

A new species of small owl of the genus *Aegolius* (Aves: Strigidae) from Quaternary deposits on Bermuda

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Abstract.—Fossil remains of a small owl found in eight separate localities on Bermuda ranging in age from the end of the last interglacial period (Marine Isotope Stage 5a, ca. 80,000 years ago) and up into the Holocene are described here as a new species, *Aegolius gradyi*, the only representative of its genus known from a remote oceanic island. This differed from its probable North American ancestor, *A. acadicus*, in its more robust hindlimb elements, smaller head, and a possible tendency for smaller wing elements. Its colonization was probably made possible by the unique conditions of suitable habitat for hunting, roosting, and nesting afforded by Bermuda, including the presence of woodpeckers (Picidae) that would have excavated nest sites suitable for the owls in the endemic palm trees (*Sabal bermudana*). From accounts dating to the early 1600s, the species appears likely to have persisted into the historic period.

Keywords: *Aegolius acadicus*, *Colaptes*, fossil birds, Holocene, Northern Saw-whet Owl, Picidae, Pleistocene, woodpeckers

The diversity of terrestrial birds in the fossil record of Bermuda (see Olson et al. 2005, Olson & Wingate 2012 for reviews of the literature) also included a very small owl that, although not abundant, was present in numerous deposits and was consistently present for a period of tens of thousands of years. It proves to be referable to the genus *Aegolius* and, as might be expected, had differentiated to a sufficient degree as to be recognized as specifically distinct from its likely mainland ancestor, the Northern Saw-whet Owl *Aegolius acadicus*. There are unique conditions offered by Bermuda that allowed it to colonize and persist since at least the beginning of the last glacial period. As with several other kinds of birds in Bermuda, this small owl evidently did not become extinct until after being seen alive in the early 1600s by pioneering English colonists on the island.

Materials and Methods

All measurements were taken with digital calipers and rounded to the nearest 0.1 mm. Comparative material examined, all from collections of the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM): 14 skeletons of *Aegolius acadicus* from Maine, Vermont, Maryland, District of Columbia, Ontario, Wyoming, Colorado, and Washington (4 males 435085, 502238, 553848, 676921; 7 females 556838, 559563, 561895–6, 621369, 623366, 635124; 3 unsexed 224818, 347240, 431077); 7 male skeletons of *Aegolius f. funereus* from Sweden (610424–610430); 2 unsexed partial skeletons of *A. f. richardsoni* from Quebec and Alaska (289422, 289861). One skeleton each of: *Athene noctua* (603596), *Glaucidium passerinum* (610391), *Micrathene whitneyi* (555314), *Otus asio* (490070),

and *Surnia ulula* (622484). No skeletons were available for *Aegolius ridgwayi* or *A. harrisii*, both of which are geographically far removed from Bermuda.

Systematics

Family Strigidae

Genus *Aegolius* Kaup, 1829

Tarsometatarsus proportionately much shorter and more robust, with hypotarsal crest much less posteriorly produced than in *Otus*, *Athene*, or *Micrathene*; tarsometatarsus much less short, squat, and robust than in *Glaucidium* or *Surnia*, with anterior and posterior surfaces of the shaft much less excavated.

Aegolius gradyi, new species

Figs. 1–3

Holotype.—Complete left tarsometatarsus (Fig. 3E) with a few associated ossified flexor tendons (USNM 525260) collected

17 Feb 1999 by S. L. Olson and D. B. Wingate.

Type locality.—Bermuda, Hamilton Parish, Wilkinson Quarry, Site UWQ1 (32°21'08.9"N, 64°42'52.2"W), a soil-filled fissure in the east face of the quarry (see Hearty et al. 2004:Fig. 6, where erroneously called UWQ4d; Olson et al. 2005:Fig. 6).

Age of holotype.—Late Pleistocene, last glacial (Marine Isotope Stage 3/2) 29,510 ± 200 ¹⁴C yr BP (Hearty et al. 2004, Olson et al. 2005).

Measurements (mm) of holotype.—Total length 23.8, proximal width 6.1, proximal depth through hypotarsus 5.6, least width of shaft 3.6, distal width 6.3, distal depth 5.0.

