

## Taxonomy and Phylogeny of the Higher Categories of Cryptodiran Turtles Based on a Cladistic Analysis of Chromosomal Data

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**Karyological data are available for 55% of all cryptodiran turtle species including members of all but one family. Cladistic analysis of these data, as well as consideration of other taxonomic studies, lead us to propose a formal classification and phylogeny not greatly different from that suggested by other workers. We recognize 11 families and three superfamilies. The platysternid and staurotypid turtles are recognized at the familial level. Patterns and models of karyotypic evolution in turtles are reviewed and discussed.**

OVER the past 10 years knowledge of turtle karyology has grown to such an extent that the order Testudines is one of the better known groups of lower vertebrates (Bickham, 1983). Nondifferentially stained karyotypes are known for 55% of cryptodiran turtle species and banded karyotypes for approximately 25% (Bickham, 1981). From this body of knowledge, as well as a consideration of the morphological variation in the order, we herein present a general review of the cryptodiran karyological literature and a discussion of the evolutionary relationships of the higher categories of cryptodiran turtles. Although this paper focuses on the Cryptodira (the largest suborder of turtles), the Pleurodira also has been well studied in terms of standard karyotypes (Ayres et al., 1969; Gorman, 1973; Bull and Legler, 1980) and a few have been studied with banding techniques (Bull and Legler, 1980).

*Historical review of taxonomic relationships.*—The primary subdivisions of the order comprising the turtles have undergone a great many name changes and rearrangements over the last 100 years. Cope (1871) presented an arrangement of the families into suborders which is still widely accepted today. Until Cope, the subordinal and suprafamilial classification of turtles was primarily based on differences in the digits among the sea turtles, the aquatic turtles and/or the terrestrial tortoises. Hoffman (1890) and Kuhn (1967) present reviews of the early classifications.

Cope recognized the currently widely accepted suborders Cryptodira and Pleurodira. Two major differences between these two suborders are in the plane of retraction of the neck

and the relationship between the shell and pelvic girdle. In the cryptodires (“hidden-necked” turtles), the neck is withdrawn into the body in a vertical plane and the pelvis is not fused to either the plastron or carapace, whereas in the pleurodires (“side-necked” turtles) the pelvic girdle is fused to both the plastron and carapace and the neck is folded back against the body in a horizontal plane. Cope’s suborder Athecae includes only the Dermochelyidae and is no longer recognized. Most authors include the Dermochelyidae among the Cryptodira (Gaffney, 1975a; Mlynarski, 1976; Wermuth and Mertens, 1977; Pritchard, 1979).

A few authors recognize the Trionychoidea (sensu Siebenrock, 1909) and/or the Chelonioidea (sensu Baur, 1893) at a suprafamilial rank equivalent with the Cryptodira and Pleurodira (Boulenger, 1889; Lindholm, 1929; Mertens et al., 1934). The suborder Cryptodira is used here in the sense of Williams (1950) and subsequent authors and includes all living non-pleurodiran turtles.

The families of the suborder Cryptodira are arranged in various superfamilies by several authors. The Testudinoidea, Chelonioidea and Trionychoidea are superfamilies common to most of the recent classifications (Williams, 1950; Romer, 1966; Gaffney, 1975a; Mlynarski, 1976). However, the limits of these taxa are not uniformly agreed upon.

The non-trionychoid freshwater and land cryptodiran turtles include the Chelydridae, Kinosternidae, Dermatemydidae, Platysternidae, Emydidae and Testudinidae and are usually placed in the Testudinoidea (Williams, 1950; Romer, 1966). Gaffney (1975a) includes the Kinosternidae and Dermatemydidae in the

Trionychoidea. Mlynarski (1976) includes only the Emydidae and Testudinidae in the Testudinoidea. He recognizes the superfamily Chelydroidea to include the Chelydridae, Dermatemydidae, Kinosternidae and Platysternidae.

The Chelonioidea includes the Cheloniidae and the Dermochelyidae (Baur, 1893; Gaffney, 1975a). Williams (1950), Romer (1966), and Mlynarski (1976) recognize a separate superfamily, the Dermochelyoidea, for the family Dermochelyidae, and include only the Cheloniidae in the Chelonioidea.

The Trionychoidea usually includes both the Trionychidae and Carettochelyidae (Mlynarski, 1976), but Williams (1950) and Romer (1966) recognize the Carettochelyidae separately in the Carettochelyoidea.

Most of the currently utilized family or subfamily level taxa have been commonly recognized since Boulenger (1889). However, there is no complete agreement regarding the level at which certain taxa should be recognized. Parsons (1968) reviewed this confusing situation with regard to the Chelydridae, Staurotypidae, Kinosternidae, Platysternidae, Emydidae and Testudinidae, as recognized here. Not mentioned by him are the inclusion of *Platysternon* in the Chelydridae (Agassiz, 1857; Gaffney, 1975b) and the recognition of the Staurotypidae (Baur, 1891, 1893; Chkhvadze, 1970).

