# Population Structure and Cryptic Evolutionary Units in the Alligator Snapping Turtle

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**Abstract:** *The alligator snapping turtle (*Macroclemys temminckii*) is a long-lived, slow-growing chelydrid turtle found in Gulf of Mexico drainages from Florida to Texas (U.S.A.). Populations are thought to be depleted throughout the range due in part to an increased harvest in the 1960s through 1980s. To identify population and evolutionary units, 420 base pairs were sequenced within the mitochondrial DNA control region of 158 specimens from 12 drainages. Results indicate substantial phylogeographic structuring and strong population-level separations among river drainages. Eight of 11 haplotypes were observed to be river-specific, providing diagnostic markers for most drainages. Three partitions are resolved in the mtDNA genealogy, corresponding to the eastern, central, and western portion of the species' range. These separations coincide with recognized biogeographic provinces. The population structure by river system indicates that many drainages are distinct management units, with the Suwannee River lineage possibly deserving special attention, based on the criterion of genetic distinctiveness. The partitioning of* M. temminckii *into river-specific populations illustrates the management framework and conservation challenges that apply to a broad array of riverine species. Drainage-specific molecular markers may be used to identify the geographic origin of turtle products in the marketplace.*

Estructura Poblacional y Unidades Evolutivas de la Tortuga *Macroclemys temminckii*

**Resumen:** *En la familia Chelydridae,* Macroclemys temminckii *es una tortuga de crecimiento lento y larga longevidad que se encuentra distribuida en las cuencas del Golfo de Mexico, desde Florida hasta Texas (U.S.A.). Se cree que las poblaciones de esta tortuga han disminuido debido a un aumento en la cacería, aproximadamente entre los años 1960s y 1980s. Con la finalidad de identificar las unidades poblacionales y evolutivas, se sequenciaron 420 pares de bases de la región control del ADN mitocondrial en 158 especimenes provenientes de 12 cuencas. Los resultados indican que entre las cuencas existe una estructura filogeográfica y una separación fuerte a nivel poblacional. Ocho de los 11 haplotipos son específicos para un río en particular y constituyen marcadores diagnósticos para la mayoría de las cuencas. Se resolvieron tres líneas evolutivas en la genealogía del ADN mitocondrial: las regiones este, central y oeste del alcance de la especie. Estas separaciones coinciden con provincias biogeográficas reconocidas. La estructura poblacional basada en cuencas riperinas indica que muchas de las cuencas constituyen unidades de manejo. La separación de* M. temminckii *en poblaciones río-específicas ilustra la necesidad de diseñar una infraestructura de manejo apropiada y refleja los retos que afronta la conservación. Marcadores moleculares específicos a una cuenca pueden ser utilizados para identificar el origen geográfico de productos provenientes de tortugas, los cuales se encuentran accesibles en el mercado.*

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## Introduction

The alligator snapping turtle (*Macroclemys temminckii*) is one of the largest freshwater turtles in the world, with records exceeding 100 kg and anecdotal reports of specimens approaching 150 kg (Pritchard 1989, 1992). Restricted to drainages of the Gulf of Mexico in the southeastern United States, *Macroclemys temminckii* is a highly aquatic turtle, found only in river systems and their associated bodies of water. Although it can lure fish with a wormlike tongue modification, the alligator snapping turtle also consumes a wide variety of mollusks, mammals, birds, vegetable matter, and other turtles (Sloan et al. 1996).

With powerful jaws and plentiful meat, *M. temminckii* plays an important role in the folklore and cuisine of the southeast United States. In the 1970s thousands of alligator snapping turtles were caught annually by professional trappers, not only to supply meat for regional consumption but also for shipment to Campbell's Soup Company and other industrial-scale processors (Pritchard 1989). Pritchard (1979, 1989) noted that population numbers have declined throughout the turtle's range as a result of unregulated harvest.

The recent exploitation of the alligator snapping turtle—along with human encroachment on riverine habitats and incidental take through commercial and recreational fishing—has raised serious conservation concerns for this species. Although a rangewide survey of morphological variation has not been conducted, Pritchard (1989) suggested that geographic variation may exist in the alligator snapping turtle and that this possibility required further investigation. Hence, one goal of this study was to test for the presence of evolutionary significant units (ESUs) in *M. temminckii*.

