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THE MANX SHEARWATER, *PUFFINUS* *PUFFINUS*, AS A SPECIES OF WORLD-WIDE DISTRIBUTION¹

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INTRODUCTION

A group of medium-sized shearwaters characterized by similar proportions and plumage pattern is recorded in the literature under the specific and subspecific names *puffinus*, *mauretanicus*, *yelkouan*, *gavia*, *huttoni*, *newelli*, *auricularis*, and *opisthomelas*. The assemblage is readily distinguishable from other shearwaters, both larger and smaller, that have been generally grouped within the genus *Puffinus*. The order in which the names are listed above is approximately that of the linear distribution of the forms from the North Atlantic eastward around the world. The zonal ranges are mainly extra-tropical and temperate in both the Northern and the Southern Hemispheres. Two forms (*newelli* of Hawaii and *auricularis* of the Revilla Gigedo Islands) nest barely within the tropics, and the breeding range of one (*puffinus*) reaches Iceland but does not cross the Arctic Circle. One form (*huttoni*) should perhaps be called subantarctic.

Six of the eight members of the group have borne distinct specific names. Mathews has even created a new genus for the species *reinholdi* (= *gavia*) in the following diagnosis: "*Reinholdia*, gen. n. Differs from *Puffinus* in its proportionately longer bill and much shorter tail, the latter [latter] being less than one-third the length of the wing and not twice the length of the exposed culmen. Type, *Puffinus reinholdi* Mathews' (Mathews, 1912, p. 107).

¹ BIRDS COLLECTED DURING THE WHITNEY SOUTH SEA EXPEDITION, No. 61.

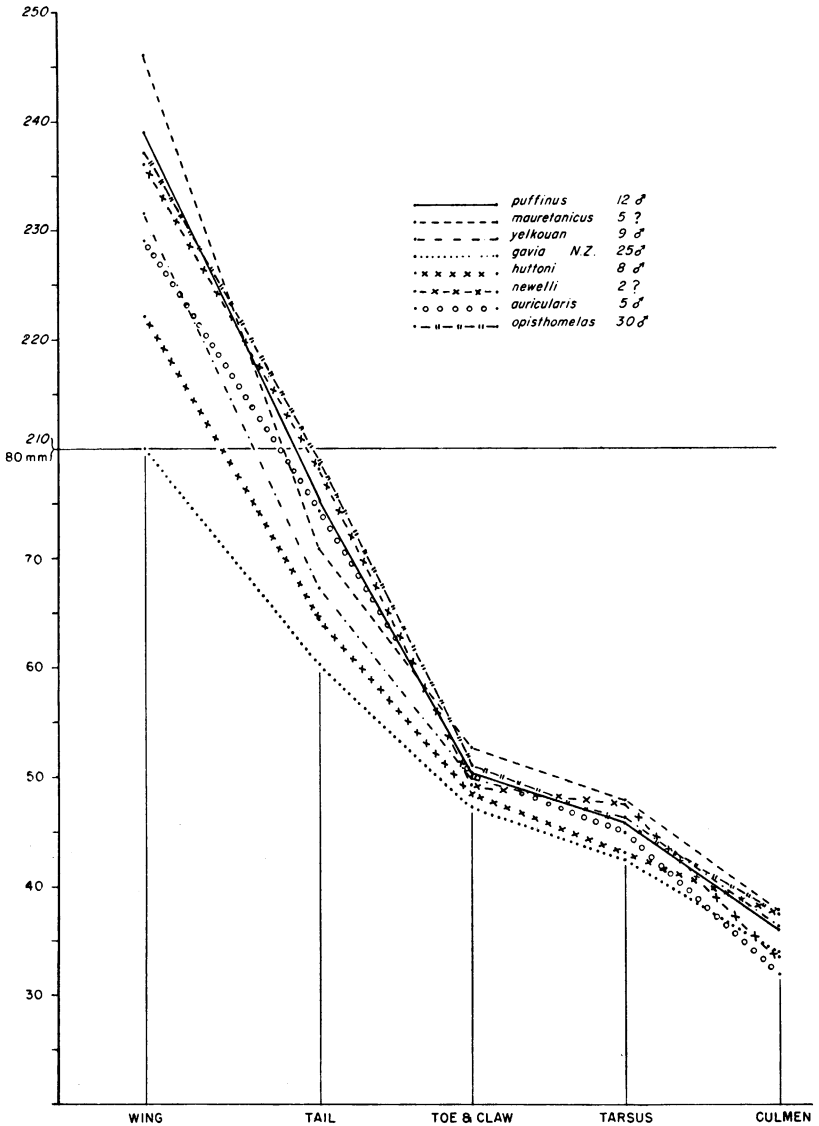


FIG. 1. Comparison of average dimensions of eight subspecies of *Puffinus puffinus*, showing close resemblance of proportions throughout the species.

Graphs prepared from measurements show that these criteria are untenable or, at any rate, not distinctive (fig. 1).

In the absence of significant disagreement in proportions,

characters of pigmentation have sometimes been used for differentiation. The Manx shearwater (*P. p. puffinus*) is dorsally "black"; the resident representatives in New Zealand (*gavia* and *huttoni*) are dorsally "brown." This distinction breaks down, however, when the group as a whole is considered, for the two races of the Manx shearwater occurring within the Mediterranean Sea are likewise brown-backed birds. So is the form *opisthomelas* of the eastern North Pacific, whereas *auricularis*, of the same general area, and *newelli*, of Hawaii, are black-backed.

