

Carotid circulation in amniotes and its implications for turtle relationships

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With 2 figures

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Abstract: The pattern of carotid blood vessel circulation in the skull of amniote vertebrates is reviewed, considering both fossil and extant taxa. Based on comparisons of early synapsids, mammaliaforms, eureptiles, parareptiles, as well as amniote outgroups, it is shown that in most amniotes the cerebral branch of the carotid artery separates from the palatal branch prior to entering the braincase, with the cerebral branch piercing the basisphenoid ventrally and exiting within the pituitary fossa, and the palatal branch continuing in an anterior direction ventral to the braincase. In squamates and parareptiles this pattern is different in that the carotid artery enters the braincase dorsolaterally to the basiptyergoid process, and the palatine and the cerebral branches separate from each other inside the bone and exit within the pituitary fossa. Birds, crown turtles, and some sauropterygians display a pattern which at least to some extent resembles that of squamates and parareptiles. Optimization of patterns of carotid circulation on a generalized amniote phylogeny with variable placement of turtles indicates that independent of turtle position, the separation of cerebral and palatal branch prior to entering the braincase must be considered plesiomorphic for amniotes. Because early turtles such as *Proganochelys* also retain the plesiomorphic condition, carotid circulation does not support a grouping of turtles within parareptiles.

Key words: Amniota, Parareptilia, Testudinata, braincase, *Arteria carotis interna*.

1. Introduction

The origin of turtles and their phylogenetic position among amniotes have captured the attention of palaeontologists and systematists since the end of the 19th century, and have become one of the most controversial topics in amniote evolution (RIEPEL 2002, 2008 and references therein). While the more traditional view supports a grouping of turtles with parareptiles such as pareiasaurs (GREGORY 1946; LEE 1993, 1995, 1997, 2001), procolophonids (REISZ & LAURIN 1991; LAURIN &

REISZ 1995), and *Eunotosaurus* (CARROLL 1988; LYSON et al. 2010), recent palaeontological and molecular studies suggest that turtles may be nested within Diapsida, related closely either to sauropterygians (RIEPEL & DEBRAGA 1996; DEBRAGA & RIEPEL 1997; RIEPEL & REISZ 1999), lepidosaurs (MÜLLER 2003, 2004; HILL 2005) or archosaurs (LØVTRUP 1977; GARDINER 1993; KUMAZAWA & NISHIDA 1999; REST et al. 2003; MEYER & ZARDOYA 2003; BHULLAR & BEVER 2009). GAUTHIER et al. (1988) also suggested that turtles form a monophyletic group with captorhinids as outgroup to Diapsida.

