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The Side-Necked Turtle Family Chelidae: A Theory of Relationships Using Shared Derived Characters

EUGENE S. GAFFNEY¹

ABSTRACT

The South American and Australian side-necked turtles of the family Chelidae are analyzed using the shared derived character technique of Hennig. The following hypotheses of monophyly are tested using the characters indicated (see fig. 10):

Group 1. Family Chelidae (*Pseudemydura*, *Emydura*, *Elseya*, *Platemys*, *Phrynops*, *Chelus*, *Chelodina*, *Hydromedusa*)

- a. Unusually developed lateral cheek emargination
- b. Loss of quadratojugal
- c. Loss of mesoplastra

Group 2. Subfamily Chelinae (*Emydura*, *Elseya*, *Platemys*, *Phrynops*, *Chelus*, *Chelodina*, *Hydromedusa*)

- a. Anterior frontal process at least partially separating nasals

Group 3. Infracfamily Chelodd (*Platemys*, *Phrynops*, *Chelus*, *Chelodina*, *Hydromedusa*)

- a. Symphyseal suture separating lower jaw rami

- b. Dorsal processes of exoccipitals meet medially above foramen magnum

c. First vertebral scute narrower than second

Group 4. Tribe Chelini (*Phrynops*, *Chelus*, *Chelodina*, *Hydromedusa*)

- a. Lateral margins of parietals distinctly reduced

Group 5. Subtribe Chelina (*Chelus*, *Chelodina*, *Hydromedusa*)

- a. Cervical vertebrae longer than dorsal vertebrae
- b. Medial portions of jugal and postorbital facing more laterally than posteriorly

Group 6. Infratribe Hydromedusad (*Chelodina*, *Hydromedusa*)

- a. Posterolateral process of parietal absent
- b. Extremely reduced horizontal process of parietal
- c. Quadrate-basisphenoid contact
- d. Four claws on forefoot

INTRODUCTION

The purpose of the present paper is to develop a theory of relationships for the side-necked tur-

tles of the family Chelidae. These turtles are found in South America, with about 12 living

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species usually recognized, and are the dominant continental turtles of Australia, where about 14 living species occur. The chelids are a predominantly carnivorous, fresh-water aquatic family that contains some of the strangest turtles (e.g., *Chelus*) as well as some of the rarest (e.g., *Pseudemydura*). There have been few attempts at explicit phylogeny reconstruction for the chelid genera and little osteologic information is available in the literature. My intention here is a phylogeny reconstruction relying primarily on cranial characters.

My method is derived from that of Hennig (1966) and others, and is often termed phylogenetic systematics or cladism. As I see it, this method is the closest approach in systematics to the logical criteria emphasized by Popper (1968) as characterizing science. Popper has argued that the best science is developed in terms of hypothesis formation and test, in which the tests attempt to falsify rather than confirm the hypothesis. In phylogeny reconstruction, hypotheses of relationship are tested by character distributions in which the characters are analyzed in terms of primitive and derived. The analysis consists of a further series of testable hypotheses. Testability, i.e., the potential to criticize and falsify a hypothesis, is the critical feature. The logical aspects of phylogenetic systematics and a summary of the method of using shared derived characters in phylogeny reconstruction are presented elsewhere (Gaffney, In press; Wiley, 1975) and the reader is referred to these works and more general references (Bonde, 1974; Brundin, 1968; Cracraft, 1972, 1974; Eldredge and Tattersall, 1975; Hennig, 1965).

Although fossil chelids are not discussed here, this is due more to the lack of skull material than lack of interest. I am currently engaged in a study of fossil chelids from Australia, including some good skull material of Miocene age. Roger Wood has (in preparation) a study of fossil chelids from South America. Other literature references on fossil chelids may be found in Kuhn (1964) and Mlynarski (1976).

The higher category classification of turtles used here is developed in Gaffney (1975), and the anatomic terminology can be found in Gaffney (1972b).

ABBREVIATIONS

ANATOMICAL

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

INSTITUTIONS

- AMNH, the American Museum of Natural History, New York
 FMNH, Field Museum of Natural History, Chicago
 NMNH, National Museum of Natural History, Smithsonian Institution, Washington, D.C.
 MCZ, Museum of Comparative Zoology, Harvard University, Cambridge
 WAM, Western Australian Museum, Perth

ACKNOWLEDGMENTS

Once again I am grateful to Dr. Samuel B. McDowell for allowing me free access to his work on chelids. Dr. Glen Storr of the Western Australian Museum very kindly lent me specimens of *Pseudemydura*. Dr. Richard Zweifel, the American Museum of Natural History, Dr. George Zug, National Museum of Natural History, Smithsonian Institution, Dr. Hymen Marx, Field Museum of Natural History, and Dr. Ernest Williams, Museum of Comparative Zoology, Harvard University, helped in finding and lending me material in their care. Mr. John Goode of Frankston, Victoria, obtained Australian specimens for me and I appreciate his help.

PREVIOUS WORK

In the section on Basic Taxa (below) I include some of the more important literature references to particular chelid genera, and here I discuss some of the more pertinent literature concerning

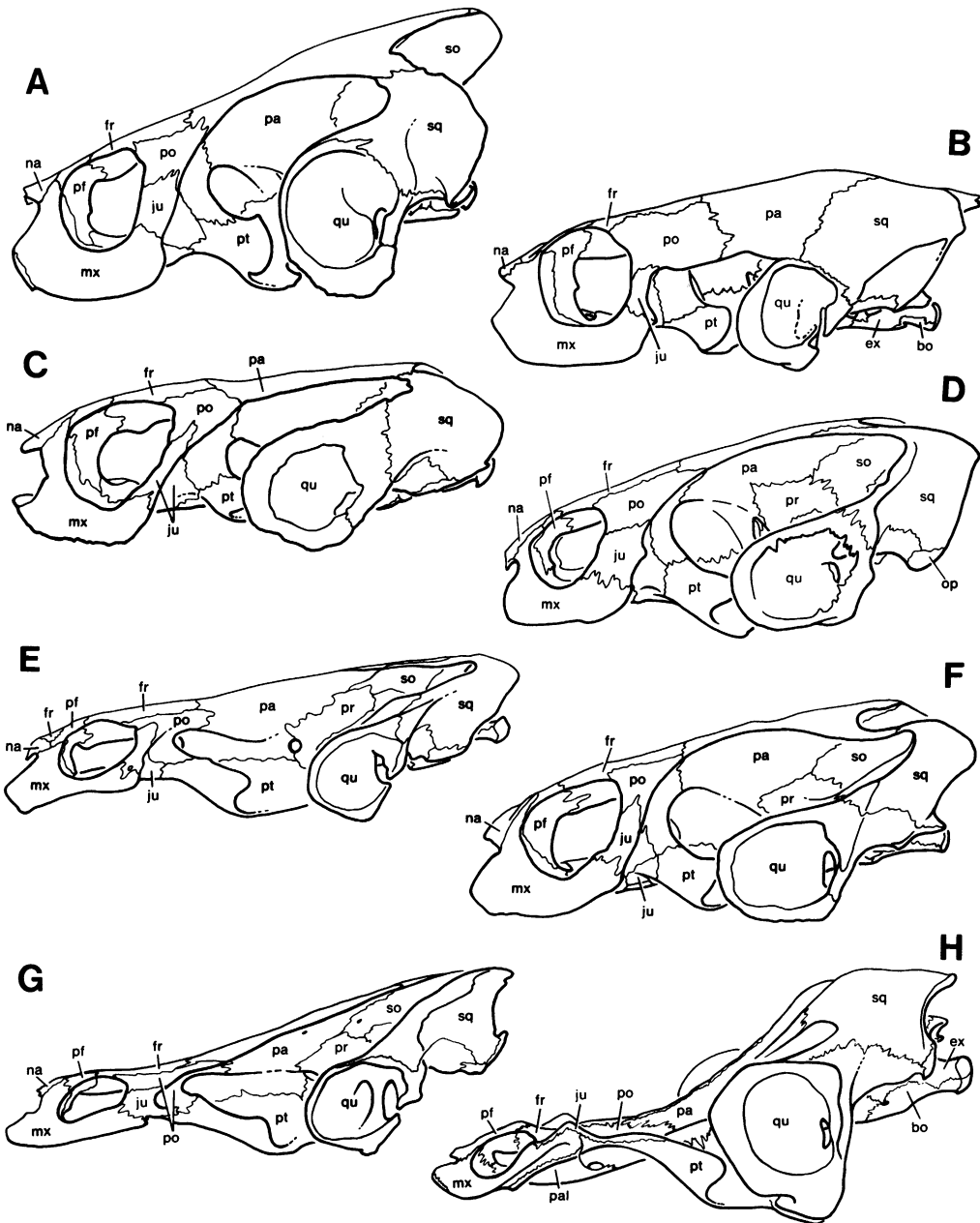


FIG. 1. Lateral views of chelid skulls, measurements are midline condylo-premaxilla length. A. *Emydura macquarrii* (AMNH 110486; 49 mm.). B. *Pseudemydura umbrina* (WAM R29341; 35 mm.). C. *Platemys platycephala* (AMNH 74811; 28 mm.). D. *Phrynops geoffroanus* (AMNH 79048; 60 mm.). E. *Hydromedusa tectifera* (FMNH 31032; 51 mm.). F. *Phrynops (Mesoclemmys) gibba* (FMNH 45669; 37 mm.). G. *Chelodina expansa* (AMNH 108948; 75 mm.). H. *Chelus fimbriata* (AMNH 108955; 104 mm.).

phylogeny and reviews of the whole family. Attempts at phylogeny reconstruction involving all or most of the genera in this family are virtually nonexistent. Boulenger (1889) and Gray (1864) presented "natural" keys, which may be interpreted as phylogenies. Burbidge, Kirsch, and Main (1974) come closest to a chelid phylogeny even though their interests were primarily in the Australian forms. On the basis of a phenetic analysis of biochemical data, they conclude that *Emydura* and *Elseya* have an ancestor in common not found in common with other forms. The three taxa *Pseudemydura*, *Emydura-Elseya*, and *Chelodina* are equally related; that is, they form a trichotomy in their analysis. Furthermore, some South American taxa were studied serologically leading to a conclusion that the Australian species form one monophyletic group and the South American species form another monophyletic group. In general, phenetic studies using morphological data can be resolved into primitive and derived character states (or convergences, etc.) and a phylogenetic study can then deal with the characters. In the case of serology and related techniques numerical methods have been suggested (e.g., Farris, 1972) to analyze phenetic data in terms of primitive and advanced characters. Nonetheless, I am not convinced of the usefulness of this approach and, in any case, Burbidge, Kirsch, and Main (1974) do not present such an analysis. Although they have produced an interesting phylogeny, albeit distinctly at variance with mine, I cannot point out areas of weakness (or strength) or attempt to resolve it with my character distributions.