A second conservation concern is the delineation of management units (MUs). Dispersal may be limited by this species' riverine habits: observational records and telemetry data (Sloan & Taylor 1987; Harrell et al. 1996) indicate that the alligator snapping turtle rarely traverses land or saline waters, with only nesting females presumed to leave the water (Ernst et al. 1994). Among other riverine turtles in the region, such as map turtles (*Graptemys*) and the loggerhead musk turtle (*Sternotherus minor*), land barriers have been found to act as geographic impediments to gene flow (Lamb et al. 1994; Walker et al. 1995).

To investigate population structure and evolutionary partitions in the alligator snapping turtle, we employed the control region of the mitochondrial genome. This segment has proven useful for resolving fine-scale population structure and intraspecific genetic variation in turtles (Lamb et al. 1994; Walker et al. 1995; Encalada et al. 1996) and other vertebrates (Quinn 1992; Stewart & Baker 1994; Zhu et al. 1994). In designing this study our goals were to chart an atlas of genetic diversity to enhance the scientific foundations for the conservation of the alligator snapping turtle and to develop molecular markers for investigations of turtle products in the marketplace.

## Methods

Twelve river systems throughout the range of the alligator snapping turtle were sampled for this study. Starting from the west, these drainages included the Trinity ($n$ = 3 turtles), Neches ($n$ = 20), Mississippi ($n$ = 23), Pascagoula ($n$ = 13), Mobile Bay ($n$ = 12), Perdido ($n$ = 1), Pensacola Bay ($n$ = 23) Choctawhatchee ($n$ = 1), Econfina ($n$ = 8), Apalachicola ($n$ = 25), Ochlockonee ($n$ = 13), and Suwannee ($n$ = 18) (Fig. 1). Turtles were collected from different locations within each river system when possible (for location data see Roman 1997). Most of the samples were collected by P.E.M. and S.D.S. between 1993 and 1997. Two specimens of the common snapping turtle (*Chelydra serpentina*) were assayed to provide a yardstick for interpretation of genetic distances within *M. temminckii.*

Blood samples were typically drawn from the caudal vein and stored in lysis buffer (100 mM Tris-HCl [pH 8], 100 mM EDTA [pH 8], 10 mM NaCl, 1.0% sodium dodecyl sulfate) in an approximate 1:10 ratio of blood to buffer, as recommended by White and Densmore (1992). Tissue samples were snipped from the tail or webbing of the rear foot of individuals that proved difficult to bleed. All turtles were released at or near the point of capture. Voucher photographs of turtles from most Florida locations have been deposited in the Florida Museum of Natural History (FMNH); tissue samples are stored in the Department of Fisheries and Aquatic Sciences at the University of Florida.

The DNA was initially extracted with standard phenol-chloroform procedures (Hillis et al. 1996) and stored in

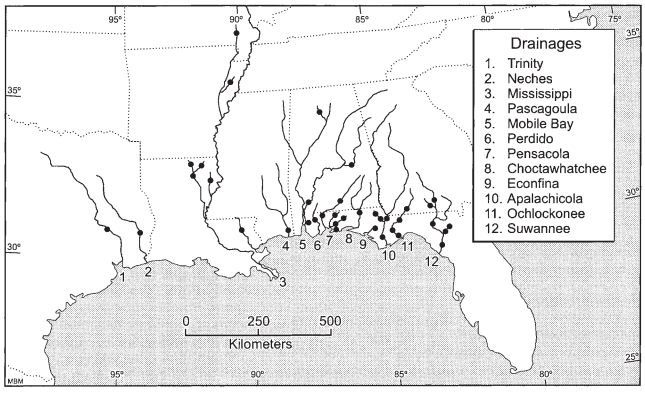


*Figure 1. Collection locales for the alligator snapping turtle. Dots indicate trapping sites. Refer to Table 2 for sample sizes of each drainage.*

500 μL of TE (10 mM Tris and 1 mM EDTA, pH 8.0). After numerous polymerase chain reaction (PCR) amplifications of extractions from the Suwannee drainage were unsuccessful, we found that isolations with a Chelex protocol yielded more consistent PCR products. A drop of blood or small tissue sample was added to a 5% Chelex solution and incubated first at 60° C for 30 minutes, then at 100° C for 15 minutes. All samples were whirled on a vortex twice during the second incubation. After cooling, the supernatant was removed and stored at 4° C. Standard precautions, including positive and negative controls, were used to assess PCR products and to guard against contamination and related problems.

