
Hybridization and skua phylogeny

Malte Andersson

Department of Zoology, Göteborg University, Box 463, SE-405 30 Göteborg, Sweden (malte.andersson@zool.gu.se)

The close similarity in mitochondrial DNA (mtDNA) between Pomarine and (North Atlantic) Great skuas, *Stercorarius pomarinus* and *Stercorarius skua*, has several possible explanations. Two of the main alternatives are stochastic lineage sorting of mtDNA and introgressive hybridization between *S. pomarinus* and *S. skua*. Here, a new probabilistic approach to testing these alternatives using different phylogenies based on external morphology, mtDNA and ectoparasites leads to rejection of the lineage sorting and corroboration of the hybridization hypothesis. If great skuas are a monophyletic group, as indicated by the present cladistic analysis based on morphology and by other evidence, the available molecular genetic data are as expected if mtDNA has been transferred from *S. pomarinus* to *S. skua* by introgressive hybridization. Further evidence from several unlinked regions of nuclear DNA is crucial for critical testing of the alternative hypotheses on skua evolution.

Keywords: phylogeny; hybridization; lineage sorting; mtDNA; ectoparasites; Stercorariidae

1. INTRODUCTION

The phylogeny of skuas Stercorariidae is puzzling in several respects. In particular, the Pomarine skua *Stercorarius pomarinus* externally resembles two smaller species, the Arctic skua *Stercorarius parasiticus* and the Long-tailed skua *Stercorarius longicaudus*. In display behaviour and molecular genetics, however, the Pomarine skua is more similar to the larger and differently coloured great skuas, often placed in a genus of their own, *Catharacta*. In particular, it is surprisingly similar to the (North Atlantic) Great skua *Stercorarius skua* in mitochondrial DNA (mtDNA) (Blechsmidt *et al.* 1993; Cohen *et al.* 1997). (The nine skua taxa discussed here are treated as one genus, *Stercorarius*; see Andersson 1999a. The Latin names used are dictated by convenience; I do not take a stance on the question of species or subspecies status for some of the great skua forms; see Furness 1987.) Note that the term 'great skuas' below refers collectively to these taxa, whereas 'Great skua' refers to the North Atlantic form, *S. skua*.

These conspicuous discrepancies and their interesting possible causes are currently debated. Apparently contradictory evidence suggests that unusual events may have occurred in the evolution of skuas (e.g. Andersson 1973, 1999a; Furness 1987; Blechsmidt *et al.* 1993; Cohen *et al.* 1997). As Braun & Brumfield (1998) remarked, debate is healthy because it stimulates additional research and new analyses that can generate fresh insights. In this paper I reanalyse and test the evidence, applying a novel approach (Andersson 1999b).

Cohen *et al.* (1997) derived a phylogeny based on mtDNA data (figure 1a), in which the North Atlantic Great skua *S. skua* is the sister of the Pomarine skua but not of the Southern Hemisphere great skuas. *Stercorarius pomarinus* and *S. skua* are remarkably similar in mtDNA, their estimated nucleotide divergence being only approximately one-third of that between *S. skua* and the other

great skuas. This result is counterintuitive in relation to external morphology, as all great skua forms are much more similar to each other than to the Pomarine skua (e.g. Furness 1987). Cohen *et al.* (1997) presented three possible explanations but regarded them all as far-fetched, as they require a remarkable convergence in the evolution of the great or the Pomarine skua morphology or an unlikely rapid origin of *S. pomarinus* through hybridization between a Great skua *S. skua* and one of the two smallest skuas, *S. parasiticus* or *S. longicaudus*.

Braun & Brumfield (1998) and Andersson (1999a) pointed out that the nuclear DNA data presented by Cohen *et al.* (1997) suggested that all great skuas form a monophyletic group, with the Pomarine skua as their sister species (figure 1b). Using maximum-likelihood analyses Braun & Brumfield (1998) also showed that an mtDNA tree where all great skuas are constrained to be monophyletic is not significantly worse than the most probable mtDNA tree. And, even if the most probable mtDNA tree is the correct one, it may still differ from the true species phylogeny due to stochastic lineage sorting (e.g. Avise *et al.* 1984). Different lineages of ancestrally polymorphic mtDNA may by chance have segregated in a fashion that falsely suggests that *S. pomarinus* and *S. skua* are sister taxa (Cohen *et al.* 1997; Braun & Brumfield 1998; Andersson 1999a).

