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Source: Bulletin of the British Ornithologists' Club, 142(1) : 111-130

Published By: British Ornithologists' Club

URL: <https://doi.org/10.25226/bboc.v142i1.2022.a6>

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Fregetta lineata (Peale, 1848) is a valid extant species endemic to New Caledonia

by Vincent Bretagnolle, Robert L. Flood, Sabrina Gaba & Hadoram Shirihai

Received 14 September 2021; revised 3 January 2022; published 11 March 2022

<http://zoobank.org/urn:lsid:zoobank.org:pub:B48F3D74-2BFE-49A1-A560-C5E59CF8FD18>

SUMMARY.—We present evidence that confirms the streaked *Fregetta lineata* is a valid extant species that breeds on New Caledonia and endorse the vernacular name New Caledonian Storm Petrel. We review taxonomic deliberations over the historic five ‘Pealea’ streaked storm petrel specimens. Three belong to the recently rediscovered New Zealand Storm Petrel *F. maoriana*. We study six biometrics of the other two identical-looking specimens, one from Samoa, the other from the Marquesas Islands, a third ‘new’ specimen collected off Brisbane, and other *Fregetta* taxa. Results of Principal Component Analyses, Discriminant Analyses, and a review of phylogenetic relationships between *Fregetta* storm petrels, *F. lineata* and *F. maoriana*, lead us to conclude that the three specimens represent a single taxon, *F. lineata*. Furthermore, *F. lineata* is clearly separated from *F. maoriana*, White-bellied Storm Petrel *F. grallaria* and Black-bellied Storm Petrel *F. tropica*. We further conclude that storm petrels photographed at sea, off New Caledonia and in the Coral Sea, are *F. lineata*. We then redescribe *F. lineata* from at-sea observations, photographs taken at sea, and study of the three museum specimens. Criteria for in-hand and at-sea identification are presented. We report the first breeding record, from New Caledonia, a grounded fledgling presumably disoriented by onshore artificial lights. We explore likely breeding locations and conservation issues.

A remarkable turn of events in recent research into Procellariiformes is recognition that five museum specimens of similar-looking streaked storm petrels, collected during natural history expeditions to the Pacific Ocean during 1827–1922, represent two ‘new’ taxa, not plumage variants of known species as argued by Murphy & Snyder (1952). ‘Streaked storm petrel’ refers to black-and-white storm petrels distinctly marked with dark streaks on a white belly. Events are all the more remarkable given that the specimens represent populations of two taxa, one discovered in 2003, the other in 2008, both of which are easily located at sea.

The puzzle of one of these taxa—the New Zealand Storm Petrel *Fregetta maoriana*, accounting for three of the historic specimens, was largely resolved over a ten-year period as follows. Two if not all three of the specimens were taken in northern New Zealand in the 19th century (Bourne & Jouanin 2004, Bourne *et al.* 2004, Medway 2004). The first sightings, in 2003, were off the Coromandel Peninsula and in the Hauraki Gulf, North Island, New Zealand (Flood 2003, Saville *et al.* 2003, Stephenson *et al.* 2008a). The first live captures, in November 2005 and January 2006, in the Hauraki Gulf, confirmed the identity (Stephenson *et al.* 2008b), and the New Zealand Rare Birds Committee accepted *F. maoriana* as a valid extant species (Scofield 2007). Breeding was confirmed in 2013 on Little Barrier Island, Hauraki Gulf (Fig. 1; Rayner *et al.* 2015, Tennyson *et al.* 2016). Conservation measures are underway.

The same process of puzzle-solving for the second taxon, New Caledonian Storm Petrel (undescribed), however, has faltered. The first sighting was in 2008 off southern New Caledonia (Howell & Collins 2008), with additional observations there in subsequent years

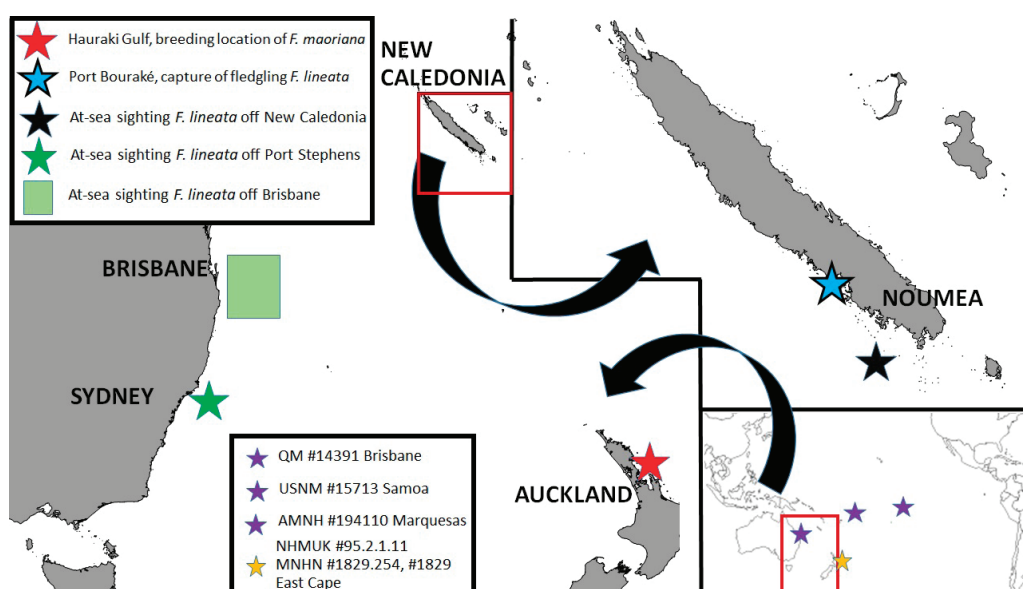


Figure 1. Map showing all locations mentioned in the text, including the breeding location of New Zealand Storm Petrel *F. maoriana*; and the locations where specimens of New Caledonian Storm Petrel *F. lineata* were collected, at-sea sightings made, and the fledgling found. There has been discussion about the origin of the specimen NHMUK 1895.2.11.1 (Galbreath 2018).

(Fig. 1; Collins 2013). The birds look similar to New Zealand Storm Petrel, but are larger and were thus presumed to be an undescribed taxon (Collins 2013). Since 2011, identical-looking streaked storm petrels have been seen regularly in the Coral Sea off eastern Australia (Fig. 1; Appendix 1 summarises all sightings known to us, 2008–21). The New Caledonian and Coral Sea storm petrels are widely assumed to be the same taxon (e.g., Howell & Zufelt 2019). However, it is not known if the two-remaining identical-looking streaked storm petrel specimens, one collected in Samoa, the other in the Marquesas, represent this taxon. Attempts to capture live birds in 2013 and 2014 were unsuccessful (C. Collins *in litt.* 2013, P. Harrison *in litt.* 2014). No findings have been published for a bird captured in the Coral Sea on 13 April 2014. The breeding location is a mystery. BirdLife Australia has deferred decisions on submissions of streaked storm petrels until the taxonomy of New Caledonian and Coral Sea storm petrels is resolved (T. Palliser *in litt.* 2021). There are no conservation measures in place.

This manuscript largely resolves the puzzle of the New Caledonian Storm Petrel. To this end, we summarise and reassess previous work on the ‘Pealea phenomenon’ (the five streaked storm petrel museum specimens, plus a newly discovered sixth specimen), discuss the taxonomy of the six specimens and *Fregetta* storm petrels in relation to biometry and genetic sequences; and conclude that the three unclassified specimens, and the New Caledonian and the Coral Sea storm petrels, are one and the same species, *Fregetta lineata* (Peale 1848). We then describe its characteristics, offer guidance for in-hand and at-sea identification, provide the first evidence of breeding, on New Caledonia, and highlight conservation priorities for this almost certainly globally threatened species.