Paratypes.—Topotypes from Wilkinson Quarry UWQ1: proximal end of right humerus USNM 545255, proximal end of left radius 545256, complete left femur 545257, proximal half of right femur 545258, distal end of left femur 545259, proximal end of left tarsometatarsus 545261, ungual phalanx 545262.

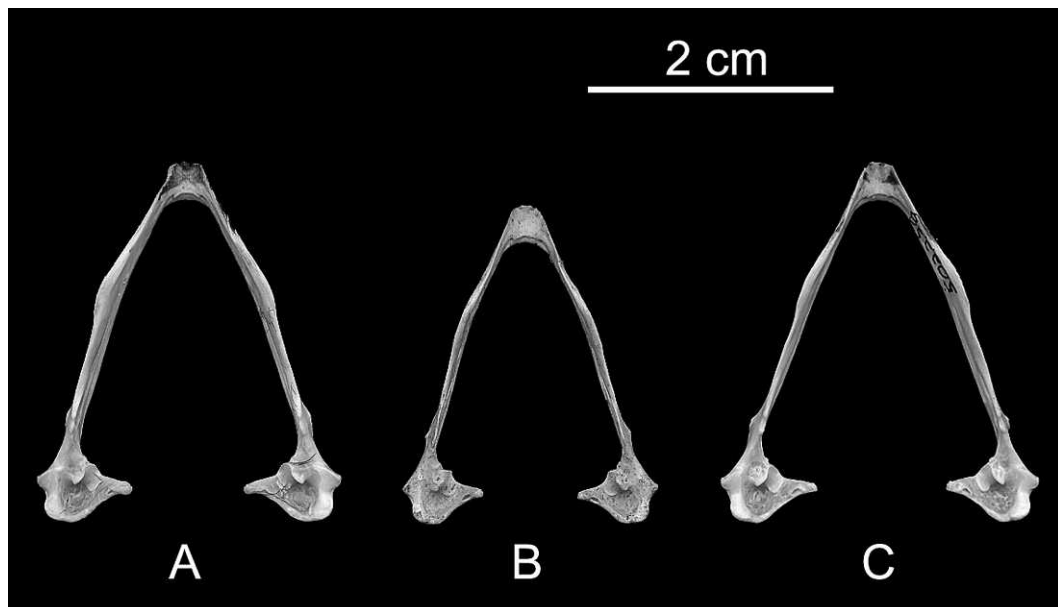


Fig. 1. Mandibles of *Aegolius* in dorsal view. A, *A. acadicus* USNM 561896; B, *A. gradyi*, USNM 545281; C, *A. acadicus* USNM 502238.

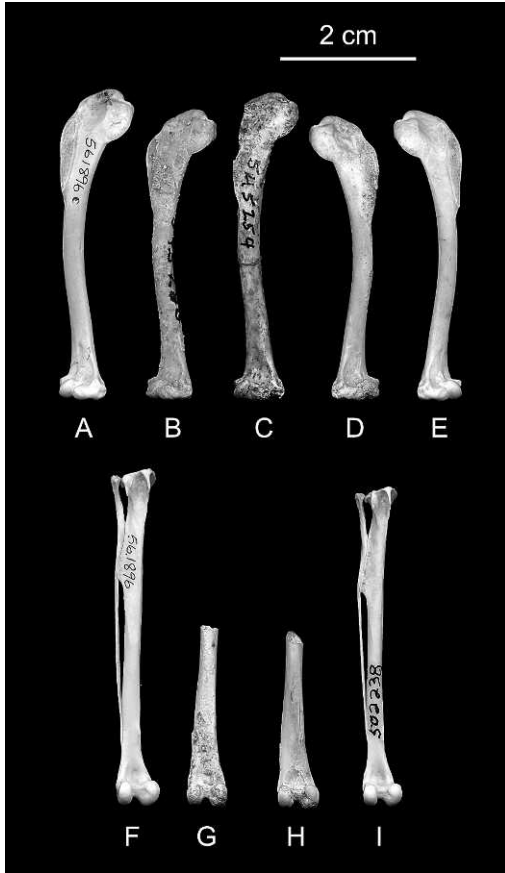


Fig. 2. Humeri in palmar view (upper row), and tibiotarsi in anterior view (lower row) of *Aegolius*. A, *A. acadicus* USNM 561896; B, *A. gradyi*, USNM 545280; C, *A. gradyi*, USNM 545254; D, *A. gradyi*, USNM 545275; E, *A. acadicus* USNM 502238; F, *A. acadicus* USNM 561896; G, *A. gradyi*, USNM 545274; H, *A. gradyi*, USNM 545272; I, *A. acadicus* USNM 502238.