Considering the total genetic evidence (including the nuclear data of Cohen *et al.* (1997)) and apparent morphological synapomorphies, Braun & Brumfield (1998) concluded that the great skuas are probably monophyletic. This is also the implicit (e.g. Andersson 1973) or explicit (Furness 1987; Andersson 1999a) view of earlier workers, but no formal cladistic analysis of skuas based on external morphology has been undertaken. This has therefore been done here.

The close similarity in mtDNA between the Pomarine and the North Atlantic Great skua has given rise to several other explanations than stochastic lineage sorting

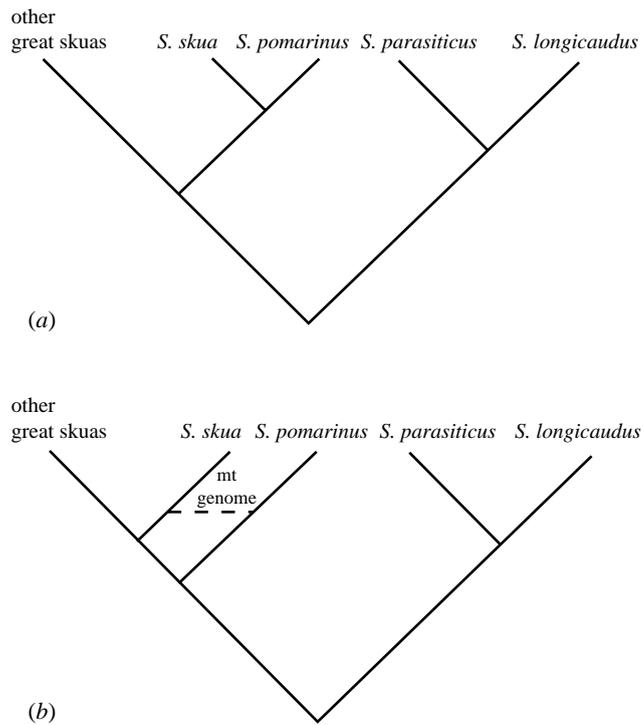


Figure 1. (a) The most parsimonious phylogenetic tree of skuas based on mtDNA sequences. The tree has been simplified from Cohen *et al.* (1997) by combining five forms of great skuas (*S. antarctica*, *S. chilensis*, *S. hamiltoni*, *S. lonnbergi* and *S. maccormicki*) in 'other great skuas'. (b) Alternative phylogeny suggested by Braun & Brumfield (1998) and Andersson (1999a) in which all great skuas, as well as the (North Atlantic) Great skua *S. skua*, form a monophyletic group. *Stercorarius skua* is here shown separate from the other great skuas only to illustrate the hypothesis of hybridization and transfer of mtDNA between *S. pomarinus* and *S. skua* (Andersson 1999a).

(e.g. Cohen *et al.* 1997; Braun & Brumfield 1998), one of which is hybridization between *S. pomarinus* and *S. skua* (Andersson 1999a). Introgressive hybridization has often been regarded as relatively unimportant in animal evolution (e.g. Mayr 1963), but increasing evidence now indicates that it can profoundly influence animal evolution (e.g. Arnold 1997; Dowling & Secor 1997; Grant & Grant 1997). It appears that the mitochondrial genome of one species sometimes has introgressed into another species which retains its own nuclear genome (reviewed by Arnold 1997; Dowling & Secor 1997). Skuas provide an interesting possible example (Andersson 1999a).

Braun & Brumfield (1998) emphasized that the cladogram suggesting that Pomarine and North Atlantic Great skuas are sister species rests solely on mtDNA sequence data (Cohen *et al.* 1997, fig. 1). In addition, Cohen *et al.* (1997) showed that the two taxa are also remarkably similar as regards ectoparasites. Both mtDNA and ectoparasites are likely to be transmitted in a hybridization event and leave clear phylogenetic long-term traces of it, as they are usually not subject to recombination or other similarly rapid change. These traits are therefore particularly useful for testing between random lineage sorting and hybridization (Andersson 1999b).

