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Junction between membranous and endochondral bones in the developing occipital squamosa

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Abstract: The occipital bone squamosa (OCS) is unique because of its double origin from both endochondral and membranous bones. The present study attempted to demonstrate the process of connection between these two bone types. We examined sagittal and frontal histological sections from 29 human fetuses with a crown-rump length ranging from 38 to 328 mm (approximately 7–39 weeks of gestational age [GA]). An initial cartilage plate appeared in the posterior side of the fourth ventricle at GA 7–8 weeks and extended inferiorly to connect with the cartilaginous basioccipital and condyle. At GA 9–10 weeks, on the superior side of the cartilage plate, membranous bone fragments appeared and adopted an arrangement resembling a chain of irregularly-shaped beads. They did not form a complete plate-like bone until late-term. At GA 11–12 weeks, endochondral ossification centers appeared at the upper and lower ends of the cartilage plate. At GA 12–15 weeks, a bar-like periosteal bone developed near and superior to the upper ossification center. Notably, sinusoidal structures, which were surrounded by growing periosteal bones, contained island-like clusters of calcified cartilage fragments. Therefore, the upper ossification center appeared likely to "migrate" downward and become distant from membranous bones. The extending periosteal bone reached and joined the membranous bone fragments. Consequently, the periosteal bones connected between the endochondral and membranous bones in the OCS. This connection was quite different from the other components of the calvaria, where membranous bones overlap the skull base cartilages at the margin.

Key words: Occipital bone, Ossification, Histology, Fetus

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Introduction

The calvaria of the head can be considered to consist of multiple plate-like membranous bones, *i.e.,* a squamosa. The frontal bone squamosa attaches to the endochondral ethmoid, and the latter rides over the former in late-term fetuses [1]. The temporal bone squamosa attaches to the sphenoid ala major, the latter of which is also a secondarily-developed membranous bone [2]. The junction between the ala major and temporal bone squamosa corresponds to the socket of the temporomandibular joint in human fetuses and neonatal period (*i.e.,* the mandibular fossa) [3, 4]. The otic capsule cartilage differentiates into most parts of the petrosa of the temporal bone, and details of its development and growth have already been described [5-7]: the otic capsule cartilage unlikely to contribute to the initial squamosa.

Among the bones that constitute the calvaria, we have considered a squamosal part of the occipital bone or the "occipital bone squamosa (OCS)" to be unique because: (1) it forms through union of the endochondral and membranous bones; (2) its cartilaginous portion, *i.e.,* the bilateral tectum posterius and the medially-located occipital superius, is

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believed to develop as early as the skull base cartilages [8-11]; and (3) its membranous bone portion forms the fragile inferior margin of the posterior fontanelle, which is still membranous and movable at birth. Therefore, the OCS seems to be composed of the early developed endochondral bone and the slowly growing membranous bone. As typically seen along the nasal capsule cartilage [1], membranous bones are likely to use a cartilage or endochondral bone as a mold and mechanical support. Does the membranous bone later develop at and along the upper end of the endochondral bone in the OCS? The aim of this study was to examine the development and growth of the OCS with special reference to when and how the endochondral and membranous bones become joined and combined.

Materials and Methods

The present study was performed in accordance with the provisions of the Declaration of Helsinki 1995 (revised in 2013). We used histological sections from 29 human fetuses (crown-rump length [CRL] 38–328 mm; gestational age [GA] approximately 7–39 weeks). Paraffin-embedded histological sections of 10 human fetuses with a CRL range of 38–97 mm (GA approximately 7–14 weeks) were part of a large collection kept at the Department of Anatomy and Embryology of the Universidad Complutense, Madrid, and had been obtained as a result of miscarriages and ectopic pregnancies at the Department of Obstetrics of the University. No information was available on the genetic background of the embryos. The sections were completely serial and stained with hematoxylin and eosin (H&E), Azan, or silver impregnation. The sectional planes were sagittal (6 specimens) or frontal (4 specimens). These sections included the whole head, or the head, neck and thorax, depending on the fetus size and sectional plane. This study was approved by the Ethics Committee of Complutense University (B08/374). All the photographs of histology sections were captured using a Nikon Eclipse 80 (Nikon).

Nine late-term fetuses and 10 mid-term fetuses (CRL 55–328 mm; GA approximately 11–39 weeks) were part of the collection kept at the Department of Anatomy, Akita University, Akita, Japan. Thus, specimens at a GA of approximately 11–14 weeks originated from both Spain and Japan: five were Japanese and two were Spanish. The 19 Japanese fetuses had been donated by their families to the Department in 1975–1985. They had been preserved in 10% w/w neutral formalin solution for more than 30 years. Data on these specimens, if present, included the date of donation and the GA, but did not include the name of the family, obstetrician or hospital, or the reason for abortion. The use of these specimens for research was approved by the Akita University Ethics Committee (No. 1428; the sixth author [G.M.] was one of the research members). Before routine procedures for paraffin embedding, the mid-term and late-term specimens were decalcified by incubating them in Plank-Rychlo solution ($AlCl_2/6H_2O$, 7.0 w/v%; HCl, 3.6; HCOOH, 4.6) at room temperature for 3–7 days. The sections were semi-serial cut at 100-mm intervals and stained with H&E, silver impregnation or Elastica-Masson (a variation of Masson-Goldner staining) [3, 12]. The sectional planes were sagittal (14 specimens) or frontal (5 specimens). Sections from smaller specimens included the whole head, while the larger head was divided into 2–4 parts before sectioning, depending on the sectional plane. All the photographs of histology sections were captured using a Nikon Eclipse 80. The present study was also approved by the Ethics Committee of Tokyo Dental College (932-2).

Finally, we need to explain about terminology used in this study. Because of limited information at the donation, the GA in the present description is often based on the basis of the CRL values. Using immunohistochemistry of proteoglycans, our group has demonstrated a mosaic of membranous and endochondral bones in the human fetal head and neck (Fig. 1) [13]. In addition, the periosteal bone is likely to surround sinusoidal tissues near the endochondral ossification center. These three modes of ossification are easy to discriminate by routine histology (Fig. 1). In the present study, the term "ossification center" will be used for such endochondral ossification, although classically this term has been applied for sites at which the initial membranous bone appears [8, 14].

