FIELDIANA
Geology

Published by Field Museum of Natural History

Volume 33, No. 9 — August 18, 1975

This volume is dedicated to Dr. Rainer Zangerl

Phylogeny of the Chelydrid Turtles:
A Study of Shared Derived Characters in the Skull.

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ABSTRACT

The turtle genera *Chelydra* (Recent, North America), *Macroclemys* (Recent, North America), *Platysternon* (Recent, Asia), *Protochelydra* (Paleocene, North America), and *Macrocephalochelys* (Pliocene, Asia) are hypothesized as a strictly monophyletic group on the basis of a shared derived character study of the skull. The five genera are therefore placed in the Family Chelydridae. The primary characters used involve the degree of temporal and cheek emargination along with changes in bone size and shape in the skull roof. *Protochelydra,* with the most extensive emarginations is proposed as the primitive end of a morphocline series culminating in *Platysternon,* which has the least emarginate condition. Cranial diagnoses for the testudinoid families Chelydridae, Emydidae, and Testudinidae are included.

INTRODUCTION

Rainer Zangerl has made outstanding contributions to our understanding of turtles, and he has created interest in developing methods of morphologic analysis. It gives me great pleasure to dedicate this paper to him.

Library of Congress Catalog Card Number: 75-16540

Publication 1205

The purpose of the present study is to develop a hypothesis of relationships among the North American snapping turtles and the Asiatic genus, *Platysternon*. Agassiz (1857) placed *Chelydra, Macroclemys* ("*Gypochelys*"), and *Platysternon* in the same family, but later Gray (1870) put *Platysternon* in its own family. Boulanger (1889, p. 45), although remarking that the "similarity of the skulls of *Platysternum* [sic] and *Macroclemmys* [sic] is very striking...," still maintained the genus in a separate family because the shell of *Platysternon* is quite distinct from snapping turtle shells. McDowell (1964) noted in passing that the affinities of *Platysternon* were with North American chelydrids, and Zug (1971) concluded that on the basis of the overall phenetic similarity of hind limb musculature characters *Chelydra* and *Platysternon* were more similar to each other than to the remaining turtles studied by him. I have here attempted to supplement these observations with a shared derived character analysis of the skull in *Chelydra, Macroclemys,* and *Platysternon.* The methods I have used are discussed by Hennig (1966), Crowson (1970), and Schaeffer et al., (1972).

In this study I have set up a series of morphoclines (see Kluge, 1971, and Schaeffer et al., 1972 for discussion of this term) for characters in the skulls of *Chelydra, Macroclemys,* and *Platysternon.* Each morphocline is discussed in a numbered series that corresponds to Table 1. The most important and difficult decision to make regarding morphoclines is the polarity, the direction of primitive and derived or advanced. This is crucial to the development of a phylogenetic hypothesis because the recognition of advanced or derived characters held in common by two or more forms is the basis of this method. I have concluded that for most of the characters used here the direction of change is *Chelydra-Macroclemys-Platysternon*—with the latter the most advanced.

I have used two methods for determining morphocline direction. The most useful is a comparison of the morphocline in question with character states in "sister" taxa. Nelson (1973) discussed this method and characterized it as an "indirect argument" involving previously proposed higher-level phylogenies (see Nelson, 1973, and references for further discussion). The higher-level phylogeny used here has been proposed in Gaffney (in press) and some understanding of this phylogenetic hypothesis is necessary in order to evaluate my decisions regarding primitive and derived conditions for chelydrids. The relative frequency of a character state within a group can also be used, rare features being considered as derived character states. These methods are hardly infallible and remain as important problem areas.

The anatomical terms used here are defined and figured in a glossary (Gaffney, 1972b.).

ACKNOWLEDGEMENTS

I am grateful to Ms. Lorraine Meeker for producing the illustrations, and my colleagues at the American Museum of Natural History for providing a stimulating environment.

ABBREVIATIONS

ang, angular
art, articular
bo, basioccipital
bs, basisphenoid
cor, coronoid
den, dentary
epi, epipterygoid
ex, exoccipital
fr, frontal
ju, jugal
mx, maxilla
na, nasal
op, opisthotic
pa, parietal
pal, palatine
pf, prefrontal
pm, premaxilla
po, postorbital
pr, prootic
pra, prearticular
pt, pterygoid
qj, quadratojugal
qu, quadrate
so, supraoccipital
sq, squamosal
sur, surangular
vo, vomer

AMNH, Department of Herpetology, American Museum of Natural History

ANALYSIS OF CRANIAL CHARACTERS IN *Chelydra, Macroclemys,* and *Platysternon*

1. Increase in relative size of dorsal lappet of prefrontal.

The increase in preorbital length is accompanied by the increase in length of the prefrontal process that forms the anterior part of the skull roof. This increase would appear to be a derived feature as the dorsal lappet of the prefrontal is smaller in baenoids.

2. Increase in posterior extent of parietal.
3. Increase in relative size of postorbital.
4. Anterior movement of dorsal portion of squamosal.
5. Decrease in extent of posterior temporal emargination or conversely, increase of skull roof covering.

Characters 2, 3, and 4 may be summarized as character 5 because basically this is how 5 is produced. Although the loss of temporal emargination in both cheek and posterodorsal areas is a critical character sequence, the direction of primitive and advanced for this morphocline is difficult to determine. In general, it can be seen rather easily that an unemarginated condition is most likely the primitive condition for Testudines. The captorhinomorphs, presumably the sister group of the turtles, are unemarginated and Zangerl (1948) has developed a morphologic argument that the solid-roofed condition is primitive. Here, however, we are comparing these three genera with other cryptodires and, more particularly, other testudinoids. Testudinoids characteristically have greatly developed cheek and posterodorsal emargination and it seems likely in view of the nearly universal occurrence of this condition in the group, that some degree of emargination is primitive. *Chelydra,* the most emarginate of the three Recent chelydrid genera, is not as emarginate as most other testudinoids and would appear to have the expected primitive condition. More importantly, however, the less emarginate condition of *Platysternon* is achieved by the presence of a large postorbital and an anterior extension of the squamosal, a rare condition among testudinoids and quite likely derived. Therefore, the more emarginate condition of *Chelydra* is here interpreted as primitive and the less emarginate condition of *Platysternon* as derived. *Macroclemys* has a relatively larger quadratojugal and the dorsal region of the squamosal is farther anterior in comparison with *Chelydra* but the degree of posterodorsal emargination is not intermediate between *Chelydra* and *Platysternon.* I interpret the postorbital and squamosal characters as shared derived for *Macroclemys* and *Platysternon.*

