

Basicranial morphology and phylogenetic position of the upper Eocene carnivoramorphan *Quercygale*

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Quercygale angustidens is a small, early carnivoramorphan from the upper Eocene of northwest Europe including the Phosphorites du Quercy, France. Although there is extensive material of the genus, very little has been published on the auditory region which is an important character complex for taxonomy and phylogenetic studies. This paper presents a detailed description of the basicranium of an undistorted partial skull of *Quercygale*. The new data form the basis for a phylogenetic analysis of *Quercygale* in the context of basal carnivoramorphan interrelationships. *Quercygale* has a mix of derived and plesiomorphic characters. The promontorium is highly derived, and unlike that of any other “miacoid”. Yet, based on the evidence from surrounding bones the bulla does not appear to be as expanded as in other closely related miacids. In the phylogenetic analysis *Quercygale* is the sister-taxon to Nimravidae and crown-group Carnivora, and it appears to be the most derived of the stem-group Miacidae. We discuss the implications that the position of *Quercygale* has on carnivoramorphan phylogenetics.

Key words: Mammalia, Miacidae, Miacoidea, *Quercygale*, carnivoran phylogeny, basicranium, Eocene, Quercy.

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Introduction

Quercygale angustidens (Filhol, 1872) is one of many small and medium sized carnivores from the Eocene–Oligocene phosphorites of the Quercy area, France (Sigé et al. 1979). Specimens attributed to *Quercygale* are known from western Europe (France, England, Switzerland) and all dated localities of *Quercygale*, as discussed by Crochet (1988), can be referred to the upper Eocene. However, some collections from the late 19th and early 20th century of the Phosphorites du Quercy that include specimens of *Quercygale* do not contain the information necessary for determining the exact location and age of these collections.

The species was first described as *Viverra angustidens* on the basis of a right ramus with m1 and alveoli of p1–p4 and m2 (Filhol 1872: pl. 13: 33–35). Fortunately, as later authors have pointed out, the m1 of “V.” *angustidens* is unique and diagnostic of the taxon. This tooth has a primitive-looking paraconid, protoconid, and very high metaconid placed in an equilateral triangle, together with a more derived-looking talonid with a central, trenchant hypoconid and posterior, very small entoconulid and hypoconulid. Thus, there is little possibility of misidentification despite the fragmentary nature of the type specimen. The same author later described an additional three mandibular rami of the species, figuring one of them (Filhol 1876). Some years later Davies (1884) de-

scribed *Viverra hastingsae* from the Headon Beds near Horwell in England. This species is in many respects similar to “V.” *angustidens*, as already noted by Schlosser (1890), and at the very least belongs in the same genus. The limited material of the English form makes it difficult to assess how closely related the two forms are, though Teilhard de Chardin (1915) believed them to be conspecific. Schlosser (1890) further noted the similarity of “*Cynodon*” *helveticus* (Rütimeyer, 1862) to “V.” *angustidens*, though he did not place the latter species in his tentative phylogeny of the Viverridae (Schlosser 1890: 4). In a contribution some years later Depéret (1910) recorded the possible presence of “V.” *angustidens* at the French site of Euzet-les-Bains. Teilhard de Chardin (1915) identified the species as a member of the Viverravinae, and transferred it to the genus *Viverravus* (Marsh, 1872a). By this time there was an abundant material of the species available in several collections. Teilhard mentions having six “more or less complete” skulls at his disposal. He figures the basicranium, both as an outline drawing (Teilhard de Chardin 1915: 3) and as a plate (Teilhard de Chardin 1915: pl. 1: 3). Unfortunately, neither of these illustrations is sufficient to give more than broad indication of the characteristics of this important anatomical region. In 1945, Kretzoi in his general review of carnivore phylogeny, erected a new genus, *Quercygale*, for “V.” *angustidens*. Kretzoi and his predecessors had based all their assessments of the taxon

on the descriptions by Filhol (1872, 1876) and Teilhard de Chardin (1915), but Piveteau (1962) added valuable information on its morphology in his study of the brain using material stored in Paris. A few years later, Beaumont (1965), apparently unaware of Kretzoi's (1945) paper, erected the genus *Humbertia* for "*V.*" *angustidens* and the related species "*Cynodon*" *helveticus* (Rütimeyer, 1862). However, Beaumont soon realized that the genera *Quercygale* and *Humbertia* were synonymous (Beaumont 1966). Despite this minor confusion, Beaumont's (1965) paper includes a comprehensive and definitive list of characters differentiating *Quercygale* from *Viverravus*. However, further work is necessary to resolve the species level taxonomy of the genus.

Up to this time, there had been near unanimity among authors subsequent to Teilhard de Chardin (1915), as well as others discussing the species (Cray 1973; Van Valen 1967a; Van Valen 1967b) in placing *Quercygale* in the Viverravinae, a subfamily of Miacidae. In the horizontal classification scheme of the time, Miacidae were considered the ancestral stock of modern carnivores. Only Kretzoi (1945) was of a different opinion, and in his avowedly vertical classification scheme, he placed *Quercygale* in its own family, the Quercygalidae, within the suborder Caniformia. Although Kretzoi's (1945) classification of the Carnivora presents many viewpoints not currently espoused, such as placing the Hyaenidae and Viverridae in the Caniformia, the opinion that *Quercygale* is a caniform has subsequently received strong support from the review of early carnivore phylogeny by Flynn and Galiano (1982). Characters presented in support of this position are the reduced P4 parastyle and protocone, and the weak but continuous lingual cingulum on the upper molars, while the single feature arguing against this allocation is the loss of M3/3.

Despite the extensive material available, very little has been published on the basicranium of *Q. angustidens*. The only basicranial character considered by Flynn and Galiano (1982) was the position of the postglenoid foramen and *Quercygale* has not been discussed in subsequent classifications of basal carnivores. The Department of Palaeozoology, Swedish Museum of Natural History, has a small collection of fossil carnivore specimens from the Quercy area including a number of specimens of *Q. angustidens*. Among these is a partial skull, NRM-PZ M2329, anteriorly broken at the level of P3, but including a complete, undistorted basicranial region (Fig. 1). This paper presents a description of the basicranium of this specimen of *Q. angustidens*. This forms the basis for a reconsideration of the phylogenetic position of *Quercygale*, in the context of basal carnivoramorph interrelationships.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; MNHN, Muséum National d'Histoire Naturelle, Paris, France; NRM-PZ, Swedish Museum of Natural History, Department of Palaeozoology, Stockholm, Sweden.

Systematic paleontology

Carnivoramorpha Wyss and Flynn, 1993

Family "Miacidae" Cope, 1883

Genus *Quercygale* Kretzoi, 1945

Humbertia de Beaumont, 1965

Type and only species: Quercygale angustidens (Filhol, 1872).

Quercygale angustidens (Filhol, 1872)

Figs. 1, 2.

Age and locality: upper Eocene, Quercy area, France.

