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Enigmatic phylogeny of skuas: an alternative hypothesis

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Last year, Cohen et al. presented molecular data suggesting the surprising result that both currently recognized genera of skuas, Stercorarius and Catharacta (Aves: Stercorariidae), are not monophyletic. However, the most enigmatic conclusion from their analysis, that S. pomarinus is sister to C. skua, rests solely on mtDNA sequence data. When the mtDNA data are analysed in a maximum likelihood framework that accounts for variation in evolutionary rates, Catharacta monophyly cannot be rejected. None of the best trees that can be derived from two nuclear data sets of Cohen et al. support the controversial pomarinus–C. skua node. We propose an alternative hypothesis, that pomarinus is sister to a monophyletic Catharacta, as the best explanation of the available molecular, morphological, and behavioural evidence.

Keywords: Stercorariidae; skua; phylogeny; lineage sorting; mtDNA; avian systematics

1. INTRODUCTION

Apparent conflicts between molecules and morphology in systematics have become almost commonplace (Balter 1997), sparking heated debate in many cases (e.g. Poe 1996; Lee et al. 1997; Sullivan & Swoford 1997). This debate is healthy because it stimulates additional research and new analyses that are generating fresh insights in a broad array of evolutionary disciplines.

A recent case in point involves the skuas, a distinctive family of predatory seabirds. Cohen et al. (1997) present molecular data bearing on skua phylogeny that pose a striking enigma. The data indicate that one of the three Stercorarius skuas, S. pomarinus (the Pomarine skua), falls within the clade comprising the Catharacta skuas, rendering both genera non-monophyletic (figure 1a). Yet these two genera are (i) quite different in outward appearance, (ii) defined by putative morphological synapomorphies (Brooke 1978; Furness 1987), and (iii) have been maintained as distinct genera in the overwhelming majority of modern treatments (e.g. AOU 1983). Cohen et al. (1997) suggest three possible explanations for the remarkable discordance between molecules and morphology in skuas, but recognize that all three explanations are ‘far-fetched’. Our purpose here is to explore this apparent paradox, and to propose a fourth hypothesis. We believe this fourth explanation best accounts for the available data, which now include plumage and skeletal morphology, behaviour, ectoparasitic lice, and a variety of molecular evidence. This explanation has the further advantage that it is readily testable.

Cohen et al. (1997) present five data sets, four of which are molecular, the fifth of which is based on ectoparasitic lice. The data are consistent in many ways, and demonstrate convincingly that pomarinus is more closely related to Catharacta than to other Stercorarius. While this is surprising in the light of the general resemblance of pomarinus to other Stercorarius, this result does not actually contradict the morphological data. As Cohen et al. point out, the Stercorarius morphotype appears to be ancestral in the Stercorariidae; therefore, it does not provide cladistic information supporting monophyly of Stercorarius. The single putative morphological synapomorphy linking pomarinus with Stercorarius, barred juvenile plumage (Brooke 1978), may instead be a symplesiomorphy in the family that has been lost in Catharacta.

What is more difficult to accept is the idea that Catharacta is also not monophyletic. The phylogeny presented by Cohen et al. places pomarinus sister to C. skua (Great skua), to the exclusion of the other five Catharacta species (figure 1a). This aspect of their phylogeny forces the authors to propose remarkable convergence in the origins of either the Catharacta or Stercorarius morphology (their hypotheses (α) and (β)) or a bizarre inter-generic hybridization event resulting in a stable hybrid species (pomarinus) that is Catharacta-like in its mitochondrial and nuclear genomes but Stercorarius-like in its external appearance (their hypothesis (γ)). It is this node which causes the bulk of the enigma they face.

Although Cohen et al. discuss five data sets, the phylogeny they present is actually derived from only one, the mitochondrial DNA (mtDNA) sequences. The mtDNA is a single, clonally inherited genetic unit. Any phylogeny based upon it must be regarded as the phylogeny of a single gene, which may or may not accurately track the species phylogeny (Nei 1987, p. 288; Maddison 1997). One set of conditions under which a gene phylogeny is likely to differ from the species phylogeny is when a series of speciation events occurs with insufficient time between them for the gene lineages to reach reciprocal monophyly. In this situation, random fixation of gene lineages in the daughter species can result in a gene tree that is incongruent with the
species tree. The small divergences among *Catharacta* species and *pomarinus* in all four genetic data sets (see Cohen 1997; note branch lengths in figure 2 herein) indicate that speciation has been rapid and relatively recent in skuas. Thus, it seems plausible that reciprocal monophyly of mtDNA may not have been reached in some lineages of the group, and that the mtDNA tree, however well-resolved it might be, simply is not the same as the species tree.

We propose an alternative hypothesis of relationship that accommodates both the morphology and the data of Cohen et al. (figure 1b). In this hypothesis, *pomarinus* is sister to a monophyletic genus *Catharacta*, reflecting the close relationship so strongly indicated by a wealth of molecular evidence. The *pomarinus*–*C. skua* node of figure 1a is presumed incorrect, either due to the gene tree–species tree problem discussed above or to inadequate resolution of the mtDNA tree (see below). Although *Stercorarius* is not monophyletic, figure 1b only requires each morphotype to evolve once (contrary to hypotheses (a) and (b) of Cohen et al.; see figure 1a). The resemblance of *pomarinus* to other *Stercorarius* is explained by assuming that *pomarinus* has retained the ancestral *Stercorarius* morphotype.

