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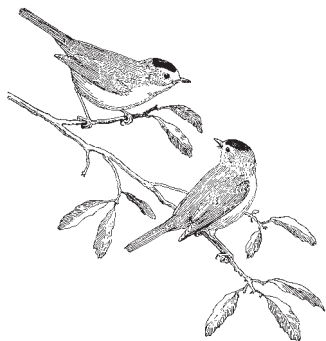
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SPECIES RANK FOR THE CRITICALLY ENDANGERED ATLANTIC LESSER FRIGATEBIRD (*FREGATA TRINITATIS*)

STORRS L. OLSON¹

ABSTRACT.—The Atlantic Lesser Frigatebird (*Fregata trinitatis*) is elevated to a separate species from *Fregata ariel* of the Indo-Pacific based on plumage differences and greater robustness of the rostrum and wing bones. The species now occurs only on the remote South Atlantic island of Trindade (South Trinidad) over 1,100 km east of mainland Brazil, although fossils establish that it once also occurred at St. Helena. *Fregata trinitatis* no longer breeds on the main island of Trindade and is only known to nest with certainty on a small rocky islet on the southern coast, where there may be fewer than 20 breeding pairs. Received 22 May 2017. Accepted 1 July 2017.

Key words: fossils, *Fregata ariel*, *Fregata minor nicolli*, geographic variation, Ilha da Trindade, South Trinidad. St. Helena.

The species level systematics of frigatebirds (*Fregata*, Fregatidae) was long poorly understood and contentious. All taxa are essentially blackish birds marked with various patches of white on the head, flanks, or abdomen, the distribution of which varies with sex and age as well as by species. Thus, for a long time only a single species was recognized, usually based on one of the two oldest names, *Pelecanus aquilus* Linnaeus (1758) or *Pelecanus minor* Gmelin (1789). The spelling *aquila*, used in combination with *Fregata*, is not the Latin noun meaning “eagle,” but the adjective meaning “black.” Later, two species were recognized on the strength of the noticeably smaller size of the Lesser Frigatebird, which took the name *Fregata ariel* (Gray 1845). Not until the researches

of Gregory Mathews (1914, 1915), followed by the comments of Rothschild (1915) and Lowe (1924), did the basis for modern species concepts of frigatebirds begin to emerge, in which five species have been recognized (although Mathews originally regarded his own taxon *magnificens* to be a subspecies of *F. minor*).

In considering the delay in recognizing species’ limits in frigatebirds, “it must be remembered that the idea of geographical isolation producing peculiar forms of such wide-spread species as [frigatebirds] was scarcely conceived” (Mathews 1915:252). For those who have seen frigatebirds crossing from ocean to ocean on a regular basis along the route of the Panama Canal, it may be difficult to comprehend the essentially sedentary nature of these birds. Murphy (1939:135) also emphasized this point: “In the steps of the process that is sometimes called ‘speciation’ we discern further evidence of

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the sedentary disposition of a bird once supposed to wander far and wide at will.” An apparent exception to sedentariness comes from young of *Fregata ariel* in the Central Pacific, which disperse great distances, mainly to the west and then north (Sibley and Clapp 1967) before returning to the Central Pacific. But the extent to which this mobility would affect genetic diversity would depend on the degree to which birds moved between breeding colonies. Satellite tracking of *Fregata magnificens* in the Caribbean and *F. minor* in the Indian Ocean showed that some birds are capable of rapid long-distance dispersal to other colonies or roosting sites but that most remain near their breeding colonies (Weimerskirch et al. 2006, 2016).

It was Mathews (1914, 1915) who first recognized that the frigatebirds from Ascension Island, South Atlantic (*Fregata aquila*), and from Christmas Island in the Indian Ocean (*F. andrewsi*) were distinct endemic species. The rapidity of evolution in this genus is underlined by the fact that the oldest subaerial rocks on Ascension Island are only about one million years of age (Nielson and Sibbett 1996), and suitable nesting habitat on Ascension has probably existed for less time than that. Christmas Island, on the other hand, is much older, with underlying rocks of Eocene and Miocene age (Trueman 1965). But *Fregata andrewsi* did not necessarily evolve on Christmas Island and may be a relict of a more widespread species that has become extinct elsewhere, paralleling the distributional history of Abbott’s Booby (*Papusa abbotti*), which once had populations in the western Indian Ocean and relatives that once occurred widely through the Pacific (Olson and Warheit 1988).

In the geologically young Galapagos Islands (Hickman and Lipps 1985), genetic data have recently corroborated what once seemed to be relatively minor morphological differences in showing that the Galapagos populations of Magnificent Frigatebird (*Fregata magnificens*) are “strongly differentiated from all conspecifics, and have probably been isolated for several hundred thousand years” (Hailer et al. 2010:817). As the name *magnificens* must attach to the Galapagos birds, if these are considered distinct at the species level, then the species represented in the rest of the former range of

magnificens must now be known as *Fregata rothschildi* Mathews 1914.

With these distributional and taxonomic facts in mind, it is worth noting that perhaps the most isolated populations of *Fregata* in the world are the two populations currently recognized as *Fregata minor nicolli* and *F. ariel trinitatis*, both currently confined to the island of Trindade (South Trinidad) in the South Atlantic Ocean, the oldest rocks of which are some 4 million years old, with much of the island-building dating to 2.3–2.9 million years ago (de Almeida 2006). Both species of frigatebird also once occurred on the equally remote South Atlantic island of St. Helena (Olson 1975), ~2,550 km NNE of Trindade (Fig. 1), the oldest rocks of which are some 14.3 million years old (Olson 1975). Lowe and Kinnear (1930:188–189) considered that the Atlantic/Caribbean vs. Indo-Pacific distribution “seems to us to be very remarkable in an ‘ocean-going’ bird like *Fregata* where physical or physiological barriers seem so difficult to define; but still more remarkable seems to be the fact that where an apparent climatic barrier in the shape of the cold ‘roaring forties’ has intervened between the Indian Ocean . . . and the Atlantic South–Trinidad [populations] it has not been effective . . .”