There are no detailed reviews of the Chelidae, but Boulenger (1889), Gray (1855, 1870), Siebenrock (1909), and Wermuth and Mertens (1961) are the best sources for lists of species and synonyms. The Australian chelids are reviewed by Goode (1967) who presented keys, figured living specimens and types, and provided a synonymy and bibliography (the last suffers from errors, however). Other important studies of the Australian taxa are: Boulenger (1888), Burbidge, Kirsch, and Main (1974), Cogger (1975, distribution maps), de Rooij (1915), Ogilby (1905), Waite (1929), and Worrell (1963); whereas Blackmore (1969), Strauch (1890), and

Werner (1909) provided more limited information.

The South American chelids are more poorly known than the Australian forms and there are no reviews of them. In addition to the works listed above, useful studies dealing with more than one genus are Froes (1957), Luederwaldt (1926), Siebenrock (1904), and Strauch (1890).

BASIC TAXA

The theory of chelid relationships developed here, uses seven generic level taxa as the fundamental units in the hypothesis. The logical nature of this hypothesis requires that these basic taxa be strictly monophyletic, but rigorous tests of monophyly, including studies of species distribution, etc., are beyond the scope of this paper. I do find it necessary, however, to make a partial examination of this problem.

My principle difficulty is the small sample of specimens available for the named genera, and the absence of any cranial material objectively identifiable for many of the species. I have done my best with the material at hand, but I suspect that some of the characters will be subject to more variation than I have indicated. Nonetheless, I doubt that a more extensive examination of specimens will seriously alter the character distributions as I have reported them. In my opinion, a more important source of further tests is in other organ systems, such as jaw musculature, hyoid apparatus, limb musculature, and limb osteology. Only by increasing the number of areas examined can phylogenetic hypotheses be discarded or substantiated.

A. *Pseudemydura*

Figures 1B, 2B, 4B, 6B

Specimens Examined. *Pseudemydura umbrina*, WAM R29341, Twin Swamp Reserve, Western Australia, Australia; *Pseudemydura umbrina*, WAM R21859, Bullsbrook Reserve, Western Australia, Australia; *Pseudemydura umbrina*, WAM R29338, Ellenbrook Reserve, Western Australia, Australia.

Discussion. *Pseudemydura umbrina* has had an interesting taxonomic history, being first named by Siebenrock (1901; figured and described in 1907; these figures are repeated in Williams,

1958) on the basis of one preserved specimen. Subsequently, Glauert (1954) described a form he called *Emydura inspectata*, which Williams (1958) identified as *Pseudemydura* thereby "rediscovering" what is possibly the rarest Recent turtle. Goode (1967) has photographs of living specimens and the Siebenrock type specimen as well as sketches of the skull. Burbidge, Kirsch, and Main (1974) gave good shell and skull figures (including the lower jaw).

I interpret the following features of *Pseudemydura* as autapomorphies; that is, derived features found only in this species:

1. Quadrate-parietal contact (fig. 1B)
2. Supraoccipital laterally expanded in contrast to other Chelidae (fig. 2B)
3. Parietal laterally expanded (fig. 2B)
4. Postorbital ventrolaterally expanded (fig. 2B)
5. Anterior extension of squamosal (figs. 1B, 2B)
6. Prearticular separating coronoid and splenial (Burbidge, Kirsch, and Main, 1974)
7. Medial approximation of maxillae along labial ridge separating or nearly separating premaxillae into anterior and posterior portions (fig. 4B)

The argument that characters 1 through 6 are autapomorphies is developed below in the section on Group 2.

B. *Emydura-Elseya*

Figures 1A, 2A, 4A, 6A, 7

Specimens Examined. *Elseya latisternum*, AMNH 103700, Bulimba Creek, Brisbane, Queensland; *Emydura macquarrii*, AMNH 77637, no data; *Emydura macquarrii*, AMNH 77648, no data; *Emydura macquarrii*, AMNH 11487, South Australia, Australia; *Emydura macquarrii*, AMNH 110486, South Australia, Australia; *Emydura macquarrii*, AMNH 110488, 40 mi. SE Mildura, Victoria, Australia; *Emydura macquarrii*, AMNH 108962, Patho, Victoria, Australia; *Emydura macquarrii*, AMNH 103702, Victoria, Australia; *Emydura krefftii*, AMNH 72406, no data; *Emydura krefftii*, AMNH 108958, Queensland, Australia; *Emydura australis*, AMNH 108957, Darwin area, Northern Territory, Australia.

Discussion. I am treating these two genera as one basic taxon because I have been unable to

differentiate them consistently using cranial characters. However, this may be due to my extremely small sample of adequately identified *Elseya* skulls. Burbidge, Kirsch, and Main (1974) and Goode (1967) used features of the intergular scute, cervical scute, skull cap, snout, and post-orbital skin tuberculation, as well as serology in the case of Burbidge, Kirsch, and Main (*ibid.*) to separate the named species into two genera.

Morphologic information substantiates *Emydura-Elseya* monophyly. *Emydura* and *Elseya* have heavier lower jaws with wider tritulating areas and slightly developed symphyseal "hooks" in contrast to all other chelids, although there is some variation in this feature. This would appear to be derived within the Chelidae but the common possession of heavy lower jaws among pelomedusids weakens the use of this feature. Also, megacephaly seems to be common in *Emydura* and *Elseya* (Goode, 1967) and may occur in other chelids such as *Phrynops*. Nonetheless, at present it seems best to treat *Emydura* and *Elseya* as a strictly monophyletic assemblage.

Other References. Boulenger (1888, 1889; skull figures); Burbidge, Kirsch, and Main (1974; skull figures); Gaffney (1975, skull figures); Goode (1967, skull figures); Gray (1863a, 1863b, 1872); Hoffmann (1890, skull figures); Krefft (1876); Loveridge (1934); Ogilby (1905); Ouwens (1914); Peters and Doria (1878); Siebenrock (1906, 1907, 1912); Vogt (1911).

C. *Platemys*

Figures 1C, 2C, 4C, 6C

Specimens Examined. *Platemys platycephala*, AMNH 74811, no data; *Platemys platycephala*, AMNH 75101, no data; *Platemys platycephala*, FMNH 45659, Loreto, Peru.

Discussion. My sample of *Platemys* skulls consists of three specimens of *P. platycephala*, which show the following autapomorphous features: truncated and reduced crista supraoccipitalis, lateral edges of parietal parallel and orbits relatively large (presumably correlated with small size of adult animals). Again, the absence of skulls identifiable as *P. pallidipectoris*, *P. spixi*, and *P. radiolata* hamper the usefulness of these criteria.

