

The Phylogenetic Position of the Recently Rediscovered Philippine Forest Turtle (Bataguridae: *Heosemys leytensis*)

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The Philippine forest turtle (*Heosemys leytensis*) is one of the least-known Asian turtles. Until recently it was only known from a single specimen, the neotype (CAS 60930). The rediscovery of this enigmatic turtle in the wild provides access to fresh genetic material, allowing us to rigorously test its phylogenetic position among Asian pond and wood turtles of the clade Bataguridae for the first time. We sequenced 1174 bp of mitochondrial DNA (*cytb*) and 1076 bp of nuclear DNA (R35 intron) from a newly acquired specimen of *H. leytensis* (PNM 8488) and compared our sequences to a previously published genetic survey of batagurids. Our main goal is to determine if *H. leytensis* is closely related to other species of *Heosemys* (*H. spinosa* [type species], *H. grandis*, *H. depressa*, and *H. annandalii* [comb. nov.]). Parsimony and likelihood analyses of mitochondrial and nuclear DNA data strongly support *H. leytensis* as the sister taxon to the Southeast Asian species *Siebenrockiella crassicollis* (commonly known as the ‘black marsh turtle’ or ‘smiling terrapin’). The close relationship between *H. leytensis* and *S. crassicollis* is a novel hypothesis, although both share an easily recognizable diagnostic feature: vertebrals 2–4 are mushroom-shaped or ‘ginkgo leaf’-shaped. In order to eliminate two potentially monotypic genera, the genus *Siebenrockiella* is phylogenetically defined to accommodate the close relationship between *S. crassicollis* and *H. leytensis* whereas a new name, *Panyaenemys*, is defined for the distinct *H. leytensis* stem lineage.

The rediscovery of wild populations of the Philippine forest turtle (*Heosemys leytensis* Taylor 1920; Fig. 1B-E) in the Palawan island group of the western Philippines (Fig. 1A; Diesmos et al. 2004a), resolved a decades-long search for this species. Prior to this, our knowledge of *H. leytensis* was restricted to the original published description (the type series was lost in the destruction of the Bureau of Science, predecessor to the National Museum of the Philippines, during World War II; Brown and Alcala 1978; Buskirk 1989), one museum specimen (CAS 60930, the neotype, Fig. 1B,C) reported by Buskirk (1989), and one specimen from Palawan (UF/FSM 67515) reported by Timmerman and Auth (1988). Thus, for over forty years, no museum specimens of *H. leytensis*

sis were known and so it remained one of the least-known Asian turtles.

The rediscovery of *H. leytensis* in the wild (Diesmos et al. 2004a) provides access to fresh genetic material, allowing us to rigorously test its phylogenetic position within the 'Asian pond and wood turtles' (Bataguridae Gray, 1870 = 'Geoemydidae Theobald, 1868'; Joyce et al. 2004) for the first time. Batagurids are a species-rich group (60+ spp.) of highly threatened (van Dijk et al. 2000), but poorly studied non-marine turtles from Asia. A taxonomic reassessment of *H. leytensis* is necessary because the content and diagnosis of batagurid genera have changed dramatically since Taylor (1920) described the Philippine forest turtle as *Heosemys leytensis* (e.g., Ernst and Barbour 1989; Iverson 1992). The twelve characters that Taylor (1920) used to diagnose *Heosemys* are now known to be either plesiomorphic for batagurids or else appear in other genera as homoplasy (Joyce and Bell 2004). One of these characters, the derived absence of a temporal arch in the skull, has played a particularly important role in maintaining *H. leytensis* in the genus *Heosemys*. Besides being noted by Taylor (1920), this character was later used by McDowell (1964) to diagnose *Heosemys* (including *H. leytensis*) and was also described in the *H. leytensis* neotype (Buskirk 1989). This character is also known in *Hieremys annandalii* (Boulenger, 1903) as well as some species of testudinoid box turtles from China and North America (*Cuora* Gray, 1855 and *Terrapene* Merrem, 1820; Zangerl 1948; McDowell 1964; Joyce and Bell 2004). Because *H. leytensis* lacks the characteristic hinged plastron of a box turtle, its referral to *Heosemys* seems logical.