Description of basicranium

The auditory region has been central to understanding carnivoramorph phylogeny for more than 150 years (Flower 1869; Hunt 1974; Turner 1848; Wang and Tedford 1994; Wesley-Hunt and Flynn 2005; Wesley and Flynn 2003; Wyss and Flynn 1993). In recent years, the discovery and study of new material of basal carnivoramorph taxa, *Tapocyon* and *Oodectes*, have significantly added to the cranial material known and the understanding of phylogenetic relationships among Viverravidae, "Miacidae" and Carnivora (Wesley-Hunt and Flynn 2005). Cranial material of *Quercygale* has been known for almost 100 years, but has yet to be incorporated into a modern phylogenetic framework. Nor has the auditory region been described in the context of basicranial evolution as we understand it today.

The following is a description of the auditory region of NRM-PZ M2329 (henceforth M2329) with comparisons and discussions of MNHN QU 17287 and MNHN QU 8755 based on personal observations of original specimens. Comparisons and observations based on text or illustrations are cited in the text. The auditory region of M2329 is in excellent condition with minimal breakage and no distortion. The specimen is a young adult with all molars fully erupted but the cranial sutures are not fully fused and can be plainly observed in the auditory region.

Petrosal and surrounding bones.—The basioccipital is relatively narrow and is ventrally convex. The lateral edges are smooth. The anteriomedial corner of the promontorium contacts the basioccipital ventrally just posterior to the basioccipital–basisphenoid suture. Anteriorly, the promontorium contacts the alisphenoid. Posteriorly, there is contact between the basioccipital and promontorium as the posterior basicapsular commissure, like that described by Wible (1983), or posterior "roof" to the inferior petrosal sinus (Fig. 2). A groove for the inferior petrosal sinus is present along the medial surface of the promontorium. It is evident that the inferior petrosal sinus was not enlarged, and exited the cranium through the basicapsular fenestra (the space posterior to the anteromedial contact between the promontorium and the basioccipital), ran under the posterior basicapsular commissure, and then joined the internal jugular vein (illustrated in Wible 1983: 285, fig. 3b).

The promontorium is elongate anteriorly and rounded, and similar in its general shape to that of *Oodectes*. The pro-

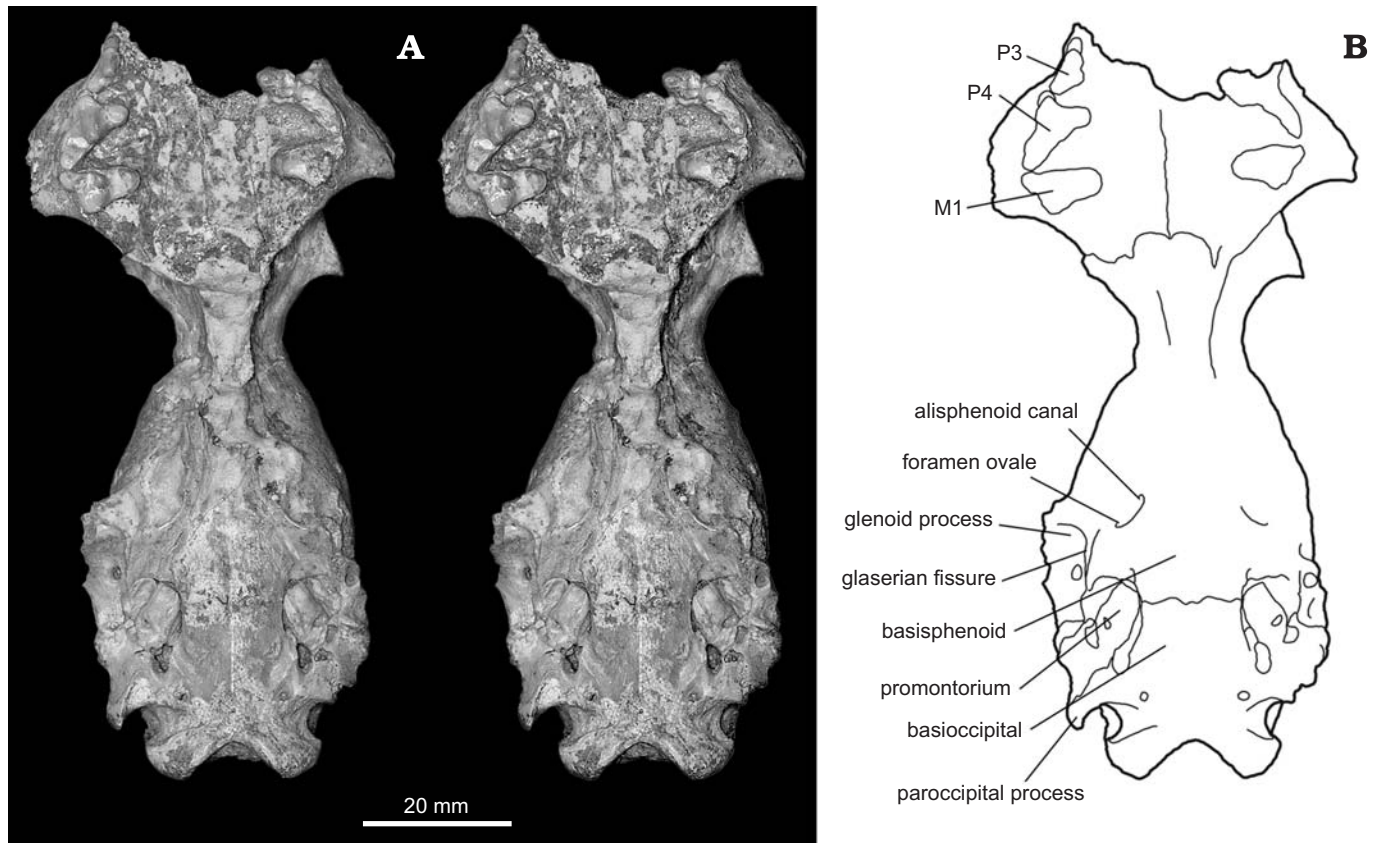


Fig. 1. *Quercyale angustidens*, upper Eocene, Quercy area, France, NRM-PZ M2329. Ventral view of the skull. A. Stereophoto. B. Explanatory drawing of the same.

montorium of *Quercyale* is distinctive from other “miacids” in that there is a ventral ridge that runs along the length of the medial edge. This ridge is strongest anteriorly and curves over itself slightly (Fig. 2). The lateral side of the ridge is rugose and appears to be an area of tympanic attachment. The ridge is not in contact with the basioccipital. No other “miacid” has this morphology. This ridge differs from the ventral petrosal process and lateral edge of the promontorium of *Proailurus* and other early feliforms in being elongate and lacking any contact with the basioccipital (see Hunt 1998 for anatomical comparison).

