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THE CRANIAL ARTERIES AND CRANIAL ARTERIAL FORAMINA OF THE TURTLE GENERA *CHRYSEMYS, STERNOTHERUS,* AND *TRIONYX:* A COMPARATIVE STUDY WITH ANALYSIS OF POSSIBLE EVOLUTIONARY IMPLICATIONS

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CONTENTS

ABSTRACT

The cranial arterial foramina and bony canals of *Chrysemys, Sternotherus,* and *Trionyx* are described and compared, and the cranial arteries that utilize these foramina and canals in the three turtle genera are also described and compared. Cranial arterial variation within a genus is slight; as a result, inferences of the general cranial arterial patterns characteristic of the Testudinidae, Kinosternidae, and Trionychidae are made. Judged by the cranial arteries the Testudinidae and Kinosternidae have had a long, separate evolution from a common ancestor. Tiionychids evolved from an earlier branch of turtles which had evolved parallel to the evolutionary path later taken by the kinosternids. Sixteen new names for anatomical features are introduced in this study.

The Trionychidae, Kinosternidae, and Testudinidae have taken three different lines of evolution in pattern of cranial arteries. As would be expected from the current taxonomy of turtles, members of the super-

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family Testudinoidea have a cranial arterial pattern basically different from that of members of the Trionychoidea (of Romer, 1956). However, this basic difference occurs only in the basisphenoid region of the skull, for most of the other cranial arteries of the soft-shelled turtles are similar to those of the Kinosternidae (of Wermuth and Mertens, 1961). With the exception of the arteries of the basisphenoid region, the trionychids and kinosternids have followed somewhat parallel lines of evolution opposed to the testudinid line.

Relatively little has been published concerning the cranial arteries of the Testudines (Testudinata). Bojanus (1819) named and illustrated almost all the head arteries of *Emys orbicularis;* Shindo (1914) described the cranial arteries of *Testudo graeca* and compared the place of origin of the mandibular artery in four species of turtles. Several other authors, such as Siebenrock (1897), Ogushi (1911), Nick (1913), and Parsons and Williams (1961), mention some of the larger arteries in their osteological studies of turtle skulls.

Girgis (1964) described the arteries of *Trionyx triunguis,* and McDowell (1961) has made the only other recent study of cranial arteries. By comparing the general cranial arterial patterns of the testudinids and kinosternids, McDowell established the existence of two different lines of cranial artery evolution in the Testudinoidea, and he also provided strong evidence for placing the Chelydridae in the testudinid line of evolution and the Dermatemydidae in the kinosternid line of evolution. Some of McDowell's findings concerning the smaller cranial arteries of the testudinids and kinosternids were not correct, but his conclusions were based on the general patterns of the larger arteries; hence these errors do not affect the validity of his conclusions to any great degree.

I. MATERIALS AND PROCEDURE

Among the Trionychidae, two injected *Trionyx spinifer,* one uninjected *Trionyx muticus,* and one uninjected *Lissemys punctata* were dissected; among the Kinosternidae, one injected *Kinosternon subrubrum,* one injected *Sternotherus*[2] *odoratus,* one uninjected *Sternotherus odoratus.* and one uninjected *Sternotherus minor;* and among the Testudinidae, two injected *Chrysemys (Pseudemys) scripta.* Partial dissections of another injected *Chrysemys scripta* and one injected *Terrapene carolina* were also made. All the dissected specimens were adult turtles. The dissections were performed under a dissecting microscope, and a dental drill with a very small bit was used to reveal the arteries within the bony canals.

The injected specimens of the above list were essential to a detailed study of the cranial arteries of the three types of turtles, for uninjected specimens yielded only a minimum of information concerning the larger cranial arteries and also yielded some information about the bony canals and foramina. The injected *Chrysemys* were obtained from commercial firms. I prepared the specimens of *Trionyx, Sternotherus,* and *Kinosternon* by injecting latex into the heart and ascending aorta of freshly killed specimens and placing the turtles in a dilute acetic acid solution for twenty-four hours to harden the latex. This procedure often produced better preparations than the commercial ones. On specimens which had been preserved for some time, however, this procedure either failed or resulted in very poor injections.

In order to extend coverage to the generic level of the detailed arterial patterns of the representative species which were dissected, the cranial arterial foramina in the skulls of

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[2] Upon the recommendation of H. M. Smith, the spelling *Sternotherus* is retained despite Tinkle's (1958: 5-6) case for *Sternothaerus*, because only "inadvertent errors" in original spellings can be corrected, whereas "incorrect transliteration" is explicitly stated in the Code *not* to be considered an inadvertent error. Furthermore the type of *Sternotherus* Bell (in Gray), 1825, must be selected from the species included in the *original* description ("*S. odorata* Gray, *S. pensylvanica* Gmelin"); no side-necked turtles were included. This requires that *Sternothaerus* Bell, 1826, be considered a different nominal genus the type of which is determined independently from that of *Sternotherus*, which is clearly the proper name for the North American kinosternid turtles related to *S. odoratus* [unless, as suggested by Romer (1966: 365) *Kinosternon* and *Sternotherus* are considered congeneric, in which case *Kinosternon* has priority].

undissected species in each genus were examined and pertinent data from the available literature were utilized. The foramina in skulls of different genera of the Trionychidae, Kinosternidae, and Testudinidae were similarly examined and the available literature utilized to establish a basis for inference of the general arterial patterns of the three families studied. Data concerning the presence or absence, relative size, and relative position of seven externally-visible cranial arterial foramina were recorded for a series of 131 skulls of adult or subadult turtles from different parts of the United States, all in the Museum of Natural History of the University of Illinois.

The following crania were examined:

Testudinidae: 34 *Chrysemys scripta,* 26 *Chrysemys picta,* 5 *Chrysemys concinna,* 3 *Graptemys geographica,* 2 *Graptemys pseudographica,* 4 *Clemmys insculpta,* 3 *Emydoidea blandingi,* 2 *Malaclemys terrapin,* 8 *Terrapene carolina,* 3 *Terrapene ornata,* 2 *Gopherus polyphemus.*

Kinosternidae: 15 *Sternotherus odoratus,* 2 *Sternotherus minor,* 1 *Sternotherus carinatus,* 2 *Kinosternon subrubrum,* 1 *Kinosternon bauri,* 1 *Kinosternon scorpioides,* 4 *Staurotypus triporcatus.*

Trionychidae: 9 *Trionyx spinifer,* 3 *Trionyx muticus,* 1 *Trionyx ferox.*

Anatomical features described in the following accounts may be visualized by reference to Figures 1-3. New terms are indicated by boldface letters wherever they first appear in the descriptive accounts.

II. THE CRANIAL ARTERIAL FORAMINA AND BONY CANALS OF *CHRYSEMYS, STERNOTHERUS* AND *TRIONYX*

Many of the cranial foramina of turtles serve as passageways for arteries, and often the size of a cranial foramen or canal is directly proportional to the size of the artery which goes through it. A detailed knowledge of the position and size of the arterial foramina and canals in turtle skulls is thus very valuable in predicting the cranial arterial pattern of those turtles. As an example, the two Jurassic turtle skulls described by Parsons and Williams (1961), judged by the large foramen stapedio-temporale, the small foramen posterius canalis carotici interni, and the foramina around the basisphenoid bone, are either on the chelydrid-testudinid line of cranial arterial evolution or are on a line of arterial evolution extremely similar to that of the modern Testudinidae (of Romer, 1956) and Chelydridae (of Wermuth and Mertens, 1961).

In the discussion of the crania of *Trionyx, Sternotherus,* and *Chrysemys,* the standard terminology established by Parsons and Williams (1961) is used. Where Parsons and Williams do not have a name for a structure, the source of the name is indicated in parentheses. New names are coined only where no other author has given the corresponding structures suitable names, and are indicated by boldface letters.

The foramen stapedio-temporale is one of the most important of the cranial arterial foramina. In *Trionyx, Chrysemys,* and *Sternotherus,* the foramen stapedio-temporale is located in or at the posterior edge of the dorsal surface of the prootic bone and opens into the fossa temporalis. In all 65 of the *Chrysemys* skulls examined, the foramen stapedio-temporale was present on each side as a very large opening. According to McDowell (1961: 33) the foramen stapedio-temporale is present in *Sternotherus* as an "occasional vestige," but it is present as a greatly reduced opening in all the 18 *Sternotherus* which I examined. In *Trionyx sinensis* (*"Trionyx japanicus"* of Ogushi) and in all *Trionyx* which I examined, the foramen stapedio-temporale is present but is not reduced as much as the foramen in *Sternotherus.* Thus both *Trionyx* and *Sternotherus* have a reduced foramen stapedio-temporale, and this stricture "of a large arterial foramen implies considerable rearrangement of the head arteries" (McDowell, 1961: 23). The aditus canalis stapedio-temporalis and the canalis stapedio-temporalis are present in all three genera and are reduced in diameter in *Trionyx* and *Sternotherus* in proportion to the reduction of the foramen stapedio-temporale in these same genera.

