Enigmatic phylogeny of skuas (Aves: Stercorariidae)

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SUMMARY

Multiple sources of evidence show that the skuas (Aves: Stercorariidae) are a monophyletic group, closely related to gulls (Laridae). On morphological and behavioural evidence the Stercorariidae are divided into two widely divergent genera, *Catharacta* and *Stercorarius*, consistent with observed levels of nuclear and mitochondrial gene divergence. *Catharacta* skuas are large-bodied and with one exception breed in the Southern Hemisphere. *Stercorarius* skuas (otherwise known as jaegers) are smaller bodied and breed exclusively in the Northern Hemisphere. Evidence from both mitochondrial and nuclear genomes and from ectoparasitic lice (Insecta: Phthiraptera) shows that the Pomarine skua, *S. pomarinus*, which has been recognized as being somewhat intermediate in certain morphological and behavioural characteristics, is much more closely related to species in the genus *Catharacta*, especially to the Northern Hemisphere-breeding Great skua, *C. skua*, than it is to the other two *Stercorarius* skuas, the Arctic skua, *S. parasiticus* and the Longtailed skua, *S. longicaudus*. Three possible explanations that might account for this discordant aspect of skua phylogeny are explored. These involve (i) the segregation of ancestral polymorphism, (ii) convergent evolution of morphology and behaviour or (iii) inter-generic hybridization. The available evidence from both nuclear and mitochondrial genomes does not exclude any of these hypotheses. Thus, resolution of this enigma of skua phylogeny awaits further work.

1. INTRODUCTION

Conflicts between molecular phylogenies and classifications based on other criteria sometimes lead to new interpretations of evolutionary patterns. Molecular phylogenies based on mitochondrial DNA (mtDNA) are particularly valuable in this regard because in most metazoa the genome of this organelle is maternally inherited without recombination, and thus acts as a reliable lineage marker (Hillis & Moritz 1990; Avise 1994). In birds, many mtDNA-based phylogenies have been produced (e.g. Richman & Price 1992; Sheldon & Bledsoe 1993; Moum *et al*. 1994), and some do indicate new and unexpected affinities (e.g. Degnan & Moritz 1992). Here, we report mtDNA and other molecular analyses conducted independently by groups in several laboratories that reveal a strikingly discordant pattern of evolution highlighted by the relationships of the Pomarine skua, *Stercorarius pomarinus*, to other taxa in the Family Stercorariidae.

Classical taxonomy treats the Stercorariidae as a monophyletic family comprising two genera, *Catharacta*

* Author for correspondence (b.l.cohen@bio.gla.ac.uk). Details of specimen provenance and some details of experimental data and results, including the consensus sequence alignment, have been omitted from the text at the request of the Editor and may be obtained from the corresponding author or from http://www.ibls.gla.ac.uk/ibls/staff/bl-cohen/blc.html.

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Table 1. *Classification of the Stercorariidae and sources of data*

(The contributing laboratories are identified by abbreviations: BR, Baton Rouge; G, Glasgow; J, Jena; T, Toronto. As indicated in the text, we have adopted a classification that does not treat named forms of *Catharacta* as sub-species. To some ornithologists, *Stercorarius* skuas are known as jaegers.)

		mode of analysis (laboratory) and number of specimens analysed							
formal name *Catharacta*	common name skua	allozyme (BR)	allozyme (T)	RAPD (T)	mtDNA RFLP (BR)	mtDNA *cytb* (G)	mtDNA *12S* (G)	mtDNA *cytb* (J)	mtDNA *cytb* (T)
antarctica	Falkland	0	1	0	0	3	1	3	1
chilensis	Chilean	0	0	0	2	1	1	8	2
hamiltoni	Tristan	0	0	0	0	5	1	3	0
lonnbergi	Brown (Sub-Anatarctic)	0	0	0	0	1	2	6	2
maccormicki	South Polar	0	1	2	0	1	1	6	2
skua	Great	1	2	2	0	4	1	4	2
Stercorarius	skua or jaeger								
longicaudus	Longtailed	7	5	2	9	5	1	4	2
parasiticus	Arctic	1	4	2	4	4	1	3	1
pomarinus	Pomarine	8	5	2	10	5	1	5	1

and *Stercorarius* (table 1). Features traditionally used to characterize the Stercorariidae include the presence of both strongly hooked talons and webs on the feet and a predominantly marine, pelagic and kleptoparasitic lifestyle. They are also the exclusive hosts of the feather louse, *Haffneria grandis* (see Timmerman 1966). The genus *Stercorarius* (jaegers to North American ornithologists) contains three species of small-bodied birds which have several features that distinguish them from the larger-bodied *Catharacta* skuas, including a distinctive alternate plumage, being dark and barred when juvenile but typically white-bellied and with elongated central tail feathers when adult. (Dark phase adults occur, but are relatively rare.) *Stercorarius* skuas also share an Arctic circumpolar breeding distribution. By contrast, *Catharacta* skuas show little plumage variation with age, juveniles are not barred, and no adult has a white-bellied plumage or central tail feathers more than marginally elongated. *Catharacta* skuas breed predominantly on Antarctic/sub-Antarctic coasts, except for the Great skua, *C. skua*, which breeds only at a few North Atlantic coastal sites (Furness 1987). The currently inferred evolutionary history of skuas supposes (as with gulls) origin of a common ancestral stock in the Northern Hemisphere, followed by colonization of the Southern Hemisphere. Then, during a period of presumed geographical isolation, the Southern Hemisphere genus, *Catharacta*, and the Northern Hemisphere genus, *Stercorarius*, differentiated. Finally, at some relatively recent time, the North Atlantic was supposedly recolonized by an ancestor of the Great skua, *C. skua* (Fisher & Lockley 1954; Furness 1987).

This background provided the starting-point for four independent and roughly contemporaneous studies of skua phylogeny. None was conceived as a full study (Baverstock & Moritz 1990); instead each was limited by approach, resources, sample size or time. Nevertheless, each study discovered evidence of an unexpected, close molecular relationship between the Pomarine skua, *Stercorarius pomarinus*, and species in the genus *Catharacta*. Presented here, the overlapping and complementary data from the four studies provide a more comprehensive view of skua phylogeny. They confirm and extend previous data (Blechschmidt *et al*. 1993; Peter *et al*. 1993; Peter *et al*. 1994; Furness *et al*. 1995), but do not unambiguously exclude any of three possible classes of hypothesis that could explain the observations. Important aspects of skua phylogenetic history remain enigmatic.

