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

EUGENE S. GAFFNEY

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

1Associate Curator, Department of Vertebrate Paleontology, the American Museum of Natural History; Adjunct Assistant Professor, Department of Geological Sciences, Columbia University.
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
- 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, prearticular
- pt, pterygoid
- qi, quadratojugal
- qu, quadrate
- so, supraoccipital
- sq, squamosal
- sur, surangular
- 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 

(1864)

even though their 

interpreted as 

(1974)

Main 

common not 

analysis 

of 

forms. The 

conclusion 

Furthermore, 

analysis. 

related; that 

form 

species 

states 

character 

can 

study 

phylogenetic 

techniques 

Nonetheless, 

suggested 

(e.g., 

data 

but 

weakness 

or strength) 

Burbidge, Kirsch, and 

sent 

an 

duced 

at variance 

an 

phylogeny, 

albeit 

areas 

increasing the 

number 

of 

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. Quadrato-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 kreffti, AMNH 72406, no data; Emydura kreffti, 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 triturating 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); Ouens (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
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); Lueuderwaldt (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 follow:

- *Rhinemys nasuta*
- *Mesoclemmys gibba*
- *Hydaspis hilarii*
- *Hydaspis geoffroyanus*
- *Hydaspis tuberosa*
- *Hydaspis rufipes*
- *Hydaspis wagleri*

Stejneger (1909) showed that the type species of *Hydaspis* Bell is *Testudo longicollis* Bell, 1828, and as this species was earlier made the type species of *Chelodina* Fitzinger, 1826, the genus *Hydaspis* is a junior synonym of *Chelodina*. He also argued that *Phrynops* Wagler, 1830, is the correct name for the taxon previously called *Hydaspis*, 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) *Hydaspis*, 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); Lueuderwaldt (1926); Medem (1960a, 1960b, 1960c, 1966, 1973); Mertens (1967, 1969, 1970); Müller (1939); Siebenrock (1904, 1905); Zangerl and Medem (1958, skull figures).
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 aperture narium externa [narrowly exposed in Chelodina] (fig. 3D)
3. Pterygoids extend anteriorly into aperture 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 aperture 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.
used to describe systematically important features.

*Other References.* Boulenger (1888); Burbidge, 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 maximi-

liani, MCZ 2856, Brazil; Hydromedusa tecti-

fera, 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 pre-

frontal 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 nare and the median

prefrontal contact occur in no other chelids (al-

though they do occur in many other turtles), and

it seems most parsimonious to consider them in-

dependently 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 Hydrom-

edusa maximiliani and H. tectifera, 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 fig-

ures); Vogt (1911); Waite (1929, skull figures); Werner

(Gaffney, 1972a) and is not unique to Hydromedusa

as stated by Wood and Moody.

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 synapomor-

phies or shared derived characters: (1) Unusu-

ally developed lateral cheek emargination; (2)

loss of quadra-tojugal; (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 emargina-

tion. Also, there is reason to think that the ex-
tensive skull roof in Pseudemydura is derived for

chelids and that the condition in Emydura is the

primitive one for chelids. The parietals, squamo-
sals, postorbitals, and supraoccipitals of Pseu-
demydura 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 pelome-

dusids or cryptodires.

A further aspect of the emphasis in chelids on

cheek emargination is the loss of the quadra-
tojugal in all members of this family. Even Pseu-
demydura, a form possessing a well-developed
temporal roof, lacks a quadra-tojugal, further sug-
gest that it evolved from a more emarginate ances-
tor. Some species of Cuora, Hieremys, Geoemyda, and

Terrapene also lack a quadratojugal, and in these forms it appears to be associ-
ated 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 fea-

ures 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, plesio-
chelyids, chelosphargine protostegids, Solnhofia,
and Proganochelys) that do have nasals, the front-
tals 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.)

