

Reflections on the Phylogenetic Position and Generic Status of Abbott's Booby *Papasula abbotti* (Aves, Sulidae)

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Abstract

Introduction: I here comment on the phylogenetic position and generic status of the rare and threatened Abbott's Booby *Papasula abbotti*. I argue that the current genus name of this species was erected from an incorrect interpretation of a phylogenetic hypothesis and a straightforward decision about its generic placement cannot be made, given the conflicts regarding the species' closer phylogenetic relationships.

Methods: I examined three published hypotheses of phylogenetic relationships for Sulidae (one based on phenotypic and two on molecular data), following Hennig's principle of reciprocal illumination, wherein a given hypothesis is evaluated by the extent to which it agrees with competing hypotheses.

Results and discussion: There is a considerable degree of congruence among the examined cladograms, the main conflict being the position of Abbott's Booby. Therefore, for the time being, I propose that in any cladistic-based classification the name '*Sula abbotti*' be placed at the level at which their relationships are more surely determined (i.e., below the family name and above *Sula* and *Morus* and labelled as 'incertae sedis') or the name *Papasula* be considered as a subgenus.

Keywords: Cladistics; Classification; Nomenclature; Seabird

Short Communication

Phylogenetic systematics, or cladistics, as proposed by Hennig [1] and developed by others [2] has become the most accepted and widely used method for inferring the evolutionary relationships among organisms. Therefore, biological classifications are expected to reflect as much as possible relationships as recovered by cladistic analyses. Nevertheless, due to several reasons, but overall because of the subjectivity of the Linnaean hierarchical system and its lack of adherence to the evolutionary paradigm, classifications did not follow the fast pace of systematics in late 20th century [3-6]. In ornithology, for example, despite earlier efforts by authors like Cracraft [7,8], the strict use of cladograms in proposing classifications has become a standard only in the last 10-15 years [9-11].

The most important principle of a cladistic-based classification is that all taxa must be monophyletic; furthermore, the relationships between sister-groups are always promptly recognized. Thus far, there are two ways for transposing information from cladograms to hierarchical classifications. The first, proposed by Hennig [1], is called 'subordination'. In this approach, each branching level in a cladogram receives a designation; moreover, and importantly, sister-taxa are always given the same taxonomic rank. In the second approach, the '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 [12,13]. These approaches have their arguments for and against; nevertheless, they are, alone or in combination, objective tools for the purpose they were devised for [4,6,13,14].

That said, I here comment on the phylogenetic position and generic status of the rare and threatened Abbott's Booby, *Papasula abbotti*. The points I shall make herein are: (1) the current genus name of this species, although supposedly erected in a cladistic context, has been proposed from a perspective closer to that of the gradistic school of systematics, which also attempts to express the so-called 'degree of divergence' among organisms [15]; and (2), a straightforward decision about its generic placement cannot be made, given the conflicts regarding the species' closer phylogenetic relationships.

Sulidae is a monophyletic family that currently includes three extant genera: *Sula*, *Morus*, and *Papasula*. Whilst the two first-named taxa respectively comprise six and three species, the latter is monotypic, being represented only by Abbott's Booby [16-19].

Besides being the sole representative of its genus, Abbott's Booby is also the rarest Sulidae. This seabird has a small population that breeds in a limited area of the Australian territory of Christmas Island, in the eastern Indian Ocean, though it formerly had a much wider breeding distribution over both Indian and Pacific Oceans [16,17,20,21]

Ridgway [22] firstly described Abbott's Booby as a member of *Sula*, where it remained until Olson and Warheit [23] proposed a new genus name for it, based on the following rationale:

Our studies of the osteology of the Sulidae confirm the distinctiveness of *Sula abbotti* and show it to be the primitive sister-group of all the remaining Sulidae

Sula abbotti possesses numerous derived characters within the Sulidae that, by themselves, would not necessarily require the erection of a new genus. However, because the species lacks other derived characters that are shared by *Morus* and *Sula*, it forms a separate

primitive clade and thus, if *Morus* and *Sula* are each recognized at the generic level, which we believe is the correct treatment, then a new genus is needed for *Sula abbotti* as well [23].