A sulcus for the internal carotid artery and promontory artery (Fig. 2) is clearly visible, running anteroposteriorly along the ventral surface of the promontorium. The sulcus begins just anterior to the medial extent of the fenestra cochleae, runs along the anterior lip of the fenestra then turns anteriorly and continues to the middle lacerate foramen. There is no sulcus for a stapedial artery present in M2329; however this morphology appears to be variable, as it is extremely distinctive in MNHN QU 8755. The stylomastoid foramen is posterolateral to the fenestra cochleae, tightly defined and anteriorly bordered by the mastoid tubercle. The mastoid tubercle is formed by the petrosal and lies laterally to the fenestra cochleae. The mastoid process is small, not distinctive and similar to that of *Prohesperocyon*. A shallow suprameatal fossa is present on the anterior face of the mas-

toid process similar to that in *Oodectes*. The mastoid shelf is smooth, similar in size to that of *Vulpavus* and relatively large compared to that of *Oodectes*. The paroccipital process is a distinct narrow process and projects posteroventrally.

The tegmen tympani is not fully ossified and a piriform fenestra is present between the petrosal and alisphenoid. (It could be argued that the piriform fenestra in this specimen should not be referred to as such, and is actually an extension of the middle lacerate foramen.) The middle lacerate foramen and piriform fenestra are separate openings in M2329, but they are joined into one vacuity in MNHN QU 17287 and MNHN QU 8755. However, in M2329 the middle lacerate foramen is not a distinct foramen as in more advanced carnivoramorphans, but a small vacuity. The canal for the facial nerve is floored by very thin bone anteromedially, and is open only at the lateral end of the canal. On the left side of M2329 the bony floor has been broken during preservation or preparation. This raises concerns, as expressed in earlier studies, about observations of fully open canals for the facial nerve and whether the open morphology is merely an artifact of preservation or preparation damage to the fragile bony floor (Wesley-Hunt and Flynn 2005; Wesley and Flynn 2003).

The epitympanic recess is shallowly excavated into the squamosal. The suture between the petrosal and the squamosal is very evident on the posterior wall of the recess. A foramen is present at this suture as in *Miacis parvivorus* Cope, 1872 and

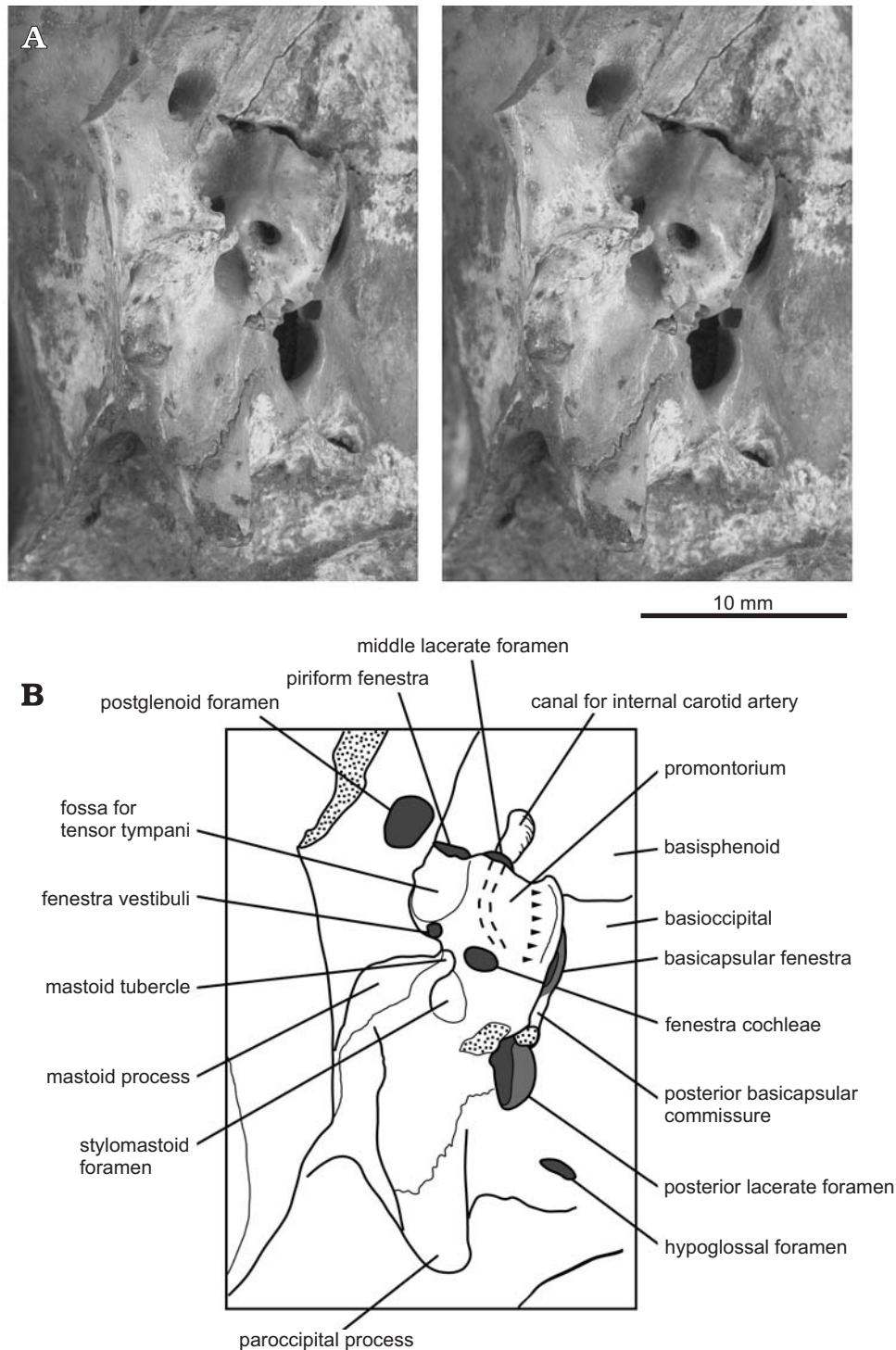


Fig. 2. *Quercygale angustidens*, upper Eocene, Quercy area, France, NRM-PZ M2329. Ventral lateral view of the right auditory region. A. Stereophoto. B. Explanatory drawing of the same. Anterior is to the top.

Oodectes. It is probable that this canal held the superior ramus of the stapedial artery as it exited the auditory region (Novacek and Wyss 1986; Wang and Tedford 1994).

The Glaserian fissure is narrow and almost closed over at its posterior dorsal extent. Lateral to the fissure, the postglenoid foramen is open, not reduced, and medial on the squamosal ridge bordering the auditory region. The alisphenoid

rises to the tegmen tympani at a shallow angle, similar to that in *Tapocyon*.