Results

A mosaic comprising three modes of ossification at the head and neck

Fig. 1 shows the combined modes of ossification in the human fetus head and neck. A typical sample was found in the occipital condyle (Fig. 1A). The membranous ossification was identified by a bone fragment (or a cluster of fragments) that was surrounded by osteoblast-like cells (Fig. 1B). The fragment was separated from the perichondrium or periosteum by loose tissues. The periosteal ossification occurred

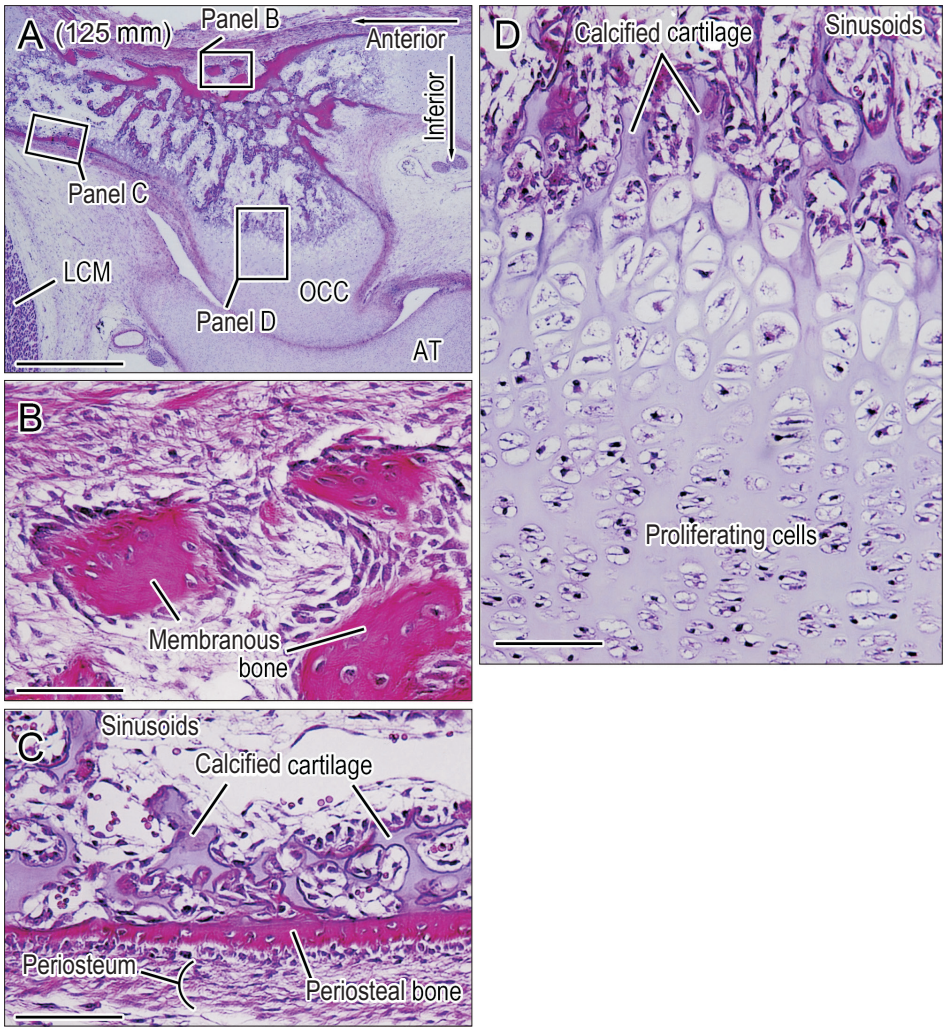

Fig. 1. Three types of ossification seen in the occipital condyle: a demonstration of the general morphology. H&E stained sagittal section of a 125-mm crown-rump length fetus (GA approximately 16 weeks). The upper side of each panel corresponds to the superior side of the head and neck. Panel (A) displays the occipital condyle and atlanto-occipital joint. Squares in panel (A) are shown in panels (B–D) at higher magnification. Panel (B) exhibits membranous bone fragments. Along the periosteum (C), a plate-like, periosteal bone appears adjacent to calcified cells originating from the endochondral ossification center. Panel (D) shows the endochondral ossification center. Scale bar=1 mm in panel (A), scale bars=0.1 mm in panels (B–D). AT, atlas; OCC, occipital bone; LCM, longus colli muscle.

along the periosteum or perichondrium, and osteoblast-like cells were arranged in line superficially or externally to the thin bony plate. Thus, the periosteal bony plate faced sinusoids containing calcified cartilages and/or endochondral bone fragments (Fig. 1C). Like the fragment of membranous bone, the periosteal bone was also likely to contain osteoblast-like cells. The endochondral ossification center was defined by a columnar arrangement of hypertrophic cartilage cells in combination with irregularly-shaped calcified cells (bone side) as well as proliferating cells (cartilage side) (Fig. 1D).

Endochondral bone of the occipital squamosa

Below, one figure represents a morphology at a specific GA or a developmental stage of the OCS and the panel A usually shows the anatomy at a lower magnification. Thus, one figure corresponds to observations of one fetus.

