

Taxonomic Observations on Extant Species and Subspecies of Slider Turtles, Genus Trachemys

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Taxonomic Observations on Extant Species and Subspecies of Slider Turtles, Genus *Trachemys*

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Slider turtles, Trachemys, have the widest distribution of any turtle genus in the New World. They range from Michigan to Argentina (Fig. 1), and approximately 26 extant forms are known. Most of them are recognized as subspecies of the megaspecies Trachemys scripta (Ernst, 1990). The taxonomy of sliders has been a source of confusion for much of the past century. However, within the last 15 years, advancements have been made toward stabilizing generic assignment (Seidel and Smith, 1986) and identification of species/subspecies (a taxonomy) in Mesoamerica (Legler, 1990), the West Indies (Seidel, 1988), and South America (Pritchard and Trebbau, 1984; Vanzolini, 1995). Nevertheless, questions and controversy remain regarding the species/subspecies status of many of the forms. Resolution has been difficult because all of the recognized taxa are either allopatric or parapatric, with only rare or questionable cases of sympatry (Bogert, 1961; Degenhardt and Christiansen, 1974; Ward, 1980; Seidel et al., 1999). A simple solution would be to recognize all of the allopatric subspecies as species (e.g., Collins, 1990; Frost and Hillis, 1990);

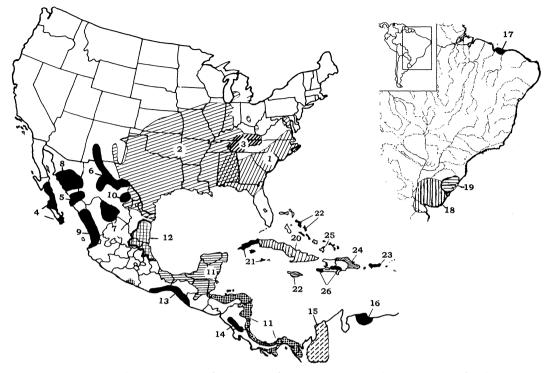


FIG. 1.Distribution of extant species and subspecies of Trachemys. Maps and ranges are modified from Seidel (1988, 1989), Ernst (1990), Legler (1990) and Iverson (1992). Numbers represent taxa listed in Table 2.

however, in my view removing a taxonomic level reduces the hierarchical and biogeographic information content of species nomenclature.

Most authors have recognized the West Indian sliders as several species, distinct from T. scripta (sensu Seidel, 1988). However, continental forms, ranging from the United States through Central America to South America have been considered by some a single polytypic species, Pseudemys (Trachemys) scripta (Smith and Smith, 1979; Legler et al., 1980; Legler, 1990), whereas others have elevated various subspecies to species rank: T. dorbigni (see Seidel, 1989), T. gaigeae (see Ernst, 1992), *Pseudemys grayi* (Williams, 1956; Wermuth and Mertens, 1961), *Pseudemys, Chrysemys,* or Trachemys ornata (Wermuth and Mertens, 1961, 1977; Weaver and Rose, 1967; Holman, 1977; Fritz, 1990), Pseudemys or Chrysemys callirostris (Mertens and Wermuth, 1955; Holman, 1977), and the more recently described T. adiutrix (Vanzolini, 1995). Partial justification has come from recognizing different courtship behavior (Davis and Jackson, 1973; Fritz, 1990; Ernst et al., 1994; Seidel and Fritz, 1997) and reproductive isolation in captivity (Alvarez del Toro, 1972). However, most species interpretations have not been tested, nor universally adopted. Furthermore, no comprehensive phylogenetic (cladistic) analysis of the continental forms of Trachemys has been attempted.

General consensus suggests that slider turtles (*Trachemys*) can be divided into three major groups: United States populations (north and east of the Rio Grande), West Indian populations, and Meso-South American populations (Legler, 1990). Recent morpho-

logical, courtship, and genetic data (Stuart and Miyashiro, 1998; Seidel et al., 1999; M. R. J. Forstner, pers. comm.) have demonstrated that T. s. elegans and gaigeae (both inhabitants of the Rio Grande system in Texas) belong to different species. Further evidence indicates that some of the tropical forms are strongly divergent, whereas others are closely related. These observations are not reflected by current nomenclature, and a taxonomic revision of T. scripta is long overdue. The objectives of the present paper are to examine morphological relationships using phylogenetic analysis; evaluate recent results based on phenetic morphology, courtship behavior, and DNA analysis; and propose a species-level taxonomy for the genus. The intent is not to present a definitive phylogeny for Trachemys but rather to resolve the nomenclatural inconsistencies and provide a more informative and perhaps more stable assignment of species. A phylogenetic species concept is generally followed but several subspecies are retained for terminal taxa with questionable evolutionary trajectories and absence of clearly defined apomorphies. In these cases explicit intraspecific relationships are not implied.

