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A new species of shearwater of the genus *Calonectris* (Aves: Procellariidae) from a middle Pleistocene deposit on Bermuda

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Abstract.—Remains of at least 26 individuals of a *Calonectris* shearwater were recovered from a Pleistocene beach deposit on Bermuda that formed when sea-level was more than 21 m above present level during an interglacial (Marine Isotope Stage 11) 400,000 yr ago. Two prefledging juveniles in the sample indicate breeding on the island. This shearwater was the general size of *C. d. diomedea* of the Mediterranean but differs in proportions and in qualitative characters and is described as *Calonectris wingatei*, new species. The species appears to have become extinct shortly after the time of deposition, when rising sea-level is also thought to have caused the extinction of the Short-tailed Albatross *Phoebastria albatrus* on Bermuda. The Neogene history of the taxa of *Calonectris* in the Atlantic basin is examined in the context of major geological and oceanographic events.

Bermuda's isolated position in the North Atlantic, 1000 km east of the North American mainland, places it within foraging distance for procellariiform birds of both temperate and subtropical waters as well as hydrographic fronts that form along the nearby Gulf Stream (Haney & McGillivary 1985). Despite this, the diversity of breeding Procellariiformes known from the island is quite low. The highly endangered Cahow *Pterodroma cahow*, once the most abundant bird on Bermuda, is the only member of the order that persists on the island. A small extinct shearwater, which provisionally takes the name *Puffinus parvus* Shufeldt (see Olson 2004a), is known only from fossils, and appears to have been succeeded, probably in historic times, by the West Indian Audubon's Shearwater *P. lherminieri*, which in turn was extirpated on Bermuda in the 20th century (Amos 1991). There are three known nesting attempts by Manx Shearwater *Puffinus puffinus*, but this species was apparently never an established resident, as the abundant fossil record from the island (Olson et al. 2005) has so far yielded only a single sternum of the species (Olson 2004a). Finally, the Short-tailed Albatross *Phoebastria albatrus* once bred on Bermuda, but the Atlantic population appears to have been extirpated by the maximum rise of sea level (>+21 m) in the Pleistocene 400,000 yr ago during Marine Isotope Stage (MIS) 11 (Olson & Hearty 2003). The former presence of a fifth species of procellariiform on Bermuda is here documented from a large assortment of fossil bones of a shearwater of the genus *Calonectris* from a single deposit that formed at the height of the same sea level rise that is postulated to have wiped out the albatross.

Three living taxa of shearwaters of the genus *Calonectris* currently breed on islands in the North Atlantic and Mediterranean, all of which had at one time been considered subspecies of a single species. Of these, it is now generally agreed that the Cape Verde Shearwater *C. edwardsi* is a distinct species by virtue of much smaller size and plumage differences (Hazevoet 1995:67), as well as by molecular differences (Gómes-Díaz et al. 2006). The Mediterranean or Scopoli's Shearwater *C. diomedea* breeds on islands in the Mediterranean Sea. The larger Cory's Shearwater *C. borealis* breeds in the North Atlantic islands of the Azores, Canaries, Salvages, Madeira, and the Berlengas Islands off of Portugal. There has been much variation in opinion as to whether this taxon deserves full specific rank or should be regarded as a subspecies of *C. diomedea* (discussed beyond).

I originally interpreted the Pleistocene accumulation from Bermuda as having been derived from beached wintering individuals of *C. d. diomedea* (Olson & Rasmussen 2001, Olson et al. 2005). With further study, I have found that these fossils belong to a previously unrecognized species, similar in size to *C. d. diomedea* but with larger hindlimbs and more robust long bones. This species was breeding on Bermuda up until the middle Pleistocene, after which it appears to have become extinct.

Materials and Methods

Modern comparative skeletal material was examined in the collections of the Division of Birds, National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). At the generic level, comparisons were made with *Fulmarus glacialis* 561911, *Pterodroma leucoptera* 615080, *Procellaria aequinoctialis* 490787, *Calonectris d. diomedea* 620711, *Puffinus* (*Hemipuffinus*) *creatopus* 559553, *P.* (*Thyellodroma*) *pacificus* 500712, *P.* (*Ardenna*) *gravis* 561135, *P.* (*Puffinus*) *griseus* 599153, *P.* (*P.*) *puffinus* 491958. At the specific level, comparisons were made with: *Calonectris d. borealis*—Massachusetts 17767, 17770, 17773–76, 17788–91, 17831, New Jersey 347825; *C. d. diomedea*—Greece 488776–77, 555936 (several individuals), Italy 612133, North Carolina 620710–18; *C. edwardsi* (trunk skeletons only)—Razo I., Cape Verdes 560762–68; and *C. leucomelas*—Halmahera, Indonesia 558350. Fossil material is housed in the Department of Paleobiology, Smithsonian Institution. Measurements were taken with digital calipers to the nearest 0.1 mm.

