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A phylogenetic framework for the terns (Sternini) inferred from mtDNA sequences: implications for taxonomy and plumage evolution

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Abstract

We sequenced 2800 bp of mitochondrial DNA from each of 33 species and 2 subspecies (35 taxa) of terns (Sternini), and employed Bayesian methods to derive a phylogeny with good branch support based on posterior probabilities. The resulting tree confirmed many of the generally accepted taxonomic groups, and led us to suggest a revision of the terns that recognizes 12 genera, 11 of which correspond to a distinct clade on the tree or a highly divergent species (1 genus was not represented in the phylogeny). As an example of how the molecular phylogeny reflects similarities in morphology and behavior among the terns, we used the phylogeny to examine the evolution of the breeding (alternate) head plumage patterns among the terns to test the hypothesis that this character is phylogenetically informative. The three basic types of head plumage (white crown, black cap, and black cap with a white blaze on the forehead) were highly conserved within clades, with notable exceptions in two white-crowned species that evolved independently among the black-capped terns. Based on the appearance of the close relatives of these exceptional species, their white crowns appear to be due to the retention of either winter (basic) plumage characteristics or perhaps juvenile characteristics when the birds molt into their breeding plumage. Examination of the evolutionary history of head plumage indicated that the white-crowned species such as the noddies (*Anous*) and the white tern (*Gygis alba*) are probably most representative of ancestral terns.

Keywords: Tern; Noddy; Charadriiformes; Plumages; Phylogeny; Taxonomy; Evolutionary history; Sternini; Sternidae; Sterninae

1. Introduction

The terns (Charadriiformes: Laridae: Sternini) are a distinctive group of seabirds that occupy aquatic environments the world over and demonstrate an interesting array of variations on a life history centered around aquatic foraging and colonial nesting. Among the terns is the Arctic tern (*Sterna paradisaea*), which migrates farther than any other animal, as well as several species with entirely sedentary life histories. The terns also demonstrate a diverse array of nesting habits, social behaviors, and molting patterns. However, understanding of the evolutionary history of these variable life history characteristics and our capacity to use the terns in comparative studies are limited by the lack of a well-supported systematic analysis of the evolutionary relationships among these birds.

According to Sibley and Monroe (1990), the terns comprise a tribe, Sternini, of 45 species in 7 genera, with

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the majority of the terns (32 species) classified under the genus *Sterna* (Table 1). Other classification schemes recognize the terns as a subfamily, Sterninae (e.g., American Ornithologist's Union, 1998, Higgins and Davies, 1996). The widely accepted classification system for the terns appears to have been influenced largely by Moynihan's (1959) taxonomic revision of the Laridae. Moynihan (1959) used his knowledge of general morphology and behavior to classify the terns as shown in Table 1, with three major groupings worthy of generic status: the noddies (*Anous*), the Inca tern (*Larosterna*), and the black-capped terns (*Sterna*). In contrast to Moynihan's extremely "lumped" revision of the terns, a more recent classification by Gochfeld and Burger (1996) divided the terns among 10 genera (Table 1). The groups recognized by both of these classification schemes are based largely on speculative criteria such as general appearance and behavior. Additionally, the utility of these morphology-and-behavior-based classifications for furthering our understanding of the evolution of life-history traits is limited because any inference about behavior or morphology from such schemes is circular.

Previous studies of evolutionary relationships among the terns are generally lacking in either their comprehensiveness or analytical rigor. In large-scale cladistic studies of the Charadriiformes only 12 species of terns were included and their relationships were unresolved (Chu, 1995; Strauch, 1978). Similarly, Sibley and Ahlquist's (1990) DNA–DNA hybridization study included only four tern species, and Hackett's (1989) sequential electrophoresis analysis included 14 tern species. Thus, these studies had relatively poor representation of the 45 extant species of terns.

The most comprehensive assessment of tern relationships that employed systematic methodology is Schnell's (1970a,b) phenetic study of the Laridae, which included 42 tern species. However, the results from this study are difficult to interpret in terms of phylogenetic relationships. Schnell (1970a,b) summarized the results of various analytical techniques applied to different morphological data sets in 14 phenograms, all of which show fundamentally different topologies. Notably, neither Hackett's (1989) nor Schnell's (1970a,b) studies were specifically attempting to construct a phylogeny of the terns. In this paper we present the first hypothesis of phylogenetic relationships among the terns using dense taxon sampling and current methods of tree-building with DNA sequence data.

To demonstrate the utility of the phylogeny in understanding how characteristics related to behavior and morphology are distributed among the terns, we examined how the three distinct forms of head plumage found in terns relate to the phylogenetic relationship defined by the tree. The majority of terns have a distinctive black cap that often contrasts markedly with gray and white body plumage. A few terns have a similar black cap but bear a white blaze on the forehead that extends from the base of the bill to just posterior to the eyes (see Fig. 1). A third type of head plumage is that of the noddies (*Anous*) and the white tern (*Gigys alba*), wherein the crown is entirely white. We used our mtDNA phylogeny to evaluate whether these head plumage-based groups correspond to groups of closely related species and to test whether head plumage is a phylogenetically conserved character.

2. Methods

2.1. Taxon sampling and DNA sequencing

Species names used throughout this paper follow Sibley and Monroe (1990). Among the taxa included in our study was the "Cayenne" tern (*Sterna sandvicensis eurygnatha*), which is widely recognized as a South American subspecies of *S. sandvicensis* (Gochfeld and Burger, 1996; Sibley and Monroe, 1990) and often hybridizes with the North American *S. s. acuflavida* subspecies (Hayes, 2004). However, *S. s. eurygnatha* is morphologically distinct from other *S. sandvicensis* subspecies (Junge and Voous, 1955) and accordingly is given species status by some authors (e.g., Harrison, 1983). We sequenced mtDNA from tissue samples of 35 tern species or subspecies and from 1 gull species (*Larus delawarensis*), which served as an outgroup, such that the total number of taxa was 36 counting the two subspecies of *S. sandvicensis* (see Table 2). We chose to use sequences from a gull, *L. delawarensis*, to root the tree based on the close phylogenetic relationship between the gulls (Larini) and the terns (Paton et al., 2003). Recognized species not included in the phylogeny are noted in Table 1. Most of the tissue samples used for DNA sequencing came from the tissue holdings at the University of Minnesota Bell Museum of Natural History and the Royal Ontario Museum. These samples were supplemented with donations from the University of Michigan Museum of Zoology, the Louisiana State University Museum of Natural Sciences, the Field Museum of Natural History, the South Australian Museum, and the Zoological Museum University of Copenhagen. Many of the samples from the Royal Ontario Museum lacked museum vouchers, but we were often able to guard against errors in identification and record keeping by sequencing at least one of the targeted DNA regions from a second member of the same species and comparing these sequences to confirm the identity of the first (Table 2).