Here I use phylogenetic analysis of the parasite data of Cohen *et al.* (1997) to distinguish between hybridiza-

tion and lineage sorting as alternative explanations for the similarity in mtDNA and ectoparasites between *S. pomarinus* and *S. skua*. The approach is more generally applicable to testing between these alternative explanations (Andersson 1999b).

2. METHODS, RESULTS AND DISCUSSION

(a) *Skua phylogeny based on external morphology*

Cladistic analysis (using PAUP 3.1; Swofford 1993) of body size and seven plumage characters in nine skua taxa, using the herring gull *Larus argentatus argentatus* as an outgroup (table 1), resulted in two shortest trees (length 12 steps, consistency index (CI) = 0.917, homoplasy index (HI) = 0.083, retention index (RI) = 0.941 and rescaled CI = 0.863). In one of the trees the South Polar skua *Stercorarius maccormicki* is the sister of the other great skuas, while in the other it is merged with this unresolved clade. In the strict consensus tree (figure 2) the Long-tailed and Arctic skuas are sister taxa, the Pomarine skua is the sister of the Long-tailed–Arctic skua clade and the six great skuas form a polytymous group of sister taxa.

To make sure that these results are not peculiar to the choice of outgroup taxon the analysis was repeated using a much smaller gull, *Larus canus* and a tern, *Anous stolidus* (see Schnell 1970; Chu 1998) as alternative outgroup taxa (data from Cramp & Simmons (1983)). This did not change the topology of the shortest trees in any way. Simultaneous inclusion of all three outgroup taxa gave the same strict consensus groupings of skuas as before, so the results are robust in relation to choice of larid outgroup. The cladistic analysis therefore corroborates the traditional view that the great skuas are a monophyletic group.

The evidence is compatible with the hypothesis that *S. maccormicki* was first among extant skuas to branch from their common ancestor (Furness 1987). In the analyses based on allozymes, Cohen *et al.* (1997; website and personal communication) also found that *S. maccormicki* differs more from *S. skua* and *S. antarctica* than they differ from each other.

The present cladogram (figure 2) agrees with the traditional view (based on morphology) that the Pomarine skua is most closely related to the two smaller species (Furness 1987). There is now, however, other strong evidence that this is not their true evolutionary relationship. Display behaviour, mtDNA, nuclear DNA and several other traits show that the Pomarine skua is more closely related to the great skuas (Andersson 1973, 1999a; Blechschmidt *et al.* 1993; Cohen *et al.* 1997; Braun & Brumfield 1998). In the following I therefore assume that, as in figure 1b, *S. pomarinus* is the sister of the great skuas. Further tests would be welcome, in particular tests based on several independent sequences of nuclear DNA.

(b) *Skua phylogeny based on ectoparasites*

The distribution of feather lice (Phthiraptera) among skuas has implications for their relationships, in particular those between *S. pomarinus* and *S. skua*, which have identical feather louse faunas (Cohen *et al.* 1997). Feather lice are usually host-specific and obligate ectoparasites which disperse between host individuals mainly during

Table 1. *Body size and plumage character classes used for cladistic analysis of nine taxa of skuas Stercorarius and an outgroup species L. a. argentatus*

(Unless stated otherwise, the data are from Furness (1987). Body masses are male–female means: 1, 0.25–0.50; 2, 0.51–1.00; and 3, 1.01–2.0 kg. For *L. a. argentatus* the body mass is that of the nominate form (Cramp & Simmons 1983). The relative tail lengths are the male–female mean lengths of the two central tail feathers relative to the adjacent feathers for *S. longicaudus*, *S. parasiticus* and *S. pomarinus*: 1, <2% difference; 2, 2–20% longer; and 3, >50% longer. The relative tail lengths for *S. skua*, *S. lonnbergi* and *L. a. argentatus* are the means of the longest central tail feather relative to adjacent feathers. (Results from measurements of skins in the Gothenburg Museum of Natural History (mean \pm s.e. (*n*)): *S. skua* 107.1 \pm 4.8 (6), *S. lonnbergi* 109.9 \pm 8.3 (3), and *L. argentatus* 100.4 \pm 1.6 (5).) Tail shape is the shape of the distal end of the two central tail feathers: 1, blunt and 2, pointed. Plumage polymorphism (dark and pale morphs): 0, absent and 1, present. The seasonal plumage is the seasonal shift between breeding and winter plumage: 0, absent and 1, present. Dorsal coloration: 1, grey; 2, grey–brown; and 3, brown. Degree of evenness of dorsal coloration: 1, even and 2, with flecking.)

