BRAINCASE STRUCTURE IN THE OLDEST KNOWN SKULL OF A THERIAN MAMMAL: IMPLICATIONS FOR MAMMALIAN SYSTEMATICS AND CRANIAL EVOLUTION

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ABSTRACT. Vincelestes neuquenianus, from the Early Cretaceous of Argentina, is the only non-tribosphenic therian mammal in which the side wall of the braincase is known. Because it has both a large alisphenoid and a well-developed anterior lamina (lamina obturans) separated by a distinct interdigitating suture, Vincelestes supports the non-homology of the sheet-like ossifications of the alisphenoid and lamina obturans. Likewise, because it shows the primitive tetrapod relation of the alisphenoid (processus ascendens) to the maxillary branch of the trigeminal nerve (V₂), as also seen in Early Jurassic mammals, it indicates that this is the outgroup condition for modern therians, retained in pouch young of didelphid marsupials. Both the embryonic lamina ascendens of the ala temporalis and the greater part of the adult alisphenoid of modern mammals are homologous with the embryonic processus ascendens and adult epipterygoid of other amniotes. Developmental studies suggest that the anterior position of the maxillary nerve with respect to the ala temporalis, seen in monotremes and a majority of marsupials and eutherians, is due to the phylogenetic anteromedial shift of the nerve with respect to the ala. The more anterior exit of the maxillary nerve is possibly related to the forward expansion of the external adductor jaw musculature, which lies posterolateral to the nerve, and to reduction of the internal adductor jaw musculature, which lies anteromedial to the nerve in sauropsids but ventral to the nerve in mammals. The greatly reduced alisphenoid and enlarged anterior lamina of monotremes and multituberculates is a derived trait which may indicate close relationship.

INTRODUCTION

Ideas on the developmental history and homologies of the ossifications forming the side wall of the mammalian braincase have had a significant impact on hypotheses of relationship among the principal groups of mammals. Differences in the structure of the side wall of the braincase were used by Hopson (1970; also see McKenna, 1975) to support a fundamental dichotomy of the Class Mammalia into the Subclass Theria (marsupials, eutherians, and Mesozoic relatives) and the Subclass Prototheria (monotremes, triconodonts, docodonts, multituberculates). These differences were first described by Watson (1916) in living mammals and later noted in fossil taxa by Kermack (1963, 1967). Whereas the lateral wall of the braincase anterior to the ear region is formed in eutherians and marsupials (fig. 1A, B) by the alisphenoid bone, usually homologized with the epipterygoid of non-mammalian amniotes, it is formed in prototherians (fig. 1C–E) primarily by an “anterior lamina,”

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Fig. 1. Lateral views of the braincase of (A-E) mammals and (F) a non-mammalian cynodont: (A) *Asioryctes nemegtensis*, a Late Cretaceous eutherian (drawn from ZPAL MgM-I/56); (B) *Dudelphis marshalli*, a Recent marsupial; (C) *Ornithorhynchus anatinus*, a Recent monotreme; (D) *Chulsanbataar vulgaris*, a Late Cretaceous multituberculate (drawn from ZPAL MgM-I/168); (E) *Morganucodon oehleri*, an Early Jurassic morganucodontid (drawn from FMNH/CUP 2320); (F) *Pachygenelus monus*, an Early Jurassic tritheledontid cynodont (drawn from SAM K1329 and K1350). Abbreviations: al, anterior lamina; as, alisphenoid; ept, epitypogoid; fr, frontal; lo, lamina obturans; os, orbitosphenoid; par, parietal; pe, periotic; pr, promontorium; pro, prootic; qr, quadrate ramus of epitypogoid; sq, squamosal; V₁, V₂, V₃, foramina for ophthalmic (V₁), maxillary (V₂), and mandibular (V₃) branches of the trigeminal nerve.
an intramembranous ossification continuous with the periotic (= petrosal) bone (Watson, 1916; Kermack, 1963; Hopson, 1964; Hopson and Crompton, 1969; Kermack and Kielan-Jaworowska, 1971). In some "prototherians," such as morganucodontids, the alisphenoid is tall though slender (fig. 1E), whereas in others, such as monotremes and most multituberculates (fig. 1C, D), it is very short and barely contributes to the braincase wall. In non-mammalian cynodonts, including the Tritheledontidae (fig. 1F), the probable sister group of Mammalia (Hopson and Barghusen, 1986), a distinct anterior lamina is not present, and the side wall of the braincase is formed in nearly equal parts by the alisphenoid and the prootic, the latter bone homologous with the anterior part of the mammalian periotic.

This view of a therian-prototherian dichotomy was challenged by a reinterpretation of braincase development in living mammals by Presley and Steel (1976) and Presley (1980, 1981), who argued that because both the anterior lamina of monotremes and most of the alisphenoid of therians form within the sphenoo-obturator membrane of the braincase wall they may be homologous ossifications; therefore, the distinctions between the braincases of therians and non-therians are trivial, a matter of whether in late developmental stages the anterior lamina fuses to the embryonic alisphenoid or to the otic capsule. Patterson (1980), Kemp (1982, 1983), and Miao (1988), among others, have accepted the arguments of Presley and Steel (1976) and Presley (1981) and consequently doubt the reality of a monophyletic group of non-therian mammals, called Prototheria by Hopson (1970) and Atheria by Kermack, Mussett, and Rigney (1973).

The theory of Presley and Steel (1976) and Presley (1981) on the developmental history and homologies of the ossifications forming the side wall of the mammalian braincase also contributes to a long-standing controversy over whether or not the alisphenoid of mammals is homologous, either wholly or in part, with the epiphragmoid of other amniotes. Part of this argument concerns whether the very small embryonic alisphenoid of monotremes represents the plesiomorphic condition for mammals, as recently advocated by Kuhn and Zeller (1987), or whether, as argued by Maier (1987, 1989), a tall ascending portion of the embryonic alisphenoid, as occurs in marsupials, is primitive, with the reduced condition of monotremes being secondary.

Cranial structure in Mesozoic therians would be expected to provide evidence for testing the conflicting views on the primitive state of the braincase in therian mammals; however, until recently, braincases of therians older than Late Cretaceous marsupials and eutherians (Kielan-Jaworowska, 1981) have not been known. Thus, the idea that Jurassic and Early Cretaceous therians lacked an anterior lamina was based on the assumption that the condition in modern therians was derived directly from a Triassic cynodont condition in which the alisphenoid is comparable in anteroposterior length and a distinct anterior lamina is lacking (fig. 1F).
Recently discovered skulls of the Early Cretaceous therian *Vincelestes neuquenianus* (Bonaparte, 1986; Bonaparte and Rougier, 1987) provide the first evidence of braincase structure in a therian mammal of pre-tribosphenic dental grade. A preliminary description of the skull and dentition was given by Bonaparte and Rougier (1987; see fig. 2A). The molars of *Vincelestes* have the characteristic “reversed triangles” pattern of therian mammals but differ from molars of tribosphenic therians in having a very small talonid without a true basin and in possessing a very small, low protocone (Bonaparte and Rougier, 1987; Rougier, unpublished observations). They are perhaps slightly more advanced toward those of tribosphenic therians than are the molars of the Late Jurassic *Peramus tenuirostris* (Bonaparte and Rougier, 1987; Butler, 1990). Therefore, *Vincelestes* may be the sister taxon of the Tribosphenida of McKenna (1975).

*Vincelestes* provides evidence relating to the evolutionary history of the mammalian cranial wall and the questions of the homology of the mammalian alisphenoid with the “reptilian” epityparygoid and the possible contribution of the anterior lamina to the therian alisphenoid. It also demonstrates, contrary to the views of Patterson (1980), Presley (1981), Kemp (1982, 1983), and Miao (1988), that the structure of the cranial wall does distinguish monotremes and multituberculates from all other mammals in which the braincase is adequately known.

The structure of the braincase of *Vincelestes* has been briefly discussed in abstracts by Rougier and Bonaparte (1988) and Hopson, Bonaparte, and Rougier (1989), and in papers by Wible and Hopson (1993) and Rougier, Wible, and Hopson (1992). However, its implications for the evolution of the braincase wall have not been explored in detail elsewhere.

**Material**

The known material of *Vincelestes neuquenianus* consists of at least nine individuals represented by six complete skulls, 17 lower jaws, and numerous disarticulated postcranial elements. All specimens are in the Neuquén Collection in the Museo Argentino de Ciencias Naturales “Bernardino Rivadaviá,” Buenos Aires. The following description of the braincase is based primarily on specimen MACN-N 05, but all the available skulls have been used to check our interpretations. The figure (fig. 2B) represents a composite of information preserved on both sides of specimen MACN-N 05.