One of the principle shell features used to

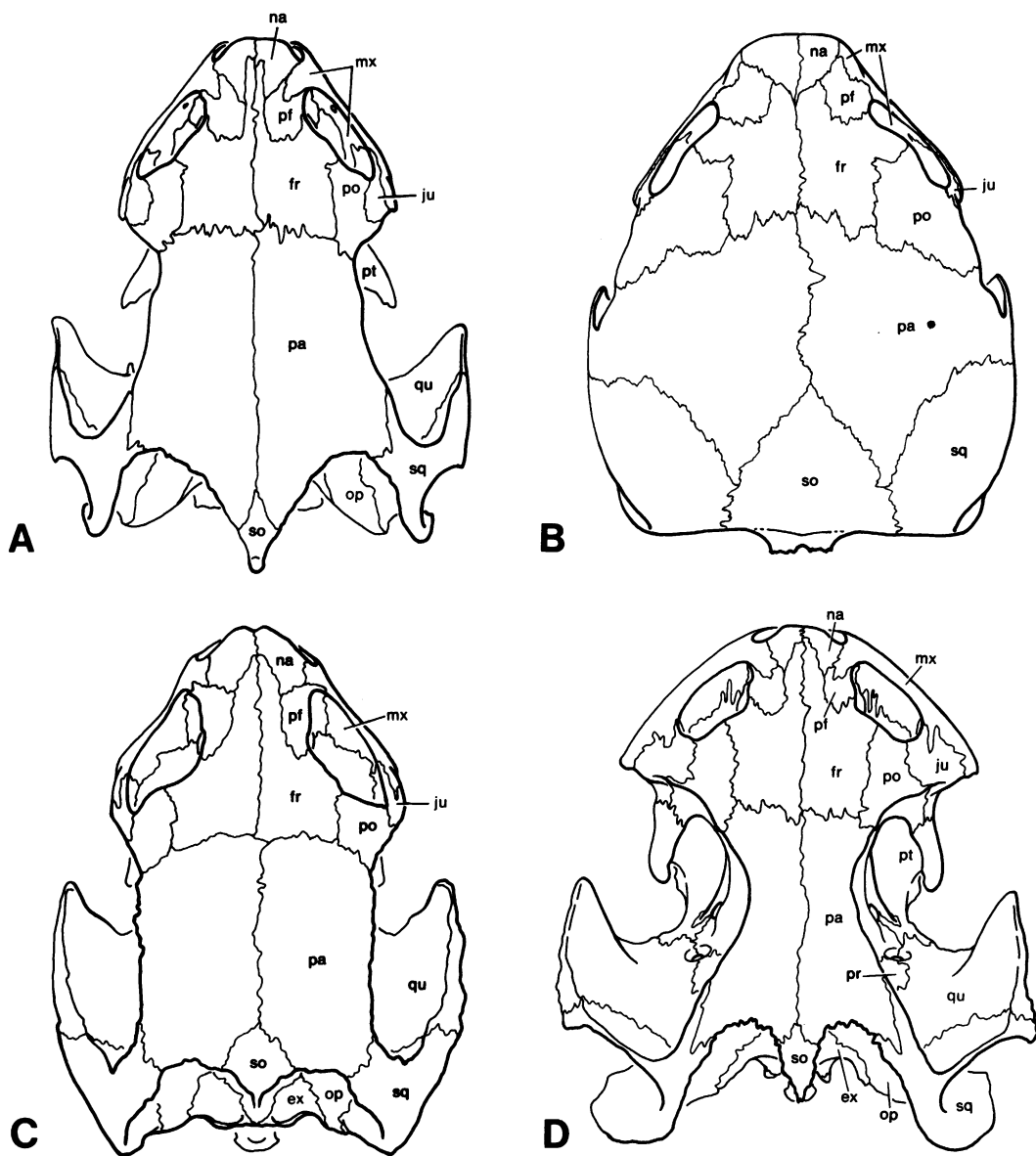


FIG. 2. Dorsal views of chelid skulls. Skull measurements in figure 1. A. *Emydura macquarrii* (AMNH 110486). B. *Pseudemydura umbrina* (WAM R29341). C. *Platemyd platycephala* (AMNH 74811). D. *Phrynops geoffroanus* (AMNH 79048).

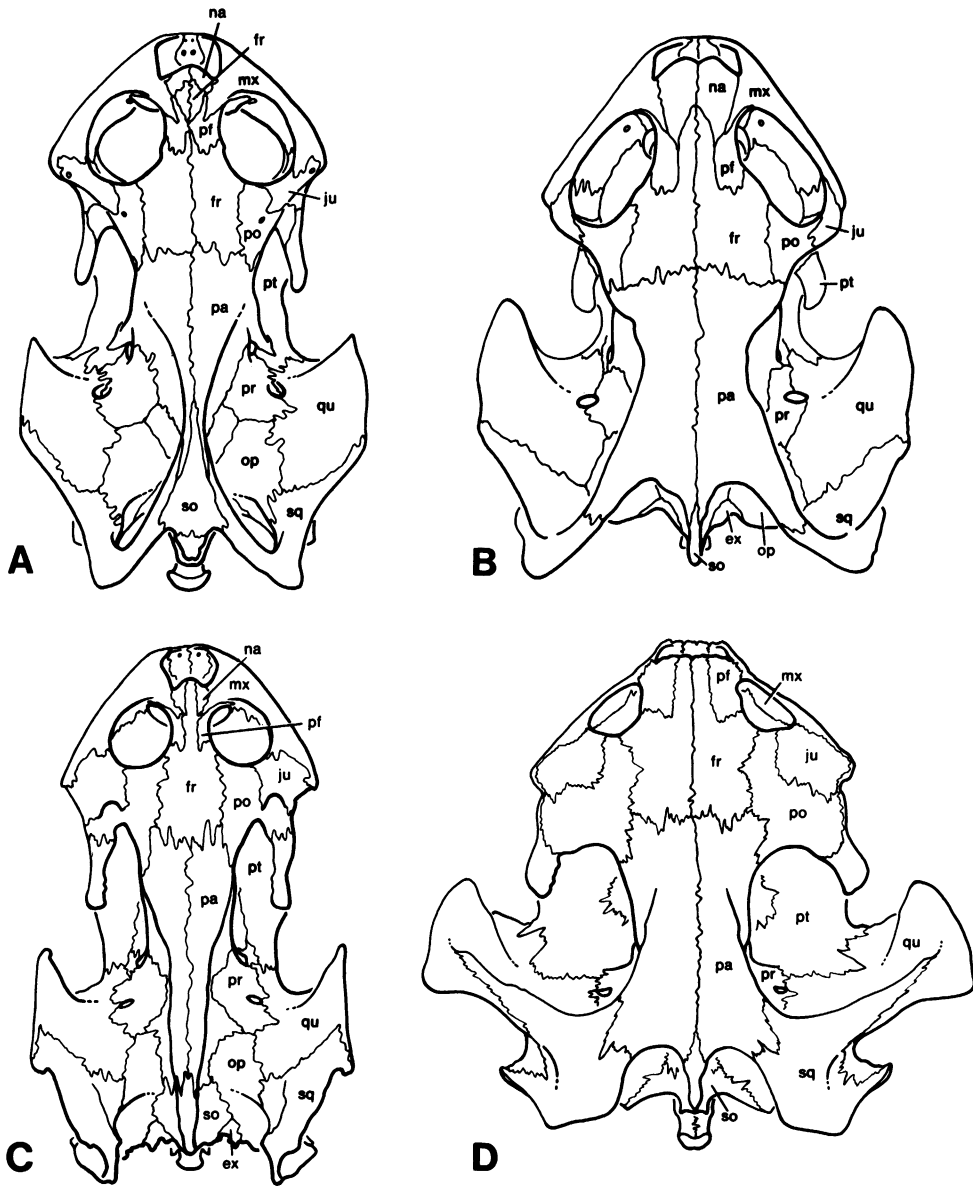


FIG. 3. Dorsal views of chelid skulls. Skull measurements in figure 1. A. *Hydromedusa tectifera* (FMNH 31032). B. *Phynops (Mesoclemmys) gibba* (FMNH 45669). C. *Chelodina expansa* (AMNH 108948). *Chelus fimbriata* (AMNH 108955).

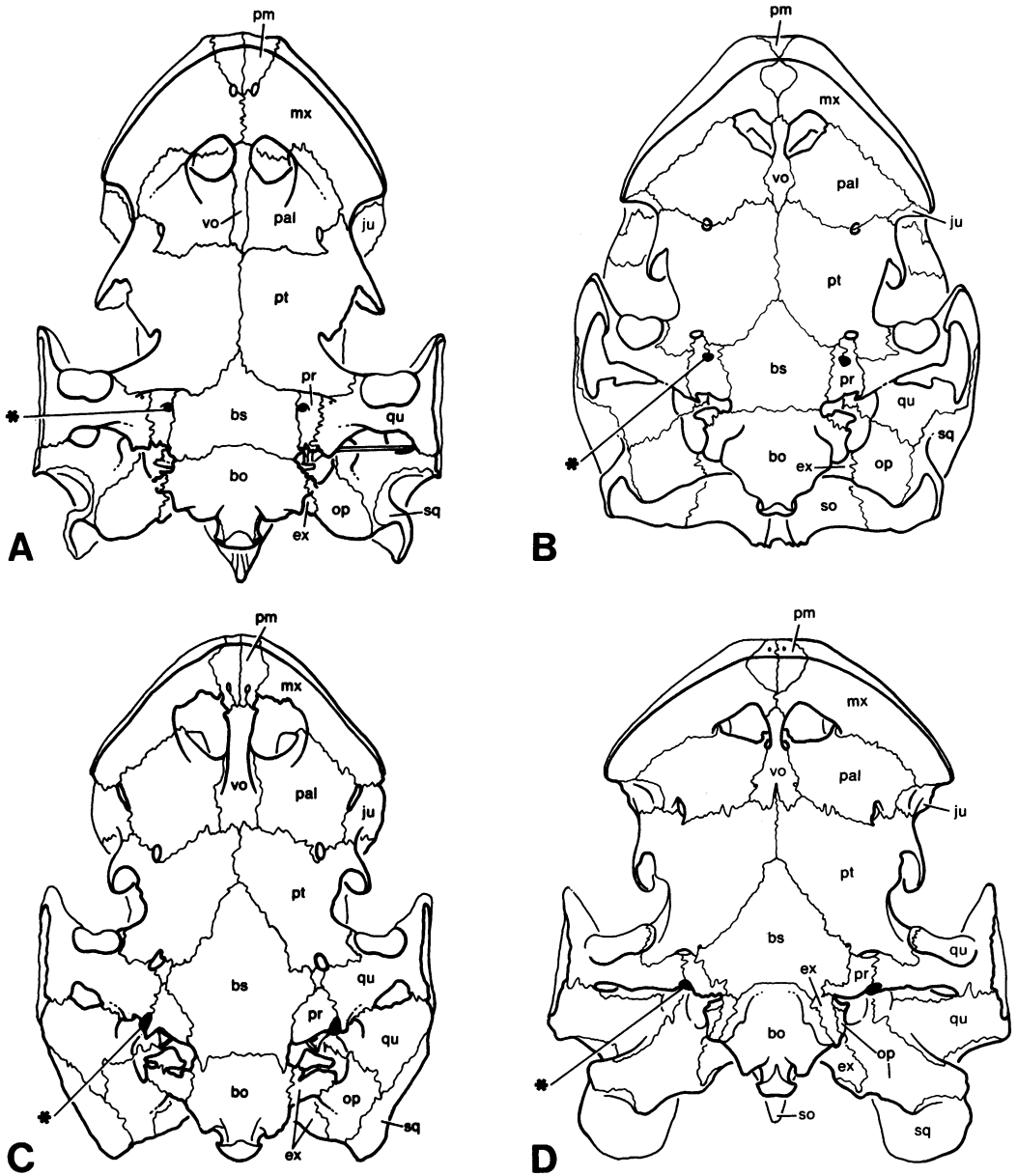


FIG. 4. Palatal views of chelid skulls. Skull measurements in figure 1. Asterisks (*) show position of foramen posterius canalis carotici interni. A. *Emydura macquarrii* (AMNH 110486). B. *Pseudemydura umbrina* (WAM R29341). C. *Platemys platycephala* (AMNH 74811). D. *Phrynops geoffroanus* (AMNH 79048).

