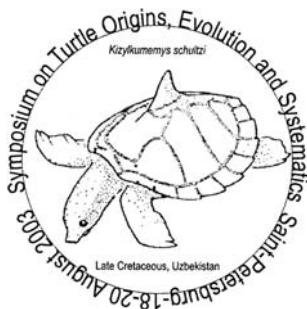


FOSSIL TURTLE RESEARCH

VOLUME 1

Proceedings of the Symposium on Turtle Origins, Evolution and Systematics

August 18 – 20, 2003,
St. Petersburg, Russia



Edited by
Igor G. Danilov and James F. Parham

St. Petersburg, 2006

FOSSIL TURTLE RESEARCH

VOLUME 1

Editors: Igor G. Danilov and James F. Parham

Proceedings of the Symposium
on Turtle Origins, Evolution and Systematics
August 18 – 20, 2003,
St. Petersburg, Russia

Published in St. Petersburg, March 2006

Papers should be cited as (e.g.): Joyce W. G. and Karl H.-V. (2006), «The world's oldest fossil turtle: fact versus fiction,» in: Danilov I. G. and Parham J. F. (eds.), *Fossil Turtle Research, Vol. 1, Russ. J. Herpetol.*, **13**(Suppl.), pp. 104-111.

This issue is published with the financial support of Dr. Ren Hirayama, grants of the President of the Russian Federation to the Leading Scientific Schools (Nsh-1647.2003.4 and Nsh-4212.2006.4), grant of the Russian Foundation for Basic Research 04-05-65000-a and with the use of the office and laboratory facilities of the Zoological Institute of the Russian Academy of Sciences.

**Cover photo: PIN 52-1a, holotype of *Yaxartemys longicauda* Riabinin, 1948,
Upper Jurassic of Kazakhstan, Karatau Ridge, vicinity of Mikhailovka village
Photograph: Igor Danilov**

PHYLOGENETIC IMPLICATIONS OF TURTLE CRANIAL CIRCULATION: A REVIEW

Heather A. Jamniczky^{1*}, Donald B. Brinkman² and Anthony P. Russell¹

The cranial arterial canals and foramina of turtles have long been a source of data for phylogenetic analyses of both extinct and extant taxa. Variation has been qualitatively documented in relation to the size, pattern, and location of the internal carotid artery and its major branches, and the diameters and locations of foramina in the basicranium through which they pass. This information has been used to erect evolutionary hypotheses of turtle relationships. Discovery and description of new fossil forms over the past four decades has overturned many of these hypotheses, however, and enigmatic taxa have been identified that do not fit proposed patterns. Reassessment using a quantitative approach reveals statistically significant differences between canals and foramina associated with the internal carotid artery and its major branches. Questions remain surrounding primary homology and systematic utility of several braincase structures and circulatory patterns, a more thorough understanding of which will require the application of a total evidence approach incorporating diverse information and emergent imaging technologies. An integrative assessment of homology in the turtle braincase, involving both extant and extinct forms, will facilitate further understanding of the evolution of the cranial arterial system.

INTRODUCTION

Turtles present a challenging puzzle to students of evolutionary biology. *Proganochelys quenstedti*, the earliest definite representative of the turtle stem lineage, appears in the fossil record some 210 million years ago (Gaffney, 1990), and the turtle body plan has since remained highly conservative. Turtles form a natural group whose monophyly has never been seriously questioned (Gaffney, 1984), but relationships among the various turtle clades continue to be debated. Several phylogenetic analyses of turtles have appeared that utilize morphological data and that incorporate both cranial and post-cranial characters (e.g.: Gaffney, 1975, 1996; Dryden, 1988; Gaffney and

Meylan, 1988; Meylan and Gaffney, 1989; Gaffney et al., 1991; Shaffer et al., 1997; Brinkman and Wu, 1999; Hirayama et al., 2000; Joyce, 2004), and patterns of turtle cranial circulation have figured prominently in most of these.

Turtle cranial circulatory anatomy was first described in the early 19th century (Bojanus, 1819). Several other works followed, detailing turtle cranial circulatory patterns and their accompanying osteology in fossil and living forms (e.g.: Siebenrock, 1897; Kesteven, 1910; Ogushi, 1911; Nick, 1912; Romer, 1956; Parsons and Williams, 1961). The notion that cranial circulatory patterns and the relative sizes of major vessels harbor important phylogenetic information was explored by McDowell (1961), Albrecht (1967, 1976), and Gaffney (1975), and these works form the basis for the continued inclusion of characters drawn from the cranial circulation in morphological phylogenetic analyses of the clade. The ability of the bony canals to preserve information about cranial circulation makes this suite of characters particularly applicable to the study of fossil taxa.

