

Editor's Note: *With the following five papers I introduce a new, occasional feature of this journal, "Conservation Forum." This will be a place where contributed papers of a controversial or especially compelling nature are published simultaneously with invited papers that explore other facets of the subject. The intent is to highlight subjects of special interest or concern and to stimulate readers' thinking in the area. In this first installment, the question of sea turtle taxonomy is addressed first in a contributed paper by Stephen Karl and Brian Bowen, then in three responses that offer different perspectives, and finally in a reply from Bowen and Karl. I invite suggestions and ideas from readers on future topics for "Conservation Forum."*

Gary K. Meffe

Evolutionary Significant Units versus Geopolitical Taxonomy: Molecular Systematics of an Endangered Sea Turtle (genus *Chelonia*)

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Abstract: *Taxonomic rank is an important criterion in assessing the conservation priority of an endangered organism: the sole member of a distinct family will generally receive a higher priority than a semi-isolated population in a polytypic species. When cryptic evolutionary partitions are discovered in endangered species, these findings are heralded as a positive step in the conservation process. The opposite action, demoting the taxonomic rank of an endangered organism, can be resisted by the conservation community because it is perceived as detrimental to preservation efforts. We explore the arguments for and against the species status of the endangered black turtle (*Chelonia agassizii*) and contribute an additional data set based on DNA sequences of single-copy nuclear loci. These data are concordant with previous mtDNA surveys in indicating no evolutionary distinction between *C. agassizii* and adjacent green turtle (*C. mydas*) populations. Although the black turtle is morphologically identifiable at a low level, much of its distinction is based on size and color differences that are highly variable throughout the range of *C. mydas*. Thus the black turtle would be more accurately classified at the subspecific or population level. There is no strong scientific case available to defend the species status of *C. agassizii*, and yet that designation has persisted for over a century. We suggest that the maintenance of this name is based on geographical and political considerations, and we propose a pragmatic category for this type of taxonomy: the geopolitical species. Furthermore, we argue against the practice of preserving species status for conservation purposes. There are several good reasons to preserve the black turtle, including morphological diversity and the possibility that it is an incipient evolutionary lineage with novel adaptations; taxonomic rank, however, is not one of them.*

Unidades Evolutivas Significativas contra Taxonomía Geopolítica: Sistemática Molecular de la Tortuga Verde Amenazada de Extinción

Resumen: *El rango taxonómico es un criterio importante en la evaluación de prioridades de conservación de un organismo amenazado: el único miembro de una familia distintiva recibirá mayor prioridad que una población semi-aislada de una especie politípica. Cuando las particiones evolutivas crípticas son descubiertas*

Paper submitted September 2, 1997; revised manuscript accepted September 23, 1998.

en especies amenazadas, estos descubrimientos son anunciados como un paso positivo en el proceso de conservación. La acción opuesta, la degradación del rango taxonómico de un organismo amenazado, puede ser resistido por la comunidad conservacionista debido a que es percibido como un retroceso en los esfuerzos de conservación. Exploramos los argumentos a favor y en contra del estatus de la tortuga negra *Chelonia agassizii*, y contibuimos con una base de datos adicional basados en secuencias de ADN de copia sencilla de un loci nuclear. Estos datos concuerdan con estudios previos de ADN mitocondrial en cuanto a la indicación de que no existe distinción evolutiva entre poblaciones adyacentes de *C. agassizii* y la tortuga verde *C. mydas*. A pesar de que la tortuga negra es morfológicamente identificable a bajo nivel, mucha de su distinción se basa en diferencias en color y tamaño, diferencias que son altamente variables a lo largo del rango de *C. mydas*. Por ello, la tortuga negra podría ser mas correctamente clasificada a nivel de subespecie o población. No existe un caso científico fuerte para defender es estatus de *C. agassizii* y sin embargo su designación ha persistido por mas de un siglo. Sugerimos que el mantenimiento de este nombre esta basado en límites geográficos y políticos y proponemos una categoría pragmática para este tipo de taxonomía: las especies geopolíticas. Mas aún, arguimos en contra de la práctica de preservación del estatus de especies con fines de conservación. Existen varias buenas razones para preservar la tortuga negra, incluyendo la diversidad morfológica y la posibilidad de que es un linaje evolutivo incipiente con adaptaciones originales, sin embargo, el rango taxonómico no es una de ellas.

It seems clear that if *Chelonia* is to get its share of concern as a group of vulnerable, threatened, and endangered forms of life, the composite nature of the *mydas* complex must be made known to conservationists and legislative governments.