It should be noted that the difference between black and brown hues in feathers is a relatively slight one from the genetic point of view. Prof. Th. Dobzhansky (*in litt.*) includes the case among many constant and non-transgressive differences in pigmentation which might conceivably be under control of a single Mendelian gene. On the other hand, the situation in the petrels under consideration may be more complicated, because it is possible that a number of color-producing genes in different loci are involved. The various factors that interact in determining plumage color in domestic fowl have not been fully worked out, but the circumstances are more explicitly understood with reference to similar shades in the coat color of mice (Sinnott, Dunn, and Dobzhansky, 1950, p. 114).

Examination of barbules from *P. p. puffinus*, *P. p. opisthomelas*, and *P. p. gavia*, thus including both "black" and "brown" contour feathers, indicates that the principal pigment in both phases is a melanin which, seen through a compound microscope under high power and oil immersion lenses, shows as discrete granules or rodlets of similar color and aspect. The melanins as a group are highly complicated, and even their chemical nature has not been completely elucidated. In their gross color values, they probably represent different stages or degrees in the oxidation of melanin-precursor substances (Nickerson, 1946, pp. 66-77). With the biochemistry of this subject we are not here concerned beyond the point of indicating that genetic changes of plumage tone from black to brown, or vice versa, are a familiar and expected evolutionary phenomenon.

No two of the eight forms of *Puffinus puffinus* share a common breeding ground. Comparison of ample series of specimens and a study of their respective dimensions make it appear that all are geographical races of one species, found almost throughout the world oceans.

An effort has been made to find distinguishing features in the relative length and weight of the bill among the eight forms here recognized. This has proved fruitless because of a complete lack of consistency. The difference in bill structure between the typical form of the Manx shearwater and its two Mediterranean representatives approximates the range of variation among all the forms. Furthermore, evidence is constantly accumulating that the bill is the most variable of the units commonly measured in systematic studies of birds. Essential differences within the group seem to be confined to size, most of the largest dimensions appearing in the Mediterranean races, and most of the smallest dimensions in the forms *auricularis* and *gavia*.

It is an interesting fact that the close resemblances between various populations of these birds that are separated by great distances have long been pointed out in comparisons such as the following:

"It has not hitherto been remarked that *P. opisthomelas* bears a strong resemblance to *P. yelkouanus* of the Mediterranean, but this is undoubtedly the case. . . Its evident affinity with a European species is a fact of singular interest" (Godman, 1908, p. 109).

"So close is the resemblance of the light phase of *P. opisthomelas* to *P. yelkouan* that I am unable to define fully their distinctive characters" (Loomis, 1918, p. 60).

". . . The best character for the separation of *P. newelli* is apparently the white central under tail-coverts (these being black in *P. auricularis*), and the absence of mottling on the sides of the neck" (Godman, 1908, p. 116).

"*Puffinus opisthomelas* Coues, of the California coast, is clearly an eastern Pacific and northern hemisphere representative of *P. gavia*. Although *opisthomelas* is of larger size, the proportions of the two species are identical. Moreover, they reveal a dual coloration of the same type (cf. Loomis, 1918, pp. 114-118, pl. xiv). The under tail-coverts of *gavia* appear to be uniformly white; those of *opisthomelas* are usually dark. However, Loomis reports that in some instances 'white nearly supplants the dark color on the shorter lower tail-coverts.' If there should prove to be an actual intergradation in this character, I should suppose that *opisthomelas* would have to be regarded as a subspecies of *gavia*" (Murphy, 1930, pp. 12-13).

Mathews (1934, pp. 178-179) lists six of the forms, including

opisthomelas, *auricularis*, and *newelli*, as subspecies of *Puffinus puffinus*, but he isolates *gavia* in another section of his paper and under the separate generic name *Reinholdia*.

Alexander (1928, p. 47) suggests that *newelli* of Hawaii may be a subspecies of *auricularis*.

Beyond all of these pertinent comments, the members of this group of petrels agree in a number of fundamental respects. They exhibit no sexual dimorphism. They are all spring breeders, the Northern Hemisphere forms apparently nesting between April and June, while *gavia* and *huttoni* nest in the corresponding months of the Southern Hemisphere spring. The latter point has particular significance because in the New Zealand area, and at islands in higher latitudes of the Atlantic and Indian oceans, there are both "summer breeding" and "winter breeding" species of petrels. Furthermore, all members of the group are burrowing birds, although in certain places the populations of several of them nest in scree or among back-beach boulders. Finally, all these petrels exhibit a relatively rapid wing beat as compared with shearwaters of different affinities, particularly the larger species. The forms *gavia* and *huttoni* are known in the Australasian area by the vernacular name "fluttering shearwaters." Bent (1922, p. 83) states that *opisthomelas* exhibits much more erratic flight, with more constant flapping, than other shearwaters off the west coast of North America.