The above discussion of the history of cryptodiran taxonomy serves to illustrate the complexity of the relationships of the inclusive taxa. The taxonomic confusion seems to result from: 1) extensive convergent evolution in certain morphological traits, 2) the failure of some workers to distinguish between shared primitive and shared derived character states and 3) the lack of a widely accepted phylogeny of turtles. Chromosomal data are used in this paper in an attempt to solve some of the evolutionary and classificatory problems. Cytogenetic information seems useful at this level because of the high degree of conservatism expressed in chelonian karyotypes (Bickham, 1981). Additionally, the application of chromosome banding techniques solves one of the most troublesome problems in phylogeny reconstruction; namely, the determination of homologous characters. When two chromosomes have identical banding patterns it can safely be concluded that they are homologous. It is sometimes difficult to determine homology among morphological characters. For example, determination of homologies among the plastral scales of various turtle fam-

ilies is difficult. The fact that a scale is in the same position in members of different families does not necessarily imply homology (Hutchinson and Bramble, 1981).

## METHODS

Details for the procedures for turtle cell culture, chromosome preparation, and banding analysis have been published (Bickham, 1975; Bickham and Baker, 1976a; Sites et al., 1979b). Chromosomes were arranged, according to the method of Bickham (1975), into three groups (A:B:C:) where group A included metacentric-submetacentric macrochromosomes, group B subtelocentric-telocentric macrochromosomes, and group C microchromosomes. The A:B:C: formula is given after the diploid number in Fig. 3 and in the text.

This paper represents a synthesis and reanalysis of (mostly) published data. In reanalyzing the data we employed cladistic methodology (Hennig, 1966) in which sister groups were established by the determination of groups that possessed shared derived characters (synapomorphies). Because banded karyotypes were not available for the most appropriate outgroup taxon (Suborder Pleurodira: Family Chelidae) we employed an "internal" method of character polarity determination. Specifically, characters that were shared among families considered to be distantly related, known from the fossil record to be early derivatives of the cryptodiran radiation, or thought to be morphologically primitive, were considered as primitive (plesiomorphic) chromosomal characters. Because of the nature of karyotypic variation in cryptodires the analysis was rather straightforward. For example, dermatemydids are among the most primitive living turtles and their fossil history extends back to the Cretaceous, as does the cheloniids which are thought to be an early offshoot of the cryptodiran line. These two families possess species with apparently identical karyotypes. It is highly unlikely that these two families possess a synapomorphy at this level of the phylogeny. This would mean that these two families were more closely related to each other than to any other families studied, an arrangement that appeared to conflict with every other line of evidence in the literature. We therefore considered this karyotype to be primitive, at least for the non-trionychoid families, and the karyotypes of other families were derived from this (see below).

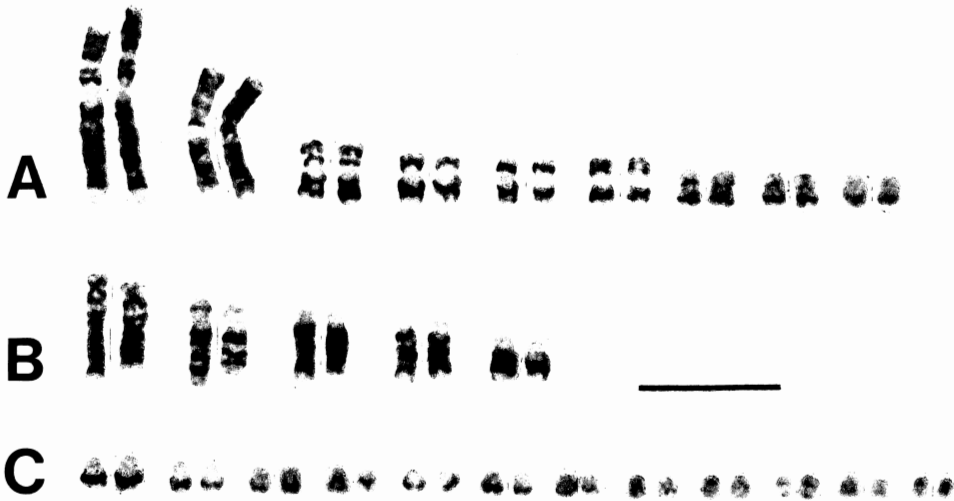


Fig. 1. G-band karyotype of a batagurine emydid (*Chinemys reevesi*,  $2n = 52$ ). The chromosomes are arranged into group A (metacentric or submetacentric macrochromosomes), group B (telocentric and subtelocentric macrochromosomes), and group C (microchromosomes).

#### RESULTS AND DISCUSSION

The following discussion is segmented into the commonly accepted family groups. In general, we have accepted each of the families as distinct entities and do not question their validity.

*Emydidae*.—The two subfamilies of emydid turtles are characterized by different karyotypes. The predominantly New World emydines have  $2n = 50$  and the predominantly Old World batagurines mostly have  $2n = 52$  (Table 1). A few batagurine species also possess  $2n = 50$  (Table 1), including *Siebenrockiella crassicolis*, the only emydid known to possess sex chromosomes (Carr and Bickham, 1981). Bickham and Baker (1976a) concluded that the primitive karyotype of the Emydidae was  $2n = 52$  and identical to that of *Sacalia bealei* and other Old World batagurines. This has been supported by recent findings that some testudinids have banded karyotypes identical to those of *Chinemys reevesi* and other batagurines (Dowler and Bickham, 1982). Fig. 1 illustrates the karyotype of a batagurine (*Chinemys reevesi*) that possesses the proposed primitive emydid karyotype.

