

Geoemyda silvatica, an enigmatic turtle of the Geoemydidae (Reptilia: Testudines), represents a distinct genus

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Abstract

The systematic position of the rare Indian turtle *Geoemyda silvatica* Henderson is examined by a phylogenetic analysis of mtDNA sequence data (cytochrome-*b* gene) of most species of Geoemydidae. *Geoemyda silvatica* represents a basal and isolated taxon within Geoemydidae, definitely not a close relative of any species of *Geoemyda* or *Heosemys*, the genera in which *G. silvatica* has been placed in the past. Therefore, the new genus *Vijayachelys* is proposed for *G. silvatica*. Cranial morphology and some other osteological characters of *Vijayachelys silvatica* are described and illustrated. Differential diagnoses are given for the type species of *Melanochelys* and the respective type species of the superficially similar genera *Geoemyda*, *Heosemys*, and *Leucocephalon*. According to Bayesian analysis of mtDNA data, *Melanochelys trijuga* could be distantly related to *V. silvatica*, whereas the morphological similarity of the other species probably is the result of a similar mode of life. The discovery of the phylogenetically isolated position of *V. silvatica* highlights the importance of the Western Ghats as a biodiversity hotspot rich in higher-level endemics.

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Introduction

One of the least known and most enigmatic chelonian species is the South Indian forest cane turtle, *Geoemyda silvatica*. This species is a representative of the mainly South and Southeast Asian family Geoemydidae (Reptilia: Testudines), and endemic to the Western Ghats Region of the Indian subcontinent (Das 1996). It was

described by Henderson (1912), based on a male and a juvenile collected in 1911 in the Cochin State Forests (Kerala, southern India), and assigned to the genus *Geoemyda* Gray, 1834. At that time, *Geoemyda* was used in a very broad sense for many semiterrestrial or terrestrial testudinoid chelonians from Central and South America as well as from South and Southeast Asia not belonging to the tortoise family Testudinidae.

For more than 70 years no additional individuals of *G. silvatica* became known to science. In an influential, sweeping revision of aquatic testudinoid

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turtles, McDowell (1964) transferred *G. silvatica* from *Geoemyda* to *Heosemys* Stejneger, 1902 without studying any forest cane turtles. In 1982, *G. silvatica* was rediscovered at its type locality (Vijaya 1982a, b, c; Groombridge et al. 1983). Based on one skull and some shells, Moll et al. (1986) provided the first osteological data for the species. A comparison with *Geoemyda spengleri*, *Heosemys grandis*, and *H. spinosa* (the latter being the type species of *Heosemys*) led Moll et al. (1986) to propose transferring *H. silvatica* back to its original genus *Geoemyda*. However, this was not generally accepted, and some authors, e.g. Ernst and Barbour (1989) and Ernst et al. (2000), continued using the combination *H. silvatica*. As the starting point of the present study we chose Moll et al.'s (1986) placement of the species in *Geoemyda*.

Thanks to the investigations by Vijaya (1982a–c), Groombridge et al. (1983), and Moll et al. (1986), we know that *G. silvatica* is a secretive, forest-dwelling, omnivorous chelonian not exceeding approximately 13 cm in shell length. Some general descriptions (e.g. Ernst and Barbour 1989; Ernst et al. 2000) and a few papers dealing with the systematics of *G. silvatica* (McCord et al. 1995; Yasukawa et al. 2001) were based entirely on data published earlier. Based on 22 morphological characters, McCord et al. (1995) considered *G. silvatica* as the sister taxon of their newly described *G. yuwonoi*, a large, forest-dwelling turtle of approximately 25 cm shell length from Sulawesi. Following a phylogenetic analysis of 35 morphological characters, Yasukawa et al. (2001) rejected this hypothesis and regarded *G. silvatica* as the sister taxon to (*Geoemyda spengleri* + *G. japonica*); the combined *Geoemyda* clade was thought to be the sister group of part of what is now considered to be *Cuora* Gray, 1855 (Honda et al. 2002), a morphologically highly distinct genus characterized by a hinged plastron.

Recently, phylogenetic hypotheses for most of the approximately 70 species of the family Geoemydidae were published, based on mtDNA and nDNA data (McCord et al. 2000; Barth et al. 2004; Spinks et al. 2004; Diesmos et al. 2005). *Geoemyda yuwonoi* was shown to represent an ancient, independent evolutionary lineage, and placed in its own genus, *Leucocephalon* McCord et al., 2000. According to those molecular data, *Leucocephalon* constitutes the sister taxon of *Notochelys platynota* (Gray, 1834), and *Cuora* the sister taxon of a clade containing the genera *Chinemys* Smith, 1931, *Mauremys* Gray, 1870, and *Ocadia* Gray, 1870, whereas *Geoemyda* represents a basal taxon of unclear relationships.

Due to its rareness in scientific collections, *G. silvatica* was not included in those investigations. Thus, the contradicting phylogenetic hypotheses for this species have never been tested using genetic data. Here, we provide the first sequence data for the mitochondrial

cytochrome-*b* gene (cyt *b*) from three individuals of *G. silvatica*, compare them with earlier-published cyt *b* sequences for other geoemydid species, and use this data set to test previous hypotheses on the position of *G. silvatica* within Geoemydidae. In addition, we provide a new diagnosis for *G. silvatica*, describe osteological features of this species, and compare them to those of some crucial other geoemydids.

Material and methods

In the past decades, a small number of *G. silvatica* entered the European pet trade, but only few specimens were preserved in scientific collections. With the exception of the specimens described below, we know of only one individual, an adult male, which is now preserved in alcohol at the Zoological Museum Amsterdam (ZMA 12536). During the 1970s, Reiner Praschag, the father of the senior author, bought several forest cane turtles that were traded as pets. One couple of these died recently. They were skeletonized and thigh muscle was extracted for genetic analysis. Small quantities of blood were obtained from a third, live individual by coccygeal vein puncture. Tissue from both dead turtles, and additional blood samples from the third individual, are stored at -70°C in the tissue collection of the Museum of Zoology, Dresden (MTD T 1628, 1630–1631). The skeleton of the male is now kept in the Museum of Zoology (Museum für Tierkunde), Dresden, under MTD 46415; the skeleton of the female in the Museum of Natural History (Naturhistorisches Museum), Vienna, under NMW 37564.

Specimens used for osteological comparisons in the present study were (abbreviations: MTD = Museum für Tierkunde Dresden; NMW = Naturhistorisches Museum Wien; SMF = Senckenberg-Museum Frankfurt; ZMH = Zoologisches Museum Hamburg):

Geoemyda spengleri: NMW 1778, NMW 37279, MTD 40796, MTD 40861, MTD 43000.