Olson and Warheit [23], however, did neither present the cladogram from where their taxonomic conclusions have been drawn nor give a reference for it. Nevertheless, I inferred from Smith [18] that such a cladogram was probably taken from the still-unpublished K. I. Warheit's 1990 Ph.D. Dissertation, which was in preparation by the time Olson and Warheit's [23] paper was published. I was unable to obtain a copy of said dissertation, but its abstract reads: 'I established a phylogenetic hypothesis for the relationships within the Sulidae [b]ased on numerical cladistic methods, using 124 discrete skeletal characters. I showed that within the Sulidae, Recent gannets (*Morus* spp.) and Recent boobies (*Sula* spp.) [sic] are each monophyletic. I also showed that Abbott's Booby (*Papasula abbotti*) is more closely related to *Sula* than to *Morus*.' I conclude that, from this excerpt, what Warheit means is that *Sula* and *Papasula* were sister-taxa to each other, and together they form the sister-group to *Morus*. My conclusion is supported by Smith [18] who, in his cladistic analysis of Pelecaniformes (*Iato sensu*), recovered those same relationships within Sulidae, and even stated (p: 20) that '*Papasula abbotti* is resolved as the sister taxon to *Sula* in the present analysis identical to the topology recovery by Warheit [190].'

It appears to me that Olson and Warheit [23] viewed a cladogram as a 'ladder of evolutionary progress' wherein the 'species-poor' sister group or branch is referred to as 'basal' or, as they [23] themselves says, 'primitive', and misinterpreted as having characters of the common ancestor. In a cladogram, all terminal taxa exhibit a mix of plesiomorphic and apomorphic character states and no objective reason exists to assume that a 'species-poor' lineage has more plesiomorphies than its 'species-rich' sister lineage [24]. The so-called 'basal-position' within an ingroup exactly means sister to the remaining taxa [24-26].

Olson and Warheit [23] listed some derived character states present in *Sula* and *Morus*, but not in Abbott's Booby (e.g., the reduced and bifurcated postorbital process, the temporal fossae meeting along the midline of the skull), which are better interpreted as homoplastic. Furthermore, the derived character states present exclusively in Abbott's Booby (e.g., the broad and bilobate paraoccipital process of the exoccipital, the laterally compressed humerus shaft; [23]) do not convey grouping information; instead, they serve to diagnose the species from other congeners.

Taking that part of Smith's [18] cladogram depicting the relationships among Sulidae (reproduced herein as Figure 1A) and assuming that the most inclusive node (i.e., that comprising the common ancestor of all terminal taxa) is to be ranked at the family level, a cladistic classification by sequencing would appear as follows:

Sulidae Reichenbach, 1849

Sula Brisson, 1760

S. abbotti Ridgway, 1893 Abbott's Booby

S. sula Linnaeus, 1766 Red-footed Booby

S. leucogaster (Boddaert, 1783) Brown Booby

S. dactylatra (Lesson, 1831) Masked Booby

S. variegata (Tschudi, 1843) Peruvian Booby

S. neboxi Milne-Edwards, 1882 Blue-footed Booby

Morus Vieillot, 1816

M. serrator Gray, 1843 Australasian Gannet

M. bassanus (Linnaeus, 1758) Northern Gannet

M. capensis (Lichtenstein, 1823) Cape Gannet

Notice that the taxa are arranged in a sequence that reflects their postulated sister-group relationships. Thus, in the classification above, '*S. abbotti*' is the sister-taxon to the clade containing all five species below it; *S. sula* is the sister-taxon to (*S. leucogaster* + (*S. dactylatra* + (*S. variegata* + *S. neboxi*))); *S. leucogaster* is the sister taxon to (*S. dactylatra* + (*S. variegata* + *S. neboxi*)); and *S. variegata* and *S. neboxi* are sister species to each other (Figure 1A). I should stress that despite differences in style (i.e., diagonal vs. rectangular branches) and position (one is rotated 90 degrees to the other) both the cladogram in Figure 1A and that of Smith [18] show the very same phylogenetic relationships.

