Phalangeal formulae of geoemydid terrapins (*Batagur*, *Callagur*, *Hardella*, *Heosemys*, *Kachuga*, *Orlitia*, *Pangshura*, *Rhinoclemmys*) reflect distinct modes of life

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Abstract. Using radiographies of manus and pes of 133 geoemydid terrapins of nine highly aquatic species (genera *Batagur*, *Callagur*, *Hardella*, *Kachuga*, *Orlitia*, *Pangshura*), four aquatic *Rhinoclemmys* species, three semiterrestrial *Heosemys* species, and three terrestrial *Rhinoclemmys* species, we confirm a correlation between mode of life and phalangeal formulae. Terrestrial geoemydid species tend to have lost phalanges or entire digits, while highly aquatic species with extensive toe webbing generally have retained the full phalangeal number in manus and pes. Phalangeal formulae of species that are not so strictly adapted to aquatic environments, and having less extensive toe webbing, are intermediate, like in the studied semiterrestrial species.

In a recent paper, Fritz et al. (2006) proposed that phalangeal formulae in geoemydid terrapins are correlated with the mode of life. Terrestrial species tend to have reduced phalangeal formulae of manus and pes, while in aquatic species no loss of phalanges or digits occurs. However, only few individuals of highly aquatic species were available in that study (one specimen each of *Malayemys subtrijuga*, *Morenia petersi*, *Pangshura smithii*, and *Siebenrockiella crassicollis*). In the present paper, we test this hypothesis by comparing phalangeal formulae of nine highly aquatic geoemydid species of the genera *Batagur*, *Callagur*, *Hardella*, *Kachuga*, *Orlitia*, and *Pangshura* with seven *Rhinoclemmys* and three *Heosemys* species. Three of the *Rhinoclemmys* species are fully terrestrial; the other four represent freshwater turtles that are less adapted to aquatic lifestyle and have less extensive toe webbing than the other previously mentioned aquatic geoemydids. Among the three semiterrestrial *Heosemys* species, two prefer terrestrial habitats as adults (*H. depressa*, *H. spinosa*) and one prefers aquatic habitats (*H. grandis*; Ernst et al., 2000; own unpublished observations).

We used radiographies of each manus and pes, taken with a faxitron x-ray cabinet, of the following 133 alcoholic specimens from the herpetological collection of the Museum of Zoology Dresden (MTD); mutilated extremities were excluded from study:

Batagur baska: MTD 39286; *Callagur borneoensis*: MTD 35072, 40209, 44004, 45366; *Hardella thurjii*: MTD 8202, 9040, 19322, 30061, 31416, 34573, 37057-8, 44428; *Heosemys depressa*: MTD 46578; *Heosemys grandis*: MTD 3687, 11502, 13788, 15708, 24354, 33832-3; *Heosemys spinosa*: MTD 8197, 9900, 17172, 24344, 30074, 37818, 43910, 44920; *Kachuga dhongoka*: MTD 8198-9, 14480-2, 28683, 31512, 42577; *Kachuga kachuga*: MTD 35022; *Orlitia borneensis*: MTD 31410, 40190, 42499; *Pangshura smithii smithii*: MTD 9038, 28417, 31739, 32145, 39306, 41535-6; *Pangshura tecta*: MTD 20140, 27949, 28480, 30082, 30084, 33817, 35803, 36681, 40067, 44850; *Pangshura tentoria tentoria*: MTD 12459, 15841, 16834, 44853; *Pangshura tentoria circumdata*: MTD 15719, 28150, 28482, 35036, 37805, 39955-9; *Pangshura tentoria flaviventer*: MTD 35148, 44237; *Rhinoclemmys annulata*: MTD 12457, 25685-8, 30046; *Rhinoclemmys diademata*: MTD 30055-6, 40287; *Rhinoclemmys funerea*: MTD 20886, 35660; *Rhinoclemmys melanosterna*: MTD 36693; *Rhinoclemmys pulcherrima pulcherrima*: MTD 32088, 32751-2, 34857, 39841; *Rhinoclemmys pulcherrima incisa*: MTD 41847, 42606-7, 44804; *Rhinoclemmys pulcherrima manni*: MTD 28472-9, 31494, 44424; *Rhinoclemmys pulcherrima rogerbarbouri*: MTD 17207-9,

