A NEW GENUS AND SPECIES OF HERON (AVES: ARDEIDAE) FROM THE LATE MIOCENE OF FLORIDA

David W. Steadman[1] and Oona M. Takano[2]

ABSTRACT

From the recently discovered Montbrook locality, Levy County, Florida (late Miocene; late Hemphillian land mammal age), a complete coracoid and nearly complete scapula represent a large heron that we name *Taphophoyx hodgei* new genus and species. While the phylogenetic affinities of *T. hodgei* are not well resolved, the tiger-herons *Tigrisoma* spp. or boat-billed heron *Cochlearius cochlearius* (both Neotropical) may be the closest living relative(s) of *Taphophoyx*, based in large part on several shared characters of the facies articularis clavicularis and facies articularis humeralis. Nevertheless, the coracoid of *Taphophoyx* has a uniquely prominent facies articularis humeralis and a uniquely sterno-ventral surface of corpus coracoidei. All 21 taxa of birds recorded thus far from Montbrook (mostly aquatic forms such as swans, ducks, geese, grebes, cormorants, ibises, sandpipers, etc.) probably represent extinct species, although *Taphophoyx hodgei* is the only one assigned to an extinct genus.

Key words: Florida, Montbrook, late Miocene, heron, Ardeidae, new taxa.

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INTRODUCTION

Understanding the evolution and historic biogeography of North American birds is possible by relating their fossil record to the biochronological system of North American Land Mammal Ages (NALMA), which complements geochronological evidence for the ages of the fossils (Woodburne, 2004). Except for the late Pliocene and Pleistocene (Blancan through Rancholabrean NALMAs) occurrences of living species (Lundelius et al., 1983; Webb et al., 2004; Emslie, 1998), the North American fossil record of herons (Ciconiiformes: Ardeidae) is not well developed. From late Miocene and early Pliocene (late Clarendonian through late Hemphillian NALMAs) fossil localities, the North American herons described thus far represent extinct species placed in living genera (Becker, 1985; Mayr et al., 2019). Thus, it is of interest that recently discovered late Miocene heron fossils from Florida differ substantially from the comparable elements in living genera of herons.

Herons are distributed nearly worldwide today, although they are most diverse in subtropical and tropical regions. A recent compilation recognizes 19 genera and 64 species of herons worldwide (del Hoyo and Collar, 2014), with 8 genera and 12 species currently inhabiting North America. Herons feed primarily in shallow fresh or estuarine waters, where fish, frogs, and crabs are their main source of food.

The heron fossils to be described here are from the Montbrook locality (Florida Museum of Natural History site LV070), south of Williston, Levy County, Florida. Based on occurrences of the rhinoceros *Teleoceras*, antilocaprid *Hexameryx simpsoni*, and canid *Borophagus hilli*, the Montbrook locality is dated biochronologically to the late Hemphillian (Hh4) NALMA, which would yield an estimated geochronological age of 5.5 to 5 million years ago (Ma; Hulbert, 2018). Among the birds that DWS has identified from Montbrook is the swan *Cygnus mariae* Bickart, which is otherwise known only from the Wickieup locality, Big Sandy Formation, Mohave County, Arizona (Bickart, 1990). Fission-track (zircon) dating of the Big Sandy Formation yielded ages of 6.1 to 4.6 Ma, with a mean of 5.5 ± 0.2 Ma (MacFadden et al., 1979), which lends further support to the estimated age of the Montbrook locality.

Discovered in 2015, Montbrook is a sandy alluvial site rather than a sediment-filled fissure/cave/sinkhole as with so many Neogene fossil sites in Florida. In terms of sheer numbers of vertebrate fossils, the Montbrook fauna is dominated by freshwater fishes, turtles, and alligators. Estuarine fish also are present. The avifauna recovered thus far at Montbrook consists mostly of aquatic birds such as swans, ducks, geese, grebes, cormorants, storks, ibises, and sandpipers (DWS personal observation). Also present are condors, vultures, hawks, galliforms, and passerines. While most of the bird fossils were recovered during excavations, those of smaller taxa have been found through screen-washing of sediments.

MATERIAL AND METHODS

All fossils from Montbrook are catalogued in the Vertebrate Paleontology Collection, Florida Museum of Natural History, University of Florida (UF), Gainesville, Florida, USA. Some fossils from other Florida sites were formerly in the fossil collection of Pierce Brodkorb, and now have the prefix UF/PB. Most modern skeletons used in this study are from the UF Ornithology Collection, some of which were formerly in the modern collection of Pierce Brodkorb (PB), as follows. *Ardea herodia*s UF 48756, 50443, 50852, *A. cocoi* UF 39955*, A. cinerea* UF 11433, 23037, 23039 (PB 19761), *Ardea* (*Casmerodius*) *albus* UF 42220, 43979, 50858, *Egretta rufescens* UF 44183, 45453, 51271, *E. thula* UF 40155, 42736, 43846, 44153, *Egretta* (*Mesophoyx*) *intermedia* UF 23001 (PB 23270), *Pilherodius pileatus* UF 22906 (PB 26929), *Syrigma sibilatrix* UF 22940, 38953, *Butorides virescens* UF 40762, 40864, 46769, 48865, *Bubulcus ibis* UF 40857, 41803, 45498, 45515, *Ardeola rufiventris* UF 38923, *Nyctanassa violacea* UF 22903 (PB 36755), 42309, 42330, 42737, 49907, *Nycticorax nycticorax* UF 20838, 22886, 22901 (PB 22328), 40152, *Botaurus lentiginosus* UF 45502, 48443, 49874, *Ixobrychus flavicollis* UF 39524, *I. exilis* UF 40336, 43058, 48784,

