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# A new species of night-heron (Ardeidae: *Nyctanassa*) from Quaternary deposits on Bermuda

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*Abstract.*—*Nyctanassa carcinocatactes* is described from Pleistocene and Holocene cave and pond deposits on the island of Bermuda. It is most similar to the Yellow-crowned Night-Heron *N. violacea* but differs in having a shorter and much heavier bill, a much more massive cranium, and more robust hindlimbs. Early historical accounts contain descriptions of what is undoubtedly this species, which was presumably exterminated subsequent to human colonization of Bermuda. The cranial and hindlimb specializations of the new species appear to be adaptations for feeding terrestrially on land crabs.

Eleven species of North American herons (Ardeidae) occur as regular visitors or vagrants to Bermuda (Amos 1991), including the Yellow-crowned Night-Heron, *Nyctanassa violacea*. In the period of reliable ornithological observation, no self-introduced herons were known certainly to breed in the islands until Green Herons, *Butorides virescens*, were found on nests in two different places in 2003 and 2004 (Wingate and Olson, pers. obs.). Yet, accounts of early visitors and settlers on Bermuda suggested that there were probably resident populations of herons in the islands. In 1603, Diego Ramirez mentioned "many very large dark herons" (Wilkinson 1950:56). Sylvanus Jourdan wrote in 1610 that "there are also great store and plenty of Herons and those so familiar and tame, that wee beate them downe from the trees with stones and staues [staves]: but such were young Herons: besides many white Herons, without so much as a blacke or grey feather on them …" (Lefroy 1981:18). Jourdan's contemporary in Bermuda, William Strachy, wrote of "white and gray Hernshawes, Bitters [herons, bitterns]" (Lefroy 1981:35). In 1623, Captain John Smith spoke of "the gray and white Hearne" and "Gray-bitterns" (Lefroy 1981:330). Juveniles of *Nyctanassa* might certainly have been taken for bitterns, and adults could be considered white and gray. Their tameness and the mention of young birds suggest a resident population.

Moore (1941) found the Yellow-crowned Night-Heron to be present in Bermuda year round and in 1940 considered that they might be breeding. Wingate (1982) reviewed the historical evidence, feeding habits, and habitat preferences of herons on Bermuda and concluded that this species would have been the most likely to have had a resident population because wetlands and shallow intertidal habitat is limited and *N. violacea*, being a crustacean feeder, was the only heron capable of exploiting the much larger area of terrestrial habitat inhabited by the blackback land crab, *Gecarcinus lateralis*. At Wingate's suggestion, the government of Bermuda was persuaded to support the

establishment of a breeding population of herons to serve as a biological control for land crabs. Some 44 nestlings of Yellow-crowned Night-Herons were translocated from Florida to Bermuda and weaned into the wild on a diet of land crabs in 1976, 1977, and 1978 (Wingate 1982). This became the epitome of a restoration and biological control success story, as the birds multiplied and spread throughout the island, reducing the land crab from the status of a major pest to merely common. The reduction was greatest—approaching 100%–on golf course fairways, lawns, and arable land, where control was most desired. (Wingate 1988).

In his review of the night-heron reintroduction in Bermuda, Wingate (1982:105) called attention to the then-recent discovery of most of the skeleton of a *Nyctanassa* in a cave in Hamilton Parish that, on Olson's assessment, was considered to represent "a distinctive endemic form characterized by a stockier build, shorter tarsus, and broader, heavier bill." Since then, additional material has been obtained, including a very distinctive cranium collected in 2004. From this we conclude that the Bermuda night-heron was sufficiently different from all populations of *Nyctanassa violacea* to merit description as a distinct species.

