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Original Article

Annakacygna, a new genus for two remarkable flightless swans (Aves, Anatidae, Cygnini) from the Miocene of Gunma, central Japan: With a note on the birds' food niche shift and specialization of wings for parental care actions

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Abstract: A new genus and two new species of flightless fossil Cygnini (Aves: Anatidae), *Annakacygna hajimei* and *A. yoshiiensis* are described from the horizon of about 11.5 Ma of the Miocene Haraichi Formation, Annaka Group of Gunma, central Japan. The type specimen of *A. hajimei* (GMNH-PV-678) is the associated skeleton of an adult bird. Osteological features of *A. hajimei* indicate that this large anatid bird belongs to tribe Cygnini as it possesses the diagnostic features of the tribe such as the long neck and long pelvis with dorsally swelling ala postacetabularis illi. *Annakacygna* were a group of flightless birds characterized by the distally small wing elements, large body, and pachyostotic bones. In addition, the autapomorphies of *Annakacygna* indicate that this bird was an animal with the body plan that specialized in breeding behavior, or sex appeal in a broad sense, and uniquely developed the filter feeding with its large head. In a sense, *Annakacygna* acquired remarkable evolutionary forms for two essential biological activities, eating and reproduction, is the "ultimate bird" ever exist. *A. yoshiiensis*, known only from the distal end of tibiotarsus (GMNH-PV-1685), was a gigantic species and showed the diversification within this unique genus in the sea of Miocene Japan.

Key Words: Miocene, Annaka Group, Cygnini, Flightless bird, *Annakacygna*

INTRODUCTION

The flightlessness, loss of flight ability, is not a rare evolutionary phenomenon in avian history (e.g., Olson, 1973, 1985; Feduccia, 1999; Livezey, 2003). Flightlessness in the narrow sense, excluding the "submarine flyers" such as penguins, that is, the negative allometry of wing musculoskeletal system against the bird's body size, seems to be a contradictory phenomenon in birds, animals whose forearms are specialized feathered wings. Large flight muscles, however, burn large calories in their physiological maintenance itself, so there is actually a big advantage to this degeneration (McNab, 1994). Flightless species are likely to appear in insular environment where there are no natural enemies and no need to take off and escape. However, since the pattern of ossification progress with growth differs depending on the major taxa of birds, there are families/orders that are prone to be flightless or not.

Anatidae is an avian group in which flightlessness occurs frequently. Totally about 27 flightless species including unnamed ones, in both fossil and modern anatids, with the earliest record from the early Miocene (Tonni, 1979; Noriega et al., 2008), are known in Anserini, Cygnini, Anatini, and Mergini (see the review of Watanabe and Matsuoka, 2014).

The "Annaka Short-winged Swan" (Matsuoka et al., 2001, 2002, 2004), the bird noted by Watanabe and Matsuoka (2014) as "an unnamed large, flightless, and probably diving anatid that resembles but is distinct from *Megalodytes morejohni*", is an example of marine flightless anatid. The fossilized nearly articulated skeleton was found and excavated by Mr. Hajime Nakajima in A. D. 2000 from the marine Miocene Haraichi Formation of the riverbed of the Usui Riber, Annaka, Gunma (Matsuoka et al., 2001). It was first identified as a possible relative of *Megalodytes morejohni* Howard, 1992, known from the Miocene of the west coast of North America (Matsuoka et al., 2001, 2002), but after the careful preparation removed all mudstone matrix from the bones, our comparative study between the skeletal elements of these birds revealed that "Annaka Short-winged Swan" is not *Megalodytes* (Matsuoka et al., 2004). In connection with this problem, though Howard (1992) originally placed *Megalodytes* in Cygnini (swans), Louchart et al. (2005) and Worthy (2008) suggested the exclusion of *Megalodytes* from this tribe. Our investigation on the phylogeny of "Annaka Short-winged Swan" has concluded that this is truly a swan, which had a unique body among all known anatid species. Therefore, as the first purpose of this paper, we describe the "Annaka Short-winged Swan" as a new genus and new species here.

And furthermore, very fortunately, the diagenetic deformation of the fossilized bones of "Annaka Short-winged Swan" is not serious, and the original shape of each skeletal element was able to be almost certainly reconstructed. Then in parallel to the phylogenetic investigation on "Annaka Short-winged Swan", with an intention to understand the functional morphology of this unique bird, the authors have developed the basic research on the musculoskeletal system of swan by using a pickled specimen of Whooper Swan (*Cygnus cygnus*): Matsuoka and Hasegawa (2007), Matsuoka et al. (2008), and Matsuoka and Seoka (2021). The second purpose of this paper is to show the ecological characteristics of "Annaka Short-winged Swan" from the viewpoint of the musculoskeletal system.

In addition, during our research, a fossil of the distal end of the tibiotarsus of a large bird found around 1995 by Mr. Toshimasa Moridaira from the riverbed of Kabura River, the location about 11.5 km east-southeast from the locality of "Annaka Short-winged Swan" was donated to GMNH in 2005. Though the specimen is fragmentary, its morphological characteristics other than its size match reasonably to that of the relevant part of "Annaka Short-winged Swan". If we postulate that these two birds had similar body shapes, that means there was the difference of 1.3 times in body length between the two. The difference is significant as an indicator of species diversity of a single avian genus. Then the larger fossil specimen is described as the second and larger species of the same genus here. This is the third purpose of this paper.

This paper adds totally 2 new species belonging to 1 new genus to the paleofauna of the marine Miocene Haraichi Formation. The serial Tomioka-Annaka groups including Haraichi Formation distributed in the southwestern part of Gunma (Oishi and Takahashi, 1990; Takahashi and Hayashi,

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2004) have produced many vertebrate and invertebrate fossils. There must have been a unique ecological and environmental background in the sea of ancient Gunma to produce the rich marine biodiversity, in which the lifestyle specialization of short-winged swans occurred. We hope this paper will contribute to the understanding of the paleontological and geological distinctiveness of the Miocene of the Japanese Archipelago.

Institutional Abbreviation—GMNH, Gunma Museum of Natural History, Tomioka, Gunma, Japan; KUGM, Department of Geology and Mineralogy, Kyoto University, Kyoto, Japan.

GEOLOGIC SETTING

The Miocene Tomioka-Annaka groups distributed in the southern part of Gunma, central Japan, consist of thick marine sediments, totally about 4000 m thick (Oishi and Takahashi, 1990; Takahashi and Hayashi, 2004). They are composed of: basal Ushibuse Formation, massive arkosic coarse sandstone of at least 400 m thick; Obata Formation, the alternation of siltstone and turbidite sandstone being 1400 m thick; Haratajino Formation, 40 m thick sandy siltstone; Niwaya Formation, 40-400 m thick sandy siltstone and sandstone including altered felsic tuff grains; Haraichi Formation, 500 m thick massive sandy siltstone; and at least 1200 m thick conglomerate, Itahana Formation, in ascending order. Between the Haratajino and Niwaya formations, the Niwaya Unconformity, that denuded the underlying rocks 500 m in maximum, divides the lower Tomioka Group (Ushibuse, Obata, and Haratalino formations) and upper Annaka Group (Niwaya, Haraichi, and Itahana formations).

The marine deposits of the Tomioka-Annaka groups yield abundant and well-preserved marine vertebrate fossils (e. g., Takakuwa et al, 2001; Matsuoka et al., 2002; Kimura et al., 2003; Takakuwa and Hasegawa, 2004; Hasegawa et al., 2005; Hasegawa and Kimura, 2008). Even only from the Haraichi Formation, many sharks (Goto et al., 1978, 1983; Takakuwa, 1999, 2005; Takakuwa et al., 2003), Allodesminae pinniped (Hasegawa et al., 2000), desmostylian mammal *Paleoparadoxia* (Hasegawa and Kimura, 2008), whales and dolphins including originally established *Joumocetus shimizui* Kimura and Hasegawa, 2010, *Kentriodon nakajimai* Kimura and Hasegawa, 2019, and *Norisdelphis annakaensis* Kimura and Hasegawa, 2020 (Hasegawa et al., 2001, 2002; Kimura et al., 2006; Kimura and Hasegawa, 2010a, 2010b, 2019, 2020, 2021), and a bird "Annaka Short-winged Swan" (Matsuoka et al., 2001, 2004) have been reported. Invertebrate fossils reported from the Tomioka-Annaka groups include: fossil decapod crustaceans (Kato, 2001), molluscs (Kurihara, 2000, 2002), barnacles (Nomura and Takakuwa, 2009), and crinoids (Takakuwa et al, 2002) and so on.

The main lithofacies of the Haraichi Formation is the blueish grey - dark grey colored massive siltstone. It is a deep-sea deposit and its environment is known through foraminifera (Kaneko and Nomura, 1998) and many vertebrate and invertebrate fossils as mentioned above. The molluscan fossils are scattered in the layers of the middle and upper part of the formation.

The fossilized almost complete skeleton of a Cygnini bird GMNH-PV-678 and a single tibiotarsus distal end of another larger bird GMNH-PV-1685 were discovered from the middle part of the Haraichi Formation, Annaka Group. The former, holotype of *Annakacygna hajimei* in this paper, is from the river floor of the Usui River of Haraichi, Annaka City, Gunma Prefecture (Matsuoka et al., 2001, 2004), and the later, holotype of *A. yoshiiensis* in this paper, is from the river floor of the Kabura River of Yoshii-machi, Takasaki City, Gunma (Fig. 1). The stratigraphic horizon where these avian fossils were yielded is the middle part of the formation and is characterized by the "*Gloripallium*" *crassivenium* Assemblage which consists of deep-sea species (Kurihara, 2000, 2002). The research on the benthic foraminifera also shows that the middle part of the Haraichi Formation including much *Uvigerina proboscidea* is a deposit of the archbenthal oceanic zone (Kaneko and Nomura, 1998).

At around the type locality of *Annakacygna hajimei*, Haraichi, Annaka, the Usui River flows roughly from southwest to northeast, and the exposed strata of the Haraichi Formation on the river floor show the WNW-ESE strike and low-angle dip toward north. That means the upper part of the river is older and the lower stream is younger in the geological sense. Looking from the excavated site of the holotype of *A. hajimei*, the tuff bed named Kitamura Tuff appears upstream and another Baba tuff appears downstream. The ^{40}Ar-^{39}Ar ages are obtained for these tuffs: 11.79±0.08 Ma for the older Kitamura Tuff, and 11.26±0.09 Ma and 11.29±0.12 Ma for the younger Baba Tuff (Odin et al., 1997). The excavated site is nearly at the middle of two tuff beds, and it is at about the horizon of the first occurrence

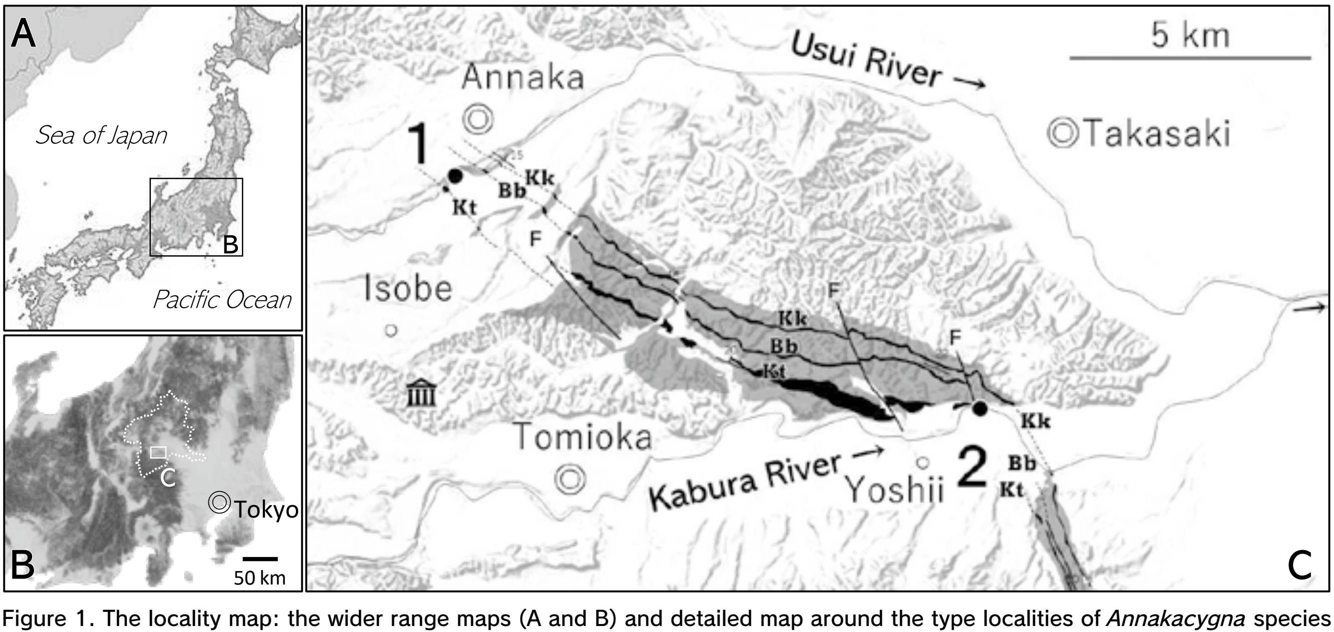

Figure 1. The locality map: the wider range maps (A and B) and detailed map around the type localities of *Annakacygna* species (C). In C map, the point 1 is the type locality of *A. hajimei*, and the point 2 is the type locality of *A. yoshiiensis*. The gray-painted area with black lines is the distribution of the Haraichi Formation, which comes stratigraphically upper (younger) as goes to northeast. Black lines are the key-tuff beds: Kt, Kitamura Tuff; Bb, Baba Tuff; and Kk, Kamikoizawa Tuff, in ascending order. F, fault.

of *Globigerina nepenthes* foraminifera (Takayanagi et al., 1976), so the age should be judged to be about 11.5 Ma.