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Table 1. Phalangeal formulae in geoemydid terrapins. N – number of specimens, n – number of extremities with respective phalangeal formula. Note that highly aquatic species tend to have three phalanges in the fifth digit. Terrestrial species have reduced phalangeal numbers in the fifth digit; the fifth toe may be entirely lost.

Species	Manus	Pes
Highly aquatic species		
Batagur baska ($N = 1$)	2-3-3-3-2 ($n = 2$)	2-3-3-3-3 ($n = 1$)
		2-3-3-3-2 ($n = 1$)
Callagur borneoensis ($N = 4$)	2-3-3-3-3 ($n = 8$)	2-3-3-3-3 ($n = 8$)
Hardella thurjii ($N = 9$)	2-3-3-3-3 ($n = 18$)	2-3-3-3-3 ($n = 17$)
		2-3-3-3-2 ($n = 1$)
Kachuga dhongoka ($N = 8$)	2-3-3-3-3 ($n = 15$)	2-3-3-3-3 ($n = 14$)
		2-3-3-3-2 ($n = 2$)
Kachuga kachuga ($N = 1$)	2-3-3-3-3 ($n = 2$)	2-3-3-3-3 ($n = 2$)
Orlitia borneensis ($N = 3$)	2-3-3-3-3 ($n = 6$)	2-3-3-3-3 ($n = 6$)
Pangshura smithii smithii ($N = 7$)	2-3-3-3-3 ($n = 14$)	2-3-3-3-4 ($n = 2$)
		2-3-3-3-3 ($n = 10$)
		2-3-3-3-2 ($n = 2$)
Pangshura tecta ($N = 10$)	2-3-3-3-3 ($n = 19$)	2-3-3-3-3 ($n = 18$)
		2-3-3-3-2 ($n = 2$)
Pangshura tentoria tentoria ($N = 4$)	2-3-3-3-3 ($n = 6$)	2-3-3-3-3 ($n = 8$)
Pangshura tentoria circumdata ($N = 10$)	2-3-3-3-3 ($n = 17$)	2-3-3-3-3 ($n = 18$)
		2-3-3-3-2 ($n = 2$)
Pangshura tentoria flaviventer ($N = 2$)	2-3-3-3-3 ($n = 4$)	2-3-3-3-3 ($n = 2$)
		2-3-3-3-2 ($n = 2$)
Aquatic species		
Rhinoclemmys diademata ($N = 3$)	2-3-3-3-2 ($n = 6$)	2-3-3-3-2 ($n = 4$)
		2-3-3-3-1 ($n = 2$)
Rhinoclemmys funerea ($N = 2$)	2-3-3-3-2 ($n = 3$)	2-3-3-3-2 ($n = 1$)
		2-3-3-3-1 ($n = 3$)
Rhinoclemmys melanosterna ($N = 1$)	2-3-3-3-2 ($n = 2$)	2-3-3-3-2 ($n = 2$)
Rhinoclemmys punctularia punctularia ($N = 9$)	2-3-3-3-3 ($n = 1$)	2-3-3-3-2 ($n = 13$)
	2-3-3-3-2 ($n = 15$)	2-3-3-3-1 ($n = 4$)
Semiterrestrial species		
Heosemys depressa ($N = 1$)	2-3-3-3-2 ($n = 2$)	2-3-3-3-1 ($n = 1$)
		2-3-3-3-0 ($n = 1$)
Heosemys grandis ($N = 7$)	2-3-3-3-2 ($n = 12$)	2-3-3-3-2 ($n = 2$)
		2-3-3-3-1 ($n = 12$)
Heosemys spinosa ($N = 8$)	2-3-3-3-2 ($n = 15$)	2-3-3-3-2 ($n = 5$)
		2-3-3-3-1 ($n = 9$)
Terrestrial species		
Rhinoclemmys annulata ($N = 6$)	2-3-3-3-2 ($n = 11$)	2-3-3-3-1 ($n = 6$)
		2-3-3-3-0 ($n = 6$)
Rhinoclemmys pulcherrima pulcherrima ($N = 5$)	2-3-3-3-2 ($n = 10$)	2-3-3-3-2 ($n = 8$)
		2-3-3-3-1 ($n = 2$)
Rhinoclemmys pulcherrima incisa ($N = 4$)	2-3-3-3-2 ($n = 8$)	2-3-3-3-2 ($n = 4$)
		2-3-3-3-1 ($n = 4$)
Rhinoclemmys pulcherrima manni ($N = 10$)	2-3-3-3-2 ($n = 20$)	2-3-3-3-2 ($n = 12$)
		2-3-3-3-1 ($n = 8$)
Rhinoclemmys pulcherrima rogerbarbouri ($N = 8$)	2-3-3-3-2 ($n = 15$)	2-3-3-3-1 ($n = 16$)
Rhinoclemmys rubida perixantha ($N = 10$)	2-3-3-3-2 ($n = 20$)	2-3-3-3-1 ($n = 16$)
		2-3-3-3-0 ($n = 3$)

