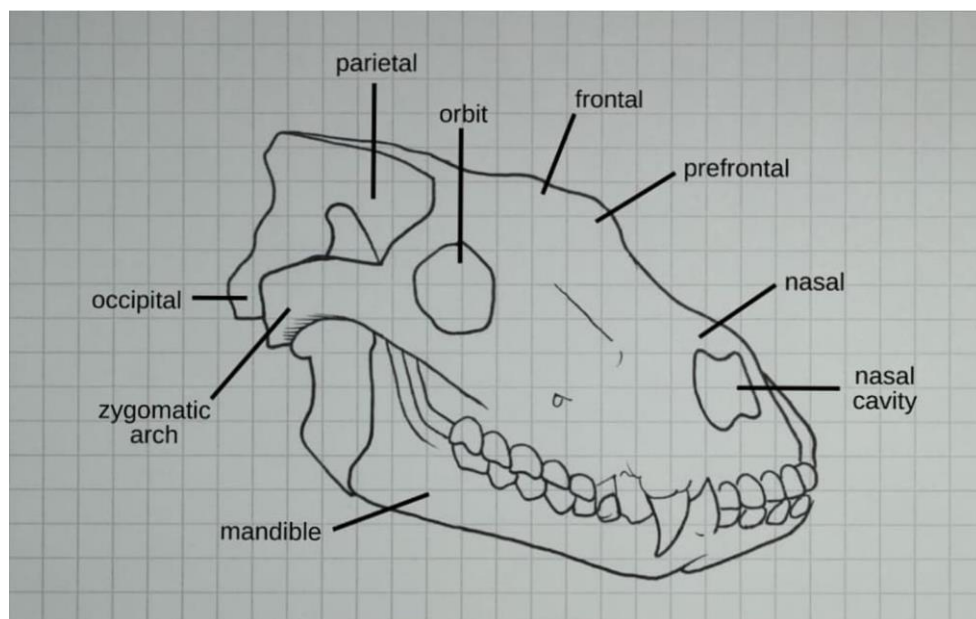
In general, mammals have a pair of occipital condyles, two openings (the acoustic meatuses) and a considerable change in the proportions of the bony elements; however, among groups of mammals there are also considerable changes in bone proportion, just considering the skull of a hippopotamus and a marmoset.

The post-orbital bone disappeared along with the other primitive orbital elements. The post-parietal bone has fused with the occipital bone (unique in humans) (JOLLIE, 1984), but the intra and interparietal bones still raise questions in evolutionary terms (MATA; MATA; AVERSI-FERREIRA, 2010; KOYABU; MAIER; SÁNCHEZ-VILLAGRA, 2012).

In primates, the dermal bones of the upper-anterior portion of the skull have become enormous to house an encephalon of immense proportions compared to other animals (PEREIRA-DE-PAULA, 2010; MONSON, 2020; ABREU et al., 2021). The periotic bone fuses with the squamous bone to form a temporal bone, and the tympanic membrane is a new structure (NODEN; TRAINOR, 2005; MONSON, 2020). The basosphenoid and presphenoid bones lie anterior to the occipital bone and a new element, the mesoethmoid bone appears in the nasal portion and fuses with the orbitoesphenoid and aliesphenoid bones. The pterygoid bones of amphibians and reptiles are represented exclusively by the aliesphenoids, but commonly, these sphenoid bones form a single, complex bone, the sphenoid (NODEN; TRAINOR, 2005; STANDRING, 2008).

The parasphenoid bone is absent in mammals. Palatine and vomer bones are preserved, but the vomer bones form a single bone in the median plane (STANDRING, 2008).

The square-jaw bone disappears, but the square and articular bones form the anvil and hammer, respectively, of the middle ear (STANDRING, 2008). Thus, the mammalian mandible is formed by the union of the dental and squamous bone, so the dental is called mandible and the squamous bone forms part of the temporal bone (HIDELBRAND; GOSLOW, 2006).

An important and interesting aspect about the human evolution starts from the modification of the jaw muscles that became weaker due to a putative mutation and allowed the growth of the hominids' encephalon (NODEN; TRAINOR, 2005). From this data, hypothetically, in association with the fact that this muscle, the masseter, originates from the supraorbital ridge in primates and australopithecines, and this origin is in the temporal of hominids, has allowed the growth of the frontal bone and the development of

the part of the brain associated with language, the fine motor coordination, the abstraction, the higher cognitive functions, the frontal lobe (MADDIN *et al.*, 2020; MONSON, 2020).