All the specimens of *Vincelestes* come from the type locality of the continental La Amarga Formation of southern Neuquén Province, Argentina (Bonaparte, 1986; Bonaparte and Rougier, 1987; Musacchio, 1971b; Leanza and Leanza, 1979; Volkheimer, Caccuri de Felice, and Sepulveda, 1977). The fossils were recovered from a single pocket in the basal unit of the La Amarga Formation, the Pichi Picún Leufú Member, which is composed principally of psammitic levels with some conglomeratic lenses and a few intercalated limonitic layers.
Fig. 2. *Vincelestes neuquenianus* Bonaparte (1986): (A) lateral view of skull and lower jaw (redrawn from Bonaparte and Rougier, 1987). (B) lateral view of the braincase, based on specimen MACN-N 05, Museo Argentino de Ciencias Naturales “B. Rivadavia”, Buenos Aires. The foramina for the maxillary (V₂) and mandibular (V₃) branches of the trigeminal nerve lie within the anterior lamina (lamina obturans). Abbreviations: al, anterior lamina; as, alisphenoid; fen ov, fenestra ovalis; fr, frontal; lat fl, lateral flange; os, orbitosphenoid; pal, palatine; par, parietal; pr, promontorium; sq, squamosal; V₁, V₂, V₃, foramina for ophthalmic (V₁), maxillary (V₂), and mandibular (V₃) branches of the trigeminal nerve.
The La Amarga Formation has been dated as being from the Late Neocomian Epoch (Early Cretaceous) by all recent workers. Studies on charophytes (Musacchio, 1971a) and ostracods (Musacchio, 1971b) support a Late Neocomian age. According to Volkheimer, Caccuravi de Felice, and Sepulveda (1977, p. 77), on the basis of palinological evidence from the Ortiz Member overlying the Pichi Picú Leufú Member (both then considered to be formations of the La Amarga Group), the Ortiz [Member] at the La Amarga locality forms a microfloristic unity with the upper part of the Agrio Formation, the latter a marine unit transitionally overlain by the La Amarga Formation. This microflora belongs to the *Cyclusphaera psilata-Classopolis* association established in the Hauterivian-Barremian beds of the Neuquén Basin (Volkheimer and Sepulveda, 1976). Simeoni and Musacchio (1986) studied ostracods from the Agrio Formation (Leanza and Leanza, 1979), their material coming from comparable levels to the palinological samples showing that the Agrio and La Amarga formations form a single microfloristic unit. These ostracods “can best be compared with those more modern ones of the La Amarga Formation” (Simeoni and Musacchio, 1986; translation from Spanish), and are interpreted as being from the early part of the Hauterivian Stage. Thus, keeping in mind all these arguments, it is probable that *Vincelestes* comes from sediments of Late Hauterivian age. However, the palinological evidence suggests that an Early Barremian age cannot be dismissed.

The following institutional abbreviations are used: FMNH/CUP, Catholic University of Peking collection housed in the Field Museum of Natural History, Chicago; MACN-N, Neuquén collection in Museo Argentino de Ciencias Naturales “Bernardino Rivadavia,” Buenos Aires; SAM, South African Museum, Cape Town; ZPAL; Institute of Paleontology, Polish Academy of Sciences, Warsaw.

**DESCRIPTION**

The braincase of *Vincelestes* (fig. 2B) possesses both a large alisphenoid and a prominent anterior lamina separated from one another by a distinct, interdigitating suture. The anterior lamina is continuous posteroventrally with that portion of the periopic which surrounds the inner ear. It has sutural contacts with the parietal dorsally and with the narrow cranial process of the squamosal posteriorly. The ventral border of the anterior lamina forms a prominent ridge, the “lateral flange,” which passes posterolaterally to meet the squamosal medial to the glenoid fossa. The lateral flange forms the outer wall of the “lateral trough,” a longitudinal depression lying between the lateral flange and the large promontorium housing the cochlea. The horizontal sheet of bone that forms the roof of the lateral trough and the floor of the the cavum epipetricum is a composite structure, as indicated by a longitudinal suture near the center of the trough. The outer portion of this sheet of bone is interpreted as being formed by the intramembranous ossification which also forms the anterior lamina, and its medial portion is considered to be formed by
appositional bone from the periotic (Wible and Hopson, 1993; Rougier, Wible, and Hopson, 1992).

The anterior lamina is pierced by the foramina for the mandibular (V₃) and maxillary (V₂) branches of the trigeminal nerve. The foramen for V₃ is the larger of the two and lies a short distance anteromedial to the squamosal glenoid, immediately above the lateral flange. The foramen for V₂ lies slightly higher on the braincase wall, immediately behind the suture with the alisphenoid. The exit for the maxillary branch of the trigeminal nerve forms a short anterolaterally-directed canal, the anteromedial surface of which extends forward on to the alisphenoid. More posteriorly, behind the suture, the anterior lamina may be seen to surround completely the nerve foramen.

On the posterodorsal portion of the anterior lamina, adjacent to the suture with the squamosal, are three smaller foramina, of which only the most posterodorsal is visible in figure 2B. These are interpreted as openings for temporal rami of the ramus superior of the stapedial artery (Rougier, Wible, and Hopson, 1992).

The alisphenoid has a long dorsal contact with the parietal and a short anterodorsal contact with the frontal. It overlaps the orbitosphenoid anterodorsally and the palate and pterygoid anteroventrally. Posteriorly, it is overlapped by the anterior lamina. On the left side of skull MACN-N 05 a rather large area of the anterior lamina above the foramen for the maxillary ramus (V₂) is missing, exposing a facet on the surface of the alisphenoid. Ventromedially, the alisphenoid is fused with the basisphenoid. Its anterior border is emarginated for the sphenobital fissure, through which the ophthalmic branch of the trigeminal nerve (V₁), as well as cranial nerves II, III, IV, and VI, left the cranial cavity. It has a short quadrate ramus which contacts the lateral flange of the anterior lamina and forms the anterolateral border of the lateral trough. A shallow groove extends forward from the foramen for the maxillary branch of the trigeminal nerve, fading out near the middle of the bone. A short distance below the foramen of the maxillary nerve is a small anterolaterally-directed foramen interpreted as a probable vascular foramen by Rougier, Wible, and Hopson (1992). Anterodorsal to this foramen is a prominent posterolaterally-directed process which may have served as an attachment area for pterygoideus musculature (see p. 291).

DISCUSSION

The manner in which the bony lateral wall of the orbitotemporal region—the area between the orbit and the otic capsule—is formed in mammals, and how the structure of this wall relates to that of living sauropsids (“reptiles” and birds), has been an enduring problem among comparative anatomists and embryologists in this century. Beginning with the developmental studies of Gaupp (1900, 1902) and including recent studies by Kuhn and Zeller (1987), Zeller (1989a, b), and Maier (1987, 1989), the question of whether the mammalian alisphenoid is homologous with the epityergoid of sauropsids has yet to receive a
definitive answer. We believe the structure of the braincase wall in *Vincelestes* provides evidence in support of this homology and that the contradictory developmental evidence can be reconciled with this conclusion.

In those sauropsids believed to retain the primitive condition of the orbitotemporal region, for example, *Sphenodon* and many lizards (Romer, 1956), the primary (endocranial) side wall of the embryonic braincase is formed by a system of cartilaginous bars separating several openings or fenestrae closed by connective tissue membranes (see fig. 5A). Lateral to this primary wall is a secondary wall formed by a slender upstanding rod of cartilage, the ascending process (processus ascendens) of the epipterygoid, and a heavy membrane in front of and behind the ascending process, the sphenoo-pturator membrane (see fig. 5B). The epipterygoid of tetrapods is homologous with the middle portion of the palatoquadrate cartilage of fishes; thus, it is derived from the first branchial arch of basal vertebrates and is not part of the braincase proper. It is joined ventrally to a basipterygoid process extending laterally from the basal plate of the braincase. The narrow, elongate space between the primary and secondary walls of the orbitotemporal region is the cavum epipetricum. This extracranial space contains the ganglia of the trigeminal and facial nerves and through it pass the branches of the trigeminal nerve before they enter the temporal fossa (see fig. 5B). In mammals, some or all of the bars of the embryonic braincase are absent (see Goodrich, 1930), and the primary lateral wall is formed principally by the dural membrane surrounding the brain. The secondary wall in mammals is completely ossified, usually as the alisphenoid, so that the cavum epipetricum now lies entirely within the bony braincase. This wall is formed by endochondral ossification of a cartilaginous process, the ala temporalis, and by desmal (appositional) ossification within the sphenoo-pturator membrane. The ala temporalis of mammals, which forms an ascending lamina and is joined to the basipterygoid or alar process of the basicranium, is comparable to the epipterygoid of sauropsids. Whether or not the two are homologous, either wholly or in part, remains controversial.