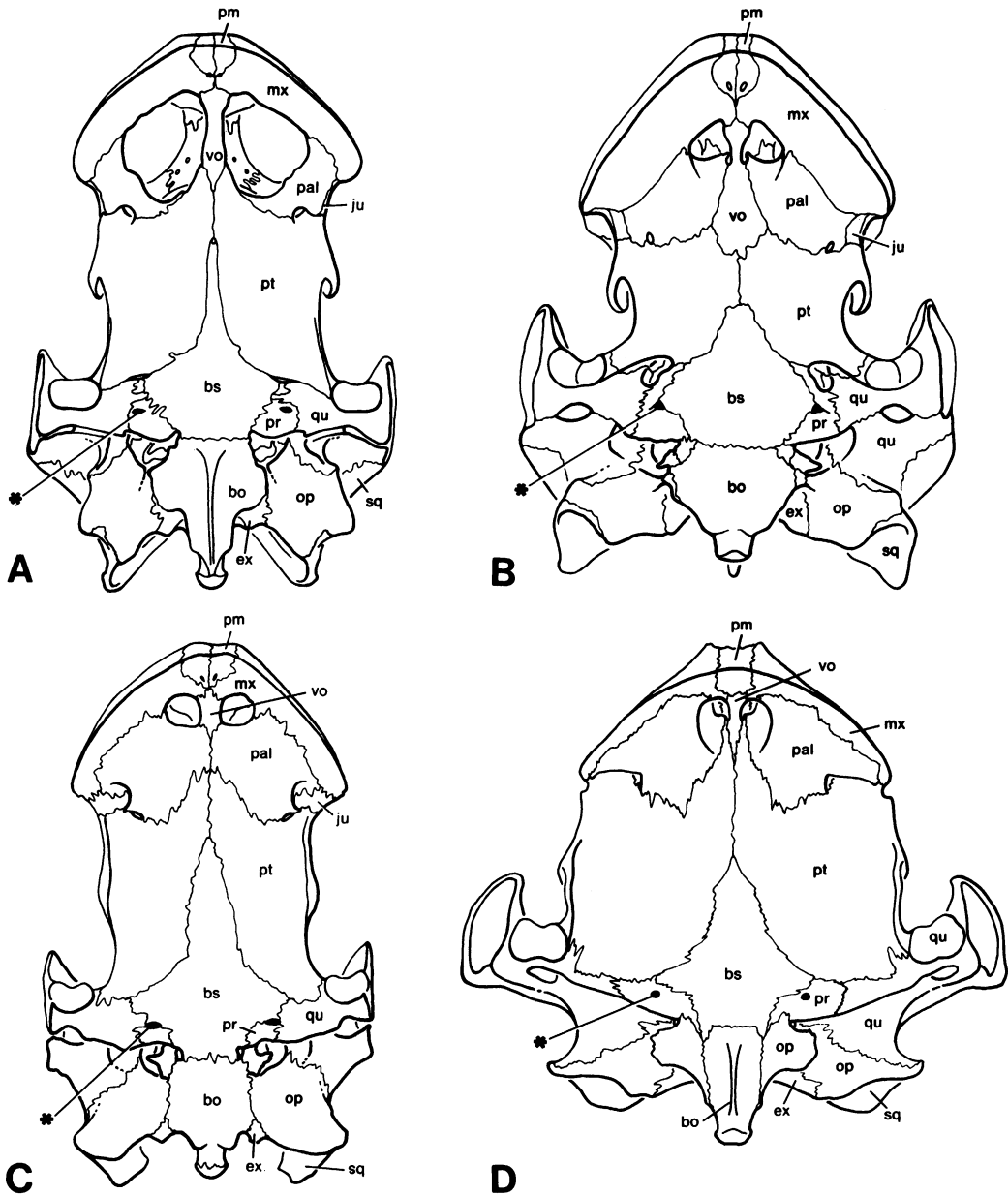


FIG. 5. Palatal views of chelid skulls. Skull measurements in figure 1. Asterisks (*) show position of foramen posterius canalis carotici interni. A. *Hydromedusa tectifera* (FMNH 31032). B. *Phrynops (Mesoclemmys) gibba* (FMNH 45669). C. *Chelodina expansa* (AMNH 108948). D. *Chelus fimbriata* (AMNH 108955).

characterize *Platemys* is the presence of a trough along the carapace midline, but this feature is apparently absent in *Platemys radiolata*, (Freiberg, 1945).

Other References. Dunn (1945); Freiberg (1945, 1947); Froes (1957); Luederwaldt (1926); Medem (1960a); Mertens (1967); Müller (1939); Siebenrock (1897, 1904, skull figures); Wagler (1830).

D. *Phrynops*

Figures 1D, 1F, 2D, 3B, 4D, 5B, 6D, 6F

Specimens Examined. *Phrynops geoffroanus*, AMNH 79048, no data; *Phrynops geoffroanus*, AMNH 58201, no data; *Phrynops geoffroanus*, AMNH 58110, ?Peru; *Phrynops (Batrachemys) nasuta*, AMNH 108908, no data; *Phrynops (Batrachemys) sp.*, AMNH 58123, Iquitos, Peru; *Phrynops (Batrachemys) nasuta*, MCZ 58099; Orinoco River, Venezuela; *Phrynops (Batrachemys) nasuta*, MCZ 1456, Pernambuco, Brazil; *Phrynops (Mesoclemmys) gibba*, FMNH 45669, Yarinacocha, Loreto, Peru; *Phrynops (Mesoclemmys) gibba*, FMNH 45671, Yarinacocha, Loreto, Peru.

Discussion. The species here included in this genus have had a particularly confusing history of generic assignment. Some of the earlier aspects may be obtained from Gray (1855, 1864, 1870). In 1909, the taxa involved were classified by Siebenrock (closely following Boulenger, 1889, and Siebenrock's own work of 1904) as follows:

Rhinemys nasuta
Mesoclemmys gibba
Hydraspis hilarii
Hydraspis geoffroyana
Hydraspis tuberosa
Hydraspis rufipes
Hydraspis wagleri

Stejneger (1909) showed that the type species of *Hydraspis* Bell is *Testudo longicollis* Bell, 1828, and as this species was earlier made the type species of *Chelodina* Fitzinger, 1826, the genus *Hydraspis* is a junior synonym of *Chelodina*. He also argued that *Phrynops* Wagler, 1830, is the correct name for the taxon previously

called *Hydraspis*, and, finding *Rhinemys* Wagler, 1830, to be a synonym of *Phrynops*, erected *Batrachemys* to replace it. Therefore, we find later works, such as Wermuth and Mertens (1961) with the following classification (give or take a few species):

Batrachemys nasuta

Batrachemys dahli (erected by Zangerl and Medem, 1958)

Mesoclemmys gibba

Phrynops geoffroanus (with three subspecies: *geoffroanus*, *hilarii*, *tuberosus*)

Phrynops rufipes

Zangerl and Medem (1958), however, in allusion to a study in progress at that time by Williams and Vanzolini (unpublished), stated that the three genera *Batrachemys*, *Mesoclemmys*, and *Phrynops* were closely related and should be placed in one genus, *Phrynops*, with the three former genera recognized as subgenera. Bour (1973) has argued that even these taxa are not objectively recognizable, but neither he nor Zangerl and Medem (*ibid.*) gave a diagnosis of *Phrynops* in the larger sense. As Bour (*ibid.*) has suggested, the Zangerl and Medem concept of *Phrynops* is essentially the same as that of Gray's (1864) *Hydraspis*, and we appear to have come full circle.

For the purposes of this study I use *Phrynops* in Bour's sense, without subgenera, even though I cannot rigorously support its strict monophyly. I have been unable to find unique derived characters in the skull of *Phrynops* but I have also been unable to find derived characters in common between some of the species in *Phrynops* and *Chelodina*, *Hydromedusa*, or *Chelus*. Therefore, at present I can falsify neither the hypothesis that *Phrynops* is monophyletic nor the hypothesis that it is paraphyletic. Even if *Phrynops* is paraphyletic it will not drastically alter the phylogenetic hypothesis advanced here.

Other References. Albrecht (1976, cranial arteries); Boulenger (1889, skull figures); Dunn (1945); Froes (1957); Gray (1873); Kanberg (1926); Luederwaldt (1926); Medem (1960a, 1960b, 1960c, 1966, 1973); Mertens (1967, 1969, 1970); Müller (1939); Siebenrock (1904, 1905); Zangerl and Medem (1958, skull figures).