In summary, the muscles of the human jaw are weaker, the skulls are thinner, and the brains are three times larger than the hominids that preceded us (STEDMAN *et al.*, 2004).

These phenomena are associated with the verticalization of the face (figure 11).

Figure 11 - Verticalization of the skull of hominids.
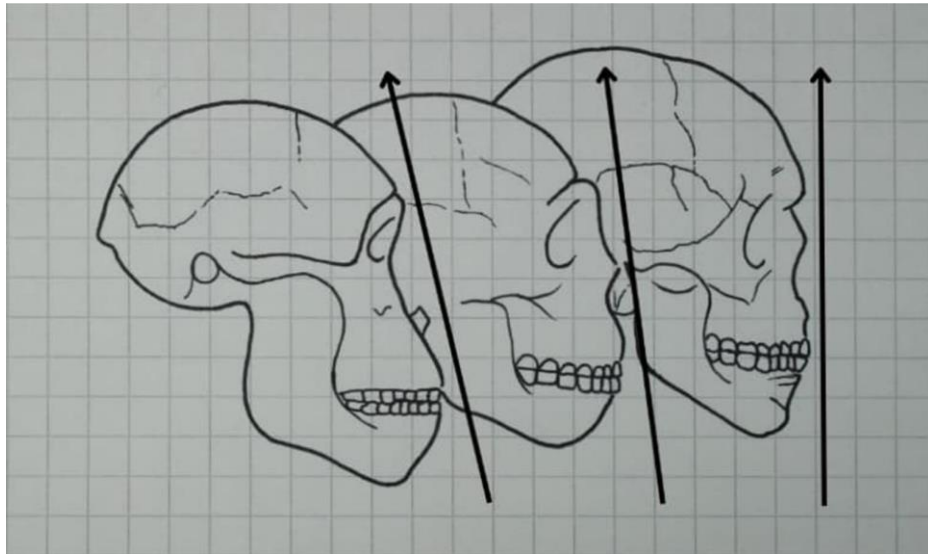
Fonte: Bento & Nogueira (2022)

Conclusions

The study of the skeletal anatomy is fundamental to the understanding of the anatomy of any species, especially if the studies are comparative.

An overview with basic but well-ordered data in terms of substitutions and phylogenetic history is fundamental to prepare future scientists in the fields of morphology, taxonomy, evolution, comparative anatomy, paleontology, forensic anatomy, inter alia.

The evolutionary history of the skull formation should be a basic subject in the teaching of anatomy, but with data that allows an understanding of the origins of bones in the most derived animals, especially primates.

REFERÊNCIAS

ABREU, T.; TAVARES, M. C. H.; BRETAS, R.; RODRIGUES, R. C.; PISSINATI, A.; AVERSI-FERREIRA, T. A. Comparative anatomy of the encephalon of new world primates with emphasis for the *Sapajus* sp. **PLos One**, v. 16, n. 9, p. e0256309, 2021.

BASTIR, M.; ROSAS, A.; STRINGER, C.; CUÉTARA, J. M.; KRUSZYNSKI, R.; WEBER, G. W. et al. Effects of brain and facial size on basicranial form in human and primate evolution. **Journal of Human Evolution**, v. 58, n.5, p. 424–31, 2010.

BIBI, F.; TYLER, F. Evolution of the bovid cranium: morphological diversification under allometric constraint. **Communications Biology**, v. 5, n. 69, p. 1-12, 2022. DOI: doi.org/10.1038/s42003-021-02877-6.

BURT. **Neuroanatomia**. Rio de Janeiro: Guanabara Koogan,1995.

CARROLL, R. L. **Vertebrate paleontology and evolution**. New York: W. H. Freeman and Company, 1990.

COSSETTE, A. P.; GRASS, A. D.; DEGUZMAN, T. The contribution of ontogenetic growth trajectories on the divergent evolution of the crocodylian skull table. **Anatomical Record**, v. 1, p. 1-22, 2021.

DE BEER, G. R. **The development of the vertebrate skull**. Chicago: University of Chicago Press, 1985.

FAMER, D. S.; KING, J. R. **Avian Biology**. New York: Academic Press, 1972.

GANS, C.; NORTHCUTT, R. G. Neural crest and the origin of the vertebrates: a new head. **Science**, v. 220, p. 268-274, 1983.

HALL, B. K. Evolutionary consequences of skeletal differentiation. **American Zoologist**, v. 15, n. 2, p. 329-350, 1975.

HILDEBRAND, M.; GOSLOW, G. **Análise da Estrutura dos Vertebrados**. 2ª ed. São Paulo: Atheneu, 2006.

