

**Cranial ontogeny of the common vampire bat *Desmodus rotundus*
(CHIROPTERA: PHYLLOSTOMIDAE): postnatal development.**

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Quiero dedicar la presente investigación a Edgar Daniel Rodríguez Rodríguez, pionero en Colombia y emprendedor en Latinoamérica en los estudios de la ecología del Oso Andino (*Tremarctos ornatus*), con quien he explorado desde hace algunos años el maravilloso mundo de la Mastozoología, y quien, dadas sus enseñanzas, ha sido no sólo un excelente profesor, sino un gran amigo.

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RESUMEN ESPAÑOL

TITULO: Cranial ontogeny of the common vampire bat *Desmodus rotundus* (CHIROPTERA: PHYLLOSTOMIDAE): postnatal development. *

AUTOR: Nicolás Rafael Reyes Amaya. **

PALABRAS CLAVES: Cráneo, Desarrollo, Suturas, Desmodus.

CONTENIDO: El cierre de las suturas craneales y la relación entre los huesos que conforman el cráneo fueron examinados en el murciélago vampiro común *Desmodus rotundus*. Las suturas mostraron un patrón abierto a largo plazo, seguido por cambios abruptos en su morfología y en su grado de desarrollo, adquiriendo formas más interdigitadas y más complejas, que fusionan los elementos óseos en las categorías de edad de subadulto y adulto. Se documenta un origen doble para el hueso frontal en el murciélago vampiro común. La prolongación de este hueso compuesto frontal y de los huesos premaxilares, además de la pérdida de solapamiento entre los huesos y la presencia de procesos óseos en las regiones preorbital, frontal y occipital son responsables de la mayor variación en el tamaño y forma del cráneo de esta especie. Todos estos cambios en el desarrollo se piensa que podrían estar estrechamente relacionados con las tensiones mecánicas que el cráneo del individuo debe soportar durante el desarrollo de la sanguivoría obligada. Este estudio constituye un aporte al conocimiento de las especializaciones morfológicas en los murciélagos filostómidos, y en un contexto ecológico y filogenético provee bases para entender las relaciones entre la ontogenia de las variaciones morfológicas y la ecología de las especies.

*Proyecto de Grado

**Facultad de Ciencias. Escuela de Biología. Director Adriana Jeréz.

RESUMEN INGLÉS

TITULO: Cranial ontogeny of the common vampire bat *Desmodus rotundus* (CHIROPTERA: PHYLLOSTOMIDAE): postnatal development. Proyecto de Grado. *

AUTOR: Nicolás Rafael Reyes Amaya. **

PALABRAS CLAVES: Skull, Development, Sutures, Desmodus

CONTENIDO: Cranial suture closures and the relation between the bones conforming the skull were examined for the common vampire bat *Desmodus rotundus*. The sutures showed a long term open pattern, followed by abrupt changes in morphology and development, acquiring more complex interdigitated shapes and fusing the bone elements in subadult and adult age categories. We documented a double origin of the frontal bone in the common vampire bat. The elongation of this composed frontal and the premaxillary bones, the loss of the overlapping between bones and the occurrence of bone processes on the preorbital, the frontal, and the occipital regions are responsible of the major variation in skull size and shape in this specie. All these changes in development are thought to be tightly related with the strains that the individual carries while develops obligate sanguivory. This study constitutes a contribution to the knowledge of the morphological specializations in phyllostomid bats. In an ecological and phylogenetic context this study provides a basis for understanding the relationship between ontogenetic morphological variations and ecology of this species.

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INTRODUCTION

Among Chiropterans the family of leaf-nosed bats, Phyllostomidae constitutes a very diverse group; ranking first in number of genera and third in number of species of bats in the world, and bearing the major morphologic and alimentary variation among the mammals (Baker et al., 2003, 2010; Simmons 2005). The feeding strategies in this clade include insectivory, sanguivory, carnivory, nectivory, frugivory and omnivory. This great diversity makes this group the perfect model for the study of adaptations and diversity patterns. Hematophagy characterizes the subfamily Desmodontinae which comprises the unique real vampire bats in the world. Desmodontinae is constituted by three extant species *Desmodus rotundus*, *Diaemus youngii*, and *Diphylla ecaudata* (Greenhall et al., 1988, 1983; Koopman, 1988; Simmons, 2005). These three species show physiological, osteological and ethological adaptations that are related to their specialized diet (Greenhall, 1983, 1988; Ferrarezzi & Giménez, 1996; Mollerach & Mangione, 2004).

Most of morphological studies on microchiropterans are focused on the description of skull characters of taxonomic utility (Davis, 1970; Machado et al., 2007; Araújo & Langguth, 2010; Orihuela, 2011). Works related with the development of the skull in this group are scarce. Fawcett (1919) and Frick (1954) used sections of prenatal skulls of to describe the development of the chondrocranium in *Myotis sp.* and *Myotis myotis*, respectively. Wible & Martin (1993) analyzed the ontogeny of the tympanic region in a compared context within Archonta. Pedersen (1995) examined the cephalometric correlation of the skull in fetuses of different bats with oral and nasal echolocation. Pedersen (1996) describes the development of auxiliary nasal foramina in rinolophid bats using cephalometry, associating it with

the echolocation function. Adams & Pedersen (2000) analyzed the development of the skull of megachiropterans and microchiropterans associated with the function of echolocation. Rocha et al. (2005) tested a new technique for observing bone tissues in embryos in *D. rotundus*, and proposed it as a useful tool to study bone development. Finally, Wyant & Adams (2007) reported the degree of ossification in fetal skeleton of *Mops condylurus* (Molossidae) relative to the greatest length of the skull.

In this study we describe the postnatal cranial development of the common vampire bat *Desmodus rotundus*, a species distributed from the North of Mexico to the North of Argentina (Greenhall, 1983; Gardner, 2007). We describe the development of the ectocranial sutures, showing the relation between the bones that constitute the skull from neonate to adult age category, as well as major changes in skull shape and determining the skull elements responsible of changes. Microchiropteran cranial variation during ontogeny is a poorly studied field, and probably not all the factors involved in the origin of morphological and functional diversity observed in adults are known. Therefore, this study not only constitutes a contribution to the knowledge of the morphological specializations in phyllostomid bats but in an ecological and phylogenetic context, provides a basis for understanding the relationship between ontogenetic morphological variations and ecology of the species (Novacek, 1993; Jablonka & Lamb, 1998; Adams & Pedersen, 2000).

2. MATERIALS AND METHODS

We analyzed an ontogenetic postnatal series of 13 individuals of *Desmodus rotundus* in different developmental stages. This sample was selected due to its

precedence from a single colony from a rocky cave located in Llano de Palmas, Rionegro, Santander, Colombia. Specimens were loaned from the Collection of Mammals of the Instituto de Ciencias Naturales (ICN) at the Universidad Nacional de Colombia. Each one of the specimens was processed by clearing and double staining of cartilage and bone following Wassersug (1976). Sex was not treated due to the small sample size.

Since the exact age was unknown, our age classification was based on morphological observations and comparisons between individuals from this sample. We established four categories: newborn (n=1), juvenile (n=4), subadult (n=3) and adult (n=5). These categories were determined based on various criteria: first, using standard morphometry for bats (Albuja, 1999; Tirira, 2007); second, by the degree of ossification of the metacarpals elements of the wing (Kunz, 1998); finally, by external characteristics of sexual maturity as the presence of testicles, lactating females and pregnant females (Racey, 1988). According to this, we have determined eight development stages contained in this four categories: neonate (A), juvenile (B, C, D, E), subadult (F, G) and Adult (H).

