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Geographic variation in the Asian big-headed turtle, *Platysternon megacephalum* (Reptilia: Testudines: Platysternidae)

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Abstract.–Currently, five subspecies of *Platysternon megacephalum* Gray, 1831 are recognized: *megacephalum* Gray, 1831, *peguense* Gray, 1870, *vogeli* Wermuth, 1969, *tristernalis* Schleich & Gruber, 1984, and *shiui* Ernst & McCord, 1987. Because two of the subspecies, *vogeli* and *tristernalis,* have geographic ranges within or overlapping others, a study was undertaken to examine their validity. A total of 136 specimens of *P. megacephalum* from throughout the species range was examined and analyzed using discriminant function analysis of morphometric data. Because discriminant function analysis is unable to separate *vogeli* with certainty and because its range overlaps that of the earlier described *peguense,* we place *vogeli* in the synonomy of *peguense.* Even though discrimininant function analysis reliably distinguishes *tristernalis*; its main characteristic (anomalous extra scales at the junction of the gular and humeral plastral scutes) occurs commonly in the other subspecies as well and does not define *tristernalis* unambiguously. Additionally, the distribution of *tristernalis* lies within that of the nominate taxon *megacephalum.* The type specimens have peculiar shell morphology, likely the result of years in captivity. We recommend *tristernalis* as a junior synonym of *megacephalum.*

The big-headed turtle, *Platysternon megacephalum* Gray 1831, is the sole living species of its clade Platysternidae. Its closest living relatives are members of the snapping turtle family, Chelydridae (Gaffney & Meylan 1988, Shaffer et al. 1997; but see Whetstone 1978, Haiduk & Bickham 1982, and Bickham & Carr 1983 for contrasting views). The species ranges from southern China (Fujian, Guangdong, Jiangxi, Yunnan, Hunan Island, and Hong Kong) southwestward through northern Vietnam, Laos, Kampuchea, and northern Thailand to southern Myanmar (Ernst & Barbour 1989, Iverson 1992). Within this range five subspecies are recognized: *Platysternon megacephulum megacephalum* Gray, 1831, in southern China; *P. m. peguense* Gray, 1870, from western Vietnam west to southern Burma; *P. m. vogeli* Wermuth, 1969, in northwestern Thailand; *P. m. tristernalis* Schleich & Gruber, 1984, from Yunnan, China; and *P. m. shiui* Ernst & McCord, 1987, in northern Vietnam and Yunnan, China.

Platysternon m. vogeli was described from two specimens whose type locality lies within the range of *P. m. peguense.* Likewise, *P. m. tristernalis* was designated from specimens collected within the range of *P. m. megacephalum.* The chief characters to differentiate *P. m. vogeli* were a short, less hooked upper jaw, a smooth posterior carapace rim, and a broad, faded plastron pattern. In *P. m. tristernalis,* three small supernumerary scales at the gular-humeral seam were its major characteristic, though these are subject to much variation within this species and other turtles. A systematic review of *P. megacephalum* was undertaken to determine the extent of geographic variation within the species, and the

validity of *vogeli* and *tristernalis*. The results of this study are presented here.

Methods

One hundred thirty-six *Platysternon* (including type specimens) from throughout the geographic range were examined (Appendix 1). Data were analyzed separately by sex to avoid bias created by sexual dimorphism. Sexes were determined by the concave plastron and the anal vent situated beyond the posterior carapacial rim in adult males (Ernst & Barbour 1989).

Straight-line measurements of each specimen were taken with dial calipers accurate to 0.1 mm. Variables measured included: the greatest carapace length (CL), carapace width (CW) and depth of shell at the level of the seam separating the second and third vertebrals (CH), marginal width (MW, the difference between the carapacial width and the width across the pleurals taken between the points of juncture of the marginals and pleurals at the level of the seam between the second and third vertebrals), greatest plastron length (PL), greatest width and length of both plastral lobes (APW, APL; PPW, PPL), least bridge length (BL), greatest width and length of the cervical scute (if present; CERW, CERL) and all vertebrals (V1W, V1L, etc.) scutes, and medial seam lengths of all plastral scutes (Gul., Hum., Pect., Abd., Fem., An.). Also noted were the number of submarginal scales on each bridge, the presence of any supernumerary scales on the anterior lobe of the plastron, the condition of the posterior plastral rim (smooth, slightly serrate, or serrate), if the lateral rim of the carapace was straight or indented at the bridge, the extent of development of the cephalic shield, the size and degree of development of the hooked upper jaw (short, S; medium, M; long, L) and the presence or absence of a postorbital stripe. The number of rows of large scales at the lateral edge of the antebrachium between the claw of the fifth digit and the first horizontal skin fold proximal to the elbow (FLSR) was also recorded.