2. MATERIALS AND METHODS

(*a*) *Organisms*

The majority of tissue and blood samples were collected from birds in breeding colonies or on migration. Samples were not taken from both members of a pair, nor from more than one chick in any brood, nor from parents and their offspring. In some cases, DNA was isolated from feathers obtained from museum collections. For simplicity, we use a classification which treats each named form of *Catharacta* as a separate species (Harrison 1985).

(*b*) *DNA sequencing*

Three laboratories sequenced polymerase chain reaction (PCR) products (table 1). Procedures used in Jena and Toronto have been reported (Blechschmidt *et al*. 1993; Friesen *et al*. 1996). In Glasgow, most samples were air-dried blood spots on filter paper or feathers from museum skins. Blood-spots were washed with methanol (Han *et al*. 1992) and dried. The smallest manageable fragment was then excised with a fresh, sterile scalpel blade and transferred to a PCR reaction vial. DNA was extracted from feather bases using a chelex procedure (Ellegren 1991). PCR and single-stranded template preparation followed a published method (Allard *et al*. 1991) using 'universal' primer pairs L14841, H15149 for the cytochrome *b* gene (*cytb*) and L1091, H1478 for the small subunit ribosomal RNA gene (*12S*) (Kocher *et al*. 1989). The template was sequenced on both strands using Sequenase 2.0, following the manufacturer's recommendations (USB/Amersham). The *cytb* fragment sequenced in Glasgow (maximum length 308 bp) will be referred to as

'*cytb*-short'; the fragment sequenced in Jena and Toronto (maximum length 1024 bp, reported length 1020 bp) as '*cytb*-long'. The *cytb*-long and *12S* sequences were concatenated to form a composite gene representing about 9% of the mitochondrial genome. New sequences reported here have been deposited in Genbank (Benson *et al*. 1994), accession numbers U76765–U76830.

(*c*) *Phylogenetic analysis of sequences*

An archive and alignment of sequences was assembled using GDE (Smith *et al*. 1994) and consensus sequences were constructed for each taxon using IUPAC ambiguity codes (International Union of Biochemistry 1984) to designate polymorphic sites. Phylogenetic distance, maximum likelihood and maximum parsimony analyses were performed with PHYLIP 3.5, fastDNAml and PAUP 3.1.1 (Felsenstein 1993; Swofford 1993; Olsen *et al*. 1994). Bootstrap frequencies were obtained from 100–500 replicate samples. Support indices (Bremer 1988; Källersjö *et al*. 1992) were obtained by finding the strict consensus of maximum parsimony trees progressively longer than the minimal tree and observing which nodes were collapsed by the added number of steps. Alternative tree topologies and character-state distributions were explored using MacClade 3.05 (Maddison & Maddison 1992). Various corrections for unseen multiple substitutions, differential weightings of transitions and transversions, and *a posteriori* re-weighting according to character rescaled consistency indices were without effect on inferred skua relationships.

(*d*) *Restriction Fragment Length Polymorphism* (*RFLP*)

In the RFLP analysis (table 1), mtDNA was purified from blood or tissue samples (Lansman *et al*. 1981; Dittmann & Zink 1991), and the fragments were resolved and recorded by standard methods (Dowling *et al*. 1990). For 14 restriction endonucleases the restriction fragment patterns could be interpreted in terms of base substitutions at 79 mapped restriction sites. The 470 nucleotides screened corresponded to approximately 3% of the mitochondrial genome. Restriction sites were recorded (1 present, 0 absent) for 25 birds in four skua taxa, and a gull outgroup, and the data matrix (available on request) was analysed by a variety of methods, with congruent results. Only the maximum parsimony analysis is reported.

(*e*) *Random Amplified Polymorphic DNA* (*RAPD*)

In the RAPD analysis PCR conditions were as follows: 25 µl reaction volumes containing 15 ng input DNA, 1U Taq polymerase (Boehringer-Mannheim), 1 × amplification buffer (Boehringer–Mannheim), 0.1 mM each dNTP, 0.36 µM primer, 35 cycles of 94 °C for 5 s, 39 °C for 30 s and 72 °C for 60 s in a Perkin Elmer-Cetus model 480 thermal cycler (Yu & Pauls 1992). One hundred 10-mer oligonucleotides with 60–70% G + C content from primer sets A, B, E, I and Z (Operon Technologies, Inc.) were screened on DNA from one *Catharacta* skua, one *Stercorarius parasiticus* and one *S. pomarinus*. Fourteen primers gave clear, reproducible patterns and these were used on two specimens from each of five taxa (table 1) with all individuals being amplified and analysed together for each primer. Amplification products were separated in 1% Synergel (Diversified Biotech), 0.6% agarose (Gibco BRL) gels for 2.5 h at 100V in 1 × TBE buffer, visualized with UV light after staining with ethidium bromide and photographed. In all, 70 unambiguous, polymorphic fragments were scored (0 absent, 1 present). The data matrix is available on request.

(*f*) *Allozymes*

Starch gel electrophoresis (Murphy *et al*. 1990) was used in two laboratories for allozyme analyses (table 1). In the larger analysis, phenotypes were determined at 42 presumed gene loci, of which ten were informative about skua relationships. Genetic distances were calculated from inferred allele frequencies using Gendist (Felsenstein 1993). Heterozygosity was calculated as the average of the frequencies of heterozygous individuals at each locus. A maximum parsimony exhaustive search analysis was made using the commonest allele at each locus treated as unordered characters (Mindell *et al*. 1989). In this analysis only three loci were informative because tied frequencies were treated as missing data. Tables showing specimens analysed, inferred genotypes and a distance matrix are available on request.

(*g*) *Ectoparasites*

Lice were extracted from live skuas using chloroform vapour in a delousing chamber (Furness & Palma 1992). Those attached to the plumage of study skins and frozen birds were found by careful combing. Species determinations were made by R. L. Palma independently of the molecular results, and voucher specimens were deposited in the Museum of New Zealand.

