

## THE ENDOCRANIAL CAVITY OF A NONMAMMALIAN EUCYNODONT, *CHINIQUEDON THEOTENICUS*, AND ITS IMPLICATIONS FOR THE ORIGIN OF THE MAMMALIAN BRAIN

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**ABSTRACT**—The braincase and endocranial cavity of a specimen of a nonmammalian eucynodont *Chiniquodon* is described and illustrated, and a tentative reconstruction of the gross anatomy of the brain offered. Salient features are the well-developed impression for the olfactory lobes, the extreme narrowness of the region available for the telencephalon, and the evidence for a large cerebellum. A two-step theory for the origin of the mammalian brain is proposed. The first step is represented by the nonmammalian cynodont level and consisted of enlargement of the cerebellum and possibly midbrain structures. This stage is associated with the evolution of more sophisticated neuromuscular control of the mandibular and locomotory apparatuses. The second step was the evolution of the mammalian six-layered neocortex, and did not occur until the origin of the mammals themselves. This stage was an integral part of a complex set of allometric changes associated with miniaturization. The origin of the neocortex was correlated with sensitivity to higher frequency sound, and a greater area of olfactory epithelium, both expected to result from miniaturization, and also with the availability of increased space within the cranial cavity expected as the adductor jaw musculature was relatively reduced in mass. Overall, neocortical function was associated with the high energy nocturnal foraging activity generally believed to have appertained in the first mammals, and also sophisticated social communication.

### INTRODUCTION

Of all the characters of mammals, none is more systematically definitive or biologically significant than the enlarged brain. After allowing for the allometric relationship between brain and body size, the brain volume of even the basal mammaliaform *Morganucodon* (Kermack et al., 1981) is significantly larger than that of a modern reptile of comparable body size (Rowe, 1996; Kielan-Jaworowska et al., 2004:fig. 3.9), and there is scarcely any aspect of mammalian physiology and behaviour that is not associated, directly or indirectly, as cause or as effect, with the enhanced central neural capacity. The phenomenal evolutionary increase in brain size is therefore of fundamental importance for understanding the origin of mammals, and this makes it all the more frustrating that so little can be inferred about the size and morphology of the brain from fossils of the various grades of nonmammalian therapsids, which in other respects illustrate so well stages in the acquisition of mammalian traits (Kemp, 2005). The problem lies quite simply in the failure of the brain fully to occupy the osteological endocranial cavity, a condition that is standard for the small-brained, nonmammalian and nonavian tetrapods (Starck, 1979). Thus there have been few attempts to reconstruct therapsid brains, and estimates of the brain volume vary widely. Expressing brain size in the standard form of an encephalization quotient, EQ: actual/expected brain weight for the body weight, as developed by Jerison (1973) and discussed by Eisenberg (1981), is even more hazardous given that body weights can also rarely be estimated with any great confidence.

Nevertheless, even the imprecise estimates of size and form that can be inferred from the cranial cavities of nonmammalian therapsids, especially nonmammalian cynodonts are of considerable interest in the light of the long-continuing debate about the homologies of the parts of nonmammalian and mammalian brains and what they imply about the origin of the latter from the former.

**Institutional Abbreviations**—**GPIT**, Institut und Museum für Geologie und Paläontologie der Universität Tübingen; **NMH**, Natural History Museum, London.

**Anatomical Abbreviations**—**ad.pr.**, anterodorsal process of the prootic; **am.cl.**, amygdalo-claustral complex; **bpt.art.**, basiptyergoid articulation; **cav.ep.**, cavum epiptericum; **cb.h.**, cerebral hemispheres; **cor.pr.**, coronoid process; **D.**, dentary; **dor.sel.**, dorsum sellae; **dorctx.**, dorsal cortex; **dorpall.**, dorsal pallium; **DVR.**, dorsal ventricular ridge; **EPT.**, epiptyergoid; **fl.fos.**, parafloccular fossa; **hipcps.**, hippocampus; **int.au.me.**, internal auditory meatus; **j.f.**, jugular foramen; **l.can.**, lower canine; **l.pt.pr.**, lateral pterygoid process; **latctx.**, lateral cortex; **latpall.**, lateral pallium; **medctx.**, medial cortex; **medpall.**, medial pallium; **nar.**, naris; **n.ri.**, nasal ridge; **neocctx.**, neocortex; **occ.con.**, occipital condyle; **ol.b.**, olfactory bulb; **olfctx.**, olfactory cortex; **OSP.**, orbitosphenoid; **osp.**, attachment edge for the orbitosphenoid; **P.**, parietal; **pi.ant.**, pila antotica; **pin.**, pineal gland; **pr.cult.**, processus cultriformis; **PT.**, pterygoid; **pt.par.f.**, pterygoparoccipital foramen; **sag.cr.**, sagittal crest; **sec.pal.**, secondary palate; **sept.**, internasal septum; **se.tur.**, sella turcica; **SMX.**, septomaxilla; **smx.f.**, septomaxillary foramen; **SO.**, supraoccipital; **SQ.**, squamosal; **u.can.**, upper canine; **unos.z.**, unossified zone; **V.**, trigeminal notch; **XII.**, hypoglossal foramen.

### MATERIAL

The specimen of the nonmammalian eucynodont *Chiniquodon* (*Probelesodon*) *theotenicus* that forms the subject of the present study is the same one that Kemp (2007) used for an investigation into the acoustic function of the postdentary and quadrate bones. It has been bisected just to the side of the midline and both halves virtually completely cleared of matrix. This has revealed considerable detail of the internal surfaces of the braincase and nasal cavity. The specimen has also been subjected to CT scanning which, while at too low a resolution to show surface features in detail, does provide sections through the cranial and nasal cavities that are not easily reconstructed directly from the specimen. Taking both techniques together, a more reliable picture of the gross anatomy of the endocranial cavity emerges, along with whatever indications of soft structures are preserved on the bone surfaces.

## SYSTEMATIC PALEONTOLOGY

CYNODONTIA Owen 1861

EUCYNODONTIA Kemp 1982

PROBAINOGNATHIA Hopson 1990

CHINQUODONTIDAE von Huene 1935–42

*CHINQUODON THEOTENICUS* von Huene 1935–42**Holotype**—GPIT 1050, partial skull.**Type Locality and Age**—Chiniqua, Rio Grande do Sul State, Brazil. Ladinian, Middle Triassic.**Referred Material**—NHM R8429, a complete skull from the Chañares River, Campo de Talapaya, La Rioja Province, Argentina, figured by Kemp (2007), who incorrectly attributed to it the catalogue number R8430. This specimen was originally referred to as *Probelesodon lewisi* Romer, but Abdala and Giannini (2002) revised the family Chiniquodontidae and showed that *P. lewisi* is a junior synonym of *Chiniquodon theotenicus*.PREVIOUS STUDIES ON THE NONMAMMALIAN  
CYNODONT BRAIN

The very limited literature then in existence on endocranial casts of nonmammalian cynodonts (referred to as cynodonts for brevity, where no ambiguity arises) was reviewed by Hopson (1979). The most important was that of the epicynodont *Nythosaurus* (possibly *Thrinaxodon*), described by Watson (1913), which consists of a cast bearing the impression of the roof of the cavity. Watson also described specimens of *Diademodon* which included a partial roof cast, and a cast of the posterior region. To this Hopson (1979) himself added a description of a specimen of the eucynodont *Trirachodon* in which both dorsal and lateral views of the endocranial cast are exposed. Although not discussed by Hopson (1979), Olson (1944) had made a reconstruction of the hindbrain region of *Thrinaxodon* based on serially ground specimens, but he did not consider the forebrain.

