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# *Paleontological and developmental evidence resolve the homology and dual embryonic origin of a mammalian skull bone, the interparietal*

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## Abstract

The homologies of mammalian skull elements are now fairly well established, except for the controversial interparietal bone. A previous experimental study reported an intriguing mixed origin of the interparietal: the medial portion being derived from the neural crest cells, whereas the lateral portion from the mesoderm. The evolutionary history of such mixed origin remains unresolved, and contradictory reports on the presence or absence and developmental patterns of the interparietal among mammals have complicated the question on its homology. Here we provide a novel perspective on the evolutionary identity of the interparietal, based on a comprehensive study across more than 300 extinct and extant taxa, integrating embryological and paleontological data. Although the interparietal has been regarded as being lost in various lineages, our investigation on embryos demonstrates its presence in all extant mammalian “orders.” The generally accepted paradigm has regarded the interparietal as consisting of two elements that are homologized to the postparietals of basal amniotes. The tabular bones have been postulated as being lost during the rise of modern mammals. However, our results demonstrate that the interparietal consists not of two but of four elements. We propose that the tabulars of basal amniotes are conserved as the lateral interparietal elements, which quickly fuse to the medial elements at the embryonic stage, and that the postparietals are homologous to the medial elements. Hence, the dual developmental origin of the mammalian interparietal can be explained as the evolutionary consequence of the fusion between the crest-derived “postparietals” and the mesoderm-derived “tabulars.

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The evolutionary identity or homology of most mammalian skull elements is now well established (1-3), although many contradictory statements still exist on the interparietal, a dermal skull roof element situated between the parietal and supraoccipital (e.g., 4, 5-8). Several authors have suggested a homology of the paired mammalian interparietals to the paired postparietals in more basal reptiles (6, 9). However, inconsistent patterns reported among mammals (7, 10, 11), and even humans (12), and a unique mixed embryonic origin (1) make the question on homology of the interparietal an unresolved issue of vertebrate anatomy.

An experimental embryological study in the mouse by Jiang et al. (13) demonstrated a striking dual developmental origin of the interparietal: the median portion is derived from the neural crest cells, whereas the lateral portion is derived from the mesoderm. This report has triggered a renewed interest among developmental biologists in the evolution of the interparietal in amniotes (1, 14, 15). Although integrating fossil record and comparative anatomical data with newly gained experimental findings should provide relevant information for the current discussions on the origin of skull roof bones, it has been hampered by terminological inconsistencies, even within the stem mammal (synapsid) lineage, and unsolved homologies across major living groups (4, 6, 7, 9, 11, 16). In humans, the interparietal develops from two pairs of ossification centers, one medial pair and one lateral pair, eventually fusing seamlessly to the supraoccipital (17). In contrast to the human pattern, it is generally regarded for mammals that the interparietal arises in development as a pair of bones that soon fuse at the midline to form a single bone (6, 8, 18). However, the absence of the interparietal has been pointed out in marsupials (11, 18), xenarthrans (19), shrews (4), seals (10), hippopotamuses (10), and pangolins (11). The classic work of de Beer (20) reported that the interparietal is lacking in monotremes, bandicoots, armadillos, and pigs.

The paucity of appropriate embryonic material across mammalian species has undoubtedly hindered evaluations as to the primordial anlage, general presence, and variation of the interparietal. As exemplified in humans, the interparietal generally fuses with neighboring bones early in the perinatal period (12). Because the majority of work has been based on mature specimens, previous observers could have been misled by the early fusion of the interparietal with other bones. Here, with the unique availability of wide taxonomic and ontogenetic sampling across all extant mammalian orders and major non-mammalian fossil taxa, we address the issues of variation, patterns, and homology of the interparietal. Our results question the generally accepted homology hypothesis, and we suggest an alternative model that explains the intriguing dual tissue origin of the interparietal. Our integrative study provides a bridge between paleontology and developmental biology and a synthetic understanding of the dermal skull roof of vertebrates.

## Results

Below we present an overview of our findings. A full description of our detailed survey is given in the supplementary information (SI Appendix). All 51 non-mammalian synapsid species examined possessed the postparietal, which has been posited as homologous to the interparietal (9), either unpaired or paired (Fig. S3 and Table S1). The Jurassic docodont mammal *Haldanodon exspectatus* reportedly possesses the interparietal (21), as do the extant monotremes including the platypus *Ornithorhynchus* (22) and the long-beaked echidna *Zaglossus* (23). A small medial membrane bone, a remnant of the interparietal, is found in the short-beaked echidna *Tachyglossus aculeatus* (24). Marsupials reportedly lack the interparietal (11), but we confirmed its presence in various species (*Trichosurus*, *Monodelphis*, *Didelphis*, *Macropus*, and *Sminthopsis*). Contrary to the reported absence of the interparietal in *Monodelphis* (25), in the examined embryonic series of the gray short-tailed opossum *M. domestica*, both the supraoccipital and interparietal are present. Here, the interparietal was found to be unpaired, paired, tripartite, and quadripartite, depending on the stage (Fig. S4).

We recorded the presence of dermal interparietal bone in four xenarthran species including the long-nosed armadillo *Dasypus hybridus* (Fig. 1*A* and Table S1). Our investigation confirmed the presence of the interparietal across afrotherians (Figs. S5*A-B*, S6, and Table S1). We identified unpaired, paired, and tripartite interparietals in the tree hyrax *Dendrohyrax arboreus*. The interparietal in the rock hyrax *Procavia capensis* was found to be unpaired, paired, tripartite, and quadripartite. In some individuals, the lateral elements fuse earlier to the supraoccipital rather than to the medial elements (Fig. S5*B*). Tripartite interparietal elements were described for the cape golden mole *Chrysochloris asiatica* (2). In sirenians (*Dugong dugon*, *Trichechus manatus*, and *T. senegalensis*) the interparietal showed a maximum of four elements. Among extinct South American notoungulates, *Toxodon* *burmeisteri*, *Typotherium cristatum*, *Nesodon imbricatus*, and *Pachyrucus* were confirmed to possess the interparietal.

We observed the interparietal universally in Euarchontoglires (Figs. 2*I-J*, S9*D-F*, and Table S1). In the kangaroo rat *Dipodomys*, the interparietal was essentially formed from four ossification centers (26). One median and two lateral elements were found in various stages of the degu *Octodon degu* (Figs. 3*B-C* and 4) and in the Patagonian cavy *Dolichotis patagonum* (Figs. 3*D-E*). Among primates, the interparietal was widely found in perinatal individuals (Fig. 2*J* and Table S1). In humans, the interparietal develops from four elements (12, 27).

Paired interparietals were recorded in lipotyphlans (Figs. 1*B*, 2*A*, and Table S1). There was no previously published information on the presence of the interparietal in moles. Nevertheless, we found thin paired membranous interparietals, which initiate their ossification from the dorsal tip of the supraoccipital and then grow gradually toward the rostral direction, in both the Iberian mole *Talpa occidentalis* (Fig. S10*A*) and the European mole *T. europaea*. Similarly, we found the developing dermal interparietal in the coast mole *Scapanus orarius* (Figs. S10*C-D*) and the Japanese mole *Mogera wogura*. Augier (4) noted that shrews have no interparietal, but we recorded this bone in various shrews (*Sorex araneus*, *S. unguiculatus*, and *Crocidura attenuata*) (Fig. 1*B*).

The interparietal is present in artiodactyls, cetaceans, perissodactyls, carnivorans, bats, and pangolins (Figs. 2*B-H*, S9*A-C*, and Table S1). The bottle-nosed dolphin *Tursiops truncatus* possesses an expanded median and two lateral interparietal elements (Fig. 2*G*).

Eales (28) described the greatly expanded four-element interparietal in the narwhal *Monodon monoceros*. The cow *Bos primigenius* exhibited quadripartite interparietal (Fig. 2*H*). The tripartite interparietal is reported for the yak *B. grunniens* (29). Wegner (1960) documented the tripartite interparietal in the jaguar *Panthera onca* and cougar *Puma concolor*. Although Giebel (10) noted that seals lack the interparietal, we observed that prenatal skulls of fur seals *Arctocephalus* (Fig. S5*G*) and *Callorhinus ursinus* (Fig. S8*B*) display enlarged interparietals and the supraoccipital is extremely reduced in size compared with the interparietal, which dominates the caudal portion of the vault. The earless seal *Phoca* is reported to exhibit the lateral interparietal element (2, 25). Gregory (30) reported that pangolins lack the interparietal, but we found its presence in an immature individual of the Chinese pangolin *Manis pentadactyla* (Fig. S5*E*).

## Discussion

**Basic structure and evolutionary patterns of the interparietal**. The presence of the interparietal is almost universal among extant mammals. Previous reports have noted that there is no interparietal in monotremes (18, 20), marsupials (11, 18), xenarthrans (11, 19, 20), moles and shrews (4), seals (10), and pangolins (30). However, we documented the presence of the interparietal in monotremes (*Ornithorhynchus* and *Tachyglossus*), marsupials (23 species), xenarthrans (*Bradypus, Dasypus*, *Tamandua,* and *Cyclopes*), moles (*Talpa*, *Mogera*, and *Scapanus*), shrews (*Crocidura*, *Suncus*, and *Sorex*), seals (*Phoca*, *Arctocephalus* and *Callorhinus*), and pangolins (*Manis*) (Table S1). Previous studies may have overlooked the presence of the interparietal because of its early fusion to adjacent bones, either the supraoccipital or the parietal. The membranous bone found rostral to the endochondral supraoccipital in these species is interpreted to be the interparietal. The case of some shrews provides an instructive example of the importance of investigating embryonic materials and understanding the topological relationships of calvarial bones. The expansion of the interparietal and the rudimentary presence of the supraoccipital, which was often found in shrews, may have misled anatomists to regard the true interparietal as the supraoccipital and to consider the interparietal to be lacking in shrews (for instance, Fig. 1*B*). Kuratani (31) observed the expansion of the dermal interparietal bone and the unique case of possible lack of the cartilaginous supraoccipital in the Asian house shrew *Suncus murinus*. In the common shrew *Sorex araneus* (Figs. S7*C-D* and S11) and the long-clawed shrew *S. unguiculatus* (Fig. S12), we observed that the membranous interparietal dorsally covers the cartilaginous supraoccipital, forming a double-layered structure with the supraoccipital. In the Asian gray shrew *Crocidura attenuata*, the presence of the dermal interparietal was obvious (Fig. 1*B*).

While the Jurassic docodont *Haldanodon* is reported to possess the interparietal (21), its absence has been noted in other basal mammalian clades, including morganucodontids, multituberculates, *Sinoconodon*, and *Vincelestes* (32). Yet, as shown in the present study, the "absence" of the interparietal cannot be generalized in these species, because the interparietal may fuse early with other bones or it may be overlooked because of the poor preservation of sutures in fossils. This is especially true for primates, in whom the interparietal fuses with the supraoccipital at very early embryonic stages [c.f. Hershkovitz (33), who commented that callitrichid monkeys lack the interparietal].

Generally, the interparietal has been regarded as comprising paired elements that often fuse with each other to form an unpaired bone (8, 9, 11, 18). In contrast, a maximum of four ossification centers were recognized from our survey in artiodactyls (Fig. 2*H*), cetaceans, rodents, sirenians, hyraxes, platypuses, opossums, and humans (Table S1). The four elements fusing with one another become paired or unpaired, depending on the species or developmental stage. The fact that the lateral elements fuse to the medial elements at the embryonic stage in many taxa makes it critically difficult to identify the lateral portions of the interparietal. Tripartite interparietals were found in opossums (Fig. 3*A*), rodents (Figs. 3*B*-*E* and 4), cetaceans (Fig. 2*G*), felids, seals, yaks, manatees, tenrecs, hyracoids, golden moles, and humans. In these taxa, the median bone is an enlarged element formed by the fusion of two medial elements, and the lateral elements are separated from this median bone. Similarly, extinct notoungulates also exhibit tripartite interparietals.

The facts presented above indicate that the interparietal consists of four basic elements: one medial pair and one lateral pair (Fig. 5*B*). In most living mammals, the lateral element fuses first with the medial element, forming paired interparietals, and later in ontogeny, the fusion occurs between the two composites, forming an unpaired interparietal. Nevertheless, in some species (rodents, cetaceans, tenrecs, hyracoids, felids, seals, manatees, yaks, golden moles, and humans), the medial elements initially fuse with each other, while the lateral elements remain separate from the medial element, producing a tripartite interparietal

(Fig. 4). Such a condition is comparable to that in most non-mammalian synapsids, in whom paired tabulars are present but are separated from the median postparietal (e.g., see *Titanophoneus* in Fig. 5*A*).

**Homology of the mammalian interparietal**. Both the postparietal and the tabular are widely present in various tetrapods, including lissamphibians, diapsids, and non-mammalian synapsids [the terminology of the postparietal has been variable depending on the authors, such as “retroparietal (34),” “dermosupraoccipital (35),” “dermooccipital (16),” and “parieto-extrascrapular (36)”] (Table S1). The stem condition of lissamphibians, as illustrated by some dissorophids, exhibits paired postparietals and tabulars (37). Although modern lissamphibians were previously suggested to have lost the postparietals (38), they are present in some living anurans such as the spadefoot toad *Pelobates* (39) and fire-bellied toad *Bombina* (40). Basal amniotes exhibit paired postparietals and tabulars (41) (Fig. S1). In contrast, no extant sauropsid reportedly possesses the postparietals, with the exception of the American alligator *Alligator mississippiensis* (42). Extant chelonians (turtles, tortoises, and terrapins) (37), squamates (18, 37, 43-45), and birds (46) lack the postparietals. However, the presence of paired postparietals is common among fossil diapsids (37, 41) (Figs. S1 and S2).

Here, we hypothesize that the medial interparietal ossification centers and lateral ossification centers of mammals are homologous to the postparietals and the tabulars, respectively, of ancestral forms (Fig. 5*A*). The spatial arrangements of these bones, the number of elements, and the intramembranous nature of these bones lend support to this postulate. The topological correspondence of the posttemporal canal in non-mammalian synapsids and in primitive mammals also gives support to this hypothesis. In non-mammalian synapsids, the tabular generally forms an arch or roof over the posttemporal canal (Fig. S3*B*, *D*, *F*) (see also ref. 47). This canal is located at the junction of the tabular, squamosal, and mastoid in *Morganucodon* (48). The posttemporal canal is found in monotremes, opossums, and armadillos (49). For example in opossums, this canal is located at the junction of the lateral interparietal, squamosal, and mastoid as in *Morganucodon* (Fig. S4) (see also ref. 50, 51).

Frequent fusions between the tabular and postparietal in non-mammalian synapsids suggest the strong coupling trend of these bones. Across the observed non-mammalian synapsids, 33 species exhibited one median postparietal and two tabulars (e.g., *Titanophoneus* in Fig. 5*A*), whereas 17 species showed only the median "postparietal" (Fig. S3 and Table S1). In the later ones, the tabular is not lost but is fused to the postparietal. Given the presence and shape of the tabular and postparietal in juveniles of *Cistecephalus microrhinus*, a Late Permian anomodont therapsid, the tabular is fused to the true postparietal to form an enlarged median "postparietal" in mature individuals of this species (52-54), which resembles the single interparietal of various extant mammals (Fig. 2*B*-*C*, and *J*).

