

A Taxonomic Reevaluation of *Phrynops* (Testudines: Chelidae) with the description of two new genera and a new species of *Batrachemys*.

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Abstract: Relationships among turtle species loosely categorized within the South American genus *Phrynops* are explored. Three once recognized genera (*Batrachemys*, *Mesoclemmys* and *Phrynops*) that were demoted to subgenera, and then synonymized with *Phrynops*, are demonstrated to warrant full recognition based on morphometric analysis, skull osteology, and mitochondrial and nuclear gene sequencing. *Mesoclemmys* is resurrected from the synonymy of *Phrynops* as a monotypic genus including *M. gibba*. The genus *Rhinemys*, previously a synonym of *Phrynops*, is resurrected for the species *R. rufipes*. ***Ranacephala* gen. nov.** is described to include the species *R. hoguei*. The genus *Batrachemys* is resurrected from the synonymy of *Phrynops* and includes *B. dahli*, *B. nasuta*, *B. raniceps*, *B. tuberculata*, and *B. zuliae*. The taxon *vanderhaegei* is placed in ***Bufocephala* gen. nov.** The genus *Phrynops* is redefined to include the taxa *P. geoffroanus*, *P. hilarii*, *P. tuberosus*, and *P. williamsi*. Cladistic analysis of morphological data supports this taxonomy. A new species of *Batrachemys* is described from the western Amazon region, and is distinguished by having facial markings in juveniles, a relatively wide head, and a flattened shell. The new species, ***B. heliostemma* sp. nov.**, is sympatric with and most similar to the recently resurrected form *Batrachemys raniceps* in the upper Amazonian region of Peru and adjacent Brazil, Ecuador, Venezuela, and Colombia. Lastly, morphometric data from living and museum specimens of all species of *Batrachemys* are presented.

Key words: Turtles, Pleurodira, chelid, genera, South America, toadhead, Iquitos, systematics.

“Turbulent” well describes the taxonomic history of the New World Pleurodira. *Phrynops* (*sensu lato*) is a chelid genus endemic to South America that includes the toadheads, a group of species whose inter-relationships have been uncertain. With the exception of the *Phrynops geoffroanus* complex, most species are poorly known, rare, or limited in distribution (Iverson, 1992). The toadheads (first defined by Gray, 1855, for the “Toad-Headed *Hydraspis*, *H. raniceps* sp. nov.”) have a sinuous and perplexing history. Multiple synonyms and poorly recorded field data abound in the literature (i.e., Wermuth and Mertens 1977).

We herein give a chronological accounting of the taxonomic history specifically of the turtles listed under *Phrynops* (*sensu lato*). Starting with his monograph of the Testudines, Schweigger (1812) described the first three toadheads, *Emys geoffroana*, *Emys nasuta* and *Emys gibba*. Noticing clear differences between the South American side-necked species in the genus *Emys* and their congeners, the Australian side-necked turtles, Fitzinger (1826), advised by Opper, erected the new genus *Chelodina* for the Australian forms, with *Emys longicollis* of eastern Australia as the generotype.

Apparently unaware of Fitzinger's work, Bell (1828) proposed the genus *Hydraspis* to include all side-necked turtles. The genotype was also *Testudo* (*Emys*) *longicollis*, and it was diagnosed as having a depressed head and body; projecting nose and narrow nostrils; a long and "extensile" neck; and an anteriorly broad first vertebral scute.

In 1830, Wagler described the monotypic genus *Phrynops* for the Brazilian species *Emys geoffroyana* Schweigger (1812). He also created the genus *Rhinemys* to subsume four other species then assigned to *Emys*: *E. rufipes* Spix (1824), *E. gibba* Schweigger (1812), *E. nasuta* Schweigger (1812) and *E. radiolata* Mikan (1820).

Realizing that Wagler had not designated a genotype for *Rhinemys*, Fitzinger (1843) specifically chose the species *E. rufipes* as the type. *Emys rufipes* Spix (1824) was not the oldest species in the genus *Rhinemys*, being preceded by *E. nasuta* Schweigger (1812:298) and *E. gibba* Schweigger (1812:299). But, as "first reviewer," Fitzinger had the right to choose whichever of Wagler's four *Rhinemys* species he deemed appropriate. It is possible that his decision was based on the fact that *E. rufipes* has the most prominent nose of the toadheads then being considered (*Rhinemys* translates to "nose-turtle").

Gray (1844) believed that *R. rufipes* and *P. geoffroyana* (= *P. geoffroyanus*) were congeneric. Since international nomenclatorial rules permit the first reviser to select the valid genus in the case of two generic names proposed on the same date, despite the fact that *Rhinemys* appeared prior to *Phrynops* (Wagler 1830: 134 vs. 135) in the same publication, Gray synonymized *Rhinemys* under *Phrynops*. Further examination of toadheads by Gray (1873a) led him to describe the monotypic genus *Mesoclemmys* for the species *Rhinemys gibba*. This genus was considered valid until assigned subgeneric status by Zangerl and Medem (1958).

Subsequent to Bell's (1828) description of *Hydraspis*, during the nineteenth and twentieth centuries, and despite both Gray's and

Wagler's work, that genus name was used erroneously (e.g., Siebenrock 1904, 1909; Luederwaldt 1926) for many of the South American chelids, including the toadheads as well as taxa currently assigned to *Platemys* and *Acanthochelys*. Since *Hydraspis* was clearly a junior synonym of *Chelodina* (same genotype; *Chelodina* has precedence), Stejneger (1909) again corrected the problem by synonymizing *Hydraspis* under *Chelodina*.

Like Boulenger, Stejneger (1909) also observed that Schweigger's (1812) *Emys nasuta* was distinct from the species then included in *Phrynops*. Since *E. rufipes* was the genotype for *Rhinemys*, and *Rhinemys* had been synonymized with *Phrynops* by Gray (1844), *E. nasuta* required a new nominal genus. Thus, Stejneger (1909) proposed the genus *Batrachemys* with *B. nasuta* as the genotype, although he provided no descriptive characteristics.

Stejneger's (1909) revision was apparently unavailable to Siebenrock (1909), who still recognized *Hydraspis* as the genus for South American toadheads of the *Phrynops geoffroyanus* complex (*P. geoffroyanus*, *P. tuberosus*, *P. rufipes* and *P. wagleri*) and used the generic designation of *Rhinemys* for the *Batrachemys nasuta* complex (at that time, using specimens of "*R. nasuta*" from Suriname to Bolivia and various localities of the upper Amazon region).

By the mid-twentieth century, the three genera – *Batrachemys*, *Phrynops* and *Mesoclemmys*, were still in use. The monotypic genus *Mesoclemmys* held *M. gibba*; *Phrynops* included *P. geoffroyanus geoffroyanus*, *P. g. tuberosus*, *P. g. hilairei* and *P. rufipes*; and *Batrachemys* included *B. nasuta*, *B. tuberculata* and *B. dahli* (Wermuth and Mertens, 1961; Pritchard, 1967).

In their description of a new toadhead from Bolívar, Colombia, Zangerl and Medem (1958) questioned the need for three genera of toadheads. They suggested that the traits supposedly diagnostic of the three genera were in fact substantial enough only for subgeneric division under the priority (oldest) name *Phrynops* (see also Lescure and Fretey 1975).

Their decision was based heavily on the unpublished work of Williams and Vanzolini.

Bour (1973; see also Bour and Pauler, 1987) considered the subgenera so poorly diagnosed as to warrant full synonymy under *Phrynops*, an arrangement followed by Vanzolini *et al.* (1980) and Rhodin *et al.* (1982). Ernst and Barbour (1989) mentioned the subgenera, but followed Bour (1973) in not recognizing them. However, some authors (e.g., Winokur and Legler 1974; Freiberg 1975; Albrecht 1976; Gaffney 1979; Winokur 1982; Lema 1994; and Cabrera 1998) retained *Batrachemys* as a full genus in their works.

Pritchard (1967, 1979) and Pritchard and Trebbau (1984) recognized the three controversial subgenera. They diagnosed the subgenus *Mesoclemmys* largely on morphological characters: small chin barbels (=barbels); the presence of zero to five often discontinuous neural bones, never contacting the nuchal (proneural) bone; less than thirty cm in shell length; a small head, pointed anteriorly as in *Batrachemys*; posteriorly wide hourglass-shaped parietals as in *Phrynops*; and parieto-squamosal arches that pass directly above the opisthotics. For the subgenus *Batrachemys*, Pritchard and Trebbau used the following characters: zero (often) to five neural bones present, never contacting the nuchal bone; comparatively short barbels; broad head; narrow, parallel-sided parietals; and slender parieto-squamosal arches located posterior to the rear margin of the opisthotic bones. They also distinguished the subgenus *Phrynops* by their six contiguous neural bones, the first of which contacts the nuchal bone; twenty-five to forty-five cm in carapace length; long barbels; broad hourglass-shaped parietals; strong parieto-squamosal arch, passing directly above the opisthotics (as with *Mesoclemmys*); and a broad, flat head with a blunt snout.

Gaffney (1977) examined cranial characters of *P. geoffroanus*, *P. (M.) gibbus*, and *P. (B.) nasutus*-complex specimens from various localities. Because he was unable to find unique derived skull characters among the species in the genus *Phrynops*, he could not resolve their

relationships (but see Shaffer *et al.* 1997, and Gaffney and Meylan 1988, for other details on chelid phylogeny). Wermuth and Mertens (1977) expressed concern regarding the recognition of subgenera within *Phrynops*, noting the unstable subgeneric differences, such as the variable neural bone arrangements.

Although inconclusive, the monophyly of the genus *Phrynops (sensu lato)* seemed to be supported by the "early" genetic data of Frair (1980, 1982) and Reed *et al.* (1991). Using mitochondrial DNA sequencing, morphological and paleontological approaches, Schaffer *et al.* (1997) provided hypotheses of chelonian phylogeny that show both the family Chelidae and the genus *Phrynops (sensu lato)* to be monophyletic. However, in an effort to resolve the conflicting taxonomic proposals, Seddon *et al.* (1997) sequenced 411 mitochondrial 12S rRNA nucleotides of 16 representative species within the 11 recognized chelid genera. Analysis using parsimony and neighbor-joining algorithms strongly supported the generic distinctiveness, or paraphyly among the subgenera of *Phrynops (sensu lato)*. *Mesoclemmys* was resolved as the sister taxon of *Batrachemys*, but *Phrynops* was most closely related to the genus *Chelus*.

Georges *et al.* (1998) broadened the study of molecular data by examining 1382 nucleotides from the 16S rRNA and CO1 mitochondrial genes and the nuclear oncogene *c-mos* from 25 chelid taxa representing all chelid genera. Their studies echoed the conclusions of Seddon *et al.* (1997) and substantively concluded that the genus *Phrynops (sensu lato)* was paraphyletic. They believed this was best resolved by elevating once again the subgenera (*Phrynops*, *Mesoclemmys*, and *Batrachemys*) to generic status. They also noted that because of the sister relationship between *Batrachemys* and *Mesoclemmys* their data could support the synonymy of those two genera (under the older name *Mesoclemmys*). However, for taxonomic stability, their final recommendation was to elevate the three subgenera to full generic status.

Cabrera (1998) reviewed the status of the three subgenera, *Batrachemys*, *Mesoclemmys*,

and *Phrynops*, and placed *P. geoffroanus*, *P. hilarii*, *P. williamsi*, *P. rufipes* and, tentatively, *P. gibbus* and *P. hoguei* in the genus *Phrynops*, while declaring that the status of *P. tuberosus* and *P. wagleri* (currently a subjective synonym of *P. geoffroanus*) was unresolved. He also recognized the genus *Batrachemys*, including *B. dahli*, *B. nasuta*, *B. raniceps*, *B. tuberculata*, *B. vanderhaegei* and *B. zuliae*. Cabrera declined to take a firm stand on the status of *Mesoclemmys* because of his lack of direct knowledge of the species involved. Based on the literature he postulated that *Mesoclemmys* could be synonymous with or subgeneric to *Phrynops*, and that it might include the species *gibbus* and *hoguei*. After examining both living and preserved specimens of all recognized species of toadheads (*Phrynops sensu lato*), we support Georges *et al.* (1998) in the recognition of the three genera *Phrynops*, *Batrachemys*, and *Mesoclemmys*.

TAXONOMIC BACKGROUND

Early taxonomy of the toad-headed turtles (= toadheads) is as follows: In 1788 Lacepède (followed by Bonnaterre 1789) cited two main classes of reptiles, belonging to the “Quadrupèdes ovipares” (four-legged, egg-laying vertebrates). *Reptilia ecaudata* (without tails) held *Rana*, *Hyla*, and *Bufo* as “genres” (genera). *Reptilia caudata* (with tails) held *Testudo* and *Lacerta* as “genres”. “Reptiles bipèdes” (two-footed) were also included in the “Quadrupèdes ovipares”, and the “Serpents” (snakes) were set apart. All chelonians (24 species) were placed in the genus *Testudo* (Linnaeus 1758), but no toadhead turtles were known at that time.

Largely through the work of Hunt (1958), it is known that in 1758 Linnaeus first used the term “Testudines” but only at a generic level referring to the plural form of *Testudo* (Bour and Dubois 1984). Batsch (1788) also used “Testudines”, but as a family name, and gave credit for first use to Linnaeus in 1758. Thus, the correct ordinal name for turtles is Chelonii

(as “les chéloniens”, Brongniart 1800). Because the ordinal name Testudines is tentatively accepted by many (e.g., Gasperetti *et al.* 1993), we will continue to use Testudines as the ordinal name for all turtles and tortoises, for the sake of nomenclatural stability.

In 1826, Fitzinger (using the manuscripts of Hemprich 1796-1825) designed the following taxonomic scheme for some chelonian taxa (i.e., South American toadheads): Class - Reptilia; Order - Monopnoa; Tribe - Testudinata; Family - Emydoidea; Genus - *Emys*. Gray (1831a) defined “Reptilia” as having vertebrae, lungs, warm [sic] red blood, heart with 1 ventricle and 2 auricles, and skin covered with scales. He defined “Testudinata” (Oppel 1811) as having ribs, vertebrae and sternum united in a bony case, usually covered with horny shields or plates, and jaws toothless.

Gaffney and Meylan (1988) elaborated upon Gray’s (1831a) definition of Testudinata to include that the post parietals are absent, lacrimal bone small or absent, teeth replaced by horny triturating surfaces, parietal (pineal) opening usually absent, stapes solid and rod-like, and postfrontal absent. The toadheads of South America presently fall under the following taxonomic hierarchy: Class - Reptilia; Order - Testudines; Suborder - Pleurodira; Family - Chelidae.

The suborder Pleurodira (Cope 1864) is distinguished by the following combination of characters (after Legler and Georges 1993): the neck flexes laterally to either side and tucks under the anterior edge of the carapace; a trochlear pulley system of the adductor muscles of the jaw utilizes the lateral process of the pterygoid bone to enhance muscular efficiency as opposed to the situation in the Cryptodira where the antero-dorsal edge of the otic capsule is used; and the pelvis is always fused to the plastron. The oldest known Chelonians (*Proterochersis* Fraas 1913), from the upper Triassic, belong to the Pleurodira.

The family Chelidae (Gray 1831a) has Gondwanan origins and first registers in the lower Cretaceous period of Patagonia (Fuente 1997). They are carnivorous (Ceï 1993). The

skull is strongly depressed; the basisphenoid is elongate, triangular, much broader behind; the basioccipital is extremely narrow and elongate (Gray 1872a). Nasal bones are present (diagnostic for the family if only living forms are considered (Gaffney 1979) in all but *Chelus*; a vomer is present and usually separating the palatines; a splenial bone is present; a post parieto-squamosal arch is present (except *Chelodina*) and the quadratojugal is absent. The central articulations of the 5th and 8th cervical vertebrae are bi-convex, and saddle joints are never present (no convex articular surface from behind fitting into a concave surface in front). A mesoplastron is absent (Legler and Georges 1993). The pelvis is fused to the carapace and plastron (or to "vertebra and sternum" as per Gray 1870); neural bones are reduced or absent; thirteen plastral scutes (including the intergular) are present; there are twelve pairs of marginal scutes; the two halves of the lower jaw are connected by a seam (not fused) at the symphysis (with the exception of the genera *Emydura* - *Elseya* - *Rheodytes* - *Elusor*); a nuchal scute is present (absent in most Australian and at least one New Guinean *Elseya*); nictitating membranes are absent; and the head is covered with soft skin or small scales. The chromosome number in the Chelidae (Bull and Legler 1978; Legler and Georges 1993) ranges from 2n=50 to 64 (96 in triploid *Platemys*).

MATERIALS AND METHODS

Specimens of all recognized species of toadheads were examined. In addition, 6 museum and 17 living specimens of an undescribed *Batrachemys* were available for study (see Tables 1-7, and Appendices A and B).

All measurements to the nearest 0.1 mm were taken with electronic calipers. The characters obtained include: head length – straight line from anterior edge of premaxilla to back of the crista supraoccipitalis (HL); head width – maximum straight width of skull at tympana (HW); head depth – maximum height of skull from ventral caudal mandible to dorsal parietal

roof (HD); interorbital width – the width of the frontal bone between the orbits taken from medial internal ridge of the orbits (IOW); parietal width – across the lateral edges of the dorsal parietal roof taken at its narrowest point (PW); carapace length – maximum straight midline from center of anterior nuchal scute to caudal seam between 12th marginals (CL); carapace width – straight line at its widest point (CW); carapace depth – maximum height of shell (CD); vertebral scute length – maximum straight midline (V1-5); vertebral scute width – straight line, at widest point (V1-5w); plastral length maximum – straight line from anteriormost point of plastron to posteriormost tip of anal scute (PWX); plastral length midline – maximum straight midline from anterior to posterior plastral margins (PLM); plastral width at anterior bridge – taken as straight line between axillary notches (PWA); plastral width at posterior bridge – straight line between inguinal notches (PWP); bridge length – from axillary to inguinal notches (BL); plastral width at outer gular/humeral seam – straight line between distal ends of gular/humeral seams (PWG); plastral width at outer femoral/anal seam – straight line between distal ends of femoral/anal seams (PWF); intergular scute – straight midline length (IG); inter-humeral, pectoral, abdominal, femoral and anal seams – maximum midline length of each seam (IH, IP, IA, IF and IAn). Sample sizes are given in Tables 2 and 5, and in Appendix A. Many unlisted living and preserved specimens of all the toadhead species were studied in the senior author's private collection.

SYSTEMATICS

In agreement with Georges *et al.* (1998) and Cabrera (1998), we herein recognize and re-diagnose the three toadhead genera: *Batrachemys*, *Mesoclemmys*, and *Phrynops*. Our diagnoses include characters of skull osteology based on material represented in Figure 1 (also see Siebenrock, 1897).

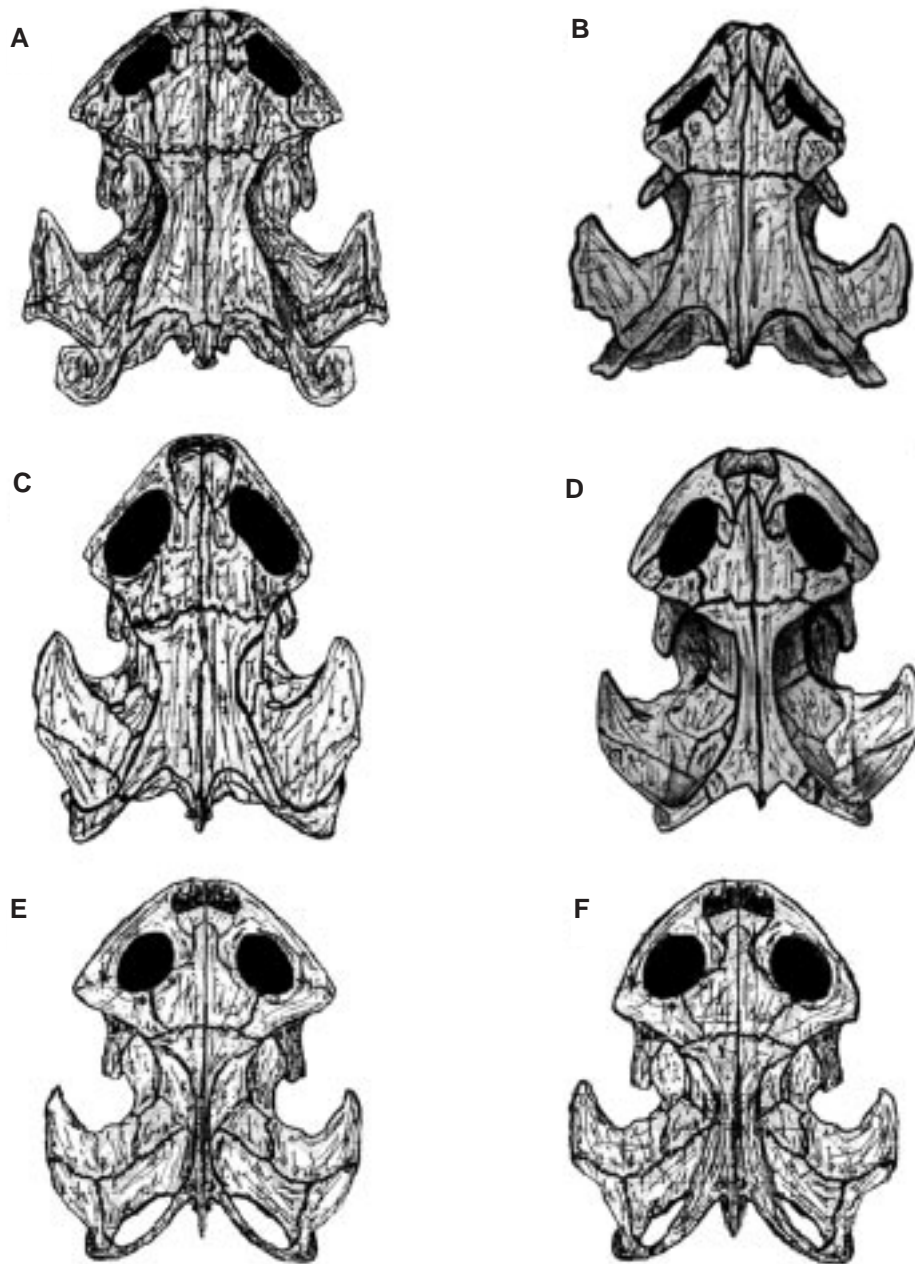


Fig. 1. Illustrations (by M.J. Ouni) of the crania of six genera of toadhead species: A) *Phrynops geoffroyanus* (after Gaffney 1977); B) *Rhinemys rufipes* (after Lamar and Medem 1982); C) *Mesoclemmys gibba* (after Gaffney 1977); D) *Bufocephala* gen. nov. *vanderhaegei* (after Bour and Pauler 1987); E) *Batrachemys raniceps* (after Boulenger 1889); F) *Batrachemys helioSTEMMA* sp. nov (based on radiograph of juvenile specimen).

TABLE 1

Character matrix for toadheads scored from data presented in Appendix B.

KEY

- #2 Head size: small=0; medium=1; broad=2
 #3 Flatness of head: flat=0; rounded=1;
 #4a Head width (HW / HL): 80-90%=0; >90%=1;
 #4b Eye orientation: laterally=0; dorsally=1;
 #5 Snout: blunt=0; pointed=1;
 #6 Barbels: small=0; long=1;
 #7 Parietal roof width: wide, >20%=0; medium, 15-20%=1; narrow, <13%=2;
 #8 Parieto-squamosal arch: substantial=0; medium=1; narrow=2;
 #10 Neural series: first neural reaches preneural=0; not=1;
 #11 Intergular/gular width: intergular wider or equal to gulars=0; intergular narrower=1;
 #12a Intergular vs interabdominal seam: IG>IAB=0; IAB>IG=1;
 #12b Interanal vs interpectoral seams: IAN>P=0; IP>IAN=1;
 #13 Shell depth: low shell=0; medium to high domed=1;
 #15 Carapacial median groove: no groove=0; present=1;
 #16 11th and 12th marginal widths: 11th>12th=0; Equal=1; 12th>11th=2;
 #17 Distal tibial scale: well developed=0; moderatel to poorly developed=1;
 #18 Upturning of lateral margin of carapace: not upturned=0; upturned=1;
 #19 Plastron coloration: Black present=0; yellow only=1

| TAXON | #2 | #3 | #4a | #4b | #5 | #6 | #7 | #8 | #10 | #11 | #12a | #12b | #13 | #15 | #16 | #17 | #18 | #19 |
|------------------------|----|----|-----|-----|----|----|----|----|-----|-----|------|------|-----|-----|-----|-----|-----|-----|
| <i>B. tuberculata</i> | 2 | 1 | 0 | 1 | 1 | 0 | 2 | 2 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 |
| <i>B. zuliae</i> | 2 | 1 | 0 | 1 | 1 | 0 | 2 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 |
| <i>B. dahli</i> | 2 | 1 | 0 | 1 | 1 | 0 | 2 | 2 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 |
| <i>R. hoguei</i> | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 9 | 1 | 1 | 0 | 1 | 1 | 2 | 0 | 1 | 1 |
| <i>R. rufipes</i> | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 1 | 0 | 1 |
| <i>P. geoffroanus</i> | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 |
| <i>M. gibba</i> | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 2 | 1 | 1 | 0 |
| <i>B. vanderhaegei</i> | 2 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 2 | 1 | 1 | 0 |
| <i>B. nasuta</i> | 2 | 1 | 0 | 1 | 1 | 0 | 2 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| <i>B. raniceps</i> | 2 | 1 | 0 | 1 | 1 | 0 | 2 | 2 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 |
| <i>B. heliostemma</i> | 2 | 1 | 0 | 1 | 1 | 0 | 2 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 |
| <i>C. fimbriata</i> | 2 | 0 | 1 | 0 | 9 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 9 |

TABLE 2

Skull measurements (in mm.) of museum specimens of six species of Batrachemys: dahli, raniceps, tuberculata, nasuta, zuliae, and heliostemma.

| Species | Index # | HL | HW | HD | IOW | PW |
|--------------------|---------|------|------|------|------|-----|
| <i>dahli</i> | | | | | | |
| f | 1 | 46.3 | 37.5 | 20.8 | 6.9 | 3.1 |
| f | 2 | 55.4 | 45.0 | 25.3 | 7.4 | 3.5 |
| f | 3 | 49.3 | 43.1 | 21.9 | 7.5 | 3.5 |
| m | 4 | 42.5 | 35.7 | 16.3 | 6.8 | 2.6 |
| j | 5 | 35.4 | 26.9 | 13.5 | 4.3 | 2.6 |
| <i>raniceps</i> | | | | | | |
| f | 6 | 56.2 | 50.1 | \ | 10.7 | 2.5 |
| m | 7 | 62.0 | 60.6 | \ | 11.4 | 5.1 |
| f | 8 | 51.9 | 45.7 | 24.2 | 10.2 | 3.9 |
| sub | 9 | 42.0 | 37.3 | 20.6 | 7.7 | 5.1 |
| j | 10 | 21.1 | 18.2 | 10.9 | 3.3 | 3.2 |
| <i>tuberculata</i> | | | | | | |
| f | 11 | 46.7 | 41.1 | 28.9 | 8.7 | 6.1 |
| f | 12 | 47.2 | 41.7 | 27.6 | 8.5 | 4.8 |
| f | 13 | 40.7 | 33.0 | 19.7 | 7.0 | 4.7 |
| m | 14 | 50.0 | 44.5 | 25.3 | 9.7 | 4.0 |
| <i>nasuta</i> | | | | | | |
| m | 15 | 81.1 | 70.5 | \ | 13.6 | 3.1 |
| f | 16 | 40.8 | 35.4 | 20.6 | 7.9 | 6.5 |
| f | 17 | 43.7 | 34.8 | 19.0 | 6.8 | 5.3 |
| un | 18 | \ | \ | \ | \ | \ |
| sk | 19 | \ | \ | \ | \ | \ |
| <i>zuliae</i> | | | | | | |
| f | 20 | 69.0 | 66.0 | \ | 10.1 | 1.6 |
| f | 21 | 74.9 | 66.1 | \ | 11.0 | 2.8 |
| f | 22 | 93.2 | 81.1 | 48.8 | 15.1 | 5.8 |
| m | 23 | 67.0 | 55.9 | 33.0 | 10.1 | 6.2 |
| sk | 24 | 57.0 | 46.3 | 22.2 | 8.0 | 1.6 |
| <i>heliostemma</i> | | | | | | |
| j** | 25 | 24.0 | 20.3 | 11.6 | 4.1 | 4.2 |
| j* | 26 | 30.1 | 26.6 | 15.6 | 4.8 | 3.3 |
| j* | 27 | 22.2 | 18.8 | 11.2 | 3.6 | 3.9 |
| f* | 28 | 37.1 | 34.7 | 18.8 | 6.4 | 5.2 |
| j* | 29 | 28.7 | 23.7 | 14.2 | 3.8 | 3.9 |

Index numbers reference collection data of museum specimens as in Appendix A. HL=Head length; HW=Head width; HD=Head depth; IOW=Interorbital width; PW=Parietal width; f=female; m=male; j=juvenile; sk=skeleton; un=unknown sex; **=holotype; *=paratype.

