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SHORT-COMMUNICATION

How many genera of Stercorariidae are there?

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ABSTRACT: In this contribution I comment on the generic taxonomy of skuas, Stercorariidae, based on the currently available hypotheses of phylogenetic relationships for the group – *i.e.*, the cladograms. Specifically, the different cladograms were examined following Hennig's principle of reciprocal illumination, in which a given hypothesis is evaluated by the extent to which it agrees with competing hypotheses. Currently, all species are often assigned to genus *Stercorarius.* However, chewing lice- (Insecta, Phthiraptera), behaviour- (territorial display and calls) and molecular-based (mitochondrial DNA) hypotheses of phylogenetic relationships all indicate that Pomarine Skua *Stercorarius pomarinus* and the species formerly placed in genus *Catharacta* are monophyletic and sister to a clade comprising Long-tailed *S. longicaudus* and Parasitic *S. parasiticus* Skuas. Therefore, contrary to the prevailing view that all species within the family should be placed in a single genus, I argue herein that in a cladistic-based classification by sequencing, both *S. parasiticus* and *S. longicaudus* should retain their generic name, whereas *S. pomarinus* should be transferred to *Catharacta*, as *C. pomarina*.

KEY-WORDS: cladistics, cladograms, classification, nomenclature, seabird.

Recently, Vogt (2008, 2014; see also Rieppel 2008) argued that Karl Popper's hypothetico-deductive method and falsificationism are not applicable to cladistics (for a contrary view *cf.* Farris 2014). According to Popper (2001 [1959]), a hypothesis is falsifiable if it prohibits at least one event that is not prohibited by the background knowledge. However, as observed by Vogt (2008: 65) "[n]either such background knowledge as for instance 'descent with modification', nor any specific tree hypothesis prohibits the occurrence of convergent evolution. This allows for both apomorphy ... and homoplasy as possible explanations ... A given tree hypothesis is logically congruent with any specific evidence of character state distribution ... [and] *does not prohibit* any specific character state distribution." In other words, in the analysis of a taxon/character matrix, when a hypothesis of primary homology is not congruent with the others, it is not refuted in a Popperian way, but parsimoniously explained as homoplasy. Naturally, a similar reasoning can be applied to the analysis of a multiple sequence alignment.

Cladistic hypotheses are statements about the phylogenetic relationships represented by the best option given the data available, but subject to confrontation with additional evidence, particularly those drawn from different sources. Therefore, as pointed out by Santos & Capellari (2009), cladograms can be compared against each other to find congruencies among them. The idea behind such a comparison is similar to Hennig's (1968 [1955]) method of "reciprocal illumination", in which two sorts of data are complementary to each other, and has the potential to enlighten one another. If, for example, two (or more) cladograms are congruent, in the sense of depicting the same or almost the same relationships, they have a better explanatory value when compared to other contradictory cladograms. On the other hand, in case of no or little congruence, then the differences should be reconciled through reanalysis of existing data and/or the analysis of new characters (Santos & Capellari 2009, Santos & Klassa 2012).

That said, in the present contribution I comment on the generic taxonomy of Stercorariidae (skuas) in light of the available hypotheses of phylogenetic relationships for the family. Specifically, I focus on detecting congruencies among the different cladograms, as outlined in the preceding paragraph. For convenience, I also provide readers with measures of support of unrefuted clades (*sensu* Grant & Kluge 2008a) obtained for each cladogram examined. The details regarding characters descriptions and character/taxon and pairwise genetic distances matrices should be consulted at the respective papers cited herein.

Stercorariidae forms a group of eight to ten species (depending on the authority) of medium- to large-sized predatory/scavenger seabirds. Traditional, pre-cladistic classifications often divided the family into two genera: *Catharacta* for the larger and, except for Great Skua *Catharacta skua*, southern hemisphere-breeding species, and *Stercorarius* for the smaller, northern hemisphere-breeding species (Peters 1934, Furness 1996, Malling-Olsen & Larsson 1997, Christidis & Boles 2008). The two genera of Stercorariidae have been accepted until the end of 1990s, when the systematics of the family was revised from a cladistic perspective.

Cohen *et al.* (1997) presented a phylogeny for Stercorariidae, based on concatenated mitochondrial (mtDNA) cytochrome *b* and 12S rRNA sequences. In their single most-parsimonious cladogram, the species were divided into two clades; the first consisting of Parasitic *S. parasiticus* and Long-tailed *S. longicaudus* Skuas, and the second, which is the sister-group to the first, of Pomarine Skua *S. pomarinus*, and the other five *Catharacta* species. Particularly in this latter group, *S. pomarinus* and *C. skua* were monophyletic and sister to a clade comprising South Polar Skua *C. maccormicki* and an apparent polytomy formed by Chilean *C. chilensis*, Brown *C. antarctica*, Tristan *C. hamiltoni*, and Subantarctic *C. lonnbergi* Skuas (Figure 1A). Furthermore, according to Cohen *et al.* (1997: 184), both their maximum-likelihood and neighbour-joining analyses resulted in the same topology.