The type locality of *Annakacygna yoshiiensis*, the river floor of the Kabura River of Yoshii-machi, Takasaki, is almost at the same horizon as *A. hajimei*, and then we can regard the age of *A. yoshiiensis* to be same as *A. hajimei*, about 11.5 Ma. A fault, however, disturbs the stratigraphy at the locality area, and the exact horizon of *A. yoshiiensis* is unclear.

SYSTEMATIC PALEONTOLOGY

Class AVES Linnaeus, 1758
Order ANSERIFORMES Wagler, 1831
Family ANATIDAE Leach, 1820
Subfamily ANSERINAE Vigors, 1825
Tribe CYGNINI Vigors, 1825

It is, honestly, hard to find any synapomorphies of recognized linages (e. g. characteristics described by Woolfenden, 1961) on such a specialized bird. However, the genus described herein can be assigned to the tribe Cignini (swans) by combination of long neck, the skeleton regarded to have 23 cervical vertebrae (synapomorphy of swans, recognized by Woolfenden, 1961), and long pelvis with dorsally swelling ala postacetabularis illi (our own view).

ANNAKACYGNA, gen. nov.

Type Species— *Annakacygna hajimei*, sp. nov.
Included Species— Type species and *A. yoshiiensis*, sp. nov.
Etymology— Combination of Annaka, the city name of type locality, and cygna, the feminine of Latin cygnus, swan.
Diagnosis— Large-sized anatid with a relatively big head and relatively reduced pectoral skeleton that is characterized by the combination of the following osteological features: cranium- wide fossa temporalis, presence of "pseudo-sagittal crest", presence of salt gland impression; lacrimal- unfused to the frontal of neurocranium; quadrate- deep impression of m. adductor mandibulae externus profundus on the lateral surface; mandible- curved strongly, long for the body, the longitudinal structure on the articular facet for quadrate; ribs- the uncinate process unfused; sternum- carina sterni reduced; scapula- small facies articularis humeralis and acromion, curved and wide corpus scapulae with developed and round extremitas caudalis; humerus- long and straight, as long as its trunk, short crista pectoralis, developed crista bicipitalis with prominent tubercules for the accessory origin of m. biceps brachii at just distal to tuberculum ventrale and the insertion of m. scapulohumeralis caudalis at the middle, small distal end; ulna- short relative to the humerus, only 57% of humeral length; radius- same as ulna short relative to the humerus, widens and flattened distally; radiale- huge relative to the wing, triangular profile in dorsoventral view, acts to limit the mobile range of wrist joint to bending posture; carpometacarpus- short and robustly build, large proximal end with strong insertion of the m. ulnimetacarpalis ventralis; pelvis- wide as a swan's, distal caudal vertebrate unfused, caudal termination of pubis deep; tibiotarsus- crista cnemialis cranialis broad and squared and extend proximally and less anteriorly, condylus lateralis and condylus medialis of distal end narrow laterally, incisura intercondylaris wide; tarsometatarsus- shaft laterally narrow. All long bones are pachyostotic.

ANNAKACYGNA HAJIMEI, sp. nov.

aff. *Megalodytes* sp.: Matsuoka et al., 2001

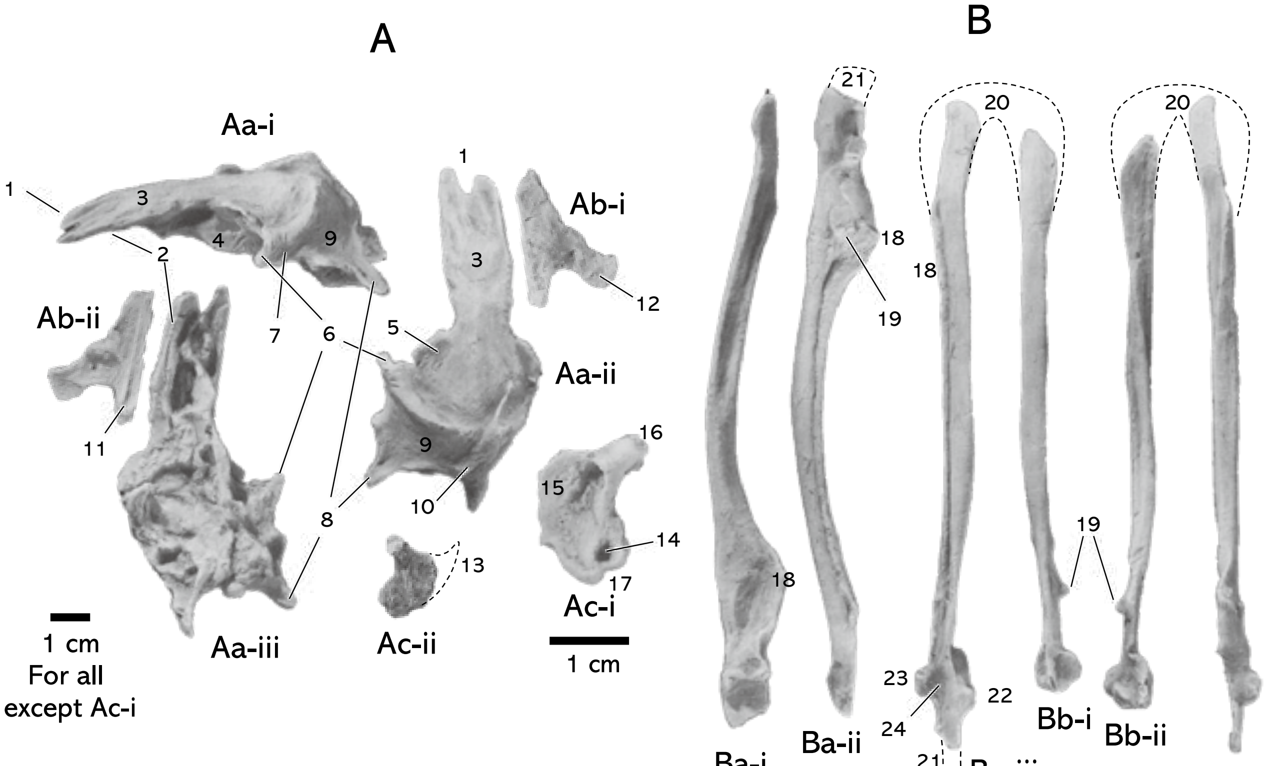

Figure 2. The skull elements (A) and mandible (B) of the holotype of *Annakacygna hajimei*. Aa, the neurocranium (Aa-i, left lateral; Aa-ii, dorsal; Aa-iii, ventral views); Ab, the right lacrimal (Ab-i, dorsolateral; Ab-ii, ventromedial views); and Ac, left quadrate (Ac-i, lateral, twice magnification than other figures; Ac-ii, medial views). Ba, the right lower mandible (Ba-i, lingual; Ba-ii, buccal; Ba-iii, ventral; Ba-iv, dorsal views); Bb, the left lower mandible (Bb-i, ventral; Bb-ii, dorsal views). 1, nasofrontal joint; 2, articular surface to the unfused lacrimal (on the lateral surface of frontal); 3, frontals; 4, orbit; 5, salt gland impression; 6, postorbital process; 7, fossa temporalis; 8, ala tympanica; 9, origin of m. depressor mandibula; 10, "pseudo-sagittal crest"; 11, articular surface to frontal; 12, ventral process = attaching surface of lig. prefrontomandibulare; 13, orbital process; 14, quadratojugal articulation; 15, origin of m. adductor mandibulae externus profundus; 16, capitulum oticum; 17, articular surface to the mandible; 18, coronoid process (proc. coronoideus); 19, lateral coronoid process (LCP); 20, pars symphysialis; 21, retroarticular process; 22, internal articular process; 23, external articular process; 24, articular surface for the quadrate.

Holotype— GMNH-PV-678, nearly complete associated but disarticulated skeleton collected January 1, 2000 by Mr. Hajime Nakajima. The specimen was collected as a large slab of siltstone (ca. 73 x 45 cm) with the bones scattered in the bedding plane (Matsuoka et al. 2001). The individual elements were then removed completely from the matrix so that they could be studied three dimensionally (Matsuoka et al. 2004). Certain elements are in nearly pristine condition, while others have suffered varying degrees of crushing and compressional distortion. The fossilized elements include: the cranium (greatly crushed); left quadrate lacking most of the orbital process; mandible lacking some portion of the symphysial area and parts of the retroarticular processes; cervical vertebrae interpreted as the 3rd-5th and 15th-23rd; thoracic vertebrae interpreted as the 1st-2nd and 5th-7th; three caudal vertebrae; pelvis with separated posterior ends of pubes; an assortment of thoracic and sternal ribs and uncinate processes, mainly from the left side; poorly preserved sternum consisting mainly of a portion of the posterior part of the carina; very poorly preserved right coracoid consisting mainly of the ventral surface imbedded in fiberglass resin; left scapula (there is no remaining part of the clavicles, if they were ossified); right and left humeri; right and left ulna, the left one is complete in length but crushed, right ulna preserved mainly as resin mold; left radius; left radiale; left carpometacarpus; left phalanx one of major alar digit; right and left femora (crushed); complete left and proximal half of right tibiotarsi; left tarsometatarsus; pedal phalanx 1 of left digit IV.

Type Locality and the geologic horizon— Near Haraichi, Annaka City, Gumna Prefecture, Japan (Fig. 1-C-point 1). The river floor of the Usui River, about 600 m down the river from the Nakahashi Bridge. 36°18'46.6"N, 138°52'07.0"E. From the middle part of Haraichi Formation, Annaka Group. About 11.5 Ma.

Measurements of Holotype in mm— Cranium: maximum length as preserved 95, least width of interorbital bridge 13.6; Mandible: greatest length 105, depth at coronoid process 17.2, depth of dentary at midpoint 6.8; Pelvis: greatest length (without pubis) 200; Sternum: maximum length as preserved 105; Scapula (left): greatest length 108, anterior width 20.8, length of glenoid facet15.1, shaft width and depth posterior to articulation 9.8 x 5.5; Humerus (right): greatest length 220, proximal width 39.9, width and depth of shaft at midpoint 9.5 x 10.3, distal width 22.2; Humerus (left): greatest length 218, proximal width 37.8, width and depth of shaft at midpoint 10.0 x 10.9, distal width 22.2; Ulna (right): greatest length 125; Ulna (left): greatest length 124, proximal depth 14.9, proximal width 15.1, distal depth 14.9; Radius (side?): greatest length 115; Radiale: maximum diameter 22.0; Carpometacarpus (left): greatest length 66, proximal depth 25.4, width of trochlea 12.7, length of alular metacarpal 16.6, distal de;pth 9.2, distal width 8.3; Phalanx 1 of major alar digit: length 24.5; Femur (right): greatest length 97, maximum proximal width 28.6+, maximum diameter of head 12.0, distal width 25.5+; Femur (left): greatest length 94, maximum proximal width 27.0+, maximum diameter of head 12.1, distal width 24.1+; Tibiotarsus (left): greatest length (including cnemial crest) 200, length from proximal articular surface to distal end 190.5, proximal width (articular surface) 21.8, length of fibular crest 41.6, width and depth of shaft 40 mm from distal end 11.0 x 8.7, distal width 21.8, depth of external condyle 20.3, depth of internal condyle 22.4; Fibula: width and depth of head 6.4 x 16.0; Tarsometatarsus (left): greatest length 110, proximal width, maximum proximal depth through hypotarsus 24.4, width and depth of shaft at midpoint 9.4 x 11.6, width through trochleae 19.2+, width and depth of trochlea II 7.6 x 14.4, width and depth of trochlea III 9.1 x 16.2, width and depth of trochlea IV 6.8 x 15.2.

Etymology— After local paleontologist Mr. Hajime Nakajima, in recognition of his outstanding contributions to vertebrate paleontology of Gunma.

Diagnosis— As for genus.

Description— The drawn figures in plates (Pls. 1-7) of this paper are the reconstructed shape of each skeletal element. See the photographs of fossil bones in Matsuoka et al. (2004). For comparison in this description, we subdivide recent swans (Genus *Cygnus*) to subgenera *Cygnus* (*C.* (*C.*) *olor*, *C.* (*C.*) *atratus*, and *C.* (*C.*) *melanocoryphus*) and *Olor* (*C.* (*O.*) *buccinator*, *C.* (*O.*) *cygnus*, *C.* (*O.*) *bewickii*, and *C.* (*O.*) *columbianus*), and use these subgenera names. The osteological names follow Baumel and Witmer (1993). As assistance for the skeletomuscular system of swans, see Matsuoka and Hasegawa (2007), Matsuoka et al. (2008), and Matsuoka and Seoka (2021).

