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CARTILAGO TENIFORMIS AND ITS DERIVATIVES: ADDITIONAL INFORMATION ON THE BASIC COMPOSITION AND EVOLUTION OF THE SKULL

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Abstract: The cephalic endoskeleton of craniate animals consists of a large number of elements. Some of them are segmentally arranged and some are not. In what follows, the contribution to the endocranium of the non-segmental component, here called the teniform cartilage, is discussed within an evolutionary framework.

Key words: non-segmental cephalic endoskeleton, basic cranial composition, endocranial evolution

Definition of problem and discussion

As argued elsewhere (Bjerring 1984), the craniate head is phylogenetically the oldest part of the body. Two main divisions of cephalic endoskeleton are recognizable, axial and pharyngoqualar (Text-fig. 1), both of which consist of serially arranged elements. These seriations coincide with each other; they have presumably arisen as a consequence of pharyngotrematosy. The perforations of this series likely functioned primarily as a ciliary filter-feeding system and each of these passageways is a pharyngothyrium (sensu Bjerring 2014). A branchyothyrium (sensu Bjerring 1984) is a gilled pharyngothyrium.

The axial endoskeletal elements are products of the upper parts of the pleurohylomeres (sensu Bjerring 2014), which are the counterparts of the epithelial segments known in craniate embryos as somites. The pharyngoqualar endoskeletal elements, collectively comprising the pharyngoqualum (sensu Bjerring 1998), derive from neural crest cells which after migration downwards lie between the pharyngothyria where they surround the interpharyngothyric parts of the pleurohylomeres, termed the parasomitic bars (sensu Bjerring 2014).

In addition to the two main divisions of segmentally arranged endoskeleton mentioned above, the craniate head includes a number of endoskeletal elements which do not exhibit a metameric arrangement. This third division of cephalic endoskeleton, generally overlooked, arises from neural crest mesenchyme, which lies dorsally to the pharyngothyria and, therefore, is not segregated into metameric masses, as are the cells that give origin to the pharyngoqualum. It would seem that the non-segmental cephalic endoskeleton was formed from continuous strips of cartilage, one on each side of the body (Text-fig. 1), which like the notochord served as an internal compression-resisting
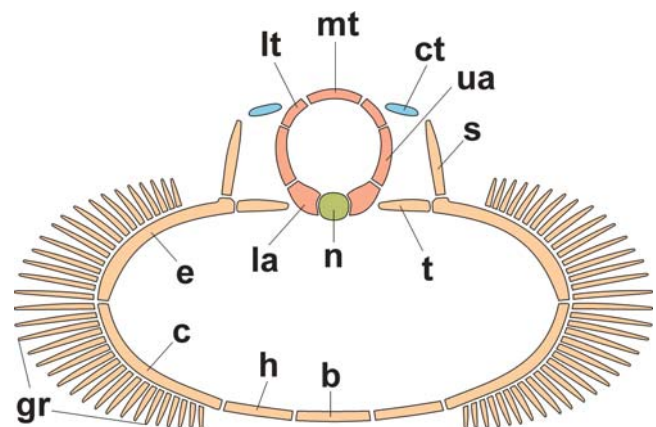
Text-fig. 1. Schematic drawing, demonstrating the basic endo-skeletal elements of the craniate head. Sclerotomic deriva-tives red and pharyngoqualar derivatives yellow. b: basal pharyngoqualar segment; c: ceratal pharyngoqualar segment; ct: cartilago teniformis (blue); e: epal pharyngoqualar segment; gr: gill rays; h: hypal pharyngoqualar segment; la: lower arcual element; lt: laterotectal element; mt: mediotectal element; n: notochord (green); s: summital pharyngoqualar segment; t: telical pharyngoqualar segment; ua: upper arcual element.

supportive structure during the beginning of cephalic history. The name given to this special category of early endoskeleton is cartilago teniformis (Bjerring 2015). During the course of evolution, the single structure of the teniform endoskeleton became fragmented and the fragments that remain in extant craniates have become incorporated into the skull.

