

A NEW GENUS OF GEOEMYDID TURTLE FROM ASIA

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(with one text-figure)

ABSTRACT.— Phylogenetic analysis of mitochondrial gene sequence variation in geoemydid turtles suggests that the genus *Geoemyda* as currently recognized is polyphyletic, and that *Geoemyda yuwonoi* is the sister taxon to *Notochelys platynota* (but the two are highly genetically divergent). We herein place *Geoemyda yuwonoi* in a new monotypic genus, *Leucocephalon*, distinguished by its maxillary contact, its lack of a quadratojugal, its large anterior plastral butresses, its humeropectoral seam posterior to the entoplastron, its long interanal seam, its primarily posteriorly directed neurals (distinctly configured), and its lack of a plastral hinge.

KEY WORDS.— *Geoemyda*, *Heosemys*, *Leucocephalon*, *Notochelys*, turtle, genus, Geoemydidae, systematics.

INTRODUCTION

Although known in the pet trade for at least a decade, the distinctive Sulawesi Forest Turtle was formally described as *Geoemyda yuwonoi* by McCord et al. in 1995 based on specimens purchased from local people by Frank Yuwono in Gorontalo, northern Sulawesi (Indonesia). Subsequent to the original description, Yuwono's supplier on Sulawesi provided additional information which suggested that the type series apparently came from the area of Marisa (00° 14' N; 120° 10' E) (Fritz and Obst, 1999; Yuwono, pers. Comm. to McCord, 2 August 2000). In any case, the natural occurrence of the species on northern Sulawesi was subsequently confirmed by Platt (1998), who field-collected specimens in a tributary creek of the Kanggol River (0° 35' N; 121° 02' E), 225 km west of the type locality and 225 km north of the second purchase site (Poso) reported by McCord et al. (1995).

McCord et al. (1995) performed a cladistic analysis of morphological characters for their new species along with those for taxa suspected to be closely related (*Cyclemys*, *Pyxidea*, and all forms placed in either *Geoemyda* or *Heosemys*).

That analysis suggested that *yuwonoi* was a member of a clade including *Geoemyda spengleri*, *G. japonica*, *G. depressa*, *G. silvatica*, and *G. leytenensis* (the last three of which have sometimes been included in the genus *Heosemys*; see reviews in Iverson, 1992), and that *Heosemys spinosa* (the type species of the genus) and *H. grandis* belonged to a separate clade. Based on this cladogram McCord et al. (1995) recommended that *yuwonoi* and the other members of its clade (except *Pyxidea*) be included in the genus *Geoemyda* until a more complete phylogenetic analysis of the Geoemydidae (sensu Bour and Dubois, in David 1994; formerly the Bataguridae) could be undertaken. However, Fritz and Obst (1996) described two additional specimens of *Geoemyda yuwonoi*, rejected the cladistic analysis in McCord et al. (1995) because it included characters prone to homoplasy, stressed the similarity between *yuwonoi* and *depressa*, and placed *yuwonoi* (and *depressa*) in the genus *Heosemys* (though without diagnosis).

Clearly there has been no consensus on the taxonomic or phylogenetic status of this com-

plex of turtles. To settle this controversy, we have been accumulating tissues from geoemydid turtles since 1991 with the vision of one day providing a phylogenetic analysis of the entire family based on mitochondrial DNA sequence variation. Sequencing of the cytochrome *b* gene for all genera and 55 of the recognized species in the family has now been completed (Spinks, Shaffer, Iverson, and McCord, unpublished), and our results suggest that the genus *Geoemyda* as defined by McCord et al. (1995) is polyphyletic (Fig. 1). Furthermore, the Sulawesi Forest Turtle is so distinctive morphologically and genetically that we here describe a new genus for this taxon.

METHODS

We obtained blood and tissue samples for 83 specimens of geoemydid turtles (representing all recognized genera, 55 recognized species, and several anomalous, undescribed, and distinctive pet trade specimens) from the collection of William P. McCord (WPM). A tissue sample from the primitive tortoise *Manouria emys* provided by P. Vander Schow served as the outgroup. Whole genomic DNA was extracted from blood or muscle tissue via SDS/protease K digestion followed by phenol/chloroform extraction (Shaffer et al., 1997). Specific regions of the mitochondrial cytochrome *b* gene were amplified using Taq-mediated PCR and sequenced on an ABI 377 automated sequencer (Applied Biosystems) using primers developed from a subset of geoemydid taxa (available from the authors on request). In order to confirm the sequences, we sequenced each species in both directions. For sequences from individual species, overlapping sequences were aligned and edited using SeqEd (Applied Biosystems, Foster City, CA) and then the complete sequences of all individuals were aligned using ClustalW (Thompson et al., 1994). All sequences will be deposited in Genbank. Alignments were unambiguous, with no insertions or deletions detected.