Family Procellariidae

Genus *Calonectris* Mathews & Iredale, 1915

The species of *Calonectris* were usually placed in the genus *Puffinus*, even after their separation had been proposed (e.g., Peters 1931). It was only following the innovative study of Kuroda (1954) that the validity of *Calonectris* came to be accepted. The long, slender rostrum allies the Bermuda species with the Puffininae as opposed to the fulmarines. As noted by Kuroda, only in *Calonectris* are the anterior intervertebral foramina of the sacrum closed by ossification. In *Calonectris* the shaft of the humerus is terete, not flattened as in subgenus *Puffinus* and to a lesser extent in *Ardenna*, but is relatively longer and more slender than in any of the taxa, except *Thyellodroma*. The brachial depression is more restricted than in *Fulmarus*, *Pterodroma*, or *Procellaria*, but is not as small and decidedly rounded in shape as in *Thyellodroma*. In *Calonectris* the shaft of the femur in medial view is slightly curved (straight in *Fulmarus*, *Pterodroma*, *Procellaria*), but decidedly less curved than in any of the species of *Puffinus*, except the subgenus *Hemipuffinus*, from which *Calonectris* differs in having the shaft relatively more slender, with the appearance of being slightly constricted near the midpoint. The inner

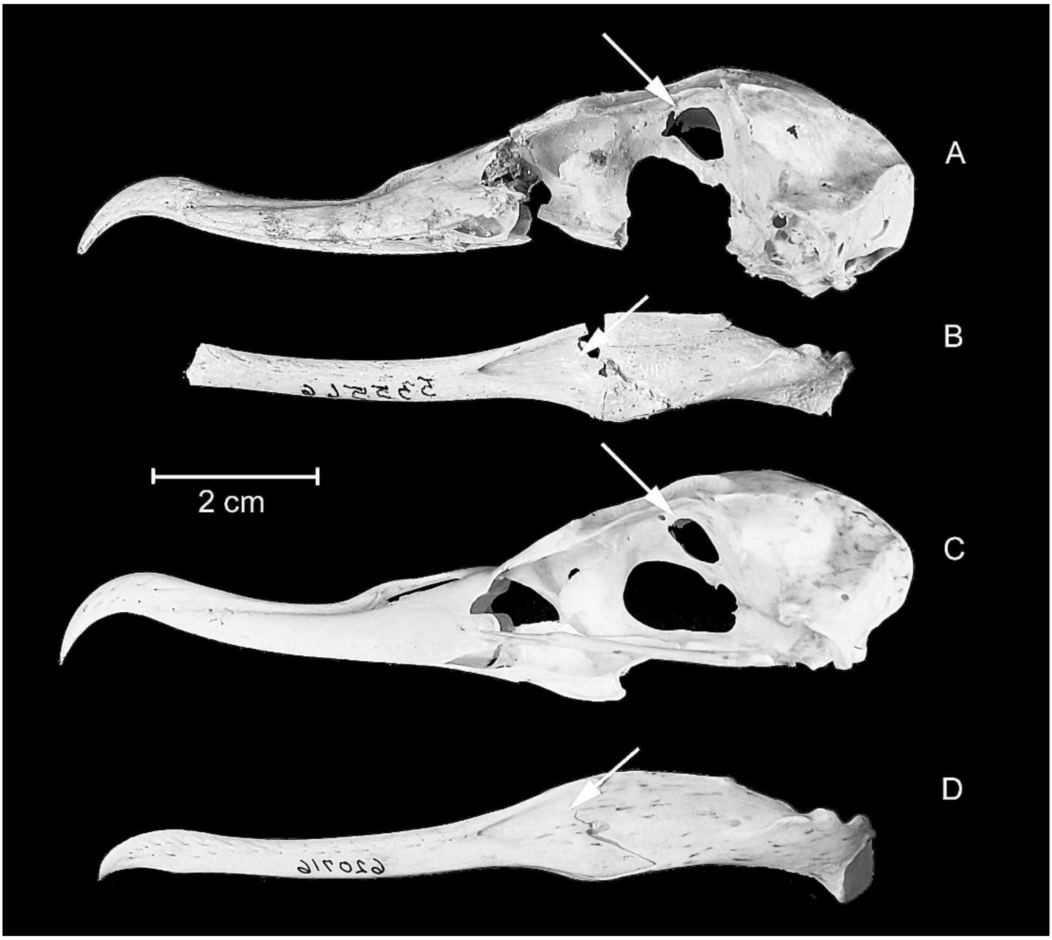

Fig. 1. Cranial elements of *Calonectris*. A, skull of *C. wingatei* holotype (USNM 535555); B, mandible of *C. wingatei* (USNM 535566); C, D, skull and mandible of *C. d. diomedea* (USNM 620716). Mandibles appear as mirror images. Arrows indicate the larger fonticulus orbitocranialis of the cranium and in the mandible the depression for the M. adductor mandibulae.

cnemial crest of the tibiotarsus is much less developed in *Calonectris* than in *Puffinus*. In all *Puffinus*, except subgenus *Hemipuffinus*, the shaft of the tarsometarsus is more laterally compressed and the inner trochlea more retracted than in *Calonectris*, in which the tarsometarsus is much more gracile than in *Hemipuffinus*. In all of these respects the Bermuda material is clearly referable to *Calonectris*.