A. F. Carr (1975)

Introduction

For much of the last century, evolutionary relationships among marine turtles have been a matter of considerable confusion and contention (reviews in Pritchard & Trebbau 1984; Pritchard 1996). Molecular genetic evaluations recently have resolved many of the major controversies (Bowen et al. 1993; Karl et al. 1995; Bowen & Karl 1996; Dutton et al. 1996; Karl 1996), but several questions relevant to the classification and conservation of marine turtles remain. There are currently seven and

sometimes eight recognized extant species divided into six genera and two families (Table 1). Nearly all species are clear, discrete evolutionary units, easily diagnosable with morphology and genetics. A notable exception, however, is the tropical herbivorous green turtle (genus *Chelonia*). Numerous regional forms are described, and subspecific status has been proposed for the green turtles in the Caribbean (*C. m. viridis*), South Atlantic (*C. m. mydas*), Indo-West Pacific (*C. m. japonica*), Gulf of California (*C. m. carrinegra*), and East Pacific (*C. m. agassizii*) (Carr 1975; reviewed in Pritchard & Trebbau 1984). Only the East Pacific population, however, is widely accepted as a legitimate taxonomic entity and is accorded full species status as *C. agassizii* (the black turtle; Pritchard & Trebbau 1984).

Black turtles are identified by a marked melanism, smaller size, and a slight dorso-ventral expansion. *C. agassizii* occurs in the East Pacific from Baja California

Table 1. Currently recognized marine turtle taxa.

Taxonomic designation	Common name	Geographic distribution
Order Testudines		
Family Dermochelyidae		
<i>Dermochelys coriacea</i>	leatherback	circumglobal: tropical, temperate, and boreal
Family Cheloniidae, Tribe Chelonini		
<i>Chelonia mydas</i>	green	circumglobal: tropical
<i>Chelonia agassizii</i>	black	eastern Pacific: tropical and temperate
Family Cheloniidae, Tribe Carettini		
<i>Caretta caretta</i>	loggerhead	circumglobal: tropical and warm-temperate
<i>Lepidochelys olivacea</i>	olive ridley	circumglobal: tropical and warm-temperate
<i>Lepidochelys kempi</i>	Kemp's ridley	Gulf of Mexico and western Atlantic: warm temperate
<i>Eretmochelys imbricata</i>	hawksbill	circumglobal: tropical
Family Cheloniidae, Tribe Natatorini		
<i>Natator depressus</i>	flatback	Australia and adjacent waters: tropical

to the Galapagos Islands and Peru, and possibly west to Hawaii and the Marshall Islands. *C. mydas* is sympatric with the black turtles in some parts of this range (Carr 1961; Pritchard 1971). Unfortunately, conflicting conclusions about the taxonomic status of the black turtle have resulted in an impasse on this issue. Some researchers continue to maintain full species status of the black turtle based on size, carapace shape, and color considerations as well as on the grounds of technical nomenclature (Pritchard 1996). Color, size, and minor differences in shell shape, however, are not considered reliable characters in systematic assessments of turtles (Gaffney 1979; Meylan 1987; Zangerl et al. 1988).

As noted by Mrosovsky (1983) and Parnham and Zug (1996), the scientific data to support the species-level designation of the black turtle are minimal. In contrast, Figueroa and Alvarado (1990) performed a principal component analysis (PCA) of eight carapace measurements taken from nesting females in Michoacan, Mexico (East Pacific) and Tortuguero, Costa Rica (Atlantic), and concluded that these populations were morphologically distinct at the species level.

Although the results of this study clearly distinguished the East Pacific and Atlantic samples, several questions remain unanswered. Given that only populations from the extreme ends of the tropical range of *Chelonia* were examined, what are the geographic limits of the two forms? The black turtle is presumed to be restricted to the eastern Pacific, but melanistic forms of green turtles have been recorded in the West Pacific and Indian Oceans (Frazier 1971). Are these members of the putative *C. agassizii*? Furthermore, sampling from two locations cannot address the possibility of a gradient in morphological characters across the global range of *Chelonia* rather than discrete species boundaries. An appropriate test must include several other populations from the Pacific and Atlantic oceans. For the black turtle to qualify as a distinct species on morphological grounds, it should occupy a unique position in multivariate space relative

to other sampled populations. An argument could be made for the species status of *C. agassizii* if the PCA indicated that the distance between the black turtle and the green turtles was greater than the distance among green turtle populations, but this condition is not met (Figueroa & Alvarado 1990). Even if it was, PCA is not a universally accepted phylogenetic tool and, as with other phenetic techniques, the correlation between distance (as defined by PCA) and taxonomic rank is not linear.

