

PHYLOGENETIC RELATIONSHIPS OF THE SOFT-SHELLED TURTLES
(FAMILY TRIONYCHIDAE)

By

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Phylogenetic analysis of nearly one hundred characters of the osteology of trionychid turtles provides abundant data on the phyletic relationships of this family to other turtles and on the interrelationships of its members. These data suggest that the family Trionychidae shares a unique common ancestor with the Dermatemydidae, Kinosternidae and Carettochelyidae, and that the Kinosternidae shares a unique common ancestor with the Trionychidae and Carettochelyidae. Furthermore, it is the staurotypine kinosternids that are most closely related to the Trionychidae and Carettochelyidae. Carettochelyids and trionychids share numerous unique features and constitute a monophyletic group.

Within the Trionychidae, the subfamilies Cyclanorbininae and Trionychinae are recognized as monophyletic clades. Recognition of three cyclanorbinine genera, Cycloderma, Cyclanorbis and Lissemys, is warranted. Within the Trionychinae, four distinct clades are recognized. The

Trionyx cartilagineus group includes Chitra indica and Pelochelys bibroni on the basis of the unique location of the foramen posterior canalis carotici interni, and features of the trigeminal region. The North American group, which includes T. triunguis, T. euphraticus, T. swinhoei, T. ferox, T. spiniferus and T. muticus, can be recognized by the presence of eight or fewer neurals (first and second are fused), deeply emarginate prefrontals and a large contribution by the parietal to the processus trochlearis oticum. The Indian group includes four species: T. gangeticus, T. hurum, T. leithii and T. nigricans. All exhibit a free first neural, five plastral callosities and intermediately extended epiplastra. Lastly, the T. steindachneri group is diagnosed by a descending spine of the opisthotic which divides the fenestra postotica in most specimens.

Two equally parsimonious arrangements of the Trionychinae differ in the placement of the North American clade. In one, this clade is the sister group of the T. cartilagineus clade; in the other it is the sister group of the T. steindachneri clade. In both, the Indian group is paraphyletic and gives rise to the T. steindachneri clade.

A tentative revision of the classification of the family Trionychidae is provided. In it, five generic names currently in the synonymy of Trionyx are resurrected to denote unique clades of trionychine turtles.

INTRODUCTION

Within recent years a fundamental revision of the systematic relationships of turtles has begun. This revision was precipitated by Gaffney (1975), who presented a reorganization of the Testudines using the phylogenetic method (as outlined in Gaffney, 1979a; Wiley, 1981). Other authors have followed Gaffney's lead in applying this method to problems in chelonian systematics, resulting in a much clearer understanding of the phylogenetic relationships among turtle taxa. Concise hypotheses of the relationship within most families are now available (Proganochelidae, Gaffney and Meeker, 1983; Chelidae, Gaffney, 1977; Baenidae, Gaffney, 1972; Meiolaniidae, Gaffney, 1983; Chelonoidea, Gaffney, 1976; Kinosternidae, Hutchison and Bramble, 1981; Emydidae, Hirayama, 1985; Testudinidae, Crumly, 1982, 1985) and are summarized by Gaffney (1984). The largest remaining family for which no such hypothesis exists is that comprising the soft-shelled turtles, Trionychidae.

This gap is significant, considering the large size, abundance and great age of the family. The Trionychidae includes more than 250 species (ca. 230 fossil and 22 extant) and occurs on every continent except Antarctica. It is a very ancient family, with definite representatives from the Cretaceous (Romer, 1956) and a probable representative from the Jurassic (Young and Chow, 1953). Representation of this family in the fossil record is considerable, although difficult to document because few

authors treat the fossils of this troublesome group. The best evidence of its ubiquity is reported by Hutchison (1982), who shows that the Trionychidae has the most continuous record of 11 reptile families examined from the Cenozoic of western North America.

Although authors do not agree on the relationships of trionychids to other turtles, I have never seen a single reference doubting the monophyly of the family. It is so distinctive that some authors have placed the family in a separate suborder equivalent to the Cryptodira and Pleurodira (Boulenger, 1889; Siebenrock, 1909; Bergounioux, 1932, 1955), an arrangement for which Loveridge and Williams (1957) found some support. Modern morphologists argue that this family is a group of aberrant cryptodires allied to the Carettochelyidae, Dermatemydidae and Kinosternidae (McDowell, 1961; Albrecht, 1967; Zug, 1971; Gaffney, 1975, 1984). But others disagree, arguing that on the basis of karyology the Trionychidae, along with the Carettochelyidae, is the sister group of all other cryptodires (Bickham, Bull and Legler, 1983). On the basis of serological tests, Frair (1983) supported the placement of the family in its own suborder.

Among those workers willing to place the Trionychidae among the Cryptodira, there is difference of opinion about which species are the closest relatives of soft-shelled turtles. Since its discovery, Carettochelys (Ramsay, 1886) has been considered to be closely related to the Trionychidae, although some authors were confused by false reports of mesoplastra in this genus (Boulenger, 1889; Pritchard, 1967). Many authors have recognized close relationship between Carettochelys and the Trionychidae (Boulenger, 1889; Baur, 1890, 1891b; Waite, 1905; Siebenrock, 1902, 1913) and some have recommended that superfamilial

status be recognized (Trionychia, Hummel, 1929; Trionychoidea, Walther, 1922).

Several morphologists (Baur, 1891a; McDowell, 1961; Albrecht, 1967; Zug, 1971; and Gaffney, 1975, 1984) have allied the Trionychidae and Carettochelyidae with the Dermatemydidae and the Kinosternidae. Gaffney (1975) applied the name Trionychoidea to this group. This enlarged concept of the Trionychoidea is in clear conflict with the frequent association of the Kinosternidae with the Chelydridae and the inclusion of these two families in a clade with the Emydidae and Testudinidae. The latter arrangement was proposed by Williams (1950) based on the morphology of the cervical vertebrae and other osteological characters and includes the Kinosterninae and Staurotypinae within the Chelydridae. The Williams arrangement has been followed by Romer (1956), Pritchard (1967, 1979a, 1979b), Mlynarski (1976) and others. Karyotypic data have recently been cited which partially support this arrangement (Bickham and Carr, 1983). It is obvious from these various arguments that the phylogenetic position of the family within the Testudines is still in question.

A narrower but equally urgent problem concerns the interrelationships within the family Trionychidae. The lack of resolution of relationships within the family is indicated by the current placement of nearly all species (ca. 235) in a single "wastebasket" genus, Trionyx. For more than fifty years since the major revision by Hummel (1929), there has been a strong tendency to synonymize trionychine genera (except Chitra and Pelochelys) with Trionyx (Bergounioux, 1955; Romer, 1956; Huene, 1956), with the result that about 40 generic names are now considered synonyms (Smith and Smith, 1979). The apparent reason for

this is not uniformity of morphology, but rather an absence of a complete and systematic interpretation of the characters. The large number of taxa and high variability of the characters makes any study of trionyhid relationships using a phenetic method extremely difficult. The most important recent studies are those of Loveridge and Williams (1957) and De Broin (1977). On the basis of osteological characters, color pattern and geography, Loveridge and Williams arrived at the arrangement redrawn as Fig. 23. The De Broin (1977) arrangement is based largely on characters of the shell and skull (especially the palate), but is given in insufficient detail to allow construction of a branching diagram. Both the Loveridge and Williams (1957) and De Broin (1977) arrangements contain features which appear in a cladistic analysis of the family based on shell morphology (Meylan, 1985).

Phylogenetic analysis provides a methodological breakthrough that may elucidate trionyhid relationships. This method results in an arrangement of taxa in a hierarchy of internested natural groups. Because uniquely derived character states are used only from that point in the hierarchy beyond which they are shared by all taxa, these states automatically form diagnoses. Recognition of the diagnostic features of monophyletic groups produces a strong hypothesis for the proper position of the Trionychidae among the Testudines and clarifies the interrelationships of its living species. In this work I have developed a hypothesis of evolutionary relationships for the 22 Recent species of the family Trionychidae. A complete revision of the entire family (fossil and extant species) lies beyond the scope of this dissertation and will take many years to complete.

The species of living trionychid turtles recognized for this study are essentially those listed by Wermuth and Mertens (1961). The only differences are 1) the use of the generic name of Trionyx for Dogania subplanus, following Loveridge and Williams (1957); and 2) the use of the name Trionyx swinhoei for the large and colorful Chinese species which these authors had relegated to the synonymy of Trionyx sinensis (De Broin, 1977; Meylan, in prep.); and 3) the relegation of Trionyx ater to subspecific level within T. spiniferus (Smith and Smith, 1979). The twenty-two species used are the same as those employed in Loveridge and Williams (1957).

Two species recognized since Wermuth and Mertens (1961) have been deemed insufficiently distinct to be used in the current study. On the basis of the absence of intergradation between Lissemys scutata and L. punctata, Webb (1982) proposed that the former be considered a full species rather than a subspecies of L. punctata (Annandale, 1912; Deraniyagala, 1939; Wermuth and Mertens, 1961). The primary morphological differences between the two are the configuration of the peripherals and the well developed plastral callosities at a small size. All superficial dermal callosities are highly variable within trionychid species, and thus additional, less variable features should be found to corroborate the validity of L. scutata before it is used as a distinct species. If valid, there is little doubt that L. punctata is its closest relative.

The name Trionyx nakornsritthamarajensis was proposed for a "rare softshell" from Thailand (Wirot, 1979). Judging from the color pattern of the specimen in the figure included with the description, this name applies to Trionyx cartilagineus.

One of the most laudable aspects of phylogenetic analysis, which is absent from phenetic methods, is that it requires an observer to look beyond the taxa of immediate interest. Decisions about the direction of evolutionary change of characters of the ingroup (the Trionychidae) requires information from related forms. Therefore this study of the relationships of the members of a single family includes an investigation of interfamilial relationships and consequently has evolved into a study of representatives of the entire order. With its scope expanded by the requirements of phylogenetic methodology, this study has produced significant data on the distribution of character states among all turtles. These data are valuable in assessing the interfamilial relationships of trionychids.

The methodology employed also provides a means for identifying those characters which have states that appear to have been gained or lost independently, or which may have undergone reversal. All of these events are termed homoplasy and are the single most confounding feature in systematics. When systematic evaluations must be made from limited data sets, as in paleontology, it is important that characters subject to homoplasy are identified. Because most fossil Trionychidae have been described from shell material, an analysis of homoplasy in shell characters is critical to future work on the systematics of fossil forms.

The descriptive portions of this study focus entirely on characters significant in producing a phylogenetic arrangement for the ingroup. They are not meant as an exhaustive survey of the osteology of the Trionychidae (see Ogushi, 1911).

The primary objectives of this project are to fill the largest remaining gap in our understanding of testudine phylogeny by 1)

determining the best placement of the Trionychidae within the Testudines; and 2) resolving relationships among the 22 extant trionychid species. In addition, it is hoped that this study will help to provide a basis for future analysis of the relationships among the ca. 230 species known only from fossil material.

METHODS

The Phylogenetic Method

Systematics is not only a means of providing names for organisms and groups of organisms, but also a method by which we can infer and express the historical data of descent. Biologists agree that all organisms have evolved by a true phylogenetic progression. The actual pedigree of taxa represents a succession of shared ancestries. Analysis of common ancestry can be a powerful explanatory tool for the co-occurrence of traits of morphology (Lauder, 1982), ecology (Stearns, 1984), physiology (McNab, 1978) and behavior (Meylan and Auffenberg, in press). But the possibility that any features are a result of phylogenetic propinquity cannot be explored unless classification reflects the correct history of descent. Consequently, it is critical for systematists to propose classifications which best reflect the descent of organisms. The phylogenetic or cladistic method is explicit in its reliance on shared derived characters, which are a function of the descent of species.

The Method

The phylogenetic method relies on the identification and use of shared derived characters to identify recency of common ancestry. Given that parallelism is the exception rather than the rule, any two taxa are more likely to have a shared trait because it was present in their common ancestor rather than because it appeared independently on two occasions.

Thus the distribution of shared derived characters among taxa can be used to build a hierarchical ranking of recency of common ancestry.

Developing this hierarchical ranking requires 1) identification of characters with appropriately distributed character states; 2) identification of primitive versus derived states for the characters; and 3) a system for the formulation of hypotheses of hierarchical relationship using the shared derived character data in the most efficient (parsimonious) manner.

Characters and Character States

The systematics of soft-shelled turtles has been based almost exclusively on skeletal morphology (see for example Baur, 1893; Siebenrock, 1902; Hummel, 1929; Loveridge and Williams, 1957; De Broin, 1977). Characters of the external soft anatomy are apparently of little use, and few studies have employed them. The exceptions are the use of color pattern (Loveridge and Williams, 1957; Webb, 1962) and the presence of femoral valves (most studies). For this reason, the character survey in the present study was restricted to skeletal morphology. A secondary advantage of this emphasis is its future direct application to the interpretation of the relationships of fossil trionychid species.

Characters of two types were sought: those uniform within the family but varying among higher taxa outside the family; and those varying among different groups of trionychid species. The former (interfamilial characters) provide a data set for hypotheses on the placement of trionychids within the Testudines. The latter (intrafamilial characters) provide a basis for developing phylogenetic hypotheses for species within the family Trionychidae.

Variation in a given character is treated as states of that character. Many of the characters used have only two states, such as presence or absence of a given bone, structure, or contact. Other characters include three or more discrete states or even continuous variation. Multistate and continuous characters pose two methodological problems. First, for purposes of analysis it is necessary to divide a continuously varying character into a number of discrete states. Secondly, it has been proposed (Gaffney, 1979a, pers. comm.) that recognition of intermediate states requires ad hoc hypotheses that evolution has occurred in certain ways, and therefore multistate characters should be avoided.

Information contained in multistate characters, or morphoclines, is extremely useful for understanding the history of descent of any group (Maslin, 1952) and has been critical in formulating a hypothesis of relationships for trionychids based on the shell alone (Meylan, 1985). The multistate characters that have been used in the present study are of three different types: 1) continuous characters of shape, size, relative position, etc., for which states have been determined by the occurrence of natural breaks along a continuum; 2) discrete characters of a meristic nature for which more than two possible states exist; and 3) two-state characters in which both states frequently occur in the same species, requiring the recognition of that third intermediate condition. I submit that in all of these cases, as for two-state characters, only a hypothesis of character polarity is necessary. By invoking the principle of parsimony we can suggest that the amount of evolutionary change required to arrive at a given state should be minimized, just as the number of postulated evolutionary changes in a clade are ordinarily

minimized by phylogenetic systematics. Why should we propose that turtles with 18 or fewer peripherals arrived at that condition directly from the primitive number, 22, when the shortest evolutionary pathway that could be used to explain this condition would be a change from a form with 20 peripherals?

Multistate discrete characters (e.g., number of peripherals or neurals) present little problem for the recognition of character states. Continuous characters of relative size must be divided into states by some artificial but objective means. As in other studies (Marx and Rabb, 1972; Drewes, 1984), I have divided continuous characters by plotting the average values for terminal taxa along a continuum, and employing natural breaks in distribution as evidence of various character states (see Fig. 9, for example). If no natural breaks in distribution occurred, the character was discarded.

The characters employed in this study are given equal weight. Certain authors, most notably Hecht and Edwards (1977), have argued that some types of characters, for example those involving loss, should be given little weight. In this study characters are weighted only in the sense that they have been included or discarded, depending on the distribution of variation. I disagree with the concept of character weighting in general, and in particular, I do not accept the supposition of Hecht and Edwards that loss is simple and subject to homoplasy, and therefore should be given low weight. The loss of a major structure such as the peripheral bones in turtles or the neural spine in snakes (a character of lowest value in the Hecht and Edwards' scheme) can occur only when a complex structural alternative (a character of highest value in the Hecht and Edwards' scheme) is available. The losses mentioned

above require the development of strong and deeply sutured rib heads in the case of certain trionychoids, and relocation of numerous muscles that originate or insert on the neural spine in snakes. This may explain why the loss of each of these features has apparently occurred only once. In both instances, loss is the immediately apparent result of a complex evolutionary event, and therefore should not be discounted.

There are two reasons to include a maximum number of characters in this analysis. First, such inclusiveness is necessary to provide results that will be of greatest value to paleontology. Paleontologists are often faced with solving systematic problems on the basis of incomplete material. By increasing the number of characters, there is an increased likelihood that characters present in any given fossil have been studied. The second reason is to provide redundancy as a test of problematic groups or possibly homoplastic character states. In this project I use about 100 characters taken from all parts of the skeletal system.

Character codes are used to assist in the identification of characters. Because there are about 100 characters discussed in this paper, some means of assisting the reader is required. The simplest solution was an alpha-numeric code. Characters of the shell are given a number only, following the code introduced in Meylan (1984) with some additions. Characters of the skull are preceded by an S if they are qualitative, except for those of the trigeminal region which are preceded by T. Quantitative (mensurative) characters of the skull are preceded by M. Characters of the lower jaw are preceded by the letter L; those of the pectoral and pelvic girdles by P; and those of the cervical and posterior body vertebrae by C; those of the extremities, both fore and hind limbs, by E; and those of the hyoid by H.

Character Polarity

Once the states of a given character have been recognized, it is essential to identify the primitive and derived extremes, or character polarity. Numerous criteria for determining the polarity of character transformations have been offered in the literature. The most often treated are outgroup comparison, commonality, evidence from the fossil record, evidence from embryology, and correlation of character states (Kluge and Farris, 1969; Marx and Rabb, 1972; Wiley, 1981). I follow Gaffney (1979a), Watrous and Wheeler (1981) and Wiley (1981) in relying on outgroup comparison as the best criterion for character polarity decisions. This criterion has been discussed at some length in recent systematic literature and methods have been outlined for making the most efficient use of outgroups when they are well established (global parsimony, Maddison, Donoghue and Maddison, 1984), or when a number of outgroups could be the sister taxon to the ingroup (outgroup substitution, Donoghue and Cantino, 1984).

In this study I have employed data from all families of turtles and the arrangement of Gaffney (1984; Fig. 10) to make use of the concept of global parsimony. That is to say, the outgroup for the Trionychidae is all other turtles. Decisions concerning polarity of characters within this family are most directly affected by the distribution of states within the Trionychoidea. The concept of the Trionychoidea is based on characters polarized at a higher level of universality.

Formulation of Phylogenetic Hypotheses

In my provisional arrangement of the Recent species of the Trionychidae based on 16 characters of shell morphology (Meylan, 1985), I

conducted the search for the most parsimonious cladogram (that requiring the fewest evolutionary steps) by hand. As additional data have been assembled for this study I have partitioned them into three sets (shell, skull, and lower jaw and nonshell postcrania). Nonetheless, as each of these data sets became very large, it has become necessary to employ a computer program to generate cladograms. I have used "PAUP" by D. Swofford, which is available through the Northeast Regional Data Center at the University of Florida.

The PAUP program emphasizes simple unrestricted parsimony procedures (Swofford, 1984). Its author finds that there is close correspondence between results obtained by hand and those generated via PAUP. One advantage in addition to the time-saving capabilities of PAUP is the MULPARS option. This option results in a listing of all "most parsimonious" trees. It seems certain that when working by hand one is unlikely to discover all such trees. The ability of the program to handle missing values improves its utility for use in the current project.

I have employed PAUP to formulate the most parsimonious hypothesis of relationship for the species within the family Trionychidae that can be derived from each of the three independent sets of osteological data. These are 1) 22 characters of the shell (an expanded version of Meylan, 1985); 2) 23 characters of the skull; and 3) 13 characters of the lower jaw and postcrania (exclusive of the shell). Additionally, an analysis of the three data sets combined was performed.

Comparison of Fundamental Hypotheses and Formulation of a General Hypothesis

Following the development of cladograms from the three separate data sets, it was desirable to formulate a single general cladogram from

them and to compare the utility of various characters, especially those of the shell, in the formulation of this general hypothesis. Two methods, analysis of the three data sets in combination and a stepwise consideration of compatible characters, have been used for this procedure. Neither the Nelson (1979) method or the similar Adams (1972) method produced a single, well-resolved cladogram of trionyhid relationships.

Terminology

Taxonomy

The names used for the Recent Trionyhididae are, with minor exception (see introduction), those employed by Wermuth and Mertens (1961). Specific epithets are often used without a generic name. Because the generic name Trionyx is currently used with about three-fourths of the species, little information is conveyed by the use of that name.

Certain collective terms are used provisionally for groups of trionyhid species throughout the text. They are used for groups which have been suggested to be monophyletic by more than one author. The Cyclanorbininae (Cyclanorbididae of Deraniyagala, 1939; or Lissemydinae, of Williams, 1950) includes Cyclanorbis elegans, Cyclanorbis senegalensis, Cycloderma aubryi, Cycloderma frenatum and Lissemys punctata. These species are considered to constitute a natural group in treatments by Deraniyagala (1939), Loveridge and Williams (1957), and Meylan (1985). The sister group of the Cyclanorbininae is the Trionychinae, which includes all non-cyclanorbine members of the family. There is good evidence that this, too, is a monophyletic group (Meylan, 1985). It has also been recognized as such by Deraniyagala (1939), and Loveridge and Williams (1957). Within the Trionychinae two species groups have been treated as

natural groups in all recent accounts: the four species of the Indian subcontinent (Trionyx gangeticus, T. leithii, T. hurum and T. nigricans); and the three North American forms (T. ferox, T. muticus and T. spiniferus) (Loveridge and Williams, 1957; De Broin, 1977; Meylan, 1985).

Names of familial and higher taxa of the Testudines follow Gaffney (1984). Monophyly of these taxa is not reexamined except for the superfamily Trionychoidea and its member families. The suffixes -oidea for superfamilies, -idae for families and -inae for subfamilies are used consistently throughout the Testudines.

Morphology

Terminology for elements of the carapace and plastron follows Loveridge and Williams (1957). The concepts of Williams and McDowell (1952) concerning the anterior lobe of the plastron are rejected. These authors suggest that the anterior midline element in trionychids is not the entoplastron, but rather a fused pair of epiplastra, and that the anteriormost paired elements are neomorphs which they term preplastra. Bramble and Carr (n.d.) have shown that, on the basis of the sites of origin and insertion of the anterior trunk musculature, this is incorrect and that the anterior plastral elements in trionychids correspond to those of other turtles. The midline element is termed the entoplastron, and the anteriormost pair are referred to as epiplastra.

For skull and lower jaw terminology, I follow Gaffney (1972, 1979b), who has developed his glossary of skull morphology in part from Parsons and Williams (1961). A variety of sources is used for the nonshell postcrania: Williams (1950) for cervical vertebrae; Baur (1891a) and Zug (1971) for the pelvic girdle; and Annandale (1912) for the hyoid.

RESULTS

Variation in Shell Morphology

Introduction

Twenty-seven characters of the carapace and plastron have been determined to be useful for establishing inter- and/or intrafamilial relationships of trionychid turtles (Table 1). They pertain to total shell size and shape and five areas of the shell: the nuchal region, the neural series, the periphery, posterior end of the carapace, and the plastron. Because of the unique nature of the shell of trionychids few of these characters are useful in testing proposed interfamilial relationships.

All character polarities discussed in this section are based on outgroup comparisons. It is therefore important that doubts about the homology of the shell of trionychids to that of other turtles be considered. Zangerl (1969) contends that the external bony layer in the Trionychidae and Dermochelyidae is composed of epithecal ossifications of more superficial origin than the dermal ossifications considered to form the shell in other turtles. This implies that the superficial layer of the shells of members of these two families are not homologous to the same layer in other turtles. The existence of a nonhomologous superficial layer seems quite possible for Dermochelys in which there is total independence of the superficial bone and the deeper dermal elements of the shell (i.e., the ribs and neural spines of vertebrae). In cross

sections these "epithecal bones" which make up the superficial bony mosaic, lack dense layers on the external and internal surfaces (Fig. 1). Thus they do not fit Zangerl's (1969) description of turtle shell bone of typical dermal origin. The case is less clear for the most superficial bony layer in the Trionychidae. In members of this family, as in other turtles, there is complete correspondence between superficial bony elements and underlying deep dermal elements of the carapace. Furthermore, cross-sections of either carapacial or plastral elements of trionychids reveal the presence of a spongy middle region with compact lamellar layers on either side (Fig. 1). This agrees with Zangerl's own description of typical dermal shell bone and fits Suzuki's (1963) description of the results of development of dermal shell bone in Pseudemys scripta. Zangerl's (1939) original argument for an epithecal origin of the superficial bone in trionychids is based on its delayed development rather than on its site of origin. The late development of the superficial layer does not have any clear bearing on the homology of its origin, and must yield to the physical evidence that in cross section trionychid shell elements do not differ significantly from other sectioned chelonian shells which are considered to be of normal dermal origin. Thus, unless other evidence can be provided, the superficial elements of trionychid shells may be regarded as homologous to those of other turtles and presumably of equivalent origin.

Shell Size and Shape

Even the smallest fragment of trionychid shell is immediately recognizable by its characteristic sculpturing. This sculpturing is never divided by scute sulci because the sulci and the epidermal scutes they delineate, which are present on the shells of most other turtles,

are always absent in trionychids. The only other living turtle which has a sculptured shell and lacks epidermal scutes is Carettochelys (character 30, Table 8).

Recent trionychids are, for the most part, large turtles and many species approach one meter in total carapace length. The carapace consists of a bony disc with cartilaginous margins. In discussion of osteological material, including this one, it is the bony disc length rather than total carapace length which is used. The largest species of trionychids have bony discs over 500 mm in length; most reach disc lengths of 300 mm (Table 2). The exceptions are few, and these are usually 200 mm or less in disc length.

Six species of Trionyx are small: Trionyx muticus, T. spiniferus, T. steindachneri, T. sinensis and T. subplanus. All of the carapacial discs of T. subplanus measured during the course of this study are under 180 mm, but one unusually large skull, BMNH 81.10.10.12 (figured as T. cartilagineus, Dalrymple, 1977), could have come from a specimen with a disc as large as 250 mm. Awaiting complete analysis of the relationship of head to shell size in this megacephalic form, T. subplanus is tentatively included among the smaller species. This list agrees in part with a list of diminutive forms assembled by De Broin (1977) based on skull size. Her inclusion of T. leithii and T. ferox as small forms, however, was clearly an artifact of small sample size.

Among other trionychoids, small size is common only in the Kinosternidae. Most known species of the Dermatemydidae and Carettochelyidae reach bony carapace lengths of 400-500 mm. Among the Kinosternidae the genus Staurotypus reaches adult sizes close to those of Dermatemys and Carettochelys; whereas Claudius, Kinosternon and

Sternotherus are smaller, usually under 200 mm. It seems likely that reduction in total size is a derived condition common to the Kinosterninae and that similar diminution occurred independently in one or more groups within the Trionychidae. Thus, small carapace size is considered to be a derived condition among trionychids (character 23, Table 3).

Sexual dimorphism in total size is well known for turtles. In certain forms the male is larger and in others the female is larger. The latter occurs most frequently among aquatic emydids but also occurs in some trionychids. Webb (1962) provides data which indicate that all three North American forms are sexually dimorphic in size. This has not been shown for any Old World forms with the possible exception of Chitra indica (Wirot, 1979). Due to its apparent absence among other trionychoids sexual dimorphism, in which the female is larger, can be considered a derived feature within the Trionychidae (character 28, Table 3).

The carapace of trionychids is unique among the Testudines in having a cartilaginous margin. This margin varies in extent and thus in flexibility. In one species (Lissemys punctata) it makes up less than 10% of the total carapace length and has in it bony elements which are most likely homologous to the peripherals of other turtles. In other forms the cartilaginous margin makes up almost one-half of the carapace length and the bony disc is thus quite reduced.

There can be little doubt that reduction of the bony disc relative to the total carapace is a derived condition, as it occurs only within this family. However, variation in this condition among trionychid species shows no natural breaks and I have not been able to convert this

continuous variable into a discrete one. It should be pointed out, however, that cyclanorbines consistently have relatively larger discs than trionychines and in this respect they represent the more primitive condition.

Elsewhere (Meylan, 1985) I have suggested that the shell outline of Cycloderma frenatum is unique in having a sharply tapering rear half of the carapace with straight to concave posteriolateral edges. After examination of numerous carapaces of Cycloderma aubryi and Lissemys punctata, it is apparent that these species share the unique carapacial outline noted above. Other trionychids, like most other testudines, have round-to-oval shells that are convex posteriolaterally (character 25, Table 3).

Nuchal Region

Dalrymple (1979) provided an excellent discussion of the role of the cervico-dorsal joint in trionychids in allowing the retraction of a long neck into a small space. In order to accommodate such modification of this joint, the entire anterior portion of the trionychid carapace must have been extensively remodeled. In most cryptodires, the first body vertebra is directly ventral to the first neural bone of the carapace and is firmly sutured to it. It is loosely jointed and usually more anteriorly located in trionychids. In Lissemys and Cycloderma, the first body vertebra lies directly below the "preneural" to which it is weakly sutured, suggesting that the "preneural" is actually a first neural (see also Baur, 1893; Hay, 1908; Carpenter, 1981). The nuchals of Lissemys and Cycloderma are also the longest (relative to their width) among the trionychids (Fig. 2). Separate anterior and posterior

costiform processes can be recognized. Grooves for the postzygapophyses of the eighth cervical vertebra are present on either side of the midline at the base of the posterior costiform process. This combination places the well-fixed first body vertebra well back from the edge of the carapace (Fig. 2B). Among trionychids the condition in Lissemys and Cycloderma most closely approaches that seen in other cryptodires. Further derived conditions apparently arose as contact between the first body vertebra and the first neural was reduced, and the nuchal came to lie above the first body vertebra.

An advanced condition of the nuchal region appears in Cyclanorbis senegalensis, in which the length of the nuchal bone is reduced, bringing the first body vertebra closer to the anterior edge of the carapace. At this stage the anterior and posterior costiform processes of the nuchal are not clearly separate (Fig. 2C), but the first neural (preneural) is still distinct from the second. A similar condition is found in Cyclanorbis elegans and in Trionyx gangeticus, T. leithii, T. nigricans, and T. hurum.

