

Vascular system associated with the sidewall of the braincase and the prootic canals of cynodonts, including mammals

C.E. Gow

Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg, 2000 Republic of South Africa

Received 29 January 1991; accepted 2 May 1991

The terminology of the cranial vascular system of cynodonts and early mammals is confusing and this confusion extends to certain associated features of the bones of the braincase. In the present paper it is attempted to clear up some of this confusion and to demonstrate that previous authors have unwittingly used the term 'prootic canal' to denote two entirely different structures. New evidence from the Tritylodontoidea allows useful speculation regarding the developmental origin of these 'prootic canals', as well as the phylogenetic origin of mammals.

Die terminologie van die kraniale bloedvate van sinodonte en vroeë soogdiere is verwarrend, en die verwarring raak ook aspekte van die breinskasmorfologie. In hierdie artikel word daar probeer om die verwarring op te klaar en bewyse te lewer dat vorige outeurs die term 'proötiese kanaal' onwetend vir twee verskillende strukture aangewend het. Die Tritylodontoidea bied nuwe inligting wat dit moontlik maak om te spekuleer oor die oorsprong tydens ontwikkeling van die proötiese kanale, asook die filogenetiese oorsprong van soogdiere.

Introduction

The developmental and evolutionary history of the sidewall of the braincase and associated vascular structures of mammals continues to attract much interest and debate amongst embryologists and palaeontologists (Kermack, Musset & Rigney 1981; Presley 1980, 1981; Crompton & Sun 1985; Kielan-Jaworowska, Presley & Poplin 1986; Maier 1989; Zeller 1989 and Wible 1989, 1990 to list just some recent papers).

The terminology of the cranial vascular system in therapsids and early mammals is confused, and this confusion extends to certain vascular canals in the bones of the braincase. For example, previous authors, often in the same paper, have used the term 'prootic canal' to denote two entirely different structures in therapsids and mammals.

The following account traces the development of the braincase in cynodont and early mammalian phylogeny and aims to sort out the difficulties in recognizing and naming homologous structures in the different groups.

Vascular system

Recently Durand (1989) has reviewed the literature and cleared up much of the confusion concerning the terminology of the vascular system of the posterior part of the therapsid skull. The main veins associated with the braincase of a typical cynodont are illustrated here in Figure 1. Durand has shown that in reptiles (including therapsids) and in mammals, the term *vena capitis lateralis* (VCL) should be reserved for the vein which ran back beneath the braincase in the cranio-quadrate passage. The *vena cerebralis media* (VCM) ran back through the cavum epiptericum to exit via the trigeminal foramen, continued back in a lateral groove on the prootic and down through the pterygo-paroccipital canal to join VCL. Within Tritylodontoidea and in early Jurassic mammals the lateral groove on the prootic becomes a closed foramen in the lateral flange of prootic; in Tritylodontidae and early Jurassic mammals the lateral

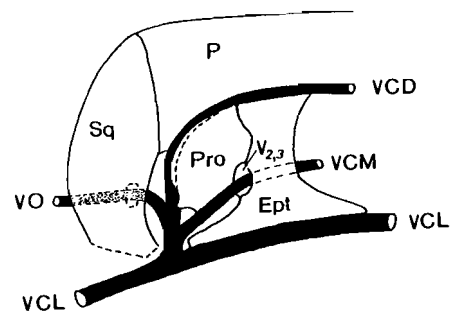


Figure 1 Veins associated with the lateral wall of the braincase in a generalized cynodont such as *Thrinaxodon* or *Probainognathus*: footplate of epityrgoid cut away to reveal the lateral head vein (VCL). See Appendix for abbreviations.

flange of the prootic is also pierced by a second foramen, this transmitted a branch of the stapedial artery (Figures 2 and 3), see also Hopson 1964; Crompton & Sun 1985, and Gow 1986.