The inescapable conclusion from the accumulated evidence is that frigatebirds, despite their seeming capacity for long-distance dispersal, especially passively by storms, are considerably more sedentary, or at least more persistently philopatric, than expected for pelagic seabirds and that speciation within modern populations of *Fregata* has been relatively rapid and recent. Thus, there is every expectation that the populations of the Atlantic that are recognized currently under the names *Fregata minor nicolli* and *F. ariel trinitatis* may very well be valid species in their own right. Geographic variation in *Fregata minor* is complex and will require more future research to resolve. The purpose of the present paper, however, is to show that there is already sufficient evidence to suggest that the Atlantic Lesser Frigatebird, which I shall hereafter refer to as *Fregata trinitatis*, merits recognition as a distinct species from Indo-Pacific Lesser Frigatebirds (*Fregata ariel*), with the two collectively hereafter being termed “lesser frigatebirds” in lower case.

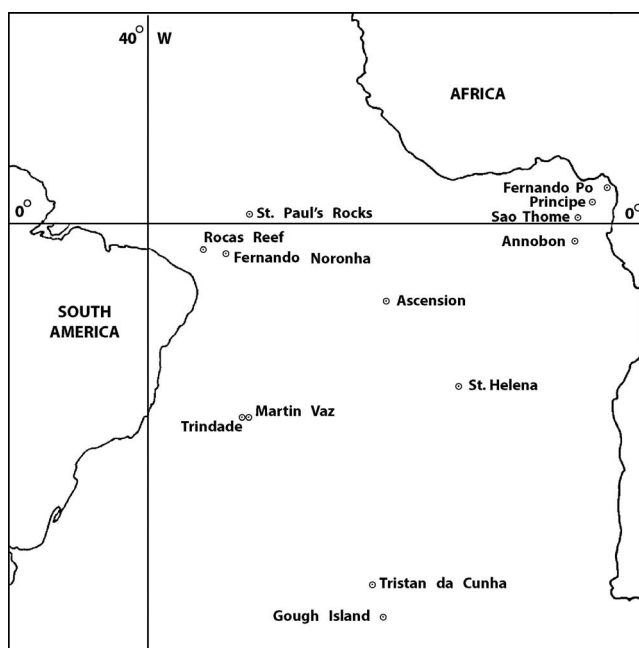


FIG. 1. Map showing positions of islands in the South Atlantic (modified from Williams 1984:394).

MATERIALS AND METHODS

Wing and culmen measurements of skin specimens of *Fregata ariel* and *F. trinitatis* are from the collections of AMNH, UMMZ, USNM, and YPM. Skeletal measurements are from 26 complete skeletons of *F. ariel* and 2 complete skeletons of *F. trinitatis*, all USNM; 4 incomplete humeri removed from skins of *F. trinitatis* (1 AMNH, 3 YPM); and an assortment of subfossil rostra, humeri, and ulnae identified as *F. trinitatis* from late Quaternary deposits at Prosperous Bay, St. Helena, Vertebrate Paleontology lot numbers USNM 241251, 241252, and 241248, respectively.

TAXONOMIC HISTORY OF LESSER FRIGATEBIRDS

Mathews (1914, 1915:287) recognized three subspecies of *Fregata ariel* in the Indo-Australian region, in the absence of good material from the Pacific, and considered the Atlantic birds to be referable to "subsp. indet." *Fregata ariel ariel* (Gray 1845; type locality Raine Island, Torres Strait, as restricted by Mathews 1914) has been applied to birds from eastern Australia east throughout the Pacific range of the species.

Fregata a. tunnyi (Mathews 1914; type locality Bedout Island off Western Australia) was described based on its supposedly larger size. *Fregata a. iredalei* (Mathews 1914; type locality Aldabra Island) has been recognized for the birds of the western Indian Ocean, based on supposedly smaller size, especially of the bill. Both Lowe (1924) and Peters (1931) considered *F. a. tunnyi* to be synonymous with *F. a. ariel*, although they recognized *F. a. iredalei*.

Following the Brazilian expedition to Trindade in 1916, de Miranda Ribeiro (1919) introduced the name *Fregata ariel trinitatis* for a single adult male specimen obtained on the island on 10 June. At this point, it is practically a *nomen nudum*. The name does not appear in the text of the account of *F. ariel* (de Miranda Ribeiro 1919) nor in the legends for the two unnumbered plates of the single specimen. The name appears only in a tabulation (p. 192, no. III) of putative new taxa "A Zoologia adquireu" (acquired [for the science of] Zoology), which included two other names proposed by de Miranda Ribeiro that have not been accepted as valid taxa: *Piscatrix sula autumnalis* and *Fregata minor januarua*. The only point of differentiation of the Trindade *F. ariel*

TABLE 1. Wing (chord) and culmen length measurements (mm) from skin specimens of lesser frigatebirds (*F. ariel*, Indo-Pacific; *Fregata trinitatis*, Trindade).

	N	Wing			Culmen		
		Range	Mean	S.D.	Range	Mean	S.D.
Indo-Pacific, male	148	442–544	506.5	14.65	74.5–94.2	83.5	3.45
Indo-Pacific, female	96	487–570	526.4	17.76	79.8–96.1	88.3	3.44
Trindade, male	5	510–533	520.0	9.30	74.1–84.0	79.3	4.21
Trindade, female	7	512–545	526.3	13.62	83.0–91.5	87.4	3.38

would be the presumption of smaller size of the bird from Trindade based on bill and wing measurements (81 mm and 510 mm, respectively) vs. a small table of measurements of Australian *F. ariel* (83–92 mm and 523–533 mm) from Mathews (1915:285).

Based on plumage differences of the population from Trindade, Lowe (1924) named a new subspecies *F. a. wilsoni*, doubtless without knowledge of de Miranda Ribeiro's (1919) earlier name. Later, Lowe became even more emphatic about the distinctiveness of the birds from Trindade, which he regarded "as a distinct species, *Fregata wilsoni*" (Lowe and Kinnear 1930:187). That de Miranda Ribeiro's name *trinitatis* was subsequently regarded as valid, beginning with Peters (1931) and in subsequent checklists (e.g., Hellmayr and Conover 1948, Dorst and Mougouin 1979), was probably because of the apparent validity of the characters used to distinguish *F. a. wilsoni* (Lowe 1924, Lowe and Kinnear 1930), a junior synonym.