taxon	body mass (kg)	relative tail length	tail shape	plumage polymorphism	seasonal plumage	dorsal coloration	colour evenness	barred juvenile plumage
<i>longicaudus</i>	1 (0.29)	3 (255)	2	1	1	2	1	1
<i>parasiticus</i>	1 (0.45)	3 (170)	2	1	1	2	1	1
<i>pomarinus</i>	2 (0.69)	3 (175)	1	1	1	2	1	1
<i>skua</i>	3 (1.41)	2 (107)	1	0	0	3	2	0
<i>antarctica</i>	3 (1.5)	2	1	0	0	3	2	0
<i>chilensis</i>	3 (1.35)	2	1	0	0	3	2	0
<i>maccormicki</i>	3 (1.32)	2	1	1	0	3	2	0
<i>hamiltoni</i>	3 (1.45)	2	1	0	0	3	2	0
<i>lonnbergi</i>	3 (1.64)	2 (110)	1	0	0	3	2	0
<i>L. argentatus</i>	3 (1.10)	1 (100)	1	0	1	1	1	0

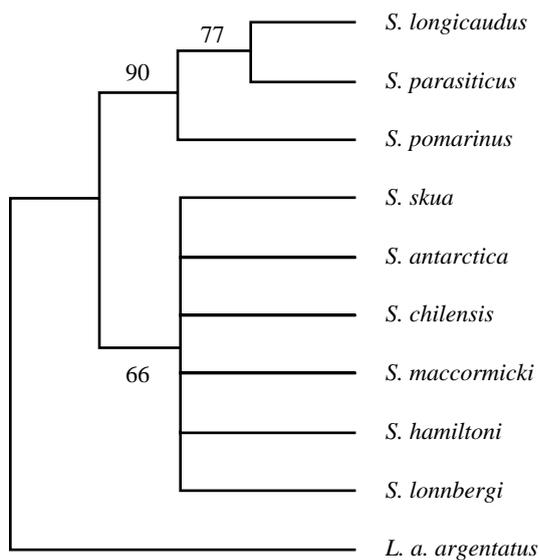


Figure 2. Cladistic phylogeny of skuas based on external morphology (body size and seven plumage characters; table 1). The tree represents strict consensus among the two most parsimonious trees (of length 12 steps) found by exhaustive search, with *L. a. argentatus* as the outgroup. The two shortest trees have CI = 0.917, HI = 0.083, RI = 0.941 and rescaled CI = 0.863. Bootstrap frequencies (%) represent a branch-and-bound search of 100 bootstrap replicates.

reproductive activities, such as copulation and parental care (Marshall 1981). As lice sometimes co-speciate with their hosts, they can provide evidence on host phylogeny (e.g. Page 1993).

There is variation among skuas as regards two taxa of feather lice: *Saemundssonina* species and *Quadriceps normifer* subspecies (Cohen *et al.* 1997). *Saemundssonina* also occurs in the outgroup *Larus* gulls, but *Q. normifer* is exclusive to

skuas (Cohen *et al.* 1997). The distribution (presence–absence matrix) of these forms of lice in skuas is summarized in table 2. Cladistic analysis of this data set (using PAUP) results in a single shortest tree (figure 3). In this tree, *S. pomarinus* and *S. skua* emerge as sister species, as in the mtDNA-based trees of Blechschmidt *et al.* (1993), Cohen *et al.* (1997) and Braun & Brumfield (1998).

Neither the parasite tree (figure 3) nor the mtDNA tree of Cohen *et al.* (1997) provide convincing evidence about the phylogeny of speciation (the mtDNA tree was discussed by Braun & Brumfield (1998)). The parasite data are few, and random events can have similar effects in the inheritance of ectoparasites as in mtDNA trees (Page & Charleston 1998). Chance may therefore have played an important role in determining the tree topology in figure 3. In addition, an alternative character coding where *Quadriceps* and *Saemundssonina* are instead coded as two unordered multistate characters results in 77 shortest trees, the strict consensus among which does not resolve any taxa. Semi-strict consensus does, however, unite *S. pomarinus* and *S. skua* in one clade and *S. antarctica*, *Stercorarius chilensis* and *S. maccormicki* in another. None of these clades is therefore contradicted by the parasite data.