The occipital squamosa cartilage appeared as a short cartilage plate at 7–8 weeks (Fig. 2). By this stage, midline cartilages at the skull base as well as vertebrae had become well differentiated, but the cartilaginous OCS was restricted to and near the fourth ventricle of the hind brain (Fig. 2A, B). The composite cartilage cells initially took a net-like arrangement (Fig. 2C) and, depending on increased deposition of extracellular matrix, became round or oval (Fig. 2D). At this stage, the perichondrium was not clear. Next, membranous bone fragments appeared and adopted an appearance resembling a chain of beads (Fig. 3A). However, this membranous bone chain was separated from the cartilaginous OCS by loose tissue until 12 weeks (Fig. 3). Fig. 3 shows a rare example of the cartilaginous OCS being composed of upper and lower plates. These plates were separated by a space (Fig. 3G) and the lower parts of the membranous bone extended inferiorly along the external aspect of the upper plate to

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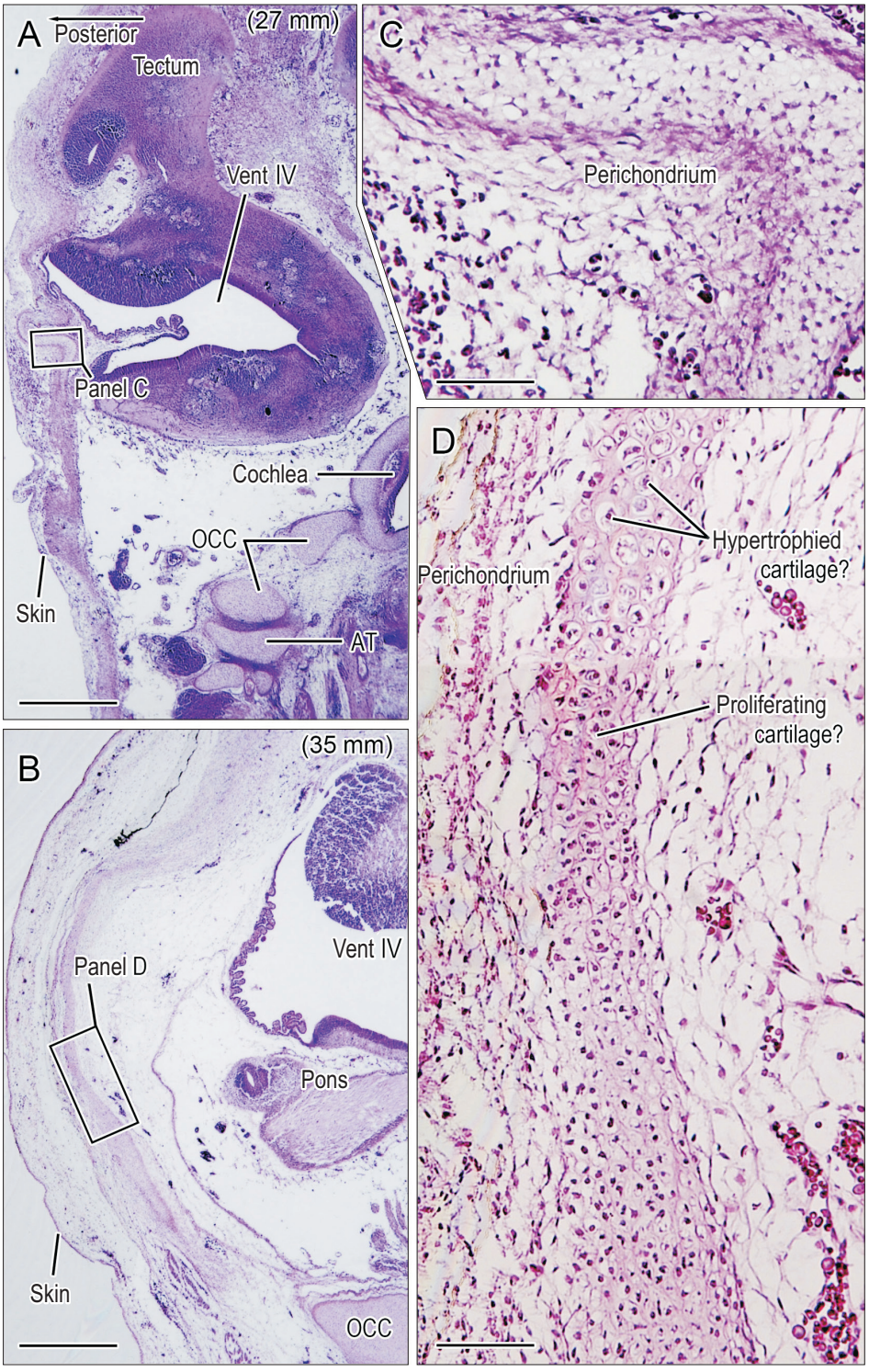

Fig. 2. Initial cartilages of the occipital squamosa. Panels (A) and (C): H&E stained sagittal sections of a 27-mm crown-rump length fetus (gestational age [GA] approximately 7 weeks), and panels (B) and (D): a 35-mm fetus (GA approximately 8 weeks). The initial cartilage plate of the occipital squamosa appears near and posterior to the fourth ventricle (vent IV in A), and soon elongates inferiorly toward the basioccipital and condyle (occipital bone [OCC]; B). The cartilage tissue is homogeneous (C, D). Scale bars=1 mm in panels (A, B); scale bars=0.1 mm in panels (C, D). AT, atlas.

reach the upper end of the lower plate (Fig. 3A–F). Superiorly, the membranous bone reached a level above the tentorium cerebelli. At and around 12 weeks, upper and lower centers of endochondral ossification appeared in the cartilaginous plate (Fig. 4A). A columnar arrangement of cartilage cells was absent and calcified cells provided a basophilic net (Fig. 4C, D). Between these two ossification centers, there was a specific cartilage area containing ballooning cells (Fig. 4B). Simultaneously, immediately superior to the cartilage, membranous bone fragments became joined to form a bar (Fig.