SIZE VARIATION IN LESSER FRIGATEBIRDS

Length Measurements from Study Skins.—Apart from the plumage differences ascribed to *F. trinitatis*, all differentiation among lesser frigatebirds has been based on supposed differences in size. To test this, I measured 256 skins of lesser

frigatebirds. These show no non-overlapping differences in size between *F. trinitatis* and *F. ariel* (Table 1). Analyses of variance (ANOVA) showed no significant differences between females in wing length ($P = 0.98$) or culmen length ($P = 0.48$), or between males in wing length ($P = 0.38$), whereas in males there was highly significant difference between males in culmen length ($P = 0.008$). This may accord with the more striking differences in bill width measurements of both sexes of *F. trinitatis* compared with *F. ariel* (Table 5).

Additional Skin Measurements.—The collectors of the Blossom Expedition of the Cleveland Museum of Natural History were assiduous about entering the total length and wingspread of each specimen of bird in the field catalog of the expedition. These measurements were presumably taken according to standard techniques such as outlined in Baldwin et al. (1931). Because such a comparatively large series of frigatebirds from Trindade will probably never be assembled again, I have presented here a summary of these measurements as a useful comparison between the two local populations (Table 2).

Egg Dimensions.—I have been able to trace only a single egg of *Fregata trinitatis* in museum collections. This was taken on the Blossom Expedition (field number 4737) and is now in the Cleveland Museum (CMNH 57), although now

TABLE 2. Total length and wingspread measurements (mm, converted from inches) of frigatebirds from Ilha da Trindade taken from the field catalog of the Blossom Expedition in the Cleveland Museum of Natural History.

	N	Total Length			Wingspread		
		Range	Mean	S.D.	Range	Mean	S.D.
<i>Fregata m. nicolli</i> , male	5	886–1,006	939	44.6	1,958–2,083	2,043	50.3
<i>Fregata m. nicolli</i> , female	15	803–1,035	976	58.3	1,974–2,197	2,090	62.6
<i>Fregata trinitatis</i> , male	5	691–803	754	42.0	1,727–1,842	1,775	46.5
<i>Fregata trinitatis</i> , female	4	823–846	839	10.8	1,784–1,905	1,854	50.5

TABLE 3. Field measurements of egg dimensions (mm) of *Fregata ariel* from Christmas Island, Pacific Ocean, compared with those of the single known egg of *F. trinitatis*.

	N	Length			Width		
		Range	Mean	S.D.	Range	Mean	S.D.
<i>Fregata ariel</i>	355	52.0–68.9	61.1	2.79	39.0–48.1	42.4	1.35
<i>Fregata trinitatis</i>			61.2			42.8	

immeasurably broken with extensive repairs. Nevertheless, its dimensions were recorded in the field catalog of *Blossom* Expedition as 61.26×42.84 mm. These measurements are exactly equivalent to the means of 355 eggs of *F. ariel* from the Pacific (Table 3).

Weight Data.—The only available weight data for *F. trinitatis* are from two males that I collected. These fall well within the range of live weights of a large series of *F. ariel* from the Pacific (Table 4), which includes individuals that may have been starving during El Niño years, accounting for the birds' reduced weights.

Summary of Size Differences.—The birds from the South Atlantic cannot be diagnosed from other lesser frigatebirds based on length measurements from skins, or length measurements of rostrum and wing bones (Table 5), although means of length measurements of culmen in males are significantly smaller. Very limited data on weight and egg dimensions of *F. trinitatis* also fall well within the range of Pacific *F. ariel*. Measures of robustness of skeletal elements of rostrum and wing, however, are notably greater in *F. trinitatis* (see below).

OSTEOLOGY AND PALEONTOLOGY OF LESSER FRIGATEBIRDS

That there might be osteological differences between *Fregata trinitatis* and *F. ariel* was first

TABLE 4. Live weights (g) of *Fregata ariel* from Christmas Island, Pacific Ocean, compared with two male specimens of *F. trinitatis* from Trindade.

	N	Range	Mean	S.D.
<i>Fregata ariel</i>				
Male	56	540–900	707	87.43
Female	71	630–1,050	832.8	78.37
<i>Fregata trinitatis</i>				
Male		780; 835		

suggested by the discovery of well-preserved fossils of two species of frigatebirds on St. Helena (Olson 1975). These were most abundant in fine aeolian sediments in Prosperous Bay Valley that are thought to be no more than a few hundred years old. The two species of frigatebirds differ in size, the smaller one being much commoner. These I identified with *F. ariel trinitatis* and *F. minor nicolli* (Olson 1975), but I noted that the shafts of the humeri of the small species were markedly more robust than in Indo-Pacific *F. ariel* (Fig. 2). Undetermined species of frigatebirds were reported from St. Helena up into the early 19th century (Olson 1975), but no specimens were ever described or preserved, and the birds are definitely extinct on the island.

The sample from St. Helena necessarily combines males and females because the fossils could not be sexed. This series was augmented by measurements from two male skeletons of *F. trinitatis* and four partial humeri removed from skins of *F. trinitatis*, as well as good series of skeletons of both sexes of *F. ariel* from the Indo-Pacific.

The length measurements of humerus, ulna, and rostrum do not differ between the two taxa, but the width measurements confirm that the wing elements and rostrum of *F. trinitatis* are appreciably more robust than in *F. ariel* (Table 5, Fig. 2).

PLUMAGE SEQUENCE IN LESSER FRIGATEBIRDS

Certain plumages differ consistently between *Fregata ariel* and *F. trinitatis*, although I have detected none between adult males. In all other plumages, Indo-Pacific *F. ariel* shows some rufous. In adult females, this is usually around the back of the neck but may also be present in the breast. Very exceptionally an adult female of *F. ariel* will lack rufous in the collar, whereas none of

TABLE 5. Bone measurements (mm) from lesser frigatebirds including fossils from St. Helena referred to *Fregata trinitatis*.

