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Short Communication

Evolutionary relationships of marine turtles: A molecular phylogeny based on nuclear and mitochondrial genes

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1. Introduction

Marine chelonians have inhabited the earth for over 100 million years, since the Cretaceous (Hirayama, 1998) and the fossil record reveals that four families were established during this period, two of which have survived into the present (Pritchard, 1996). The Dermochelyidae contains only the leatherback turtle, *Dermochelys coriacea*, while the second family, the Cheloniidae, is commonly thought to include six species classified into five genera (Fig. 1). Early molecular phylogenetic studies supported recognition of the olive ridley, *Lepidochelys olivacea*, and Kemp's ridley, *L. kempii*, as separate species (Bowen et al., 1991, 1993; Dutton et al., 1996) and removal of the flatback turtle, *Natator depressus*, from genus *Chelonia* (Dutton et al., 1996; see also Limpus et al., 1988 and Zangerl et al., 1988). There is general agreement that the leatherback, *Dermochelys coriacea*, is the sister-taxon to a clade comprising all other extant sea turtles (e.g., Gaffney and Meylan, 1988; Pritchard, 1996), and one phylogenetic hypothesis (Fig. 1a; see Iverson et al., 2007) is broadly supported by the most recent research (Bowen and Karl, 1996; Dutton et al., 1996; Parham and Fastovsky, 1997).

Despite the application of molecular approaches, there are still conflicting hypotheses about the evolutionary relationships of widely distributed but highly threatened marine turtles (Bowen et al., 1993; Dutton et al., 1996), and further study is needed (Bowen and Karl, 2007; Iverson et al., 2007). In the past, questions were raised as to the placement of the geographically restricted flatback, *Natator depressus*, which nests only in Australia (see Bowen et al., 1993; Dutton et al., 1996; Pritchard, 1996). The evolution of feeding ecology in marine turtles remains puzzling, and two alternative hypotheses of carnivorous versus herbivorous origins have been proposed to account for spongivory in hawksbill turtles (Bowen and Karl, 1996), a rare dietary choice in reptiles and vertebrates (Meylan, 1988). The possibility of an omnivorous ancestor has not been as fully explored. Additionally, full consensus has not yet been reached on the taxonomic status of the Eastern Pacific (EP) green turtle (*Chelonia mydas*; see Kamezaki and Matsui, 1995; Parham and Zug, 1996; Pritchard, 1996). However, to date DNA results reveal no species-level or evolutionary distinctiveness of *C. mydas* of the EP (Bowen et al., 1992, 1993; Bowen and Karl, 1996; Karl and Bowen, 1999).

Although recently there has been intense scientific focus on the evolutionary relationships among all turtles (see Iverson et al., 2007), our understanding of marine turtle phylogeny from a genetic perspective still remains largely based on mitochondrial DNA studies (Bowen et al., 1993; Dutton et al., 1996; but see Bowen and Karl, 1996), despite recognized problems in relying solely on mtDNA. To address the lingering controversies and to recover a definitive marine turtle phylogeny, we sequenced five nuclear DNA markers (*BDNF*, *Cmos*, *R35*, *Rag1*, and *Rag2*) and two mitochondrial genes (*12S* and *16S*) in the seven widely recognized marine turtle species, the taxonomically ambiguous Eastern Pacific green turtle, and four outgroups. We used comprehensive phylogenetic methods, improving upon previous work by including multiple outgroups and examining both nuclear and mitochondrial markers. Using this approach we tested hypotheses about the evolutionary relationships of marine turtles, including the placement of the geographically restricted flatback turtle, and the origin of the rare spongivorous dietary habit of hawksbill turtles.

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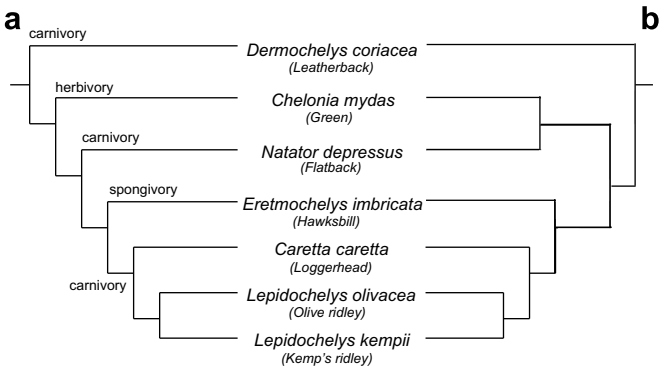

Fig. 1. (a) Consensus phylogenetic relationships of marine turtles based on previous studies (after Iverson et al., 2007); (b) Evolutionary relationships revealed in this study.