Genomic DNA was isolated using either a DNeasy Tissue Kit (Qiagen, Valencia, CA) or by following a variation on the phenol–chloroform extraction protocol of Hillis et al. (1996). Mitochondrial DNA from part of the cytochrome *b* (cyt *b*) gene, the entire NADH 2 (ND2)

Table 1
Classifications of the terns from past studies and the recommended classification based on the mtDNA phylogeny

Moynihan (1959)	Sibley and Monroe (1990)	Gochfeld and Burger (1996)	Suggested
Anous	*Anous*	Noddies	Noddies
Dark noddies	*Anous stolidus*	*Anous*	*Anous*
Anous stolidus	*Anous minutus*	*Anous stolidus*	*Anous stolidus*
A. minutus	*Anous tenuirostris*	*A. minutus*	*A. minutus*
A. tenuirostris	*Procelsterna*	*A. tenuirostris*	*A. tenuirostris*
Intermediate noddies	*Procelsterna cerulea*	*Procelsterna*	*Procelsterna*
A. cerulea	*P. albivitta*	*Procelsterna cerulea*	*Procelsterna cerulea*[a]
A. albivitta	*Gygis*	*P. albivatta*	*P. albivitta*[b,a]
White noddies	*Gygis alba*	*Gygis*	*Gygis*
A. alba	*Gygis microrhyncha*	*Gygis alba*	*Gygis alba*
Larosterna	*Phaetusa*	Atypical black-capped terns	*Gygis microrhyncha*[a,b]
Inca tern	*Phaetusa simplex*	*Phaetusa*	Brown-winged terns
Larosterna inca	*Larosterna*	*Phaetusa simplex*	*Onychoprion*
Sterna	*Larosterna inca*	*Gelochelidon*	*Onychoprion fuscata*
Little terns	*Chlidonias*	*Gelochelidon nilotica*	*O. lunata*
Sterna albifrons	*Chlidonias albostriatus*	*Hydroprogne*	*O. anaethetus*
S. superciliaris	*C. hybridus*	*Hydroprogne caspia*	*O. aleutica*
S. nereis	*C. leucopterus*	Inca tern	Little terns
S. lorata	*C. niger*	*Larosterna*	*Sternula*
Gull-billed tern	*Sterna*	*Larosterna inca*	*Sternula albifrons*
S. nilotica	*Sterna nilotica*	Marsh terns	*S. antillarum*
Large-billed tern	*S. caspia*	*Chlidonias*	*S. superciliaris*
S. simplex	*S. aurantia*	*Chlidonias niger*	*S. nereis*
Marsh terns	*S. maxima*	*C. leucopterus*	*S. lorata*[a]
S. niger	*S. elegans*	*C. hybridus*	*S. saundersi*[a]
S. leucoptera	*S. bengalensis*	Typical black-capped terns	*S. balaenarum*[a]
S. hybrida	*S. bergii*	*Sterna*	Atypical black-capped terns
Crested terns	*S. bernsteini*	*Sterna aurantia*	*Phaetusa*
S. caspia	*S. sandvicensis*	*S. dougallii*	*Phaetusa simplex*
S. maxima	*S. dougallii*	*S. striata*	*Gelochelidon*
S. bergii	*S. striata*	*S. sumatrana*	*Gelochelidon nilotica*
S. sandvicensis	*S. sumatrana*	*S. hirundinacea*	*Hydroprogne*
S. elegans	*S. hirundinacea*	*S. vittata*	*Hydroprogne caspia*
S. bernsteini	*S. hirundo*	*S. virgata*	Inca tern
S. eurygnatha	*S. paradisaea*	*S. paradisaea*	*Larosterna*
Typical black-capped terns	*S. vittata*	*S. aleutica*	*Larosterna inca*
Sterna dougallii	*S. virgata*	*S. hirundo*	Marsh terns
S. sumatrana	*S. forsteri*	*S. forsteri*	*Chlidonias*
S. hirundinacea	*S. trudeaui*	*S. repressa*	*Chlidonias niger*
S. vittata	*S. albifrons*	*S. acuticauda*	*C. leucopterus*
S. virgata	*S. saundersi*	*S. albostriatus*	*C. hybrida*
S. paradisaea	*S. antillarum*	*S. trudeaui*	*C. albostriatus*
S. aleutica	*S. superciliaris*	Small terns	Typical black-capped terns
S. striata	*S. lorata*	*S. albifrons*	*Sterna*
S. forsteri	*S. nereis*	*S. saundersi*	*Sterna dougallii*
S. trudeaui	*S. balaenarum*	*S. superciliaris*	*S. striata*
S. repressa	*S. repressa*	*S. nereis*	*S. sumatrana*
S. balaenarum	*S. acuticauda*	*S. lorata*	*S. hirundinacea*
S. lunata	*S. aleutica*	*S. balaenarum*	*S. vittata*
S. anaethetus	*S. lunata*	Brown-winged terns	*S. paradisaea*
S. fuscata	*S. anaethetus*	*S. fuscata*	*S. hirundo*
S. acuticauda	*S. fuscata*	*S. lunata*	*S. forsteri*[b]
S. aurantia		*S. anaethetus*	*S. trudeaui*[b]
S. albostriatus		Crested terns	*S. acuticauda*[a]
S. hirundo		*Thalasseus*	*S. aurantia*[a]
		Thalasseus maximus	*S. repressa*[a]
		T. bergii	*S. virgata*[a]
		T. sandvicensis	Crested terns
		T. elegans	*Thalasseus*
		T. bernsteini	*Thalasseus maximus*
		T. bengalensis	*T. bergii*

(*continued on next page*)

Table 1 (*continued*)

Moynihan (1959)	Sibley and Monroe (1990)	Gochfeld and Burger (1996)	Suggested
			T. sandvicensis sandvicensis
			T. s. eurygnatha
			T. elegans
			T. bengalensis
			T. bernsteini[a]

Informal groups are designated by non-italic type.

[a] Not included in mtDNA tree; group membership is speculative.

[b] Group membership only weakly supported by mtDNA tree; perhaps a crested tern.