Heosemys spinosa: NMW 1201, NMW 1782, NMW 34555, SMF 7670, SMF 7704-7705, SMF 32967-32968, SMF 32996, ZMH R04454.

Leucocephalon yuwonoi: MTD 40171, MTD 41576, MTD 44789, MTD 45153, MTD 45165.

Melanochelys trijuga: NMW 1783, NMW 37159, MTD 40839, MTD 40844.

In the description of craniological characters we follow Gaffney's (1979) terminology. The length of the triturating surface is measured from the median suture between the maxillae or praemaxillae to the suture between maxilla and jugal. The width of the triturating surface is defined as the distance between the labial ridge and the lingual ridge (Gaffney 1979), at mid-length (of the length as defined above).

Table 1. Geoemydid and outgroup taxa, and corresponding GenBank accession numbers

Taxon	Accession number	Source
<i>Batagur baska</i> (Gray, 1830)	AY434600	Spinks et al. (2004)
<i>Callagur borneoensis</i> (Schlegel & Müller, 1844)	AY434601	Spinks et al. (2004)
<i>Chinemys megalcephala</i> Fang, 1934	AJ519499	Barth et al. (2004)
<i>Chinemys nigricans</i> (Gray, 1834)	AJ519500	Barth et al. (2004)
<i>Chinemys reevesii</i> (Gray, 1831)	AJ519497	Barth et al. (2004)
<i>Cuora amboinensis amboinensis</i> (Daudin, 1802)	AJ564447	Barth et al. (2004)
<i>Cuora aurocapitata</i> Luo & Zhong, 1988	AY434626	Spinks et al. (2004)
<i>Cuora flavomarginata</i> “sinensis” (Hsü, 1930)	AY434570	Spinks et al. (2004)
<i>Cuora galbinifrons</i> Bourret, 1939	AJ564448	Barth et al. (2004)
<i>Cuora mccordi</i> Ernst, 1988	AY434568	Spinks et al. (2004)
<i>Cuora mouhotii</i> (Gray, 1862)	AY434604	Spinks et al. (2004)
<i>Cuora pani</i> Song, 1984	AY434574	Spinks et al. (2004)
<i>Cuora picturata</i> Lehr, Obst & Fritz, 1998	AY434576	Spinks et al. (2004)
<i>Cuora trifasciata</i> (Bell, 1825)	AY434627	Spinks et al. (2004)
<i>Cuora zhoui</i> Zhao, Zhou & Ye in Zhao, 1990	AY434584	Spinks et al. (2004)
<i>Cyclemys shanensis</i> Annandale, 1918	AJ604513	Schilde et al. (2004)
<i>Cyclemys</i> sp.	AY434617	Spinks et al. (2004)
<i>Cyclemys</i> sp.	AY434577	Spinks et al. (2004)
<i>Cyclemys</i> sp.	AY434579	Spinks et al. (2004)
<i>Geoclemys hamiltonii</i> (Gray, 1831)	AY434573	Spinks et al. (2004)
<i>Geoemyda japonica</i> Fan, 1931	AY434602	Spinks et al. (2004)
<i>Geoemyda spengleri</i> (Gmelin, 1789)	AJ564449	Barth et al. (2004)
<i>Hardella thurjii</i> (Gray, 1831)	AY434603	Spinks et al. (2004)
<i>Heosemys depressa</i> (Anderson, 1875)	AY434607	Spinks et al. (2004)
<i>Heosemys grandis</i> (Gray, 1860)	AY434566	Spinks et al. (2004)
<i>Heosemys spinosa</i> (Gray, 1831)	AY434578	Spinks et al. (2004)
<i>Hieremys annandalei</i> (Boulenger, 1903)	AJ564451	Barth et al. (2004)
<i>Kachuga dhongoka</i> (Gray, 1834)	AJ564452	Barth et al. (2004)
<i>Leucocephalon yuwonoi</i> (McCord, Iverson & Boeadi, 1995)	AJ564450	Barth et al. (2004)
<i>Malayemys subtrijuga</i> (Schlegel & Müller, 1844)	AJ519502	Barth et al. (2004)
<i>Mauremys annamensis</i> (Siebenrock, 1903)	AJ564456	Barth et al. (2004)
<i>Mauremys caspica caspica</i> (Gmelin, 1774)	AJ564453	Barth et al. (2004)
<i>Mauremys japonica</i> (Temminck & Schlegel, 1835)	AJ564458	Barth et al. (2004)
<i>Mauremys leprosa</i> (Schweigger, 1812)	AJ564457	Barth et al. (2004)
<i>Mauremys mutica mutica</i> (Cantor, 1842)	AJ564459	Barth et al. (2004)
<i>Mauremys rivulata</i> (Valenciennes in Bory de Saint-Vincent et al., 1833)	AJ564455	Barth et al. (2004)
<i>Melanochelys trijuga edeniana</i> Theobald, 1876	AJ564461	Barth et al. (2004)
<i>Melanochelys trijuga edeniana</i> Theobald, 1876	AY434629	Spinks et al. (2004)
<i>Morenia ocellata</i> (Duméril & Bibron, 1835)	AY434605	Spinks et al. (2004)
<i>Notochelys platynota</i> (Gray, 1834)	AJ564462	Barth et al. (2004)
<i>Ocadia sinensis</i> (Gray, 1834)	AJ564463	Barth et al. (2004)
<i>Orlitia borneensis</i> Gray, 1873	AJ564464	Barth et al. (2004)
<i>Pangshura smithii smithii</i> (Gray, 1863)	AY434589	Spinks et al. (2004)
<i>Pangshura tecta</i> (Gray, 1831)	AY434583	Spinks et al. (2004)
<i>Pangshura tentoria circumdata</i> (Mertens, 1969)	AY434610	Spinks et al. (2004)
<i>Rhinoclemmys annulata</i> (Gray, 1860)	AY434621	Spinks et al. (2004)
<i>Rhinoclemmys areolata</i> (Duméril & Bibron in Duméril and Duméril, 1851)	AY434611	Spinks et al. (2004)
<i>Rhinoclemmys diademata</i> (Mertens, 1954)	AY434616	Spinks et al. (2004)
<i>Rhinoclemmys funerea</i> (Cope, 1876)	AY434599	Spinks et al. (2004)
<i>Rhinoclemmys melanosterna</i> (Gray, 1861)	AY434590	Spinks et al. (2004)
<i>Rhinoclemmys punctularia punctularia</i> (Daudin, 1802)	AY434595	Spinks et al. (2004)
<i>Rhinoclemmys rubida</i> (Cope, 1870)	AY434625	Spinks et al. (2004)
<i>Sacalia bealei</i> (Gray, 1831)	AJ519501	Barth et al. (2004)
<i>Sacalia quadriocellata</i> (Siebenrock, 1903)	AJ564465	Barth et al. (2004)
<i>Siebenrockiella crassicolis</i> (Gray, 1831)	AY434571	Spinks et al. (2004)
<i>Siebenrockiella leytensis</i> (Taylor, 1920)	AY952911	Diesmos et al. (2005)