2. Materials and methods

2.1. Taxonomic sampling and laboratory methods

We obtained blood or tissue samples from marine turtles nesting at beaches of the Atlantic and Pacific Oceans (with the exception of the Kemp's ridley turtle sampled from a feeding ground; Table 1), and from four outgroups. We employed the primers listed in Table A1 (Supplementary Data) to amplify and sequence two mitochondrial and five nuclear markers using previously described laboratory methods (Le et al., 2006). We aligned the sequence data using the program Sequencher v4.6 (Gene Codes Corporation) or ClustalX v1.83 (Thompson et al., 1997) with default settings for complete alignment.

2.2. Phylogenetic analysis

Data were analyzed using maximum parsimony (MP) as implemented in PAUP* v4.0b10 (Swofford, 2001) and Bayesian analysis as implemented in MrBayes v3.1 (Huelsenbeck and Ronquist, 2001). For maximum parsimony, we conducted heuristic analyses with 100 random taxon addition replicates using the tree-bisection and reconnection (TBR) branch swapping algorithm in PAUP, with no upper limit set for the maximum number of trees saved. Bootstrap support (BP; Felsenstein, 1985) was evaluated using 1000 pseudoreplicates and 100 random taxon addition replicates. Bremer indices (BI; Bremer, 1994) were determined using TreeRot v3 (Sorenson and Franzosa, 2007). All characters were equally weighted and unordered. For Bayesian analyses we used the optimal model determined using Modeltest v3.7 (Posada and Crandall, 1998) with parameters estimated by MrBayes v3.1. Analyses were conducted with a random starting tree and run for 5×10^6 generations. Four Markov chains, one cold and three heated (utilizing default heating values), were sampled every 1000 generations. Log-likelihood scores of sample points were plotted against the number of generations to detect stationarity of the Markov chains. Trees generated prior to stationarity (21 trees in both combined and mixed-model Bayesian analyses) were removed from the final analyses using the burn-in function. Two independent analyses were run simultaneously. The posterior probability values (PP) for all clades in the final majority rule consensus tree are reported. We ran analyses on both combined and partitioned datasets to examine the robustness of the tree topology (Nylander et al., 2004; Brandley et al., 2005). In the partitioned analyses, we divided the data into fifteen separate partitions, including *12S*, *16S*, and *R35*, with the other twelve partitions based on gene codon positions (first, second, and third) in *BDNF*, *Cmos*, *Rag1*, and *Rag2*. Optimal models of molecular evolution for each partition were selected using the Akaike information criterion (AIC) in Modeltest and then assigned to these partitions in MrBayes (Table A2, Supplementary Data). Model parameters were calculated independently for each data partition using the UNLINK command. We consider bootstrap values $\geqslant$70% potentially strong support (Hillis and Bull, 1993) and PP values $\geqslant$95% strong support for a clade.

Table 1
Sampling locations at nesting beaches in the Atlantic or Pacific Oceans

Taxon	Sample site (n)[a]	
	Atlantic	Pacific
Dermochelys coriacea	Mayumba, Gabon (1)	New South Wales, Australia (1)[b]
Chelonia mydas	Atol das Rocas, Brazil (1)	Heron Island, Queensland, Australia (1)
	Trindade Island, Brazil (1)	—
Eastern Pacific	—	Michoacán, Mexico (2)
Natator depressus	—	Queensland, Australia (1)
Eretmochelys imbricata	Puerto Rico, USA (1)	Queensland, Australia (1)
Caretta caretta	Georgia, USA (1)	Mon Repos, Queensland, Australia (1)
Lepidochelys olivacea	Ada Foah, Ghana (1)[b]	Northern Territory, Australia (1)
Lepidochelys kempii	New York, USA (1)[c]	—

[a] Sample size is indicated in parentheses.
[b] A taxon represented by two individuals due to samples that were degraded or difficult to amplify.
[c] Sample collected at a feeding rather than nesting area.

2.3. Time calibration

Divergence times were calculated using a relaxed clock model (Drummond et al., 2006) as implemented in the computer program BEAST v1.4.5 (Drummond and Rambaut, 2006). The program BEAUti v1.4.5 was used to set criteria for the analysis. Nodes corresponding to the most recent common ancestors of three clades: (1) all sea turtle species; (2) *Caretta* and *Lepidochelys*; and (3) *Lepidochelys kempii* and *L. olivacea* were constrained respectively to: (1) 110 million years with a 95% confidence interval from 100 to 120; (2) 16 million years with 95% confidence interval from 12 to 20; and (3) 5 million years with 95% confidence interval from 4 to 6. These dates are based on reasonably strong fossil evidence (Carr, 1942; Hendrickson, 1980; Zangerl, 1980; Dodd and Morgan, 1992; Hirayama, 1998) and supported by genetic studies (*Lepidochelys, Caretta*: Bowen et al., 1991). A GTR model using gamma + invariant sites with four gamma categories was used along with the assumption of a relaxed molecular clock. As for the priors, we used all default settings, except for the Tree Prior category that was set to Yule Process as suggested in the BEAST manual. A UPGMA tree was used as a starting tree. The analysis was run for 5×10^6 generations with a 1000-step thinning. The posterior sample was examined in Tracer v1.4. Burn-in was set to 500. The final tree with divergence estimates and their 95% highest posterior densities (HPD) was computed in TreeAnnotator v1.4.5. BEAST, BEAUti, TreeAnnotator, and Tracer are available from http://beast.bio.ed.ac.uk.

