

ON THE EPIPTERYGOID—ALISPHEOID TRANSITION IN THERAPSIDA

By

T. H. BARRY

South African Museum, Cape Town

(With 22 figures in the text)

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INTRODUCTION

Mainly as a result of the researches of Gaupp (1902), Allis (1919), Broom (1907, 1909 and 1914), Fuchs (1912) and Gregory and Noble (1924) it is now generally accepted that the reptilian epipterygoid and mammalian alisphenoid, although superficially different in many respects, are homologous structures. The views of these workers have received support from embryologists, comparative anatomists and palaeontologists alike over the last few decades and the theory has now virtually become axiomatic.

In modern reptiles there is a marked degree of variation in the development of the epipterygoid, ranging from the primitive, rather solid, construction of the bone in *Sphenodon*, to the absence or vestigial development of the bone in adult Ophidia and Crocodilia with the Lacertilia displaying a thin columnar structure. The relationship of the branches of the trigeminal nerve to the bone, remains constant throughout the class, the profundus emerging anterior to the epipterygoid and the maxillary and mandibular branches posterior to the bone.

In mammals the development of the alisphenoid as a relatively broad and flattened bone is fairly constant except in *Echidna* where it appears to be absent. In mammals, however, the relationship of the branches of the trigeminal nerve to the alisphenoid varies. This ranges from the 'reptilian' type, where the bone lies between the profundus and maxillary branches, found in *Didelphis*, through stages where first the maxillary and then also the mandibular branches pierce the bone, to where the profundus and maxillary branches both emerge anterior to the alisphenoid.

The palaeontological evidence for the homology of the reptilian epipterygoid and the mammalian alisphenoid presented in the early years (mainly by Broom) naturally reflects the inadequate state of knowledge of the early reptile fossils at the time. Although seldom stated explicitly there was a strong tendency to see in the lacertilian condition the basic type from which the mammalian condition could be derived.

As far back as 1907 Broom stated that palaeontological evidence supported the view that the alisphenoid of mammals had evolved from the reptilian epipterygoid concluding:

'In the very primitive reptiles, of which *Procolophon* may be taken as a type, we have a lizard-like columella cranii. In the early types, which have specialized along the mammalian line, such as the Therocephalians, we still have a columella cranii. In the even more mammal-like anomodonts, such as *Dicynodon* and *Oudenodon*, there is a columella cranii, but no alisphenoid. When we come to examine the Cynodonts—those remarkable reptiles, so very nearly related to the Mammals as to be regarded by many as the group ancestral to them—we find a broad flattened bone, which most anatomists would not hesitate to call the alisphenoid, and yet there can be little doubt, it is only the columella cranii of the anomodont flattened out' (p. 114).

In 1914 Broom offered more direct evidence to substantiate his view stating:

'A short epipterygoid is known in *Diadectes* and a long lizard-like columella cranii is met with in *Procolophon*. A short epipterygoid occurs in the Pelycosaur *Dimetrodon*. In Anomodonts the epipterygoid is present as a long slender rod—in some species rounded and in others much flattened . . . and its lower end is considerably expanded antero-posteriorly, giving it a long suture with the pterygoid. In Gorgonopsians the epipterygoid is a long, much flattened rod which inferiorly has probably similar relations to the pterygoid as seen in the Anomodonts. In the Therocephalians the epipterygoid is only satisfactorily known in *Scylacosaurus*. Here, . . . it is a relatively short, flattened structure with a very wide base which lies along the pterygoid. In the Cynodonts, at least in the higher forms as exemplified by *Diademodon* and *Cynognathus*, in the region occupied by the epipterygoid in the Therocephalians there is a very much larger bone which there can

be little doubt is also an epipterygoid development. The upper part is greatly expanded antero-posteriorly and forms much of the cranial wall. The lower portion of the bone is so much more developed than in the Therocephalian that it completely replaces the posterior part of the pterygoid, . . . and extends outwards as far as the quadrate. There can be little doubt that while this bone is homologous with the epipterygoid of the lower forms, it is also the homologue of the mammalian alisphenoid' (p. 30).

In the next thirty years very little advance was made. In 1944 Olson still describes the structural changes undergone by the epipterygoid in the transition from the primitive reptilian condition to that of mammals as follows:

'In primitive reptiles the bone is composed of a restricted basal portion and a slender ascending ramus, the columella cranii. In somewhat more advanced forms, the basal portion is expanded into a posterior quadrate ramus and an anterior pterygoid process. At this stage the ascending ramus remains a thin rod. In the advanced mammal-like reptiles, the ascending ramus is much expanded and has attained intimate association with the periotic behind and the parietal above. The quadrate and pterygoid processes are somewhat elongated' (p. 110).

In the twenty years that have elapsed since Olson wrote the foregoing descriptions of the palatoquadrate of all the principal groups of reptiles and of the forms ancestral to the reptiles have become available. A restatement of the course of the evolution of the epipterygoid-alisphenoid has therefore become necessary. In the following pages a short review of the present state of our knowledge of this element is given. Although the epipterygoid is a distinct element in the early tetrapod skull its evolution cannot be discussed in isolation since both the number of palatoquadrate ossifications and the extent of these elements vary. An account of the palatoquadrate as a whole will therefore be given and the evolutionary trends evident in its ossifications discussed.

My interest in the transformation of the epipterygoid (and quadrate in so far as it affected the epipterygoid) originated while studying serially ground sections of the skull of the anomodont *Pristerodon buffaloensis*. This technique revealed important features of the palatoquadrate complex which would not have been readily seen in material cleaned in the normal way. As some of these features contradict vital points in the evolutionary sequences as interpreted by Broom and Olson, an account of the *Pristerodon* palatoquadrate will be presented first and will be followed by a general review of the transformation of the palatoquadrate.

MATERIAL

A skull of *Pristerodon buffaloensis* Toerien, No. B.P.I. 339, was made available for sectioning by Dr. A. S. Brink, Assistant Director of the Bernard Price

Institute for Palaeontological Research, Johannesburg. It was discovered in 1956 by Mr. James W. Kitching of the same Institute in *Cistecephalus* Zone strata on the farm Kirkvors, today known as De Hoop, approximately two miles north-west of Murraysburg, Cape Province. *Pristerodon* belongs to the family Endothiodontidae of the Sub-order Anomodontia (Sub-class Synapsida; Order Therapsida).

THE PALATOQUADRATE OF *PRISTERODON*

The ossified palatoquadrate of *Pristerodon buffaloensis* is represented by the separated epipterygoid and the quadrate (figs. 1 and 4). Viewed laterally the epipterygoid is L-shaped, with both the vertical and the horizontal limbs well developed. The vertical limb (or columella cranii) is relatively thin and extends upward and slightly forward to meet a ventrally extending ridge originating

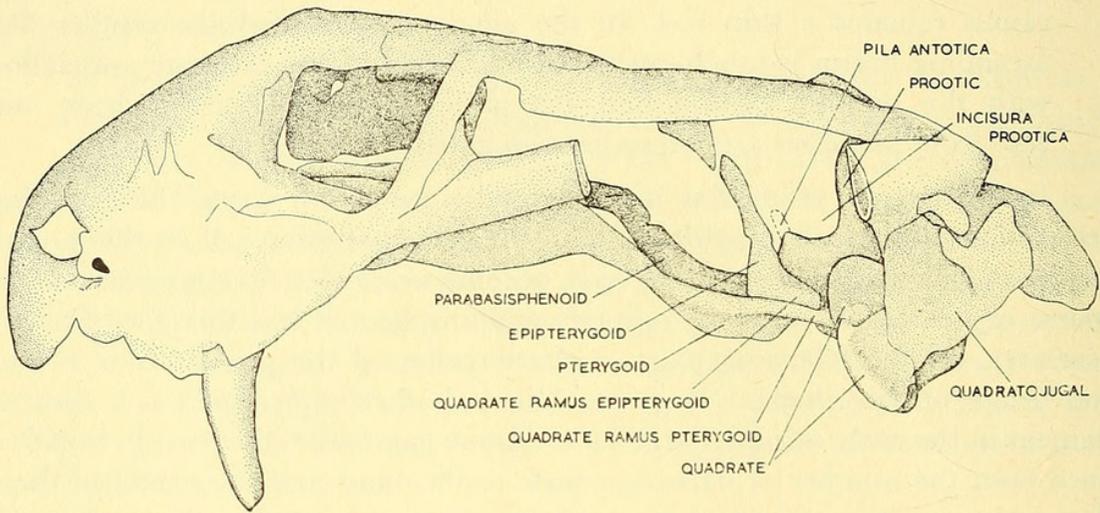


FIG. 1. *Pristerodon buffaloensis*. Lateral view of skull reconstructed from serial sections. Squamosal cut away to show palatoquadrate complex.

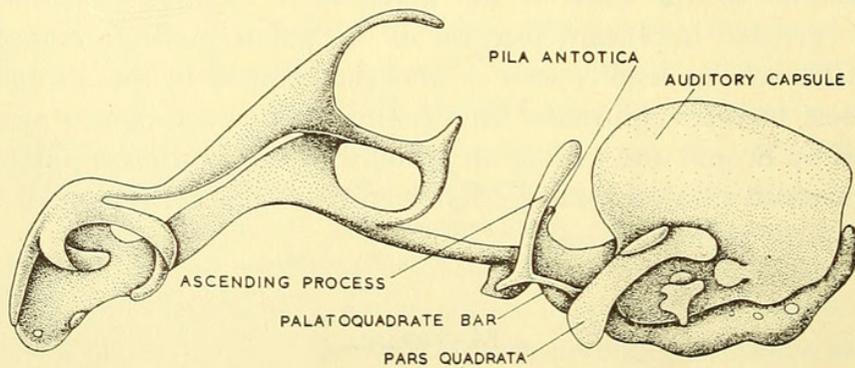


FIG. 2. *Tropicolotes tripolitanus*. Lateral view of skull of 15.2 mm. embryo. (After Kamal, 1960.)

from the under-surface of the parietal. The posteriorly directed horizontal portion is thickest near the angle of the bone, tapering posteriorly to become rod-shaped (quadrate ramus of the epipterygoid). The entire base of the epipterygoid is applied to the dorsal and/or dorso-lateral surface of the quadrate ramus of the pterygoid. The quadrate rami of both the pterygoid and the epipterygoid are directed postero-laterally, towards the inner surface of the quadrate.

