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Accepted: 7 July 1997.

Journal of Herpetology, Vol. 31, No. 4, pp. 507–513, 1997

Taxonomic Revision of the South American Subspecies of the Turtle *Kinosternon scorpioides*

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ABSTRACT.—**The taxonomic status of *Kinosternon scorpioides seriei* Freiberg, and *K. s. carajasensis* Cunha is reviewed. The diagnostic characters from their original descriptions were reassessed. Morphometric distinction was evaluated with principal components, UPGMA cluster, and discriminant function analyses. The presumed distinctive characters showed extensive overlap among both subspecies and the nominal race, and no new character could be found to discriminate among the three subspecies. The taxonomic significance of their supposed allopatry is discussed. It is suggested that both *K. s. seriei* and *K. s. carajasensis* be placed in the synonymy of *K. s. scorpioides*.**

The South American subspecies of *Kinosternon scorpioides* include *K. s. scorpioides* (Linné, 1766), *K. s. seriei* Freiberg, 1936, and *K. s. carajasensis* Cunha, 1970. *Kinosternon s. pachyurum* Müller and Hellmich, 1936, is regarded as a synonym of *K. s. seriei* (Freiberg, 1938; Berry, 1978; Cei, 1993). These forms are supposedly well-delimited geographically: *Kinosternon s. seriei* inhabits the Gran Chaco, *K. s. carajasensis* occurs only in the Serra dos Carajás, State of Pará, Brazil, and the nominal form is widespread in northern South America (Pritchard and Trebbau, 1984). However, subspecific identification of specimens without locality data is often difficult, due to overlapping of diagnostic characters.

Kinosternon s. seriei and *K. s. carajasensis* were described on small, perhaps inadequate samples. As a result, their validity, or that of their diagnostic characters, has been doubted repeatedly (e.g., Pritchard, 1979; Vanzolini et al., 1980; Vanzolini, 1981; Pritchard and Trebbau, 1984; Cabrera, 1995).

In his description of *K. s. seriei*, Freiberg (1936) gave not a diagnosis, but a brief description based on three specimens representing both sexes, with measurements and illustrations. Under the subheading "Observaciones" Freiberg summarized the features that he felt would distinguish this subspecies (see below).

Cunha (1970) described *K. s. carajasensis* on the basis of six individuals, juvenile and adult, representing both sexes, four of them forming the type series. He provided a diagnosis, with measurements and some drawings, comparisons to related forms, and a map of the Serra dos Carajás. Later, Cunha et al. (1985) treated this form as a synonym of *K. s. scorpioides* with a brief justification: "... presently admitted as a synonym of (*K.*) *scorpioides scorpioides*, notwithstanding showing marked variations" (our translation).

In order to assess the validity of, or relationships among these three South American races of *K. scorpioides*, we conducted this review.

MATERIALS AND METHODS

This study was approached from two levels: (1) morphological features relevant to the recognition of these subspecies, according to their original descriptions, were analyzed and compared; (2) a numerical analysis was performed, including both "diagnostic" and other mensural characters from the shell.

The samples comprised turtles with carapace length >110 mm from throughout the range of the nominal race in Brazil, plus all available specimens of *K. s. seriei* in the South American collections surveyed, and all the type series of

K. s. carajasensis, except one juvenile (see Appendix 1).

Shell and scute measurements (to the nearest 0.5 mm) were recorded, including proximal dorsal width of the nuchal (=cervical) scute (PN); distal dorsal width of the nuchal scute (DN); midline length of the nuchal scute (NL); maximum width of the first vertebral (=central) scute (WVI); maximum carapace length (CL); maximum carapace width (CW); midline length of gular scute (GL); midline length of the plastral forelobe (PFL); maximum length of the plastral hindlobe (PHL); maximum plastron length (PL); height of the anterior shell opening, measured from the ventral plane to the medial anterior border of the carapace (AH). Because the interfemoral (IF) and interanal (IA) seams are frequently asymmetrical in this species, the length of the medial border of the right and left of each pair of scutes for each specimen was measured, and the respective means were calculated. Maximum measurements are not always coincident with midline measurements. To facilitate comparisons with earlier papers, our scute terminology follows conventional use, in spite of the probable homology of plastral scutes as proposed by Hutchison and Bramble (1981).