The origin of the  $2n = 50$  emyidine karyotype

is unclear (Bickham and Baker, 1976a). There is no karyotypic evidence to indicate emydines are at all closely related to *Rhinoclemmys*, the only New World batagurine genus (Carr, 1981). There may be some hint of the batagurine-emydine transition in the finding of several species of Asiatic batagurines with  $2n = 50$  (Table 1). Any relationship of the emydines to the  $2n = 50$  batagurines will require evidence from other character systems in order to establish its existence.

*Testudinidae*.—The karyology of this family is not as well studied as that of the Emydidae but it seems certain that the primitive karyotype is  $2n = 52$ . Some species are known to possess G-band patterns identical to those of certain batagurines including *Geochelone pardalis*, *G. elongata* and *G. elephantopus* (Dowler and Bickham, 1982). C-band variation exists among species of *Geochelone*, and the karyotypes of *Gopherus* species differ from *Geochelone* species by the morphology and location of the nucleolar organizing region (NOR) (Dowler and Bickham, 1982). Although this family is nearly world-wide in distribution and morphologically diverse, the available data indicate a high degree of karyological conservatism.

TABLE 1. DIPLOID NUMBERS OF CRYPTODIRAN TURTLES. Each reference is listed under the currently recognized name if different from that under which it was originally reported. Unpublished data have been processed in our lab.

Taxon	Diploid number	Source
<b>EMYDIDAE</b>		
<b>EMYDINAE</b>		
<i>Emys orbicularis</i>	50	Matthey, 1930, 1931; Wickbom, 1945; Polli, 1952; Matthey and Van Brink, 1957; Van Brink, 1959; Ivanov, 1973
<i>Chrysemys picta</i>	50	Van Brink, 1959; Forbes, 1966; Killebrew, 1977a
<i>C. p. belli</i>	50	Glascok, 1915; Van Brink, 1959; Forbes, 1966; Stock, 1972; DeSmet, 1978
<i>C. p. dorsalis</i>	50	Forbes, 1966
<i>C. p. marginata</i>	50	Jordan, 1914; Forbes, 1966
<i>C. (Pseudemys) scripta elegans</i>	50	Forbes, 1966; Stock, 1972; Bickham and Baker, 1976a; Killebrew, 1977a
	52	DeSmet, 1978
<i>C. s. ornata</i>	50	Stock, 1972
<i>C. s. callirostris</i>	50	Killebrew, 1977a
	52	DeSmet, 1978
<i>C. concinna</i>	50	Forbes, 1966; Gorman, 1973; Bickham and Baker, 1979
<i>C. c. mobilensis</i>	50	Forbes, 1966
<i>C. c. texana</i>	50	Killebrew, 1977a
<i>C. floridana</i>	50	Stock, 1972; unpublished
<i>C. f. hoyi</i>	50	Killebrew, 1977a
<i>C. rubriventris</i>	50	Gorman, 1973
<i>C. nelsoni</i>	50	Gorman, 1973; Killebrew, 1977a
<i>C. decorata</i>	50	Gorman, 1973; Bickham and Baker, 1976a, b, 1979
<i>C. terrapen</i>	50	Bickham and Baker, 1976a, b
<i>C. malonei</i>	50	Unpublished
<i>C. stejnegeri vicina</i>	50	Bickham and Baker, 1976a, b
<i>Graptemys geographica</i>	50	Forbes, 1966; McKown, 1972; Killebrew, 1977a
<i>G. pseudogeographica</i>	50	Forbes, 1966; Stock, 1972; Bickham and Baker, 1979
<i>G. o. ouachitensis</i>	50	Forbes, 1966; McKown, 1972
<i>G. o. sabinensis</i>	50	McKown, 1972; Killebrew, 1977a
<i>G. kohni</i>	50	McKown, 1972; Stock, 1972; Killebrew, 1977a
<i>G. barbouri</i>	52	McKown, 1972
	50	Killebrew, 1977a
<i>G. pulchra</i>	52	McKown, 1972
<i>G. versa</i>	50	McKown, 1972; Unpublished
<i>G. caglei</i>	50	McKown, 1972; Killebrew, 1977a
<i>G. flavimaculata</i>	50	McKown, 1972; Killebrew, 1977a
<i>G. nigrinoda</i>	50	McKown, 1972; Killebrew, 1977a
<i>G. oculifera</i>	50	McKown, 1972; Killebrew, 1977a
<i>Terrapene ornata</i>	50	Stock, 1972; Bickham and Baker, 1976a; Killebrew, 1977a

TABLE 1. CONTINUED.