The ‘Pealea’ storm petrels

The five streaked storm petrel specimens (Fig. 2) have been the subject of much controversy and confusion over the last 70 years (Murphy & Snyder 1952, Cibois *et*



Figure 2. The five historic and one recently discovered museum specimens of New Caledonian Storm Petrel *Fregetta lineata* and New Zealand Storm Petrel *F. maoriana*. (A) *F. lineata*, collected 1839, perhaps 23–25 November, Samoa by T. R. Peale during the US Explorer Expedition, held at National Museum of Natural History, Washington DC (USNM 15713). (B) *F. lineata*, collected 15 September 1922, presumably at sea, off Ua Pou Island, Marquesas Islands by R. H. Beck during the Whitney South Seas Expedition, held at American Museum of Natural History, New York (AMNH 194110). (C) *F. maoriana*, collected January–March 1827 by Quoy & Gaimard (1830) during first voyage of the *Astrolabe*, held at Museum national d'Histoire naturelle, Paris (MNHN C.G. 1829.254 (14393), C.G. 1829 (14372)). (D) *F. maoriana*, presented by George Carrick Steet of London in February 1895, possibly collected in the Hauraki Gulf, New Zealand (Bourne *et al.* 2004), held at the Natural History Museum, Tring (NHMUK 1895.2.11.1). (E) *F. lineata* (left) and Black-bellied Storm Petrel *F. tropica* (right), beach-cast, Stradbroke Island, Brisbane, Queensland, Australia, held at Queensland Museum, Brisbane (respectively, QM 14391 collected July 1973; and QM 31216, collected 22 May 1999) (Vincent Bretagnolle, except D: Mark Adams, © Natural History Museum, London)

al. 2015, Robertson *et al.* 2016). Their unique streaked appearance gave rise to the term 'Pealea phenomenon'. The specimens have been variously assigned to five genera, *Thalassidroma* Gould, 1844, *Fregetta* Bonaparte, 1855, *Pealea* Ridgway, 1886, *Fregettornis* Mathews, 1914, and *Pealeornis* Mathews, 1932, based on morphometrics and details of foot structure (measurements of all five specimens in Appendix 2).

Murphy & Snyder (1952) concluded that the three New Zealand specimens 'maoriana' were pale-morph Wilson's Storm Petrels *Oceanites oceanicus*, that the Samoan specimen 'lineata' was an aberrant Black-bellied Storm Petrel *Fregetta tropica*, and that the Marquesan specimen 'guttata' was an aberrant White-bellied Storm Petrel *F. grallaria*. This taxonomic treatment collapsed with the rediscovery of, and realisation that, New Zealand Storm Petrel *F. maoriana* is a valid species that accounts for the New Zealand specimens (Robertson *et al.* 2011, Robertson *et al.* 2016).

The status of the other two specimens remained an open question. However, it became apparent that they bear strong resemblance to the New Caledonian and Coral Sea storm petrels. The oldest of the two specimens was collected in 1839 at Samoa by T. R. Peale (hence 'Pealea phenomenon') during the US Explorer Expedition. It is held at the National Museum of

Natural History, Smithsonian Institution, Washington DC (USNM 15713). The specimen was described as a new species *Thalassidroma lineata* (Peale 1848, and in Cassin 1858). Mathews (1933) placed this taxon in *Pealea*. The original description (see Cassin 1858: 403–405) includes a drawing by Peale, also reproduced in Bourne (2008), of an underwing pattern that we will demonstrate below is diagnostic of New Caledonian Storm Petrel.

The other specimen was collected on 15 September 1922, presumably at sea, off Ua Pou Island, Marquesas Islands, by R. H. Beck during the Whitney South Seas Expedition. It is at the American Museum of Natural History, New York (AMNH 194110). The specimen was described as a new species *Fregetta guttata* (Murphy 1930) and was subsequently placed in *Fregetornis* (Mathews 1933). Both Mathews and Murphy argued that these two specimens differ notably, but only on the basis of foot structure (Murphy 1930, Mathews 1933).

There is a third, ‘new’ (recently discovered), specimen. During a visit in 2017 to Queensland Museum in Brisbane, VB found two storm petrel specimens with dark markings on a white belly (QM 31216 and QM 14391; biometrics in Appendix 2; Fig. 2). Both were labelled Black-bellied Storm Petrel *F. tropica*. They are beach-cast specimens collected on Stradbroke Island, off Brisbane. The dark belly markings qualify them as candidate *F. lineata*. However, one has dark streaks, whereas the other appears more like *F. tropica*, having dark spots, although its belly feathers are heavily abraded.

The next section presents multivariate analyses of six biometrics of *Fregetta* museum specimens. Analyses incorporate the two specimens from Brisbane and those from Samoa and the Marquesas. The aim is to investigate how the specimens and species relate to one another.

Multivariate analyses of *Fregetta* and suspected *F. lineata* specimens

We conducted a series of multivariate analyses on six biometrics: bill width, bill depth at gonys; and culmen, wing, tail and tarsus lengths. The sample ($n = 261$) comprised adults collected at colonies, held at museums worldwide, and measured by VB. Mean measurements are shown in Fig. 3. Analyses were conducted using the packages FACTORMINE and MASS from R software. Biometric characters were centred and scaled prior to analyses.

Principal Component Analyses.—Principal Component Analysis (PCA) was performed as a descriptive multivariate analysis. In the first PCA, specimens from breeding archipelagos were grouped and averaged, including *F. tropica* (11 populations), small White-bellied Storm Petrels *F. grallaria* (six populations), the large *F. [g.] titan* (from Rapa Island), and *F. maoriana* (from New Zealand). The two Brisbane specimens and the specimens ‘*lineata*’ from Samoa and ‘*guttata*’ from Ua Pou were treated individually. Results are shown in Fig. 4A. The first principal component (Dim 1; Fig. 4A) was a body size axis (especially wing length; see Fig. 5). Dim 1 clearly separates the smallest *F. maoriana* (purple) from the largest *F. [g.] titan* (blue). *F. tropica* (green) and *F. grallaria* (orange and red) were fairly evenly spread, with *F. grallaria* having an overall smaller size and notably shorter tarsi, although some individuals (mainly from the western Pacific, but also the South Atlantic) had tarsi nearly as long as *F. tropica* (Fig. 3). QM 31216 (light green) clumped with *F. tropica* (dark green), whilst QM 14391 clumped with ‘*lineata*’ and ‘*guttata*’ (black). All three were at the small end of the size range of *F. grallaria*, having slightly shorter wings, a shorter tail than other *Fregetta* (but longer than *F. maoriana*), and tarsus length intermediate between *F. tropica* and *F. grallaria* (Fig. 3). This morphometric analysis supports the separation of *F. maoriana*, highlights the distinctiveness of the ‘*lineata*, *guttata*, QM 14391’ specimens within *F. grallaria*, and aligns QM 31216 with *F. tropica*.

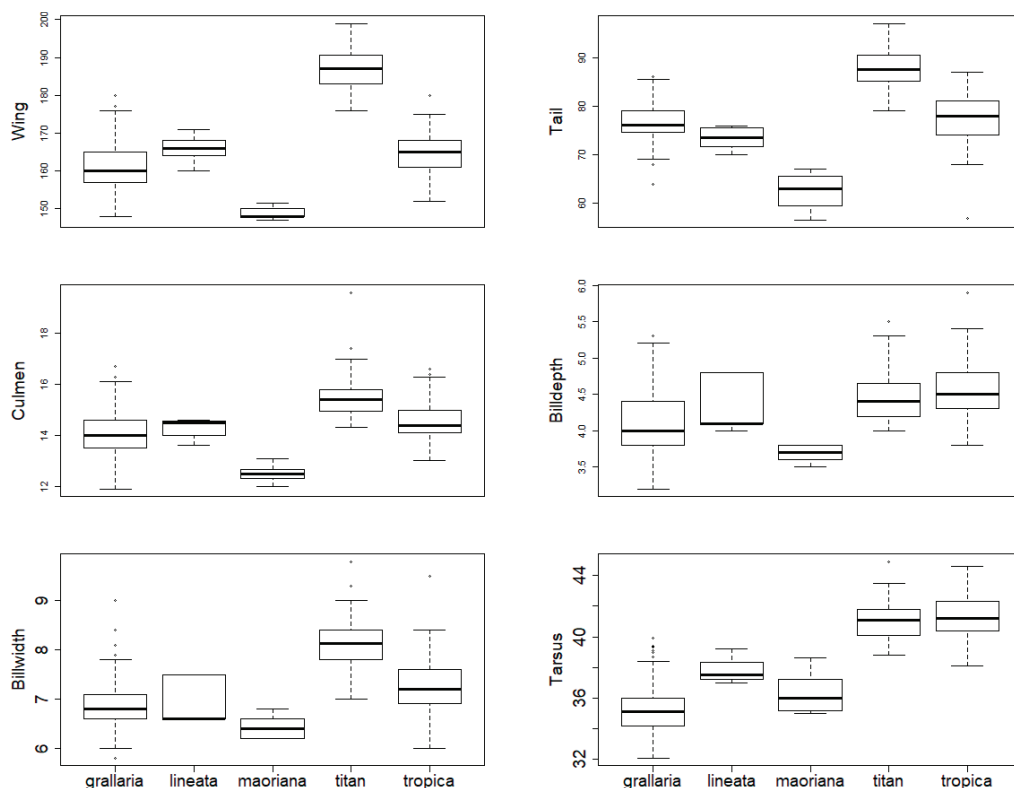
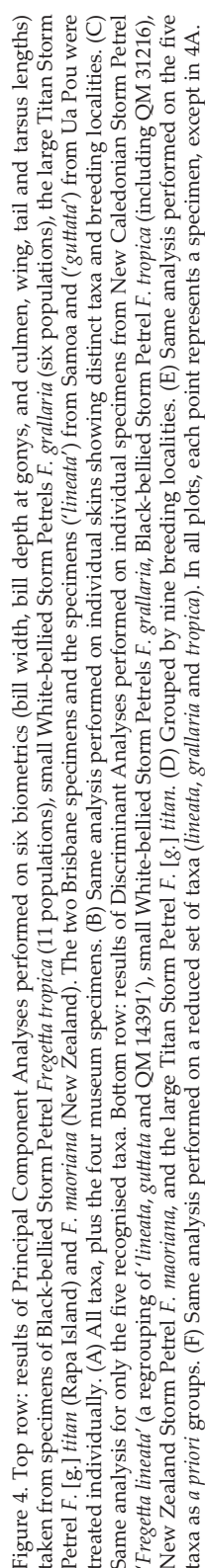