The interparietal has been regarded as an intramembranous bone formed dorsally to the tectum posterius, generally developing as a pair (7). Goodrich (9) suggested that the origin of the mammalian skull from a reptilian-like condition was brought about by the evolutionary loss of the prefrontal, postfrontal, postorbital, and quadratojugal. In his view, the postparietal pair has remained as the interparietal pair. Similarly, Gross and Hanken (1) and Morris-Kay (3) have noted that the mammalian interparietal is homologous to the postparietal bone of “archaic reptiles.” In contrast, our investigation demonstrates that the interparietal is constituted of four rather than just two elements. Such a developmental pattern of the modern mammalian interparietal from four dermal ossification centers is not fully explained, and thus this generally accepted paradigm on the homology of the interparietal (6, 8, 9, 18, 20) cannot be supported. Furthermore, the “interparietal” frequently documented in non-mammalian synapsids (e.g., 41, 53) is inconsistent. In cases where the bone labeled “interparietal” is isolated from the tabular, calling it the “postparietal” or “medial interparietal” would be appropriate.

Although the tabular is fused to the medial interparietal in some species of Dicynodontia (e.g., *Dicynodon*, *Diictodon*, and *Emydops*), it is clearly present and proportionally large in many other non-mammalian synapsids (Table S1). Among extinct basal mammals, the tabular is present in *Morganucodon*, but its relative size is much reduced compared to those in non-mammalian synapsids (48). *Haldanodon* shows an unpaired interparietal. The interparietal is not reported in multituberculates, but we assume their interparietal is fused to the supraoccipital. Thus, it appears that in crown-group mammals the tabular became reduced in size and fused to the medial interparietal.

According to Sidor (55), who studied the variation and evolution of cranial elements in synapsids leading to the living mammal crown group, there are, surprisingly, no fossil species that lack the tabular, whereas the extant lineage studied (*Ornithorhynchus*, *Didelphis*, and *Homo*) were reported to lack this bone. Nonetheless, as in the case of *Homo*, the lateral interparietal pair, which we hypothesize to be homologous to the tabulars, is identifiable in embryos (Fig. S13) (12, 27). Although the "simplification trend" of the mammalian skull (55) still holds, the general assumption that the tabular is lost in the modern mammalian lineage (18, 21, 55) is questionable. Broom (35) and von Huene (56) noted that the postparietal found in fossil amphibian-like land vertebrate *Diadectes* (Fig. 5*A*) should be considered homologous to the postparietal of the stegocephalians. Furthermore, Jarvik (57) proposed that the postparietal and tabular of basal tetrapods are homologous to the medial and lateral extrascapulars, respectively, of osteolepiform fishes. If these scenarios are to be supported, the medial and lateral extrascapulars of osteolepiforms should be regarded as conserved in mammals as the four basic elements constituting the interparietal.

As noted earlier, dual origin of the interparietal has been reported in the mouse, the medial portion being derived from the neural crest cells and the lateral portion from the mesoderm (Fig. 5*D*) (13). At least four segments are necessary to account for such mixed arrangements (Fig. 5*C*). We found (see also ref. 26) that the rodent interparietal originates from four ossification centers. Therefore, the two medial interparietal elements may correspond to the neural crest cell-derived portion and the lateral elements to the mesoderm-derived portion. Thus, the dual origin found for the interparietal (13) could be regarded as the evolutionary consequence of the fusion between the crest-derived "postparietals" and the mesoderm-derived "tabulars."

Gross and Hanken (1) noted that the location of the interparietal in the mouse corresponds to that of the "parietal" in the avian skull, a bone for which a controversy exists on its neural crest (58) or mesodermal origin (59). From embryological (i.e., dual mesenchymal origin) and topographical (or anatomical) grounds, Noden and Schneider (59) proposed that the bone conventionally labeled "parietal" in the chick would more appropriately be termed "interparietal" and "frontal" as "frontoparietal." In the chick, the boundary between frontal and parietal overlies the otic capsule, whereas in the mouse, this boundary occurs over the orbit (59). Although the developmental origin of the avian "parietal" [the "interparietal" of Noden and Schneider (59)] is controversially reported to be exclusively derived from the mesoderm (59) or exclusively from the neural crest cells (58), no studies have been conducted to test the dual embryonic origin for the avian "parietal" (1). If the avian "parietal" is validated to be derived from both the neural crest cells and the mesoderm, it will indicate that the mammalian interparietal is homologous to the avian "parietal."

The early ontogenetic fusion of the lateral and medial interparietal elements in living mammals may have been acquired in the synapsid lineage with encephalization and changes in molecular signaling. There is now good evidence that calvarial suture closures are associated with the expression of transforming growth factor β receptor genes (*Tgfbr1* and *Tgfbr2*) and fibroblast growth factor receptor genes (*Fgfr1* and *Fgfr2*) (60). Mutations in these molecules and the increased signaling of transforming growth factor β (TGF-β) or fibroblast growth factor (FGF) provokes early suture closure in humans—the so-called craniosynostosis syndrome (60, 61). However, inactivation of *Tgfbr2* in the mouse leads to the absence of the interparietal and parietal (62), suggesting the critical role of TGF-β signaling in the dermal skull roof development (see also ref. 63). In addition, recent findings demonstrate that *Tgfbr2* activity is required for axon formation and neuronal migration in the developing mammalian neocortex (64) and that expression of *Fgfr1* and *Fgfr2* determines brain size (65, 66). Richtsmeier et al. (67) have pointed out the analogy between human craniosynostosis and the simplification trend of cranial bone elements in synapsid evolution. Given the phenotypic integration of brain and neurocranium growth, they suggested the possible shared genetic pathways for brain development and skull tissue growth. It is quite intriguing to recognize that humans, which exhibit the most aberrant case of encephalization in vertebrate evolution (68) are, at the same time, the species that shows one of the most complete and accelerated fusion of the interparietal among mammals. Investigators may profit from testing whether encephalization and suture fusions in the skull roof are pleiotropically caused by changes in TGF-β and/or FGF signaling.

In conclusion, the discovery of the four-element nature of the interparietal (Fig. 5*B*) provides a synthetic understanding of the dermal skull roof of mammals. The “three-element interparietal” can be interpreted as consisting of one median bone, produced by the fusion of the medial interparietal elements, and two lateral interparietal elements. The “two-element interparietal” consists of a right and a left bone, each of which is the fusion of the medial and lateral interparietal elements. The “one-element interparietal” is interpreted as the fusion of all four elements (two medial and two lateral interparietal elements) into one median bone. However, it must be noted that the lateral interparietal elements may be fused earlier to the supraoccipital or to the parietal than to the medial interparietal in some cases (e.g., hyraxes). In terms of homology (Fig. 5*A*), the lateral interparietal elements derived from the mesoderm and the medial elements derived from the neural crest cells appear to correspond to the tabular and postparietal elements, respectively, of basal tetrapods. If future experimental studies on species other than the mouse similarly confirm the dual origin of the interparietal, our hypothesis shall be further supported.

Lastly, it is worth noting that wormian bones are rarely found anterior to the true interparietal in hyraxes, horses, cows, and primates (Fig. S14). This anomalous dermal bone has been referred to as “os Incae” in humans (12) and “preinterparietal” in other mammals (7). Whether the preinterparietal is a simple developmental anomaly or a trait obtained *de novo* in some mammals remains uncertain. Future investigations on developmental and evolutionary patterns of the preinterparietal are needed to further understand the anatomy of the mammalian skull.

## Methods

We investigated more than 3,000 skulls of 318 species in the context of studies on ossification sequences and sutural fusion in mammals (69, 70) and conducted a comprehensive review on literature describing amniote skulls (Table S1). Fetal or perinatal stages were studied to document whether the interparietal was recognizable and to record the number of interparietal ossification centers and contacts. Following de Beer (20) and Wegner

(7), we defined the interparietal as an intramembranous bone that is formed dorsally to the tectum posterius and posteriorly to the parietal. Documentation was based on macerated skulls and cleared and stained specimens as well as on microtomographic scans (Anthropological Institute, University of Zurich, μCT80, Scano Medical, Bassersdorf, Switzerland). 3D visualization was conducted in Amira 5.3 (Visage Imaging, Richmond, Australia). A missing distinctive interparietal could be due to real loss or primordial fusion with one of the adjacent bones. Therefore, we restricted our observations to the recording of interparietals and omitted any speculation based on the “absence” of clear signs of this element.

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## Figure legends

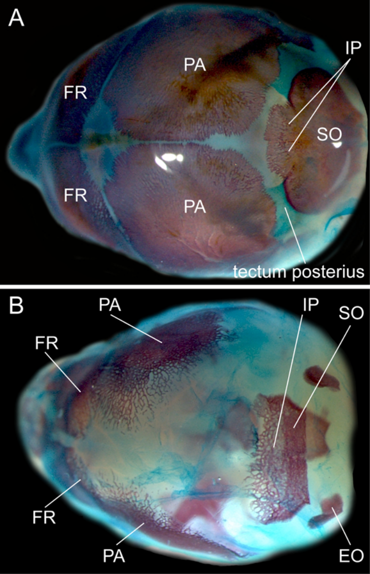
Fig. 1. Dorsal view of cleared and stained embryonic specimens. (*A*) Specimen of southern long-nosed armadillo (*Dasypus hybridus*). Note the dermal interparietal growing from the anterior tip of the cartilaginous supraoccipital. (*B*) Specimen of Asian grey shrew (*Crocidura attenuata*). Note the typical reticular appearance of the interparietal seamlessly attached to the anterior tip of the supraoccipital. IP, interparietal; SO, supraoccipital; PA, parietal; FR, frontal.

Fig. 2. Microtomographic reconstructions of the embryonic skulls in various species (caudal view). (*A*). Amur hedgehog (*Erinaceus amurensis*). (*B*) Cat (*Felis cattus*). (*C*) Japanese deer (*Cervus nippon*). (*D*) Horseshoe bat (*Rhinolopus cornutus*). (*E*) Hardwicke's woolly bat (*Kerivoula hardwickii*). (*F*) Blanford's bat (*Hesperoptenus blanfordi*). (*G*) Bottlenose dolphin (*Tursiops truncatus*). (*H*) Cow (*Bos primigenius*). (*I*) Large Japanese field mouse (*Apodemus speciosus*). (*J*) Japanese macaque (*Macaca fuscata*). IP, interparietal; SO, supraoccipital; BO, basioccipital; EO, exoccipital; SQ, squamosal; PE, petrosal; PA, parietal.

Fig. 3. Lateral view of skulls of opossum and rodents. (*A*) dorsal view of a white-eared opossum (*Didelphis albiventris*). (*B*) and (*C*) Degu (*Octodon degu*) skulls of different stages. (*D*) Perinatal skull of Patagonian cavy (*Dolichotis patagonum*). Note the lateral interparietal element (LI). (*E*) A close-up image of (*D*). IP, interparietal; LI, lateral interparietal element ; SO, supraoccipital; SQ, squamosal; PE, petrosal; PA, parietal.

Fig. 4. Dorsal view of embryonic skulls of degu (*O. degu*). (*A*) Note the lateral interparietal elements (highlighted with arrows) lying lateral to the median interparietal (IP). (*B*) A more advanced individual of degu. Note the lateral interparietal elements (highlighted with arrows). IP, interparietal; SO, supraoccipital; PA, parietal.