*Comparative material examined.*—12 complete and 2 partial skeletons of *Nyctanassa violacea* from Louisiana (1M, 1F), Florida (2M), Haiti (2M, 1F), Swan Island (unsexed), Barbuda (1F), Panama (1F), Galapagos (1M, 1 unsexed), and Mexico (2 unsexed partial), National Museum of Natural History, Smithsonian Institution (USNM) 7762, 11110, 18028, 18501, 288582, 318840–318842, 491403, 502477, 558045, 610610–610611, 611552. This series includes 3 nominal subspecies (Hellmayr & Conover 1948): *N. v. violacea*, *N. v. bancrofti*, and *N. v. pauper*. It was augmented by a skull, mandible, tibiotarsus, and tarsometatarsus removed from a skin of *Nyctanassa violacea gravirostris* (USNM 117501) from Socorro Island, Mexico. *Nycticorax nycticorax* 489903 (M), 501625 (F) and *Botaurus lentiginosus* 559802 (M), 501939 (F) were also used in the comparisons. Two additional skin specimens of *N. v. gravirostris* were also examined (50860, 50862) along with skins presumed to be of *N. v. bancrofti* from Isla San Martín (528976) and Isla Natividád (102233), Baja California, Mexico.

## Systematics

### Family Ardeidae

### Genus *Nyctanassa* Stejneger, 1887

Payne and Risley (1976) made a strong case for maintaining *Nyctanassa* distinct from *Nycticorax*. The skeletal characters most diagnostic and observable in the fossil material are the absence of the anterior cranial fenestra ("supraorbital foramen" of Adams 1955:60, and Payne and Risley 1972:91) and the much longer and more slender tarsometatarsus in *Nyctanassa* as opposed to *Nycticorax*. Also, we note that the humerus is relatively shorter and more robust with a more projecting pectoral crest in *Nyctanassa* compared with *Nycticorax*. In these respects, the Bermuda heron is clearly referable to *Nyctanassa*.

Kurochkin (1976) named a new species, *Nyctanassa kobdoena*, based on a single distal end of a tarsometatarsus from the Pliocene of Mongolia. We doubt that *Nyctanassa* could be diagnosed on this portion of the skeleton alone. The taxa of *Nyctanassa* are entirely New World in distribution, within which they are mainly coastal crustacean specialists, so it is doubtful that a close relative would have inhabited the interior of Asia. Although *Nyctanassa kobdoena* is certainly a heron, its generic placement is doubtful.

Fig. 1. Right lateral, dorsal, and ventral (top to bottom) views of skulls of *Nyctanassa carcinocatactes* (upper in each pair—rostrum USNM 326181, holotype; neurocranium USNM 529355, paratype) and *N. violacea* (USNM 18020). Scale = 2 cm.


Fig. 2 Wing bones of night herons (A–C, left humeri in palmar view; D–E, right humeri in anconal view; F–G, right carpometacarpi in palmar view). A, *Nycticorax nycticorax* (USNM 489903); B, E, *Nyctanassa violacea* (USNM 18028); C, *N. carcinocatactes* (USNM 326181, holotype); *N. carcinocatactes* (USNM 530025, paratype); F, *N. violacea* (USNM 501477); G, *N. carcinocatactes* (USNM 326181 holotype). Scale = 2 cm.

***Nyctanassa carcinocatactes***, new species
Figs. 1–3

*Holotype.*—Associated incomplete skeleton, USNM 326181, consisting of the rostrum anterior to the nostrils, basicranium, both quadrates, a fragment each of right and left dentaries, right and left postdentary bones of the mandible, 17 presacral vertebrae, the head of one vertebral rib, 3 fragments of pelvis, sternum consisting mainly of carina, manubrium, and part of the right posterior sternal plate, both scapulae (right lacking posterior half), both coracoids, both humeri, right ulna lacking olecrenon, left ulna lacking a small piece of shaft, left radius, distal end of right radius, right ulnare, both carpometacarpi, phalanx 1 of right major alar digit, right femur lacking part of shaft, left femur lacking proximal end, right tibiotarsus, left tibiotarsus lacking proximal end, left tarsometatarsus. Collected January 1982 by Robert F. Baird.

*Type locality.*—Bermuda, Hamilton Parish, Devil's Sinkhole, 32°20′20.9″N, 64°42′24.5″W (see Olson et al. 2005).

*Age.*—Quaternary and most likely Holocene, because the sinkhole in which it was found appears to have opened by roof collapse within the last few thousand years.