At about the same time Quiroga (1979, 1980, 1984) described endocranial casts and attempted brain reconstructions of four eucynodonts, and Kemp (1979) published a reconstruction of the brain of the basal cynodont *Procynosuchus* on the basis of a skull completely cleared of matrix by acetic acid.

The most recent review of the literature on nonmammalian cynodont and Mesozoic mammaliaform endocranial casts and reconstructed brains is that of Kielan-Jaworowska et al. (2004). It indicates that virtually all authors agree the cynodont brain was only slightly larger than that of basal amniotes, and in particular that the cerebral hemispheres were long, thin, and tubular in form, so quite unlike this region of mammals. To attempt to quantify this impression, they tabulated the various published estimates of the Encephalization Quotient (EQ, actual/expected brain weight, Jerison, 1973) of cynodonts and early mammals, relative to the regression line of body weight against brain size of living mammals. The estimates are variable, ranging from 0.1 by Jerison (1973) for the epicynodont *Thrinaxodon*, to 0.22 by Quiroga (1980) for the eucynodont *Massetognathus*, but all are consistently much lower than for any of the Mesozoic mammals that have been studied in this respect (see Kielan-Jaworowska, 1984a, b, 1986). In fact, the quoted estimates of Kielan-Jaworowska et al. (2004) for the latter are even more variable than for cynodonts. Their quoted estimates for the EQ range from as low as 0.36 in the Cretaceous eutherian *Kennalestes*, through 0.49 in the Jurassic *Triconodon*, to a high of 0.7 in *Zalambdalestes*, another Cretaceous eutherian. For multituberculates alone, the estimates vary from 0.49 to 0.71. The most recent study of a Mesozoic mammal endocranial cavity is the important one on the South American Cretaceous theriiform *Vincelestes* by Macrini et al. (2007). They estimated an EQ for the brain including the olfactory bulbs of 0.27 or 0.37, depending on the value of the exponent applied. Actually, considerable variance in brain size

in the taxon even after allowing for body size should be expected, since it is also true of modern mammals. For example, Eisenberg and Wilson (1981) found an EQ range of 0.5–1.09 within the single marsupial family Didelphidae, and Eisenberg (1981) reported values from 0.40 to 1.43 in a variety of small mammals of roughly comparable body weights, with some correlation with aspects of their respective modes of life. Furthermore, body weight is difficult and often virtually impossible to estimate accurately in fossil material. Indeed, Quiroga (1979) had to base his calculations for cynodonts on skull length, which itself is unlikely to have a precise relationship to body mass. However, the greatest source of uncertainty in estimating EQ's for cynodonts lies in the measurement of brain volume itself. All the references to brain size in cynodonts are based mainly, if not exclusively on the impression of the brain on the skull roof. Unfortunately, the depth of the forebrain with its cerebral hemispheres is entirely unknown, and only the hindbrain, namely the medulla and the cerebellum leave convincing impressions on the internal surfaces of the bony braincase. The assumption appears to have been made that the cynodont forebrain was essentially like that of modern reptiles, in so far as the dorso-ventral depth was no greater than the lateral breadth. The one study where this assumption was not made was that of Kemp (1979), who argued that if it is accepted that the brain could have been deep and narrow, rather than strictly tubular, then its volume could have been and probably was significantly larger than those of basal amniote brains.

The present specimen offers an opportunity for a new, potentially more accurate estimate of the brain size and anatomy of a nonmammalian eucynodont, because the internal surfaces of the bony braincase itself have been exposed, and the skull is sufficiently undistorted for CT scanning to provide satisfactory transverse sections of the endocranial cavity.

THE ENDOCRANIAL CAVITY OF *CHINQUODON*

Early work by Watson (1911, 1913), Broili and Schröder (1934, 1935) and Parrington (1946) established the main external features of the cynodont braincase, while the first to describe in detail the internal structure was Olson (1944) in his comparative cranial study based on a series of serially ground therapsid specimens. This included two Lower Triassic cynodonts, identified as *Galesaurus* ('cynodont A') and *Thrinaxodon* ('Cynodont B'). Fourie (1976) also studied a serially ground specimen of a *Thrinaxodon* skull, adding a great deal more detailed information. The first description based on an entire skull in which the internal as well as the external surfaces were exposed was Kemp's (1979) study of an acetic acid prepared specimen of the Late Permian, primitive cynodont *Procynosuchus*. Later, the same author described another bisected and internally prepared brain case, that of the eucynodont *Luangwa* (Kemp, 1980). A few other partial descriptions of the internal surfaces and features of the cynodont braincase have appeared since, such as that of Abdala and Teixeira (2004), also of *Luangwa*. The structure of the braincase and endocranial cavity of *Chiniquodon* (Figs. 1–4) corresponds to the general cynodont structure, although there are significant differences from *Procynosuchus*.

A shallow, concave depression occupying the full width of the underside of the paired frontals is agreed by all authors to indicate the position of the olfactory bulbs (Fig. 3:ol.b). It is clearly demarcated in front by a pair of oblique ridges separating it from the paired deep lateral recesses at the hindmost part of the nasal cavity, immediately anterior to the orbital walls. A very slight ridge divides the front part of the depression for the olfactory bulb into left and right sides, possibly representing the base of a dorsal remnant of the nasal septum, but further back there is no indication of a paired nature. The posterior limit of the bulbs is not clearly indicated, but corresponds to a gradual transition