In the most complete morphological analysis to date, by Kamezaki and Matsui (1995) examined skull characters from seven *Chelonia* nesting beaches, including two Atlantic, one East Pacific, one West Pacific, and two Indian Ocean samples. The result of a PCA indicates that the East Pacific form is the most distinct cluster. But this distinction is based on the first canonical axis (size), and turtles from Guyana (Atlantic), Costa Rica (Atlantic), and Japan (Pacific) also are predominant nonoverlapping groups. Of particular note, the Costa Rican population used by Figueroa and Alvarado (1990) clusters separately from other Atlantic (as well as Pacific) populations in most of the analyses. Considered as a whole, these data demonstrate considerable interlocation variation in the morphology of green turtles worldwide but do not indicate a species-level distinction of East Pacific populations from other green turtles. Kamezaki and Matsui (1995) recommend a subspecific assignment for *C. agassizii*.

Molecular genetic analyses have provided a contrasting arrangement of relationships within *Chelonia*. Bowen et al. (1992) examined mitochondrial DNA (mtDNA) in 226 specimens from 15 nesting locations, including samples of at least 10 individuals from every major ocean basin inhabited by *Chelonia*. A prominent feature of the mtDNA phylogeny is the grouping of haplotypes into two primary clusters corresponding to the major oceanic basins: Atlantic Ocean and Mediterranean Sea versus the Indian and Pacific Oceans (Fig. 1). This division is concordant with recognized biogeographic barriers to the dispersal of

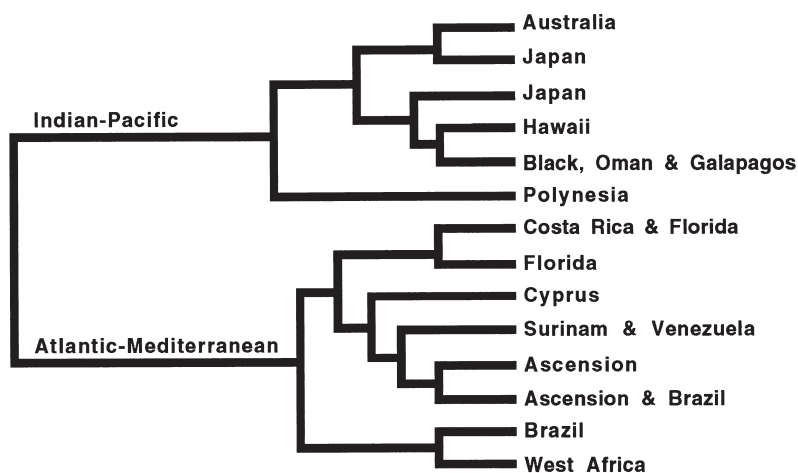


Figure 1. A UPGMA phenogram of relationships among haplotypes in *Chelonia* populations based on mtDNA restriction fragment analysis (adapted from Bowen et al. 1992).

tropical fauna: the southern extensions of Africa and South America (Briggs 1974). But the mtDNA analysis does not indicate that the black turtle represents a unique lineage relative to other green turtle populations and hence does not support the taxonomic or evolutionary distinctiveness of East Pacific *Chelonia* populations. In fact, the single mtDNA haplotype that characterized black turtles also was found in green turtles from Hawaii and the Indian Ocean. If divisions were to be drawn from these data, they would be made between the Atlantic-Mediterranean and the Indian-Pacific groups.

In a companion study, Karl et al. (1992) used restriction site polymorphisms in single-copy nuclear DNA to elucidate the degree of genetic differentiation between nesting colonies and to test for male-mediated gene flow. Although the study was not designed to assess the status of *C. agassizii*, Karl et al. noted that a phylogenetic analysis of the nuclear haplotypes did not indicate consistent clustering of *C. agassizii* individuals relative to *C. mydas*. They concluded that the East Pacific turtles do not form a discrete evolutionary lineage. The Atlantic-Mediterranean and Indian-Pacific clusters observed in mtDNA were not supported in the analysis, but this conclusion was provisional because of the overall low level of diversity observed with restriction-site analyses.

In an attempt to resolve the phylogenetic questions surrounding *C. agassizii*, we sequenced a total of 1337 nucleotides from three of the nuclear DNA loci used in Karl et al. (1992). Sequence analysis permits the resolution of all nucleotide substitutions at these loci. This enhanced resolution is used to motivate a discussion of evolutionary significant units (ESUs) in the green turtle and the persistence of taxonomic designations based on geographic or political considerations. Given that *Chelonia* populations have declined in the last several decades (Bjorndal 1995), the taxonomic status of the east Pacific form may have repercussions well beyond the museums and academic circles where this debate began. We use the molecular data and resulting phylogenetic conclusions to prompt a discussion of the factors that work against taxonomic realignment of endangered species.