Fig. 5. Evolutionary and development pattern of the interparietal. (*A*) Cladogram and caudal view of skulls of Early Permian lissamphibian *Diadectes*, Late Permian therapsid *Titanophoneus*, and human fetus. The medial interparietal (postparietal) are given in blue, and the lateral interparietal (tabular) is shown in pink. (*B*) Diversity of the interparietal elements. Single, paired, or tripartite interparietal is consequently produced, depending on the fusion pattern of the four elements. (*C*) Suggested basic structure of the interparietal. The interparietal is suggested to be consisted of two medial elements and two lateral elements. (*D*) Tissue origins of the mouse skull vault [after Jiang et al. (13)]. The interparietal has dual origins, the median portion derived from the neural crest and the lateral part from the mesoderm. NA, nasal; FR, frontal; PA, parietal; IP, interparietal; SO, supraoccipital; SQ, squamosal.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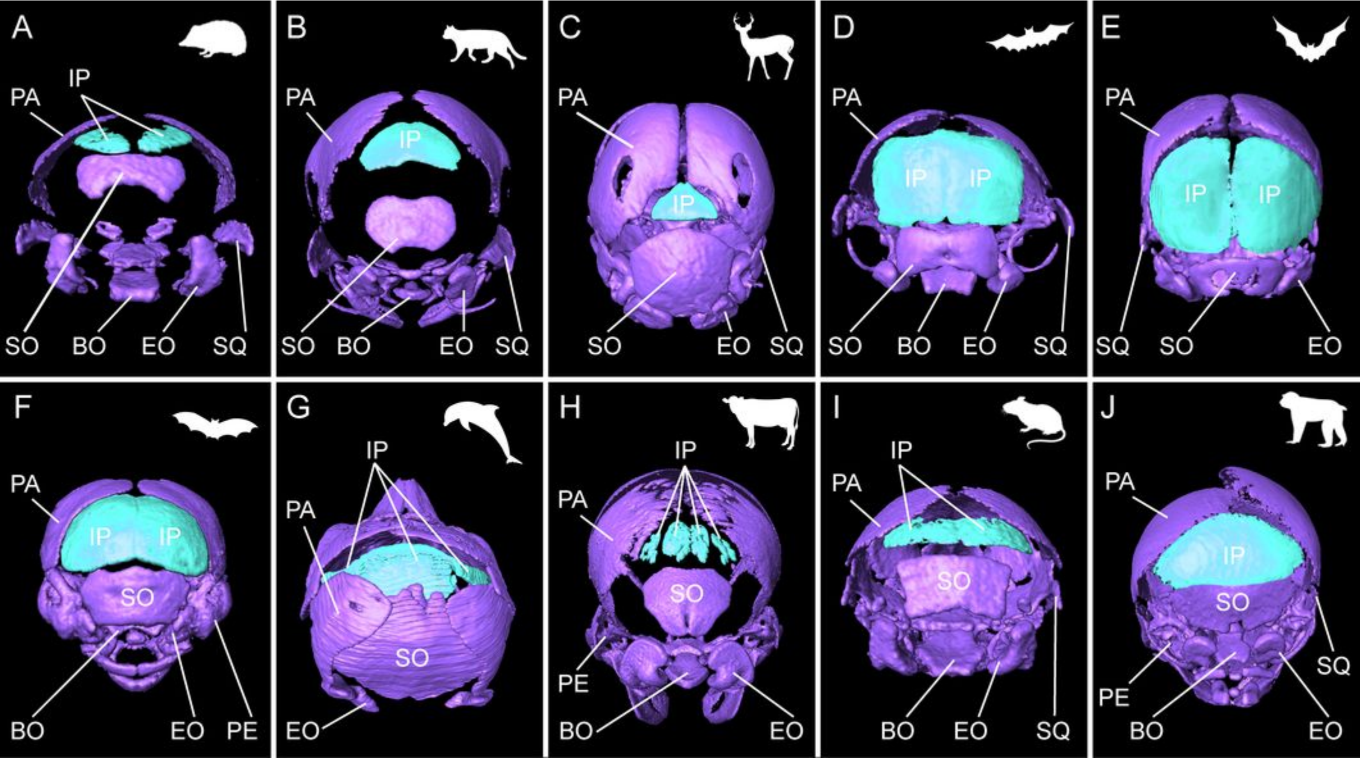
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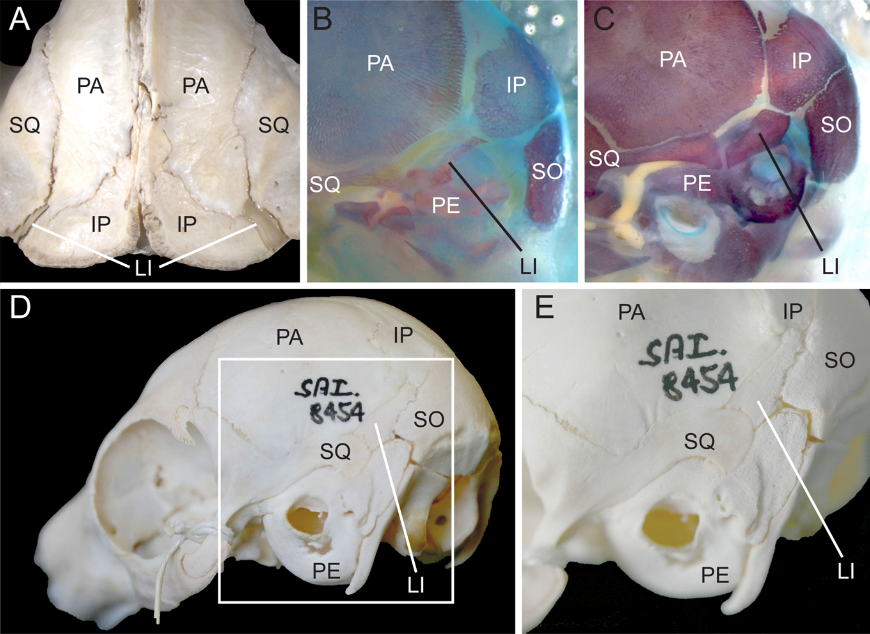
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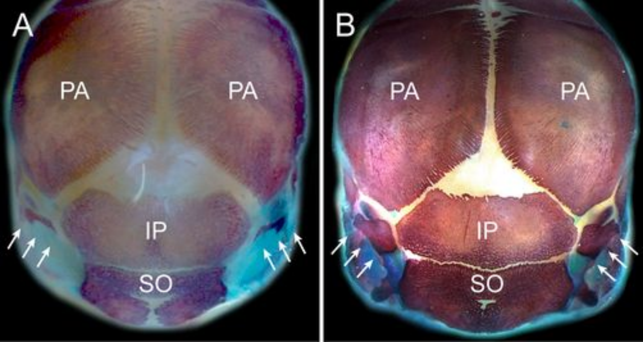
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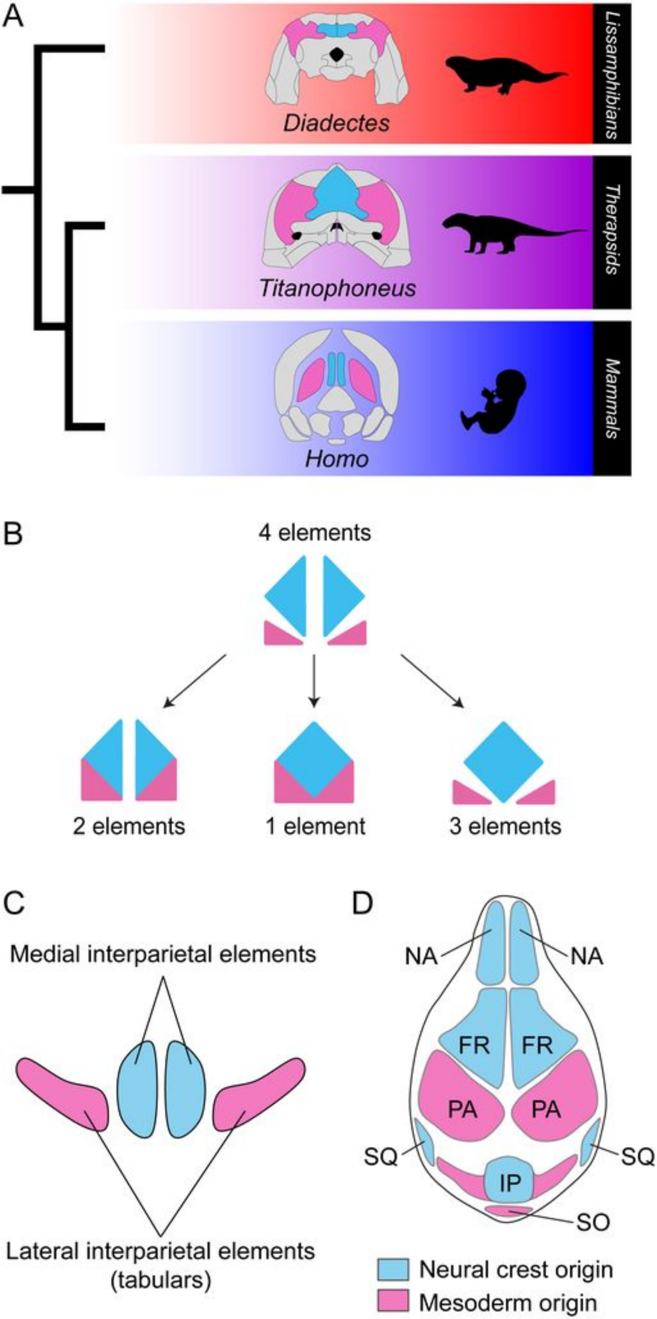
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(tabulars)
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FR
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SQ
SQ
IP
SO
Neural crest origin
Mesoderm origin

# SUPPLEMENTARY INFORMATION

# *Paleontological and developmental evidence resolve the homology and dual embryonic origin of a mammalian skull bone, the interparietal*

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## Part A. Supplementary descriptions on the interparietal of studies species

### Fish, stem tetrapods and, lissamphibians

Sarcopterygians such as *Youngolepis praecursor* and actinopterygians including *Moythomasia nitida*, *Kansasiella eatoni* are documented to possess paired postparietal (1, 2). Already in *Ichthyostega* the postparietals are medially fused - but not in other early tetrapods (3, 4). *Acanthostega* had both postparietal and tabular (5). Many fossil batrachomorpha (sensu 6) have retained paired postparietals, including *Eryops*, *Diplocaulus*, *Phlegethontia* (*Dolichosoma*), *Branchiosaurus* (7), and *Apateon dracyiformis* (8). *Palaeogyrinus* (*Palaeoherpeton*) is documented to possess a paired postparietal by Romer and Parsons (1). Although Jarvik (3) identified a small unpaired dermal ossification at the dorsal side of the foramen magnum of *Rana*, extant lissamphibians are commonly recorded as missing postparietals (9). On the other hand, *Eocaecilia micropodia*, which is considered to represent the stem condition of lissamphibian (10), and a member of diadectomorph *Limnoscelis* exhibit a paired postparietal (11). *Anthracosaurus* shows paired postparietal (12). At least some dissorophids (*Doleserpeton*), a putative stem group of all or some lissamphibians possess paired postparietals (13, 14). Although most modern anurans are supposed to have lost the postparietal, it is present in some living groups such as *Pelobates* (15) and *Bombina* (16).

### Stem-amniotes and sauropsids

Basal amniotes such as, *Paleothyris* (17), *Seymouria* (Figs.1*A* and 2*B*) (18), and *Kotlassia* (11) exhibit paired postparietals. Broom (19) documented the unpaired postparietal in *Diadectes* and *Chilonyx* and noted that, from the direction of the fibres of this medial element, it seems probable that it originated from two ossification centers.

On the other hand, no extant sauropsid seems to possess postparietal, except for *Alligator mississippiensis* (20). Here, the bone is a small dermal plate lying ventrally and posteriorly to the posterior margin of the parietal and dorsally to the trabecular bone, forming a dorsal surface of the supraoccipital portion of the neural endocranium. Chelonians (the clade uniting turtles, tortoises and terrapins) seems to lack the postparietal; there is no postparietal found in *Proganochelys*, *Caretta*, *Lepidochelys*, *Chelonia* and *Emys* (11, 21, 22). No postparietal is found in either the embryonic *Pelodiscus sinensis* (23) or *Emydura subglobosa* (24). Several works on squamates confirm the lack of the postparietal in this group: apparently *Lacerta* (25), *Varanus* (11), *Tupinambis* (21)*,* and *Ctenosaura* (26), as well as the comprehensive study of Conrad (27) and the recent description of an Eocene “lizard” from

Messel in Germany (28). *Sphenodon* has no postparietal (11, 21), and this is confirmed in fetal stages as well (29). No placodont and in fact no other sauropterygian posess a postparietal bone (30). On the other hand, among fossil diapsids, the presence of paired postparietal is documented in *Araeoscelis* by Parrington (18), and in *Protorothyris* (Fig. S1*B*), *Euparkeria* (Fig. S1*C*), *Milleratops* (or juvenile? of *Milleretta*) (Fig. S1*D*)*, Milleretta* (Fig. S1*E*) *Machaeroprosopus* (Fig. S2*C*), *Youngina* (Fig. S2*D*) by Romer (11). The anapsid reptile *Labidosaurus* (Fig. S2*B*) shows an unpaired postparietal (18).

Extinct and extant birds apparently lack the postparietal (31, 32). In his careful study Müller (33) reported that *Rhea* and other primitive birds have no potsparietal. Jollie (21) who depicts the cranium of a freshly hatched chick shows no sign of an postparietal. There is no potsparietal in *Protoavis* (34) nor in *Archaeopteryx* (35). Raath (36) who showed a detailed drawing of the occiput records no potsparietal for *Syntarsus* (*Megapnosaurus*).

Non-mammalian synapsids: “pelycosaurids” and “therapsids”

Among pelycosaurs, a paraphyletic grouping of basal synapsids, *Ophiacodon uniformis* (37), *Edaphosaurus pogonias* (37-39) and for *Theropleura retroversa* (Fig. 3*A*) (40) reportedly has a single bone labeled as postparietal which lies just dorsal to the supraoccipital, contacting the tabulars laterally and the parietal dorsally. Parrington (18) documented the presence of the paired postparietal and paired tabular in *Dimetrodon*, *Diops*, and *Theropleura*.

*Thrinaxodon liorhinus* (Fig. 3*B*) is reported to possess an enlarged unpaired postparietal and paired tabular (41). Various therapsids such as *Diarthrognathus* (42), *Myosaurus gracilis* (43), *Rechnisaurus cristarhynchus* (44), *Ennatosaurus tecton* (45), *Ecteninion lunensis* (46), *Emydops* (47), *Kombuisia frerensis* (48), *Scylacops*, *Cynognathus*, *Ulemosaurus*, *Synostoephalus*, *Lycedops* (Fig. 3*C*), *Bauria* (11), *Hofmeyria* (Fig. 3*D*), *Hyenosaurus* (Fig. 3*E*) (49), *Procynosuchus* (50), *Titanophoneus*, *Aneugomphius (51), Lystrosaurus amphibius* (52) are reported to possess the postparietal. The monographic work of Broom on non-mammalian synapsids (53) provides the illustrations of more than 40 species, depicting the postparietal in which postparietals are labeled.

Docodonts

*Haldanodon exspectatus* was reported to possess a triangular median interparietal (54).

## Monotremes

According to de Beer (55), Kuhn (56), Zeller (57), and Jollie (21), monotremes do not have the interparietal and rather possess a very expanded supraoccipital. On the other hand, van Bemmelen (58) reported that *Ornithorhynchus* possesses an interparietal. Here, he labeled the medial interparietal as a "medial parietal" and the lateral interparietal as a "lateral parietal". Landry (59) commented that the interparietal appears in the embryonic *Zaglossus* (long-beaked echidna) as a large element covering the back end of the brain case. Kierdorf and Kierdorf (60) reported a small medial membrane bone of only transient occurrence observed in *Tachyglossus aculeatus* (61), which is possibly a remnant of the interparietal element in this species.

## Marsupials

From our embryonic specimens, we confirmed the presence of the interparietal in *Trichosurus*, *Monodelphis*, *Macropus,* and *Sminthopsis*. Owen (62) reported that *Macropus*, *Hypsiprymnus*, *Petaurus*, *Phalanger*, *Myrnecobius*, and *Phascolomys* exhibit the interparietal. An unparied interparietal was described in postnatal *Didelphis marsupialis* (63), and in *Monodelphis* by Clark and Smith (64). Wible (65) noted that this bone apparently fuses seamlessly with the supraoccipital along the nuchal crest. In our ontogenetic series, the interparietal was found to be unpaired, paired, tripartite, and quadripartite (Figs. S4*A*-*D*). *Myrmecobius fasciatus* (Dasyuromorphia) is reported to have an enlarged interparietal (66). As pointed out by Wible (65), since the bone seamlessly fuses with the supraoccipital, the interparietal is often erroneously labeled in adults as part of the supraoccipital bone. Abdala (67) reported the fusion of the unpaired interparietal to the suprapoccipital in *Didelphis albiventris*. The interparietal of *D. albiventris* was found to be quadripartite (Figs. S4*E* and *F*). Forasiepi (68) documented the presence of the unpaired interparietal in the fossil metatherian *Arctodictis sinclairi*. Voss and Jansa (69) discussed the presence of the interparietal in some didelphids and reported this bone in stem metatherians. According to these authors, the presence of a "large undivided interparietal bone that is wedged between the parietals anteriorly and fused to the supraoccipital posteriorly" may be a didelphid synapomorphy. The search for morphological synapomorphies for didelphids makes this question worthwhile, but the hypothesis seems questionable considering the difficulty of assessing the condition in basal crown-group Marsupialia such as *Herpetotherium* (70). The different interpretations on the condition of *Pucadelphys* (71) and *Mayulestes* (72), which have been described or illustrated as possessing different conditions, may be best explained by the fact that different stages of cranial vault sutural fusion may have been considered. Wegner (73) reported the presence of the interparietal in *Bettongia*, *Petaurus*, *Dedrolagus*, *Phalanger*, *Wombatus*, *Phascolarctos*, *Trichosurus*, *Onychogale*, and *Sarcophilus* and commented that the interparietal is a persistant bone in marsupials.

Notoungulates

*Toxodon burmeisteri*, *Typotherium cristatum*, *Nesodon imbricatus*, and *Pachyrucus* exhibit the median interparietal and lateral interparietals (74).