3. RESULTS

(*a*) *Evidence from the mitochondrial genome*

(i) *DNA sequences*

The *cytb*-long region was sequenced from between four and ten individuals, and the *12S* rRNA segment from between one and four individuals of all nine skua taxa (table 1). Several lines of evidence excluded the possibility that these sequences derive from nuclear pseudogenes: (i) there were no in-frame stop codons in the *cytb* sequences; (ii) most substitutions in *cytb* were third codon position transitions; (iii) the range of inferred amino acid substitutions was consistent with functional mtDNA coding sequences; (iv) the *12S* sequences were alignable with homologous bird sequences and gave no indication of aberrant secondary structure; and (v) using one specific pair of *cytb* and *12S* primers, it was possible to amplify, by PCR, both genes on a single (*ca*. 4 kb) fragment (Willcox, unpublished data), consistent with the mitochondrial gene order established for other birds (Desjardins & Morais 1990; Ramirez *et al*. 1993). Most importantly, RFLP analysis of purified skua mtDNA gave congruent phylogenetic results (see below). Comparison of sequences from the different laboratories showed very good agreement. Observed levels of within-taxon divergence in skuas were low (details available on request), and multiple individual sequences were therefore reduced to consensus sequences. Between-taxon distances, based on the consensus concatenated *cytb*-long + *12S* sequences, are given in table 2.

Table 2. *Between-taxon divergence in concatenated mitochondrial* cytb-*long and* 12S *consensus sequences*

	above diagonal: parsimony distances (absolute) below diagonal: estimated nucleotide divergence (% Jukes–Cantor distance)									
taxon	1	2	3	4	5	6	7	8	9	10
1. *Larus canus*	—	146	142	146	143	146	146	146	152	148
2. *Catharacta antarctica*	12.59	—	0	1	0	2	17	81	93	17
3. *C. chilensis*	12.16	0.14	—	1	0	2	17	79	90	17
4. *C. hamiltoni*	12.43	0.22	0.07	—	1	2	17	80	92	17
5. *C. lonnbergi*	12.31	0.14	0.00	0.70	—	1	17	79	89	17
6. *C. maccormicki*	12.50	0.29	0.14	0.15	0.07	—	17	81	91	17
7. *C. skua*	12.50	1.37	1.22	1.26	1.23	1.22	—	83	96	5
8. *Stercorarius longicaudus*	14.49	7.93	7.70	7.95	7.69	7.85	8.01	—	41	83
9. *S. parasiticus*	15.82	9.65	9.26	9.66	9.22	9.32	9.73	6.94	—	93
10. *S. pomarinus*	12.72	1.47	1.32	1.35	1.32	1.32	0.44	8.11	9.60	—

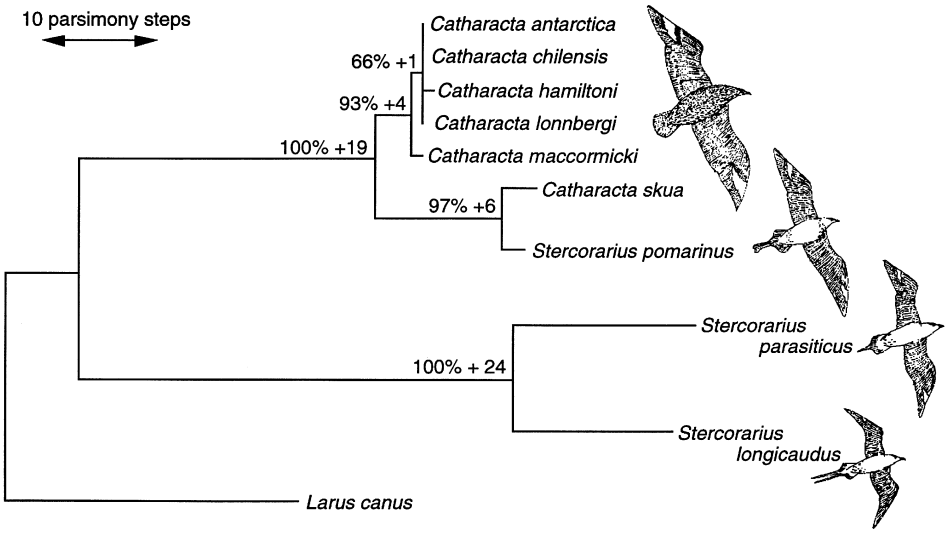

Figure 1. Maximum parsimony tree. (This one tree of 148 steps, consistency index = 0.757, retention index = 0.746, was found by branch and bound search using ACCTRAN optimization, with zero-length nodes collapsed, of 109 informative sites of concatenated skua *cytb*-long and *12S* consensus sequences. Bootstrap frequencies (%) were based on a branch and bound search of 100 bootstrap replicates of the informative sites. Bremer support indices (marked +) indicate the number of additional steps required to collapse the adjacent node. The sketches, which are approximately to scale, represent a typical *Catharacta* skua, and the Pomarine, Arctic and Longtailed skuas.)

Independent evidence from morphology indicates that gulls (larids) are the sister-group of skuas (Chu 1995) and therefore provide a suitable proximate outgroup (Nixon & Carpenter 1993; Smith 1994). Preliminary maximum parsimony and other analyses (not shown) with concatenated *cytb*-long and *12S* sequences from other candidate outgroups (composite sequences from congeneric species indicated by spp.) including alcids (*Alca torda*, *Fratercula arctica*, *Uria aalge*), a charadriid (*Calidris* spp.) and a pelecanid (*Pelecanus* spp.) indicated that alcids were also an appropriate outgroup. But since morphological evidence indicates that larids are closer to skuas than alcids, and including alcids was without effect on the skua tree, a larid outgroup was adopted. Both *cytb*-long and *12S* fragments were available for only one larid, *Larus canus*. Although this sequence lacked 99 bp at the 3′ end of the *12S* fragment, it was usable because this region contained no variable sites informative of skua relationships. Analyses combining gull *cytb*-long from several species with the available complete *12S* sequence (*L. dominicanus*, Genbank accession number X82525) confirmed that the missing data in *L. canus* were without effect on the skua tree. For some seabird taxa only *cytb*-short sequences were available (e.g. Sternidae). Parsimony analyses of these sequences confirmed that larids were the sister-group of skuas, and that this fragment alone gave the same skua tree topology. The *12S* fragment alone also gave similar results (details not shown).