The quadrate is relatively large, has the shape of an inverted Y in cross-section, the upper leg lying in a deep antero-posteriorly directed ventral pocket of the squamosal. It is suturally attached to two other elements only, the quadratojugal on the outside and the stapes to which it is attached through a short horizontal ridge projecting medially from the inner condyle. Antero-dorsally to this ridge there is a longitudinal groove in the vertical face of the quadrate, extending backwards from the anterior border for approximately one-third of the length of the vertical plate (fig. 4). Throughout its length this groove is seen to follow remarkably closely a course parallel to the posterior portion of the quadrate ramus of the pterygoid, the latter bone terminating close to, but free from the inner surface of the quadrate, approximately half-way along its length. A distinct rounded bulge terminates the groove in the left quadrate. As the groove follows what could have been the course of a posterior extension of the horizontal limb or quadrate ramus of the epipterygoid it would seem reasonable to assume that the groove housed a cartilaginous rod connecting the quadrate with the epipterygoid.

The occurrence of a solid link between the quadrate and epipterygoid in an adult *Pristerodon*, recalls conditions found in the developmental stages of the skull in many recent reptiles and in developmental stages of *Sphenodon* (fig. 3) as well as in the adult. The complex, as reconstructed in *Pristerodon*,

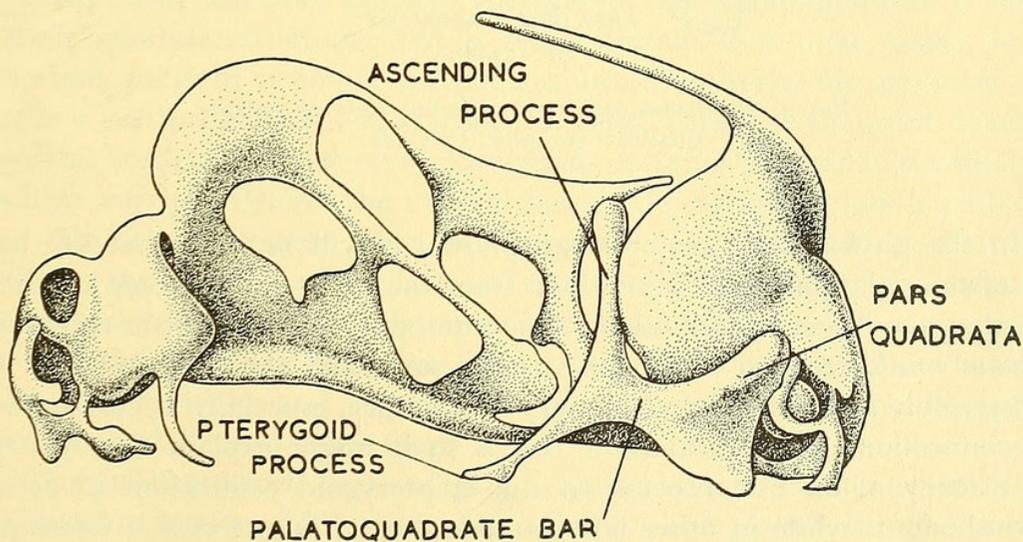


FIG. 3. *Sphenodon punctatus*. Embryo. Lateral view of skull. (After Howes & Swinnerton, 1901.)

shows a remarkable resemblance to the palatoquadrate of *Zonurus (Condylus)*, as featured by Broom (1925), and of the 15.2 mm. developmental stage of the Egyptian lizard *Tropicolotes tripolitanus* (fig. 2), described by Kamal (1960). Similarly the relationship between the horizontal limb and the quadrate ramus of the pterygoid in *Pristerodon* is mirrored by conditions found in *Sphenodon*, the base of the palatoquadrate cartilage occupying the dorsal and dorso-lateral surface of the quadrate ramus of the pterygoid in both forms.

In this connection it is important also to consider the relationship of the nerves to the complex, and especially that of the trigeminal nerve to the epipterygoid. In recent reptiles the nerve emerges from the braincase through the incisura prootica. The profundus branch then passes medially to the epipterygoid while the maxillary and mandibular rami pass behind the epipterygoid. In *Pristerodon* there are no indications of the routes followed by the presumed branches of the trigeminal nerve but judging by the nerve foramina and grooves found in some early gnathostomes and tetrapods it would seem indicated that present-day relationships had an early origin.

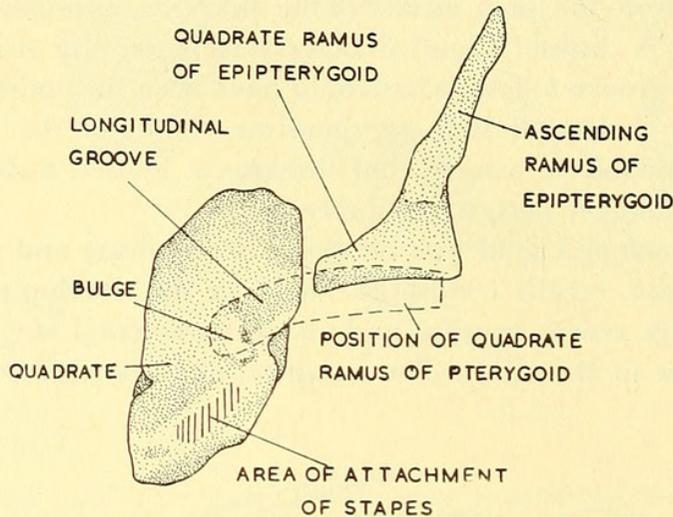


FIG. 4. *Pristerodon buffaloensis*. Medial view of palatoquadrate complex. Left side.

In the phylogenetic review that follows, it will be seen that the basic form of the palatoquadrate is retained from the early gnathostome condition up to the early 'stem reptile' stage. The number of ossifications in the palatoquadrate would seem to vary from stage to stage and even within stages and could possibly be of minor evolutionary importance, especially as cartilaginous inter-connections are indicated. If this is so it might explain the apparent inconsistency of an otic process on the epipterygoid ossification in certain labyrinthodonts while in other labyrinthodonts and later forms it forms part of the quadrate ossification. After the attainment of the basic reptile stage, or possibly even already during the labyrinthodont stage the palatoquadrate

begins to undergo evolutionary change which will have far reaching effects. The development is channelled into two main streams; one leading towards the expansion of the epipterygoid and reduction of the quadrate, as exemplified in those trends showing mammalian affinities, and another resulting in the retention of the quadrate and reduction of the epipterygoid in trends showing reptilian affinities.

PHYLOGENY

The first adequately known vertebrates are agnathous forms found in the Late Silurian. Jawed vertebrates have as yet not been discovered in the Silurian but the variety of these forms in the Lower Devonian indicates they must have been undergoing development in the Silurian (Romer, 1955).

PLACODERMI

The early Devonian gnathostomes are predominantly placoderms. Although widely varied in appearance, the jaw apparatus is usually of a relatively primitive type. Amongst them the acanthodians are generally regarded as the earliest and most archaic and their morphology could, therefore, throw light on the problems connected with the formation and evolution of the primitive jaws.

According to Watson (1937) the acanthodian palatoquadrate is large and superficially divisible into two elements, a short horizontal suborbital or palatal portion and a large vertical postorbital or paraotic portion. In the genera *Climatius* and *Cheiracanthus* the palatoquadrate is ossified as a single unit, but in *Mesacanthus* and *Ischnacanthus* the palatal and paraotic portions are ossified independently. In *Acanthodes* (fig. 5), the last surviving member of the group, and therefore possibly specialized, the palatoquadrate is ossified as three separate structures, but it seems certain that these bones, in life, comprised parts of a single palatoquadrate. Anteriorly the paraotic plate ends in a vertical border, which forms the hind margin of the orbit. From the top of this border the bone curves downwards posteriorly to end in the thickened quadrate condyle. Behind the vertical border the paraotic plate is perforated by a foramen, extremely large in *Cheiracanthus*, which could possibly have served for the exit of the maxillary and mandibular branches of the trigeminal. The palatal portion of the palatoquadrate terminates anteriorly at a point in line with the middle of the orbit. This is some distance behind the front end of Meckel's cartilage and would appear to indicate that the palatoquadrate was continued forward as cartilage.

The palatoquadrate does not seem to have contact with the neurocranium in *Climatius*, but in *Mesacanthus*, *Cheiracanthus* and *Acanthodes*, the paraotic flange bears an otic process which articulates with the skull behind the post-orbital process. The palatal part of the bone has a basal articulation.