Watson (1916) was the first to note that in monotremes the bony side wall of the braincase is formed in a strikingly different way from that of therians. In the latter, the region anterior to the ear is enclosed by the alisphenoid (fig. 1A, B), which Watson considered to be partly homologous with the epipterygoid of non-mammalian amniotes. In monotremes the adult alisphenoid is greatly reduced in size, and the greater part of the braincase wall, at least in the platypus *Ornithorhynchus*, is formed by an anterior extension into the sphenoo-pturator membrane of an ossification which, in the developmental stages studied by Watson, is continuous posteriorly with the otic capsule (fig. 1C). This intramembranous ossification was called the "anterior process of the periotic" by Watson, the "anterior lamina of the periotic" by Hopson (1964), and the "lamina obturans" by Vandevoeck (1964, p. 156).
In the echidna *Tachyglossus*, the pattern of ossification of the secondary side wall is more complex than in *Ornithorhynchus*, including, in addition to a small contribution from the alisphenoid, intramembranous contributions from surrounding elements, for example, the palatine, "ectopterygoid" (= "echidna pterygoid"), squamosal, and periotic, which invade the sphenoid-obturator membrane, and, late in ontogeny, from the lamina obturans (Kuhn and Zeller, 1987). The ossification of the lamina obturans begins in several isolated centers, variable in number and location within the sphenoid-obturator membrane, which fuse to surrounding elements relatively late in life (MacIntyre, 1967; Kuhn, 1971, Griffiths, 1978). Hopson (1970), Kuhn and Zeller (1987), and Zeller (1989a) consider the echidna condition to be a secondary specialization within monotremes, with the condition in the platypus more closely resembling the condition in the ancestral monotreme.

Kermack and Mussett (1958) described an anterior lamina of the periotic in the Early Jurassic mammal *Morganucodon* (fig. 1E) and suggested a relationship of morganucodontids, then considered to be docodonts, with monotremes. Kermack (1963) later described an anterior lamina in the Late Jurassic triconodontid *Trioracodon* and suggested its presence in multituberculates. This was subsequently verified by Hopson and Crompton (1969, p. 45) in isolated multituberculate periotics from the Late Cretaceous of North America and by Kielen-Jaworowska (1970) in multituberculate skulls from the Late Cretaceous of Mongolia (fig. 1D). Hopson (1964), Kermack (1967), Hopson and Crompton (1969), and Kermack and Kielen-Jaworowska (1971) considered the presence of an anterior lamina in non-therian mammals (that is, mammals lacking the characteristic reversed-triangles molar pattern of therians) as evidence of relationship. Hopson (1970) formalized this concept by grouping the non-therian mammals, that is, monotremes, triconodonts (including morganucodontids), docodontids, and multituberculates, in the Subclass Prototheria on the basis of the presence of an anterior lamina of the periotic (then inferred for docodontids, but recently described in the docodontid *Haldanodon* by Lillegraven and Krusat, 1991). Kermack, Mussett, and Rigney (1973) allied the same taxa as the mammalian Subclass Atheria.

Objections to a dichotomy of mammals based on braincase structure were raised by Presley and Steel (1976) and Presley (1980, 1981), whose
Figure 3

A

B

Braincase of non-tribosphenic therian mammal
developmental studies led them to conclude that no fundamental distinction exists between the structure of the braincase wall in monotremes and modern therians. Presley (1981) demonstrated that in the platypus *Ornithorhynchus*, the lamina obturans (anterior lamina) ossifies within the sphenoid-obturator membrane entirely separate from the otic capsule (see 1 and 2 in fig. 3A) and only later in development becomes synostosed to it (3 in fig. 3A; see also Zeller, 1989a, b). Thus, it is not an outgrowth of the periptychial as believed by Watson (1916) and many later workers (Kermack, 1967; Hopson and Crompton, 1969; Kermack and Kielen-Jaworowska, 1971; Kielen-Jaworowska, 1981) but an independent ossification in the sphenoid-obturator membrane, not unlike that of the echidna. Because the greater part of the therian alisphenoid also forms as an intramembranous ossification in the sphenoid-obturator membrane, Presley extended use of the term “lamina obturans” to include “the very similar field of membrane bone here in therians” (Presley, 1981). He considered there to be “no fundamental difference between therians and monotremes in the early development of this bone. Differences arise only when it fuses with its neighbours” (Presley, 1981). He further pointed out that “If Mesozoic, like Recent, mammals formed membrane bone in the area of the lamina obturans, it follows that any form in the fossil record with an expanded epitypogoidal, an anterior process of the petrosal [=periptychial], or both, could, by a simple change in the affinity of synostosis during development (Presley and Steel, 1976), come to possess therian anatomy” (Presley, 1981). In this, he has been followed by Patterson (1980), Kemp (1982, 1983, 1988), and Miao (1988). Figure 4, modified from diagrams of Presley and Steel (1976) and Kemp (1982, 1983), illustrates the hypothesis that the lamina obturans forms the greater part of the braincase wall in both monotremes (B) and therians (C).

Presley and Steel (1976) and Presley (1981) have also cast doubt on the homology of the cartilaginous ascending process of the “reptilian” epitypogoidal with the usually much smaller ascending lamina of the mammalian ala temporalis or embryonic alisphenoid. The idea that the ascending process of non-mammalian amniotes and the ascending lamina of mammals are not homologous, the latter being a neomorph, was first put forward by Gaupp (1900, 1902) and has subsequently been supported by Watson (1916), DeBeer (1926, 1937), Kuhn (1971), and Kuhn and Zeller (1987), as well as by Presley and Steel (1976) and Presley (1980, 1981). The principal argument for lack of homology is their different relations to the maxillary ramus of the trigeminal nerve (V2). In non-mammalian amniotes, including non-mammalian cynodonts (see figs. 1F, 5A, B), this nerve leaves the skull in company with the mandibular branch of the trigeminal nerve (V3) behind the epitypogoidal (Romer, 1956), therefore, behind the ascending process. In some living mammals, notably didelphid marsupials (Maier, 1987), the maxillary nerve also leaves the skull behind the ala temporalis (fig. 5C). However, in a majority of mammals (all monotremes and many marsupials and eutherians; Maier, 1987), the nerve passes from the skull with, or close to, the ophthalmic branch of the trigeminal (V1) in front of the dorsally-directed
Fig. 4. Diagrammatic representation of the homologies of the embryonic components of the lateral wall of the mammalian braincase put forward by Presley and Steel (1976), Presley (1981), and Kemp (1982, 1983): (A) the primitive condition in mammals, both therian and non-therian, in which the lamina obturans (= anterior lamina) is fused to the periotic (otic capsule) and is pierced by V₂ and V₃, the epipterygoid and its embryonic precursor, the processus ascendens, resemble those of non-mammalian amniotes, and the squamosal has a small cranial process contacting the otic capsule and anterior lamina; (B, C) the modern mammalian condition in which the dorsal process of the adult epipterygoid has been lost and only the quadrat ramus remains; (B) the monotreme condition in which the lamina obturans forms the greater part of the braincase wall, the processus ascendens has been lost, and the alisphenoid is formed by a small neomorphic lamina ascendens which has grown up between V₂ and V₃ from the remnant of the quadrat ramus of the epipterygoid; (C) the modern therian condition in which a processus ascendens anterior to V₂ is present in some marsupials but is replaced in other therians by a neomorphic lamina ascendens between V₂ and V₃; these remnants of the epipterygoid fuse with the lamina obturans to form the large alisphenoid; the cranial process of the squamosal of modern therians expands anteriorly to form part of the side wall between the lamina obturans and the periotic. Dotted lines indicate the embryonic processus ascendens. Broken lines indicate fusion of separate embryonic ossifications. In C, the processus ascendens is fused to the lamina obturans. Modified from Presley and Steel (1976) and Kemp (1982, 1983). Abbreviations: as, alisphenoid; ept, epipterygoid; lam asc, lamina ascendens; lam obt, lamina obturans; per, periotic; pr asc, processus ascendens; qr, quadrat ramus of epipterygoid; sq, squamosal; V₁, V₂, V₃, ophthalmic, maxillary, and mandibular rami of trigeminal nerve.