Taxon	Diploid number	Source
<i>T. carolina</i>	[32]*	Jordan, 1914
	50	Forbes, 1966; Huang and Clark, 1967; Clark et al., 1970; Stock and Mengden, 1975; Bickham and Baker, 1979
<i>T. c. triunguis</i>	50	Forbes, 1966; Stock, 1972; Killebrew, 1977a
<i>T. coahuila</i>	50	Killebrew, 1977a
<i>Deirochelys reticularia</i>	50	Stock, 1972; Killebrew, 1977a
<i>D. r. chrysea</i>	50	Forbes, 1966
<i>Malaclemys terrapin</i>	50	Forbes, 1966; Stock, 1972
<i>M. t. littoralis</i>	50	McKown, 1972
<i>Emydoidea blandingi</i>	50	Forbes, 1966; Stock, 1972
<i>Clemmys insculpta</i>	48	Forbes, 1966
	50	Stock, 1972; Bickham, 1975, 1976
<i>C. guttata</i>	48	Forbes, 1966
	50	Stock, 1972; Bickham, 1975
<i>C. m. marmorata</i>	50	Stock, 1972; Bickham, 1975
<i>C. m. pallida</i>	50	Killebrew, 1977a
<i>C. muhlenbergi</i>	50	Bickham, 1975
<b>BATAGURINAE</b>		
<i>Sacalia bealei</i>	52	Bickham, 1975; Bickham and Baker, 1976a
<i>Mauremys caspica leprosa</i>	50	Killebrew, 1977a
	52	Bickham, 1975, 1976
<i>M. c. rivulata</i>	52	Bickham, 1975, 1976
<i>M. mutica</i>	52	Nakamura, 1935, 1937, 1949; Stock, 1972; Gorman, 1973; Bickham, 1975; Killebrew, 1977a
<i>M. japonica</i>	52	Nakamura, 1935; Sasaki and Itoh, 1967; Becak et al., 1975
<i>Rhinoclemmys pulcherrima</i>	52	Bickham and Baker, 1976a, b
<i>R. punctularia punctularia</i>	56	Barros et al., 1975; Bickham and Baker, 1976a, b
<i>R. p. melanosterna</i>	52	Killebrew, 1977a
<i>R. funerea</i>	52	Killebrew, 1977a; Carr, 1981
<i>R. areolata</i>	52	Carr, 1981
<i>R. rubida</i>	52	Carr, 1981
<i>Geoemyda spengleri</i>	52	Nakamura, 1937, 1949
<i>Heosemys spinosa</i>	52	DeSmet, 1978; Carr, 1981
<i>Melanochelys trijuga coronata</i>	50	DeSmet, 1978
<i>Chinemys reevesi</i>	52	Sasaki and Itoh, 1967, Takagi and Sasaki, 1974; Killebrew, 1977a; Sites et al., 1979a; Dowler and Bickham, 1982; Haiduk and Bickham, 1982
<i>Cyclemys dentata</i>	50-52	Gorman, 1973
	52	Nakamura, 1949; Stock, 1972; Killebrew, 1977a; DeSmet, 1978; Haiduk and Bickham, 1982
<i>Pyxidea mouhoti</i>	52	Carr, 1981
<i>Cuora amboinensis</i>	50	Gorman, 1973

TABLE 1. CONTINUED.

Taxon	Diploid number	Source
	52	Killebrew, 1977a; Haiduk and Bickham, 1982
<i>C. flavomarginata</i>	52	Nakamura, 1949; Sasaki and Itoh, 1967; Gorman, 1973
<i>Kachuga tecta</i>	52	Singh, 1972; Stock, 1972
<i>K. smithi</i>	52	Killebrew, 1977a
<i>K. trivittata</i>	52	DeSmet, 1978
<i>K. dhongoka</i>	52	Singh, 1972
<i>Ocadia sinensis</i>	50	Stock, 1972
	52	Nakamura, 1949; Killebrew, 1977a; Carr, 1981
<i>Malayemys subtrijuga</i>	50	Carr, 1981
	52	Killebrew, 1977a
<i>Orlitia borneensis</i>	50	Carr, 1981
<i>Siebenrockiella crassicollis</i>	50	Stock, 1972; Bickham and Baker, 1976a; Carr and Bickham, 1981
<i>Callagur borneoensis</i>	52	Carr, 1981
<i>Hieremys annandalei</i>	52	Carr, 1981
TESTUDINIDAE		
<i>Gopherus agassizi</i>	52	Atkin et al., 1965; Ohno, 1967, 1971; Huang and Clark, 1969; Jackson and Barr, 1969; Stock, 1972; Gorman, 1973
<i>G. berlandieri</i>	52	Stock, 1972; Gorman, 1973; Killebrew and McKown, 1978; Dowler and Bickham, 1982
<i>G. polyphemus</i>	54	Forbes, 1966
	52	Dowler and Bickham, 1982
<i>Kinixys belliana belliana</i>	52	Killebrew and McKown, 1978
<i>Testudo hermanni</i>	52	Stock, 1972
<i>T. graeca</i>	52	Huang and Clark, 1969; Clark et al., 1970; Shindarov et al., 1976
	54-60	Matthey, 1930
<i>Geochelone denticulata</i>	52	Sampaio et al., 1969, 1971; Bickham, 1976; Bickham and Baker, 1976a, b
<i>G. carbonaria</i>	52	Forbes, 1966; Sampaio et al., 1971; Stock, 1972; Bickham and Baker, 1976b
<i>G. chilensis</i>	52	Unpublished
<i>G. elephantopus</i>	52	Goldstein and Lin, 1972; Benirschke et al., 1976; Dowler and Bickham, 1982
<i>Geochelone elongata</i>	52	DeSmet, 1978; Dowler and Bickham, 1982
<i>G. pardalis</i>	52	Dowler and Bickham, 1982
<i>G. gigantea</i>	52	Benirschke et al., 1976
<i>Malacochersus tornieri</i>	52	Dowler and Bickham, 1982
PLATYSTERNIDAE		
<i>Platysternon megacephalum</i>	54	Gorman, 1973; Haiduk and Bickham, 1982
STAUROTYPIDAE		
<i>Claudius angustatus</i>	54	Bull et al., 1974; Moon, 1974
	56	Gorman, 1973
<i>Staurotypus triporcatus</i>	54	Bull et al., 1974; Moon, 1974; Killebrew, 1975

TABLE 1. CONTINUED.