Branch and bound maximum parsimony searches of the consensus sequence alignment found a single tree (figure 1, length = 148 steps, consistency index = 0.757, retention index = 0.746), and trees with identical topology also resulted from maximum likelihood and neighbour-joining distance analyses (not shown). These trees indicate that the Arctic skua, *Stercorarius parasiticus* and the Longtailed skua, *S. longicaudus*, form a strongly-supported clade which is the sister-group of all *Catharacta* skuas and differs from them markedly

(table 2). Thus, the mtDNA evidence strongly supports division of skuas into two clades. However, as noted before (Blechschmidt *et al*. 1993; Peter *et al*. 1994; Furness *et al*. 1995), the tree also shows that one member of the genus *Stercorarius*, the Pomarine skua, *S. pomarinus*, belongs in the *Catharacta* clade, where it is strongly supported as the sister-group of *C. skua*. Moreover, the *C. skua* + *S. pomarinus* clade is the sister-group of the short-branched clade of Southern Hemisphere *Catharacta* skuas. As implied by the bootstrap and Bremer support indices in figure 1, when the Pomarine skua was constrained to join the *Stercorarius* clade, tree length increased substantially (9–21 % depending on constraint position). Thus, it is highly unparsimonious to group the Pomarine skua, *S. pomarinus*, with its congeners the Longtailed skua, *S. longicaudus*, and the Arctic skua, *S. parasiticus*. Constraining the Pomarine skua to be the basal member of the *Catharacta* clade led to a 4 % increase in tree length. When individual, rather than consensus sequences were used for phylogenetic reconstruction, the Southern Hemisphere taxa, *Catharacta antarctica*, *C. chilensis*, *C. hamiltoni*, *C. lonnbergi* and *C. maccormicki* did not form discrete assemblages (not shown), indicating that mtDNAs of these taxa are not fully differentiated. Other clades were unaltered when individual sequences were used.

(ii) *RFLP analysis*

Whereas sequence analysis focuses on specific mtDNA segments that are potentially unrepresentative, RFLP analysis of purified mtDNA examines a quasi-random sample of the entire mitochondrial genome. An exhaustive maximum parsimony search of the presence–absence coded matrix (data available on request) of 79 restriction sites, 23 of which were parsimony-informative, found two minimal trees (length = 75 steps, consistency index = 0.89, retention index = 0.65). The strict consensus of these trees linked the Pomarine skua, *Stercorarius pomarinus*, and a representative *Catharacta skua*, *C. chilensis*, in a clade with 100 % bootstrap support and Bremer support index + 9, and excluded it from the clade containing the other *Stercorarius* skuas, *S. longicaudus* and *S. parasiticus* (tree not shown). Thus, the RFLP data strongly confirm the sequence result that places the Pomarine skua, *S. pomarinus*, in the *Catharacta* clade.

(*b*) *Evidence from the nuclear genome*

The evident discordance between the matrilineal mtDNA genotype of the Pomarine skua, *Stercorarius pomarinus*, and its traditional classification in the genus *Stercorarius* calls for the addition of data from the nuclear genome, which may also reveal the contributions of patrilineal ancestors, although its power to reconstruct phylogeny is lower (Moore 1995). Random amplified DNA fragments (RAPDs) and allozymes provide two sources of nuclear gene evidence that are generally capable of resolving species-level relationships (Williams *et al*. 1990; Avise 1994), and both have been employed on small samples from a selection of skua taxa.

(i) *RAPDs*

Interpretation of the RAPD data demands caution because indistinguishable agarose gel mobility is a weak indicator of fragment homology, and because fragments are potentially non-independent, non-allelic and dominant. Of the 70 fragments recorded (details available on request), 14 were present in all tested individuals of the South Polar skua, *Catharacta maccormicki* and the Great skua, *C. skua*, but were absent from all tested individuals of the Longtailed skua, *Stercorarius longicaudus* and the Arctic skua, *S. parasiticus*. Of these 14 fragments, only one was not found in both individuals of the Pomarine skua, *S. pomarinus*. Conversely, 14 other fragments were present in all tested individuals of the Longtailed and Arctic skuas, *S. longicaudus* and *S. parasiticus*, but absent from *Catharacta* spp. Of these 14, only one was also found in both individuals of the Pomarine skua. (Due to their distribution amongst RAPD primers, only a minority of the two sets of 14 informative fragments could have been alleles.) A distance matrix (available on request) based on all 70 RAPD fragments also confirms the close association between the Pomarine and *Catharacta* skuas.

(ii) *Allozymes*

Two independent allozyme analyses (table 1) gave similar results. In the more informative study, phenotypes due to 42 presumed gene loci were determined on 21 individuals from six skua taxa and one gull. Of the 42 loci, ten differed amongst skuas and 32 were either monomorphic in skuas or differed only between skuas and the gull. Inferred genotypes and a table of genetic distances calculated from allele frequencies at informative loci are available on request. As expected, all skua taxa are approximately equidistant from the gull. The Longtailed skua, *Stercorarius longicaudus*, and the Arctic skua, *S. parasiticus*, differ from one another by about 4 %, and differ from *Catharacta* spp. by 6–16 %. The *Catharacta* species differ from one another by 0.3–4 %. The Pomarine skua, *S. pomarinus*, differs from *Catharacta* spp. by 3–5 %, and differs from the other *Stercorarius* species by about 8 %. Thus, although sample sizes were small, the allozyme data agree with mtDNA and RAPDs in suggesting a closer relationship between the Pomarine skua and *Catharacta* skuas than between the Pomarine skua and other *Stercorarius* skuas. Average heterozygosity values were 0.2 in the Great skua, *C. skua*, and 0.025–0.12 in the three *Stercorarius* species. A similar level of nuclear gene diversity has been noted before in skuas (Hackett 1989). In a maximum parsimony analysis of the allozyme data, the Pomarine skua, *S. pomarinus*, was placed in the *Catharacta* clade in 77 % of bootstrap replicates.