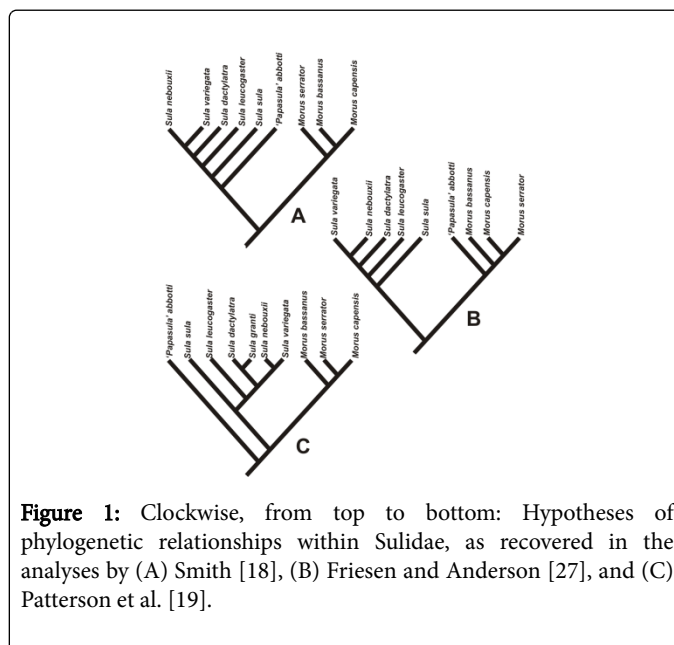


Figure 1: Clockwise, from top to bottom: Hypotheses of phylogenetic relationships within Sulidae, as recovered in the analyses by (A) Smith [18], (B) Friesen and Anderson [27], and (C) Patterson et al. [19].

I think it is pertinent here to explain why I chose the sequencing method. The subordination approach, although nomenclature more precise, has two main disadvantages. Firstly, it often requires the use of too many Linnaean categories to represent every branching in a cladogram, and secondly, often results in many redundant taxa (i.e., a monotypic taxon at several levels; [6]). Because the sequencing approach requires a lower number of categories and results in much less redundancy of names [4,13,14], it is better suited for classifying taxa in the family, genus, and species groups, whose nomenclature is governed by International Code of Zoological Nomenclature [26]. In zoology, the number of categories at these levels is restricted (eight from superfamily to species); therefore, depending on the number of taxa, the subordination method alone is not feasible [4,13].

The phylogenetic relationships among Sulidae have also been investigated using cladistic analyses of molecular datasets. Friesen and Anderson [27] and Patterson et al. [19] published hypotheses based on, respectively, 807 base pairs of mitochondrial DNA cytochrome *b* sequences and five nuclear intron loci plus the complete mitochondrial

cytochrome *b* sequences. In the first study, Abbott's Booby was recovered as sister-taxon to a clade containing Australasian, Northern, and Cape Gannets (Figure 1B), whereas in the second, it was resolved as the sister-taxon to a clade comprising all other species (Figure 1C).