Tigrisoma mexicanum UF 38926, 42715, *T. lineatum* UF 22875 (PB 21581), *T. fasciatum* UF 43434. We also examined a modern skeleton of *Cochlearius cochlearius* from the Museum of Vertebrate Zoology, University of California (MVZ 86641). Measurements were taken using digital calipers with 0.01 mm increments, rounded to the nearest 0.1 mm. The measurements include only one individual for each living species because our goal was merely to give a general idea of the size of the extinct Montbrook heron. Photographs were taken with a Canon EOS 5D Mark II digital camera.

Osteological terminology follows, as closely as possible, that of Baumel and Witmer (1993). We note here that terminology for the coracoid, an essential part of the avian shoulder, can be confusing. Four other bones articulate with the coracoid (furcula, humerus, scapula, and sternum, the first three being part of the shoulder). In defining terms, Clark (1993: 12) says ": **Regio omalis [Omus]** The shoulder is the arbitrarily delimited region of junction of the wing and trunk. The Greek term Omos is used … in its Latin transliteration, Omus." Among words listed by Brown (1956: 709) for shoulder is "Gr. *Omos*, m. shoulder, upper arm; *akromion*, n. point of the shoulder blade; ..." When referring to the end of the coracoid that is opposite from the sternal end, we will call it the "omal" end to satisfy reviewers, even though only the furcula articulates with the coracoid at this end, separate from where the other two bones of the avian shoulder (humerus, scapula) join the coracoid. In Figures 1–5, we place numbered arrows for each of the 13 diagnostic characters of the new genus and species, except for character 7, which is difficult to discern in photographs.

SYSTEMATIC PALEONTOLOGY

Order PELECANIFORMES[1]

Family ARDEIDAE Leach

TAPHOPHOYX new genus

Type species.—*Taphophoyx hodgei* new species.

Zoobank nomenclatural act.—D11FE128-3D90-43A9-BE10-F8C5DFB290F5.

[1]formerly Ciconiiformes.

Diagnosis.—A large heron (Table 1) that differs from all other ardeid genera examined in these characters. CORACOID: 1. In medial aspect, the facies articularis clavicularis is more diagonal (less perpendicular) to long axis of corpus coracoidei than in all except *Tigrisoma* spp. and *Cochlearius cochlearius*. 2. In medial aspect, the facies articularis clavicularis lacks a distinct dorsal protuberance (present in all others except *Cochlearius cochlearius*). 3. In ventral aspect, the sternal end of facies articularis clavicularis is more rounded than in all except *Tigrisoma mexicanum*, *Egretta rufescens*, and *Cochlearius cochlearius*. 4. In medio-clavicular aspect, the profile of facies articularis clavicularis is more rounded than in all except *Tigrisoma fasciatum*, *T. lineatum*, and *Pilherodius pileatus*. 5. In lateral, ventral, or dorsal aspect, the sternal margin of facies articularis humeralis is perpendicular to facies articularis scapularis (as in *Tigrisoma mexicanum*, *T. lineatum*, and *Cochlearius cochlearius*) but joins much more gradually in all others. 6. In ventral aspect, the sternal end of facies articularis humeralis protrudes more abruptly (nearly perpendicularly) from corpus coracoidei. 7. The medio-ventral margin of corpus coracoidei is more rounded (flatter in all others). 8. The depression of sterno-ventral surface of corpus coracoidei is deeper. 9. In medial aspect, the medio-sternal margin of facies articularis sternalis is more concave than in all except *Casmerodius albus*, *Egretta rufescens*, *Mesophoyx intermedia*, *Nyctanassa violacea*, and *Cochlearius cochlearius*. 10. The medio-ventral surface of facies articularis sternalis is more expanded omally than in all except *Botaurus lentiginosus*. SCAPULA: 11. In medial aspect, tuberculum coracoideum blends into facies articularis humeralis (separated by distinct notch in all others except *Ardea herodias* and *Tigrisoma mexicanum*). 12. In either medial or lateral aspect, facies articularis humeralis is less protrudent from corpus scapulae than in all except *Casmerodius albus* and *Nyctanassa violacea*. 13. In either medial or lateral aspect, facies articularis clavicularis is less protrudent proximally than tuberculum coracoideum (more protrudent in all others except *Tigrisoma mexicanum* and *Cochlearius cochlearius*).

Table 1. Measurements (in mm) of the coracoid and scapula in herons. Cc, corpus coracoidei; fac, facies articularis clavicularis; fah, facies articularis humeralis; tc, tuberculum coracoideum. Depth = dorso-ventral distance; length = distance along sterno-omal axis; width = medio-lateral distance.

