LARGER PETRELS OF THE GENUS 
PTERODROMA¹

BY ROBERT CUSHMAN MURPHY AND JESSIE M. PENNOYER

This paper is a study of 15 forms of the genus *Pterodroma*. Their association is based less on obviously close interrelationship than on the fact that none of the forms discussed appears to be a member of any other group or superspecies.

The affinities of the species and subspecies listed are indicated by general resemblances and, in the case of several forms represented in the American Museum of Natural History by skeletons as well as skins, by virtual identity of anatomical structure. We have compared, for example, skulls of the species *neglecta*, *arminjoniana*, and *ultima* and can find no detail that would distinguish one from another. The foregoing three species belong to the surface-nesting division of the genus *Pterodroma*, and might perhaps be expected to share a structural uniformity. However, the skulls of various burrowing species prove to differ from those of surface nesters in no way other than size.

Comparison of skulls and skeletons of the species *lessonii* with those of *incerta* shows uniformity in size and detail except for slightly greater interorbital breadth in *incerta*. The least width between the fossae of the supraorbital glands in two skulls of *incerta* is 7 mm. and 8.8 mm. In three of *lessonii*, the same dimension is 3.8, 4.5, and 5.3 mm. Too much reliance cannot be placed on this interorbital dimension, however, because a series of seven skulls of a single species, *neglecta*, shows an individual variation proportionate to the cited interspecific variation.

Skulls and body skeletons of *lessonii* and *macroptera* reveal no perceptible differences.

¹ Birds Collected During the Whitney South Sea Expedition, No. 60.
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Taking into account structure, plumage pattern, and habits, we have arranged the 15 forms of petrels in an order differing considerably from that of recent systematic lists and in our opinion more nearly approaching a sequence that reflects descent and kinship.

The differences among the members of this group of petrels fall into several categories, all of which are worthy of brief mention and tabulation (table 1). First among these is one already referred to above, relating to breeding habits. Nine species and subspecies burrow in the ground, laying the egg in a subterranean chamber that may in certain instances be at a distance of 2 meters or more from the entrance. The other six species and subspecies are the surface nesters, which incubate in the open or sometimes in superficial niches and chinks of cliffs. Mathews (1936, p. 376, and elsewhere) has stated that these two types of reproductive habit are associated with very different responses when nesting birds are disturbed. The burrowing species, he maintains, defend themselves violently with feet and claws, while the surface-nesting species are so gentle as to allow themselves to be handled with impunity. On this basis he has even divided the genus *Pterodroma* into two named groups exhibiting respective "temperamental differences."

While there may be a certain degree of truth in the observations on which this distinction is based, it is likely that Mathews has overemphasized it. Surface-nesting petrels, including *Pterodroma neglecta*, sometimes react in a vociferous and bellicose manner, and a typical burrowing petrel (*Pterodroma cahow*) has been found on occasion to be completely gentle or almost apathetic when pulled out of its nest or lifted off its egg (Murphy and Mowbray, 1951, pp. 271–275).

Another marked difference in the forms under consideration relates to zonal distribution on the surface of the globe. We find examples characteristic, respectively, of the tropical, subtropical, and subantarctic zones of ocean water. Representatives of each of these three groups may have a circumpolar distribution. This is particularly noteworthy in the case of a tropical species (*arminjoniana*) in view of present continental barriers, which would appear to separate lower latitudes of the world ocean into two or even three mutually exclusive basins.

Special attention should be called to the fact that petrels belonging to different but adjacent oceanic zones are in some in-
stances extremely closely related. Thus a subtropical species of the South Atlantic (and possibly Indian) oceans, namely, *Pterodroma incerta*, differs from a subantarctic and probably circum-polar species, *Pterodroma lessonii*, only in pigmental characters of a type familiar among both birds and mammals bred under conditions of laboratory control. *P. incerta* has brown plumage, while *lessonii* has little or no brown pigment in its feathers and is therefore gray where the other species is brown. Even though we can in this instance draw conclusions only by analogy, we are justified in assuming that genetically *incerta* and *lessonii* are sibling species and that the differences visible to the eye are associated with different responses to climatic environment.

While the association of petrels with definite oceanic zones is fairly sharp and rigid, at least with respect to breeding grounds, we find a slight overlap, particularly at nesting stations close to the convergence between tropical and subtropical ocean water. Thus in the central South Pacific, two tropical species (*alba* and *arminjoniana*) share certain marginal nesting islands with two subtropical species (*neglecta* and *ultima*). In table 1, the presence of petrels at what might be called extralimital breeding grounds (as distinguished from those within the normal or prevailing zone) is indicated by a check (x) enclosed within parentheses. Petrels require islands for nesting, and, within certain zonal limits, the mere availability of an island seems to be more important than its precise location.

Oceanic ranges during the non-breeding season are under considerably more elastic meteorological or oceanographic control. Thus among typically subantarctic petrels, such as *lessonii* and especially *inexpectata*, the normal flight ranges extend deeply into the antarctic zone of surface water, even though their breeding stations lie north of the Antarctic Convergence.

In still another manner expressive of an environmental response, the petrels of this assemblage differ among themselves in that the reproductive period of certain species falls in the spring and summer of the Southern Hemisphere, whereas other species are winter breeders. Still a third category is represented among certain tropical and subtropical species that have a prolonged breeding season or one that seems to show still inexplicable differences from one island group to another.

Falla (1934, p. 259) has made the interesting suggestion, with reference to the resident petrels of New Zealand, that the extent
of the annual migration may determine the breeding dates, the highly migratory species returning regularly to lay eggs in the southern springtime, whereas the sedentary or permanently resident petrels are winter breeders, with more flexible calendars and a more extended reproductive season. This generalization may apply especially to north-south, rather than east-west, migration. Falla himself refers to the extensive travels of *P. macroptera*, a winter breeder, *across* the meridians of longitude. On the other hand, this species is not known to cross the tropics into the Northern Hemisphere.

Finally, as regards characters of plumage, we can recognize among the petrels under consideration several types: two of the forms have a cloudy, mottled, and indefinite plumage pattern; nine others show sharply defined, symmetrical, and uniform patterns, which exhibit only a single phase; four forms are strongly dichromatic, having white-breasted and all-black phases, as well as intermediates which, in the species *neglecta*, run almost the whole gamut of possible patterns between the extremes (fig. 3).

In addition to such differences of pattern, these petrels also exhibit a gradation in the cuneation of the tail. At one end of the series, rectrices lengthening towards the central pair produce a strongly wedged outline (as in *incerta*), whereas at the other end of the series, *neglecta* has a comparatively square or gently rounded tail.

No group of petrels includes better examples of sibling species than the one under consideration. In the case of *lessonii* and *incerta*, the two members of the pair are distinguishable at sight. Of the genotypes we have no knowledge, but the phenotypes differ strongly in their respective tones of pigmentation. Furthermore, they are allopatric birds, confined to different oceanic zones.

*Pterodroma alba* and *P. arminjoniana heraldica*, on the other hand, are sympatric sibling species, and certain examples of the second of these petrels bear an extraordinarily close resemblance to most specimens of *alba*, a fact fully discussed in the systematic section of this paper.

Recent studies of bird behavior have shown that intraspecific recognition is commonly based not on perception of "wholeness" but rather of particular and striking marks in plumage or on unfeathered integument. It is highly probable that spots in the lining of the wing, white shafts of primary quills, or similar insignia serve such a purpose for several species of *Pterodroma*
FIG. 1. Diagrams of under-wing pattern in species of *Pterodroma*. A. *P. inexpectata*. B. *P. rostrata, macroptera, incerta, and lessonii* (all four species have exactly the same pattern, although tone of pigmentation is variously blackish brown, brown, and gray). C. *P. solandri*. D. *P. alba*. E. *P. arminjoniana heraldica* (white-breasted and black phases have similar wing linings). F. *P. ultima*. G. *P. neglecta* (white primary shafts).
which mingle at the nesting grounds. Such an extremely conspicuous mark as the nearly black bar on the prevailing white under wing of *Pterodroma inexpectata* may surely be assumed to be as important for recognition by other birds of its own species as it is by naturalists in the field!

In continuation of this thought, we have had careful semi-diagrammatic drawings made of the several types of under-wing patterns represented among the species discussed in this paper (fig. 1). In view of the extraordinary diversity of plumage pattern found among four petrels occupying (in part) common nesting grounds (*neglecta, arminjoniana, alba, and ultima*), the fixed pattern of the wing lining probably has a bearing on reproductive isolation. It is equally likely that the pattern and quality of call notes are also important in recognition, but information on this must await more intensive field study.

All these petrels have similar natal plumages of dark down, in some cases brown, in others dusky gray, but not infrequently changing in the prevailing color tone between the protoptyle and mesoptyle stages.