Although *H. leytensis* shares the absence of the temporal arch with other *Heosemys*, it is morphologically divergent from other *Heosemys* in other respects. For example, *H. leytensis* usually has mushroom-shaped or 'ginkgo leaf'-shaped vertebral scales 2–4 (Fig. 1B, E), a feature that is otherwise restricted to the 'smiling terrapin' of southeast Asia, *Siebenrockiella crassicollis* (Gray 1831) (Fig. 1F–G). Additionally, the projecting gular region (anterior region of the plastron) of *H. leytensis* clearly distinguishes it from all other batagurid lineages, including other species referred to *Heosemys*. In this character, it superficially resembles some species of terrestrial tortoises (Testudinidae Gray, 1825), the sister-taxon to batagurids (Spinks et al. 2004).

Given the extensive homoplasy within batagurid morphology (Joyce and Bell 2004) and the overall distinctiveness of *H. leytensis*, it is difficult to confidently place *H. leytensis* into any existing genus on morphological grounds alone. Moreover, weak nodes generated from cladistic analyses of morphological variation in Bataguridae (Hirayama 1985; McCord et al. 1995) are strongly rejected by molecular studies (McCord et al. 2000; Spinks et al. 2004). For this reason, we tested the phylogenetic position of *H. leytensis* with cladistic analyses of mitochondrial and nuclear DNA sequences.

Our primary goal was to determine whether *H. leytensis* should continue to be recognized as a member of the genus *Heosemys*. But in order to avoid confusion, we must establish an explicit concept of *Heosemys* and what species names this informal clade name should include. Spinks et al. (2004) reported DNA sequences from three species of *Heosemys* including one sample attributed to the type species *Heosemys spinosa* (Gray, 1831). According to their study, *Heosemys* form a well-supported clade with *Hieremys annandalii*, and so Spinks et al. (2004) raised the possibility that *H. annandalii* might be better placed within an expanded *Heosemys*. However, Spinks et al. (2004) refrained from making a taxonomic change pending future evidence for the possible placement of *Hieremys annandalii* relative to *Heosemys* species. We think this reticence is unwarranted inasmuch as *Hieremys* Smith, 1916 is a monotypic genus and *H. annandalii* forms a well-supported clade with other *Heosemys*. The Spinks et al. (2004) suggestion to expand the older genus name (*Heosemys*) to the well-supported node creates a much more stable taxonomy. Under this scheme, the widely-used genus name will remain stable regardless of the ultimate resolution of the position within the *Heosemys* basal polytomy. We refer *Hieremys annandalii* to the genus *Heosemys*, but