Only in migratory propensities do there seem to be noteworthy differences among members of this *puffinus* group. The distinction may be more apparent than real because of our lack of information regarding the life history and travels of several forms. Typical *Puffinus puffinus puffinus* migrates from western Europe far into the South Atlantic, reaching latitudes off Argentina. The Mediterranean races are, so far as is known, more nearly sedentary, although *mauretanicus*, of the western end of that sea, has been captured repeatedly in the British Isles and at other localities facing the open Atlantic. The New Zealand races, *gavia* and *huttoni*, are alleged to make no more than limited migrations and have been taken only as far distant from nesting grounds as the Australian coast (>1000 geographic miles). Off western North America, the difference in the migratory traits of *auricularis*, and of *opisthomelas*, which flies seasonally northward as far as Vancouver Island, has been exaggerated (Loomis, 1918, p. 120). The form *auricularis* is now known not only from its nest-

ing stations on the Revilla Gigedos, but also at sea northward to Cape San Lucas and southward to the vicinity of Clipperton Island, a span of some 1800 geographic miles (Bent, 1922, p. 85). The Hawaiian *newelli* has not been collected outside the archipelago, but the serious reduction or near extinction of the population might sufficiently account for this fact.

The problems and consequences of relationship among all these petrels may be expressed in simplified form as follows:

The races *auricularis* and *newelli* can be distinguished from the typical race of *Puffinus puffinus* chiefly by slight differences of size and pattern. The same is true as regards discrimination between the forms *yelkouan*, *gavia*, and *opisthomelas*. Therefore, unless *puffinus* and *yelkouan* are specifically distinct (which no recent investigator has had the temerity to allege), all the petrels under consideration in this paper belong to the same species.

A HYPOTHESIS OF DISTRIBUTION

If the distribution of these petrels be weighed in relation to the prevailing pigmentation of the dorsal surface, it might appear that the forms with black backs had dispersed in a westward direction from western Europe. Thus the breeding range of *P. p. puffinus* has reached Bermuda in the western North Atlantic; that of *auricularis* is confined to the Revilla Gigedo Islands in the eastern Pacific, south of the twentieth parallel of north latitude and more than 300 geographic miles from the Mexican mainland; that of *newelli* to Hawaii, about 2500 miles farther west, on approximately the same parallel.

The brown-backed forms, on the other hand, might be considered to have dispersed in an easterly direction, the successive representatives being *mauretanicus* in the western Mediterranean, *yelkouan* in the Adriatic-Levantine area, *gavia* and *huttoni* in and about New Zealand, and *opisthomelas* across the whole breadth of the Pacific, nesting on islands close to the coast of Baja California.

There are large spatial gaps in this sequence, the first being the extent of the Indian Ocean. Here, however, the explanation may lie merely in current lack of information. As regards sea birds, the area is still the least explored part of the world ocean, and from time to time petrels such as *Pterodroma arminjoniana*, hitherto believed restricted to the Pacific, turn up as breeding species of the Indian Ocean (Murphy and Irving, 1951, p. 2).

Another possibility is that of extinction during the nineteenth century of Indian Ocean petrels at Amsterdam and Saint Paul Islands, which lie on the same latitude as the present breeding grounds of *gavia* in New Zealand (*ibid.*, pp. 2-3).

Such a speculative hypothesis as is outlined in the previous several paragraphs would account for the contemporary juxtaposition of the black-backed *auricularis* and the brown-backed *opisthomelas* in the subtropical zone of the eastern North Pacific. They might be said to have met and overlapped after their dis-

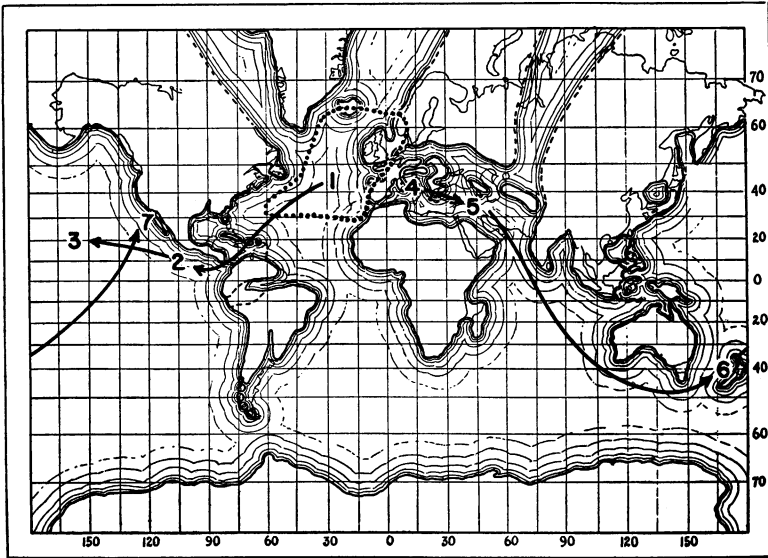


FIG. 2. Present-day distribution of seven of the forms of *Puffinus puffinus* on a map of the Oligocene period. Numbers as in taxonomic list.

persal in opposite directions around the globe. If *auricularis* and *opisthomelas* were the sole representatives of this group of petrels, they could be recognized only as fully discrete species. Traced back, however, eastward and westward, respectively, through the successive populations of their relatives, they seem to stem from the two western European forms *P. puffinus puffinus* and *P. puffinus mauretanicus*, which have been universally accepted as subspecies.

Figure 2 denotes the present-day ranges of seven of the eight subspecies acknowledged in this paper, plotted upon a chart

showing the relations of land and water in the Oligocene period. No dating of evolutionary phenomena is implied. During the Oligocene an open sea route around the world was available, but intercontinental breaches in one direction or the other also existed in later Tertiary time, or perhaps as recently as during stages of subsidence within the Pleistocene.

