Neural bone patterns and
the phylogeny of the turtles of the
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Earlham College

Abstract

Neural bone patterns for turtles of the subfamily Kinosterninae are analyzed phylogenetically to produce a cladogram for all known species. Although this cladogram is not highly concordant with previously hypothesized species group relationships, when the data set is expanded to include presence or absence of clasping organs and first vertebral width, more concordant cladograms are produced. The synonymy of *Sternotherus* with *Kinosternon* is upheld. The results suggest that kinosternine neural patterns are subject to some homoplasy; however, when analyzed with other characters that are less likely to be homoplasic, significant phylogenetic information can emerge.

Introduction

The alpha taxonomy of the Recent mud and musk turtles of the subfamily Kinosterninae is finally becoming clear (see Berry, 1978; Berry and Iverson, 1980; Berry and Legler, 1980; Berry et al. MS; Iverson, 1976, 1978a, 1978b, 1979, 1981, 1986; Iverson and Berry, 1979; Legler, 1965; Reynolds and Seidel, 1983; Seidel and Lucchino, 1981). However, until Seidel et al. (1986) analyzed protein variation, no phylogenetic hypothesis for all known species in the subfamily had appeared in the literature. Hypotheses based on external plastral morphometrics are nearing completion (Iverson, MS), and these will soon be tested with data sets based on chemical composition of musk, skull morphology, and bony shell morphology. Analysis of shell morphology has begun and preliminary results on patterns of variation in the neural series and their implications for the relationships among the members of the subfamily Kinosterninae are presented here.

Materials and Methods

Skeletal specimens in my personal collection (to be deposited in the Florida State Museum collection: UF) representing 16 of the 19 recognized, Recent kinosternine species (Table 1) and one undescribed Recent species were examined for neural bone patterns. At least ten specimens from diverse parts of the range were examined for each species except *Kinosternon acutum* (N=2) and *K. creaseri* (N=4). For this analysis within-species variation in neural pattern is not discussed; only the modal-configuration for each species is identified and used in this analysis.

For species unrepresented in my collection, data were supplied as follows: the modal pattern for *K. angustipons* is assumed to be the one illustrated by Legler (1965); for *K. dunni*, that for a single specimen examined by Peter Meylan (pers. comm. based on AMNH 112397); and for *Kinosternon depressum*, the same as that of its sister taxon *K. minor* (the synonymy of the genus *Sternotherus* with *Kinosternon* follows Seidel et al., 1986, hence the use of the species names *carinatum*, *depressum*, and *odoratum*).

Neural formulae similar to those used by Auffenberg (1974) are used to describe neural patterns. A neural formula is preceded by an N if the first neural contacts the nuchal bone or a C if the first costals are in contact anterior to the first neural. The formula ends with an S if the last neural contacts the suprapygal, or with a C if posterior costals are in contact posterior to the last neural. Numbers indicate the number of other bones contacted by each neural. Angle brackets indicate the direction of symmetry for hexagonal (or pentagonal) neurals, with the open side of the bracket directed toward the short-sided end of the next neural. For example, the hypothetical formula N4<6<6486>6>6>S would represent a turtle with eight neurals, the first tetragonal and contacting the nuchal, the second and third hexagonal with the three adja-

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cent short sides directed anteriorly), the fourth tetragonal, the fifth octagonal, the sixth through eighth hexagonal with the short sides directed posteriorly, and the eighth neural contacting the suprapygal.

Cladistic methodology (see Wiley, 1981) was used in phylogeny construction. Polarity decisions were made by outgroup comparisons. Outgroups include members of the appropriate sister groups identified by Hutchison and Bramble (1981): *Xenochelys* (from Hay, 1908), representatives of the Staurotypinae (from specimens in my collection or that of UNAM at the Estacion Biologica "Los Tuxtlas"), *Hoplochelys* (from Hay, 1908 and Gilmore, 1919), *Dermatemys* (from Boulenger, 1889 and Peter Meylan, pers. comm.), and *Baptemys* (from Hay, 1908).