3. Results

The final matrix that was subjected to phylogenetic analyses included 404 aligned bp of *12S*, 579 bp of *16S*, 717 bp of *BDNF*, 602 bp of *Cmos*, 984 bp of *R35*, 2860 bp of *Rag1*, and 1194 bp of *Rag2* for a total of 7340 bp. The GenBank Accession numbers for these sequences are listed in Table A3 (Supplementary Data). The sea turtle data set included 17 indels. Of these, 14 were 1 bp long and found within *12S*, *16S* and the *R35* intron. The remaining three indels were: (1) a 28 bp insertion in Atlantic and Western Pacific green

turtles within the *R35* intron; (2) a 12 bp insertion in the *Rag1* gene of *Caretta caretta* (Atlantic and Pacific); and (3) a 3 bp deletion in *Rag2* of *Eretmochelys imbricata*. The nucleotide composition of sites polymorphic in more than one individual in green turtles is shown in Table A4 (Supplementary Data).

Using Maximum Parsimony (MP) and Bayesian analyses, we recovered the phylogenetic trees shown in Figs. 1b and 2. All of the phylogenetic methods used in this study generated trees with an identical topology and strong levels of support for all nodes. In the MP cladogram, all nodes received high bootstrap support. MP analyses of nuclear and mitochondrial partitions also indicated the same topology (Supplementary Data Figs. A1–A2). Time calibration analysis demonstrated that the Chelonini split from Carettini about 63 MYA (95% HPD: 35.59 MYA–91.38 MYA), while *Natator* separated from *Chelonia* about 34 MYA (95% HPD: 14.08 MYA–60.05 MYA), and *Eretmochelys* split from *Caretta* and *Lepidochelys* about 29 MYA (95% HPD: 16.52 MYA–44.27 MYA; Supplementary Data Fig. A3). The divergence between Atlantic and Indo-Pacific green turtles is estimated at about 7 million years (95% HPD: 1.92 MYA–13.47 MYA; Supplementary Data Fig. A3).

4. Discussion

Our phylogenetic results differ from those recovered in previous molecular studies by strongly supporting a sister-taxon relationship between the flatback (*Natator depressus*) and green turtles

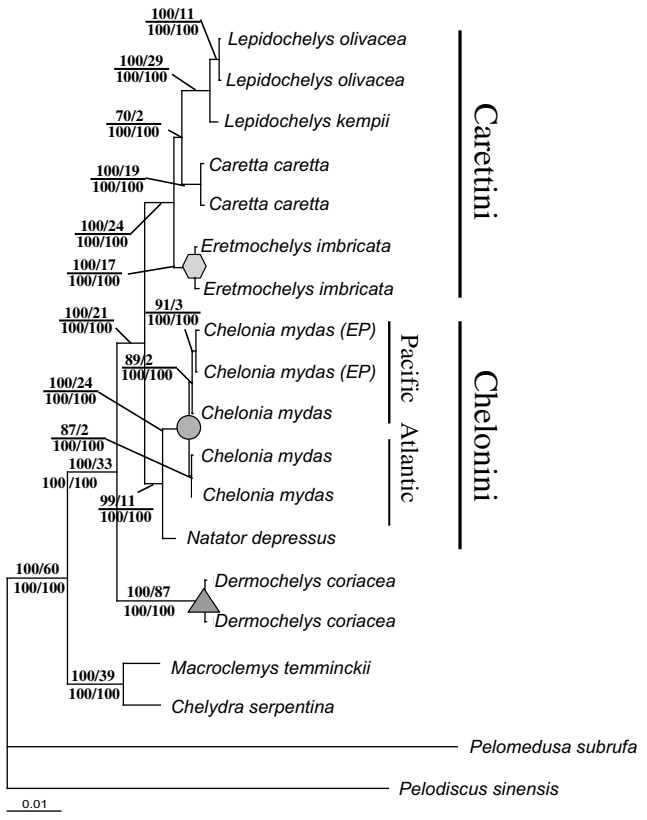

Fig. 2. Single tree generated from the MP and Bayesian analyses of combined mitochondrial and nuclear genes with branch length estimated by the Bayesian analyses. For the MP analysis, tree length = 1502, consistency index (CI) = 0.868, and retention index (RI) = 0.84. Of the 7340 total characters, 1177 were variable characters and 480 of these were parsimony-informative. The numbers above branches are MP bootstrap and Bremer values (Bremer, 1994), and those below the branches are posterior probability values (PP) from combined and mixed-model Bayesian analyses, respectively. The triangle, hexagon, and circle show jellyfish carnivory, spongivory, and herbivory feeding modes, respectively.

