
POSTNATAL ONTOGENY OF THE SKULL IN
THE EXTANT NORTH AMERICAN TURTLE
STERNOTHERUS ODORATUS
(CRYPTODIRA: KINOSTERNIDAE)

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ABSTRACT

There are few published data addressing the types, levels, and patterns of intraspecific variation in gross anatomical structures for nonavian reptiles, especially considering the widespread interest in their morphology and evolutionary history. This study examines variation in both discrete and continuous characters of the postnatal skull for a single population of the kinosternid turtle *Sternotherus odoratus*. The primary purpose of the study was to elucidate those features that exhibit transformations (and by default those that do not) in the latter two-thirds of postnatal ontogeny—that portion heavily relied upon in phylogenetic analyses of macroanatomical features and most often preserved in the vertebrate fossil record. Data are presented for cranial characters historically used to elucidate phylogenetic relationships in turtles and to assess fossil specimens taxonomically.

Results indicate that the number of characters exhibiting postnatal variation, and the levels at which they vary, are surprisingly high considering the conservative nature of both the taxonomic sample and the pool of examined characters. Features associated with the feeding apparatus are among the most variable cranial structures—for both continuous and discrete characters. A relatively large number of discrete transformations occur in structures derived from those cranial elements preformed in cartilage. This concentration demonstrates that developmental trajectories apomorphic for deep nodes in vertebrate phylogenetic history result in relatively late-stage postnatal transformations and high levels of variation in characters informative at much more restricted taxonomic levels. This study provides a baseline of data that future studies examining the ontogenetic and evolutionary history of variation can build upon and it represents a necessary step in understanding the complex system by which variability in developmental modules becomes integrated in the reptile skull.

INTRODUCTION

The relationship between ontogenetically correlated and phylogenetically informative transformations in anatomical structure (as inferred from observed differences in a series of semaphoronts) has a long and complicated history in biology (Gould, 1977; Mayr, 1982). It therefore is somewhat surprising that the amount of published information documenting ontogenetic variation in the nonavian reptile skull is not more substantial, especially considering both the taxonomic diversity within Reptilia and the historic and current interest this group receives from comparative morphologists, paleontologists, and systematists. Much of the work that is available on nonavian reptile cranial ontogeny addresses the sequence in which cranial ossifications appear and/or the topological relations of features during embryonic and early postnatal development (e.g., Bellairs and Kamal, 1981 [and references therein]; Kuratani, 1987, 1989; Eßwein, 1992; Rieppel, 1992a, 1992b, 1993a, 1993b; Rieppel and Zaher, 2001; Klembara, 2001, 2004; Maisano, 2002; Sheil, 2003, 2005; Sheil and Greenbaum, 2005; Tulenko and Sheil, 2007). Considerably fewer data are

available that describe the shape and structural transformations during later stages of postnatal development despite the fact that it is this portion of ontogeny most often relied upon in the delineation of morphological characters for phylogenetic analysis and in assessing the nature of observed variations in fossil specimens.

The number of studies explicitly describing postnatal transformations in cranial form in extinct nonavian reptile taxa (e.g., Sander, 1989; Carr, 1999; O'Keefe et al., 1999; Rauhut and Fechner, 2005; Horner and Goodwin, 2006; Goodwin et al., 2006) may actually be comparable to the number published for living species. The seemingly greater interest in studying late-stage ontogenetic transformations in extinct species might be understandable because of the array of unique skeletal features known only in extinct forms (e.g., Weishampel, 1981); however, it also is curious for at least two additional reasons. The first is rather obvious and lies in the general difficulty of attaining adequate sample sizes in the fossil record that support meaningful conclusions regarding the source of observed variation. That is, does an observed variant represent ontoge-

netic, sexual, individual, teratologic, taphonomic, or phylogenetic/taxonomic information—or some combination within this perceived hierarchy? Notable exceptions exist (e.g., Gao and Shubin, 2001), but certainly expanded samples are more readily available from extant species. Second, there is increased recognition in the biological community that homology can be assessed at the level of process and at the level of structure (see Wagner, 1996; Gilbert and Bolker, 2000). This concept is not new (see Panchen, 2001; Hall, 2003) and more accurately reflects the need to assert homology at more specific structural levels. Nevertheless, detailed studies of postnatal ontogenetic transformations in phylogenetically strategic extant taxa are not only a largely untapped source of systematically informative morphological data, but also could constitute an explicit phylogenetic framework in which to test transformational hypotheses for lesser-known extant and extinct forms.

For turtles, the only published study that explicitly examines postnatal growth trajectories and late-stage transformations in the skull (as a whole) of a living species is Dalrymple (1977) for the North American trionychid *Apalone ferox*. Because such data are available from only a single species, comparisons with a second species (extant or extinct and irrespective of how closely related the two species are) become explicitly nonphylogenetic because the polarity of observed similarities or differences cannot be established. This absence of a phylogenetic perspective may be especially noteworthy in this example, as the skull of *A. ferox*, and trionychids in general, is highly derived within turtles regardless of the systematic position of trionychids within Testudines (Gaffney, 1979; Shaffer et al., 1997; Near et al., 2005).

The purpose of this study is to increase the relatively depauperate published information regarding late-stage ontogenetic change (or perhaps lack of change) in the skull of extant reptiles by documenting postnatal transformations in the skull of the stinkpot, *Sternotherus odoratus* (Latreille). Emphasis is placed on documenting the presence or absence of discrete transformations as well as establishing growth trajectories for continuous characters. Results are assessed with

regard to comparable data from the skull of *Apalone ferox* (Dalrymple, 1977).

STERNOTHERUS ODORATUS AND ITS PHYLOGENETIC RELATIONSHIPS

The stinkpot, *Sternotherus odoratus*, is a relatively small-bodied turtle inhabiting the freshwater lakes and streams of North America from southern Maine, southeastern Canada, and Wisconsin south to Florida and south-central Texas (Iverson, 1992). *Sternotherus odoratus* is omnivorous with smaller individuals (under approximately 50 mm carapace length), feeding on aquatic insects, algae, and carrion, whereas larger individuals feed on an even greater diversity of food items (Mahmoud, 1968; Berry, 1975; Ernst and Barbour, 1989).

Sternotherus odoratus is one of at least 25 living cryptodire species that comprise Kinosternidae (Siebenrock, 1907; Ernst and Barbour, 1989; Iverson, 1991). These species currently are allocated to four extant genera: *Claudius*, *Staurotypus*, *Sternotherus*, and *Kinosternon*; the latter contains the majority of species-level diversity (at least 16 of 25 species; Iverson, 1991). Monophyly of Kinosternidae is supported by a series of morphological synapomorphies that include shell, nonshell postcranial, and cranial osteological characters (Meylan and Gaffney, 1989). Kinosternidae generally is accepted as the extant sister taxon to the Central American river turtle, *Dermatemys mawii*, within Kinosternoidea (fig. 1A; Meylan and Gaffney, 1989). The higher-level relationships within Cryptodira currently are subjects of disagreement among turtle systematists, and many competing hypotheses have been published regarding the sister taxon of Kinosternoidea (e.g., Trionychoidea, Meylan and Gaffney, 1989; Shaffer et al., 1997; Chelydridae, Near et al., 2005; and Chelonoidea, Lee et al., 2004; Krenz et al., 2005). Despite the lack of consensus regarding its sister taxon, Kinosternoidea regularly is found to be part of a relatively restricted clade that is the sister group to Testudinoidea (pond turtles and tortoises).

Few phylogenetic analyses are published that explore species-level relationships within Kinosternidae. Based on the analysis of

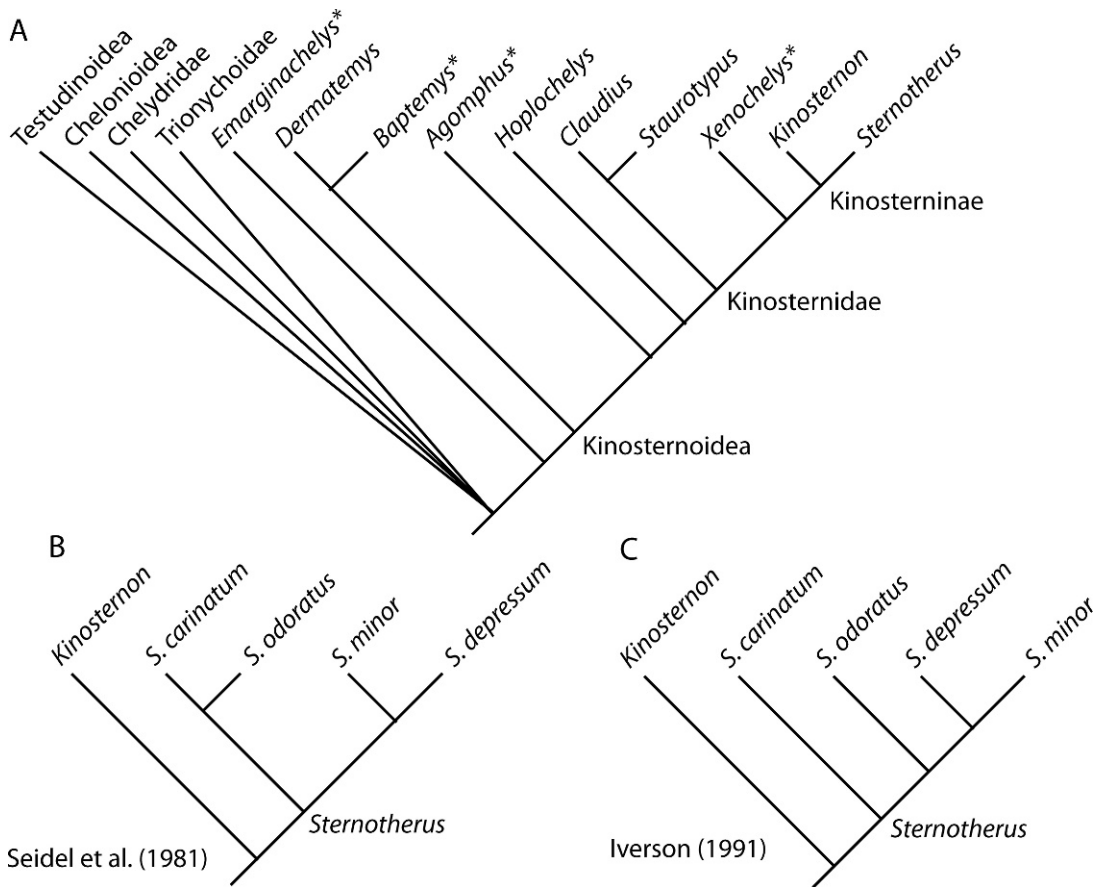


Fig. 1. Phylogenetic hypotheses regarding the systematic position of *Sternotherus odoratus*. The sister taxon to Kinosternoidea within Cryptodira is currently a point of contention (Meylan and Gaffney, 1989; Krenz et al., 2005; Near et al., 2005). Kinosternoidea here is considered to reflect the crown-clade of Kinosternidae + *Dermatemys*. This usage follows Joyce et al. (2004) and reflects the unresolved position of *Emarginachelys* (Shaffer et al., 1997). Asterisks (*) denote extinct lineages.

protein electromorph data, Seidel et al. (1981) concluded that *Sternotherus odoratus* is the sister taxon to *S. carinatum* (fig. 1B). That analysis, however, was restricted to *Sternotherus*. A subsequent expanded electrophoretic analysis (Seidel et al., 1986) concluded that *Kinosternon* is paraphyletic with respect to *Sternotherus*. Phylogenetic signals derived from patterns of neural bones in the carapace failed to support a monophyletic *Sternotherus* and determined that “*Sternotherus*” is not the sister taxon to *Kinosternon* (Iverson, 1988). A series of phylogenetic analyses based on much more expansive character data that included post-cranial osteological characters, cytochrome *b*

sequence data, and protein electromorph product supports a monophyletic *Sternotherus* comprising four living species (*S. carinatum*, *S. depressum*, *S. minor*, and *S. odoratus*) with *S. odoratus* being the sister taxon to a clade that includes *S. depressum* and *S. minor* (fig. 1C; Iverson, 1991, 1998).

Despite the historical importance that cranial morphology plays in turtle systematics (e.g., Gray, 1870; Baur, 1890, 1893; Siebenrock, 1897; McDowell, 1964; Gaffney, 1975, 1984; Gaffney and Meylan, 1988), no comprehensive study of cranial anatomy in kinosternid turtles is published, and no cranial characters are included in any modern phylogenetic analysis aimed specifically at

resolving the relationships within Kinosternidae. The skull of *Sternotherus odoratus* may be the best known among kinosternids, despite the fact that a comprehensive description is not available in the literature. Most of the recently published cranial data for *S. odoratus* are the result of *S. odoratus* being commonly utilized as a representative kinosternid in higher-level phylogenetic analyses of turtle relationships (e.g., Shaffer et al., 1997) or as an outgroup in phylogenetic studies that target the evolutionary history within more restricted turtle clades (most notably Testudinoidea; e.g., Stephens and Wiens, 2003; Joyce and Bell, 2004). Important observations on the cranial anatomy of *S. odoratus* also are available in Siebenrock (1897, 1907; general morphology and osteology), Poglayen-Neuwall (1953, 1954; myology), Albrecht (1967, 1976; cranial circulation and osteology), Parsons and Stephens (1968; nasal capsule), and Gaffney (1979; osteology).

MATERIALS AND METHODS

EXAMINED SPECIMENS

The material component of this study is based on 38 specimens of *Sternotherus odoratus* collected November 13, 1966, from the San Marcos River in the city of San Marcos, Hays County, Texas, and subsequently skeletonized using dermestid beetles. The San Marcos River begins within the city of San Marcos as a series of natural springs in the Edwards Aquifer that flow southeast toward the Gulf of Mexico as part of the Guadalupe River drainage. The exact pool or pools from which the San Marcos River sample (SMRS) was collected is not known, but it is likely that they were collected from Spring Lake, Aquarena Center (29°56'N, 97°55'W), which is a large spring-fed pool that forms the primary headwaters of the San Marcos River (Tyler, 1996; Rose et al., 1998; Swannack and Rose, 2003; Towns et al., 2003). The San Marcos River lies near, but well within, the southwestern margin of the range of *S. odoratus*.

Twenty-one females (55.3%) and 17 males (44.7%) comprise the SMRS, with the size of the specimens ranging from 44.9 to 90.1 mm in carapace length (table 1). Because soft-

tissues were not collected and preserved, the only gender information available is that provided by the original collector. The specimens are housed in the Texas Memorial Museum (TMM) and denoted both in the museum and in this paper by the letter M. The SMRS provides an opportunity to assess the morphological variation that occurred in that population during a narrow interval of time because all the specimens were collected the same day. Population-level studies of morphological variation are important because they provide a baseline of variation data on which future studies can build. Delineating the source of observed variation in anatomical systems requires replication (Jones and German, 2005). This means that in order to support conclusions regarding the source of observed variation at one level (e.g., ontogeny, geography, phylogeny), variation in that system has to be studied at a minimum of two levels. A sample drawn from a single population, though potentially exhibiting characteristics peculiar to that population, also eliminates the influence of geography and most associated environmental variables that may contribute to variation observed in a normal species sample (microgeographic and microenvironmental differences potentially remain influential; e.g., Thorpe and Brown [1989], Freeman-Gallant [1996], Verdade et al. [2002]). The SMRS is particularly informative because all specimens were collected on the same day, thereby largely negating the influence of temporal variation on the skeletal structure (e.g., Edgren, 1960). The relative lack of reported sexual dimorphism in *Sternotherus odoratus* and the relatively small size of the SMRS reduce both the necessity and ability to compare more refined partitions that would increase the independence of the results.

AGE ESTIMATION OF THE SAN MARCOS RIVER SAMPLE (SMRS)

The San Marcos River sample (SMRS) was divided into two primary age classes that are referred to as “juvenile” and “adult.” This division is less refined than preferable but was necessary in order to maintain a large enough sample size in each class to permit substantive comparisons and conclusions. Maturity as-

TABLE 1
Measurements Used to Classify Specimens of *Sternotherus odoratus* from the SMRS
(*N* = 38) as Juveniles or Adults

CL = carapace length, PL = plastron length, GSL = greatest skull length, CBL = condylobasal length. All measurements were taken along a straight line and are in millimeters. ? represents a measurement that could not be recorded because of the disarticulated nature of the specimen.

	CL	PL	GSL	CBL		CL	PL	GSL	CBL
Juvenile Males (<i>N</i> = 5)					Juvenile Females (<i>N</i> = 10)				
M-2992	44.9	29.1	13.0	?	M-2960	?	30.2	13.7	?
M-2980	49.8	32.1	19.8	16.9	M-2971	47.2	32.1	18.9	16.6
M-2986	50.1	33.4	19.8	16.9	M-2974	47.3	31.8	18.7	15.8
M-2993	53.2	35.6	21.2	18.1	M-2978	?	31.8	?	?
M-2981	53.8	36.4	20.6	17.1	M-2994	49.1	34.4	19.4	16.4
					M-2990	?	?	20.2	?
					M-2995	54.1	37.7	21.5	18.1
					M-2991	53.2	37.8	21.7	?
					M-2968	54.9	37.5	21.8	18.5
					M-2965	57.9	39.9	22.4	19.3
Adult Males (<i>N</i> = 12)					Adult Females (<i>N</i> = 11)				
M-2997	59.4	39.4	24.1	20.6	M-2977	62.1	43.2	23.9	20.1
M-2976	60.7	40.8	23.2	20.5	M-2969	63.4	44.5	23.4	19.9
M-2987	60.7	40.7	23.8	20.9	M-2964	69.6	44.8	26.4	22.8
M-2996	66.6	43.5	27.2	23.4	M-2959	70.4	47.3	27.4	23.4
M-2988	69.0	47.7	28.6	24.7	M-2970	70.9	51.9	25.6	22.2
M-2989	69.7	?	26.1	22.5	M-2958	74.0	53.3	27.1	23.2
M-2979	71.9	48.2	26.6	23.1	M-2967	74.1	48.0	27.9	23.2
M-2984	?	?	31.1	26.4	M-2973	76.5	49.3	29.8	25.2
M-2975	79.2	53.5	31.0	26.9	M-2966	79.3	51.9	33.5	28.1
M-2985	?	?	32.8	27.4	M-2956	80.1	60.9	29.6	24.6
M-2982	?	?	33.3	?	M-2961	81.0	59.5	30.6	26.5
M-2983	90.1	60.9	39.3	31.9					

assessments were based primarily on carapace lengths using data presented by Tinkle (1961), who studied body size and sexual maturity in *Sternotherus odoratus* across much of its geographic range. The presence of significant latitudinal variation in both overall body size and size at maturity in *S. odoratus* prompted Tinkle to divide his sample into northern and southern halves based on collection locality, with the southern sample including specimens from Alabama, Arkansas, Florida, Georgia, Louisiana, Tennessee, and Texas. His criteria for sexual maturity in males of the southern group included enlargement of the testes, presence of an enlarged and convoluted vas deferens, and presence of tailed spermatozoa in the testes or vas deferentia. His criteria for sexual maturity in females of the southern group included yolk-filled ovarian follicles of a certain size, ovulation scars in the ovary, and eggs in the oviduct (Tinkle, 1961). I

divided the SMRS into juveniles and adults based on the carapace lengths of the smallest, southern male and female specimens determined by Tinkle (1961) to meet the criteria for sexual maturity (cutoff between juveniles and adults set at 60 mm carapace length for females and 55 mm for males). It is probable that some specimens from the SMRS classified as adults were not sexually mature when collected; this most likely occurred with females based on the disparity in size between the smallest mature and largest immature females found by Tinkle (1961). The division used in this study maintains a reasonable ratio in sample size between the classes while basing the division on a biologically meaningful parameter (as opposed to simply dividing the samples based on median values; see Zug, 1991). Another possibility for classifying individuals as juveniles or adults would be to use discriminant function analysis of

cranial size and shape; however, since determination of cranial shape change during postnatal growth is one of the primary goals of the study, this method was not employed.

Specimens whose carapace lengths were not available owing to disarticulation were categorized based either on plastron length, total skull length, or condylobasal length (depending on which was available for the particular specimen). Each of these variables correlates strongly with carapace length (fig. 2). I compared the age estimations based on carapace length against other skeletal indicators commonly used for estimating skeletal maturity in turtles. These indicators included closure of the costoperipheral fontanelles, closure of the ectepicondylar foramen of the humerus, and closure of the otic fontanelle (Zug et al., 1986; Zug, 1991). The correlation of these skeletal transformations with body size as estimated by shell length and the attainment of sexual maturity is of particular interest to paleontologists who rely largely on such transformations to assess the maturity of fossil specimens (although see Erickson, 2005).

QUALITATIVE DESCRIPTIONS

Emphasis was placed on the description of characters drawn from published phylogenetic analyses of turtle relationships. These analyses include those addressing higher-level relationships within turtles (Gaffney, 1975, 1984, 1996; Gaffney and Meylan, 1988; Shaffer et al., 1997), relationships within Trionychoidea (Meylan, 1987; Meylan and Gaffney, 1989; Meylan et al., 2000), and relationships within Testudinoidea (Crumly, 1982; Hirayama, 1985; Burke et al., 1996; Yasukawa et al., 2001; Stephens and Wiens, 2003). Studies of testudinoid phylogeny are included because Testudinoidea is widely considered to be closely related to Kinosternoidea (although they are not necessarily sister taxa, see above), and therefore constitutes an important outgroup for comparative studies within Kinosternidae (and vice versa). In addition, cranial morphology has played a far more important role in exploring phylogenetic relationships within Testudinoidea than it has in studies of kinosternid systematics. One result of this inequality is that

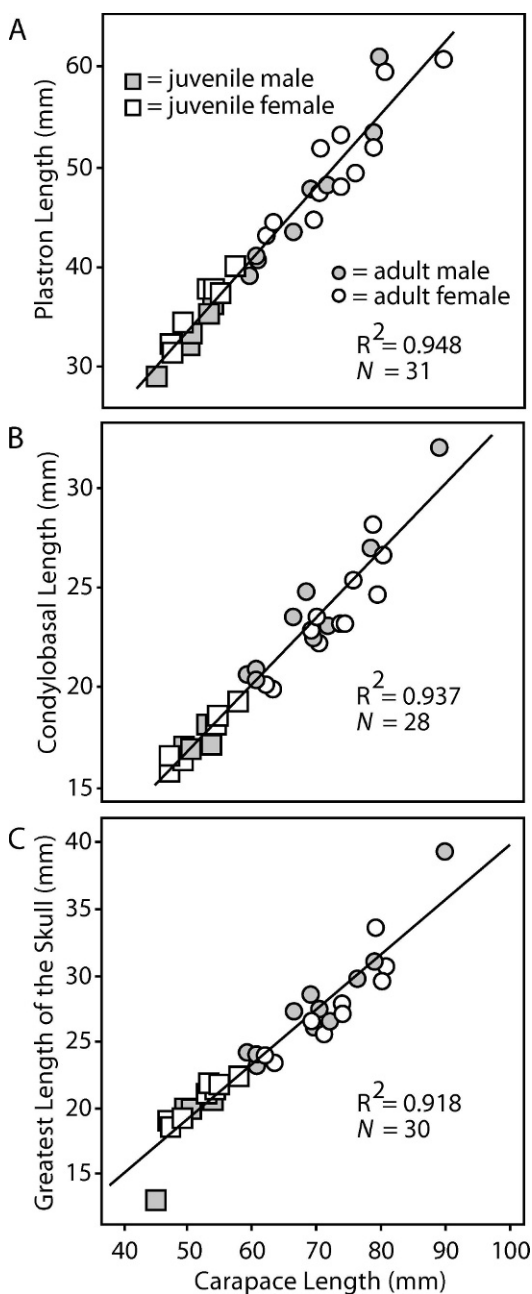


Fig. 2. Relationship between carapace length and plastron length (A), condylobasal length (B), and greatest length of the skull (C) for *Sternotherus odoratus* from the SMRS.

characters drawn from testudinoid studies more comprehensively encompass the morphology of the skull and thus may be useful for exploring cranial variation within Kino-

sternidae. Although a comparative morphology of the kinosternid skull lies well outside the scope of this study, I did attempt to place the observed morphologies of the SMRS into a broad phylogenetic context based both on personal observations of specimens and the available literature. A more thorough comparative analysis will be published elsewhere. Descriptive terminology largely follows Gaffney (1972, 1979). Anatomical abbreviations are provided in appendix 1.

Discrete character states were scored and recorded for each specimen as they are described in appendix 2. The character state observed in the majority of SMRS specimens is listed in appendix 3, whereas the scorings for individual specimens are provided in appendix 4. Several characters described originally as discrete may be represented more precisely as a morphometric index (e.g., shape of the foramen orbitonasale equaling the greatest length of the foramen divided by its greatest width), so where possible these characters were modified. In addition to published phylogenetic characters, numerous discrete variables were examined that currently are not included in any known phylogenetic analysis of turtles (referred to hereafter as “unpublished” characters; although, this is somewhat misleading because many characters are noted in published morphological descriptions of turtle skulls—the primary source being Gaffney, 1979). As with the continuous characters, these observations were included to more fully document postnatal morphological variation.

Postnatal transformations in discrete cranial characters are inferred here based largely on the qualitative description of differences observed between the smallest (presumed youngest) and largest (presumed oldest) specimens in the sample following the methods of Giannini et al. (2004). However, because such differences may reflect variation more accurately explained by phenomena other than ontogeny (e.g., sexual, individual, teratological, or stochastic patterns of structural complexity), variation throughout the sample is noted with the frequency of each variant presented as a percentage of the sample. For some characters, such as those observable only on disarticulated elements, the reported frequencies are based on low sample sizes; however, frequency data based

on samples as low as five were shown to be phylogenetically informative (Wiens, 1995, 1999), and therefore are reported here. Character-state frequencies are compiled and reported as percentages for the SMRS as a whole, as well as for subdivisions of the sample (juvenile, adult, male, female; appendix 5). Variation scores are compiled and reported for each character that exhibits some level of variation within the SMRS. Variation scores for characters with only two character states are equal to the percentage of specimens exhibiting the character state whose variation frequency is less than 50%. For example, if for a two-state character, half the observed specimens exhibit character state 0 and half the specimens exhibit character state 1, then the variation score for that character is 50. For characters with more than two character states, the variation score is equal to the sum of frequencies for those character states that most closely approximate but do not exceed 50%. The variation score cannot exceed 50. For example, if a character has three states that are exhibited in the sample with respective frequencies of 25, 15, and 60%, then the variation score for that character is 40%. The purpose of the variation score is to reflect the level of variation in each character, and facilitate statistical comparisons of variation between characters with different numbers of character states. Significant differences in mean variation scores (expressed as a percentage of the sample) are assessed using paired-samples t-tests. Levene’s test is used to test the assumption that variances are equal. Significant differences in the expression of character states between the different data partitions (e.g., juvenile versus adult, male versus female) are assessed using Mann-Whitney nonparametric tests for two-independent samples (Zar, 1999).

Frequency data and variation scores are also compiled and summarized for character allocations based on anatomical partitioning of the skull. Two partitioning schemes are employed (table 2). The first scheme is based on a topological division of characters that estimates the major functional units of the skull. These partitions, which include dermal roofing, palatal, palatoquadrate, braincase, and lower jaw elements, follow the divisions

TABLE 2

Allocation of Cranial Elements to the Two-Partitioning Schemes Utilized in This Study

The qualitative observations detailed in the description are organized based on a topological/functional scheme following Gaffney (1979). The number and percentage of examined characters from appendix 2 are given for each partition.

Development-Based Partitions	
Dermatocranium (103; 71.0%)	prefrontal, frontal, parietal, jugal, quadratojugal, squamosal, postorbital, premaxilla, maxilla, palatine, vomer, pterygoid, dentary, angular, surangular, coronoid
Neurocranium (30; 20.7%)	supraoccipital, parabasisphenoid, exoccipital, prootic, opisthotic
Splanchnocranium (12; 8.3%)	epipterygoid, quadrate, columella auris, articular
Topological/Functional-Based Partitions	
Dermal Roofing (22; 15.9%)	prefrontal, frontal, parietal, jugal, quadratojugal, squamosal, postorbital
Palatal (44; 30.4%)	premaxilla, maxilla, palatine, vomer
Palatoquadrate (31; 21.4%)	pterygoid, epipterygoid, quadrate, columella auris
Braincase (32; 22.1%)	supraoccipital, parabasisphenoid, exoccipital, prootic, opisthotic
Lower Jaw (16; 11.0%)	dentary, angular, surangular, coronoid, articular

of the skull used in the descriptive studies of Gaffney (e.g., Gaffney, 1979). The second scheme partitions the cranial characters based on the developmental origin of the bones involved in the characters and includes dermatocranium, neurocranium, and splanchnocranium (Goodrich, 1930); this is also the scheme used here to organize the qualitative observations. Most characters are allocated easily to one of the divisions, but some characters are formed from elements from two or more of the partitions. In such cases, an attempt was made to assess the dominant factor contributing to the observed variation. For example, character 60 (pterygoids divided by basisphenoid; Shaffer et al., 1997) involves elements from the palatoquadrate and braincase partitions of the skull, as well as the dermatocranium and neurocranium; however, the observed variation in this character appears to be based on the degree of ossification of the pterygoids rather than any morphological transformation of the basisphenoid and therefore this character is allocated to and analyzed as part of the

palatoquadrate and dermatocranial cranial partitions.

Bilateral asymmetry was reported for every examined discrete character. When totaling the percentages of variation and for the calculation of variation scores, asymmetrical specimens were counted as exhibiting whichever character state increased the total variation for that character. This approach inflates variation levels relative to alternative approaches (e.g., consistently counting asymmetrical characters as exhibiting the derived state), but more accurately reflects the amount of morphological variation in the sample.

Standard two-dimensional chi-square tests of independence were used to search for statistically significant correlations in observed levels of variation between those phylogenetic characters that exhibit some level of variation. This test was run on every possible pair of characters using $\alpha = 0.05$ as the level of significance. The Yates continuity correction was applied in cases with only one degree of freedom (degrees of freedom being

based on the number of character states; e.g., two possible characters states, 0 and 1, equals one degree of freedom) (Zar, 1999). It is important to stress that the purpose of applying these tests is to explore the data for potentially nonindependent variations that may subsequently prove to be biologically relevant. When running such a large number of tests, there is a strong likelihood that some positive correlations will be retrieved through random chance alone. In addition, the sample sizes for many of these character combinations are relatively small, with expected values often falling below 5. With low expected values, the χ^2 values may be inflated upward and thus also lead to statistically significant correlations that are not biologically meaningful (Cochran, 1954). In an attempt to avoid reporting character correlations that are obvious false positives, while still using the test to explore the data, I checked each significant pairwise correlation by examining the character matrix to make sure that the variant morphologies (i.e., those found in a minority of the specimens) for both characters occur in at least some of the same specimens. A similar approach was used to explore for potential correlations in the Permian dicynodont *Diictodon* (Sullivan and Reisz, 2005).

CONTINUOUS CHARACTER VARIATION AND ALLOMETRY

Continuous characters in the form of straight-line measurements were recorded to the nearest 0.1 mm from each of the SMRS specimens using digital calipers. Because the skulls of seven of the SMRS specimens are disarticulated, variation for continuous characters is based on 31 specimens (10 juveniles, 21 adults, 14 males, 17 females). The measurements were drawn largely from the literature but also include previously unreported dimensions that were added in order to more completely represent skull size and shape. The continuous characters and the sources from which they were drawn (if applicable) include (fig. 3): (1) *greatest skull length* (Tinkle, 1958; Dalrymple, 1977; Stephens and Wiens, 2003; measured from the tip of the snout to the caudal extremity of the supraoccipital); (2) *condylobasal length* (Dal-

rymple, 1977; Stephens and Wiens, 2003; measured from the tip of the snout to the caudal end of the occipital condyle); (3) *maximum skull width* (Tinkle, 1958; Stephens and Wiens, 2003); (4) *cranial height* (vertical distance between basioccipital-parabasisphenoid suture [which is visible in all examined specimens] to parietal/supraoccipital suture along crista supraoccipitalis); (5) *greatest width of apertura narium externa*; (6) *greatest height of apertura narium externa at midline*; (7) *minimum interorbital width* (Dalrymple, 1977); (8) *frontal length* (Stephens, 1998; maximum length of the frontal measured along the parasagittal axis); (9) *greatest length of orbit* (Dalrymple, 1977; Stephens, 1998); (10) *minimum width of postorbital arch* (Dalrymple, 1977; Stephens and Wiens, 2003; measured midway between dorsal origin and contact with zygomatic arch); (11) *minimum dorsoventral width of zygomatic arch* (Stephens and Wiens, 2003); (12) *width of maxillary triturating surface* (McDowell, 1964; Dalrymple, 1977; Stephens and Wiens, 2003; measured laterally and perpendicular to the long axis of the triturating surface, which runs oblique to the long axis of the skull [can include the palatine contribution if it exists]); (13) *palatal width* (Stephens, 1998; distance between medial margin of right and left foramen palatinum posterius); (14) *minimum width of pterygoid waist* (Williams, 1952; Tinkle, 1958; Dalrymple, 1977); (15) *width between lateral margins of right and left processus pterygoideus externus*; (16) *pterygoid suture* (Stephens, 1998; length of the pterygoid-pterygoid suture, viewed ventrally); (17) *pterygoid suture + parabasisphenoid* (Stephens, 1998; distance between the parabasisphenoid-basioccipital suture and the vomer-pterygoid suture as viewed ventrally and measured along the central axis); (18) *least length across dorsal surface of otic chamber* (Tinkle, 1958; measured along the long axis of the otic chamber, which runs oblique to the long axis of the skull); (19) *intersquamosal width* (Tinkle, 1958; Stephens, 1998; distance between the caudal-most portion of each squamosal); (20) *basicranial width* (measured across ventral floor of braincase between medial margins of right and left foramen posterius canalis caroticus internus); (21) *greatest width of lower tritu-*

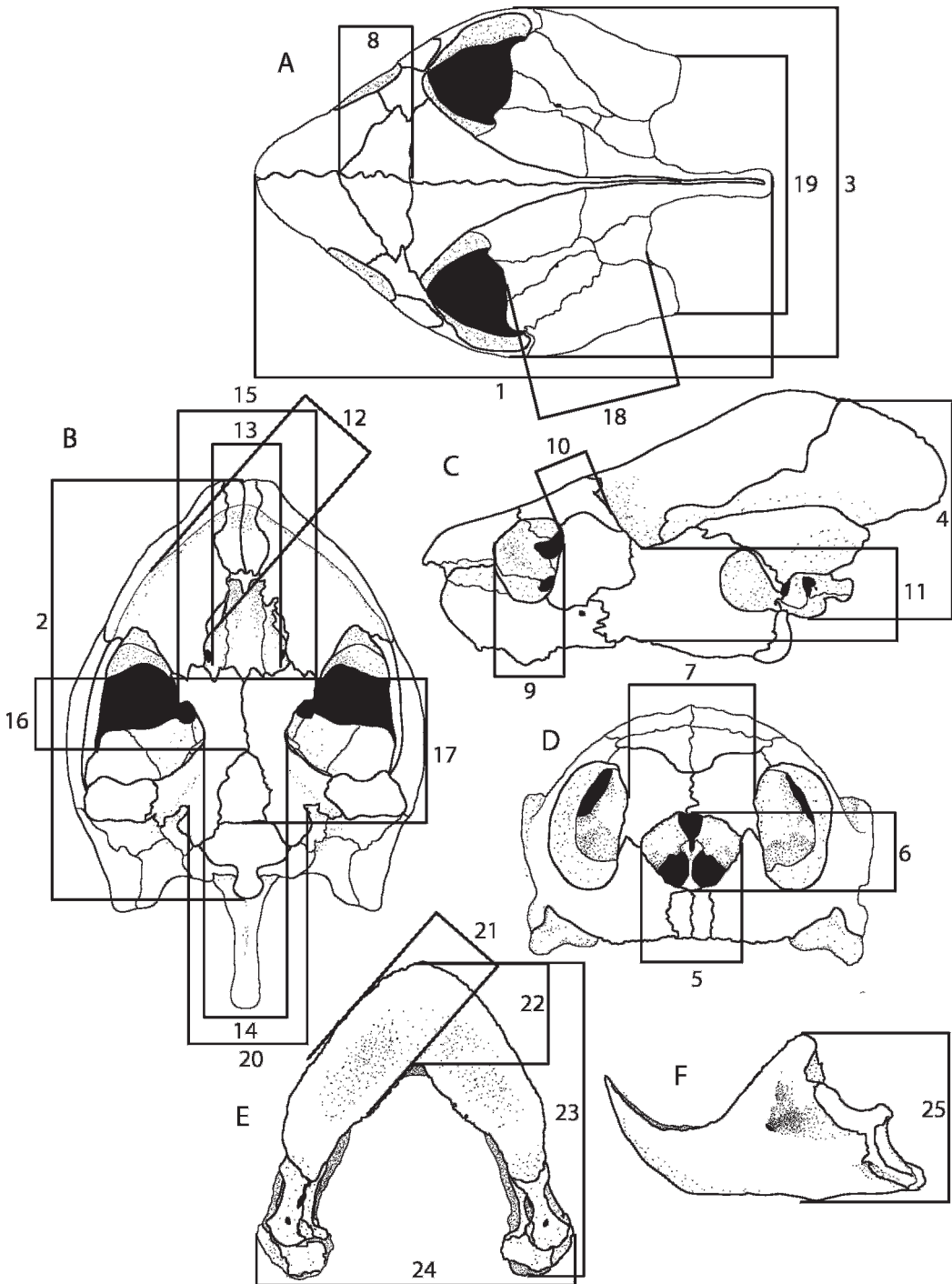


Fig. 3. Continuous characters included in morphometric and growth analyses. Numbers refer to character descriptions in text. Dorsal view of skull (A), ventral view of skull (B), left lateral view of skull (C), rostral view of skull (D), dorsal view of lower jaw (E), and left lateral view of lower jaw (F).

rating surface (Dalrymple, 1977; Stephens, 1998); measured laterally and perpendicular to the long axis of the triturating surface, which runs oblique to the rostrocaudal axis of the mandible); (22) *rostrocaudal length of the lower triturating surface* (measured along the mandibular symphysis); (23) *greatest length of mandible*; (24) *greatest width of mandible*; (25) *height of lower jaw*.

These measurements, which reflect the major dimensions and overall shape of the skull and lower jaws, were analyzed using bivariate regression and multivariate principal components analyses (PCA) largely for the purpose of determining growth trajectories for different portions of the skull. Bivariate analyses using greatest length of the skull as a measure of overall size (Radinsky, 1981a, 1981b; Emerson and Bramble, 1993) were used to assess the growth trajectories of the other 24 continuous characters diagrammed in figure 3. Growth was examined using the equation $\log y = \log b_0 + b_1 \log x$, which is the log transformation of the power growth equation $y = b_0 x^{b_1}$ (Gould, 1966; Alexander, 1985; Abdala and Giannini, 2000; Abdala et al., 2001), where y is the focus variable, b_0 is the y-intercept, x is the total length of the skull, and b_1 is the slope of the line (coefficient of allometry; see Gayon, 2000). Deviations from isometry were assessed by testing the significance of the allometry coefficients with two-tailed t-tests under the null hypothesis $b_1 = 1.0$, fixing type I error rate first at $\alpha = 0.01$ and then at $\alpha = 0.05$. Two significance tests were employed because the primary purpose of these statistical procedures is to explore the data—coefficients that are significant at high and marginal levels of confidence are of interest (i.e., $0.05 > P > 0.01$; Abdala and Giannini, 2000; Giannini et al., 2004). t -scores were calculated under the null hypothesis that $b_1 = 1.0$ using the equation $t = (b_1 - 1)/\sigma_b$ (where σ is the standard error; Zar, 1999) with isometry being the condition in which the allometry coefficient is statistically indistinct from the null hypothesis (unity; Giannini et al., 2004). Statistically significant deviations in which $b_1 < 1.0$ represent negative allometry, whereas those in which $b_1 > 1.0$ represent positive allometry.

In order to increase the reliability of estimating the relationship between each

variable and overall size, two regression methods were used to determine the coefficient of allometry (b_1). Least squares regression is a commonly applied regression technique (performed here using SPSS, 2000); however, there are problems with its application to biological growth. Least-squares regression assumes there is a variable that truly is independent (i.e., devoid of both measurement error and natural variation), which certainly is not the case with greatest length of the skull (Radinsky, 1981a, 1981b; Niklas, 1994). Consequently, coefficients of allometry were calculated using reduced major axis regression (RMA; Bohonak, 2002). RMA is more appropriate for studying biological growth because the two variables under study are interchangeable, meaning that the dependence on a size relationship is not explicit, thus allowing variation in both variables (Sokal and Rohlf, 1981; Niklas, 1994). Least squares and RMA are correlated arithmetically through the correlation coefficient with their differences representing shifts in scale between b_1 (Niklas, 1994). The size of these shifts depends on the amount of variation explained by size (the correlation coefficient [R value]); these techniques were applied to cranial growth in marsupial mammals by Abdala and Giannini (2000), Abdala et al. (2001), Flores et al. (2003, 2006), and Giannini and Abdala (2004).

Principal components analyses were run on the data from these 25 measurements for two primary purposes. First, PCA was simply used to explore the nature of size and shape variation within the TLS as a whole and between various subdivisions of the sample (i.e., juvenile vs adult, male vs female). For these initial exploratory analyses, PCA was performed on untransformed data. All PCA were executed in SPSS (2000).

Secondly, PCA was used to derive multivariate coefficients of allometry based on the generalization of the allometry equation proposed by Jolicoeur (1963a) and as applied by Jolicoeur (1963b), Voss et al. (1990), Voss and Marcus (1992), O'Keefe et al. (1999), Giannini et al. (2004), and Flores et al. (2006). In contrast to bivariate allometry, which estimates the relationship between two selected variables, one of which is used to represent overall size (i.e., greatest length of the skull in this study), multivariate analysis considers size

as a latent variable affecting all examined variables simultaneously. The first eigenvector of a principal component analysis generally expresses the allometric relationships between the examined variables and size, if those eigenvectors are extracted from a variance-covariance matrix of variables transformed to natural logarithms (Jolicoeur, 1963a, see Giannini et al., 2004). Therefore, multivariate allometry is assessed through comparison with a hypothetical isometric eigenvector that is expressed as $1/p^{0.5}$ where p equals the number of examined variables (Giannini et al., 2004). The expected isometry value for each of these 25 variables is therefore equal to $1/25^{0.5}$, or 0.200. PCA requires a complete design (no missing values); therefore only 30 of the total SMRS of 38 specimens contributed to the multivariate results (because only 30 specimens had complete values).

The significance of observed deviations from the theoretical isometric eigenvector of 0.200 was assessed following the methodology outlined by Giannini et al. (2004), in which the data are resampled using a first-order jackknife approach (Manly, 1997). This approach involved successively removing one specimen at a time from the sample and recalculating the subsample eigenvectors using PCA as described above. Each set of eigenvectors derived from this subsampling technique can be conceptualized as a set of pseudovalues (surrogates of the true coefficients). More specifically, each pseudovalue is calculated as $\hat{e}_j^* = n \hat{e} - (n-1) \hat{e}_{-j}$, where $\hat{e}$ is the observed multivariate coefficient of allometry (value of the first unit eigenvector) for each examined variable, and $\hat{e}_{-j}$ is the value of the coefficient of allometry obtained with specimen j removed (Manly, 1997; Giannini et al., 2004). The mean of the corresponding pseudovalues for a given variable represents the jackknife estimate of the multivariate allometry coefficient of that variable, and the difference between that mean and the observed coefficient of allometry based on PCA of all characters is an estimate of the sampling bias that may be present in the one-sample coefficient derived from the analysis including all specimens (Giannini et al., 2004). The standard deviation of each set of pseudovalues was calculated and used to establish a 99% confidence

interval for the mean pseudovalue (i.e., jackknife estimate of the coefficient of allometry). Following the methodology of Giannini et al. (2004), a significant departure from isometry was considered to occur when the 99% confidence interval does not include the expected value under isometry (0.200); additionally, the possible influences of extreme values was assessed by trimming the largest and smallest pseudovalues for each variable and recalculating the 99% confidence intervals.