The specimens of the samples vary considerably in CL (mm): *K. s. scorpioides* ($\bar{x}$ = 141.1 ± 12.9, range = 116–166, N = 40); *K. s. seriei* ($\bar{x}$ = 156.6 ± 17.4, range = 135–181, N = 9); *K. s. carajasensis* ($\bar{x}$ = 125.3 ± 3.5, range = 122–129, N = 3). Therefore, all characters were standardized for body size by linear regression of each variable against CL, using the residuals in the statistical calculations. The use of residuals has been controversial (see review in Jungers et al., 1995). However, we submitted our raw data to DM RAW (ratios formed by dividing each variable by the geometric mean, the latter computed as the *n*th root of the product of all n variables; Jungers et al., 1995), as an alternative size-adjustment method, and the results obtained were virtually identical to those using residuals. The use of residuals as input variables was preferred because it has proved useful in taxonomic studies of turtles (e.g., McCord and Iverson, 1991; Iverson and McCord, 1994).

ANOVA and MANOVA tests were performed between *K. s. scorpioides* and *K. s. seriei*; *K. s. carajasensis* was excluded due to small sample size. A principal components analysis (PCA) of the character correlation matrix, a UPGMA cluster analysis using Squared Euclidean Distance, and a canonical discriminant function analysis (DFA) were performed using the residuals of each character, with the exception of CL, PN, DN, and NL. The last three characters were excluded because they showed no linear relationship to CL. Only one male specimen (the type) and two females of *K. s. carajasensis* were available for analysis. Therefore, these specimens were included as ungrouped (i.e., classified a posteriori) in the DFA of *K. s. scorpioides* versus *K. s. seriei*. In all cases males and females were analyzed separately to reduce the effects of sexual dimorphism. All morphometric analyses were conducted using SPSS (SPSS Inc., 1990) software.

Results

The "Diagnostic" Characters.—Freiberg (1936: 171) gave diagnostic value to the following features in distinguishing *Kinosternon scorpioides seriei* from *K. s. scorpioides* (our translation hereafter):

(1) "... nuchal scute as wide in its base as it is long; ..." In nine studied specimens of *K. s. seriei*, both of the paratypes roughly meet that condition; in two others the nuchal scute is a tiny triangle with its base cephalad (AC 384, FML 00043); in two other specimens the scute is inappreciable from dorsal view (FML 00026, 00029); in two others it is trapezoidal, longer than wide (FML 00007, MACN 11968), and in the remaining one it is trapezoidal, wider than long.

(2) "... (inter) anal seam three or four times (longer than) the (inter) femoral seam; ..." Nearly all the *K. s. seriei* sample fulfills this condition (range IA/IF = 2.05–4.35, $\bar{x}$ = 3.36, N = 9), except MACN 11968 (IA/IF = 2.38), and one paratype (MACN 1247; IA/IF = 2.05). However, that ratio is not exclusive to chacoan specimens. In *K. s. carajasensis* the ratio IA/IF averages 2.89 (range = 2.44–3.27, N = 3). Some specimens of the nominal form (MZUSP 5, 1044, 1050, 2169, 2178, 2929, 2933, 3095) are similar (range = 3–3.52, $\bar{x}$ = 3.22) to *K. s. seriei*, and the ratio approximates to four in MZUSP 2736, 2938, and 3088. The IA/IF ratio does not exhibit clinal variation (Fig. 1).

(3) "... femoro-abdominal seam very broad, and with intercalary cornified plates ...." The "cornified plates" are actually remnants of the fragmented adcephalic margin of the femoral plates. This is clearly evident following the outline of the last growth rings on these plates in specimens with intense plastral wear (e.g., MACN 13885 and FML 00029). In specimens with little plastral wear (e.g., FML 00043) those supposed intercalary plates are always absent (i.e., last growth rings are complete).