	<i>F. ariel</i> (Indo-Pacific)															
	Male				Female				St. Helena				Trindade			
	N	Range	Mean	S. D.	N	Range	Mean	S. D.	N	Range	Mean	S. D.	N	Range	Mean	S. D.
Hum																
Length	13	143.4–155.7	150.1	3.43	13	151.8–163.7	156.9	3.41	22	147.0–160.0	152.6	3.52	2	146.8–148.8	147.8	1.41
Width	13	8.7–9.5	9.1	0.22	13	9.2–10.2	9.6	0.28	22	9.4–11.4	10.4	0.57	3	9.4–10.0	9.7	0.29
Ratio L/W	13	15.6–17.4	16.5		13	15.2–17.1	16.3		22	13.7–15.8	14.7		2	15.5–15.6	15.5	
Ulna																
Length	13	189.3–201.9	196.7	3.76	13	195.7–212.0	202.8	4.68	16	188.0–204.0	195.5	4.90	2	192.4–194.4	193.4	1.40
Width	13	7.6–8.6	8.1	0.23	13	7.7–9.0	8.4	0.33	16	8.3–10.0	8.89	0.53	2	7.9–.5	8.2	0.44
Ratio L/W	13	22.2–25.4	24.3		13	22.3–25.9	24.2		16	20.4–23.1	22.0		2	22.9–24.4	23.7	
Culmen																
Ridge Width	13	3.3–4.5	4.0	0.34	13	3.6–4.8	4.2	0.35	6	4.2–5.0	4.7	0.28	2	4.2–4.3	4.3	0.11
W post. nostril	13	15.8–16.9	16.2	0.32	13	16.0–17.9	16.6	0.58	6	22.2–24.3	22.7	0.73	2	16.2–16.7	16.5	0.33
Length	13	76.3–86.5	81.2	2.70	13	81.4–88.5	85.2	2.08	6	75.1–85.1	79.6	3.33	2	80.7–81.3	81.0	0.40
Ratio L/W	13	4.8–5.4	5.0		13	4.8–5.5	5.1		6	3.3–3.7	3.5		2	4.8–5.0	4.9	

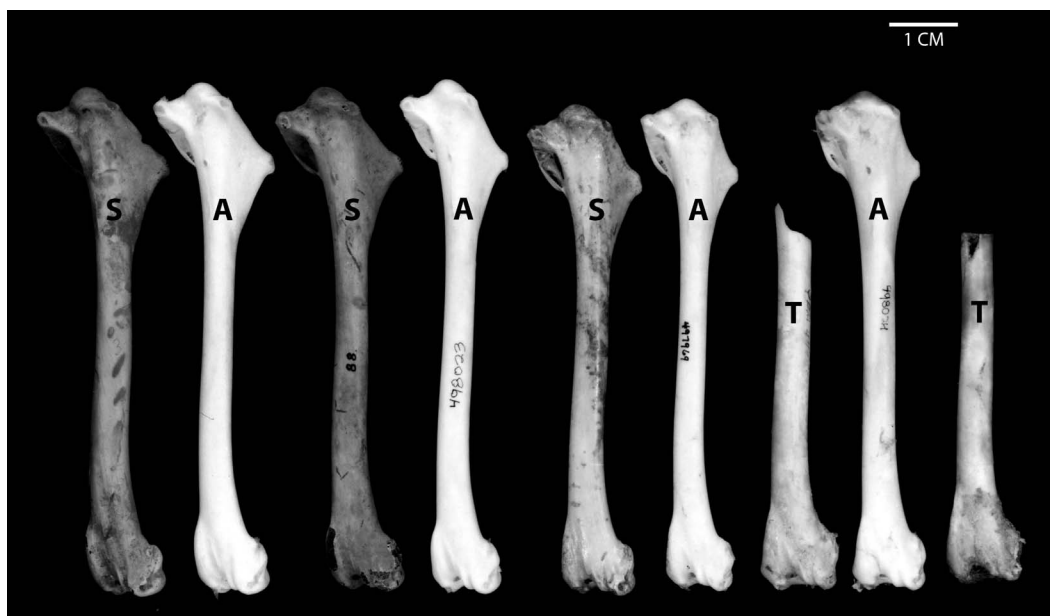


FIG. 2. Right humeri of lesser frigatebirds in anconal view: S = subfossil bones from Prosperous Bay, St. Helena, assigned to *F. trinitatis* (USNM 241251); T = bones removed from skins of *F. trinitatis* from Ilha da Trindade (YPM 44456; YPM 44454); A = *Fregata ariel* from Howland Island, Pacific Ocean (USNM 488390 female, USNM 498023 female, USNM 497969 male, USNM 498024 female).

the existing specimens of *F. trinitatis* adult or younger, show any sign of rufous. Apparently, the only indication so far that rufous may be present in *F. trinitatis* was my observation, at considerable distance, of a nestling juvenile with a rufous head. If this is typical of juveniles of the species, then the rufous must be a very evanescent plumage, because none of the available specimens of *F. trinitatis* is in juvenile plumage or retains any portion of such plumage.

As noted by Mathews (1915:286) in *Fregata ariel* “bird[s] [seem] to moult from the rusty-red coloured juvenile dress direct into the fully adult plumage.” This is confirmed by specimens in which both reddish juvenile feathers of the head are mixed with the iridescent black feathers of the adult plumage (Frontispiece, Fig. 3).

This is not the case in *F. trinitatis*, which has an intermediate immature or subadult plumage. Lowe’s (1924:310) perception of the nature of the bird from Trindade was based entirely on the three specimens in the British Museum taken on three different expeditions, one by Nicoll and two by Wilson, the last of which “both have brown heads and both have the white of the flanks

running well back into the axilla” (emphasis his). He was uncertain about the sex or age of these specimens “but, whatever they are, the brown head phase is either peculiar to the South Trinidad *ariel* or it so happens that this phase has never been noted or collected before throughout the whole range of the species.” He concluded that “other races of *F. ariel* moult straight from the white-headed [with rusty feathers] state into the glossy purple” and that “whatever the sequences may ultimately prove to be, there is some justification for thinking that a brown phase may be peculiar to South Trinidad,” for which reason he proposed his new subspecies *F. a. wilsoni*, doubtless without knowledge of de Miranda Ribeiro’s (1919) earlier name. Lowe later became even more emphatic about the distinctiveness of the bird from Trindade; he stated that the plumage “represents one of two things, viz. either a young phase of plumage which, by a curious chance, has not previously been met with by collectors throughout the entire range of the *ariel* group, or a phase which is anomalous” so that it is “wiser, until other material arrives to clear up the point, to regard the South



FIG. 3. Head and neck plumage of lesser frigatebirds: A, *F. ariel* adult female, Cargados Carajos (USNM 487605); B, *F. ariel* female changing from juvenile to adult, Borneo (USNM 182210); C, *F. trinitatis* subadult female, Ilha da Trindade (AMNH 269346); D, *F. ariel* juvenile female, Borneo (USNM 182211).