Convolvulus Cave: also once referred to as “Bournes Quarry Cave,” complete right ulna 545263, complete right radius 264890.

Walsingham Cave, higher, drier portion: proximal two-thirds of right humerus 545264.

Fern Sink Cave: surface deposits, complete left tarsometatarsus 545265.

Government Quarry: fissure fill upper level, Aug 1981, R. Baird, left carpometacarpus lacking minor metacarpal 545267.



Fig. 3. Femora in anterior view (upper row), and tarsometatarsi in anterior view (lower row) of *Aegolius*. A, *A. acadicus* USNM 561896; B, *A. gradyi*, USNM 545257; C, *A. acadicus* USNM 502238; D, *A. acadicus* USNM 561896; E, *A. gradyi*, holotype USNM 545260; F, *A. gradyi*, USNM 545266; G, *A. acadicus* USNM 502238.

Sibleys Cave, Heron Head Pocket: complete right tarsometatarsus 545266.

Admirals Cave: lower unit *u* proximal half of right ulna 545268, upper *u* distal end of right ulna 545269, upper 10 cm of *u* transitioning to *v* proximal two-thirds of right ulna 545270, lower *u/v* distal end of left humerus and piece of shaft 545271, upper *u/v* distal end of right tibiotarsus 545272, lower *v* distal end of right tibiotarsus 545273, south pocket of *v* distal end

Table 1.—Measurements of *Aegolius* (mm). For *A. acadicus* $n=14$, except mandible = 11, femur = 13. Distal depth of tibiotarsus is through the internal condyle. Proximal depth of tarsometatarsus is through the hypotarsus.

Measurement	<i>A. acadicus</i> range (mean)	<i>A. gradyi</i>
MANDIBLE length	30.3–31.9 (31.0)	27.7
HUMERUS length	40.2–45.4 (43.1)	42.3, 45.0
proximal width	7.6–8.8 (8.3)	7.5, 8.2, 8.3
least shaft width	2.6–3.3 (3.0)	2.9, 3.1, 3.3
distal width	7.3–8.2 (7.7)	7.7, 7.9
ULNA length	46.7–53.4 (49.8)	47.0
RADIUS length	45.3–51.3 (47.7)	45.1
CARPMETACARPUS length	20.5–23.5 (22.0)	21.0, 21.5
proximal depth	5.0–5.6 (5.2)	5.2, 5.5
FEMUR length	31.7–35.3 (33.8)	35.8
proximal width	5.6–6.4 (6.0)	6.6, 6.7
least width shaft	2.3–2.7 (2.5)	2.9, 3.0
distal width	5.6–6.5 (5.9)	5.9, 6.9
TIBIOTARSUS		
least width shaft	2.1–2.6 (2.4)	2.6, 2.6
distal width	5.4–6.2 (5.8)	5.5+, 5.9, 6.1
distal depth	4.3–4.9 (4.7)	4.3, 4.4, 4.7
TARSOMETATARSUS length	23.1–25.5 (23.9)	23.1, 23.4, 23.8
proximal width	5.1–5.9 (5.5)	5.3, 5.4, 5.6, 6.1
proximal depth	4.9–5.8 (5.5)	4.9, 5.6, 5.7
least shaft width	2.6–3.3 (3.0)	3.3, 3.3, 3.6
distal width	5.3–6.6 (6.1)	5.9, 6.1, 6.3
distal depth	4.3–5.2 (4.7)	4.7, 5.0, 5.1

of right tibiotarsus 545274, unit *v* equivalent under block of loose flowstone complete left humerus 454275, same locality proximal half left ulna 545276, unit *x* distal portion of right ulna 545277, unit *x* right carpometacarpus lacking minor metacarpal 545278, unit *y* proximal end of left ulna 545279, NE upper red talus complete right humerus 545280.