Combined, the nuclear gene RAPD and allozyme analyses strongly confirm the evidence from mtDNA that the Pomarine skua, *S. pomarinus*, is genealogically much closer to members of the genus *Catharacta* than it is to other species of the genus *Stercorarius*. The nuclear gene data provide no critical evidence about the ancestry of the Pomarine skua, although a simplistic interpretation of the RAPD data suggests that about

Table 3. *Feather louse taxon distribution on skuas and gulls*

(For taxa that were rare or not found, the number of lice and the number of hosts examined are indicated in parentheses.)

	louse taxa			
hosts	*Haffneria grandis*	*Austromenopon* spp.	*Quadraceps normifer* subspp.	*Saemundssonia* spp.
Stercorarius				
longicaudus	present (Emerson 1972)	*fuscofasciatum*	*normifer*	*cephalus*
parasiticus	rare (1/80+)	*fuscofasciatum*	*parvopallidus*	*inexspectata*
pomarinus	abundant	*fuscofasciatum*	*stellaepolaris*	*stresemanni*
Catharacta				
skua	abundant	absent (0/53)	*stellaepolaris*	*stresemanni*
antarctica	abundant	absent (0/78)	*alpha*	*stresemanni*
chilensis	abundant	*fuscofasciatum*	*alpha*	*stresemanni*
hamiltoni	abundant	*fuscofasciatum*	absent (0/26)	*stresemanni*
lonnbergi	abundant	*fuscofasciatum*	absent (0/29)	*stresemanni*
maccormicki	abundant	*fuscofasciatum*	*alpha*	*stresemanni*
Larus				
spp.	absent (0/tens)	*transversum*	absent (0/tens)	*lari*

one-fifteenth part of its nuclear genome is divergent from the typical *Catharacta* genome and could be of *Stercorarius* origin.

(*c*) *Evidence from ectoparasites*

Feather lice are obligate plumage ectoparasites. With few exceptions their dispersal is confined within the host population and occurs mainly during breeding activities (Marshall 1981). Lice and hosts often show co-speciation and the distribution of these ectoparasites (table 3) may therefore be treated (with reservations) as analogous to a heritable character (Page 1993; Paterson *et al*. 1993). *Haffneria grandis* is a monotypic genus exclusive to the Stercorariidae, but it is rare on *Stercorarius longicaudus* and *S. parasiticus*. *Austromenopon* lice occur on many members of the Charadriiformes, Procellariiformes and some Pelecaniformes, as well as on Laridae and Stercorariidae (Pilgrim & Palma 1982). Similar forms occur on Laridae and Stercorariidae, but they are distinguished here and by some other authors (Clay 1959). Thus, the distributions of both *Haffneria* and *Austromenopon* are consistent with monophyly of the Stercorariidae. *Quadraceps normifer* is exclusive to the Stercorariidae, where it has differentiated into at least four subspecies (e.g. Emerson 1972), one of which, *Q. normifer stellaepolaris*, precisely reflects the unexpected close relationship between the Pomarine skua, *S. pomarinus*, and the Great skua, *Catharacta skua*. The three species of the louse genus *Saemundssonia* are morphologically distinct and again show an association between the Pomarine and *Catharacta* skuas (table 3).

4. DISCUSSION

Molecular and morphological evidence both show that the Stercorariidae are a monophyletic group. Both also agree that this clade is divided into two subclades or lineages, but they do not agree on the composition of the subclades. Morphology and behaviour correspond to the current genera *Catharacta* and *Stercorarius*; but the molecular evidence places the Pomarine skua, *S. pomarinus*, in the *Catharacta* rather than the *Stercorarius* lineage and, moreover, shows it to be extremely close in mtDNA genotype to the Great skua, *C. skua*. Ectoparasite evidence reinforces this conclusion quite remarkably: the Pomarine skua, *S. pomarinus*, shares its *Saemundssonia* louse with all forms of *Catharacta* but not with its *Stercorarius* congeners, yet only one of the *Catharacta* taxa ever breeds in the same hemisphere as the Pomarine skua. Moreover, one subspecies of *Quadraceps* occurs only on *S. pomarinus* and *C. skua*, the Pomarine and Great skuas. That the Pomarine skua has *Catharacta*-like properties is not novel (Schnell 1970; Andersson 1973; Furness 1987). These include body size intermediate between the smaller *Stercorarius* and larger *Catharacta* lineages, *Catharacta*-like male-to-female size ratio and an intermediate long call sonogram. Moreover, the Pomarine and Great skuas share particular forms of the long call display. But none of these features has been considered sufficiently important in taxonomy to outweigh the shared *Stercorarius*-like plumage, feeding and breeding behaviours and distributions that appeared to unite the three *Stercorarius* species, although Andersson (1973) perceptively proposed recent common ancestry of the Pomarine and Great skuas, *S. pomarinus* and *C. skua*.

Both detailed morphological comparisons (Strauch 1978; Mickevitch & Parenti 1980; Chu 1995) and mtDNA phylogeny identify gulls as the sister-group of skuas. Gulls share with *Stercorarius* skuas a barred juvenile plumage and white-breasted alternate adult plumage. Thus, outgroup rooting suggests that basal skuas were morphologically *Stercorarius*-like and therefore that the *Catharacta*-like morphological lineage is derived. Outgroup rooting is less helpful in determining the polarity of mtDNA evolution. It confirms monophyly of the Stercorariidae, but does not identify

an ancestral mtDNA lineage; instead, two highly divergent mtDNA lineages are seen to co-exist. (Molecular convergence between these lineages requires so many independent mutational substitutions that it can be ignored.) From this starting-point, we will discuss three alternative hypotheses that attempt to explain the observed diversity of morphology in the *Catharacta*-like mtDNA lineage of skuas.

(*a*) *Ancestral polymorphism of mtDNA*; *convergent origin of* Catharacta-*like morphology*

Monophyly of the Stercorariidae implies that the population of the last common ancestor of *Catharacta* and *Stercorarius* contained a variety of mtDNA genotypes which shared some ancestral traits but whose range of divergence included forms ancestral to the extant C-type and S-type lineages (*Catharacta* and *Stercorarius* types respectively). Let us suppose that by stochastic processes (Avise *et al*. 1984) the C-type mtDNA segregated into the common ancestor of the *Catharacta* lineage (including the Pomarine skua), whilst the S-type mtDNA segregated into the common ancestor of the Arctic and Longtailed skuas, *Stercorarius parasiticus* and *S. longicaudus*. On this hypothesis the Pomarine skua, *S. pomarinus*, actually represents most closely the unaltered, ancestral *Catharacta* lineage, from which arose the Southern Hemisphere *Catharacta* species and the Great skua, *C. skua*, both of which independently lost alternate plumage and gained in body size, etc., perhaps as correlated responses to adopting a more kleptoparasitic lifestyle. This independent acquisition of *Catharacta*-like morphology is obviously unparsimonious, as is any rearrangement of the mtDNA tree that would be required to avoid it. One possible implication of this ancestral polymorphism hypothesis is that the C-type mtDNA might also be present in the *Stercorarius* lineage, but has remained undiscovered. Technically, unsatisfactory sequences from two Longtailed skua museum skins suggested that this might be so, but contamination was not excluded (Cohen, unpublished data).