Bulla.—A firmly attached ossified bulla is not present in *Quercygale*, and no ossified bulla is preserved in any specimens. However, there is evidence on the surrounding bones that some form of bulla was present, whether ossified but

weakly attached, or fully or partially cartilaginous. On both the left and right side of the M2329 there is an indentation at the suture between the squamosal, petrosal and alisphenoid, anteromedial to the epitympanic recess and medial to the posterior extent of the Glaserian fissure. This indentation is rugose and the point of contact with the anterior crus of the ectotympanic as it is in modern carnivores and other “miacids”. There is no evidence of a smooth indentation on the alisphenoid caused by the anterior face of the ectotympanic as a result of anterior expansion of the bulla, as observed in other taxa (see Hunt 1998). Therefore, *Quercygale* probably did not have an anteriorly expanded bulla. The medial ridge of the promontorium is the most definitive evidence of contact with the tympanic, most likely the caudal entotympanic due to its linear anteroposterior extent. This ridge (Fig. 2) is smooth on the medial face and rugose on the lateral face. The rugosity extends on to the ventral surface but is limited to the medial edge of promontorium. A similar morphology can be observed on *Miacis sylvestris* (Marsh, 1872b) (AMNH 129284), however, no distinct ridge is present, just a wide roughened surface on the medial edge of the promontorium. This ridge morphology is unique to *Quercygale* among the “miacids” and Carnivora. On the ventral surface of the promontorium, medial to the anterior edge of the foramen cochlea there is a small divot or dimple that stands out from the surrounding attachment surface. This divot is of itself not noteworthy on *Quercygale*, as it is just part of the larger entotympanic attachment surface, but this feature is also present on *Oodectes*, *Miacis parvivorus*, and *Tapocyon*. These specimens do not have the extensive entotympanic attachment surfaces observed in *Quercygale*, so the more concrete association of this divot with an entotympanic attachment in *Quercygale* bolsters the argument for an entotympanic attachment in the other specimens. The roughened surface anteromedially on the promontorium supports the inferred presence of a rostral entotympanic. The medial extent of the bulla appears to be the medial ridge of the promontorium: there is no evidence of a medially expanded bulla. The apron of the promontorium posterior to the fenestra cochleae is rugose and suggests an attachment surface for the caudal entotympanic as is observed in *Nandinia* and *Tapocyon*. The mastoid shelf is smooth, as is the paroccipital process, and therefore the entotympanic was probably not expanded posteriorly past the promontorium. As observed in *Tapocyon*, *Oodectes* and *Nandinia*, there is no evidence that the caudal entotympanic was attached to the paroccipital process in *Quercygale*.

Internal carotid artery.—The carotid artery follows a course very similar to its condition in *Miacis sylvestris*. When the internal carotid artery enters the middle ear cavity it splits into a stapedial and a promontory branch. The presence of the stapedial artery is problematic. There is no evidence of a sulcus for a stapedial artery in the specimen M2329, nor in MNHN QU 17287. However, in MNHN QU 8755 the sulcus is very clear. In addition, although no sulcus is present for the stapedial artery in M2329, a canal is present, entering the

posterior wall of the epitympanic recess, presumably the course for the superior ramus of the stapedial artery to exit the middle ear cavity (Novacek and Wyss 1986; Wang and Tedford 1994). The sulcus for the promontory artery is, however, clearly defined in all the specimens observed. The simplest conclusion is that the stapedial artery is present in *Quercygale*, but that the sulcus for the stapedial artery is variably developed. *Quercygale* is one of the few genera of “Miacoida” in which it is possible to study variation in basicranial anatomy from multiple specimens.

The internal carotid artery is transpromontorial (Wible 1983, 1986) running along the promontorium on the ventrolateral surface toward the middle lacerate foramen. The artery passes anterior to the foramen and turns around on itself, forming an anterior loop before entering the brain cavity through the middle lacerate foramen (Fig. 2). This anterior loop is present in more derived “miacids” such as *Tapocyon*, *Miacis sylvestris*, and *Prohesperocyon*.

Phylogenetic analysis

Methods and data.—The phylogenetic analysis is based on Wesley-Hunt and Flynn (2005) to whom we refer for detailed information on the character matrix (cf. Appendix 1). There are some minor alterations made to the matrix for the purposes of this paper. Characters 43 and 44 of Wesley-Hunt and Flynn (M1 metastyle projection and M1 parastyle projection, respectively) have been replaced by a composite character with three states, 0 = metastyle projecting further labially, 1 = metastyle and parastyle with equal projections, 2 = parastyle projecting further labially. This was done because of the realization that characters 43 and 44 of Wesley-Hunt and Flynn (2005), due to their definition, are only semi-independent, with state 1 of character 43 being nearly the same as state 0 of character 44. This change has, in fact, not affected the analysis. Despite this minor change, we have retained the character numbering of Wesley-Hunt and Flynn (2005). Thus, our characters are numbered 1–99, but exclude #44. In addition, one stem-group taxon, *Viverravus acutus* Matthew and Granger, 1915, was added here (Polly et al. in press), and six crown-group taxa removed [*Otarocyon macdonaldi* Wang, Tedford, and Taylor, 1999, *Pteronarctos goedertae* Barnes, 1989, Otariidae, *Mephitis* sp., *Ailurus fulgens* F. Cuvier, 1825, and *Procyon lotor* (Linnaeus, 1758)], because these are redundant to the issues addressed in the present paper.

A total of 36 taxa were thus analysed using a matrix of 98 characters, of which one, placement of the middle lacerate foramen, was ordered (on the basis of analyses carried out by Hunt (1987, 1998). Tree topologies were evaluated using the heuristic search algorithms of PAUP* version 4.0b10 for Macintosh (Swofford 1998), with ACCTRAN optimization. The heuristic searches carried out 100 random addition sequence iterations. Bremer support values were calculated using TreeRot, version 2 (Sorenson 1999) and tree manipulation was carried out with Mesquite, version 1.05 (Maddison and Maddison 2004).

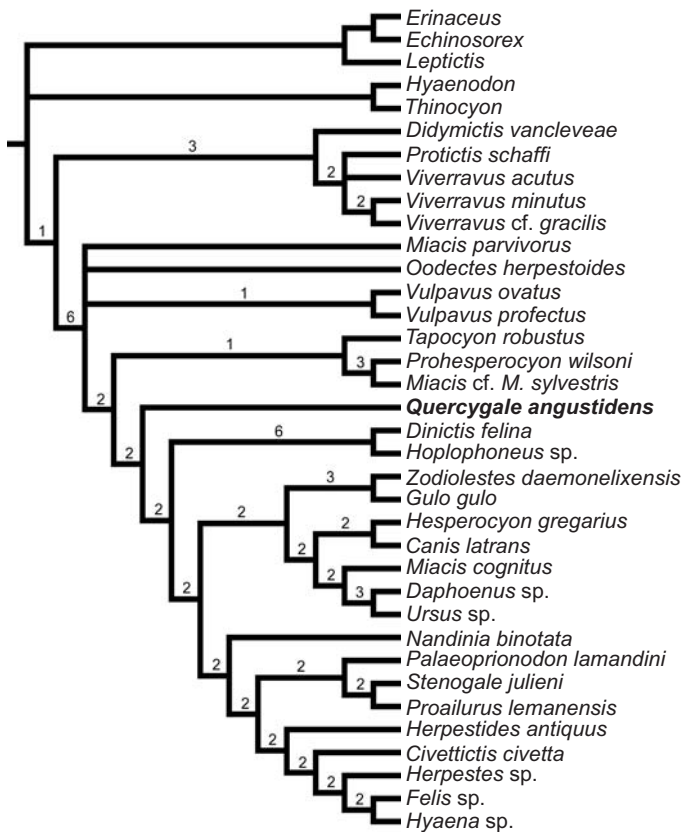


Fig. 3. Systematic position of *Quercygale*. Strict consensus of 12 most parsimonious trees; heuristic search—100 random addition sequence iterations; tree length 386 steps; consistency index = 0.339, retention index = 0.657, rescaled consistency index 0.223. Bremer support values for each ingroup node are labeled.

