A synopsis of Projeto TAMAR was presented in 1992 during the IV Encontro Brasileiro de Herpetólogos and subsequently published (Baptistotte, 1994). One of TAMAR's consistent priorities has been to develop collaborative arrangements with national and international organizations, investigators, and conservationists, and this policy continues to prevail.

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Systematics of the *Pseudemys concinna-floridana* Complex (Testudines: Emydidae): An Alternative Interpretation

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The complex relationships among the many forms of cooters (i.e., the *Pseudemys concinna-floridana* complex) in the southeastern United States have served as fodder for turtle systematists for decades (e.g., Carr, 1935, 1937, 1938, 1952; Crenshaw, 1955; Ward, 1984; Dundee and Rossman, 1989). Unfortunately, several recent authors (Frost and Hillis, 1990; Collins, 1991; Seidel, 1994) may have depended at least in part upon inadequate information for their summaries or analyses, which I believe led them to erroneous conclusions.

While I respect Seidel's (1994) innovative attempt to address one of chelonian systematics' most vexing questions, years of personal field observations of these turtles, mostly in northern Florida and adjacent states, as well as knowledge of their osteology as a result of conducting an extensive study of their fossils (Jackson, 1977), have led me to different conclusions. An examination of Seidel's morphometric data, based on museum specimens, has not caused me to alter these conclusions.

I have not conducted an exhaustive systematic analysis of the genus, nor have I examined specimens from throughout its range. I primarily address disagreements I have with Seidel's conclusions as they relate to cooters in northern Florida, an area where I have studied the taxa in question for two decades.

Because he believes that cranial musculature and osteology "are of little use in field identification or in evaluation of fluid-preserved material," Seidel quickly dismissed the analysis of Ward (1984), which relied heavily on these characters. While not in complete agreement with Ward's findings, I nonetheless affirm the importance of such characters in systematics. Surely Seidel would not deny the value of such characters as karyotype, electrophoretic pattern, vocalization, and behavior in systematics, yet which of these is useful with preserved specimens? Based on years of observation of thousands of *Pseudemys*, I long ago concluded that their high levels of intraspecific variation in scute and shell proportions diminish the overall utility of morphometric relationships in systematic analyses, although certain characters (e.g., nuchal scute proportions) are diagnostic. It is principally among largely homogeneous turtle groups (e.g., the genus *Kinosternon*, members of which are relatively uniform in shape and coloration) that biologists have been forced to rely extensively on such tools. Seidel (1994) noted that "many of the character states in *Pseudemys* are based upon continuous variables with considerable overlap." Nonetheless, despite extensive variation, color patterns do exhibit certain central themes that seem especially useful in discriminating species (e.g., Conant and Collins, 1991).

Further, other generally used characters vary more than is typically appreciated. For example, the upper tomial notch and bordering cusps, often used to distinguish the *Pseudemys rubriventris* group, occur in the *P. concinna* line as well, not just throughout such western taxa as *P. texana* and *P. gorzugi*, but even as an intrapopulational variant within rivers of the Florida panhandle (e.g., the Wakulla and Apalachicola). The frequency of these characters in this lineage may increase as one moves westward; they are seemingly absent in peninsular Florida, infrequently present in the Florida panhandle, and common in western forms such as *P. texana*. Additionally, I noted earlier (as cited by Seidel, 1994) the unreliability of trophic structures such as these as taxonomic characters for this group of emydids (Jackson, 1978).

Below, I address my three principal disagreements with Seidel (1994): the elevation of both *P. concinna suwanniensis* and *P. floridana peninsularis* to specific status and the combining of the remaining *P. concinna* and *P. floridana* into a single species with two subspecies, *P. concinna concinna* and *P. concinna floridana*.