	Coracoid						Scapula	
Species	Total length	Depth of fac	Max length of fah	Max width of fah	Least width of cc	Width of sternal end	Length through tc & fah	Width through fah & fac
Taphophoyx hodgei	70.0	11.4	11.4	7.8	6.2	21.4	11.4	14.9
Tigrisoma mexicanum	63.3	9.0	8.7	6.9	5.0	19.2	10.5	13.6
Tigrisoma lineatum	58.5	8.1	7.6	5.2	4.4	15.5	8.3	11.0
Tigrisoma fasciatum	51.3	7.3	6.4	5.2	4.0	12.8	7.2	10.1
Cochlearius cochlearius	48.0	7.6	7.3	5.0	3.8	14.4	7.8	9.3
Ardea herodias	74.7	13.8	12.3	8.0	6.2	24.1	12.3	16.0
Ardea cocoi	72.2	11.9	11.6	7.7	6.1	20.6	11.9	16.7
Ardea cinerea	63.4	11.9	11.3	7.7	5.8	21.6	11.8	14.6
Casmerodius albus	55.9	10.7	9.1	6.2	5.0	18.4	10.3	12.1
Egretta rufescens	47.6	8.5	8.3	5.9	4.1	17.2	8.6	9.9
Egretta thula	36.9	6.5	7.0	4.4	3.4	12.8	6.3	8.3
Mesophoyx intermedius	41.2	6.6	6.7	4.5	3.6	13.0	7.7	9.8
Pilherodius pileatus	46.0	6.8	7.5	5.0	3.6	15.1	---	9.2
Syrigma sibilatrix	38.1	7.4	6.2	4.4	3.6	13.7	7.2	8.6
Butorides virescens	35.6	5.0	4.7	3.3	2.7	9.1	5.3	6.0
Bubulcus ibis	37.6	6.1	6.5	3.8	3.1	11.1	6.9	7.7
Ardeola rufiventris	35.1	5.1	4.9	3.4	2.6	9.2	5.0	6.8
Nyctanassa violacea	48.3	7.8	6.5	4.7	3.9	15.0	7.7	9.0
Nycticorax nycticorax	52.7	8.1	7.5	5.6	4.3	15.6	8.4	9.9
Botaurus lentiginosus	55.1	8.0	6.7	5.7	4.3	15.6	8.4	9.7
Ixobrychus flavicollis	42.8	5.2	4.7	3.6	2.6	10.0	5.1	7.4