Taxon	Diploid number	Source
	56	Gorman, 1973
<i>S. salvini</i>	54	Bull et al., 1974; Moon, 1974; Sites et al., 1979a, b
<b>CHELYDRIDAE</b>		
<i>Chelydra s. serpentina</i>	52	Forbes, 1966; Stock, 1972; Gorman, 1973; Bickham and Baker, 1976a; Killebrew, 1977b; DeSmet, 1978
<i>C. s. osceola</i>	52	Gorman, 1973; Haiduk and Bickham, 1982
<i>C. s. acutirostris</i>	52	Haiduk and Bickham, 1982
<i>Macroclmys temminckii</i>	52	Forbes, 1966; Gorman, 1973; Killebrew, 1977b; Haiduk and Bickham, 1982
<b>KINOSTERNIDAE</b>		
<i>Kinosternon flavescens</i>	56	Stock, 1972; Killebrew, 1975
<i>K. subrubrum</i>	54	Forbes, 1966
	56	Stock, 1972; Gorman, 1973
<i>K. s. hippocrepis</i>	56	Killebrew, 1975
<i>K. s. steindachneri</i>	56	Killebrew, 1975; Sites et al., 1979b
<i>K. leucostomum</i>	56	Gorman, 1973; Moon, 1974
<i>K. l. postinguinale</i>	56	Killebrew, 1975
<i>K. hirtipes</i>	56	Killebrew, 1975
<i>K. integrum</i>	56	Unpublished
<i>K. herrerae</i>	56	Unpublished
<i>K. scorpoides</i>	56	Bickham and Baker, 1976b
<i>K. s. scorpoides</i>	56	Barros et al., 1972; Killebrew, 1975
<i>K. s. carajasensis</i>	56	Barros et al., 1972
<i>K. s. abaxillare</i>	56	Moon, 1974; Sites et al., 1979b
<i>K. s. cruentatum</i>	56	Killebrew, 1975; Sites et al., 1979b
<i>K. bauri</i>	56	Gorman, 1973; Moon, 1974; Killebrew, 1975; Sites et al., 1979b
<i>Sternotherus odoratus</i>	50	Risley, 1936
	54	Forbes, 1966
	56	Stock, 1972; Gorman, 1973; Killebrew, 1975
<i>S. carinatus</i>	56	Stock, 1972; Killebrew, 1975
<i>S. minor</i>	56	Moon, 1974; Bickham and Baker, 1979; Sites et al., 1979b
<b>DERMATEMYDIDAE</b>		
<i>Dermatemys mawii</i>	56	Carr et al., 1981
<b>CHELONIIDAE</b>		
<i>Caretta caretta</i>	52	Nakamura, 1937
	56	Unpublished
	58	Nakamura, 1949
<i>Chelonia mydas</i>	55	Nakamura, 1949
	56	Makino, 1952; Waddell and Sigel, 1965; Bickham et al., 1980
<i>Eretmochelys imbricata</i>	56	Unpublished

TABLE 1. CONTINUED.

Taxon	Diploid number	Source
<b>TRIONYCHIDAE</b>		
<i>Trionyx spiniferus</i>	58	Forbes, 1966
	66	Stock, 1972; Bickham et al., 1983
<i>T. muticus</i>	56	Forbes, 1966
	66	Stock, 1972
<i>T. ferox</i>	66	Atkin et al., 1965; Ohno, 1967; Bickham et al., 1983
<i>T. sinensis</i>	63–64	Oguma, 1936, 1937
	66	Susuki, 1950; Bickham et al., 1983
<i>T. cartilagineus</i>	66	Gorman, 1973
<i>Lissemys punctata</i>	66	Singh et al., 1970; Stock, 1972; Gorman, 1973
<i>Dogania subplana</i>	66	Stock, 1972
<b>CARETTOCHELYIDAE</b>		
<i>Carettochelys insculpta</i>	68	Bickham et al., 1983

\* Reported as N = 16.

*Platysternidae*.—The standard karyotype of the single species of platysternid (*Platysternon megacephalum*) has  $2n = 54$  (Haiduk and Bickham, 1982). This species appears to have close affinities to the Emydidae but is karyotypically distinct from all emydids thus far studied. Because *P. megacephalum* and emydids do apparently have synapomorphic chromosomes that are not shared with chelydrids, Haiduk and Bickham (1982) considered *P. megacephalum* to comprise a family distinct from the Chelydridae (sensu Gaffney, 1975b) and resurrected the Platysternidae (Gray, 1870), a move also suggested by Whetstone (1978).