In addition, careful notes were made of head, neck, limb, carapace and plastron patterns, and colors were recorded from living turtles and color transparencies. Specimens were assigned to subspecies according to these characters, and their collection locality.

Statistical techniques were executed using SAS 6.12. Levels of significance were set a priori at $\alpha = 0.05$.

Results

Normal plots by sex and subspecies showed no strong deviation from normality for the morphological variables used in multivariate analyses, so the untransformed variables were used. MANOVA (using pooled covariance matrices) indicated significant differences between subspecies were present in both the female and the male samples. A statistically conservative pairwise comparison (Roy & Bose 1953) showed that for both sexes only *shiui* was significantly different from the other taxa.

Canonical discriminant analyses using resubstitution had overall error rates of 8.6% for females and 10.5% for males, but when using cross validation (the preferred method) these rates increased to 40% for females and 57.6% for males. Removal of gular and humeral data (characters important in *tristernalis*) did not significantly affect these results.

Under cross validation, only one of three female *vogeli* was properly identified (one each of the remaining female specimens was improperly placed with *megacephalum* and *peguense*); but *megacephalum* (67% accurately identified, 17% as *peguense,* 11% as *vogeli,* and 6% as *shiui*), peguense (55% accurately identified, 36% as *megacephalum,* and 9% as *vogli*), and *shiui* (67% accurately identified, and 33% as *megacephalum* appeared valid. The inclusion of both *megacephalum* and *peguense* in *vogeli* suggests invalidity of the latter taxon. For

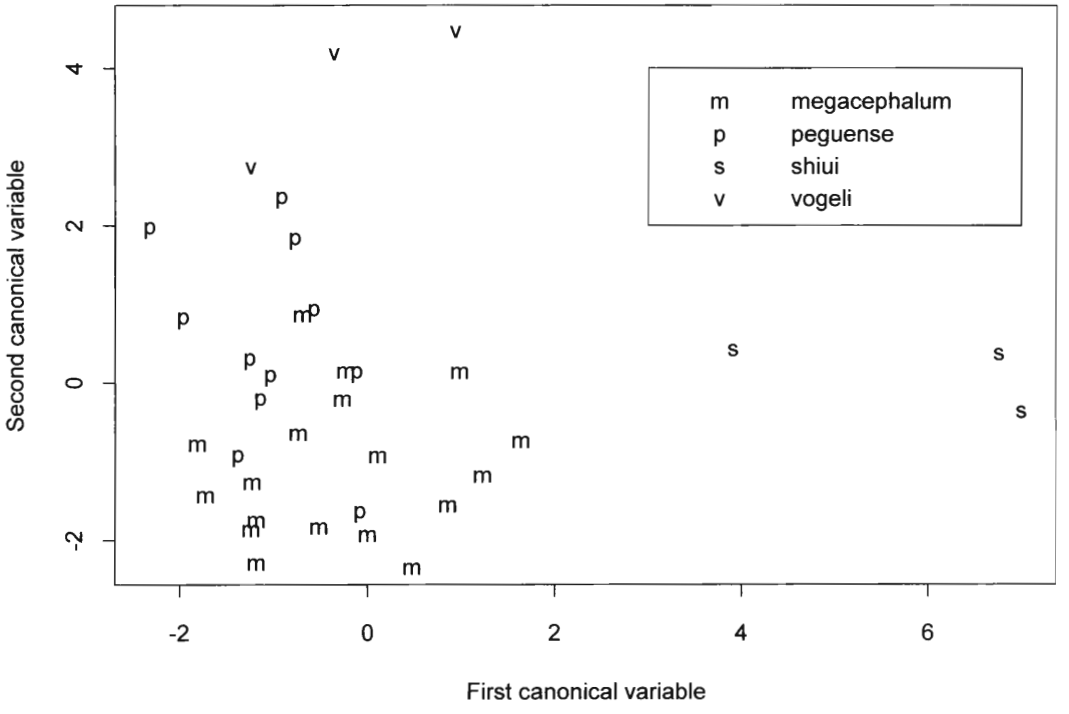

Fig. 1. Plot of the first two canonical variables of females.