A major derivative of the teniform cartilage is an anuran embryonic structure that Gaupp (1893) called taenia tecti marginalis. This element extents forwards above the otic capsule from the tectum posterius to the pila antotica (pila

prootica according to Gaupp). Accordingly, this anuran endoskeleton comprises an otic as well as a temporal part. The latter is anteriorly continued by what Gaupp (1893) refers to as the "dorsal Randspange", a cartilaginous rod that runs dorsally in the orbital region towards the nasal capsule on the same side, connecting the antotic and preoptic pilae. Gaupp's "dorsal Randspange" is referred to by de Beer (1937) as the orbital cartilage.

In a paper on the endocranium of a 31 mm sand lizard (*Lacerta agilis* LINNAEUS, 1758) embryo Gaupp (1900) uses the term taenia marginalis for a cartilaginous structure, which according to his opinion, corresponds to the two anuran structures he earlier called taenia tecti marginalis and the "dorsal Randspange". Anteriorly, this lacertilian cartilage meets the part of the endocranium that Gaupp designated the planum supraseptale. As shown by de Beer (1930) the planum supraseptale represents a pair of orbital cartilages that have been pressed together between the eyes. Each of the orbital cartilages develops an anteriorly directed process, the anlage of the sphenethmoidal commissure. This commissure subsequently becomes attached to the primordium of the nasal capsule roof, an element of independent origin called the cartilago parietotectalis. It thus follows that in the sand lizard the endocranium includes on each side a longitudinal row of elements which are neither axial nor pharyngoqualar (Text-fig. 2).

A corresponding row of endocranial elements occurs in mammals. From back to front, these mammalian elements are known as commissura parietooccipitalis, lamina parietalis, commissura orbitoparietalis, ala orbitalis or orbital cartilage, commissura sphenethmoidalis or commissura orbitonasalis and cartilago parietotectalis or cartilago tecti nasi (Text-fig. 3).

As exemplified by the cat embryo (Terry 1917) the parietal plate and the orbital cartilage may arise as independent chondrifications. During development, the parietal plate grows forwards into the temporal region to reach the orbital cartilage and thus forms the orbitoparietal commissure. Subsequently the parietal plate fuses with the lateral part of the tectum posterius and the orbital cartilage with the roof of the nasal capsule at the sphenethmoidal commissure.

