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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

systematic work with cooters. Problems inherent to the strict biological species concept stem from its disregard for evolutionary history, as well as the dilemmas of how to thoroughly test reproductive compatibility, detecting sibling (cryptic) species, inconsistencies in gene exchange among sympatric and parapatric populations (introgression), and highly variable rates of gene flow. Much has been written on these shortcomings and pitfalls (see reviews by Ehrlich, 1961; Sokal and Crovello, 1970; Cracraft, 1983, 1987; Otte and Endler, 1989; Frost and Hillis, 1990; and Frost et al., 1992).

Typical of many commentators, Jackson (1995) cites statements from Seidel (1994) out of context, while ignoring many relevant points. For example, Jackson infers that my disagreement with Ward's (1984) conclusions (which Jackson seems to support) is evidence that I dismiss the importance of osteological characters. It should be obvious that not nearly enough skeletal material is available to evaluate variation throughout the range of *Pseudemys*, whereas there are large series of fluid-preserved specimens in museum collections. The majority of skeletons are assigned to species based on traditional, external morphological characters. Ward (1984) indicated that markings and coloration are too variable to be reliable for diagnosing cooter species. If, as he suggests, only osteological characters reliably separate *P. concinna* from *P. floridana*, then these species should be considered cryptic (sibling) based on their external morphology. Note that Ward (1984) does not provide a list of museum catalogue numbers and general localities for specimens he examined (something fundamental to all reliable taxonomic papers). I have examined many skulls and shells of *Pseudemys* and found that skeletal characters cited in Ward (1984) often are not diagnostic of his proposed species *P. concinna* and *P. floridana*. Nevertheless, my belief that osteological material is useful in turtle systematics (and *Pseudemys* in particular) should be obvious to anyone familiar with my work (Seidel, 1981, 1988; Seidel and Palmer, 1991). All characters that are genetically determined have potential systematic value, and those that can be quantified will yield the most objective results.

Jackson's (1995) conclusion that variation in scute and shell proportions has little value in *Pseudemys* systematics is also perplexing. What is his evidence for this? It is curious that Jackson recognizes the significance of scute and shell measurements in other turtles (e.g., *Kinosternon*), and then admits the value of some of these characters in *Pseudemys*. He either ignores or is unaware of the literature which clearly demonstrates the taxonomic value of scute and shell proportions in *Pseudemys* and related genera (Seidel, 1988; Legler, 1990; Iverson and Graham, 1990; Seidel and Palmer, 1991).

Cooter turtles frequently assigned to *P. concinna* and *P. floridana* range throughout much of the southern and central United States. Jackson (1995) states that he has not examined these turtles over much of their range, and admits that his experience comes mostly from observations in northern Florida and personal communications. However, without data he proclaims them distinct species. Bold conclusions such as this, based on hearsay and observations restricted to a small geographic region, are precisely why the systematics of *Pseudemys* has remained so poorly understood. I have observed *Pseudemys* in the field for more than thirty years and have made collections from New Jersey to Florida to New Mexico. I have also examined more than a thousand specimens, from every geographic region in which they occur. Based on exhaustive data analysis, I have concluded that *P. concinna* and *P. floridana* are not morphometrically distinct over large portions of their ranges. There are indeed "*concinna*" populations inhabiting Piedmont sections of rivers, which have markings quite distinct from "*floridana*" populations on the coastal plains. In Seidel (1994) I clearly recognize the "sympatry" which Jackson argues is evidence for two "biological species." At some localities (e.g., near Aiken, South Carolina) the two forms occur in close proximity, *concinna* inhabiting rivers and *floridana* in nearby lentic habitats. It is easy to understand how observers in these areas would strongly argue for two species. Nevertheless, the two distinct forms (color pattern morphotypes) do not commonly, if ever, occur in the same body of water. Therefore, they are not microsympatric and probably have little opportunity to exchange genes. Most modern systematists recognize that populations in a species may be reproductively isolated in some geographic areas, maintaining distinct character states, while gene flow may be common elsewhere (e.g., in the salamander *Ensatina eschscholtzii*, Wake et al., 1986). Jackson disregards my data which shows that *concinna* and *floridana* intergrade in many areas, especially along the Fall Line of the Atlantic slope. Furthermore, hatchlings from individual clutches of eggs, produced by "intergrade" females in North Carolina, display a full range of diagnostic markings between these morphotypes (North Carolina State Museum specimens 19711, 19432, 24030, 24525-36). Seidel and Palmer (1991) presented a numerical assessment of color patterns and marking variation between *concinna* and *floridana* in Atlantic slope drainages. It is clear that no set of proposed diagnostic characters consistently separates these forms throughout their collective range. Mount (1975), Fahey (1980), and Dundee and Rossman (1989) could not readily distinguish these turtles in many areas of Alabama and Louisiana. Following Carr's (1952) arrangement, I concluded (Seidel, 1994) that *concinna* and *floridana* should be considered subspecies of a wide-ranging polymorphic species.