The *suwanniensis* Problem

Although he was not the first to do so (see Frost and Hillis, 1990; Collins, 1991), Seidel's elevation of *P. c. suwanniensis* to specific status was based on limited and inaccurate information. Seidel admitted that "few characters

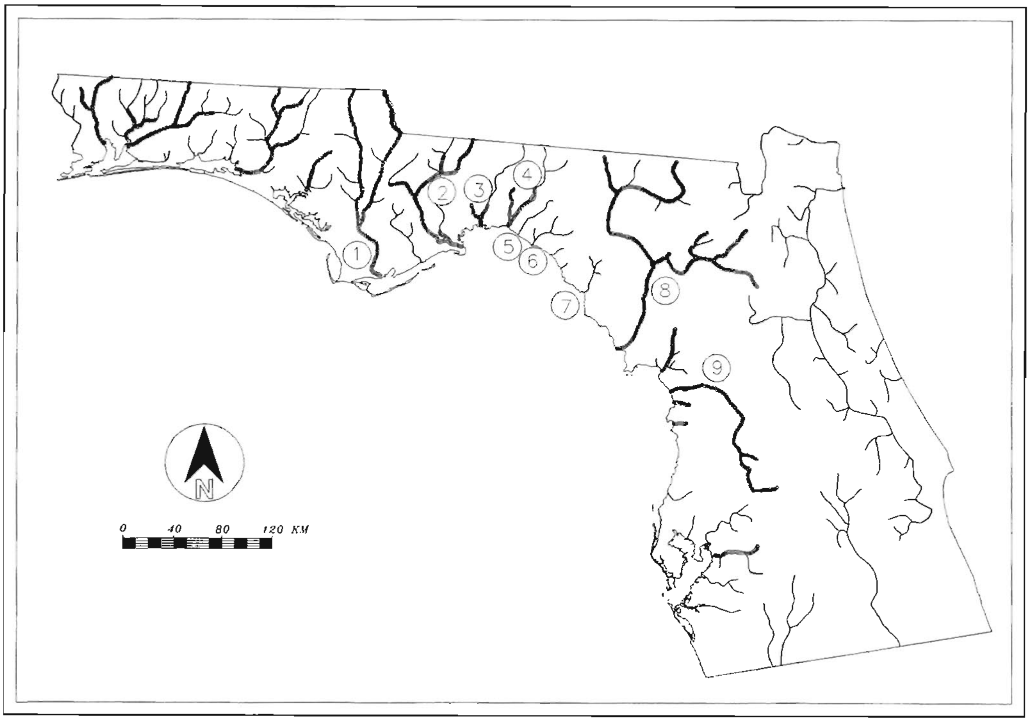

Figure 1. Minimum known distribution of *Pseudemys concinna* (*sensu lato*) in Florida; shading indicates segments of rivers known to be inhabited by the species. Rivers named in text: 1) Apalachicola, 2) Ochlockonee, 3) Wakulla-St. Marks, 4) Wacissa-Aucilla, 5) Econfina, 6) Fenholloway, 7) Steinhatchee, 8) Suwannee, 9) Withlacoochee. Specimens from the Ochlockonee River eastward conform generally to the definition of *P. c. suwanniensis*, which intergrades with other forms from the Apalachicola River westward.

separate the recognized forms of river cooters." Further, despite noting that "morphometric analysis (PCA) did not separate [*suwanniensis*] from other populations of *P. concinna*," he nonetheless recommended that it be considered a distinct species, largely because cluster analysis separated it from other forms, and it "appears to be allopatric to other *P. concinna*." As I will show, the latter contention is incorrect. Seidel tried to strengthen his case by listing presumably unique ecological characteristics (limited terrestrial activity, cryptic nesting behavior, migrations) that he gleaned from already conjectural literature. However, to my knowledge, terrestrial activity is limited in all *P. concinna* (principally restricted to basking and nesting), the nesting habits of *suwanniensis* are not exceptionally cryptic (I have marked nearly 300 nesting females in one population!), and there is no documentation of directed "migrations" to sea water.

The misconception that *suwanniensis* is allopatric with other river cooters (i.e., *P. concinna*; Frost and Hillis, 1990; Collins, 1991; Seidel, 1994) stems principally from generalized, and not altogether accurate, range maps, such as those found in standard field guides (e.g., Conant and Collins, 1991, which fails to include a substantial inhabited portion of the Suwannee River basin). Better depictions of the species' range throughout Florida are presented by Auffenberg (1978) and Jackson (1992; note: published map inadvertently omitted the Wacissa-Aucilla River), who highlight only *rivers* inhabited by *P. concinna*. Application of the concept of allopatry to aquatic organisms requires the infusion of common sense. Are we to consider isolated populations of largemouth bass, bullfrogs, greater sirens, and banded water snakes to represent allopatric taxa simply because there may presently be 30–40 km of uninhabitable dry land between occupied wetlands? I should hope not. Clearly, no riverine species is likely to occur where there are no rivers, and, in the case of river cooters in Florida, a river may need to be of some minimum size to support cooters.