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

<sup>a</sup>(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 Elseya and Pseudemydura as sister taxa, that is, with an ancestor in common not in common with any other turtle. However, Pseudemydura and Elseya 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 falls 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
would have the primitive chelid possessing most of the features of Emydura except the nasofrontal 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, Pleiosuchia, 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 symphysal suture separating the two lower jaw rami. Pseudemydura and Emydura have the rami fused as do all other turtles except for Hesperoestudo, 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...
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 Boulen-ger, 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

<table>
<thead>
<tr>
<th>Feature Description</th>
<th>Pseudemydura</th>
<th>Emydura &amp; Elseya</th>
<th>Platemys</th>
<th>Phrynops</th>
<th>Chelus</th>
<th>Chelodina</th>
<th>Hydromedusa</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Nasals</td>
<td>present</td>
<td>present</td>
<td>present</td>
<td>present</td>
<td>absent</td>
<td>present</td>
<td>present</td>
</tr>
<tr>
<td>2. Anterior process of frontal</td>
<td>absent</td>
<td>present</td>
<td>present</td>
<td>present</td>
<td>present</td>
<td>present</td>
<td>present</td>
</tr>
<tr>
<td>3. Nasals completely separated by anterior frontal process</td>
<td>no</td>
<td>no</td>
<td>no</td>
<td>no</td>
<td>nasals absent</td>
<td>yes</td>
<td>no</td>
</tr>
<tr>
<td>4. Prefrontalals exposed along dorsal margin of apertura narium externa</td>
<td>no</td>
<td>no</td>
<td>no</td>
<td>no</td>
<td>broadly</td>
<td>narrowly</td>
<td>no</td>
</tr>
<tr>
<td>5. Prefrontalals meet in midline so that frontals are exposed anterior and posterior to prefrontal contact</td>
<td>no</td>
<td>no</td>
<td>no</td>
<td>no</td>
<td>no</td>
<td>no</td>
<td>yes</td>
</tr>
</tbody>
</table>
### TABLE 2 – (Continued)

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

1977
<table>
<thead>
<tr>
<th></th>
<th>Pseudemydura</th>
<th>Emydura &amp; Elseya</th>
<th>Platemys</th>
<th>Phrynops</th>
<th>Chelus</th>
<th>Chelodina</th>
<th>Hydromedusa</th>
</tr>
</thead>
<tbody>
<tr>
<td>16.</td>
<td>Medial portions of jugal and postorbital facing more laterally than posteriorly</td>
<td>no</td>
<td>no</td>
<td>no</td>
<td>no</td>
<td>yes, entirely on external surface of skull</td>
<td>yes</td>
</tr>
<tr>
<td>17.</td>
<td>Dorsal processes of exoccipitals meet above foramen magnum</td>
<td>no</td>
<td>no</td>
<td>yes</td>
<td>yes</td>
<td>yes</td>
<td>yes</td>
</tr>
<tr>
<td>18.</td>
<td>Cavum tympani extended laterally</td>
<td>no</td>
<td>no</td>
<td>no</td>
<td>no</td>
<td>yes</td>
<td>no</td>
</tr>
<tr>
<td>19.</td>
<td>Maxilla reduced in exposure on triturating surface so that palatine bears lingual ridge</td>
<td>no</td>
<td>no</td>
<td>no</td>
<td>no</td>
<td>yes</td>
<td>no</td>
</tr>
<tr>
<td>20.</td>
<td>Medial maxillary contact dividing premaxillae longitudinally</td>
<td>yes</td>
<td>no</td>
<td>no</td>
<td>no</td>
<td>no</td>
<td>no</td>
</tr>
<tr>
<td>21.</td>
<td>Vomer-palatine contact</td>
<td>yes</td>
<td>yes</td>
<td>yes</td>
<td>yes</td>
<td>no, due to anterior pterygoid processes reaching vomer</td>
<td>yes</td>
</tr>
<tr>
<td>22.</td>
<td>Large bony apertura narium interna formed by reduction of palatines</td>
<td>no</td>
<td>no</td>
<td>no</td>
<td>no</td>
<td>no</td>
<td>no</td>
</tr>
</tbody>
</table>
TABLE 2 – (Continued)