For phylogenetic analysis, all 26 currently recognized taxa throughout the range of *Trachemys* (Fig. 1) were examined, including more than 1200 specimens (see Appendix 1). Fifty-two characters, based on markings, shell measurements, soft anatomy and osteological features, were initially examined. Smith and Smith (1979), Seidel (1988), Legler (1990), and Seidel et al. (1999) have demonstrated that these kinds of characteristics are useful in distinguishing forms of

TABLE 1. Matrix for cladistic analysis of Trachemys. Characters A-W are identified below and states are indicated present (1-3) or absent (0). The primitive (plesiomorphic) conditions are considered to be the states present in Pseudemys and/or Graptemys (the outgroup) and the other character states are considered derived (apomorphic). A, plastron length/carapace length > 0.89 (1). B, cervical scute underlap (ventral length)/carapace length (1 = <0.035, 2 = 0.037-0.050, 3 = >0.055). C, vertebral scute I anterior width/carapace length (0 = <0.150, 1 = 0.154-0.167, 2 = >0.175). D, male foreclaw length (third ungual manus)/carapace length (0 = 0.036-0.060, 1 = 0.077-0.086, 2 = >0.090). E, male snout length (from orbit)/maximum head width > 0.290 (1). F, maximum cranium depth/condylobasal length > 0.315 (1). G, maximum female carapace length > 350mm (1). H, squamosal bone tapered posterodorsally (0), blunt posterodorsally (2), or intermediate (1) (Seidel, 1988). I, pygal bone extended beyond marginal-vertebral seam (Hay, 1908) (1). J, mandibular tomium serrate (1). K, choanal papilla present (Parsons, 1968) (1). L, old males with solid black (melanistic) posterior carapace (Seidel, 1988) (1). M, ocellate yellow-orange lines with dark borders (1) or reticulations (2) on carapace. N, dark line symmetrical (dendritic) plastron figure (0), partially disconnected dark spots or ocelli (1), isolated spots or ocelli (2). O, supratemporal (postorbital) stripe yellow (0), orange (1), or red (2). P, supratemporal stripe contacts orbit of eye (1). Q, yellow "Y" figure on gular surface (1). R, ventral surface of mandible rounded (1) not flat (0). S, upper (alveolar) surface of mandible broad (1). T, cutting surface of upper jaw not cusped but medially forms an angle or shallow notch (1). U, zygomatic arch relatively narrow (1). V, narial opening of cranium relatively narrow (1). W, entoplastron not elongate (0), at least as broad as it is long (Jackson, 1988). Characters R-V (Seidel and Smith, 1986).