Presumably, fusion of the first neural to the second occurred only after the first body vertebra, through reduction of its neural arch, had become free of the first neural. This evidently left the overlying neural element available for further modification. Fusion of the first and second neurals occurs in all Chitra, Pelochelys, and Recent Trionyx except T. hurum, T. leithii, T. nigricans, and T. gangeticus (except for one BMNH specimen that is kyphotic). Up to about 10% of certain Trionyx species (T. ferox, T. formosus, T. triunguis) show separate first and second neurals.

The extreme of development in this suite of characters is found in Chitra (Fig. 2D). In C. indica, prezygapophyses of the first body vertebra are immediately adjacent to the anterior rim of the carapace, and the nuchal is reduced to a narrow sliver of bone. A single costiform process occurs on the anterior margin, and depressions which allow passage of the postzygapophyses of the eighth cervical are present just inside the rim of the carapace. In Chitra there is also a new pair of processes at the posterior edge of the nuchal.

Variation in the nuchal region has been analyzed through the use of four characters (Tables 1, 3). The primitive condition for nuchal shape (character 1) is that most similar to that of other turtles, i.e., as wide or nearly as wide as long. Costiform processes (character 2) are not present in adult Carettochelys, but in some juveniles of the related genus Anosteira, there are two pairs (Bramble, pers. comm.). In other trionychoids (Kinosternidae and Dermatemydidae) there is one pair in adults. But in newly hatched Dermatemys (BMNH 1984.1291) there are, in fact, two pairs. A cleared and stained hatchling Sternotherus minor in the UF collection also has two pairs of costiform processes. Thus it seems likely that two pairs are present early in the ontogeny of all trionychoids. In the Dermatemydidae and Kinosternidae the anterior of the two pairs disappears with age while in the Trionychidae the two pairs occur separately in some forms (Lissemys punctata and both species of Cycloderma) and appear to be united in all others. Because it is the condition common to all trionychoids the possession of two pairs of costiform processes is considered primitive for trionychids.

Most cryptodires have the first body vertebrae at the posterior edge of the nuchal. Through evolutionary foreshortening, the anterior edge of

the nuchal apparently moves toward the first body vertebra. Proximity of the anteriormost body vertebra to the margin of the carapace is considered derived (character 3, Table 3).

The trionychid "preneural" is here considered to be the first neural (see also Hasan, 1941). As suggested by Webb (1962) and Gaffney (1979c), fusion of the first neural to the second neural must be a derived character state (character 4). No non-trionychid member of the Trionychoidea has two neurals between the first pleurals, but there are two body vertebrae between the first pleurals of all trionychids. In T. ferox two neurals form (one on each of the first two body vertebrae) and then they fuse into a single element (Carpenter, 1981; present study).

The carapace of adult turtles is ordinarily a solid bony structure without openings or fontanels. Peripheral fontanels are not uncommon: they occur in juveniles of all cryptodires and are retained in some adult chelydrids, cheloniids, and trionychids. In trionychids, peripheral fontanels are difficult to visualize because the peripheral bones are lacking. Fontanels on the midline are much less common. They occur above the ilia in very old individuals of some testudinoids (e.g., Terrapene, Cuora, Gopherus, Homopus) and above the scapulae (=suprascapular fontanels) in certain trionychids and at least one testudinid, Homopus.

Suprascapular fontanels are probably present early in the development of all trionychids. They are closed at hatching in some forms (Lissemys punctata) but remain open throughout life in others (Trionyx subplanus, T. spiniferus [except some old males], T. muticus and T. steindachneri). In most trionychids suprascapular fontanels close up at some point between hatching and adult size (Table 4). Insufficient

data on the timing of closure in most species prevents the use of this character. Early loss of the fontanels is likely the primitive condition and life-long retention derived.

The Neural Series

The above argument shows that in the Trionychidae the "preneural" of many authors is probably the first neural. Thus the most complete neural series in trionychids includes nine elements between the nuchal and eighth pleurals. The normal pattern in cryptodires is a continuous series of neurals from the nuchal to the suprapygal, usually with some uniform orientation. All trionychids lack a suprapygal, and the eighth pleurals meet at the midline (except in Trionyx subplanus). The most complete series of nine neurals, with all or the majority (numbers 2-7) hexagonal and uniformly facing posteriorly, is likely to be the most primitive condition among living trionychids (Fig. 3A). It is also the condition present in the Jurassic species Sinaspideretes wimani Young and Chow (1953), which appears to be the oldest known trionychid.

Modification of the presumed primitive condition results from four apparently independent changes: (1) the fusion of the first and second neural (treated above, character 4); (2) interruption of the neural series by pleurals meeting at the midline (character 15); (3) variation in the number of neurals expressed on the dorsal surface of the carapace (character 13, Table 5); and (4) variation in the location at which orientation of the neurals reverses (character 16, Table 6). There are also interspecific differences in the amount of variability in the point of neural reversal (character 14). That is to say, in some species the location of reversal is always the same neural; in others, reversal

occurs only at either of two adjacent neurals; and in still others, it may occur anywhere along the neural series (Table 7).

Interruption of the neural series by pleurals meeting at the midline is not common among cryptodires. Most species have a neural series which is uninterrupted from the nuchal to the suprapygals. In dermatemydids and kinosternids, posterior pleurals may meet on the midline but in this case the posteriormost neurals do not appear so they can not be isolated from the anterior portion of the series. In Carettochelys pleurals often meet along the midline, isolating sections of the neural series. The neurals of Carettochelys are quite narrow and thus appear to be less generalized than those of trionychids. Relying on global parsimony in establishing polarity in this case, the absence of pleural interruption of the neural series must be considered primitive for the Trionychidae.

Actually, interruption of the neural series is rare in trionychids. The last neural is isolated from the rest of the neural series in occasional specimens of Lissemys punctata (2 of 19), Trionyx ferox (5 of 31), T. gangeticus (1 of 7) and T. hurum (1 of 5). More frequent neural isolation occurs only in the two species of Cyclanorbis. Siebenrock (1902) discussed the marked variability of the neural series in these two species in his paper which establishes the existence of the two forms on osteological grounds. Both Cyclanorbis species can have long continuous rows of neurals or many isolated neurals. Although C. senegalensis tends to have more isolated neurals than C. elegans, the most reliable diagnostic features of these two species are found in the plastron. C. senegalensis is unique among living trionychids in possessing gular callosities. C. elegans is unique among cyclanorbines in having

callosities of the fused hyo-hypoplastra that are flat or concave along their anterior edge.

The number of neurals appearing on the surface of the carapace in trionychids varies from three to ten. The occurrence of a tenth neural is very rare (3 of 242 specimens, two Trionyx subplanus and one T. cartilagineus) and seems to be anomalous. Thus, nine neurals form the most complete series, and the possession of nine neurals is considered to be the fundamental condition for trionychids. This is not supported by evidence from the outgroups. The entire superfamily seems to have lost, or be in the process of losing, posterior neurals which makes arriving at a primitive number based on the trionychoids quite difficult.

Looking outside of the Trionychoidea, one finds nine neurals commonly in the Chelydridae, where they are packed closely together posteriorly. In the Cheloniidae, Chelonia mydas and E. imbricata frequently have two neurals between the first pair of pleurals, as is proposed to be primitive for trionychids (see for example Fig. 85 in Deraniyagala, 1939). Other sea turtles have higher numbers of neurals but this is due to division of neural elements (Zangerl and Turnbull, 1955); nine neurals may actually be the primitive number for these species as well.

Variation in the number of neurals among living trionychids is given in Table 5. The number of neurals (character 13, Tables 1, 3) is treated as five character states, with nine neurals considered most primitive and seven or fewer neurals most derived.

Nearly all neurals of trionychids are six-sided. Anterior and posterior ends of each neural contact adjacent neurals, the four lateral sides contact adjacent pleurals. The lateral sides consist of two

unequal pairs (Fig. 4). In the anterior part of the neural series the short lateral sides face posteriorly, but in the posterior part of the series (in most species) they face anteriorly. Thus, there is usually a reversal in orientation of these antero-posteriorly assymetrical elements in every neural series.

Reversal of orientation occurs in two ways (Fig. 4). More commonly it occurs via a four-sided neural (= a "diaphragmatic" neural of Hummel, 1929). This four-sided neural and the adjacent pleurals contact the three posterior-facing short sides of the next anterior neural, and the three anterior-facing short sides of the next posterior neural (Fig. 4A). The second and less common reversal occurs via two successive assymetrical pentagonal neurals (Fig. 4B). The anterior of the pair contacts an anterior short side of one of the next posterior pair of pleurals, while the posterior neural contacts a short posterior side of the preceding pleural on the opposite side.

In the presumed primitive neural arrangement, reversal of neural orientation, if it occurs at all, is posteriorly located. But in many forms, reversal occurs anteriorly and this is considered to be derived. Such reversal usually accompanies other changes from the primitive neural configuration. Reversals can occur from neural one through eight and multiple reversals are common in some species (Tables 6, 7). Where multiple reversals occur the location of the most posterior one is thought to indicate the degree of anterior migration of neural reversal. Data on location of neural reversal are treated as five states of character 16 (Tables 1, 3), with most anterior being most derived. Data on the amount of intraspecific variability in the location of the last

neural reversal are treated via three states of character 14 (Tables 1, 3), with the most variable being considered most derived.

Shell Periphery

With the exception of the Trionychidae, the margins of all testudine carapaces are rigid. This is due to the presence of peripheral bones that form a complete ring around the carapace. In nearly all turtles this ring is composed of 22 peripherals, a nuchal and a pygal. Only in the Trionychoidea is there reduction and complete loss of any of these elements. In all kinosternids and Carettochelys there is one fewer peripheral on each side (total of 20). The peripherals of Carettochelys are not sutured to the pleurals, which is also true for the only trionychid which retains bones in the periphery, Lissemys punctata (character 5A, Table 3). The homologies of the bones in the shell periphery of Lissemys have been questioned by many authors. Boulenger (1889), Loveridge and Williams (1957), Zangerl (1969) and others have considered these bones to be neomorphic structures. Walther (1922), Webb (1982) and Meylan (1984) have treated the peripherals of Lissemys as homologs of the peripherals of other turtles. Although these elements are found only in the carapace posterior to the bridge and they lack one-to-one correspondence with the pleurals, there is other evidence which suggests that they are degenerated peripherals and not neomorphs. In cross-section the peripheral ossifications of Lissemys are like those of other turtles in that they consist of two laminar layers of bone which converge distally (Fig. 5). Between these two layers is cancellous bone. Lissemys peripherals differ from those of other turtles principally in the absence of the proximal portion. Unless some developmental constraint that results in the formation of V-shaped elements in the

periphery of all turtle shells can be identified, it may be best to consider these details of morphology as evidence of homology.

Peripherals are found in the carapace of Lissemys only posterior to the bridge and are usually about 14 in number (Deraniyagala, 1939).

Peripherals are absent in all other trionychids. The reduction and loss of bones in the periphery is clearly derived (character 5, Tables 1, 3, 8).

Although the rib heads of each pleural bone normally reach the centrum of the corresponding neural, the contact is not always a strong one. Only in trionychids and Carettochelys among the Cryptodira have I found strong, interlocking sutures (character 28, Tables 1, 8). Dennis Bramble (pers. comm.) has suggested that the peripheral bones of most turtles form a locking ring around the shell that keeps it from expanding laterally when a dorso-ventral force is applied and that these strengthened contacts between the rib-heads and centra may be an alternate means of countering such forces. Thus the carapace of Carettochelys may be "preadapted" for the loss of peripherals.

Both Lissemys punctata and Cyclanorbis senegalensis possess a prenuchal that is an isolated element that lies above the neck, just anterior to the nuchal (character 6, Tables 1, 3). The prenuchal is a neomorph not found in any other cryptodire, and its appearance is a derived condition.

Posterior End of Carapace

In nearly all turtles, the eighth and last pair of pleurals forms as significant a portion of the carapace as those which precede it.

Although the eighth pleurals of trionychids develop allometrically, being

relatively larger in adult turtles than in juveniles, it is still possible to detect a difference in their size among species. In some forms they are large, in others somewhat reduced, and in yet others they are absent. The presence of large eighth pleurals provides a complete complement of pleural bones. The reduction of this complete complement is considered to be derived. Large eighth pleurals are present in all cyclanorbines as well as all Old World trionychines, except Trionyx euphraticus. There is a trend toward the loss of the eighth pleurals in New World forms (character 8, Tables 1, 3).

The ilia of cyclanorbines, except Cyclanorbis elegans, articulate with the eighth pleurals, as they do in other cryptodires. In all trionychines and in C. elegans the ilia articulate with the tough connective tissue just posterior to the end of the shell. The presence of depressions for the ilia on the 8th pleurals is considered primitive, their absence derived (character 20, Table 3).

Plastron

The plastron of most cryptodires includes nine elements (one pair each of epi-, hyo-, hypo- and xiphiplastra and a single entoplastron). These nine elements are well sutured to one another and form a solid bony structure. The same nine elements are present in all trionychids (Bramble and Carr, n.d.) but they are relatively incomplete; they are often not sutured to one another and do not normally result in a single solid structure. Where plastral sutures are present in trionychids they occur between the superficial dermal callosities with minor contributions from underlying elements. The presence of sutures, and thus of the callosities that allow them to occur, is interpreted as a primitive condition.

A suture is found between the hyo- and hypoplastra of all trionychids, and in many fusion occurs along this suture. The xiphiplastral callosities make contact at the midline in large Lissemys, Cycloderma, and Trionyx, but only in Lissemys punctata and Cycloderma aubryi does a sutured contact occur. This suture fuses in very old individuals of these two species. Sutures are absent between epi- and entoplastron, entoplastron and hypoplastra, hypo- and xiphiplastra, and along the midline (except for the xiphiplastra of the two species noted above) in all Recent trionychids.

The number of plastral callosities in all trionychids increases with age but is stable in large adults (character 9). Callosities are present on all nine plastral elements in certain species and this is proposed as the primitive condition. The callosities covering the hyo- and hypoplastron on each side are here considered to be a single structure making seven the primitive number. Seven callosities are found in Lissemys, Cycloderma and some Trionyx. Derived conditions include both an increase and a decrease in the number of callosities (character 9, Tables 1, 3). Only Cyclanorbis senegalensis has increased the number of callosities by the addition of a gular pair. The cyclanorbine Cyclanorbis elegans parallels the trend in the Trionychinae in having marked reduction in the number of callosities to two.

Although the fusion of two plastral elements is certainly derived, it can occur only when the primitive condition, a suture between two elements, is present. Thus the xiphiplastral suture in Lissemys punctata and Cycloderma aubryi suggests that they are primitive. However, xiphiplastral fusion is unique to these forms among trionychids and is considered a shared derived state (character 11, Table 3).

Hyo-hyoplastral sutures occur at some stage in the ontogeny of all extant trionychids. Recent cyclanorbines share the common character state of hyo-hyoplastral fusion at a very small size (as small as 62 mm disc length). Fusion of the hyoplastra to the hypoplastra occurs in all adult Trionyx ferox and in adults of some populations of T. triunguis. The presence of hyo-hyoplastral fusion is considered to be derived and to occur independently in cyclanorbines and trionychines (characters 10A, 10B, Tables 1, 3).

The xiphi-hyoplastral union in trionychids is of two types. In all trionychines the two anterior xiphiplastral processes lie on either side of the most lateral of the three posterior processes of the hypoplastron. In cyclanorbines the two anterior processes of the xiphiplastron lie on either side of the middle of the three posterior processes of the hypoplastron. The trionychine condition occurs in cheloniids, Carettochelys and among kinosternids (Kinosternon, Sternotherus, and Staurotypus), suggesting that it is the primitive condition. Thus the presence of the hypoplastron lateral to the xiphiplastron at their junction is considered to be a derived condition unique to cyclanorbine trionychids (character 12, Table 3).

Relative to the epiplastra of other Testudines those of trionychids are quite reduced in basic structure. The deep element, which may or may not be covered by a callosity, is I- or J-shaped. The J-shaped elements have a long ramus that is oblique to the midline and has a long contact with the entoplastron. They also have an anterior projection of variable length that roughly parallels the midline. I-shaped elements consist of only the anterior portion and have minimal contact to the entoplastron. J-shaped epiplastra are found in all trionychids except Lissemys

punctata, Cycloderma aubryi, and Cycloderma frenatum, which have the alternate I-shape.

Long medial contact between the epiplastra and the entoplastron occurs in all turtles in which these elements are present. The posterior contact of the J-shaped epiplastra to the entoplastron maintains this contact and thus the J-shape is considered primitive, the I-shaped derived (character 18, Table 3).

The anterior extension of J-shaped epiplastra varies in length among the species in which it is found. The extension beyond the entoplastron varies from 0.165 to 0.48 times the width of the hypoplastron of the right side (Table 9). It is difficult to be certain which length of the extension is primitive for trionychids but it seems clear that the marked extension of Trionyx cartilagineus, T. subplanus, T. sinensis and T. steindachneri is derived. As suggested by De Broin (1977), the species of the Indian subcontinent have epiplastra of intermediate length relative to the most elongate forms and other trionychids. Variation in this feature is treated as three states of character 19 with the longest extension considered to be most derived (character 19, Table 3).

The boomerang shape of the entoplastron of trionychids is unique among turtles (character 21, Table 8). Zangerl (1939) has implied that a T-shaped entoplastron is primitive for reptiles. The entoplastron in trionychids apparently arises from a proliferation and bending of the transverse portion of the "T", combined with suppression of development of the longitudinal portion. The amount of bending of the transverse bar varies among trionychids and results in an angle of 62 to 122 degrees between the two posteriolaterally directed rami. Variation within each species spans about 15 degrees. Variation among species is quite

continuous, with no natural breaks. Establishing a polarity for this character has not been possible because no other members of the Trionychoidea have similar entoplastron morphology. This fact, combined with problems of variability, has made it impossible to include angle of the entoplastron as a character in intrafamilial analysis.

Plastral reduction in trionychids includes a marked reduction in the length of the bridge. Bridge length was compared to hypoplastron width as an index of this reduction. Bridge length varies from more than three-quarters of hypoplastron width (Cycloderma aubryi) to about one-eighth hypoplastron width (Trionyx subplanus). But variation falls into two discrete groups: those species in which the bridge is well over one-half hypoplastron width, and those species with a bridge less than one-half hypoplastron width. The former group includes all cyclanorbines except Cyclanorbis elegans; the latter includes all trionychines plus Cyclanobis elegans.

Long plastral bridges occur in Dermatemys and Carettochelys but not in kinosternids. They are also long in testudinoids, with the exception of the most kinetic forms. Thus a long bridge is considered to be primitive, a short bridge derived (character 22, Tables 1, 3, 8).

In addition to being short, the bridges of trionychid turtles lack ascending buttresses and sutured contacts to the elements of the carapace. Ascending processes cross the peripherals in both the axillary and inguinal regions in pleurodires and testudinoids except for those taxa which well develop plastral kinesis. In Dermatemys only the axillary buttress reaches the pleurals. In all other living families the buttresses are quite reduced and do not cross the peripherals (character 26, Tables 1, 8). The distribution of the states of this character can

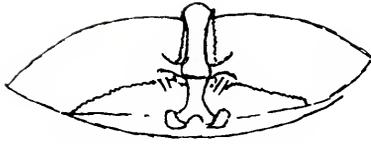
be explained about as parsimoniously by loss or by gain of buttresses if only Recent forms are examined. Buttresses occur in such extinct families as the Baenidae, Plesiochelyidae, and Meiolaniidae, however, suggesting that their presence is in fact the primitive condition.

In a few taxa that lack large plastral buttresses, the bridge is further weakened by the absence of strong sutures between the carapace and plastron. This occurs in chelydrids, cheloniids, Claudius, Carettochelys and trionychids. The absence of sutures at the bridge is considered derived (character 27, Tables 1, 8).

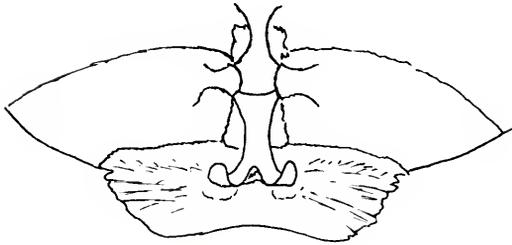
Figure 1. Cross sections of the shell of three cryptodiran turtles.
Top, Trionyx ferox, UF 54212, X 10; middle, Chrysemys picta, UF 37557,
X 5; bottom, Dermochelys coriacea, UF 37557, X 20.



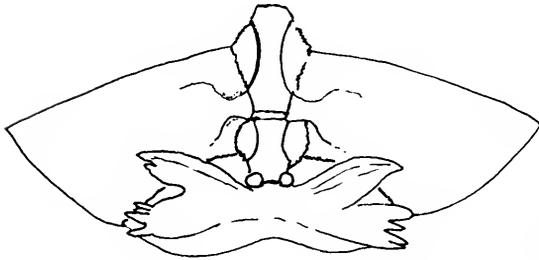
Figure 2. Internal view of the nuchal region of four trionychoid turtles. A, Carettochelys insculpta, UF 43823; B, Cycloderma frenatum, UF 52704; C, Trionyx ferox, UF 53383; D, Chitra indica, PCHP unnumbered.



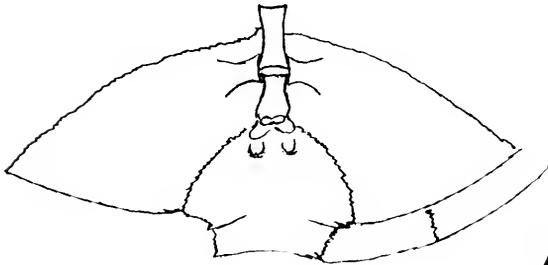
D



C



B



A

Figure 3. Variation in the neural series in the Trionychidae. Arrows indicate proposed progression of change in the trionychid neural series. A, Cycloderma frenatum, TM unnumbered; B, hypothesized intermediate condition; C, Trionyx formosus, BMNH 1947.3.6.9; D, Trionyx ferox, PCHP 1171; E, Lissemys punctata, BMNH 88.12.3.4; F, Cyclanorbis senegalensis, after Villiers, 1955.

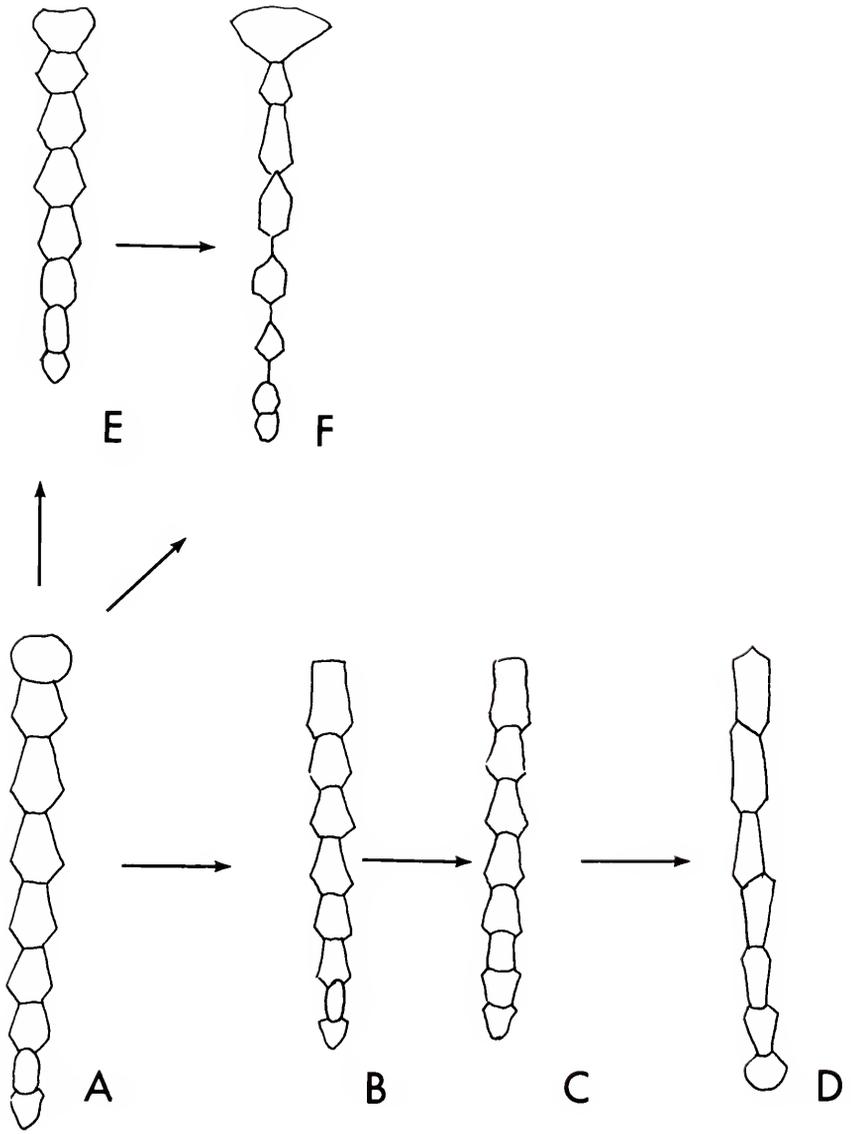
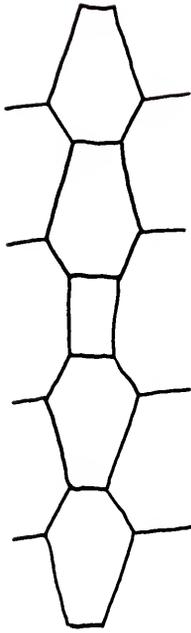
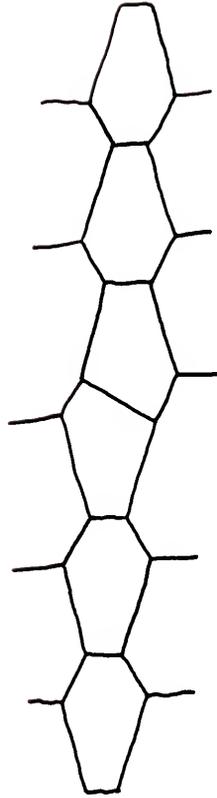


Figure 4. Two types of reversal in the neural orientation of trionychids. A, reversal via a four-sided neural; B, reversal via two assymetrical pentagonal neurals.



A



B

Figure 5. Cross sections of the peripherals of two cryptodires. Top, Lissemys punctata, UF 56017; bottom, Chrysemys picta, UF 40615; both X 20.

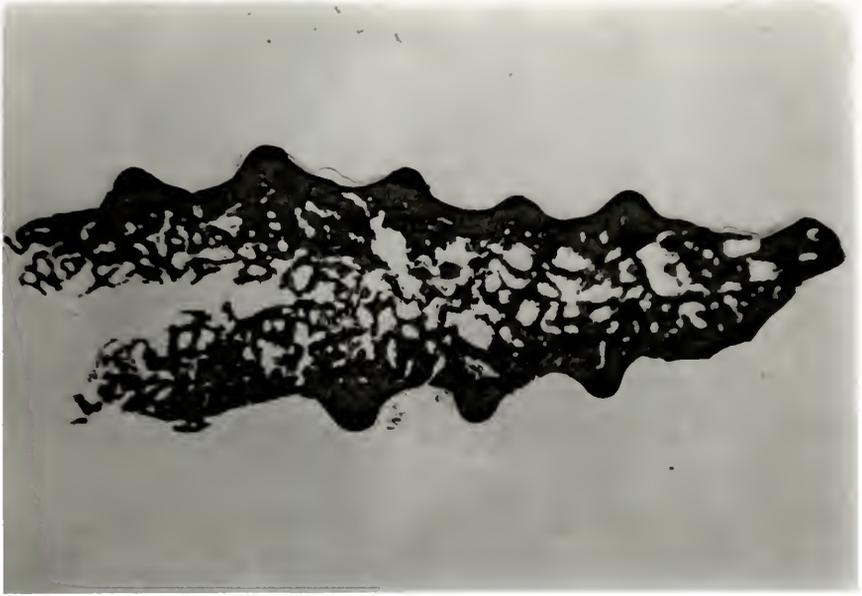


Table 1. Shell characters and character states used for resolving phylogenetic relationships of Recent trionychid turtles. For each character the most primitive state is number 1.

Characters	Character States
1) width/length of nuchal bone	1) less than 2 2) greater than 2 3) greater than 3 4) greater than 4
2) anterior and posterior costiform processes of nuchal bone united	1) no 2) yes
3) position of anterior edge of first body vertebra relative to nuchal bone	1) posterior edge of nuchal 2) middle of nuchal 3) anterior edge of nuchal
4) first and second neurals fused	1) no 2) yes
5) total number of peripherals	1) 22 2) 20 3) 14-18 4) 0
5A) peripherals sutured to pleurals	1) yes 2) no
6) prenuchal bone	1) absent 2) present
8) size of eighth pleurals	1) large 2) reduced or absent
9) number of plastral callosities	1) seven 2) five 3) four 4) two 5) none 0) nine
10A) hyoplastra and hypoplastra fuse just after hatching	1) no 2) yes
10B) hyoplastra and hypoplastra fuse in adults	1) no 2) yes
11) fusion of xiphiplastra	1) absent 2) present

Table 1--continued.

Characters	Character States
12) hypo-xiphiplastral union	1) xiphiplastra lateral to hypoplastra 2) hypoplastra lateral to xiphiplastra
13) number of neurals (fused 1 and 2 counted as 2)	1) nine 2) eight or nine 3) eight 4) seven or eight 5) seven or fewer
14) variability in position of neural reversal	1) always at same neural 2) always at adjacent neurals 3) highly variable
15) pleurals which meet at the midline	1) eighth only 2) seventh and eighth or eighth only 3) sixth, seventh and eighth or seventh and eighth 4) more than sixth, seventh and eighth 0) none
16) point of reversal of orientation of neurals	1) at neural eight 2) at neural seven 3) at neural six or seven 4) at neural six 5) at neural four, five or six
18) epiplastron shape	1) J-shaped 2) I-shaped
19) length epilastra anterior to entoplastron contact	1) short 2) intermediate 3) long
20) depressions on eighth pleurals for contact of ilia	1) present 2) absent
21) shape of entoplastron	1) antero-posteriorly elongate or round 2) "boomerang-shaped"
22) bridge length	1) long

Table 1--continued.