Another important arterial foramen is the foramen posterius canalis carotici interni.[3] In *Chrysemys* and *Sternotherus* this foramen is located at the ventromedial corner of

[3] Spelling courtesy Dr. Donald P. Rogers, modified from that used by Parsons and Williams.

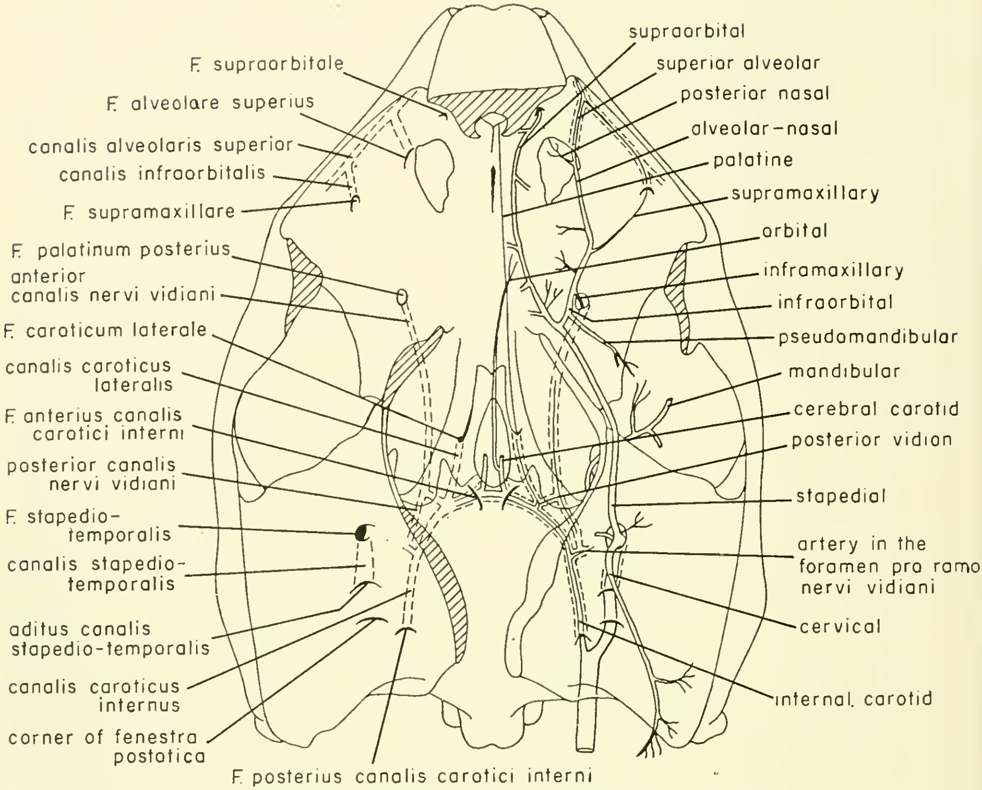

Figure 1. Semidiagrammatic dorsal view of the cranial arteries (right side) and cranial arterial foramina and canals (left side) of *Chrysemys scripta.*

the fenestra postotica, whereas in *Trionyx* the foramen posterius canalis carotici interni is separated by a broad bar of the pterygoid bone from ventrolateral fenestra postotica. The foramen posterius canalis carotici interni is very small in *Chrysemys,* but is relatively much larger in *Sternotherus* and *Trionyx.*

In all three genera, the foramen posterius canalis carotici interni leads into the canalis caroticus internus which curves anteriomedially on each side of the cranium through the pterygoid and basisphenoid bones to an opening in the basisphenoid at the posterior end of the sella turcica known as the foramen anterius canalis carotici interni.[4]. As would be expected from the relative sizes of the foramen posterius canalis carotici interni, the canalis caroticus internus of *Chrysemys* is a narrow canal, whereas in *Sternotherus* and *Trionyx* it is a much wider canal. The foramen anterius canalis carotici interni is located in the dorsum sellae of the basisphenoid bone medial to the processus clinoideus. In *Chrysemys* and *Sternotherus* this is a fairly small foramen, but in *Trionyx* the foramen anterius canalis carotici interni is a very large foramen. Again, the relative sizes of these canals and foramina imply quite different cranial arterial patterns in this region of the skulls of the three genera.

In *Chrysemys, Sternotherus,* and *Trionyx,* the canalis caroticus internus on each side of the skull gives off an anterior canal in the pterygoid bone which opens into the sulcus cavernosus directly lateral to the basisphenoid. In *Chrysemys* this small canal goes for some way through the pterygoid bone and opens into the cavum cranii through an extremely small foramen lateral to the middle of the rostrum basisphenoidale. On the other hand, this canal is very

[4] Spelling courtesy Dr. Donald P. Rogers, modified from that used by Parsons and Williams.

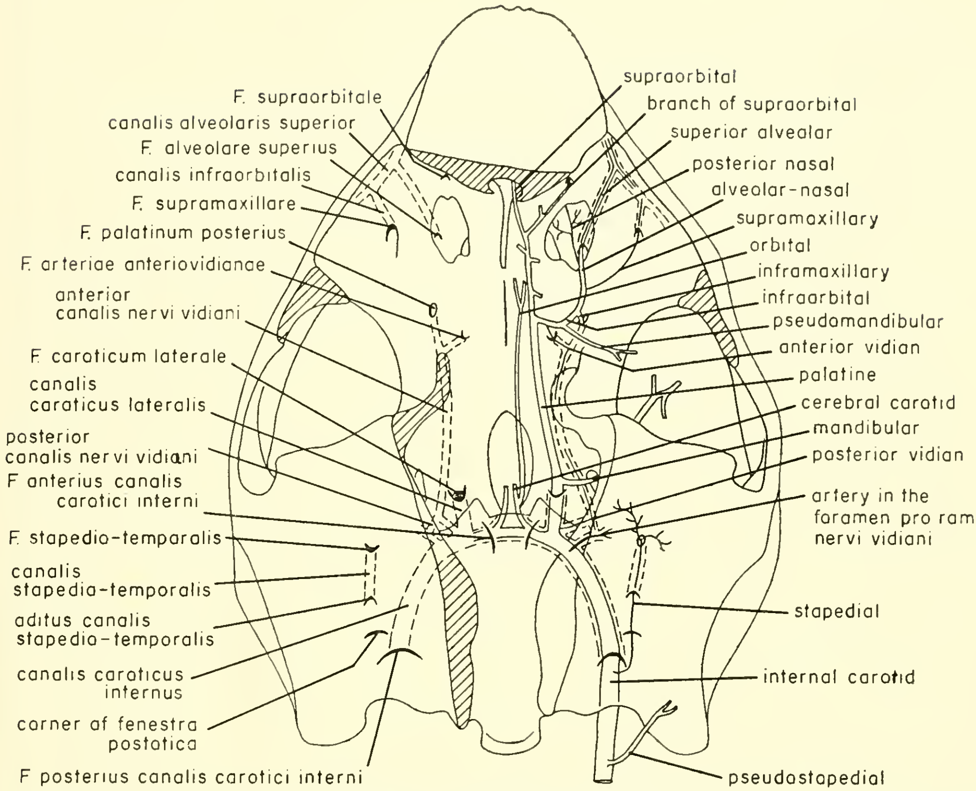

Figure 2. Semidiagrammatic dorsal view of the cranial arteries (right side) and cranial arterial foramina and canals (left side) of *Sternotherus odoratus.*

large in *Sternotherus,* and it goes only a short distance through the pterygoid bone before it opens into the cavum cranii by means of a larger foramen which is directly lateral to the dorsum sellae. Similarly in *Trionyx,* this large canal arises from the canalis caroticus internus, goes a short way through the pterygoid bone, and opens into the cavum cranii through a large foramen lateral to the dosum sellae. This foramen in *Trionyx* may be slightly smaller than the foramen in *Sternotherus,* but in both groups it is much larger than that of *Chrysemys.* Furthermore, this foramen in the pterygoid bone of *Chrysemys* is more anteriorly-located than the foramen in the pterygoid bones of *Sternotherus* and *Trionyx.* Nevertheless, the canal in each genus is very similar in relative position in the pterygoid bone and in relation to the other canals, and hence the canal and foramen are probably homologous in *Chrysemys. Sternotherus,* and *Trionyx.*

The canal and foramen described above have been given a variety of names. Siebenrock (1897) showed this foramen labeled f.c.i.' in trionychids and kinosternids and he also discussed its occurrence in the Chelidae. Ogushi (1911: 29) called this foramen and canal of *Trionyx* "die Fenestra lateralis canalis carotici." Finally, McDowell (1961) found that the palatine artery goes through this canal in testudinids and kinosternids, and he called the canal the canalis arteriopalatinus and the foramen the foramen arteriopalatinum. However, the palatine artery no longer traverses this foramen in *Trionyx,* and hence McDowell's names no longer suffice. Following Ogushi's example, I call this canal the **canalis caroticus lateralis** and its opening the **foramen caroticum laterale** in all turtle genera.