Table 1. (continued)

Taxon	Accession number	Source
Outgroups (Testudinidae)		
<i>Indotestudo travancorica</i> (Boulenger, 1907)	AY434644	Spinks et al. (2004)
<i>Manouria emys</i> (Schlegel & Müller, 1844)	AY434563	Spinks et al. (2004)

For phylogenetic analyses we decided to use the mitochondrial *cyt b* gene. It is known to be phylogenetically highly informative in geoemydid turtles (Barth et al. 2004; Spinks et al. 2004), and due to these studies a good coverage of most geoemydid taxa is available from GenBank (see Table 1). Accession numbers for *G. silvatica* sequences from the present study are AJ973610–AJ973612.

Molecular techniques

Total genomic DNA of small aliquots of the *G. silvatica* samples was extracted according to Gustinich et al. (1991). PCR and sequencing primers were mt-a-neu (5'-CTC CCA GCC CCA TCC AAC ATC TCA GCA TGA TGA AAC TTC G-3') of Lenk and Wink (1997), H-15909 (5'-AGG GTG GAG TCT TCA GTT TTT GGT TTA CAA GAC CAA TG-3') of Lenk et al. (1999), and (5'-TGA GGA CAA ATA TCA TTC TGA GG-3'), which is a slightly modified version of mt-C2 of Wink and Sauer-Gürth (2000). PCR was conducted in an Eppendorf Mastercycler. Cycling procedure was: initial denaturation 5 min at 95 °C; 40 cycles, denaturation 1 min at 95 °C, primer annealing for 1 min at 50 °C, extension for 2 min at 72 °C, and stop reaction for 10 min at 72 °C. PCR products were purified using the Invisorb Spin PCRapid Kit from Invitex. Cycle sequencing was performed with the following conditions for 25 cycles: 10 s at 96 °C, 5 s at 50 °C, and 4 min at 60 °C. Products were resolved on an ABI 3100 Genetic Analyzer (Applied Biosystems). The sequences obtained were approximately 1050–1100 bp long.

Phylogenetic analyses

Our analyses are based on an alignment of 1014 bp of the mitochondrial *cyt b* gene of *G. silvatica* with sequences available from GenBank for more than 50 representatives of all geoemydid clades and two testudinids as outgroup taxa (Table 1). Alignments across taxa were made by using ClustalX v.1.83 (Thompson et al. 1997) with default parameters.

Phylogenetic relationships were estimated with Neighbor-Joining (NJ), using the program package MEGA 2.1 and PAUP*4.0b10 (Swofford 2002), with Maximum Parsimony (MP) and Maximum Likelihood (ML) using PAUP*4.0b10, and with Bayesian analysis using

MRBAYES v3.0B4 (Huelsenbeck and Ronquist 2001). For all reconstructions except Bayesian analysis, the robustness of the branching pattern was tested by bootstrapping (Felsenstein 1985).

For the reconstruction of NJ trees (Saitou and Nei 1987) the Tamura–Nei model (Tamura and Nei 1993), a pairwise deletion, and 10,000 bootstrap replicates were chosen. To find the most appropriate model and parameters of DNA nucleotide substitution, we performed an hierarchical likelihood ratio test with MOD-ELTEST v.3.6 (Posada and Crandall 1998). The GTR model (Lanave et al. 1984; Tavaré 1986; Rodríguez et al. 1990; Yang 1994) combined with a proportion of invariable sites $I = 0.4241$ and a gamma distribution shape parameter $G = 0.9453$ was the best fitting of 56 tested models. The selected model and parameters were used to perform ML and Bayesian analyses. For ML and MP analyses we used the heuristic search method with 10 random stepwise additions and the TBR branch swapping option. For MP analysis, 1000 bootstrap replicates and a permutation test with 100 steps were conducted. For ML analysis, only 100 bootstrap replicates were run. Bayesian analyses were run for 1,000,000 generations, with a sampling frequency of 10 generations. From the 100,000 trees found, we determined a subset of trees for building our consensus tree by inspecting likelihood values of trees saved by MRBAYES, and set the burn-in to 1000 trees discarded to ensure that stable likelihood values were achieved.

Results

Alignment of the three *G. silvatica* sequences showed no nucleotide differences. Base frequencies in the 1041 bp long sequence AJ973611 were $A = 0.3256$, $C = 0.2997$, $G = 0.1009$, and $T = 0.2738$. The bias against guanine is characteristic for mitochondrial but not for nuclear genes (Desjardins and Morais 1990). The alignment of 1014 bp with the geoemydid taxa listed in Table 1 resulted in 479 constant and 535 variable positions, of which 448 are parsimony-informative and 87 are singletons. While all tree-building methods agree in some well-supported clades, the basal relationships within Geoemydidae are badly resolved under ML, MP and NJ, with bootstrap values for most nodes below 50. Bayesian analysis provides the best resolution of basal