Figure 3. Means of six biometrics (bill width, bill depth at gonyes, and culmen, wing, tail and tarsus lengths) of small White-bellied Storm Petrels *Fregetta grallaria* (all taxa aggregated), New Caledonian Storm Petrel *F. lineata*, New Zealand Storm Petrel *F. maoriana*, the large Titan Storm Petrel *F. [g.] titan*, and Black-bellied Storm Petrel *F. tropica* (for methodology see main text).

These results were confirmed by two further PCAs run on individual specimens. For the *F. maoriana*, 'lineata' and 'guttata' specimens, we used measurements taken by various researchers, as if they were independent samples, yielding, respectively, seven and 11 'specimens' (complete list and measurements in Appendix 2). In the PCAs, individuals were grouped by breeding locality (Fig. 4B) or by taxonomy (Fig. 4C). Both PCAs indicated that 'lineata', 'guttata' and QM 14391 clumped between *F. grallaria* and *F. tropica*, overlapping slightly with both. Also, many *F. grallaria* specimens overlapped with *F. tropica*. Lastly, once again, *F. maoriana* and *F. [g.] titan* map as extreme opposites (Figs. 4B–C).

Discriminant Analyses.—Discriminant Analysis (DA) maximises multivariate differences between groups (taxa). It establishes classification of individuals from their biometrics based on canonical discriminant functions. DA was performed on individuals grouped by nine breeding localities (Fig. 4D), five taxa (Fig. 4E), and a reduced set of three taxa (Fig. 4F). The five taxa were 'F. lineata' (a regrouping of 'lineata', 'guttata', and QM 14391'), *F. grallaria*, *F. tropica* (including QM 31216), *F. maoriana*, and *F. [g.] titan*. Error-classification rates are derived as apparent rates when using all individuals as a train dataset, or more robust estimates of error rates when using the cross-validation and leave one out procedure. The same six centred and scaled variables from PCA were used in DA.

First, a stepwise DA indicated that all six variables entered the model (with threshold significance level for dropping a variable established at 0.01), thus all six variables were retained (data not shown). Then, using Linear Discriminant Analysis (LDA), we found



apparent classification-error rate was only 10.34% ($n = 261$) when applied to all breeding localities as groups (Fig. 4D). Five of seven *F. lineata* were correctly assigned, as were all *F. maoriana* and all *F. [g.] titan*, and nearly all *F. tropica* and *F. g. segethi*. Using a cross-validation procedure for error-rate estimation led to a slight increase, as expected, of 13.0% error rate.

A second LDA was run on the five taxa as *a priori* groups (Fig. 4E). Apparent error-rate classification was lower, at 8%, but just two *F. lineata* were correctly classified. Quadratic Discriminant Analysis (QDA) was also used, as it is less conservative (permitting different variance matrices for different groups), while using a quadratic classification decision boundary. QDA significantly improved the apparent error rate (3.8%), notably with all seven *F. lineata* specimens now being correctly assigned to their group. However, using the cross-validation calibration, the error rate was 8.8%. Restricting DA to *F. lineata*, *F. grallaria* and *F. tropica* did not significantly alter the results, but placed *F. lineata* between *F. grallaria* and *F. tropica* in multivariate space (Fig. 4F), notably due to intermediate values in tarsus length (Figs. 3 and 6).

The three *F. lineata* specimens are larger than *F. maoriana* in all measurements (Fig. 3, Appendix 2), albeit with very slight overlap in bill width. Within each taxon, measurements vary to some extent between individuals, as reported by relatively high standard error values in wing and tail measurements (Appendix 2). Intra-taxon variation, however, is particularly pronounced for the three *F. lineata* specimens. Part of this variation is due to observer measurement error, and possibly also to specimen age. The within-individual range of variation (i.e., measurements made by three or four different observers) is actually higher than the within-population variation of *F. maoriana*. For example, the two specimens of *F. maoriana* held at the Muséum national d'Histoire naturelle, Paris, were measured by four different observers, and standard errors in measurements vary between 0.13 mm (culmen length in one specimen) and 2.25 mm (tail length in the other). Tarsus length also varies both within and between the three *F. lineata* specimens. Streaks on their bellies are also quite variable, as in *F. maoriana* (e.g., Flood 2003, Stephenson *et al.* 2008b), but are completely unique to *F. lineata* and *F. maoriana*. Neither taxon shows an absence of streaks, but their extent and arrangement are variable and distinctive (see below).

Phylogenetic relationships between *Fregetta* storm petrels

Recent genetic work shed light on the *Fregetta* complex, but also added uncertainties and confusion. These have confirmed that live *F. maoriana* and the three *F. maoriana* specimens are the same taxon (Robertson *et al.* 2011). They are distinct from and not close to *Oceanites* and lie within *Fregetta* (Robertson *et al.* 2011, 2016). This is supported by evidence from Mallophaga: *Philoceanus fasciatus*, a species found on both *F. tropica* and *F. grallaria*, has been collected on *F. maoriana*, and is morphologically very different from both *Philoceanus robertsi*, parasitic on *Oceanites oceanicus*, and *Philoceanus garrodiae*, parasitic on Grey-backed Storm Petrel *Garrodia nereis* (Stephenson *et al.* 2008b).

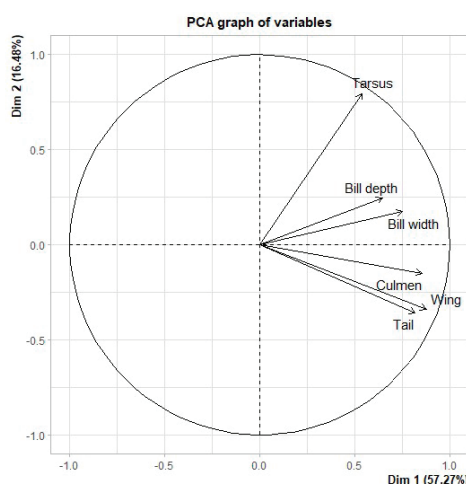


Figure 5. Principal Component Analysis showing contribution of variables to axes 1 and 2.

