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Phylogenetic relationships within the *Laridae* (Charadriiformes: *Aves*) inferred from mitochondrial markers

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Abstract

Gulls (*Aves*: *Laridae*) constitute a recent and cosmopolite family of well-studied seabirds for which a robust phylogeny is needed to perform comparative and biogeographical analyses. The present study, the first molecular phylogeny of all Larids species ($N = 53$), is based on a combined segment of mtDNA (partial cytochrome *b* and control region). We discuss our phylogenetic tree in the light of previous suggestions based on morphological, behavioral, and plumage characters. Although the phylogeny is not fully resolved, it highlights several robust species groups and confirms or identifies for the first time some sister relationships that had never been suggested before. The Dolphin Gull (*Leucophaeus scoresbii*) for instance, is identified as the sister species of the Grey Gull (*Larus modestus*) and the Ross's Gull (*Rhodostethia rosea*) forms a monophyletic group with the Little Gull (*Larus minutus*). Our results clearly demonstrate that the genus *Larus* as currently defined is not monophyletic, since current taxonomy of gulls is based on the use of convergent phenotypic characters. We propose a new systematic arrangement that better reflects their evolutionary history.

Keywords: Gulls; *Larus*; Cytochrome *b*; Control region; Bayesian inference; Phylogeny; Systematics

1. Introduction

The gulls (*Laridae*) constitute a cosmopolite family of about 50 extant species with most diversity in temperate regions of both hemispheres (Burger and Gochfeld, 1996). Gulls are generalist seabirds equally adept at flying, walking and swimming. They occupy a large variety of habitats from the high Arctic and Antarctic to sea coasts, lakes, reservoirs, rivers, cities and even interior deserts. Their closest relatives have long assumed to be terns (*Sternidae*), skuas (*Stercorariidae*,) and skimmers (*Rynchopidae*) (Peters, 1934; Chu, 1998). Recent molecular phylogenies have shown that alcids (*Alcidae*) are actually members of the same clade, and that skuas and alcids are probably sister taxa. The skuas- alcids clade is sister to a clade including larids, terns, and skimmers, but relationships between these three latter groups remain uncertain (Ericson et al., 2003; Paton et al., 2003). In this paper, we follow Burger and Gochfeld (1996) to assign a family rank to gulls although alternative taxonomic treatments have been proposed (Dickinson, 2003; Sibley and Monroe, 1990).

The relationships among gulls are still the focus of controversial debates. Most studies of evolutionary relationships among gulls were based on plumage and morphological characters (Chu, 1998; Dwight, 1925; Strauch, 1978) or behavioral characters (Moynihan, 1959). Dwight (1925) split the *Laridae* family into two large groups: (1) the *Larae* comprises large species with a white head in breeding plumage (except *Larus*

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ichythyaetus, *L. fuliginosus*, *L. hemprichii*, *L. leucophthalmus*) and (2) the *Xemae* includes small species with often a dark hood in breeding plumage. Within each group, some peculiar species were assigned to monospecific genera (*Gabianus pacificus*, *Leucophaeus scoresbii*, *Pagophila eburnea* for *Larae*; *Xema sabini*, *Rhodostethia rosea and Creagrus furcatus* for *Xemae*) or to genus with two species in the case of the Kittiwakes (*Rissa*). Similarly, Moynihan (1959) on the basis of behavior, vocalizations, and plumage also proposed to divide gulls into two large groups assigned to the subgenus *Larus* and *Xema*. The main difference with Dwight's classification concerned the placement of species with a dark hood or a dark plumage that were further divided into 'masked' and 'primitive' hooded species groups. On the basis of osteological and integumentary characters, Chu (1998) assigned gull species to 'Sternines' that comprised the 'masked' species group as well as *Rissa*, *Xema*, *Pagophila*, *Rhodostethia* and to 'Larines' corresponding to Dwight's *Larae* plus Moynihan's "primitive" hooded species.

Phylogenetic analyses of mitochondrial DNA (mtDNA) sequences (Crochet et al., 2000) supported the hypothesis that the "hooded" species belonged to two basal lineages as suggested by Chu (1998). In addition, this study revealed several species-groups that were strongly supported by mtDNA data but were mostly incongruent with previous hypothesis on gulls' relationships. These inconsistencies mostly stemmed from the labile nature of morphological characters, presumably as a result of strong selection pressures, resulting in numerous instances of convergence between unrelated species or quick divergence of closely related species (Crochet et al., 2000). Several species were missing in the data set of Crochet et al. (2000), which makes it difficult to use these results for comparative and biogeographical analyses. Furthermore, results of Crochet et al. (2000) demonstrated that the current nomenclature of the Laridae (using the genus name *Larus* for most species but a few morphologically divergent ones, see Burger and Gochfeld, 1996) is inadequate, as *Larus* as currently used is not a monophyletic clade. A complete evaluation of Larid systematics was nevertheless impossible as long as no complete phylogeny was available. Numerous discrepancies between molecular and morphological phylogenies highlighted the need for a complete molecular phylogeny of the Laridae.

In this study, we propose a molecular phylogeny based on a mtDNA composite segment (parts of cytochrome *b* and control region) including for the first time all gull species recognized by Burger and Gochfeld (1996)—which we follow for species names—and further assigning a species rank to *michahellis* and *smithsonianus* (Crochet et al., 2002; Liebers et al., 2001, 2004). Our objectives were to complete the phylogeny proposed by Crochet et al. (2000), including the 21 species that were missing, and to evaluate the impact on the phylogeny of the use of recent Bayesian reconstruction methods compared to more traditional maximum parsimony and maximum likelihood methods. From our consensus phylogeny we recommend several changes in taxonomic classification and discuss our results in the light of previous classifications based on plumage, morphology and behavior.

2. Methods

2.1. Sampling

The list of the sequenced specimens is given in Table 1. Samples were taken from both feathers and muscles collected in the field by several contributors (30 species) or from tissue collection (19 species). In addition, museum specimens (from the Paris museum [MNHN], Table 1) were used for six species. At least two specimens per taxon were analyzed for more than 50% of the species included in the phylogenetic analyses to check for possible mistakes in tissue sampling or laboratory work.