On the basis of fairly extensive measurements, there seems to be little or no evidence of sexual dimorphism in any member of the group except one of the two subspecies of *Pterodroma arminjoniana*. When the five usual dimensions of 20 specimens of *P. arminjoniana arminjoniana*, almost equally divided as to sex, were plotted in the form of frequency distribution graphs, males were found to be consistently larger than females. The relationship in the length of the tarsus is illustrated in figure 4. These data were subjected to statistical trial by the *t*-test, as described by Snedecor (1946, pp. 41–42). This technique yields the standard deviation of the mean of samples drawn from a single population and enables estimation of the .95 "fiducial interval," within which averages of other samples of the population will fall unless there is a one in 20 mischance in sampling. Computation of these intervals for the tarsal measurements of male and female *Pterodroma arminjoniana arminjoniana* gives ranges which do not overlap, indicating a significant size difference between the sexes of this subspecies. Here the range for the population average was 35.9 to 37.6 mm. for males and 34.5 to 35.4 mm. for females.

In order to facilitate comparison, the dimensions of all 15 forms of petrels have been summarized in tables 2 and 3. The statistical treatment includes derivation of the standard deviation and co-
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efficient of variation for series represented by an adequately large number of specimens.

There is a remarkable consistency in the variability of dimensions among the different members of the group, and likewise between the sexes of each, with the single exception noted above. The measurements of *Pterodroma arminjoniana heraldica, ultima, alba, neglecta neglecta*, and *neglecta juana*, all reveal parallel variations, the wing in every case showing the lowest coefficient of variation, the tail (or in *neglecta*, by a very slight margin, the tarsus) the greatest. In no case is the coefficient of variability greater than .376 per cent. In some forms the females appear to show greater variability than the males, but as this difference is nowhere more than .9 per cent it is probably not significant.

For numerous measurements, comparisons, and bibliographical responsibilities we are indebted to Miss Susan Irving. Drs. Ernst Mayr and Dean Amadon have helped greatly by critical discussion and suggestions and by reading the entire text.

**Pterodroma macroptera**

This large, black, and conspicuous petrel is of subantarctic and barely subtropical distribution, the latitudinal extremes of its breeding range being bounded by Tristan da Cunha and southwestern Australia on the north and by Kerguelen on the south. The two island groups named are, respectively, close to the Subtropical and the Antarctic Convergences (Murphy, 1936, p. 67). Throughout this comparatively narrow belt, *Pterodroma macroptera* is apparently of circumpolar distribution. According to Falla (1937, p. 180), the two or more races of the species range farther to the east and west of their nesting grounds than any other Procellariiformes except the albatrosses. With the exception of Kerguelen Island, all the known breeding stations lie between latitudes 30° and 40° S., and the distribution at sea is chiefly between latitudes 30° and 50° S.

The type locality of the species is the seas off the Cape of Good Hope, where the bird has long been familiar to sailors. Falla has called attention to the sharp oceanographic break between that area and the much colder surface waters of the southern Indian Ocean. For such reasons, it would seem likely that the typical race nests at Tristan da Cunha, and that the Kerguelen Island population may differ subspecifically. Unfortunately, the material available is insufficient for settling that taxonomic prob-
lem in the present study. We have seen but one Kerguelen specimen, and the measurements of others recorded by Falla and by Jouanin (1951, p. 349) do not differ noticeably from those of our Atlantic birds. It may be remarked that the Crozet Islands, which are also a breeding station, are climatically somewhat intermediate between Tristan and Kerguelen. As noted by Falla, the subspecific distinctness of the bird inhabiting the New Zealand area is obvious.

This petrel nests in burrows, and its season of reproduction is that of the Southern Hemisphere winter period from Tristan da Cunha and the Australian coast as far southward as glacial Kerguelen. In the more temperate parts of the range, the nesting season is extraordinarily prolonged.

_Pterodroma macroptera_ is one of the largest members of its genus, with a strongly cuneate tail and black bill and feet to match its dark plumage. Alleged sexual dimorphism is probably based on evidence too scanty to have statistical significance. Falla found that New Zealand and Indian Ocean males had slightly larger bills than females, but the opposite chances to be true among the South Atlantic specimens we have examined. There seems to be no appreciable discrepancy among our 45 New Zealand adults of both sexes.

_Pterodroma macroptera macroptera_  
_Procellaria macroptera_ A. Smith, 1840, Illustrations of the zoology of South Africa, pt. 2, pl. 52 (seas off the Cape of Good Hope).

The South Atlantic specimens examined include two from Tristan da Cunha, one from Inaccessible Island in the same group, and several collected in various latitudes northward to 19° S., and even to the Gulf of Guinea. The last two may be regarded as extralimital. The southernmost position for a bird collected in the Atlantic is latitude 49°20' S., longitude 6° E., not far from Gough Island, which is probably a breeding station. Eleven such specimens, several of which lack sex determination and other data, agree with the single Kerguelen Island bird in being of smaller size and distinctly less "gray-faced" than representatives of the species from the New Zealand area. As indicated above, however, comparison of an adequate series of specimens from Kerguelen with birds from more northerly areas is much needed.

A male collected by Mrs. Mary K. Rowan at Tristan da Cunha on June 24, 1949, is in fresh plumage, with the head completely
dark and with scarcely any of the basal white showing on the throat feathers. Another male, taken on the "Blossom" expedition of the Cleveland Museum of Natural History on August 27, 1925, in latitude 27°52'S., longitude 8°26'W., about 10° north of Tristan, shows considerable light mottling on the throat, and is browner and more faded than the Rowan specimen. Bierman and Voous (1950, p. 84) note that this petrel is distinguishable in life from Procellaria aequinoctialis by the browner appearance of its dark plumage.

At Tristan da Cunha, where this petrel is known as the "black eaglet," it is said that eggs are laid in July, which would agree with the seasonal régime of the New Zealand race in approximately the same latitude. At Kerguelen, Studer (1879, p. 109) describes "Procellaria Atlantica" (one of the synonyms of this species) incubating on November 13 an egg which hatched December 2. In view of the thorough investigations by Falla, it appears likely that Studer was in error as to the species or the date. Falla had abundant opportunity to watch reproductive activities at Kerguelen, and he reports that eggs are laid in June and that fledglings take to sea in November. The Kerguelen breeding period thus appears to fall about a month in advance of that in New Zealand, and it is probable that in a locality at the verge of antarctic surface water the life history of the species is under stricter calendar control than in a less rigorous climatic belt.

**Pterodroma macroptera gouldi**

*Aestrelata gouldi* Hutton, 1869, Ibis, p. 351 (New Zealand seas).

*Pterodroma macroptera albani* Mathews, 1912, Austral Avian Rec., vol. 1, p. 30 (Rabbit Island, Western Australia).

This Pacific race is distinct from that of the Atlantic in averaging larger, in having a generally heavier bill, with a long maxillary unguis, and in the pronouncedly gray face. Even a fledgling chick taken at Cuvier Island, New Zealand, on January 19, 1926, is as gray-masked as adult birds in fresh plumage. Mathews' type of *albani*, now in the American Museum collection, is a relatively small example, although falling within the range of the New Zealand series from which it is in no way distinguishable. Serventy and Whittell (1951, p. 100) state that this petrel nests on many islands along the south coast of Australia between Albany and Cape Arid, and that storm-drifted birds have been found on Western Australian beaches as far north as Pelsart Island.
the latter fact they have inferred the existence of a still undiscovered breeding station on the west coast, possibly at the Abrolhos Islands.

The American Museum collection includes a number of older specimens from New Zealand and the surrounding waters as far southward as the Auckland Islands. The Whitney South Sea Expedition series was taken mostly at sea between the North Island of New Zealand and the Kermadec group, between November 30 and December 8, 1925. Positions indicated on the labels of some 40 specimens are at the following latitudes and longitudes: $34^\circ$ S., $176^\circ$ W.; $37^\circ$ S., $180^\circ$ W.; $38^\circ$ S., $179^\circ$ W. All these skins are relatively "white-faced," in rather sharp contrast to Atlantic examples and our single specimen from the Indian Ocean. The plumage appears somewhat lighter and browner or less sooty than that of the Atlantic birds, but this may be due in part to wear and fading, because certain other New Zealand examples are characterized by fresh, dark, and glossy feathering. The Whitney expedition birds are also mostly marked as having reduced gonads, which would be expected at the indicated season.

The birds in this New Zealand series are almost uniformly larger than Atlantic specimens. Their bills have pronounced whitish or buffy chalky streaks, particularly on the maxilla, which appear to be due to a salty deposit of some sort.

Falla (1934, p. 255) writes of this petrel in New Zealand: "it may be said that it breeds on every islet where burrows can be made, on all suitable cliffs, along the mainland coast, and sometimes a mile or two inland." A full list of its New Zealand breeding stations would include hundreds of islands, islets, and capes. It is a winter breeder, the bulk of the eggs being laid in late July and August, but the nesting season of the subspecies as a whole is so prolonged that only for a single midsummer month or thereabouts (January, February) are examples likely to be completely absent from breeding stations. Serventy and Whittell report that at Eclipse Island, off southwestern Australia, the laying of eggs begins late in May, the month corresponding with the Northern Hemisphere November. On an islet in King George Sound, birds have been found incubating in the middle of June (Allen, 1938, p. 317).

At Cuvier Island, New Zealand, Beck, the leader of the Whitney expedition, found that feral cats were the principal enemy of this petrel on its nesting ground.
Pterodroma solandri


Procellaria phillipii Gray, 1862, Ibis, p. 246 (Norfolk Island).