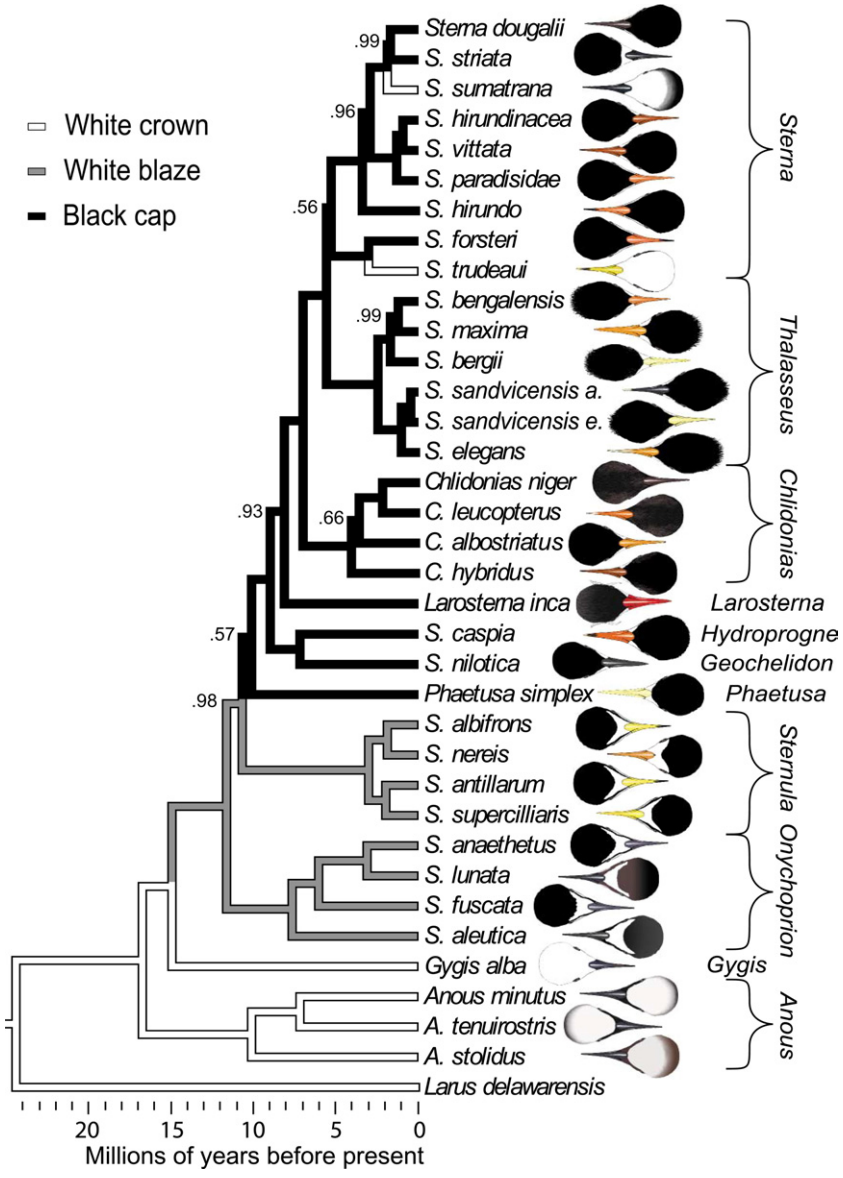

Fig. 1. Mitochondrial DNA phylogeny of the terns. Branch lengths indicate divergence times according to the scale below the tree. Posterior probabilities are listed only for branches with values less than 1. Dorsal views of the heads of all species in the tree are shown, and branch shading illustrates the evolutionary history of head plumage types. Text and brackets to the right of the figure indicate the recommended genus-level revision of the naming system (note that the genus *Procelsterna* is missing because we lacked tissue for it and could not include it in the phylogeny). A color version of this figure given in Appendix A.

gene, and part of the 12S ribosomal subunit (12S) were amplified by polymerase chain reaction (PCR; Saiki et al., 1988). Primers used in association with each mtDNA region were as follows: ND2: L5215 (Hackett, 1996), H1064 (Drovetski et al., 2004), metL (5′-AAGCTAT CGGGCCCATACCCG-3′; O. Haddrath, unpublished),

Table 2
Museum specimens used in this study

Specimen	Verification
Ring-billed Gull (*Larus delawarensis*); Washington, USA; BMNH [5027]	Voucher
Black Noddy (*Anous minutus*); Hawaii, USA; UMMZ 233348 [T-748]	cyt *b*
Brown Noddy (*A. stolidus*); Hawaii, USA; BMNH 44974 [X8367]	Voucher
Lesser Noddy (*A. tenuirostris*); Ascension Island; ZMUC 113341 [C1067]	None
White tern (*Gygis alba*); Hawaii, USA; LSUMNS B-35109 [DLD7544]	12S, cyt *b*, ND2
Large-billed tern (*Phaetusa simplex*); Rio Grande do Sul, Brazil; ROM [L50140]	None
Inca tern (*Larosterna inca*); Captive; UMMZ 234198 [T-971]	12S, cyt *b*, ND2
Black tern (*Chlidonias niger*); Kargopol'skiy rayon, Russia; BMNH 44291 [AWJ063]	12S, cyt *b*, ND2
Black-fronted tern (*C. albostriatus*); New Zealand; ROM [BFT001]	None
Whiskered tern (*C. hybridus*); W. Australia; ROM [AJD6149]	12S, cyt *b*, ND2
White-winged tern (*C. leucopterus*); W. Australia; ROM [SSB030]	None
Aleutian tern (*Sterna aleutica*); Alaska, USA; BMNH 42083 [JK9404]	Voucher
Amazon tern (*S. supercilliaris*); Para, Brazil; ROM [G29502]	12S, cyt *b*, ND2
Antarctic tern (*S. vittata*); Antarctica; LSUMNS B-9899	12S, cyt *b*, ND2
Arctic tern (*S. paradisaea*); Mezenskiy rayon, Russia; BMNH 44530 [AWJ101]	12S, cyt *b*, ND2, voucher
Black-naped tern (*S. sumatrana*); Micronesia; FMNH 346067	12S, cyt *b*, ND2
Bridled tern (*S. anaethetus*); W. Australia; ROM [AJB5615]	None
Caspian tern (*S. caspia*); Minnesota, USA; BMNH 42160 [JK9424]	12S, cyt *b*, ND2, voucher
Cayenne tern (*S. sandvicensis eurygnatha*); Para, Brazil; ROM [G12327]	12S, cyt *b*, ND2
Common tern (*S. hirundo*); Kargopol'skiy rayon, Russia; BMNH 44288 [AWJ060]	12S, cyt *b*, ND2, voucher
Crested tern (*S. bergii*); New S. Wales; ROM [AJB5621]	12S, cyt *b*, ND2
Elegant tern (*S. elegans*); Baja California Sur, Mexico; LSUMNS B-5788	None
Fairy tern (*S. nereis*); S. Australia; SAM ABTC2326	12S, cyt *b*
Forster's tern (*S. forsteri*); Minnesota, USA; BMNH 44052 [X8202]	voucher
Gray-backed tern (*S. lunata*); Hawaii, USA; BMNH 44973 [X8536]	voucher
Gull-Billed tern (*S. nilotica*); Rio Negro, Argentina; ROM [G3]	None
Least tern (*S. antillarum*); Louisiana, USA; LSUMNS B-8423 [DLD2137]	12S, cyt *b*, ND2
Lesser crested tern (*S. bengalensis*); W. Australia; ROM [AJB6104]	12S, cyt *b*, ND2
Little tern (*S. albifrons*); W. Australia; ROM [AJB6071]	12S, cyt *b*, ND2
Roseate tern (*S. dougallii*); Massachusetts, USA; BMNH 44190 [X8594]	voucher
Royal tern (*S. maxima*); Rio Grande do Sul, Brazil; ROM [NO7420]	12S, cyt *b*
Sandwich tern (*S. sandvicensis acuflavida*); Louisiana, USA; LSUMNS B-8458 [SJH21]	12S, cyt *b*, ND2
Sooty tern (*S. fuscata*); New S. Wales, Australia; ROM [AJB5625]	12S, ND2, voucher
South American tern (*S. hirundinacea*); Buenos Aires, Argentina; ROM [Sth001]	None
Snowy-crowned tern (*S. trudeaui*); Rio Grande do Sul, Brazil; ROM [J14824]	None
White-fronted tern (*S. striata*); New Zealand; ROM [WFT001]	12S, cyt *b*, ND2