* corresponding author

¹ Vertebrate Morphology and Palaeontology Research Group, Department of Biological Sciences, University of Calgary, Calgary, Alberta, T2N 1N4, Canada. E-mail: hajamnic@ucalgary.ca

² Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, T0J 0Y0, Canada

Herein we review the use and interpretation of turtle cranial circulatory patterns in studies of cryptodiran turtle phylogeny and evolution, in light of a recent re-evaluation (Jamniczky and Russell, 2004) of some of these characters and the recent discovery of a number of new fossil turtle skulls (Brinkman, unpublished data) of uncertain affinity. All anatomical terminology follows Gaffney (1972), and clade names follow those of Gaffney and Meylan (1988) with respect to circumscribed content (but see Joyce et al. [2004] for a new, rank-free scheme).

BRANCHES OF THE INTERNAL CAROTID ARTERY

The paired internal carotid arteries supply the majority of blood to the head of a turtle, each one entering the skull via a foramen posterior canalis carotici interni, the position of which is discussed in detail below, and traveling, variably enclosed in bone, along the basisphenoid and pterygoid (Fig. 1; McDowell, 1961). The internal carotid artery gives off two major branches in the braincase area. The stapedia artery (except in those taxa in which it is absent; see below) branches off first at the rear of the skull, passes through the aditus canalis stapedio-temporalis and the canalis stapedio-temporalis, and exits onto the surface of the skull in the temporal fossa via the foramen stapedio-temporale, an opening formed, in the Casichelydia, by the prootic and quadrate bones (Albrecht, 1967). This branch point is not preserved in osteological specimens, since it occurs before the vessels enter the skull. The palatine artery (in all major clades except Trionychoidea, which has a pseudopalatine artery, and in those taxa in which it is absent; see below) branches off anterior to the stapedia artery, and travels, again variably enclosed in bone, through the canalis caroticus lateralis, exiting the braincase into the sulcus cavernosus via the foramen caroticum laterale (Albrecht, 1967). Corrosion-cast preparations of *Chelydra serpentina*

reveal that the canals and foramina through which these vessels pass accurately reflect the size of the vessel in life (Jamniczky and Russell, 2004).

The patterns and relative sizes of the branches of the internal carotid artery have been studied most thoroughly and used most frequently in phylogenetic analyses of extant cryptodiran turtles. McDowell (1961) made the first qualitative comparisons of relative size and pattern among the major branches of the internal carotid artery in extant cryptodires, a work later extended by Albrecht (1967, 1976) to include all major extant turtle clades. Cheloniidae and *Dermochelys coriacea* were found to have large, equally sized stapedia and palatine arteries; Chelydridae (including *Platysternon megacephalum*), Testudinidae, «Bataguridae», and Emydidae share the state of a palatine artery that is reduced in diameter relative to that of the stapedia artery, or occasionally absent; Kinosternoidae, Trionychoidea, and likely *Carretochelys insculpta* share the state of a stapedia artery that is reduced in diameter relative to that of the palatine or pseudopalatine artery, or occasionally absent (Albrecht, 1967, 1976). These patterns are summarized in Figure 2.

Based upon his observations and those of McDowell (1961), Albrecht (1967, 1976) suggested that the primitive turtle arterial pattern consisted of equally sized stapedia and palatine arteries, as seen in chelonioid turtles. Such an interpretation requires that the testudinoid (Emydidae + «Bataguridae» + Testudinidae) condition, wherein the palatine artery is greatly reduced relative to the stapedia artery, and the trionychoid (Trionychoidea + Kinosternoidae) condition, wherein the stapedia artery is greatly reduced in diameter relative to that of the palatine or pseudopalatine artery, both be considered derived conditions. Gaffney (1975) discovered a greatly reduced foramen caroticum laterale, indicating a reduced palatine artery as evident in Testudinoidea, in extinct chelonioids including *Toxochelys latiremis*, baenids, and other living reptiles, and therefore