Trinidad form provisionally as a distinct species, *Fregata wilsoni*." (Lowe and Kinnear 1930:187).

With the ampler series from the *Blossom* expedition, it is clear that this subadult plumage, in which the top of the head and hindneck are dark brownish and the throat a smoky gray (Frontispiece, Fig. 3), is distinctive. Possibly what Harrison (1983) took to be the "subadult female" plumage of *F. ariel* may have been based on brown-headed specimens of *F. trinitatis*, but the available series of such specimens, if correctly sexed, contains both males and females. I have seen no similar plumage in any specimens of Indo-Pacific *F. ariel*, so that the brown-headed "phase" appears to be a character unique to *F. trinitatis*.

ILHA DA TRINDADE AND ITS FRIGATEBIRDS

The geographical focus of this inquiry is the very small and remote Brazilian island in the South Atlantic Ocean known in Portuguese as Ilha da Trindade, and in English usually as South Trinidad. It is all too frequently misspelled "Trinidad," which is not correct in either language. It is a volcanic peak with a surface area of 10 km² arising over 1,100 km east (20° 29.3' 31.7" S, 29° 20.6' 17.9" W) of the mainland of Brazil. It forms part of a diminutive archipelago with the islets of Martin Vaz (0.36 km²) ~48 km to the east (Alves and da Silva 2016). Martin Vaz is the accepted official spelling used here but the spellings "Martim" and "Vas" occur throughout the literature in every possible combination with the other spellings.

Hogs (*Sus scrofa*) and goats (*Capra aegagrus hircus*) were first introduced to Trindade by Edmond Halley, of comet fame, as early as 1700 (Eyde and Olson 1983). Human settlements on the island were sporadic and short-lived until a permanent garrison of a few naval personnel was established in 1957, occupying buildings on the northeast side. Meanwhile, the dense forest cover on most of the island began to disappear by the 19th century, probably because of lack of regeneration caused by foraging goats (Eyde and Olson 1983).

On 20 Aug 1874, astronomer James Ludovic Lord Lindsay, later 26th Earl of Crawford, obtained specimens of birds at Trindade, including two frigatebirds. At least one of these was received by the British Museum and was assigned to the larger of the two species of *Fregata* then recognized (Ogilvie-Grant 1898) and is therefore referable to *F. minor nicolli*. At this time it was noted that the birds were "found...sitting on the island" (Saunders 1880:163).

Author Edward F. Knight incorporated observations from his second visit to Trindade (20 Nov to 29 Dec 1889) in his novel *The Cruise of the "Alerte"* (Knight 1892) in which he mentions, in addition to the melancholy dead forests, that there were large nesting colonies of frigatebirds, boobies, and petrels (Alves and da Silva 2016).

The naturalist and Antarctic explorer Edward Wilson obtained a single specimen of *Fregata ariel* at Trindade on 13 September 1901 on the

southward leg of the *Discovery* expedition (Wilson 1904, 1967). Sharpe (1904) noted that this was the first example of the species *ariel* known for Trindade or the South Atlantic. Wilson and A. Cherry-Garrard collected one of each species of frigatebird offshore at Trindade on the southward voyage of the *Terra Nova* expedition on 26 July 1910, but saw none after landing (Wilson 1967). All these specimens of frigatebirds made their way to the British Museum, where described and discussed in detail by Lowe (1924) and Lowe and Kinnear (1930).

Nicoll (1906:673) accompanied Lord Lindsay to Trindade on his return trip in the *Valhalla* from 3–5 Jan 1905 and reported that the larger of the two frigatebirds (now *F. minor*) was “very common . . . but was not breeding at the time of our visit,” whereas only a single specimen of *F. ariel* was obtained “from the yacht as she lay off the island,” this being only the second specimen for the island (Nicoll 1908). He also noted that apparently “neither of these frigate birds was nesting on South Trinidad during our visit, but they may breed on the neighbouring islets of Martin Vas [sic], in the immediate vicinity of which we found them numerous” (Nicoll 1908:49). Mathews (1915) saw no specimens from Trindade and mentioned only two in the British Museum.

Murphy (1915), in the whaling brig *Daisy*, collected specimens in the waters around Trindade on 8 April 1913 and noted both species of frigatebirds, although he took no specimens himself. He noted that all individuals he saw that he assigned to “*Fregata ariel* (Gould) subsp.?” were immatures and noted that a specimen caught on a fish hook “was skinned by the captain [B. D. Cleveland] of the *Daisy*, and is now, I believe, in the Milwaukee Museum” (Murphy 1915:346). Murphy described the plumage and mentioned the supposedly small size of this specimen. The only frigatebird from Trindade in the collections of the Milwaukee Public Museum (MPM 1164), which I borrowed and examined, has a wing chord of 724 mm and a culmen length of 115 mm, indicating a bird much too large for any lesser frigatebird (see Table 1); therefore, the specimen must be referred to *Fregata minor nicolli*. Murphy’s description of the plumage agrees reasonably well with the specimen except that the “chestnut stripe” does not extend to the mentum but is confined to the lower throat and

upper breast. This pattern of chestnut does not occur in *F. trinitatis*.

Lowe (1924:309) listed five specimens of *F. minor nicolli* in the British Museum taken at Trindade on 29 Oct 1913 by Stammwitz but no specimens of *F. ariel* by that collector. Percy Stammwitz was a taxidermist at the British Museum, who accompanied Major G. E. H. Barrett-Hamilton on a mission to investigate the whaling industry at South Georgia (Lockyer 1913). The register of the BMNH bird collection also indicates that two Brown Noddies (*Anous stolidus*) and three White Terns (*Gygis alba*) were taken on the same day (R. Prys-Jones, pers. comm.). One of those was indicated as a “pullus” (chick), which could only have been taken by a shore party. Evidently their vessel must have stopped for one day of collecting at Trindade on the way south, which has not otherwise been noted in the ornithological literature.

