

Osteology in the *Cuora galbinifrons* complex suggests conspecificity of *C. bourreti* and *C. galbinifrons*, with notes on shell osteology and phalangeal formulae within the Geoemydidae

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Abstract. Thirty-six complete skeletons, three shells, and x-rays of the extremities of 32 additional turtles of the *Cuora galbinifrons* complex have been compared with 38 other geoemydid species from 19 genera. *Cuora bourreti* differs from *C. galbinifrons* and *C. picturata* by a lost phalanx in the fourth finger and fourth toe. Individuals with a shell shape intermediate between *C. bourreti* and *C. galbinifrons*, as found on Hainan Island (China), have either the reduced phalangeal formula of *C. bourreti* (manus: 2-3-3-2-2, pes: 2-3-3-2-1) or the complete number of phalanges (manus: 2-3-3-3-2, pes: 2-3-3-3-1). Only in *C. flavomarginata* did we also register a lost phalanx in the fourth digit of manus and pes; in the pes of *C. mouhotii* the same character state may occur. In *C. flavomarginata* the fifth digit of the pes is also lacking. Some other terrestrial and semiterrestrial geoemydids (*Cuora mccordi*, *Heosemys spinosa*, and in part *C. mouhotii* and *Leucocephalon yuwonoi*) display a similar pattern of phalangeal reduction, resulting in the loss of the fifth digit of the pes. Likewise, in tortoises (Testudinidae), a further group of terrestrial chelonians, and the terrestrial turtle genus *Terrapene* (Emydidae) the loss of phalanges or complete digits is known to occur. *Malayemys subtrijuga*, *Morenia petersi*, *Pangshura smithii* and *Siebenrockiella crassicolis* differ from all other studied geoemydid taxa by an additional phalanx in the fifth digit of the manus (2-3-3-3-3); one *P. smithii* has on one body side three phalanges in the fifth digit of the pes (2-3-3-3-3). These are highly aquatic turtles with extensive toe webbing. Probably, longer digits (and thus a higher phalangeal number) are a favorable prerequisite for swimming while phalangeal loss seems to be the consequence of walking.

Cuora bourreti and *C. picturata* have consistently in the bony carapace a very rare character state regarding the articulation of the rib tips with the peripheral plates. In both species the rib tips are intercalated between two peripheral plates in the bridge region. Intercalated rib tips like those in *C. bourreti* and *C. picturata* were found only in *C. m. mouhotii*, but not in the southern subspecies *C. mouhotii obsti*. In *C. galbinifrons* and all other geoemydid taxa studied the rib tips articulate on the bridge within the underlying peripheral and not between two peripherals. In turtles morphologically intermediate between *C. bourreti* and *C. galbinifrons* both characters states are found. This suggests that such individuals are hybrids or intergrades. Three known-locality specimens from Hainan Island display both extremes and an intermediate character state. This, together with external morphology and the occurrence of both phalangeal formulae in approximately the same frequency on that island, argues for genetic introgression of *C. bourreti* on the Hainan population of *C. galbinifrons*. We conclude that our findings qualify *C. galbinifrons* and *C. bourreti* under the Biological Species Concept as conspecific.

Introduction

Indochinese box turtles of the *Cuora galbinifrons* complex (Testudines: Geoemydidae) occur in Vietnam, neighboring Laos and on Hainan Island (China) (Bourret, 1939; Lehr et al., 1998a, b; Fritz et al., 2002; Stuart and Parham, 2004); reports for Cambodia and southern mainland China have been doubted

in one of the most recent investigations (Stuart and Parham, 2004). This group comprises three small terrestrial species (*C. bourreti* Obst and Reimann, 1994; *C. galbinifrons* Bourret, 1939; *C. picturata* Lehr, Fritz and Obst, 1998) that are able to close the shell by a plastral hinge, like other *Cuora* species. Until recently, these taxa were treated as subspecies of *C. galbinifrons* (Obst and Reimann, 1994; Lehr et al., 1998a, b; Fritz et al., 2002). Due to an over-exploitation for food in recent years, turtles of the *C. galbinifrons* complex are critically endangered (IUCN, 2002). As a by-product of harvesting wild populations for the Chinese food markets, many Indochinese box turtles ap-

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peared in the international pet trade. This situation stimulated several investigations concerning their taxonomy and conservational status as reviewed in Stuart and Parham (2004).

Cuora galbinifrons is distributed in North Vietnam, on Hainan Island (China) and perhaps in southern mainland China. Stuart and Parham (2004) and Stuart and Platt (2004) attribute also specimens from eastern-central Laos to *C. galbinifrons*. This species has a flat, elongated shell without a dark lateral band and a black plastron. The soft parts are often intensely patterned with red. *Cuora bourreti* is known from Central Vietnam. Its shell is moderately domed and with a dark lateral band. The plastron is blotched. As in *C. picturata*, the soft parts never have a red pattern. *Cuora picturata* from southern Vietnam differs from *C. bourreti* by its extremely domed carapace, the lower position of the dark carapacial lateral band and in the color pattern of the soft parts (Lehr et al., 1998a, b). Some authors (e.g., Iverson and McCord, 1992) referred Indochinese box turtles from Hainan Island (China) to two further taxa, *Cuora galbinifrons hainanensis* (Li, 1958) and *C. g. serrata* Iverson and McCord, 1992. Recently, the latter taxon was shown to represent hybrids of *C. mouhotii* and *C. galbinifrons* (Parham et al., 2001). Lehr et al. (1998b) have demonstrated that Indochinese box turtles from Hainan Island exhibit some characters intermediate between *galbinifrons* and *bourreti*; e.g., the plastron can have a blotched pattern like in *bourreti*. These authors suggested that this reflects a former intergradation of *galbinifrons* and *bourreti* during a glacial low sea-level period when Hainan was part of the Southeast Asian mainland. As the Hainan turtles morphologically resemble *galbinifrons* more than *bourreti*, Lehr et al. (1998b) recommended treating *C. g. hainanensis* (Li, 1958) as a junior synonym of *C. galbinifrons* Bourret, 1939. Later, Fritz et al. (2002) demonstrated that *galbinifrons* and *bourreti* intergrade in southern North Vietnam. Stuart and Parham (2004) reported that within *C. galbinifrons* three major

