Molecular Phylogenetics and Evolution 97 (2016) 170-176

Contents lists available at ScienceDirect





Molecular Phylogenetics and Evolution

journal homepage: www.elsevier.com/locate/ympev

Phylogenetic affinities of the *Fregetta* storm-petrels are not black and white ${}^{\bigstar}$



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ARTICLE INFO

Article history: Received 15 April 2015 Revised 20 December 2015 Accepted 10 January 2016 Available online 20 January 2016

Keywords: Phylogeny Fregetta storm-petrels Cytochrome b gene β-fibrinogen gene Procellariiformes South Atlantic Ocean

ABSTRACT

The *Fregetta* storm-petrels generally are regarded to comprise two species: black-bellied storm-petrels *F. tropica* (monotypic) breed at Antarctic and sub-Antarctic islands (46–63°S), and white-bellied storm-petrels *F. grallaria* breed at south temperate islands (28–37°S), with four recognized subspecies. Confusion surrounds the status of birds at Gough Island (40°S), central South Atlantic, which have been attributed usually to a white-bellied form of black-bellied storm-petrel *F. t. melanoleuca*. We use cyto-chrome *b* and nuclear β -fibrinogen gene sequences to show that *F. t. melanoleuca* are present during the breeding season at Gough and islands in the nearby Tristan da Cunha archipelago (37°S), exhibiting limited divergence from *F. t. tropica*. We also show that there is greater diversity among *F. grallaria* populations, with eastern South Pacific *F. g. segethi* and *F. g. titan* differing by c. 0.011, and both differing from western South Pacific nominate *f. g. grallaria* by c. 0.059. The Tristan archipelago supports a population of *F. grallaria* closely allied to the nominate form, as well as a distinct form identified as *F. g. leucogaster*. Further research is needed to assess how *F. grallaria* and *F. tropica* segregate in sympatry at Tristan and Gough, and why this is the only location where both species have white-bellies.

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1. Introduction

The storm-petrels of the Southern Hemisphere genus *Fregetta* Bonaparte (sub-family Oceanitinae) traditionally contains two species (e.g. Jouanin and Mougin, 1979;): the black-bellied storm-petrel, *F. tropica* (Gould, 1844) that breeds in the Antarctic and sub-Antarctic; and the temperate-breeding white-bellied storm-petrel, *F. grallaria* (Vieillot, 1818). The taxonomy of the *Fregetta* storm-petrels has been debated vigorously over the last 100 years (e.g. Salvadori, 1908; Mathews, 1933; Murphy and Snyder, 1952), with various sub-specific designations proposed and revised (Mathews, 1933; Murphy and Snyder, 1952), and confusion remains as to whether a white-bellied form of *F. tropica* exists on

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Gough Island (40°S, 10°W) in the mid-South Atlantic (Clancey, 1981; Brooke, 2004; Ryan, 2007). Robertson et al. (2011) showed using phylogenetic analyses that the New Zealand storm-petrel (*Oceanites maorianus*) is not an *Oceanites*, but is better placed with *F. grallaria* and *F. tropica* in the genus *Fregetta*, and suggested the name *Fregetta maoriana*. Recently, Cibois et al. (2015) clarified the identity of an unusual '*pealea*' specimen (American Museum of Natural History 194110) collected off the Marquesas Islands, concluding that it was closely related to the *F. grallaria* clade but that its exact placement was uncertain. They also suggested that *F. grallaria* was not monophyletic, based on a short cytochrome *b* sequence from a Natural History Museum, London, specimen (1953.55.101) collected on Gough Island and assigned to *F. g. leucogaster*.

Fregetta taxonomy has been based on various morphological characters (Marchant and Higgins, 1990; Stephenson et al., 2008) including chin and throat feather coloration (bases white in

 $^{^{\}star}$ This paper was edited by the Associate Editor Edward Louis Braun.

F. tropica, not in *F. grallaria*; but see Stephenson et al., 2008); toe projection beyond the tail tip in flight (absent in *F. grallaria*; but see Howell, 2010); tarsal scale pattern (holothecal in *F. tropica*, scutellated in *F. grallaria*); morphometrics (bill, tarsus, toes longer in *F. tropica*; wings relatively longer in *F. grallaria*); and toe morphology and symmetry (Marchant and Higgins, 1990; Stephenson et al., 2008). Various combinations of these characters have been used in revisions of *Fregetta* taxonomy (Salvadori, 1908; Kinghorn and Cayley, 1922; Mathews, 1932a, 1933; Murphy and Snyder, 1952). However, many of the early taxonomic revisions were based on the examination of single specimens of unknown breeding provenance (Murphy, 1936; Murphy and Snyder, 1952).

Recently several researchers have called for a revision of *F. grallaria*, suggesting that some subspecies might warrant full species status due to plumage and morphological differences (e.g. Stephenson et al., 2008; Howell, 2014). Currently, four subspecies are recognized for *F. grallaria* (nominate *grallaria*, *titan*, *segethi* and *leucogaster*) and one or two subspecies for *F. tropica* (nominate *tropica* and *melanoleuca*), depending on the status of the Gough population (cf. Marchant and Higgins, 1990; Brooke, 2004; Onley and Scofield, 2007; Dickinson and Remsen, 2013). *F. g. grallaria* breeds on the Lord Howe islands (32°S, 159°E) in the Tasman Sea, and the

Kermadec Islands (29°S, 178°W) north of New Zealand (Fig. 1). The nominate form is unusual in being polymorphic, with some blackbellied forms at Lord Howe islands (Fig. 2; Marchant and Higgins, 1990) and a less extensive degree of polymorphism at the Kermadec Islands (Tennyson and Taylor, 1990). F. g. titan of Rapa Island (28°S, 144°W) in the Austral Islands, French Polynesia, was defined on size, being larger than F. g. segethi from the Juan Fernandez Islands (34°S, 81°W) in the eastern South Pacific (Murphy, 1924, 1928). Finally, F. g. *leucogaster* breeds at the Tristan da Cunha group (37°S, 12°W) and perhaps Gough Island (Brooke, 2004) in the central South Atlantic, and a tiny relict population breeds at St Paul Island (39°S, 77°E) in the southern Indian Ocean (Tollu, 1984; Worthy and Jouventin, 1999). This form probably also bred at nearby Amsterdam Island (38°S, 77°E) prior to the arrival of rats and other introduced mammals (Worthy and Jouventin, 1999). F. t. tropica breeds in three regions further south than F. grallaria (Brooke, 2004): at sub-Antarctic islands south of New Zealand (Auckland, Antipodes and Campbell, 49–52°S) and in the southwest Indian Ocean (Kerguelen, Crozets and the Prince Edwards, 46-50°S), and at peri-Antarctic islands in the South Atlantic and Scotia Sea area (South Georgia, South Orkneys, South Shetlands, Bouvet and probably the South Sandwich Islands, 54-63°S).



Fig. 1. Sampling locations of the New Zealand storm-petrel *Fregetta maoriana* (pentagon), white-bellied storm-petrels *F. grallaria* (circle) and black-bellied storm-petrels *F. tropica* (square) used in the analysis. Open symbols are breeding locations not sampled in this study.

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