Crystal Cave: complete mandible 545281 (formerly 346839 in ornithology collection; see Olson et al. 2005:229 for some of the history of this specimen).

Measurements of paratypes.—See Table 1.

Ages of paratypes.—This small owl, though scarce, is present virtually throughout the extraordinarily detailed sequence of deposits in Admirals Cave (Hearty et al. 2004), in levels ranging back through the entire last glacial period (MIS 4-2) and at least to the very end of the last interglacial

(MIS 5a), ca. 80,000 years ago. It is likewise present in the two early Holocene units (*x* and *y*) and in the surface deposits in Fern Sink Cave, which are also Holocene (Hearty et al. 2004). The ages of the other cave deposits in which owl fossils were found are all considered to fall within this late Quaternary time period (Olson et al. 2005).

Etymology.—To Frederick V. Grady, my companion in the field on many trips to Bermuda, Hawaii, and the West Indies. A diligent and indefatigable collector of vertebrate fossils, Grady's extraordinary ability and perseverance in identifying and sorting small fossils from vast amounts of washed and screened matrix have added immeasurably to knowledge of paleoenvironments everywhere he has worked.

Diagnosis.—A species of *Aegolius* smaller than *A. funereus*. Generally similar in

size to *A. acadicus* but shafts of hindlimb elements more robust. Femur with neck narrower but rotular groove wider. Condyles of tibiotarsus noticeably less deep than in *A. acadicus* in distal, lateral, and medial views. Posterior wing of internal cotyla of tarsometatarsus projects more posteriorly, not angled medially as in *A. acadicus*; hypotarsus decidedly less deep. Bicipital crest of humerus smaller and more rounded, pectoral crest not as extensive in length or width compared with *A. acadicus*. Mandible smaller, decidedly less bowed, dorsal edge of posterior portion of dentary much less flared than in *A. acadicus*.

Description.—In overall size *Aegolius gradyi* is generally similar to *A. acadicus*. Although the lengths of hindlimb elements overlap, in the Bermudan owl they are decidedly more robust. There was evidently also a tendency towards reduction in size of the wing and in muscle attachments on the crests of the humerus. The single available complete fossil ulna and radius are each at or below the minimum for *A. acadicus*, although fragmentary specimens of those elements suggest that some individuals were larger, so that there was probably more overlap. Likewise, the two available fossil carpometacarpi are below the mean size of *A. acadicus* although still within the range of that species. The surprisingly small size of the single available mandible may represent the low end of variation in size in *A. gradyi*, yet nevertheless may be an indication that the size of the head in the insular species may have been smaller, for which there are plausible evolutionary explanations (see below).

Remarks.—Even without morphological differentiation, the number and distribution of fossils are certain evidence that there was a resident population of *Aegolius* on Bermuda through at least the last glacial period and into the Holocene and probably the historic period. Bermuda at any time would have presented an envi-

ronment quite distinct from that occupied by the Northern Saw-whet Owl *A. acadicus*, yet Bermuda presented certain conditions that may easily have “pre-adapted” that species for colonizing such a new environment.

Aegolius acadicus breeds across North America, mainly in northern forest in the east but extending farther south in mountainous areas, particularly in the west. Although present in the breeding range throughout the year, good numbers migrate to more southerly quarters for the winter (Beckett & Proudfoot 2011) and vagrant individuals have strayed to Bermuda at intervals, mainly in fall and winter (November–April; Amos 1991). During the last glacial period, the breeding distribution of *A. acadicus* would have been depressed far to the south of its present range, putting most of the eastern populations closer to Bermuda throughout the year and thus probably facilitating colonization at a time when Bermuda was reaching its maximum land area during a period of lowered sea level (Hearty & Olson 2010, Olson & Hearty 2010).