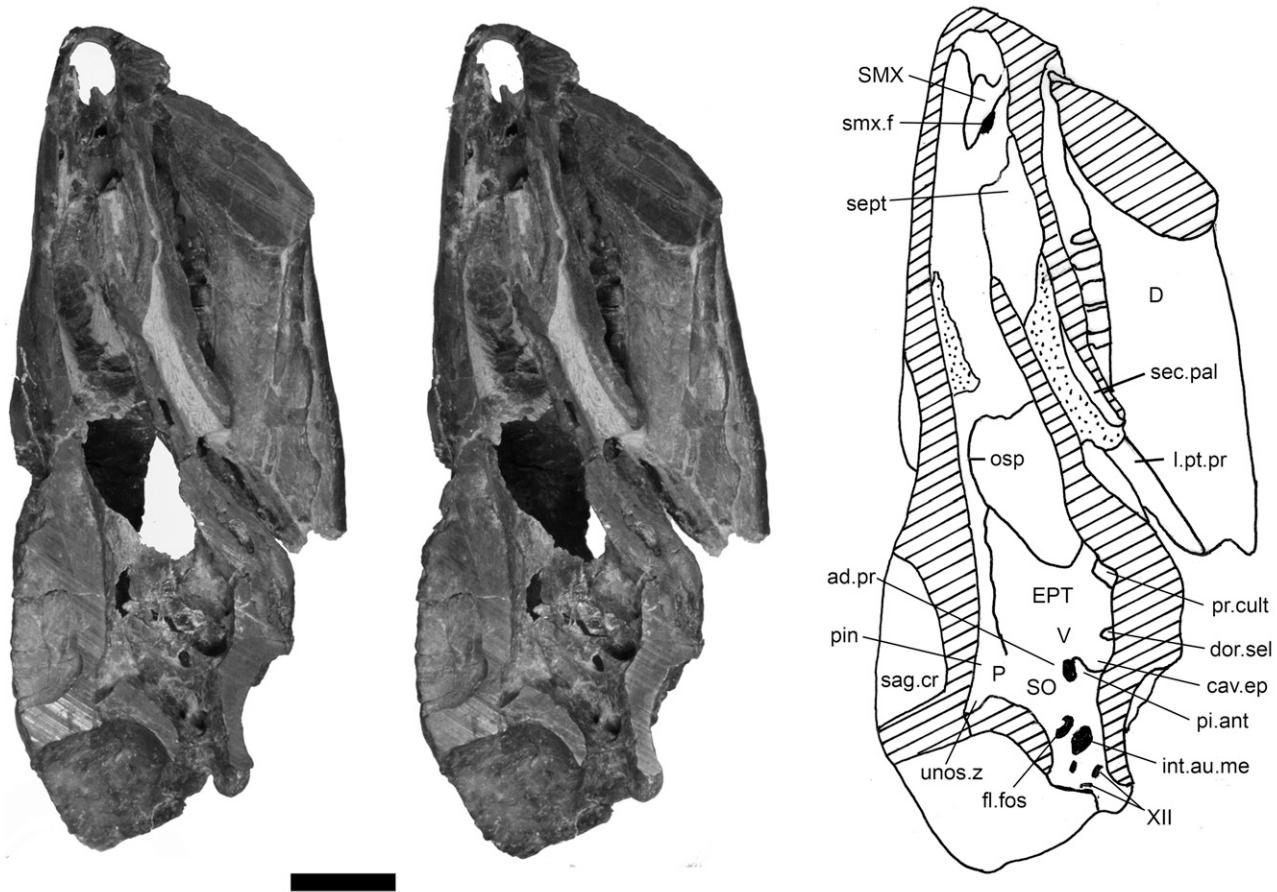


FIGURE 1. *Chiniquodon theotenicus*, NHM R8429. Stereophotograph of the left half of the skull viewed from medially. Scale bar equals 2 cm.

from the slight concavity to an equally slight convexity at about the level of the start of the epipterygoid. The undersurface of the frontal bone here is very finely rugose, with small ridges and minute foramina.

The orbitosphenoid (Fig. 2:OSP) is ossified, unlike the condition in more basal cynodonts. As in all nonmammalian therapsids where it is preserved, it is a single, median bone. In the specimen, the right side has remained attached to the frontal bone, although it has been displaced a little towards the midline. The left side was removed during preparation of the skull, but its original line of attachment is clearly appreciated (Fig. 1:OSP), as it follows the lateralmost edge of the frontal, between the orbital wall anteriorly and the antero-dorsal part of the epipterygoid (Fig. 1:EPT) posteriorly. Both the anterior and posterior edges of the orbitosphenoid attenuate slightly so the midline of the bone is shorter than the lateral edges. The orbitosphenoid defines the cavity in which the olfactory bulbs lay, and therefore allows an accurate estimate of the maximum possible size of those structures.

Behind the impression of the olfactory bulbs, the roof of the braincase over the presumed region of the cerebral hemispheres consists of the ventral surface of the parietal bones (Fig. 3:cb.h). It is concave laterally, but very slightly convex from front to back, and so is unlikely to be a direct impression of a bulbous cerebrum. Furthermore, there is no trace of a midline ridge to indicate a division into right and left hemispheres. This part of

the skull roof continues posteriorly until a more prominent median spherical depression occurs in the roof, just in front of the supraoccipital (Fig. 1:pin). Behind the depression lies the unossified region (Figs. 1–3:unos.z) between the parietal and interparietal bones above and the supraoccipital below that is characteristic of all cynodonts. There is no sign at all of the pineal canal and foramen characteristic of more basal cynodonts, unless it be the depression in the roof just mentioned. The surface texture of the parietal roof of the braincase is finely rugose, like the olfactory bulb region. The fine striations run generally antero-posteriorly. However, the surface of the posterior depression is smooth and virtually free of markings.

The side wall of the braincase behind the orbitosphenoid consists of the expanded ascending process of the epipterygoid, a characteristic cynodont feature matched elsewhere only in the whaitsiid therocephalians (Kemp, 1972). Both epipterygoids are slightly damaged dorsally, but taken together represent virtually all the internal surface, and are complete enough to give a good indication of the maximum breadth of the parts of the brain that would have lain between them. The epipterygoid overlaps but probably did not contact the orbitosphenoid antero-dorsally, and it has a long suture with the basisphenoid ventrally (Fig. 4:bpt.art), the cynodont homologue of the basiptyergoid articulation. Behind the latter region, the epipterygoid extends postero-laterally as the quadrate ramus, and between this and the periotic medially lies the cavum epipticum (Fig. 1:cav.ep), a structure



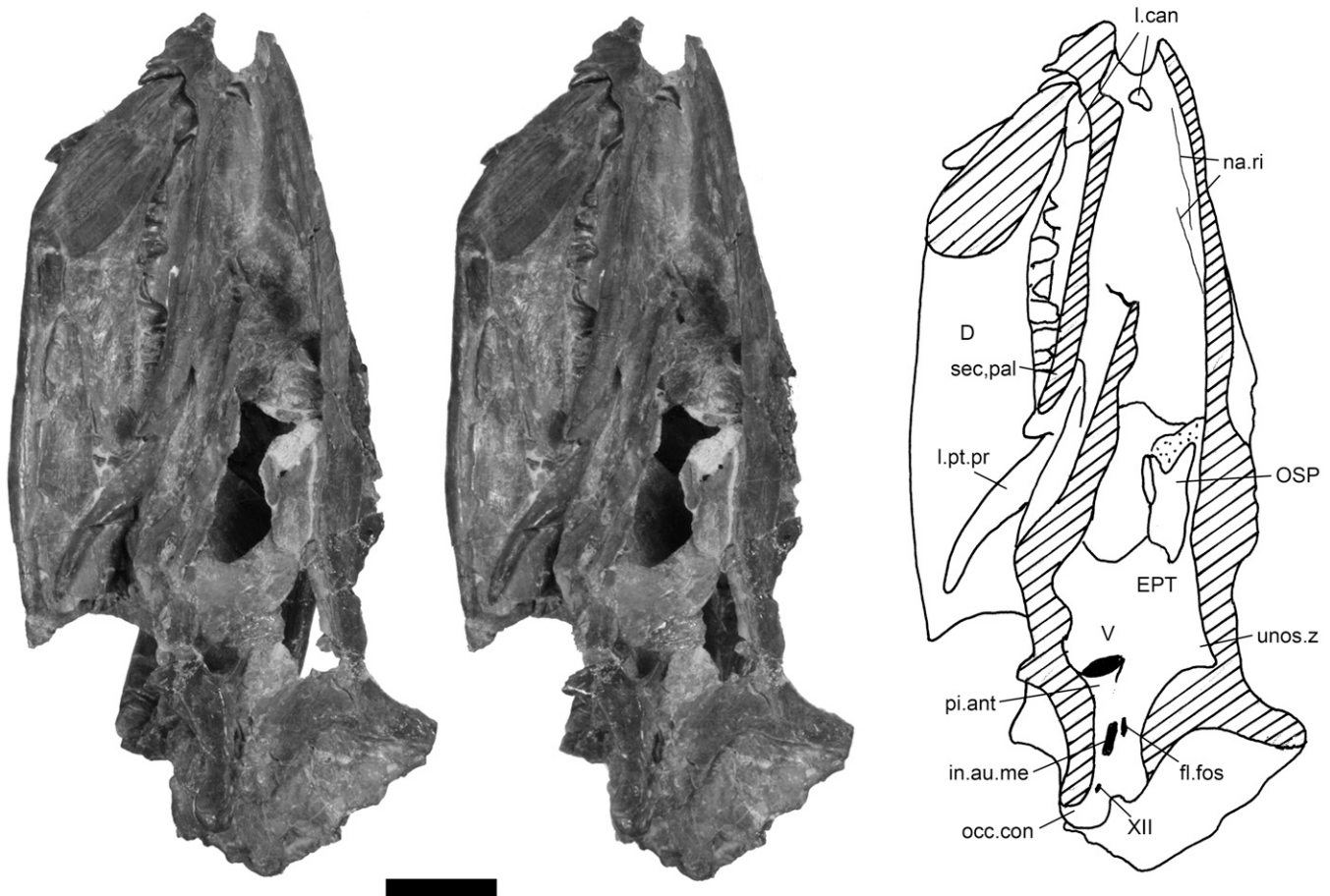


FIGURE 2. *Chiniquodon theotenicus*, NHM R8429. Stereophotograph of the right half of the skull viewed from medially. Scale bar equals 2 cm.

much discussed in the context of the origin of the mammalian braincase (e.g., Hopson, 1964; Kermack and Kielan-Jaworowska, 1971). The line of contact between the left epipterygoid and parietal bone (Fig. 1) coincides with a ridge of the side wall of the braincase, but this may be at least in part an artefact due to slight crushing of the skull. Unfortunately, this region of the right side is missing and so no confirmation of the presence of such a ridge is possible. Otherwise, the internal surface of the epipterygoid is virtually completely devoid of any features that indicate the position or form of the brain that lay between them.