A small ventrally-directed canal is associated with the canalis caroticus lateralis in *Chrysemys* and *Sternotherus.* The canalis carotico-pharyngealis (McDowell) of *Chrysemys* is a small ventral canal which

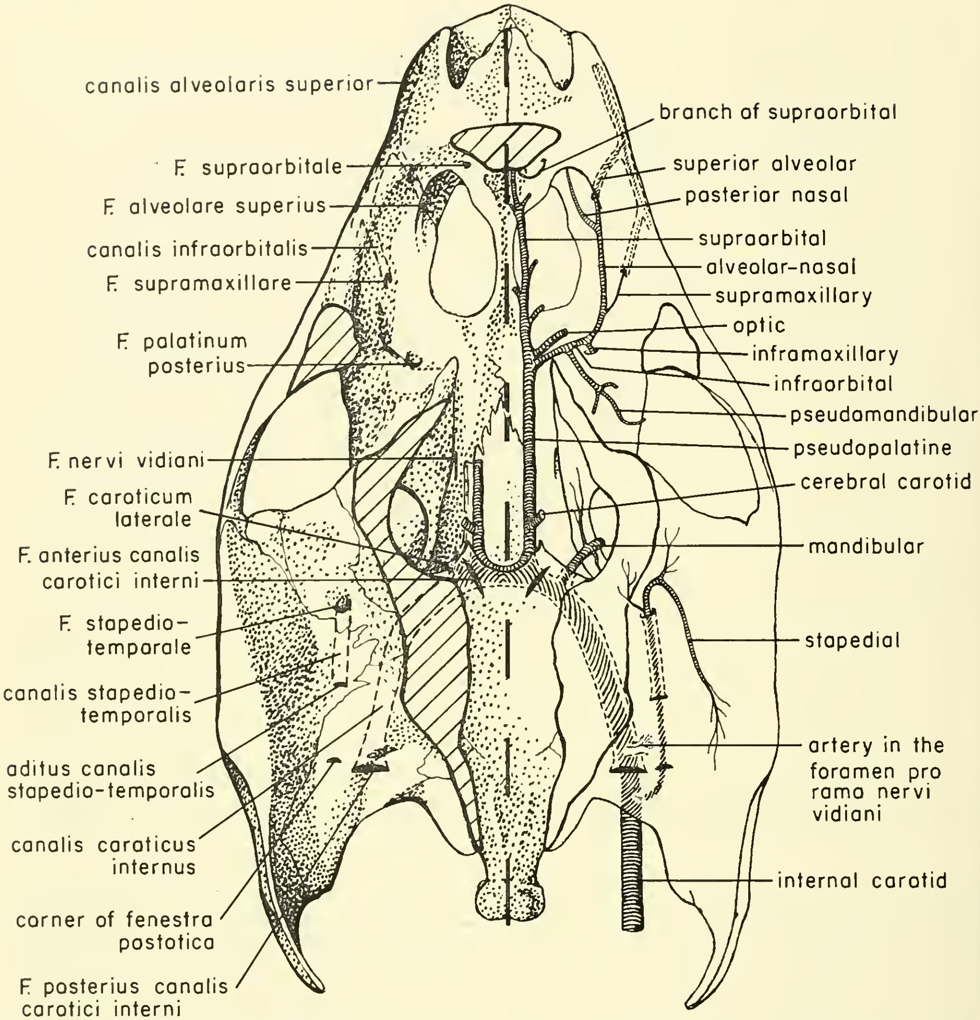

Figure 3. Semidiagrammatic dorsal view of the cranial arteries (right side) and cranial arterial foramina and canals (left side) of *Trionyx spinifer.*

arises near the posterior end of the canalis caroticus lateralis and goes ventrally through the pterygoid bone to exit through the foramen carotico-pharyngeale (McDowell). This foramen was present as a very small opening in the ventral surface of the pterygoid bone anterolateral to the middle of the ventral surface of the basisphenoid bone in all 65 of the *Chrysemys* examined. The diameters of the foramina were variable, and sometimes the foramina were barely visible; the number of foramina carotico-pharyngeale was also variable, for there often were two or three foramina on each side and in four specimens the foramen was not visible on one side of the skull. In *Sternotherus,* the canalis carotico-pharyngealis arises directly at the origin of the canalis caroticus lateralis and goes ventrally in the pterygoid bone to open at the foramina carotico-pharyngeale. This foramen and canal are usually slightly larger than those of *Chrysemys,* and the foramen carotico-pharyngeale of *Sternotherus* is located in the pterygoid bone lateral to the anterior tip of the ventral surface of the basisphenoid, anteriorly in relation to the foramen in *Chrysemys.* Although they were present in all the

Chrysemys and *Sternotherus* examined, the foramina carotico-pharyngeale were absent in all the *Trionyx* examined.

The canalis carotico-pharyngealis of *Chrysemys* and *Sternotherus* is associated with the canals for the vidian nerve. In *Chrysemys*, the vidian nerve enters the canalis caroticus internus by means of the foramen pro ramo nervi vidiani, which connects the canalis caroticus internus with the canalis cavernosus and is visible as a large opening in the dorsal wall of the canalis caroticus internus medial to the condylus mandibularis. From this foramen, some nerves enter a small, anterolaterally-directed canal in the pterygoid which goes lateral and parallel to the canalis caroticus internus anteriorly to the region of the canalis carotico-pharyngealis; for convenience, I call this nerve canal the posterior canalis nervi vidiani. Other nerves exit from the foramen pro ramo nervi vidiani and traverse the canalis caroticus internus anteriorly to enter the canalis caroticus lateralis. These nerves then divide; some branches go through the canalis caroticus lateralis and exit on the dorsal surface of the pterygoid bone whereas other nerves go ventrally, entering the canalis carotico-pharyngealis and finally joining the nerves of the posterior canalis nervi vidiani by means of an anterolateral canal which connects the canalis carotico-pharyngealis with the posterior canalis nervi vidiani. These nerves in the bony canals then enter the anterior canalis nervi vidiani which goes through the pterygoid and palatine bones from the region of the canalis carotico-pharyngealis to the foramen palatinum posterius; the nerves then traverse this foramen to enter the orbit. The vidian canal pattern is thus much more complicated than indicated by McDowell.

The canals for the vidian nerve of *Sternotherus* are very similar to those of *Chrysemys*. The posterior canalis nervi vidiani, connection of the canalis nervi vidiani with the canalis carotico-pharyngealis, anterior canalis nervi vidiani, and the connection of the anterior canalis nervi vidiani with the foramen palatinum posterius are present. However, there are some differences from the bony canal pattern of *Chrysemys*. First of all, the foramen pro ramo nervi vidiani is smaller in diameter and is located near the base of the canalis caroticus lateralis, therefore farther anterior than in *Chrysemys*. Furthermore, the anterior canalis nervi vidiani connects with another anterior canal in the pterygoid bone just posterior to its connection with the foramen palatinum posterius. This anterior canal angles anterodorsally to open on the dorsal surface of the pterygoid bone through a small foramen anterior to the anterior end of the crista pterygoidea, posteromedial to the dorsal foramen palatinum posterius. This short anterior canal connects with very small canals opening in the ventral surface of the palatine bone medial to the ventral foramen palatinum posterius; I call these ventral openings the **foramina arteriaevidianae** and the larger opening on the dorsal bone anteroventral from the processus inferior parietalis I call the **foramen arteriae anteriovidianae.** The extremely small, variable foramina arteriaevidianae were present in all 18 of the *Sternotherus* skulls examined. These foramina are lacking in *Chrysemys* and *Trionyx*.

The vidian nerve pattern of *Trionyx* is very simple in comparison with the complex patterns of *Chrysemys* and *Sternotherus*. The nerves enter the canalis caroticus internus through the foramen pro ramo nervi vidiani, which is similar in size and position to the foramen of *Chrysemys*. The nerves then continue on from the canalis caroticus lateralis and exit into the sulcus cavernosus by means of the foramen caroticum laterale; the nerves go a short way over the dorsal surface of the pterygoid bone to enter the foramen nervi vidiani (Siebenrock) at the medial base of the crista pterygoidea ventral to the anterior edge of the foramen nervi trigemini. The foramen nervi vidiani leads to the canalis nervi vidiani which goes through the pterygoid and palatine bones to another canal in the palatine bone which in turn carries the vidian nerves to the foramen palatinum posterius. From the foramen palatinum posterius, the vidian nerves of *Trionyx* enter the orbit, as in *Chrysemys* and *Sternotherus*. Thus *Trionyx* differs from *Chrysemys* and *Sternotherus* in having no canalis carotico-pharyngealis, no posterior canalis nervi vidiani, and no connection between the canalis nervi vidiani and the canalis caroticus lateralis. The vidian nerve canals of *Chrysemys* and *Sternotherus* contain small arteries, but no artery was found in the vidian canal of *Trionyx*.