Results and Discussion

Six modal neural patterns (Fig. 1) are evident among the kinosternines (including *Xenochelys*). Comparisons with the neural patterns of the nearest relatives of the subfamily (Fig. 2; as identified by Hutchison and Bramble, 1981) reveal several important character state differences and their probable polarities. The ancestral neural pattern for this group (exhibited by *Baptemys* and many other living and extinct cryptodires and pleurodires) is apparently a complete series of eight anteriorly short-sided neurals (the first tetragonal) contacting the nuchal anteriorly and the suprapygal posteriorly (i.e., N4<6<6<6<6<6<6<6S). Reductions in the number of neurals and the loss of contact with the nuchal and suprapygal are clearly apomorphic (and correlated). Kinosternines are unique among turtles in the predominance of posteriorly short-sided neurals (most closely approached by trionychids; Meylan, 1987), and the reversal from anteriorly short-sided to posteriorly short-sided neurals is certainly derived. Based on the assumption that a transformation series has occurred among the kinosternines, increase in the amount of reversal apparently has occurred via the posterior shift in the location of the tetragonal neural, with those neurals anterior to the tetragonal one exhibiting short sides posteriorly (compare the series A through D in Fig. 1). Thus the further posterior the reversal of neural orientation, the more derived the condition.

The most parsimonious cladogram based on these characters (Table 1) and proposed polarities appears in Figure 3. This tree is striking in the degree to which it contradicts the recognition of the previously hypothesized, supposedly monophyletic, kinosternine species groups (Table 2). Most significantly, it suggests that two of the best defined species groups, the *Sternotherus* and *scorpioides* groups (sensu Berry, 1978 and Bramble et al., 1984) are not monophyletic. This makes interpreting the value of neural patterns for phylogeny construction in kinosternine turtles difficult.

Other studies (Iverson, MS) suggest that plastral morphology alone (including relative scute shapes and hindlobe kinesis) is also of very limited value for hypothesizing phylogenetic relationships, because of the high degree of correlation among plastral components and overall plastron size. Similarly, nasal scale shape is of little value since virtually the entire range of variation is known from the single species *Kinosternon hirtipes* (Iverson, 1981). However, each of these character sets, when analyzed in the context of a larger data set that presumably includes characters not as subject to homoplasy, may still provide important phylogenetic information.

At present I can identify only two additional characters that are potentially useful to the development of a kinosternine phylogeny. The first is the presence or absence of clasping organs (opposing rough scale patches on the crus and thigh of males; called

vinculae by Smith and Smith, 1980). Because these organs are found in all members of the subfamily Staurotypinae (presumably the sister group of the Kinosterninae; Gaffney, 1975, Hutchison and Bramble, 1981, and Bramble et al., 1984; but see Bickham and Carr, 1983), because they are found in most members of the subfamily Kinosterninae, and because they are used in such a crucial (presumably conservative) aspect of reproduction in the group (i.e. mating), their presence in the Kinosterninae is considered to be plesiomorphic. Only one species group of kinosternines (the *"scorpioides"* group) lacks clasping organs, and its members share other characters (including those listed in Table 2).

Because I believe it is doubtful that clasping organs have been lost more than once in this subfamily, I weigh this character very heavily. Allowing it to provide the primary structure to the phylogeny substantially alters the cladogram based only on neural characters (Fig. 4), and requires that the pattern of loss of nuchal contact, completion of neural reversal, and reduction to five neurals has evolved twice independently. However, with this provision the cladogram is highly concordant with the previously hypothesized species groups (Table 2). If clasping organ loss was homoplasic (and the neural cladogram accurate), that loss would have had to occur at least four times independently in the kinosternines. This makes Figure 4 the more parsimonious phylogeny.

A second useful non-neural character is the width of the first vertebral scute. A narrow scute (i.e. widely separated from contact with the second marginals and barely if at all overlapping the first peripheral bones) is considered primitive in the Kinosternidae because it is exhibited by its sister group, the genus *Hoplochelys*, as well as the staurotypines (except *Claudius)* and *Xenochelys*. Including this character in the phylogeny basically affects only the relative position of two species: *K. herrerai* (narrow first vertebral scute) and *K. flavescens* (wide scute). Either *K. herrerai* reevolved a narrow first vertebral scute and *K. flavescens* independently evolved a wide one (Fig. 4), or *herrerai* is the sister taxon to *odoratus, flavescens* is not closely related to the *Sternotherus*-like forms, and the pattern of loss of nuchal contact, completion of neural reversal, and reduction to five neurals evolved at least three times independently (Fig. 5). I believe this last phylogeny is less likely than that shown in Figure 4.