Skull—(Figs. 2-A, 3-A; Pl. 2) The skull is very crushed and lacks the beak portion in the holotype fossil. However, it can be complemented and reconstructed by the complete mandible and then we can view its original shape. We see the proportion of this bird was "head-heavy". The reconstructed length of the upper beak, estimated in relation to the mandible, is about 10 cm.

The neurocranium is flattened and distorted, and its ventral

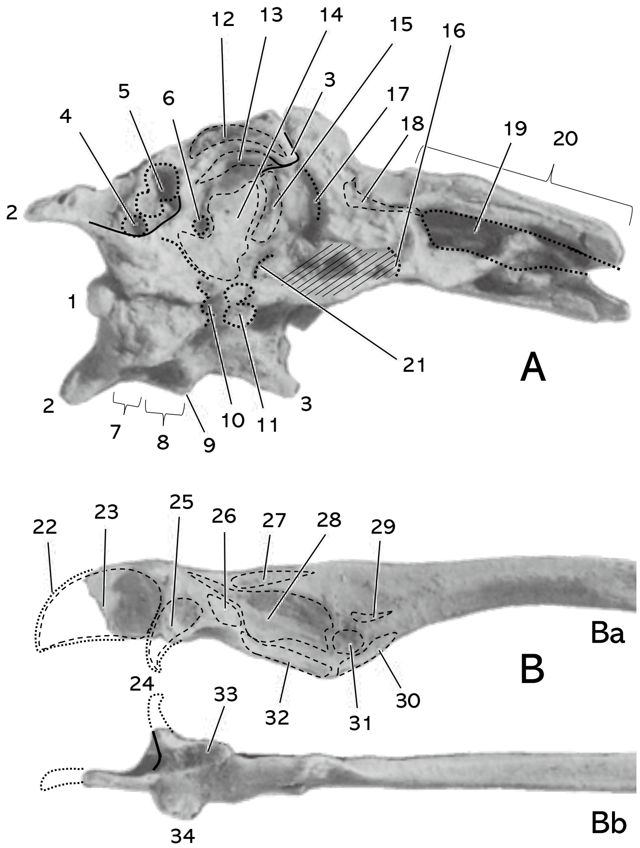

Figure 3. The ventral surface of cranium (A) and the medial (Ba) and dorsal (Bb) surfaces of the right mandible of holotype of *Annakacygna hajimei*. 1, condylus occipitalis; 2, os exoccipitale : ala tympanica; 3, proc. postorbitalis; 4, fenestra vestibuli; 5, cotylae quadratica squamosi et otici; 6, foramen n. maxillomandibularis; 7, meatus acusticus externus; 8, quadrate fossa; 9, "articular tubercle"; 10, tuba auditiva communis; 11, facies articularis pterygoidea, rostrum parasphenoidale; 12, origin of m. adductor mandibulae externus superficialis (A-port.); 13, origin of m. adductor mandibulae externus medialis; 14, origin of m. protractor quadratus; 15, origin of m. pseudotemporalis superficialis; 16, origin of m. protractor pterygoideus (anterior margin); 17, fonticuli orbitocraniales (crushed); 18, sulcus olfactorius; 19, nasal cavity; 20, facies articulalis lacrimalis; 21, foramen n. ophthalmici; 22, insertion of m. depressor mandibulae (anterolateral part); 23, insertion of m. depressor mandibulae (ventromedial part); 24, proc. mandibulae medialis (= internal articular process: IAP); 25, origin of m. pterygoideus ventralis lateralis; 26, insertion of m. pterygoideus dorsalis medialis; 27, origin of m. intermandibularis ventralis; 28, insertion of m. pterygoideus dorsalis lateralis; 29, origin of m. intermandibularis dorsalis; 30, insertion of m. pseudotemporalis superficialis; 31, origin of m. branchiomandibularis; 32, insertion of pseudotemporalis profundus; 33, cotyla medialis; 34, proc. mandibulae lateralis (= external articular process: EAP)

surface may look difficult to interpret. But, even in the current state of the significantly deformed fossil, following characteristics are preserved. Nasofrontal joint is completely unfused and separated. Lacrimal is unfused to neurocranium and the articular surface on the lateral surface of frontal has a long anteroposteriorly extending ridge in the middle. Frontals are apparently relatively narrow. Frontals and lacrimals, though completely flattened, are originally swollen slightly but not large as in *Olor*. Over the posterior margin of the orbit, there is a distinct shelf of bone, and on the dorsal surface, there is a distinct notch between it and the postorbital process, which is the impression of passing salt gland. Postorbital process is short and wide. Fossa temporalis is very small, limited only at the base of short postorbital process. Ala tympanica is very long, narrow, and posterolaterally directed. The origin of m. depressor mandibula is vast, in which the posterolateral end is ala tympanica, and the left and right vast origins of this muscle meet at the midline to form a "pseudo-sagittal crest".

The unfused lacrimal is V-shaped, with one side for the articular surface to frontal. This thin and flat element is large and well developed as in *Olor* but highly unusual in not being fused. The V-shape is formed from the long dorsal articulating surface and the large posteriorly directed ventral process with a rounded notch in the posterior margin. Lack of fusion is possibly a result of pedomorphosis in response to possibly unusual kinesis associated with the unique feeding mechanism. The articular surface has a long anteroposteriorly extending groove in the middle. The attaching surface of lig. prefrontomandibulare, the tip of another side of "V", is small and not like in *Cygnus*. There is a small foramen in the middle of the ventral process. Together with frontals, though completely flattened, it shows indications of the original swollen form.

A quadrate, only from the left side and lacking much of the orbital process, is dorsoventrally high, and the caudal margin is well round. Capitulum oticum has the normal double head, which is short, rounded, and faces dorsal. The pit for quadratojugal articulation is small and deep. The origin of m. adductor mandibulae externus profundus is wide and deeply impressed on the lateral surface. This element is quite thin and differs from other Anseriformes in that the articular surface with the mandible is a single, antero-posteriorly oriented condyle. Such condyle-shaped articular surface must be the adaptation for the developed upper jaw retraction unique to this bird. Such kinetic characteristics of this bird will be discussed in the following chapter.

Mandible—(Figs. 2-B, 3-B; Pl. 2) This element is extraordinarily different from that in any other Anseriformes. The rami are very long, slender, and deeply bowed ventrally when viewed laterally. The coronoid process (Proc. coronoideus) is situated far posteriorly so that the length of the ramus anterior to the coronoid process is about 4 times the length of the distance from coronoid process to the posterior margin of the articular surface, in contrast to about 2 times in *Olor*. The lateral coronoid process (LCP) locates just below the top of the coronoid process, that shows, among the lower jaw adductors, the muscles that insert anterior to LCP are significantly degenerated, and the proportion of those that insert the area posterior to LCP is relatively large. The symphysial portions are not complete on either side, as the bone becomes very thin and fragile here. Its original shape that formed evidently broad pars symphysialis can be reconstructed by extending the relatively well-preserved parts, lateral margin of left dentary is and medial margin of right dentary. After the fossil deformation is restored, the dorsoventral profile of the lower mandible is about an elongated Ω-shape, with the pars symphysialis (anterior end) spreading out laterally and the middle part narrowed medially. The retroarticular process was well developed but is broken on both sides, so the posterior termination is unclear. In dorsal view the articulation area appears narrower. The internal articular process, preserved only on the right side, is slightly abraded but small. The external articular process is wide and low. The articular surface for the quadrate is parallel with the ramus and not strongly angled as in *Olor*.

Cervical and free thoracic vertebrae —(Fig. 4) Totally 17 cervical and thoracic vertebrae are preserved in the type specimen. Most of them are much distorted by crushing, but well preserved to determine their original positions. The successive and gradually transforming vertebrae are evidence of a long neck, and through the comparison, they are identified to be the 3rd to 5th and 15th to 23rd cervical vertebrae and 1st, 2nd, and 5th to 7th thoracic vertebrae. The 23rd cervical vertebra and the 7th thoracic vertebra are the last ones of each series. The cervical and thoracic vertebrae of this bird are in general similar to the vertebral series of *Cygnus*, especially to *C. atratus* as the length of vertebral column matches. In contrast, the total shape of each fossil vertebra is wider and heavier than in modern *Cygnus* species. In comparison to the *C. artatus*

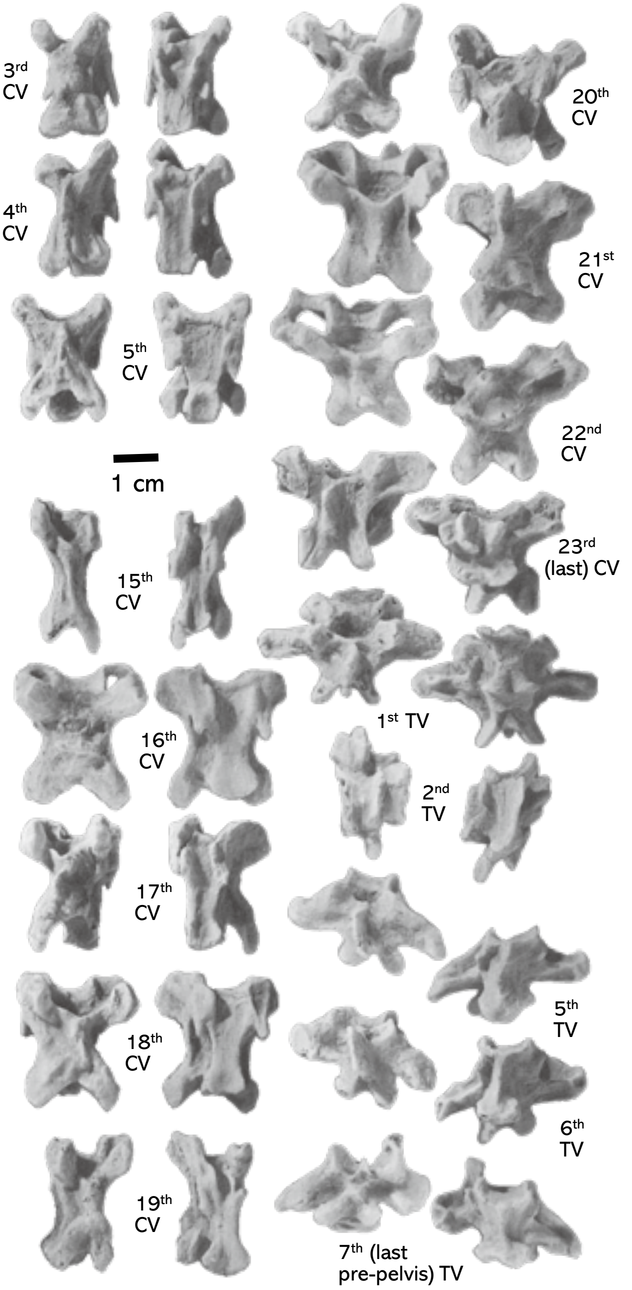

Figure 4. The cervical and free thoracic vertebrae of the holotype of *Annakacygna hajimei*. The identification of each vertebra is as numbered in the figure. The dorsal view in the left and the ventral view in the right of set figure of each vertebra. Top to cranial. CV, the cervical vertebra; TV, thoracic vertebra.

vertebrae: the anterior C3 to C5 are larger, and posterior C15 to C23 are shorter and more robust. Process ventralis of distal cervical vertebrae and proximal thoracic vertebrae (around C20-T2) are much developed and larger than the ones of compared modern *Cygnus*. Thoracic vertebrae have a shorter and robust build. The transverse process of T2 is much narrower. T4 is shorter and the ventral process is much longer and more blade-like. The dorsal processes of T5 and T6 are higher and shorter. The transverse process of T7 is narrower. These unique morphologies indicate the strong and very-mobile action of neck that is consistent with the "head-heavy" proportion of this bird.

Ribs—(Fig. 5) Those preserved are mainly of the left side. It is difficult to decide the numbers of position but seems to be the mid-posterior portion of the rib cage. Though the exact positions are not found, they are robust in general. What is highly unique on these ribs is that the uncinate processes (UP in figure) are unfused. The articular surface between the rib body and the uncinate process, the shallow depression on the rib body, is smooth.

Sternum—(Fig. 6-B, Pl. 3-C) This element is very poorly preserved, especially the caudal portion of the facies muscularis sterni is crushed and partly the fragments are overlapped, and the anterior margin of this bone appears to have suffered breakage, so its full extent is difficult to know. However, fortunately, the ventral margin of carina sterni is reasonably preserved. In any case compared with volant swans it was very reduced.

The carina is low and thin and certainly was not excavated for the trachea as in *Olor*. Eight or seven process costalis are visible. Sulcus articularis coracoideus is narrow and oblique to the midline. On both facies muscularis sterni and carina sterni, the linea intermuscularis is visible: on facies muscularis sterni the cranial end of the line is about the middle portion of the sulcus articularis coracoideus and the line goes caudally to the point about to the caudal termination of carina sterni; and on carina sterni the line is about half its depth. Even in this crushed fossil, it is obvious that the lateral portion of facies muscularis sterni is laterally narrow and absolutely small. Then the m. coracobrachialis posterior must be very small.