We have followed Loomis (1924, p. 282) in rejecting Gmelin's name melanopus in favor of Gould's solandri. Latham's English description (1785, p. 408) of the "Black Toad Petrel" and Gmelin's Latin characterization of the same bird show that both authors were referring to a much smaller species. In addition, their details of plumage and pattern cannot well be reconciled with the species under consideration.

Gould's description of solandri is reasonably satisfactory, considering its brevity. His dimensions, however, show one obvious misprint in that the tarsus is recorded as having a length of 3/4, instead of 1 3/4, inches. Finally, it should be remembered that both Latham and Gmelin credited melanopus to North America, and that Mathews later arbitrarily changed this type locality to Norfolk Island.

This is quite obviously the species which Governor Phillip (1789, p. 161) described and figured as the "Norfolk Island Petrel," and which Gray subsequently described as "Procellaria phillipii."

Godman (1908, p. 219) has suggested that Pterodroma solandri may be a dark form of lessonii, being larger than the Atlantic macroptera in several dimensions, and having the bases of the inner primaries white. However close its measurements may be to those of lessonii, it differs significantly in having a squarer tail and in the fact that it nests in a more genial oceanic zone, being subtropical instead of prevailingly subantarctic. Its egg (from the few published measurements) appears to be considerably smaller than that of lessonii. It resembles Pterodroma ultima, though with less white on the throat and a squarer tail.

The American Museum possesses a large series of this petrel from the Rothschild collection, all of which were taken by Roy Bell at Lord Howe Island in months of 1913 and 1914 covering practically every season of the year. The named localities on Lord Howe include Little Slope, Black Face, Mt. Ledgbird, and Lower Road. The area occupied by the petrel colonies extends from an altitude of 2000 feet, at the summit of Mt. Gower, almost down to sea level.

Mathews (1928, p. 18) states that the breeding season is from
May and June to August, and that 15 eggs in his possession were collected on Mt. Gower, on May 30, 1914. They were all taken from chambers at the ends of burrows.

Thus solandri, like macroptera, might appear to be a winter-nesting petrel. Nevertheless, chicks from Lord Howe in the American Museum collection are dated April and August, as well as October, which would suggest that, as in the case of macroptera, the nesting season of the population as a whole is very prolonged. This would accord with tradition at Norfolk Island, where the species, as the famous "Bird of Providence," was exploited to extinction in the late eighteenth century (Whitley, 1934, p. 48).

Pterodroma solandri is to be regarded as a subtropical petrel known exclusively from the Tasman Sea and closely adjacent waters. Its only nesting sites are Lord Howe Island and (formerly) Norfolk Island. Peters' references (1931, p. 63) to breeding grounds in the Tuamotu and Austral Islands are evidently based on erroneous identifications in the literature.

Pterodroma solandri is predominantly slate gray, but the plumage shows considerable variation in the extent and quality of a brownish cast over the ventral surface, throat, head, tail, wings, and the basal parts of the feathers on the back. This variability is due mainly to molt, wear, and fading. Fledglings and immature examples in still unworn plumage show many white-edged feathers on the back. For a period after molt and renewal in the adults, there is a silvery sheen on the lower back, tail, and wings, due to the grayish central parts of the new feathers which contrast with their darker borders. There is much evidence that the exact time of molt has a wide range, in correspondence with the dates of oviposition, hatching of eggs, etc. In general the bluish gray dorsal cast is most evident among May birds, while those taken in November are browner and considerably more mottled as a result of feather abrasion. The mottling or scalloping is especially conspicuous on the facial feathers, which have white bases, and many such birds show a pronounced whitish hmask surrounding the bill. On the other hand, the long series of specimens includes also a few October and November birds in fresh plumage.

All adults have pale inner webs on the wing quills, and in many the axillaries and feathers of the flanks are slightly tipped with white. The robust bill is black, but the skin color of the feet and legs seems to vary from uniform black to a black that is
definitely tinged with brown or even with yellow on the tarsus and the proximal parts of the toes. Fledglings can be distinguished from mature birds by their relatively slender bills, but we have no information as to how long such a criterion remains useful.

**Pterodroma lessonii**


In the original description, Garnot showed his carelessness by citing north, instead of south, latitude, and by omitting directional symbols of the longitude. Since the latter was undoubtedly a meridian measured from Paris rather than from Greenwich, the type locality would be a little west of Magellanic South America.

*Pterodroma lessonii* is a petrel of the cooler or subantarctic zone of the Pacific and Indian oceans. Away from its nesting stations, it ranges far southward across the Antarctic Convergence, foraging in surface waters as cold as $-1^\circ$ C., and keeping in general to waters not warmer than 15° C. (Bierman and Voous, 1950, p. 87). Along with *Pterodroma incerta*, to which it is closely related, it is one of the largest members of its group, a bird of distinctive pattern and burrowing habit.

In the absence of evidence that the species is known in the Falklands area, it is hardly clear why Mathews (1913, p. 37) substituted “Falklands Island Seas” for the position originally named by Garnot. Information received from Dr. Holger Holgersen of the Stavanger Museum (in litt.) reports this petrel as common just off the Pacific entrance of the Strait of Magellan on December 9, 1947. This position is very close to the type locality. Later in the course of his Pacific cruise, Dr. Holgersen saw the species frequently, but never to the south of the Antarctic Convergence.

It is not unlikely that *Pterodroma lessonii* is replaced in the South Atlantic by a representative species, namely, *Pterodroma incerta*. It has been suggested, indeed, that *lessonii* is merely a color phase of *incerta*. Both birds have a dark under wing, white breast, and pink or flesh-colored feet, distally blackish or brownish; but *incerta* is predominantly a brown bird, while
lessonii is gray. In considering lessonii as a variant of incerta, Murphy (1936, p. 703) overlooked a discrepancy shown by the under tail-coverts, which are brown in incerta, but white in lessonii instead of the gray to be expected if the differences were due to mutation. Moreover the two are divided by their zonal preferences, incerta belonging to a warmer oceanic area.

The close relationship of both of these species with Pterodroma macroptera, a "melanistic mutant," has also been pointed out. American Museum specimens of lessonii include birds collected during the Whitney South Sea Expedition in latitude 50° S., longitude 179° W., February, 1926, and others taken at Antipodes Islands nesting grounds in the same period. We also possess older specimens from the Auckland Islands, the Antipodes, Macquarie, and Kerguelen, as well as the beach-drift example from New South Wales to which Mathews applied the subspecific name australis. A downy chick taken at Greenland Harbor, Kerguelen Island, by Robert Hall on January 30, 1898, indicates that the nesting season begins very early in the Southern Hemisphere spring. This young bird is clad in fuscous gray or almost liver-colored down except for the throat, which is sparsely covered with whitish down. It agrees entirely with chicks from the Antipodes Islands.

The downy chicks taken by R. H. Beck at Antipodes on February 23 and 26 are of an appropriately larger size than the Kerguelen nestling. Two Rothschild collection chicks of similar size, taken by Travers at the Antipodes, are labeled "June, 1895," but Falla has left in the tray a memorandum stating that, from his personal knowledge of Travers' travels these specimens are incorrectly labeled as to date. There are therefore no data to throw out of joint our conclusions regarding the spring and summer nesting of this species throughout its subantarctic range.

Most of the Whitney expedition specimens taken at sea are marked as having small gonads, although several females still revealed enlargement of the ovaries. Beck's notes from Antipodes on February 23 state that the majority of the adult birds seemed then to have passed their active breeding period. The burrows were scattered about everywhere on the islands, the tunnels in some instances extending for several feet just beneath the surface of the ground. One or more pairs were encountered still in the process of digging, although other nests already contained young chicks. The burrows were damp, and in some in-
stances partly filled with puddles of rain water, but the nest platforms, topped with grass stems and feathers, were dry. In one place, 17 skulls of this petrel were found on the ground, representing birds which had been captured and eaten by skuas. The burrows were mainly on the slopes and in valleys of the island, the summit being occupied by albatrosses.

**Pterodroma incerta**

*Procellaria incerta* Schlegel, 1863, Muséum d’histoire naturelle des Pays-Bas, vol. 6, Procellariae, p. 9 ("Mers australes" = South Atlantic Ocean).

*Pterodroma incerta* is a zonal representative of *P. lessonii*, exhibiting genetic differences in color and very slightly in pattern, as discussed under the preceding species. It may possibly be a longer-winged petrel than *lessonii*, although a comparison based on 28 specimens of one species and only 13 of the other is not necessarily significant (table 2).

It may also be a South Atlantic representative species of *lessonii*, although this is not certain because the subantarctic flight range of the latter may yet prove to be completely circumpolar. At any rate, *incerta* inhabits a warmer oceanic zone and breeds at the verge of subtropical waters. The certainly known nesting stations are restricted entirely to the islands of the Tristan da Cunha group in the South Atlantic. Zoogeographic evidence, as well as abundant records of the species from the western Indian Ocean, makes it extremely likely that St. Paul and Amsterdam Islands are, or formerly were, breeding stations. The question of extinction of petrels at the latter islands has been discussed in a former publication (Murphy and Irving, 1951, p. 2).