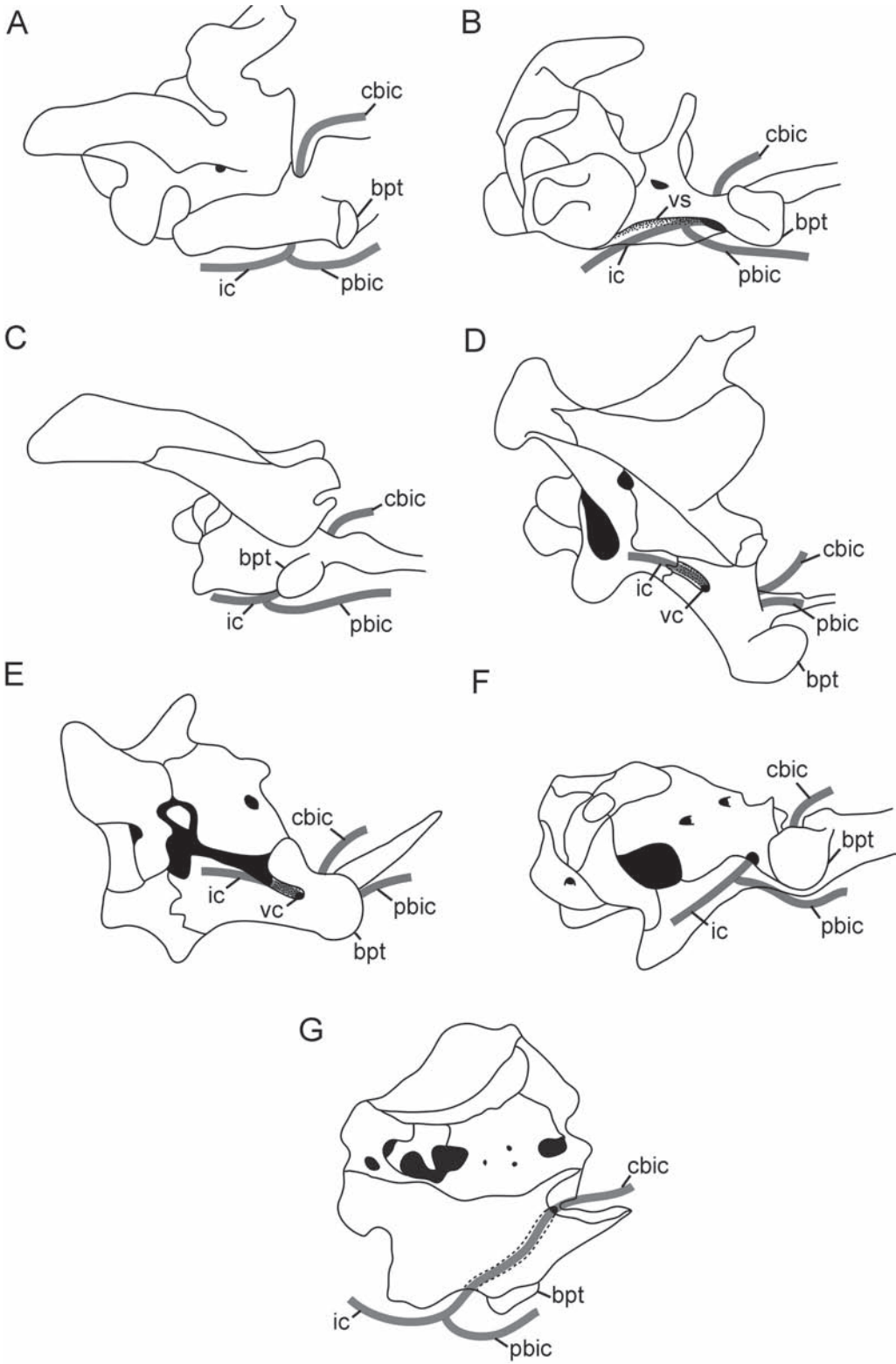


Fig. 1.

As part of the controversy on turtle origins, the homology of several characters postulated to be synapomorphies of turtles and their proposed sister groups have been discussed. Among those, the homology of the acromion (LEE 1996, 1998; RIEPPEL 1996), the hooked fifth metatarsal (RIEPEL & REISZ 1999; LEE 1997; FRABREZI et al. 2008), the laterosphenoid (GAFFNEY 1990; BHULLAR & BEVER 2009), and the dermal armour (RIEPEL & REISZ 1999; JOYCE et al. 2009; SCHEYER & SANDER 2009) figured most prominently. Recently, STERLI et al. (2010) described the parabasisphenoid complex of several fossil turtles and observed that in most turtles the parasphenoid expands posteriorly below the basisphenoid, covering the latter ventrally and variably enclosing the internal carotid artery in bone. In the course of this study it became apparent that no comprehensive overview of the carotid circulation in amniotes exists in the literature. In this contribution, we therefore examine the basicranium of basal amniotes and review the evolution of the carotid circulation to establish the primary homology of the involved structures, focusing on the basal members of the different major clades. Also, we optimize patterns of carotid circulation on various amniote phylogenies and discuss the results in light of the different views of turtle relationships.

