

A Review of the Comparative Morphology of Extant Testudinoid Turtles (Reptilia: Testudines)

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Abstract. - With an expansive geographic distribution, an excellent fossil record, and over 140 recognized extant species, testudinoid turtles constitute one of the most diverse and widespread clades of turtles. The current understanding of the distribution of morphological characters among testudinoid turtles is poor. Improved knowledge will help to facilitate accurate identification of fossil remains, and to provide a reliable morphological data set for phylogenetic analyses. We provide a critical review of skeletal and scute characters commonly utilized in previous systematic analyses of Testudinoidea. Description and illustration of character states, discussion of their distribution within Testudinoidea, and polarity determinations for 93 characters are provided. Our preliminary results indicate that ontogenetic changes in skeletal structure are an important source of variation within Testudinoidea. Sexual variation, ontogenetic variation, and intra- and inter-population variation are inadequately documented for most testudinoid taxa. Furthermore, data matrices of morphologic characters in the existing literature must be carefully reconsidered. Previously published morphologic data provide reasonably strong support for the monophyly of 'Testudinidae.' Strong morphologic support for a monophyletic 'Emydidae' is lacking, and 'batagurid' monophyly has not been rigorously tested in the literature. Because a new research cycle centered on testudinoid phylogeny is now under way, it is essential to critically re-examine the underlying assumptions and working hypotheses that have governed this field of study over the last 20 years.

Key words. - Testudines, Testudinoidea, Testudinidae, Emydidae, Bataguridae, Geoemydidae, morphology, systematics.

Introduction

Pond turtles and land tortoises (collectively, Testudinoidea) form one of the largest and most widespread clades of living turtles, with more than 140 extant species and an almost worldwide distribution. The discovery and description of many new fossil testudinoids in the last half century, combined with the emergence and ascendancy of molecular techniques in systematics, provide new opportunities to explore the evolutionary history of the group in unprecedented detail. Concomitant with the appearance of these new data sets and analytical techniques comes an increasing appreciation for conservation efforts to preserve these turtle lineages and help to secure their future in the face of increasing human predation and habitat encroachment. This is true especially for the Asian representatives of this clade (e.g., van Dijk et al., 2000) but also is relevant at a more generalized and inclusive level (e.g., Rhodin, 2000).

Our recent attempts to diagnose fossil testudinoids reliably and to place them within a phylogenetic context led to the recognition that a critical re-evaluation of morphological data and purported synapomorphies for the

subclades of testudinoid turtles is desirable. A more thorough understanding of morphological data sets will provide not only a means by which molecular trees may be independently assessed, but also will form an essential foundation for diagnosing and interpreting fossil specimens. This in turn will facilitate the integration of fossil taxa into future systematic analyses, and will enhance our understanding of the paleobiogeography and divergence times of extant lineages.

The recent flurry of published works appears to represent the beginning of a new research cycle (*sensu* Kluge, 1991) in testudinoid systematics. We suggest that an important part of this cycle will be a critical re-examination of the working hypotheses that have governed testudinoid systematics since the publication of McDowell's (1964) seminal work on the group. A key component of this will be the assessment of fundamental, often unstated, assumptions that underlie current hypotheses of relationship. Our contribution to this research cycle is the first critical reappraisal of morphological characters applied to testudinoid systematics since the work of Hirayama (1985). The emerging improvement in our understanding of testudinoid relationships based on molecular sequence data will certainly

ly result in numerous new questions (e.g., regarding paleobiogeography, the timing of sequence and evolutionary divergences, and the evolution of morphological adaptations) that will demand a clearer understanding of testudinoid morphology.

The purpose of this paper is to present a preliminary revision and discussion of the morphological characters previously utilized in investigations of testudinoid systematics. Our goal here is not to produce a phylogenetic hypothesis (indeed, we deliberately eschew such a production), but rather to evaluate the morphological data that have been, and will be, used to generate such hypotheses. To enhance our discussion and facilitate improved communication about testudinoid morphology, we provide illustrations of all characters states we discuss.

Abbreviations. - Institution and collection abbreviations: CAS, California Academy of Sciences, San Francisco, California; CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; FMNH, Field Museum of Natural History, Chicago, Illinois; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; KU, The University of Kansas Natural History Museum, Lawrence, Kansas; LMNH, Louisiana Museum of Natural History, Baton Rouge, Louisiana; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; TNHC, Texas Natural History Collections, Texas Memorial Museum, Austin, Texas; TUMNH, Tulane University Museum of Natural History, New Orleans, Louisiana; YPM, Yale Peabody Museum, New Haven, Connecticut.

Abbreviations used in figures: AB, abdominal scute; af, articular facet; an, angular; bo, basioccipital; CE, cervical scute; co, costal bone; ent, entoplastron; epi, epipterygoid; fdm, foramen dentofaciale majus; fr, frontal; fpp, foramen palatinum posterius; HU, humeral scute; hyo, hyoplastron; hypo, hypoplastron; ju, jugal; MA, marginal scute; mx, maxilla; ne, neural bone; pa, parietal; pal, palatine; PEC, pectoral scute; pf, prefrontal; PL, pleural scute; pm, premaxilla; po, postorbital; pt, pterygoid; qj, quadratojugal; qu, quadrate; VE, vertebral scute; vf, vomerine foramen; vo, vomer.

Material and Methods

We examined 309 testudinoid specimens representing 93 species, but focused our efforts on 46 representative species. The list of specimens examined is provided in Appendix 1. Turtle shell nomenclature follows Zangerl (1969) and cranial nomenclature follows Gaffney (1972). Of the 46 focal species, most were recognized as

valid species by Ernst and Barbour (1989), with the exception of *texana*, which they placed within ‘*concinna*.’ Generic allocations for testudinoid species varied widely over the last 50 years and are subject to differing opinions today, particularly because the monophyly of many testudinoid genera remains untested. We consequently suppress the use of generic names wherever possible and use species epithets only. This procedure also has the advantage of precisely associating observations with species only instead of higher taxonomic categories. Most extant turtles have distinct species names, but among those turtles discussed in this review the species epithets *insculpta*, *nelsoni*, *oculifera*, *ornata*, and *platynota* each appear twice (*insculpta* under *Glyptemys* and *Carettochelys*; *nelsoni* under *Pseudemys* and *Terrapene*; *oculifera* under *Graptemys* and *Psammobates*; *ornata* under *Pseudemys* and *Terrapene*; *platynota* under *Geochelone* and *Notochelys*). For clarity in these instances, we indicate our usage with a single-letter generic abbreviation. A complete list of all currently recognized testudinoid species and all outgroup species used herein is provided in Appendix 2 together with a list of their various generic assignments used in the last 50 years.

Our use of the classic higher categories is always restricted to their phylogenetic crown. ‘*Emydinae*’ (sensu McDowell, 1964) are also referred to as ‘*Emydidae*,’ ‘*emydids*,’ or North American pond turtles; ‘*Batagurinae*’ (sensu McDowell, 1964) as ‘*Bataguridae*,’ ‘*batagurids*’ or Asian pond turtles; and ‘*Testudinidae*’ (sensu McDowell, 1964) as ‘*testudinids*’ or (land) tortoises. We make no *a priori* assumptions of monophyly for any of these categories, and retain single quotations around these names throughout the text to emphasize our uncertainty.

We attempted to examine most significant morphological characters commonly utilized in systematic studies of testudinoids, but the majority of our observations concern the skeletal system and scute characters. Almost all characters were derived from the literature. Major sources for each category were: ‘*Batagurinae*’ (Hirayama, 1985; McCord et al., 1995; Yasukawa et al., 2001); ‘*Testudinidae*’ (Crumly, 1982, 1985, 1994); and ‘*Emydinae*’ (Gaffney and Meylan, 1988; Burke et al., 1996). Additional characters were also found in Mlynarski (1976), Shaffer et al. (1997), and other sources cited in the character discussions. With few exceptions, morphological features were examined on specimens themselves; evaluations based on previously published literature are indicated where applicable. Sexual dimorphism, ontogenetically influenced polymorphisms, and geographic variation in morphology are not well explored in testudinoid turtles. These areas are in need of much more research. A full exploration of

such variation is beyond the scope of this work, but we are able to make some preliminary observations regarding morphological change through ontogeny in some anatomical systems.

Polarizing characters with the help of outgroups proved to be a difficult task, mostly because all relevant extant sister taxa are highly specialized after more than 65 million years of independent evolution. Furthermore, hypotheses of the systematic relationships of the major groups of cryptodires reveal a highly unstable picture (e.g., Bickham, 1981; Gaffney, 1975, 1985; Gaffney et al., 1991; Shaffer et al., 1997) making it impossible to make any *a priori* decisions regarding the succession of outgroups. We consequently assessed polarity for most characters by examining select outgroup taxa and the ingroup taxa. Where polarity is not clear from outgroup comparison, we sometimes relied upon ingroup commonality. To allow full transparency, we discuss every polarity decision at the end of each character description.

Outgroup taxa include the cryptodires *caretta*, *odoratus*, *serpentina*, and *spinifera*, and the pleurodires *gibba*, *siebenrocki*, *subglobosa*, and *subrufa*. For a number of characters, especially of the shell, neither ingroup nor outgroup analysis of extant taxa proved useful. In these instances, polarity was based on literature descriptions of the “lindholmemydid” taxa *Gravemys*, *Lindholmemyx*, and *Mongolemys*. These Cretaceous, Asian, fossil taxa are not well described in the literature, but sufficient material and description exists to use these taxa to help polarize character states (e.g., Khosatzky and Mlynarski, 1971; Sukhanov, 2000; Danilov and Sukhanov, 2001). The group may not be monophyletic, but putative members currently are hypothesized to sit along the phylogenetic stem of Testudinoidea (Danilov and Sukhanov, 2001). We purposefully did not use the fossil taxon ‘*Echmatemys*’ as an outgroup taxon (Hirayama, 1985), because its phylogenetic position outside of Testudinoidea or even ‘Batagurinae’ is not sufficiently demonstrated.

All figures were produced using digital photography and processed using Adobe Photoshop. Images were digitally enhanced using the burn and burnish tools and the unsharp mask filter option.

Taxonomic and Systematic Background. - Despite the increased attention directed towards testudinoids by scientists, hobbyists, and nonprofessional enthusiasts in the last thirty-five years, our collective conceptualization of the higher-level (beyond the specific and generic) systematics within this clade remained virtually unchanged since the work of McDowell (1964). The various taxonomies in current use owe their existence in large part to historical contexts that are not well appreciated by

many authors. A brief summary is given here.

During the second half of the 19th century, a number of attempts were made to work out higher-level testudinoid relationships and to apply taxonomic conventions that were designed (to a greater or lesser extent) to communicate conceptualizations of these relationships. In his synopsis on the turtles of North America, Agassiz (1857) united all pond turtles into the Emydoidae and subdivided this group into a three monotypic subfamilies (Deirochelyoidae for *reticularia*, Emydoidae for *blandingii*, Cistudinina for *T. ornata* and *carolina*) followed by the subfamilies Clemmydoidae (for *G. insculpta*, *guttata*, *marmorata*, and *muhlenbergii*) and Nectemydoidae (for those species currently placed in the genera *Pseudemys*, *Trachemys*, *Graptemys*, *Malaclemys* and *Chrysemys*). Most land tortoises were placed in Testudinidae by Theobald (1868); he also included all ‘leaf turtles and tortoises’ (e.g., *amboinensis*, *emys*, *dentata*, *grandis*, *tricarinata*) in Geoemydidae, and an eclectic group of aquatic turtles, including *mega-cephalum*, *serpentina*, kinosternids, and all remaining testudinoids, in Emydidae. Subsequently, all land tortoises (including *emys* and *impressa*) were united in the Testudinidae by Gray (1870). Those species currently placed in *Pseudemys* and *Trachemys* were assigned by Gray (1870) to the Pseudemydidae; the Asian taxa *baska*, *borneoensis*, *thurjii*, *kachuga*, and *ocellata* were assigned to the Bataguridae, and all hinged pond turtles, ‘true terrapins,’ and ‘snail-eating pond turtles’ to the Holarctic families Cistudinidae, Emydidae, and Malaclemmydidae, respectively.

Despite these early attempts, most subsequent authors (e.g., Boulenger, 1889; Siebenrock, 1909; Lindholm, 1929; Smith, 1931; Bourret, 1941) ignored (or were unaware of) these works and simply divided all testudinoid turtles into two speciose subgroups: tortoises (Testudinidae or Testudininae) and pond turtles (Emydidae or Emydinae). This situation remained static for nearly 100 years until the comprehensive and influential work of McDowell (1964). He not only divided all known pond turtles into several species complexes (‘*Hardella*,’ ‘*Batagur*,’ ‘*Orlitia*,’ ‘*Geoemyda*,’ ‘*Chrysemys*,’ ‘*Deirochelys*,’ and ‘*Emys*’ complexes), but also concluded that pond turtles can be divided clearly into two subgroups, the predominantly North American ‘Emydinae’ and the Asian and central American ‘Batagurinae.’ Furthermore, McDowell (1964) reasoned that tortoises are not the sister group of pond turtles, but rather were likely derived from a ‘batagurine’ ancestor. These conclusions were later corroborated by the first, and to date only, comprehensive morphological cladistic analysis of ‘batagurine’ systematics (Hirayama, 1985).

The influence of McDowell’s (1964) work is best understood when considering its continuous impact on

subsequently proposed phylogenies. Despite differences of opinion regarding generic- and species-level systematic arrangements, virtually all major synthetic works in the last thirty years followed McDowell's (1964) subdivision of pond turtles into the 'Batagurinae' and 'Emydinae' (e.g., Mlynarski, 1976; Pritchard, 1979; Ernst and Barbour, 1989), even though 'Batagurinae' may best be regarded as a paraphyletic taxon (McDowell, 1964; Hirayama, 1985). The fundamental division proposed by McDowell is also reflected in more recent studies centered on using various molecular techniques to elucidate phylogeny, the majority of which dealt with treatments of in-group relationships *within* one or the other of McDowell's groups (Sites et al., 1984; Bickham et al., 1996; Carr and Bickham, 1986; Wu et al., 1999; McCord et al., 2000; Feldman and Parham, 2002; Honda et al., 2002; Iverson et al., 2002; Stephens and Wiens, 2003).

Admittedly, the list of autapomorphic characters compiled by Crumly (1985) for the 'Testudininae' compellingly corroborates the hypothesis of tortoise monophyly. However, most characters that currently unite 'Emydinae' or 'Batagurinae + Testudininae' seem to support these groupings weakly, because the derived states typically are not found within all species of the ingroup and commonly also are observed in species of the alleged sister group (e.g., Hirayama, 1985; Gaffney and Meylan, 1988). In addition, several of the characters that purportedly distinguish 'Batagurinae + Testudininae' from the 'Emydinae' probably should be considered primitive for the entire group (Gaffney and Meylan, 1988). Even if some characters do successfully unite a group, monophyly is not established until the involved characters are demonstrated to be derived within Testudinoidea. Furthermore, the simple demonstration of monophyly for a given group does not automatically imply that it must be the sister to the remaining taxa. For instance, 'Emydinae' may be monophyletic, but monophyly does not necessarily demand that 'Emydinae' be regarded as the sister to 'Batagurinae + Testudininae.' It is at least plausible that 'Emydinae' is situated within 'Batagurinae,' a possibility that is not adequately explored and tested in the literature.

Similarly, most of the groupings considered by Gray (1855, 1870) and Agassiz (1857) were not discussed in recent literature, even though they might be valid. For instance, given the considerable list of morphological similarities that are shared by hinged turtles of the New and Old World (e.g., development of a plastral hinge, reduction of posterior neural elements, fusion of the femoral trochanter, great reduction of the temporal arch) perhaps Gray (1870) was truly visionary in uniting these turtles as the 'Cistudinidae.' Only a global cladistic analysis with no *a priori* assumption regarding internal relationships can evaluate these alternatives and

produce testable results. It is toward this end that we offer our critical reappraisal of morphological characters in testudinoids.

Results and Discussion

Cranium

(1) *Shape of the fissura ethmoidalis*; 0 = narrow or closed, keyhole-shaped, Fig. 1; 1 = very wide, Fig. 2 (modified from Crumly, 1982, 13; Hirayama, 1985, 1; McCord et al., 1995, 5).

The general configuration of the fissura in 'emydids' and 'batagurids' is keyhole-shaped (McDowell, 1964). Different proportions and widths are apparent (especially in the ventral part of the fissura), and were scored by Hirayama (1985) and Crumly (1982) as discrete character states. Our survey of many taxa reveals morphological intermediates, and the expression of various states appears to have an ontogenetic component in which younger individuals exhibit a relatively larger fissura, which corresponds to a less-ossified nasal cavity. However, a rather significant morphological gap can be observed between tortoises and pond turtles. For the purpose of this review, we lumped Hirayama's (1985) states into our state 0, and Crumly's (1982) into our state 1. The scoring presented by Hirayama (1985) and McCord et al. (1995) permitted phylogenetic resolution within 'batagurids', and that of Crumly (1982) within tortoises. Our revised scoring permits support only for the hypothesis of a monophyletic 'Testudinidae.'

Polarity: Pleurodires lack a defined fissura ethmoidalis. A keyhole-shaped fissura ethmoidalis is present in *spinifera*, *odoratus*, *caretta*, *serpentina*, and *Mongolemys*, and this condition is considered primitive for testudinoids.

(2) *Medial inflection of the inferior descending processes of the frontal*; 0 = absent, or very small, Fig. 3; 1 = present, well-developed, medial contact present or almost present, Fig. 4 (modified from Hirayama, 1985, 2).

In most turtles, a gutter (the sulcus olfactorius) is formed along the ventral surface of the frontals. This gutter transmits the olfactory nerve. The lateral rims of the sulcus sometimes form processes that descend ventromedially to surround the nerve from below (McDowell, 1964). According to Hirayama (1985) these processes are well-developed, or are in contact medially, in *ocellata* and *hamiltonii*. We confirm the presence of well-developed processes in these taxa and add *petersi*, *N. platynota*, and all sampled tortoises to the list. We recommend that this character not be subdivided into additional character states, because the descending processes of the frontals grow larger through ontogeny.

Polarity: A medial inflection is absent in all outgroups and the vast majority of the ingroup. We consider its presence to be derived.

(3) *Frontal contribution to the orbital rim*; 0 = present, no prefrontal/postorbital contact on dorsal surface, Fig. 5; 1 = absent, frontal excluded from orbital rim by prefrontal/postorbital contact, Fig. 6 (modified from Crumly, 1982, 17; Hirayama, 1985, 3; Shaffer et al., 1997, 97; Yasukawa et al., 2001, 1).

Three states for this character were scored by Hirayama (1985) and Yasukawa et al. (2001): frontal contribution always or usually present, frontal sometimes excluded from orbital rim, and frontal always excluded from orbital rim. Our sample size for many taxa does not permit a reliable assessment of intraspecific variation in this character, and thus our initial scores differed for some taxa from those of Hirayama (1985). We add *petersi* and *N. platynota* to the list of taxa in which the frontal appears always to be excluded. For those taxa that sometimes exclude the frontals, we confirm this polymorphic condition in *crassicolis*, and add *agassizii* and *annulata*. Our sample was too small to confirm the reported polymorphic condition in *amboinensis*, and *pulcherrima* by Hirayama (1985) and Yasukawa et al. (2001), but we scored these taxa as polymorphic based on their observations. We also followed Crumly (1982) by coding *pardalis* as polymorphic, even though we were not able to observe this in our sample. Our coding differs from that of Shaffer et al. (1997) for *Heosemys* and *reevesii*. In their analysis, they used *spinosa* (in which the frontal contributes to the orbital rim), but we used *grandis* (in which it does not). In both specimens of *reevesii* available to us, the frontal clearly does not participate in the orbital margin. Given the contrary statement by Shaffer et al. (1997), *reevesii* may be polymorphic for this character.

Polarity: The frontal participates in the orbital rim in pleurodires and *spinifera*, it is excluded in *odoratus* and *caretta*, and it is polymorphic in *serpentina*. No pattern is apparent within the ingroup. Given that the frontal clearly contributes to the orbital rim in *Mongolemys*, we consider its absence to be derived.

(4) *Contact between jugal and pterygoid*; 0 = present, medial process of jugal well-developed and touching the pterygoid, Fig. 7; 1 = absent, medial process reduced, Fig. 8 (modified from Hirayama, 1985, 11, 12; McCord et al., 1995, 3; Burke et al., 1996, 23; Yasukawa et al., 2001, 4, 5).

The jugal of most testudinoid turtles is expanded at its ventral end to form a medial process that contacts the pterygoid medially (McDowell, 1964). Presence or absence of the medial process, and presence or absence

of a medial contact with the pterygoid were treated as two characters by Hirayama (1985) and Yasukawa et al. (2001). The scoring for the two characters appears to be redundant and we followed the recommendation of Gaffney and Meylan (1988) by combining them.

We confirm the loss of a medial contact between the jugal and the pterygoid in *galbinifrons*, *flavomarginata*, and *mouhotii* (Hirayama, 1985; Yasukawa et al., 2001), but we found this condition to be polymorphic in *spengleri* (also reported by McCord et al., 1995), and in *trijuga*. Our observations are concordant with those of Burke et al. (1996).

Polarity: A contact between the jugal and pterygoid is present in *spinifera*, *odoratus*, and *serpentina*, but is absent (although the two bones closely approach one another) in *caretta*. We conclude that the contact between the two bones is the primitive condition for testudinoids and that their separation is derived, a conclusion also reached by Hirayama (1985). Our polarity determination is opposite that used by McCord et al. (1995), who mistakenly claimed to have derived their polarity assessment from Hirayama (1985).

(5) *Contact between jugal and palatine*; 0 = absent, Fig. 9; 1 = present, Fig. 10 (Gaffney and Meylan, 1988, F5.4).

The presence of a contact between the medial process of the jugal and the palatine was used previously in support of a monophyletic Deirochelyinae (Gaffney and Meylan, 1988). We confirm the formerly observed distribution of this character within 'emydids' with the exception of *reticularia*, which does not exhibit a contact. A contact is present in numerous 'batagurids,' such as *borneoensis*, *reevesii*, and *hamiltonii*, but was absent in all examined members of 'Testudinidae.'

Polarity: A contact between the jugal and the palatine is present in *caretta*, *odoratus*, and pleurodires, but is absent in *spinifera* and *serpentina*. A contact is absent in *Mongolemys*. We consequently consider its presence to be derived.

(6) *Contact of the epipterygoid with the jugal*; 0 = clearly absent, Fig. 11; 1 = present, or almost present, epipterygoid forms a long lateral process that approaches the jugal, Fig. 12 (Gaffney and Meylan, 1988, F8.1; Shaffer et al., 1997, 106).

According to Gaffney and Meylan (1988) the epipterygoid and the medial process of the jugal approach one another or are in contact in *reticularia* and the various species they included in *Pseudemys* and *Trachemys*. They also noted a contact between these two elements in species they classified in *Graptemys*, but the condition in those taxa was interpreted to be a result of

the medial expansion of the jugal and not a lateral expansion of the epipterygoid, and consequently was regarded as non-homologous (Gaffney and Meylan, 1988). We confirm the contact or near contact of these two elements in *reticularia*, *decorata*, *scripta*, *alabamensis*, *P. nelsoni*, *rubriventris*, *texana*, *flavimaculata*, *geographica*, *kohnii*, *nigrinoda*, *G. oculifera*, *ouachitensis*, and *versa*, and also report it in *picta* and *terrapin*. Contact was clearly absent in the specimens of *barbouri*, *ernsti*, and *gibbonsi* we examined. We made no assessments of homology, but accept any contact between these two elements as the derived state (as was done by Shaffer et al., 1997). Among ‘batagurids,’ we also found a close approach in *reevesii*.

Polarity: A contact, or near contact, between the epipterygoid and the jugal is absent in all outgroups and the vast majority of the ingroup. We consider its presence to be derived.

(7) *Contact of the inferior process of the parietal with the medial process of the jugal; 0 = absent, Fig. 13; 1 = present, Fig. 14 (Hirayama, 1985, 13).*

Our coding differs significantly from that of Hirayama (1985). In *reevesii*, *N. platynota*, and *bealei* we found no contact between the parietal and jugal, although these were the only three taxa in which Hirayama (1985: table 2) scored it to be present. However, we found a pronounced contact between these two elements in *subtrijuga*, a species scored by Hirayama (1985: table 2) as lacking such a contact, but shown on his tree (Hirayama, 1985: fig. 2) as a unique ‘batagurid’ feature convergent with some ‘emydids.’ Among ‘emydids,’ a well-developed contact occurs in *barbouri* and other broad-headed species currently classified in *Graptemys*.

Polarity: There is no contact between the inferior process of the parietal and the medial process of the jugal in all outgroups and the vast majority of the ingroup. A contact is considered to be the derived condition.

(8) *Contact of the inferior process of the parietal with the maxilla; 0 = absent, Fig. 13; 1 = present, Fig. 14 (Hirayama, 1985, 14).*

Our coding differs from that of Hirayama (1985). According to his character matrix (table 2) a contact should be present between the inferior process of the parietal and the maxilla in *reevesii* and *mouhotii*, but his cladogram (fig. 2) indicated that the presence of a contact should be regarded as a uniquely derived autapomorphy of *subtrijuga*. We found no contact in *reevesii* or *mouhotii*. Of the testudinoid species we examined, *subtrijuga* is the only one that shows this feature.

Polarity: There is no contact between the inferior

process of the parietal and the maxilla in all outgroups. Its presence is considered to be derived.

(9) *Extent of quadratojugal; 0 = quadratojugal well developed, firmly attached to jugal, Fig. 15; 1 = quadratojugal present, contact lost with jugal, Fig. 16; 2 = quadratojugal so heavily reduced that it appears to be absent in many skeletal specimens, Figs. 17, 18 (modified from Hirayama, 1985, 16; Shaffer et al., 1997, 47; Burke et al., 1996, 21; McCord et al., 1995, 6; Yasukawa et al., 2001, 7, 8).*

Variation in the structure of the temporal region of turtles was discussed in detail by Zdansky (1924) and comments specific to testudinoids were provided by Zangerl (1948) and McDowell (1964). We originally scored the reduction of the quadratojugal as three different characters: loss of contact with the jugal, loss of contact with the squamosal, and the apparent loss of the quadratojugal. All five logically possible combinations were observed, but in most testudinoid turtles the temporal arch is so slender that the contact between the quadratojugal and squamosal is commonly reduced to a sliver that would have to be scored as ‘just barely present’ or ‘just barely absent.’ We therefore abandoned our efforts to evaluate the contact between the quadratojugal and squamosal. Our observations generally agree with those of McDowell (1964), Hirayama (1985), Burke et al., (1996), McCord et al. (1995), and Yasukawa et al. (2001).

We purposefully avoid addressing the apparent lack of a quadratojugal in many species as an absence, because previous work by Zdansky (1924) showed that the quadratojugal of some ‘batagurids’ is so poorly ossified and connected to the surrounding elements that it tends to be lost in skeletal specimens (Figs. 17, 18). An example of this problem can be found among the many conflicting statements made regarding the presence of this element in *N. platynota* (e.g., Smith, 1931; Bourret, 1941; McDowell, 1964; Ernst and Barbour, 1989).

Polarity: The quadratojugal is present and firmly attached to the jugal in all outgroups, with the exception of chelids. Its reduction is considered to be derived.

(10) *Contribution of jugal to the rim of upper temporal emargination (Hirayama, 1985, 15); 0 = absent, Figs. 19, 20; 1 = present, Fig. 21.*

Participation of the jugal in the rim of the upper temporal emargination was reported previously in *hamiltonii* and *ocellata* (Hirayama, 1985). We confirm its presence in both species, but in one of the *hamiltonii* specimens we examined (MCZ 120333) the jugal forms a significant part of the rim only on one side of the skull; on the other side, which appears abnormal and likely represents a teratology, it does not. In all other species

available to us, the jugal does not participate in the rim. In *subtrijuga*, the jugal is excluded from the upper temporal emargination by narrow extensions of the postorbital and quadratojugal (Fig. 20).

Polarity: The jugal participates in the upper temporal rim of *spinifera*, but it is excluded in *odoratus*, *caretta*, *serpentina*, *Mongolemys*, and most pleurodires. We consider the participation of the jugal in the rim of the upper temporal emargination to be the derived condition within testudinoids.

(11) *Contact between the quadratojugal and the articular facet of the quadrate; 0 = absent, Fig. 22; 1 = present, quadratojugal sends a process ventrally along the rim of the cavum tympani and touches the lateral edge of the articular facet, Fig. 23 (modified from Hirayama, 1985, 17).*

The original character definition (Hirayama, 1985, character 17) is inappropriate, because the *jugal* does not contact the articular surface of the quadrate in any turtle except for *madagascariensis* and *dumerilianus* (Gaffney and Meylan, 1988). However, because Hirayama indicated in his tree that the only 'batagurid' taxon to exhibit this character is *subtrijuga*, we assume that he was referring to a contact between the *quadratojugal* and the articular facet of the quadrate, a characteristic of *subtrijuga* only among testudinoids. A contact between the two elements was reported previously for *reevesii* in the character matrix published by Hirayama (1985), but we conclude that this must be a publishing error, because it stands in conflict with his tree. In the specimens of *reevesii* available to us, there is no contact. It is possible that the scoring for *subtrijuga* and *reevesii* were flipped, at least in part, in the Hirayama (1985) matrix (in which the taxa were listed next to one another).

Polarity: A contact between the quadratojugal and the articular surface of the quadrate is absent in *spinifera*, but present in *odoratus*, *caretta*, and *serpentina*, and consequently could be considered primitive. However, based on ingroup commonality and the absence of a contact in *Mongolemys*, we consider a contact to be derived for Testudinoidea.

(12) *Contact between quadratojugal and maxilla; 0 = absent, Fig. 22; 1 = present, Figs. 23, 24 (Hirayama, 1985, 18).*

According to Hirayama (1985), among 'batagurids' a contact between the quadratojugal and maxilla is only present in *subtrijuga* and *reevesii*. We did not find a contact in our specimens of *reevesii*, but confirm its presence in *subtrijuga*.

Gaffney and Meylan (1988) listed a contact between the quadratojugal and maxilla as a synapomorphy for Platysternina {*megacephalum* + '*Chelydrosis*'}

and as an independently evolved synapomorphy for Kinosternidae, whereas Shaffer et al. (1997) noted a contact to be present in Kinosternidae, *C. insculpta*, and *megacephalum*. Our observations confirm the presence of a contact in all of these extant groups. Among testudinoids, *subtrijuga* is unique in having an extensive contact in lateral view (Fig. 23). In several 'emydids,' a contact is present on the inside of the temporal arch (*barbouri*, and *nigrinoda*; polymorphic in *geographica*, *G. oculifera*, and *texana*; Fig. 24). For now, we scored all taxa as present, regardless of whether the contact is visible in lateral view, medial view, or both. In several other 'emydid' taxa, the bones closely approach one another, but do not actually meet, on the inside of the temporal arch (*alabamensis*, *ernsti*, *flavimaculata*, *gibbonsi*, *kohnii*, *P. nelsoni*).