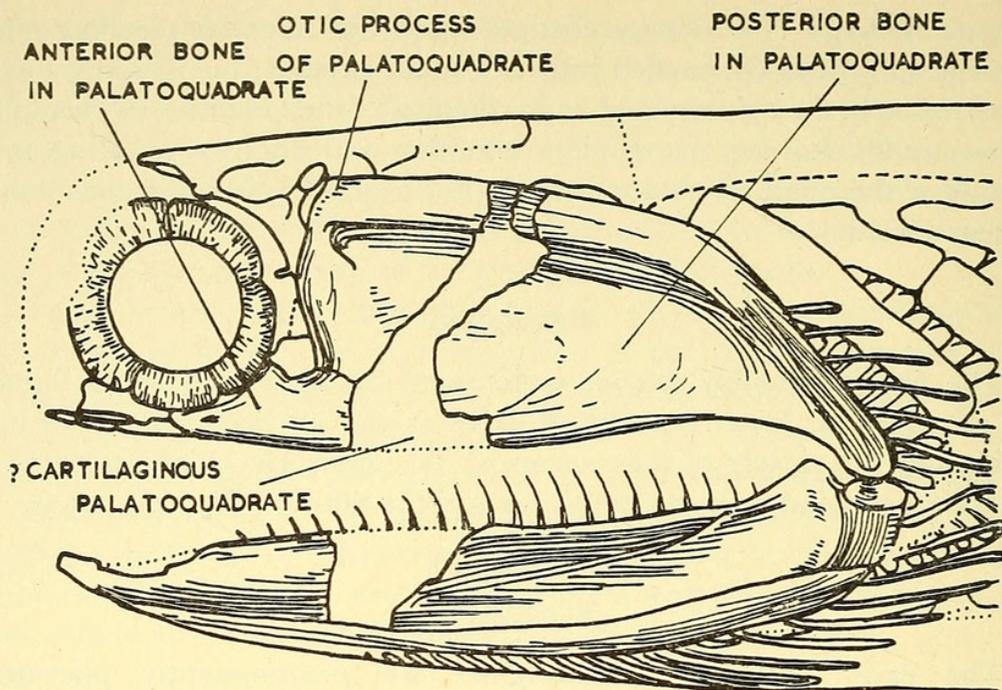


FIG. 5. *Acanthodes* sp. Reconstruction of the skull from specimens from the Lebach ironstones. Complete except for squamation. (After Watson, 1937.)

According to Watson (1937) the palatoquadrate in arthrodires is directly comparable with that occurring in several acanthodians. In *Pholidosteus* the palatoquadrate has two ossifications, an anterior which articulates with the ventral part of the neurocranium just behind the olfactory capsules, and a posterior quadrate.

CROSSOPTERYGII

In the Crossopterygii the processes and future subdivisions of the palatoquadrate become more apparent.

In *Eusthenopteron* the palatoquadrate is a single ossification with, according to Jarvik (1954), five distinguishable parts; an anterior pars autopalatina, articulating with the ethmoidal region and the anterior neural endocranium; a basal process articulating with the basiptyergoid process; an antero-dorsally directed ascending process which articulates with the supraptyergoid process of the neural endocranium; a paratemporal process, which articulates with the anterior end of the otic shelf and a thickened pars quadrata posteriorly. A thin film of bone, dotted with large fenestrae, makes up the rest of the palatoquadrate (fig. 6).

Jarvik states that the profundus passed medially to the ascending process while the maxillary and mandibular branches of the trigeminal probably passed through the notch between the ascending and paratemporal processes.

Osteolepis macrolepidotus similarly possesses a completely ossified palato-

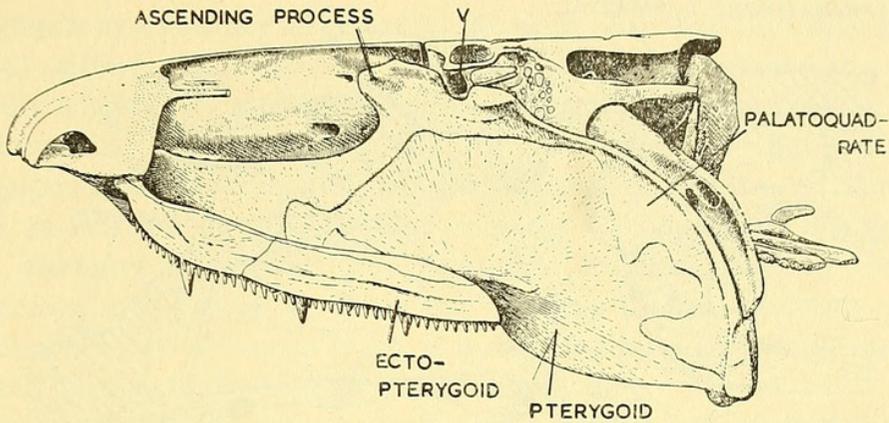


FIG. 6. *Eusthenopteron foordi*. Lateral view of skull with dermal bones removed. (After Jarvik, 1954.)

quadrate (Watson, 1954). But in *Megalichthyes* (Watson, 1925), the palatoquadrate is ossified as a continuous series of bones. Of these the anterior one, which extends into the basal process, represents the epipterygoid, the posterior the quadrate.

LABYRINTHODONTIA

The Coal Measure embolomorous anthracosaurs *Palaeogyrinus decorus* and *Eogyrinus altheyi* (Panchen, 1964) both display well developed palatoquadrates. In *Palaeogyrinus* (fig. 7) a large facet forms the anterior termination of a massive buttress, shaped like the mouth of a horn, which tapers forward as the palatal ramus. The latter appears to have rested on the horizontal palatal ramus of the pterygoid, but its lower edge cannot be made out. In mesial view the columella cranii appears as a slender rod extending dorsally until it expands to form an anteriorly directed process and a second vertical process. Panchen believes that the anteriorly directed process, the dorso-mesial surface of which is grooved, formed the dorsal edge of a notch for the profundus and that the second process probably divided the maxillary and mandibular branches of the trigeminal nerve. In lateral view the columella is continuous with a sheet of bone covering the whole of the upper half of the quadrate ramus of the pterygoid and which runs from the level of the cranial base to the quadrate condyle. A similar expansion is present in *Edops* (Romer and Whittier, 1942). Panchen believes that the epipterygoid may have extended as cartilage further down the quadrate ramus of the pterygoid and there seems also to have been a broad process projecting downward and backward from the level of the basis cranii. There is also a complex articulation for the basipterygoid process of the basisphenoid formed by both epipterygoid and pterygoid.

The quadrate is small in *Palaeogyrinus* but is a much more extensive ossification in *Edops*.

Panchen states that the considerable ossification in the cartilaginous palatoquadrate shown by these forms, and probably by *Eogyrinus* must be

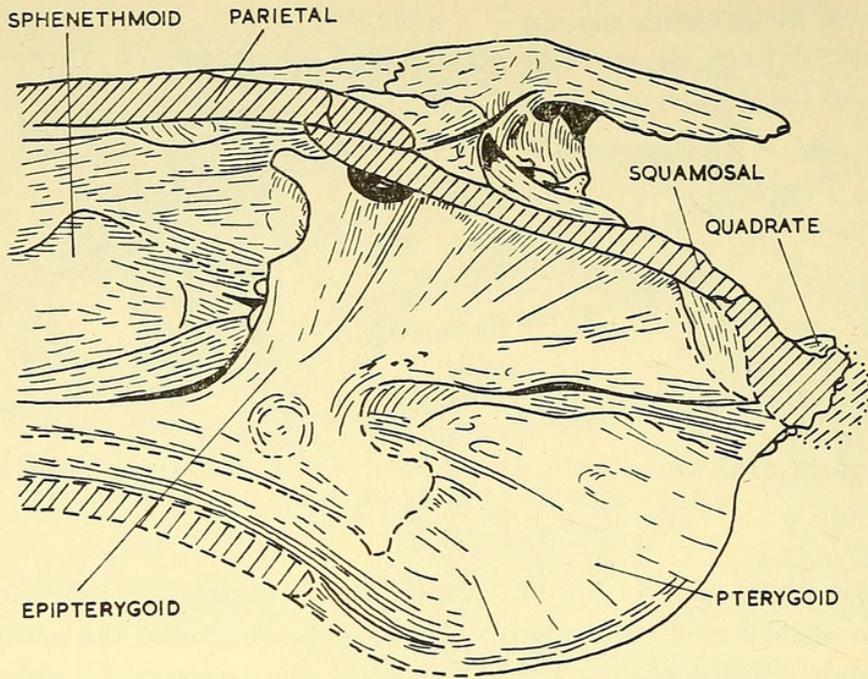


FIG. 7. *Palaeogyrinus*. Lateral view of suspensorial region as though sectioned through a plane parallel to the quadrate ramus. (After Panchen, 1964.)

interpreted as a primitive condition and that a progressive reduction of the epipterygoid ossification is to be seen in later labyrinthodonts.

Although Triassic labyrinthodonts are not on the phylogenetic line leading to reptiles, the structure of the palatoquadrate is nevertheless of interest. It consists of two parts, a horizontal cartilaginous anterior part and a mainly vertical ossified posterior part (Sushkin, 1899; Watson, 1919 and 1926, and Säve-Söderbergh, 1936). The vertical part had, at least in *Lyrocephalus*, basal, ascending and otic processes. Säve-Söderbergh maintains that all these processes were embodied in the epipterygoid in the most completely ossified individuals, but that in *Aphaneramma* and *Platystega* the ascending process only was included in the epipterygoid. The epipterygoid was joined to the quadrate ossification by means of a cartilaginous link which rested in a groove of the ramus of the pterygoid.

We may therefore assume that the palatoquadrate survived in labyrinthodonts complete from the quadrate to at least the front end of the epipterygoid.

COTYLOSAURIA

Whether or not the seymouriamorphs are considered amphibians or reptiles, the skull of primitive forms such as *Seymouria* and *Kollasia* show that they are not far removed from the anthracosaurian amphibians from which the seymouriamorphs and more advanced reptiles have been derived (Romer, 1956). The epipterygoid, which is not well known and seems to be slow to

ossify, extends as a rod-like structure to the skull roof. The primitive quadrate, when well ossified, ran forward to meet the epipterygoid. When the quadrate is less fully ossified, a cartilaginous area may have bridged the gap between the quadrate and the epipterygoid (fig. 8). It is presumed that the tendency for the epipterygoid to remain unossified is a degenerate feature (Romer, 1956).