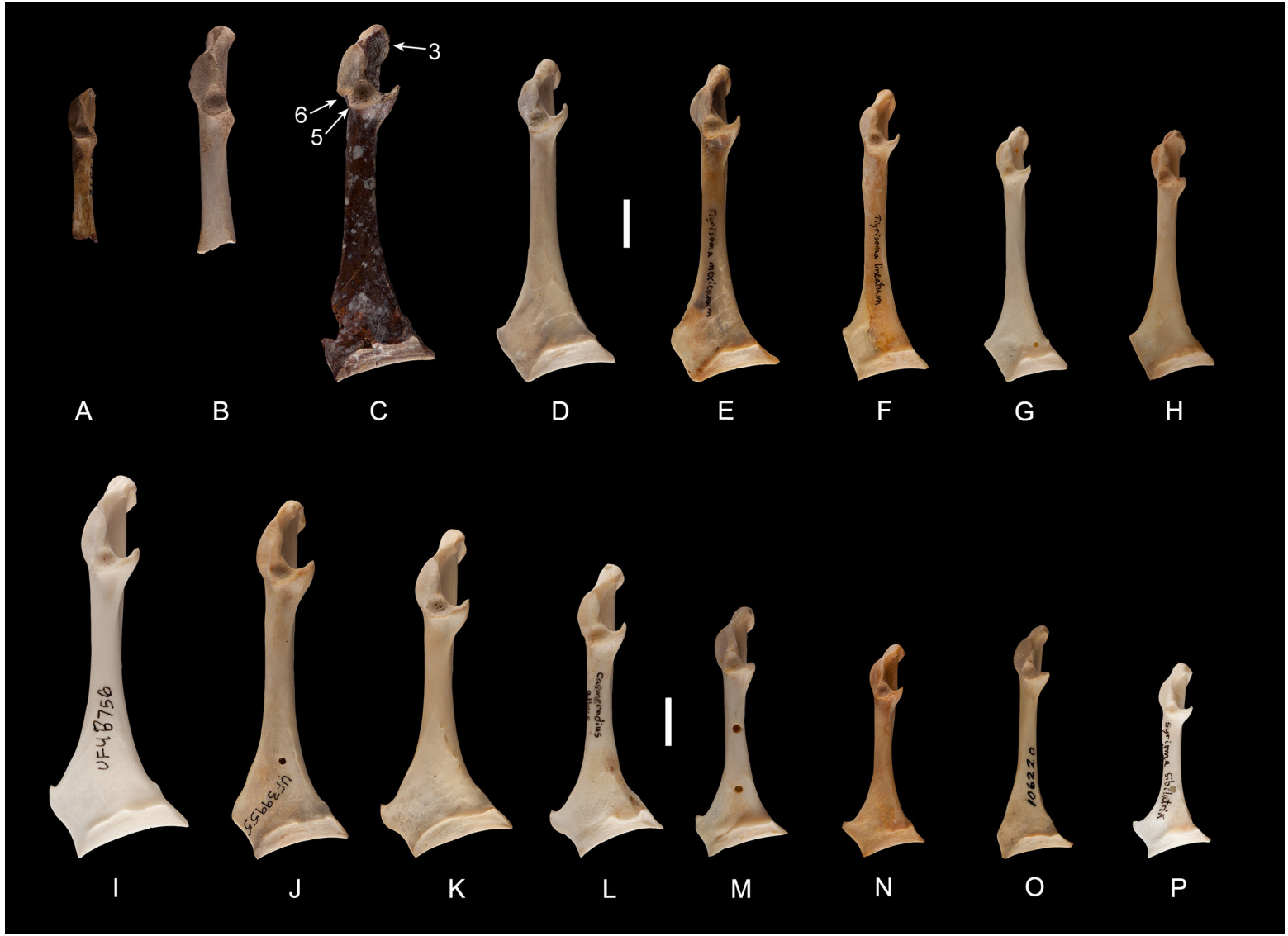

Figure 1. The coracoid of herons in dorsal aspect. A. *Egretta* sp., UF/PB 7925 (fossil), Bone Valley, Florida. B. *Ardea polkensis*, UF/PB 7924 (fossil), Bone Valley, Florida. C. *Taphophoyx hodgei* new genus and species, UF 425443 (fossil), Montbrook, Florida. D. *Tigrisoma mexicanum*, UF 42715, Honduras. E. *Tigrisoma mexicanum*, UF 38926, Guatemala. F. *Tigrisoma lineatum*, UF 22875, captive. G. *Tigrisoma fasciatum*, UF 43434, Peru. H. *Cochlearius cochlearius*, MVZ 86641, El Salvador. I. *Ardea herodias*, UF 48756, Florida. J. *Ardea cocoi*, UF 39955, Guyana. K. *Ardea cinerea*, UF 23039, Holland. L. *Casmerodius albus*, UF 42220, Florida. M. *Egretta rufescens*, UF 45453, Florida. N. *Mesophoyx intermedius*, UF 23001, Japan. O. *Pilherodius pileatus*, UF 22906, captive. P. *Syrigma sibilatrix*, UF 38953, Argentina. Scale bars = 10 mm.

Etymology.—*Taphophoyx* is derived from the Greek words *taphos*, meaning grave or tomb, and *phoyx*, meaning heron (Brown, 1956:381, 408). Both words are masculine. The first half of the name *Taphophoyx* refers to the large concentration of fossils of gomphotheriid proboscideans at Montbrook, rendering the site the paleo-equivalent of an "elephant graveyard."

Comparisons with other fossil Ardeidae.—Outside of North America, three extinct genera of herons have been described from early Miocene localities (ca. 11–12 million years older than the Montbrook locality); fortunately, each is represented by a partial (omal end) coracoid. The first, *Matuku* from the St. Bathans Fauna of New Zealand (~19–16 Ma), was described as not closely related to any particular genus or lineage of heron (Scofield et al., 2010). *Matuku* differs markedly from *Taphophoyx* in these characters: 1. In medial aspect, processus acrocoracoideus more pointed (less rounded); 2. In medial aspect, facies articularis clavicularis perpendicular to long axis of corpus coracoidei (diagonal in *Taphophoyx*); 3. In lateral aspect, facies articularis humeralis placed closer to omal end; and 4. In lateral aspect, processus procoracoideus less protrudent from corpus coracoidei.

The second described early Miocene extinct genus, *Pikaihao* from the same locality as *Matuku*, is a small form regarded as allied to the bitterns (Botaurinae; Worthy et al., 2013). *Pikaihao* differs markedly from *Taphophoyx* in characters 2 and 4 of *Matuku* (above), as well as having more pointed (less rounded) omal and sternal margins of facies articularis humeralis.

The third early Miocene genus, *Zeltornis* from Libya, was a huge heron (larger than in any living species) believed to be related to *Cochlearius* or *Nycticorax* (Balouet, 1981). Known only from the omal half of a coracoid, the measurements of *Zeltornis* as given by Balouet (1981; translated from the French) are: maximum width of the head – 20.9 mm; minimum width of the head – 12.9 mm; maximum length of the glenoid facet (= facies articularis humeralis) – 17.8 mm. These same three measurements in *Taphophoyx* are 11.4 mm, 7.3 mm, and 11.6 mm, which range from ~54% to ~65% of the comparable values in *Zeltornis*. *Taphophoyx* differs further from *Zeltornis* in three of the six characters (1, 5, and 6) in the diagnosis of *Taphophoyx* that can be evaluated.

Other early Miocene heron fossils are of even more uncertain affinities, namely the small European forms variously called *Proardeola walkeri*, *Ardea aurelianensis*, or *Proardea amissa*, which represent one or more *Ardeola*-sized taxon (Olson, 1985; Scofield et al., 2010; Zelenkov, 2011), and Ardeidae sp. from Thailand (Cheneval et al., 1991).

Middle Miocene heron fossils include *Ardea sytchevskayae* from the Sharga locality in Mongolia (~12 Ma), based on a large coracoid (Zelenkov, 2011, 2016), and *Ardea* sp. from the Sand Canyon Beds (early Barstovian NALMA; ~16–15 Ma) of Nebraska (Becker, 1986), based on a tarsometatarsus. The coracoid of *A. sytchevskayae* differs from that of *Taphophoyx* and is typical of that in *Ardea* spp. in being slender in dorsal or ventral aspect, in having the facies articularis humeralis located more toward the omal end, and in having the facies articularis clavicularis less diagonal to the long axis of corpus coracoidei. Also from Sharga is a single quadrate described as a new genus, *Nyctisoma* (Elzanowski and Zelenkov, 2015) with some similarities to *Nycticorax*, *Tigrisoma*, and perhaps the extinct *Pikaihao*. From the Maboko Formation, Kenya (~15–14 Ma), a small ardeid quadrate and tarsometatarsus were referred to cf. *Pikaihao* (Mayr, 2014; also see Worthy et al., 2013).