Behind the epipterygoid lies the periotic, which shows rather more indications of the possible brain structure. The antero-dorsal process (Fig. 1:ad.pr) has a long suture with the epipterygoid and forms the upper margin of the trigeminal notch (Figs 1, 2:V). The lower border of the notch is formed by the pila antotica (Figs 2–4:pi.ant), which has broken on both sides. (When the specimen was first prepared by the author several years ago, the right pila antotica was complete. Unfortunately, the distal half has since been broken off and lost.) The more posterior landmarks of the periotic are the parafloccular fossa (Figs. 1, 2:fl.fos) and below it the combined opening of the internal auditory meatus and jugular canal (Figs. 1, 2:int.au.me), the former leading to the labyrinth region and fenestra ovalis and the latter to the jugular foramen.

The roof of this hind region of the cranial cavity is formed by the supraoccipital. The internal surface is concave from side to

side, and slightly convex from antero-dorsal to postero-ventral, where it curves around to become the roof of the hind part of the brain cavity and the foramen magnum. The surface of the bone is smooth and non-rugose and lacks structural features. Above the supraoccipital lies the unossified zone (Figs 1–3:unos.z) remarked upon above. The supraoccipital floor of this zone lacks a periosteal finish, unlike the sides and roof which are formed by the parietal and presumably interparietal dermal bones.

Anterior to the epipterygoids, the braincase floor is formed by the pterygoids, which together are a broad, horizontal trough (Fig. 4). Where it runs medially to the epipterygoid, the lateral part of each pterygoid becomes a vertical sheet, with a narrow cleft between it and the median parasphenoid. This is the closed interpterygoid vacuity. The processus cultriformis of the parasphenoid (Fig. 4:pr.cult) is a short, median process supported by the low median septum of the pterygoids. Behind the processus cultriformis lies the basicranial region of the basisphenoid. On each side it is a narrow wing of bone, slightly concave laterally and slightly convex antero-posteriorly. It makes a relatively very long suture with the base of the epipterygoid. At the posterior extent of the connection there is a small, but very distinct median process, and behind this a fine median ridge. Two small foramina arranged in tandem open on the ridge. It is generally supposed that this part of the basisphenoid is a narrow sella turcica housing the pituitary gland. Marking the hind end of the sella turcica, between the paired bases of the pilae antoticae lies a small dorsum sellae (Figs. 1, 4:dor.sel).

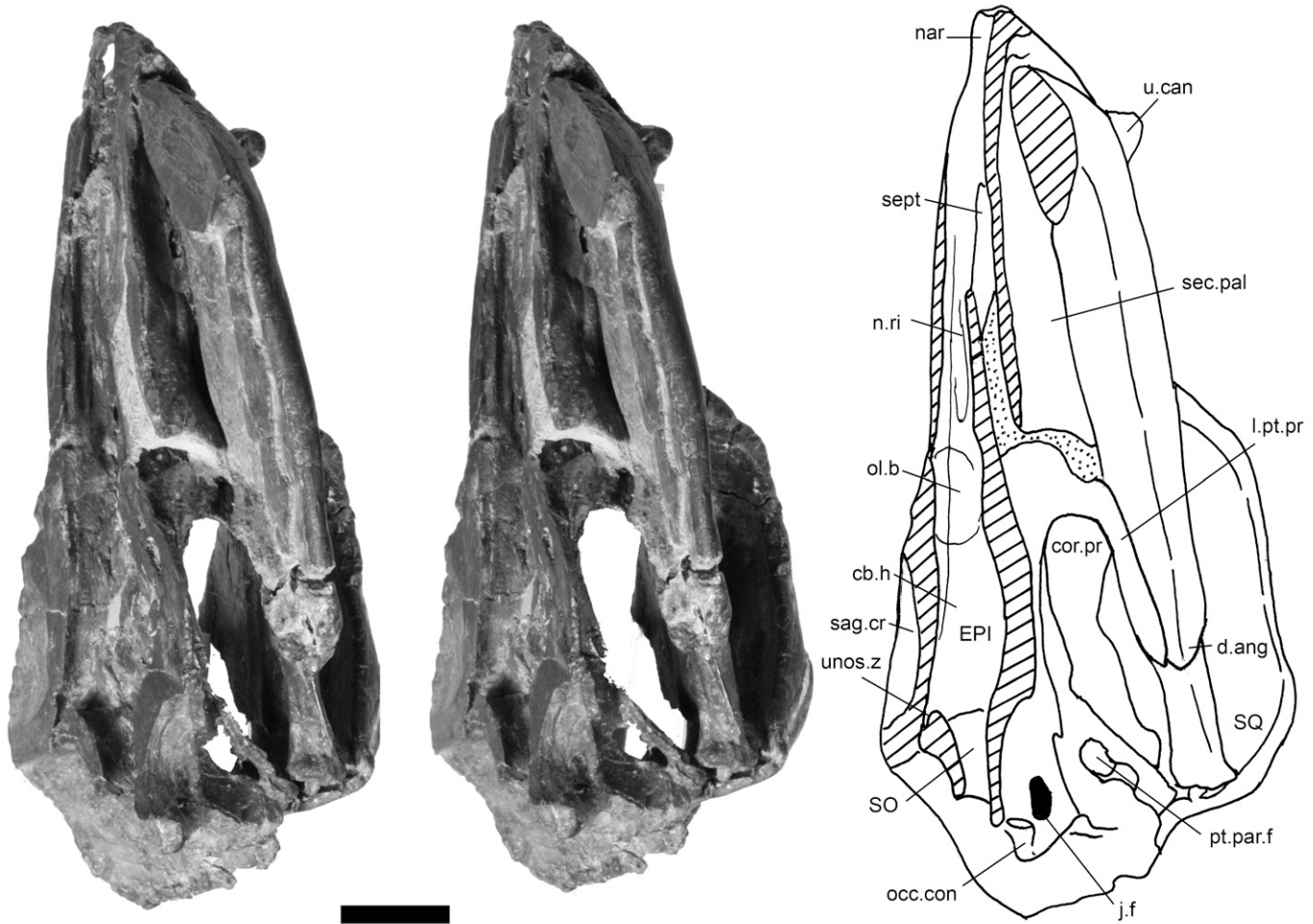


FIGURE 3. *Chiniquodon theotenicus*, NHM R8429. Stereophotograph of the left half of the skull viewed from ventrally and slightly medially. Scale bar equals 2 cm.