males, the cross validation technique also revealed much overlap between the various taxa. The two male tristernalis were accurately identified, as were 71% of male *shiui* (18% as *megacephalum,* and 6% as *peguense*); but only 40% each of *megacephalum* (40% as *shiui,* and 10% as *peguense*) and *peguense* (40% as *shiui,* and 10% as *megacephalum*) were properly identified. Only one of two male *vogeli* was properly identified (the other was placed with *megacephalum*), further suggesting invalidity of the taxon.

Examining a plot of the first two canonical variables from females (no female *tristernalis* were available) resulted, as expected from the resubstitution results, in good separation of *shui,* but not very good separation for megacephalum, *peguense* and *vogeli* (Fig. 1). The plots of *megacephalum* and *peguense* overlapped, and *vogeli* formed an extension of *peguense.* Invalidity of *vogeli* is further supported by its sharing plastron and head patterns with *peguense.* Partial univariate *f*-statistics identified Pect., Fem., and APW as the most important characters separating females.

The same plot for males (Fig. 2) shows good separation for male *peguense, tristernalis* and *vogeli,* but not for *megacephalum* and *shui.* Partial univariate *f*-statistics identified APW, PPW, and An as the most important characters separating males.

Logistic regression ($P < 0.0001$) of the snout and jaw hook indicated that these supposedly important features for separating *peguense* and *vogeli* increase with size and are not reliable taxonomic characters for distinguishing the two taxa.

Discussion

Discriminant function analysis with cross validation, although sample sizes were small, did not properly classify more than 50% of male *vogeli,* and more than 33% of females–males were misidentified as *megacephalum*; females as either *megacephal-*

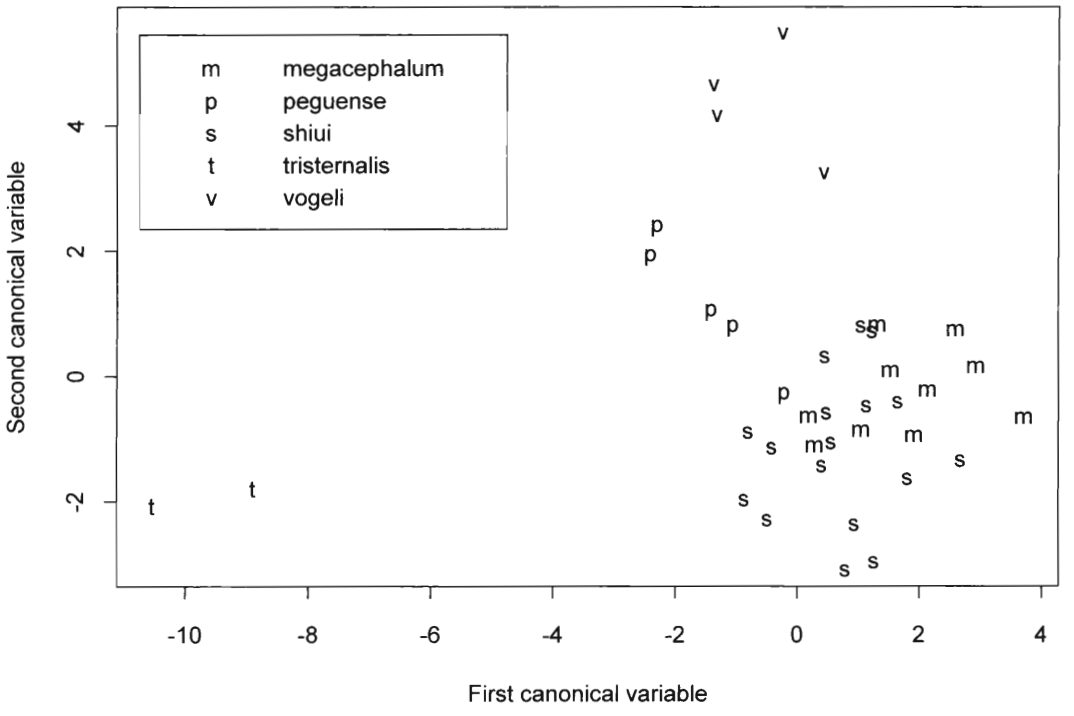

Fig. 2. Plot of the first two canonical variables of males.