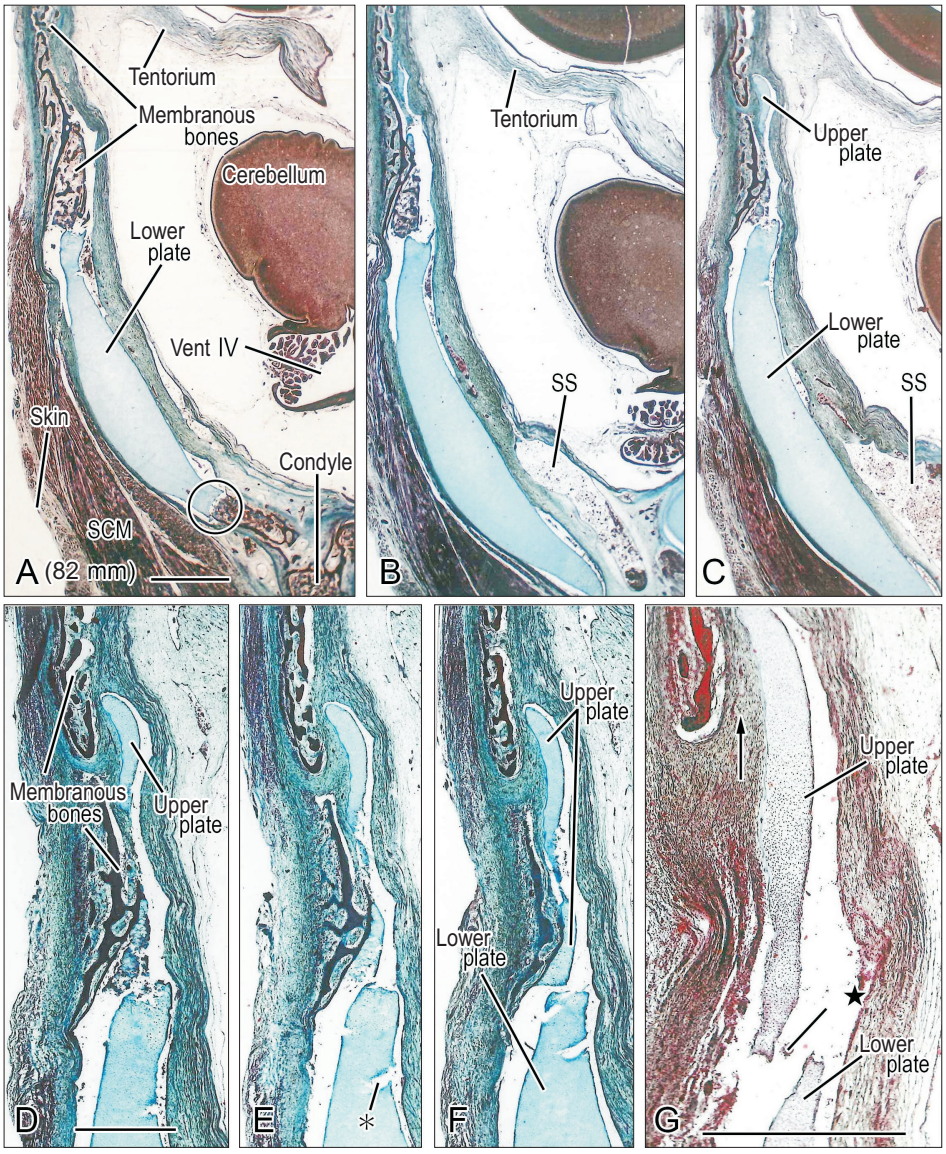

Fig. 3. The cartilaginous occipital squamosa without an ossification center does not attach to a membranous squamosa. Azan-stained sagittal sections of an 82-mm crown-rump length fetus (gestational age approximately 12 weeks). The upper side of each panel corresponds to the superior side of the head. Panel (A) (or G) displays the medial (or lateral) plane in the figure. Panels (C) and (D) show the same section at different magnifications. The early cartilaginous squamosa is composed of the upper and lower plates, which are separated by a space (star in G). The endochondral ossification center is indicated by a circle in panel (A). The membranous bone was separated from the cartilaginous plate (arrow in G). Asterisk in panel (E) indicates tissue damage during the histological procedure. Panels (A–C) or panels (D–F) were prepared at the same magnification. Scale bars=1 mm in panels (A, D, G). Tentorium, tentorium cerebelli; SCM, splenius capitis muscle; SS, sigmoid sinus.

4E), which was surrounded by osteoblast-like cells (Fig. 4F). The upper center was still separated from the membranous bones by loose fibrous tissue.

Junction between endochondral and membranous bones

The connection between the cartilage and membranous bone occurred more than 5–25 mm below the future fonticulus posterior (or the posterior margin of the developing parietal bone) depending on size of the specimen. The junction was characterized by bulky or stout periosteal bones. By 14–15 weeks, the periosteal bone had surrounded or lined the sinusoidal tissues superior to the upper ossification center (Figs. 5, 6). The sinusoidal tissue contained island-like clusters of endochondral bone fragments and calcified cartilage that had originated from the upper endochondral ossification center. These endochondral elements became attached to and intermingled with membranous bone fragments. Notably, the calcified cartilage tended to lie at a site distant from (*i.e.,* superior to) the upper ossification center (Fig. 6C, D). This isolated calcified cartilage was continuous with, or fused to, a membranous bone fragment and/or a periosteal bone bar.

The periosteal bone was continuous with the perichondrium of the cartilaginous OCS and surrounded by no or few osteoblast-like cells, in contrast to the abundant cells surrounding the membranous bone fragment (Fig. 6E). Membranous bones extended inferiorly along the external