Common and scientific names from Sibley and Monroe (1990) are followed by the specimen's locality, its museum of origin, and the accession and field numbers if available (field numbers are in brackets). Sequences or vouchers used to validate species identity are listed in the verification column. Museum abbreviations are as follows: BMNH, University of Minnesota Bell Museum of Natural History; ROM, Royal Ontario Museum; UMMZ, University of Michigan Museum of Zoology; LSUMNS, Louisiana State University Museum of Natural Sciences; FMNH, Field Museum of Natural History; SAM, South Australian Museum; and ZMUC, Zoological Museum University of Copenhagen.

and ASN (5′-GATCRAGGCCCATCTGTCTAG-3′; O. Haddrath, unpublished); 12S: L1537 (5′-CAATCTT GTGCCAGCCACCGCGG-3′; O. Haddrath, unpublished) and 12Send (5′-GTGCACCTTCCGGTACACT TACC-3′; O. Haddrath, unpublished); cyt *b*: B52 (5′-GNAAATCYCACCCNCTWCTHAAAAT-3′; O. Haddrath, unpublished) and B6 (T. Burt, pers. comm.). The thermal cycles used for PCR amplification are described in Buehler and Baker (2003) and in Drovetski et al. (2004). PCR products were cleaned using a Qiaquick PCR Purification Kit (Qiagen Valencia, CA).

With the exception of two ND2 sequences, all sequencing was performed by the University of Minnesota Advanced Genetic Analysis Center on ABI 377 automated sequencers. ND2 sequences from *S. trudeaui* and *S. bergii* were pieced together from parts of the gene sequenced manually using a Thermo Sequenase Cycle Sequencing Kit (Amersham–Pharmacia Biotech, Amersham, UK), from partial sequences produced by the Advanced Genetic Analysis Center, and from sequence generated by a Licor 4200 long-read DNA sequencer at the Royal Ontario Museum. Sequences were edited and aligned using Sequencher v4.1.2 (Gene Codes, Ann Arbor, MI). We were able to align the 12S sequence without adding gaps for all but one taxon, *Sterna anaethetus*, which required a 1-bp gap. Examination of amino acid sequences confirmed the mitochondrial origin of the protein-coding genes. The final edited data set included 2800 bp for each taxon: 1050 bp for cyt *b*, 1041 bp for ND2, and 709 bp for 12S. There were few missing bases for most taxa with the exception of *Anous minutus*, for which we lacked over 500 bp from the cyt *b* gene. All sequences used for phylogenetic inference are deposited in GenBank (Accession Nos. AY631284–AY631391).

2.2. Phylogenetic and evolutionary analyses

We generated the final mtDNA phylogeny using Bayesian inference with the program MrBayes v3.0 (Huelsenbeck and Ronquist, 2001). We chose this method of analysis because it allowed us to use a partitioned likelihood model wherein all parameter values were generated separately for each DNA region. For each partition, we specified a general time reversible model with empirical base frequencies and with rate variation among sites modeled as a gamma distribution. The Markov chain Monte Carlo (MCMC) search was run with four chains that were incrementally "heated" according to the default values of the program to ensure an adequate search of the tree space. The chain ran for 2,000,000 generations with trees sampled every 2000 generations. A graph of −log likelihood vs. generation (not shown) revealed that the −log likelihood leveled off after approximately 30,000 generations; thus, we discarded trees from the first 100,000 generations as a conservative "burn-in." A phylogeny was constructed from the remaining 951 trees by compiling a majority-rule consensus tree in PAUP* v4.0b2a (Swofford, 1999). Because the trees from every 2000th generation were a sample from the posterior distribution of most likely trees (Tierney, 1994), the probability of each node can be estimated based on the proportion of trees in the sample that support the node. In addition to the Bayesian phylogenetic analysis, we performed heuristic searches using maximum parsimony (MP) and maximum likelihood (ML) in PAUP to determine to the extent to which these different methodologies agree in their resulting tree topologies, and we calculated ML bootstrap values for the Bayesian tree topology with 100 bootstrap replications.

We consulted Gochfeld and Burger (1996) in scoring winter plumage characters associated with each species and subspecies. Head plumage characteristics were mapped onto the phylogeny using a simple parsimony model in the Mesquite software package (Maddison and Maddison, 2003).