Characters	Character States
23) largest adult size 200 mm or less (disc length)	1) no 2) yes
25) carapace straight or concave posteriolaterally	1) no 2) yes
26) plastral buttresses reach across peripherals to contact pleurals	1) both axillary and inguinal 2) axillary only 3) neither
27) carapace sutured to plastron all across bridge	1) yes 2) no
28) rib heads strongly sutured to vertebral centra	1) no 2) yes
29) sexual dimorphism in disc length	1) no 2) yes
30) shell sculptured and lacking epidermal scutes	1) no 2) yes

Table 2. Maximum known size of Recent trionychids (character 23).

Species	Specimen	Length of Bony disc (mm)
aubryi	BMNH 61.7.29	365
bibroni	BMNH 80.4.25.6	415
cartilagineus	ZSM 832/1920	316
elegans	NMW 1437	475
euphraticus	cited in Siebenrock, 1913	282
ferox	UF 45341*	371
formosus	cited in Annandale, 1912	274
frenatum	BMNH (Type of <i>Aspidochelys livingstoni</i>)	535
gangeticus	cited in Annandale, 1912	485
hurum	cited in Annandale, 1912	416
indica	MNHNP 1880-182	550
leithii	EOM 2819	380
muticus	UMMZ 128086	124
nigricans	cited in Annandale, 1912	403
punctata	cited in Deraniyagala, 1939	370
senegalensis	BMNH 1949.1.3.51	325
sinensis	ZSM 429/1911	201
spiniferus	UF 37228	186.5
steindachneri	MNHNP unnumbered	170
subplanus	calculated from skull BMNH 81.10.10.12	ca.250
swinhoei	calculated from Fig. 1A, Heude, 1880	490
triunguis	KNM-VP-ER-8123	410

*Allen (1982) reports a larger specimen of Trionyx ferox but a disc length is not available.

Table 3. Modal character states for shell characters of the Recent Trionychidae that are used in the analysis of intrafamilial relationships. For descriptions of the characters and character states see Table 1. Periods indicate missing values.

Species	Characters										
	1	2	3	4	5	6	8	9	10A	11	12
<i>aubryi</i>	2	1	2	1	4	1	1	1	2	2	2
<i>bibroni</i>	3	2	2	2	4	1	1	3	1	1	1
<i>cartilagineus</i>	3	2	2	2	4	1	1	2	1	1	1
<i>elegans</i>	2	2	2	1	4	1	1	4	2	1	2
<i>euphraticus</i>	3	2	2	2	4	1	2	4	1	1	1
<i>ferox</i>	3	2	2	2	4	1	2	3	1	1	1
<i>formosus</i>	2	2	2	2	4	1	1	3	1	1	1
<i>frenatum</i>	2	1	1	1	4	1	1	1	2	1	2
<i>gangeticus</i>	3	2	2	1	4	1	1	2	1	1	1
<i>hurum</i>	3	2	2	1	4	1	1	2	1	1	1
<i>indica</i>	3	2	3	2	4	1	1	3	1	1	1
<i>leithii</i>	3	2	2	1	4	1	1	2	1	1	1
<i>muticus</i>	4	2	2	2	4	1	2	1	1	1	1
<i>nigricans</i>	3	2	2	1	4	1	1	2	1	1	1
<i>punctata</i>	2	1	1	1	3	2	1	1	2	2	2
<i>senegalensis</i>	3	2	2	1	4	2	1	0	2	1	2
<i>sinensis</i>	4	2	2	2	4	1	1	1	1	1	1
<i>spiniferus</i>	3	2	2	2	4	1	2	1	1	1	1
<i>steindachneri</i>	2	2	2	2	4	1	1	3	1	1	1
<i>subplanus</i>	4	2	2	2	4	1	1	3	1	1	1
<i>swinhoei</i>	.	.	.	2	4	1	2	4	1	1	1
<i>triunguis</i>	3	2	2	2	4	1	1	3	1	1	1

Table 3--continued.

Species	Characters											
	13	14	15	16	17	18	19	20	22	23	25	29
<i>aubryi</i>	2	1	2	1	1	2	1	1	1	1	2	1
<i>bibroni</i>	2	1	1	3	2	1	1	2	2	1	1	1
<i>cartilagineus</i>	1	1	1	2	2	1	3	2	2	1	1	1
<i>elegans</i>	2	1	2	1	1	1	1	2	2	1	1	1
<i>euphraticus</i>	3	1	2	3	2	1	1	2	2	1	1	1
<i>ferox</i>	3	3	2	4	2	1	1	2	2	1	1	2
<i>formosus</i>	1	1	1	2	1	1	1	2	2	1	1	1
<i>frenatum</i>	2	1	2	2	1	2	1	1	1	1	2	1
<i>gangeticus</i>	2	2	2	3	1	1	2	2	2	1	1	1
<i>hurum</i>	1	2	2	3	1	1	2	2	2	1	1	1
<i>indica</i>	1	1	1	3	1	1	1	2	2	1	1	2?
<i>leithii</i>	2	1	1	3	1	1	2	2	2	1	1	1
<i>muticus</i>	2	3	2	4	3	1	1	2	2	2	1	2
<i>nigricans</i>	1	1	2	3	.	1	2	2	2	1	1	1
<i>punctata</i>	4	1	2	2	1	2	1	1	1	1	2	1
<i>senegalensis</i>	5	.	4	.	1	1	1	1	1	1	1	1
<i>sinensis</i>	2	3	2	4	2	1	2	2	2	2	1	1
<i>spiniferus</i>	3	3	2	4	3	1	1	2	2	2	1	2
<i>steindachneri</i>	2	1	2	2	1	1	3	2	2	2	1	1
<i>subplanus</i>	1	2	0	2	3	1	3	2	2	2	1	1
<i>swinhoei</i>	1	1	2	2	1	1	1
<i>triunguis</i>	3	1	2	3	2	1	1	2	2	1	1	1

Table 4. Occurrence of suprascapular fontanels (character 17) in the carapace of Recent trionychids. Disc length for the largest specimen with fontanels (A), smallest specimen without fontanels (B), and largest specimen examined for fontanels (C) are given for each species.

Species	A	B	C
aubryi	none	131.0	365.0
bibroni	71.0	200.0	415.0
cartilagineus	174.0	172.0	316.0
elegans	none	182.0	475.0
euphraticus	273.0	217.0	273.0
ferox	237.0	120.5	315.0
formosus	none	156.0	156.0
frenatum	none	180.0	535.0
gangeticus	106.0	205.0	460.0
hurum	none	132.0	292.0
indica	none	180.0	550.0
leithii	none	205.0	380.0
muticus	124.0	none	124.0
punctata	none	60.0	277.5
senegalensis	none	113.0	294.5
sinensis	140.0	117.0	242.0
spiniferus	males 89.5 females 186.5	85.0 none	89.5 186.5
steindachneri	170.0	none	170.0
subplanus	177.0	none	177.0
triunguis	83.5	197.0	410.0

Table 5. Number of neurals in Recent trionychid turtles. Values represent the frequency of occurrence for the sample. A fused first and second neural is counted as two elements. Trionyx formosus, T. nigricans and T. swinhoi are excluded due to insufficient sample size.

Species	N	3	4	5	6	7	8	9	10
aubryi	17						0.71	0.29	
bibroni	10					0.10	0.20	0.70	
cartilagineus	18						0.17	0.78	0.06
elegans	14					0.21	0.43	0.36	
euphraticus	6						1.00		
ferox	31					0.06	0.88	0.06	
frenatum	5					0.20	0.20	0.60	
gangeticus	7						0.71	0.29	
hurum	5						0.20	0.80	
indica	13							1.00	
leithii	3						0.33	0.67	
muticus	7						0.43	0.57	
punctata	19					0.21	0.74	0.05	
senegalensis	17	0.06	0.06	0.18	0.47	0.18	0.06		
sinensis	25						0.40	0.60	
spiniferus	18					0.06	0.88	0.06	
steindachneri	3						0.33	0.67	
subplanus	10							0.80	0.20
triunguis	14						0.92	0.08	

Table 6. Location of reversal in neural orientation in Recent trionychids. Location of the most posterior reversal is given as a frequency of occurrence at or between neurals. Values which do not sum to 1.0 are due to individuals with no neural reversal (see Table 7). Trionyx formosus, T. nigricans and T. swinhoei are excluded due to insufficient sample size; in T. senegalensis the neural series is too fragmented to allow the detection of reversals.

Species	N	4/5 or anterior	5	5/6	6	6/7	7	7/8	8
aubryi	17							0.12	0.06
bibroni	10		0.10	0.30	0.50	0.10			
cartilagineus	18				0.28	0.17	0.44	0.06	0.11
elegans	14								0.43
euphraticus	6		0.17	0.33	0.33	0.17			
ferox	31	0.16	0.13	0.19	0.32	0.19			
frenatum	5					0.20	0.40		0.20
gangeticus	7				0.57		0.43		
hurum	5				0.40	0.20	0.40		
indica	13			0.08	0.92				
leithii	3	0.33			0.33		0.33		
muticus	7		0.14	0.14	0.57	0.14			
punctata	19						0.32	0.11	
sinensis	25	0.08		0.08	0.12	0.28	0.40	0.04	
spiniferus	18	0.28	0.11	0.33	0.06	0.17	0.06		
steindachneri	3					0.33	0.33		
subplanus	8					0.25	0.63	0.13	
triunguis	14			0.08	0.69	0.08	0.15		

Table 7. Number of reversals of orientation in the neural series of Recent trionychids. Number of reversals is given as a frequency.

Species	N	0	1	2	3
aubryi	17	0.82	0.18		
bibroni	10		1.00		
cartilagineus	18		1.00		
elegans	14	0.57	0.43		
euphraticus	6		1.00		
ferox	31		0.66	0.31	0.03
frenatum	5	0.20	0.80		
gangeticus	7		1.00		
hurum	5		1.00		
indica	13		1.00		
leithii	3		1.00		
muticus	7		0.86		0.14
punctata	19	0.58	0.42		
sinensis	25		0.80	0.16	0.04
spiniferus	18		0.44	0.28	0.28
steindachneri	3	0.33	0.67		
subplanus	8		1.00		
triunguis	14		1.00		

Table 8. Modal character states for shell characters of the Recent Trionychidae that are used in the analysis of interfamilial relationships. For descriptions of characters and character states see Table 1.

Taxa	Character States						
	5	5A	21	26	27	28	30
Trionychidae	3/4	2	2	3	2	2	2
Carettochelys	2	2	1	3	2	2	2
Claudius	2	1	1	3	2	1	1
Staurotypus	2	1	1	3	1	1	1
Kinosterninae	2	1	1	3	1	1	1
Dermatemys	1	1	1	2	1	1	1
Chelydridae	1	1	1	3	2	1	1
Platysternon	1	1	1	3	2	1	1
Cheloniidae	1	2	1	3	2	1	1
Emydidae	1	1	1	1	1*	1	1
Testudinidae	1	1	1	1	1	1	1
Pleurodira	1	1	1	1	1*	2	1

* except in kinetic forms

Table 9. Extension of the right epiplastron beyond the entoplastron relative to total hypoplastron width of the right side (character 19). Sample size, average and one standard deviation are given for each species. Species with I-shaped epiplastra and T. nigricans are not included.

Species	N	\bar{X}	± 1 S.D.
bibroni	3	0.165	0.042
cartilagineus	4	0.482	0.022
elegans	2	0.356	0.019
euphraticus	2	0.263	0.025
ferox	13	0.228	0.019
formosus	1	0.287	
gangeticus	2	0.314	0.038
hurum	2	0.358	0.010
indica	5	0.230	0.011
leithii	3	0.312	0.021
muticus	3	0.183	0.017
senegalensis	3	0.280	0.015
sinensis	13	0.423	0.036
spiniferus	10	0.248	0.024
steindachneri	2	0.418	0.014
subplanus	5	0.479	0.039
swinhoei	1	0.221	
triunguis	3	0.228	0.023

Variation in Skull Morphology

Introduction

The value of the trionychid skull in systematics has been recognized by numerous authors (Gray, 1864, 1869, 1873a, 1873b; Boulenger, 1889; Hummel, 1929; Loveridge and Williams, 1957; De Broin, 1977). As pointed out by Loveridge and Williams (1957) there has been too much emphasis on the size and form of the jaws and too little on details of morphology and contacts of skull elements. Numerous authors have expressed concern about the validity of characters of the size and shape of the jaws (Boulenger, 1889; Villiers, 1958; Barghusen and Parsons, 1966; Eiselt, 1976; De Broin, 1977). But only Dalrymple's (1977) account of variation in the skull of Trionyx ferox treats the correlation of skull size and shape to environmental factors in a detailed and systematic fashion. Dalrymple has found that the most variable features of size and shape of the skull of T. ferox are those which relate to feeding. Those structures which provide sites of origin or passage for jaw musculature increase allometrically with age, and the amount of relative increase is highly variable. Furthermore, the development of features related to feeding can occur independently of one another. This high degree of variability in characters of the feeding apparatus indicates that they are not useful systematic features, as had been suspected.

In this study quantitative characters of the jaws and associated structures (palatal groove, supraoccipital spine) are avoided. Treatment of the skull concentrates on contacts between elements and between elements and features of external morphology. Because complete interspecific comparison is the goal of this study, data from sectioned skulls (8 of 22 trionychid species available) will not be treated. This

is the first study of trionychnid systematics for which at least one skull of every currently recognized Recent species was available.

The skull characters and character states which are treated in this section are summarized in Table 10. The details of distribution of the states of characters important for resolving relationships within the Trionychnidae are given in Table 11. The states for characters important for resolving interfamilial relationships are given in Table 12. Character states which are autapomorphic for a living trionychnid species are listed in Table 13. Discussion of these characters is arranged by region of the skull beginning anteriorly and proceeding posteriorly, with the dorsal surface treated first.

Nasal Region

The premaxillae of cryptodires are usually paired elements that make up the ventral edge of the apertura narium externum. Among trionychnoids this is true only for dermatemydids and kinosternids. In Carettochelys, as well as all trionychnids, these normally paired elements are fused to one another (character S15, Tables 10, 12; Fig. 6 A, B, D). In trionychnids this fused premaxillary differs further from those of the outgroups in being excluded from the apertura narium exturnum by the maxillae which meet dorsally to it (character S16, Table 12; Fig. 6 A, B).

In three trionychnids the premaxillary is either often absent (Chitra indica, 4 of 10), or nearly always absent (Cycloderma frenatum, 4 of 5; Pelochelys bibroni; 6 of 7) (character S59, Table 11). The loss of this element is clearly derived.

Because nasals are absent in all trionychids, as they are in all living cryptodires (Gaffney, 1979b), the prefrontals are the anteriormost paired elements on the dorsal surface of the skull. Thus, the prefrontals form the dorsal border of the apertura narium externum. Laterally these elements contact the maxillae and border the anterior portion of each orbit between the maxilla and frontal. In most cryptodires the descending processes of the prefrontals contact the vomer and palatines. There is significant variation among trionychids in these contacts. There is also useful variation in the degree of emargination of the prefrontals at the dorsal edge of the apertura narium externum and in the degree of separation of the maxillae and frontals along the anterior margin of the orbit.

Through reduction of the prefrontals, vomer and palatines, contact between the prefrontals and palatal elements in trionychids is greatly reduced, or lost. The prefrontal-palatine contact found in most cryptodires is lost in all trionychids (Gaffney, 1979b) and this loss can be considered a shared derived character for the family (character S9, Table 12). Contact between the vomer and prefrontals is the common condition among trionychids, as it is for all testudines. It is absent only in Cycloderma aubryi, Cycloderma frenatum, Cyclanorbis senegalensis and Chitra indica, and is clearly a derived condition (character S7, Table 11).

With the exception of two very primitive forms, Proganochelys and Kallokibotion, testudines have an unpaired apertura narium externum with a nearly straight to somewhat anteriorly convex dorsal margin that is usually formed by the prefrontals (Fig. 6 C, D). This is true for the outgroups and for some living species of trionychids. The remaining

trionychids show some degree of emargination of the prefrontals and thus alteration of this primitive shape of the external narial opening. With one exception emargination occurs laterally and is either shallow or quite deep (character S13A, Table 11; Fig. 6 A, B). Only in Cyclanorbis elegans does emargination occur medially (character S13B, Table 13). The condition in C. elegans is considered to occur independently from that in other emarginate forms. Weak lateral emargination is considered to be intermediate between the strongly emarginate and non-emarginate conditions.

It is the prefrontal that normally separates the maxilla from the frontal at the anterior edge of the orbit in turtles. In a single trionychid, Trionyx subplanus, the maxillae contact the frontals lateral to the prefrontals in about one-half of the specimens examined. In the others, these elements are quite close and their proximity can be considered a unique feature of this species (character S49, Table 13).

Orbital Region

A frequently used character in trionychid systematics is the relationship between the width of the postorbital bar and orbit diameter. The postorbital bar varies in width among the species of this family from two times wider than the orbit to one-sixth of orbit width. Variation in the width of the postorbital bar relative to the width of the orbit is not continuous but constitutes four separate sets of species.

The outgroups vary in width of postorbital bar between state two (equal to or wider than orbit) and state three (one-half to one-third width of orbit). Only Claudius, with a very narrow postorbital bar (state 4), and Platysternon and the chelonoids, which lack temporal emargination (state 1), show the extreme conditions. In the current

context it seems most appropriate to consider most divergent postorbital bar widths to be derived relative to the combined intermediate groups.

Skull Emargination

The advanced cryptodires (Chelomacryptodira of Gaffney, 1984), the Trionychoidea and Testudinoidea, have highly developed temporal emargination. But these two superfamilies differ greatly in the degree of cheek emargination that they exhibit.

As reviewed by Gaffney (1979b) there has always been a problem identifying landmarks suitable for making comparisons between taxa. The use of exposed elements seems to be most appropriate, but use of exposure of the postorbital as an index of temporal emargination in trionychids is problematical. All trionychids have very deep temporal emargination that leaves the processus trochlearis oticum fully exposed, and the communication of the fossa temporalis dorsalis with the fossa temporalis ventralis is visible over a significant distance. With this degree of temporal emargination the postorbital bone, which makes up a significant portion of the postorbital bar, is usually exposed. This is true for all outgroup trionychoids and testudinoids examined. The postorbital in trionychids is one of several skull elements which has undergone extreme reduction. This reduction is so extreme that contact between the jugal and parietal occurs below the skull surface in all trionychids (character S6, Table 12) and these two elements make up much of the postorbital bar. In some trionychids jugal-parietal contact is so strong that it is present on the skull surface and the postorbital is isolated from temporal emargination. Isolation of the postorbital from the temporal emargination might seem quite primitive and it certainly is if isolation

is via parietal-squamosal or parietal-squamosal-quadratojugal contact. But isolation via jugal-parietal contact is a derived feature found only among trionychids (character S5, Table 12).

Jugal-parietal contact on the skull surface can vary within a single trionychid species. This variable condition is considered to be intermediate between the primitive absence of jugal-parietal contact on the skull surface and its presence which is certainly derived (character S5, Table 11).

Lateral to the temporal emargination in trionychids is a very narrow bar formed by the jugal and quadratojugal. The trionychids parallel the condition seen in some emydids of extreme quadratojugal reduction. But unlike the case in emydids this element is never lost. In all trionychids the quadratojugal does not contact the maxilla and postorbital but only the jugal. Posteriorly it sutures to the quadrate and squamosal. In other living trionychoids the contact of the quadratojugal to the postorbital is maintained and the quadrato-jugal maxillary contact is maintained except in some Dermatemys (UF 29168; Fig. 172 in Gaffney, 1979b). Reduced contacts of the quadratojugal is considered derived within the Trionychoidea (characters S1, S4, Table 12).

Because of the reduced size of the quadratojugal, the jugal and squamosal lie quite close to one another in all trionychids. In six species they are occasionally in contact. This is considered to be the derived state for character S2 (Table 11).

Strong cheek emargination, which accompanies temporal emargination in testudinoids, is not found among living trionychoids. Although cheek emargination is visible in Dermatemys, Carettochelys and kinosternids, it does not extend above an imaginary line extending horizontally from the

lower edge of the orbit (character S10, Table 12). In testudinoids, on the contrary, cheek emargination is quite well developed and extends well dorsal to such a line (except in Malayemys). In all testudinoids and trionychoids except for the Trionychidae, cheek emargination is limited anteriorly by the maxillary. In the Trionychidae, cheek emargination occurs within the jugal when it is present (character S12, Table 12). Because of flexure of the snout in trionychids, ventral emargination of the jugal does reach above the lower rim of the orbit in a few cases. But emargination occurs only within the jugal and is the site of origin of the *M. zygomatico-mandibularis* (Dalrymple, 1977), a muscle which is unique to trionychids. Therefore, it is likely that cheek emargination in trionychids is not homologous to that of other turtles and that restriction of true cheek emargination ventral to the lower rim of the orbit can be considered a derived feature of the Trionychoidea (character S10, Table 12).

Stapedial Foramen

The most significant differences between testudinoid and trionychoid turtles is in the pattern of blood flow to the head (McDowell, 1961; Albrecht, 1967; Gaffney, 1975, 1979b). This is reflected in variation of the size of the stapedial foramen and in the morphology of the prootic and parietal adjacent to this foramen. In testudinoids the majority of anterior blood flow is via the stapedial artery. Therefore the foramen stapedio-temporale is large and there is often a groove in the prootic and parietal for the large stapedial artery. In trionychoids, the stapedial artery is reduced because most of the anterior blood flow is via the internal carotid artery. In this superfamily the foramen stapediotemporale tends to be reduced or absent and rarely is there

evidence of a groove for the stapedia artery on the prootic or parietal (character S43, Table 12). These feature are important at the family level, there is little variation within the Trionychidae.

The Processus Trochlearis Oticum and the Quadrate

The processus trochlearis oticum is a distinctive feature of the Cryptodira. It is over this structure that the majority of the jaw adductor musculature lies. This is in contrast to the condition in Pleurodira in which the lower jaw adductors operate over a process of the pterygoid. In most cryptodires the majority of the processus is formed by the quadrate.

In trionychids the processus trochlearis oticum can be quite large and it always involves the quadrate, prootic and parietal (Table 14). In thirteen species the quadratojugal is included in at least some individuals. Within the Trionychidae, three useful patterns of variation are noted: the inclusion of the quadratojugal into the processus trochlearis oticum, reduction in the contribution made by the quadrate, and increase in the contribution made by the parietal. The first occurs when the quadratojugal sends a medial process across the anterior edge of the quadrate. It results in reduction of the quadrate contribution and is absent from the processus in all outgroups. It is thus considered to be derived within the Trionychidae (character M16, Table 11). In trionychids unlike other cryptodires the quadrate makes up less than one-third of this structure (character M17, Table 12).

There is additional variation among trionychids in the amount of parietal contribution. In the majority the parietal contribution is small, always less than one sixth of the total (Table 14). In the North

American forms, and also Cyclanorbis elegans, Trionyx euphraticus, T. nigricans, T. swinhoei and T. triunguis the parietal contribution is slightly larger, about one-fourth or more of the processus trochlearis oticum (character M19, Table 11). The contribution of the parietal to this structure in other cryptodires is quite limited or absent. Thus the large contribution in trionychids is clearly derived.

In very few chelonians does the quadrate completely surround the collumela (Gaffney, 1979b). This occurs in the Trionychidae, Carettochelys, Chelydridae and Testudinidae (Tables 10, 12).

The Trigeminal Region

The trigeminal foramen lies lateral to the braincase and below the processus trochlearis oticum of cryptodires. In trionychids it is a large opening providing an exit for the maxillary and mandibular branches of the trigeminal nerve as well as the mandibular artery (Gaffney, 1979b). In trionychids the parietal, prootic, quadrate, pterygoid and epipterygoid may contact this foramen but there is significant inter- and intraspecific variation in the degree and form of contact of each element (Fig. 7).

An epipterygoid is present in all trionychid species but tends to fuse to the pterygoid in larger individuals (Table 15). Fusion occurs less frequently (perhaps later in life) in trionychines than in cyclanorbines. Variation in the length of retention of a distinct epipterygoid is treated via three states of character T7 (Tables 10, 11). This element usually fuses to the pterygoid in older adults of most cryptodires. Long-term retention of the epipterygoid is therefore considered to be a derived and possibly paedomorphic feature.

Because the epipterygoid is an important landmark in describing variation in the morphology of the trigeminal region of trionychids, descriptions of this region are based on individuals in which this element is not yet fused to the pterygoid. Complication of these descriptions arises because the epipterygoid is a superficial element of variable shape and size that can cover certain contacts in some individuals of a given species but not in others. This results in the ungainly appearance of the three states of character T2B (Table 10) in which all states include the possibility of no pterygoid-trigeminal contact (the case when the epipterygoid is large), but show different forms of pterygoid-trigeminal contact if the epipterygoid is not enlarged. When the pterygoid does contact the foramen nervi trigemini the contact may occur posteriorly between the prootic and epipterygoid (state 1), ventrally between the epipterygoid and quadrate (state 0), anteriorly between the parietal and epipterygoid (state 2), or in no individuals at all (character T2A, state 2). See Table 11 for distribution of these character states.

Contact of the pterygoid to the foramen nervi trigemini between the prootic and epipterygoid (state 1, character T2) occurs in Trionyx formosus, T. gangeticus, T. hurum, T. nigricans and Lissemys punctata and results in the isolation of the quadrate from the foramen nervi trigemini (Fig. 7 D, F). In both Cyclanorbis species and both Cycloderma species the quadrate is also isolated from the foramen nervi trigemini. But in this case it is the epipterygoid that meets the prootic posteriorly and thus intervenes (character T4, state 2; Fig 7 E). When the epipterygoid fuses to the pterygoid, the two groups mentioned above (those with state

1 of character T2 and those with state 2 of character T4) look identical but they arrive at this condition via very different pathways.

Significant variation in this region among the outgroups makes assigning polarities to characters of contact of the epipterygoid to the foramen nervi trigemini difficult. Identification of polarity for other contacts in the trigeminal region seems clear. In no other trionychoid does the epipterygoid contact the prootic posteriorly (Fig. 7 A, B, D) as it does in Cyclanorbis and Cycloderma (character T4, Table 11; Fig. 7 E) or anteriorly as it does in some or all members of certain trionychine species (character T3, Table 11; Fig. 7 H). Similarly, all trionychoid outgroups have contact between the epipterygoid and palatine (Fig. 7 A, B, C) and the absence of this contact in some or all members of a species is considered derived (character T1, Tables 10, 11).

An important feature of the Trionychoidea (sensu Gaffney, 1979b) is participation of the palatine in the formation of the lateral wall of the braincase. This occurs in all trionychoids examined and can be seen just anterior to the foramen nervi trigemini (Fig. 7 A-H). In trionychoids the pterygoid is excluded from the interorbital fenestra by the expanded palatines. In testudinoids and in other turtles the pterygoid either reaches the interorbital fenestra or is immediately adjacent to it (character 14, Table 12).

The Occipital Region

There are numerous systematically useful characters visible on the skull in posterior view. One of these is a reflection of the importance of the internal carotid artery (Albrecht, 1967; McDowell, 1961; Gaffney, 1975, 1979b). The large diameter of the canalis carotici interni and the straight path that it follows in trionychoids can be observed even in

articulated skulls. A stiff wire, slightly narrower than the canal, will pass into the foramen posterius canalis carotici interni and out of the foramen anterius canalis carotici interni with ease (character S31, Table 12). In large trionychids the latter opening is clearly visible through the former. This is in contrast to the case in other cryptodires in which this canal makes an S-shaped curve or a high angle bend (see Figs. 25-29 in Gaffney, 1979b). It seems likely that this straight, wide path facilitates blood flow through the internal carotid in trionychoids.

The location of the foramen posterius canalis carotici interni in the Trionychidae is also of some interest. In all species of this family it is completely surrounded by the pterygoid. The same is true for Carettochelys, but in kinosternids it can be open dorsally to the fenestra postotica (Staurotypus) or be bordered dorsally by the prootic (Kinosternon). In Dermatemys and in most testudinoids it is open dorsally to the fenestra postotica (character S30, Table 12).

In some trionychids the foramen posterius canalis carotici interni is quite ventrally located and is reminiscent of the condition in the Paracryptodira. However, in all other trionychoids and other Eucryptodira it is posteriorly located. Thus the presence of these foramina on the ventral surface of the skull is considered derived.

Variation in the location of the foramen posterius canalis carotici interni within the Trionychidae is best described in relation to a crest of bone which is a lateral extension of the tuberculum basioccipitales. In no member of this family is this foramen located above such a crest, but in Pelochelys bibroni, Chitra indica, Trionyx cartilagineus and T. nigricans (only one specimen available) it is found within the crest.

The latter condition is considered to be primitive relative to the ventral position found in all other species (character S34, Table 11).

The foramen jugularis posterius is located lateral to the foramen magnum in turtles and is visible in posterior view. In most cryptodires it is surrounded by the exoccipital or exoccipital and opisthotic (Fig. 8 A, B, C). In some cheloniids, some trionychids, some Claudius and Platysternon, this opening is continuous with the fenestra postotica (Fig. 8 E, F). Isolation of the foramen jugularis posterius from the fenestra postotica when present in the Trionychidae occurs in a unique manner, that is by contact of the pterygoid to the opisthotic (Fig. 8, D, F). In all cyclanorbines the pterygoid arches dorsally to meet the opisthotic (Fig. 8 D). In the trionychines infrequent isolation occurs via the descent of a narrow process of the opisthotic across an otherwise open fenestra postotica (8 F). These two types of isolation of the foramen jugulare posterius appear to be independent evolutionary events (Loveridge and Williams, 1957) and are treated as such in the analysis of intrafamilial relationship (characters S32A, S32B, Table 11).