Primers employed by Lamb et al. (1994) were modified to amplify PCR products from a portion of the $tRNA^{PRO}$ gene and adjoining 5′ end of the mtDNA control region in alligator snapping turtles (5′ TCT TCC TAG AAT AAT CAA AAG 3′ in the $tRNA^{PRO}$ gene; 5′ ATG ACC CTG AAG AAA GAA CCA G 3′ in the central control region). The PCR amplifications included 35 cycles: 1 minute 94° C, 1 minute 50° C, 2 minutes 72° C. Using the manufacturer's recommended conditions, we conducted single-stranded DNA-sequencing reactions with a robotic work station (Applied Biosystems model 800), and we analyzed the labeled extension products with an automated DNA sequencer (Applied Biosystems model 373A). Fragments were aligned and edited with Sequencher version 3.0 (Gene Codes Corporation). Reverse sequences were obtained for representatives of each haplotype and for any sequences with ambiguous nucleotide designations.

We used the Kimura two-parameter model (PHYLIP version 3.57, Felsenstein 1993) to estimate nucleotide sequence divergence ($d$) between mtDNA haplotypes. Sequence distances were clustered by the neighbor-joining method (Saitou & Nei 1987) algorithm in PHYLIP, and trees were evaluated by means of bootstrap values based on 2000 replicates. We conducted a maximum parsimony analysis using the branch-and-bound option in PAUP (version 3.1.1, Swofford 1993), with *C. serpentina* as an outgroup. Consistency index (CI) and retention index (RI) values were determined by this approach. An unrooted parsimony network was constructed by hand to infer phylogeographic relationships among drainages.

We estimated within-drainage and overall genetic variation in the form of haplotype ($h$) and nucleotide ($\pi$) diversities (Nei 1987, equations 8.4 and 10.5). We performed a chi-square test of haplotype frequency differences between drainages with the program CHIRXC (Zaykin & Pudovkin 1993), using 250 randomizations of the original data matrix to estimate a probability distribution for each test (Roff & Bentzen 1989). We estimated the proportion of gene diversity within and between drainages with $\phi_{ST}$ values using AMOVA version 1.5 (Excoffier et al. 1992). Using equation 14 in Slatkin and Barton (1989), we determined the average migration rate ($Nm$) between drainages by the private-allele method (Slatkin 1985).

River systems with sample sizes less than $n = 8$ (Trinity, $n = 3$; Perdido, $n = 1$; and Choctawhatchee, $n = 1$) were excluded from chi-square tests of independence and population estimates of genetic diversity. These samples, however, were included in species-wide estimates of haplotype diversity and nucleotide diversity.

## Results

Amplification products consisted of approximately 500 base pairs. From these we were able to resolve a fragment of 420 base pairs in all samples. This fragment includes 53 base pairs of the $tRNA^{PRO}$ gene and 367 base pairs at the 5′ end of the control region. In the 158 samples of *M. temminckii*, 21 variable nucleotide sites were observed, including 4 transversions and 18 transitions (site 289 contained both a transition and a transversion), which define 11 haplotypes. Representative haplotypes from Mississippi, Apalachicola, and Suwannee drainages have been deposited in GenBank under accession numbers AF056522–AF056524. Sequences are available from the authors on request.

Genetic distances between haplotypes varied from $d = 0.0024$ to $d = 0.0341$. Within-drainage haplotype diversity and nucleotide diversity were zero for all river systems except Mobile Bay, Pensacola Bay, and the Apalachicola (Table 1). Overall haplotype diversity was $h = 0.830$, and overall nucleotide diversity was $\pi = 0.0145$.

Haplotype distributions among locations have a very strong geographic component (Table 2). Four drainages contained only endemic haplotypes. Pensacola Bay drainages had two endemic haplotypes: one found in both the Escambia and Blackwater rivers, the other

**Table 1. Haplotype ($h$) and nucleotide ($\pi$) diversity for alligator snapping turtles.**

| *Drainage** | *Haplotype diversity* (h) ± *SE* | *Nucleotide diversity* ($\pi$) |
|---|---|---|
| Neches | 0.00 | 0.00 |
| Mississippi | 0.00 | 0.00 |
| Pascagoula | 0.00 | 0.00 |
| Mobile Bay | 0.41 ± 0.13 | 0.00098 |
| Pensacola | 0.50 ± 0.05 | 0.00120 |
| Econfina | 0.00 | 0.00 |
| Apalachicola | 0.29 ± 0.11 | 0.00072 |
| Ochlockonee | 0.00 | 0.00 |
| Suwannee | 0.00 | 0.00 |
| Overall | 0.830 | 0.0145 |