An alternative possibility is that the parasite shared only by *S. pomarinus* and *S. skua*, *Quadriceps normifer stellaepolaris*, is ancestral to the *S. pomarinus*–great skua clade. However, if, as seems probable (Furness 1987), *S. maccormicki* branched from the common great skua ancestor before any other extant great skua did so (see above), *Q. n. stellaepolaris* is unlikely to be ancestral to the *S. pomarinus*–great skua clade. This is because *S. maccormicki* shares another subspecies of the parasite, *Quadriceps normifer alpha*, with two other great skua forms, *S. antarctica* and *S. chilensis*. Again, sequence data from several unlinked regions of nuclear DNA are needed for more

Table 2. *Forms of Quadraceps and Saemundssonina feather lice found among skuas Stercorariidae*

(1, presence and 0, absence of the louse taxon. Data from Cohen *et al.* (1997). Two great skua forms in which no *Quadraceps* individuals were found, *S. hamiltoni* and *S. lonnbergi*, have been excluded.)

skua taxon	louse taxon							
	<i>Q. n. stellaepolaris</i>	<i>Q. n. normifer</i>	<i>Q. n. parvopallidus</i>	<i>Q. n. alpha</i>	<i>S. stresemanni</i>	<i>S. cephalus</i>	<i>S. inexpectata</i>	<i>S. lari</i>
<i>S. pomarinus</i>	1	0	0	0	1	0	0	0
<i>S. longicaudus</i>	0	0	1	0	0	0	1	0
<i>S. parasiticus</i>	0	1	0	0	0	1	0	0
<i>S. skua</i>	1	0	0	0	1	0	0	0
<i>S. antarctica</i>	0	0	0	1	1	0	0	0
<i>S. chilensis</i>	0	0	0	1	1	0	0	0
<i>S. maccormicki</i>	0	0	0	1	1	0	0	0
<i>Larus spp.</i>	0	0	0	0	0	0	0	1

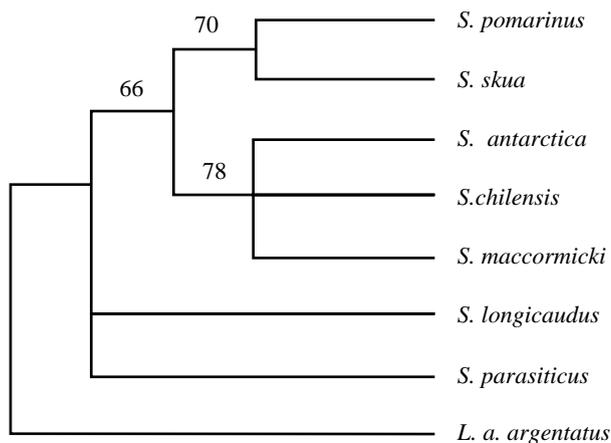


Figure 3. Cladistic phylogeny of skuas based on ectoparasite data (from table 3 in Cohen *et al.* (1997)). With exception for *S. longicaudus* and *S. parasiticus* being unresolved, the tree in its essential features is identical to the most parsimonious tree based on mtDNA (Cohen *et al.* 1997; see also figure 1a). In particular, *S. pomarinus* and *S. skua* also emerge as sister species here. The two parasite taxa showing informative variation between skuas (*Q. normifer* subspecies and *Saemundssonina* species) were used for estimation of the tree (see table 2). The single most parsimonious tree was found by exhaustive search of the three phylogenetically informative forms among the seven forms of ectoparasites in table 2 (*Q. n. stellaepolaris*, *Q. n. alpha* and *Saemundssonina stresemanni*). Bootstrap frequencies (%) represent a branch-and-bound search of 100 replicates.

decisive evidence on this as well as most other uncertain aspects of evolution in skuas.