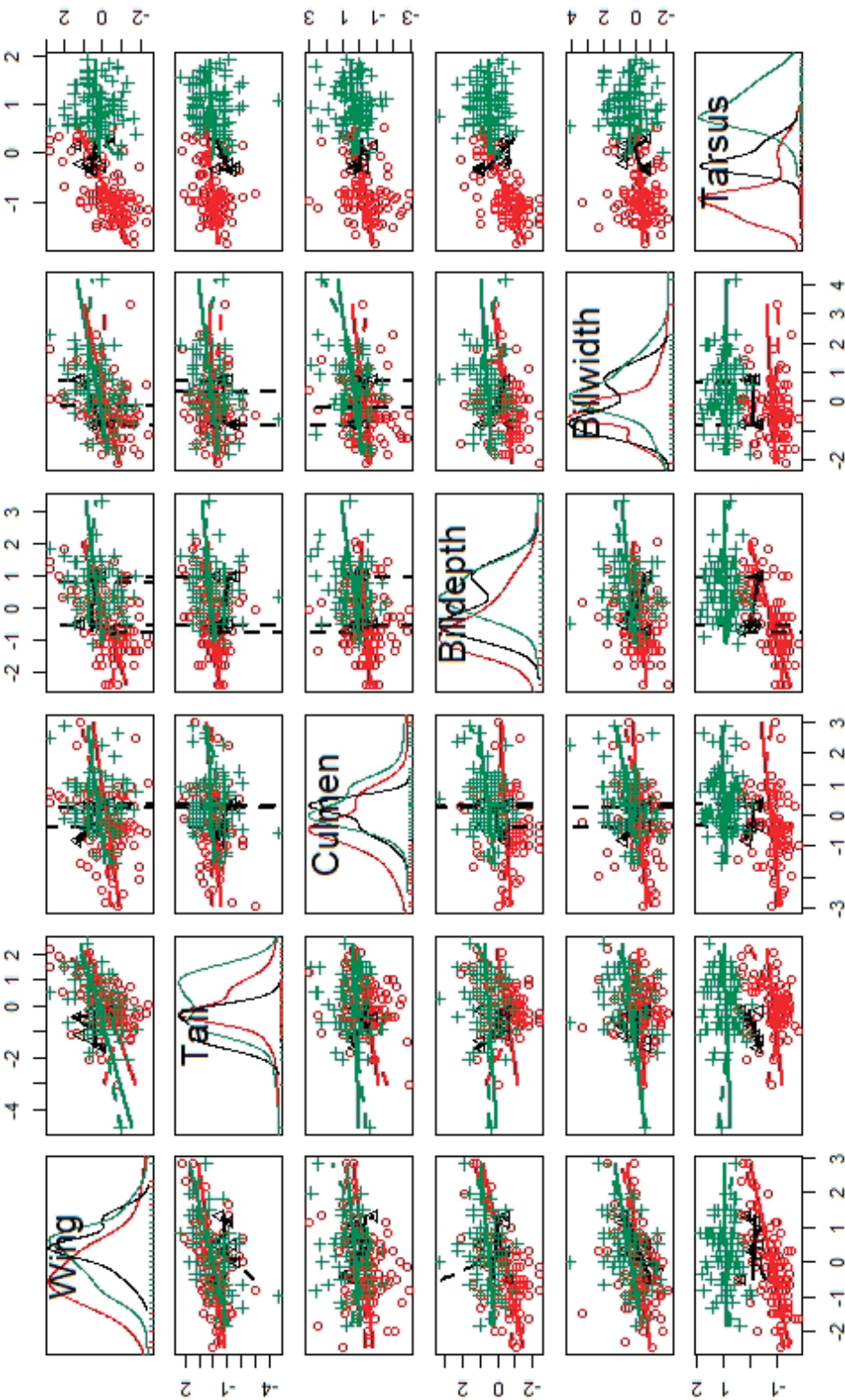


Figure 6. Comparative measurements of New Caledonian Storm Petrel *Fregetta lineata* (black), White-bellied Storm Petrel *F. grallaria* (red) and Black-bellied Storm Petrel *F. tropica* (green). Data are presented as a correlation matrix for each pair of morphometric variables, with the diagonal in the matrix showing the distribution of each variable per taxon. Colour chart as in Fig. 4F.

Three studies provide *Fregetta* phylogenetic trees; based on either short (c.500 bp; Cibois *et al.* 2015), long (960 bp; Robertson *et al.* 2016), or complete *cyt-b* sequences (Robertson *et al.* 2011); as well as seventh intron of beta Fib (Robertson *et al.* 2011, 2016). This diversity of genetic material led to contrasting conclusions. *F. maoriana* was closer to *F. tropica* than *F. grallaria* in both complete *cyt-b* and nuclear intron (Robertson *et al.* 2011), closer to *F. tropica* than *F. grallaria* in short *cyt-b* (Cibois *et al.* 2015), but closer to *F. grallaria* in long *cyt-b* and closer to *F. tropica* in nuclear intron (Robertson *et al.* 2016). In addition, *F. lineata* AMNH 194110 was sequenced and results indicate that it diverges from *F. maoriana* and, based on partial *cyt-b* sequence (557 bp), is more closely related to *F. grallaria*, especially *F. [g.] titan*, than to *F. tropica* (Cibois *et al.* 2015, Robertson *et al.* 2016). A matter of note, Robertson *et al.* (2016) commented that Cibois *et al.* (2015) were wrong to include NHMUK 1953.55.101 (collected on Gough Island, South Atlantic, held at the Natural History Museum, Tring) as *F. grallaria*. However, the sequence was taken from Robertson *et al.* (2011), as recorded in GenBank, so the original error is owned by the latter.

Our findings show that USNM 15713 and AMNH 194110 are the same taxon, *F. lineata*, based on morphometrics, although no genetic data are available for the USNM specimen. Interestingly, the Brisbane specimen QM 14391 was sequenced and clumped with *F. [g.] titan* (Robertson *et al.* 2011), as did the Ua Pou specimen AMNH 194110 (Cibois *et al.* 2015), supporting the case for aggregating them. Incidentally, whilst QM 14391 is labelled *F. tropica*, Robertson *et al.* (2016) treated it as *F. grallaria*, presumably because sequences clade with *F. grallaria* rather than *F. tropica*. However, systematics of the group are complicated by the opaque taxonomy of the genus *Fregetta* itself (Howell 2010, 2012), with more than 20 different names proposed for these birds, and the complex situation in Tristan da Cunha, South Atlantic (Brooke 2004, Howell 2012, Flood & Fisher 2013). In particular, taxonomy of the *F. grallaria* and *F. tropica* complexes are not resolved (Crochet 2008, Howell 2010, 2012, Robertson *et al.* 2016). That said, there is consensus that the four *Fregetta* taxa (*F. grallaria*, *F. tropica*, *F. lineata* and *F. maoriana*) form a monophyletic clade, based on mtDNA and nuclear DNA, albeit a single gene in both cases (Robertson *et al.* 2011, Cibois *et al.* 2015, Robertson *et al.* 2016). This clade is distinct from *Oceanites* and supports the generic denomination *Fregetta*.

Taxonomic conclusions

From these univariate and multivariate analyses, we conclude that the three specimens 'lineata', 'guttata', and QM 14391 represent a single taxon, for which the oldest available name is *lineata*. This group is clearly separated from *F. maoriana* by measurements, and *F. grallaria* and *F. tropica* by dark streaks on a white belly. Phylogenetically, *F. lineata* is close to *F. [g.] titan*, as assessed by the *cyt-b* sequences of two of the three specimens. Moreover, we conclude that birds photographed off New Caledonia and in the Coral Sea are identical to the three museum specimens and are the same taxon *F. lineata*. Taxonomic conclusions for the AMNH and UNSM specimens were presented by Murphy (1924), Murphy & Snyder (1952) and Matthews (1933). We conclude that *F. lineata* is a valid species, not a morph, nor a subspecies. The next section redescribes *F. lineata* by drawing on our at-sea observations, photographs taken at sea, and study of the three museum specimens.

New Caledonian Storm Petrel *Fregetta lineata*

Holotype.—The oldest of the three *F. lineata* specimens (USNM 15713; Fig. 2) was collected on Upolu, Samoa, in 1839 by T. R. Peale and described in detail by Mathews (1933). It is the type specimen of *Thalassidroma lineata* Peale (1848, Deignan 1961). However,

the specimen has not been sequenced, unlike the other two. Probably, the specimen was collected in November 1839, perhaps during 23–25 November, when Peale visited the island. The species was said to be nesting in holes high in the mountains (Mathews 1933), ‘very high up in the mountains’ (Murphy & Snyder 1952), possibly the highest point Mt. Fito (c.1,100 m). Historic records state that a native collected the specimen for Peale, and the latter mentioned these birds were from the mountains. However, the precise circumstances are unclear and it is possible that the storm petrel breeding in the mountains was Polynesian Storm Petrel *Nesofregetta fuliginosa* (Bourne 2008), and that the specimen was collected at sea, as Peale mentioned these birds were commonly observed there. Murphy & Snyder’s (1952) conclusion that the specimen is *F. tropica*, which is not known to breed in the tropics, led Bourne (2008) to propose that it was collected by Peale in the southern seas and accidentally exchanged with the holotype of Collared Petrel *Pterodroma brevipes* (USNM 15459; also collected by Peale). As it is not *F. tropica* (see above), there is no reason to doubt the locality. USNM 15713 has not been genetically sequenced, its age is unknown, and the skin is damaged.