**Drainages with* $n < 8$ *are excluded from individual estimates of diversity but included in overall estimates.*

**Table 2. Haplotype distribution for the alligator snapping turtle.**

| | *Haplotype* | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Drainage* | *A* | *B* | *C* | *D* | *E* | *F* | *G* | *H* | *I* | *J* | *K* |
| Trinity | 3 | | | | | | | | | | |
| Neches | 18 | | | | | | | | | | |
| Mississippi | 23 | | | | | | | | | | |
| Pascagoula | | 13 | | | | | | | | | |
| Mobile Bay | | | 9 | 3 | | | | | | | |
| Perdido | | | 1 | | | | | | | | |
| Pensacola | | | | | 14 | 9 | | | | | |
| Choctawhatchee | | | | | | | | 1 | | | |
| Econfina | | | | | | | | | | 8 | |
| Apalachicola | | | | | | | 3 | 21 | 1 | | |
| Ochlockonee | | | | | | | | 13 | | | |
| Suwannee | | | | | | | | | | | 18 |

found in the Yellow River, and both found in the East Bay River. The Mississippi and two drainages to the west were fixed for the same haplotype (A). Mobile Bay shared haplotype C with the Perdido River; the adjacent Apalachicola, Ochlockonee, and Choctawhatchee drainages shared haplotype H. With only three haplotypes found in more than one drainage, Monte Carlo chi-square tests of frequency differences among river systems were highly significant ($\chi^2 = 824.3$, df = 80, $p < 0.001$). Very strong population structuring was also indicated by a $\phi_{ST}$ value of 0.978, possibly the highest value reported in the literature for conspecific populations. Given this exceptionally high value, the estimated migration rate was correspondingly low, $Nm \approx 0.1$. This value indicates that dispersal between drainages is too low to influence demographic processes.

The topology produced by a neighbor-joining analysis was concordant with a hand-generated parsimony network (Fig. 2). Both methods partitioned the 11 mtDNA haplotypes into three major groups: the western assemblage includes 6 haplotypes; the central lineage includes 4 haplotypes; and a single divergent eastern haplotype was observed only in the Suwannee drainage. This Suwannee lineage represents the deepest partition in the control-region phylogeny. In the neighbor-joining tree, bootstrap analyses supported the three groups with values from 86% to 92%, with an average sequence divergence between lineages of 2.45%. The maximum parsimony method was consistent with the branching of this tree, except that parsimony failed to resolve the topology of the cluster containing haplotypes B, C, and D and the cluster containing haplotypes H, I, and J. Both the consistency index (0.89) and the retention index (0.83) demonstrated a good fit of this tree to the original data. Sequences from the common snapping turtle ($d = 0.1027-0.1253$ from the alligator snapping turtle) were most similar to the divergent Suwannee haplotype in all analyses.