The earliest known reptiles date from the Carboniferous but knowledge of their anatomy is fragmentary. Abundant forms appear in the Upper Carboniferous and Lower Permian but as these include not only primitive forms but also more advanced types, it is certain that a very important section of the early history of the reptiles is still unknown.

In diadectids both epipterygoid and quadrate are greatly developed. *Diadectes* itself features a quadrate of considerable height and width but little length (Romer, 1956). In the South African pareiasaurs both epipterygoid and quadrate are plate-like. The epipterygoid, which has a slender ascending process, furthermore stands transversely on the quadrate ramus of the pterygoid near its articulation with the basiptyergoid process (Boonstra, 1934). According to Romer (1956) the margins of the base of the epipterygoid in pareiasaurians are unfinished, indicating a cartilaginous connection with the quadrate which has a similarly unfinished surface facing towards the epipterygoid.

The captorhinomorphs *Limnosceles*, *Captorhinus* and *Labidosaurus* from the Lower Permian of the American Southwest are among the oldest cotylosaurs

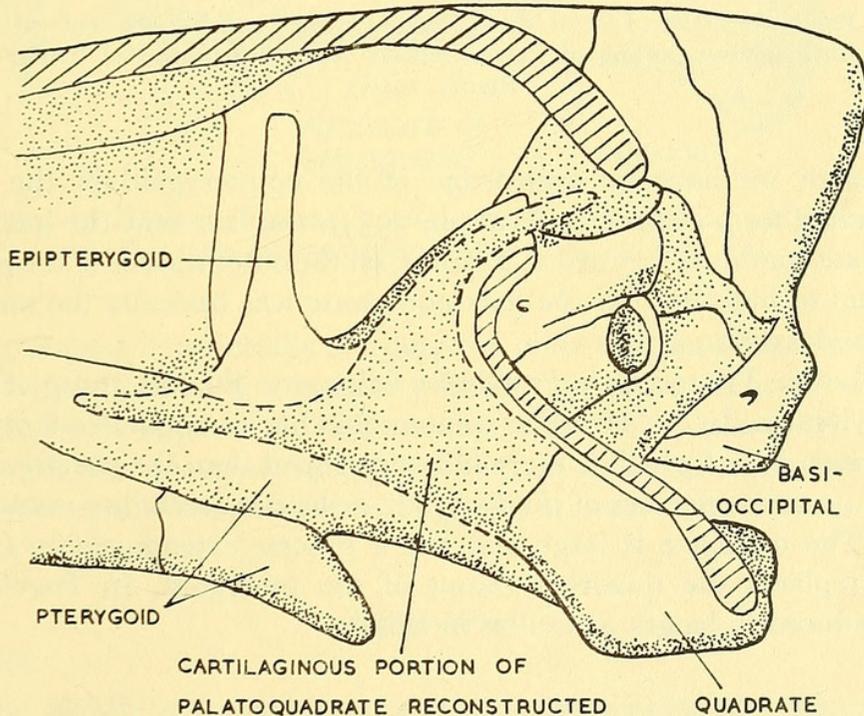


FIG. 8. *Seymouria*. Lateral view of the skull with dermal bones removed. Cartilaginous portion of palatoquadrate reconstructed. (After Romer, 1956.)

of which we have detailed knowledge. Here the quadrate also consists of a vertical sheet of bone with an essentially flat outer surface and an epipterygoid, separated from the quadrate but presumably attached to it in life by cartilage, with a rod-like ascending process (fig. 9).

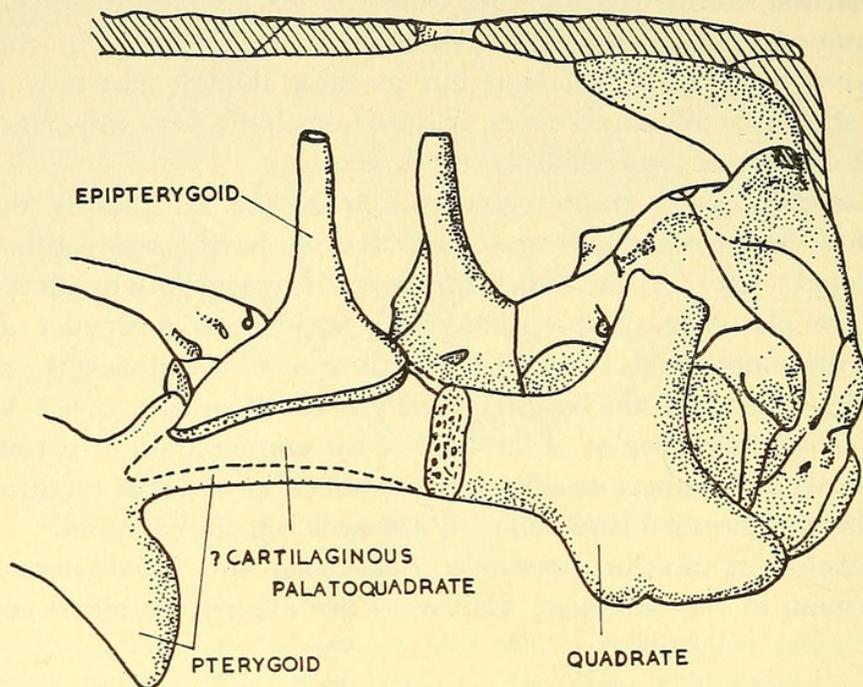


FIG. 9. *Captorhinus*. Lateral view of the skull with dermal bones removed. Cartilaginous portion of palatoquadrate tentatively indicated. (After Romer, 1956.)

Although we have no knowledge of the epipterygoid in the aberrant early Permian form *Bolosaurus* (Watson, 1954), the fact that the inner part of the quadrate continues forward as a ramus, on the outer surface of the pterygoid, would seem to indicate that the palatoquadrate was basically the same as the general cotylosaurian type.

The Lower Triassic form *Procolophon* belongs to the last group of survivors of the cotylosaurs. In this form the epipterygoid has an expanded footplate, the anterior extension of which is more fully developed than the posterior portion. From the posterior portion of the footplate a slender ascending ramus extends dorsally. The quadrate is large and has a process extending forward which partially replaces the quadrate ramus of the pterygoid. In *Procolophon* the latter is reduced in length as well as in height.

PELYCOSAURIA

If, as is generally accepted, the Pelycosauria represent an early stage in mammalian history and that they possess ' . . . many archaic features which

illustrate the structure of the primitive reptilian stock' (Romer & Price, 1940: 1), then it should not be surprising to find that this group still displays a palatoquadrate complex in which the epipterygoid and quadrate portions are linked. This condition would merely represent the retention in this group of the basic gnathostome condition of a unified palatoquadrate as exemplified in the placoderms, and retained, with modifications, in the crossopterygians, labyrinthodonts and probably also the early stem reptiles.

The epipterygoid has a wide base closely applied to the lateral surface of the anterior portion of the quadrate ramus of the pterygoid (fig. 10). Anteriorly a slender extension curves down along a groove on the dorsal surface of the palatal ramus of the pterygoid. A continuation of this groove in some cases beyond the anterior end of the bone suggests a further cartilaginous extension of the palatoquadrate. The slender rod-like portion of the epipterygoid gains contact, in *Dimetrodon*, with the anterior surface of the paroccipital process.

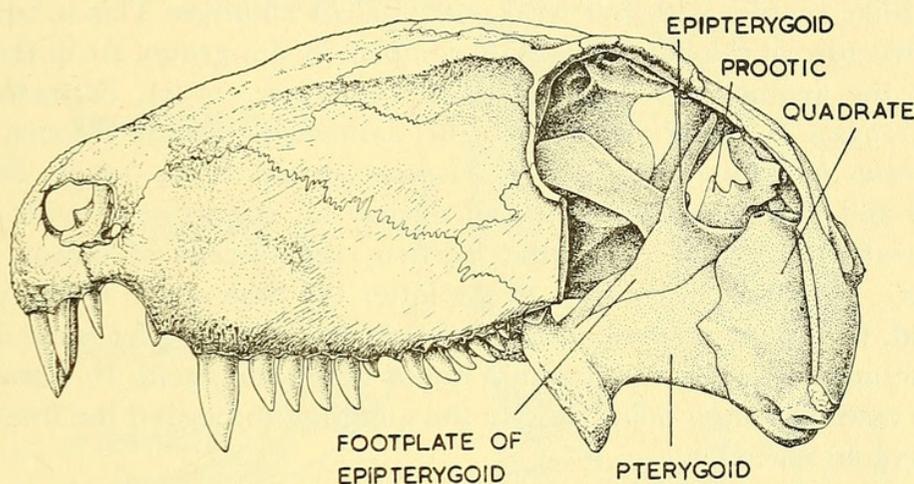


FIG. 10. *Dimetrodon limbatus*. Lateral view of skull with dermal bones cut off to show palatoquadrate. (After Romer & Price, 1940.)

The quadrate is essentially a triangular plate varying greatly in extent in the few forms where it is adequately known. In some cases in which it is well developed it appears to gain contact with the epipterygoid along the dorsal margin of the internal surface of the pterygoid (fig. 10), while in others in which the bone is more restricted in size, it appears to have been continued forward as cartilage.

THERAPSIDA

Dinocephalia

Of the slightly more advanced mammal-like reptiles, the therapsids, the *Dinocephalia* are generally regarded as the oldest and in many respects the most primitive suborder. In them, according to Boonstra (personal communication), the epipterygoid is small or reduced except in the titanosuchid genus

Anteosaurus. In the latter the bone extends right up to the skull roof, has an expanded waist and a relatively long anterior footplate. In *Jonkeria* (titano-suchid) the footplate is also extended anteriorly but dorsally the epipterygoid only reaches halfway to the roofing bones while the footplate as well as the dorsal ramus are reduced in the tapinocephalid *Struthiocephalus*. In none of the Dinocephalia do we find evidence of a posterior extension to the footplate which could have formed a link between the epipterygoid and the quadrate. According to Watson (1914) the Dinocephalia, as a group, has a very special importance because alone amongst the therapsids it retained a large quadrate. This feature as well as the absence of the quadrate ramus of the epipterygoid indicates affinities with the reptilian rather than the mammalian lines of evolution.