(c) *Hybridization or lineage sorting?*

The strong similarity in mtDNA as well as parasites between *S. pomarinus* and *S. skua* is remarkable (Cohen *et al.* 1997), because most other evidence suggests that great skuas are a monophyletic group (see above and Furness 1987; Braun & Brumfield 1998). Why then are *S. pomarinus* and *S. skua* most similar to each other in both mtDNA and ectoparasites? Besides hybridization, lineage sorting might lead to such an outcome (e.g. Page & Charleston 1998). What is the probability that random lineage sorting of parasites will produce a pattern where *S. pomarinus* and *S. skua* are most similar to each other, precisely the result

that is expected if there has been hybridization and transfer of both mtDNA and ectoparasites between *S. pomarinus* and *S. skua*? If some simplifying assumptions are made, this probability is estimated at <0.0006 (see Appendix A). It is small enough that lineage sorting can be refuted in favour of hybridization as the reason why *S. pomarinus* and *S. skua* are most similar to each other in mtDNA as well as ectoparasites.

(d) *Direction of mtDNA transfer*

The results presented by Cohen *et al.* (1997) and Braun & Brumfield (1998) permit another test of two predictions from the hybridization hypothesis, bearing on the direction of mtDNA transfer. If *S. skua* has received its mtDNA from *S. pomarinus* (Andersson 1999a), then *S. skua* should be more similar to *S. pomarinus* than to the members of the great skua clade in mtDNA. Moreover, *S. skua* then should also differ more in mtDNA from the other great skuas than they differ between each other, since the (mtDNA-donating) Pomarine skua has probably been separated from these other forms for a longer time (figure 1b), as indicated by nuclear DNA data (see below) and morphology. If *S. skua* differs less in mtDNA from one or more of the other great skuas than they differ between each other, this is evidence against the hypothesis that *S. skua* received its mtDNA from *S. pomarinus*.

The data presented by Cohen *et al.* (1997, table 3) show, however, that the two predictions from the hybridization hypothesis are upheld. In mtDNA, *S. skua* is more similar to *S. pomarinus* than to any great skua form and *S. skua* differs more from them than they differ between each other.

An alternative explanation for these results is that mtDNA was transferred to *S. pomarinus* from *S. skua* and that the latter diverged earlier from the great skua common ancestor than did the other great skuas, explaining why *S. skua* is less similar to them in mtDNA. However, if so, *S. skua* should also differ more in nuclear DNA from the other great skuas than they differ between each other. This is not the case in the allozyme distance matrix of Cohen *et al.* (1997; website and personal communication). Indeed, that data set suggests that *S. skua* and *S. antarctica* are more closely related than *S. antarctica* and *S. maccormicki* (Braun & Brumfield 1998). All these results are as expected if mitochondria passed

from the Pomarine to North Atlantic Great skua and not the opposite way. (Cohen *et al.* (1997) reviewed recent sympatry between the two species and Andersson (1999a) suggested a possible historical scenario of hybridization.)

3. CONCLUSIONS

The cladogram based on external morphology (figure 2) corroborates the traditional view that all great skuas form a monophyletic group. This view is also supported by nuclear genetic data (Cohen *et al.* 1997; Braun & Brumfield 1998). The present analyses provide evidence against lineage sorting and for hybridization as the cause of the close similarity in mtDNA and ectoparasites between the Pomarine and the North Atlantic Great skua. Genomic data presented by Cohen *et al.* (1997 and website) are also in line with the idea (Andersson 1999a) that mitochondria have been transferred from *S. pomarinus* to *S. skua* through introgressive hybridization.

This tentative conclusion as well as the alternative explanations need further testing, which can be done by constructing skua phylogenies from a number of unlinked nuclear DNA sequences. If such analysis supports the mtDNA tree of Cohen *et al.* (1997), *S. pomarinus* and *S. skua* are most probably sister species. Then, an extraordinary morphological convergence with other skuas must have taken place in one of these two species (Cohen *et al.* 1997). If, on the other hand, nuclear DNA sequences yield trees which differ from the mtDNA tree but, like the morphology-based cladogram presented here, support monophyly of the great skuas including *S. skua*, then the hypothesis that *S. skua* and *S. pomarinus* are sister species is refuted. Such a result would further corroborate the hypothesis that mtDNA and feather lice have been transferred between these two species through hybridization. Further evidence that *S. maccormicki* was first among the extant great skuas to branch from their common ancestor would also support hybridization as the explanation for the ectoparasite identity between *S. pomarinus* and *S. skua*.