VCM is present in early mammalian embryos but has often been referred to as VCL, e.g. Simpson 1938; Crompton & Sun 1985; Gow 1986 and Wible 1989, 1990. In late monotreme and marsupial embryos a tributary draining the prootic sinus is all that remains of VCM: this vein passes through what is called a prootic canal but is in fact homologous with a foramen in the lateral flange of prootic in Jurassic mammals, as will be seen presently. This canal is apparently not present in embryos of eutherian mammals (Wible 1990).

The *vena capitis dorsalis* (VCD) lay in a lateral groove on the parietal in early cynodonts (e.g. *Procynosuchus* Kemp 1979), but in later forms this groove is situated further ventrally on the contact between parietal and epityrgoid plus prootic (e.g. *Thrinaxodon*, *Probainognathus* Figure 1). In Tritylodontidae VCD runs in a 'tunnel' just within the lateral surface of parietal covered by a thin sheet

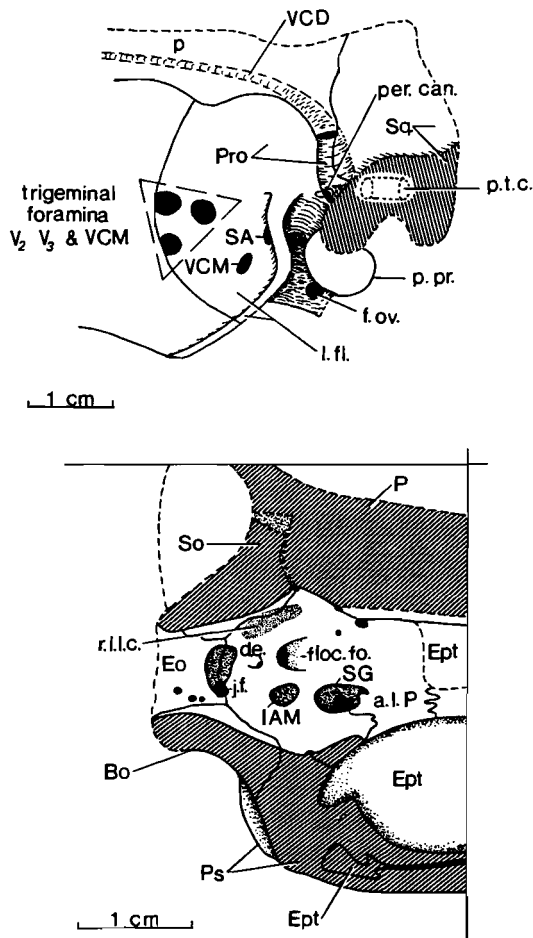


Figure 2 *Tritylodon* BP/1/5104a. Isolated braincase sagittally sectioned. Top — in lateral view. To display foramina in lateral flange of petriotic and the position of the lateral opening of the petriotic canal. Functions are not assigned to foramina in the trigeminal region as there is still uncertainty about this. Note: ventral part of braincase omitted for clarity. Bottom — in median view. The endocranial opening of the petriotic canal is in the apex of the floccular fossa. Topographic relationships to other endocranial landmarks are clear. (In *Tritylodon* an anterodorsal process of prootic excludes the epipterygoid from the recess for the semilunate ganglion, as is the case in mammals.) See Appendix for abbreviations.

of bone. In the early mammal *Morganucodon*, VCD becomes in the terminology of Kermack *et al.* (1981), the *vena temporo orbitales*, still in an extracranial position. Wible (1989) has proposed that the traditional course of VCD was in fact occupied by the stapedia artery. This notion is not supported by the present investigation as will become apparent.

The traditional view (dating from Watson 1920) is that VCD was joined by the *vena occipitalis* entering from the post temporal canal, the combined vein joining VCM as it entered the pterygo-paroccipital canal. Watson (1920) suggested that in *Diademodon* (his *Gomphognathus* and *Protacmon*) VCD was joined by a vein from the endocranial transverse sinus which exited via an ill-defined unossified gap between the parietal and prootic. Fourie (1974) suggested this vein could also have been present in *Thrinaxodon*.