The American Museum possesses specimens of this petrel from Tristan da Cunha and from not distant parts of the South Atlantic between latitudes 24° and 39° S., and longitudes 31° and 47° W. Bierman and Voous (1950, p. 84) observed the species in summer (December), south of southernmost Africa in latitude 42° S., well within the subantarctic zone of surface water (surface temperature 9° C.)

The inhabitants of Tristan appear to recognize a relatively close relationship between *P. incerta* and *P. macroptera* because they call the former the "white-breasted black eaglet." The nesting season at Tristan is not yet known with certainty, the only recorded egg being of doubtful identity (Murphy, 1936, p. 702).
Pterodroma rostrata

*Pterodroma rostrata* is a tropical species of relatively restricted range in the Pacific Ocean. Little is known of its distribution and habits, but it occupies insular groups between the Tropic of Capricorn and the Equator, namely, the islands of the Marquesas, Society, and the Solomon or neighboring archipelagoes, and New Caledonia. It is a burrowing species, breeding in the Southern Hemisphere winter season. Downy chicks have been taken in October and November at two breeding stations of the typical form.

![Image of Pterodroma rostrata](image)

**Fig. 2.** Two subspecies of *Pterodroma rostrata* differing in size. Upper: *P. r. rostrata* female, Moorea Island, Society group. Lower: *P. r. becki* female, type.

The species is characterized by a very definite plumage pattern: brown, slightly darker than, but close to, the Clove Brown of Ridgway, on dorsal surface, head, neck, and sides; ventral surface white, caudad from a distinct line of demarcation, including the under tail-coverts; the concealed parts of the dark plumage are grayish, and the feet parti-colored. Two subspecies are here recognized.
Pterodroma rostrata rostrata

Procellaria rostrata Peale, 1848, United States exploring expedition ... under ... Charles Wilkes, vol. 8, p. 296 (Tahiti, Society Islands).


Examination of Brasil's type of trouessarti in the Muséum National d'Histoire Naturelle in Paris shows that there are no grounds for recognition of an endemic subspecies at New Caledonia. The describer compared his single New Caledonian bird with two old examples from the Marquesas and Tahiti, both of which had dimensions in the lower ranges of typical rostrata. It is possible that the differences are correlated with age, because the type of trouessarti is evidently a mature bird. Its primaries had been clipped in life, as though it had been kept for some time as a captive. Its four available dimensions are as follows: tail, 114; culmen, 36; depth of bill in front of nostril, 12.8; tarsus, 49; middle toe and claw, 63 mm., all of which fit well into the series of measurements of Marquesas and Society Islands specimens summarized in table 2.

The American Museum has one downy young taken at "Hovailov," at an altitude of 1000 feet above sea level in New Caledonia, on October 26, 1914, by P. D. Montague. It is intermediate in size between similar chicks collected at Hatutu Island and Tahuata Island, Marquesas group, on October 12 and November 27, respectively. This would suggest a common calendar in the stages of life history over all the nesting range.

Pterodroma rostrata becki


To date only the type specimen of this remarkable form has been reported upon in print. It is a female collected January 6, 1929. On May 18 of the same year, Hannibal Hamlin, who succeeded R. H. Beck as field leader of the Whitney South Sea Expedition, captured a male specimen northeast of Rendova Island. This example has a slightly more robust bill than the type, with which it agrees in every essential respect. Dimensions of both specimens appear in table 1.

As previously noted (Murphy, 1928, p. 1), this form is a miniature of typical rostrata of the central Pacific archipelagoes. In
length of wing and tail, it seems to be about 15 per cent smaller than the mean of *rostrata*, and in other dimensions, fully 25 per cent smaller. Although the distinction in size is perhaps greater than in other recognized subspecies of petrels, there seems to be no good reason for not regarding the small form as a race of *rostrata*. Its unknown nesting sites are probably in the Solomon Islands area.

**Pterodroma brevirostris**


The type specimen in the Paris Museum is labeled Cape of Good Hope. Kerguelen Island, which appears to be the only known breeding station, has subsequently been designated as type locality, but the question still hinges on the actual provenance of the type specimen.

We have been able to find for examination only seven examples of this fluffy, drab, curiously nondescript petrel, which looks as though its closest affinities might be with *Pterodroma inexpectata*. Falla (1937, p. 186) has suggested that *brevirostris* may be “a dark phase of *P. mollis*,” partly because he frequently observed both forms together in the Indian Ocean.

This conclusion we regard as unlikely for a number of reasons. First, the under surface of the quills and the distal parts of the feet are paler than in *mollis* (i.e., the opposite of what might be expected if Falla’s supposition were correct). Second, *brevirostris* seems to be a relatively short-tailed petrel. Third, it has a distinctive quality of plumage texture which is somewhat hard to define. Fourth, *brevirostris* and *mollis* breed in different oceanic zones, notwithstanding the fact that their flight ranges may overlap.

Although *brevirostris* has been repeatedly credited as a breeding species of Tristan da Cunha, the evidence has never been forthcoming. We know, on the other hand, that it nests at Kerguelen Island, which lies on the Antarctic Convergence, and that it ranges regularly southward into the belt of pack ice, as far as latitude 70°S. It has rarely been observed north of about 45°S., and there can be no certainty that the type specimen of 1820 was actually collected near the Cape of Good Hope.

The species is to be classed as an antarctic or “high subantarctic” petrel, whereas *mollis* is marginally subtropical, with pres-
ent or former breeding stations at Tristan da Cunha, Gough, St. Paul, and Amsterdam Islands.

The concealed parts of the feathers in *brevirostris* are everywhere white or hoary gray under the dark gray surface, and the entire plumage is exceptionally thick and soft.

It is, of course, a summer breeder. Eggs have been taken at Kerguelen in October, downy young in December, fledglings in January.

Bierman and Voous (1950, p. 85) report that a specimen of this petrel collected in latitude 55° S., longitude 16°50’ E. weighed 310 grams. They report also that it ranges far into the Antarctic zone, feeding in surface water with temperatures between +2° and −2° C.

**Pterodroma inexpectata**

*Procellaria inexpectata* FORSTER, 1844, Descriptiones animalium, ed. Lichtenstein, p. 204 (Antarctic Ocean).


The mottled or, one might say, motley plumage of this species shows a wide range in aspect. Its texture and its general pattern, except in the wing lining, suggest kinship with *Pterodroma brevirostris*. Some of our specimens are almost clear gray ventrally, caudad from the breast, while others show so much of the concealed portions of the plumage that they are mainly, and sometimes asymmetrically, whitish on the belly. The barring on lower throat and breast is also highly variable, forming in some instances a more or less distinct collar. The variation as a whole is obviously related to wear, the specimens with abraded feather endings showing more and more of the whitish under plumage. Falla (1937, p. 186) has particularly noted the dark band on the under wing, which is a diagnostic mark.

A fledgling from Antipodes Island is still largely covered with gray down which has an almost purplish cast. The new contour plumage of its wings is light or “bluish” gray, and the feathers of the forehead and anterior crown have a strongly scaled appearance, each dark center being outlined with white. Adults in fresh plumage have similar foreheads, but in most examples the area is darker owing to abrasion of the feather margins.

*Pterodroma inexpectata* is a burrowing, summer-nesting petrel which formerly had one of the most extensive breeding ranges
of any member of its genus. According to Falla, it once lived throughout the forest over the greater part of all three main islands of New Zealand, and on most of the outliers, including the Chatham and Bounty Islands, the Aucklands, and the Antipodes. Quite possibly the enormous distribution of the species, including regular migrations to American and Alaskan waters, and accidental occurrence in New York State, has been due to the extremely large population of this petrel in primitive times.

At any rate, the surviving numbers of _Pterodroma inexpectata_ are relatively small because, after the introduction of wild and domestic predatory animals, it rapidly disappeared on the New Zealand mainland breeding grounds. Its present nesting range is limited chiefly to islets in New Zealand sounds and bays, to the coastal islets of Stewart Island, and to the more distant outliers. Presumably the native predatory marsupials prevented establishment of the species at Tasmania, which is an otherwise suitable habitat. The type specimen of Mathews' race _thompsoni_, from the Tasmanian coast, agrees with New Zealand birds.

Falla records the probable presence of _Pterodroma inexpectata_ in the pack ice beyond latitude 66° S., due south of Western Australia. This was in January, early in the Southern Hemisphere summer and close to the height of the New Zealand breeding season. Falla cites further antarctic records from the reports of Peale and Clarke. It is therefore likely that this species, like _Pterodroma brevirostris_, migrates very far south of its temperate and subantarctic nesting grounds, as well as far to the north across the Equator and into the subarctic Pacific.

The American Museum possesses a series from the Rothschild, Buller, and Mathews collections, as well as 10 specimens taken during the Whitney South Sea Expedition between latitudes 38° and 49° S., and longitudes 175° E. and 179° W., December, 1925, to February, 1926. The positions are all east of New Zealand, south almost to the latitude of Antipodes Islands.