Results.—Of the 98 characters, 89 were parsimony-informative for the present set of taxa. The parsimony analyses using PAUP* found 12 most parsimonious trees, each of length 386, consistency index 0.339, retention index 0.657, and rescaled consistency index 0.223. The heuristic searches found these 12 trees about half the time, but only one tree island was recovered, with other searches stopping at solutions known to be suboptimal for this data set. The strict consensus tree of these 12 trees is shown in Fig. 3, which also shows the Bremer support values for each ingroup node.

The differences between the topology obtained in this study and that of Wesley-Hunt and Flynn (2005) are small but interesting. Within the Carnivora (crown-group), the topologies are identical, with two exceptions. The Nimravidae, which in their topology was the sister taxon to Feloidea, here becomes sister taxon to the remaining Carnivora. This reflects the historically unstable placement of Nimravidae (Hunt 1987; Neff 1983; Werdelin 1996; Wyss and Flynn 1993) and others. It is worth noting that both nimravid taxa used herein belong to the Nimravidae *sensu stricto*, and that this variable placement therefore does not reflect the debate regarding whether the barbooufelids represent a family distinct from the Nimravidae (Morlo et al. 2004). In addition, the present analysis moves the Amphicyonidae and “*Miacis*”

cognitus Gustafson, 1986 into successive sister-group positions relative to Ursidae and interchanges the positions of Mustelidae and Canidae. These differences can in part be ascribed to the reduced number of caniform taxa included in the analysis, but the closeness of Amphicyonidae and Ursidae has been observed in other analyses of carnivoran phylogeny (Wyss and Flynn 1993).

Among the stem lineage taxa, *Viverravus acutus* is placed together with other members of *Viverravus* in the Viverravidae of Wesley-Hunt and Flynn (2005). Resolution of the cladogram is reduced above the Viverravidae, and *Miacis*, *Oodectes*, and *Vulpavus* form an unresolved polychotomy. In our analysis, *Prohesperocyon* and *Miacis* cf. *M. sylvestris* form a clade together with *Tapocyon*, while in the analysis of Wesley-Hunt and Flynn (2005), the latter taxon was placed one step higher in the phylogeny. Finally, *Quercygale*, our target taxon in this analysis, is placed between the *Tapocyon* clade and the Carnivora, as the most derived “Miacidae” in the formulation of Wesley-Hunt and Flynn (2005).

A number of characters are of particular importance to the placement of *Quercygale* in the phylogeny (see Table 1). Character #7, proportion of frontal and parietal midline length, excludes *Quercygale* from crown-group Carnivora (including Nimravidae); #16, hypoglossal foramen position, separates *Quercygale* (and *Tapocyon*, *Prohesperocyon*, and *Miacis* cf. *M. sylvestris*) from *Vulpavus* and less derived taxa; #18, fenestra cochleae position, on the other hand, unites *Quercygale* with *Tapocyon* and other “Miacidae” of Wesley-Hunt and Flynn (2005) and excludes them from crown-group Carnivora. The state of the crown-group represents a reversal to the primitive condition exhibited by the outgroups and Viverravidae; #23, anterior loop of internal carotid artery, unites *Quercygale* and the *Tapocyon* clade with nimravids and caniforms; #25, position of the internal

Table 1. Character matrix for *Quercygale*. Refer to the Appendix 1 for character descriptions and Wesley-Hunt and Flynn (2005) for more detailed discussion.

Characters	0 0 0 0	0 0 0 0	1 1 1 1	1 1 1 1	1 1 1 1
	1 2 3 4	5 6 7 8 9	0 1 2 3 4	5 6 7 8 9	
<i>Quercygale</i>	1 0 0 1	1 2 0 0 0	0 0 0 1 0	0 1 ? 1 0	
	2 2 2 2 2	2 2 2 2 2	3 3 3 3 3	3 3 3 3 3	
	0 1 2 3 4	5 6 7 8 9	0 1 2 3 4	5 6 7 8 9	
	1 1 0 1 1	0 1 0 1 0	1 0 0 0 0	0 0 0 0 1	
	4 4 4 4 4	4 4 4 4 4	5 5 5 5 5	5 5 5 5 5	
	0 1 2 3 4	5 6 7 8 9	0 1 2 3 4	5 6 7 8 9	
	0 1 0 2 -	1 0 0 1 0	0 1 1 1 1	2 1 1 0 1	
	6 6 6 6 6	6 6 6 6 6	7 7 7 7 7	7 7 7 7 7	
	0 1 2 3 4	5 6 7 8 9	0 1 2 3 4	5 6 7 8 9	
	0 0 ? 0 0	0 0 0 0 0	? ? 0 ? ?	? ? ? 0 0	
	8 8 8 8 8	8 8 8 8 8	9 9 9 9 9	9 9 9 9 9	
	0 1 2 3 4	5 6 7 8 9	0 1 2 3 4	5 6 7 8 9	
	0 0 0 0 0	0 1 0 1 ?	? ? ? ? ?	? ? ? ? ?	

carotid artery, is another character that excludes *Quercygale* and other “Miacidae” from crown-group Carnivora; #26, apron shelf on promontorium, on the other hand, unites *Quercygale* (as well as *Tapocyon* and *Vulpavus ovatus* Matthew, 1909) with crown-group Carnivora; #32, squamosal/alisphenoid contact from anterior crus, also excludes *Quercygale* from crown-group Carnivora, as does #34, extent of flange on basioccipital lateral edge; #45, parastyle direction, however, unites *Quercygale* and the *Tapocyon* clade with crown-group Carnivora; #52, M1 size, also unites *Quercygale* and *Tapocyon* with crown-group Carnivora, as does #53, presence/absence of M3; #56, P4 protocone size, also unites *Quercygale* and the *Tapocyon* clade with crown-group Carnivora, while #66, position of postorbital constriction, excludes them from crown-group Carnivora; finally, #88, presence/absence of m3, is again a character that unites *Quercygale* (but not the *Tapocyon* group) with crown-group Carnivora. In summary, the analysis points to a number of characters that are important to placing *Quercygale* near crown-group Carnivora (and *Tapocyon*), but other characters definitely exclude *Quercygale* from the crown-group.