Aegolius acadicus is a very small owl and normally feeds almost exclusively on mice, especially *Peromyscus*. It occasionally preys on birds, with the largest normally being about the size of the Northern Cardinal *Cardinalis cardinalis* (Johnsgard 1988), although species as improbably large as a pigeon (*Columba livia*) have also been reported (Cannings 1993). Insects (Cannings 1993) and intertidal invertebrates (Hobson & Sealy 1991, Sealy 1999) are also included in the diet of *A. acadicus*, and vagrants to Bermuda have been observed feeding on moths under streetlights (D. B. Wingate, in litt. 29 Oct 2011). As there never were any native mammals on Bermuda apart from bats (Grady & Olson 2006), which may never have been present in great numbers, *Aegolius gradyi* probably fed to a large extent on birds and the then-ubiquitous skink, which was present on Bermuda for hundreds of

thousands of years (Olson et al. 2006). Another equally long-term resident (Olson & Hearty 2009) was a large, endemic, terrestrial finch, *Pipilo naufragus* Olson & Wingate (2012), derived from the Eastern Towhee *P. erythrophthalmus*. This was larger than its mainland ancestor but with reduced wings. Another component of the pre-human terrestrial avifauna that would have served well as prey for a small owl was a large endemic warbler (Parulidae) (Olson & Hearty 2009). Large insects would have been one of few other food choices, one example being the endemic cicada *Tibicen bermudiana*, whose presence was mentioned as early as 1619, although the species is now feared to be at or near extinction (Wilson & Hilburn 1991). Another insect that may also have disappeared is the flightless grasshopper *Paroxya bermudensis* Rehn (1909), the largest individuals of which were only about 2.5 cm long. It is quite conceivable that other large species of insects existed in Bermuda prior to human colonization and became extinct before being recorded. Although intertidal organisms may have played a part in the diet of the Bermuda owl, as for *A. acadicus brooksi* on the Queen Charlotte Islands of British Columbia (Hobson & Sealy 1991, Sealy 1999), the smaller tidal range on Bermuda would expose less area below tideline. During the low sea levels of glacial periods the shoreline would mainly have been cliffs in any case.

As a consequence of having to feed mainly on birds and lizards, *Aegolius gradyi* had probably become much more diurnal than *A. acadicus*, which is almost strictly nocturnal. The latter has the appearance of being big-headed, owing mainly to the high degree of development of the auditory apparatus, which suggests that “the birds probably can capture prey in total or near-total darkness” (Johnsgard 1988:236). Although the use of auditory clues might still have been useful in hunting birds scratching about in dense

cover during the day, the decreased need for auditory acuity or for refined night vision resulting from diurnal hunting habits, may have led to decrease in size of both the ears and eyes in *A. gradyi*. Evolution of smaller head size in *A. gradyi* is suggested by the quite small size of the single available mandible. The differences from *A. acadicus* in the distal end of the tibiotarsus and the proximal end of the tarsometatarsus suggest that there were different mechanical constraints on the intertarsal joint, which probably reflects differences in the predominant prey.

It has also been suggested that in *A. acadicus* the “relatively light wing loading ... provides for higher maneuverability and allows them to hunt in relatively heavy, shrub-dominated cover” (Johnsgard 1988:236). This ability would certainly have been an advantage in the dense scrub cover that must have prevailed in much of pre-human Bermuda (Olson & Wingate 2012). The only potential predator of *Aegolius gradyi* would have been the very scarce endemic hawk *Bermuteo avivorous* (Olson, 2008).

Another precondition afforded by the Bermuda environment would have been availability of nest sites. *Aegolius acadicus* typically nests in old woodpecker holes, particularly those excavated by flickers (*Colaptes*). Although very scarce in the fossil record, there was at least one species of resident woodpecker on Bermuda, a flicker (*Colaptes* sp.) of smaller size than *Colaptes auratus* of the mainland of eastern North America (Olson pers. obs.). One of the dominant components of the flora of Bermuda was the palmetto *Sabal bermudana*, a living species known from abundant fossils dating back at least to the last interglacial period (Hearty & Olson 2011). The relatively soft trunks of *Sabal* palm trees are favored by woodpeckers for constructing their nest holes wherever the two occur together. Thus the presence of the palm, and at least a flicker (*Colaptes*), would have insured nesting cavities suit-

able for *Aegolius* owls throughout Bermuda. The predilection of *Aegolius acadicus* for roosting in conifers would also have been met by the Bermuda cedar (*Juniperus bermudiana*), another formerly dominant component of the flora though now greatly decimated (Challinor & Wingate 1971).