Several of the Whitney expedition birds were undergoing molt and replacement of the flight quills when they were collected in mid-February. In one or more specimens, new growth has proceeded as far as the third from the outermost primary. All but one are noted as showing reduced gonads, the single exception being a female taken on December 2, 1925, in which the ovaries were greatly enlarged. Presumably the others had laid eggs on dates between December and February.
Pterodroma neglecta

We have had the good fortune to examine more than 500 examples of this widely distributed petrel, which is known only from the Pacific Ocean, and to compare our specimens with all related species within the genus *Pterodroma*. In the American Museum collections from the Brewster-Sanford Expedition and the Whitney South Sea Expedition are skins from scores of insular localities and neighboring oceanic points, representing every stage of growth and every phase of plumage. Many additional specimens have been seen and measured by the senior author in European museums and elsewhere.

![Image of Pterodroma neglecta specimens](image_url)

*Fig. 3.* Normal individual variation in *Pterodroma neglecta neglecta*. Left to right: Male, Ducie Island; female, Rapa Island; male, Ducie Island; female, Oeno Island; male, Ducie Island; male, latitude 29° S., longitude 177° W.; male, Ducie Island.

The populations of *Pterodroma neglecta* recall those of domesticated birds, such as *Columba livia*, because of the wide range of plumage pattern. The blackish and the white-breasted phases are linked by a series of intermediates representing nearly every possible blend. In addition, asymmetrical and partially albinistic styles crop out in a significant proportion of all populations.
Because of such extreme variability of plumage, random examples of *neglecta* are likely to bear a close superficial resemblance to certain other species of the genus *Pterodroma*. The over-all range is from rather light gray to sooty brown, or nearly black. A collar on the breast of whitish birds varies individually all the way from complete absence through gray-washed, peppered, and wavy or barred designs to one of solid dark brown. Therefore, from trays containing large series of skins, it is possible to pick examples of *Pterodroma neglecta* which in general aspect almost duplicate representatives of the species *arminjoniana*, *rostrata*, *macroptera*, and even *lessonii*.

Light-breasted specimens of this petrel have parti-colored feet, the distal half of the toes and webs, the outermost toe, and the distal end of the tarsometatarsus being blackish, the remainder of leg and foot whitish or flesh-colored. Most examples in intermediate plumage show similar skin colors on the legs and feet. In birds of wholly dark phase, the condition seems to be variable, some having parti-colored legs and feet exactly like those of the light birds, whereas in a few others the skin color seems to be black and is so marked on many labels. Dr. J. P. Chapin has noted on the label of a black bird collected by himself at Ducie Island that the proximal parts of foot and tarsus were brown in life, a hue deepening distally to black. This pattern still shows vaguely in the dried skin.

The constant specific characters which distinguish *neglecta* from all its congeners are: a relatively short and squarish tail, the presence of white or ivory-white shafts on the primaries (usually extending well towards the tip on the outermost quill), and an under wing pattern which includes a highly conspicuous, elongate subterminal patch formed by the white (or in a few instances silver-gray) inner webs of the primary quills.

The above-mentioned diagnostic features seem invariable. In most black examples of the species, the patch on the under wing is as white as in the palest of the gray-backed, white-breasted, and white-headed specimens. One among many dark birds, on the other hand, may have under wing markings of silvery gray rather than white, but even such examples have quill shafts which, in the whiteness of their external aspect, leave no doubt as to specific identity.

The following tabulation records the relative proportions of white-breasted, all-dark, and intermediate adult birds in the Ameri-
can Museum collection from a number of breeding localities. To a certain extent, the sorting is arbitrary because, while the extremes can be allocated without difficulty, the intermediates cover a broad range of variation. Furthermore, since the basal parts of the plumage are everywhere white in this species, feather wear inevitably produces a certain degree of mottling. In the tabulation below, white-breasted birds, with or without dark collar, are grouped in the "light" column, and birds of prevailing gray or brownish black plumage, with uniform ventral surface, in the "dark" column.

There is evidence of a cline of increasing degree or proportion of whiteness from east to west across the South Pacific. Thus birds of light phase reach an extreme in intensity, if not in numbers, at the Kermadec and Lord Howe Islands at the western end of the breeding range. Conversely, the blackest of the dark examples seem to be most characteristic of Juan Fernandez and San Ambrosio, at the eastern end of the breeding range.

<table>
<thead>
<tr>
<th>Light</th>
<th>Intermediate</th>
<th>Dark</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mas Atierra, Juan Fernandez</td>
<td>3</td>
<td>47</td>
</tr>
<tr>
<td>San Ambrosio</td>
<td>0</td>
<td>7</td>
</tr>
<tr>
<td>Ducie</td>
<td>36</td>
<td>19</td>
</tr>
<tr>
<td>Henderson</td>
<td>5</td>
<td>7</td>
</tr>
<tr>
<td>Oeno</td>
<td>6</td>
<td>8</td>
</tr>
<tr>
<td>Tuamotu Islands</td>
<td>9</td>
<td>8</td>
</tr>
<tr>
<td>Rapa, Austral group</td>
<td>7</td>
<td>14</td>
</tr>
<tr>
<td>Kermadec</td>
<td>23</td>
<td>21</td>
</tr>
<tr>
<td>Lord Howe</td>
<td>2</td>
<td>1</td>
</tr>
</tbody>
</table>

We conclude, on a basis of measurements rather than of plumage, that the populations of *neglecta* comprise two geographic races, one of which belongs to the eastern South Pacific, nesting at Juan Fernandez and San Ambrosio Islands, east of the meridian of 80° W.; and the second to the central and western part of the same ocean between Ducie Island (longitude 124°48' W.) and the coast of Australia. This petrel does not breed, or no longer breeds, at Easter Island, so that a gap of considerably more than 2000 geographic miles now appears to separate the two nearest nesting stations of the eastern and western populations.

Unlike *arminjoniana*, which is a tropical species, *neglecta* is typically a petrel of the subtropical oceanic zone, its breeding places lying chiefly between the Tropic of Capricorn and the Kermadec (close to latitude 30° S.) and Juan Fernandez (latitude
33°40' S.) Islands. In the southeastern part of the Tuamotu Archipelago, not far from the populous breeding grounds of Oeno, Henderson, and Ducie Islands, it nests at several stations which lie technically within the tropics. In this area, the breeding grounds of neglecta overlap those of arminjoniana. No doubt both species also occupied Pitcairn Island in times before its settlement by the mutineers of the "Bounty" and their descendants.

In the eastern Pacific the flight range of Pterodroma neglecta extends, at least casually, northward into and across the tropics as far as the west coast of Mexico. Less is known with reference to east-west dispersal within the breeding range, and nothing about north-south flights in the western Pacific. Most series of specimens have been collected in rather close proximity to nesting islands, and, as noted above, there is a wide spatial gap between the eastern and western populations.

This petrel is a surface nester, and there is some evidence of an almost year-round breeding period, probably with a seasonal node of maximal egg laying at any one locality. The American Museum possesses series of eggs collected at Mas Atierra Island, Juan Fernandez, between mid-December and mid-January; from Ducie and Oeno Islands in late March and mid-April, respectively; and from the Kermadec group in mid-November. Oliver (1930, p. 142) reports that on Sunday Island of the Kermadecs fresh eggs have been observed between October 20 and December 6. He adds, however, that on Meyer Island, in the same group, the laying season comes four months later, eggs being found from the end of February well into April, the young birds leaving the island in July and August.

**Pterodroma neglecta neglecta**

*Procellaria neglecta* Schlegel, 1863, Muséum d'histoire naturelle des Pays-Bas, vol. 6, Procellariae, p. 10 (Sunday Island, Kermadec group).


Peters (1931, p. 63) and certain other recent authors have replaced Schlegel's specific name *neglecta* by *phillipii* of G. R. Gray, which was first published in 1862, one year earlier than *neglecta*. Gray's name was based not on specimens but on the description of the "Norfolk Island Petrel" in Phillip's account of the voyage to Botany Bay (1789, p. 161 and plate). Reference to this source shows beyond any doubt that the bird referred to by
Phillip was not Schlegel’s species but was undoubtedly *solandri*. Quite aside from evidence in the description is the statement that his Norfolk Island petrel “burrows in the sand like a rabbit, lying hid in the holes throughout the day.” *Pterodroma neglecta* is everywhere a surface-nesting rather than a burrowing bird. Finally it should be noted that Norfolk Island lies outside the breeding range of *neglecta*, which, with the other evidence, vitiates the opinion of Loomis (1924, p. 282) that Governor Phillip’s description and plate refer to “one of the variations of the Neglected Petrel.”

The American Museum possesses one specimen attributed to Norfolk Island, but its true provenance is extremely doubtful. It is marked as collected by P. Metcalfe previous to January 17, 1888. The data on the label were subsequently recorded after receipt of a letter from Metcalfe to W. M. Crowfoot. If this specimen actually represents a Norfolk Island record, it may be regarded as purely accidental.

All our specimens collected between the vicinity of Ducie Island and just off the east Australian coast, in latitude 30° S., where a dark male was obtained by the Archbold expedition on April 16, 1934, may be allocated to the typical race, regardless of possible small and poorly defined populational differences.