Discussion

Quercygale appears to be highly derived both in dentition and in basicranial anatomy, yet plesiomorphic in some of its morphology. It has a relatively derived auditory region when compared to other “miacoids”, for example, the morphology of the promontorium in *Quercygale* is not seen in any other “miacid” or carnivoran. In addition there is a clear attachment surface for the caudal entotympanic on the promontorium, and an anterior loop to the carotid artery is present. However, based on the evidence from surrounding bones, the bulla does not appear to be as expanded as in *Tapocyon* or *Prohesperocyon*; in fact, the bulla in *Quercygale* does not appear to be expanded at all, anteriorly, medially or posteriorly. The open piriform fenestra is also a more primitive condition.

This morphological assessment is reflected in the position of *Quercygale* in the phylogeny presented herein. It is placed as the sister-taxon to crown-group Carnivora (but see below for a consideration of the latter), and both the node below and that above *Quercygale* has Bremer support of two, so that the shortest tree that does not include *Quercygale* in this position is at least two steps longer. Many authors (Beaumont 1965; Flynn and Galiano 1982; Van Valen 1967a) have suggested a close relationship between *Quercygale* and *Tapocyon*, and this is borne out in the present analysis. However, we here suggest that *Quercygale* is more derived in the direction of crown-group Carnivora, particularly in the loss of M3 and m3 and possibly some other features; *Quercygale* is more hypercarnivorous than *Tapocyon* in other dental features as well. Given the uncertainties inherent in the present analysis, as well as that of Wesley-Hunt and Flynn (2005), it is not impossible that *Tapocyon* and *Quercygale* may eventually be found to form a monophyletic group, possibly to-

gether with *Prohesperocyon* and *Miacis* cf. *M. sylvestris*. In any case, the position of *Quercygale* in the vicinity of the *Tapocyon* clade shows that the transition from “Miacidae” to Carnivora was a general trend in the middle and late Eocene, with taxa from both North America and Eurasia involved.

Be that as it may, the present analysis also has some implications for the overall phylogeny of Carnivoramorpha. First of all, if the position of Nimravidae recovered herein is confirmed, this would place the family outside the crown-group Carnivora, defined phylogenetically as all extant Carnivora and their cladistically nearest relatives (see Wyss and Flynn 1993). The position of Nimravidae thus remains a key issue in carnivoran phylogenetics. Second, the appearance of a monophyletic clade including *Tapocyon* may be an indication that with additional data, a monophyletic Miacidae (or Quercygalidae) may be found to exist. Third, the placement of *Quercygale* and Nimravidae affects the diagnosis of Carnivora as given by Wesley-Hunt and Flynn (2005) in so far as loss of M3 can no longer be considered a synapomorphy of Carnivora. Even if Nimravidae were found to belong within the crown-group, the loss of M3 in *Quercygale* places the loss of M3 outside Carnivora, since this taxon lacks the other character states diagnostic of Carnivora (flange on basioccipital lateral edge well-developed [34(2)], expanded braincase, fronto-parietal suture anteriorly located [66(1)]).

The present analysis of the basicranial morphology of *Quercygale* and accompanying phylogenetic analysis shows that with more data we find more variations on the theme of how a carnivoramorphan basicranium can be constructed. The new data provide us with a refined understanding of basal carnivoramorphan interrelationships. The backbone of the phylogeny of Carnivoramorpha now seems quite stable, with a basal, monophyletic Viverravidae, a miacid stem-lineage and a crown-group Carnivora. However, many details are still unstable between analyses, such as the position of Nimravidae and whether there is a monophyletic clade intermediate in position between Viverravidae and Carnivora. The present analysis places *Quercygale* as the most derived miacid. Only further study of more taxa can determine the validity of this position.

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Appendix 1

Character states and descriptions (characters derived from other studies are noted and cited). For discussion of characters, refer to Wesley-Hunt and Flynn (2005).