Few, if any, other small oceanic islands exist that could have provided suitable vegetation for hunting, roosting, and nesting, as well as woodpeckers to excavate nest holes, that would have been required for a small species of *Aegolius* to colonize. Thus, on Bermuda, the most important accommodation that the owls would have had to make to their new environment was a fairly dramatic shift in prey selection, though not one that was completely outside the normal feeding variation known for the colonizing species.

That the endemic *Aegolius* persisted into the historic period is suggested by some of the earliest accounts of the island. Among other birds noted by William Strachey during his exile on Bermuda in 1609–1610 were “White and gray Hernshawes, Biters, Teale, Snites, Crowes, and Hawkes, of which in March wee found diuers Ayers, Goshawkes and Tassells, Oxenbirds, Cormorants, Bald-Cootes, Moore-Hennes, Owles, and Battes in great store” (Strachey 1625:1740). Some thirteen years later, Captain John Smith was a little more specific in his report of aspects of the English settlement as of 1623: “there were a kinde of small Owles in great abundance, but they are now all slaine or fled” (in Lefroy 1981:331). There has been no trace of any other kind of owl on Bermuda than *Aegolius gradyi*, so that we must assume that the owls seen by the early colonists were the same species that we find as fossils. Decline of both cedar and palmetto following human colonization (Rueger & von Wallmenich 1996) and massive importation of an alien biota including predators and competitors (Sterrer et al. 2004) would have sealed the fate of *Aegolius gradyi* along with many other organisms.

Discussion

Owls are frequently an important component of island ecosystems and a variety of genera have colonized even distant archipelagos (Pavia 2008), although species of *Aegolius* have done so infrequently. *Aegolius martae* Pavia (2008) from the Pleistocene of Sardinia was a very large, robust species, larger than *A. funereus*, that occupied an island “intermediate” between continental and oceanic in that the fauna of Sardinia included non-volant mammals but no mammalian carnivores (Pavia 2008).

More instructive in regard to *Aegolius gradyi*, is the resident population of the Queen Charlotte Islands, British Columbia, *A. acadicus brooksi*. This differs from *A. a. acadicus* in being much darker in plumage and in vocalizations, although the two taxa are similar in size (Sealy 1998). No intermediates are known despite the fact that individuals of *A. a. acadicus* occur on the Queen Charlotte Islands as visitors (Sealy 1998). The degree of genetic differentiation of *A. a. brooksi* was found to be compatible with its status as a subspecies of *A. acadicus* (Topp & Winker 2008), with an estimated divergence time of 51,500–64,375 years before present. Although there was a land connection between the mainland and the Queen Charlotte Islands in the last glacial period at least between 12,750 and 13,250 years ago (Hetherington et al. 2003), because of glaciation, tectonic rebound, and fluctuating sea-levels the geological and biotic history of the area is complex and it would probably be difficult to determine the age of an effective isolating mechanism for *A. a. brooksi*.

On Bermuda, the isolating mechanism was in effect from the moment of colonization, and the fossil record indicates that *Aegolius gradyi* was resident at least as long ago as the end of the last interglacial period and, thus, may have been isolated for a far longer period of time than *A. a.*

brooksi was on the Queen Charlottes. Any interaction with incoming vagrants of *A. acadicus* from the mainland would have been far less frequent than the appearance of *A. acadicus* on the Queen Charlotte Islands, where no introgression has apparently taken place. *Aegolius* was apparently resident on Bermuda before the colonization and differentiation of the distinctive flightless rail *Rallus recessus* Olson & Wingate (2001) within the last glacial period (Olson & Hearty 2010), so there would have been sufficient time for differentiation of the owl at the specific level and no information exists to support a subspecies-level relationship between *A. gradyi* and *A. acadicus*.

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