process of the embryonic ala temporalis (fig. SE). An intermediate condition exists in some marsupials and eutherians in which the maxillary nerve passes through a foramen in the ala temporalis (DeBeer, 1937; Maier, 1987).
Fig. 5. Semi-diagrammatic representations of the developing braincase of (A, B) a sauropod embryo and (C, D, E) three pouch young marsupial mammals, showing the varying relations of the maxillary ramus (V2) of the trigeminal nerve to the ascending process (= ala temporalis) of the epipterygoid (= alisphenoid): (A) lateral view of the embryonic braincase in a sauropod, based on Lacerta, showing the primitive amniote relations of the branches of the trigeminal nerve to the ascending process; (B) the same in dorsal view, showing the position of the sphenobasilar membrane and the relations of the three embryonic masses of mandibular adductor musculature to the branches of the trigeminal nerve; (C) a didelphid in which the V2 lies posterior to the ala temporalis, as in non-mammalian amniotes; (D) the dasyurid Smilanthopsis in which V2 passes through a foramen in the ala temporalis; a similar condition occurs in some eutherians; (E), a macropodid in which V2 lies entirely medial to the ala temporalis, as also occurs in a majority of eutherians. A, C–E adapted from Maier (1989); B adapted from Heaton (1980). Abbreviations: ala temp, ala temporalis; cav ep, cavum epiphrericum; fen ov, fenestra ovalis; gg, gasserian ganglion of trigeminal nerve; MAMI, MAME, MAMP, internus, externus, and posterior masses of the adductor mandibulae musculature; ot cap, otic capsule; pant, pila antotica; pr asc, processus ascendens; s-o mem, sphenobasilar membrane; V1, V2, V3, ophthalmic, maxillary, and mandibular branches of the trigeminal nerve.

Presley (1981) describes a processus ascendens, between V1 and V2, in the marsupial Didelphis and a lamina ascendens, between V2 and V3, in the monotremes Ornithorhynchus and Tachyglossus and in the eutherian Erinaceus. As noted above, he considers these two types of dorsally-directed process of the mammalian ala temporalis to be non-homologous, distinguishing between them as follows (see fig. 4): “I use 'processus' ascendens' for the part of the ala between ophthalmic and maxillary
nerves; ‘lamina ascendens’ for the part of the ala between maxillary and mandibular nerves” (Presley, 1981; see also Goodrich, 1930, p. 271).

In contrast, as discussed below, a number of other workers (see reviews by Maier, 1987; and Miao, 1988) have accepted the homology of the dorsally-directed process of the mammalian alisphenoid with that of the sauropsid epipterygoid.

_Vincelestes_ demonstrates that the side wall of the braincase in early therians was basically like that of early non-therian mammals such as _Morganucodon_ (fig. 1E; Kermack, Mussett, and Rigney, 1981) and _Sinocodon_ (Crompton and Sun, 1985; Crompton and Luo, 1992). Therefore, contrary to the views of Kermack and co-workers (Kermack, 1967; Kermack and Kielan-Jaworowska, 1971; Kermack, Mussett, and Rigney, 1973, 1981) and Hopson and Crompton (1969), the presence of a well-developed anterior lamina pierced by V₂ and V₃ was a primitive feature of all mammals and does not characterize a prototherian or atherian clade. The fossil evidence suggests that from this primitive mammalian condition were derived the specialized conditions of: (1) marsupials and eutherians in which the alisphenoid has completely replaced the anterior lamina in the braincase wall; and (2) monotremes and multituberculates, and perhaps triconodontids, in which the anterior lamina has almost completely replaced the alisphenoid, now greatly reduced in size, in the braincase wall. Clearly, a separation of all mammals into two monophyletic groups based on the structure of the side wall of the braincase is no longer tenable, but, contrary to the views of Presley (1981), Patterson (1980), Kemp (1982, 1983, 1988), and Miao (1988), it may still be possible to draw some phylogenetic implications from the structural variation seen in the lateral wall of the mammalian braincase.

The structure of the side wall of the braincase in _Vincelestes_, taken in conjunction with recent studies of the development of the temporal region in living mammals (Maier, 1987, 1989; Zeller, 1989a, 1989b), calls into question the view advanced by Presley and Steel (1976) and Presley (1980, 1981) that the ossification formed in the sphenoid-obliterator membrane (that is, the lamina obturans) is the homologous element in both therians, where it contributes to the expanded alisphenoid, and non-therians, where it contributes to the anterior lamina. In addition, the paleontological and developmental evidence casts doubt on the view of Presley and other workers (Gaupp, 1900, 1902; Watson, 1916; Kuhn, 1971; Kuhn and Zeller, 1987) that the ascending process of the sauropsid epipterygoid is not homologous with the ascending lamina of the mammalian alisphenoid.

In the following sections, we consider the developmental and paleontological evidence relating to the following questions:

1. Is the intramembranous ossification of the alisphenoid of modern therians homologous with the lamina obturans of monotremes, or are they distinct, non-homologous ossifications?

2. Is the processus ascendens of the epipterygoid of non-mammalian amniotes homologous with the lamina ascendens of the mammalian alisphenoid, or are they distinct, non-homologous structures?
3. Does the structure of the secondary side wall of the braincase provide evidence on the interrelationships of the major groups of mammals?

Homologies of the Ossifications in the Spheno-Obturator Membrane

Maier (1987) has clearly demonstrated that during early postnatal development the ala temporalis in the pouch young of the didelphid marsupial Monodelphis domestica resembles the reptilian epitympanic in having a tall ascending process lying in front of and medial to the maxillary ramus of the trigeminal nerve \((V_2)\). A similar condition was described by Fuchs (1915) and Presley (1981) in Didelphis. Maier also describes a fibrous layer between the ala temporalis and the stout alar process of the basicranial axis, suggesting that this corresponds to “the ancient basipterygoid joint of lower vertebrates” between the epitympanic and basipterygoid process (Maier, 1987, p. 77). As described by Maier, the alisphenoid begins to ossify at the level of the cartilaginous ascending process, the anterior, upper, and posterior borders of which become covered by perichondral bone lamellae. This ossification spreads into the sphenoid-obturatos membrane as appositional bone and surrounds the maxillary nerve to enclose it in a foramen rotundum (1 in fig. 3B). The ossification continues to expand dorsally (2 in fig. 3B), and then extends posteriorly as an “epitympanic process” which contacts the otic capsule and fills most of the space in the braincase wall occupied by the sphenoid-obturator membrane (3 in fig. 3B). Between the ventromedial part of the epitympanic process and the otic capsule is an elongate fissure, the proximal end of which is widened as an “incisura ovalis” for the mandibular branch of the trigeminal nerve \((V_3)\). The gap between the posterodorsal part of the alisphenoid and the parietal becomes closed by the squamosal, which spreads forward into the sphenoid-obturator membrane.

Clark and Smith (1989) describe a similar ossification pattern for the developing alisphenoid in both Monodelphis and the kangaroo Macropus, which suggests that it is the general pattern for marsupials. In addition, Presley (1981) states that in all recent therians ossification appears in the sphenoid-obturator membrane “close to the ala and extends back to suture with the squamosal and tegmen tympani.” This characteristic therian ossification pattern of the alisphenoid may be compared with the ossification pattern described above for the lamina obturans (anterior lamina) of the monotreme Ornithorhynchus. In therians, as exemplified by Monodelphis (fig. 3B), the intramembranous portion of the alisphenoid ossification is initiated adjacent to the ala temporalis and only at a fairly late ontogenetic stage expands posteriorly to contact the otic capsule. In contrast, the lamina obturans of Ornithorhynchus begins to ossify in the dorsal part of the sphenoid-obturator membrane, quite distant from the ala temporalis, and only late in ontogeny does it expand anteroventrally to contact the small alisphenoid (fig. 3A). Thus, even though both elements form in the sphenoid-obturator membrane, the developmental evidence
indicates that they are distinct, therefore non-homologous, ossifications. Were the adult alisphenoid to be a composite ossification, including both appositional bone formed in association with the ala temporalis and membrane bone homologous with the lamina obturans, one would expect to see in the early development of modern therians both centers of ossification, widely separated from one another, in the sphenoid obturator membrane. Therian mammals show no intramembranous ossification that is clearly identifiable with the initial stages of ossification of the lamina obturans in Ornithorhynchus (Kuhn and Zeller, 1987, p. 66).