It should be emphasized that the directional implications in figure 2 have been drawn merely to create a hypothetical frame of reference. We possess evidence neither on the original center of dispersal of this group of petrels, nor on the routes traversed by forms ancestral to the present well-defined populations. All that can be affirmed with high probability is that before the latest closure of waterways between North and South America, and between Africa and Eurasia, members of the species attained an almost cosmopolitan subtropical and temperate distribution.

For measurement of specimens, plotting, comparison, and statistical work in this study, the author is indebted to two successive assistants, Miss Susan Irving and Miss Jessie M. Penoyer. The latter has also pointed out characters of plumage which distinguish such closely related forms as *gavia* and *huttoni*. Counsel on several other aspects of the investigation has been given by Drs. Ernst Mayr, Dean Amadon, and Norman D. Newell, all of the scientific staff of the American Museum of Natural History, by Prof. B. H. Willier of the Johns Hopkins University, and by Dr. Karl F. Koopman. Miss Constance D. Sherman translated the Swedish paper by Fontaine listed in the Bibliography.

TAXONOMY

THE BLACK-BACKED RACES

1. *Puffinus puffinus puffinus*

Procellaria puffinus BRÜNNICH, 1764, Ornithologia borealis, p. 29 (Faeroe Islands).

The Manx shearwater of the North Atlantic has acquired the most extensive breeding range of any member of the species. Islets off the British, Irish, and French coasts, Iceland, Bermuda, the Azores, Madeira, the Salvages, and the Desertas are all present or recent nesting stations (fig. 2). Murphy (1936, p. 677) has recorded autumn migrants of several different years from the coast of Argentina.

The descriptive characteristics of the form in all stages of growth and its life history (fig. 3) are now known more fully than

JAN.	NO BIRDS AT OR NEAR BREEDING GROUND	PERIOD OF ABSENCE
FEB.	FIRST BIRD RECORDED ON ISLAND FEB. 2 BIRDS FOUND SINGLY IN OLD BURROWS AT FIRST; BEGIN CALLING ONE WEEK AFTER LANDING, PLENTIFUL BY NIGHT TOWARD END OF MONTH	ARRIVAL OF BREEDING BIRDS-COURTSHIP, MATING, PREPARATION OF BURROWS
MAR.	BURROWING BEGINS AFTER MARCH 21, BIRDS FOUND IN PAIRS IN BURROWS REGULARLY AT NIGHT	
APR.	TERRITORIAL STRUGGLES FIRST COPULATION OBSERVED APRIL 11 GATHERING OF NEST MATERIAL FIRST EGG RECORDED MAY 1	
MAY	<i>Egg of May 7 laid</i> LAST RECORDED DATE OF LAYING MAY 24	INCUBATION 51-54 DAYS
JUNE	INCUBATION BY BOTH MALE AND FEMALE ALTERNATING IN SHIFTS OF 3 TO 5 DAYS OR LONGER <i>Egg of May 7 hatched June 26</i>	
JULY	YOUNG BROODED CONTINUOUSLY FOR ONE WEEK LAST RECORD OF HATCHING JULY 19	
AUG.	YOUNG VISITED ONCE NIGHTLY FOR FEEDING 8th TO 60th DAY ADULTS BEGIN MOLT. MESOPTYLE DOWN APPEARS ABOUT 16th DAY, REACHES MAXIMUM ABOUT 35th DAY QUILLS APPEAR ABOUT 42nd DAY PARENTS ABANDON YOUNG 60th-62nd DAY <i>Parents of May 7th egg deserted Aug. 27</i>	GROWTH OF CHICK FROM HATCHING TO DEPARTURE 72-74 DAYS
SEPT.	CHICKS STAY IN BURROW, STARVE AND LOSE LAST OF DOWN FOR 6 DAY PERIOD, THEN EMERGE AT NIGHT ONLY, 4-5 DAYS <i>Chick of May 7 left for sea Sept. 7</i> CHICKS LEAVE FOR SEA AT AVERAGE AGE OF 73 DAYS	
OCT.	AUTUMN MIGRATION LAST CHICKS GONE BY MID-OCTOBER	
NOV.	OCCASIONAL RECORDS OF BIRDS NEAR BREEDING GROUND	PERIOD OF ABSENCE
DEC.	NO BIRDS AT OR NEAR BREEDING GROUND	

FIG. 3. Summary of the life history of *Puffinus puffinus puffinus* at Skokholm, Pembrokeshire. Data from Lockley, 1942.

those of any other petrel (Witherby *et al.*, 1940, p. 42; Lockley, 1942). Dimensions of 20 adults from the British Isles, measured

in the course of the present study, are summarized in table 1. Measurements of an additional series in the American Museum and elsewhere, including the South Atlantic specimens, agree with those of the British examples.

The wing expanse of eight Scilly Island birds, measured in the flesh and noted on the labels, ranged between 749 and 813 mm., without indication of sexual discrepancy. The body length among the same birds was 235–251 mm., and the weight 406–510 grams.

2. *Puffinus puffinus auricularis*

Puffinus auricularis TOWNSEND, 1890, Proc. U. S. Natl. Mus., vol. 13, p. 133 (Clarion Island, Revilla Gigedo group).