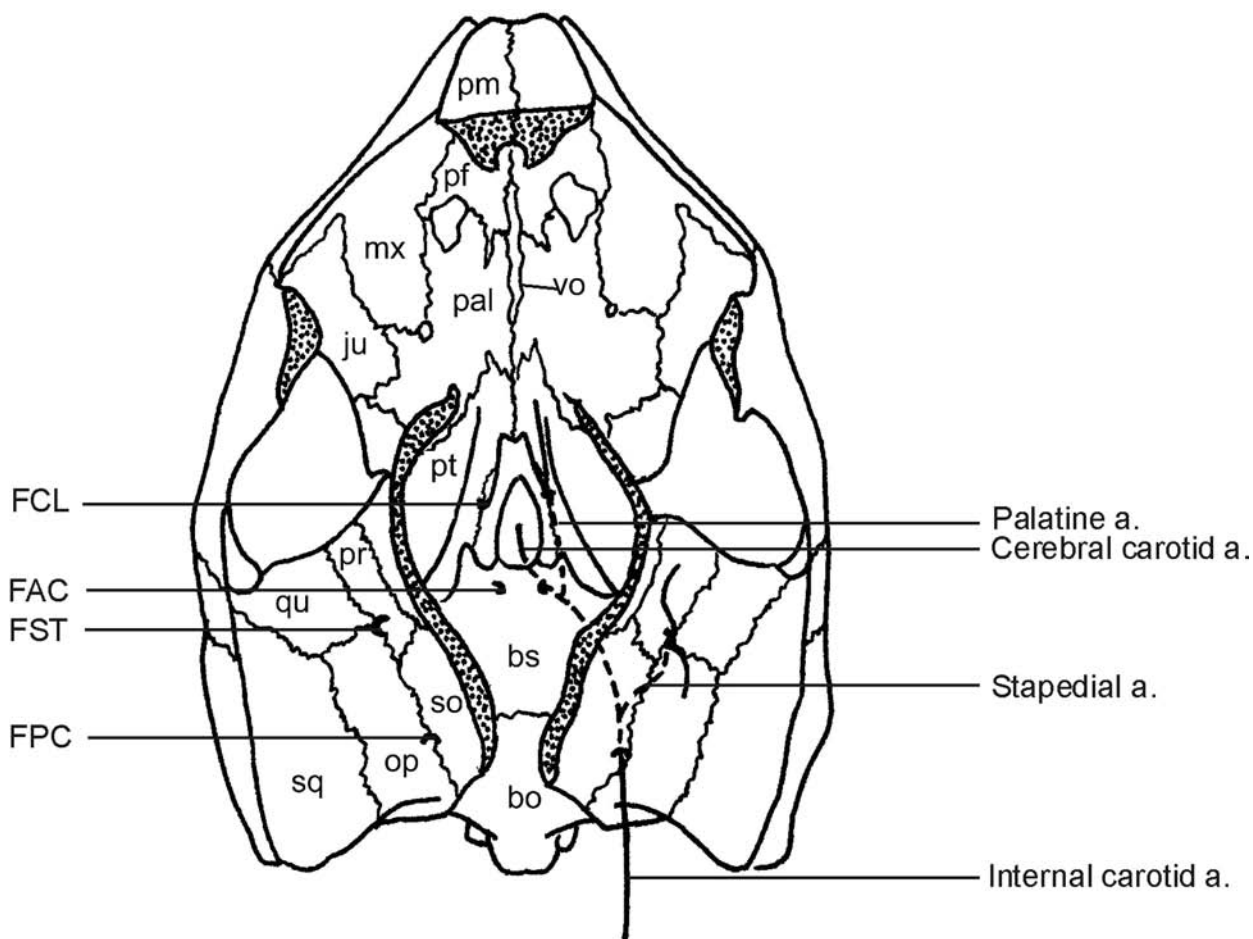


Fig. 1. Dorsal view of the skull of *Trachemys scripta*, with skull roof removed, showing the locations of cranial arterial foramina assessed in this study. Solid line indicates visible vessel, dashed line indicates vessel within bony canal, and stippling indicates cut surface. Note: FPC is on the ventral surface of the skull, but is indicated here for clarity. Redrawn and modified from Albrecht (1967, Fig. 1), with suture locations approximated based on Gaffney (1979, Fig. 65).

Abbreviations: **a.**, artery; **bo**, basioccipital; **bs**, basisphenoid; **FAC**, foramen anterior canalis carotici interni; **FCL**, foramen caroticum laterale; **FPC**, foramen posterior canalis carotici interni; **FST**, foramen stapedio-temporale; **ju**, jugal; **mx**, maxilla; **op**, opisthotic; **pal**, palatine; **pf**, prefrontal; **pm**, premaxilla; **pr**, prootic; **pt**, pterygoid; **qu**, quadrate; **so**, supraoccipital; **sq**, squamosal; **vo**, vomer.

argued for a primitive pattern resembling the testudinoid condition, interpreting the trionychoid and chelonioid patterns as independently derived. Subsequent authors (Gaffney and Meylan, 1988; Gaffney et al., 1991, Brinkman and Nicholls, 1993; Gaffney, 1996; Shaffer et al., 1997) have accepted as the primitive pattern a condition in which the internal carotid and palatine arteries are of similar diameter and are somewhat smaller than the

stapedial artery, based on the findings of Meylan and Gaffney (1989) who noted that many primitive cryptodires have a relatively large foramen caroticum laterale. Under this scenario, the reduced diameter of the palatine artery relative to that of the internal carotid of chelydrid, testudinoid, trionychoid, and baenid turtles is considered derived.