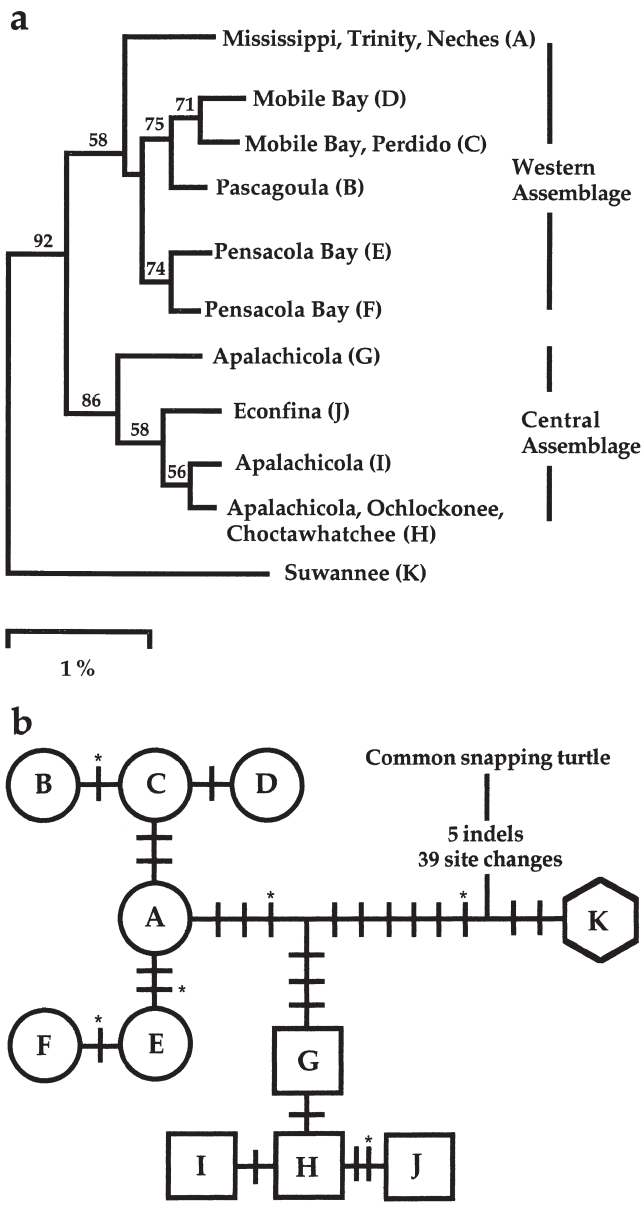


*Figure 2. Phylogenetic relationships among mtDNA haplotypes for the alligator snapping turtle; neighbor-joining tree (a) and parsimony network, including the common snapping turtle (b). Numbers on the tree indicate levels of bootstrap support greater than 50%. On the parsimony network, circles designate the western, Mississippi-influenced haplotypes, squares denote the central lineage, and the hexagon indicates the Suwannee; asterisks denote instances of presumed homoplasy (not shown for common snapping turtle).*

## Discussion

### Population Structure

Control-region sequences for the alligator snapping turtle reveal substantial population subdivision among the

various drainages. The highly aquatic nature and habitat limitations of *M. temminckii* may help explain the depth of these breaks. Harrell et al. (1996) conducted a telemetry study of 12 juvenile alligator snapping turtles in Louisiana with a total of 1327 location fixes. They recorded no overland movement. Sloan and Taylor (1987) monitored the activities of 11 adult alligator snapping turtles; although the turtles used culverts to travel between water bodies, no terrestrial locations were documented in more than 14 months of study. As with freshwater fishes, the opportunities for interdrainage dispersal for *M. temminckii* seem to be restricted to events such as drainage confluences during low sea level, estuarine and inland flooding, and stream captures. With an overall $\phi_{ST}$ value of 0.978, it is clear that these are rare events.

One exception to the strong structuring of *M. temminckii* haplotypes was the occurrence of haplotype A in three drainages (Mississippi, Trinity, and Neches), represented by trapping locations separated by more than 750 km. A likely explanation for the paucity of genetic variation in the Trinity and Neches rivers is that populations in these smaller drainages may be the product of relatively recent colonization events. Low diversity in the Mississippi River, which included samples from Louisiana, Missouri, and Arkansas, is more difficult to explain.

The largest river in North America, the Mississippi is a relatively old drainage, and fossil evidence indicates that *Macroclemys* occurred there in the Miocene (Zangerl 1945), although perhaps not continuously since then. Much of the Mississippi was glaciated during the Pleistocene (Mayden 1988), presumably restricting the northern distribution of *M. temminckii*. Frigid glacial runoff may have extirpated the alligator snapping turtle from the main channel and northern tributaries of the Mississippi or may have reduced suitable habitat to a few southern tributaries (Mayden 1988; Walker & Avise 1998). Under this scenario, it is possible that remnant populations from these tributaries, or from the Neches or Trinity rivers, dispersed back through the Mississippi after a glacial episode.

It is notable that this Mississippi-distributed haplotype (A) may indicate the ancestral source of turtles in the Pascagoula, Mobile Bay, and Pensacola drainages. Many coastal-plain rivers were completely flooded by seawater or greatly reduced in size during the Pliocene (Bermingham & Avise 1986). As Lamb et al. (1994) noted for map turtles, opportunities for endemic lineages to develop in the Pascagoula and Pensacola Bay drainages probably occurred after sea-level lowering in the Late Pliocene.