The floor of the hindbrain region (Fig. 4), posterior to the dorsum sellae and pilae antoticae is formed by the basisphenoid and basioccipital bones, although no clear suture between them is visible. It is smooth, and gently concave from side to side, and a pair of slight swellings lie immediately medial to the internal auditory meatus. A number of foramina for cranial nerves are evident. The trigeminal notch marks the exit of the trigeminal nerve, of course. A smaller foramen at the base of the pila antotica is usually taken to be the exit for cranial nerve VI, and a foramen immediately anterior to the internal auditory meatus as that for cranial nerve VII. There is a possible small foramen immediately behind the internal auditory meatus, and two well marked hypoglossal nerve foramina on the side, close to the foramen magnum.

#### RECONSTRUCTION OF THE BRAIN

It is an unfortunate but inescapable fact that the detailed form of the brain of *Chiniquodon* cannot be discerned from the shape of the endocranial cavity because much of the brain did not impress itself on the cavity walls. As in living reptiles, it must have been well enough supported by the connective tissue meninges and suspending, strap-like funiculi (Starck, 1979), which possibly spanned considerable distances between the bone of the cranial cavity wall and the neural tissue of the brain itself (Fig. 5). It is therefore extremely unlikely that much more detail of nonmammalian cyno-

dont brain anatomy will ever be available than that revealed by the present specimen, and moreover previous interpretations of the brain size and form have probably rather over-interpreted the osteological anatomy. Nevertheless, the endocranial cavity does at least impose constraints on the possible maximum size of parts of the brain, and as it happens this actually reveals a very interesting anomaly concerning the evolutionary origin of the mammalian brain, which is discussed in the next section.

The parts of the brain (Fig. 6) that can be most confidently reconstructed are the olfactory bulbs. As all previous authors have agreed, the concave underside of the frontal bones reflects quite closely the size of the bulbs, and in the case of *Chiniquodon* the maximum possible lateral and dorso-ventral extents are also indicated by the ossified orbitosphenoid. As so conceived, they are greater in length and appear to have been larger, relative to other parts of the brain, than in most tetrapods (e.g., Kappers et al., 1936), including living mammals (Walker et al., 2008), and certainly constitute a significantly higher proportion of the forebrain as a whole.

The cerebral hemispheres are a good deal more controversial. All previous authors except Kemp (1979) have described them as long, thin and tubular in cynodonts. This interpretation is based on the latero-medially concave form of the roof of the cranial cavity behind the olfactory bulb impressions. But this region of the roof is also slightly convex from front to back, and so is very unlikely to be a direct impression of the dorsal surface



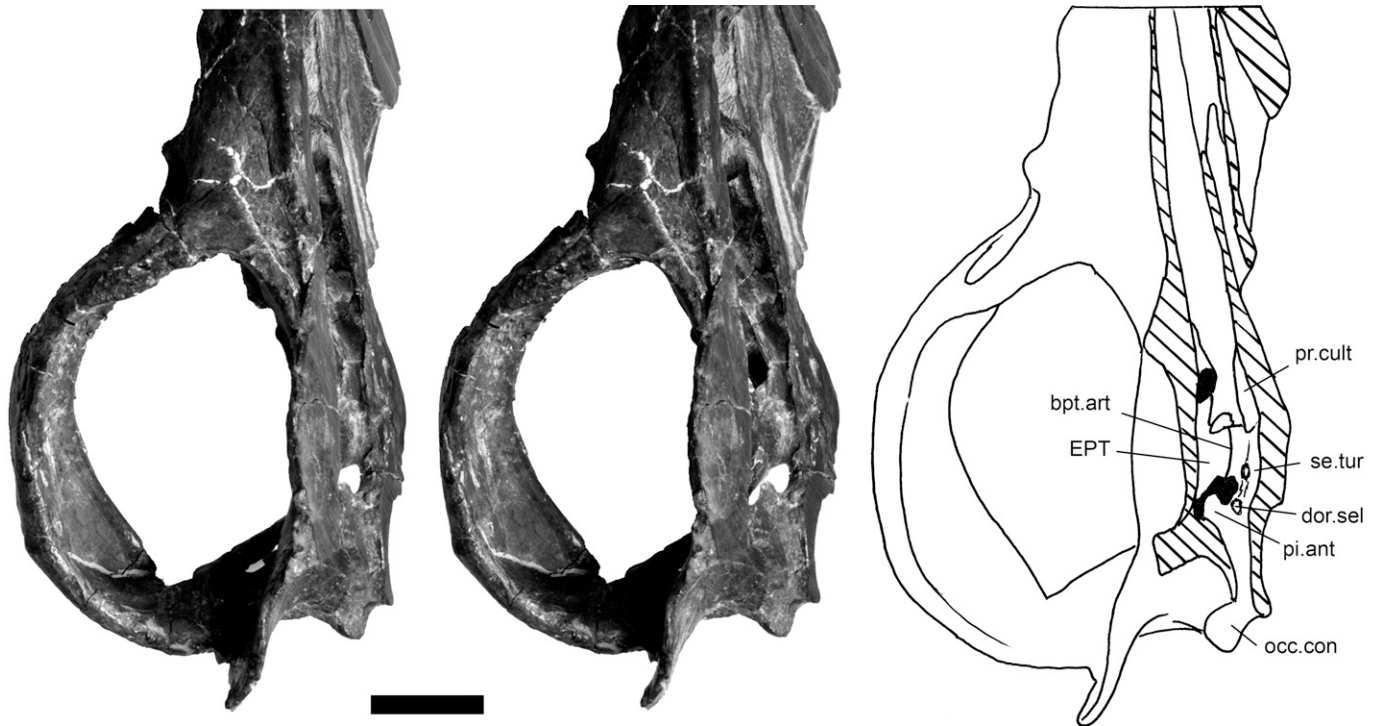


FIGURE 4. *Chiniquodon theotenicus*, NHM R8429. Stereophotograph of the left half of the skull viewed from dorsally and slightly medially. Scale bar equals 2 cm.

of what was presumably at least a linear and more probably a convex dorsal profile of the hemispheres. Furthermore, to interpret them as tubular requires the assumption that the cerebrum was approximately circular in cross section, and therefore no deeper than wide, which gives them an extraordinarily small volume. However, as there is no ossified floor to the cranial cavity in the region of the cerebral hemispheres, no indication of the dorso-ventral extent of the hemispheres is possible and therefore they could have been substantially deeper than wide. The reconstruction in Figure 6 allows for this possibility, although it must be stressed that there is no positive evidence for it at all. Whatever their depth may have been, the maximum medio-lateral extent of the cerebral hemispheres is constrained by the distance between the epipterygoids forming the side walls of the endocranial cavity in this region, and this is remarkably narrow compared to all living amniotes (Kappers et al., 1936; Hopson, 1979; Northcutt, 1981; Aboitiz et al., 2002), an anomaly discussed in the next section.

As shown by Quiroga (1979) in *Chiniquodon* and *Massetognathus*, there is also no indication on the roof of the endocranial cavity of the posterior limit of the cerebral hemispheres, although he did find evidence from the impression on the roof of the possible posterior termination of these structures in the smaller eucynodont *Probainognathus* (Quiroga, 1980).