The adcephalic margin of the femoral plates seems prone to fracture, perhaps due to aging or by simple abrasion. The result is a broader exposition of the underlying cartilage, that allows the plastral hindlobe to move, in worn turtles. As expected, specimens of *K. s. scorpioides*

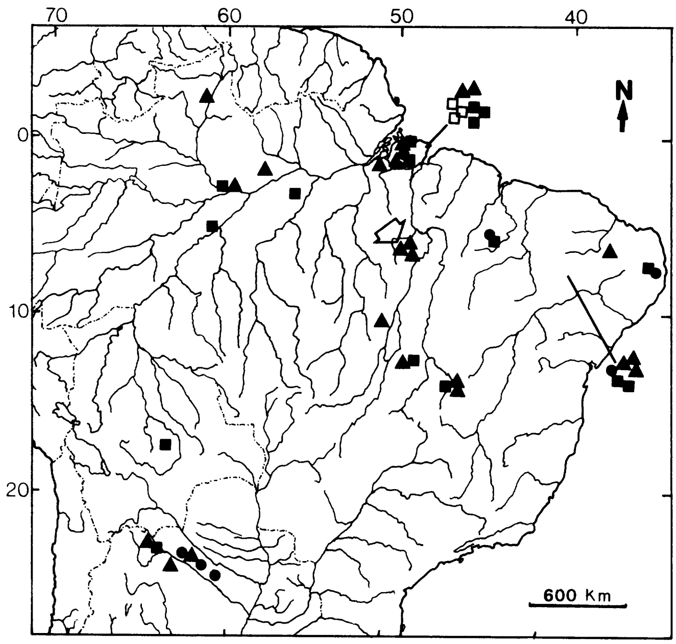

FIG. 1. Geographic distribution of the interanal seam length/interfemoral seam length (IA/IF) in *Kinosternon scorpioides carajasensis* (arrow), *K. s. seriei* (Bolivian and Argentine records), and *K. s. scorpioides* (all others). Each symbol represents one specimen. Ratios are: 1 (□); 2 (■); 3 (▲); 4 (●). For visual clarity each ratio was adjusted to the nearest integer.

(AC 177, MZUSP 1049, 2780, 3142) having worn plastron exhibit "intercalary cornified plates."

(4) "...head, neck, tail, and limbs gray." The color of the skin in live or fresh-killed chacoan specimens (AC 384, FML 00043) is essentially the same as in the nominal form (e.g., description and specimens photographed in Pritchard and Trebbau, 1984).

(5) "... of larger size and more corpulent." See Morphometric analyses below.

In his diagnosis of *Kinosternon s. carajasensis*, Cunha (1970:5) detailed features of this subspecies that we are not able to test completely, because our sample comprised only specimens in the type series. However, it is noteworthy that in the extensive MZUSP collection there is not a single specimen determined by the curators as, or assignable to, *K. s. carajasensis*. Based on our inspection of those specimens, we note the following.

(1) The paramesial keels of the carapace are indeed very low in comparison to the median keel, but only in two specimens. One of the paratypes (MPEG 13) is little different from those in the nominal form (e.g., MZUSP 3136), which is likewise variable in the relative height of its keels, including cases of asymmetry.

(2) "... nuchal scute extremely small in dorsal view; ..." This is not a diagnostic feature, because in *K. s. scorpioides* the nuchal scute also may be tiny in relation to body size (e.g., MZUSP 1045, 2176) or even inappreciable from dorsal view (MZUSP 2929, 2938), just as in *K. s. seriei* (see above).

(3) "... skull large in relation to body size, ..." Although we lacked a cranial series of this subspecies to compare, specimens of the other two subspecies (e.g., MZUSP 5, FML 00043) drew our attention for their large heads with respect to their body size. Moreover, a relatively larger head in males is assumed to be a sexually dimorphic character (Pritchard and Trebbau, 1984).

Morphometric Analyses.—Univariate tests (ANOVA) for males showed significant differences between *Kinosternon s. scorpioides* and *K. s. seriei* in CW ($F_{1,18} = 8.43$, $P = 0.009$), and IA ($F_{1,27} = 5.39$, $P = 0.028$) characters. However, CW was the only character showing heteroscedasticity to Bartlett-Box Test. In the female ANOVAs, CW and IA also showed significant differences between subspecies ($F_{1,15} = 7.15$, $P = 0.017$, and $F_{1,17} = 5.05$, $P = 0.039$, respectively).