Coracoid—(Fig. 6-A, Pl. 3-B) Only the right coracoid remains and the fossil, which is preserved as a resin mold, consists only of the ventral surface and not much else can be ascertained. The total profile looks like that of *Chendytes*, the Pleistocene flightless duck of the western coast of North America (see Miller et al., 1961; Watanabe and Matsuoka, 2014 for the figures), in these points: narrow and dorsoventrally high profile; flat and non-pneumatic body; the cranial top (process acrocoracoideus) reduced and looks just club-like as the facies articularis clavicularis does not develop, and almost invisible on it; facies auricularis humeralis appears reduced; and proc. procoracoidei is weak with a blunt tip. Process lateralis is not prominent, and the lateral margin of this bone is straight to the lateral termination of the caudal (sternal) margin. Angulus medialis slightly expands cranially, not in acute angle.

Scapula—(Fig. 6-C, Pl. 3-A) The holotype has a complete left scapula. The blade (corpus scapulae) curves laterally and dorsally convex and is wide and thick in its entire length. So, it looks much stronger than the scapula of volant Anseriformes and might not look like that of a flightless bird. The distal two-thirds of the blade is rotated to face the dorsal surface (facies lateralis) more laterally in the articulated skeleton. The posterior termination (extremitas caudalis) is round. On this wide blade, the origin of m. scapulohumeralis caudalis is wide and much more developed than volant swans. On the lateral (axillary) margin of the blade, at the position of about one-fourth from the proximal tip of the entire bone, the attaching position of the scapular anchor of m. deltoideus major forms a small projection. Along with the margo dorsalis, m. rhomboideus superficialis leaves a strong line at its insertion. On the ventral surface (facies costalis) of the blade, the origin of m. subscapularis is developed and gives the largest curvature of dorsal convexity at this position. Probably to provide room for this developed muscle, the scapula is convex dorsally.

In contrast to the wide blade, the articular end is narrow. Facies articularis humeralis is small. Acromion is low but thick and has a flat face on the cranial termination. The sulcus between acromion and facies articularis humeralis is deep, and the caudal continuity of acromion forms a sharp ridge on the dorsal surface of the bone. Tuberculum coracoideum is pronounced and rounded. This articulating structure to the coracoid protuberates slightly ventrally, then the morphology may suggest an acute angle to the coracoid in life, not the obtuse-angled articulation common in flightless birds.

Humerus—(Fig. 7-A, Pl. 4-A) Both right and left bones are complete. Overall length is nearly the same as with the

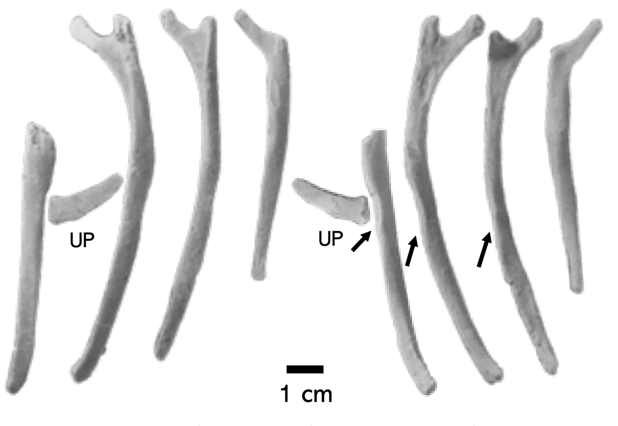

Figure 5. Examples of the ribs of the holotype of *Annakacygna hajimei*. The lateral surface in the left of the figure and the medial surface in the right. UP, the unfused uncinate processes. Note the depression (arrows), where is the articular point to the uncinate process, on the mid-portion of the caudal margin of the body.

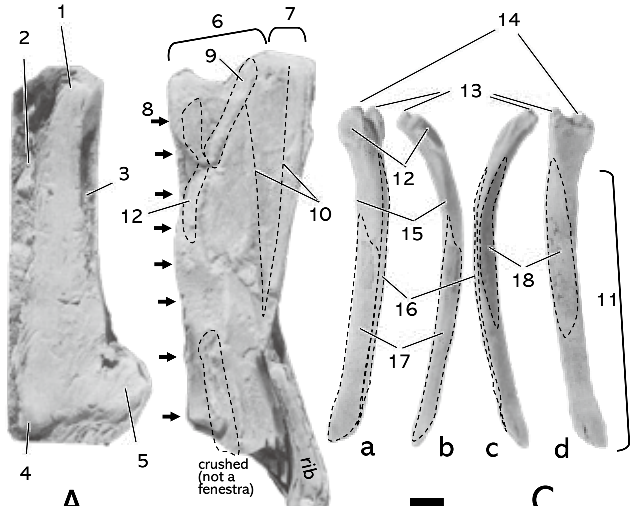

Figure 6. The coracoid (A), sternum (B), and scapula (C) of the holotype of *Annakacygna hajimei*. A, the right coracoid; B, the crushed sternum, showing the right side; C, the complete left coracoid. Ca, dorsal; Cb, lateral; Cc, medial; Cd, ventral views. 1, process acrocoracoideus; 2, facies auricularis humeralis; 3, process procoracoidei; 4, process lateralis; 5, angulus medialis; 6, facies muscularis sterni; 7, carina sterni; 8 (arrows), process costalis; 9, sulcus articularis coracoideus; 10, linea intermuscularis; 11, corpus scapulae; 12, facies articularis humeralis; 13, acromion; 14, tuberculum coracoideum; 15, projection for the scapular anchor of m. deltoideus major; 16, insertion of m. rhomboideus superficialis; 17, origin of m. scapulohumeralis caudalis; 18, origin of m. subscapularis.

modern black swan (*C.* (*C.*) *atratus*). It is, however, extraordinary in that the shaft (corpus humeri) is long but almost completely straight, with no sigmoid curvature in the dorsovental dimension. The lateromedial view shows the remnant of the sigmoidal curve, being nearly ∫ (long s) shape. The proximal end appears expanded in lateromedial dimension, being a palm-like shape due mainly to the reduced crista pectoralis and rounded crista bicipitalis: the crista pectoralis is short and reduced, and on the contrary, well-developed tubercular muscle attachment points are on the ventroposterior margin of crista bicipitalis and they are making the outline of the proximal end of the humerus more rounded. The tubercules are the accessory origin of m. biceps brachii at just distal to tuberculum ventrale and the insertion of m. scapulohumeralis caudalis at the middle of crista bicipitalis. Its size of the latter tubercle is clearly larger than other structures in relative size at the proximal end of the humerus, and even larger in absolute size than that of whooper swan (*C*, (*O.*) *cygnus*, a large volant swan).

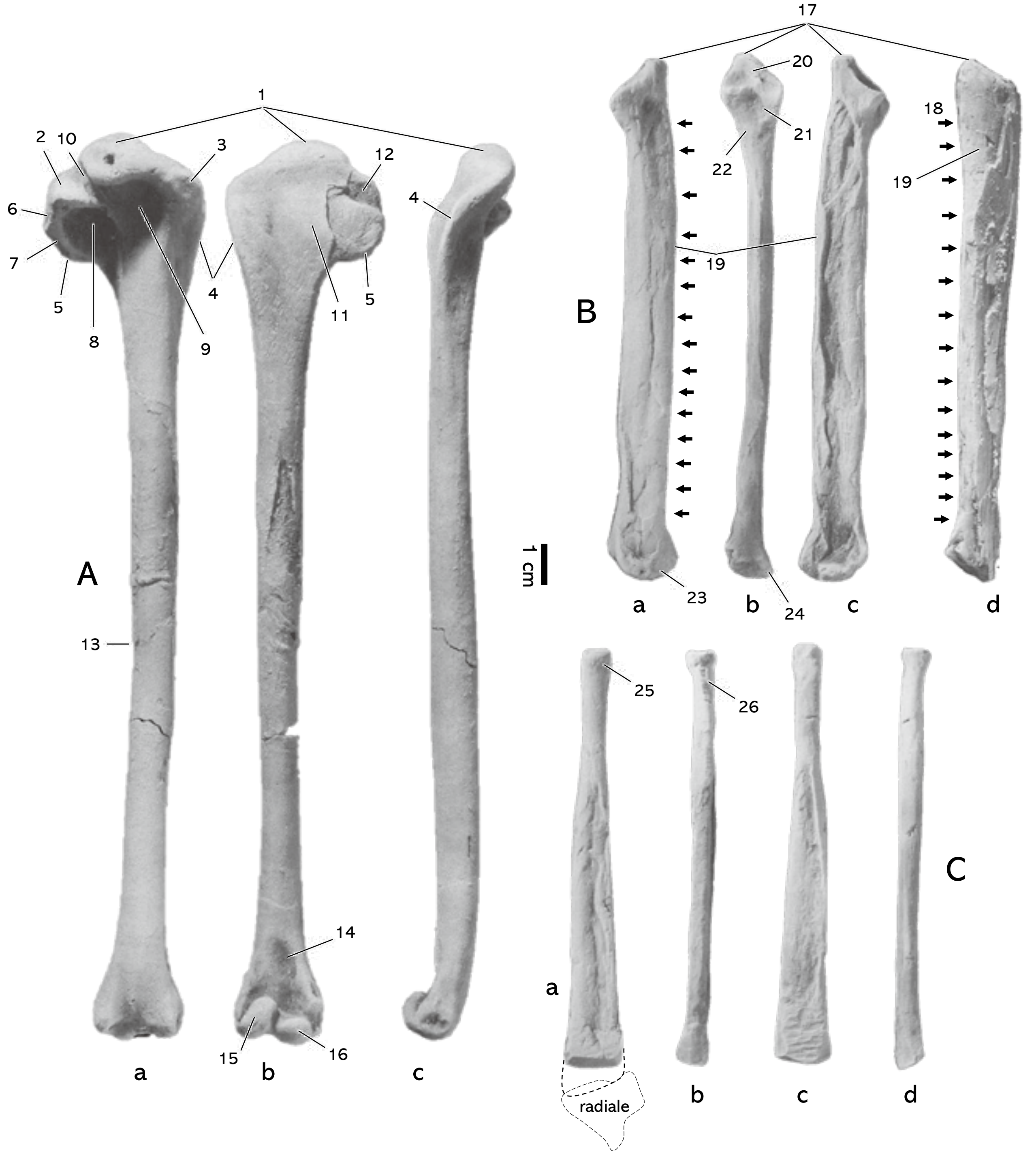

Figure 7. The humerus (A), ulna (B), and radius (C) of the holotype of *Annakacygna hajimei*. Aa and Ab, the right humerus (Aa, caudal; Ab, cranial views); Ac, dorsal view of left humerus; Ba, Bb and Bc, the left ulna (Ba, dorsal; Bb, cranial; Bc, ventral views); Bd, the right ulna, caudal view; C, the left radius (Ca, dorsal; Cb, cranial (= ulnar); Cc, ventral; Cd, caudal views). 1, caput humeri; 2, tuberculum ventrale; 3, tuberculum dorsale = the insertion of m. supracoracoideus; 4, crista pectoralis; 5, crista bicipitalis; 6, accessory origin of m. biceps brachii; 7, insertion of m. scapulohumeralis caudalis; 8, fossa pneumatricipitalis; 9, origin of the dorsal head of m. humerotriceps; 10, incisura capitis; 11, intumescentia; 12, sulcus lig. transversus; 13, corpus humeri; 14, fossa m. brachialis; 15, condylus dorsalis; 16, condylus ventralis; 17, olecranon; 18, papillae remigiales caudalis; 19, margo caudales; 20, crista intercotylaris; 21, incisura radialis; 22, depressio m. brachialis; 23, labrum condyli; 24, condyles ventralis; 25, "dorsal tubercle"; 26, facies articularis ulnalis.

The head (caput humeri) is low in axial dimension and the caudal surface is somewhat flat. The single ventral fossa pneumatricipitalis is large and deeply excavated occupying almost the whole bicipital area. It is unclear whether there were any pneumatic openings in this fossa, as in modern swans, but this is unlikely given the very pachyostotic nature of the bone. The area beneath the head, the area of the origin of the dorsal head of m. humerotriceps, is also deeply excavated, very unlike modern swans. Incisura capitis is deep and connects smoothly to the depression for the origin of m. humerotriceps. Tuberculum dorsale, the insertion of m. supracoracoideus is low but significantly wide. In the cranial surface of the proximal end, crista pectralis doesn't slope up cranially, and is in an almost flat plane of Intumescentia. Sulcus lig. transversus is wide but relatively shallow.

The distal end of the humerus is narrow with the much reduced condylus dorsalis and ventralis. The cond. dorsalis is shorter and more rounded. Fossa m. brachialis is pronounced and more vertically oriented and situated closer to the ventral margin of the shaft.

This element is highly pachyostotic, with very thick cortical walls and a very small lumen. Measurement at the broken part of shaft shows the ratio of bone against the diameter is 57%.

Ulna—(Fig. 7-B, Pl. 4-C) The left ulna is complete but crushed badly, and the right one has preserved only the caudal surface mainly as a resin mold. What is highly unique on this element is its shortness: extremely shortened, being only about 57% of the length of the humerus, whereas in modern swans the forearm is nearly the same length as the humerus. The shaft is straight. The right one, though incomplete, shows the shaft to have been rounded in cross section. Totally 14 or so papillae remigiales caudalis are visible on the round margo caudales. Olecranon is low. The proximal articular surface is more angled, on the contrary more perpendicular in volant anatids. Crista intercotylaris is relatively developed. Incisura radialis is long and well developed. Depressio m. brachialis is not deep, but wide and elongate distally. On the distal end, labrum condyli caudally is pointed. Condyles ventralis is low but wide.