This hypothesis also accounts for the similarity of *pomarinus* to *Catharacta* observed in a phenetic study of 50 skeletal characters (Schnell 1970), as well as behavioural similarities in calls and displays (Andersson 1973). In fact, Andersson seems to have proposed essentially the same hypothesis of relationship entailed in figure 1b when he wrote 'the most likely explanation for this [behavioural similarity] seems to be that the Pomarine and Great skuas diverged from each other at a time when the predecessor of the two smaller species had already branched from the common skua ancestor' (Andersson 1973, p. 14). Although he did not explicitly state that he considered *Catharacta* monophyletic, Andersson treated the South Polar skua (*C. s. maccormicki*) as a subspecies of the Great skua (*C. s. skua*) in the same section, so the idea seems implicit.

2. METHODS, RESULTS AND DISCUSSION

(a) Mitochondrial data

Given the two competing hypotheses of relationship contained in figures 1a and 1b, it is natural to ask whether the mtDNA sequence data support one hypothesis significantly more than
Figure 2. Maximum-likelihood estimate of skua phylogeny based on mtDNA sequence data of Cohen et al. (1997). Numbers refer to percentage of 100 unconstrained likelihood bootstrap replicates in which each node occurs. Only values greater than 50% are shown. Branch lengths are proportional to the expected number of substitutions per site (ENSS). Likelihood parameters for the general time reversible (GTR) substitution model (Lanave et al. 1984) with among-site rate heterogeneity following a gamma distribution (F; Yang 1993) were estimated separately on the cytochrome b (cyt b) and 12S ribosomal RNA (12S) data. The GTR+F likelihood model was used because it fit the data significantly better based on likelihood ratio tests (Goldman 1993) than other models available in PAUP* (e.g. GTR+F versus HKY85+F, $\chi^2=21.02$, d.f. = 5, $p < 0.05$). Because the estimated parameters (i.e. rate matrix and gamma-shape parameter) were very similar for both genes, cyt b and 12S sequences were combined. Using all 1415 bp of sequence data, likelihood parameters for the GTR+F model were estimated using the successive approximations approach suggested by Swofford et al. (1996, p. 445), beginning with a neighbour-joining tree (Saitou & Nei 1987) constructed from HKY85 (Hasegawa et al. 1995) genetic distances assuming no among-site rate heterogeneity. The parameter estimates used were rate matrix: $A-C = 2.329 \times 10^{-8}$, $A-G = 1.826 \times 10^{-8}$, $A-T = 8.528 \times 10^{-8}$, $C-G = 7.613 \times 10^{-8}$, $C-T = 3.455 \times 10^{-8}$, $G-T = 1$; gamma-shape parameter, $a = 0.0974665$.

Although we believe model-based likelihood methods are better suited for phylogenetic analysis of sequence data, in the interest of completeness we also performed KH and Templeton (1983) tests on optimal trees from unconstrained and constrained unweighted parsimony analyses analogous to those presented by Cohen et al. Our analysis of 102 informative sites resulted in a single most parsimonious tree (145 steps) identical in topology to that presented by Cohen et al. Discrepancies in the number of informative sites and tree length from that presented in Cohen et al. (109 informative sites, tree length 148) are due to an improvement in the ability of PAUP* to detect uninformative characters in certain situations involving polymorphic terminal taxa. This improvement does not affect their phylogenetic conclusions. A search in which Catharacta was constrained monophyletic resulted in an unweighted parsimony framework (58% versus 97%; figure 2). To understand why this node is less robust under maximum likelihood, it is important to note that the branch lengths in the pomarinus–Catharacta clade are all quite short. This results from the fact that the maximum-likelihood model accounts for the substantial variation among sites in evolutionary rates present in this data set (see figure 2 legend).

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in a single most parsimonious tree (151 steps) that placed pomarinus basal to the Catharacta clade. The KH test found the unconstrained tree to be better than the constrained tree (T = 2.1591, p = 0.0032). There was no significant difference as judged by the Templeton test (z = 1.8904, n.s.).

(b) Nuclear data

Thus, maximum-likelihood methods indicate that the tree of figure 1a is not a significantly better explanation of the mtDNA data than the tree of figure 1b, and parsimony methods indicate that it is at best marginally so. However, even if there was a significant difference, the gene tree—species tree problem would remain. Whether a particular gene tree is congruent with the species tree can best be tested by independent estimates of the species tree based on other data (i.e. other genes, morphology, behaviour, etc.). Cohen et al. describe two nuclear data sets (allozymes, RAPDs) that can be used for this purpose. However, they do not present trees based on these data, concluding instead that the nuclear gene data strongly confirm the close relationship of pomarinus to Catharacta, but provide no critical evidence about the ancestry of the Pomarine skua.