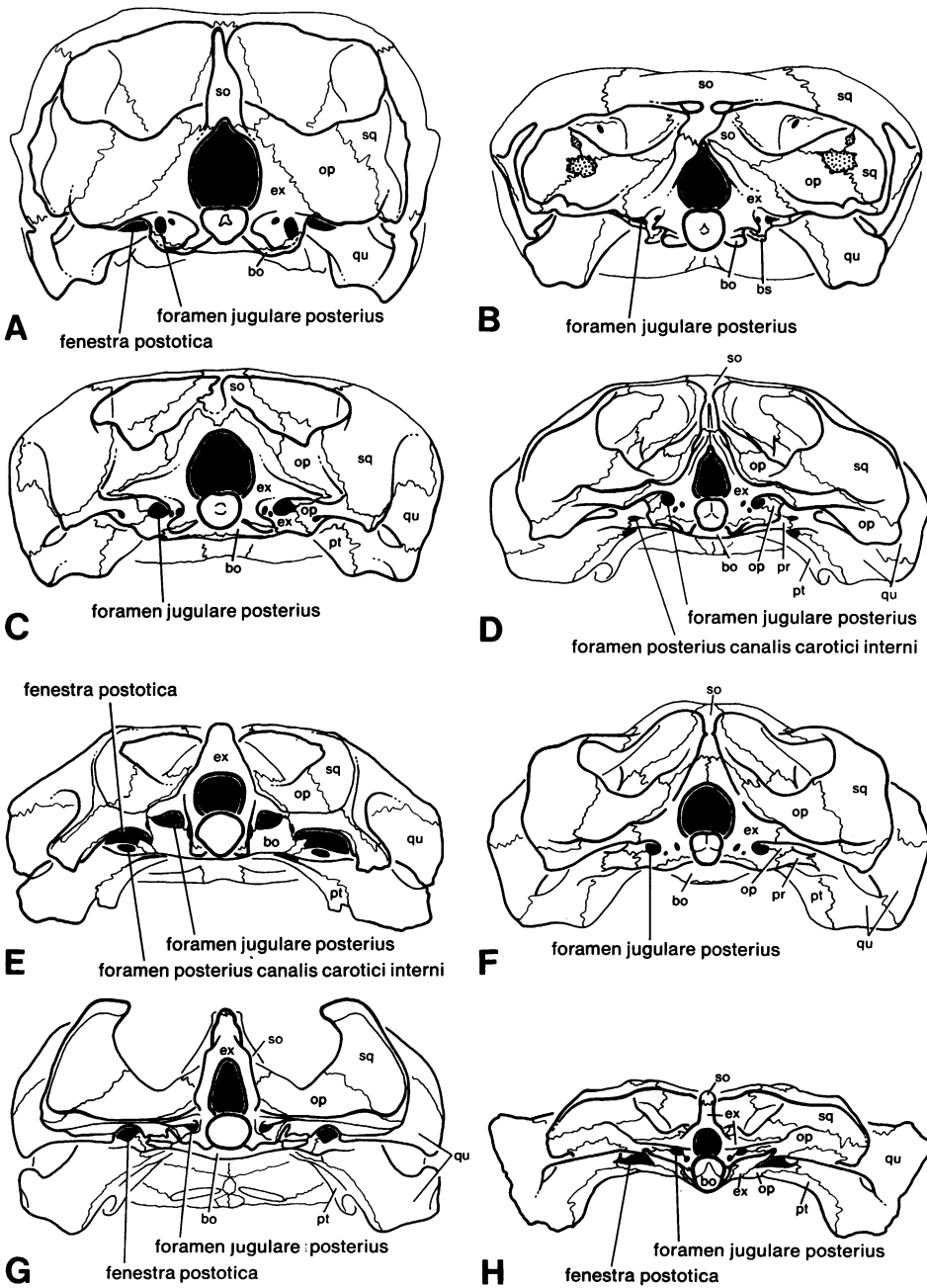


FIG. 6. Occipital views of chelid skulls. A. *Emydura macquarrii* (AMNH 76199). B. *Pseudemydura umbrina* (WAM R29341). C. *Platemys platycephala* (AMNH 74811). D. *Phrynops Geoffroanus* (AMNH 79048). E. *Hydromedusa tectifera* (NMNH 15189). F. *Phrynops (Mesoclemmys) gibba* (FMNH 45669). G. *Chelodina expansa* (AMNH 108948). H. *Chelus fimbriata* (AMNH 108955).

E. *Chelus*

Figures 1H, 3D, 5D, 6H

Specimens Examined. *Chelus fimbriata*, AMNH 108955, no data; *Chelus fimbriata*, AMNH 111962, no data; *Chelus fimbriata*, AMNH 6596, no data; *Chelus fimbriata*, AMNH 43298, no data.

Discussion. Only one Recent species of this genus is usually recognized, but in any case, *Chelus* is riddled with autapomorphies and looks as if it had been run over by a truck. The following cranial features I interpret as unique derived characters for this taxon:

1. Nasals absent (fig. 3D)
2. Prefrontal broadly exposed along dorsal margin of apertura narium externa [narrowly exposed in *Chelodina*] (fig. 3D)
3. Pterygoids extend anteriorly into apertura narium interna and often separate vomer from palatines (fig. 5D)
4. Extreme flattening of skull, particularly in center (fig. 1H)
5. Cavum tympani extended laterally to considerable degree (fig. 3D)
6. Medial processes of jugal and postorbital lie entirely on external surface of skull [see discussion under Group 5] (fig. 3D)
7. Maxilla relatively reduced in exposure on triturating surface so that palatine bears lingual ridge (fig. 5D)

Other References. Boulenger (1889, skull figures); Dunn (1945); Froes (1957); Fuchs (1931, lower jaw figures); Gregory (1946, skull figures); Hoffmann (1890); Luederwaldt (1926); Medem (1960a); Muller (1939); Siebenrock (1897, skull figures); Wagler (1830, skull figures).

F. *Chelodina*

Figures 1G, 3C, 5C, 6G, 8

Specimens Examined. *Chelodina steindachneri*, AMNH 101978, Woodstock, Western Australia, Australia; *Chelodina longicollis*, AMNH 108953, no data; *Chelodina longicollis*, AMNH 108950, no data; *Chelodina longicollis*, AMNH 108947, no data; *Chelodina longicollis*, AMNH

108951, Patho, Victoria, Australia; *Chelodina longicollis*, AMNH 76569, no data; *Chelodina longicollis*, AMNH 108952, Patho, Victoria, Australia; *Chelodina novaeguineae*, AMNH 57589, Mabaduane, Papua, New Guinea; *Chelodina novaeguineae*, AMNH 86547, Armraynald, Queensland, Australia; *Chelodina expansa* (?), AMNH 103699, Bulimba Creek, Brisbane, Queensland, Australia; *Chelodina expansa*, AMNH 108948, Patho, Victoria, Australia; *Chelodina expansa*, AMNH 108949, Patho, Victoria, Australia; *Chelodina rugosa* (?), AMNH 104338, Mt. Burnett, Western Australia, Australia; *Chelodina rugosa*, AMNH 82532, Cape York Peninsula, Queensland, Australia; *Chelodina rugosa*, AMNH 108954, Darwin area, Northern Territory, Australia.

Discussion. *Chelodina* has a series of characters that I am hypothesizing as autapomorphies or unique derived characters.

1. Nasals usually separated by anterior processes of frontals (fig. 3C)
2. Frontals fused along midline (fig. 3C)
3. Temporal bar absent (fig. 3C)
4. Extensive quadrate-basisphenoid contact (fig. 5C)

Characters 1 and 2 are unique in turtles, although the frontal in *Chelus* reaches the margin of the apertura narium externa the nasals are absent in that form. The temporal bar is absent in some cryptodires but the remaining roofing bones are of distinctly different morphology. An extensive quadrate-basisphenoid contact occurs in pelomedusids (e.g., *Podocnemis*) but again, the morphology of the bones involved is inconsistent with the hypothesis that the contacts are homologous. A limited quadrate-basisphenoid contact occurs in *Hydromedusa* and I hypothesize that the limited condition is primitive for *Hydromedusa* and *Chelodina*.

These characters are consistent with strict monophyly of *Chelodina*. Burbidge, Kirsch, and Main (1974) presented serologic data which they conclude also argues for *Chelodina* monophyly.

Rhodin and Mittermeier (1976) gave good descriptions and figures of the skull in *Chelodina siebenrocki* and their new species, *C. parkeri*. They provided a glossary of anatomical terms

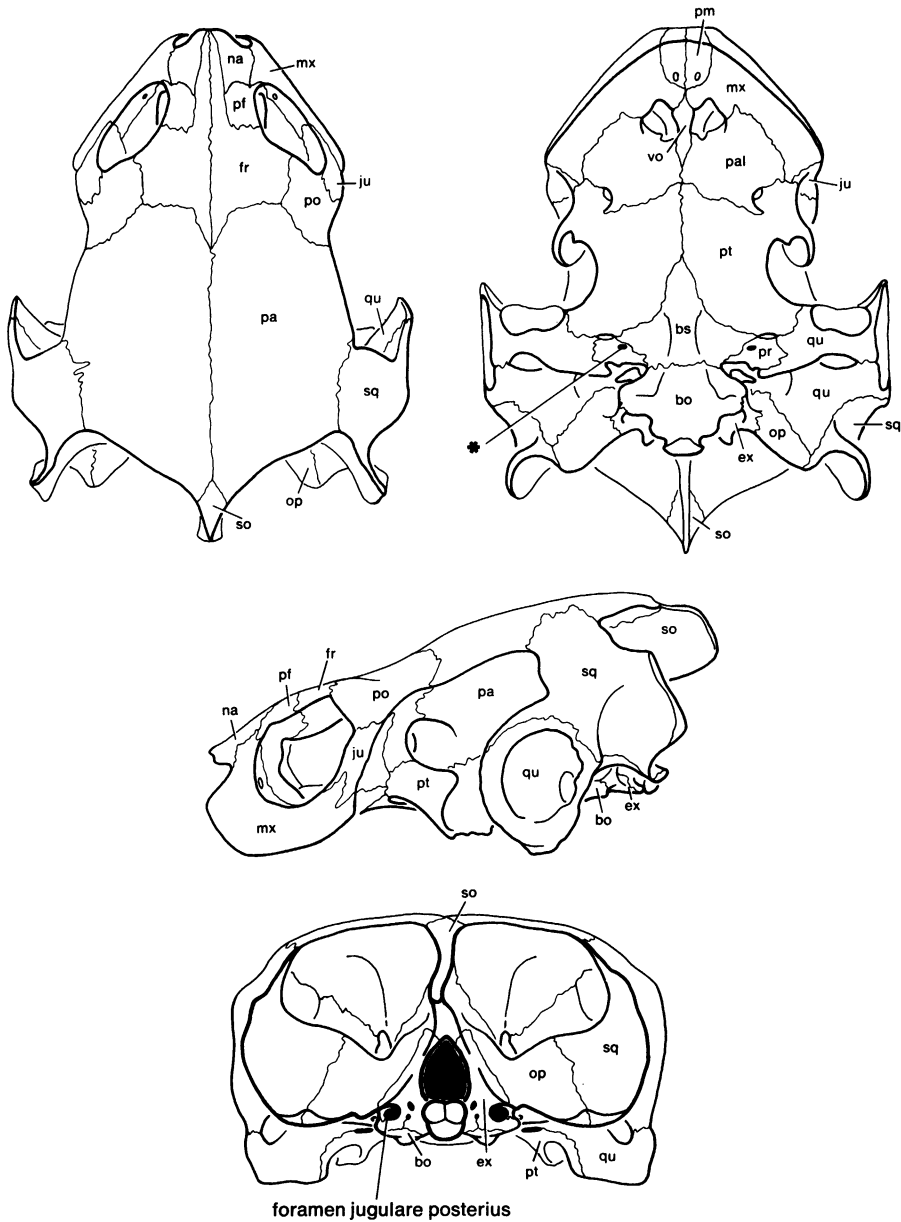


FIG. 7. *Elseyia latisternum* (AMNH 103700; 53 mm.).

used to describe systematically important features.