The foramen palatinum posterius is present in all the skulls of the three genera as an opening on the posterior floor of the orbit, anterior to the crista pterygoidea. In *Trionyx*, the foramen palatinum posterius is connected by a small, posteromedially-directed canal in the palatine bone which opens ventrally through a variable number of small foramina. These foramina are located in the palatine bone posteromedial from the ventral opening of the foramen palatinum posterius, and I call these the **foramina palatinum accessorium.** The canal connecting the foramina palatinum accessorium with the foramina palatinum posterius is called the canalis palatinus major et minor by Ogushi, but I shall use the simpler term **canalis intrapalatinus.** The canalis intrapalatinus transports arteries and nerves and also serves as the anterior opening of the canalis nervi vidiani. The foramina palatinum accessorium and the canalis intrapalatinus were present in all the *Trionyx* examined, but they were not present in any of the *Sternotherus* or *Chrysemys* crania.

Besides the foramen palatinum posterius, there are also a number of other arterial foramina in the orbital region of the three genera. The foramen orbito-nasale is a large foramen on the anterior floor of the orbit in *Trionyx, Chrysemys,* and *Sternotherus.* The smaller foramen alveolare superius is located at the lateral edge of the foramen orbito-nasale; the foramen alveolare superius leads into the anterolaterally-directed canalis alveolaris superior which goes through the maxillary bone, branching into the lateral canalis alveolaris superior which goes anteriorly and posteriorly along the ventrolateral edge of the maxillary bone.

Posterolateral from the foramen alveolare superius there is a small foramen located in the maxillary bone of the floor of the orbit. This small foramen, the **foramen supramaxillare** (new term, adapted from Bojanus) leads into a narrow, anterolaterally-directed canal, the canalis infraorbitalis (Ogushi), which connects with the lateral canalis alveolaris superior. The foramen supramaxillare was present in all 96 of the *Chrysemys, Sternotherus,* and *Trionyx* skulls examined.

Another extremely small arterial foramen is located on the prefrontal bone in the anterodorsal part of the orbit, dorsolateral from the dorsal edge of the fissura ethmoidalis. This opening, the **foramen supraorbitale,** leads into an extremely narrow canal which goes anteriorly through the prefrontal bone and terminates by opening into the fossa nasalis. In *Chrysemys,* the canal leads to the anterior end of the dorsal part of the prefrontal bone, and its openings there are often visible on dry skulls. Despite its small size, the foramen supraorbitale was present in all 96 of the *Chrysemys, Sternotherus,* and *Trionyx* skulls examined. Thus the arterial foramina and canals of the orbit are nearly identical in *Chrysemys, Sternotherus,* and *Trionyx.*

There are also a number of other cranial arterial foramina common to the three genera, such as the foramen nervi trigemini, the fossa meckelii, and the fissura ethmoidalis, but these are very large openings which contain much more than arteries and are fairly similar in *Trionyx, Chrysemys,* and *Sternotherus.* The foramina praepalatinum also transports arteries; these foramina are present as paired, very small openings in *Chrysemys* and *Sternotherus,* but in *Trionyx* the two foramina praepalatinum are fused to form a very large opening into the fossa nasalis.

In general, the differing cranial arterial foramina of *Trionyx, Sternotherus,* and *Chrysemys* were found to be quite constant in all the skulls of each genus examined, and only the smallest foramina were subject to minor individual variations. To summarize, the larger cranial arterial foramina and canals of *Trionyx* are very similar to those of *Sternotherus,* as evidenced by the reduced foramen stapedio-temporale, the large foramen posterius canalis carotici interni, the large canalis caroticus internus, the large canalis caroticus lateralis, and the large foramen caroticum laterale. *Chrysemys* differs from *Trionyx* and *Sternotherus* in having a very large foramen stapedio-temporale, a small foramen posterius canalis carotici interni, a small canalis caroticus internus, and a very small canalis caroticus lateralis with more anteriorly-located foramen caroticum laterale. *Chrysemys* and *Sternotherus* have a complex vidian nerve canal complex and foramina carotico-pharyngeale which are not present in *Trionyx,* and *Trionyx* has a very large foramen anterius canalis carotici interni which is small in *Chrysemys* and *Sternotherus.* The foramen supraorbitale, foramen supramaxillare, canalis infraorbitalis, foramen alveolare superius, canalis alveolaris superior, foramen palatinum posterius, and foramen orbito-nasale are very similar in all three genera. The foramina arteriaevidianae and foramen arteriae anteriovidianae are peculiar to *Sternotherus*, and the foramen palatinum accessorium and canalis intrapalatinus are peculiar to *Trionyx*. Finally, it should be re-emphasized that all the above facts concerning foramina and canals are directly related to the different cranial arterial patterns of *Chrysemys*, *Sternotherus*, and *Trionyx*.

III. CRANIAL ARTERIAL FORAMINA AND CANALS ON A FAMILIAL LEVEL

McDowell (1961) described the general foramina and canals of the Testudinidae, with emphasis on the large foramen stapedio-temporale, small canalis caroticus internus, and very small canalis caroticus lateralis. From the studies of Siebenrock and McDowell and my own studies of the crania of seven testudinid genera, I conclude that the above are constant features in the Testudinidae. Furthermore the foramen palatinum posterius, foramen praepalatinum, foramen supramaxillare, foramen supraorbitale, and the foramen carotico-pharyngeale were present in all the testudinid skulls which I examined. The foramina cartoico-pharyngeale seemed to be most variable in the testudinids, for they were very small in *Chrysemys*, *Graptemys*, and *Malaclemys* and fairly large in *Clemmys*, *Emydoidea*, *Terrapene*, and *Gopherus*. In *Gopherus*, there was a single large foramen carotico-pharyngeale located in the basisphenoid, and a peculiar foramen arteriomandibulare (McDowell) was also present. The other arterial foramina studied also differed slightly in size and position in the different genera. McDowell failed to note the connection between the vidian canals and the canalis carotico-pharyngealis and he was not correct in stating that the canalis carotico-pharyngealis is a branch of the canalis caroticus internus (1961: 27).

Siebenrock and McDowell also described some of the foramina and canals of the Kinosternidae, emphasizing the large canalis caroticus internus, the large canalis caroticus lateralis, and the greatly reduced foramen stapedio-temporale. McDowell stresses the reduced or "absent" foramen stapedio-temporale and states that it is present as an occasional vestige in the Kinosternidae (1961: 33). On the other hand, Siebenrock disagrees with this viewpoint and states that the foramen stapedio-temporale "fehlt aber bei keiner Art" (1897: 266). The foramen is present in all the 26 skulls I examined, except in one large skull of *Kinosternon scorpiodes*, and its absence in this specimen may have been due to old age. Hence McDowell's statement should be changed to say that the foramen stapedio-temporale is occasionally absent in the Kinosternidae. Examination of the three genera of Kinosternidae also revealed the presence of the foramen palatinum posterius, foramen supramaxillare, foramen supraorbitale, foramen arteriaevidianae, and foramen carotico-pharyngeale in all specimens; the foramen praepalatinum was not present in *Staurotypus*.

The foramina and canalis of the other genera of the Trionychidae have not been described in as much detail as they have for different genera in the other two families. Siebenrock noted the large foramen posterius canalis carotici interni and the large foramen caroticum laterale, and he made an important observation about the "besondere Grösse" (1897: 262) of the foramen anterius canalis carotici interni which by his system separated the trionychids from all other turtles. From the illustrations of the skulls of the Trionychidae in Wermuth and Mertens (1961) it can also be concluded that the reduced foramen stapedio-temporale is a constant feature of the trionychids.

To generalize from the above facts, the relative sizes and presence of the foramen stapedio-temporale, the canals and foramina of the basisphenoid region, and the foramina of the orbital region were found to be constant characteristics of the testudinids and kinosternids. From this it follows that the general arterial pattern of these two families can be validly inferred from the detailed arterial patterns of *Chrysemys* and *Sternotherus*. Less is known about the other genera of the Trionychidae, but it can be inferred that the general arterial patterns in the basisphenoid region and in the foramen stapedio-temporale are constant in all the trionychids and that the arterial pattern in these regions is the same as that of *Trionyx*.

IV. THE CRANIAL ARTERIES OF *CHRYSEMYS*

The common carotid artery courses up the side of the neck, giving off small branches into the adjacent muscles. Behind the skull, the common carotid artery branches into the ventral arteria carotica externa (external carotid artery), which supplies the tissue around the hyoid apparatus under the tongue, and the arteria carotica interna (internal carotid artery). The internal carotid artery goes anteriorly a short way to the region directly posterior to the fenestra postotica, where it gives rise to a large, dorsolateral branch, the arteria stapedialis (stapedial artery). The internal carotid artery then continues on into the foramen posterius canalis carotici interni.