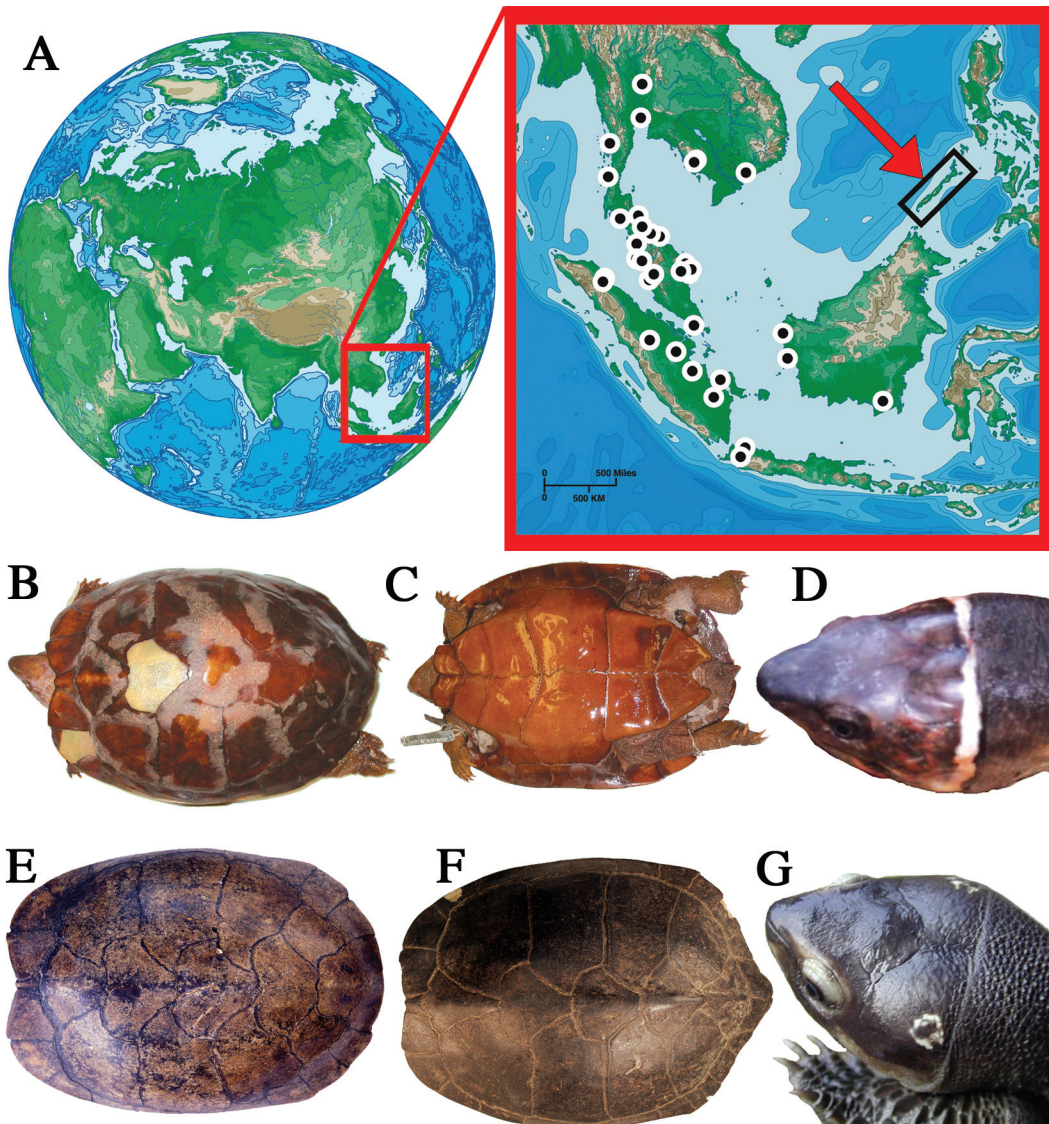


FIGURE 1. A: Map showing the known distribution of *Siebenrockiella crassicollis* (dots) based on Iverson (1992) and Stuart and Platt (2004). The black rectangle includes the known and hypothesized range of *Heosemys leytensis* based on Diesmos et al. (2004b); B-C: Neotype specimen of *Heosemys leytensis* (CAS 60930), dorsal [note the missing 'ginkgo leaf'-shaped vertebral 2] (B) and ventral view (C); D: Dorsal view of *H. leytensis* head showing diagnostic markings; E: Dorsal view of *H. leytensis* possibly from Dumaran Island (see Diesmos et al., 2004a); F: Dorsal view of *S. crassicollis* (FMNH 224070); G: View of *S. crassicollis* head showing the diagnostic markings.

refrain from defining the genus *Heosemys* phylogenetically until we discuss our results, especially regarding the placement of *H. leytensis*. In summary, our concept of *Heosemys* is the clade that includes the type species *Heosemys spinosa*, the aforementioned *Heosemys* [orig. *Cyclemys*] *annandalii* (Boulenger, 1903) comb. nov., *Heosemys grandis* (Gray, 1860), and *Heosemys depressa* (Anderson, 1875).

INSTITUTIONAL ABBREVIATIONS.— CAS, The California Academy of Sciences, San Francisco,

California, USA; FMNH, The Field Museum of Natural History, Chicago, Illinois, USA; PNM, National Museum of the Philippines, Manila, Philippines; UF, Florida Museum of Natural History, University of Florida, Gainesville, Florida.

MATERIALS AND METHODS

Ethanol-preserved muscle was taken from a museum specimen of *Heosemys leytensis* (PNM 8488, see Material Examined). Total genomic DNA was extracted from the muscle using PureGene Animal Tissue DNA Isolation Protocol (Gentra Systems, Inc.). Primers for amplifying and sequencing parts of *cytb* and tRNA-Thr (collectively 'cytb') were taken from Spinks et al. (2004) and R35 primers were taken from Fujita et al. (2004). PCR products were electrophoresed in a 1% low melt agarose TALE gel stained with ethidium bromide and visualized under ultraviolet light. The bands containing DNA were excised and agarose was digested from bands using GELase (Epicentre Technologies). PCR products were sequenced in both directions by direct double-strand cycle sequencing using Big Dye version 3.1 chemistry (Perkin Elmer). Cycle-sequencing products were precipitated with ethanol, 3 M sodium acetate, and 125 mM EDTA, and sequenced with a 3730 DNA Analyzer (ABI). Sequences were edited and protein-coding regions were translated into amino acids with Sequencher version 4.1 (Genecodes).