While Kinosternoidae and Trionychoidae are currently united on the basis of the shared posses-

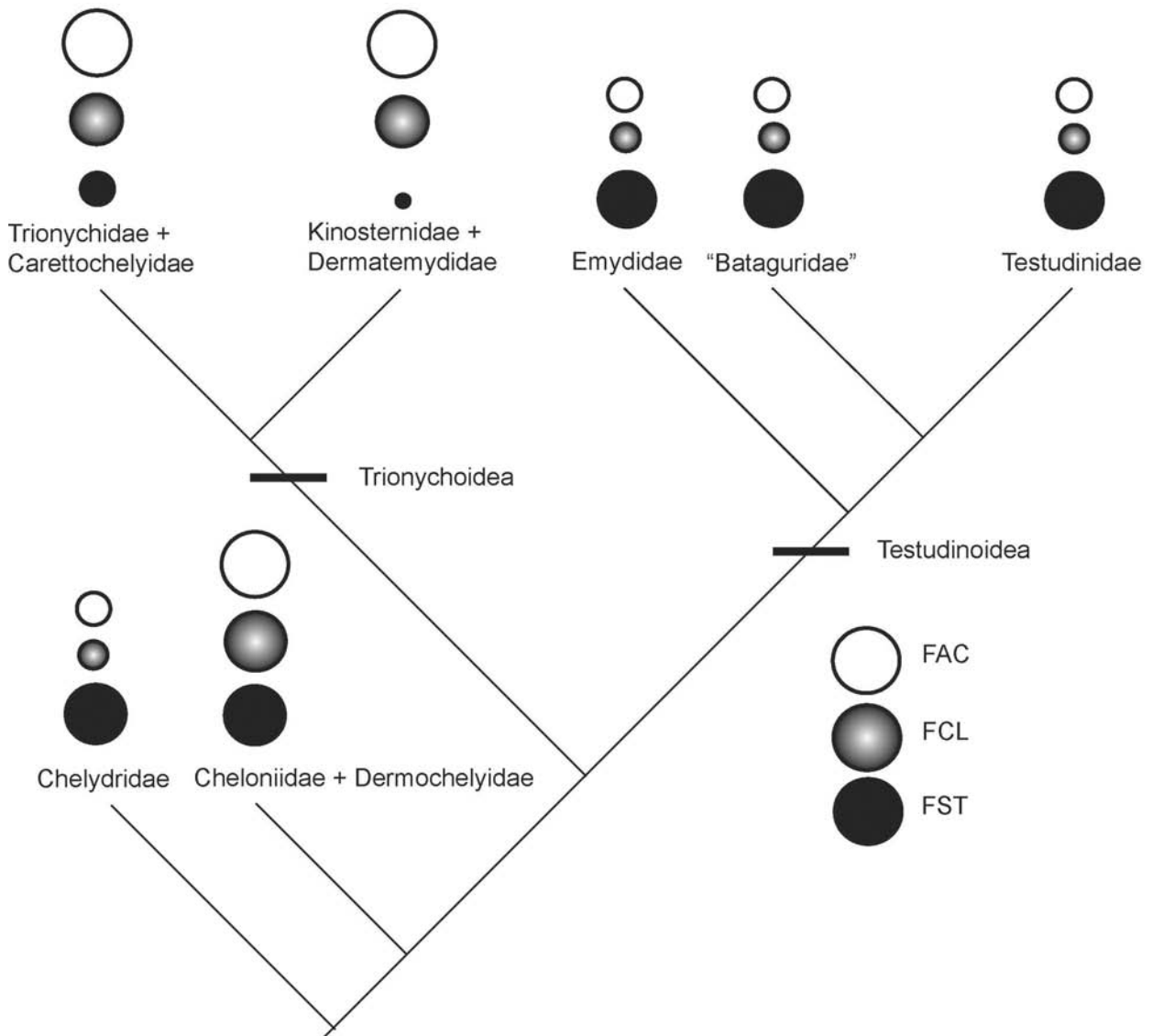


Fig. 2. Patterns of relationship between and within the turtle clades Trionychoidea and Testudinoidea, after Gaffney & Meylan (1988), and relative sizes of cranial arterial foramina after McDowell (1961) and Albrecht (1967, 1976). Relative diameters are exaggerated for clarity, and are not to scale.