Polarity: A contact is present between the quadratojugal and maxilla in *odoratus*, but absent in *spinifera*, *caretta*, *serpentina*, and *Mongolemys*. We consider the presence of a contact to be derived for Testudinoids.

(13) *Medial contact of the maxillae along the anterior margin of the jaw; 0 = absent, Figs. 25, 26; 1 = present, Fig. 27 (modified from Hirayama, 1985, 20; McCord et al., 1995, 2; Yasukawa et al., 2001, 10).*

In most testudinoids, the anteromedial ends of the maxillae are separated medially by the premaxillae along the anterior margin of the jaw (Fig. 25). Hirayama (1985) noted that the maxillae have a medial contact in some 'batagurids,' which was confirmed by McCord et al. (1995) and Yasukawa et al. (2001) for *spengleri* and several other species that they included in the genus *Geoemyda*. We found a broad medial contact of the maxillae in *spengleri* and *annulata* (Fig. 27). In some species, the maxillae approach one another along the ventral rim of the nasal opening (e.g., *amboinensis*, *mouhotii*, *pulcherrima*, *crassicolis*), but a well-developed contact is never present (Fig. 26).

Polarity: The maxillae do not meet medially along the anterior margin of the jaw in *odoratus*, *caretta*, *serpentina*, and *Mongolemys*. A medial contact is present in *spinifera* but only along the ventral border of the external nares. We consider a medial contact along the anterior margin of the jaw to be the derived condition within Testudinoidea.

(14) *Size of the foramen orbito-nasale; 0 = small, less than 1/6 of orbit length, Figs. 28, 29; 1 = large, more than 1/6 of orbit length, Fig. 30 (modified from Hirayama, 1985, 33; Gaffney and Meylan, 1988, F9.3, F10.2, G10.3, H11.1, H16.3; Crumly, 1982, 25; Crumly, 1994, 12).*

We were cautious when first approaching this character due to the inconsistent usage and definition of

'small' and 'large' by various authors. However, after assessing the size of this foramen based on its size relative to the length of the orbit, we were surprised to see that we were able to reproduce Hirayama's (1985) scoring for the 'batagurids' without too many difficulties. In contrast, our initial observations of tortoises were in stark contrast to those of Crumly (1982, 1985, 1994) and Gaffney and Meylan (1988). This may be due to the thin nature of the palatine of many tortoises, and the relative ease with which that part of the palate can be damaged during skeletal preparation and handling. Furthermore, the foramen becomes progressively more closed with increased ontogenetic age (Crumly, 1982). We encountered similar problems in attempting to score *reticularia* and *blandingii*. Because we deem this character to be potentially useful for helping to resolve phylogeny within 'batagurids' and 'emydids,' we decided to score all testudinoids with delicate palatines (i.e., all tortoises, *reticularia*, and *blandingii*) as 'unknown.' We acknowledge that our redefinition of the character is still subjective and somewhat problematic, but using this definition we were able to unambiguously score all the ingroup taxa we examined.

Polarity: The foramen orbito-nasale is large in *serpentina*, *odoratus*, and *spinifera*, but small in *caretta*. We consider presence of a large foramen orbito-nasale to be the derived condition within testudinoids, because the foramen is small in *Mongolemys*.

(15) *Contact between maxilla and vomer; 0 = present, Fig. 31; 1 = absent, vomer separated from the maxilla by the premaxilla, Fig. 32 (Hirayama, 1985, 31; Crumly, 1982, 21; Yasukawa et al., 2001, 14).*

We generally agree with previous scorings for this character (Hirayama, 1985, Crumly, 1982, Yasukawa et al., 2001). We confirm the absence of a contact in *amboinensis* and *pulcherrima*, but our scoring differs slightly for those taxa that Hirayama (1985) coded as 'intermediate apomorphic,' a character state that we interpret as polymorphism. Of those taxa that Hirayama (1985) and Yasukawa et al. (2001) scored as intermediate (*flavomarginata*, *casifica*, *annulata*), our sample size is too small to confirm whether both character states are present. We consequently follow these authors by scoring those taxa as polymorphic.

Polarity: A contact between the maxilla and vomer is present in all outgroups. The loss of this contact is derived for testudinoids.

(16) *Size of the foramen palatinum posterius; 0 = large, Fig. 33; 1 = small, Fig. 34 (modified from Hirayama, 1985, 22; Gaffney and Meylan, 1988, F2.2, F6.1; McCord et al., 1995, 4; Yasukawa et al., 2001, 12).*

Our characters 16 and 17 were published originally

by Hirayama (1985) as one character that combined two morphological features: the size of the foramen palatinum posterius (f.p.p.) and participation of the pterygoid in the margin of the f.p.p. Although four possible combinations of these features are logically possible, only two were originally included (participation present, f.p.p. large; participation absent, f.p.p. small). Gaffney and Meylan (1988) also used this character within 'emydids,' but their character applied only to the exclusion of the pterygoid from the f.p.p. We decided to subdivide Hirayama's (1985) character into one character that describes the size of the f.p.p. and a second that addresses the position of the pterygoid relative to the f.p.p.

We found no difficulty in identifying the f.p.p. as 'large' or 'small,' (Figs. 33 and 34, respectively), and no ambiguous condition was encountered. Because our character definition only includes two character states, our scorings do not reflect those of other workers with a more limited target group (e.g., McCord et al., 1995). In juveniles the f.p.p. tends to be larger, but during later ontogenetic stages the f.p.p. is slowly reduced in size.

Polarity: The f.p.p. is small in *odoratus*, *spinifera*, and most pleurodires; it is absent in *caretta*, but is large in *serpentina* and *Mongolemys*. We consider a small f.p.p. to be the derived state.

(17) *Position of the pterygoid relative to foramen palatinum posterius (f.p.p.); 0 = pterygoid situated posterior to the f.p.p., Fig. 33; 1 = pterygoid situated posterior to the f.p.p., but sends a process anterior and lateral to the f.p.p., Fig. 34.*

Our survey of testudinoids indicated that reliable assessment of participation of the pterygoid in the f.p.p. may be difficult because many species show an ontogenetic change in configuration of this part of the palate. In juveniles, the f.p.p. typically includes the pterygoid in its posterior margin. During later ontogenetic stages the pterygoid is excluded. In spite of this, it appears that the relative position of the pterygoid tends to stay constant during ontogeny.

Polarity: The anterior end of the pterygoid is situated posterior to the f.p.p. in *odoratus*, *serpentina*, most pleurodires, and *Mongolemys*, but is situated lateral to the f.p.p. in *spinifera*. We consider a posterior position to be primitive for Testudinoidea.

(18) *Epipterygoid participation in the trigeminal foramen; 0 = absent, Fig. 35; 1 = present, epipterygoid clearly separates the parietal and pterygoid in lateral view, Fig. 36.*

The anteroventral rim of the trigeminal foramen of most testudinoid turtles is formed by the parietal and pterygoid. The epipterygoid commonly comes close to the foramen, but does not form part of it. In *spengleri*

and *mouhotii*, the epipterygoid consistently participates in the margin of the trigeminal foramen thus separating the parietal and pterygoid, at least in lateral view.

Polarity: The epipterygoid forms part of the anteroventral rim of the trigeminal foramen in the majority of outgroups, with the exception of pleurodires that lack a definitive ossified epipterygoid (Gaffney, 1979). The condition is unclear for *Mongolemys*. However, within the ingroup we found this character only in the seemingly rather specialized turtles *spengleri* and *mouhotii*. We consequently consider its presence to be secondarily derived.

(19) *Vomerine foramen*; 0 = absent, Fig. 37; 1 = present, Fig. 38 (Gaffney and Meylan, 1988, H4.1; Crumly, 1994, 15).

The vomerine foramen (= anteromedial vomerine aperture of Crumly, 1982 and 1994 [in part]) is a small opening that pierces the vomer along the midline just posterior to the foramen praepalatium (Bramble, 1971). The presence of a vomerine foramen was noted in *agassizii* and *berlandieri* by Bramble (1971), and was used by Gaffney and Meylan (1988) to unite various species currently placed in *Gopherus* as a clade. Its irregular presence in *elegans*, *elongata*, *chilensis*, and *radiata* was reported by Crumly (1982). Specimens in our sample enable us to confirm its presence in *agassizii*, *berlandieri*, and *chilensis*.

Polarity: The vomerine foramen occurs in only a few 'testudinids' and it is absent in all outgroups. Its presence is considered derived for Testudinoidea.

(20) *Development of the foramen praepalatium as a canal (canalis praepalatium) that is concealed by a bony secondary palate in ventral view*; 0 = absent, Fig. 39; 1 = present, Fig. 40 (modified from Hirayama, 1985, 24).

In most testudinoids, the foramen praepalatium is a small opening that connects the nasal cavity with the roof of the oral cavity (Fig. 39). However, in a number of taxa with extensively developed secondary palates, the anterior nasal artery passes through an elongated canal that is concealed in ventral view by the bony secondary palate (e.g., *baska*, *tentoria*, *petersi*; Fig. 40). We refer to this structure as the canalis praepalatium. Our scorings are fully consistent with those of Hirayama (1985).

Polarity: The foramen praepalatium is absent in *spinifera* (Gaffney, 1979) and *caretta* (Nick, 1912), and is developed as a true foramen that is exposed in ventral view in *odoratus*, *serpentina*, and *Mongolemys*. The development of a canalis praepalatium is considered the derived condition within Testudinoidea.

(21) *Contact between pterygoid and basioccipital*; 0 = present, Fig. 41; 1 = absent, Fig. 42 (modified from Gaffney and Meylan, 1988, F1.1, F10.3, H18.3; Crumly, 1994; Shaffer et al., 1997, 103).

Two of the most often-cited characters that purportedly help to distinguish the 'Emydidae' from the 'Bataguridae' are the batagurine process and the contact between the pterygoid and the basioccipital (McDowell, 1964). Both traits are commonly combined as one character (e.g., Gaffney and Meylan, 1988) and even seem to have been confused with one another (e.g., Mlynarski, 1976; Shaffer et al., 1997). The batagurine process is a poorly-defined feature that, in McDowell's original usage (1964) appears to consist of a lateral process of the basioccipital that floors the recessus scalae tympani. Many testudinoid species (including non-'batagurines') have a laterally-projecting process of the basioccipital; it may or may not floor the recessus scalae tympani, but it is often obscured from view in articulated specimens. When disarticulated material is examined, a broader distribution of this feature (assuming it is interpreted as we have done above) across testudinoids is revealed.

Within Testudinoidea, the pterygoid commonly sends a process posteriorly and contacts the basioccipital just lateral to the basisphenoid. This character appears to be absent in most 'emydids,' but is present in *terrapin* and those species that are currently attributed to *Graptomys* (Gaffney and Meylan, 1988). We noticed a strong ontogenetic component to this character within 'emydids.' The pterygoid is commonly rather short during younger ontogenetic stages, but finally reaches the basioccipital in later stages. For instance, among our specimens of *terrapin*, *orbicularis*, and *texana*, the pterygoid does not contact the basioccipital in younger individuals, but a clear contact is present in adults. We score such species as polymorphic, but note that ontogenetically influenced polymorphisms are not well explored in turtles.

Among 'batagurids,' we noted a similar pattern. Contrary to general belief we were not able to observe a contact between the pterygoid and the basioccipital in all taxa traditionally classified in this group (e.g., *trijuga*, *pulcherrima*, *sinensis*). As with the 'emydids,' there seems to be an ontogenetic effect in which younger specimens tend not to have a contact. Where recognized, we scored these species as polymorphic.

We found much conflicting data regarding the distribution of this character among tortoises (Crumly, 1982, 1985, 1994; Gaffney and Meylan, 1988). Among the specimens we examined, we note the complete absence of a contact only in *graeca*; polymorphisms were observed in *polyphemus* and *horsfieldi*. Again, an ontogenetic component is apparent.

Polarity: A contact between the pterygoid and

basioccipital is present in all outgroups. Its absence is considered to be derived.

(22) *Contact of the pterygoid with the articular facet of the quadrate*; 0 = absent, Fig. 43; 1 = present, Fig. 44 (Hirayama, 1985, 38).

According to the data matrix published by Hirayama (1985) he only observed this contact in *reevesii*, however, in his tree (fig. 2) the contact is mapped as an autapomorphy of *subtrijuga*. We confirm the presence of a contact between the posterior process of the pterygoid and the articular surface of the quadrate in *subtrijuga*. It is the only taxon we examined that displays the derived condition.

Polarity: A contact between the pterygoid and the articular surface of the quadrate is absent in all outgroups and the vast majority of the ingroup. We consider its presence to be derived.

(23) *Closure and depth of the incisura columella auris*; 0 = absent, incisura is open, Fig. 44; 1 = present, incisura closed, Fig. 45 (Crumly, 1985; Gaffney and Meylan, 1988, H1.3).

The incisura columella auris is a notch that is formed by the quadrate and that holds the stapes and eustachian tube (Gaffney, 1972). In a number of turtles, the incisura closes to fully surround the stapedial shaft (Gaffney and Meylan, 1988). Within testudinoids, the incisura evidently is closed in most tortoises (Crumly, 1985). We are able to confirm the presence of such a closed incisura in all 'testudinids' we examined with the exception of one specimen of *kleinmanni* (CAS 228431), the smallest of the species now classified in *Testudo*. In a number of 'batagurids' and 'emydids' the incisura commonly is very narrow and even appears to be closed, however, a closer look under the microscope combined with a probing needle reveals that this apparent closure is produced by dry tissues that remain in this area in many articulated skulls. The only 'batagurid' for which we sometimes found a closed incisura is *N. platynota*; in that species the quadrate does not fuse together forming a solid ring behind the incisura, but this is also the case for many tortoises (e.g., some *belliana*, *emys*, some *homeana*, some *kleinmanni*). In some cases, the polymorphism we noted (e.g., in *belliana* and *homeana*) appears to be a result of ontogenetic age, with older individuals displaying a greater degree of fusion at the posterior part of the incisura.

Polarity: The polarity of this character is somewhat ambiguous, because the incisura columella auris is closed in *serpentina* and *spinifera*, but open in *caretta* and *odoratus*. We conclude that its presence is derived within testudinoids because it is absent in *Mongolemys*.

Mandible

(24) *Angular contribution to the sulcus cartilaginis Meckelii*; 0 = present, the angular contributes to the sulcus and is as long or longer than the prearticular, Fig. 47; 1 = absent, the angular is shorter than the prearticular, Fig. 48 (modified from Gaffney and Meylan, 1988, F1.4).

A broad contact of the angular with Meckel's cartilage was used by McDowell (1964) to characterize the 'Emydinae' and later used by Gaffney and Meylan (1988) as a synapomorphy to unite the same grouping. As it was originally worded, this character is difficult to observe in its literal sense for most museum specimens, because the Meckel's cartilage usually is not present in modern and fossil skeletal specimens. We suggest that the spirit of McDowell's (1964) character can be evaluated by examining the participation of the angular in the sulcus cartilaginis Meckelii. We confirm that a small to broad angular contribution is present in all 'emydids' with the exception of *rubriventris*. In most 'batagurids,' the angular is a short bone that does not participate in the sulcus and barely spans half the distance the prearticular does. However, a small but clear contribution to the sulcus is present in an eclectic group comprised of *baska*, *dentata*, *thurjii*, *punctularia*, and some *grandis*. We were not able to carefully evaluate potential polymorphisms in these taxa.

Polarity: An angular contribution to the sulcus cartilaginis Meckelii is present in all cryptodiran outgroup taxa. We consider its absence to be derived.

(25) *Contact between surangular and dentary*; 0 = simple contact, Fig. 49; 1 = strongly interdigitated suture, Fig. 50 (Crumly, 1982, 12; Crumly, 1985; Gaffney and Meylan, 1988, H6.1).

In most testudinoids, the surangular and dentary meet along the lateral side of the mandible in a simple, overlapping contact. According to Crumly (1982, 1985), this contact is stabilized through a finger-like process of the surangular that interdigitates with the dentary in all tortoises except *emys*, *impressa*, and those species he classified in *Gopherus*. We confirm the absence of this character in *agassizii*, *berlandieri*, *emys*, *impressa*, and *polyphemus*, but also did not observe it in *areolatus*.

Polarity: An interdigitated contact between the surangular and dentary is absent in all outgroups and the majority of the ingroup. We consider its presence to be derived.

(26) *Height of the processus coronoideus*; 0 = as high as dentary, Fig. 51; 1 = rising significantly above the dentary, Fig. 52 (modified from Hirayama, 1985, 45).

The coronoid of most turtles is a small bone that produces a minor knobby projection that rises only little

above the adjacent dentary, if at all. According to McDowell (1964) and Hirayama (1985) the coronoid is larger and rises moderately above the dentary in *borneensis* and *crassicollis*, and in *reevesii* and *subtrijuga* the coronoid is very large and produces a robust process that sits high above the dentary. We confirm these observations, however, we were also able to observe moderately developed coronoid processes in *kachuga* and *tentoria*. Among ‘emydids,’ we also observed moderately developed coronoids in *barbouri*, *ernsti*, *flavimaculata*, *geographica*, *gibbonsi*, *kohnii*, and *terrapin*. Unlike Hirayama (1985), we only utilize one derived character state, because it is difficult to objectively measure and discretize the relative height of the coronoid among turtles.

Polarity: The coronoids of *caretta*, *serpentina*, and *odoratus* are small and do not rise above the dentary, but the coronoid of *spinifera* is well developed and forms a moderate process. The lower jaw is not described for *Mongolemys*. We consider well-developed coronoids to be derived within testudinoids.

(27) *Foramen dentofaciale majus*; 0 = small, Fig. 53; 1 = large and situated within a large lateral fossa, Fig. 54 (Hirayama, 1985, 47).

The foramen dentofaciale majus of most testudinoids is a small opening that is situated on the lateral side of the mandible, just ventral and slightly anterior to the coronoid. The foramen dentofaciale majus is greatly enlarged in *thurjii* and *ocellata* and is situated at the anterior end of an expanded lateral fossa (Hirayama, 1985). We confirm the enlargement in those taxa, and further note its presence in *petersi*.

Polarity: The foramen dentofaciale majus is small in all outgroups and the vast majority of the ingroup. Its presence is considered to be derived.

Triturating Surfaces

(28) *Participation of palatine in the triturating surface of the upper jaw*; 0 = absent, Fig. 55; 1 = present, Figs. 56, 57 (Hirayama, 1985, 26; Gaffney and Meylan, 1988, F2.1).

In some testudinoids, the palatine has a ventrolateral maxillary process that participates in the triturating surface of the upper jaw. The degree of participation varies among taxa, and within some species. A clear and extensive participation is present in *barbouri*, *ernsti*, *geographica*, *gibbonsi*, *petersi*, *rubriventris*, *scripta*, *terrapin*, *texana*, and *versa*. It is weakly developed in *hamiltonii*, *ocellata*, *G. oculifera*, *ouachitensis*, *reevesii*, *subtrijuga*, and some individuals of *baska*.

Participation was used by Gaffney and Meylan (1988) to unite *Terrapene* spp., *blandingii*, *guttata*, *G. insculpta*, *marmorata*, *muhlenbergii*, and *orbicularis* as

a clade within the ‘Emydidae.’ In our observations, however, this participation also is absent among other ‘emydids’ such as *flavimaculata*, *kohnii*, *nigrinoda*, *picta*, and *reticularia* (we were not able to evaluate adequately the potential for polymorphism in these taxa). In addition, it appears that the absence of a palatine participation represents the plesiomorphic state for testudinoids, thus eliminating its value for diagnosing monophyletic groups.

Polarity: The palatine does not participate in the triturating surface of *spinifera*, but does so in *odoratus*, *caretta*, and *serpentina*. The palatine does not participate in the triturating surface of *Mongolemys* and only occurs in Testudinoids with highly derived secondary palates. We consequently consider the participation of the palatine in the triturating surface to be derived within testudinoids.

(29) *Participation of the vomer in the triturating surface of the upper jaw*; 0 = absent, Figs. 56, 57, 58; 1 = present, Fig. 59 (Hirayama, 1985, 25).

The triturating surface is the grinding surface of the jaw. In most turtles, it is formed on the upper jaw predominantly by the maxilla and premaxilla. However, in turtles with extensive secondary palates the vomer may also participate. In *texana*, the vomer may have a ventral projection that barely separates the maxillae in the midline, but it does not participate in the triturating surface proper because it sits in a dorsal concavity within the palate (Fig. 56). Our scorings differ from those of Hirayama (1985) for *mouhotii* (which Hirayama scored as “intermediate apomorphic” and we score as absent because it does not have a secondary palate) and *subtrijuga* (in our specimens the vomer does not descend to the palatal surface, but this species may be polymorphic). This character is polymorphic in *barbouri*.

Polarity: Because the vomer does not participate in the triturating surface of *odoratus*, *spinifera*, *caretta*, *serpentina*, and *Mongolemys*, its participation is considered to be the derived condition for Testudinoidea.

(30) *Presence and number of lingual ridges of the triturating surfaces of the upper and lower jaws*; 0 = no lingual ridges present, Fig. 60; 1 = one lingual ridge present, Figs. 61-62; 2 = two lingual ridges present (modified from Hirayama, 1985, 29, 44; Gaffney and Meylan, 1988, F7.2, F9.1)

Most turtles lack lingual ridges on their triturating surfaces (Fig. 60), but one or two such ridges are developed in a number of testudinoids (Figs. 61-62). These ridges run parallel to the labial surface of the maxilla and dentary, and typically do not meet their counterpart on the midline. They are not necessarily a continuous structure (Fig. 61), and may be divided into several com-

ponents. In some cases, an extensive ridge-like structure can create the appearance of an additional ridge at the extreme lingual margin of the maxilla bordering the internal nares; however, we consider these to be the thickened rim of the internal nares rather than an additional ridge. Among 'batagurids' and 'emydids,' one lingual ridge is present in *alabamensis*, *borneoensis*, *decorata*, *kachuga*, *P. nelsoni*, *ocellata*, *petersi*, *rubriventris*, *scripta*, *sinensis*, *tentoria*, *texana*, and *thurjii*. Two lingual ridges are developed in *baska*. We found lingual ridges in all tortoises we examined except *erosa*, *belliana*, and *homeana*.

Hirayama (1985) originally scored this character as two separate characters, one for the mandible and one for the maxilla. In our observations, the triturating surface of the lower jaw closely mimics that of the upper jaw, creating an occlusal surface that closely reproduces the function of cusps in mammalian cheek teeth. Both characters were scored in parallel in Hirayama's matrix, and we see no reason to consider them independent.

Polarity: All outgroups lack lingual ridges on the triturating surfaces. We consequently consider their presence to be derived.

(31) *Well-developed serrations on labial or lingual ridges of the triturating surfaces of the upper and lower jaws; 0 = absent, Fig. 60; 1 = present, Fig. 61 (modified from Hirayama, 1985, 21, 27, 41, 43, 46; Gaffney and Meylan, 1988, F9.2; Yasukawa et al., 2001, 11).*

Well-developed serrations on the lingual and labial ridges of the upper and lower jaws are developed in several 'batagurids' and 'emydids'. A number of tortoises and other 'batagurids' (e.g., *carbonaria*, *pardalis*, *sulcata*, *annulata*, and *areolata*) exhibit serrations on their ramphothecae, but unlike the bony, tooth-like serrations of *borneoensis*, *thurjii*, *petersi*, or *texana*, these crenulations are weakly developed, leaving very little or no trace of serrations on the underlying bone. In comparison to those taxa with well-developed serrations, it is very difficult to establish a consistent scoring system for taxa with fine crenulations, because many specimens will not exhibit any serrations, probably due to wear of the ramphothecae. Unlike Hirayama (1985) and Yasukawa et al. (2001) we scored all taxa with such weak serrations as absent.

Unfortunately, even in those taxa with well-developed serrations, the serrations are not always evenly developed on all ridges. We consequently combined all of Hirayama's (1985) characters relating to serrations into one character. Because serrations commonly occur on all available ridges, this treatment will also help to avoid unconsciously weighting the presence of serrations with up to five characters. In those taxa that have them, the ridges themselves often have very different

morphologies; this character needs to be critically reevaluated with adequate sample sizes for the relevant taxa.

Polarity: All of our outgroup taxa and the majority of the ingroup taxa lack strong serrations. We interpret their presence to be derived.

(32) *Median ridge or sulcus of the triturating surface of the upper jaw; 0 = both structures absent, Fig. 60; 1 = median ridge present, Fig. 62; 2 = median sulcus present, Fig. 63 (modified from Hirayama, 1985, 30; Crumly, 1985, 1994, 4; Gaffney and Meylan, 1988, H3.1).*

In a number of testudinoid turtles with partially developed secondary palates and lingual ridges, additional structures are formed along the midline of the upper jaw that typically correspond to reciprocal structures of the lower jaw. The upper jaw of *petersi* is characterized by a narrow sulcus (Fig. 63) and the mandible exhibits a low median ridge. On the other hand, in *baska*, *borneoensis*, *thurjii*, *kachuga*, *agassizii*, *berlandieri*, and *polyphemus*, a ridge runs along the midline (Fig. 62), which typically corresponds to a sulcus in the lower jaw. An incipient ridge also was reported in *emys* (Crumly, 1994), but we were not able to confirm this on the specimen available to us.

Polarity: A median ridge is absent in all outgroups and the vast majority of the ingroup. Its presence is considered to be derived.

(33) *Posterior extension of the lower triturating surface behind the symphysis of the dentary; 0 = absent, Fig. 64; 1 = present, Fig. 65 (Hirayama, 1985, 42; Gaffney and Meylan, 1988, G5.2).*

In several 'batagurids,' the triturating surface of the dentary forms a shelf along the midline that extends so far posteriorly that the symphysis cannot be seen when the mandible is observed in dorsal view (McDowell, 1964). Our scorings fully agree with those of Hirayama (1985) for the 'Bataguridae,' but we disagree with Gaffney and Meylan (1988) who asserted that this character also occurs in some 'Emydidae.' Admittedly, several species currently placed in the genera *Graptemys*, *Pseudemys*, and *Trachemys* have greatly expanded triturating surfaces of the dentary, but in all of the specimens available to us, the symphysis is always visible in dorsal view.

Polarity: An extended triturating surface of the dentary does not occur in any outgroup taxon. We consider its presence to be derived.

Carapace

(34) *Carapace strongly tricarinate in adult; 0 = absent, Figs. 66, 67; 1 = present, Fig. 68 (modified from*

Hirayama, 1985, F; McCord et al., 1995, 10; Yasukawa et al., 2001, 24).

Three distinct carapacial ridges are present in the adults of *reevesii*, *hamiltonii*, *spengleri*, *subtrijuga*, *trijuga*, and *mouhotii*. We cannot replicate Hirayama's (1985) placement of this character as an autapomorphy in *hamiltonii*. In our observations, the carinae in *hamiltonii* are not better developed than in some other taxa. In fact, they are more weakly developed than those in *mouhotii* (Fig. 68). Because keels are present in the young and subadults of such taxa as *crassicolis* (Fig. 67), *mutica*, and *sinensis*, but disappear with age, and because we were not able to observe the juveniles of most species, we restricted this character to those species that exhibit well-developed tricarinae as adults. Three keels were reported to be present in the adults of *dentata* (McCord et al., 1995), but we cannot confirm this (tricarinae are not present on our younger specimens).

Polarity: Tricarinae are absent in our outgroup species (*caretta*, *odoratus*, *serpentina*, *spinifera*, *gibba*, *siebenrocki*, *subglobosa*, and *subrufa*), but do appear occasionally in some of their close relatives, such as *scorpioides*, *temminckii*, and *fimbriatus*. We consider the presence of tricarinae to be derived within Testudinoidea.

(35) Significant serration of the posterior peripherals; 0 = absent, Fig. 66; 1 = present, Fig. 68 (modified from Hirayama, 1985, D; McCord et al., 1995, 11; Yasukawa et al., 2001, 23).

We generally agree with previous observations reported for this character (Hirayama, 1985). However, because the carapace rim is at least slightly serrated in almost all turtles, we rephrase the character definition to include only significantly serrated posterior peripherals as found, for example, in *crassicolis*, *dentata*, *grandis*, *mouhotii*, *N. platynota*, and *spengleri*. Among the 'emydids' and 'testudinids,' the peripherals of *barbouri*, *erosa*, *flavimaculata*, *geographica*, *homeana*, *kohnii*, *nigrinoda*, *oculifer*, *G. oculifera*, *pseudogeographica*, and *versa* also are serrated. It is important to note that our scores are based on the peripheral bones; the amount of carapacial serration greatly depends on the presence or absence of the marginal scutes in the specimens used, because the scutes greatly accentuate the amount of serration, if present. We find no conflict with the codings of McCord et al. (1995) and Yasukawa et al. (2001).

Polarity: Serrated posterior peripherals are present in *caretta*, but absent in *odoratus*, *serpentina*, and most pleurodires. However, due to ingroup commonality and its absence in taxa placed within "Lindholmemydidae" we conclude that its presence is derived.

(36) Carapace of adult tectiform in cross-section with a strong posterior projection on the third vertebral scute; 0 = absent, Fig. 69; 1 = present, Fig. 70 (Hirayama, 1985, N).

According to Hirayama (1985), this character only occurs in *tecta* and *tentoria*. For our sample, we were able to confirm its presence in *tecta* and *tentoria* and also observed it in *barbouri* (*barbouri* and other species now classified in *Graptemys* may be sexually dimorphic for this character). The descriptive term 'tectiform' is somewhat problematic, because any turtle shell can be considered 'roofed' (Fig. 69). We regard a carapace as tectiform if its sides are more-or-less flat and meet along the midline at a rather sharp angle (Fig. 70). Many testudinoids, and notably those 'emydids' currently classified within *Graptemys*, have a somewhat tectiform carapace as juveniles, but that morphology typically is lost in the adults.

Polarity: Because all outgroups and the majority of the ingroup do not have a tectiform carapace, we consider its presence to be derived.

(37) Shape and orientation of the second neural; 0 = second neural hexagonal, short sides positioned anteriorly, Fig. 71; 1 = second neural hexagonal, short sides positioned posteriorly, Fig. 72; 2 = second neural octagonal, Fig. 73 (modified from Hirayama, 1985, G; Yasukawa et al., 2001, 25).

(38) Shape and orientation of the third neural; 0 = third neural hexagonal, short sides positioned anteriorly, Fig. 71; 1 = third neural hexagonal, short sides positioned posteriorly, Fig. 72; 2 = third neural square, Fig. 74; 3 = third neural octagonal, Fig. 75 (modified from Hirayama, 1985, G; Yasukawa et al., 2001, 25).

Originally, Hirayama (1985) only discussed the orientation of the neurals in general, which is fully sufficient for his 'batagurid' ingroup, because almost all individuals exhibit his two suggested character states. However, in most tortoises the second and/or third neurals are not hexagonal, but rather are square or octagonal, making it impossible to assign them to one of Hirayama's (1985) character states. We consequently split Hirayama's original character into two characters, restricted their application to the second and third neural, and added additional character states.

Our observations generally agree with those of Hirayama (1985) and Yasukawa et al. (2001) for 'batagurids,' with the exception of *annandalei* in which we found the short side of the second and third neurals to be positioned anteriorly, and not posteriorly as was indicated by Hirayama (1985).