Anomodontia

The anomodonts are generally regarded to be an aberrant group of mammal-like reptiles with but weak mammalian affinities. This is borne out by the structure of the palatoquadrate complex in this group. As in the Dinocephalia the anomodonts *Kannemeyeria erithrea* (Case, 1934), *Dicynodon kolbei* (Broom, 1932), *D. sollasi* (Watson, 1948), *Lystrosaurus murrayi* (Broom, 1932), *Daptocephalus leoniceps* (Ewer, 1961), *Kingoria nowacki* (Cox, 1959), *Dicynodon grimbeeki* and *Pristerodon buffaloensis*, all display an epipterygoid with a long, thin dorsally projecting columellar portion, reminiscent of recent reptiles (see later). However, in contrast to the latter the base of the epipterygoid is expanded, to varying degrees, in all of the above, extending for some distance along the upper edge of the quadrate ramus of the pterygoid. In *Kannemeyeria* the base extends from a point close to the quadrate to beyond the front of the interpterygoid space.

In the anomodonts investigated, there is no direct contact between the epipterygoid and the quadrate (fig. 11), but there is a distinct probability that a cartilaginous link existed in life in some of these forms, as has been shown

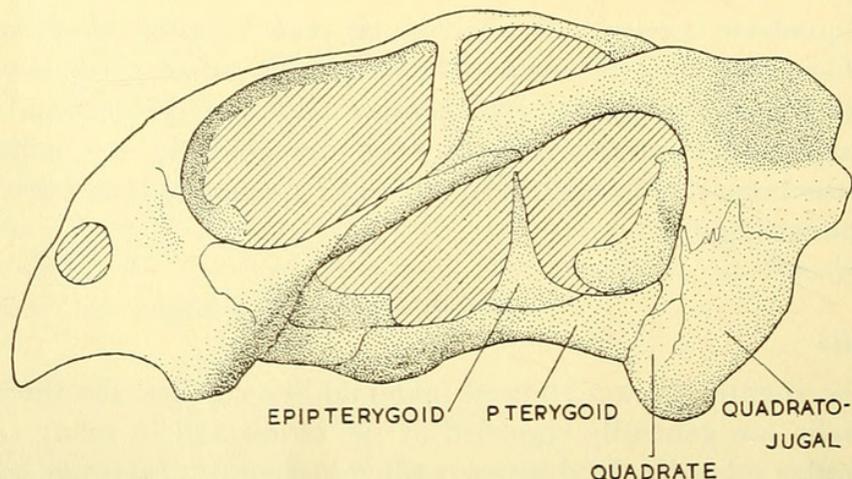


FIG. 11. *Dicynodon* sp. Lateral view of skull.

for *Pristerodon*. However, the general tendency within the group is for the bar, linking the epipterygoid to the quadrate portion, to become reduced; an evolutionary trend, as will be shown later, that was present also in the line that culminated in modern reptiles.

Gorgonopsia

In all known *Gorgonopsia* the epipterygoid is high and relatively narrow, with a well-developed footplate. In '*Lycaenodon*' (fig. 12), *Scymnognathus*, *Leptotrachelus*, *Cynariops* (Boonstra, 1934a) and *Aelurognathus* (Haughton, 1924), the footplate has a long tapering anterior extension, with a short posterior extension ending some distance away from the quadrate. Boonstra found no evidence in this group of a widening of the vertical portion of the epipterygoid.

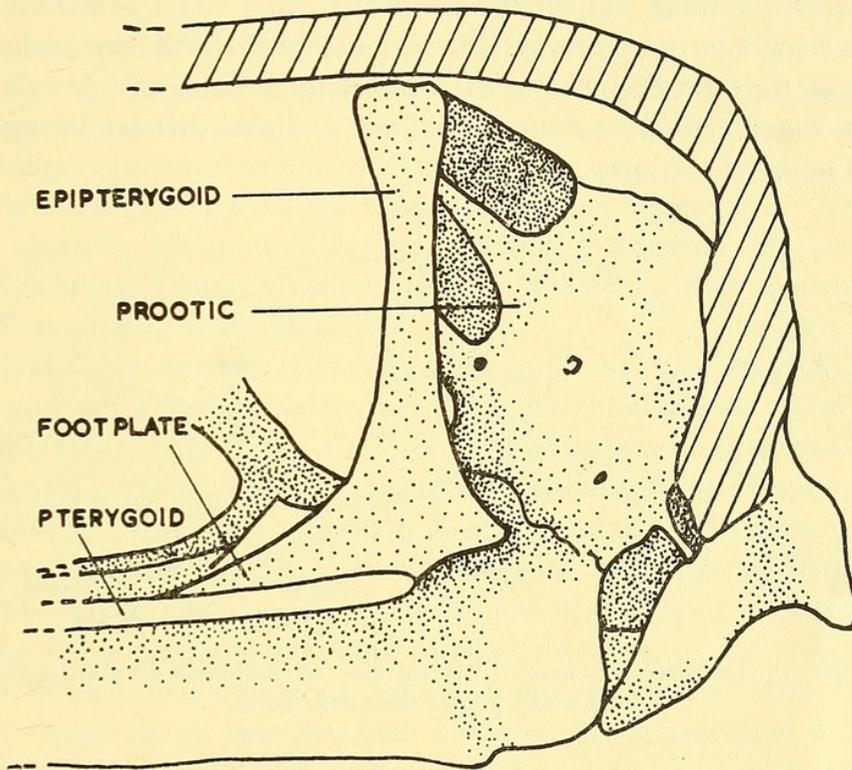


FIG. 12. '*Lycaenodon*'. Lateral view of skull with dermal bones cut away.
(After Boonstra, 1934a.)

Terocephalia

In the early *Tapinocephalus* Zone forms such as the pristerognathids *Scylacosaurus* and *Scymnosaurus* (Boonstra, 1934b, 1954), and most of the primitive therocephalians, the vertical portion of the epipterygoid is still relatively narrow, but in *Glanosuchus macrops* (Boonstra, 1954) the epipterygoid has become dumb-bell-shaped, although still not much widened. The base has no noteworthy posterior process. However, in the lycosuchid *Trochosaurus major* (Boonstra, 1934b) occurring in the same zone, the epipterygoid has

developed into a large, broad plate which obscures the lateral opening into the pituitary fossa and the foramina for the Vth and VIth nerves. The epipterygoid here is more than twice as broad as in any known gorgonopsian and has the appearance of a cynodont epipterygoid. It differs from that known in *Scymnosaurus* and *Scylacosaurus* in having an expanded upper end in addition to a wide footplate, a condition reaching its greatest development in the later whaitsids (Boonstra, 1934).

Of the *Cistecephalus* Zone Theriocephalia, *Euchambersia mirabilis* (Boonstra, 1936) also shows the dorsally and ventrally expanded condition (fig. 13) but the shaft of the bone does not show much expansion. In the scaloposaurid *Ictidosuchops intermedius* (Crompton, 1955), however, the shaft is a broad one, and ends in a slightly more expanded dorsal portion which fits into a shallow depression in the antero-dorsal wall of the prootic, consequently forming part of the true lateral wall of the braincase. The anterior extension of the footplate is long, but the posterior one is short. At the juncture of the posterior extension and the ascending ramus there is a shallow notch which most probably housed the maxillary or both the maxillary and mandibular branches of the trigeminal nerve (Crompton, 1955).

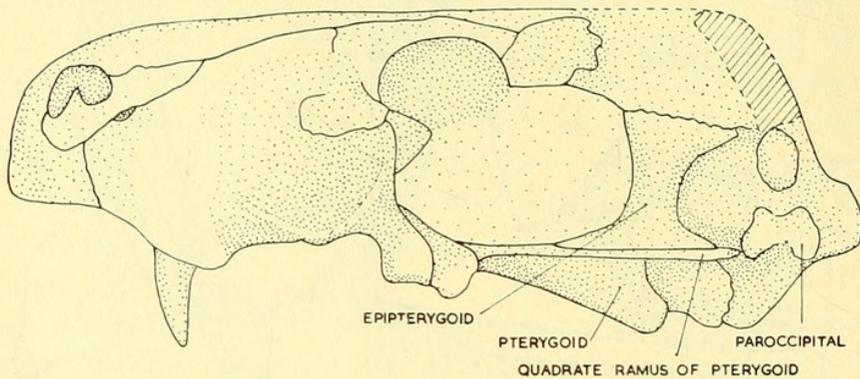


FIG. 13. *Euchambersia mirabilis*. Lateral view of skull with dermal bones cut away. (After Boonstra, 1936.)

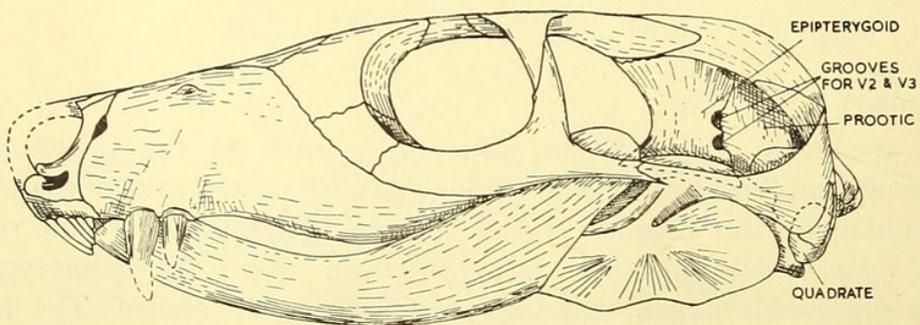


FIG. 14. *Aneugomphius ictidoceps*. Lateral view of skull with outlines of palatoquadrate bones indicated. (After Brink, 1956.)