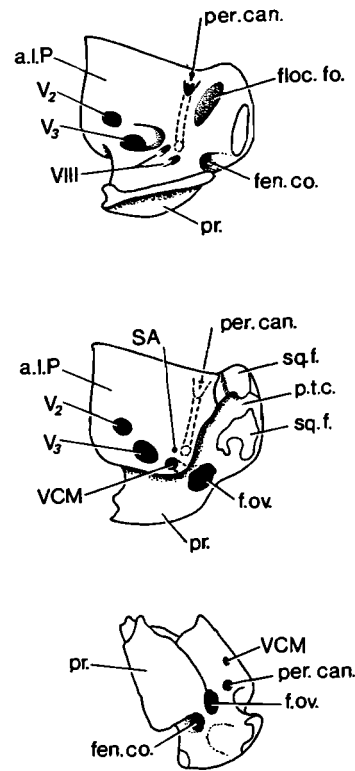


Figure 3 *Morganucodon* petrosal in, from top to bottom, median, lateral and ventral views. After Kermack *et al.* (1981 Figure 71) with the course of the petriotic canal indicated by dashed lines. See Appendix for abbreviations.

However, recent careful re-examination proves that no such gap existed in *Procynosuchus* (confirming Kemp 1979), nor was it present in *Cynosaurus* or *Galesaurus*. In these genera blood from the endocranial cavity could have been drained only via the trigeminal or jugular foramina. The need for an additional vein arose later, as we shall see.

The presence of the vein draining the endocranial transverse sinus described by Watson (1920) for *Diademodon* is thus at best variable in cynodonts and certainly not capable of conclusive demonstration.

Prootic canals

The term prootic canal has been most confusing. Wible (1990) asserts that the prootic canal runs through the anterior lamina of the petrosal. Presumably this is what appears to be the case in mammalian embryos: It is not true of what is generally termed the prootic canal in *Morganucodon* and its allies and a homologous structure in *Tritylodontidae* as will be shown below. Crompton & Sun (1985 p. 114) propose the following as a synapomorphy of Mammalia: ‘... additional ossification of the external surface of the petrosal so as to enclose the head vein in a prootic canal’. This quote is a clear description of the venous foramen in the lateral flange and does not describe the genesis of the structure called prootic canal in their paper.

Presley (1980 p. 160) also describes a prootic canal homologous with a foramen in the cynodont lateral flange, as follows:

‘The anterior lamina of the petrosal in advanced

therapsids is often separated from the lateral flange by vascular markings, either a groove or foramina, leading toward the trigeminal exit. In mammals distributors of the stapedia artery are the vessels most consistently found in this region. That such arteries, rather than the more usually discussed veins, could be the relevant vessels in therapsids may be worth considering, especially since the primitive presence of the infraorbital ramus (of the stapedia artery) might account for the origin of the alisphenoid (prootic) canal, found both within monotremes and ditremes'.

The above three papers all describe the prootic canal as though it were homologous with a foramen in the lateral flange of the prootic. In actual fact the prootic canal which is so well known in *Morganucodon* (Kermack *et al.* 1981) and present in *Sinoconodon* (Crompton & Sun 1985) and *Megazostrodon* (Gow 1986), clearly penetrates the petrosal from a dorsal endocranial to a latero-ventral extracranial position (Figure 3). The prootic canal transmitted a new vein which joined the head vein complex as we shall see presently. This canal lies behind the lateral flange of prootic — it is therefore inconceivable that such a structure could be associated with the anterior lamina of petrosal.

The prootic canal in cynodonts

Kuhne (1956) described a venous canal in the tritylodontid *Oligokyphus* which leaves the skull via the apex of the floccular fossa to link up with VCD near its junction with the occipital vein. Kermack *et al.* (1981) regarded this as a unique feature of tritylodonts. In fact, it is probably common to most if not all Tritylodontoidea (*sensu* Hopson & Barghusen 1986): it is argued here that this canal is the exact homologue of the mammalian prootic canal (the palaeontologists' prootic canal, not the embryologists'). This new vein would appear to confirm that the prominent dorso-lateral groove on the side of the cynodont braincase did indeed carry a vein (Watson 1920) not an artery (Wible 1989).