All three of these alternative cladograms support the close relationship of eastern United States *Kinosternon* with the members of the genus *Sternotherus* (sensu Stejneger, 1923; among others), and they suggest that the genus *Kinosternon* of all recent authors (except Romer, 1966 and Seidel et al., 1986) is paraphyletic. These three cladograms also suggest that *Kinosternon* may be paraphyletic with respect to the genus *Xenochelys*, despite the fact that the latter retains the primitive entoplastron (shared with the staurotypines and dermatemydids). They further suggest that *K. herrerai* is not the sister group of the rest of the *Kinosternon* (sensu stricto) as suggested by Bramble et al (1984).

I believe that despite the likelihood that neural patterns exhibit some homoplasy, they provide useful information about the phylogenetic relationships within the Kinosternine. Unfortunately I am yet unable to explain any of the various kinosternine neural patterns in adaptive terms (e.g. in relation to shell morphology, reproduction, ecology, or any other character set). Perhaps my more detailed studies of variation in the shapes and alignments of other bones and scutes in this group will suggest adaptive explanations. It is interesting that adaptive explanations of neural patterns in the Old World's ecological equivalent of the New World Kinosterninae (the Pelomedusidae; Broadley, 1983) have been equally elusive.

Acknowledgments

Table 1. Neural bone characters and polarities for kinosternid turtles.

Character	Primitive condition	Derived condition
Number of neurals	Eight	Progressive reduction from seven to five
Contact between nuchal and first neural	Contact	Loss of contact
Contact between suprapygal and neural series	Contact	Loss of contact
Orientation of short sides of hexagonal neurals	Short sides directed anteriorly; no short sides directed posteriorly	Progressive increase in number of posteriorly short-sided neurals

Table 2. Species groups of kinosternine turtles based on shared (not necessarily derived) characters, including those morphological, biochemical, and ecological. Order of groups is alphabetical and contains no phylogenetic information.

Group	Members	Shared characters

hirtipes	*hirtipes*
	sonoriense
		clasping organs present
		reduced plastron (some highly)
		triangular to quadrangular anterior
		   humeral (= pectoral) scute
		basically tricarinate
		wide first vertebral
		mottled to striped head pattern
		nasal scale furcate, very reduced,
		   or bell-shaped
		non-distinctive proteins
		no terrestrial estivation
		extended "spring" seasonal reproductive
		   pattern
		apparently no embryonic diapause
		species allopatric
		subtropical distribution

leucostomum	*leucostomum*
	   (incl. *spurrelli*)
	angustipons
	dunni
		clasping organs present
		reduced plastron in some
		triangular anterior humeral
		basically unicarinate
		wide first vertebral
		basically broad striped head pattern
		nasal scale bell-shaped
		distinctive proteins (at least in *leucostomum*)
		exhibit terrestrial estivation (at least
		   leucostomum)
		"extended" reproductive pattern (at least
		   leucostomum)
		exhibit embryonic diapause (at least
		   leucostomum)
		species sympatric
		tropical distribution

scorpioides	*scorpioides*
	   (incl. *cruentatum*
	   and *abaxillare*)
	acutum
	alamosae
	creaseri
	   integrum
	   oaxacae
	n. sp. (Jalisco
	   and Colima)
		no clasping organs (apomorphic)
		reduced plastron in few
		triangular anterior humeral
		basically tricarinate
		wide first vertebral
		mottled to striped head pattern
		nasal scale bell-shaped
		non-distinctive proteins
		exhibit terrestrial estivation
		"summer" reproductive pattern
		exhibit embryonic diapause (at least
		   scorpioides and *acutum*)
		species mostly allopatric
		tropical distribution

Table 2 *(continued)*

Group	Members	Shared characters

Sternotherus	*carinatus*
	depressus
	minor
	odoratus
		clasping organs present
		highly reduced plastron
		posterior plastral hinge akinetic
		quadrangular anterior humeral
		basically tricarinate with high
		   medial keel
		narrow first vertebral
		spotted to mottled to striped head pattern
		nasal scale furcate
		distinctive (*subrubrum*-like) proteins
		no terrestrial estivation
		"spring" or (southerly) "fall-spring"
		   reproductive pattern
		no embryonic diapause
		species often sympatric
		temperate to sub-tropical distribution

subrubrum	*subrubrum*
	baurii
		clasping organs present
		plastron not reduced
		triangular anterior humeral
		basically unicarinate or smooth
		narrow first vertebral
		mottled to striped head pattern
		nasal scale bell-shaped or furcate (rare)
		distinctive (*Sternotherus*-like) proteins
		exhibit terrestrial estivation
		"spring" or (southerly) "fall-spring"
		   reproductive pattern
		almost no embryonic diapause (very rarely
		   in *baurii*)
		species sympatric
		temperate to sub-tropical distribution