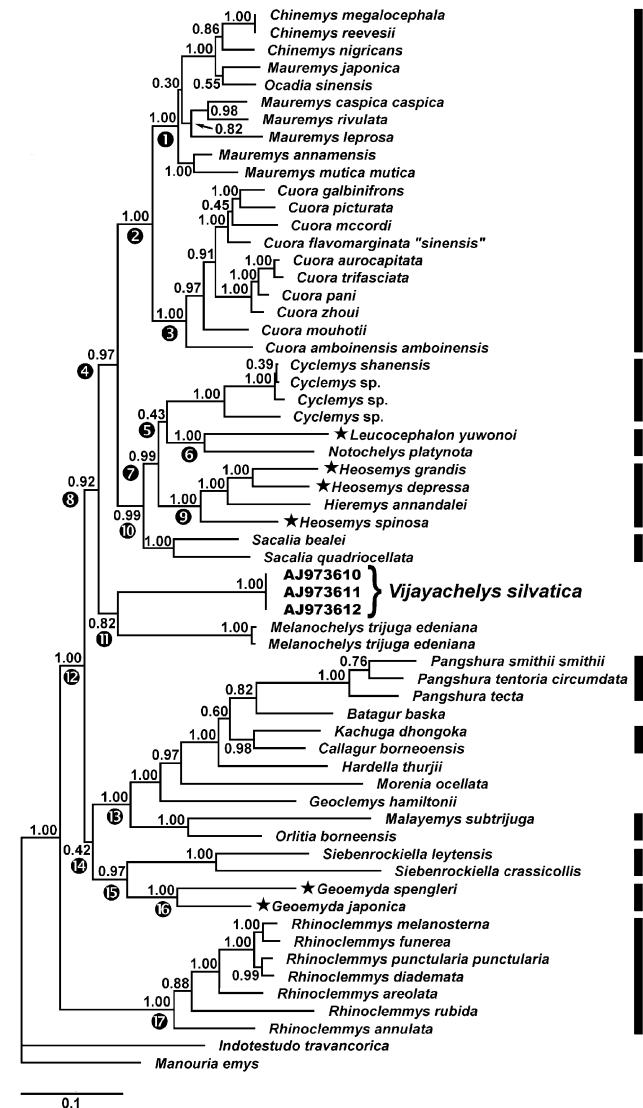
relationships (Fig. 1). However, this should be interpreted carefully. It is well-known that Bayesian support values may be overestimated and lead to erroneous conclusions (Erixon et al. 2003; Simmons et al. 2004). MP analysis resulted in 12 most parsimonious trees that differed only regarding in-group relations of the (*Chinemys*, *Mauremys*, *Ocadia*) clade, and within *Cyclemys*.

It is important that under all tree-building methods *G. silvatica* groups with neither of the genera it was previously placed in (*Geoemyda* or *Heosemys*: Henderson 1912; McDowell 1964; Moll et al. 1986; Yasukawa et al. 2001) or associated with (*Leucocephalon*: McCord et al. 1995). Instead, only *M. trijuga* could be distantly related to *G. silvatica*. However, the (*M. trijuga* + *G. silvatica*) clade is only weakly supported: by a posterior probability value of 0.82 under Bayesian analysis, or with a bootstrap value of 20 under ML

and of 23 under MP analysis. NJ does not support this clade at all.

The clades (*G. japonica* + *G. spengleri*), (*Heosemys* + *Hieremys*), and (*Leucocephalon* + *Notochelys*) form well-supported monophyla that are recovered in all tree-building methods. These clades are nested, with high Bayesian support, within other groups (nodes 10 and 15 in Fig. 1). *Geoemyda silvatica* is outside of all of these clades and represents a basal, isolated taxon. Sequence divergence values support the distinctness of *G. silvatica* (Table 2) as well. Whereas within the *Heosemys*–*Hieremys* clade and between *G. japonica* and *G. spengleri* uncorrected *p* distances are 0.097 and 0.114, respectively, values for *G. silvatica* versus (*Heosemys* + *Hieremys*) and versus (*G. japonica* + *G. spengleri*) are distinctly higher, 0.137 and 0.151, respectively. These values even exceed the level of differentiation between the two monotypic genera *Leucocephalon* and *Notochelys* (uncorrected *p* distance: 0.125).

Fig. 1. Bayesian tree of *cyt b* sequences from Geoemydidae; rooted with two testudinid species. For most accession numbers see Table 1. Branch lengths are Bayesian estimates and proportional to scale, with unit corresponding to average nucleotide changes per site. Taxa thought before to be closely related or congeneric with *Vijayachelys silvatica* are denoted by asterisks. Black bars indicate well-supported monophyla under all tree-building methods. Numbers at nodes represent posterior probabilities. Numbers in black circles indicate bootstrap support values for crucial nodes under ML (100), MP (1000 replicates), and NJ (10,000 replicates) as follows: (1) holophyly of *Chinemys*, *Mauremys*, *Ocadia*: 74/77/96; (2) holophyly of *Chinemys*, *Cuora*, *Mauremys*, *Ocadia*: 75/92/99; (3) holophyly of *Cuora*: 98/92/98; (4) holophyly of *Chinemys*, *Cuora*, *Cyclemys*, *Heosemys*, *Hieremys*, *Leucocephalon*, *Mauremys*, *Notochelys*, *Ocadia*, *Sacalia*: 7/–/–; (5) holophyly of *Cyclemys*, *Leucocephalon*, *Notochelys*: –/–/–; (6) holophyly of *Leucocephalon*, *Notochelys*: 61/80/78; (7) holophyly of *Cyclemys*, *Heosemys*, *Hieremys*, *Leucocephalon*, *Notochelys*: 30/–/–; (8) holophyly of *Chinemys*, *Cuora*, *Cyclemys*, *Heosemys*, *Hieremys*, *Leucocephalon*, *Mauremys*, *Melanochelys*, *Notochelys*, *Ocadia*, *Sacalia*, *Vijayachelys*: –/–/–; (9) holophyly of *Heosemys*, *Hieremys*: 82/93/98; (10) holophyly of *Cyclemys*, *Heosemys*, *Hieremys*, *Leucocephalon*, *Notochelys*, *Sacalia*: 16/37/54; (11) holophyly of *Melanochelys*, *Vijayachelys*: 20/23/–; (12) holophyly of *Batagur*, *Callagur*, *Chinemys*, *Cuora*, *Cyclemys*, *Geoclemys*, *Geoemyda* sensu stricto, *Hardella*, *Heosemys*, *Hieremys*, *Kachuga*, *Leucocephalon*, *Malayemys*, *Mauremys*, *Melanochelys*, *Morenia*, *Notochelys*, *Ocadia*, *Orlita*, *Pangshura*, *Sacalia*, *Siebenrockiella*, *Vijayachelys* (Geoemydidae exclusive of New World *Rhinoclemmys*): 34/41/47; (13) holophyly of *Batagur*, *Callagur*, *Geoclemys*, *Hardella*, *Kachuga*, *Malayemys*, *Morenia*, *Orlita*, *Pangshura*: 79/39/42; (14) holophyly of *Batagur*, *Callagur*, *Geoclemys*, *Geoemyda* sensu stricto, *Hardella*, *Kachuga*, *Malayemys*, *Morenia*, *Orlita*, *Pangshura*, *Siebenrockiella*: –/–/–; (15) holophyly of *Geoemyda* sensu stricto, *Siebenrockiella*: 38/30/68; (16) holophyly of *Geoemyda* sensu stricto, *Siebenrockiella*: 93/95/98; (17) holophyly of *Rhinoclemmys*: 100/100/100.