For each sex, MANOVA tests showed no significant differences ($F = 1.69$, df = 10, $P = 0.213$, in males, and $F = 2.01$, df = 7, $P = 0.185$, in females) between *K. s. scorpioides* and *K. s. seriei*. CW probably reflects dissimilar body shapes. IA seems to be the only character with different averages for both sexes of both subspecies: *K. s. scorpioides*: $\bar{x} = -0.52$, SD = 2.48, N = 23, and $\bar{x} = -0.53$, SD = 2.28, N = 14

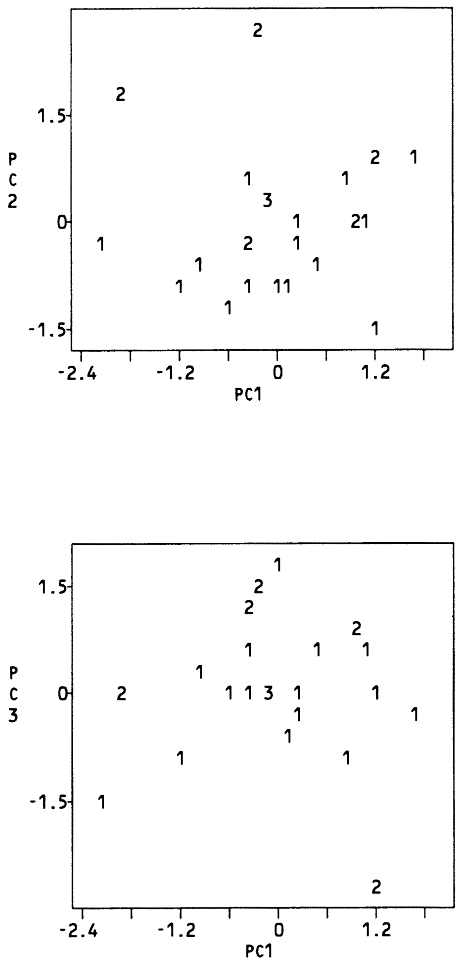

FIG. 2. Plot of males of *Kinosternon s. scorpioides* (1), *K. s. seriei* (2), and *K. s. carajasensis* (3) based on principal components analysis of size-adjusted residuals of measurable characters. Each number represents one specimen.

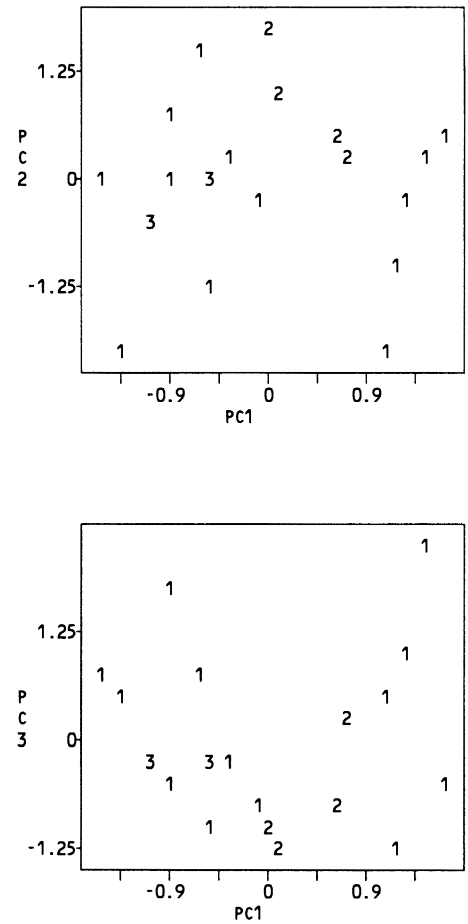

FIG. 3. Plot of females of *Kinosternon s. scorpioides* (1), *K. s. seriei* (2), and *K. s. carajasensis* (3) based on principal components analysis of size-adjusted residuals of measurable characters. Each number represents one specimen.

(males and females, respectively); *K. s. seriei*: $\bar{x} = 2.41$, SD = 2.94, N = 5, and $\bar{x} = 2.15$, SD = 1.02, N = 4 (males and females, respectively). However, the small samples of *K. s. seriei* and high correlation of IA with body size obliges caution in the application of this single character to a diagnosis.

The PCA results for males (Fig. 2) and females (Fig. 3) showed no clear separation among the three subspecies. The first principal component (PC1) accounted for 31.5% of the total variation in males, and 37.6% in females. Characters most influential to PC1 were PHL and PL in males, and PHL, IA, and PL in females (Table 1). On this axis both males and females of *K. s. seriei* and *K. s. carajasensis* fell within the variation of *K. s. scorpioides* (Figs. 2 and 3).