Measurements.—Wing length 163 mm; tail length 70 mm; culmen (bill length from feathers) 14.5 mm; bill depth (top of maxillary unguis to base of mandibular unguis) 4.8 mm; bill width at base 6.6 mm; tarsus length 37.3 mm.

Second oldest specimen.—AMNH 194110 from the Marquesas (Fig. 2) was described in detail by Murphy (1924) and is a female collected on 15 September 1922 by R. H. Beck, off Ua Pou, Marquesas. It is currently labelled *Fregetta guttata* (Mathews 1933, LeCroy 2017) and is the holotype of *F. guttata* (LeCroy 2017). Murphy (1924) initially considered the specimen to be the same taxon as *F. lineata* (Peale 1848), and noted an intermediate structure (foot, nails, rectrices, etc.) between *F. grallaria* and *F. tropica*. Mathews (1933) misinterpreted Murphy (1924), confusing *F. lineata* and *F. [g.] titan*, and concluded AMNH 194110 represented a new species, even proposing a new genus. However, *contra* Mathews (1933), Murphy & Snyder (1952) found the differences insufficient to recognise a new taxon and assigned it to *F. grallaria*, considering ‘*lineata*’ to be a synonym of ‘*grallaria*’ (see also LeCroy 2017). Measurements are given in Appendix 2.

Description.—Consult Figs. 7–9. *Foreparts* Head, neck and throat to upper breast blackish brown (old feathers brownish and new ones glossed black). Throat of worn birds may show central pale mottling. *Underparts* Lower breast, belly to upper ventral region, and flanks contrastingly white with characteristic oval-shaped blackish streaking (feather centres). Streaking somewhat variable in size and shape, but typically each streak broadens at feather tip. Streaks on flanks widest and densest, those on central belly narrowest, and form rows of oval dapples. Dark upper breast border tends to form triangular extensions into sides of white breast. *Underwing* Striking pattern with following specific characteristics. Broad blackish-brown leading edge, its border contiguous with dark upper breast. Dark leading edge of inner wing involves lesser secondary-coverts, and on outer wing the lesser and central median primary-coverts. Greater primary-coverts mostly greyish black. Median and greater primary-coverts narrowly tipped and edged white. Flight feathers essentially uniform greyish black. Resultant pattern is dark with restricted white underwing panel, which mostly involves median and greater secondary-coverts. However, some greater secondary-coverts can be dark centred, further restricting area of white panel. *Upperparts* Mantle to back and scapulars essentially blackish brown, shiny greenish / greyish on catching the light. Some mantle and scapular feathers narrowly tipped whitish. Small uppertail-coverts browner, rest white forming a well-defined wide U shape that wraps onto white underside. *Upperwing* Colour as upperparts, but upperwing-coverts a shade browner, forming an indistinct paler panel. *Tail* Blackish brown with white basal area on underside



Figure 7. New Caledonian Storm Petrel *Fregetta lineata*, off Nouméa, New Caledonia, January 2020 (Hadoram Shirihai, © Tubenoses Project)

mostly concealed by blackish-brown lateral undertail-coverts (with thin white edges) but visible on spread tail. *Bare parts* Essentially black.

In-hand identification.—*F. lineata* is distinct from *F. grallaria* in structure and measurements. Only a few *F. grallaria* are flecked / streaked on belly (Fig. 8). Murphy & Snyder (1952) stated that such markings are commonly found in *F. grallaria*. However, they are found on just eight of 68 adults collected near the Juan Fernández Islands (Chile), and seven of 35 adult *F. [g.] titan*. Similar statistics occur for *F. tropica* (AMNH). Our experience of *F. grallaria* and *F. [g.] titan* in the South Pacific, and c.35 *F. tropica* specimens from New Zealand, leads to the conclusion that streaking is scarce and irregular, and variable in width and density, unlike the three *F. lineata* specimens (see Flood 2003, Stephenson *et al.* 2008b). Variation in intermediate-morph *F. g. grallaria* from Lord Howe and Kermadec Islands amounts to gradual darkening on the axillaries and flanks, not streaking on the belly, and all but the darkest individuals have a pale belly (Marchant & Higgins 1990, Stephenson *et al.* 2008b).

Identification at sea and plumage variation.—*F. lineata* can reliably be identified at sea with good views and, ideally, in sharp photographs on which it is possible to evaluate details.

Separation from Fregetta storm petrels.—Usually, *F. tropica* has a thick dark central belly-stripe, sometimes narrow, scarcely broken, and a different structure and behaviour (see below). Usually, *F. grallaria* has a pure white belly, but a few have irregular thinly distributed flecks / streaks. Scarcely, individuals from all populations of *F. grallaria* have flanks streaking, narrow and close to feather shafts, never in rows of oval dapples characteristic of *F. lineata*, or straighter lines characteristic of *F. maoriana* (Fig. 8). A few extreme examples of *F. g. grallaria* from Lord Howe display broader flanks streaking, but never across the whole belly (Fig. 8). Also, unlike *F. grallaria*, *F. lineata* (and *F. maoriana*) have a narrower white 'rump patch' on the long uppertail-coverts and a more restricted white underwing panel. Lastly, *F. lineata* (and *F. maoriana*) lack extensive and broad white fringing on fresh upperparts as in most populations of *F. tropica* and *F. grallaria*.



Figure 8. Comparison of 'streaked' White-bellied Storm Petrel *Fregetta g. grallaria* with New Zealand Storm Petrel *F. maoriana* and New Caledonian Storm Petrel *F. lineata*. (A) White-bellied Storm Petrel, Lord Howe Island, Australia, April 2019 (David Newell, www.birdlifephotography.org.au). (B) White-bellied Storm Petrel, Lord Howe Island, February 2017 (Mark Lethlean, www.birdlifephotography.org.au). (C) White-bellied Storm Petrel, Lord Howe Island, date unknown (Jack Shick, www.lhirodenteradicationproject.org/plants-animals/birds). (D) New Zealand Storm Petrel, Hauraki Gulf, North Island, New Zealand, November 2018 (Hadoram Shirihai, © Tubenoses Project). (E) New Caledonian Storm Petrel, off Nouméa, New Caledonia, January 2020 (Hadoram Shirihai, © Tubenoses Project). (F) New Caledonian Storm Petrel, off Nouméa, New Caledonia, January 2020 (Hadoram Shirihai, © Tubenoses Project). Rarely, individuals of all populations of *F. grallaria* have limited fine streaking, for example (A) and (B), narrow and close to feather shafts, never in rows of oval dapples characteristic of *F. lineata*, for example (E) and (F), or forming straighter lines characteristic of *F. maoriana* (D). A few extreme examples of *F. g. grallaria* from Lord Howe possess broader flanks streaking, e.g. (C), but never covering the whole belly.

Separation from F. maoriana.—Consult Figs. 8–9. Similar-looking but individually variable *F. lineata* is larger, longer winged and longer legged, with different belly streaking and underwing pattern. Belly streaking of *F. lineata* is typically denser and bolder. White underwing panel of *F. lineata* typically narrower and less clean-looking (more underwing-coverts have broad dark centres). Border of dark on breast rounder in *F. lineata*, curving from sides of lower breast to central upper breast, but clearly straighter in *F. maoriana*. White 'rump patch' on long uppertail-coverts averages narrower and rounder in *F. lineata*. Both species show variation in belly streaking. For example, *F. lineata* score 4 (16.7% of birds) shows narrower less coalescing streaking, suggesting most heavily streaked *F. maoriana* score 1 (9.3% of birds). *F. lineata* score 1 (23.3% of birds) uniquely patterned, with continuous and dense rows of oval dapples, rather than the more straight-lined streaks