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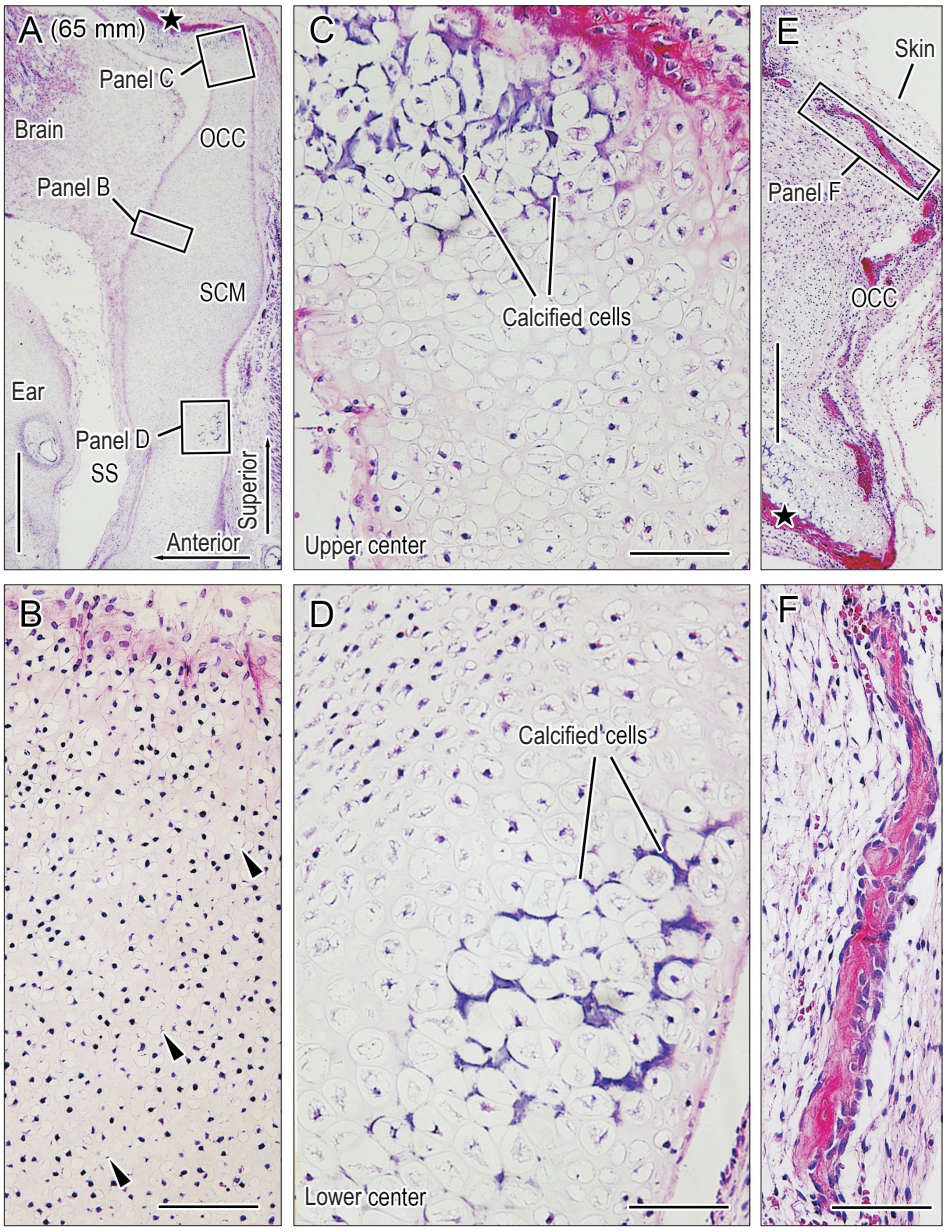

Fig. 4. Cartilaginous occipital squamosa with two ossification centers appears continuous with a membranous squamosa. H&E stained sagittal section of a 65-mm crown-rump length fetus (gestational age approximately 12 weeks). The upper side of each panel corresponds to the superior side of the head. Panel (A) displays an inferiorly-located cartilaginous plate, while panel (E) displays the superiorly-located membranous bones. Stars in panels (A) and (E) indicate the corresponding site. Squares in panel (A) are shown in panels (B–D) at higher magnification. Panel (F) is a higher-magnification view of the square in panel (E). Panels (C) and (D) exhibit the upper and lower endochondral ossification centers, respectively. A cartilage layer with ballooning cells (arrowheads in B) is sandwiched between these ossification centers. Membranous bone fragments are located just beneath the skin (E), and each of the fragments is surrounded by osteoblast-like cells (F). Scale bars=1 mm in panels (A, E); scale bars=0.1 mm in panels (B–D, F). SCM, splenius capitis muscle; SS, sigmoid sinus; OCC, occipital bone.

aspect of the periosteal bone (Figs. 5B, 6D) and the external growth of the membranous bone later extended to reach the cartilaginous plate (Fig. 7A, B). A columnar arrangement of cartilage cells in the ossification center became evident with increasing age (Fig. 5C vs. Fig. 7C, D). A site-dependent difference in the density of osteoblast-like cells around the bone became more evident (Fig. 7E, F). A specific cartilage containing ballooning cells continued to exist between the two ossification centers (Fig. 7G).

Overall, it seemed likely that superior growth of the periosteal bone allowed it to first connect the cartilaginous OCS to the membranous bone chain. Later, conversely, the membranous bones grew inferiorly and covered the periosteal bone. Notably, the isolated, superior clusters of endochondral bone fragments and/or calcified cartilages were present at a level that surrounded or was lined by the periosteal bone.

Discussion

The present study appears to be the first to have demonstrated double endochondral ossification centers in the cartilaginous OCS. These double centers sandwiched a cartilage zone with ballooning cells and less matrix, apparently corresponding to a “resting cartilage zone” (future bone