In *Theriognathus microps* (Boonstra, 1934), *Notosollasia laticeps* (Boonstra, 1934) and *Aneugomphius ictidoceps* (Brink, 1956), as in all known whaitsids, the epipterygoid is broad and flat with greatly expanded dorsal and ventral ends (fig. 14). The base is long and in most forms posteriorly overlaps the prootic obscuring the incisura prootica. The hind wall of the epipterygoid in *Aneugomphius* shows two deep notches, probably for the exit of the maxillary and mandibular branches of the trigeminal nerve.

Cynodontia

Brink (1960) states that the epipterygoids of the primitive cynodont *Scalopocynodon gracilis* are ' . . . Cynodont-like in being broadly expanded, but Therocephalian-like in their feeble overlap of the prootics' (p. 145). The anterior extension of the footplate is long and broad while the remainder of the ventral margin follows the dorsal margin of the quadrate ramus of the pterygoid (fig. 15). Brink made the interesting observation that the anterior margin of the epipterygoid is very thick. This may well support the view that this portion of the vertical limb is the more stable and is older phylogenetically than the thinner, posterior section of the limb. The quadrate is in the shape of a wedge lodged loosely in a cavity anteriorly in the squamosal. The anterior margin is straight, blunt and vertical, while the posterior margin is sharp and broadly curved. The quadrate is a much smaller bone than the epipterygoid and is well separated from the latter.

In *Thrinaxodon liorhinus* (Parrington, 1946) the epipterygoid is greatly expanded and dorsally is broadly in contact with the prootic. The quadrate ramus of the epipterygoid joins the prootic, but does not reach the quadrate, leaving a large foramen between the epipterygoid and prootic for the maxillary and mandibular rami. The quadrate, which is about one-third the size of the epipterygoid, has a wide, dumb-bell-shaped articulating surface and a thin, slightly curved dorsal process which medially is greatly strengthened by a pillar-like development which continues to the apex of the bone.

In an unidentified cynodont, which compares closely with *Trirachodon*, Parrington (1946) found two foramina between the epipterygoid and prootic. A groove comparable with that leading into the single foramen in *Thrinaxodon*, leads into the lower, larger foramen from below and behind. The dorsal smaller foramen is probably new. Parrington states that the significance of this development lies in the possibility that the maxillary left the skull by the upper foramen, which is apparently mainly enclosed by the epipterygoid, and is equivalent to the foramen rotundum, and the mandibular by the lower, larger foramen, the equivalent of the foramen ovale. The size of both foramina indicates that blood vessels accompanied the nerves.

In *Diademodon mastacus* (Brink, 1955) the foramen for the trigeminal is also divided into two, although incompletely in this species (fig. 16). The foramen lies slightly above and behind the pituitary fossa. The epipterygoid itself covers the anterior half of the prootic. The footplate is extensive and

extends forward as a very thin tapering process while it reaches the quadrate with its posterior extension.

In the cynognathids, the thin plate-like epipterygoid overlaps the anterior superior process of the prootic. The footplate of the base is extensive. It sends back a posterior extension which occupies the position of the quadrate ramus of the pterygoid and which reaches the relatively reduced quadrate.

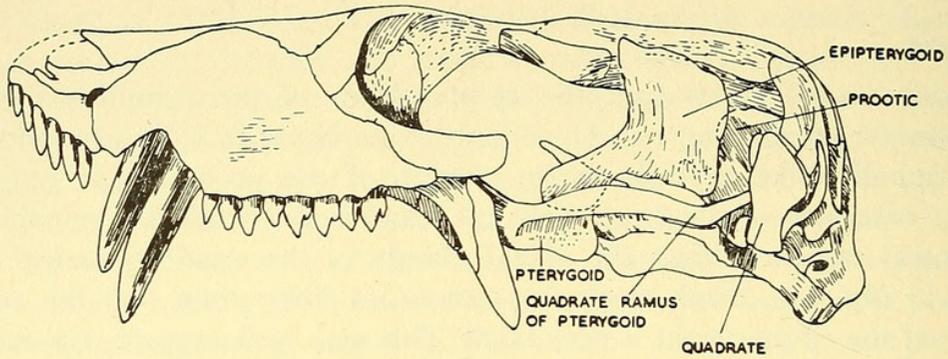


FIG. 15. *Scalopocynodon gracilis*. Lateral view of skull with dermal bones cut away. (After Brink, 1960.)

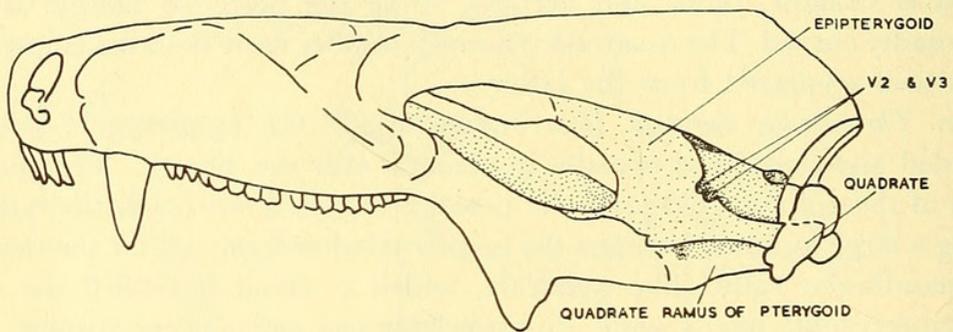


FIG. 16. *Diademodon mastacus*. Lateral view of skull with dermal bones cut away. (After Brink, 1955.)

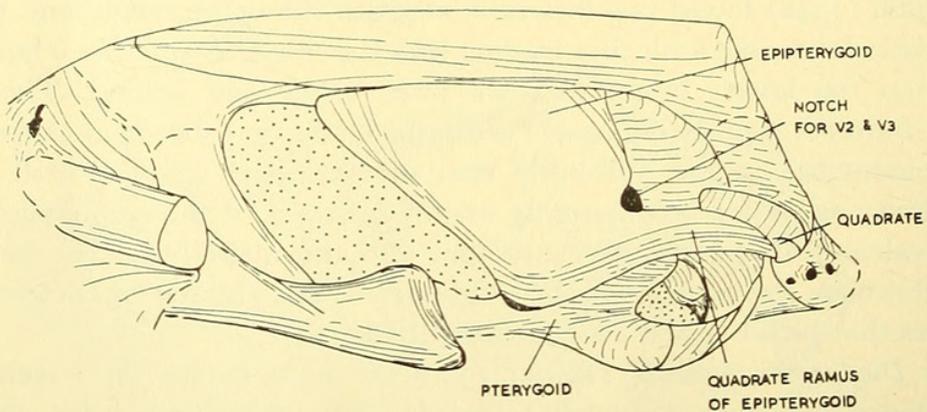


FIG. 17. *Diarthrognathus broomi*. Lateral view of skull. (After Crompton, 1958.)

Ictidosauria

In *Diarthrognathus broomi* the dorsal portion of the epipterygoid is extremely broad and overlaps the prootic above the prootic incisure. Here the posterior edge of the epipterygoid is slightly indented for the maxillary and mandibular branches of the trigeminal nerve (fig. 17). Crompton (1958) states that although it is difficult to ascertain, it would appear that the quadrate ramus of the epipterygoid meets the antero-medial edge of the quadrate. The quadrate is much reduced, S-shaped in occipital view, and the articular surface is markedly concave. This latter feature, according to Crompton, is of great significance as in all known therapsids, including *Bienotherium* and *Oligokyphus*, the articular face of the quadrate is either flat or convex, but never concave. It is also significant that the mammalian malleus (articular) possesses a convex articular surface which meets a convex articular face in the incus (quadrate).

In *Bienotherium* (Hopson, 1964) the epipterygoid and the anterior part of the prootic together form the side wall of the brain case (fig. 18). The quadrate ramus of the epipterygoid is more vertically orientated and deeper than in

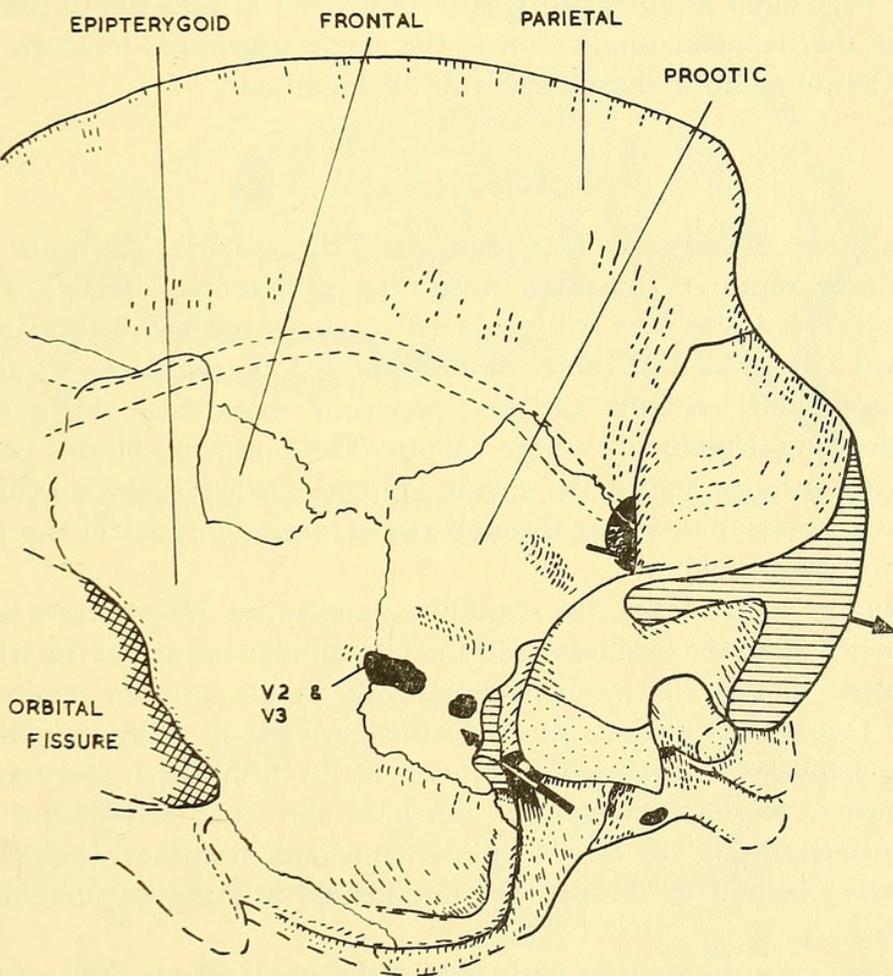


FIG. 18. *Bienotherium yunnanense*. Lateral view of braincase reconstructed from serial sections. (After Hopson, 1964.)