It should be noted that our inferences of carotid circulation in fossil amniotes are nested within the phylogenetic bracket of extant amniote relationships. As such, they rest on the assumption that the braincase morphologies of the individual fossil taxa can be homologized with those of their extant relatives, for which, in all major clades, both the hard part anatomy and the course of the internal carotid artery are known in great detail. Because it has been shown that the hard part anatomy of the amniote braincase sufficiently reflects the pattern of carotid circulation (see e.g. OELRICH 1956), we consider this approach appropriate for the present study.

2. Results

2.1. Carotid circulation in Synapsida and early Eureptilia

In early synapsids such as the pelycosaurian-grade synapsids *Dimetrodon* and *Haptodus* (ROMER & PRICE 1940; CURRIE 1977) and also in mammaliaforms such as *Morganucodon* (KERMACK et al. 1981), the cerebral (internal) branch of the carotid artery pierces the (para) basisphenoid to enter the hypophyseal fossa medial to the base of the basiptyergoid process on the ventral side of the braincase, whereas the palatal branch of the artery continues ventrally to the braincase in an anterior direction, medial to the basiptyergoid processes (Fig. 1A). The entrance foramina for the paired cerebral branch are clearly visible in ventral view. In early eureptiles this pattern is very similar; in the Late Carboniferous captorhinid *Concordia* the groove of the cerebral artery, or 'Vidian sulcus', can be seen on the ventral surface of the (para)basisphenoid and trends anteriorly, passing medial to the basiptyergoid process with the posterior foramen for the entrance of the cerebral carotid (foramen carotici cerebri posterior) being situated on the ventral side (MÜLLER & REISZ 2005: fig. 2). A similar pattern is retained in the moradisaurine captorhinid *Labidosaurus* (MODESTO et al. 2007: fig. 5) and in *Captorhinus* (HEATON 1979), whereas the (para)basisphenoid becomes slightly expanded laterally and comes to underlie the course of the cerebral artery ventrally, thus forming a more prominently expressed Vidian sulcus, which opens laterally (Fig. 1B).

2.2. Carotid circulation in Diapsida

A pattern similar to that of synapsids and non-diapsid eureptiles is also observed in early diapsids, as evidenced by the Late Permian *Youngina* (EVANS 1987) and the Middle Triassic thalattosaur *Askeptosaurus*

Fig. 1. The braincase and the pattern of the internal carotid artery in selected amniotes (A – F right lateral view, G internal view of the left side). **A** – the synapsid *Dimetrodon* (after ROMER & PRICE 1940); **B** – the early eureptile *Captorhinus* (after HEATON 1979); **C** – the early archosauriform *Fugusuchus* (after GOWER & SENNIKOV 1996); **D** – the squamate *Ctenosaura* (after OELRICH 1956); **E** – the parareptile *Procolophon* (after CARROLL & LINDSAY 1985); **F** – the reptiliomorph *Seymouria* (after WHITE 1939); **G** – the Triassic turtle *Proganochelys* (after GAFFNEY 1990). Abbreviations: bpt, basiptyergoid process; cbic, cerebral branch of the internal carotid artery; ic, internal carotid artery; pbic, palatal branch of the internal carotid artery; vc, Vidian canal; vs, Vidian sulcus. Not to scale.

(MÜLLER 2005), which both show an open Vidian sulcus passing medial to the basiptyergoid process. In lepidosaurs, the situation is more complex: whereas in *Sphenodon* the same pattern as in early diapsids is observed (RIEPEL 1980), squamates show the Vidian sulcus to be closed and transformed into a Vidian canal, with the entrance foramen for the internal carotid artery (= foramen posterior canalis carotici interni, GAFFNEY 1979) positioned dorsolateral, and somewhat posterior, to the basiptyergoid process (OELRICH 1956; Fig. 1D). The division of the carotid artery into a cerebral and palatal branch takes place inside the (para) basisphenoid, with the palatine artery exiting lateral to the crista trabecularis within the anterodorsal part of the (para)basisphenoid, and the cerebral branch exiting dorsal to the crista trabecularis.