Calonectris wingatei, new species
Figs. 1–4

Holotype.—USNM 535555 articulated cranium and rostrum lacking the quadratojugals and all elements of the palate; collected 9 Aug 1984 by S. L. Olson, D. B. Wingate, and Frederick V. Grady.

Type locality.—Bermuda, Hamilton Parish, Calonectris Quarry, 32°20′20.9″N, 64°42′24.5W″ (see Olson et al. 2005). The site where the fossils were collected, called Calonectris Quarry, was exposed in the Government Quarry on the western side of Castle Harbour on the eastern end of Bermuda. It was described briefly by Olson & Hearty (2003) and Olson et al. (2005) and in detail by Olson & Hearty (2009) because of its importance in providing multiple lines of evidence for sea-

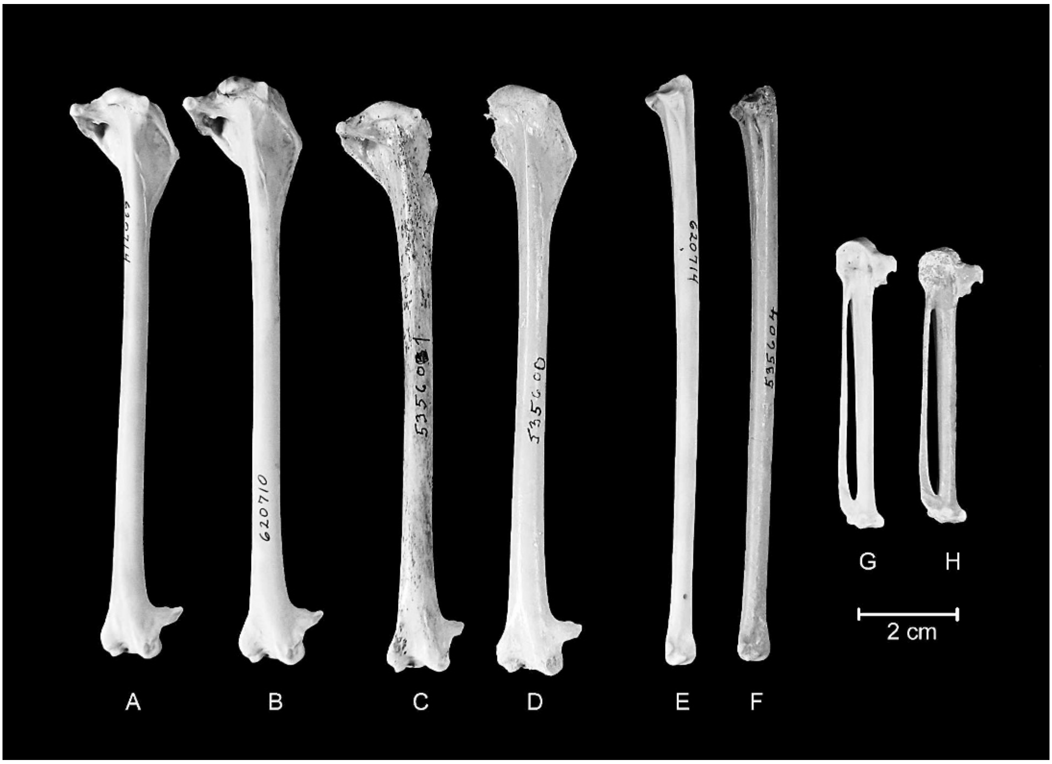

Fig. 2. Wing elements of *Calonectris*. A, B, E, G, *C. d. diomedea*. C, D, F, H, *C. wingatei*. A–D, right humeri (USNM 620714, 620710, 535601, 535600). E, F, right ulnae (USNM 620714, 535604); G, H, left carpometacarpi (USNM 620716, 535605). Note the stouter shafts in *C. wingatei*.

level having exceeding 20 m above present in the Middle Pleistocene. The associated fauna (Olson & Hearty 2009) consisted of terrestrial and marine invertebrates, fish, three species of seabirds in addition to *Calonectris* (*Pterodroma cahow*, *Puffinus parvus*, *Phoebastria albatrus*), three species of land birds, a skink (Olson et al. 2006), and a vagrant bat (Grady & Olson 2006).