Abbreviations: **FAC**, foramen anterior canalis carotici interni; **FCL**, foramen caroticum laterale; **FST**, foramen stapedio-temporale.

sion of a reduced stapelial artery (Gaffney, 1975), problems of homology of the vessels branching off the internal carotid artery anteriorly in these groups has brought this unification into question. In Kinosternoidae, a large palatine artery branches off the internal carotid artery and passes through

the foramen caroticum laterale, and continues anteriorly to give rise to the mandibular artery, while the internal carotid artery becomes known as the cerebral carotid artery (Albrecht, 1967). In Trionychoidea, the internal carotid artery gives rise to the mandibular artery, which passes

through the foramen caroticum laterale, and then continues anteriorly to give rise to a large pseudopalatine artery from which the cerebral carotid artery subsequently branches (Albrecht, 1967). The apparent substitution of the pseudopalatine for the palatine artery in Trionychidae suggests separate evolution of the two circulatory systems. In keeping with this interpretation, Albrecht (1976) hypothesized three main lines of turtle evolution, represented by the Testudinoidea, Kinosternoidea, and Trionychoidea, with the Chelydridae following a parallel trajectory to the Testudinoidea.

Jamniczky and Russell (2004), in a quantitative re-examination of these characters, found statistical support for the size-related differences described above, lending further weight to the argument that these patterns do contain robust phylogenetic signal. This study also found evidence, however, for reconsideration of primary homology assessment in the anterior region of the internal carotid artery. Present work is revealing that removing the constraints of nominalism and re-assessing the true locus of homology in the cranial circulation may lead to changes in the way that this region is used in phylogenetic analyses (Jamniczky, unpublished data).

EVOLUTION OF THE INTERNAL CAROTID CANAL

The opening through which the internal carotid artery enters the skull, and the extent and thickness of the floor of the canal housing this artery, have been used extensively in interpreting the phylogenetic position of extinct forms and the possible evolutionary trajectories of extant taxa (e.g. Gaffney, 1975; Brinkman and Nicholls, 1993; Brinkman and Wu, 1999). Interpretations of this feature and its implications have varied, and have stimulated ongoing debate. Gaffney (1975) first suggested that the location of the foramen posterior canalis carotici interni (fpc), by which the internal carotid artery enters the skull, separates

primitive turtles from their more derived relatives (Fig. 3a). Gaffney (1975) united turtles with an fpc located midway along the basisphenoid-ptyergoid suture, a relatively cranial position, into the Paracryptodira (Fig. 3a), and further united those turtles with an fpc located at or near the posterior end of the pterygoid, a more caudal position, into the Eucryptodira, indicating that this may be the most important synapomorphy uniting Eucryptodira (Gaffney, 1975, p. 427). Gaffney (1975) considered both groups to be derived from an unknown primitive condition.

Evans and Kemp (1976) and Rieppel (1980) interpreted the changing position of the fpc as morphoclinally-based (Fig. 3b). They hypothesized a primitive condition in which the fpc was located anteriorly, rendering the Paracryptodira plesiomorphic rather than synapomorphic for this condition. The fpc is postulated to have migrated posteriorly over the course of the evolution of the clade, and the most derived forms display its caudalmost location (Rieppel, 1980). Subsequent workers agreed with this assessment and interpretation of the primitive condition (Gaffney, 1979; Gaffney and Meylan, 1988; Gaffney et al. 1991).

More recently, Brinkman and Nicholls (1993) revived the notion of Paracryptodira and Eucryptodira as independently derived clades, but offered a third interpretation of the position of the fpc (Fig. 3c). In this interpretation, the primitive condition is an internal carotid artery that is fully exposed ventrally, up to and including the branch point of the palatine artery, as seen in *Kallokibotion bajazidi* (Gaffney and Meylan, 1992). In Paracryptodira, the floor of this canal initially appeared anterior to the branch point and extended rearward, while in Eucryptodira, the floor initially appeared posterior to the branch point and extended forward, eventually covering the majority of the artery (Brinkman and Nicholls, 1993).

The presence in a large number of extinct and extant eucryptodires of an opening exposing the branch point of the palatine artery while