A morphology largely similar to early diapsids can be seen in archosauromorphs such as *Prolacerta* (EVANS 1986) and the rhynchosaurs *Hyperodapedon* and *Stenaulorhynchus* (BENTON 1983) as well as in the earliest known archosauriforms (GOWER & SENNIKOV 1996; GOWER & WEBER 1998; GOWER & WALKER 2002; Fig. 1C). More derived crurotarsan ('crocodilian-line') archosaurs show the posterior foramen for the entrance of the cerebral artery (foramen carotici cerebralis posterior) to be situated on the lateral surface of the parabasisphenoid, whereas the palatine branch is interpreted by GOWER (2002) to continue in an open channel and to branch off the cerebral artery before the latter enters the braincase. In crocodiles, the evolution of a secondary palate and the resulting fusion of the dermal palate to the basicranium resulted in a more posteriorly situated entrance of the internal carotid into the braincase through the basioccipital (RIEPEL 1993), whereas embryological evidence suggests that ancestrally the internal carotid entered the braincase laterally (GOWER & WEBER 1998). Modern crocodiles also lack the palatine artery (SHINDO 1914).

In birds, there is a lateral Vidian canal through which the internal carotid artery enters the braincase, splitting into cerebral and palatine branches inside the bone, with the latter exiting dorsal to the basiptyergoid process (STARCK 1979), and the cerebral branch exiting through the pituitary fossa. In comparison to squamates, the posterior entrance foramen of the Vidian canal is situated further posteriorly in birds.

The pattern of internal carotid circulation is not completely understood in Sauropterygia. In all sauropterygians, with the exception of Plesiosauridae and Plesiosauria, the dermal palate ossifies extensively: the pterygoids extend posteriorly almost to the level

of the occipital condyle (less so in placodontoids and cyamodontoids) and close the interptyergoid vacuity, obscuring the basicranium in ventral view. In Placodontoidea and Cyamodontoidea, the internal carotid passes through the posteriorly open cranioquadrate passage, but anterior to this passage its course is mostly unknown (RIEPEL 1995, 2000, 2001). According to RIEPEL (2001), there is some indication that the internal carotid enters the basicranium between the basisphenoid and the otic capsule (mostly the prootic) in one species of *Cyamodus*, which resembles the condition in squamates. However, whether or not the split between the cerebral and palatine branches occurs within the bone remains unknown. A peculiar internal carotid circulation is documented in *Simosaurus*, *Nothosaurus*, and *Cymatosaurus* (RIEPEL 1994, 2001; RIEPEL & WERNEBURG 1998): the ossification of the pterygoid in the posterior part of the skull is remarkably developed and extensively sutured to the basioccipital, significantly reducing the posterior opening of the cranioquadrate passage. In these taxa, the internal carotid enters the skull posteriorly in the quadrate ramus of the pterygoid, runs through this bone for a short distance, exits into the cranioquadrate space, and travels forward into a groove on the dorsolateral part of the basioccipital and basisphenoid. The internal carotid then enters the basicranium between the basisphenoid and otic capsule and divides into cerebral and palatine branches within the bone. In Pistosauridae and Plesiosauria, the ossification of the pterygoid is less pronounced posteromedially and the interptyergoid vacuity is open, revealing the basicranium in ventral view (O'KEEFE 2001). In taxa where this area is sufficiently preserved (i.e. only some plesiosaurs), paired foramina for the internal carotid (probably the cerebral branch only) are present on the ventral surface of the basisphenoid, which recalls the plesiomorphic amniote condition, and the internal carotid likely passes through the posterior interptyergoid vacuity, splitting into cerebral and palatine branches outside the bone.