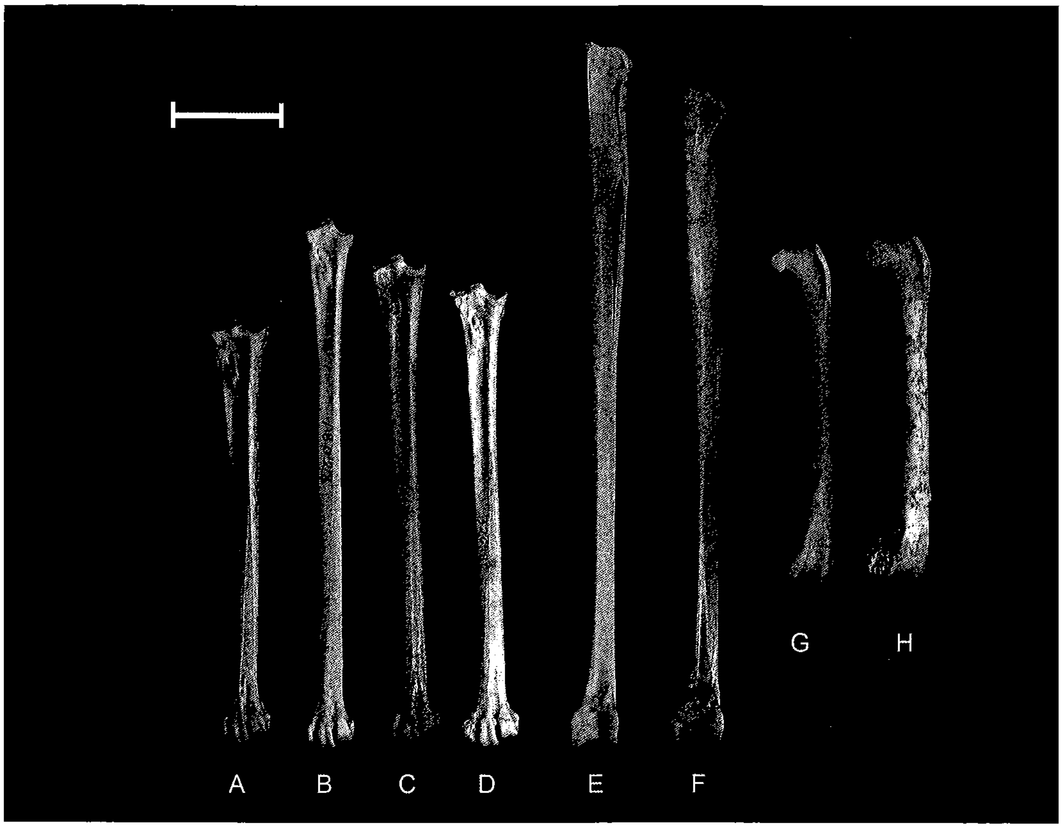


Fig. 3. Hindlimb elements of night herons in anterior view (A–D, left tarsometatarsi; E–F, left tibiotarsi,G–H, left femora). A, *Nycticorax nycticorax* (USNM 489903); B, E, G, *Nyctanassa violacea* (USNM 18028); C, *N. carcinocatactes* (USNM 326010, paratype); D, *N. carcinocatactes* (USNM 326181, holotype); F, *N. carcinocatactes* (USNM 326005, paratype); H, *N. carcinocatactes* (AMNH 27706; paratype). Scale = 2 cm.

*Measurements of holotype.*—See Tables 1–3.

*Paratypes.*—USNM 529355, neurocranium; USNM 529356, cervical vertebra 15; USNM 529357, cervical vertebra anterior to 15; Sibley's Cave (see Olson et al. 2005), collected 12 February 2004 by S. L. Olson and F. V. Grady. The cranium was found when excavating by hand in a rather large pocket of dusty sediment in Sibley's cave. At that time, although it was rather heavily encrusted with travertine, the break at the naso-frontal hinge appeared fresh. All the sediment in the pocket was removed from the cave and sieved through fine mesh but no additional heron bones were encountered except the two vertebrae. The appearance of a fresh break could have arisen from the thin bone at the hinge being chipped during the excavation process, as the rostrum definitely was not present. Snails of the species *Poecilizonites nelsoni* occurred in pockets slightly lower in the cave, indicating deposition during the last glacial period and the heron bones may date to that time as would be concordant with the encrustation of the cranium.