mtDNA clades exist, corresponding to the taxa *galbinifrons*, *bourreti* and *picturata*. By adopting the Phylogenetic Species Concept, these authors suggested elevating *galbinifrons*, *bourreti* and *picturata* to species level. An mtDNA sequence from a Hainan box turtle clustered within the *galbinifrons* clade, and Stuart and Parham (2004) concluded that Indochinese box turtles from Hainan Island represent *C. galbinifrons*.

Since 1999, more than 300 complete chelonian skeletons have been prepared in the Museum of Zoology Dresden, among them 36 representatives of the *C. galbinifrons* complex. In the present paper we use this collection, three shells and x-rays of 32 additional turtles of the *C. galbinifrons* complex to determine whether differences in external morphology and the mitochondrial genome are reflected by osteology.

Materials and Methods

Alcohol preserved specimens of the *Cuora galbinifrons* complex and of other geoemydid turtles were skeletonized manually. Epidermal scutes were removed from one half of the shell by cutting vertebral scutes sagittally. Vertebral columns and extremities were prepared as far as possible in that bones remained in situ, held by sinews. All bones were individually numbered. A few specimens were prepared only as bony shells (see below). For this study only adult-sized or close to adult-sized turtles were used.

The following specimens were compared for osteological differences, all from the collection of the Museum of Zoology Dresden (Museum für Tierkunde Dresden = MTD):

Cuora bourreti ($n = 16$): MTD 30988, 40489-40490 (Hué, Central Vietnam), 40851, 41824, 41868 (Hué, Central Vietnam), 41938-41939, 42493, 42635, 42894, 44172, 44241, 44268-44270.

Specimens morphologically intermediate between *Cuora bourreti* and *C. galbinifrons* ($n = 7$): MTD 30435, 38770 (shell), 40849 (Hainan), 42895-42896 (Hainan), 44112, 44417.

Cuora galbinifrons ($n = 10$): MTD 30051, 31697, 31805 (Tam Dao, Vietnam), 36695, 38769 (shell), 38771 (shell), 44120-44121, 44242, 44267.

Cuora picturata ($n = 6$): MTD 31861 (southern Annam, Vietnam), 34568-34569 (southern Annam, Vietnam), 42633, 44125-44126.

For assessing the number and arrangement of metacarpal, carpal, tarsal and metatarsal elements and phalangeal numbers of the manus and pes, x-rays of the following additional

32 alcoholic specimens have been taken with a faxitron x-ray cabinet:

Cuora bourreti ($n = 8$): MTD 41165 (Annam, Vietnam), 41283, 41798-41799, 41856-41857, 41937, 41940.

Specimens morphologically intermediate between *Cuora bourreti* and *C. galbinifrons* ($n = 8$): MTD 27210 (Hainan), 31121-31122 (Hainan), 34038 (Hainan), 40015-40016 (Xinzheng, Hainan), 40022 (Tongzha, Hainan), 40394 (Hainan).

Cuora galbinifrons ($n = 9$): MTD 35902, 37255, 39849-39850, 40850, 41276, 41278, 41603, 41803.

Cuora picturata ($n = 7$): MTD 41848, 42872-42874, 43691-43692, 43732.

Many studied individuals originated from the international pet trade. Locality data are given above only for specimens with reliable geographic origin. Most *Cuora galbinifrons* from Hainan were obtained in the center of the island, except MTD 27210, which has no detailed locality data.

For comparative purposes the following 108 shells and skeletons of other geoemydids were studied, representing 19 genera and 38 species, i.e., more than half of the 60-70 species of the family (Fritz, 2001). The covered taxa correspond to most of the major geoemydid clades that have been identified by mtDNA and nDNA sequences (Spinks et al., 2004). Specimens with complete autopodial skeletons used for comparing phalangeal formulae are asterisked:

Callagur borneoensis: MTD 41360; *Chinemys reevesii*: MTD 38777-38779, 41541*, 44132*; *Cuora amboinensis*: MTD 3940, 42510-42511, 43356, 43903; *Cuora amboinensis amboinensis*: MTD 940-943, 24240, 44243*; *Cuora amboinensis kamaroma*: MTD 41167*; *Cuora aurocapitata*: MTD 45154*; *Cuora flavomarginata*: MTD 31695, 38768, 43360*, 44249*, 44459*, 45159*, 45372*; *Cuora mccordi*: MTD 45162*; *Cuora mouhotii mouhotii*: MTD 31688, 41168, 43909*; *Cuora mouhotii obsti*: MTD 40853*, 42636*; *Cuora pani*: MTD 41372*, 41891*; *Cuora zhoui*: MTD 45158*, 45163*; *Cyclemys atripons-pulchriata* complex: MTD 42549*; *Cyclemys dentata*: MTD 40835*, 41949*; *Cyclemys oldhamii*: MTD 40544-40545*, 49652; *Cyclemys shanensis shanensis*: MTD 40300*, 40390; *Cyclemys shanensis tcheponensis*: MTD 45035; *Geochemys hamiltonii*: MTD 12364*; *Geoemyda spengleri*: MTD 40796*, 40861*-40862*, 43000*; *Heosemys grandis*: MTD 42507, 42515; *Heosemys spinosa*: MTD 40859*; *Hieremys annandalei*: MTD 40863*, 42506; *Leucocephalon yuwonoi*: MTD 40171*, 41576*, 44789*, 45153*, 45165*; *Malayemys subtrijuga*: MTD 4358, 12595-12596, 24239, 42514, 43351*; *Mauremys annamensis*: MTD 38780-38783, 40829*, 41851*; *Mauremys caspica*: MTD 8482*, 40854*; *Mauremys "iversoni"*: MTD 40653*; *Mauremys leprosa*: MTD 3555, 4762, 8483, 31689, 43362*; *Mauremys mutica*: MTD 41973*, 43365*; *Mauremys rivulata*: MTD 38749, 40855*-40856, 41980*-41981*, 41988*; *Melanochelys trijuga edeniana*: MTD 40844*-40845*; *Morenia petersi*: MTD 42833*; *Notochelys platynota*: MTD 41948*; *Ocadia sinensis*: MTD 41897*, 42703; *Pangshura smithii*: MTD 38790, 43355*; *Pangshura tecta*: MTD 3561; *Pangshura tentoria circumdata*: MTD 24241; *Sacalia bealei*: MTD 38750-38752, 40858*, 42812*, 42999*;

Sacalia quadriocellata: MTD 40860*; *Rhinoclemmys didemata*: MTD 31694; *Rhinoclemmys punctularia*: MTD 31457; *Siebenrockiella crassicollis*: MTD 4359*.

Results

Regarding craniology, the number and arrangement of metacarpalia, carpalia, metatarsalia and tarsalia no consistent differences were found between the studied taxa of the *Cuora galbinifrons* complex. Also, there occur no obvious differences between the sexes or subadult and adult turtles, with the exception of obscured bony shell sutures in aged individuals (see below). The fore legs have five, the hind legs only four claws. However, in the pes is a fifth digit with one tiny phalanx present. In the manus, a pisi-form is normally lacking. We noted in the carpus of aged individuals a general tendency towards a fusion of the centralia as well as of the ulnare and the intermedium; rarely also the distal carpalia may be fused. Analogous fusions are observed in the tarsalia of aged specimens (fig. 1). In the phalangeal numbers of *C. bourreti* we found a major difference compared with *C. galbinifrons* and *C. picturata*. Most *C. bourreti* lost one phalanx of the fourth finger and fourth toe while this character state occurs only rarely in the other two species. This difference is statistically highly significant between *C. bourreti* and *C. galbinifrons* as well as between *C. bourreti* and *C. picturata* (χ^2 test for both combinations: $p < 0.001$ for manus and pes). In 90% of all studied *C. bourreti* ($n = 24$) the phalangeal formula of the manus is 2-3-3-2-2. Only 10% have the formula 2-3-3-3-2 that occurs in 85% of *C. galbinifrons* ($n = 17$) and *C. picturata* ($n = 13$). In the pes, 100% of the *C. bourreti* ($n = 24$) have the reduced phalangeal formula 2-3-3-2-1, which is found in only 18% of the *C. galbinifrons* ($n = 17$) and 8% of the *C. picturata* ($n = 13$). Two of the studied individuals were asymmetric with different phalangeal formulae of the manus on both body sides (one *C. bourreti*, one *C. galbinifrons*). Turtles with color pattern and