The only known breeding stations of Townsend's shearwater are at Clarion, Socorro, and San Benedicto Islands of the Revilla Ggedos, west of Mexico.

The original describer and most subsequent authors have compared the form with *opisthomelas* (Loomis, 1918, p. 119). Its evident affinities are much closer with the Atlantic race, *P. p. puffinus*, of which it is a very slightly smaller counterpart except in the following particulars: (1) the under tail-coverts are pre-vaillingly blackish; (2) there is usually more solid black (less mottled) plumage at the sides of the neck and breast; and (3) in occasional specimens a mottled collar almost separates the throat from the breast. In large series of Atlantic *puffinus*, however, certain specimens show an approach to each or all of these conditions.

The dimensions of 13 adults of *auricularis* (table 1) closely agree with those of 16 published by Loomis (1918, p. 122). This race averages smaller in the length of wing and bill than the subspecies *puffinus*, but is approximately equal in other dimensions. The wing expanse of a female collected north of the Revilla Ggedo Islands on July 1 was 787 mm., which is midway in the range of wing spreads of birds of the Atlantic race. An egg recorded by Bent (1922, p. 85) also falls within the size range of eggs of typical *puffinus*.

3. *Puffinus puffinus newelli*

Puffinus newelli HENSHAW, 1900, Auk, vol. 17, p. 246 (Maui Island, Hawaii).

This race is confined to the Hawaiian group, where it formerly bred on at least four of the main islands.

The type and one other example at the Bishop Museum, Honolulu, have been examined and measured by the writer. Manuscript notes, prepared by Dr. Dean Amadon during a long stay in Hawaii, indicate that only seven specimens of this bird have ever been recorded, and that five of these can no longer be traced. It is possible, however, that a nesting population still exists on Kauai, which the mongoose has not yet reached.

The measurements in table 1 hardly offer an adequate basis for comparison with the subspecies *puffinus* and *auricularis*. Godman's remarks on apparent differences in plumage are quoted on page 4 of this paper.

Satisfactory characterization of the race, which probably has validity, will have to await further study. On present evidence it would appear that *newelli* shows closer resemblances to typical *puffinus*, of the Atlantic, than to its nearer neighbor, *auricularis*, of the Pacific.

The same phenomenon is more strikingly paralleled in the European races *puffinus*, *mauretanicus*, and *yelkouan*. The first and the third of these resemble each other much more than either resembles the spatially intermediate second form. Such circumstances have been discussed as a common or general evolutionary trend by Nichols (1916, p. 565). The thesis, as it might here prove applicable, is that when related forms are geographically in touch (e.g., *puffinus-mauretanicus* and *mauretanicus-yelkouan*), they tend to develop strongly marked superficial characters, thus widening the gap. It is not difficult to comprehend how natural selection might lead to such a result.

THE BROWN-BACKED RACES

4. *Puffinus puffinus mauretanicus*

Puffinus puffinus mauretanicus LOWE, 1921, Bull. Brit. Ornith. Club, vol. 41, p. 140 (Algiers).

In this race we encounter the first of a series of populations that are definitely brown on the dorsal surface, thus differing from the Atlantic Manx and the two Pacific subspecies already discussed. The latter are black-backed, beginning with the plumage that succeeds the nestling down.

The difference in hue between *mauretanicus* and *puffinus* is close to that between the Fuscous and the Sooty Black, respectively, of Ridgway (1912). Neither shade is an exact match,

TABLE 1
DIMENSIONS OF THE RACES OF *Puffinus puffinus*

		Wing	Tail	Culmen	Tarsus	Toe and Claw
<i>puffinus</i>	12 ♂	232-246 (239)	71.9-88.6 (75.1)	34.2-38.5 (35.9)	43.7-49.0 (45.8)	47.8-51.3 (50.4)
British Isles area	8 ♀	226-241 (235)	68.8-76.0 (72.7)	33.1-37.5 (34.8)	42.6-46.4 (44.9)	49.7-53.0 (51.0)
<i>auricularis</i>	5 ♂	220-237 (229)	67.5-77.6 (74.4)	30.6-34.4 (31.9)	42.9-46.4 (44.9)	48.4-51.5 (50.0)
	8 ♀	223-238 (227)	72.5-77.2 (75.2)	28.9-34.4 (31.6)	43.5-46.0 (44.7)	47.5-50.5 (48.5)
<i>newelli</i>	2?	222-242 (236)	75.0-81.5 (78.3)	33.4-33.8 (33.6)	47.0-48.0 (47.5)	47.0-51.5 (49.3)
<i>maurelanicus</i>	5?	239-254 (246)	68.4-73.7 (70.8)	35.9-39.4 (37.7)	47.2-48.6 (47.9)	52.2-53.5 (52.7)
<i>yelkouan</i>	9 ♂	226-242 (231.5)	64.4-70.3 (67.2)	33.2-39.2 (36.2)	44.0-47.5 (46.2)	48.2-51.1 (49.9)
	12 ♀	227-244 (234.5)	65.7-72.9 (69.2)	33.6-36.8 (35.4)	43.9-48.0 (45.3)	48.9-51.8 (50.5)