2.2. DNA extraction, PCR amplification, and sequencing

Mitochondrial DNA extraction, amplification, and sequencing were done either in Montpellier or in Paris. The protocols used in Montpellier have been previously published (Crochet et al., 2000, 2002; Crochet and Desmarais, 2000). The protocols used in Paris are given here: DNA was extracted from tissue samples using the CTAB procedure Winnepenninckx et al., 1993. Domains II and III of the control region and a part of the cytochrome *b* gene were amplified and sequenced. Cytochrome *b* was amplified using amplification primers L14967 (5′-CATCCAACATCTCTGCTTGATGAAA-3′) and H15938 (5′-ATGAAGGGATGTTCTACTGG TTG-3′). L refers to light strands and H refers to heavy strands, and the numbers refer to the position of the 3′ nucleotide of the primer on the White Leghorn chicken (*Gallus gallus*) mtDNA sequence (Desjardins and Morais, 1990). The amplification primers for the control region were L438 (5′-TCACGTGAAATCAGCAACC C-3′) (Wenink et al., 1993) and H1248 (5′-CATCTTCA GTGCCATGCTTT-3′) (Crochet and Desmarais, 2000). For museum specimens, three overlapping segments of the control region were amplified separately (see Crochet et al., 2000 for details on the procedures). The amplifications were performed in a final volume of 25 or 50 μL. Cycling conditions were 92 °C for 40 s, respectively 54 °C for the cytochrome *b* and 58 °C for the control region for 40 s, 72 °C for 60 s for 30 cycles. Primers L14967 and H15503 (5′-GATCCTGTTTCGTGGAGGAAGGGT-3′) were used as cytochrome *b* sequencing primers. L438, L699 (5′-ATAAACCCCTCCAGTGCACC-3′) and

Table 1
List of species and samples used in this study

Taxon	Number[a]	Locality, Country	Source, voucher	GenBank[b] Accession Nos. Cyt *b*	GenBank[b] Accession Nos. D-Loop
Leucophaeus scoresbii	3	Tierra del Fuego, Xii Region, Punta, Percy, north corner of Bahia Gente Grande, Chile.	P. Sweet, AMNH[c], GBN 168, 169, 170	AY964933	AY964953
Larus pacificus	2	Boston Bay, Port Lincoln, South Australia; Gladstone, Tasmania. Australia.	CSIRO[d],45402, 46714	AY964934	AY964954
Larus belcheri	2	Atacama, Pan de Azucar National Park, Chile.	P. Sweet, AMNH GBN 22, 23	AY964935	AY964955
Larus atlanticus	3	Caleta Malaspina, Golfo San Jorge, Chubut; Islote Arroyo Jabali Oeste, Buenos Aires. Argentina.	P. Yorio	AY964936	AY964956
Larus crassirostris	1	Teuri Island, Hokkaido, Japan.	C. Michiyo	AY964937	AY964957
Larus modestus	1	Guayas, Ecuador.	J. Fjeldså, ZMUC[e]	AY964938	AY964958
Larus heermanni	1	Grays Harbor, WA, USA.	D.L. Dittmann, LSUMZ[f], B-20534	AF268506	AF268541
Larus leucophthalmus	4	Tiran Island, Sinaï, Egypt.	Y. Yom-Tov, Tel Aviv University Zoo, ring number = E2758	AY964939	AY964959
Larus hemprichii	1	Hormuz straits.	MNHN[g] (no number)	AY964952	AY964960
Larus canus	1	Nolsoy, Faeroe Islands, Denmark.	J. Fjeldså, ZMUC	AF268504	268539
Larus audouinii	5	Ebro delta, Spain.	Y. Kayser, M. Genovart	AF268514	AF268542
Larus delawarensis	2	Lake Ontario, Canada.	C. Weseloh	AF268505	AF268542
Larus californicus	2	Mono Lake, CA, USA.	R. Bradbury, J. Jehl	AF268503	AF268532
Larus marinus	>10	Brittany, France.	B. Cadiou, P. Yésou	AF268496	AF268529
Larus dominicanus	2	Kerguelen Islands; New Zealand.	MNHN 1951–668; M. Renner	AF444529	AF444258
Larus glaucescens	4	Kachemak Bay, Alaska, USA; British Columbia, Canada.	D. A. Bell, MVZ[h] 172505, 172539, 172543	AY964940	AY964961
Larus occidentalis	1	Grays Harbor WA, USA.	D.L. Dittmann, LSUMZ, B-20480	AF268502	AF268538
Larus livens	2	San Pedro Martir Island, Mexico.	R. Bradbury, B. Tershy	AF268501	AY964957
Larus hyperboreus	2	Russia.	P. Ericson, SMNH[i] NRM 946577, 946581	AF268500	AF268535
Larus glaucoides	1	Nolsoy, Faeroe Islands, Denmark.	J. Fjeldså, ZMUC	AF268499	AF268533
Larus thayeri	3	Monterey Bay, California, USA.	C. Cicero, MVZ 175953, 175954, 175955	AY615704	AY615691
Larus smithsonianus	2	Iles Sainte-Maries, Québec, Canada.	G. Chapdelaine, J.-F. Rail	AF 444266	AF 444257
Larus argentatus	>15	Brittany, France.	J.-M. Pons, P. Yésou	AF268495	AF268530
Larus michahellis	>30	Camargue, France.	P.-A. Crochet	AF268493	AF268527
Larus cachinnans	1	Danube delta, Romania.	N. Sadoul	AY964941	AY964963
Larus armenicus	2	Yerevan, Armenia.	V. Ananian	AY964942	AY964964
Larus schistisagus	2	Teuri Island, Hokkaido, Japan.	C. Michiyo	AF444263	AF444262
Larus fuscus	>10	Brittany, France.	J.-M. Pons, P. Yésou	AF268494	AF268531
Larus ichthyaetus	1	Kuwait.	D.L. Dittmann, LSUMZ B-15647	AF268544	AF268511
Larus brunnicephalus	1	Koko Nor, Qinghai Hu, China.	P. Alström	AY964943	AY964965
Larus cirrocephalus	2	Guayas, Equator.	J. Fjeldså, ZMUC	AF268518	AF268550
Larus hartlaubii	1	Table Bay docks, Cape Town, South Africa.	O. Hyuser	AY964944	AY964966
Larus novaehollandiae	2	Shoalwater Bay, Rockhampton, Queensland; Point Turton area, Yorke Peninsula, South Australia. Australia.	CSIRO[d], 43805, 46600	AY964945	AY964967
Larus scopulinus	1	South Island, New Zealand.	J. Fjeldså, ZMUC	AF268516	AF268528
Larus bulleri	1	New Zealand.	M. Renner	AY964946	AY964968
Larus maculipennis	2	Calleta Tirna, Chile.	P. Sweet, AMNH GBN 82, 83	AY964947	AY964969
Larus ridibundus	12	Dombes, Forez, France.	A.-C. Prévot-Julliard	AF268515	AF268549
Larus genei	2	Camargue, France.	P.-A. Crochet	AF268513	AF268547

Table 1 (*continued*)