Jackson (1995) states that my elevation of *P. f. peninsularis* to specific status is "not consistent with the facts" which he then fails to present. His argument that *P. concinna* and *P. (f.) floridana* are sympatric in some regions outside Florida is irrelevant to this issue, which is whether or not *peninsularis* is specifically distinct from what he considers *P. f. floridana*. Jackson claims that *P. f. floridana* and *P. f. peninsularis* share a basic morphology and that they intergrade in northern peninsular Florida based on turtles he subjectively considers intermediate. However, he presents no data and makes this determination exclusively from the appearance of coloration and markings. I have found that

species of *Pseudemys* may exhibit convergent patterns of pigmentation in areas where their ranges contact. It is well known that color patterns of turtles (including diagnostic features) may in some instances be influenced by environment (Mount, 1975; Etchberger et al., 1993; Seidel, 1994). Superficial examination of markings, without rigorous character analysis or voucher specimens, can easily lead to erroneous conclusions. In contrast to Jackson, my assessment (Seidel, 1994) of *P. (f.) peninsularis* is based on standard systematic methods: quantitative character state evaluation (including markings, bone contour, and scute morphology) and analysis of variation by cluster analysis, principal components (PCA), and cladistics (PAUP). Turtles I examined from northern peninsular Florida (Jackson's purported zone of intergradation) are not morphometrically intermediate. These turtles plot well within a central cluster of *P. peninsularis* specimens (Seidel, 1994, Fig. 3). Jackson is correct that my conclusions are not congruent with his "facts," if by this he means his assertions and conjecture. My "facts" strongly indicate that *P. peninsularis* is a distinct (non-intergrading) peninsular species, diagnosable by quantifiable, apomorphic character states. The fossil material from Florida, which Jackson spuriously claims is indication of separate *concinna* and *floridana* lineages, implicitly supports separation of *concinna* or *suwanniensis* from *peninsularis*.

Among the eight species of *Pseudemys* that I recognize (Seidel, 1994), *P. suwanniensis* is perhaps the least distinctive. Nevertheless, there are several characters that separate it from its closest congener, *P. concinna*, to which it is allopatric. *Pseudemys suwanniensis* is a cooter that inhabits the Suwannee River system and smaller Florida rivers south to Tampa Bay. Jackson (1995) claims that *suwanniensis* is not allopatric to *P. concinna*. However, he presents a map (Jackson, 1995, Fig. 1) which shows at least a 100 km hiatus between the mouth of the Suwannee River and mouths of the Wacissa, Aucilla, and Wakulla rivers, the nearest systems known to be inhabited by *P. concinna*. To my knowledge, if populations are not allopatric, they must be either parapatric or sympatric. Again, Jackson provides no evidence for the latter and indeed seems to contradict himself. Nevertheless, the real issue is whether *P. suwanniensis* is diagnosable. I acknowledge that Jackson has seen a large number of *P. concinna* during his ecological studies in northern Florida. However, his identification of turtles in the field using binoculars or photographs is hardly responsible taxonomy. Jackson referred to 10 specimens of *P. concinna* (in his personal collection) from the Wakulla River, which he claims match my characterization of *P. suwanniensis*. Why did he not present measurements of these turtles using my diagnostic characters: cervical scute length, projection of nuchal bone, curvature of epiplastral lip? My recognition of *P. suwanniensis*, as any taxonomic conclusion, is certainly subject to rigorous scientific scrutiny. However, Jackson's conclusions drawn in the absence of data are unacceptable. He has an excellent opportunity to carefully examine (and measure) large numbers of cooters in a critical portion of their range. I encourage him to do so!

Finally, Jackson (1995) makes an appeal for the application of biomolecular methods to clarify the systematic confusion in *Pseudemys*. He overlooks the protein data I present (Seidel, 1994) and is apparently unaware of the extensive mitochondrial DNA study by Davis (1994, and *pers. comm.*). Similar to my results, Davis found very little molecular variation in *Pseudemys*, especially between *floridana* and *concinna*. It is noteworthy that the DNA data reveal only one distinct (divergent) lineage in the genus, that being *P. gorzugi*. Jackson parenthetically questions the validity of this species, again without any reasonable justification.