Although the lamina obturans in the echidna Tachyglossus ossifies adjacent to the alisphenoid, it forms very late in ontogeny and even in adult specimens may not fuse with adjacent bones (Kuhn and Zeller, 1987). This pattern is believed by Kuhn and Zeller (1987, p. 66) to be a secondary specialization within Monotremata, the cranial displacement of the lamina being due to the incorporation of the squamosal, "ectopterygoid," and "processus anterior perioticci" into the caudal wall of the cavum epipetricum. The slender squamosal and relatively open middle ear of Ornithorhynchus more closely resemble these regions of the skull in early mammals (for example, Morganucodon) than do the greatly expanded squamosal and more enclosed middle ear of Tachyglossus (Wible and Hopson, 1993). Likewise, the lamina obturans of the platypus and the presumably homologous anterior lamina of early mammals are characterized by ossification and fusion to the periotic early in ontogeny, whereas the pattern of late ossification and fusion to surrounding bones appears to be unique to the echidna. Therefore, we agree with Kuhn and Zeller that the condition of the lamina obturans in Ornithorhynchus is more plesiomorphic than is that of Tachyglossus.

The paleontological evidence also supports the non-homology of the alisphenoid and anterior lamina (presumably homologous with the monotreme lamina obturans) inasmuch as in all fossil taxa with an anterior lamina that are known from complete, well-preserved skulls (for example, Sinoconodon, Morganucodon, various Mongolian multituberculates, Lambdopsalis, and Vincelestes), a distinct suture separates the two bones (see figs. 1D,E, 2B). Vincelestes, as the putative outgroup to modern therians (Rougier, 1990; Wible, 1990; Wible and Hopson, 1993), is especially important in casting doubt on the supposed homology of the lamina obturans with the intramembranous portion of the alisphenoid.

In non-mammalian cynodons (fig. 1F) and in mammals other than modern therians (fig. 1C–E), the cranial moieties of the squamosal is narrow anteroposteriorly, being restricted to the region of the otic capsule, and does not contribute to the cranial wall. In these taxa the anterior lamina forms the secondary lateral wall of the braincase between the alisphenoid and the narrow cranial process of the squamosal. This primitive mammalian condition also pertains in Vincelestes (fig. 2B). In eutherians and marsupials (fig. 1A, B), the cranial moieties of the squamosal has a large anterior portion which contributes broadly to the secondary cranial wall (Wible, 1991, p. 7; Maier, 1987), and an anterior lamina is
absent. Presley and Steel (1976), Presley (1981), and Kemp (1982, 1983) have argued that all that remains of the primitive cynodont epiphyseal in living mammals is the ventral part of the ala temporalis (which they consider to be homologous with the quadrato ramus of the primitive epiphyseal) and that the greater part of the modern therian alisphenoid, which ossifies intramembranously, is derived from the anterior lamina (lamina obturans) of an early mammal such as Morganucodon (fig. 4). Kemp speculates that “the expansion of the cranial process of the squamosal in modern therians affected the later developmental stages of the braincase, prevented the anterior lamina from fusing any longer with the periotic, and thus caused it to fuse with the alisphenoid instead” (Kemp, 1983, p. 374).

The evidence of *Vincelestes*, in which the ascending portion of the alisphenoid hardly differs from that of modern therians either in degree of anteroposterior expansion or in position relative to the otic capsule (compare fig. 2B with fig. 1A,B), argues against equating the intramembranous portion of the alisphenoid with the anterior lamina. If the anterior lamina has become indistinguishably fused with any adjacent membrane bone in modern therians, the topographic evidence of figure 1A and B would suggest that it represents the anterior moiety (cranial process) of the squamosal. Although developmental evidence certainly does not support this homology (see Maier, 1987), neither does it support the homology for which Presley and Kemp argue.

Furthermore, Miao (1988, p. 60) has pointed out that “Presley’s hypothesis would be seriously challenged if it were shown that . . . a mammal (fossil or living) with an extensive anterior lamina in front of the petrosal has the lamina laterally overlapped by the alisphenoid, or contrariwise.” As noted above, the anterior lamina of *Vincelestes* overlaps the posterior margin of the alisphenoid, thus providing further support for our view that these elements are developmentally-independent ossifications.

The argument of Presley and Steel (1976) and Presley (1981) for the homology of the mammalian alisphenoid with the cynodont anterior lamina, rather than with the expanded ascending portion of the cynodont epiphyseal, is based on the similar relations of the alisphenoid and anterior lamina to branches of the trigeminal nerve. If the modern therian alisphenoid is homologous with the primitive cynodont epiphyseal, as argued above, then the differences in their relations to the maxillary ramus of the trigeminal nerve must be explained. This is done in the following section.

**Homology of “Reptilian” Epiphyseal and Mammalian Alisphenoid**

The view that the “alisphenoid cartilage” (that is, ala temporalis) of embryonic mammals corresponds to the epiphyseal of therapsids and other “reptiles” was first proposed by Broom (1909). Fuchs’s (1915) demonstration that in *Didelphis* embryos the ala temporalis lies in front of the second branch of the trigeminal nerve, as it does in non-mammalian
amniotes, supported Broom’s interpretation. Goodrich (1930) agreed that the lamina ascendens of mammals “in all probability corresponds to the processus ascendens of lower Tetrapods” (Goodrich, 1930, p. 436–437) and suggested that “the mammalian processus ascendens spread backward so as to pass on both sides of the maxillary nerve, and that then the anterior limb disappeared while the posterior persisted” (Goodrich, 1930, p. 271). DeBeer (1937, p. 421), too, suggested that the processus ascendens gave rise to the “typical mammalian ala temporalis” by lapping back around the maxillary nerve.

As noted above, many workers have argued that the mammalian ala temporalis is not homologous with the reptilian processus ascendens, primarily on the basis of their differing relations to the maxillary branch of the trigeminal nerve. Gaupp (1900, 1902), Watson (1916), Kuhn (1971), Presley and Steel (1976), and Kuhn and Zeller (1987) believed that the lamina ascendens is an independent upgrowth from the base of the ala temporalis, quite distinct from the “reptilian” ascending process of the epitypogoid.

DeBeer (1926, p. 334) accepted Broom’s theory that “the mammalian ala temporalis and alisphenoid was evolved from the ascending process and epitypogoid of [therapsid] reptiles,” but, nevertheless, he noted that in those mammals in which the cartilage of the embryonic alisphenoid is pierced by the maxillary nerve, this cartilage is a composite structure, formed by processus ascendens in front of the nerve and by ala temporalis [=lamina ascendens] behind the nerve. “When this structure ossifies it produces a combined epitypogoid and alisphenoid” (DeBeer, 1926, p. 327). He went on to note that in those eutherians in which the cartilage separating V₁ from V₂ has disappeared, only the ala temporalis [=lamina ascendens] is left and this ossifies as the “true alisphenoid.” Thus, in DeBeer’s view, the ala temporalis is derived from the ascending process by lapping back around V₂ and “may therefore be held to be partially homologous with it” (DeBeer, 1926, p. 334).

Such distinctions between parts of a single embryonic structure (that is, the ascending process of the epitypogoid = the ala temporalis of the alisphenoid) appear to us unnecessarily rigid. If the distinction between ascending process and ascending lamina is to be consistently applied because of their topographic relations to the branches of the trigeminal nerve, then what does one call the parts of the cartilaginous process that lie below and above the foramen for V₂, for they lie neither between V₁ and V₂ nor between V₂ and V₃. Maier (1987, p. 75) points out that “such a formal approach certainly cannot satisfactorily solve the underlying problems.” We agree with Maier that this distinction is not fundamental, believing that the ala has changed its topographic relation to the maxillary nerve by an evolutionary shifting of the nerve anteriorly “through” a unitary cartilage, the processus ascendens = ala temporalis. Thus, at some phylogenetic stage the embryonic ala will have been notched from behind, as described by Maier (1987) in Monodelphis. At a later phylogenetic stage, when the nerve has migrated farther forward, the bar behind
the nerve will extend to and join the upper part of the ala. At a still later stage, with further anterior migration of the nerve, the bar in front of the nerve will become incomplete, whereas that behind the nerve will increase in diameter. Finally, the nerve will lie entirely anterior to the ala, and the cartilage will be a single solid process again. One could plausibly argue that the portion of the ala that lies immediately behind the maxillary nerve is not homologous with that portion that in the ancestor lay immediately anterior to the nerve. But how does one argue that the portions above and below the level of the nerve are not homologous?