2.3. Estimating divergence times

A likelihood ratio test indicated that the full data set (with outgroup removed) did not adhere to a model of evolution with a molecular clock enforced ($df = 33$, $\chi^2 = 167.87$, $p < 0.001$). Similarly, likelihood ratio tests examining each DNA region separately also showed that only sequence data from 12S appeared to be clocklike (12S: $df = 33$, $\chi^2 = 29.80$, $p = 0.63$; ND2: $df = 33$, $\chi^2 = 217.12$, $p < 0.001$; cyt *b*: $df = 30$, $\chi^2 = 43.66$, $p = 0.10$). Thus, we generated divergence times by applying Sanderson's (1997) non-parametric rate smoothing method in the program r8s v1.50 (Sanderson, 2002) to the likelihood branch lengths generated in the Bayesian analysis from the entire data set. We calibrated divergence times by assigning dates to two speciation events. The first calibration point was the gull–tern split estimated by Paton et al. (2003) to have occurred 24.4 million years before present (MYBP). The second was the divergence of *Chlidonias niger* and *C. leucopterus*. Howard (1946) found *C. niger* fossils in Oregon dating to approximately 2 MYBP, suggesting that the latter date corresponds roughly with *C. niger*'s colonization of the Northwestern United States. Because all *Chlidonias* terns other than *C. niger* are restricted to the old world, we assigned a date of 2 MYBP as a minimum divergence of this species from its sister species, *C. leucopterus*.

3. Results

3.1. Tree topologies and branch support

Bayesian analysis produced a generally well-supported tree with several distinct clades of species and with only three poorly supported nodes based on posterior probabilities (Fig. 1; a color version of this tree is given in the supplementary material available online, as described in Appendix A). The three weak nodes involved the positions of *Phaetusa simplex*, *C. hybridus*, and the clade formed by *S. forsteri* and *S. trudeaui*. Among the trees sampled in the Bayesian analysis, *P. simplex* occasionally formed a clade with *S. caspia* and *S. nilotica* or grouped as a distant sister species to the small terns (*Sternula* in Fig. 1). A similar situation describes the poor posterior probability support associated with the *S. fosteri–S. trudeaui* clade, which either grouped in a basal position with the crested terns (*Thalaseus* in Fig. 1), was positioned as a sister group to both crested terns and black-capped terns (*Sterna* in Fig. 1), or was grouped in a basal position with the black-capped terns as shown in Fig. 1. The third branch with a low posterior probability is the one grouping *C. niger*, *C. leucopterus*, and *C. albostriatus*. The uncertainty of this node is due to the fact that *C. albostriatus* was the most basal of the *Chlidonias* terns in roughly one-third of the trees sampled from the MCMC chains, as opposed to *C. hybridus* being the most basal *Chlidonias* tern as shown in Fig. 1.

Both of the most optimal ML and MP trees differed from the Bayesian tree in that the *S. forsteri–S. trudeaui* clade was sister to the crested terns (*Thalasseus* in Fig 1) and the other black-capped terns (*Sterna* in Fig. 1). In addition the MP tree grouped *L. inca* with *S. caspia* and *S. nilotica* and placed *P. simplex* in a clade with the little terns (*Sternula* in Fig 1). ML bootstrap support for the Bayesian tree topology was poorer than the posterior probabilities (Fig. 2). However, we stress that because the ML model of evolution was not partitioned as was the Bayesian model, the bootstrapping analysis did not account for different levels of homoplasy in each gene

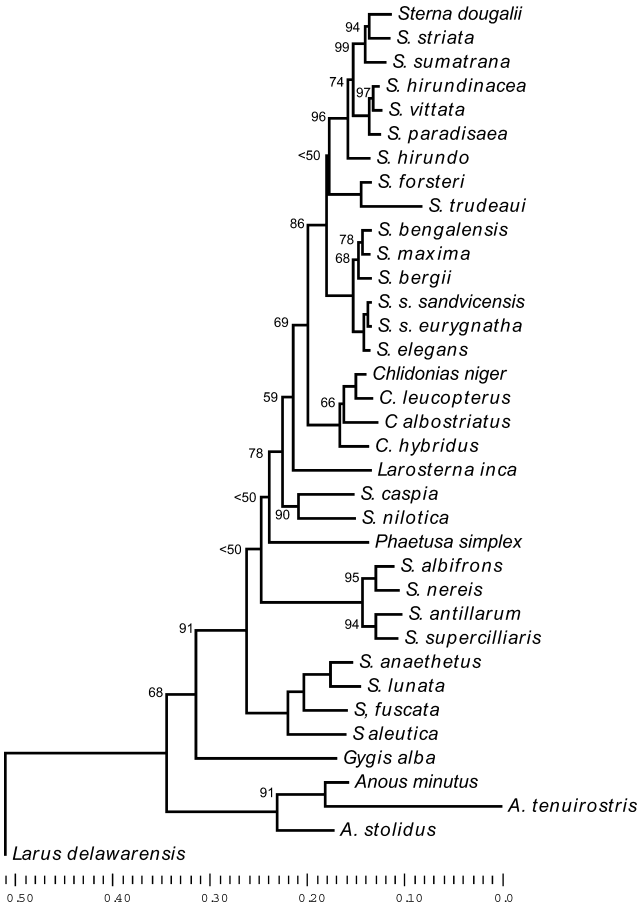

Fig. 2. Unsmoothed phylogram of the Bayesian tree topology showing ML distances (scale shown below the tree) and ML bootstrap support indices (number of supported nodes in 100 replications). Nodes that lack numbers had bootstrap scores of 100.

region, making it less suitable for our data. Therefore, we emphasize the results from the Bayesian support indices over the ML bootstrapping.

Many of the clades defined by the Bayesian tree corresponded well with informal groups described in Gochfeld and Burger (1996). These groups are the noddies (*Anous*, *Gygis*, and *Procelsterna*), the brown-winged terns (four species of *Sterna*), the small terns (four species of *Sterna*), the marsh terns (*Chlidonias*), the crested terns (*Thallasseus* in Gochfeld and Burger (1996)), and the typical terns (several *Sterna* species). *S. caspia* and *S. nilotica* form another distinctive clade but these species were each placed in monotypic genera by Gochfeld and Burger (1996). Finally, two species, *P. simplex* and *L. inca*, do not appear to belong to any of these morphologically conservative clades.

3.2. Sequence divergence

A matrix of percent sequence divergence is presented in Table 3. Sequence divergence between the terns and the gull outgroup averaged 12.8%. Among the ingroup taxa, pairwise sequence divergence ranged from 0.29% (*S. sandvicensis* vs. *S. eurygnatha*) to 16% (*Anous minutus* vs. *S. supercilliaris*; Table 3), which corresponded to divergence times of approximately 300,000 years ago and 15.7 MYBP, respectively, assuming that our divergence-time estimates are accurate. Based on the estimate of the gull–tern split at 2.4. MYBP, most of the speciation that gave rise to the current assemblage of tern species occurred within the last 10 million years. The mtDNA tree makes evident the presence of several highly divergent taxa, including *Gygis alba*, *P. simplex*, and *L. inca*, all of which split from their closest relatives more than 8 million years ago (Fig. 1) and bear several morphologically distinct features (e.g., almost entirely white plumage in *G. alba*, extremely large bill in *P. simplex*, and moustache ornament in *L. inca*).