Polarity: The short side of the second and third neural bones faces posteriorly in *odoratus* and *spinifera* but

anteriorly in *caretta*. The shape of the second and third neurals is extremely variable in *serpentina*. However, in *Lindholmemyx* and *Mongolemyx* the short side of the second and third neurals is positioned anteriorly. We consider that condition to be primitive for Testudinoidea.

(39) *Medial contact of the seventh and/or eighth costal bones; 0 = absent, Fig. 76; 1 = present, Fig. 77 (Hirayama, 1985, V; Yasukawa et al., 2001, 26).*

In some testudinoid turtles, the posterior costal bones meet along the midline due to the reduction of the posterior neural elements. The original character definition provided by Hirayama (1985) and Yasukawa et al. (2001) was worded to indicate a contact between the seventh and eighth costal bones among some 'batagurids.' We are unable to reproduce their results if the character definition is taken literally. For example, in all our specimens of *amboinensis* and *galbinifrons*, the eighth costals meet on the midline, but the seventh costals do not. However, if the character definition is modified to include any contact of the seventh or eighth costals, our results are concordant with those of Hirayama (1985) and Yasukawa et al. (2001). In addition to the Asian box turtles, we report a medial contact of the posterior costals in *baska*, *carolina*, *coahuila*, *T. nelsoni*, *T. ornata* and *rubida*.

Polarity: A medial contact of the seventh and/or eighth costals is absent in *serpentina*, but present in *spinifera*, *caretta*, many kinosternids, and many pleurodires. Although a composite reconstruction of a putative "lindholmemydid" from the Early Cretaceous of Japan was illustrated with the seventh costals in contact at the midline (Hirayama et al., 2000, fig. 11), such a contact is absent in other specimens of *Lindholmemyx* and *Mongolemyx*. Its presence within testudinoids is predominantly in the highly derived box turtles, and we conclude that its presence is derived for Testudinoidea.

(40) *Cervical scute; 0 = present, Fig. 78; 1 = absent, Fig. 79 (modified from Crumly, 1985, 1994, 34; Gaffney and Meylan, 1988, H5.2, H10.1; Shaffer et al., 1997, 41).*

The presence and shape of the cervical scute is used commonly to determine phylogenetic relationships within tortoises. According to Crumly (1985) the cervical scute is very narrow or absent in all tortoises except *agassizii*, *berlandieri*, *emys*, *flavomarginatus*, *impressa*, and *polyphemus*. We generally agree with these observations, but when this character is applied to all testudinoids intraspecific variation is so great that the character becomes essentially useless. We consequently limit our scoring to the mere presence or absence of the cervical scute. We confirm the observations of Gaffney and

Meylan (1988) that this scute is absent in *carbonaria*, *chilensis*, *elegans*, *nigra*, *pardalis*, and *sulcata* and additionally code *homeana* and *erosa* as polymorphic.

Polarity: The cervical scute is present in all cryptodiran outgroups that have scutes on their carapace. We consider its absence to be derived.

(41) *Number of vertebral scutes; 0 = five, Fig. 80; 1 = six or more, Fig. 81 (Hirayama, 1985, P).*

We confirm Hirayama's (1985) observation that there are at least six vertebral scutes in *N. platynota*. Additional scutes occasionally occur in other species, but are best considered abnormalities; they typically lack the symmetrical associations with adjacent pleural scutes seen in *N. platynota*.

Polarity: All testudinoids, except for *N. platynota*, have five vertebral scutes. We consider the presence of six scutes to be derived.

(42) *Position of the anterior sulcus of the fourth vertebral scute; 0 = sulcus lies on the fifth neural, Fig. 82; 1 = sulcus lies on fourth neural, or on the suture between the fourth and fifth neural, Fig. 83; 2 = sulcus lies on the sixth neural, or on the suture between the fifth and sixth neural, Fig. 84 (modified from Hirayama, 1985, L+M).*

(43) *Position of the posterior sulcus of the fourth vertebral scute; 0 = sulcus lies on the eighth neural, or on the homologue of the eighth neural, if the seventh is reduced (e.g., in most tortoises), Fig. 85; 1 = sulcus lies on the seventh neural, or on the suture between the seventh and eighth neural, Fig. 86; 2 = eighth neural absent, sulcus overlies costals that meet at the midline, Fig. 87 (modified from Hirayama, 1985, L+M).*

The size of the fourth vertebral scute was addressed with two characters by Hirayama (1985) but the total range of morphological variability in testudinoids is not encompassed by his character definitions. In most testudinoids, the fourth vertebral scute covers the posterior half of the fifth neural bone, the sixth and seventh neurals, and the anterior half of the eighth neural. A number of variations are known, and simply counting the number of neural bones covered by this scute results in problems by creating a false perception of homology. For instance, a fourth scute that partially overlies the fourth and seventh neurals and fully covers the fifth and sixth, can strictly be said also to cover four neurals, but the elements involved are only partially homologous with the common condition. We attempt to resolve these issues by establishing two new characters that preserve what we think was Hirayama's (1985) original intent, but that permit a more accurate representation of the association between the fourth vertebral scute and the underlying neural bones.

Some problems that are associated with scoring this character include the prevalence of scute abnormalities among testudinoids (e.g., Coker, 1905, 1910; Newman, 1906; Zangerl and Johnson, 1957). Specimens exhibiting such abnormalities were scored as unknown. The notable exception to this is *N. platynota*, in which a sixth, or even a seventh, vertebral scute is always present.

Polarity: Determining the polarity through outgroup relationship is somewhat difficult, because almost every outgroup exhibits a different condition, especially for the posterior sulcus. Based on ingroup commonality, and the presence of our zero state in both *Lindholmemyx* and *Mongolemyx*, we consider the sulci of the fourth vertebral scute to be primitively situated on the fifth and eighth neural bones.

(44) *Posterior margin of first vertebral scute significantly narrower than its anterior margin; 0 = absent, Fig. 88; 1 = present, Fig. 89 (modified from Hirayama, 1985, C).*

When originally proposed, this character was applied to a posterior constriction of all vertebral scutes (Hirayama, 1985). If strictly applied, this character is absent in all taxa, because the fifth vertebral scute never is constricted along its posterior edge relative to the anterior edge. If each scute is viewed by itself, it becomes apparent that especially the fourth vertebral scute tends to be narrowed posteriorly, as can be observed in all species now classified in the genera *Graptemyx*, *Heosemyx*, *Trachemyx*, and *Testudo* among others. According to Hirayama (1985), posterior narrowing is limited to *crassicolis* and *borneensis* and unites them as a synapomorphy. We were able to replicate this distribution only if the character definition was restricted to the first vertebral scute, in which the posterior margin is significantly narrower than its anterior margin in those two species only. In making this change, however, this character becomes at least partly redundant with characters 45 and 47.

Polarity: Outgroup analysis reveals that posterior narrowing of the first vertebral scute is present only in *odoratus*; it is absent in *Lindholmemyx* and *Mongolemyx*. We regard the presence of a posterior narrowing of the first vertebral scute to be derived.

(45) *Anterior half of the first vertebral scute much narrower than posterior half, especially in adults; 0 = absent, Fig. 90; 1 = present, Fig. 91 (modified from Hirayama, 1985, R).*

We confirm the clear presence of an anteriorly narrowed first vertebral scute in *dentata* and *spinosa* as reported by Hirayama (1985), and note that *grandis* is polymorphic. Because the anterior sulcus of the first ver-

tebral scute commonly is restricted to the nuchal bone in several other taxa, but the scute shows no anterior narrowing, we limit the original character definition to the shape of the first vertebral scute only. This peculiar morphology seems to be the result of growth that is limited to the anterior edge and the posterior half of the lateral edge of the first vertebral scute. As a consequence, this character is not apparent in juveniles, but becomes increasingly accentuated in adults.

Polarity: Anterior narrowing of the first vertebral scute is absent in all outgroups and within the large majority of the ingroup. We consider its presence to be derived.

(46) *Significant contact of the tenth marginal scute with the fifth vertebral scute; 0 = absent, Fig. 92; 1 = present, Fig. 93 (modified from Hirayama, 1985, K).*

Contact of the tenth marginal scute with the fifth vertebral scute was reported previously only in *baska*, *smithii*, *tecta*, and *tentoria* (Hirayama, 1985). We are able to confirm the presence of a very well developed contact in all but *smithii* (not seen), and we add *spinosa* to the list of species in which this contact may occur (it is polymorphic for *spinosa*; contact is present in CAS 228368, but absent in the smaller CAS 228459, so ontogenetic differences may explain the polymorphism). We also note slight contacts in some specimens of other species (e.g., *agassizii*, *borneensis*, *carbonaria*, *homeana*, *orbicularis*, *pardalis*, and *polyphemus*), but by rewording Hirayama's (1985) original character to include only significant contact, we are able to retain what we believe was his original intent.

Polarity: Due to the absence of contact in all outgroups in which it is applicable and the predominance within the ingroup, we consider its presence to be derived.

(47) *Contact of the second marginal scute with the first vertebral scute; 0 = absent, Fig. 94; 1 = present, Fig. 95 (Hirayama, 1985, O; see also Tinkle, 1962, table 1, 'Seam A').*

According to Hirayama (1985), the first vertebral scute usually (>90%) contacts the second marginal scute in *japonica*, *leprosa*, and *caspica*. He also noted that the scutes are sometimes in contact in *N. platynota* and *bealei*. For our sample, we are able to confirm this contact as a polymorphism for *bealei*, *caspica*, *japonica*, and *leprosa*, but the contact is clearly absent in all our specimens of *N. platynota*. We also note that these scutes are sometimes in contact in *picta*, *amboinensis*, *orbicularis*, and *terrapin*. Together with all of the above, these taxa were scored as polymorphic. The only taxa to exhibit a consistently well-developed contact are *reticularia* and *blandingii*.

Polarity: A clear contact between the second marginal scute and the first vertebral scute does not exist in *caretta* or *serpentina*, but both morphologies occur in kinosternids and pleurodires. The scutes are not in contact in *Lindholmemyd* and *Gravemyd*, but they are in contact in *Mongolemys*. The polarity for this character is ambiguous.

(48) *Contact of the sixth marginal scute with the third pleural scute; 0 = absent, Fig. 96; 1 = present, Fig. 97 (modified from Hirayama, 1985, B; see also Tinkle, 1962, table 3, 'Seam C').*

The contact between the sixth marginal and third pleural scutes is easily enough rendered as a simple 'presence or absence' character, but this hides the range of possible morphological variation. The degree of contact can range from extensive to a condition where the two scutes just barely contact at their corners. Several taxa exhibit a condition where these scutes either barely touch or do not touch one another at their corners, but whenever several specimens were available to us, they typically turned out to be polymorphic. For this reason Gaffney and Meylan (1988) called this character 'dubious.' We scored such borderline cases as polymorphic, even if not enough specimens were available to corroborate this.

We confirm Hirayama's (1985) observations regarding the absence of a contact between these scutes in *baska*, *ocellata*, *tecta*, *tentoria*, and *thurjii*, and we add *petersi* and *spinosa* to that list. Taxa that we score as polymorphic include *annandalei*, *borneensis*, *borneensis*, *caspica*, *crassicolis*, *grandis*, *hamiltonii*, *japonica*, *punctularia*, *reevesii*, *sinensis*, *subtrijuga*, and *trijuga*. Whereas all 'emydids' lack a contact, tortoises exhibit both character states.

The presence of a contact between the sixth marginal scute and the third pleural scute was considered by Hirayama (1985) to unite crown group 'batagurids' and 'testudinids' as a synapomorphy. Given the patchy distribution of this character, and widespread polymorphism, it seems to be of little use.

Polarity: A contact between the sixth marginal scute and the third pleural scute is absent in most outgroups. The exception is *caretta*; this is not surprising because *caretta* has five instead of four pleural scutes. We consider the presence of a contact to be derived.

(49) *Twelfth marginal scute; 0 = two present, their common sulcus only partially subdivides the pygal bone, Fig. 98; 1 = two present, but their common sulcus fully subdivides the pygal bone, Fig. 98; 2 = both twelfth marginal scutes fused along the midline, Fig. 99 (modified from Mlynarski, 1976; Crumly, 1985, 1994, 35; Gaffney and Meylan, 1988, H2.1).*

According to McDowell (1964, p. 240 and table 1 number 4) members of the 'Emydinae' can be distinguished from the 'Batagurinae' based on an incomplete subdivision of the pygal bone by the median sulcus of the posterior-most marginals. We found exceptions with *picta*, *N. platynota*, *pulcherrima*, *reevesii*, *reticularia*, and *spengleri*, which do not always clearly exhibit the pattern that would be predicted by McDowell's (1964) statement, but we note that the expression of this character will depend significantly on the shape of the pygal bone. In all tortoises except *emys* and *impressa*, the twelfth marginal scutes are fused to form a single supra-caudal scute that covers the posterior part of the carapace (Crumly, 1985). For this condition, we created a third character state.

Polarity: The twelfth marginal scutes are fully separated in all outgroups that have them, and their common sulcus fully subdivides the pygal bone. The pygal bone in "lindholmemydids" is polymorphic, with the 0 state found in *Lindholmemyd* and *Mongolemys*, and the 1 state in *Gravemyd*. Either state 0 or state 1 is primitive for Testudinoidea; the midline fusion of the twelfth marginals is a derived feature for 'Testudinidae'.

Bridge

(50) *Sutured contact between plastron and carapace; 0 = present, plastron and carapace are tightly connected by an osseous bridge, Fig. 100; 1 = absent, plastron is attached to carapace by connective tissue, Fig. 101 (modified from Hirayama, 1985, Q; Shaffer et al., 1997, 58; Yasukawa et al. 2001, 21a).*

(51) *Presence and development of anterior buttresses; 0 = anterior buttresses absent, Fig. 102; 1 = anterior buttresses present but small, and not in contact with the first costal bones, Fig. 103; 2 = anterior buttresses long and thin and just barely in contact with the costal bones, if at all, Fig. 104; 3 = anterior buttresses well developed and in clear contact with the first costal bones, Fig. 105; 4 = anterior buttresses very large and in direct contact with the first dorsal rib, Fig. 106 (modified from Hirayama, 1985, Q; Gaffney and Meylan, 1988, A14.2; Yasukawa et al., 2001, 28).*

(52) *Presence and development of posterior buttresses; 0 = posterior buttresses absent, Fig. 107; 1 = posterior buttresses present but small, and not in contact with the costal bones, Fig. 108; 2 = posterior buttresses long and thin and just barely in contact with the costal bones, if at all, Fig. 109; 3 = posterior buttresses well developed and in clear contact with costal bones V and VI, Fig. 110; 4 = posterior buttresses well developed but only in clear contact with costal bone V, Fig. 111 (modified from Hirayama, 1985, Q; Gaffney and Meylan, 1988, A14.2, Shaffer et al., 1997, 55; Yasukawa et al., 2001, 29).*

(53) *Medially-directed pivoting process for plastral hinge developed on fifth peripheral bone*; 0 = absent, Fig. 112; 1 = present, Fig. 113.

(54) *Complete or almost complete overlap of hyoplastron/hypoplastron suture by the pectoral/abdominal sulcus*; 0 = absent, Fig. 114; 1 = present, Fig. 115 (modified Gaffney and Meylan, 1988, F3.2; Burke et al., 1996, 16; McCord et al., 1995, 13; Yasukawa et al., 2001, 21b).

In most testudinoid turtles, the plastron is attached to the carapace via a fully ossified bridge and variably developed plastral buttresses. In species with a kinetic plastron, the bridge is typically absent and the plastron is attached to the carapace via connective tissues (e.g., *amboinensis*, *blandingii*, *carolina*, *dentata*, *galbinifrons*, *mouhotii*, *orbicularis*, *T. ornata*). The original configuration of this character tied the presence of plastral kinesis to the reduction of the buttresses (Hirayama, 1985). However, within testudinoid turtles the morphology of the buttresses varies significantly and independently from plastral kinesis. We consequently split this character into three discrete characters concerned with the morphology of the bridge and the buttresses.

We also developed two new characters that pertain to the morphology of the bridge region: the presence of medially-directed processes on the fifth peripherals that act as pivots for the plastral bones during shell closure (Bramble, 1974) and a revised plastral kinesis character (Gaffney and Meylan, 1988; McCord et al., 1995) that considers plastral-kinesis to be well developed only in those taxa in which the pectoral/abdominal sulcus fully overlaps the hyoplastron/hypoplastron suture, allowing optimal movement between the two plastral lobes. Most taxa with plastral kinesis also have well-developed pivoting processes on the fifth peripherals, but notable exceptions are *orbicularis* and *N. platynota*. In *blandingii*, the process is modified into an anteroposteriorly-elongated, flattened process that extends along most or all of the length of the fifth peripheral (Fig. 113). In some specimens of *blandingii*, a similar structure is developed on the sixth peripheral as well.

Polarity: Reconstructing the basal condition for these characters within testudinoids is difficult, because all living cryptodiran outgroups do not have plastral buttresses and commonly lack osseous bridges. However, the bridge of *Gravemys*, *Mongolemys*, and *Lindholmemyx* is osseous, shows no signs of kinesis, and (at least in *Lindholmemyx*) the anterior and posterior buttresses are well developed and touch the costal bones. We consider that morphology to be primitive for Testudinoids.

(55) *Contact between inguinal and femoral scutes*; 0 = absent, Fig. 116; 1 = present, Fig. 117 (Crumly, 1985, 1994, 42; Gaffney and Meylan, 1988, H3.3, H15.2).

Within tortoises the complete or frequent absence of a contact between the inguinal scute and the femoral scute was used previously to hypothesize the monophyly of several smaller clades, for example {*graeca* + *hermanni* + *horsfieldi* + *kleinmanni* + *marginata* + *tornieri*} (Crumly, 1985) and {*agassizii* + *berlandieri* + *flavomarginatus* + *polyphemus*} (Gaffney and Meylan 1988). We confirm the absence of a contact in representatives of the first group, but not in the second. Among the second group (traditionally classified together in *Gopherus*) the contact is strongly reduced, but still is present. Among 'batagurids' and 'emydids,' a contact is absent in all taxa with the noteworthy exception of *hamiltonii*.

Polarity: Determining the polarity for this character is somewhat difficult because all living outgroups have an arrangement of plastral scutes that is rather different from testudinoids. However, based on ingroup commonality and the absence of a contact in the "Lindholmemydidae," we conclude that the presence of a contact between the inguinal and femoral scutes should be considered derived for Testudinoidea.

(56) *Presence of musk glands*; 0 = inguinal and axillary gland present; 1 = axillary gland present only; 2 = musk glands absent (modified from Crumly, 1985).

(57) *Presence of anterior musk duct foramina*; 0 = musk glands and their foramina present, Fig. 118; 1 = musk glands present, but foramina not developed; 2 = musk glands and foramina absent (modified from Hirayama, 1985, A; Gaffney and Meylan, 1988, F1.2, F5.3; Burke et al., 1996, 20).

(58) *Presence of posterior musk duct foramina*; 0 = musk glands and their foramina present, Fig. 119; 1 = musk glands present, but foramina not developed; 2 = musk glands and foramina absent (modified from Hirayama, 1985, A; Gaffney and Meylan, 1988, F1.2, F5.3; Burke et al., 1996, 20).

According to Hirayama (1985), the presence of musk duct foramina characterizes the paraphyletic assemblage 'Batagurinae' (sensu Hirayama, 1985, not Gaffney and Meylan, 1988). We believe the difference of opinion between Hirayama (1985) and Gaffney and Meylan (1988) regarding this character is based on failure to make clear the distinction between the presence of musk glands and the presence of musk duct foramina. Musk glands are developed in almost all extant turtles (Waagen, 1972), and we consequently agree with Gaffney and Meylan (1988) that their presence should be considered primitive for all cryptodiran turtles.

However, even though most turtles have musk glands, true musk duct *foramina* are developed only in some pleurodires (e.g., *Chelodina*, *Emydura*), some ‘emydids,’ and all ‘batagurids,’ making a monophyletic Testudinoidea (sensu Hirayama, 1985) possible. Distinct musk duct grooves are present on the anterior peripherals of Kinosternidae, and tiny *foramina* are sometimes associated with these (Hutchison, 1991).

Because the presence of musk glands does not necessarily result in the development of musk duct *foramina*, we decided to score these two characters separately. We relied on an unpublished thesis on the musk glands of turtles (Waagen, 1972) to determine the presence of musk glands for most taxa. In scoring taxa not investigated by Waagen (1972) we only recorded presence of musk glands if musk duct *foramina* provided positive evidence for their presence (e.g., *baska*, *bealei*, *borneensis*, *galbinifrons*, *kachuga*, *mouhotii*, *petersi*, *pulcherriima*, *spengleri*, and *tentoria*). Many tortoises, consequently, had to be scored as unknown, because they were not analyzed by Waagen (1972) and do not exhibit musk duct *foramina* (e.g., *elongata*, *homeana*, *horsfieldi*, and *pardalis*).

Our scoring of the musk duct *foramina* is derived from a combination of osteological observation and data provided by Waagen (1972). Taxa not reported to possess musk glands (Waagen, 1972) were checked for musk duct *foramina*, but none were found. For those species that Waagen reported as having musk glands, we sought musk duct *foramina* on osteological specimens. Several taxa with musk glands, but only lightly ossified bridges, do not exhibit musk duct *foramina* (e.g., *blandingii*, *dentata*, *flavomarginata*, *orbicularis*, and *pulcherriima*) or show an asymmetry with *foramina* only visible anteriorly (e.g., *N. platynota*). In taxa that possess them, the musk duct *foramina* are sometimes contained entirely within the peripherals (e.g., *N. platynota*), and sometimes between the peripheral and the plastral buttress (e.g., *reevesii*).

Polarity: Given the presence of musk glands in all extant outgroups (Waagen, 1972), their absence should be considered derived. Musk duct *foramina* are not described for “lindholmemydids” but J. H. Hutchison specifically searched for them in *Mongolemys* specimens housed at IVPP and found no trace of them. Because musk duct *foramina* are developed in the vast majority of the ingroup, we consider their absence to be derived for testudinoids.

Plastron

(59) *Extensive overhanging lip of the epiplastra*; 0 = absent, Fig. 120; 1 = present, Fig. 121 (Gaffney and Meylan 1988, H5.1, 9.2).

In most testudinoid turtles, the epiplastra are rather

flat with a slight increase in thickness along the anterior margin. In contrast, many tortoises have strongly thickened epiplastral margins that sometimes form an overhanging lip along the interior rim of the plastron. According to Gaffney and Meylan (1988) the presence of such an overhang of the epiplastral unites all tortoises except those classified in the genera *Manouria* (Fig. 120) and *Gopherus*, with a reversal occurring in giant insular forms. We confirm this general pattern, but we note the absence of an overhang in *tornieri*. A interior overhang is absent also in all extant ‘emydids’ and ‘batagurids,’ but a small overhang is present in extinct *Ptychogaster* and *Echmatemys* (Mlynarski, 1976, figs. 78, 81), taxa generally considered to belong to either the ‘Emydidae’ or ‘Batagurinae.’

Polarity: An overhanging lip on the epiplastra is absent in all outgroups and the majority of the ingroup. We consider its presence to be derived.

(60) *Intersection of the entoplastron by the humeropectoral sulcus*; 0 = absent, Fig. 122; 1 = present, Fig. 123 (Hirayama, 1985, X; Crumly, 1985; Gaffney and Meylan, 1988, F5.1; McCord et al., 1995, 15).

This character was used to help resolve relationships within ‘batagurids’ by Hirayama (1985) but we were unable to replicate his results in our analysis. We agree with Crumly (1985) that the sulcus crosses the entoplastron in at least one species classified in the genus *Indotestudo* (i.e., *elongata*), but the sulcus is at the entoplastron/hyoplastron suture in our specimen of *forsteni*. The condition in species now commonly classified in *Testudo* varies widely (e.g., the suture crosses the entoplastron in *graeca* and *horsfieldi*, but does not in *hermanni* or *kleinmanni*). We also agree with Gaffney and Meylan (1988) on their distribution of this character among the ‘Emydidae,’ however, our scoring for *picta*, *orbicularis*, and *blandingii* is polymorphic, because the sulcus generally runs along the suture between the entoplastron and the hypoplastra, but may barely fall on either side.

Polarity: The polarity is ambiguous if only extant taxa are considered. The plastron of most outgroups is too different from that of testudinoids to be of any use for polarizing this character. For instance, the plastron of *spinifera* lacks scutes, and that of *serpentina*, *odoratus*, and *caretta* is too heavily modified to enable a meaningful comparison. Both character states are commonly found in ‘batagurids,’ ‘emydids,’ and testudinids, making an ingroup analysis futile. The humeropectoral sulcus is distinctly posterior to the epiplastron in *Gravemys* and *Mongolemys*, so we consider an intersection of this suture with the entoplastron to be derived.

(61) *Anal notch of the plastron*; 0 = present, Fig. 124; 1 = greatly reduced, Fig. 125; 2 = absent, Fig. 126 (modified from Hirayama, 1985, W; Yasukawa et al., 2001, 22).

The plastron of most testudinoid turtles has a significant anal notch. The absence of such an anal notch for *amboinensis*, *galbinifrons*, and *flavomarginata* was reported by Hirayama (1985) and we confirm those observations. An anal notch also is absent in *belliana*, *carolina*, *coahuila*, *erosa*, *homeana*, *T. nelsoni*, and *T. ornata*. To accommodate the presence of a reduced anal notch we modify Hirayama's (1985) character by creating a third character state. A reduced anal notch is found in *blandingii*, *orbicularis*, *N. platynota*, and *reticularia*. In at least one species (*mouhotii*), a distinct anal notch is present in larger individuals, but small specimens have a reduced notch (scored as polymorphic in our matrix); this suggests that development of an anal notch may be subject to ontogenetic variation in at least some testudinoids.

Polarity: In *caretta* and *serpentina* an anal notch is not present, however, their plastra are narrow and tapered posteriorly. The fleshy plastron of *spinifera* is smooth along its posterior margin, but this cannot be observed in osteological preparations. A notch is weakly developed in at least some *Lindholmemyx*, but is absent in *Mongolemyx*. A notch is present in kinosternids, pleurodires, most of the ingroup, and in *Gravemys*. We conclude that its absence should be considered derived for our ingroup.

(62) *Anal scutes fused*; 0 = absent, Fig. 127; 1 = present, Fig. 127 (Hirayama, 1985, Z).

The anal scutes of adult *galbinifrons*, and *flavomarginata* are at least slightly fused, especially along their posterior medial border. We fully agree with Hirayama's (1985) treatment for this character. Anal scute fusion can be identified easily in macerated specimens (Fig. 127), because the anal scutes will not separate from one another, as will all other scutes.

Polarity: Anal scute fusion is absent in the vast majority of turtles, and is considered to be the primitive condition.

(63) *Plastral scutes with vibrant, radiating color pattern*; 0 = absent, Fig. 128; 1 = present, Fig. 129 (Hirayama, 1985, S; McCord et al., 1995, 16 Yasukawa et al., 2001, 32).

Vibrant, radiating color patterns of the plastral scutes of *dentata*, *grandis*, and *spinosa* were noted by Hirayama (1985) and McCord et al. (1995). We add *tcheponensis* to this list, as well as the 'testudinids' *geometricus* and *P. oculifera*. In our specimens, the pattern of *dentata* and *tcheponensis* is not as vibrant as in *gran-*

dis and *spinosa*.

Polarity: Vibrant, radiated color patterns are missing in all outgroups and the majority of the ingroup. Their presence is derived.

Postcranium and Soft Tissue

(64) *Development of a suprascapula*; 0 = absent; 1 = present, Fig. 130 (Gaffney and Meylan, 1988, F3.1; Burke et al., 1996, 11).

(65) *Development of an episcapula*; 0 = absent; 1 = present, Fig. 130 (Gaffney and Meylan, 1988, F4.1; Burke et al., 1996, 11).

The presence of both a suprascapula and an episcapula apparently is limited to *blandingii* and the species currently classified in *Terrapene*. A suprascapula is also present in *orbicularis*. Both structures are involved in the locking mechanism of the anterior plastral lobe during shell closure (Bramble, 1974). These structures are difficult to verify in most osteological preparations, because they may dissociate from the scapula and be difficult to recognize, and because they may ossify only in older individuals. The specimen we dissected to illustrate these features (TNHC 62532, a *T. ornata* with carapace length of 103 mm) has a completely cartilaginous episcapula, and a predominantly cartilaginous suprascapula (Fig. 130). It is therefore much easier to confirm their presence than verify their absence. We followed Bramble's (1974) account of these structures and scored our matrix accordingly, as probably did Gaffney and Meylan (1988) and Burke et al. (1996).

Polarity: Suprascapulae and episcapulae are absent in all outgroups and the majority of the ingroup. Their presence is considered to be derived.

(66) *Shape of coracoid blade*; 0 = long and narrow, Fig. 131; 1 = short and very wide, Fig. 131 (Crumly, 1985, 1994; Gaffney and Meylan, 1988, H1.7).

The coracoid blade of all 'emydids' and 'batagurids' is an elongate bone with a narrow, short shaft and a long, wedge-shaped coracoid blade that is about two times wider than the base. In tortoises, this bone is still wedge-shaped, but relatively much shorter and with a blade that is considerably wider, typically four times the width of the base (Crumly, 1985, 1994; Gaffney and Meylan, 1988). We agree with previously published observations.

Polarity: The coracoid blade of *caretta*, *serpentina*, and *odoratus* is long and narrow and that of *spinifera* is long, but not wedge-shaped. We consider a long and narrow coracoid blade to be primitive for Testudinoidea.

(67) *Number of manual claws*; 0 = five, Fig. 132; 1 = four, Fig. 133 (modified from Hirayama, 1985, J).

Most testudinoid turtles have five manual claws with the exception of *baska* and *horsfieldi*, both of which have only four. We did not verify this character independently for all species, due to an overall lack of articulated skeletons and our limited access to pickled specimens. However, because the number of claws of the forelimbs is an easily determinable, discrete number that is regularly noted and described in the literature, we scored all remaining taxa from the comprehensive information provided by Ernst and Barbour (1989).

Polarity: Five manual claws are present in *serpentina*, *odoratus*, and almost all pleurodires (excluding species currently classified in *Chelodina* and *Hydromedusa*); three are present in *spinifera*, and two in *caretta*. The condition in “lindholmemydids” is unknown. Based on ingroup commonality, we consider five claws to be primitive for the ingroup.

(68) *Number of phalanges of manus and pes; 0 = digital formula of 2-3-3-3-3 or 2-3-3-3-2, Fig. 132; 1 = digital formula with less than 2-3-3-3-2, Fig. 133 (Crumly, 1985; Gaffney and Meylan, 1988, H1.1).*

The digital formula of most testudinoid turtles is 2-3-3-3-3 or 2-3-3-3-2. Among tortoises, the manus and pes are greatly shortened and the digital formula is typically reduced to 2-2-2-2-2 or less (Auffenberg, 1974:135-136; Crumly, 1985). Due to the dissociated nature of most of the material we viewed, we were not able to verify the digital formulae of most of the turtle taxa we included. However, when articulated hands and feet were present, we never found anything to contradict the statements made above. We scored all tortoises based on information provided by Auffenberg (1974) and Crumly (1985).