Uncertain	*herrerai*	clasping organs present highly reduced plastron posterior plastral hinge akinetic quadrangular anterior humeral basically unicarinate narrow first vertebral mottled head pattern nasal scale furcate non-distinctive proteins no terrestrial estivation apparently "spring" seasonal reproductive pattern apparently no embryonic diapause allopatric with *hirtipes* group sub-tropical distribution

Table 2 *(continued)*

| Group	Members	Shared characters
Uncertain	*flavescens*	clasping organs present plastron not reduced triangular anterior humeral basically unicarinate or smooth wide first vertebral mottled to uniform dark above — light below head pattern nasal scale furcate, but very reduced non-distinctive proteins exhibit terrestrial estivation "spring" to "summer" (moisture-related) reproductive pattern apparently no embryonic diapause narrowly sympatric (ecologically parapatric) relative to *subrubrum* and *hirtipes* groups
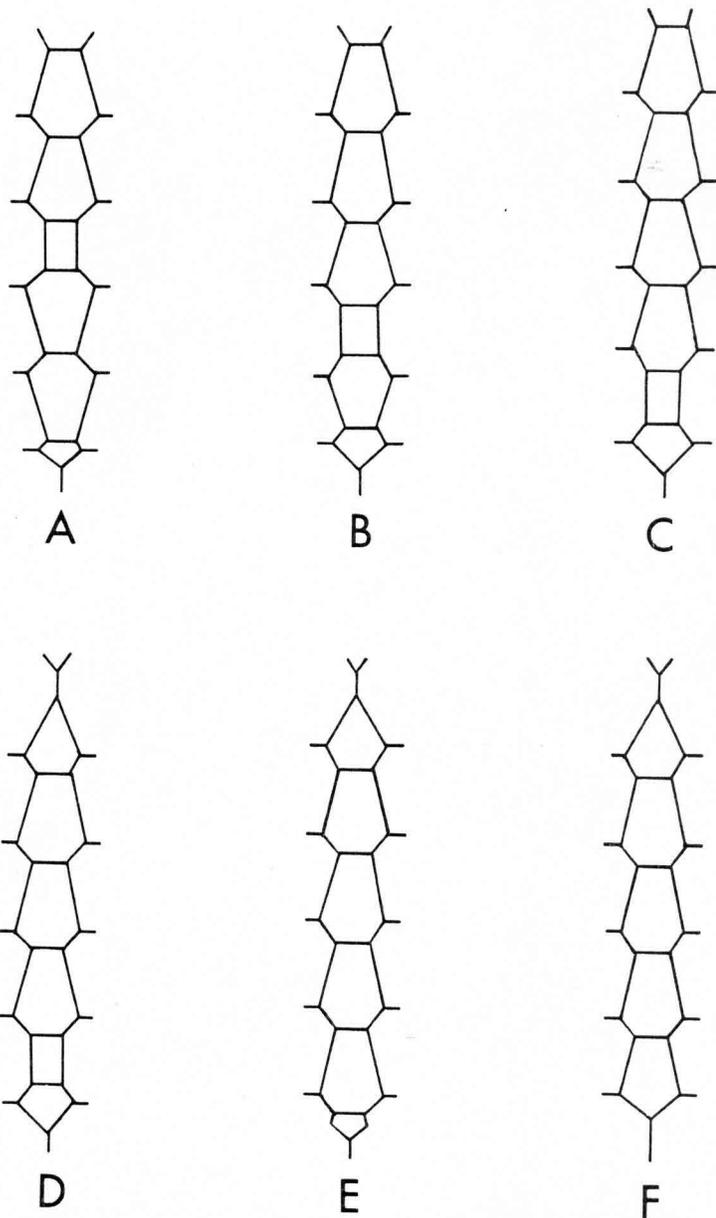
Fig. 1. Variation in modal neural bone pattern (anterior to the top) in kinosternine turtles. Modal pattern A is exhibited by *K. minor* (N6>6>4<6<6<5C); B, by *K. baurii* (N6>6>6>4<6<5C); C, by *Xenochelys*, and *Kinosternon alamosae, K. carinatum, K. flavescens*, and *K. subrubrum* (N6>6>6>6>4<5C); D, by *K. creaseri* and *K. odoratum* (C5>6>6>6>4<5C); E, by *K. hirtipes, K. integrum, K. oaxacae*, and *K. sonoriense*; and F, *K. acutum, K. angustipons, K. dunni, K. herrerai, K. leucostomum, K. scorpioides*, and *K.* sp.(C5>6>6>6>5C).
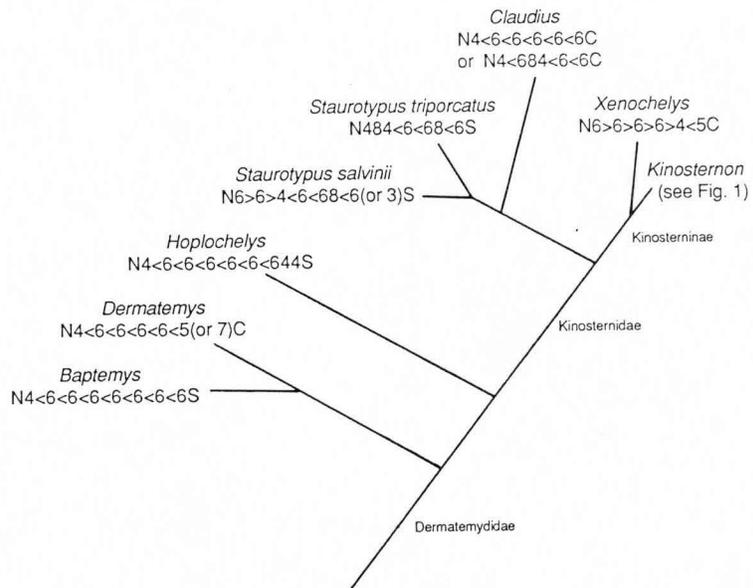
Fig. 2. Phylogenetic relationships of kinosternid turtles and near relatives (after Hutchison and Bramble, 1981), with neural formulae indicated. See text for interpretation of formulae.
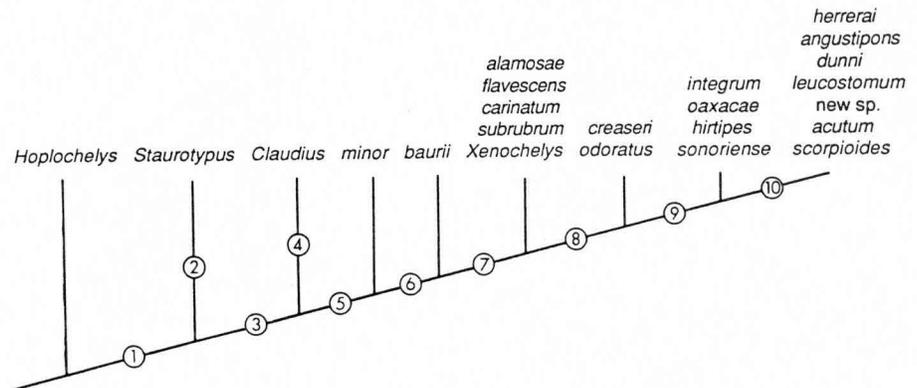