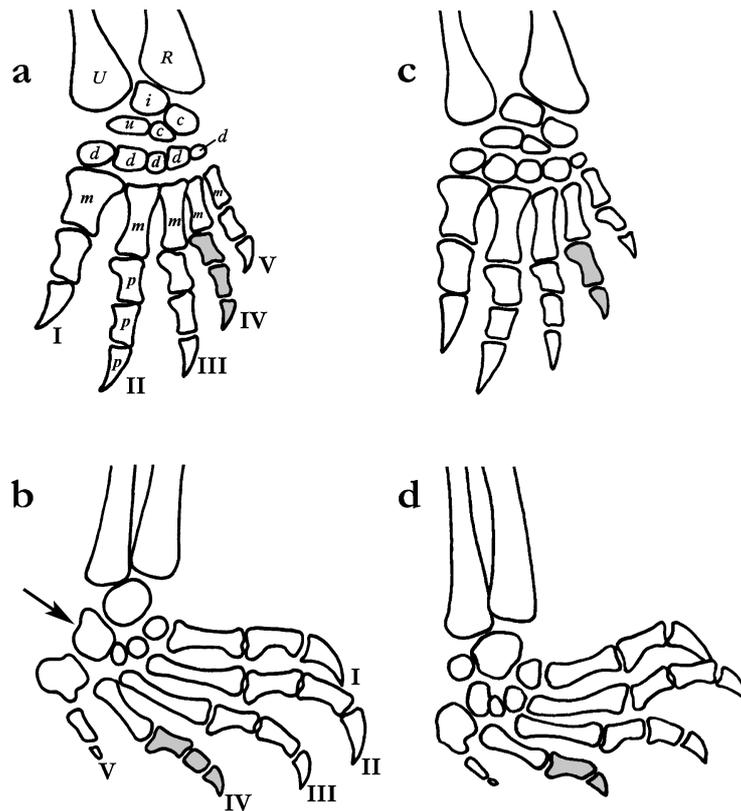


Figure 1. Manus (top) and pes (bottom) of *Cuora galbinifrons* (a: MTD 41276; b: MTD 39850) and an Indochinese box turtle from Hainan Island (c, d: MTD 40022). Note the lost phalanx in the fourth digit in (c) and (d) and the partially fused tarsalia in (b), indicated by the arrow. Abbreviations: *U* ulna, *R* radius, *i* intermedium, *u* ulnare, *c* centralia, *d* distal carpalia, *m* metacarpalia, *p* phalanges. Redrawn from x-ray photographs.

shell shape intermediate between *C. bourreti* and *C. galbinifrons* also have an intermediate position regarding their phalangeal number in that individuals with a lost phalanx in the fourth finger and toe occur more frequently than in our samples of *C. galbinifrons* and *C. picturata* (fig. 2; table 1).

Among our comparative material there is some variation regarding the phalangeal formulae, mainly in the fifth toe. The fifth digit of the pes is either completely lacking or has one to three phalanges. Less variation is found regarding the fifth finger, where most taxa have two phalanges. A reduced phalangeal number in the fourth finger and fourth toe, like in *C. bourreti* and some *C. galbinifrons* and *C. picturata*, is found only in the manus of *C. flavomarginata* and in the pes of *C. flavomarginata* and

some *C. mouhotii*. The fifth digit of the pes is lost in *C. flavomarginata*, *C. mccordi*, *Heosemys spinosa*, and in part in *C. mouhotii* and *Leucocephalon yuwonoi* (table 2). *Malayemys subtrijuga*, *Morenia petersi*, *Pangshura smithii* and *Siebenrockiella crassicollis* differ from all other taxa by an additional phalanx in the fifth digit of the manus (2-3-3-3-3); the *P. smithii* specimen has on one body side three phalanges in the fifth digit of the pes (2-3-3-3-3).

Besides the already known obvious differences in carapace shape (Lehr et al., 1998a, b), *C. bourreti* and *C. picturata* differ in shell osteology from *C. galbinifrons* by the location of the articulation of the rib tips into the peripheral bones in the bridge region. In most testudinoid turtles the rib tips insert approximately medially into the underlying peripheral plate. This is also

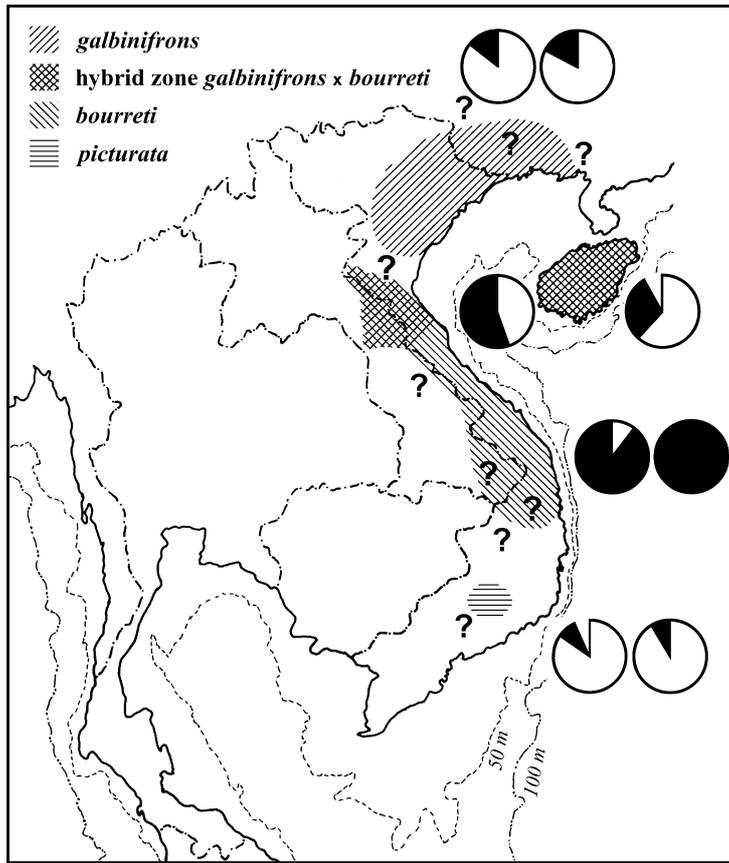


Figure 2. Frequency distributions of phalangeal formulae in the *Cuora galbinifrons* complex (left: manus, right: pes). Distribution ranges are approximations and question marks denote uncertainties. The complete phalangeal formula (manus: 2-3-3-3-2, pes: 2-3-3-3-1) is symbolized in white, the reduced formula (manus: 2-3-3-2-2, pes: 2-3-3-2-1) in black. Lacking percentages correspond to individuals with incomplete autopodial skeletons (compare table 1). In the last glacial, the coastline was embedded between the depicted 50 m and 100 m bathymetric contours and Hainan Island part of the Southeast Asian continent.