6. Decrease in size of jugal.

7. Decrease in exposure of jugal on cheek margin.

8. Increase in size of quadratojugal.

9. Decrease in extent of cheek emargination.

The argument here is essentially the same as with characters 2 - 5. The Testudinoidea would appear to have had a common ancestor with some degree of cheek emargination (with broad exposure of the jugal) because this feature is so common among known members of the group. Furthermore, *Platysternon* is unique in having a jugal with no exposure along the ventrolateral margin of the skull. *Macroclemys* approaches the *Platysternon* condition but still retains orbital exposure and a slight ventral exposure. The *Platysternon* condition is interpreted as derived and *Macroclemys* is interpreted as sharing these derived features with *Platysternon.*

10. Development of premaxillary "hook."

Chelydrids are characterized by having a variably developed symphyseal projection on the premaxillae. Within the Cryptodira the presence of such a "hook" would appear to be derived. *Chelydra* has the least prominent development of the "hook," while *Macroclemys* has it best developed and *Platysternon* is intermediate. This can be interpreted as a shared derived character held in common by *Platysternon* and *Macroclemys.*

11. Reduction of median ridge on ventral surface of vomer.

In *Chelydra* and many other cryptodires, a broad ridge on the ventral surface of the vomer tends to separate the paired troughs leading into each apertura narium interna. The ventral surface of the ridge has a lateral expansion on each side that also tends to define the choanal channels. *Platysternon* and *Macroclemys* lack this ridge morphology and the ridge itself is reduced to only the anterior part of the vomer. I interpret the reduction of this ridge as derived but the direction of this morphocline is certainly dubious.

12. Reduction of vertical flange on processus pterygoideus externus.

Chelydra and most cryptodires have a vertical plate on the lateral margin of the processus pterygoideus externus. This plate bears part of the mundplatte and apparently acts as a guide for the lower jaw during adduction. The extent of the vertical flange is reduced in *Macroclemys* and only a small spine persists in *Platysternon.* The reduction of the flange appears to be a derived feature for testudinoids because it is well developed in baenoids and most eucryptodires.

13. Development of snout constriction.

14. Labial ridge tending to curve inward.

These features are related to each other and presumably involve the development of a premaxillary "hook." *Platysternon* and *Macroclemys* have well-developed "hooks," relatively elongate snouts, and a straight or medially concave labial ridge. In *Chelydra* the labial ridges are concave laterally and there is no snout constriction.

15. Constriction of pterygoid "waist."

The paired pterygoids of cryptodires narrow midway along their length to form a "waist"-like outline in ventral view. *Macroclemys* and *Platysternon* are distinctly narrower in this area than *Chelydra* and most other cryptodires. This feature would appear to be related to a change in the size and attachment area of the M. adductor

Table 1. A comparison of *Chelydra* with *Macroclemys* and *Platysternon.*

Character	*Chelydra*	*Macroclemys* and *Platysternon*
1. Relative size of dorsal lappet of prefrontal	smaller	larger
2. Posterior area of parietal	less extensive	more extensive
3. Relative size of postorbital	smaller	larger
4. Anterodorsal extension of squamosal	absent	present
5. Relative extent of posterior temporal emargination	larger	smaller
6. Relative size of jugal	larger	smaller
7. Degree of jugal exposure on cheek margin	larger	smaller
8. Relative size of quadrato-jugal	smaller	larger
9. Degree of cheek emargination	more extensive	less extensive
10. Premaxillary "hook" development	smaller	larger
11. Median ridge on ventral surface of vomer	strongly developed	weakly developed
12. Vertical flange on processus pterygoideus externus	well developed	reduced
13. Snout constriction	absent	present
14. Labial ridge of skull	convex laterally	concave laterally or straight
15. Pterygoid "waist"	relatively broad	relatively narrow
16. Symphyseal "hook" on lower jaw	reduced	prominent
17. Relative length of lower jaw symphysis	short	long

mandibulae internus muscle group (Schumacher, 1954, 1955a, 1955b). The M. pterygoideus attachment site around the margin of the pterygoid moves medially in the *Chelydra-Macroclemys-Platysternon* series. In *Chelydra* the attachment areas are well separated, in *Platysternon* they meet in the midline, and in *Macroclemys* they are intermediate. The quadrate ramus of the pterygoid bears part of the M. pterygoideus attachment area. In *Chelydra* this area is separated posteromedially from the occipital muscle attachment sites, while in *Macroclemys* and *Platysternon* the pterygoideus and occipital muscle sites meet along the posteromedial margin of the pterygoid and form a ridge. These muscle attachment sites are rather variable among turtles but I think that the condition seen in *Chelydra* is primitive.

16. Development of prominent symphyseal "hook" on lower jaw.

As with the skull, *Platysternon* and *Macroclemys* have a well-developed symphyseal "hook," while in *Chelydra* it is less prominent. In this case, the "hook" is higher in *Macroclemys* than in *Platysternon.* The development of a symphyseal "hook" would seem to be a derived character because of its rarity in testudinoids and other cryptodires.

17. Development of broad symphyseal area on lower jaw.

Presumably this feature is correlated with the "hook" development, but, in any case, *Macroclemys* and *Platysternon* have a lower jaw symphysis with a greater anteroposterior length than *Chelydra.* Although there is some expansion of the triturating area itself, most of the increase in symphyseal length occurs posterior to the lingual ridge. If this feature is considered independent of the "hook" development, I do not know whether it is primitive or derived with respect to other testudinoids.

Protochelydra

Erickson (1973) has described a chelydrid of Paleocene age from North Dakota, the skull of which is fairly well preserved. Although there are some errors in the restoration (Erickson, 1973, fig 2; the limited posterior extent of the pterygoid disagrees with the text description and is almost certainly wrong), I will assume that the figures are essentially correct and use them as a basis of comparison with the three living genera.[1] Many of the characters I have used are not determinable but some of the more important ones, concerning the skull roof, can be distinguished.