TABLE 3

Carapace measurements (in mm.) of several museum specimens of Batrachemys: dahli, raniceps, tuberculata, nasuta, zuliae, and heliostemma.

| Species | Index # | CL | CW | CD | V1 | V1w | V2 | V2w | V3 | V3w | V4 | V4w | V5 | V5w |
|--------------------|---------|-------|-------|------|-------|-------|-------|------|------|------|------|------|------|------|
| <i>dahli</i> | | | | | | | | | | | | | | |
| f | 1 | 155.9 | 113.7 | 51.3 | 32.6 | 50.7 | 25.8 | 31.3 | 23.2 | 28.6 | 23.3 | 24.6 | 23.1 | 39.3 |
| f | 2 | 174.6 | 128.7 | 54.3 | 37.0 | 50.9 | 30.2 | 33.9 | 26.2 | 29.5 | 24.9 | 25.6 | 26.1 | 44.3 |
| f | 3 | 192.5 | 140.8 | 57.4 | 39.0 | 59.9 | 32.3 | 35.8 | 31.0 | 33.9 | 34.5 | 29.1 | 28.4 | 44.5 |
| m | 4 | 147.3 | 110.0 | 44.6 | 29.3 | 39.4 | 23.0 | 27.5 | 21.4 | 25.2 | 20.1 | 19.9 | 22.7 | 33.6 |
| j | 5 | 110.5 | 84.0 | 33.7 | 23.1 | 30.7 | 18.5 | 23.2 | 15.4 | 21.8 | 15.8 | 18.4 | 18.5 | 23.3 |
| <i>raniceps</i> | | | | | | | | | | | | | | |
| f | 6 | 198.7 | 148.3 | 61.7 | 41.2 | 52.3 | 30.7 | 35.7 | 28.2 | 32.9 | 25.7 | 28.1 | 31.2 | 52.6 |
| m | 7 | 224.8 | 172.6 | 74.5 | 44.6 | 57.3 | 32.0 | 38.2 | 29.5 | 33.2 | 34.4 | 29.9 | 41.1 | 76.0 |
| f | 8 | 165.5 | 122.2 | 50.5 | 31.5 | 46.3 | 26.8 | 34.7 | 25.1 | 29.9 | 20.0 | 25.9 | 24.6 | 32.3 |
| sub | 9 | 135.8 | 105.0 | 44.6 | 26.4 | 35.4 | 18.5 | 27.9 | 20.1 | 24.9 | 19.0 | 23.3 | 19.3 | 32.7 |
| j | 10 | 57.0 | 46.6 | 17.3 | 10.6 | 13.6 | 7.8 | 18.5 | 7.4 | 16.8 | 7.4 | 14.0 | 11.7 | 14.2 |
| <i>tuberculata</i> | | | | | | | | | | | | | | |
| f | 11 | 175.9 | 121.9 | 64.7 | 37.1 | 50.5 | 28.5 | 35.9 | 26.2 | 32.3 | 27.9 | 26.4 | 31.0 | 40.7 |
| f | 12 | 163.6 | 121.5 | 62.7 | 40.2 | 55.9 | 25.5 | 34.9 | 25.0 | 32.6 | 26.8 | 24.8 | 24.8 | 36.1 |
| f | 13 | 151.4 | 107.8 | 49.2 | 31.4 | 53.6 | 19.9 | 30.7 | 19.0 | 26.0 | 14.5 | 22.2 | 24.0 | 28.3 |
| m | 14 | 190.0 | 130.3 | 65.4 | 44.3 | 57.7 | 29.7 | 35.3 | 28.0 | 30.3 | 28.4 | 25.0 | 28.8 | 33.3 |
| <i>nasuta</i> | | | | | | | | | | | | | | |
| m | 15 | 274.3 | 204.3 | 74.5 | 54.4 | 69.2 | 39.2 | 47.6 | 42.2 | 42.9 | 40.1 | 36.3 | 52.1 | 83.3 |
| f | 16 | 155.6 | 115.5 | 49.3 | 32.1 | 46.1 | 23.9 | 37.0 | 20.8 | 33.5 | 23.5 | 30.1 | 30.4 | 44.9 |
| f | 17 | 151.3 | 115.8 | 44.2 | 30.8 | 43.6 | 23.4 | 33.7 | 23.4 | 30.7 | 23.4 | 26.8 | 23.0 | 31.7 |
| un | 18 | 161.3 | 128.9 | 51.1 | 33.32 | 46.5 | 26.79 | 32.2 | 22.8 | 29.6 | 20.5 | 23.7 | 31.0 | 36.6 |
| sk | 19 | 317.1 | 226.3 | 90.3 | 73.38 | 103.4 | 51.82 | 62.8 | 50.0 | 57.5 | 51.0 | 51.1 | 53.7 | 83.8 |
| <i>zuliae</i> | | | | | | | | | | | | | | |
| f | 20 | 244.2 | 179.0 | 78.6 | 53.3 | 70.6 | 40.5 | 40.0 | 38.1 | 37.4 | 43.1 | 32.8 | 36.0 | 66.5 |
| f | 21 | 239.7 | 180.5 | 80.7 | 55.3 | 78.8 | 38.9 | 42.6 | 36.7 | 36.2 | 40.2 | 30.8 | 35.0 | 63.2 |
| f | 22 | 280.1 | 200.1 | 93.9 | 70.4 | 75.7 | 40.1 | 44.3 | 40.5 | 39.6 | 46.3 | 35.3 | 40.6 | 78.6 |
| m | 23 | 220.0 | 147.6 | 71.1 | 49.5 | 54.7 | 32.9 | 35.8 | 28.0 | 32.1 | 30.7 | 27.8 | 33.5 | 55.3 |
| sk | 24 | 184.3 | 138.1 | 60.5 | 39.9 | 57.9 | 30.2 | 33.2 | 28.1 | 30.4 | 26.4 | 25.7 | 27.4 | 43.2 |
| <i>heliostemma</i> | | | | | | | | | | | | | | |
| j** | 25 | 71.3 | 56.2 | 18.5 | 13.6 | 19.8 | 10.1 | 19.7 | 10.0 | 19.5 | 9.9 | 16.3 | 12.3 | 13.5 |
| j | 26 | 112.8 | 87.1 | 32.1 | 22.4 | 36.5 | 16.2 | 35.9 | 14.7 | 30.3 | 15.9 | 25.3 | 18.4 | 25.6 |
| j* | 27 | 61.6 | 48.6 | 17.7 | 11.5 | 17.2 | 8.5 | 18.2 | 8.1 | 18.5 | 7.9 | 14.9 | 11.6 | 16.4 |
| f* | 28 | 130.3 | 103.3 | 39.2 | 26.2 | 39.4 | 21.1 | 34.2 | 20.3 | 34.4 | 18.6 | 30.8 | 25.4 | 33.0 |
| j* | 29 | 97.1 | 71.7 | 27.1 | 19.7 | 28.3 | 13.6 | 26.2 | 12.8 | 23.9 | 13.5 | 20.5 | 16.4 | 22.3 |

Index numbers reference collection data of specimens as in Table 3. CL=Carapace length; CW=Carapace width; CD=Carapace depth; V'#'= vertebral number length; V'#'w= vertebral number width.

TABLE 4

Plastron measurements (in mm.) of several museum specimens of Batrachemys: dahli, raniceps, tuberculata, nasuta, zuliae, and heliostemma.

| Species | Index # | PLX | PLM | PWA | PWP | BL | PWG | PWF | IG | IH | IP | IA | IF | IAN |
|--------------------|---------|-------|-------|-------|-------|------|------|------|------|------|------|------|------|------|
| <i>dahli</i> | | | | | | | | | | | | | | |
| f | 1 | 139.1 | 125.9 | 72.1 | 54.6 | 36.8 | 49.3 | 40.0 | 32.6 | 9.4 | 17.3 | 18.8 | 27.6 | 17.3 |
| f | 2 | 152.9 | 139.9 | 78.2 | 62.9 | 35.9 | 59.2 | 44.7 | 30.4 | 16.8 | 19.6 | 23.6 | 25.8 | 21.7 |
| f | 3 | 171.0 | 157.5 | 85.0 | 63.7 | 43.9 | 63.8 | 45.2 | 35.7 | 18.7 | 21.4 | 30.1 | 30.5 | 19.6 |
| m | 4 | 130.9 | 120.1 | 64.4 | 48.0 | 28.5 | 47.9 | 33.0 | 30.0 | 11.4 | 15.0 | 18.1 | 28.0 | 13.7 |
| j | 5 | 96.7 | 87.7 | 46.2 | 36.6 | 24.3 | 35.6 | 26.8 | 20.3 | 9.4 | 13.9 | 14.2 | 14.6 | 11.7 |
| <i>raniceps</i> | | | | | | | | | | | | | | |
| f | 6 | 173.8 | 159.4 | 92.6 | 79.8 | 43.8 | 60.3 | 63.6 | 36.9 | 14.7 | 26.9 | 28.6 | 29.6 | 19.5 |
| m | 7 | 201.0 | 180.2 | 104.1 | 88.6 | 51.6 | 66.5 | 68.9 | 39.4 | 30.6 | 16.7 | 30.0 | 42.2 | 21.7 |
| f | 8 | 147.2 | 134.0 | 77.9 | 66.4 | 35.7 | 52.9 | 52.0 | 32.5 | 16.0 | 16.6 | 22.3 | 25.8 | 16.8 |
| sub | 9 | 124.9 | 113.9 | 66.1 | 58.1 | 29.5 | 48.4 | 41.9 | 25.4 | 14.2 | 19.8 | 15.7 | 22.3 | 13.5 |
| j | 10 | 46.5 | 44.3 | 22.9 | 21.4 | 12.3 | 14.7 | 14.2 | 10.2 | 4.0 | 6.0 | 6.6 | 9.7 | 5.6 |
| <i>tuberculata</i> | | | | | | | | | | | | | | |
| f | 11 | 158.5 | 148.7 | 86.6 | 76.7 | 43.0 | 56.3 | 52.3 | 33.1 | 22.3 | 14.2 | 25.6 | 26.7 | 23.7 |
| f | 12 | 152.6 | 145.5 | 86.8 | 76.5 | 40.4 | 59.5 | 53.4 | 33.4 | 19.1 | 12.7 | 29.8 | 25.2 | 23.0 |
| f | 13 | 142.0 | 135.8 | 78.6 | 67.8 | 40.7 | 52.5 | 47.5 | 33.8 | 14.7 | 11.1 | 24.9 | 21.4 | 26.4 |
| m | 14 | 178.8 | 168.1 | 91.5 | 78.2 | 43.8 | 64.7 | 61.6 | 42.2 | 18.8 | 13.3 | 32.7 | 29.5 | 27.3 |
| <i>nasuta</i> | | | | | | | | | | | | | | |
| m | 15 | 235.9 | 213.6 | 134.9 | 113.5 | 56.8 | 84.9 | 85.4 | 46.9 | 27.0 | 19.9 | 42.8 | 39.5 | 30.4 |
| f | 16 | 133.2 | 125.0 | 68.3 | 59.0 | 34.2 | 48.5 | 42.0 | 26.0 | 19.1 | 17.0 | 18.4 | 23.3 | 15.5 |
| f | 17 | 133.8 | 123.2 | 75.6 | 62.3 | 35.0 | 51.7 | 44.6 | 32.2 | 12.1 | 16.7 | 18.1 | 21.2 | 18.1 |
| un | 18 | 145.3 | 134.8 | 85.4 | 74.0 | 34.6 | 53.2 | 48.8 | 31.6 | 18.2 | 19.5 | 19.1 | 22.7 | 21.9 |
| sk | 19 | 272.9 | 255.5 | 147.7 | 123.5 | 76.1 | 96.1 | 91.7 | 49.9 | 36.5 | 36.3 | 56.1 | 45.9 | 26.8 |
| <i>zuliae</i> | | | | | | | | | | | | | | |
| f | 20 | 210.8 | 194.0 | 94.1 | 79.3 | 58.5 | 69.2 | 62.2 | 39.0 | 26.2 | 22.9 | 38.6 | 42.8 | 19.8 |
| f | 21 | 220.9 | 208.3 | 105.5 | 83.3 | 62.7 | 78.8 | 62.4 | 44.5 | 31.2 | 20.8 | 35.1 | 46.5 | 24.7 |
| f | 22 | 240.4 | 223.1 | 111.4 | 93.3 | 68.2 | 89.4 | 70.2 | 43.9 | 38.7 | 20.5 | 42.5 | 52.5 | 23.0 |
| m | 23 | 178.9 | 162.3 | 87.1 | 66.8 | 44.3 | 59.3 | 55.2 | 36.1 | 25.3 | 14.3 | 27.4 | 40.1 | 16.0 |
| sk | 24 | 163.0 | 149.1 | 76.8 | 59.9 | 37.1 | 58.7 | 45.0 | 33.2 | 22.8 | 15.0 | 22.7 | 33.1 | 16.7 |
| <i>heliostemma</i> | | | | | | | | | | | | | | |
| j** | 25 | 58.2 | 53.9 | 28.7 | 24.6 | 15.0 | 18.4 | 16.1 | 11.0 | 6.8 | 8.4 | 8.2 | 9.0 | 6.6 |
| j* | 26 | 97.1 | 87.2 | 51.7 | 42.9 | 21.6 | 36.6 | 29.5 | 19.3 | 12.7 | 11.6 | 13.1 | 16.2 | 12.7 |
| j* | 27 | 50.5 | 46.4 | 25.4 | 22.6 | 10.4 | 16.3 | 15.9 | 8.2 | 6.3 | 7.2 | 7.7 | 9.3 | 6.0 |
| f* | 28 | 119.8 | 109.4 | 61.7 | 52.2 | 28.7 | 43.2 | 35.2 | 27.9 | 13.2 | 13.4 | 18.4 | 23.1 | 12.1 |
| j* | 29 | 79.0 | 75.3 | 40.8 | 36.2 | 19.9 | 30.3 | 24.0 | 16.9 | 8.3 | 11.6 | 11.9 | 15.0 | 9.1 |

Index numbers reference collection data of specimens as in Table 3. PLX=Plastral length maximum; PLM=Plastral length midline; PWA=Plastral width at anterior bridge; PWP=Plastral width at posterior bridge; BL=Bridge length; PWG=Plastral width at outer gular/humeral seam; PWF=Plastral width at outer femoral-anal seam; IG=Intergular length; IH=Interhumeral seam; IP=Interpectoral seam; IA=Interabdominal seam; IF=Interfemoral seam; IAN=Interanal seam.

TABLE 5

Carapace measurements (in mm.) of living specimens, in the collections of W. P. McCord and Chris Hansen, representing five species of Batrachemys: raniceps, tuberculata, nasuta, zuliae, heliostemma and Bufocephala vanderhaegei.

| Species | CL | CW | CD | V1 | V1w | V2 | V2w | V3 | V3w | V4 | V4w | V5 | V5w |
|---------------------|-------|-------|------|------|------|------|------|------|------|------|------|------|------|
| <i>nasuta</i> | | | | | | | | | | | | | |
| f | 223.7 | 169.2 | 61.7 | 42.8 | 66.6 | 32.5 | 45.1 | 36.6 | 39.9 | 26.7 | 37.0 | 34.2 | 49.1 |
| f | 246.6 | 182.2 | 74.7 | 49.0 | 69.8 | 37.2 | 44.3 | 48.9 | 41.1 | 33.1 | 32.3 | 37.4 | 65.6 |
| f | 237.6 | 181.8 | 69.4 | 48.4 | 76.1 | 34.8 | 47.9 | 44.7 | 41.4 | 31.1 | 37.8 | 35.2 | 52.5 |
| m | 281.0 | 213.2 | 84.5 | 58.6 | 79.6 | 41.8 | 48.9 | 43.7 | 42.2 | 34.7 | 34.0 | 59.2 | 63.8 |
| m | 213.9 | 162.3 | 63.8 | 39.6 | 59.0 | 31.8 | 42.4 | 33.2 | 37.8 | 32.9 | 29.8 | 33.9 | 46.2 |
| m | 217.7 | 160.5 | 63.9 | 42.9 | 66.3 | 32.9 | 40.9 | 33.3 | 36.1 | 32.8 | 32.3 | 35.1 | 48.7 |
| m | 177.3 | 139.8 | 54.3 | 35.6 | 52.4 | 25.5 | 37.7 | 29.1 | 34.0 | 22.0 | 30.0 | 30.4 | 40.2 |
| m | 177.4 | 140.2 | 53.5 | 35.8 | 53.8 | 24.6 | 39.3 | 27.7 | 33.6 | 23.2 | 30.9 | 30.5 | 40.3 |
| <i>tuberculata</i> | | | | | | | | | | | | | |
| f | 232.6 | 171.9 | 84.7 | 50.1 | 61.5 | 44.0 | 43.6 | 34.7 | 35.9 | 25.6 | 29.2 | 31.7 | 46.3 |
| f | 160.0 | 117.0 | 53.2 | 32.1 | 46.0 | 25.0 | 33.9 | 24.5 | 30.9 | 22.5 | 24.8 | 26.3 | 35.6 |
| f | 202.7 | 149.1 | 76.0 | 43.9 | 56.7 | 32.6 | 36.8 | 32.1 | 34.5 | 33.0 | 29.3 | 30.7 | 51.9 |
| f | 234.9 | 186.4 | 76.6 | 48.6 | 83.7 | 40.3 | 46.8 | 39.0 | 42.2 | 38.2 | 36.0 | 40.3 | 57.8 |
| f | 191.0 | 149.8 | 72.4 | 42.6 | 65.2 | 32.6 | 31.0 | 31.0 | 29.3 | 27.6 | 23.9 | 26.3 | 45.8 |
| f | 207.0 | 147.8 | 73.1 | 42.7 | 63.7 | 35.1 | 38.6 | 32.7 | 34.2 | 33.5 | 28.5 | 31.0 | 44.7 |
| f | 208.1 | 141.8 | 68.4 | 42.1 | 62.7 | 31.9 | 36.0 | 28.2 | 32.0 | 31.6 | 27.0 | 27.9 | 44.3 |
| m | 173.8 | 123.7 | 61.9 | 34.3 | 51.0 | 29.1 | 33.1 | 27.2 | 29.7 | 25.8 | 23.0 | 30.8 | 40.9 |
| <i>raniceps</i> | | | | | | | | | | | | | |
| f | 194.0 | 137.3 | 61.1 | 42.2 | 53.8 | 28.0 | 37.8 | 27.0 | 32.2 | 25.8 | 28.0 | 29.6 | 47.1 |
| f | 220.9 | 160.7 | 71.0 | 42.3 | 58.6 | 33.2 | 42.4 | 30.4 | 37.2 | 31.6 | 31.7 | 35.0 | 57.8 |
| f | 139.8 | 100.0 | 47.8 | 29.4 | 40.6 | 20.7 | 27.7 | 19.6 | 24.8 | 17.7 | 21.2 | 22.5 | 32.2 |
| f | 129.8 | 95.9 | 43.1 | 28.1 | 36.2 | 18.1 | 27.3 | 17.6 | 24.0 | 16.1 | 20.5 | 20.5 | 30.6 |
| m | 120.1 | 88.5 | 39.6 | 22.3 | 30.6 | 16.9 | 27.1 | 17.0 | 24.2 | 16.3 | 20.5 | 19.0 | 29.5 |
| m | 149.2 | 106.9 | 46.4 | 32.4 | 48.0 | 22.5 | 34.1 | 19.6 | 27.9 | 17.6 | 24.5 | 25.9 | 36.0 |
| m | 123.7 | 95.9 | 38.8 | \ | \ | \ | \ | 17.3 | \ | 14.5 | \ | 20.7 | \ |
| m | 125.7 | 93.8 | 39.6 | 24.6 | 31.0 | 17.1 | 28.7 | 16.6 | 24.9 | 16.3 | 20.1 | 21.5 | 28.4 |
| m | 187.2 | 137.2 | 59.9 | 39.9 | 41.4 | 29.1 | 33.4 | 27.2 | 28.9 | 26.4 | 25.6 | 30.2 | 48.7 |
| m | 219.3 | 156.4 | 62.8 | 42.7 | 48.1 | 31.6 | 35.3 | 29.3 | 31.8 | 28.3 | 29.9 | 38.3 | 56.4 |
| j | 114.7 | 86.2 | 35.2 | 25.2 | 33.3 | 15.7 | 23.5 | 15.1 | 30.1 | 15.0 | 18.6 | 17.3 | 21.6 |
| j | 105.1 | 83.0 | 36.4 | 22.7 | 30.5 | 14.9 | 24.8 | 13.4 | 22.2 | 13.4 | 18.0 | 17.2 | 22.8 |
| <i>heliostemma</i> | | | | | | | | | | | | | |
| f | 140.6 | 108.8 | \ | 28.6 | 49.5 | 21.3 | 40.5 | 19.2 | 39.2 | 19.9 | 34.6 | 24.6 | 36.5 |
| f | 156.5 | 118.9 | \ | 34.1 | 51.3 | 24.0 | 40.1 | 23.8 | 37.3 | 22.0 | 33.5 | 25.1 | 32.1 |
| f | 142.4 | 111.2 | 44.5 | 27.2 | 48.3 | 20.5 | 39.0 | 18.1 | 38.2 | 20.3 | 34.6 | 23.8 | 37.4 |
| f | 155.4 | 122.4 | 45.7 | 33.2 | 47.9 | 23.2 | 38.6 | 21.3 | 35.5 | 21.3 | 28.7 | 24.3 | 32.7 |
| m | 149.3 | 108.7 | 45.0 | 26.7 | 44.2 | 22.6 | 36.7 | 19.4 | 34.4 | 20.3 | 31.1 | 24.1 | 36.9 |
| m | 161.8 | 116.8 | 47.3 | 31.6 | 50.0 | 24.1 | 38.8 | 22.8 | 37.9 | 22.8 | 31.7 | 28.1 | 39.7 |
| m | 161.4 | 122.3 | 49.8 | 33.6 | 50.6 | 22.4 | 38.7 | 22.1 | 36.4 | 22.2 | 31.9 | 25.1 | 32.1 |
| j | 128.1 | 98.1 | 40.9 | 23.2 | 40.4 | 19.4 | 31.8 | 16.9 | 31.2 | 18.2 | 26.6 | 19.9 | 29.9 |
| j | 113.7 | 87.6 | 31.8 | 22.3 | 36.3 | 16.3 | 35.7 | 15.9 | 31.0 | 17.2 | 25.7 | 19.1 | 26.3 |
| <i>zuliae</i> | | | | | | | | | | | | | |
| f | 248.0 | 181.0 | \ | 55.0 | 74.0 | 42.0 | 43.0 | 40.0 | 38.0 | 40.0 | 31.0 | 38.0 | 66.0 |
| f | 286.0 | 192.0 | \ | 61.0 | 79.0 | 49.0 | 43.0 | 43.0 | 40.0 | 43.0 | 36.0 | 52.0 | 71.0 |
| f | 264.0 | 189.0 | \ | 59.0 | 81.0 | 45.0 | 50.0 | 38.0 | 43.0 | 46.0 | 39.0 | 39.0 | 78.0 |
| f | 277.0 | 188.0 | \ | 59.0 | 77.0 | 44.0 | 42.0 | 51.0 | 35.0 | \ | \ | \ | \ |
| f | 235.1 | 163.3 | 70.7 | 51.0 | 70.3 | 37.9 | 39.1 | 34.9 | 36.8 | 37.0 | 31.0 | 34.3 | 63.6 |
| m | 208.3 | 142.5 | 67.1 | 47.8 | 55.1 | 35.1 | 35.1 | 31.8 | 30.1 | 26.8 | 26.9 | 45.4 | 53.0 |
| m | 198.0 | 144.0 | \ | 43.0 | 59.0 | 33.0 | 38.0 | 27.0 | 33.0 | 32.0 | 29.0 | 37.0 | 68.0 |
| m | 148.0 | 108.0 | \ | 28.0 | 41.0 | 27.0 | 31.0 | 20.0 | 28.0 | 20.0 | 21.0 | 30.0 | 44.0 |
| j | 128.0 | 97.0 | \ | 25.0 | 40.0 | 20.0 | 28.0 | 19.0 | 27.0 | 17.0 | 21.0 | 27.0 | 34.0 |
| <i>vanderhaegei</i> | | | | | | | | | | | | | |
| f | 231.4 | 166.1 | 76.3 | 52.9 | 73.8 | 28.5 | 40.6 | 30.8 | 37.1 | 29.7 | 30.6 | 36.8 | 45.9 |
| f | 215.3 | 145.6 | 74.5 | 44.8 | 56.3 | 30.7 | 32.4 | 30.2 | 30.5 | 29.0 | 26.8 | 30.6 | 60.2 |
| f | 233.1 | 167.5 | 74.3 | 56.3 | 74.2 | 30.9 | 41.8 | 34.4 | 39.0 | 32.4 | 32.3 | 39.8 | 46.6 |
| m | 192.1 | 157.1 | 62.5 | 45.0 | 59.9 | 31.0 | 37.3 | 33.2 | 33.1 | 24.0 | 27.6 | 26.5 | 35.1 |

See Table 3 for abbreviations.