We described completely the skull at the age category of neonate, and after that, all the changes in the next age stages were registered until the adult stage. Anatomical descriptions followed the nomenclature of *Nomina Anatomica Veterinaria* (1994), including the sutures. Our classification was modified according to the presence of sutures in the species, following the model proposed by *Nomina Anatomica Veterinaria* (1994) (see table 1). The skull regions were determined based on Giannini et al. (2006) with modifications, and we recognize four regions: rostral, dorsal, lateral, and occipital. We registered: the position of the ectocranial bones, the changes of form of these bones, and their fusion sequence, including a description of the shape of the suture. General changes in skull shape,

as well as the identification of which bones were responsible for such changes in each developmental stage were also recorded. The sutures development followed Chopra (1957), who distinguish three stages: open, closing and closed. In open sutures neighbor bones are easily recognized; sutures can be separated or close together, but the suture is not yet ossified. In closing sutures the bones are close together and the ossification has already started. Although each bony element can still be distinguished, they can be fused in some regions of their contact surface. Finally, closed sutures are completely ossified and the bones are fused but the suture may or may not be visible. The morphologic classification of the sutures follow Evans (1993), who distinguishes four forms: serrated, foliated, squamosal and plane. A serrated suture is that in which the borders of the neighboring bones have dentate irregularities that tends to join one with the other; a foliated suture the one in which the borders of the neighbor bones have wide irregularities with foliated form, that tends to join one with the other; a squamosal suture is that where one of the neighbor bones is overlapping the other, generally each of them having a beveled edge which joins during the ossification process; a plane suture is such that the borders of the neighbor bones have no irregularities and they are juxtaposed one with the other.

The material was examined using stereoscopic microscope, using drawings and photographs of the postnatal stages in study to describe: changes in shape, position and relation of the ectocranial elements, also describing the fusion process of these elements and the major variations in the cranial design among the different developmental stages. Because the mandible consists of a single bone element with a single suture, it was excluded from this study.

2. RESULTS

The rostral region of the skull of *Desmodus rotundus* is composed of the paired premaxillary, maxillary, lacrimal, nasal and frontal bones, which constitute 33% of the skull in the adult. In the neonate, each frontal is formed by two elements, and thus has a double origin (Fig. 1, A, 2, A); each frontal is formed anteriorly by a thin rectangular element called the anterior frontal (af), and posteriorly by a bigger element, called posterior frontal (posf). These bony elements in advanced developmental stages (stage F) will constitute the pair of frontal bones (fr) (Fig. 1, A). The dorsal region of the skull, or roof, is made up of the paired parietal bones (Fig. 1, A). The lateral region consists of the paired jugal and squamosal bones (Figure 1 B). Finally, the occipital region consists of the paired exoccipital and interparietal bones and a single supraoccipital bone (Fig, 1, C).

In *Desmodus rotundus*, cranial sutures remain open for much of postnatal development, even until the last stage of development of juveniles (stage E). However, the frontal suture (fs), sutura premaxillolacrimalis (spmxl), sutura sagittalis (ss), sutura parietointerparietalis (spip) and sutura interparietalis (sip), begin to close or are completely closed between stages A (neonate) and C (intermediate category of juvenil age). All the sutures are completely closed in the adult stage, thus, the skull is a unit without distinguishable bone elements. Most of the ectocranial sutures show abrupt changes in their degree of development, in one stage it is completely open and in the next it is closing or even completely closed in some cases. We observed three morphological types of sutures: serrated, plane and squamous; there was no presence of foliated sutures during development. Morphological changes were observed in some sutures along the development. We observed only one case in which a suture (sutura frontoparietalis, sfp) had two morphological variations during different development stages.

The general form of the skull of *Desmodus rotundus* shows drastic changes in the rostral and occipital regions along its development. Compared to the newborn, adults exhibit a pronounced snout and an elongated occipital region (Fig. 2, 9). Towards the rostral region these changes are mainly due to a marked prolongation of the bone elements and the loss of bone overlap in neonate. Conversely changes in the occipital region are primarily due to a significant growth of bony elements and changes in their shape. Additionally, the development of the preorbital frontal process (pfp), the occipital process (op), and the nuchal crest (nc) also alters markedly the shape of the skull in advanced stages of development (Fig. 9).

2.1 STAGE A: NEONATE (FIG. 2)

The skull exhibits a short rostral region. Posteriorly the cranial vault has a rounded shape. At this particular stage all skull bones are quite distinctive in shape and position, but some of them are not yet fully developed. Several bone elements are overlapping each other and others are juxtaposed. Evidence of suture closure is present only in the frontal suture (fs) and sutura sagittalis (ss).

Rostral Region (Fig. 2, A): The premaxillary bone is paired and rectangular shaped. It forms the anterior and lateral edges of the nostril. Posteriorly, it overlaps the lateral edge of the nasal bone, and laterally it articulates with the maxillary pair. Each premaxillary exhibits a pair of encrypted deciduous caniform incisors. Behind them there is a unique definitive incisor, that in this stage is encrypted within each premaxillary. The lacrimal is a small square-shaped bone located between the premaxillary and the orbital fossa. Each maxillary is triangular in shape and

exhibits a deciduous canine and a deciduous premolar. These are not yet erupted at this stage, similarly to the permanent canine and premolar teeth located behind them. There is also an un-erupted molar tooth in the maxillary. The paired maxillary bones meet the premaxillary anteriorly and the jugal posteriorly. The maxillary elements extend forming the zygomatic process of the maxilla (zpmx). The nasal bones are short and form a convex arc that defines the posterior region of the nasal cavity, they overlap the anterior frontals posteriorly. The latter are rectangular and arched bones, forming a second convex arc above the nasals. The anterior frontals are covered posteriorly by the posterior frontals. Each posterior frontal is big with a quadrangular shape; they meet posteriorly the parietal pair, which is overlapping them. The frontal suture (fs) is squamous and connect the anterior and posterior frontal bones. Such suture is closing in a portion greater or equal to 75% of its contact surface. In the region between the anterior and posterior the supraorbital foramen (sofa) is observed.

Lateral Region (Fig. 2, B): The jugal is narrow with a rectangular shape, and does not contact the maxillary or squamous bones. The squamous is ovoid in shape and overlaps the parietal bones. Each squamous exhibits the zygomatic process of the squamous (zpsq) in the anterior edge.

Dorsal Region (Fig. 2, C): The parietal bones are the only elements of this region. They form the roof of the skull, constituting over 50% of the cranial vault. At the neonatal stage, the parietal bones are not fully differentiated, and the frontoparietal foramen (fpf) is present between the parietal and posterior frontal bones. Laterally, the parietal is in contact with the squamosal and caudally with interparietal and exoccipital bones. The sutura sagittalis (ss) is serrated and is observed between the parietal bones, it is closing over 75% of the contact surface.

Occipital Region (Fig. 2, D): The interparietal bone is paired; each one is a roughly squared element. Anteriorly, they are slightly covered by the parietals; posteriorly, they meet laterally the exoccipital bones and medially the unique supraoccipital bone. The paired exoccipitals, roughly quadrangulars are overlapping the supraoccipital and parietal bones. The supraoccipital is a rectangular single bone, and its anterior edge is slightly overlapped by the interparietal bones.