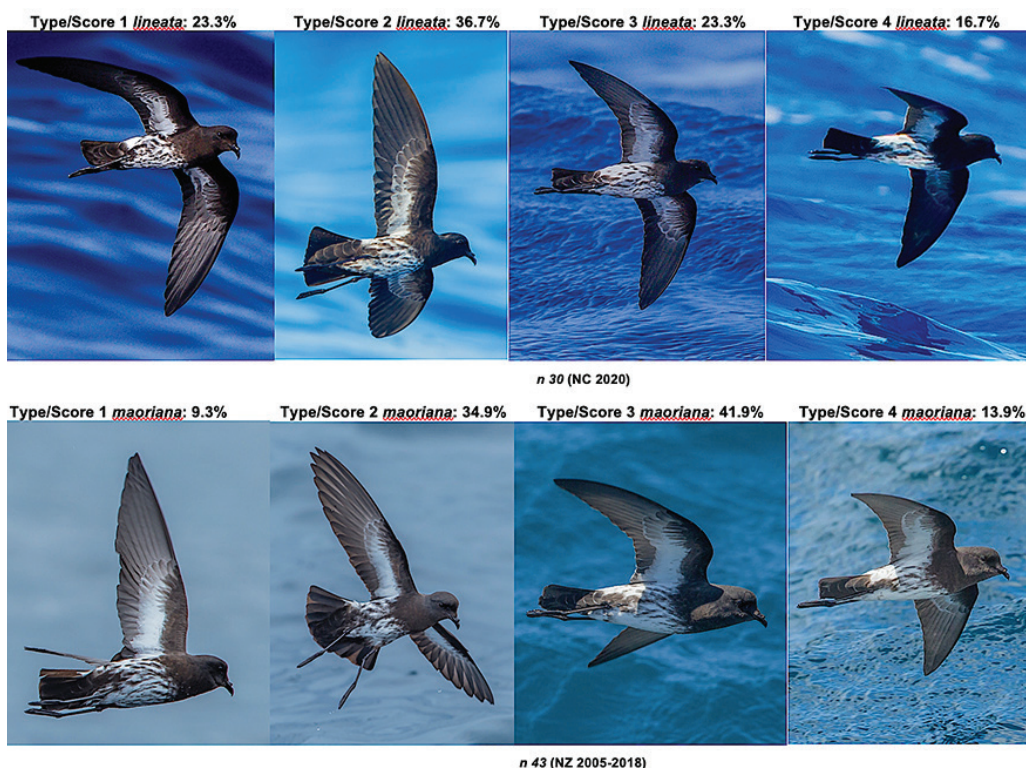


Figure 9. Comparison of underparts and underwing patterns of New Caledonian Storm Petrel *Fregatta lineata* ($n = 30$), off Nouméa, New Caledonia, January 2020 (top row) and New Zealand Storm Petrel *F. maoriana* ($n = 43$), Hauraki Gulf, North Island, New Zealand, November 2018 (bottom row). Variation is scored into four main types for each species, from the heaviest marked (score 1) to lightest marked (score 4). *Underparts streaking* Both species can show similar coverage of streaking on the white belly and a tendency for denser and / or thicker streaks on the flanks. Score 1 for *F. lineata* (23.3% of birds) is uniquely patterned, with continuous and dense rows of oval dapples, rather than straighter lines of *F. maoriana*. Score 2 for *F. lineata* (36.7%) is the most common and similar to the coverage and shape of streaking as the similarly common score 2 for *F. maoriana* (34.9%). Streaking on *F. lineata* tends to be denser and bolder giving the impression it is wider. The unstreaked belly area tends to be cleaner white in *F. maoriana*. Border of dark breast The border in *F. lineata* is positioned higher than in *F. maoriana*, towards the centre of the upper breast, creating a rounder and less straight border than *F. maoriana*. *Underwing pattern* In *F. lineata*, the dark leading edge to the inner wing involves lesser secondary-coverts. The longest of these have partially dark bases creating a characteristic ragged border, with strongly marked bases in 83.3%, limited dark bases in the remaining 16.7%. By contrast, the dark leading edge in *F. maoriana* invariably shows a clear-cut border on the coverts, only occasionally with a few dark spots in the longest lesser coverts, and never forming a continuous ragged border as in *F. lineata*. Usually, some greater secondary-coverts and most / all greater primary-coverts in *F. lineata* have broad dark centres. Thus, the white underwing panel of *F. lineata* is noticeably less extensive than in *F. maoriana* (Hadoram Shirihi, © Tubenoses Project)

of *F. maoriana* (for explanation of scoring see Fig. 9). Borderline cases of belly streaking separated when underwing pattern diagnostic. Underwing of *F. lineata* diagnostic when shows partially dark row of longest lesser secondary-coverts, creating characteristic ragged border to dark leading edge, and has dark centres to greater secondary-coverts. Conversely, a clear-cut border and all-white greater secondary-coverts are diagnostic of *F. maoriana* (e.g., as evidenced by the first proven record of *F. maoriana* away from New Zealand, off Fiji; Flood & Wilson 2017). Also consider jizz and behaviour as follows.

Jizz and behaviour.—Once learnt, *F. lineata* is readily identifiable by jizz, flight and feeding behaviour. Compared to other *Fregatta* storm petrels, including *F. maoriana*, note the slimmer build, with proportionately longer and narrower wings, elongated rear body, and

long squarer-ended tail. *F. lineata* has a less square, more angular forehead profile, longer neck, and quite long and thick bill that curves downward. It also has long legs, notably the tibia, which can approach the very long legs of White-faced Storm Petrel *Pelagodroma marina*, best appreciated when foot-pattering (Fig. 7). Feet relatively 'huge', accentuating impression of 'walking on water'. Unlike other *Fregetta* that freely 'ski' using one foot, this species only occasionally performs short 'skis'. Rather, it employs both feet simultaneously, occasionally followed by a short 'ski'. *F. maoriana* 'skis' on one foot in travelling flight, but not habitually like *F. tropica* and *F. grallaria*. Travelling flight striking, comprising glides and flaps on stiff wings, close to the sea surface. Collects prey from sea surface like other *Fregetta*. A bird once dived c.30 cm to collect small pieces of fish. On several occasions, foraging birds challenged Tahiti Petrel *Pseudobulweria rostrata* and Gould's Petrel *Pterodroma leucoptera*, quickly snatching fish pieces, then escaping. *F. lineata* may associate with *P. leucoptera* as they often arrive simultaneously at chum, and *F. lineata* is always present at large feeding aggregations of *P. leucoptera*. Also, *F. lineata* constantly follows feeding Copper Sharks *Carcharhinus brachyurus*.

Breeding New Caledonian Storm Petrel *Fregetta lineata*

First confirmed breeding in New Caledonia.—On 26 September 2014, a juvenile *F. lineata* was caught by inhabitants of New Caledonia. Information is sparse, but it was found on the shore of mainland New Caledonia, in an inhabited area (Fig. 1), and the juvenile probably was disoriented by street lights, as happens elsewhere with petrels, shearwaters and storm petrels (Rodríguez *et al.* 2017). Photographs were taken that day at Port Bouraké, in front of Îlot Leprédour (Fig. 10). In 2009, this islet became a nature reserve of the Province Sud. Eradication of European Rabbits *Oryctolagus cuniculus* from the islet is underway. The photographs were first sent to L. Renaudet (of the Société Calédonienne d'Ornithologie), who forwarded them to VB for identification. The bird had down on its head and nape, indicating a recent fledgling and confirming breeding on New Caledonia. No feather or blood samples were taken, and the bird was released. This is the only definite record of *F. lineata* on land and the only one indicative of breeding.

What is the breeding season in New Caledonia?—A fledgling in September points to winter breeding in the Southern Hemisphere. A six-month season is expected given the size of *F. lineata*. Thus, based on the fledgling, March–April is the likely egg-laying period. This corresponds with the majority of sightings in March and April off New Caledonia (Appendix 1). Further, numerous sightings as early as January off New Caledonia in 2020 suggest that egg laying may occur over an extended period, possibly January–April. In January 2020, off New Caledonia, birds were in rather fresh plumage, but tail and breast feathers were worn. The lack of primary moult and feather condition indicate that at least some were engaged in pre-breeding or breeding activities. (Primary moult of successful breeding storm petrels generally commences post-breeding.) Sightings off Australia perhaps correspond mainly to non-breeders. Indeed, birds there in March often had rather worn plumage and in April 2014 active wing moult was noted, which would not be expected in breeding adults. That said, some did not show obvious wear or moult.