(*b*) *Ancestral polymorphism of mtDNA*; *convergent origin of* Stercorarius-*like morphology*

According to this hypothesis, molecular divergence of the ancestral *Stercorarius* and *Catharacta* lineages proceeds as already suggested, but with the *Catharacta* lineage uniformly losing the ancestral alternate plumage characters, etc. The Pomarine skua, *S. pomarinus*, is then interpreted as a member of the *Catharacta* lineage that converged secondarily in both morphology and behaviour towards *Stercorarius* skuas, presumably as correlated changes associated with adoption of a less kleptoparasitic lifestyle. If so, its small genetic divergence from the Great skua, *C. skua*, means that the required changes in morphology and behaviour have occurred rapidly, after the origin of the Southern Hemisphere forms. Plausibly, the most obvious change—in plumage—could have involved regulatory elements such as must exist to control the barred juvenile to white-fronted adult plumage transition. If so, this pathway, was 'on' in the common ancestor of gulls and skuas and remained 'on' in the *Stercorarius* lineage, but was set 'off' in the *Catharacta* lineage and returned to 'on' in the population that gave rise to the Pomarine skua, *S. pomarinus*. Comparable lineage-specific changes have been reported in the timing of plumage development characters in other Charadriiform birds (Chu 1994). We cannot realistically speculate about the genetic bases of the behavioural and other morphological similarities between the Pomarine skua and other *Stercorarius* skuas, *S. longicaudus* and *S. parasiticus*, but it is worth noting that neither the Pomarine nor Great skuas are notably deficient in nuclear gene diversity. This implies the absence of major bottlenecks due to selection or chance effects, and is perhaps an argument for pleiotropy and against rapid convergence. Hedges & Sibley (1994) suggested that when, as here, molecular data produce a robust phylogeny that conflicts with morphology, the morphological characters should be reassessed. Perhaps a detailed morphological study (*pace* Strauch 1978) would reveal that similarity between the Pomarine skua, *S. pomarinus*, and other *Stercorarius* species is only skin-deep.

(*c*) *Divergence followed by inter-generic hybridization*

Given the high frequency of hybridization amongst bird species (Short 1969; Grant & Grant 1992; de Querioz & Gauthier 1994), it is appealing to propose the origin of the Pomarine skua by ancestral hybridization. According to this hypothesis, the Pomarine skua would have originated from matings between presumed ancestral female Great skua(s), *C. skua*, and male *Stercorarius* skua(s), possibly *S. parasiticus*, and this has already been proposed on preliminary mtDNA sequence evidence (Blechschmidt *et al*. 1993; Peter *et al*. 1993; Peter *et al*. 1994; Furness *et al*. 1995). However, hybridization between bird genera occurs more rarely than between species and may require weak mate recognition (Grant & Grant 1992), for which there is no indication amongst present-day skuas. Nevertheless, inter-generic hybridization might well have been triggered by rarity of conspecific mate encounters during the supposed recent initiation of Northern Hemisphere breeding by the Great skua, *C. skua* (Furness 1987). Since the Pomarine skua's mitochondrial and nuclear genomes are both *Catharacta*-like, it is necessary to further propose that a stable hybrid species emerged only after a period of backcrossing, preferentially to *Catharacta*-like parents.

A hypothetical behavioural mechanism to promote inter-generic hybridization and biased backcrossing can be constructed as follows. Differences in the time of arrival at the nestsite of males and females of different Southern Hemisphere species result in hybrid matings by otherwise unmated, early-arriving female skuas (Devillers 1978; Pietz 1987; Parmelee 1988). Similar sex and species differences in time of arrival of Great and Arctic skuas also occur (Furness 1987). Thus, conditions favouring inter-generic hybridization are a realistic possibility. Differential time of arrival at the

breeding site and the size disparity of skua pairs (the female always being larger than the male) could also serve as pre-mating mechanisms of reproductive isolation to produce the necessary bias in backcross direction, favouring backcrosses to *Catharacta* or intercrosses with hybrid males. Taken at face value the RAPD data suggest at least three rounds of backcrossing. Given hybridization and biased backcrossing, reproductive isolation could have developed between the incipient Pomarine skua and its *Catharacta* parent through differences in behaviour. Whereas the Great skua, *C. skua*, is almost exclusively a pelagic predator and kleptoparasite, the Arctic skua, *S. parasiticus*, also breeds on the tundra where it feeds on small mammals, terrestrial birds and insects. The Pomarine skua, *S. pomarinus*, today (in the breeding season) has a distinctive ground-feeding habit (Andersson 1973). Therefore, the ancestral parental Great skua, *C. skua*, and the later backcross hybrid birds could have come largely to occupy allopatric territories, one coastal, the other more inland. (Due to recent range expansion, Great skuas now breed in small numbers on the coast of Novaya Zemlya and the Kola peninsula, sympatric with Pomarine skuas, but there are no data on interbreeding at these sites.) Apart from its many *ad hoc* elements, obvious difficulties of the hybridization hypothesis are that (i) Haldane's (not inalienable) rule (Wu *et al*. 1996) predicts reduced female fertility, and (ii) nuclear gene diversity in the Pomarine skua is perhaps too high to accommodate the major population bottleneck implied by the origin of this species by inter-generic hybridization.

(*d*) *Status of Southern Hemisphere* Catharacta *species and the historical biogeography of skuas*

If our trees are correctly polarized, the Southern Hemisphere *Catharacta* group is of relatively recent origin and shares a common ancestor with the ancestor of the Northern Hemisphere-breeding Great skua, *C. skua*, and the Pomarine skua *Stercorarius pomarinus*. The relative lack of genetic differentiation amongst Southern Hemisphere skuas is well explained on the basis of recent invasion of territory and a relatively large population of wide-ranging birds. It is consistent with field observation of hybrid matings (Pietz 1987), and with the existence in some localities of (presumably hybrid) individuals that cannot be securely classified by morphology alone (Devillers 1978; Pietz 1987; Parmelee 1988). Presumably the Southern Hemisphere group was founded by birds from a more northerly breeding site, whereas the Northern Hemisphere population of the Great skua, *C. skua*, came from a more southerly breeding site. Do current migration routes of *Catharacta* species point to a common breeding area in middle latitudes, perhaps at a time when both boreal regions were less hospitable? If so, when did the poleward migration of breeding sites occur, and is its timing consistent with observed levels of divergence and diversity? We have avoided addressing such questions on account of uncertainty about rates of molecular evolution in skuas and lack of data on their pre-historic (Pleistocene and later) distributions.