The position and form of the cerebellum are more confidently assessed because of the presence of a parafloccular fossa on either side of the posterior braincase. As other authors agree, their presence implies that the cerebellum occupied the full width of the braincase at this level, a conclusion supported by the smooth bone surface and concave form of this part of the supraoccipital and periotic components of the braincase. The question of how far dorsally the cerebellum reached is not so readily answered. The surface of the supraoccipital is convex from top to bottom and is therefore unlikely to be reflecting the shape of the cerebellum. As in all cynodonts, the dorsal region of the supraoccipital gives way to an unossified zone that is roofed

by the parietal and perhaps partly the interparietal. Olson (1944) regarded this simply as a failure of ossification of the supraoccipital, though why this should happen is unclear. In contrast, Kielan-Jaworowska et al. (2004) argued that this space was occupied by a mammal-like mid-dorsal vermis of the cerebellum, on the grounds that the concavity is continuous with the adjacent parts of the cranial cavity and is a consistent feature within cynodonts. If they are correct, then the cerebellum must have been remarkably large to have stretched from parafloccular fossae to the unossified zone, and not at all of a characteristic mammalian shape. Another possible interpretation of this region

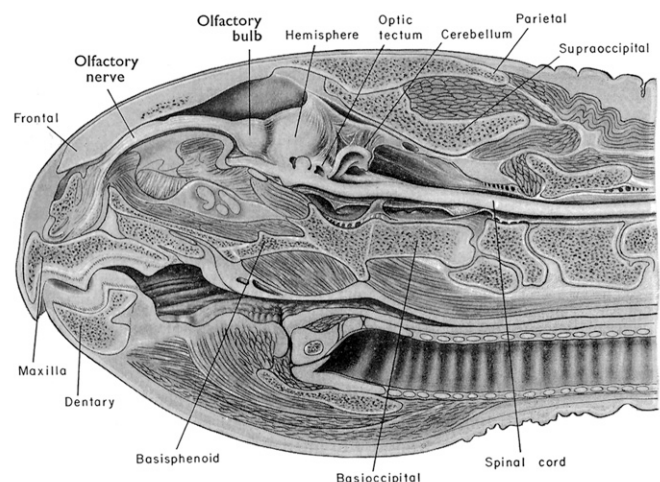


FIGURE 5. Sagittally sectioned skull of the turtle *Chelone mydas* to show the relationship between the endocranial cavity, brain, and meninges of a recent reptile. Reproduced with permission from Starck (1979).

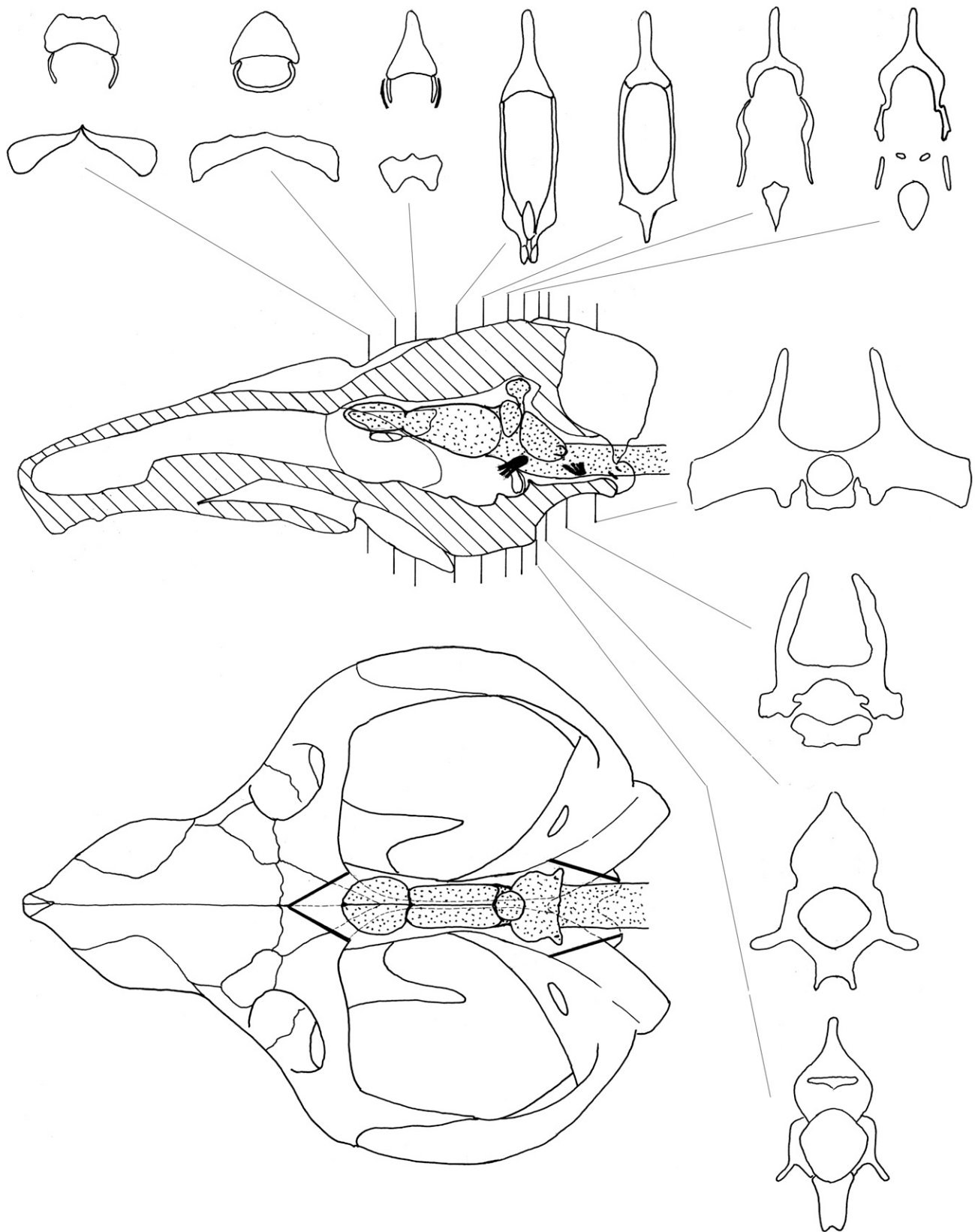


FIGURE 6. Reconstruction of the brain within the endocranial cavity of the eucynodont *Chiniquodon thetensis* in medial and dorsal views. Transverse sections of the whole skull corresponding to the positions indicated, based on CT scans.

is that the dorsal depression between the parietal and interparietal bones in the region marks the position of a superior sagittal sinus, as suggested by Rowe et al. (1995).

The only possible direct evidence bearing on the nature of the midbrain between cerebral hemispheres and cerebellum is the presence of the smooth, quite deep concavity in the parietal roof (Fig. 1:pin). This corresponds in position to the internal end of the broad pineal canal that leads to the open pineal foramen in *Procynosuchus* (Kemp, 1979) and other basal cynodonts such as *Thrinaxodon* (Fourie, 1974). It is therefore possible that the concavity was associated with a pineal gland. It is also possible that mid-brain structures, an optic tectum or mammalian colliculi were well developed, and the relatively small size of the cerebral hemispheres would tend to support this.

The brain stem corresponds well to that described by Olson (1944), with an impression of the medulla oblongata leading via the midbrain to the thalamus region, and the points of exit of cranial nerves V, VII, IX, X, and XII indicated by foramina. The pituitary may well have occupied the sella turcica just forwards of the bases of the pilae antoticae, as in tetrapods generally and, assuming this was so, it suggests that the brain stem lay close to the floor of the endocranial cavity posterior to the pituitary. In front of the pituitary and the presumed overlying hypothalamus region, it is not possible to determine the relative size of thalamus to cerebral hemispheres.

The reconstruction of the brain in Figure 5 should not be taken too literally on account of the caveats mentioned. The brain *could* have been of this size and gross anatomy, but it could also have been a good deal smaller and the relative sizes of the parts could have been somewhat different.