The second principal component (PC2) accounted for 28.9% of the remaining variation in males and 18.5% in females. The most influential characters loading on PC2 were IA, IF, and CW in males, and CW in females (Table 1). On this axis only males of *K. s. seriei* were partially separated from the males of the nominal subspecies (Fig. 2). The third principal component (PC3) accounted for 16.1% of the remaining variation in males, and 14.2% in females. Characters most influential were WVI for males, and IF and WVI in females (Table 1).

The cluster analysis produced dendrograms (Fig. 4) in which specimens of neither *K. s. seriei* and *K. s. carajasensis* were homogeneous. The DFA was congruent with the PCA in that a clear separation among the three subspecies was not evident (Fig. 5). The first canonical discriminant function explained 60% of the variability among

TABLE 1. Loadings for the most influential characters from principal components analysis. Characters coded in text.

	Males			Females			
	PC1	PC2	PC3	PC1	PC2	PC3	PC4
Residuals							
WVI	0.104	−0.013	−0.720	0.075	0.239	0.771	−0.317
CW	−0.156	0.794	0.281	0.019	0.811	−0.016	−0.401
IA	0.199	0.917	−0.140	0.830	0.208	−0.232	−0.177
IF	0.114	−0.852	−0.046	−0.042	−0.066	0.899	0.155
PHL	0.910	0.127	−0.073	0.881	0.072	0.071	−0.271
PL	0.853	−0.289	0.221	0.789	0.356	0.344	0.278
AH	−0.709	−0.207	0.367	−0.217	−0.060	−0.068	0.872
Eigenvalue							
	2.83	2.60	1.45	3.38	1.66	1.28	1.04
Cum. Percent							
	31.5	60.4	76.5	37.6	56.1	70.3	81.9

males of both subspecies (Eigenvalue = 1.49, df = 6, P = 0.033). For females, the discriminant function (Eigenvalue = 1.56, df = 3, P = 0.005) explained 61% of the variation between groups, but 100% of the specimens of *K. s. scorpioides* were correctly classified (Table 2). *Kinosternon s. carajasensis* (ungrouped cases) was classified as *K. s. scorpioides* (one male and one female), or as *K. s. seriei* (the remaining female).

DISCUSSION

Our results indicate that the characters selected by Freiberg (1936) and Cunha (1970) to define *Kinosternon scorpioides seriei* and *K. s. carajasensis*, respectively, are not diagnostic of the subspecies, and do not distinguish them from the nominal form. The morphometric analyses also failed to reveal new characters useful to diagnose one or another subspecies.

In addition to the "diagnostic" characters analyzed in this paper, Freiberg (1936) cited two features when describing *K. s. seriei*: short, unsharpened claws and, in females, tail without spur; attributes repeated in Freiberg (1977). Since these characters could be wrongly interpreted as unique to the subspecies, it should be noted that (1) the paratype MACN 1247 has the claws very worn or cut off; the paratype MACN 7058 has the forelimbs mutilated (missing hands) but it has claws on its hindfeet. All other whole chacoan specimens surveyed by us have well-developed claws; (2) all the females do have a very small (up to 4 mm, but clearly distinct) horny spur on the tip of the tail. Surprisingly, in refering to Brazilian specimens (*K. s. scorpioides*) Luederwaldt (1926) also erroneously reported that females lack a tail spur.

The recognition of *K. s. seriei* and *K. s. carajasensis* seems to be thus relatively supported only by body size and geographic isolation. *Kinosternon s. seriei* is generally larger than *K. s. scorpioides*, whereas *K. s. carajasensis* is usually smaller than the others. Body size in *Kinosternon s. seriei* may be affected by the environment. Pritchard and Trebbau (1984) have reported lower growth rates in individuals of the nominal race from forested habitats than those from nonforested situations.

The geographic isolation of *Kinosternon s. seriei* from populations of *K. s. scorpioides* of northern South America is controversial. It cannot be stated that the species is absent in intervening areas, because a complete exploration of these regions is lacking. To the data mapped by Iverson (1992) should be added central Bolivia (MACN 11968) and Paraguay, whence it has been reported by Bertoni (1939—cited in Talbot, 1979), and recently confirmed by Norman (1994), although neither one specifying subspecies. *Kinosternon s. scorpioides* is reasonably well represented in the still incompletely explored Amazon river basin. It seems evident that as the exploration of intervening zones advances, the supposed geographic gap between the two populations is diminishing.