In conclusion, we have described discordant morphological and molecular evolution in skuas and have suggested three possible, but far-fetched explanations, none of which is convincingly excluded by available nuclear and mitochondrial genome or other evidence. It has been said that ' … when you have eliminated the impossible, whatever remains, however improbable, must be the truth!' (Conan Doyle 1903). Here, the genealogical relationships of the Pomarine skua are improbably discordant, and we have eliminated nothing. The true history of this species is likely to remain enigmatic unless future morphological work sheds new light on skua relationships, or new molecular work uncovers diagnostic nuclear markers or a greater variety of mitochondrial genotypes. Further work on the evolution of the Stercorariidae is desirable.

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REFERENCES

Allard, M. W., Ellsworth, D. L. & Honeycutt, R. L. 1991 The production of single-stranded DNA suitable for sequencing using the polymerase chain reaction. *BioTechniques* **10**, 24–26.

Andersson, M. 1973 Behaviour of the pomarine skua *Stercorarius pomarinus* Temm. with comparative remarks on Stercorariinae. *Ornis scand.* **4**, 1–16.

Avise, J. C. 1994 *Molecular markers, natural history and evolution*. London: Chapman & Hall.

Avise, J. C., Neigel, J. I. & Arnold, J. 1984 Demographic influences on mitochondrial DNA lineage survivorship in animal populations. *J. molec. Evol.* **20**, 99–105.

Baverstock, P. R. & Moritz, C. M. 1990 Sampling Design. In *Molecular systematics* (ed. D. M. Hillis & C. M. Moritz), pp. 13–24. Sunderland, MA: Sinauer Associates.

Benson, D. A., Boguski, M., Lipman, D. L. & Ostell, J. 1994 GenBank. *Nucl. Acids Res.* **22**, 3441–3444.

Blechschmidt, K., Peter, H.-U., Korte, J. D., Wink, M., Seibold, I. & Helbig, A. J. 1993 Untersuchungen zur molekularen Systematik der Raubmowen (Stercorariidae). Zoologische Jahrbücher Abteilung für Systematik **120**, 379–387.

Bremer, K. 1988 The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. *Evolution* **42**, 795–803.

Chu, P. C. 1994 Historical examination of delayed plumage maturation in the shorebirds (Aves: Charadriiformes). *Evolution* **48**, 327–350.

Chu, P. C. 1995 Phylogenetic reanalysis of Strauch's

osteological data set for the Charadriiformes. *Condor* **97**, 174–196.

Clay, T. 1959 Key to the species of *Austomenopon* Bedford (Mallophaga) parasitic on the Charadriiformes. *Proc. R. ent. Soc. Lond.* B **28**, 157–168.

Conan Doyle, A., 1903 *The sign of four*. London: Smith, Elder & Co.

De Querioz, K. & Gauthier, J. 1994 Towards a phylogenetic system of biological nomenclature. *Trends Ecol. Evol.* **9**, 27–30.

Degnan, S. M. & Moritz, C. 1992 Phylogeography of mitochondrial DNA in two species of white-eyes in Australia. *Auk* **109**, 800–811.

Desjardins, P. & Morais, R. 1990 Sequence and gene organization of the chicken mitochondrial genome. *J. molec. Biol.* **212**, 599–634.

Devillers, P. 1978 Distribution and relationships of South American skuas. *Gerfaut* **68**, 374–417.

Dittmann, D. L. & Zink, R. M. 1991 Mitochondrial DNA variation amongst phalaropes and allies. *Auk* **108**, 771–779.

Dowling, T. E., Moritz, C. & Palmer, J. 1990 Nucleic acids II. Restriction site analysis. In *Molecular systematics* (ed. D. M. Hillis & C. Moritz), pp. 250–317. Sunderland, MA: Sinauer Associates.

Ellegren, H. 1991 DNA typing of museum birds. *Nature, Lond.* **354**, 113.

Emerson, K. C. 1972 *Checklist of the Mallophaga of North America* (*North of Mexico*). *Part IV. Bird host list*. 216 pp. Dugway, Utah: Deseret Research Centre.

Felsenstein, J. 1993 PHYLIP (Phylogeny Inference Package). Seattle, Washington: Department of Genetics, University of Washington. Distributed by the author.

Fisher, J. & Lockley, R. M. 1954 Sea-birds. London: Collins.

Friesen, V. L., Baker, A. J. & Piatt, J. F. 1996 Phylogenetic relationships within the Alcidae (Charadriiformes: Aves) inferred from total molecular evidence. *Molec. Biol. Evol.* **13**, 359–367.

Furness, R. W. 1987 *The Skuas*. Calton, Staffs.: Poyser.

Furness, R. W., Cohen, B. L., Peter, H.-U. *et al.* 1995 Mitochondrial DNA and ectoparasites indicate evolution through intergeneric hybridization within the family Stercorariidae (Aves). In *Threats to seabirds*, p. 22. Sandy: Seabird Group.

Furness, R. W. & Palma, R. L. 1992 Phthiraptera of petrels and skuas from Gough Island, South Atlantic Ocean. *Seabird* **14**, 33–42.

Grant, P. R. & Grant, R. 1992 Hybridization of bird species. *Science, Wash.* **256**, 193–197.

Hackett, S. J. 1989 Effects of varied electrophoretic conditions on detection of evolutionary patterns in the Laridae. *Condor* **91**, 73–90.

Han, C. Y., Lin, B. K. & Lin, H. J. 1992 Methanol for preparing hair bulbs for PCR. *Nucl. Acids Res.* **20**, 6419–6420.

Harrison, P. 1985 *Seabirds, an identification guide*. London: Christopher Helm.

Hedges, S. B. & Sibley, C. G. 1994 Molecules vs morphology in avian evolution: The case of the 'pelicaniform' birds. *Proc. natn. Acad. Sci. USA* **91**, 9861–9865.