Afrotheria

Giebel (75) and Lawlor (76) documented the presence of this bone across Hyracoidea. Our own investigations confirmed its presence in *Heterohyrax brucei* and *Procavia capensis* (Fig. S5*B*). In addition to this, we indentified unpaired, paired, and tripartite (one triangular large medial and paired lateral elements) interparietals in *Dendrohyrax abroreus*. Similarly, unpaired, paired, tripartite (one triangular large medial and paired lateral elements), and maximally quadruple (medially paired and laterally paired) interparietals were found in *P. capensis*. Wegner (73) reported that *P. capensis* shows a tripartite interparietal consisted of one large medial and two lateral elements. Parker (77, 78) documented the interparietal in *Microgale longicaudata* (Figs. S6*A* and *B*), *Tenrec ecaudatus* (Figs. S6*G* and *H*), and *Hemicentetes madagascarensis* (Figs. S6*C* and *D*). In *M. longicaudata*, he also noted the presence of the “supratemporals”, which shall be rather called tabular, lying lateral to the interparietal. In tenrecs (*Potamogale velox*, *Hemicentetes semispinosus,* and *Tenrec ecaudatus*), Schunke and Zeller (79) observed that the interparietal bone is unpaired and separated from the supraoccipital in embryos. In *Hemicentetes semispinosus*, the interparietal fuses first with the supraoccipital. The interparietal is formed considerably later in *Potamogale* compared to *Hemicentetes* and remains separated from the supraoccipital for some time (79). Leimgruber (80) also reported a notably developed interparietal bone in *Tenrec*. In *Setifer* the interparietal bone fuses shortly after its origin with the supraoccipital bone (81). Similarly, one median and two lateral interparietals were described for *Chrysochloris asiatica* (82). The African elephant is reported to possess a small interparietal which is present at birth and fuses with other bones with growth (83). Giebel (75) reported that paired interparietals are found in young individuals of the elephant. De Beer (55) noted that the interparietals fuse with the parietals in sirenians. The golden mole *Eremitalpa* is reported to possess an unpaired interparietal bone (81). According to our investigations, a neonate *Macroscelides proboscideus* shows a large interparietal (Fig. S5*A*), and a neonate of *Orycteropus afer* shows a very large interparietal. Parker (77, 78) documented the interparietal in *Rhynchocyon cirnei* (Figs. S7*E* and *F*) and greatly expanded interparietal for *O. afer* (Figs. S5*G* and *H*). We found mutli-elemented interparietal bones in *Dugong dugon*, *Trichechus manatus*, and *T. senegalensis*. The interparietal is reported also in *Rytina* by Wegner (73). He also noted the presence of the tabular, an extra bone lateral to the interparietal, in *T. manatus*.

## Xenarthra

Kingsley (84) noted that no xenarthrans posseses the interparietal. On the contrary, our investigation found a paired interparietal in *Cyclopes didactylus*, an unpaired interparietal in *Tamandua tetradactyla* (Fig. S5*D*), and an unpaired interparietal in a prenatal *Bradypus tridactylus*. Similarly, Wegner (73) reported its presence in *Bradypus tridactylus* and *C. didactylus*. Our own examination on perinatal *Bradypus tridactylus* (Fig. S5*C*) also confirmed the presence of the interparietal. De Beer (55) noted that *Dasypus* lacks the interparietal, but our own investigation found a dermal interparietal bone in *Dasypus hybridus* (Fig. 1*A*).

## Euarchontoglires

The interparietal bone is commonly found in rodents and lagomorphs. This bone in Glires is relatively enlarged (85). Beer (86) conducted a survey on the presence of the interparietal in 21 *Dipodomys* species, sampling 2360 prenatal and postnatal specimens. In *Dipodomys*, the interparietal was basically formed from four ossification centers and finally united into an unpaired shield-shaped structure. In the monographic work by Tullberg (87), the interparietal can be found in figures for more than 40 genera. We found unpaired interparietals in *Pedetes capensis*, *Galea musteloides*, *Hydromys chrysogaster*, *Jaculus jaculus*, *Micromys minutus*, and *Apodemus speciosus* (Figs. 2*I* and S9*D*). In addition, three interparietal bones, one medial and two lateral, were found in various stages of *Octodon degu* (Figs. 4*A-C* and 5). Similarly, median interparietals and two lateral interparietals were found in two juveniles from different localities of *Dolichotis patagonum* (Figs. 3*D* and *E*). In *Lepus*, the interparietal remains fuses with the parietal in mature individuals. Our neonatal *Oryctolagus cuniculus* shows an unpaired interparietal. Starck (22) noted that, although the interparietal generally remains independent from other bones in the Lagomorpha and Rodentia, the interparietal often fuses with the parietal rather than with the supraoccipital in rodents. Our CT investigation on the newborn of *D. patagonum* confirmed such trend of fusion with the parietal. Similarly, the interparietal fuses with the parietal in *Pteromys volans* and *Spermophilus undulatus*. We confirmed that the interparietal fuses with the parietal in *Petaurista leucogenys* and *Pteromys momonga*.

Parker (77) documented the presence of the interparietals in *Cynocephalus volans* and *Galeopterus variegatus* (Figs. S6*E* and *F*). The presence of this bone in *Galeopterus* was documented also by Giebel (75). Wortmann (88) and Zeller (89) documented the presence of the interparietal in *Tupaia belangeri*. This investigation was confirmed in our investigation on young newborn *Tupaia belangeri.*

Among primates, young individuals of *Daubentonia madagascariensis* and *Cebus* are reported to possess the interparietals (75). There are many studies reporting the existence of the interparietal in humans (e.g., 90, 91) (Fig. S13). The presence of the interparietal is reported in the newborn *Hylobates syndactylus*, and *Pan troglodytes* (75). Kingsley (84) and Eaglen (92) noted that lemurids frequently show unpaired interparietals. Wegner (73) described the enlarged interparietal in *Loris tardigradus* and *D. madagascariensis.* Our own investigation confirmed the presence of the interparietal in the fetal skull of *Pan troglodytes* (Fig. S8*C*) and in young *Galago senegalensis* (Fig. S5*I*). In addition, our microCT examination on fetal specimens clearly showed the presence of the membranous interparietal in *Macaca fascicularis* (Fig. S9*E*) and in *M. fuscata* (Figs. 2*J* and S9*F*). In macaques, the interparietal develops after the supraoccipital and then rapidly fuses with this bone. Starck (93) reported that he failed to find the interparietal in a late fetal stage of *Propithecus*, although he noted a clear membranous “bone growth” at the dorsal margin of the supraoccipital, presumably an interparietal, was visible. In new world primates, Hershkovitz (94) documented the frequent presence of the interparietal across Cebidae, and Chopra (95) reported its presence in *Saimiri*.

## Laurasiatherians

The presence of paired interparietal was documented in *Solenodon paradoxus* (96). In juvenile *Solenodon* there is a paired interparietal, the two parts of which become fused between them and with their neighboring bones (96). From our original investigation on embryonic specimens, we confirmed that *Erinaceus europaeus* (Figs. S7*A* and *B*) and *E. amurensis* (Fig. 2*A*) possess paired interparietals. The presence of the interparietal is also documented in *Echinosorex* (75). There is little published information on the presence of the interparietal in moles, possibly due to their very early closure of cranial sutures. Although Goswami and Prochel (97) noted that there is no evidence of presence of the interparietal in *T.*

*europaea*, our investigation in embryonic specimens found thin paired membranous interparietals which initiate their ossification from the dorsal tip of the supraoccital and then grow gradually toward the rostral direction in both *T. occidentalis* (Fig. S10*A*) and *T. europaea*. The suture between the interparietal and the supraoccital closes rapidly. We also found the developing dermal interpartal at the anterior tip of the supraoccipital in an embryonic specimen of *Scapanus orarius* (Figs. S10*C* and *D*) and *Mogera wogura*. De Beer (98) documented the interparietal in the *Sorex araneus* (Figs. S11*A* and *B*). He described that the supraoccipital is partly covered by the dermal interparietal. On the other hand, Augier (99) noted that soricids have no interparietal, but the supraoccipital forms a dermal second center of ossification in the expanded tectum posterius. Kuratani (100) observed the expansion of the dermal interparietal bone and the extremely unique case of the lack of the cartilaginous supraoccipital in *Suncus murinus*. We found dermal interparietal bones in embryonic specimens of *Sorex unguiculatus* and *Crocidura attenuata*. In *Sorex unguiculatus*, the interparietal seemed to dorsally cover the supraoccipital, forming a double layered structure with the supraoccipital (Fig. S12). In *C. attenuata,* the cartilaginous supraoccipital is small but evident, and the dermal interparietal grows toward the anterior direction (Figs. 1*B* and S10*G-H*). On the other hand, in the specimens of *C. watasei* and *Suncus murinus* we studied, the dermal interparietal bone was apparently present but the cartilaginous supraoccipital was not clearly identified at least in our ontogenetic series. Recently, presence of the interparietal was commonly found in myosoricine shrews (*Surdisorex*, *Congosorex*, and *Myosorex*) (101). Parker (78) described the interparietal in *Sorex vulgaris* (*araneus*) (Figs. S7*C* and *D*).

The reconstruction of CT images of embryonic whale specimens showed that *Tursiops truncatus* possesses an expanded interparietal (Fig. 2*G*). We found the interparietal also in *Phocoena phocoena* the harbour porpoise. Eales (102) described the greatly expanded four-element interparietals in *Monodon monoceros*. The interparietal is also reported for other cetaceans (*Balaenoptera borealis*, *B. musculus*, *Delphinus delphinus*, and *Inia geoffrensis*) (73, 103-105). Recent investigation on embryonic *Stenella attenuata* documented the presence of the interparietal (106). The interparietal is large and square-shaped bone, stretching toward the medial plane and making up part of the dorsal roof of the braincase. However, we assume that the bones labeled as “right and left ossifications centers of the supraoccipital” (see Fig. 6*C* of ref. 106) are not part of the cartilaginous supraoccipital given their dermal appearance. We postulate that the “right and left ossifications centers of the supraoccipital” in Moran (106) are one of the ossification centers of the interparietal (see ref.

102), thus exhibiting three interparietals. According to Starck (107), the interparietal fuses with the supraoccipital in cetaceans.

In a late fetal cranium of *Capreolus capreolus* large and paired interparietals were visible (Fig. S5*H*). Similarly, we found the interparietal in a young *Tragelaphus scriptus*. Our CT examination on embryonic specimens demonstrated paired interparietals in *Cervus nippon* (Fig. 2*C*) and *Bos primigenius* (Fig. S9*B*). Quadrupartite interparietal was also found in *B. primigenius* (Fig. 2*H*). The interparietal and two lateral elements are depicted for a fetal *B. grunniens* by Starck (see Table 34 of ref. 108). Kierdorf and Kierdorf (60) reported the interparietal in four *Cervus* species (*C. elaphus*, *C. nippon*, *C. duvauceli* and *C. eldi*). Shapiro and Robinson (109) described an enlarged interparietal in *Odocoileus virginanus*. According to Rörig (110), the interparietal is present in *Capreolus capreolus* and in *Dama dama*. The interparietal found in *Alces alces* apparently fuse to the parietal. A pair of the interparietal is reported in *Muntiacus reevesi* (111). In many late fetal sheep *Ovis dalli* skulls, we found that the interparietal is almost always clearly distinguished. An infantile skull of *O. dalli* shows a paired interparietal. Paired interparietals are found in a prenatal *Vicugna pacos* (Fig. S8*A*). A two-day old calf of *Kobus ellipsiprymnus* shows clearly separated and paired interparietals. *Tragulus* is reported to possess the interparietal (73).

It is reported that the interparietal is highly common among ursids, including *Ailuropoda melanoleuca* (73). *Canis* is reported to have paired interparietals and also a median interparietal that immediately fuses with the supraoccipital (55). *Lutra lutra* reportedly possess an interparietal bone which is triangular in shape and has external sagital crest (crista sagittalis externa) (112). *Mustela* and *Procyon lotor* (113), *P. pygmaeus* (114) are reported to have interparietals in the posterior end of the skull roof. *Vulpes vulpes* is reported to possess the interparietal (115). *Panthera leo*, *P. onca*, and *Puma concolor* are reported to show the interparietal by Wegner (116). He also noted that the interparietals are tripartite in *P. onca* and *P. concolor*. According to our microCT images of a late fetal *Felis domestica* (Figs. 2*B* and S9*C*), the interparietal is even larger than the supraoccipital. An unpaired interparietal was found in *Panthera pardus*. Although Giebel (75) noted that phocids lack the interparietal, our prenatal *Arctocephalus* (Fig. S5*G*) and *Callorhinus ursinus* skulls (Fig. S8*B*) apparently displayed enlarged dermal interparietals. *Phoca* is reported to exhibit the lateral interparietal element (82, 116). Here, we observed that supraoccipital is extremely reduced in size compared to the interparietal which dominates the caudal portion of the vault. In some neonate dog skulls, the supraoccipital sends a prominent dorsal process between the parietals; in *Speothos*, it is incompletely separated from the supraoccipital. Gregory (117) described that

*Manis spp.* lack the interparietal, but our examination found the interparital which fuses with the supraoccpital (Fig. S5*E*).

We confirmed the presence of the interparietal in our young individual of *Equus* (Fig. S5*F*). Giebel (75) reported that diamond shaped unpaired interparietal is often found in embryonic and young individuals. There are studies that report the existence of paired interparietal in *Tapirus* (tapir) (118-120). Kingsley (84) noted that the interparietal fuses with the parietals in *Equus* and *Tapirus*. Cuvier (121) reported the presence of the interparietal in *Rhinoceros* and *Diceros*.

We found paired interparietals in the embryonic specimens of *Hipposideros*, *Kerivoula* (Fig. 2*E*), *Hesperoptenus* (Fig. 2*F*), *Rhinolophus* (Fig. 2*D* and S9*A*). The interparietal fused with the supraoccipital and then with the parietal. Fawcett (122) showed a figure of *Miniopterus* that has large and paired interparietal. The interparietal is reported to be present in *Roussettus* (123) and *Artibeus* (124). As documented by Giannini et al. (125) among the Megachiroptera, in *Pteropus lylei* the interparietals are an unpaired bone clearly distinguishable in adults, as is also the case in *Dobsonia pannietensis*.

## Part B. Supplementary Figures

Abbreviations: BO, basioccipital; EO, exoccipital; FR, frontal; IP, interparietal; MA, mastoid; MX, maxilla; NA, nasal; OO, opisthotic (paroccipital); PA, parietal; PE, petrosal; PO, postorbital; PP, postparietal; PTC, posttemporal canal; Q, quadrate; QJ, quadrojugal; SO, supraoccipital; SQ, squamosal; ST, supratemroal;  TA, lateral interparietal element (tabular).