2.2 STAGE B: JUVENILE (FIGURE 3)

Overall, skull bones remain distinctive so that the only suture completely closed is the sutura premaxilolacrimalis (spxl). It is also noted that the overlap between the bones decreases noticeably when most elements have increased in size. The cranial vault is enlarged in respect to the neonate and the skull presents an ovoid shape.

Rostral Region (Fig. 3, A): Each premaxillary has enlarged anteriorly and is fused with the lacrimal, therefore the sutura premaxilolacrimalis (spxl), which consists of the squamous (sq), is closed. The two deciduous caniform incisors begin to erupt. The nasals are roughly square and less covered by the premaxillary. The posterior frontal (posf) is bigger, losing much of the overlap of the parietal laterally. The frontal suture (fs) still remains closing in 75% or more of its extension, however only some parts of the bones are fused.

Lateral Region (Fig. 3, B): The jugal bone has increased in size, and is observed in close proximity with the zygomatic process of the maxilla and the squamosal. The zygomatic process of the squamous (zpsq) shows significant prolongation.

Dorsal Region (Fig. 3 C): The parietal bones are fully differentiated anteriorly, and the frontoparietal foramen (fpf) in this stage is small.

Occipital Region (Fig. 3 D): Posteriorly each interparietal is swollen towards the middle region, which constitutes the occipital process (op). The exoccipitals no longer overlap the supraoccipital in its lateral edges.

2.3 STAGE C: JUVENILE (FIG. 4)

At this stage the great majority of the components have increased in size, particularly the anterior frontal and the posterior frontal bones. These show a marked elongation generating greater projection of rostral region.

Rostral region (Fig. 4, A): Anteriorly, the premaxillary bones increase their contact surface near the midline. The permanent incisor teeth begin to erupt just behind the deciduous caniform incisors. In each maxillary, the zygomatic process of the maxilla (zpmx) has significantly widened and extended; both canine teeth, the deciduous and the permanent ones, are observed in the process of eruption. The nasal bones have changed to a roughly trapezoidal shape and now appear bigger. The anterior frontals are markedly enlarged, thickening the convex arc that they form above the nasals.

Lateral region (Fig. 4, B): no noticeable changes are observed in this region at this stage.

Dorsal Region (Fig. 4, C): The frontoparietal foramen (fpf) is very small due to the significant growth of the posterior frontals and the parietals. The sutura saggitalis (ss) is closing over 100% of the parietals.

Occipital Region (Fig. 4, D): The interparietals are no longer overlapped by the parietals and now they are juxtaposed to them. The sutura parietointerparietalis (spip) is closing in a length greater than or equal to 25% of its contact area, showing the morphology of a serrated suture. The sutura interparietalis (sip), which is serrated, is closing over a length greater than or equal to 50%.

2.4 STAGE D: JUVENILE (FIG. 5)

The skull shape has changed dramatically in the rostral region. The increased sizes of the premaxillaries, the nasals and frontals make the snout look apparently lengthened, and the skull presents a stylized shape.

Rostral Region (Fig. 5, A): In this stage, the nasals present an elongated rectangular shape. The frontal suture (fs), between the anterior and posterior frontals is squamous and this is observed closing in 100% of the length of contact. This suture clearly defines the supraorbital foramina (sofa).

Lateral region (Fig. 5, B): no noticeable changes are observed in this region at this stage.

Dorsal Region (Fig. 5, C): The parietal bones are fully differentiated and now are markedly larger, overlapping the posterior edge of the frontals. Therefore, the frontoparietal foramen (fpf) is no longer observed at this stage.

Occipital region (Fig. 5, D): The sutura parietointerparietalis (spip), with serrated morphology, is closing in 75% or more of the length of contact between the parietals and the interparietals. The sutura interparietalis (sip), which is serrated, is closing over 75% or more of its contact area. The sutura occipitointerparietalis (soipa) is squamous, and is observed closing over 75% or more of contact between the supraoccipital and interparietals.

2.5 STAGE E: JUVENILE (FIG. 6)

In this stage the snout is swollen between the posterior region of the premaxillary bones and the anterior region of frontal, just ahead of the optic fossa; this is called the preorbital frontal process (pfp).

Rostral Region (Fig. 6, A): The sutura maxilloincisiva (smi), with serrate morphology, is closing in a length less than or equal to 25% of the contact area between the premaxilla and the maxilla. The nasals and frontals are fusing;

therefore, the sutura frontonasalis (sfn), which is squamous, is closing over 100% of their contact surface. The frontals, anterior and posterior, are fusing in the midline; since the sutura interfrontalis (sif), which is plane (pl), is closing in a length greater than or equal to 75% of its contact surface. In the maxillary, the permanent premolar and the molar begin to replace deciduous teeth, and the deciduous premolar is no longer observed.

Lateral region (Fig. 6, B): The sutura squamosa (ssq), between the squamous and parietal bones, is closing in a portion less than or equal to 25% of its length. This is a squamous shaped suture.

Dorsal region (Fig. 6, C): no noticeable changes are observed in this region in this stage.

Occipital Region (Fig. 6, D): Fusion of the interparietals is complete and the serrated sutura interparietalis (sip) is closed. The exoccipital and supraoccipital are fusing in a length not greater than 25% of its contact surface, since the sutura occipitalis (soc), which is plane, is closing. The exoccipital bones no longer overlap the parietals, now they are juxtaposed.

2.6 STAGE F: SUBADULT (FIG. 7)

In this stage a higher fusion among the skull bones is observed, but most elements are visible. The rostrum continues to be prolonged by the increasing size of the premaxillary and nasal elements. The preorbital frontal process (pfp) is

accentuating. The postorbital constriction (pc) in the frontal bones (anterior and posterior) is observed. Dorsal and occipital regions also exhibit changes, since the parietals and the supraoccipital increase their size and the interparietals get reduced, lengthening the cranial cavity. The nuchal crest (nc) is observed in the supraoccipital by the projection of the sutura occipitointerparietalis (soipa).

Rostral region (Fig. 7, A): Between the premaxillaries appears the sutura interpremaxillaris (sipmx), with plane morphology, which is closing in 100% of its length. Between the premaxillaries and the nasals appears the sutura premaxilonasalis (spmxxn), with serrated morphology, is closing along a length greater than or equal to 50% of its contact surface. The premaxillaries have fused completely with the maxillaries since the sutura maxilloincisiva (smi), which is serrated, is completely closed. The permanent incisors, canines, premolars and molars are present. The deciduous incisors are still observed. The fusion of the nasal bones is complete, and the sutura internasalis (sina), with plane morphology, is closed. The lacrimal bone, which is already fused with the premaxillary since stage B, fuses with the maxillary, since the sutura maxilolacrimalis (smxl), which is squamous, is closed. The anterior and posterior frontal bones are fused, since the frontal suture (fs), that is a squamous, is completely closed. The same occurs with the sutura interfrontalis (sif), which is plane. The sutura frontopremaxilaris (sfpmx) is now closing in 75% or more of its contact surface and presents a serrated morphology. The frontals are fusing with the nasal, since the sutura frontonasalis (sfn) is closing over 100% of its contact surface; this suture varies morphologically from a squamous shape to a serrated shape in this stage. The sutura zygomaticomaxillaris (szmx) is closing over 100% of its contact surface.