TABLE 6

Plastral measurements (in mm.) of living specimens representing five species of Batrachemys: raniceps, tuberculata, nasuta, zuliae, heliostemma and Bufocephala vanderhaegei.

| Species | PLX | PLM | PWA | PWP | BL | PWG | PWF | IG | IH | IP | IA | IF | IAN |
|---------------------|-------|-------|-------|-------|------|------|------|------|------|------|------|------|------|
| <i>nasuta</i> | | | | | | | | | | | | | |
| f | 192.3 | 180.4 | 106.0 | 92.8 | 44.6 | 80.3 | 70.8 | 44.7 | 21.5 | 26.0 | 27.8 | 23.8 | 33.0 |
| f | 217.7 | 202.5 | 123.7 | 101.6 | 52.0 | 72.8 | 76.8 | 47.0 | 23.7 | 22.7 | 35.5 | 39.3 | 32.2 |
| f | 209.3 | 191.6 | 115.7 | 96.2 | 50.0 | 74.2 | 72.8 | 47.6 | 20.9 | 26.2 | 29.1 | 34.6 | 28.4 |
| m | 239.6 | 225.2 | 134.7 | 114.6 | 57.6 | 82.1 | 81.1 | 50.0 | 30.4 | 25.1 | 40.8 | 42.7 | 30.3 |
| m | 190.1 | 174.5 | 108.6 | 90.6 | 45.3 | 68.9 | 68.2 | 39.2 | 24.1 | 23.6 | 27.0 | 28.8 | 26.8 |
| m | 189.2 | 176.9 | 105.4 | 89.1 | 43.4 | 72.0 | 62.4 | 42.7 | 24.9 | 22.6 | 29.8 | 36.1 | 22.5 |
| m | 155.3 | 146.4 | 88.1 | 75.5 | 34.9 | 65.5 | 54.9 | 38.2 | 15.8 | 22.4 | 21.5 | 20.6 | 27.1 |
| m | 156.7 | 146.4 | 87.2 | 74.9 | 33.9 | 65.9 | 54.7 | 38.2 | 15.9 | 21.9 | 20.1 | 20.6 | 26.9 |
| <i>tuberculata</i> | | | | | | | | | | | | | |
| f | 216.6 | 207.1 | 123.7 | 109.8 | 62.6 | 74.1 | 79.2 | 50.7 | 22.2 | 13.5 | 45.8 | 38.3 | 35.2 |
| f | 142.1 | 138.3 | 81.8 | 73.3 | 38.0 | 53.7 | 56.8 | 32.6 | 18.1 | 9.4 | 26.2 | 24.6 | 23.7 |
| f | 196.8 | 191.5 | 105.3 | 95.0 | 58.1 | 66.2 | 70.8 | 45.5 | 22.4 | 17.9 | 37.3 | 36.3 | 30.2 |
| f | 226.4 | 218.4 | 126.5 | 116.2 | 70.3 | 83.3 | 74.3 | 51.8 | 22.4 | 20.3 | 45.1 | 42.4 | 33.5 |
| f | 175.1 | 168.8 | 108.5 | 92.1 | 52.7 | 55.3 | 67.0 | 40.5 | 17.7 | 12.3 | 35.3 | 30.6 | 29.6 |
| f | 195.3 | 186.2 | 107.6 | 95.6 | 57.9 | 71.9 | 71.2 | 42.7 | 24.7 | 13.3 | 40.3 | 28.0 | 34.4 |
| f | 182.1 | 174.9 | 100.0 | 90.6 | 53.3 | 60.4 | 61.1 | 39.2 | 25.1 | 12.7 | 37.2 | 32.4 | 24.2 |
| m | 164.4 | 156.4 | 79.9 | 66.4 | 47.1 | 55.9 | \ | \ | \ | \ | \ | \ | \ |
| <i>raniceps</i> | | | | | | | | | | | | | |
| f | 166.5 | 152.9 | 83.7 | 77.5 | 39.3 | 62.0 | 53.6 | 34.2 | 18.6 | 20.6 | 26.7 | 34.1 | 13.6 |
| f | 207.6 | 190.9 | 106.2 | 92.1 | 57.2 | 69.8 | 71.6 | 39.9 | 25.1 | 30.2 | 35.4 | 35.4 | 23.1 |
| f | 122.1 | 113.1 | 64.6 | 58.5 | 30.1 | 41.9 | 38.7 | 24.7 | 14.8 | 13.8 | 17.7 | 24.3 | 13.6 |
| f | 120.3 | 110.0 | 62.6 | 54.4 | 27.7 | 40.5 | 40.9 | 24.7 | 16.0 | 12.6 | 17.0 | 20.9 | 14.2 |
| m | 107.1 | 99.3 | 56.2 | 52.0 | 25.7 | 39.0 | 35.8 | 20.7 | 15.6 | 12.6 | 14.6 | 20.0 | 12.5 |
| m | 135.8 | 124.6 | 69.2 | 64.3 | 32.3 | 50.8 | 44.5 | 27.1 | 18.8 | 16.7 | 15.8 | 29.7 | 13.4 |
| m | 112.4 | 101.7 | 58.1 | 50.6 | 27.2 | 42.6 | 37.0 | 25.7 | 10.6 | 17.5 | 10.6 | 18.9 | 14.2 |
| m | 113.1 | 101.3 | 59.1 | 52.9 | 27.5 | 41.9 | 37.1 | 24.5 | 12.5 | 13.5 | 14.6 | 20.5 | 11.5 |
| m | 166.1 | 151.3 | 85.7 | 81.9 | 45.1 | 51.0 | 62.1 | 29.5 | 19.5 | 19.9 | 26.3 | 31.6 | 20.7 |
| m | 196.5 | 173.9 | 105.0 | 86.6 | 50.2 | 71.2 | 66.8 | 41.4 | 19.1 | 24.5 | 27.8 | 35.6 | 19.8 |
| j | 98.4 | 89.4 | 54.6 | 48.7 | 24.5 | 33.2 | 34.9 | 22.0 | 11.3 | 12.3 | 12.1 | 17.0 | 11.2 |
| j | 95.5 | 84.9 | 50.5 | 45.3 | 22.5 | 38.0 | 31.7 | 18.9 | 11.1 | 13.5 | 10.1 | 17.9 | 10.6 |
| <i>heliostemma</i> | | | | | | | | | | | | | |
| f | 111.7 | \ | 65.2 | \ | \ | \ | \ | \ | \ | \ | \ | \ | \ |
| f | 124.9 | \ | 74.6 | \ | \ | \ | \ | \ | \ | \ | \ | \ | \ |
| f | 113.8 | 121.2 | 65.6 | 57.2 | 30.6 | 46.0 | 38.8 | 27.5 | 14.2 | 17.2 | 13.8 | 21.5 | 16.3 |
| f | 121.2 | 134.8 | 76.2 | 35.3 | 30.7 | 50.2 | 44.9 | 31.4 | 13.1 | 13.5 | 18.1 | 22.6 | 16.8 |
| m | 113.8 | 124.3 | 64.3 | 53.7 | 29.1 | 51.7 | 40.0 | 27.5 | 14.5 | 17.1 | 12.6 | 21.6 | 16.0 |
| m | 128.0 | 140.4 | 75.4 | 62.7 | 32.6 | 56.7 | 40.8 | 32.5 | 14.2 | 19.8 | 16.4 | 23.4 | 18.9 |
| m | 125.9 | 139.0 | 76.3 | 62.7 | 33.0 | 54.3 | 43.5 | 30.7 | 15.8 | 15.2 | 16.4 | 25.3 | 18.8 |
| j | 103.1 | 111.8 | 57.2 | 49.6 | 27.3 | 42.5 | 33.9 | 24.4 | 12.7 | 15.0 | 13.6 | 19.0 | 13.5 |
| j | 95.7 | 87.5 | 51.8 | 43.1 | 21.1 | 37.1 | 29.9 | 18.5 | 12.7 | 11.8 | 12.8 | 15.8 | 12.1 |
| <i>zuliae</i> | | | | | | | | | | | | | |
| f | 213.0 | 191.0 | 105.0 | 86.0 | 56.0 | 75.0 | \ | 41.0 | 32.0 | 20.0 | 33.0 | 53.0 | 18.0 |
| f | 225.0 | 211.0 | 116.0 | 88.0 | 61.0 | 73.0 | \ | 41.0 | 38.0 | 17.0 | 42.0 | 50.0 | 23.0 |
| f | 232.0 | 212.0 | 108.0 | 86.0 | 63.0 | 72.0 | \ | 39.0 | 36.0 | 22.0 | 48.0 | 54.0 | 22.0 |
| f | 215.0 | 196.0 | 35.0 | 82.0 | 52.0 | 72.0 | \ | 41.0 | 32.0 | 23.0 | 35.0 | 50.0 | 24.0 |
| f | 202.3 | 188.3 | 98.0 | 76.8 | 53.7 | 76.1 | 57.1 | 37.5 | 26.7 | 24.9 | 31.7 | 42.0 | 22.5 |
| m | 178.3 | 163.9 | 80.7 | 60.9 | 40.2 | 67.7 | 53.8 | 35.9 | 25.7 | 16.1 | 25.8 | 37.4 | 18.7 |
| m | 171.0 | 157.0 | 78.0 | 35.0 | 39.0 | 60.0 | \ | 37.0 | 27.0 | 17.0 | 25.0 | 31.0 | 18.0 |
| m | 128.0 | 119.0 | 65.0 | 49.0 | 28.0 | 52.0 | \ | 26.0 | 17.0 | 13.0 | 14.0 | 27.0 | 14.0 |
| j | 110.0 | 104.0 | 56.0 | 44.0 | 29.0 | 39.0 | \ | 22.0 | 15.0 | 14.0 | 14.0 | 21.0 | 16.0 |
| <i>vanderhaegei</i> | | | | | | | | | | | | | |
| f | 197.3 | 181.0 | 113.6 | 100.1 | 50.2 | 67.7 | 73.9 | 40.4 | 26.9 | 19.2 | 30.4 | 36.9 | 24.9 |
| f | 192.9 | 179.6 | 103.9 | 87.2 | 48.3 | 66.6 | 72.4 | 38.3 | 31.4 | 11.8 | 33.9 | 39.1 | 23.5 |
| f | 199.1 | 182.8 | 115.2 | 100.5 | 49.2 | 69.4 | 74.4 | 39.5 | 27.4 | 17.3 | 30.2 | 37.0 | 25.3 |
| m | 171.3 | 156.5 | 91.8 | 79.8 | 37.0 | 59.9 | 61.4 | 37.4 | 20.0 | 17.1 | 24.1 | 32.2 | 23.0 |

See Table 4 for abbreviations.

TABLE 7

Skull measurements (in mm.) of living specimens representing five species of *Batrachemys*: *raniceps*, *tuberculata*, *nasuta*, *zuliae*, *heliostemma* and *Bufocephala vanderhaegei*.

| Species | HL | HW | HD | IOW | PW |
|---------------------|------|------|------|------|-----|
| <i>nasuta</i> | | | | | |
| f | 63.4 | 53.2 | 28.5 | 11.2 | 6.6 |
| f | 69.9 | 62.3 | 33.0 | 13.9 | 5.8 |
| f | 66.5 | 59.2 | 30.7 | 12.3 | 5.3 |
| m | 88.9 | 75.2 | 41.8 | 16.2 | 7.2 |
| m | 68.4 | 57.2 | 31.7 | 8.9 | 5.6 |
| m | 61.3 | 54.5 | 30.4 | 11.1 | 6.6 |
| m | 50.9 | 45.6 | 25.0 | 8.4 | 5.8 |
| m | 51.4 | 45.6 | 24.6 | 8.6 | 5.8 |
| <i>tuberculata</i> | | | | | |
| f | 65.2 | 57.7 | 34.6 | 14.8 | 7.0 |
| f | 47.3 | 40.6 | 25.1 | 8.4 | 4.5 |
| f | 57.5 | 50.2 | 28.7 | 9.7 | 4.8 |
| f | 65.8 | 58.0 | 37.3 | 14.6 | 6.2 |
| f | 53.9 | 46.3 | 28.2 | 10.4 | 7.0 |
| f | 58.2 | 52.3 | 30.7 | 11.2 | 7.1 |
| f | 56.2 | 48.7 | 27.1 | 10.3 | 4.3 |
| m | 50.9 | 42.4 | 24.7 | 10.4 | 4.4 |
| <i>raniceps</i> | | | | | |
| f | 56.1 | 51.4 | 25.9 | 11.8 | 3.5 |
| f | 69.8 | 58.6 | 28.8 | 11.7 | 4.2 |
| f | 43.6 | 39.5 | 20.6 | 7.9 | 3.5 |
| f | 41.7 | 36.9 | 19.4 | 7.1 | 2.8 |
| m | 37.5 | 35.1 | 17.8 | 5.2 | 3.1 |
| m | 47.0 | 42.3 | 19.8 | 9.0 | 2.7 |
| m | 39.4 | 33.6 | 17.9 | 6.6 | 3.4 |
| m | 38.0 | 34.2 | 17.8 | 7.2 | 3.6 |
| m | 52.3 | 48.0 | 22.4 | 10.0 | 3.2 |
| m | 67.3 | 54.5 | 28.2 | 12.5 | 3.6 |
| j | 37.5 | 32.2 | 17.8 | 6.8 | 4.0 |
| j | 33.6 | 30.4 | 15.6 | 5.3 | 2.8 |
| <i>heliostemma</i> | | | | | |
| f | 35.6 | 34.2 | 7.7 | 6.9 | 7.3 |
| f | 41.2 | 37.8 | 9.8 | 8.3 | 7.7 |
| f | 39.8 | 35.0 | 19.8 | 5.6 | 6.6 |
| f | 42.4 | 36.4 | 20.3 | 6.8 | 6.7 |
| m | 41.6 | 36.1 | 18.9 | 6.3 | 4.7 |
| m | 46.5 | 38.3 | 20.6 | 7.5 | 4.9 |
| m | 44.7 | 38.6 | 20.1 | 7.3 | 5.8 |
| j | 36.5 | 31.5 | 16.5 | 3.8 | 4.2 |
| j | 32.6 | 26.8 | 16.5 | 6.0 | 4.0 |
| <i>zuliae</i> | | | | | |
| f | 76.0 | 65.0 | 34.0 | 26.0 | 4.0 |
| f | 88.0 | 82.0 | 45.0 | 26.0 | 7.0 |
| f | 81.0 | 67.0 | 37.0 | 24.0 | 7.0 |
| f | 77.0 | 66.0 | 38.0 | 28.0 | 8.0 |
| f | 67.8 | 61.2 | 36.4 | 9.8 | 5.3 |
| m | 63.2 | 52.6 | 29.7 | 9.2 | 6.5 |
| m | 63.0 | 52.0 | 34.0 | 23.0 | 5.0 |
| m | 46.0 | 37.0 | 22.0 | 16.0 | 7.0 |
| j | 38.0 | 35.0 | 18.0 | 15.0 | 3.0 |
| <i>vanderhaegei</i> | | | | | |
| f | 57.4 | 47.7 | 24.2 | 10.6 | 8.0 |
| f | 54.7 | 46.7 | 25.8 | 10.7 | 4.1 |
| f | 57.1 | 47.4 | 23.7 | 10.8 | 6.0 |
| m | 45.2 | 39.8 | 22.0 | 9.7 | 8.5 |

See Table 2 for abbreviations.

After reviewing both osteological and morphological characteristics of currently recognized species within the genera *Batrachemys*, *Mesoclemmys* and *Phrynops* (Appendix B), we find the need for further taxonomic clarification. Our data compel us to leave the “*Phrynops geoffroanus* complex” (including *P. geoffroanus* [generotype], *P. tuberosus*, *P. williamsi* and *P. hilarii*) in the genus *Phrynops*; to re-allocate *P. rufipes* and *P. hogei* each to their own monotypic genus; to leave *Mesoclemmys gibba* as generotype of the monotypic genus *Mesoclemmys*; to leave the “*Batrachemys nasuta* complex” (*B. nasuta* [generotype], *B. raniceps*, *B. dahli*, *B. zuliae* and *B. tuberculata*) in the genus *Batrachemys*; and to create a monotypic genus for *Batrachemys vanderhaegei*.

Since *Phrynops (Rhinemys) rufipes* is the generotype of *Rhinemys*, which as a genus was earlier (Gray, 1844) synonymized with *Phrynops* (see above), we herein resurrect the genus name *Rhinemys* for this species. Of the 19 characters (Appendix B) examined, *Rhinemys rufipes* and members of the *P. geoffroanus* complex share only 32% (i.e., # 2, 3, 8, 9, 10, and 18), whereas compared to each other, the four members of the *P. geoffroanus* complex (*P. geoffroanus*, *P. tuberosus*, *P. williamsi* and *P. hilarii*) share 84%. This justifies the removal of the species *rufipes* from the genus *Phrynops*.

Phrynops hogei Mertens, 1967, was originally described in the genus *Phrynops*; however, this species is distinct from all other members of that genus as defined herein. It is said to be the most osteologically divergent member of the genus *Phrynops* (Rhodin, in Reed *et al.* 1991). When compared to the *P. geoffroanus* complex, it shares at most 37% of the characters tabulated in Appendix B (i.e., # 6, 7, 9?, 10?, 11, 14, and 15). We herein propose the new monotypic genus *Ranacephala*, to include the species *R. hogei* as the generotype. In addition, *Rhinemys rufipes* shares at most 37% of the characters in Appendix B (i.e., # 5, 7, 9?, 10?, 13, 16, and 19) with *Ranacephala hogei*, supporting the recognition of these two forms in separate genera.

Similarly, as noted by two other investigators (Bour, 1973; Bour and Pauler, 1987), we believe that the affinities of *Batrachemys vanderhaegei* lie somewhere between *Mesoclemmys* and *Batrachemys*. *Batrachemys vanderhaegei* shares 37% of the characters in Appendix B (i.e., # 1, 5, 9, 11, 16, 18 and 19) with *M. gibba*; 37% of the characters in Appendix B (i.e., # 5, 6, 9, 11, 14, 15 and 19) with *B. nasuta*; and 32% of the characters in Appendix B (i.e., # 3, 6, 9, 14, 15, 18) with *B. tuberculata*. For comparison, the members of the “*Batrachemys nasuta* complex” (*B. dahli*, *B. nasuta*, *B. raniceps*, *B. tuberculata*, *B. zuliae*) share at least 79% (all but # 1, 11, 12, 19) of the characters represented in Appendix B. This demonstrates that the affinities of *B. vanderhaegei* do not lie with either *Mesoclemmys* or *Batrachemys*. The new monotypic genus name *Bufocephala* is herein proposed, to include the generotype *B. vanderhaegei*.

In order to test our generic arrangement for the toadheads, we undertook a cladistic analysis (using PAUP 3.1) of the characters scored in Table 1. The resulting cladogram (Fig. 2) further supports our taxonomic conclusions.

MESOCLEMMYS Gray 1873a

Type Species. – *Emys gibba* Schweigger 1812, by monotypy.

Vernacular Name. – The Humpbacked Toadheads (*gibba* = Latin for “hump”, “bump”).

Etymology. – Greek, *mesos* for “middle” or “in between”, and Greek, *klemmys* for “turtle.” The “intermediate turtle”- “between *Hydraspis* and *Platemys*,” according to Gray, 1873b: 305.

Grammatical gender: feminine.

Diagnosis and Description. - The genus *Mesoclemmys* is part of the toadhead complex of chelid turtles with the following characteristics: A head width between the tympana 15-20% of the median straight length of the carapace. Three to four neural bones (sometimes none) are usually present. The first neural bone

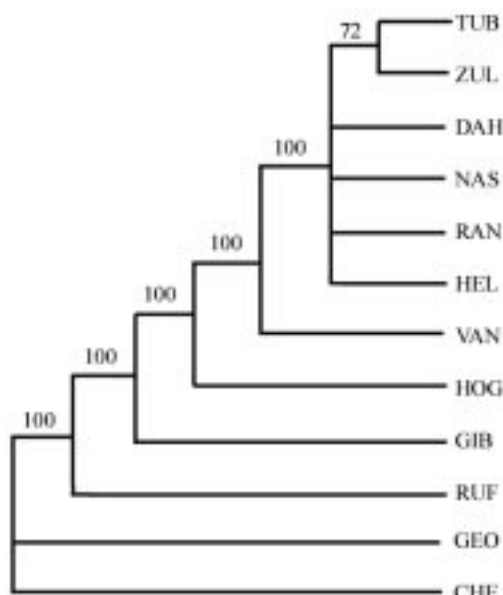


Fig. 2. Strict consensus tree of relationships of toadheads, based on maximum parsimony analysis (PAUP 3.1) of 18 characters coded in Table 1 (based on data in Appendix B). Outgroup taxon is *Chelus fimbriata*. 50% Majority Rule, shortest trees (29) had 38 steps (CI=0.58; RI=0.69).

is absent, allowing the first costals to contact medially. The neurals, when present, may or may not be in a contiguous row. The nuchal reaches the anterior margin of the carapace. There is no large, round scale present distally on the antero-medial row of tibial scales. The 11th marginal is narrower than the supracaudals. The lateral borders of the carapace narrow mildly, with a strong upward curve. The vertebrals are arched, with the median keel on vertebrals 3, 4, and 5 poorly developed. The anterior end of the plastron is equal to or wider than the posterior end. The interanal plastral seam is shorter than the interhumeral seam. The dorsum of the head is covered by many small scales. The paired barbels are short to medium in size.

Skull. – The skull is relatively smaller than other toadheads. The nasal is long and thin. The quadrate points considerably inward. The exoccipital, supraoccipital, ophisthotic (a cartilaginous bone that ossifies in the posterior half of the otic capsule, according to Gaffney, 1979) and squamosal bones are reduced. The parietals are wide above (dorsally) and some-

what hourglass-shaped. At the narrowest point the parietal roof width is never less than the horizontal diameter of the orbit. The parieto-squamosal arches are narrow and pass above, but not posterior to the rear margin of the opisthotic bones. There is lack of symphyseal fusion in the mandible. The chelid foramen (McDowell, 1983) or foramen retropterygoideum (Bour and Pauler, 1987) is well developed.

Comparisons. – *Mesoclemmys*, as a genus, was originally created because *Emys gibba* was distinct from the other toadheads. It shares some features of both *Phrynops* and *Batrachemys*. For example, the snout is pointed (as in *Batrachemys*), the parietals are broadened above (as in *Phrynops*), the parieto-squamosal arches are narrow (as in *Batrachemys*); the parieto-squamosal arches pass directly above but not posterior to the rear margin of the opisthotic bones (as in *Phrynops*), and the first neural bone is absent, allowing the first pair of costals to contact medially (as in *Batrachemys*).

Content. – *Mesoclemmys gibba* (Schweigger, 1812). Only one monotypic species is recognized, but there is clearly an east-west cline, for instance with the head coloration, darker westwards (Bour and Pauler, 1987:7).

Distribution. – Orinoco to Amazon river basins in Colombia, eastern Ecuador, Peru, Venezuela, the Guianas and northern Brazil; Trinidad (Iverson, 1992).

Preserved Material Examined. – See Appendix A (Also many specimens in senior author's preserved and live collection).

PHRYNOPS Wagler 1830

Type Species. – *Emys geoffroana* Schweigger 1812, by monotypy.

Vernacular Name. – The Bearded Toadheads.

Etymology. – Greek, *phryne* for “toad” and Greek, *ops* for “appearance.” The “Toad-like Turtle.” (cf. Wagler, 1830: 135).

Grammatical gender: masculine (Bour 1973).

Diagnosis and Description. - The genus *Phrynops* is a member of the toadhead complex of chelid turtles, with the following characteristics: The head is flat and wide, with a blunt snout, and has a width between the tympana 15-20% of the median straight length of the carapace. Five to seven neural bones are present, usually in a contiguous anterior series. The first neural bone is present, contacting the proneural, and separates the first pair of costals. The carapace is relatively flat. The entoplastron is reduced, separating only the epiplastrals and very little of the hyoplastrals. The 11th marginals are wider than the supracaudals. The lateral borders of the carapace are not upturned and without narrowing. There is no large round scale present at the distal end of the antero-medial row of tibial scales. The interanal seam of the plastron is longer than the interhumeral seam. The paired barbels usually are long.

Skull. - The nasal bone is short and thick. Both the jugal and postorbital are long and wide, so the orbits are situated somewhat dorsally on the skull. The maxilla is long and wide so the front of the face is rounded. There is a lack of symphyseal fusion in the mandible. The parieto-squamosal arch is substantial and passes above but not posterior to the rear margin of the opisthotic bones. The parietals are broadened, often hourglass-shaped above (dorsally). At the narrowest point the parietal roof width is never less than the horizontal diameter of the orbit. The chelid foramen is present in the genotype *P. geoffroanus* (R. Bour and E. Gaffney pers. comm.), and in the other presently recognized species of the *P. geoffroanus* complex (R. Bour pers. comm.).

Comparisons. - See Appendix B to compare 19 characters of every toadhead genotype.

Content. - *Phrynops geoffroanus* (Schweigger 1812); *P. tuberosus* (Peters 1870); *P. hilarii* (Duméril and Bibron, 1835); *P. williamsi* Rhodin and Mittermeier, 1983.

Distribution. - Orinoco to Amazon and São Francisco to Paraná and adjacent river

basins of Colombia, Venezuela, the Guianas, Brazil, Paraguay, Uruguay and northeastern Argentina (Iverson, 1992).

Preserved Material Examined. - See Appendix A (Also many specimens in senior author's preserved and live collection).

Comment. - Although disputed by some, *Phrynops tuberosus* was recognized as a full species originally by Peters (1870), and since by Froes (1957), Rhodin and Mittermeier (1983), David (1994), Fritz *et al.* (1994) and again herein.

BATRACHEMYS Stejneger 1909

Type Species. - *Emys nasuta* Schweigger 1812, by original designation of Stejneger.

Vernacular Name. - The Northern Toadheads.

Etymology. - Greek, *batrachos* for "frog," and Greek, *emys* for "freshwater turtle." The "Frog Turtle."

Grammatical gender: feminine.

Diagnosis and Description. - The genus *Batrachemys* is a member of the toadhead group of chelid turtles with the following characteristics: The snout is pointed. The carapace is relatively broad, as is the head, whose width between the tympana is 20% or more of the median straight length of the carapace. The neck is relatively thin and short. Zero to five reduced neural bones (usually 3 - 4) may be present and are sometimes discontinuous. The first neural is absent, allowing the first pair of costal bones to contact medially (as with *Mesoclemmys*, but not *Phrynops*, which has a first neural). The interanal seam of the plastron is usually longer than the interhumeral seam, but sometimes equal or shorter. The 11th marginals are narrower than or equal to the width of the supracaudals. A well-developed scale is present at the distal end of the antero-medial row of tibial scales. The paired barbels are small.

Skull. - The nasal bone is short and thick. The jugal and postorbital are short and wide, situating the orbit at the center of the maxilla. The prefrontal and frontal are somewhat smaller,

not reaching as far forward as in *Phrynops*. There is lack of symphyseal fusion in the mandible. The parieto-squamosal arch is narrow and posteriorly displaced, reaching caudally beyond the posterior margin of the opisthotic bones. The parietal roof is somewhat parallel-sided, narrow, and sometimes ridged. The width of the parietal roof at its narrowest point is less than the horizontal diameter of the orbit. The chelid foramen is present in all species presently included in this genus (Bour and Pauler, 1987).