Radius—(Fig. 7-C, Pl. 4-B) The only remaining left bone is nearly complete but lacks the distal end. Together with ulna, this element is shortened.

The shape of this bone, definitely not entirely the result of crushing, is, authors believe, the oddest radius of any bird, and the articulated distal wing skeleton of this bird is the "strangest" bird wing.

The shaft is rounded in cross section for the proximal quarter. But then begins expanding distally until it becomes very broad and flat in the distal end. The proximal articulation is reduced, and the "dorsal tubercle" (no name in Nomina Anatomica Avium) in the proximal end, which is knob-like and very large in modern swans, is totally low and almost unrecognizable. Facies articularis ulnalis is strong and distally long. Sulcus tendinous in the distal portion of the dorsal surface is hard to find because of crushing. The distal termination is missing in the fossil, however the shape must have been oblique to the shaft axis with longer cranial margin than the caudal to form a reasonable wrist joint.

Radiale—(Fig. 8) This odd-shaped bone, huge for the body size, was first interpreted as a patella in previous reports, but appeared to be the left radiale. It is a very large, well-developed bone. The dorsoventral view of radiale shows an approximately equilateral triangular outline, which is significantly different from the normal morphology that is close to a quadrangle. The two sides of the triangle are the articular surfaces to radius and carpometacarpus, and the other side is the one to face cranially and acts as the "belt pulley" of m. ulnimetacarpalis ventralis. Articulation to the radius is quite distinct. Articulation to the carpometacarpus is flat and vast. Its large size accords with the huge development of the proximal end of the carpometacarpus. Because of its triangular shape, this bone acts as the "wedge", limits the wrist joint motion not to open straightly. The characteristics of the wrist joint will be discussed later.

Carpometacarpus—(Fig. 9-A, Pl. 4-D) The left bone is complete. This is an extraordinary element in being short, half the length of that of a volant swan, but with the proximal end extremely large with very well defined processes and articular surfaces demonstrating active use of this element and exhibiting no signs of "degeneration". The trochlea carpalis is very wide proximally, being as large or larger than in modern swans. The facies articularis ulnocarpalis is greatly expanded ventrally with a squared rather than rounded distal outline. The insertion of the m. ulnimetacarpalis ventralis on the dorsal surface of the proximal end of carpometacarpus has an abnormally large tubercular shape. The pisiform process bears a large and flattened surface, and at behind and below the fossa it is very deeply excavated. The proc. extensoorius of the alular metacarpal is low and more posteriorly directed. The interemetacarpal space is very narrow and the distal articulation is very reduced.

Phalanx proximalis digiti majoris—(Fig. 9-B, Pl. 4-E) This is another odd-shaped bone. It is a truly misshapen element that would barely be recognizable save for the well-developed proximal articular surface with the carpometacarpus. There is a deep excavated trough on what would normally be the dorsal surface, rotated into almost the caudal position. The abnormally deeply recessed dorsal surface of this bone can be understood as a structure to hold the primaries firmly for that purpose. The ventral surface is convex, with the cross section of mid-bone being C-shaped open dorsocaudally. There is an indistinct distal articular surface suggesting there may have been a small phalanx 2.

Pelvis and free caudal vertebrae—(Fig. 10, Pl. 5) Pelvis is almost complete in the holotype. The fossil is slightly flattened dorsoventrally, but after the compression is compensated, the overall profile is gently arched and convex dorsally with the anterior portion of ala preacetabulare ilii more expanded. A strikingly unusual feature on this bone is that the part of caudal vertebrae of synsacrum is short and the caudal termination of pelvis is recessed deeply in the middle, as the posterior ends of the posterior extension of the ilia are to extend posteriorly. Then the pelvis is short, especially at the postacetabular portion, and wide and crista iliaca dorsalis much less prominent than with a swan. The postacetabular portion of synsacrum in dorsal view is more depressed below to ala

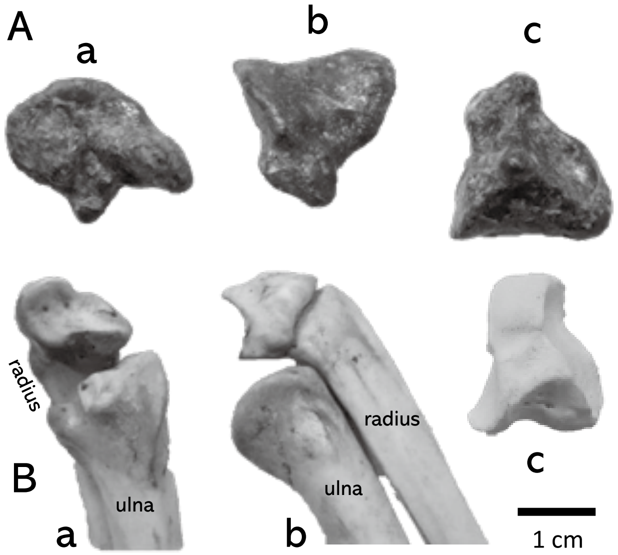

Figure 8. The left radiale (Os carpi radiale) of the holotype of *Annakacygna hajimei* (A) and radiale and surrounding bones of modern swans for comparison (B). Aa, the articular surface to carpometacarpus, dorsal to top; Ab, the dorsal view, cranial to top; the ventral view, caudal to top; Ba, same view to Aa, the articulated radiale, radius, and ulna of *Cygnus atratus*; Bb, same view to Ab, same specimen with Ba; Bc, same view to Ac, of *Cygnus olor*.

postacetabularis ilii. The series of synsacral vertebrae consists of totally 16 vertebrae, and includes three cranial-most vertebrae that have foveae costales. Intervertebral fenestrae are much larger than the ones in modern *Cygnus*. The foramen acetabuli is large and the margin of the acetabular is sharp. The antitrochanter faces somewhat cranially, and the caudal lip points dorsocaudally. The tuberculum praeacetabulare is low. The distal ends of the pubes flare out from the narrow shaft but are simply rounded at the end and do not become a large, expanded foot.

Three free caudal vertebrae have been found in the holotype. All of them are large and strongly developed, and it may be hard to believe that they are the caudal vertebrae of a bird. Both proc. dorsalis and proc. transversus are small and blunt, indicating their original position at the cranial portion among the series of free caudal vertebrae.

Femur—(Fig. 11-A; Pls. 6-C, 7-A) Both right and left bones are in the holotype, but the fossils are compressed and crushed so the detail of this element is obscured. Crista trochanteris is reduced, and then the external margin in the proximal view is narrow. The head is decidedly rounder and more distinctly set off from the rest of the bone. The scar for ligamentum teres (round ligament of femur) is deep and distinct. In lateral view, the trochanter is rounded, not like in *Cygnus* which is nearly square in outline. The shaft in lateral view appears curved, although crushing renders this less certain. The distal end is relatively narrow. The ridge-like anterior portion of condyles lateralis looks narrower in the fossil, but could be restored more inflated shape and extends anteriorly. Sulcus intercondylaris is crushed in fossil, but originally wide and deep. In the posterior view of the dirtal end, the lateral portion is much larger than condylus medialis. Condylus medialis is narrow and more vertically oriented. Trochlea fibularis is large, but crista tibiofibularis is shorter and not extending far posteriorly.

Tibiotarsus and fibula—(Fig. 11-B, C; Pls. 6-B and 7-B, C) Left tibiotarsus is complete and right tibiotarsus lacks the distal portion. On tibiotarsus, crista cnemialis cranialis is very different in shape from modern *Cygnus*: being broad and squared, extending proximally and less anteriorly. Crista cnemialis lateralis is small and more angled distally. In proximal view the articular surface is more squared, the internal cotyla not extending as far posteriorly. Crista fibularis is well developed. The insertion of m. popliteus is laterally small but strongly swells. The distal end comes medially. Sulcus extensoris is wide and deep. Pons supratendineus is relatively small. Canalis extensorius is oval in shape and relatively large for a swan. At the distal end, condylus lateralis and condylus medialis are laterally narrow, and incisura intercondylaris is much wider especially in distal view. Both condylus lateralis and condylus medialis are small, not extending as far anteriorly. Condylus lateralis in lateral view is incised proximally and so is less rounded in shape. This element is highly pachyostotic.

The fibulae were fossilized in, or nearly in, the articulated position with the tibiotarsi. In comparison with the tibiotarsus, the length of fibula is shorter than in modern swans. It is not because of the breakage of the distal tip. The distal tip is perfectly preserved in the fossil, especially in the left bone, and the shortness is because of less-ossification in its distal portion. The proximal portion of this bone is well developed. Caput fibulae is broad in lateral view. Sulcus for the accessory part of m. flexor perforatus digiti III is deeply impressed. Spina fibulae is short and robust.

Tarsometatarsus—(Fig. 11-D; Pls 6-A and 7-D) Left tarsometatarsus is complete, beautifully preserved with just slight deformation laterally compressed. On the fossil, the trochleae of the distal end look markedly laterally compressed and narrow and the intertrochlear notches are much narrower. But after the deformation correction, the distal end was wider laterally, and the proximal end is narrower than the distal end in total profile. Apart from the problem of diagenetic deformation,

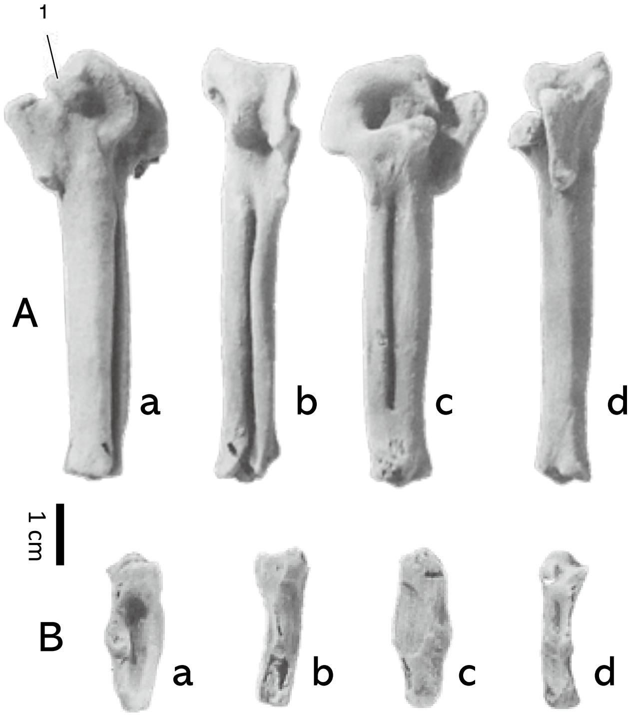

Figure 9. The left carpometacarpus (A) and phalanx proximalis digiti majoris (B) of the holotype of *Annakacygna hajimei*. Aa, dorsal; Ab. caudal; Ac, ventral: Ad, cranial; Ba, dorsal (slightly dorsocaudal); Bb, caudal; Bc, ventral (ventrocranial); Bd, cranial views. 1, the tubercle for the insertion of m. ulnimetacarpalis ventralis.

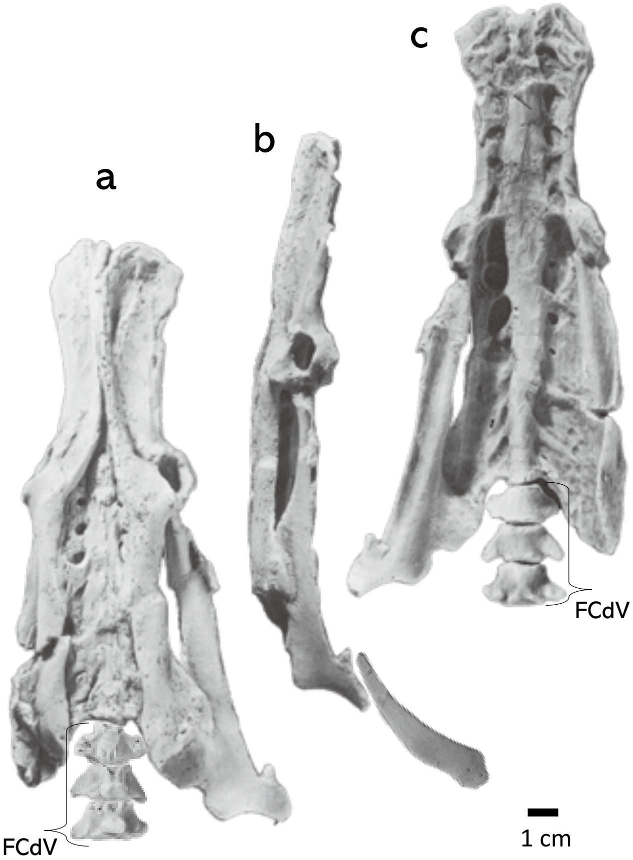

Figure 10. The pelvis and free caudal vertebrae (FCdV) of the holotype of *Annakacygna hajimei*. a, dorsal; b, lateral; c, ventral views.

originally, this element has a laterally narrow profile, and the cross section of the shaft is anteroposteriorly long. Facies dorsalis of the shaft angled medially, with the relatively distinct lateral margin. In the dorsoventral view of the proximal end, the medial rim of cotyla medialis is not angled sharply upward. The proximal articular surface is relatively narrow. The medial part of the hypotarsus extends farther posteriorly. The internal trochlea (IV) is elevated and retracted laterally relative to the middle trochlea (III).