Other References. Boulenger (1888); Burbridge, Kirsch, and Main (1974, skull figures); Fry (1915); Gaffney (1975, skull figures); Glauert

(1922); Goode (1967, skull figures; 1968); Goode and Russell (1968); Gray (1856, 1869, skull figures); Hoffmann (1890, skull figures); Loveridge (1934); Ogilby (1890, 1905); Schnee (1899); Siebenrock (1897, 1905, 1914, skull fig-

ures); Stejneger (1909); Vestjens (1969); Vogt (1911); Waite (1929, skull figures); Werner (1901); Worrell (1961).

G. *Hydromedusa*

Figures 1E, 3A, 5A, 6E

Specimens Examined. *Hydromedusa maximiliani*, MCZ 2856, Brazil; *Hydromedusa tectifera*, NMNH 15189; *Hydromedusa tectifera*, FMNH 31032.

Discussion. *Hydromedusa* has the following unique derived features:

1. Relatively large bony apertura narium interna formed by reduced ossification of palatine [the fleshy internal narial openings may not be enlarged] (fig. 5A)
2. Prefrontals meet in midline and may overlap anterior processes of frontals so that frontals are exposed anterior and posterior to the prefrontal contact (fig. 3A)
3. The cervical (nuchal) scute is relatively large and separated from the anterior edge of the shell by medial contact of the first pair of marginal scutes (Boulenger, 1889)

The large bony internal nares and the median prefrontal contact occur in no other chelids (although they do occur in many other turtles), and it seems most parsimonious to consider them independently derived in *Hydromedusa* rather than a primitive retention. The shell feature is unique among turtles.

Wood and Moody (1976) provide figures for the shells and descriptions of the shells in *Hydromedusa maximiliani* and *H. tectifera*,¹ as well as shell characters allowing recognition of these two forms.

Other References: Froes (1957); Hay (1908, skull figures); Luederwaldt (1926); Mertens (1967); Müller (1939); Peters (1839, skull figures); Wagler (1830, skull figures).

PHYLOGENETIC HYPOTHESIS

The following sections should be read with the cladogram (fig. 10) in mind. The group numbers refer to numbers on the cladogram. A sum-

¹ Note that the recessed nuchal bone with peripheral bones meeting medially found in *Hydromedusa maximiliani* also occurs in the extinct baenoid *Compsemys* (Gaffney, 1972a) and is not unique to *Hydromedusa* as stated by Wood and Moody.

mary of the shared derived characters may be found in the Abstract. See also table 2 for cranial characters discussed here and in the Basic Taxa section.

GROUP 1—FAMILY CHELIDAE

Table 1 is a comparison of Pelomedusidae and Chelidae using a series of characters that test monophyly for both families. I have elsewhere (Gaffney, 1975) argued that pleurodires are strictly monophyletic, and that discussion should be consulted. I am including Recent and fossil taxa to the extent that they are available.

The chelids have the following synapomorphies or shared derived characters: (1) Unusually developed lateral cheek emargination; (2) loss of quadratojugal; (3) loss of mesoplastra.

Although *Pseudemydura* has relatively less cheek emargination than the other chelids it still differs strongly from pelomedusids in the shape and number of bones bordering the emargination. Also, there is reason to think that the extensive skull roof in *Pseudemydura* is derived for chelids and that the condition in *Emydura* is the primitive one for chelids. The parietals, squamosals, postorbitals, and supraoccipitals of *Pseudemydura* are different in their extension and shape not only from other chelids but also from pelomedusids. If the *Pseudemydura* pattern were primitive, one would expect to find it in pelomedusids or cryptodires.

A further aspect of the emphasis in chelids on cheek emargination is the loss of the quadratojugal in all members of this family. Even *Pseudemydura*, a form possessing a well-developed temporal roof, lacks a quadratojugal, further suggesting that it evolved from a more emarginate ancestor. Some species of *Cuora*, *Hieremys*, *Geoemyda*, and *Terrapene* also lack a quadratojugal, and in these forms it appears to be associated with well developed cheek emargination.

Chelids lack mesoplastra, the presence of which is presumably primitive for pleurodires. Although mesoplastra were lost independently within the cryptodires, there is no evidence that this has happened more than once within the pleurodires.

GROUP 2—SUBFAMILY CHELINAE

Pseudemydura has a number of unique features but only one of them would appear to be

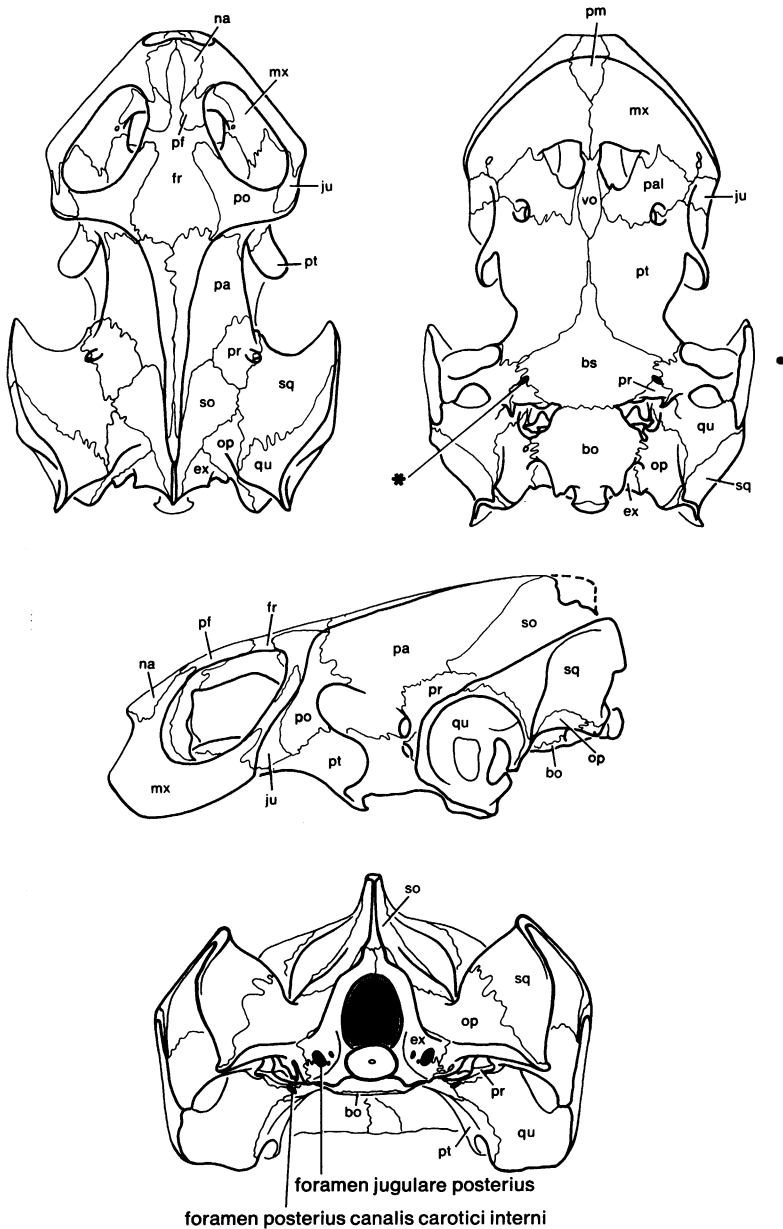


FIG. 8. *Chelodina novaeguineae* (AMNH 57589; 41 mm.).

primitive for the Chelidae. In all other chelids the frontal has a process that extends anteriorly (with the other frontal) along the median suture to partially separate the nasals. In *Pseudemydura* (figs. 2, 3) the nasals slightly separate the frontals and there is only a short anterior process on the

frontal. No other living turtles possess nasals but in fossil turtles (baenoids, toxochelyids, plesiochelyids, chelosphargine protostegids, *Solnhofia*, and *Proganochelys*) that do have nasals, the frontals do not separate the nasals. Therefore, the condition in all chelids except *Pseudemydura*

TABLE 1
A Comparison of the Pelomedusidae and Chelidae
(Including information on Recent and fossil forms.)

Character	Pelomedusidae	Chelidae
1. Nasals	absent	present (except in <i>Chelus</i>)
2. Prefrontals	meet in midline	do not meet in midline (except in <i>Hydromedusa</i>)
3. Posterior temporal emargination	varies from virtually absent (e.g., <i>Dacquemys</i>) to extensive (e.g., <i>Pelomedusa</i>)	usually poorly developed with persistent squamosal-parietal contact (except in <i>Chelodina</i>)
4. Cheek (lateral temporal emargination)	variable, but never developed to the extent seen in Chelidae	developed to an unusual degree with only a parietal-squamosal bar remaining
5. Quadratojugal	present	absent
6. Triturating surface	usually broader	usually narrower
7. Vomer	usually absent	present
8. Splenial	absent	present
9. Mesoplastra	present	absent
10. Cervical (nuchal) scute	absent	present (except in most <i>Eleya</i> and as an infrequent variation)
11. Cervical vertebrae ^a	second biconvex	fifth and eighth biconvex

^a(Williams, 1950)

would appear to be derived for pleurodires and a useful test for monophyly of the non-*Pseudemydura* chelids.

I am interpreting the other unique features of *Pseudemydura* as autapomorphies, that is, derived characters found only in this species and, therefore, not useful in phylogeny reconstruction.