Reanalysis of the nuclear data sets reveals that the best trees that can be derived from either of them supports the close relationship of pomarinus to Catharacta, but contradicts the pomarinus—C. skua node of the mtDNA tree. That this might be true can be seen by inspection of the distance matrices (Cohen 1997). The RAPD distance matrix indicates that C. skua and C. maccormicki are more similar to each other than either is to pomarinus (skua and maccormicki are the only Catharacta taxa in the RAPD data matrix). Minimum evolution (Kidd & Sgaramella-Zonta 1971) and FM (Fitch & Margoliash 1967) analyses confirm this similarity, yielding a tree with Catharacta monophyletic. Parsimony analysis of the RAPD data yields four most parsimonious trees, all of which have C. maccormicki sister to pomarinus. The shortest trees (90 steps) are only one step shorter than a tree in which Catharacta is monophyletic. Thus, neither distance nor parsimony trees derived from the RAPD data contain a pomarinus—C. skua node.

Using BIOSYS (Swoford & Selander 1981), distance matrices (Cavalli-Sforza & Edwards 1967; Nei 1972) were calculated from the original 42-locus allozyme data set provided by A. Baker (including allele frequency data for the outgroups Larus fuscus, L. mexicanum, and Sterna hirundo). In each case, C. skua and C. antarctica are more similar to one another than either is to pomarinus (skua and antarctica and maccormicki are the only Catharacta taxa in the allozyme data matrix). In fact, one allele at the guanine deaminase (GDA) locus represents an unambiguous synapomorphy for C. skua and C. antarctica. Given that the mtDNA data are also derived from a single genetic unit, we consider GDA by itself to be an important conflict for the mtDNA tree of figure 1a.

A frequency parsimony analysis of the allozyme data was performed by converting the BIOSYS file to a FREQPARS file using the FORTRAN program BIO2FREQ (Swoford & Berlocher 1987; program available via anonymous FTP at onyx.sj.edu). The FREQPARS file was imported into PAUP* and a branch-and-bound search was performed (for details of the FREQPARS analysis utilizing PAUP*, see Berlocher & Swoford 1997). The three most parsimonious FREQPARS trees (49.916 steps) have C. skua sister to C. antarctica. A tree with Catharacta constrained monophyletic is only 1.1 steps longer (a FREQPARS step is equivalent to an allelic frequency change of 0.5). UPGMA (unweighted pair group method), neighbour-joining, and minimum evolution trees were also constructed using the chord distance (Cavalli-Sforza & Edwards 1967); all of these also have C. skua sister to C. antarctica.

3. CONCLUSIONS

(a) Phylogeny

In summary, none of the best trees derived from the nuclear data sets includes the pomarinus—C. skua node found in the mtDNA tree, and near optimal trees exist in each case in which Catharacta is monophyletic. While neither nuclear data set can be used to exclude confidently one or other of the topologies in question, the same can probably be said of the mtDNA data as explored above. Given the conflict between data sets and the gene tree—species tree problem, a more conservative interpretation of the total genetic evidence (mitochondrial and nuclear) would be that it supports a clade composed of pomarinus plus all Catharacta, but no further resolution within that clade is yet possible. When the several apparent morphological synapomorphies that unite Catharacta are considered (Furness 1987), it seems more reasonable to suppose that the group is monophyletic (figure 1b).

Distinguishing between these two hypotheses of relationship (figures 1a and 1b) should be straightforward. Any independent estimate of the species tree that resolves the nodes within the pomarinus—Catharacta clade will corroborate one of these hypotheses (or one of the other possible resolutions within the clade), and refute the rest. In principle, it would be possible to make such an estimate from morphological or behavioural data, if such information exists for all the forms of Catharacta. However, given that genetic samples from all named forms of Catharacta and Stercorarius are in hand in several laboratories, it seems most likely that independent estimates of the species tree will come from DNA sequences of nuclear genes.

(b) Taxonomy

The phylogeny in figure 1b makes Stercorarius non-monophyletic, while that of figure 1a renders both Stercorarius and Catharacta non-monophyletic. In either case, a different generic treatment of the group is required. One possibility is to treat all skuas in a single genus, Stercorarius, as recommended by Hartert (1912), Moynihan (1959) and Andersson (1973). However, if the topology of figure 1b proves correct, it would also be reasonable to retain Stercorarius and Catharacta, and place pomarinus in a separate genus. This treatment would have the advantage of recognizing the morphological distinctiveness that separates pomarinus from Catharacta, while highlighting the true phylogenetic structure of the group. The disadvantage of this arrangement is that it would erect separate genera for two groups (pomarinus and Catharacta) which, based on their genetic similarity, probably share a more recent common ancestor than do the two remaining species of Stercorarius. Accumulation of genetic and palaeontological data may make recency of common ancestry a desirable metric of categorical rank in future. At present, there is only a loose correlation between the two in avian taxonomy (e.g. Brumfield et al. 1997). The dual goals of recognizing phylogeny and morphological similarity take priority in current usage, and this second treatment is the
one we favour if figure 1b is the correct phylogeny. The generic name with priority for *pomarius* under this scenario seems to be *Coprothes* Reichenbach 1850.

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