Comparisons. – See Appendix B to compare 19 characters of every toadhead genotype.

Content. – *Batrachemys nasuta* (Schweigger 1812); *B. dahli* (Zangerl and Medem 1958); *B. zuliae* (Pritchard and Trebbau 1984); *B. tuberculata* (Luederwaldt 1926); *B. heliostemma* sp. nov.; *B. raniceps* (Gray 1855; synonymized under *R. nasuta* by Boulenger 1889; resurrected by Bour and Pauler 1987).

Distribution. – Includes *B. heliostemma* sp. nov. in the upper Amazon basin from southern Venezuela, western Brazil, northeastern Peru, and eastern Ecuador to southeastern Colombia, overlapped by *B. raniceps* found in the upper Orinoco to Amazon river basins in eastern Colombia, southern Venezuela, Peru, Brazil and Bolivia; *B. tuberculata* in eastern Brazil in the Rio São Francisco and adjacent basins; *B. nasuta* in the Guianas and adjacent Brazil; *B. dahli* in northeastern Colombia; and *B. zuliae* found in the basins draining with the western shore of Lake Maracaibo, Venezuela (Iverson, 1992).

Preserved Material Examined. – See Appendix A (Also many specimens in senior author's preserved and live collection).

Comment. – *Batrachemys* (as represented by *B. dahli*) is the only living chelid genus found west of the Andes Mountains (Medem 1966).

RHINEMYS Wagler 1830 gen. resurrected.

Type Species. – *Emys rufipes* Spix 1824, by subsequent designation of Fitzinger 1843.

Vernacular Name. – The Red Toadheads.

Etymology. – From the Greek *rhinos* meaning “nose,” and the Greek *emys* meaning “freshwater turtle.” The “Big-nosed Freshwater Turtle.”

Grammatical gender: feminine.

Diagnosis. – A toadhead turtle of the family Chelidae distinguished from all others by having red coloration of the head and limbs. Further distinguished by having a medium-sized head (similar to *P. geoffroanus* and *B. vanderhaegei*); nostrils (snout) much more prominent than any other toadhead; barbels small (as in all *Batrachemys*; not as large as *Phrynops*); the widest parietal roof in any toadhead (over 30% HW in juveniles); 5-8 neural bones (as in *Phrynops*; more than *Mesoclemmys* and *Batrachemys*); the first neural touching the proneural (as in *Phrynops*); the intergular wider than the gulars (as with all toadheads but *R. hoguei*, *P. geoffroanus*, *B. tuberculata* and *B. heliostemma*); the interfemoral plastral seam longest (as in *B. dahli* and often in *P. geoffroanus*); a domed carapace (as in *R. hoguei* and *M. gibba*); a vertebral keel present (as in *M. gibba*); a carapacial groove absent (as in *M. gibba*); the 11th marginals narrower than the 12th (as in *R. hoguei*, *B. vanderhaegei* and *M. gibba*); a mildly developed antero-medial distal tibial scale (as in *M. gibba*); no upturn of lateral marginals (as in *P. geoffroanus*); and a solid yellow plastron (as in *R. hoguei*, *B. dahli* and *B. zuliae*). The chelid foramen is present (R. Bour pers. comm. from examination of the holotype).

Description. – A full description of the only included species (*E. rufipes*) is provided in the original description by Spix (1824), again by Medem (1975), and with further details provided by Lamar and Medem (1982); see also Appendix B.

Comparisons. – See Appendix B to compare 19 characters of every toadhead genotype.

Content. – Includes only *Rhinemys rufipes*.

Distribution. – Primarily the mid- to upper Amazon Basin, but see Lamar and Medem (1982) for further details.

Preserved Material Examined. – See Appendix A. (Also 4 living specimens in the senior author's collection).

RANACEPHALA gen. nov.

Type Species. – *Phrynops hoguei* Mertens 1967, by present designation.

Vernacular Name. – The Rio Paraiba Toadheads.

Etymology. – Latin, *rana* for “frog,” and Greek, *kephale* for “head.” The “Froghead Turtle.” (The generotype was named in honor of Dr. A. R. Hoge, from the Instituto Butantan in São Paulo, Brazil).

Grammatical gender: feminine.

Diagnosis. – A toadhead turtle of the family Chelidae distinguished by having a distinct bicolor head (as in *B. nasuta*); a relatively small head (as in *M. gibba*); a pointed snout (as in all toadheads but the *P. geoffroanus* complex); large barbels (most similar to *P. geoffroanus*); wide parietal roof width in adults (as in *M. gibba* and *P. geoffroanus*); intergular scute narrower than gulars (as in *P. geoffroanus*, *B. tuberculata*, and *B. heliostemma*); interabdominal seam (of plastral seam formula) longest (unique to *R. hoguei*); carapace domed (as in *R. rufipes* and *M. gibba*); the lack of a vertebral keel (as in all toadheads but *R. rufipes* and *M. gibba*); carapacial median groove present in mature adults (as in all toadheads but *R. rufipes* and *M. gibba*); 11th marginal narrower than 12th (as in *R. rufipes*, *M. gibba* and *B. vanderhaegei*); the antero-medial distal tibial scale is well developed, (as in *B. zuliae*, *B. raniceps*, *B. tuberculata*, *B. nasuta* and *B. heliostemma*); the lateral marginals upturned (as with all toadheads but *R. rufipes* and *P. geoffroanus*, but with *Ranacephala* the upturn is “sharp” as in *M. gibba*, *B. vanderhaegei*, *B. dahli*, *B. zuliae*, and *B. tuberculata*); and plastron solid yellow (as in *R. rufipes*, *B. dahli* and *B. zuliae*). The chelid foramen is thought to be present, but this is not confirmed (R. Bour pers. comm.). Data on the neural series are unconfirmed at this time due to lack of skeletonized specimens.

Description. – A full description of the only included species (*P. hoguei*) is provided by Mertens (1967) and further details are given by Rhodin *et al.* (1982); see also Appendix B.

Comparisons. – See Appendix B to compare 19 characters of every toadhead genotype.

Content. – Includes only *Ranacephala hoguei* (Mertens 1967).

Distribution. – Found in low-lying areas of the Rio Paraiba drainage of Rio de Janeiro, and southern Minas Gerais, north to coastal Espírito Santo in Brazil (Mittermeier *et al.* 1980).

Preserved Material Examined. – See Appendix A.

BUFOCEPHALA gen. nov.

Type Species. – *Phrynops vanderhaegei* Bour 1973, by present designation.

Vernacular Name. – The Southern Toadheads.

Etymology. – Latin, *bufo* for “toad,” and Greek, *kephale* for “head.” The “Toadhead Turtle.” (The generotype was named in honor of Maurice Vanderhaege, a cheloniophile and friend of R. Bour).

Grammatical gender: feminine.

Diagnosis. – A toadhead turtle of the family Chelidae distinguished by having a generally blackish head in adults (as in *M. gibba* and *B. heliostemma*); a medium-sized head (as in *R. rufipes* and *P. geoffroanus*); a horizontal “bar” in the iris of the eye [= iris] (as in *B. dahli* and *B. zuliae*); nose pointed (as in all toadheads except the *P. geoffroanus* complex); small barbels (as in all toadheads but *R. hoguei*, and the *P. geoffroanus* complex); parietal roof width moderate, as in no other toadhead; reduced neural series (as in all toadheads [*R. hoguei* ?] but the *P. geoffroanus* complex and *R. rufipes*), but unique in having a usually discontinuous series, often with a first neural present, that does not touch the proneural; intergular wider than gulars (as in all toadheads but *R. hoguei*, *P. geoffroanus*, *B. tuberculata* and *B. heliostemma*); plastral seam

formula starts with IG>IF>Iab (as in *B. dahli*, *B. raniceps*, *B. nasuta*, *B. heliostemma*, and sometimes *M. gibba* and *P. geoffroanus*); the carapace is mildly domed (unique to *B. vanderhaegei*); no carapacial median keel (as in all toadheads but *R. rufipes* and *M. gibba*); carapacial median groove present in adults (as in all toadheads but *R. rufipes* and *M. gibba*); 11th marginals narrower than 12th (as in *R. hoguei*, *R. rufipes* and *M. gibba*); the antero-medial distal tibial scale moderately developed (as in *B. dahli* and *P. geoffroanus*); the lateral marginal scutes upturned (as in all toadheads but *R. rufipes* and *P. geoffroanus*, but with *Bufocephala* the upturn is “sharp”, as in *M. gibba*, *R. hoguei*, *B. dahli*, *B. zuliae* and *B. tuberculata*); there is obvious narrowing of the lateral marginals of the carapace, a unique condition among toadheads; plastron generally black with yellow background (as in many *M. gibba*, and similar to that in *B. raniceps*, *B. nasuta* and *B. heliostemma*); axillary scutes absent in the Paraguayan population (as in *R. rufipes*, *B. zuliae*, and sometimes *B. nasuta* and *B. dahli*). The chelid foramen is present (Bour and Pauler 1987).

Description. – A full description of the only included species (*B. vanderhaegei*) is provided in the original description by Bour (1973) with further details given by Bour and Pauler (1987); see also Appendix B.

Comparisons. – See Appendix B to compare 19 characters of every toadhead genotype.

Content. – Includes only *Bufocephala vanderhaegei*.

Distribution. – Basins of Paraguay and Parana rivers in Paraguay, Brazil and northern Argentina.

Preserved Material Examined. – See Appendix A. (Also 10 living specimens in the senior author’s collection).

A NEW SPECIES OF *BATRACHEMYS*

In the early 1990’s, one of the authors (WWL) observed several distinctive toadheads near Iquitos, Peru, in the western Amazon basin. In 1984, Roy W. McDiarmid had also collected this distinct toadhead during the Cerro de La Neblina expedition, Venezuela. Independently, Roger Bour discovered a young specimen in the collections of the British Museum. Then at approximately the same time, Chris Hansen of Florida recognized the same taxon among juvenile offspring from a shipment originating in Iquitos that had passed through the pet trade facility at which he was employed.

All specimens, brought to the attention of the senior author displayed bright yellow-orange facial bands (Figs. 3 and 4) which easily separated them from all other toadheads. These specimens from populations in the Iquitos region of eastern Peru and the Neblina region of southern Venezuela in the upper Amazon clearly represent an undescribed species belonging to the genus *Batrachemys* as defined herein.

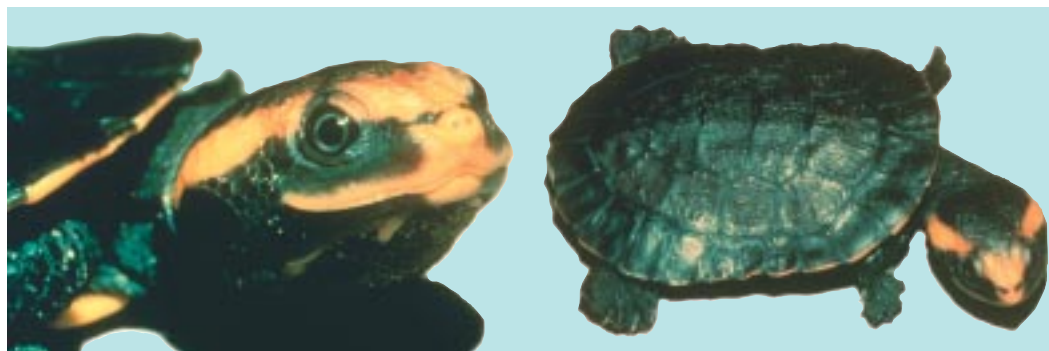


Fig. 3. Juvenile *Batrachemys heliostemma* sp. nov., (68.7 mm. carapace length) exhibiting its unique yellow-orange facial bands. This head pattern is lost with age, eventually becoming black. Same specimen appears as adult in figure 8-B.

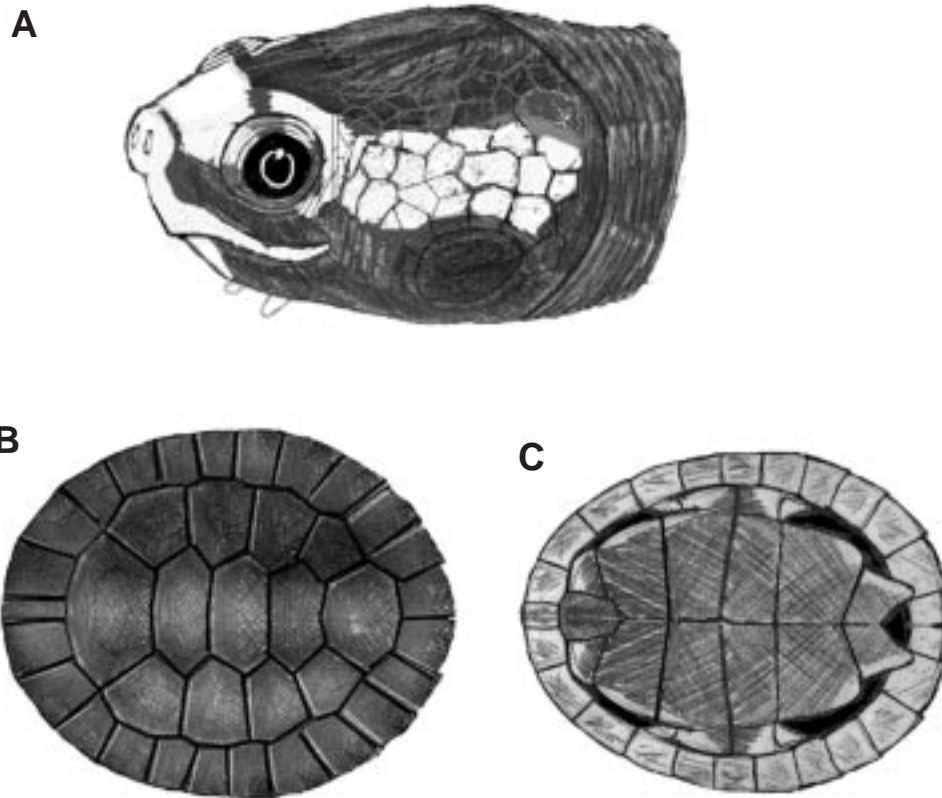


Fig. 4. *Batrachemys heliostemma* sp. nov.: Artistic rendering (by M.J. Ouni) of the head (top), carapace (lower left), and plastron (lower right) of juvenile. Specimen alive in the collection of Carlos Rivera.

AMAZON TOADHEAD

Batrachemys heliostemma sp. nov.

Holotype. – Smithsonian Institution (USNM) 541895, juvenile preserved in alcohol, measuring 71.3 mm carapace length, from the base of Pico da Neblina (situated on the Venezuela/Brazil border) on the left bank of Río Baria (=Río Mawarinuma) [4° 95' N, 66° 10' W], a tributary of the Rio Negro, Amazonas, Venezuela, collected by Roy W. McDiarmid on 17 March, 1984 (Figs. 5 and 6a-c).

Paratypes. – Leiden Museum (RMNH) 31998, juvenile preserved in alcohol, measuring 112.8 mm carapace length, from Callao, on the north bank of the Río Tapiche [5° 21' S, 47° 9' W],

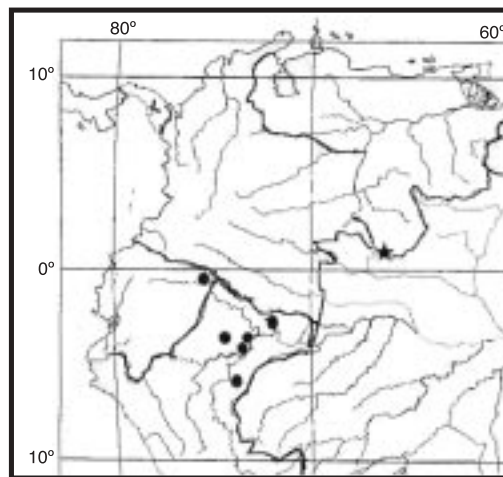


Fig. 5. The distribution of *Batrachemys heliostemma* sp. nov. in Ecuador, Peru, and Venezuela, South America (star indicates holotype; dots indicate other documented localities).

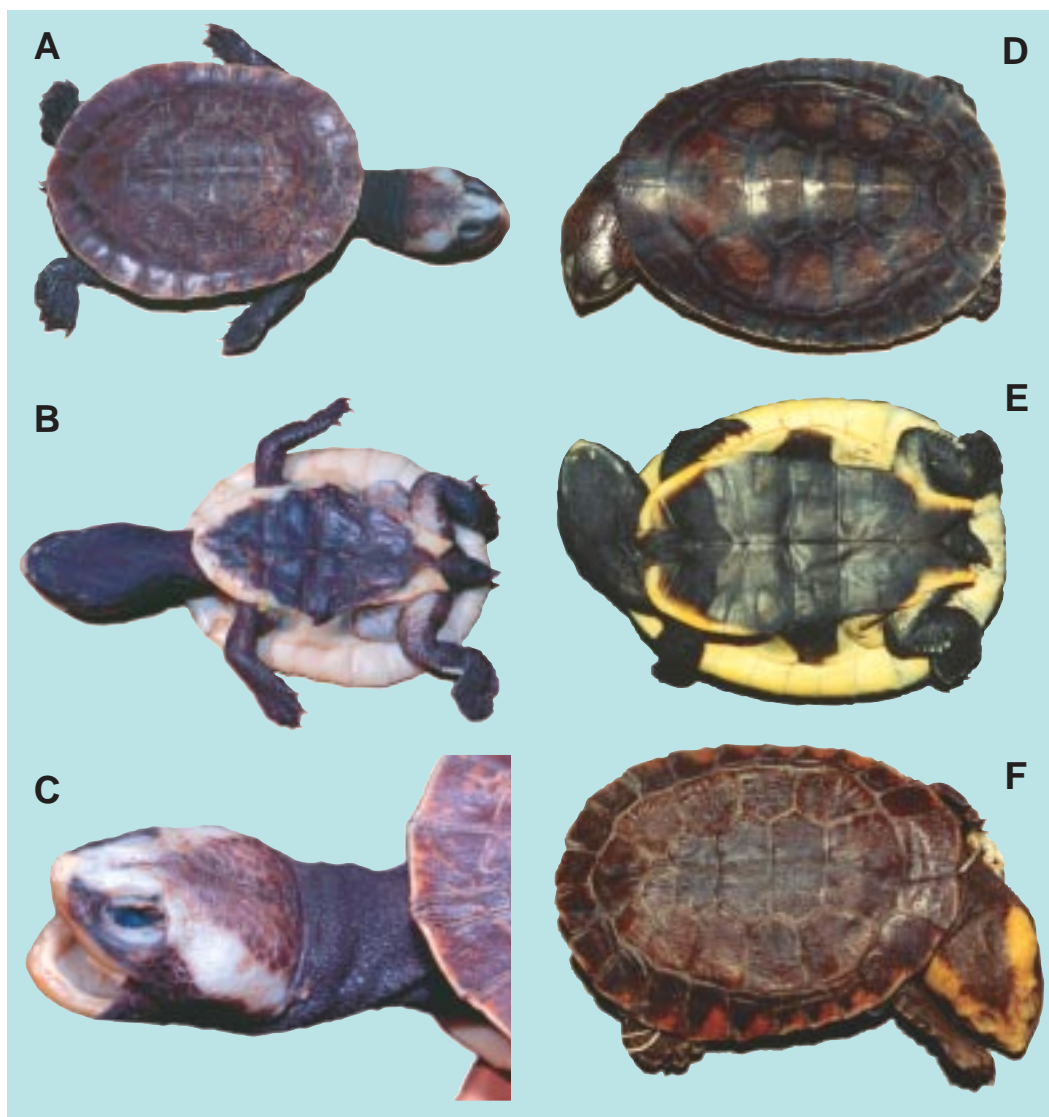


Fig. 6. *Batrachemys heliostemma* sp. nov.: A-C) Holotype: carapace, plastral and head views. D) Leiden paratype, dorsal view. E) Leiden paratype, ventral view. F) Natural History Museum paratype, dorsal view.

near the mouth of the Río Blanco, a tributary of the Río Ucayali, Loreto, Peru, collected by Federico Medem on 9 September 1972 (Fig. 6d and e). RMNH 31999, same data as Leiden Museum (RMNH) 31998. Natural History Museum (NHM; =ex BMNH) 1904.7.26.1, juvenile, in alcohol, from Igape-Assu, Pará, Brasil (Fig. 6f). Its novelty was noticed by R. Bour in 1987, who withheld describing a new species from such a unique young specimen

but of dubious origin (I. Pauler pers. comm.). The collection date is unknown. (C. McCarthy, pers. comm., indicates this specimen was part of a collection made by Monsieur A. Robert and purchased through an animal dealer, Mr. A. Rosenberg. The collection of which it was a part includes species from a wide area of the Amazon basin and we thus do not accept the Pará locality as valid for *B. heliostemma*. Moreover, the locality

cannot be located in any Brazilian gazetteer). Field Museum of Natural History (FMNH) 218500, subadult, in alcohol, from Marian, Napo, Ecuador, collected by R. M. Timm, on 7 October 1983.

Referred Specimens. – Live specimens from the collections of Chris Hansen, Boca Raton, Florida, USA (said to be from Iquitos, Peru), and Carlos Rivera of Iquitos, Peru, collected in the vicinity of Iquitos, Peru. A live adult male collected at Quebrada Pañayacu, Río Pucacuro (2° 57'9" S, 75° 07'2" W) [tributary of the Río Tigre], Peru, collected by P. Soini.

Distribution. – Widely distributed but seemingly localized through the upper Amazon basin, from southern Venezuela, western Brazil, northeastern Peru, and eastern Ecuador to southeastern Colombia. Sympatric chelids are *Batrachemys raniceps*, *M. gibba*, *P. geoffroanus*, *Chelus fimbriata*, *Rhinemys rufipes* and *Platemys platycephala*.

Diagnosis. – A medium- to large-sized toadhead turtle of the genus *Batrachemys* that is distinguished from members of other toadhead genera by its large, wide, rounded head; its narrow parietal roof and parieto-squamosal arch; its reduced neural bone series; the combination of its relatively "shallow" carapace, having a median groove, lacking a keel, absence of lateral marginal narrowing, and presence of mild lateral marginal upturning; the presence of a large antero-medial distal tibial scale; and its distinct plastral pattern (see also Appendix B and Fig. 7).

Batrachemys heliostemma is distinguished from its congeners by its distinct head coloration; diminished size of neck tubercles; lack of horizontal line in the iris; greater parietal roof width; its carapace widest at M7; 4th vertebral scute always wider than long; 11th marginals equal to or wider than 12th; mild upturning of lateral marginals; intergular scute narrower than gulars; greater width of the anterior plastral lobe; its plastral seam formula; and its plastral pattern (see Fig. 8).

Among its congeners *Batrachemys heliostemma* is sympatric with and most similar to *B. raniceps*. The two forms share a rela-

tively similar head size and shape, a pointed nose, small barbels, a similar neural bone series, a similar plastral seam formula, lack of keels, a shallow carapace groove, a well-developed distal antero-medial tibial scale, and similar plastral patterns. However, *B. heliostemma* sp. nov. differs from *B. raniceps* by having a different head pattern and coloration, a broader parietal roof, a more substantial parieto-squamosal arch, an intergular narrower than its gulars (opposite in *B. raniceps*), a flatter shell, and 11th pair of marginals equal or wider than 12th (equal in *B. raniceps*).

Etymology. – The name is a combination of Greek *helios*, "sun," and Greek *stemma* (grammatical gender neutral), "wreath," in reference to the bright yellow-orange facial bands found in many juveniles that extend like a wreath from the supra-tympanum over and across the eyes, ending and joining at the tip of the nose. As the grammatical gender of *Batrachemys* is feminine, the binominal combination is *Batrachemys heliostemma*.

DESCRIPTION

Carapace. – The nuchal is usually long and thin. The vertebral scutes are all wider than long, the first and fifth being longest; width decreases from V1-V4, then V5 usually widens. Costals decrease in size from 1st to 4th. Marginals brown to black like the rest of the carapace, with the posterior edge of preceding scute slightly overlapping the anterior edge of the following scute, from M8-11; usually a small notch between the supracaudals; and M4-7 slightly upturned. In stripe-faced juvenile specimens M2-11 may be 'scalloped' with yellow coloring antero-laterally. Maximum width usually at M7.

Plastron. – The intergular scute bisects 25% of the humeral scutes, and is usually narrower than the gulars at the anterior margin of the plastron. The only consistent feature of the plastral seam formula in the specimens studied is that IG>IF> all others. The anterior plastral lobe is wider than the posterior plastral lobe

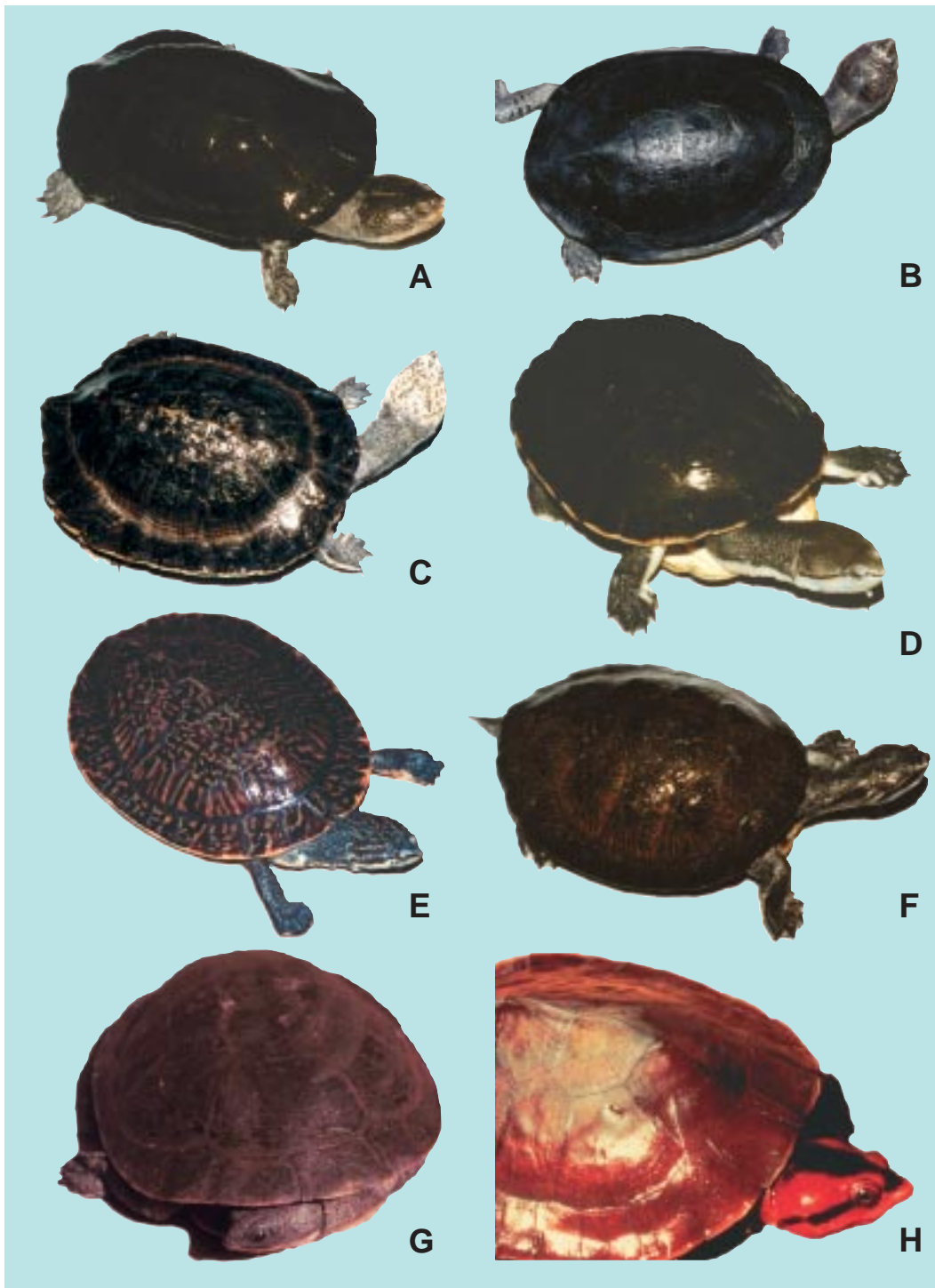


Fig. 7. Toadheads of the genera *Bufocephala*, *Mesoclemmys*, *Phrynops*, *Ranacephala* and *Rhinemys*: A) *B. vanderhaegei*; B) *M. gibba*; C) *P. geoffroanus*; D) *P. hilarii*; E) *P. tuberosus*; F) *P. williamsi*; G) *R. hoguei* (photo by P.C.H. Pritchard); H) *R. rufipes*.