Table 1. Phalangeal formulae in the *Cuora galbinifrons* complex. Sums of character states do not necessarily correspond to sample sizes and sums of percentages not necessarily to 100 because some specimens had mutilated or disarticulated extremities. Asymmetric individuals with different phalangeal formulae on both body sides are divided between both classes. For Indochinese box turtles intermediate between *C. bourreti* and *C. galbinifrons* all individuals combined (including turtles without known geographic origin) and only specimens originating on Hainan Island are shown.

		<i>galbinifrons</i> n = 17	intermediates n = 13	Hainan only n = 11	<i>bourreti</i> n = 24	<i>picturata</i> n = 13
Manus	2-3-3-3-2	14.5	6	6	2.5	11
	2-3-3-2-2	2.5	7	5	21.5	1
Pes	2-3-3-3-1	14	8	6	0	12
	2-3-3-2-1	3	4	4	24	1
Percentages						
Manus	2-3-3-3-2	85	46	55	10	85
	2-3-3-2-2	15	54	45	90	8
Pes	2-3-3-3-1	82	62	55	0	92
	2-3-3-2-1	18	31	36	100	8

Table 2. Phalangeal formulae in other geoemydid taxa. Question marks denote lost or possibly lost phalanges during preparation or due to injuries. The studied *Pangshura smithii* is asymmetric; the second character state is bracketeded.

Taxon	<i>n</i>	Manus	Pes
<i>Chinemys reevesii</i>	2	2-3-3-3-2	2-3-3-3-1
<i>Cuora a. amboinensis</i>	1	2-3-3-3-2	2-3-3-3-2
<i>Cuora a. kamaroma</i>	1	2-3-3-3-2	2-3-3-3-1
<i>Cuora aurocapitata</i>	1	2-3-3-3-2	2-3-3-3-2
<i>Cuora flavomarginata</i>	5	2-3-3-2-2	2-3-3-2-0
<i>Cuora mccordi</i>	1	2-3-3-3-2	2-3-3-3-0
<i>Cuora m. mouhotii</i>	1	2-3-3-3-2	2-3-3-2-0
<i>Cuora m. obsti</i>	2	2-3-3-3-2	2-3-3-3-1 (<i>n</i> = 1) 2-3-3-2-0 (<i>n</i> = 1)
<i>Cuora pani</i>	2	2-3-3-3-2	2-3-3-3-1
<i>Cuora zhoui</i>	2	2-3-3-3-2	2-3-3-3-1
<i>Cyclemys atripons-pulchristriata</i> complex	1	2-3-3-3-2	2-3-3-3-2
<i>Cyclemys dentata</i>	2	2-3-3-3-2	2-3-3-3-2
<i>Cyclemys oldhamii</i>	1	2-3-3-3-2	2-3-3-3-2
<i>Cyclemys s. shanensis</i>	1	2-3-3-3-2	2-3-3-3-2
<i>Geoclemys hamiltonii</i>	1	2-3-3-3-2	2-3-3-3-2
<i>Geoemyda spengleri</i>	4	2-3-3-3-2	2-3-3-3-1
<i>Heosemys spinosa</i>	1	2-3-3-3-?	2-3-3-3-0
<i>Hieremys annandalei</i>	1	2-3-3-3-2	2-3-3-3-2
<i>Leucocephalon yuwonoi</i>	5	2-3-3-3-2	2-3-3-3-1 (<i>n</i> = 3) 2-3-3-3-0 (<i>n</i> = 2)
<i>Malayemys subtrijuga</i>	1	2-3-3-3-3	2-3-3-3-2
<i>Mauremys annamensis</i>	2	2-3-3-3-2	2-3-3-3-2
<i>Mauremys caspica</i>	1	2-3-3-3-2	2-3-3-3-1
<i>Mauremys "iversoni"</i>	1	2-3-3-3-2	2-3-3-3-1
<i>Mauremys leprosa</i>	1	2-3-3-3-2	2-3-3-3-1
<i>Mauremys mutica</i>	2	2-3-3-3-2	2-3-3-3-1
<i>Mauremys rivulata</i>	4	2-3-3-3-2	2-3-3-3-2 (<i>n</i> = 1) 2-3-3-3-1 (<i>n</i> = 3)
<i>Melanochelys trijuga edeniana</i>	2	2-3-3-3-2	2-3-3-3-1
<i>Morenia petersi</i>	1	2-3-3-3-3	2-3-3-3-2
<i>Notochelys platynota</i>	1	2-3-3-3-2	2-3-3-3-1
<i>Ocadia sinensis</i>	1	2-3-3-3-2	2-3-3-3-2
<i>Pangshura smithii</i>	1	2-3-3-3-3	2-3-3-3-3 (2-3-3-3-2)
<i>Sacalia bealei</i>	3	2-3-3-3-2	2-3-3-3-2 (<i>n</i> = 2) 2-3-3-3-? (<i>n</i> = 1)
<i>Sacalia quadriocellata</i>	1	2-3-3-3-2	2-3-3-3-2
<i>Siebenrockiella crassicollis</i>	1	2-3-3-3-3	2-3-3-3-2

the case in *C. galbinifrons*, while in *C. bourreti* and *C. picturata* the rib tips articulate in the bridge region generally between two peripheral bones (fig. 3). In *C. galbinifrons* the free rib end of costal 2 penetrates the fourth peripheral plate, the free rib end of costal 3 the fifth peripheral, and the free rib end of costal 4 fuses medially with the sixth peripheral. In the other two taxa, the costals obviously are located more posteriorly, resulting in an articulation of the respective free rib tips between the fourth and fifth, the fifth and sixth, and the sixth and seventh periph-

erals. For the character state found in *C. bourreti* and *C. picturata*, we introduce here the term "intercalated rib tips". This character state has to the best of our knowledge not previously been described from any testudinoid turtle.