RESULTS

AGE ESTIMATION

SHELL LENGTH AND ONTOGENETIC CLASSIFICATION: The carapace length of hatchling *Sternotherus odoratus* is 20–22 mm (Ernst and Barbour, 1989), with adults sometimes reaching carapace lengths of over 130 mm; specimens in the northern part of the range are on average larger than those in the south (Tinkle, 1961; Reynolds and Seidel, 1982). The carapaces of the SMRS range in length from 44.9 to 90.1 mm (table 1). Approximately the first 20–25% of the postnatal ontogeny of this population (based on a hatchling carapace length of 20 mm and a carapace length of 90 to 100 mm for the largest and oldest specimens), therefore, is not represented in the SMRS. The absence of this portion of the ontogeny may be caused by a bias in the collection technique or it may represent a skewed size distribution within the population because of differential growth rates (juveniles may grow faster than older individuals; Zug, 1991) or a demographic bias in population structure. The portion of the ontogeny that is represented in SMRS seemingly would be the most likely to be represented in the fossil record (and in phylogenetic analyses) based on the robustness of the ossifications (skeletal mass; Iverson, 1982), and therefore the most important for the goals of this study.

The smallest male and female specimens from the southern sample that met the criteria for sexual maturity had carapace lengths of 54 and 61 mm, respectively (Tinkle, 1961). The largest male and female specimens from the southern sample of Tinkle (1961) that lacked

the criteria for maturity measured 56 and 78 mm carapace length, respectively. The average size of sexually mature individuals was 65 mm in southern males and 82 mm in southern females. The smallest SMRS specimens whose carapace lengths exceed the smallest specimens meeting the criteria for sexual maturity by Tinkle (1961) are M-2997 (59.4 mm) and M-2977 (62.1 mm) for males and females, respectively (table 1). These specimens were considered the smallest adults in the SMRS, with smaller specimens considered juveniles. This scheme of classification identifies 15 juvenile and 23 adult specimens constituting the SMRS. Bivariate regression analyses of plastron length of these specimens indicate that the later two-thirds of postnatal ontogeny in *Sternotherus odoratus* are represented fairly continuously by the SMRS (fig. 2).

COSTOPERIPHERAL FONTANELLES: Closure of the costoperipheral fontanelles closely approximates the estimation of sexual maturity based on carapace length (fig. 4A). For both males and females, the costoperipheral fontanelles were completely closed in the largest specimen allocated to the juvenile group based on carapace length, with all smaller specimens retaining fontanelles. M-2997, the smallest female allocated to the adult group, was the only adult that retained remnants of the costoperipheral fontanelles.

ECTEPICONDYLAR FORAMEN: In both males and females of the SMRS, closure of the ectepicondylar foramen, which lies on the radial side of the humerus and transmits the radial nerve (Williston, 1925), was delayed relative to both the obliteration of the costoperipheral fontanelles and the estimation of sexual maturity based on carapace length (fig. 4B). The smallest male specimen (CL = 69.0 mm) to contain a closed ectepicondylar foramen is M-2988, and in this specimen the foramen is closed only on the right humerus (remains open on the left humerus). Two larger male specimens (M-2975 and 2982) also exhibit bilateral asymmetries in the closure of the ectepicondylar foramen. The only male specimen that contains completely closed ectepicondylar foramina on both the right and left side is M-2983, the largest male in the SMRS. The smallest female specimen to exhibit a closed ectepicondylar foramen is

M-2958, and only one humerus is preserved with this specimen. The next largest female specimen (M-2967) exhibits bilateral asymmetry in the closure of its foramina. The successively larger females exhibit symmetric closure of the foramen, with the exception of M-2956, which contains open foramina on both sides. Closure of the ectepicondylar foramen in the SMRS, therefore, is correlated with size but exhibits considerable variation and is delayed relative to other estimates of skeletal maturity analyzed here. Individual variation in the ontogenetic closure of the ectepicondylar foramen is particularly significant considering that closure of this foramen is thought to be informative in higher-level reptile phylogeny (Laurin and Reisz, 1995; DeBraga and Rieppel, 1997).

OTIC FONTANELLE: A fontanelle between the prootic, opisthotic, and supraoccipital is present in the roof of the otic capsule during development. This feature is obvious in turtles whose otic capsules are exposed dorsally because of extensive temporal emargination (fig. 4C; Gaffney, 1979). The timing of closure of this fontanelle was compared with an estimation of maturity based on carapace length, but only a loose correspondence was found between the two (fig. 4C). The largest of the juvenile females (M-2965), based on carapace length, exhibits an open otic fontanelle, whereas in the smallest adult males (M-2997 and M-2976) the fontanelle is closed. The fontanelle in all juvenile males and females remains open, however three adult females (M-2977, M-2969, and M-2970) also retain the fontanelle. Two adult females whose fontanelle is closed exhibit carapace lengths that are less than that of M-2970.

QUALITATIVE OBSERVATIONS

GENERAL: The skull of *Sternotherus odoratus* overall is relatively short and broad with the greatest width falling along a transverse line that approximates the rostral margin of the otic capsules (the position of this widest point appears to shift slightly caudal during ontogeny; figs. 5, 6). Rostral and caudal to this point, the skull narrows considerably, resulting in a roughly circular shape when viewed dorsoventrally. This circular shape is

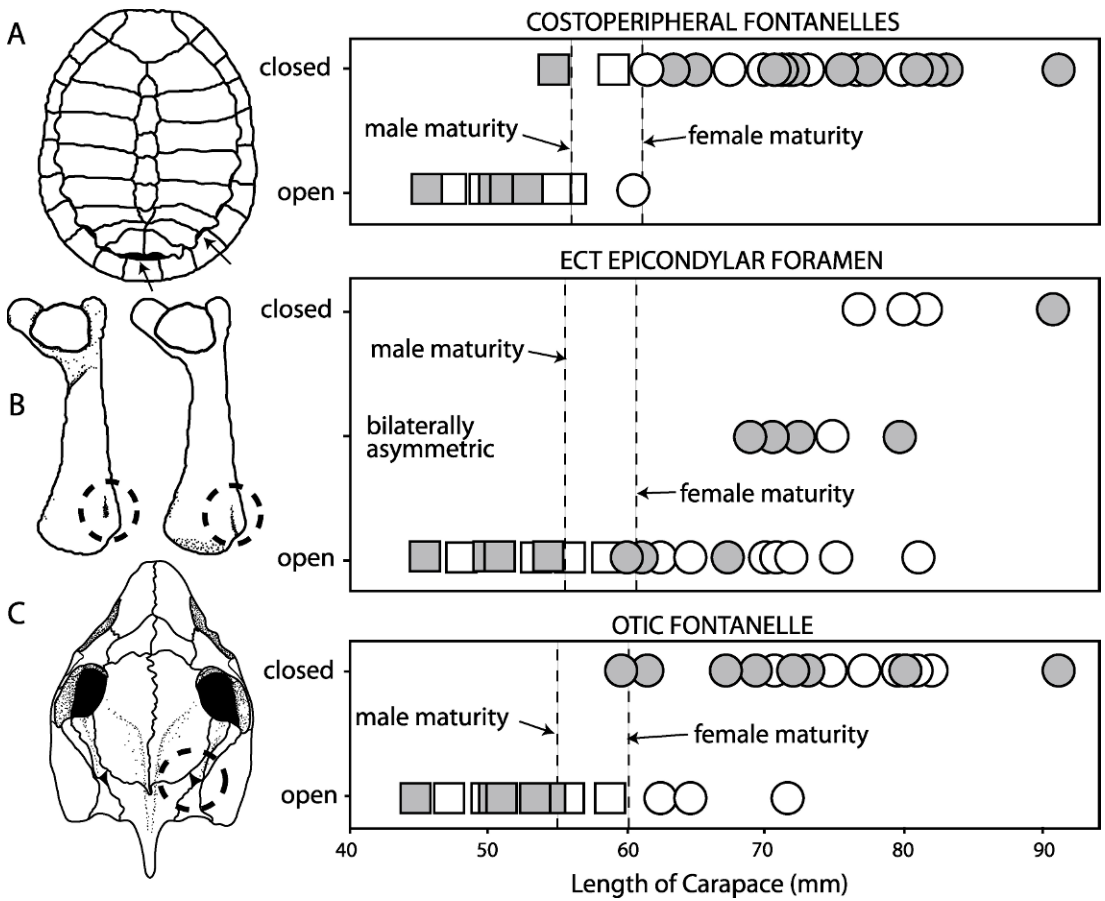


Fig. 4. Illustrations of three skeletal characters often used to estimate maturity in turtles and their graphical relationship with greatest length of the carapace for *Sternotherus odoratus* from the SMRS. These characters include closure of the costoperipheral fontanelles (A), closure of the ectepicondylar foramen in the humerus (B), and closure of the otic fontanelle (C). Shaded squares represent juvenile males, clear squares represent juvenile females. Shaded circles represent adult males, clear circles represent adult females. The transformation of these features during postnatal ontogeny has a variable relationship with the average carapace length at which specimens become sexually mature in southern populations of *S. odoratus* (dashed lines; Tinkle, 1961).

exaggerated in the largest specimens, possibly in response to allometric growth of the adductor musculature forcing the zygomatic arch to flare laterally as the muscles pass medial to this structure (Schumacher, 1973; Dalrymple, 1977). This expansion is also expressed in a strong postnatal expansion of the crista supraoccipitalis, which increases the height of the skull (fig. 7). The lower jaw is robust with a moderately expanded triturating surface, a strong coronoid process, and a rostral margin that is broadly rounded in lateral view (fig. 8).

DERMAL ROOFING REGION: Seven paired bones, the prefrontal, frontal, parietal, jugal, quadratojugal, squamosal, and postorbital, constitute the dermal roofing elements. The temporal region is strongly emarginated in the smallest and largest specimens such that the dorsal surface of the otic capsule is fully exposed, the parietal and squamosal no longer are in contact, and the postorbital is exposed caudally. Advanced temporal emargination that exposes the postorbital caudally is plesiomorphic for extant cryptodires (Gaffney and Meylan, 1988; Shaffer et al., 1997),

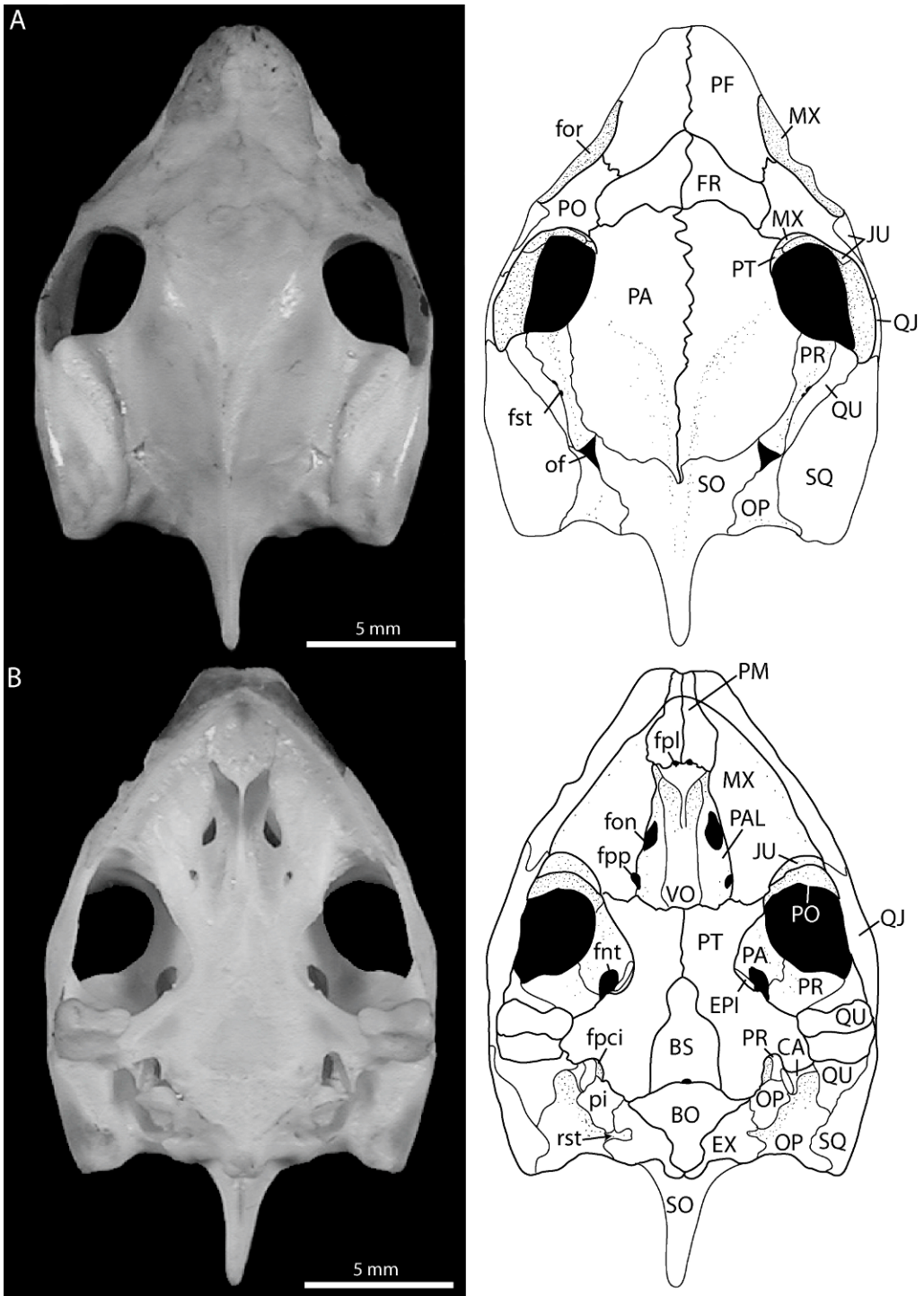


Fig. 5. Photographs and line drawings of the dorsal and ventral views of the skull of *Sternotherus odoratus* based on the least mature specimen from the SMRS (M-2980).

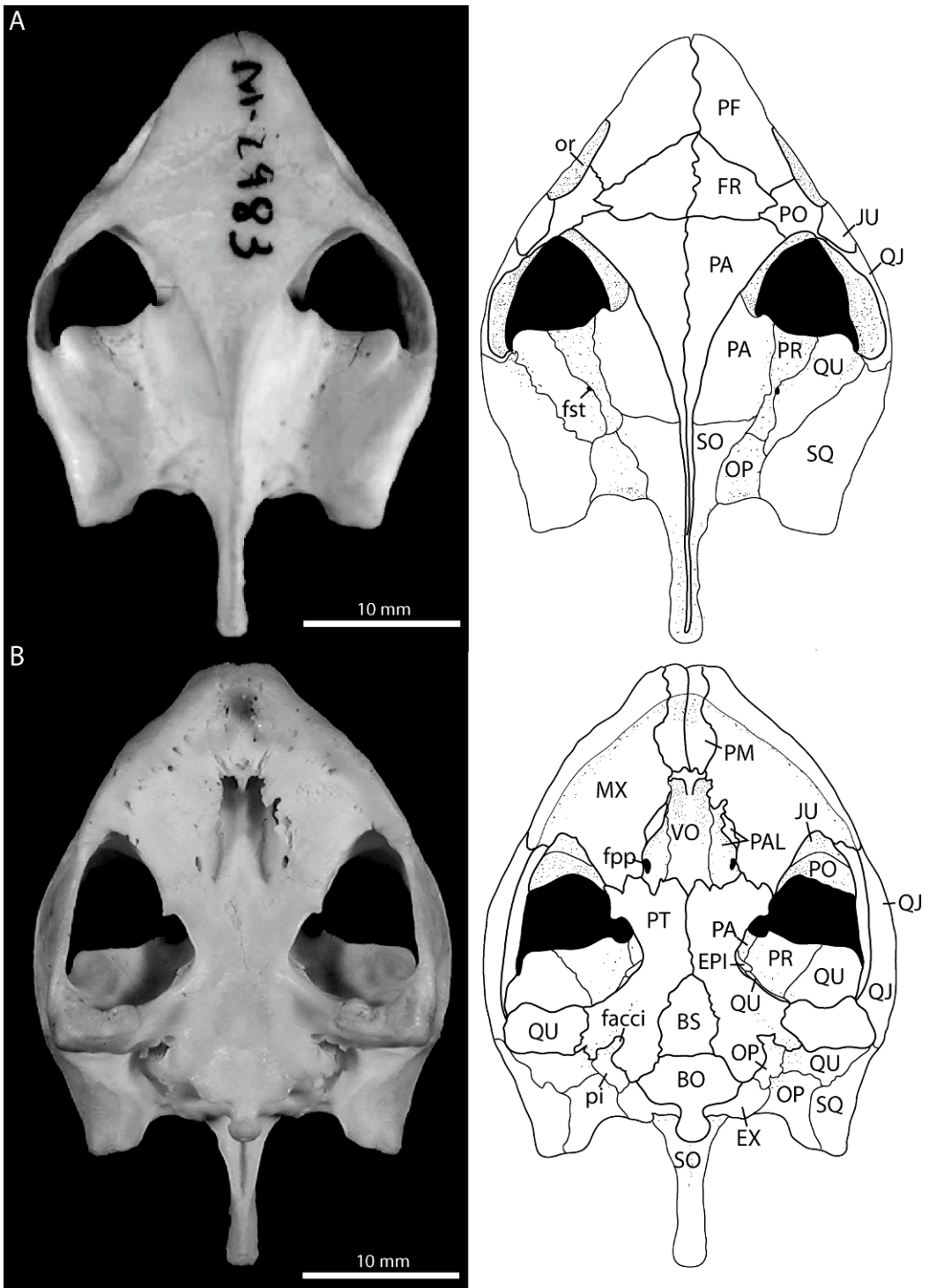


Fig. 6. Photographs and line drawings of the dorsal and ventral views of the skull of *Sternotherus odoratus* based on the most mature specimen from the SMRS (M-2983).

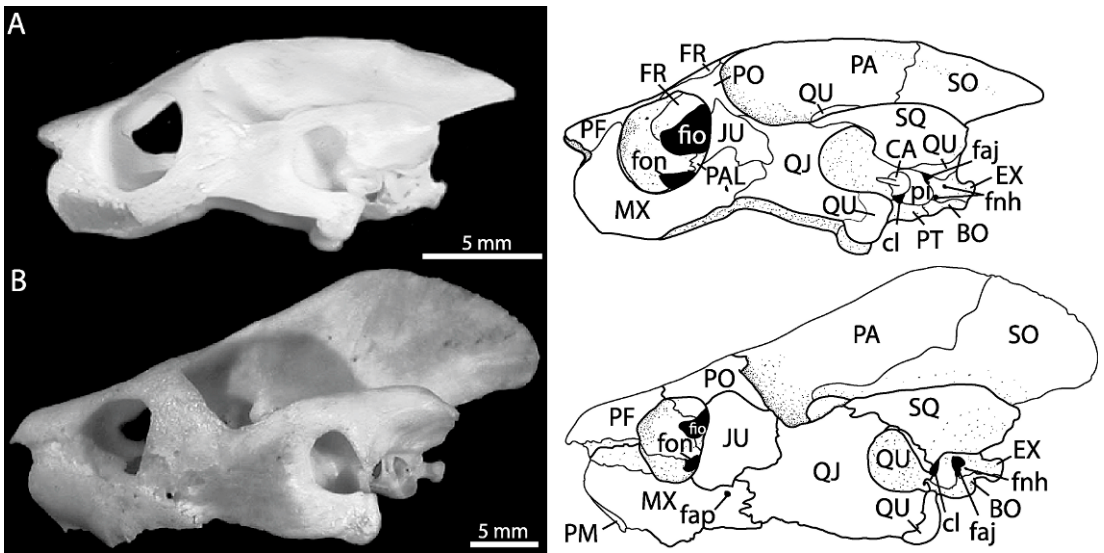


Fig. 7. Photographs and line drawings of the left lateral view of the skull of *Sternotherus odoratus* based on the least mature (M-2980, **A**) and most mature (M-2983, **B**) specimens from the SMRS.

whereas the absence of a parietal-squamosal contact is a derived character supporting a Trionychoidea-Testudinoidea clade (Gaffney, 1996). The rostral border of the temporal emargination extends slightly further rostral relative to the orbit in juveniles owing to a widening of the postorbital bar in adults (figs. 5 and 6). The zygomatic arch is strongly developed and deep, resulting in relatively little cheek emargination (particularly along the ventral margin: fig. 7). Cheek emargination is more pronounced in immature specimens where the dorsal extent of emargination reaches the ventral margin of the cavum tympani (fig. 7A). The dorsal rim of cheek emargination clearly lies below this landmark in larger, more mature specimens (fig. 7B). The failure of cheek emargination to reach the level of the orbit is a shared feature of kinosternids, staurotypines, and *Dermatemys*, but is absent in *Batemys* and *Emarginachelys* (Meylan and Gaffney, 1989).

The prefrontal is flattened dorsally except at its rostral end, where it arches downward to form the upper margin of the apertura narium externa. This aperture is wider than tall (table 3) with the only exception being an obviously teratological specimen (M-2987) whose left side is distinctly deformed (fig. 9). The lateral margins of the prefrontals taper

rostrally, but remain spaced so that the minimum interorbital distance is equal to or greater than the width of the nasal chamber (table 3), which is the common cryptodire condition. An hourglass-shaped prefrontal is present in some kinosternids (e.g., *Staurotypus triporcatus*) and is a derived feature within Testudinoidea (McDowell, 1964; Burke et al., 1996; Stephens and Wiens, 2003).

The ventral prefrontal process contributes to the rostral wall of the fossa orbitalis and caudal wall of the nasal cavity, forms a strong sutural contact with the vomer (a derived feature of cryptodires among extant turtles; Gaffney, 1996) and palatine, and contributes to the rostral margins of the foramen orbitonasale and foramen interorbitale. The extent of the prefrontal-palatine contact increases with overall size (fig. 10), making absence of this osseous contact conceivable early in postnatal ontogeny. The ventral process is consistently pierced by the foramen supraorbitale (Albrecht, 1967). The length of the foramen orbitonasale, which transmits the posterior nasal artery from the fossa orbitalis to the fossa nasalis (Albrecht, 1967), is greater than one-sixth the orbital length (table 3). The width of this foramen is equal to or greater than the width of the palatine process of the vomer in

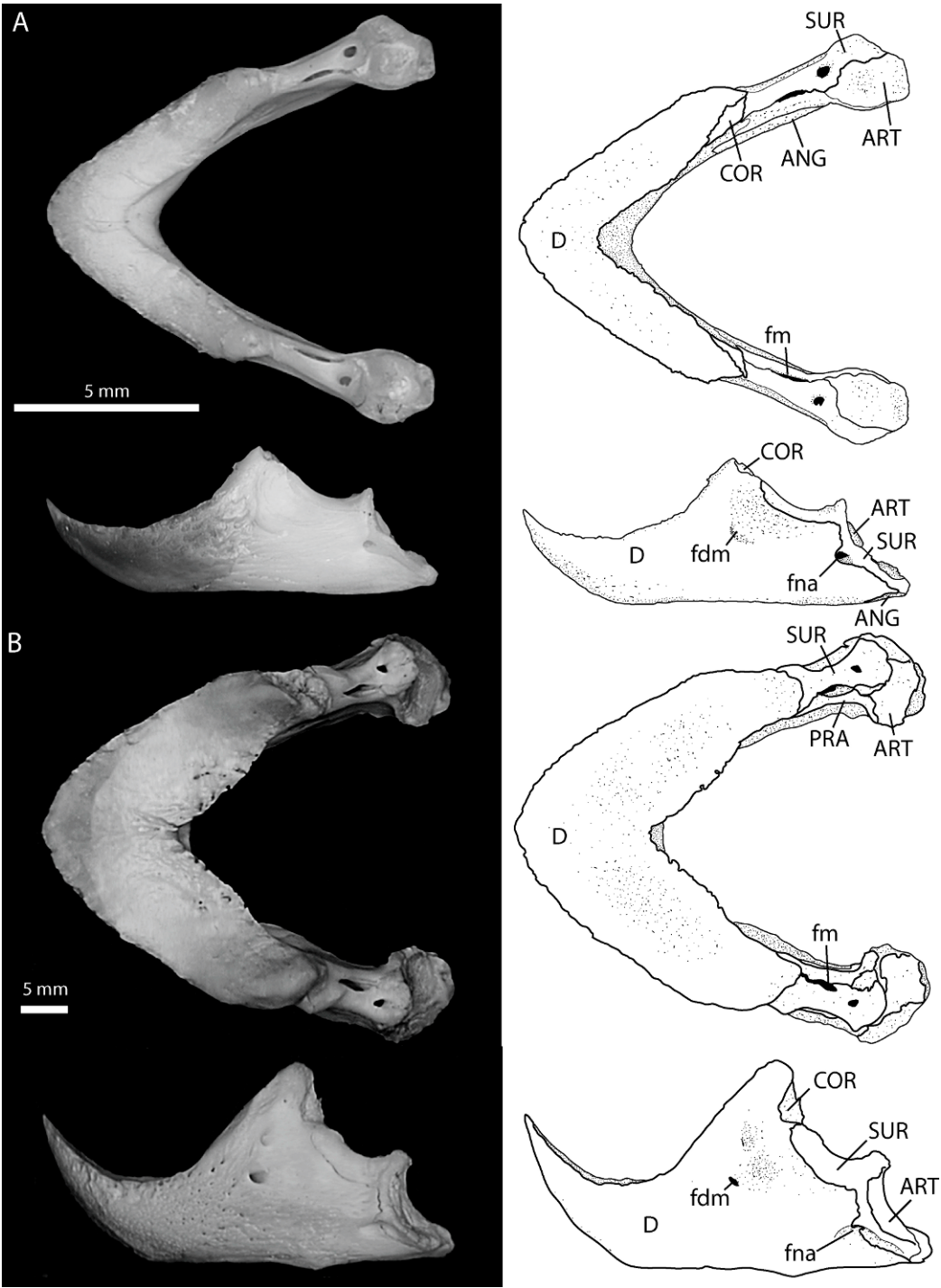


Fig. 8. Photographs and line drawings of the dorsal and left lateral view of the lower jaw of *Sternotherus odoratus* based on the least mature (M-2980, A) and most mature (M-2983, B) specimens from the SMRS.

TABLE 3
Descriptive Statistics for Selected Morphometric Characters from Dermal Roofing
Elements of *Sternotherus odoratus* from the SMRS

Characters are arranged based on their order of appearance within the descriptive text. All measurements are in millimeters.

	<i>N</i>	Mean	SD	Range
Apertura narium externa height/width				
Total	32	0.79	0.065	0.65–0.92
Juveniles	11	0.74	0.048	0.65–0.80
Adults	21	0.81	0.060	0.70–0.92
Nasal chamber width/minimum interorbital width				
Total	32	0.59	0.073	0.43–0.73
Juveniles	11	0.62	0.062	0.48–0.71
Adults	21	0.58	0.076	0.43–0.73
Foramen orbitonasale length/orbital length				
Total	32	0.55	0.050	0.44–0.67
Juveniles	11	0.51	0.022	0.48–0.54
Adults	21	0.56	0.054	0.44–0.67
Palatine process of vomer width/foramen orbitonasale width				
Total	32	0.88	0.160	0.59–1.27
Juveniles	11	0.82	0.090	0.71–1.00
Adults	21	0.91	0.180	0.59–1.27
Foramen orbitonasale width/length				
Total	32	0.59	0.073	0.43–0.73
Juveniles	11	0.62	0.062	0.48–0.71
Adults	21	0.58	0.076	0.43–0.73
Fissura ethmoidalis width (ventral)/width (dorsal)				
Total	32	0.65	0.085	0.50–0.78
Juveniles	11	0.62	0.062	0.55–0.78
Adults	21	0.65	0.089	0.50–0.77

the smallest specimens but narrows (relatively) with cranial growth and is narrower than this process in most mature specimens. The overall shape of the foramen orbitonasale also differs between the smallest and largest specimens, being rounded (length and width subequal) in immature specimens and elongate in mature specimens (diameter of the longitudinal axis two or more times that of the perpendicular axis). *Sternotherus odoratus* generally is considered to exhibit a relatively large, elongate foramen orbitonasale (Joyce and Bell, 2004), which is the most common condition among cryptodires.

The fissura ethmoidalis, which transmits the olfactory nerves (cranial nerve I), is teardrop-shaped and approximates a narrow or closed condition (Loveridge and Williams, 1957: figs. 10, 11; Joyce and Bell, 2004: figs.

1, 2). The shape of this opening (based on a ratio of greatest dorsal width to mid-height width: table 3) does not change appreciably during postnatal ontogeny (table 3). In contrast, the fissura ethmoidalis of testudinoids narrows during postnatal growth, becoming more rectangular (Loveridge and Williams, 1957; Crumly, 1982; Joyce and Bell (2004). This disparity may reflect a heterochronic shift (the polarity of which cannot currently be established) in which the ossified caudal wall of the fossa nasalis matures earlier in *S. odoratus* than in testudinoids.

The prefrontal process of the frontal (Bertl and Killebrew, 1983) is not well developed dorsally, resulting in an extensive prefrontal-prefrontal contact. The process does pass consistently above the fissura ethmoidalis to contribute to the roof of the fossa nasalis

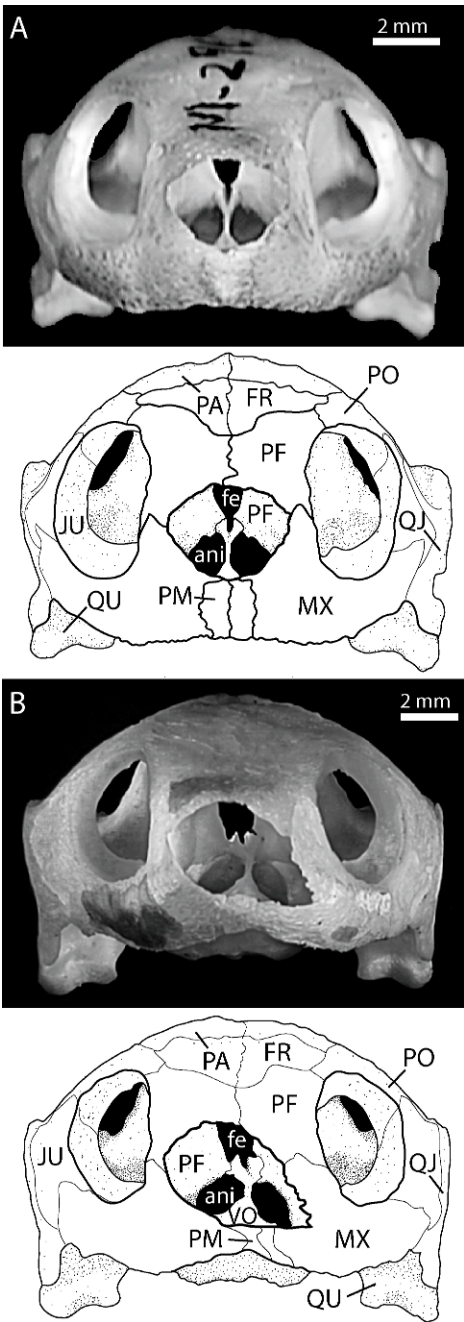


Fig. 9. Photographs and line drawings of the rostral view of M-2995 (A), an immature female, and M-2987 (B), an adult male exhibiting teratological variation in the rostral portion of the skull. This variation is most clearly expressed in the shape of the apertura narium externa, fissura ethmoidalis, premaxillae, and vomer.

(plesiomorphic for kinosternids). A majority of specimens (78.8%) exhibit a blunt or rounded, rather than acute, prefrontal process when viewed dorsally (fig. 11), but a wide range of morphologies that do not exhibit a clear ontogenetic trend are present in the SMRS. This variation complicates the scoring of discrete character states as described by Stephens and Wiens (2003). The presence of a midline cranial scute is marked in the largest specimen by a well-delineated sulcus that partly obscures the prefrontal-frontal contact; this sulcus is not evident in juveniles or smaller adults. Cranial scute sulci are plesiomorphic for kinosternids, being present in *Staurotypus*, *Dermatemys*, *Baptemys*, and *Emarginachelys* (Meylan and Gaffney, 1989). The frontal consistently participates in the dorsal margin of the orbit. A consistent participation may be derived for Kinosternidae (Meylan and Gaffney, 1989), but its presence as a polymorphic character in *Dermatemys mawii* (Bienz, 1895) suggests that this transformation has a longer or more complex evolutionary history within kinosternoids.

The parietal is the primary component in the cranial roof. It angles dorsally just behind the prefrontal-frontal suture and terminates at the apex of a crista supraoccipitalis, which is well developed in adults (see supraoccipital). The dorsal plate consistently lacks a parietal foramen. The processus inferior parietalis extends ventrally to form consistent contacts with the palatine, epipterygoid, and pterygoid; together, these elements form the lateral wall of the cavum cranii. A strong dorsal process of the palatine contacts the descending process of the parietal and is plesiomorphic for kinosternids (apomorphy of Trionyochoidea; Shaffer et al., 1997). The dorsal process is swollen rostrally (increasingly so during postnatal growth) and narrows caudally toward the cavum epiptericum. It is difficult to evaluate whether the width of this process equals at least one-quarter the distance between the caudal margins of the right and left interorbital foramina, as described by McDowell (1964) and Stephens and Wiens (2003) as a derived condition within Testudinoidea. These distances cannot accurately be measured in articulated specimens because the caudal wall of the fossa nasalis obscures the necessary line of sight.

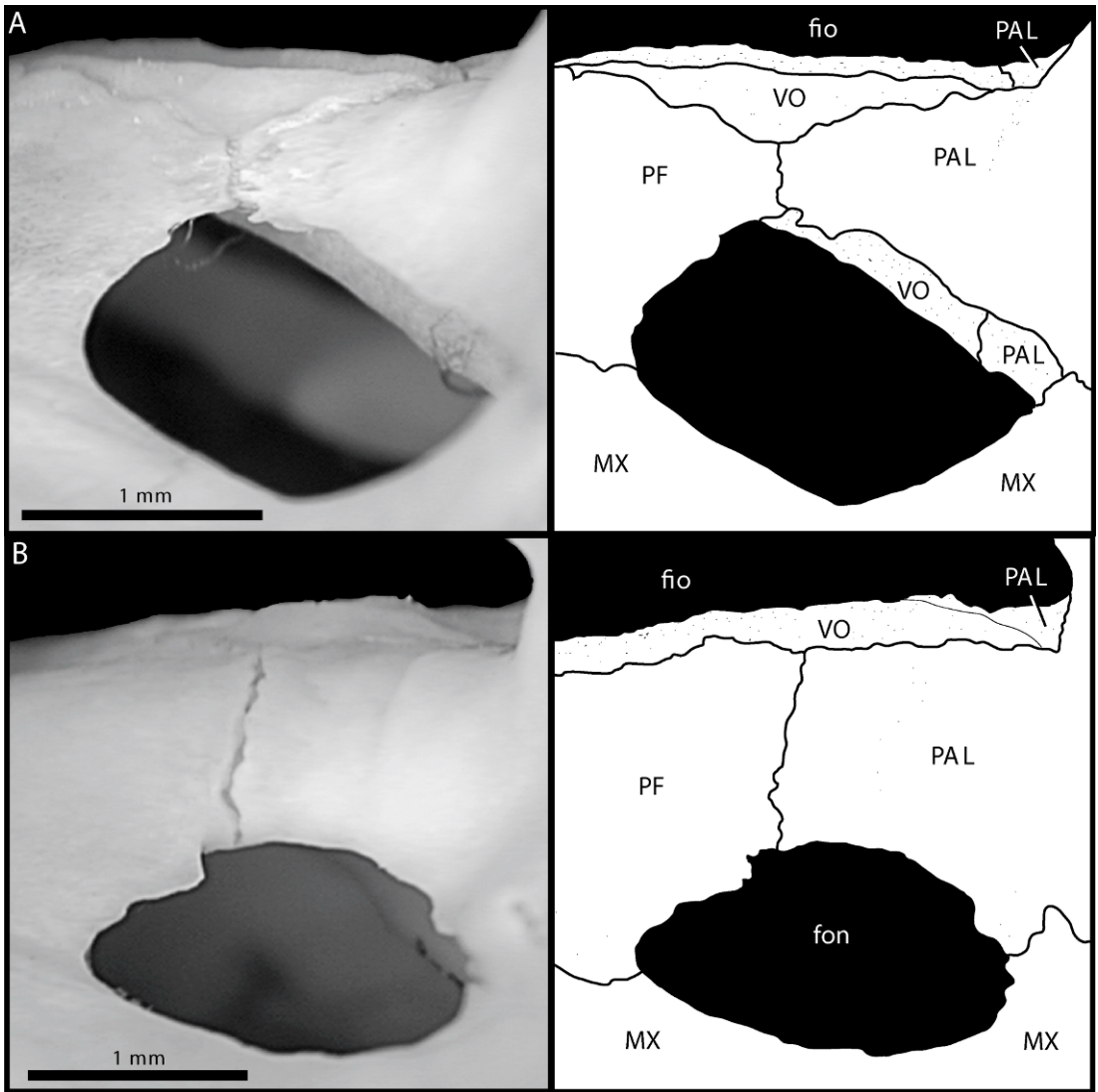


Fig. 10. Photographs and line drawings of the interorbital region in M-2968 (A) and M-2983 (B). Note differences in the breadth of contact of the prefrontal (PF) and palatine (PAL) above the foramen orbitonasale (fon).

The processus inferior parietalis lacks contact with the maxilla and medial process of the jugal as found in some derived testudinoids (e.g., *Graptemys barbouri*, *Malayemys subtrijuga*; Joyce and Bell, 2004).

The processus inferior parietalis, along with the prootic, quadrate, and epipterygoid, contributes to the foramen nervi trigemini. This foramen is not clearly divided into maxillary and mandibular components in any SMRS specimen, but several variations

do occur in relatively large individuals. A small foramen at the dorsal margin of the foramen nervi trigemini (in the parietal contribution) is present on the right side of M-2983 and is represented as a groove on the opposing side (fig. 12A, B). A similar groove is found in nine other specimens and thus is present in 30.3% of the SMRS (bilateral asymmetry in M-2997). A relatively small, distinct, process and several smaller processes forming partial foramina occur along the

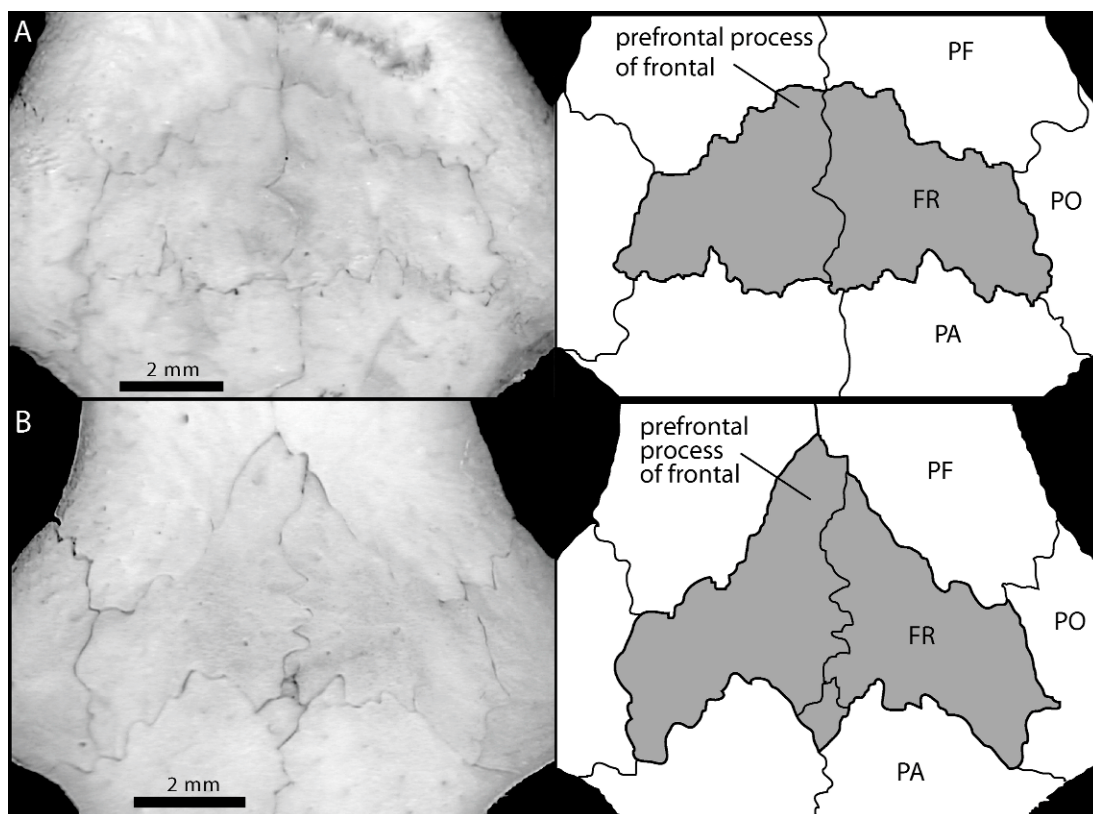


Fig. 11. Photographs and line drawings of the dorsal roof showing the relative development of the prefrontal process of the frontal in M-2985 (A) and M-2965 (B). Also note that the frontal does not participate in the orbit or temporal fenestration.

dorsal margin in M-2988 (fig. 12C). These processes are formed to a lesser degree in M-2977. A secondary process of the parietal extends caudoventrally from the processus inferior parietalis and consistently contacts the crista pterygoidea to form the rostral margin of the foramen nervi trigemini. The bone is thin directly rostral to this process, and in small specimens ossification is incomplete negating a parietal-ptyergoid contact medial to the epiptyergoid.

In lateral view (fig. 7), the jugal contributes consistently to the caudolateral margin of the orbit and variably to the rim of the temporal emargination (fig. 13). Absence of the latter contribution is generally considered to characterize *Sternotherus odoratus* (probably as the plesiomorphic condition for kinosternids; Joyce and Bell, 2004). The medial process of the jugal forms consistent

contacts with the maxilla, palatine, and ptyergoid, but consistently fails to contact the descending process of the parietal. The confluence between the fossa orbitalis and fossa temporalis inferior is constricted in the most mature specimens by a dorsal thickening of the medial process of the jugal and caudolateral margin of the palatine. This postnatal thickening can capture the maxillary (V_2) nerve along its path toward the foramen supramaxillare, as evidenced by a small foramen and groove on the right side of M-2985 (fig. 14).