The stapedial artery gives off a fairly large branch which goes around the posterior part of the skull to supply the tissue of the incisura columellae auris, and then the stapedial artery enters the fenestra postotica. In the cavum acustico-jugulare anterior to the columella, the stapedial artery gives rise to a ventral branch, the arteria mandibularis (mandibular artery). Contrary to McDowell, the mandibular artery is large and not "minute" (1961: 28) in size. The mandibular artery goes through the canalis cavernosus and into the muscles of the fenestra subtemporalis by means of the foramen cavernosum and the foramen nervi trigemini. The mandibular artery goes ventrally through the muscles of the fenestra subtemporalis, giving off many branches, and then enters the fossa meckelii. In this fossa, the mandibular artery gives off branches which remain in the canalis cartilaginis meckelii, branches which exit from the bone through a large medial foramen ventral to the processus coronoideus, and small branches which go posteroventrally to exit from the mandible through small foramina in the lateral bone near the area articularis mandibularis.

From the cavum acustico-jugulare, the large stapedial artery enters the aditus canalis stapedio-temporalis and goes through the canalis stapedio-temporalis to the foramen stapedio-temporale. In the temporal fossa, the stapedial artery gives rise to a large posterior branch, the arteria cervicalis (cervical artery), which supplies muscles of the temporal fossa and dorsal neck muscles behind the head. The stapedial artery curves anterodorsally in a groove in the lateral surface of the parietal bone and branches into the arteria supraorbitalis and the arteria infraorbitalis under the postorbital bone.

The arteria supraorbitalis (supraorbital artery) is usually the smaller of the two branches of the stapedial artery. It curves over the dorsomedial part of the eyeball, giving off many branches to the eyeball, small branches into the prefrontal bone, and a small branch into the foramen supraorbitale. This last branch goes through its foramen and canal in the prefrontal bone to supply the anterior tissue of the fossa nasalis. In one *Chrysemys* which I dissected, the supraorbital artery was larger than the infraorbital artery and was divided into two large branches. One branch formed a loop on the posteromedial surface of the eyeball, sending many branches to the adjacent tissue. The other branch went anteromedial to the eyeball and was located in the middle of the orbit, not in the dorsal part of the orbit as in the normal supraorbital artery. Furthermore, this anterior branch of the supraorbital artery sent a small dorsal branch into the foramen supraorbitale, but it also sent a large branch into the fissura ethmoidalis.

The arteria infraorbitalis (infraorbital artery) runs ventrally in the posterior part of the orbit, supplying the eyeball and also giving rise to the small arteria pseudomandibularis (pseudomandibular artery) which supplies the anterior muscles of the fenestra subtemporalis. On the floor of the orbit, the infraorbital artery gives rise to three branches, the arteria supramaxillaris (supramaxillary artery) the **arteria inframaxillaris** (inframaxillary artery) and the **arteria alveolare-nasalis** (alveolar-nasal artery).

The largest of the three arteries, the alveolar-nasal artery, goes anteriorly on the ventral surface of the eyeball across the floor of the orbit and into the membrane covering the foramen orbito-nasale. Here the alveolar-nasal artery branches into the lateral arteria alveolaris superior (superior alveolar artery) and the anterior arteria posterior nasalis (posterior nasal artery). The posterior nasal artery goes through the foramen orbito-nasale to supply the tissue of the posterior part of the fossa nasalis. The superior alveolar artery goes through the foramen alveolare superius and into the canalis alveolaris superior, where it sends small branches into the maxillary bone, to the lateral skin, and to the tissue of the nasal capsule.

The supramaxillary artery is a very small artery passing anteriorly on the lateral floor of the orbit and entering the canalis infraorbitalis by way of the foramen supramaxillare. Its function probably is that of supplying the branches of the trigeminal nerve within the canalis infraorbitalis and canalis alveolaris superior.

The inframaxillary artery runs directly ventrad through the foramen palatinum posterius to emerge on the roof of the mouth. The inframaxillary artery then goes anteriorly in the tissue medial to the border of the triturating surface, sending many small branches into the adjacent tissue and into the maxillary bone. The arteries of each side anastomose, forming the "U-shaped artery" of McDowell, and a branch on each side, the arteria anterior nasalis (anterior nasal artery) extends from the anastomosis into the foramen praepalatinum and then into the tissue of the fossa nasalis.

The small internal carotid artery enters the canalis caroticus internus and curves anteromedially to the foramen anterius canalis carotici interni. Shortly after entering its canal, the internal carotid artery gives off an extremely small dorsal branch which goes into the foramen pro ramo nervi vidiani and supplies some of the tissue in the canalis cavernosus. Anteriorly in its canal, the internal carotid artery gives off a small branch which enters the canalis caroticus lateralis; this branch is the base of the arteria palatina (palatine artery). This base of the palatine artery gives rise to two other arteries, the **arteria carotico-pharyngealis** (pharyngeal carotid artery) and the **arteria posterior vidiana** (posterior vidian artery). The small pharyngeal carotid artery arises as a ventral branch of the base of the palatine artery; it goes through the canalis carotico-pharyngealis and out the foramen carotico-pharyngeale to supply the adjacent tissue on the roof of the mouth. The very small posterior vidian artery arises at the same place on the base of the palatine artery and goes through the canal which connects the canalis carotico-pharyngealis with the canalis nervi vidiani. Then the posterior vidian artery sends extremely small branches into the posterior canalis nervi vidiani and into the anterior canalis nervi vidiani. Contrary to McDowell, the posterior vidian artery does not extend the length of the vidian canal, for it ends in the canal and probably supplies only the tissue within the canal. McDowell also erred in stating that the pharyngeal carotid artery arises as a branch of the internal carotid artery (1961: 29). After giving off the above two arteries at its base, the minute palatine artery exits from the foramen caroticum laterale into the cavum cranii and runs lateral to the rostrum basisphenoidale and lateral to the cartilage which fills the sulcus vomeri to the tissue which fills the fissura ethmoidalis. There is no anastomosis of the palatine artery in the cavum cranii with the posterior vidian artery as found by Mc Dowell, and the palatine artery anteriorly appears to be a functionless vestige.

After giving off the base of the palatine artery, the internal carotid artery on each side goes out the foramen anterius canalis carotici interni to form a large anastomosis in the dorsum sellae of the basisphenoid. Contrary to McDowell (1961: 31), this anastomosis is not the circle of Willis, for the circle of Willis is formed dorsal to it on the ventral surafce of the brain. The arteria carotica cerebralis (cerebral carotid artery) extends dorsally from each side of the anastomosis. Before entering the brain, each cerebral carotid artery gives off a small artery, the arteria orbitales (orbital artery), which goes anteriorly under the brain, dorsally through the interorbital tissue, and into the orbit to supply the ocular muscles (*fide* Burda).

The cerebral carotid arteries go on to the ventral surface of the brain lateral to the pituitary body. There the cerebral carotid arteries on each side give off a posterior branch and an anterior branch. The anterior branch on each side gives rise to a large arteria cerebri media (middle cerebral artery), which angles anterodorsally up the middle of the cerebrum; the middle cerebral artery on each side has small branches which anastomose in front of the optic chiasma, and other more anterior branches are the arteria cerebri anterior (anterior cerebral artery) and the arteria olfactoria (olfactory artery). The posterior branch of the cerebral carotid artery gives rise to a large arteria cerebri posterior (posterior cerebral artery) which goes along the posterior margin of the cerebrum and sends branches dorsally to terminate in the choroid plexus of the third ventricle. The posterior branches of the cerebral carotid artery on each side then anastomose under the medulla oblongata to form the arteria basilaris (basilar artery); the basilar artery also receives blood from spinal arteries. The anastomosis for the basilar artery and the anterior anastomosis together form the circle of Willis.

V. THE CRANIAL ARTERIES OF *STERNOTHERUS*

The common carotid artery goes up the side of the neck and gives rise ventrally to external carotid artery, as in *Chrysemys*. Just anterior to the external carotid artery, the internal carotid artery gives rise to a large dorsal branch which goes through the neck muscles to supply the muscles above the fossa temporalis. This branch takes over the function of the cervical branch of the stapedial artery in *Chrysemys*, and hence I call it the **arteria pseudostapedialis** (pseudostapedial artery).

Before entering the foramen posterius canalis carotici interni, the internal carotid artery gives off a small dorsolateral branch which goes around the posterior part of the skull to supply the tissue of the incisura columellae auris; this branch is extremely similar to the branch from the stapedial artery of *Chrysemys*. McDowell found no stapedial artery in the canalis stapedio-temporalis and foramen stapedio-temporale of the one injected *Sternotherus* which he dissected, and he concludes that the foramen stapedio-temporale is "purely venous" in function (1961: 33). Contrary to that statement, a minute stapedial artery is present in *Sternotherus*. The stapedial artery arises as a minute branch of the larger dorsolateral branch mentioned above, and it goes through the fenestra postotica, cavum acustico-jugulare, aditus canalis stapedio-temporalis, canalis stapedio-temporalis, and foramen stapedio-temporale, just as in *Chrysemys*. The stapedial artery emerges from the foramen stapedio-temporale, sending extremely small branches into the epithelium under the muscles of the temporal fossa, and it also sends one small branch into the supraoccipital bone. The stapedial artery of *Sternotherus* does not give rise to the mandibular artery and is greatly reduced in comparison with the stapedial artery of *Chrysemys*. McDowell's one specimen of *Sternotherus* may have been poorly injected, causing him to completely miss this evolutionarily-important artery.