*Staurotypidae*.—This group is usually considered to be a subfamily (Staurotypinae) of the Kinosternidae. Standard karyotypes of all three species in this group are known (Table 1; see especially Bull et al., 1974). The two species of *Staurotypus* are distinctive in possessing an XX/XY sex chromosome system (Bull et al., 1974; Sites et al., 1979a). *Claudius angustatus*, like nearly all other turtle species studied, does not possess heteromorphic sex chromosomes but appears to be otherwise karyotypically identical to *Staurotypus* (Bull et al., 1974). Sites et al. (1979a, b) report banded karyotypes of *S. salvini* and show that this species possesses a biarmed second group B macrochromosome that appears to be homologous to an identical

element in emydids and testudinids (and platysternids based on standard chromosome morphology). This chromosome is acrocentric in chelydrids, kinosternids, dermatemydids and cheloniids (Fig. 2). We conclude that the biarmed condition is derived. Centric fusion of the ancestral acrocentric macrochromosome with a microchromosome accounts for the presence of a subtelocentric macrochromosome in the common ancestor of the Emydidae, Testudinidae, Platysternidae and Staurotypidae. This is indicative of the staurotypids belonging to a clade that does not include kinosternids (*Kinosternon* and *Sternotherus*). This seems irreconcilable with

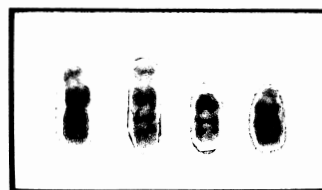


Fig. 2. G-band patterns of the second group B chromosomes of (left to right) a staurotypid, an emydid, a kinosternid and a cheloniid. The long arms of all 4 taxa are identical; the short arms of the staurotypid and emydid are euchromatic and identical, however, the short arms of the kinosternid and the cheloniid are small and heterochromatic; see text for further discussion.



the current classification; it is therefore proposed that the Staurotypinae be elevated to familial rank.

*Chelydridae*.—The two extant species of this family have been studied for both standard (Table 1) and banded karyotypes (Haiduk and Bickham, 1982). *Chelydra serpentina* and *Macrolemys temminckii* both have  $2n = 52$  but differ in the morphology of certain chromosomes. Haiduk and Bickham (1982) conclude that these two species do not share any derived chromosomal characteristics with each other or with any other families of Cryptodira. However, the karyotype of *M. temminckii* could be derived from that of *C. serpentina*. The latter is considered the primitive karyotype for the family.

*Kinosternidae*.—This family is comprised of two genera and about 18 species and has been well studied karyotypically (Table 1). Early, and apparently inaccurate, reports aside (Table 1), all species thus far examined appear to possess  $2n = 56$ . Banded karyotypes (Bickham and Baker, 1979; Sites et al., 1979b) indicate all species possess a large, subtelocentric macrochromosome not found in any other group of turtles. Kinosternids do not share any derived chromosomal characters with any other turtle family, including the staurotypids with which they are usually considered confamilial. An interesting variation was found in this family by Sites et al. (1979b). Heterochromatin that stains dark in both G- and C-band preparations was found in *Sternotherus minor*, *Kinosternon baurii* and *K. subrubrum*, but not found in *K. scorpioides*. The presence of this type of heterochromatin was considered to be a derived character (it is not found in closely related families) shared among the three species that possess it, indicating that the genus *Sternotherus* has affinities with temperate species of *Kinosternon*.

*Dermatemydidae*.—The single extant species of this family (*Dermatemys mawii*) possesses  $2n = 56$  (Table 1). There are no uniquely derived elements and this species shares no derived chromosomes with any other family.

*Cheloniidae*.—Members of this family possess  $2n = 56$  (Table 1). Banding data indicate cheloniids and dermatemydids are karyotypically indistinguishable (Bickham et al., 1980; Carr et al., 1981). Early reports of other diploid numbers and sex chromosomes have not been sub-

stantiated by recent studies using current techniques.

*Trionychidae*.—Members of both subfamilies (Cyclanorbininae and Trionychinae) have  $2n = 66$  (Table 1). Reports of other diploid numbers have been unsubstantiated in subsequent studies. The report of  $2n = 52-54$  in *Trionyx leithii* (Singh et al., 1970) was due to the misidentification of this specimen (*Kachuga dhongoka*, Emydidae; Singh, 1972). The  $2n = 66$  karyotype was considered by Bickham et al. (1983) to be the primitive karyotype for the family. Banding comparisons between *Trionyx* and *Chelonia* revealed little homology between the Trionychidae and Cheloniidae (Bickham et al., 1983).

*Carettochelyidae*.—The single extant species (*Carettochelys insculpta*) has  $2n = 68$  (Bickham et al., 1983). Although no banding data have been reported for this species, the standard karyotype is very similar to the  $2n = 66$  karyotype of trionychids.

*Taxonomy*.—The acceptability of using karyotypic data in order to draw phylogenetic inferences and erect a classification at the level of family and higher is based upon the conservatism of the karyotypic character system. By character system, we refer to a suite of characters and character states which may be presumed to be closely enough related to be within the realm of influence of the same set of evolutionary constraints. According to this line of reasoning then, karyotypic data constitute a character system separate from the character systems associated with electrophoretic data or cranial osteology, etc. The level at which characters are relatively constant within a group is the point at which those characters are of systematic utility and those characters are said to be conservative (Farris, 1966). Our studies and a review of the pertinent literature indicate that family level groups within the Cryptodira are characteristically karyotypically homogeneous and that the significant variation (in the phylogenetic sense) is observable interfamilially. It is upon these premises that we propose the classification in Table 2 based upon our cladistic analysis of the karyotypic data.

This classification is conservative in that all families commonly recognized are maintained, even though in two instances there are family pairs which we cannot karyotypically distinguish [i.e., Cheloniidae-Dermatemydidae and

TABLE 2. TAXONOMIC ARRANGEMENT OF THE HIGHER CATEGORIES OF CRYPTODIRAN TURTLES.