Between the Apalachicola and Ochlockonee rivers on the west and the Suwannee River on the east (i.e., the alleged gap separating *suwanniensis* from *concinna*) are a number of rather small river systems draining directly into the Gulf (Fig. 1). The Wakulla-St. Marks River system, the first drainage east of the Ochlockonee, supports a substantial population of river cooters (Fig. 2) whose reproductive biology I have studied for several years (Jackson, 1987, 1989, 1994). River cooters also are abundant in the next drainage eastward, the Wacissa-Aucilla River system (these data are readily available from the state Natural Heritage Program; Iverson and Etchberger, 1989, also note specimens from these rivers). Differences between turtles in these two systems and those in the Suwannee and Withlacoochee to the south are so slight that even subspecific separation would not be justified. Ten depredated adult female specimens from the Wakulla River, the shells and bones of which are currently in my collection pending completion of my studies, match Seidel's characterization of *P. c. suwanniensis* (interestingly, carapaces of turtles in this population, and potentially others, appear much blacker and less patterned in life, perhaps suggestive of a response of melanin to sunlight). Furthermore, cooters in all of these rivers are similar ecologically and behaviorally (e.g., similar food habits, basking patterns, microhabitat use, and reproductive parameters). The few rivers lying between the Wacissa-Aucilla and Suwannee – the Econfina, Fenholloway, and Steinhatchee – are all small, have been poorly explored herpetologically (hence might be inhabited by a few river cooters), support relatively little aquatic vegetation (i.e., cooter food), and in one case (Fenholloway, a designated "industrial river") receive heavy pollution input. Thus, I contend that there is no taxonomically significant geographic gap isolating populations that Seidel would separate out as *P. suwanniensis*. The purported allopatry does *not* exist.

It may be pertinent at this point to caution systematists about relying too heavily on allopatry as a basis for subdividing populations into distinct species. For example, Seidel cited the "broadly disjunct geographic ranges" of the three red-bellied turtles (*P. alabamensis*, *P. nelsoni*, and *P. rubriventris*) as evidence of speciation, yet he failed to mention that Pleistocene fossils from South Carolina (Dobie and Jackson, 1979) effectively bridge one of the major gaps. Current distributions do not necessarily reflect the distributions under which isolating mechanisms may or may not have evolved. Ultimately, of course, it is coexistence in *sympatry* that best confirms the separate species status of two populations and which likely reflects the conditions under which isolating mechanisms developed.

To further my understanding of the relationships of southern river cooters, I traveled to east-central Alabama in September 1994 to visit Horseshoe Bend National Military Park on the Tallapoosa River, a tributary of the Alabama-Tensaw drainage that empties into Mobile Bay on the Gulf

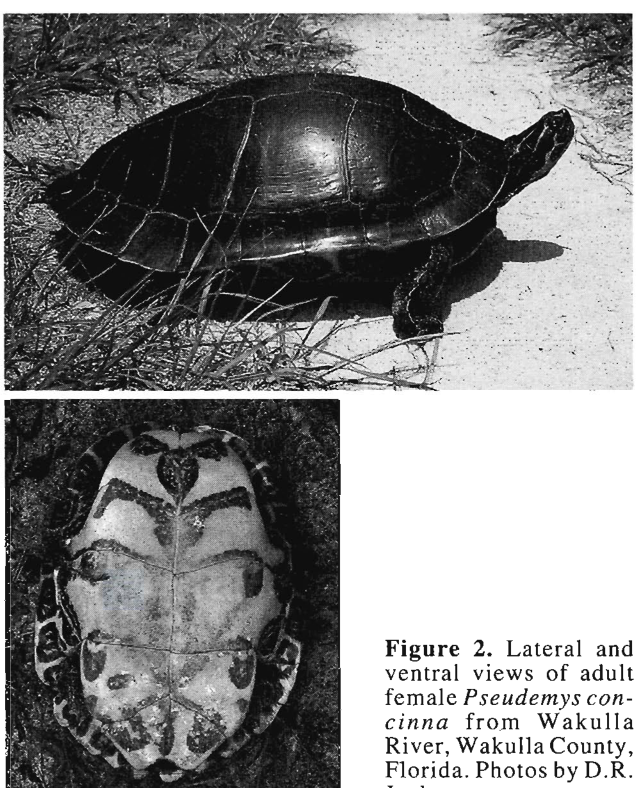

Figure 2. Lateral and ventral views of adult female *Pseudemys concinna* from Wakulla River, Wakulla County, Florida. Photos by D.R. Jackson.