This series of dorsolateral endocranial elements can also be identified in fishes whose anatomical features place them in the key position as progenitors of limbed craniates. Thus in the Devonian osteolepiform *Eusthenopteron foordi* WHITEAVES, 1881 (Text-fig. 4), which was studied using serially ground sections, the tectum orbitae (corresponding to the sphenethmoidal commissure and a part of the taenia marginalis) exists in the form of a backward directed rod-shaped process of the tectum nasi. This capsular roof corresponds to the taenia marginalis ethmoidalis of Hammarberg (1937) and Betmar (1966). The tip of the above-mentioned rod-shaped process lacks a periosteal lining and must therefore have continued as cartilage. This cartilaginous posterior part of the tectum orbitae, one may assume, ended where the margin of the endocranial roof juts out in front of the intracranial juncture apparatus (sensu Bjerring 1998), because this marginal endocranial part, too, is without a periosteal lining. The orbital tectum of *Eusthenopteron foordi* is very similar to that of *Polypterus*
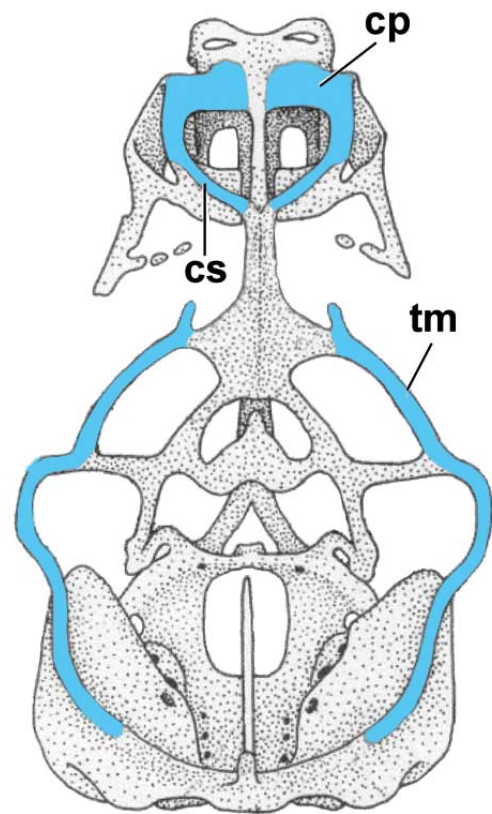
Text-fig. 2. Dorsal view of endocranium of a 31 mm sand lizard (*Lacerta agilis*). Derivatives of the teniform cartilages blue. cp: cartilago parietectalis (cartilago tecti nasi); cs: sphenethmoidal commissure; tm: taenia marginalis. (Modified from Gaupp 1900.)
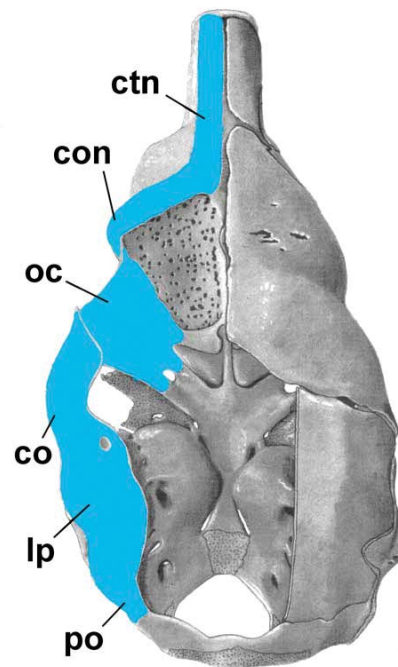
Text-fig. 3. Dorsal view of endocranium of armadillo (*Dasypus novemcinctus*); some dermal allostoses from the right side are included. Derivatives of the teniform cartilage blue. co: orbitoparietal commissure; con: sphenethmoidal (orbitonasal) commissure; ctn: cartilago tecti nasi; lp: parietal lamina; oc: orbital cartilage (ala orbitalis); po: parieto-occipital commissure. (Modified from Reinbach 1952.)
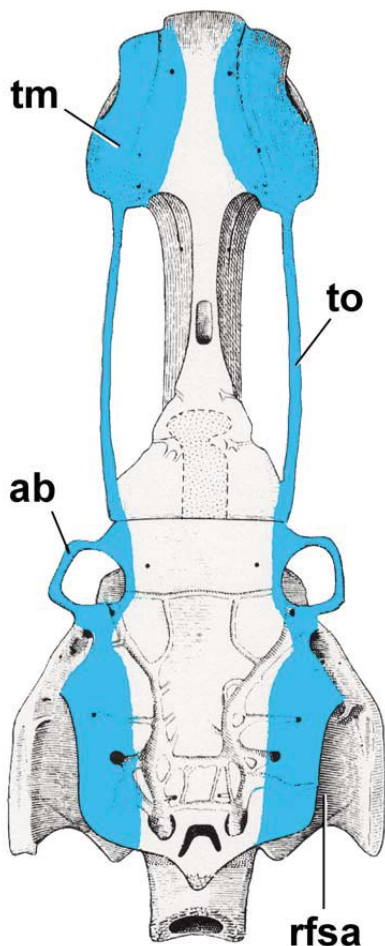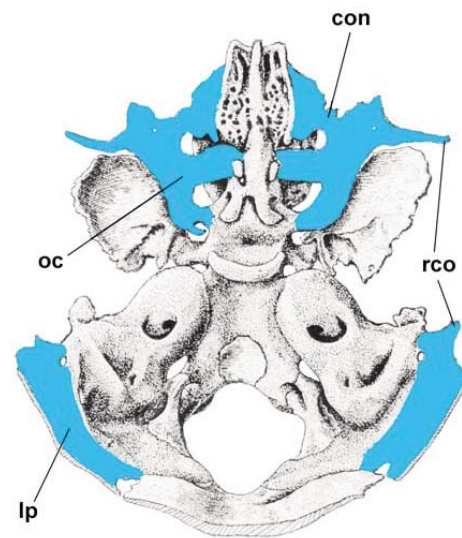
Text-fig. 4. Dorsal view of endocranium of a Devonian osteo-lepiform (*Eusthenopteron foordi*). Derivatives of the teniform cartilages blue (cf. fig. 7 in Bjerring 2015). ab: anterolateral bar of otico-occipital (Jarvik 1954) which corresponds to the orbitoparietal commissure of the armadillo; rfsa: endoskeleton above the supra-auditive fossa which corresponds to the parietal lamina of the armadillo; tn: tectum nasi; to: tectum orbitae which corresponds to the orbital cartilage and the orbitonasal commissure of the armadillo.