2.3. Carotid circulation in Parareptilia

In parareptiles the situation is very similar to that seen in squamates, as already noted by SHISHKIN (1968) for the procolophonoid *Phaantosaurus*. In this taxon, but also in other procolophonoids such as *Leptopleuron* (SPENCER 2000) and *Procolophon* (CARROLL & LINDSAY 1985) a Vidian canal is present, and its posterior entrance foramen is in the same position as that of squamates (Fig. 1E). Similarly, the division of the carotid

artery into cerebral and palatal branches occurs within the bone, with the cerebral branch exiting dorsally into the pituitary fossa and the palatal artery leaving through a foramen anteromedial to the basiptyergoid process (SHISHKIN 1968). In the sister clade to Procolophonoidea, which consists of 'nycteroleters' and pareiasaurs (MÜLLER & TSUJI 2007; TSUJI & MÜLLER 2009), current evidence suggests that the pattern is largely identical. The pareiasaur *Pareiasuchus* from the Late Permian of South Africa also shows a Vidian canal on the dorsolateral surface of the parabasisphenoid (HAUGHTON 1929), and the same appears to be true for the Russian taxon *Deltavjatia* (LINDA TSUJI, pers. comm.). In this context it should be noted that LEE et al. (1997) describe an unusual configuration of 'anterior' and 'posterior' foramina on the ventral surface of the parabasisphenoid, between the basiptyergoid processes, in a newly prepared specimen of *Pareiasuchus*. While the posterior foramen seems to exit on the dorsal surface of the basiptyergoid process, the course of the anterior foramen is unclear (LEE et al. 1997). Also a juvenile specimen of *Deltavjatia* apparently shows a foramen similar to the anterior one described by LEE et al. (1997; LINDA TSUJI, pers. comm.). However, because both taxa possess foramina on the dorsolateral side of the basiptyergoid process that are similar to what has been described as posterior foramina of the vidian canal in procolophonoids, we consider the condition of the carotid artery identical in pareiasaurs. A minor difference from the procolophonoid condition may be that the paired palatal branch exits via a single foramen in the anterodorsal area of the parabasisphenoid (HAUGHTON 1929) and not medial to the basiptyergoid processes; however, this interpretation requires further study.

The lateral surface of the parabasisphenoid is poorly known in the 'nycteroleters'; however, the ventral surface of this element in all taxa that preserve a braincase never possesses foramina for the potential entrance of the internal carotids (JM, pers. observ.). In addition, TSUJI (2006) describes the dorsal surface of the parabasisphenoid in *Macroleter*, figuring the sulcus for the course of the palatal branch in the anterolateral area of the pituitary fossa, and thus dorsal to the basiptyergoid processes, excluding a condition as observed in eureptiles and synapsids. The described configuration in *Macroleter* may be regarded as 'intermediate' between the anteriorly situated paired exit foramina of the palatal branches as seen in procolophonoids, and the single foramen in the anterodorsal part of the parabasisphenoid as described for pareiasaurs.

Millerettids, which are among the most basal parareptiles currently known (TSUJI & MÜLLER 2009; CISNEROS et al. 2008), also possess a Vidian canal with an entrance posterolateral to the basiptyergoid processes, and similar to procolophonoids the palatal branch exits anteromedially (GOW 1972). Mesosaurs, the sister group to all other parareptiles (TSUJI & MÜLLER 2009), are somewhat difficult to interpret. MODESTO (2006) describes the presence of Vidian grooves on the ventral surface of the parabasisphenoid in *Mesosaurus*, but at the same time notes the absence of entrance foramina for the internal carotids and therefore suggests the presence of a lateral Vidian canal as in millerettids and procolophonoids. Such a configuration would imply that the palatal artery did not run dorsal or anteromedial to the basiptyergoid processes, but in an open channel ventral to the basicranium. Further anatomical investigations are needed to resolve this issue.

2.4. Carotid circulation in stem amniotes

In the taxa outside Amniota, but within Reptiliomorpha, the configuration is similar to that described for early eureptiles and synapsids, i.e. the cerebral branches of the internal carotids pierce the (para)basisphenoid ventrally and the palatine branch seems to continue in an open channel ventral to the basicranium (e.g. *Seymouria* and *Chroniosuchus*, SHISHKIN 1968; Fig. 1F).