Pedal phalanx— Only a single element is preserved. It appears to correspond to the left p. 1 of digit IV. It is smaller than the same element in *Cygnus* (*Olor*) *cygnus* and possibly narrower distally.

Comparison

The osteology of *Annakacygna hajimei* indicates that this bird belongs to tribe Cygnini as the large anatid possesses the diagnostic features such as the long neck and long pelvis with dorsally swelling ala postacetabularis illi. The wing, on the other hand, in which the distal elements (ulna, radius, and carpometacarpus) are obviously short for the body size, indicates that this was a flightless bird. In addition to the "short-winged" proportion, the "head-heavy" body was revealed after the careful preparation on skeletal elements. This is not a bird belonging any Cygnini genera previously described by Howard (1964, 1992); Louchart (2005); or Worthy (2008).

As reviewed in Watanabe and Matsuoka (2014), within Anatidae, flightlessness has evolved in several major lineages including Anserini, Cygnini, Anatini, and Mergini. The fossil species are: from the early Miocene, the oldest known flightless anatid, *Cayaoa bruneti* Tonni, 1979; *Megalodytes morejohni* Howard, 1992 from the middle Miocene of California; diverse forms of flightless anatids from Quaternary deposits of the Hawaiian Islands (*Chelychelynechen quassus* Olson and James, 1991; *Thambetochen xanion* Olson and James, 1991; *T. chauliodous* Olson and Wetmore, 1976; *Ptaiochen pau* Olson and James, 1991; *Branta rhuax* (Wetmore, 1943, formerly *Geochen* Wetmore, 1943), *B. hylobadistes* Olson and James, 1991; and *Talpanas lippa* Olson and James, 2009, in Iwaniuk, 2009); a possible flightless anatid from Rota, Mariana (Steadman, 1992), gigantic *Cygnus falconeri* Parker, 1865 from the Pleistocene of Malta, Mediterranean Sea; *Cnemiornis calcitrans* Owen, 1866 from the South Island of New Zealand;

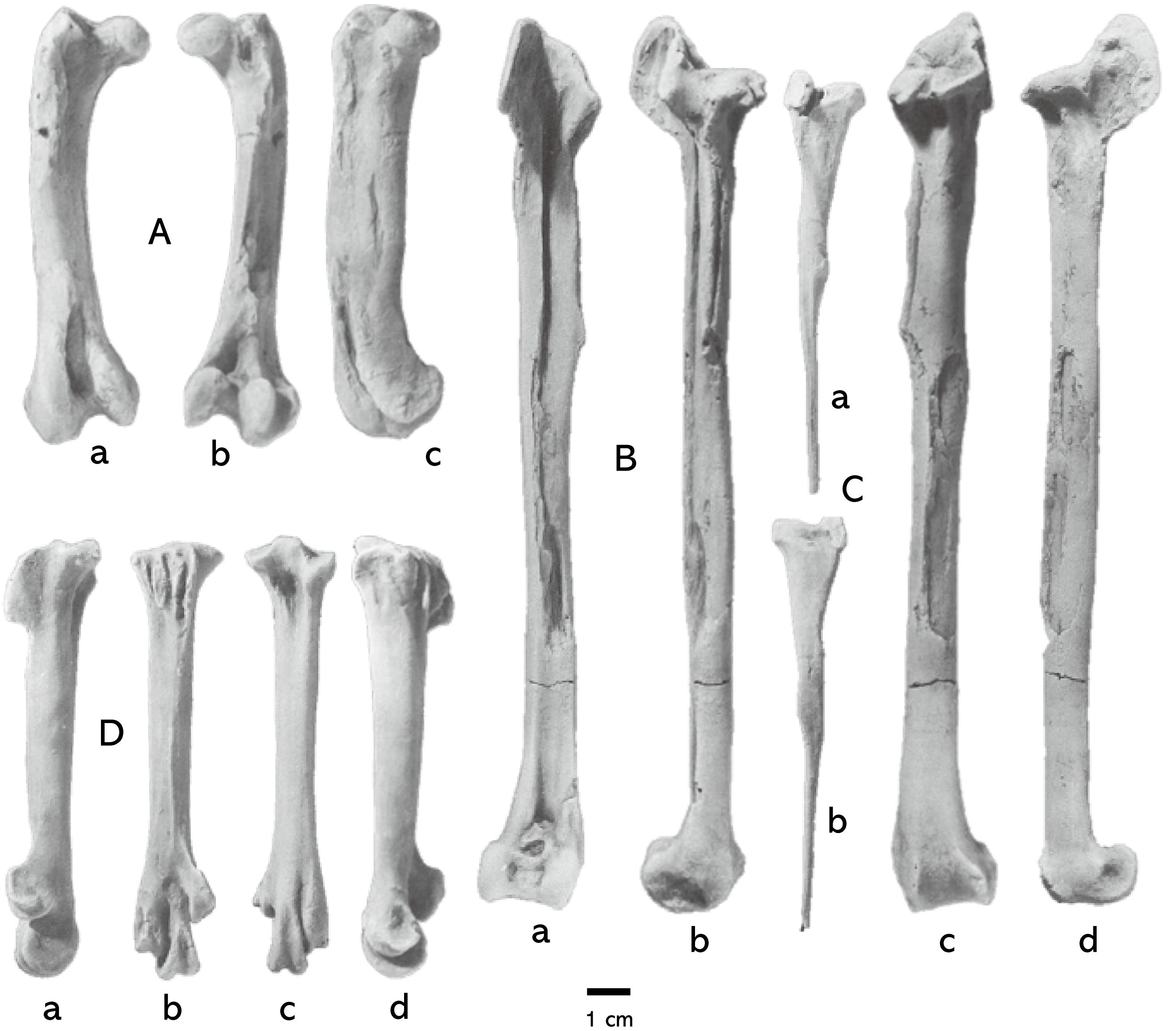

Figure 11. The right femur (A), the left tibiotarsus (B), the left fibula (C), and the left tarsometatarsus (D) of the holotype of *Annakacygna hajimei.* Aa, cranial; Ab, caudal: Ac, medial; Ba, cranial; Bb, lateral; Bc, caudal; Bd, medial; Ca, lateral; Cb, medial; Da, medial; Db, caudal; Dc, cranial; Dd, lateral views.

Cnemiornis gracilis Forbes, 1892 from the North Islands of New Zealand; *Chenonetta finschi* (van Beneden, 1875) (formerly *Euryanas* Oliver, 1930) from the Quaternary of New Zealand; the recently extinct *Mergus australis* from the Auckland Islands; a possible undescribed species of *Mergus* from Chatham Island (Millener, 1999); *Anas marecula* Olson and Jouventin, 1996 from the Holocene of Amsterdam Island, southern Indian Ocean; *Chendytes lawi* Miller, 1925 from the Pleistocene and Holocene of California to Oregon; *Chendytes milleri* Howard, 1955 from the lower Pleistocene of Channel Islands of California (Howard, 1955); and *Shiriyanetta hasegawai* from the Pleistocene of northern Japan (Watanabe and Matsuoka, 2014). Recent *Anas aucklandica* on Auckland Islands, *Anas nesiotis* on Campbell Island, and three steamer ducks (*Tachyeres leucocephalus*, *T. brachypterus*, and *T. pteneres*) distributed in South America are flightless.

In comparison to these flightless anatids, *Annakacygna* is a large Cygnini bird. As a possible Miocene marine Cygnini, the type specimen of *Annakacygna hajimei* was once classified as aff. *Megalodytes* sp. (Matsuoka et al., 2001, 2004). On *Megalodytes*, though Howard (1992) did not clearly state whether it was flightless, Matsuoka et al. (2001, 2004) asserted its flightlessness from humeral morphology. Louchart et al. (2005) and Worthy (2008) later suggested the exclusion of *Megalodytes* from Cygnini. During our research, Gunma Museum of Natural History obtained the replica of *Megalodytes* specimens from Los Angeles County Museum, and so we could examine them.

After the direct comparison of these two birds, we concluded that the two birds are clearly different, as follows. *Megalodytes morejohni* is, in comparison to *Annakacygna hajimei*: the tibiotarsus is much smaller at the proximal part of the shaft and flattened on the posterior face. Its shaft is about as wide as in *Annakacygna* although the bone is much shorter, so the proportions of the two are very different. The fibular crest is more prominent and there is a crest on the medial margin of the proximal end that is not present in *Annakacygna*. The medial condyle in medial view is much shorter than in *Annakacygna*. The femur of *Megalodytes* is smaller. The internal condyle is lower and not as extended posteriorly and is in lateral view rounded, not pointed as in *Annakacygna*. The bicipital crest of the humerus tapers into the shaft and is not squared as in *Annakacygna*. The pectoral crest is better developed, more parallel with the shaft, not tapering into the shaft as in *Annakacygna*. In medial view the distal edge of the ventral tubercle is closer to being perpendicular with the shaft as opposed to more angled in *Annakacygna*.

ANNAKACYGNA YOSHIIENSIS, sp. nov.

Holotype— GMNH-PV-1685 (Figure 12-A), the distal end of the right tibiotarsus, collected around 1995 by the late Mr. Toshimasa Moridaira.

Type Locality and the geologic horizon— Near Maniwa, Yoshii-machi, Takasaki City, Gumna Prefecture, Japan (Fig. 1-C-point 2). The river floor of the Kabura River, about 400 m down the river from the Tagobashi Bridge. 36° 16'9"N, 138° 59'44"E.

From the middle part of the Haraichi Formation, Annaka Group. Around 11.5 Ma (almost same as the horizon of the type locality of *A. hajimei*, but because of the existence of a fault near the locality, the exact horizon is unclear).

Measurements of Holotype— Width of the distal end of tibiotarsus (right), 27.8 mm. Depth of the distal end of tibiotarsus, 29.4 mm.

Etymology— After the name of type locality town, Yoshii-machi.

Diagnosis— The distal end of tibiotarsus is similar to *Annakacygna hajimei* in shape. It is in contrast much larger than the type species, about 1.3 times larger.

Description— The holotype is a single distal end of the right tibiotarsus. The fracture surface is fresh and sharp, and must

Figure 12. The holotype distal end of right tibiotarsus of *Annakacygna yoshiiensis* (A) and the corresponding part of *A. hajimei* (B). The B (*A. hajimei*) images are reversed from the photo of left bone, because right tibiotarsus lacks the distal portion in the holotype skeleton of *A. hajimei*, for viewers' convenience. For both A and B: a, cranial; b, medial; c, lateral; d, distal views. Ae, condition of pachyostosis.

have been longer and more complete in the strata. The fossil distal end comes medially from the center of the shaft. Though the anterior surface of the shaft is damaged, sulcus extensoris is wide and deep. Pons supratendineus is also damaged but seems originally incompletely ossified and small. Canalis extensorius is small and laterally a long rectangle in shape. Condylus lateralis and condyles medialis are laterally narrow, and incisura intercondylaris is wide and deep. Both condylus lateralis and condyles medialis are small, not extending as far anteriorly. Condylus lateralis in lateral view is incised proximally and so is less rounded in shape. Highly pachyostotic.

Note— Above-described characteristics are very similar to the same part of *Annakacygna hajimei*. However, the size differs significantly. The size difference of 1.3 times cannot to be considered intraspecific variation (Figure 13). Therefore, we establish a new species belonging to *Annakacygna*.

DISCUSSION

The unique musculoskeletal system of *Annakacygna*

Head

Though the cranial skeleton of *Annakacygna hajimei* lacks the beak portion in the holotype fossil, we can reconstruct the original shape of head based on the complete mandible (Plate 2) and then we can view its musculoskeletal system (Plate 8-9) and consider the eating habits of this bird. The holotype skeleton shows that the mandible was longer and robustly built compared with the trunk size, and the proportion of this bird was relatively "head-heavy" (Plate 1). In the lateral view, the lower mandible curves concavely to form a deep space in the middle. The proc. coronoideus of the lower mandible is located posteriorly, close to the quadratomandibular joint, and the dentary occupies a large portion on the entire mandible. The missing upper beak should have a correspondingly large, deep, and forward-spreading shape, and it is probable that the appearance must have resembled the skull of shovelers.

The places where the muscles involved in the opening and closing of the jaws attachment are also peculiar (Figure 14-15, Plate 8-9). The origin of the lower jaw depressor (m. depressor mandibulae) in the posterior portion of the neurocranium is enormous in size, and the left and right muscles meet at the midline to form a "pseudo-sagittal crest". There is probably no other bird like this. The posterior tip of the lower mandible is missing on both the left and right. But at least the base is deep and indicating the original posteriorly extended shape, and therefore we can recognize that the insertion of m. depressor mandibulae was developed significantly as a whole.

The lower jaw adductors (superficial mm. adductor mandibulae externus superficialis, externus medialis, externus profundus, and posterior, and deep mm. pseudotemporalis superficialis and profundus) originate from and insert on anteroposteriorly short areas. That means the assembly of lower jaw adductors are short anteroposteriorly, and, moreover, it has the characteristic that it is located almost in the vertical direction. Such musculoskeletal condition indicates that the jaw movement of *Annakacygna* was mainly a seesaw-like repetition of simple adduction (closing) and abduction (opening) of the quadratomandibular joint, with the antagonization of anteroposteriorly short lower jaw adductors and huge lower jaw depressor. Even in the same swan tribe, the appearance of *Annakacygna* jaw muscles is completely different from the one of ordinary swans that eat mainly plant materials by cutting fibers using the anteroposteriorly long lower jaw adductors and the action including the component of strong backward pulling. An example of a similar bird in Anatidae is shovelers.