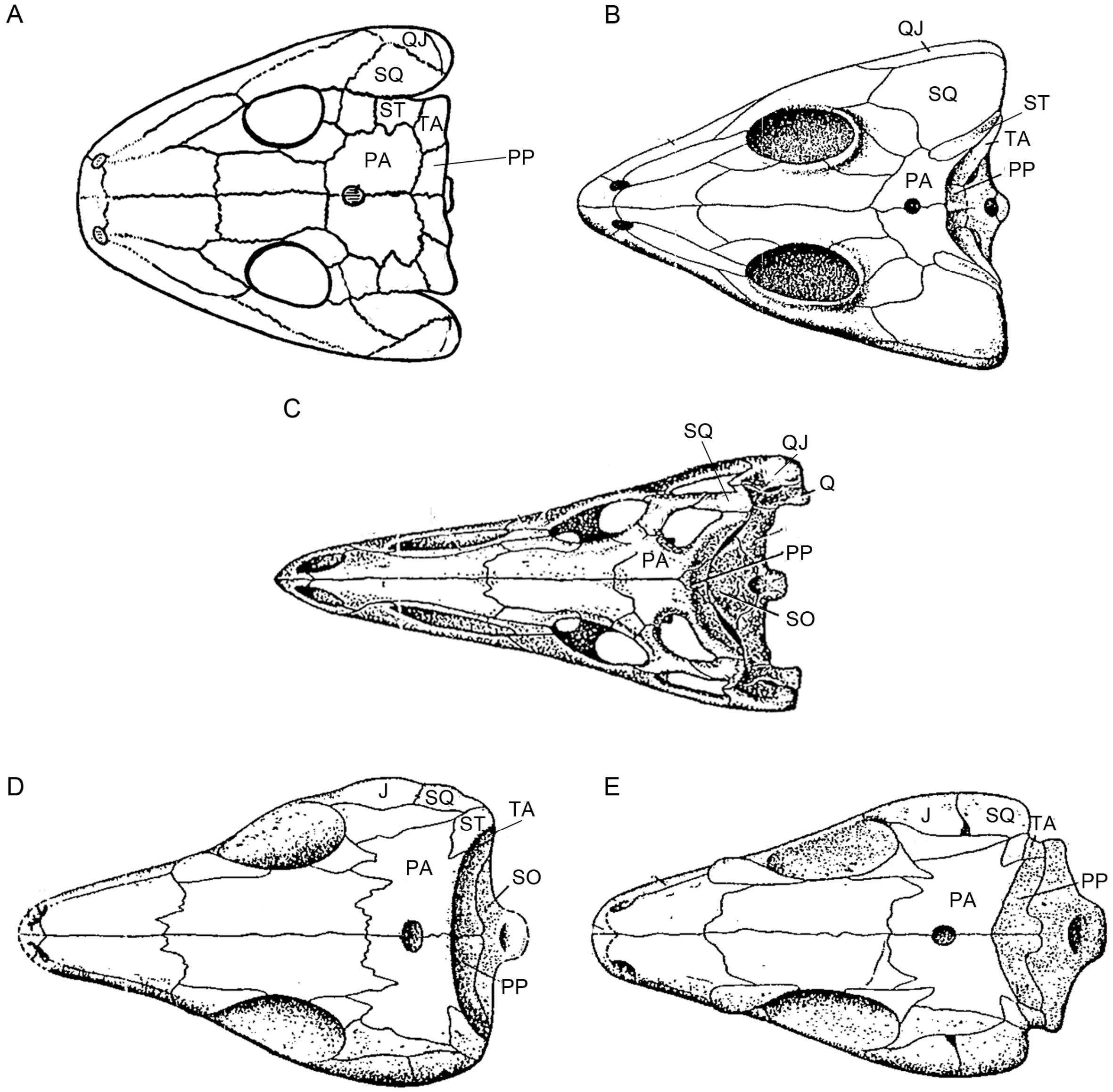


**Figure S1. Dorsal views of the skulls of stem amniotes and sauropsids.** (*A*) *Seymouria baylorensis* [redrawn from Parrington (18)], (*B*) *Protorothyris*, (*C*) *Euparkeria*, (*D*) *Milleretops* (or juvenile? of *Milleretta*), and (*E*) *Milleretta* [redrawn from Romer (11)].

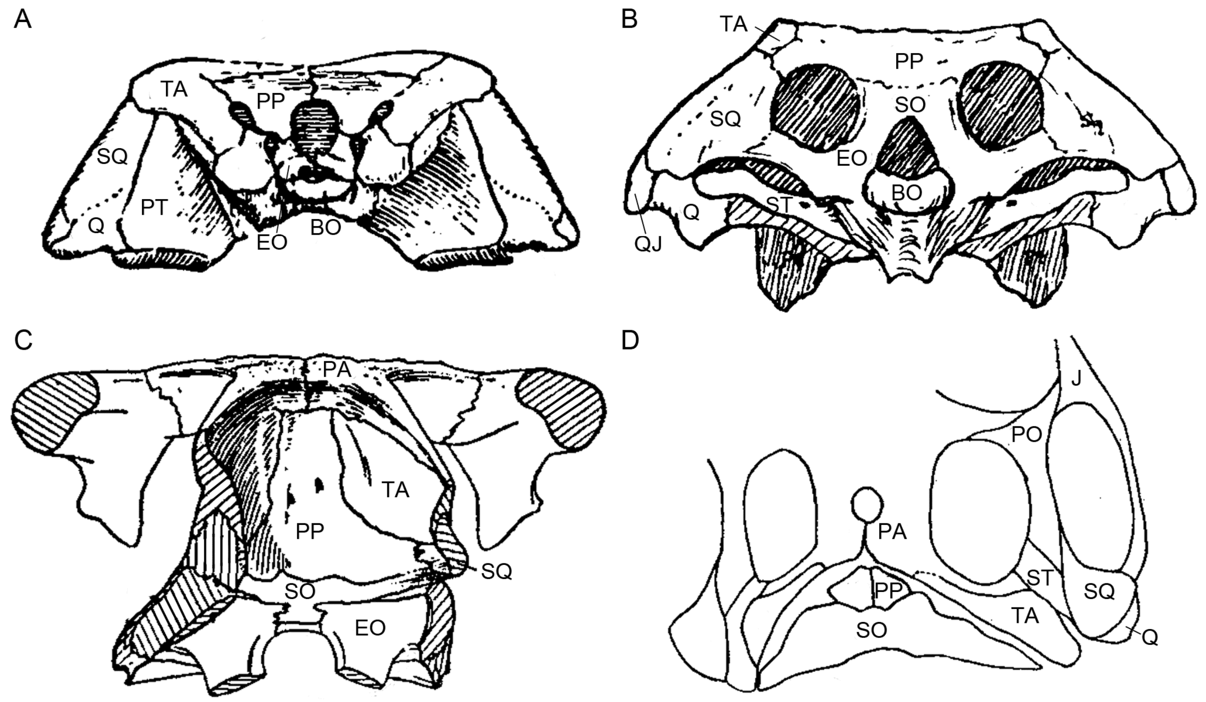


**Figure S2. Occipital region of stem amniotes and sauropsids.** (*A*) *Seymouria baylorensis*, (*B*) *Labidosaurus*, (*C*) *Machaeroprosopus gregorii*, and (*D*) *Youngina capensis* [adopted from Parrington (18)]. The bones labeled as IP in the original reference are renamed as PP for consistencies.

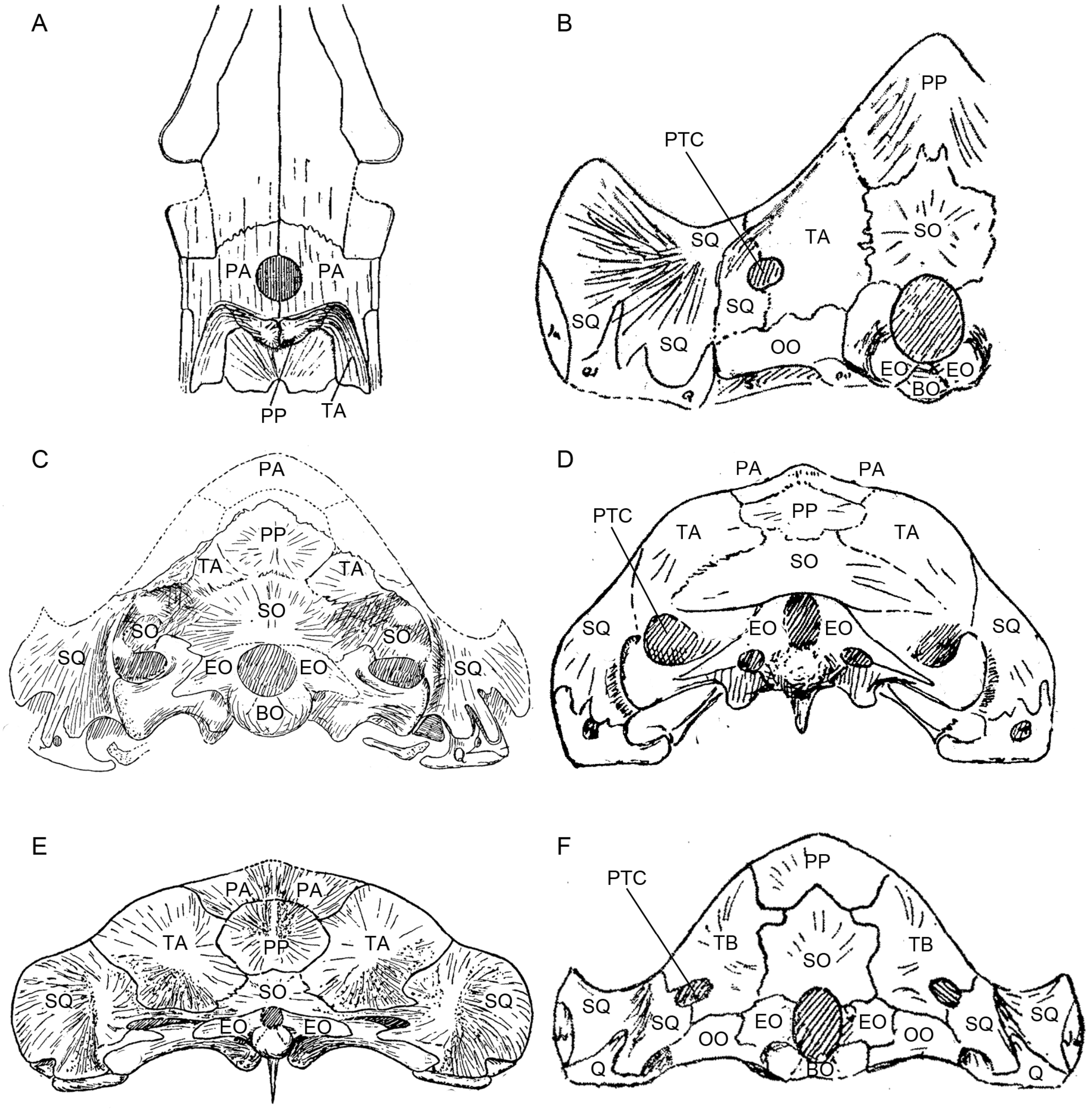


**Figure S3. Occipital region of non-mammalian synapsids.** (*A*) *Theropleura* [redrawn from Parrington (18)], (*B*) *Thrinaxodon liorhinus* (redrawn from Broom (53)), (*C*) *Lycedops*, (*D*) *Hofmeyria*, (*E*) *Hyenosaurus* [redrawn from Broom (49)] , and (*F*) *Galesaurus planiceps* [adopted from Broom (53)]. The bones labeled as IP in the original references are renamed as PP for consistencies.

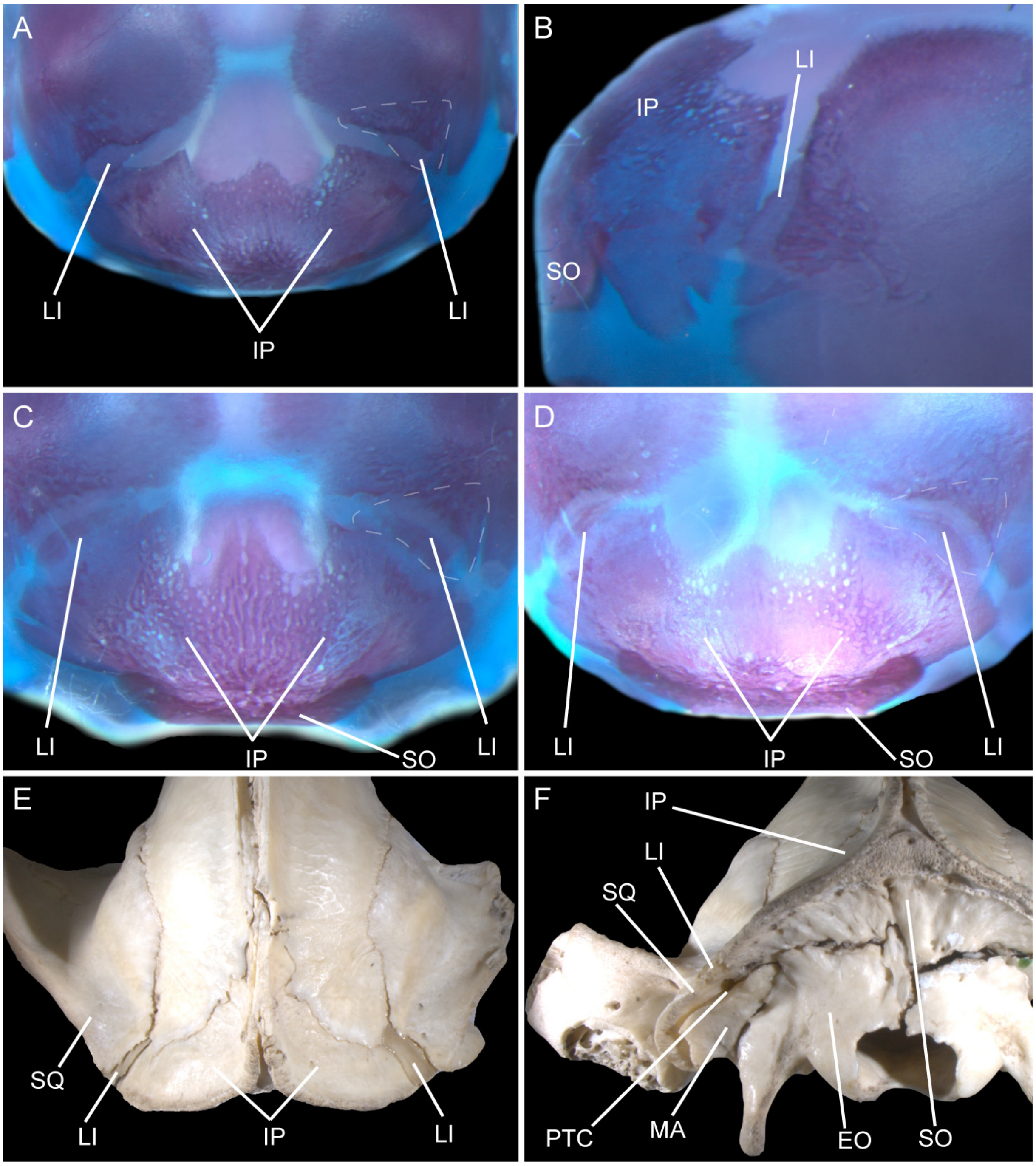


**Fig. S4. Occipital region of opossums.** (*A*) dorsal view and (*B*) lateral view of a 15 day *Monodelphis domestica* (gray short-tailed opossum) (PIMUZ-635D3/5), (*C*) dorsal view of a 15 day *M. domestica* (PIMUZ-635D2/5), (*D*) dorsal view of a 15 day *M. domestica* (PIMUZ-635D4/5), (*E*) dorsal view and (*F*) caudal view of a young *Didelphis albiventris* (white-eared opossum). The lateral interparietal elements (LI) are found laterally to the medial interparietals (IP) and are partly covered by the parietals in *M. domestica* (*A-D*). The lateral interparietal elements (LI) are found laterally to the medial interparietal elements (IP) in *D. albiventris* (*E-F*). The posttemporal canal (PTC) is found at the junction of the lateral interparietal (LI), squamosal (SQ), and mastoid (MA) (*F*).