Genesis of the prootic canal

Early cynodonts have separate prootic and opisthotic bones. The position of the suture between these bones is fundamental to understanding the prootic canal, because it is in this suture that the canal formed. In tritylodontids the prootic and opisthotic bones fuse to form the petiotic bone, and in mammals the compound bone develops a new structure, the promontorium, and is then called the petrosal bone.

In the cynodont *Thrinaxodon*, prootic and opisthotic bones are not fused, indeed in the specimen illustrated here it was possible to remove these bones from the skull and separate them (Figure 4). Laterally the suture between these bones lies beneath the junction of the occipital vein and VCD, while medially it runs through the floccular (subarcuate) fossa. All known non-gomphodont cynodonts apparently have a floccular fossa which is a primitively imperforate depression.

In tritylodonts (Figure 2) the floccular fossa is a deep, backwardly directed, funnel-shaped recess with a foramen at the apex where it is hidden from view. A canal runs from

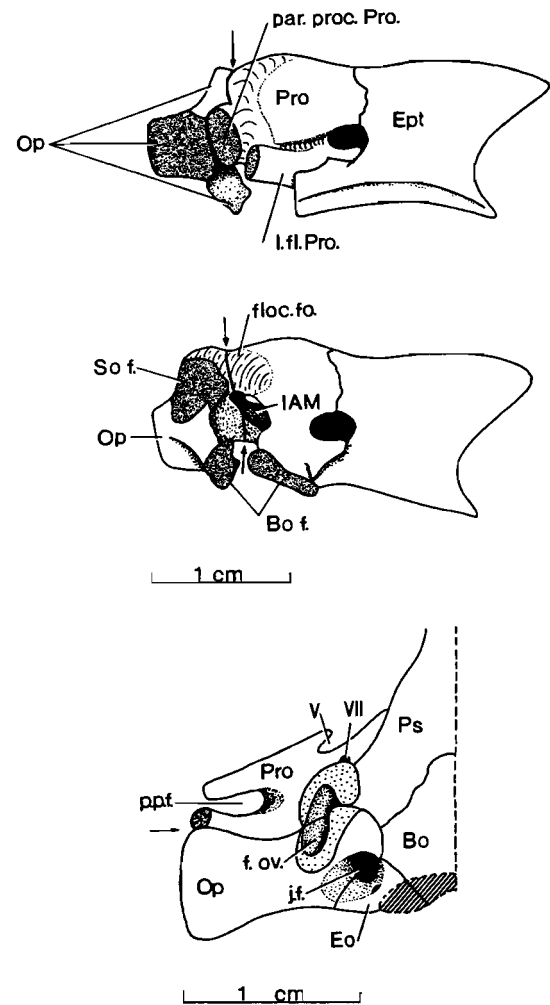


Figure 4 Braincase of *Thrinaxodon*, primarily to show the suture between prootic and opisthotic (arrowed) and its position relative to the floccular fossa. See text for discussion. Top to bottom — Lateral, medial and ventral views. See Appendix for abbreviations.

this foramen through the thickness of the petiotic bone, dorsal and lateral to the inner ear canals, to emerge in a deep depression in the channel for the head veins medial to the junction of the occipital and dorsal head veins (thus a union of three major vessels at this point). Although in tritylodonts the prootic and opisthotic are indistinguishably fused, the position of this venous canal strongly suggests that it must have formed in the gap between these bones as they ossified during development. It is nevertheless desirable to confirm this in a cynodont in which prootic and opisthotic are still separated by a distinct suture.

The specimens of *Thrinaxodon* and *Tritylodon* described above are exceptional in that they have been dissected and fully prepared in acid. A search for corroborative detail among other members of the Tritylodontoidea has been difficult because of the deep-seated situation of the prootic canal. In the case of one damaged specimen of *Diademodon* (BP/1/37760) the dorso-lateral flange of prootic on one side was removed and here the presence of a lateral foramen for the prootic canal is confirmed; it lies on the opisthotic/prootic suture as predicted.