Suborder Cryptodira
Superfamily Cheloniodea
Family Cheloniidae
Family Dermochelyidae
Superfamily Testudinoidea
Family Emydidae
Family Testudinidae
Family Platysternidae
Family Staurotypidae
Family Chelydridae
Family Kinosternidae
Family Dermatemydidae
Superfamily Trionychoidea
Family Trionychidae
Family Carettochelyidae

Testudinidae-Emydidae (in part)]. The classification departs from those that are commonly accepted in several respects, two of which deserve further attention. The first is the removal of the Dermatemydidae and Kinosternidae (plus Staurotypidae as herein conceived) from the Trionychoidea (sensu Gaffney, 1975a). Although Gaffney (1975a) and Zug (1971) present morphological evidence for a relationship between these groups, the karyotypic evidence clearly indicates that these groups are from lineages which have been separated for a long period of time. No karyotypic apomorphies are shared between the Trionychoidea, and the Dermatemydidae and Kinosternidae and in fact few symplesiomorphies remain (Bickham et al., 1983; Carr et al., 1981).

The Staurotypidae as herein recognized deserves special attention. The karyotypic data clearly indicate not only a relatively large karyotypic distance between the commonly recognized Kinosterninae and Staurotypinae, but also a clearly identifiable difference in direction of karyotypic evolution in that the Staurotypidae can be allied synapomorphically in a derived clade which does not include the Kinosternidae. Even if a karyotypic convergence on the apomorphic character allying the Staurotypidae with the Platysternidae, Testudinidae, and Emydidae has occurred, the fact remains that the Kinosternidae and Staurotypidae would still be karyotypically distinct (and nonrelatable), at least to as great a degree as are any of the other families. In the context of this paper and our data-base we are left with no recourse except

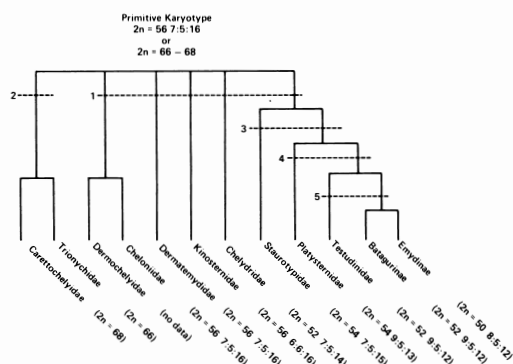


Fig. 3. Cladogram showing the hypothesized relationships of the higher categories of cryptodiran turtles. The diploid number and the number of chromosome pairs in groups A:B:C (Fig. 1) in the proposed primitive karyotype of each family (and both subfamilies of Emydidae) are shown. Because the trionychoid families are so divergent, the A:B:C formulas are not given (Bickham et al., 1983). Characters 1–5 are listed and discussed in the text.

to recognize the Staurotypinae as a separate family, the Staurotypidae. This conclusion is incongruent with data from other character systems. Many morphological studies report similarities between the Kinosternidae and Staurotypidae (among these Williams, 1950; Parsons, 1968; Zug, 1971). Most such studies have not attempted cladistic analyses (two exceptions are Gaffney, 1975; Hutchison and Bramble, 1981). There seems no obvious or simple manner in which to reconcile the conflicting data from the karyotypic character system and the overwhelming amount of data from various morphological character systems. In recognizing the Staurotypidae, we have made explicit our prediction of its relationships to other testudinoid families. Independent confirmation or refutation of these relationships will determine the merit of this move.

The three superfamilies are all considered to be holophyletic. Fig. 3 presents a cladogram that we believe best reflects the branching sequence of the evolution of this group. The Testudinoidea and Cheloniodea may be sister groups but this is as yet unproved. The primitive karyotypes of these two taxa are identical,  $2n = 56$  (character 1 in Fig. 3), and very different from that of the Trionychoidea,  $2n = 66-68$  (character 2 in Fig. 3), but we do not yet know the polarity of these character states (Bickham et al., 1983).

All testudinoid and chelonioid turtles possess at least seven group A macrochromosomes (character 1 in Fig. 3). Among the testudinoid families, a clade that includes Staurotypidae, Platysternidae, Testudinidae, and Emydidae can be identified by the presence of a biarmed second group B macrochromosome (character 3 in Fig. 3; Fig. 2). Another clade includes the Platysternidae, Testudinidae and Emydidae all of which primitively possess nine group A macrochromosomes (Fig. 1; character 4 in Fig. 3). A clade including the Emydidae and Testudinidae is characterized by a  $2n = 52$  9:5:12 primitive karyotype (Fig. 1; character 5 in Fig. 3). Species of the emydid subfamily Emydinae all possess a karyotype derived from the primitive 9:5:12 arrangement (Bickham and Baker, 1976a).

The Dermatemydidae, Kinosternidae and Chelydridae possess no chromosomal synapomorphies and the branching sequence of these families is not obvious from chromosomal, morphological or serological data. However, the Chelydridae is usually considered to be most closely related to the Emydidae (McDowell, 1964; Zug, 1971; Frair, 1972; Haiduk and Bickham, 1982) and the dermatemydids, morphologically one of the most primitive families of turtles, are considered closely allied to the Kinosternidae (Zug, 1971; Frair, 1972; Gaffney, 1975b).