AMNH 27706 (Dept. of Ornithology), complete left femur, slightly abraded; Government Quarry, Hamilton Parish (see Olson et al. 2005). This bone was among a small lot collected by Robert C. Murphy in a cave in Government Quarry (see Olson et al., 2005), 3 Feb 1951. The

Table 1.—Cranial measurements (mm) of *Nyctanassa*. The sample of *N. violacea* includes three nominal subspecies (*violacea, bancroft, pauper*) and the measurements include range and mean (above) and standard deviation (below). * = holotype.

| Measurement | *N. violacea* (N = 13) | *N. carcinocatactes* n. sp. | *N. v. gravirostris* |
|---|---|---|---|
| Cranium length from posterior margin of lacrimal | 47.9–52.5 (50.3) 1.34 | 56.3 | — |
| Least width of interorbital bridge | 14.7–20.3 (17.4) 1.80 | 21.3 | 15.7 |
| Cranium width at postorbital processes | 31.6–36.2 (33.7) 1.43 | 39.6 | 31.2 |
| Quadrate length through otic process | 17.8–20.9 (19.0) 0.89 | 20.3* | 18.4 |
| Rostrum length from articulation of quadratojugal bar | 57.4–63.8 (59.9) 1.73 | 56.3* | 56.5 |
| Rostrum width at quadratojugal bar | 16.0–18.9 (17.3) 0.77 | 20.7* | 17.8 |
| Rostrum width at anterior margin of nostril | 13.5–16.3 (15.0) 0.87 | 17.1* | 15.4 |
| Culmen ridge width | 4.4–5.8 (4.9) 0.39 | 6.7* | 5.0 |
| Least depth of mandibular ramus | 8.0–9.8 (9.1) 0.51 | 9.6* | 8.4 |
| Width of mandibular articulation | 11.8–14.4 (12.6) 0.76 | 14.3* | — |

other material consists of *Pterodroma cahow* (left dentary, left mandibular articulation, juvenile right ulna, and radius lacking distal end), *Puffinus parvus* (shaft of right humerus), and bones of *Rattus* obviously of much more recent age than the others. There is no estimate of the age of the material beyond the assumption of Quaternary.

USNM 530025, complete right humerus, collected 13 February 2002 by Olson, Wingate, and P. J. Hearty; USNM 530026; distal half of left tarsometatarsus, collected 24 February 1979 by D. B. Wingate; Fern Sink Cave (see Olson et al. 2005). Both Holocene and last glacial age deposits occur in Fern Sink Cave. The specimens were found near the surface indicating Holocene but were encrusted with travertine suggesting the older interval.

USNM 326001, right coracoid; USNM 529359, left coracoid; USNM 325999, complete right humerus; USNM 529358, right humerus with damaged distal end; USNM 326008, USNM 326009, left and right radii; USNM 326006, USNM 326007, complete right ulnae; USNM 326002, complete right tibiotarsus; USNM 326005, complete left tibiotarsus; USNM 326004, left tibiotarsus lacking part of proximal articulation; USNM 326003 proximal 2/5 of left tibiotarsus; USNM 326010, complete left tarsometatarsus; USNM 326011, left tarsometatarsus lacking proximal end; USNM 326012, proximal ⅔ of right tarsometatarsus; all from Holocene dredging spoil at Spittal Pond (see Olson et al. 2005). Minimum number of individuals, 3.

*Measurements of paratypes.*—See Tables 1–3.

*Etymology.*—From Greek, *karkinos*, crab, and *kataktes*, breaker, in reference to the probable feeding specialization of the species as indicated by its bill shape. The name is analogous to that of the European Nutcracker *Nucifraga caryocatactes* (Aves: Corvidae).

*Diagnosis.*—A very robust, heavy-legged species of *Nyctanassa* with a very short, heavy bill. Rostrum shorter and considerably wider than in any population of *N. violacea*, with dorsal (culmen) ridge much wider. Cranium much more massive. Proportions of hindlimb very different: femur length near maximum, tibiotarsus below average in length, and tarsometatarsus near or below the minimum length in *N. violacea*, but all width measurements are greater than in that species. The differences in proportions and robustness are demonstrated visually in Fig. 4.