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APPENDIX A. PROBABILITY THAT LINEAGE SORTING MAKES *S. POMARINUS* AND *S. SKUA* MOST SIMILAR AS REGARDS BOTH ECTOPARASITES AND mtDNA

Gene and species phylogenies can differ because of random events. When there is stochastic lineage sorting, different alleles or mtDNA haplotypes need not follow the same branching pattern as the species tree (e.g. Avise *et al.* 1984; Pamilo & Nei 1988; Doyle 1997; Maddison 1997). Discordance between an mtDNA tree and phylogenetic trees based on nuclear DNA or other characters might therefore be caused by such random events. This could explain why *S. pomarinus* and *S. skua* are sister taxa in the mtDNA tree (Cohen *et al.* 1997), although morphology and nuclear DNA suggest that the great

skuas are a monophyletic group and behaviour and genomic evidence suggest that *S. pomarinus* is their sister taxon (Andersson 1973, 1999a; Braun & Brumfield 1998).

As an alternative to lineage sorting, Andersson (1999a) suggested hybridization and mtDNA transfer between *S. pomarinus* and *S. skua*. Mitochondria from one taxon often seem to have been incorporated by another taxon that retains its nuclear genome (reviewed by Arnold 1997; Dowling & Secor 1997).

In addition, *S. pomarinus* and *S. skua* have identical ectoparasites (Cohen *et al.* 1997). As feather lice are usually passed between mates and from parent to offspring (Marshall 1981), they are likely to be transferred between species if there is introgressive hybridization (e.g. Patton *et al.* 1984). Parasites may, however, also be subject to similar random processes as genes, including duplication, horizontal transfer and loss through stochastic lineage sorting (Page & Charleston 1998). Random events in the transmission of feather lice therefore might give rise to the pattern that is also expected if there has been hybridization and transfer of mtDNA and lice between *S. pomarinus* and *S. skua*.

As stochastic lineage sorting assumes randomness, it is accessible to probabilistic testing (Andersson 1999b). What is the probability that lineage sorting (null hypothesis) leads to a parasite pattern that goes at least as far as the observed one or further in the direction expected under the (alternative) hybridization hypothesis? If that probability is sufficiently small, the null hypothesis of random sorting can be rejected in favour of the hybridization hypothesis.

Consider the great skua–Pomarine skua clade in figure 1b (the right-hand part of the tree is irrelevant to the present problem). There is parasite variation within that clade in the form of two different subspecies of *Q. normifer* (Cohen *et al.* 1997; see table 2). As there is not yet enough nuclear genetic, morphological or behavioural data to resolve the phylogeny of great skuas convincingly (see Cohen *et al.* 1997; Braun & Brumfield 1998; and figure 2), they are here left unresolved in a polytomous tree (figure 4).

From the point of view of the hybridization hypothesis, the most strongly corroborative outcome is that *S. pomarinus* and *S. skua*, and only they, share the same *Quadriceps* form, and that the other three species share the other *Quadriceps* form. What is the probability that random sorting will produce this pattern? Using some simplifying assumptions, an approximate estimation of this probability can be done.

Assume that both forms of *Quadriceps* are present in the common ancestor of great skuas and *S. pomarinus* (figure 4), for example because of earlier host switching or within-host speciation of parasites (Page & Charleston 1998). Assume further that each of the two parasite forms has the same probability p in each phylogenetic branching event to enter and survive in each new branch, until the next branching event in that new branch. The probability of not entering or surviving is $q = 1 - p$. Given that the parasite survives until the next branching event takes place, the same probabilities then apply in each of the new branches.