A year later, Braun & Brumfield (1998) reanalysed the Cohen *et al.*'s (1997) data using a maximum-likelihood approach and cladogram searches constrained for the monophyly of *Catharacta*. They recovered a cladogram similar to that of Cohen *et al.* (1997), the difference being the position of *S. pomarinus* as sister-taxon to a clade comprising the *Catharacta* species (Figure 1B). However, as the authors themselves point out (p. 997), unconstrained analysis by both maximum parsimony and maximum likelihood approaches resulted in a cladogram topologically identical to that obtained by Cohen *et al.* (1997; *cf.* Figures 1A and 1C). Braun & Brumfield (1998) defended their findings by arguing that they were more consistent with pre-cladistic, plumage-, body mass-, and behaviour-based hypotheses of a "natural" *Catharacta*. They furthermore suggested that, if their cladogram (Figure 1B) proves "correct", it would be reasonable to place *S. pomarinus* in its own genus, for which *Coprotheres* would be available.

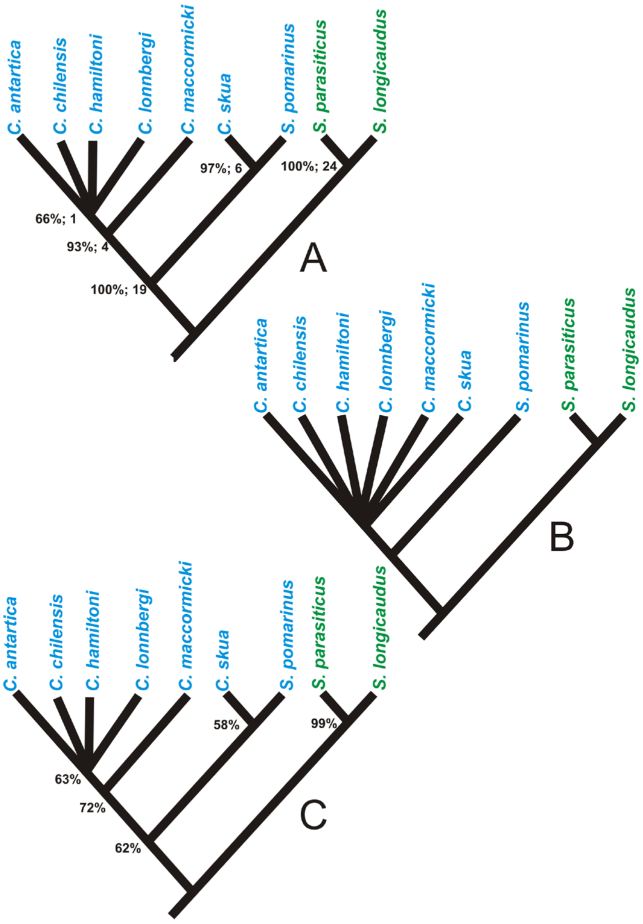

FIGURE 1. Clockwise, from top to bottom: Hypotheses of phylogenetic relationships within Stercorariidae, as recovered in the analyses by Cohen *et al.* (1997; (**A**) and Braun & Brumfield (1998; both constrained (**B**) and unconstrained (**C**) for the monophyly of *Catharacta*). Numbers refer to percentage bootstrap (100 replicates) and Goodman-Bremer support (Grant & Kluge 2008b). Note that Braun & Brumfield (1998) did not provide support values for their constrained cladogram.

Andersson (1999a) proposed two additional hypotheses of phylogenetic relationships within Stercorariidae: one based on body-mass and plumage characters (phenotype), the other based on presence or absence of ectoparasite chewing lice taxa (Insecta, Phthiraptera). In the phenotype-based cladogram, the species were divided in two clades; a "traditional", monophyletic *Stercorarius* sister to a trichotomy of *C. antarctica*, *C. chilensis*, and *C. maccormicki* (Figure 2A). In the cladogram derived from chewing lice data, *S. pomarinus* and *C. skua* were monophyletic and sister to a polytomy containing the other *Catharacta* species (Figure 2B). Andersson (1999b) also published a further hypothesis, this time based on behavioural characters (*i.e.*, territorial displays and calls). Although his analysis included only four out of seven–ten species of the family, *S. pomarinus* and *C. skua* were recovered as monophyletic, and placed sister to *S. parasiticus* plus *S. longicaudus* (Figure 2C). Andersson (1999b: 212) noted that "the traditional placement of the Pomarine Skua in the same genus as the two smaller *Stercorarius* forms, and not together with the larger *Catharacta* species to which *[S.] pomarinus* is clearly much more closely related, ignores the cladistic evidence and makes *Stercorarius* a paraphyletic genus." Nevertheless, his main recommendation was to merge all species into a single genus, the older *Stercorarius*. Andersson (1999b: 212) further commented that "if *Catharacta* is retained ... the generic name of *[S.] pomarinus* should be changed to *Catharacta*, as there is now massive evidence for closer relatedness of the Pomarine to the larger *Catharacta* skuas than to the two smaller *Stercorarius* species."