Taxon	Number[a]	Locality, Country	Source, voucher	GenBank[b]Accession Nos. Cyt *b*	GenBank[b] Accession Nos. D-Loop
Larus philadelphia	1	Grays Harbor WA, USA.	D.L. Dittmann, LSUMZ B-21799	AF268517	AF268548
Larus saundersi	2	Youngjongdo Inchon; Hyungsan river, South Korea.	Harkjin Kim, Woosoo Kim	AY964948	AY964970
Larus serranus	1	Chimborazo, Ecuador.	J. Fjeldså, ZMUC	AF268512	AF268546
Larus melanocephalus	2	Camargue, France.	P. Defos du Rau, Tour du Valat	AF268510	AF268543
Larus relictus	1	Hu-Han, China.	J. Fjeldså, ZMUC	AY964949	AY964971
Larus fuliginosus	2	Galapagos, Equator.	D. Anderson	AY964950	AY964972
Larus atricilla	1	Grand Connétable Island, French Guyana, France.	O. Tostain	AF268509	AF268552
Larus pipixcan	1	Punta Canero, Guayas, Equator.	J. Fjeldså, ZMUC	AF268508	AF268551
Larus minutus	1	Biarritz, France.	MNHN 1990-747	AF268524	AF268555
Pagophila eburnea	1	Groenland, Denmark.	MNHN 1911-978	AF268521	AF268556
Rhodostethia rosea	1	Sweden.	J. Fjeldså, ZMUC	AY964951	AY964973
Xema sabini	1	Royan, France.	MNHN 1970-864	AF268520	AY964966
Creagrus furcatus	1	Alaza Island, Galapagos, Ecuador.	MNHN 1970-864	AF268519	AF268553
Rissa brevirostris	1	Buldir Island, Alaska, USA.	R. Bradbury, F. Williams	AF268523	AF268558
Rissa tridactyla	1	Brittany, France.	E. Danchin	AF268522	AF268557
Sterna sandvicensis	1	Grand Connétable Island, French Guyana, France.	O. Tostain	AF268525	AF268560
Sterna maxima	1	Grand Connétable Island, French Guyana, France.	O. Tostain	AF268526	AF268559
Hamaetopus ater				AY074886	AY074886
Calidris alpina				U34686	L20137

Species are listed following the taxonomy of Burger and Gochfeld (1996).

[a] Number of sequenced haplotypes per species.

[b] GenBank accession number of each haplotype included in analyses.

[c] American Museum of Natural History.

[d] Australian National Wildlife Collection.

[e] Zoological Museum of the University of Copenhagen.

[f] Louisiana State University Museum of Natural Science.

[g] Muséum national d'Histoire naturelle.

[h] Museum of Vertebrate Zoology.

[i] Swedish Museum of Natural History.

L892 (5′-GTGTAGTGCTCAATGGACATG-3′) were used as sequencing primers for domains II and III of the control region. Negative controls were included with each PCR reaction. Segments of approximately 300 base pairs for the cytochrome *b* and 660 bp for the control region were obtained after purification (QiaQuick PCR purification kit, Qiagen) by direct sequencing performed on an automated sequencer (CEQ 2000 XL) following the supplier's procedures (Beckmann).

2.3. Phylogenetic analyses

Phylogenetic trees were reconstructed with the maximum parsimony, maximum likelihood and Bayesian methods.

2.3.1. Sequences comparisons

As the level of genetic divergence among species was moderate, cytochrome *b* and control region sequences with indels were aligned manually. We examined reading frames and tested for incongruencies between the phylogenies resulting from cytochrome *b* and the control region to exclude the possibility of our using numts in our analyses (see Crochet and Desmarais, 2000; Crochet et al., 2000 for more details).

A sequenced cytochrome *b* segment of 275–300 bp long was obtained for all species For all species, we also obtained a 650–661 bp long segment for the control region except in the case of *Larus fuliginosus* for which it was only possible to obtain a 205 bp segment from the domain III. When several haplotypes were available per species, we randomly selected one haplotype to perform phylogenetic analyses except for species represented by many specimens for which the most frequent haplotype was selected (see Crochet et al., 2000 for details).

2.3.2. Maximum parsimony analyses

We used the partition homogeneity test (Farris et al., 1994, 1995; Swofford, 2003) to examine whether there was evidence for different phylogenetic signals between

cytochrome *b* and the control region. As no significant differences were found between our mitochondrial markers, phylogenetic analyses were performed on a composite sequence of 894 bp after the removal of ambiguous gaps.

The maximum parsimony (MP) analysis was conducted on PAUP 3.1.1 (Swofford, 1993) with differential weighting of the character-state transformations as detailed in Hassanin et al. (1998a,b) for each substitution type (i.e., A-G, C-T, A-C, A-T, C-G, G-T), the amount of homoplasy was measured through the consistency index excluding uninformative characters (CIex), and the saturation was assessed graphically by plotting the pairwise number of observed differences against the corresponding pairwise number of inferred substitutions calculated by PAUP (the slope of the linear regression [S] was used to evaluate the level of saturation). The reliability of the nodes was assessed by bootstrap percentages (BP; Felsenstein, 1985). The bootstrap values were computed after 1000 replicates of the closest stepwise addition of taxa. Indels were coded as missing data.

2.3.3. Maximum likelihood analyses

The maximum likelihood (ML) analyses were performed with PHYML (Guindon and Gascuel, 2003). MODELTEST 3.06 (Posada and Crandall, 1998) was used for choosing the model of DNA substitution that best fits our data. The selected likelihood model was the general time reversible model (Yang, 1994) with among-site substitution rate heterogeneity described by a gamma distribution and a fraction of sites constrained to be invariable. The BPs were computed by generating 1000 bootstrapped data sets with the program SEQBOOT in the PHYLIP package Version 3.6b (Felsenstein, 2004).

2.3.4. Bayesian inference

Bayesian analyses were performed with Mr. Bayes 3.0b4 (Huelsenbeck and Ronquist, 2001). The chosen likelihood model was GTR+G+I. Different models were used for each of the two partitions, i.e., Cyt *b* (275 bp) and control region (619 bp). All analyses were conducted with five independent Markov chains run for 1 million Metropolis-coupled MCMC generations, with tree sampling every 100 generations, and burn-in of 1000 trees. The analyses were run twice using different random starting trees to evaluate the convergence of the likelihood values and posterior clade probabilities (Huelsenbeck et al., 2002).

3. Results

3.1. Sequence comparisons

Within *Laridae,* the control region including the domain II and the hypervariable domain III did not evolve faster than the cytochrome *b*. This unexpected pattern of variation is discussed in a previous paper (Crochet and Desmarais, 2000). Parts of the cytochrome *b* and of the control region sequenced were very similar in the fraction of sites that were variable and potentially phylogenetically informative (within ingroup cytochrome *b* variations, 28.4% and 18.5% of variable and informative sites, respectively; within ingroup control region variations, 27.6% and 18.4 % of variable and informative sites, respectively). Divergences between mitochondrial composite sequences ranged from 0.1% to 0.2% (between *L. michahellis* and *L. marinus* and between *L. schistisagus* and other northern gull species) to 10.9% between *L. philadelphia* and *L. minutus*.