RESULTS AND DISCUSSION

Our final data set consisted of 968 to 1139 nucleotides of the cytochrome *b* gene encompass-

ing 85% to 100% of the gene. 521 nucleotide sites were parsimony-informative, 92 variable sites were parsimony-uninformative and 526 sites were constant across all taxa. Phylogenetic analyses were conducted under parsimony, using PAUP* 4.0b3a (provided by David L. Swofford) and, to assess statistical reliability, we bootstrapped our data set 100 times (Felsenstein, 1985). All characters were equally weighted and a heuristic search produced 126 equally parsimonious trees that were combined into a 50% majority rule consensus tree. The complete results of our phylogenetic analysis will be published separately; we here present only that part of the consensus tree relevant to the systematic position of *yuwonoi* (Fig. 1). Our phylogenetic analysis leaves little doubt that 1) the Sulawesi Forest Turtle is not closely related to other species currently or previously included in *Geoemyda* or *Heosemys* (genetic distance > 12%; Table 1), 2) it is most closely related to *Notochelys platynota* (though still 12% distant), 3) the genus *Geoemyda* should be restricted to *G. spengleri* (the type species) and *G. japonica*, and 4) in order to avoid paraphyly, *Hieremys annandalei* should perhaps be included in the genus *Heosemys* (as suggested earlier by Williams (in Loveridge and Williams, 1957), although that change should probably await a reexamination of the morphology. Unfortunately, we still lack sequence data for "*Geoemyda*" *leytensis* and "*G.*" *silvatica*, and thus their generic placement is uncertain. We therefore recommend that they tentatively be placed in the genus *Heosemys* as recommended by some (but not all) previous authors (review in Iverson, 1992).

SYSTEMATICS

LEUCOCEPHALON NEW GENUS SULAWESI FOREST TURTLES

Geoemyda Gray 1834 (in part; see McCord et al., 1995).

Heosemys Stejneger 1902 (in part; see Fritz and Obst, 1996).

Type species. - *Geoemyda yuwonoi* McCord, Iverson & Boeadi, 1995.

Diagnosis. - A genus of geoemydid turtle that is distinguished by having the maxillae in con-

TABLE 1: Relevant portion of uncorrected ("p") distance matrix for 83 geoemydids representing at least 55 species.

	Gj	Gs	Np	Ly	Ha	Hs	Hd
<i>Geoemyda japonica</i>	—						
<i>Geoemyda spengleri</i>	0.106	—					
<i>Notochelys platynota</i>	0.153	0.151	—				
<i>Leucocephalon yuwonoi</i>	0.157	0.152	0.123	—			
<i>Hieremys annandalii</i>	0.138	0.132	0.139	0.128	—		
<i>Heosemys spinosa</i>	0.137	0.140	0.133	0.134	0.097	—	
<i>Heosemys depressa</i>	0.149	0.141	0.133	0.133	0.091	0.090	—
<i>Heosemys grandis</i>	0.138	0.145	0.132	0.135	0.089	0.100	0.078
(3 specimens)	-0.143	-0.154	-0.147	-0.145	-0.095	-0.113	-0.084