Hillis, D. M. & Moritz, D. 1990 *Molecular systematics*. Sunderland, MA: Sinauer.

International Union of Biochemistry 1984 *Enzyme nomenclature*. Orlando, Fl.: Academic Press.

Källersjö, M., Farris, J. S., Kluge, A. G. & Bult, C. 1992 Skewness and permutation. *Cladistics* **8**, 275–287.

Kocher, T. D., Thomas, W. K., Meyer, A., Edwards, S. V., Pääbo, S., Villablanca, F. X. & Wilson, A. C. 1989 Dynamics of mitochondrial DNA evolution in animals: amplification and sequencing with conserved primers. *Proc. natn. Acad. Sci. USA* **89**, 6196–6200.

Lansman, R. A., Shade, R. O., Shapira, J. F. & Avise, J. C. 1981 The use of restriction endonucleases to measure mitochondrial DNA sequence relatedness in natural populations. III. Techniques and potential applications. *J. molec. Evol.* **17**, 214–226.

Maddison, W. P. & Maddison, D. R. 1992 MacClade. Sunderland, MA: Sinauer Associates.

Marshall, A. G. 1981 *The ecology of ectoparasitic insects*. London: Academic Press.

Mickevitch, M. F. & Parenti, L. R. 1980 [Review of] The phylogeny of the Charadriiformes (Aves): a new estimate using the method of character compatibility analysis. *Syst. Zool.* **29**, 108–113.

Mindell, D. P., Sites, J. W. & Graur, D. 1989 Speciation evolution: a phylogenetic test with allozymes in *Sceloporus* (*Reptilia*). *Cladistics* **5**, 49–61.

Moore, W. S. 1995 Inferring phylogenies from mtDNA variation: mitochondrial-gene trees versus nuclear-gene trees. *Evolution* **49**, 718–126.

Moum, T., Johansen, S., Erikstad, K. E. & Piatt, J. F. 1994 Phylogeny and evolution of the auks (subfamily Alcinae) based on mitochondrial DNA sequences. *Proc. natn. Acad. Sci. USA* **91**, 7912–7916.

Murphy, R. W., Sites, J. W. J., Buth, D. G. & Haufler, C. H. 1990 Proteins I: Isozyme electrophoresis. In *Molecular systematics* (ed. D. M. Hillis & C. Moritz), pp. 45–126. Sunderland, MA: Sinauer Associates.

Nixon, K. C. & Carpenter, J. M. 1993 On outgroups. *Cladistics* **9**, 413–426.

Olsen, G. J., Matsuda, H., Hagstrom, R. & Overbeek, R. 1994 fastDNAml: a tool for construction of phylogenetic trees of DNA sequences using maximum likelihood. *Cabios* **10**, 41–48.

Page, R. D. M. 1993 Parasites, phylogeny and cospeciation. *Int. J. Parasitol.* **23**, 499–506.

Parmelee, D. F. 1988 The hybrid skua: a Southern Ocean enigma. *Wilson Bull.* **100**, 345–346.

Paterson, A. M., Gray, R. D. & Wallis, G. P. 1993 Parasites, petrels and penguins: does louse presence reflect seabird phylogeny? *Int. J. Parasitol.* **23**, 515–526.

Peter, H.-U., Blechschmidt, K., de Korte, J., Wink, M., Helbig, A. J. & Seibold, I. 1993 Neues über antarktische und arktische Raubmöwen. In *Deutsche Gesellschaft für Polarforschung* 17. Internationale Tagung in Obergurgl. Tagungsband, pp. 67–68.

Peter, H.-U., Blechschmidt, K., Furness, R. W., Cohen, B. L., Wilson, R. H. & de Korte, J. 1994 Molecular systematics of skuas. *J. Ornithol.* **135**, 320.

Pietz, P. J. 1987 Feeding and nesting ecology of sympatric south polar and brown skuas. *Auk* **104**, 617–627.

Pilgrim, R. L. C. & Palma, R. 1982 A list of the chewing lice (Insecta: Mallophaga) from birds in New Zealand. *Notornis* **29**, 1–32.

Ramirez, V., Savoie, P. & Morais, R. 1993 Molecular characterization and evolution of a duck mitochondrial genome. *J. molec. Evol.* **37**, 325–331.

Richman, A. D. & Price, T. 1992 Evolution of ecological differences in the Old World leaf warblers. *Nature, Lond.* **355**, 817–821.

Schnell, G. G. 1970 A phenetic study of the suborder Lari (Aves), parts I–II. *Syst. Zool.* **19**, 35–57, 264–302.

Sheldon, F. H. & Bledsoe, A. H. 1993 Avian molecular systematics, 1970s to 1990s. *A. Rev. Ecol. Syst.* **24**, 243–278.

Short, L. L. 1969 Taxonomic aspects of avian hybridization. *Auk* **86**, 84–105.

Smith, A. B. 1994 Rooting molecular trees: problems and strategies. *Biol. J. Linn. Soc.* **51**, 279–292.

Smith, S. W., Overbeek, R., Woese, C. R., Gilbert, W. & Gillevet, P. M. 1994 The Genetic Data Environment, an expandable GUI for multiple sequence analysis. *Cabios* **10**, 671–675.

Strauch, J. G. J. 1978 The phylogeny of the Charadriiformes (Aves): a new estimate using the method of character compatibility analysis. *Trans. Zool. Soc. Lond.* **34**, 263–345.

Swofford, D. L. 1993 PAUP: phylogenetic analysis using parsimony, version 3.1. Computer program distributed by Dr D. Swofford, Smithsonian Institution, Washington, D.C., USA.

Timmerman, G. 1966 *Haffneria* nov. gen., ein neues Mallophagengenus von Raubmöwen. *Mitt. Hamburg. Zool. Mus. Inst.* **63**, 85–89.

Williams, J. G. K., Kubelik, A. R., Livak, K. J., Rafalski, J. A. & Tingey, S. V. 1990 DNA polymorphisms amplified by arbitrary primers are useful as genetic markers. *Nucl. Acids Res.* **18**, 6531–6535.

Wu, C.-I., Johnson, N. A. & Palopoli, M. F. 1996 Haldane's rule and its legacy: why are there so many sterile males? *Trends Ecol. Evol.* **11**, 281–284.

Yu, K. & Pauls, K. P. 1992 Optimization of the PCR program for RAPD analysis. *Nucl. Acids Res.* **20**, 2606.

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