Table 2.—Measurements (mm) of pectoral elements of *Nyctanassa*. The sample of *N. violacea* includes three nominal subspecies (*violacea, bancroft, pauper*) and the measurements include range and mean (above), *n* and standard deviation (below). * = holotype.

| Measurement | *N. violacea* | *N. carcinocatactes* n. sp. |
|---|---|---|
| CORACOID | | |
| Length with sternal end flat on caliper | 46.8–52.1 (49.4)<br>12 1.43 | 48.7, 50.2, 50.4* |
| Least width of shaft | 3.8–4.4 (4.1)<br>12 0.18 | 4.2*, 4.3, 4.3 |
| Width of sternal end | 14.0–17.4 (16.1)<br>12 0.94 | 16.4+, 17.0*, 17.3, |
| HUMERUS | | |
| Length | 99.1–112.9 (105.4)<br>13 4.24 | 106.4, 107.5*, 109+, 109.8 |
| Width of shaft at midpoint | 5.5–6.8 (6.2)<br>13 0.38 | 6.9*, 6.9, 7.0, 7.2 |
| Distal width | 13.8–15.5 (14.7)<br>13 0.53 | 15.3, 15.4*, 15.7, 16.2 |
| ULNA | | |
| Length | 110.3–131.0 (120.6)<br>12 5.69 | 119.4, 121.1*, 121.9 |
| Proximal depth | 9.2–10.8 (10.1)<br>13 0.49 | 10.4, 10.5, 10,8* |
| Depth of shaft at midpoint | 4.4–5.3 (4.8)<br>12 0.36 | 4.9, 5.0*, 5.5 |
| CARPOMETACARPUS | | |
| Length | 53.2–63.4 (58.4)<br>11 3.25 | 56.3* |
| Proximal depth | 10.5–11.5 (11.2)<br>12 0.29 | 11.6* |
| MAJOR DIGIT PHALANX 1 | | |
| Length | 19.6–23.0 (21.8)<br>12 1.20 | 21.1* |
| Proximal width | 4.8–5.4 (5.1)<br>12 0.23 | 5.7* |
| Proximal depth | 4.4–4.9 (4.5)<br>12 0.16 | 5.0* |
| Greatest depth | 6.3–7.5 (6.8)<br>12 0.40 | 7.3* |

*Description*.—The rostrum is very distinctive in being extremely short and heavy, much more so than even in *N. v. gravirostris*. The neurocranium is concomitantly much more massive than in *N. violacea*, being both longer and much wider, especially noticeable in the frontal area between the orbits. The flange of the frontal that projects along the posterior articulation with the lacrimal is much better developed (broken on the left side). The postorbital processes are much better developed, extending beyond the zygomatic processes (whereas the opposite pertains in *N. violacea*), making the notch between the processes much more pronounced. Temporal fossae much larger and more excavated, indicating greater development of the temporalis musculature than in *N. violacea*. Foramen magnum and occipital condyle larger than in *N. violacea*. The paroccipital process of the exoccipital is much wider, with its medial corner forming a distinct pointed process that is fused with the overlying bone in *N. violacea*. The external auditory meatus is much larger and of a very different shape from that in *N. violacea*.

Table 3.—Measurements (mm) of hindlimb elements of *Nyctanassa*. The sample of *N. violacea* includes three nominal subspecies (*violacea, bancroft, pauper*) and the measurements include range and mean (above), *n* and standard deviation (below). * = holotype (femur length is an estimate from both sides).

| Measurement | *N. violacea* | *N. carcinocatactes* n. sp. | *N. v. gravirostris* |
|---|---|---|---|
| FEMUR | | | |
| Length | 63.1–68.0 (65.5)<br>10 1.50 | 67.7*, 68.0 | |
| Proximal width | 10.7–12.0 (11.4)<br>11 0.39 | 12.4, 12.6* | |
| Shaft width at midpoint | 4.5–5.4 (4.9)<br>12 0.32 | 5.1, 5.3* | |
| Distal width | 10.6–12.2 (11.5)<br>12 0.50 | 12.9+, 13.0 | |
| TIBIOTARSUS | | | |
| Length from proximal articular surface | 121.9–138.0 (130.6)<br>13 5.33 | 124.8*, 127.1, 128.3, 129.0 | |
| Width of shaft below fibular crest | 4.9–6.2 (5.5)<br>13 0.35 | 5.7, 5.7. 6.1*, 6.1, 6.5 | |
| Distal width | 9.1–9.9 (9.4)<br>13 0.28 | 9.9*, 10.3, 10.4, 10.6 | 9.5 |
| TARSOMETATARSUS | | | |
| Length | 90.4–105.2 (97.4) | 90.2*, 96.2 | 82.3 |
| Proximal width | 9.8–10.7 (10.3)<br>13 0.22 | 10.5, 11.0*, 11.4 | 9.7 |
| Shaft width at midpoint | 3.9–5.6 (4.5)<br>13 0.43 | 4.9*, 4.9, 4.9, 5.0 | 3.9 |
| Distal width | 9.5–10.7 (10.3)<br>13 0.34 | 11.3*, 11.4, 11.4 | 10.5 |