um or *peguense*. The subspecies *vogeli* shares a black-bordered postorbital stripe, unpatterned jaws, and a dark plastron pattern with *peguense*. The two subspecies reportedly differ in the length of upper jaw hook, the condition of the posterior carapace rim, and the condition of the dark plastron pattern (Ernst & Barbour 1989). The upper jaw of *vogeli* is not short and not strongly hooked, that of *peguense* is supposedly strongly hooked; the posterior carapace rim of *vogeli* is smooth and unserrate, that of *peguense* is serrate; and *vogeli* has a larger, faded plastron pattern, *peguense* a dark seam-following plastron pattern. These three characters are ontogenetic, change with growth, and should not be considered valid for separating the two taxa. The snout and upper jaw of all *P. megacephalum* are relatively short at hatching, but lengthen with age (Table 1). Similarly, a serrate posterior carapace rim is normally a juvenile condition in turtles, and the rim becomes less serrate with growth, until very smooth in large adults. The dark seam-following pattern of juvenile turtles usually spreads from the seams to cover progressively more of the plastron surface, and eventually fades and is no longer dark in adults (species in the North American emydine genera *Graptemys, Pseudemys* and *Trachemys* are good examples; Ernst et al. 1994). Elimination of these three characters makes a stronger case for placing *vogeli* in the synonymy of *peguense*. Also, *peguense* was described from three juvenile syntypes (BMNH 1946.9.7.42, 1946.1.22.21, 1946.1.22.22), but the holotype and paratype of *vogeli* (SMNS 4573 and 3755, respectively) are adults. Therefore, we believe *vogeli* to be the adult stage of *peguense* and recommend that it be placed in the synonomy of *peguense*.

Two juveniles with 95 mm and 102 mm carapace lengths from Hainan Island, China within the geographical range of *shiui* exhibited the three characters discussed above, but the posterior carapace rim was

Table 1.—Condition of upper jaw in *Platysternon megacephalum.*

Taxon (n)	Sex (n)	*Jaw condition*		
		Short	Medium	Long (Hooked)
megacephalum (20)				
	F (7)	0	1	6
	M (9)	0	5	4
	J (4)	1	3	0
peguense (16)				
	F (3)	0	0	3
	M (0)	0	0	0
	J (13)	9	4	0
shiui (17)				
	F (7)	0	3	4
	M (6)	0	4	2
	J (4)	0	4	0
tristernalis (2)				
	M (2)	0	0	2
vogeli (10)				
	F (4)	0	0	4
	M (0)	0	0	0
	J (6)	4	1	1

only "slightly serrated" and the turtles resembled *P. t. peguense*; adults from Hainan Island resembled *shiui* (de Bruin & Artner 1999). Consequently de Bruin & Artner (1999) proposed that *shiui* was merely the adult of *peguense.* We have examined *shiui* (102–106 mm CL) from northern Vietnam that lacked a postorbital stripe, a dark plastral pattern, and a serrate posterior carapace rim. They, however, had *shiui* head and carapace patterns. If juvenile *shiui* look like young *peguense,* they must lose the three pertinent characters before reaching a carapace length of 102 mm, which is unlikely. We have also examined adult *Platysternon* from Hainan which resembled both *shiui* and *peguense* (FMNH 6631, 6632; UMMZ 129833). This raises questions as to what is occurring there. Are the two subspecies naturally present, and has intergradation taken place? Has *peguense* been introduced for the food trade? More study is needed to address these points.