Methods

DNA Sequencing

The samples included in this study are a subset of those used by both Bowen et al. (1992) and Karl et al. (1992); they consist of two individuals from Florida, U.S.A., one from Ras Al Had, Oman, two from French Frigate Shoals, Hawaii (U.S.A.), three from Ascension Island, one from Quintana Roo, Mexico (Atlantic), and five from Isabela Island, Galápagos, Ecuador. Nuclear DNA sequences were determined for three single-copy nuclear loci from each individual as well as from a single individual each of

Table 2. Variable nucleotide positions at three nuclear loci from green, black, hawksbill, and loggerhead turtles*

	CM-12 position number:	CM-14 position number:	CM-45 position number:
Florida	11111122222333333444	111111222222223333333344	112222223333444
Florida	444457714455812258001233233	2334702456702466667890111233478900	11137999341222356128334
Quintana Roo	24577699675660451352456756	32577017281148601234709356634941446	14801448579805345910529894
Ascension	CGTCCCTGAC--A-CGGCGGGGCGATGA	AGATTTGACTCCGTNGAGAGCCCCCTTCCGAGCTNC	CCCATACNNTT-CTA---CTTCCAGCT
AscensionA.....N.....CN.....C..GNTG...C.....T.....
AscensionA.....N-NNNNNNNNNNY.A.A...CC.....G..C..C...GTT...T.....T.....
AscensionA.....N-NNNNNNNNNNA.....CG.....T.....A.N...C.G...C.....T...N...
HawaiiA.....G-.....C.NNNCA.....GT.....C.C.T...T...T.N...
HawaiiA.G.A.TGAA..T.....AAC.G.-GN..CG.....T.....C..C.T.....T.....NNN
HawaiiTGAA..T.....AAC.G.-C.A.A...CG.....C.....C..C.N..C.....T.C.T...
OmanTGAA..T.....AAC.G.-Y.ATA.TT.CG..A.....C..G.G.CA..C.....T.C.TG...
BlackTGAA..T.....AA..G.-R.....CG.....C..C.G.....T.....T.....
BlackTGAA..T.....AA..G.-A.....T.CG.....C..C.C.....N.....T...T...
BlackTGAA..T.....AAC.G.-N.....CG.....T.....C.C.....A.....T.C.T...
BlackTGAA..T.....AAC.G.-C.A..T..TT.CG..A.G.....C.T.....T.....T...T...
BlackTGAA..T.....AAC.G.-N.....CG.....A.T.....C..C.C.....N.....T.N.TNNNN
BlackTGAA..T.....AAC.G.-NANN.A...NCG...N..T..NNNCTT.C.C.....N.....T...T...
EretmochelysTTTGA..GT...ACTGNNN.T..GA...ACG----.NT..TCTT.C.G.G...CCGT...TTATGCA..TAG
CarettaT.T.TTGA..GT..AA.ACTG..A...GCCGT..CTTATG...NNNNA...GCCGT..CTTATG...NNNN

*Nucleotide designation follows standard conventions: period (.), same as reference sequence; dash (-), undetermined base. Position numbers are referenced 5' to 3' to the sequences recorded in GenBank.

Caretta caretta and *Eretmochelys imbricata*. These two species were chosen because they are among the closest extant relatives to *Chelonia* (Bowen & Karl 1996).

Total cell DNA isolated from all individuals was subjected to polymerase chain reaction amplification with the nuclear DNA primers CM-12, CM-14, and CM-45, as described by Karl and Avise (1993). Free nucleotides and unused primers from successful amplifications were removed by centrifugal filtration with Millipore Ultrafree-MC (30,000 MW) filter units. Purified and concentrated amplified DNA was sequenced with an ABI automated DNA sequencer (DNA Sequencing Core, University of Florida). Sequences have been deposited in GenBank under accession numbers U73532, U73533, U73535-U73548, U73550-U73556, U73558-U73561, U73563, U73565-U73569, U76647-U76653, and U76655-U76663.

Data Analysis

We aligned all sequences manually using the computer program SeqEd (Applied Biosystems). Gaps were introduced into the sequence as necessary to increase sequence similarity. Multiple, contiguous gaps were condensed to a single gap whenever the sequence information present was invariant. Gaps were treated both as new states and as missing data in phylogenetic analyses. Analyses were conducted using each locus alone and all three combined. When combined, all individuals listed in Table 2 possessed unique composite genotypes, so no pooling of alleles was necessary.

Aligned sequences were analyzed by unweighted parsimony using the branch-and-bound algorithm of PAUP (version 3.1.1; Swofford 1991). Bootstrapping was performed in PAUP (heuristic search using three random additions of taxa, MULPARS, nearest-neighbor branch swapping, and steepest descent) or by using the SEQBOOT, DNADIST (maximum likelihood distances), NEIGHBOR, and CONSENSE programs of PHYLIP (version 3.572; Felsenstein 1989). Maximum likelihood distances were calculated with empirically derived nucleotide composition and transition to transversion ratios of 1:1. All trees were rooted with *Caretta caretta* and *Eretmochelys imbricata*.