Homology of prootic canal of cynodonts

To equate this prootic canal in Tritylodontoidea with the prootic canal of *Morganucodon* (Figure 3) and its allies may at first seem precarious, as the two forms appear to be rather different and the foramina at each end of the canal appear to be so differently situated in each. In fact it is the consistent position of the prootic canal relative to other fundamentally important structures that is significant here. In both cases the prootic canal runs dorsal and lateral to the inner ear canals (which are known to straddle the prootic/opisthotic suture in tetrapods).

In *Tritylodon* the external foramen is laterally situated behind the dorsal part of the lateral flange of the prootic at about the same level as the post temporal canal: in early mammals it is seen in ventral view, but its position is the same relative to surrounding structures, it lies posterior to the foramen in the lateral flange for VCM, anterior to the post temporal canal, and lateral to the fenestra vestibuli. Migration within these limits is not affected by any other structures penetrating the periotic/petrosal. Similarly with the endocranial foramen which in *Tritylodon* lies within the floccular (subarcuate) fossa while in *Morganucodon* it lies anterodorsal to the latter. Here again there are no structures which would prevent some migration of the foramen. It is not the intention here to imply any phylogenetic link or ranking between *Tritylodon* and *Morganucodon*, only to establish homology. Phylogenetic considerations will be treated separately in the discussion.

Discussion

In light of the foregoing it is desirable to define what is

meant by prootic canal, as this term has been used for two different canals in the prootic. It is thus proposed that one of these be known as the canal of the lateral flange. The lateral flange of advanced cynodonts (tritylodontids and early mammals) bears two prominent foramina (Figures 2 and 3), one unquestionably transmitted a vessel which emerged from the trigeminal foramen, this is most likely to have been a branch of the *vena cerebialis media*. The other foramen transmitted a branch of the stapedial artery. To the present author's understanding only one foramen is recognizable in the lateral flange region of mammalian embryos and it transmits a vein (Wible 1990). Presley (1980) suggested that the 'prootic canal' (canal of the lateral flange) may have transmitted the infraorbital ramus of the stapedial artery. Of course it is perfectly possible that in recent mammals the two foramina have merged, if so there would be no conflict between these two interpretations, the single foramen transmitting both a vein and an artery.

The venous tract which completely penetrates the periotic/petrosal in Tritylodontoidea and Morganucodontidae, is present in adult *Ornithorhynchus*, and which Kermack *et al.* (1981) refer to as the prootic canal, is clearly a different structure. Perhaps the best term for this canal would be periotic canal, in reference to its origin between prootic and opisthotic. One must infer from Wible (1990) that this is the 'prootic canal' he describes in the petrosals of Cretaceous marsupials (while in his description of embryos he is referring to the canal of the lateral flange), since he homologizes this 'prootic canal' with that of *Morganucodon*.

Prootic canals have interesting phylogenetic implications for cynodonts. They are not known in non-gomphodont