The range of *K. s. carajasensis*, the Serra Norte from the Carajás System, is formed by plateaus (600–800 m above sea level) with steep borders. Nevertheless, faunal interchange with its surroundings seems likely, because the reptile fauna of the Serra Norte (77 species) is chiefly an Amazonian or a wide-ranging one (Cunha et al., 1985). These authors considered as probably endemic a single species, the colubrid snake *Liophis carajasensis*. For turtles, however, having obtained some additional specimens of *Kinosternon* from Carajás, Cunha et al. (1985) found no reasons to recognize *K. s. carajasensis* as a distinct taxon.

We concur with Vanzolini (1992) that the rec-

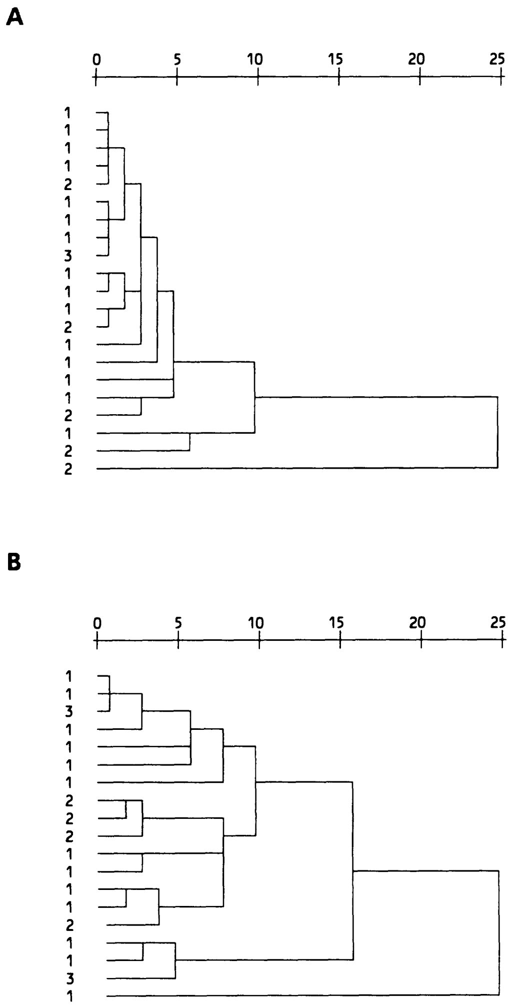

FIG. 4. UPGMA dendrograms of males (A), and females (B) of *Kinosternon s. scorpioides* (1), *K. s. seriei* (2), and *K. s. carajasensis* (3). Each number represents one specimen.

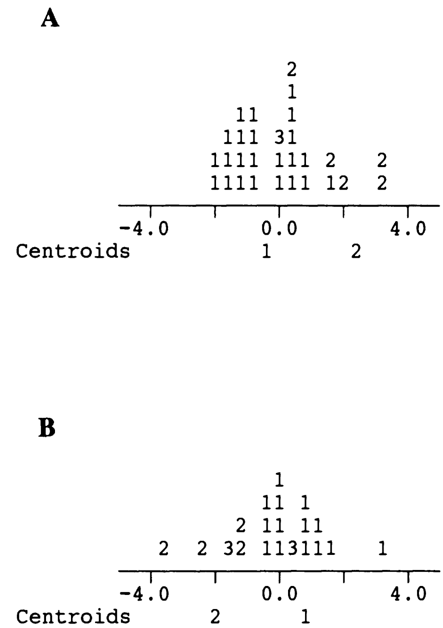

FIG. 5. Histograms of discriminant scores for first canonical function for males (A), and females (B) of *Kinosternon s. scorpioides* (1), *K. s. seriei* (2), and *K. s. carajasensis* (3, classified a posteriori). Each number represents one specimen.

ognition of a subspecific taxon is justified when the geographic and genetic conditions that define the subspecies concept are fulfilled. There is no evidence of geographic intergrading ("hybrid zone") among members of these populations of *Kinosternon*. Our results also show that phenotypic differences consistent enough to recognize South American subspecies other than the nominal form are lacking. Therefore, we suggest that both *K. s. seriei* and *K. s. carajasensis* be placed in the synonymy of *K. s. scorpioides*.