Although there is some variation (table 3), the character state is very constant in the third costal (χ^2 test comparing *C. bourreti* and *C. picturata*, respectively, with *C. galbinifrons*: $p < 0.001$). All *C. bourreti* and *C. picturata* have here rib tips intercalated between the two adjacent peripheral plates, while in all *C. gal-*

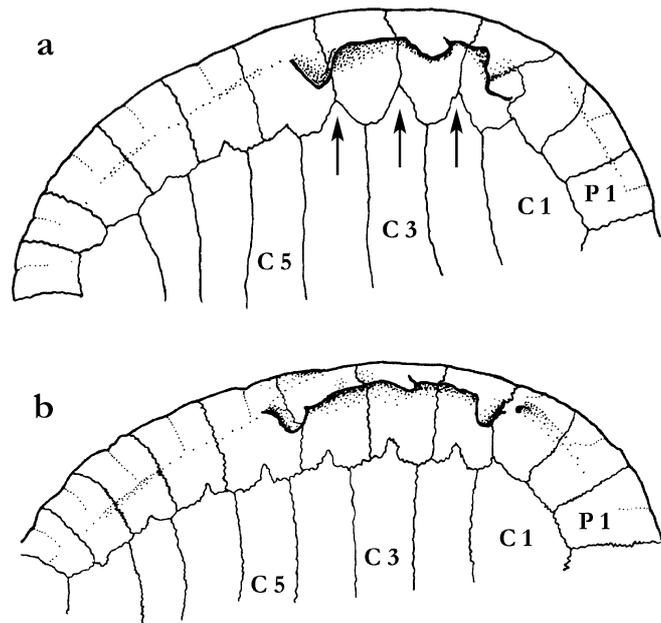


Figure 3. Visceral aspects of the carapace of *Cuora bourreti* (a: MTD 41868) and *Cuora galbinifrons* (b: MTD 30051). The anterior side is on the right. P1 = first peripheral; C1 = first costal plate, etc. Arrows indicate in *C. bourreti* costal tips intercalated between two peripherals. Note that costal tips articulate within the underlying peripherals in *C. galbinifrons*.

binifrons the rib tip of the third costal articulates medially within one peripheral. Only the second free rib tip is also rarely in *C. galbinifrons* intercalated between two peripherals (2 of 7 specimens). Nevertheless, there is a highly significant difference between *C. bourreti* and *C. galbinifrons* (χ^2 test: $p < 0.001$) in the location of the second free rib tip (intercalated vs. not intercalated) but not when comparing *C. picturata* with *C. galbinifrons* (χ^2 test: n. s.); the frequency distribution differs at the 0.05 level in *C. bourreti* and *C. picturata*. In the location of the fourth rib tip, the difference between *C. bourreti* and *C. galbinifrons* is significant (χ^2 test: $p < 0.01$), the difference between *C. picturata* and *C. galbinifrons* weakly significant (χ^2 test: $p < 0.05$), and between *C. bourreti* and *C. picturata* not significant.

Among more than 100 skeletons of 38 species of 19 of the approximately 25 geoemydid genera (Fritz, 2001), we found intercalated rib tips as in *C. bourreti* and *C. picturata* only in *C. mouhotii mouhotii* ($n = 3$) but not in representatives of the subspecies *C. mouhotii obsti*

($n = 2$). In *C. m. obsti* and most other studied taxa, the rib tips articulate in the bridge region into the middle of the underlying peripheral, as in *C. galbinifrons*. In *C. flavomarginata* ($n = 7$), *C. mccordi* ($n = 1$) and *Leucocephalon yuwonoi* ($n = 5$) the rib tips articulate in the posterior half of the underlying peripheral. This highlights the exceptionality of intercalated rib tips among geoemydids. Remarkably, two skeletons of individuals morphologically intermediate between *C. bourreti* and *C. galbinifrons* also have intercalated third rib tips (MTD 30435, 40849). In a further specimen (MTD 42896) the character state is intermediate in that the rib tips approach and touch the suture between two neighboring peripherals but do not intrude between them. MTD 40849 and 42896 are known to be from Hainan Island.

Parenthetically, it may be noted that in old individuals the bony shell sutures fuse and obscure completely (*C. bourreti*: MTD 40489-40490, 41939, 44268, 44270; *C. bourreti* × *C. galbinifrons* intermediates: MTD 38770; *C. galbinifrons*: MTD 36695, 44242, 44267;

Table 3. Location of the articulation of 2nd to 4th rib tips with peripheral plates in the *Cuora galbinifrons* complex. The asterisked values indicate that an intermediate character state is found in one individual from Hainan Island attributed to the “within groups” (see text for further explanation). One of the other two known-locality specimens from Hainan has intercalated rib tips, the other not.