We compared new *cytb* and R35 sequences with the sequences reported by Spinks et al. (2004). Sequences were aligned by eye into the matrix used by Spinks et al. (2004) and deposited into TreeBASE (www.treebase.org, accession number S1002). Our sequences (*cytb*, 1174 bp; R35, 1076 and 1078 bp) were longer than those used in the Spinks et al. (2004) alignment; the extra base pairs were excluded from the analysis. For the parsimony analysis of combined data sets, we included 72 of the 79 taxa sequenced by Spinks et al. (2004), excluding seven putative hybrids. Some of these hybrids were described as new species from pet trade samples leading to taxonomic confusion that is not yet fully resolved (Parham et al. 2001; Wink et al. 2001; Spinks et al. 2004). We avoid these issues by removing the suspect taxa from consideration. We feel that we are justified in doing this because an initial phylogenetic analysis (not shown) demonstrated that *H. leytensis* is not closely related to any of these taxa and the inclusion or exclusion of these sequences does not affect the phylogenetic position of *H. leytensis*. Besides *H. leytensis*, the only addition to the Spinks et al. (2004) data set was the sequence of one vouchered *Siebenrockiella crassicollis* sample from Cambodia (see below).

In addition to the aforementioned combined analysis, we analyzed the mitochondrial and nuclear data sets separately in order to compare the potential congruence or conflict in the phylogenetic signal of our markers. We also performed a maximum likelihood and Bayesian analyses on a restricted data set that includes 28 of the 79 species from Spinks et al. (2004). These 28 sequences represent all the non-hybrid taxa from the Spinks et al. (2004) study that have both *cytb* and R35 sequenced. The restricted data set is still appropriate for placing *H. leytensis* because it contains every major lineage (i.e., genus) of batagurid.

Parsimony analyses were performed using the 1000 random addition-sequence replicates of the heuristic search algorithm in PAUP*4.0b10 (Swofford 2002). Support for the parsimony analyses was determined using bootstrap and decay indices. For the combined analysis, we used 1000 bootstrap replicates with 10 random addition-sequence replicates each. Decay indices were calculated using a PAUP command file generated by MacClade 4.0 (Maddison and Maddison 2000). For the likelihood analyses, we used hierarchical likelihood-ratio tests with ModelTest (Posada and Crandall 1998) to determine which model was appropriate. For the standard likelihood analysis the model GTR+I+G was selected, with proportion of invariable sites 0.3836, gamma distribution

shape parameter 0.4762, and base frequencies as A=0.3198, C=0.3039, G=0.1336, and T=0.2427. Maximum likelihood analyses were performed with 100 random addition replicates with stepwise addition of taxa using the heuristic search algorithm and TBR branch swapping. For the Bayesian analysis, we separated the *cytb* and R35 data into their own partitions and estimated the best models for each (GTR+I+G and HKY respectively). Using these parameters, we performed three mixed-model analyses of five million generations and four chains each using MrBayes v3.0b4 (Huelsenbeck and Ronquist 2001). We plotted the log likelihood scores against generation to determine when the analysis achieved stationarity for each analysis. In each case, the seven thousand trees recovered prior to stationarity were discarded as ‘burn in’ and a 50% majority rule consensus was used to determine the posterior probabilities for each clade.