Our American Museum series includes many skins from the Rothschild collection, obtained by Travers and others at Sunday Island and elsewhere in the Kermadec group. These bear dates running from December, 1894, to as recently as July, 1913. The vernacular name, “winter mutton bird,” has been written on some of the labels, which indicates local recognition of the fact that some species of petrels return to breed during the Southern Hemisphere summer, and others in the opposite season. It is not quite clear, however, to just what part of the year “winter” refers at the Kermadec Islands.

According to Whitney South Sea Expedition experience at the Kermadecs, the southeastern Tuamotus, Ducie, Oeno, Rapa, Ravaivai, and other islands close to the Tropic of Capricorn, the breeding season of this petrel is either variable or prolonged. Eggs, for example, were collected at Ducie Island on March 22, at Oeno on April 18, and at Sunday Island, Kermadec group, on November 18. As noted above, Oliver has reported quite different nesting seasons for the species at two neighboring islands of the Kermadecs.
At Ducie Island, Chapin collected a male nestling, associated with an adult, on January 3, 1935. The chick was just beginning to lose the long gray down from the face and throat. Its stomach contained squid mandibles. At the same island Beck collected a newly hatched chick, with its parent, on March 20, and at the same date there were plenty of fresh eggs. Here, then, is further evidence of a prolonged or all-year nesting period.

In any one locality, it is probable that molt is seasonally associated with the reproductive period. Among our November birds taken at or near the Kermadec Islands, a good proportion have missing central rectrices and new or not fully grown wing quills.

In the American sector of the range, the Brewster-Sanford Expedition obtained a considerable series of eggs of *P. neglecta juana* at Juan Fernandez in December and January. The dimensions of the American Museum eggs of both subspecies are summarized in table 4.

<table>
<thead>
<tr>
<th></th>
<th>Ducie Island</th>
<th>Oeno Island</th>
<th>Sunday Island</th>
<th>Juan Fernandez</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number</td>
<td>11</td>
<td>5</td>
<td>4</td>
<td>10</td>
</tr>
<tr>
<td>Average</td>
<td>63.9 × 46.3</td>
<td>62.5 × 46.8</td>
<td>65.4 × 46.6</td>
<td>65.2 × 45.9</td>
</tr>
<tr>
<td>Longest</td>
<td>69.0 × 49.7</td>
<td>64.5 × 47.9</td>
<td>67.2 × 46.4</td>
<td>68.0 × 45.9</td>
</tr>
<tr>
<td>Shortest</td>
<td>60.4 × 44.7</td>
<td>61.2 × 44.9</td>
<td>64.0 × 45.4</td>
<td>60.7 × 45.0</td>
</tr>
<tr>
<td>Broadest</td>
<td>69.0 × 49.7</td>
<td>63.7 × 48.3</td>
<td>64.9 × 48.5</td>
<td>66.4 × 50.5</td>
</tr>
<tr>
<td>Narrowest</td>
<td>64.4 × 44.6</td>
<td>61.2 × 44.9</td>
<td>64.0 × 45.4</td>
<td>60.7 × 45.0</td>
</tr>
</tbody>
</table>

Skins in the American Museum include birds from Mt. Gower, Lord Howe Island, among which is the type of an unacceptable race, *quintali* Mathews. These specimens were obtained by Roy Bell, who recorded on his labels that they were taken about 1000 feet below the summit of the mountain, that the petrels of this species never burrow, and that the surface nests are made up of an accumulation of leaves that may weigh as much as 4 pounds.

Whitney expedition specimens collected at Rapa, the southernmost island of the Austral group, in February, 1922, exhibit almost the full range in plumage pattern presented by the species as a whole. The extremes include both dusky and whitish birds,
some of the latter having pale gray heads and a minimum of mottling on the ventral surface. Well-grown downy chicks taken at Rapa on February 16 all seem to be coming into dark-phase contour plumage, but this is no more than a coincidence, because light-phase fledglings are well represented from near-by parts of the Pacific.

In the Tuamotu group, specimens were collected in late May and June, 1922, at the islands of Maria, Nengo Nengo, and Ahunui. All these localities are relatively near the outliers of Oeno, Henderson, and Ducie, which are one of the great centers of population of the species.

At Ducie Island, on March 25, E. H. Quayle of the Whitney expedition corps made entries in his notebook from which the following is transcribed: "I spent at least an hour wandering through the groups of nesting shearwaters, looking for unusual phases of plumage. *P. neglecta* certainly has a variety of hues, from the dark brown birds with brown breast and dark legs to the extremely white-breasted and almost white-headed examples, which have the upper third of the toes and the tarsus whitish. The smaller shearwater (*Pterodroma arminjoniana heraldica*) varies less than *neglecta*.

The notes of both Beck and Quayle report that at Ducie Island and elsewhere four species of surface-nesting petrels (*neglecta, alba, arminjoniana,* and *ultima*) mingle more or less on the nesting ground, but that in each particular cluster of breeding birds one species usually predominates. They also found nests of *neglecta* close to those of red-tailed tropic birds (*Phaethon*).

**Pterodroma neglecta juana**


Average larger size (table 2) clearly distinguishes the eastern South Pacific race of this petrel. Less definite distinctions of plumage have been referred to above. The plumages of the race have been fully discussed by Murphy (1936, p. 704).

The subtropical zonal proclivities of the species *neglecta* are strongly suggested by the breeding distribution of the eastern Pacific race. At Juan Fernandez its nesting grounds are confined to the inner islands of Mas Atierra and Santa Clara, which lie in water of lower average temperature than the outer island of Mas Afuerra. The latter, incidentally, is a nesting station of at
least two other species of the genus *Pterodroma* of definitely tropical affinities.

Farther northward in this same part of the eastern Pacific, which is partly under the influence of the Peru current, *P. neglecta juana* similarly breeds on San Ambrosio Island rather than on the outer or western island of San Felix.

Loomis (1918, p. 103) has noted that this race of *neglecta* occasionally migrates across the Equator into the Northern Hemisphere. A specimen from the Rothschild collection can now be cited to extend slightly the northward migration. It is a female taken by R. H. Beck in latitude 21°10' N., longitude 115°38' W., on July 1, 1897. The position is near the Revillo Gigedo Islands. The specimen had been labeled "*Pterodroma heraldica,*" but it proves to be an example of *Pterodroma neglecta juana*.

As regards plumage, we have seen no representative of the race *juana* either as completely white on the ventral surface, as pale on the head, or as devoid of a pectoral band as many specimens of the western Pacific race taken in colonies between Ducie, the Kermadecs, and Lord Howe.

The alimentary tracts of eight specimens collected by Chapin in the neighborhood of San Ambrosio Island all contained mandibles and pens of squids. Measurements of the eggs of this race are listed in table 4.

**Pterodroma alba**


*Aestrelata oliveri* MATHEWS AND IREDALE, 1914, Austral Avian Rec., vol. 2, p. 113 (Kermadec Islands).

Murphy (1928, p. 2) has reported in detail on part of the series of this tropical, surface-nesting petrel collected during the Whitney South Sea Expedition. The specimens came from the Line group (Christmas Island), the Marquesas, and the Phoenix Islands. The breeding season appears to be prolonged, as among certain other tropical petrels, because fledglings were taken at Hatutu Island of the Marquesas in September and October,
whereas young in all stages of growth were encountered at Christmas Island in February.

Many more specimens were collected by the Whitney expedition staff at Ducie, Oeno, and Henderson Islands, in March and April, 1922, and a single adult at Tikahau Island, in June 1923. Tikahau is in the western part of the Tuamotu Archipelago (latitude 15° S). The other three islands are easterly outliers of that group, just south of the Tropic of Capricorn.

*Pterodroma alba* is therefore typically a tropical zone petrel, the breeding range of which lies in the central Pacific from slightly north of the Equator to about latitude 24° S. Its zonal relationships are thus extremely similar to those of *Pterodroma arminjoniana heraldica*. *P. alba*, however, while similar in range, general appearance, and in surface-breeding habit, is a well-marked species of only a single plumage phase, whereas both the races of *arminjoniana* are strongly dichromatic. Furthermore, in *alba* the entire head except the pale throat and a white circumorbital line, are of a nearly uniform brown hue, whereas in *arminjoniana*, the feathers of forehead and lores tend to be strongly scaled by light terminal margins.

Since the former report, the American Museum has acquired with the Rothschild collection the types of *Oestrelata wortheni* and *Aestrelata oliveri*. Both of these agree in all respects with our series. The former was taken at sea, slightly east of halfway between the Marquesas and Galápagos Islands. The type of *oliveri* is labeled Sunday Island, Kermadec group, March 7, 1913. It is the only specimen known from such a southerly locality (latitude 29° S.) and is probably to be regarded as an accidental record.

In describing *wortheni*, Rothschild compared his specimen with *Pterodroma magentae*, an alleged species still known only from the unique type in the Museum at Turin, Italy. We have been unable to arrive at any confident conclusions regarding the identity and relationships of *magentae*, and the question can perhaps never be settled until the type specimen can be compared with several other Pacific petrels.

Measurement of some 90 adult specimens of *P. alba*, collected throughout the breeding range between Christmas and Ducie Islands, reveals no more than a possible suggestion of populational variability. Thus there are no grounds for racial discrimination.