of Mexico (river cooters inhabit most or all of the river systems between Mobile Bay and the Apalachicola). Here Fahey (1987) studied aspects of the ecology of *P. concinna*. During my visit I observed approximately 50 cooters, representing a good cross-section of sex and age classes, in their natural habitat; some of these were viewed at very close range with binoculars which presented excellent views of carapacial, plastral, and skin color patterns, as well as general shell morphology (all representing potentially diagnostic characters). These observations left me with no doubt that the Tallapoosa River turtles differed very little (perhaps very slightly lower in shell profile) from, and represented the same species as, turtles in the Apalachicola, Wakulla, Wacissa, Suwannee, and Withlacoochee rivers of Florida. In fact, although it is beyond the scope of this essay, I join others (e.g., Ernst and Barbour, 1989; Ernst et al., 1994; J.L. Dobie, *pers. comm.*) who question the specific distinctness from *P. concinna* of such taxa as *P. gorzugi* and *P. texana* (see Ward, 1984, and Seidel, 1994), based on cursory observations of photographs and specimens in the field and museums; biomolecular analyses would be most useful.

From the perspectives of habitat and biogeography, there is little reason that river cooters from different river systems along the Gulf coast should be highly distinct genetically. Although the species principally inhabits riverine systems, its salinity tolerance seems high for a freshwater turtle. Carr (1952) remarked on the large aggregations of Suwannee cooters feeding in the coastal seagrass flats off the mouth of the Suwannee River (surely representing a mix of fresh and sea water), while I have observed these turtles in brackish waters (along with saltmarsh vegetation and fishes, blue crabs, and bottle-nosed dolphins) in the lower St. Marks River (below the Wakulla), as well as barnacles on the shells of cooters (likewise mentioned by Carr, 1952) in the fresh waters of the upper Wakulla River (suggesting movements upstream from more saline waters). Sea levels at least 100 m lower than present during glacial episodes of the late Tertiary and Quaternary are known to have exposed vast expanses of continental shelf in the Gulf of Mexico (Frey, 1965; Vail and Hardenbol, 1979). While biogeographers have generally considered the resulting "Gulf Coast Corridor" in terms of its role in the dispersal of terrestrial animals, it surely facilitated the movements of aquatic species as well. The lower reaches of currently disjunct river systems would have been much less spatially separated, and some may even have joined. Swift et al. (1986) cited repeated falls in sea level as providing the principal mechanism for dispersal of lowland freshwater fishes among Gulf coastal rivers from the Late Oligocene throughout the Pleistocene. Conversely, there is also ample evidence of headwater stream faunal transfers in this region (Chambers, 1978; Swift et al., 1986; Gilbert, 1987). Such increased proximities and faunal exchanges among Gulf Coast drainages best account for certain distributional patterns of both vertebrates and invertebrates, particularly for aquatic species that surmounted the gap between the present Apalachicola/Ochlockonee and Suwannee systems (e.g., Jackson, 1975; Chambers, 1978;

Swift et al., 1986; Gilbert, 1987). In particular, the virtual identity of the freshwater ichthyofaunas of the Ochlockonee, Suwannee, and intervening drainages (Swift et al., 1986) underscores the unlikeliness of a taxonomically meaningful gap existing here for freshwater turtles.

The *floridana* and *peninsularis* Problem

Seidel's elevation of *P. floridana peninsularis* to specific status, and his failure to recognize conspecific taxa outside peninsular Florida, are not consistent with the facts. Easily identifiable "Florida cooters" (i.e., *P. floridana* as traditionally recognized; e.g., Conant and Collins, 1991; Ernst et al., 1994) inhabit ponds and lakes throughout much of western Florida and adjacent southern Alabama (e.g., Thomas, 1972), Georgia (*pers. obs.*), and South Carolina (e.g., Gibbons and Coker, 1977; K. Buhlmann, *pers. comm.*). In these areas, sympatric *P. concinna* is clearly distinct both morphologically and in terms of preferred habitat use (i.e., riverine systems). In contrast, *P. floridana* in these areas shares basic morphology with, and uses similar habitat (i.e., typically lentic waters) to, peninsular Florida populations of *P. f. peninsularis*; the species exhibits extensive variation in color pattern, shell shape, and rugosity, but this variation nonetheless revolves around a common theme (typically including a plain yellow plastron, bars rather than very fine concentric markings on the costals, and often an incomplete set of submarginal spots). An intergradation zone (between traditional *P. f. floridana* and *P. f. peninsularis*) occurs in northern peninsular Florida (e.g., Alachua County), such that some specimens have "hairpins" (i.e., confluence of supratemporal and paramedian stripes atop the head, a *peninsularis* character; see Carr, 1952, Fig. 54D), others lack them, and still others have a hairpin on one side but not the other (*pers. obs.*).