The probability P_{tot} under the null hypothesis of obtaining the pattern in figure 3 can now be calculated as

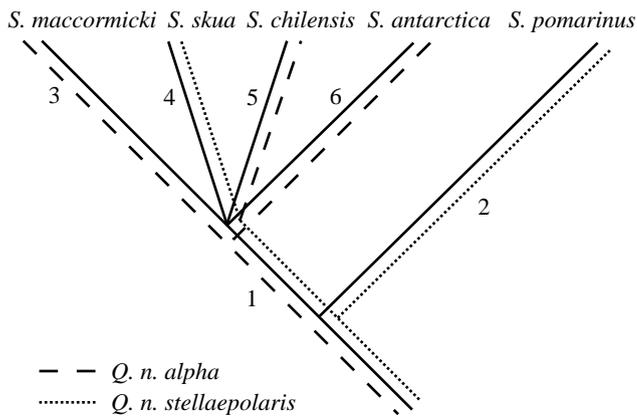


Figure 4. Stochastic lineage sorting of feather lice, two subspecies of *Q. normifer*, might give rise to the same observed pattern of similarities among Pomarine and great skuas as does mtDNA variation. The likelihood that this will happen through random sorting is estimated in the main text. Bold lines: hypothetical phylogeny of great and Pomarine skuas based on morphology and nuclear genes. Hatched lines: transmission under the random lineage sorting hypothesis of the two forms of *Q. normifer* ssp., leading to the presently observed distribution of *Q. normifer* subspecies among these skuas.

the product of the two independent probabilities P_a and P_s of obtaining the observed patterns for *Q. n. alpha* and *Q. n. stellaepolaris*, respectively. These probabilities are as follows (progressing in the order of branch numbers in the tree; figure 4):

$$P_a = pqppqp = p^4 q^2,$$

$$P_s = ppqpqq = p^3 q^3,$$

and

$$P_{\text{tot}} = P_a P_s = p^7 q^5 = p^7 (1 - p)^5.$$

In addition, this probability must be doubled as there is an identical possible pattern of character distribution among these skuas, but with reversed parasite identity.

In reality, p will probably vary with, for example, branch length (time), parasite biology and other factors. Assuming a single value for p is a heuristic simplification, but it should not lead to systematic bias in the present context. The value of p is not known, but a useful result is obtained by calculating the maximum possible value of P_{tot} , a conservative procedure that minimizes the risk of refuting a true null hypothesis (Andersson 1999b). The maximum is found by differentiating P_{tot} with respect to p and setting the derivative to zero, which gives $p = 7/12$, $P_{\text{tot}} = (7/12)^7 (5/12)^5$ and $2P_{\text{tot}} \cong 0.0006$. This can be shown to be a maximum point, as the second derivative is less than zero.

It is also possible to estimate the likelihood of the observed pattern or a more strongly corroborative one from the perspective of the hybridization hypothesis for a tree that includes the two great skuas (*Stercorarius hamiltoni* and *Stercorarius lonnbergi*; Cohen *et al.* 1997) in which no *Quadriceps* form has been found. It can be shown that the corresponding probability for this enlarged tree with six instead of four great skua forms is $2P_{\text{tot}} \cong 0.0005$.

In both the above cases the observed outcomes and other equally or more extreme possible outcomes in the direction expected from the hybridization hypothesis have a low probability of arising by chance under the null hypothesis of random lineage sorting. They are, however, as expected if hybridization and transfer of parasites has taken place between *S. pomarinus* and *S. skua*. The results therefore refute the random sorting hypothesis and corroborate the hybridization hypothesis.

This conclusion might be mistaken, for example, if both parasite forms (*Q. n. alpha* and *Q. n. stellaepolaris*) co-occur in one or more skuas but the double presence has escaped notice. The relatively high number of skua individuals examined (Cohen *et al.* 1997) speaks against this possibility, but it cannot be definitely refuted. Another possibility is that the parasite *Q. n. stellaepolaris* was ancestral in the *S. pomarinus*–great skua clade and remained unchanged in the *S. skua* branch, but evolved anagenetically into *Q. n. alpha* before cladogenesis of the other great skuas took place. This seems unlikely, as some evidence suggests that *S. maccormicki*, also a host of *Q. n. alpha*, was first among the extant great skuas to branch from their common ancestor (see above) and for other reasons (Andersson 1999b). It can be shown that if the location of *S. maccormicki* in figure 4 is shifted accordingly, the probability that lineage sorting has produced the observed parasite distribution becomes even smaller.

Further tests, such as those suggested above based on several independent sequences of nuclear DNA, are needed to discriminate between the alternative explanations.

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