In the carpometacarpus, the minor metacarpal is more bowed, the intermetacarpal space is wider, and the proximal symphysis is shorter, deeper, and less constricted. Phalanx 1 of major digit is more robust.

Although the tarsometatarsus is relatively long by comparison with *Nycticorax nycticorax* or *Botaurus lentiginosus*, thus being in agreement with *Nyctanassa*, the element in the Bermuda bird is at or below the low end of length variation in *N. violacea* and its appearance of being more robust is borne out by measurements (Table 3).

*Remarks*.—Wetmore (1946) revised *Nyctanassa violacea* and recognized six subspecies: nominate *N. v. violacea* breeding in the eastern United States probably to eastern Mexico and migrating south to the West Indies and Middle America as far south as Panama; *N. v. cayennensis* from northern South America; *N. v. pauper* of the Galapagos; *N. v. bancrofti* throughout the West Indies and also the Pacific coast of western Mexico; *N. v. caliginus* from Panama and the Pacific coasts of Colombia and Ecuador; and *N. v. gravirostris* from Socorro Island, Mexico. Of these, the last three are characterized by heavy bills, with *N. v. gravirostris* supposedly having the thickest bill of all.

In looking at skeletons, it is apparent that there is considerable variation in the heaviness of the bill, but it is not certain that this is consistently geographical in nature, so that segregating either skins or skeletons on this basis becomes subjective. The bird from Socorro Island, *N. v. gravirostris*, was said by van Rossem (1943:266) to be "characterized by a very heavy bill, gross throughout its length, and short, thick tarsi." In the one partial skeletal specimen we examined, the bill is comparatively short and stout and the tarsometatarsus very short in comparison