#### DISCUSSION: IMPLICATIONS FOR THE ORIGIN OF THE MAMMALIAN BRAIN

##### The Problem of the Origin of the Mammalian Cerebral Hemispheres

Despite the extremely limited information that can be gleaned with any confidence about the anatomy of the brain, the structure of the cranial endocast of this and other nonmammalian cynodonts has important implications for the evolution of the highly characteristic, greatly expanded brain of the mammals. There is a very considerable anomaly apparent in the small size and lack of lateral expansion of the cerebral hemispheres in cynodonts, especially the eucynodonts such as *Chiniquodon*, which are so remarkably mammalian in other features (reviewed by Kemp, 2005). Their jaw musculature is elaborated in such a way as to be capable of producing both the large bite forces and the precision of movement of the mandible necessary for accurately occluding, multi-cusped teeth. Similarly, the limb musculature and skeleton have been radically re-designed to permit the inherently unstable, and therefore highly agile gait associated with parasagittal limb posture and feet placed underneath the body. Both these evolutionary transitions would have required the correlated evolution of more sophisticated neuromuscular activity, both somatosensory and motor. There is also considerable evidence pointing to a significantly elevated metabolic rate in cynodonts, notably the secondary palate and likely presence of a diaphragm, and the very existence of the greater food processing and locomotor abilities (Kemp, 2006). Amongst modern amniotes, the five-to tenfold elevation of the metabolic rates of the two endothermic taxa, mammals and birds, are associated with their very large brains (Kemp, 2006). Yet nonmammalian cynodonts possessed cerebral hemispheres that were certainly no larger than found in the most simple-toothed, sprawling gaited, ectothermic tetrapods found today (e.g., Kappers et al., 1936).

A good deal of attention has been paid over the last few years to the problem of the evolution of the enlarged, six-layered

mammalian neocortex (isocortex) from the telencephalon of their basal tetrapod ancestors, and in particular which parts of the mammalian cerebral hemispheres, if any, are homologous with which parts of the modern sauropsid brain (Ulinski, 1986; Northcutt and Kaas, 1995; Aboitiz et al., 2002; Butler and Molnár, 2002; Molnár and Butler, 2002; Aboitiz et al., 2003; Montagnini and Treves, 2003). All the discussions recognise two basic alternative theories, originally referred to by Northcutt (1981; Northcutt and Kaas, 1995) as the Recapitulation Hypothesis and the Outgroup Hypothesis respectively (Fig. 7).

The Recapitulation Hypothesis proposes that the dorsal ventricular ridge (DVR) of modern reptiles, a column of neural tissue that lies in the floor of the lateral cerebral ventricle, is the homologue of one or more parts of the neocortex of mammals. Therefore the common ancestor of reptiles and mammals possessed a DVR, and the evolution of the mammalian neocortex occurred at least in large part by DVR cells spreading laterally to emerge on the dorsal cortex. There are a number of versions of this view (e.g., Butler, 1994; Karten, 1997), with differences in exactly which parts of the mammalian pallium are supposedly so derived (see Butler and Molnár, 2002 for a brief review). Butler and Molnár (2002) took a novel view to account for the inconsistency of the evidence, arguing that rather than a structural point-to-point set of homologies between the respective parts of the reptilian DVR and the mammalian neocortex, there is a 'field' homology, in the sense that the same developmental field that in reptiles produces the DVR, produces in mammals various parts of the pallium including the lateral neocortex, claustrum-piriform region, and the basolateral part of the amygdala.

The Outgroup Hypothesis in contrast argues that there is no homology between the reptilian DVR and the mammalian neocortex. The differences in the anatomy, development and hodology (neural pathways) between the two structures is so great that they are best regarded as independent elaborations in two respective lineages, from a common ancestor that possessed a much more primitive tetrapod pallium. Again, within this general concept there are differing views focussing on how primitive and amphibian-like this common ancestor was, and how exactly the mammalian neocortex came about (e.g., Northcutt, 1981; Ulinski, 1986; Aboitiz et al., 2002, 2003).

##### An Alternative View of the Origin of the Mammalian Brain

The reconstruction of the cynodont brain presented here on the evidence of the endocranial cavity of *Chiniquodon*, limited and relatively indeterminate as that evidence is, supports the Outgroup Hypothesis, but also suggests a resolution of the anomaly of small cerebral hemispheres coupled with elaboration of the neuromusculature of the mandibular and locomotory apparatuses. First of all, it is unrealistic to reconstruct the non-mammalian cynodont telencephalon as tubular, as virtually all earlier authors have done. Modern reptilian cerebral hemispheres are broader than high in transverse section (e.g., Senn, 1979; Northcutt, 1981), and if this principle were applied to the cynodont endocranial cavity, an allowance made for even quite thin meninges, and the length taken as indicated, then the hemispheres would be extraordinarily long and thin, and utterly unlike those of any other vertebrate brain in shape. A relatively huge thalamus would have been necessary to connect the hemispheres to the rest of the brain stem. But even allowing for a somewhat greater depth of cerebrum as reconstructed here, it is difficult to see how such narrow cerebral hemispheres would have had enough space to accommodate a reptile-like DVR. It seems inescapable that the gross anatomy and therefore probably the basic internal morphology of the cynodont cerebral hemispheres were essentially amphibian and not reptilian-like, in agreement with the Outgroup Hypothesis. The suggested ventral expansion, especially towards the more posterior part, would