Characters	A	В	С	D	Е	F	G	Н	I	J	K	L	Μ	N	0	Р	Q	R	S	Т	U	V	W
Outgroup	1	2	1	2	0	1	1	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1
elegans	1	3	1	1	0	1	0	2	1	0	0	1	0	2	2	1	1	1	0	1	1	1	0
scripta	1	3	0	2	0	1	0	2	1	0	0	1	0	2	0	1	1	1	0	1	1	1	0
gaigeae	1	1	2	0	1	1	0	0	1	0	0	0	1	0	1	0	1	1	0	1	1	1	0
taylori	0	1	2	0	0	1	0	2	0	1	0	0	1	0	2	1	1	1	0	1	1	1	0
hartwegi	1	1	2	0	0	1	0	0	1	0	0	0	1	0	1	0	0	1	0	1	1	1	0
yaquia	1	2	2	0	0	1	0	0	1	1	0	0	1	0	1	1	1	1	0	1	1	1	0
nebulosa	0	1	1	0	1	1	1	0	1	0	1	0	2	1	1	0	0	1	0	1	1	1	0
hiltoni	0	1	1	0	1	1	1	0	0	0	1	0	2	1	1	0	0	1	0	1	1	1	0
ornata	0	1	2	0	0	1	1	0	1	1	0	0	1	0	1	1	1	1	0	1	1	1	0
cataspila	0	1	2	0	1	1	0	1	0	1	0	0	1	0	0	1	1	1	0	1	1	1	0
venusta	1	1	2	0	0	0	1	1	0	1	0	0	1	0	0	1	1	1	0	1	1	1	0
grayi	1	2	2	0	1	0	1	2	0	1	0	0	1	0	0	1	1	1	0	1	1	1	0
emolli	0	1	2	0	0	0	1	1	1	0	0	0	1	0	1	0	1	1	0	1	1	1	0
callirostris	1	2	1	0	0	1	0	2	0	1	0	0	1	0	2	0	0	1	0	1	1	1	0
chichiriviche	0	2	1	0	0	1	1	2	0	1	0	0	1	0	2	0	0	1	0	1	1	1	0
dorbigni	1	2	2	0	0	1	0	2	0	0	0	0	1	0	1	1	1	1	0	1	1	1	0
decussata	0	2	0	1	0	0	1	0	0	0	0	0	1	0	1	0	1	1	0	1	1	1	0
terrapen	0	2	2	1	0	1	0	2	0	0	0	0	1	0	1	0	1	1	0	1	1	1	0
decorata	0	2	2	1	1	1	1	2	0	0	0	0	1	2	0	0	1	1	0	1	1	1	0
stejnegeri	0	2	1	2	1	1	0	2	0	0	0	1	1	0	2	0	1	1	0	1	1	1	0
vicina	0	2	1	2	1	1	0	2	0	0	0	0	1	0	2	0	1	1	0	1	1	1	0
malonei	0	2	0	2	1	1	0	2	0	0	0	0	1	0	2	0	1	1	0	1	1	1	0
angusta	0	2	0	1	0	0	1	0	0	0	0	0	1	0	1	0	1	1	0	1	1	1	0
troostii	1	3	1	2	0	1	0	2	1	0	0	1	1	2	0	1	1	1	0	1	1	1	0
brasiliensis	1	2	2	0	0	1	0	2	0	0	0	0	0	0	1	1	1	1	0	1	1	1	0
adiutrix	0	2	2	0	0	1	0	2	1	0	0	0	1	0	1	1	1	1	0	1	1	1	0

Trachemys. However, identifying characters that are phylogenetically informative at low taxonomic levels (species/subspecies) is difficult, especially regarding polarization (Arnold, 1981). Because 29 of the 52 characters were not informative due to extensive variation within taxa or excessive variability in the outgroup (questionable polarization), phylogenetic evaluation was based on 23 characters (A–W, Table 1). Cladistic relationships were defined by phylogenetic analysis using parsimony (PAUP vers. 4.0b4a, D. L. Swofford, Sinauer Associates, Sunderland, MA, 1998; and WinClada vers. 0.9.99M244). The parameters included a heuristic search for multiple, equally parsimonious trees via branch-swapping. The maximum number of trees was not designated and all characters received equal weight. Polarities of character states (Table 1) were based on outgroup comparisons and trees rooted with *Graptemys* and *Pseudemys* (evidence that these two genera are the closest outgroups and that *Trachemys* is monophyletic appears in Seidel and Smith, 1986).

Because the number of taxa included was large (26) relative to the number of useful characters (23), it was not surprising that the PAUP algorithm found 86 equally parsimonious trees. Nevertheless, a 50% majority-rule consensus tree (Fig. 2) illustrates hierarchi-

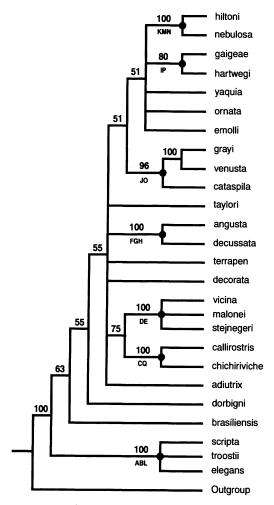


FIG. 2. Fifty percent majority-rule consensus tree (derived from WinClada) rooted with an outgroup of *Pseudemys* and *Graptemys*. The length is 81 and the rescaled consistency index is 0.36. Numbers indicate the frequency (percentage) each branch occurred among all equally parsimonious trees. Solid circles represent nodes for terminal clades with strong support (80–100%), indicative of conspecific taxa (Table 2). Letters represent characters (identified in Table 1), which provide branch support for terminal clades.