The Cheloniidae and Dermochelyidae are considered to comprise the suborder Chelonioidae. There are no karyotypic data available for *Dermochelys coriacea* so the relationship between this species and cheloniids has yet to be tested chromosomally. But, these two families are closely related morphologically and serologically (Frair, 1979). We follow most other workers in giving this group full superfamilial status, recognizing that they have invaded an adaptive zone, the marine environment, that is distinctly different from that of most other turtles. It must be emphasized that *Chelonia mydas* (Chelonioidae) and *Dermatemys mawii* (Testudinoidae) appear karyotypically identical and we interpret this to be the primitive karyotype of these two superfamilies.

The superfamily Trionychoidea includes only the Trionychidae and Carettochelyidae. These two taxa are closely related chromosomally as well as morphologically and their karyotypes are distinctly different from those of species of the other two superfamilies. Some workers have included the Kinosternidae and Dermatemy-

didae in the Trionychoidea (Gaffney, 1975a). The chromosomal data do not support such an arrangement because of the disparity in diploid number and chromosome morphology between testudinoids (including kinosternids and dermatemydids) and trionychoids (Bickham et al., 1983).

*Chromosomal evolution.*—We conclude, for two reasons, that the primitive karyotype of the suborder Cryptodira is most likely the  $2n = 56$  karyotype of cheloniid and dermatemydid turtles. First, these are among the most ancient families in the suborder (both date from the Cretaceous), and second, this karyotype is highly generalized and could have given rise to the diversity of karyotypes in the suborder by a minimum number of events. A primitive karyotype more similar to that of trionychoid turtles ( $2n = 66-68$ ) cannot entirely be ruled out (Bickham et al., 1983). Comparisons with karyotypes of the species of Pleurodira do not solve the problem because species of the Chelidae are known to possess diploid numbers in the  $2n = 56$  range as well as the  $2n = 66$  range (Bull and Legler, 1980). However, the primitive karyotype of the Pleurodira was considered by Bull and Legler (1980) to be  $2n = 50-54$  which is consistent with our hypothesis of a  $2n = 56$  ancestral karyotype for the Cryptodira.

If the above hypothesis is true, then chromosomal evolution in the Trionychoidea involved an increase in the diploid number by a reduction in the number of macrochromosomes and an increase in the number of microchromosomes. However, chromosomal evolution in the Testudinoidea reduced the diploid number by an increase in the number of macrochromosomes and reduction of the number of microchromosomes.

Bickham and Baker (1979) note that species within a family or subfamily possess identical or very similar karyotypes. However, karyotypic comparisons among families and subfamilies almost always reveal variation. A more refined analysis of the pattern of karyotypic variation in turtles (Bickham, 1981) suggests that the rate of karyotypic evolution has decelerated and that Mesozoic turtles evolved at a rate twice as fast as their descendants. Additionally, the kinds of chromosomal rearrangements incorporated during the diversification of cryptodiran families differ from the kinds of rearrangements incorporated during the evolution of modern species.

The above described pattern of karyotypic evolution is consistent with the canalization model of chromosomal evolution (Bickham and Baker, 1979). Under this model, evolution of the karyotype is driven by natural selection because the chromosomal rearrangements alter genetic regulatory systems. Changes that are adaptive accumulate more rapidly during the early radiation of a lineage. As time goes on more and more adaptive linkage groups are produced. Further chromosomal rearrangement tends to break up adaptive gene sequences and the rate of chromosomal evolution slows down. Thus, in an ancient group such as turtles, the process of canalization has had such a long period of time to act that karyotypic evolution among modern forms is virtually nonexistent. However, when karyotypic comparisons are made of taxa that diverged early during turtle evolution, such as comparisons of the primitive karyotypes of families, variation is found to be more pronounced.

Models that explain karyotypic evolution by population demography, such as deme size, do not apply to turtles. The classical model of chromosomal speciation (White, 1978) requires fixation of chromosomal rearrangements in small demes due to genetic drift or inbreeding. There is some question as to whether chromosomal speciation is in fact a viable process (Bickham and Baker, 1979, 1980; Futuyma and Mayer, 1980), but even if it is, it certainly is not operative in turtles. There are no known chromosomal races in turtles. This could be explained by turtles characteristically not having small population sizes or other demographic factors that promote the fixation of chromosomal rearrangements by genetic drift or inbreeding. However, turtles display such a diversity of demographic characteristics (Auffenberg and Iverson, 1979; Bury, 1979; Bustard, 1979) that this explanation seems untenable.

Turtles exhibit a diverse array of morphological types and occur in nearly all habitats available to reptiles. Some, such as the migratory sea turtles, are highly vagile but others, such as tortoises, have relatively low vagility. Reproductive rates also vary. The green turtle may lay as many as 200 eggs in a single clutch, some emydids may lay only a single large egg. While there are certainly many species that characteristically have large population sizes, we can point to many that probably do not. For example, kinosternids and emydids that occur in the arid western United States and Mexico

often are found in isolated stock tanks, ponds, intermittent streams and permanent springs. Population sizes are often small and there is probably very little migration among populations.

Many of the above mentioned biological characteristics of turtles conceivably could promote chromosomal speciation. That it does not occur in a major radiation (Cryptodira) does not mean that the process is not viable in other taxa, but its absence is somewhat unexpected. In conclusion, population parameters are poorly correlated with chromosomal variability in turtles and in principle we agree with the criticisms of the chromosomal speciation models espoused by Bickham and Baker (1979, 1980) and Futuyma and Mayer (1980).

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