The accumulation clearly formed as a beach deposit, the birds having been washed into a crevice that was probably near the maximum of normal wave runup on a sloping beach. The elevation of the site was determined by transit survey as being exactly 70 ft (21.3 m) above present sea level.

Age.—Middle Pleistocene, Marine Isotope Stage 11, 400,000 yr BP (Olson & Hearty 2003, 2009). A +21 m sea stand in MIS 11 has also been documented at two localities in the Bahamas (Hearty et al. 1999) and was later confirmed at another site on Oahu, Hawaiian Islands (Hearty 2002) and elsewhere. This event would have had a major impact on seabirds worldwide.

Measurements of holotype (mm).—Total length 101.8, length of rostrum from nasofrontal hinge 55.5, length of cranium from nasofrontal hinge 47.5, width of nasofrontal hinge 13.4, least width of interorbital bridge 10.4, greatest width of cranium (at postorbital processes) 35.9, depth of rostrum at nasofrontal hinge 11.4.

Paratypes.—535627 rostrum and dorsal surface of cranium; USNM 535552–54, 535556 crania; 535557, 525628–30 rostra; 535558 anterior half of rostrum; 535559–65 rostral hooks; 535565–78 incomplete mandibulae; 535579 left lacrimal; 535580–84, 535632–34, 535653 right