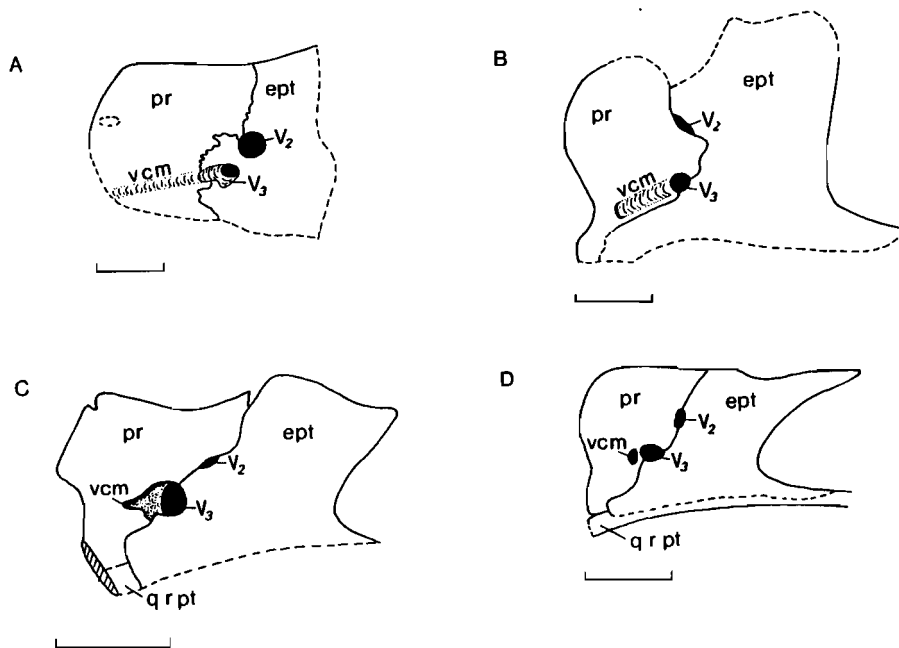


Figure 5 Lateral portion of prootic and epitygoid in a series of tritylodontoid cynodonts showing capture of VCM by lateral flange. (a) *Diademodon* BP/1/4677. The course of VCM is indicated by a faint groove on the prootic. More complete specimens show this groove entering the pterygoparoccipital canal. Dashed ellipse indicates position of lateral opening of periotic canal behind the lateral flange (see text). (b) Unidentified gomphodont from the Santa Maria Formation of Brazil. BP/1/5295. VCM now penetrates lateral flange of prootic. (c) *Trirachodon* BP/1/5050. Foramen for VCM in lateral flange is here situated closer to the trigeminal foramina. (d) *Massetognathus* BP/1/4245. Foramen for VCM in lateral flange now very close to the foramen the vein shares with V₃. All scale bars 1 cm. See Appendix for abbreviations.

cynodonts until their sudden appearance in the early mammals, which have a fully developed lateral flange with both foramina, and a periotic canal completely penetrating the petrosal. The gradual development of the venous foramen in the lateral flange is recorded in Tritylodontoidea (Figure 5), but the arterial foramen appears suddenly in Tritylodontidae. A periotic canal completely penetrating the periotic and apparently fully homologous with the similar structure in early mammals may prove to be present in all Tritylodontoidea.

In view of the above some might suggest that Mammalia are derived from somewhere within Tritylodontoidea, though differences such as the dentition make this unlikely. Others might prefer to believe that the similarities in the braincases of the two groups are due to convergence. A more conservative variant of the first alternative would be that Tritylodontoidea and Mammalia are sister groups, but this is still only partially true. What seems most probable is that Tritylodontoidea are the sister clade of another middle Triassic to lower Jurassic cynodont clade which includes Mammalia, but several key members of which are not represented in the known fossil record. These two major clades being derived from a form in which the periotic canal between opisthotic and prootic was already present. This canal is not recorded in any non-gomphodont cynodont and it seems inconceivable that it could suddenly have appeared *de novo* in early mammals, given the evolutionary and developmental history outlined for it in this paper. An extension of this proposal is the possibility that Tritylodontoidea may be polyphyletic, and that Diademodontidae, Traversodontidae and Tritylodontidae, in view of their distinctly different postcanine tooth crown morphology, could be successive derivatives from the hypothetical generalist clade which culminated in Mammalia.

References

- CROMPTON, A.W. & SUN, AI-LIN. 1985. Cranial structure and relationships of the Liassic mammal *Sinoconodon*. *Zool. J. Linn. Soc.* 85: 99–119.
- DURAND, J.F. 1989. Aspects of the cranial morphology of the therocephalian *Moschorhinus* (Reptilia: Therapsida). Ph.D. thesis, University of the Witwatersrand, Johannesburg.
- FOURIE, S. 1974. The cranial morphology of *Thrinaxodon liorhinus* Seeley. *Ann. S. Afr. Mus.* 65(10): 337–400.
- GOW, C.E. 1986. A new skull of *Megazostrodon* (Mammalia,