This particular hypothesis, namely that *Pseudemydura* is the sister taxon to the other chelids is perhaps the weakest aspect of my chelid phylogeny, and I would like to discuss some alternatives at this point. One alternative (fig. 9A) would have *Emydura* and *Pseudemydura* as sister taxa, that is, with an ancestor in common not in common with any other turtle. However, *Pseudemydura* and *Emydura* have few unique characters in common. The cervical vertebrae (particularly the anterior ones) of these two genera do have zygapophyses that are more widely separated than in other chelid genera but this feature is presumably primitive for pleurodires and quite unsatisfactory for corroborating monophyly.

Similarly the second alternative (fig. 9B) also fails from the lack of a derived character in common between *Pseudemydura* and all chelids except *Emydura*.

My contention that *Pseudemydura* is the sister taxon to all other chelids should not be thought of as an argument that all of its morphology is primitive. The nasal-frontal morphology does seem primitive, but other distinctive features of the skull roof seem to be autapomorphies or advanced features unique to this species. The extensive temporal roof of *Pseudemydura* is best interpreted as a unique derived condition for chelids rather than a primitive one. In fact, comparison with pelomedusids and cryptodires suggests to me that the *Emydura* type of temporal roof with an extensive lateral or cheek emargination and a shallow posterior emargination is probably primitive for chelids. The absence of a quadratojugal in *Pseudemydura* is consistent with a hypothesis of expansion of the parietals, postorbitals, and supraoccipital into the emarginated areas. In other words, my hypothesis of relationships

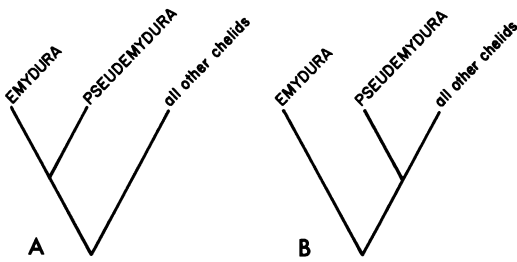


FIG. 9. Alternate hypotheses relating *Emydura*, *Pseudemydura*, and remaining chelids. A third, but preferred alternative, is presented in figure 10. See text for discussion.

would have the primitive chelid possessing most of the features of *Emydura* except the nasal-frontal morphology in which it would resemble *Pseudemydura*.

In the lower jaw of *Pseudemydura* the prearticular extends anteriorly to separate or nearly separate the coronoid and splenial (Burbidge, Kirsch, and Main, 1974, p. 389). In all other chelids the coronoid and splenial have an extensive contact. Few turtles retain a splenial, but in those that do (i.e., *Solnhofia*, baenids, *Plesiochelys*), the coronoid and splenial have a well-developed contact. Therefore, the prearticular extension in *Pseudemydura* is best interpreted as a unique derived character.

GROUP 3—INFRAFAMILY CHELODD

Platemys, *Phrynops*, *Chelus*, *Chelodina*, and *Hydromedusa* all have a symphyseal suture separating the two lower jaw rami. *Pseudemydura* and *Emydura* have the rami fused as do all other turtles except for *Hesperotestudo*, *fide* Bramble, [MS], whereas most reptiles have the rami separated. The appropriate out-group comparison must be with cryptodires rather than other reptiles and I conclude that separate rami are a derived feature corroborating common ancestry of *Platemys*, *Phrynops*, *Chelus*, *Chelodina*, and *Hydromedusa*.

Another feature with this distribution involves the dorsal processes of the exoccipitals (fig. 6). In the five genera indicated these dorsal processes extend dorsomedially to meet each other in a sagittal suture above the foramen magnum and prevent the usual exposure of the supraoccipital

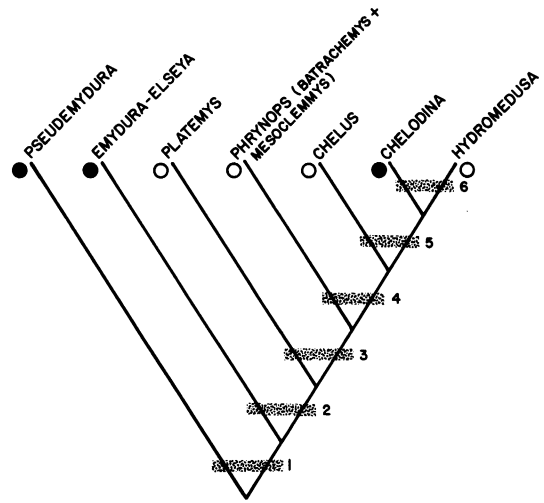


FIG. 10. A theory of relationships of the chelid turtles. The numbers and associated bars refer to groups and character distributions discussed in the text (see Abstract for list). The solid black circles are Australian genera, the open circles South American.

on the dorsal margin of the foramen. In *Emydura* and *Pseudemydura* the exoccipitals do not meet, although they very nearly do so in *Pseudemydura*.

As noted by Boulenger (1889), *Emydura* and *Elseya* have the first vertebral scute narrower than the second, whereas the other chelids have the first vertebral wider than the second. *Pseudemydura* (unknown to Boulenger) also has the first vertebral scute narrower than the second, giving this character the same distribution as the two characters discussed above. A comparison of this condition with pelomedusids unfortunately does not allow a useful test of polarity (primitive vs. derived). Pelomedusids have both conditions although *Pelusios* and *Pelomedusa*, forms that I would consider as generally plesiomorphic pelomedusids, have the narrower first vertebral scute. In any case, the character does not falsify the hypothesis advanced here.

GROUP 4—TRIBE CHELINI

In *Phrynops*, *Chelus*, *Chelodina*, and *Hydromedusa* the lateral margins of the parietals are distinctly reduced in comparison to the degree of

emargination seen in *Emydura* and *Platemys* (figs. 2, 3). I interpret this more emarginate condition as derived for the four taxa indicated and suggest that this is consistent with the hypothesis that they are strictly monophyletic. A reduced squamosal-parietal arch also characterizes this group, except *Chelus*.

The above four genera also differ from other chelids in generally having neurals; the other genera usually lack them (table 3; see also Boulenger, 1889 for figures). *Chelodina* has neurals in only one species, *C. oblonga* (Burbidge, Kirsch, and Main, 1974), however. The presence of neurals would presumably be primitive and their absence derived, making this character distribution an important contradiction to my hypothesis. Nonetheless, I am concluding that it is more par-

simonious to accept my hypothesis and reject the neural bone test because the latter is only one character, whereas my hypothesis suggests several. The acceptance of neural absence as being consistent with strict monophyly of *Pseudemydura*, *Emydura-Elseya*, and *Platemys* requires a number of *ad hoc* hypotheses to invoke character convergence. The rejection of the neural features requires the acceptance of one of the following *ad hoc* hypotheses: (1) the absence of neurals is a primitive feature for chelids and the presence of neurals in the Tribe Chelini (Group 4) is an example of convergence, or (2) the three generic level taxa lacking neurals lost them independently. Neither hypothesis is supported by other tests and this remains an important problem area.

TABLE 2
Cranial Features of Chelid Genera

	<i>Emydura</i> &		<i>Platemys</i>	<i>Phrynops</i>	<i>Chelus</i>	<i>Chelodina</i>	<i>Hydromedusa</i>
	<i>Pseudemydura</i>	<i>Elseya</i>					
1. Nasals	present	present	present	present	absent	present	present
2. Anterior process of frontal	absent	present	present	present	present	present	present
3. Nasals completely separated by anterior frontal process	no	no	no	no	nasals absent	yes	no
4. Prefrontals exposed along dorsal margin of aperturarium externa	no	no	no	no	broadly	narrowly	no
5. Prefrontals meet in midline so that frontals are exposed anterior and posterior to prefrontal contact	no	no	no	no	no	no	yes

TABLE 2 — (Continued)

	<i>Emydura</i> &						
	<i>Pseudemydura</i>	<i>Elseya</i>	<i>Platemys</i>	<i>Phrynops</i>	<i>Chelus</i>	<i>Chelodina</i>	<i>Hydromedusa</i>
6. Frontals fused	no	no	no	no	no	yes	no
7. Dorsal portion of postorbital	large	small	small	small	small	small	small
8. Temporal arch	very extensive; formed by parietal, squamosal and supraoccipital	moderate; formed by squamosal and parietal	moderate; formed by squamosal and parietal	moderate; formed by squamosal and parietal	moderate; formed by squamosal and parietal	absent	very slender; formed by squamosal and supraoccipital
9. Skull flattened	no	no	no	no	extreme	moderate	moderate
10. Dorsal (horizontal) portion of parietal	broadly covers adductor fossa	covers central area of adductor fossa but not lateral area	covers central area of adductor fossa but not lateral area	covers little of adductor fossa but still present (although greatly reduced in some)	covers little of adductor fossa	absent; covers none of adductor fossa	absent; covers none of adductor fossa
11. Lateral edges of parietals	sub-parallel but laterally extensive	tapering anteriorly	parallel	wasp-waisted	wasp-waisted	tapering posteriorly, greatly reduced	tapering posteriorly, greatly reduced
12. Supraoccipital-parietal contact	present	absent	absent	absent	absent	absent (temporal bar absent)	present
13. Quadrate-parietal contact	present	absent	absent	absent	absent	absent	absent
14. Dorsal horizontal portion of supraoccipital	broadly expanded	not expanded	slightly expanded	not expanded	not expanded	not expanded	slightly expanded
15. Crista supraoccipitalis	does not extend beyond foramen magnum	extends beyond foramen magnum and condylus occipitalis	more reduced than in any other chelid, does not extend beyond foramen magnum	extends beyond foramen magnum and condylus occipitalis	does not extend beyond foramen magnum	does not extend beyond foramen magnum	does not extend beyond foramen magnum

TABLE 2 - (Continued)