cal relationships which are generally congruent with the biogeography of *Trachemys*. Although the tree is polytomous, several major clades are apparent: central and eastern United States forms (*elegans*, *scripta*, *troostii*), Northern Mexico isolates (*yaquia*, *ornata*, *gaigeae*, *hartwegi*, *nebulosa*, *hiltoni*, dis *emolli*), and a Mesoamerican coastal series (*cataspila*, *venusta*, *grayi*). The West Indian *Trachemys* (*terrapen*, *decorata*, *decussata*, *angusta*, *stejnegeri*, *vicina*, *malonei*) appear para- or polyphyletic. Terminal clades which appear in 80–100% of the trees found, (Fig. 2) suggest very close common ancestry, and are here interpreted as polytypic species: *T. scripta* (ssp. *elegans*, *scripta*, and *troostii*); *T. decussata* (ssp. *decussata* and *angusta*); *T. stejnegeri* (ssp. *stejnegeri*, *vicina*, and malonei); T. callirostris (ssp. callirostris and chichiriviche); T. venusta (ssp. cataspila, venusta, and grayi); T. gaigeae (ssp. gaigeae and hartwegi); and T. nebulosa (ssp. nebulosa and hiltoni). Characters which support these lineages (branches) are identified in Figure 2.

Similar to present results, Legler's (1990) phenetic analysis found morphological similarities among isolated populations in northern Mexico. The inclusion of emolli (an isolate from Nicaragua) within this group (Fig. 2) is probably the result of shared homoplasous character states (e.g., B, I or P, Table 1). The divergent position of taylori is also consistent with Legler's analysis, as is the clade formed of coastal Mesoamerican sliders (cataspila, venusta, grayi). For South American sliders, the sister group of callirostris and chichiriviche was not surprising considering their similarity and geographic proximity in northern Venezuela (Pritchard and Trebbau, 1984). However, the absence of a dorbigni, brasiliensis group was unexpected. The "outgroup" positions of dorbigni and brasiliensis appear to be the result of shared primitive character states and treating them as conspecifics could invoke paraphyly. Nevertheless, these two forms are very similar, broadly disjunct from other sliders (Fig. 1), and may intergrade where their ranges contact in southern Brazil (Seidel, 1989). For these reasons brasiliensis is presently retained as a subspecies of *T. dorbigni*. The relationship of adiutrix (northern Brazil) to other South American sliders warrants further examination.

Starkey (1997) analyzed mitochondrial DNA in a variety of Trachemys and found substantial variation among many of the forms, apparently much more than in the related genus Pseudemys (S. K. Davis, unpubl. data). Using a neighbor joining phylogram, Starkey's most divergent lineage was a clade of scripta, elegans, and troostii, which collectively formed the sister group to gaigeae. Although gaigeae is not conspecific with these sliders, hybridization (introgression) and some degree of genetic convergence with *elegans* may be occurring in the Rio Grande (Seidel et al., 1999; M. R. J. Forstner, pers. comm.). Hybridization may also be occurring between elegans in the Rio Grande system (Rio Salado) and taylori in Mexico (Legler, 1963, 1990), although taylori, like gaigeae, has a courtship behavior different from elegans (Davis and Jackson, 1973; Fritz, 1990). Starkey's (1997) results indicate that taylori, yaquia, emolli, and dorbigni are strongly divergent from each other (separate species?) as well as from other Meso- and South American forms. Unfortunately, nebulosa, hiltoni, hartwegi, ornata, malonei, adiutrix, and brasiliensis were not sampled. In contrast to Seidel (1988) and present results (Fig. 2), Starkey (1997) suggested that the West Indian species of Trachemys are a monophyletic lineage. However, the species relationships of Seidel (1988) are generally upheld by his DNA data. It is noteworthy that both types of male sexual dimorphism (snout and foreclaw elongation), which are presumably related to dichotomous courtship patterns (Legler, 1990; Stuart and Miyashiro, 1998), are represented among West Indian Trachemys (Table 1). Divergent reproductive behavior, in addition to the presence of variable forms of male melanism (Seidel, 1988), suggests multiple origins for West Indian sliders.