In nearly all trionychids, as in most other trionychoids and in chelydrids (including Platysternon) and chelonioids, there is contact between the exoccipital and pterygoid. Only in Trionyx triunguis does the basioccipital intervene between these elements, separating them as it does in most testudinoids. In the current context this is a unique feature most useful for the recognition of T. triunguis (character S57, Table 13). Separation of the pterygoid from the exoccipital may be a shared derived feature of the Testudinoidea.

The crista dorsalis occipitalis is a small tubercle on the dorsal surface of the basioccipital found within the braincase. When present

this tubercle is visible (under correct lighting) through the foramen magnum. Gaffney (1979b) reports that it is variably developed in most turtles but that it is missing in Trionyx ferox. I find this structure to be absent in all trionychoids and testudinids examined, but clearly visible in cheloniids, dermochelyids, chelydrids, and emydids (except Rhinoclemys pulcherimma). This is therefore a useful character at the interfamilial level (character S29, Table 12).

Palate

The most striking differences between the palates of trionychoids and those of other cryptodires is the presence of a median foramen anterior to the apertura narium internum and the presence of unconstricted pterygoids. This midline opening is usually of large size and is called the foramen intermaxillaris. It varies in size in the Trionychoidea (see below, character M4) but it always separates the vomer from the premaxilla. The same structure appears to be present in Carettochelys where it is continuous with the apertura narium internum. In Carettochelys the vomer and maxillae do not meet anterior to the apertura narium internum and the posterior limits of the foramen intermaxillaris remain undefined.

A structure that appears to be homologous to the foramen intermaxillaris is present in mature individuals of all three living staurotypine kinosternids and in Xenochelys formosus (Oligocene of South Dakota, Williams, 1952). The deep pit in the premaxillae, which accommodates the symphyseal projection of the lower jaw in all kinosternids, opens dorsally in large individuals of both species of Staurotypus, in Claudius and in Xenochelys. This does not occur in large individuals of any other living forms with strongly hooked lower jaws

such as chelydrids (including Platysternon). This trait, which appears late in life in staurotypines, may have come to arise earlier in carettochelyids, which also have sharply hooked lower jaws. Once present, this novelty apparently remained in trionychids in spite of the fact that they have unhooked lower jaws (character S19, Table 12).

Variation in the size of the intermaxillary foramen among trionychids has been utilized by several authors (Loveridge and Williams, 1957; De Broin, 1977). Comparison of the length of the intermaxillary foramen relative to the total skull length is not satisfactory; the distribution of this character for trionychids is quite continuous (Fig. 9). It should be noted, however, that all of the members of a proposed monophyletic group (Meylan, 1985), the North American forms plus Trionyx swinhoei, T. euphraticus and T. triunguis have the highest values for the ratio of intermaxillary foramen length to total skull length.

This character can be utilized if examined in terms of its size relative to the primary palate. Variation in the ratio of length of the intermaxillary foramen to length primary palate among trionychids falls into five distinct groups (Fig. 9, Table 10). Identification of a character polarity for the states of this character is difficult. The intermaxillary foramen in other trionychoids is highly specialized in one case (Carettochelys) and incompletely developed in the other (Staurotypinae). It appears prudent to assume that the medium size classes together approximate the primitive state and that the most divergent conditions (states 0 and 2) are derived within the Trionychidae (character M4, Tables 11, 13).

The vomer is one of several elements which is reduced in the Trionychidae. In most turtles it lies between the paired maxillae and

palatines. Anteriorly it reaches the premaxillae and posteriorly it often contacts the paired pterygoids. When an intermaxillary foramen is present, premaxillary contact is prevented. In some trionychids the vomer divides the maxillae completely and reaches the intermaxillary foramen between them. This most closely approximates the condition in the outgroups in which no intermaxillary foramen is present and is therefore considered to be the primitive condition for the relationship of the vomer to the maxillae (character S20, Table 11).

In other trionychids the maxillae meet on the midline of the palate ventral to the vomer. Depending on the degree of reduction of the vomer and the length of this intermaxillary suture, the vomer may still enter the intermaxillary foramen by reaching it dorsally over the united maxillae. Reduction of the vomer to the extent that it does not reach anteriorly to the intermaxillary foramen is interpreted as the derived state of character 21 (Table 11).

Posteriorly, the vomer of most cryptodires reaches between the paired palatines as far as the pterygoids. This is true of Dermatemys and kinosternids but not Carettochelys or any trionychids. The failure of the vomer to reach as far posterior as the palatines is considered a derived condition (character S22, Table 12).

In most chelonians the vomer is the only unpaired midline element reaching the transverse pterygoid-palatine suture. In Carettochelys and all trionychids (except T. euphraticus), only an enlarged basisphenoid does so. This unique contact of palatal elements has been recognized as evidence of unique common ancestry of these two taxa (Baur 1891b; Meylan, 1985). It is treated as such here (character S18, Table 12). The

absence of contact of palatines and basisphenoid in most specimens of T. euphraticus appears to be a unique reversal (character S18, Table 13).

The vomer of turtles does not normally contact the basisphenoid, but with the anterior elongation of the latter in trionychids comes a greater possibility that such contact might occur. Siebenrock (1897) reports vomer-basisphenoid contact on the dorsal surface of the palate in Pelochelys. In two of the seven Pelochelys skulls examined during this study (USNM 231523 and NMW 1857) contact between these elements is present on the palate. This condition is unique to Pelochelys among the Trionychidae (character S23, Table 13). In Cycloderma frenatum the vomer is absent. This is a unique condition among trionychids (character S60, Table 13).

At or near the palatine-pterygoid suture in all chelonians is located a pair of ventral openings in the palate, the foramina palatinum posterius. These openings are never large in trionychids. They may be entire, divided into two openings, or divided into numerous small openings not larger than the nutritive foramina of the palate. Small size of these openings may be shared by all trionychoids as well as some testudinoids, but the variation in the division of this opening is useful within the Trionychidae, and in particular among the Cyclanorbinae (character S26, Tables 11). Division of the foramen palatinum posterius is considered derived.

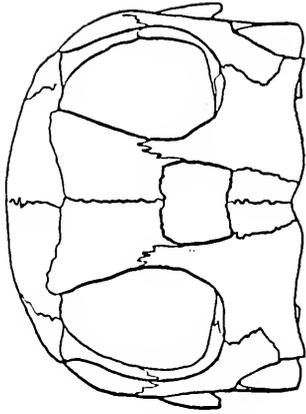
The contacts of the foramina palatinum posterius also vary among the living species of the Trionychidae. In most forms, as in most chelonians, these foramina contact the palatine and the pterygoid and/or maxillary. In a limited number of trionychids this opening is restricted

to the palatine, which is considered to be a derived condition (character S27, Table 11).

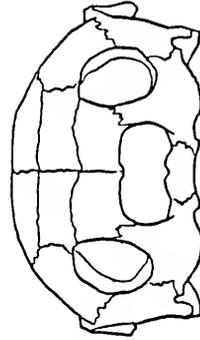
The processus pterygoideus externus of cryptodires usually takes the form of a moderate to short posterior or posteriolateral projection from the anteriolateral edge of the pterygoid just anterior to some degree of medial constriction. They are found in nearly all cryptodires and they vary considerably in degree of development. In trionychids there is no medial constriction of the pterygoids and no free projection of this process. In Carettochelys, the pterygoids are only slightly constricted and the processus pterygoideus externus projects very weakly or not at all. In other trionychoids these processes may be present (Kinosternon, Staurotypus, some Dermatemys, some Claudius) or absent (some Claudius, some Dermatemys, Xenochelys), but they are never as large and posteriorly projecting as in the Chelydridae or some of the Emydidae. Reduction of this projecting quality could be a shared derived feature of the Trionychoidea. It occurs elsewhere among the Cheloniidae (Chelonia), Emydidae (Malayemys) and Testudinidae (several genera). The absence of a projecting processus is certainly derived for the Trionychidae and possibly for the Trionychidae plus Carettochelys (character S25, Table 12).

The elongate basisphenoid of trionychids varies in shape. In most species, as in the outgroups, it has a subtriangular shape although somewhat more elongate. In a few forms medial constriction of the basisphenoid occurs either occasionally or frequently. The presence of an hour-glass shaped basisphenoid is considered derived within the Trionychidae (character S58, Table 11).

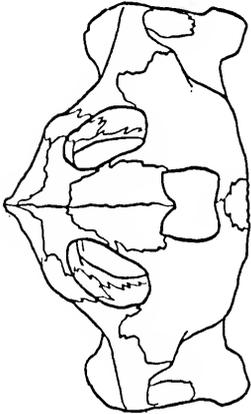
Figure 6. Frontal views of the skull of four cryptodiran turtles showing fusion of the premaxillae in trionychids (A, B) and carettochelyids (D), exclusion of the premaxillae from the apertura narium externum in trionychids (A, B), and slight (A) to extensive (B) emargination of the anterior border of the prefrontals. A, Trionyx cartilagineus, RH 129, X 0.65; B, Trionyx ferox, PM unnumbered, X 1; C, Chelonia mydas, UF 55880, X 0.50; D, Carettochelys insculpta, UF 43888, X 0.65.



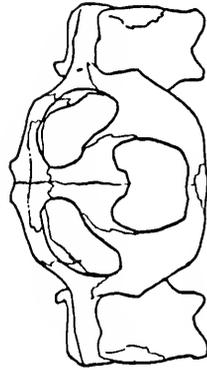
C



D



A



B

Figure 7. The trigeminal region of eight trionychoid turtles showing contacts of the skull elements around the foramen nervi trigemini and participation by the palatine in the lateral wall of the brain case. The foramen interorbitale is crosshatched, the foramen nervi trigemini is stippled. Abbreviations: e, epipterygoid; pal, palatine; par, parietal; pr, prootic; pt, pterygoid; q, quadrate. A, Dermatemys mawii, BMNH 1911.1.28.1; B, Staurotypus salvinii, BMNH 1879.1.7.5; C, Carettochelys insculpta, BMNH 1903.4.10.1; D, Lissemys punctata, UF 56017; E, Cyclanorbis elegans, BMNH 1954.1.14.3; F, Trionyx hurum, BMNH 86.8.16.2; G, Trionyx triunguis, BMNH 62.3.20.8; H, Chitra indica, ISNB 3295.

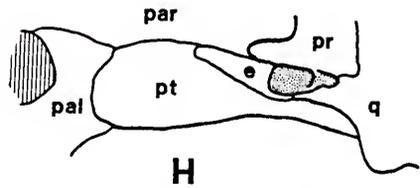
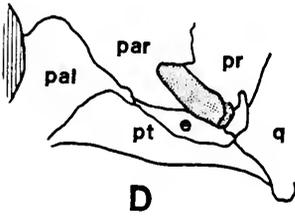
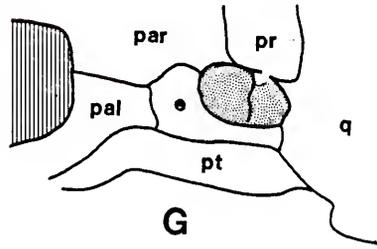
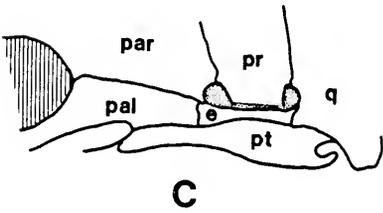
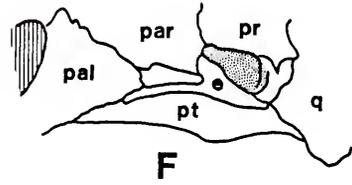
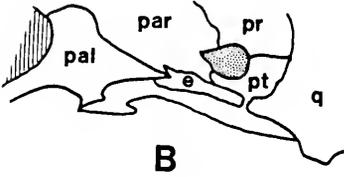
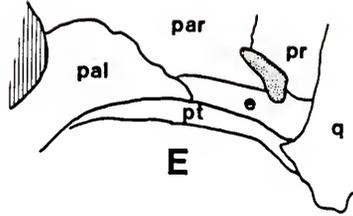
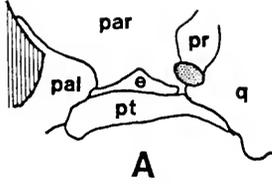
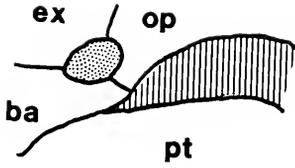
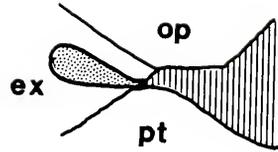


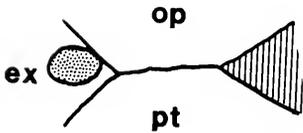
Figure 8. Diagramatic representations of contact between the foramen jugulare posterius (stippled) and the fenestra postotica (crosshatched) in six trionychoid turtles. Abbreviations: ba, basioccipital; ex, exoccipital; op, opisthotic; pt, pterygoid. A, Staurotypus triporcatus, UF 13482; B, Dermatemys mawii, UF 29168; C, Carettochelys insculpta, UF 43888; D, Cycloderma frenatum, NMZB 1245, E, Pelochelys bibroni, USNM 231523; F, Trionyx subplanus, UF 56317.



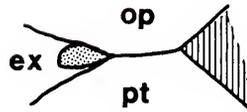
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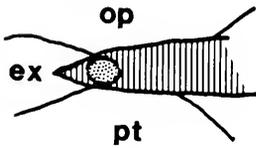
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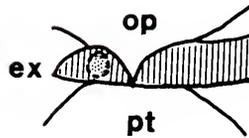
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D



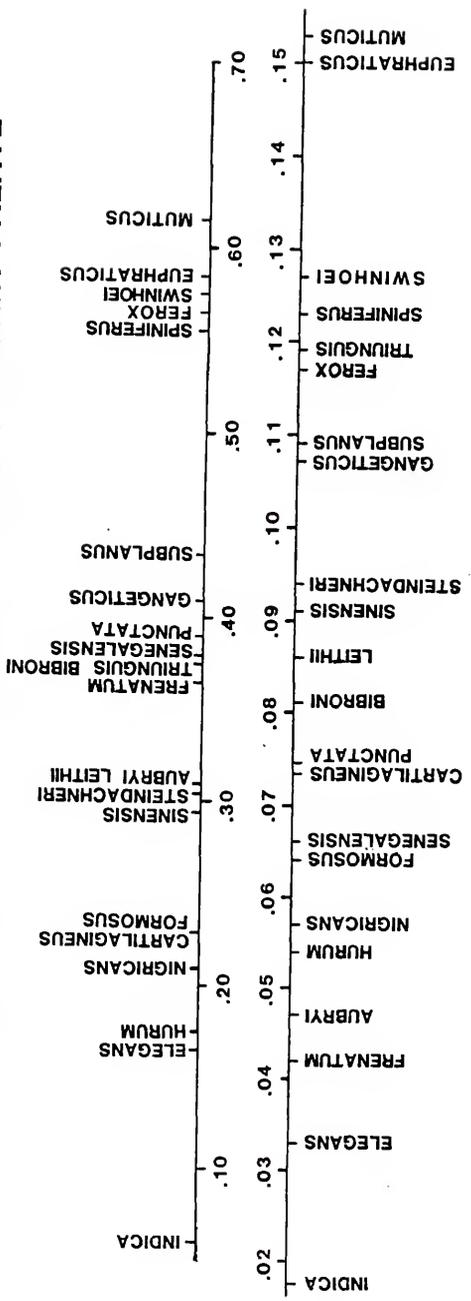
E



F

Figure 9. Comparison of two continuous characters examined during the course of study of the variation in size of the foramen intermaxillaris. Foramen intermaxillaris/length primary palate falls into five discrete classes and is used in the cladistic analysis. Foramen intermaxillaris/total skull length shows no such discrete classes and could not be used.

LENGTH INTERMAXILLARY FORAMEN / LENGTH PRIMARY PALATE



LENGTH PRIMARY PALATE / TOTAL SKULL LENGTH



Table 10. Systematic characters and character states of the trionychid skull. All skull characters are preceded by the letter S except those of the trigeminal region (T) and those which are based on measurements (M).

Characters	Character States
S1) quadratojugal contacts maxillary	1) yes 2) occasionally 3) no
S2) jugal contacts squamosal	1) no 2) in one-half of sample
S4) quadratojugal contacts postorbital	1) yes 2) no
S5) jugal contacts parietal on skull surface	1) no 2) in one-half of sample 3) yes
S6) jugal contacts parietal within fossa temporalis	1) no 2) yes
S7) vomer contacts prefrontal	1) yes 2) no
S8) incisura collumella auris closed	1) no 2) yes
S9) palatines contact prefrontals lateral to vomer	1) yes 2) no
S10) cheek emargination extends above lower edge of orbit	1) yes 2) no
S12) anterior limit of cheek emargination formed by	1) maxilla 2) jugal
S13a) dorsal edge of apertura narium externum laterally emarginate	1) no 2) weakly 3) strongly
S13b) dorsal edge of apertura narium externum medially emarginate	1) no 2) yes
S14) palatine forms a significant part of the lateral wall of the brain case	1) no 2) yes
S15) premaxillae fused into single element	1) no 2) yes

Table 10--continued.

Characters	Character States
S16) premaxillae enter apertura narium exturnum	1) yes 2) no
S18) basisphenoid contacts palatines	1) no 2) yes
S19) foramen intermaxillaris	1) absent 2) present
S20) vomer divides maxillae	1) yes 2) no
S21) vomer reaches intermaxillary foramen	1) yes 2) no
S22) vomer contacts pterygoid	1) yes 2) occasionally 3) no
S23) vomer contacts basisphenoid	1) no 2) occasionally
S25) processus pterygoideus exter- nus projects from pterygoid	1) yes 2) no
S26) size of foramen palatinum posterius	1) large 2) small 3) small and divided 4) many small openings
S27) foramen palatinum posterius forms in	1) palatine and pterygoid and/or maxilla 2) palatine only
S29) crista dorsalis basiocci- pitalis present	1) yes 2) no
S30) foramen posterius canalis carotici interni completely within pterygoid	1) no 2) yes
S31) canalis carotici interni straight and wide	1) no 2) yes
S32a) foramen jugulare posterius excluded from fenestra postoti- ca by pterygoid arching to contact opisthotic	1) no 2) yes

Table 10--continued.

Characters	Character States
S32b) foramen jugulare posterius excluded from fenestra postotica by descending process of opisthotic which reaches pterygoid	1) no 2) yes
S34) foramen posterius canalis carotici interni relative to lateral crest of basioccipital tubercle	1) above 2) in it 3) below
S43) groove for some portion of stapodial artery visible on prootic or descending process of parietal	1) yes 2) no
S49) maxilla contacts frontal in front of orbit	1) no 2) yes
S57) exoccipital contacts pterygoid	1) no 2) yes
S58) basisphenoid shape	1) not medially constricted 2) occasionally medially constricted 3) medially constricted
S59) premaxilla absent	1) no 2) occasionally 3) usually
S60) vomer lost	1) no 2) yes
T1) epipterygoid, if present, contacts the palatine	1) yes 2) in ca. 50% 3) no
T2A) contact between pterygoid and foramen nervi trigemini occurs when epipterygoid is present	1) yes 2) no
T2B) when epipterygoid is present pterygoid contacts foramen nervi trigemini	0) between epipterygoid and quadrate or not at all 1) between prootic and epipterygoid or not at all 2) between epipterygoid and parietal or not at all
T3) epipterygoid contacts prootic anterior to foramen nervi trigemini	1) no 2) in ca. 50% 3) yes

Table 10--continued.

Characters	Character States
T4) epipterygoid contacts prootic posterior to foramen nervi trigemini	1) no 2) yes
T7) epipterygoid fuses to pterygoid	1) in subadults 2) in adults only 3) never
M4) average ratio of intermaxillary foramen length to length primary palate	0) 0.07 1) about 0.20 to 0.40 2) about 0.60
M8) postorbital bar relative to orbit diameter	0) about 2 times orbit 1) about equal to orbit to 1/3 of orbit 2) less than 1/5 orbit
M16) quadratojugal participates in processus trochlearis oticum	1) no 2) yes
M17) quadrate make up of the processus trochlearis oticum	1) greater than 50% 2) 33 to 50% 3) less than 33%
M19) proportion of processus trochlearis oticum made up by parietal	1) 15.6% or less 2) 22.1% or more

Table 11. Character states for characters of the trionychid skull that have been found to be useful in assessing intrafamilial relationships. Numbers refer to character states outlined in Table 10. Periods indicate missing values.

Species	Characters										
	S2	S5	S7	S13A	S20	S21	S26	S27	S32A	S32B	S34
aubryi	1	3	2	2	2	2	4	2	2	1	3
bibroni	1	3	1	1	1	1	2	1	1	1	2
cartilagineus	1	1	1	2	2	2	2	1	1	1	2
elegans	1	3	1	1	2	2	3	2	2	1	3
euphraticus	1	1	1	2	1	1	2	1	1	1	3
ferox	1	1	1	3	1	1	2	1	1	1	3
formosus	2	3	1	2	2	2	2	1	1	1	3
frenatum	1	3	2	1	2	2	4	2	2	1	3
gangeticus	1	1	1	2	2	2	2	1	1	1	3
hurum	1	2	1	3	2	2	2	1	1	1	3
indica	1	3	2	1	1	1	2	1	1	1	2
leithii	2	2	1	2	2	2	2	1	1	1	3
muticus	2	2	1	3	1	2	2	1	1	1	3
nigricans	2	1	1	2	2	2	2	1	1	1	2
punctata	1	2	1	1	2	1	2	2	2	1	3
senegalensis	1	3	2	2	1	1	3	2	2	1	3
sinensis	2	2	1	3	2	2	2	2	1	2	3
spiniferus	1	1	1	3	1	1	2	1	1	1	3
steindachneri	1	3	1	3	2	2	2	1	1	2	3
subplanus	1	2	1	3	2	2	2	1	1	2	3
swinhoei	2	1	1	2	1	1	2	2	1	1	3
triunguis	1	1	1	3	2	2	2	1	1	1	3

Table 11--continued.

Species	Characters											
	S58	S59	T1	T2A	T2B	T3	T4	T7	M4	M8	M16	M19
aubryi	1	1	2	2	.	1	2	1	1	1	1	1
bibroni	1	3	3	1	0	2	1	2	1	1	1	1
cartilagineus	2	1	2	1	0	2	1	3	1	1	2	1
elegans	1	1	1	2	.	1	2	2	1	1	2	2
euphraticus	2	1	1	1	0	1	1	3	2	1	2	2
ferox	1	1	1	1	0	1	1	3	2	1	2	2
formosus	3	1	1	1	1	1	1	3	1	1	1	1
frenatum	1	2	3	2	.	1	2	2	1	1	2	1
gangeticus	3	1	1	1	1	1	1	2	1	1	2	1
hurum	3	1	1	1	1	2	1	3	1	1	1	1
indica	1	2	3	1	0	3	1	3	0	0	1	1
leithii	3	1	1	1	0	1	1	3	1	1	1	1
muticus	1	1	1	2	.	1	1	2	2	2	2	2
nigricans	3	1	3	1	1	1	1	3	1	1	1	2
punctata	1	1	2	1	1	1	1	1	1	1	1	1
senegalensis	1	1	3	2	.	1	2	1	1	1	1	1
sinensis	3	1	1	1	2	1	1	3	1	1	2	1
spiniferus	2	1	1	1	.	1	1	3	2	2	2	2
steindachneri	3	1	1	2	.	3	1	3	1	2	1	1
subplanus	2	1	1	1	.	1	1	2	1	2	2	1
swinhoei	1	1	1	1	0	1	1	3	2	1	2	2
triunguis	1	1	1	1	0	1	1	2	1	1	2	2

Table 12. States of skull characters important in interfamilial analyses. Numbers represent the character states listed in Table 10.

Taxa	Characters										
	S1	S4	S6	S8	S9	S10	S12	S14	S15	S16	S18
Trionychidae	3	2	2	2	2	2	2	2	2	2	2
Garettochelys	1	1	1	2	1	2	1	2	2	1	2
Staurotypus	1	1	1	1	1	2	1	2	1	1	1
Claudius	1	1	1	1	1	2	1	2	1	1	1
Kinosternon	1	1	1	1	1	2	1	2	1	1	1
Dermatemys	2	1	1	1	1	2	1	2	1	1	1
Cheloniidae	3	1	1	1	1	2	2	1	1	1	1
Chelydridae	3	1	1	2	1	1	1	1	1	1	1
Platysternon	1	1	1	2	1	2	1	1	1	1	1
Emydidae	2	1	1	1	1	1	1	1	1	1	1
Testudinidae	2	1	1	2	1	1	1	1	1	1	1
Pleurodira	3	1	1	1	1	1	3	1	1	1	1

Table 12--continued.

Taxa	Characters							
	S19	S22	S25	S29	S30	S31	S43	M17
Trionychidae	2	2	2	2	2	2	2	3
Carettochelys	2	2	2	2	2	2	2	2
Staurotypus	2	1	1	2	1	2	2	2
Claudius	2	1	1	2	1	2	2	1
Kinosternon	1	1	1	2	1	2	2	2
Dermatemys	1	1	1	2	1	2	2	3
Cheloniidae	1	1	2	1	1	1	2	2
Chelydridae	1	1	1	1	1	1	1	1
Platysternon	1	1	1	1	1	1	1	1
Emydidae	1	1	1	1	1	1	1	1
Testudinidae	1	1	2	2	1	1	1	1
Pleurodira	1	3	1	2	1	1	2	-

Table 13. Autapomorphic skull features of trionychid turtles.

Character	Species	Autapomorphic State
S13B	<i>Cyclanorbis elegans</i>	apertura narium externum medially emarginate
S18	<i>Trionyx euphraticus</i>	basisphenoid fails to contact palatines
S23	<i>Pelochelys bibroni</i>	vomer contacts basisphenoid
S49	<i>Trionyx subplanus</i>	maxillae contact frontals in orbit
S57	<i>Trionyx triunguis</i>	pterygoid isolated from exoccipital by basioccipital
S60	<i>Cycloderma frenatum</i>	vomer is absent
S61	<i>Cycloderma aubryi</i>	jugal excluded from orbit
M4	<i>Chitra indica</i>	intermaxillary foramen quite reduced
M8	<i>Trionyx subplanus</i>	postorbital bar one-ninth of orbit diameter

Table 14. Average contribution of quadratojugal, quadrate, prootic and parietal to the processus trochlearis oticum of Recent trionychid turtles.

Species	N	Quadrato- jugal	Quadrate	Prootic	Parietal
aubryi	8	0.000	0.227	0.607	0.166
bibroni	7	0.000	0.207	0.602	0.117
cartilagineus	7	0.007	0.239	0.655	0.139
elegans	5	0.011	0.236	0.565	0.221
euphraticus	9	0.020	0.166	0.557	0.266
ferox	11	0.032	0.290	0.396	0.260
formosus	4	0.000	0.294	0.635	0.071
frenatum	4	0.026	0.130	0.734	0.136
gangeticus	7	0.007	0.137	0.720	0.144
hurum	6	0.000	0.213	0.744	0.054
indica	8	0.000	0.312	0.626	0.062
leithii	3	0.000	0.249	0.684	0.091
muticus	5	0.027	0.072	0.581	0.320
nigricans	1	0.000	0.200	0.500	0.292
punctata	6	0.000	0.192	0.717	0.094
senegalensis	6	0.000	0.177	0.671	0.152
sinensis	9	0.005	0.154	0.728	0.122
spiniferus	8	0.019	0.262	0.527	0.225
steindachneri	1	0.000	0.180	0.819	0.000
subplanus	6	0.088	0.180	0.625	0.112
swinhoei	1	0.033	0.100	0.500	0.300
triunguis	10	0.004	0.189	0.584	0.223

Table 15. Occurrence of fusion of the epipterygoid to the pterygoid in trionychid turtles. Condylar length (in mm) of the largest skull with a free epipterygoid (A), the smallest skull with a fused epipterygoid (B), and largest skull measured (C) are given for each species.

Species	N	A	B	C
aubryi	7	94.5	88.0	122.0
bibroni	7	119.0	119.0	119.0
cartilagineus	7	131.5	none	131.5
elegans	5	125.0	122.0	130.0
euphraticus	9	83.3	none	83.3
ferox	9	110.0	none	110.0
formosus	4	79.0	none	79.0
frenatum	4	107.3	134.0	134.0
gangeticus	7	110.0	111.0	111.0
hurum	4	99.0	none	99.0
indica	8	195.0	none	195.0
leithii	3	108.0	none	108.0
muticus	3	39.5	41.5	41.5
nigricans	1	105.0	none	105.0
punctata	6	50.0	38.0	81.5
senegalensis	6	80.3	75.0	117.5
sinensis	9	58.5	none	58.5
spiniferus	8	59.5	none	59.5
steindachneri	1	43.8	none	43.8
subplanus	4	61.6	104.5	104.5
swinhoei	1	67.0	none	67.0
triunguis	10	153.0	143.5	153.0

Variation in the Mandible and Nonshell Postcrania

Introduction

Although the non-shell postcranial elements of turtles have been shown to provide valuable systematic data and are important in currently used arrangements, they have not been used extensively. The most important modern studies of the systematic value of non-shell postcrania are Williams (1950) and Zug (1971). The Williams (1950) monograph on the cervical articulations of turtles forms the foundation of the most frequently used modern classifications of turtles (see discussion). Zug (1971) provided data on the pelvic girdle and hind limbs which has since been cited as evidence for the recent realignment of certain cryptodires (Gaffney, 1975, 1984).

In the current attempt to determine the best hypothesis of relationships for trionychids, data from the cervical series and posterior body vertebrae, the hyoid and the pelvic and pectoral girdles have been found to be extremely valuable. Characters of the appendages and caudal vertebrae are of less use. The lower jaw has been included with the nonshell postcrania in an effort to balance the size of the three osteological data sets.

With the exception of the hyoid and the lower jaw, the characters treated in this section are most valuable in determining interfamilial relationships of trionychids. The hyoid and lower jaw are also important at this level but prove to be of additional value in the study of intrafamilial relationships.