the cynodonts and could have reached the quadrate. The ascending ramus is broad and high with a posterior border which is overlapped laterally, above the trigeminal foramen, by the prootic. This latter is the reverse of the usual reptilian condition in which the prootic lies medial to the epipterygoid, and is ascribed by Hopson to the development of a forward extension of the anterior portion of the prootic in such a way that it lies lateral to the cavum epiptericum. In *Bienotherium* both this extension—the ventro-lateral flange—and the anterodorsal border of the prootic extend well forward of the prootic incisure, an observation which has led Hopson to conclude that the prootic component of the trigeminal foramen in this form is not strictly homologous with the prootic incisure in cynodonts, because the former is merely a notch in the anterior border of the ventro-lateral flange. This conclusion seems to be supported by the fact that the trigeminal foramen pierces the side wall of the skull anterior to the depression of the semilunar ganglion. It also indicates that the maxillary and mandibular branches extend in an anterior direction through the cavum epiptericum in *Bienotherium*, whereas normally, in those forms with broadened epipterygoids, they pass in a posterior direction.

The trigeminal foramen is slightly constricted at mid-length presumably indicating the incipient subdivision of the single trigeminal foramen into the separate foramina rotundum and ovale of mammals.

TRICONODONTA

In a group of Mesozoic mammals, the Triconodonta, the brain case has an essentially reptilian structure. According to Kermack (1963) *Triconodon mordax* and *Trioracodon ferox* still possessed a cavum epiptericum lying outside the ossified lateral wall of the braincase (formed by the petrosal) and as in *Morganucodon* and possibly all pre-Cretaceous mammals, the alisphenoid formed the lateral boundary of the cavum. The ramus profundus passed out through the anterior end of the cavum epiptericum while the maxillary and mandibular nerves passed out through two foramina formed in the posterior edge of the alisphenoid.

According to Kermack, the semilunar ganglion in *Morganucodon* lay inside the primary wall of the braincase and the mandibular branch of the trigeminal nerve passed through the foramen pseudovale in the anterior lamina of the petrosal. The lamina extends much further forward in *Morganucodon* than it does in cynodonts. The maxillary branch of the fifth nerve presumably left the braincase, passing through the notch at the front end of the anterior lamina. After crossing the cavum epiptericum both branches would have left it by passing behind or through the alisphenoid in some way reminiscent of cynodonts.

In basic construction the braincase of the triconodonts differs from that of an advanced therapsid only in the narrower cavum epiptericum in the former, a difference due to the relatively larger size of the brain in mammals.

LIVING REPTILES AND MAMMALS

Amongst recent reptiles *Sphenodon* has virtually retained its larval palatoquadrate in the adult (compare figs 3 and 19) but in the lizards *Lacerta* (Gaupp, 1906), *Cordylus*, *Eremias* and *Mabuia* (Broom, 1903), *Tropicolotes* (Kamal, 1960), *Varanus* (Frazetta, 1962), *Tupinambis* (Jollie, 1960) and many others, and in the chelonians *Emys* (Kunkel, 1912) and *Chrysemys* (Shaner, 1926), the palatoquadrate complex undergoes considerable changes during ontogeny. Ossifications within the complex culminate in the formation of widely separated epipterygoid and quadrate portions, while the rest of the palatoquadrate is resorbed. The quadrate is retained as a comparatively strong element while the epipterygoid is whittled down to a narrow rod-like structure (fig. 20). The base of the bone is not expanded. It has, however, a cartilaginous epiphysis, fitting into the fossa pterygoidei which may be linked with the quadrate through a strand of connective tissue, both epiphysis and connecting strand probably representing remnants of the palatoquadrate cartilage.

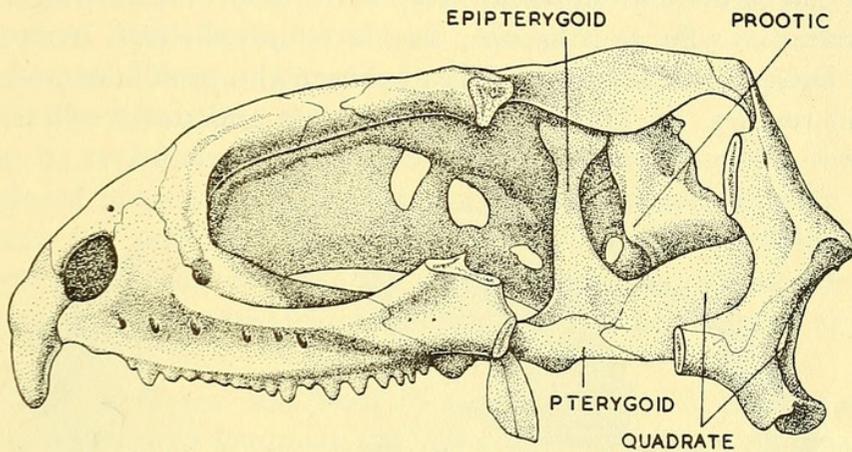


FIG. 19. *Sphenodon punctatus*. Lateral view of the skull with dermal bones cut off to show palatoquadrate.

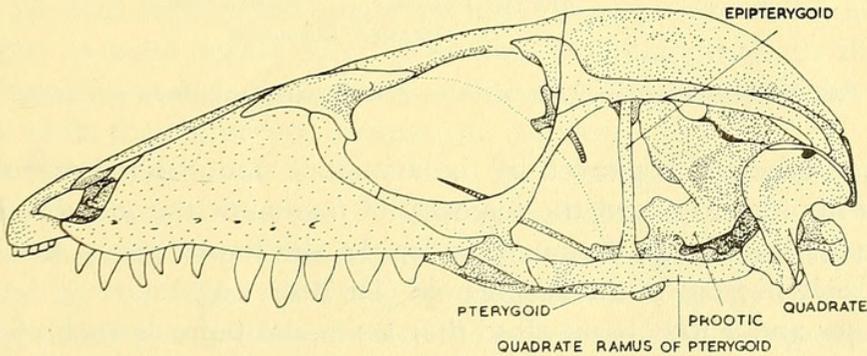


FIG. 20. *Tupinambis nigropunctatus*. Lateral view of skull. (After Jollie, 1960.)

Further reduction of the epipterygoid has taken place in the lizards *Agama*, *Lyriocephalus* and *Calotes* (Ramaswami, 1946), *Ophiocephs* and *Anniella* (Jollie, 1960), *Phrynocephalus* (Siebenrock, 1895), *Physignatus*, *Chlamydosaurus* and *Amphibolurus* (Beddard, 1905), where the epipterygoid is very short. However, in the Chamaeleontidae, Dibamidae (Boulenger, 1887) and apparently most Amphisbaenidae (known only in *Trogonophis*, Bellairs, 1950), the epipterygoid is absent. In the Chelonia the epipterygoid is still present but very small (Parker, 1880) while it is much reduced or vestigial in Ophidia and Crocodilia, although the embryos of crocodiles still show the ascending process (Parker, 1883; Shiino, 1914). In birds it appears to be absent (Goodrich 1930), the quadrate being the only part of the palatoquadrate to be retained in the adult.

Where present the epipterygoid lies lateral to the lateral head vein, postero-lateral to the profundus and antero-medial to the maxillary and mandibular branches and the orbital artery.

In mammals the alisphenoid appears to be lost in *Echidna*. In this feature, as will be seen later, *Echidna* probably shows reptilian affinities. In *Dasyurus* the dorsal end of the ala temporalis fuses with the orbital cartilage, but in all other mammals, as far as is known, the ala temporalis ends freely (De Beer, 1937). In *Didelphis* the alisphenoid lies between the profundus and maxillary rami, as in reptiles. In *Trichosurus*, *Mus*, *Mustela* and many others (De Beer,

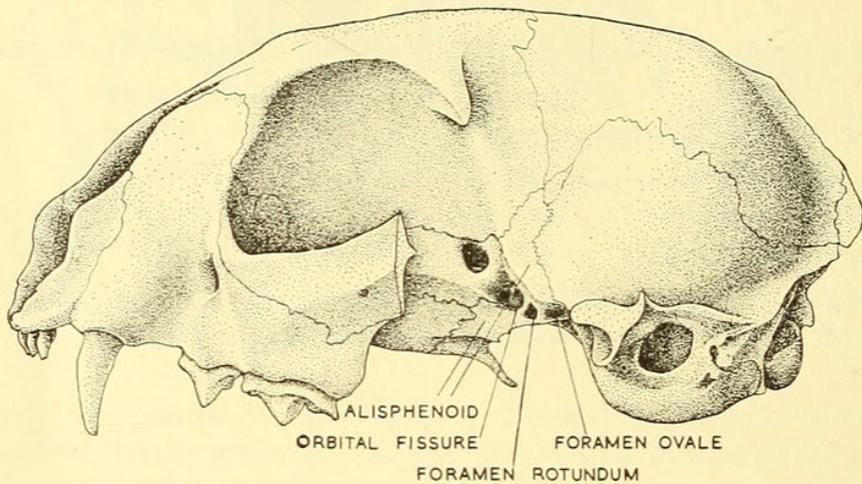


FIG. 21. *Felis domestica*. Lateral view of skull with jugal arch cut away.