The Brazilian government asserted a presence on Trindade in 1916 with a military contingent. A commission from the National Museum (Comissão do Museu Nacional), through the coordination of the museum’s director Bruno Alvares da Silva Lobo (Lobo 1919), was also dispatched to make a physiographic and zoological reconnaissance of the island. The expedition was headquartered in the area of beaches along the northeastern side of the island (Lobo 1919). Specimens were obtained over a period of 6 months, which resulted in the collection of 26 skins and 27 eggs of *Fregata minor*, but only a single specimen of *Fregata ariel*, which became the holotype of *F. a. trinitatis* de Miranda Ribeiro (1919). Also, a mounted adult male of *F. trinitatis* on exhibit at MNRJ may have come from the expedition of 1916, although I could find no data for it. At this time frigatebirds were encountered nesting on dead trees on the main island (de Miranda Ribeiro 1919: fig. 6). There are also three rather enigmatic specimens of *F. minor nicolli* (MNRJ 18975, 18964, and 21386) labeled as being collected by P. P. Peixoto on 15 Jan 1921, although I have found no other evidence of an expedition to Trindade in that year.

By far the most extensive sojourn of natural history collecting at Trindade was carried out by the *Blossom* Expedition of the Cleveland Museum of Natural History, which was intended to visit West Africa and Brazil and all the South Atlantic islands including South Georgia, although the last

was never attained. The expedition's vessel was a small 3-masted sailing schooner rechristened the *Blossom* but that had no auxiliary engine or other means of propulsion save wind. The ship was commanded by Texas naturalist George Finlay Simmons instead of the experienced old whaling master George Comer, who was originally intended to skipper the vessel. Although Simmons was "to assume the title of captain . . . it was purely a courtesy title as he had no such maritime rating." (Rockwell 1955:123). Simmons' (1927) popular account touches only lightly on the hardships endured by the crew of the *Blossom* because of inexperience and poor planning as later detailed by taxidermist Robert Rockwell (1932, 1955). Nevertheless, the collectors and preparators of the expedition were extremely dedicated and hard-working.

The *Blossom* collectors obtained a few birds, but no frigatebirds, at Martin Vaz on 21–22 December 1924, despite the fact that Simmons (1927), cited later by Murphy (1936), averred that both species of frigatebirds were encountered there and then later at Trindade. On the other hand, Rockwell (1932, 1955) mentioned "thousands" of seabirds at Martin Vaz and the few specimens that were collected; he said nothing of frigatebirds, so Simmons' recollection may be questioned.

The *Blossom* crew then went on to collect well over 200 specimens of birds plus other vertebrates, invertebrates, plants, and mineral specimens on Trindade from 23 December 1924 to 26 January 1925. These included at least 20 skins and 1 egg of *Fregata minor nicolli* and 8 skins and 1 egg of *F. trinitatis* as well as 4 specimens in formalin, at least one of which was *F. trinitatis*. Three others are not identified, although the dimensions given are closest to *F. trinitatis* but if not fully grown might represent *F. minor*. Although a few of the *Blossom* specimens of birds remain in the Cleveland Museum (CMNH: 2 *Fregata minor*), most were dispersed through sale or exchange, with the bulk going to Yale (YPM) and others to University of Michigan (UMMZ) and the American Museum of Natural History (AMNH).

As had the Brazilian expedition of 1916, the *Blossom* encountered frigatebirds breeding on dead tree trunks on the main island (Simmons 1927, Rockwell 1955). Rockwell (1955:195) noted that: "We had no trouble securing the birds we wanted for specimens. We seldom needed to shoot

them, and nearly all our catch was taken by hand." The *Blossom* anchored off the southern tip of the island and from there worked up the steep slopes of the southern side. Perhaps this venue resulted in the expedition obtaining many more specimens of *Fregata trinitatis* than the expedition of 1916, quartered on the northern side of the island.

In 1950, the Brazilian government sent a scientific expedition to Trindade, from 17–31 May, but with only 9 days of fieldwork (Alves and da Silva 2016). The birds from this expedition were reported by Novaes (1952), who noted up to five individuals of *Fregata minor nicolli*, which he regarded as a resident species being present and feeding on hatchling turtles (*Chelonia*). He failed to mention two specimens (MNRJ 25096, 25097) taken by the expedition. *Fregata trinitatis*, which Novaes treated as a species "migratoria" (i.e., non-resident), was not encountered, which may be taken as a possible indication that the expedition members did not cross to the south side of the island, where that species nests.

I stayed on Trindade making observations and collecting specimens of natural history from 13 December 1975 until 10 February 1976 (Olson 1981). Frigatebirds were scarce, and I managed to secure only two *Fregata trinitatis* (weight 780 g and 835 g) and three *F. minor nicolli* (1,160 g, 1,280 g, and 1,290 g). All five were males and were prepared as flat skins and skeletons. On the north side of the island, where I spent most of my time, frigatebirds were generally very sporadic in occurrence, usually only as single birds or pairs. On 11 January 1976, a few minutes after sunset I observed a male *F. trinitatis* pursued by a larger female frigatebird of indeterminate species, which kept up its pursuit high over Pão de Açúcar until the poor male regurgitated his dinner, which was handily caught by the female. Sightings became more regular beginning 30 January 1976, and by 3 February they were regular along the beaches of the northeast shore, where the birds were preying on hatchling green turtles (*Chelonia mydas*). I got the impression that *F. minor* had appeared almost out of nowhere for the hatching event, perhaps coming from Martin Vaz. One *F. minor* that I collected on 4 February contained remains of three turtle hatchlings, and one of two collected on 6 February contained remains of six turtles, whereas the other had only a few remnants of a flying fish (Exocoetidae).