*Pterodroma alba* bears an extraordinarily close resemblance to
TABLE 5
AVERAGE DIMENSIONS OF Pterodroma alba POPULATIONS, SEXES COMBINED

<table>
<thead>
<tr>
<th>Population</th>
<th>Wing</th>
<th>Tail</th>
<th>Culmen</th>
<th>Depth</th>
<th>Tarsus</th>
<th>Toe and Claw</th>
</tr>
</thead>
<tbody>
<tr>
<td>Christmas Island (27)</td>
<td>277.9</td>
<td>114.5</td>
<td>28.1</td>
<td>8.9</td>
<td>33.9</td>
<td>44.6</td>
</tr>
<tr>
<td>Phoenix Group (16)</td>
<td>276.9</td>
<td>114.1</td>
<td>28.1</td>
<td>8.9</td>
<td>33.5</td>
<td>44.3</td>
</tr>
<tr>
<td>Marquesas Group (14)</td>
<td>276.6</td>
<td>114.0</td>
<td>27.6</td>
<td>8.8</td>
<td>34.2</td>
<td>44.6</td>
</tr>
<tr>
<td>Oeno Island (6)</td>
<td>275</td>
<td>110.9</td>
<td>27.2</td>
<td>8.9</td>
<td>33.2</td>
<td>44.8</td>
</tr>
<tr>
<td>Ducie Island (14)</td>
<td>273</td>
<td>108.1</td>
<td>27.0</td>
<td>8.7</td>
<td>33.5</td>
<td>44.4</td>
</tr>
<tr>
<td>Henderson Island (1)</td>
<td>284</td>
<td>111.7</td>
<td>27.1</td>
<td>9.0</td>
<td>33.7</td>
<td>45.2</td>
</tr>
<tr>
<td>Tikahau Island (1)</td>
<td>270</td>
<td>110.6</td>
<td>25.5</td>
<td>8.5</td>
<td>32.3</td>
<td>43.9</td>
</tr>
</tbody>
</table>

Pterodroma arminjoniana heraldica in its light-breasted phase. P. alba is a species of relatively uniform plumage, whereas its neighbor heraldica runs a very wide gamut of individual variation. In examples with a dark and heavy breast band, the resemblance to alba is extraordinarily close.

Generally speaking, the differences between the two may be summarized as follows: in the white-breasted phase, heraldica invariably has a scaled forehead and lores owing to white terminal margins on the feathers; in alba, these areas are uniformly brown. In the dark phase of heraldica, no such scalation is present, but alba has no dark phase. In P. alba, the almost invariably complete pectoral collar is of a solid brownish black hue, only slightly less intense than that of the dorsal surface. In heraldica of the white-breasted phase, the corresponding collar is always lighter (grayish rather than blackish brown), and is also usually banded or mottled in a pepper-and-salt effect. The individual range of heraldica is very wide, some examples showing only a trace of the collar, whereas in others it is so heavy as to be almost solidly gray. Such darker specimens are also likely to have a grayish wash over all the white ventral surface, and in occasional birds, asymmetrical dark patches appear on the belly and flanks. Finally, the patterns of the under tail-coverts in the two species show a difference which is characteristic in the great majority of specimens. In P. alba these coverts are almost invariably white, crossed by a banded pattern of grayish black. In heraldica, they are prevailingly darker and are more often mottled than banded, but a small proportion of the specimens have under tail-coverts which are scarcely distinguishable from those of alba.

A summary of the dimensions of eight eggs of Pterodroma alba,
collected at Christmas Island in February and at the Tonga group in July, is as follows: average, 56.06 by 42.54; longest, 59.4 by 42.0; shortest, 52.9 by 43.0; broadest, 43.5 by 57.7; narrowest, 39.4 by 53.1.

**Pterodroma arminjoniana**

This petrel, of complicated taxonomic history, is a tropical, surface-nesting, circumpolar species of many plumage phases. It is closely related to at least three other members of its genus, namely, *neglecta*, *alba*, and *ultima*. It nests, however, at stations shared by all of these, a warrant of its specific distinctness. It occupies islands in the tropical parts of all three of the southern oceans (Atlantic, Indian, and Pacific), and in the last-named its breeding range extends slightly southward of the Tropic of Capricorn.

Historically, *arminjoniana* has been regarded as an exclusively South Atlantic species, its wide range in the Pacific being hitherto masked by Salvin's name *heraldica*, which has only subspecific value.

The species is to be regarded as relatively sedentary. It apparently occupies its breeding islets throughout the year and makes no long, regular migrations. Records of birds at great distances from breeding stations, as in the Northern Hemisphere, have been shown to be due to tropical storms of hurricane type (Murphy, 1936, p. 710).

Since *arminjoniana* is a circumpolar petrel, despite its tropical proclivities, its route of original dispersal is much more likely to have been south of Africa (latitude 35° S.) than south of South America (latitude 59° S.). The new discovery of the species as an Indian Ocean resident, here first reported, strengthens this hypothesis. We have no means of knowing, however, whether or not the distribution route dates from a period of a tropical water gap between North and South America.

If *arminjoniana* attained its circumpolar distribution during a period of present continental barriers, it is highly probable that the directional spread was westward, terminating in the South Atlantic. For reasons well understood, the isotherms of surface water strike the eastern coasts of Australia and South Africa at markedly higher latitudes (±10°) than the western coasts of the same continents. A world ocean map of Spilhaus (1942, p. 434) shows the condition strikingly with respect to the mean iso-
therm of 20°C. (a subtropical temperature). Such an oceanographic pattern close to the Cape of Good Hope would interpose only a slight barrier to the passage of tropical petrels, man-o'-war birds (Fregata), and terns (Gygis and Sterna fuscata) from the Indian Ocean to the Atlantic.

**Pterodroma arminjoniana arminjoniana**


The synonymy of the Trindade Island Petrel, which includes the specific names trinitatis, sandaliata, wilsoni, and chionophara, is listed by Hellmayr and Conover, as well as by Mathews (1934, p. 168). This is a petrel of polymorphic color phases, one of which (“wilsoni”) is intermediate between the brown-and-white pattern of the type and the wholly dark phase (“trinitatis”). Hellmayr and Conover have recently listed arminjoniana as a subspecies of neglecta, which is inadmissible for reasons stated above.

Dimensions of nine males and 10 females appear in table 1. All the specimens were collected at or around Trindade Island, South Atlantic, except one female of uncertain source, which was purchased in Leadenhall Market, London, December 26, 1889, subsequently finding its way into the Rothschild collection. The label of the London specimen states that its wing expanse was 965.2. The average body length and wing spread of “Blossom” expedition specimens in the Cleveland Museum of Natural History, as recorded from flesh measurements, were as follows:

<table>
<thead>
<tr>
<th></th>
<th>Length</th>
<th>Wing Spread</th>
</tr>
</thead>
<tbody>
<tr>
<td>Five males</td>
<td>378 mm.</td>
<td>992 mm.</td>
</tr>
<tr>
<td>Four females</td>
<td>379</td>
<td>971</td>
</tr>
</tbody>
</table>

From *Pterodroma neglecta* both of the subspecies of *arminjoniana* differ in having a relatively longer tail, dark quill shafts, dark inner vanes of primaries, and in never being white-headed (except in the sport described as “chionophara”). The light phase always has a finely barred, dusky collar, dividing white throat from white breast.
In the South Atlantic, *arminjoniana* nests only at Trindade and the neighboring rocks of Martim Vaz, just beyond latitude 20° S., and therefore well within the tropics. It is interesting to note that the recently discovered nesting ground of the Indian Ocean population lies on almost exactly the same parallel of latitude as the South Atlantic stations.

![Diagram](image)

**Fig. 4.** Sexual dimorphism, as shown by length of the tarsus, in *Pterodroma arminjoniana arminjoniana* (right pair of graphs), and its absence in *P. a. heraldica* (left pair). The frequency distribution of other standard systematic measurements in these two races shows a similar relation. Nine males and 11 females of *P. a. arminjoniana*; 97 males and 67 females of *P. a. heraldica*.

The first record from the Indian Ocean is based on three specimens sent to us for identification by the British Museum. These were collected on the nest, and in one instance sitting upon an egg, at Round Island, off Mauritius, on November 27, 1949, by Mr. J. Vinson.

The three specimens we have seen and measured comprise one light-breasted bird with speckled face and mottled collar, one uniformly dark bird, and one of intermediate stage showing a
dark pileum and a heavy blackish wash on the flanks. The light bird and the intermediate specimen have parti-colored feet, while in the dark specimen the legs and feet are entirely black. The light specimen has prevailingly white under tail-coverts marked by gray transverse bands, whereas both the intermediate and the dark specimens have dark under tail-coverts. The three phases therefore completely agree with the resident birds of Trindade of the Atlantic, which in the past have been described as several distinct species.

The Indian Ocean specimens are quite indistinguishable from South Atlantic examples but are definitely larger than birds in our extensive South Pacific series.