3.2. Phylogenetic relationships

The tree topologies obtained from MP, ML, and Bayesian analyses were very similar except for a few weakly supported nodes (see below). The Bayesian tree is depicted in Fig. 1 with posterior probabilities (PP), MP, and ML bootstrap percentages (MP_{BP}, ML_{BP}) given for nodes well supported by at least one of the three methods (PP $\geqslant$ 0.95, or $MP_{BP} \geqslant 50\%$, or $ML_{BP} \geqslant 50\%$). The nodes that were well supported in the Bayesian approach also received a high support under MP and ML analyses (except one node) while the reverse was not verified for a few nodes (see Fig. 1 and electronic appendices B and C for ML and MP trees).

The monophyly of the Laridae was tested using *Calidris alpina* (*Scolopacidae*) and *Haematopus ater* (*Haematopodidae*) as outgroups. The exclusion from our ingroup of the two tern species (*Sternidae*) was then highly supported in bootstrap and Bayesian values whatever the method applied (Fig. 1).

Our data set yielded several well-defined species groups of comparatively recent origin, but the basal relationships among these terminal clades were often poorly resolved.

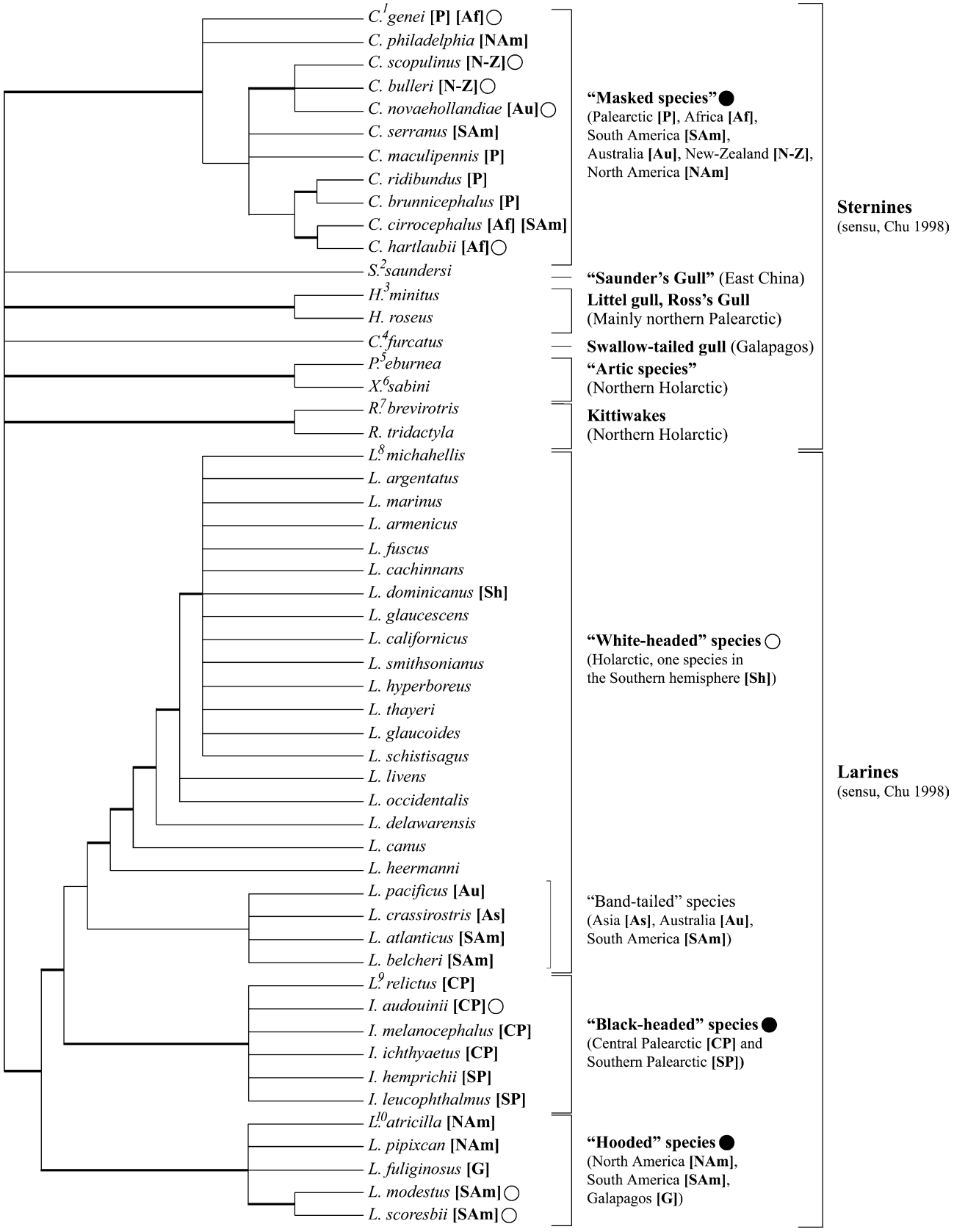
3.2.1. Composition of the species groups and relationships within species groups

Most Larid species fall into four main groups (masked species, white-headed species, black-headed species, hooded species), all of which have moderate to strong support under all methods of analysis. These groups corroborate those previously identified by Crochet et al. (2000) with a lower taxonomic sampling. Three other well supported groups are made of two species each (Figs. 1 and 2). Two of them were already grouped together in the same genus (*Rissa tridactyla* and *R. brevirostris*) but the other had not been associated in the traditional classifications of the Laridae (*Larus minutus* with *Rhodostethia rosea*; *Pagophila eburnea* with *Xema sabini*). Two species remain without close relatives: *Larus saundersi* has a poorly supported position

Fig. 1. Bayesian tree based on combined mtDNA (parts of Cyt *b* and control region) depicting phylogenetic relationships among 53 gull' species. Numbers indicate posterior probability (PP)/MP bootstrap support/ML bootstrap support. Unlabelled nodes received PP < 0.95, MP_{BP} < 50%, and ML_{BP} < 50%. For the sake of clarity, hatched branches have been divided by four. Species' names according to Burger and Gochfeld (1996).

(PP = 0.62, MP_{BP} = 30, and ML_{BP} = 20) close to the "masked" species group and *Creagrus furcatus* occupies a basal position with low to moderate support in MP, ML, and Bayesian analyses (Fig. 1).