TABLE 1—Continued

		Wing	Tail	Culmen	Tarsus	Toe and Claw
<i>gavia</i>						
New Zealand						
	25♂	189-220 (210)	56.3-63.3 (60.1)	31.7-36.1 (34.0)	39.0-45.8 (42.3)	43.2-51.0 (47.2)
	30♀	195-219 (208)	55.8-64.6 (59.4)	29.4-34.7 (33.1)	38.2-43.6 (41.7)	43.3-50.1 (46.8)
<i>gavia</i>	9♂	190-216 (206)	58.2-64.0 (61.2)	31.2-34.4 (32.7)	38.2-43.2 (41.3)	42.9-47.5 (46.1)
Australia						
	17♀	199-213 (206)	55.0-64.4 (60.0)	31.4-34.2 (33.0)	39.0-43.0 (41.4)	43.8-48.0 (46.6)
<i>huttoni</i>	8♂	215-228 (222)	60.7-67.0 (64.5)	36.4-38.3 (37.5)	42.4-43.9 (43.0)	47.5-49.7 (48.4)
New Zealand	9♀	215-229 (222)	62.5-70.3 (65.8)	34.4-37.2 (35.9)	40.0-42.7 (41.6)	45.2-48.1 (46.7)
<i>opishomelas</i>	30♂	213-251 (237)	72.4-82.6 (78.4)	35.4-41.2 (37.5)	43.6-48.1 (45.8)	48.1-55.1 (50.9)
	19♀	214-246 (237)	74.7-81.4 (78.3)	34.2-37.8 (36.9)	43.2-47.9 (45.5)	48.0-52.2 (50.5)

but the fresh plumage in *puffinus* is blacker than the Blackish Brown series of Ridgway. On a more subjective basis, there can be no question to any observer that *mauretanicus* is a brown bird and *puffinus* a black one.

Appropriately called the "Balearic shearwater," it now appears that *mauretanicus* is not the resident race of the "western Mediterranean" but rather of only the westernmost basin, which comprises a very small proportion of that sea. The fact that the two Mediterranean races were not distinguished until 1921 has led to confusion in the literature. The other Mediterranean form, *yelkouan*, nests westward as far as Corsica and Sardinia, and mingles at sea with *mauretanicus* about the Balearic Islands. The two subspecies are of such different appearance as to be readily distinguishable at sight, as the writer learned while cruising in the Mediterranean in 1926.

Mr. Philip W. Munn, who formerly resided at Alcudia, Mallorca, has reported (*in litt.*) that the eastern Mediterranean shearwater is seen among the flocks of *mauretanicus* only during the winter season.

The Balearic shearwater differs from the Levantine (*yelkouan*) in that it makes more or less regular movements through the Strait of Gibraltar into the Atlantic and to western European coasts. Prof. V. C. Wynne-Edwards (*in litt.*) states that on September 10, 1933, he saw numbers of *mauretanicus* in the English Channel, and that "the wings are . . . flapped faster" than those of *Puffinus gravis*. This is significant because the rapid wing beat of the group with which we are dealing is noted in published observations and reflected in at least one vernacular name.

The heavy brown lateral wash on the plumage of *mauretanicus* from head and breast to flanks, and the wholly brown axillaries and under tail-coverts, are diagnostic. It is also probably the largest race of the species in length of wing and bill.

5. *Puffinus puffinus yelkouan*

Procellaria yelkouan ACERBI, 1827, Biblioteca Italiana, vol. 47, p. 297 (The Bosphorus).

Although brown-backed and black-backed, respectively, *yelkouan* and *puffinus* resemble each other in having nearly identical patterns. The distribution of dark dorsal and white ventral plumage is similar. The axillary feathers of *yelkouan* are, however, distally brownish for about half of their length, and the

under tail-coverts are prevailing dark, even though some specimens show median mottled or pure white feathers.

The type locality of this form is the famous strait between the Black Sea and the Sea of Marmora. Its range includes the Black Sea and all parts and arms of the Mediterranean, but the westernmost breeding sites appear to be on islets off Sardinia and Corsica. The next islands westward, namely, the Balearics, are occupied by the very distinct subspecies, *mauretanicus*.

The American Museum possesses specimens of *yelkouan* from islands in the Aegean Sea, the Tremite islands in the Adriatic, elsewhere along the coasts of Italy, Sicily, and Tunisia, the Cerbicale Islands off Corsica, and the islets of Vacca and Toro off the southeastern tip of Sardinia. Many of these were taken at the nest. We know from Godman's text (1908, p. 108) that our examples collected at the Cerbicales by Whitehead, on May 2, 1884, were incubating eggs.

This so-called Levantine shearwater is the Manx shearwater of the whole Mediterranean basin except the westernmost part between Algeria and Morocco on the south and Spain and France on the north. In the Adriatic this shearwater is known to Italian fishermen as "Berta minore" to distinguish it from the "big Bertha" (*Puffinus kuhli kuhli*).

Measurements of 21 adults of *yelkouan* (table 1) suggest that it is a relatively short-tailed race, but that in other respects its size and proportions agree closely with those of *P. p. puffinus*. Its resemblance to the three races discussed below is evident and impressive.

6. *Puffinus puffinus gavia*

Procellaria gavia FORSTER, 1844, Descriptiones animalium, ed. Lichtenstein, p. 148 (Queen Charlotte Sound, New Zealand).

Puffinus reinholdi reinholdi MATHEWS, 1912, The birds of Australia, vol. 2, p. 74 (New Zealand).