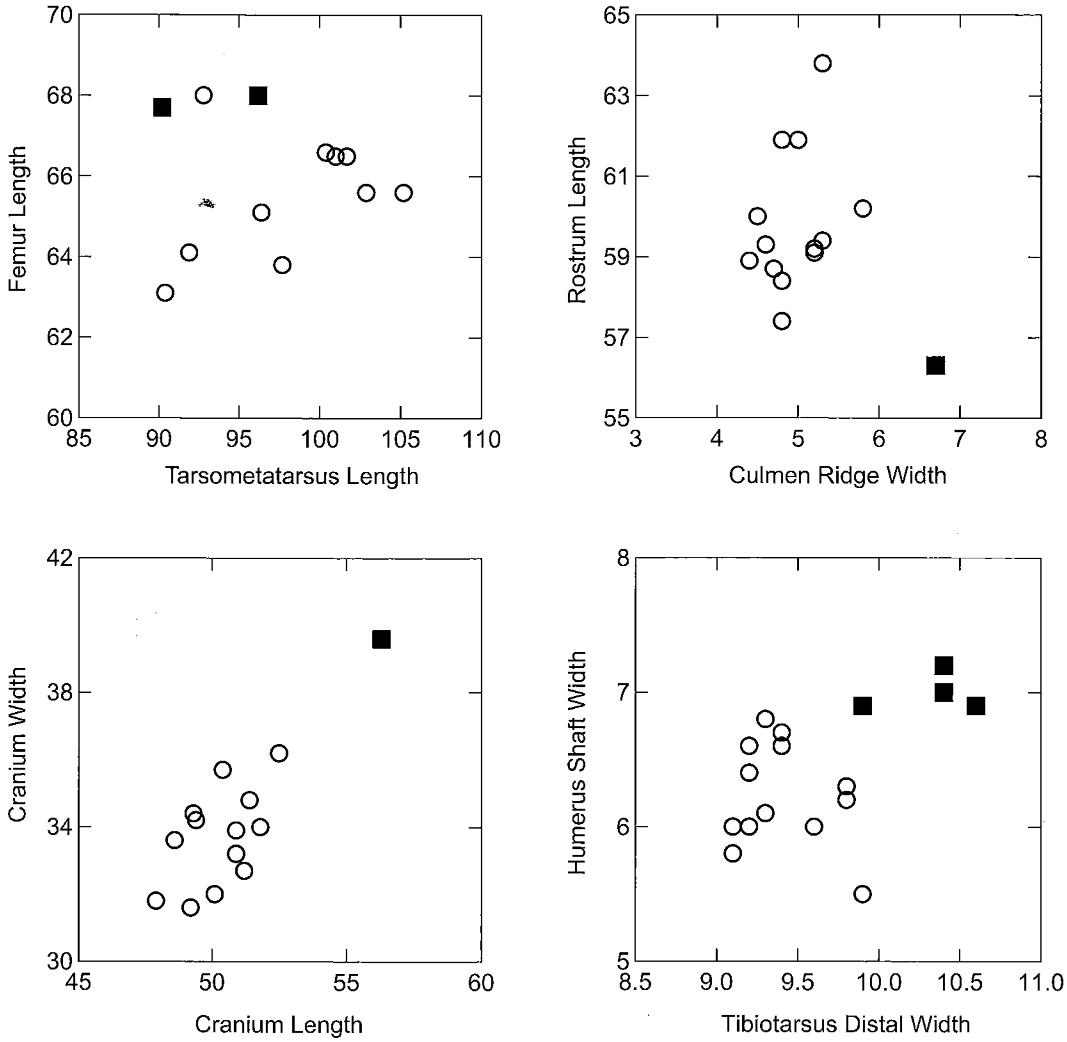


Fig. 4. Bivariate plots of various skeletal measurements of *Nyctanassa* to show the distinctiveness of the Bermuda species *N. carcinocatactes* (black squares) from *N. violacea* (open circles).

with the other individuals of *N. violacea* examined. In three skin specimens of *N. v. gravirostris* examined, the appearance of the bill being short and stout was artificially enhanced by the fact that the tip of the bill in all specimens was heavily worn and blunted, as was true also of single specimens of *N. v. bancrofti* from Isla San Martín and Isla Natividád, Baja California.

Herons of the genus *Nyctanassa* are crustacean specialists, usually feeding on smaller species such as fiddler crabs (*Uca*) or crayfish (Cambaridae) (Watts 1995). On Socorro Island, however, *N. v. gravirostris* feeds mainly on the large land crab *Gecarcinus planatus*, which makes up about 93% of its diet based on analysis of pellets, with scorpions and other invertebrates making up the remainder (Rodriguez-Estrella et al. 1996). From its habits, Walter (1998) characterized it as a terrestrial landbird. Given that the amount of wetland habitat on Bermuda was minuscule compared to the amount of terrestrial habitat occupied by land crabs, the habits of *N. carcinocatactes* were probably similar. Wading birds that adopt a strictly terrestrial habit would be expected to evolve shorter and more robust legs, and this is borne out by the measurements of *N. v. gravirostris* and *N. carcinocatactes*.

Night herons have been more successful at establishing endemic species on oceanic islands than other groups of herons. Those known so far have all been referred to the genus *Nycticorax* and all are extinct and known only from bones and sometimes also from the accounts of old voyages. These include *Nycticorax olsoni* of remote, barren Ascension Island in the South Atlantic (Bourne et al. 2003); *N. duboisi, N. mauritianus*, and *N. megacephalus* in the Mascarene islands of Reunion, Mauritius, and Rodrigues, respectively (Mourer-Chauviré et al. 1999); *N. kalavikai* from Niue, and an unnamed species from 'Eua, Tonga, both in the central South Pacific (Steadman et al. 2000). The bird from Niue was hypothesized to have fed on land crabs. In all cases, the islands inhabited had limited or nonexistent aquatic habitats so that all of these herons would have had to be essentially terrestrial, as we suggest for *Nyctanassa carcinocatactes* on Bermuda.