In conclusion, present results, as well as studies over the last 15 years, indicate that many of the taxa TABLE 2. A proposed taxonomy for species and subspecies of *Trachemys*. Distinguishing characteristics are given for polytypic species which contain new or restricted combinations of subspecies. See Smith and Smith (1979), Pritchard and Trebbau (1984), Seidel (1988, 1989), Legler (1990), Ernst (1990) and Vanzolini (1995) for descriptions and illustrations. The numbers identify geographic ranges in Figure 1.

	Trachemys scripta (Schoepff), 1792:16-isolated spots or ocelli on plastron, old males with solid black
	posterior carapace, elongated cervical scute underlap, elongated male foreclaws.
1	T. s. scripta (Schoepff), 1792:16
2	T. s. elegans (Wied), 1839:213
3	T. s. troostii (Holbrook), 1836:55
	Trachemys nebulosa (Van Denburgh), 1895:84-cervical scute underlap short, male snout elongate, mark-
	ings on carapace irregular or reticulate.
4	T. n. nebulosa (Van Denbrugh), 1895:84
5	T. n. hiltoni (Carr), 1942:1
	Trachemys gaigeae (Hartweg), 1939:1—supratemporal marking orange and not contacting orbit, plastral
	pattern reduced and narrow, pygal bone elongate.
6	T. g. gaigeae (Hartweg), 1939:1
7	T. g. hartwegi (Legler), 1990:89
8	Trachemys yaquia (Legler and Webb), 1970:158
9	Trachemys ornata (Gray), 1831:30
10	Trachemys taylori (Legler), 1960:75
	Trachemys venusta (Gray), 1855:24-vertebral scute broad, mandibular tomium serrate, supratemporal
	stripe yellow and contacting orbit, carapace ocelli complete.
11	T. v. venusta (Gray), 1855:24
12	T. v. cataspila (Günther), 1885:4
13	T. v gravi (Bocourt), 1868:121
14	Trachemys emolli (Legler), 1990:91
	Trachemys callirostris (Gray), 1855:25-supratemporal stripe red and not contacting orbit, "Y" figure
	absent from gular surface.
15	T. c. callirostris (Gray), 1855:25
16	T. c. chichiriviche (Pritchard and Trebbau), 1984:191
17	Trachemys adiutrix Vanzolini, 1995:112
	Trachemys dorbigni (Duméril and Bibron), 1835:272
18	T. d. dorbigni (Duméril and Bibron), 1835:272
19	T. d. brasiliensis (Freiberg), 1969:301
	Trachemys decussata (Gray), 1831:28
20	T. d. decussata (Gray), 1831:28
21	T. d. angusta (Barbour and Carr), 1940:402
22	Trachemys terrapen (Lacépède), 1788:129
	Trachemys stejnegeri (Schmidt), 1928:147
23	T. s. stejnegeri (Schmidt), 1928:147
24	T. s. vicina (Barbour and Carr), 1940:408
25	T. s. malonei (Barbour and Carr), 1938:76
26	Trachemys decorata (Barbour and Carr), 1940:409

(subspecies) of *T. scripta* are broadly allopatric and morphologically distinct. That, combined with evidence of biochemical divergence (Seidel, 1988; Starkey, 1997) and variation in courtship behavior, implicitly supports recognizing most of these taxa as species. Table 2 presents a proposed taxonomy for sliders in the genus *Trachemys*, partitioned into 15 species, eight of which are polytypic. This represents greater species diversity than previous arrangements and could enhance conservation efforts, especially in the Neotropics where protection is often limited to the species level.

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APPENDIX 1

In addition to the 750+ *Trachemys* specimens listed in Seidel (1988) and Seidel et al. (1999), the following specimens were examined. Abbreviations for museums follow Leviton et al. (1985) except for MES (reference collection of author) and PCHP (collection of Peter Pritchard).

Trachemys scripta scripta.—MES 1952. NCSM 7162, 9268–69, 10358, 11873, 13811, 14939, 15115, 16453, 17580, 19175, 20997–98, 21625, 23082, 23879, 24008, 28885. PCHP 303, 306, 331, 1595, 1699, 2695, 4007. UF 11934, 13502, 13506–07, 13572, 13608, 13669, 30108, 65846. USNM 51358–60, 91308.

Trachemys scripta elegans.—MES 1787, 1878, 1948–51, 1953. MSB 23773, 37594, 42230, 42417, 42561–62. TCWC 51831, 61776. USNM 83173–77, 83178–79, 83184–86. UU 4164, 17523.