A well-developed quadratojugal exhibits broad, consistent contacts with the jugal and maxilla to form a strong zygomatic arch. A maxilla-quadratojugal contact evolved numerous times within Cryptodira, but is absent in *Emarginachelys* and dermatemydids, and may be derived for kinosternids

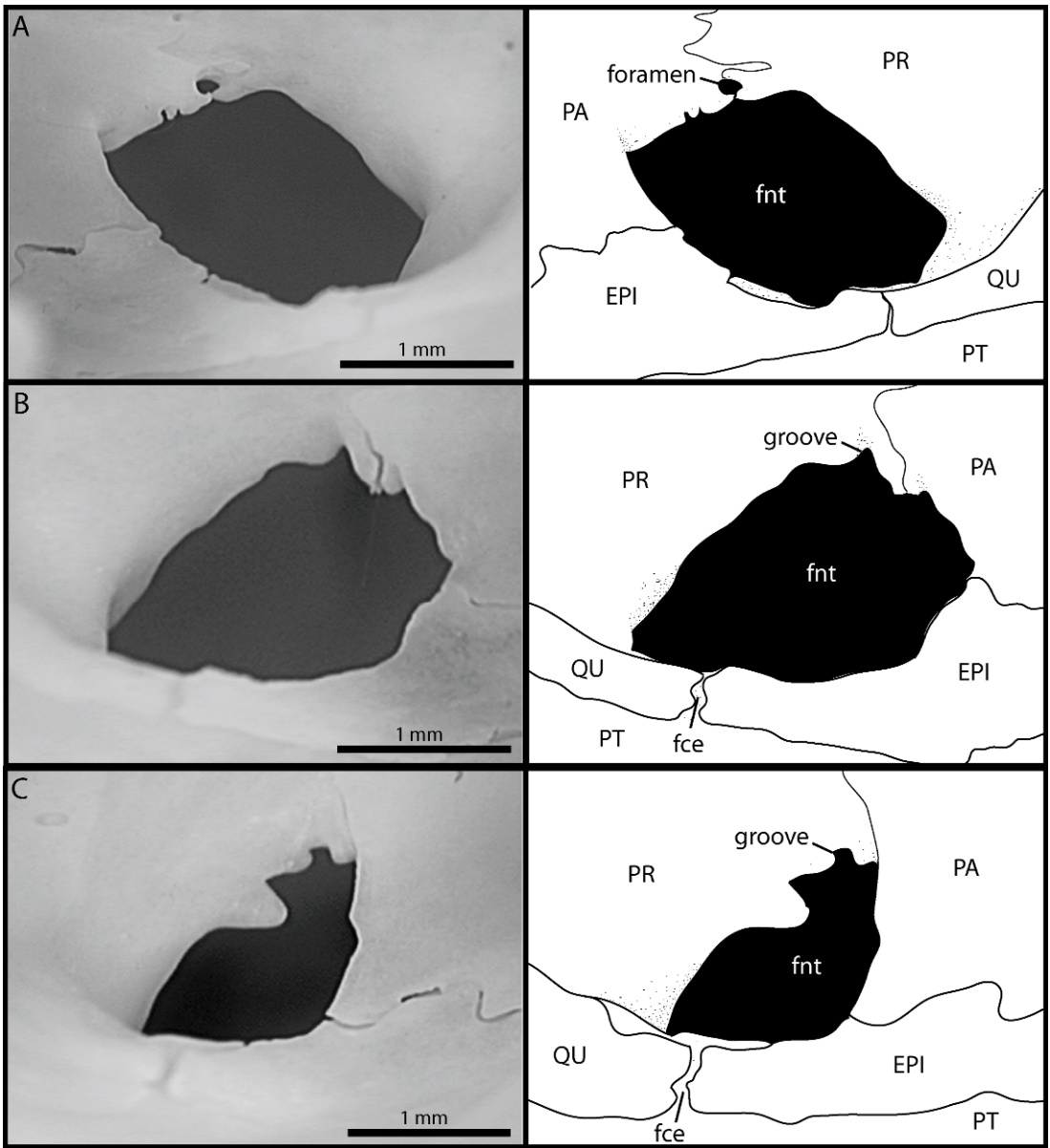


Fig. 12. Photographs and line drawings of the foramen nervi trigemini in right lateral (M-2983, **A**) and left lateral (M-2983, **B**; M-2988, **C**) views. Note the small foramen or groove in the dorsal margin of the foramen nervi trigemini that occurs as a variant in the SMRS.

(Meylan and Gaffney, 1989; Shaffer et al., 1997). The quadratojugal sweeps caudally below the cavum tympani to consistently contact the processus articularis of the quadrate. Contact with the articular facet is absent, but near contact is present in most mature specimens (fig. 15). A strong qua-

dratojugal-squamosal contact consistently occurs above the cavum tympani. The squamosal, with the processus paraoccipitalis of the opisthotic, forms a distinct ridge that separates the origins of the *M. adductor mandibulae pars superficialis* (dorsomedial) and *M. depressor mandibulae* (ventrolateral-

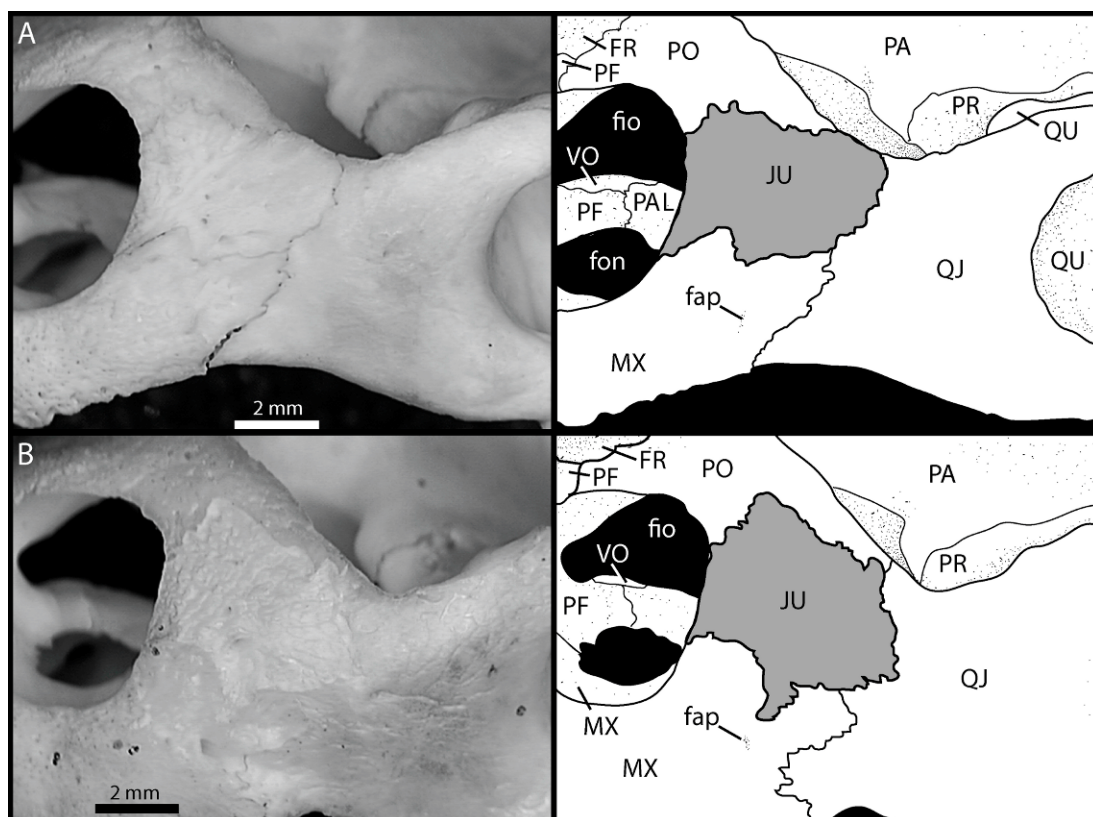


Fig. 13. Photographs and line drawings of the left lateral surface of the skull showing the presence (A, M-2984) and absence (B, M-2983) of a contribution from the jugal to the rostral rim of the upper temporal fenestra.

ly; Schumacher, 1973). The prominence of this ridge and its associated fossa increases with growth (also true in *Apalone ferox* to an extreme degree; Dalrymple, 1977). The ridge and fossa are better developed on the opisthotic in small specimens and on the squamosal in large specimens, suggesting an ontogenetic shift in the position or relative size of these cranial muscles.

PALATAL REGION: The palatal elements include the paired premaxilla, maxilla, and palatine, as well as the median vomer. The premaxillae, in all but two of the more mature specimens, are overlain by small medial extensions of the maxillae that meet along the midline in a pattern similar to that described as a derived condition within Trionychidae (Meylan, 1987; Shaffer et al., 1997). This median maxillary contact is slightly recessed within the rostral margin of

the fossa nasalis in about half the sample (46.7%, $n = 30$), such that the premaxillae contribute to the ventral margin of the apertura narium externa despite rostral contact of the maxillae (fig. 16A, B). This recessed contact is not present in any of the smallest, least mature specimens. Unlike in *Carettochelys* and some trionychids (Meylan, 1987; Shaffer et al., 1997), the maxillae consistently fail to meet along the rostral margin of the jaw below the premaxilla.

The rostroventral margin of the premaxilla generally contributes to a smooth, continuous labial ridge of the upper triturating surface. In mature specimens, the premaxillae extend slightly ventral to the maxillary contribution of the labial ridge, thereby forming a short, beaklike structure (fig. 7B; as in some testudinoids, see Joyce and Bell [2004]). The maxillary portion of the labial

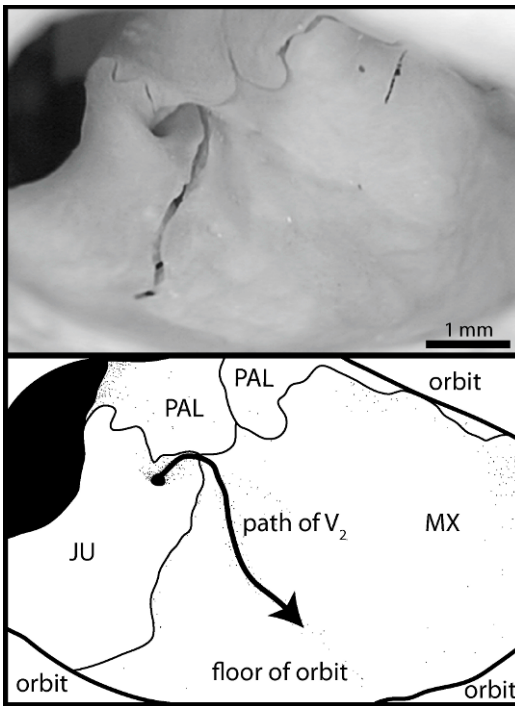


Fig. 14. Photograph and line drawing of the caudal margin of the right orbital floor in M-2985 as seen through the orbit. A relatively large and distinct foramen is present in the medial process of the jugal in this specimen, which represents a variant condition for the SMRS. The maxillary branch of the trigeminal nerve may pass through this foramen before traveling rostrally along the floor of the orbit to the foramen supramaxillare.

ridge in these mature specimens arches away from the premaxilla to form a cusplike structure at approximately the rostral margin of the orbit (fig. 7B); smaller specimens lack these cusps. The palatal process of the premaxilla contacts the vomer caudally but lacks the nasal process of some emydids (Killebrew, 1979; Bertl and Killebrew, 1983; Stephens and Wiens, 2003). The palatal process consistently participates in the paired foramen praepalatinum (fig. 17), which is visible ventrally in over half the specimens (64.5%; McDowell, 1964). In the remaining specimens, increased premaxillary ossification near the vomer contact result in the posterior nasal artery passing from the palate to the fossa nasalis through a short canal. The caudal foramen of this canal is visible in

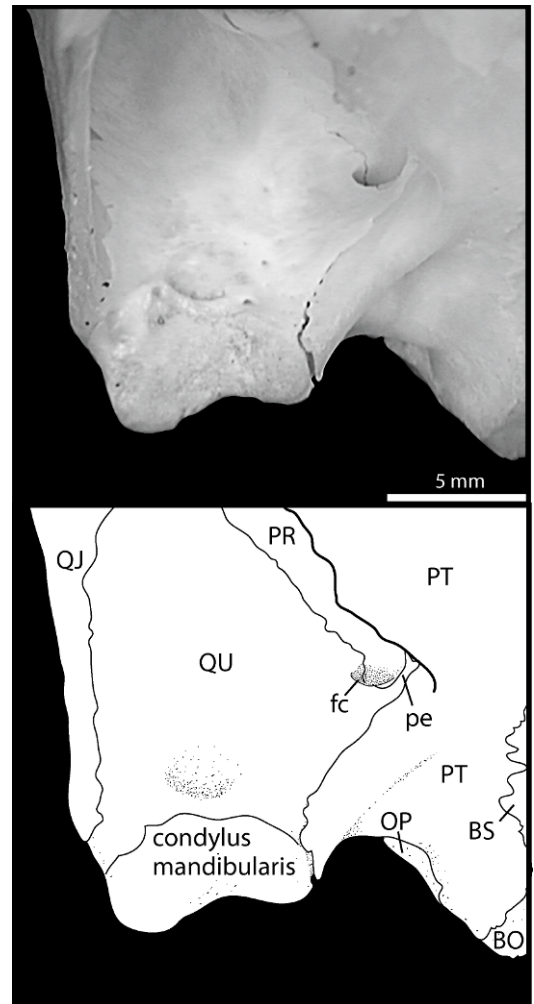


Fig. 15. Photograph and line drawing of the rostroventral surface of the left quadrate and basicranium of M-2981. Note the relatively close approximation of the laterally positioned quadratojugal to the articular surface of the quadrate, and contact between the quadrate ramus of pterygoid and the articular surface of quadrate.

posterior view only. The canal, when present, is not developed to the extent found in some testudinoids (e.g., *Morenia petersi*; Joyce and Bell, 2004). Increased ossification of the premaxillae also results in the foramen praepalatinum transforming from a position between the premaxillae and vomer (61.3% of the SMRS, including the smallest specimens) to one fully within the premaxillae (most mature specimens).

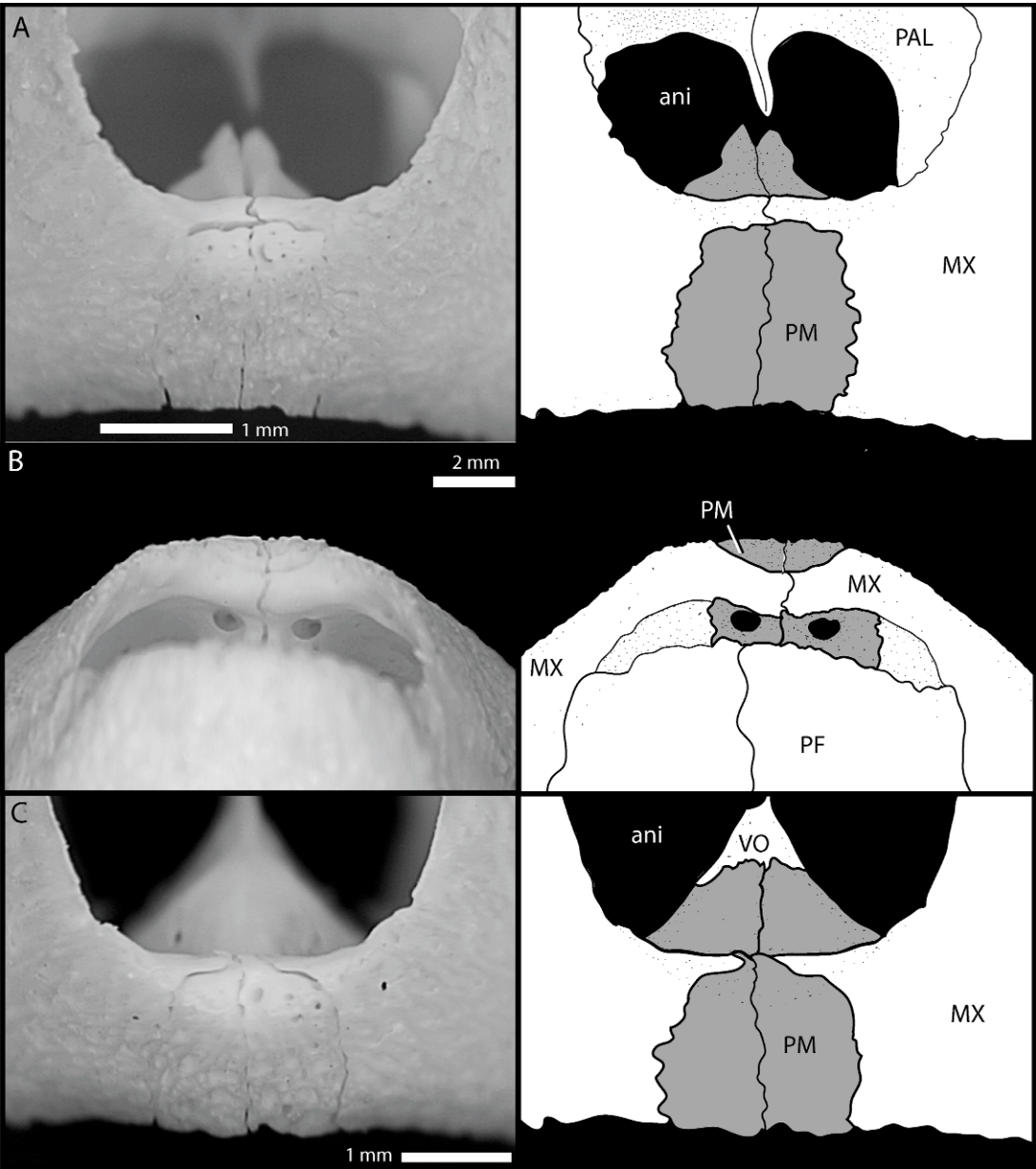


Fig. 16. Photographs and line drawings of the relationships of the premaxillae, maxillae, and ventral margin of the apertura narium externa. The most common condition within the SMRS is for the maxillae to send small secondary processes over the premaxillae to form the ventral margin of aperture (A, M-2967). This medial contact can be recessed such that the premaxillae still contribute to the ventral margin of aperture (B, M-2967). Sometimes the maxillae fail to meet medially above the premaxillae (C, M-2956).

The facial surface of the maxilla consistently contributes to the ventral rim of the orbit and apertura narium externa, which is emarginated dorsally in all specimens (Wil-

liams, 1952; Meylan, 1987). A triangular or rectangular sulcus extends along the maxilla-prefrontal suture on the lateral surface of the skull between the apertura narium externa

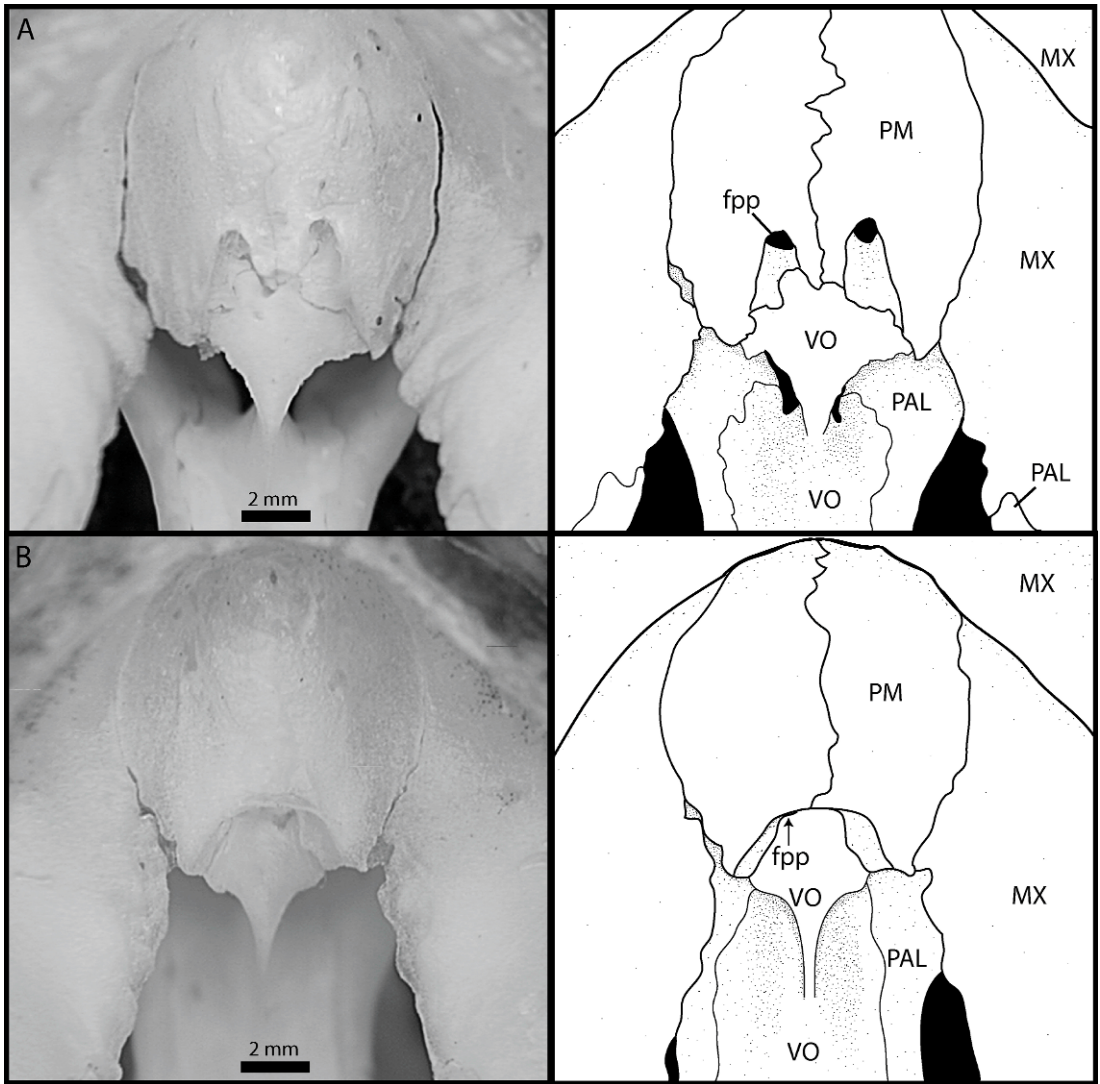


Fig. 17. Photographs and line drawings of the palatal surface of M-2989 (A) and M-2958 (B). The paired foramina praepalatinum are exposed ventrally in M-2989, whereas they are concealed by caudal development of the premaxillae on the secondary palate in M-2958. Ventral exposure of these foramina is the most common condition within the SMRS.

and rostral margin of the fossa orbitalis (fig. 7B). This sulcus lies between the dorsal sculpturing of the snout and the protrusion of the maxilla covered by the rhinotheca and is most distinct in the largest specimens. The lateral surface of the alveolar process of the maxilla consistently exhibits a large foramen alveolare posterius near its caudal suture with the quadratojugal (figs. 7, 13). This foramen is plesiomorphic for kinosternids (present in

Dermatemys and testudinoids), and is one of three consistent openings of a maxillary canal system that transmits the arteria alveolare superius, arteria supramaxillare, and the maxillary branch of the trigeminal nerve (V_2 ; Albrecht, 1967). A foramen supramaxillare is present on the floor of the fossa orbitalis, and the foramen alveolare superior lies at the ventrolateral margin of the fossa nasalis, and the foramen alveolare superior

lies at the ventrolateral margin of the fossa near the rostral margin of the foramen orbitonasale. The latter foramen is positioned slightly rostral to the foramen orbitonasale in all specimens except a single adult male (M-2989), where it lies just inside the rostral rim of the foramen orbitonasale. A large foramen or series of smaller foramina often are present within the maxilla along the lateral margin of the fossa orbitalis (near the orbital rim). The number and exact position of these foramina are highly variable and do not appear to correlate with postnatal growth.

The ventral surface of the maxilla is the primary component of the upper triturating surface, which forms a partial secondary palate. The lateral breadth of this surface expands during postnatal ontogeny and increasingly obscures the foramen orbitonasale in ventral view (figs. 5, 6). The triturating surface receives a significant contribution from the palatine in all but the smallest articulated specimen (M-2980; fig. 5), in which it appears to be largely or completely absent (fig. 5); other small individuals exhibit this contribution. A palatine contribution to the upper triturating surface evolved a number of times during turtle evolution (Gaffney, 1979) and is present in *Staurotypus* but absent in *Dermatemys* and *Emarginachelys* (Bienz, 1895; Whetstone, 1978). The upper triturating surface is simple as it lacks the lingual ridge, median maxillary ridge or sulcus, lateral concavities, maxillary "tooth," and well-developed serrations that characterize the complex feeding surfaces in *Dermatemys* and *Baptmys* (Meylan and Gaffney, 1989). The rostromedial portion of the upper triturating surface is generally flat and relatively smooth. In the largest specimen, this surface exhibits a pocket that accepts the upturned rostral margin of the lower jaw (see below), comparable to that in *Xenochelys* (Williams, 1952).

The vomer includes a rostral process that sweeps dorsally to form the base of the fissura ethmoidalis, a descending process that approximates but does not contribute to the triturating surface (as in some testudinoids; Joyce and Bell, 2004), and an elongate horizontal process that extends caudally to form a large portion of the primary palate.

The descending process consistently contacts the premaxillae rostrally but forms lateral contacts with the maxillae in only the largest most mature specimens (21.4% of the sample). Maxillary contacts clearly are lacking in the smallest specimens and are not extensive in the specimens that do exhibit them (*Sternotherus odoratus* is generally considered to contain this contact; Joyce and Bell, 2004).

The palatal process of the vomer contacts the right and left pterygoids; however, in four specimens (11.4%; two juvenile, two adult) the palatines meet along the midline of the skull at the caudal end of the vomer and obscure the pterygoid-vomer contact in ventral view (fig. 18A). This medial contact of the palatines was not previously described in kinosternoids, although it evolved many times within Cryptodira (Hirayama et al., 2001; Joyce and Norell, 2005). The shape of the palatal process along the pterygoid suture is variable, with 64.3% of the specimens exhibiting a broadly rounded or slightly jagged margin (fig. 18B; including the least mature individuals). The remaining 35.7%, including the largest individuals, exhibit a trident-shaped caudal margin with the medial prong contacting the pterygoid and the lateral portions contacting the palatines (fig. 18A, C). This morphology presumably represents the flared condition described by Stephens and Wiens (2003). Variation in this contact depends largely on the differential development of the pterygoids. The position of the vomer-ptyergoid contact approaches the caudal margin of the palate (here defined as a transverse line extending between the caudal margins of the alveolar processes of the maxillae) in 71.0% of the specimens. The vomer-ptyergoid contact is distinctly behind this palatal margin in 22.6% of the SMRS (all adults), and in two specimens (6.5%) is positioned distinctly rostral to the caudal margin of the palate.

The dorsal process of the palatine contacts the processus inferior parietalis to form the rostral portion of the lateral wall of the cavum cranii (see above). The palatine contribution to this wall is greater laterally than medially. The process thickens during ontogeny but its relative contribution to the wall does not change appreciably. A rostral process of the palatine interrupts the caudal

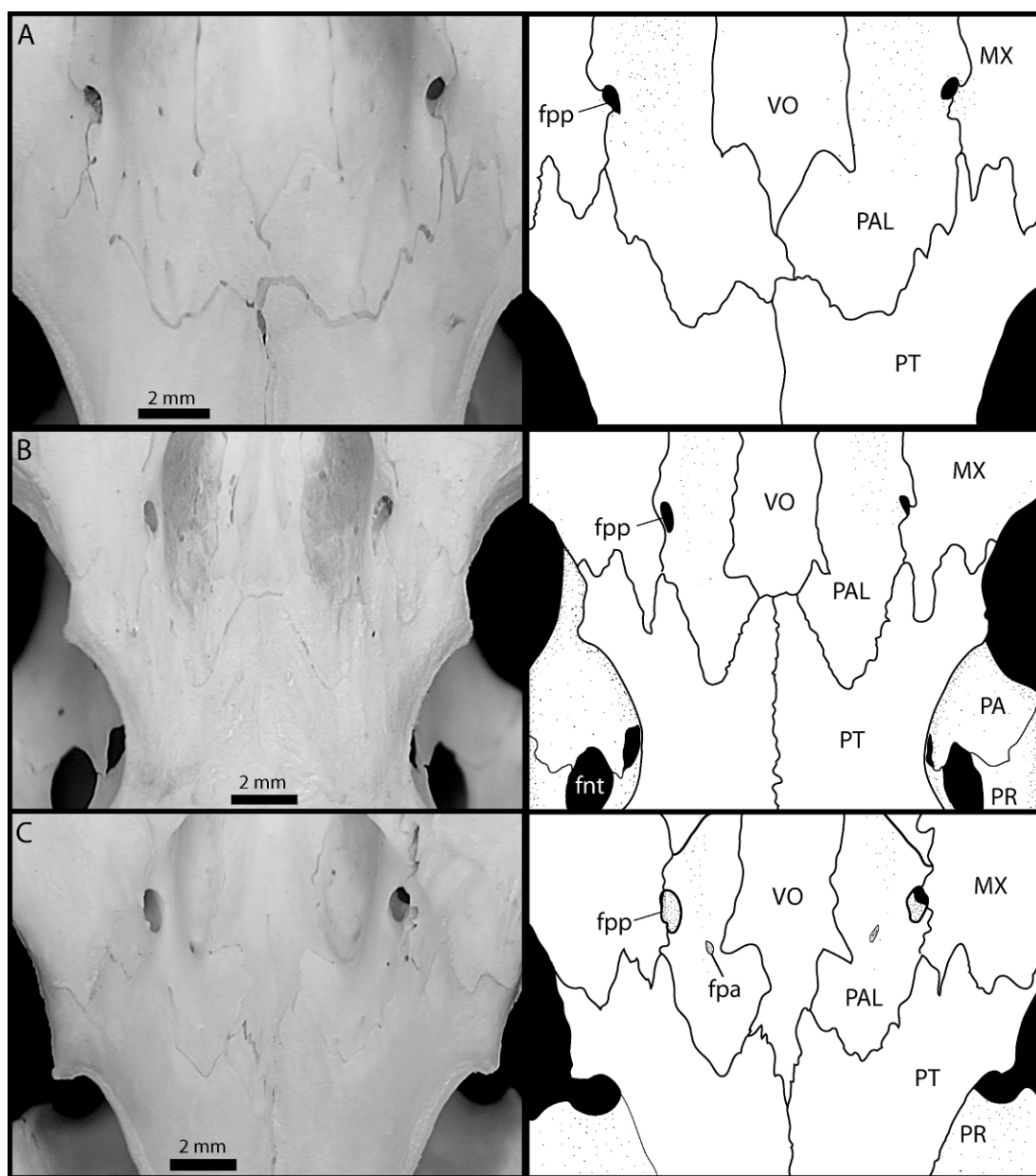


Fig. 18. Photographs and line drawings of the palatal surface of M-2979 (A), M-2974 (B), and M-2983 (C). The palatines obscure the vomer-ptyergoid contact in M-2974. The shape of the vomer-ptyergoid contact can be broadly rounded or obtuse as in M-2974 or the vomer can terminate caudally at a single point as in M-2983. The development of the rostral margin of ptyergoid appears to be the major factor controlling the morphology of this character.

margin of the foramen orbitonasale in at least two mature specimens (5.6%). The partial bisection of this foramen is a derived character within testudinoids (Stephens and

Wiens, 2003), and its absence appears to be plesiomorphic for kinosternids.

The paired foramen palatinum posterius, which transmits the inframaxillary artery

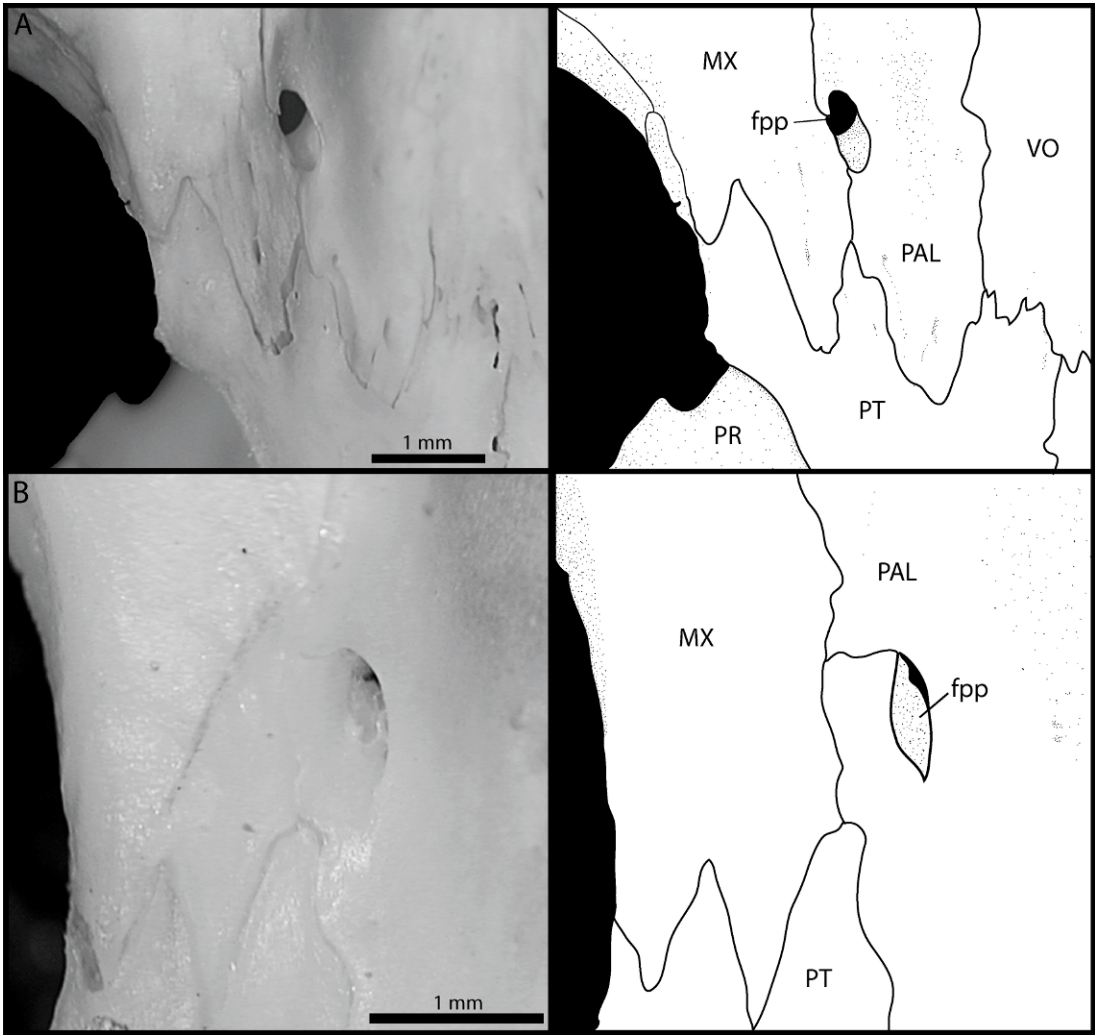


Fig. 19. Photographs and line drawings of the palatal surface of M-2985 (A) and M-2999 (B) showing the contacts of the palatine, maxilla, and foramen palatinum posterius. The most common condition in the SMRS is for the maxilla to form the lateral margin of this foramen (A). The palatines sometimes meet lateral to the foramen palatinum posterius on the ventral surface of the palate.

onto the palatal surface (Albrecht, 1967; Gaffney, 1979), is clearly and consistently visible ventrally. This foramen opens ventrally between the palatine and maxillae in most specimens, although in the most mature individuals (13.5%), the palatine excludes maxillary participation by completely encircling the foramen palatinum posterius on the palatal surface (fig. 19). This exclusion is a left-right asymmetry in two adult specimens (M-2969, right; M-2956, left). The foramen palatinum poster-

ius is smaller than the foramen orbitonasale and narrower than the palatine process of the vomer, both conditions being common among kinosternids. Its shape exhibits some variation, being circular in some specimens and elongate in others (table 4); however, this variation is not closely correlated with overall skull size. An elongate foramen palatinum posterius is the most common condition among kinosternids.

The caudal wall of the foramen palatinum posterius is penetrated consistently by a

TABLE 4
Descriptive Statistics for Selected Morphometric Characters from Palatal Elements of
Sternotherus odoratus from the SMRS

Characters are listed according to their order of appearance within the descriptive text. All measurements are in millimeters.

	N	Mean	SD	Range
Foramen palatinum posterius width/foramen orbitonasale width				
Total	30	0.18	0.047	0.08–0.27
Juveniles	10	0.18	0.059	0.08–0.27
Adults	20	0.18	0.041	0.12–0.26
Foramen palatinum posterius width/palatine process of vomer width				
Total	31	0.20	0.056	0.10–0.33
Juveniles	10	0.22	0.065	0.10–0.33
Adults	21	0.20	0.051	0.13–0.33
Foramen palatinum posterius width/length				
Total	31	0.49	0.127	0.25–0.75
Juveniles	10	0.54	0.177	0.25–0.75
Adults	21	0.46	0.092	0.30–0.60

relatively large rostral opening of the anterior canalis nervi vidiani, which transmits branches of the vidian nerve (VII) and vein to the foramen palatinum posterius where they pass dorsally to enter the orbit (Albrecht, 1967). This opening can be difficult to see in an articulated specimen but generally is visible through the fossa orbitalis (fig. 20). A much smaller foramen is variably present (59.5%) on the ventral surface of the palate just caudomedial to the foramen palatinum posterius (fig. 18C). Of the 22 specimens that exhibit this foramen, 15 (77.3%) do so as a right/left asymmetry (8 right/7 left). This foramen may represent the foramen palatinum accessorium that communicates with the foramen palatinum posterius through the canalis intrapalatinus in *Apalone* (Albrecht, 1967). This opening, however, is smaller and closer to the foramen palatinum posterius than in *Apalone*, and Albrecht (1967) found no evidence of these structures in the 15 specimens of *Sternotherus odoratus* he examined. Small foramina are consistently present in the ventral surface of the palatine at or near its suture with the pterygoid. These openings represent the foramen arteriaevidianae and vary considerably in number, ranging from one to four per side (mode = 2, 50%). The foramen arteriaevidianae and the

foramen palatinum accessorium transmit small branches of the vidian nerve to the surface of the palate (Albrecht, 1967). A larger foramen that probably represents the foramen arteriae anteriovidianae of Albrecht (1967) is present on the dorsal surface of the palatine, caudal to the foramen palatinum posterius and rostral to the cavum cranii (fig. 20). This foramen is a right/left asymmetry in five specimens (13.5%, four right, one left) and is present in the rostral margin of the lateral wall of the cavum cranii in a single specimen (M-2958). The only noted difference between this foramen and the foramen arteriae anteriovidianae as described by Albrecht (1967) is that the SMRS foramen lies within the palatine rather than the pterygoid. This foramen is part of a canal that enters the palatine from the pterygoid (see below) and extends rostrally through the base of the dorsal palatine process (fig. 20). The bifurcation in this canal, which results in the dorsal foramen arteriae anteriovidianae, occurs near the caudal margin of the palatine, whereas bifurcations resulting in the foramina arteriaevidianae and foramen palatinum accessorium occur rostrally near the foramen palatinum posterius. The considerable variation observed in the foram-

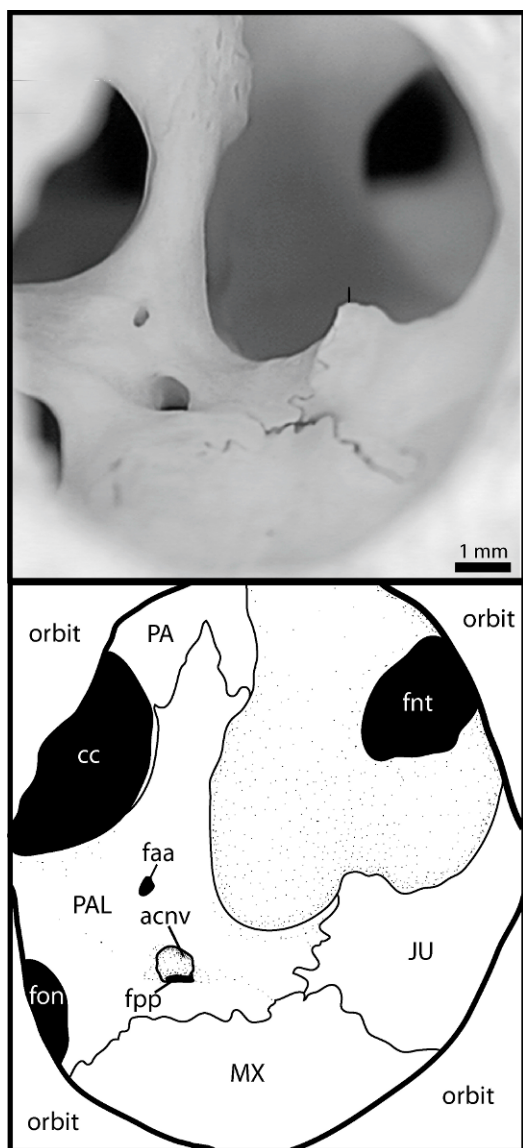


Fig. 20. Photographs and line drawings of the caudal margin of the left orbital floor and rostral margin of the cavum cranii as viewed through the left orbit of M-2966. A rostral opening of the vidian canal (acnv) lies in the caudal margin of the foramen palatinum posterior. The foramen arteriae anteriovidianae (faa) is a second rostral opening of a vidian canal that transmits a branch of the vidian nerve and vein onto the dorsal surface of the palate.

ina associated with the rostral extent of the vidian canal(s) is not closely correlated with postnatal ontogeny.

PALATOQUADRATE REGION: The palatoquadrate region is composed of the paired quadrate, epipterygoid (both splanchnocrania), and pterygoid (dermatocranium). The processus epipterygoideus of the quadrate extends rostrally along the medial margin of the cavum epiptericum. In the smallest specimens, this process fails to contact the epipterygoid because a distinct fossa cartilaginosis epipterygoidei is present (fig. 12B, C), whereas, the near complete ossification of the palatoquadrate cartilage in this area facilitates this contact in the most mature specimens (12.9%; fig. 12A). Obliteration of the fossa cartilaginosis epipterygoidei is a right/left asymmetry in M-2973. The processus epipterygoideus participates in the ventral margin of the foramen nervi trigemini in 16.7% of specimens (which vary widely in size), whereas in the remaining 83.3%, the pterygoid forms this margin. The quadrate consistently forms the caudal margin of the trigeminal fenestra. Exclusion of the pterygoid from this opening is the most common condition among kinosternoids.

The incisura columellae auris is open in all specimens, and in the smallest individuals this space is unrestricted dorsally and ventrally (fig. 21C). A vertical ridge extends from the ventral margin of the incisura and restricts this opening caudally; this is a common postnatal transformation that is present in 73.7% of the sample (including the largest specimens; fig. 21A). This ridge is bilaterally asymmetric in two specimens (M-2976 and M-2996), and absent in two adults (M-2956 and M-2966) whose incisura is restricted by downward growth of its dorsal margin (fig. 21B).