Systematics

Geoemyda silvatica represents a basal, isolated taxon within Geoemydidae that merits recognition as a distinct genus because in phylogenetic reconstructions it is located outside of all well-supported geoemydid clades. In the past, *G. silvatica* was assigned either to *Geoemyda* Gray, 1834 (type species: *Testudo spengleri* Gmelin, 1789) or to *Heosemys* Stejneger, 1902 (type species: *Emys spinosa* Gray, 1831). As placement in these genera is ruled out, and no other available genus name can be combined with *G. silvatica*, we propose to erect a new genus here.

Vijayachelys gen. nov.

Derivatio nominis. Composed of chelys (χέλυς), a Greek word for turtle, and the name of the late Indian herpetologist Jaganath Vijaya, who devoted her life to the herpetology of India and focused on turtles. The rediscovery of the forest cane turtle is her achievement. During her surveys she caught and marked more than 125 forest cane turtles, and lived more than 5 months in a cave to study the turtles in their habitat. The genus name *Vijayachelys* is of female gender.

Type species. *Geoemyda silvatica* Henderson, 1912.

Diagnosis. For diagnostic characters of external morphology, see Moll et al. (1986), Ernst and Barbour (1989), and Ernst et al. (2000). The diagnosis below focuses on osteological characters.

Small sized geoemydid: carapace in males up to 125 mm long, 83 mm wide, 43 mm high; carapace in females up to 131 mm long, 92 mm wide, 46 mm high (Moll et al. 1986). Carapace tricarinate, margin not or weakly serrated. Humeropectoral seam crosses entoplastron near its posterior margin, or bordering posterior margin of entoplastron. Connection between carapace and plastron ligamentous; reduction of bony articulation stronger in females than in males. Upper (2nd) suprapygal distinctly smaller than lower (1st) suprapygal. Skull without temporal arch. Beak with a median hook, maxillae in contact frontally, only partly separated by praemaxillae (according to Moll et al. 1986), or praemaxillae not visible in frontal view (in specimens examined in present study). Orbits large; frontal contributes considerably to orbital rim. Prootic in dorsal view extended frontally. Jugal–maxillary contact separated from pterygoid–maxillary contact by a gap, thus jugal not contacting pterygoid. Processus pterygoideus externus feebly developed; contact between maxilla and pterygoid narrow. Triturating surface of upper jaw narrow, more than four times longer than wide. Foramen palatinum posterius approximately 1.5 times longer than wide; pterygoid laterally emarginated and medially constricted, fossa temporalis inferior large

and voluminous, making room for musculus adductor mandibularis; processus trochlearis oticum small. Tail moderately long in male, abruptly narrowing after cloaca; tail very short in female.

Other crucial taxa

In the following, we provide differential diagnoses for the crucial species (in alphabetical order) *Geoemyda spengleri*, *Heosemys spinosa*, *Leucocephalon yuwonoi*, and *Melanochelys trijuga*, representing the type species of the respective genera. *Geoemyda spengleri* and *L. yuwonoi* superficially resemble *Vijayachelys silvatica*; previously, all three species were placed in *Geoemyda* (Henderson 1912; Moll et al. 1986; McCord et al. 1995; Yasukawa et al. 2001). McCord et al. (1995) suggested *V. silvatica* as the sister taxon of *L. yuwonoi*, a species since transferred to the monotypic genus *Leucocephalon* (McCord et al. 2000). *Heosemys spinosa* is of relevance as the type species of the genus *Heosemys* Stejneger, 1902, in which *V. silvatica* was placed by some authors (McDowell 1964; Ernst and Barbour 1989; Ernst et al. 2000). We include also *M. trijuga*, because this species could be distantly related to *V. silvatica* according to Bayesian analysis of mtDNA data. Character states of *V. silvatica* are given in brackets, unless otherwise stated.

Geoemyda spengleri (Gmelin, 1789) – type species of *Geoemyda* Gray, 1834

Of similar size as *Vijayachelys silvatica*.

Shell: Anterior margin of carapace slightly serrated, posterior margin strongly serrated (distinctly less serrated or unserrated). Gulars very short and quadrangular (very short but triangular). Upper suprapygal only slightly smaller than lower (distinctly smaller).

Skull: Temporal arch present (absent). Parietal without prominent crest (pronounced crest extends from posterior part of parietal onto supraoccipital).

Tail: Long in both sexes; in very long males, gradually narrowing toward tip (in moderately long males, abruptly narrowing after cloaca; tail very short in females).

Heosemys spinosa (Gray, 1831) – type species of *Heosemys* Stejneger, 1902

Carapace length up to approximately 23 cm (Ernst et al. 2000); males clearly exceeding females (up to approximately 13 cm; males slightly smaller than females).

Shell: Males with elongated shell; females with nearly circular shell when viewed from above; anterior carapacial margin slightly, hind margin strongly serrated in both sexes; shell with one pronounced median keel (tricarinate, elongated shell in both sexes, carapacial margin unserrated or slightly serrated). Gular scutes

Table 2. Genetic distances (uncorrected *p* distances; expressed as percentages) between crucial geoemydid taxa and clades

	<i>Heosemys+</i> <i>Hieremys</i>	<i>Geoemyda</i> <i>japonica+</i> <i>G. spengleri</i>	<i>Leucocephalon+</i> <i>Notochelys</i>	<i>Vijayachelys</i> <i>silvatica</i>
<i>Heosemys+Hieremys</i>	0.097			
<i>Geoemyda japonica+G. spengleri</i>	0.144	0.114		
<i>Leucocephalon+Notochelys</i>	0.138	0.154	0.125	
<i>Vijayachelys silvatica</i>	0.137	0.151	0.146	—

Within-group distances are presented in bold on the diagonal.

triangular, not conspicuously short (very short and triangular). Anterior and posterior plastral buttresses in males firmly articulating with carapace (feebly connected over ligament). In females anterior plastral buttresses firmly articulating with carapace (ligamentous connection); in both species articulation between posterior plastral buttresses and carapace replaced by wide ligamentous connection; however, in *H. spinosa* a weak hyo-hypoplastral hinge is present that partially divides epidermal scutes (hinge lacking in *V. silvatica*, plastral scutes not divided).

Skull: Upper jaw medially notched, notch flanked on each side by distinct cusp (medially hooked). Praemaxillae in frontal view distinct, large, separating maxillae completely and forming part of tomium (praemaxillae may be invisible in frontal aspect; if visible, praemaxillae only incompletely separating maxillae; praemaxillae not participating in formation of tomium). Jugal contacting pterygoid (not contacting pterygoid). Fissura ethmoidalis broad (narrow). Parietal not produced as prominent crest in its posterior part (pronounced crest continues from posterior part of parietal onto supraoccipital). Foramen palatinum posterius approximately two times longer than wide (approximately 1.5 times longer than wide). Processus trochlearis feebly developed (small but distinct).