Moving to the late Miocene, the new genus and species *Ardeagrandis arborea* was described from a huge but fragmentary tarsometatarus from Moldova (Kurochkin and Ganya, 1972). All North American late Miocene (late Clarendonian through Hemphillian NALMA) fossils of herons have been referred to living genera, including *Ardea*, *Egretta*, *Ardeol*a (*Butorides*), and *Nycticorax* (Brodkorb, 1955, 1963; Becker, 1985). We have examined the specimens from localities in Florida (UF 3285, 19001, 21138, 25759, 25939, 25940, 26082), agreeing in each case with Becker's identifications. Concerning coracoids in particular, the specimen from Bone Valley, Florida (late Hemphillian,

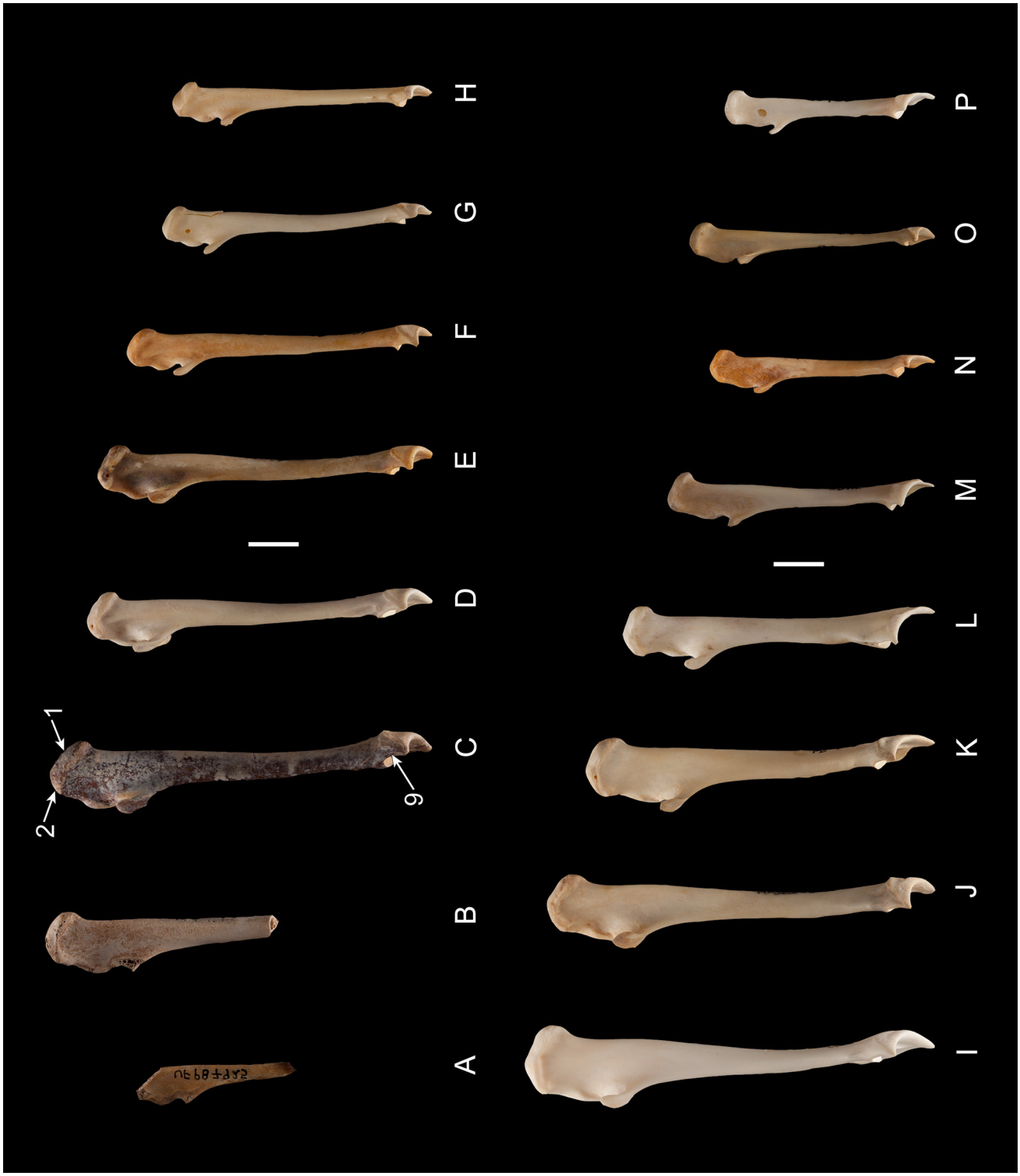

Figure 2. The coracoid of herons in medial aspect. Specimens as in Figure 1. Scale bars = 10 mm.

UF/PB 7924; Figs. 1B, 2B, 3B) referred to *Ardea polkensis* by Becker (1985) indeed agrees with *Ardea* rather than *Taphophoyx* in all seven of the characters (#1–7 above) that can be assessed. Similarly, the coracoid from Bone Valley (UF/PB 7925; Figs. 1A, 2A, 3A) that Becker (1985) referred to *Egretta* sp. agrees with modern *Egretta* rather than *Taphophoyx* in all four characters that can be evaluated (#4-7 above). The same applies to a previously unreported Bone Valley specimen (UF/PB 9230), which is a similarly sized omal end of a coracoid of *Egretta* sp.