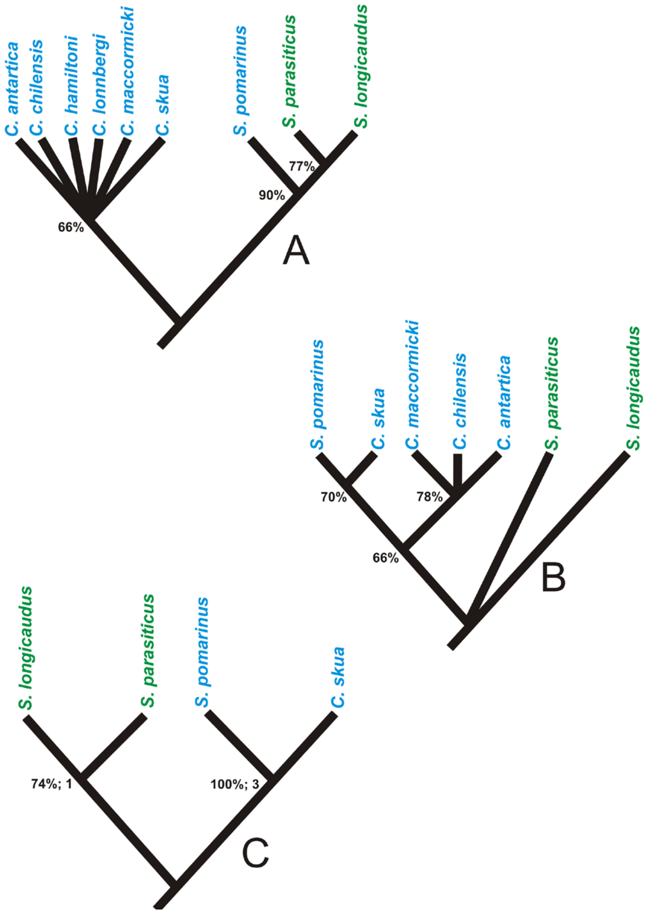

FIGURE 2. Clockwise, from top to bottom: Hypotheses of phylogenetic relationships within Stercorariidae, as recovered in the analyses by Andersson (1999a; body mass and plumage characters (**A**) and presence or absence of ectoparasite chewing lice taxa (**B**)), and Andersson (1999b; territorial display and calls (**C**)). Numbers refer to percentage bootstrap (100 replicates) and Goodman-Bremer support (Grant & Kluge 2008b).

More recently, Chu *et al.* (2009) performed a cladistic analysis of Stercorariidae on the basis of 141 osteological characters. They found a single most parsimonious tree in which the relationships among Stercorariidae fit a comb-shaped or pectinate topology (*i.e.*, that topology wherein every bifurcation leads to one terminal taxon). This can be parenthetically expressed as follows: (*S. longicaudus* + (*S. parasiticus* + (*S. pomarinus* + (*C. maccormicki* + (*C. skua* + (*C. antarctica* + (*C. chilensis* + *C. lonnbergi*))))))).

In the early 2000s, ornithologists in general, and technical committees responsible for developing and maintaining checklists of birds for countries or other political units in particular, all embraced the idea of having a single genus of Stercorariidae (*e.g.*, American Ornithologists' Union 2000, Sangster *et al.* 2004, Christidis & Boles 2008, Gill & Donsker 2015, Remsen *et al.* 2015). Apparently, the only exception to this general agreement was by the Checklist Committee Ornithological Society of New Zealand (2010: 223), which retained both *Catharacta* and *Stercorarius*, but placed *S. pomarinus* in *Coprotheres*.

Two methods for transposing information from cladograms to hierarchical Linnaean classifications have been proposed so far. The first, put forward by Hennig (1968 [1955]), is called "subordination". In this approach, each branching level in a cladogram receives a designation; furthermore, and importantly, sister-taxa are always given the same taxonomic rank. In the second approach, called "sequencing", progressively nested sister-group relationships are given the same taxonomic rank, with the first taxon in a sequence being sister to the subsequent taxa (Nelson 1973). Naturally, these approaches have their arguments for and against; nevertheless, they, alone or in combination, are objective and instrumental tools for the purpose they were devised for (Amorim 2002, Schuh & Brower 2009).