The inclusion of *Larus pacificus*, *L. belcheri*, *L. atlanticus*, and *L. crassirostris* in the white-headed species group has a rather moderate support under MP and ML analyses and a low PP support (Figs. 1 and 2) and


C.[1] genei [P] [Af]○
C. philadelphia [NAm]
C. scopulinus [N-Z]○
C. bulleri [N-Z]○
C. novaehollandiae [Au]○
C. serranus [SAm]
C. maculipennis [P]
C. ridibundus [P]
C. brunnicephalus [P]
C. cirrocephalus [Af] [SAm]
C. hartlaubii [Af]○
S.[2] saundersi
H.[3] minitus
H. roseus
C.[4] furcatus
P.[5] eburnea
X.[6] sabini
R.[7] brevirotris
R. tridactyla
L.[8] michahellis
L. argentatus
L. marinus
L. armenicus
L. fuscus
L. cachinnans
L. dominicanus [Sh]
L. glaucescens
L. californicus
L. smithsonianus
L. hyperboreus
L. thayeri
L. glaucoides
L. schistisagus
L. livens
L. occidentalis
L. delawarensis
L. canus
L. heermanni
L. pacificus [Au]
L. crassirostris [As]
L. atlanticus [SAm]
L. belcheri [SAm]
L.[9] relictus [CP]
I. audouinii [CP]○
I. melanocephalus [CP]
I. ichthyaetus [CP]
I. hemprichii [SP]
I. leucophthalmus [SP]
L.[10] atricilla [NAm]
L. pipixcan [NAm]
L. fuliginosus [G]
L. modestus [SAm]○
L. scoresbii [SAm]○
"Masked species"●
(Palearctic [P], Africa [Af],
South America [SAm],
Australia [Au], New-Zealand [N-Z],
North America [NAm]
"Saunder's Gull" (East China)
Littel gull, Ross's Gull
(Mainly northern Palearctic)
Swallow-tailed gull (Galapagos)
"Artic species"
(Northern Holarctic)
Kittiwakes
(Northern Holarctic)
"White-headed" species○
(Holarctic, one species in
the Southern hemisphere [Sh])
"Band-tailed" species
(Asia [As], Australia [Au],
South America [SAm])
"Black-headed" species●
(Central Palearctic [CP] and
Southern Palearctic [SP])
"Hooded" species●
(North America [NAm],
South America [SAm],
Galapagos [G])
Sternines
(sensu, Chu 1998)
Larines
(sensu, Chu 1998)

thus remains tentative. The position of *L. heermannii*, *L. canus*, *L. delawarensis*, *L. occidentalis*, and *L. livens* as early offshoots before the diversification of the *L. argentatus* complex is better established. The *Larus argentatus* complex in the broad sense (14 species, Figs. 1 and 2) constituted a highly supported clade made up of species that are genetically very similar (PP = 1; overall average K2P distance = 0.06). The relationships within this complex are mostly unresolved; only the node linking *L. californicus* and *L. smithsonianus* to the northern-pacific species (*glaucoides*, *schistisagus*, *glaucescens*, *hyperboreus*, *thayeri*) received a high PP support and a moderate support in ML analyses (Fig. 1). The node gathering the two South American species *L. belcheri* and *L. atlanticus* is not well supported (PP = 0.45, BP_{ML} = 31, and BP_{MP} = 46) and the genetic distance found between them is roughly twice the genetic distance separating *L. atlanticus* from *L. crassirostris*, a far East Asian species (K2P distance *atlanticus*/*belcheri* = 0.017; K2P distance *atlanticus*/*crassirostris* = 0.009).

Within the "hooded" species group, an unexpected sister relationship between *Larus modestus* and *Leucophaeus scoresbii* received a strong support in all three methods (PP = 1, BP_{ML} = 72, and BP_{MP} = 78). The three *scoresbii* specimens that we sequenced exhibit the same cytochrome *b* haplotype and two D-loop haplotypes differing by only two mutations. All individuals clustered within the "hooded" species whatever the D-loop haplotype used, eliminating the risk of sampling or sequencing errors. *L. fuliginosus* was also included within the "hooded" species group together with *L. pipixcan* (PP = 90, BP_{ML} = 72, and BP_{MP} = 87), whereas the clade comprising *L. modestus* and *L. scoresbii* was the first taxon to split off at the base of this species group.

The relationships among the "black-headed" species group are not well established. The Mediterranean gull (*Larus melanocephalus*) has a poorly supported basal position under ML and Bayesian analyses (BP_{ML} = 43, PP = 0.91). The newly added *L. relictus* and *L. leucophthalmus* undisputedly belong to this species group, *L. relictus* occupying the basal position under MP analysis (BP_{MP} = 51).

The last group corresponds to the "masked" species and is supported by high MP, ML, and Bayesian support values (PP = 0.99, BP_{MP} = 85, and BP_{ML} = 93). Within the "masked" species group, the node linking *Larus bulleri*, *L. scopulinus*, and *L. novaehollandiae* receives a high support under the MP and ML analyses (BP_{MP} = 79, BP_{ML} = 81) and a moderate one with the Bayesian method (PP = 0.94). The sister relationship between *L. cirrocephalus* and *L. hartlaubii* is strongly supported as well as the one of *L. ridibundus* with *L. brunnicephalus* (Fig. 1).

3.2.2. Relationships among species groups

A large clade, highly supported in all analyses (BP_{MP} = 88, BP_{ML} = 82, and PP = 1), unites the three species groups ("white-headed" species, "black-headed" species, "hooded" species) and corresponds to the Larines of Chu (1998) (Fig. 2). Within this "larine" clade, the "hooded" species group is always identified as the most basal unit, with strong ML and MP support and high Bayesian PP (Figs. 1 and 2). The relationships among other group species included in the Sternines by Chu (1998) (Figs. 1 and 2) was undetermined under the three methods.

4. Discussion

4.1. Larid monophyly

Whether the gulls constitute a monophyletic assemblage or not has been the focus of several studies with contradictory results. Some studies recognized a discrete gull group (e.g., Chu, 1998; Hoffman, 1984; Sibley and Ahlquist, 1990) whereas others provided little or no support for the monophyly of gulls (Schnell, 1970a,b; Strauch, 1978). Our molecular results support the idea that gulls constitute a monophyletic clade, since our sternid representatives often considered as the Larids' sister group (Sibley and Ahlquist, 1990) were always excluded from the ingroup in all our phylogenetic analyses when using *Haematopus ater* and *Calidris alpina* as outgroups. Moreover, the Inca tern *Larosterna inca* and other atypical terns not included in our analyses should not group with gulls according to a recent tern phylogeny (Bridge et al., 2005). A definitive answer to this question would nevertheless require inclusion of skimmers which could be the sister group of gulls (Paton et al., 2003). Monophyly of gulls is nevertheless supported by Paton et al. (2003), who found that *Rissa tridactyla* and *Larus marinus* (which are among the most divergent species among gulls) are much more closely related than either of them is to their skimmer representative.