Text-fig. 5. Dorsal view of endocranium of 93 mm human fetus. Derivatives of the teniform cartilages blue. con: orbitonasal commissure; lp: parietal lamina; oc: orbital cartilage; rco: remnants of orbitoparietal commissure. (Modified from Reinbach 1963; cf. Bersch and Reinbach 1970.)

senegalus (CUVIER, 1829) (Bjerring 2014). In the Middle Devonian fish *Youngolepis praecursor* CHANG et YU, 1981, on the other hand, the tectum orbitae covers the orbit completely (Chang 1982).

Posterior to the tectum orbitae, the margin of the endocranial roof of *Eusthenopteron foordi* protrudes like eaves. In the temporal region, this projecting overhang (called the anterolateral bar of the otico-occipital by Jarvik (1954)) is perforated exposing the underside of the adjacent dermal skull roof, which here articulates with the ascending mid-portion of the palatoquadrate (see Bjerring 2015, fig. 8A), a contact that corresponds to the human sphenoparietal suture. In the otic region, the lateral edge of the endocranial roof partly covers the fossa supra-auditiva ("fossa Bridgei"), a depression in the otic capsule serving as a myodome (Bjerring 2015, fig. 8C).

Thus, it seems that, as in the sand lizard, all of the original cartilago teniformis persists in the endocranium of *Eusthenopteron foordi*. However, this is not always the case. For example, in the bowfin, *Amia calva* LINNAEUS, 1766, the

roof of the nasal capsule is absent (Hammarberg 1937) and in the longfinned pilot whale, *Globicephala melas* (TRAILL, 1809), there is no sphenethmoidal commissure (Schreiber 1916). Moreover, in the human embryo the orbitoparietal commissure is generally absent (Text-fig. 5), but Augier (1934) described a remnant of this commissure in the form of an element he calls the cartilage rétroalaire. Furthermore, in the chimpanzee, *Pan troglodytes* (BLUMENBACH, 1775)*,* there is no parietal plate (Starck 1960).