Now, taking into account the congruencies among those cladograms in Figures 1A, B and 2B, C, one can conclude that, regardless of intragroup resolution, *S. pomarinus* does belong to a clade with *Catharacta.* As seen above, this is just the conclusion that authors have come to (Cohen *et al.* 1997, Braun & Brumfield, 1998, Andersson, 1999a, b). Assuming the most inclusive nodes (*i.e.*, those including the common ancestor of all terminal taxa) of Figures 1A, B and 2C (the most inclusive node of Figure 2B is unresolved, but note that *S. pomarinus* is monophyletic with *C. skua*) to be ranked at the family level, as a wealth of evidence indicates (*e.g.*, Furness 1996, Chu *et al.* 2009, Ericson *et al.* 2003), then in a cladistic-based classification by sequencing, the two lineages branching from those nodes should be assigned to different genera, *contra* Andersson's (1999b) proposal of a single genus, but concurrent with his "alternative" suggestion to transfer *S. pomarinus* to *Catharacta*. Indeed, the only topology in which all terminal taxa would be given the same genus is that recovered by Chu *et al.* (2009: 616).

Stercorarius was introduced by Brisson (1760, 1: 56; 6: 149), with type species *Stercorarius* (Le Stercoraire) Brisson = *Larus parasiticus* Linnaeus, 1758, by tautonomy (*fide* Peters 1934, Hellmayr & Conover 1948). Therefore, both *S. parasiticus* and *S. longicaudus* can retain their generic name. The oldest name on genus level for the other clade, containing *S. pomarinus* and the *Catharacta* species, is *Catharacta* Brünnich (1764: 32) – type-species: *C. skua* Brünnich, by subsequent designation of Reichenbach (1852: v). Accordingly, *S. pomarinus* should be transferred to *Catharacta* as *C. pomarina*, a combination used previously by Mathews (1912: 182). The specific epithet was changed to "*pomarina*" to agree with the gender of the genus, as required by article 34.2

of the International Code of Zoological Nomenclature ("The Code"; ICZN 1999).

As mentioned above, Braun & Brumfield (1998) recommended to place *C. pomarina (= S. pamarinus)* in *Coprotheres*. According to them (p. 998), "[t]his treatment would have the advantage of recognizing the morphological distinctiveness that separates *[S.] pomarinus* from *Catharacta*". However, emphasizing the "distinctiveness" of a given taxa from, rather than its "similarities" with, its closest-related taxon/taxa is not strictly consistent with the cladistic principles, as proposed by Hennig (1968 [1955]). Instead, this is a way of thinking that recalls that of the gradistic school of systematic, which, in classifying taxa above the species-group level, also attempts to express the so-called degree of divergence among organisms (*e.g.*, Mayr 1969).

A few words are pertinent here in order to explain why the sequencing method was chosen in place of that by subordination. The subordination approach, though more precise from a nomenclatural standpoint, has two main disadvantages. Firstly, it often requires the use of too many Linnaean categories to represent every branching in a cladogram; and secondly, it often results in many redundant taxa (*i.e.*, a monotypic taxon at several levels). Because the sequencing approach requires a lower number of Linnaean categories, and also results in much less redundancy of names (Amorim 2002, Schuh & Brower 2009), it is better suited for classifying taxa in the family, genus, and species groups, whose nomenclature is governed by "The Code" (ICZN 1999). In zoology, the number of categories at these levels is extremely restricted (a total of eight from superfamily to species); therefore, depending on the quantity of taxa included in an analysis, the subordination method alone is simply not feasible (Amorim 2002, Schuh & Brower 2009).

A cladistic-based classification by sequencing of Stercorariidae derived from Braun & Brumfield's (1998) hypothesis, which is congruent with results of Andersson (1999a, b), would be as follows:

Stercorariidae Gray, 1871
  Stercorarius Brisson, 1760
    S. parasiticus (Linnaeus, 1758)
    S. longicaudus Vieillot, 1819
  Catharacta Brünnich, 1764
    C. pomarina (Temminck, 1815)
    C. skua Brünnich, 1764, *sedis mutabilis*
    C. maccormicki (Saunders, 1893), *sedis mutabilis*
    C. lonnbergi Mathews, 1912, *sedis mutabilis*
    C. hamiltoni (Hagen, 1952), *sedis mutabilis*
    C. chilensis (Bonaparte, 1857), *sedis mutabilis*
    C. antarctica (Lesson, 1831), *sedis mutabilis*

Note that taxa are arranged in a sequence that reflects their postulated sister-group relationships. Thus, in the classification above, *C. pomarina* is the sister taxon to an unresolved clade containing the other six species in *Catharacta* (*cf.* Figure 1B). Wiley (1981) proposed the term "*sedis mutabilis*" ("of changeable seating") to indicate when a taxon are part of a politomy.

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