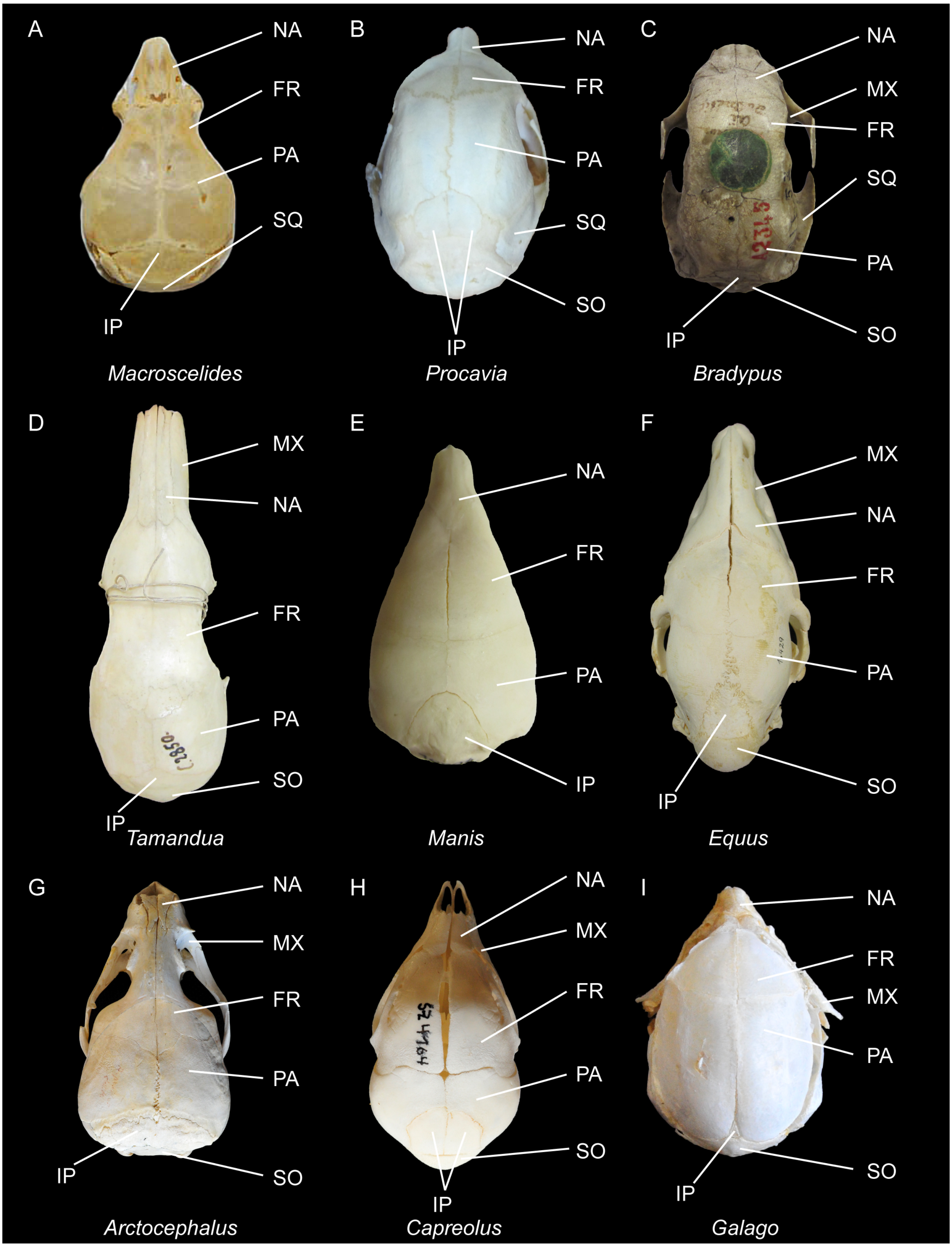


**Figure S5. Dorsal views of the skulls of selected mammals.** (*A*) *Macroscelides proboscideus* (short-eared elephant-shrew), (*B*) *Procavia capensis* (rock hyrax), (*C*) *Bradypus tridachtylus* (pale-throated sloth), (*D*) *Tamandua tetradactyla* (lesser anteater), (*E*) *Manis pentadactyla* (pangolin), (*F*) *Equus grevyi* (Grévy's zebra), (*G*) *Arctocephalus sp*. (fur seal), (*H*) *Capreolus capreolus* (European roe deer), (*I*) *Galago senegalensis* (Senegal bushbaby).

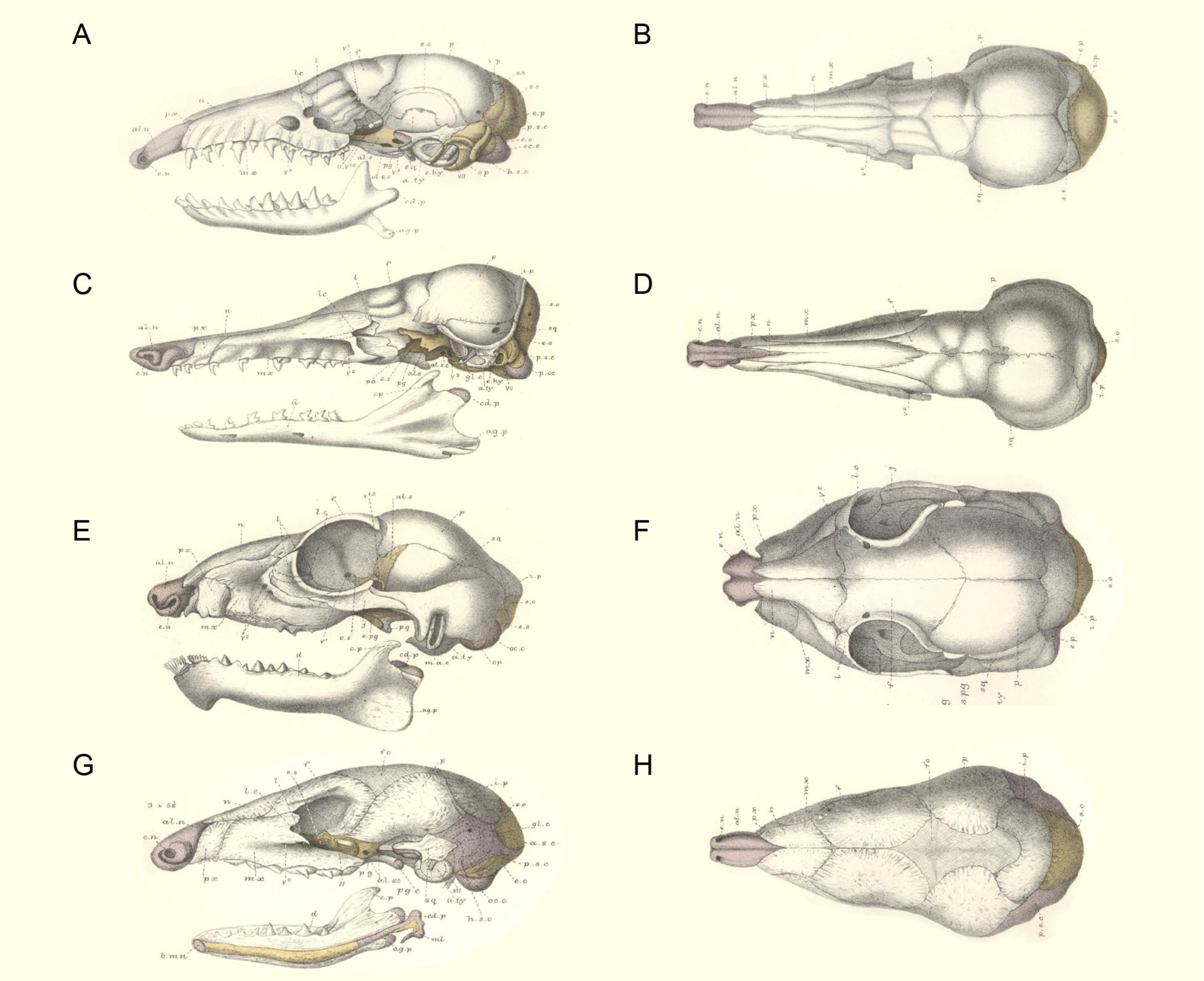


**Figure S6. Mammalian embryonic specimens described by Parker (78).** Note the interparietal bone labeled as "*i.p*" and the lateral interparietal element as "*s.t.*" (*A*) lateral and (*B*) dorsal view of *Microgale longicaudata* (lesser long-tailed shrew tenrec), (*C*) lateral and (*D*) dorsal view of *Hemicentetes madagascarensis* (lowland streaked tenrec), (*E*) lateral and (*F*) dorsal view of *Galeopterus variegatus* (Sunda flying lemur), (*G*) lateral and (*H*) dorsal view of *Tenrec ecaudatus* (tailless tenrec).

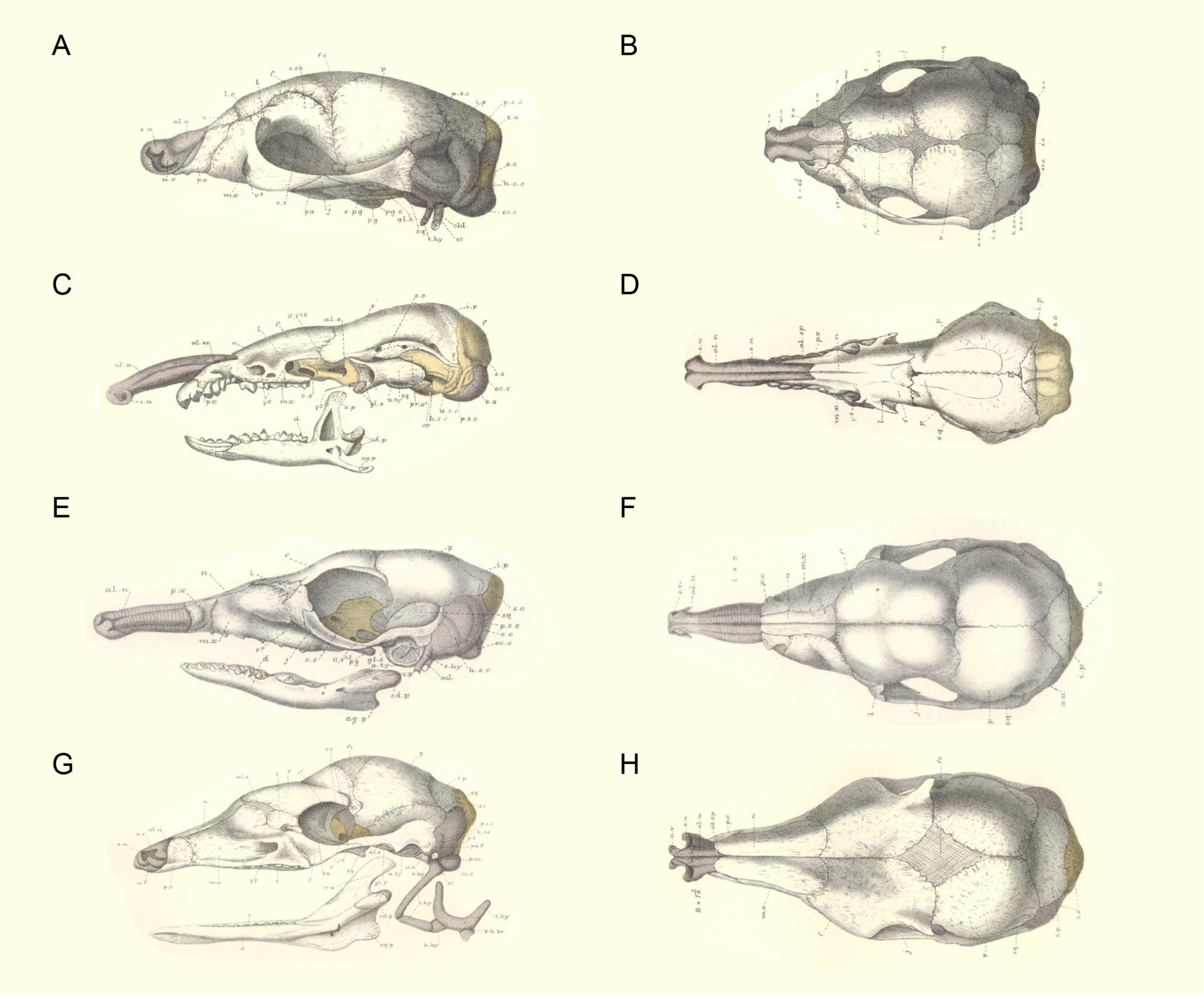


**Figure S7. Mammalian embryonic specimens described by Parker (77, 78)**. Note the interparietal bone labeled as "*i.p*". (*A*) lateral and (*B*) dorsal view of *Erinaceus europaeus* (European hedgehog), (*C*) lateral and (*D*) dorsal view of *Sorex araneus* (common shrew), (*E*) lateral and (*F*) dorsal view of *Rhynchocyon cirnei* (checkered elephant shrew), (*G*) lateral and (*H*) dorsal view of *Orycteropus afer* (aardvark).

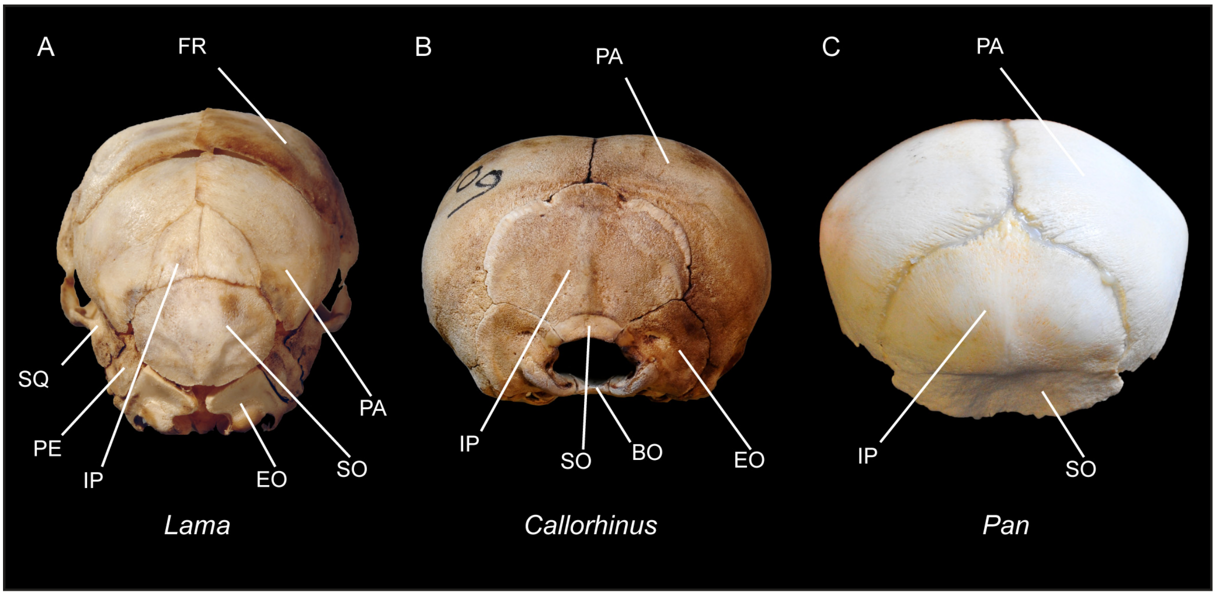


**Figure S8. Caudal view of the skulls.** (*A*) *Vicugna pacos* (alpaca), (*B*) *Callorhinus urusinus* (northern fur seal), and (*C*) *Pan troglodytes* (chimpanzee).