TAPHOPHOYX HODGEI new species

Holotype.—Complete left coracoid, UF 425443 (Figs. 1C, 2C, 3C). Montbrook site (LV070), Levy County, Florida. Collected in grid square 15S x 9E by Toni-Ann Benjamin on 9 November 2017.

Paratype.—Left scapula lacking distal part of blade, UF 431654 (Figs. 4A, 5A). Montbrook site (LV070), Levy County, Florida. Collected in grid square 16S x 9E by Sharon Shears on 16 November 2017.

Zoobank Nomenclatural Act.—D423D7E9-6D28-49D1-8004-135C342BDAC0.

Species Diagnosis.—As for the genus *Taphophoyx*.

Etymology.—The species name *Taphophoyx hodgei* is to honor Mr. Eddie Hodge, who has been most generous to the Florida Museum of Natural History in providing logistical help and in granting permission to excavate and study the fossils discovered on his land.

Remarks.—The two specimens of *Taphophoyx hodgei*, which are the only heron fossils known from Montbrook, were found in adjacent 1-m^2 squares, which suggests that they belong to the same individual. This likelihood increases further by the fossils being a left coracoid and left scapula, which articulate with each other. Among the 10 characters of the coracoid, *Taphophoyx hodgei* agrees with *Cochlearius cochlearius* in five of them, and with one or more species of *Tigrisoma* in four of them. For the scapula, these agreement values are one of three characters for *Cochlearius cochlearius*, and two of three characters for *Tigrisoma* spp.

Compared to those of living species, the measurements of *Taphophoyx hodgei* are most similar to those of *Ardea cinerea* and *A. cocoi* (Table 1). These two large herons have body masses of 1020-2073 g (mean 1443 g) and 1148-1465 g (mean 1306 g), respectively (Dunning, 2008:29).

DISCUSSION

Phylogenetic relationships within the Ardeidae are not well understood, with conflicting proposals based on morphological data, molecular data, and combinations thereof (Payne and Risley, 1976; Sheldon et al., 1995, 2000; McCracken and Sheldon, 1998; Huang et al., 2016; Mayr et al., 2019). We note here that molecular data for phylogenetic analyses are typically based on a single individual tissue sample per species, something that is unavoidable in certain instances, just as with fossils. Thus, we hesitate to place *Taphophoyx* in a phylogenetic context other than to speculate that, based upon the available coracoid and scapula, it may be more closely related to the tiger-herons (*Tigrisoma* spp.) or boat-billed heron (*Cochlearius cochlearius*) than to other living genera of herons. Both of these Neotropical genera occur today as far north as northern Mexico, and likely were more widespread in the Pleistocene (Olson and Suárez, 2008), so the late Neogene existence of a related genus in Florida (and undoubtedly elsewhere in North America) is reasonable.

Thus far, the coracoid and scapula from Montbrook are the only solid evidence of an extinct genus of heron from North America. From the much older (early Miocene; Hemingfordian NALMA; ~18.5 Ma) Thomas Farm locality in Florida, extensive screen-washing of sediments over the past 15 years has produced six fossils (a highly fragmentary coracoid and carpometacarpus, and four pedal phalanges) of a small heron. This material is inadequate for assignment beyond the family level; all other birds from Thomas Farm represented by diagnostic fossils are accommodated in extinct genera (Steadman, 2008).

The late Miocene bird community from Montbrook is dominated by aquatic species such