Trachemys scripta troostii.—MES 1946–47, 1954. UMMZ 96261–63, 218733–35. USNM 86717–18, 86724, 86758–59, 86761, 86786–87.

Trachemys nebulosa nebulosa.—MES (uncataloged). PCHP 403–04. USNM 12622, 240694. UU 12450–51, 12749, 14797.

Trachemys nebulosa hiltoni.—KU 46678, 47585–88, 63601, 63604–09. UU 3824–37, 3831–32, 3840, 3845.

Trachemys gaigeae gaigeae —KU 51202–03, 51208, 51212, 51215, 51219, 51315, 91380. MCZ 31974. MSB 22406, 54750. SRSU 5669, 5930. UU 12406.

Trachemys gaigeae hartwegi.—KU 29357. MCZ 4550– 51. UF 39634, 62933–34. USNM 105265, 105267, 105269. UU 4701, 12504, 17583.

Trachemys yaquia.—UF 52756–62. UU 6030, 6033, 12487.

Trachemys ornata.—KU 63610–11, 78979. UF 48172, 22382. USNM 66198, 238183. UU 3803–04, 3810, 3813, 11147–49, 11154, 11375, 12920, 12923.

Trachemys taylori.—KU 53785, 53787. MES 107. MSB 30552–57, 30559, 30561–63. UF 48101–02, 48092–93. USNM 30560, 159579, 166365. UU 3854, 3861, 11253–56.

Trachemys venusta venusta.—CM 62091, 91077–80, 91082, 96016–18, 96029, 96037, 96040, 96043, 96051, 105873–74, 112796–812, 117679–80, 117682–83, 117685–87, 117689, 117693–94, 124230. KU 85532, 102542, 171406. MCZ 7868, 16770–76, 19351–53, 31484, 31963–64, 34356, 53150, 55121, 71641–42. MES 129. MSB 30549–51. PCHP 4196. UF 7689, 10299, 13479–80 (4), 24071, 37161, 40813, 43106, 50473–75, 50477–80, 50809, 90020, 99978–79. USNM 51068, 53883, 54085, 54088, 55603, 61246, 103707, 129587, 129609, 134440, 136612, 222426, 292553. UU 6164, 6598, 6602, 6693, 6832–40, 6842–49, 6859, 6881, 6899, 6923, 6940, 6962, 9659, 9670, 9679, 9681, 9701–03, 11334, 11342.

Trachemys venusta cataspila.—PCHP 1251, 1840. TCWC 26495, 26497–98, 53145–47. USNM 30746.

Trachemys venusta grayi.—MCZ 4982–87. PCHP 4008. USNM 46281–82, 109086. UU 11362, 11367, 11370, 11372–74.

Trachemys emolli.—KU 85531, 128705–06. PCHP 3359, 4732, 4737. TCWC 56903–09. UU 6701, 6760, 6762, 13026.

Trachemys callirostris callirostris.—FMNH 74893–94, 194301. KU 94578. MCZ 54715–16, 57241–48. MES 1711, 1783. PCHP 15828–31, 2772. UF 22375, 22383, 43107, 49088, 49171–79. UMMZ 110564–65, 126861 (8). Trachemys callirostris chichiriviche.—MCZ 172053. PCHP 1465, 1470, 1472, 1520, 1524–25, 2662, 2736–37, 4799. UF 53333–34.

Trachemys adiutrix.—USNM 329467.

Trachemys dorbigni dorbigni.—CM 57095–99, 62078, 96001–02. MCZ 1890, 174751. PCHP 2064, 3015. USNM 107788.

Trachemys dorbigni basiliensis.—MCZ 33502, 51445. PCHP 2954, 3181.