The small extra scutes at the gular-humeral seam in *tristernalis* are developmental anomalies, not fixed characters, and should not be used for designating taxa. Subdivisions at the borders of scutes create smaller, additional scutes, and can occur at any position on a turtle's shell (Zangerl & Johnson 1957, Zangerl 1969). Such supernumerary scutes are commonly found when a series of turtles of like taxon are examined (Parker 1901, Newman 1906, Coker 1910, Babcock 1930, Hildebrand 1930, Grant 1937, Lynn 1937, Lynn & Ullrich 1950, Sturn & Brattstrom 1958, Zangerl & Johnson 1967, Baker 1968, Bonaric & Bons 1971, Ernst 1971, Schwartz & Peterson 1984), are known from all turtle families with scutes (Ewert 1979), and probably occur in all turtle genera with scutes (Ernst, pers. obs.). Such anomalies are common at the gular-humeral seam in *Platysternon megacephalum* (Table 2), including in two of three syntypes of *peguense* (BMNH 1946.1.22.21, 1946.1.22.22), and therefore, because supernumerary scutes are found in all subspecies of *P. megacephalum, tristernalis* is considered invalid. This taxon

Table 2.—Supernumerary scutes at the gular: humeral interface in *Playsternon megacephalum*.

Taxon (n)	Sex (n)	Number of extra scutes (n)
mecagephalum (2)		
	F (1)	1
	M (1)	1
peguense (11)		
	F (3)	1, 2 (2)
	M (2)	1, 2
	J (6)	1 (4), 2 (2)
shiui (2)		
	M (1)	1
	J (1)	1
tristernalis (2)		
	M (2)	3, 4
volgeli (5)		
	F (4)	1 (3), 2
	J (1)	1

should be relegated to the synonymy of the subspecies *megacephalum,* which it most closely resembles and within whose range its type-locality lies.

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Appendix 1

Platysternon megacephalum examined.

Specimens from the following collections were examined: British Museum of Natural History (BMNH); California Academy of Sciences (CAS); Field Museum of Natural History (FMNH); George Mason University (GMU); Museum National d'Histoire Naturelle, Paris (MNHP); National Natuurhistorisch Museum, Leiden (RMNH); Naturhistorisches Museum Wien, Vienna (NHMW); Natur-Museum Senckenberg, Frankfurt-am-Main, Germany (SMF); Staatliches Museum Naturkunde, Stuttgart (SMNS); Staatliches Museum für Tierkunde, Dresden (MTKD), United States National Museum of Natural History (USNM); University of Michigan Museum of Zoology (UMMZ); William P. McCord, Hopewell Junction, New York, personal collection (WPM); William H. Randel, Hatboro, Pennsylvania, personal collection (WHR), Zoologisches Institut und Museum Hamburg (ZMH), and the Zoologische Staatssammlung München (ZSM).

Platysternon megacephalum megacephalum (51): BMNH 1870.1.14.26, 1946.9.7.42(47a)–holotype, 1954.5.4.3, 1983.6.60; CAS 12343, 16529, 74579; FMNH 15909, 24230, 51627; GMU 1102; MNHN 1945; NMW 1748, 19652, 19653-1, 19653-2, 19654, 29477; SMF 33094, 34457, 37021, 40210, 40211, 40212, 40213, 59446, 60053, 65758, 69147, 69774, 69794, 71654; UMMZ 129761; USNM 66454, 73119, 73120, 73121, 73122, 136016, 286813; WPM 1–11.

Platysternon megacephalum peguense (42): BMNH 1882.10.7.1, 1887.11.2.1, 19214.1.195, 1921.4.1.196, 1927.5.20.45, 1946.1.22.21–syntype, 1946.1.22.22–syntype; CM 89809, 89814; FMNH 6628, 6631, 6632; GMU 2985, 3407; MNHN 1893-301, 1935-467, 1982-251; NMW 20825, 29287; SMF 21489, 57544, 66464, 66465, 69684, 69955, 70531, 72682, 73011; UMMZ 101652, 101665, 101666, 112313, 129833, 141782; USNM 068166, 129761, 339715, 339716, 339717; WHR 31; WPM 1–2.

Platysternon megacephalum megacephalum x Platysternon megacephalum peguense (1): BMNH 1983.6.59.

Platysternon megacephalum shiui (26): BMNH 1979.64; GMU 3408, 3821; MNHN 1935–121; NMW 1144; RMNH 6489, 14908; USNM 266160–holotype, 266161–paratype; WHR 30; WPM 1–8, 12–16.

Platysternon megacephalum tristernalis (2): ZSM 318/1980–paratype, 319/1980–holotype.

Platysternon megacephalum vogeli (14): MTKD 19219, 40714, 40715, 40793, 41342; SMNS 3755–paratype, 4573–holotype; WHR 1; WPM 1; ZMH R01081, R01088, R04051; ZSM 220/1982, 55/1990.