4. Discussion

4.1. Taxonomic implications

Classification schemes for the terns range from the conservative revision by Moynihan (1959) that recognized only three genera to the recent classification by Gochfeld and Burger (1996) with 10 genera (Table 1). The widely accepted checklist by Sibley and Monroe (1990) falls between these two extremes, recognizing seven genera among 45 species (Table 1). Our phylogeny indicates that all of these classification schemes are flawed because they include paraphyletic genera. The most general shortcoming is the failure to recognize the small terns (*S. albifrons* and allies) and the brown-winged terns (*S. fuscata* and allies) as groups distinct from the typical black-capped terns, which causes taxonomy to conflict with monophyletic groups. In developing a classification scheme that corresponds with phylogenetic relationships, we see two possible naming systems. The first, and more conservative, resembles Moynihan's view of the terns, recognizing only three genera: *Anous*, *Gygis*, and *Sterna*. This revision would leave *Anous* and *Gygis* unchanged but would group all other terns under the genus *Sterna* (including *Chlidonias*). Our alternative classification scheme would modify that of Gochfeld and Burger (1996; see Table 1) to include two additional genera in recognition of the distinct clades formed by the brown-winged and small terns, bringing the number of genera among the terns up to 12 (Table 1; Fig. 1).

There are no objective methods for choosing between these scenarios, as each allows for monophyletic genera. However, we favor the latter classification scheme because it is more illustrative of the structure of the phylogeny and more informative regarding the ecology, plumage, and natural history of the species comprising each of the major clades. Thus, in addition to the genera

Table 3
Pairwise percent genetic divergences among the terns and a gull (*Larus delawarensis*) outgroup

		36	35	34	33	32	31	30	29	28	27	26	25	24	23	22	21	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2
1	*Larus delawarensis*	13.5	13.1	15.1	13.1	12.2	11.9	12.1	13.1	13.8	13.5	14.1	13.7	13.2	13.9	12.8	13.1	13.6	13.4	13.1	13.0	12.6	12.8	12.9	13.3	12.8	14.3	12.8	13.0	12.9	13.0	13.4	13.1	13.6	13.9	12.9
2	*Sterna vittata*	13.3	13.0	14.6	7.8	7.7	7.5	7.3	13.4	9.0	10.7	11.3	11.3	11.1	11.5	6.3	6.3	8.5	4.8	6.4	6.3	11.2	3.7	1.1	11.6	6.6	12.2	8.8	1.8	6.5	6.6	4.8	4.6	11.4	8.0	
3	*S. trudeaui*	14.4	13.3	14.9	9.1	9.1	8.9	8.4	13.5	9.6	10.8	11.5	11.3	11.1	11.7	8.3	7.9	9.6	8.3	8.2	4.9	11.0	7.8	7.9	11.4	8.1	12.0	9.9	7.7	8.3	8.4	8.3	7.9	11.4		
4	*S. supercilliaris*	14.9	13.6	16.0	11.0	10.7	10.6	10.6	13.9	11.3	11.3	5.2	11.7	11.6	3.8	10.8	10.9	11.0	11.4	11.0	11.0	11.3	11.1	11.1	11.7	10.6	5.1	10.6	11.1	11.2	11.2	11.7	11.4			
5	*S. sumatrana*	13.6	12.9	14.6	7.7	7.7	7.8	7.3	13.4	9.0	10.1	10.7	10.6	11.0	11.5	6.3	6.2	8.1	3.6	6.4	6.1	10.8	4.3	4.6	11.0	6.5	11.6	9.0	4.6	6.5	6.5	3.5				
6	*S. striata*	14.1	13.5	15.0	8.2	8.2	8.1	7.7	13.8	9.4	10.7	11.2	11.1	11.3	11.9	6.6	6.5	8.6	3.3	7.1	6.4	11.3	4.5	4.6	11.5	6.8	11.8	9.4	4.6	7.1	7.3					
7	*S. s. eurygnatha*	14.2	12.9	15.5	7.8	7.1	7.4	7.0	13.1	8.5	10.6	11.1	10.3	10.6	11.3	2.4	2.6	8.6	7.1	1.0	6.0	10.3	6.2	6.6	10.7	2.6	11.9	8.4	6.4	0.3						
8	*S. sandvicensis*	14.0	12.8	15.5	7.9	7.1	7.3	7.1	13.0	8.4	10.7	11.1	10.4	10.6	11.2	2.4	2.7	8.6	7.1	1.0	5.8	10.3	6.1	6.5	10.7	2.6	11.8	8.5	6.3							
9	*S. paradisaea*	13.1	13.1	14.4	7.9	7.5	7.6	7.2	12.9	8.9	10.5	10.9	11.1	10.8	11.2	6.2	6.1	8.2	4.7	6.3	5.9	10.8	4.0	1.6	11.1	6.3	11.7	8.7								
10	*S. nilotica*	13.9	12.9	15.3	8.9	8.2	7.9	8.1	12.7	8.6	10.2	10.3	10.1	10.3	10.7	8.2	8.1	7.1	9.6	8.7	8.1	10.3	8.6	8.6	10.4	8.2	11.3									
11	*S. nereis*	14.8	13.8	15.9	11.4	11.5	11.1	11.1	13.7	12.0	11.7	3.3	11.7	11.9	5.3	11.6	11.6	11.3	11.7	11.7	11.1	11.6	11.4	11.7	12.1	11.5										
12	*S. maxima*	13.8	12.7	15.3	7.9	7.0	7.4	6.9	12.7	8.1	10.5	10.7	10.1	10.3	11.0	1.2	1.7	7.9	6.7	2.4	5.8	10.0	5.7	6.5	10.3											
13	*S. lunata*	13.8	13.1	14.8	11.2	10.4	10.4	10.5	12.6	10.9	11.0	11.4	7.4	3.9	11.9	10.3	10.3	10.0	11.6	10.7	10.8	6.6	10.6	11.3												
14	*S. hirundinacea*	13.1	12.9	14.3	7.5	7.3	7.1	6.7	13.3	8.5	10.6	10.8	11.0	10.9	11.2	6.2	6.1	8.5	4.8	6.3	6.1	10.7	3.7													
15	*S. hirundo*	13.1	12.6	14.0	7.3	7.2	6.7	6.7	13.3	8.9	10.3	10.8	10.6	10.3	11.3	5.7	5.5	8.2	4.6	6.0	5.8	10.4														
16	*S, fuscata*	13.0	13.3	14.2	11.2	10.0	10.0	10.0	12.0	10.8	10.3	10.5	7.3	6.2	11.8	10.2	10.0	9.7	11.3	10.2	10.2															
17	*S. forsteri*	13.6	12.9	14.7	8.1	7.4	7.3	7.2	12.9	8.6	10.0	10.7	10.7	10.5	11.0	5.8	5.4	8.1	6.5	5.8																
18	*S. elegans*	14.2	13.0	15.5	8.0	7.3	7.3	7.1	12.8	8.1	10.5	11.1	10.5	10.7	11.1	2.3	2.5	8.7	6.9																	
19	*S. dougalii*	14.1	13.6	14.7	8.3	8.1	8.1	8.0	13.6	9.2	10.6	11.0	11.4	11.3	11.4	6.6	6.5	8.8																		
20	*S. caspia*	13.6	12.6	15.3	8.5	8.7	8.5	8.4	12.6	8.5	9.5	10.5	9.7	9.8	11.2	8.3	8.0																			
21	*S. bergii*	13.7	12.5	15.1	7.6	6.8	6.8	6.7	13.0	8.2	10.6	10.8	10.0	10.2	11.0	1.9																				
22	*S. bengalensis*	13.9	13.0	15.2	8.0	7.0	7.3	7.0	12.8	8.3	10.3	10.7	10.1	10.2	11.1																					
23	*S. antillarum*	14.2	13.3	15.3	10.8	10.6	10.5	10.4	13.7	11.3	11.0	5.0	11.5	11.9																						
24	*S. anaethetus*	13.6	12.8	14.5	10.9	10.5	10.3	10.6	12.1	10.6	10.6	10.9	7.2																							
25	*S aleutica*	13.4	13.2	15.0	10.8	10.2	10.4	10.2	12.5	10.5	10.6	11.1																								
26	*S. albifrons*	14.6	13.5	15.1	10.6	10.9	10.7	10.5	13.7	11.4	11.2																									
27	*Phaetusa simplex*	14.3	13.4	14.5	10.2	9.6	10.3	9.7	13.2	11.0																										
28	*Larosterna inca*	14.4	13.3	15.3	8.9	8.7	8.1	8.3	12.7																											
29	*Gygis alba*	13.9	13.2	14.5	12.8	12.1	11.8	12.0																												
30	*Chlidonias niger*	13.1	11.8	14.4	4.3	4.0	2.1																													
31	*C. leucopterus*	12.8	11.7	14.2	4.5	4.5																														
32	*C. hybridus*	12.9	11.9	14.4	4.9																															
33	*S. albostriatus*	13.9	12.2	15.0																																
34	*Anous tenuirostris*	8.8	11.1																																	
35	*A. stolidus*	7.8																																		
36	*A. minutus*																																			