Lateral Region (Fig. 7, B): The sutura squamosa (ssq) is closing along its entire length. The parietals are fusing with the exoccipitals; since the sutura exoccipitoparietalis (seopa), which is serrated, is closing in a length less than or equal to 50% of the contact surface. The sutura zigomaticotemporal (szt) is closing over 100% of its contact surface.

Dorsal Region (Fig. 7, C): The sutura sagittalis (ss) is closed, and the parietals are fused. Between the frontals and the parietals, the sutura frontoparietalis (sfp) is closing over 100% of its contact surface and presents in this stage two morphological types, serrated in its central region, and squamosal to its lateral region. The postorbital constriction (pc) is very conspicuous.

Occipital Region (Fig. 7, D): The supraoccipital bone has increased in size significantly in dorsoventral direction. The interparietals, already fused in a single element, are completely fused with the parietals, since the serrated suture parietointerparietalis (spip) is completely closed. The sutura occipitalis (soc), with squamous morphology, is completely closed.

2.7 STAGE G: SUBADULT (FIG. 8)

The skull shows the cranial configuration observed in adult stage. The rostrum and the skull vault are markedly prolonged. All bone elements are fused since all sutures are completely closed. The preorbital frontal processes (pfp), as well as the postorbital constriction (pc) are very conspicuous in this stage. The paired nasals start to elevate respect to the other rostral elements. The nuchal crest (cn),

formed by the projection of the sutura occipitointerparietalis is higher than in previous stages, however it does not reach the size observed in adults.

Rostral Region (Fig. 8, A): All elements are fused; therefore the serrated sutures frontonasalis (sfn), frontopremaxillaris (sfpmx) premaxilonasalis (spmxn) interpremaxillaris (sipmx) and the squamous suture zygomaticomaxillaris (szmx) are completely closed and are not observed in this stage. Only the permanent teeth are present.

Lateral Region (Fig. 8, B): All sutures in this region are closed and are no longer visible. The sutura squamosa (ssq) with squamous morphology, the serrate sutures called exoccipitosquamous (eosqs) and the exoccipitoparietalis sutura (seopa) are already closed. The jugal is a robust bone, which elongates anteroposteriorly; this is fused to the squamous and the maxillary bones, since the squamous suturas zygomaticotemporalis (szt) and zygomaticomaxillaris (szmx) are closed.

Dorsal Region (Fig. 8, C): The parietals are fused completely to the frontals and the sutura frontoparietalis (sfp), which is fully closed and no longer visible; as well as all other sutures of this skull region.

Occipital Region (Fig. 8, D): The supraoccipital bones are completely fused with the interparietals; therefore the squamous suture called sutura occipitointerparietalis (soipa) is closed. All sutures in this region of the skull are completely closed and thus are not visible.

2.8 STAGE H: ADULT (FIG. 9)

The skull of *Desmodus rotundus* shows the adult configuration appearing as a unit. All the skull elements are fused and the sutures are not visible. The preorbital frontal process (pfp) is observed largely swollen, just before the optical fossa. The nasals, already fused, exhibit an evident increase on its angle of elevation in respect to the rest of the rostrum, being almost horizontal. The postorbital constriction (pc) is very sharp. The skull presents a low sagittal crest (sc), while the nuchal crest (nc) is quite pronounced. A quite pronounced occipital process (op) is located at the intersection of these two crests.

3. DISCUSSION

In this paper we provide the first description and analysis of the postnatal development in the skull of *Desmodus rotundus*. In general, the adult skull exhibits a pronounced snout and an elongated occipital region compared with the short snout and round skull of the neonate. Towards the rostral region these changes are mainly due to marked prolongation of the frontal and premaxillary bone elements. On the other hand, the marked enlargement of the vault is mainly due to the loss of bones overlap present in the neonate. Furthermore, the sutures remain open until advanced stages of development, yet however all the sutures are completely closed and not visible in the adult stage. Such sutures show abrupt changes in advanced stages of development. Lastly, the presence of an additional paired bone, called anterior frontal (af), is described.

The double origin for the frontal bone has not been documented in mammals. There is no possibility that this bone constitutes a prefrontal, because the two bone elements contact in the midline of the skull, mammals are characterized by the absence of the prefrontal, and finally this element begins to fuse early with the frontal bone to constitute the definitive frontal bone. For other mammals, bones with similar pattern of development, in which the two elements begins to fuse early to constitute the definitive bone element, have been also observed with a double origin (de Beer, 1937; Koyabu et al., 2012). A recent study of the interparietal bone demonstrates a dual origin from neural crest and mesoderm for that bone in mammals, and that characteristic is a synapomorphy for the group since its is shared for 300 extinct and extant taxa (Koyabu et al., 2012). In this study, the description of the cranial bone elements of *Desmodus rotundus* reveals a double origin in the development of the paired frontal bones, although, there has been observed that the mammalian frontal and squamosal bones are neural crest derived, in contrast to the parietal and interparietal (Gillian & Morriss-Kay, 2001). This characteristic, a double origin for the frontal, could be a synapomorphic character of all Phyllostomidae or Microchiroptera, since Giannini et al. (2006) does not report this condition in *Pteropus* (Megachiroptera: Pteropodidae), but similar ontogenetic studies are necessary in other bat species.

The trend of premaxillary bones reduction in most chiropterans (Wible & Novaceck, 1988; Novacek, 1993) is not applied in *Desmodus rotundus*, since the premaxillary bones show a significant size compared with the other elements of the rostral region; the magnitude of these bones is probable related with the specialized big caniniform incisor tooth associated to its diet. In this work we found that *Desmodus rotundus* presents two deciduous incisors, in contrast to just one permanent incisor. This is consistent with Phillips (1971), who found the same pattern in the bat genus *Macrotus* bat genera. It contrast with many other mammals in which the deciduous dentition corresponds exactly with the permanent one. This fact

suggests that the two set of teeth are under separate genetic control (Adams & Pedersen, 2000). In bats, the deciduous teeth usually are shed as the permanent teeth erupt (Phillips, 1971). It was observed in *D. rotundus* that the two deciduous incisors teeth are present a great part of the development with the unique permanent incisor already erupted. Birney & Timm (1975) found a similar pattern in the desmodontine *Diphylla ecaudata*, where the second deciduous incisor is shed late. It would be interesting to evaluate whether this condition is a diagnostic character as this two species belong to Desmodontinae, and his relation to hematophagous evolution in this clade.

In general, the sutures in *Desmodus rotundus* shows a progressive sequence of closure: i) beginning in the neonate with some rostral and dorsal sutures; ii) continuing in the juvenile with other rostral sutures and starting some lateral and occipital sutures; iii) finally in the subadult, all remaining sutures. This sequence, analyzed in a broader specimen series could describe a pattern; but it is unknown whether it is conserved for all microchiropterans or if it is exclusive for each genera or species according to specific ecological needs like in some terrestrial mammals (Wilson & Sanchez-Villagra, 2009; Sanchez-Villagra, 2010; Flores & Barone, 2012).