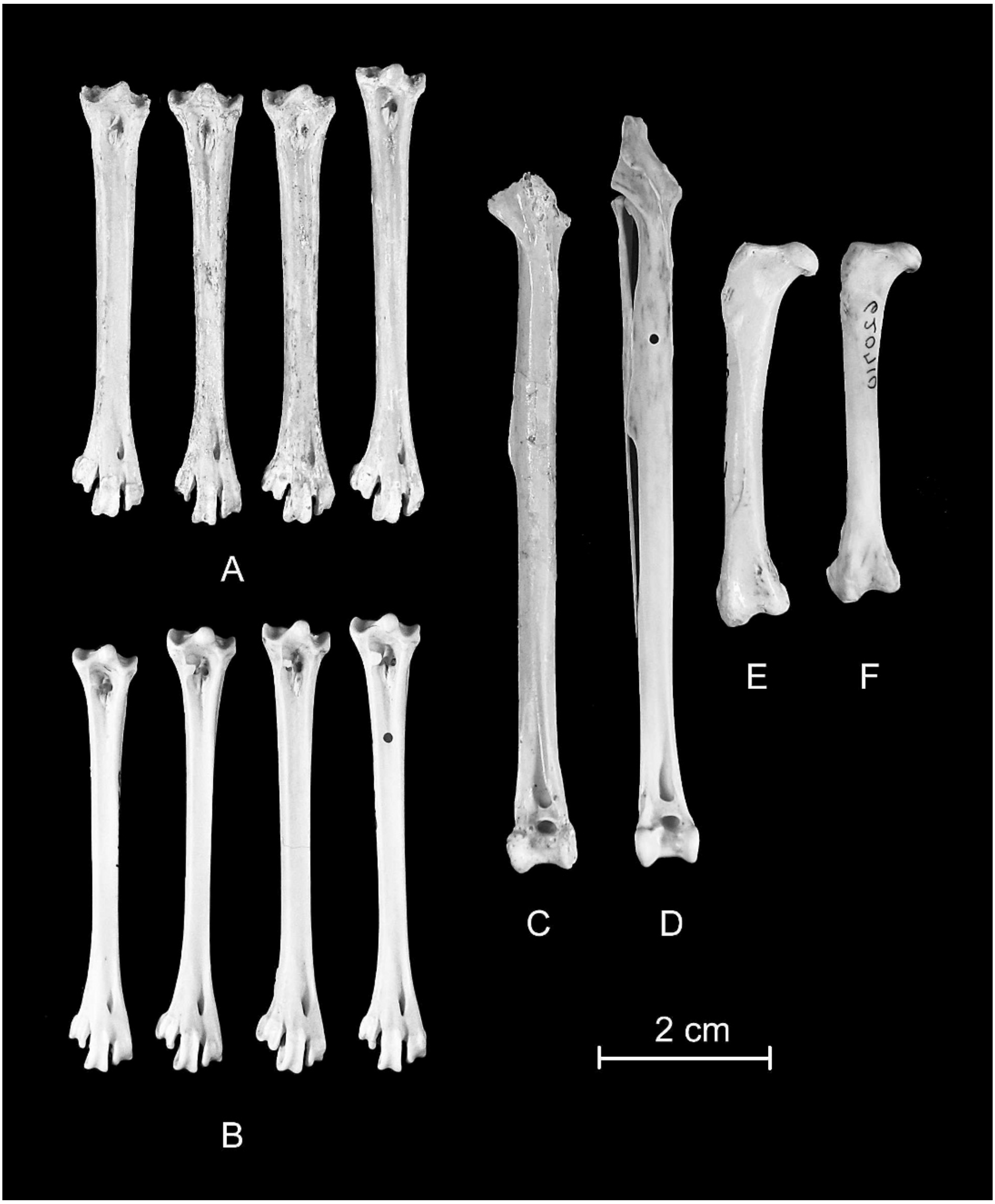

Fig. 3. Hindlimb elements of *Calonectris*. A, C, E, *C. wingatei*. B, D, F. *C. d. diomedea*. A, left tarsometatarsi (left to right, USNM 535647, 535648, 535646, 535645); B, *C. d. diomedea* (left to right, USNM 620714, 620711, 620716, 620710); C, D, right tibiotarsi (USNM 535617, 620710); E, F, right femora (USNM 535621, 620710). Note the much stouter shafts in *C. wingatei*.

coracoids; 535585–90, 535654–56 left coracoids; 535659 right clavicle; 535649 sternum lacking much of right side; 535591, 535631, 535650 anterior portions of sterna; 535651–52 synsacra; 535592–93, 535657–58 right scapulae; 535594–97 left scapulae; 535598–601, 535635–36, 535663–67 right humeri; 535602–03, 535637–38, 535660–62, left humeri; 535604, 535639–40, 535668–71 right ulnae; 535641, 535672–

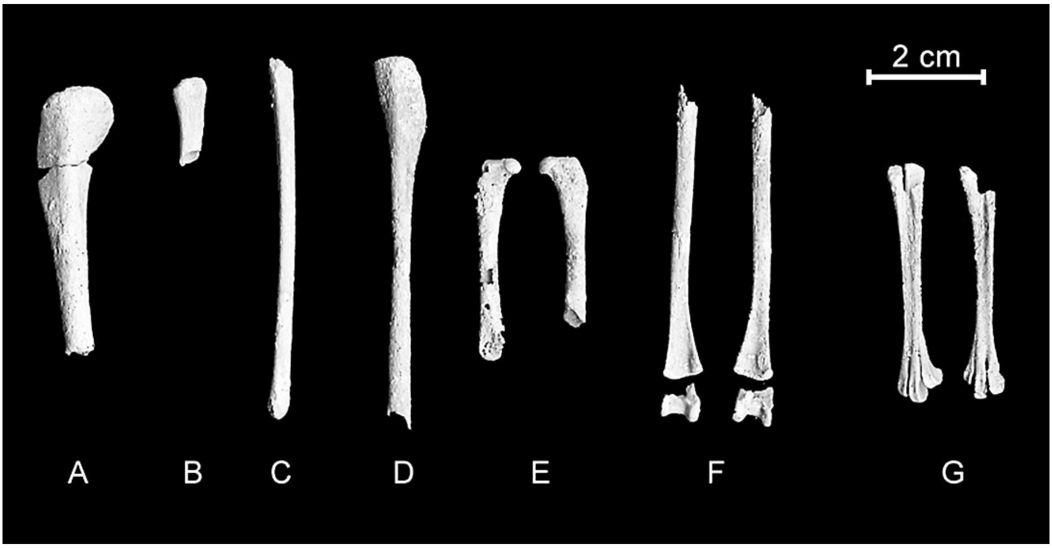

Fig. 4. Bones of prefledging juveniles of *Calonectris wingatei*. A–B, humerus and ulna(?) of an older individual (USNM 535682) than C–G (USNM 535681), which are probably from a single individual; C, ulna; D, right humerus; E, right and left femora; F, right and left tibiotarsi with unfused tarsals; G, right and left tarsometatarsi lacking proximal tarsals.

74 left ulnae; 535675–79 right radii; 535605–07, 535680 left carpometacarpi; 535608–09 right carpometacarpi; 535610–12, 535642 right phalanx 1 of major alar digit; 535613–15, 535643 left phalanx 1 of major alar digit; 535616 right tibiotarsus lacking inner cnemial crest; 535617 left tibiotarsus lacking inner cnemial crest; 535618 distal half of left tibiotarsus; 535619 distal two-thirds of right tibiotarsus; 535620 proximal third of right tibiotarsus; 535621 left femur; 535622 right femur; 535623 left femur lacking distal end; 535644 right tarsometatarsus; 535624, 535645–48 left tarsometatarsi; 535625 proximal end of right tarsometatarsus; 535626 distal end of left tarsometatarsus. 535681 postcranial elements of a very young, prefledging juvenile; 535682 proximal end of left humerus and proximal ulna(?) of a somewhat older juvenile. There are many more specimens, mainly fragmentary, in the collections but that were not used for comparisons or measurements and have not been cataloged. The minimum number of individuals is 26, including the two juveniles.

Measurements of paratypes.—See Table 1.