Numbers in the left most column correspond to both species names and numbers in subsequent column headings.

used in Gochfeld and Burger (1996), we suggest resurrecting the genera *Onchycoprion*, which Wagler (1832) created in his synonymous description of *S. fuscata* (see Coues, 1897), and *Sternula*, which Gould (1843) generated in the original description of *S. nereis*, to distinguish the brown-winged clade and the small terns, respectively (Table 1, Fig. 1). Designation of several monospecific genera (i.e., *Phaetusa*, *Larosterna*, *Gelochelidon*, and *Hydroprogne*) used by Gochfeld and Burger (1996) is warranted both to maintain some degree of continuity with currently used naming systems and to designate these four species as being morphologically unique and highly divergent among the terns. We are unable to offer empirically based taxonomic recommendations regarding *Procelsterna* because no tissues were available to us, but considering its distinctive plumage, we suspect that it should retain its own generic status.

The mtDNA phylogeny resolves several disputed aspects of tern taxonomy. For instance, recent considerations of *S. dougallii* have noted that this species bears similarities to both the crested terns and the typical terns, and were unable to assign this species to either of these groups (Gochfeld and Burger, 1996, Gochfeld et al., 1998). The mtDNA phylogeny places *S. dougallii* squarely among the typical terns. Similarly, the classification of *C. albostriatus* within either *Chlidonias* or *Sterna* has been subject to considerable confusion because like the other *Chlidonias* terns it has markedly dark plumage and disperses inland for breeding. However, *C. albostriatus* does not share the distinctive marsh nesting habits of the other *Chlidonias* species. Our results confirm that this taxon belongs in *Chlidonias* and that its plumage reflects its systematic affinities more strongly than does the absence of marsh nesting. We were unable to obtain tissue samples of two-other dark-plumaged terns, *S. acuticauda* and *S. repressa*, for our phylogenetic analysis, but the plumages and behavior of these birds are similar to those of other *Chlidonias* terns. Notably, aside from its dark plumage *S. acuticauda* is an inland nesting species associated primarily with freshwater habitats. Hence, it is possible that one or both of these species belong to the genus *Chlidonias* rather than *Sterna*. However, the dark plumages of *S. acuticauda* and *S. repressa* may also reflect Gloger's rule in that these South Asian species live in warm and sunny environments. Thus, we refrain from recommending taxonomic shifts for *S. acuticauda* and *S. repressa* without further supporting evidence.

Unfortunately, a number of other disputed issues regarding tern systematics remain unresolved. For example, although the mtDNA tree confirms suspicions that *S. trudeaui* and *S. forsteri* are sister species (Gochfeld and Burger, 1996; McNicholl et al., 2001; Schnell, 1970b), it is unclear whether these species should be grouped with the crested terns (*Thalasseus* in Fig. 1) or the typical terns (*Sterna* in Fig. 1). The mtDNA phylogeny favors grouping *S. trudeaui* and *S. forsteri* as sister to the typical terns. However, this determination is based on a node with a posterior probability of 0.56, with the remainder of the posterior distribution favoring placement of the *S. trudeau–S. forsteri* clade among the crested terns or as sister to both the crested and black-capped terns. Based on their small size (compared to most of the crested terns), their temperate breeding ecology, and their lack of a distinct crest, *S. trudeaui* and *S. forsteri* are outwardly more similar to the typical terns than to the crested terns. Thus, most of the available evidence favors keeping *S. trudeaui* and *S. forsteri* as members of *Sterna*; however, further examination of the taxonomic position of these sister species is needed.