Alone among the forms of petrels discussed in this paper, the South Atlantic series of *P. arminjoniana arminjoniana* shows a consistent sexual dimorphism. Average differences in the dimensions of 20 adults almost equally divided as to sex, as shown in table 1, might not be considered significant owing to the smallness of the sample. Since, however, the same size relationship appears in frequency distribution graphs plotted from these same specimens (fig. 4), the matter is noted for the attention of future workers. No equally clear indications of a size difference between the sexes occur in the Pacific race (*heraldica*) of this species (cf. also p. 7).

**Pterodroma arminjoniana heraldica**

*Aestrelata heraldica* Salvin, 1888, Ibis, p. 357 (Chesterfield Island, northwest of New Caledonia).


It is curious that this widely distributed petrel has not long been recognized as the Pacific representative of the Atlantic *arminjoniana*. The two forms have precisely the same proportions and plumage pattern, and both of them differ from *Pterodroma neglecta* in having dark shafts on the wing quills. Only the extreme bases of these structures become pale in the races of *arminjoniana*, whereas in *neglecta*, the greater part of the shaft is white or ivory, even in birds of black phase. Both of the races of *arminjoniana* are polychromatic, but a white-headed condition (common in *neglecta*) is lacking.

The type locality of the subspecies *heraldica* is a small unit of a
line of reefs and shoals lying on latitude 20° S. and close to longitude 159° E., midway between the northern tip of New Caledonia and the Great Barrier Reef of northeastern Australia. The entire breeding range extends across the South Pacific from Easter Island almost to Australia, between the approximate parallels of 8° and 27°10' S.

The American Museum representation of *heraldica* was obtained chiefly during the Whitney South Sea Expedition, but also in part by J. P. Chapin on the cruise of the schooner "Zaca." Our specimens cover the following localities and periods:

<table>
<thead>
<tr>
<th>Localities</th>
<th>Periods</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ducie Island</td>
<td>March, 1922</td>
</tr>
<tr>
<td>Henderson Island</td>
<td>March and April, 1922</td>
</tr>
<tr>
<td>Oeno Island</td>
<td>April, 1922</td>
</tr>
<tr>
<td>Tuamotu group (Vanavana, Maria, Tenarunga, Timoe)</td>
<td>April, May, June, 1922</td>
</tr>
<tr>
<td>Marquesas group (Uapu Island)</td>
<td>September and October, 1922</td>
</tr>
<tr>
<td>Tonga group (Hongahapai and Hongatonga)</td>
<td>July, 1925</td>
</tr>
<tr>
<td>Easter Island</td>
<td>January, 1935</td>
</tr>
<tr>
<td>At sea, latitude 25° S., longitude 129° W., and latitude 26°58' S., longitude 133°16' W. (near Pitcairn Island)</td>
<td>March, 1922</td>
</tr>
</tbody>
</table>

Populational peculiarities are a highly striking feature of the race *heraldica*, but they offer no ground for systematic discrimination. The Easter Island specimens, including the type of "*pachae*" in the Royal Natural History Museum at Stockholm, are matched in every respect by birds from many other localities.

In the central and western Pacific, the statistical ratio between birds of the white-breasted and the blackish phases, as shown by museum specimens, bears a harmonious relation to the proportions observed in the field, as recorded in the journals of several members of the personnel of the Whitney South Sea Expedition. The following count is based on our entire American Museum series from nesting grounds:

<table>
<thead>
<tr>
<th>White-breasted</th>
<th>All Black</th>
</tr>
</thead>
<tbody>
<tr>
<td>Easter Island</td>
<td>1</td>
</tr>
<tr>
<td>Marquesas group</td>
<td>21</td>
</tr>
<tr>
<td>Ducie Island</td>
<td>42</td>
</tr>
<tr>
<td>Oeno Island</td>
<td>22</td>
</tr>
<tr>
<td>Henderson Island</td>
<td>5</td>
</tr>
<tr>
<td>Tuamotu group</td>
<td>3</td>
</tr>
<tr>
<td>Tonga group</td>
<td>18</td>
</tr>
</tbody>
</table>

<p>| | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0</td>
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<tr>
<td></td>
<td>2</td>
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<td></td>
<td>2</td>
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<tr>
<td></td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>53</td>
</tr>
<tr>
<td></td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>0</td>
</tr>
</tbody>
</table>

It should be remembered that the phase represented by the smaller number of specimens is likely to be overweighted because
of human selection in the field. Indeed, the notes of R. H. Beck and his associates repeatedly state that among the nesting petrels they sometimes had to hunt solicitously in order to obtain samples of minority plumage phases.

Taking Ducie and Henderson Islands, which lie in the same oceanic zone about 220 nautical miles apart, as examples of stations at which different plumage phases of this petrel vastly predominate, we have searched the field notes of Messrs. Beck and Quayle for eye-witness accounts. The following records are freely transcribed:

At Henderson Island, we passed up innumerable dark petrels of this species while looking for light ones. In fact, it took us a long while to find five of the latter after we had taken and skinned more than 50 of the black birds (Quayle).

The great bulk of this species at Henderson was black. Among many hundreds attracted to bait a half mile off the coast, not more than four (and perhaps only two) were light-breasted. Ashore, the ratio of black to light was certainly more than 40 to 1 (Beck).

At Ducie Island, the population of heraldica was of the order of 230,000 birds, predominantly white-breasted and white-throated. Black birds were hard to find, though occasionally we located one, paired with a light bird. I would judge that dark birds made up less than one-tenth of the whole population. Although the two abundant resident species (neglecta and heraldica) are thoroughly intermixed on the nesting grounds, there still seems to be a decided tendency toward agglomeration of either species in small groups (Quayle).

At Ducie we could inspect many hundreds of these petrels merely by walking among the tangled trees. The birds had just selected nesting sites and were mostly in pairs (March 20). Occasionally we saw one in black plumage, like those of Henderson Island (Beck).

It has been pointed out (Murphy, 1936, pp. 693–697) that dichromatism in petrel populations probably has a temporal as well as a spatial periodicity. In other words, the proportions of white-breasted and black birds in a particular population are likely to change in different periods of years. Père Labat (1724, vol. 1, pt. 2, p. 109), for example, described the petrels of Guadeloupe, West Indies, as black birds (Pterodroma caribbaea phase). Du Tertre (1667, vol. 2, p. 257), at an earlier date, had found the same population to be made up of white-breasted birds (Pterodroma hasitata phase).

At a date three or more decades after the visits of the Whitney expedition, it would be highly interesting to ascertain whether the populations of Pterodroma arminjoniana heraldica are still prevailingly black at Henderson Island and prevailingly white-breasted at the neighboring islands of Ducie and Oeno.
Young in the nest of this petrel were collected only at the Tonga group, on July 24, 1925, by Beck and his fellow workers. However, most of the birds from other localities, and at widely different dates, appeared to be in or close to their breeding season. It is likely that the season of reproduction is prolonged or nearly continuous, at least in lower latitudes of the range. Certainly the nesting stations are occupied throughout the year, as in the case of the Atlantic race.

The downy young from the Tonga group closely resemble chicks of *Pterodroma alba* from Christmas Island and the Marquesas. As they lose their down, however, the distinguishing characters in the contour plumage of each species immediately appear on the forehead, lores, and under tail-coverts.

*Pterodroma arminjoniana heraldica* is slightly smaller than the nominate race of the Atlantic and Indian oceans. The phases of plumage are completely parallel. Traces of albinism turn up now and then, as among Atlantic birds. One female from Ducie Island is prevailing white over the back, with a scattering of albinistic feathers in the crown, rump, and tail-coverts.

A summary of the dimensions of 29 eggs of *P. arminjoniana heraldica*, collected at Oeno Island in April and at Ducie Island in March, is as follows: average, 59.12 by 42.7; longest, 62.7 by 42.2; shortest, 56.1 by 41.1; broadest, 59.7 by 45.8; narrowest, 60.3 by 40.9.

**Pterodroma ultima**

*Pterodroma ultima* MURPHY, 1949, Ornithologie als biologische Wissenschaft (Festschrift zum 60. Geburtstag von Erwin Stresemann), Heidelberg, p. 89 (Oeno Island, subtropical South Pacific).

Common in the central subtropical Pacific, this large petrel, very recently described, is known only from Rapa Island and Bass Rocks (Austral group), and from several outliers of the Tuamotu Archipelago (Timoe Atoll, Maria, Ducie, and Oeno Islands).

Birds taken at Bass Rocks in February, and at Rapa and Oeno in mid-April, were almost all in breeding condition. The species is a surface nester. At Rapa, Beck extracted a female from a niche in a cliff. Such sites are frequently occupied by other surface-nesting petrels, such as *P. arminjoniana* at Trindade.

This species is of entirely sooty and slaty plumage except for a scaled forehead (in fresh plumage) and a mottled throat, where the basally white feathers are more or less deeply exposed. The legs
and feet are parti-colored (black and fleshy or bluish white). Wear produces a considerable superficial change in appearance, without affecting the general pattern.

The species somewhat resembles *macroptera* and *solandri* but is smaller than either. It also resembles the dark phase of *Pterodroma armijoniana heraldica*, but it is a larger petrel and is not dichromatic. It breeds at a number of the same insular stations as *heraldica*, *neglecta*, and *alba*.

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