Polarity: All outgroups and the majority of the ingroup do not have a reduced digital formula. We consequently consider the reduced formula to be derived.

(69) *Webbing between digits; 0 = present, well developed, Fig. 134; 1 = absent, or at least strongly reduced, Fig. 135 (Hirayama, 1985, b).*

Due to their semi-aquatic nature, most testudinoids have well-developed webbing between the digits of their hands and feet. In more terrestrial species, however, the webbing often is reduced. Unfortunately, there seems to be a gradient in the development of webbing, from extremely well developed (e.g., *baska*, *reticularia*) to moderately developed (e.g., *dentata*, *guttata*) to virtually non-existent (e.g., *spengleri*). We nevertheless were able to reproduce Hirayama's (1985) distribution for the ‘batagurids’ with the exception of *grandis* and *spinosa*, which have reduced webbing (*grandis* is the only ‘borderline’ taxon we found, but its webbing is reduced relative to those taxa we scored as having well-developed

webbing). Among ‘emydids,’ we note that the webbing is heavily reduced in *carolina*, *T. nelsoni*, and *T. ornata*. All tortoises lack webbing.

Polarity: All outgroups and the majority of ingroup taxa have webbed hands and feet. We consider the absence of webbing to be derived.

(70) *Sexual size dimorphism; 0 = absent; 1 = present, female much larger than male (Gaffney and Meylan, 1988, F5.2; Burke et al., 1996, 37).*

In almost every species of turtle, there is some expression of sexual size dimorphism (Berry and Shine, 1980; Gibbons and Lovich, 1990). The difference in size between the sexes can be expressed as a ratio and typically shows considerable variation depending on the population (Gibbons and Lovich, 1990). We initially tried to score this character with three character states, as done by Burke et al. (1996), differentiating between species with larger males, larger females, and equally sized sexes, but we abandoned that, because exact data are missing for most ‘batagurid’ taxa. We consequently only score taxa as being sexually dimorphic if females are at least 1.4 times larger than the males. Our scores are derived from Gibbons and Lovich (1990) and Ernst and Barbour (1989).

Polarity: Sexual size dimorphism is prevalent in most outgroups. In *spinifera* the female is much larger, in *odoratus* and *serpentina* the male tends to be slightly smaller, in *caretta* the sexes are of similar size. The outgroup polarity is thus ambiguous, but in the majority of the ingroup pronounced sexual dimorphism is absent.

Problematic Characters

We encountered difficulties in evaluating a number of previously used characters, and we provide some summary statements for those in this section. Most of these characters were not pursued thoroughly in our study because we were not able to understand the original descriptions, were unable to recover discrete character states, or because at an early point in our investigation of the character we detected significant variation in expression of character states within taxa. In the latter case greater sample sizes or new methodological techniques (e.g., Wiens, 1995; Smith and Gutberlet, 2001) will be required to tease out a phylogenetic signal.

(A) *Frontal contribution to the supratemporal rim (Hirayama, 1985, 4).*

The anterior extent of the upper temporal emargination is difficult to define in many taxa, and is impossible to determine in those with a fully emarginated temporal region (e.g., *T. ornata*). The result is a high degree of ambiguity and a general lack of discrete character states.

(B) *Contact between postorbital and quadrate* (Hirayama, 1985, 10).

In the vast majority of ingroup taxa, there is no contact between the postorbital and the quadrate. Such a contact was observed only in *japonica* and *punctularia* by Hirayama (1985). In specimens of *japonica* available to us, we were not able to confirm this contact. CAS 228348 is a skeleton from a diseased specimen of *punctularia*. On the right side of the skull there is a possible (but only slight) contact. It is possible that the contact is actually between the postorbital and the quadratojugal (Fig. 136). We also found a minimal contact in one specimen of *annulata*. Given these diverging observations and the minute contact that is present in our material, we regard (for now) any contact within the ingroup as an abnormality.

(C) *Absence of the "posterior process of the postorbital"* (Hirayama, 1985, 8).

We cannot determine unambiguously what Hirayama (1985) meant by this character. In our assessment of testudinoids, both a posterolateral and a postero-medial process of the postorbital can occur. In Hirayama's (1985) analysis, only *grandis* and *spinosa* lack a "posterior process of the postorbital." These species are also the only 'batagurid' taxa to fully lack a temporal arch. We suspect that this character may somehow be referring to a lack of a bony temporal arch.

(D) *Processus inferior parietalis "medially approximating each other; cranial cavity anteroventrally narrowing"* (Hirayama, 1985, 5; McCord et al., 1995, 7; Yasukawa et al., 2001, 2).

We acknowledge the validity of this character as was originally worded by McDowell (1964). However, we find it difficult to determine how strongly the constriction of the brain case must be before it can be considered present. We were unable to develop unambiguous discrete character states for this feature.

(E) *Subdivision of the foramen nervi trigemini* (Crumly, 1982; Hirayama, 1985, 6).

This character was used originally by Crumly (1982) to infer phylogenetic relationships within 'Testudinidae'. For his ingroup, Crumly (1982) observed a great amount of polymorphism, with no single species either completely lacking or always exhibiting a subdivision of the foramen. He also noted asymmetry for this character between the left and right side of some individuals. We confirm the common presence of a subdivided trigeminal foramen in representatives of 'Testudinidae,' and the occasional presence in individuals of 'Emydidae' and 'Bataguridae' (e.g., *areolata*, *dentata*, *flavimaculata*, *N. platynota*, and *rubida*). A signifi-

cant amount of variation can be observed in two specimens of *borneensis* available to us, that exhibit left/right asymmetry and the full spectrum from a fully intact (Fig. 137), to partially subdivided (Fig. 138), to fully subdivided (Fig. 139) trigeminal foramen. Given that most taxa are represented by three or fewer skulls in our study, it is apparent that we are not able to fully document the amount of variation exhibited by testudinoids.

(F) *Contact between postorbital and squamosal* (Hirayama, 1985, 9).

Gaffney et al. (1991) noted that absence of this contact is associated with the upper temporal emargination and considered it informative at the level of their analysis. Within our ingroup, all turtles have substantial upper temporal emarginations, resulting in the contact being just barely present, or just barely absent, or polymorphic (e.g., *picta*, *petersi*, *texana*, *crassicolis*). See comments above under character 9.

(G) *Median premaxillary notch* (Hirayama, 1985, 19; Yasukawa et al., 2001, 9)

(H) *Large cusps near the suture of the premaxillae and maxillae* (Hirayama, 1985, 28).

Initially, we were faced with the problem of defining these two characters independently from one another, because the presence of two tightly spaced, opposing cusp-like structures along any margin will automatically result in the development of a median notch. An additional problem relating to these characters is the question of whether these features should be observed on the ramphotheca or the maxilla.

Large, tooth-like cusps are clearly present in a number of taxa (e.g., *thurjii*) but so is the full spectrum of smaller cusps, making it impossible to clearly define discrete character states. Furthermore, if all species were evaluated for medial notches that existed even if the cusps were removed, all taxa in our sample would show a medial notch. We were unable to develop a consistent method for scoring this character for all testudinoid species.

(I) *"Antero-medial portion of the upper triturating surface formed by premaxillae and maxillae"* (Hirayama, 1985, 23; Yasukawa et al., 2001, 13).

We are neither able to replicate the full meaning of this character nor formulate truly discrete character states. A connection with the development of the secondary palate is evident, but the morphology of this region seems to be sufficiently covered by a number of other characters.

(J) *Participation of the vomer in the foramen praepalat-inum* (Crumly, 1982, 10; Hirayama, 1985, 32; Yasukawa et al., 2001, 15).

Within testudinoid turtles, the foramen praepalat-inum perforates the nasal cavity at the border between the premaxilla and the vomer. When the foramen is positioned slightly more anteriorly, it is fully surrounded by the premaxilla, when it is minutely farther posterior it is surrounded by the vomer. Considering the impact of such minute changes, it is not surprising that our scoring for this character generally seems to be in conflict with that of Hirayama (1985) and Crumly (1982). This character appears to be subject to great intraspecific variation.

(K) *Foramen palatinum posterius enclosed within the brain cavity* (Hirayama, 1985, 34).

According to Hirayama (1985), in *reevesii* (only) the foramen palatinum posterius is enclosed within the region of the brain cavity due to a flared descending process of the parietal. We cannot confirm this observation for any testudinoid turtles (including three specimens of *reevesii*).

(L) *Participating bones in the processus trochlearis oticum* (Hirayama 1985, 37; Gaffney and Meylan, 1988, Gaffney et al. 1991, 6; McCord et al., 1995, 8; Shaffer et al., 1997, 74, 258 Yasukawa et al., 2001, 18).

The relative participation of the prootic, parietal, and quadrate to the processus trochlearis oticum was used previously by a number of authors to infer phylogenetic relationships within turtles. Our observations confirm the great variety of morphologies that can be observed in this region. However, the amount of intraspecific variation is considerable and the full spectrum of possible morphologies seems to be filled, making it difficult to discern discrete character states. Future research in the area may result in more clearly defined discrete character states.

(M) *Length of the crista supraoccipitalis* (Hirayama, 1985, 40).

A long crista supraoccipitalis was observed by Hirayama (1985) for *borneensis*. The character states he used are defined by relative length of the crista supraoccipitalis to the “condylo-basal length.” Unfortunately, we could not replicate this because it is not clear exactly how the length of the crista was measured. Furthermore, a true morphological gap seems to be missing between the admittedly very long crista of *borneensis* and other ‘batagurids’ with an elongated crista. This character is problematic, because it is poorly defined and lacks discrete character states.

(N) *Bony sutures and sulci lost in old adults* (Hirayama, 1985, I).

According to Hirayama (1985), loss of sutures and sulci occurs in *baska*, *borneensis*, and *borneensis* only. We are able to confirm this, but we do not have individuals of all other species that are sufficiently old enough to positively confirm that they also do not exhibit this feature at old age. In subsequent treatments, loss of sutures and loss of sulci should be treated as separate characters.

(O) *Ossification of cornu branchiale II* (Hirayama, 1985, 48; Yasukawa et al., 2001, 20).

This character was used previously to unite tortoises with a number of ‘batagurid’ taxa (Hirayama, 1985). The hyoid apparatus of turtles is often disarticulated in skeletal preparations, making it difficult to positively confirm if an ossified cornu branchiale is present or absent. However, for those taxa for which we were able to observe the hyoid apparatus, we were not able to confirm Hirayama’s (1985) observation of a reduced cornu branchiale II in some ‘batagurids’ (e.g., *galbinifrons*, *spengleri*). Instead, these taxa exhibit a cornu branchiale II that is not significantly different from most other ‘batagurids.’

(P) *Double articulation between the fifth and sixth cervical vertebrae* (Hirayama, 1985; Gaffney and Meylan, 1988, F1.5).

Most articular surfaces of the cervical column are rather homogenous within all testudinoid turtles (Williams, 1950). A double articulation between the fifth and sixth cervical previously was considered to be a unique character that unites the ‘Emydinae’ (McDowell, 1964). This character also was used by Hirayama (1985) and with reservations by Gaffney and Meylan (1988). Our observations generally confirm the presence of a more or less clear double articulation in most ‘emydids,’ however, this feature is also present in a number of ‘batagurids’ confirming that this character is highly variable within the ingroup (Williams, 1950; Gaffney and Meylan, 1988). Unfortunately, discrete character states are lacking; we were able to observe the full morphological spectrum from a clear singular articulation to a clear double articulation.

(Q) *Scapular prong with lateral concavity* (Hirayama, 1985, E).

Hirayama (1985) reported this character as an autapomorphy for *subtrijuga* only. However, we cannot identify this morphology in any of our specimens of *subtrijuga*.

(R) *Large facet of the ilium for the testoscupularis and testoliacus* (Hirayama, 1985, T; Yasukawa et al., 2001, 34)

(S) *Extensive development of both testoscupularis and testoliacus* (Hirayama, 1985, U).

An extensive development of the testoscupularis and testoliacus muscles together with an associated large scar on the ilium was reported by Bramble (1974) for Asian and North American box turtles. Whereas we have no reason to doubt his assessment of the development of these muscles for box turtles, we were not able to score this character for most of the remaining taxa. The shape of the ilium was explored and illustrated for some 'emydids' and 'batagurids' by Yasukawa et al. (2001:122-123).

(T) *Ossification of the epipubis* (Gaffney and Meylan, 1988, F5.5).

The identification (and confirmation of presence or absence) of an ossified epipubis (Fig. 141) is somewhat difficult for most species, because it seems to ossify rather late in ontogeny, and can fall off during preparation. Our tentative observations confirm the presence of an ossified epipubis in numerous adult 'emydids' and 'batagurids,' typically terrestrial forms (e.g., *T. ornata*, *G. insculpta*, *N. platynota*, *yuwonoï*). An improved sample of adult specimens of all taxa, however, is necessary to reveal the true distribution of this character.

(U) *Diploid Number of Chromosomes* (Hirayama, 1985, Ø; Shaffer et al., 1997, 43).

The diploid number of chromosomes was used by Carr and Bickham (1986) to hypothesize a sister group relationship between the 'Emydinae' and *subtrijuga*, followed by *borneensis* and *crassicollis* and finally the rest of the 'Batagurinae.' Whereas most 'batagurids' allegedly have 52 chromosomes, *subtrijuga*, *borneensis*, *crassicollis*, and 'emydids' are supposed to have 50 chromosomes. We view these results with caution, because a brief review of the relevant literature reveals great differences in chromosomal counts for a variety of taxa. For instance, according to the work of Killebrew (1977) and Bickham (1981), *amboinensis* has 52 chromosomes, however, Gorman (1973) reported only 50. Similar conflicts can also be found for *dentata* (Bickham, 1981; DeSmet, 1978; Gorman, 1973; Stock, 1972), *subtrijuga* (Bickham, 1981; Killebrew, 1977), *trijuga* (DeSmet, 1978; Carr and Bickham, 1986), *sinensis* (Bickham, 1981; Killebrew, 1977; Stock, 1972), *crassicollis* (Killebrew, 1977; Stock, 1972; Bickham and Baker, 1976), and some of the species currently placed in *Graptemys* (Killebrew, 1977; McKown 1972), *Trachemys* (DeSmet, 1978; Killebrew, 1977; Stock,

1972) and *Mauremys* (Killebrew, 1977; Stock, 1972). This conflict in primary data is probably best understood when considering the nature of testudinoid chromosomes: whereas 14 pairs of chromosomes have a considerable size, all of the remaining ones are extremely small. Given these circumstances, it seems reasonable to hypothesize that one pair of chromosomes may be unrecognized during analysis.

(V) *Plica media spade-shaped* (Gaffney and Meylan, 1988, F7.1).

The penile soft anatomy of turtles was comprehensively reviewed by Zug (1966) and one of his characters, the shape of the plica media, was used by Gaffney and Meylan (1988) to unify species placed in *Chrysemys*, *Deirochelys*, *Trachemys*, and *Pseudemys* as a monophyletic group. In his detailed description of the plica media, Zug (1966) referred to the shape of this structure as being "spade-shaped" in those taxa, but made similar claims for other taxa too. Furthermore, based on the illustrations that were provided by Zug (1966) for other taxa, the plica media of species placed in *Graptemys*, *Malaclemys*, *Rhinoclemmys*, and *Platysternon* appear "spade-shaped" also, even though Zug (1966) did not explicitly use those descriptive words. This anatomical system should be carefully reevaluated for all testudinoids, with special attention given to definition of discrete characters.

(W) *Ossifications within the fenestra postotica*.

In some taxa, portions of the fenestra postotica are closed or obscured by ossifications (noted, but without exemplars, by Gaffney, 1972). In our largest specimen of *grandis* (CAS 228443) a short, spike-like ossified process extends posterodorsally from the dorsal edge of the quadrate process of the pterygoid, and crosses the fenestra postotica. It is situated ventral to the stapes (columella auris), medial to the incisura columella auris, and lateral to the fenestra ovalis (Fig. 141). In some specimens, the dorsal tip of a similar structure approaches or meets a posterodorsally-inclined process that extends from the dorsal surface of the pterygoid, near the suture with the prootic. In our largest specimen of *N. platynota* (CAS 228342) the two processes meet to enclose the stapelial shaft in a ring of bone situated at approximately the midpoint between the fenestra ovalis and the medial opening of the incisura columella auris. Our other, smaller, specimen of *N. platynota* shows no development of these processes. It seems likely that there is an ontogenetic component in the expression of this feature. It does not appear to have any systematic significance, but in any case it is not widespread within Testudinoidea.

Conclusions

Our observations can be used to draw some tentative conclusions regarding the current level of understanding about morphological variation within testudinoid turtles. In addition, we provide some cautionary statements about the quality of morphological data now in use for assessing systematic relationships among these turtles. It is clear from a perusal of the relevant literature, and from our data, that there is reasonably strong morphological support for a monophyletic 'Testudinidae.' Support for monophyly of 'emydines' and 'batagurines' is not as impressive. The paraphyly of 'Batagurinae' (with respect to 'Testudinidae') was explicitly proposed by Hirayama (1985) and has been generally accepted since that time, although some strides have been made towards resolving relationships among some 'batagurine' taxa. The monophyly of 'Emydinae' seems to have been implicitly assumed by many workers, but remains to be established in the context of a rigorous phylogenetic analysis of all relevant taxa. The interpretation of several morphological features shared between some 'emydines' and some 'batagurines' as either convergence or synapomorphy remains an important and interesting challenge. For example, there are intriguing morphological similarities between *subtrijuga* and some species classified in the genus *Graptemys* (e.g., contact of the jugal and descending process of the parietal; contact of the quadratojugal with the articular facet of the quadrate; contact between the quadratojugal and the maxilla; ventral process of the pterygoid approaching the articular surface of the quadrate). These similarities may be due to functional convergence as a result of a molluscivorous diet, but they raise questions about the propriety of utilizing *subtrijuga* as an outgroup for systematic studies of 'emydines' (e.g., Burke et al., 1996). Additional similarities are reported for chromosome numbers in *subtrijuga* and 'emydines' (see 'Problematic Character' U, above).

A seriously deficient understanding of morphological variation is one of the greatest inadequacies of current perspectives on morphological data in turtles generally, and testudinoids specifically. Few published studies have been conducted to evaluate the range and causes of sexual, ontogenetic, intra- and inter-population variation in morphological characters within testudinoids. Our preliminary considerations of ontogenetic variation, combined with reports of sexual variation (e.g., Berry and Shine 1980; Gibbons and Lovich, 1990; Stephens, 1998) and new studies exploring the complex interactions of morphological evolution with behavioral characteristics and environmental conditions in turtles (e.g., Lindeman, 2000; Herrel et al., 2002; Joyce and Gauthier, 2003; Claude et al., 2003) emphasize the importance of pursuing these questions further. Our decision not to

produce a phylogenetic hypothesis in this paper was based primarily on two considerations. The first is the relatively small sample size we used for many taxa in this study (although it is comparable to sample sizes from other, previously published, studies), and the fact that several taxa are not represented in our work. The second consideration is our sense that the current understanding of morphological variation in testudinoid turtles is insufficiently mature to permit reliable phylogenetic hypotheses based solely on morphological data. The most expedient way to address the need for greater documentation of variation within testudinoid species is to utilize existing museum collections to the greatest extent possible, and secondarily to develop responsible collecting programs that are designed with this need in mind.

Our results also indicate that morphological data matrices currently in the literature should not be taken at face value. We had particular difficulties replicating some of the scoring in the Hirayama (1985) matrix. That seminal analysis (completed prior to the widespread use of computer-assisted analytical methods in systematics) laid the foundation for nearly all subsequent work on 'batagurine' morphology (including our own), and its importance in shaping our current conceptualization of 'batagurine' phylogeny cannot be overstated. The work of pathfinders in all fields of inquiry is often subjected to the greatest scrutiny by the next generation of researchers. Our statements and contradictory observations in this paper in no way denigrate Hirayama's work; instead, we view our efforts as minor attempts to correct the few inconsistencies in his analysis, and to contribute our observations to the body of knowledge that he began to synthesize 20 years ago.

The accurate interpretation and understanding of the morphological descriptions of previous authors were among the great challenges we faced when we began our studies of testudinoid skeletal morphology. Much of our confusion could have been averted if adequate illustrations accompanied all published character descriptions, but such documentation often is an expensive undertaking. Our photographs of character states discussed in this paper are intended to facilitate communication among turtle enthusiasts, and to provide a baseline for future comparisons and discussions about testudinoid morphology. We hope that adequate illustration of all newly proposed characters will become standard practice among turtle systematists. It seems likely that our interpretations of characters will differ in some respects from those of our colleagues, and we anticipate that our decisions regarding 'problematic characters' (discussed above), and our choices with respect to 'lumping' or 'splitting' previously published character states, will generate much spirited discussion in the years ahead.



Figure 1. Character 1(0): CAS 228437, *texana*, anterior view.



Figure 2. Character 1(1): CAS 228404, *belliana*, anterior view.

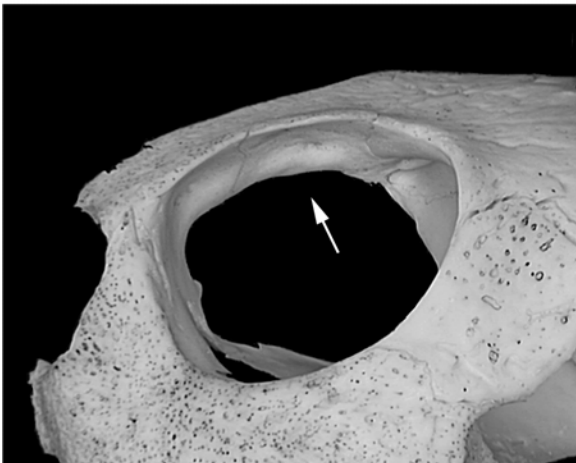


Figure 3. Character 2(0): CAS 228458, *texana*, left lateral view.

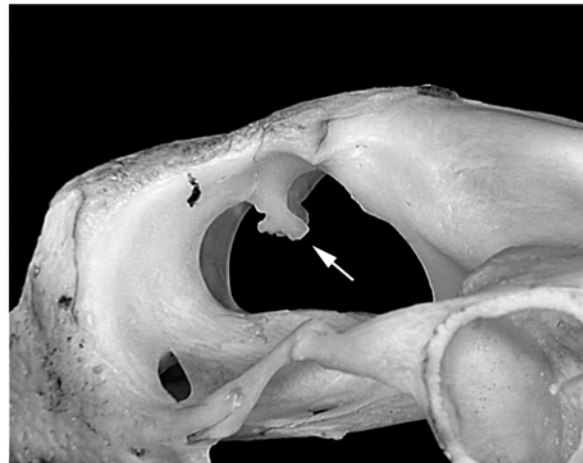


Figure 4. Character 2(1): CAS 228404, *belliana*, left lateral view.

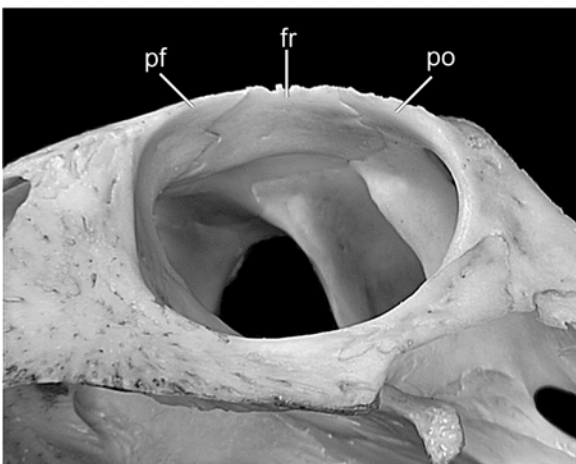


Figure 5. Character 3(0): CAS 228444, *mouhotii*, left ventrolateral view of orbit.

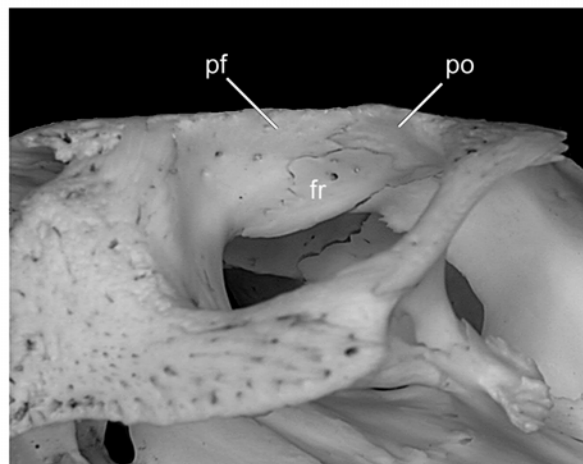


Figure 6. Character 3(1): CAS 228443, *grandis*, left ventrolateral view of orbit.

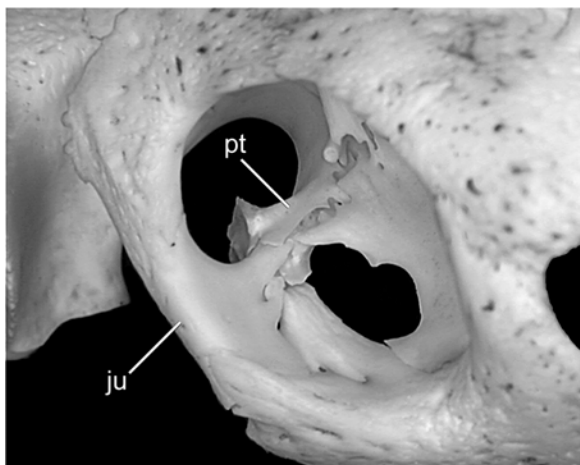


Figure 7. Character 4(0): CAS 228443, *grandis*, right anterolateral view of orbit.

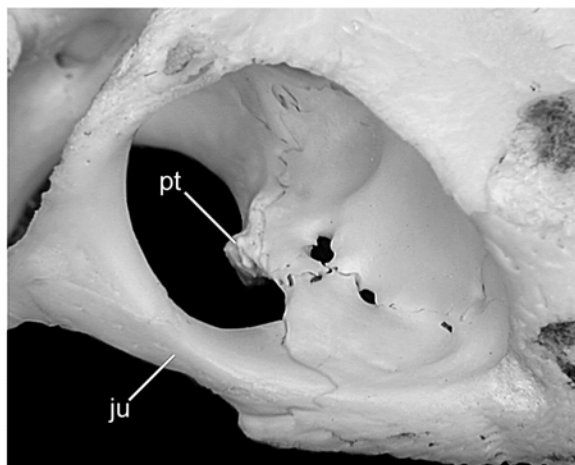


Figure 8. Character 4(1): CAS 228420, *mouhotii*, right anterolateral view of orbit.

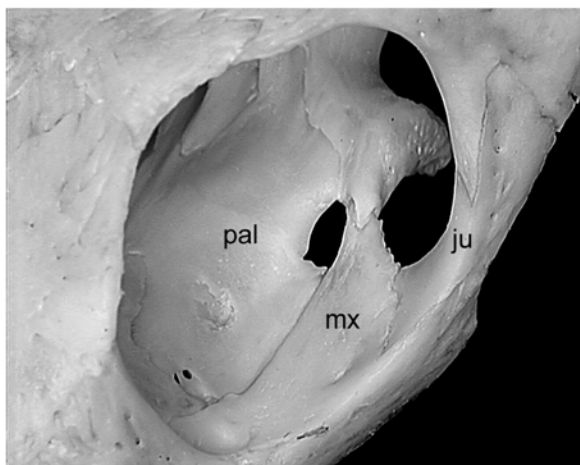


Figure 9. Character 5(0): CAS 228444, *mouhotii*, left anterolateral view of orbit.

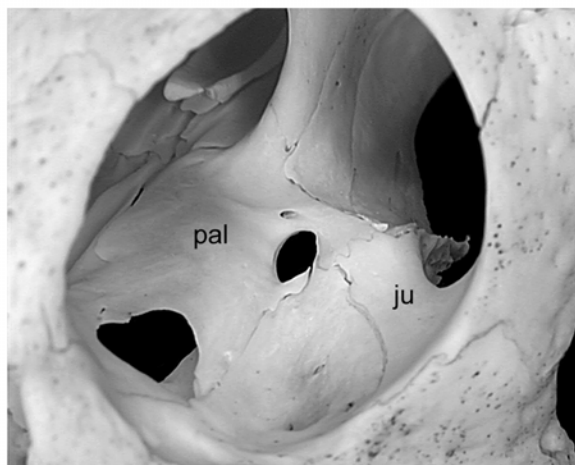


Figure 10. Character 5(1): CAS 228438, *texana*, left anterolateral view of orbit.

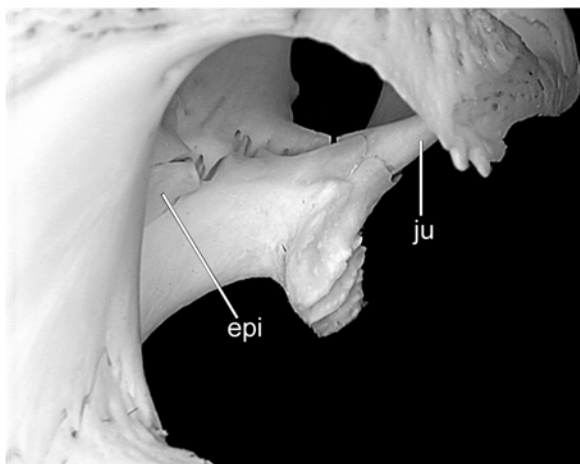


Figure 11. Character 6(0): CAS 228443, *grandis*, right posterolateral view.

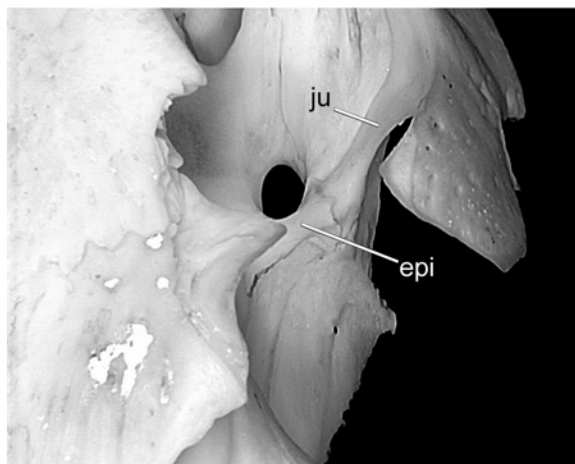


Figure 12. Character 6(1): CAS 228439, *texana*, right posterolateral view, postorbital removed.

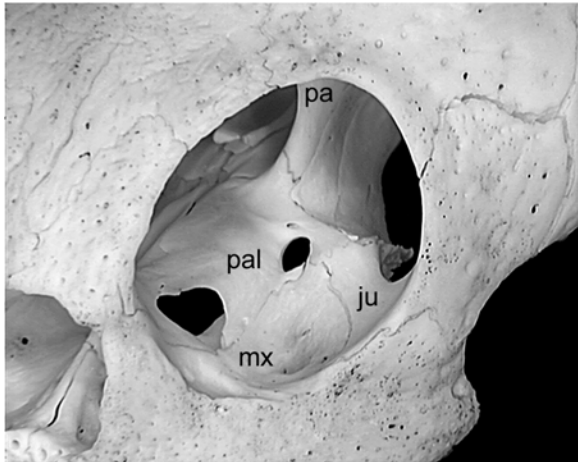


Figure 13. Character 7(0) and 8(0): CAS 228438, *texana*, left anterolateral view of orbit.