Fig. 3. Most parsimonious phylogenetic tree of kinosternid turtles based only on neural pattern variation, with numbers coding proposed derived character states: 1) reduction to seven neurals; 2) neural six octagonal; 3) reduction to six neurals; 4) neural three octagonal and neural four tetragonal; 5) shift to posteriorly short-sided neurals anterior to tetragonal neural three; 6) shift to posteriorly short-sided neurals anterior to tetragonal neural four; 7) shift to posteriorly short-sided neurals anterior to tetragonal neural five; 8) loss of contact between nuchal and neural one; 9) complete shift to all posteriorly short-sided neurals (i.e., reversal complete); and 10) reduction to five neurals.
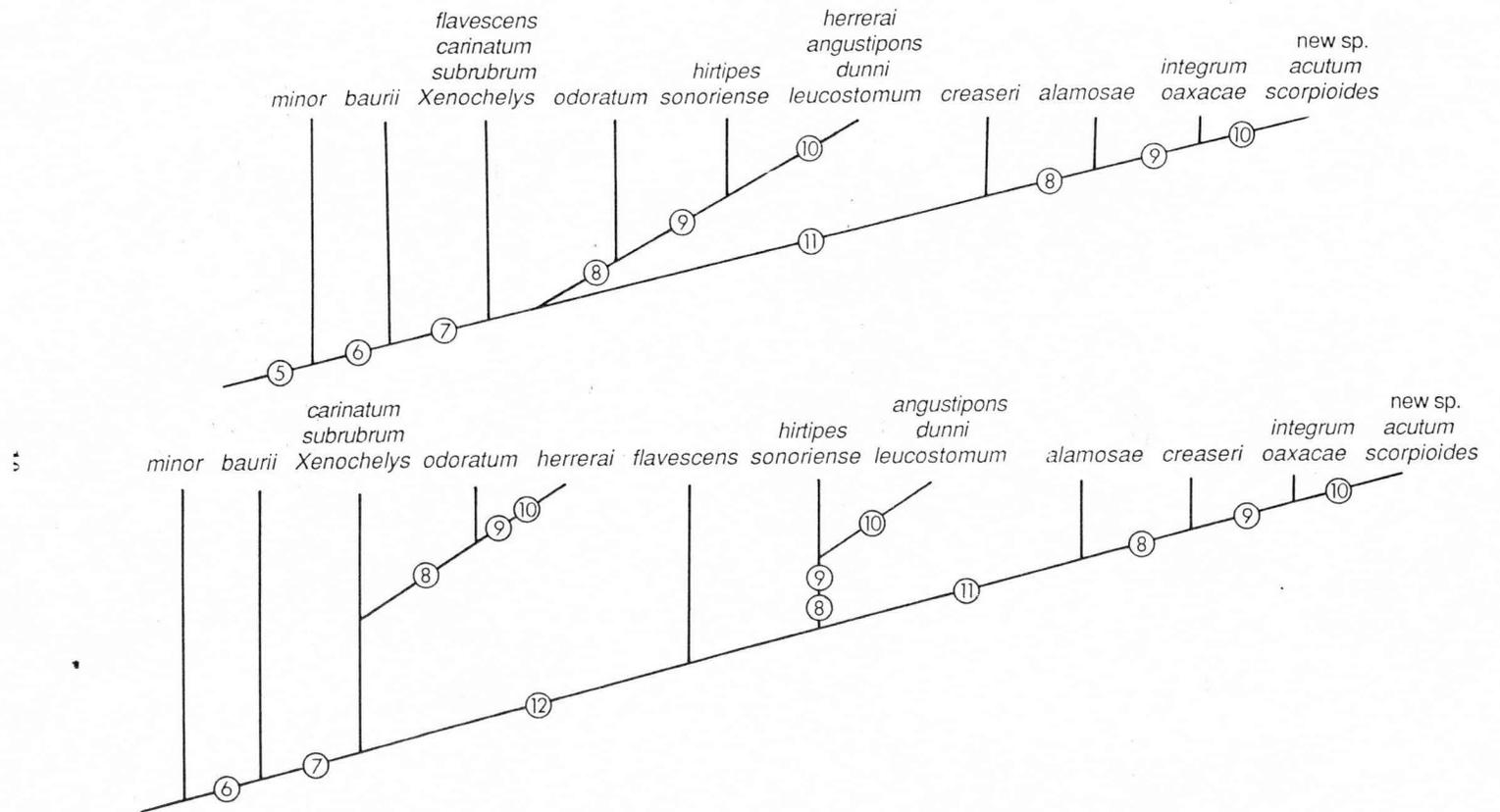
Fig. 4. Hypothesized phylogeny of the Kinosterninae. Derived character states are numbered as in Figure 3, except 11) loss of clasping organs. Repeated character numbers are those believed to have evolved more than once in this phylogeny. Fig. 5. Hypothesized phylogeny of the Kinosterninae. Derived character states are numbered as in Figures 3 and 4, except 12) increased first-vertebral width. Repeated character numbers are those believed to have evolved more than once in this phylogeny.