The dorsal temporal emargination in *Protochelydra* is more extensive than in the three living genera. The posterolateral area of the parietal and the parietal-postorbital suture are reduced in comparison to *Chelydra,* the most emarginate of the living genera.

[1] Another trivial error is the misidentification of the *incisura columellae auris* in figure 3 and the text on page 6. In both places this structure is referred to as the *fenestra ovalis;* the latter, however, lies more medially in the skull, contains the footplate of the stapes, and is formed primarily by the prootic and opisthotic — not by the quadrate.

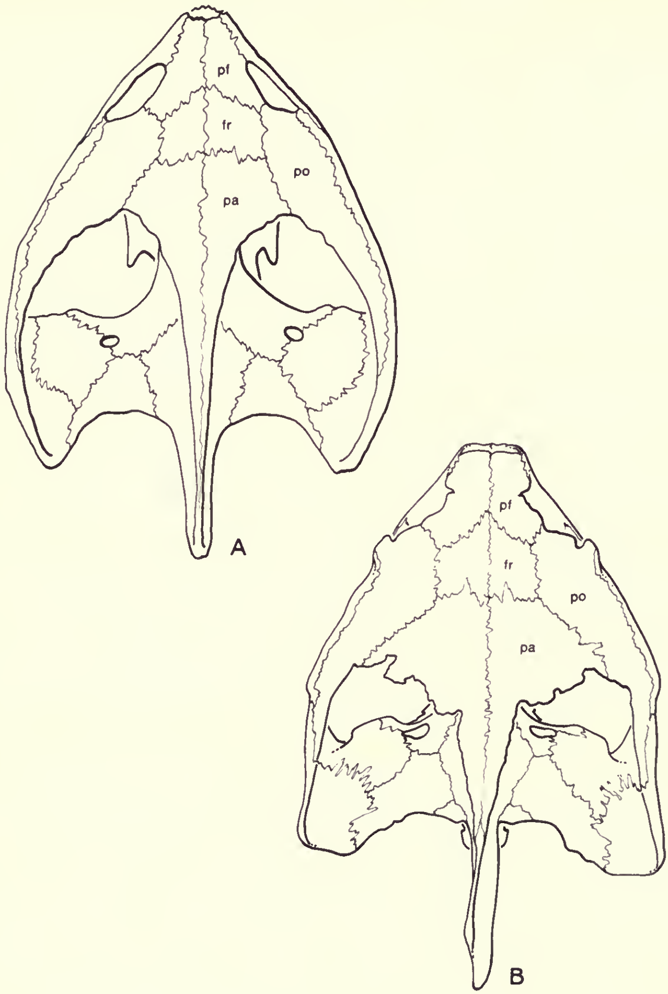


FIG. 1. Dorsal views of chelydrid skulls. **A**, *Protochelydra zangerli*, Paleocene, North America, restoration from Erickson (1973). **B**, *Chelydra serpentina*, Recent, North America, AMNH 5305.

The cheek emargination and the jugal are larger in *Protochelydra* than in the living forms and the quadrato-jugal appears smaller in *Protochelydra* than in the living chelydrids. The premaxillary "hook," vomerine ridge, processus pterygoideus externus flange, degree of snout constriction, and pterygoid "waist" all appear to be about the same in *Chelydra* and *Protochelydra*. The morphocline set up for the three living chelydrids can be extended in what is

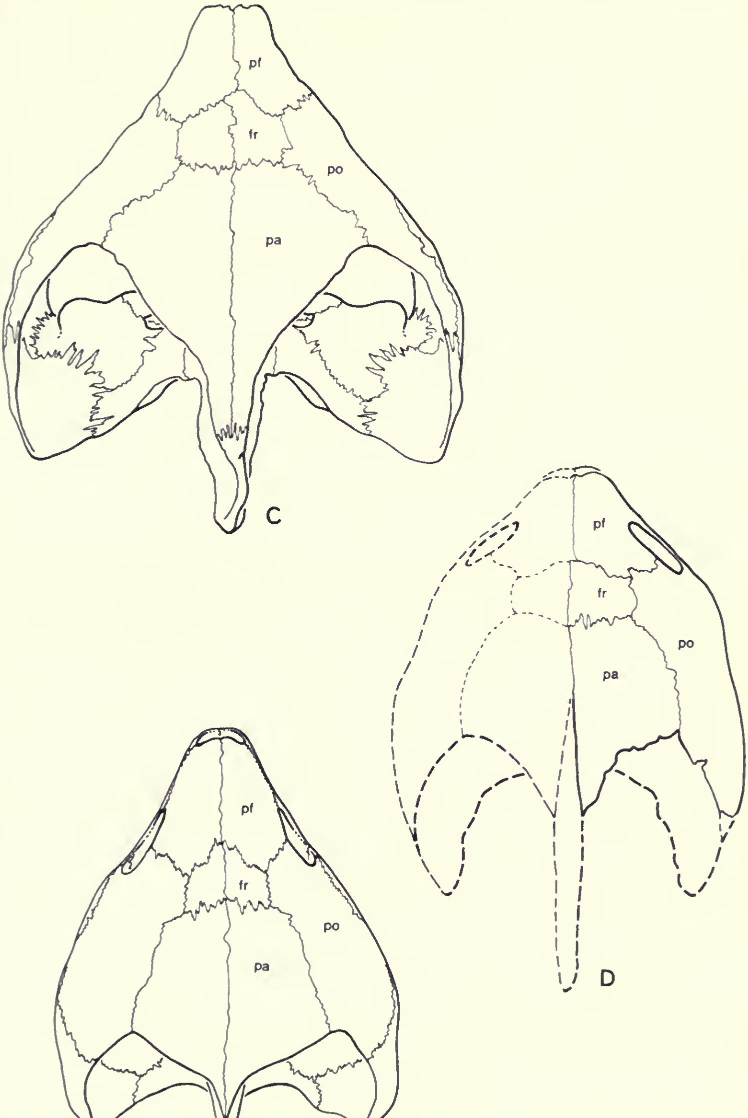


FIG. 1. (*continued*). **C**, *Macroclemys temminckii,* Recent, North America, AMNH 58251. **D**, *Macrocephalochelys pontica,* Pliocene, Asia, restoration from Pidoplichko and Tarashchuk (1960). **E**, *Platysternon megacephalum,* Recent, Asia, AMNH 92740.

here hypothesized as the primitive direction. If this is done it can be seen that *Protochelydra* possesses a more primitive state for the following characters (see table for key to numbers): 2, 3, 5, 6, 7, 8, 9. *Protochelydra,* then, may be hypothesized as the "sister" taxon for the other three chelydrids. The three living forms may be considered to be a strictly monophyletic group because they possess some advanced characters not possessed by *Protochelydra.*

The age of *Protochelydra* is consistent with my hypothesis of relationships and with the direction of the morphocline. However, it does not really supply a useful test of the hypothesis because, although stratigraphically older taxa are more likely to possess primitive characters they often do not, and there is no non-morphologic method to determine this (Schaeffer et al., 1972). *Protochelydra* is not consistent with the ancestral morphotype of the living chelydrids. The expanded triturating surface would appear to be a uniquely derived character and would bar it from potential ancestry of the later chelydrids.