Mandible

The lower jaw of trionychids is remarkable for its very high coronoid processes and large retroarticular processes (Boulenger, 1889)

and for the significant contribution to the area articularis mandibularis made by the surangular. The retroarticular process is much larger than in other turtles (except Carettochelys) and adds 10% or more to the total length of the structure (character L12, Tables 16, 18).

As observed by Gaffney (1979b) the prearticular and surangular of trionychids are frequently in contact restricting or subdividing the fossa meckelii. In 82% (81/98) of the trionychids examined the prearticular and surangular meet either on the posterior edge of the fossa meckelii (36/98) or divide it by meeting across the middle (45/98). There is no clear pattern of variation among the species within the family. All three conditions occur in three taxa; two of three conditions occur in 11 others. The high incidence of surangular-prearticular contact across the fossa meckelii could be considered a shared derived feature of the family Trionychidae. However, it occurs in several other taxa and absence of a clear distribution makes this character unusable. In Carettochelys one-half of the specimens (N=4) examined show this contact. Elsewhere among cryptodires it occurs in some Kinosternon, and Dermatemys, in Platysternon and in some pleurodires.

In most turtles the area articularis mandibularis is made up by the articular with little or no contribution from the surangular. Only in the Trionychidae and Carettochelys does the surangular make up one-half or more of this surface. The surangular is always included in this area in other trionychoids but always forms less than one-half of the articular surface. In Testudinoids and Chelydrids the surangular is frequently absent from the area articularis mandibularis and when present contributes less than one-half of the articular area. The large

contribution by the surangular in trionyichids must be considered derived. The condition in other trionyichoids appears to be intermediate between the state in the Trionyichidae and that in other turtles (character L4, Table 18).

An important systematic character in the lower jaw of trionyichids is the presence of a sagittal ridge on the triturating surface at the symphysis (De Broin, 1977). This ridge usually forms within a depression on an otherwise flat surface. Such a single ridge does not occur in other turtles and appears to be derived within the Trionyichidae. Among the members of this family such a ridge occurs only in the Indian species, and in Trionyx cartilagineus and T. formosus (character L6, Table 17). A ridge is also present in the largest individuals of T. subplanus.

The foramen nervi auriculotemporalis is a single or multiple opening in the surangular ventral to the area articularis mandibularis. Gaffney (1979b) reports multiple openings for this foramen only in Podocnemis expansa, however I find two or more lateral openings in some specimens of almost every species of trionyichid. Additional pleurodires (Pelusios castaneus) and also some emydids (Cuora, Graptemys, and Geoclemys also have multiple lateral openings in the surangular). The occurrence of multiple lateral openings in the surangular, representing a divided foramen nervi auriculotemporalis, is considered derived (character L8A, Table 18).

Gaffney (1979b) mentions an additional, apparently unnamed foramen in the surangular that communicates with the foramen nervi auriculotemporalis and the fossa meckelii. Unlike the foramen nervi auriculotemporalis, it opens dorsally not laterally. It is mentioned as

occurring in Staurotypus and Terrapene. I have noted this opening in all kinosternids examined, and in Platysternon, but in no other taxa. The occurrence of the opening can clearly be considered derived and it appears to be a shared derived character for the Kinosternidae (character L8B, Table 18).

On the lingual surface of the jaw, in the suture between the prearticular and the angular, there may appear two foramina, the foramina intermandibularis oralis and caudalis. In most turtles there is evidence of both. In trionychids the anterior one (oralis) is never present and the posterior one (caudalis) may be present or absent in some species, but is always absent in others (character L10, Table 17). This uniform absence of the foramen intermandibularis caudalis is considered to be derived within the Trionychidae.

Hyoid

The hyoid of most cryptodires is not an elaborate structure. It typically consists of a single basal unit, the corpus hyoideum, which may or may not be ossified, and two pairs of branchial horns, the anterior pair of which is always ossified. By contrast, the hyoid of trionychids always consists of a minimum of ten ossifications and may include as many as 40. The corpus hyoideum is composed of either three pairs of ossifications (one pair of basihyals and two pairs of basibranchials), or four pairs of ossifications (an additional pair is present anterior to the basihyals). The first branchial horn always consists of a single ossification while the second branchial horn consists of one to 18.

Ossification of the corpus hyoideum from numerous centers has been recognized as a unique feature of the Trionychidae (Siebenrock, 1913;

Romer, 1956) (character H1, Table 18). This highly developed structure is also known to vary among the species of the Trionychidae (Annandale, 1912; Siebenrock 1913), and characters of the hyoid appear to be useful in assessing intrafamilial relationships. Claudius is the only cryptodire that ossifies the corpus hyoideum from three centers.

Most members of the Trionychidae have six ossifications of the corpus hyoideum throughout life. However, in eight species the corpus has six ossifications in subadults but a total of eight ossifications at full maturity (character H1, Table 17). This exceptionally high number in these select species is considered to be a further derived state.

The first branchial horn is a single ossification in all adult cryptodires examined in the course of this study. The second branchial horn, when ossified, also consists of a single element, except in some trionychids. In all of the Cyclanorbinae and in Trionyx hurum it ossifies from a single center. In the remainder, it ossifies from as few as two to as many as 18 centers. Interspecific variability in the number of centers of ossification in the second branchial arm falls into two seemingly natural groups with two exceptions. In most Old World forms the second horn includes six or fewer ossifications. Only among living New World species and T. euphraticus does it always consist of seven or more (character H3, Table 17). In T. gangeticus it consists of five to 14 centers ($X=8.4$) and in T. sinensis it consists of three to nine centers ($X=5.1$). These two species are assigned to a group based on their average number of ossifications. As is the case for the corpus hyoideum, a high number of ossifications in the second branchial horn is considered derived.

In Chitra indica and Pelochelys bibroni the second branchial horn consists of three ossifications which are very broad and strongly sutured to one another. This is a unique condition within the Trionychidae (character H4, Table 17).

The corpus hyoideum of cyclanorbine trionychids can always be recognized by the close contact and anterior projection of the basihyal pair which is always the anteriormost of three pairs of ossified elements. Projections of this kind do not occur in trionychines with six basal elements, or in the corresponding elements in those species with eight basal ossifications. Anterior projection of the bony corpus is therefore considered derived for the Cyclanorbinæ (character H5, Table 17).

Cervical and Body Vertebrae

As early as 1876 it was recognized that trionychids had unique cervical articulations (Vaillant, 1876) and the cervical series continues to be used as strong evidence for monophyly of the Trionychidae (Boulenger, 1889; Siebenrock, 1902; Loveridge and Williams, 1957) and for monophyly of the Trionychidae plus Carettochelyidae (Meylan, 1984). In both families all cervicals are opisthocoelous (character C1, Table 18) except for the eighth in trionychids, which has no central contact to the first body vertebrae (character C2, Table 18). All other cryptodires have at least one biconvex vertebra (number 2,3, or 4), some procoelous vertebrae, and contact between the centrum of the first body vertebra and the centrum of the eighth cervical (Williams, 1950).

The members of the Trionychidae are also unique in having no ventral process on the eighth cervical. A single or double process is present on the eighth cervical of all other cryptodires (character C3A, Table 18).

Its absence in this family can be correlated with the unique neck-packing mechanism described by Dalrymple (1979). The double ventral process of the eighth cervical, which is found only in kinosterninds and Carettochelys, is considered to be derived (character C3B, Table 18).

The only relief on the ventral surface of the eighth cervical of trionychids is a small posterior keel found in a few large species (character C4, Table 17). Such keels are absent in other trionychooids and are considered to be derived within the family.

Like other cryptodires, most trionychids lack dorsal processes of the cervicals. However, four species have very well developed dorsal processes on the middle to posterior cervical vertebrae (character C5, Table 17). The presence of these processes is considered derived.

Chelonians have ten body vertebrae between the cervicals and the sacrals, and they normally have eight pairs of pleural bones. Thus, two body vertebrae are not associated with a pair of pleurals. One of these is the first body vertebra. It sends transverse processes posterolaterally to join the anterior edge of the ribs associated with the first pair of pleurals. The other vertebra which is without associated pleurals is the tenth. The tenth body vertebra may be firmly fixed by transverse processes which brace it against a tuberosity on the eighth pleural, or it may be somewhat less well fixed and have only remnants of transverse processes (Zug, 1971). In the Kinosternidae the ninth body vertebra is like the tenth in having no contact between the transverse processes and the carapace. In this family both the ninth and tenth vertebrae exhibit some freedom of movement.

The distribution of these three conditions of the posterior body vertebrae (character C6, Table 18), from nine and tenth fixed to ninth

only fixed, to ninth and tenth free, suggests that reduced articulation between the shell and these posterior vertebrae is derived.

Pelvis

Numerous features of the trionychid pelvic girdle are useful in phylogenetic analysis. There are no fewer than ten characters which are germane to establishing interfamilial relationships. Three of these are used in the intrafamilial analysis as well. The pelvic girdle is treated as follows: ilium first, and then puboischiatic plate from anterior to posterior.

The ilia in most turtles extend dorsally from the acetabulum to meet the carapace and transverse processes of the sacral vertebrae. The main axis of the ilium is straight in all turtles except trionychids (Zug, 1971). In trionychids they are strongly flexed posteriorly (character P2, Table 18). Zug (1971) indicates that these posteriorly curved ilia do not articulate with the carapace in trionychids. This is certainly the case in all trionychine trionychids, but carapacial contact does occur in some cyclanorbines (see discussion of shell character 20).

Hirayama (1985) as cited by Gaffney (1984) has suggested that medial curvature of the ilia is a feature unique to the Testudinoidea. I believe he means medial curvature because I find medially curved ilia are present in all testudinoids examined. In numerous trionychoids including some trionychids, (character P1, Table 17), Carettochelys, Dermatemys and most kinosternids (character P1, Table 18) the ilia are also medially curved. The character state is therefore shared by all of Gaffney's (1984) Chelomacryptodira (Trionychoidea plus Testudinoidea). Its absence

in most trionychids can be considered a loss of the condition, and thus derived within the family.

The dorsal end of the ilium of all turtles, except trionychids and smaller kinosternids, is antero-posteriorly expanded. This distal sagittal crest is the site where the transverse processes of the sacral vertebrae articulate. Based on a single individual, Zug (1971) describes the distal end of the ilium of Dermatemys as being unexpanded. In four Dermatemys and in three Carettochelys (not examined by Zug) available for this study the distal ilia are antero-posteriorly expanded. The absence of this distal expansion is considered derived (character P3 , Table 18).

The thelial process, site of attachment for the iliotibialis muscle, has been considered to be a unique feature of the Kinosternidae (Zug, 1971). A topographically and morphologically similar structure occurs on the ilium of all three Carettochelys pelves available to me. In addition, a small tubercle, in the position of the thelial process, is present in two of six individuals of Lissemys punctata examined. The presence of a thelial process is considered to be derived for kinosternids and Carettochelys (character P4, Table 18).

The epipubis is a small plate of cartilage or bone which extends anteriorly in a horizontal plane from the region of the pubic symphysis. Hay (1908) has suggested that an unossified epipubis is primitive for turtles. Although it is the last center in the pelvic girdle to ossify it does ossify in all cryptodires except the most derived trionchoids (Carettochelyidae and Trionychidae) most cheloniids (Baur, 1891a, reports that some old cheloniids ossify the prepubis) and testudinids. The lack of ossification of the prepubis appears to be a derived, and possibly pedomorphic feature (character P6, Table 18).

The pectineal processes extend from the body of the pubis in an anterior or anterolateral direction. In most cryptodires they are small relative to the length of interpubic contacts. The members of the Trionychidae are unique in having pectineal processes which are as wide or wider than the length of interpubic contact (character P9, Table 18).

The pectineal processes and the epipubes of trionychids lie in a single plane and they all lie flat against the plastron (Zug, 1971). In nearly all other cryptodires no such common plane exists. The exceptions are living chelonoids and Claudius, but in these taxa the anterior pubic region does not lie flat on the plastron. In skeletons of very young specimens of Kinosternon and Sternotherus the entire pubis is quite flat. It appears that the pelvis first ossifies in a single plane and with age gains three-dimensional qualities. Thus the occurrence of a flat pubis in trionychids may be a retention of the juvenile state (character P7, Table 18).

The thyroid fenestra is the major opening in the puboishiatric plate. In turtles it is often partially or completely divided by bone. Bony division occurs in two non-homologous ways: by ossification of the median gastroid cartilage or by junction of medial extensions of the pubes and ischia (Walker, 1973).

A closed thyroid fenestra is the common condition among Recent turtles (character P5, Table 18; Baur, 1891a; Zug, 1971). But the bony junction in chelydrids and Dermatemys occurs through ossification of the medial gastroid cartilage, a structure which is found in all open forms (Baur, 1891a). This is a minor modification of an otherwise completely open condition. Very distinct reduction and division of the thyroid fenestra occurs by extension of the pubis and ischium into the fenestra.

Among living cryptodires this occurs only in Platysternon, kinosternine kinosternids and testudinoids.

Baur's (1891a) interpretation of this character is that an open thyroid fenestra is primitive and a divided fenestra derived. Data from living turtles support this hypothesis. However, Proganochelys (Gaffney, MS), some chelonioids and some baenids (Hay, 1908) have the thyroid fenestra divided by ischial-pubic contact. If the closed condition is found among other extinct families, the use of global parsimony may require this state to be recognized as primitive. Should this be the case, then an open foramen could be used as a shared derived character within the Chelydridae, the Chelonioidea and Trionychoidea. For the present, Baur's interpretation is accepted.

Baur (1891a) indicates that expansion of the undivided thyroid fenestra in trionychids is a uniquely derived condition. This fenestra is open widely, and ischial extension into it is minimal (Dermatemys and staurotypines) or absent (most trionychids and Carettochelys) in all trionychoids except for kinosternines. When the ischia do extend into the thyroid fenestra in species of the Trionychidae, this is considered to occur by reversal to the primitive condition. It appears only in Lissemys punctata, Cycloderma aubryi, and C. frenatum (character P8, Table 17).

Most trionychids, and in fact most cryptodires, have distinct, posteriorly directed processes of the ischia, the metischial processes. In seven species of trionychids (the Cyclanorbinæ, Trionyx euphraticus and T. ferox) these processes exist only as postero-medial expansions of the ischia and not as free projections. Outgroup taxa which also lack ischial processes include Claudius, Staurotypus, some Kinosternon, some

Dermatemys and some cheloniids (character P12, Tables 17, 18). Because metischial processes are present in Carettochelys (the proposed sister group for the Trionychidae), some members of the other two trionychoid families and most other turtles, their presence is judged to be primitive within the Trionychidae and their absence derived.

One additional character of the pelvis, which bears on the current problem only in that it supports monophyly of the Kinosternidae, is the occurrence of a distinct notch in the acetabulum at the junction of the ilium and ischium. Such a notch is present in Staurotypus, Claudius and most Kinosternon (character P13, Table 18).

Pectoral Girdle

The pectoral girdle of all turtles is a triradiate structure composed of two elements, the scapula and coracoid. From the acetabulum the main body of the scapula extends dorso-medially to the carapace in the region of the first body vertebra. The acromion process of the scapula extends anteromedially to the plastron. The coracoid joins the scapula only at the acetabulum and projects posteromedially towards the midline of the plastron. The relative lengths of these three projections and the angles between them vary in a systematically useful manner. Their use in systematics up to this time appears to be limited (Meylan and Auffenberg, in press).

In most turtles, the dorsal projection of the scapula is the longest of the three pectoral processes. The only exceptions are the chelonioids, trionychine trionychids and Carettochelys in which the coracoid is longer (character P16, Tables 17, 18). The shortest projection is the acromion process of the scapula except in the Testudinoidea in which the coracoid is always shortest (character P14,

Table 17). An exceptionally long or exceptionally short coracoid is considered to be derived.

Two angles in the pectoral girdle, one between the acromion process and main body of the scapula and the other between the acromion and the coracoid, were measured. In most cryptodires the former angle approaches 90 degrees and is always much greater than the latter. The same is true for majority of trionychids although the larger angle tends to be somewhat less (65-75 degrees). In six taxa the acromion-scapula angle is lower still and the coracoid-acromion angle is higher, so that there is little or no difference between them. The similarity of these two angles is considered to be a derived character state within the Trionychidae (character P15, Table 17).

Appendicular Skeleton

The humerus and femur of trionychids are remarkably similar in general appearance. Both form gentle S-shaped curves, both have two large proximal trochanters which are free from each other and both have weakly differentiated distal tubercles. The humerus can be distinguished from the femur most easily by the presence of an entepicondylar groove that is always open in this family. Furthermore the lesser trochanter of the humerus lies in an antero-posterior plane that runs through the main axis of the humerus. The greater trochanter of the humerus and both trochanters of the femur lie at a high angle to this plane.

The condition of the entepicondylar foramen of the humerus is constant in the Trionychidae, but it can be open or closed in pleurodires, Kinosternon, Dermatemys and among the various genera of emydids. It closes with age in chelydrids, and is apparently always

closed in Carettochelys. It is always open in cheloniids and staurotypines. Because the closed condition is found in some members of all three outgroup trionychoid families, the consistently open condition in the Trionychidae is unique within the superfamily (character A1, Table 18).

The carpus and tarsus of trionychids do not differ significantly from those of other turtles (Hay, 1908; Ogushi, 1911). The carpus consists of ten elements: an intermedium, ulnare, and pisiform, two centralia, and five carpals. Unlike the case in most other turtles, the trionychids do not have the intermedium between the distal ends of the radius and ulna; instead these forearm elements have a strong contact. The only other taxa in which this occurs are the families Cheloniidae and Testudinidae (character A4, Table 18).

Among trionychids there is a uniform number of phalanges in digits one, two and three (those which are clawed) but a variable number in digits four and five. The most common phalangeal formula for turtles is 2-3-3-3-3 (Romer, 1956). In trionychids those digits which are clawed, 1, 2 and 3 retain this number. Those which have no claws (digits 4 and 5) may differ from this most common, and according to Hay (1908), primitive number. In almost every trionychid for which an articulated manus is available the fourth digit has at least four phalanges, a few have five and Lissemys and Chitra have as many as six. Only Cyclanorbis senegalensis (one specimen available) appears to retain the primitive number of three elements. Despite this exception, hyperphalangy of the fourth digit is considered to be a derived feature of the Trionychidae. Hyperphalangy of the fifth digit of the manus is less common in the Trionychidae. although there is some interspecific variation within the

data set for both of these characters, the data are not sufficient to allow use of this character in the intrafamilial analysis.

Hyperphalangy of the fourth digit of the pes is also commonplace for trionychids. There is variation among family members but, like the manus, the data are insufficient to include them in the analysis of intrafamilial relationships. Hyperphalangy is treated as a single character (character A2, Table 18) and is used only in the interfamilial analyses.

Table 16. Systematic characters and character states of the lower jaw and nonshell postcrania of trionychid turtles. The letter preceding each character indicates the portion of the skeleton to which the character pertains: A, appendicular skeleton; C, cervical and body vertebrae; H, hyoid; L, lower jaw; P, pectoral and pelvic girdle.

Characters	Character States
A1) entepicondylar foramen open along humerus	1) no 2) variable 3) yes
A2) hyperphalangy of manus digits 4 and 5, pes digit 4	1) no 2) yes
A4) radius and ulna in contact adjacent to manus	1) no 2) yes
A6) number of clawed digits of manus	1) 5 2) 3 or fewer 3) 2 or fewer
C1) cervical centra 2-7 opisthocoelus	1) no 2) yes
C2) centra of 8th cervical and first body vertebrae in contact	1) yes 2) no
C3A) ventral process on 8th cervical	1) present 2) absent
C3B) ventral process on 8th cervical	1) single 2) double
C4) ventral keel on 8th cervical present and limited to posterior end	1) no 2) yes
C5) strong dorsal processes on cervicals	1) no 2) yes
C6) number of posterior body vertebrae with transverse processes not reaching pleurals	1) 0 2) 1 3) 2
H1) number of ossifications in corpus hyoideum	1) 1 2) 3 3) 6 4) 8

Table 16--continued.

Characters	Character States
H3) number of ossifications in second branchial horn	1) 1 only 2) 6 or fewer 3) 7 or more
H4) ossifications of second branchial horn broad and strongly sutured	1) no 2) yes
H5) basihyals in close contact and projecting anteriorly	1) no 2) yes
L4) surangular forms part of area articularis mandibularis	1) less than 1/2 to 0 2) less than 1/2 3) greater than or equal to 1/2
L6) symphyseal ridge strong and present in a depression	1) no 2) yes
L8A) foramen nervi auriculotemporalis with two lateral openings	1) no 2) yes
L8B) foramen nervi auriculotemporalis with one lateral and one dorsal opening	1) no 2) yes
L10) foramen intermandibularis caudalis enclosed by prearticular	1) sometimes 2) never
L12) retroarticular process large, about one tenth of total lower jaw	1) no 2) yes
P1) ilia curve medially	1) no 2) yes
P2) ilia curve posteriorly	1) no 2) yes
P3) ilia antero-posteriorly expanded at distal end	1) yes 2) no
P4) thelial process present	1) no 2) yes
P5) pubis and ischium closely opposed or in contact across thyroid fenestra	1) no 2) yes
P6) epipubic region ossifies	1) yes 2) no

Table 16--continued.

Characters	Character States
P7) pectineal processes and inter- pubic suture lie in a single plane	1) no 2) yes
P8) ischia extend into thyroid- fenestra	1) yes 2) no
P9) pectineal processes equal to or wider than interpubic contact	1) no 2) yes
P12) metischial processes present and distinct	1) yes 2) no
P13) ilio-ischial notch	1) absent 2) present
P14) coracoid shortest of three pectoral processes	1) no 2) yes
P15) angle of acromion process to scapula approaches that of coracoid to acromion	1) no 2) yes
P16) coracoid longest of three pectoral processes	1) no 2) yes

Table 17. Character states of characters found to be useful in hypothesizing relationships among Recent trionychid turtles. See Table 16 for explanation of characters and character states. Periods indicate missing values.

Species	Characters												
	L6	L10	P1	P8	P12	C4	C5	P15	P16	H1	H3	H4	H5
aubryi	1	2	2	1	2	1	2	1	1	2	1	1	2
bibroni	1	1	1	2	1	2	2	2	2	3	2	2	1
cartilagineus	2	1	1	2	1	2	1	1	2	3	2	1	1
elegans	1	2	1	2	2	1	1	2	1	2	1	1	2
euphraticus	1	2	1	2	2	2	1	1	2	3	3	1	1
ferox	1	1	1	2	2	1	1	1	2	3	3	1	1
formosus	2	2	1	2	2	1	1
frenatum	1	2	2	1	2	1	2	1	1	2	1	1	2
gangeticus	2	1	1	2	1	1	1	1	2	2	3	1	1
hurum	2	1	1	2	1	1	1	1	2	3	1	1	1
indica	1	2	1	2	1	2	2	2	2	3	2	2	1
leithii	2	1	1	2	1	1	1	1	2	2	2	1	1
muticus	1	1	1	2	1	1	1	2	2	2	2	1	1
nigricans	2	1	1	2	1	1	1	1	2	2	2	1	1
punctata	1	2	1	1	2	1	1	1	2	2	1	1	2
senegalensis	1	2	2	2	2	1	1	2	1	2	1	1	2
sinensis	1	1	1	2	1	1	1	1	2	2	2	1	1
spiniferus	1	1	1	2	1	1	1	2	2	2	3	1	1
steindachneri	1	1	.	2	2	2	1	1
subplanus	2	1	1	2	1	1	1	1	2	3	2	1	1
swinhoefi	1	2	.	2	3	.	1	1
triunguis	1	1	1	2	1	1	1	1	2	2	2	1	1

Table 18. Distribution of the states of characters of the mandible and nonshell postcrania used to develop a hypothesis of relationship of the Trionychidae to other turtles. See Table 16 for explanation of characters and character states. Characters marked with an asterisk are variable (see Table 17). Periods indicate missing values.

Taxa	Characters								
	A1	A2	A4	A6	C1	C2	C3A	C3B	C6
Trionychidae	3	2	2	2	2	2	2	.	2
Carettochelys	1	1	2	3	2	1	1	2	2
Claudius	3	1	1	1	1	1	1	2	3
Staurotypus	3	1	1	1	1	1	1	2	3
Kinosterninae	2	1	1	1	1	1	1	2	3
Dermatemys	2	1	1	1	1	1	1	1	2
Chelydridae	2	1	1	1	1	1	1	1	2
Platysternon	1	1	1	1	1	1	1	1	1
Cheloniidae	3	1	2	3	1	1	1	1	1
Emydidae	2	1	1	1	1	1	1	1	1
Testudinidae	2		1	1	1	1	1	1	1
Pleurodira	2	1	1	1	1	1	.	.	1

Table 18--continued.

Taxa	Characters								
	H1	L4	L8A	L8B	L12	P1	P2	P3	P4
Trionychidae	3 or 4	3	2	1	2	*	2	2	1
Garettochelys	1	3	1	1	2	2	1	1	2
Claudius	2	2	1	2	1	2	1	1	2
Staurotypus	1	2	1	2	1	2	1	1	2
Kinosterninae	1	2	1	2	1	2	1	2	2
Dermatemys	1	2	1	1	1	2	1	1	1
Chelydridae	1	1	1	1	1	1	1	1	1
Platysternon	1	1	1	2	1	1	1	1	1
Cheloniidae	1	2	1	1	1	1	1	1	1
Emydidae	1	1	2	1	1	2	1	1	1
Testudinidae	1	1	1	1	1	2	1	1	1
Pleurodira	1	1	2	1	1	1	1	1	1

Table 18--continued.

Taxa	Characters								
	P5	P6	P7	P8	P9	P12	P13	P14	P16
Trionychidae	1	2	2	*	2	*	1	1	*
Garettochelys	1	2	1	2	1	1	1	1	2
Claudius	1	1	2	1	1	2	2	1	1
Staurotypus	1	1	1	1	1	2	2	1	1
Kinosterninae	2	1	1	1	1	1	2	1	1
Dermatemys	1	1	1	1	1	1	1	1	1
Chelydridae	1	1	1	1	1	1	1	1	1
Platysternon	2	1	1	1	1	1	1	1	1
Cheloniidae	1	2	2	1	1	2	1	1	2
Emydidae	2	1	1	1	1	1	1	2	1
Testudinidae	2	2	1	1	1	1	1	2	1
Pleurodira	1	.	1	.	1	.	1	1	1

DISCUSSION

The Higher Relationships of the Trionychidae

Monophyly of the Trionychoidea

The characters examined during the course of this study support the hypothesis that the families Dermatomydidae, Kinosternidae, Carettochelyidae and Trionychidae form a monophyletic group. These relationships were proposed by Gaffney (1975) who grouped them together as the superfamily Trionychoidea (Fig. 10). Relationship of the Trionychidae to the Kinosternidae and Dermatomydidae was first proposed late in the last century by Baur (1891a). Although it has subsequently been supported by the work of Albrecht (1967), Zug (1966; 1971) and Gaffney (1975, 1979b, 1984), it is not frequently cited (an exception is Smith and Smith, 1979). An alternative proposed by Williams (1950, 1952) has received wider use (Dowling and Duellman, 1973; Goin and Goin, 1962, 1971; Porter, 1972; Pritchard, 1979a, 1979b; Romer, 1956, 1966; Wermuth and Mertens, 1961; Zug, 1966). The Williams' arrangement places the family Trionychidae alone in the superfamily Trionychoidea. The Kinosternidae (as the Kinosterninae and Staurotypinae) is included in the Chelydridae which, along with the Dermatomydidae, is considered part of the Testudinoidea (Fig. 11). The Carettochelyidae is confined to its own superfamily, the Carettochelyoidea.

Gaffney (1984) summarized the evidence for using the superfamily Trionychoidea (sensu Gaffney, 1975) which until now consisted largely of characters of the cranial arteries. Additional characters of the skull,

lower jaw, shell and body vertebrae are here shown to support this inclusive view of the Trionychoidea (Table 19). Furthermore, the criteria which Williams (1950) used to include the Kinosternidae in the Testudinoidea are shown to be plesiomorphic or subject to homoplasy.

A critical feature of Gaffney's (1975, 1984) definition of the Trionychoidea is the inclusion of the Carettochelyidae. Previously, the carettochelyids have been thought of alternatively as pleurodires (Boulenger, 1889), as the missing link between trionychids and chelonoids (Strauch, 1890), or as a link between dermatemydids and kinosternids, and the Trionychidae (Baur, 1891a; Gaffney, 1975 and others). It is abundantly clear from the present analysis that the last of these three alternatives is the one best supported by available data.

Although the present study has not reexamined characters of the cranial arteries (McDowell, 1961; Albrecht, 1967; and Gaffney, 1975, 1979b, 1984), two of the external skull characters examined here reflect the different arterial patterns that distinguish trionychoids from testudinoids. The small size of the stapedia artery in trionychoids is reflected by the absence of any grooves or furrows to accommodate this vessel where it crosses the prootic and the descending process of the parietal (character S43, state 2). In chelydrids, emydids and testudinids, by contrast, there is a distinct though variably developed furrow or groove for the stapedia artery. In certain taxa (Chelydra, Melanochelys, Terrapene) these grooves extend for long distances. In other forms, especially testudinids, they are short but deep and found only adjacent to the foramen stapedio temporale.

The second arterial feature noted here reflects the increased importance of the internal carotid artery in Recent trionychoid skulls.

In this superfamily, a stiff wire of a diameter just less than the foramen posterior canalis carotici interni, will pass easily from this foramen through the foramen anterior canalis carotici interni and into the brain case (character S31, state 2). This is possible because the canalis carotici follows a very straight path. In other living cryptodires the path followed by the internal carotid artery is less direct as can be seen in Figs. 26-29 in Gaffney, 1979b.

A useful feature of the skull used by Gaffney (1975) which does not involve blood flow pattern is the inclusion of the palatine in the lateral wall of the braincase. In all turtles other than trionychoids, palatine participation is insignificant or absent (character S14, state 2). In trionychoids it is quite extensive, often extending posteriorly to the epipterygoid (Fig. 7).