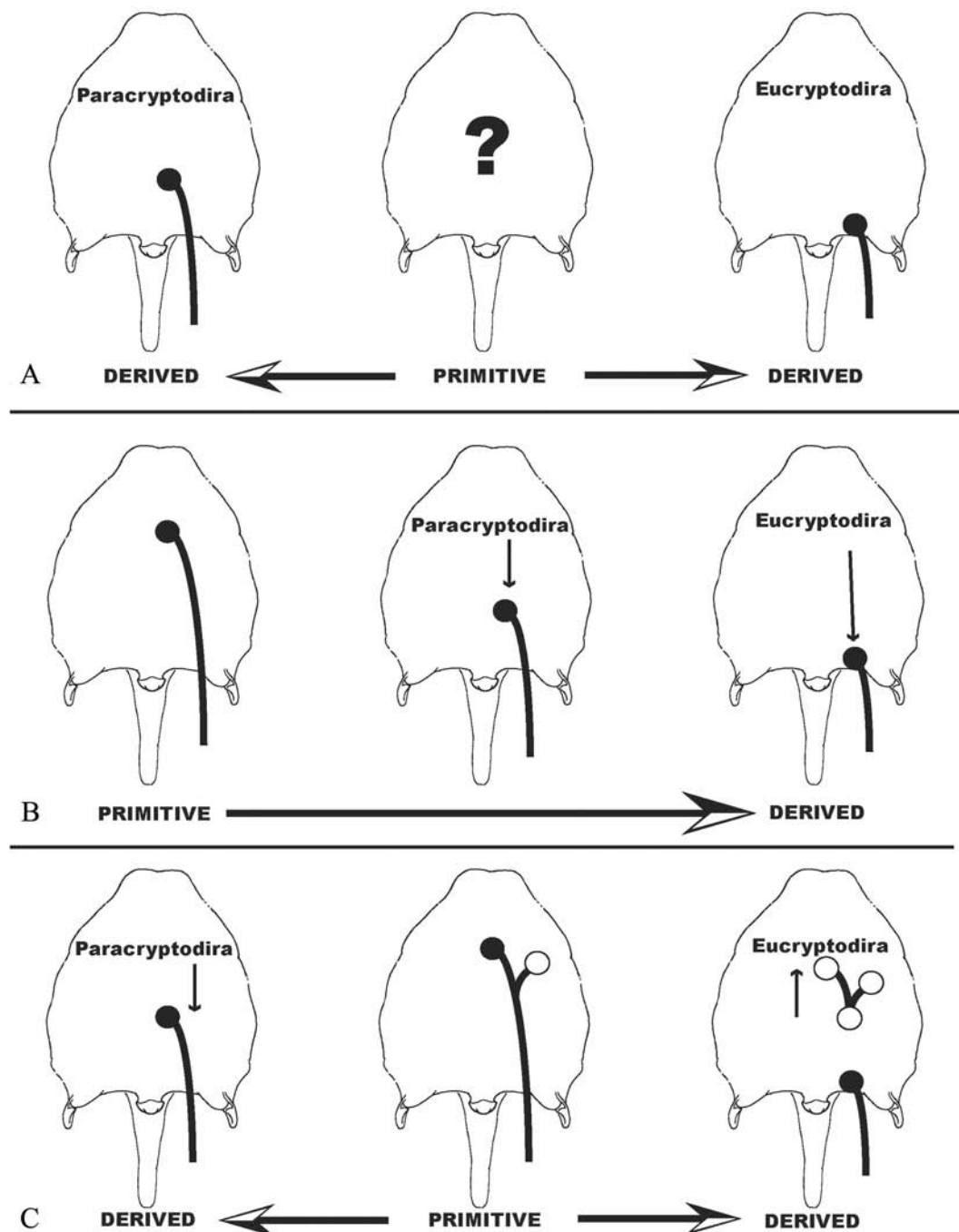


Fig. 3. Summary of three possible scenarios for the evolution of the position of the foramen posterior canalis carotici interni in Paracryptodira and Eucryptodira. Heavy line indicates internal carotid artery; black circle indicates foramen posterior canalis carotici interni; open circles indicate other openings. Position and size of structures are exaggerated for clarity. A – independent derivation in Paracryptodira and Eucryptodira, according to Gaffney (1975). B – Morphocline erected by Evans and Kemp (1976) and Rieppel (1980). Arrow indicates direction of migration of foramen posterior canalis carotici interni. C – Independent derivation in Paracryptodira and Eucryptodira, according to Brinkman and Nicholls (1993). Arrow indicates direction of development of new floor for canalis caroticus internus.

the remainder of the canalis caroticus internus is floored, termed the foramen basisphenoidale (Gaffney, 1983), lends support to this interpretation (Brinkman and Nicholls, 1993). Primitive eucryptodires such as *Ordosemys leios* (Brinkman and Wu, 1999), *Xinjiangchelys latimarginalis*, and *Sinemys lens* (Brinkman and Nicholls, 1993) show large such openings, while more derived eucryptodires, including the extinct *Adocus beatus* and several extant genera (Meylan and Gaffney, 1989), show relatively much smaller openings. The presence of a large foramen basisphenoidale in primitive eucryptodires indicates that the anteriorly directed flooring of the internal carotid canal is not yet complete in these forms, with more derived forms showing no opening at all (Brinkman and Nicholls, 1993). Evidence acquired to date mostly strongly supports this interpretation, summarized in Figure 4.