Fig. 2. Consensus phylogenetic tree from the Bayesian, maximum likelihood and maximum parsimony analyses. Thick branches indicate nodes strongly supported by the three methods (PP ⩾ 0.95/BP ⩾ 75 %). Indicated groups are clades referred to in the text. Genus names according to the taxonomic rearrangement proposed in this study: [1] *Chroicocephalus*; [2] *Saundersilarus*; [3] *Hydrocoloeus*; [4] *Creagrus*; [5] *Pagophila*; [6] *Xema*; [7] *Rissa*; [8] *Larus*; [9] *Ichthyaetus*; [10] *Leucophaeus*. ○ species without a black cap and ● species with a black cap among the four most speciose species groups. The four band-tailed species occupy a basal position within the "white-headed" species group with a moderate support under MP and ML analyses (BP_{ML} = 54, BP_{MP} = 68).

4.2. Main species groups

We are confident that the main species groups identified in this study represent true phylogenetic relationships. First, they are identified under all methods of tree construction (distance (not shown), MP, ML, Bayesian) with strong support. Second, although they are at odds with previous phylogenetic hypotheses based on external characters or osteology, they are supported by similarities in voice, behavior, or the plumages of juvenile and immature birds (see Crochet et al., 2000). Inclusion of additional species did not change the composition of the species groups compared with the results of Crochet et al. (2000). Inter-species relationships within the major species groups were often poorly defined because of the low amount of genetic variation between species and the apparently rapid diversification within species group, but the possibility of hybridization between species (Pierotti, 1987) might further obscure true species relationships (Crochet et al., 2002; Liebers et al., 2004; Liebers and Helbig, 2002).

Despite the addition of numerous species, *Pagophila* and *Xema*, two very different artic species, are still identified as sister taxa, as are both species of *Rissa*. Among the species not available in Crochet et al. (2000), *Rhodostethia rosea* is identified as the sister species of *Larus minutus*. The position of the Ross's Gull within the Laridae has long been a matter of debate (Burger and Gochfeld, 1996). Our results strongly support the grouping of the Ross's Gull (*Rhodostethia rosea*) with Little Gull (*Larus minutus*) ($BP_{MP} = 78$, $PP = 1$). A close relationship between these two species, whose adult plumage sequence and juvenile plumage exhibit marked similarities, was proposed by Dwight (1925), Moynihan (1959), and Chu (1998), who noted the presence of a reduced skull ossification found only in the *minutus–rosea* clade. Congruent results obtained from molecular, plumage and osteological data strengthen the confidence in the sister relationship between these two species. Last, the basal position of *Creagrus furcatus*, in MP, and ML, and Bayesian analyses is only moderately supported in our analyses ($PP = 0.84$, $BP_{ML} = 55$, and $BP_{MP} = 48$). However, this study clearly refutes the previous hypothesis based on similarities in bill and plumage coloration of a close relationship with *X. sabini* (Chu, 1998; Moynihan, 1959). This species deserves additional molecular studies to firmly establish its phylogenetic position within Larids.

The White-eyed Gull *Larus leucophthalmus* is unambiguously identified by our results as a member of the "black-headed" species group, but its relationships with *L. hemprichii*, with which it shares the same general distribution range and similar plumages, remain unresolved. *Larus relictus* is also a member of the "black-headed" species group, as predicted from its similarities with *L. melanocephalus* and *L. ichthyaetus* (Auezov, 1971; Kitson, 1980; Lönnberg, 1931). It is genetically well divergent from these two species (K2P distances = 4.1% and 5.2%, respectively).

One relationship that was never predicted before is the inclusion of the Dolphin Gull *Leucophaeus scoresbii* in the "hooded" species group together with *Larus pipixcan*, *atricilla*, and *modestus*. The Dolphin Gull is a very peculiar South American species, which exhibits unique behavior, plumage, and chick pattern, and it is consequently often placed in the monospecific genus *Leucophaeus* (Dwight, 1925; Burger and Gochfeld, 1996). It has also been combined with the Pacific Gull in the genus *Gabianus* on basis of its strongly hooked bill (Peters, 1934), or placed near the band-tailed species (*pacificus, belcheri, atlanticus*) by Moynihan (1959) and Devillers (1977a) on basis of plumage and breeding behavior. Interestingly, Moynihan (1959) noted, however, that some of its displays are particularly reminiscent of those of the Skuas (*Lari, Stercorariidae*) and Moynihan's "primitive hooded gulls", which comprised *Larus atricilla* and *Larus pipixcan* (two members of our "hooded" species group, Fig. 2). Yet, Moynihan placed the Dolphin Gull in its own group on basis of peculiar behavioral characters. We sequenced three Dolphin gulls, which had the same cytochrome *b* haplotype and two very similar D-loop segments. These three Dolphin Gull specimens were always included in the "hooded" species group with high bootstrap scores. We are thus confident that its placement in the "hooded" species group correctly reflects the evolutionary history of this peculiar species.

The last member of the "hooded" species group is the Lava Gull (*Larus fuliginosus*), an endemic species from the Galapagos archipelago, which clustered with the Franklin's Gull (*Larus pipixcan*) ($PP = 90$, $BP_{ML} = 72$, and $BP_{MP} = 87$). Our molecular study thus confirms that the Lava Gull is not closely related to the other dark plumage species *L. hemprichii*, *L. leucophthalmus*, and *L. heermani*, contrary to what was often suggested (Chu, 1998), strengthening the case for convergence in plumage melanism among tropical gulls possibly due to common environmental constraints including overexposure to the sun. In the case of the Lava Gull, dark plumage has also been suggested as an adaptation to the predation pressure exerts on nests by *Fregata magnificens* (Snow and Nelson, 1984) and to interspecific competition with other scavengers (Hailman, 1963). Interestingly, several other plumage characters (traces of a well-defined sooty brown hood, whitish eye-ring), together with size, structure, and some behavioral displays, also suggest a close relationship with the Laughing Gull and the Franklin's Gull, two members of our "hooded" species group (Moynihan, 1959, 1962).

The four band-tailed species inhabiting South America (*atlanticus*, *belcheri*), Australia (*pacificus*), and Asia (*crassirostris*) have sometimes been considered as a