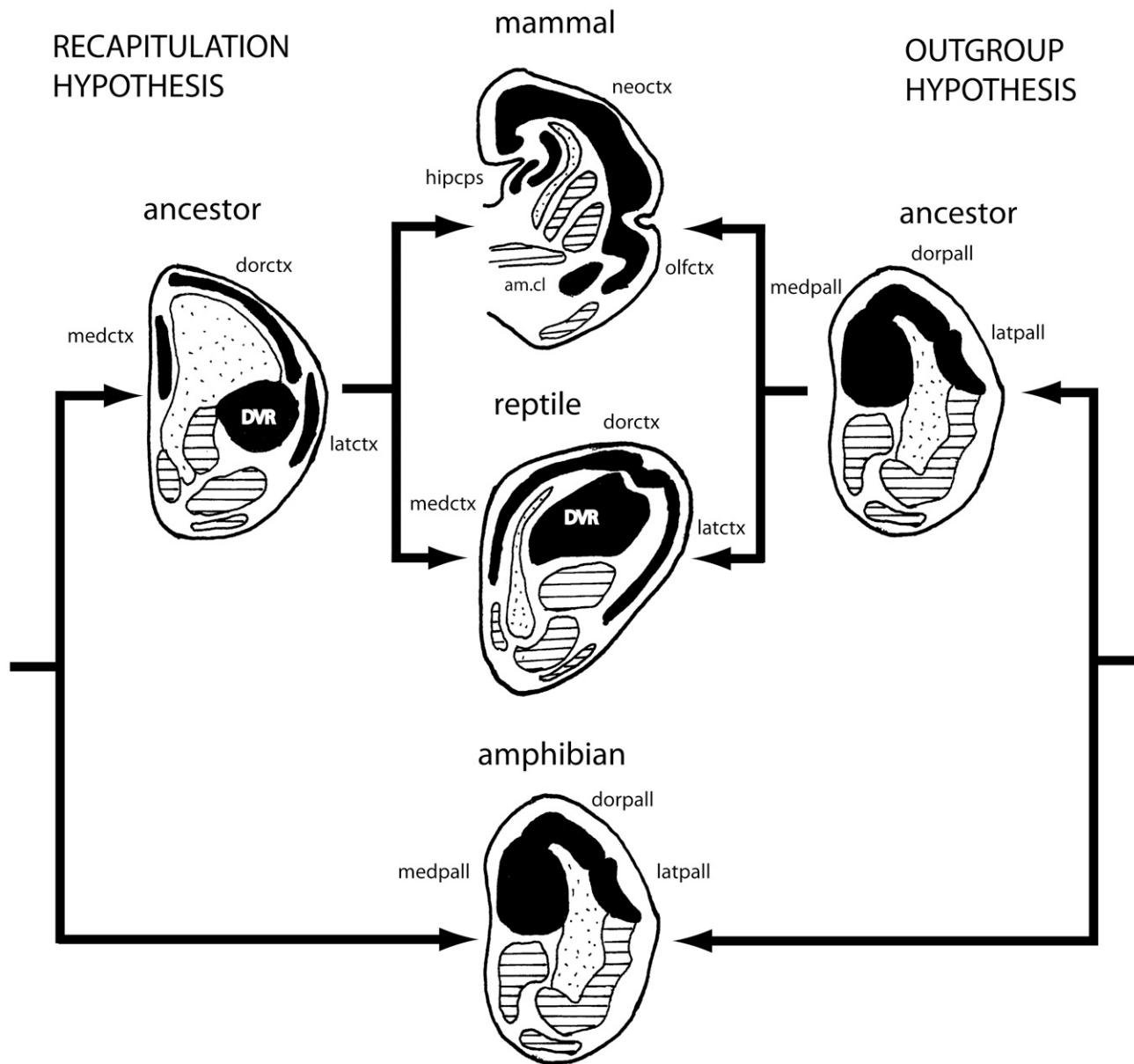


FIGURE 7. The alternative hypotheses, recapitulation and outgroup, of the origin of the mammalian neocortex. See text for explanation. Lateral ventricles are stippled. Derivatives of pallium are black. Derivatives of basal telencephalon and striatus depicted with hatching. Redrawn after Northcutt and Kaas (1995) and Aboitiz et al. (2003).

correspond to what in amniotes generally is the auditory cortex or piriform region of the cortex.

However, the evidence also points to a significantly enlarged cerebellum in the hindbrain region, certainly larger and therefore presumably more complex than that of living reptiles. The width is evidently greater than that of the cerebrum, and there is enough space to have accommodated a considerable antero-dorsal dimension. Indeed, the cerebellum of the modern, similar body-sized mammal *Didelphis virginiana* fits comfortably into the hind part of the endocranial cavity of *Chiniquodon* (personal observation using a latex endocranial cast of *Didelphis*).

The form of the mid-brain region of the brain is obscure, but there is the capacity for an optic tectum/collicular region that is better developed, or at least more dorsally exposed than in mod-

ern mammals. The reconstruction of the brain of the eucynodont *Probainognathus* by Quiroga (1980), as accepted by most subsequent authors (e.g., Ulinski, 1986; Rowe, 1996; Aboitiz et al., 2002; Kielan-Jaworowska et al., 2004) although questioned by Aboitiz et al. (2003) and Gilissen and Smith (2003), shows a slight expansion at the posterior end of the tubular hemispheres on the basis of an impression in the endocranial cast. However, given the comments above on the shape of the hemispheres, it is a great deal more probable that this region was actually occupied by mid-brain structures.

These notes on the likely gross anatomy of the cynodont brain, limited as they must be, suggest that the mammalian brain evolved in two distinct stages. The first is represented by the nonmammalian cynodonts and consisted of enlargement of the

cerebellum and perhaps also the midbrain structures. The cerebral hemispheres remained primitively small, with no elaboration of cortical structures or development of a dorsal ventricular ridge. The second stage is represented by the mammals themselves and consisted of expansion of the telencephalic pallial structures to form the six-layered neocortex. Significantly, these two hypothesized stages coincide with two major shifts in the morphology and inferred biology in the lineage leading to mammals (see Kemp, 2005 for a review of cynodont functional anatomy). The cynodonts are characterised by their complex, occluding posterior teeth and a unique reorganization of the jaw musculature to create a bite that is simultaneously forceful and precise. The locomotory system includes a very mammal-like design, particularly of the hindlimb but also including increased mobility of the mobile shoulder girdle and a wide range of possible forelimb movements. These and other features, such as large amplitude mobility of the head on the atlas-axis complex, all point to a substantial increase in the level of sophistication of the neuromuscular control of the movements. It may be speculated that the neurological basis for this lay in elaboration of the proprioceptive sensory input to, and forward and backward feedback controls within the cerebellum (Mauk et al., 2000), probably with the evolution of new forward projections to the midbrain to be coordinated there with visual input.

The evolution of mammals from a eucynodont ancestral stage was associated with a process of miniaturization: the great majority of Mesozoic mammals were small animals, and the ancestral state is inferred to have been a body mass of perhaps 10g (Kielan-Jaworowska et al., 2004). This great reduction in size had several correlated consequences that must have impacted on the animal's biology. One concerned sound reception. Cynodonts are believed to have used their postdentary bones, quadrate, and stapes by essentially the same pressure transduction mechanism as in modern mammals to detect air-borne sound waves and transmit them to the cochlea. However, because of the high mass and low compliance of the system in cynodonts, Kemp (2007) estimated that the sensitivity was probably limited to relatively low frequencies of around 1-2kHz. With miniaturization of the body as a whole, the mass of the accessory jaw bones decreased, allometrically as well as absolutely, and this allowed the new dentary-squamosal jaw articulation to form. The combination of the reduction in mass of the accessory bones and their freedom from a mechanical function as part of the lower jaw and the jaw hinge immediately rendered the system sensitive to much higher frequency sound. This would have enhanced the effectiveness of hearing for active foraging for insects by a nocturnal animal, and also for effective aural-based social communication such as between parent and offspring. A comparable situation concerning olfaction may also have arisen at this time. The extent, if any, of nasal conchae or turbinates in the nasal cavity covered with olfactory epithelium is unclear. The widely quoted direct evidence for the existence for turbinates in cynodonts (Hillenius, 1994) actually consists only of slight ridges in various parts of the nasal cavity wall, and no sign of ossified structures has yet been reported. Nevertheless, assuming olfactory turbinate bones or cartilages were indeed present, the process of miniaturization and the concomitant general increase in surface area to volume ratio would tend to result in an increase in the relative surface area of such structures, and presumably the potential sensitivity and discriminatory properties of the olfactory system. It has long been remarked that olfaction played a particularly significant role in the evolution of the mammalian brain (e.g., Jerison, 1973), in association with the adoption of nocturnal habits. Comparably with hearing, it would be expected that such enhanced olfactory abilities were associated with social communication too.

Coinciding with these putative shifts in sensory sensitivities, miniaturization also has significant allometric effects on the

gross anatomy of the skull. One is that the size of jaw musculature is expected to scale with surface area rather than with body mass, explicable because muscle force is related to cross sectional area of muscle, and related to the maintenance of approximately constant pressure over the occlusal surface area of the dentition. A second is that, as is very well documented, brain size also tends to scale approximately with body surface area (i.e., mass<sup>0.67</sup>) and not with body mass itself (Jerison, 1973; Harvey and Krebs, 1990), so smaller animals have relatively larger brains (Jerison, 1973; Eisenberg, 1981). Taking these two allometric relationships together implies that a relatively larger space became available for cranial expansion between the epipterygoids as the adductor musculature of the temporal region became relatively smaller, and that this coincided with the need for a relatively larger endocranial cavity. This would surely have been a time of evolutionary reorganization of the brain.

Looking at the overall consequences of the process of miniaturization, uniquely at this moment in the history of the synapsid lineage the anatomical potential for lateral expansion of the brain occurred simultaneously with the potential for greatly enhanced auditory and olfactory sensory input. The brain size was freed from some of the constraints imposed by the mechanical and structural requirements of the skull, and able to evolve rapidly and radically by expansion of the dorsal pallium into the six-layered neocortex, with its characteristic organization into the pattern of projection and association centers familiar in modern mammals. Thus the animals became adapted by higher levels of sensory discrimination, social organization, and learning capacity to a hitherto unexploited mode of life—that of a high energy, continuously active, nocturnal, insectivorous mode of life (Aboitiz et al., 2003).

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