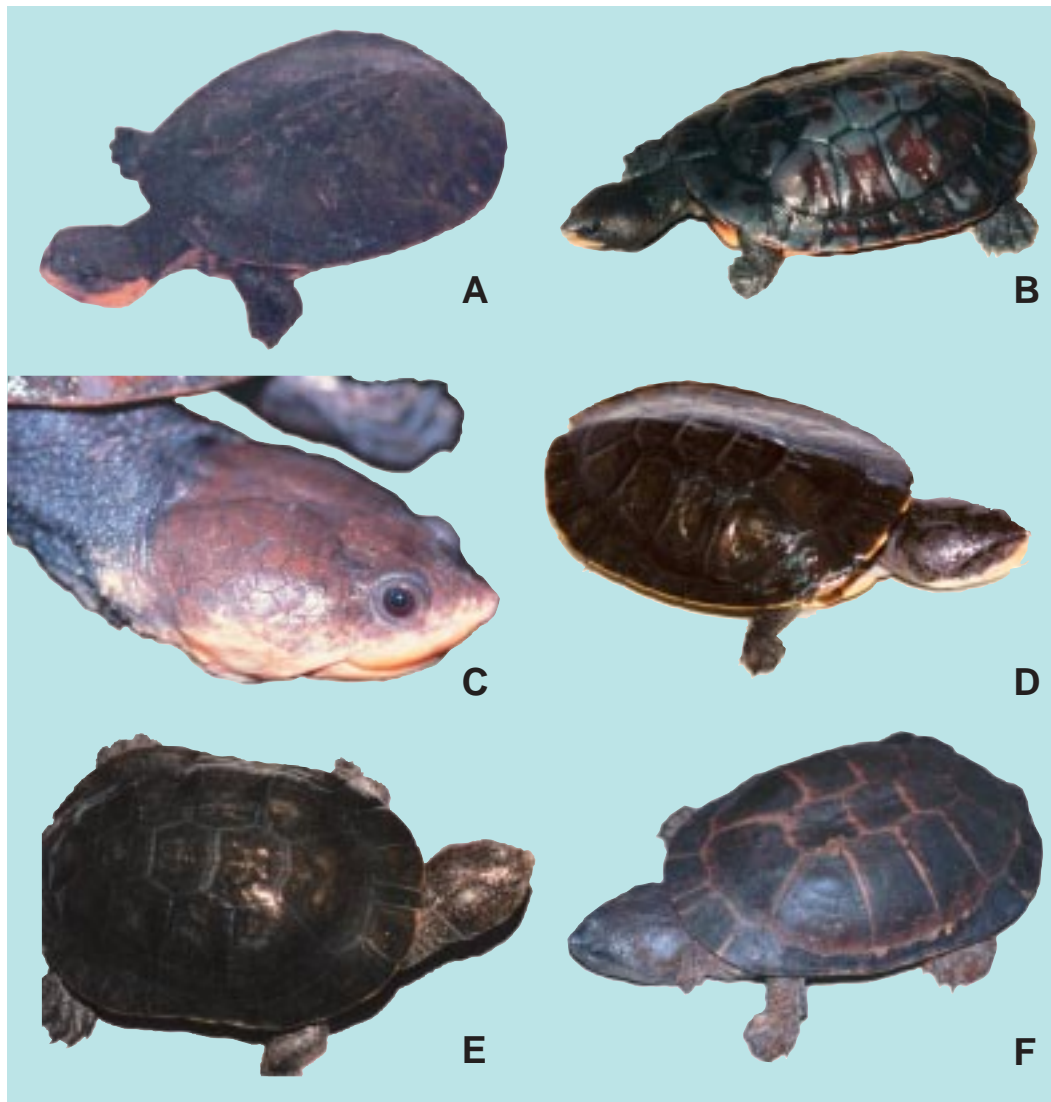


Fig. 8. Toadheads of the genus *Batrachemys*: A) *B. dahli*; (photo courtesy of Reptilia Magazine); B) *B. heliostemma*; C) *B. nasuta*; D) *B. raniceps*; E) *B. tuberculata*; F) *B. zuliae*.

(see PWA versus PWP, and PWG versus PWF in Table 6) and it is rounded in front. The posterior lobe is deeply notched behind. The juveniles with yellow/orange head-bands tend to have less dark pigmentation on the undersides of the marginals than those specimens without head bands, but with age melanism increases in all. Axillary and inguinal scutes are present.

Head and Limbs. – Two juvenile head patterns exist. Some specimens are entirely

melanistic, while others are hatched with a bold, bright yellow-orange “horse-shoe-shaped wreath” that goes from the tip of the nose over and through the eye, and ends dorsal to the tympanum on either side.

Both color phases show pale coloration of the upper and lower jaw, being palest in the head-banded specimens. The ventral aspect of the mandibles is always discontinuously pale. The barbels are always pale, the tympanum

always black. The upper jaw has a slight notch medially, and the lower jaw has a definite "hook" medially that opposes the notch in the upper jaw. Eventually, the yellow-orange head bands on the "light" phase juveniles fade, and by the subadult stage all specimens are melanistic and identical in head coloration. The temporal muscles are well developed. The neck is black and has fine tubercles.

The dorsal and ventral surfaces of the forelimbs are black, although only the dorsal sides on the hindlegs are all black. The ventral surface of only the femoral area is yellowed or pale. The antero-medial row of tibial scales can be all pale, have only the distal scale pale, or be all black. The most distal scale is highly developed. The tail of the male is larger than the female's, and is always black.

All five digits of the forelimbs have black nails. Only the four medial of the five digits of the hind limbs have nails. The feet are extensively webbed. A wild-caught and apparently very old male was an overall horn (olive) color.

Osteology. – Although no prepared skulls were available for direct study, the heads of several museum and living specimens were measured. These specimens possess several consistent characters. The skull is relatively large, its width averaging 25% of carapace length. The shape, as demonstrated by HW/HL = 88% (average), is round. The width of the parietal roof in juveniles averages a moderate 15% of skull width. The neural series usually consists of 3 to 4 continuous bones with the first neural absent, and therefore no contact occurs between neurals and the proneural.

Size and Sexual Dimorphism. – Males (~20 to 31 cm) and females (~25 to 31 cm), are similar in size with the exception of males possessing a larger tail.

DISCUSSION

Dixon and Soini (1977) listed two species of toadheads in the Iquitos area, *M. gibba* and *B. nasuta* (population there currently known as *B. raniceps*). *Batrachemys heliostemma* adds a

third species to the list (see Figs. 5 and 9e). Although *B. heliostemma* seems to be broadly sympatric with *B. raniceps* and *M. gibba* in the Iquitos area, the possibility exists that they are not microsympatric. In August of 1997 one of us (WWL) observed two juvenile *B. heliostemma* in the lower reaches of Quebrada Tamshiyacu, an affluent of the Amazon River that enters from the east below the town of Tamshiyacu, close to Iquitos, but on the opposite bank of the Amazon. *Batrachemys raniceps* primarily inhabit lower, flooded forest habitats in the Iquitos region, whereas the two juvenile *B. heliostemma* observed in 1997, and a subadult observed from the Río Tapiche were inhabiting streams of high, non-flooded forest areas. Lamar has also observed specimens from high forest regions along the Río Itaya, south of Iquitos, and the Río Yahuas-yacu, north of Iquitos, but on the same side of the river. In the Iquitos region, *M. gibba* is found in both seasonally flooded and non-flooded situations. Little data are available on the Venezuelan, Colombian, Ecuadorian or Brazilian populations but they are likely to occupy a similar niche to that observed in Peru.

Though many juveniles exhibit the beautiful yellow or orange facial markings, these colors are lost gradually with age. Melanism was completed by the age of two years (based on counting carapace scute annuli) in all known subadult specimens, leaving an almost completely black animal. As the head bands fade, specimens with less intensity in color of these markings give way to mottling of the (once solid) bands, then to a small patch of white pigmentation between the now black scales on the side of the face. Eventually, the pale and dark color phase specimens become indistinguishable. At this time, no biological significance can be assigned to this distinctive feature of *B. heliostemma*.

Habitat. – Though historically collected throughout an array of Amazonian habitats, *B. heliostemma* has been observed only in high, non-flooded forest situations in near permanent water bodies such as oxbow lakes and slow-moving streams. It is likely that some

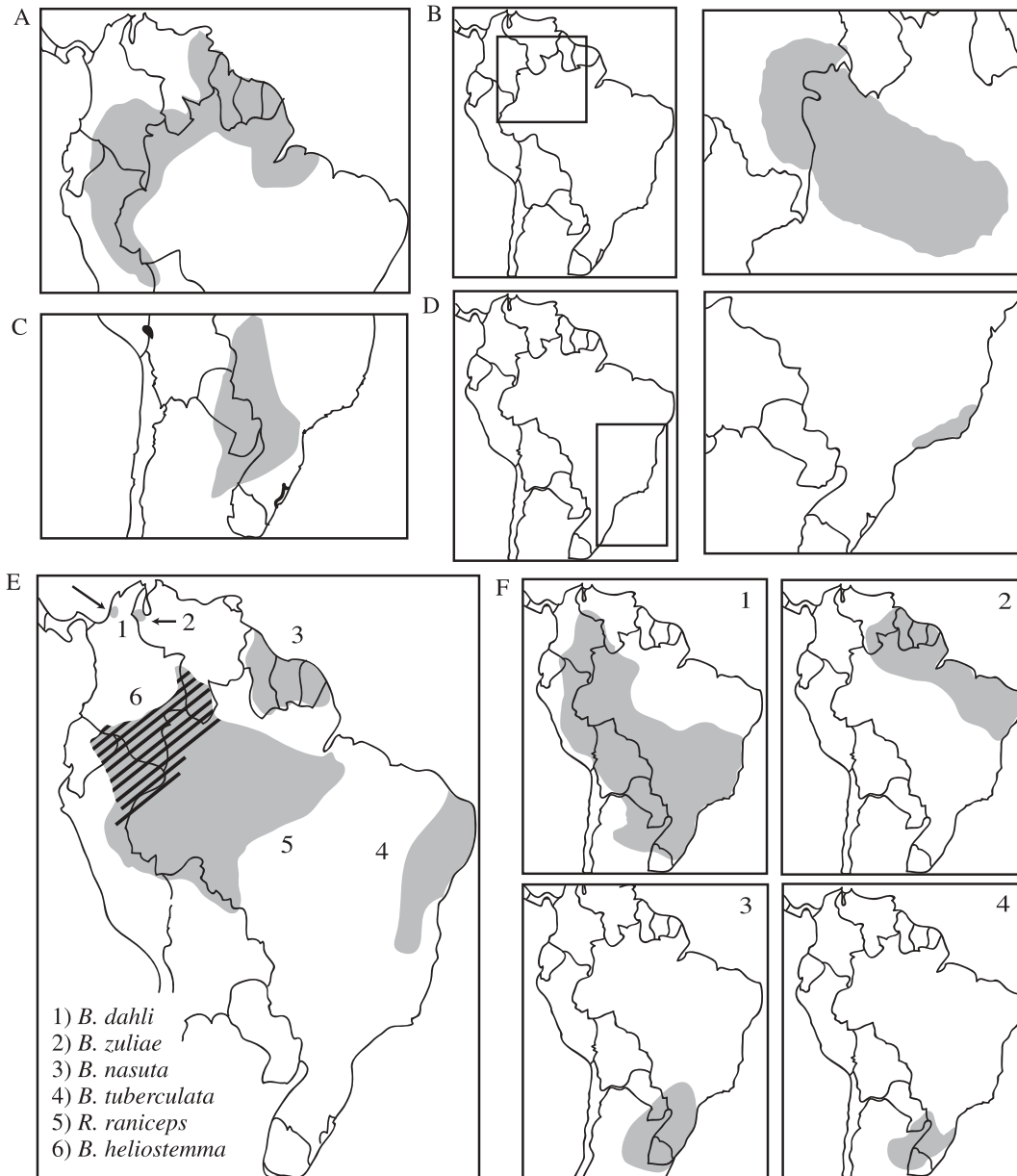


Fig. 9. (A-F) The distributions of the chelid genera of toadheads in South America (artwork by M.J. Ouni), generally taken from Iverson, 1992, but including data from personal communication and field notes: (A) *Mesoclemmys*; (B) *Rhinemys*; (C) *Bufocephala*; (D) *Ranacephala*; (E) *Batrachemys*; (F) *Phrynops* (1. *P. geoffroanus*; 2. *P. tuberosus*; 3. *P. hilarii*; 4. *P. williamsi*).

specimens may venture into lower, flooded-forest situations. However, they seem to prefer shallow and clear waters over the turbid, deeper waters of saturated lowlands.

Ecology. – Little is known of behavior or feeding preferences of this species in the wild. Two adults were caught by Pekka Soini (in a 2-2 1/2 m deep, quiet “blackwater” pond at the

mouth of the fast-moving Quebrada Pañayacu, a blackwater tributary of the Río Pucacuro, Loreto) in a gill net feeding on fish. Captive specimens have taken well to small worms, live and dead fish, and commercial pelleted food. We have observed specimens in the wild that were active at night. Handling of just-caught wild specimens results in the release of offensive Rathke's gland secretions.

DIAGNOSTIC COMPARISONS

Comparisons were made with living and/or preserved specimens of all other relevant species presently listed in the genera *Batrachemys*, *Bufocephala*, *Mesoclemmys*, *Phrynops*, *Ranacephala*, and *Rhinemys* (Appendix B). *Batrachemys heliostemma* can be differentiated from species in the *P. geoffroanus* complex (*P. geoffroanus*, *P. hilarii*, *P. tuberosus* and *P. williamsi* (Fig. 7c-f) – but especially from *P. geoffroanus*, with which it is partially sympatric) by coloration of the head, carapace and plastron; by the relatively larger size and rounder shape of the head; by the shorter length of the barbels; by its narrower parietal roof and parieto-squamosal arch; by the reduced neural series not touching the proneural; by its plastral seam formula; by its well developed distal tibial scale and by the presence of a mild upturning of its lateral marginal scutes on the carapace.

Batrachemys heliostemma can be differentiated from *Rhinemys rufipes* (Fig. 7h), with which it is partially sympatric, by its head, carapace and plastron coloration; its relatively larger head size and rounder head shape; the narrower parietal roof and parieto-squamosal arch; the reduced features of its neural series; the opposite situation with the gular/intergular width comparisons; the differences in plastral seam formula; the carapacial features of being much flatter, without a keel, and having a median groove; having the 11th marginals equal or wider than 12th marginal pair; having slight lateral marginal upturning; and by a more developed distal antero-medial tibial scale.

Batrachemys heliostemma is distinguished from *Ranacephala hogei* (Fig. 7g) by its head, carapace and plastral coloration; by its relatively larger, wider and rounder head with smaller barbels; by its narrower parietal roof; by a different plastral seam formula; by a shorter bridge (in *R. hogei* the bridge nearly equals the posterior plastral lobe in length); by its flatter shell; by the 11th marginals being equal to or wider than the 12th marginals; and by being widely separated geographically.

Batrachemys heliostemma can be distinguished from *Mesoclemmys gibba* (Fig. 7b), with which it is sympatric, by the coloration of its head (especially the juvenile banded phase) and plastron; its relatively larger and rounder head; its narrower parietal roof, and narrower parieto-squamosal arch; its shorter barbels; its intergular narrower than gulars; its differences in plastral seam formula; its carapacial flatness, lack of a keel, and presence of a median groove; its 11th marginals being equal to or wider than the 12th; its mildly upturned lateral marginals; and its greatly developed distal antero-medial tibial scale.

Batrachemys heliostemma can be distinguished from *B. vanderhaegei* (Fig. 7a) by the color of its head (especially the juvenile banded phase) and plastron; its relatively larger, rounder head; its narrower parietal roof width in adults; its usually contiguous neural series lacking a first neural bone; its intergular being narrower than its gulars at the anterior margin of the plastron; its different plastral seam formula; its carapacial flatness; its 12th marginals being equal or wider than 12th marginals; its mild upturning of the lateral marginal scutes; its lack of lateral carapacial narrowing; and its greatly developed antero-medial distal tibial scute. *Batrachemys heliostemma* is not sympatric with *B. vanderhaegei*.

Batrachemys heliostemma and its congeners (*B. dahli*, *B. nasuta*, *B. raniceps*, *B. tuberculata*, *B. zuliae*) all possess large, rounded heads; tube-shaped nostrils projecting over the upper jaw; small barbels; narrow parietal roof and parieto-squamosal arch in adults; similar reduced neural series; relatively flat shells,

lack of keel, and median carapacial groove in adults; and some degree of lateral carapacial upturning. However, head and neck coloration are important characters for distinguishing species of this genus. None of the other species in this genus possess the yellow/orange facial bands of a "light phase" *B. heliostemma* at any stage, and none has an overall black head and neck (except for the temporary juvenile facial bands) as does *B. heliostemma*. *Batrachemys nasuta* has a bicolor dark-over-light pattern; and *B. dahli*, *B. zuliae* and *B. raniceps* all have varying patterns of cephalic black lines. In *B. tuberculata* the head has a gray background with black patches and vermiculations dorsally, and a gray/yellow (orange variations in hatchlings) mottled throat. Only *B. heliostemma* has a solid black tympanum (all specimens).

Only *B. tuberculata* has prominent neck tubercles and elevated head scales. They all have very wide, rounded heads, but the head of *B. dahli* is narrower (lowest HW/HL %) and slightly smaller in relation to carapace length than the others. Among the *Batrachemys* only *B. zuliae* and *B. dahli* have horizontal "bars" in the iris. All six species have eyes oriented somewhat dorsally, and small barbels. As for parietal roof width, *B. heliostemma* may possess the widest with an average of 15% PW/HW (all others 11% or less), but it should be considered that all "in hand" specimens of *B. heliostemma* used for this study were small to large juveniles, whereas mostly subadults and adults were used for its congeners. It should be noted that as a rule, younger specimens in all *Batrachemys* usually have a higher PW/HW% than adults (Bour and Pauler 1987), and that the parietal width does not increase in direct proportion to head width, as a turtle in this complex grows (a feature also in *R. hoguei* where juveniles can have a 10-12% higher PW/HW% than adults). The PW/HW% of an adult *B. heliostemma* is likely to be 10-12%, supported by field observation (WWL) and in photos (see Fig. 8b) of legally unobtainable wild, adult specimens. This may still be a relatively wide parietal roof width for a *Batrachemys*, but helps to further separate it

from *B. vanderhaegei* which has a 15% PW/HW ratio in adult specimens.

The neural bone series has the same reduced features in all *Batrachemys* (*B. dahli* often has none; Zangerl and Medem 1958); the carapace of *B. heliostemma* is widest at M7, giving it a more rounded appearance than *B. raniceps* and *B. dahli* which have the greatest carapace width at M8 (all other *Batrachemys* lie somewhere in between). Depth of shell, lack of keel, and shallow median carapacial groove (deepest in *B. tuberculata*) are similar in all members of this genus.

The 4th vertebral scute is consistently wider than long in *B. heliostemma*, *B. raniceps*, and *B. nasuta*; is variable in *B. dahli*, and is longer than wide in *B. zuliae* and *B. tuberculata*. In *B. heliostemma* and *B. zuliae*, the 11th marginals are equal to or wider than 12th marginals, whereas in all other *Batrachemys* they are equal. All *Batrachemys* species share the feature of upturned lateral marginals in subadults and adults (but more sharply in *B. tuberculata*, *B. zuliae*, and *B. dahli*) and do not show lateral carapacial narrowing.

Batrachemys heliostemma shares with *B. tuberculata* having an intergular scute narrower than its gulars, which is the opposite of all other congeners. In *B. heliostemma* the anterior plastral lobe is noticeably broader than in *B. raniceps*, but not as much as in *B. tuberculata*. Even the posterior plastral lobe of *B. tuberculata* is much broader than all other *Batrachemys*, for which the posterior plastral lobe narrows greatly (going caudally) as compared to the anterior plastral lobe. The plastral seam formulae of all but two *Batrachemys* species are consistent in the first half of the formula being IG>IF>Iab. The exceptions are *B. tuberculata* with IG>Iab>IF (long Iab associated with a long bridge), and *B. zuliae* with IF>IG>Iab, both still maintaining the same three designated seams (in different order) as the three longest in the formula. The latter half of the plastral seam formula varies greatly among all *Batrachemys*, with *B. heliostemma* being most similar to *B. raniceps*. All *Batrachemys* but *B. dahli* (moderately developed), have a well-developed distal

antero-medial tibial scale. The plastral pattern of *B. heliostemma* closely resembles that of *B. nasuta* and *B. raniceps* with dark central coloring, whereas *B. zuliae*, *B. dahli*, and *B. tuberculata* (with reduced central dark area) have basically yellow plastra.

In the genus *Batrachemys*, only *B. raniceps* is sympatric with *B. heliostemma*. *Batrachemys nasuta* is found in the Guianas, *B. zuliae* in northwestern Venezuela, *B. dahli* in northwestern Colombia, and *B. tuberculata* in the Rio São Francisco drainage of Bahia, Brazil (see Fig. 9).

We accept the redescription of the holotype of *B. nasuta* by Bour (1973) and Lescure and Fretey (1975). Among other characters, they found the specimen to have neither cephalic black lines, nor black 'zones' on the marginal undersides. Thus, the holotype most closely matches the Guyana/Suriname population of *Batrachemys*.

In summary, we recognize the following species arranged in six genera:

Family: Chelidae Gray 1831a

Genus: *Batrachemys* Stejneger 1909

- B. dahli* (Zangerl and Medem 1958)
- B. heliostemma* sp. nov.
- B. nasuta* (Schweigger 1812)
- B. raniceps* (Gray 1855)
- B. tuberculata* (Luederwaldt 1926)
- B. zuliae* (Pritchard and Trebbau 1984)

Genus: *Bufocephala* gen. nov.

- B. vanderhaegei* (Bour 1973)

Genus: *Mesoclemmys* Gray 1873a

- M. gibba* (Schweigger 1812)

Genus: *Phrynops* Wagler 1830

- P. geoffroanus* (Schweigger 1812)
- P. hilarii* (Duméril and Bibron 1835)
- P. tuberosus* (Peters 1870)
- P. williamsi* Rhodin and Mittermeier 1983

Genus: *Ranacephala* gen. nov.

- R. hogei* (Mertens 1967)

Genus: *Rhinemys* Wagler 1830

- R. rufipes* (Spix 1824)

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RESUMEN

Se investigaron las afinidades entre las especies de tortugas agrupadas casualmente dentro del género suramericano *Phrynops*. Tres géneros anteriormente reconocidos (*Batrachemys*, *Mesoclemmys*, y *Phrynops*), que fueron subsecuentemente colocados como sub-géneros, y luego puestos bajo sinonimia de *Phrynops*, se reconocen ahora como géneros válidos basándose en análisis morfométrico, osteología craneal y de secuencias génicas, nucleares y

mitocondriales. *Mesoclemmys* se reconocen como género válido, monotípico, conteniendo la especie *M. gibba*, y no como sinónimo del género *Phrynops*. El género *Rhinemys*, previamente sinónimo de *Phrynops*, se reconocen como género monotípico y conteniendo la especie *R. rufipes*. Se describen *Ranacephala* gen. nov. e incluyendo la especie *R. hogeii*. Se reconocen el género *Batrachemys* no como sinónimo de *Phrynops* sino como género válido e incluyendo las especies: *B. dahli*, *B. nasuta*, *B. raniceps*, *B. tuberculata*, y *B. zuliae*. La especie *vanderhaegei* se coloca en *Bufocephala* gen. nov.. El género *Phrynops* se definen de nuevo e incluye las especies: *P. geoffroanus*, *P. hilarii*, *P. tuberosus*, y *P. williamsi*. Esta taxonomía está apoyada por análisis cladístico. Se describe una especie nueva de *Batrachemys* desde la region peruana de Iquitos, y que se destaca por la presencia de patrones distintivos en las caras de juveniles, por su cabeza relativamente ancha y por su caparazón de forma aplastada. La especie nueva, *B. heliostemma* sp. nov., se asemeja a *Batrachemys raniceps*, reconocida nuevamente. Ambas son simpátricas en la region altamazónica de Perú y los países adyacentes Brazil, Ecuador, Venezuela y Colombia. Finalmente, se presentan los datos morfométricos tomados de ejemplares vivos y de museo para todas las especies del género *Batrachemys*.

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APPENDIX A

Index to museum specimens used for Tables 2, 3 and 4. Museum acronyms (see Iverson 1992: viii) for these specimens and others cited in the text are: AMNH= American Museum of Natural History; CAS=California Academy of Sciences; CM= Carnegie Museum; CRI= Chelonian Research Institute; FMNH= Field Museum of Natural History; MCZ=Museum of Comparative Zoology, Harvard University, Cambridge; MNHN= Museum National d'Histoire Naturelle, Paris; MZUSP=Muzeu de Zoologie Universidade de São Paulo; NHM= Natural History Museum, London (=ex British Museum of Natural History); NMW= Naturhistorisches Museum, Wien 1, Austria; RMNH=Rijksmuseum van Natuurlijke Historie, Leiden; SMF=Natur-Museum und Forschung-Institut Senckenberg; UF= University of Florida; USNM= National Museum of Natural History, Smithsonian Institution; ZMB= Museum für Naturkunde, Universität Humboldt, Berlin; ZSM(ZSMH, Bour and Pauler 1987:4)= Zoologisches Sammlung des Bayerischen Staates, München.

Batrachemys dahl

- 1) FMNH #83042, adult female, dried, Sincelejo, Bolívar, Colombia, May 1956.
- 2) FMNH #81991, adult female, alcohol, paratype.
- 3) FMNH #83043, adult female, dried, Sincelejo, Bolívar, Colombia, June 25, 1956.
- 4) FMNH #83044, adult male, dried, Sincelejo, Bolívar, Colombia, June 24, 1956.
- 5) FMNH #81992, juvenile, alcohol, paratype, Sincelejo, Bolívar, Colombia, Aug. 13, 1956.