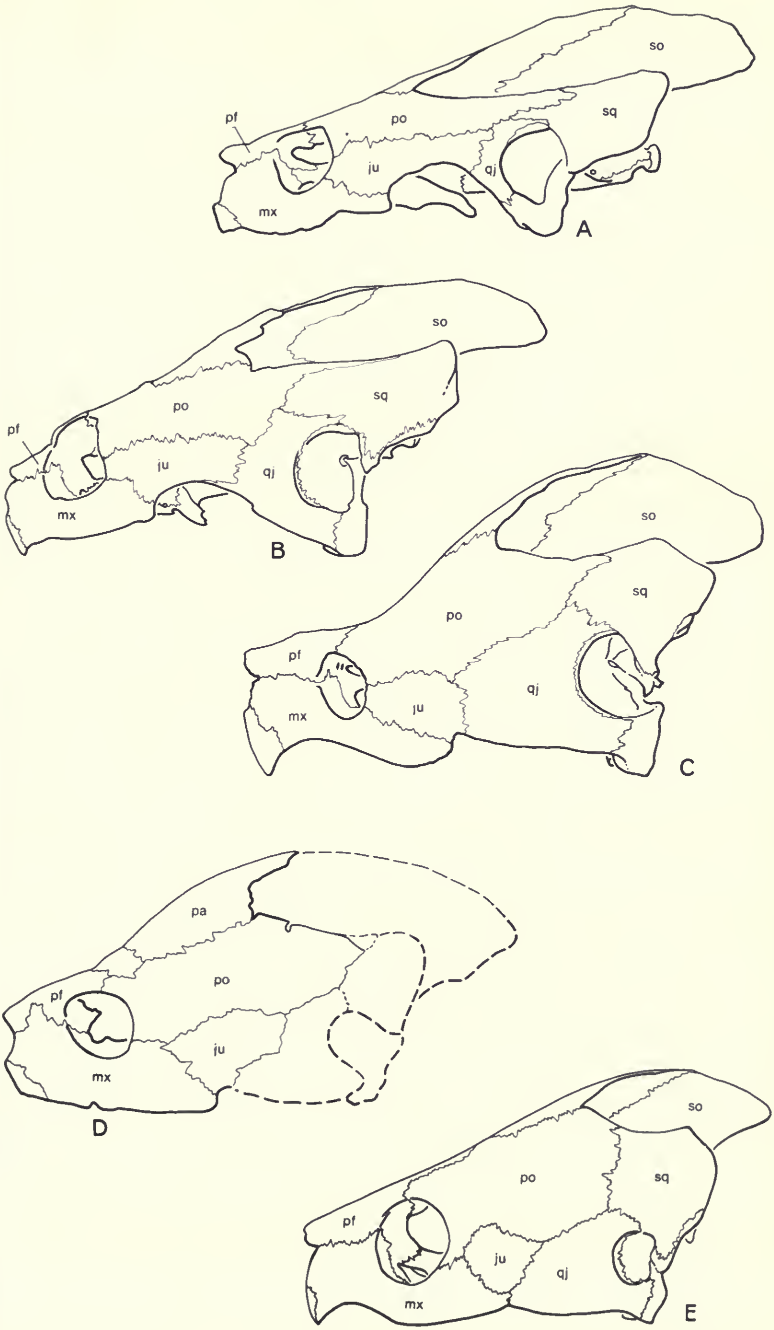
Macrocephalochelys

Pidoplichko and Tarashchuk (1960)[1] described a partial skull, *Macrocephalochelys pontica* from the Pliocene of the Ukraine and concluded that it was a near relative of *Platysternon.* Only the skull roof and cheek were figured, but the limits of the cheek and temporal emarginations and jugal sutures can be seen. The postorbital and maxilla meet behind the orbit as in *Platysternon* and, if the figure is correct, the ventral exposure of the jugal is reduced, as in *Macroclemys.* The prominent premaxillary "hook" appears to be absent and this may be a specialization unique to this form or due to preservation. The well-developed postorbital-maxilla contact is a shared derived character held in common with *Platysternon* and on this basis I would hypothesize that *Macroce-*

[1] I am indebted to S. B. McDowell who brought this reference to my attention.

Opposite:

FIG. 2. Lateral views of chelydrid skulls. **A,** *Protochelydra zangerli,* Paleocene, North America, restoration from Erickson (1973). **B,** *Chelydra serpentina,* Recent, North America, AMNH 5305. **C,** *Macroclemys temminckii,* Recent, North America, AMNH 58251. **D,** *Macrocephalochelys pontica,* Pliocene, Asia, restoration from Pidoplichko and Tarashchuk (1960). **E,** *Platysternon megacephalum,* Recent, Asia, AMNH 92740.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phalochelys has an ancestor in common with *Platysternon* that neither form has in common with other known turtles. This is in agreement with Pidoplichko and Tarashchuk's conclusions.

The other visible features of the skull roof agree with *Macroclemys;* that is, the degree of cheek and posterodorsal emargination is about the same in both genera. A more phenetic classification would probably ally *Macrocephalochelys* with *Macroclemys* and, in fact, Ckhikvadze (1971) has placed this genus in the Chelydridae (excluding *Platysternon*). Nonetheless, the presence in *Macrocephalochelys* of a shared derived character held in common with *Platysternon* is sufficient, at present, to develop a hypothesis of its relationships.