Acknowledgments.—We thank Ana M. Ramos Costa and Paulo Vanzolini (Museu de Zoologia da Universidade de São Paulo, MZUSP); Teresa Sáuer de Avila-Pires (Museu Paraense Emílio Goeldi, Belém, MPEG); Gustavo Carrizo and Esperanza Varela de Olmedo (Museo Argentino de Ciencias Naturales, Buenos Aires, MACN); Raymond Laurent, Gustavo Scrocchi, and Sonia Kretzchmar (Fundación Miguel Lillo, Tucumán, FML) for free access to, or loan of, specimens in their care, and for providing working space. We are grateful to Richard Seigel and two anonymous reviewers for comments that improved the manuscript. This research was funded by SECYT-UNC (Secretaría de Ciencia y Tecnología de la Universidad Nacional de Córdoba), and by SECITECOR (Secretaría de Ciencia y Tecnología de la Provincia de Córdoba, Argentina).

TABLE 2. Summary of classification results of discriminant function analysis. Abbreviations: sc = *Kinosternon s. scorpioides*; se = *K. s. seriei*; un = ungrouped (actually *K. s. carajasensis*). Percent of "grouped" cases correctly classified: 92.86% (males), 88.89% (females).

Actual group	No. of cases	Predicted group membership (%) sc	se
Males			
sc	23	22 (95.7)	1 (4.3)
se	5	1 (20)	4 (80)
un	1	1 (100)	0 (0)
Females			
sc	14	14 (100)	0 (0)
se	4	2 (50)	2 (50)
un	2	1 (50)	1 (50)

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Accepted: 9 July 1997.

Appendix 1

Specimens Examined

Collection acronyms are as indicated in Acknowledgments, except AC = Personal collection of the senior author.

Kinosternon scorpioides scorpioides.—Brazil. Amazonas: Manicoré (MZUSP 2911); Itapiranga (MZUSP 2181); Manaus (AC 177); Itacoatiara (MZUSP 2780). Goiás: Barra do Rio São Domingos (MZUSP 1044, 1048, 1050); (Rio) Cana Brava (MZUSP 1045, 1049). Maranhão: (MZUSP 5); Barra do Corda (MZUSP 2736, 2737). Mato Grosso: Barra do (Rio) Tapirapé (MZUSP 2185). Pará: Breves (MZUSP 2180); Chaves (MZUSP 2176, 2177); Souré (MZUSP 2170, 2171, 2172, 2173, 2174, 2175, 2746, 2747); Rio Xingu (MZUSP 3132, 3136); Gurupá (MZUSP 2182); São Luís, Rio Tapajós (MZUSP 2184); Rio Ganhoão (MZUSP 2178, 2179). Paraíba: Gurinhém, Fazenda Salgado (MZUSP 3088, 3112); Coremas (MZUSP 2169). Pernambuco: 5 Km E of Exu (MZUSP 2929, 2931); Exu (MZUSP 2933, 2938; 2939, 3047). Rondônia: Rio Machado, Cachoeira de Nazaré (MZUSP 3095). Roraima: Serra da Lua (MZUSP 3142).

Kinosternon scorpioides seriei.—Argentina. Formosa: Departamento Bermejo, Estación Chiriguanos (AC 384, alive); Departamento Matacos, Ingeniero Juárez (MACN 13885); Departamento Patiño, Las Lomitas (FML 00029). Salta: Departamento Anta, 100 km NE of Joaquín V. González (FML 00043); Departamento Orán, Tabacal (MACN 1247, paratype; the holotype—same number, different sex—remained missing during this work; it was rediscovered in early 1996, and could not be included in this study); Orán (MACN 7058, paratype); Departamento Rivadavia, Los Blancos (FML 00007); "Chaco salteño" (FML 00026). Bolivia. Departamento Santa Cruz, Buena Vista (MACN 11968).

Kinosternon scorpioides carajasensis.—Brazil. Pará: Serra dos Carajás, Serra Norte (MPEG 15, holotype; MPEG 13 and MPEG 14, paratypes).