RESULTS

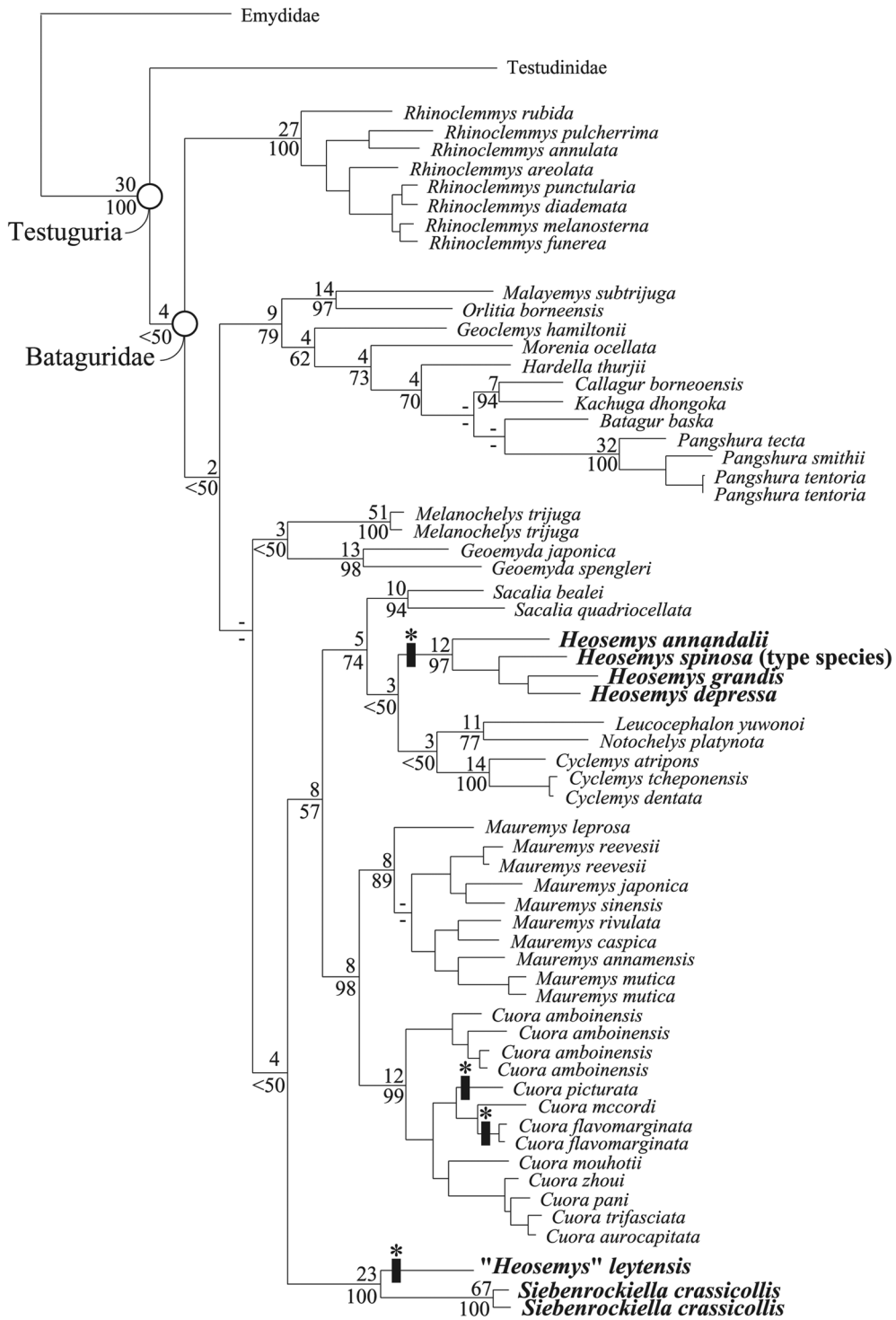
In our initial analyses, the sequence from our sample of *H. leytensis* is consistently placed as the sister taxon to *S. crassicolis* with high statistical support. None of the samples from the Spinks et al. (2004) study have vouchered specimens, so we confirmed our initial results by sequencing a vouchered specimen of *S. crassicolis* from Cambodia (see Material Examined). All tree statistics were calculated with the additional sample included. All analyses (parsimony, likelihood, Bayesian) place *H. leytensis* and *S. crassicolis* as sister taxa (Fig. 2). In the parsimony and Bayesian analyses, *H. leytensis* and *S. crassicolis* are united with high statistical support (100% parsimony bootstrap, 23 decay index, 100% Bayesian posterior probability). Parsimony analyses of the separate *cytb* and R35 data sets (not shown) show that the *H. leytensis* + *S. crassicolis* clade is independently supported by our mitochondrial and nuclear markers. Meanwhile, the other species of the genus *Heosemys* form a well-supported clade that is separated from *H. leytensis* + *S. crassicolis* clade by several branches (Fig. 2).

DISCUSSION

Our study demonstrates that the continued placement of *H. leytensis* in the genus *Heosemys* is no longer tenable. Inasmuch as the other species of *Heosemys* form a well-supported clade, which is readily-diagnosable with molecular and morphological data, we phylogenetically define the genus *Heosemys* as the crown clade arising from the last common ancestor of *Heosemys* [orig. *Emys*] *spinosa* (Gray, 1831), *Heosemys* [orig. *Geoemyda*] *grandis* (Gray, 1860), *Heosemys* [orig. *Geoemyda*] *depressa* (Anderson, 1875), and *Heosemys* [orig. *Cyclemys*] *annandalii* (Boulenger, 1903).