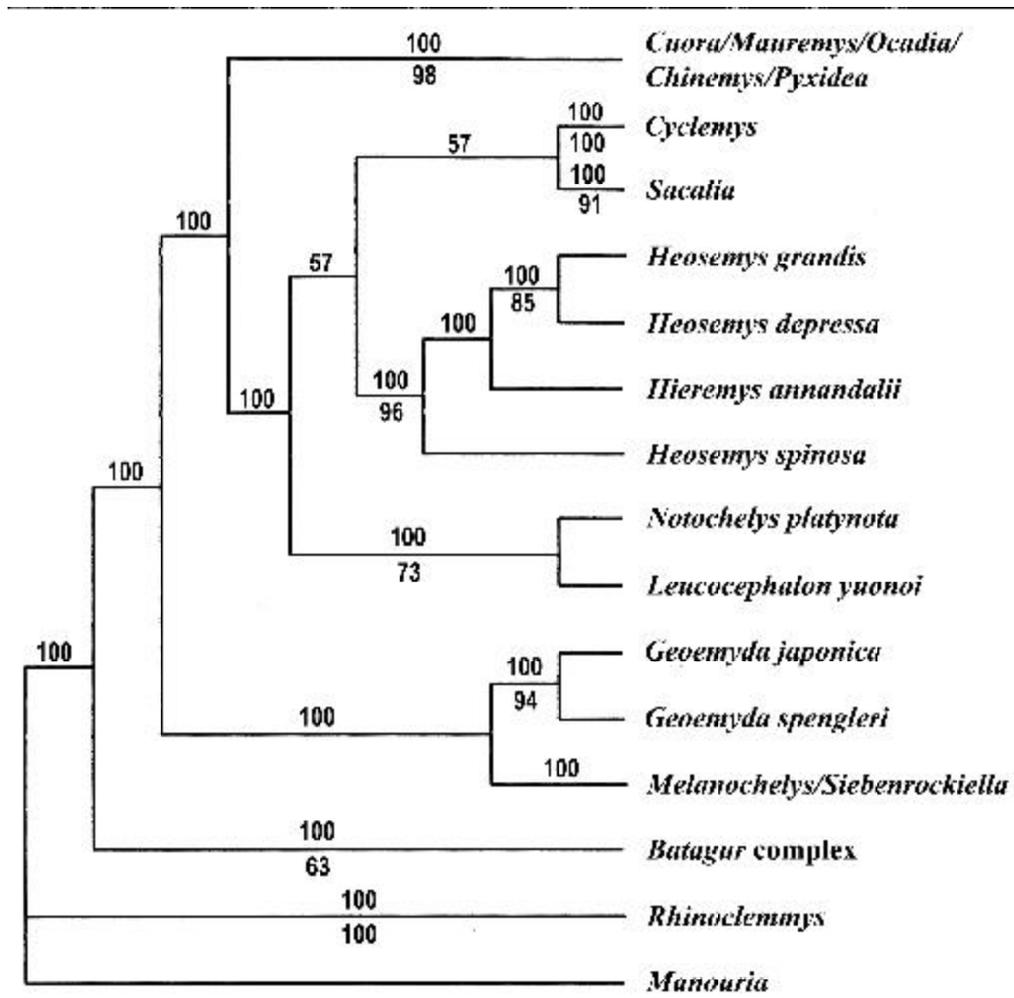


FIGURE 1: Majority rule consensus tree of relationships within the Geoemydidae as determined from parsimony analysis of mitochondrial DNA sequence data. Full cladogram (3457 steps; CI = 0.26) for 83 geoemydid specimens and one tortoise has been collapsed to focus on the genera most closely allied to *Leucocephalon yuwonoi*. Numbers above nodes are percent of shortest trees with this topology; numbers below nodes are percent bootstrap support (> 50%).

tact anteriorly (as in *Geoemyda* as defined here; separated by the premaxilla in *Notochelys* and all *Heosemys* but *H. silvatica*), lacking a quadratojugal (as in *Heosemys*; present in *Geoemyda* and *Notochelys*, though weakly attached in the latter; see McDowell 1964), having no plastral hinge in the adult (as in *Geoemyda* and *Heosemys*; a hinge between the hyo- and hypoplastron in *Notochelys*), having a solid bony bridge (as in *Geoemyda* and *Heosemys*; ligamentous in *Notochelys*), having large anterior plastral buttresses (almost no anterior buttresses in *Notochelys*; although both possess well-developed posterior buttresses, contrary to McDowell, 1964), having the plastral plane well below the plane of the margin of the carapace (as in *Geoemyda* and *Heosemys*; nearly in the same plane in *Notochelys*), having the humeropectoral seam posterior to entoplastron (the seam crossing the entoplastron in *Geoemyda*, *Notochelys*, and all *Heosemys* but *H. silvatica*), having the interanal seam (typically) as the longest plastral midline seam (the interabdominal seam is typically longest in *Notochelys*, *Heosemys*, and *Geoemyda*), having eight neural bones (nine in *Notochelys*) with the first five posteriorly directed and six-sided and the eighth anteriorly directed and six-sided (the first quadrangular, the second through seventh anteriorly directed and six-sided, and the eighth posteriorly directed and six-sided in *Notochelys*).

Description: McCord et al. (1995) provided a full description of the species, including additional external morphological characters that diagnose the species, and hence, the genus. Table 1 in that publication also reviewed the morphological characters of each of the species currently or previously included in *Geoemyda* or *Heosemys*.

Content.- Includes only *Leucocephalon yuwonoi*.

Distribution and biogeography.- *Leucocephalon yuwonoi* is known only from northern Sulawesi, Indonesia, and is one of only two geoemydid turtles known east of Wallace's Line (Iverson, 1992). Its sister taxon, *Notochelys platynota*, occupies a complementary range on the larger Indonesian islands to the west (as well as on the main land), suggesting a vicariant event.

The close geological and zoogeographic affinity of northern Sulawesi and Borneo (Audley-Charles et al., 1972; Auffenberg, 1980; Yoshii and Greenslade, 1993) also argues that *L. yuwonoi* evolved in isolation from the common ancestor of *Notochelys* and *Leucocephalon*.

Etymology.- From the Greek *leukos*, meaning white, and *kephale*, meaning head, referring to the sexually dimorphic white markings on the head of this species, which are more extensive and reach to the dorsum of the head in males.

Skeletal material examined.- *Leucocephalon yuwonoi*: PCHP 4984, 4669, 4949, 4657; UF 97335, 109835. *Notochelys platynota*: JBI uncatalogued (one specimen); PCHP 3649-50, 4594, 4698, 4939-40, 4961, uncatalogued (one specimen). Note that whole animals in this study include those recorded in McCord et al. (1995) and Iverson and McCord (1997), as well as 20 *Leucocephalon* and six *Notochelys* alive in the collection of WPM.

ACKNOWLEDGEMENTS

Wayne King and Kenney Krusko (UF; Florida Museum of Natural History, Gainesville), and Peter Pritchard and Richard Cripps (PCHP; Chelonian Research Institute, Oviedo, Florida) allowed JBI access to their respective collections. Patrick Baker facilitated the examination of material in McCord's (WPM) collection. Paul Vander Schow provided tissues from *Manouria*.

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Received: 17 April 2000.

Accepted: 26 August 2000.