The very large internal carotid artery curves anteromedially through the canalis caroticus internus to the foramen anterius canalis carotici interni. The internal carotid artery gives off an extremely small branch, smaller than that of *Chrysemys*, into the foramen pro ramo nervi vidiani. More anteriorly, the internal carotid artery gives rise to the large palatine artery in the canalis caroticus lateralis. The palatine artery immediately gives rise to the ventral pharyngeal carotid artery; this artery is much larger than that of *Chrysemys*, and its ventral branches run anteriorly and posteriorly to supply much of the tissue of the roof of the mouth. In fact, these branches of the pharyngeal carotid arteries are sometimes visible when a live *Sternotherus* opens its mouth . In the pterygoid bone, the pharyngeal carotid artery gives rise to a very small posterior vidian artery which goes only a short way into the anterior and posterior canalis nervi vidiani, as in *Chrysemys*.

The internal carotid arteries anastomose in the dorsum sellae and give rise to the cerebral carotid arteries and orbital arteries which proceed to the eye and to the brain, just as in *Chrysemys*; the branches of the cerebral carotid arteries in the brain are also similar to those of *Chrysemys*. My injected specimen of *Sternotherus* had no anastomosis between the internal carotid arteries, but this was clearly an individual variation, for the anastomosis was present in the other dissected *Sternotherus*.

The large palatine artery emerges from the foramen caroticum laterale and immediately gives rise to a large lateral branch, the mandibular artery, which exists through the foramen nervi trigemini to supply the muscles of the fenestra subtemporalis and the mandible as in *Chrysemys*. In the cavum cranii, the mandibular artery on each side gives off a fairly large artery which goes posterodorsally to connect with the basilar artery on the brain; these branches are not found in *Chrysemys*.

The palatine artery continues on in the cavum cranii medial to the ventral processus inferior parietalis and divides into the supraorbital artery and infraorbital artery just as it leaves the cavum cranii. The supraorbital artery is very similar to the large supraorbital artery of the aberrant *Chrysemys*. The supraorbital artery runs anteromedial to the eye in the middle of the orbit, sending many branches to the eye; after sending a small dorsal branch into the foramen supraorbitale, the supraorbital artery sends branches into the fissura ethmoidalis.

The infraorbital artery, pseudomandibular artery, supramaxillary artery, inframaxillary artery, anterior nasal artery, alveolar-nasal artery, superior alveolar artery, and posterior nasal artery are so similar to the same arteries in *Chrysemys* that a redescription is not necessary. However, one small branch of the infraorbital artery in *Sternotherus* was not observed in *Chrysemys*. This small branch, the **arteria anterior vidiana** (anterior vidian artery) enters the foramen arteriae anteriovidianae and goes posteroventrally through the palatine bone to the region of the foramina arteriaevidianae. The anterior vidian artery in this region medial to the foramen palatinum posterius sends a very small branch into the anterior canalis nervi vidiani, and it also sends a variable number of branches through the foramina arteriaevidianae to supply a small area of tissue on the dorsal roof of the mouth.

To generalize, the cranial arteries in the brain region, orbital region, nasal region, and mandibular region are very similar in *Sternotherus* and *Chrysemys*. The major arterial differences in the two genera involve the size and function of three major arteries and the place of origin of three additional arteries. In *Chrysemys,* the stapedial artery is large, the internal carotid artery is small, and the palatine artery is minute; in *Sternotherus*, the stapedial artery is minute, the internal carotid artery is large, and the palatine artery is large. In *Chrysemys*, the mandibular artery, supraorbital artery, and infraorbital artery arise from the stapedial artery; in *Sternotherus,* these same three arteries arise from the palatine artery. *Sternotherus* also has pseudostapedial arteries, anterior vidian arteries, and branches from the mandibular arteries to the brain which are not present in *Chrysemys*.

VI. THE CRANIAL ARTERIES OF *TRIONYX*

The common carotid artery goes up the side of the neck and gives off the external carotid artery, as in *Sternotherus* and *Chrysemys*. Directly behind the skull, the large internal carotid artery gives off a smaller dorsolateral branch, the stapedial artery. Before entering the fenestra postotica, the stapedial artery gives rise to a branch which goes around the posterior part of the skull to the tissue of the incisura columellae auris, just as in *Chrysemys* and *Sternotherus*. In *Trionyx,* the stapedial artery is smaller than the internal carotid artery, but it is not greatly reduced as in *Sternotherus*. After traversing the dorsolateral corner of the fenestra postotica, the cavum acusticojugulare, the aditus canalis stapedio-temporalis, the canalis stapedio-temporalis, and the foramen stapedio-temporale, the stapedial artery enters the temporal fossa as a medium-sized artery which supplies only the muscles of the temporal fossa.

Shortly after entering the canalis caroticus internus, the large internal carotid artery sends a small branch dorsally into the foramen pro ramo nervi vidiani; this branch is similar to that of *Chrysemys* and is larger than that of *Sternotherus*. The internal carotid artery curves anteromedially in its canal and gives off a large branch into the canalis caroticus lateralis. This branch exists from the foramen caroticum laterale and from the foramen nervi trigemini to supply the muscles of the fenestra subtemporalis and to enter the fossa meckelii, where arteries are distributed as in *Chrysemys* and *Sternotherus*. In short, the mandibular artery arises as a branch of the internal carotid artery and utilizes the canalis caroticus lateralis, which conducts the palatine artery in *Sternotherus* and *Chrysemys*.

The internal carotid artery directly posterior to the foramen anterius canalis carotici interni is much larger than the internal carotid artery in the same region of *Sternotherus* and *Chrysemys*. Because of this, the anastomosis in the dorsum sellae of *Trionyx* is also larger than the anastomosis in the other two genera. From each side of the anastomosis, an artery emerges into the cavum cranii; this artery is much larger than the cerebral carotid artery of *Sternotherus* and *Chrysemys*. In the cavum cranii, this large artery goes anteriorly lateral to the pituitary body a short distance and then gives off a dorsal branch on each side which is clearly the cerebral carotid artery. The cerebral carotid arteries branch on the anterior and posterior ventral surface of the brain, giving rise to the middle cerebral artery and its branches, the posterior cerebral artery, the basilar artery, and the circle of Willis, just as in *Sternotherus* and *Chrysemys.*

After giving off the cerebral carotid artery, the large artery runs anteriorly in the cavum cranii medial to the ventral processus inferior parietalis, and just as it leaves the cavum cranii, the large artery branches into the orbit. Except for its origin, this large artery of *Trionyx* is very similar to the palatine artery of *Chrysemys* and *Sternotherus.* However, the position of origin from the internal carotid artery is an important point which very likely indicates that the large artery of *Trionyx* is not homologous with the palatine artery of the other two genera. Hence I call this artery the **arteria pseudopalatina** (pseudopalatine artery). To recapitulate, the pseudopalatine artery of *Trionyx* is a branch of the internal carotid artery which goes through the foramen anterius canalis carotici interni and gives rise to the cerebral carotid artery and the arteries of the orbit. In contrast, the palatine artery of *Sternotherus* is a large branch of the internal carotid artery which goes through the foramen caroticum laterale and gives rise to the mandibular artery and the arteries of the orbit; the palatine artery of *Chrysemys* is a minute branch of the internal carotid artery which goes through the foramen caroticum laterale and terminates without branching.

Medial to the anterior end of the crista pterygoidea, the pseudopalatine artery branches into three arteries which run anteriorly, anterodorsally, and ventrolaterally in the orbit. The fairly large anterior branch is the supraorbital artery, which runs anteromedially in the middle of the orbit, sending many branches to the eye and adjacent tissues. The main branch of the supraorbital artery then enters the fissura ethmoidalis, where it branches extensively to supply the tissue of the fossa nasalis. One of the anterior branches of the supraorbital artery a short distance inside the fissura ethmoidalis gives rise to a small posterior branch which exists from the posterior part of the fissura ethmoidalis and goes dorsally to enter the foramen supraorbitale. From the foramen, the small supraorbital branch enters its own canal in the prefrontal bone to supply the anterior nasal tissue.