Cranial sutures in *Desmodus rotundus* remain open until the last stage of development of the juvenile age category (stage E). This is particularly important considering the fact that this species exhibits drastic transformations in size and shape during development (Herring, 1972); and the sutures are essential for skull growth, since they are the major sites of bone expansion during postnatal craniofacial growth (Opperman, 2000). Subsequently most of these sutures show abrupt changes in their degree of development, varying in some cases from being completely open in one stage, to being completely closed in the other. In this

sense, the abrupt changes in suture development are associated with drastically changes in general skull shape, especially in subadult F and G stages of development. These abrupt changes in the sutures are probably related to the fact that the major cranial characteristics observed in adult stage start their development in these transitional stages between the last juvenile stage and the first subadult stage. However, the development of such adult characteristics at this stages allows this species to occupy a specific ecological niche related with the hematophagy. It probably corresponds to an ontogenetic period when the species is learning about specific life cycle behaviors, such as the alimentary strategy.

The more common suture morphology in the skull of *Desmodus rotundus* is the serrated shape, which implies a close interdigitation of the bone elements (Chopra, 1957). Sutures are known to be responsible for absorbing and transmitting mechanical stresses generated during activities, and the more complex suture shapes, as serrated, support greater strains (Rafferty & Herring, 1999; Mao et al., 2003; Flores & Barone, 2012). This is especially important in a bat that needs to cut the thick tegument of preys like *Bos taurus* and *Equus ferus caballus* to feed on their blood (Aguirre et al., 2002). Also the sutural ontogenetic changes are influenced by extrinsic and intrinsic forces that act over the skull (Jaslow, 1990). Therefore the change of suture morphology during the development in *Desmodus rotundus* from a squamous to a serrated shape (sutura frontonasalis) is probably associated with the development of the behavior of feeding techniques, because this phenomenon is observed in sutures from other mammal skulls associated with changes in diet due to mechanical strains (Flores & Barone, 2012).

The features of ossification patterns of the skull are useful to distinguish different age categories among the individuals of a species. In this sense, we found

important characteristics that could be useful for the age determination in this species: the frontoparietal foramen (fpf), present in the neonate stage, disappear in the juvenile stage (D); the sutura premaxilolacrimalis is closed until the early juvenile stage B, distinguishing this stage from the neonate stage A; different sutures were closed during the later juvenile stage (E, F, G); the sutura interparietalis (sip) is closed completely until juvenile stage E, and remarkable sutures as sutura sagitalis (ss), sutura interfrontalis (sif) and sutura internasalis (sina) are completely closed until the early subadult stage F; the deciduous dentition is shed completely until the late subadult stage G just before the adult age category; the zygomatic arch is completely formed until the later subadult stage G too, which implies that the sutura zygomaticomaxillaris (szmx) and the sutura zygomatico temporalis (szt) are completely closed until this stage.

These characteristics observed in the skull development are likely related with other aspect of his behavioral biology, since common vampire bat feeding is very particular, and this is the major factor that causes variations in this species respect to the other members of his family (Baker et al., 2010). *Desmodus rotundus* has an exceptionally long duration of juvenile development with suckling up to 10 months (Schmidt & Manske, 1973; Wilkinson, 1984,1985). After 2 months, juvenile are fed with regurgitated blood from their mothers, and at four months they start to drink blood by themselves. The first feeding expeditions are made with the tutoring of the mother (Schmidt et al., 1980; Wilkinson, 1985). Therefore, it is apparent that the developmental transition from a juvenile skull with a relatively easy diet comprised mainly of milk and blood to a subadult and adult skull specialized for sanguivory, with nutritional independence, implies changes in skull related whit ossification pattern, which are necessary for biomechanical function in adult stage.

The obligated hematophagy of this species force it to develop special skills. Neurologically, *Desmodus rotundus* exhibit the major neocortical volume between 276 species of bats in which this characteristic have been studied (Baron et al., 1996; Bhatnagar, 2008). This aspect has special interest because the relative size of chiropteran brain is associated with their aerial niche. The ones who forage in more complex environments present a bigger brain (Eisenberg & Wilson, 1978). In this study, we found that the cranial vault of *D. rotundus* develops a grater size, allowed by the overlapping of the ectocranial bones in the neonatal and juvenile stages. This overlapping have been found in other mammals like *Saimiri boliviensis* (Flores & Barone, 2012) and *Homo* (de Beer, 1937), and it allows the skull to growth rapidly in volume to store a big brain. Besides, the increasing of the supraoccipital bone and the vertical orientation in the occipital region observed in *D. rotundus* might be related with the enlargement of the cerebellum as in some other mammals (Zeller, 1987). It is known the development of this cerebral region in Phyllostomidae (Henson, 1970) and specially in the Desmodontinae subfamily (Mc Daniel, 1976).

Desmodus rotundus also shows a great development of olfactory structures (Baron et al., 1996). This feature is related probably with the notable development of the skull nasorostral region expressed in the development of the preorbital frontal process (pfp). Fawcett (1919) reports a similar development in the rostral region in the chondrocranium of *Miniopterus schreibersii* (Miniopteridae), which exhibits the recessus frontalis, a cavity located behind the nasal foramen and related with the development of the olfactory system. This preorbital frontal process (pfp) is not reported in other descriptions of the adult skull of *D. rotundus* and is probably related to a greater development of the olfactory system. It is important to evaluate the variation of this rostral region, since the formation of the preorbital frontal process could be a variation for this population or a trait important to study in the determination of species in *Desmodus*. While some authors consider

Desmodus rotundus as a single species throughout its distribución (Koopman, 1988; Simmons, 2005), presently this genus is considered as polytypic, with two subspecies recognized: *Desmodus rotundus murinus* in Mesoamerica and *Desmodus rotundus rotundus* in South America (Greenhall & Schmidt, 1988; Orihuela, 2011). Recent genetic studies with cytochrome b in Brazil have recognized four geographical clades, separated by extremely high levels of sequence divergence (ranging from 6% to 11%), the highest ever described for a neotropical bat species and cannot be explained by female philopatry alone (Martins et al., 2007). More recently, Martins & Hubbe (2012) found that this genetic diversity is supported by significant statistical morphometry. In this sense, the genus *Desmodus* probably presents cryptic diversity. This study comprises a baseline for future comparative works, since we could understand the origin of the morphological variation in this species at postnatal stages. This analysis allows evaluating if the cranial variation in size may be explained by the bone overlapping and late sutures fusion, as well as analyzing the ontogenetic variation of different traits with taxonomic utility. The study of morphologic variation is very important in this clade because present widespread distribution, genetic diversity and fossil sample. Therefore, this study contributes to understand the ontogenetic processes responsible of the diversity observed in *Desmodus*.

4. CONCLUSIONS

The sutures showed a long term open pattern, followed by abrupt changes in morphology and development, acquiring more complex interdigitated shapes and fusing bone elements in subadult and adult age categories. We documented a double origin of the frontal bone in the common vampire bat. The elongation of the composed frontal and premaxillary, the loss of the overlapping between bones and the occurrence of bone processes on the preorbital, the frontal, and the occipital

regions are responsible of the major variation in skull size and shape. All these changes in development are thought to be tightly related with the strains that the individual carries while develops obligate sanguivory.