PROSPECTUS

Turtles are an enigmatic group of organisms that have evolved a body plan that has proved adaptable and sufficient for survival across a large span of geological time, and across a broad array

of ecosystems (Ernst and Barbour, 1989; Gaffney, 1990). A total evidence approach to both morphology and phylogeny will help better understand turtle relationships. Questions remain regarding the primitive turtle basicranial pattern, the homology of the palatine and pseudopalatine arteries, and the extent to which basicranial circulation alone can indicate relationships. The possible phylogenetic significance of other features of the basicranial region, such as the foramen pro ramo nervi vidiani, the processus interfenestralis, and variation in the development of the sella turcica, has yet to be explored. Further work on the turtle basicranium and circulatory patterns, incorporating information from developmental studies and advanced imaging techniques, will shed further light on these problems and their significance to turtle evolution.

Acknowledgments. Thanks to Walter Joyce and an anonymous reviewer for comments that improved the quality of the manuscript. The Natural Sciences and Engineering Research Council of Canada (HAJ, APR) and the Alberta Ingenuity Fund (HAJ) provided support.

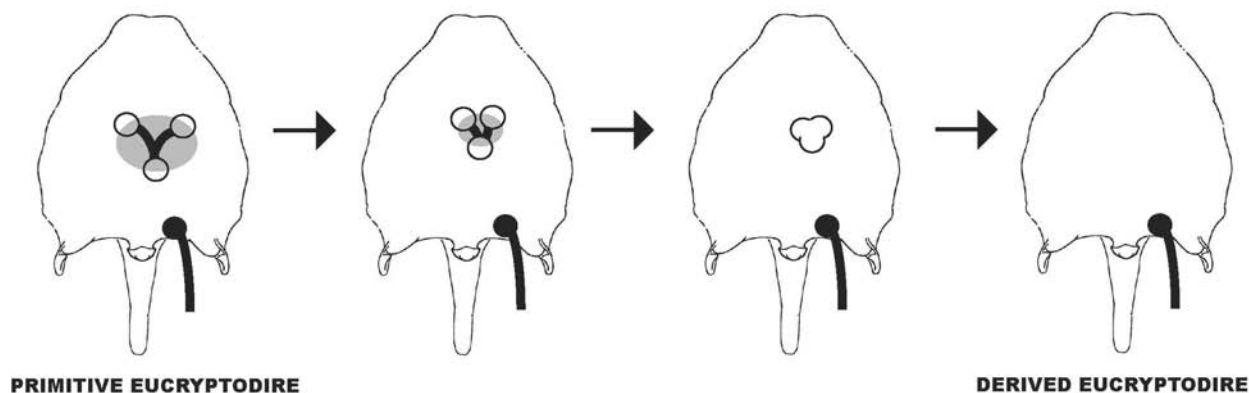


Fig. 4. Evolutionary trajectory (based on available evidence – see text for details) resulting in complete flooring of the canalis caroticus internus in Eucryptodira. Grey circle indicates ventrally exposed area of canalis caroticus internus, considered homologous with foramen caroticum basisphenoidale; heavy line indicates internal carotid artery; black circle indicates foramen posterior canalis carotici interni; open circles indicate other openings. Position and size of structures are exaggerated for clarity.