The hypothesis that *H. leytensis* and *S. crassicolis* are sister taxa within Bataguridae is a novel result. Both *H. leytensis* and *S. crassicolis* share two diagnostic characters that may have been inherited from a common ancestor: 1) Vertebrae 2–4 are ‘ginkgo leaf’-shaped. *Orlitia borneensis* Gray 1873 has a superficially similar condition, but it is restricted to the first vertebral; 2) Light spots or lines in the posterior dorsal region of the head. In *S. crassicolis* (Fig. 1G), this character occurs as two circles or spots that may fade with age (Lim and Das 1999) whereas in *H. leytensis* (1C) it is a straight line that is faint or absent in 35% of individuals (Diesmos et al. 2004a, b). A similar, but more dramatic, condition of posterior head marking occurs in parallel in the ‘eyed turtles’ of the genus *Sacalia* Gray 1870.

Additional morphological comparisons of *S. crassicolis* and *H. leytensis*, including skeletal material, may reveal more potential synapomorphies. Meanwhile, the character that has long been used to place *H. leytensis* in the genus *Heosemys*, the absence of a complete temporal arch, is more



50 changes

homoplastic than previously thought. If this character is optimized onto the phylogeny (Fig. 2), it predicts that the temporal arch was lost at least three independent times within Bataguridae: once in the *H. leytensis* stem-lineage, once in the in the *Heosemys* stem lineage, and at least once within *Cuora*. A polytomy at the base of *Cuora* (e.g., Spinks et al., 2004; Parham et al., 2004) and a poor understanding of the morphological variation in extent of the temporal arch (see Joyce and Bell 2004) preclude a definitive assessment of the polarity of this character within *Cuora*.

From a biogeographic perspective, the *S. crassicolis* + *H. leytensis* clade seems plausible. *Heosemys leytensis* is known only from the Palawan Pleistocene Aggregate Island Complex (or Palawan PAIC; Brown and Diesmos 2001). Although the Palawan region contains a significant level of endemism in fauna and flora not found in the Sundaic region (see Widmann 1998, McGuire and Alcalá 2000, Brown and Guttman 2002, Evans et al. 2004), in general the fauna of the Palawan PAIC has a much closer affinity to the Islands of the Sunda Shelf (e.g., Kalimantan/'Borneo', Madura, Sumatra) than do the other Philippine islands (Heaney 1986; Brown and Diesmos 2001).

Therefore, the close relationship of *H. leytensis* to a Sunda Shelf species (*S. crassicolis*) is not surprising. The combined distribution of the *S. crassicolis*+*H. leytensis* clade (Fig. 1A) is very similar to that of *Cyclemys dentata* (Gray 1831) and *Cuora amboinensis* (Daudin 1802), the two other turtle species known from Palawan PAIC (Iverson 1992). Their shared distributions may indicate that these three lineages may have a shared biogeographical history as well, the details of which could be compared through additional DNA sequencing of *S. crassicolis*, *Cu. amboinensis* and *Cy. dentata* from throughout their range.

Given the strong phylogenetic signal placing it as the sister taxon to *S. crassicolis*, we feel justified in referring *H. leytensis* to a phylogenetically defined *Siebenrockiella* Lindholm 1929. By using the genus name *Siebenrockiella* to highlight this close relationship, we eliminate two monotypic genera (*Siebenrockiella* and a hypothetical new genus for *H. leytensis*) from a literature that is lamentably crowded with monotypic genera (Spinks et al. 2004). Polytypic genera are functionally superior to monotypic genera because they maximize the information content in each widely-used name (Parham and Feldman 2002; Feldman and Parham 2004). With this in mind, we phylogenetically define *Siebenrockiella* as the crown clade arising from the last common ancestor of *Siebenrockiella* [orig. *Emys*] *crassicolis* (Gray 1831) and *Siebenrockiella* [orig. *Heosemys*] *leytensis* (Taylor 1920) (comb. nov.).