Where exactly does it breed?—All islets in the southern lagoon of New Caledonia have been visited and carefully searched, with several nights spent on most of them (Benoit & Bretagnolle 2002). No storm petrel was ever seen, no *Fregetta* whistling call was heard and, as far as we know, none of the many ornithologists who subsequently visited the islets has reported storm petrels. The only known storm petrel colony in New Caledonia was located in December 1999 in the interior of an islet off northern New Caledonia (VB pers. obs.). Seven to nine burrows with entrances of c.5–7 cm width were located in sand. No particular



Figure 10. New Caledonian Storm Petrel *Fregetta lineata*, Port Bouraké, New Caledonia, 26 September 2014; the first documented fledgling; note traces of down on head, stripes on belly diagnostic of *F. lineata*, narrow white fringes on dorsal feathers and upperwing (the latter most typical of *F. grallaria*) (photographer unknown, images supplied by L. Renaudet)

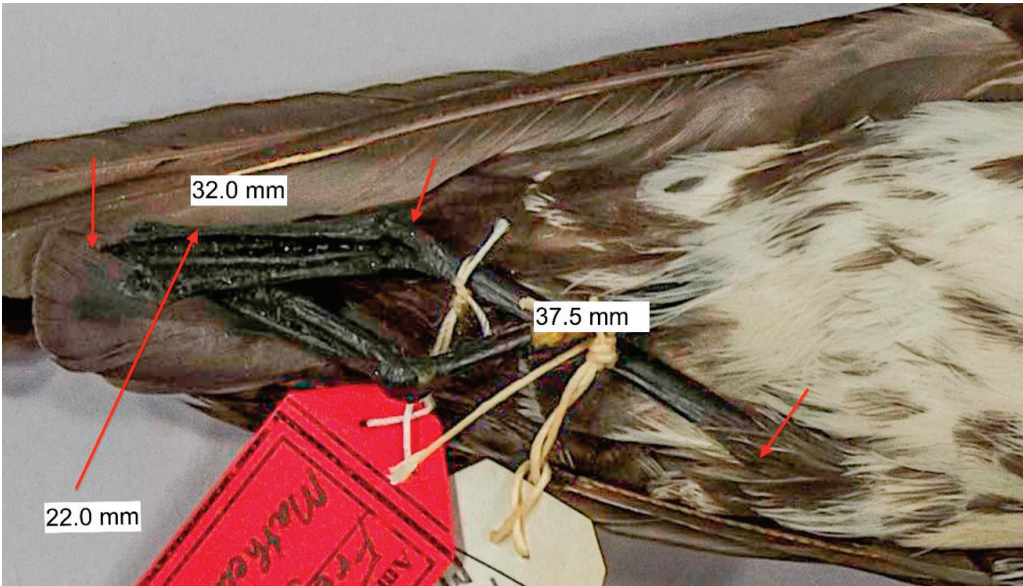


Figure 11. New Caledonian Storm Petrel *Fregetta lineata* held at the American Museum of Natural History, New York (AMNH 194110); the annotations demonstrate that the middle toe and claw measure 32 mm, and the published measurement of 22 mm is incorrect (Hadoram Shirihai)

smell was detected and nothing was observed in the burrows. They were not disturbed as burrows in sand are easily and irreparably damaged. It was not possible to spend the night on the islet, but during several nights on neighbouring islets no storm petrel was seen or heard. Polynesian Storm Petrel *Nesofregetta fuliginosa*, a long-suspected breeder in New Caledonia, was believed to be the burrow owner. In May 2000, M. Pandolfi spent a night at the colony, heard whistling calls, but did not see or catch any storm petrels. Winter breeding supported the assumption that *N. fuliginosa* was involved. However, the following summer rats *Rattus rattus* were found on the islet. Although successfully eradicated in 2008, no one has located storm petrels on subsequent visits and no burrow has been found (J. Baudat & P. Villard pers. comm. 2008–18). The species of storm petrel involved remains unknown.

F. lineata may breed either inland or on islets in Bouloupari Lagoon (not visited). These islets are atypical and quite unlike southern lagoon islets. Some are rocky and most are surrounded by mangroves. The most suitable location would be Leprédour Islet where introduced mammals were recently eradicated. Any storm petrel population on the islet would likely have recovered somewhat, leading to at-sea sightings, as suggested for *F. maoriana* which breeds on Little Barrier Island where cats were recently eradicated. Alternatively, breeding may occur on mainland New Caledonia; a likely location is the Tontouta River valley where *Pterodroma leucoptera* breeds. High forested peaks along the coast, such as Dent de Saint Vincent, are also suitable search locations.

Apart from New Caledonia, the Marquesas Islands, where AMNH 194110 was collected, could hold a breeding population. The presence of subfossil bones attributed to *Fregetta* on Ua Huka and Tahuata (Steadman 2006) might evidence the past presence of *F. lineata*. In addition, on 30 September 2013, one or two streaked storm petrels were seen south-west of Fatu Hiva, which provides hope that the streaked storm petrel survives in the Marquesas (Flood & Wilson 2017). However, in September–October 2021, an 18-day seabird survey circumnavigating the islands recorded numerous storm petrels, but no streaked birds (Flood *et al.* 2022). Perhaps seas around the Marquesas form part of the non-breeding range, given that the AMNH specimen and the recent sightings were in September, at the end of the likely breeding season in New Caledonia discussed above. Also, *F. lineata* could breed and survive on Samoa, where USNM 15713 was collected (especially if the bird was collected on land, see above). Mt. Fito would be a likely breeding locality, although again, the seas around Samoa could form part of the non-breeding range, as the specimen was collected in November.

Conservation

It is now vitally important to find breeding burrows where immediate protective measures will be required. Based on the numbers seen at sea, both off Australia and New Caledonia, the population is perhaps in the order of 100–1,000 pairs and almost certainly globally threatened. Compared to breeding on islets, nesting in the mountains would be far more difficult to confirm and conservation management far more difficult to implement. Thus, our primary recommendation is to search for evidence of breeding on islets, in April or May, using spotlighting which is known to attract storm petrels. Nocturnal searches are preferable as a first step, which is quite manageable given the small number of islets. If successful, this should be followed by catching and fitting birds with radio tags. If unsuccessful, searches on the main island should be undertaken. It is worth recalling that *F. maoriana* survived undetected on Little Barrier Island for more than 100 years, breeding in large forests and on cliffs, despite the presence of cats and rats (Rayner *et al.* 2015).

Acknowledgements

Thanks to Ludovic Renaudet for sending photographs of the fledgling *F. lineata*, Mireille Pandolfi and Pascal Villard for their help in searching for storm petrels on the northern islets, and Julien Baudat for sharing his knowledge of seabirds. VB thanks the many museum curators, too numerous to name individually, who permitted and supported his visits for storm petrel studies. RLF thanks Mark Adams of NHMUK for supplying at short notice a photograph of NHMUK 1895.2.1.11. HS particularly thanks Gabriel Levionnois for assisting three days of pelagic work off New Caledonia in January 2020, the masterful skippering of his boat making possible high-quality photographs, and his great enthusiasm to learn about seabird conservation on his island home. Also, much appreciation goes to François Levionnois and Odile Thomas for their warm hospitality during HS's long stay in New Caledonia, January–August 2020. HS also expresses his thanks to the Jorvall Foundation for many years of support of avian taxonomic research. Thanks to an anonymous reviewer, and to Chris Collins and Paul Walbridge for helpful advice. Guy Kirwan provided help in editing the text, and we thank him for supplying additional references that were initially missed.

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Appendix 1: at-sea observations of New Caledonian Storm Petrel off New Caledonia and in Coral Sea

The recent history of the New Caledonian Storm Petrel *Fregetta lineata* begins with observation of a streaked storm petrel by C. Collins, RLF, S. N. G. Howell *et al.* during the 2008 Western Pacific Odyssey (WPO, Heritage Expeditions). The location was c.25 nm south-west of New Caledonia at c.22°40'S, 166°23'E (Howell & Collins 2008). None was seen during the 2009 WPO, nor the previous one in 2007, but singles were found in the same area during the 2010, 2011 and 2012 voyages (Table 1). Since then, many have been observed and photographed in the same region (Table 1). On 31 January 2020, 25 nm south of Nouméa, New Caledonia, in deep waters just outside the lagoon at c.22°50.22'S, 166°26.17'E (Fig. 1), 24 were attracted to chum, to date the largest single-day count.