Results and Discussion

Although the debate over *C. agassizii* has not been resolved by prior research efforts, recent data indicate that the black turtle is not a unique phylogenetic unit. The mtDNA data previously presented and nuclear DNA sequence data presented below support the Atlantic-Mediterranean versus Indian-Pacific groupings. Neither data set contains a monophyletic group of black turtles, nor are black turtles grouped apart from green turtles.

We sequenced approximately 437, 455, and 449

nucleotides from the three loci, CM-12, CM-14, and CM-45, revealing 27, 35, and 26 variable positions, respectively (Table 2). Individually, the loci vary considerably in their ability to resolve relationships. CM-12 is the only locus that robustly resolves the Atlantic-Mediterranean and Indian-Pacific groups. Neither of the other loci provides strong support for this division or for any associations among *Chelonia* samples; these results are consistent among all analytical approaches. All loci individually and together show strong bootstrap support for grouping of all *Chelonia* to the exclusion of both *C. caretta* and *E. imbricata* (Fig. 2). When all loci are combined, the mean genetic distance among *Chelonia* samples ranges from 0.3 to 2.1% when corrected for missing data. A prominent feature of the combined analysis is strong support for the Atlantic-Mediterranean versus Indian-Pacific grouping found with mtDNA (Fig. 2). A branch-and-bound analysis of all data results in 71 equally parsimonious trees. A 50% majority-rule consensus tree supports some intraregional relationships (e.g., Florida individuals always group together). Associations within the major *Chelonia* lineages, however, are mostly unresolved. Neither parsimony nor distance methods differ in their ability to resolve regional relationships. We attribute the lack of phylogenetic structure within ocean basins to rookery turnover and to rare exchanges between nesting colonies. In no analyses do the black turtles cluster unequivocally outside of a monophyletic green turtle clade. On the basis of these data, the black turtle does not appear to be more divergent than other regional forms of the green turtle.

Chelonia is not the only sea turtle genus with a controversial taxonomic history. The Kemp's ridley (*Lepidochelys kempi*) and olive ridley (*L. olivacea*) sea turtles also are easily distinguished by coloration but difficult to distinguish by the external morphological characters typically used to assign species status (Pritchard 1969). The Kemp's ridley is the most endangered sea turtle, and the species status of this form, like that of the black turtle, carries significant legal implications for protection. Unlike the black and green turtles, however, the Kemp's and olive ridleys are well separated in molecular genetic evaluations (Bowen et al. 1993; Bowen & Karl 1996), a finding that has been used to bolster conservation efforts for *L. kempi*.

Evolutionary Significant Units and Conservation

The need to recognize individual biota for conservation purposes has rekindled a debate over species definitions and prompted some innovative solutions (Cracraft 1983; Ryder 1986; Avise & Ball 1990; Wayne 1992). One emerging solution is to draw a distinction between species in the organismal sense and units of evolutionary diversity in a conservation context. The ESU has been proposed as a unit of conservation (Vogler & DeSalle 1992; Moritz 1994; Waples 1995) and is now widely applied