Etymology.—Dedicated to David B. Wingate, premier naturalist and conservationist of Bermuda, savior of the Cahow, and paleontological explorer and facilitator.

Diagnosis.—A species of *Calonectris* smaller than *C. diomedea borealis* (Table 1), larger than *C. edwardsi* or *C leucomelas*, which latter is quite distinct from any of the Atlantic taxa. Similar in size to *C. d. diomedea* (Table 1) but with femur absolutely larger and all long bones more robust (Table 2). In the cranium, the fonticulus orbitocranialis is larger and more irregularly ossified anteriorly than in *C. d. diomedea* (Fig. 1). The mandibular ramus is generally deeper, with the symphysis longer, wider, and deeper than in *C. d. diomedea*. The external fossa on the dentary for the attachment of part of M. adductor mandibulae is markedly deeper and more extensive in the fossils than in *C. d. diomedea* (Fig. 1).

Description.—The large series of shearwater bones from Calonectris Quarry are

Table 1.—Skeletal measurements (lengths in mm) of *Calonectris*. From left to right and top to bottom the figures represent range, mean, *n*, and standard deviation.

Measurement	*C. d. borealis*	*C. wingatei*	*C. d. diomedea*
Cranium	45.4–49.3 (47.0) 12 1.32	45.0–47.0 (46.4) 5 0.72	43.2–47.6 (45.1) 13 1.26
Rostrum	58.4–66.3 (61.7) 12 2.38	51.3–56.4 (53.5) 5 1.83	54.6–61.0 (57.9) 13 1.75
Humerus	122.3–135.5 (128.3) 12 4.18	116.1–127.2 (120.4) 21 2.50	111.7–124.3 (122.5) 15 3.10
Ulna	124.9–137.1 (129.9) 12 4.02	96.8–126.3 (120.0) 12 7.50	117.8–127.4 (122.5) 15 2.88
Carpometacarpus	60.2–69.2 (64.1) 12 2.67	56.7–61.5 (58.2) 8 1.61	57.5–62.1 (60.0) 13 1.59
Femur	40.5–47.6 (43.8) 12 1.97	43.2–45.4 (44.3) 2 1.56	37.1–42.9 (40.0) 11 1.99
Tarsometatarsus	51.1–59.7 (56.7) 12 2.84	52.2–56.9 (53.8) 6 1.82	50.9–54.6 (52.9) 12 1.39

from a species much larger and more robust than *C. edwardsi*, as seen in visual comparison of the coracoids and femora in 7 trunk skeletons of that species. The length measurements of the femora of *C. edwardsi* (35.4–37.9 mm, mean 36.4) are far below those of the two intact femora of *C. wingatei* (43.2 and 45.4 mm). The Pacific species *C. leucomelas* is a much more gracile bird with a longer, more slender bill than in the Bermudan fossils.

It has been well established that *C. d. borealis* is larger than *C. d. diomedea* based on measurements, body weight, and egg weight (Jouanin 1976, Massa & Lo Valvo 1986, Granadeiro 1993). Within each taxon there is geographic size variation and males are larger than females (Wink & Ristow 1979, Witt et al. 1984, Massa & Lo Valvo 1986, Granadeiro 1993). In the series of skeletons of *C. d. diomedea* and *C. d. borealis* measured here (Table 1), there is slight overlap between the taxa in all measurements, with the larger extremes of *C. d. diomedea* falling within the range of smaller individuals of *C. d. borealis*. *Calonectris wingatei* is clearly smaller than *C. d. borealis* (with the exception of cranium length, which scarcely differs among the three samples).

Although *C. wingatei* is in the general size range of *C. d. diomedea*, it was a decidedly more robust bird (Figs. 2, 3), particularly in the hindlimb. There is no overlap at all in tarsal width between the two (Table 2), and only one measurement each for femur and tibiotarsus of *D. wingatei* was less than the maximum for *C. d. diomedea*. The two exceptions could very well have come from immature birds. There was no overlap in the width of the

Table 2.—Shaft widths (mm) at midpoint of limb bones of *Calonectris*. From left to right the figures represent range, mean, and *n*.

Measurement	*C. wingatei*	*C. d. diomedea*
Humerus	5.6–6.9 (5.9) 15	5.3–6.0 (5.5) 15
Ulna	4.7–5.3 (4.9) 11	4.1–4.6 (4.4) 14
Carpometacarpus	3.6–4.7 (4.2) 9	3.7–4.1 (3.9) 13
Femur	3.9–4.6 (4.2) 6	3.6–4.0 (3.8) 14
Tibiotarsus	3.9–4.6 (4.3) 5	3.7–4.2 (4.0) 12
Tarsometatarsus	3.7–4.3 (4.0) 6	2.9–3.4 (3.2) 12

shaft of the ulna (Table 2), and only two carpometacarpi of *C. wingatei* were less than the maximum for *C. d. diomedea*. Although there is overlap in the shaft widths of the humerus, all measurements of *C. wingatei* exceed the mean for *C. d. diomedea* and nearly 40% are at (1) or exceed (5) the maximum in that taxon. In length, the leg elements are absolutely larger (femur) or average larger in *C. wingatei*, whereas the rostrum and wing elements all average smaller than in *C. d. diomedea*, so that *C. wingatei* appears to have been a heavy-set bird with relatively smaller wings than *C. d. diomedea*. This suggests the possibility that the Bermuda bird may have been more sedentary and may not have performed long migrations.