		<i>bourreti</i> <i>n</i> = 16	intermediates <i>n</i> = 7	<i>galbinifrons</i> <i>n</i> = 10	<i>picturata</i> <i>n</i> = 6
Rib tip 2 inserts	within 4 th peripheral	0	4	5	2
	between 4 th and 5 th peripheral	11	2	2	3
Rib tip 3 inserts	within 5 th peripheral	0	4*	7	0
	between 5 th and 6 th peripheral	11	2*	0	5
Rib tip 4 inserts	within 6 th peripheral	4	6*	7	2
	between 6 th and 7 th peripheral	7	0*	0	3
Aged individuals with unsutured bony shell capsule		5	1	3	1
Percentages (only individuals with visible sutures considered)					
		<i>n</i> = 11	<i>n</i> = 6	<i>n</i> = 7	<i>n</i> = 5
Rib tip 2 inserts	within 4 th peripheral	0	67	71	40
	between 4 th and 5 th peripheral	100	33	29	60
Rib tip 3 inserts	within 5 th peripheral	0	67*	100	0
	between 5 th and 6 th peripheral	100	33*	0	100
Rib tip 4 inserts	within 6 th peripheral	36	100*	100	40
	between 6 th and 7 th peripheral	64	0*	0	60

C. picturata: MTD 44126), so that the bony shell is an unsutured, solid capsule. This resulted in a reduced number of specimens in which the bony elements of the shell could be studied (table 3).

Discussion

A reduction of the phalangeal number in the fourth finger and fourth toe, as occurs in *C. bourreti* and some *C. galbinifrons* and *C. picturata*, was found among our studied comparative material only in *C. flavomarginata*; *C. mouhotii* may also have a reduced phalangeal number in the fourth digit of the pes. We do not regard the resemblance of the character states in *C. flavomarginata* and the *C. galbinifrons* complex as supporting a *Cistoclemmys* clade, which has been repeatedly suggested for these taxa (Bour, 1980; Hirayama, 1985; Yasukawa et al., 2001). The species of the *C. galbinifrons* complex, *C. flavomarginata* and *C. mouhotii* are terrestrially living turtles. It is likely that their phalangeal loss is correlated with this ecological adaptation because all geoemydids

in which we registered a completely lost fifth digit in the pes are also terrestrial or semi-terrestrial (*Cuora flavomarginata*, *C. mccordi*, *C. mouhotii*, *Heosemys spinosa*, *Leucocephalon yuwonoi*). Likewise, in tortoises (Testudinidae), another group of terrestrial chelonians, and the terrestrial turtle genus *Terrapene* (Emydidae) the loss of phalanges or complete digits is known to occur (Crumly, 1985; Minx, 1992; Crumly and Sánchez-Villagra, 2004). In contrast, the highly aquatic geoemydids *Malayemys subtrijuga*, *Morenia petersi*, *Pangshura smithii* and *Siebenrockiella crassicollis* were shown in the present study to have higher phalangeal numbers than other Geoemydidae. In aquatic turtles the extremities have extensive toe webbing. Therefore, longer digits (and thus a higher phalangeal number) are likely to be a favorable prerequisite for swimming while phalangeal loss could be the consequence of an adaptation to walking.

The character state of rib tips articulating between two peripherals, described here for *Cuora bourreti* and *C. picturata*, is extremely rare among geoemydids and other testudinoid tur-

tles. Normally, the rib tips insert within the underlying peripheral plate. This is likely to contribute to a mechanical stabilization of the shell. We do not know why the rib tips moved backward in *C. bourreti* and *C. picturata*, but this could be related with their specialized shell architecture. Both taxa possess, in contrast to *C. galbinifrons* and most geoemydids, a moderately to highly domed carapace. However, the sole other taxon in which we also discovered intercalated rib tips (*C. m. mouhotii*) has a totally different, strongly flattened and tricarinate shell.

Based on mtDNA sequences, Stuart and Parham (2004) found a very weakly supported sister relationship between *C. galbinifrons* and *C. bourreti*, despite the fact that *C. bourreti* and *C. picturata* are morphologically more similar in that both have a domed shell, a dark carapacial lateral band, a blotched plastral pattern and lack the intensely red coloration of the soft parts of many *C. galbinifrons*. Our osteological data for the shell reflect this general morphological similarity of *C. bourreti* and *C. picturata*, while the phalangeal formulae do not. However, as the complete phalangeal formulae of *C. galbinifrons* and *C. picturata* are likely to represent the plesiomorphic character state, this does not conflict with the hypothesis of a closer relationship between *C. bourreti* and *C. picturata*.

Fritz et al. (2002) demonstrated that Indochinese box turtles from southern North Vietnam (Ha Tinh and Quang Binh provinces) are morphologically intermediate between *C. bourreti* and *C. galbinifrons* and interpreted this as intergradation of two subspecies. Our osteological data further support that gene flow between both taxa exists. We found among turtles with an intermediate external gross morphology individuals with the reduced phalangeal formula, as typical for *C. bourreti*, in approximately the same frequency as individuals with the complete phalangeal formula as in *C. galbinifrons* (fig. 2). Moreover, we discovered among the intermediate turtles two individuals with intercalated rib tips and one with an intermediate character state. Stuart and Parham (2004) claimed that the

Vietnamese box turtles described by Fritz et al. (2002) as intergrades of two subspecies represent rather interspecific hybrids. Their approach is mainly based on a different species concept, and a discussion of this is beyond the scope of the present paper. However, we wish to point out that our osteological findings qualify *C. bourreti* and *C. galbinifrons* under the Biological Species Concept (Mayr, 1942, 1963, 2000) as conspecific. Our osteological data do not shed any new light on the question of whether *C. picturata* could be also a subspecies of *C. galbinifrons*. Taking the morphological similarity to *C. bourreti* into account, this could well be.