Tail: Extremely short in both sexes (moderately long in males, very short in females).

***Leucocephalon yuwonoi* (McCord, Iverson and Boeadi, 1995) – type species of *Leucocephalon* McCord et al., 2000**

Carapace length up to approximately 27 cm in males, up to 22 cm in females (McCord et al. 1995; Fritz and Obst 1999); in *V. silvatica* up to approximately 13 cm, males somewhat smaller than females.

Shell: Carapacial margin flaring, hind margin strongly serrated (not flaring and unserrated or slightly serrated). Bridge in both sexes massively ossified with well-developed plastral buttresses firmly articulating with carapace (weak plastral buttresses connected to carapace by ligament). Gulars very short and quadrangular (very short and triangular). Humeropectoral seam

always located behind, thus never encroaching upon, entoplastron (may encroach upon entoplastron near its posterior margin). Gular-humeral seam parallel to humeropectoral seam (not parallel).

Skull: Distinctly more robust and wider than in *V. silvatica*. Parietal margin rounded, slightly diverging posteriorly (straight-sided). Complete temporal arch may rarely be present (temporal arch absent). Processus trochlearis oticum protruding and large (small but distinct). In ventral view foramen orbitonasale well visible (hidden behind lingual ridge of maxilla). Processus pterygoideus externus well developed (feebly developed). Fissura ethmoidalis wide (narrow). Ventral end of jugal contacting anterolateral process of pterygoid (not contacting pterygoid). Vomer posteriorly blunt, not extending between pterygoids (intruding deeply as pointed process between pterygoids).

***Melanochelys trijuga* (Schweigger, 1812) – type species of *Melanochelys* Gray, 1869**

Maximum carapace length ranging in the six subspecies from 22 cm (ssp. *trijuga*) to 38 cm (ssp. *parkeri*; Ernst et al. 2000); in *V. silvatica* up to approximately 13 cm. Limbs flattened, digits nearly fully webbed (limbs not flattened, digits not webbed).

Shell: Carapace shape similar in both species. Gular scutes large (short), intergular seam approximately of same length as interhumeral seam length (approximately 25–33% of interhumeral seam length).

Skull: General shape resembling *V. silvatica*, but complete temporal arch and well-developed quadratojugal of varying shape present (temporal arch absent, quadratojugal lacking or extremely small). Praemaxillae separating maxillae in frontal view (praemaxillae lacking or, if present, only partly dividing maxillae). Maxillae without median hook (distinct, projecting median hook present). Postorbital in *M. trijuga* slightly wider than in *V. silvatica*. Prootic anteriorly narrowed (anteriorly widened). In dorsal view parietal contacting quadratum in front of prootic (no contact). Foramen praepalatinum entirely enclosed by praemaxilla (foramen praepalatinum located at hind margin of praemaxilla, not entirely enclosed by praemaxilla). Foramen palatinum posterius

two times longer than wide (1.5 times longer than wide). Dorsal margin of otic chamber in lateral view slightly concave (convex). Condylus mandibularis extending below anterior margin of otic chamber (condylus located below hind part of otic chamber).

Osteological description of *Vijayachelys silvatica*

See Figs. 2–4. In the following data, those on the left of the slash (/) refer to male specimen MTD 46415, those on the right of the slash to female specimen NMW 3756.

Shell: Carapace length 105 mm/127 mm, width 80 mm/92 mm, height 37 mm/approximately 46 mm. Height of female shell not measured exactly, because plastron cut off along bridge during dissection. Plastron length max. 92, 85 mm on midline/max. 118, 109 mm on midline. Axillary and inguinal buttresses connected to carapace by ligament, thus connection between carapace and plastron rather weak, especially in posterior half. Axillary buttresses located at 3rd peripheral and 1st costal; inguinal buttresses firmly connected in male, feebly connected in female, with 7th peripheral and 5th costal. Neural formula in MTD 46415 and NMW 37564: 6–6–6–4–8–4–6–6; among four