In his recent review of the question, Maier (1987) points out that the ascending process of the ala temporalis has a “reptilian” position in all four didelphid genera that have been studied, as well as in the bandicoot *Perameles* (fig. 5C). In some marsupials (the dasyurid *Smithopsis*, the bandicoot *Isodon*, the wombat *Vombatus*, and the phalangerid *Trichosurus*), the ascending process is pierced by the maxillary ramus (V₂; fig. 5D), whereas in others, such as the dasyurid *Dasyurus* and the kangaroos *Petrogale* and *Macropus*, the ascending process lies between the maxillary (V₂) and mandibular rami (V₃), as it does in a majority of eutherians (fig. 5E). Although no eutherian is known to possess the “reptilian” position of the ala temporalis anterior to V₂, some eutherians (for example, many carnivores, primates, and the hyrax *Procavia*, Maier, 1987; *Tupaia*; Zeller, 1987) show the “intermediate” condition in which the ala temporalis is pierced by V₂. In a later paper, Maier argues, “we have within marsupials a morphological series linking <reptilian> with <eutherian> conditions. All circumstances indicate that the ala temporalis in all these taxa are [sic] homologous, but that their [sic] spatial relationship with the trigeminal branches is variable, sometimes even within families” (Maier, 1989, p. 397).

Maier argues that the dorsally-directed process of the ala temporalis is homologous throughout amniotes and that in many mammals there has been a shifting of the position of the ala with respect to the branches of the trigeminal nerve. “Therefore,” he states, “it seems quite unnecessary to make a formal distinction between an anteriorly situated ascending process (being homologous to the epitypargoid) and a posteriorly lying Lamina ascendens (corresponding to a neomorphic mammalian alisphenoid) as suggested by De Beer (1926; 1937) and Presley and Steel (1976)” (Maier, 1987, p. 86).

Kuhn and Zeller (1987, p. 65) acknowledge that in didelphids the structure that they term the “Lamina ascendens of the Ala temporalis” lies anterior to the maxillary branch of the trigeminal nerve; however, because of the variability of its position in other marsupials, they question “which of these states are [sic] plesiomorphic for marsupials.” They argue, for reasons discussed below, that the common ancestor of monotremes and therians “must have had a small, basal epitypargoid of about the dimensions of the Ala temporalis of monotremes” (Kuhn and Zeller, 1987, p. 67), so that “the Lamina ascendens is a therian neomorph” (Kuhn and Zeller, 1987, p. 65). The tall “Lamina ascendens” of some
marsupials, then, is a secondary specialization within this group, "possibly as an adaptation of mechanics of the skull to sucking on a nipple at a very immature developmental state" (Kuhn and Zeller, 1987, p. 67). Though they do not explicitly say so, they presumably also consider the anterior position of the "Lamina ascendens" with respect to $V_2$ in didelphids and *Perameles* to be secondarily derived rather than primitive.

The opposing views of Maier and of Kuhn and Zeller on the size of the ala temporalis and its relation to the maxillary nerve in the common ancestor of monotremes and therians cannot be conclusively tested with reference to fossils because of the absence of information on early development in extinct forms. However, it is possible to draw some inferences from the structure of the adult braincase in non-mammalian therapsids and early mammals about the probable condition of the embryonic ascending process *cum* ala temporalis and the position of the maxillary nerve with respect to it. In addition, information on the phylogenetic positions of living mammals showing different states of these features can aid in assessing which states are primitive.

In early therapsids, such as anomodonts and gorgonopsians, the secondary wall of the orbitotemporal region is formed by the epipterygoid, which forms a tall slender rod that extends dorsally to the level of the parietal, as in primitive amniotes (Romer, 1956; Barry, 1965). We presume that in the developing therapsid skull the ascending process was a tall slender cartilage attached to the sphenoid membrane (fig. 5A, B), as it is in embryos of *Sphenodon* and most lizards (Säve-Söderburgh, 1947), and that the bony element formed primarily through endochondral ossification. The trigeminal nerve left the primary cranial cavity via the prootic incisure, a notch in the anterior border of the prootic bounded anteroventrally by the ossified pila antotica (fig. 5A), also as in *Sphenodon* and most lizards (Romer, 1956). It is presumed that the maxillary ($V_2$) and mandibular ($V_3$) branches of the trigeminal nerve exited from the cavum behind the epipterygoid, as in other primitive amniotes (fig. 5A, B).

In therocephalians and early cynodonts, the epipterygoid is moderately expanded anteroposteriorly, suggesting that it ossified partly as endochondral bone in the ascending process and perhaps partly as appositional bone in the sphenoid membrane. It also has an elongate posteroventral process, the quadrate ramus, directed toward the jaw joint. In cynodonts the anterodorsal border of the prootic forms a sutural contact with the posterodorsal margin of the epipterygoid, and the ventrolateral part of the prootic forms a longitudinally-oriented process, the lateral flange, which contacts the quadrate ramus of the epipterygoid (fig. 1F). These dorsal and ventral contacts of the epipterygoid and prootic lay in the plane of the sphenoid membrane, lateral to the cavum epipetricum and the primary cranial wall (represented by the prootic incisure and the pila antotica), and it is probable that both elements were formed in part by membrane bone. The new secondary braincase wall in cynodonts, formed by epipterygoid and prootic,
encloses a large foramen through which part of the trigeminal nerve left the skull. In herbivorous cynodonts (Gomphodontia) this foramen is subdivided by a bar of bone to produce two smaller foramina that lie on the epitygroid-prootic contact. This bar in Diademodon is formed by the epitygroid in some specimens (Gow, 1986) and by the prootic in others (Hopson, personal observation). The subdivision of the trigeminal foramen provides the best evidence that both the maxillary and mandibular branches of the trigeminal nerve left the braincase behind the epitygroid in non-mammalian therapsids (see also Presley and Steel, 1976, p. 453). As in all living tetrapods, the ophthalmic branch of the trigeminal would have passed forward within the cavum epiptericum to leave the braincase anterior to the epitygroid.

The epitygroid of non-mammalian cynodonts is intermediate in its features between the slender epitygroid of primitive amniotes and the expanded alisphenoid of early mammals, but its relations to the branches of the trigeminal nerve were as in living sauropsids: it lay behind the ophthalmic (V₁) ramus and anterior to the maxillary (V₂) and mandibular (V₃) rami. We see no reason to doubt that a fully-developed ascending process occurred in the embryonic skull.

In the earliest mammals known from complete skulls, the Early Jurassic Sinoconodon, Morganucodon (fig. 1E), and Megazostrodon, the epitygroid has the same relations to surrounding bones as does that of a late non-mammalian cynodont such as Pachygenelus (fig. 1F; epitygroid is used here to indicate strict homology with this element in non-mammalian cynodonts; compare Gow; 1986, p. 15). In Morganucodon (Kermack, Mussett, and Rigney, 1981), Megazostrodon (Gow, 1986), and, to a lesser degree, in Sinoconodon (Crompton and Luo, 1993), the epitygroid is more slender than that of Pachygenelus and most Triassic cynodonts. In both Sinoconodon and Morganucodon, two foramina perforate the anterior part of the periotic, that is, the now-fused prootic and opisthotic of “reptiles.” These are usually interpreted, correctly we believe, as the exits for the maxillary and mandibular rami of the trigeminal nerve from the cavum epiptericum. The thin bone surrounding these foramina, which forms a more extensive lateral wall to the cavum than does the prootic of non-mammalian cynodonts, is the anterior lamina, generally interpreted as an intramembranous ossification in the sphenopohre oburator membrane. Megazostrodon has but a single large trigeminal foramen between the epitygroid and periotic, but as Gow notes, “the exact conformation of this area may prove variable due to overgrowth of membrane bone” (Gow, 1986, p. 15). As with advanced non-mammalian cynodonts, there is no reason to doubt that the epitygroid of Early Jurassic mammals was formed in the embryo from a fully-developed processus ascendens of what may now be termed the ala temporalis.

The side wall of the braincase of Vincelestes (fig. 2B), with respect to the features considered here, differs in no significant way from that of Morganucodon (fig. 1E), except that the epitygroid/alisphenoid (as this
transitional element may be called) is anteroposteriorly longer and the quadrate ramus is shorter. The foraamina of the maxillary and mandibular rami of the trigeminal nerve are more widely separated in *Vincentelos*, but both penetrate the anterior lamina as in *Morganucodon*. The epitypogoid/alisphenoid also contacts the same surrounding bones in *Vincentelos*, except anteroventrally where, due to the great reduction in size of the pterygoid, the palatine also contacts it. Therefore, it is most likely that the epitypogoid/alisphenoid of *Vincentelos* is strictly homologous with that of the earliest mammals and non-mammalian cynodonts and that in the embryo the ala temporalis had a tall processus ascendens, homologous with that of primitive therapsids and other early amniotes.