1. Lacrimal facial process: 0: broad rostral flange; 1: small, present on face; 2: not present on face; 3: orbital flange reduced to area around lacrimal foramen (in part Wyss and Flynn 1993; character 7).
2. Ventral exposure of premaxilla; posterior extent of premaxilla, lateral to palatal foramen: 0: lateral to canine; 1: anterior to canine.
3. Shape of infraorbital foramen: 0: elongate; 1: round.
4. Position of infraorbital foramen: 0: above P3; 1: above anterior edge of P4; 2: above mid-posterior portion of P4.
5. Length of palate—position of the posterior edge of palatine midline relative to tooth row (modified from Bryant 1991; character 2): 0: posterior to upper tooth row; 1: anterior or equal to upper tooth row.
6. Palatine canal primary anterior opening (Bryant 1991; character 3): 0: opening through palatine; 1: at maxilla-palatine suture; 2: opening through maxilla.
7. Relative length of frontal and parietal at midline: 0: parietal greater than frontal; 1: parietal equal or sub equal to frontal; 2: frontal midline much longer than parietal.
8. Postorbital process: 0: prominent; 1: small, reduced.
9. Paroccipital process size: 0: well developed; 1: reduced.
10. Paroccipital process shape: 0: simple process; 1: laterally flattened, thin, but is distinct process; 2: cupped around bulla, process not distinct; 3: absent.
11. Placement of postglenoid foramen: 0: medially placed; 1: more lateral, external, very near edge of skull.
12. Postglenoid foramen: 0: present; 1: greatly reduced, or missing.
13. Shape of mastoid process: 0: forming a distinct process, extending out farther than paroccipital process, or subequal; 1: blunt, rounded, does not protrude significantly, more a swelling of the mastoid; 2: thin plate, no distinct process.
14. Direction of mastoid process extension: 0: lateral-ventral; 1: ventral; 2: lateral; 3: none, or only swelling.
15. Condylod (hypoglossal) foramen position relative to posterior lacerate foramen: 0: distant; 1: close (less than the diameter of the hypoglossal foramen away); 2: conjoined with posterior lacerate foramen.
16. Condylod (hypoglossal) foramen position relative to groove between the occipital condyle and the paroccipital process: 0: in line or within groove; 1: anterior to groove.
17. Posterior lacerate foramen: 0: present as a vacuity between the promontorium and the basioccipital; 1: present as an individual foramen.
18. Fenestra cochleae (rotunda) position relative to mastoid tubercle (Wesley-Hunt and Flynn 2005: fig. 8): 0: posterior to mastoid tubercle; 1: anterior, subequal to mastoid tubercle.
19. Relative distance between the foramen ovale and the alisphenoid canal: 0: separated by at least the diameter of the alisphenoid canal; 1: separated only by a thin wall; 2: no alisphenoid canal present.
20. Ossification of tegmen tympani: 0: facial nerve exposed ventrally; 1: facial nerve partially embedded within tegmen tympani and floored in anteromedial segment; 2: facial nerve beneath a bony sheath, which defines the fossa for tensor tympani muscle (in part Wang and Tedford 1994; character 3).
21. Contact of promontorium and basioccipital: 0: promontorium isolated; 1: promontorium in contact with basioccipital (Wang and Tedford 1994; character 4).
22. Composition of mastoid tubercle: 0: formed by petrosal; 1: formed by squamosal (modified from Wang and Tedford 1994; character 6).
23. Anterior loop of internal carotid artery (Wesley-Hunt and Flynn 2005: fig. 8): 0: absent; 1: present—excavation in basisphenoid; 2: present—but extrabullar (in part Wang and Tedford 1994; character 7).
24. Suprameatal fossa (fossa on squamosal anterior to mastoid): 0: absent; 1: small; 2: large, well developed (in part Wang and Tedford 1994; character 8).
25. Position of internal carotid artery: 0: laterally positioned, transpromontorial, runs close to margin of fenestra cochleae, presence of a promontory artery, groove for stapedial artery may or may not be present; 1: transpromontorial but medially positioned, course far from fenestra cochleae; 2: medial, extrabullar, inside a bony canal formed by the caudal entotympanic. (in part Wang and Tedford 1994; character 11; see also Hunt 1987).
26. Apron shelf on promontorium posterior to fenestra cochleae for entotympanic attachment (anatomical reference: Hunt 1998): 0: absent; 1: blunt—surface present posterior to fenestra cochleae, but no extensive attachment possible; 2: extended, large area for attachment, may roof posterior bullar chamber.
27. Ventral process of promontorium (anatomical reference: Hunt 1989, 1998): 0: absent; 1: present, medially positioned on promontorium; 2: present, anteriorly positioned.
28. Shape of the promontorium, anterior extension: 0: elongate, apron extension tapers to a point anteriorly, almond-like in appearance; 1: elongate, rounded anteriorly; 2: blunt, quickly truncating; 3: elongate, apron is broad, flat extension, not almond shaped and not blunt.
29. Facet on promontorium indicative of ectotympanic contact (anatomical reference: Hunt 1998): 0: absent; 1: present.
30. Surface of the anterior-medial promontorium or tympanic wing of basisphenoid: 0: smooth; 1: roughened surface associated with attachment of rostral entotympanic, or rostral entotympanic present.
31. Inferior petrosal sinus: 0: small; 1: greatly enlarged (Wang and Tedford 1994; character 16); 2: excavation into basioccipital extremely deep (Wyss and Flynn 1993; character 22).
32. A deep, well-developed fossa or pit on the squamosal/alispheoid recording the contact with the anterior crus or anterior face of the ectotympanic (Wesley-Hunt and Flynn 2005: fig. 8, and Hunt 1998): 0: absent, may have slight/shallow indentation; 1: present, well developed, or bulla present and fully ossified.
33. Shelf between mastoid process and paroccipital process: 0: laterally wide, curved trough with smooth surface; 1: laterally wide, could have flat surface, rugose or bulbous, no smoothed out trough; 2: very thin, outside edge could be raised; 3: no shelf present.
34. Extent of flange on basioccipital lateral edge bordering auditory region: 0: absent; 1: small, nascent; 2: well developed when compared to basal “miacids”.
35. Evidence on basisphenoid and basioccipital for marked medial inflation of the entotympanic (anatomical reference: Hunt 1998): 0: absent; 1: present—inflation of entotympanic pushing medially onto and over the basioccipital.
36. Evidence of marked posterior inflation of the entotympanic; entotympanic attached during life to paroccipital process or to extensive area posterior to the petrosal (anatomical reference: Hunt 1998): 0: absent; 1: present.
37. Fossa for the stapedius muscle: 0: borders tightly defined, and anteriorly bound by the mastoid; 1: general area of muscle insertion, open, less defined.
38. Epitympanic wing of the petrosal forms ventral floor to the anterior medial corner of the fossa for the tensor tympani muscle (Wesley-Hunt and Flynn 2005: fig. 9): 0: absent; 1: present, but relatively flat and horizontal; 2: ventral floor present, but not horizontal, instead it forms a delicate “tube”, the bony floor is not extension of petrosal.
39. Fossa for the tensor tympani muscle, defined and deep, excavating well dorsal of the level of the fenestra vestibuli (Wesley-Hunt and Flynn 2005: fig. 8): 0: absent, fossa for the tensor tympani muscle shallow, not strongly defined; 1: present, defined and deep; 2: shallow/absent—tensor tympani inserts on eustachian canal (in part Wyss and Flynn 1993).
40. Placement of middle lacerate foramen (Wesley-Hunt and Flynn 2005: fig. 8): (Ordered) 0: foramen a vacuity—not defined anteriorly nor posteriorly, positioned directly anterior to petrosal; 1: foramen anteriorly defined, posteriorly bordered by petrosal—positioned equal or posterior to basisphenoid/basioccipital suture; 2: foramen defined anteriorly, petrosal may be undefined posterior border, foramen positioned in basisphenoid (or edge of alispheoid) just anterior to basisphenoid/