In addition to developing a conservative nomenclature for the widely-used genus name, we also want to name the stem-lineage that includes the morphologically and molecularly divergent *S. leytensis*. For example, compared to *S. crassicolis*, *S. leytensis* has a proportionately larger head and correspondent nuchal emargination, is larger in overall body size, and has an extremely protruding gular region of the plastron (Diesmos et al. 2004b). The morphological distinctiveness of the two known *Siebenrockiella* species is demonstrated by the fact that no author has ever suggested a close relationship between them until now. Moreover, the genetic distinctiveness of the *S. leytensis* lineage is shown by a high sequence divergence from *S. crassicolis* (~13% *cytb*) that is greater than that shown by other batagurid congeners (5.0-10.7%, see Spinks et al. 2004). In order

FIGURE 2 (left). Parsimony phylogram of one of the four most parsimonious trees (4387 steps) recovered by the parsimony analysis of the combined *cytb* and R35 data set for batagurid turtles. For taxonomy of suprageneric clades see Joyce et al. (2004). The four equally parsimonious results differ in the placement of species within the genus *Mauremys* or between suprageneric genera not related to *Heosemys* or *Siebenrockiella*. Nodes that are not supported in all of the four equally parsimonious trees are indicated by '-' on either side of the stem. The numbers at each of the other nodes represent support values. The top numbers are decay indices and the bottom numbers are parsimony bootstrap percentages. Support values for species clades within genera are not shown but see Spinks et al. (2004). The batagurid lineages that lose a complete temporal arch are shown by '*-*

to provide a name for this distinct lineage that is divorced from the vagaries of species concepts, we name a new subgenus, *Panyaenemys*, for *S. leytensis*.

SYSTEMATICS

Panyaenemys, new clade name, new subgenus

TYPE SPECIES: *Siebenrockiella leytensis* (Taylor, 1920) comb. nov.

We designate a type species for this phylogenetically defined clade name so that it is valid under the rules of the International Code of Zoological Nomenclature (1999).

ETYMOLOGY.— *Panyaen-*, from the word ‘panya-en’ which means ‘enchanted’ in the language of the Pala’wan (one of seven ethnic groups that inhabit the Palawan islands). A resident of Palawan interviewed by ACD during forest surveys in November, 2003 referred to a *S. leytensis* as a ‘panya-en’, because it is apparently a favorite pet of forest spirits; *-emys*, turtle.

PHYLOGENETIC DEFINITION.— We define *Panyaenemys* as the most inclusive clade containing *Siebenrockiella* [orig. *Heosemys*] *leytensis* (Taylor 1920) but not *Siebenrockiella* [orig. *Emys*] *crassicollis* (Gray 1831).

DIFFERENTIAL DIAGNOSIS.— The sole known member of the subgenus *Panyaenemys* can be distinguished from all other turtles by the combination of the following four characters: 1) Strongly projecting epiplastra; 2) ‘Ginkgo leaf’-shaped vertebral scales 2-4; 3) No temporal arch in the skull; 4) Light lines on the back of the head.

MATERIAL EXAMINED

HEOSEMYS LEYTENSIS.— PHILIPPINES: CAS 60930, the neotype specimen discussed in detail by Buskirk (1989) and Diesmos et al. (2004a); PHILIPPINES: PNM 8488, GenBank accession numbers = AY954911 (*cytb*) and AY954914 (R35), a dead specimen that was donated to the National Museum of the Philippines (PNM) by a wildlife collector in 2003 and examined by Diesmos et al. (2004b). The specimen was apparently bought from a wildlife trader from Palawan. An additional 47 live specimens of *H. leytensis* in captivity were examined by Diesmos et al. (2004b) comprised of 34 turtles on Palawan being held by a private collector and 13 government-confiscated turtles housed at the Wildlife Rescue Center of the Protected Areas and Wildlife Bureau, Quezon City, Philippines.

SIEBENROCKIELLA CRASSICOLLIS.— CAMBODIA: FMNH 259055 (see Stuart and Platt 2004), GenBank accession numbers = AY954912 (*cytb*) and AY954913 (R35), Koh Kong Province, Sre Ambel District, Prek Kroch River (tributary of Sre Ambel River), 11°06’20”N 103°39’35”E, <10 m elevation, in a flooded paddy at edge of mangrove and *Melaleuca* forest, captured by a fisherman in bamboo fish trap set at that location, 27 August 2000, B.L. Stuart and S.G. Platt; UNCERTAIN/MALAYSIA?: FMNH 224070, Perak, Batu Gajah, purchased in a pet shop, 19 November 1975, E.O. Moll.

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