LITERATURE CITED

uffenberg, W. 1974. Checklist of fossil land tortoises (Testudinidae). Bull Florida State Mus. Biol. Sci. 18(3):121-251.

erry, J. F. 1978. Variation and systematics in the *Kinosternon scorpioides* and *K. leucostomum* complexes (Reptilia: Testudines: Kinosternidae) of Mexico and Central America. Ph.D. Diss., Univ. Utah, Salt Lake City, Utah.

erry, J. F. and J. B. Iverson. 1980. A new species of mud turtle, genus *Kinosternon*, from Oaxaca, Mexico. J. Herpetol. 14:313-320.

erry, J. F. and J. M. Legler. 1980. A new turtle (genus *Kinosternon*) from Sonora, Mexico. Contrib. Sci. Natur. Hist. Mus. Los Angeles Co. (325):1-12.

erry, J. F., M. E. Seidel, and J. B. Iverson. MS. A new species of mud turtle (genus *Kinosternon*) from Jalisco and Colima, Mexico. In prep.

ickham, J. W. and J. L. Carr. 1983. Taxonomy and phylogeny of the higher categories of cryptodiran turtles based on cladistic analysis of chromosomal data. Copeia 1983:918-932.

ramble, D. M., J. H. Hutchison, and J. M. Legler. 1984. Kinosternid shell kinesis: Structure, function, and evolution. Copeia 1984:456-475.

roadley, D. G. 1983. Neural pattern — A neglected taxonomic character in the genus *Pelusios* Wagler (Pleurodira: Pelomedusidae). pp. 159-68. *In:* A. G. J. Rhodin and K. Miyata (eds.), Advances in herpetology and evolutionary biology. Mus. Comp. Zool. Harvard. Cambridge, Mass.

ilmore, C. W. 1919. Reptilian faunas of the Torrejon, Puerco, and underlying upper Cretaceous formations of San Juan County, New Mexico. U.S. Geol. Surv. Prof. Papers 119:1-71.

[ay, O. P. 1908. The fossil turtles of North America. Carnegie Inst. Washington Publ. 75.

lutchison, J. H. and D. M. Bramble. 1981. Homology of the plastral scales of the Kinosternidae and related turtles. Herpetologica 37:73-85.

verson, J. B. 1976. The genus *Kinosternon* in Belize (Testudines: Kinosternidae). Herpetologica 32:258-262.

_____ 1978a. Variation in striped mud turtles, *Kinosternon baurii* (Reptilia, Testudines, Kinosternidae). J. Herpetol. 12:135-142.

_____ 1978b. Distributional problems of the genus *Kinosternon* in the American southwest. Copeia 1978:476-479.

_____ 1979. A taxonomic reappraisal of the yellow mud turtle, *Kinosternon Plavescens* (Testudines: Kinosternidae). Copeia 1979:212-225.

_____ 1981. Biosystematics of the *Kinosternon hirtipes* species group (Testudines: Kinosternidae). Tulane Stud. Zool. Bot. 23:1-74.

_____ 1986. Notes on the natural history of the Oaxaca mud turtle, *Kinosternon oaxacae*. J. Herpetol. 20:119-123.

verson, J.B. MS. Phylogenic hypothesis for the evolution of *Kinosternon* turtles. Submitted.

_____ and J. F. Berry. 1979. The genus *Kinosternon* in northeastern Mexico. Herpetologica 35:318-324.

.egler, J. M. 1965. A new species of turtle, genus *Kinosternon* from Central America. Univ. Kansas Publ. Mus. Natur. Hist. 15:615-625.

Vieylan, P. A. 1987. The phylogenetic relationships of soft-shelled turtles (family Trionychidae). Bull. Amer. Mus. Natur. Hist. 186:1-101.

leynolds, S. and M. E. Seidel. 1983. Morphological homogeneity in the turtle *Sternotherus odoratus*(Kinosternidae) throughout its range. J. Herpetol. 17:113-120.

lomer, A. S. 1966. Vertebrate Paleontology. Third edition. University of Chicago Press. Chicago, Illinois.

Seidel, M. E., J. B. Iverson, and M. D. Adkins. 1986. Biochemical comparisons and phylogenetic relationships in the family Kinosternidae (Testudines). Copeia 1986:285-294.

_____ and R. V. Lucchino. 1981. Allozymic and morphological variation among the musk turtles *Sternotherus carinatus*, *S. depressus*, and *S. minor* (Kinosternidae). Copeia 1981:119-128.

Smith, H. M. and R. B. Smith. 1980. Herpetology of Mexico. Vol 6. Turtles of Mexico. John Johnson, Burlington, VT.

Stejneger, L. 1923. Rehabilitation of a hitherto overlooked species of musk turtles of the southern states. Proc. U. S. Natl. Mus. 62(6):1-3.

Wiley, E. O. 1981. Phylogenetics: The theory and practice of phylogenetic systematics. John Wiley and Sons, New York.

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