- Triconodonta) from the Elliot Formation (Lower Jurassic) of Southern Africa. *Palaeont. afr.* 26(2): 13–23.
- HOPSON, J.A. 1964. The braincase of the advanced mammal-like reptile *Bienotherium*. *Postilla*. No. 87: 1–30.
- HOPSON, J.A. & BARGHUSEN, H.R. 1986. An analysis of therapsid relationships. In: *The ecology and biology of mammal-like reptiles*. (Eds) P.D. MacLean, J.J. Roth, E.C. Roth & N. Hotton III. Smithsonian Institution Press, Washington, D.C.
- KEMP, T.S. 1979. The primitive cynodont *Procynosuchus*: functional anatomy of the skull and relationships. *Phil. Trans. R. Soc. Lond. ser. B.* 285(1005): 73–122.
- KERMACK, K.A., MUSSET, F. & RIGNEY, H.W. 1981. The skull of *Morganucodon*. *Zool. J. Linn. Soc.* 71: 1–158.
- KIELAN-JAWOROWSKA, Z., PRESLEY, R., & POPLIN, C. 1986. The cranial vascular system in taeniolabidoid multituberculate mammals. *Phil. Trans. R. Soc. Lond. B* 313(1164): 525–602.
- KUHNE, W.G. 1956. The Liassic Therapsid *Oligokyphus* pp. 149. British Museum (Natural History) London.
- MAIER, W. 1989. Ala temporalis and alisphenoid in therian mammals. In: *Trends in Vertebrate Morphology*. (Eds) H. Splechtma & H. Hilgers. *Progress in Zoology/Fortschritte der Zoologie* 35: 397–400.
- PRESLEY, R. 1980. The braincase in Recent and Mesozoic therapsids. *Mem. Soc. geol. Fr. N.S.* 139: 159–162.
- PRESLEY, R. 1981. Alisphenoid equivalents in placentals, marsupials, monotremes and fossils. *Nature* 294: 668–670.
- SIMPSON, G.G. 1938. Osteography of the ear region in monotremes. *Amer. Mus. Novit.* 978: 1–15.
- WATSON, D.M.S. 1920. On the Cynodontia. *Ann. Mag. Nat. Hist.* (9)6: 506–524.
- WIBLE, J.R. 1989. Vessels on the side wall of the braincase in cynodonts and primitive mammals. In: *Trends in Vertebrate Morphology*. (Eds) H. Splechtma & H. Hilgers. *Progress in Zoology/Fortschritte der Zoologie* 35: 406–408.
- WIBLE, J.R. 1990. Petrosals of late Cretaceous marsupials from north America, and a cladistic analysis of the petrosal in therian mammals. *J. Vert. Paleont.* 10(2): 183–205.
- ZELLER, U. 1989. The braincase of *Ornithorhynchus*. In: *Trends in Vertebrate Morphology*. (Eds) H. Splechtma & H. Hilgers. *Progress in Zoology/Fortschritte der Zoologie* 35: 386–389.

Appendix 1 Abbreviations

alP	anterior lamina of the prootic	pr	promontorium
Bo	basioccipital	Pro	prootic
Bo f	basioccipital facet	Ps	parasphenoid
de	ductus endolymphaticus	ptc	post temporal canal
Eo	exoccipital	rlc	recess for lateral lobe of cerebellum
Ept	epipterygoid	SA	stapedial artery
f ov	foramen ovale	Sw	squamosal
fen co	fenestra cochleae	SG	semilunate ganglion
floc fo	floccular fossa	So	supraoccipital
IAM	internal auditory meatus	So f	supraoccipital facet
jf	jugular foramen	V ₂	maxillary nerve
C fl Pro	lateral flange of prootic	V ₃	mandibular nerve
Op	opisthotic	VIII	auditory nerve
P	parietal	VCD	<i>vena capitis dorsalis</i>
par proc pro	paroccipital process of prootic	VCL	<i>vena capitis lateralis</i>
Per	periotic	VCM	<i>vena cerebialis media</i>
per can	periotic canal	VCT	<i>vena cerebialis transversus</i>
ppf	pterygo-paroccipital foramen	VO	<i>vena occipitalis</i>