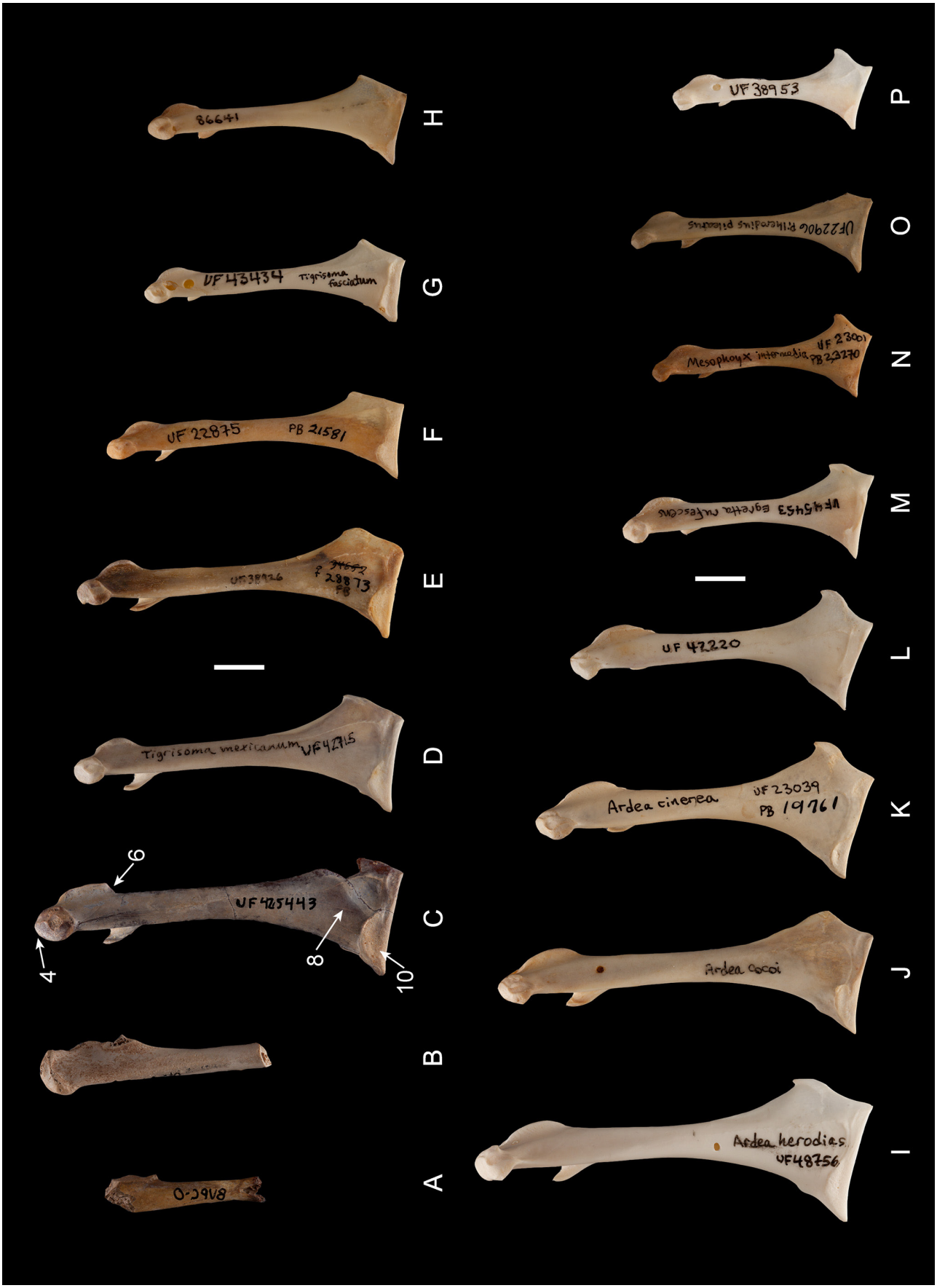

Figure 3. The coracoid of herons in ventral aspect. Specimens as in Figure 1. Scale bars = 10 mm.

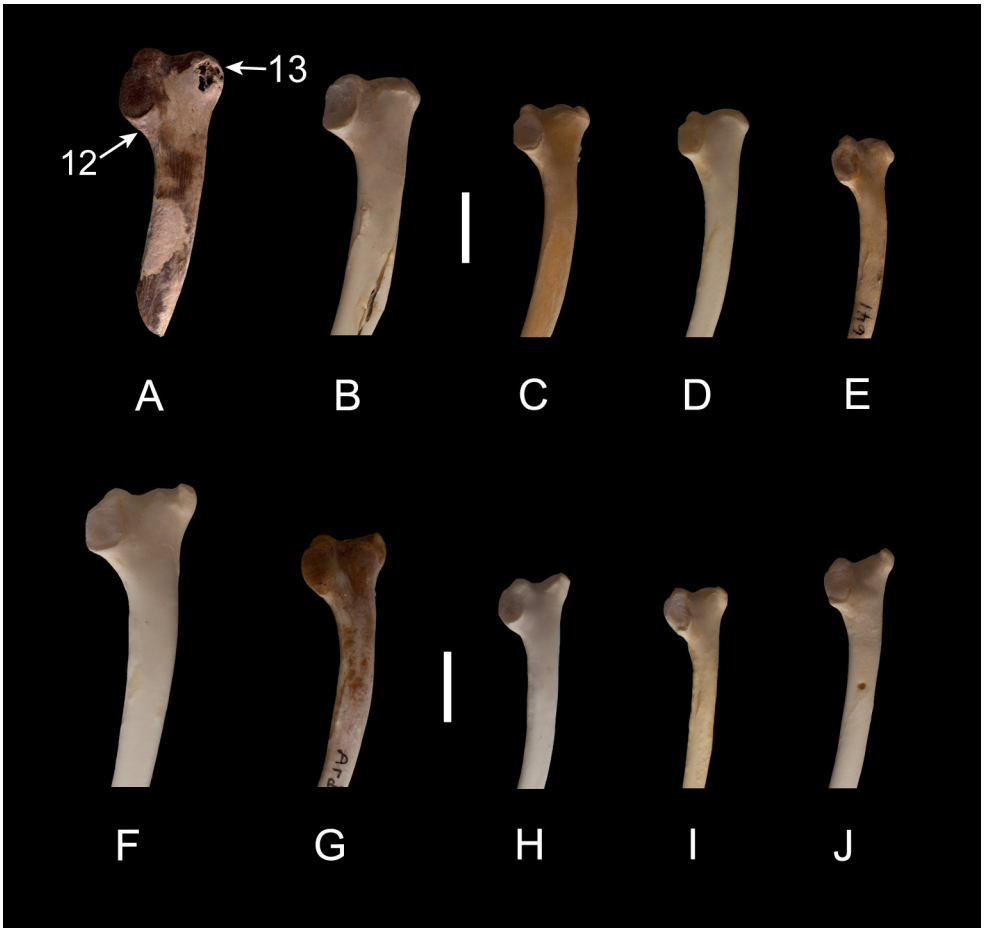

Figure 4. The scapula of herons in lateral aspect. A. *Taphophoyx hodgei* new genus and species, UF 431654 (fossil), Montbrook, Florida. B. *Tigrisoma mexicanum*, UF 42715, Honduras. C. *Tigrisoma lineatum*, UF 22875, captive. D. *Tigrisoma fasciatum*, UF 43434, Peru. E. *Cochlearius cochlearius*, MVZ 86641, El Salvador. F. *Ardea herodias*, UF 48756, Florida. G. *Casmerodius albus*, UF 42220, Florida. H. *Egretta rufescens*, UF 51271, Florida. I. *Nyctanassa violacea*, UF 22903 (PB 36755), Florida. J. *Botaurus lentiginosus*, UF 52331, Florida. Scale bars = 10 mm.