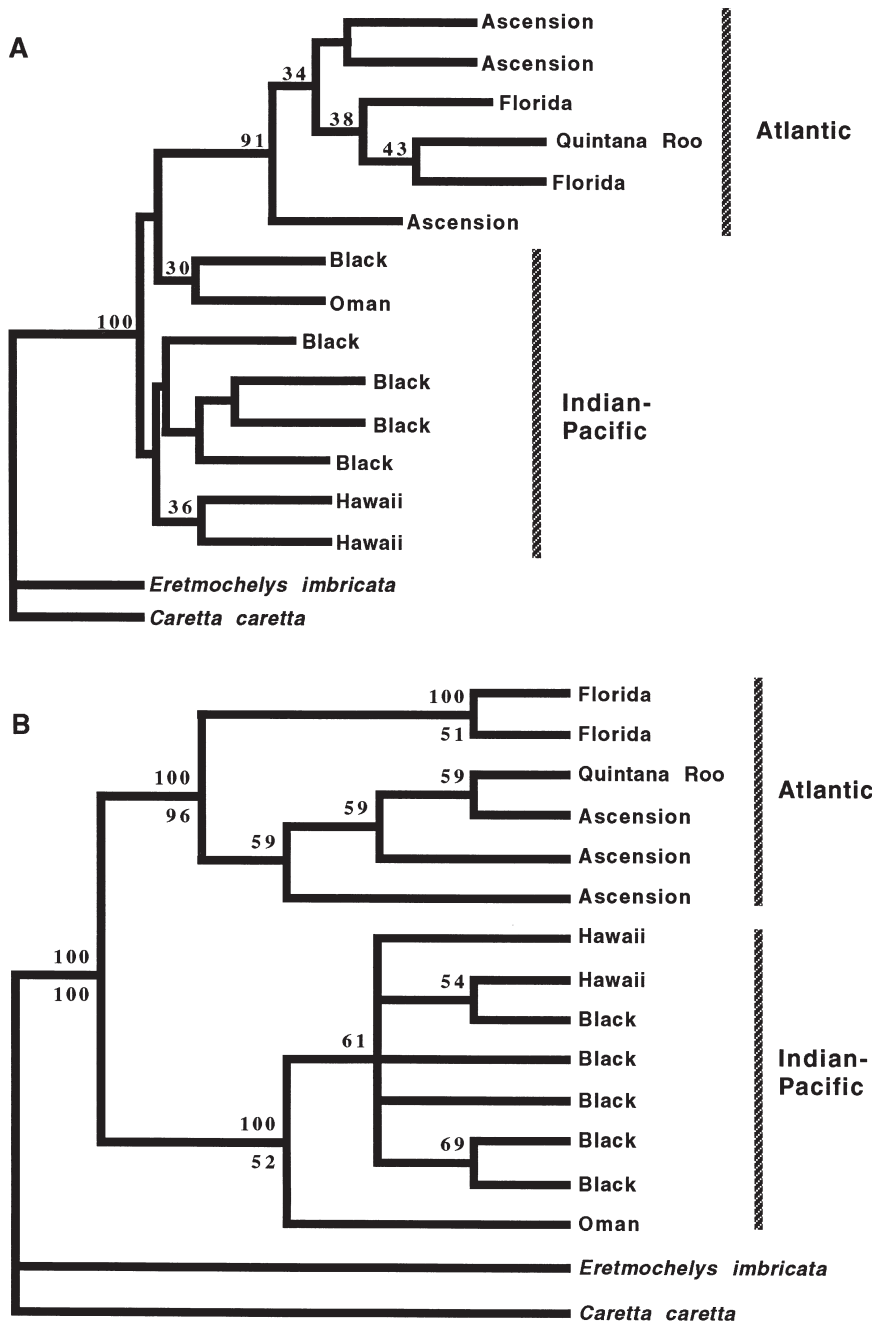


Figure 2. Relationships among *scnDNA* types in *Chelonia* populations based on combined data from three nuclear loci. Neighbor joining tree of maximum likelihood distances (A). Numbers at nodes represent percent bootstrap support from 300 replicates. Unnumbered nodes were supported at less than 30%. A 50% majority-rule consensus tree of 71 equally most parsimonious trees using a branch and bound algorithm (B). Numbers above nodes represent the percentage of all trees containing that node. Numbers below nodes are percent bootstrap support using a heuristic search, three random additions of taxa, and 100 bootstrap replicates.

for policy purposes. In terms of conventional taxonomy, an ESU often corresponds to species or subspecies boundaries, but in some circumstances can extend to isolated populations. How does the black turtle fit into conventional definitions of the ESU? Moritz (1994) proposed the following definition of an ESU based on genetic criteria: "ESUs should be reciprocally monophyletic for mtDNA alleles and show significant divergence of allele frequencies at nuclear loci." Under this definition, ESUs in green turtles would clearly correspond to the Atlantic-Mediterranean and Indian-Pacific units, supporting the previously proposed subspecies *C. m. mydas* (Linnaeus 1758) and *C. m. japonica* (Thunberg 1787) re-

spectively. On the basis of a relatively large genetic sample, these units are characterized by fixed differences in mtDNA, significant allele frequency shifts in nDNA (Karl et al. 1992), and a clean distinction in phylogenetic analyses (Figs. 1 & 2, respectively). Although many of the intraregional green turtle population subsegments also would correspond to ESUs based upon mtDNA data, they fail the criterion of significant allele frequency differences at single-copy nuclear loci (Karl et al. 1992).

A second ESU definition (Waples 1991), widely applied in North America and having the weight of law in many cases, has a somewhat broader guideline: "An ESU is a population (or group of populations) that (1) is sub-

stantially reproductively isolated from other conspecific populations, and (2) represents an important component in the evolutionary legacy of the species." In this case, there are two criteria, and the applicability of each can be weighed separately. First, are black turtles substantially reproductively isolated? Much of the east Pacific biota probably is. Coastal faunas in this region are isolated from the shallow habitats of the central and western Pacific by a vast oceanic expanse in which primary productivity is low. Briggs (1974) referred to this as the east Pacific barrier, and it is possible that this represents an isolating barrier to the black turtle. Sea turtles, however, can migrate thousands of kilometers between feeding and nesting areas, and at least one species is known to cross the Pacific Ocean during developmental migrations (Bowen et al. 1995). Hence, it is not likely that geographic separations are a barrier to exchange between Pacific populations of *Chelonia*. The close relationship of the black turtle and Indian Ocean green turtles (Figs. 1 & 2) reinforces the point that they have not been isolated over recent evolutionary time. Intrinsic reproductive barriers between the black turtle and Pacific green turtles are unlikely given that even the most divergent species in the family Cheloniidae are capable of producing viable hybrids (Karl et al. 1995).