B. raniceps

- 6) CRI #4915, adult female, skeleton, Iquitos, Loreto, Peru.
- 7) CRI #3409, adult male, dried.
- 8) FMNH #229983, adult male, alcohol, Leticia, Amazonas, Colombia.
- 9) CM #58619, subadult male, dried.
- 10) CRI #813, juvenile, dried, Leticia, Amazonas, Colombia.

B. tuberculata

- 11) CM # R3146, female, dried, Bahia, Brazil, by J.D. Haseman, Jan. 4, 1908.
- 12) CM # R3144, female, dried.
- 13) CRI # 3408, adult female, dried, Brazil.
- 14) CRI #4094, adult male, dried, Rio São Francisco, Brazil.

B. nasuta

- 15) CRI # 1831, adult male, dried, Kwamelasamoetoe Village, Suriname.
- 16) CRI # 1060, adult female, dried.
- 17) CRI # 1832, adult female, dried, Kwamelasamoetoe Village, Suriname.
- 18) CRI # 4713, adult female, dried, Sipaliwini, Suriname by T. Hensen.

- 19) FMNH #98962, skeleton.

B. zuliae

- 20) CRI #1700, adult female, dried, Caño Madre Vieja, Zulia, Venezuela.
- 21) CRI #1701, adult female, dried, Caño Madre Vieja, Zulia, Venezuela.
- 22) UF #51340, adult female, dried, paratype, Parque del Sur, Maracaibo, Venezuela, by P.A. Pritchard.
- 23) CRI #1689, adult male, dried, Caño Madre Vieja, Zulia, Venezuela.
- 24) UF #53440, skeleton, paratype, El Rosario, El Guayabo, District Colón, Zulia, Venezuela, by E. Urdañeta, Aug. 1981.

B. heliostemma

- 25) USNM 541895, juvenile, alcohol, holotype, Río Baria, Neblina, Amazonas, Venezuela by Roy W. McDiarmid, 1984, Mar.
- 26) RMNH #31998, juvenile, alcohol, paratype, Callao, Río Tapiche, Loreto, Peru by Federico Medem, 1972, Sept.
- 27) NHM #1904.7.26.1, juvenile, alcohol, paratype, "Igapé-Assu, Pará, Brasil" by A. Roberts.
- 28) FMNH #218500, subadult, alcohol, paratype, Marian, Napo, Ecuador by R.M. Timm, 10/7/83.
- 29) RMNH #31999, same data as above in #26, paratype.

Ranacephala hoguei

- 30) CM #3132, juvenile, alcohol, Minas Gerais, Brazil, by J.D. Haseman, 1908.
- 31) CAS #13458, Rio Parahyba (Rio Paraíba, Fazenda Feliz Remanso, Pinheiral) Estado do Rio de Janeiro, Brazil, 1948.

Phrynosops tuberosus

- 32) CRI #1327, subadult female, dried, Río Caroni, Venezuela, by Dr. P. Pritchard.
- 33) CRI #4485, adult female, dried, Irewg River, Guyana, by W. Hale, 1995.
- 34) CM #R3141, adult male, dried, Pinahy, Lagas de Paragua, Brazil, by J.D. Haseman, 1908.

Rhinemys rufipes

- 35) CRI #2897, adult female, dried, Río Tí-Paraná, Vaupés, Colombia, by Klaus Methner, 1985.
- 36) CRI #152, adult male, alcohol, Leticia, Amazonas, Colombia (Tarpon Zoo).

Mesoclemmys gibba

- 37) CRI #1945, alcohol, Suriname by Dr. P. Pritchard, 1984.
- 38) CRI #6149, dried, Guyana, by K. Herzog, 1999.
- 39) CRI #2931, dried, Suriname, (pet trade) by W.P. McCord, 1989.

Bufocephala vanderhaegei

- 40) MNHN-Z #1977-50 (Bour, 1987).
- 41) MNHN-Z #1977-51 (Bour, 1987).

APPENDIX B

List of 19 diagnostic characters and their character states for the following species: *Batrachemys raniceps*; *Batrachemys heliostemma*; *Batrachemys nasuta*; *Batrachemys dahli*; *Batrachemys zuliae*; *Batrachemys tuberculata*; *Bufocephala vanderhaegei*; *Chelus fimbriata*; *Mesoclemmys gibba*; *Phrynops Geoffroanus*; *Ranacephala hogeii*; *Rhinemys rufipes*.

KEY

- 1) Color of head.
- 2) Size of head relative to carapace.
- 3) Flatness of head.
- 4) Shape of head.
- 5) Snout.
- 6) Length of barbels.
- 7) Parietal roof.
- 8) Parieto-squamosal arch.
- 9) Number of neural bones.
- 10) Presence of first neural.
- 11) Width of intergular scute compared to gulars (at anterior plastron).
- 12) Plastral seam formula.
- 13) Depth of carapace.
- 14) Presence of carapacial keel.
- 15) Presence of median groove in carapace.
- 16) Width of 11th marginals (measured side to side, or intermarginal seam to intermarginal seam) compared to supracaudals.
- 17) Large distal scale medial tibial row of scales.
- 18) Uprturned lateral borders of carapace.
- 19) Plastral pattern.

Batrachemys dahli

- 1) Dorsally gray to slate-gray; mouth, barbels, tympanum and throat all light. Cephalic black line running from nostril through eye and ending over dorsal tympanum. Lateral bar present in iris.
- 2) Large HW/PL = 24%.
- 3) Rounded to well developed temporal muscles.
- 4) Pointed anteriorly, widening gradually as goes caudally. HW 83% of HL. Eyes oriented slightly dorsally.
- 5) Pointed.
- 6) Small.
- 7) Narrow, PW/HW = 8%.
- 8) Narrow.
- 9) 0-4 (often none).
- 10) No.
- 11) Wider than gulars.
- 12) $IG > IF > IAb > IP > IAn > IH$.
- 13) Relatively flat.
- 14) No.
- 15) Yes, shallow.
- 16) 11th marginal equal to 12th in width.
- 17) Moderately developed.
- 18) Yes, sharply.
- 19) Yellow.

Batrachemys heliostemma

- 1) Head color generally black, with bilateral orange facial bands on some specimens. Tympanum is solid black.
- 2) Large HW/CL = 25%.
- 3) Rounded with well developed temporal muscles.
- 4) Width (juveniles) 88 % length, pointed anteriorly, widening rapidly; eyes oriented somewhat dorsally.
- 5) Pointed.
- 6) Small.
- 7) Moderate (15% HW) juvenile width (10-12% expected in adults).
- 8) Narrow-moderate (juveniles).
- 9) 3-4.
- 10) No.
- 11) Usually narrower than gulars.
- 12) $IG > IF > IAb \geq IP > IH \geq IAn$.
- 13) Flat.
- 14) Adults no (slight in juveniles).
- 15) Yes, in adults only (shallow).
- 16) 11th are equal or wider than 12th in juveniles.
- 17) Yes, well developed.
- 18) Yes, but not sharply.
- 19) Yellow background with large central dark area, covering most of all scutes, extending centrally over bridges. Underside of marginals is yellow in most juveniles with pigment on antero-intermarginal seam in some, developing same pigment in all with age.

Batrachemys nasuta

- 1) Brown-black dorsally, light mouth, chin, barbels, tympanum; dark central throat.
- 2) Wide and large, HW/CL ~ 27%.
- 3) Rounded, well developed temporal muscles.
- 4) Eyes oriented somewhat dorsally. Head overall round (width 89% of length).
- 5) Pointed.
- 6) Small.
- 7) Narrow (10% HW) somewhat parallel sided.
- 8) Narrow.
- 9) Usually 3-4 (usually contiguous).
- 10) No.
- 11) Wider than gulars.
- 12) $IG > IF > IAb \geq IAn > IP > IH$.
- 13) Relatively flat.
- 14) Adults no (juveniles slight).
- 15) Shallow V2,3,4 only in mature adults.
- 16) Fairly equal.
- 17) Strongly developed.
- 18) Yes but not as sharply as *Mesoclemmys gibba*.
- 19) Generally black on yellow background with minimal dark areas only on underside of last four pairs of marginals (juveniles and adults).

Batrachemys raniceps

- 1) Gray-black dorsally, pale mouth, chin, barbels and tympanum; black central throat, cephalic black lines (solid or broken) present from nose to eye to dorsal

- tympanum and outlining (laterally) the parietal roof (crest).
- 2) Wide and large HW/CL = 27%.
 - 3) Rounded, well developed temporal muscles.
 - 4) Head overall round, eyes oriented somewhat dorsally, width 89% of length.
 - 5) Pointed.
 - 6) Small.
 - 7) Narrow (~8% HW) somewhat parallel sided.
 - 8) Narrow.
 - 9) Usually 3-4.
 - 10) No.
 - 11) Wider or equal to gulars.
 - 12) $IG > IF > IAb > IP \geq IH \geq IAn$. (I-anal may lengthen to longer than IP and IH with age).
 - 13) Relatively flat.
 - 14) Adults no (juveniles slight).
 - 15) Shallow V2,3,4 only in mature adults.
 - 16) Equal.
 - 17) Yes, well developed.
 - 18) Yes but not sharply.
 - 19) Black on yellow plastron but with age further darkening, including all intermarginal seams.

Batrachemys tuberculata

- 1) Dorsally gray with random small black blotches on most head scales, which are more elevated than in most toad-head turtles; mouth and barbels light. Tympanum either light with gray blotch or all gray. Throat either all gray or light to gray mottling.
- 2) Large HW/CL = 25%.
- 3) Rounded to well developed temporal muscles.
- 4) Round, HW 88% of HL. Eyes oriented somewhat dorsally.
- 5) Pointed.
- 6) Small (but stout).
- 7) Narrow, PW/HW = 11%.
- 8) Narrow.
- 9) Usually 3-4.
- 10) No.
- 11) Usually not as wide as gulars at anterior border of the plastron.
- 12) $IG > IAb > IF > IAn > IH > IP$
- 13) Relatively flat.
- 14) No.
- 15) Yes, shallow.
- 16) 11th marginals equal to 12th in width.
- 17) Yes, highly developed.
- 18) Yes, sharply (not in hatchlings).
- 19) Yellow with minimal midline gray mottling.

Batrachemys zuliae

- 1) Dorsally gray to slate-gray, throat pale gray to gray. Mouth, chin barbels and tympanum light. Cephalic black line runs from nostril through the eye, ending after passing over tympanum. Lateral bar present in iris.
- 2) Large, HW/CL = 27%

- 3) Rounded with well developed temporal muscles.
- 4) Head overall round, HW 87% of HL. Eyes oriented somewhat dorsally.
- 5) Pointed.
- 6) Small.
- 7) Narrow. PW/HW = 7%.
- 8) Narrow.
- 9) Usually 3-4. 10) No.
- 11) Wider than gulars.
- 12) $IF > IG > IAb > IH > IAn > IP$
- 13) Relatively flat.
- 14) No.
- 15) Yes, shallow.
- 16) 11th marginals are equal or wider to 12th.
- 17) Yes, very developed.
- 18) Yes, sharply.
- 19) Yellow.

Bufocephala vanderhaegei

- 1) Black dorsally, light or dark vermiculated mouth, chin, barbels and tympanum, with dark throat; eye has lateral bar in iris.
- 2) Moderately wide HW/CL ~20%.
- 3) Mildly rounded with slightly elevated head scales.
- 4) Pointed anteriorly, widening rapidly; eyes oriented laterally (width 86% length).
- 5) Pointed.
- 6) Small.
- 7) Moderate width (15% HW) halfway between hourglass and parallel sided in contour.
- 8) Moderate.
- 9) 3-4 (often discontinuous).
- 10) Often present, but not touch proneural.
- 11) Wider than gulars.
- 12) $IG > IF > IAb > IH > IAn > IP$.
- 13) Mildly domed.
- 14) No.
- 15) Yes in adults (V2 and V3).
- 16) 11th narrower.
- 17) Moderately developed.
- 18) Yes, sharply. Plus see lateral carapace obviously narrows.
- 19) Generally black with yellow background.
- 20) Aggressive when handled.

Chelus fimbriata (Schneider, 1783)

- 1) Tan/ brown adults, orange-red juveniles, black cephalic lines present as anteriorly directed "V" on dorsal head.
- 2) Broad (large) HW/CL = 33%.
- 3) Flat.
- 4) Skull wider than long, much wider in rear of skull, arrowhead shaped, eyes oriented laterally, width 110% of skull length.
- 5) Nostrils long, narrow, fleshy double-tube.
- 6) Long.
- 7) Wide (hourglass) ~ 21% HW.
- 8) More than substantial.

- 9) 6-8 (Usually 7), are wide, (1/2 width of vertebral scute), continuous.
- 10) Yes (reaches proneural).
- 11) Intergular usually wider, sometimes equal.
- 12) IF>IH>IP>IG>IAb>Ian (Peru); IF>IH>IP>IG>IAb>IAN>G (Guyana). ('IG' is actually intergular scute length, whereas 'G' is really the true intergular seam length in Guianan specimens).
- 13) Fairly flat (not including keels).
- 14) Yes, 3 keels present (very knobby).
- 15) No median groove.
- 16) 11th marginals equal to 12th pair in width.
- 17) Distal tibial scale – moderately developed (Peru); Poorly developed (Guyana).
- 18) Lateral borders are not upturned.
- 19) Plastral pattern is generally a vague dark pattern over most of a yellow or pink plastron (Peru); All yellow (Guyana).

Mesoclemmys gibba

- 1) Adults usually black dorsally, light or dark vermiculated mouth, chin, barbels and tympanum, with dark throat.
- 2) Relatively small HW/CL = 18%.
- 3) Fairly flat with flat head scales.
- 4) Pointed anteriorly (Width ~82% length), widening gradually distally; eyes oriented laterally.
- 5) Mildly pointed.
- 6) Small – medium.
- 7) Hourglass, wide, ~23% HW.
- 8) Narrow.
- 9) 0-4 (usually 3-4).
- 10) Absent.
- 11) Wider than gulars.
- 12) IG>IAb>IF>IH>IAN>IP.
- 13) Domed.
- 14) Yes.
- 15) No.
- 16) 11th narrower.
- 17) Mildly developed.
- 18) Yes (sharply).
- 19) Generally black with yellow background.
- 20) Non-aggressive when handled.

Phrynops geoffroanus

- 1) Pale background with black (solid or broken) head stripes laterally and dorsally.
- 2) Medium, HW/ CL ~ 17%.
- 3) Flat.
- 4) Fairly blunt (width ~98% length), widening rapidly as goes caudally; eyes oriented laterally.
- 5) Relatively blunt.
- 6) Large.
- 7) Wide (hourglass ~ 21% HW).
- 8) Substantial.
- 9) 5 – 7.
- 10) Yes (touches proneural).
- 11) Narrower.
- 12) IF><IG>IAb>IAN>IH>IP.

- 13) Fairly flat.
- 14) None.
- 15) Yes (2-4th vertebral scutes).
- 16) 11th are wider.
- 17) Moderately developed.
- 18) No.
- 19) White-yellow/ orange/ red, with irregular dark vermiculations on each scute.

Ranacephala hogei

- 1) Bicolor – dark brown or gray dorsally w/ dark zwine red line dorso-laterally / yellow-white ventrally (females). Dark brown or gray / yellow-white (males). (Even tympanum is bicolor).
- 2) Small, HW/CL ~ 13 - 14% (adults)
- 3) Slightly rounded.
- 4) Pointed and narrow anterior, wider posterior (near arrow-head shape), eyes oriented laterally; max width ~ 86% HL.
- 5) Strongly pointed.
- 6) Large.
- 7) Wide (hourglass) ~22% HW (adults) (Mertens,1967; Luederwaldt, 1926).
- 8) Moderate.
- 9) Unknown.
- 10) Unknown.
- 11) Narrower than gulars.
- 12) IAb>IF> IG>IAN>IH>IP.
- 13) Domed.
- 14) None.
- 15) Yes, 2-4th vertebral scutes (Mertens 1967).
- 16) 11th slightly narrower.
- 17) Strongly developed.
- 18) Yes (3-5th marginals), sharply.
- 19) Yellow (no markings).

Rhinemys rufipes

- 1) Red(can be brown in large females) with broad black head stripes laterally and dorsomedially.
- 2) Medium, HW/CL = 17%.
- 3) Fairly flat.
- 4) Strongly pointed anteriorly, much wider posteriorly (almost arrowhead shape); eyes oriented laterally, width ~94% length.
- 5) Strongly pointed.
- 6) Small.
- 7) Wide (hourglass ~31% HW).
- 8) Substantial.
- 9) 5-8.
- 10) Yes (touches proneural).
- 11) Wider than gulars.
- 12) IF>IG>IAb>IH>IAN>IP.
- 13) Domed.
- 14) Pronounced vertebral keel.
- 15) No.
- 16) 11th marginal slightly narrower.
- 17) Mildly developed.
- 18) No.
- 19) Yellow (no markings).

APPENDIX C

The following chronological chresonymy (Smith and Smith 1973) presents original descriptions, synonyms, new combinations, authors, dates and pagination of first-use authorship for the toadheads and is the result of reviewing (with full citation) the reference list herein. Authors of original descriptions are indicated by lack of colon or parentheses in the nominal-complex (Dubois 2000), and for these the type locality along with data for all available types is given. "In part" connotes inappropriate synonymy (=inapp. syn.) and that the author(s) included other forms (correctly or incorrectly) under the same name at that time. Explanation for names not presently in use is given. A bracketed [] name is the currently accepted genus and species for that given synonym.

***Batrachemys nasuta* (Schweigger 1812)**

Emys nasuta Schweigger 1812:298. Holotype: MNHN 4140. Type locality: "Patria Ignota" (locality unknown). Designated as "Amérique méridionale" (South America) by Duméril and Bibron (1835:437). Restricted to "Rivières Ouaqui et Inini, bassin du Maroni en amont de Maripasoula, Guyane française" by Bour and Pauler (1987:6). Synonymized with *Platemys schweiggerii* after *Emys nasuta* was excluded from inapp. syn. with *Emys depressa* Merrem under *Platemys newwiedii* by Duméril and Bibron (1835:425).

Emys viridis Spix 1824: Kaup (1828:1150; in part). [= *Phrynops Geoffroanus* (Schweigger 1812:299)].

Emys rufipes Spix 1824: Kaup (1828:1150; in part). [= *Rhinemys rufipes* (Spix 1824:7)].

Emys stenops Spix 1824: Kaup (1828:1151; in part); Froes (1957:18; in part). See Hoogmoed and Gruber 1983:351. [= *Mesoclemmys gibba* (Schweigger 1812:299)].

Emys barbatula Gravenhorst 1829:15. Holotype: Presumed originally in the Museum of Natural History, Wroclaw University (WU), Poland, said to be destroyed (Roger Bour pers. comm.); see illustrations in original description. Type locality unknown. Synonymized with *Rhinemys nasuta* by Boulenger (1889:218). [= *Batrachemys nasuta* (Schweigger 1812:298)].

Rhinemys nasuta (Schweigger 1812): Wagler (1830:134); Boulenger (1889:218; in part). Both *Emys depressa* Merrem and *Emys stenops* Spix are excluded from synonymy with *Rhinemys nasuta* under *Platemys schweiggerii* by Duméril and Bibron (1835:435). Also see inapp. syn. of *Rhinemys nasuta* by Boulenger (1889:218) with *Hydraspis spixii* (not

Duméril and Bibron, = *Batrachemys raniceps*) Gray 1853:134 and *Hydraspis raniceps* Gray 1855:55 [= *Batrachemys nasuta* (Schweigger 1812:298)].

Hydraspis barbatula (Gravenhorst 1829): Gray (1831b:43). Synonymized with *Rhinemys nasuta* by Boulenger (1889:218) [= *Batrachemys nasuta* (Schweigger 1812:298)].

Emys nasua Schweigger 1812: Gray (1831b:41). *Ex errore* (spelling error).

Platemys schweiggerii Duméril and Bibron 1835:435. Holotype: MNHN 4140 (same as for *Emys nasuta* Schweigger 1812:298). *Nomen novum* (new replacement name) for *Emys nasuta* Schweigger 1812. Type locality: "de l'Amérique méridionale" (South America). Named in honor of August Friedrich Schweigger. Synonymized under *Hydraspis nasuta* by Gray (1844:40). [= *Batrachemys nasuta* (Schweigger 1812:298)].

Hydraspis (Rhinemys) nasuta (Schweigger 1812): Bonaparte (1836:8).

Emys platycephala (Schneider 1792): Temminck and Schlegel (1838:46; in part). Also, synonymized under *Hydraspis nasuta* by Gray (1844:40; in part). Both are inapp. syn. of *Emys (Testudo) platycephala* (Schneider 1792:261) [= *Platemys platycephala* (Schneider 1792:261)].

Hydraspis nasuta (Schweigger 1812): Gray (1844:40).

Hydraspis spixii (Duméril and Bibron 1835): Gray (1855:54; in part, M. Clausen collection). Inapp. syn. of *Hydraspis (Platemys) spixii* (Duméril and Bibron 1835:409) with *Rhinemys nasuta*. See same Clausen type specimen appropriately used for *Hydraspis spixii* (Duméril and Bibron) in Gray (1844:39); in Gray (1873a:66), and Gray (1873b:305) as *Acanthochelys spixii*; and in Boulenger 1889:227 as *Platemys spixii* (= *Emys depressa* Spix 1824:5). Then also see inapp. syn. of *Hydraspis spixii* in Gray (1853:134; in part), as non Duméril and Bibron under *Rhinemys nasuta* by Boulenger (1889:218; in part). *Hydraspis spixii* (Gray 1853:134; in part) is described with "head very large; neck smooth"; and from the Bates collection (= *Batrachemys raniceps*). Gray 1852 (=1853); see Gray 1855:55; Vanzolini 1977:74. [= *Acanthochelys spixii* (Duméril and Bibron 1835:409)].

Platemys canaliculata (Spix 1824): Schlegel in Gray (1855:54; in part). Inapp. syn. of *Platemys (Emys) canaliculata* (Wagler 1830:135) (= *Emys canaliculata* Spix 1824:10) [= *Platemys platycephala* (Schneider 1792:261)].

- Platemys raniceps* (Gray 1855): Strauch (1862:47; in part); also in Boulenger (1889:219; in part). Inapp. syn. of *Platemys (Hydraspis) raniceps* (Gray 1855:55) [= *Batrachemys raniceps* (Gray 1855:55)].
- Platemys nasuta* (Schweigger 1812): Strauch (1862:47).
- Hydraspis (Rhinemys) gibba* (Schweigger 1812): Gray (1864:130; in part). See inapp. syn. of *Hydraspis nasuta* under *Hydraspis (Rhinemys) gibba* (Schweigger 1812:299) [= *Mesoclemmys gibba* (Schweigger 1812:299)].
- Hydraspis raniceps* Gray 1855: Gray (1873a:64; in part, by locality); Boulenger (1889:218; in part, under *Rhinemys nasuta*). Was never meant by Gray 1853:134 (as *Hydraspis spixii* non Duméril and Bibron) or 1855:55, by locality alone, to be *Batrachemys nasutus*; see inapp. syn. of *Hydraspis raniceps*, Bates collection [= *Batrachemys raniceps* (Gray 1855:55)], with *Batrachemys nasuta* and *Batrachemys nasutus* by Wermuth and Mertens (1961:304) and (1977:132); again with *Phrynops (Batrachemys) nasutus nasutus* by Lescure and Fretey (1975:1318); also see Bour and Pauler 1987:8.
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- Hydraspis maculata* Gray 1873a:65. Holotype: NHM (ex BMNH) 66.8.14.233. Type locality: "S. America". Synonymized with *Rhinemys nasuta* by Boulenger (1889:219). [= *Batrachemys nasuta* (Schweigger 1812:298)].
- Phrynops walbaumi* Fitzinger in Siebenrock (1904:20). Reference specimen (according to the museum specimen tag): NMW 24932. Locality: "Rio Guapore, near Mato Grosso," Brasil. Holotype belonging to the "*Phrynops raniceps* group" (Roger Bour pers. comm.). Inapp. syn. by Siebenrock (1904:20) under *Rhinemys nasuta* [= *Batrachemys raniceps* (Gray 1855:55)]. *Nomen nudum* (published without a valid description; not an available name, therefore not a true synonym). Named in honor of Johann Julius Walbaum.
- Batrachemys nasuta* (Schweigger 1812): Stejneger (1909:127).
- Platemys miliusii* Duméril and Bibron 1835: Froes (1957:18; in part). See Hoogmoed and Gruber 1983:351 [= *Mesoclemmys gibba* (Schweigger 1812:299)];
- Phrynops (Batrachemys) nasuta* (Schweigger 1812): Zangerl and Medem (1958:376); Medem (1960:284; in part, see inapp. syn. with *Hydraspis raniceps* Gray 1855:55).
- Rhinemys tuberculata* Luederwaldt 1926: Wermuth and Mertens (1961:304; in part). [= *Batrachemys tuberculata* (Luederwaldt 1926:437)].
- Phrynops (Batrachemys) nasutus* (Schweigger 1812): Mertens (1970:19).
- Phrynops (Batrachemys) nasutus nasutus* (Schweigger 1812): Mertens (1970:19); Lescure and Fretey (1975:1318).
- Phrynops nasutus* (Schweigger 1812): Bour (1973:177).
- Phrynops wermuthi* Mertens 1967: Bour (1973:182; in part). [= *Batrachemys raniceps* (Gray 1855:55)].
- Phrynops nasutus nasutus* (Schweigger 1812): Bour (1973:185).
- Batrachemys dahli* (Zangerl and Medem 1958)**
- Phrynops (Batrachemys) dahli* Zangerl and Medem 1958:377. Holotype: FMNH 75980. Type locality: "vicinity of Sincelejo, Bolívar, Colombia." Named in honor of George Dahl.
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- Batrachemys dahli* (Zangerl and Medem 1958): Wermuth and Mertens (1961:304).
- Phrynops dahli* Zangerl and Medem 1958: Bour (1973:180).
- Phrynops (Batrachemys) nasutus dahli* Zangerl and Medem 1958: Müller (1987:199). Inapp. syn. having *Phrynops dahli* as subspecies of *Phrynops (Batrachemys) nasutus* (Schweigger 1812:298). [= *Batrachemys dahli* (Zangerl and Medem 1958:377)].
- Batrachemys tuberculata* (Luederwaldt 1926)**
- Rhinemys tuberculata* Luederwaldt 1926:437 & 460. Syntypes: MZUSP 43 and 81; lectotype: MZUSP 43 by Bour and Pauler 1987:9. Type locality: "Villa Nova, (Est. da Bahia)," Brazil.
- Phrynops nasutus* (Schweigger 1812): Müller (1937:610; in part (by locality), "Ceará, 150 km SSW of Fortaleza, Rio São Francisco, Brazil") [= *Batrachemys nasuta* (Schweigger 1812:298)].
- Batrachemys tuberculata* (Luederwaldt 1926): Froes (1957:18).
- Phrynops (Batrachemys) tuberculata* (Luederwaldt 1926): Zangerl and Medem (1958:376).