Comparison of the epitypogoid/alisphenoid of *Vincentelos* with the alisphenoid of a didelphid marsupial (fig. 1B) shows that the two bones also have the same contacts with surrounding bones, except that in the didelphids the anterior moiety of the squamosal has replaced the anterior lamina in the secondary side wall. We know that the alisphenoid in didelphids develops from an embryonic precursor which has the main features of the primitive amniote processus ascendens, that is, a tall slender process reaching the orbitoparietal commissure (taenia marginalis), an open joint with the basipterygoid process, and a position anterior to the maxillary ramus of the trigeminal nerve (Maier, 1987). These features are known in the embryos of living saurians and are inferred from adult morphology to have been present in non-mammalian therapsids, early Jurassic mammals, and the non-tribosphenic therian *Vincentelos*. Therefore, we see no reason to doubt the homology of the didelphid alisphenoid with the epitypogoid of sauropsids and primitive therapsids. Furthermore, because of the phylogenetic position of *Vincentelos* as the probable sister taxon of Tribosphenida and the basal position of “didelphoids” within Marsupialia (Kirsch and Archer, 1982; Reig, Kirsch, and Marshall, 1987, p. 82), we accept Maier’s view, contrary to Kuhn and Zeller (1987), that the didelphid condition represents the plesiomorphic condition for marsupials and, by extension, for all living therians.

The position of the ala temporalis relative to the maxillary nerve cannot be documented in most fossil mammals in which a separate foramen rotundum is present in the alisphenoid, for it may have had any of the three positions that occur in living mammals (fig. 5C-E). Even in those fossils lacking a foramen rotundum, in which the maxillary nerve left the braincase anterior to the alisphenoid, it is possible that the embryonic ala temporalis lay anterior to the nerve but did not become ossified into the alisphenoid.

The fossil evidence, we believe, supports Maier’s view of the homology of the ascending process of the epitypogoid (=ascending lamina of the ala temporalis in mammals) throughout amniotes and that its variable position in mammals with respect to the maxillary branch of the trigeminal nerve is due to a phylogenetic shift in the position of the nerve from behind the ala to in front of it. The best evidence for such a shift is seen in
those embryonic marsupials and eutherians in which the nerve lies in an “intermediate” position, passing through a foramen within the cartilagi-
inous ala. We view the range of positions occupied by the maxillary nerve with respect to the cartilaginous bar in the side wall as evidence for a transformation series in which the nerve migrated anteriorly “through” a single cartilaginous unit. This appears to be much more likely than that the ascending process anterior to V₂ was reduced in size and ultimately lost and a neomorphic ascending lamina then grew up behind the nerve (see fig. 4C), as advocated by Gaupp (1902), Watson (1916), Presley and Steel (1976), Presley (1981, 1989), and Kuhn and Zeller (1987). A functional reason for the phylogenetic shift of the maxillary nerve to a more anteromedial position is presented below.

This interpretation implies that the condition of the side wall of the braincase in monotremes and multituberculates (fig. 1C, D), where the adult alisphenoid is a very small element extending but a short distance above the basicranium, and the anterior lamina forms the greater part of the ossified side wall, is a secondary one. Kuhn and Zeller (1987, p. 65) argue that the common ancestor of monotremes and therians must have had “a small, basal alisphenoid, similar to that of Recent monotremes.” Otherwise, they argue, it would be difficult to understand why a tall epipterygoid, such as occurs in non-mammalian cynodonts: (1) was not used in the braincase of monotremes; (2) changed its topographic relation to the maxillary nerve in therians; and (3) develops in therians quite differently from a reptilian epipterygoid and shows such a high degree of ontogenetic variability among therians. These three problems are dis-
cussed below.

1. The first of these queries cannot be answered because we are essentially ignorant of the factors that influenced the development of the skull in Mesozoic mammals. The altricial (essentially fetal) condition of monotreme hatchlings and marsupial neonates is probably plesiomor-
phic for mammals (Hopson, 1973; Tyndale-Biscoe and Renfree, 1987); therefore hatchlings or neonates of all non-eutherian Mesozoic mammals would have begun suckling while the skull was still in a fetal condition. Maier (1987) regards the tall ala temporalis in marsupials to be a mechanical support for the primary side wall of the braincase, which he believes would be stressed by the jaw muscles during suckling. We regard the tall ala of marsupials to be a probable primitive retention and not, as proposed by Kuhn and Zeller (1987, p. 67), a neomorphic fetal adapta-
tion (although union with the orbitoparietal commissure may be). With regard to monotremes, Maier argues that the lack of development of the ala temporalis may have been compensated for by expansion of the cartilaginous structures of the chondrocranium, notably the orbitoparietal commissure (= taenia marginalis; fig. 3A). However, this does not explain why the ala temporalis of monotremes lost its function as a structural support in the skull.

2. The change of the relation of the ala temporalis to the maxillary nerve in most, though not all, therians and in monotremes may be
related primarily to the forward migration of the point of exit of the nerve from the cavum epipitericum which has occurred to a lesser or greater degree in all mammals, including the earliest fossil taxa. This, in turn, may be related to the reduction of the internus component of the adductor jaw musculature and expansion of the externus component. Lakjer (1926) separated the adductor jaw muscles (M. adductor mandibulae) of lower tetrapods into three major groups according to their relations to the maxillary and mandibular branches of the trigeminal nerve (fig. 5B; see Ostrom, 1961, Barghusen, 1973, and Heatton, 1980, for summaries in English). The external adductor (M. adductor mandibulae externus) lies lateral to the maxillary and mandibular branches, the internal adductor (M. a. m. internus) lies anterior and medial to the maxillary branch, and the posterior adductor (M. a. m. posterior) lies posterior and medial to the mandibular branch. The adductor jaw muscles of modern sauropsids include components of all three subdivisions (fig. 5B). Barghusen (1973) restored a similar pattern of jaw muscles in the early “mammal-like reptile” Dimetrodon, including large internal adductor components, that is, a pseudotemporalis taking origin from the epipterygoid and adjacent undersurface of the skull roof and a posterior pterygoideus taking origin from the ventrolateral surface of the pterygoid bone (Barghusen, 1973, figs. 5, 7B).

In mammals, the great bulk of jaw-closing musculature filling the temporal fossa (temporalis, masseter, external (lateral) pterygoid) is derived from the external adductor mass. The temporalis attachment on the braincase extends well down the side wall, even on to the alisphenoid, and the external pterygoid often attaches to the alisphenoid between the foramina for the maxillary and mandibular nerves (Hiiemae and Jenkins, 1969; Turnbull, 1970). The only major remaining component of the internal adductor (M. a. m. i.) is the mammalian internal (medial) pterygoid, homologous with either the M. a. m. i. pseudotemporalis (Brock, 1938) or part of the M. a. m. i. pterygoideus (Crompton, 1963) of primitive amniotes, which attaches to the braincase below the level of the trigeminal foramina (Hiiemae and Jenkins, 1969; Turnbull, 1970). Thus, an anterior migration of its exit foramen would have removed the maxillary nerve from proximity to the attachment sites of the external adductor muscles. Furthermore, the elimination of internal adductor (pseudotemporalis) musculature from a position anterior and medial to the maxillary nerve removed the obstruction that could have prevented the nerve from shifting to a position internal to the alisphenoid in the secondary braincase wall.

We conclude that the anterior migration of the maxillary branch of the trigeminal nerve in mammals, “through” a more or less stationary alisphenoid cartilage, was functionally related to the expansion of the external adductor musculature on the side wall of the braincase in the space between the exit foramina of V₂ and V₃.

3. The high degree of ontogenetic variability in development of the therian alisphenoid relates in part to its position relative to the maxillary
nerve, as discussed above, and to the great variation in size of the ala temporalis in eutherians. As suggested by Maier (1987, p. 87), the reduction of the ala in eutherians may be related to their prolonged intrauterine development and lack of need to strengthen the side wall of the braincase at an early developmental stage as would be true for marsupials and, presumably, most Mesozoic mammals. As noted above, the altricial condition seen in hatchling monotremes and neonate marsupials is probably primitive for mammals.