	<i>Emydura</i> &		<i>Platemys</i>	<i>Phrynops</i>	<i>Chelus</i>	<i>Chelodina</i>	<i>Hydromedusa</i>
	<i>Pseudemydura</i>	<i>Elseya</i>					
16. Medial portions of jugal and postorbital facing more laterally than posteriorly	no	no	no	no	yes, entirely on external surface of skull	yes	yes
17. Dorsal processes of exoccipitals meet above foramen magnum	no	no	yes	yes	yes	yes	yes
18. Cavum tympani extended laterally	no	no	no	no	yes	no	no
19. Maxilla reduced in exposure on triturating surface so that palatine bears lingual ridge	no	no	no	no	yes	no	no
20. Medial maxillary contact dividing premaxillae longitudinally	yes	no	no	no	no	no	no
21. Vomer-palatine contact	yes	yes	yes	yes	no, due to anterior pterygoid processes reaching vomer	yes	no, due to enlarged apertura narium interna reducing palatine
22. Large bony apertura narium interna formed by reduction of palatines	no	no	no	no	no	no	yes

TABLE 2 - (Continued)

	<i>Emydura</i> &						
	<i>Pseudemydura</i>	<i>Elseya</i>	<i>Platemys</i>	<i>Phrynops</i>	<i>Chelus</i>	<i>Chelodina</i>	<i>Hydromedusa</i>
23. Quadrate-basisphenoid contact	absent	absent	absent	absent	absent	extensive	limited
24. Symphyseal suture separates lower jaw rami	no	no	yes	yes	yes	yes	yes
25. Relatively massive mandibles with symphyseal "hooks"	absent	present	absent	absent	absent	absent	absent
26. Prearticular separates or nearly separates coronoid splenial	yes	no	no	no	no	no	no

GROUP 5—SUBTRIBE CHELINA

Boulenger (1889, p. 207) divided the "Chelydidae" into two sections: "I. Neck longer than the dorsal vertebral column. . . ." and "II. Neck shorter than the dorsal vertebral column. . . ." and this distinction, as emphasized by Goode (1967) and Burbidge, Kirsch, and Main (1974) still has usefulness for systematists. The extremely long cervical vertebrae of *Chelus*, *Chelodina*, and *Hydromedusa* may be hypothesized as a shared derived character testing the monophyletic nature of this group. In all other chelids the cervicals are shorter than the length of the vertebrae attached to the carapace and, as this latter condition is found in nearly all other turtles (as far as I know), it is presumably primitive.

Another feature found only in *Chelus*, *Chelodina*, and *Hydromedusa* involves the jugal and postorbital bones (figs. 1, 2, 3).¹ In pleurodires

¹Rhodin and Mittermeier (1976) described the jugal and postorbital areas in *Chelodina* and developed a useful terminology for it. Their figures 4 and 6 should be consulted as an aid to identification.

the jugal along with the postorbital make up the characteristic postorbital wall found in this group (Gaffney, 1975). The jugal usually forms the more lateral portion of the wall, whereas the postorbital forms the more medial area. As in cryptodires the jugal of pleurodires may reach the palatine but there is always a strong contact with the anterior edge of the pterygoid, presumably to aid in support of the uniquely pleurodiran processus trochlearis pterygoidei. In the primitive condition both bones consist of two portions, a medial section exposed behind the fossa orbitalis and forming the front of the fossa temporalis inferior, and a lateral portion exposed on the external surface of the skull. This situation occurs in pelomedusids, which is the basis for considering it primitive. It also occurs in *Emydura*, *Pseudemydura*, *Platemys*, and *Phrynops*. In *Chelus*, *Chelodina*, and *Hydromedusa*, however, the medial portion, which is covered by musculature (except in *Chelus*, see below), is turned outward to face somewhat more laterally rather than more posteriorly as in other chelids (*Chelodina novaeguineae*, fig. 8, is less like the other forms of *Chelodina* and more like

TABLE 3
Postcranial Features of Chelid Genera

	<i>Pseudemydura</i>	<i>Emydura</i>	<i>Eseya</i>	<i>Platemys</i>	<i>Phrynops</i>	<i>Chelus</i>	<i>Chelodina</i>	<i>Hydromedusa</i>
1. Cervical vertebrae longer or shorter than dorsal vertebrae	shorter	shorter	shorter	shorter	shorter	longer	longer	longer
2. Cervical (nuchal) scute	small and marginal	small and marginal	usually absent	small and marginal	small and marginal	small and marginal	small and marginal	large and separated from shell margin
3. Neural bones	absent	absent	absent	absent	variable, four to six	seven	variable, zero to eight	seven
4. Intergular scute entirely separating gular scutes	yes	yes	yes	yes	yes	no, gulars meet posteriorly ^a	no, gulars meet anteriorly	yes
5. Intergular scute entirely separating humeral scutes and anterior portion of pectoral scutes	yes	no	no	no	no	no	yes	no
6. Claws on forefoot	five	five	five	five	five	five	four	four
7. First vertebral scute wider or narrower than second vertebral scute	narrower	narrower	narrower	wider	wider	wider	wider	wider

^aExcept in fossil *Chelus* reported by Wood (1976).

Emydura, but I interpret this as a secondary condition). *Chelus*, on the other hand, is extreme in its degree of rotation of the medial portions of the jugal and postorbital. The medial areas in *Chelus* lie entirely on the surface of the skull, are not covered by musculature, and have no demarcation between medial and external surfaces. This condition of *Chelus* I interpret as uniquely derived or autapomorphic, as it does not occur in any other turtle.

It is interesting to note that Wood (1976) has recently described a Miocene *Chelus*, *C. colombianus*, which differs from *C. fimbriatus* in having an intergular enclosed by gulars (one individual apparently has an extra set of gulars) much as in *Chelodina*. This suggests the hypothesis that an enclosed intergular may be primitive for *Chelodina*, *Hydromedusa*, and *Chelus*. In any case, either the enclosed intergular evolved twice, or the open intergular evolved twice.

GROUP 6—INFRA TRIBE HYDROMEDUSAD

The genera *Chelodina* and *Hydromedusa* are very similar in skull morphology. They both have relatively long, thin, and flat skulls, although *Chelodina novaeguineae* (fig. 8) is deeper than other *Chelodina*. Both taxa have extremely reduced temporal roof coverings and a markedly narrow parietal area between the temporal fossae (figs. 2, 3). The interorbital distance is narrower than in other chelids and the orbits face dorsally to a greater extent than a flattened form such as *Chelus*. The posterolateral process of the parietal, seen in other chelids (except *Pseudemydura*, apparently in coincidence with other unique features of the temporal roof) are absent in *Hydromedusa* and *Chelodina*. *Chelodina* is the only chelid to entirely lack a temporal bar of some sort, whereas in *Hydromedusa* an anteromedial

process of the squamosal reaches the parietal and the latter bone has no lateral component in this region.

Chelodina and *Hydromedusa* also usually have a quadrate-basisphenoid contact, usually ventral to the prootic, but always leaving some of that bone exposed (figs. 4, 5). The contact is well developed in *Chelodina* but limited in *Hydromedusa*, barely taking place in some instances. My sample of *Hydromedusa* (three skulls) is too limited to determine variation of this feature, but I would not be surprised to see the contact absent in some specimens. Nonetheless, there are a number of unique features in common between *Hydromedusa* and *Chelodina* and I hypothesize that they are a strictly monophyletic group with respect to other chelids.

As noted by Boulenger (1889) *Chelodina* and *Hydromedusa* have four claws on their forefeet rather than five as in all other chelids and pelomedusids. I regard this as a derived feature also.

CLASSIFICATION

In my opinion, a classification should be a redundant reflection of a phylogenetic hypothesis. Further discussion of this point of view may be found in Gaffney (1975, In press) and McKenna (1975). Although stability is often considered an important quality of classifications, I believe that it is often a spurious and misleading indication of the attainment of phylogenetic "truth." All of our notions about phylogeny are hypotheses that could be wrong; they can never be proved correct. If a classification is to have wide-ranging biologic usefulness, it must be susceptible to change. The classification presented here is as unstable as the phylogenetic hypothesis presented here.

CLASSIFICATION OF THE CHELID TURTLES

- Infraorder Pleurodira (Cope, 1868b)
 Family Pelomedusidae Cope, 1868a
 Family Chelidae¹ Gray, 1825
 Subfamily Pseudemydurinae, new
 Pseudemydura
 Subfamily Chelinae Gray, 1825, new rank
 Infrafamily Emydurodd,² new
 Emydura
 Elseya
 Infrafamily Chelodd Gray, 1825, new rank
 Tribe Platemini, new
 Platemys
 Tribe Chelini Gray, 1825, new rank
 Subtribe Hydraspina³ Bonaparte, 1838, new rank
 Phrynops
 Subtribe Chelina Gray, 1825, new rank
 Infratribe Chelad⁴ Gray, 1825, new rank
 Chelus
 Infratribe Hydromedusad, new
 Chelodina
 Hydromedusa

¹The family name of this group of turtles has been spelled in a number of ways but most commonly Chelyidae. However, I am here following Williams (1950) and Wermuth and Mertens (1961), among others, in the use of Chelidae. As far as I can see, the oldest valid name for this family is Chelidina Gray, 1825, which becomes Chelidae with the addition of the appropriate ending. There could be some question as to whether or not Chelides Cuvier, 1817, might not be valid, but I am taking the view that it was not explicitly stated as a family level taxon.

The spelling variations are primarily due to the fact that although *Chelus* Dumeril, 1806, was the first spelling of this genus, it was later "corrected" to *Chelys* and many family level taxa were based on the latter spelling, which was popular during the 19th century. Kuhn

(1967) gave a number of these spellings and a very useful guide to the higher categories.

²Elsewhere (Gaffney, 1972a) I use the arbitrarily chosen ending -odd for infrafamily and continue the practice here.

³Bonaparte (1838) originally named a family level taxon, Hydraspina, based on the genus *Hydraspis*, a name now considered a synonym of *Chelodina* (see text and Stejneger, 1909). However, when Bonaparte used *Hydraspis* it referred to what is now *Phrynops* and, as I understand the rules on family level taxa, the name Hydraspina must go with *Phrynops*.

⁴As there are no rules or suggestions dealing with tribal level endings, I arbitrarily choose -ad as the ending for infratribe.

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