- Batrachemys nasuta* (Schweigger 1812): Wermuth and Mertens (1961:304; in part). [= *Batrachemys nasuta* (Schweigger 1812:298)].
- Phrynopys* (*Batrachemys*) *tuberculatus* (Luederwaldt 1926): Mertens (1970:19); Iverson (1986:228).
- Phrynopys tuberculatus* (Luederwaldt 1926): Mertens (1970:19); King and Burke (1989:124).
- Phrynopys tuberculatus tuberculatus* (Luederwaldt 1926): Bour (1973:184); Wermuth and Mertens (1977:133).
- Phrynopys* (*Phrynopys*) *tuberculatus* (Luederwaldt 1926): Freiberg (1981:69). Inapp. syn., since *Batrachemys* would be the correct subgenus for this species.
- Phrynopys* (*Phrynopys*) *tuberculatus tuberculatus* (Luederwaldt 1926): Freiberg (1981:69). Inapp. syn., since *Batrachemys* would be the correct subgenus for this species.
- Batrachemys zuliae* (Pritchard and Trebbau 1984)**
- Phrynopys* (*Batrachemys*) *zuliae* Pritchard and Trebbau 1984:135. Holotype: UF 53439. Type locality: Caño Madre Vieja, Edo. Zulia, Venezuela.
- Phrynopys zuliae* Pritchard and Trebbau 1984: Bour and Pauler (1987:3,4).
- Batrachemys raniceps* (Gray 1855): comb. nov. [new combination].**
- Hydraspis spixii* (Duméril and Bibron 1835): Gray (1853:134; in part, Bates collection). Reference specimen: "adult stuffed specimen; head very large; neck smooth" from "Brazils, Para". NHM (ex BMNH) 1947.3.5.92; also the same specimen in Gray 1855:55 as *Hydraspis raniceps* and in Gray (1873a:65) see the same specimen again, specimen "a", as *Hydraspis raniceps*. Thus inapp. syn. with *Hydraspis spixii* (Duméril and Bibron). See *Hydraspis spixii* non Duméril and Bibron (Gray 1853) appropriately synonymized with *Hydraspis raniceps* Gray 1855:55 by Boulenger (1889:218) (= *Batrachemys raniceps*). [= *Acanthochelys spixii* (Duméril and Bibron 1835:409)].
- Hydraspis raniceps* Gray 1855:55. Holotype: none properly designated. Lectotype: NHM (ex BMNH) "adult (stuffed)" specimen; Bates collection, 1947.3.5.92 (formerly NHM 51.8.12.1) designated by Bour and Pauler 1987:8. Type locality: "Brazils; Para." Also in Gray (1873a:64; in part); see inapp. syn. of specimens c, d, e and possibly b, which are *Batrachemys nasutus* by locality.
- Platemys raniceps* (Gray 1855): Strauch (1862:47).
- Hydraspis gaudichaudii* (Duméril and Bibron 1835): Gray (1872a:19; in part). Holotype: MNHN 2101. Type locality: "Brésil." Synonymized under *Platemys* (*Emys*) *radiolata* (Mikan 1820) by Mertens and Wermuth (1955:405). Inapp. syn. of *Hydraspis* (*Platemys*) *gaudichaudii* (Duméril and Bibron 1835:427) [= *Acanthochelys radiolata* (Mikan 1820; unpaginated)].
- Rhinemys nasuta* (Schweigger 1812): Boulenger (1889:218; in part). [= *Batrachemys nasuta* (Schweigger 1812:298)].
- Platemys nasuta* (Schweigger 1812): Strauch (1890:104; in part). [= *Batrachemys nasuta* (Schweigger 1812:298)].
- Phrynopys walbaumi* Fitzinger in Siebenrock (1904:20). Reference specimen: NMW 24932. Locality: "Rio Guapore, near Mato Grosso," Brasil. See inapp. syn. under *Rhinemys nasuta* by Siebenrock (1904:20). Holotype belonging to the "*Phrynopys raniceps* group" (Roger Bour pers. comm.); see also Bour 1973:186 [= *Batrachemys raniceps* (Gray 1855:55)]. *Nomen nudum* (published without a valid description; not an available name, therefore not a true synonym).
- Phrynopys* (*Batrachemys*) *nasuta* (Schweigger 1812): Medem (1960:284; in part). [= *Batrachemys nasuta* (Schweigger 1812:298)].
- Phrynopys wermuthi* Mertens 1969:132. Holotype: SMF 66246. Type locality: "Amazonian Peru." Synonymized under *Phrynopys raniceps* (Gray 1855:55) by Bour and Pauler (1987:8) [= *Batrachemys raniceps* (Gray 1855:55)]. Named in honor of Heinz Wermuth.
- Phrynopys* (*Batrachemys*) *nasutus wermuthi* Mertens 1969: Mertens (1970:19); and Müller (1987:199). Inapp. syn. having *Phrynopys wermuthi* as subspecies of *Phrynopys nasutus* (Schweigger 1812:298). Synonymized under *Phrynopys raniceps* (Gray 1855:55) by Bour and Pauler (1987:8) [= *Batrachemys raniceps* (Gray 1855:55)].
- Phrynopys nasutus* (Schweigger 1812): Bour (1973:182; in part, as *Phrynopys wermuthi*). [= *Batrachemys nasuta* (Schweigger 1812:298)].
- Phrynopys nasutus wermuthi* Mertens 1969: Bour (1973:182). Inapp. syn. having *Phrynopys wermuthi* as subspecies of *Phrynopys nasutus* (Schweigger 182:298). Synonymized with *Phrynopys raniceps*

(Gray 1855:55) by Bour and Pauler (1987:8) [= *Batrachemys raniceps* (Gray 1855:55)].

Phrynops (Phrynops) tuberculatus wermuthi Mertens 1969; Freiberg (1981:69; in part). Inapp. syn. having *Phrynops wermuthi* as subspecies of *Phrynops tuberculatus* (Luederwaldt 1926:437). Also inapp. syn. since *Batrachemys* would have been the correct subgenus in 1981. Synonymized with *Phrynops raniceps* (Gray 1855:55) by Bour and Pauler (1987:8) [= *Batrachemys raniceps* (Gray 1855:55)].

Phrynops raniceps (Gray 1855): Bour and Pauler (1987:8).

Batrachemys heliostemma sp. nov.
No synonyms. Holotype: USNM 541895.

***Bufocephala vanderhaegei* (Bour 1973): comb. nov.**

Phrynops schopfii Fitzinger in Diesing (1840:237). Reference specimen: NMW15762. Type locality: "zu Cujaba" (Cuiabá, Mato Grosso, Brazil). [= *Bufocephala vanderhaegei* (Bour 1973:183)]. *Nomen nudum* (published without valid description; not an available name, therefore not a true synonym; Bour and Pauler 1987:10). Named in honor of Johann David Schoepff.

Batrachemys nasuta (Schweigger 1812): Müller (1937:610; in part, "aus Paraguay"), also Müller (1939:94; in part, "ins mittlere Paraguay"); also Mertens (1967:72; in part; specimen SMF 62533, "bei Caieiras, Sao Paulo, Brasilien"). Inapp. syn. of all, by locality. [= *Batrachemys nasuta* (Schweigger 1812:298)].

Phrynops paraguayensis Vanzolini in Donoso-Barros (1965:5). No type designated (Bour & Pauler 1987:10). Locality: "rio Paraguay." [= *Bufocephala vanderhaegei* (Bour 1973:183)]. *Nomen nudum* (published without valid description; not an available name, therefore not a true synonym; Bour and Pauler 1987:10).

Phrynops tuberculatus vanderhaegei Bour 1973:184. Holotype: MNHN 1977.50. Type locality: near "Asunción, Paraguay". Restricted to "Tobati (25° 05' S, 57° 04' W), La Cordillera, Paraguay" by Bour and Pauler (1987:10). Inappropriate designation having *Phrynops vanderhaegei* as subspecies of *Phrynops tuberculatus* (Luederwaldt 1926:437). Elevated to full species by Pritchard (1979:793) [= *Bufocephala vanderhaegei* (Bour 1973:184)].

Phrynops (Batrachemys) vanderhaegei Bour 1973; Pritchard (1979:793).

Phrynops (Phrynops) tuberculatus vanderhaegei Bour 1973; Freiberg (1981:69). Inapp. syn. having *Phrynops vanderhaegei* as a subspecies of *Phrynops tuberculatus* (Luederwaldt 1926:437). Also inapp. syn. since *Batrachemys* would have been the correct subgenus in 1981. Elevated to full species by Pritchard (1979:793) [= *Bufocephala vanderhaegei* (Bour 1973:184)].

Phrynops gibbus (Schweigger 1812): McDiarmid and Foster (1987:3; in part). Inapp. syn. of *Phrynops gibbus* (Schweigger 1812:299) due to its phenotypic resemblance to *Bufocephala vanderhaegei* [= *Mesoclemmys gibba* (Schweigger 1812:299)].

Phrynops vanderhaegei Bour 1973; Bour and Pauler (1987:10).

***Mesoclemmys gibba* (Schweigger 1812)**

Testudo geometrica Linnaeus 1758:199; in part. Syntype (juvenile *Mesoclemmys gibba* (Schweigger 1812:299)) from "Museum Adolphi Friderici Regis", presently in the collections of the Swedish Museum of Natural History, Stockholm. Type locality: "Asia". See Bour and Pauler (1987:7). [= *Psammobates geometricus* (Linnaeus 1758:199)].

Emys gibba Schweigger 1812:299. Holotype: MNHN 8756. Type locality: "Patria Ignota" (locality unknown). Designated as "Amérique méridionale" (South America) by Duméril and Duméril (1851:20). Restricted to near "Cayenne, Guyane française" by Bour and Pauler (1987:7).

Emys stenops Spix 1824:12; Plate III. Holotype: ZSMH 2454/0. Type locality: "ad ripam fluminis Solimoens" (Amazonas, Brazil). Synonymized with *Platemys miliusii* after *Emys stenops* was excluded from synonymy with *Rhinemys nasuta* under *Platemys schweiggeri* by Duméril and Bibron (1835:435); later synonymized with *Phrynops gibbus* by Bour (1973:178). [= *Mesoclemmys gibba* (Schweigger 1812:299)].

Emys nasuta Schweigger 1812; Kaup (1828:1151; in part); Mertens (1970:19; in part). See both inappropriately synonymize *Emys stenops* Spix 1824:12, and only Mertens (1970:19) inappropriately synonymize *Platemys miliusii* Duméril and Bibron 1835:431 with *Emys nasuta* Schweigger 1812:298. [= *Phrynops Geoffroyanus* (Schweigger 1812:302)].

Hydraspis stenops (Spix 1824): Bell (1828:512) [= *Mesoclemmys gibba* (Schweigger 1812:299)].

Rhinemys gibba (Schweigger 1812): Wagler (1830:135).

- Chelys (Hydraspis) rufipes* (Spix 1824): Gray (1831a:16; in part). [= *Rhinemys rufipes* (Spix 1824:7)].
- Chelys (Hydraspis) cayennensis* (Schweigger 1812): Gray (1831a:17; in part). Inapp. syn. of *Emys cayennensis* Schweigger 1812:298 [= *Podocnemis unifilis* Troschel 1848:647]; see Mittermeier and Wilson 1974:158; Hoogmoed and Gruber 1983:343; and Iverson 1992:77.
- Hydraspis rufipes* (Spix 1824): Gray (1831b:41; in part). [= *Rhinemys rufipes* (Spix 1824:7)].
- Hydraspis cayennensis* (Schweigger 1812): Gray (1831b:42; in part); also Gray (1855:55; in part). Inapp. syn. of *Emys cayennensis* Schweigger 1812:298 [= *Podocnemis unifilis* Troschel 1848:647]; see Mittermeier and Wilson 1974:158; Hoogmoed and Gruber 1983:343; and Iverson 1992:77.
- Platemys gibba* (Schweigger 1812): Duméril and Bibron (1835:416).
- Platemys miliusii* Duméril and Bibron 1835:431. Holotype: MNHN8755. Type locality: from "Cayenne" (French Guyane). Synonymized under *Hydraspis gibba* by Boulenger (1889:224). [= *Mesoclemmys gibba* (Schweigger 1812:299)]. Named in honor of Baron Pierre-Bernard de Milius.
- Hydraspis gibba* (Schweigger 1812): Fitzinger (1835:126).
- Emys platycephala* (Schneider 1792): Temminck and Schlegel (1838:47; in part, as *Emys stenops*). Inapp. syn. of *Emys (Testudo) platycephala* (Schneider 1792:261). Synonymized under *Phrynops miliusii* by Gray (1844:42). [= *Platemys platycephala* (Schneider 1792:261)].
- Phrynops miliusii* (Duméril and Bibron 1835): Gray (1844:42) [= *Mesoclemmys gibba* (Schweigger 1812:299)].
- Phrynops gibbus* (Schweigger 1812): Diesing (1850:406).
- Platemys canaliculata* (Spix 1824): Schlegel in Gray (1855:54; in part). Inapp. syn. of *Platemys (Emys) canaliculata* (Wagler 1830:135) (= *Emys canaliculata* Spix 1824:10) [= *Platemys platycephala* (Schneider 1792:261)].
- Rhinemys nasuta* (Schweigger 1812): Gray (1855:56; in part). Inapp. syn. of *Rhinemys (Emys) nasuta* (Schweigger 1812:298) [= *Batrachemys nasuta* (Schweigger 1812:298)].
- Hydraspis miliusii* (Duméril and Bibron 1835): Gray (1855:56; in part). Synonymized under *Hydraspis gibba* by Gray (1870:74). [= *Mesoclemmys gibba* (Schweigger 1812:299)].
- Hydraspis (Rhinemys) gibba* (Schweigger 1812): Gray (1864:130; in part). Also see inapp. syn with *Hydraspis (Rhinemys) nasuta* (Schweigger 1812:298). [= *Mesoclemmys gibba* (Schweigger 1812:299)].
- Hydraspis nasuta* (Schweigger 1812): Gray (1864:130; in part); also Gray (1870:74; in part). [= *Batrachemys nasuta* (Schweigger 1812:298)].
- Hydraspis gordonii* Gray 1868:563. Holotype: NHM (ex BMNH) 1947.3.4.18. Type locality: "Trinidad, near the mountain of Tamana." Synonymized under *Hydraspis gibba* by Boulenger (1889:224). [= *Mesoclemmys gibba* (Schweigger 1812:299)].
- Hydraspis wagleri* (Duméril and Bibron 1835): Gray (1870:74; in part). Inapp. syn. of *Hydraspis (Platemys) wagleri* (Duméril and Bibron 1835:422) [= *Phrynops geoffroanus* (Schweigger 1812:302)].
- Testudo leithii* Carter 1852: Gray (1871:340 in part). Inapp. syn. of *Testudo leithii* Carter (not Günther) 1852:1. Assigned new genus (*Carteremys*) by Williams 1953:5 [= *Carteremys leithii* (fossil) (Carter 1852:1)].
- Hydraspis leithii* (Carter 1852): Gray (1871:340; in part). Inapp. syn. of *Hydraspis (Testudo) leithii* (Carter (not Günther) 1852:1). Assigned new genus (*Carteremys*) by Williams 1953:5 [= *Carteremys leithii* (fossil) (Carter 1852:1)].
- Emys barbatula* Gravenhorst 1829: Gray (1872a:19; in part). Inapp. syn. of *Emys barbatula* Gravenhorst 1829:15 [= *Batrachemys nasuta* (Schweigger 1812:298)].
- Mesoclemmys gibba* (Schweigger 1812): Gray (1873b:306).
- Hydraspis bicolor* Gray 1873b:304. Holotype: NHM (ex BMNH) 72.10.16.80. (New # 1947.2.22.86). Type locality: "Demerara Falls," Guyana. Synonymized under *Hydraspis gibba* by Boulenger (1889:224). [= *Mesoclemmys gibba* (Schweigger 1812:299)].
- Emys radiolata* Mikan 1820: Boulenger (1889:224; in part). [= *Acanthochelys radiolata* (Mikan 1820)].
- Platemys radiolata* (Mikan 1820): Boulenger (1889:224; in part). Inapp. syn. of *Platemys radiolata* Duméril

and Bibron 1835:412 (= *Emys radiolata* Mikan 1820) [= *Acanthochelys radiolata* (Mikan 1820)].

Hydraspis nasuta (Schweigger 1812): Boulenger (1889:224; in part). Inapp. syn. of *Hydraspis nasuta* (Gray 1855:55) (= *Emys nasuta* Schweigger 1812:298) [= *Batrachemys nasuta* (Schweigger 1812:298)].

Batrachemys nasuta (Schweigger 1812): Froes (1957:18; in part). [= *Batrachemys nasuta* (Schweigger 1812:298)].

Phrynops (Mesoclemmys) gibba (Schweigger 1812): Zangerl and Medem (1958:376).

Phrynops rufipes (Spix, 1824): Wermuth and Mertens (1961:334; in part) [= *Rhinemys rufipes* (Spix 1824:7)].

Mesoclemmys giba (Schweigger 1812): Donoso-Barros (1965:13) *Ex errore* (spelling error).

Phrynops nasutus (Schweigger 1812): Mertens (1970:19; in part). [= *Batrachemys nasuta* (Schweigger 1812:298)].

Phrynops (Mesoclemmys) gibbus (Schweigger 1812): Medem (1973:91).

Phrynops (Mesoclemmys) "sp." Fretey 1975:674. Locality: "Guyane française". Synonymized under *Phrynops (Mesoclemmys) gibbus* by Hoogmoed and Gruber (1983:351). [= *Mesoclemmys gibba* (Schweigger 1812:299)].

Phrynops (Mesoclemmys) miliusii (Duméril and Bibron 1835): Fretey (1975:675). [= *Mesoclemmys gibba* (Schweigger 1812:299)].

Phrynops gibba (Schweigger 1812): Pritchard (1979:432).

***Phrynops hilarii* (Duméril and Bibron 1835)**

Phrynops (Emys) geoffroana (Schweigger 1812): Wagler (1830:136; in part). Appropriately synonymized with *Emys viridis* Spix, but then inapp. syn. with misidentified *Phrynops geoffroana* plate 5 in the same publication (= *Phrynops hilarii*, Roger Bour pers. comm.) [= *Phrynops geoffroanus* (Schweigger 1812:302)].

Phrynops geoffroana (Schweigger 1812): Wagler (1830:Table V. (=plate 5); in part), and see Wagler (1833: plate 26; in part) Inapp. syn. since both plates depict *Phrynops hilarii* (Roger Bour pers. comm.) [= *Phrynops geoffroanus* (Schweigger 1812:302)].

Emys geoffreana Schweigger 1812: Duméril and Bibron (1835:418; in part). Incorrect subsequent spelling

since (Roger Bour pers. comm.) Duméril and Bibron correctly attributed the specific name to Schweigger, thus cannot be used as a substitute name (ICZN Code, 33.3). Appropriately synonymized with Duméril and Bibron 1835:418 adult *Platemys geoffreana* specimen, with *Phrynops (Emys) geoffroana* (Wagler 1830:136), and with both *Emys viridis* Spix 1824:3 and *Hydraspis viridis* (Spix, 1824:3). See also inapp. syn. with Duméril and Bibron 1835:422 misidentified juvenile (MNHN 2100) Buenos Ayres specimen collected by d'Orbigny (= *Phrynops hilarii*, Roger Bour pers. comm.), and Wagler (1830 and 1833, plates 5 and 26, both under *Phrynops geoffreana*, in Duméril and Bibron 1835:418, both = *Phrynops hilarii*) [= *Phrynops geoffroanus* (Schweigger 1812:302)].

Platemys geoffreana (Schweigger 1812): Duméril and Bibron (1835:418; in part). Appropriately synonymized with *Emys geoffreana* Schweigger (Duméril and Bibron 1835:418), with *Phrynops (Emys) geoffroana* (Wagler 1830:136), and with both *Emys viridis* Spix 1824:3 and *Hydraspis viridis* (Spix, 1824:3). This is a redescription of the *Emys geoffroana* Schweigger 1812:302 holotype, but see inapp. syn. with the Duméril and Bibron 1835:422 "envoyé des Buenos Ayres" juvenile specimen (= *Phrynops hilarii*) and Wagler (1830 and 1833, plates 5 and 26, = *Phrynops hilarii*). But see also appropriate synonymy by Boulenger (1889:222; in part) of *Platemys geoffreana* juvenile specimen from Buenos Ayres (= *Phrynops hilarii*) Duméril and Bibron 1835:421(=422), under *Hydraspis hilarii* [= *Phrynops geoffroanus* (Schweigger 1812:302)].

Phrynops geoffreana (Schweigger 1812): Duméril and Bibron (1835:418; in part). See intended appropriate synonymy with *Emys geoffroana* Schweigger 1812:302 as *Platemys geoffreana* (Schweigger); with *Emys geoffreana* Schweigger; with *Emys viridis* Spix 1824; and *Hydraspis viridis* (Spix 1824); thus also appropriate synonymy with *Phrynops geoffroana* Wagler (1830:136 Schweigger/ *viridis*). But also see unintended inapp. syn. with Duméril and Bibron 1835:422 juvenile from Buenos Ayres specimen (= *Phrynops hilarii*), and with Wagler (1830 and 1833, plates 5 and 26, = *Phrynops hilarii*) [= *Phrynops geoffroanus* (Schweigger 1812:302)].

Emys viridis Spix 1824: Duméril and Bibron (1835:418; in part), seen as both *Emys viridis* Spix 1824, and *Hydraspis viridis* (Spix 1824). Appropriately synonymized with *Platemys geoffreana* (adult specimen); *Emys geoffreana* Schweigger; and *Phrynops geoffroana* (Wagler 1830:136 Schweigger/ *viridis*); all from Duméril and Bibron (1835:418). See also inapp. syn. with Duméril and Bibron 1835:422 juvenile Buenos Ayres specimen (= *Phrynops hilarii*), and

- Wagler (1830 and 1833 plates 5 and 26, as *Phrynops geoffreana*, =*Phrynops hilarii*) [= *Phrynops geoffroanus* (Schweigger 1812:302)].
- Platemys hilarii* Duméril and Bibron 1835:428. Holotype: MNHN 8757. Type locality: "Brésil" (named in honor of Auguste de Saint-Hilaire). See inapp. syn. by Troschel in Schomburgk (1848:647).
- Hydraspis hilarii* (Duméril and Bibron 1835): Gray (1844:40). Incorrect subsequent spelling.
- Phrynops geoffroyana* (Schweigger 1812): Gray (1844:41; in part); Gray (1864:130; in part). Incorrect subsequent spelling. Synonymized appropriately by Gray (1844:41) with *Phrynops geoffroana* Wagler (1830:136 Schweigger), *Emys geoffroana* Schweigger in Duméril and Bibron (1835:418), *Platemys geoffreana* (adult specimen) Duméril and Bibron 1835:418, and *Emys viridis* Spix 1824 (=Schweigger); but inapp. syn. with *Phrynops geoffroana* Wagler (1830 and 1833 plates 5 and 26, =*Phrynops hilarii*) and Duméril and Bibron 1835:422 Buenos Ayres juvenile specimen (= *Phrynops hilarii*). Also see Gray (1864:130) appropriately (intended or not?) synonymize *Phrynops geoffroana* (Wagler 1830:plate 5, =*Phrynops hilarii*), as *Phrynops geoffroyana*, under *Hydraspis* (*Phrynops*) *geoffroyana* Buenos Ayres (=Duméril and Bibron 1835:422, =*Phrynops hilarii*). Also see Boulenger (1889:222; in part) appropriately synonymize *Phrynops geoffroyana* (non Schweigger) with *Phrynops geoffroana* Wagler (1830; 1833, plates 5 and 26; in part, =*Phrynops hilarii*), and with Duméril and Bibron's 1835:422; in part, juvenile Buenos Ayres specimen (= *Phrynops hilarii*), under *Hydraspis hilarii*. But then see inapp. syn. by Boulenger of *Phrynops* (*Emys*) *geoffroana* (Schweigger/ *viridis*) Wagler (1830:136; in part) under *Hydraspis hilarii*. [= *Phrynops geoffroanus* (Schweigger 1812:302)].
- Hydraspis geoffroyana* (Schweigger 1812): Gray (1855:57; in part); Gray (1864:130; in part); Siebenrock (1905:426; in part). Both Gray (1855:57) and Gray (1864:130) specifically include the Duméril and Bibron 1835:422 Buenos Ayres locality (= *Phrynops hilarii*). See inapp. syn. by Siebenrock (1905:426) with Wagler (1830 and 1833 plates 5 and 26, =*Phrynops hilarii*) [= *Phrynops geoffroanus* (Schweigger 1812:302)].
- Hydraspis* (*Phrynops*) *geoffroyana* (Schweigger 1812): Gray (1864:130; in part). Here, Gray refers only to the Duméril and Bibron 1835:422, Buenos Ayres locality (= *Phrynops hilarii*), and synonymizes with *Phrynops geoffroyana* Wagler (1830: plate 5, = *Phrynops hilarii*). [= *Phrynops geoffroanus* (Schweigger 1812:302)].
- Platemys geoffreyana* (Schweigger 1812): Hensel (1868:350); Boulenger (1889:222; in part). Incorrect subsequent spelling. Inapp. syn. of *Platemys geoffreyana* Hensel (1868:350, refers to Duméril and Bibron 1835:418 (Schweigger), not Duméril and Bibron 1835:422 Buenos Ayres, = *Phrynops hilarii*) by Boulenger (1889:222; in part), under *Hydraspis hilarii*. By locality "In der Provinz Rio-Grande do Sul" may include *Phrynops williamsi* Rhodin and Mittermeier 1983 [= *Phrynops geoffroanus* (Schweigger 1812:302)].
- Spatulemys lasalae* Gray 1872b:463. Holotype: NHM (ex BMNH) 1947.3.5.93. Type locality: "Río Paraná, Corrientes" Province, Argentina. Synonymized under *Hydraspis hilarii* by Boulenger (1889:222). [= *Phrynops hilarii* (Duméril and Bibron 1835:428)].
- Hydraspis geoffroyana hilarii* (Duméril and Bibron 1835): Siebenrock (1905:426). Inapp. syn. having *Hydraspis hilarii* as subspecies of *Hydraspis geoffroyana* (Schweigger 1812:302). [= *Phrynops hilarii* (Duméril and Bibron 1835:428)].
- Phrynops hilarii* (Duméril and Bibron 1835): Stejneger (1909:127).
- Phrynops geoffroana hilarii* (Duméril and Bibron 1835): Müller (1939:95). Inapp. syn. having *Phrynops hilarii* as subspecies of *Phrynops geoffroana* Schweigger (1812:302). [= *Phrynops hilarii* (Duméril and Bibron 1835:428)].
- Phrynops* (*Phrynops*) *hilarii* (Duméril and Bibron 1835): Zangerl and Medem (1958:376).
- Phrynops geoffroanus hilarii* (Duméril and Bibron 1835): Wermuth and Mertens (1961:333). Inapp. syn. having *Phrynops hilarii* as subspecies of *Phrynops geoffroanus* (Schweigger 1812:302). [= *Phrynops hilarii* (Duméril and Bibron 1835:428)].
- Phrynops* (*Phrynops*) *geoffroanus hilarii* (Duméril and Bibron 1835): Pritchard (1967:234). Inapp. syn. having *Phrynops hilarii* as subspecies of *Phrynops geoffroanus* (Schweigger 1812:302). [= *Phrynops hilarii* (Duméril and Bibron 1835:428)].
- Phrynops geoffroanus* (Schweigger 1812)**
- Emys geoffroana* Schweigger 1812:302. Holotype: MNHN 9417 (taken from the Lisbon collections during the Napoleonic wars). Type locality: "in Brasilia" (named in honor of Etienne Geoffroy Saint-Hilaire).
- Emys depressa* Merrem 1820:22. (Not *Emys depressa* Spix 1824:5; lectotype ZSM 3003/0; see Hoogmoed and Gruber 1983:344, = *Acanthochelys spixii* (Duméril

and Bibron 1835:409). Holotype: ZSM 167/25, collected by Wied-Neuwied. Type locality: "Estado de Rio de Janeiro, Brasilien." Synonymized with *Platemys newwedii* after *Emys depressa* Merrem was excluded from synonymy with *Rhinemys nasuta* under *Platemys schweigerii* by Duméril and Bibron (1835:425). [= *Phrynops Geoffroanus* (Schweigger 1812:302)].