SHELL MORPHOLOGY

The primary area of taxonomic interest in most turtle studies has been the shell morphology. *Platysternon* has a distinctly different shell pattern from *Chelydra* and *Macroclemys* (see Boulanger, 1889, for shell figures) and, although cranial similarities to *Macroclemys* have been noted (Boulanger, 1889, p. 45), the emydid-like shell has resulted in the separation of *Platysternon* from *Chelydra* and *Macroclemys.* According to the phylogenetic hypothesis advanced here, however, the cruciform, *Chelydra*-like shell is primitive for the Chelydridae and the more ossified shell of *Platysternon* is advanced. There are a number of supposed examples among chelonioids where an emarginate or reduced bony shell appears to have evolved independently, but there seem to have been no suggestions that a more ossified shell evolved from a less ossified one. However, I think that the condition in *Platysternon* can be interpreted as a case of increased shell ossification. *Platysternon* differs from emydids and resembles chelydrids in having a relatively narrow bridge, ligamentous attachment of the plastron to the carapace, and lacking plastral buttresses. The relatively broad, anteriorly concave nuchal bone is also similar to chelydrids. The principal difference between *Platysternon* and other chelydrids is the broad epiplastron and xiphiplastron of *Platysternon.* These features may have evolved in *Platysternon* independently of their occurrence in other testudinoids.

DIAGNOSES OF FAMILIES IN THE TESTUDINOIDEA

My concept of the Family Chelydridae differs from most previous authors (but not Agassiz, 1857) in including *Platysternon.*

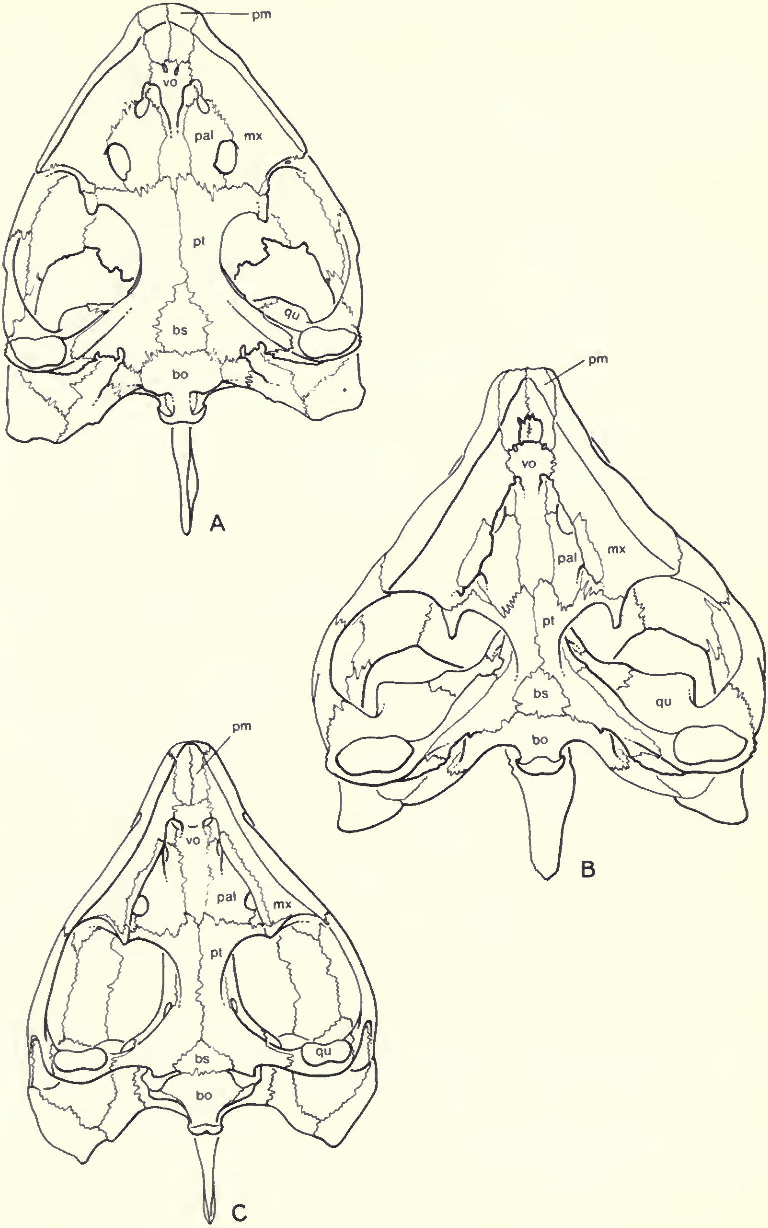

FIG. 3. Palatal views of chelydrid skulls. **A**, *Chelydra serpentina,* Recent, North America, AMNH 5305. **B**, *Macroclemys temminckii,* Recent, North America, AMNH 58251. **C**, *Platysternon megacephalum,* Recent, Asia, AMNH 92740.

Consequently, a new diagnosis is offered for the family, and, so that features may be compared more easily, cranial diagnoses of the other testudinoid families are also given.

Chelydridae

Skull roof: Temporal emargination not as extensive as in other Testudinoidea; parietal, postorbital, and squamosal exposed along temporal margin. Frontal does not enter orbital margin, reduced in comparison to Testudinidae and many Emydidae. Maxilla and quadratojugal may (*Platysternon*) or may not be in contact. Descending processes of prefrontal usually closely approximated ventrally resulting in a narrow fissura ethmoidalis, as in most Emydidae (*Macroclemys* has a moderately wide fissura ethmoidalis, but it is not as wide as in Testudinidae). Postorbital well developed and more extensive than in other Testudinoidea. Jugal may or may not enter orbit.

Palate: Maxillary triturating surface narrow or moderately expanded (*Protochelydra*), no approach to secondary palate. High labial ridge, low or absent lingual ridge, no accessory ridges. Foramen palatinum posterius small or large. Premaxillae developed into a prominent hook-like projection (less so in *Chelydra* and *Macrocephalochelys*). No development of palatal trough on vomer, palatines, and pterygoids as can be seen in Testudinidae. Processus pterygoideus externus variably developed.

Braincase: Quadrate forming a completely enclosed incisura columellae auris. Processus trochlearis oticum moderately well developed. Ventromedial process of frontal seen in Testudinidae absent. Processus inferior parietalis not reduced, similar to most Emydidae.