18187, 24350-1, 29942, 32080; *Rhinoclemmys punctularia punctularia*: MTD 26086, 26580, 28069, 30053, 31813, 32092, 39707, 42961, 44905; *Rhinoclemmys rubida perixantha*: MTD 17184, 17186-8, 24477, 25713-5, 32089, 38708.

Our findings corroborate the hypothesis of Fritz et al. (2006) that terrestrial geoemydid species tend to have lost phalanges or entire digits (table 1). In contrast, despite some individual

variation in the fifth digit, highly aquatic species generally have retained the full phalangeal formula of 2-3-3-3-3 in manus and pes or even have an additional fourth phalanx in the fifth toe (*Pangshura s. smithii*); the full phalangeal number is constituting a favourable prerequisite for swimming in these terrapin species having extensive toe webbing (Fritz et al., 2006). *Batagur baska* could represent an exception to this rule in having a 2-3-3-3-2 formula in the manus; however, this large, highly aquatic riverine species has somewhat paddle-like forelimbs with only four instead of five claws (Ernst et al., 2000), so that a distinct morphological pattern could be involved. Phalangeal formulae of species that are not so strictly adapted to aquatic environments, and having less extensive toe webbing, are intermediate, like in the studied semiterrestrial species.

Our findings also underline that environmental pressure may lead via selection to similar, homoplastic morphological characters in species not closely related. The same general pattern of phalangeal loss also occurs in terrestrial chelonians (Emydidae: *Terrapene*, Minx, 1992; Testudinidae, Crumly, 1985; Crumly and Sánchez-Villagra, 2004) being only distantly related with the geoemydids studied by Fritz et al. (2006) or in the present paper. However, in testudinids most variation occurs in the manus (Crumly and Sánchez-Villagra, 2004), while in geoemydids phalangeal formulae for the manus are less variable than phalangeal formulae for the pes (Fritz et al., 2006; this study). In *Terrapene*, variation in manus and pes is approximately of the same extent (Minx, 1992).

The most reduced phalangeal formulae occur in the most terrestrially adapted species, with lost phalanges in digits I-V in testudinids (Crumly and Sánchez-Villagra, 2004) or digits II-V in *Terrapene nelsoni* and *T. ornata* (Minx, 1992). With three exceptions, phalangeal loss is restricted in terrestrial geoemydids to digit V. Only in *Cuora flavomarginata*, *C. galbinifrons* and *C. mouhotii* a phalanx is also lost in the fourth digit of manus or pes (Fritz et al., 2006; Praschag et al., 2006; this study), suggesting that the extent of phalangeal loss could be correlated with the degree of and timeframe for adaptation to terrestriality in all three families.

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