Emys viridis Spix 1824:3. Holotype: ZSMH 3008/0. Type locality: "in aquis lacustribus fluminis Carinhanhae, confluentis Sti Francisci" (Rio Carinhanhae and Rio San Francisco, Brazil). Synonymized appropriately with Wagler (1830:136 Schweigger) but inappropriately with Wagler (1830 and 1833, plates 5 and 26, = *Phrynops hilarii*), as *Phrynops Geoffroyana* by Gray (1844:41), and as *Phrynops Geoffreana* by Duméril and Bibron (1835:418); then again appropriately synonymized under *Platemys Geoffreana* (Schweigger) and *Emys Geoffreana* Schweigger, but inappropriately synonymized with the Buenos Ayres specimen (= *Phrynops hilarii*), by Duméril and Bibron (1835:418) where also, as *Hydraspis viridis* it was excluded from synonymy with *Emys rufipes* Spix, and inappropriately synonymized with *Platemys miliusii* [= *Phrynops Geoffroanus* (Schweigger 1812:302)].

Chelodina Geoffroana (Schweigger 1812): Fitzinger (1826:45).

Emys nasuta Schweigger 1812: Kaup (1828:1150; in part, as *Emys viridis* Spix 1824:3). *Emys nasuta* was excluded from synonymy with *Emys depressa* Merrem under *Platemys newwedii* by Duméril and Bibron (1835:425). [= *Batrachemys nasuta* (Schweigger 1812:298)].

Emys rufipes Spix 1824: Kaup (1828:1150; in part, as *Emys viridis* Spix 1824:3). *Emys rufipes* was excluded from synonymy with *Hydraspis viridis* under *Platemys Geoffreana* by Duméril and Bibron (1835:418). [= *Rhinemys rufipes* (Spix 1824:7)].

Hydraspis viridis (Spix 1824): Bell (1828:512). Synonymized under *Platemys Geoffreana* by Duméril and Bibron (1835:418). [= *Phrynops Geoffroanus* (Schweigger 1812:302)].

Phrynops (Emys) Geoffroana (Schweigger 1812): Wagler (1830:136; in part). See appropriately synonymized with *Platemys Geoffreana* (Schweigger), *Emys Geoffreana* Schweigger, *Hydraspis viridis* (Spix) and *Emys viridis* Spix, all in Duméril and Bibron (1835:418); but then inapp. syn. with *Phrynops hilarii* in plate 5 of the same publication, plate 26 of Wagler (1833), and the Duméril and Bibron 1835:422 juvenile Buenos Ayres specimen (all = *Phrynops hilarii*) [= *Phrynops Geoffroanus* (Schweigger 1812:302)].

Phrynops Geoffroana (Schweigger 1812): Wagler (1830:Table V. (=plate 5); in part); Wagler (1833: plate 26; in part). Inapp. syn. since both plates depict *Phrynops hilarii*. [= *Phrynops Geoffroanus* (Schweigger 1812:302)].

Chelys (Hydraspis) depressa (Merrem 1820): Gray (1831a:16). [= *Phrynops Geoffroanus* (Schweigger 1812:302)].

Chelys (Hydraspis) planiceps (Schoepff 1801): Gray (1831a:16; in part). Inapp. syn. of *Testudo planiceps* Schoepff 1801:115 [= *Platemys platycephala* (Schneider 1792:261)].

Chelys (Hydraspis) viridis (Spix 1824): Gray (1831a:16). [= *Phrynops Geoffroanus* (Schweigger 1812:302)].

Emys Geoffroyana Schweigger 1812: Gray (1831a:16; in part). Incorrect subsequent spelling. See inapp. syn. with *Testudo platycephala* Schneider 1792:261 and *Emys caniculata* Spix 1824:10 [= *Phrynops Geoffroanus* (Schweigger 1812:302)].

Hydraspis planiceps (Schoepff 1801): Gray (1831b:40; in part). Inapp. syn. of *Testudo planiceps* Schoepff 1801:115 [= *Platemys platycephala* (Schneider 1792:261)].

Hydraspis depressa (Merrem 1820): Gray (1831b:41). Appropriately synonymized under *Hydraspis Geoffroyana* by Boulenger (1889:223). Also appropriate synonymy by Gray (1855:56) with *Hydraspis depressa* (Merrem) in Gray (1831b:41); *Emys depressa* Merrem 1820:20; and *Platemys newwedii* (Merrem) Duméril and Bibron 1835:425. But then see inapp. syn. with *Hydraspis depressa* (Merrem 1820:20) by Gray (1855:56; in part). Reference specimen: Gray catalogue number NHM (ex BMNH) "51.b" (non Merrem; non Spix), Schomburgk collection. Specimen currently catalogued as *Phrynops Geoffroana tuberosa* (C. McCarthy pers. comm.). Locality: "British Guiana". Also see NHM "51.b" (as non Merrem) appropriately synonymized under *Hydraspis tuberosa* by Boulenger (1889:223). [= *Phrynops Geoffroanus* (Schweigger 1812:302)].

Phrynops viridis (Spix 1824): Gray (1831b:76). Synonymized under *Emys Geoffroyana* by Gray (1831b:77). [= *Phrynops Geoffroanus* (Schweigger 1812:302)].

Emys Geoffreana Schweigger 1812: Duméril and Bibron (1835:418; in part). Incorrect subsequent spelling. Appropriately synonymized with Duméril and Bibron 1835:418 adult *Platemys Geoffreana* specimen, with *Phrynops (Emys) Geoffroana* (Wagler 1830:136), and with both *Emys viridis* Spix 1824:3

and *Hydraspis viridis* (Spix, 1824:3). See also inapp. syn. with Duméril and Bibron 1835:422 juvenile (MNHN 2100) Buenos Ayres specimen (= *Phrynops hilarii*), and Wagler (1830 and 1833, plates 5 and 26) both under *Phrynops geoffreana* (both = *Phrynops hilarii*) [= *Phrynops geoffroanus* (Schweigger 1812:302)].

Platemys geoffreana Duméril and Bibron 1835:418; in part. Appropriately synonymized with *Emys geoffreana* (Schweigger) (Duméril and Bibron 1835:418), with *Phrynops (Emys) geoffroana* (Wagler 1830:136), and with both *Emys viridis* Spix 1824:3 and *Hydraspis viridis* (Spix, 1824:3). This is a redescription of the *Emys geoffroana* Schweigger 1812:302 holotype, but see inapp. syn. with the Duméril and Bibron 1835:422 “envoyé des Buenos Ayres” juvenile specimen (= *Phrynops hilarii*) and Wagler (1830 and 1833, plates 5 and 26, = *Phrynops hilarii*). But see also appropriate synonymy by Boulenger (1889:222; in part) of *Platemys geoffreana* juvenile specimen from Buenos Ayres (= *Phrynops hilarii*) Duméril and Bibron 1835:421(=422), under *Hydraspis hilairii* [= *Phrynops geoffroanus* (Schweigger 1812:302)].

Phrynops geoffreana (Schweigger 1812): Duméril and Bibron (1835:418; in part). See intended appropriate synonymy with *Emys geoffroana* Schweigger 1812:302 as *Platemys geoffreana* (Schweigger); with *Emys geoffreana* Schweigger; with *Emys viridis* Spix 1824; and *Hydraspis viridis* (Spix 1824); thus also appropriate synonymy with *Phrynops geoffroana* Wagler (1830:136 Schweigger/ *viridis*). But also see unintended inapp. syn. with Duméril and Bibron 1835:422 juvenile from Buenos Ayres specimen (= *Phrynops hilarii*), and with Wagler (1830 and 1833, plates 5 and 26, = *Phrynops hilarii*) [= *Phrynops geoffroanus* (Schweigger 1812:302)].

Platemys wagneri Duméril and Bibron 1835:422. Holotype: MNHN 8758. Type locality: “Brésil” (from collection of August de Saint-Hilaire). Synonymized under *Hydraspis wagneri* by Gray (1844:40). [= *Phrynops geoffroanus* (Schweigger 1812:302)]. Named in honor of Johann Georg Wagner.

Platemys newwedii Duméril and Bibron 1835:425. *Nomen novum* (new replacement name) for *Emys depressa* Merrem 1820. Holotype: ZSM 167/?5 (same as *Emys depressa* Merrem 1820:22). Type locality: “Brésil”. Synonymized under *Hydraspis depressa* (Merrem) by Gray (1844:39) and Gray (1855:56). [= *Phrynops geoffroanus* (Schweigger 1812:302)]. Named in honor of Prince Maximilian Wied-Neuwied.

Hydraspis (Phrynops) geoffroana (Schweigger 1812): Fitzinger (1835:126).

Emys geoffroiana Schweigger 1812: Temminck and Schlegel (1838:46). Incorrect subsequent spelling.

Emys platycephala (Schneider 1792): Temminck and Schlegel (1838:46; in part). Synonymized under *Hydraspis depressa* (Merrem) and *Phrynops geoffroyana* by Gray (1844:39 & 41). Inapp. syn. of *Emys (Testudo) platycephala* (Schneider 1792:261) [= *Platemys platycephala* (Schneider 1792:261)].

Phrynops geoffroanus (Schweigger 1812): Diesing (1840:237).

Hydraspis wagneri (Duméril and Bibron 1835): Gray (1844:40). Synonymized under *Hydraspis geoffroyana* by Luederwaldt (1926:430), and under *Phrynops geoffroanus geoffroanus* by Mertens and Wermuth (1955:404). [= *Phrynops geoffroanus* (Schweigger 1812:302)].

Emys geoffroana Schweigger 1812: Gray 1844:41; in part). Incorrect subsequent spelling. Appropriately synonymized with *Phrynops geoffroana* Wagler (1830:136, =Schweigger), *Emys viridis* Spix 1824:3 (=Schweigger), and *Platemys geoffreana* Duméril and Bibron 1835:418; in part (=Schweigger), but see inapp. syn. with *Phrynops geoffroana* Wagler (1830 and 1833, plates 5 and 26, = *Phrynops hilarii*), and Duméril and Bibron 1835:422; in part, as juvenile Buenos Ayres specimen (= *Phrynops hilarii*) [= *Phrynops geoffroanus* (Schweigger 1812:302)].

Phrynops geoffroyana (Schweigger 1812): Gray (1844:41; in part); Gray (1864:130; in part). Synonymized appropriately by Gray (1844:41) with *Phrynops geoffroana* Wagler (1830:136 Schweigger), *Emys geoffroana* Schweigger in Duméril and Bibron (1835:418), *Platemys geoffreana* (adult specimen) Duméril and Bibron 1835:418, and *Emys viridis* Spix 1824 (=Schweigger); but inapp. syn. with *Phrynops geoffroana* Wagler (1830 and 1833 plates 5 and 26, = *Phrynops hilarii*) and Duméril and Bibron 1835:422 Buenos Ayres juvenile specimen (= *Phrynops hilarii*). Also see Gray (1864:130) appropriately (intended or not?) synonymize *Phrynops geoffroana* (Wagler 1830:plate 5, = *Phrynops hilarii*), as *Phrynops geoffroyana*, under *Hydraspis (Phrynops) geoffroyana* Buenos Ayres (=Duméril and Bibron 1835:422, = *Phrynops hilarii*). Also see Boulenger (1889:222; in part) appropriately synonymize *Phrynops geoffroyana* (as non Schweigger) with *Phrynops geoffroana* Wagler (1830; 1833, plates 5 and 26; in part, = *Phrynops hilarii*), and with Duméril and Bibron’s 1835:422; in part, juvenile Buenos Ayres specimen (= *Phrynops hilarii*), under *Hydraspis hilarii*. But then see inapp. syn. by Boulenger of *Phrynops (Emys) geoffroana*

- (Schweigger/ *viridis*) Wagler (1830:136; in part) under *Hydraspis hilarii*. [= *Phrynops Geoffroyana* (Schweigger 1812:302)].
- Hydraspis rufipes* (Spix 1824): Gray (1844:41; in part) [= *Rhinemys rufipes* (Spix 1824:7)].
- Platemys canaliculata* (Spix 1824): Schlegel in Gray (1855:54; in part). Inapp. syn. of *Platemys (Emys) canaliculata* (Wagler 1830:135) (= *Emys canaliculata* Spix 1824:10) [= *Platemys platycephala* (Schneider 1792:261)].
- Hydraspis Geoffroyana* (Schweigger 1812): Gray (1855:57; in part); Gray (1864:130; in part); Siebenrock (1905:426; in part). Both Gray (1855:57) and Gray (1864:130) specifically include the Duméril and Bibron 1835:422 Buenos Ayres locality (= *Phrynops hilarii*). See inapp. syn. by Siebenrock (1905:426) with Wagler (1830 and 1833 plates 5 and 26, = *Phrynops hilarii*) [= *Phrynops Geoffroyana* (Schweigger 1812:302)].
- Platemys depressa* (Merrem 1820): Strauch (1862:47). [= *Phrynops Geoffroyana* (Schweigger 1812:302)].
- Platemys Geoffroyana* (Schweigger 1812): Strauch (1862:47).
- Hydraspis (Phrynops) Geoffroyana* (Schweigger 1812): Gray (1864:130; in part). Here, Gray refers only to the Duméril and Bibron 1835:422, Buenos Ayres locality (= *Phrynops hilarii*), and synonymizes with *Phrynops Geoffroyana* Wagler (1830: plate 5, = *Phrynops hilarii*). [= *Phrynops Geoffroyana* (Schweigger 1812:302)].
- Platemys Geoffroyana* (Schweigger 1812): Hensel (1868:350); Boulenger (1889:222; in part). Incorrect subsequent spelling. Inapp. syn. of *Platemys Geoffroyana* Hensel (1868:350, refers to Duméril and Bibron 1835:418 (Schweigger), not Duméril and Bibron 1835:422 Buenos Ayres, = *Phrynops hilarii*) by Boulenger (1889:222; in part), under *Hydraspis hilarii*. By locality "In der Provinz Rio-Grande do Sul", may include *Phrynops williamsi* Rhodin and Mittermeier 1983 [= *Phrynops Geoffroyana* (Schweigger 1812:302)].
- Platemys Geoffroyana* (Schweigger 1812): Hensel (1868:354; in part). By locality ("Rio Cadéa") may include *Phrynops williamsi* [= *Phrynops Geoffroyana* (Schweigger 1812:302)].
- Rhinemys Geoffroyana* (Schweigger 1812): Baur (1890:485).
- Hydraspis Boulengeri* Bohls 1895:53. Holotype: NHM (ex BMNH) 1947.3.5.94 (originally 96.5.11.1). Type locality: "im Aquidaban, Tagatiya und anderen linken Nebenflüssen des Paraguaystomes beobachtet habe" (in the Aquidaban, Tagatiya and other tributaries of the left bank of the Paraguay river). Synonymized under *Hydraspis Geoffroyana* by Siebenrock (1909:576). [= *Phrynops Geoffroyana* (Schweigger 1812:302)].
- Hydraspis lutzii* Ihering in Luederwaldt (1926:441). Holotype: MZUSP 31. Type locality: "Mogy-guassu (Est. de S. Paulo)", Brazil. Synonymized under *Phrynops Geoffroyana Geoffroyana* by Mertens and Wermuth (1955:333). [= *Phrynops Geoffroyana* (Schweigger 1812:302)].
- Phrynops Geoffroyana Geoffroyana* (Schweigger 1812): Müller (1939:95).
- Phrynops (Phrynops) Geoffroyana* (Schweigger 1812): Zangerl and Medem (1958:376).
- Phrynops Geoffroyana Geoffroyana* (Schweigger 1812): Wermuth and Mertens (1961:333).
- Phrynops (Phrynops) Geoffroyana Geoffroyana* (Schweigger 1812): Pritchard (1967:234).
- Phrynops (Phrynops) Geoffroyana* (Schweigger 1812): Pritchard (1967:234); also Freiberg (1981:69).
- Emys depressa* Spix 1824: Vanzolini (1981:19; in part). See Hoogmoed and Gruber, 1983:345. Inapp. syn. of *Emys depressa* Spix 1824:5 [= *Acanthochelys spixii* (Duméril and Bibron 1835:409)].

***Phrynops tuberosus* (Peters 1870)**

Platemys hilarii Duméril and Bibron 1835: Troschel in Schomburgk (1848:647; in part). Reference specimen (non Duméril and Bibron 1835:428): ZMB (Berlin) 166. Locality: "Cotinga flusse am Roraimagebirge in British-Guiana" (Cotinga River, near the Roraima Mountains, British Guiana). Inapp. syn. by Troschel (1848) with *Platemys hilarii* Duméril and Bibron 1835:428. See appropriate synonymy of Troschel (1848) under *Hydraspis tuberosa* by Boulenger (1889:223). [= *Phrynops hilarii* (Duméril and Bibron 1835:428)].

Hydraspis depressa (Merrem 1820): Gray (1855:56; in part). See inapp. syn of reference specimen: Gray catalogue number NHM (ex BMNH) "51.b" (non Merrem; non Spix), Schomburgk collection. Specimen currently catalogued as *Phrynops Geoffroyana tuberosa* (C. McCarthy pers. comm.). Locality: "British Guiana". Also see NHM "51.b" (as non Merrem) appropriately synonymized under

- Hydraspis tuberosa* by Boulenger (1889:223). [= *Phrynops geoffroanus* (Schweigger 1812:302)].
- Platemys tuberosa* Peters 1870:311. Holotype: ZMB (Berlin) 166 (same holotype as Troschel 1848). Type locality: "British Guiana".
- Hydraspis tuberosa* (Peters 1870): Gray (1870:75).
- Platemys depressa* (Merrem 1820): Boulenger (1889:223; in part). Inapp. syn. of *Platemys (Emys) depressa* (Merrem) Strauch (1862:153), under *Hydraspis tuberosa* [= *Phrynops geoffroanus* (Schweigger 1812:302)].
- Phrynops tuberosa* (Peters 1870): Stejneger (1909:127).
- Hydraspis geoffroyana* (Schweigger 1812): Luederwaldt (1926:430; in part). Incorrect subsequent spelling. Inapp. syn. of *Hydraspis tuberosa* (Peters 1870) noting that adult *Hydraspis tuberosa* have never been found, inferring synonymy with *Hydraspis geoffroyana* [= *Phrynops geoffroanus* (Schweigger 1812:302)].
- Phrynops geoffroana tuberosa* (Peters 1870): Müller (1939:95). Inapp. syn. having *Phrynops tuberosa* as subspecies of *Phrynops geoffroana* (Schweigger 1812:302) [= *Phrynops tuberosus* (Peters 1870:311)].
- Phrynops (Phrynops) tuberosa* (Peters 1870): Zangerl and Medem (1958:376).
- Phrynops geoffroanus tuberosus* (Peters 1870): Wermuth and Mertens (1961:333; in part). Inapp. syn. having *Phrynops tuberosus* as subspecies of *Phrynops geoffroanus* (Schweigger 1812:302) [= *Phrynops tuberosus* (Peters 1870:311)].
- Phrynops (Phrynops) geoffroanus tuberosus* (Peters 1870): Pritchard (1967:234). Inapp. syn. having *Phrynops tuberosus* as subspecies of *Phrynops geoffroanus* (Schweigger 1812:302) [= *Phrynops tuberosus* (Peters 1870:311)].
- Phrynops (Phrynops) tuberosus* (Peters 1870): Freiberg (1981:69).
- Phrynops tuberosus* (Peters 1870): Rhodin and Mittermeier (1983:59).
- Phrynops williamsi* Rhodin and Mittermeier 1983**
- Platemys geoffroyana* (Schweigger 1812): Hensel (1868:350; in part), by locality ("In der Provinz Rio-Grande do Sul") since *Phrynops williamsi* Rhodin and Mittermeier 1983:59 (see Paratype ZMB 6858) not yet recognized as distinct. Incorrect subsequent spelling. (= *Platemys geoffreana* Duméril and Bibron 1835:418; = *Emys geoffreana* Schweigger (Duméril and Bibron 1835:418)) [= *Phrynops geoffroanus* (Schweigger 1812:302)].
- Platemys geoffroyana* (Schweigger 1812): Hensel (1868:354; in part), by locality ("Rio Cadéa") since *Phrynops williamsi* Rhodin and Mittermeier 1983:59 (see Paratype ZMB 6858) not yet recognized as distinct. Incorrect subsequent spelling. (= *Platemys geoffreana* Duméril and Bibron 1835:418; = *Emys geoffreana* Schweigger (Duméril and Bibron 1835:418)) [= *Phrynops geoffroanus* (Schweigger 1812:302)].
- Hydraspis geoffroyana* (Schweigger 1812): Boulenger (1889:223; in part), phenotypically ("Body...rayed with brown") and by locality since *Phrynops williamsi* Rhodin and Mittermeier 1983:59 not yet recognized as distinct. (= *Emys geoffroana* Schweigger 1812:302) [= *Phrynops geoffroanus* (Schweigger 1812:302)].
- Phrynops geoffroyana* (Schweigger 1812): Vaz-Ferreira (1955:25; in part), by locality since *Phrynops williamsi* Rhodin and Mittermeier 1983:59 not yet recognized as distinct. (= *Emys geoffroana* Schweigger 1812:302) [= *Phrynops geoffroanus* (Schweigger 1812:302)].
- Phrynops geoffroana geoffroana* (Schweigger 1812): Mertens and Wermuth (1955:404; in part), by locality since *Phrynops williamsi* Rhodin and Mittermeier 1983:59 not yet recognized as distinct. [= *Phrynops geoffroanus* (Schweigger 1812:302)].
- Phrynops geoffroanus geoffroanus* (Schweigger 1812): Wermuth and Mertens (1961:333; in part), by locality since *Phrynops williamsi* Rhodin and Mittermeier 1983:59 not yet recognized as distinct. [= *Phrynops geoffroanus* (Schweigger 1812:302)].
- Phrynops geoffroanus* (Schweigger 1812): Freiberg (1970:190; in part), by locality since *Phrynops williamsi* Rhodin and Mittermeier 1983:59 not yet recognized as distinct. [= *Phrynops geoffroanus* (Schweigger 1812:302)].
- Phrynops geoffroana* (Schweigger 1812): Achaval (1976:26; in part), by locality since *Phrynops williamsi* Rhodin and Mittermeier 1983:59 not yet recognized as distinct. [= *Phrynops geoffroanus* (Schweigger 1812:302)].
- Phrynops williamsi* Rhodin and Mittermeier 1983:59. Holotype: MCZ 64135. Designated type locality: "Rio Cadéa, Rio Grande do Sul, Brazil." Named in honor of Ernest Edward Williams.

Phrynops (Phrynops) williamsi Rhodin and Mittermeier 1983; Iverson (1986:230).

***Ranacephala hoguei* (Mertens 1967): comb. nov.**

Mesoclemmys sp. (Schweigger 1812): Luederwaldt (1926:450; in part; see corresponding photos of Turtles #47 and #96). Locality: "Rio Parahyba, (Est. do Rio de Janeiro)". Inapp. syn. of *Mesoclemmys* which has a different locality (range) and misleading phenotypic resemblance to *Ranacephala hoguei* (= *Mesoclemmys* Gray 1873a:66) [= *Mesoclemmys gibba* (Schweigger 1812:299)].

Mesoclemmys gibba (Schweigger 1812): Ruschi (1966:1-6; in part). Locality: Espírito Santo, Brazil, where *Mesoclemmys* does not occur (Rhodin 1982:181). Inapp. syn. of *Mesoclemmys gibba* due to its having a different locality (range) and misleading phenotypic resemblance to *Ranacephala hoguei* [= *Mesoclemmys gibba* (Schweigger 1812:299)].

Phrynops (Phrynops) hoguei Mertens 1967:74. Holotype: SMF 62530. Type locality: "Rio Pequena, südwestlich von São Paulo, Brasilien, Instituto Butantan" (locality *ex errore*, see text). Named in honor of Alphonse Richard Hoge.

Phrynops hoguei Mertens 1967: Müller (1987:197).

***Rhinemys rufipes* (Spix 1824)**

Emys rufipes Spix 1824:7. Holotype: ZSM 3006/0. Type locality: "ad ripam fluminis Solimoëns", Brazil. See inapp. syn. with *Platemys miliusii* after *Emys rufipes* was excluded from synonymy with *Hydraspis viridis* under *Platemys geoffreana* by Duméril and Bibron (1835:418). [= *Rhinemys rufipes* (Spix 1824:9)].

Emys nasuta Schweigger 1812: Kaup (1828:1150; in part). [= *Batrachemys nasuta* (Schweigger 1812:298)].

Emys viridis Spix 1824: Kaup (1828:1150; in part). [= *Phrynops geoffroanus* (Schweigger 1812:302)].

Hydraspis rufipes (Spix 1824): Bell (1828:512).

Rhinemys rufipes (Spix 1824): Wagler (1830:134).

Chelys (Hydraspis) rufipes (Spix 1824): Gray (1831a:16).

Emys stenops Spix 1824: Gray (1831a:16; in part; 1831b:41; in part); Wermuth and Mertens (1961:334; in part); and Vanzolini (1981:19; in part). See Hoogmoed and Gruber 1983:351. [= *Mesoclemmys gibba* (Schweigger 1812:299)].

Hydraspis viridis (Spix 1824): Gray (1831b:41; in part). [= *Phrynops geoffroanus* (Schweigger 1812:302)].

Platemys rufipes (Spix 1824): Duméril and Bibron (1835:435).

Emys platycephala (Schneider 1792): Temminck and Schlegel (1838:47; in part). Also synonymized under *Phrynops rufipes* by Gray (1844:41; in part). Both are inapp. syn. of *Emys (Testudo) platycephala* (Schneider 1792:261) [= *Platemys platycephala* (Schneider 1792:261)].

Phrynops rufipes (Spix 1824): Gray (1844:41).

Platemys canaliculata (Spix 1824): Schlegel in Gray (1855:54; in part). Inapp. syn. of *Platemys (Emys) canaliculata* (Wagler 1830:135) (= *Emys canaliculata* Spix 1824:10). [= *Platemys platycephala* (Schneider 1792:261)].

Phrynops (Phrynops) rufipes (Spix 1824): Zangerl and Medem (1958:376).