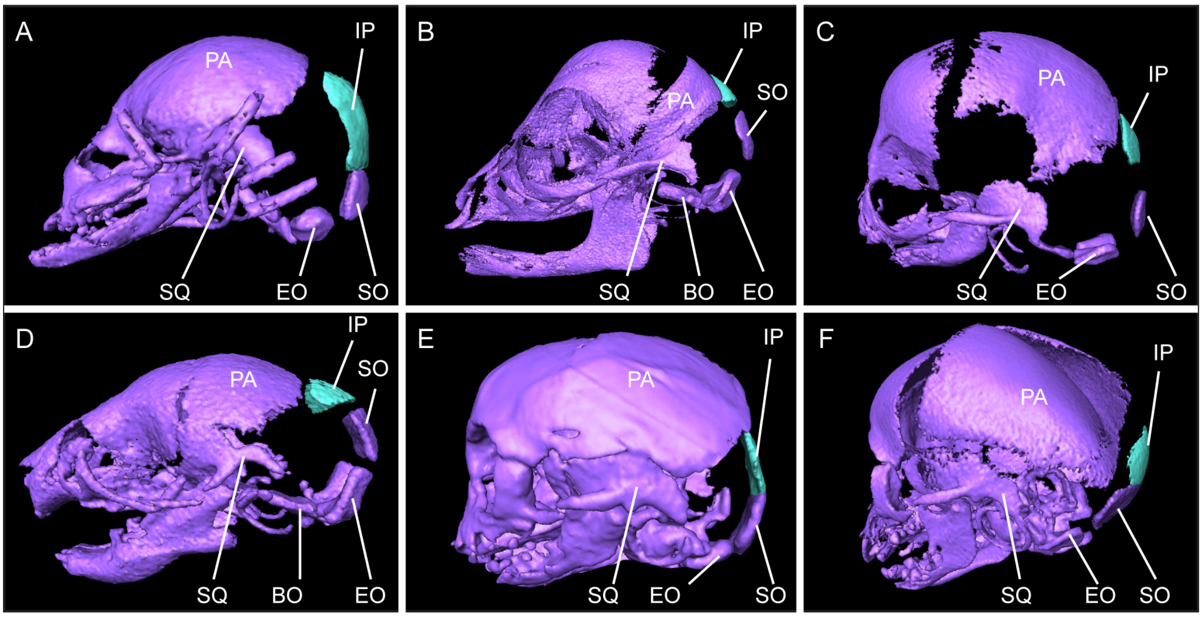


**Figure S9. CT reconstructions of the embryonic skulls (lateral view).** (*A*) *Rhinolopus sp.* (horseshoe bat), (*B*) *Bos primigenius* (cow), (*C*) *Felis cattus* (cat), (*D*) *Apodemus speciosus* (large Japanese field mouse), (*E*) *Macaca fascicularis* (long-tailed macaque), and (*F*) *Macaca fuscata* (Japanese macaque).

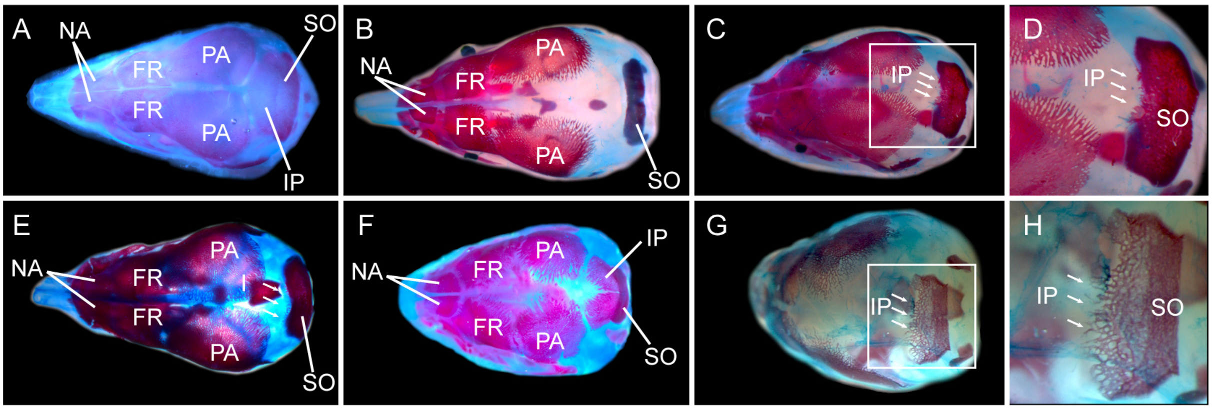
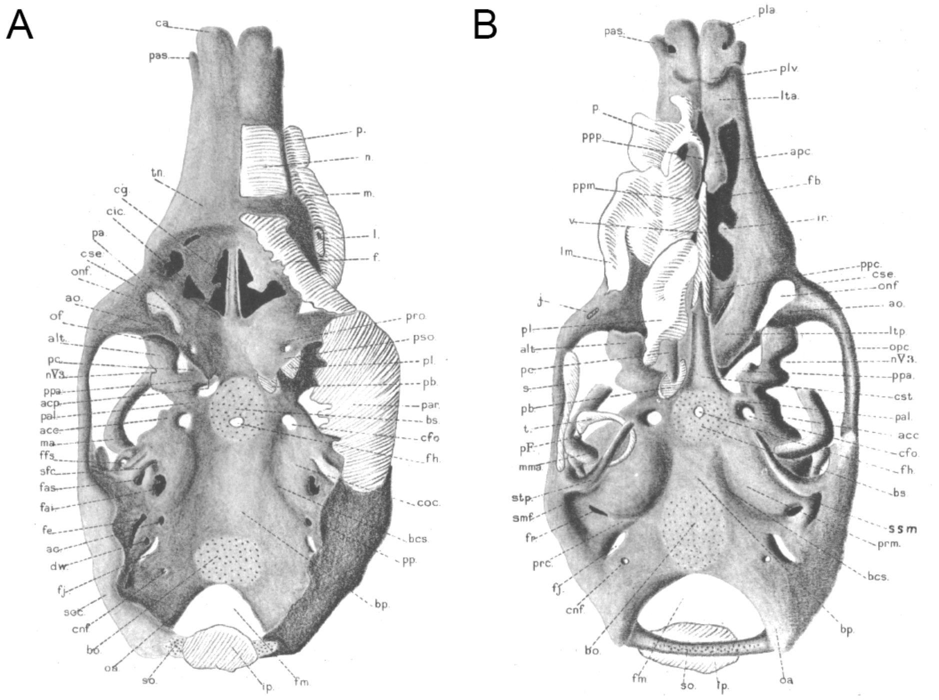


**Figure S10. Double-stained embryonic specimens of moles, hedgehogs, and shrews.** (*A*) *Talpa occidentalis* (Iberian mole). Note the interpairtal expanding anterior to the supraoccipital. (*B*) *Scapanus orarius* (coast mole). The interparietal is not yet ossified in this individual. (*C*) *S. orarius*. The interparietal has started to ossify from the anterior tip of the supraoccipital. (*D*) *S. orarius*. Close-up picture of (*C*). Note the small dermal outgrowth from the anterior tip of the supraoccipital. (*E*) *Mogera wogura* (Japanese mole). The interparietal has started to ossify. Note the dermal bone growing from the anterior tip of the supraoccipital. (*F*) *Erinaceus europaeus* (European hedgehog). Paired interparietal can be observed. (*G*) *Crocidura attenuata* (Asian grey shrew). Note the dermal bone (interparietal) attached to the anterior tip of the supraoccipital. (*H*) *C. attenuata*. Close-up picture of (*G*).



*Sorex* (dorsal)

*Sorex* (ventral)

**Figure S11. An embryonic skull of *Sorex araneus* (common shrew) described by de Beer (98).** (*A*) dorsal and (*B*) ventral view. Note the interparietal (*ip*) dorsally covers the supraoccipital (*so*), forming a double layered structure.

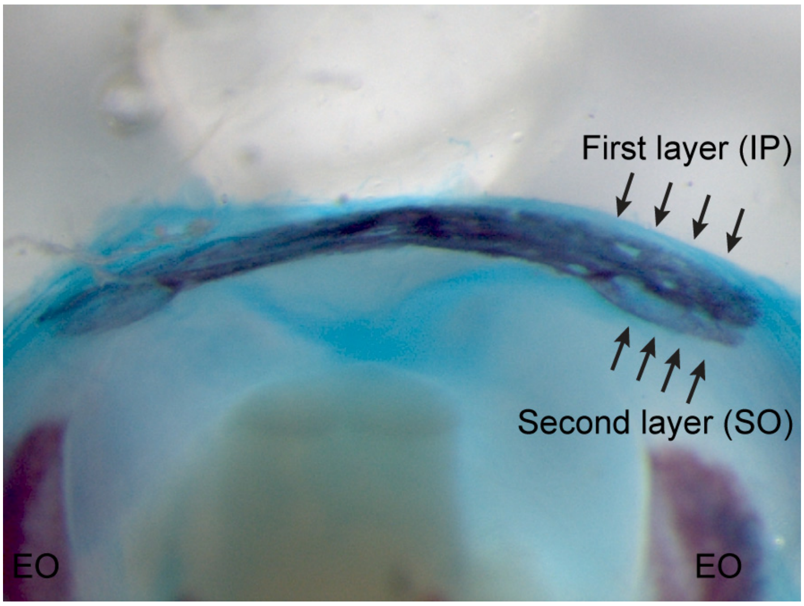


**Figure S12. Caudal view of the occipital region in a double-stained embryonic specimen of *Sorex unguiculatus* (long-clawed shrew).** The interparietal (IP) is covering the supraoccipital (SO), forming two layers of bones. This covering pattern is comparable to that of *S. araneus* (Fig. S11).

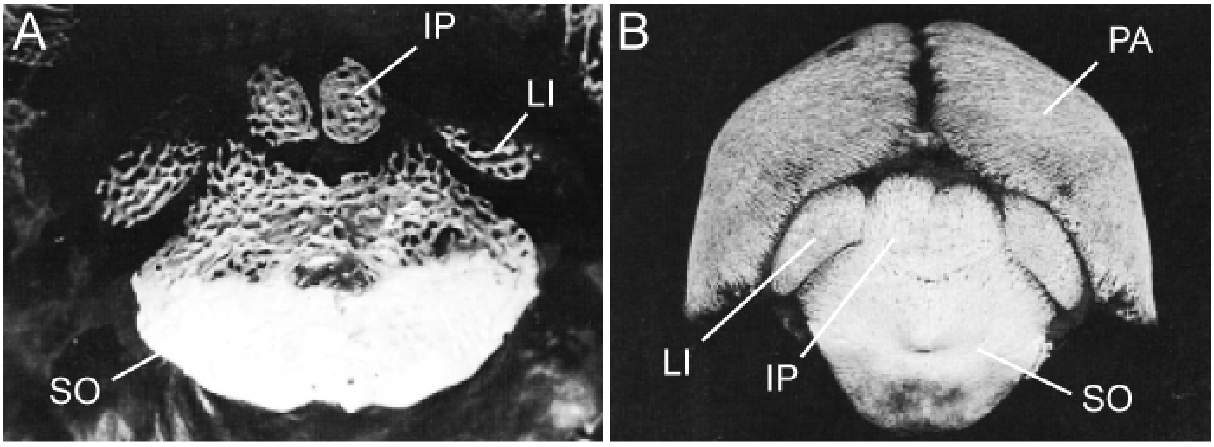


**Fig. S13. Interparietal development in *Homo sapiens*.** (*A*) Occipital squama of a 4th month fetus. (*B*) Occipital squama in a 5th month fetal skull. Note that the interparietal develops from four ossification centers (IP and LI) [reprinted from Matsumura et al. (91) with permission, courtesy of John Wiley & Sons].

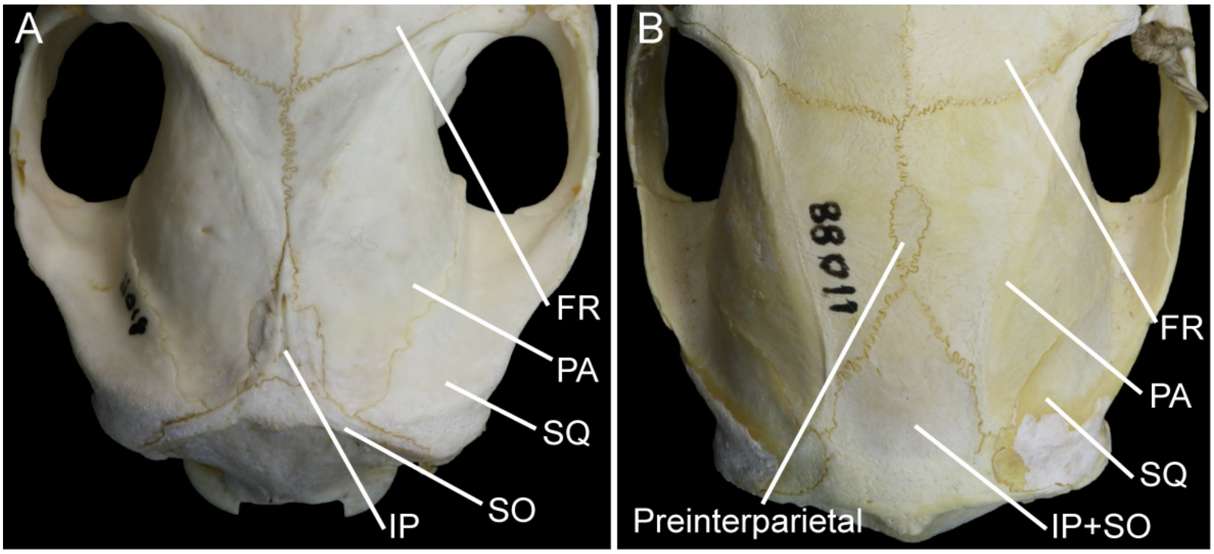


**Fig. 14. Preinterparietal in *Procavia capensis* (rock hyrax).** (*A*) the preinterparietal is not present, (*B*) the preinterparietal is present anterior to the interparietal (IP).

## Part C. Supplementary Table

Table S1. Observed pattern of the interparietal (or postparietal).

| | | Observed element number | First fusion with |
|---|---|---|---|
| Fish, stem tetrapods, and lissamphimbians | | | |
| | *Youngolepis praecursor* | 4 | none |
| | *Moythomsia nitida* | 4 | none |
| | *Kansasiella eatoni* | 4 | none |
| | *Ichthyostega* | 1 | none |
| | *Eryops* | 4 | none |
| | *Diplocaulus* | 4 | none |
| | *Phlegethontia (Dolichosoma)* | 4 | none |
| | *Branchiosaurus* | 4 | none |
| | *Apateon drachyiformis* | 4 | none |
| | *Palaeogyrinus (Palaeoherpeton)* | 4 | none |
| | *Eocaecilia micropodia* | 4 | none |
| | *Limnoscelis* | 4 | none |
| | *Doleserpeton* | 4 | none |
| | *Acanthostega* | 4 | none |
| | *Rana* | 1 | none |
| | *Pelobates* | 4 | none |
| | *Bombina* | 4 | none |
| | *Anthracosaurus* | 4 | none |
| Stem-amniotes and sauropsids | | | |
| | *Paleothyris* | 4 | none |
| | *Seymouria* | 4 | none |
| | *Kotlassia* | 4 | none |
| | *Diadectes* | 4 | none |
| | *Chilonyx* | 4 | none |
| | *Alligator mississippiensis* | 2 | none |
| | *Proganochelys* | none | - |
| | *Caretta* | none | - |
| | *Lepidochelys* | none | - |
| | *Chelonia* | none | - |
| | *Emys* | none | - |
| | *Pelodiscus sinensis* | none | - |
| | *Emydura subglobosa* | none | - |
| | *Lacerta* | none | - |
| | *Varanus* | none | - |
| | *Tupinambis* | none | - |
| | *Ctenosaura* | none | - |
| | *Sphenodon* | none | - |
| | *Placodus* | none | - |
| | *Araeoscelis* | 4 | none |
| | *Youngina* | 4 | none |
| | *Euparkeria* | 1 | none |
| | *Machaeroprosopus* | 3 | none |
| | *Milleretta* | 4 | none |
| | *Milleratops* (or juvenile? of *Milleretta*) | 4 | none |
| | *Protorothyris* | 4 | none |
| | *Labidosaurus* | 4 | none |
| | *Archaeopteryx* | none | - |
| | *Rhea* | none | - |
| | *Gallus gallus* | none | - |
| | *Protoavis* | none | - |
| | *Syntarsus* | none | - |

The observed number of interparietal elements, the bone to which the interparietal fuses, and the presence of lateral interparietal elements (tabular) are documented. The observed number of elements includes the number of tabulars for non-mammalian vertebrates.