Similarly, we cannot conclusively address the controversy regarding whether to designate *S. sandvicensis sandvicensis* and *S. s. eurygnatha* as different species. The small (0.29%) genetic divergence suggests that these two taxa should be regarded as subspecies; however, they may also constitute two species that have diverged quite recently. The decision to split these taxa into two species requires further research with many vouchered samples from throughout their ranges, particularly in the Caribbean where the two subspecies commonly hybridize (see Hayes, 2004).

4.2. Divergence time uncertainties

In calibrating our tree according to the 24.4 MYBP estimate of the tern–gull split by Paton et al. (2003), we observed a low rate of sequence divergence: roughly 0.5% per million years. In their phylogenetic study of the gulls, Crochet et al. (2000) calibrated sequence divergence against the DNA–DNA hybridization data of Sibley and Ahlquist (1990) and concluded that the gull–tern split occurred 13.5 MYBP. Using this estimate as a calibration gives a more typical divergence rate of roughly 1% per million years and indicates that the divergence times in Fig 1 are overestimates. However, there is also some indication that we have underestimated divergence times in that Olson and Rasmussen (2001) describe what is probably an early Pliocene (3.7–4.8 MYBP) bone fragment from Northeastern United States, which closely resembles modern *S. maxima*. This specimen could represent an ancestral member of the crested tern group that preceded several speciation events during the last 5 million years as indicated by our divergence estimates. Alternatively, this fossil could indicate that *S. maxima* was present in North America long before our estimate of its origin at 1.0 MYBP, suggesting that our estimated divergence times are too recent.

The incorporation of the earliest *C. niger* fossils in North America (Howard, 1946) as a calibration point may be seen as problematic because C. niger could have arisen in Eurasia long before its colonization of North America. However, omission of this calibration point dates the *C. niger–C. leucotperus* split at 1.6 MYBP,

which is probably inaccurate because it follows the deposition of *C. niger* fossils in North America. Thus, inclusion of this calibration point serves to improve the accuracy of our dating scheme, although it almost certainly estimates a minimum divergence time for *C. niger* and *C. leucotperus* rather than an actual divergence time. We direct those wishing to examine the effects of different calibrations of our tree to Appendix A in the online version of this article, which contains a Supplementary data file that includes trees calibrated with and without the *C. niger* fossil data and according to the gull–tern-split estimates of both 24.4 MYBP and 13.5 MYBP.

4.3. Correspondence between phylogeny and general morphology

Examination of interspecific variation in the general appearance of terns in light of our mtDNA phylogeny reveals several interesting insights into plumage evolution in this group. In particular, the plumage on the forehead, crown, and nape of terns in breeding (alternate) plumage carries a strong phylogenetic signal. The most parsimonious reconstruction of ancestral head plumage patterns indicates that the ancestor to all terns probably had a mostly white head similar to many of the "white-headed" gull species (Crochet et al., 2000; Moynihan, 1959; Fig. 1). A black cap with a white blaze on the forehead is present in the brown-winged terns as well as the small terns, and it appears to be symplesiomorphic in these two groups (Fig. 1). The majority of the terns have a full black cap, with two notable exceptions. Both *S. sumatrana* and *S. trudeaui* stand out among their allies in that the black caps associated with their breeding plumages are much reduced—almost absent in *S. trudeaui*, which bears only an elongated black eye patch on an otherwise white head (Fig. 1). The breeding plumage of *S. trudeaui* bears a striking resemblance to the winter plumage of its sister taxon, *S. forsteri*. Similarly, the other nearly white-headed species, *S. sumatrana*, is sister to a clade formed by the roseate tern (*S. dougallii*) and the white-fronted tern (*S. striata*), and the unusual breeding plumage of *S. sumatrana* resembles that of its close relatives in two ways. First, the winter plumage of *S. dougallii* is very similar to the breeding plumage of *S. sumatrana*. Second, the black cap of *S. striata* does not extend anteriorly all the way to the base of the bill, such that it resembles an intermediate between *S. sumatrana* and *S. dougallii* (Fig. 1). Thus, although it is likely that both *S. trudeaui* and *S. sumatrana* replace their crown plumage as part of their partial pre-breeding molt, they appear to have retained the white-crown that characterizes the winter plumages of their relatives. However, as molt in these species is poorly documented, it is also possible that *S. trudeaui* and *S. sumatrana* forgo the pre-breeding molt of their head plumage, which would also give rise to their unusual breeding plumages.

Voelker (1996) suggested that the annual cycling between black caps (breeding plumage) and mottled or white head (winter plumage) in most terns is an adaptation associated with social signaling that allows non-breeding wintering birds to avoid conflicts with breeding congeners resident on the non-breeder's wintering areas. Following on this line of reasoning, the reduction of the black cap in *S. trudeaui* and *S. sumatrana* may be a characteristic retained from the winter or sub-adult plumages that was favored by evolution because of reduced aggression from black-headed congeners. Alternatively, the white heads may serve to improve recognition of conspecifics as both of these species nest in areas populated by black-capped species.

Morphological and behavioral features have been key to prior classifications of the terns, and the high degree to which such prior classifications correspond with the topology of our tree demonstrates that many of these characters, particularly plumage patterns, generally agree with phylogenetic relationships inferred from mtDNA sequences. Although this study indicates that general plumage characteristics can provide good evidence of taxon relationships, many have concluded that plumage characteristics are too labile for use in avian systematics because of the numerous potential influences on the evolution of plumage coloration, such as sexual selection, species recognition, predator avoidance, and thermoregulatory considerations (reviewed in Omland and Lanyon, 2000). In their phylogenetic study of the gulls, Crochet et al. (2000) determined that the black cap in gulls has no value in determining species relationships. Furthermore, based on the prevalence of black caps in the terns, skimmers (Rynchopinae) and skuas (Stercorarinae), they speculated that the black cap represents a common ancestral state within gulls and the other charadriiform families. However the basal position of *Anous* and *Gygis* in our phylogeny contradicts this view with respect to terns, as the parsimony-based reconstruction of plumage states for terns indicates that a white crown represented the ancestral state. However, likelihood-based reconstruction indicates a probability of 0.81 for the white-crown ancestral state. A forthcoming phylogeny of the gulls with improved resolution (Crochet, pers. comm.) may help resolve this issue and determine whether the black caps common among the charadriiform seabirds are an example of widespread convergent evolution.

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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.2004.12.010. Nexus tree file containing unscaled branch lengths for the terns phylogeny as well as trees with smoothed branch lengths illustrating alternative divergence times based on different calibration schemes.

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