There are at present three species of land crabs on Bermuda. The land hermit *Coenobita clypeatus*, which would probably only fall prey to night-herons at small sizes when they could be consumed protective mollusk shell and all; the blue land crab *Cardisoma guanhumi*, adults of which are much too large to be eaten by *Nyctanassa*; and the blackback land crab *Gecarcinus lateralis*, which is the principal prey of the translocated breeding population of *Nyctanassa violacea* on Bermuda today.

The junior author has observed the technique used by this heron for capturing and eating land crabs on numerous occasions. There are three or four stages to the process, depending on the size of the crab:

Stage 1. *Hunting and capture*. If the crab is intercepted out in the open away from its burrow, it is run down and grabbed in the heron's beak. Otherwise the heron stands poised and motionless over a burrow entrance, waiting until a crab emerges within reach to grab.

Stage 2. *Dismemberment*. If the crab has been captured amidst dense vegetation the heron quickly carries it on foot or in flight to an open area where the prey has less chance of escaping if dropped. It is then held by the legs or pincers and shaken vigorously until most or all of the appendages fall off by autotomy or are wrenched off. In the case of small crabs these appendages may be eaten later, but in the case of full-grown crabs they are invariably left uneaten. Pellets of undigested shell from a previous meal are sometimes regurgitated at this point.

Stage 3. *Swallowing*. If the crab is small enough the dismembered crab body is swallowed whole. In the case of full-grown crabs, however, the bodies are too large to swallow and further processing is required.

Stage 4. *Removal of the carapace*. The heron drops the dismembered crab body on the ground, then rears up to full height with bill pointed straight down and delivers a hammer blow on the carapace. After several such blows the carapace either separates from the rest of the body or breaks into pieces, which fall away. After all this processing it is usually only the posterior half of the body that is ultimately eaten.

Circumstances on Bermuda dictate that *Gecarcinus lateralis* makes up about 90% of the diet of the translocated population of *N. violacea*, yet it takes an individual anywhere from 15 to 30 min to process a full-grown crab from capture to consumption, with perhaps as much as half of the potential food value being left uneaten. Presumably the distinctive skeletal adaptations of *N. carcinocatactes*, notably the more robust bill and the wider gape, would have enabled it to process the same prey in less time and with more effective utilization of the carcass.

There was a fourth species of land crab on Bermuda of as yet undetermined relationships (William Hart, Warren Blow, pers. comm.), possibly a different species of *Gecarcinus*. This was larger than *G. lateralis* and occurs in various fossil deposits along with the remains of the other three species of land crabs. It is uncertain just when this species became extinct on Bermuda, but its disappearance could be linked to human-caused perturbations such as the introduction of hogs (*Sus scrofa*) or even direct predation by early human colonists of Bermuda. It may be that the cranial adaptations of *N. carcinocactes* permitted feeding on this larger species of crab as well.

Whereas fossils of *N. carcinocatactes* are not particularly common, they have been found in a diversity of cave and lacustrine localities. The fact that the bird occurs in cave deposits supports the hypothesis of a terrestrial feeding habit.

Natural extinctions on Bermuda appear to be caused mainly by interglacial rises in sea level that greatly reduce land area (Olson and Hearty 2003, Hearty et al. 2004, Olson et al. 2005), but *N. carcinocatactes* survived the present interglacial until human colonization, so could presumably weather any adversity that did not eliminate its supply of land crabs.

How long *Nyctanassa* existed on Bermuda prior to the Holocene is uncertain. We feel confident that some of the fossil material dates back to the last glacial period (Marine Isotope Stages MIS 2–4), although no bones of this species were encountered in the long sequence in Admirals Cave, which spans the last major interglacial (MIS 5) to the Holocene (Hearty et al. 2004). This might simply be a reflection of the small size of the opening through which most of the cave sediments entered. The heron has never been found in earlier deposits in the penultimate glacial stage, which contain endemic birds that probably evolved over a period involving two glacial stages (MIS 8 and 6) and a weak intervening interglacial (MIS 7) (see Olson et al. 2005; Olson et al., in press). During this time Bermuda was home to an endemic crane, *Grus latipes* (Wetmore 1960; Olson and Wingate 2000), which may have filled the niche of a large crab-eating bird. Thus, it is possible that *Nyctanassa carcinocatactes* evolved only since the extinction of the crane during MIS 5.

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