There are three additional features of the trionychoid skull which can be added to the evidence for monophyly. Cheek emargination is extremely weak (character S10, state 2) (Gaffney, 1979b); a basioccipital tubercle is always absent (character S29, state 2); and the participation of the quadrate in the processes trochlearis oticum is reduced (character M17).

Only living chelonioids (Cheloniidae, Dermochelyidae) and Platysternon share with the trionychoids greatly reduced cheek emargination. In none of these taxa does it extend above the lower rim of the orbit. The presence of well developed cheek emargination in the Pleurodira, baenids, pleiochelyids and most chelydrids suggests that its absence in the Chelonioidea and Trionychoidea is derived.

The absence of a basioccipital tubercle in certain cryptodires is most easily explained as a single loss in the Trionychoidea and as a

single loss in the advanced Testudinoidea (Rhinoclemmys and the Testudinidae, except Gopherus). The reduction of quadrate contribution to the processus trochlearis oticum also appears to have occurred in parallel, once in the chelonoids and once in the trionychoids.

A single character of the lower jaw lends support to the argument for monophyly of the Trionychoidea. Throughout the superfamily there is always contribution by the surangular to the area articularis mandibularis (character L4, state 2). In certain forms it makes up the majority of this surface; in others it makes up a smaller part. It is never absent from this area, as in some testudinoids and chelydrids.

Reduction and loss of plastral buttresses is a useful feature of the shell of trionychoids (character 26, state 2 or 3). The presence of two pairs of well developed buttresses in the Pleurodira, Pleurosternidae, Baenidae, meiolanids and testudinoids is used here as evidence that they were present in the primitive cryptodires and have subsequently been reduced to one pair or lost in chelydrids, chelonoids and trionychoids. Even if absence of plastral buttresses were to be shown to be the primitive condition for cryptodires, the character is still a very useful one. Testudinoids could then be recognized as having two pairs of well developed plastral buttresses except for the most kinetic forms (Cuora, Terrapene). No trionychoid taxa could be included in such a group.

An important character of the posterior body vertebrae is used here as evidence of monophyly of the Trionychoidea. As mentioned by Zug (1971), the tenth body vertebra, which is immediately anterior to the sacral pair, has very reduced transverse processes in members of this superfamily. These processes do not reach the inner surface of the carapace as they do in Recent chelonoids, testudinoids and Platysternon

(character C6, state 2). Chelydra and Macroclemys have the trionychoid condition which suggests the alternative that the absence of contact of the transverse processes of the tenth body vertebra to the shell is actually primitive. If this is the case, then this character would be equivalent to the alternate possibility given for the plastral buttresses. That is, the occurrence of complete tenth transverse processes would be derived for the Chelonioidea and Testudinoidea and this would exclude any trionychoids from either of these taxa.

In summary, there are seven osteological characters, in addition to the two that correlate with blood flow patterns, that suggest that the Trionychoidea (sensu Gaffney, 1975) is monophyletic. The most commonly cited alternative, which places the Dermatemydidae and Kinosternidae along with the Chelydridae in the Testudinoidea, requires that all nine characters used here occur twice, once in the Trionychoidea and once in the Testudinoidea.

Observations on the morphology of the cloacal region support monophyly of the Trionychoidea. All four families lack cloacal bursae (Smith and James, 1958). This can be cited as additional evidence with the assumption that loss has occurred independently in chelonoids and testudinids. The penis in all four families has a singly or doubly bifurcate seminal groove (Zug, 1966), a condition that occurs elsewhere only in the Testudinidae.

The evidence presented by Williams (1950) for including the Kinosternidae (as the Kinosterninae and Staurotypinae) within the Chelydridae consists of two pleisiomorphic characters, and three highly variable characters. The existence of costiform processes of the nuchal is widespread among cryptodires and is most clearly visible in hatchlings

and juveniles. Their retention in adults could be considered a shared derived character of the chelydrids and kinosternids but they are also retained in adult Dermodochelys, Dermatemys and trionychids. Their presence is probably primitive for the Cryptodira.

The evidence from the cervical formula is similarly of little value. The presence of a single biconvex vertebra and a doubly procoelus eighth cervical is used as evidence of relationship of chelydrids and kinosternids. But these features are also present in chelonoids and dermatemydids which suggests that they are actually primitive for cryptodires. Independent modification of this cervical formula supports monophyly of the Testudinoidea (usually two biconvex cervicals in the cervical series) and the Carettochelyidae plus Trionychidae (no biconvex cervicals, numbers two through seven opisthocelous).

Williams (1950) cites a variable number of marginals, 23 or 25, as a character of his Chelydridae. The number of marginal scales reflects variation in the number of peripheral bones (Hutchison and Bramble, 1981). The Williams' arrangement would require that reduction in the number of peripheral bones from 22 to 20 occur twice, once in his Testudinoidea and once in his Carettochelyoidea. In the arrangement advocated here this can be treated as a single event and as part of a transformation series which culminates in complete loss of peripherals in the Trionychidae.

Broad unridged alveolar surfaces occur in numerous unrelated taxa in addition to those included in Williams' Chelydridae. They apparently correlate with a durophagous diet (Pritchard, 1984) and are not strong evidence of common ancestry of such a group. The cruciform plastron is a similarly variable character being absent within Williams' Chelydridae

(many Kinosternon species) and present outside of this family (certain trionychine trionychids and extinct carettochelyids). There is no strong case for including the Kinosternidae within the Chelydridae on osteological grounds.

Bickham and Carr (1983) suggest that the staurotypines are the sister group of the Testudinoidea (in which they include Platysternon) which supports the Williams (1950) arrangement in part. These authors rely on the recognition of a homologous derived chromosome in the Staurotypinae, Emydidae and Testudinidae. The crux of their argument is that the same microsome is fused to the same identifiable acrocentric macrosome in these three taxa. However, the combined microsome is euchromatic and homology of the short arm of their biarmed second group B macrosome seems tentative at best. It is clear that their results are in irreconcilable conflict with the morphological evidence. Their observation that the Trionychoidea and Carettochelyidae have been separated from the Dermatemydidae and Kinosternidae "for a long period of time" has no bearing on the cladistic relationships of these families.

The data examined in the current study support alliance of the Kinosterninae and Staurotypinae with the other trionychoids as suggested by Baur (1891a) and advocated by Gaffney and others. Additional characters which indirectly indicate monophyly of the Trionychoidea (sensu Gaffney) are shared by members of the Kinosternidae, Carettocheyidae and Trionychidae. But these characters suggest an alternative to the dichotomous view of the Trionychoidea used in Gaffney (1975, 1984) shown in Figure 10.

Monophyly of the Kinosternidae, Carettochelyidae and Trionychoidea

Gaffney (1984) views the Trionychoidea as consisting of two clades, one includes the Dermatemydidae and Kinosternidae, and the other includes the Trionychoidea and Carettochelyidae (Figs. 10, 12 A). Hutchison and Bramble (1981) detail the relationships within the dermatemydid-kinosternid clade. They cite Albrecht (1967), Gaffney(1975), McDowell (1961), Zug (1966) and Frair (1964) for evidence of the monophyly of these two families. They do not subscribe to the idea that the Dermatemydidae and Kinosternidae share a unique common ancestor with the Trionychoidea and Carettochelyidae. They believe that the evidence cited by Gaffney (1975, 1984)--similarity in blood flow patterns--is convergent. As evidence they cite the presence of a large foramen stapedio-temporale in Adocus, a primitive dermatemydid. A large foramen stapedio-temporale appears in many trionychoidea but apparently a large stapedia artery does not (Gaffney, 1979b). The occurrence of a large foramen stapedio temporale in these taxa is due to the retention of the primitive condition.

The osteological characters examined in the current study suggest an alternative to both the Gaffney (1975, 1984) and the Hutchison and Bramble (1981) arrangements (Fig. 12 C, D). Within the monophyletic Trionychoidea the Trionychoidea and Carettochelyidae share a unique common ancestor; these two families plus Claudius may share a unique common ancestor (Fig. 12 D), or alternately the Staurotypinae, Carettochelyidae and Trionychoidea may share a common ancestor not shared by the Kinosterninae and Dermatemydidae (Fig. 12 C); and in either case the Dermatemydidae is the sister group to all other members of the Trionychoidea.

This arrangement is supported by 28 characters from the present study, 17 of which suggest monophyly of the Trionychidae plus Carettochelyidae (Table 20). These characters can be integrated with those used by Gaffney (1984) and Hutchison and Bramble (1981) to support one or the other of two alternative arrangements shown in Figure 12 C or D as the most parsimonious for the Trionychoidea.

Monophyly of the Kinosternidae, Carettochelyidae and Trionychidae is suggested by two characters of the shell, one of the cervical series and one of the pelvis. In all members of these three families there are 20 or fewer peripherals (character 5, state 2) and plastral buttresses are absent (character 26, state 3). The ventral process of the eighth cervical is divided except in the trionychids in which this process is absent (character C3B, state 2). In the pelvis, a thelial process is present in kinosternids and Carettochelyids but is absent in nearly all trionychids (observed only in two specimens of Lissemys, UMMZ 129396, MHNG 615.87) (character P4, state 2).

The inclusion of the Trionychidae and Carettochelyidae in the same clade as the Kinosternidae in the Hutchison and Bramble (1981) arrangement requires that these taxa share the features shown to be derived for the dermatemydids plus kinosternids in that study. Scutes are absent from all trionychids. In carettochelyids only the vertebral scutes develop and these are lost soon after hatching (Zangerl, 1959). Thus the many characters of scalation used by Hutchison and Bramble (1981) do not enter into the current argument. Many of the remaining characters of their dermatemydid-kinosternid clade are shared by the Trionychidae and Carettochelyidae: posterior lobe reduced in width; stapelial artery reduced; large costiform processes; reduction of

plastral bridge. Two other characters which they use, megacephaly and the development of a tricarinate carapace, are actually quite variable within the Dermatemydidae and Kinosternidae. Megacephaly is as well developed in some trionychids (Trionyx cartilagineus and especially T. subplanus) as it is in megacephalous kinosternids (Claudius angustatus, Sternotherus minor).

The tricarinate carapace is certainly absent in some dermatemydids and in the majority of many kinosternines. The reduction of carapacial keeling could very likely be a result of the flattening of the shell which occurs in the clade leading to trionychids.

The one remaining non-scute character which Hutchison and Bramble (1981) consider to be evidence of monophyly of the Kinosternidae plus Dermatemydidae, exclusive of the Trionychidae and Carettochelyidae, is the loss of sculpturing of the shell. There would have to be reversal in this character to allow the arrangement advocated here.

Two of the nonscute characters cited by Hutchison and Bramble (1981) for monophyly of the Kinosternidae are characters which I cite as evidence for the monophyly of the Kinosternidae, Trionychidae and Carettochelyidae. These are the possession of 20 (or fewer) peripherals (character 5, state 2) and the presence of a divided ventral process of the eighth cervical (character C3B, state 2).

Other characters that these authors cite for the monophyly of the Kinosternidae do not necessarily exclude the Trionychidae and Carettochelyidae from this clade. These include: the loss of neural eight; the tendency for development of a secondary palate; and development of impressed musk ducts in the anterior peripherals.

I believe that their reference to the loss of neural eight actually pertains to the loss of neural nine. There is no neural element sutured to the first body vertebra in any kinosternid so it can be said that the first neural is absent. If eight neurals are present the posteriormost is number nine, and not number eight. Although most kinosternids have seven (numbers two through eight) or fewer neurals, both Staurotypus species have eight (numbers two through nine) on occasion (UF 58976, BMNH 1871.1.7.5). Other than lacking a first neural, this is identical to the proposed primitive number for trionychids.

The development of a secondary palate is not widespread enough among kinosternids to be a valid shared derived feature of this family. Hutchison and Bramble (1981) cite Gaffney (1979b) in support of this feature. Gaffney mentions the presence of a secondary palate only in two genera (Staurotypus and Xenochelys). The palate in the other genera of this family are not remarkably elongate. This character seems to be of value at a lower level of universality than it is used in the Hutchison and Bramble arrangement.

Impressed musk ducts are clearly visible on the interior surface of the anterior peripherals (usually numbers two, three and four) of all kinosternids. In Carettochelys, there is no duct impression but there is a canal through the second peripheral. The interior opening of this canal is at the same level as the impressed duct in kinosternids, the exterior opening is identical in position to the anterior musk duct opening in trionychids. It is apparent that all trionychoids have anterior musk ducts which exit just dorsal to the fore limbs. In kinosternids they leave an impression in the anterior peripherals, in Carettochelys they leave no impression but apparently pass through the

second peripheral. Trionychids have no anterior peripherals so the path of the musk duct cannot be traced in osteological material. The condition in Carettochelys could be viewed as a modification of that seen in the kinosternids.

From the osteological evidence it appears that the best arrangement for the Trionychoidea is to utilize the Dermatemydidae as a sister group to the other three families. Furthermore, it is apparent that certain kinosternids have closer affinities to the carettochelyids and trionychids than others.

Monophyly of the Staurotypinae, Carettochelyidae and Trionychidae

One line of evidence pursued in the present study supports monophyly of the Staurotypinae, Carettochelyidae and Trionychidae, and evidence from Hutchison and Bramble (1981) supports this view. The palate of all three living species of staurotypines develop a foramen intermaxillaris (character S19). In staurotypines it does not appear until maturity but it forms in exactly the same manner as in carettochelyids and trionychids. It lies between the vomers and premaxillae with maxillae defining the lateral edges. In staurotypines it allows the symphyseal hook of the lower jaw to pass into the nasal capsule. In other cryptodires with well developed symphyseal hooks, this region of the palate is usually deeply impressed (Chelydra, Macroclemys, Platysternon) or the premaxillae may be slightly divided (Deirochelys) but in no other turtles is there an opening comparable to the foramen intermaxillaris.

All four of the non-scute features used by Hutchison and Bramble (1981) for evidence of monophyly of the staurotypinae are shared by the Trionychidae and Carettochelyidae. These are 1) costal bone four spans peripheral six (carettochelyids); 2) the anterior lobe is kinetic; 3)

there are very short plastral buttresses; and 4) scapular attachment is transferred from entoplastron to epiplastron. The second and third features I find to be useful at a higher level and I have used it as evidence for monophyly of the Kinosternidae, Carettochelyidae and Trionychidae. Attachment of the scapulae to the epiplastra via the acromial ligament has been verified for Carettochelys and the Trionychidae (Bramble and Carr, MS).

Four features which suggest that all kinosternids share a unique common ancestor with the Carettochelyidae and Trionychidae, and five others which suggest that the affinities of the latter two families lie specifically with the Staurotypinae have been discussed above. Two additional characters shared by Claudius and the Trionychidae but absent in Carettochelys should also be mentioned. These two characters concern the morphology of the corpus hyoideum and the form of the epipubic region of the pelvis. The corpus hyoideum of all cryptodires ossifies as a single unit except in Claudius and trionychids (character H1, state 2). In Claudius it forms from three centers, in the trionychids it forms from six or eight. The epipubic region of Claudius is like that of trionychids in that it forms a common plane with the interpubic symphysis and the pectineal processes (character P7, state 2). The distribution of these characters could be equally explained by: 1) appearance in a unique common ancestor of these three taxa and subsequent loss in Carettochelys or 2) independent appearance in Claudius and the trionychidae. The former would further restrict the affinities of kinosternids and the carettochelyid-trionychid clade but there is currently no evidence to accept the former arrangement (Fig. 12 D) over the latter (Fig. 12 C).

The osteological data as treated in the present study support an arrangement of the families of the Trionychoidea that has not been considered previously. That is, monophyly of all or part of the Staurotypinae, Carettochelyidae and Trionychidae (Fig. 12 C or D). That the entire Kinosternidae might be the sister group to the carettochelyid-trionychid clade (Fig. 12 B) is an alternate possibility to this arrangement.

Monophyly of the Kinosternidae exclusive of the Trionychidae and Carettochelyidae is suggested by three characters in addition to those treated by Hutchison and Bramble (1981). These are 1) the presence of one dorsal and one lateral opening of the foramen nervi auriculotemporalis (character L8B, state 2); 2) two, rather than one, posterior body vertebrae having transverse processes that fail to reach the carapace (character C6, state 3); and 3) the presence of an ilioischial notch (Zug, 1971) (character P13, state 2). However, the most parsimonious arrangement of the osteological data results in the equal length arrangements shown in Fig. 12 C and D.

Monophyly of Carettochelys and the Trionychidae

Since it was first described, Carettochelys has often been associated with the Trionychidae (Baur, 1891b; Ramsay, 1886; Walther, 1922, Siebenrock, 1909; Hummel, 1929). It is clear from the characters considered in the current study that this association is very well supported by osteological data (Table 20). Ten of the features shared by these two families occur in no other cryptodire. Five others are present in these two families and among the Chelonioidea. However, the many unique features of the Chelonioidea (Gaffney, 1975, 1984) and the many

unique features of the Trionychoidea discussed above, suggest that these five character states have been attained in parallel. Three of them are states of characters which may only reflect the modification of limbs and girdles for a highly aquatic mode of life: coracoid longest pectoral process (Pl6); reduction in number of claws (A6); and contact of radius and ulna adjacent to the manus (A4). In addition to the ten osteological characters that are unique to these two families, trionychids are also the only turtles known to have a fleshy proboscis.

Monophyly of the Trionychidae

Monophyly of the family Trionychidae has, to my knowledge, never been questioned. All recent systematic studies treat the family as a monophyletic unit (De Broin, 1977; Gaffney, 1975, 1979b, 1984; Bickham and Carr, 1983; Meylan, 1985), but the osteological evidence for monophyly has never been compiled. Therefore, the unique features of the family are listed in Table 21. In combination they result in the unique overall morphology of this distinctive family of turtles.

Relationships among the Recent Trionychidae

Computer-assisted analyses of independent data sets from the skull, shell and nonshell postcrania reveal that there are numerous possibilities for explaining the character state distributions of each by using hypotheses of descent that require a minimum number of evolutionary steps. By recognizing unresolvable areas in the multiple, equal-length arrangements suggested by each data set, a single solution or consensus tree for that data set was obtained. These fundamental cladograms vary between data sets in the degree of resolution of interfamilial

relationships, in their internal consistency (the amount of parallelism and reversal required by the distribution of the character states), and most importantly, in their topology. The relationships suggested by analysis of the skull data (Fig. 15) differ from that obtained by analysis of shell data (Fig. 14). The poor resolution achieved by the small nonshell postcranial data set (Fig. 16) limits the comparability of the topology resulting from its analysis to those resulting from analysis of shell or skull characters.

Results of analyses of the three separate data sets (i.e., the fundamental cladograms, Figs. 14, 15 16) could not be resolved into a single general cladogram following the methods of Nelson (1979). Therefore, these results are contrasted and compared to one another and to six equally parsimonious trees based on an analysis of all three data sets combined. This comparison suggests a choice of two alternate trees as the best hypotheses for the relationships of soft-shelled turtles from osteological evidence (Figs. 20, 21).

Evidence from Shell Morphology

A previous examination of variation in shell morphology (Meylan, 1985) has indicated that there is sufficient variation among the shells of trionychids to allow resolution of the relationships of 20 of the 22 living species. The arrangement which resulted from that study is based on 16 characters and the most parsimonious tree was produced by hand (Fig. 19). That data set has been upgraded for the current study. The data matrix includes 40% more entries (21 characters X 22 taxa vs. 16 characters X 20 taxa). With this increased data matrix a search for the most parsimonious tree by hand proved to be too time consuming. A tree-producing package, PAUP (Phylogenetic Analysis Using Parsimony), by David

Swofford (Version 2.3, 1984) was used to determine the most parsimonious arrangement of the Trionychidae based on shell data. Analysis of 21 characters of the shell of all 22 Recent species of the Trionychidae using PAUP produces a dozen equally parsimonious trees. This is due entirely to alternate topologies of the unresolvable portions of the trees. Two clades that appear in all of the shortest length trees cannot be resolved by the data in the shell data set alone. These problematical clades are a group of Cyclanorbines, Cycloderma aubryi, Cycloderma frenatum and Lissemys punctata, and the Indian species of the genus Trionyx. These two clades are shown to be unresolved in the tree which best represents the relationships of the Trionychidae based on shell morphology alone (Fig. 14).

These results are generally compatible with those of Meylan (1985). The monophyly of the Trionychinae is supported. Monophyly of the Indian species and its position as the sister group to the remaining Trionychinae is also repeated. The Asian species occupy the middle ground between the Indian clade and a previously recognized clade leading to the North American forms.

The most obvious divergences from the previous arrangement (Meylan, 1985) are the failure to recognize a monophyletic Cyclanorbinae and the recognition of most Asian species as a monophyletic group. In this regard these results support the conclusions of De Broin (1977) who suggests that the Cyclanorbinae may not be monophyletic and that the Trionychinae includes three monophyletic groups, the Indian forms (her Aspiderites), most other Asian forms (her Amyda), and a group which culminated in the North American forms (her Platypeltis).

The failure of analysis of the current shell data to support a monophyletic Cyclanorbinae, contrary to the case in Meylan (1985), can be attributed to the inclusion of several new characters not considered in that study. Cyclanorbis elegans shares with the Trionychinae a reduction in length of the bony bridge and articulation of the ilia against the cartilaginous part of the shell rather than on the bony disk (characters 20 and 22). These characters work in concert with reduced plastral callosities, a short nuchal bone and the united anterior and posterior costiform processes (characters 1, 2 and 9) to suggest that the two Cyclanorbis species share a unique common ancestor with the Trionychinae. However, the distribution of two characters which support monophyly of the Cyclanorbinae (characters 10 and 12) in Meylan (1985) are explained as unique reversals to the primitive condition for all trionychnines in Figure 14. Characters of the skull and nonshell postcrania considered below and the results from all three data sets analysed together firmly support monophyly of the Cyclanorbinae and the recognition of this subfamily is ultimately indicated by this study.

In the arrangement based on shell morphology, monophyly of the Indian species is supported by the occurrence of five plastral callosities in all species (character 9), this occurs elsewhere only in Trionyx cartilagineus, and on the occurrence of epiplastral projections of intermediate length (character 19), which occur elsewhere only in T. sinensis. It is also possible that the existence of two neurals between the first pleurals is a derived feature arrived at independently in the Cyclanorbinae and the Indian forms.

Monophyly of the Asian clade (Pelochelys bibroni through Trionyx subplanus) in Fig. 14 is supported only by an apparent reversal. The

eighth pleurals are the only pair that meet on the midline, a condition which occurs elsewhere only in Trionyx leithii. Monophyly of T. triunguis, T. euphraticus, T. swinhoei, the three North American forms and T. sinensis, is suggested by a unique reduction in the total number of neurals (character 13) although there is a reversal in this condition in the most derived forms.

Evidence from Skull Morphology

Like the variation in the trionyhid shell, variation in the trionyhid skull is sufficient to allow nearly complete resolution of the relationships of all 22 living species. Analysis of 23 characters of the trionyhid skull using PAUP results in a minimum-length tree of 99 evolutionary steps. Three equally parsimonious trees produced by PAUP differ only in minor changes in the positions of Trionyx formosus and T. leithii. Variation in the three trees is represented in the single solution cladogram by a trichotomy (Fig. 15). They agree completely in the remainder of their structure.

The three equally parsimonious arrangements all support a monophyletic Cyclanorbininae as the sister group to a monophyletic Trionychinae. Lissemys punctata is always the sister group to all other cyclanorbinines. Chitra indica and Pelochelys bibroni form a clade which is the sister group to the remaining Trionychinae. Trionyx cartilagineus is the sister group to two remaining major monophyletic units, the North American group with T. triunguis, T. euphraticus and T. swinhoei on the one hand, and the Indian and Asian Trionyx species on the other. Unlike the arrangement based on shell morphology, T. sinensis is placed among the Asian clade and T. subplanus is the sister group to the North American clade.

Although the arrangement based on skull data alone is initially more appealing for several reasons, its internal consistency is lower than that derived from shell data. The distribution of nearly two-thirds of the character states in the skull cladogram must be explained by reversal or parallelism. The appealing features of the skull arrangement include its support of both subfamilies, the Cyclanorbinæ and Trionychinae, as monophyletic units and its overall similarity to the arrangement in Meylan (1985) which in turn approaches arrangements proposed by Loveridge and Williams (1957) and De Broin (1977).

Evidence from Nonshell Postcrania and Lower Jaw

Only thirteen characters of the lower jaw and nonshell postcrania were found to display useful interspecific variation among living trionychids. This is far too few to allow complete resolution of the relationships of the Recent Trionychidae. Two pairs of species share identical character state distributions (Cycloderma aubryi and Cycloderma frenatum; Trionyx nigricans and T. leithii) and three other species share another distribution (T. steindachneri; T. sinensis, and T. triunguis). Furthermore, two additional species, T. swinhoei and T. formosus, have numerous missing values. The lack of resolvability and the presence of many missing values result in hundreds of equally parsimonious trees. But even among the numerous trees there is a fair amount of consistency.

Examination of a large subset (N = 45) of these trees reveals that nine clades appear in every one. These provide important evidence for interfamilial relationships and are shown in a consensus tree (Fig. 16). Most importantly, the Cyclanorbinæ and Trionychinae are recognized in every case. The former has a unique configuration of the corpus hyoideum

(character H5), lacks distinct metischial processes (character P12) and never has the foramen intermandibularis caudalis defined by bone (character L10). The latter has multiple ossifications of the second branchial horn (character H3) and the coracoid is longer than the scapula (character P16) in every case (and also in Lissemys punctata).

A unique reversal to the primitive condition of ischial projections into the thyroid fenestra (character P8) and reduction of the acromion process to scapula angle (character P15), each identify a separate clade within the Cyclanorbinæ.

Among the Trionychinae, one large subset of taxa, the four Indian species plus Trionyx formosus, T. cartilagineus, Chitra indica and Pelochelys bibroni are recognized as a single clade largely on the basis of a symphyseal ridge (character L6). Four characters of the non-shell postcrania support monophyly of Chitra and Pelochelys.

The remaining trionychine species always include three additional clades. Trionyx muticus and T. spiniferus share a rare configuration of the scapula (character P15). T. subplanus, T. euphraticus, T. swinhoei and T. ferox have eight ossifications of the corpus hyoideum (character H1). T. euphraticus and T. ferox have a high number of ossifications in the second branchial horn (character H3) and lack distinct methischial processes (character P12).

Although variation in the characters of the lower jaw and non-shell postcrania are insufficient to allow formulation of an independent arrangement of the Recent trionychids, certain of these characters are important in corroborating clades identified by the shell and skull data sets. Also, some characters which have proven unimportant at this level

are essential to formulation of a hypothesis for the higher relationships of the Trionychidae.

Formulation of a General Hypothesis of Relationships for the Trionychidae

The methods available for constructing consensus trees (Adams, 1972) and (Nelson, 1979) will not completely resolve the relationships among Recent soft-shelled turtles. The Adams (1972) method combines information from nodes present in every rival tree. There is only one node, that representing the Trionychinae, found in all three fundamental cladograms. The Nelson (1979) method combines replicated nodes as the foundation for a consensus tree, uncombinable nodes are discarded and combinable nodes which are unreplicated but compatible with one another are added to the replicated nodes. Only six nodes are replicated in two or more of the fundamental cladograms in this study and four combinations of combinable unreplicated nodes can be added to produce a consensus tree which contains an equal amount of cladistic information (an equal number of nodes). As an alternative, I have made a clade-by-clade comparison of the trees resulting from analysis of the shell (Fig. 14) data to that resulting from the data on the skull (Fig. 15) and the mandible and nonshell postcrania (Fig. 16). These results are then compared to those based on a separate PAUP analysis of all three data sets combined. All three trees based on independent data sets and those from the combined data set consist of basal cyclanorbines, and a series of similar combinations of Indian, Asian and North American species. It is simplest to compare and combine results by proceeding up the phylogenetic tree.

Monophyly of the Cyclanorbinae has been advocated by several students of trionychid systematics (Boulenger, 1889; Deraniyagala, 1937; Loveridge and Williams, 1957; Meylan, 1985). It is supported strongly by

the nonshell data sets (Figs. 15, 16) but does not appear in the arrangement based on the shell alone (Fig. 14). As pointed out in Meylan (1985) the unique cyclanorbine xiphiplastral-hypoplastral joint and early fusion of the hyo- and hypoplastra (characters 10, 12) can be considered shared derived characters for the subfamily rather than unique reversals for the Trionychinae as they are shown in Fig. 14. These two characters, in combination with the unique cyclanorbine hyoid (character H5) restriction of the fenestra postotica by an ascending pterygoid arch (character S32A), the absence of distinct metishial processes (character P12) and other characters of the skeleton and soft parts (including femoral flaps) suggest that recognition of a monophyletic Cyclanorbiniae would ultimately lead to a more parsimonious arrangement of the Trionychidae. If the shell arrangement (Fig. 14) is used, the distribution of seven nonshell characters common to these five taxa would require 21 evolutionary steps. On the other hand addition of the shell data to the skull arrangement would require only seven added steps, provided that the two species of Cyclanorbis are considered to be monophyletic. Monophyly of the Cyclanorbiniae is indicated in all six equally parsimonious trees based on the combined data set.

Resolution of the Cyclanorbiniae is best completed by recognizing three monophyletic genera, Lissemys, Cyclanorbis and Cycloderma, with Lissemys being the sister group to the other genera. This arrangement requires that two steps be added to account for independent acquisition of epiplastron shape and shell shape (characters 18 and 25) in Lissemys and Cycloderma. But the retention of the shell topology would require independent acquisition of seven characters in Cycloderma and Cyclanorbis and would add seven evolutionary steps. Among the characters supporting

monophyly of Cyclanorbis plus Cycloderma are the reduced size of the coracoid (character P16), medial curvature of the ilia (lost in Cyclanorbis elegans; character P12); the presence of small and multiply-divided foramina palatinum posterius (character S26) and exclusion of the quadrate from the trigeminal foramen by the epipterygoid (character T4). Three of the four species also lack prefrontal-vomer contact which occurs elsewhere only in Chitra indica (character 7).