In a classification by the sequencing method [12,13] from Friesen and Anderson's [27] cladogram, Abbott's Booby would be transferred to *Morus*. On the other hand, the Patterson [19] cladogram would be translated into a classification wherein Abbott's Booby is monotypic at subfamily, genus, and species levels:

Sulidae Reichenbach, 1849 180

'Subfamily A-inae' [*Papasula abbotti*' (Ridgway, 1893)]

'Subfamily B-inae'

Sula Brisson, 1760

S. sula Linnaeus, 1766

S. leucogaster (Boddaert, 1783)

S. dactylatra (Lesson, 1831)

S. granti Rothschild, 1902 Nazca Booby

S. neboxi Milne-Edwards, 1882

S. variegata (Tschudi, 1843)

Morus Vieillot, 1816 190

M. bassanus (Linnaeus, 1758)

M. serrator Gray, 1843

M. capensis (Lichtenstein, 1823)

To avoid confusion, since I am not concerned with formally revising the taxonomy of Sulidae, no names were proposed for those 'hypothetical' subfamilies in the scheme immediately above. Furthermore, with respect to Abbott's Booby, the generic name alone was omitted by following the suggestion of Christoffersen [28] that, in case of redundancy, the name of the most inclusive taxon should be only followed by the name, in square brackets, of the least inclusive taxon.

When comparing the cladograms in Figure 1, we see that despite differences in the terminals, type of evidence (phenotypic vs. molecular data), and optimality criteria (Maximum parsimony, Neighbor-joining, and Bayesian inference), there is a considerable degree of agreement among them in terms of phylogenetic relationships. The main incongruence is the position of Abbott's Booby Figure 1A-C.

Vogt [29,30] has recently argued that Karl Popper's hypothetico-deductive method and falsificationism are not applicable to cladistics [31]. According to Popper [32], a hypothesis is falsifiable if it prohibits at least one event that is not prohibited by the background knowledge. However, as observed by Vogt [29] '[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. 'Put in other way, in the analysis of a taxon/character matrix, when a hypothesis of primary homology [33] is not congruent with the others, it is not refuted in a strict Popperian

way, but parsimoniously explained as homoplasy. Naturally, a similar reasoning applies to the analysis of a multiple sequence alignment.

A cladistic hypothesis is a statement about the phylogenetic relationships represented by the best option given the data available, but subject to confrontation with additional hypotheses, especially those drawn from different sources. Therefore, as pointed out by Santos and Capellari [34], cladograms can be compared against each other to find congruencies among them. The idea behind such a comparison is similar to Hennig's [1] method of 'reciprocal illumination', wherein 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 better explanatory power 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 [34].

Patterson et al. [19] argued that incomplete lineage sorting and long-branch attraction have probably confounded the phylogenetic placements of Abbott's Booby as the sister-taxon to the *Morus* clade in the analysis by Friesen and Anderson [27]. Nevertheless, even regarding this relationship as 'less likely' due to problems in using mitochondrial DNA alone to infer phylogenetic relationships, there remains the conflict between Smith's [18] and Patterson et al. 's [19] cladograms.

I should mention at this point that, although being an important aspect of cladistic analysis, measures of clade support cannot be viewed as empirical tests for the hypothesized relationships; instead, they only evaluate the relative strength of evidence. All clades present in a consensus cladogram are supported by the available evidence. Therefore, degree of support per se does not provide rational bases for confidence or 'disbelief' in a clade as more probable, reliable or worthy of taxonomic recognition [35,36].

Therefore, if further analyses, especially those based on different evidences, confirm the findings of Patterson [19] then, the originally unnecessarily-coined name *Papasula* would be available for the species under discussion. However, for the time being, I propose to follow the recommendation of Patterson and Rosen [37] that taxa of uncertain position should be placed at the level at which their relationships are more surely determined and labelled as '*incertae sedis*'. Thus, in a cladistics classification, '*Sula abbotti*' would be listed just below the family name and above *Sula* and *Morus*, to make clear that there is still conflicting information regarding the species' close phylogenetic affinities. Other solution, perhaps less orthodox, is to propose *Papasula* as a subgenus to include Abbott's Booby, although this does not reflect any particular hypothesis on the species' phylogenetic affinities.

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Conflict of Interest

The author confirms that this article content has no conflict of interest.

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