The Question of Conspecificity of *concinna* and *floridana* Outside of Florida

Seidel's failure to distinguish two species of cooters from Atlantic-slope drainages is especially perplexing. He noted that two forms occupy the region: a *floridana* morphotype that inhabits lentic waters and a *concinna* morphotype that inhabits rivers. He admitted in an earlier paper (Seidel and Palmer, 1991) that, within the coastal plain, the two forms occur in close geographic proximity, except for separation by preferred habitat, while he added that they differ in terms of shell depth, head-striping, and carapacial and plastral patterns (differences that he illustrated and subsequently formalized in a key separating the two species). Recent observations by K. Buhlmann (*pers. comm.*) confirm this to be the case in South Carolina, where *P. concinna* lives in the Savannah River and *P. floridana* inhabits Carolina bays (freshwater ponds); hatchlings are readily distinguishable. Seidel's inability to distinguish these two species *morphometrically* hardly makes them conspecific (either as subspecies or ecotypes, both of which he suggested), but rather reflects the low sensitivity of his methods in distinguishing these two taxa. It is not uncommon for species to be similar morphometrically but to differ significantly in other important features (e.g., chromosome number and vocal pattern in hylid frogs or coloration and mitochondrial DNA in plethodontid salamanders). When two broadly sympatric populations are morphologically distinct, breed true (i.e., produce others like themselves), fail to intergrade throughout vast areas of sympatry, and exhibit distinctly different habitat preferences (lentic vs. lotic), there can be little reason *not* to consider them as distinct species. Further, fossil evidence (Jackson, 1977, and unpublished records) from Florida clearly supports the separation of both lineages (*concinna* and *floridana*) since at least the Pleistocene.

Conclusion

I strongly recommend that biologists reject the elevation of *suwanniensis* and *peninsularis* to specific status and, instead, retain them as populations (or subspecies if preferred) of the *distinct* species *P. concinna* and *P. floridana*, respectively. The generally accepted taxonomic arrangement – followed, although differing in details, by Ward (1984), Ernst and Barbour (1989), Conant and Collins (1991), and Ernst et al. (1994) – best fits current data on morphology, ecology, and biogeography. Those choosing to recognize *P. suwanniensis* and *P. peninsularis* as full species must not only expand their proposed distributional limits greatly but also present strong evidence of their relatively high levels of genetic isolation from geographically proximate populations traditionally referred to the same species.

Relationships among turtles of the *Pseudemys concinna-floridana* lineage are exceedingly complex. Detailed work, incorporating a broad spectrum of approaches applied to specimens from throughout the group's range, will be necessary to resolve systematic questions. In systematic studies of complex taxa, the value of first-hand experience with the animals in the field cannot be overstated.

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How Many Species of Cooter Turtles and Where is the Scientific Evidence? – A Reply to Jackson

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The following is a response to Jackson (1995) who proposes a species taxonomy for cooter turtles (*Pseudemys*) as an alternative to mine (Seidel, 1994). Obviously Jackson and I have different notions of what constitutes species and how they can be tested in the context of evidence, sound scientific methods, and the objectives of evolutionary biology. Few would argue that there is any group of North American turtles more taxonomically challenging than *Pseudemys*. This may be one of the few points on which Jackson and I agree.

Jackson (1995) adheres strictly to the "biological species concept" (i.e., of Mayr, 1942). This definition rests solely on the idea that "species-ness" is determined by reproductive compatibility, either actual or potential, and without regard to real evolutionary relatedness. In Seidel (1994) I concluded that reproductive compatibility among populations of *Pseudemys* must be extremely variable. Carr (1952) also arrived at this conclusion early in his pioneer