REFERENCES

- Albrecht P. W.** (1967), «The cranial arteries and cranial arterial foramina of the turtle genera *Chrysemys*, *Sternotherus*, and *Trionyx*: a comparative study with analysis of possible evolutionary implications,» *Tulane Stud. Zool.*, **14**(3), 81-99.
- Albrecht P. W.** (1976), «The cranial arteries of turtles and their evolutionary significance,» *J. Morphol.*, **149**(2), 159-182.
- Bojanus L. H.** (1819), *Anatome Testudinis europaeae*, Jozephus Zawadzki, Vilna.
- Brinkman D. B. and Nicholls E. L.** (1993), «The skull of *Neurankylus eximius* (Testudines: Baenidae) and a reinterpretation of the relationships of this taxon,» *J. Vertebr. Paleontol.*, **13**(3), 273-281.
- Brinkman D. B. and Wu X. C.** (1999), «The skull of *Ordosemys*, an Early Cretaceous turtle from Inner Mongolia, People's Republic of China, and the interrelationships of Eucryptodira (Chelonia, Cryptodira),» *Paludicola*, **2**(2), 134-147.
- Dryden L. S.** (1988), *Paraphyly of the Cryptodira and phylogenetic systematics of turtles*, MS Thesis, University of Kansas, Lawrence.
- Ernst C. H. and Barbour R. W.** (1989), *Turtles of the World*, Smithsonian Inst. Press, Washington.
- Evans J. and Kemp T. S.** (1976), «A new turtle skull from the Purbeckian of England and a note on the early dichotomies of cryptodire turtles,» *Palaeontology*, **19**(2), 317-324.
- Gaffney E. S.** (1972), «An illustrated glossary of turtle skull nomenclature,» *Amer. Mus. Novit.*, **2486**, 1-33.
- Gaffney E. S.** (1975), «A phylogeny and classification of higher categories of turtles,» *Bull. Amer. Mus. Nat. Hist.*, **155**(5), 387-436.
- Gaffney E. S.** (1979), «Comparative cranial morphology of recent and fossil turtles,» *Bull. Amer. Mus. Nat. Hist.*, **164**(2), 1-376.
- Gaffney E.S.** (1983), «Cranial morphology of the extinct horned turtle, *Meiolania platyceps*, from the Pleistocene of Lord Howe Island,» *Bull. Amer. Mus. Nat. Hist.*, **175**(4), 361-480.
- Gaffney E. S.** (1984), «Historical analyses of theories of chelonian relationship,» *Syst. Zool.*, **33**(3), 283-301.
- Gaffney E. S.** (1990), «The comparative osteology of the Triassic turtle *Proganochelys*,» *Bull. Amer. Mus. Nat. Hist.*, **194**, 1-263.
- Gaffney E. S.** (1996), «The postcranial morphology of *Meiolania platyceps* and a review of the Meiolaniidae,» *Bull. Amer. Mus. Nat. Hist.*, **229**, 1-166.
- Gaffney E. S. and Meylan P. A.** (1988), «A phylogeny of turtles,» in: Benton M. J. (ed.), *The Phylogeny and Classification of the Tetrapods, Volume 1: Amphibians, Reptiles, Birds*, Clarendon Press, Oxford, pp. 157-219.
- Gaffney E. S. and Meylan P. A.** (1992), «The Transylvanian turtle *Kallokibotion*, a primitive cryptodire of Cretaceous age,» *Amer. Mus. Novit.*, **3040**, 1-37.
- Gaffney E. S., Meylan P. A. and Wyss A. R.** (1991), «A computer assisted analysis of the relationships of the higher categories of turtles,» *Cladistics*, **7**(4), 313-335.
- Hirayama R., Brinkman D. B. and Danilov I. G.** (2000), «Distribution and biogeography of non-marine Cretaceous turtles,» *Russ. J. Herpetol.*, **7**(3), 181-198.
- Jamniczky H. A. and Russell A. P.** (2004), «Cranial arterial foramen diameter in turtles: a quantitative assessment of size-independent phylogenetic signal,» *Anim. Biol.*, **54**, 417-436.
- Joyce W. G.** (2004), *Phylogeny, nomenclature, and ecology of Mesozoic turtles*, PhD Thesis, Yale University, New Haven.
- Joyce W. G., Parham J. F. and Gauthier J. A.** (2004), «Developing a protocol for the conversion of rank-based taxon names to phylogenetically defined clade names, as exemplified by turtles,» *J. Paleont.* **78**(5), 989-1013.
- Kesteven H. L.** (1910), «The anatomy of the head of the green turtle *Chelone midas*, Latr., Part I. The skull,» *J. Proc. Roy. Soc. New South Wales*, **44**, 368-400.

- McDowell S. B.** (1961), «On the major arterial canals in the ear-region of testudinoid turtles and the classification of the Testudinoidea,» *Bull. Mus. Compar. Zool. Harvard*, **125**(3), 23-39.
- Meylan P. A. and Gaffney E. S.** (1989), «The skeletal morphology of the Cretaceous cryptodiran turtle, *Adocus*, and the relationships of the Trionychoidea,» *Amer. Mus. Nov.*, **2941**, 1-60.
- Nick L.** (1912), «Das Kopfskelet von *Dermochelys coriacea* L.,» *Zool. Jb. Abt. Anat. Ont. Tiere*, **33**, 1-238.
- Ogushi K.** (1911), «Anatomische Studien an der japanischen dreikralligen Lippenschildkröte (*Trionyx japonicus*). Part I,» *Mitt. Morphol. Jb.*, **43**, 1-106.
- Parsons T. S. and Williams E. E.** (1961), «Two Jurassic turtle skulls: a morphological study,» *Bull. Mus. Comp. Zool. Harvard*, **125**(3), 43-107.
- Rieppel O.** (1980), «The skull of the Upper Jurassic cryptodire turtle *Thalassemys*, with a reconsideration of the chelonian braincase,» *Palaeontographica A*, **171**, 105-140.
- Romer A. S.** (1956), *The Osteology of the Reptiles*, University of Chicago Press, Chicago.
- Shaffer H. B., Meylan P. and McKnight M. L.** (1997), «Tests of turtle phylogeny: molecular, morphological, and paleontological approaches,» *Syst. Biol.*, **46**(2), 235-268.
- Siebenrock F.** (1897), «Das Kopfskelet der Schildkröten,» *Sitzber. K. Akad. Wiss. (Wien), Math.-Naturwiss. Kl.*, **106**(1), 245-328.