## Table S1 (continued).

| | | Observed element number | First fusion with |
|---|---|---|---|
| Non-mammalian synapsids | | | |
| | *Ophiacodon uniformis* | 3 | none |
| | *Edaphosaurus pogonias* | 3 | none |
| | *Theropleura retroversa* | 3 | none |
| | *Dimetrodon* | 4 | none |
| | *Varanosaurus* | 4 | none |
| | *Diopus* | 4 | none |
| | *Mesenosaurus* | 4 | none |
| | *Thrinaxodon liorhinus* | 3 | none |
| | *Diarthrognathus* | 3 | parietal |
| | *Myosaurus gracilis* | 3 | none |
| | *Rechnisaurus cristarhynchus* | 1 | none |
| | *Ennatosaurus tecton* | 4 | none |
| | *Ecteninion lunensis* | 3 | none |
| | *Emydops* | 3 | none |
| | *Kombuisia frerensis* | 3 | none |
| | *Scylacops* | 3 | none |
| | *Cynognathus* | 3 | none |
| | *Ulemosaurus* | 4? | none |
| | *Synostoephalus* | 3 | none |
| | *Lycedops* | 3 | none |
| | *Bauria* | 3 | none |
| | *Hofmeyria* | 3 | none |
| | *Hyenosaurus* | 3 | none |
| | *Procynosuchus* | 3 | none |
| | *Titanophoneus* | 3 | none |
| | *Galesuchus gracilis* | 3 | none |
| | *Eoarctops vanderbyli* | 3 | none |
| | *Scylacognathus parvus* | 3 | none |
| | *Scylacops capensis* | 3 | none |
| | *Gorgonops torvus* | 3 | none |
| | *Lycaenops ornatus* | 3 | none |
| | *Sycosaurus laticeps* | 3 | none |
| | *Oudenodon bainii* | 1 | none |
| | *Tropidostoma dubium* | 1 | none |
| | *Dicynodon leptoscelus* (*Dicynodontia indet.*) | 1 | none |
| | *Sintocephalus alticeps* | 1 | none |
| | *Diictodon feliceps* | 1 | none |
| | *Aulacocephalodon baini* | 1 | none |
| | *A. laticeps* | 1 | none |
| | *A. whaitisi* | 1 | none |
| | *Platycyclops haughtoni* | 1 | none |
| | *Emydops longiceps* | 1 | none |
| | *E. trigoniceps* | 1 | none |
| | *E. longus* | 1 | none |
| | *Cistecephalus microrhinus* | 1-3 | none |
| | *Lystrosaurus maccaigi* | 1 | none |
| | *L. murrayi* | 1 | none |
| | *L. curvatus* | 1 | none |
| | *L. maccaigi* | 3 | none |
| | *Galesaurus planiceps* | 3 | none |
| | *Trirachodon kannemeyeri* | 1 | none |

## Table S1 (continued).

| | | | Observed element number | First fusion with |
|---|---|---|---|---|
| Docodonts | | | | |
| | | *Haldanodon exspectatus* | 1 | ? |
| Monotremes | | | | |
| | | *Ornithorhynchus* | 1 | supraoccipital |
| | | *Zaglossus* | 1 | supraoccipital |
| | | *Tachyglossus aculeatus* | 1 | supraoccipital |
| Marsupials | | | | |
| | | *Trichosurus* | 1-2 | supraoccipital |
| | | *Monodelphis* | 1-4 | supraoccipital |
| | | *Macropus* | 1-2 | supraoccipital |
| | | *Sminthopsis* | 1-2 | supraoccipital |
| | | *Macropus* | 1-2 | supraoccipital |
| | | *Hypsiprymnus* | 1-2 | supraoccipital |
| | | *Petaurus* | 1-2 | supraoccipital |
| | | *Phalanger* | 1-2 | supraoccipital |
| | | *Myrnecobius* | 1-2 | supraoccipital |
| | | *Phascolomys* | 1-2 | supraoccipital |
| | | *Didelphis marsupialis* | 1-2 | supraoccipital |
| | | *Myrmecobius fasciatus* | 1-2 | supraoccipital |
| | | *Didelphis albiventris* | 1-2 | supraoccipital |
| | | *Arctodictis sinclairi* | 1-2 | supraoccipital |
| | | *Bettongia* | 1-2 | supraoccipital |
| | | *Petaurus* | 1-2 | supraoccipital |
| | | *Dedrolagus* | 1-2 | supraoccipital |
| | | *Phalanger* | 1-2 | supraoccipital |
| | | *Wombatus* | 1-2 | supraoccipital |
| | | *Phascolarctos* | 1-2 | supraoccipital |
| | | *Trichosurus* | 1-2 | supraoccipital |
| | | *Onychogale* | 1-2 | supraoccipital |
| | | *Sarcophilus* | 1-2 | supraoccipital |
| Notoungulates | | | | |
| | Toxodontids | *Toxodon burmeisteri* | 3 | ? |
| | | *Nesodon imbricatus* | 3 | ? |
| | | *Pachyrucus* | 3 | ? |
| | Mesotherids | *Typotherium cristatum* | 3 | ? |
| Afrotherians | | | | |
| | Afrosoricids | *Tenrec ecaudatus* | 1-2 | supraoccipital |
| | | *Hemicentetes madagascarensis* | 1-2 | supraoccipital |
| | | *H. semispinosus* | 1-2 | supraoccipital |
| | | *Microgale longicaudata* | 3 | supraoccipital |
| | | *Potamogale velox* | 1 | supraoccipital |
| | | *Setifer* | 1 | supraoccipital |
| | | *Eremitalpa* | 1-2 | ? |
| | Hyracoids | *Heterohyrax brucei* | 1 | supraoccipital |
| | | *Procavia capensis* | 1-4 | supraoccipital |
| | | *Dendrohyrax abroreus* | 1-3 | supraoccipital |
| | Proboscids | *Loxodonta africana* | 1 | supraoccipital |
| | Macroscelids | *Macroscelides proboscideus* | 1 | supraoccipital |
| | Tubulidentates | *Orycteropus capensis* | 1 | supraoccipital |
| | | *Rhynchocyon cirnei* | 1 | supraoccipital |
| | Sirenians | *Dugong dugon* | 1-4 | parietal |
| | | *Trichechus manatus* | 1-4 | parietal |
| | | *T. senegalensis* | 1-4 | parietal |
| | | *Rytina* | 1 | ? |
| | | *Chrysochloris asiatica* | 3 | ? |
| Xenarthrans | | | | |
| | Pilosans | *Cyclopes didactylus* | 1-2 | supraoccipital |
| | | *Bradypus tridactylus* | 1 | supraoccipital |
| | | *Tamandua tetradactyla* | 1 | supraoccipital |
| | Cingulates | *Dasypus hybridus* | 1-2 | supraoccipital |

Table S1 (continued).

| | | | Observed element number | First fusion with |
|---|---|---|---|---|
| Euarchontoglires | | | | |
| | Rodents | *Dipodomys spp.* | 1-4 | ? |
| | | *Pedetes capensis* | 1-2 | ? |
| | | *Galea musteloides* | 1-2 | ? |
| | | *Hydromys chrysogaster* | 1-2 | ? |
| | | *Jaculus jaculus* | 1-2 | ? |
| | | *Micromys minutus* | 1-2 | ? |
| | | *Apodemus speciosus* | 1-2 | ? |
| | | *Octodon degu* | 1-3 | parietal |
| | | *Dolichotis patagonicum* | 1-3 | parietal |
| | | *Pteromys volans* | 1 | parietal |
| | | *Pteromys momonga* | 1 | parietal |
| | | *Spermophilus undulatus* | 1 | parietal |
| | | *Petaurista leucogenys* | 1 | parietal |
| | Lagomorphs | *Lepus* | 1-2 | parietal |
| | | *Oryctolagus cuniculus* | 1 | parietal |
| | Dermopterans | *Cynocephalus volans* | 1 | supraoccipital |
| | | *Galeopterus variegatus* | 1 | supraoccipital |
| | Scandentians | *Tupaia belangeri* | 1 | supraoccipital |
| | Primates | *Daubentonia madagascariensis* | 1 | supraoccipital |
| | | *Cebus* | 1 | supraoccipital |
| | | *Hylobates syndactylus* | 1 | supraoccipital |
| | | *Pan troglodytes* | 1 | supraoccipital |
| | | *Homo sapiens* | 1-4 | supraoccipital |
| | | *Eulemur* | 1-2 | supraoccipital |
| | | *Propithecus* | 1 | supraoccipital |
| | | *Loris tardigradus* | 1 | supraoccipital |
| | | *Galago senegalensis* | 1 | supraoccipital |
| | | *Macaca fuscata* | 1 | supraoccipital |
| | | *M. fascicularis* | 1 | supraoccipital |
| | | *M. mulatta* | 1 | supraoccipital |
| | | *Saimiri* | 1 | supraoccipital |
| Laurasiatherians | | | | |
| | Lipotyphlans | *Solenodon paradoxus* | 1-2 | parietal |
| | | *Erinaceus europaeus* | 1-2 | supraoccipital |
| | | *E. amurensis* | 1-2 | supraoccipital |
| | | *Echinosorex* | 1-2 | supraoccipital |
| | | *T. europaea* | 1-2 | supraoccipital |
| | | *T. occidentalis* | 1-2 | supraoccipital |
| | | *Scapanus orarius* | 1-2 | supraoccipital |
| | | *Mogera wogura* | 1-2 | supraoccipital |
| | | *Surdisorex norae* | 1 | ? |
| | | *S. polulus* | 1 | ? |
| | | *S. schlitteri* | 1 | ? |
| | | *Congosorex phillipsorum* | 1 | ? |
| | | *C. polli* | 1 | ? |
| | | *C. verheyeni* | 1 | ? |
| | | *Myosorex varius* | 1 | ? |
| | | *M. cafer* | 1 | ? |
| | | *M. longicaudatus* | 1 | ? |
| | | *M. eisentrauti* | 1 | ? |
| | | *M. gnoskei* | 1 | ? |
| | | *M. jejei* | 1 | ? |
| | | *M. babaulti* | 1 | ? |
| | | *M. bururiensis* | 1 | ? |
| | | *M. rumpii* | 1 | ? |
| | | *M. okuensis* | 1 | ? |
| | | *M. geata* | 1 | ? |
| | | *M. kihaulei* | 1 | ? |
| | | *M. tenuis* | 1 | ? |
| | | *M. zinki* | 1 | ? |
| | | *Sorex araneus* | 1 | supraoccipital |
| | | *S. unguiculatus* | 1 | supraoccipital |
| | | *Suncus murinus* | 1 | supraoccipital |
| | | *Crocidura attenuata* | 1 | supraoccipital |
| | | *C. watasei* | 1 | supraoccipital |

Table S1 (continued).

| | | Observed element number | First fusion with |
|---|---|---|---|
| Cetaceans | *Tursiops truncatus* | 1-3 | ? |
| | *Phocoena phocoena* | 1 | ? |
| | *Monodon monoceros* | 1-4 | ? |
| | *Balaenoptera borealis* | 1 | supraoccipital |
| | *B. musculus* | 1 | supraoccipital |
| | *Delphinus delphinus* | 1 | ? |
| | *Inia geoffrensis* | 1 | ? |
| | *Stenella attenuata* | 3 | supraoccipital |
| Artiodactyls | *Capreolus capreolus* | 1-2 | parietal |
| | *Tragelaphus scriptus* | 1-2 | parietal |
| | *Cervus nippon* | 1-2 | parietal |
| | *C. elaphus* | 1-2 | parietal |
| | *C. duvauceli* | 1-2 | parietal |
| | *C. eldi* | 1-2 | parietal |
| | *Odocoileus virginanus* | 1 | parietal |
| | *Dama dama* | 1-2 | parietal |
| | *Alces alces* | 1-2 | parietal |
| | *Bos primigenius* | 1-4 | parietal |
| | *Bos grunniens* | 1-3 | ? |
| | *Muntiacus reevesi* | 1-2 | parietal |
| | *Ovis dalli* | 1-2 | parietal |
| | *O. dalli* | 1-2 | parietal |
| | *Lama pacos* | 1-2 | parietal |
| | *Kobus ellipsiprymnus* | 1-2 | parietal |
| | *Tragulus* | 1-2 | parietal |
| Carnivorans | *Ailuropoda melanoleuca* | 1 | supraoccipital |
| | *Ursus* | 1 | supraoccipital |
| | *Canis* | 1-2 | supraoccipital |
| | *Speothos* | 1 | supraoccipital |
| | *Lutra lutra* | 1 | supraoccipital |
| | *Mustela* | 1 | supraoccipital |
| | *Procyon lotor* | 1 | supraoccipital |
| | *P. pygmaeus* | 1 | supraoccipital |
| | *Vulpes vulpes* | 1 | supraoccipital |
| | *Panthera leo* | 1 | supraoccipital |
| | *P. onca* | 1-3 | supraoccipital |
| | *P. pardus* | 1 | supraoccipital |
| | *Puma concolor* | 1-3 | supraoccipital |
| | *Felis domestica* | 1-2 | supraoccipital |
| | *Arctocephalus* | 1 | supraoccipital |
| | *Callorhinus ursinus* | 1 | supraoccipital |
| | *Phoca* | 1-3 | supraoccipital |
| Pholidotans | *Manis* | 1 | supraoccipital |
| Perissodactyls | *Equus* | 1-2 | parietal |
| | *Tapirus* | 1-2 | parietal |
| | *Rhinoceros* | 1 | parietal |
| | *Diceros* | 1 | parietal |
| Chiropterans | *Hipposideros* | 1-2 | supraoccipital |
| | *Kerivoula* | 1-2 | supraoccipital |
| | *Hesperoptenus* | 1-2 | supraoccipital |
| | *Rhinolophus* | 1-2 | supraoccipital |
| | *Miniopterus* | 1-2 | supraoccipital |
| | *Roussettus* | 1 | supraoccipital |
| | *Artibeus* | 1 | supraoccipital |
| | *Pteropus lylei* | 1 | supraoccipital |
| | *Dobsonia pannietensis* | 1 | supraoccipital |

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