I found no evidence of nesting by *F. minor* anywhere on the main island of Trindade nor on any of the adjacent islets. I did, however, observe *F. trinitatis* nesting on the largest islet at Ponta do Sul at the southern tip of the main island, where I first observed this species from a distance on 27 December 1975, including two that were simultaneously harassing Sooty Terns (*Onychoprion fuscatus*). On 4 January 1976, I observed birds with nests on the west side of the islet on very steep rocky slopes with bits of grass. Three females had nests within 30–60 cm of each other and had rather large downy white young with no scapular feathers showing. A male circling over these birds did not display and was not noticed and landed nearby, where hidden from view by a rock. Two males were later noted sitting, but I was unable to tell if they were with young birds or not. The salmon-colored soles of the feet as well as the white wing bars of females were quite conspicuous even at that considerable distance of my observations with binoculars. On 10 January 1976, I estimated a minimum of 15 nests of *F. trinitatis* at this same locality, with both males and females on nests, some with spread wings at about 1030 hrs Brazil Time (BRT). Males were not seen to display, and no piracy was observed. On 24 January 1976 at the breeding site off Ponta do Sul, with the aid of a telescope, I observed a juvenile with two females of *F. trinitatis* feathered as follows: all the back and most of the wing blackish but white down extending out the wing coverts and present on belly to chin. The head was definitely reddish but appeared more ochraceous than I remembered in Pacific specimens of *F. ariel*. In any case it was not white or brown and gray as in the subadult plumage. The two females showed no trace of reddish on the neck or elsewhere, confirming observations from skins of *F. trinitatis*.

Williams (1984) considered that *Fregata trinitatis* bred at both Trindade and Martin Vaz, but the latter appears to have been based on the rather dubious mention by Simmons (1927), followed by Murphy (1936). Williams (1984) further regarded *F. minor* as breeding only at Martin Vaz, but that may have been only a surmise based on my report (Olson 1981). Neither *Fregata trinitatis* nor *F. minor* was found at Martin Vaz from 19–21 March 1990 (Antas 1991).

From 18 February to 12 April 1986, A. Filippini recorded a maximum of six *Fregata minor* hunting

turtle hatchlings along the northeastern beaches of Trindade (Antas 1991).

Luigi (1993) reported few details about frigatebirds observed on Trindade from 1987, confirming the presence of *Fregata trinitatis* at Ponta do Sul but seldom seen elsewhere, whereas *F. minor* was often seen patrolling the northeastern beaches for baby turtles.

R. J. V. Alves (Alves and da Silva 2016; R. J. V. Alves, pers. comm.) and party landed by helicopter on Martin Vaz in January 1995 and in 2002, and although they encountered nesting boobies (*Sula*), no frigatebirds were seen.

da Fonseca Neto (2004:119) reported on studies of seabirds conducted during five expeditions to Trindade from August 1994 to February 2000, the months of the intervening visits not being specifically stated. Frigatebirds of both species were “observed sporadically, and they were not breeding in the studied periods”, although the areas studied included Ponta do Sul. *Fregata trinitatis* was observed on only five occasions flying over the northeastern beaches, whereas *Fregata minor* was seen almost daily on the same shores. Adult males of the larger species were also observed gathering nesting material (sedges and a dry branch) on two occasions in September 1994 and flying east towards points on Trindade, but I point out that that would also be in the direction of the Martin Vaz islets.

Port et al. (2016) reported observations of frigatebirds at Trindade from 19 February to 19 April 2013 which included surveys on foot in all parts of the island and several trips circumnavigating the island by inflatable boat. They could account for a minimum of only 4 individuals of *Fregata minor nicolli* (2 adult males, 1 adult female, 1 juvenile) and 6 individuals of *F. trinitatis* (2 adult males, 2 adult females, 2 juveniles). Presumably these figures reflect the maximum number of any given plumage seen at one time, although the actual number of frigatebirds present at the island may have been greater. All records of *F. trinitatis*, including perched birds, were from the same western side of the islet at Ponta do Sul where I observed this species in 1975–1976.

Unlike St. Helena, where the fossil record indicates that *Fregata trinitatis* was the more abundant of the two species of frigatebirds occurring there, all available evidence from at

least 1874–2013 on Trindade indicates that *F. minor nicolli* was more frequently encountered than *F. trinitatis*. Meanwhile, the status of frigatebirds at Martin Vaz has remained uncertain.

CONSERVATION

The conservation status of *Fregata trinitatis* and *F. minor nicolli* is dire in the extreme. At one time the largest populations were probably those of St. Helena, but frigatebirds of any kind disappeared from there in the 19th century. There is no realistic hope of their populations ever being restored. The continued survival of these taxa therefore depends on the populations of Trindade and Martin Vaz, which exist in very low numbers and are in imminent danger of extinction. These populations are regarded to be critically endangered (“Criticamente em Perigo”) by da Fonseca Neto (2004).

Trees suitable as nesting sites for frigatebirds began to disappear from Trindade in the early 19th century, probably because of lack of forest regeneration caused by destruction of vegetation by goats (Eyde and Olson 1983). Frigatebirds were still nesting on the remains of trees on the main island of Trindade in 1916 and 1925 but appear to have been gone by 1950; they were certainly absent by my visit in 1975–1976. At that time, the only breeding frigatebirds were probably fewer than 20 pairs of *F. trinitatis* on a small islet off the southern point of the island, where they nested on the ground. Ground nesting would probably not be feasible for frigatebirds on the main island of Trindade because of the large numbers of voracious, omnivorous land crabs, *Johngarthia* (formerly *Gecarcinus*) *lagostoma*. I postulated that the absence of breeding procellariiform birds at Fernando de Noronha and Ascension Islands might be explained by the presence of these land crabs, as opposed to St. Helena where there were no land crabs and where the procellariiform fauna was diverse (Olson 1981). That the only procellariiform on Trindade, the Trindade Petrel (*Pterodroma arminjoniana*) nests only in inaccessible sites on cliffs may not be because of introduced mammalian predators (Williams 1984) but could be a naturally evolved response to the presence of land crabs.

Although I published a guess that there were “probably no more than 50 individuals,” of

Fregata trinitatis on Trindade (Olson 1981:489) this was misquoted by da Fonseca Neto (2004:133) as “mais de [more than] 50 indivíduos,” and the number was even further inflated to 50 pairs by Williams (1984) and Antas (1991), when in fact my estimate of 50 individuals was highly optimistic. I found no evidence of nesting of *F. minor nicolli* at Trindade, which suggested at that time that the only remaining breeding site might be at Martin Vaz, but that has never been confirmed.