Lower jaw: Triturating surface narrow, labial ridge subequal or slightly higher than lingual ridge. Prominent symphyseal hook present (although somewhat reduced in *Chelydra*). Processus coronoideus low. Surangular largely covered by dentary, only narrowly exposed laterally as in Emydidae.

Emydidae

Skull roof: Temporal emargination variable but at least parietal, postorbital, and squamosal exposed along temporal margin with some forms exposing in addition the quadratojugal, jugal, and (rarely) the frontal. Loss of the quadratojugal occurs in some forms

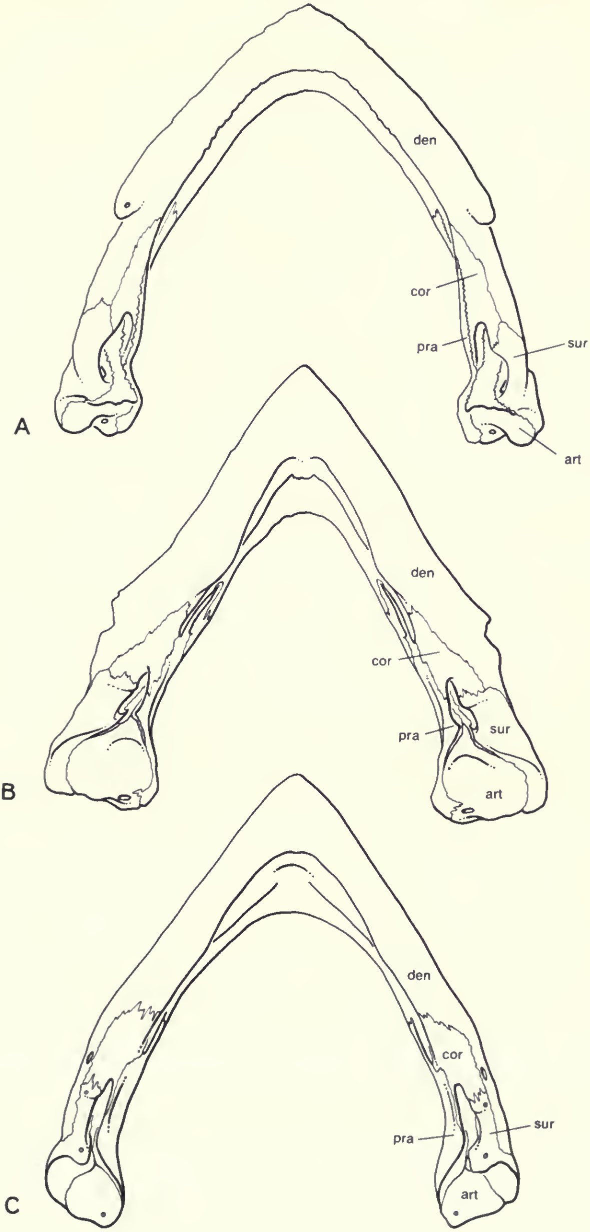

FIG. 4. Dorsal views of chelydrid lower jaws. **A**, *Chelydra serpentina*, Recent, North America, AMNH 5305. **B**, *Macroclemys temminckii*, Recent, North America, AMNH 58251. **C**, *Platysternon megacephalum*, Recent, Asia, AMNH 92740.

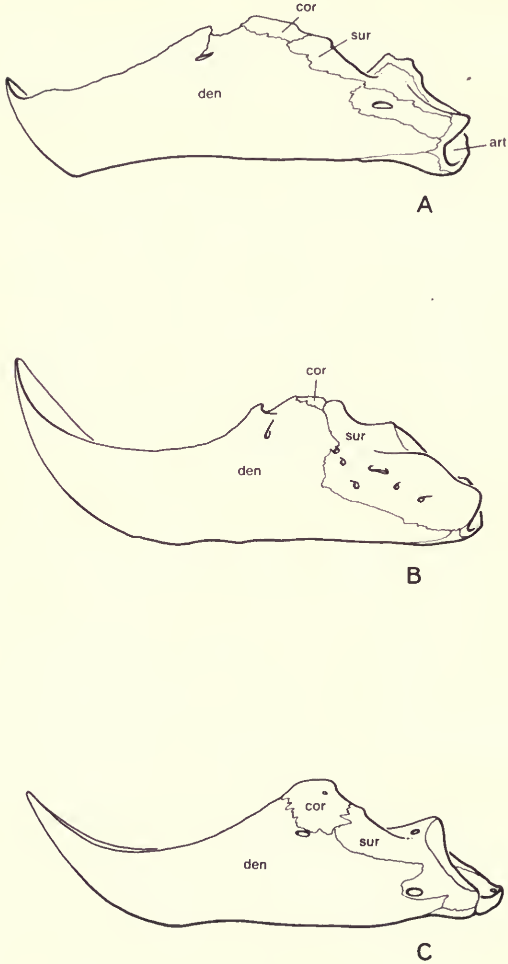

FIG. 5. Lateral views of chelydrid lower jaws. **A**, *Chelydra serpentina,* Recent, North America, AMNH 5305. **B**, *Macroclemys temminckii,* Recent, North America, AMNH 58251. **C**, *Platysternon megacephalum,* Recent, Asia, AMNH 92740.

(*Terrapene, Geoemyda*) with consequent absence of zygomatic arch. Frontal may or may not enter orbital margin. Maxilla and quadratojugal rarely in contact. Descending processes of prefrontals typically very closely approximated ventrally (at most only moderatly separated) resulting in a narrow fissura ethmoidalis similar to Chelydridae but as opposed to Testudinidae. Postorbital well developed but not as extensive as in Chelydridae; never absent. Jugal entering orbit.

Palate: Maxillary triturating surface highly variable, ranges from narrow (as in *Deirochelys*) to well-developed secondary palate (as in *Chinemys*). High labial ridge, variable lingual ridge, accessory ridges absent in many forms, one or two (extreme seen in *Batagur*) present in others. Foramen palatinum posterius small (most emydids) to unusually large (e.g., *Deirochelys*). Premaxillae not developed into a prominent hook-like projection as in most Chelydridae. No development of palatal trough on vomer, palatines, and pterygoids as seen in Testudinidae. Processus pterygoideus externus usually well developed as in *Chelydra*.