However, the cranial skeleton of *Annakacygna* is very different from the one of shovelers in detail (Figures 14-15). The superficial m. adductor mandibulae externus superficialis portions are relatively small, and m. adductor mandibulae posterior and m. adductor mandibulae externus profundus are relatively large. These two relatively large muscles are the ones that originate from the lateral side of the quadrate, and then they are also the upper jaw retractors at the same time act as the lower jaw adductors. In the fossil, the origin of m. adductor mandibulae externus profundus on the lateral side of the quadrate is a strong impression, indicating that this muscle was truly developed. There is no doubt that as *Annakacygna* closed her mouth in the process of seesaw-like lower mandible actions, the upper beak retraction ("push-covering") worked well at the same time.

Now we can understand consistently the enigmatic features of the cranial skeleton of *Annakacygna*, such as: the unfused nasofrontal joint, the long and anteroposteriorly grooved structure for the quadrate glenoid on the lower mandible, and the unfused lacrimal bone, as, respectively, the reflection of the extremely high kinetic mobility of the upper beak (prokinesis), the receiving structure for the pendulum movement of the quadrate, and the mechanism that reduces the strong stress by lig. prefrontomandibulare that occurs at the pendulum movement of the quadrate.

All osteological features and the muscles reconstructed from them, and the resulting jaw movements and cranial kinesis, indicate that the bird was a highly adapted filter feeder. In the sense of functional morphology, its degree is much more advanced than shovelers. The oral side of stratum corneum of the upper and lower beaks probably were lined with soft and long lamellae. *Annakacygna* can be positioned as a phylogenetic branch that has shifted the food niche to a planktonic diet from the herbivorous diet that is common in ordinary swans.

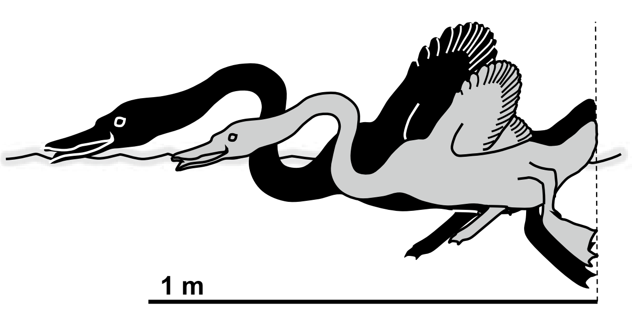

Figure 13. The image of size difference between *Annakacygna yoshiiensis* (black bird in back) and *A. hajimei* (grey one in front).

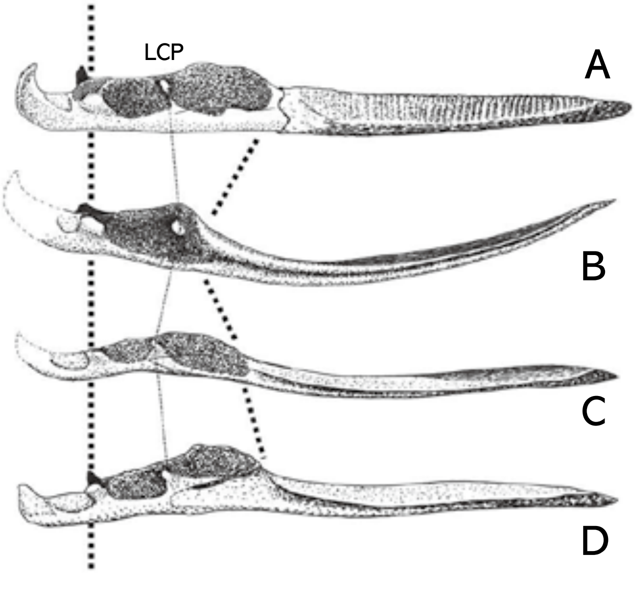

Figure 14. Comparison of the lateral view of lower mandible in some anatids. A, *Cygnus cygnus*, a modern swan; B, *Annakacygna hajimei*; C, "*Anas*" *clypeata*, a shoveler; D, *Anas platyrhynchos*, a common duck. Doted area is the insertion of lower jaw adductors. LCP, lateral coronoid process.

Ribs

Annakacygna has the unique feature that none of the uncinate processes of the ribs fuse to any costa vertebralis. This is strange for a bird. Since screamers, the most primitive lineage of Anseriformes, do not have ossified uncinate process on their ribs (Figure 16), a possibility that the unfused uncinate process of *Annakacygna* is a primitive character of Anseriformes may be presumed. However, in general, this can be understood as a neotenic evolutionary phenomenon that evolved from the volant ancestor whose uncinate processes were fused to ribs. It is probable that the demand for toughness of the thoracic cage weakened as the bird become flightlessness, resulting in such a loose state.

Pelvis and free caudal vertebrae

The pelvis of *Annakacygna* is short and wide as of a swan, somewhat looking like those of coscoroba swan and geese. It never seems like the one of long and narrow pelvis characteristic to foot-propelled diving birds. As noted below, however, the foot (tarsometatarsus) of *Annakacygna* is laterally narrow and reminds us of the foot-propelled habit of this marine bird. Then at a glance the characteristics of pelvis and tarsometatarsus are contradictory. But, the narrow tarsometatarsus, an evolutionary phenomenon to reduce water resistance, can occur independently, and the wide pelvis of *Annakacygna* should be understood as the adaptation to something else. We suppose it was the adaptation to stabilize the body in a wavy marine habitat.

A strikingly unusual feature on the pelvis is that part of the caudal vertebrae of synsacrum is short and the caudal termination of the pelvis is recessed deeply in the middle, as the posterior ends of the posterior extension of the ilia are to extend posteriorly. In addition, three free caudal vertebrae have been discovered, and all of them are large and well developed and it is hard to believe that they are the caudal vertebrae of a bird. With long and robust caudal vertebrae, the tail of *Annakacygna* might act strongly and be widely mobile. This view is supported by the deep caudal termination of the pubis, giving a wide area for the attaching tail depressors (mm. pubocaudalis externus et internus: Plate 10).

How did *Annakacygna* use such a strong, muscular tail? The answer can be obtained by considering it in combination with the following peculiar wings.

Wing

Flightlessness is not a rare evolutionary phenomenon in birds. *Annakacygna* is a flightless bird with distally small wings. The humerus is straight, and the forearm and hand elements (ulna, radius, and carpometacarpus) are significantly shorter than the size expected in volant species. *Annakacygna* was a bird characterized by the wings, especially in the distal portion, that were clearly miniaturized relative to the body. The full-body image was literally as it was named "Annaka Short-winged Swan".

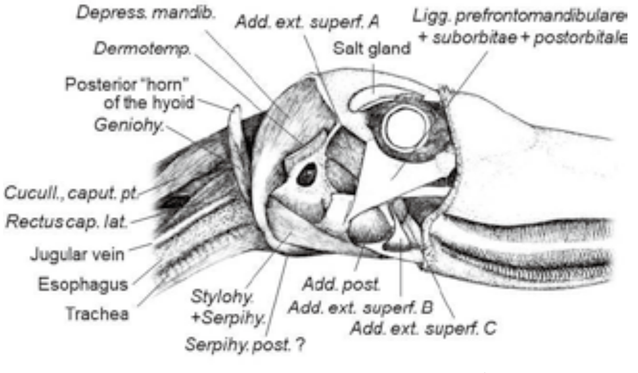

Figure 15. The reconstructed jaw muscles of *Annakacygna hajimei*. The image is reversed from the one in Plate 8.

In general, neoteny is considered as a key to explain the flightlessness in birds (e. g., Olson, 1973; Feduccia, 1999). On *Annakacygna*, the low carina sterni and the short distal wing elements seem to be possible examples of neotenic evolution at first glance. However, as discussed below, the wings of *Annakacygna* also have various characteristics that cannot be regarded as simple "degeneration". Also, an evidence of neoteny in flightless birds is the obtuse angle between the coracoid and the scapula (Olson, 1973), but in *Annakacygna*, this joint is probably reconstructed as an acute angle. In the pectoral and wing girdles, the form is not the product of simple neotenic evolution on this bird.

Again, *Annakacygna* is a flightless bird. The shape of shoulder and wrist joints and these prospected movements, however, are more highly developed and specialized than in volant birds.

We see the peculiar use of wings in this bird (Plate 10). First, we show the characteristics of the shoulder joint. In the humerus, to the very straight corpus humeri, the proximal end widens greatly to the dorsoventral direction. On the proximal end of humerus, the crista pectoralis, the insertion of m. pectoralis, is certainly short and degenerative, where the proximal end is constricted, but the other muscles (including m. supracoracoideus) are not degenerated as seen on m. pectoralis. The osteology suggests that *Annakacygna* could not fly, but the shoulder joint had high motility substantially equivalent to that of the flying species.

In addition, the proximal end of the humerus demonstrates the unique additional function of the shoulder joint. One factor in the widened contour of the proximal end of the humerus of

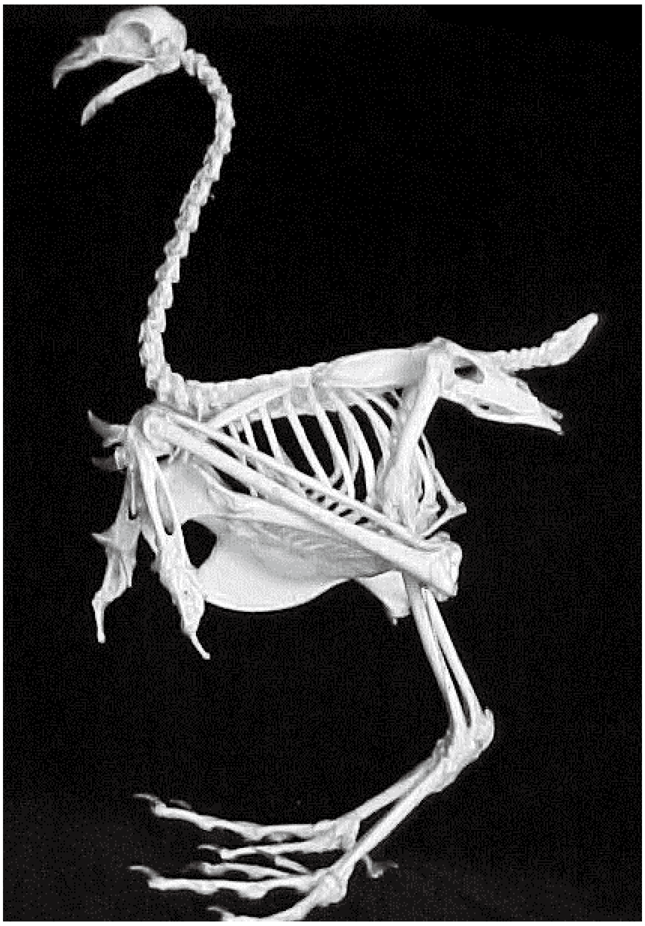

Figure 16. The skeleton of *Chauna torquata*, Southern Screamer (Anhimidae). The specimen is housed in Department of Geology and Mineralogy, Faculty of Science, Kyoto University.

Annakacygna is the presence of a well-developed tubercular muscle attachment point in the middle of the posterior margin of crista bicipitalis. This tubercule is the insertion of m. scapulohumeralis caudalis. In the wing musculoskeletal system of *Annakacygna*, m. scapulohumeralis caudalis was clearly more developed as it was larger than with volant species. The wide and thick blade of the scapula also shows this.

The function of m. scapulohumeralis caudalis is to raise the upper arm posteriorly (backward elevation) in the shoulder joint. M. subscapularis, another muscle act for the backward elevation of the humerus, is also developed in *Annakacygna* as the insertion on the tuberculum ventral of the humerus is large.

The backward elevation of the wing is a movement that does not occur very often in normal birds, and is performed momentarily when the wing is folded. Why did *Annakacygna* have the wing musculoskeletal structure that developed such a minor movement? The answer will be considered together with the following "strange" wrist joint.

The second enigma on the wing is the morphology of the wrist joint. The wrist joint of *Annakacygna* is arguably the strangest structure among all birds. The authors initially misidentified the gigantic os carpi radiale as the patella (Matsuoka et al., 2001; 2004). The radius was also a peculiar form that widens distally, but the authors also misjudged it formally as just broken and deformed due to diagenetic pressure and did not consider the functional morphology of this before. Correct identification and positioning of os carpi radiale and correct restoration of the radial morphology (Figure 8) revealed the highly unique characteristics of the distal wing of *Annakacygna*. The os carpi ulnare is missing in the fossil, but it is not important here because it does not contribute to the angle of the wrist joint.

The wrist joint has a form in which a triangular "wedge", that is the radiale, is driven into its radial part. Then even when the wings fully open, the wrist joint does not extend (radial flexion) straight and stops at a position of about 135 degrees, and with the same constraint, even when flexed (ulnar flexion), the wrist joint cannot fold the wings any more than at the position of about 60 degrees. Thus, it is considered that there is only about 75 degrees of wrist movement area (Figure 17).