as swans, ducks, grebes, cormorants, herons, and ibises, whether considered from the number of taxa or the number of individual fossils. The Montbrook avifauna does not include the more strictly marine taxa that are so common in the roughly contemporaneous Palmetto Fauna from the Bone Valley phosphate mining district, such as loons, albatrosses, shearwaters, sulids, and alcids (Brobkorb, 1955; Becker, 1987). While many of the birds discovered at Montbrook are compatible with an estuarine environment, the fossils are just as likely to have been deposited in a freshwater setting.

Finally, we note that the Montbrook avifauna promises to become considerably richer as field and lab work continue. Of the 20+ taxa of birds recognized thus far by DWS, 12 are known from single specimens; we are far from reaching diminishing returns at this unusual site.

ACKNOWLEDGMENTS

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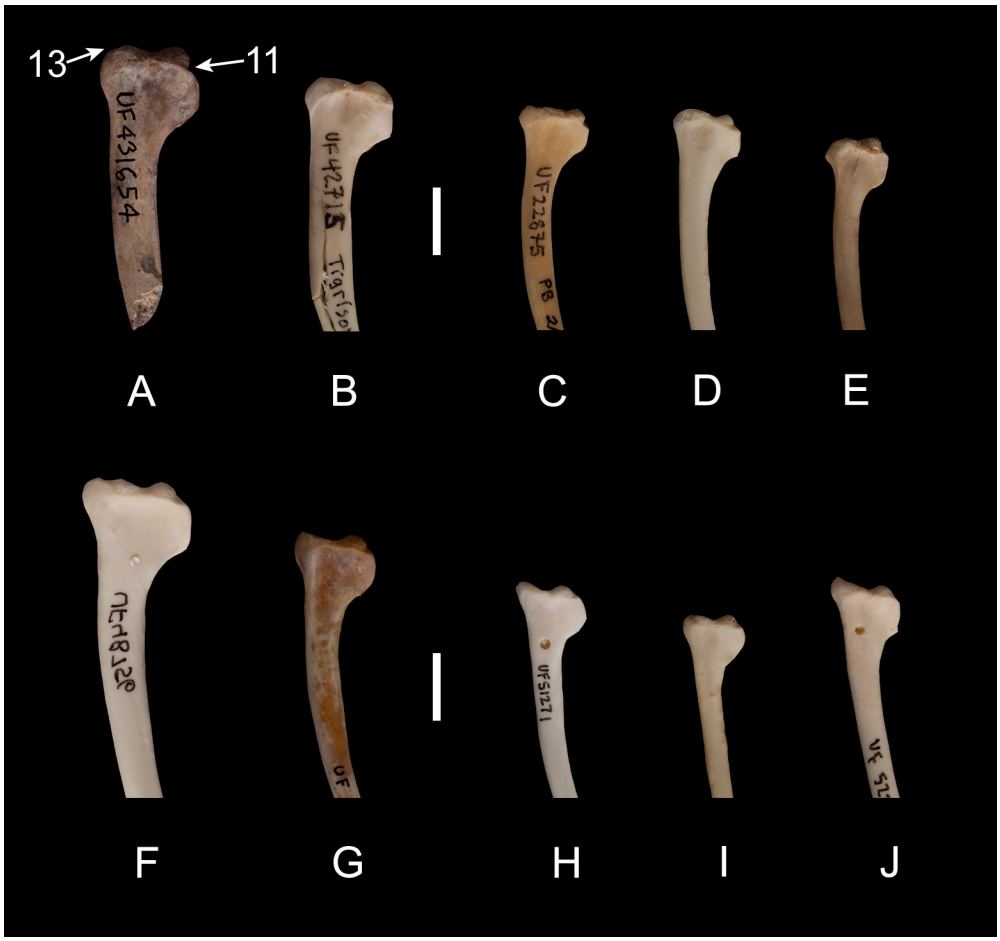

Figure 5. The scapula of herons in medial (costal) aspect. A. *Taphophoyx hodgei* new genus and species, UF 431654 (fossil), Montbrook, Florida. B. *Tigrisoma mexicanum*, UF 42715, Honduras. C. *Tigrisoma lineatum*, UF 22875, captive. D. *Tigrisoma fasciatum*, UF 43434, Peru. E. *Cochlearius cochlearius*, MVZ 86641, El Salvador. F. *Ardea herodias*, UF 48756, Florida. G. *Casmerodius albus*, UF 42220, Florida. H. *Egretta rufescens*, UF 51271, Florida. I. *Nyctanassa violacea*, UF 22903 (PB 36755), Florida. J. *Botaurus lentiginosus*, UF 52331, Florida. Scale bars = 10 mm.

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