- basioccipital suture; 3: foramen defined anteriorly and posteriorly completely bordered by basisphenoid, foramen positioned far anterior to basisphenoid/basioccipital suture (anatomical reference: Hunt 1987, 1998):
41. M1: a defined cingulum continuous around the lingual face of the protocone: 0: absent; 1: complete cingulum present; 2: anterior segment of cingulae absent or smaller than posterior cingulae (in part Wang and Tedford 1994; character 2).
 42. M1: protocone height relative to paracone: 0: protocone shorter than paracone; 1: protocone equal or subequal to height of paracone.
 43. M1 metastyle and parastyle projection: 0: metastyle projecting further labially; 1: metastyle and parastyle with equal projections; 2: parastyle projecting further labially.
 44. Removed from analysis, as discussed in text.
 45. M1: parastyle direction: 0: buccally with anterior direction; 1: buccally; 2: no parastyle present.
 46. M1: size: 0: well developed; 1: markedly reduced.
 47. M1: size of posterior lingual cingular shelf at base of protocone: 0: posterior lingual cingular shelf equal or subequal to anterior cingulum; 1: posterior lingual cingular shelf more pronounced, larger than anterior cingulum.
 48. M1: relative height of paracone and metacone: 0: equal or subequal; 1: paracone taller than metacone.
 49. M1: relative height of paraconule and metaconule: 0: paraconule greater than metaconule; 1: paraconule equal or subequal to metaconule; 2: both absent; 3: metaconule enlarged, greater than paraconule.
 50. M1: presence of hypocone: 0: absent; 1: present (distinct cusp); 2: present, formed by swelling of entire cingulum ridge (Wyss and Flynn 1993; character 44).
 51. M1: width of parastylar shelf: 0: lack of a shelf; 1: broad; 2: narrow, consisting mainly of ridge.
 52. Presence of M2: 0: present; 1: residual or reduced, simplified morphology, less than half the size of M1; 2: absent.
 53. Presence of M3: 0: present; 1: absent.
 54. P4/m1 carnassial shear: 0: absent; 1: present (Wyss and Flynn 1993; character 31).
 55. P4: size of parastyle cusp: 0: absent; 1: well developed, defined cusp; 2: present as bulge on cingulum, reduced.
 56. P4: protocone: 0: large, well developed; 1: reduced or absent (Bryant 1991; Flynn 1998; Wyss and Flynn 1993).
 57. P4: size of metastylar blade: 0: short; 1: elongate.
 58. Posterior accessory cusps on P3: 0: one cusp present; 1: two cusps present; 2: absent.
 59. m2 talonid morphology: 0: high trigonid with extremely elongate talonid due to large hypoconulid, tooth elongate oval outline; 1: talonid not elongate, tooth oval outline, no enlarged hypoconulid; 2: low trigonid, extremely elongate with low, well-developed talonid cusps; 3: absent (revised from Flynn 1998).
 60. Palatine, relative size: 0: midline length of palatine less than midline length of maxilla; 1: midline length greater than midline length of maxilla. (Wyss and Flynn 1993; character 2).
 61. Posterior width of palate (*versus* width between canines): 0: wider than width at canines; 1: nearly equal (resulting in nearly parallel tooth rows). (Wyss and Flynn 1993; character 3).
 62. Turbinal bones: 0: simple development of maxilloturbinals in nasal cavity; 1: maxilloturbinals large and branching, excluding nasoturbinals from narial opening. (Wyss and Flynn 1993; character 4).
 63. Posterior projection of nasals: 0: nasals terminate anterior to, or in extreme anterior region of, orbit, projecting at most slightly between frontals; 1: nasals project deeply between frontals, far posterior of anterior orbital rim; 2: nasals with W-shaped termination; 3: nasals with flat termination. (Wyss and Flynn 1993; character 6).
 64. Jugal: 0: reaches lacrimal, or is separated from it by only thin sliver of maxilla; 1: widely separated from lacrimal, maxilla broadly laps posteriorly over anterior orbital rim. (Wyss and Flynn 1993; character 8).
 65. Anterior extent of palatine in orbit: 0: broadly contacts lacrimal; 1: fails to contact lacrimal. (Wyss and Flynn 1993; character 10).
 66. Postorbital constriction: 0: just anterior to fronto-parietal suture, near posterior margin of frontal; 1: braincase expanded, with frontals making much greater contribution; fronto-parietal suture located more anteriorly in frontal. (Wyss and Flynn 1993; character 11).
 67. Posterior entrance of carotid artery into auditory capsule: 0: posterior entry, artery not enclosed in osseous tube; 1: posterior entry, artery enclosed in tube; 2: anterior entry, artery enclosed in osseous tube; 3: anterior entry, artery not enclosed in tube. (Wyss and Flynn 1993; character 16).
 68. Entotympanic: 0: fails to ossify, or is only weakly attached to auditory capsule; 1: ossified at least partially, and firmly fused to the skull. (Wyss and Flynn 1993; character 17).
 69. Ectotympanic contributes to external auditory meatal tube: 0: no; 1: yes. (Wyss and Flynn 1993; character 18).
 70. Ectotympanic septum: 0: absent; 1: present. (Wyss and Flynn 1993; character 19).
 71. Entotympanic septum: 0: absent; 1: present. (Wyss and Flynn 1993; character 20). In this analysis Hyaenidae was coded as the derived condition based on Ivanoff (2001).
 72. Fenestra cochleae: 0: approximately equal in size to fenestra ovalis, cochlear fossula not developed; 1: at least three times the area of oval window, cochlear fossula well developed. (Wyss and Flynn 1993; character 24).
 73. Malleus, muscular process: 0: present; 1: absent. (Wyss and Flynn 1993; character 26).
 74. Malleus, processus gracilis and anterior lamina: 0: well developed; 1: reduced. (Wyss and Flynn 1993; character 27).
 75. Major a2 arterial shunt: 0: small; 1: large, intracranial rete. (Wyss and Flynn 1993; character 28).
 76. Major a4 arterial shunt: 0: absent; 1: present. (Wyss and Flynn 1993; character 29).
 77. Major anastomosis x: 0: absent; 1: present. (Wyss and Flynn 1993; character 30).
 78. i1: 0: present; 1: absent. (Wyss and Flynn 1993; character 32).
 79. P1: 0: present; 1: absent. (Wyss and Flynn 1993; character 33).
 80. P3 lingual cusp: 0: absent; 1: present. (Wyss and Flynn 1993; character 34).
 81. P4 metastyle: 0: V- or slit-shaped notch; 1: notch absent. (Wyss and Flynn 1993; character 36).
 82. P4 protocone: 0: medial or posterior to paracone; 1: anterior to paracone. (Wyss and Flynn 1993; character 37).
 83. P4 hypocone: 0: absent; 1: present. (Wyss and Flynn 1993; character 39).
 84. p1: 0: present; 1: absent. (Wyss and Flynn 1993; character 40).
 85. m1 talonid: 0: present; 1: absent. (Wyss and Flynn 1993; character 41).
 86. Lower molars: 0: subequal in size; 1: m1 much larger than m2–3, and progressive decrease in size from m1–3. (modified from Wyss and Flynn 1993; character 42).
 87. M2 hypocone: 0: absent; 1: present. (Wyss and Flynn 1993; character 47).
 88. m3: 0: present; 1: absent. (Wyss and Flynn 1993; character 51).
 89. Baculum: 0: small and simple or absent; 1: long, stylized. (Wyss and Flynn 1993; character 52).
 90. Scapula, postscapular fossa: 0: absent; 1: present. (Wyss and Flynn 1993; character 53).
 91. Tail: 0: long; 1: reduced. (Wyss and Flynn 1993; character 54).
 92. Scaphoid and lunare: 0: unfused; 1: fused. (Wyss and Flynn 1993; character 55).
 93. Hallux: 0: present; 1: greatly reduced or absent. (Wyss and Flynn 1993; character 56).
 94. Femur, third trochanter: 0: present; 1: absent. (Wyss and Flynn 1993; character 57).
 95. Cowper's (bulbourethral) gland: 0: present; 1: absent. (Wyss and Flynn 1993; character 58).
 96. Prostate gland: 0: small/vestigial; 1: large, ampulla bilobed. (Wyss and Flynn 1993; character 59).
 97. Kidneys: 0: simple; 1: conglomeratic. (Wyss and Flynn 1993; character 60).
 98. Anal glands: 0: simple; 1: enlarged and having enlarged anal sac. (Wyss and Flynn 1993; character 63).
 99. Terminal phalanges: 0: fissured; 1: simple. (Wyss and Flynn 1993; character 64).