In the two monotremes of the Australian region, the platypus (*Ornithorhynchus anatinus* (SHAW, 1799)) and the spiny anteater (*Tachyglossus aculeatus* (SHAW, 1792)), according to de Beer (1937), the endocranium corresponds with that of placental mammals by the inclusion of an orbitonasal commissure, an orbital cartilage, an orbitoparietal commissure and a parietal plate (lamina supracapsularis). This view, however, is probably incorrect, inasmuch as the backward expansion of the telencephalon relative to the endocranium occurs differently within these two groups of tetrapods. More precisely, in the embryogeny of monotremes the cerebral hemispheres expand posteriorly inside the endocranium whereas the corresponding brain parts in the embryos of placental mammals grow backwards outside the endocranium (cf. Bjerring 1995, 1998). The implication is, then, that the monotreme cerebrum lies in an undivided hollow, the cavitas encephalica endocranii, and that the cerebrum of placentals is accommodated in a bipartite hollow, the cavitas encephalica cranii, one part of which is the neocavum and the other the compartitio trunci encephalicae (Bjerring 2015). The two last-mentioned spaces are separated by the tentorium cerebelli, which is a component part of the endocranium (Bjerring 1995, 2015). In some placental mammals, the tentorium cerebelli is more or less covered by allostotic bone forming the tentorium osseum (cf. Bayer 1898).
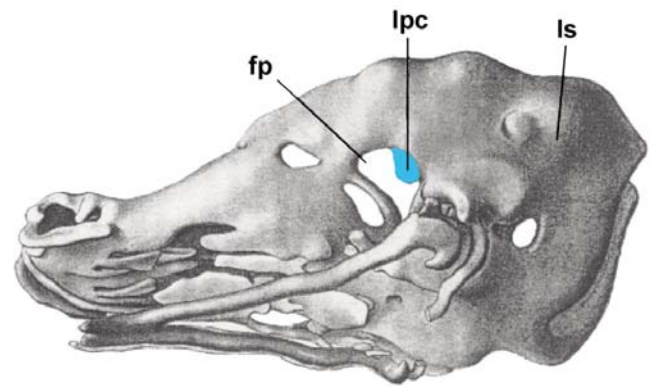
An endocranium within which the telencephalon expands backwards need not incorporate new endoskeletal elements
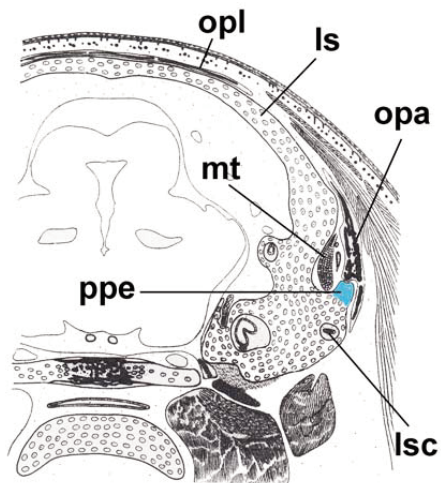
Text-fig. 6. *Ornithorhynchus anatinus*. Transverse section through the otic region of the head of a 180-mm specimen. ls: supracapsular lamina; lsc: lateral semicircular canal; mt: musculus temporalis; opa: parietal bone; opl: pluteal bone; ppe: parietal process of endocranium (blue). (Modified from Zeller 1989.)
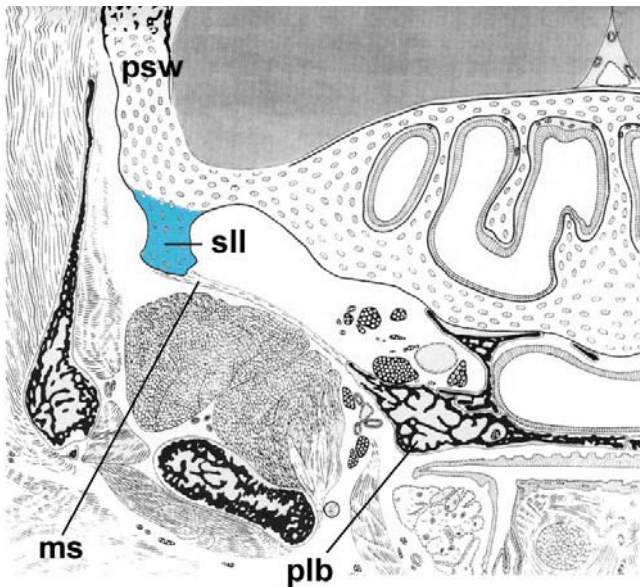

Text-fig. 7. *Tachyglossus aculeatus*. Ventrolateral view of the head endoskeleton of a specimen shortly after it had left the pouch. fp: foramen prooticum; lpc: limbus praecapsularis (blue); ls: supracapsular lamina. (Modified from Gaupp 1913.)