natural group (Devillers, 1977a; Moynihan, 1959) based on some common morphological features, especially their dark subterminal tail band. In our phylogeny, these four species occupy a basal position in the "white-headed" species group but do not form a clade. Nevertheless, their relationships are not well supported, and should be considered as undetermined. Our phylogenic tree nevertheless demonstrates that, contrary to previous suggestions (Dwight, 1925; Wolters, 1975), the Pacific Gull (*Larus pacificus*) is closely related to other band-tailed species and does not deserve to be placed in a separate genus either alone or with the Dolphin Gull (Dickinson, 2003; Dwight, 1925; Morony et al., 1975). The Olrog's Gull (*Larus atlanticus*), an Argentina endemic species, had long been treated as a subspecies of the Belcher's Gull (*Larus belcheri*), which breeds in the Humboldt Current area (Burger and Gochfeld, 1996; Olrog, 1958). Further studies demonstrated that Olrog's Gull differs in size, proportions, adult and juvenile plumages, eye-ring color (Devillers, 1977b; Olrog, 1967), and parental behavior (Devillers, 1977b). We sequenced two Belcher's Gulls that had the same cytochrome *b* haplotype and diverged by one mutation on the D-loop segment and three Olrog's Gulls for which we obtained two cytochrome *b* haplotypes and three D-loop haplotypes. One of our Olrog's Gull had a very different haplotype, nearly identical to those obtained for the sympatric Kelp Gull *Larus dominicanus* (no difference in cytochrome *b*, one mutation in D-loop). This could be explained by a mistake in tissue sampling or by horizontal transfer from the Kelp Gull to the Olrog's Gull (see Crochet et al., 2002, 2003 for other examples in "white-headed" gulls). Depending on the haplotypes (but always excluding the *dominicanus* haplotype), the genetic distance between *belcheri* and *atlanticus* varied from 1.6 to 1.9%, comparable to the distance between *L. atlanticus* and *L. pacificus*, confirming the specific status assigned to the Olrog's Gull (Burger and Gochfeld, 1996).

Bayesian analysis recovered basically the same relationships among the other "white-headed" species as Crochet et al. (2000) based on less taxa. The Herring Gull species group (the "fuscus-clade" in Crochet et al. (2002)) is still identified as a strongly monophyletic group (Bayesian PP = 1, $BP_{ML} = 92$, and $BP_{MP} = 93$) of poorly differentiated species of recent origin whose relationships remain difficult to elucidate (see Crochet et al. (2002) for a detailed discussion of this group). The Slaty-backed Gull (*Larus schistisagus*), and Glaucous-winged Gull (*Larus glaucescens*), American gull (*Larus smithsonianus*), Pontic gull (*Larus cachinnans*) and Armenian Gull (*Larus armenicus*) are typical member of this "fuscus-clade", as recently demonstrated also by Liebers et al. (2004).

Most species predicted by Crochet et al. (2000) to be members of the "masked-species" group were unambiguously classified as such by our results: *Larus maculipennis*, *L. bulleri*, *L. novaehollandiae*, *L. hartlaubii*, *L. brunnicephalus*. This "masked" species group was also identified by Moynihan (1959) on the basis of behavioral characters. Most relationships within this group were moderately supported (Figs. 1 and 2). However, it is worth nothing that in their study of molecular phylogeny of masked gulls, Given et al. (2005) using the same taxonomic sample (without *L. brunnicephalus*, and *L. saundersi*) and a longer composite mtDNA segment (3600 bp) found the same topology with high bootstrap values. The basal position of *L. genei* and *L. philadelphia* with respect to the rest of the masked gulls is established by the two studies. The three Australasian species, namely the Black-billed Gull (*Larus bulleri*), the Silver Gull (*Larus novaehollandiae*) and the Red-billed Gull (*Larus scopulinus*) constitute a well supported clade. Another robust clade includes the African and American *L. cirrocephalus* and the purely African *L. hartlaubii*. *Larus hartlaubii* has always been considered as closely related with *L. scopulinus* and *L. novaehollandiae*, and they are most often treated as subspecies or members of the same superspecies (Burger and Gochfeld, 1996; Sibley and Monroe, 1990). These relationships are not supported-by neither our results nor those of Given et al. (2005), but we cannot exclude that the grouping of these taxa on our mtDNA tree according to geographical units results from horizontal transfer through hybridization. The Brown-hooded Gull (*La. maculipennis*) from South America is very similar to the Black-headed Gull in behavior (Moynihan, 1959), plumage pattern and bill shape (see Hellmayr, 1932). Despite these strong similarities, these two taxa are only distantly related.

The only species that was predicted by Crochet et al. (2000) to be a member of the "masked" species group, but which was not clearly identified as such by our genetic results, is the Saunders's Gull *Larus saundersi*. The phylogenetic position of the Saunders's Gull is not solved in our molecular analyses. Chu (1998) found that it clustered with the "masked-species" with a low support. Clearly, further molecular studies would be necessary to determine the phylogenetic position of this species, but it is evidently not as closely related to the typical "masked" species as these species are to each others.

Dwight (1925), Moynihan (1959), or Chu (1998) did not manage to uncover the composition of most of the species groups, especially the "hooded" and "black-headed" species, and failed to identify the position of many atypical species. This is probably because they gave too much weight to adult plumage characters, in particular dark hood and mantle color, as well as to features such as bill shape or size, which are all subject to rapid changes as shown by the lack of congruence between their systematic hypothesis and the molecular phylogeny. Dark hood, for example, seems to be an ancestral state in gulls that has repeatedly been lost and is not useful in reconstructing

evolutionary relationships within Laridae (Chu, 1998), while plumage coloration is under strong selection pressures that leads to convergent acquisition of common features by unrelated species (Crochet et al., 2000).

4.3. Relationships among species groups

The overall Bayesian topology produced in this study with 53 species is concordant with the ML topology published in Crochet et al. (2000) based on 33 species. Nevertheless, the branching order between the well-supported species groups still suffers from a lack of resolution. Homoplasy is not a likely explanation for this lack of resolution as Crochet et al. (2000) found no saturation for the cytochrome *b* segment and a limited amount of saturation only for the control region segment among gull species. Further studies with longer mtDNA markers together with nuclear markers could improve the resolution of basal nodes, but it seems likely that deep relationships will remain fuzzy because gull evolution seems to follow a pattern of rapid initial cladogenesis followed by recent and concomitant speciation events, obscuring phylogenetic relationships, as in other avian groups (Friesen et al., 1996; Richman and Price, 1992).

The only nodes among species group that are well supported in most analyses are those linking the "white-headed" and "black-headed" species groups and the node linking the "hooded" species to this clade. The group made of these three species groups corresponds to the "larine" gulls of Chu (1998), identified on the basis of morphological and plumage characters. The close relationships between the "white-headed" species and the "black-headed" + "hooded" species gain further support from the behavioral data of Moynihan (1959), even if this author gave more weight to the plumage characters (absence or presence of a dark head) than to its behavioral data and grouped the "black-headed" and "hooded" species with the masked species. Relationships among the other main clades corresponding to Chu's "sternines" are not resolved in our phylogenetic analyses (see Fig. 2).