The osseous signature denoting the path of the chorda tympani branch of the facial (VII) nerve out of the cavum acusticojugulare portion of the middle ear is highly variable (fig. 22). In 34.2% of the SMRS, including the smallest individuals, the foramen chorda tympani superius and foramen chorda tympani inferius lie completely within the quadrate on at least one side of the skull, and the canal connecting them (canalis chorda tympani quadrati, Gaffney, 1972, 1979) is comp-

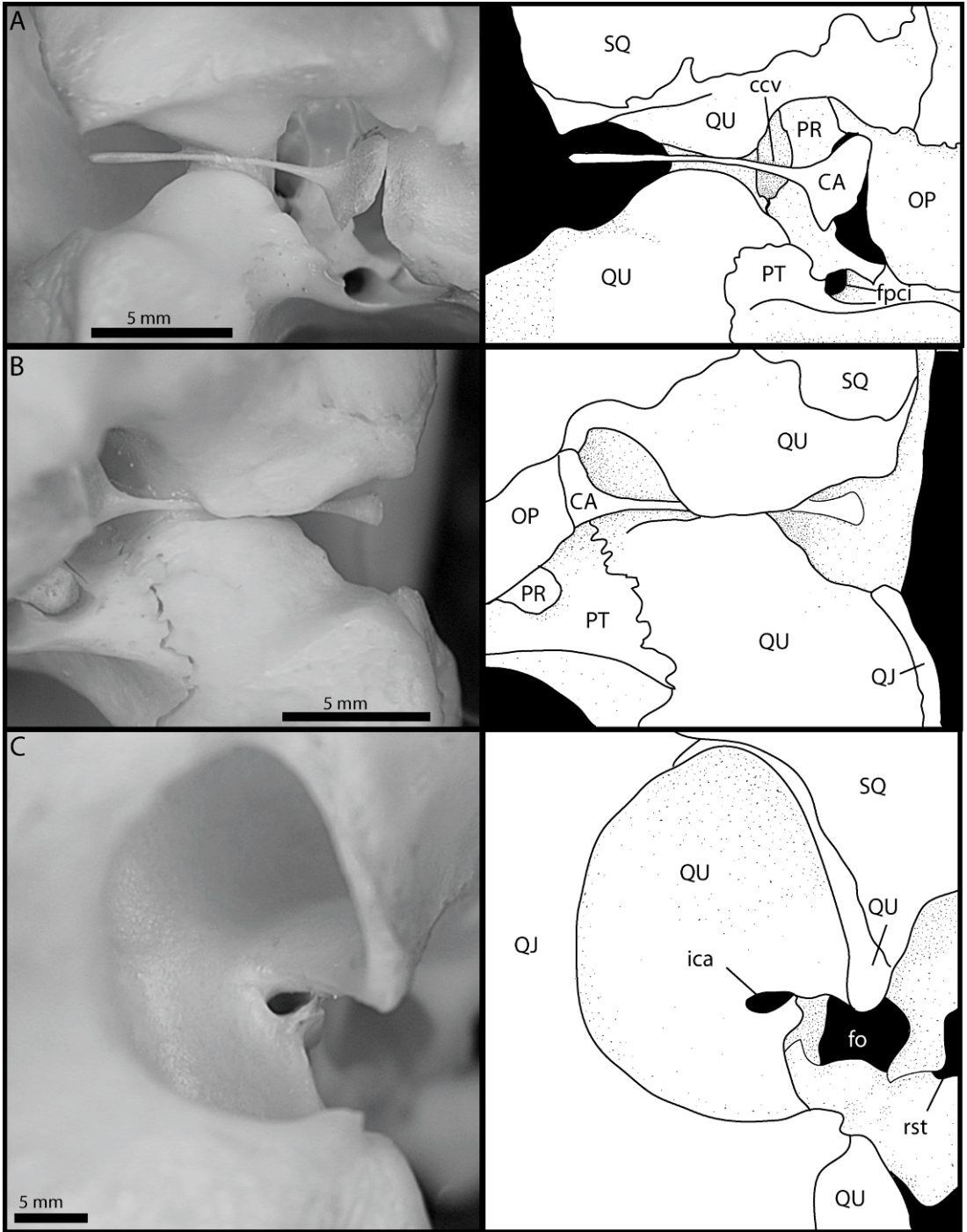


Fig. 21. Photographs and line drawings of the incisura columella auris and surrounding basicranial region in M-2975 (A, left), M-2966 (B, right), and M-2983 (C, left). The incisura is open caudally in M-2975, restricted caudally by a descending secondary process of the quadrate in M-2966, and restricted by an ascending secondary process of the quadrate in M-2983.

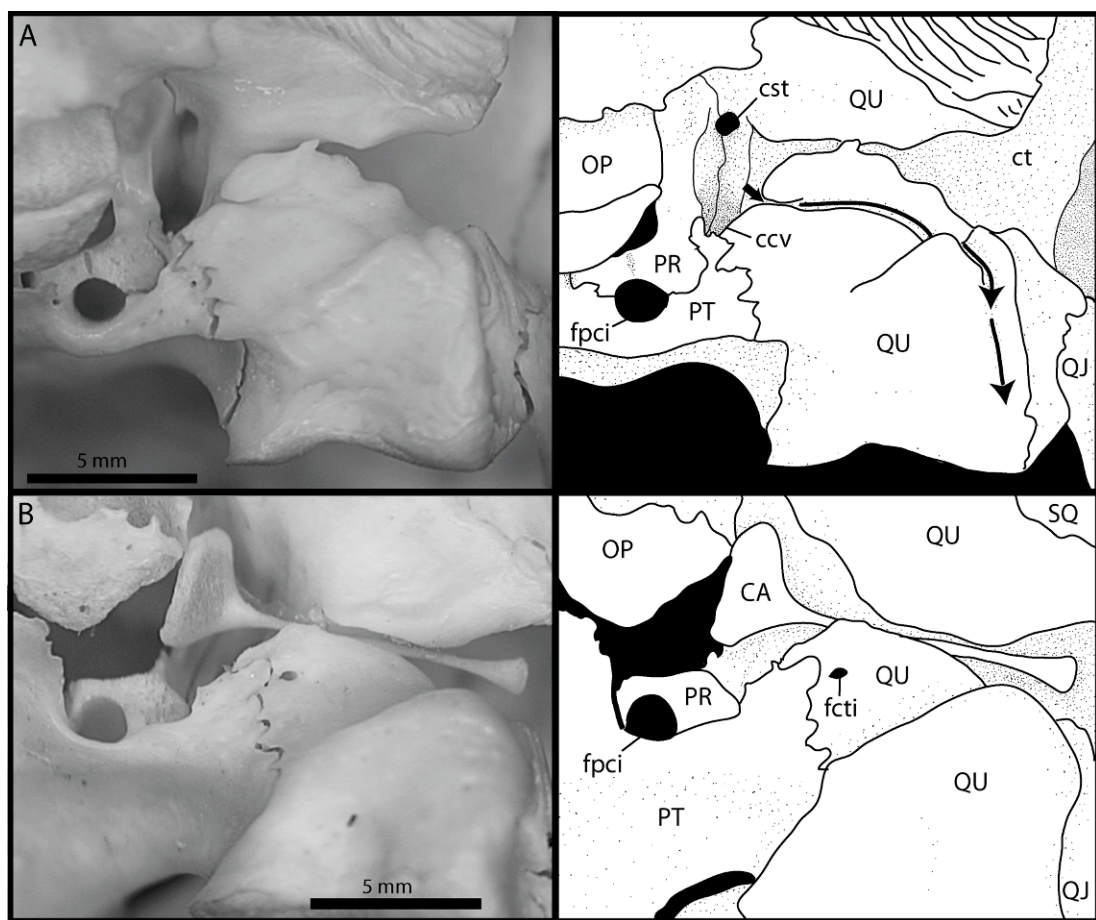


Fig. 22. Photographs and line drawings of the basicranial region of M-2984 (A) and M-2966 (B) in caudoventral view. In M-2984, the chorda tympani nerve passes through a groove in the quadrate rather than through a fully enclosed foramen (canalis chorda tympani quadrati) as seen in M-2966. The path of the chorda tympani external to this opening is preserved in M-2984 and denoted here by an arrow.

letely enclosed in bone (i.e., a true canal; fig. 22B). In 39.5% of the specimens, the path lies completely within the quadrate but takes the form of a groove rather than a canal (fig. 22A). A position between the quadrate and pterygoid characterizes at least one side in 39.1% of the SMRS, including the largest specimen (30.4% as a canal and 8.7% as a groove). An osseous signature for the chorda tympani nerve is absent on at least one side of the skull in 10.5% of the SMRS. The morphology of this path is a bilaterally asymmetric feature in 18.4% of the specimens. The path of the chorda tympani nerve is especially well preserved in a mature male (M-2984) where it is visible entering the

foramen chorda tympani superius from the cavum acuticojugulare before crossing the processus articularis of the quadrate on its way to the lower jaw (fig. 22A). In M-2964, the foramen chorda tympani inferius penetrates the medial margin of a small, distinct quadrate fossa just below the incisura columella auris. These variant morphologies do not exhibit a clear correlation with postnatal growth. Variation in the cranial path of the chorda tympani nerve has not been explicitly surveyed in turtles.

The epipterygoid consistently fails to contact the jugal or prootic (both are plesiomorphic for kinosternids). Rostral contact of the epipterygoid with the palatine, which is

common among cryptodires including kinosternids, is highly inconsistent in the SMRS—present in 51.7% of observable specimens. Variation in this contact seemingly should be related to differing levels of ossification of the epipterygoid, and therefore strongly correlated with ontogenetic stage; however, such a correlation is not evident (adult percentage only slightly higher than juvenile [52.6% and 50.0%, respectively]). In addition, some of the smallest specimens exhibit this contact (e.g., M-2980), whereas the largest specimen (M-2983) lacks it. The epipterygoid separates the parietal and pterygoid in lateral view and thus participates in the foramen nervi trigemini in 55.9% of specimens including the largest individual (fig. 12). This participation is absent in the remaining percentage, which includes the smallest individual. (Joyce and Bell [2004] describe this contact as present in *Sternotherus odoratus*.) The foramen nervi trigemini in two adults (M-2970 and M-2975) exhibits an epipterygoid contribution on one side of the skull only (the parietal and pterygoid form this margin on the opposing side).

The pterygoid maintains a consistent rostral contact with the palatine, maxilla, jugal, parietal, epipterygoid, and opposing pterygoid (all plesiomorphic for kinosternids). A rostromedial contact with the vomer is present in 88.6% of specimens but obscured in four specimens because of a midline contact of the palatines (see above). The processus pterygoideus externus is present with some variation in its development (figs. 5, 6). Its lateral margin is highly rounded in smaller individuals and becomes relatively pronounced in larger specimens (e.g., M-2983 and M-2995). A distinct vertical flange is absent in all specimens, but the thickness of this process increases through ontogeny (nearly flat in the smallest specimens). Development of this process is never as strong as in some cryptodires (e.g., chelydrids, *Platysternon megacephalum*, trionychids; Gaffney, 1979; Shaffer et al., 1997).

Caudally, the pterygoid contains a large process that consistently sweeps back to brace the quadrate against the braincase and flooring the middle ear (a derived feature of cryptodires among extant turtles; Gaffney and Meylan, 1988; Gaffney, 1990). This caudomedial process consistently contacts

the parabasisphenoid and basioccipital (cryptodire apomorphy, is reversed in some testudinoids; see Joyce and Bell, 2004). Variable pterygoid contacts with the processus interfenestralis of the opisthotic (16.1%) and the exoccipital (12.9%) are present only in larger specimens. The lateral margin of the exoccipital extends ventrally to separate the basioccipital from the processus interfenestralis (see discussion of recessus scalae tympani below). The largest specimen in the SMRS (M-2983) exhibits a broad exoccipital-opisthotic contact suggesting this may be a consistent morphology among older individuals. This contact may be derived within Kinosternoidea (absent in *Dermatemys*; Bienz, 1895). The quadrate ramus of the pterygoid forms a consistent contact with the processus articularis of the quadrate but only contacts the condylus mandibularis in three specimens (8.6%; fig. 15). In two specimens, condylar contact is a right/left asymmetry. Considerable variation in the proximity of the pterygoid to the condyle occurs in both age groups. This contact was considered present in *Sternotherus odoratus* (Joyce and Bell, 2004).

A distinct foramen caroticopharyngeale (figs. 5, 6), which transmits branches of both the caroticopharyngeal artery and vidian (VII) nerve, is present on the ventral surface of the pterygoid in all specimens; however, in two juveniles and one adult (M-2993, M-2981, and M-2956, respectively) this foramen is present on only one side. These small foramina lack the subdivisions, described in some testudinoids (Gaffney and Meylan, 1988; Stephens and Wiens, 2003). The foramina caroticopharyngeale generally are positioned adjacent to the rostral margin of the parabasisphenoid but vary considerably in their exact location (no apparent correlation with ontogeny). In 68.4% of the SMRS (including the smallest and largest individuals), this foramen is rostral to the parabasisphenoid, and in 10.5% its position relative to the parabasisphenoid is bilateral asymmetric. The foramen caroticopharyngeale penetrates the parabasisphenoid-pterygoid suture (McDowell, 1964) on the right side of a single juvenile skull (M-2986). A ventral pterygoid fossa, just medial to the processus articularis and lateral to the parabasisphenoid, houses the origin of the M. pterygoi-

deus pars ventralis (Schumacher, 1973) but does not house the foramen caroticopharyngeale in any specimen. The fossa deepens and becomes more distinct with growth. *Sternotherus odoratus* was scored as lacking the fossa (Stephens and Wiens, 2003). Their description of the fossa, however, included a qualifier that it houses a foramen caroticopharyngeale (which may explain our observational discrepancy).

The caudal border of the pterygoid forms the ventral margin of the fenestra postotica, a large caudal opening through which the internal carotid artery, stapedial artery, and are transmitted into and out of the skull (McDowell, 1961; Gaffney, 1979). The internal carotid artery passes rostrally through a canal formed between the pterygoid and prootic (see below). The canal branches, sending the cranial carotid artery into the parabasisphenoid and sella turcica and the stapedial artery through the foramen caroticum laterale (McDowell, 1961; Albrecht, 1967). The canalis caroticus internus and canalis caroticus lateralis are thus ventrally completely embedded in bone even in the smallest specimens (derived feature of cryptodires among extant turtles; Gaffney, 1996). A dorsal process of the pterygoid generally extends medially above the palatine artery to contact the ventral margin of the prootic and form the roof of the foramen caroticum laterale (fig. 23A). This process stops short of completely forming the medial wall of this foramen (which is completed by the parabasisphenoid). In at least one immature specimen (M-2960), the dorsomedial extension of this process fails to develop so that the foramen caroticum laterale is roofed completely by the prootic (fig. 23B).

The width of the foramen posterius canalis caroticus internus ranges between 0.4 and 0.9 mm with little variation between the right and left sides of the skull. The size of this foramen is equal or nearly equal to that of the foramen caroticum laterale (the foramen caroticum laterale is sometimes slightly smaller but never larger). The width of the foramen caroticum laterale is 20 to 60% greater than that of the foramen anterius canalis caroticus interni within the sella turcica. Sample size is low for these comparisons because the requisite measurements are impossible to take on an articulated skull; see table 5). These

proportions reflect a plesiomorphic condition within Kinosternidae (but perhaps derived for Kinosternoidea) in which the primary blood supply to the head (with the exception of the brain) is through the palatine artery rather than through the pseudopalatine branch of the internal carotid artery (as in trionychids) and the stapedial artery (as in testudinoids; McDowell, 1961; Albrecht, 1967, 1976; Gaffney, 1979; Meylan and Gaffney, 1989; see below for comparison of these foramina with those of the stapedial artery).

A distinct circular fossa (here referred to as the vidian fossa) lies in the dorsal surface of the pterygoid at the position of the foramen caroticum laterale or directly rostral to it. Within this fossa is a pair of foramina, one directed rostrally and one caudally (fig. 24A). The rostral foramen is the caudal opening of the canalis nervi vidiani that splits within the pterygoid, sending one branch (canalis caroticopharyngeale) to open ventrally as the foramen caroticopharyngeale and another branch (anterior canalis nervi vidiani) rostrally through the pterygoid and palatine to open in the caudal margin of the foramen palatinum posterius (see above). The anterior canalis nervi vidiani passes rostrally through the pterygoid in the base of the crista pterygoidea near its lateral margin with the fossa temporalis inferior (fig. 24B). This canal can be exposed laterally (fig. 24C) but generally is not.

The caudal opening within the vidian fossa is the rostral foramen of the posterior canalis nervi vidiani that enters the pterygoid directly below the foramen pro ramo nervi vidiani in the floor of the canalis caroticus internus (see below; fig. 25A). If this interpretation is correct, then the fibers of the vidian nerve that pass through the posterior canalis nervi vidiani rejoin the rest of the vidian nerve within this fossa and then pass together through the rostral foramen of the canalis nervi vidiani. This condition differs somewhat from the description of Albrecht (1967) who observed the posterior canalis nervi vidiani joining the anterior canalis nervi vidiani within the pterygoid (not within a fossa) and well rostral to the foramen caroticum laterale.

The vidian nerve enters the canalis caroticus internus from the canalis cavernosus

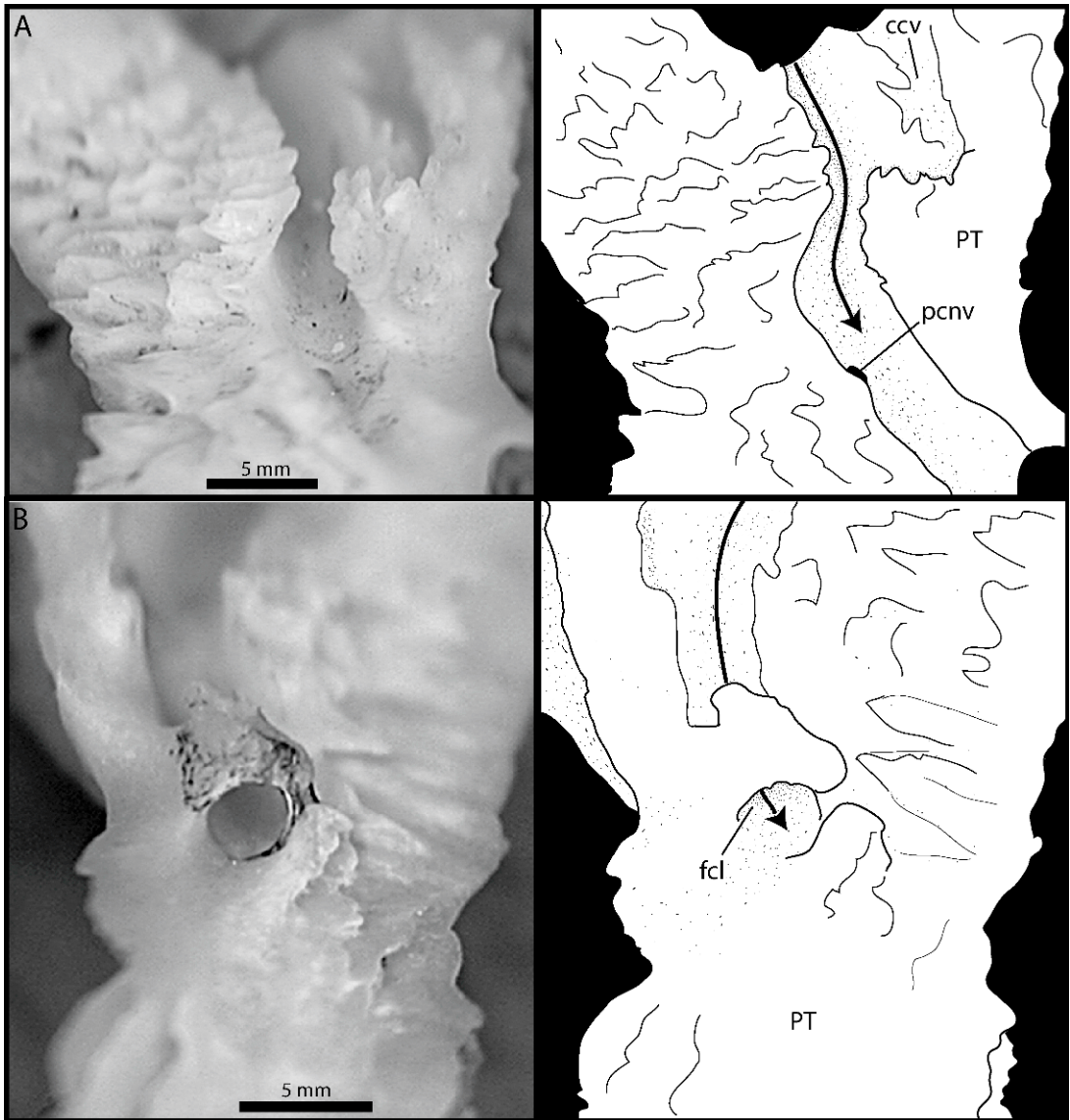


Fig. 23. Photographs and line drawings of the dorsal surface of the pterygoid in M-2960 (A, left) and M-2990 (B, right). The foramen caroticum laterale, which transmits the palatine artery rostrally, was closed dorsally in M-2960 by the overlying prootic, whereas in M-2990 the dorsal margin of this foramen is formed by the pterygoid. The pterygoid falls just short of forming the entire medial margin of the foramen caroticum laterale in M-2990. This margin would have been closed medially by the parabasisphenoid. Arrows show path of internal carotid artery.

through the foramen pro ramo nervi vidiani (Albrecht, 1967; Gaffney, 1979). The structure of this foramen varies considerably. The ventral margin is consistently formed by the pterygoid. The caudal and most of the dorsal margin generally are formed by the pterygoid

(fig. 25A), with the prootic often making a small contribution owing to incomplete ossification of the pterygoid above the foramen. The prootic can form the entire dorsal margin in larger individuals (fig. 25B). Some amount of bilateral asymmetry in the

TABLE 5
Descriptive Statistics for Selected Morphometric Characters from Palatoquadrate,
Braincase, and Lower Jaw of *Sternotherus odoratus* from the SMRS

Characters are listed according to their order of appearance within the descriptive text. All measurements are in millimeters. VI = abducens nerve.

	N	Mean	SD	Range
Foramen anterius canalis caroticum interni width/foramen caroticum laterale width				
Total	8	0.77	0.155	0.60–1.00
Juveniles	5	0.76	0.153	0.60–1.00
Adults	3	0.78	0.193	0.67–1.00
Width of foramen stapediotemporale/width of foramen caroticum laterale				
Total	8	0.49	0.182	0.25–0.75
Juveniles	5	0.43	0.191	0.25–0.75
Adults	3	0.50	0.144	0.50–0.75
Fenestra perilymphatica width/foramen posterius canalis caroticus internus width				
Total	8	1.10	0.220	0.80–1.40
Juveniles	5	1.06	0.276	0.80–1.40
Adults	3	1.18	0.062	1.14–1.25
Distance between right and left foramen posterius canalis caroticus internus				
Total	8	2.25	0.831	1.17–3.67
Juveniles	5	1.87	0.673	1.17–2.67
Adults	3	2.89	0.737	2.20–3.67
Distance between rostral VI foramina/distance between caudal VI foramina				
Juveniles	5	0.91	0.058	0.84–0.96
Adults	3	1.07	0.064	1.04–1.15
Lower triturating surface lateral width /rostromedial width				
Total	38	0.75	0.088	0.54–0.95
Juveniles	15	0.77	0.090	0.61–0.95
Adults	23	0.73	0.085	0.33–0.86

composition of the dorsal margin is common (50% of observed specimens). The medial wall of the canalis cavernosus that forms the rostral margin of the foramen pro ramo nervi vidiani generally is well ossified, even in small specimens, but remains unossified in a very small specimen (M-2991; fig. 25C). Ossification of the medial wall of the canalis cavernosus caudal to the foramen pro ramo nervi vidiani exhibits considerable variation that includes complete ossification resulting in the formation of a caudal margin of the foramen pro ramo nervi vidiani that lacks a caudal foramen, minimal ossification resulting in the lack of a caudal wall of the foramen pro ramo nervi vidiani, and partial ossification that results in a small but distinct second foramen positioned caudal to the foramen pro ramo nervi vidiani. This second foramen is only partly delineated

in bone in some specimens. What passes through this foramen when it is present is unclear but it may be that the vidian nerve splits in the canalis cavernosus rather than splitting after it passes into the canalis caroticum internus. Once in the canalis caroticus internus, the vidian nerve sends a branch directly into the pterygoid through the posterius canalis nervi vidiani and a second (and possibly third) branch rostrally to the foramen caroticum laterale and eventually into the anterior canalis nervi vidiani (Albrecht, 1967). Variation in the ossification around the foramen pro ramo nervi vidiani consequently results in considerable size variation for this foramen, which was reported to be smaller in *Sternotherus odoratus* than in either *Chrysemys* or *Apalone* (Albrecht, 1967). The posterior canalis nervi vidiani is consistently

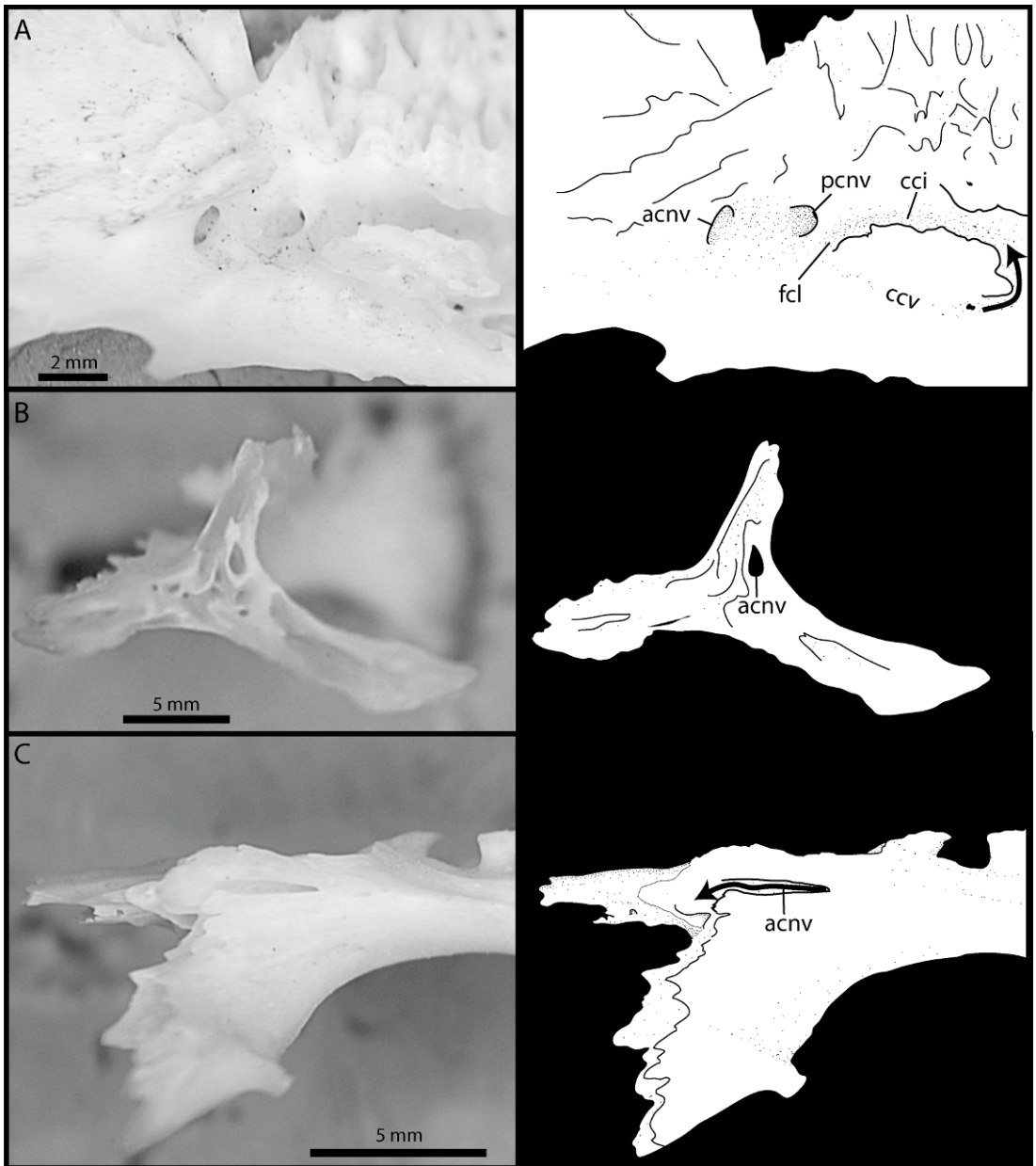


Fig. 24. Photographs and line drawings of the dorsal surface of the pterygoid in M-2960 (A, left), the rostral end of the pterygoid in M-2982 (B, left), and lateral view of the rostral half of the pterygoid in M-2960 (C, left). A fossa lying just rostral to the foramen caroticum laterale houses foramina involved in the transmission of the vidian nerve and vein. The anterior canalis nervi vidiani (acnv) transmits the vidian nerve and vein rostrally through the crista pterygoidea before it eventually bifurcates sending branches of the vidian onto the dorsal and ventral surfaces of the palate. Arrows mark the path of the vidian nerve through the foramen pro ramo nervi vidiani (A) and the anterior canalis nervi vidiani (C).

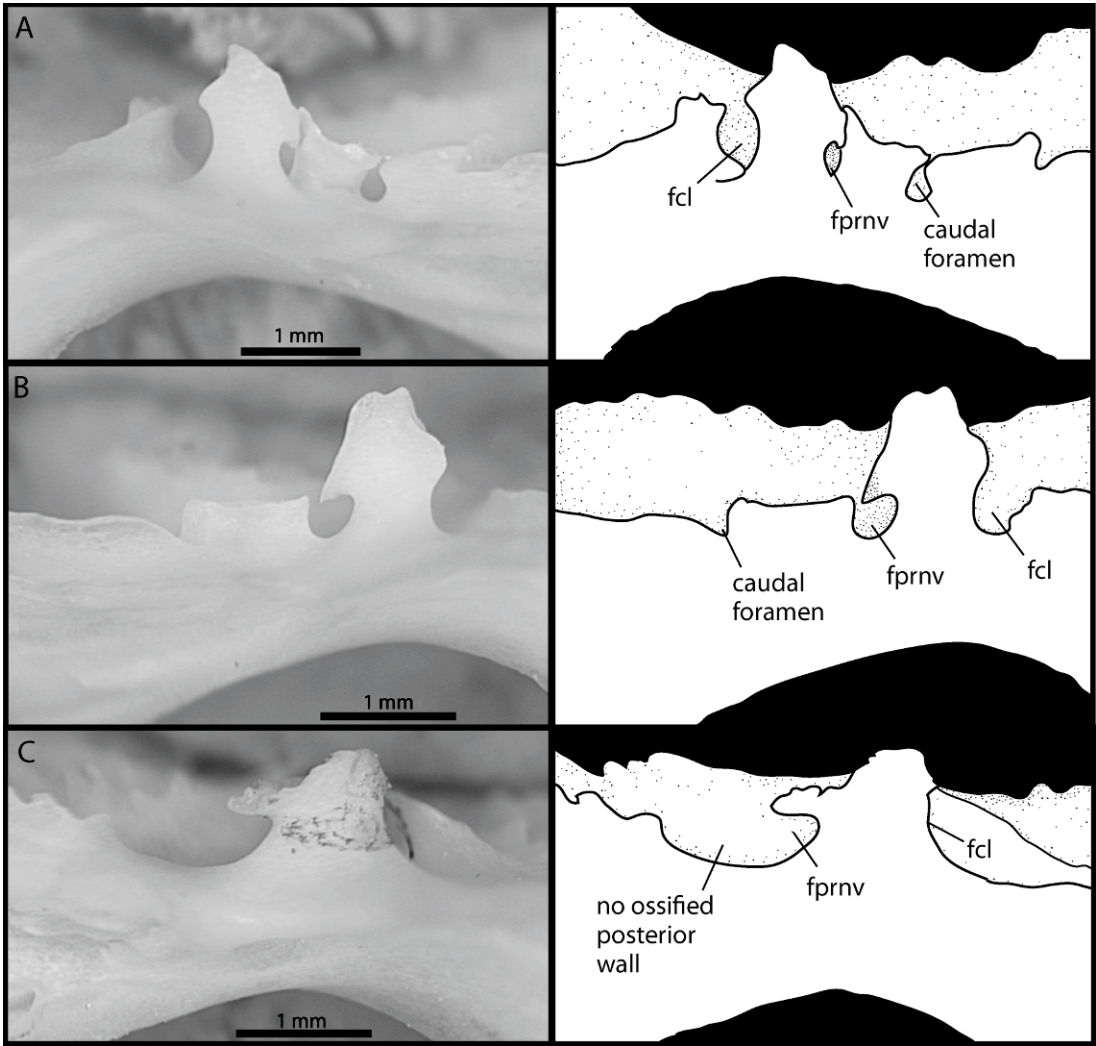


Fig. 25. Photographs and line drawings of the pterygoid in dorsolateral view showing the ossified dorsal wall that separates the canalis cavernosus (foreground) and the internal carotid canal, which terminates rostrally with the foramen caroticum laterale (fcl). This wall is penetrated by the foramen pro ramo nervi vidiani, which transmits the vidian nerve from the canalis cavernosus to the internal carotid canal. The ossification of the wall around this foramen is variable in the SMRS as seen in M-2992 (A, left), (B, right), and M-2991 (C, right). The prootic, which is not articulated in these photographs, lies above the pterygoid and participates in the foramen caroticum laterale and foramen pro ramo nervi vidiani.

present and enters the pterygoid inside the canalis caroticus internus at the base of the foramen pro ramo nervi vidiani. This entry generally occurs through a single foramen in juveniles and a pair of foramina in adults; however, variation does exist and because disarticulated specimens are required to examine this character, these observations are based on a small sample size.

The crista pterygoidea participates in the ventral margin of the foramen nervi trigemini in all specimens with the exception of a single adult (M-2976; 3.1%; also lacking from the right side of a juvenile, M-2995). When absent, a pterygoid contribution is negated by the complete ossification of the epipterygoid and obliteration of the fossa epipterygoideus cartilaginis. It is within this fossa

that the pterygoid contribution is most consistent, although a contribution above the epipterygoid is not uncommon (fig. 12). Absence of this participation is the most common condition among kinosternids including *Dermatemys*, so its presence may be derived within the group.

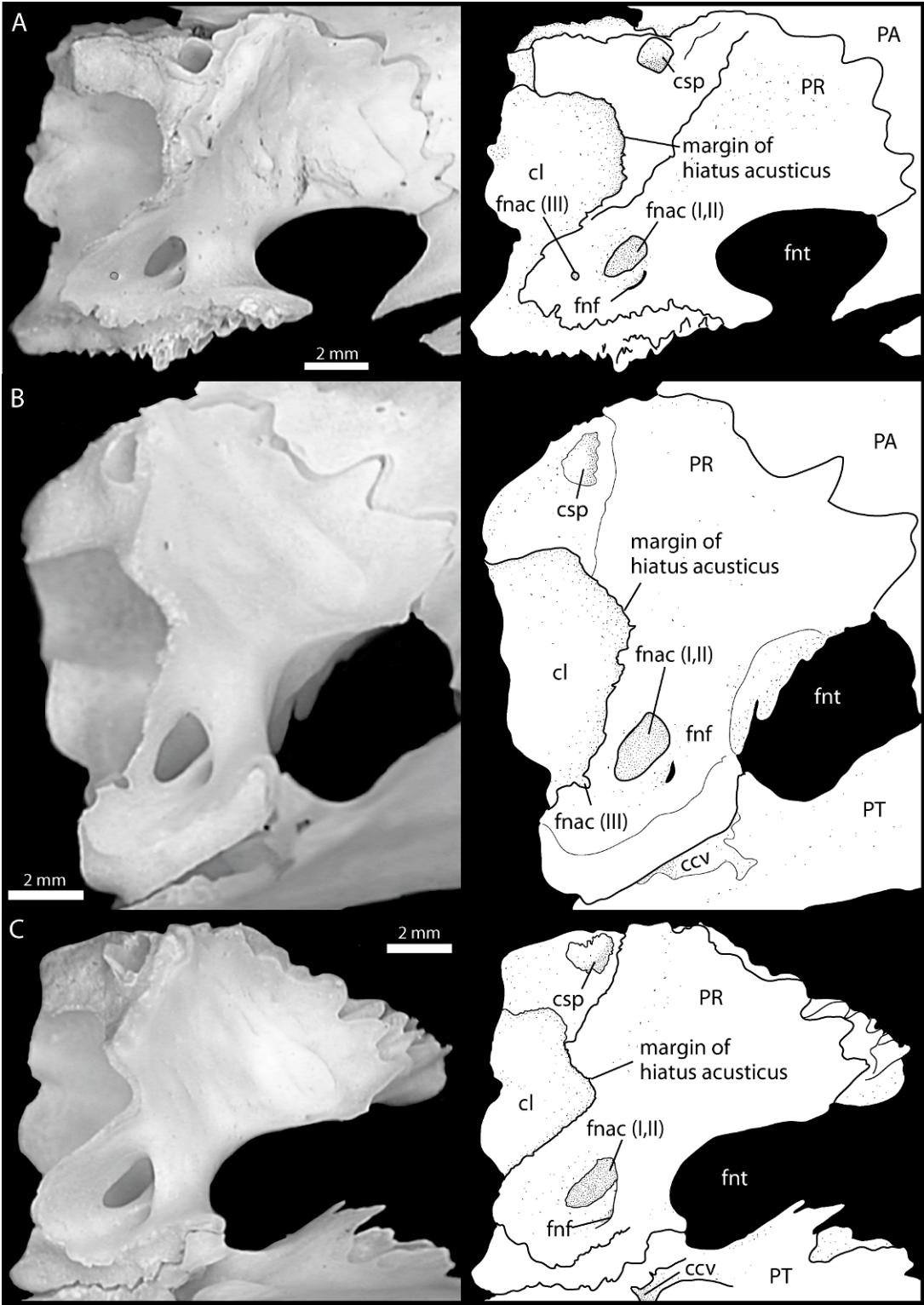
BRAINCASE REGION: The braincase includes the midline supraoccipital, basioccipital, and parabasisphenoid and the paired exoccipital, prootic, and opisthotic. The external surface of the supraoccipital is dominated by the crista supraoccipitalis (fig. 7). This crest is peaked in most specimens (65.7%; including the smallest individuals) such that the rostral and caudal halves are straight and angle away from each other (Stephens and Wiens, 2003). The crest is arched dorsally in 31.4% of the SMRS (mostly adults) and is straight along at least three-quarters of its length in a single adult female (M-2959; 2.9%). A broadly rounded caudal terminus of the crista supraoccipitalis, which is the plesiomorphic condition for Kinosternidae, is present in 65.7% of the SMRS, including the most mature specimens. The position of the crest's apex relative to the parietal-supraoccipital suture is variable. It is positioned at the suture in 62.9%, rostral to the suture in 25.7% (including the largest specimen), and caudal to the suture in 11.4% of the specimens. Although the large degree of postnatal variation in the shape of the crista supraoccipitalis undoubtedly affects this position, the observed variations are not clearly correlated with skull size. The caudoventral margin of the crest in the largest specimens exhibits a pronounced thickening (fig. 5). This may be the rudimentary development of an ossified supraoccipital tendon that forms a prominent bony shelf as a derived feature in some turtles (e.g., *Apalone*; Dalrymple, 1977; *Carettochelys* and *Podocnemis*; Gaffney, 1979).

The supraoccipital contributes to the vestibular portion of the cavum labyrinthicum (all extant turtles, Gaffney, 1979, 1990). The foramen aquaducti vestibuli, which transmits the endolymphatic duct from the endolymphatic sac in the cavum cranii to the sacculus (Baird, 1960, 1970), penetrates the rostrome-dial wall of this contribution even in the smallest specimens. In two juvenile speci-

mens, this foramen lies in the margin of the supraoccipital and hiatus acusticus, thus being formed half in bone and half in cartilage. The foramen can lie fully within the supraoccipital on one or both sides of the skull in both juveniles and adults specimens. A sagittally section specimen of *S. odoratus* illustrated by Gaffney (1979: 179; maturity assessment based on advanced development of the crista supraoccipitalis) does not exhibit a foramen aquaducti vestibuli, presumably because the endolymphatic duct passed through the hiatus acusticus. Therefore, considerable individual variation in the ossification of the hiatus acusticus does occur. The foramen vasis vestibuli, described as lying in the medial wall of the cavum labyrinthicum near the foramen aquaducti vestibuli in a trionychid and possibly some specimens of *Caretta* and *Chelydra* (Gaffney, 1979: 191) was not observed in the SMRS.

The dorsal surface of the prootic, even in the smallest specimens, contains a relatively broad process trochlearis oticum, a thickening in cryptodires that bears a synovial joint over which the main adductor tendon system changes from a predominantly horizontal to a vertical orientation (Schumacher, 1973; Gaffney, 1979). The quadrate contributes significantly to this process laterally, and the parietal overlies its most medial edge. The relative contribution of the parietal varies but always accounts for less than one-third of the width of this structure. The process becomes more perpendicular with respect to the long axis of the skull and forms a distinct medial saddle through ontogeny (as in *Apalone ferox*; Dalrymple, 1977).

The prootic and quadrate form the canalis stapedi-temporalis, a nearly vertical canal that transmits the stapedia artery from the cranioquadrate portion of the cavum acusticojugulare to the floor of the fossa temporalis superior. The greatest diameter of the foramen stapedi-temporale ranges from 0.1 to 0.4 mm and is consistently smaller than the foramen caroticum laterale (table 5). The presence of this canal and foramen is nearly consistent, which concurs with the observations of Albrecht (1967) but differs from those of McDowell (1961) who stated that the foramen stapedi-temporale occurred only occasionally in *Sternotherus*. A single



adult (M-2995) lacks the canal and foramen, but only on the right side. A reduction in the size of these structures canal is derived for Kinsoternoidea, whereas their complete absence is a synapomorphy diagnosing Dermatemydidae (Baur, 1888, 1896; Meylan and Gaffney, 1989).

The medial wall of the prootic houses the fossa acusticofacialis. The common condition among reptiles is for this fossa to be penetrated by three foramina, one transmitting the facial (VII) nerve into the canalis cavernosus and two transmitting the primary branches of the vestibulocochlear (VIII) nerve into the cavum labyrinthicum (Baird, 1970; Wever, 1978; fig. 26). The fossa acusticofacialis is not visible in articulated specimens of *S. odoratus*. Therefore, observations of variation are restricted to disarticulated skulls. The foramen nervi facialis is consistently present, as is a large, elongate, caudally positioned foramen nervi acustici. The latter foramen transmits the two primary branches of the vestibulocochlear nerve (fig. 26). The normal division of this opening into a pair of smaller foramina is absent in all observed specimens and must ossify late in postnatal ontogeny. The osseous signature of a third branch of VIII is variably present. This foramen can be distinct and lie well away from the rostral margin of the hiatus acusticus (fig. 26A), can be partially formed in the margin of the hiatus acusticus (fig. 26B), or be absent altogether (fig. 26C). This variation depends largely on the degree to which the otic capsule is ossified medially and, not surprisingly, is correlated with postnatal ontogeny; all adults exhibit some osseous signature of a third branch of VIII. However, a distinctly developed foramen for a third branch is present in at least one juvenile (M-2992) demonstrating that the size of the hiatus acusticus can be decoupled from general growth trajectories to at least some degree. A sagittally sectioned adult *S. odor-*

atus exhibits three vestibulocochlear foramina (Gaffney, 1979: 179).

As in all turtles, the glossopharyngeal (IX) nerve passes through the cavum labyrinthicum in the SMRS (Siebenrock, 1897; Gaffney, 1979; Rieppel, 1980). It enters the cavum through the foramen medialis nervi glossopharyngei, which can lie within the hiatus acusticus or penetrate the processus interfenestralis of the opisthotic. The nerve then traverses the caudal wall of the cavum labyrinthicum before entering a short canal through the processus interfenestralis (via the foramen internum nervi glossopharyngei). The most variable of these structures in turtles is the foramen medialis nervi glossopharyngei (Gaffney, 1979) (fig. 27). In the SMRS, the relative size and closure of this foramen vary roughly with age, but are not reliable predictors of any precise postnatal stage. The distance from the medial to internal foramen varies with growth of the processus interfenestralis (Gaffney, 1979), as does the distinctiveness of the shallow groove that transmits IX medially. The medial foramen varies in its relative position within the processus interfenestralis and the degree to which it is enclosed in bone. A fully formed foramen (fig. 27) is present in 40.0% of juveniles and 82.6% of adults.

The fenestra perilymphatica (fig. 27) transmits the periotic sac from the cavum labyrinthicum to the recessus scalae tympani portion of the cavum acusticojugulare through the process interfenestralis (Baird, 1960, 1970; Gaffney, 1979). The medial margin of this fenestra is ossified completely in 57.9% of specimens (fig. 27A), bilaterally asymmetrical in M-2956, and is open medially in the remaining specimens (fig. 27B). Closure is present in 73.9% of adults and 33.3% of juveniles; however, this margin is completely ossified in M-2992, one of the smallest specimens in the sample. The fenes-

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Fig. 26. Photographs and line drawings of the medial surface of the left prootic in M-2982 (A), M-2992 (B), and M-2996 (C) showing the variable morphology of the fossa acusticofacialis. Note the single large opening that transmits at least two branches of the vestibulocochlear nerve. A third branch of VIII may pass through a fully enclosed smaller foramen (A), a partial foramen in the margin of the hiatus acusticus (B), or presumably, when no secondary foramen is present, through the hiatus acusticus (C).