Monophyly of Cyclanorbis is suggested by ischial extension into the thyroid fenestra (character P8), reduced angle of the acromion process to body of scapula (character P15), wide nuchal (character 1), united costiform processes (character 2), and the location of the first body vertebra in the middle of the nuchal bone (character 3). Cycloderma has a unique condition of the foramen palatinum posterius; it is represented by many very fine openings hardly distinguishable from the nutritive foramina of the palate (character 26). The two species of the genus also share characters of shell shape, epiplastron shape (characters 18, 25) and the presence of enlarged dorsal processes on the cervical series which occur elsewhere only in Chitra and Pelochelys (character C5).

The six equally parsimonious trees for the combined data set match three different arrangements of the Cyclanorbinae (Fig. 17) to two arrangements of the Trionychinae (Fig. 18). One of the alternative cyclanorbine arrangements is that advocated above. The other two require either a paraphyletic Cyclanorbis or a paraphyletic Cycloderma.

Choice between these equally parsimonious arrangements for the Cyclanorbinae rests on considerations of the characters themselves. Variability in the number of pleurals that meet on the midline (character 15) provides useful data that enhance the argument for recognition of a

monophyletic Cyclanorbis. The modal condition of the neural series was used to score taxa in Table 3. However, the highly derived condition (state 4 of character 15), common in Cyclanorbis senegalensis, is also known to occur in Cyclanorbis elegans (see section on neurals under variation in shell morphology). Using Cartmill's (1978) philosophy, that occasionally derived is in fact derived, the rare occurrence of a high number of pleurals meeting at the midline in Cyclanorbis elegans reinforces the suggestion of monophyly for this genus which appears in two of the three alternate topologies for the Cyclanorbinae (Fig. 17).

Recognition of a monophyletic Cyclanorbis reduces the choice of topologies for the Cyclanorbinae to those shown in Fig. 17 B and C. Examination of the characters which support monophyly of Cycloderma (Fig. 17 B) versus that which supports monophyly of Cycloderma aubryi plus Cyclanorbis (Fig. 17 C) provide useful results relevant to determining the relative reliability of these two alternate arrangements. The two characters which argue for monophyly of Cycloderma include one unique evolutionary event (reduction of the foramen palatinum posterius to a series of fine openings, characters S26) and a feature that occurs elsewhere on only one occasion (presence of large dorsal spines on the cervical vertebrae, character C5). The average consistency of these characters is 0.750. The average consistency of the three characters which support monophyly of Cycloderma aubryi and Cyclanorbis (Fig. 17 C) is much less, 0.431. These include anterior location of the first body vertebra (character 3, C = 0.667), location of neural reversal (character 16, C = 0.375) and emargination of the prefrontals in the aperturum narium externum (character S13A, C = 0.250). On the strength of its higher consistency at the critical level, it is suggested that the

arrangement of the Cyclanorbinae that appears in Figure 17 B is the most reliable hypothesis.

The shell (Fig. 14) and both nonshell arrangements (Figs. 15 and 16) support a monophyletic Trionychinae. In all, nine characters support the recognition of this subfamily (Figs. 20, 21). Unique features of the Trionychinae include advancement of the point of reversal of neural orientation at least to neural six or seven and the presence of multiple ossifications of the second branchial horn (characters 16, H3). Four other features of the Trionychinae appear independently in one or both Cyclanorbis species (characters 1, 2, 20, 22).

The basic difference between the arrangement of the Trionychinae determined from shell versus skull data is the combination of the Asian and North American clades to the exclusion of the Indian clade in the shell arrangement and the combination of the Indian, North American and parts of the Asian clades to the exclusion of Chitra, Pelochelys and Trionyx cartilagineus in the skull arrangement. These differences are based on very few characters. More importantly, the four major clades which appear in the analysis of all data sets combined appear in one or both cases. At this point it seems best to consider the evidence for recognition of the major clades within the Trionychinae. Consideration of a hypothesis about their interrelationship can then follow.

Four groups of species within the Trionychinae are represented as distinct clades or are in close proximity in at least two of the three arrangements based on the three independent data sets and in all most parsimonious arrangements based on united data sets. These are termed the North American clade, the Indian clade, the Trionyx cartilagineus clade and the T. steindachneri clade.

The North American clade includes at least three Old World species, Trionyx triunguis, T. euphraticus and T. swinhoei, as well as the three North American forms, T. ferox, T. muticus and T. spiniferus. This clade also includes T. sinensis in the arrangement based on shell data. All members of this group have eight or fewer neurals (character 13), deeply emarginate prefrontals (character S13A) and a large contribution by the parietal to the processus trochlearis oticum (character M19). Except for T. triunguis, the members of this clade also have a large intermaxillary foramen (character M4), second branchial horns which ossify from seven or more centers (character H3) and small to absent eighth pleurals (character 8).

The Indian clade includes Trionyx gangeticus, T. leithii, T. hurum and T. nigricans. The evidence that this group should be recognized comes entirely from the shell. All four species have a maximum of five plastral callosities, epiplastral extensions of intermediate length and two neurals between the first pair of pleurals (characters 4, 9 and 19). The presence of two neurals between the first pair of pleurals may be primitive for the Trionychinae but in that case an extra neural must have been added to the anterior end of the neural series in the common ancestor of all trionychids. Only one appears between the first pleurals in carettochelyids, kinosternids, and dermatemydids. The addition of this extra neural and the subsequent fusion called for in Meylan (1985) requires two independent evolutionary steps. The occurrence of two neurals between the first pleurals could alternatively be explained by its independent appearance in the Cyclanorbinae and in the Indian forms of Trionyx. In the various arrangements under consideration here T.

formosus and some of the members of the T. steindachneri group may be included in the Indian clade.

The Trionyx steindachneri group appears to include T. sinensis and T. subplanus. Although three taxa are not combined in any of the three cladograms based on the three separate data sets, they form a monophyletic group in all six of the equally parsimonious cladograms resulting from analysis of all data combined (Figs. 18, 20, 21). The most important character of this group is the unique division of the fenestra postotica by a descending process of the opisthotic in T. sinensis, T. steindachneri and T. subplanus. Furthermore, in T. sinensis the pterygoid contacts the foramen nervi trigemini anterior to the epipterygoid. This is compatible with lack of contact of these structures in T. subplanus and T. steindachneri but not with contact of the pterygoid and foramen nervi trigemini posterior to the epipterygoid (see discussion of character T2B) which is found in all members of the North American clade--a clade which includes T. sinensis in Fig. 14 and in Meylan (1985). T. sinensis also lacks the high number of ossifications in the second branchial arch, the significant contribution of the parietal to the processus trochlearis oticum, the large intermaxillary foramen and the secondarily enlarged vomer found in all members of the North American clade (characters H3, M19, M4, S20, and S21). Recognition of a T. sinensis, T. steindachneri and T. subplanus clade requires that the highly variable neural formula with the last reversal in neural orientation occurring at neural six (characters 14 and 16) and the reappearance of callosities on all plastral elements (character 9) occur independently in T. sinensis and in the North American clade. However, reversal of reduction in the eighth peripheral

and reversal in the occurrence of sexual size dimorphism which are required in the shell arrangement are not required if T. sinensis is withdrawn from the North American clade.

The last of the four groups of species within the Trionychinae includes Trionyx cartilagineus, Chitra indica and Pelochelys bibroni. These three species have the foramen posterius canalis carotici interni lying within, rather than below, the lateral crest of the tuberculum basioccipitale, a condition which is seen elsewhere only in the single available skull of T. nigricans (character 34). The epipterygoid frequently contacts the prootic anterior to the foramen nervi trigemini (character T3), and the eighth cervical vertebra has a distinct subcentral ridge (character C4) in all three. Furthermore, these taxa all have a hyoid with eight elements in the corpus hyoideum which occurs elsewhere only in T. subplanus and in three species of the North American clade. The highly derived nature of Chitra and Pelochelys is suggested by their many shared derived features and the unique features of Chitra.

The shell characters that conflict with the nonshell evidence for monophyly of these three taxa are relatively minor. An extra posterior neural may appear at times in Chitra indica and Trionyx cartilagineus and neural reversal may occur one neural more posteriorly in some cases (characters 13 and 16). The clearest conflict in character distribution is the presence of elongate anterior epiplastral projections (character 19) in T. cartilagineus and in the Indian and T. steindachneri groups. Recognition of these groups requires that elongate epiplastra arise independently on three occasions.

The combination of species of the Trionychinae into clades seems clear and it results in the recognition of groups which other authors

have recognized and even named in the past. To finish the task of determining the best hypothesis for relationships among all members of this subfamily it is necessary to identify the interrelationships of these four clades. Unfortunately, there are few characters which contribute to the understanding of the relationship of these clades to one another and several alternative hypotheses are possible.

Based on the presence of a symphyseal ridge (character L6) (which is absent in species with a short symphysis or reduced overall size) and a constricted basisphenoid (character S58), all of the Indian and Asian forms could be separated from the North American clade (Fig. 22). Within this Indian and Asian clade the Trionyx cartilagineus group stands out as being highly derived. A sister group to the T. cartilagineus group could be defined on two features of the skull: contact of the jugal and squamosal across the quadratojugal (character S2) and contact of jugal and parietal on the skull surface (character S5). These characters occur in some individuals of nearly every species in the Indian clade group and in T. sinensis. Only the latter character is present in T. steindachneri and T. subplanus but the distribution of other characters suggests that the absence of the former is best considered as a reversal.

This arrangement (Fig. 22) is the most parsimonious one that will preserve the four species groups as monophyletic units. It is four steps longer than the two shortest trees based on analysis of the skull, shell, mandible and nonshell postcrania combined.

The two alternate arrangements of the Trionychinae based on the analysis of the combined data sets differ only in the placement of the four trionychine clades (Figs. 20, 21). In both, the Indian species group is paraphyletic and the only difference is that the North American

forms are the sister group to the Trionyx cartilagineus group on the one hand, and to the T. steindachneri group on the other. No supplementary evidence is available to support one of these arrangements over the other. Consequently, until additional data can be collected and analyzed, the arrangements shown in Figures 20 and 21 must be considered equally plausible most parsimonious hypotheses for the interfamilial relationships of the Trionychidae.

Comparison of Results to the Prevailing Hypotheses of Trionychid Relationships

Although there is extensive literature on the taxonomy of soft-shelled turtles, few authors have considered the systematic relationships of all of the family members. The few exceptions are Hummel (1929), Loveridge and Williams (1957) and De Broin (1977). Of these, the Loveridge and Williams treatment gives the most complete consideration of intrafamilial relationships.

These three major systematic studies all recognize at least three of the five species groups thought to represent monophyletic (or paraphyletic) clades in the current study. All three use the concept of the Cyclanorbinæ. The Indian and North American groups retain their identity in all three. The uniqueness of the genera Pelochelys and Chitra is recognized in each, as is the possible relationship of Trionyx sinensis to T. steindachneri.

Since the time of Boulenger (1889) and Fitzinger (1889), soft-shelled turtles which hide their hind feet with flaps of skin have been recognized to be unique relative to other soft-shelled turtles. Only De Broin (1977) questions the monophyletic nature of this subfamily. The twelve shared, derived features of this subfamily (Figs. 20, 21) strongly

support its continued recognition. Furthermore, the nine derived features of the Trionychinae indicate monophyly for the remaining trionychids which have previously been placed together without attention to their unique common ancestry.

Loveridge and Williams (1957) detail the relationships of the African members of the Cyclanorbinae in terms of a progression of the most primitive, Cyclanorbis elegans, to the most derived, Cycloderma aubryi, based on three skull characters. The arrangement of the Cyclanorbinae given in their Fig. 50 (reproduced here as Fig. 23) is identical to one of three alternatives for the Cyclanorbinae derived in my work (Figure 17 A) but not chosen as the best solution. However, in their text they support monophyly of Cyclanorbis and Cycloderma, as is suggested by the data considered in the current study.

The Indian clade is recognized in all three systematic studies considered. This has been based in part on the presence of a preneural although this may be primitive for the family. Hay (1903) proposed the name Aspideretes for those fossil and Recent trionychine species with a preneural. Hummel (1929) endorses the use of this term as a subgenus, and De Broin (1977) recognizes it alternatively as a valid genus or subgenus. In spite of its apparent paraphyletic nature, recognition of this distinctive taxon may best promote a more complete understanding of trionychine relationships.

De Broin (1977) and Loveridge and Williams (1957) find Trionyx formosus and T. cartilagineus to be closely related to the Indian clade. The results of this study suggest that T. formosus is the sister group of the four Indian species (but that it does not share the features of

Aspideretes). T. cartilagineus is thought to share a unique common ancestor with Chitra and Pelochelys.

The North American clade is as frequently recognized as the Indian clade. It includes Trionyx triunguis, T. euphraticus, T. swinhoei and the three living North American species, T. muticus, T. spiniferus and T. ferox. No previous studies have included T. triunguis in this group. Loveridge and Williams (1957) place T. triunguis in a sister group to the North American clade along with T. sinensis and T. steindachneri. These three species are united only on the basis that they all fail to share features of the distinctive groups which these authors recognize. De Broin (1977) considers T. triunguis as the remnant of a group that evolved independently from that which led to the North American forms. Based on the osteological features considered here, T. triunguis is best considered the sister group of the remainder of the North American clade. The remainder of this clade is recognized in these three systematic works and the name Platypeltis Fitzinger, 1935, is applied to it by Hummel (1929). De Broin (1977) would restrict the use of the name Platypeltis to the three North American forms and resurrect the name Rafetus Gray 1864 for T. swinhoei and T. euphraticus. These last two species fit the diagnosis for Platypeltis (reduction of the eighth peripherals) and so recognition of Rafetus in addition to Platypeltis may not be necessary. Furthermore, if Rafetus is used for T. swinhoei and T. euphraticus then the generic name Apalone Rafinesque 1832 would have to be applied to the three North American forms.

Fortunately, the systematic position of Trionyx triunguis is clear. It can stand alone in the arrangement of the family as described above. This is important taxonomically because it is the type species of

Trionyx. The long muzzle of this species makes it phenetically distinct and the separation of the exoccipital from the pterygoid by the basisphenoid (character S57) is unique and makes it cladistically recognizable.

In past considerations of trionychnid relationships the species Trionyx sinensis and T. steindachneri appear to have been left over after other more distinctive taxa had been extracted from the Trionychninae. Loveridge and Williams (1957) mention the unique feature shared by these two taxa (and also T. subplanus), division of the fenestra postotica by a ventral process of the opisthotic, but they do not make full use of this unique quality. In addition to this skull character, these two species and T. subplanus share characters of reduced total size and an extremely short nuchal bone. Smith and Smith (1979) indicate that the generic name Amyda Geoffroy has Trionyx cartilagineus as its type species and thus cannot be applied to this clade as has been suggested by De Broin (1977) and Hummel (1929). The first available name is Pelodiscus Fitzinger for which T. sinensis is the type species.

The last of the four trionychnine clades recognized in the current study includes Pelochelys, Chitra and Trionyx cartilagineus. More than 100 years ago Gray (1873a) recognized a unique relationship between Chitra and Pelochelys by making them the only members of his subfamily Chitraina of the family Chitridae. Although no authors have followed this arrangement, none have disputed it.

The sister group relationship of Trionyx cartilagineus to Chitra and Pelochelys proposed here is novel. But based on a unique location of the foramen posterior canalis carotici interni (character S34), frequent contact of the epipterygoid and prootic anterior to the foramen nervi

trigemini (character T3), absence of contact of epipterygoid and palatine (character T1) and the presence of a fine ridge on the centrum of the eighth cervical vertebra (character C4), the sister relationship of T. cartilagineus to these unique genera is well supported. Recognition of the T. cartilagineus clade as a single genus seems undesirable given the established quality of the names Pelochelys and Chitra. But T. cartilagineus deserves distinction from the rest of the genus Trionyx. In this case the generic name Amyda Geoffroy, for which Testudo cartilaginea Boddaert (1770) is the type species, should be applied to T. cartilagineus (Smith and Smith, 1977).

In summary, the clades recognized by phylogenetic analysis are in nearly every case not totally novel. All have had generic or subgeneric names applied to them. The unique qualities of these clades are not currently conveyed by the broad use of the name Trionyx but could be by the use of the available generic names as in the tentative classification in Table 22. The continued use of the Trionyx with Chitra and Pelochelys for trionychine turtles is misleading and conveys little information. If more complete resolution of the relationships of the four clades identified can be achieved, further increase in information content of trionychid classification could result from the use of tribes to contain genera of unique common ancestry.

Trends and Mechanisms in Soft-Shell Turtle Evolution

Although it is possible to trace the changes in character states during the course of evolution of trionychids, many possibilities exist that might explain why these changes have occurred. Four scenerios could explain portions of the unique morphology of trionychids: 1) selection

for greater snapping ability (Pritchard, 1984); 2) selection for high-speed swimming (Pritchard, 1984; pers. obs.); 3) selection for greater aquatic fossoriality (Pritchard, 1984; Bramble, pers. comm.); and 4) a trend toward increased reproductive output.

The apparently critical evolutionary step which allows the unique loss of peripherals in trionyichids occurs in carettochelyids. This is the very tight and broad suturing of the rib heads to the vertebral centra. The development of massive rib heads provides a locking mechanism alternate to the presence of peripherals (Bramble, pers. comm.). In fact, the peripherals are not sutured to the pleurals in Carettochelys.

The absence of peripherals can most easily be explained by developmental truncation. In the embryonic turtle, ossification centers in the disc margin (those which result in the peripherals, nuchal and pygal bones), are the last to form (Zangerl, 1969). Consequently, the trionyichid shell may be paedomorphic; that is, the final step in carapace development never occurs. If Bramble's hypothesis about the locking function of the peripherals is correct, broadly developed rib head sutures are necessary in the absence of peripheral elements. This feature is one which the present phylogenetic analysis suggests would appear in a common ancestor of the Carettochelyidae and Trionyichidae.

Paedomorphosis may be the mechanism by which the unique trionyichid shell morphology evolved. However, few other features of soft-shelled turtles can be ascribed to a truncation of development. The only characters which might also be a result of paedomorphosis are those of the pubic elements. As noted, the pectineal processes of the pubic bones lie in a single plane as appears to be the case early in ontogeny of

other turtles. Furthermore, ossification of the prepubic region, which occurs in most living cryptodires, never occurs in trionychids. The absence of other paedomorphic features of soft-shelled turtle morphology suggests that developmental truncation has not been an important influence on the evolution of the group.

The most completely described adaptive hypothesis for the unique shell form of trionychids is that of Pritchard (1984). He suggests that Chitra is the best model for the ancestral trionychid, and that the unique body form of trionychids is an adaptation for a rapid predatory strike (one of his three listed adaptations for piscivory). His evidence is partly based on the similarity of the skull of Chitra to that of Chitracephalus dumonii Dollo from the Jurassic or Cretaceous of Europe, and partly on his observation that Chitra is the most developed piscivore among the trionychids and that other forms have secondarily become more generalized.

Other than their similar skull shape, there is nothing to suggest that Chitracephalus is related to the trionychids (Gaffney, 1979b). Pritchard himself states that the long, narrow skull found in these two forms appears a number of times in turtle evolution. He cites Glyptops, a baenoid, and Deirochelys, an emydid, as examples. The superficial similarity of Chitracephalus and Chitra goes beyond the overall skull shape, both have large and well developed hyoids. However, judging from Figure 1 in Dollo (1884), the corpus hyoideum in Chitracephalus is not composed of multiple ossifications. This is evidence that Chitracephalus has no close relationship to the Trionychidae.

Further arguments against using Chitra as the ancestral trionychid can be taken directly from the phylogenetic analyses conducted in the

present study. The many unique features of Chitra (and Chitra plus Pelochelys) would have to be lost secondarily in all other trionychids. A good example is the extensive postorbital bar. The hypothesis supported by the phylogenetically analysed data suggests that a very narrow postorbital bar first allowed contact of the jugal and parietal and that expansion of this contact is secondarily enlarged in Chitra and other species in the family with long, narrow skulls. Other features, including extensive hyperphalangy (Boulenger, 1889), the presence of large dorsal spines on the fifth and sixth cervicals, the narrow symphysis, the very short nuchal bone with the first body vertebra located at the anterior margin and the unique hyoid with a massive corpus hyoideum of eight ossifications and large second branchial arch of three strongly sutured ossifications, would all have to appear and then be lost in the course of trionychid evolution. It is far more parsimonious to consider the genus Chitra as a highly specialized trionychid (with all of its derived features appearing only once). Conversely, Pritchard's (1984) argument that Lissemys punctata is the most derived of trionychids remains unsupported. The view that it is the most primitive (Walther, 1922; Deraniyagala, 1939) is corroborated in the current study.

Pritchard (1984) suggests that swimming prowess and aquatic fossoriality are two secondary advantages of modification of shell shape in trionychids. Bramble (pers. comm.) has also pointed out that fossorial activity is enhanced by the shape of the trionychid carapace. Certainly, the flattened body form of trionychids provides reduced resistance to motion through fluids, be they water, sand or mud. It is only after the loss of peripherals in trionychids that there has been a remarkable decrease in the relative proportion of the total carapace made

up by the bony disc. A concomitant increase in the flexible margin, which would assist in aquatic fossoriality, also occurs at this stage indicating that fossoriality may in fact be a secondary result of peripheral loss, and not necessarily the cause for their loss.

Although trionychids have reduced shells they are found living with turtle-eating crocodylians throughout much of their range. Their survival under such circumstances may be ascribed to crypsis or to their swimming speed. It has been my observation that Trionyx ferox is the fastest swimming turtle that one encounters in clear Florida spring runs. Selection for better swimming ability could explain the acquisition of numerous derived features noted during the course of this study, especially those of the shell and girdles.

Trends toward reduction in shell size, including reduction in the number of peripherals, neurals, and plastral callosities, and reduction in the size of the eighth pleurals and the nuchal bone could all be attempts to lighten the shell, with shell streamlining as the result. Reduction of the bridge is important in allowing maximum retraction of the hind limbs for a maximum power stroke in swimming.

Loss of epidermal scutes may also act to reduce the weight of the shell. If Coldiron (1974) is correct in his hypothesis that dermal bone sculpturing acts to disperse stresses on broad areas of dermal bone (crocodylian and labryinthodont skulls), sculpturing could be an alternative shell-strengthening mechanism to epidermal scutes in trionychids.

Acquisition of hyperphalangy can be correlated with increased swimming prowess. Strong contact of the radius and ulna stiffens the forearm and probably produces a better paddle in trionychids,

carettochelyids and cheloniids. The reduction of the transverse processes of the tenth body vertebra that occurs in all trionychoids might increase the capacity of the pelvic girdle to rotate and thus contribute to the very long hind-limb power stroke of trionychids (Zug, 1971). The expanded pectineal processes of the pelvic girdle and the relatively enlarged coracoids both provide additional surface area for muscle attachment. Thus it appears that selection for improved swimming speed would account for many of the derived features noted to occur in the Trionychidae.

Another equally interesting possibility is suggested by Gould (1977), who discussed increased reproductive output as an impetus for major morphological modification. If accelerated maturity through paedomorphosis of shell development significantly reduces age at maturity, one might expect it to occur when increased reproductive output was required. The paedomorphic shell of trionychids might also act as a more flexible egg case and allow greater reproductive effort on the part of the females. Testing this hypothesis for the Trionychidae cannot be accomplished with osteological data but rather requires data on life history traits. Unfortunately, such data are rare for trionychids.

The limited data available on age at reproductive maturity does not strongly support this hypothesis. Reproduction in trionychids is best known for three of smallest forms: Trionyx muticus, Trionyx spiniferus, and Trionyx sinensis. The available data on age at sexual maturity for these and other aquatic turtles has been summarized by Bury (1979). He notes that for aquatic turtles in general males mature earlier than females and that smaller species mature earlier than larger species. Male Trionyx of the three species listed above usually mature in four

years (Webb, 1962; Plummer, 1977), which is equal to or less than that of males of other species which mature at a similar size. Estimates of age at maturity for female Trionyx of four temperate species varies from six to nine years for the North American forms (Webb, 1962; Plummer, 1977) and is given as six years for the Chinese soft-shell, Trionyx sinensis (Mitzukari, 1905). Maturity does not occur significantly earlier in female soft-shells than in females of other aquatic species which mature at a similar size.

Limited data indicates that female soft-shells may be capable of carrying larger clutches than other turtles of similar size. Clutch size in the smaller species mentioned varies from ten to twenty or more eggs. Clutch sizes for female T. muticus given by Plummer (1977) are slightly to significantly greater than clutch sizes for three female emydid species of equal plastron length given by Gibbons et al. (1982). This may only be a reflection of smaller egg size in trionychids. Data on reproductive effort (ratio of clutch mass to female mass) do not exist, but will be necessary to determine whether a relative difference in clutch size actually exists. The reproductive potential of large species is depicted in a figure in Wirot (1979). He shows a freshly butchered Chitra indica with 105 shelled eggs and three separate sets of developing follicles. If this species breeds every year, its reproductive output could match or surpass that of chelonioids.

Increased reproductive output facilitated by the paedomorphic features of trionychids could be a strong selective factor in the evolution of the family. However, more complete data on life history traits of the members of this family will be required to examine this possibility.

Figure 10. A phylogenetic arrangement of living turtles based on Gaffney (1984) with recognition of the Bataguridae from Hirayama (1985). Character states indicating monophyly of the Trionychoidea are enumerated in Figure 13.



Figure 11. A phylogenetic tree of the Testudines based on the classification in Williams (1950).

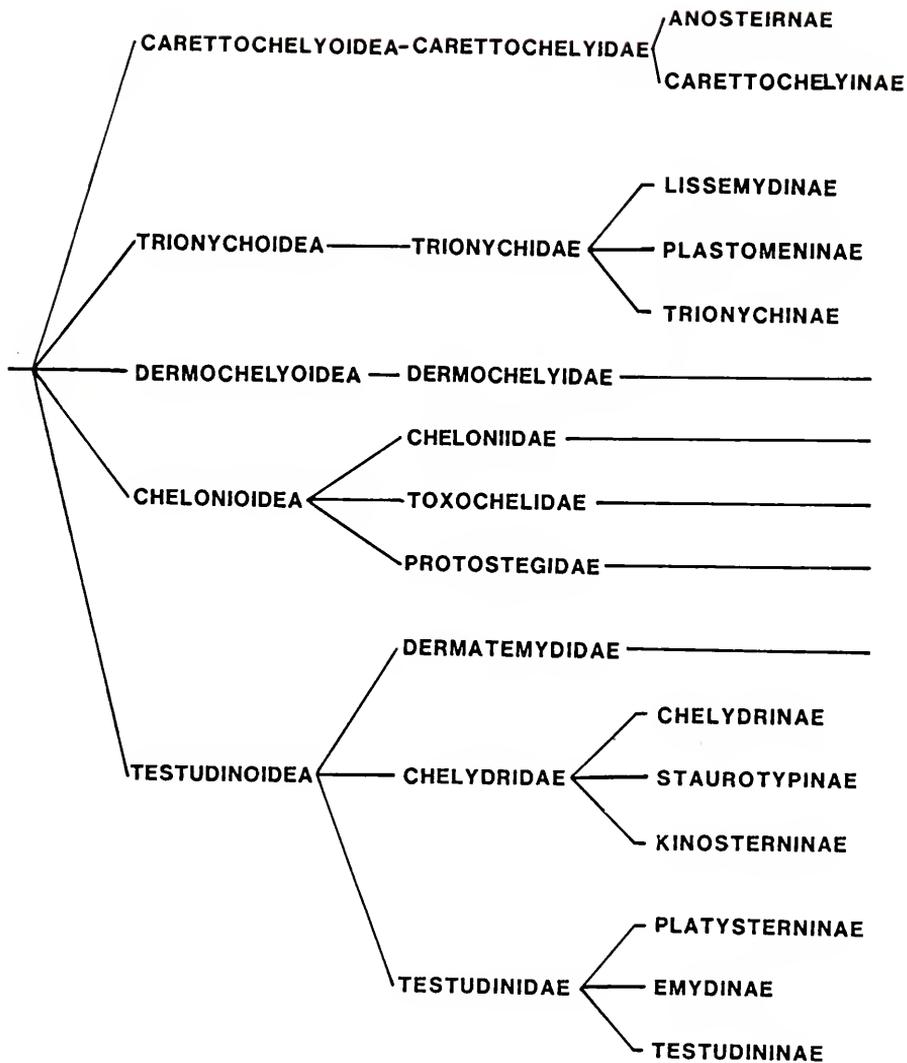
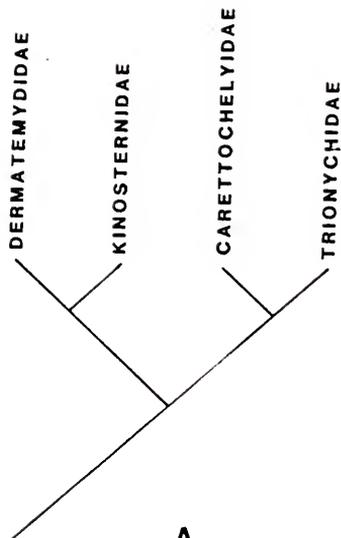
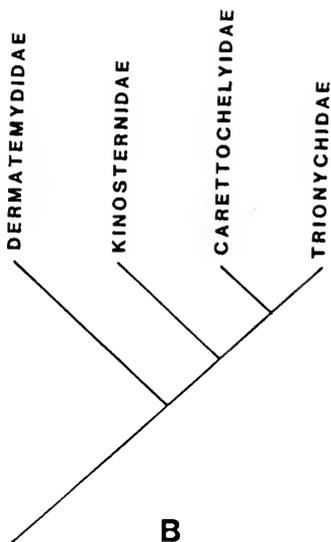


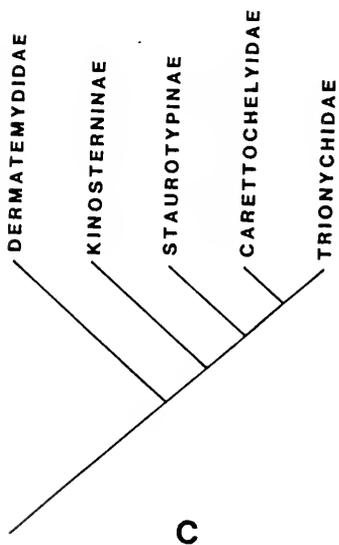
Figure 12. Four alternate classifications of the Trionychoidea. See discussion section for supporting characters.