2.5. Carotid circulation in turtles

The oldest and phylogenetically basalmost turtles, such as *Proganochelys quenstedti*, *Palaeochersis talampayensis*, *Australochelys africanus*, *Kayentachelys aprix*, *Condorchelys antiqua*, and *Heckerochelys romani* (the condition in *Odontochelys* is unfortunately not known), all display the same carotid configuration as seen in synapsids and early eureptiles, meaning that the palatal branch of the carotid artery runs openly and ventral to the basicranium, and the cerebral branch pierces the (para)basisphenoid medial to the basiptyergoid process on the ventral surface of the bone (Fig. 1G; GAFFNEY 1983; STERLI & DE LA FUENTE 2010). As mentioned above, in later turtles this pattern becomes extensively modified due to a closure of the interptyergoid vacuity and extensive ossification of the (para)basisphenoid complex, thus enclosing the internal carotid artery largely in bone (STERLI & DE LA FUENTE 2010; STERLI et al. 2010).

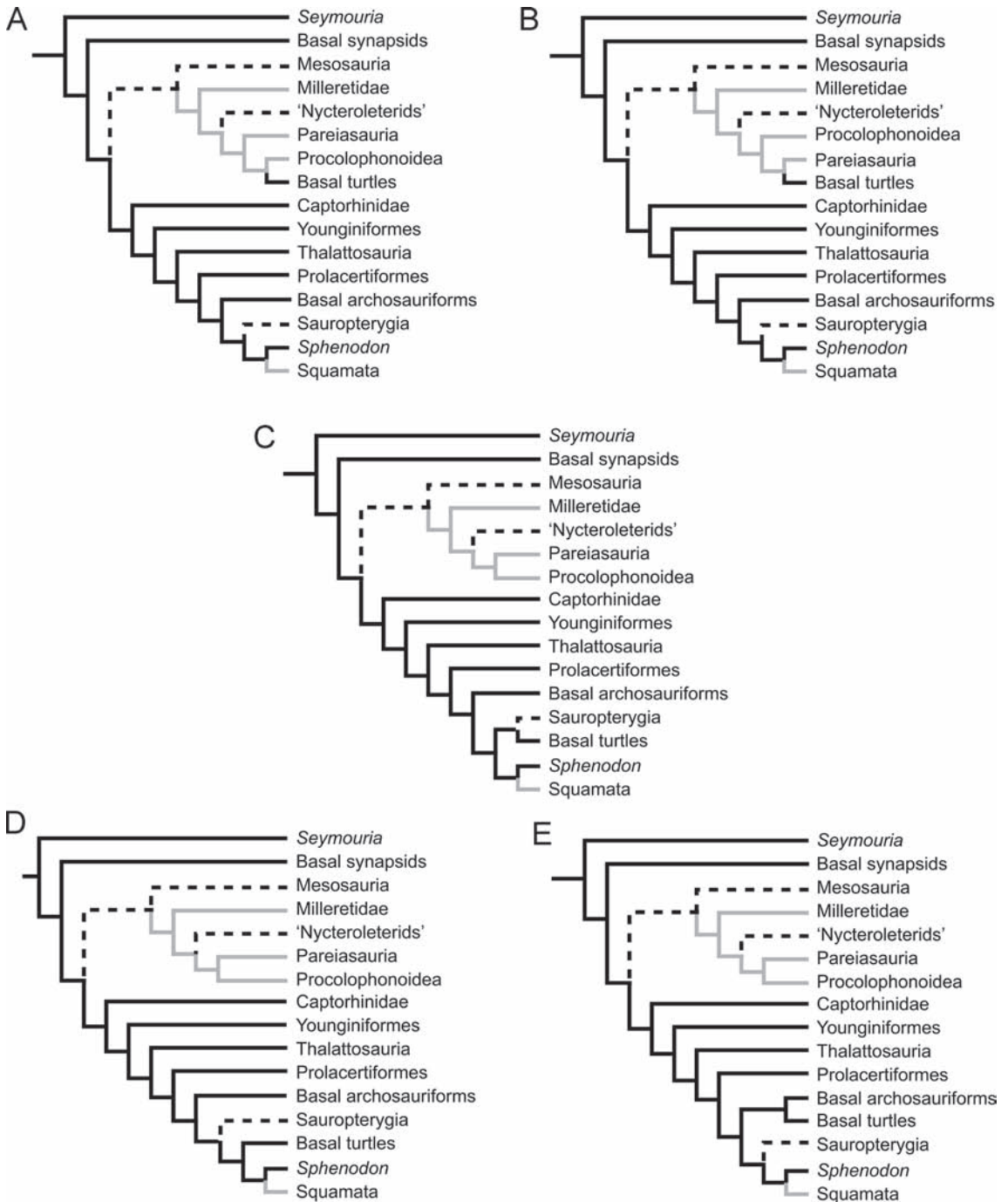


Fig. 2. Optimization of the character 'bifurcation of the internal carotid artery into cerebral and palatine arteries covered by bone: no (0), yes (1)' on different phylogenies of the major clades of amniotes. **A** – after LAURIN & REISZ (1995); **B** – after LEE (1993); **C** – after RIEPPEL & DEBRAGA (1996); **D** – after MÜLLER (2003); **E** – after BHULLAR & BEVER (2009). Black lines denote state 0; grey lines denote state 1; dashed lines denote unknown state or ambiguous optimization.

3. Discussion

The results of the present survey have important implications for the ongoing debate about whether turtles are parareptiles, more specifically closely related

to Procolophonoidea, Pareiasauria, or *Eunotosaurus*, or if they should be considered diapsids and thus part of Eureptilia (see TSUJI & MÜLLER 2009 for a review). Using a generalized amniote phylogeny, we mapped

the character 'bifurcation of the internal carotid artery into cerebral and palatine arteries covered by bone: no (0), yes (1)' to evaluate the evolution of each of this character in the different scenarios proposed for the origin of turtles (Fig. 2). Character mapping was performed using the software package TNT (GOLOBOFF et al. 2008). The optimization of this character (Fig. 2) suggests that the plesiomorphic condition for amniotes was to have the bifurcation into cerebral and palatine arteries not covered ventrally by bone and that the enclosure of these arteries in bone was