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ANNEXES

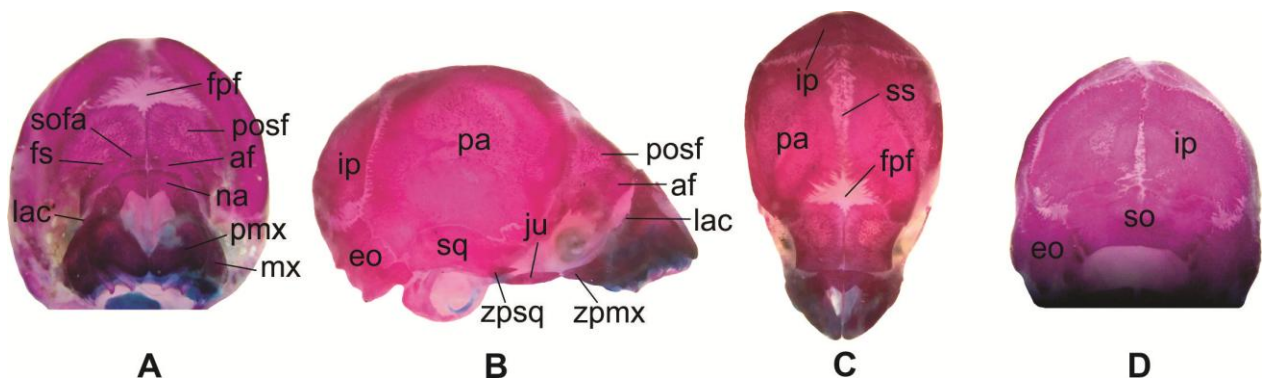
Table 1. Conditions of Ectocranial Suture morphology.

Age Categories		Newborn (1)				Juvenile (4)								Subadult (3)								Adult (5)								
		Development stages				A (1)		B (1)		C (1)		D (1)		E (1)		F (1)		G (2)		H (5)										
Region	Sutures	% A	% C	F	S	% A	% C	F	S	% A	% C	F	S	% A	% C	F	S	% A	% C	F	S	% A	% C	F	S					
Rostral	Frontal	≤25	≥75		Sq	≤25	≥75		Sq	≤25	≥75		Sq	0	100		Sq	0	0	x	Sq	0	0	x	Sq	0	0	x	Sq	
	Frontonasalis	100	0			100	0			100	0			100	0			Sq	0	100		Srr	0	0	x	Srr	0	0	x	Srr
	Frontopremaxillaris	100	0			100	0			100	0			100	0			≤25	≥75		Srr	0	0	x	Srr	0	0	x	Srr	
	Interfrontalis	100	0			100	0			100	0			100	0			≤25	≥75		Pl	0	0	x	Pl	0	0	x	Pl	
	Interpremaxillaris	100	0			100	0			100	0			100	0			0	100		Pl	0	0	x	Pl	0	0	x	Pl	
	Internasalis	100	0			100	0			100	0			100	0			0	0	x	Pl	0	0	x	Pl	0	0	x	Pl	
	Maxilolacrimalis	100	0			100	0			100	0			100	0			0	0	x	Sq	0	0	x	Sq	0	0	x	Sq	
	Maxilloincisiva	100	0			100	0			100	0			100	0			≥75	≤25		Srr	0	0	x	Srr	0	0	x	Srr	
	Premaxilolacrimalis	100	0			0	0	x	Sq	0	0	x	Sq	0	0	x	Sq	0	0	x	Sq	0	0	x	Sq	0	0	x	Sq	
	Premaxilonasalis	100	0			100	0			100	0			100	0			≤50	≥50		Srr	0	0	x	Srr	0	0	x	Srr	
Zigomaticomaxilaris	100	0			100	0			100	0			100	0			0	100			0	0	x	Sq	0	0	x	Sq		
Dorsal	Frontoparietalis	100	0			100	0			100	0			100	0			0	100		Sq/Srr	0	0	x	Sq/Srr	0	0	x	Sq/Srr	
	Sagittalis	≤25	≥75		Srr	≤25	≥75		Srr	0	100		Srr	0	100		Srr	0	0	x	Srr	0	0	x	Srr	0	0	x	Srr	
Lateral	Exoccipitosquamous	100	0			100	0			100	0			100	0			100	0			0	0	x	Srr	0	0	x	Srr	
	Exoccipitoparietalis	100	0			100	0			100	0			100	0			≥50	≤50		Srr	0	0	x	Srr	0	0	x	Srr	
	Squamosa	100	0			100	0			100	0			100	0			≥75	≤25		Sq	0	100		Sq	0	0	x	Sq	
	Zigomaticotemporalis	100	0			100	0			100	0			100	0			0	100			0	0	x	Sq	0	0	x	Sq	
Occipital	Interparietalis	100	0			100	0			≤50	≥50		Srr	≤25	≥75		Srr	0	0	x	Srr	0	0	x	Srr	0	0	x	Srr	
	Occipitointerparietalis	100	0			100	0			100	0			≤25	≥75		Sq	≤25	≥75		Sq	≤25	≥75		Sq	0	0	x	Sq	
	Occipitalis	100	0			100	0			100	0			≥75	≤25		Pl	0	0	x	Pl	0	0	x	Pl	0	0	x	Pl	
	Parietointerparietalis	100	0			100	0			≤75	≥25		Srr	≤25	≥75		Srr	≤25	≥75		Srr	≤25	≥75		Srr	0	0	x	Srr	

Morphology and closure percentage in *Desmodus rotundus* sutures at the four age stages. Neonate to adult; and their eight development stages (letters A to H). Abbreviations: %A , percentage open; %C, percentage closing; f, fused; serr, serrated; sq, squamous; pl, plane. Parentheses indicate the number of the sample. Percentages was made qualitatively.

Frontal, lateral and caudal views of the skull of a subadult of *Desmodus rotundus* in the Subadult F stage. Dotted lines show sutures that are not visible in that stage. A. Rostral and Dorsal region. B. Lateral region. C. Occipital region. Abbreviations: af, anterior frontal; c, canine; di, deciduous incisive; eo, exoccipital; eosqs, exoccipitosquamous suture; fr, frontal; fs, frontal suture; i, incisive; ip, interparietal; ju, jugal; lac, lacrimal; m, molar; mx, maxilla; na, nasal; op, occipital process; pa, parietal; pc, postorbital constriction; pm, premolar; pmx, premaxilla; posf, posterior frontal; sfp, sutura frontoparietalis; sif, sutura interfrontalis; sina, sutura internasalis; sipmx, sutura interpremaxillaris; sip, sutura interparietalis; smi, sutura maxilloincisiva; smxl, sutura maxilolacrimalis; so, supraoccipital; soc, sutura occipitalis; sofa, supraorbital foramina; soipa, sutura occipitointerparietalis; spmxn, sutura premaxilonasalis; spmxl, sutura premaxilolacrimalis; spip, sutura parietointerparietalis; szmx, sutura zygomaticomaxillaris; sq, squamosal; ss, sutura sagittalis; ssq, sutura squamosa; seopa, sutura exoccipitoparietalis; szt, sutura zygomaticotemporalis; zpmx, zygomatic process of the maxilla; zpsq, zygomatic process of the squamous.