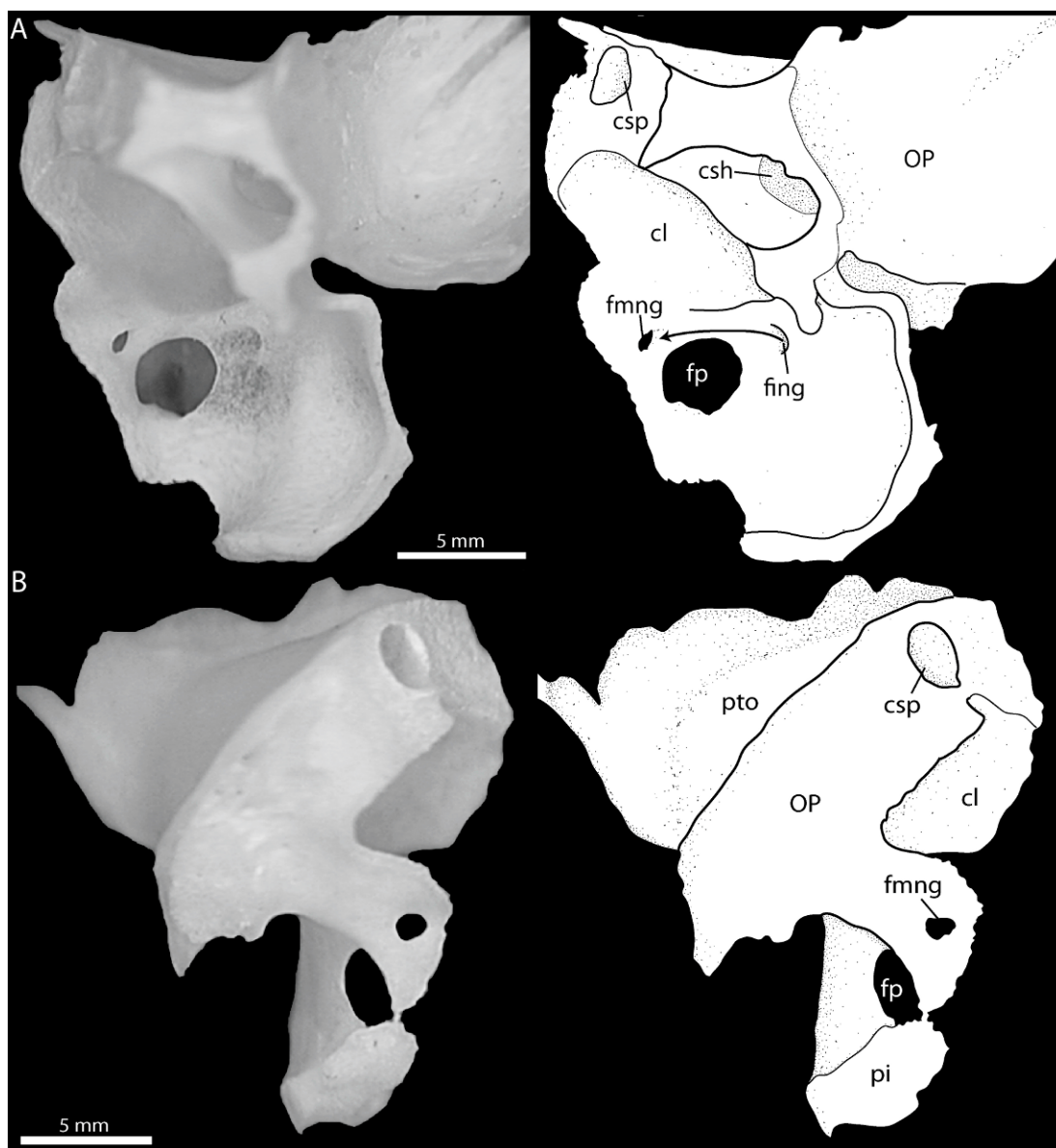


Fig. 27. Photographs and line drawings of the left opisthotic in rostral (M-2964, **A**) and medial (M-2992, **B**) views. The arrow marks the path of the glossopharyngeal nerve along the caudal wall of the cavum labyrinthicum (cl), which is formed by the processus interfenestralis of the opisthotic (pi). Note the differences in the ossification of the medial wall of the fenestra perilymphatica in the two specimens.

tra perilymphatica was not completed by the basioccipital in any SMRS specimen.

The fenestra ovalis houses the footplate of the columella auris and is the most prominent opening in the lateral wall of the cavum labyrinthicum. The ventral margin of the fenestra, as formed by the cartilaginous otic

capsule, generally remains unossified. The largest specimen in the sample (M-2983) is the only individual whose ventral margin is formed by the prootic rostrally and opisthotic caudally (fig. 28A). In all other specimens, this margin is formed by the pterygoid and in at least one larger individual a small contri-

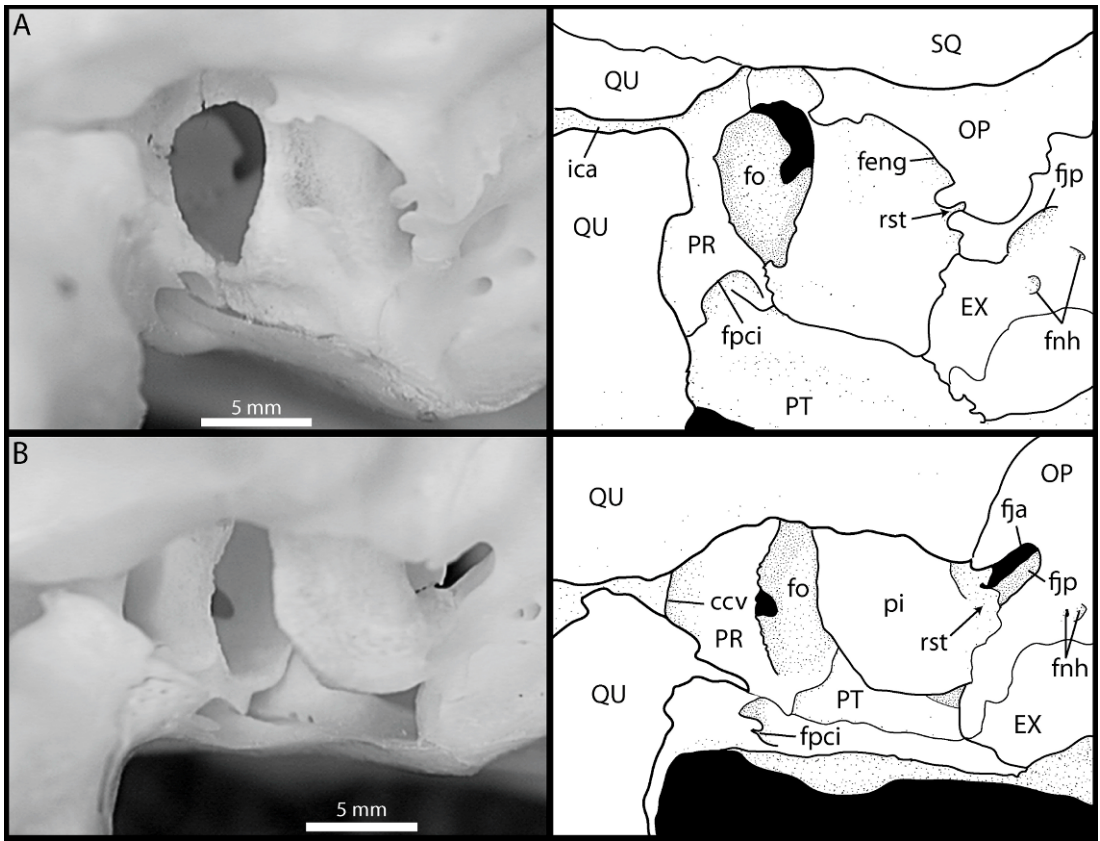


Fig. 28. Photographs and line drawings of the left basicranial region in posterolateral view through the fenestra postotica in M-2983 (A) and M-2995 (B). Note the increased ossification in M-2983 (a large, mature male) relative to M-2995 (an immature male). This increased ossification is especially apparent around the fenestra ovalis (fo) and the lateral margin of the foramen jugulare posterius (fjp). The columella auris is absent in both specimens.

bution from the lateral edge of the parabasi-sphenoid (M-2966). The foramen posterior canalis carotici interni is formed between the descending process of the prootic (dorsally) and the pterygoid (ventrally). With the exception of the largest specimen, the descending process of the prootic is recessed such that the canalis caroticus internus begin caudally as a groove in the pterygoid rather than as a true osseous canal (fig. 28B). The caudal shift in the relative position of the prootic such that it overlies the caudal margin of the pterygoid and forms the dorsal margin of a completed foramen posterior canalis carotici interni (fig. 28A) is a late-stage, postnatal transformation.

The embryonic metotic fissure remains undivided postnatally in turtles (Rieppel,

1985). This space forms the caudomedial portion of the cavum acusticojugulare and is generally referred to as the recessus scalae tympani (Gaffney, 1979). The recessus scalae tympani is defined osteologically by the processus interfenestralis of the opisthotic (rostrally) and the exoccipital (caudally; fig. 29A). Its medial wall contains a large communication with the cavum cranii (foramen jugulare anterius) through which pass the vena cerebialis posterior, vagus (X) nerve, and accessory (XI) nerve, and is typically formed in turtles by a combination of the opisthotic and exoccipital with variable contributions from the basioccipital (Gaffney, 1979). In the SMRS, the exoccipital contains a short process that sweeps rostrally beneath the foramen jugulare anterius to

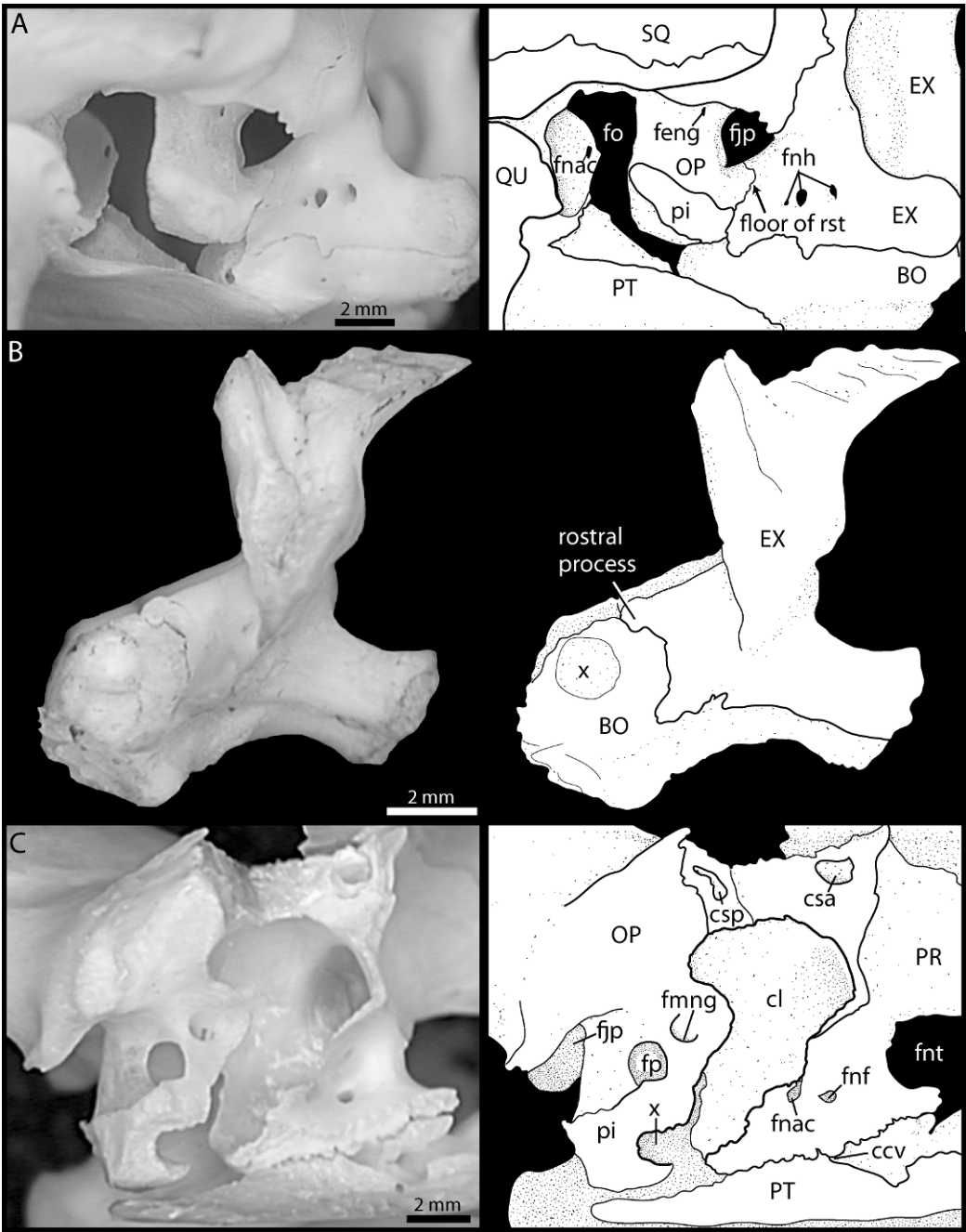


Fig. 29. Photographs and line drawings of the left basicranial region in M-2969 (A), the exoccipital and basioccipital in left lateral view in M-2960 (B), and the medial view of the prootic and opisthotic in M-2964 (C). The floor of the recessus scalae tympani is formed by a caudal shelf of the opisthotic and a rostral extension of the exoccipital. X in M-2960 marks a concavity in the basioccipital that accepts the distal end of the cochlear duct (cochlear recess). X in M-2964 marks the notch in the processus interfenestralis of the opisthotic through which the cochlear duct extends caudomedially.

contact or nearly contact the processus interfenestralis (fig. 29B). A similar rostral extension was described in emydids (McDowell, 1964). The floor of the recessus scalae tympani in cryptodires generally is formed by some combination of the pterygoid, exoccipital, and basioccipital (Gaffney, 1979). The floor in the SMRS is formed by variable contributions from the exoccipital and a caudoventral extension of the processus interfenestralis (fig. 29A). This shelf of the opisthotic is extensive even in the smallest specimens and often is clearly grooved. These contributions fail to meet along the entire length in only a single adult (M-2994), which produces a narrow gap through which a small dorsal ridge of the basioccipital is exposed. The phylogenetic polarity of this construction is unclear, but the floor of the recessus scalae tympani in *Dermatemys* is formed fully by the basioccipital.

The hiatus postlagenum is a communication between the cavum labyrinthicum and the recessus scalae tympani that was defined by McDowell (1964: 246) as "a gap in the suture between the basioccipital and the processus interfenestralis of the opisthotic, ventral to the perilymphatic foramen and immediately posterior to the lagena." This space purportedly is present in all turtles except kinosternoids (including *Dermatemys*), where it is obliterated by the squamous overlap of the basioccipital by the processus interfenestralis (McDowell, 1964: 250). The hiatus postlagenum is consistently absent in the SMRS. A rostral notch in the ventromedial margin of the processus interfenestralis does open into the caudomedial corner of the cavum labyrinthicum. The basioccipital contains a flattened surface that rests against this notch and thus helps to enclose the cavum labyrinthicum. This surface contains a concavity that matches the diameter of the notch and may have been filled by the distal extension of the cochlear duct (lagena), which is positioned caudally in turtles (de Burlet, 1934; Baird, 1960). These cochlear recesses are present in the SMRS with the exception of two small specimens indicating that ossification around the distal end of the cochlear duct occurs postnatally (fig. 29C).

The exoccipital is pierced by the relatively large foramen jugulare posterius and usually

a pair of smaller hypoglossal foramina (fig. 30). The foramen jugulare posterius transmits the posterior head vein, and in some cases the vagus (X) and accessory (XI) nerves, from the recessus scalae tympani to outside the skull (Gaffney, 1979). In most turtles, the foramen jugulare posterius is closed off from the fenestra postotica by an osseous bar formed by a combination of the exoccipital and opisthotic (with the foramen itself being closed laterally by the exoccipital; Gaffney, 1979). The foramen in the SMRS remains confluent with the fenestra postotica (fig. 30A) in all specimens except the largest in the sample (fig. 30B) where a lateral contact of the exoccipital, with a small contribution from the opisthotic most notably on the right side, closes the foramen. The same specimen (M-2983) exhibits numerous small processes that extend into the cavum acusticojugulare (from the prootic) and fenestra postotica. Some of these processes extend from the exoccipital and opisthotic along the margin of the fenestra postotica and delineate the path of the glossopharyngeal nerve. This nerve exits along the opisthotic on the left side and along the exoccipital on the right side. A foramen jugulare posterius that is laterally confluent with the fenestra postotica is the common condition among kinosternoid turtles, although its' relatively late ontogenetic transformation in the SMRS complicates assessing its presence/absence.

The majority of specimens (71.1%), including the smallest and largest individuals, contain two hypoglossal foramina, both of which are formed entirely within the exoccipital. Numerous other morphological combinations and asymmetries are present. These include: two foramina on each side, the second of which is bounded ventrally by the basioccipital (juveniles and adults); three foramina, all of which are in the exoccipital; three foramina on the left and two on the right (all in the exoccipital); two foramina on the left, the second of which is bounded ventrally by the basioccipital, and three foramina on the right, all in the exoccipital. The number of hypoglossal foramina in the reptile basicranium generally decreases over ontogeny (Bellairs and Kamal, 1981), but in the SMRS the percentage of adult specimens

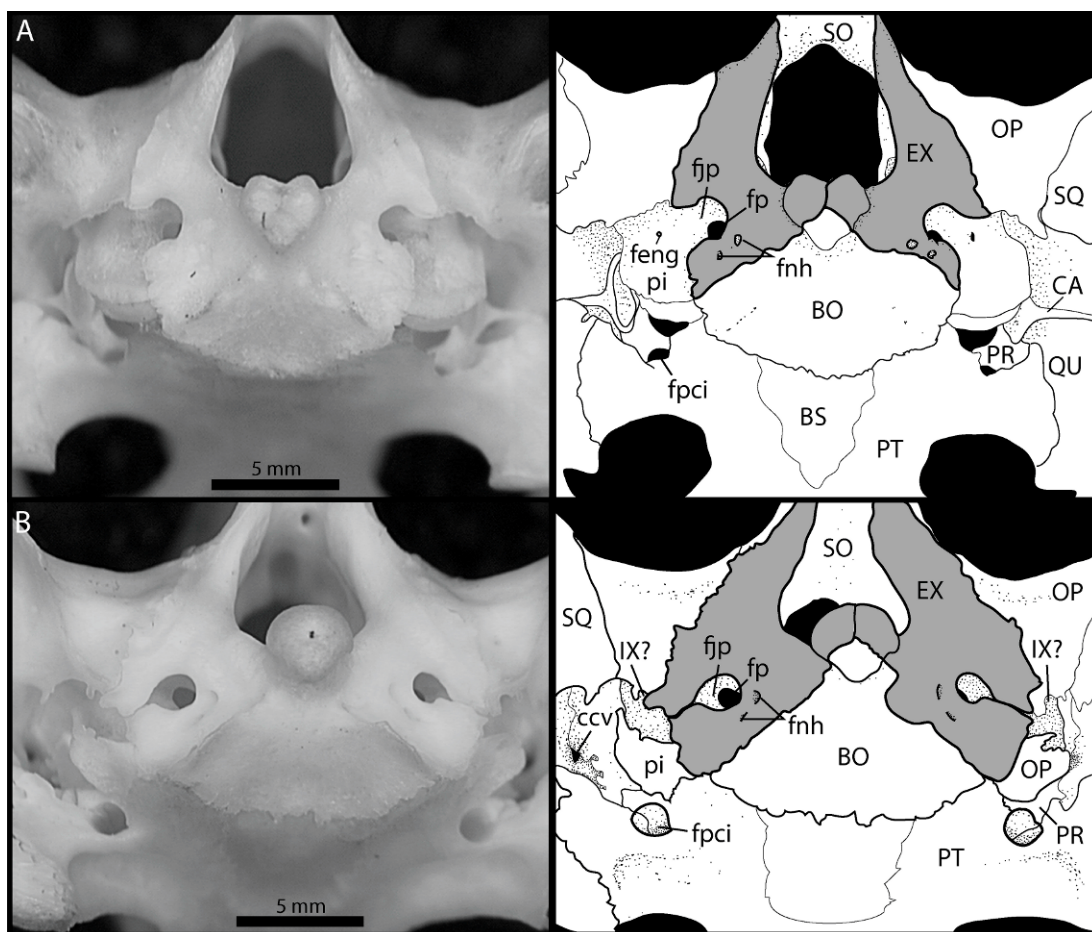


Fig. 30. Photographs and line drawings of the occipital and basicranial regions in M-2980 (A) and M-2983 (B) (the least and most mature specimens in the SMRS). Note the relative ossification of the exoccipitals. IX? (B) marks the possible path of the glossopharyngeal nerve out of the recessus scalae tympani, which is delimited by small, processlike ossifications around the rim of the fenestra postotica.

exhibiting three hypoglossal foramina was nearly equal to that of juveniles (reduction may have occurred earlier in ontogeny). Historically, the number and position of hypoglossal foramina are not considered in phylogenetic analyses of turtle interrelationships; however, their inclusion in phylogenetic and taxonomic assessments of other reptile lineages is not uncommon (e.g., saurischian dinosaurs; Makovicky and Norell, 1998).

The process paroccipitalis of the opisthotic is tightly sutured to the squamosal even in the smallest specimens and contributes to a prominent arching ridge that marks the separation of the *M. adductor mandibulae*

and *M. depressor mandibulae*. As noted above, the prominence of this ridge and the related expansion of a distinct fossa (that lies largely within the squamosal) for the *M. depressor mandibulae* are significantly greater in larger individuals. A tightly sutured process paroccipitalis is a plesiomorphic feature of extant cryptodires (Gaffney et al., 1991).

The fenestra basicranialis is a large, median opening in the chondrocranial planum basale that divides the basal plate into rostral and caudal halves. These halves ossify as the basisphenoid and basioccipital, respectively (Bellairs and Kamal, 1981). A remnant of this fenestra is retained on the ventral

surface of the skull in 65.8% of the specimens (fig. 31). All juveniles and 43.5% of adults exhibited a remnant of this feature, indicating that the full ossification of this margin occurs relatively late in postnatal ontogeny. The presence/absence of a remnant of the fenestra basicranialis may correspond to the presence/absence of a medial notch at the parabasisphenoid-basioccipital suture as described for some testudinoids (Stephens and Wiens, 2003).

The parabasisphenoid-basioccipital suture is formed as the concave caudal margin of the parabasisphenoid accepts the convex rostral margin of the basioccipital. Dorsally, the parabasisphenoid forms a thin, upturned ridge along this margin. This dorsal structure is present even in the smallest specimens (e.g., M-2960), although ontogenetically it starts as a pair of dorsal processes rather than a completed ridge (fig. 32A–C). The shape of this margin is variable. The margin can be relatively straight (5.6%; adults only, fig. 31A), curved rostrally (30.6%, juveniles and adults), or straight medially but sloped laterally (63.9%, juveniles and adults, fig. 31B). The latter condition forms when strong caudolateral processes of the parabasisphenoid underlie the basioccipital, and the fenestra basicranialis is retained. A fully curved margin results when the processes develop but the fenestra is closed. A straight margin forms when these processes fail to develop. A small caudomedial projection of the parabasisphenoid (as described by Stephens and Wiens, 2003) was not observed in any SMRS specimen.

A distinct, semicircular fossa housing the insertion of the *M. rectus capitis* is a common feature of kinosternoids and is present in 68.4% of the SMRS. In adults and large juveniles, the fossa is delineated rostrally by a distinct ridge (McDowell, 1964: fig. 31). This rostral margin lies along the parabasisphenoid-basioccipital suture in 42.3% of the specimens exhibiting this fossa, whereas in the remaining 37.7%, which includes the largest specimens in the sample, the margin is distinctly rostral to the suture. This suggests a postnatal shift in its relative position on the braincase. The ventral surface of the parabasisphenoid lacks paired pits (Stephens and Wiens, 2003).

The shape of the parabasisphenoid, as exposed on the ventral surface of an articu-

lated skull, varies considerably in the SMRS, but this variation is not strongly correlated with overall skull size. The rostral margin is broadly rounded, rather than acute, in 88.6% of the SMRS. This percentage includes the smallest and largest individuals and reflects the plesiomorphic morphology for Kinosternidae. The lateral margins are convex caudally and concave laterally in 42.1% of the sample, including the smallest and largest specimens (fig. 5). A fully convex lateral margin is present in 31.6% of the SMRS (fig. 6). Straight margins that angle toward the midline (fig. 31A) and concave lateral margins are found in 23.7% and 2.6% of the specimens, respectively. This shape does vary among kinosternid taxa, as well as within Testudinoidea where it was applied as a character in systematic analyses (Killebrew, 1979; Stephens and Wiens, 2003).

The tuberculum basioccipitale are completely absent in the smallest specimens but are present as a pair of ridges that form a horizontal shelf rather than a true ventrally directed process (fig. 31A) in most of the sample, indicating that their acquisition occurs relatively early in postnatal ontogeny. The presence of this structure is plesiomorphic for Kinosternoidea; however, a transformation from a ventrally directed process (as found in *Dermatemys*; Bienz, 1895) to a horizontal shelf may be derived within this clade. This shelf in the SMRS lies beneath the foramen nervi hypoglossi and extends ventrolaterally at approximately a 40° angle from a point near the condylus occipitalis to the caudal end of the pterygoid directly below the foramen jugulare anterius.

The rostral margin of the parabasisphenoid is dominated (dorsally) by the ossified trabeculae and rostrum basisphenoidale (Pehrson, 1945). A distinct rostrum that is separated, at least for a portion of its length, from the trabeculae and tapers to a point is present in most specimens (82.9%; fig. 32A). In 17.1% of the sample, including one of the smallest specimens (M-2990), ossification along the lateral margins of the rostrum joins this structure to the trabeculae along its entire length. This ossification results in the process losing its rodlike shape and becoming more platelike (fig. 32B). The fusion of the median

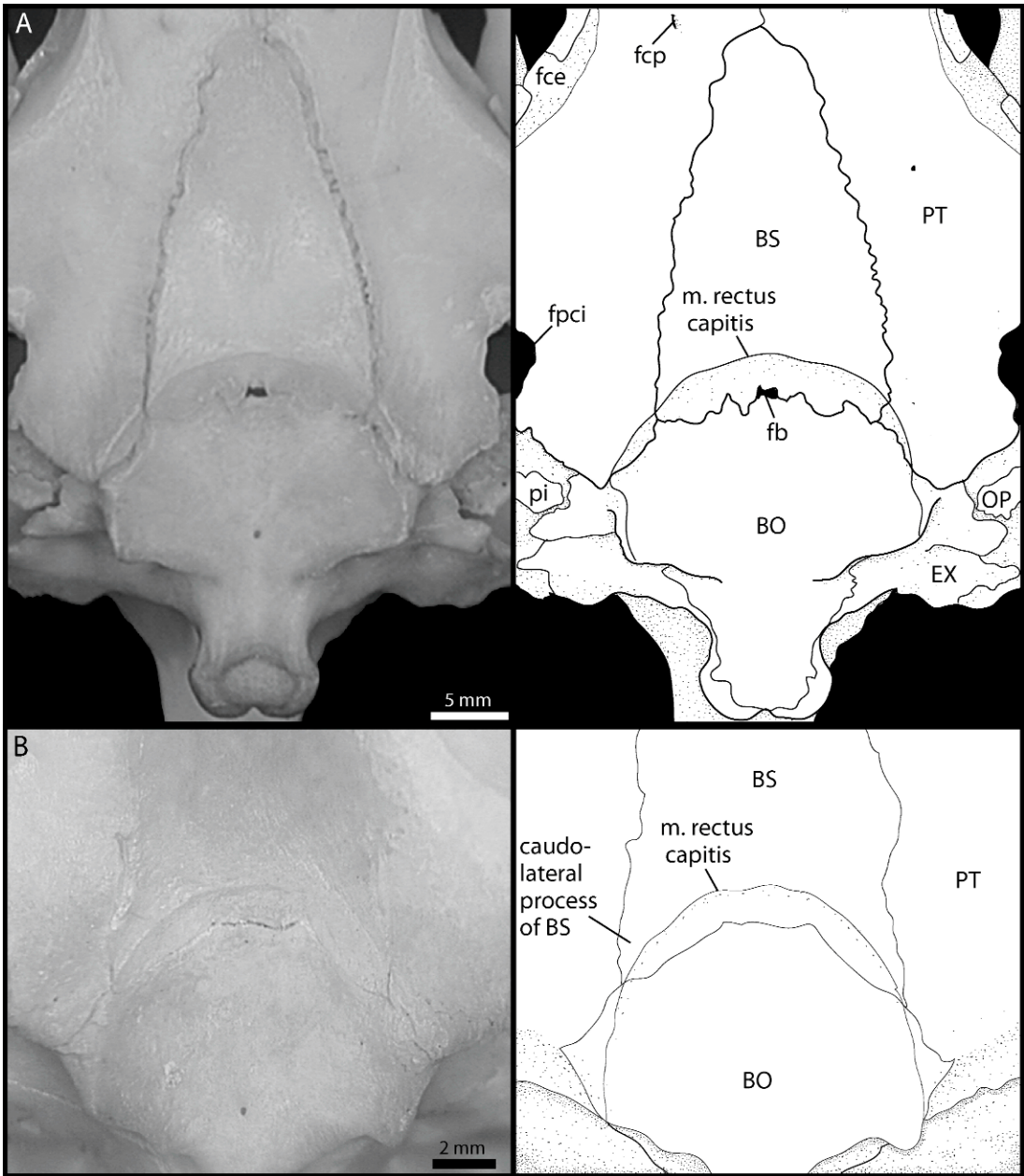


Fig. 31. Photographs and line drawings of the basicranial region of M-2984 (A) and M-2967 (B) showing the morphology of the parabasisphenoid-basioccipital suture. The suture in M-2984 is relatively straight and exhibits a remnant of the fenestra basicranialis (fb). The suture in M-2967 is rostrally curved and marked by two caudolateral processes of the parabasisphenoid. The fenestra basicranialis is obliterated. A rostrally convex ridge marking the insertion of the *M. rectus capitis* is present and has a rostral position on the parabasisphenoid in both specimens.

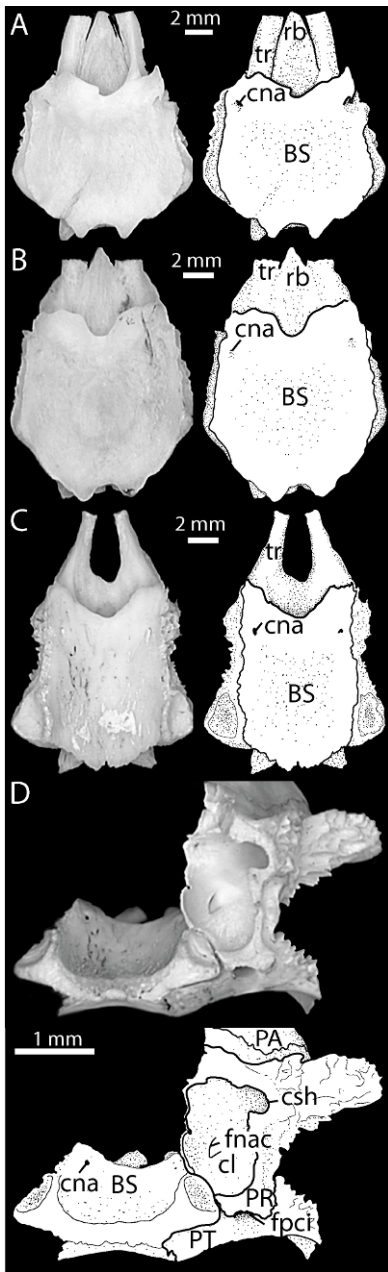


Fig. 32. Photographs and line drawings of the dorsal surface of the parabasisphenoid in M-2990 (A), M-2978 (B), and M-2982 (C), and a caudal view of the parabasisphenoid in articulation with the prootic and pterygoid in M-2982 (D). Note the variable development of the rostrum basisphenoidale (rb), trabeculae (tr), and the caudolateral concavities that contribute to the ventral margin of the cavum labyrinthicum (cl).

process to the trabeculae begins proximally at the rostral margin of the sella turcica and progresses distally over postnatal ontogeny. The trabeculae in all but the smallest specimens extend further anterior than the rostrum basisphenoidale (fig. 32C). The trabeculae angle rostromedially and nearly contact each other medially in two adults (M-2959 and M-2987).

The dorsum sellum overhangs and partly conceals the sella turcica from dorsal view even in the smallest specimens (a common feature in Testudines other than sea turtles; Shaffer et al., 1997). Clinoid processes are present but vary in their development. Not even in the largest specimens, however, are these processes comparable to those in taxa with extensive ossification of the pila prootica and long processus clinoides (e.g., *Terrapene* and *Emydura*; Gaffney, 1979). The canalis caroticus internus consistently enters the parabasisphenoid along a horizontal line that extends rostrally to the trabeculae and a transverse line that extends medially to a point just behind the rostro-dorsal margin of the dorsum sellum. This foramen lies below a relatively broad shelf that forms the articulation surface with the prootic (this shelf is not well developed in the smallest specimens). The foramen varies between 0.3 and 0.6 mm and corresponds closely in size with the foramen anterior canalis carotici interni that opens into the sella turcica. The distance between the right and left foramen is between 1.17 and 3.67 times larger than the width of the foramina themselves (table 5). This ratio is larger in adults and closely approximates the derived condition as scored by Shaffer et al. (1997) for chelonoids.

The paired abducens (VI) nerve enters the caudal surface of the dorsum sellae along its dorsolateral margins and exits the rostral surface beneath the process clinoides. The pathway through the dorsum sellum is rostromedial in juveniles and rostromedial in adults (table 5). The right abducens canal is not completed in bone in a single juvenile (M-2990), but rather extends along the lateral margin of the processus clinoides as a partly enclosed groove.

The caudodorsal surface of the parabasisphenoid contains (along its lateral margins)

a pair of relatively large, concave surfaces that are ventrolaterally angled and contribute to the ventromedial wall of the cavum labyrinthicum (Siebenrock, 1897; fig. 32C, D). These surfaces are undeveloped in 31.6% of the specimens, all of which are juveniles, are partly developed but not concave in 28.9%, which includes three relatively large juveniles and approximately one-third of the adults. The remaining 65.2% of the adults exhibit a surface that is fully developed and concave. No juveniles exhibit fully developed surfaces, indicating they are the product of relatively late postnatal transformations.

LOWER JAW: The lower jaw consists of the articular, angular, surangular, coronoid, and dentary (fig. 8). The apex of the lower jaw, formed by the dentary, is not broadly rounded (as described by Stephens and Wiens, 2003) but rather exhibits a distinct angle that does not appear to change appreciably during ontogeny. The rostroventral margin of the dentary, when viewed laterally, is broadly rounded and distinctly upturned into a hooked configuration that may be derived within Kinosternoidea (absent in dermatemydids). The extent and angle of the hook increases during growth (fig. 8). The ventromedial surface of the dentary is flattened in rostral view (McDowell, 1964). The triturating surface of the dentary is simple (comparable to the upper surface; see above). The lingual margin is distinct even in the smallest specimens and is separated from the underlying ramus of the dentary by a sharp angularity (Stephens and Wiens, 2003). The triturating surface is relatively narrow in smaller specimens but broadens and becomes more spatulate with growth. This expansion results in the lateral portion of the triturating surface distinctly overhanging the underlying mandibular ramus (Stephens and Wiens, 2003). In contrast, the rostromedial portion of the feeding surface expands to a position that is even with, but does not extend caudal to, the mandibular symphysis (Joyce and Bell, 2004). The rostromedial portion of the triturating surface is about 75% longer than the lateral portion is wide (table 5). Significant intra-specific variation in the relative proportions

of the triturating surface is present (table 5; see below).

The foramen dentofaciale majus is positioned in the rostral wall of a shallow fossa within the lateral surface of the dentary (fig. 7). The size of this foramen is highly variable, as is the number of foramina that penetrate the fossa. This variation does not exhibit an obvious correlation with overall size, although the depth and degree of sculpting of the adductor fossa does increase during postnatal ontogeny. The foramen dentofaciale majus never reaches the size found in some testudinoids (e.g., *Hardella thurjii* and *Morenia*; Joyce and Bell, 2004). The angular consistently extends farther rostrally than the prearticular. This portion of the angular provides a distinct contribution to the ventral margin of the sulcus cartilaginis meckelii in 93.5% of the specimens (including the smallest and largest individuals). In two adults (M-2959 and M-2987), the angular bends slightly ventral and does not contribute to this sulcus. This character has a relatively complex evolutionary history within cryptodires, but angular participation in the sulcus is plesiomorphic in kinosternoids (Gaffney and Meylan, 1988; Shaffer, 1997; Joyce and Bell, 2004).

The foramen intermandibularis caudalis is present, being formed completely within the angular in 72.0% of the SMRS including the largest specimens and between the angular and the prearticular in the remaining 28.0%, which includes the smallest specimens. Its position between these two bones is a right/left asymmetry in one juvenile and three adults.

The surangular consistently underlies the dentary along a simple suture that lacks the rostral strut of some tortoises (Crumly, 1982; Gaffney and Meylan, 1988; Joyce and Bell, 2004). The surangular contributes approximately the lateral one-fourth to one-third of the area articularis mandibularis (proportion increases dorsally; fig. 8). The dorsal surface of the surangular is penetrated by a relatively large foramen that lies just behind and slightly lateral to the dorsal opening of Meckel's fossa with which it communicates (fig. 8). In more mature specimens, the surangular extends dorsally around this opening, forming a tubelike structure. This

foramen is present in a small number of other cryptodires, including *Staurotypus* and *Terrapene* (Gaffney, 1979). The lateral surface of the surangular is penetrated by the foramen nervi auriculotemporalis, which communicates with the dorsal foramen and the fossa meckelii. In lateral view, this foramen is bounded rostrally by the caudal margin of the dentary in all but a single adult specimen (M-2966), whose foramen auriculotemporalis is formed entirely within the surangular.

The coronoid is robust but does not extend above the dentary contribution to the coronoid process (even in the most mature specimens where it is best developed). Although the relative height of this process increases postnatally, it is not tall relative to that of, for example, trionychids (Meylan and Gaffney, 1989). The coronoid process moves from a position approximately in the rostro-caudal midline of the lower jaw in the smallest specimens to a caudal position in adults (fig. 8); both in contrast to the rostral position present in trionychids (Meylan and Gaffney, 1989). The processus coronoideus lacks a caudally directed hook that is a derived feature of some tesudinoids (Bertl and Killam, 1983; Stephens and Wiens, 2003).

METRIC VARIATION

Descriptive statistics of the 25 linear measurements examined as continuous characters (fig. 3; numbers in text refer to this figure) are available in table 6. Principal components analysis of these measurements on 38 SMRS specimens indicates that over 80% of the variation within the sample falls along the first principal component (PC1; fig. 33). This skewed distribution, in combination with the consistently high correlation coefficients (i.e., all positive loadings) for each measurement with PC1 (table 7), indicates that this axis primarily reflects size variation. Juveniles tend to score low on PC1, but significant overlap with the adult subsample (fig. 34). There is no discernible separation of males and females along PC1 (or PC2 and PC3). All characters are significantly correlated with size at the 0.01 level based on their correlation coefficients. Greatest skull length (1; numbers refer to fig. 3) and condylobasal length (2) are most

closely correlated with PC1, whereas the width of the primary palate (13) and length of the pterygoid-ptyergoid suture (16) exhibit the lowest correlation coefficients for PC1 (table 7).

PC2 and PC3, which are uncorrelated with both PC1 and each other and therefore represent dimensions of shape variation, account for 4.7% and 3.7% of the sample variance, respectively (fig. 33). Juveniles and adults exhibit a relatively small degree of overlap along PC2 (fig. 34B). The variables with the largest positive correlation coefficients with PC2 include length of the pterygoid-ptyergoid suture (16), distance between the parabasisphenoid-basioccipital suture and vomer-ptyergoid suture (17), and length of the frontal-frontal suture (8; table 7). Variables exhibiting the largest negative loadings for PC2 include length of the otic chamber (18), width of the pterygoid waist (14), and width of the basicranium (20; table 7). The ventral surface of the skull therefore is a major source of shape variation within the SMRS and a primary contributor to morphometric separation between juvenile and adult specimens of *S. odoratus*. Little morphometric separation occurs among any of the examined subsamples along PC3 (fig. 34B). Measurements contributing most to what separation does occur along this axis are width of the primary palate (13, positive) and length of the lower triturating surface (22, negative; table 7).

When the mandibular characters are excluded, juveniles and adults exhibit a complete morphometric separation (fig. 34C), but this separation requires both axes and the morphometric separation resulting from shape variation recovered (PC2) in the first analysis (i.e., with jaws) largely disappears (fig. 34C). The shape of the lower jaw through postnatal ontogeny contributes significantly to total shape variation.

CRANIAL GROWTH

BIVARIATE ANALYSES: The rate of change for individual continuous characters 2–25 with respect to size (estimated using greatest length of the skull) is shown in table 8. The proportion of variation within each of the examined characters that can be attributed to overall size is estimated by the R^2 values,

TABLE 6
Descriptive Statistics for 25 Continuous Characters (Ch.; see fig. 4)
Statistics are provided for the following SMRS groups: total sample (T), juveniles (J), adults (A), males (M), and females (F).