The main threats to recolonization of the main island by frigatebirds once came from cats, which are direct predators, and goats, which prevent forest growth and the redevelopment of trees as nesting sites. Doubtless because the island lacks beaches accessible for careening vessels, Trindade has been spared invasion by rats (*Rattus* spp.), although house mice (*Mus musculus*) are present and abundant. Mice, especially in the absence of competing species of rodents, can pose a serious threat to ground-nesting insular seabirds on oceanic islands (Angel et al. 2009), and on Trindade may be quite arboreal as well.

Hogs persisted on the island past the middle of the 20th century but were eliminated, along with donkeys and sheep by order of the military command by 1965 (da Silva and Alves 2011). I saw no evidence of hogs anywhere on the island during my stay.

Feral cats (*Felis catus*) were present in substantial numbers on Trindade and doubtless have played a significant role in the reduction and near extirpation of many of the breeding seabirds of the island. Cats were shown to have a very detrimental effect on Ascension Frigatebirds (*Fregata aquila*) attempting only to roost on the main island of Ascension (Olson 1977). Eradication of feral cats on Ascension resulted on partial restoration of some seabird populations but did not eliminate threats from other sources such as rats (Ratcliffe et al. 2009). Frigatebirds, however, have not resumed breeding on the main island of Ascension.

Cats have been successfully eradicated from numerous small islands with the almost immediate recovery of at least some seabird populations (Nogales et al. 2004, Rauzon et al. 2008). This was accomplished largely through poisoning campaigns. A shooting campaign by the Brazilian Navy appears to have resulted in the elimination of cats from Trindade by 1994, so that numerous

marine sniper teams who forayed and camped throughout the island between 1998 and 2005 did not encounter any cats (R. J. V. Alves, pers. comm.).

Eradication of goats, which were still present on Trindade in good numbers into the early 21st century, became a high priority. Techniques and potential strategies for goat removal are summarized by Daly (1989) and include shooting. Again, the Brazilian military took seriously its stewardship of the island and sent in teams of marine snipers so that the last goats were eliminated by 2005, with nearly immediate recovery of some components of the native vegetation (da Silva and Alves 2011). One wonders, however, if forest regeneration could take place in time to save either species of frigatebird given their current extremely low numbers. For this reason the next step being contemplated now is the erection of artificial breeding and roosting perches in areas most suitable for frigatebirds (R. J. V. Alves, pers. comm.).

Although, because of the elimination of introduced mammals, the future of frigatebirds at Trindade looks somewhat less bleak than only a few years ago, it still seems perilous in the extreme. As yet we do not have an accurate estimate of numbers of each species nor any information about where the larger species may be breeding, if it still does. We can only hope that the days of *Fregata trinitatis* are not to be few in number. It would be regrettable if this rarest of all frigatebirds, one of the rarest seabirds in the world, were to join the shades of all the other species of birds pummeled into extinction in the past three or four millennia by the expansion of humanity to oceanic islands; to become only a shadow (Fig. 4) in the mind's eye of the few who have ever heard of it, and with nothing left to learn about it save what can be acquired from the few relics preserved in museums.

CONCLUSION

Frigatebirds (Pelecaniformes, Fregatidae) defy our expectations of large, far-ranging, pelagic seabirds. It is inappropriate to view them through the same lens as albatrosses and petrels (Procellariiformes) which may have nearly unlimited dispersal ability and in which species appear to evolve slowly but may persist



FIG. 4. Silhouette of a male *Fregata trinitatis* in intricate aerial positioning movement. Made from a photograph by Ruy Barreto dos Santos on Ilha da Trindade, January 2014. Note how the wings appear to be functioning independently of one another, the tail has been reconfigured from a fork to a point, and even both tiny feet have been brought into play to assist in maneuvering. Photograph supplied by Ruy Valka Alves; silhouette made by Christina Gebhard.

for long geological periods unchanged. In contrast, frigatebirds, although capable of dispersal, tend to be highly sedentary and strongly philopatric, so that isolation, as in land birds, may provide a driving force for speciation. We are now beginning to appreciate that frigatebirds may speciate in geologically short periods of time, as best exemplified by those endemic to the young islands of Ascension and the Galapagos.

With the Atlantic Lesser Frigatebird confined to the remote island of Trindade, and formerly to St. Helena, both of which are millions of years older than Ascension or any of the Galapagos, the populations are starkly isolated from their nearest relatives in the Indian and Pacific oceans by unfavorable geographic and oceanic conditions. Thus, the stage was certainly set for a speciation event and the evidence marshalled here is interpreted as proving that such a speciation event has taken place.

The Atlantic birds evidently have a juvenile plumage with a rufous head as in Indo-Pacific *Fregata ariel*, but this appears to be very evanescent and must be quickly lost as there is no hint of rufous in any of the subsequent plumages, whereas in *F. ariel* there is some rufous in the plumage of all but adult males. In *F. ariel*, the head feathers molt directly from the rufous juvenile plumage into the glossy black adult

plumage, whereas the Atlantic birds have a distinctive subadult plumage in which the head is mottled brown, with a smoky gray throat.

In the Atlantic birds, two measurements of bill width indicate a considerably stouter bill than in *F. ariel*, and bill lengths of males are statistically significantly smaller than in *F. ariel*. In Atlantic birds, the ulnae, and especially the humeri, are markedly more robust than in *F. ariel*. This indicates that these populations have had to make evolutionary adaptations in both feeding apparatus and in locomotion, presumably to accommodate unique conditions met with in the Atlantic.

These differences should be quite sufficient an argument for raising the Atlantic Lesser Frigatebird, *Fregata trinitatis*, to full specific rank, separate from Indo-Pacific Lesser Frigatebird, *F. ariel*. Unfortunately, *Fregata trinitatis* now remains on Trindade in extremely small numbers and is in imminent danger of extinction. Successful removal of all introduced mammals from Trindade save house mice, *Mus musculus*, may have improved the chances of survival of frigatebirds on the island, but whether populations can recover from such low numbers remains to be seen.

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