The second criterion concerns evolutionary legacy, potentially a difficult term to define (Bowen 1998). Waples (1995) offers the following: "The evolutionary legacy of a species is the genetic variability that is a product of past evolutionary events and that represents the reservoir upon which future evolutionary potential depends." This definition, like the ESU of Waples (1991), can be considered in two parts. The condition of genetic variability is similar to the ESU defined by Moritz emphasizes the genetic signatures of previous evolutionary divergence. The black turtle cannot be supported as an ESU using this criterion because no analysis to date has indicated significant genetic divergence between black and green sea turtles. What about the second criterion of future evolutionary potential? The east Pacific populations are at the extreme of the range of *Chelonia* and live in cooler waters than other green turtles. Moreover, this form is morphologically distinct (albeit at a low level) in spite of close genetic similarity to other Pacific and Indian Ocean populations of green turtle. It has been recognized that new species may arise as ecotypes in such fringe environments (Endler 1977), and under strong selection these populations may speciate prior to complete reproductive isolation (Smith et al. 1997). Likely signatures of such incipient species include forms that are morphologically or behaviorally distinct but genetically indistinguishable or distinguishable only at the population level (Chouinard et al. 1996; Schluter 1996; Taylor et al. 1997). While we cannot be certain if the east Pacific form ever will become "*C. agassizii*," the distinctiveness of this form can be detected with morphology (Kamezaki & Matsui 1995) and

population-level genetic partitions (Bowen & Karl 1996). It therefore seems defensible that the black turtle is a geminate species and qualifies under the ESU criterion of "future evolutionary potential."

Green and Black: Geographically and Politically Defined Species

The species name *agassizii* has been advocated throughout this century (Carr 1961; Ernst & Barbour 1989; Pritchard 1971) with effectively no supporting scientific data. Certainly one factor in the persistence of this assignment is the restricted range of the black turtle nesting populations, which coincides with geographical, political, and cultural boundaries. In the last 400 years, species with broad marine distributions were routinely given multiple names in different locations (for examples in sea turtles see Pritchard & Trebbau 1984). With improvement in scientific communication and taxonomy over the last century, many of these regional names have been synonymized. This trend may be abating, however, as conservationists cling to dubious taxonomy for the sake of protecting wildlife within existing legal frameworks. Mrosovsky (1983) noted that the dire conservation status of the black turtle has been invoked as an argument for preserving species status. Hence, the artificial geopolitical designations of the past are being perpetuated principally for management and regulatory reasons.

We propose the label *geopolitical species* (GS) for taxonomic designations that persist, but for which there are essentially no supporting data. Geopolitical species are groups of individuals confined to geographically or politically defined areas and are accorded species status independent of morphological, genetic, and reproductive criteria. The GS is a pragmatic designation based not on science but on the recognition that some species names are perpetuated primarily on geographical, political, or cultural grounds.

Most organismal biologists, when introduced to the GS, can readily provide examples from their own field. For example, the sardines (*Sardinops* spp.) occupying Japan, California, Chile, Australia, and southern Africa are almost indistinguishable in terms of morphology, yet species names for each regional form have persisted for seven decades (Grant et al. 1998). In a review of the genus *Sardinops*, Parrish et al. (1989) conclude that the only reason these forms were designated as separated species was that they lived in separate locations. Hence, the concept of the GS can be applied to one of the most abundant and—due to its commercial importance—best-studied fishes in the world.

Many geopolitical species are the product of an earlier age of exploration, when naturalists described the biota of a particular region without access to specimens from adjacent regions. Given the limits on travel and scientific

access, it was inevitable that multiple names would arise for single species, and in most cases the rules of taxonomy have eliminated these *nomina nuda* over the years. The remaining *nomina nuda* (or GSs) are artifacts of the political, geographical, cultural, and linguistic boundaries that continue to separate biologists.

It is important to recognize that GS status does not necessarily imply taxonomic invalidity. Rather, it indicates that a scientific case for an existing taxonomic designation has not been made. In many cases, geopolitical species based on biogeographical considerations may turn out to be valid by accepted scientific criteria. In other cases, taxonomies based on a few specimens collected long ago may persist only because they coincide with geopolitical boundaries. The latter circumstance is almost certainly the case for the black turtle, described by Bocourt (1868) based on a limited number of specimens. Once this species was examined with modern approaches, distinctions between Pacific *C. mydas* and putative *C. agassizii* appear only at the subspecies level in terms of morphology (Kamezaki & Matsui 1995) and only at the population level in terms of DNA sequence data. In spite of this, the species level distinctiveness of the black turtle continues to be defended based on morphology and geographic probability (Pritchard 1996; Mrosovsky 1983; Parnham & Zug 1996). This position is consistent with a GS assignment.