Taphonomy and extinction of Calonectris *on Bermuda*.—A minimum of 24 adult individuals is indicated. Disproportionate representation of wing and pectoral girdle elements compared with hindlimb and cranial bones suggests that most of the birds died at sea and were in various stages of decomposition when washed ashore (Olson & Hearty 2009). Two individuals are early juvenile birds that would have been too young to fly and that must have hatched on the island. The bones are still very porous and unformed, and the tarsals are unfused to the metatarsals or the tibiae (Fig. 4). That at least two individuals are represented is indicated by humeri and ulnae of different sizes and stages of development.

Ordinarily, one would expect to see indication of higher mortality among juveniles than adults. The disproportion of adults to juveniles in the sample might be explained by the fact that in at least some populations of *Calonectris*, approximately 75% of individuals occupying a breeding colony may be non-breeders (Araujo et al. 1976).

A more likely possibility is that by the time sea level reached 21 m above present levels there would have been very little land area or suitable nesting sites for *Calonectris* left on Bermuda and normal population dynamics would have been disrupted. In a long-lived seabird such as a species of *Calonectris*, a large adult population might persist for years after recruitment had fallen below levels sufficient to sustain the species. Not long after the Calonectris Quarry bones were deposited, sand generated and exposed by the falling MIS 11 sea was blown over the site, completely burying the former sea-cliff above the deposit and probably obliterating most or all suitable nesting crevices for *Calonectris*.

Two juvenile albatrosses in the same deposit with the bones of *Calonectris* represent the last known occurrence of resident albatrosses in the North Atlantic (Olson & Hearty 2003). The only older locality in Bermuda from which vertebrate fossils have been recovered is the storm deposit at Green Island and vicinity on the south shore that was the site of an albatross colony near present sea level that formed at the beginning of the same interglacial stage as the Calonectris Quarry site (Olson & Hearty 2003). This was a sandy beach ridge that would have been unsuitable as a breeding site for *Calonectris* shearwaters and the only bird remains found here were those of albatrosses, with the exception of a single fragment of rostrum of a Great Auk *Pinguinus impennis* (Olson 2004b).

Prior to the catastrophic MIS 11 inundation was a very long stable period of some half million yr during which sea levels, while fluctuating, were always below their present level, exposing the entire Bermuda platform (Olson et al. 2005, 2006). *Calonectris* probably throve on Bermuda at that time, but no vertebrate fossil deposits of that age have ever been found on the island (Olson et al. 2005). On the other hand, many deposits younger than Calonectris Quarry, containing tens of thousands of bird bones representing most of the past 200,000 yr of Bermuda's history have been found

(Hearty et al. 2004, Olson et al. 2005), none of which are referable to *Calonectris*. Thus, the Bermuda species of *Calonectris* probably became extinct shortly after the only known aggregation of its bones was deposited in the middle Pleistocene.

Paleogeographical history of Calonectris *in the Atlantic*.—The earliest fossil record for *Calonectris* is a small species in middle Miocene deposits of the Calvert Formation of Maryland and Virginia, about 14 million yr in age (Olson unpublished). It is uncertain what the relationships of that species may have been to the larger members of the genus. Nearly 10 million yr elapsed before the next occurrence of the genus in the early Pliocene. Two fragmentary fossils from South Africa were referred to a *Calonectris* that would probably have been nearest to *C. d. borealis* in size (Olson 1985). Three species were recorded from the early Pliocene Yorktown Formation in North Carolina, between 4 and 5 million yr of age (Olson & Rasmussen 2001). One of these was a giant species, *C. krantzi*, that was roughly the size of some of the species of *Procellaria*. The other two were identified on size as probable temporal representatives of *C. borealis* and *C. diomedea*. On re-examination of the material this assessment will require some modification. The specimen referred to *C. d. borealis* appears to be correctly assigned. The femur referred to *C. d. diomedea*, however, is quite small, and is possibly better referred to *C. edwardsi*. Because *C. d. diomedea* had presumably not differentiated as early as the early Pliocene (see below), the three humeri referred to that taxon by Olson & Rasmussen (2001) could well have come from individuals of *C. wingatei* or its direct antecedent.