Text-fig. 8. *Tachyglossus aculeatus*. Transverse section through the temporal region of the adult head. Membranous parts blue, autostoses brown and allostoses purple. gg: ganglion gasseri; lop: lamina obturatoria periotici; ms: sphenobturatory membrane; mt: musculus temporalis; oo: os obturans; opa: parietal bone. (Modified from Kuhn and Zeller 1987.)

for the confinement of the brain. Therefore, the parts of the monotremous skeleton, which Gaupp (1908), Kuhn (1971), and Zeller (1989) have designated as the orbitonasal commissure, the orbital cartilage, the orbitoparietal commissure and the supracapsular lamina are not homologous with the placental skull elements usually referred to by the same terms. The elements of the monotreme endocranium previously enumerated are quite surely contributions originating from somitic mesenchyme and belonging to the laterotectal series (cf. Text-fig. 1).

In the platypus, in a far advanced period of ontogeny, a process on the otic capsule dorsal to the lateral semicircular canal develops (Text-fig. 6). Zeller (1989) calls it the processus opercularis and suggests that its homologue is the structure in the mole (*Talpa europaea* LINNAEUS, 1758) referred to by the same name (Fischer 1901); this structure was later renamed the processus pleuroticus (Bjerring 1993). The previously mentioned therian process is united ventrally with the edge of the posterior part of the tegmen tympani and extends upwards laterally to the jugular vein towards the place where the orbitoparietal commissure is attached to the parietal plate. Thus, Fischer's opercular process is in the main located in the temporal region of the endocranium. Zeller's opercular process, however, is located in the otic region of the endocranium where it contributes to the formation of a myodome for the musculus temporalis. This means that there is reason to believe in a nonhomology between Fischer's and Zeller's process. Elsewhere (Bjerring 1993) it has been argued that the former process represents modified gill rays of the fourth or hyoid pharyngoqualar arch. The latter process, on the other hand, occupies such a position that it should probably be regarded as a homologue of a remnant of the therian parietal plate. This process of the platypus is hereinafter termed the processus parietalis endocranii. A possible corollary of this view is that the dermal allostosis developing adjacent to the endocranial parietal process
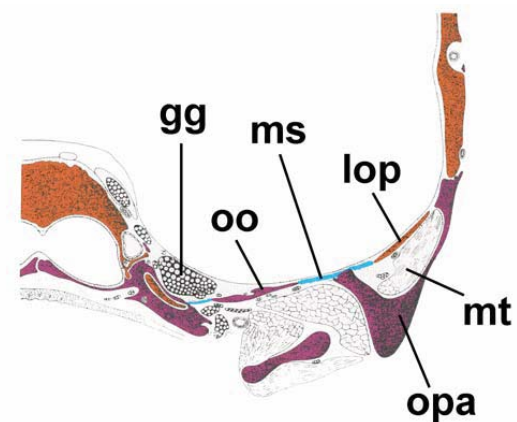
represents a homologue of the human parietal bone and is not a squamosal bone as stated by Zeller (1989).The squamosal bone is defined by Hallmann (1837) as the pars squamosal of the temporal bone, a mucosal allostotic structure. In the platypus, this mucosal allostosis, it would seem, occurs in the temporal part of the sphenobturatory membrane in the form of the obturans bone, which, as suggested elsewhere (Bjerring 1998), derives from spiracular allostoses.

In the ontogeny of the spiny anteater, according to Gaupp (1908) and Kuhn (1971), the foramen prooticum is enclosed dorsally by an endocranial commissure, which is involved in the demarcation of the cavitas encephalica endocranii. During later development, this axial part of the nascent endocranium increases in size and from its ventral edge arises an outgrowth that projects sideways outside the foramen prooticum where it ends freely. Gaupp (1908) calls it the limbus praecapsularis (Text-fig. 7). This limbic part of the cartilaginous endocranium does not confine the ipsilateral cerebral hemisphere but serves as the attachment for the