Braincase: Quadrate forming a nearly but usually not completely enclosed incisura columellae auris. Processus trochlearis oticum variably developed. Ventromedial process of frontal seen in Testudinidae absent. Processus inferior parietalis usually not reduced as in most Testudinidae.

Lower jaw: Triturating surface variable, may be expanded (e.g., *Chinemys*) or narrow (e.g., *Deirochelys*). Symphyseal hook usually absent or at least not developed as in *Macroclemys*. Processus coronoideus very high (e.g., *Chinemys*) or low. Surangular largely covered by dentary, only narrowly exposed laterally, as in Chelydridae but in contrast to Testudinidae.

Testudinidae

Skull roof: Temporal emargination well developed, parietal, postorbital, quadratojugal, squamosal, and sometimes jugal exposed along temporal margin. Postorbital and zygomatic arches reduced in comparison to most other Testudinoidea. Frontal may or may not enter orbital margin. Maxilla not in contact with quadratojugal. Descending processes of prefrontals typically more or less widely separated inferiorly resulting in a wide fissura ethmoidalis in comparison to Emydidae and Chelydridae. Postorbital tending to be reduced, rarely absent. Jugal entering orbit.

Palate: Maxillary triturating surface somewhat variable, ranges from narrow (e.g., *Kinixys*) to moderately expanded (e.g., *Geochelone*) but not forming a secondary palate as in many Emydidae. High labial ridge, low to absent lingual ridge, one accessory ridge is often present paralleling the labial and lingual ridges. Foramen palatinum posterius small in comparison to *Chelydra* but similar to most Emydidae (not *Deirochelys*). Premaxilla not developed into a prominent hook-like projection as in most Chelydridae. Vomer,

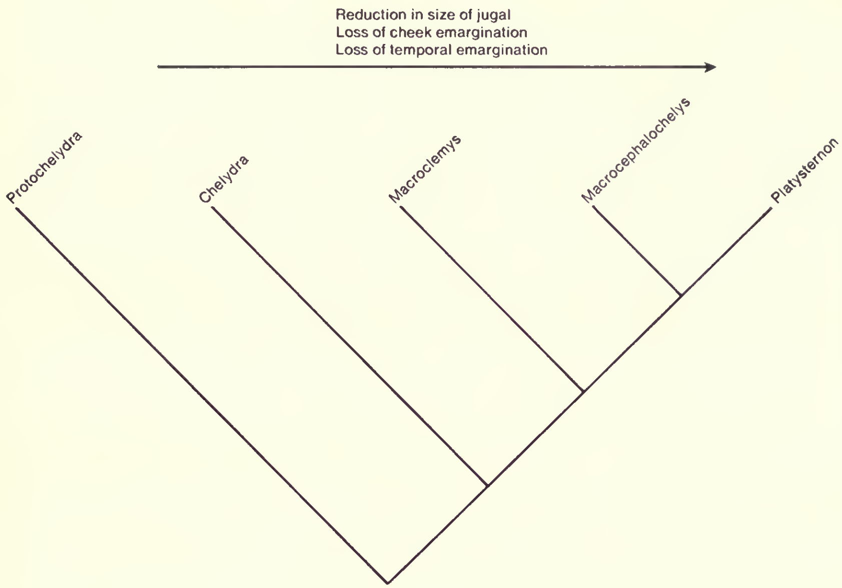

FIG. 6. A theory of relationships for the chelydrid turtles. The arrow shows the hypothesized direction (from primitive to derived) of the three indicated morphoclines. The diagram is intended to show the relative positions of common ancestors but does not show stratigraphic position or other adaptational features.

palatines, and pterygoids forming a ventrally concave trough extending from the apertura narium interna posteriorly to the region of the pterygoid "waist." A median ridge is usually developed on the vomer and pterygoids that separates the trough into two lateral halves. Processus pterygoideus externus reduced in comparison to *Chelydra* and most Emydidae.

Braincase: Quadrate forming a completely enclosed incisura columellae auris. Processus trochlearis oticum moderately well developed, within range seen in Emydidae. Ventromedial process of frontal forms partly enclosed sulcus olfactorius. Processus inferior parietalis reduced in comparison to many Emydidae but not as in Cheloniidae.

Lower jaw: Triturating surface narrow in comparison to some Emydidae (such as *Chinemys*), but usually developed into a trough with labial and lingual ridges parallel to one another and about equally high. Symphyseal hook as seen in Chelydridae absent. Surangular not covered by dentary, often extensively exposed laterally in contrast to condition in most Testudinoidea. Processus coronoideus relatively low as in *Chelydra* and as opposed to some Emydidae (e.g., *Chinemys*).

CLASSIFICATION

There has been much argument and little agreement about the purposes of a classification. As I have discussed elsewhere (Gaffney, in press), in my opinion, phylogenetic diagrams are to be preferred over classifications and, within the limits of practicality, a classification should exactly reflect a phylogenetic hypothesis. In this paper I am presenting a classification of snapping turtles and their near relatives. This classification is a written version of the phylogenetic hypothesis presented here using the full hierarchy available in the Linnaean system. Although stability is often considered an important attribute of classifications, my classification of the Chelydridae must be changed if a new phylogenetic hypothesis is developed, if new fossil material becomes available, or even if new sutural interpretations are offered. It seems to me, however, that the bibliographic and curatorial advantages of stability in higher categories are rather minor in view of the greater biologic usefulness of phylogenetic information. In this sense stability in higher taxa is often a spurious and misleading indication of the attainment of phylogenetic "truth." The purpose of the classification presented here is to reflect a phylogenetic hypothesis and to name monophyletic groups.

CLASSIFICATION OF CHELYDRID TURTLES

Family Chelydridae Swainson, 1839[1]

Subfamily Protochelydrinae, new

Chelydrid turtles having a relatively larger jugal and greater posterodorsal and cheek emargination than in Chelydrinae; triturating surfaces of skull relatively wide in comparison to most Chelydrinae; posteriorly directed ridge on ventral surface of pterygoid present; plastron cruciform, as in *Chelydra* and *Macroclemys*, but apparently lacking median fontanelles.