An important paleoenvironmental factor influencing the evolution of procellariiform birds in the Atlantic was the so-called Messinian Salinity Crisis at the end of the Miocene, which lasted about 400,000 yr and ended some 5.3 million yr ago (Gautier et al. 1994, Suc & Clauzon 1996). At this time the Mediterranean Sea was cut off from the Atlantic and was either nearly dry or consisted of highly saline lakes (Stanley 1990). In either case, there would have been no suitable habit for procellariiform birds in the Mediterranean basin at this time, as noted by Voous (1976), and probably for a considerable period thereafter, until the basin refilled and oceanographic conditions stabilized sufficiently for the establishment of marine ecosystems with all the elements lower on the food web than surface-feeding predatory birds. Thus, given that *C. borealis* was the likely progenitor of *C. diomedea*, the latter is not likely to have differentiated until well into the Pliocene at the earliest. Molecular evidence appears to support this as well (see below).

Until recently, *C. borealis* was usually considered to be a subspecies of *C. diomedea* but a case for specific status for these shearwaters was summarized by Sangster et al. (1999), who, under *Calonectris borealis*, stated that "Cory's Shearwater and Scopoli's Shearwater *C. diomedea* are specifically distinct based on phylogeographic analysis of allozymes (Randi et al. 1989) and mitochondrial DNA (Heidrich et al. 1996, 1998), qualitative differences in vocalisations (Bretagnolle & Lequette 1990) and analysis of morphological characters (Granadeiro 1993, Gutiérrez 1998)." This statement does not accurately reflect the results reported in the papers cited, however, which were either equivocal, did not address the issue, or came to exactly the opposite conclusion.

Individuals of *C. d. borealis* occur in the Mediterranean in colonies of *C. d. diomedea*, either as non-breeders (Lo Valvo & Massa 1988), paired with another individual of *C. d. borealis* (Sánchez Codoñer & Albufera 1994), or possibly forming mixed pairs with *C. d. diomedea* (Thibault & Bretagnolle 1998). Rabouam et al. (2000) concluded from their genetic studies that the two taxa were subspecies that had only recently differentiated. Penhallurick & Wink (2004:139) considered that within *Calonectris* "the Mediterranean and the Atlantic lineages differ morphologically and genetically, but distances are rather small, suggesting that *C. d. diomedea* and *C. d. borealis* should be treated as subspecies." In a phylogeographic genetic evaluation of the *Calonectris* species complex, Gómez-Díaz et al. (2006) found a low but consistent level of genetic difference between *C. d. diomedea* and *C. d. borealis*, also suggesting a relatively recent divergence time for these taxa, which they treated as subspecies. In addition, they found that a population breeding at Almeria on the Mediterranean coast of Spain was clearly assignable to *C. d. borealis*, suggesting that the Almeria-Oran oceanographic front was a more important barrier to these taxa than the Straits of Gibraltar. Although the subspecies concept is in many cases inappropriately applied in Procellariiformes, this is one instance when it use appears justified.

Calonectris d. borealis breeds on islands that are in areas of cold-water upwelling such as the Azores Current and the Canary Current, whereas *C. d. diomedea* is an occupant of the warmer waters of the Mediterranean with a main wintering area now apparently in the vicinity of the Gulf Stream in the western Atlantic. Although both taxa occur in the western North Atlantic off North Carolina (Lee 1995), *C. d. diomedea* may predominate at times, as shown by a series of nine *Calonectris* collected off North Carolina on 15 Sep 1995, all of which proved to be *C. d. diomedea* (USNM 620710–620718). On the other hand, most of the individuals occurring in cold South African waters are *C. d. borealis* (Camphuysen & van der Meer 2001) rather than *C. d. diomedea* as had been thought previously (Mougin et al. 1988). Thus the size differences in these taxa could simply be a reflection of environmental responses, with the larger form in colder regions in accordance with Bergman's Rule.

If body size is affected by sea-surface temperatures, one would expect any *Calonectris* occupying the warmer waters around Bermuda to be smaller than *C. d. borealis*, as was *C. wingatei*, which may have bred on Bermuda and occupied the warmer waters of the western North Atlantic for millions of years as the warm-water counterpart of *C. d. borealis* on the other islands of the northern North Atlantic. When the Mediterranean became available for colonization, *C. d. borealis* entered and gave rise to the smaller *C. d. diomedea* as an adaptation to the warmer waters, thus becoming convergently similar in size to *C. wingatei*. If the Bermudan species occupied the western North Atlantic year round, it is conceivable that suitable warm-water wintering habitat may have been more of a limiting factor for *C. d. diomedea* than breeding habitat in the Mediterranean. Perhaps *C. d. diomedea* did not begin wintering in the western North Atlantic until after the extinction of *C. wingatei* in the Middle Pleistocene.

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