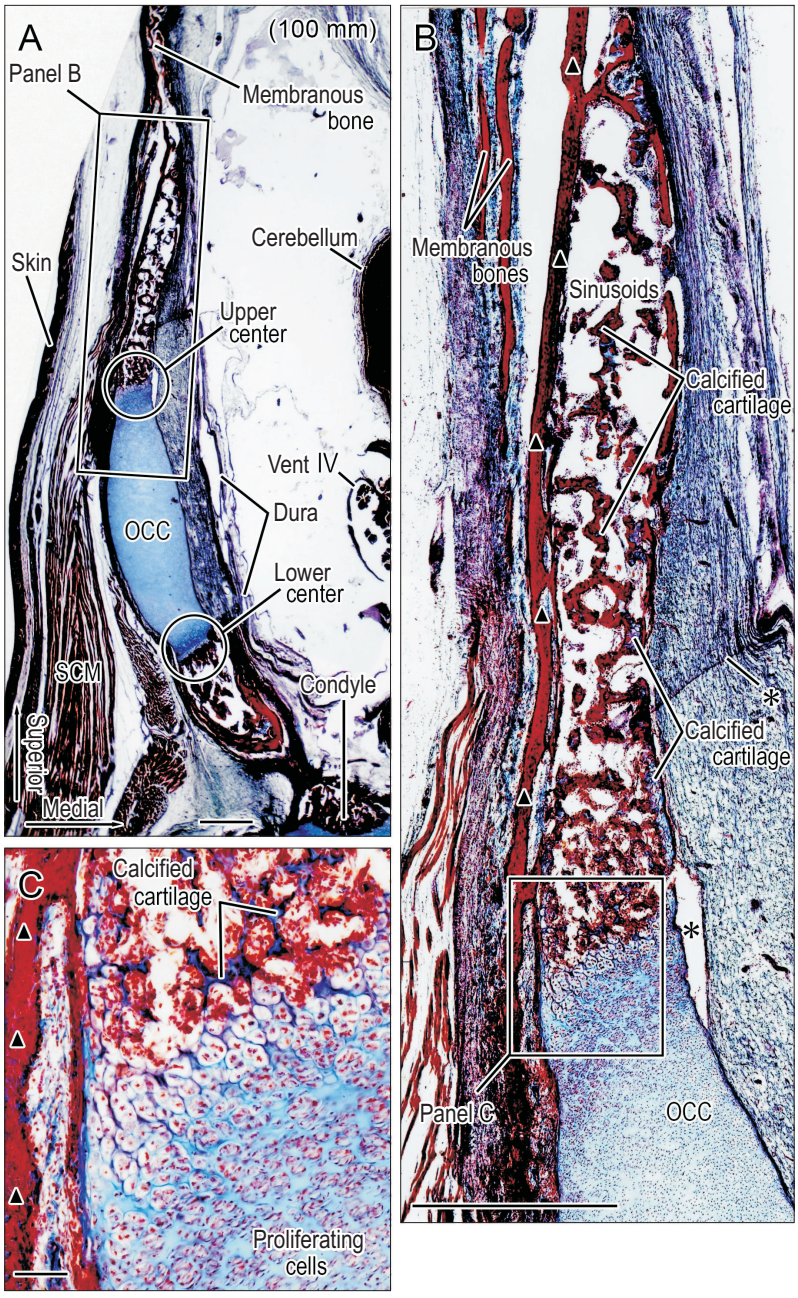

Fig. 5. Long periosteal bone lining the external aspect of the endochondral bone area. Azan-stained sagittal section of a 100-mm crown-rump length fetus (gestational age approximately 14 weeks). The upper side of each panel corresponds to the superior side of the head. Panel (A) displays the upper and lower centers of endochondral ossification (two circles). The square in panel (A) (or B) is shown in panel (B) (or C). A stout bar of periosteal bone (triangles in B, C) grows superiorly and connects the cartilage plate to the membranous bone. Abundant calcified cartilages are scattered in the sinusoidal tissue (B). Asterisks in (B) indicate an artifactual space. Scale bars=1 mm in panels (A, B); scale bar=0.1 mm in panel (C). SCM, splenius capitis muscle; OCC, occipital bone.

junction; [15, 16]) between endochondral ossification centers in the midline cartilage mass at the skull base (*i.e.,* the ethmoid–presphenoid–basisphenoid–basioccipital). Smith and colleagues considered that the resting zone facilitates and regulates bone growth. Likewise, Opperman (2000) [17] noted a suture between membranous bones of the rodents' calvaria as a morphological aspect of the bone growth and examined a sequence of molecular markers expressed in the bone reconstruction. The membranous-endochondral junction in the OCS resembled a "suture" for his subject because of folded and/or overlapped membranous bones contained. However, periosteal ossification seemed to be out of his focus.

Classically, it has been considered that the overlapping membranous bones as well as the overlap between the membranous and endochondral bones at the junction contribute significantly to bone growth that determines orofacial patterning [18-23]. Therefore, this type of bone junction was termed a "growing suture" [24]. In contrast, because stout periosteal bones were evident, the endochondral-membra-

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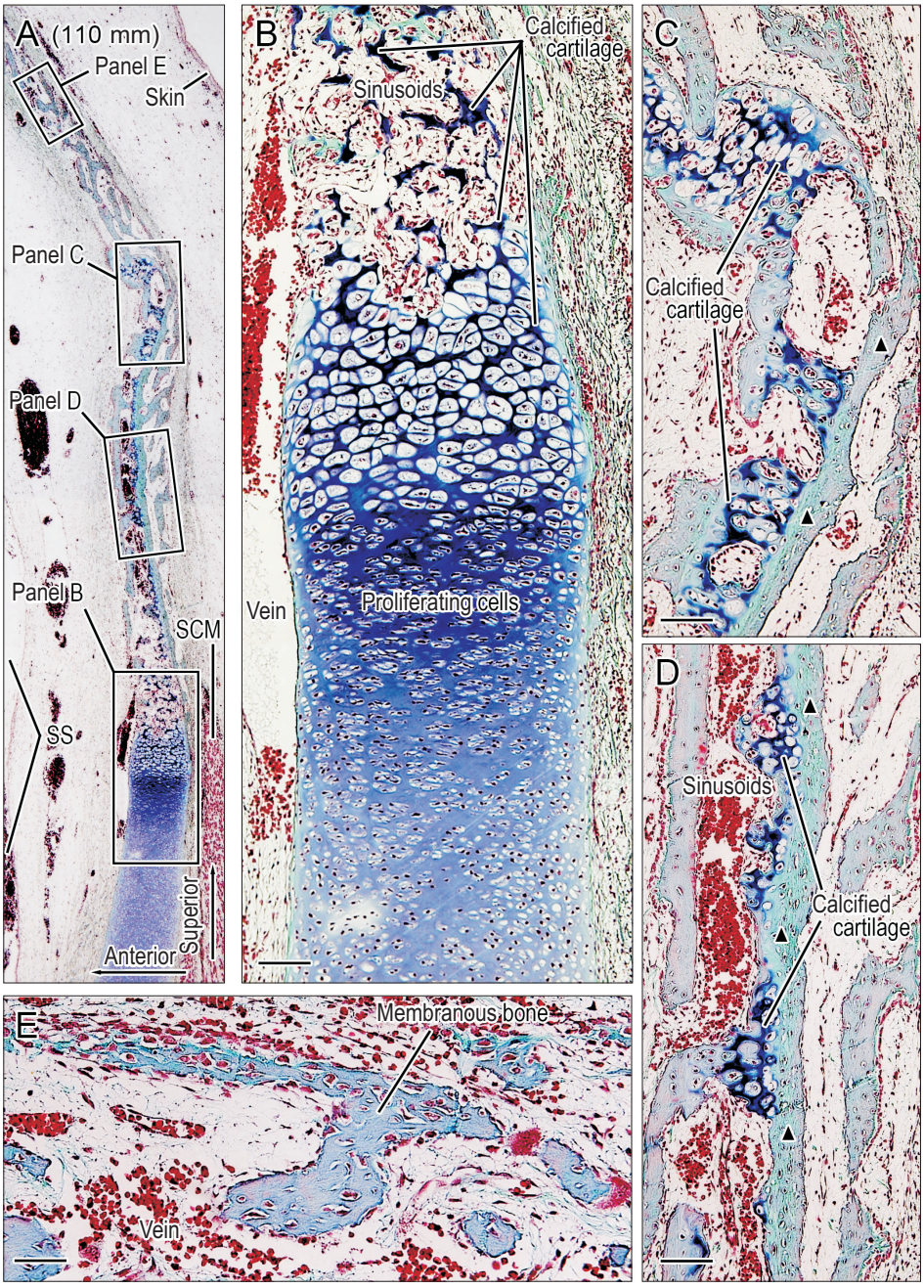