Reinholdia reinholdi byroni MATHEWS, 1913, Austral Avian Rec., vol. 1, p. 187 (off Wollongong, New South Wales).

Reinholdia reinholdi melanotis MATHEWS, 1916, Bull. Brit. Ornith. Club, vol. 36, p. 89 (Kaipara Beach, North Island, New Zealand).

Cinathisma cyaneoleuca HULL, 1916, Emu, vol. 15, p. 205 (at sea near Brush Island, New South Wales).

The four type specimens of Mathews and of Hull are in the American Museum of Natural History.

In replacing Forster's original name by "*reinholdi*," Mathews

argued that *gavia* was unidentifiable or that it applied to another and smaller species of petrel. Loomis (1918, p. 61) has shown plainly that the evidence is not wholly one-sided: Forster's description fits this bird in some particulars, even if not in all. Furthermore, the name *gavia* is well established and is still accepted by New Zealand ornithologists.

Falla (1934, p. 252) reports that examples of this shearwater from northern New Zealand are smaller than birds from Cook Strait, and that Mathews' subspecific name *byroni* may prove applicable to the former. Clark and Fleming (1948, p. 187) have added some illuminating notes to the same theme. No one knows more about the circumstances and probabilities than Falla and Fleming, but, for lack of sufficient critical material, the author of the present paper must leave determination of the number of discrete populations of "*gavia* type" to New Zealand students. The comparisons and measurements of American Museum specimens indicate two clearly marked forms, *gavia* and *huttoni*, the breeding areas of which appear to belong to different oceanic zones.

Puffinus puffinus gavia is a match for the race *yelkouan* except in the following minor respects: (1) smaller size (the average difference is not more than 10 per cent in any dimension and less in most); (2) slightly darker (but still white-tipped) axillary feathers; (3) wider individual variability in the mottling at the sides of the neck; and (4) under tail-coverts consistently white, instead of prevailingly or laterally grayish brown as in *yelkouan*.

Reference to table 1 will show that there is no difference in size between 55 examples of *gavia* collected in and around New Zealand and 26 taken in Australian waters. Nor is there any evidence of a resident population of *gavia* (or of a close relative) anywhere in Australia. The description by Mathews of an alleged Australian race, and his treatment of the whole subject in "The birds of Australia," have led to false assumptions on that score.

Males and females of *gavia* are obviously of equivalent size. We have therefore considered statistically the measurements of all our specimens from New Zealand and Australia, of which only the summarized dimensions are recorded in table 1. The result appears in table 2. As in the case of *Puffinus pacificus* (Murphy, 1941, p. 17), the wing length can be regarded as the most stable of the sets of measurements calculated, since its coefficient of variation amounts only to 3 per cent.

Serventy (1939, p. 95) has reported at length upon the status of both *gavia* and *huttoni* in Australian waters and has listed the pertinent bibliography of 29 titles. His measurements of specimens of *gavia* from New South Wales agree well with those of New Zealand birds obtained by Rollo H. Beck during the Whitney South Sea Expedition. These have already been reported upon by Murphy (1930, p. 12), but in his paper of that date examples of the subspecies *huttoni* were incorporated in the description and measurements. Serventy (1939, p. 104) was correct in inferring that the measurements represented a "mixed catch." The specimens came from numerous islands in Hauraki Gulf and from other New Zealand coastal areas.

TABLE 2
COMBINED MEASUREMENTS OF EIGHTY-ONE MALES AND FEMALES
OF *Puffinus puffinus gavia*

		Standard Deviation	Coefficient of Variation
Wing	189-220 (208 ± .718)	6.26	3.007
Tail	55.0-64.6 (59.9 ± .267)	2.361	3.93
Culmen	29.4-36.1 (33.3 ± .141)	1.2125	3.63
Tarsus	38.2-45.8 (41.8 ± .174)	1.563	3.74
Toe and Claw	42.9-51.0 (46.8 ± .207)	1.791	3.81

Following are notes on the type specimens of forms that are regarded as synonyms of *Puffinus puffinus gavia*:

Puffinus reinholdi reinholdi Mathews, A.M.N.H. No. 527750, an adult male, labeled merely New Zealand and no. 128a in the collection of Sir Walter Buller. This is a relatively large bird, although none of its dimensions exceed the maxima recorded in table 1. The axillary feathers are typical of the race *gavia*.

Reinholdia reinholdi byroni Mathews, A.M.N.H. 527764, a doubtful male which had been a mounted specimen, acquired from Messrs. Tost and Rohu, taxidermists, of Sydney, Australia, and labeled "*Oestrelata cookii*, Eastern Australia," without date. On the back of the original label, Mathews has written "Byron

Bay = Five Islands, N. S. Wales." The exceptionally dark brown dorsal coloration of this specimen is due to the fact that it is in very fresh plumage. It is doubtful whether the quills of wing and tail had obtained quite their full growth. Their appearance, together with the weakness of the bill, makes it seem likely that this was a young bird not long out of the nest. Its dimensions are small, although still within the range of those in table 1.

Reinholdia reinholdi melanotis Mathews, A.M.N.H. 527748, a male washed up on Kaipara Beach, near Helensville, Waitemata County, North Island, New Zealand, January 10, 1915, and obtained by Robin Kemp. In its rich brown plumage and in all other respects, this specimen matches the type of *byroni*. It also looks like a youthful bird. The claw of the middle toe is unworn and long (9 mm.), which accounts for the discrepancy in toe measurements.