Ch.	Group	N	SD	Mean	Range	Ch.	Group	N	SD	Mean	Range
1	T	31	25.494	4.8134	18.7–39.3	11	T	30	4.070	0.8330	2.9–5.3
	J	10	20.410	1.2784	18.7–22.4		J	10	3.140	0.2271	2.9–3.6
	A	21	27.914	3.8658	23.2–39.3		A	20	4.535	0.5932	3.7–5.3
	M	14	25.886	5.4183	19.8–39.3		M	14	4.214	0.8883	2.9–5.3
	F	17	25.171	4.3981	18.7–33.5		F	16	3.944	0.7882	2.9–5.1
2	T	31	21.729	3.9464	15.8–31.9	12	T	30	3.263	0.8996	2.0–6.5
	J	10	17.370	1.0843	15.8–19.3		J	10	2.510	0.2470	2.0–2.9
	A	21	23.805	2.9677	19.9–31.9		A	20	3.640	0.8708	2.6–6.5
	M	14	22.121	4.3640	16.9–31.9		M	14	3.364	1.0710	2.5–6.5
	F	17	21.406	3.6718	15.8–28.1		F	16	3.175	0.7434	2.0–4.8
3	T	31	15.281	2.7950	11.1–23.1	13	T	30	3.573	0.6416	2.6–4.8
	J	10	12.300	0.6733	11.1–13.5		J	10	2.860	0.1838	2.6–3.2
	A	21	16.700	2.2264	13.5–23.1		A	20	3.930	0.4589	3.1–4.8
	M	14	15.400	3.2251	12.0–23.1		M	14	3.586	0.6815	2.6–4.8
	F	17	15.182	2.4848	11.1–19.8		F	16	3.563	0.6270	2.6–4.8
4	T	30	9.717	1.8677	7.0–13.0	14	T	30	4.473	0.5866	3.1–5.2
	J	10	7.550	0.3864	7.0–8.3		J	10	3.870	0.4620	3.1–4.7
	A	20	10.745	1.3835	8.8–13.0		A	20	4.775	0.3697	4.0–5.2
	M	14	9.893	1.9297	7.4–13.0		M	14	4.414	0.5985	3.1–5.2
	F	16	9.563	1.8608	7.0–13.0		F	16	4.525	0.5905	3.5–5.2
5	T	32	3.800	0.5364	3.0–5.0	15	T	30	6.593	1.0485	4.8–8.6
	J	11	3.227	0.1348	3.0–3.5		J	10	5.440	0.3688	4.8–6.1
	A	21	4.100	0.4025	3.4–5.0		A	20	7.170	0.7505	6.0–8.6
	M	14	3.921	0.6229	3.0–5.0		M	14	6.614	1.0883	5.1–8.3
	F	18	3.706	0.4544	3.1–4.6		F	16	6.575	1.0479	4.8–8.6
6	T	32	3.013	0.5841	2.0–4.2	16	T	30	2.830	0.6109	1.5–3.9
	J	11	2.391	0.1921	2.0–2.8		J	10	2.530	0.5208	2.0–3.8
	A	21	3.338	0.4318	2.6–4.2		A	20	2.980	0.6084	1.5–3.9
	M	14	3.193	0.6245	2.4–4.2		M	14	2.936	0.5786	2.0–3.8
	F	18	2.872	0.5256	2.0–4.0		F	16	2.738	0.6417	1.5–3.9
7	T	33	5.715	1.2833	4.1–9.7	17	T	30	6.787	1.0285	5.1–9.0
	J	11	4.436	0.2420	4.1–4.9		J	10	5.840	0.4033	5.1–6.4
	A	22	6.355	1.0940	4.7–9.7		A	20	7.260	0.9110	5.6–9.0
	M	15	5.993	1.4023	4.3–9.7		M	14	7.007	1.2275	5.5–9.0
	F	18	5.483	1.1643	4.1–8.3		F	16	6.594	0.8087	5.1–8.4
8	T	30	3.900	0.6449	2.9–5.9	18	T	30	7.750	1.2440	5.9–9.8
	J	10	3.450	0.3408	2.9–4.1		J	10	6.400	0.3018	5.9–7.0
	A	20	4.125	0.6480	3.0–5.9		A	20	8.425	0.9380	6.9–9.8
	M	14	3.964	0.7919	2.9–5.9		M	14	7.793	1.2767	6.2–9.7
	F	16	3.844	0.5033	3.0–5.0		F	16	7.713	1.2553	5.9–9.8
9	T	33	4.927	0.7147	3.7–6.7	19	T	30	12.920	2.2998	9.8–18.9
	J	11	4.200	0.2490	3.7–4.6		J	10	10.730	0.6093	9.8–11.7
	A	22	5.291	0.5773	4.4–6.7		A	20	14.015	2.0275	11.3–18.9
	M	15	5.027	0.7968	4.0–6.7		M	14	13.200	2.6798	10.4–18.9
	F	18	4.844	0.6501	3.7–5.9		F	16	12.675	1.9659	9.8–16.2
10	T	30	2.037	0.5660	1.2–3.6	20	T	30	6.053	0.9350	3.9–7.6
	J	10	1.460	0.1955	1.2–1.7		J	10	5.040	0.5232	3.9–5.9
	A	20	2.325	0.4564	1.7–3.6		A	20	6.560	0.6278	5.5–7.6
	M	14	2.121	0.6179	1.3–3.6		M	14	6.13	0.8820	4.9–7.6
	F	16	1.963	0.5252	1.2–2.9		F	16	5.981	1.0021	3.9–7.4

TABLE 6
(Continued)

Ch.	Group	N	SD	Mean	Range
21	T	38	2.355	0.7020	1.5–5.0
	J	14	1.793	0.2235	1.5–2.2
	A	23	2.735	0.6436	2.0–5.0
	M	17	2.594	0.8212	1.5–5.0
	F	22	2.132	0.5393	1.5–3.7
22	T	38	3.187	1.0923	1.8–7.4
	J	15	2.347	0.5125	1.8–3.5
	A	23	3.735	1.0219	2.5–7.4
	M	17	3.582	1.3083	1.8–7.4
	F	22	2.818	0.7878	1.8–4.7
23	T	32	13.784	2.5835	9.6–21.2
	J	12	11.250	0.8827	9.6–12.5
	A	20	15.305	1.9869	12.8–21.2
	M	16	14.163	2.9502	9.6–21.2
	F	17	13.182	2.3104	9.6–17.9
24	T	33	13.370	2.3787	9.3–19.5
	J	12	10.950	0.8152	9.3–12.3
	A	21	14.752	1.7798	12.0–19.5
	M	17	13.494	2.6267	9.3–19.5
	F	17	13.006	2.3012	9.3–17.8
25	T	38	4.850	1.3121	3.1–9.1
	J	15	3.667	0.3848	3.1–4.7
	A	23	5.622	1.1062	4.0–9.1
	M	17	5.141	1.5516	3.1–9.1
	F	21	4.614	1.0622	3.3–7.1

which vary widely between approximately 24 and 99% (e.g., length of the pterygoid-ptyergoid suture (16) and condylobasal length (2), respectively; see fig. 35). Nine of the 24 continuous characters exhibit R^2 values that exceed 90%. Overall, the rates of change during postnatal ontogeny tend toward negative allometry with the coefficient of variation being greater than 1.0 in only six characters based on least squares regression and nine characters with reduced major axis regression (RMA). The coefficients of allometry produced under the two regression techniques are in general agreement; therefore, it follows that conclusions regarding relative growth within the skull also agree. These coefficients are higher (both positively and negatively) under RMA than least squares for all variables with the exception of the width of the lower triturating surface along the mandibular symphysis (22). Slightly higher values for RMA relative to least squares regression are expected based on previous studies (e.g., Giannini et al., 2004).

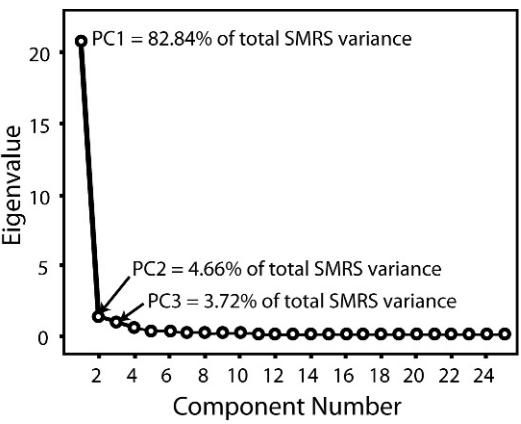


Fig. 33. Scree plot showing the distribution of eigenvalue scores for each principal component derived from the analysis of 25 continuous characters from the skull and lower jaws of *Sternotherus odoratus* from the SMRS. PC1, which generally represents size, constitutes a large percentage (over 80%) of the total sample variance. The first three principal components account for more than 90% of the total sample variance.

Coefficients of allometry based both on least squares and RMA agree that condylobasal length (2), greatest skull width (3), skull height (4), height of the apertura narium externa (6), and width of the zygomatic arch (11) scale isometrically with greatest skull length (table 7). A total of 12 (least squares) and 11 (RMA) characters exhibit slopes that diverge significantly from the expected condition of isometry ($b_1=1$) when the critical value is assessed at a 0.01 confidence level. Only one of these characters, greatest height of the lower jaw (25) scales with significantly positive allometry under both regression models. Other characters that scale with significant levels of positive allometry based on RMA are postorbital bar width (10), and width of the upper (12) and lower (21) triturating surfaces. These variables exhibit marginally significant positive values under least squares. Length of the lower feeding surface along the midline of the jaw (22) increases in relative size during growth at a significant level under least squares but only at a moderately positive rate under RMA.

Characters that significantly decrease in relative size during postnatal growth (negative allometry) based on both bivariate regression models are apertura narium ex-

TABLE 7
Component Matrix Showing Correlation Coefficients (R; loadings) of 25 Continuous Characters (Ch.) from Skull and Mandible of *Sternotherus odoratus* from the SMRS

Correlation coefficients are for the first three principal components derived from principal components analyses. The first analysis included the continuous characters from the lower jaw; the second analysis excluded them. See text for character descriptions.

Ch.	With lower jaws			Without lower jaws		
	PC1	PC2	PC3	PC1	PC2	PC3
1	0.993	0.023	−0.037	0.986	0.012	−0.069
2	0.993	0.003	0.001	0.986	0.009	−0.040
3	0.989	−0.010	−0.013	0.981	−0.009	−0.031
4	0.965	−0.177	0.043	0.976	−0.125	0.035
5	0.949	0.002	0.019	0.953	0.041	−0.075
6	0.955	−0.029	−0.025	0.955	−0.027	−0.024
7	0.951	0.123	−0.138	0.945	0.071	−0.205
8	0.833	0.298	−0.086	0.752	0.278	−0.213
9	0.957	−0.037	−0.066	0.952	−0.053	−0.074
10	0.906	−0.128	−0.198	0.907	−0.177	−0.153
11	0.921	−0.259	0.111	0.925	−0.164	0.117
12	0.927	0.075	−0.225	0.918	0.000	−0.244
13	0.591	−0.044	0.627	0.613	0.171	0.689
14	0.806	−0.281	0.290	0.837	−0.130	0.255
15	0.948	−0.195	0.079	0.961	−0.122	0.052
16	0.528	0.666	0.377	0.541	0.763	0.010
17	0.869	0.323	0.231	0.875	0.394	0.042
18	0.937	−0.295	0.085	0.954	−0.214	0.109
19	0.908	−0.107	−0.038	0.906	−0.102	−0.009
20	0.896	−0.232	0.046	0.904	−0.175	0.059
21	0.926	0.189	−0.161	na	na	na
22	0.894	0.250	−0.240	na	na	na
23	0.982	0.040	−0.099	na	na	na
24	0.980	−0.046	−0.064	na	na	na
25	0.975	0.133	−0.076	na	na	na

terna width (5), orbit width (9), width of the pterygoid waist (14), width of palate (15), length of the pterygoid-ptyergoid suture (16), distance between the parabasisphenoid-basi-occipital and vomer-ptyergoid sutures (17), and length of the otic capsule (18). Length of the frontal-frontal suture (8), skull width between apices of the squamosal (19), basi-cranium width (20), and lower jaw length (23) all trend towards negative allometry (al-though not at significant levels under RMA). Orbit width (9) exhibits the highest t-value of those expressing negative allome-try, followed closely by interorbital width (7) (−5.270 and −5.098, respectively).

MULTIVARIATE ANALYSES: Observed mul-tivariate coefficients of allometry varied between 0.106 (8, length of the frontal-frontal suture) and 0.275 (22, width of the lower triturating surface along the midline), when

expected coefficient under isometry = 0.200 (table 9). Other variables exhibiting relatively large departures from the expected coefficient under isometry, and thus suggesting positive allometry, include postorbital bar width (10), lower jaw height (25), and width of the lower triturating surface (21; table 9). Additional characters with relatively large values sugges-tive of negative allometry include width of the pterygoid waist (14) and length of the pterygoid-ptyergoid suture (16; table 9). The smallest departures from isometry are found in interorbital width (7) and greatest skull length (1). Average estimated bias based on jackknife values calculated from trimmed and untrimmed values both were small (0.0013 and 0.0012, respectively). The average stan-dard deviation is only slightly larger for the untrimmed values relative to the trimmed dataset (0.0041 and 0.0035, respectively),

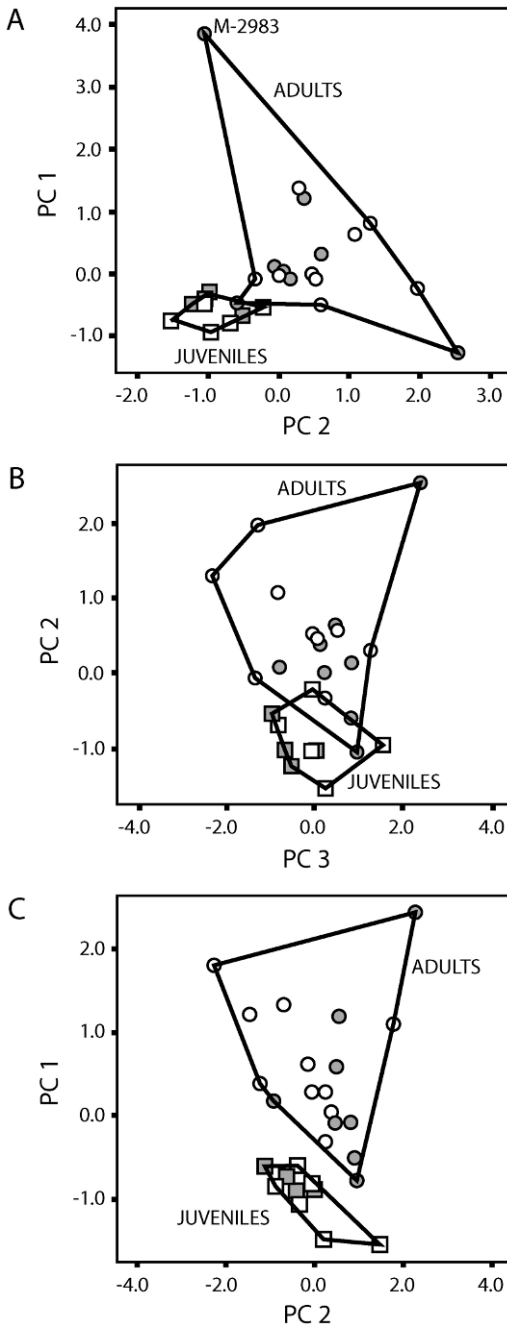


Fig. 34. Plots of principal components scores derived from 25 continuous characters for *Sternotherus odoratus* from the SMRS. Plots **A** and **B** represent scores based on 25 continuous characters from the skull and lower jaws. Plot **C** represent principal component scores derived from 20 continuous characters from the skull only. Circles

which indicates that trimming the largest and smallest values from each of the examined variables did not significantly affect the allometry statistics.

Growth trends based on the distribution of the 99% confidence intervals compare closely between untrimmed and trimmed datasets. Of the 25 examined continuous characters, 19 (76%) exhibit significant levels of negative allometry based on both datasets (table 9). The highest levels of negative allometry were found in the length of the frontal-frontal suture (8), width of the pterygoid waist (14), and length of the pterygoid-ptyergoid suture (16). Six of the 25 examined characters (24%) exhibit significantly positive multivariate coefficients of allometry based on the untrimmed dataset. These characters include interorbital width (7), postorbital bar width (10), width of the upper (12) and lower triturating surfaces (21), width of the lower triturating surface along the midline of the jaw (22), and lower jaw height (25). The highest levels of positive allometry are found in the width of the lower triturating surface along the midline of the lower jaw (22). Width of the upper triturating surface exhibits isometry when only the trimmed data are considered. General interpretations of growth based on trajectories revealed from the four methods utilized in this study are largely congruent (table 10). For example, none of the characters was interpreted to have negative allometry based on one method but positive allometry based on a second method; however, only seven of the 25 variables were interpreted as having the same ontogenetic trajectory based on all four analyses of growth. These characters include width of the apertura narium externa (5), orbit length (9), width of the pterygoid waist (14), palatal width (15), distance between the parabasisphenoid-basioccipital suture and the pterygoid-vomer suture (17), otic capsule length (18), and lower jaw height (25). Only lower jaw height (25) is positively allometric based on all four methods (table 10). Bivar-

←

represent adults. Squares represent juveniles. Shaded symbols represent males. The morphometric space occupied by juveniles and adults are delimited by minimum polygons.

TABLE 8
Results of Bivariate Allometry Analyses on *Sternotherus odoratus* from the SMRS

Characters (Ch.) refer to figure 4. Expected coefficient of allometry under isometry is 1.0 for all variables. Abbreviations: *N*, sample size; *R*², adjusted coefficient of determination; *b*₁, coefficient of allometry; SE, standard error for *b*₁; *t*_{iso}, *t*-value for *b*₁; GT, growth trend; =, null hypothesis of isometry not rejected; +/−, positive or negative allometry at *p* < 0.01; +/−_m, marginal positive or negative allometry at 0.05 > *p* > 0.01. Significance based on the distribution of the calculated *t*-score under a normal probability curve with degrees of freedom = *N* − 2.

Ch.	<i>N</i>	<i>R</i> ²	Least squares				Reduced major axis			
			<i>b</i> ₁	SE	<i>t</i> _{iso}	GT	<i>b</i> ₁	SE	<i>t</i> _{iso}	GT
2	31	0.990	0.974	0.018	−1.444	=	0.979	0.018	−1.105	=
3	31	0.976	0.958	0.028	−1.500	=	0.970	0.028	−0.976	=
4	29	0.946	0.957	0.044	−0.977	=	0.984	0.044	−0.372	=
5	30	0.861	0.682	0.052	−6.115	−	0.735	0.052	−5.098	−
6	30	0.886	0.943	0.064	−0.891	=	1.001	0.064	0.016	=
7	31	0.909	1.087	0.064	1.359	=	1.140	0.064	2.188	+ _m
8	29	0.449	0.566	0.121	−3.587	−	0.845	0.121	−1.281	=
9	31	0.904	0.730	0.113	−6.136	−	0.768	0.044	−5.27	−
10	29	0.814	1.292	0.119	2.454	+ _m	1.433	0.119	3.639	+
11	29	0.784	0.953	0.096	−0.490	=	1.077	0.096	0.802	=
12	29	0.865	1.209	0.092	2.272	+ _m	1.300	0.092	3.261	+
13	29	0.908	0.916	0.056	−1.500	=	1.483	0.186	2.597	+ _m
14	29	0.687	0.606	0.079	−4.987	−	0.731	0.079	−3.405	−
15	29	0.897	0.781	0.051	−4.294	−	0.825	0.051	−3.431	−
16	29	0.237	0.602	0.208	−1.914	=	1.237	0.208	1.139	=
17	29	0.703	0.640	0.080	−4.500	−	0.764	0.080	−2.95	−
18	29	0.893	0.781	0.052	−4.212	−	0.826	0.052	−3.346	−
19	29	0.816	0.794	0.073	−2.820	−	0.879	0.073	−1.663	=
20	29	0.719	0.701	0.084	−3.560	−	0.826	0.084	−2.067	− _m
21	31	0.834	1.252	0.104	2.420	+ _m	1.371	0.104	3.567	+
22	31	0.799	1.367	0.140	2.621	+ _m	1.088	0.048	1.833	=
23	28	0.956	0.891	0.038	−2.868	−	0.918	0.039	−1.972	=
24	28	0.941	0.896	0.044	−2.364	− _m	0.924	0.044	−1.738	=
25	31	0.949	1.281	0.055	5.109	+	1.315	0.055	5.727	+

iate methods tended to be more conservative in that a much higher number of characters were interpreted as exhibiting isometric growth trajectories than with multivariate analysis. This undoubtedly results from the fact that the bivariate analyses are considering the trajectories of each measurement relative only to greatest skull length in contrast to the multivariate methods, which incorporate size as a latent variable affecting all characters simultaneously.

DISCUSSION

DISCRETE VARIATION

I scored 144 discrete characters for each of the 38 SMRS specimens. One-hundred fourteen of these characters were drawn from

previously published phylogenetic analyses of turtle interrelationships, including those applied previously to the resolution of phylogenetic relationships within Kinosternoidea. Over 45% of these characters exhibited some level of variation. Approximately 31% of the characters drawn from phylogenetic analyses exhibited some level of variation.

Thirty-five of the 113 (31.0%) discrete characters drawn from previous phylogenetic analyses exhibit some level of intrapopulation- al variation (appendix 3). The average level of variation for these 35 characters based on the variation score is slightly greater than 20% (table 11). These variation scores approach a bimodal distribution when placed in bins of 5%, with 48.6% of the characters varying at levels between 5 and 15% and 28.6% of the characters varying at levels between 30 and

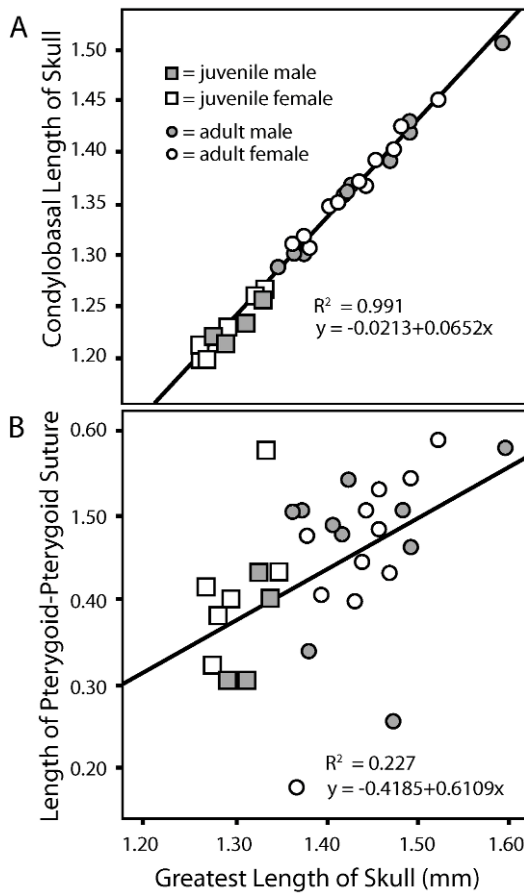


Fig. 35. Examples of allometry trends in *Sternotherus odoratus* based on least squares regression model showing the best (A) and worst (B) fitted regressions on greatest length of the skull. The data are in millimeters and are log transformed.

40%. Thirty-one of the 32 discrete characters that are not drawn from phylogenetic studies exhibit some level of variation (table 11). This high proportion is not surprising since these characters were included largely because variation in their expression was observed. The mean variation score among these characters is 34.1, approximately 14% higher than that of the variable published characters. The percentage of examined discontinuous characters exhibiting variation within the SMRS increases to 45.5% when all variable characters are considered together. The inclusion of the unpublished characters increases the relative

proportion of characters with high levels of variation and raises the average variation score to slightly over 25.

ONTOGENY: The mean variation score is lower in juveniles than adults for both published characters alone and for all discrete characters (table 11). However, these differences may simply reflect the larger number of adults. They are not significant based on paired-samples t-tests ($\alpha = 0.05$) for the published characters alone ($t = -0.824$; $N = 35$) or when they are combined with the variable unpublished characters ($t = -1.487$; $N = 66$). Juveniles expressed higher variation scores in 17 of the 35 variable published characters (48.6%) and 18 of the 31 variable unpublished characters (58.1%). These data, therefore, support no specific trends regarding an overall increase or decrease in levels of discrete cranial variation with age.

Despite the statistical similarity in the overall levels of variation between juveniles and adults, certain characters do show distinctly different variation scores between ontogenetic subsamples. Variation scores for 16 of the 35 variable published characters (45.7%) differ between juveniles and adults at levels exceeding 10% (table 12). In nine of these characters (11, 41, 42, 76, 78, 83, 87, 88, and 108) (25.7%), the difference in variation scores exceeds 20%, and for five characters (14.3%) the difference in variation scores exceeds 30% (table 12). These five characters include presence of avomer-maxillae contact (41), presence of a small vomerine foramen (42), relative size of perilymphatic fenestra (83), and the morphology (87) and shape (88) of the basisphenoid-basioccipital suture. When all variable discrete characters are considered, the characters whose variation scores differ between juveniles and adults by 10% or more increase modestly to 50%, those that differ by 20% or more increase to 32.1%, and those that differ by 30% or more increase slightly to 16.7% (table 11).

The variation score for juveniles exceeds that for adults in 10 of the 16 published characters in which the score differed between age classes by 10% or more, and juveniles exceed adults in four of the five published characters where the score difference exceeds 30%. However, overall support for a trend in which juveniles exhibit higher

TABLE 9
Results of Multivariate Analysis of Cranial Allometry in *Sternotherus odoratus* from the SMRS

Characters (Ch.) refer to figure 3. Abbreviations: =, null hypothesis of isometry not rejected; +/−, positive or negative allometry at $p < 0.01$. The first three columns are results based on all data. Remaining columns show jackknife results using untrimmed and trimmed sets of pseudovectors (see text). Allometry coefficient is the first eigenvector per variable. Resampled coefficient is the first-order jackknife value. Bias is the difference between the resampled and observed allometry coefficients.

Ch.	Expected isometry coefficient	Observed allometry coefficient	Observed departure	Untrimmed values				Trimmed values			
				Resampled allometry coefficient	Bias	99% confidence interval	Growth trend	Resampled allometry coefficient	Bias	99% confidence interval	Growth trend
1	0.200	0.191	−0.009	0.190	−0.0007	0.187–0.194	−	0.191	−0.0005	0.188–0.193	−
2	0.200	0.186	−0.014	0.185	−0.0006	0.182–0.189	−	0.186	−0.0005	0.183–0.188	−
3	0.200	0.184	−0.016	0.183	−0.0012	0.180–0.186	−	0.183	−0.0010	0.180–0.186	−
4	0.200	0.187	−0.013	0.184	−0.0026	0.180–0.189	−	0.185	−0.0024	0.181–0.188	−
5	0.200	0.133	−0.067	0.132	−0.0013	0.129–0.134	−	0.132	−0.0012	0.130–0.134	−
6	0.200	0.183	−0.017	0.182	−0.0015	0.177–0.186	−	0.182	−0.0013	0.178–0.186	−
7	0.200	0.207	0.007	0.206	−0.0006	0.202–0.211	+	0.207	−0.0002	0.203–0.210	+
8	0.200	0.106	−0.094	0.110	−0.0037	0.104–0.116	+	0.110	0.0036	0.105–0.115	−
9	0.200	0.139	−0.061	0.138	−0.0013	0.135–0.141	−	0.138	−0.0012	0.135–0.140	−
10	0.200	0.255	0.055	0.253	0.0020	0.248–0.259	+	0.253	−0.0019	0.248–0.258	+
11	0.200	0.192	−0.008	0.190	0.0019	0.187–0.193	−	0.190	−0.0020	0.187–0.193	−
12	0.200	0.233	0.033	0.233	−0.0002	0.228–0.238	+	0.233	0.0000	0.194–0.237	≡
13	0.200	0.173	−0.027	0.173	−0.0002	0.170–0.176	−	0.173	−0.0000	0.170–0.176	−
14	0.200	0.114	−0.086	0.114	0.0004	0.111–0.118	−	0.115	0.0007	0.112–0.117	−
15	0.200	0.153	−0.047	0.151	−0.0022	0.147–0.155	−	0.151	−0.0020	0.148–0.154	−
16	0.200	0.116	−0.084	0.115	−0.0013	0.108–0.122	−	0.115	−0.0012	0.110–0.120	−
17	0.200	0.128	−0.072	0.126	−0.0021	0.122–0.130	−	0.126	−0.0019	0.123–0.130	−
18	0.200	0.153	−0.047	0.151	−0.0019	0.148–0.154	−	0.151	−0.0019	0.149–0.154	−
19	0.200	0.155	−0.045	0.154	−0.0007	0.151–0.158	−	0.154	−0.0006	0.152–0.157	−
20	0.200	0.143	−0.057	0.141	0.0021	0.137–0.145	−	0.141	−0.0019	0.138–0.144	−
21	0.200	0.242	0.042	0.244	−0.0023	0.239–0.250	+	0.244	0.0022	0.239–0.249	+
22	0.200	0.275	0.075	0.275	−0.0004	0.269–0.280	+	0.275	−0.0003	0.270–0.280	+
23	0.200	0.176	−0.024	0.175	−0.0009	0.172–0.179	−	0.175	−0.0007	0.172–0.178	−
24	0.200	0.175	−0.025	0.176	0.0006	0.172–0.179	−	0.176	0.0009	0.172–0.179	−
25	0.200	0.245	0.045	0.245	−0.0003	0.242–0.249	+	0.245	0.0004	0.242–0.249	+

TABLE 10
Gross Comparisons of Growth Trends in the Skull of *Sternotherus odoratus*

Abbreviations: =, isometric; +/-, positive or negative allometry at $p < 0.01$; LS, least squares regression; RMA, reduced major axis.

Ch.	Bivariate		Multivariate	
	LS	RMA	Untrimmed	Trimmed
1	na	na	—	—
2	=	=	—	—
3	=	=	—	—
4	=	=	—	—
5	—	—	—	—
6	=	=	—	—
7	=	=	+	+
8	—	=	—	—
9	—	—	—	—
10	=	+	+	+
11	=	=	—	—
12	=	+	+	=
13	=	=	—	—
14	—	—	—	—
15	—	—	—	—
16	—	—	=	=
17	—	—	—	—
18	—	—	—	—
19	—	=	—	—
20	—	=	—	—
21	=	+	+	+
22	=	=	+	+
23	—	=	—	—
24	=	=	—	—
25	+	+	+	+

levels of discrete character variation is tenuous at best. The only possible exception is among those characters exhibiting the most dramatic change in variation (over 30%) for which it appears that variation is decreasing with growth.

There are no obvious correlations between those nine characters exhibiting variation score differences between age classes of 20% or more and the cranial partitions from which they are derived. Characters 11, 41, 42, and 108 are influenced predominantly by dermatocranial elements, whereas characters 76, 78, 83, 87, and 88 are neurocranial. None of the small number of splanchnocranial characters exhibit these relatively large ontogenetic differences in variation levels. Of the 12 unpublished characters exhibiting a difference in variation scores that exceeds 20% between juveniles and adults, nine (114, 115, 116, 127, 128, 129,

TABLE 11
Descriptive Statistics for Published, Unpublished, and Total Characters for Turtles Exhibiting Variation within the SMRS

Min. = minimum variation score, max. = maximum variation score.

	Min.	Max.	Mean
Published Characters ($N = 35$)			
Total	26.0	45.7	20.04
Juveniles	0.0	50.0	16.54
Adults	0.0	47.6	19.13
Males	0.0	50.0	22.46
Females	0.0	47.4	20.43
Unpublished Characters ($N = 31$)			
Total	2.9	50.0	34.10
Juveniles	0.0	50.0	21.16
Adults	0.0	50.0	25.91
Males	0.0	50.0	26.92
Females	0.0	47.6	26.67
All Characters ($N = 66$)			
Total	2.6	50.0	25.02
Juveniles	0.0	50.0	18.71
Adults	0.0	50.0	22.32
Males	0.0	50.0	24.07
Females	0.0	47.6	23.36

131, 132, and 133) are dermatocranial, two neurocranial (closure of the foramen medialis nervi glossopharyngei, 134, and presence of a concavity in the dorsolateral surface of the basioccipital, 136), and one splanchnocranial (development of the processus pterygoideus of the quadrate, 122). A clear pattern is similarly lacking when these characters are distributed based on the functional/topological partitioning of the skull. One dermal roofing, two palatal, five braincase, and one lower jaw character(s) are drawn from the published pool of variable characters (no palatoquadrate). Seven of the unpublished characters exhibiting this large difference are formed within the palatoquadrate region, with three, two, one, and one character(s) derived from the dermal roofing, braincase, palate, and lower jaw, respectively.

A number of characters differ in the state exhibited by the majority of juveniles and adults or contain a state exhibited either in juveniles or adults (but not both)—differences that are interpreted here as ontogenetic changes in postnatal morphology. Published phylogenetic characters include general expan-

TABLE 12
Differences in Variation Scores between Juveniles and Adults (J–A) and between Males and Females (M–F) for Discrete Characters Exhibiting Variation within the SMRS

Negative values refer to differences in which the juveniles and males have larger variation scores than adults and females, respectively. MW refers to two-tailed significance values of the Mann-Whitney nonparametric tests for two independent samples (based on Z scores). Significance is placed at 0.05, with significant values noted in boldface.

Ch.	J–A	MW	M–F	MW
Published (<i>N</i> = 35)				
5	–18.2	0.137	2.2	0.848
6	0.0	1.000	–4.4	0.663
11	22.8	0.138	–14.5	0.320
20	6.5	0.717	–3.6	0.833
28	3.3	0.711	–11.8	0.177
29	–6.3	0.651	–4.0	0.419
30	–9.1	0.252	12.5	0.109
32	1.4	0.940	13.5	0.444
33	10.5	0.574	–5.5	0.760
35	7.7	0.193	6.7	0.248
41	–33.3	0.043	14.3	0.366
42	–30.4	0.029	7.7	0.564
43	8.0	0.519	2.8	0.804
44	–19.9	0.314	10.4	0.576
45	–16.8	0.185	–0.8	0.881
48	–9.1	0.252	1.9	0.848
55	8.4	0.508	24.4	0.048
59	–4.3	0.376	5.9	0.641
65	–19.0	0.146	–10.9	0.393
66	0.0	0.197	8.3	0.390
67	2.4	0.758	1.1	0.879
69	6.7	0.216	5.9	0.266
70	–4.3	0.419	5.9	0.266
75	4.1	0.663	1.2	0.889
76	23.5	0.048	–25.0	0.147
77	18.9	0.262	–1.7	0.919
78	–22.3	0.563	21.7	0.251
83	40.0	0.112	–6.7	0.860
87	–43.5	0.000	23.3	0.138
88	–40.9	0.002	18.0	0.189
95	–5.9	0.599	–8.3	0.450
97	0.9	0.962	–1.7	0.851
106	–4.3	0.419	5.9	0.266
108	20.0	0.000	–25.3	0.101
110	–11.8	0.230	2.1	0.797
Unpublished (<i>N</i> = 31)				
114	–29.1	0.099	3.5	0.733
115	–35.0	0.001	12.0	0.498
116	–21.7	0.064	–14.1	0.217
117	10.0	0.590	4.4	0.799
118	–7.8	0.645	–9.7	0.554
120	–5.9	0.580	1.8	0.865

TABLE 12
(Continued)

Ch.	J–A	MW	M–F	MW
121	–16.0	0.146	2.5	0.838
122	–43.5	0.000	12.6	0.422
123	5.0	0.733	–15.8	0.257
124	–8.1	0.294	17.4	0.136
125	–3.3	0.412	–1.7	0.749
126	2.6	0.895	2.4	0.595
127	–23.8	0.097	1.8	0.577
128	–21.1	0.125	–18.2	0.159
129	–33.3	0.197	33.3	0.197
130	6.7	0.870	–6.7	0.870
131	–33.3	0.197	33.3	0.197
132	40.0	0.237	–40.0	0.393
133	20.0	0.040	–16.7	0.127
134	22.6	0.022	–14.6	0.343
135	2.9	0.030	–13.5	0.092
136	50.0	0.109	–8.3	0.789
137	–4.5	0.460	6.7	0.260
138	7.3	0.680	7.3	0.418
139	–14.8	0.001	8.9	0.288
140	–6.7	0.610	–6.7	0.610
141	0.0	1.000	13.0	0.217
142	–14.8	0.001	8.9	0.288
143	15.0	0.419	10.2	0.576
144	–5.6	0.395	–6.0	0.333

sion of adductor chamber resulting in a tall and rounded crista supraoccipitalis (76), subacute caudal termination of crista supraoccipitalis (77), apex of crista supraoccipitalis positioned rostrally (78), relative (108) and general (106) expansion of lower triturating surface; ossification of the primary palate resulting in maxillae-vomer contact (41), exclusion of vomer for foramen praepalatium (33), vomerine foramen (42), ossification of the ascending process of the palatoquadrate cartilage so that the epipterygoid contributes to the foramen nervi trigemini (59), closure of the fenestra basicranialis posterior (87), increasing diameter of the fenestra perilymphatica relative to the foramen posterior canalis carotici interni (83), and an increasingly convex lateral margin of the parabasisphenoid (97). Significant variation in the expression of character states between juveniles and adults, as revealed by Mann-Whitney nonparametric tests for two independent samples, is present in six of these published characters (41, 42, 76, 87, 88, and 108; table 12). Each of these phylogenetic characters also exhibits large ontogenetic differences in variation scores (see above).

Stephens and Wiens (2003) found that a rounded crista supraoccipitalis was the non-variable condition in both *Sternotherus odoratus* and *Kinosternon subrubrum* and the most common condition among testudinoids. The expanded and rounded crista supraoccipitalis present in the largest SMRS *S. odoratus* is more exaggerated than the rounded crest of such testudinoids as *Emys orbicularis* (Bojanus, 1819–1821) and *Pseudemys texana* and the kinosternoids *Emarginachelys* (Whetstone, 1978) and *Dermatemys mawii* (Bienz, 1895). This distribution suggests that the expanded crista supraoccipitalis in *S. odoratus* is the product of a derived transformation at some position within Kinosternoidea but one that may be highly plastic within turtles (e.g., also present in the chelydrid *Macrochelys temminckii*; Sheil, 2005). The extant cryptodire with a crista supraoccipitalis most similar to that of mature *S. odoratus* may be the enigmatic big-headed turtle, *Platysternon megacephalum*; the phylogenetic position of *P. megacephalum* is long debated, but it may be the sister taxon of emydids within testudinoids (Parham et al., 2006). It may be noteworthy that the crista supraoccipitalis in the extant emydid *Pseudemys texana*, although somewhat rounded in adult specimens, becomes increasingly straight during the later stages of postnatal growth (Bever, 2008). This suggests that not only does the adult shape of the crest have a complex evolutionary history within cryptodiran turtles, but that the growth trajectories resulting in these adult shapes have equally complex evolutionary patterns. The phylogenetic histories of the adult shapes and the growth trajectories that produce them are not necessarily congruent and it is unclear whether a phylogenetic analysis of the growth trajectories of this, or other, structures would result in a less homoplastic phylogenetic signal—but it is possible. A rounding of the caudal terminus and a rostral shift in the position at which the crest slopes ventrally are both restricted to the largest SMRS specimens and thus correlated with a general postnatal expansion of the adductor chamber. A subacute caudal terminus and a caudal position of the ventral slope are both morphologies that likely would be considered apomorphic within Kinosternoidea—making

the recognition that these character states are retained relatively late in the postnatal ontogeny of *S. odoratus* important for interpreting the phylogenetic implications of these conditions in single specimens.

A relatively expanded rostromedial portion of the triturating surface is a common adult character state in derived cryptodires that likely is the plesiomorphic condition for both Kinosternoidea and Testudinoidea (Stephens and Wiens, 2003). The opposing condition, where the lateral triturating surface is relatively expanded, transforms as a derived character state within both Deirochelyinae and Bataguridae (Stephens and Wiens, 2003), but also is present in the kinosternoid *Dermatemys mawii*—which complicates optimization of this character at the base of the kinosternid tree. A spatulate triturating surface of the dentary is present only in the largest and most mature SMRS specimen, indicating that this expansion occurs late in postnatal ontogeny. (A spatulate surface is derived within cryptodires; Gaffney, 1979; Stephens and Wiens, 2003.) A vomer-maxilla contact, which occurs largely through the postnatal expansion of the maxilla on the primary palate, is a common adult morphology among kinosternids but is absent in *Dermatemys*. The postnatal acquisition of this contact, therefore, is likely derived within Kinosternoidea, as it is within Testudinoidea (e.g., *Cuora amboinensis*, *Testudo graeca*; Joyce and Bell, 2004). Whereas the smallest and largest specimens clearly exhibit a foramen praepalatinum that is fully formed within the premaxillae, to the exclusion of the vomer, there does appear to be considerable variation in the presence or timing of this remodeling of the rostromedial portion of the palate during postnatal ontogeny. Participation of the vomer in the foramina praepalatinum (visible ventrally) is the plesiomorphic condition for kinosternids based on the morphology of *Dermatemys mawii* and *Staurotypus triporcatus* (Bienz, 1895; Meylan and Gaffney, 1989; see Joyce and Bell, 2004 for the distribution of these morphologies within testudinoids). This remodeling of the primary palate relatively late in postnatal ontogeny also determines whether the paired foramen praepalatinum is visible in ventral view or enclosed in a short canal (32); a

foramen that is visible ventrally is the plesiomorphic condition for Kinosternoidea.

Continued ossification of the endochondral elements of the splanchno- and neurocranium results in a number of phylogenetically informative transformations. An expansion of the epipterygoid so that it contributes to the trigeminal foramen is absent in most cryptodires, including *Dermatemys mawii*, and therefore is likely a derived feature within Kinosternoidea. The presence of a medial notch in the basisphenoid-basioccipital suture was considered a derived feature within Testudinoidea by Stephens and Wiens (2003), who scored it as variably or consistently present in numerous deirochelyids but consistently absent in *Kinosternon subrubrum* and *Sternotherus odoratus* (in contrast to the SMRS). I interpret this medial notch to be the postnatal retention of the basicranial fontanelle, whose obliteration through continued ossification of the basal plate is a postnatal transformation in the SMRS and the only other turtle where its postnatal ontogeny has been explicitly studied—the deirochelyid emydid, *Pseudemys texana* (Bever, 2008). This obliteration occurs later in the postnatal ontogeny of *S. odoratus* than was found in a comparable postnatal series of *P. texana*, indicating that the timing of ontogenetic closure for this fontanelle does exhibit variation in cryptodires. The phylogenetic polarity of this timing cannot currently be established without the explicit descriptions of postnatal ontogeny in additional turtle taxa; however, based on the reported distribution of this medial notch by Stephens and Wiens (2003), the relatively early obliteration is the plesiomorphic condition for cryptodires, making its delayed retention in *S. odoratus* derived at some level.

The size of the fenestra perilymphatica is purported to contain a phylogenetic signal since it is considerably larger than the canalis caroticus internus in Pelomedusidae, Chelidae, Chelydridae, Emydidae, Testudinidae, and Cheloniidae (Gaffney, 1979, 1990, 1996; Brinkman and Nicholls, 1993). The relative size of the fenestra also was hypothesized to be somewhat dependent on age—being larger in juveniles and smaller in adults (Brinkman and Nicholls, 1993). This trajectory is expected because soft tissues of the central

nervous system and sensory organs generally develop early in ontogeny, with the surrounding skeletal material growing subsequently around them. The diameter of this fenestra in *S. odoratus* cannot be measured reliably in articulated specimens; in the eight disarticulated SMRS specimens, the diameter of the fenestra ranged from slightly smaller than the foramen posterior canalis carotici interni to considerably larger (table 5). In contrast to the observations of Brinkman and Nicholls (1993), the only specimens in which the fenestra perilymphatica was smaller than the canalis caroticus internus were juveniles; however, variation was extensive among the juveniles, because the relatively largest fenestra also occurred in a juvenile (M-2960).

The shape of the parabasisphenoid on the ventral surface of an articulated skull was found to be a highly variable character within Testudinoidea by Stephens and Wiens (2003) but one that was consistently convex in both *Kinosternon subrubrum* and *Sternotherus odoratus*. The considerable variation and inferred postnatal transformation of this shape within the SMRS complicate the perceived condition of *S. odoratus* and render the optimization of a convex lateral margin the plesiomorphic condition for Testudinoidea questionable.

Other discrete characters not drawn from phylogenetic analyses that exhibit postnatal transformations in *Sternotherus odoratus* based on the SMRS include: dorsoventral expansion of zygomatic arch (115); exclusion of maxilla from foramen palatinum posterius (116); increased number of foramina arteriaevidianae (119); decreasing ossification of pterygoid surrounding foramen pro ramo nervi vidiani (131, 133); penetration of crista pterygoideus caudal to canalis nervi vidiani by one or two foramina (132); exclusion of dentary from rostral margin of foramen auriculotemporalis by surangular (144); ossification of fossa cartilaginis epipterygoidei, forming quadrate-epipterygoid contact (121); quadrate participating in foramen nervi trigemini (122); path of chorda tympani branch of the facial nerve increasingly enclosed by quadrate (125); caudal shift in relative position of foramen caroticopharyngeale (128); exclusion of pterygoid from foramen caroticum laterale by prootic (129);

formation of *M. rectus capitis fossa* on basioccipital/basisphenoid (139); formation of parabasisphenoid contribution to cavum labyrinthicum (142); formation and deepening of cochlear recess (136); rostralateral shift of abducens canal (141); closure of foramen jugulare posterius from fenestra postotica (137); ossification of processus interfenestralis of such that foramen medialis nervi glossopharyngei (134) and fenestra perilymphatica (135) are completed in bone. Mann-Whitney tests indicate that characters 115, 122, 133, 134, 135, 139, 142 are expressed differently in juveniles and adults (table 12).