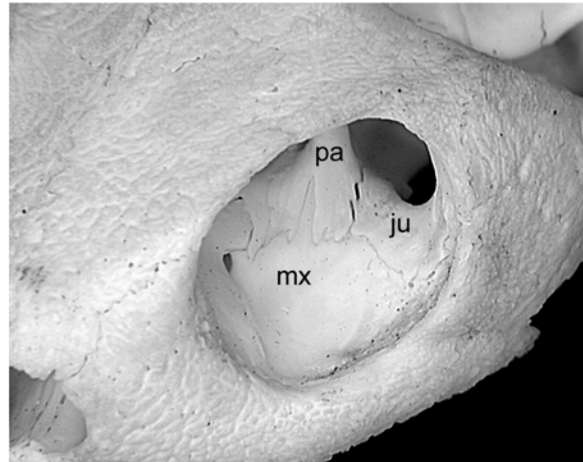


Figure 14. Character 7(1) and 8(1): CAS 228445, *subtrijuga*, left anterolateral view of orbit.

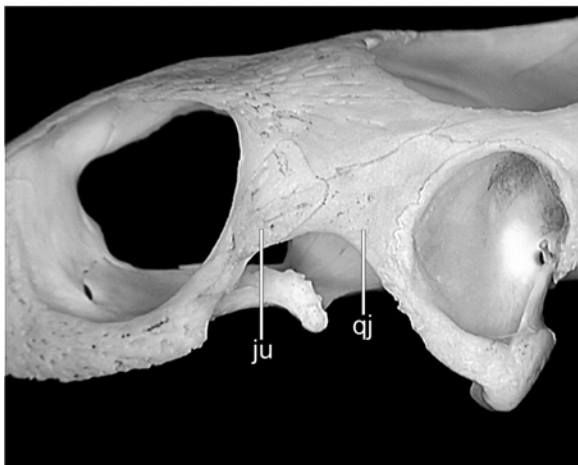


Figure 15. Character 9(0): CAS 228447, *orbicularis*, left lateral view.

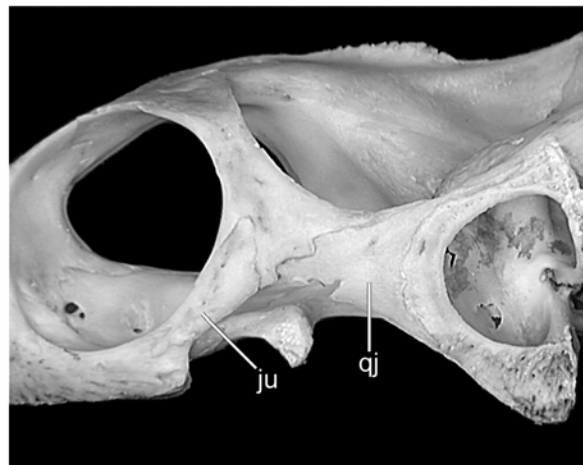


Figure 16. Character 9(1): CAS 228444, *mouhotii*, left lateral view.



Figure 17. Character 9(2): YPM 14074, *galbinifrons*, left lateral view.



Figure 18. Character 9(2): YPM 14080, *galbinifrons*, left lateral view.



Figure 19. Character 10(0): CAS 228444, *mouhotii*, left lateral view.



Figure 20. Character 10(0): CAS 228446, *subtrijuga*, left lateral view.

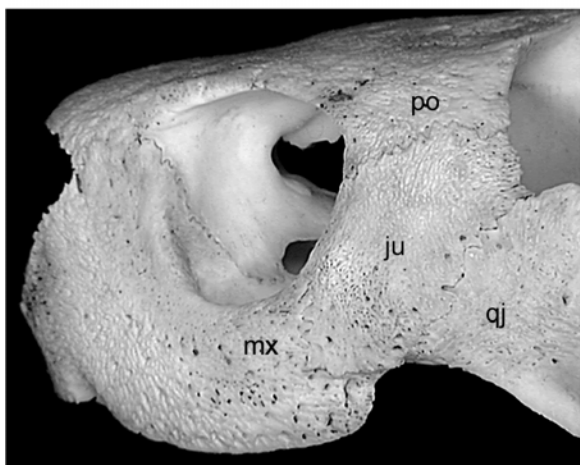


Figure 21. Character 10(1): YPM 10339, *hamiltonii*, left lateral view of orbit.

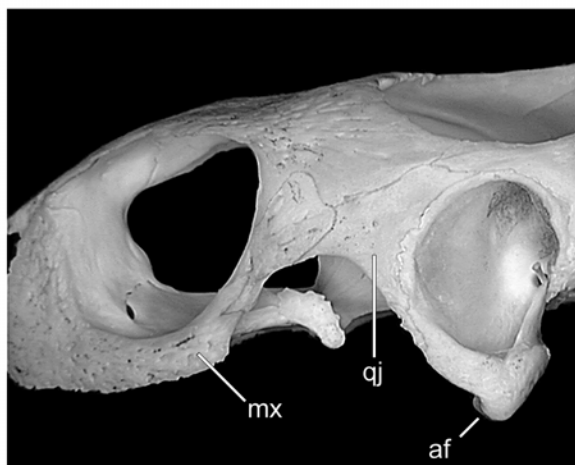


Figure 22. Character 11(0) and 12(0): CAS 228447, *orbicularis*, left lateral view.

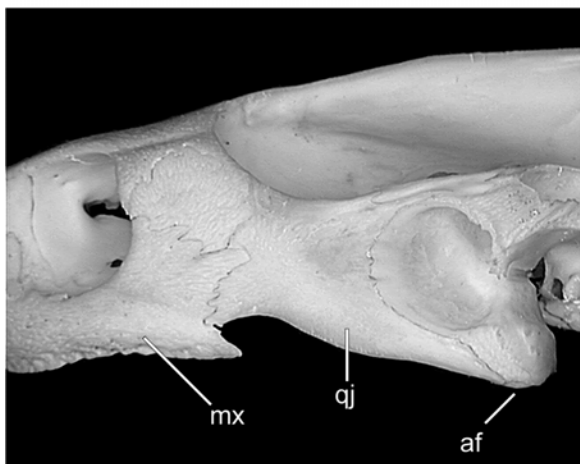


Figure 23. Character 11(1) and 12(1): CAS 228446, *subtrijuga*, left lateral view.

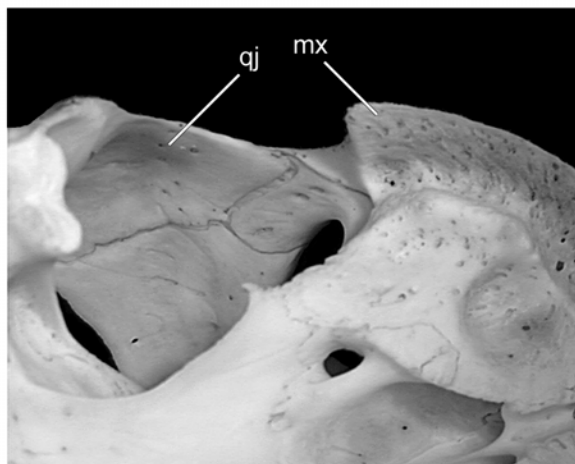


Figure 24. Character 12(1): CAS 228438, *texana*, right posteroventral view of lower temporal fossa.

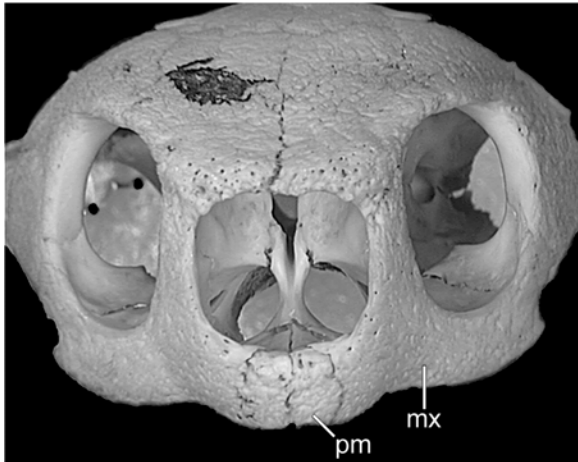


Figure 25. Character 13(0): CAS 228361, *reevesii*, anterior view.

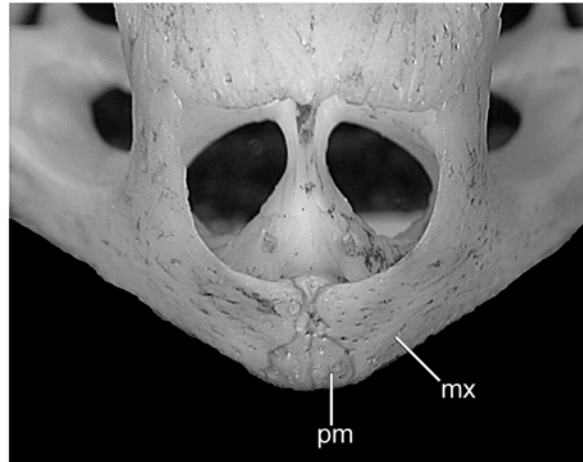


Figure 26. Character 13(0): CAS 228419, *amboinensis*, anterior view.

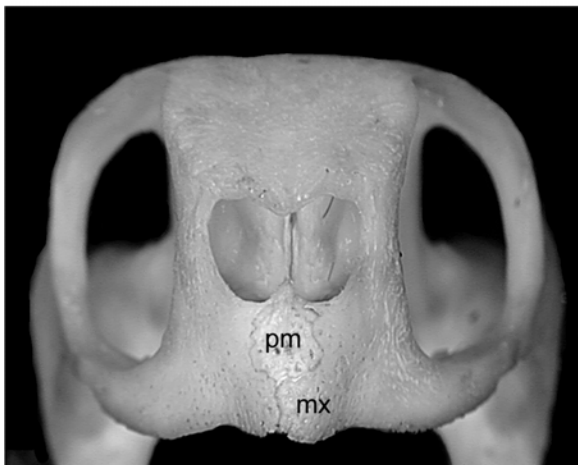


Figure 27. Character 13(1): CAS 228371, *spengleri*, anterior view.

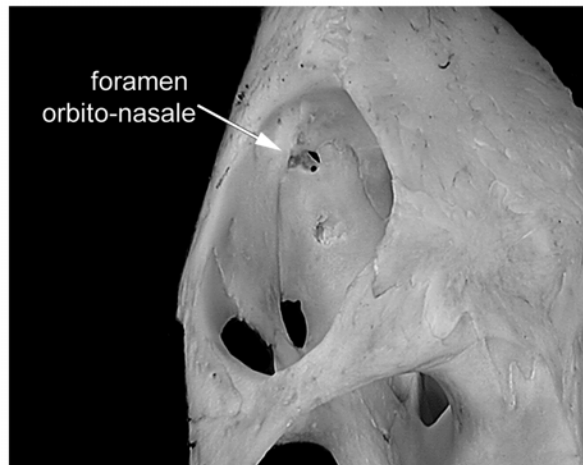


Figure 28. Character 14(0): CAS 228444, *mouhotii*, left posterolateral view of orbit.

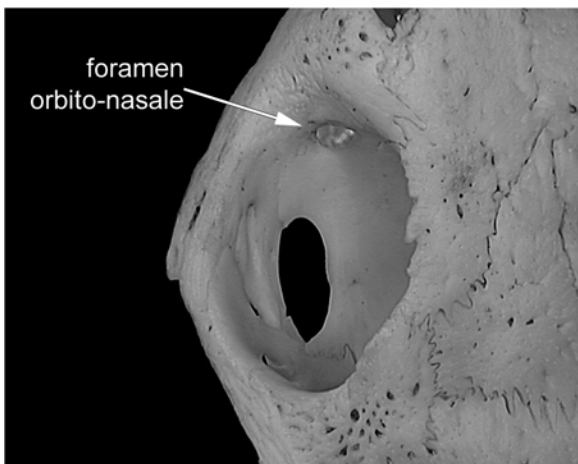


Figure 29. Character 14(0): CAS 228443, *grandis*, left posterolateral view of orbit.

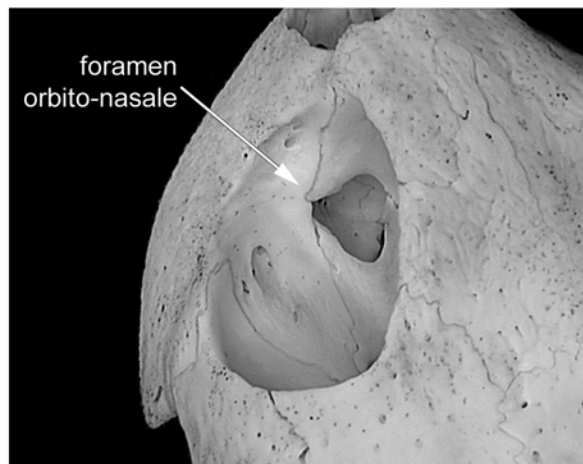


Figure 30. Character 14(1): CAS 228438, *texana*, left posterolateral view of orbit.

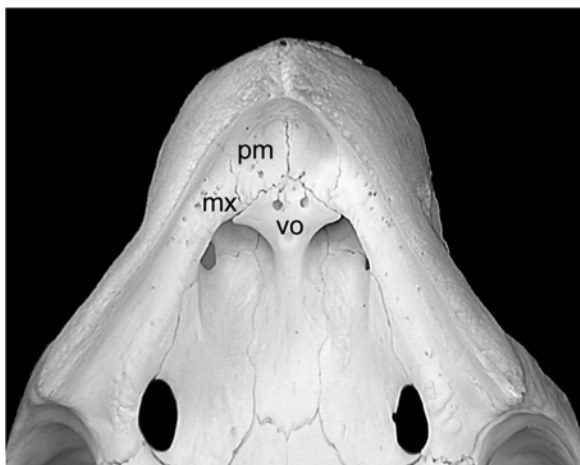


Figure 31. Character 15(0): CAS 228342, *N. platynota*, ventral view of palate.

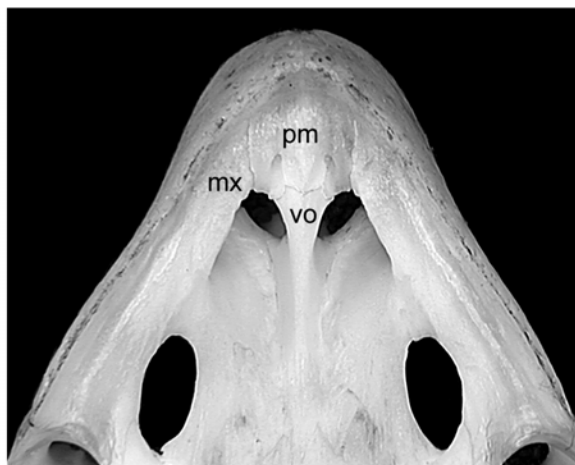


Figure 32. Character 15(1): CAS 228419, *amboinensis*, ventral view of palate.

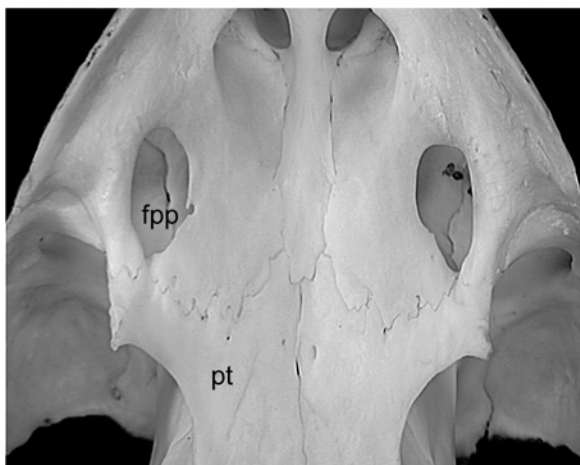


Figure 33. Character 16(0) and 17(0): CAS 228447, *orbicularis*, ventral view of palate.

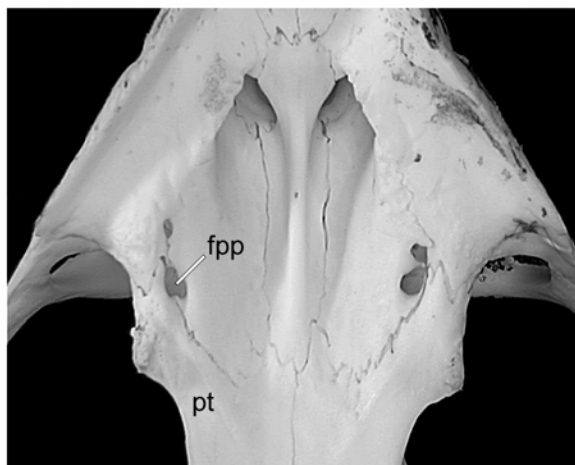


Figure 34. Character 16(1) and 17(1): CAS 228420, *mouhotii*, ventral view of palate.

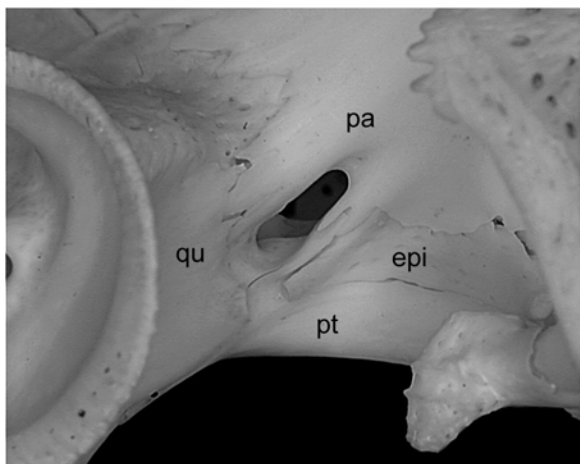


Figure 35. Character 18(0): CAS 228443, *grandis*, right lateral view of trigeminal foramen.

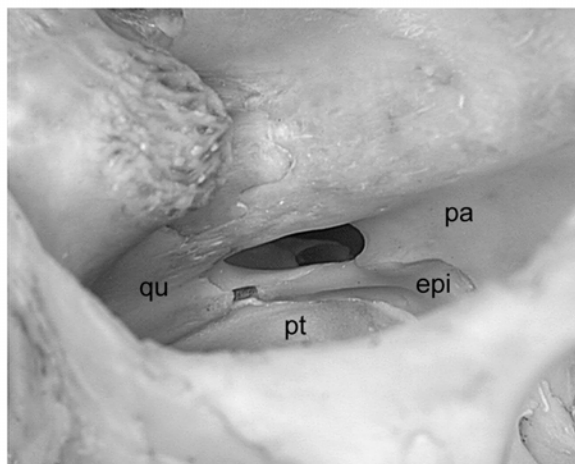


Figure 36. Character 18(1): CAS 228444, *mouhotii*, right dorsolateral view of trigeminal foramen.



Figure 37. Character 19(0): CAS 228447, *orbicularis*, ventral view of palate.



Figure 38. Character 19(1): TMM 2813, *berlandieri*, ventral view of palate.



Figure 39. Character 20(0): CAS 228335, *crassicollis*, ventral view of palate.

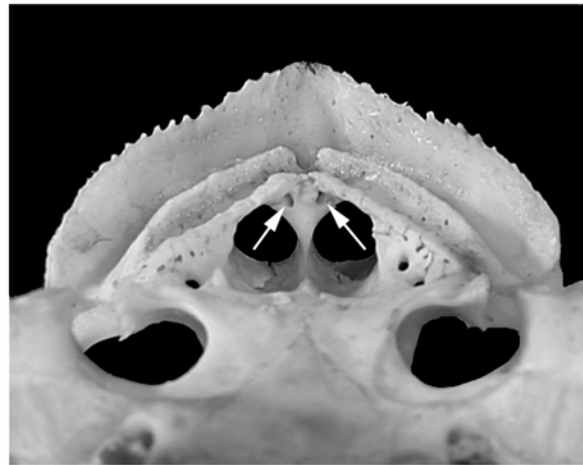


Figure 40. Character 20(1): FMNH 259430, *tentoria*, posteroventral view of palate.

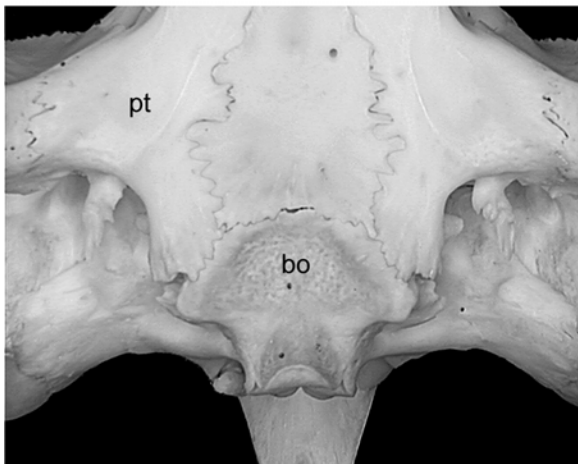


Figure 41. Character 21(0): CAS 228443, *grandis*, ventral view of brain case.

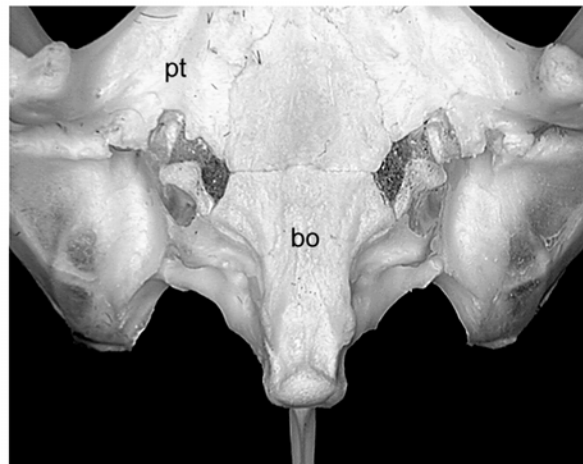


Figure 42. Character 21(1): CAS 228338, *reticularia*, ventral view of brain case.

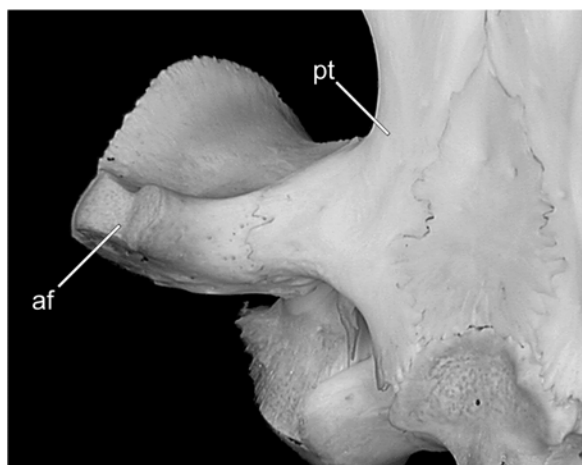


Figure 43. Character 22(0): CAS 228443, *grandis*, ventromedial view of right basicranium.

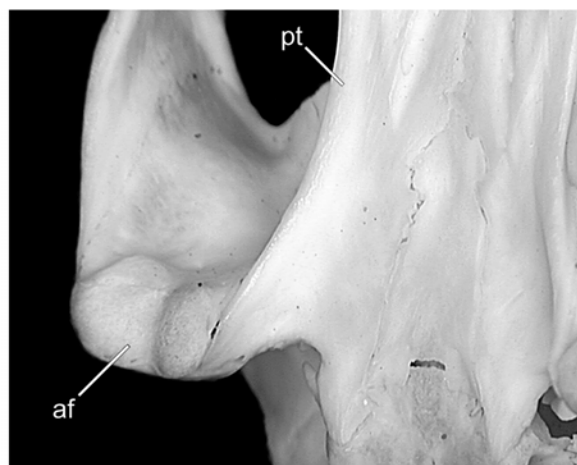


Figure 44. Character 22(1): CAS 228445, *subtrijuga*, ventromedial view of right basicranium.



Figure 45. Character 23(0): CAS 228437, *texana*, right lateral view of quadrate.



Figure 46. Character 23(1): CAS 228342, *N. platynota*, right lateral view of quadrate.

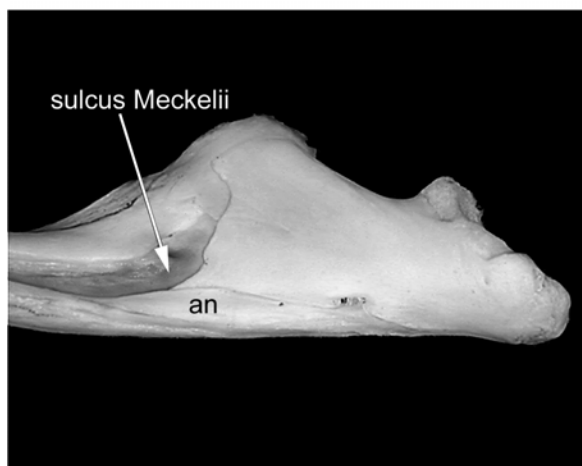


Figure 47. Character 24(0): CAS 228447, *orbicularis*, right lateral view of mandible.

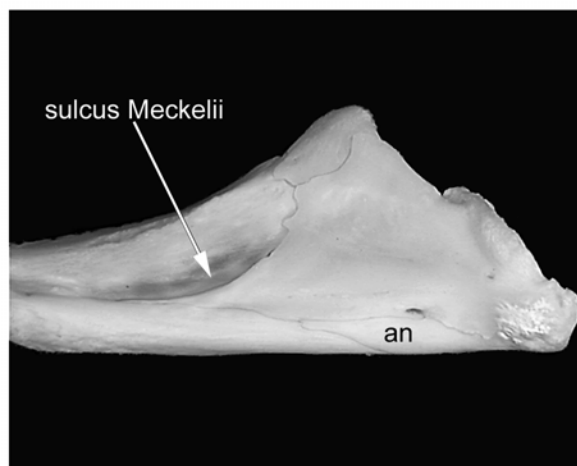


Figure 48. Character 24(1): CAS 228335, *crassicollis*, right lateral view of mandible.

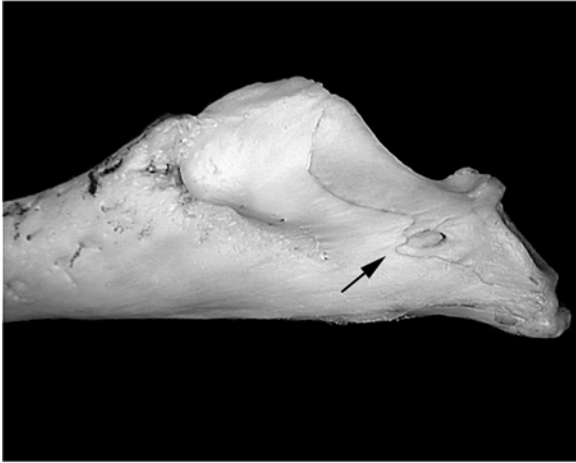


Figure 49. Character 25(0): CAS 228447, *orbicularis*, left lateral view of mandible.

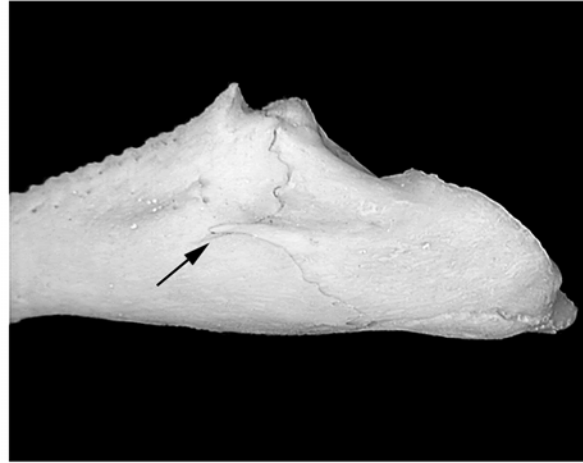


Figure 50. Character 25(1): CAS 228411, *carbonaria*, left lateral view of mandible.



Figure 51. Character 26(0): CAS 228404, *belliana*, left lateral view of mandible.

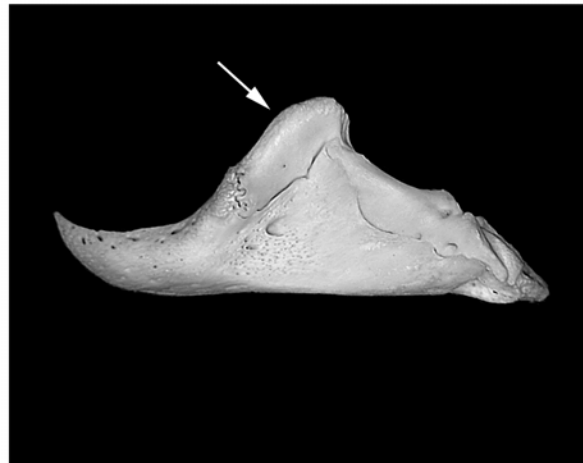


Figure 52. Character 26(1): CAS 228361, *reevesii*, left lateral view of mandible.

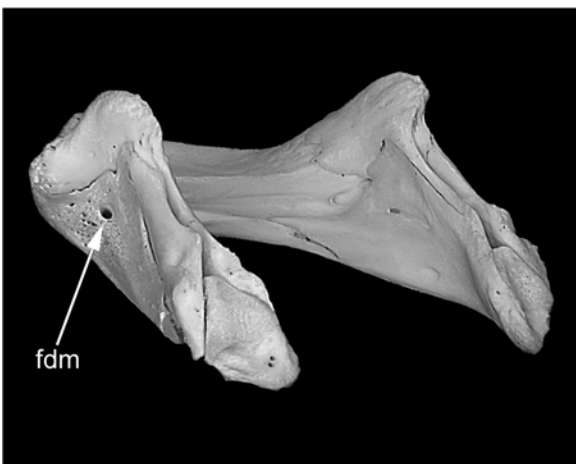


Figure 53. Character 27(0): CAS 228361, *reevesii*, left posterolateral view of mandible.

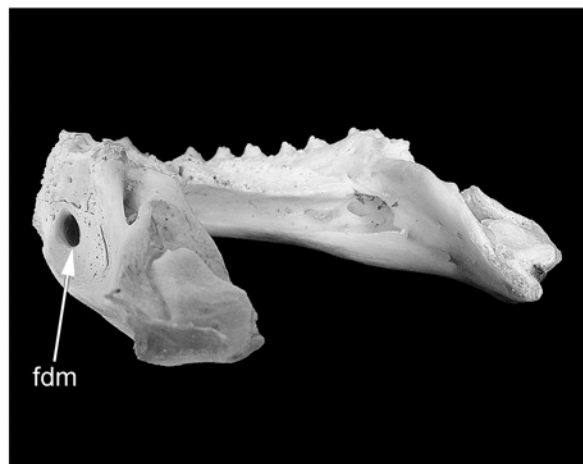


Figure 54. Character 27(1): YPM 10861, *thurjii*, left posterolateral view of mandible.