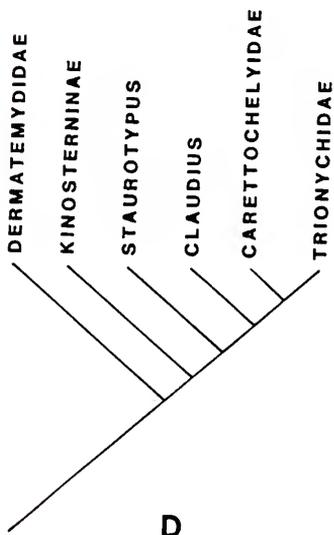
A



B



C



D

Figure 13. The distribution of character states for one of two most parsimonious arrangements of the Trionychoidea. See Table 20 for shared derived features of the Trionychidae plus Carettochelyidae, and Table 21 for unique features of the Trionychidae. A solid circle indicates a character state appearing only once; a large open circle indicates a character state appearing twice; a small open circle indicates a character state that occurs three or more times; and a star following a character state indicates that it occurs as a reversal.

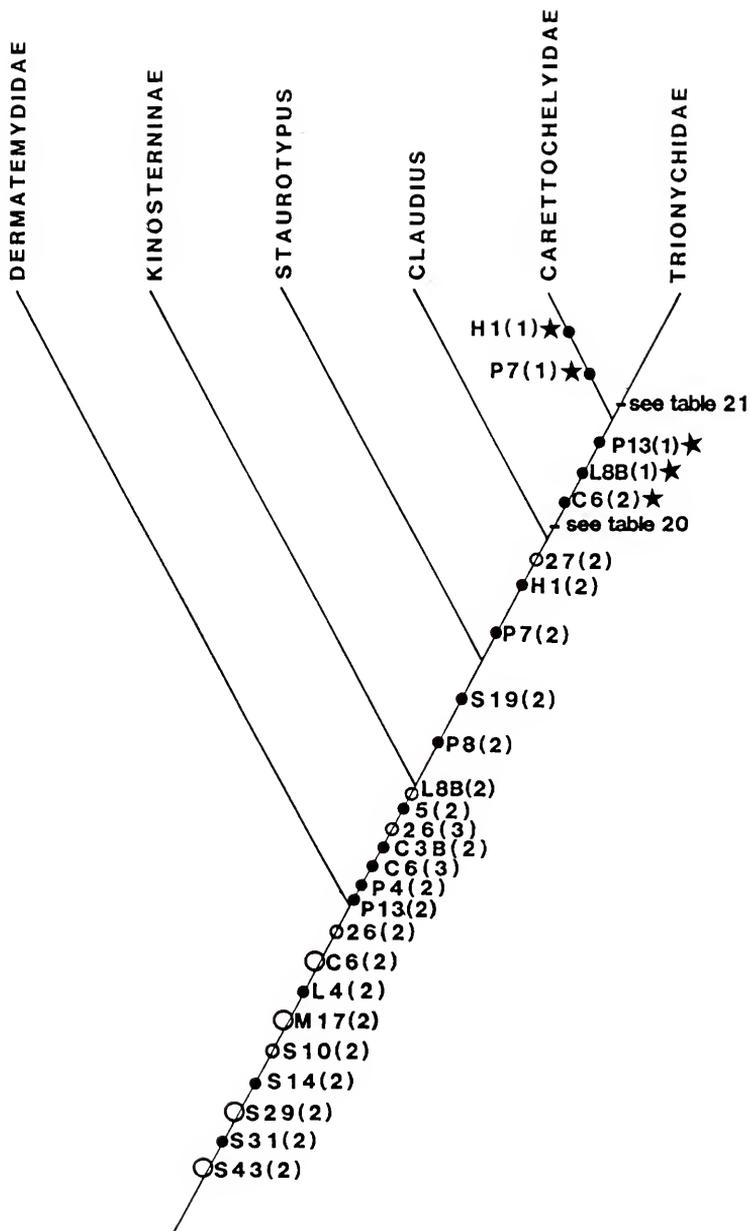


Figure 14. The distribution of character states in the most parsimonious arrangement of extant soft-shelled turtles based on 22 characters of shell morphology. A solid circle indicates a character state appearing only once; a large open circle indicates a character state appearing twice; a small open circle indicates a character state that occurs three or more times; and a star following a character state indicates that it occurs as a reversal.

Figure 15. The distribution of character states in the most parsimonious arrangement of extant soft-shelled turtles based on 23 characters of skull morphology. A solid circle indicates a character state appearing only once; a large open circle indicates a character state appearing twice; a small open circle indicates a character state that occur three or more times; and a star following a character state indicates that it occurs as a reversal.

Figure 16. The distribution of character states in the most parsimonious arrangement of extant soft-shelled turtles based on 13 characters of the mandible and nonshell postcrania. A solid circle indicates a character state appearing only once; a large open circle indicates a character state appearing twice; a small open circle indicates a character state that occurs three or more times; and a star following a character state indicates that it occurs as a reversal.

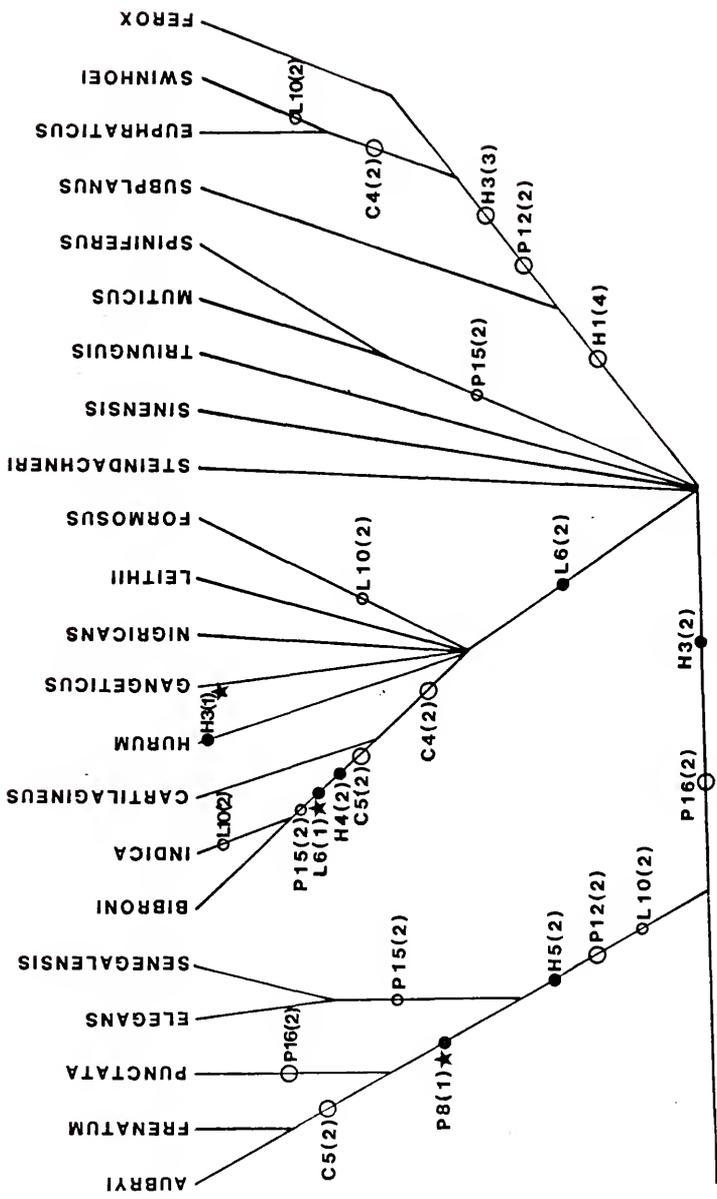


Figure 17. Three alternate topologies for the Cyclanorbinae appearing in the six most parsimonious cladograms based on the shell and nonshell data sets combined.

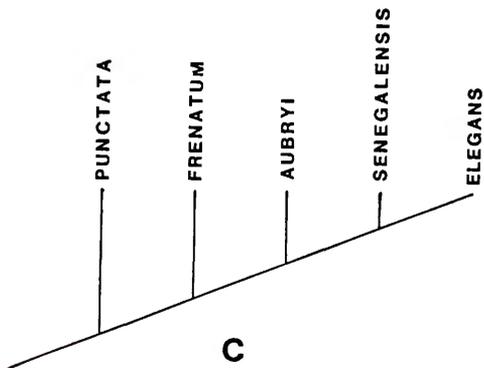
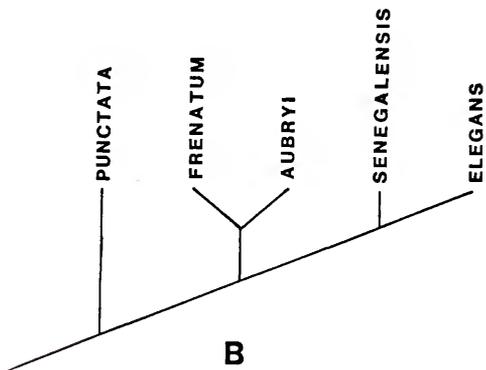
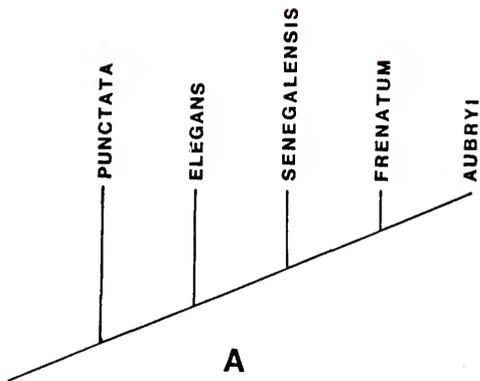


Figure 18. Two alternate topologies for the Trionychinae appearing in the six most parsimonious cladograms based on the shell and nonshell data sets combined.

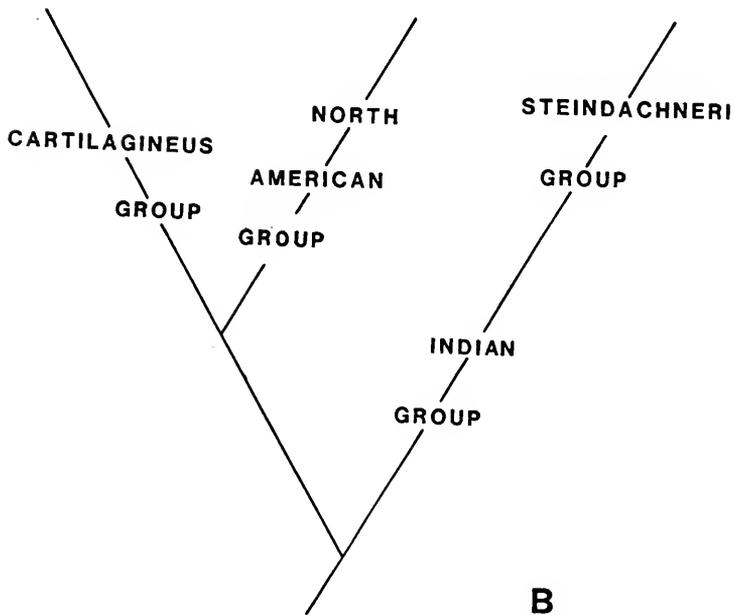
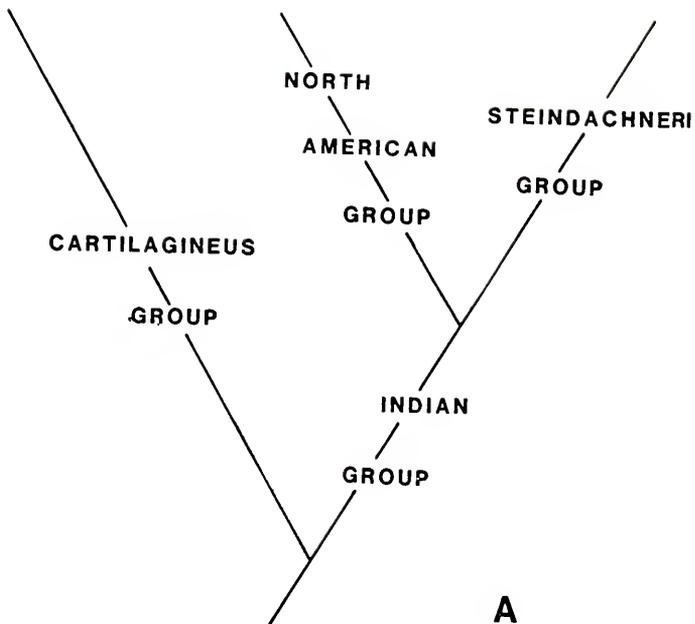


Figure 19. A phylogenetic arrangement of 20 living species of soft-shelled turtles based on 16 characters of the shell (from Meylan, 1984).

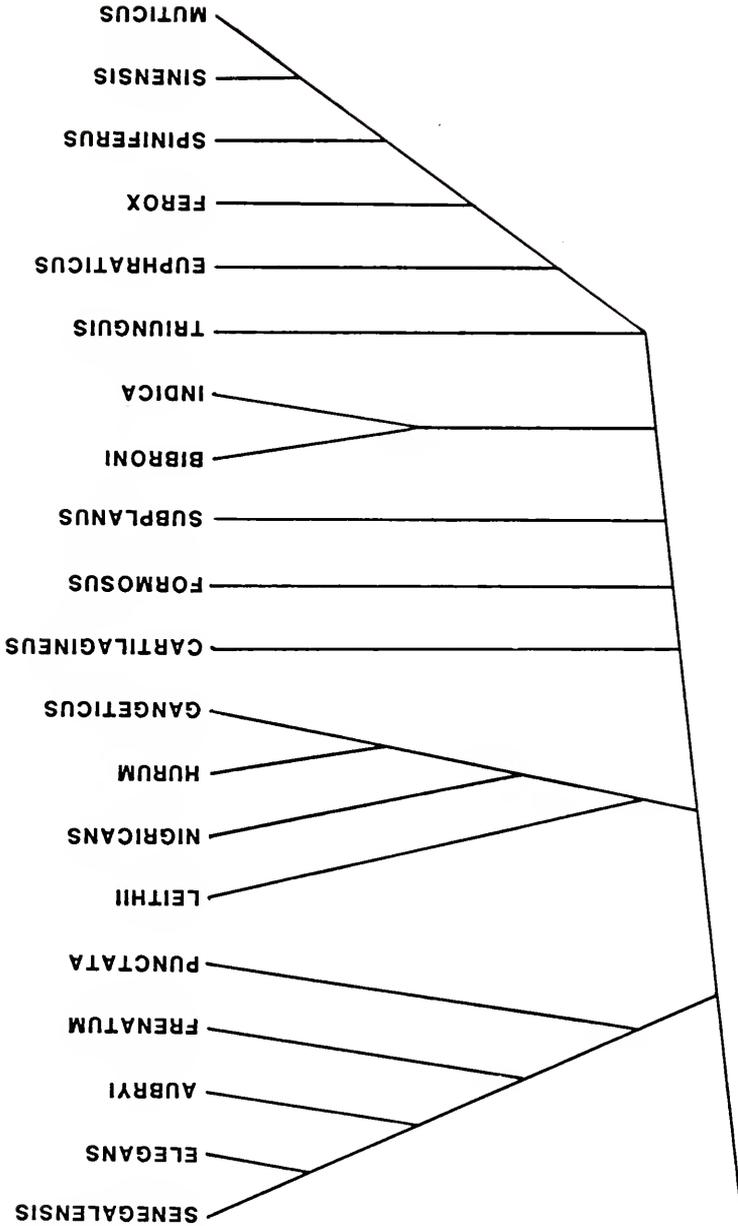


Figure 20. The topology and distribution of character states for one of the two most parsimonious arrangements of the living Trionychidae. A solid circle indicates a character state appearing only once; a large open circle indicates a character state appearing twice; a small open circle indicates a character state that occurs three or more times; and a star following a character state indicates that it occurs as a reversal.

Figure 21. The topology for the second of two most parsimonious arrangements of the living Trionychidae.

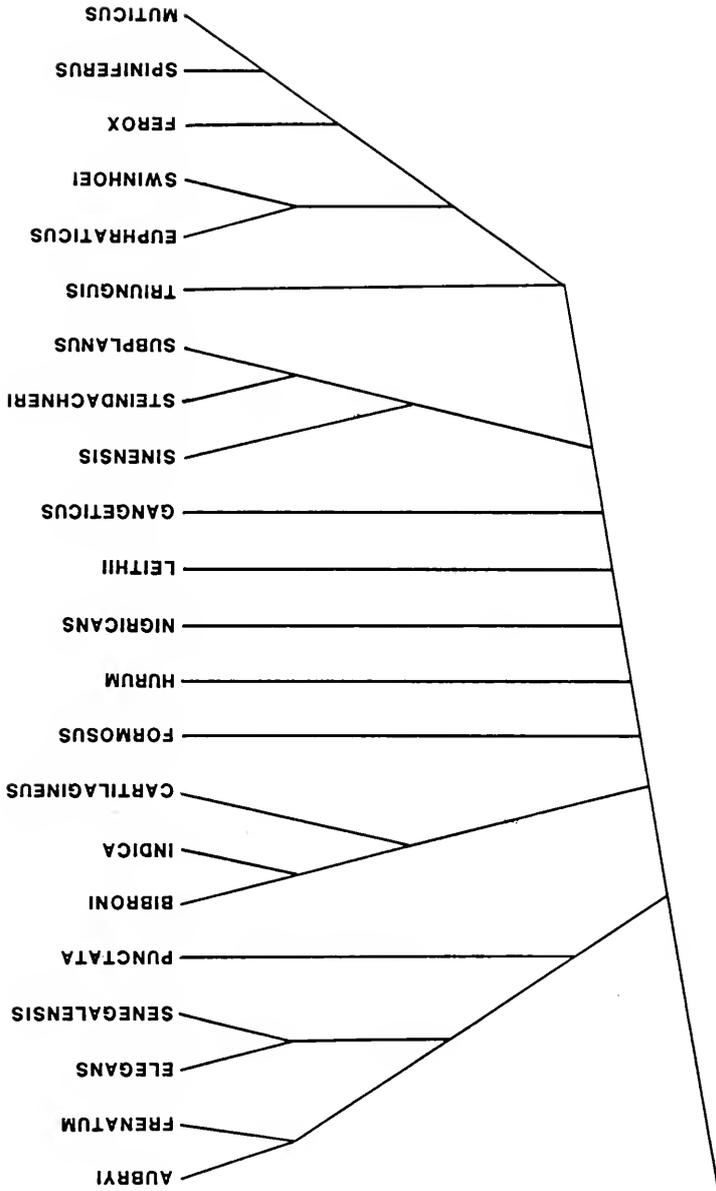


Figure 22. The topology of the most parsimonious cladogram that preserves monophyly of all four trionychine clades identified during this study.

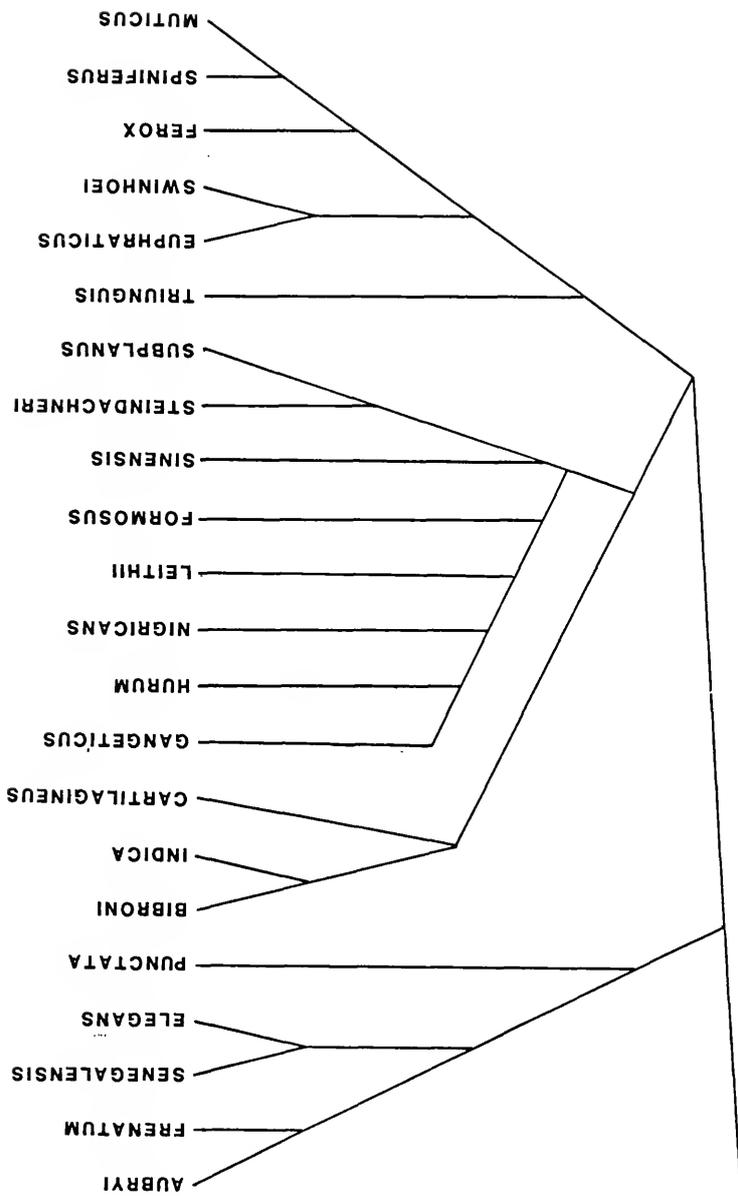


Figure 23. A phylogenetic tree for the Trionychidae redrawn from Figure 50 in Loveridge and Williams (1957).

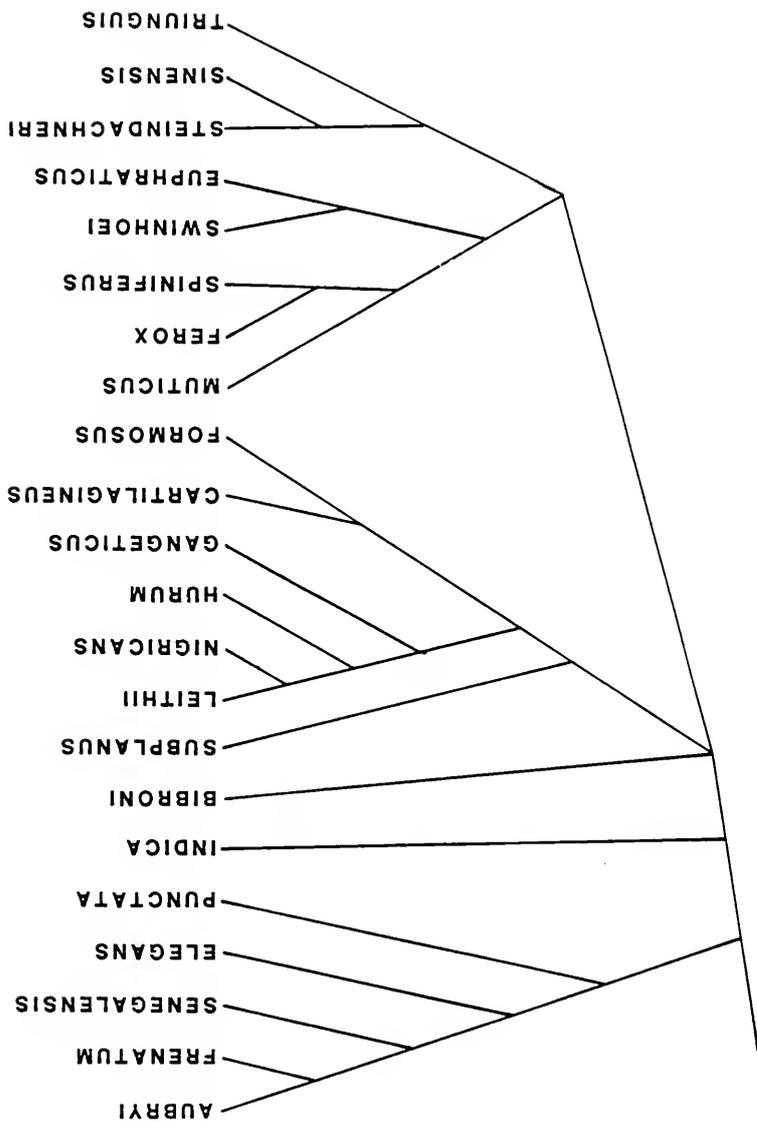


Table 19. Shared derived osteological characters of the Trionychoidea.

Character Code	Derived State
26	plastral buttresses reduced or absent
S10	cheek emargination reduced
S14	palatines contribute significantly to braincase
S29	crista dorsalis basioccipitalis absent
S31	canalis carotici straight and wide
S43	no groove for stapedia artery on prootic or parietal
M17	quadrate contribution to processus trochlearis oticum less than 50%
L4	surangular always present in area articularis mandibularis
C6	transverse processes of ninth body vertebra do not articulate with carapace

Table 20. Shared derived characters of the Trionychidae and Carettochelyidae. States for characters 5A through C1 are unique among the Cryptodira. States for characters S25 through P16 are also found among the Chelonioidea. The state for S8 is also found in the Chelydridae; that for 27 is also found in both the Chelonioidea and Chelydridae.

Character Code	Character State
5A	peripherals never sutured to pleurals
28	rib heads strongly sutured to vertebral centra
30	shell is sculptured and without epidermal scutes
S15	premaxillae fused
S18	basisphenoid contacts palatines
S22	vomer not in contact with pterygoids
S30	foramen posterius canalis carotici interni completely within pterygoid
L4	50% or more of area articularis mandibularis formed by surangular
L12	retroarticular process forms about one tenth of mandible length
C1	cervical centra 2-7 opisthocelous
S25	processus pterygoideus not projecting
A4	radius and ulna in contact adjacent to manus
A6	number of clawed digits three or fewer
P6	epipubic region never ossifies
P16	coracoid longest of three pectoral processes
S8	quadrate enclosing stapes
27	carapace not sutured to plastron

Table 21. Uniquely derived features of the Trionychidae.

Character Code	Character State
5	18 or fewer peripherals; no pygal or supragpygal
21	boomerang-shaped entoplastron
S4	quadratojugal not in contact with postorbital
S6	jugal contacts parietal
S16	premaxillae excluded from apertura narium externum
A2	hyperphalangy of manus digits 4 and 5, pes digit 4
A6	three clawed digits in manus
C2	centra of eighth cervical and first body vertebra not in contact
C3A	no ventral processes on eighth cervical
H1	corpus hyoideum composed of six or eight ossifications
P2	ilia curve posteriorly
P7	pectineal processes in a single plane and in broad contact with plastron
P9	pectineal processes equal to or wider than interpubic contact

Table 22. A tentative classification of the Trionyichidae.

Trionyichidae (Fitzinger) Bell, 1819

Cyclanorbinae Hummel, 1929

Cycloderma Peters, 1854

Cycloderma aubryi (A. Dumeril), 1856

Cycloderma frenatum Peters, 1854

Cyclanorbis Gray, 1852

Cyclanorbis senegalensis (Dumeril and Bibron), 1835

Cyclanorbis elegans (Gray), 1869

Lissemys Malcolm Smith, 1931

Lissemys punctata (Lacepede), 1788

Trionyichinae (Fitzinger) Lydekker, 1819

Chitra Gray, 1844

Chitra indica (Gray), 1831

Pelochelys Gray, 1864

Pelochelys bibroni (Owen), 1853

Amyda Geoffroy, 1809

Amyda cartilaginea (Boddaert), 1770

Aspideretes Hay, 1904

Aspideretes gangeticus (Cuvier), 1825

Aspideretes hurum (Gray), 1831

Aspideretes leithii (Gray), 1872

Aspideretes nigricans (Anderson), 1875

Nilssonina Gray, 1872

Nilssonina formosus (Gray), 1869

Table 22--continued.

Trionyx Geoffroy, 1809

Trionyx triunguis (Forsk.) 1775

Platypeltis Fitzinger, 1835

Platypeltis euphraticus (Daudin), 1802

Platypeltis swinhoei (Gray), 1823

Platypeltis ferox (Schneider), 1783

Platypeltis spiniferus (Le Sueur), 1827

Platypeltis muticus (Le Sueur), 1827

Pelodiscus Gray, 1844

Pelodiscus subplanus (Geoffroy), 1809

Pelodiscus sinensis (Wiegmann), 1835

Pelodiscus steindachneri (Siebenrock), 1906

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BIOGRAPHICAL SKETCH

Peter Andre Meylan was born in Lancaster, Pennsylvania, on 28 May, 1953. In 1971, he graduated from New Providence High School in New Providence, New Jersey. He entered the University of Florida in September, 1971 and received his Bachelor of Science degree in zoology in December, 1976. In May, 1980 he completed the requirements for the Master of Science degree in zoology, for which he studied the Pleistocene squamates from the Inglis local fauna. He expects to receive the Doctor of Philosophy degree in zoology at the University of Florida in September, 1985.

He has served as the manager of the herpetology collection of the Florida State Museum from August, 1974 to September, 1985. He will continue his career in biology as the Carter Fellow in Vertebrate Paleontology at the American Museum of Natural History.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



Walter Auffenberg, Chairman
Distinguished Service Professor
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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



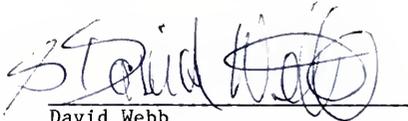
Douglas Jones
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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



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This dissertation was submitted to the Graduate Faculty of the Department of Zoology in the College of Liberal Arts and Sciences and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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