<table>
<thead>
<tr>
<th></th>
<th>Emydura &amp; Pseudemydura</th>
<th>Elseya</th>
<th>Platemys</th>
<th>Phrynops</th>
<th>Chelus</th>
<th>Chelodina</th>
<th>Hydromedusa</th>
</tr>
</thead>
<tbody>
<tr>
<td>23. Quadrate-basisphenoid contact</td>
<td>absent</td>
<td>absent</td>
<td>absent</td>
<td>absent</td>
<td>absent</td>
<td>extensive</td>
<td>limited</td>
</tr>
<tr>
<td>24. Symphy-seal suture separates lower jaw rami</td>
<td>no</td>
<td>no</td>
<td>yes</td>
<td>yes</td>
<td>yes</td>
<td>yes</td>
<td>yes</td>
</tr>
<tr>
<td>25. Relatively massive mandibles with symphy-seal &quot;hooks&quot;</td>
<td>absent</td>
<td>present</td>
<td>absent</td>
<td>absent</td>
<td>absent</td>
<td>absent</td>
<td>absent</td>
</tr>
<tr>
<td>26. Prearticular separates or nearly separates corono-noid splenial</td>
<td>yes</td>
<td>no</td>
<td>no</td>
<td>no</td>
<td>no</td>
<td>no</td>
<td>no</td>
</tr>
</tbody>
</table>

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 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 palate 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

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

*Except 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—INFRATRIBE 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 quadrato-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 Emydourida,2 new
      Emydura
      Elseya
  Infrafamily Chelodda Gray, 1825, new rank
    Tribe Platemini, new
      Platemys
  Tribe Chelini Gray, 1825, new rank
    Subtribe Hydraspina3 Bonaparte, 1838, new rank
      Phrynops
    Subtribe Chelinae Gray, 1825, new rank
      Infrafamily Chelida,4 Gray, 1825, new rank
        Chelus
        Infratrib Chelidinae, new
          Chelodina
          Hydromedusa

1 The 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 Chelidinae 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.

2 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.

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

4 Bonaparte (1838) originally named a family level taxon, Hydraspidae, 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 Hydraspidae must go with Phrynops.

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

LITERATURE CITED

Albrecht, P. W.

Bell, T.

Blackmore, E. H.

Bonaparte, C. E.

Bonde, Niels

Boulenger, G. A.

Bour, Roger

Bramble, Dennis Marley

Brundin, Lars

Burbidge, Andrew A., John A. W. Kirsch, and A. R. Main

Cogger, H.

Cope, Edward D.


Cracraft, Joel


Cuvier, Georges

Dumeril, A. M. Constant

Dunn, E. R.

Eldredge, Nilas, and Ian Tattersall

Farris, James S.

Fitzinger, L.

Freiberg, Marcos A.


Froes, Oscar Miranda

Fry, D. B.

Fuchs, Hugo

Gaffney, Eugene S.
1972a. The systematics of the North American family Baenidae (Reptilia, Cryptodira).


Glauert, L.


Goode, John


Gray, John Edward


Gregory, William King


Hay, O. P.


Hennig, Willi


Hoffmann, C. K.


Kanberg, Hans


Krefft, G.


Kuhn, O.


Loveridge, A.


Luederwaldt, Hermann


McKenna, Malcolm C.


Medem, Fred


Mertens, Robert


Mlynarski, Marian

Müller, Lorenz

Ogilby, J. D.


Ouwens, P. A.

Peters, Wilhelm

Peters, W., and G. Doria

Popper, Karl

Rhdin, Anders G. J., and Russell A. Mittermeier

Rooij, Nelly de

Schnee, P.

Siebenrock, F.


1909. Synopsis der rezenten Schildkröten, mit Berücksichtigung der in historischer
Stejneger, Leonhard
Strauch, Alexander
Vestjens, W. J. M.
Vogt, T.
Wagler, J.
Waite, E. R.
Wermuth, H., and R. Mertens
Werner, F.
Wiley, E. O.
Williams, Ernest E.
Wood, Roger Conant
Wood, Roger C., and Richard T. J. Moody
Worrell, E.
Zangerl, Rainer, and Fred Medem