Figure 55. Character 28(0): CAS 228342, *N. platynota*, ventral view of palate.



Figure 56. Character 28(1) and 29(0): CAS 228437, *texana*, ventral view of palate.

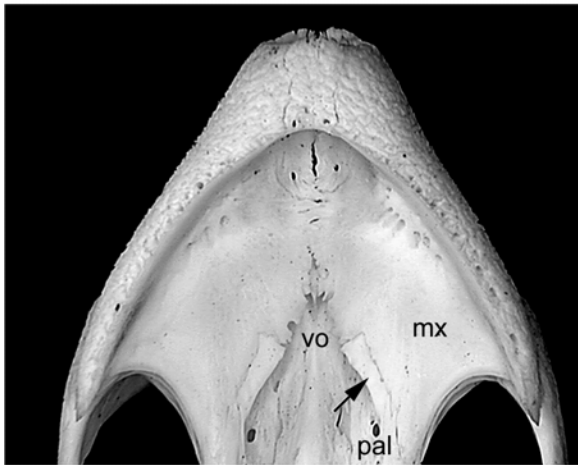


Figure 57. Character 28(1) and 29(0): CAS 228445, *subtrijuga*, ventral view of palate.

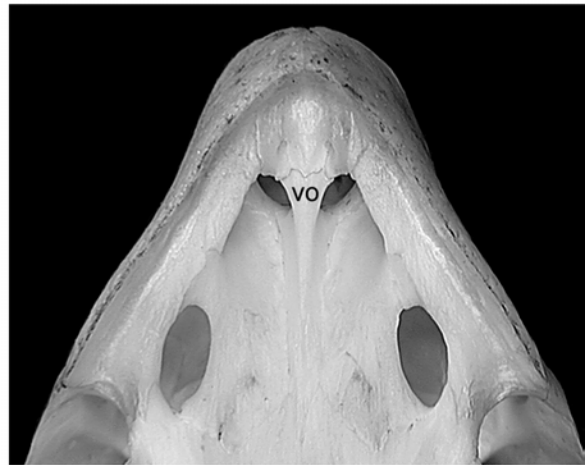


Figure 58. Character 29(0): CAS 228419, *amboinensis*, ventral view of palate.



Figure 59. Character 29(1): CAS 228361, *reevesii*, ventral view of palate.



Figure 60. Character 30(0), 31(0), and 32(0): CAS 228447, *orbicularis*, oblique ventral view of palate.



Figure 61. Character 30(1) and 31(1): CAS 228437, *texana*, oblique ventral view of palate.



Figure 62. Character 30(1) and 32(1): TMM 2813, *berlandieri*, ventral view of palate.

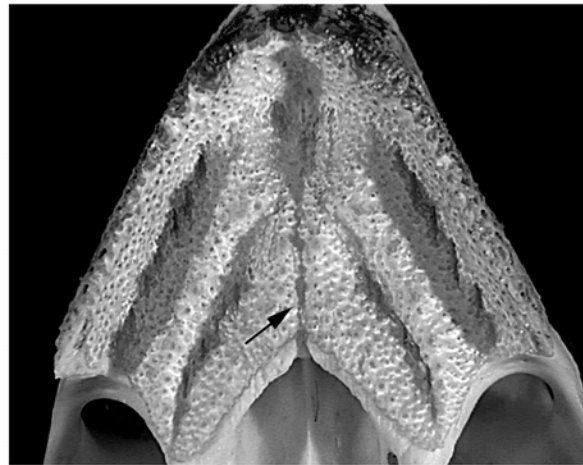


Figure 63. Character 32(2): CM 124246, *petersi*, ventral view of palate.



Figure 64. Character 33(0): CAS 228443, *grandis*, dorsal view of mandible.



Figure 65. Character 33(1): CAS 228361, *reevesii*, dorsal view of mandible.



Figure 66. Character 34(0) and 35(0): CAS 228448, *blandingii*, dorsal view of carapace.

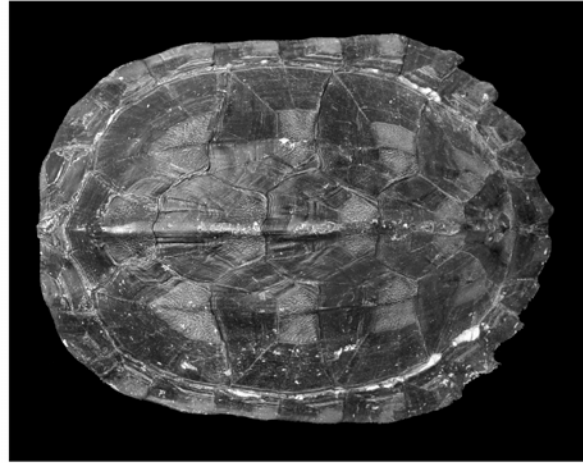


Figure 67. Character 34: CAS 228451, *crassicollis*, dorsal view of juvenile carapace showing tricarinae.



Figure 68. Character 34(1) and 35(1): CAS 228444, *mouhotii*, dorsal view of carapace.

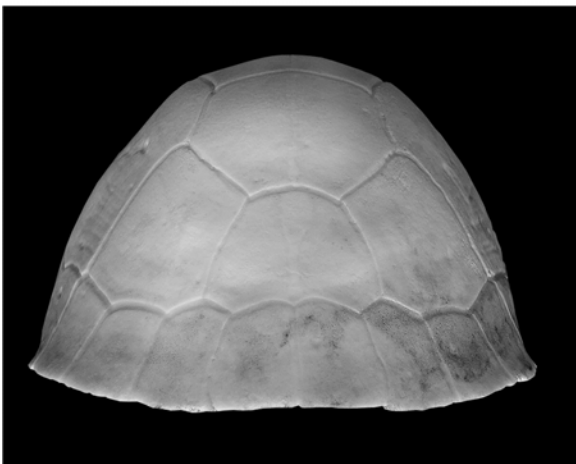


Figure 69. Character 36(0): CAS 228376, *galbinifrons*, posterior view of shell.

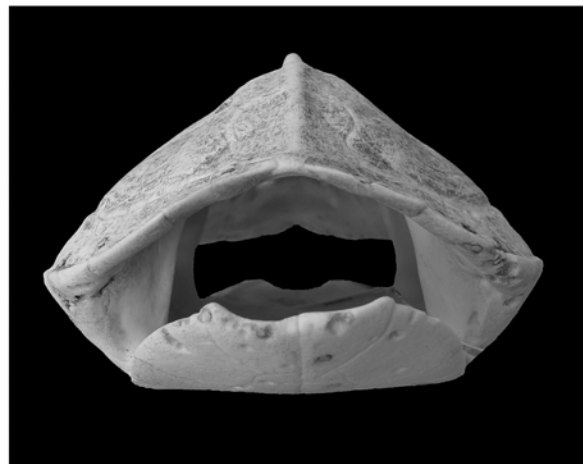


Figure 70. Character 36(1): CM 259430, *tentoria*, anterior view of shell.

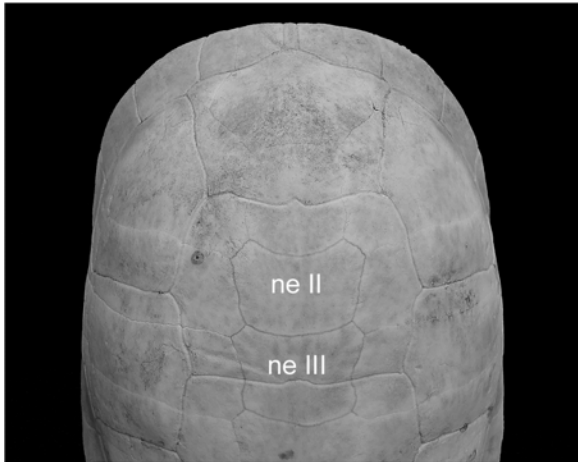


Figure 71. Character 37(0) and 38(0): CAS 228346, *blandingii*, dorsal view of carapace.

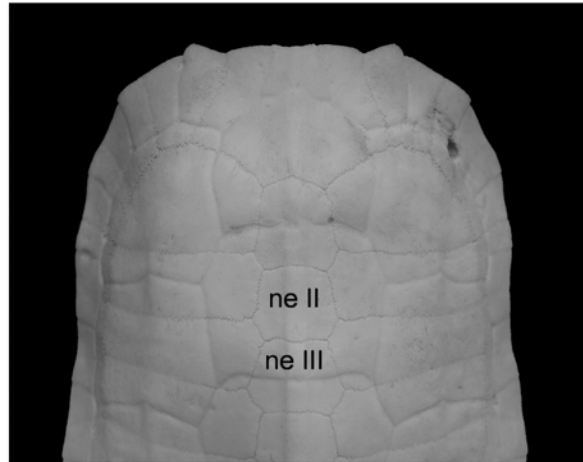


Figure 72. Character 37(1) and 38(1): CAS 228343, *spengleri*, dorsal view of carapace.

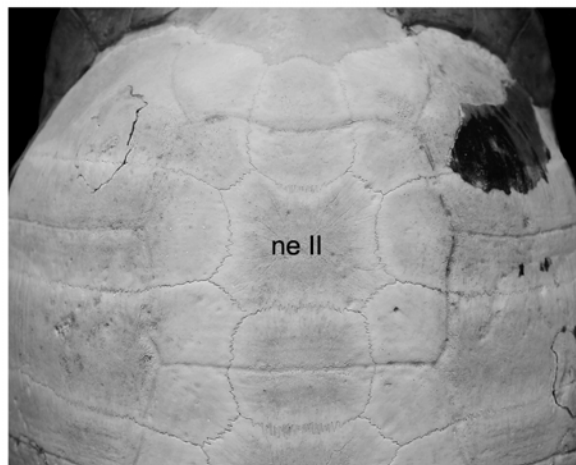


Figure 73. Character 37(2): CAS 228408, *elongata*, dorsal view of carapace.

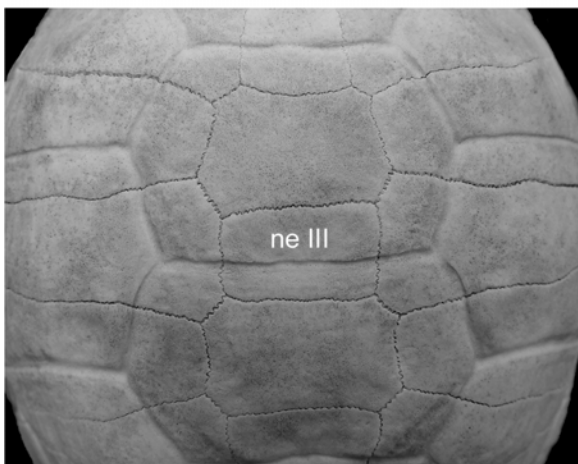


Figure 74. Character 38(2): CAS 228399, *horsfieldi*, dorsal view of carapace.

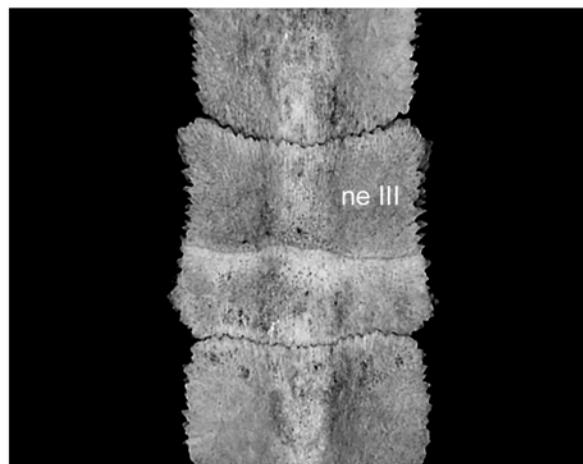


Figure 75. Character 38(3): CAS 228445, *subtrijuga*, dorsal view of neurals II - IV.

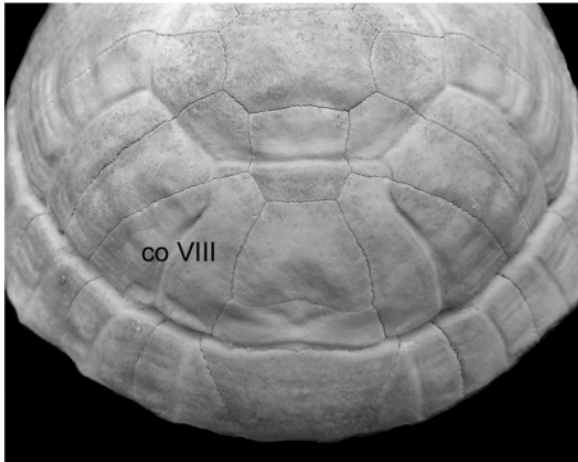


Figure 76. Character 39(0): CAS 228399, *horsfieldi*, posterodorsal view of carapace.

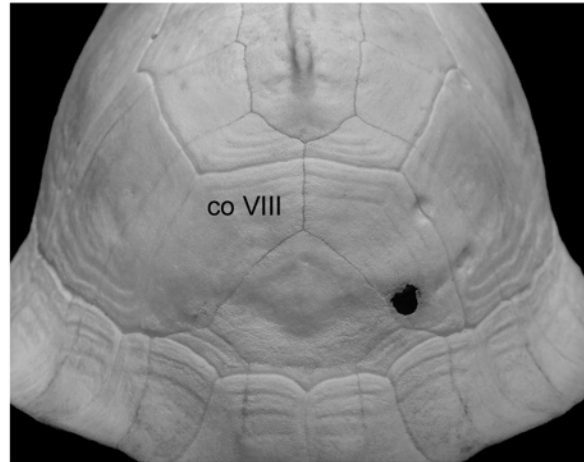


Figure 77. Character 39(1): CAS 228375, *carolina*, posterodorsal view of carapace.

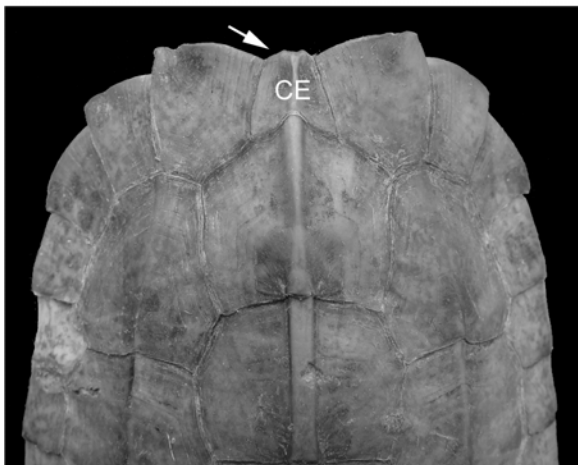


Figure 78. Character 40(0): CAS 228371, *spengleri*, dorsal view of carapace.

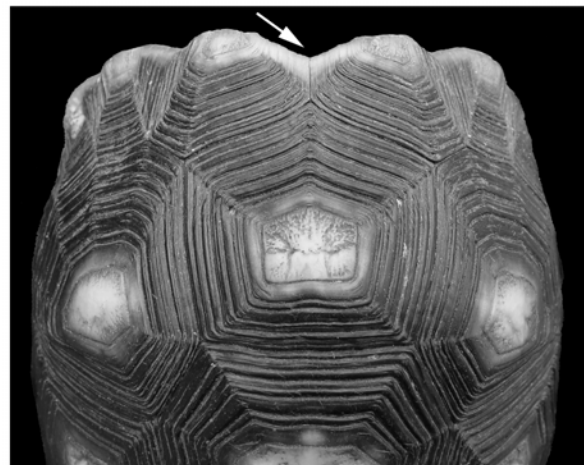


Figure 79. Character 40(1): CAS 228430, *carbonaria*, anterodorsal view of carapace.

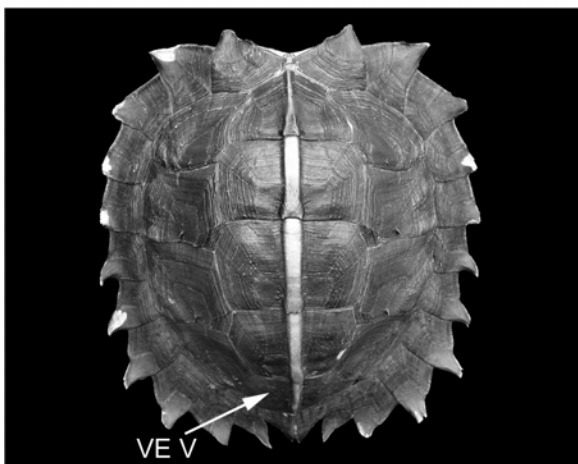


Figure 80. Character 41(0): CAS 228368, *spinosa*, dorsal view of carapace.

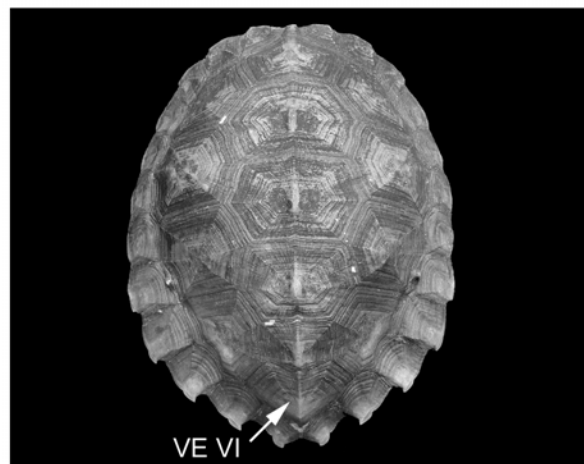


Figure 81. Character 41(1): CAS 228450, *N. platynota*, dorsal view of carapace.

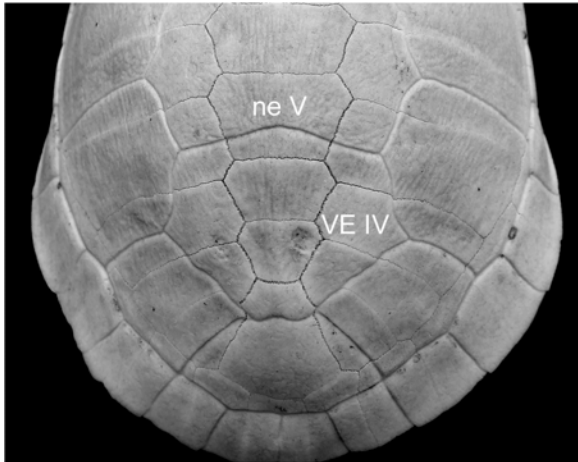


Figure 82. Character 42(0): CAS 228338, *reticularia*, posterodorsal view of carapace.

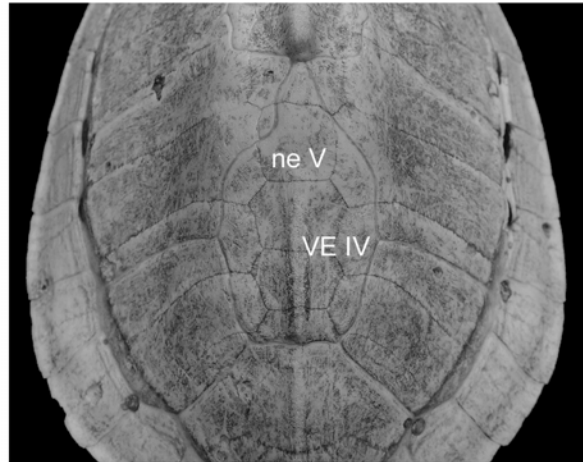


Figure 83. Character 42(1): FMNH 259430, *tentoria*, posterodorsal view of carapace.

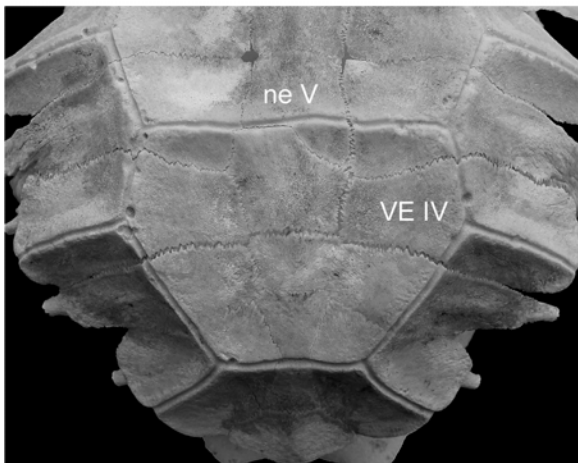


Figure 84. Character 42(2): CAS 228344, *emys*, posterodorsal view of carapace.

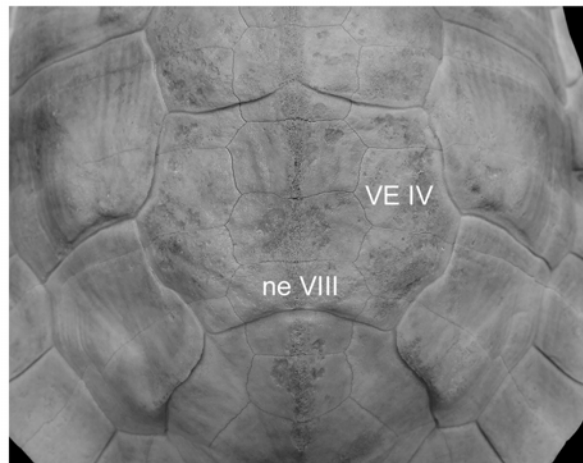


Figure 85. Character 43(0): CAS 228413, *insculpta*, posterodorsal view of carapace.

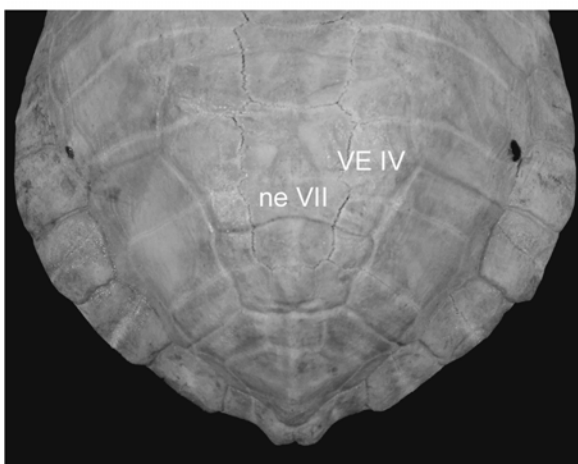


Figure 86. Character 43(1): YPM 14678, *platynota*, posterodorsal view of carapace.

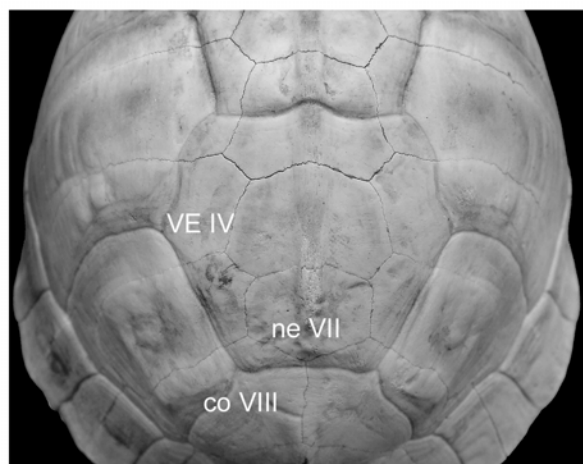


Figure 87. Character 43(2): CAS 228345, *amboinensis*, posterodorsal view of carapace.

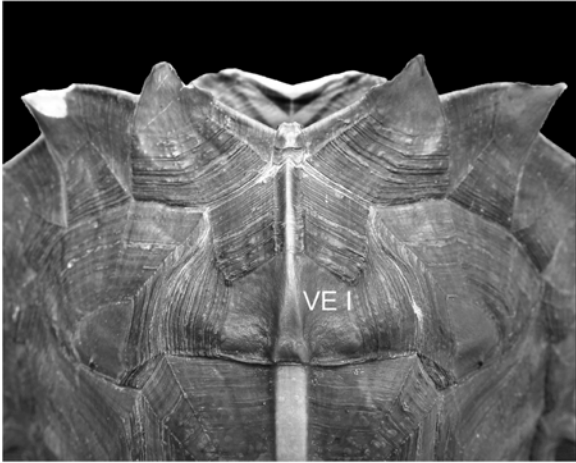


Figure 88. Character 44(0): CAS 228368, *spinosa*, dorsal view of carapace.

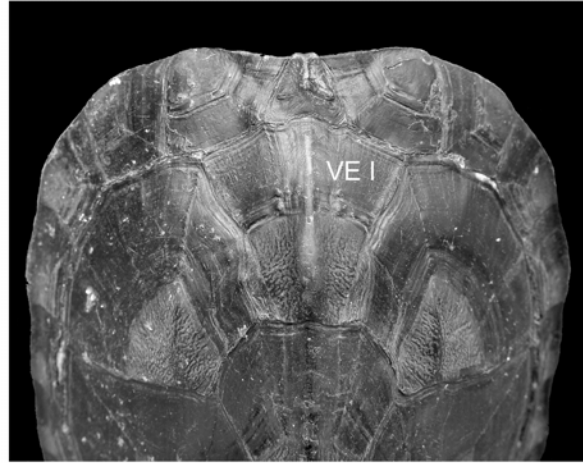


Figure 89. Character 44(1): CAS 228335, *crassicollis*, dorsal view of carapace.

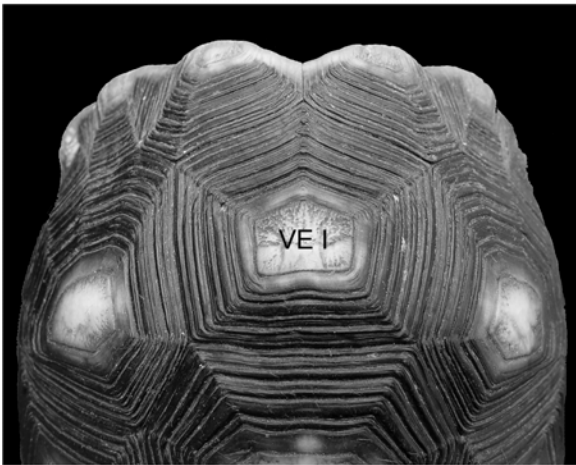


Figure 90. Character 45(0): CAS 228430, *carbonaria*, anterodorsal view of carapace.

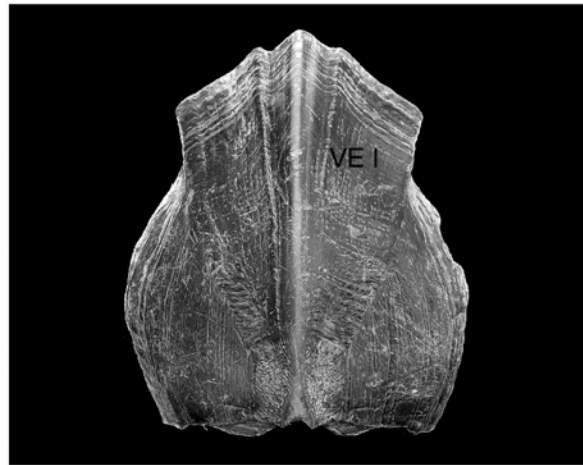


Figure 91. Character 45(1): CAS 228341, *grandis*, dorsal view of first vertebral scute, anterior to top.

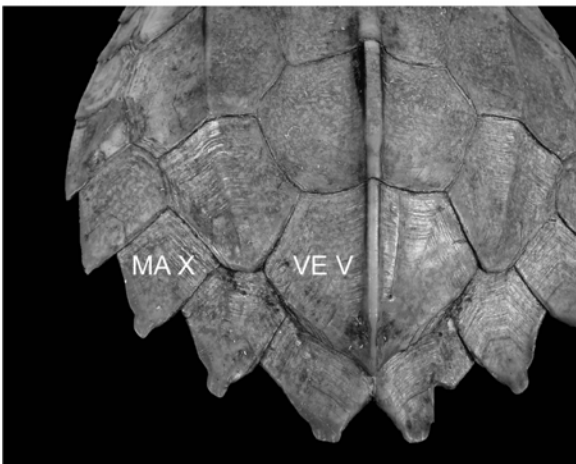


Figure 92. Character 46(0): YPM 11653, *spengleri*, posterodorsal view of carapace.

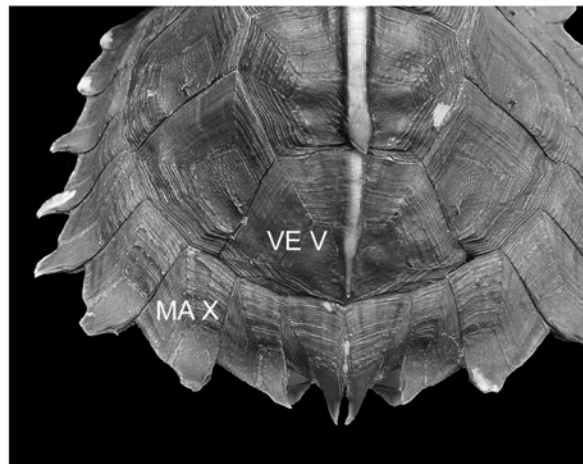


Figure 93. Character 46(1): CAS 228368, *spinosa*, posterodorsal view of carapace.

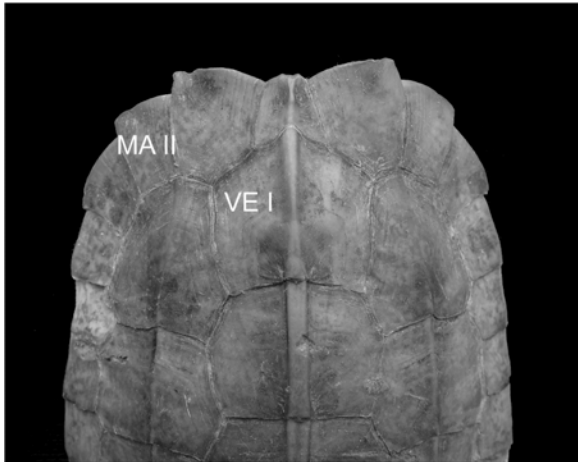


Figure 94. Character 47(0): CAS 228371, *spengleri*, dorsal view of carapace.

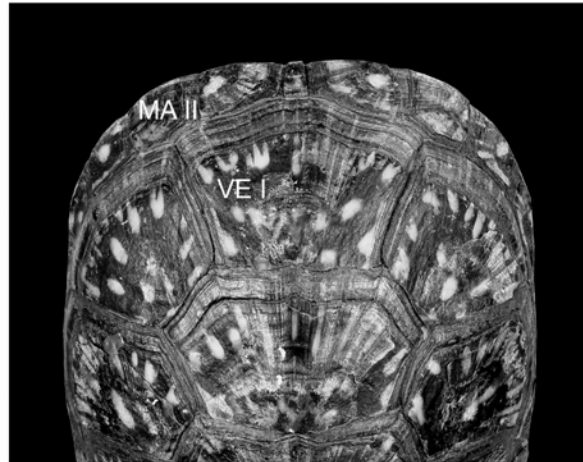


Figure 95. Character 47(1): YPM 10382, *blandingii*, dorsal view of carapace.