**Phylogenetic Implications of Braincase Structure in Mammals**

Figure 6 is a diagrammatic representation of our conclusions concerning the evolutionary history of the side wall of the mammalian braincase. In the outgroup condition (A), seen in carnivorous Triassic cynodonts and Early Jurassic tritheledontids, the epitygroid is expanded and contacts the anterior end of the prootic ossification of the otic capsule which probably includes an intramembranous component. The relations of the three branches of the trigeminal nerve (V) are primitive for amniotes, with V₄₋₅ leaving the skull through a single opening and V₁ passing forward in the cavum epiptericum medial to the epitygroid. The embryonic processus ascendens (homologous with the ala temporalis of mammals) is indicated by a dotted line. The squamosal bone (not shown) contacts the lateral surface of the otic capsule but does not enter into the cranial wall. In an Early Jurassic mammal (B) such as *Sinoconodon* or *Morganucodon*, the relations of the trigeminal nerve to the epitygroid *cum* alisphenoid are the same, but the maxillary and mandibular nerves (V₂₋₃) leave the braincase via separate foramina in the presumed intramembranous ossification of the anterior lamina (lamina obturans). These relations persist in Jurassic and Early Cretaceous non-tribosphenic therians (C), such as *Vincelestes*, in which some expansion of the alisphenoid has taken place. In the common ancestor of marsupials and eutherians (D), the anterior lamina (lamina obturans) has been lost. The alisphenoid has a large intramembranous component that forms as appositional bone adjacent to the persisting tall ala temporalis of the early neonate and expands primarily posteriorly, both phylogenetically and ontogenetically (see open arrow), to contact, or nearly contact, the otic capsule; the remaining gap between alisphenoid and otic capsule is filled by the anteriorly-expanded cranial process of the squamosal. Didelphid marsupials retain the primitive relations of V₂ to the ala temporalis, but in more derived marsupials and in eutherians V₂ either passes through a foramen in the ala temporalis or passes forward medial to the ala. In monotremes, multituberculates, and perhaps in triconodontids (E), the embryonic ala temporalis and the intramembranous ossification of the alisphenoid are both greatly reduced; the place of the ascending portion of the alisphenoid in the side wall of the braincase is taken by a lamina obturans which expands primarily anteriorly (see open arrow), though it also expands posteriorly to a lesser degree to contact and fuse with the otic capsule. The latter condition is derivable from that which presum-
ably characterized all Early Jurassic mammals, whether therian or non-therian, and the Early Cretaceous therian *Vincelestes*. The branching off of those taxa with a reduced alisphenoid and a greatly expanded anterior lamina could have occurred at any time in the Early or Middle Jurassic and, in the case of monotremes, possibly even as late as the Early Cretaceous (black arrows with "?").

We conclude (fig. 6) that: (1) the loss of the lamina obturans and backward expansion of the alisphenoid is a synapomorphy of marsupials and eutherians and presumably of any group with which either shares a common ancestor (for example, delthatheriids; Kielan-Jaworowska and Nesov, 1990); (2) the great reduction of the alisphenoid ossification and anterior enlargement of the lamina obturans in monotremes and multituberculates (Kielan-Jaworowska, 1971; secondarily reversed in *Lambdopsa-lis*; Miao, 1988) is a unique feature of these groups; whether it is homologous or convergent, however, is extremely uncertain.

The description of the Early Cretaceous monotreme, *Steropodon galmani* (Archer and others, 1985), with molars having a "reversed triangles" pattern similar to that of the Late Jurassic non-tribosphenic therian *Peramus* (Kielan-Jaworowska, Crompton, and Jenkins, 1987) has been generally received as conclusive evidence that monotremes are therians. That early therians had an anterior lamina in their braincase, from which the monotreme condition could easily be derived, strengthens this conclusion. However, in their postcranial skeleton, monotremes are much more primitive than the Late Jurassic dryolestoid "eupantothere", *Henkelotherium guimarotae*, recently described by Krebs (1991), in which the postcranium is strikingly similar to that of modern therians. As noted by Krebs, this derived locomotor morphology must have "been reached by the common ancestor of *Henkelotherium* and the modern Theria, i.e. by an Amphitherium-like eupantothere of the Middle Jurassic" (Krebs, 1991, p. 10; also see Prothero, 1981), so that the monotremes must have separated from the line leading to modern Theria by the Middle Jurassic. At the present time we wish to suspend judgment concerning the relationships of monotremes.

Current views on the relationships of multituberculates are even more diverse. Most specialists on the group consider them to be non-therians, having branched off from early mammalian stock (see Miao, 1988). The morphology of the rather simple molar teeth of the oldest multituberculates, the paulchoffatiids (Hahn, 1969), strongly suggests that they were derived from ancestral molars in which the main cusps lay in a longitudinal row. This view is strengthened by Sigogneau-Russell's (1989) recent study of haramiyid teeth, which emphasizes the dental similarity of these enigmatic Late Triassic-Early Jurassic mammals to multituberculates.

A contrary view is presented by Rowe and Greenwald (1987), Rowe (1988), and Greenwald (1988), who consider multituberculates to be the sister taxon of marsupials plus eutherians, largely on the basis of derived
Fig. 6. Diagrammatic representation of the evolutionary history of the side wall of the mammalian braincase proposed here. (A) the ancestral condition, represented by a non-mammalian cynodont; (B) an Early Jurassic mammal, such as Morganucodon; (C) an Early Cretaceous non-tribosphenic therian, such as Vincelestes; (D) a Late Cretaceous therian, represented by a didelphid marsupial; (E) the monotreme, multituberculate, and, perhaps, triconodontid condition, which is derivable from that of a primitive mammal, whether therian or non-therian (see arrows with "?"). The anterior lamina is indicated by tone; the processus ascendens/ala temporalis is indicated by dotted lines. The height of the ala temporalis pertains to its state (known or inferred) in early neonates, as indicated in fig. 5. The white arrows in D and E indicate the principal direction of growth of the ossification in the sphenoid-obturator membrane with respect to the ala temporalis. Abbreviations: al, anterior lamina (= lamina obturans); ala tem, ala temporalis; as, alisphenoid; ept, eipipterygoid; fen ov, fenestra ovalis; ot cap, otic capsule; pr asc, processus ascendens; V₁, V₂, V₃, ophthalmic, maxillary, and mandibular branches of trigeminal nerve.

resemblances in the postcranial skeleton which previous workers (Simpson and Elftman, 1928; Krause and Jenkins, 1983) considered to be convergences. However, Wible's (1991) reanalysis of the cranial (only) characters used by Rowe (1988) in his PAUP analysis of mammalian
phylogeny, separates the Multituberculata from the marsupials and eutherians, placing them as the outgroup to all living mammals. We consider current knowledge of multituberculate morphology, particularly that of the oldest members of the group, to be inadequate for providing convincing evidence of relationship to any other group of mammals. However, the similarities in braincase structure to monotremes, and perhaps to triconodontids (see below), are derived resemblances and so should be given weight in any consideration of multituberculate affinities.

Triconodontids have a large anterior lamina (Kermack, 1963; Crompton and Jenkins, 1979; Crompton and Sun, 1985), but the condition of the alisphenoid is not known with certainty. Crompton and Jenkins (1979, fig. 3–5C) illustrate a tall alisphenoid in contact with the anterior border of the anterior lamina in a “triconodontine” based in part “on undescribed material from the Early Cretaceous Cloverly Formation.” We have examined these specimens and are unsure of the limits of the anterior lamina and the possible alisphenoid. Therefore, although present evidence indicates the presence of a large anterior lamina in triconodontids, we are uncertain of the condition of the alisphenoid in this group.

In summary, the side wall of the braincase of monotremes and multituberculates, and possibly triconodontids, possesses derived features that could be regarded as synapomorphies uniting these groups. At present, we believe, the evidence for relationships of each of these taxa to other mammals is sufficiently contradictory that we do not wish to give undue weight to their shared braincase specializations. Nevertheless, we believe that the evidence provided by braincase structure should not be dismissed, as has been done by numerous workers influenced by the work of Presley and Steel (1976) and Presley (1981).

ACKNOWLEDGMENTS

Dr. J. F. Bonaparte, who collected all known material of Vincelestes neuquenianus, invited JAH to collaborate with him and GWR on a study of the braincase of this very important mammal; we thank him for giving us this opportunity to describe the braincase of Vincelestes. For permission to study specimens in their care, we thank: Dr. M. A. Cluver, South African Museum, Cape Town; Professor A. W. Crompton, Museum of Comparative Zoology, Harvard University; Dr. J. Hooker, The Natural History Museum, London; Professor Z. Kielen-Jaworowska, Paleontologisk Museum, Oslo; Dra. Marta Piantida, Museo Argentino de Ciencias Naturales, Buenos Aires; Dr. W. D. Turnbull, Field Museum of Natural History; and Lic. Diego Verzi, Facultad y Universidad de La Plata. The manuscript has benefitted from critical readings by Drs. E. F. Allin, J. F. Bonaparte, D. Miao, R. Presley, and J. R. Wible. The illustrations were prepared by Claire Vanderslice. Rougier’s research is supported by a CONICET Doctoral Fellowship. Hopson’s research is supported by National Science Foundation Research Grant BSR-8906619 which also
funded a three month research and study visit to the United States by Rougier in 1989–1990.

It is a pleasure to dedicate this paper to Dr. John Ostrom, to whom J. A. H. is grateful for support and friendship at the beginning of his career in vertebrate paleontology.

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