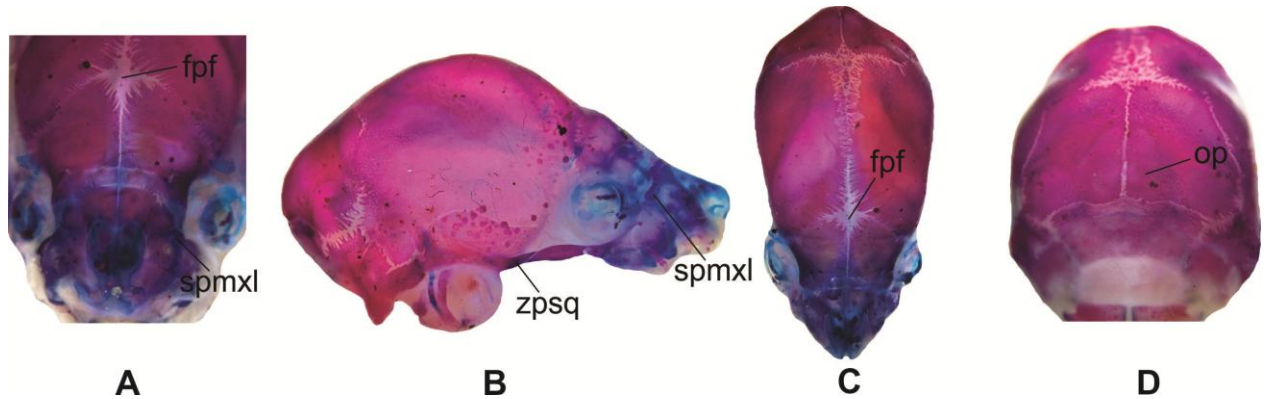
Figure 2. *Desmodus rotundus* skull in A stage of development



A, Rostral; B, lateral; C, dorsal and D, occipital regions. Abbreviations: pmx, premaxilla; mx, maxilla; lac, lacrimal; na, nasal; fr, frontal; af, anterior frontal; posf, posterior frontal; fs, frontal suture; sofa, supraorbital foramina; fpf, frontoparietal

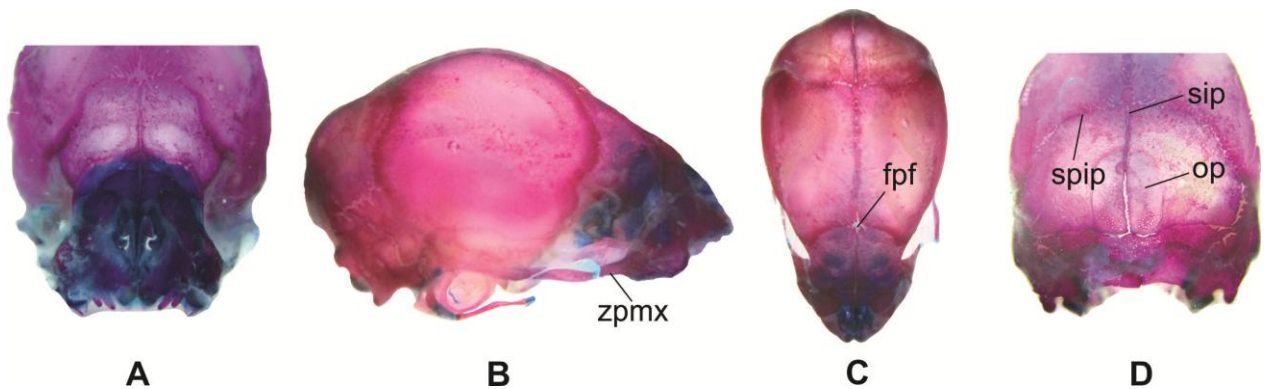
foramen; pa, parietal; ss, sutura sagittalis; ju, jugal; sq, squamosal; zpmx, zygomatic process of the maxilla; zpsq, zygomatic process of the squamous; eo, exoccipital; ip, interparietal; so, supraoccipital.

Figure 3. *Desmodus rotundus* skull in B stage of development.



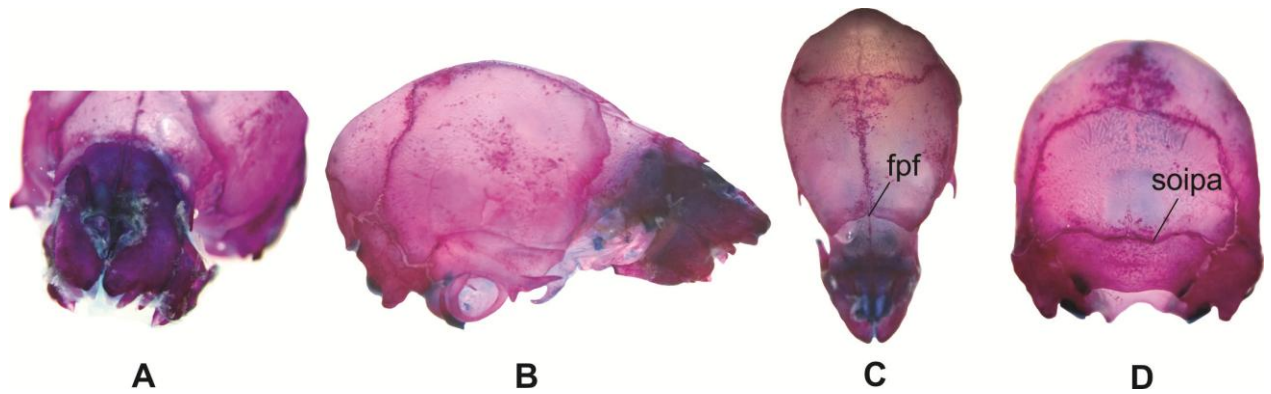
A, Rostral; B, lateral; C, dorsal and D, occipital regions. Abbreviations: spmxl, sutura premaxilolacrimalis; zpsq, zygomatic process of the squamous; fpf, frontoparietal foramen; op, occipital process.

Figure 4. *Desmodus rotundus* skull in C stage of development.



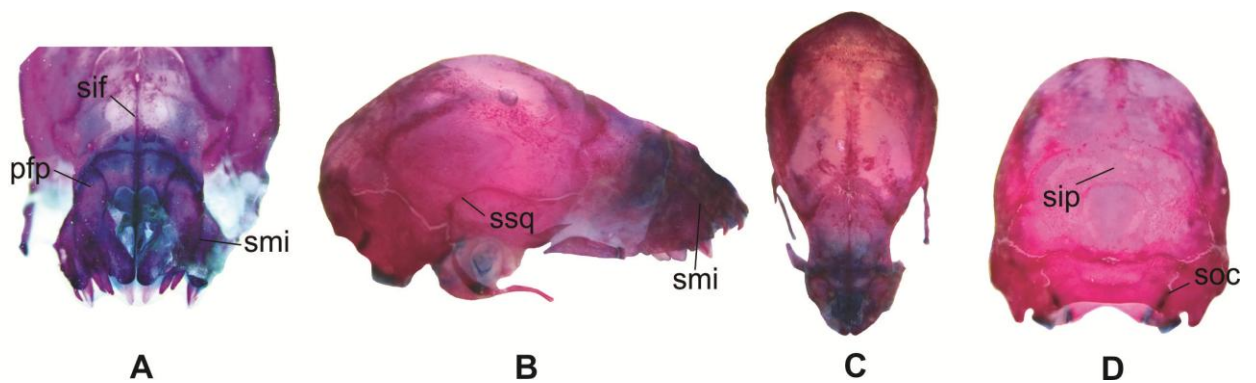
A, Rostral; B, lateral; C, dorsal and D, occipital regions. Abbreviations: fpf, frontoparietal foramen; zpmx, zygomatic process of the maxilla; spip, sutura parietointerparietalis; sip, sutura interparietalis; op, occipital process.