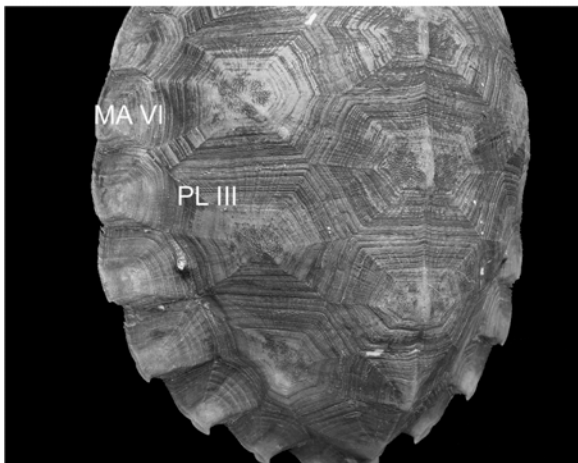


Figure 96. Character 48(0): CAS 228450, *N. platynota*, left dorsolateral view of carapace.

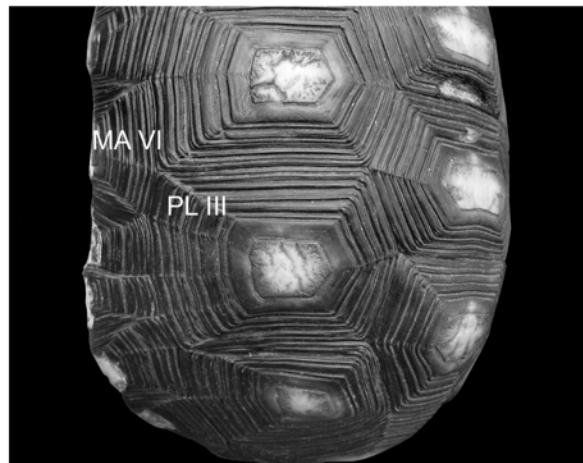


Figure 97. Character 48(1): CAS 228430, *carbonaria*, left dorsolateral view of carapace.

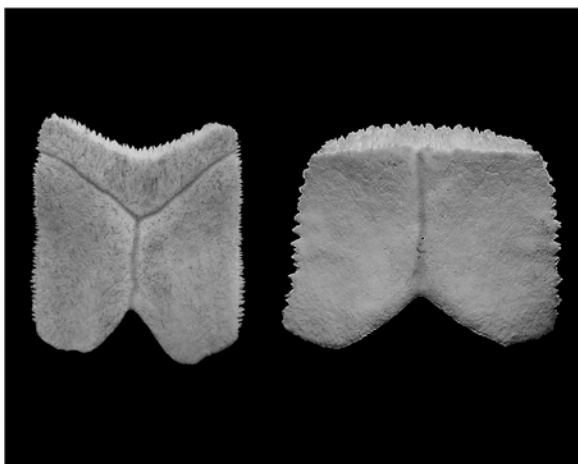


Figure 98. Character 49(0): CAS 228458, *texana* (left); 49(1): CAS 228341, *grandis* (right); dorsal view of pygals.

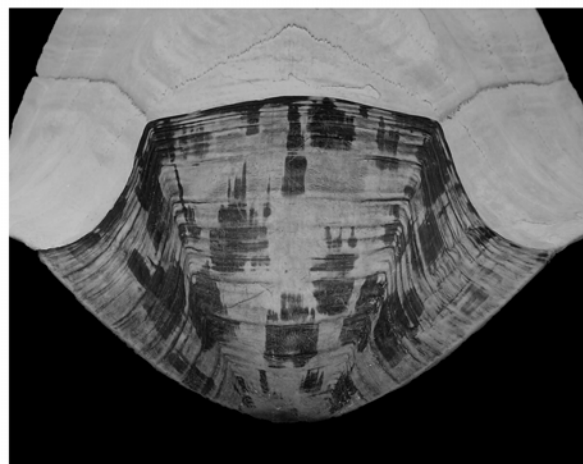


Figure 99. Character 49(2): CAS 228449, *pardalis*, posterior view of carapace.

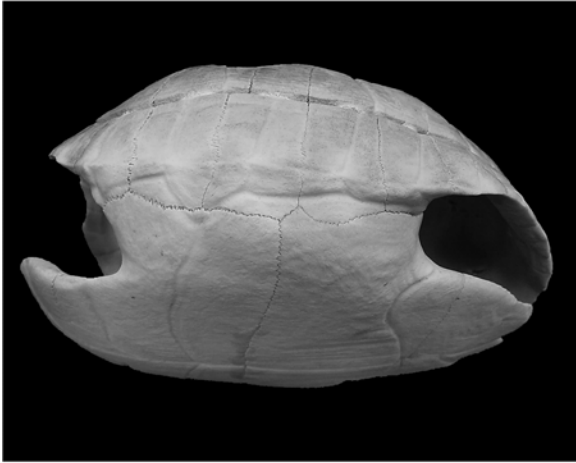


Figure 100. Character 50(0): CAS 228399, *horsfieldi*, lateral view of carapace.



Figure 101. Character 50(1): CAS 228375, *carolina*, lateral view of carapace.

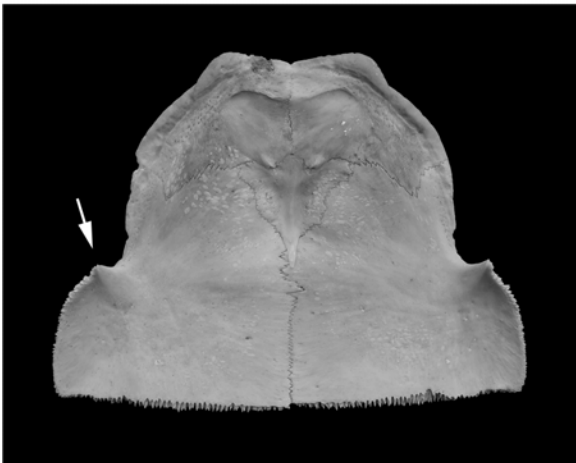


Figure 102. Character 51(0): CAS 228342, *platynota*, ventral view of anterior plastral lobe.

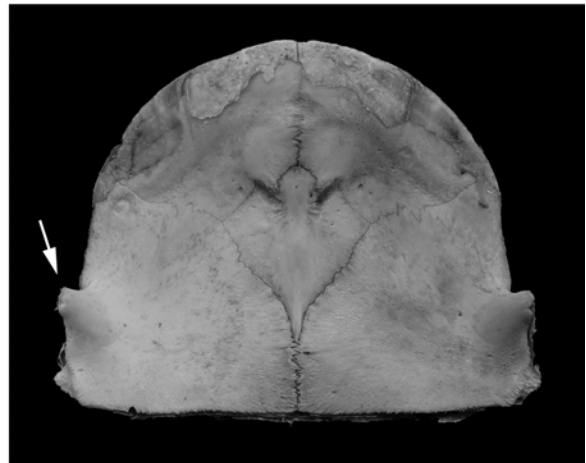


Figure 103. Character 51(1): CAS 228419, *amboinensis*, ventral view of anterior plastral lobe.

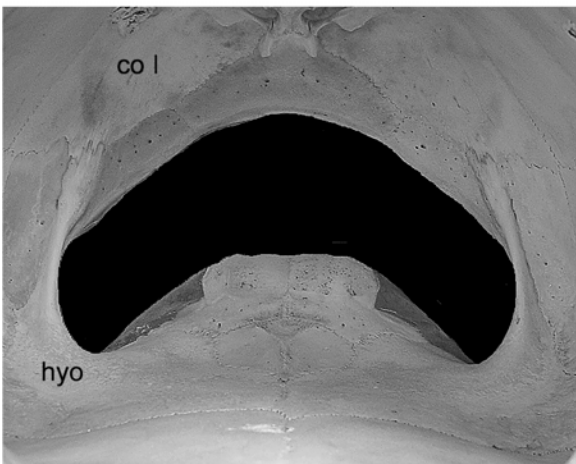


Figure 104. Character 51(2): CAS 228408, *elongata*, internal view of shell from posterior.

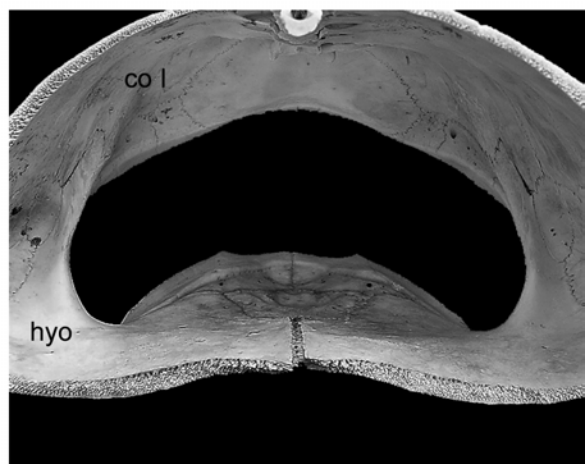


Figure 105. Character 51(3): CAS 228406, *insculpta*, internal view of shell from posterior.

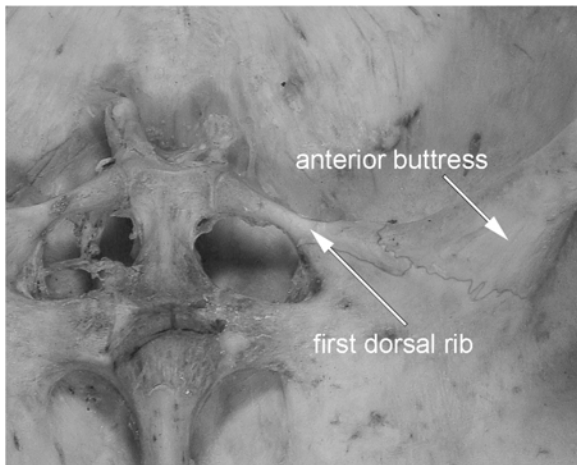


Figure 106. Character 51(4): YPM 14073, *thurjii*, left ventral view of first thoracic rib.



Figure 107. Character 52(0): YPM 691, *carolina*, ventral view of posterior plastral lobe.

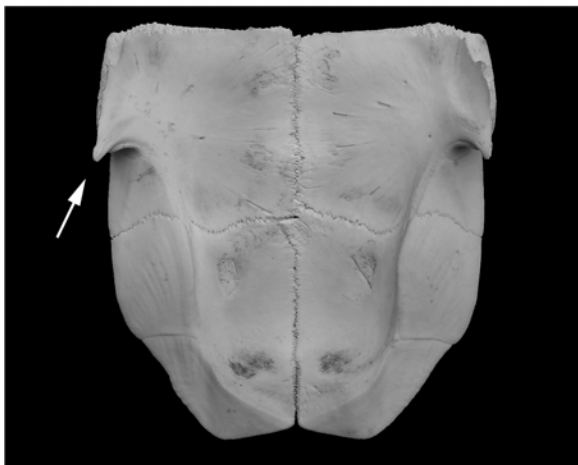


Figure 108. Character 52(1): CAS 228434, *blandingii*, ventral view of posterior plastral lobe.

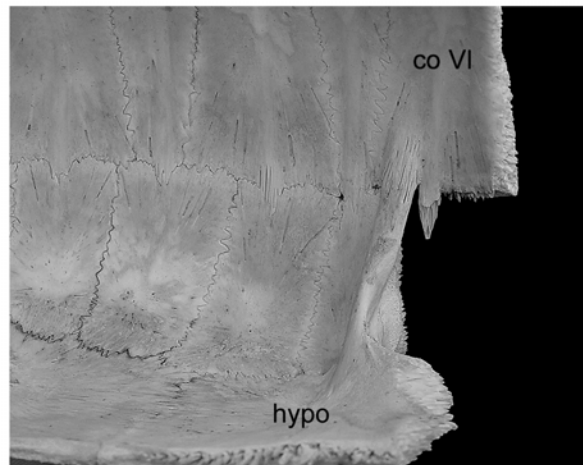


Figure 109. Character 52(2): CAS 228349, *pardalis*, medial view of partial right shell.

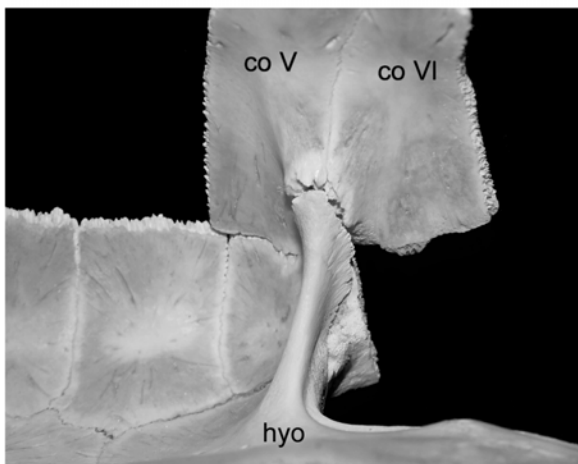


Figure 110. Character 52(3): CAS 228361, *reevesii*, medial view of partial right shell.

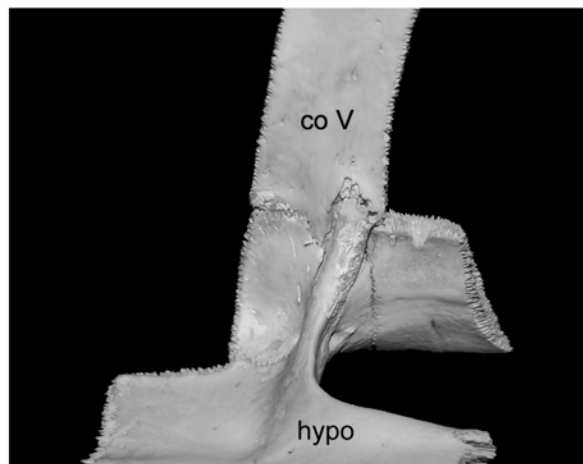


Figure 111. Character 52(4): CAS 228341, *grandis*, medial view of partial right shell.



Figure 112. Character 53(0): CAS 228447, *orbicularis*, ventral view of carapace.

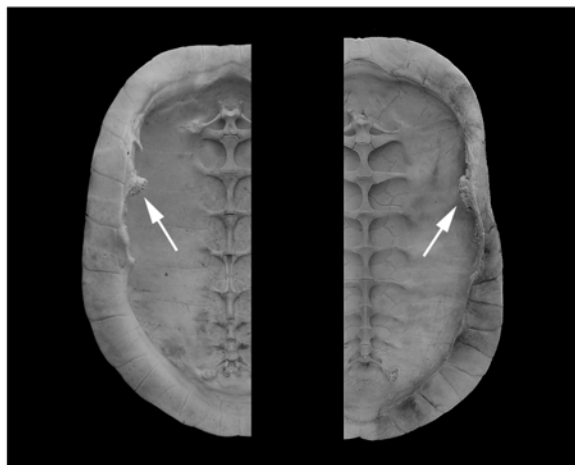


Figure 113. Character 53(1): CAS 228345, *amboinensis* (left); CAS 228373, *blandingii* (right); ventral view of carapaces.

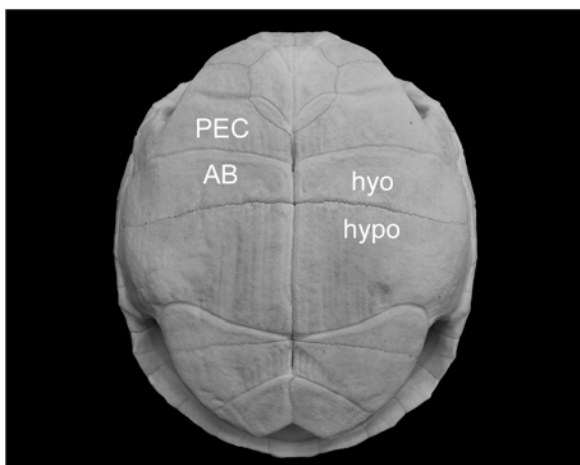


Figure 114. Character 54(0): CAS 228399, *horsfieldi*, ventral view of shell.

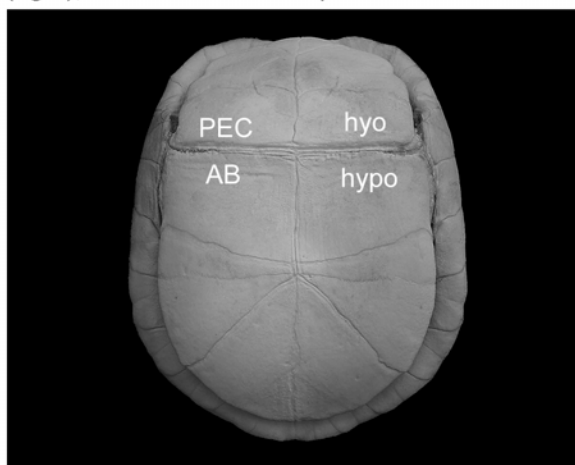


Figure 115. Character 54(1): CAS 228345, *amboinensis*, ventral view of shell.



Figure 116. Character 55(0): CAS 228403, *tornieri*, right posterolateral view of carapace.

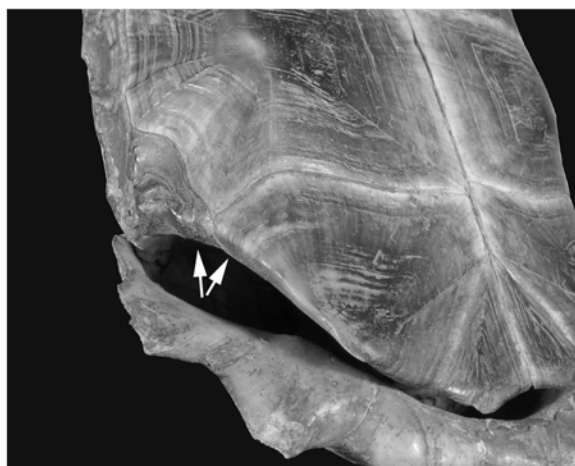


Figure 117. Character 55(1): YPM 12653, *erosa*, right posterolateral view of carapace.

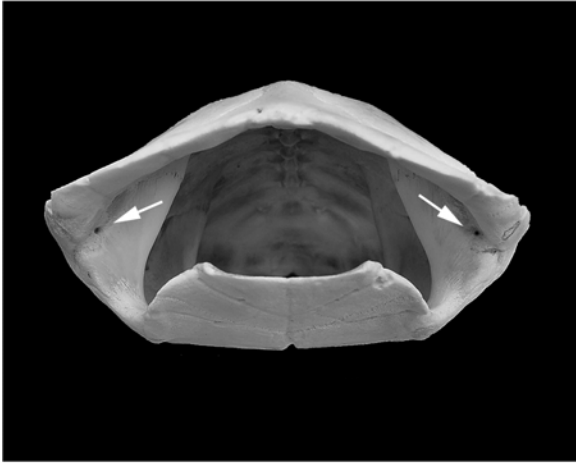


Figure 118. Character 57(0): CAS 228335, *crassidactylus*, anterior view of shell.

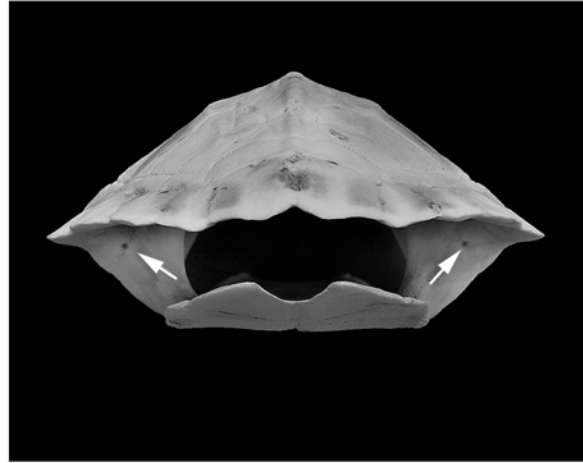


Figure 119. Character 58(0): CAS 228335, *crassidactylus*, posterior view of shell.

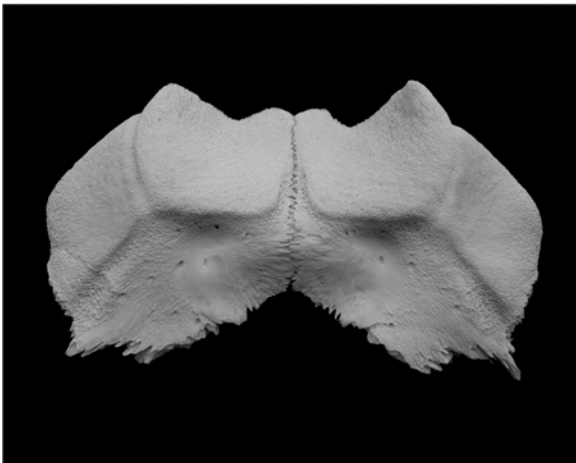


Figure 120. Character 59(0): CAS 228416, *impressus*, dorsal view of epiploastrum.



Figure 121. Character 59(1): CAS 228397, *carbonaria*, dorsal view of epiploastrum.

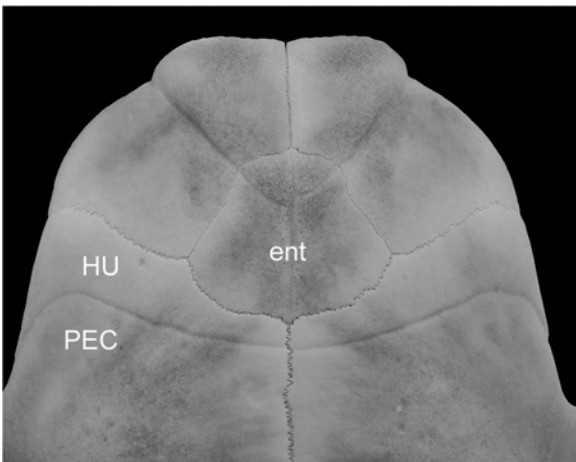


Figure 122. Character 60(0): CAS 228437, *texana*, ventral view of anterior plastral lobe.

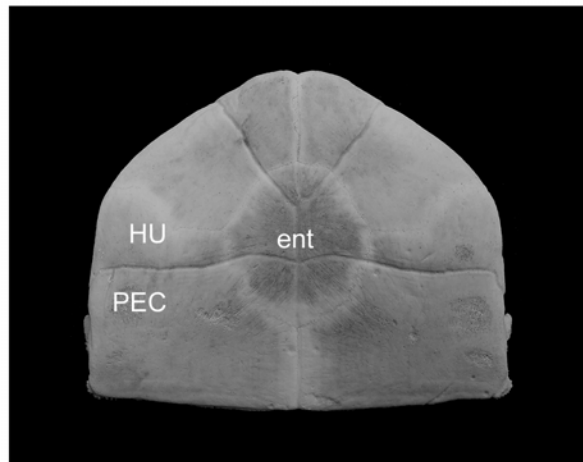


Figure 123. Character 60(1): CAS 228345, *amboinensis*, ventral view of anterior plastral lobe.

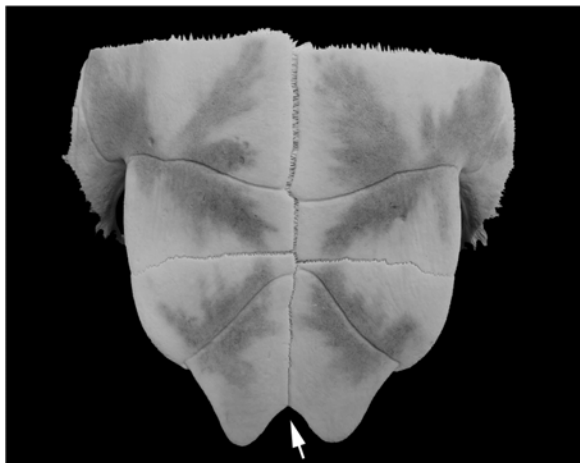


Figure 124. Character 61(0): CAS 228437, *texana*, ventral view of posterior plastral lobe.

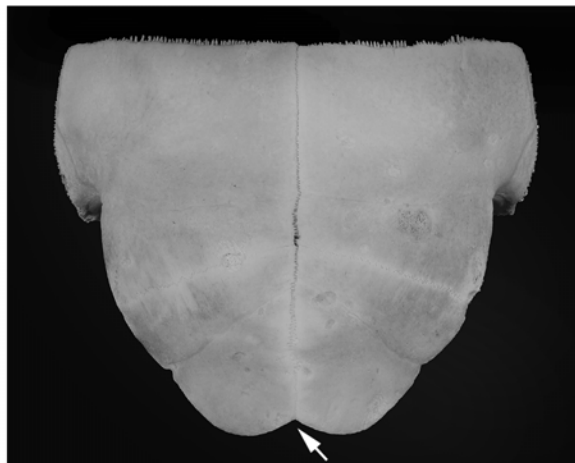


Figure 125. Character 61(1): YPM 14678, *N. platynota*, ventral view of posterior plastral lobe.

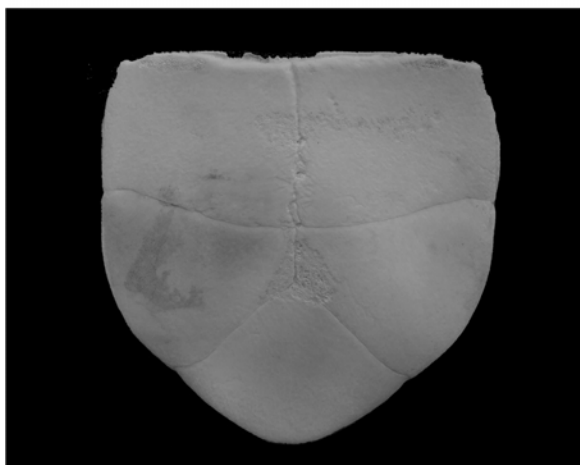


Figure 126. Character 61(2): CAS 228376, *galbinifrons*, ventral view of posterior plastral lobe.

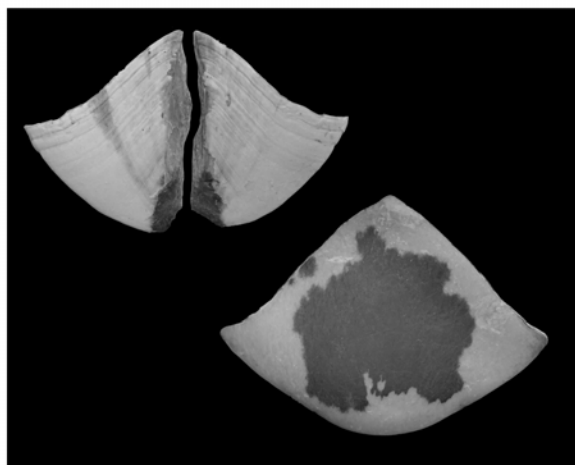


Figure 127. Character 62(0): CAS 228345, *amboinensis* (left); 62(1): CAS 228376, *galbinifrons* (right); ventral view of anal scutes.



Figure 128. Character 63(0): CAS 228450, *platynota*, ventral view of plastron.

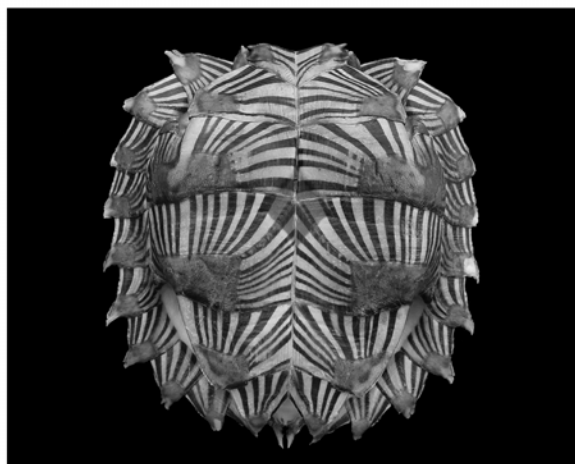


Figure 129. Character 63(1): CAS 228368, *spinosa*, ventral view of plastron.

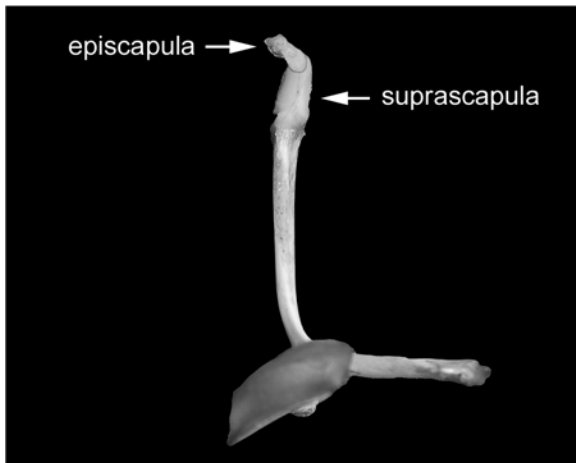


Figure 130. Character 64(1) and 65(1): TNHC 62532, *ornata*, lateral view of right scapulacoracoid.



Figure 131. Character 66(0): CAS 228345, *amboinensis* (left); 66(1): CAS 228397, *carbonaria* (right); coracoids.



Figure 132. Character 67(0) and 68(0): YPM 14677, *blandingii*, top view of lower arm and manus.

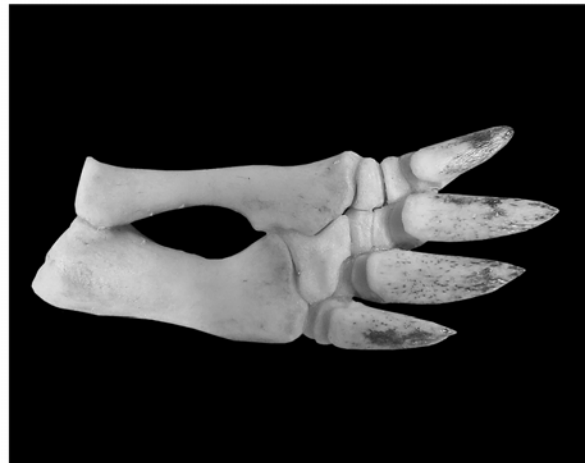


Figure 133. Character 67(1) and 68(1): YPM 16450, *horsfieldi*, top view of lower arm and manus.

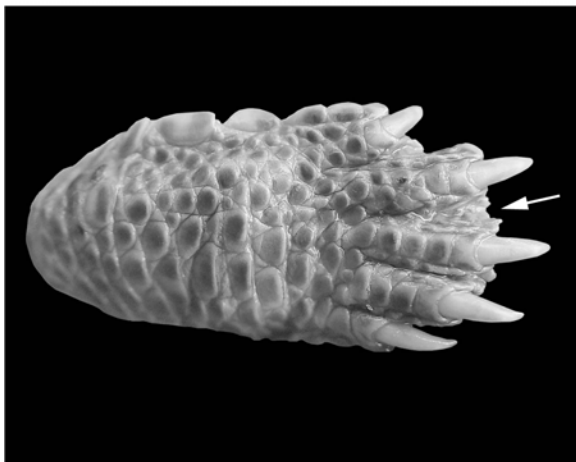


Figure 134. Character 69(0): YPM 2983, *terrapin*, top view of lower arm and manus.



Figure 135. Character 69(1): YPM 14445, *spengleri*, top view of lower arm and manus.