The fairly large anterodorsal branch of the pseudopalatine artery is situated in the dorsal part of the posteromedial part of the orbit. This artery becomes associated with the optic nerve, and it supplies the eye. There is no orbital artery branching from the cerebral carotid artery of *Trionyx,* but this anterodorsal artery probably has approximately the same function as the orbital artery of the other two genera. I call this artery the **arteria optica** (optic artery); there is no optic artery in *Sternotherus* or in *Chrysemys.*

The ventrolateral branch of the pseudopalatine artery in the orbit is the infraorbital artery. In the posterior part of the orbit, the infraorbital artery gives rise to the pseudomandibular artery which goes dorsally to supply the muscles under the postorbital bar and then ventrally to supply the tissue of the lateral part of the mandible; the pseudomandibular artery of *Trionyx* is much larger than the same artery in *Sternotherus* and *Chrysemys.* The infraorbital artery continues ventrolaterally and gives rise to the inframaxillary artery, which enters the foramen palatinum posterius. In the ventral foramen palatinum posterius, the inframaxillary artery gives rise to a small branch which goes through the canalis intrapalatinus, exits from the foramen palatinum accessorium, and supplies the adjacent tissue on the roof of the mouth. The inframaxillary artery itself exits from the foramen palatinum posterius and runs anteriorly in the tissue medial to the border of the triturating surface, giving off many small branches to the adjacent tissue and to the maxillary bone. The arteries of each side then form a narrow anastomosis which sends small branches dorsally to the mouth tissue. The anterior nasal artery on each side extends from the anastomosis into the foramen praepalatinum and then into the nasal tissue.

The infraorbital artery goes a short distance anteriorly in the orbit and divides into the supramaxillary artery and the alveolar-nasal artery. The very small supramaxillary artery enters the foramen supramaxillare and supplies the tissue within the canalis infraorbitalis and canalis alveolaris superior. The alveolar-nasal artery goes anteriorly on the orbit floor and divides into two arteries in the foramen orbito-nasale; the smaller posterior nasal artery goes through the foramen orbito-nasale to supply the posterior nasal tissue, whereas the superior alveolar artery enters the canalis alveolaris superior to supply the lateral side of the maxillary bone and adjacent tissue.

To compare and summarize, the major arterial differences between *Trionyx* and the other two genera occur in the basisphenoid region of the skull. In *Trionyx*, the anastomosis of the internal carotid arteries in the dorsum sellae gives rise to the very large pseudopalatine artery, whereas in *Chrysemys* and *Sternotherus* the small anastomosis in the dorsum sellae gives rise to the cerebral carotid artery. The cerebral carotid artery of *Trionyx* is a branch of the pseudopalatine artery. In *Chrysemys* and *Sternotherus*, the palatine artery is a branch of the internal carotid artery which exits through the canalis caroticus lateralis, but in *Trionyx* the mandibular artery is a branch of the internal carotid artery which exits through the canalis caroticus lateralis. The mandibular artery of *Chrysemys* is a branch of the stapedial artery, and the mandibular artery of *Sternotherus* is a branch of the palatine artery. A branch from the mandibular artery to the brain is present only in *Sternotherus*. In spite of their different origins, the mandibular artery of each genus exits from the foramen nervi trigemini, goes through the fenestra subtemporalis, enters the fossa meckelii, and branches similarly in the mandible. Furthermore, the branches of the cerebral carotid arteries in the brain are very similar in the three genera.

The origin of the arteries of the orbital and nasal regions is a direct consequence of the rearrangement of the arteries in the basisphenoid region. In *Trionyx*, the pseudopalatine artery gives rise to the infraorbital and supraorbital arteries, and the stapedial artery supplies only the muscles of the temporal fossa. In *Chrysemys*, the large stapedial artery gives rise to the infraorbital and supraorbital arteries and to the cervical artery, which supplies the muscles of the temporal fossa; the palatine artery of *Chrysemys* is minute. In *Sternotherus*, the large palatine artery gives rise to the infraorbital and supraorbital arteries, and the stapedial artery is minute; only *Sternotherus* has a pseudostapedial artery which supplies the muscles of the temporal fossa.

The arteries of the orbit are suprisingly similar in the three genera, but there are minor differences. The supraorbital artery of *Chrysemys* is often smaller and more dorsally located than the supraorbital artery of the other two genera, and the branch of the supraorbital artery into the foramen supraorbitale arises more anteriorly in *Trionyx*. The infraorbital artery of *Sternotherus* gives rise to the anterior vidian artery, which is lacking in the other two genera, and the inframaxillary artery of *Trionyx* has a small branch into the canalis intrapalatinus which is absent in the other two genera. But the supramaxillary artery, inframaxillary artery and its anastomosis, anterior nasal artery, pseudomandibular artery, alveolar-nasal artery, superior alveolar artery, and posterior nasal artery are present in *Trionyx, Sternotherus,* and *Chrysemys*.

The internal carotid arteries are large in *Sternotherus* and *Trionyx* but small in *Chrysemys*. The branches from the internal carotid arteries into the foramen pro ramo nervi vidiani are larger in *Trionyx* and *Chrysemys* than in *Sternotherus*. The pharyngeal carotid artery of *Sternotherus* is larger than that of *Chrysemys*, and this artery is not present in *Trionyx*. The posterior vidian arteries of *Chrysemys* and *Sternotherus* are very similar and are not present in *Trionyx*. Finally, the orbital arteries of *Chrysemys* and *Sternotherus* are alike and are not present in *Trionyx*, which has a peculiar optic artery.

VII. THE GENERAL ARTERIAL PATTERNS ON A FAMILIAL LEVEL

Variations in cranial arteries within a genus seem to be very minor. The cranial arteries of the two *Trionyx spinifer* and the one dissected *Trionyx muticus* were nearly identical, and agree in most details with those of *Trionyx triunguis* described by Girgis (1964) except for the anastomosis he described between the mandibular and stapedial arteries. With the exception of the supraorbital artery, the arterial pattern was the same in all three dissected *Chrysemys*. The cranial anastomoses are somewhat variable, for one *Sternotherus* had no anastomosis between the internal carotid arteries, and one *Kinosternon* had no anastomosis between the inframaxillary arteries.

However, there may be characteristic variants in cranial arterial pattern among the genera of one family. Within the Testudinidae, the arteries of *Testudo graeca* (according to Shindo) seem to be nearly the same as those of *Chrysemys*, but in the other genera the following variations have been noted: in *Gopherus* and *Geochelone*, the mandibular artery arises from the stapedial artery, but it sometimes exits into the temporal fossa through its own foramen arteriomandibulare and not through the foramen cavernosum as in *Chrysemys* (according to McDowell); in *Emys orbicularis*, the mandibular artery arises from the infraorbital artery and only a small vestige remains of the mandibular artery which arises from the stapedial artery (according to Bojanus and Shindo); in some other genera such as *Terrapene*, the pharyngeal carotid artery is larger than that of *Chrysemys*, and still other genera have a larger palatine artery (according to McDowell). Within the Kinosternidae, the *Kinosternon subrubrum* which I dissected differs from *Sternotherus* in the following ways: the alveolar-nasal artery arises as a branch of the inframaxillary artery and runs dorsally through the foramen orbito-nasale to divide into the posterior nasal and superior alveolar arteries; the anterior vidian artery is slightly larger than that of *Sternotherus*, and it extends the full length of the anterior vidian canal. Within the Trionychidae, the uninjected *Lissemys punctata* which I dissected appeared to have branches of the infraorbital artery different from those of *Trionyx*. From the above, the arteries of the orbit and their branches seem to be variable in the different genera of each family, and hence these arteries cannot be included in considerations of the general arterial pattern at the family level, as seen in the Testudinidae, Kinosternidae, and Trionychidae.

In summary, many cranial arteries are, or appear to be, variable in occurrence among the different genera. Until more information is available, these arteries must be excluded from a description of the general arterial patterns at the family level. From the dissections and crania examined by myself and other authors, it can be seen that the general cranial arterial patterns of the three families can be characterized by the following:

Testudinidae: The large stapedial artery exits from the foramen stapedio-temporale, gives rise to the arteries of the orbit and often gives rise to the mandibular artery. The small internal carotid artery in the canalis caroticus internus gives rise to the minute, vestigial palatine artery which exits through the foramen caroticum laterale; the internal carotid arteries anastomose in the dorsum sellae and give rise to the cerebral carotid arteries.

Kinosternidae: The stapedial artery is a minute vestige which exits through a greatly reduced foramen stapedio-temporale. The large internal carotid artery in the canalis caroticus lateralis gives rise to the large palatine artery, which exits from the foramen caroticum laterale, gives rise to the arteries of the orbit and also gives rise to the mandibular artery; the internal carotid arteries anastomose in the dorsum sellae and give rise to the cerebral carotid arteries.

Trionychidae: The stapedial artery is smaller than the testudinid stapedial artery but is much larger than the stapedial artery of kinosternids. The large internal carotid artery in the canalis caroticus internus gives rise to the fairly large mandibular artery, which exits from the foramen caroticum laterale; the internal carotid arteries anastomose in the dorsum sellae and give rise to the large pseudopalatine artery. The pseudopalatine arteries give rise to the cerebral carotid arteries and to the arteries of the orbit.