Further to this, in 2011 D. Mantle and P. Walbridge came across identical-looking storm petrels in the Coral Sea, off Queensland, Australia (<http://www.sossa-international.org/>). Subsequently, many have been logged over seamounts in the Coral Sea, c.300 km east of Queensland, more rarely further south, off the adjacent state of New South Wales (Table 1). Some birds of those off New South Wales may have been New Zealand Storm Petrels. On 13 April 2014, one was caught and released. 'Coral Sea Storm Petrel' is the proposed alternative vernacular name.

Birds have been recorded in January–April off New Caledonia, although we know of no pelagic trip there May–November. We know of records in December–June and October off Queensland, with max. numbers in April, but none during pelagic trips in July–December (<http://www.sossa-international.org/>).

TABLE 1

At-sea records of New Caledonian Storm Petrel *Fregetta lineata* 2008–21. Some birds off New South Wales may have been New Zealand Storm Petrels *F. maoriana*. Includes all records noted in publications and online. Some sightings may not have been located or reported. Distances approximate. Nouméa is capital of New Caledonia. NSW = New South Wales; QLD = Queensland, Australia. ‘SOSSA 2012’ = a report in 2012 by Southern Ocean Seabirds Study Association. Ditto subsequent years. Source for Rob Hynson www.pbbase.com/rob_hynson/image/123145261; for Alan Stuart www.thinkingaboutbirds.com/that-storm-petrel.php; for Heritage Expeditions, page recently removed from www.heritage-expeditions.com/.

Year	Location	Date	No.	Notes	Source
2008	25 nm S of Nouméa, 22°40’S, 166°23’E	7 Apr	1		Howell & Collins (2008)
2010	25 nm S of Nouméa	?	1		Collins (2013)
2010	Off Ulladulla, NSW	29 Mar	1	Moulting	Rob Hynson
2011	25 nm S of Nouméa	?	1		Collins (2013)
2011	32 nm ENE of Southport, QLD	18 Jun	1	Morning	SOSSA 2011
2012	Off SE New Caledonia	Apr	1		Collins (2013)
2012	35 nm NE of Brisbane, QLD, 27°S, 154°E, to 27°S, 155°E	14 Apr	6	Morning (4), late afternoon (2)	SOSSA 2012
2012	85 nm E of Brisbane, QLD, 28°S, 155°E	15 Apr	4	Morning and early afternoon	SOSSA 2012
2013	30 nm ENE of Southport, QLD, 27°S, 153°E to 27°S, 154°E	19 Jan	2	Morning	SOSSA 2013
2013	Off S New Caledonia	20 Mar	10		Collins (2013)
2013	Off S New Caledonia	21 Mar	1		Collins (2013)
2013	Off S New Caledonia	Apr for 6 days	21		P. Harrison (<i>in litt.</i> 2014)
2014	85 nm ENE of Brisbane, QLD, 27°S, 155°E	12 Apr	4	1 at 17.00 h	SOSSA 2014
2014	85 nm ESE of Brisbane, QLD, 28°S, 155°E	13 Apr	21	1 captured in moult; morning	SOSSA 2014
2014	28 nm ENE of Southport, QLD, 27°S, 153°E	19 Apr	1	At 11.35 h	SOSSA 2014
2015	Off Port Stephens, NSW	Jun	1		Alan Stuart
2018	Off Brisbane, QLD	21 Apr			SOSSA 2018
2018	Off Brisbane, QLD	30 Jun			SOSSA 2018
2019	12 nm W Nouméa	22 Mar	>1		Heritage Expeditions
2019	Off QLD	19 Oct	>1		ebird.org/species/necstp1
2020	25 nm S of Nouméa	21 Jan	10	Some worn, none moulting	This study
2020	25 nm S of Nouméa	31 Jan	24	Some worn, none moulting	This study
2020	25 nm S of Nouméa	20 Feb	6	Some worn, none moulting	This study
2020	South Britannia Seamount, NSW	28 Mar	1		ebird.org/species/necstp1
2021	Off Port Stephens, NSW, 32°48’S, 152°39’E	17 Jan	1	11.30–12.30 h	SOSSA 2021
2021	Off Southport, QLD	14 Feb	1		ebird.org/species/necstp1
2021	Off QLD	13 Mar	>1		ebird.org/species/necstp1
2021	South Britannia Seamount, NSW	14 Mar	>1		ebird.org/species/necstp1
2021	Off Port Stephens, NSW	28 Mar	1		Eremaea BirdLines 2021
2021	Off Kempsey, NSW	3 Apr	1	Worn primaries	ebird.org/species/necstp1
2021	Off Southport, QLD	18 Dec	1	First Dec record	P. Walbridge (<i>in litt.</i>)

Appendix 2
Biometrics (mm) of all known museum specimens of New Caledonian Storm Petrel *Fregatta lineata* and New Zealand Storm Petrel *F. maoriana*. AMNH = American Museum of Natural History, New York. NHMUK = Natural History Museum, Tring. QM = Queensland Museum, Brisbane. USNM = National Museum of Natural History, Smithsonian Institution, Washington DC. Taxon is *Fregatta*. I = island. N = number (1, unless otherwise stated). NZ = New Zealand. S = sex (male / female) VB = Vincent Bretagnolle. Notes: ¹ The value 22.0 mm in Murphy & Snyder (1952) is dubious. On reassessment, it should read 32.0 mm (see Fig. 11); ² The value 34.5 mm (Mathews 1933) is dubious and likely erroneous.

Specimen reg. no.	Museum / Reference	Taxon	S	N	Location	Observer / source	Date collected	Wing	Tail	Culmen	Bill depth	Bill width	Tarsus	Middle toe and claw
194110	AMNH	<i>lineata</i>	F		Ua Pou, Marquesas	VB	15/9/1922	171	75	13.6	4.1	7.5	38.7	
						Shirihai (2015)		170	72	14.5			37.5	32.0
						Murphy & Snyder (1952)		165	73.5	14.0			38	22.0 ¹
15713	USNM	<i>lineata</i>	M		Upolu, Samoa	VB	?/11/1839	163	70	14.5	4.8	6.6	37.3	
						Mathews (1933)		166	76	14.0			34.5 ²	31.0
						Murphy & Snyder (1952)		166	71.2	14.6			37.0	28.6
14391	QM	<i>lineata</i>	-		Stradbroke I	VB	?/7/1973	160	76	14.6	4.0	6.6	39.2	
31216	QM	<i>tropica</i>	M		Stradbroke I	VB	22/5/1999	157	75	14.5	4.4	6.9	41.4	
	Mean ± SE			3				162.8 (3.01)	74.0 (1.35)	14.3 (0.23)	4.3 (0.18)	6.7 (0.40)	39.2 (0.85)	
1895.2.1.11	NHMUK	<i>maoriana</i>	-		North I, NZ	VB	4/3/1868	150	67	12.1	3.5	6.8	35.9	
						Murphy & Snyder (1952)		151.5	64.2	12.5			35.0	27.2
						Bourne (2004)		148	67	12.5			35.0	
C.G. 1829.254 (14393)	MNHN	<i>maoriana</i>	M		North I, NZ	VB	4/2/1827	150	58	13.1	3.8	6.2	38.6	
						Murphy & Snyder (1952)		147	56.6	12.7			35.3	27.6
						Jouanin (2004)		148	65	12.5			37.0	28.0
						(Bourne 2004)		148	66	12.0			37.0	27.5
C.G. 1829 (14372)	MNHN	<i>maoriana</i>	-		North I, NZ	VB	4/2/1827	150	62	12.6	3.7	6.4	38.4	
						Murphy & Snyder (1952)		148	58	12.5			35.1	27.2
						Jouanin (2004)		150	63	13.0			37.5	28.0
						Bourne (2004)		148	61	12.0			36.0	27.0
	Mean ± SE			3				150 (0)	62.3 (2.25)	12.6 (0.25)	3.7 (0.08)	6.5 (0.15)	37.6 (0.75)	
Live birds	Rayner <i>et al.</i> (2014)	<i>maoriana</i>	M	20	Hauraki Gulf, NZ		2005–12	151.8 ± 3.6	64.8 ± 3.6	12.7 ± 0.63			35.0 ± 1.5	
			F	7	Hauraki Gulf, NZ		2005–12	153.6 ± 3.7	64.1 ± 2.8	12.6 ± 0.60			35.3 ± 0.8	
	Stephenson <i>et al.</i> (2008)	<i>maoriana</i>		4			2005–06	148.7 ± 3.7	66.0 ± 1.5	13.4 ± 0.3			35.9 ± 0.9	29.5 ± 1.2