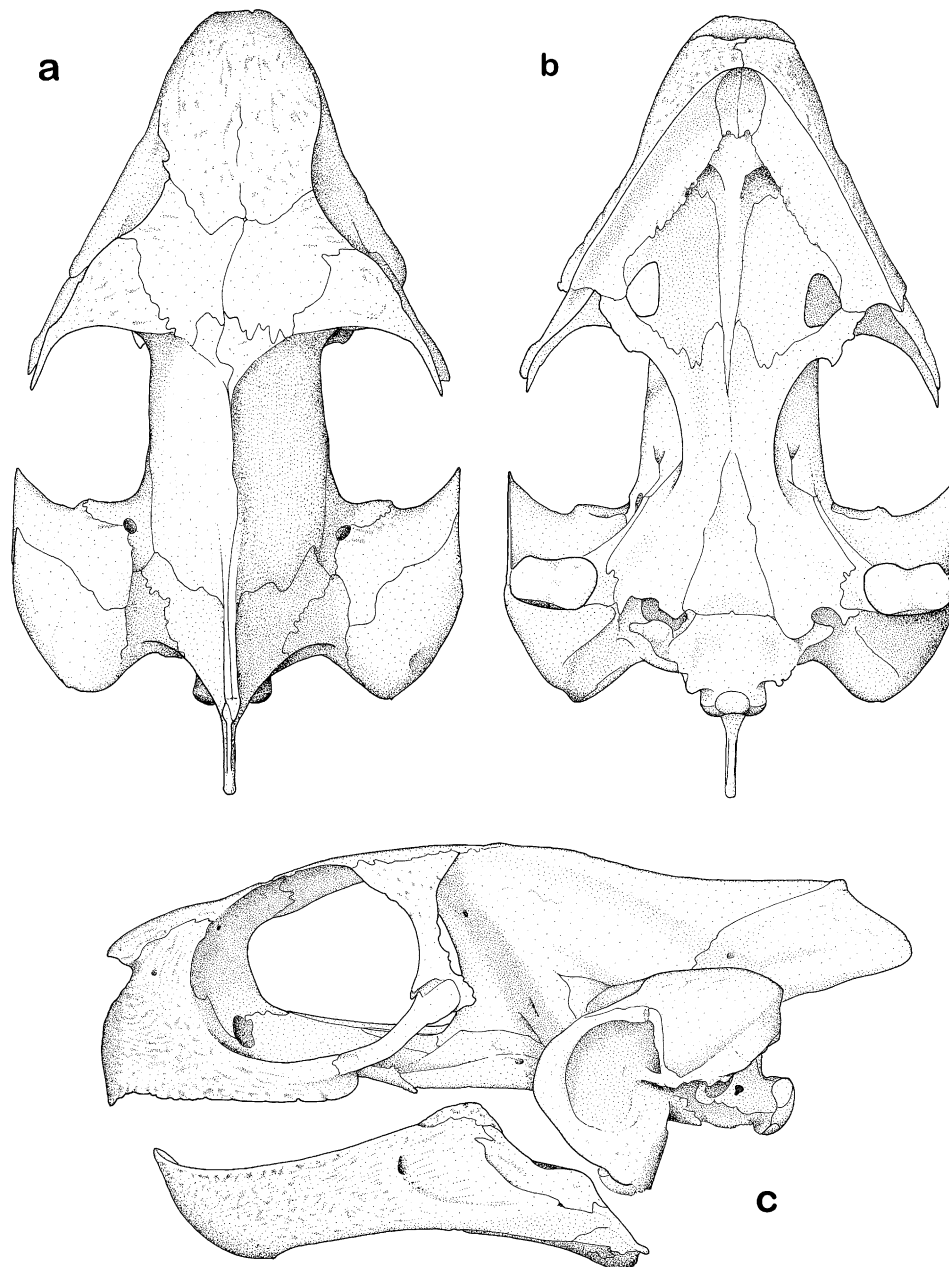


Fig. 2. (a) Dorsal, (b) ventral, and (c) lateral aspect of the skull of a male *Vijayachelys silvatica* (MTD 46415); lower jaw not shown in (a) and (b). Drawings by Ch. Schmidt.

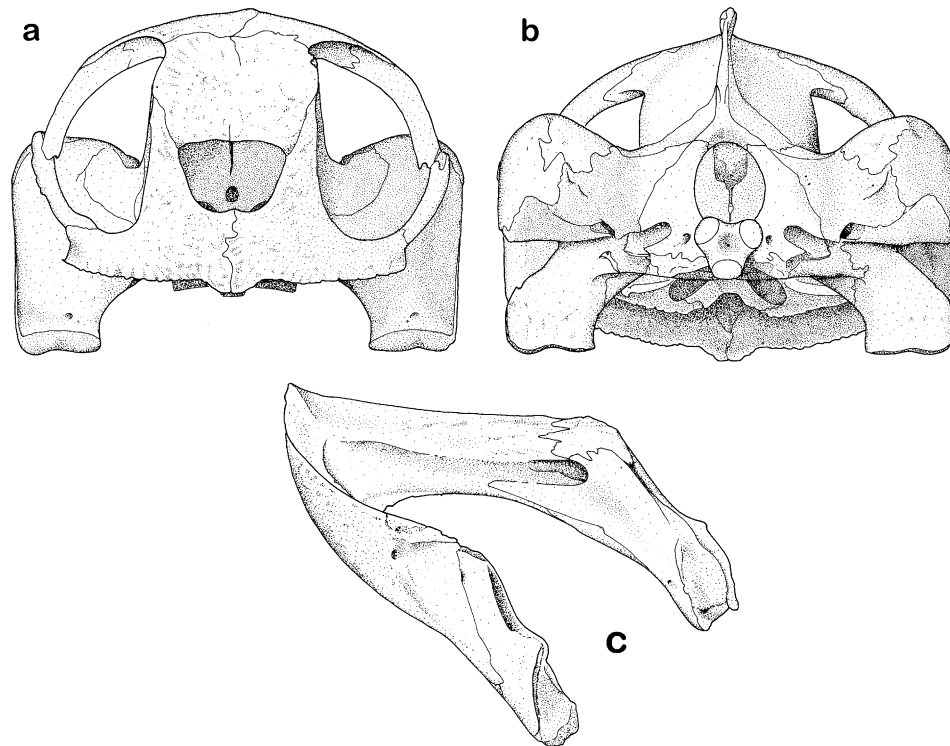


Fig. 3. (a) Frontal and (b) occipital aspect of the skull, (c) dorsolateral aspect of the lower jaw of a male *Vijayachelys silvatica* (MTD 46415); lower jaw not shown in (a) and (b). Drawings by Ch. Schmidt.

additional specimens, only one (of unknown sex and age, described by Moll et al. 1986) displayed the same formula, the others: 6–4–8–4–8–4–7–5, 4–6–8–4–8–4–8–4, 5–7–6–4–8–4–6–7. Entoplastron pear-shaped in ventral (exterior) view, with narrow end pointing anteriorly. At its posterior end, humeropectoral sulcus encroaches upon entoplastron, separating two narrow portions near its posterior margin. According to Moll et al. (1986), humeropectoral seam may also be excluded from entoplastron, bordering its posterior margin. In dorsal (visceral) view, entoplastron in female very stoutly pear-shaped, with broader end pointing to anterior; near its posterior end a small, shallow tubercle visible.

Skull: Total length 31.9/36.0 mm, length from apex to condylus occipitalis 27.5/31.5 mm; width 17.9/21.2 mm; height (without lower jaw) approximately 14/16 mm. Triturating surface of upper jaw left 11.5/14.0 mm long, 2.6/2.4 mm wide; right 11.8/14.0 mm long, 2.5/2.5 mm wide. Maxillae forming distinct median hook, labial ridge slightly serrated irregularly. On both skulls in frontal view no distinct praemaxillae visible between maxillae, in contrast to skull described by Moll et al. (1986). In dorsal view, praefrontal bones medially incompletely separated, only distally and proximally discernible suture present. Frontal bones not protruding between praefrontals, in contrast to skull figured in Moll et al. (1986). Frontal contributes considerably to orbital rim; suture between praefrontal and frontal at anterior third of orbital margin. Postorbital elongated, in lateral

view its narrowest part only 1/5 as wide as length of suture between frontal and postorbital; posteroventral corner somewhat enlarged as a process with irregular posterior margin. No closed temporal arch present. Quadratojugal completely lacking in male specimen, in female extremely small, vestigial quadratojugal present on left side, adhering to the anterior margin of quadratum. Jugal more slender than postorbital. Ventral end of jugal only contacting maxilla; this contact separated by a distinct gap from contact of maxilla with anterolateral process of pterygoid. Posterior part of parietal produced as prominent median crest, which continues on supraoccipital. Suture between parietal and supraoccipital in lateral view running caudally towards dorsal margin, with which it forms acute angle. In dorsal view, on dorsal margin of crest connection between these two bones asymmetrical and slightly thickened. Prootic anteriorly enlarged. In ventral view, praemaxillae distinct. Foramen praepalatinum small, located in suture between praemaxilla and vomer. Maxillae forming narrow triturating surface. Vomer posteriorly acute, with straight sides, clearly extending between pterygoids in MTD 46415 (male), only feebly extending in NMW 37564 (female). Foramen orbitonasale tiny, in ventral view hidden behind lingual ridge of maxilla. Foramen palatinum posterius approximately 1.5 times longer than wide, located between palatine, maxilla and pterygoid. Pterygoid laterally emarginated and medially constricted; pterygoids with processus