Figure 5. *Desmodus rotundus* skull in D stage of development.



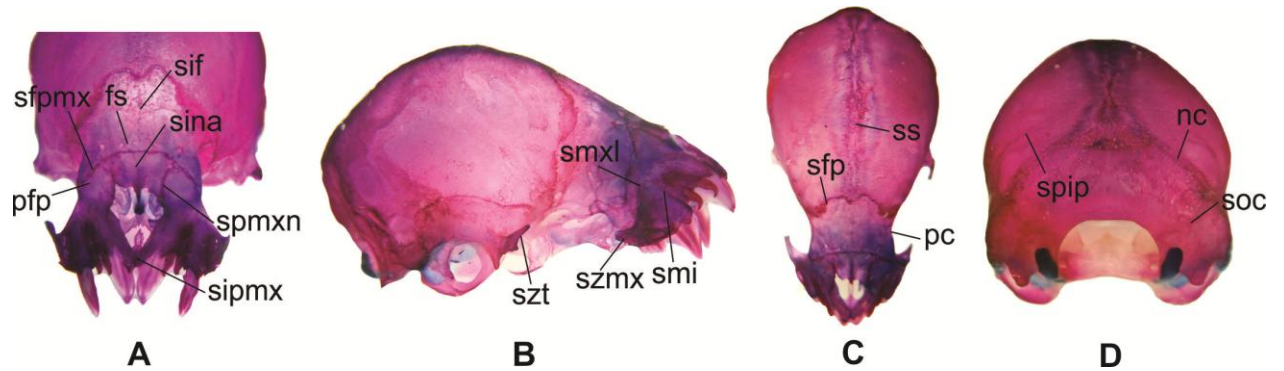
A, Rostral; B, lateral; C, dorsal and D, occipital regions. Abbreviations: fpf, frontoparietal foramen; soipa, sutura occipitointerparietalis.

Figure 6. *Desmodus rotundus* skull in E stage of development.



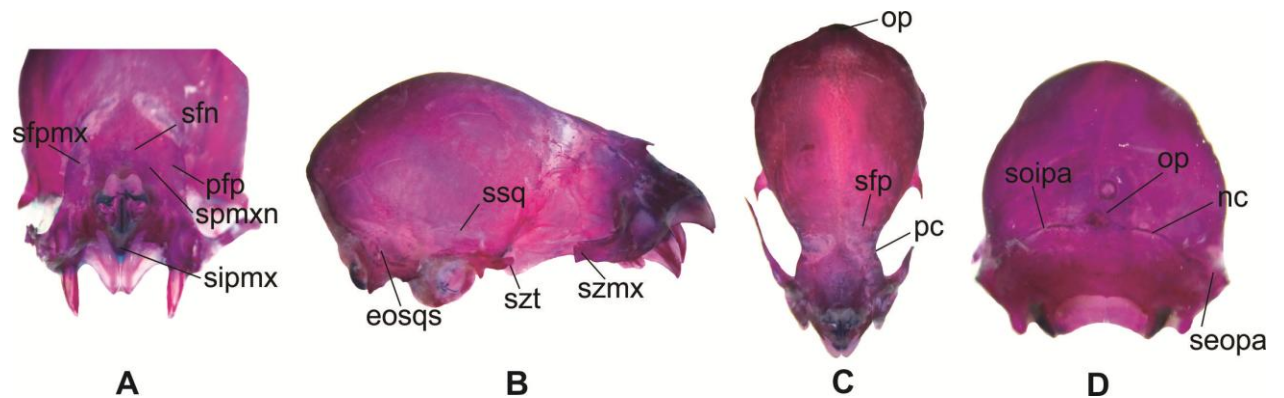
A, Rostral; B, lateral; C, dorsal and D, occipital regions. Abbreviations: sif, sutura interfrontalis; smi, sutura maxilloincisiva; ssq, sutura squamosa; sip, sutura interparietalis; soc, sutura occipitalis; pfp, preorbital frontal process.

Figure 7. *Desmodus rotundus* skull in F stage of development.



A, Rostral; B, lateral; C, dorsal and D occipital regions. Abbreviations: pfp, preorbital frontal process; sina, sutura internasalis; fs, frontal suture; sfp, sutura frontoparietalis; smpxn, sutura premaxilonasalis; sipmx, sutura interpremaxillaris; smi, sutura maxilloincisiva; szmx, sutura zygomaticomaxillaris; pc, postorbital constriction; spip, sutura parietointerparietalis; ss, sutura sagittalis; szt, sutura zygomaticotemporalis; soc, sutura occipitalis; nc, nuchal crest.

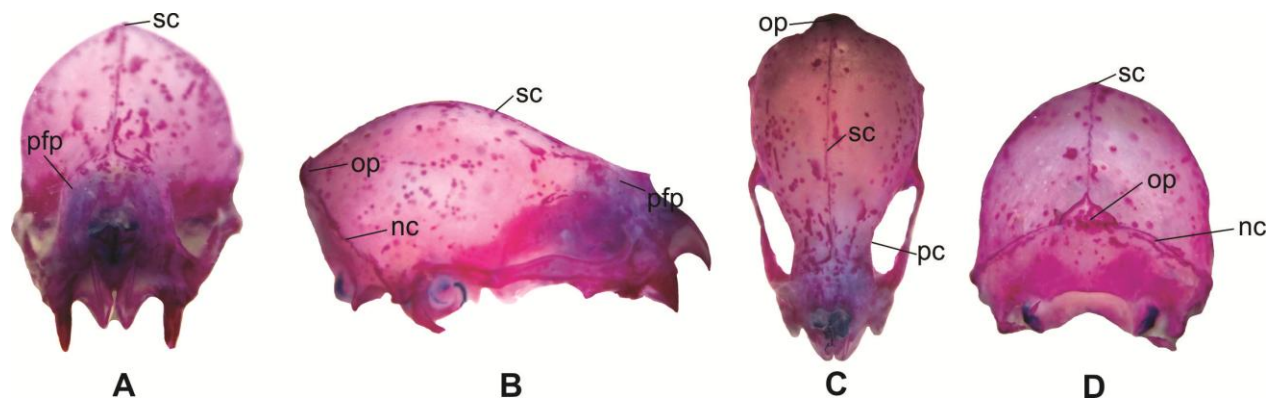
Figure 8. *Desmodus rotundus* skull in G stage of development.



A, Rostral; B, lateral; C, dorsal and D occipital regions. Abbreviations: pfp, preorbital frontal process; sfn, sutura frontonasalis; sfp, sutura frontoparietalis; smpxn, sutura premaxilonasalis; sipmx, sutura

interpremaxillaris; szmx, sutura zygomaticomaxillaris; pc, postorbital constriction; sfp, sutura frontoparietalis; szt, sutura zygomaticotemporalis; ssq, sutura squamosa; eosqs, exoccipitosquamous suture; seopa, sutura exoccipitoparietalis; soipa, sutura occipitointerparietalis; op, occipital process; nc, nuchal crest.

Figure 9. *Desmodus rotundus* skull in H stage of development.



A, Rostral; B, lateral; C, dorsal and D occipital regions. Abbreviations: pfp, preorbital frontal process; pc, postorbital constriction; op, occipital process; nc, nuchal crest; sc, sagittal crest.