JOLLIE, M. The vertebrate head – segmented or a single morphogenetic structure? **Journal of Vertebrate Paleontology**, v. 4, p. 320-29, 1984.

KOYABU, D.; MAIER, W.; SÁNCHEZ-VILLAGRA, M. R. Paleontological and developmental evidence resolve the homology and dual embryonic origin of a mammalian skull bone, the interparietal. **PNAS**, v. 109, n. 35, p. 14075-80, 2012.

LAUDER, G. V.; LIEM, K. F. Patterns of diversity and evolution in ray-finned fishes. **Fish Neurobiology**, v. 1, p. 1-24, 1983.

LEE, H. W.; ESTEVE-ALTAVA, B.; ABZHANOV, A. Evolutionary and ontogenetic changes of the anatomical organization and modularity in the skull of archosaurs. **Scientific Reports**, v. 10, n. 1, p. 16138, 2020.

MADDIN, H. C.; PIEKARSKI, N.; REISZ, R. R.; HANKEN, J. Development and evolution of the tetrapod skull–neck boundary. **Biological Reviews**, v. 95, n. 3, p. 573-591, 2020.

MATA, J. R.; MATA, F. R.; AVERSI-FERREIRA, T. A. Analysis of bone variations of the occipital bone in man. **International Journal of Morphology**, v. 28, n. 1, p. 243-48, 2010.

MONSON, T. A. Patterns and magnitudes of craniofacial covariation in extant cercopithecids. **Anatomical Record,** v. 303, p. 3068-84, 2020.

MOORE, K. L.; PERSAUD, T. V. N.; TORCHIA, M. G. **The developing Human: Clinically Oriented Embriology**. 10th ed. Philadelphia: W. B. Saunders, 2015.

NOBLE, G. K. **The Biology of the Amphibia**. New York: McGraw-Hill Book, 1931.

NODEN, D. M.; TRAINOR, P.A. Relations and interactions between cranial mesoderm and neural crest populations. **Journal of Anatomy**, v. 207, p. 89-120, 2005.

O'RAHILLY, R.; MULLER, F. **Basic Human Anatomy: A Regional Study of Human Structure.** Philadelphia: W. B. Saunders Co Ltd; 1983.

ORR, R. T. **Biologia dos Vertebrados**. 5ª ed. Saom Paulo: ROCA; 2000.

STEDMAN, H. H.; KOZYAK, B. W.; NELSON, A.; THESIER, D. M.; SU, L. T.; LOW, D. W.; BRIDGES, C. R.; SHRAGER, J. B.; MINUGH-PURVIS, N.; MITCHELL, M. A. Myosin gene mutation correlates with anatomical changes in the human lineage. **Nature**, v. 428, n. 6981, p. 415–418, 2004.

PEREIRA-DE-PAULA, J.; PRADO, Y. C. L.; TOMAZ, C.; AVERSI-FERREIRA, T. A. (Rylands, 2000). Anatomical Study of the Main Sulci and Gyri of the Cebus Libidinosus Brain (Rylands, 2000), **Neurobiologia**, v. 2, v. 2, p. 65-78, 2010.

ROMER, A. S. **Osteology of the Reptiles**.Chicago: University of Chicago Press, 1956.

STANDRING, S. **Grays Anatomy. The Anatomical Basis of Clinical Practice**. 40th ed. Amsterdam: Elsevier, 2008.

STORER, T. I.; USINGER, R. L.; STEBBINS, R. C.; NYBAKKEN, J. W. **General Zoology**. 6ª ed. São Paulo: Companhia Editora Nacional, 1986.

TERRAY, L.; DENYS, C.; GOODMAN, S. M.; SOARIMALALA, V.; LALIS, A.; CORNETT, R. Skull morphological evolution in Malagasy endemic Nesomyinae rodents. **Plos One**, v. 17, n. 2, p. e0263045, 2022.

THOMSON, K. S. The adaption and evolution of early fishes. **Quarterly Review of Biology**, v. 46, n. 2, p. 139-166, 1971.

TORREY, T. W. **Morfogénesis de los Vertebrados**. Limusa: México; 1978.

WAKE, D. B. Comparative osteology and evolution of the lungless salamanders, Family Plethodontidae. **Memoirs of the Southern California Academy of Sciences**, *v.* 4, p. 1-111, 1966.

WEAVER, T. D.; STRINGER, C. B. Unconstrained cranial evolution in Neandertals and modern humans compared to common chimpanzees. **Proceedings of Royal Society B**, v. 262, p. 20151519, 2015.