In the central lineage, unique haplotypes were found in relatively small drainages. Even Econfina Creek, which is depauperate in freshwater fish species (Swift et al. 1986) and before this study had no record of *M. temminckii* (Pritchard 1992), yielded a unique haplotype for the eight turtles analyzed. The more widespread haplotype H, found in the adjacent Apalachicola, Ochlockonee, and Choctawhatchee rivers, may reflect stream capture by the Ochlockonee from the Apalachicola (Gilbert 1987), as well as the fact that the Apalachicola once coursed through the valley now occupied by the Choctawhatchee River (Puri & Vernon 1964). Such large-scale geological events aside, most river systems have characteristic haplotypes that are either endemic or shared only with adjacent drainages.

It remains to be determined whether subtle demographic partitions exist within drainages. In Pensacola Bay, the two western rivers, Escambia and Blackwater, share a single haplotype (E), the Yellow River has a unique haplotype (F), but both haplotypes occur in the East Bay River, perhaps indicating recent movement. Elsewhere, samples are either too scarce or, as with the Mississippi, genetic diversity is too low ($\pi = 0$) to provide sufficient resolution to identify within-drainage partitions.

### Biogeography and Evolutionary History

With nucleotide divergences up to 3.4%, it is evident that *M. temminckii* lineages have been isolated over recent evolutionary history. Estimates of DNA sequence divergence have been used to date evolutionary events, based on a provisional assumption of uniform rates of mutation. Encalada et al. (1996) proposed a divergence rate of 1.2–2.4% per million years for the control region in green turtles (*Chelonia mydas*). A similar rate applied to the control region of the alligator snapping turtle indicates that extant populations may have shared a common ancestor in the late Pliocene or early Pleistocene, yet fossil records for the genus *Macroclemys* date back at least 12–20 million years (Zangerl 1945). Although molecular clocks must be interpreted with caution, alligator snapping turtle populations evidently coalesced within the past few million years—perhaps 10% of the time frame for *Macroclemys* in the fossil record.

The deepest mtDNA lineages in the alligator snapping turtle are similar in magnitude to those found between species of map turtles (Lamb et al. 1994), which display considerable variation in size, head markings, and carapacial morphology (Conant & Collins 1991; Ernst et al. 1994). Although a rigorous rangewide survey of morphological variation of *M. temminckii* has not been conducted, geographic variation in skull shape has been noted (Pritchard 1989), and an east-west split in this morphological feature may coincide with the genetic break between the Pensacola and Choctawhatchee drainages (S.D.S., personal observation). The alligator snapping turtle, however, seems to display less phenotypic diversity than other freshwater turtles. Certainly the deep split found for the Suwannee lineage was unanticipated on the basis of external morphology alone.

In contrast to the strong phylogeographic structure in *M. temminckii*, the common snapping turtle exhibits almost no mtDNA variation in eastern North America (Phillips et al. 1996; Walker et al. 1998). This uniformity and the turtle's ability to disperse over land and water suggest that the common snapping turtle may be considered a single ESU (Walker et al. 1998). Molecular evidence for the alligator snapping turtle, however, indicates the existence of three major evolutionary lineages or ESUs.

The distribution of mtDNA lineages among Gulf Coast drainages may be tied to isolation and dispersal events associated with marine transgressions and regressions from the late Pliocene through the Pleistocene, as is suspected for other freshwater species in the region (Bermingham & Avise 1986; Lamb et al. 1994). In particular, the presence of a large sand-hill region separating Pensacola Bay drainages from river systems to the east may have served as a long-standing barrier to dispersal, fostering the split between the western and central groups. Even if sea levels rose 5–10 m, these sand hills could continue to serve as a terrestrial barrier. This split in the mtDNA phylogeny of the alligator snapping turtle is consistent with a major break in the distribution of amphibians and reptiles at Pensacola Bay (Conant & Collins 1991), and Avise (1992) has noted intraspecific phylogenetic breaks for the freshwater fishes in this vicinity.