1937) the alisphenoid is pierced by the maxillary ramus (foramen rotundum), while in *Felis* (fig. 21), and the majority of mammals the mandibular ramus too may pass through it (foramen ovale). In the fourth group the maxillary emerges freely in front of the alisphenoid (De Beer, 1937).

Edinger and Kitts (1954) state that the mandibular branch of the trigeminal appears to have been variable in its relations to the alisphenoid in living mammals as the foramen ovale is absent in some of them. Several

genera of extant *Perissodactyla* and *Artiodactyla* lack the foramen but in both these orders a separate foramen ovale was the usual condition in the early Tertiary. Comparison of fossil and recent material suggests a similar trend in certain families of the *Rodentia* and *Insectivora*. They relate the formation of the foramen ovale with an earlier palaeoneurological development when the mandibular nerve came to branch off the trigeminal stem intracranially, during or near the origin of mammals. It is only in some later forms that the nerve used the foramen lacerum for its passage from the braincase. This probably indicates that its absence is a secondary condition and possibly reveals an evolutionary trend within the mammals to abolish the separate exit of the mandibular nerve.

CONCLUSIONS

The evolutionary history of the palatoquadrate has been followed, as far as the availability of information on fossil material permits, from the early gnathostome condition to that in recent reptiles and mammals. It has been shown that the primitive palatoquadrate was a solid structure, consisting mostly of several ossifications, with four main processes for its attachment to the neurocranium. These are the otic, ascending, basal and pterygoid processes. In tetrapods the ossifications are reduced to two.

During its evolutionary history the palatoquadrate shows a tendency to become reduced in size, the pterygoid process shortens considerably while the area between the otic and ascending processes becomes deeply excavated thereby accentuating and demarcating the epipterygoid and quadrate portions. The demarcation of these two elements becomes more pronounced as evolution progresses.

Conditions in recent and fossil forms show that the palatoquadrate of both recent reptiles and mammals are deducible from the early gnathostome condition and that they evolved through the placoderm, crossopterygian, labyrinthodont and early stem reptile stages. In the groups leading to or showing affinities with the lines leading to modern reptiles, the trend is towards the progressive reduction of that part of the palatoquadrate anterior to the quadrate. In most reptiles the epipterygoid is the only part of this area to be retained but in some recent forms even this too disappears. In those lines leading towards mammals the opposite occurred and regression of the quadrate took place while the epipterygoid expanded (fig. 22).

From the foregoing it is clear that the phylogenetic and ontogenetic evidence do not support the view that the epipterygoid in the primitive reptile possessed a restricted base. The latter condition is a specialized reptilian one as is proved by conditions obtaining in adult forms of many recent reptiles. It is a stage in the gradual reduction of the epipterygoid in this group. Olson's (1944) views on the evolutionary development of the epipterygoid, must then differ from those given here.

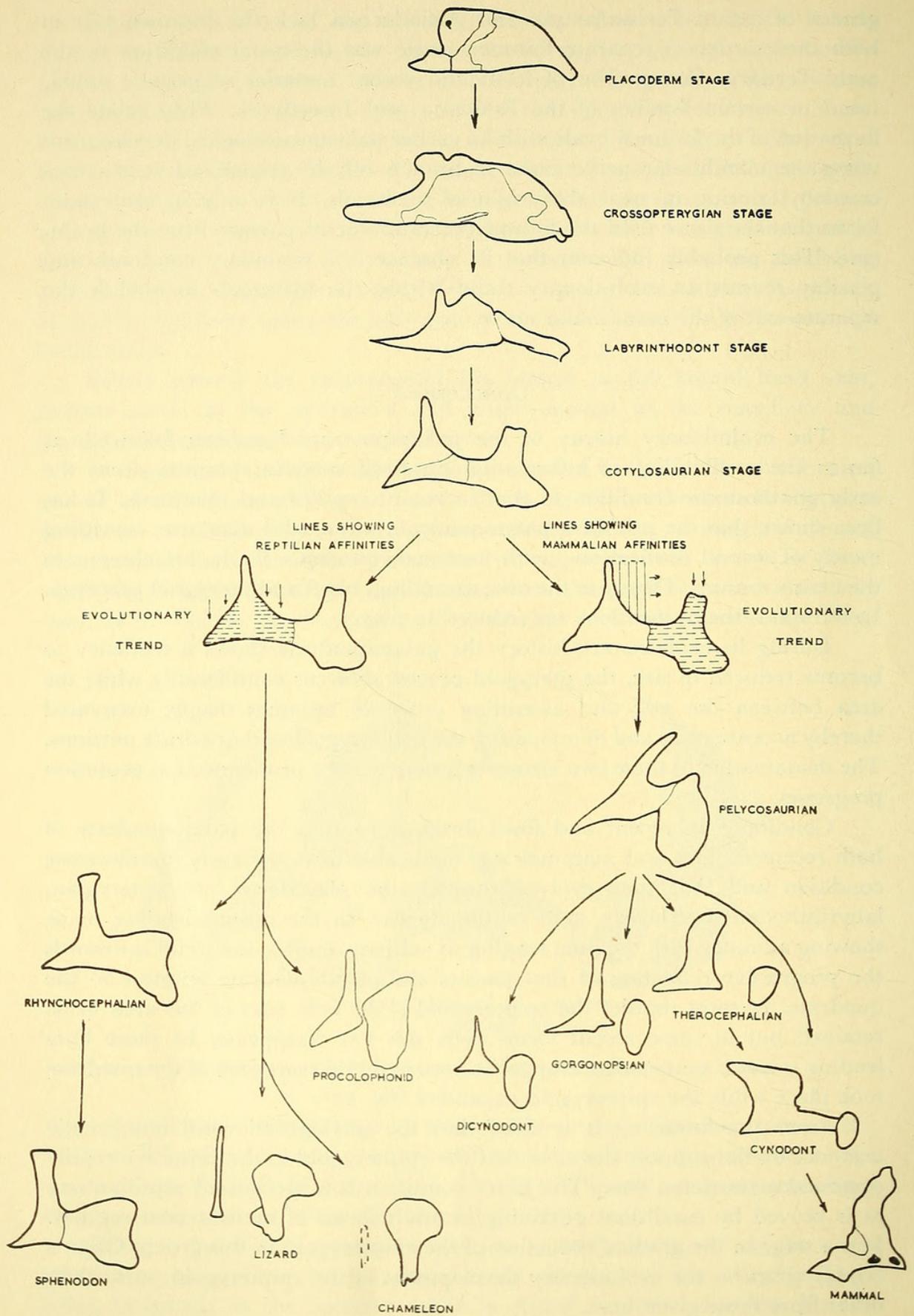


FIG. 22. Schematic presentation of probable evolutionary trend in development of palatoquadrate leading towards recent reptiles and mammals.

Although the therapsids show a marked degree of variability in the structure of the epipterygoid, we find that the groups which show mammalian affinities have also retained certain basic features of the early tetrapod palatoquadrate complex. The most noticeable of these is the retention of the extensive base of the epipterygoid, indicating that a considerable portion of the base of the palatoquadrate anterior to the quadrate, of the early labyrinthodont and stem reptile, had been retained.

Two further features are closely linked with the development of the alisphenoid in mammals. Firstly the expansion posteriorly of the rod-like ascending process of the epipterygoid and secondly, the increase in size of the brain in forms approaching the transitional stage.

Backward extension of the ascending process would result in the maxillary and mandibular branches of the trigeminal nerve being pushed backward by the epipterygoid as the latter progresses past the incisura prootica through which the trigeminal emerges.

The increase in size of the brain in mammals and the consequent lateral expansion of the braincase, could conceivably result in the nerves becoming trapped between the posteriorly extending epipterygoid and the expanding braincase. Close contact between the epipterygoid and braincase could force the nerves to seek an exit through the epipterygoid. Whether this results in the formation of a notch only, a foramen or two foramina depends largely on the separate development of the epipterygoid and prootic, the way these bones make contact and where this contact is made. In this way the maxillary ramus can emerge through the foramen rotundum while the mandibular emerges farther back through its own foramen ovale or merely through a notch in the posterior portion.

If the expansion of the braincase is continued anteriorly the cavum epiptericum would be obliterated, as it has been in mammals. This could mean that the pila antotica, which forms the inner wall of the cavum in reptiles, could have been pushed against the alisphenoid and as the pila will then virtually have become redundant, there is no need for it to develop in mammals. The possibility that this could have happened is strengthened by the fact that isolated cartilaginous fragments of the pila antotica have been found in many higher mammals, e.g. *Lepus* (Voit, 1909), *Homo* (Macklin, 1914), *Felis* (Terry, 1917), *Didelphys* (Töplitz, 1920), *Halicore* (Matthes, 1921) and *Tarsius* (Henckel, 1927).

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SUMMARY

The serial sectioning of the skull of the anomodont *Pristerodon buffaloensis* has produced valuable evidence regarding the structure of the palatoquadrate complex and the evolution of the therapsid epipterygoid. A short review is given of the structure of the palatoquadrate in the most important known fossil vertebrate groups.

It is emphasized that the mammalian alisphenoid should not be looked upon as a transformation of the rod-like epipterygoid, as found in more specialized true reptiles as Broom and others implied, but that both conditions are derived from a common ancestral type.

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