SEXUAL DIMORPHISM: Males and females of *Sternotherus odoratus*, unlike many turtles (e.g., chelydrids, deirochelyines; Berry and Shine, 1980), do not exhibit significant differences in adult body size. This relative absence of sexual dimorphism generally is thought to hold true (with obvious exceptions) for most aspects of gross morphology, including cranial osteology (see Materials and Methods). The mean level of discrete character variation is slightly higher in males than females (as it was for the continuous characters), but as with the age classes, the differences are not significant (table 11). Males exhibit higher levels of variation in only 14 published (40.0%) and 13 unpublished characters (41.9%). In comparison with the age-class data, relatively few characters exhibit distinctly different variation scores between males and females. Only 13 (37.1%) of the variable published characters and 14 of the variable unpublished characters (45.1%) exhibit a variation score that differs between males and females at levels of 10% or more, and the number of characters differing at levels exceeding 20 and 30% is only five (14.3%) and zero (0.0%), respectively, for published characters and three (9.7%) for unpublished characters (each of which exceeds a 30% difference) (table 12). Fourteen (45.1%) of the unpublished characters have variation scores that differ by more than 10% between males and females.

None of the explicitly examined discrete characters consistently exhibited different states in males and females. Mann-Whitney tests determined that males and females differed significantly in their expressed character states for a single published character

(position of the pterygoid relative to the foramen palatinum posterius, 55; table 12). Even in this character, the states expressed in the majority of males and females are the same, with the difference being in the amount of variation (approximately 30% of males contain a pterygoid process that extends rostralateral to the foramen whereas only 5% of females exhibit such a process). In a relatively small number of characters, all of which are unpublished, a particular state was not expressed in males or females, or the state expressed in the majority of males differed from that in the majority of females (appendices 4, 5). These characters include: absence of an osseous signature of chorda tympani nerve (only in males; 125), foramen arteriaevidianae single opening (more common in females; 119), rostral position of the foramen caroticopharyngeale (more common in males; 128), dorsal margin of foramen caroticum formed by pterygoid (consistent in females; 129), presence of a distinct rostral margin of foramen pro ramo nervi vidiani (consistent in females; 131), single foramen for posterior canalis nervi vidiani (present only in females; 133), epipterygoid-palatine contact (more common in females; 126), distinct *M. rectus capitis fossa* (more common in males; 139), rostralateral trajectory of abducens canal (more common in males; 141), and retention of an unossified medial wall of the fenestra perilymphatica (more common in females; 135). The majority of these characters are among those interpreted as transforming during postnatal ontogeny. It seems likely that most of these simply reflect the uneven distribution of males and females among age classes or the uneven distribution of size within those age classes. Resolving the influence of sex on the distribution of these, or similar, variation data will require larger samples that allow more refined data partitioning.

POLYMORPHISM: The remaining characters exhibiting variation within the SMRS do so with a pattern that is not obviously correlated with either sex or ontogenetic divisions and therefore are inferred to represent polymorphisms (Wiens, 1999; epigenetic polymorphisms of Berry and Searle, 1963 and Hanken and Hall, 1993; natural individual variation of Hilton and Bemis, 1999, and

Hilton, 2002). Several of these polymorphic characters are derived from the primary palate and rostrum.

Relatively rare polymorphisms in the SMRS whose presence would be considered a derived feature within Kinosternoidea are: round rather than elongate foramen orbitonasale (6), partial bisection of foramen orbitonasale (48), acute terminus of prefrontal process of frontal (11), exclusion of premaxillae from apertura narium externa (28), hooked process of premaxilla (30), pterygoid lateral to foramen palatinum posterius (55), rostral position of vomer-ptyergoid contact (45), and absence of vomer-ptyergoid contact (43). Exclusion of the premaxillae from apertura narium externa probably represents the plesiomorphic condition for Cryptodira, whereas participation is a derived character shared by *Carretochelys*, trionychids, and kinosternoids (Shaffer et al., 1997). The pterygoid-vomer suture in most SMRS specimens lies behind the caudal margin of the palate, which is the plesiomorphic position within Cryptodira. A rostral position is a derived feature that generally characterizes the testudinoid skull (Stephens and Wiens, 2003). A vomer-ptyergoid contact is absent in a small number of SMRS specimens owing to a medial contact of the palatines that obscures, but probably does not prevent, this contact on the ventral surface of the palate. The absence of a vomer-ptyergoid contact was considered a derived character diagnosing *Carretochelys* and trionychids as a clade (Gaffney, 1990; Shaffer et al., 1997).

The shape of the vomer-ptyergoid suture (44), when visible, is highly polymorphic in the SMRS. An acute morphology is the most common condition among cryptodires and likely is plesiomorphic for Kinosternoidae (Gaffney, 1979; Stephens and Wiens, 2003). Jugal participation in temporal emargination also is highly polymorphic in the SMRS. This participation has been surveyed primarily for testudinoids (Hirayama, 1985), but its absence is by far the most common condition among cryptodires (Joyce and Bell, 2004) and likely represents the plesiomorphic condition for kinosternoids. The presence of a small foramen positioned within the palatine slightly caudal to the foramen palatinum posterius

(118) and the absence of a foramen arteriae anteroividianae (120) are two additional characters from the palate expressed as polymorphisms in the SMRS.

The caudal region of the skull, including the braincase, contributes a number of polymorphic characters to SMRS variation. Absence of foramen caroticopharyngeale (67), contact of foramen caroticopharyngeale with pterygoid-parabasisphenoid suture (69), presence of rostralateral projection of parabasisphenoid rostrum (70), absence of pterygoid contribution to foramen nervi trigemini (75), acute rostral terminus of parabasisphenoid (95), convex parabasisphenoid-basioccipital suture (88), and exclusion of angular from sulcus cartilaginis meckelii (110) are relatively rare polymorphisms. Their presence would be considered derived within Kinosternoidea (if scored on an $N = 1$ sample). A number of additional characters from the area in and around the braincase, which have never been included in a phylogenetic analysis of turtle interrelationships, exhibit discrete variation in the SMRS; they are inferred here as polymorphisms. These characters include: parietal foramen dorsal to trigeminal fenestra (114), process of quadrate within cranioquadrate space (123), restriction of incisura columella auris (124), pterygoid-opisthotic contact (127), dorsal margin of foramen pro ramo nervi vidiani formed by pterygoid, prootic, or combination of the two (130), three hypoglossal foramina formed in part by basioccipital (138), and prearticular in foramen intermandibularis posterius (143).

BILATERAL ASYMMETRY: Eleven published characters (31.4%) exhibiting variation within the SMRS are bilaterally asymmetrical in at least one specimen. These characters include: jugal participation in rim of temporal emargination (20), foramen praepalatium as canal (32), vomer participation in foramen praepalatium (33), pterygoid position relative to foramen palatinum posterius (55), epiptyergoid participation in trigeminal fenestra (59), pterygoid-exoccipital contact (65), pterygoid contact with articular facet of quadrate (66), presence and position of foramen caroticopharyngeale (67, 69), rostralateral process of parabasisphenoid (70), and pterygoid contribution to foramen nervi trigemini (75). Sixteen unpublished characters

exhibit bilateral asymmetry in at least one specimen (51.6%). These include: parietal foramen above trigeminal foramen (114), maxillary participation in foramen palatinum posterius (116), restriction of incisura columella auris (124), chorda tympani nerve and pterygoid-opisthotic contact (125), epipterygoid-palatine contact (126), pterygoid-opisthotic contact (127), position of foramen caroticopharyngeale (128), ossification around vidian nerve (118, 120, 130, 132, 133), medial closure of fenestra perilymphatica (135), delineation of cochlear recess (136), number and position of hypoglossal foramina (138), and contribution of prearticular to foramen intermandibularis posterius (143). Two published characters: jugal participation in upper temporal emargination (20) and position of pterygoid relative to foramen palatinum posterius (55), are bilaterally asymmetrical in more than 10% of the SMRS (17.1 and 10.8%, respectively). Nine unpublished characters are bilaterally asymmetrical in more than 10% of the SMRS (118, 43.2%; 120, 10.8%; 124, 18.4%; 128, 10.5%; 130, 57.1%; 132, 28.6%; 133, 25.0%; 138, 13.2%; and 143, 24.0%). Three of the five unpublished characters that are asymmetrical in greater than 20% of the SMRS are associated directly with the path of the vidian nerve (118, 130, 132, and 133). Qualitative assessment of the distribution of these asymmetries reveals no obvious pattern with respect to size, sex, or side of the skull.

CRANIAL PARTITIONS AND VARIATION: Partitioning of the 144 examined cranial characters based on their developmental origin results in 71% of the characters being classified as dermal (dermatocranium), slightly over 20% neurocranial endochondral, and slightly greater than 8% splanchnocranial endochondral (table 13). Of those 66 variable characters within the SMRS, 60.6% are dermatocranial, 27.3% are neurocranial, and 12.1% are splanchnocranial. These percentages closely approximate their expected percentages based on their representation in the character matrix; the dermatocranium is slightly underrepresented, whereas the neurocranium and splanchnocranium are slightly overrepresented. Dermatocranial characters exhibit the lowest mean score and the highest standard deviation. The eight splanchnocra-

nial characters exhibit the largest mean variation score followed closely by those of the neurocranium. When the neurocranial and splanchnocranial characters are pooled as endochondral characters, their mean level of variation is 28.9%, which is approximately 20% greater than the mean variation score for dermatocranial characters.

The distribution of partitioned characters for the variable published characters alone is 71.4% dermatocranial, 22.9% neurocranial, and 5.7% splanchnocranial. Variations within and among these three developmental partitions show that, among the published characters, the highest mean level of variation is among the neurocranial characters (28.5%) with splanchnocranial and dermatocranial characters varying at mean levels of 22.3 and 17.2%, respectively (table 13). The mean level of variation for the pooled endochondral characters is 27.2%, which is slightly more than 10% greater than that of dermatocranial characters. When only published characters are considered, endochondral characters exhibit a mean variation score of 27.2% in comparison to the 17.2% mean variation for dermatocranial characters. Overall, endochondral characters vary at higher levels than those of the dermatocranium.

Character partitioning based on a topological/functional scheme reveals that 15.9% are derived from the dermal roofing elements, 30.4% palate, 21.4% palatoquadrate, 22.1% braincase, and 11.0% lower jaw. Four variable characters (6.1%) are from the dermal roof, 20 (30.3%) from the palate, 20 (30.3%) from palatoquadrate elements, 17 (25.8%) from the braincase, and 5 (7.6%) from the lower jaw. Therefore, the dermal roof contributes significantly fewer variable characters than predicted based on their proportional contribution in the dataset. The lower jaw contributes a slightly lower than expected percentage, the palate and braincase contributions closely approximate their expected proportion, and the palatoquadrate elements contribute a higher than expected proportion. Dermal roofing elements exhibit the highest average variation score, which is caused in part by the low sample size; however, this average score is much higher than that of the lower jaw,

TABLE 13
Allocation of Cranial Characters to the Two-Partitioning Schemes

Schemes are described in text. Numbers following the partition titles (e.g., dermatocranium) refer to the total number of characters allocated to that partition and the associated percentage. For each partition, characters are subdivided into those drawn from published phylogenetic studies (publ.) and those that are not (unpubl.).

Development-Based Partitions	
Dermatocranium (103; 71.0%)	
publ. (87): 1–55, 60–69, 71–74, 80, 84, 85, 97, 100–113	
unpubl. (16): 114–120, 128–133, 143, 144	
Neurocranium (30; 20.7%)	
publ. (20): 70, 76–79, 82, 83, 86–96, 98, 99	
unpubl. (10): 127, 134–142	
Splanchnocranium (12; 8.3%)	
publ. (6): 56–59, 75, 81	
unpubl. (6): 121–126	
Topological/Functional-Based Partitions	
Dermal Roofing (22; 15.9%)	
publ. (20): 1, 2, 7–12, 15–21, 24–26, 34, 80	
unpubl. (2): 114–115	
Palatal (44; 30.4%)	
publ. (39): 76–79, 81–84, 86–96, 98, 99	
unpubl. (5): 116–120	
Palatoquadrate (31; 21.4%)	
publ. (18): 56–59, 63–69, 71–75, 85, 97	
unpubl. (13): 121–133	
Braincase (32; 22.1%)	
publ. (23): 70, 76–79, 81–84, 86–96, 98, 99	
unpubl. (9): 134–142	
Lower Jaw (16; 11.0%)	
publ. (14): 100–113	
unpubl. (2): 143, 144	

which has a comparably low sample size (table 14). Among the palate, palatoquadrate, and braincase, each of which have comparable sample sizes, the palatoquadrate and braincase show similar mean levels of variation with the palatal elements considerably less variable.

When only the 113 published characters are considered, dermal roofing elements contribute 17.7% of the characters, palatal 34.5%, palatoquadrate 15.9%, braincase 20.4%, and lower jaw 12.4%. As a percentage of the subset of 35 variable published characters, the highest proportion is derived from the palate (42.9%) with 22.9, 20, 8.6, and 5.7% derived

from the braincase, palatoquadrate, lower jaw, and dermal roofing elements, respectively. The variation scores among published characters are largest in the dermal roof (33.5) and braincase (28.5), with the palate, palatoquadrate, and lower jaw exhibiting a mean variation score of 16.7, 16.6, and 13.6, respectively (table 14). Overall, the dermal roof varies at the highest level; however, the significance of these high scores is spurious because of the low number of characters from this region. The relatively high levels of variation expressed in the braincase characters are more strongly supported by a larger sample size that eases comparisons with the other cranial partitions (table 14).

Standard chi-square tests of independence for all 595 possible pairwise combinations of the 35 phylogenetic characters exhibiting variation within the SMRS resulted in 28 character pairs (4.7%) in which the variable character states are significantly correlated to each other (nonindependent). These statistically nonindependent combinations comprise characters in which the variant morphology is present in a very low percentage of the sample. In such cases, and when running such a large number of pairwise tests, there is a strong likelihood of finding nonindependent character combinations through random chance alone. The expected percentage of statistically nonindependent character combinations based on chance alone is approximately 5% (Zar, 1999), which is almost exactly the percentage recovered. Application of a Bonferonni correction resulted in the significance level (*p*) falling from 0.05 to 0.00008 (= 0.05/595). Of the 28 statistically nonindependent character combinations initially deemed significant, only two pairs of character combinations retained a statistically significant correlation. Both pairs include the shape of the dorsal surface of the crista supraoccipitalis (76) and palatal characters (table 15).

GROWTH

Although there is a growing body of literature examining morphometric variation in the reptile skull and its ecological, phylogenetic, and functional correlates, most of these studies concentrate on phylogenetic

TABLE 14
Descriptive Statistics for Variation Scores from the 66 Discrete Characters Exhibiting
Variation within the SMRS

Characters are partitioned based on the developmental and topological/functional origin of the bones.

	<i>N</i>	Min.	Max.	Mean	SD
Developmental Partitions					
Total sample (66 variable characters)					
Dermatocranium	40	2.6	50.0	22.48	16.091
Neurocranium	18	2.6	44.7	27.78	12.914
Splanchnocranium	8	6.3	48.3	29.26	15.592
Endochondral	26	2.6	48.3	28.93	13.474
Published only (35 variable characters)					
Dermatocranium	25	2.6	45.7	17.17	13.266
Neurocranium	8	2.6	37.5	28.45	13.508
Splanchnocranium	2	6.3	38.2	22.25	22.557
Endochondral	10	2.6	38.2	27.21	14.328
Topological/Functional Partitions					
Total sample (66 variable characters)					
Dermal roofing	4	21.2	45.7	35.13	11.487
Palatal	20	2.7	50.0	19.91	13.725
Palatoquadrate	20	2.6	50.0	26.94	17.664
Braincase	17	2.6	44.7	29.53	12.906
Lower jaw	5	2.6	31.6	14.38	14.212
Published only (35 variable characters)					
Dermal roofing	2	21.2	45.7	33.45	17.324
Palatal	15	2.7	38.7	16.67	11.304
Palatoquadrate	7	2.6	42.1	16.57	16.453
Braincase	8	2.6	37.5	28.45	13.507
Lower jaw	3	2.6	31.6	13.57	15.739

patterns of allometry based on relatively small samples of adult specimens (e.g., Marugán-Lobón and Buscalioni, 2003; Claude et al., 2004). Few studies examine growth trajectories of cranial morphometry within species, and even fewer do so at the population level. The study by Dalrymple (1977) on growth and variation in the skull of a single population of the Florida Softshell Turtle, *Apalone ferox* (Trionychidae), represents the most comparable dataset to that presented here for the SMRS *Sternotherus odoratus*. Twelve of the 25 continuous characters analyzed here (1, 2, 3, 4, 7, 9, 10, 12, 13, 14, 21, and 22) are the same as those examined by Dalrymple (1977), who used bivariate regressions to study growth, which facilitates direct comparisons between the two studies.

Growth trajectories of the skull during postnatal ontogeny in *Sternotherus odoratus* and *Apalone ferox*, as might be expected,

exhibit some similarities and differences. Both taxa exhibit positive allometry in the growth of the postorbital bar and interorbital breadth, and negative allometry in the expansion of orbital diameter. The orbit thus attains a particular size relatively early in ontogeny and then largely maintains that size for the duration of postnatal growth, whereas the facial skeleton grows with positive allometry around the orbit (the result being a relatively small orbit in large individuals). These growth patterns probably result from the accelerated differentiation of the central nervous system and sensory capsules, which may be the plesiomorphic condition not only for turtles, but also for Reptilia (Hall and Portier, 1994), Amniota (Abdala et al., 2001; O'Higgins et al., 2001), and likely Vertebrata (Emerson and Bramble, 1993).

This pattern of relatively early maturation of the nervous system also manifests itself in the early enlargement of the braincase and

TABLE 15
Two-Way Tables Showing Number of Specimens Exhibiting Each Combination of
Character States

χ^2 value, degrees of freedom (df), and p -value are given for the two pairs of qualitative characters determined to be significantly nonindependent based on two-way chi-square tests of independence after the application of a Bonferroni correction.

A. Dorsal surface of crista supraoccipitalis (76) and position of vomer-ptyergoid contact relative to caudal palatal margin (45).			
	rounded	Dorsal surface of crista straight	peaked
<i>Vomer-ptyergoid</i>			
at margin	14	1	6
rostral	1	9	1
caudal	6	0	1
$\chi^2 = 26.454$, $df = 4$, $p = 0.000026$.			
B. Dorsal surface of crista supraoccipitalis (76) and vomeral participation in foramen praepalatium (33).			
	rounded	Dorsal surface of crista straight	peaked
<i>Vomer participation</i>			
present	0	1	11
absent	16	0	0
$\chi^2 = 28.0$, $df = 2$, $p = 0.0000008$.			

otic capsules, with subsequent negative allometric growth relative to overall size (e.g., measurements 18 and 20). Although the braincase and otic capsules achieve a relatively large size early in postnatal ontogeny (along with the soft anatomical structures of the central nervous system that they enclose), ossification of the cartilaginous braincase and otic capsule is largely delayed relative to that of dermally derived elements of the cranial roof. Maturation of ossified structures in the otic capsule and braincase also continues throughout most of postnatal ontogeny—well into that portion of ontogeny occupied by sexually mature adults. Examples of this delayed maturation in *Sternotherus odoratus* include closure of the basicranial and otic fontanelles; closure of the perilymphatic foramen, foramen medialis nervi glossopharyngei, and foramen jugulare posterius; restriction of the hiatus acusticus; ossification of the ventral margin of the fenestra ovalis; obliteration of the fossa cartilaginous epiptyergoidei (splanchnocranium); and formation of the tuberculum basioccipitale. Thus, the endochondral skeleton housing the brain and sensory capsules develops relatively early, but continues to mature throughout much of ontogeny, re-

sulting in a considerable number of relatively late-stage postnatal transformations in characters drawn from this anatomical region. This delayed maturation may reflect the delayed onset of ossification in the neurocranium and sensory capsules relative to the dermatocranium that appears to be the common and possibly plesiomorphic condition for Amniota (Nesslinger, 1956; Rieppel, 1992a, 1992b, 1993a, 1993b; Sheil, 2003, 2005; Sheil and Greenbaum, 2005).
The postnatal cranial ontogenies of *Sternotherus odoratus* and *Apalone ferox* also share a tendency toward positive allometric growth in the size of the feeding surfaces (12, 21, 22), which are also the features making the contribution to overall morphometric cranial variation. (The latter also agrees with the conclusions of Crumly [1984] for Galapagos tortoises.) This similarity suggests that positive allometry of the triturating surfaces may be plesiomorphic for trionychids and that the extremely wide surfaces of adults in forms like *A. ferox* represent an elaboration of an already present growth trajectory. The maxillary feeding surface of *A. ferox* increases during postnatal growth with a higher coefficient of allometry than does the lower triturating surface, whereas the opposite is

true in *S. odoratus*. The polarity of these differences cannot be established by comparing two taxa; however, considering the derived nature of the feeding surfaces of *A. ferox* among other cryptodires, it may be more likely that the morphology of the feeding apparatus in *S. odoratus* more closely reflects the plesiomorphic cryptodire condition (rather than a derived ontogenetic trajectory for the lower feeding surface of *S. odoratus*, which also is possible). The width of the primary palate (13) is largely the same in these two species since it scales isometrically with cranial length. (This width does trend toward negative allometry in *S. odoratus* based on a multivariate approach.)

The allometric expansion of the triturating surfaces during postnatal growth occurs concurrently with other postnatal transformations associated with the functional ability of these turtles to open and close the lower jaw with increasing force. Height of the crista supraoccipitalis (4), which provides the surface of origination for the *M. adductor mandibulae externus pars profundus* (Schumacher, 1973) and thus is closely integrated anatomically with the cranial feeding mechanism, scales with significant positive allometry in the population of *Apalone ferox* (Dalrymple, 1977). Qualitative comparison of the smallest and largest specimens in the SMRS indicates that its transformation during postnatal ontogeny is considerable. The coefficient of allometry for cranial height in the SMRS as a whole, however, does not differ significantly from isometry or tends slightly toward negative allometry, and a bivariate comparison of the untransformed values for this metric against length of the skull indicates that growth more closely follows an S-shaped curve. One possible reason for this disparity between the two taxa is that the exact measurement used to summarize the height of this feature is not identical in this study with that of Dalrymple (1977). Dalrymple measured only the crista supraoccipitalis—which is difficult to replicate consistently in *Sternotherus odoratus*. Instead, the growth of this structure was studied based on its height above the ventral surface of the basicranium. The seemingly illogical isometric or negative growth trajectory for the height of the crista supraocci-

tal in *S. odoratus* may reflect a relative dorsoventral shortening of that portion of the braincase not incorporated by the measurement of Dalrymple (1977). The presence of dorsoventral compression in the caudal portion of the skull is supported by the increased approximation of the pterygoid and quadratojugal with the articular facet of the quadrate in the lower jaw. Therein, the position of the parietal-supraoccipital suture was used as the landmark for measuring the height of the crista supraoccipitalis—a position that exhibits some variation with respect to the vertical apex of this structure. Other discrete transformations associated with increased mechanical force of the lower jaw include increased sculpting of the caudal surface of the skull formed by the squamosal and paroccipital process (origin of *M. depressor mandibulae* and *M. adductor mandibulae pars superficialis*), thickening of the processus pterygoideus externus, increased height of the processus coronoideus, and increased ossification of the rostromedial portion of the upper triturating surface. The latter transformation affects the presence of a vomer-maxilla contact and the structure of the foramen praepalatium, both of which were used as characters in phylogenetic analyses of turtle interrelationships (i.e., Stephens and Wiens, 2003).

The cranial ontogenies of *Sternotherus odoratus* and *Apalone ferox* (in addition to the height of the crista supraoccipitalis) differ in the relative increase of condylobasal length, cranial width, and width of pterygoid waist. Each of these metrics trends toward negative allometry in *S. odoratus*, whereas they grow with strong positive allometry in *A. ferox*. Thus, the skulls of *S. odoratus* and *A. ferox* become increasingly rounded during postnatal ontogeny but attain this shape via different growth trajectories. The skull of *S. odoratus* becomes rounded because both its length and width scale with negative allometry relative to overall size, whereas the skull of *A. ferox* becomes rounded because its length and width scale with positive allometry relative to overall size. The phylogenetic polarity of these differences currently cannot be established. As with height of the crista supraoccipitalis, the width of the skull and dorsoventral height of the zygomatic arch

differ qualitatively between small and large individuals in the SMRS whose coefficients of allometry do not differ significantly from isometry.

The lateral margins of the pterygoids delineate the medial margins of the fossa temporalis inferior. Therefore, the breadth of the pterygoid waist is associated anatomically with the morphology of that chamber and presumably the muscles that are housed therein. A relatively broad waist was described as a distinctive feature of the Oligocene kinosternid *Xenochelys* (Williams, 1952). The probable growth trajectories for the pterygoid waist are difficult to project in other extant kinosternoids based on adult morphology alone (e.g., *Emarginachelys* [Whetstone, 1978], *Dermatemys* [Bienz, 1895], *Staurotypus* spp. [Gaffney, 1979], although *Claudius* appears to have a relatively narrow pterygoid waist (Gaffney, 1979). The polarity of a negative growth trajectory for this metric cannot be established for *Sternotherus odoratus*; however, the trajectory does emphasize the importance of ontogenetic histories of characters deemed important for understanding the evolutionary history of kinosternoid turtles and other vertebrate lineages.

CONCLUSIONS

This study examined the cranial morphology of the extant cryptodire *Sternotherus odoratus* based on a sample drawn from a single population representing a significant portion of this species' postnatal ontogeny. The result is the first relatively comprehensive description of the skull of an extant kinosternid. More importantly, the data derived from this study provide details of the nature of morphological transformations and variation (for both discrete and continuous characters) during the postnatal ontogeny of the skull that previously were not available in the anatomical literature concerning both turtles and reptiles in general. The extent of postnatal change was surprisingly high considering the conservative nature of the sample—conservative not only because the study estimates the variation present in a single population on a single day, but because a majority of the examined characters were drawn from published phylogenetic analyses

and, therefore, should theoretically exhibit relatively low levels of intraspecific variation.

Most of the postnatal transformations in the discrete cranial morphology of *Sternotherus odoratus* were found in structures formed within the endochondral elements of the neurocranium and otic capsule, which not only begin ossification relatively late but also mature more slowly than elements of the dermatocranium. This overall pattern of development probably is not unique to *S. odoratus* and may even be plesiomorphic for Vertebrata. This plesiomorphic pattern of development results in a modular (sensu Wagner, 1996) expression of variation during postnatal ontogeny that probably also is derived at a relatively deep position in chordate phylogeny. These plesiomorphic developmental trends, however, result in ontogenetic transformations and variation in characters purportedly informative at much more restricted levels of vertebrate history (e.g., Kinosternidae; see also Rieppel and Crumly [1997]). It currently is unclear how heterochronic transformations in the timing of this postnatal maturation have affected the expression of these phylogenetic characters.

As in previous studies (e.g., Dalrymple, 1977), the largest contributors to postnatal variation among the continuous characters are those dimensions that represent the feeding apparatus and trophic function. This variation and its associated growth trajectories may represent an adaptation to a dietary shift in larger individuals, which entails increased omnivory and the ingestion of more hard-textured food items. Such an explanation commonly is evoked for turtle taxa that exhibit large feeding surfaces and, as adults, feed on hard-shelled prey items like snails (Dalrymple, 1977; Lindeman, 2000; Claude et al., 2004). This trend in *Sternotherus odoratus* also may simply represent the retention of an ancestral ontogenetic trajectory that allows an increasingly diverse diet among adults, and therefore represents a plesiomorphic rather than a derived condition (based on the criteria set forth by de Queiroz, 1985). The mechanical influences of cranial function, not surprisingly, are important proximal causes of postnatal variation in the skull of all vertebrates, including *S. odoratus*. This, however, does not mean that

more ultimate causation in the evolution of developmental trajectories and the expression of variation during ontogeny is not phylogenetically informative, as often is implied when functional causation is invoked to explain adult morphology.

Variation is necessary for evolutionary change. Delimiting the sources of observed variation often is difficult because most, if not all, anatomical variations are derived from the integration of multiple factors being expressed (or at least conceptualized) at different hierarchical levels (e.g., phylogenetic, geographic, individual, sexual, ontogenetic). Despite theoretical advances in integrating ontogenetically correlated anatomical data into an evolutionary framework (e.g., Gilbert and Bolker, 2000), and the fact that variation as the expected condition in biological systems has been one of the primary tenets driving modern biology since the importance of variation was articulated by Darwin (1859), descriptive studies documenting the types, distribution, and frequency of anatomical variation are lacking for most biological groups and morphological systems—including the skeletal system of nonavian reptiles. The primary purpose of this study was to assess the nature of morphological transformations in the reptile skull during the later portion of postnatal ontogeny (that portion most often used in morphological phylogenetic analyses and preserved in the fossil record). This assessment was based on a sample that provided some control on the influence of geographic, stratigraphic, and phylogenetic variation; such variables are difficult to account for when analyzing samples from mixed extant populations and from nearly all fossil accumulations. This study, therefore, provides baseline data for future studies that will expand our understanding of the ontogenetic and phylogenetic patterns of cranial modularity that affect the expression of intraspecific variation in anatomical systems.

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APPENDIX 1

List of Anatomical Abbreviations

BONES

ANG	angular
ART	articular
BO	basioccipital
BS	parabasisphenoid
CA	columella auris
COR	coronoid
D	dentary
EPI	epipterygoid
EX	exoccipital
FR	frontal
JU	jugal
MX	maxilla
NA	nasal
OP	opisthotic
PA	parietal
PAL	palatine
PF	prefrontal
PM	premaxilla
PO	postorbital
PR	prootic
PRA	prearticular
PT	pterygoid
QJ	quadratojugal
QU	quadrate
SO	supraoccipital
SQ	squamosal
SUR	surangular
VO	vomer

STRUCTURES

aam	area articularis mandibularis
acnv	anterior canalis nervi vidiani
ane	apertura narium externa
ani	apertura narium interna
ast	aditus stapediotemporalis
can	canalis nervi abducentis
cc	cavum cranii
cci	canalis caroticus internus
cev	canalis cavernosus
cl	cavum labyrinthicum
cm	condylus mandibularis
csa	canalis semicircularis anterior
csb	canalis semicircularis horizontalis
csp	canalis semicircularis posterior
cst	canalis stapediotemporalis
ct	cavum tympani
faa	foramen arteriae anteriovidianae
faj	foramen jugulare posterius
fap	foramen alveolare posterius

fb	fenestra basicranialis
fc	foramen cavernosum
fce	fossa cartilaginis epipterygoidei
fcl	foramen caroticum laterale
fcp	foramen caroticopharyngeale
fcti	foramen chorda tympani inferius
fdm	foramen dentofaciale majus
fe	fissura ethmoidalis
feng	foramen externum nervi glossopharyngei
fig	foramen internum nervi glossopharyngei
fio	foramen interorbitale
fja	foramen jugulare anterius (medial aperture of recessus scalae tympani)
fjp	foramen jugulare posterius
fm	fossa meckelii
fmng	foramen medialis nervi glossopharyngei
fna	foramen nervi auriculotemporalis
fnab	foramen nervi abducentis
fnac	foramen nervi acustici
fnf	foramen nervi facialis
fnh	foramen nervi hypoglossi
fmt	foramen nervi trigemini
fo	fenestra ovalis
fon	foramen orbitonasale
fp	fenestra perilymphatica
fpa	foramen palatinum accessorium
fpci	foramen posterior canalis carotici interni
fpl	foramen praepalatium
fpp	foramen palatinum posterius
fprnv	foramen pro ramo nervi vidiani
fst	foramen stapediolum
ica	incisura columellae auris
of	otic fontanelle
or	fossa orbitalis
pcnv	posterior canalis nervi vidiani
pe	processus epipterygoideus
pi	processus interfenestralis
pto	processus trochlearis oticum
rb	rostrum basisphenoidale
rst	recessus scalae tympani
tr	trabeculae of parabasisphenoid

APPENDIX 2

Characters Drawn from Published Phylogenetic Studies

The author(s), date(s), and original character number(s) or letters are supplied for each character (where applicable), followed by the character states.

(1) *Lateral edges of prefrontal in dorsal view* (Burke et al., 1996: 22; Stephens and Wiens, 2003: 50): taper rostrally [0]; lateral edges parallel or form hourglass shape [1]. (2) *Minimum interorbital distance* (McDowell, 1964; Stephens and Wiens, 2003: 51): exceeds greatest width of apertura narium externa [0]; less than greatest width of apertura narium externa [1]. (3) *Prefrontal-vomer contact* (Gaffney, 1996: 3): absent [0]; present [1]. (4) *Length of foramen orbitonasale*

(Hirayama, 1985: 33; Gaffney and Meylan, 1988; Crumly, 1982: 25; Crumly, 1994: 12; modified by Joyce and Bell, 2004: 14): small, less than one-sixth of orbital length [0]; large, greater than one-sixth of orbital length [1]. (5) *Width of foramen orbitonasale* (Stephens and Wiens, 2003: 19): less than greatest width of palatine process of vomer [0]; equal to or greater than greatest width of palatine process of vomer [1]. (6) *Shape of foramen orbitonasale* (Stephens and Wiens, 2003: 21): elongate rostrocaudally, diameter of longitudinal axis two or more times diameter of perpendicular axis [0]; rounded with length and width subequal [1]. (7) *Shape of fissura ethmoidalis* (Loveridge and Williams, 1957; Crumly, 1982: 13; Hirayama, 1985: 1; Joyce and Bell, 2004: 1): narrow or closed [0]; very wide [1]. (8) *Frontal contribution to orbital margin* (McDowell, 1964; Crumly, 1982: 17; Hirayama, 1985: 3; Shaffer et al., 1997: 97; Yasukawa et al., 2001: 1; Stephens and Wiens, 2003: 54; Joyce and Bell, 2004: 3): absent [0]; present [1]. (9) *Frontal contribution to rostral margin of supratemporal fossa* (Hirayama, 1985: 4; Joyce and Bell, 2004: A): absent [0]; present [1]. (10) *Prefrontal process of frontal* (Bertl and Killebrew, 1983; Stephens and Wiens, 2003: 52): absent [0]; present [1]. (11) *Rostral termination of prefrontal process of frontal* (Stephens and Wiens, 2003: 53): blunt or rounded [0]; acute [1]. (12) *Parietals very small* (Shaffer et al., 1997: 52): no [0]; yes [1]. (13) *Parietal-palatine contact* (McDowell, 1964; Stephens and Wiens, 2003: 64): absent, elements separated by pterygoid [0]; present [1]. (14) *Contact of processus inferior parietalis with maxilla* (Hirayama, 1985: 14; Joyce and Bell, 2004: 8): absent [0]; present [1]. (15) *Contact of processus inferior parietalis with medial process of jugal* (Hirayama, 1985: 13; Joyce and Bell, 2004: 7): absent [0]; present [1]. (16) *Rostral border of processus inferior parietalis* (McDowell, 1964; Stephens and Wiens, 2003: 63): thin [0]; thick, with at least one-quarter the distance between caudal margins of right and left interorbital foramina [1]. (17) *Foramen nervi trigemini* (modified from Crumly, 1982; Hirayama, 1985: 6; Joyce and Bell, 2004: E): foramen not divided into maxillary and mandibular foramina [0]; divided [1]. (18) *Jugal contribution to lateral margin of orbit* (Bertl and Killebrew, 1983; Stephens and Wiens, 2003: 55): absent [0]; present [1]. (19) *Postorbital exposed caudally by temporal emargination* (Shaffer et al., 1997: 109): absent [0]; present [1]. (20) *Contribution of jugal to rim of temporal emargination* (Hirayama, 1985: 15; Joyce and Bell, 2004: 10): absent [0]; present [1]. (21) *Maxilla-quadratojugal contact* (McDowell, 1964; Hirayama, 1985: 18; Shaffer et al., 1997: 98; Stephens and Wiens, 2003: 65; Joyce and Bell, 2004: 12): absent [0]; present [1]. (22) *Jugal-palatine contact* (Gaffney and Meylan, 1988; Stephens and Wiens, 2003: 66; Joyce and Bell, 2004: 5): absent, excluded by maxilla [0]; present [1]. (23) *Jugal-ptyergoid contact* (McDowell, 1964; Hirayama, 1985: 11, 12; Burke et al., 1996: 23; Yasukawa et al., 2001: 4, 5; Stephens and Wiens, 2003: 68; Joyce and Bell, 2004: 4): absent [0]; present [1]. (24) *Jugal-quadratojugal contact* (Hirayama, 1985: 16; Shaffer et al., 1997: 47; Burke et al., 1996: 21; Yasukawa et al., 2001: 7, 8; Stephens and Wiens, 2004: 60, 61; Joyce and Bell, 2004: 9): quadratojugal well developed, firmly at-

tached to jugal [0]; quadratojugal present, contact lost with jugal [1]; quadratojugal reduced, appears absent in skeletal specimens [2]. (25) *Contact between quadratojugal and articular facet of quadrate* (modified from Hirayama, 1985: 17; Joyce and Bell, 2004: 11): absent [0]; present [1]. (26) *Quadratojugal-squamosal contact* (Gaffney and Meylan, 1988): absent [0]; present [1]. (27) *Fusion of premaxillae* (Meylan, 1987: 44; Shaffer et al., 1997: 81): paired [0]; fused [1]. (28) *Participation of premaxilla in apertura narium externa* (Shaffer et al., 1997: 87): present [0]; absent [1]. NOTE: Absence results from medial contact of maxillae dorsal to premaxillae in rostral view. When this maxillary contact is slightly recessed so that it is just within the fossa nasalis, participation of the premaxillae in the apertura narium externa can occur in conjunction with a rostral contact of maxillae. (29) *Medial contact of maxillae along rostral margin of jaw (ventral to the premaxillae)* (Hirayama, 1985: 20; Yasukawa et al., 2001: 10; modified by Joyce and Bell, 2004: 13): absent [0]; present [1]. (30) *Rostroventral border of premaxilla* (Hirayama, 1985: 19, 28; Yasukawa et al., 2001: 9; Stephens and Wiens, 2003: 29; Joyce and Bell, 2004: G, H): smooth [0]; smooth but with notch [1]; notch defined by two cusps [2]; hooked beak [3]. (31) *Nasal process of premaxilla* (Killebrew, 1979; Bertl and Killebrew, 1983; Stephens and Wiens, 2003: 49): absent [0]; present [1]. (32) *Development of foramen praepalatium as a canal (canalis praepalatium) that is concealed by a bony secondary palate in ventral view* (McDowell, 1964; Hirayama, 1985: 24; Stephens and Wiens, 2003: 30; Joyce and Bell, 2004: 20): absent [0]; present [1]. (33) *Vomer participation in foramen praepalatium* (Crumly, 1982: 10; Hirayama, 1985: 32; Yasukawa et al., 2001: 15; Joyce and Bell, 2004: J): present [0]; absent [1]. (34) *Lateral edge of apertura narium externa emarginate dorsally* (Williams, 1952; Meylan, 1987: 41): no [0]; yes [1]. (35) *Participation of palatine in upper triturating surface* (Hirayama, 1985: 26; Gaffney and Meylan, 1988; Stephens and Wiens, 2003: 24; Joyce and Bell, 2004: 28): excluded entirely [0]; present [1]. (36) *Presence and number of lingual ridges of upper and lower triturating surfaces* (Hirayama, 1985: 29, 44; Gaffney and Meylan, 1988; Joyce and Bell, 2004: 30): absent [0]; one lingual ridge present [1]; two lingual ridges present [2]. (37) *Median ridge or sulcus of upper triturating surface* (Hirayama, 1985: 30; Gaffney and Meylan, 1988; Crumly, 1994: 4; Stephens and Wiens, 2003: 26; Joyce and Bell, 2004: 32): both structures absent [0]; median ridge present [1]; median sulcus present [2]. (38) *Maxillary "tooth" on upper triturating surface* (Meylan and Gaffney, 1989; Shaffer et al., 1997: 73): absent [0]; present [1]. (39) *Well-developed serrations on labial or lingual ridges of triturating surfaces* (Hirayama, 1985: 21, 27, 41, 43, 46; Gaffney and Meylan, 1988; Yasukawa et al., 2001: 11; Stephens and Wiens, 2003: 31; Joyce and Bell, 2004: 31): absent [0]; present [1]. (40) *Participation of vomer in upper triturating surface* (McDowell, 1964; Hirayama, 1985: 25; Stephens and Wiens, 2003: 25; Joyce and Bell, 2004: 29): absent [0]; present [1]. (41) *Vomer-maxilla contact* (Crumly, 1982: 31; Hirayama, 1985: 31; Yasukawa et al., 2001: 14; Joyce and Bell, 2004: 15): absent [0]; present [1]. (42) *Vomerine foramen* (Gaffney

and Meylan, 1988; Crumly, 1994: 15; Joyce and Bell, 2004: 19): absent [0]; present [1]. (43) *Vomer-ptyergoid contact in ventral view* (Shaffer et al., 1997: 75): absent [0]; present [1]. NOTE: Considered absent when palatines meet medially and obscure vomer-ptyergoid suture. (44) *Shape of vomer-ptyergoid contact* (Stephens and Wiens, 2003: 15): vomer does not come to distinct point at contact with pterygoids on ventral surface of palate, suture is broadly rounded at contact or forms jagged horizontal line [0]; vomer tapers to single point at contact with pterygoids and often flares just rostral to contact [1]; vomer bifurcate at contact with pterygoids [2]; vomer trifurcate [3]; vomer with four distinct points [4]; vomer with five distinct points [5]. (45) *Position of vomer-ptyergoid contact* (modified from Stephens and Wiens, 2003: 16): at caudal border of palate [0]; rostral to caudal border of palate [1]; behind caudal border of palate [2]. NOTE: This character requires that the caudal margin of the palate be defined formally. I define this margin as lying along a transverse line that extends between the caudal margins of the maxilla on the ventral surface of the skull. (46) *Palatines truncated rostrally* (Shaffer et al., 1997: 76): no [0]; yes [1]. (47) *Palatine contribution to braincase* (Meylan and Gaffney, 1989; Shaffer et al., 1997: 68): absent [0]; present [1]. (48) *Bisection of foramen orbitonasale by process of palatine* (Stephens and Wiens, 2003: 20): not bisected, one opening present [0]; bisected partly or completely by thin process of palatine [1]. (49) *Presence of foramen palatinum posterius* (Shaffer et al., 1997: 66): present [0]; absent [1]. (50) *Position of foramen palatinum posterius* (Stephens and Wiens, 2003: 18): occurs at bottom of furrow formed by caudoventral projection of palatine and maxilla [0]; clearly visible [1]. (51) *Foramen palatinum posterius enclosed within brain cavity* (Hirayama, 1985: 34; Joyce and Bell, 2004: K): no [0]; yes [1]. (52) *Size of foramen palatinum posterius relative to foramen orbitonasale* (Hirayama, 1985: 22; Gaffney and Meylan, 1988; Yasukawa et al., 2001: 12; Stephens and Wiens, 2003: 22): larger [0]; smaller [1]. (53) *Size of foramen palatinum posterius relative to palatine process of vomer* (Burke et al., 1996: 18; Stephens and Wiens, 2003: 17): narrower than or equal to greatest width of palatine process of vomer [0]; wider than palatine process of vomer [1]. (54) *Pterygoid participation in foramen palatinum posterius* (Gaffney and Meylan, 1988; Stephens and Wiens, 2003: 23): absent [0]; present [1]. (55) *Position of pterygoid relative to foramen palatinum posterius* (Joyce and Bell, 2004: 17): caudal [0]; caudal to foramen palatinum posterius but with a rostromedial process [1]. (56) *Quadrate with ventral process extending medially to braincase below cranioquadrate space* (Gaffney and Meylan, 1988; Gaffney et al., 1991): absent [0]; present [1]. (57) *Incisura columellae auris* (Crumly, 1985; Gaffney and Meylan, 1988; Shaffer et al., 1997: 59; Joyce and Bell, 2004: 23): absent, incisura open [0]; present, incisura closed [1]. (58) *Epiptyergoid-jugal contact* (Gaffney and Meylan, 1988; Shaffer et al., 1997: 106; Stephens and Wiens, 2003: 67; Joyce and Bell, 2004: 6): absent [0]; present [1]. (59) *Epiptyergoid participation in foramen nervi trigemini* (Joyce and Bell, 2004: 18): absent [0]; present [1]. (60) *Pterygoids divided by parabasi-*