Figure 136. CAS 228348, *punctularia*, right lateral view.



Figure 137. FMNH 224107, *borneoensis*, left anterolateral view of trigeminal foramen.

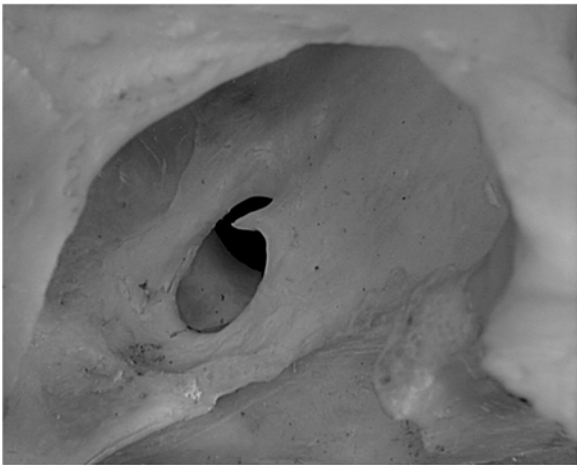


Figure 138. FMNH 224107, *borneoensis*, right anterolateral view of trigeminal foramen.

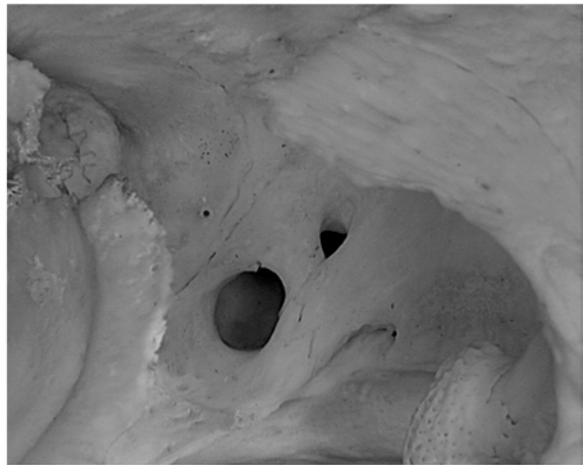


Figure 139. FMNH 224122, *borneoensis*, right anterolateral view of trigeminal foramen.



Figure 140. CAS 228378, *carolina*, dorsal view of pelvis.

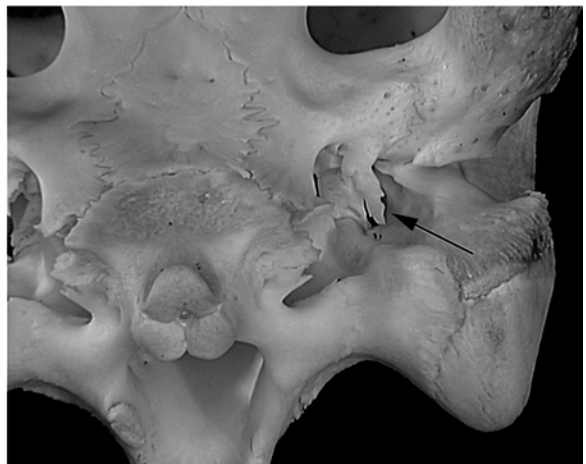


Figure 141. CAS 228443, *grandis*, posteroventral view of otic region.

As practicing vertebrate paleontologists, we also hope that our efforts here will stimulate additional investigation and publication of the extensive fossil record of testudinoid turtles. Morphology is, of course, of paramount importance for the interpretation of fossils. Our visits to many museums in the last several years revealed an abundance of unpublished testudinoid fossil material. Although a phylogenetic analysis was not a goal of this research, we adopt the convenient and now familiar means of summarizing morphological data by providing a character matrix that summarizes some of our observations. Although character data can be used to assist paleontologists in diagnosing fossil testudinoid specimens, we also encourage paleontologists to utilize our study as a starting point for basic morphologic descriptions. Description of differential diagnostic characters generally is an adequate minimum for the erection of a new taxon. However, such a diagnosis is, in itself, not particularly helpful to systematists trying to score a matrix and place a fossil into a broader phylogenetic context. Descriptions of new fossil specimens (and taxa) will be most useful if they include discussions of character state data for all preserved anatomical regions. This current summary of morphological characters that traditionally are used in systematic treatments of testudinoids can be used as a preliminary guide to the anatomical regions and features that would be most useful when included as part of a description of new fossil material.

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Appendix 1

List of specimens used.

agassizii, CAS 33867, FMNH 216746, FMNH 250843; *alabamensis*, CM 95968, CM 95991; *amboinensis*, CAS 153872, CAS 228345, CAS 228369, CAS 228412, CAS 228419, FMNH 224009; *annandalei*, FMNH 258876, FMNH 258879, FMNH Moll3036; *annulata*, CAS SUR7425, CM 87903, YPM 15410; *arachnoides*, MCZ 54050; *areolatus*, MCZ 42214; *areolata*, CM 47957, CM 87904; *barbouri*, CAS SUR12063, TUMNH 15400, TUMNH 15428, TUMNH 15429, TUMNH 16899; *baska*, FMNH 224095, FMNH 224097, FMNH 224213, FMNH 224124, FMNH 224226; *bealei*, CM 118554, FMNH 255270, FMNH 226542; *belliana*, CAS 228394, CAS 228404; *berlandieri*, TNHC 2813; *blandingii*, CAS 12837, CAS 228346, CAS 228373, CAS 228434, CAS 228448, YPM 14677, YPM 10382; *borneensis*, FMNH 224001, FMNH 224003, FMNH 224004, FMNH 224005, FMNH 224140; *borneoensis*, FMNH 224107, FMNH 224122, FMNH 224129, FMNH 251499, MCZ 42198; *carbonaria*, CAS 228397, CAS 228411, CAS 228427, CAS 228430; *caretta*, CAS 8383, FMNH 31021; *carolina*, CAS 228375, CAS 228378; *caspica*, CAS 141118, CM 118517, FMNH 19714, FMNH 74505, FMNH 98764; *chilensis*, CM 112252; *coahuila*, KU 46929, KU 92623, MCZ 120335; *crassicolis*, CAS 228335, CAS 228451, FMNH 11091, MCZ 7821, MCZ 134451; *decorata*, CM 118590; *dentata*, CAS 134332, KU 47170, MCZ 29567, CAS 228333, CAS 228362, CAS 228414; *elegans*, CAS 228396; *elongata*, CAS 228408, FMNH 183740, FMNH 257382; *emys*, CAS 228344, FMNH 63749, FMNH 224034; *ernsti*, TUMNH 13460, TUMNH 13462, TUMNH 16899; *erosa*, YPM 12653; *flavimaculata*, TUMNH 15375, TUMNH 15404, TUMNH 15747, TUMNH 15787; *flavomarginata*, CAS 18040, CAS 228356, CAS 228357, CAS 228359, FMNH 216515; *flavomarginatus*, MCZ 164926; *forsteni*, CAS 228433; *galbinifrons*, CAS 228358, CAS 228360, CAS 228367, CAS 228376, YPM 14074, YPM 14080; *geographica*, CAS 12809, TUMNH 15391, TUMNH 15392, TUMNH 15410, TUMNH 15430; *geometricus*, MCZ 32184; *gibba*, CAS 228392; *graeca*, CAS 217732, CAS 228435, LMNH 54855, LMNH 54861; *grandis*, CAS 228341, CAS 228443, FMNH 224038, YPM 15431; *guttata*, CAS 8696, CAS 228372, CAS 228386, FMNH 211573; *hamiltonii*, MCZ 120333, YPM 10399; *hermanni*, CAS 228400, CAS 228401, CAS 228402; *homeana*, CAS 228409, CAS 228423, CAS 228428, CAS 228429, CAS 228455, FMNH 19794; *horsfieldi*, CAS 120707, CAS 228398, CAS 228399, CAS 228421, CAS 228425, YPM 16450; *impressa*, CAS 228416; *G. insculpta*, CAS 228406, CAS 228407, CAS 228413; *japonica*, YPM 15482, YPM 15486; *kachuga*, FMNH 224128, FMNH 224152; *kleinmanni*, CAS 228422, CAS 228426, CAS 228431; *kohnii*, TUMNH 10237, TUMNH 12121, TUMNH 14544, TUMNH 15678; *leprosa*, CM 137031; *marmorata*, CAS no number, CAS 188533, CAS 220052, FMNH 22076; *mouhotii*, CAS 228365, CAS 228374, CAS 228420, CAS 228444; *muhlenbergii*, LMNH 55352, MCZ 52248; *mutica*, LMNH 54883; *P. nelsoni*, CM 67311; *nigra*, CAS 8125, CAS 8289; *nigrinoda*, TUMNH 15147, TUMNH 15317, TUMNH 15408, TUMNH 15750; *ocellata*, CAS 228336; *G. oculifera*, TUMNH 26, TUMNH 3359, TUMNH 7548, TUMNH 12402, TUMNH 16928; *P. oculifera*, CAS 165598, CAS 220645, CAS 220646; *odoratus*, YPM 13622, CAS 228351, CAS 228352, CAS 228353; *orbicularis*, CAS 173223, CAS 228347, CAS 228415, CAS 228447, LMNH 10347, YPM 15479; *T. ornata*, CAS 228381, CAS 228382, CAS 228383, CAS 228384, TNHC 62532; *ouachitensis*, CM 61656, CM 84696; *pardalis*, CAS 148630, CAS 228349, CAS 228410, CAS 228418, CAS 228432, CAS 228449; *petersi*, CAS 8608, CM 124246, CM 124247; *picta*, CAS 13889, CAS 228379, CAS 228380, CAS 228385; *N. platynota*, CAS 228342, CAS 228450, CM 118586, FMNH 224216, YPM 14678; *polyphemus*, CAS 14090, LMNH 43344, LMNH 43354, LMNH 59320; *pulcherrima*, CAS 11754, CAS 228355, CAS 228366, CAS 228377; *pulchra*, LMNH 48092; *punctularia*, YPM 465, CAS 228348; *reevesii*, CAS 31437, CAS 228361, CAS 228364; *reticularia*, CAS 228338, CAS 228388, LMNH 14565, LMNH 14569, LMNH 49145, LMNH 54856, LMNH 78580; *rubida*, CM 87907, CM 87908; *rubriventris*, CM 34409, CM 45188; *scripta*, CAS SUR8642, CAS 228436, CAS 228442, LMNH 15684; *serpentina*, CAS 228452, YPM 6369, CAS 228457; *siebenrocki*, CAS 228393; *signatus*, CAS 228405, MCZ 42217, MCZ 42218; *sinensis*, CAS 18031, CAS 228339; *spengleri*, CAS 21008, CAS 228331, CAS 228332, CAS 228343, CAS 228371, YPM 11653, YPM 14445; *spinifera*, CAS 65705, CAS 228350, CAS 228354, YPM 656; *spinosa*, CAS 228368, CAS 228459; *subglobosa*, CAS 228334; *subtrijuga*, CAS 16996, CAS 228445, CAS 228446, CAS 228453, CAS 228454; *sub-rufa*, CAS 228389, CAS 228390, CAS 228391; *tchepo-nensis*, CAS 228363, CAS 228370; *tecta*, CM 89923; *tentoria*, FMNH Moll3026, FMNH Moll3028, FMNH Moll3032, FMNH 259430; *tentorius*, MCZ 41944, MCZ 46604; *terrapin*, CAS 43640, CAS 228340, CAS 228387, YPM 2983; *texana*, CAS 30965, CAS 228437, CAS 228438, CAS 228439, CAS 228440, CAS 228441, CAS 228456, CAS 228458; *thurjii*, FMNH 224135, FMNH 224153, MCZ 62523, MCZ 62524, YPM 14072, YPM 14073, YPM 14074; *tornieri*, CAS 139704, CAS 228395, CAS 228403, CAS 228417, CAS 228424; *tri-*

fasciata, CAS 228337, MCZ 5218; *trijuga*, CAS 12463, CM 89921, CM 124227, YPM 15453; *versa*, TUMNH 4484, TUMNH 10510, TUMNH 16192; *yuwonoi*, YPM 12626.

Appendix 2

Generic synonymies for all currently recognized testudinoid species and all outgroup species used herein. Synonymies are based only on common usage during the last 50 years.

Ingroup

<i>adiutrix</i>	<i>Chrysemys</i> , <i>Pseudemys</i> , <i>Trachemys</i>	<i>dussumieri</i>	<i>Aldabrachelys</i> , <i>Dipsochelys</i> , <i>Geochelone</i> , <i>Megalochelys</i>
<i>agassizii</i>	<i>Gopherus</i> , <i>Xerobates</i>	<i>elegans</i>	<i>Geochelone</i>
<i>alabamensis</i>	<i>Chrysemys</i> , <i>Pseudemys</i>	<i>elongata</i>	<i>Geochelone</i> , <i>Indotestudo</i>
<i>amboinensis</i>	<i>Cuora</i>	<i>emolli</i>	<i>Chrysemys</i> , <i>Pseudemys</i> , <i>Trachemys</i>
<i>angulata</i>	<i>Chersina</i> , <i>Goniochersus</i> , <i>Neotestudo</i> , <i>Testudo</i>	<i>ernsti</i>	<i>Geochelone</i> , <i>Manouria</i>
<i>annamensis</i>	<i>Annamemys</i> , <i>Mauremys</i>	<i>erosa</i>	<i>Graptemys</i>
<i>annandalii</i>	<i>Hieremys</i>	<i>femoralis</i>	<i>Kinixys</i>
<i>annulata</i>	<i>Callopsis</i> , <i>Geoemyda</i> , <i>Nicoria</i> , <i>Rhinoclemmys</i>	<i>flavimaculata</i>	<i>Homopus</i>
<i>arachnoides</i>	<i>Pyxis</i>	<i>flavomarginata</i>	<i>Graptemys</i> , <i>Malaclemys</i>
<i>areolata</i>	<i>Callopsis</i> , <i>Geoemyda</i> , <i>Nicoria</i> , <i>Rhinoclemmys</i>	<i>flavomarginatus</i>	<i>Cistoclemmys</i> , <i>Cuora</i> , <i>Geoemyda</i>
<i>areolatus</i>	<i>Homopus</i>	<i>floridana</i>	<i>Gopherus</i>
<i>aurocapitata</i>	<i>Cuora</i>	<i>forsteni</i>	<i>Chrysemys</i> , <i>Pseudemys</i>
<i>barbouri</i>	<i>Graptemys</i> , <i>Malaclemys</i>	<i>funerea</i>	<i>Geochelone</i> , <i>Indotestudo</i> , <i>Manouria</i>
<i>baska</i>	<i>Batagur</i>	<i>gaigeae</i>	<i>Callopsis</i> , <i>Geoemyda</i> , <i>Rhinoclemmys</i>
<i>bealei</i>	<i>Clemmys</i> , <i>Sacalia</i>	<i>galbinifrons</i>	<i>Chrysemys</i> , <i>Pseudemys</i> , <i>Trachemys</i>
<i>belliana</i>	<i>Kinixys</i>	<i>geographica</i>	<i>Cistoclemmys</i> , <i>Cuora</i>
<i>berlandieri</i>	<i>Gopherus</i>	<i>geometricus</i>	<i>Graptemys</i> , <i>Malaclemys</i>
<i>blandingii</i>	<i>Emydoidea</i> , <i>Emys</i> , <i>Neoemys</i>	<i>gibbonsi</i>	<i>Psammobates</i>
<i>borneensis</i>	<i>Orlitia</i>	<i>graeca</i>	<i>Graptemys</i>
<i>borneoensis</i>	<i>Callagur</i>	<i>grandis</i>	<i>Testudo</i>
<i>boulengeri</i>	<i>Homopus</i>	<i>guttata</i>	<i>Geoemyda</i> , <i>Heosemys</i>
<i>caglei</i>	<i>Graptemys</i>	<i>hamiltonii</i>	<i>Clemmys</i>
<i>callirostris</i>	<i>Chrysemys</i> , <i>Pseudemys</i> , <i>Trachemys</i>	<i>hermanni</i>	<i>Geoclemys</i>
<i>carbonaria</i>	<i>Chelonoidis</i> , <i>Geochelone</i>	<i>homeana</i>	<i>Testudo</i>
<i>carolina</i>	<i>Terrapene</i>	<i>horsfieldi</i>	<i>Kinixys</i>
<i>caspica</i>	<i>Clemmys</i> , <i>Mauremys</i>	<i>impressa</i>	<i>Agrionemys</i> , <i>Testudo</i>
<i>chilensis</i>	<i>Chelonoidis</i> , <i>Geochelone</i>	<i>G. insculpta</i>	<i>Geochelone</i> , <i>Manouria</i>
<i>coahuila</i>	<i>Terrapene</i>	<i>japonica</i>	<i>Calemys</i> , <i>Clemmys</i> , <i>Glyptemys</i>
<i>concinna</i>	<i>Chrysemys</i> , <i>Pseudemys</i>	<i>kachuga</i>	<i>Clemmys</i> , <i>Mauremys</i>
<i>crassicolis</i>	<i>Siebenrockiella</i>	<i>kleinmanni</i>	<i>Kachuga</i>
<i>decorata</i>	<i>Chrysemys</i> , <i>Pseudemys</i> , <i>Trachemys</i>	<i>kohnii</i>	<i>Pseudotestudo</i> , <i>Testudo</i>
<i>decussata</i>	<i>Chrysemys</i> , <i>Pseudemys</i> , <i>Trachemys</i>	<i>leprosa</i>	<i>Graptemys</i>
<i>dentata</i>	<i>Cyclemys</i> , <i>Geoemyda</i>	<i>leytensis</i>	<i>Clemmys</i> , <i>Mauremys</i>
<i>denticulata</i>	<i>Chelonoidis</i> , <i>Geochelone</i>	<i>lobatsiana</i>	<i>Geoemyda</i> , <i>Heosemys</i>
<i>depressa</i>	<i>Geoemyda</i> , <i>Heosemys</i>	<i>marginata</i>	<i>Kinixys</i>
<i>dhongoka</i>	<i>Kachuga</i>	<i>marmorata</i>	<i>Testudo</i>
<i>diademata</i>	<i>Geoemyda</i> , <i>Rhinoclemmys</i>	<i>melanosterna</i>	<i>Clemmys</i> , <i>Emys</i>
<i>dorbigni</i>	<i>Chrysemys</i> , <i>Pseudemys</i> , <i>Trachemys</i>	<i>mouhotii</i>	<i>Geoemyda</i> , <i>Rhinoclemmys</i>
		<i>muhlenbergii</i>	<i>Cuora</i> , <i>Cyclemys</i> , <i>Geoemyda</i> , <i>Pyxidea</i>
		<i>mutica</i>	<i>Calemys</i> , <i>Clemmys</i> , <i>Glyptemys</i>
		<i>nasuta</i>	<i>Clemmys</i> , <i>Mauremys</i>
		<i>natalensis</i>	<i>Callopsis</i> , <i>Geoemyda</i> , <i>Rhinoclemmys</i>
		<i>nebulosa</i>	<i>Kinixys</i>
		<i>P. nelsoni</i>	<i>Chrysemys</i> , <i>Pseudemys</i> , <i>Trachemys</i>
		<i>T. nelsoni</i>	<i>Chrysemys</i> , <i>Pseudemys</i>
		<i>nigra</i>	<i>Terrapene</i>
		<i>nigricans</i>	<i>Chelonoidis</i> , <i>Geochelone</i>
		<i>nigrinoda</i>	<i>Chinemys</i>
		<i>ocellata</i>	<i>Graptemys</i> , <i>Malaclemys</i>
		<i>G. oculifera</i>	<i>Morenia</i>
		<i>P. oculifera</i>	<i>Graptemys</i> , <i>Malaclemys</i>
		<i>oldhamii</i>	<i>Psammobates</i>
			<i>Cyclemys</i>

<i>orbicularis</i>	<i>Emys</i>
<i>T. ornata</i>	<i>Terrapene</i>
<i>P. ornata</i>	<i>Chrysemys, Pseudemys, Trachemys</i>
<i>ouachitensis</i>	<i>Graptemys</i>
<i>pani</i>	<i>Cuora</i>
<i>pardalis</i>	<i>Geochelone</i>
<i>petersi</i>	<i>Morenia</i>
<i>picta</i>	<i>Chrysemys</i>
<i>planicauda</i>	<i>Acinixys, Pyxis</i>
<i>G. platynota</i>	<i>Geochelone</i>
<i>N. platynota</i>	<i>Notochelys</i>
<i>polyphemus</i>	<i>Gopherus, Xerobates</i>
<i>pseudogeographica</i>	<i>Graptemys, Malaclemys</i>
<i>pulcherrima</i>	<i>Callopsis, Geoemyda, Rhinoclemmys</i>
<i>pulchra</i>	<i>Graptemys, Malaclemys</i>
<i>pulchriata</i>	<i>Cyclemys</i>
<i>punctularia</i>	<i>Geoemyda, Rhinoclemmys</i>
<i>quadriocellata</i>	<i>Clemmys, Sacalia</i>
<i>radiata</i>	<i>Asterochelys, Geochelone</i>
<i>reevesii</i>	<i>Chinemys</i>
<i>reticularia</i>	<i>Deirochelys</i>
<i>rubida</i>	<i>Callopsis, Geoemyda, Nicoria, Rhinoclemmys</i>
<i>rubriventris</i>	<i>Chrysemys, Pseudemys</i>
<i>scripta</i>	<i>Chrysemys, Pseudemys, Trachemys</i>
<i>signatus</i>	<i>Homopus</i>
<i>silvatica</i>	<i>Geoemyda, Heosemys</i>
<i>sinensis</i>	<i>Ocadia</i>
<i>smithii</i>	<i>Kachuga, Pangshura</i>
<i>spekii</i>	<i>Kinixys</i>
<i>spengleri</i>	<i>Geoemyda</i>
<i>spinosa</i>	<i>Geoemyda, Heosemys</i>
<i>stejnegeri</i>	<i>Chrysemys, Pseudemys, Trachemys</i>
<i>subtrijuga</i>	<i>Malayemys</i>
<i>sulcata</i>	<i>Geochelone</i>
<i>syhetensis</i>	<i>Kachuga, Pangshura</i>
<i>taylori</i>	<i>Chrysemys, Pseudemys, Trachemys</i>
<i>tcheponensis</i>	<i>Cyclemys, Geoemyda</i>
<i>tecta</i>	<i>Kachuga, Pangshura</i>
<i>tentoria</i>	<i>Kachuga, Pangshura</i>
<i>tentorius</i>	<i>Psammobates</i>
<i>terrapen</i>	<i>Chrysemys, Pseudemys, Trachemys</i>
<i>terrapin</i>	<i>Malaclemys</i>
<i>texana</i>	<i>Chrysemys, Pseudemys</i>
<i>thurjii</i>	<i>Hardella</i>
<i>tornieri</i>	<i>Malacochersus</i>
<i>travancorica</i>	<i>Geochelone, Indotestudo</i>
<i>tricarinata</i>	<i>Geoemyda, Melanochelys</i>
<i>trifasciata</i>	<i>Cistoclemmys, Cuora</i>
<i>trijuga</i>	<i>Geoemyda, Melanochelys</i>
<i>trivittata</i>	<i>Kachuga</i>
<i>venusta</i>	<i>Chrysemys, Pseudemys, Trachemys</i>
<i>versa</i>	<i>Graptemys, Malaclemys</i>
<i>wernerii</i>	<i>Testudo</i>

<i>yaquia</i>	<i>Chrysemys, Pseudemys, Trachemys</i>
<i>yniphora</i>	<i>Asterochelys, Geochelone</i>
<i>yunnanensis</i>	<i>Cuora</i>
<i>yuwonoi</i>	<i>Geoemyda, Leucocephalon, Notochelys</i>
<i>zhoui</i>	<i>Cuora</i>

Outgroup

<i>caretta</i>	<i>Caretta</i>
<i>dumerilianus</i>	<i>Peltocephalus, Podocnemis</i>
<i>C. insculpta</i>	<i>Carettochelys</i>
<i>fimbriatus</i>	<i>Chelus</i>
<i>gibba</i>	<i>Phrynops, Mesoclemmys</i>
<i>madagascariensis</i>	<i>Erymnochelys, Podocnemis</i>
<i>megacephalum</i>	<i>Platysternon</i>
<i>odoratus</i>	<i>Kinosternon, Sternotherus, Sternotherus</i>
<i>scorpioides</i>	<i>Kinosternon</i>
<i>serpentina</i>	<i>Chelydra</i>
<i>siebenrocki</i>	<i>Chelodina, Macrochelodina</i>
<i>spinifera</i>	<i>Apalone, Trionyx</i>
<i>subglobosa</i>	<i>Emydura, Tropicochelymys</i>
<i>subrufa</i>	<i>Pelomedusa</i>
<i>temminckii</i>	<i>Macroclemys, Macrochelys</i>

Appendix 3

Distribution of character states for 70 characters among 46 species of testudinoid turtles; a = 0/1; b = 0/2; c = 0/3; d = 0/1/2; e = 1/2; f = 1/3; g = 2/3.

<i>agassizii</i>					
11a10	00000	000?0	11010	00110	00001
01000	03200	00000	00120	22001	22200
00000	10110				
<i>amboinensis</i>					
00a00	00010	00001	00000	00010	00000
00000	01110	00200	0a011	11110	00001
20000	00000				
<i>annandalei</i>					
0010?	00020	00011	10001	00010	00000
00100	01100	00000	00a10	34000	00001
00000	0000?				
<i>annulata</i>					
00a00	00010	0010a	00000	00010	00000
00000	03100	00000	000?0	11000	0?01
00000	00010				
<i>barbouri</i>					
00001	11000	01010	10000	10000	101a0
00001	10000	00000	00000	34000	22200
00000	00001				
<i>baska</i>					
00001	00000	00010	10001	00000	00a02
11100	00010	00000	10110	43000	00000

00000	01000					00100	00010				
<i>bealei</i>						<i>guttata</i>					
00000	00010	00000	10000	00010	00000	00010	00000	00000	00000	10000	00000
00000	00000	0??00	0a010	34000	0000?	00000	00000	00000	00000	34000	10201
00000	00000					00000	00000				
<i>blandingii</i>						<i>hamiltonii</i>					
00000	00000	000?0	00000	10000	00000	01101	00001	00000	10000	00010	00110
00000	0c000	00000	01001	11110	1120a	00111	00000	00000	00a10	33001	0000a
10011	00000					00000	00000				
<i>borneensis</i>						<i>homeana</i>					
00100	00000	00010	00000	00010	10000	11010	00000	000?1	11000	00111	00000
00000	00000	00010	00a10	33000	00000	00001	0110a	00000	00020	22001	???1a
00000	00000					20000	10110				
<i>borneoensis</i>						<i>horsfieldi</i>					
00001	00000	00010	10001	00010	00001	11010	00000	000?0	11000	a0111	00001
11100	00000	00100	00a10	43000	00000	00000	03200	00000	00020	22000	???11
00000	00000					00000	11110				
<i>carbonaria</i>						<i>kachuga</i>					
11010	00000	000?a	11000	00111	00001	00101	00000	00010	10001	00010	10001
00000	01201	00000	00120	22001	22210	11100	00000	01000	10110	43000	00000
00000	10110					00000	0000?				
<i>caspica</i>						<i>mouhotii</i>					
00000	00010	0000a	00000	00010	00000	00010	00010	00000	11100	00010	00000
00000	00000	00000	0aa10	34000	00001	00011	01100	00000	00011	11110	00001
00000	00000					a0000	00010				
<i>crassicollis</i>						<i>P. oculifera</i>					
00a00	00000	00000	10000	00010	10000	11010	00000	000??	11000	00111	00001
00001	00000	00010	00a10	33000	00001	00001	01200	00000	00120	22001	???10
00000	00000					00000	10110				
<i>elongata</i>						<i>orbicularis</i>					
11010	00000	000?a	11000	00111	00001	00000	00000	00000	00000	a0000	00000
00000	03200	00000	00020	22001	???11	00000	00000	00000	0a001	11010	1120a
00000	10110					10010	00000				
<i>dentata</i>						<i>T. ornata</i>					
00000	00010	00000	00000	00000	00000	00010	00010	00000	00000	10000	00000
00001	01100	00001	00011	11000	01101	00000	00010	00200	00001	00110	ed201
00100	00000					20011	00010				
<i>emys</i>						<i>pardalis</i>					
11010	00000	000?a	11000	00110	00001	11010	00000	000?a	11000	00111	00001
00000	01000	02000	00aa0	22001	???00	00000	0f201	00000	00120	22001	???10
00000	10110					00000	10110				
<i>flavomarginata</i>						<i>petersi</i>					
00010	00020	0000a	00000	00010	00000	01100	00000	00010	10001	00010	01111
00000	01110	00100	00011	11110	?1101	12100	02000	00100	00110	34000	00000
21000	00010					00000	00001				
<i>graeca</i>						<i>picta</i>					
11010	00000	000?1	11000	10111	00001	00001	10000	00010	00000	10000	00000
00000	03200	00000	00a20	22000	22211	00000	00000	00000	0a0a0	34000	2220a
00000	10110					00000	0000a				
<i>grandis</i>						<i>N. platynota</i>					
0010a	00020	00000	00000	000a0	00000	01101	00010	00000	00000	00a10	00000
00001	01100	0000a	00a10	34000	00001	00001	00000	10100	00001	03010	00101

10000	00000					00000	10110
<i>polyphemus</i>							
11010	00000	000?0	11000	a0110	00001		
01000	0a200	00000	00120	22001	22200		
00000	10110						
<i>pulcherrima</i>							
00a00	00010	00001	00000	a0010	00000		
00000	01100	00000	000a0	14000	01?01		
00000	00000						
<i>reevesii</i>							
00101	10000	00000	10000	00010	10110		
00110	00000	00000	00aa0	33000	00001		
00000	00000						
<i>reticularia</i>							
00000	10000	000?0	00000	10000	00000		
00000	00000	00000	010a0	34000	22200		
10000	00001						
<i>scripta</i>							
00001	10000	00010	10000	10000	00101		
10000	00000	00000	00000	34000	22200		
00000	0000a						
<i>sinensis</i>							
00001	00000	00010	10001	10010	00001		
00000	00000	00000	00aa0	33000	00001		
00000	00000						
<i>spengleri</i>							
000a0	00000	00100	10100	00010	00000		
00011	01100	00000	00000	34000	00001		
00000	00010						
<i>subtrijuga</i>							
00100	01100	11000	10000	01010	10100		
00110	00g00	00000	00a10	33000	00000		
00000	00000						
<i>tentoria</i>							
00001	00000	00010	10001	00010	10001		
10100	10000	01000	10110	43000	00000		
00000	0000?						
<i>terrapin</i>							
00001	10000	00010	10000	a0000	10100		
00000	00000	00000	0a000	34000	ed200		
00000	00001						
<i>texana</i>							
00001	10000	0a010	10000	a0000	00101		
10000	00000	00000	00000	34000	22200		
00000	0000a						
<i>thurjii</i>							
00001	00000	00010	10001	00000	01011		
11100	00000	00100	00110	43000	00000		
00000	00001						
<i>tornieri</i>							
11010	00000	000?1	11000	00111	00001		
00000	0??00	00000	00020	22000	2220a		