Protochelydra

Subfamily Chelydrinae Swainson, 1839, new rank

Chelydrid turtles usually having a relatively smaller jugal and more reduced posterodorsal and cheek emargination than in Protochelydrinae; triturating surfaces of skull relatively narrow in comparison to Protochelydrinae; posteriorly

[1] Swainson's original spelling "Chelidridae" (1839, p. 116) actually has priority according to the recent nomenclature rules concerning family level taxa but this spelling has not been used for some time.

directed ridge on ventral surface of pterygoid absent; plastron usually cruciform with median fontanelles (but not in *Platysternon*).

Tribe Chelydrini Swainson, 1839, new rank

Turtles of the Subfamily Chelydrinae with a relatively larger jugal and more extensive posterodorsal and cheek emargination than in Platysternini; postorbital, quadrato-jugal, dorsal lappet of prefrontal, posterior area of parietal, premaxillary "hook," and symphyseal "hook" on mandible all relatively smaller than in most Platysternini; anterodorsal extension of squamosal seen in most Platysternini absent; median ridge on ventral surface of vomer strongly developed in contrast to Platysternini; vertical flange on processus pterygoideus externus well developed in contrast to Platysternini; pterygoid "waist" relatively broad in contrast to Platysternini.

Chelydra

Tribe Platysternini Gray, 1870, new rank

Turtles of the Subfamily Chelydrinae with a relatively smaller jugal and less extensive posterodorsal and cheek emargination than in Chelydrini; postorbital, quadratojugal, dorsal lappet of prefrontal, posterior area of parietal, premaxillary "hook," and symphyseal "hook" on mandible all relatively larger than in Chelydrini; anterodorsal extension of squamosal present; median ridge on ventral surface of vomer not strongly developed as in Chelydrini; vertical flange on processus pterygoideus externus weakly developed in contrast to Chelydrini; pterygoid "waist" relatively narrower than in Chelydrini.

Subtribe Macroclemydina, new

Turtles of the Tribe Platysternini usually lacking a well-developed maxilla-postorbital contact seen in the Subtribe Platysternina.

Macroclemys

Subtribe Platysternina Gray, 1870, new rank

Turtles of the Tribe Platysternini having a well-developed maxilla–postorbital contact.

Platysternon
Macrocephalochelys

REFERENCES

Agassiz, Louis

1857. North American Testudinata, vol. 1, pt. 2, pp. 233-452. *In* Contributions to the natural history of the United States, Little, Brown & Co., Boston.

Boulenger, George A.

1889. Catalogue of the chelonians, rhynchocephalians and crocodiles in the British Museum (Natural History). New Edition. London, British Museum (Nat. Hist), 311 pp.

CKHIKVADZE, VIACHESLAV M.

1971. First find of a Tertiary turtle of the family Platysternidae. [Translated from Russian.] Paleontal. Zhur., **1971**, no. 4, pp. 137-139.

CROWSON, R. A.

1970. Classification and biology. New York, Atherton Press, Inc., 350 pp.

ERICKSON, BRUCE R.

1973. A new chelydrid turtle *Protochelydra zangerli* from the Late Paleocene of North America. Scientific Publ. Sci. Mus. Minnesota, n.s., **2,** no. 2, pp. 1-16.

GAFFNEY, EUGENE S.

1972a. The systematics of the North American family Baenidae (Reptilia, Cryptodira). Bull. Amer. Mus. Nat. Hist., **147,** art. 5, pp. 241-320.

1972b. An illustrated glossary of turtle skull nomenclature. Amer. Mus. Nov., no. 2486, pp. 1-33.

In press. Phylogeny and classification of the higher categories of turtles. Bull. Amer. Mus. Nat. Hist., **155,** art. 5, pp. 387-436.

GRAY, JOHN EDWARD

1870. Supplement to the catalogue of shield reptiles in the collection of the British Museum. Part I. Testudinata (tortoises). Brit. Mus. (Nat. Hist.), London, pp. ix-120.

HENNIG, WILLI

1966. Phylogenetic systematics. Univ. Illinois Press, Urbana, 263 pp.

KLUGE, ARNOLD G.

1971. Concepts and principles of morphologic and functional studies, pp. 3-41. *In* Waterman, Allyn J. et al., Chordate structure and function, Macmillan Co., New York.

McDOWELL, SAMUEL B.

1964. Partition of the genus *Clemmys* and related problems in the taxonomy of the aquatic Testudinidae. Proc. Zool. Soc. London, **143,** pp. 239-279.

NELSON, GARETH J.

1973. The higher-level phylogeny of vertebrates. Syst. Zool., **22,** no. 1, pp. 87-91.

PIDOPLICHKO, IVAN G. and B. I. TARASHCHUK

1960. New genus of large-headed (macrocephalous) turtle from the Pontion beds in the environs of Odessa. [In Ukranian with Russian summary.] Zbirn. Prats. Zool. Mus. Akad. URSR, no. 29, pp. 105-110.

SCHAEFFER, BOBB, MAX K. HECHT, and NILES ELDREDGE

1972. Paleontology and phylogeny, vol. 6, pp. 31-46. *In* Dobzhansky, T. et al., eds., Evolutionary biology, Appleton-Century-Crofts, New York.

SCHUMACHER, G. H.

1954. Beiträge zur Kiefermuskulatur der Schildkröten. I. Mitteilung. Wissenschaftliche Zeitschr., Univ. Greifswald, Jahrg. 3, Math.-Naturwiss., pp. 457-518.

1955a. Beiträge zur Kiefermuskulatur der Schildkröten. II Mitteilung. Wiss. Z. Univ. Greifswald, Jahrg. 4, Math.-Natursiss., pp. 501-518.

1955b, Beiträge zur Kiefermuskulatur der Schildkröten, III. Mitteilung. Wiss. Z. Univ. Greifswald, Jahrg. 4, Math.-Naturwiss., pp. 559-587.

Swainson, William

1839. The natural history of fishes, amphibians, and reptiles, or monocardian animals. Vol. 2, pp. vi-452. Longman, Orme, Brown, Green & Longmans, London.

Zangerl, Rainer

1948. The methods of comparative anatomy and its contribution to the study of evolution. Evolution, **2,** pp. 351-374.

Zug, George R.

1971. Buoyancy, locomotion, morphology of the pelvic girdle and hindlimb, and systematics of cryptodiran turtles. Misc. Publ., Mus. Zool., Univ. Michigan, no. 142, pp. 1-98.