VIII. POSSIBLE EVOLUTIONARY IMPLICATIONS

McDowell hypothesized a primitive cranial arterial pattern in which there is both a large stapedial artery and a large palatine artery (1961: 34). The testudinids may have evolved from this primitive pattern by enlarging the stapedial artery and greatly reducing the palatine artery, whereas the kinosternids possibly evolved in such a way that the stapedial artery was greatly reduced and the palatine artery was enlarged. This is all quite easy to understand, but the trionychid arterial pattern is much more difficult to derive from this primitive pattern, for trionychids have a reduced stapedial artery with no palatine artery.

The cranial arteries of the testudinids and kinosternids seem to give clear evidence for the separate evolution of these two families of turtles. The different sizes of the palatine and stapedial arrteries, the different origins of the mandibular artery and the arteries of the orbit, the presence of the kinosternid pseudostapedial artery and anterior vidian artery, and the branches from the mandibular arteries to the brain in kinosternids all point toward a long, separate evolution of the Kinosternidae and Testudinidae. As McDowell pointed out, the arterial pattern of each of these two families cannot be derived from the other arterial pattern. However, cranial arteries also provide evidence for the placement of these two families in a common superfamily. The presence of a palatine artery in the canalis caroticus lateralis, the origin of the cerebral carotid arteries, the presence of the orbital arteries, the similar arteries of the orbit, brain, and mandible, the presence of pharyngeal carotid arteries, and particularly the similar canals, foramina and arteries of the vidian nerve complex all point toward a common origin of these two types of testudinoid turtles.

Trionyx resembles *Chrysemys* and *Sternotherus* in having similar arteries of the brain, orbit, and mandible. Trionychids in general have followed the kinosternid type of cranial arterial evolution as opposed to the testudinid type, for soft-shelled turtles possess a large internal carotid artery and a stapedial artery which is not as large as the stapedial artery of testudinids. This similarity in basic cranial arterial patterns in the Kinosternidae and Trionychidae may be a case of parallel evolution, but it also may lend support to the opinion that these two families "are relatively closely related" (Webb, 1962: 443).

The presence of the pseudopalatine artery in the dorsum sellae, the origin of the mandibular artery from the internal carotid artery and its presence in the canalis caroticus lateralis, and the complete absence of the palatine and orbital arteries all point toward a trionychid arterial evolution which is extremely different from the arterial evolution of *Chrysemys* and *Sternotherus*. It seems very possible that the trionychids and kinosternids evolved in a parallel manner insofar as they enlarged the internal carotid artery, and a branch of the enlarged internal carotid artery gave rise to the arteries of the orbit. However, the trionychids evolved completely separately from the kinosternids thereafter, for they acquired a pseudopalatine artery in the foramen anterius canalis carotici interni, whereas the kinosternids developed a palatine artery in the canalis caroticus lateralis. This completely separate evolution of the three families from a common ancestor requires a primitive arterial pattern different from that hypothesized by McDowell, but I do not know what that primitive pattern would be.

On the other hand, the trionychids and kinosternids may have arisen from a common ancestor or from similar ancestors in which the internal carotid artery was large, the palatine artery in the canalis caroticus lateralis was large, the cerebral carotid arteries near the dorsum sellae gave rise to the orbital arteries, and the stapedial artery was similar to that of modern trionychids. From this hypothetical, primitive pattern, the kinosternids might have evolved by reducing the stapedial artery but retaining the other arteries. An anastomosis between the primitive mandibular artery and the palatine artery, and the degeneration of the primitive posterior mandibular artery may have resulted in the origin of the mandibular artery from the palatine artery.

The trionychids hypothetically could have evolved from this primitive pattern in a complex manner. For some reason, the palatine artery of the trionychid ancestor perhaps began to degenerate, and this degeneration could have caused the orbital artery to enlarge, for the orbital arteries of some recent turtles anastomose with the supraorbital and infraorbital arteries. As this degeneration and subsequent enlargement took place, an anastomosis may have developed between the palatine artery and mandibular artery, which primitively probably exited from the foramen cavernosum as a branch of the stapedial artery. This anastomosis resulted in the complete disappearance of the anterior part of the primitive palatine artery, causing the orbital arteries to supply all the blood to the orbital and nasal regions. The posterior, primitive mandibular artery then completely degenerated, and the anastomosis allowed blood to flow from the internal carotid artery to the mandible. Thus the hypothetical formation of the generalized trionychid arterial pattern was complete. It thus may be the case that the pseudopalatine artery of trionychids is homologous with the orbital artery of kinosternids, and the base of the trionychid mandibular artery may be homologous with the base of the kinosternid palatine artery.

It should be noted that the arterial pattern of *Trionyx* and the general arterial pattern of the trionychids can be derived in the above manner from the cranial arteries of *Sternotherus* and the general arterial pattern of the kinosternids. Furthermore, as Shindo noted, the mandibular artery of modern turtles is quite variable, and thus its different origins from the palatine artery, internal carotid artery, or stapedial artery of different turtles is not too surprising.

In my opinion, the similar small arteries, foramina, and canals associated with the vidian nerves of *Chrysemys* and *Sternotherus* show that the testudinids and kinosternids are fairly closely related, and these two families probably evolved from a common ancestor, as hypothesized by McDowell. Perhaps earlier, this common ancestor of the testudinids and kinosternids gave rise to a branch of turtles which evolved a cranial arterial pattern similar to the pattern the kinosternids would later acquire. In other words, the ancestor of the trionychids may have evolved in a manner parallel to the cranial arterial evolution later taken by the kinosternids. The trionychids may have arisen from this older branch in the manner described above.

In order to determine the closeness of the relationship between kinosternids and trionychids and the cranial arterial patterns of the ancestors of the trionychids, kinosternids, and testudinids ,many more detailed descriptions of the arterial foramina and bony canals of fossil skulls must become available. From these descriptions, the general arterial patterns can validly be inferred, as was done earlier for the Jurassic skulls described by Parsons and Williams. Much more work also needs to be done with the cranial arteries of all the genera in a single turtle patterns of the sea turtles and side-necked turtles have never been described in detail, and a detailed description of the cranial arteries of all the genera in a single turtle family has never been published.

IX. CONCLUSION

In this paper, the cranial arterial foramina and bony canals of *Chrysemys, Sternotherus,* and *Trionyx* are described and compared, and the cranial arteries which utilize these foramina and canals in the three turtle genera are also described and compared. Skull studies and published knowledge show that cranial arterial variation within a genus is slight and permit inference of the general cranial arterial patterns characteristic of the Testudinidae, Kinosternidae, and Trionychidae. Detailed knowledge of the cranial arteries gives evidence for assuming a long, separate evolution of the Kinosternidae and Testudinidae from a common ancestor, and evolution of the Trionychidae from an earlier branch of turtles which had evolved parallel to the evolutionary path later taken by the kinosternids. Finally, it should be re-emphasized that the cranial arteries of turtles are indeed evolutionarily significant, and more work in this field may help to clear up many of the current problems of turtle taxonomy.

X. TERMINOLOGY

The anatomical terms used in this paper which are not used by Parsons and Williams (1961) are listed below. The oldest source used by this author for each term is cited, and those terms for which no author is cited are original. Cited sources are not necessarily the first in which the terms were used.

arteria alveolare-nasalis
arteria alveolaris superior (Shindo, 1914)
arteria anterior nasalis (Shindo, 1914)
arteria anterior vidiana
arteria basilaris (Bojanus, 1819)
arteria carotico-pharyngealis
arteria carotica cerebralis (Siebenrock, 1897)
arteria carotica externa (Bojanus, 1819)
arteria carotica interna (Siebenrock, 1897)
arteria cerebri anterior (Shindo, 1914)
arteria cerebri media (Shindo, 1914)
arteria cerebri posterior (Shindo, 1914)
arteria cervicalis (Bojanus, 1819)
arteria inframaxillaris
arteria infraorbitalis (Shindo, 1914)
arteria mandibularis (Shindo, 1914)
arteria olfactoria (Bojanus, 1819)
arteria optica
arteria orbitalis (Shindo, 1914)
arteria palatina (Shindo, 1914)
arteria posterior nasalis (Shindo, 1914)
arteria posterior vidiana

arteria pseudomandibularis (McDowell, 1961)
arteria pseudopalatina
arteria pseudostapedialis
arteria stapedialis (Parsons and Wililams, 1961, but not listed)
arteria supramaxillaris (Bojanus, 1819)
arteria supraorbitalis (Bojanus, 1819)
canalis carotico-pharyngealis (McDowell, 1961)
canalis caroticus lateralis
canalis infraorbitalis (Ogushi, 1911)
canalis intrapalatinus
foramen arteriae anteriovidianae
foramen arteriaevidianae
foramen arteriomandibulare (McDowell, 1961)
foramen carotico-pharyngeale (McDowell, 1961)
foramen caroticum laterale
foramen nervi vidiani (Siebenrock, 1897)
foramen palatinum accessorium
foramen supramaxillare
foramen supraorbitale

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