(*Chelonia mydas*; BP = 99%, PP = 100%). Although recent research consistently grouped the flatback with the Carettini tribe (e.g. Dutton et al., 1996; Parham and Fastovsky, 1997), this species was until recently classified as *Chelonia depressa* (Garman, 1880; Limpus et al., 1988; Zangerl et al., 1988), and its sister-taxon relationship with *C. mydas* is supported by mtDNA control region and ND4 data (Dutton et al., 1996; Bowen and Karl, 2007).

By placing the flatback outside the Carettini tribe, the previous hypothesis that the hawksbill turtle's spongivorous dietary habit developed from a carnivorous ancestor (Bowen et al., 1993; Dutton et al., 1996) becomes less obvious. The hawksbill is now hypothesized to be a basal and distinct lineage rather than a taxon embedded within a carnivorous clade. In addition, although the dietary preferences of hawksbills are primarily for sponges, their food can also include items such as plants, algae, and animals other than sponges that may dominate the diet in certain areas (reviewed by Bjorndal, 1996). Similarly, turtles that are mainly carnivorous such as the loggerhead, the ridleys, and the flatback, also consume plants and algae (reviewed by Bjorndal, 1996). Green turtles, which tend to specialize on algae or sea grass as adults, have carnivorous young (Bjorndal, 1996; Reich et al., 2007) and adult diets may include animals (Bjorndal, 1996; Seminoff et al., 2002). Based on our phylogenetic results and dietary reconstruction, we hypothesize the ancestral state of all sea turtles is carnivorous (Fig. 1b). However the reconstruction of dietary habits is not unambiguous, as the origins of spongivory in *Eretmochelys* could also be explained by transitions from omnivory to spongivory, with an omnivorous common ancestor to all sea turtles. If hawksbill, green, and leatherback turtles are nonetheless considered to be specialists over evolutionary time, with the bulk of their diet consisting of limited items, then a specialized diet in marine turtles evolved independently three times (i.e., spongivory in the hawksbill, jellyfish carnivory in the leatherback, and herbivory in the green turtle; Fig. 2).

Our results substantiate and extend findings of previous molecular studies, which also revealed the sister-taxon relationship of the ridleys, the close affiliation between *Lepidochelys* and the loggerhead turtle, and the basal position of *Dermochelys* relative to other marine turtles (Bowen et al., 1993; Dutton et al., 1996). Our study joins past work by indicating the paraphyly of the Eastern Pacific green turtle with respect to other green turtles (Bowen et al., 1992; Bowen and Karl, 1996; Karl and Bowen, 1999), and revealing a deep split between Atlantic and Pacific green turtle lineages. Our Bayesian analysis dates this divergence back to about 7 MYA (95% HPD: 1.92 MYA–13.47 MYA; Supplementary Data Fig. A3), predating other vicariant events known to divide marine taxa such as the formation of the Isthmus of Panama (about 3–3.5 MYA). However, effects of the formation of the Isthmus may have been felt prior to the closure itself, and previous estimated divergence times between Atlantic and Pacific green turtles based on a molecular clock (Encalada et al., 1996) were consistent with the formation of the Isthmus, a time period included in the confidence interval of our current estimate.

Of interest, our estimated divergence time of about 7 MYA between Atlantic and Pacific green turtles follows the closure of the Tethys Sea (14–18 MYA; Vrielynck et al., 1997; Rögl, 1998), an event that prevented mixing between many tropical marine species of the Atlantic and Indo-Pacific (Rosen, 1988). The cooling of southern ocean temperatures from the mid to late Miocene (from 15–17 MYA to about 6 MYA) is consistent with a split about 7 MYA due to cold temperatures blocking dispersal via southern routes. Indeed, the divergence between the green turtle populations in separate ocean basins is generally attributed to the biogeographic barrier to the dispersal of tropical species formed by the relatively cold waters of the southern tips of South Africa and South America. However, microsatellites and mtDNA phylogeographic studies suggest

relatively recent linkages between green turtles of the Atlantic, Indian, and Pacific (Roberts et al., 2004; Bourjea et al., 2007), and there is general agreement that limited gene flow prevents Atlantic and Pacific green turtle lineages from being considered separate species. This phylogenetic study, thus, provides a foundation for more detailed research in evolutionary biology, clarifies systematic issues of these highly threatened species, and significantly contributes to the resolution of the "turtle tree of life."

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ympev.2008.08.004.

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