Text-fig. 9. *Tachyglossus aculeatus*. **Transverse section through the orbital region of the head of a juvenile specimen. ms: sphenobturatory membrane; plb: palatine bone; psw: primary endocranial sidewall; sll: secondary lateral lamella of Kuhn (1971); this endocranial process (blue) is here interpreted as a derivative of the cartilago teniformis. (From Kuhn and Zeller 1987.)**
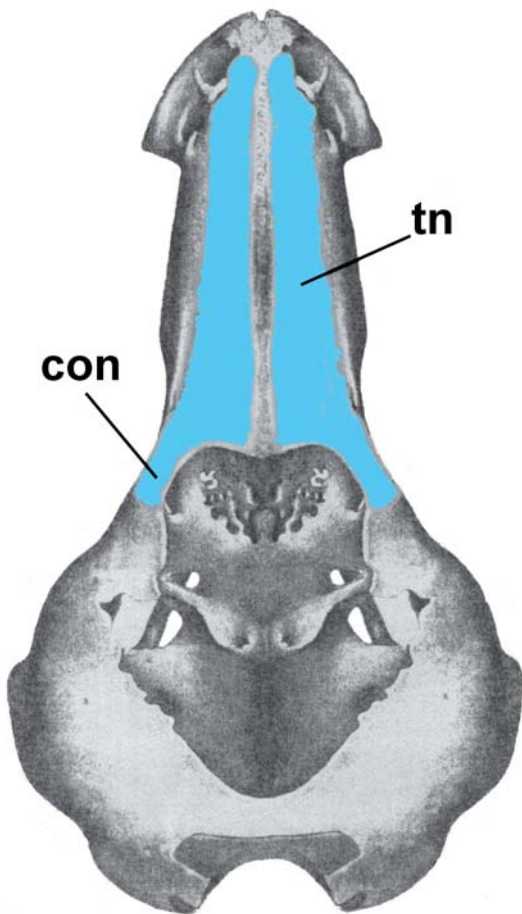
Text-fig. 10. Dorsal view of endocranium of a ca. 53 mm *Tachyglossus aculeatus*. **Derivatives of the teniform cartilages blue. con: orbitonasal commissure; tn: tectum nasi. (Modified from Kuhn 1971.)**

sphenobturatory membrane. Subsequently, the limbus praecapsularis ossifies and forms a bony endoskeletal projection called lamina obturatoria periotici (Text-fig. 8). Following the formation of this autostosis, a greater part of the neighboring wall of the cavitas encephalica endocranii undergoes resorption and the lamina obturatoria periotici is now utilized in the enclosure of the cerebrum. The result of all this is that the limbus praecapsularis of the spiny anteater can be classified neither as axial nor as pharyngoqualar endoskeleton.

Besides the limbus praecapsularis, the developing endocranium of the spiny anteater presents one more outgrowth from its primary sidewall. This alary endocranial addition is called by Kuhn (1971) the secondary lateral lamella of the preoptic pila (see also Kuhn and Zeller 1987). It arises late in ontogeny as a descending offshoot from the part of the endocranial sidewall that is contiguous to the distal end of Kuhn's preoptic pila and, ventrally, passes over into the sphenobturatory membrane (Text-fig. 9). In the juvenile spiny anteater, the distal part of Kuhn's pila praeoptica undergoes resorption and almost coincidently, the adjacent lateral endocranial lamella becomes converted from cartilage into bone. Thereby, a new space is added to the cavitas encephalica endocranii. According to Kuhn (1971), the lamella at issue is a neoformation unique to the spiny anteater. It would seem, however, that it phylogenetically stems from the tectum orbitae of some piscine progenitors of the four-legged craniates.

In addition to these two contributions to the braincase of the spiny anteater, the teniform cartilage provides, as in therians, the tectum nasi and its connection with the fore part of the primary endocranial sidewall (Text-fig. 10).

Conclusion

In summary, from the facts presented above, it is probable that in the deep past of craniate history on each side of the evolving head there was a dorsolaterally placed rod-like endoskeletal element, which extended the whole length of this evolving body part and like the notochord served as an internal compression-resisting supportive structure. This non-metameric neural crest derivative is termed the cartilago teniformis. While metamerically arranged axial and pharyngoqualar elements as well as allostotic elements, were gradually consolidating, the teniform cartilage became involved in this evolutionary process and ended up as part of the cranium.

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