Fig. 6. Cartilaginous occipital squamosa with two ossification centers appears continuous with a membranous squamosa. Elastica-Masson stained sagittal sections of a crown-rump length 115-mm fetus (gestational age approximately 15 weeks). The upper side of each panel corresponds to the superior side of the head. The occipital bone squamosa (A) appears as a mosaic of the endochondral and membranous bones. Squares in panel (A) are shown in panels (B–E) at higher magnification, respectively. Panel (B) exhibits the upper endochondral ossification center as well as the sinusoids containing calcified cartilage and bone fragments. Notably, the inferior part of the membranous bones also contains calcified cartilage (C, D). A stout periosteal bone is indicated by triangles in panels (C) and (D). Panel (E) shows pure membranous bones without calcified cartilages. Scale bar=1 mm in panel (A); scale bars=0.1 mm in panels (B–E). SCM, splenius capitis muscle; SS, sigmoid sinus.

nous-bone junction in the OCS resembles a growing diaphysis of long bones rather than the suture or bone junction. We speculated a lower migration of the upper ossification center (Fig. 8; details, see the paragraph below) appeared to make the OCS larger and longer. Notably, the periosteal bone was clearly discriminated from membranous bone bars surrounded by osteoblast-like cells.

The periosteal bone of a long diaphysis in the extremities seems to maintain bone strength against bending or twisting stress due to early contraction of associated muscles. Likewise, the bulky periosteal bone of the OCS appears to mechanically support the delayed enlargement of the cerebellum and tectum of the brain. We noted that the long periosteal bone was lined by or surrounded sinusoidal tissues containing endochondral bone fragments and calcified cartilages. This was also evident in the occipital condyle (Fig. 1C). These structures were most likely to originate from the upper ossification center and maintain their original