Cinathisma cyaneoleuca Hull, A.M.N.H. 427791, a female taken at sea between Ulladulla and Brush Island, New South Wales, December 5, 1915, by A. F. Basset Hull and H. S. Grant. This specimen is in all respects an average *gavia*.

TABLE 3

MEASUREMENTS OF SYNONYMIC TYPE SPECIMENS OF *Puffinus puffinus gavia*

	Wing	Tail	Culmen	Tarsus	Toe and Claw
<i>Puffinus reinholdi reinholdi</i>	214	60.5	36.1	44.8	51.0
<i>Reinholdia reinholdi byroni</i>	190	58.0	31.8	40.5	42.9
<i>Reinholdia reinholdi melanotis</i>	189	58.5	31.2	38.7	46.3
<i>Cinathisma cyaneoleuca</i> (length in flesh, 337)	199	55.3	32.8	41.5	46.4

7. *Puffinus puffinus huttoni*

Puffinus reinholdi huttoni MATHEWS, 1912, The birds of Australia, vol. 2, p. 77 (Snares Islands, south of New Zealand = locality probably uncertain).

Puffinus leptorhynchus MATHEWS, 1937, Bull. Brit. Ornith. Club, vol. 57, p. 143.

Puffinus gavia, MURPHY, 1930, Amer. Mus. Novitates, no. 419, p. 12 (part).

The type specimen of *huttoni* (A.M.N.H. No. 527761) reached the American Museum by way of the Mathews and Rothschild collections. Capture of the specimen has been attributed to Travers and to Dannefaerd. On the original label is written in

ink "Puffinus gavia ♀," and below, in pencil, "Snares Isl." Both of these are in Dannefaerd's handwriting, as has been determined by comparing the notations with those on the labels of other birds known to have been taken by the same collector. The penciled notation, "Snares Isl.," need not be regarded, however, as assurance that the bird was collected on a Snares Island breeding ground. It may have been shot in waters close to the islands, which would offer no proof of its nesting station, or it may even have been mislabeled in the course of Dannefaerd's hurried voyages on the New Zealand government vessel that serviced the subantarctic islands.

Indeed we may be almost certain that this specimen was subsequently labeled as to locality, because a second example, a male (A.M.N.H. No. 527760), bears a similar label and this bird proves to be not *huttoni* but *gavia* (cf. Hartert, 1926, p. 348).

The doubts concerning the type specimen have here been emphasized because its source has already been questioned by New Zealand ornithologists and because no examples of the race were found on the main island of the Snares group during a visit of two weeks in which the writer participated at the height of the breeding season in 1947. In any event, the known distribution of *huttoni* makes it appear virtually certain that it nests in a higher latitudinal zone than *gavia* and well to the south of the subtropical convergence. (Cf. Serventy, 1939, p. 103 and fig. 5.)

In the original description, Mathews pointed out the distinguishing characteristics of the race, namely, large size, the heavy brown wash or mottling on the sides of the neck and chest and the flanks, the brownish flecking of the wing lining, and the dark axillaries. The last character may be stressed, for it seems to be completely diagnostic. Among 18 examples in the American Museum collection, the axillary feathers are dark to the tips, whereas every one of a much larger series of *gavia* shows a narrow white distal band on these same feathers.

The Whitney South Sea Expedition specimens of *huttoni* were all collected off the Banks Peninsula, South Island, New Zealand, on January 28 and 29, 1926. Most of them are marked as birds that had passed the breeding stage, but in a few the gonads were still somewhat enlarged. All of them are characterized by heavy brownish flecking on the neck, which differs from the report (Murphy, 1930, p. 12) published before *huttoni* and *gavia* had been distinguished. Certain birds labeled "lat. 44° S., long.

173° W.," and previously so recorded, were actually taken in longitude 173° *east*, as determined by reference to the field journals. The corrected locality is close to the central eastern coast of the South Island.

8. *Puffinus puffinus opisthomelas*

Puffinus opisthomelas COUES, 1864, Proc. Acad. Nat. Sci. Philadelphia, no. 2, p. 139 (Cape San Lucas, Baja California).

The black-vented shearwater is said to be the most abundant species of the genus *Puffinus* along the western coast of North America. A large series measured in the American Museum represents localities from near Cape Blanco, Costa Rica (latitude 9° N.), northward to central California. Birds from the insular breeding grounds off Baja California have been examined in the Carnegie Museum, Pittsburgh, and elsewhere. Measurements of 49 specimens are summarized in table 1, which shows that the sexes are as precisely alike in size as they are in appearance. The same conclusions are to be drawn from Loomis' (1918, p. 119) figures based upon more than 100 specimens. These are in agreement with those in table 1, except as regards length of tarsus. At the American Museum we endeavor to take this dimension in such a manner as to have it equal the length of a disassociated tarsometatarsal bone. Certain ornithologists, including the late Mr. Loomis, have evidently measured study skins by a technique that yields a figure slightly below the full length of this bone. In other respects the writer has always found his measurements wholly comparable with those of Loomis.

The resemblances between the races *yelkouan* and *opisthomelas* are pointed out above. As regards Murphy's (1930, p. 12) comparison of *opisthomelas* and *gavia*, it should be noted that this applies even more specifically to *huttoni*, which at that date was confused with *gavia*.

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