4.4. Timing of gulls' evolution

Our data do not provide much new information for the dating of the main evolutionary events in gulls phylogeny, as the main gull lineages were all included in the study of Crochet et al. (2000). The timing provided by Crochet et al. (2000) and based on a simple calibration of mtDNA divergence rate for transversions only could be improved by the use of more sophisticated methods since the evolution of the control region segment differ significantly from a clock-like evolution (Crochet and Desmarais, 2000). Nevertheless, the main source of uncertainty over the timing of gull evolution is the calibration of the tree. Crochet et al. (2000) used the terns—gulls split as calibration point, using a 13.5 MYA divergence time based on the DNA–DNA hybridization data of Sibley and Ahlquist (1990). A recent phylogeny of the terns (Bridge et al., 2005) used the same point for calibration but dated it at 24.4 MYA based on Paton et al. (2003). This nearly two-fold increase of the terns—gulls divergence time would result in an estimate of the timing for the initial divergence among gulls of 4.6 to 10.8 MYA, compared with the original timing of 2.6 to 5.9 MYA proposed by Crochet et al. (2000).

It should be noted that the 13.5 MYA calibration for the gulls—tern split results in a divergence rate for gull mtDNA close to the classical 2% divergence per million years (see Crochet et al., 2000) while the calibration used by Bridge et al. (2005) results in a very slow divergence rate of 0.5 % per million years. Last, the study of Paton et al. (2003) used as a source to calibrate the gulls—tern split also provides a dating for the divergence of *Rissa tridactyla* and *Larus marinus* (at the basis of the gulls tree) at 3.3 MYA, fitting well with the dating proposed by Crochet et al. (2000). As can be seen from these conflicting results, the main factor precluding a reliable dating of gulls evolution is thus clearly the lack of reliable calibration point.

4.5. Morphological evolution

One of the most striking results of the previously published incomplete gull phylogeny was the lack of concordance between plumage characters and species relationships. This result can now be expended to other morphological characters such as bill shape and bill size, which have also been used in the past to define supposedly natural groups in gulls. The atypical bill shape of the Pacific Gull (*Larus pacificus*) and the Dolphin Gull (*Leucophaeus scoresbii*) have lead to them being often classified in genera other than *Larus* (see above). In fact, our molecular phylogeny identifies them as close relatives of species with typical bill shape, illustrating that rapid change in morphology can occur within gulls, mirroring the pattern of plumage evolution.

This situation of multiple incongruence between morphological characters and phylogeny in gulls contrast with the good agreement between plumage patterns and phylogeny in terns (Bridge et al., 2005). For example, there are three basic head patterns in terns: mainly white head, a white blaze and a partly black cap, or a full black cap. Most of the species groups in terns include only species of the same type of head pattern. The only two exceptions are two white-headed species included in the *Sterna* clade, where most species have a full black cap. There is thus a better agreement in terns than in gulls between previous systematic hypotheses and phylogeny.

4.6. Taxonomic recommendations

Our results show that the genus *Larus*, as currently recognized, is not monophyletic. To match nomenclature with phylogeny, three options are possible. The first option, as suggested by Moynihan (1959) and Chu (1998), is to place all gulls in the genus *Larus*. The second option is to assign a generic rank to each of the two main gull clades. The third is to revalidate several genus names which are no longer in use. In his cladistic study, Chu (1998) argued for placing all gull species in the genus *Larus*, despite the fact that this is the less informative taxonomic alternative. This treatment would avoid assigning a genus rank to groups poorly supported by osteological and integumentary characters, but it would remove from usage several well-established names such as *Rissa*, *Pagophila*, *Rhodosthetia*, or *Xema* (Burger and Gochfeld, 1996). Recognizing two genera (*Larus* for the larines gulls and *Xema* for the sternines gulls, see Fig. 2) translates into nomenclature a result that is only weakly supported by our molecular study. It also conceals most of the diversity of the larine and sternine gulls, and would also remove the same well-established genera. The third option would give genus rank to each of our main species groups. In this taxonomic treatment, each nomenclature change is strongly supported by our genetic results and often by behavioral and morphological data. The Larids would then be divided into 1—*Rissa* (*R. tridactyla, R. brevirostris*); 2—*Creagrus furcatus*; 3—*Hydrocoloeus* Kaup, 1829 (*H. minutus*, *H. roseus*, these two sister species differ in adult plumage but share numerous phenotypic and behavioral similarities which justify a placement in the same genus); 4—*Pagophila eburnea*; 5—*Xema sabini* (these last two species are maintained in two separate genus because of their morphological, ecological, and behavioral differences); 6—*Chroicocephalus* Eyton, 1836 for the "masked" species; 7—*Leucophaeus* Bruch, 1853 for the 'hooded' species group; 8—*Ichthyaetus* Kaup, 1829 for the 'black-headed' species group; 9—*Larus* for the "white-headed" species and 10—*Saundersilarus saundersi*. Although the "black-headed," "hooded," and "white-headed" species groups form a monophyletic clade in all analyses, the amount of divergence (genetic, morphological, and behavioral) among them is similar to the divergence among the other genera of gulls, and we prefer to treat them as distinct genera. *S. saundersi* shares some plumage characters with *Chroicocephalus* and since we cannot exclude that it is the sister group of this genus, it could be included in it. We prefer to use the monospecific genus *Saundersilarus* Dwight, 1926 in accordance with its morphological peculiarities (see Burger and Gochfeld, 1996), its amount of genetic divergence and its uncertain relationships. See the Nomenclatural appendix for additional information on the five genus names we propose to revalidate.

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Appendix A. Nomenclatural appendix

Genus *Hydrocoloeus* Kaup, 1829

Reference: Kaup, 1829. Skizzirte Entwicklungs-Geschichte und natürliches System der europäischen Thierwelt, p. 113, 196.

Type species: *Larus minutus* Pallas, 1776 by subsequent designation (Gray, 1842 A List of the Genera of Birds, ed. 2, App. p. 15).

Genus *Chroicocephalus* Eyton, 1836

Reference: Eyton, 1836. A catalogue of British birds, p. 53.

Type species: *Larus capistratus* Temminck, 1820 (= *Larus ridibundus* Linné, 1766) by subsequent designation (Gray, 1840 List Genera of Birds, p. 79).

Genus *Leucophaeus* Bruch, 1853

Reference: Bruch 1853. Monographische Uebersicht der Gattung Larus Lin. Journal für Ornithologie 1853, 1, p. 108.

Type species : *Leucopheus haematorhynchus* King, 1828 (= *Larus scoresbii* Traill, 1823).

Genus *Ichthyaetus* Kaup, 1829

Reference: Kaup, 1829. Skizzirte Entwicklungs-Geschichte und natürliches System der europäischen Thierwelt, p. 102.

Type species: by tautonymy *Larus Ichthyaetus* Pallas, 1773.

Genus *Saundersilarus* Dwight, Jr., 1926

Reference: Dwight, Jr., 1926. A New Name for *Saundersia*, Dwight. Auk, 43, p. 228.

nomen novum pro Saundersia Dwight, Jr., 1925, *nec Saundersia* Schiner, 1868 Novara-Reise p. 333 (Diptera).

Type species: *Chroicocephalus saundersi* Swinhoe, 1871.

Appendix B. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ympev.2005.05.011.

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