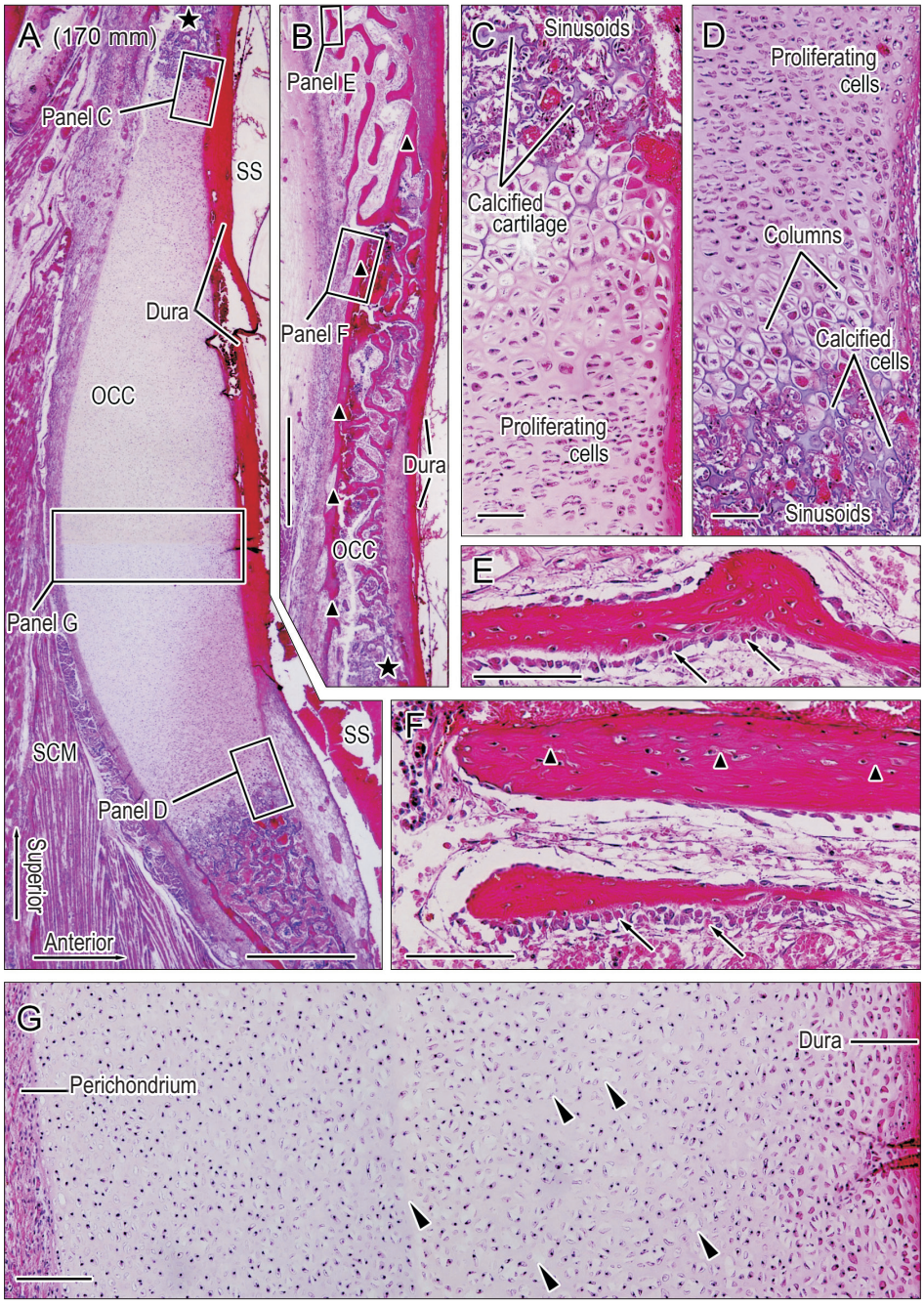

Fig. 7. A resting cartilage layer sandwiched by the upper and lower ossification centers in the cartilaginous occipital squamosa. H&E stained sagittal section of a crown-rump length 170-mm fetus (gestational age approximately 19 weeks). The upper side of each panel corresponds to the superior side of the head. Panel (A) displays the inferiorly-located cartilage plate, while panel (B) displays the superiorly-located membranous bone. Stars in panels (A) and (B) indicate the corresponding site. Squares in panel (A) (or B) are shown in panels (C, D, G) (or E, F) at higher magnification, respectively. Panel (F) also shows a periosteal bone bar (triangles) without osteoblast-like cells. The upper and lower ossification centers contain the proliferating and hypertrophic cell layers (C, D). Panels (E) and (F) show membranous bone bars surrounded by osteoblast-like cells (arrows). A resting cartilage area contains abundant ballooning cells (arrowheads in G). Scale bars=1 mm in panels (A, B); scale bars=0.1 mm in panels (C–G). SCM, splenius capitis muscle; SS, sigmoid sinus; OCC, occipital bone.

position in the bone due to possible lower migration of the center (Fig. 8). The distribution of the isolated endochondral elements might predict the initial site of the endochondral-membranous bone junction. Conversely, the superiorly-extending periosteal bone might bring us an impression of the lower migration of the ossification center.

According to Yamamoto et al. (2023) [1], the lower end of the growing frontal (membranous) bone contains cartilage-like tissue. The large mass of the nasal bone (also membranous) contains cartilage-like tissue at the upper end. We speculate that these unique cartilages might originate from the adjacent cartilaginous ethmoid or nasal capsule cartilage by analogy with the cartilage-membranous bone junction in the OCS. At the early stage, the initial membranous bone was located external to the cartilaginous OCS at the junction (Fig. 3A). Notably, the frontal bone develops along the inferior aspect of the cartilaginous ethmoid and ala minor of the sphenoid, *i.e.*, the "external" side of the cartilage relative to

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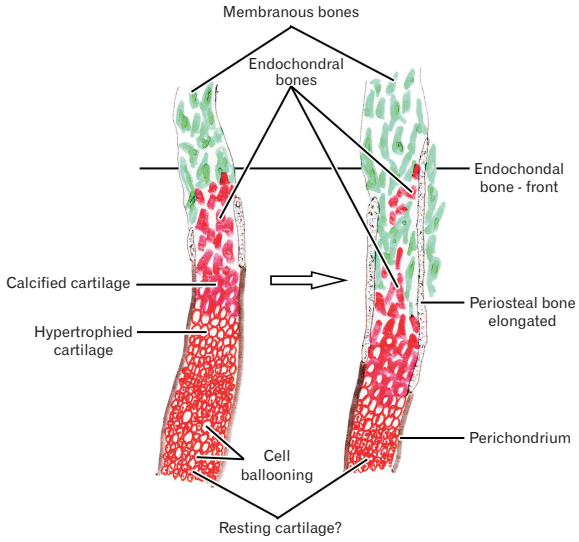

Fig. 8. Inferior migration of the upper endochondral ossification center in the cartilaginous occipital squamosa: a hypothesis. The left-hand illustration displays the early stage, while the right-hand illustration shows the later stage. The upward-growing periosteal bones connect the cartilaginous plate to the membranous bone and surround the sinusoidal tissue. The latter contains island-like clusters of endochondral bone and/or calcified cartilage together with membranous bone fragments. Therefore, inferior migration of the endochondral ossification center appears to depend on the superior growth of the periosteal bone. During this process, endochondral and membranous bones mix to provide the definite union. The initial position of the ossification center is indicated by a line labeled "endochondral bone front." The cartilage plate might contain a "resting cartilage."

the brain [1, 2]. Likewise, the maxilla as well as the lacrimal and palatine bones (all membranous bones) develop along the external side of the nasal capsule cartilage, the shape of which is determined by endodermal invagination [1].

Nevertheless, at and around the developing nasal cavity, these membranous bones are unlikely to accompany a periosteal bone. The periosteal bone appeared to be one particularly unique feature of the OCS (see Introduction). It is also worth noting that at the sacro-iliac joint, secondarily-developed membranous bones cover the endochondral ilium to create complete joint congruity [18]. Recent research has shown that markers specific to cartilage appear in tendon tissue during the healing process of damage to the muscle attachment area to bone [25, 26]. It has also become clear that the expression of factors that control muscle growth is essential for the growth process of the muscle-tendon junction [27]. In the future, it will be necessary to elucidate the factors necessary for membranous ossification.

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Author Contributions

Conceptualization: KI, KK, JFRV. Data acquisition: KI, ST, SA, GM, JFRV. Data analysis or interpretation: KI, KK, RS, KM, GM, SA. Drafting of the manuscript: KI, KK, GM. Critical revision of the manuscript: KK, RS, KM, ST, GM, JFRV, SA. Approval of the final version of the manuscript: all authors.

Conflicts of Interest

No potential conflict of interest relevant to this article was reported.

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