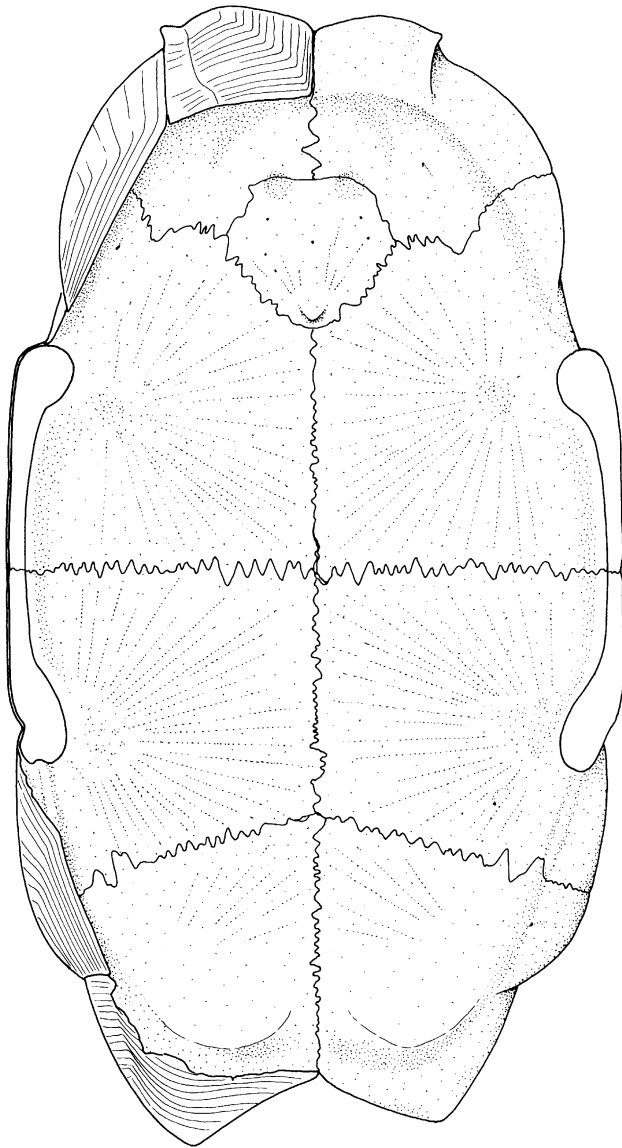


Fig. 4. Visceral (dorsal) aspect of the plastron of a female *Vijayachelys silvatica* (NMW 37564); epidermal scutes removed on right side. Note entoplastral shape. Drawing by Ch. Schmidt.

pterygoideus externus, which is reduced and acute on left side and obtuse on right side in MTD 46415 (male); reverse conditions are observed in NMW 37564 (female). Posterior end of pterygoid rounded in ventral view. Basisphenoid triangular. Basisoccipital with strong lateral processus interfenestralis. Condylus mandibularis located below midlength of otic chamber. Condylus occipitalis with three condylar surfaces and pit between them.

Lower jaw: Total length 19.6/21.2 mm, width 15.8/18.8 mm. Dentary with slight median hook, labial ridge almost smooth. Angular separated from sulcus cartilagineus meckelii by part of praearticular. Area articularis

mandibularis formed by articular, lateral margin by surangular, and medial margin by praearticular.

Formula for cervical vertebrae in both specimens: 2(–(3(–(4)–)5)–)6)–)7(–(8)). There is a double articulation between the fifth and sixth cervical vertebrae, as in the individual described by Moll et al. (1986).

Phalangeal formula of manus: 2–3–3–3–2; of pes: 2–3–3–3–1.

Tail with 22 vertebrae in male and 20 in female.

Discussion

The Western Ghats Region of India is a well-known biodiversity hotspot (Myers et al. 2000). The phylogenetic distinctness of *Vijayachelys silvatica* is another example underscoring the richness of this region in higher-level endemics (Biju and Bossuyt 2003; Bossuyt et al. 2004; Helgen and Groves 2005). Previous allocations of *V. silvatica* to the genera *Geoemyda* or *Heosemys* were based on morphological characters such as superficial resemblance, size, shape of the beak and shell, of bones, foramina and fissures in the skull, and presence or absence of a temporal arch (Moll et al. 1986; McCord et al. 1995; Yasukawa et al. 2001). It is beyond the scope of the present paper to re-evaluate these data in detail. However, we wish to point out that these characters are not complex morphological structures, but often related to the mode of life, and thus prone to homoplasy. Moreover, individual variation has been studied in osteological characters only rarely. For example, the temporal arch is known to have been lost in several geoemydid clades independently (Moll et al. 1986; Diesmos et al. 2005). But even within the same taxon variation may occur. Among five *Leucocephalon yuwonoi* skulls we noticed one (MTD 41576) with a complete temporal arch on the left side; on the right side the arch is interrupted, as is the case in the other four skulls.

Vijayachelys silvatica shares some conspicuous external traits, such as the hooked beak or tricarinate carapace, with other forest-dwelling geoemydids (*Geoemyda japonica*, *G. spengleri*, *Leucocephalon yuwonoi*, and *Cuora mouhotii*). Moreover, *G. japonica*, *G. spengleri*, and *L. yuwonoi* have very short gular scutes like those in *V. silvatica*. This suggests that selection results in similar phenotypes in distantly related geoemydids with a similar mode of life. It will be an important future challenge to establish a new morphological data matrix for geoemydids, using more complex morphological structures, and allowing the identification of reliable synapomorphies.

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ERRATUM

Erratum to “*Geoemyda silvatica*, an enigmatic turtle of the Geoemydidae (Reptilia: Testudines), represents a distinct genus” [Org. Divers. Evol. 6 (2006) 151–162]

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Due to an unfortunate error in type-setting, part of a species diagnosis is incorrect.

On p.156, under the heading

Geoemyda spengleri (Gmelin, 1789)—type species of *Geoemyda* Gray, 1834

read:

Tail: Long in both sexes; very long in males, gradually narrowing toward tip (moderately long in males, abruptly narrowing after cloaca; tail very short in females).

We apologize for any inconvenience caused.

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