Overall, the methods and conclusions drawn by Jackson illustrate very well why complex species relationships remain poorly understood. His "alternative interpretation" of *Pseudemys* is essentially void of scientific evidence. Unfortunately, it will be followed by those who resist progress in our understanding of evolutionary history and hold on to overly simplistic and unnatural species concepts.

Literature Cited

CARR, A.F. 1952. Handbook of Turtles. Ithaca, New York: Cornell Univ. Press, 542 pp.

CRACRAFT, J. 1983. Species concepts and speciation analysis. In: Johnston, R.F. (Ed.), Current Ornithology, Vol. 1. New York: Plenum Press, pp. 159-187.

CRACRAFT, J. 1987. Species concepts and the ontology of evolution. Bio. Philos. 2:329-346.

DAVIS, S.K. 1994. Molecular systematics of emydid turtles. Athens, Georgia: 37th Ann. Meet. Soc. Stud. Amphib. Rept., Abstracts.

DUNDEE, H.A., AND ROSSMAN. D.A. 1989. The Amphibians and Reptiles of Louisiana. Baton Rouge: Louisiana State Univ. Press, 300 pp.

EHRLICH, P.R. 1961. Has the biological species concept outlived its usefulness? Syst. Zool. 10:167-176.

ETCHBERGER, C.R., EWERT, M.A., PHILLIPS, J.B., AND NELSON, C.E. 1993. Environmental and maternal influences on embryonic pigmentation in a turtle (*Trachemys scripta elegans*). J. Zool. Lond. 230:529-539.

FAHEY, K.M. 1980. A taxonomic study of the cooter turtles, *Pseudemys floridana* (Le Conte) and *Pseudemys concinna* (Le Conte), in the lower Red River, Atchafalaya River, and Mississippi River basins. Tulane Stud. Zool. 22:49-66.

FROST, D.R., AND HILLIS, D.M. 1990. Species in concept and practice: herpetological applications. Herpetologica 46:87-104.

FROST, D.R., KLUGE, A.G., AND HILLIS, D.M. 1992. Species in contemporary herpetology: comments on phylogenetic inference and taxonomy. Herpetol. Rev. 23(2):46-54.

IVERSON, J.B., AND GRAHAM, T.E. 1990. Geographic variation in the redbelly turtle, *Pseudemys rubriventris* (Reptilia: Testudines). Ann. Carnegie Mus. 59:1-13.

JACKSON, D.R. 1995. Systematics of the *Pseudemys concinna-floridana* complex (Testudines: Emydidae): an alternative interpretation. Chelonian Conservation and Biology 1(4):329-333.

LEGLER, J.M. 1990. The genus *Pseudemys* in Mesoamerica: taxonomy, distribution, and origins. In: Gibbons, J.W. (Ed.). Life History and Ecology of the Slider Turtle. Washington: Smithsonian Inst. Press, pp. 82-105.

MAYR, E. 1942. Systematics and the Origin of Species. New York: Columbia University Press, 334 pp.

MOUNT, R.H. 1975. The Reptiles and Amphibians of Alabama. Auburn: Auburn Univ. Agric. Exp. Stn., 347 pp.

OTTE, D., AND ENDLER, J.A. 1989. Speciation and its consequences. Sunderland, Massachusetts: Sinauer Assoc., Inc.

SEIDEL, M.E. 1981. A taxonomic analysis of pseudemyd turtles (Testudines: Emydidae) from the New River, and phenetic relationships in the subgenus *Pseudemys*. Brimleyana 6:25-44.

SEIDEL, M.E. 1988. Revision of the West Indian emydid turtles (Testudines). Amer. Mus. Novitates 2918:1-41.

SEIDEL, M.E. 1994. Morphometric analysis and taxonomy of cooter and red-bellied turtles in the North American genus *Pseudemys* (Emydidae). Chelonian Conservation and Biology 1(2):117-130.

SEIDEL, M.E., AND PALMER, W.M. 1991. Morphological variation in turtles of the genus *Pseudemys* (Testudines: Emydidae) from central Atlantic drainages. Brimleyana 17:105-135.

SOKAL, R.R., AND CROVELLO, T.J. 1970. The biological species concept: a critical evaluation. Am. Nat. 104:127-153.

WAKE, D.B., YANEY, K.P., AND BROWN, C.W. 1986. Intraspecific sympatry in a "ring species," the plethodontid salamander *Ensatina eschscholtzii* in southern California. Evolution 40:866-868.

WARD, J.P. 1984. Relationships of chrysemyd turtles of North America (Testudines: Emydidae). Spec. Publ. Texas Tech. Mus. 21:1-50.

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