sphenoid (Shaffer et al., 1997): no [0]; yes [1]. (61) Processus externus of pterygoid (Shaffer et al., 1997: 77): present [0]; absent [1]. (62) Vertical flange on processus pterygoideus externus (Gaffney et al., 1991; Gaffney, 1996: 4): absent [0]; present [1]. (63) Middle ear with ossified floor formed by caudoomedial process of pterygoid (Gaffney and Meylan, 1988; Gaffney et al., 1991; Gaffney, 1996: 8): present [0]; absent [1]. (64) Pterygoid-basioccipital contact (Gaffney and Meylan, 1988; Crumly, 1994; Shaffer et al., 1997: 103; Stephens and Wiens, 2003: 47; Joyce and Bell, 2004: 21): present [0]; absent [1]. (65) Pterygoid-exoccipital contact (McDowell, 1964; Stephens and Wiens, 2003: 48): absent [0]; present [1]. (66) Contact between pterygoid and articular facet of quadrate (Hirayama, 1985: 38; Joyce and Bell, 2004: 22): absent [0]; present [1]. (67) Foramen caroticopharyngeale on ventral surface of pterygoid (Gaffney and Meylan, 1988; Stephens and Wiens, 2003: 32): absent [0]; present [1]. (68) Size and morphology of foramen caroticopharyngeale (Gaffney and Meylan, 1988; Stephens and Wiens, 2003: 33): large, easily seen with naked eye, subdivision of foramen visible just below surface [0]; small, barely visible to naked eye, subdivisions not visible [1]. (69) Position of foramen caroticopharyngeale (McDowell, 1964; Stephens and Wiens, 2003: 34): contacts pterygoid-parabasisphenoid suture [0]; does not contact suture [1]. (70) "Wings" on rostral projection of parabasisphenoid, often contacts foramen caroticopharyngeale (Stephens and Wiens, 2003: 38): absent [0]; present [1]. (71) Depression in pterygoid just lateral to parabasisphenoid (Stephens and Wiens, 2003: 36): absent [0]; present, foramen caroticopharyngeale usually occurs in the walls of this depression [1]. (72) Canalis caroticus internus formed entirely by pterygoid caudally (Gaffney and Meylan, 1988; Gaffney et al., 1991; Gaffney, 1996: 9): formed partly or not by pterygoid [0]; formed entirely by pterygoid without contribution from parabasisphenoid [1]. (73) Canalis caroticus internus and canalis caroticus lateralis completely embedded in bone (Gaffney, 1996): both canals open ventrally [0]; both canals embedded in bone [1]; internal carotid canal open, canalis caroticus lateralis closed [2]. (74) Size of foramen caroticum laterale relative to foramen anterius canalis caroticus interius (Gaffney, 1975; Meylan and Gaffney, 1989; Shaffer et al., 1997: 91): smaller than or equal [0]; larger [1]. (75) Pterygoid contribution to foramen nervi trigemini (Bertl and Killebrew, 1983; Stephens and Wiens, 2003: 69): does not contribute to ventral border, dorsal projection of pterygoid separated from foramen nervi trigemini by rostral projection of quadrate and caudal projection of epipterygoid and/or parietal [0]; contributes to ventral border of foramen nervi trigemini [1]. (76) Dorsal surface of supraoccipital crest in lateral view (Stephens and Wiens, 2003: 56): rounded [0]; straight, forming a continuous line along more than three-quarters of its length [1]; peaked such that both rostral and caudal halves of crest are straight, but caudal half slopes ventrally at an angle from rostral half [2]. (77) Caudal termination of supraoccipital crest (Stephens and Wiens, 2003: 58): rounded [0]; acute to subacute [1]. (78) Ventral slope of supraoccipital crest, when crest is sloped (Stephens

and Wiens, 2003: 57): begins rostral to supraoccipital-parietal suture [0]; begins at supraoccipital-parietal suture [1]; begins caudal to supraoccipital-parietal suture [2]. (79) Processus trochlearis oticum formed by prootic and quadrate (Gaffney, 1975; Gaffney et al., 1991): absent [0]; present [1]. (80) Parietal makes up one-third or more of processus trochlearis oticum (Hirayama, 1985: 37; Gaffney and Meylan, 1988; Gaffney et al., 1991: 6; Shaffer et al., 1997: 74; Yasukawa et al., 2001: 18; Joyce and Bell, 2004: L): no [0]; yes [1]. (81) Size of canalis stapediotemporalis relative to canalis caroticum laterale (modified from Shaffer et al., 1997: 67): larger [0]; smaller [1]. (82) Hyomandibular branch of facial nerve (Gaffney et al., 1991): lies within canalis cavernosus [0]; lies in its own canal [1]. (83) Size of perilymphatic foramen relative to foramen posterius canalis carotici interni (Gaffney, 1990, 1996: 15; Brinkman and Nicholls, 1993): larger [0]; smaller [1]. (84) Canalis caroticus internus at least partly formed by pterygoid (Gaffney et al., 1991; Gaffney, 1996): no [0]; yes [1]. (85) Foramen posterius canalis carotici interni (Gaffney and Meylan, 1989; Gaffney, 1996: 10): not formed by parabasisphenoid and pterygoid [0]; formed by parabasisphenoid and pterygoid, midway along parabasisphenoid/pterygoid suture [1]; formed solely by pterygoid [2]. (86) Processus paroccipitalis of the opisthotic (Gaffney et al., 1991): loosely articulated, if at all, to squamosal and quadrate [0]; tightly sutured to squamosal and quadrate [1]. (87) Parabasisphenoid-basioccipital suture (Stephens and Wiens, 2003: 42): not notched [0]; with medial notch [1]. NOTE: Notch may represent remnant of fenestra basicranialis posterior. (88) Shape of parabasisphenoid-basioccipital suture (Bertl and Killebrew, 1983; Stephens and Wiens, 2003: 41): straight [0]; rostrally convex [1]; straight medially, but lateral edges slope caudally [2]; rostrally concave [3]. (89) Basioccipital process of parabasisphenoid, small caudomedial projection of parabasisphenoid (Stephens and Wiens, 2003: 43): absent [0]; present [1]. (90) Paired pits on ventral surface of parabasisphenoid (Brinkman and Peng, 1993a, 1993b; Gaffney, 1996): absent [0]; present [1]. (91) Occipital condyle (Shaffer et al., 1997: 44): includes basioccipital [0]; excludes basioccipital [1]. (92) Exoccipitals meet dorsal to foramen magnum (Shaffer et al., 1997: 51): no [0]; yes [1]. (93) Sella turcica (Shaffer et al., 1997: 65): partly concealed by dorsum sellae [0]; not concealed by dorsum sellae [1]. (94) Paired foramina anterius canalis carotici interni (Shaffer et al., 1997: 64): separated by space less than two to three times their diameter [0]; separated by space two to three times greater than their diameter or more [1]. (95) Shape of rostral tip of parabasisphenoid (Stephens and Wiens, 2003: 39): acute [0]; rounded [1]. (96) Foramen at rostral tip of parabasisphenoid (Stephens and Wiens, 2003: 40): absent [0]; present [1]. NOTE: It is unclear what passes through this foramen. Stephens and Wiens (2003) noted that when this foramen is present, the shape of the rostral tip of the parabasisphenoid cannot be scored because that tip is not fully ossified. This character, therefore, may be addressing ossification of the parabasisphenoid, rather than the presence of a structure creating a foramen in this region during development. (97) Lateral edges of

rostral projection of parabasisphenoid in ventral view (Killebrew, 1979; Stephens and Wiens, 2003: 37): convex [0]; concave [1]; convex caudally, concave rostrally [2]; straight [3]; convex rostrally, concave caudally [4]. (98) Tuberculum basioccipitale (Stephens and Wiens, 2003: 45): absent [0]; present [1]. (99) Orientation of tuberculum basioccipitale (Stephens and Wiens, 2003: 46): directed caudally [0]; directed ventrally [1]. (100) Apex of lower jaw (Seidel and Palmer, 1991; Stephens and Wiens, 2003: 70): angled [0]; rounded [1]. (101) Rostral margin of dentary in lateral view (McDowell, 1964; Stephens and Wiens, 2003: 71): rounded [0]; forms 90° angle ventrally with ventral margin of dentary [1]. (102) Rostral margin of lower jaw hooked dorsally (Stephens and Wiens, 2003: 74): no [0]; yes [1]. (103) Ventromedial surface of dentary in rostral view (McDowell, 1964; Stephens and Wiens, 2003: 72): rounded [0]; flattened [1]. (104) Median ridge of lower triturating surface of dentary (McDowell, 1964; Stephens and Wiens, 2003: 78): absent [0]; present and separate from and lateral to lingual ridge [1]. (105) Edge of triturating surface of dentary (McDowell, 1964; Stephens and Wiens, 2003: 76): with distinct lingual border, a sharp angularity setting off horizontal triturating surface from medial surface of dentary [0]; lacks distinct lingual border and slopes gradually toward vertical medial face of dentary [1]. (106) Triturating surface of dentary (Stephens and Wiens, 2003: 75): not spatulate [0]; broad and spatulate [1]. (107) Caudal extension of lower triturating surface behind symphysis of dentary (Hirayama, 1985: 42; Gaffney and Meylan, 1988; Joyce and Bell, 2004: 33): present [0]; absent [1]. (108) Rostromedial width of triturating surface of dentary (McDowell, 1964; Stephens and Wiens, 2003: 77): in dorsal view not sharply defined rostromedially, width of rostromedial and lateral triturating surfaces roughly equal [0]; sharply defined rostromedially, width of rostromedial surface at least twice the width of lateral surface [1]. (109) Foramen dentofaciale majus (Hirayama, 1985: 47; Joyce and Bell, 2004: 27): small [0]; large and situated within large lateral fossa [1]. (110) Angular contribution to sulcus cartilaginis meckelii (McDowell, 1964; Gaffney and Meylan, 1988; Shaffer et al., 1997: 40; Stephens and Wiens, 2003: 79; Joyce and Bell, 2004: 24): present, angular contributes to sulcus and is as long or longer than prearticular [0]; absent, angular shorter than prearticular [1]. (111) Surangular-dentary contact (Crumly, 1982: 12; Crumly, 1985; Gaffney and Meylan, 1988; Joyce and Bell, 2004: 25): simple contact [0]; strongly interdigitating suture formed by rostrally projecting strut of surangular [1]. (112) Height of coronoid (Hirayama, 1985: 45; Joyce and Bell, 2004: 26): as high as dentary [0]; rising significantly above dentary [1]. (113) Processus coronoideus (Bertl and Killebrew, 1983; Stephens and Wiens, 2003: 80): not hooked [0]; hooked [1].

Additional Discrete Characters Exhibiting Variation in the SMRS

(114) Foramen in parietal near dorsal margin of foramen nervi trigemini: absent [0]; present, either as a groove or completed foramen [1]. (115) Cheek emargination even or dorsal to ventral margin of cavum

tympani: present [0]; absent, remains below cavum tympani [1]. (116) Foramen palatinum posterius in ventral view: formed between palatine medially and maxilla laterally [0]; surrounded by palatine [1]. (117) Shape of foramen palatinum posterius in ventral view: greatest length of foramen 2× its greatest width or more [0]; greatest length less than 2× greatest width [1]. (118) Small foramen positioned within palatine slightly caudal to foramen palatinum posterius on ventral surface of palate: absent [0]; present [1]. (119) Foramina arteriaevidianae: absent [0]; present, single foramen [1]; present, two foramina [2]; present, three foramina [3]; present, four foramina [4]. (120) Foramina arteriae anteriovidianae: absent [0]; present, in caudal wall of foramen palatinum posterius [1]; present, positioned between foramen palatinum posterius and rostral margin of lateral wall of cavum cranii [2]. (121) Epipterygoid-quadrate contact: absent, epipterygoid and processus epipterygoideus separated by fossa cartilaginis epipterygoidei [0]; present, fossa cartilaginis epipterygoidei obliterated by advanced ossification of the palatoquadrate cartilage [1]. (122) Participation of quadrate in foramen nervi trigemini: absent, dorsal margin of processus epipterygoideus of quadrate excluded from foramen by crista pterygoidea of pterygoid [0]; present [1]. (123) Horizontal process of quadrate extending medially within cranioquadrate portion of cavum acusticojugulare to nearly make contact with prootic: absent [0]; present [1]. (124) Restriction of incisura columellae auris: absent, incisura open [0]; present, restricted by vertical ridge of quadrate extending dorsally [1]; present, restricted by vertical ridge of quadrate extending ventrally [2]. (125) Osseous signature of chorda tympani branch of facial (VII) nerve: absent, no obvious canal or groove, chorda tympani nerve presumably passes out of cavum acusticojugulare through fenestra postotica [0]; canalis chorda tympani quadrati formed completely within quadrate [1]; completely within quadrate but groove rather than canal [2]; canal, between quadrate and pterygoid [3]; groove, between quadrate and pterygoid [4]; canal or groove, completely within pterygoid [5]. (126) Epipterygoid-palatine contact: absent [0]; present, rostral margin of epipterygoid contacts caudal margin of dorsal process of palatine along lateral wall of cavum cranii [1]. (127) Pterygoid-opisthotic contact: absent [0]; present, contact between dorsal surface of pterygoid and ventral surface of processus interfenestralis of opisthotic [1]. (128) Position of foramen caroticopharyngeale relative to rostral margin of parabasisphenoid in ventral view: caudal [0]; rostral [1]. (129) Dorsal margin of foramen caroticum laterale: formed at least partly by pterygoid [0]; formed completely by prootic [1]. (130) Dorsal margin of foramen pro ramo nervi vidiani: dorsal margin completed by pterygoid [0]; dorsal margin partly formed by pterygoid with contribution from prootic [1]; dorsal margin completed by prootic [2]. (131) Rostral margin of foramen pro ramo nervi vidiani: complete ossification of pterygoid in this area resulting in completed rostral margin [0]; minimal ossification resulting in lack of an rostral margin formed by pterygoid [1]. (132) Caudal margin of foramen pro ramo nervi vidiani: complete ossification of pterygoid in this area resulting in

APPENDIX 4

Scorings for Discrete Characters Listed in Appendix 2 that Exhibit Variation within the SMRS (R and L refer to right and left and denote a bilateral asymmetry)

	5	6	11	20	21	28	29	30	32	33	35	41	42	43	44	45	48	55	59	65	66	67	69
Juvenile Males (N = 5)																							
M-2992	?	?	?	1	1	1	?	0	?	?	?	?	0	?	?	?	?	1	?	?	?	1	1
M-2980	0	1	0	0	1	1	1	0	0	0	0	1	0	1	0	0	0	1R	0	0	0	1	1
M-2986	0	0	0	?	1	1	0	0	0	0	1	1	0	1	1	0	0	0	0	0	0	1	1R
M-2993	0	0	1	1	1	1	1	0	0	1	1	1	0	1	0	0	0	0	1	0	0	1	1
M-2981	0	0	0	1L	1	1	1	0	1L	1L	1	1	0	0	?	0	0	1R	0	0	?	1L	1
Juvenile Females (N = 10)																							
M-2960	?	?	?	0	1	1	1	0	?	?	1	?	?	?	?	?	0	0	0	?	0	1	1
M-2971	0	0	0	1	1	1	1	0	1R	0	1	1	0	1	0	0	0	0	0	0	0	1	1
M-2974	0	0	1	1R	1	1	1	0	0	0	1	1	0	1	0	1	0	0	0	0	0	1	1
M-2978	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?	?	?	1	1
M-2994	0	0	0	1	1	1	1	0	0	0	1	1	0	0	?	1	0	0	1	0	0	1	1
M-2990	0	0	0	1L	1	1	1	0	0	1	1	1	0	1	1	0	0	0	1	?	0	1	1
M-2995	0	0	1	1	1	1	1	0	0	1	1	1	0	1	0	0	0	0	1	0	0	1	1
M-2991	?	?	?	?	?	?	?	1	0	?	1	?	0	1	?	?	0	?	1	?	0	1	1
M-2968	0	0	0	1	0	0	0	0	1	0	1	1	0	1	0	0	0	0	1	0	0	1	1
M-2965	0	0	1	1L	?	?	?	0	0	0	1	?	0	1	0	0	0	0	0	0	0	1	1
Adult Males (N = 12)																							
M-2997	0	0	0	1	1	1	1	0	0	0	1	1	0	1	0	0	0	0	0	0	1L	1	1
M-2976	0	0	1	0	1	1	1	0	1	0	1	1	0	1	0	0	0	0	1	0	0	1	1
M-2987	0	0	0	0	?	?	0	0	0	0	1	1	0	1	1	2	0	0	0	0	0	1	1
M-2996	0	0	0	0	0	1	1	0	?	?	1	?	0	1	?	?	0	0	?	?	0	1	1
M-2988	0	0	0	0	0	1	1	0	1	0	1	1	0	1	0	2	0	1	1	0	0	1	1
M-2989	0	0	0	1	1	1	1	0	1	1	1	1	0	1	0	2	0	0	1	0	0	1	1
M-2979	1	0	0	1	1	1	1	0	0	1	1	1	1	0	?	0	0	0	0	0	0	1	1
M-2984	0	0	0	1R	1	1	1	3	1	0	1	0	0	1	1	0	0	0	1	0	0	1	1
M-2975	0	0	0	1R	1	1	1	0	0	0	1	0	0	1	1	2	1	1R	1L	0	0	1	1
M-2985	0	0	0	1	1	1	1	?	?	?	1	1	0	1	0	0	?	0	1	0	0	1	1
M-2982	?	?	?	1	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	1	1
M-2983	1	0	0	0	1	1	1	3	1	1L	1	0	1	1	1	0	0	0	1	1	1	1	1

APPENDIX 4
(Continued)

	5	6	11	20	28	29	30	32	33	35	41	42	43	44	45	48	55	59	65	66	67	69
Adult Females (N = 11)																						
M-2977	0	0	1	0	1	1	0	0	0	1	?	0	1	0	0	0	0	1	0	0	1	1
M-2969	0	0	1	1	1	1	0	0	1	1	1	1	1	0	0	0	0	1	0	0	1	1
M-2964	0	0	0	0	?	0	0	?	?	1	?	0	0	?	?	0	0	0	0	0	1	1
M-2959	1	1	0	1L	1	1	0	0	0	1	1	0	1	0	0	0	0	0	1	0	1	1
M-2970	0	0	0	0	1	1	0	0	1R	1	1	1	1	1	0	0	0	1R	0	0	1	1
M-2958	0	0	0	1	1	1	0	1	1	1	1	0	1	0	0	0	0	1	1R	1R	1	1
M-2967	0	0	0	1	1	1	0	1	0	1	?	0	1	0	2	0	0	1	0	0	1	1
M-2973	0	0	0	1	1	1	0	0	0	1	0	0	1	1	0	0	0	1	0	0	1	1
M-2966	0	0	0	1R	1	1	0	0	0	1	0	0	1	0	0	0	0	1	0	0	1	1
M-2956	1	1	0	0	0	0	0	0	1	1	1	0	1	1	2	0	0	0	0	0	1L	1
M-2961	0	0	0	1	1	1	0	0	0	1	1	1	1	1	2	1	1L	1	1	0	1	1
70 75 76 77 78 83 87 88 95 97 106 108 110 114 115 116 117 118 119 120 121 122																						
Juvenile Males (N = 5)																						
M-2992	0	?	?	?	?	?	1	2	?	2	0	0	0	?	?	0	?	0	1	1	?	?
M-2980	0	1	2	1	1	?	1	2	1	2	0	0	0	0	0	0	0	1	2	1	0	0
M-2986	0	1	0	0	?	?	1	2	1	2	0	1	0	0	0	0	1	1R	3	1	0	0
M-2993	0	1	2	1	1	?	1	2	1	2	0	1	0	?	0	0	1	1	2	1	0	0
M-2981	0	1	0	0	?	?	1	1	1	3	0	0	0	0	0	0	0	1	2	1	0	0
Juvenile Females (N = 10)																						
M-2960	0	?	0	0	1	0	1	2	1	3	0	0	0	?	?	0	?	0	2	1	?	?
M-2971	0	1	0	0	2	?	1	2	1	2	0	0	0	0	0	0	1	1R	1	1	0	0
M-2974	0	1	0	0	2	?	1	2	1	2	0	0	0	?	?	0	0	1L	2	1	0	0
M-2978	0	?	?	?	?	?	1	2	?	0	0	?	?	?	?	0	?	0	1	1	?	?
M-2994	0	1	0	1	1	?	1	2	0	2	0	0	0	1	0	0	?	1	1	1	0	1
M-2990	0	1	2	1	1	1	1	2	1	0	0	0	0	?	?	0	?	1R	2	1	?	?
M-2995	0	1L	2	1	1	?	1	2	1	1	0	0	0	0	0	0	0	1L	2	1	0	1
M-2991	0	?	2	0	1	0	1	2	1	0	0	0	0	?	?	?	?	?	1	?	?	?
M-2968	0	1	0	0	1	?	1	2	1	2	0	0	0	0	0	0	0	0	3	1	0	0
M-2965	0	1	2	0	1	?	1	2	1	2	0	1	0	0	0	0	1	0	2	1R	0	0

APPENDIX 4
(Continued)

	70	75	76	77	78	83	87	88	95	97	106	108	110	114	115	116	117	118	119	120	121	122
Adult Males (N = 12)																						
M-2997	0	1	2	1	2	?	0	1	1	0	0	1	0	1R	1	0	0	1L	3	1	0	0
M-2976	0	0	0	0	1	?	0	2	1	2	0	1	0	0	0	0	1	1R	1	1	1	1
M-2987	0	0	0	0	1	?	0	1	1	2	0	1	1	1	1	0	0	0	2	1R	0	0
M-2996	0	?	0	0	1	0	0	?	1	0	0	1	?	0	?	0	?	0	2	1	?	?
M-2988	0	1	0	0	1	?	1	0	?	1	3	0	1	0	1	0	0	1R	2	1R	0	?
M-2989	0	1	0	1	0	?	1	2	1	3	0	1	0	0	0	0	0	0	2	1	0	0
M-2979	0	1	0	0	1	?	1	2	1	0	0	1	0	0	0	0	1	1R	4	1	0	0
M-2984	0	1	0	0	0	?	1	0	1	0	0	1	0	1	1	0	0	0	3	1	0	0
M-2975	1R	1	0	0	0	?	0	1	1	2	0	1	0	0	1	0	0	1	3	1	0	0
M-2985	0	1	0	0	0	?	0	2	0	0	0	1	?	0	1	0	1	0	3	1	0	0
M-2982	0	?	?	?	?	0	0	?	?	0	0	1	?	0	?	0	?	1L	3	1	?	?
M-2983	0	1	0	0	0	?	0	1	1	3	1	1	0	1	1	1	0	1	2	1	1	0
Adult Females (N = 11)																						
M-2977	0	1	0	0	1	?	1	1	1	2	0	1	0	1	1	0	1	0	3	1	0	0
M-2969	0	1	0	0	1	?	1	1	0	3	0	1	0	1	1	1R	1	0	2	1	0	1
M-2964	0	1	0	0	1	?	0	2	1	3	0	1	1	0	?	0	0	0	2	1	0	0
M-2959	0	1	1	0	1	?	1	2	1	0	0	1	0	0	0	0	0	0	3	1R	0	0
M-2970	0	1	0	0	1	?	1	1	1	2	0	1	0	0	1	0	0	1L	2	1	0	0
M-2958	0	1	2	1	1	?	1	2	1	3	0	1	0	0	0	1	0	0	2	1	0	0
M-2967	0	1	0	0	0	?	0	2	1	2	0	1	0	1	0	0	0	1L	4	1	0	0
M-2973	0	1	2	0	0	?	0	1	0	0	0	1	0	0	0	?	1	1	2	1	1	0
M-2966	0	1	0	0	0	?	1	1	1	3	0	1	0	0	1	1	0	1L	2	1	1	0
M-2956	0	1	0	1	2	?	0	1	1	2	0	1	0	0	1	1L	0	1R	4	1	0	0
M-2961	0	?	0	0	1	?	0	2	1	0	0	1	0	1	0	0	?	1R	3	1	0	1
Juvenile Males (N = 5)																						
M-2992	0	0	2	?	?	?	1	0	A	?	?	1	1	0	?	?	0	0	0	0	1	0
M-2980	0	0	2	1	0	?	1	?	?	?	?	1	0	?	1	B	0	1	?	0	1	0
M-2986	0	1	2	0	0	?	1	?	?	?	?	0	0	?	1	1	0	0	?	0	0	0
M-2993	0	1	C	0	0	?	1	?	?	?	?	0	0	?	1	0	0	0	?	0	0	0
M-2981	0	1	2	1	0	?	1	?	?	?	?	1	1	?	1	0	0	0	?	0	1R	0

APPENDIX 4
(Continued)

	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144
Juvenile Females (<i>N</i> = 10)																						
M-2981	0	1	2	1	0	1	?	?	?	?	?	1	1	?	1	0	0	?	?	0	1R	0
M-2960	0	1	3	?	?	1	0	?	?	A	1	1	0	1	1	0	1	0	?	0	?	0
M-2971	0	1	0	1	0	1	?	?	?	?	?	1	1	1	1	0	0	?	?	0	0	0
M-2974	0	0	2	0	0	1	?	?	?	?	?	0	0	?	1	0	0	?	?	0	0	0
M-2978	0	1	4	?	?	?	0	2	?	?	?	1	1	1R	?	0	0	0	?	?	?	0
M-2994	0	1	D	1	0	1	?	?	?	?	?	0	0	?	1	0	0	?	?	0	0	0
M-2990	0	0	4	?	?	?	1	0	0	1	1	0	0	0	1	0	0	?	?	?	?	0
M-2995	0	1	2	1	0	1L	?	?	?	?	?	1	1	?	1	0	1	?	?	1	0	0
M-2991	0	1	0	?	?	1	0	2	?	?	1	0	0	1	?	0	0	?	?	0	?	?
M-2968	0	1	3	0	0	1L	?	?	?	?	?	0	0	?	1	0	1	0	?	1	1	0
M-2965	0	1	4	0	0	1L	?	?	?	?	?	0	0	?	1	0	0	?	?	1	0	?
Adult Males (<i>N</i> = 12)																						
M-2997	0	1	1	?	1	0	?	?	?	?	?	0	1	?	1	0	2	?	?	2	0	0
M-2976	0	A	2	1	0	0	?	?	?	?	?	1	1	?	1	0	1	0	?	1	0	0
M-2987	0	0	2	0	0	1	?	?	?	?	?	1	1	?	1	0	1	0	?	1	1R	0
M-2996	0	A	3	?	0	1	0	1	?	?	2	0	0	?	1	0	1	0	?	1	?	0
M-2988	0	1	1	1	0	1	?	?	?	?	?	1	1	?	1	0	2	0	?	2	0	0
M-2989	1	1	1	1	0	1L	?	?	?	?	?	1	1	?	1	E	2	0	?	2	0	0
M-2979	1	1	3	0	0	1	?	?	?	?	?	1	1	?	1	0	2	0	?	2	?	?
M-2984	1	1	2	0	0	1	?	?	?	?	?	1	1	1	1	0	2	0	?	2	?	?
M-2975	1	0	4	1	0	0	?	?	?	?	?	1	1	?	1	B	2	0	?	2	0	0
M-2985	1	1	F	0	1L	0	?	?	?	?	?	1	1	?	1	0	2	1	?	2	?	?
M-2982	1	0	1	?	?	1	1	2	1	1	?	1	1	1	?	0	0	?	?	2	?	?
M-2983	1	1	G	0	1	1	?	?	?	?	?	1	1	?	0	0	2	?	?	2	?	0
Adult Females (<i>N</i> = 11)																						
M-2977	0	0	0	0	0	0	?	?	?	?	?	1	0	?	1	C	1	1	?	1	0	0
M-2969	1	1	1	0	0	0	?	?	?	?	?	1	1	?	1	2	1	0	?	1	?	0
M-2964	0	1	1	?	0	0	?	A	0	1	C	1	1	1	1	0	1	0	1	?	?	0
M-2959	0	1	C	1	1	1	?	?	?	?	?	1	1	?	1	0	1	0	?	1	0	0
M-2970	0	1	4	1L	0	1	?	?	?	?	C	1	0	?	1	1	1	0	?	1	1L	?
M-2958	0	1	H	1	1	1	?	?	?	?	?	1	1	?	1	0	2	0	?	2	0	?
M-2967	1	1	3	0	0	0	?	?	?	?	?	1	1	?	1	0	2	1	?	2	?	0

APPENDIX 5

Summary of Discrete and Variation Scores for Characters Exhibiting Variation within the SMRS

Character (Ch.) numbers refer to character descriptions in appendix 2. 0, 1, 2, 3 refer to states of those character and the percentage (%) of specimens exhibiting those states. V refers to Variation Scores (see Materials and Methods). For character states 2 and 3, percentages are given in parentheses.

Ch.	5	6	11	20	28	29	30	32	33	35	41	42	43	44	45	48	55	59
Total Sample																		
N	33	33	33	35	32	34	36	31	31	37	28	36	35	28	31	36	37	34
0	29	30	26	19	2	4	34	20	19	1	6	29	4	18	22	34	31	13
%	87.9	90.9	78.8	54.3	6.3	11.8	94.4	64.5	61.3	2.7	21.4	80.6	11.4	64.3	71.0	94.4	83.8	38.2
1	4	3	7	16	30	30	0	11	12	36	22	7	31	10	2	2	6	21
%	12.1	9.1	21.2	45.7	93.8	88.2	0.0	35.5	38.7	97.3	78.6	19.4	88.6	35.7	6.5	5.6	16.2	61.8
2									0(0.0)					7(22.6)				
3							2(5.6)											
V	12.1	9.1	21.2	45.7	6.3	11.8	5.6	35.5	38.7	2.7	21.4	19.4	11.4	35.7	29.0	5.6	16.2	38.2
Juveniles																		
N	11	11	11	12	12	12	13	11	11	13	10	13	12	9	11	14	14	13
0	11	10	7	6	1	1	13	7	6	1	0	13	2	7	9	14	11	7
%	100.0	90.9	63.6	50.0	8.3	8.3	100.0	63.6	54.5	7.7	0.0	100.0	16.7	77.8	81.8	100.0	78.6	53.8
1	0	1	4	6	11	11	0	4	5	12	10	0	10	2	2	0	3	6
%	0.0	9.1	36.4	50.0	91.7	91.7	0.0	36.4	45.5	92.3	100.0	0.0	83.3	22.2	18.2	0.0	21.4	46.2
V	0.0	9.1	36.4	50.0	8.3	8.3	0.0	36.4	45.5	7.7	0.0	0.0	16.7	22.2	18.2	0.0	21.4	46.2
Adults																		
N	22	22	22	23	20	22	22	20	20	24	18	23	23	19	20	22	23	21
0	18	20	19	13	1	3	20	13	13	0	6	16	2	11	13	20	20	6
%	81.8	90.9	86.4	56.5	5.0	13.6	90.9	65.0	65.0	0.0	33.3	69.6	8.7	57.9	65.0	90.9	87.0	28.6
1	4	2	3	10	19	19	0	7	7	24	12	7	21	8	0	2	3	15
%	18.2	9.1	13.6	43.5	95.0	86.4	0.0	35.0	35.0	100.0	66.7	30.4	91.3	42.1	0.0	9.1	13.0	71.4
2							0(0.0)								7(35.0)			
3							2(9.1)											
V	18.2	9.1	13.6	43.5	5.0	13.6	9.1	35.0	35.0	0.0	33.3	30.4	8.7	42.1	35.0	9.1	13.0	28.6
Males																		
N	15	15	15	16	15	15	16	14	14	15	14	17	15	12	14	15	17	14
0	13	14	13	9	0	1	14	8	9	1	4	13	2	7	10	14	12	7
%	86.7	93.3	86.7	56.3	0.0	6.7	87.5	57.1	64.3	6.7	28.6	76.5	13.3	58.3	71.4	93.3	70.6	50.0

APPENDIX 5
(Continued)

Ch.	5	6	11	20	28	29	30	32	33	35	41	42	43	44	45	48	55	59
1	2	1	2	7	15	14	2	6	5	14	10	4	13	5	0	1	5	7
%	13.3	6.7	13.3	43.8	100.0	93.3	12.5	42.9	35.7	93.3	71.4	23.5	86.7	41.7	0.0	6.7	29.4	50.0
2							0(0.0)								4(28.6)			
3							0(0.0)											
V	13.3	6.7	13.3	43.8	0.0	6.7	12.5	42.9	35.7	6.7	28.6	23.5	13.3	41.7	28.6	6.7	29.4	50
Females																		
N	18	18	18	19	17	19	20	17	17	20	14	19	19	16	17	21	20	20
0	16	16	13	10	2	3	18	12	10	0	2	16	2	11	12	20	19	8
%	88.9	88.9	72.2	52.6	11.8	15.8	90.0	70.6	58.8	0.0	14.3	84.2	10.5	68.8	70.6	95.2	95.0	40.0
1	2	2	5	9	15	16	0	5	7	20	12	3	17	5	2	1	1	12
%	11.1	11.1	27.8	47.4	88.2	84.2	0.0	29.4	41.2	100.0	85.7	15.8	89.5	31.3	11.8	4.8	5.0	60.0
2							0(0.0)								3(17.6)			
3							2(10.0)											
V	11.1	11.1	27.8	47.4	11.8	15.8	0.0	29.4	41.2	0.0	14.3	15.8	10.5	31.3	11.8	4.8	5.0	40.0
Total Sample																		
Ch.	65	66	67	69	70	75	76	77	78	83	87	88	95	97	106	108	110	115
N	31	35	38	38	38	31	35	35	35	8	38	36	35	38	38	38	31	33
0	27	32	2	1	37	2	23	23	9	5	13	2	4	12	37	12	29	23
%	87.1	91.4	5.3	2.6	97.4	6.5	65.7	65.7	25.7	62.5	34.2	5.6	11.4	31.6	97.4	31.6	93.5	69.7
1	4	3	36	37	1	29	1	12	22	3	25	11	31	1	1	26	2	10
%	12.9	8.6	94.7	97.4	2.6	93.5	2.9	34.3	62.9	37.5	65.8	30.6	88.6	2.6	2.6	68.4	6.5	30.3
2							11(31.4)		4(11.4)			23(63.9)		16(42.1)				
3														9(23.7)				
V	12.9	8.6	5.3	2.6	2.6	6.5	34.3	34.3	25.7	37.5	34.2	36.2	11.4	42.1	2.6	31.6	6.5	30.3
Juveniles																		
N	10	12	15	15	15	11	13	13	13	5	15	15	13	15	15	15	14	10
0	10	12	1	1	15	1	6	7	2	2	0	0	1	3	15	12	14	9
%	100.0	100.0	6.7	6.7	100.0	9.1	46.2	53.8	15.4	40.0	0.0	0.0	7.7	20.0	100.0	80.0	100.0	90.0
1	0	0	14	14	0	10	0	6	10	3	15	1	12	1	0	3	0	1
%	0.0	0.0	93.3	93.3	0.0	90.9	0.0	46.2	76.9	60.0	100.0	6.7	92.3	6.7	0.0	20.0	0.0	10.0
2							7(53.8)		1(7.7)			14(93.3)		9(60.0)				
3														2(13.3)				

APPENDIX 5
(Continued)

Ch.	65	66	67	69	70	75	76	77	78	83	87	88	95	97	106	108	110	115
V	0.0	0.0	6.7	6.7	0.0	9.1	46.2	46.2	15.4	40.0	0.0	6.7	7.7	40.0	0.0	20.0	0.0	10.0
Adults																		
N	21	23	23	23	23	20	22	22	22	3	23	21	22	23	23	23	17	23
0	17	20	1	0	22	1	17	16	7	3	13	2	3	9	22	0	15	14
%	81.0	87.0	4.3	0.0	95.7	5.0	77.3	72.7	31.8	100.0	56.5	9.5	13.6	39.1	95.7	0.0	88.2	60.9
1	4	3	22	23	1	19	1	6	12	0	10	10	19	0	1	23	2	9
%	19.0	13.0	95.7	100.0	4.3	95.0	4.5	27.3	54.5	0.0	43.5	47.6	86.4	0.0	4.3	100.0	11.8	39.1
2							4(18.2)		3(13.6)			9 (42.9)		7(30.4)				
3														7(30.4)				
V	19.0	0.0	4.3	0.0	4.3	5.0	22.7	27.3	45.4	0.0	43.5	47.6	13.6	39.1	4.3	0.0	11.8	39.1
Males																		
N	14	15	17	17	17	14	15	15	15	3	17	15	15	17	17	17	14	15
0	13	13	1	1	16	1	12	10	6	2	8	2	1	6	16	3	13	10
%	92.9	86.7	5.9	5.9	94.1	7.1	80.0	66.7	40.0	66.7	47.1	13.3	6.7	35.3	94.1	17.6	92.9	62.5
1	1	2	16	16	1	13	0	5	7	1	9	5	14	0	1	14	1	5
%	7.1	13.3	94.1	94.1	5.9	92.9	0.0	33.3	46.7	33.3	52.9	33.3	93.3	0.0	5.9	82.4	7.1	31.3
2							3(20.0)		2(13.3)			8(53.3)		7(41.2)				
3														4(23.5)				
V	7.1	13.3	5.9	5.9	5.9	7.1	20.0	33.3	46.7	33.3	47.1	13.3	6.7	41.2	5.9	17.6	7.1	31.3
Females																		
N	17	20	21	21	21	17	20	20	20	5	21	21	20	21	21	21	20	18
0	14	19	1	0	21	1	11	13	3	3	5	0	3	6	21	9	19	13
%	82.4	95.0	4.8	0.0	100.0	5.9	55.0	65.0	15.0	60.0	23.8	0.0	15.0	28.6	100.0	42.9	95.0	72.2
1	3	1	20	21	0	16	1	7	15	2	16	6	17	1	0	12	1	5
%	17.6	5.0	95.2	100.0	0.0	94.1	5.0	35.0	75.0	40.0	76.2	28.6	85.5	4.8	0.0	57.1	5.0	27.8
2							8(40.0)		2(10.0)			15(71.4)		9(42.9)				
3														5(23.8)				
V	17.6	5.0	4.8	0.0	0.0	5.9	45.0	35.0	25.0	40.0	23.8	28.6	15.0	42.9	0.0	42.9	5.0	27.8
Total Sample																		
Ch.	116	117	118	119	120	121	122	123	124	125	126	127	128	129	130	131	132	133
Total Sample																		
N	30	37	30	37	38	37	31	38	30	38	37	29	31	38	8	8	8	8

APPENDIX 5
(Continued)

Ch.	116	117	118	119	120	121	122	123	124	125	126	127	128	129	130	131	132	133
0	17	32	20	15	0	4	27	25	25	10	3	14	26	16	7	1	7	2
%	56.7	86.5	66.7	40.5	0.0	10.8	87.1	65.8	83.3	26.3	8.1	48.3	83.9	42.1	87.5	12.5	87.5	25.0
1	13	5	10	22	6	33	4	13	5	26	9	15	5	22	1	4	1	4
%	43.3	13.5	33.3	59.5	15.8	89.2	12.9	34.2	16.7	68.4	24.3	51.7	16.1	57.9	12.5	50.0	12.5	50.0
2					19(50.0)					2(5.3)	12(32.4)					3(37.5)		
3					9(23.7)						8(21.6)							2(25)
4					4(10.5)						5(13.5)							
V	43.3	13.5	33.3	40.5	50.0	10.8	12.9	34.2	16.7	31.6	32.4	48.3	16.1	42.1	12.5	50.0	12.5	50.0
Juveniles																		
N	10	14	10	14	15	14	10	15	10	15	15	10	10	15	5	5	5	5
0	10	14	6	5	0	1	10	15	8	4	2	5	10	4	5	1	5	2
%	100.0	100.0	60.0	35.7	0.0	7.1	100.0	100.0	80.0	26.7	13.3	50.0	100.0	26.7	100.0	20.0	100.0	40.0
1	0	0	4	9	5	13	0	0	2	11	1	5	0	11	0	2	0	1
%	0.0	0.0	40.0	64.3	33.3	92.9	0.0	0.0	20.0	73.3	6.7	50.0	0.0	73.3	0.0	40.0	0.0	20.0
2					8(53.3)						7(46.7)					2(40.0)		
3					2(13.3)						2(13.3)							
4					0(0.0)						3(20.0)							
V	0.0	0.0	40.0	35.7	46.7	7.1	0.0	0.0	20.0	26.7	46.7	50.0	0.0	26.7	0.0	40.0	0.0	40.0
Adults																		
N	20	23	20	23	23	23	21	23	20	24	22	19	21	23	3	3	3	3
0	7	18	14	10	0	3	17	10	17	7	1	9	16	12	2	0	2	0
%	35.0	78.3	70.0	43.5	0.0	13.0	81.0	43.5	85.0	29.2	4.5	47.4	76.2	52.2	66.7	0.0	66.7	0.0
1	13	5	6	13	1	20	4	13	3	15	8	10	5	11	1	2	1	3
%	65.0	21.7	30.0	56.5	4.3	87.0	19.0	56.5	15.0	62.5	36.4	52.6	23.8	47.8	33.3	66.7	33.3	100.0
2					11(47.8)					2(8.3)	5(22.7)					1 (33.3)		0 (0)
3					7(30.4)						6(27.3)							
4					4(17.4)						2(9.1)							
V	35.0	21.7	30.0	43.5	47.8	13.0	19.0	43.5	15.0	38.1	50.0	47.4	23.8	47.8	33.3	33.3	33.3	0.0
Males																		
N	14	17	14	17	17	17	14	17	13	17	17	13	14	17	3	3	3	3
0	7	16	9	9	0	2	12	10	12	7	0	7	12	5	2	0	2	0
%	50.0	94.1	64.3	53.0	0.0	11.8	85.7	58.8	92.3	41.2	0.0	53.8	85.7	29.4	66.7	0.0	66.7	0.0
1	7	1	5	8	2	15	2	7	1	10	6	6	2	12	1	2	1	3

APPENDIX 5
(Continued)

Ch.	134	135	136	137	138	139	140	141	142	143	144
Adults											
N	3	23	23	4	22	23	23	20	3	23	14
0	0	4	7	0	1	17	0	16	0	0	11
%	0.0	17.4	30.4	0.0	4.5	74.0	0.0	80.0	0.0	0.0	78.6
1	2	19	16	4	21	3	8	4	3	8	3
%	66.7	82.6	69.6	100.0	95.5	13.0	34.8	20.0	100.0	34.8	21.4
2	1 (33.3)					3(13.0)	15 (65.2)			15(65.2)	
V	0.0	17.4	30.4	0.0	4.5	26.0	34.8	20.0	0.0	34.8	21.4
Males											
N	2	17	17	4	15	17	17	15	3	17	12
0	0	4	5	1	1	13	5	13	1	5	8
%	0.0	23.5	29.4	25.0	6.7	76.5	29.5	86.7	33.3	29.5	66.7
1	0	13	12	3	14	3	3	2	2	3	4
%	0.0	76.5	70.6	75.0	93.3	17.6	17.6	13.3	66.7	17.6	33.3
2	2 (100.0)					1(5.9)	9(52.9)			9(52.9)	
V	0.0	23.5	29.4	25.0	6.7	23.5	47.1	13.3	33.3	47.1	33.3
Females											
N	6	21	21	6	19	21	21	20	5	21	13
0	0	8	12	2	0	14	7	16	4	7	10
%	0.0	38.1	57.1	33.3	0.0	66.7	33.3	80.0	80.0	33.3	76.9
1	5	13	9	4	19	3	8	4	1	8	3
%	83.3	61.9	42.9	66.7	100.0	14.3	38.1	20.0	20.0	38.1	23.1
2	1 (16.7)					4(19)	6(28.6)			6(28.6)	
V	16.7	38.1	42.9	33.3	0.0	33.3	38.1	20.0	20.0	38.1	23.1

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