acquired independently in several clades such as crown turtles, squamates, some sauropterygians, birds, and parareptiles. Because basal turtles and basal diapsids show the plesiomorphic condition for amniotes, and at least all parareptiles exclusive of Mesosauridae have the bifurcation embedded in the (para)basisphenoid, the optimization of this character is more parsimonious when turtles are nested in Diapsida than in Parareptilia (2 steps and 3 steps, respectively). From this it also follows that the plesiomorphic condition of the amniote carotid circulation is for the internal carotid to split into the cerebral and palatine branches before entering the skull and that the cerebral artery pierces the (para)basisphenoid from below, exiting into the dorsum sellae, with the palatine artery continuing anterior and medial to the basitrabecular (= basiptyergoid) processes. This is evidenced by the fact that the entrance of the cerebral artery into the braincase occurs through paired foramina on the ventral surface of the basisphenoid when the arterial bifurcation is outside the basicranium, whereas the entrance of the internal carotid is displaced to a dorsolateral position when the bifurcation is inside the braincase.

If turtles were nested within parareptiles, one would expect an arterial pattern similar to the one described above, with the internal carotid artery entering the braincase on the lateral surface of the parabasisphenoid and splitting into cerebral and palatal branches within the Vidian canal. Instead, the condition seen in early turtles is identical to that of early eureptiles and synapsids, and represents the plesiomorphic condition for amniotes. As such, the anatomy of the basicranium of early turtles is another morphological structure, which, like the vomer (DAMIANI & MODESTO 2001), the scapula (RIEPEL 1996), the temporal region (MÜLLER 2003), and the laterosphenoid (BHULLAR & BEVER 2009), seems to contradict a turtle-parareptile relationship. Unfortunately, a more precise phylogenetic position of turtles cannot be assessed here using this single character, because early turtles retain the plesiomorphic amniote condition

of the carotid circulation pattern. Our contribution nonetheless emphasizes the imminent necessity of reconsidering primary homology statements of important morphological characters in order to gain a better understanding of both amniote phylogeny and turtle relationships.

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