Based on color pattern characters, Lehr et al. (1998b) believed that Hainan box turtles represent a further *bourreti* × *galbinifrons* intergrade population, which was cut off from the mainland by rising sea levels in postglacial times (compare fig. 2). Lehr et al. (1998b) recommended lumping Hainan Island turtles nomenclaturally with mainland *galbinifrons* because they resemble this taxon morphologically more than *bourreti*, despite a clear influence of *bourreti*. Based on one mtDNA sequence, Stuart and Parham (2004) attributed Indochinese box turtles from Hainan Island to *C. galbinifrons*, without appreciating that Lehr et al. (1998b) demonstrated that shell shape and color pattern of Hainan turtles is intermediate between *bourreti* and *galbinifrons*. Among our three studied skeletons from Hainan Island we found one specimen with intercalated rib tips (MTD 40849), one with rib tips articulating within the underlying peripherals (MTD 42895) and the third turtle showed an intermediate character state (MTD 42896). Taking the rareness of intercalated rib tips in geoemydid turtles into account, this, together with our findings regarding the phalangeal formulae is strong evidence of a genetic impact of *bourreti* on Hainan box turtles and suggests a hybrid origin of that island population. This argues for caution when considering mtDNA data only, especially for limited sample sizes, as mtDNA data reflect only maternal lines but do not mirror neces-

sarily introgression phenomena or gene flow (see also Wilson et al., 1985; Birky, 1991; Hay et al., 2003; Ballard and Whitlock, 2004). For example, also some other turtles attributed by Stuart and Parham (2004) and Stuart and Platt (2004) to *C. galbinifrons* could well represent intergrades between *C. galbinifrons* and *C. bourreti* according to the southern location of their collection sites in eastern-central Laos (17°50'N 105°35'E, 17°32'N 105°04'E) and Vietnam (19°03'N 104°37'E; Stuart and Platt, 2004). The occurrence of an mtDNA haplotype clustering with *galbinifrons* in one of these individuals (Stuart and Parham, 2004) provides only evidence that the maternal ancestor of the studied individual was a *C. galbinifrons*.

A remarkable by-product of the present study is the discovery that among the studied 38 other geoemydid species intercalated rib tips occur only in *Cuora mouhotii*. *Cuora mouhotii* was until recently considered to represent a distinct genus (*Pyxidea*), but its mtDNA haplotypes nest within *Cuora* (Honda et al., 2002; Parham et al., 2004; Stuart and Parham, 2004). Therefore, Honda et al. (2002) recommended putting *mouhotii* into *Cuora*. This is followed here. *Cuora mouhotii* is a polytypic species with two recognized subspecies that occur widely sympatrically with the *C. galbinifrons* complex. The taxonomic differentiation of *C. mouhotii* parallels the *C. galbinifrons* complex in that a northern taxon, *Cuora mouhotii mouhotii* (Gray, 1862) lives in approximately the same area as *C. galbinifrons*. The distribution of a southern taxon, *C. m. obsti* Fritz, Lehr and Andreas, 1998 corresponds to *C. bourreti* (Fritz et al., 1998, 2002). Interestingly, in *C. mouhotii* the intercalated rib condition occurs in the northern subspecies *mouhotii*, which is sympatric with *C. galbinifrons*, the only taxon of the *C. galbinifrons* complex in which this character state does not occur. The southern subspecies *C. mouhotii obsti* that apparently has no intercalated rib tips, is sympatric with *C. bourreti* that has intercalated rib tips. *Cuora mouhotii* is known to hybridize sporadically with *C. gal-*

binifrons and *C. bourreti* (Parham et al., 2001; Stuart and Parham, 2004). As the intercalated rib tips occur both in the *C. galbinifrons* complex and the *C. mouhotii* subspecies crosswise, it is unlikely that this is due to hybridization or introgression. We believe that this character was independently acquired by *C. m. mouhotii* and the *C. galbinifrons* complex.

Asiatic box turtles of the genus *Cuora* (Geoemydidae) resemble in many morphological and ecological traits the North American box turtle genus *Terrapene* (Emydidae). Both in *Cuora* and *Terrapene* phalangeal loss and a plastral hinge occur, the latter allowing complete shell closure (Minx, 1992; Ernst et al., 1994; Dodd, 2001). Strikingly, also old *Terrapene* individuals tend to have completely fused bony shell sutures (Dodd, 2001; Holman and Fritz, 2005), as described for the *Cuora galbinifrons* complex in this study. Further research is needed for a better understanding of the evolutionary and environmental forces leading to such parallel evolved traits, but also to unique character states like the intercalated rib tips found only in the *C. galbinifrons* complex and *C. m. mouhotii*.

Acknowledgements. The MTD skeleton collection could not be established without the work of our preparators. Henry Heidecke coordinated this work over several years. Thanks to Edgar Lehr for technical support. Axel Zarske assisted with the x-rays. Elmar Meier provided information about the behavior of *Cuora mccordi*. James Parham and Bryan Stuart commented extensively on an earlier draft of this paper.

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Received: January 19, 2005. Accepted: July 4, 2005.