Unlike the split between Pensacola and Choctawhatchee bays, which reflects a well-documented break in faunal composition, the Suwannee has almost identical fish fauna to that of the nearest major Gulf Coast drainage, the Ochlockonee (Swift et al. 1986). In the alligator snapping turtle phylogeny, however, this single drainage represents the deepest evolutionary break. A likely explanation for this deep divergence is that a remnant population, perhaps from as long ago as the Pliocene, may have persisted in the Suwannee because cold glacial runoff was probably not an influence on this southern low-altitude drainage. It is interesting that this lineage was found to be the closest to *C. serpentina.*

### Conservation Implications

The river-specific structure of the alligator snapping turtle—showing demographic and perhaps evolutionary independence among populations—has immediate application to management plans. This case history highlights the inherent vulnerability of slow-growing riverine species, which may be easily harvested, quickly depleted, and slow to recover. Habitat alterations, in the form of dams and agricultural modifications, have been extensive throughout the species' range and no doubt influence this recovery. The genetic data indicate that the extirpation of the alligator snapping turtle from a single drainage could entail the loss of divergent haplotypes, and negligible interdrainage gene flow would prevent natural recolonization within the foreseeable future. Based on the criterion of phylogenetic distinctiveness (Avise 1989), turtles in the Suwannee merit a high conservation priority because this river is the sole locale of a highly divergent lineage.

Many riverine species are subject to similar conservation concerns. Dynesius and Nilsson (1994) surveyed 139 of the largest river systems in the northern third of the world and found that 77% were strongly or moderately affected by fragmentation or water-flow modifications. As a result, many ecosystems have been lost and populations of riverine species fragmented. Within the range of the alligator snapping turtle, Lydeard and Mayden (1995) noted that the aquatic systems of Alabama are hotspots of biodiversity, although no critical habitat has been protected and most species remain unstudied. In the data they reviewed, 10% of fishes, 69% of mussels, 65% of gill-breathing snails, and 43% of freshwater turtles in Alabama were recognized as extinct, endangered, threatened, or of special concern. Many other river systems host organisms that are similarly underprotected and poorly researched.

In the absence of genetic or tagging data, wildlife managers may define management units on a river-specific basis for many aquatic, salt-intolerant species. On a broader scale, phylogeographic provinces may be consistent across taxa, as is the case with many freshwater turtles (Walker & Avise 1998).

A decade ago Pritchard (1989) argued for federal protection of the alligator snapping turtle because of pressures from harvest and human encroachment. As a result of suspected population declines, most states in which the alligator snapping turtle resides have already restricted harvest; only Louisiana continues to permit commercial exploitation. A study of the status of alligator snapping turtles in Arkansas, which borders Louisiana to the north, provided evidence that turtles may have been overharvested in this state. In counties open to "turtling" before 1993, the frequency of turtles presumed to have reached sexual maturity was lower than in those counties that prohibited trapping (Wagner et al. 1998).

In Florida, conservation methods include a ban on commercial harvest, which appears to be effective. Moler (1996) noted that trapping success during biological surveys for *M. temminckii* was 3–4 times greater in Florida—which has prohibited commercial take since 1973—than it was in a Georgia river that sustained heavy harvests until 1983. Size distribution also differed: turtles more than 22.5 kg were proportionally more than twice as common in Florida than in Georgia.

The high market value of turtle meat, which currently sells for up to $9 a pound in New Orleans, and the large size and habitat limitations of *M. temminckii* make this species especially vulnerable to overharvest. Sloan and Lovich (1995) reported that one Louisiana buyer processed approximately 1200 alligator snapping turtles in 3 years. Even many Louisiana turtle trappers agree that

much of their state is commercially "fished out" (Pritchard 1989).

In Alabama and Florida, there has been evidence of poaching to supply Louisiana's marketplace (C. Parnell, personal communication; P.E.M., personal observation). Polymerase chain reaction technology, which allows for the recovery of genetic material from processed and minute amounts of material, may provide a means of detecting such activities (Baker et al. 1996). Based on the drainage-specific markers identified here, illegally harvested snappers can now be discerned even after they have been transported across state lines and butchered. Only turtles with the widespread western haplotype A, of the Trinity, Neches, and Mississippi rivers, can be legally harvested for sale. For drainages represented by all of the other haplotypes, commercial harvest is prohibited by state laws.

Molecular genetic testing can become an important means of monitoring the trade in turtle products in the United States and internationally. If *Macroclemys* from other states is sold in Louisiana, this commerce constitutes a violation of U.S. law (the Lacey Act), which restricts the movement of animals in violation of any federal, state, or foreign regulations. We have developed a simple restriction-fragment protocol that distinguishes alligator snapping turtle meat from that of common snapping turtles (Roman et al., unpublished). Combined with DNA sequencing, this protocol can provide a robust tool for effective law enforcement on a state, national, and international level.

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