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On the Nomenclature of the Skink (*Mabuya*) Endemic to the Western Atlantic Archipelago of Fernando de Noronha, Brazil

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The skink genus Mabuya currently comprises more than 100 species worldwide (Greer and Broadley, 2000; Greer and Nussbaum, 2000). Approximately 20 species are known for the Neotropics (Mijares-Urrutia and Arends R., 1997; Greer et al., 2000; Rodrigues, 2000). As is the case for many of the Old World species, systematics of the Neotropical forms remain unsatisfactorily resolved. One of the South American taxa, currently referred to as Mabuya maculata, is endemic to the archipelago of Fernando de Noronha, in the western Atlantic, approximately 200 km off the northeast Brazilian coast. Specimens from Fernando de Noronha differ from other Mabuya species in numerous morphological features, especially strongly keeled dorsal scales, uniform coloration without a trace of striping, and unusually high dorsal, ventral, and midbody scale counts (e.g., Dunn, 1935; Peters and Donoso-Barros, 1970). As a result, they have been linked to the Cape Verde Islands Mabuya species, rather than to any of the New World congeners (e.g., Dunn, 1935; Horton, 1973). In spite of the Noronha species' distinctiveness and restricted geographic range, the question of which is the valid name because it has been much discussed since its first description over 160 years ago and, in our opinion, is not yet resolved.

The *Mabuya* from Fernando de Noronha was first described by Gray (1839) as *Tiliqua punctata*. On the same page of the same work, Gray described a second skink, *Tiliqua maculata*, from Demerara, British Guiana (now Guyana). Since then, both names have been alternatively considered synonymous and distinct by various authors (for a thorough review of the literature see Travassos, 1946, 1948).

Boulenger (1887) was the first to allocate Gray's species to the genus *Mabuya* Fitzinger, 1826, and was also the first to consider them synonymous, based on examination of the types at the British Museum of Natural History (BMNH). Acting as first revisor in the sense of the Code of Zoological Nomenclature, Boulenger gave the name *punctata* priority over *maculata*.

Andersson (1900) noted the homonymy between Gray's species and *Lacerta punctata* Linnaeus, 1758, which he considered a synonym of *Mabuya homalocephala* (Wiegmann); he thus replaced the name *punctata* by its junior synonym *maculata*.

Dunn (1935), apparently unaware of Andersson's work, disputed Boulenger's (1887) synonymy of maculata with punctata and restored the latter name for the Noronha species; he also synonymized M. maculata with M. mabouya mabouya (Lacépède, 1788). Mabuya mabouya mabouya, as defined by Dunn, is now known to represent a composite of several different species (e.g., Hoge, 1946; Reboucas-Spieker, 1974, 1981; Avila-Pires, 1995; Mayer and Lazell, 2000). Dunn apparently made these decisions based on Gray's descriptions and on the examination of four specimens from Fernando de Noronha and six from the Guianan region. He did not examine Gray's types.

Schmidt (1945) agreed with Dunn's synonymy of *M.* maculata with *M.* mabouya but, considering the homonymy noted by Andersson (1900), proposed the new name atlantica to replace the preoccupied name punctata.

Travassos (1946) disagreed with Dunn (1935) and considered both of Gray's species indistinguishable; unaware of both Andersson's (1900) and Schmidt's (1945) contributions, he retained the name M. punctata (he further presented a synonymy and bibliography). Later, Travassos (1948) again reviewed the literature concerning the Fernando de Noronha Mabuya, presenting a more complete reference list. He agreed with Andersson (1900) in considering Lacerta punctata L. a Mabuya, based on pictures of the type and a letter of U. Bergstrom of the Stockholm Museum of Natural History confirming that the type is indistinguishable from M. homalocephala. Nevertheless, Travassos (1948) disagreed with Schmidt (1945) in considering Gray's two species distinct from each other and dropped Schmidt's epithet atlantica in favor of the older maculata, thus reinstating Andersson's (1900) arrangement. Travassos did not examine Gray's types (two of M. punctata and two of M. maculata), and his decisions were based on data supplied to him by the British Museum staff. Nevertheless, his arrangement has remained in use ever since, although some recent publications have referred to the Noronha species by the name punctata (e.g., Brygoo, 1985; Greer et al., 2000; Greer and Broadley, 2000; Greer and Nussbaum, 2000), apparently caused by the authors not being aware of the last nomenclatural changes (Brygoo, 1985; A. E. Greer, pers. comm.).

Two additional names have been included in the synonymy of *M. punctata* (Gray): *Mabuya punctatissima* O'Shaugnessy, 1874, synonymized by Boulenger (1887) and *Trachylepis* (*Xystrolepis*) punctata Tschudi, 1845, synonymized by Travassos (1946). *Mabuya punctatissima* was described by O'Shaugnessy (1874) based

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Standards in Herpetology and Ichthyology: Part I. Standard Symbolic Codes for Institutional Resource Collections in Herpetology and Ichthyology

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