While the temptation exists to maintain species status for management purposes, the GS category probably applies to a minority of endangered species. More common is the protection of subsections of a species range based on geopolitical boundaries. We propose the designation of a *geopolitical management unit* (GMU) for these cases. North American examples of GMUs include the gray wolf (*Canis lupus*), grizzly bear (*Ursus arctos horribilis*), and bald eagle (*Haliaeetus leucocephalus*). Although large numbers exist in Alaska and British Columbia (almost to the point of nuisance), in the lower 48 states these species have been nearly or completely extirpated. To protect these species in the southern end of their range, wildlife managers have successfully listed them under the provisions of the U.S. Endangered Species Act (ESA) without meeting the criterion of evolutionary separation. In fact, Pennock and Dimmick (1997) list a total of 25 (of 29) taxa currently listed and protected under the ESA as distinct population segments. Only four of these species (desert tortoise [*Gopherus agassizii*], chinook salmon [*Oncorhynchus tshawytscha*], sockeye salmon [*O. nerka*], and Umpqua River cutthroat trout [*O. clarki clarki*]) currently meet the genetic criteria for an ESU (Moritz 1994) in that they have been demonstrated to represent distinct evolutionary lineages. Many if not all of the remaining taxa could be recognized as geopolitical management units.

Recently, the U.S. Fish and Wildlife and National Marine Fisheries Services have been criticized for using the ESU

as a criterion for protection under the Endangered Species Act. Pennock and Dimmick (1997) are concerned that the application of ESUs reduces the role of demographic, behavioral, cultural, economic, and geographic justifications for protection. We agree with Pennock and Dimmick (1997) that the Endangered Species Act should include considerable flexibility in defining population segments for protection (see Waples 1998). We disagree with their argument that such flexibility is required to protect species that are "extinct in part of their range." From a biological perspective, extinction is the total elimination of a unique, identifiable unit. Removal of individuals from a segment of a species range is more correctly referred to as extirpation. If species are listed as endangered in only part of their range (as is the case for Bald Eagles and other examples cited in Pennock and Dimmick [1997]), then the unit of protection is not a species and the species is not truly in danger of extinction. We do not argue against protective measures for these groups, only against the use of the labels "endangered" or "species" (in a biological sense) for protective measures based on political boundaries or geographic considerations. These seem to be de facto applications of the GS and GMU that perhaps demonstrate the legitimate role of these designations in conservation.

Prospectus

The *mydas-agassizii* debate has rekindled in part because of dire trends in these east Pacific populations. Black turtles are subject to harvesting pressures both on the nesting beaches and in nearby waters (Pritchard 1996). As the lack of genetic separation between green and black turtles became apparent over the last 5 years, some conservationists who embraced the genetic findings for the Kemp's ridley turtle studiously ignored identical genetic assays for *C. agassizii*. Even more alarming are declarations that such information is a disservice to conservation. We are disturbed by the implication that scientific data are at odds with conservation goals and are sympathetic to the fishery scientists who have lived with this paradox for decades (Hutchings et al. 1997).

The controversy over evolutionary significant units in green turtles is approaching a resolution. The primary genetic partition in this species is between the Atlantic-Mediterranean and Indian-Pacific groups, corresponding to the previously proposed subspecies designations *C. m. mydas* (Linnaeus 1758) and *C. m. japonica* (Thunberg 1787), respectively. The available data do not warrant species-level taxonomic recognition for any regional morphotype of *Chelonia* (including the east Pacific black turtle). This may be perceived as an argument to lower conservation priorities for east Pacific turtles, but preservation of regional green turtle populations is a concern apart from taxonomic criteria and species designations.

nations. Many nesting populations of sea turtles already are protected without the benefit of taxonomic rank. In these cases conservation priorities are appropriately based on a variety of information including geographical considerations and subtle morphological or genetic attributes rather than unsubstantiated nomenclature.

Acknowledgments

Geopolitical species were first suggested to S. A. K. by R. Vrijenhoek at Rutgers University, to whom we are indebted. For logistic support we thank E. Almira, A. L. Bass, E. Severance, S. Shanker, D. Sweger, M. Zacks, and the DNA Sequencing Core at the University of Florida. We thank J. Quattro, P. Pritchard, and anonymous reviewers for helpful comments. J. Spotilla provided editorial comments on a previous version. This research was supported by a National Science Foundation (NSF) Conservation and Restoration Program grant to B. W. B. and a NSF Systematic Program grant to S. A. K.

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