One more strange thing about the wrist joint is the huge insertion of the m. ulnimetacarpalis ventralis. This muscle originates in the distal part of the ventral surface of the ulna, then becoming a strong tendon and appears on the dorsal side by passing the cranial surface of pulley-like os carpi radiale, and inserts on this point. The function of this muscle is the "hyperpronation" of the palm, which causes upward elevation of the primaries beyond the wrist joint. It seems no clear antagonistic muscle exists for this muscle, and the repositioning might be caused by the tension of the ligaments. It is certain that the "hyperpronation" of the hand was a routine movement for this animal, as the articular surface between os carpi radiale and carpometacarpus is very large and flat and is responsible for this movement.

The above noted three strange features: the upper arm adapted to backward elevation, the wrist joint that keeps the style of ulnar flexion, and the routine hyperpronation in the wrist joint, are enigmatic when seen individually. But, when we consider the three in combination, we can get a good view of how *Annakacygna* used her wings (Plate 10).

The backward elevation of the wings at the shoulder joint is, as pointed out above, an action that occurs momentarily when the wings are folded toward the body. The skeletal figure of Plate 1 depicts the state of the wing at this moment. At this moment, the elbow is raised high to the back, reaching anterior to the pelvis. Then the wrist comes to the side of the anterior end of the pelvis, and as the wrist joint is in a ulnar flexion state, the carpometacarpus and distal elements are in the position almost parallel to the femur.

This is nothing but the swan "piggyback" style. Among the modern swans, the three species belonging to subgenus *Cygnus* (mute swan, *Cygnus* (*Cygnus*) *olor*; black swan, *C.* (*C.*) *atratus*; and black-necked swan, *C.* (*C.*) *melanocoryphus*) have a habit of protecting chicks by piggybacking while on water. Also, unlike the whooper swan and the tundra swan (species of the subgenus *Olor*) that actively communicate by voice, these three species do not make much sound, and, for communication between couples, they make a visual appeal by active shaking of their wings folded on back.

Doesn't the piggyback design of *Annakacygna* wings and the musculoskeletal system reflect the behavioral pattern of subgenus *Cygnus*? Though strange and enigmatic wings, once viewed in the context of carrying chicks, it is clear that the wings act as a cradle for chicks. In that case, the muscular and highly mobile tail, mentioned above, would form the back wall of the cradle, with the added function of tail swinging for communication. It follows that hyperpronation of the wrist would indicate active shaking of primaries for display. Also, the abnormally deeply recessed dorsal surface of Phalanx proximalis digiti majoris can be understood as a structure to hold the primaries firmly for that purpose. All mysteries are thus solved.

Considering that the wings and musculoskeletal structure of this flightless bird are designed to protect offspring and provide means for visually display, we conclude that these structures do not indicate degeneration but rather development for these functions.

Foot

The tarsometatarsus of *Annakacygna* is laterally narrow and the cross-section of the shaft is ellipse anteroposteriorly long. If this bone was found alone, we would not be able to identify it correctly as of a swan.

The laterally narrow tarsometatarsus, found in loons and grebes, is an adaptive form that reduces water resistance during foot-propelled motion in water. *Annakacygna* might not have dived very deep, but it was certainly a sea dweller, and the shape of the tarsometatarsus must be an adaptation for aquatic life. Other evidence is that the tibiotarsus of *Annakacygna* has a well-developed crista cnemialis cranialis, which looks similar to that of albatrosses (large petrels) and sulid gannets and anhingas. It also means that the major knee extensors, mm. femorotibialis externus and medialis were developed.

The narrowness of the tarsometatarsus of *Annakacygna* is due to the degeneration of the foot extensor. The extensor digitorum longus, the main foot extensor running alongside the anterior surface of tarsometatarsus, of *Annakacygna* is quite different from the one of ordinary anatids: being wide and leaving a strong groove on bone to make the shape of the cross section of the tarsometatarsus shaft trapezoidal anteriorly wide in ordinary anatids, but in *Annakacygna* this muscle leave no clear traces. On the other hand, the insertion of the m. tibialis cranialis is

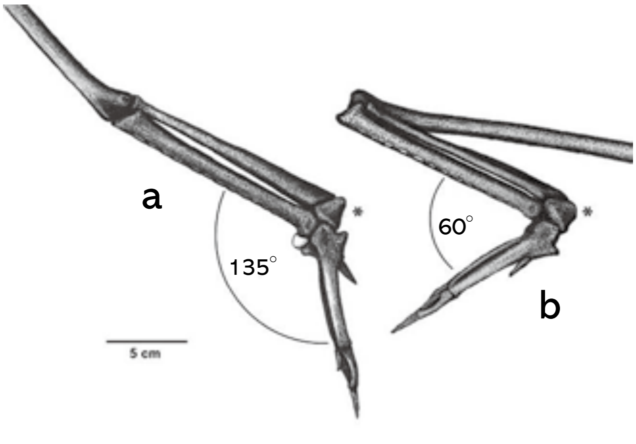

Figure 17. The wing actions in *Annakacygna hajimei*. Right wing. The fully extended (a) and completely folded (b) postures. Asterisk is the radiale.

wide and deep on the anterior surface of the proximal end of tarsometatarsus, and there was sufficient space in the incisura intercondylaris at the distal end of the tibiotarsus for its passage, so the dorsiflexion of the ankle joint was strong. In the life of *Annakacygna*, during her paddling in water, the webbed foot is passively folded with the dorsiflexion of the ankle. Then the foot extensor become degenerative, we hypothesize.

As opposed to the extensors, the strong hypotarsus tells us that the foot flexors were well developed. On the back of the shaft of the tarsometatarsus, there must be a thick flexor tendon and the skin covering it, and it is probable that the tarsometatarsus had an increasingly long oval cross section in life.

There are also differences from the evolutionary features of the skeleton of foot-propelled diving birds, loons and grebes, as proposed by Storer (1960, 1971). According to Storer, the femur becomes thicker and shorter in addition to the lateral narrowness of tarsometatarsus, but this does not occur in *Annakacygna*. The measurements in mm on the three hindlimb bones (one individual for each species, from KUGM osteological specimen), the greatest length of femur, the axal length of tibiotarsus, and the greatest length of tarsometatarsus of *Annakacygna hajimei*, *Cygnus* (*Olor*) *cygnus*, and *Cygnus* (*Cygnus*) *atratus* are, respectively, 99, 191, 112.5; 111, 196, 117; 82.5, 157, 94 (mm). To the all species, the ratio of each bone to the total of three bones are 24.6-26.1:46.0-46.2:27.6-28.1, having a nearly constant ratio.

Thick and short femurs (extension of the distal element among hindlimb elements) and slimming of the tarsometatarsus have been considered as set evolutionary phenomena, but *Annakacygna* indicates that the evolutionary features that reduce water resistance, narrowness of tarsometatarsus, can occur independently.

Pachyostosis

The skeletal elements of *Annakacygna* show remarkable pachyostosis, thickening of bones (see the X-ray images on Matsuoka et al., 2004). The Measurement at the broken part of shaft of humerus shows the ratio of bone against the diameter to be 57%, and other long bone elements, though not measured, also show a high degree of pachyostosis.

Pachyostosis is a phenomenon often seen in flightless diving birds and is generally understood to be an evolutionary phenomenon that makes the body heavier for easier diving. However, it is probable that *Annakacygna* did not dive. Since it developed a vigorous seesaw-type jaw movement and prokinesis of the upper beak, it is reasonable to think that it was foraging on the water surface as a filter feeder, and it was different from the ordinary swans who use their long necks to feed on plant materials under water. *Annakacygna* might no longer even put her neck in the water.

We hypothesize that the pachyostotic heavy body was probably to stabilize the body on rough seas. By making the waterline lower (of course not so low as to endanger piggybacking chicks) with the lower center of gravity this bird must have gained stability in choppy waters.

CONCLUDING REMARK

Two species of the genus *Annakacygna* are known: *A. hajimei* which is about the same size as the modern black swan (except for the large size of the head and wide and heavy body), and *A. yoshiiensis* which is a giant bird that is much larger than the modern mute swan and weighed a considerable amount considering its pachostotic bone. It is surprising that two such related "monster birds" that had evolved a highly unique morphology coexisted in one area.

The almost bizarre body characteristics of *Annakacygna* are thought to have been uniquely developed on this bird as autapomorphies. The peculiar wings and tail were specialized to protect the chicks riding on back and to confirm family bonds. It was an animal with a body plan that specialized in breeding behavior, or sex appeal in a broad sense.

Annakacygna was also an animal that uniquely developed filter feeding with its atypically large head. The Miocene sea of the future Annaka-Tomioka-Takasaki region of Gunma, Japan was inhabited by a rich diversity of animals including plant-eating sea turtles (Hasegawa et al., 2005). In the historical geology of the Japanese Archipelago, it was just the age when the diatomaceous hard shale of the Onnagawa Formation, an oil reservoir, was deposited widely in northeastern Japan. It should be remained that the time and place of *Annakacygna* diverged was just when and where the surface productivity of marine ecosystem increased significantly. *Annakacygna* swans may have adapted just to this spatiotemporal environment.

In a sense, *Annakacygna*, which had acquired remarkable evolutionary forms for the two biological imperatives, eating and reproduction, is the "ultimate bird" that ever existed.

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群馬県の中新統から産出した顕著なる無飛翔鳥２種を含むハクチョウ族（カモ科）の新属*Annakacygna*：特にその食性シフトと育雛のための翼の特殊化について

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要旨：群馬県の中新統，富岡－安中層群は豊富な脊椎動物化石を産することで知られる．本論文はここに1新属2新種の鳥類を加える．新属名は*Annakacygna*で，全身骨格（群馬県立自然史博物館標本GMNH-PV-678）をホロタイプとする模式種*A. hajimei*と，右脛足根骨遠位端（GMNH-PV-1685）をホロタイプとする*A. yoshiiensis*の２種である．共に安中群原市層（およそ11.5 Maの層準）から発見された．*Annakacygna hajimei*のホロタイプはこれまでアンナカコバネハクチョウと呼称してきたものである．*A. hajimei*は，大型かつ頸が長く，頸椎数が23と復元されること，またその長い骨盤は腸骨の後方進展部が背側に盛り上がっていることなどの骨学的特徴があり，ハクチョウ族の一員に同定される．一方で翼の要素をみると，尺骨・橈骨・手根中手骨といった遠位の要素が上腕骨に対して著しく短く，上腕骨はS字状の湾曲を失った直線的なもので，無飛翔性の種であることを示す．その翼にはさらに特異な筋骨格系上の特徴があって，第一に上腕骨を肩関節で背側に引き上げる姿勢（後方挙上）に適応しており，第二に，前腕－手根中手骨は翼を閉じたときも手首関節が曲がりきらない著しく特殊化した形態であった．これは親がヒナを背に乗せて運搬する生態に特殊化したものと考えられる．また頭部においては，現生のハクチョウ類とは大いに異なり，下顎の筋突起よりも前方の歯骨部分が後方部分よりも著しく大きく発達し，かつ湾曲している．このような嘴は水面での濾過食に適応した形態で，生時にはラメラ状の角板が並んでいたと考えられる．*Annakacygna*ほど著しい濾過食種のガンカモ類は化石・現生を問わずこれまで知られていない．生物としてのなすべき二つのこと，すなわち日々食い個体として生きながらえること，そして家族の絆を結び世代をつないで種の存続を図ること，その両面に，著しい進化形態を獲得している*Annakacygna*は，ある意味で究極の鳥として生物学上特記される存在であると考える．さらに，*Annakacygna*属には大きさが大きく異なる２種が知られた．２種は同一海域に共存していたと考えられ，原市層堆積当時の海洋の豊かな生産性を背景として放散したものであろう．

キーワード：中新世，安中層群，ハクチョウ族，無飛翔性鳥類，アンナカキグナ属

Explanation of Plates

Plate 1. The skeleton of *Annakacygna hajimei*.
In standing and wing folded posture. The white elements/parts were not found in the fossil.

Plate 2. The reconstructed skull and mandible of *Annakacygna hajimei*.
A, the dorsal view of the skull; B, the lateral view of articulated skull and mandible; C, the dorsal (the left half of the image) and ventral (the right half) of mandible.

Plate 3. The reconstructed scapula (A), coracoid (B), and sternum (C) of *Annakacygna hajimei*.
Aa, lateral; Ab, ventral, Ac, dorsal; B, ventral; Ca, lateral; Cb, ventral views.

Plate 4. The reconstructed humerus (A), radius (B), ulna (C), carpometacarpus (D), and phalanx proximalis digiti majoris (E) of *Annakacygna hajimei*.
All left side bones. Aa, cranial; Ab, caudal; Ba, dorsal; Bb, ventral; Bc, caudal; Ca, caudal; Cb, ventral; Da, dorsal; Db, caudal; Dc, ventral; Ea, dorsal; Eb, caudal; Ec, ventral views.

Plate 5. The reconstructed pelvis of *Annakacygna hajimei*.
a, dorsal; b, ventral views.

Plate 6. The lateral view of reconstructed tarsometatarsus (A), tibiotarsus + fibula (B), femur (C), and pelvis of *Annakacygna hajimei*.
All left side bones.

Plate 7. The reconstructed femur (A), tibiotarsus (B), fibula (C), and tarsometatarsus (D) of *Annakacygna hajimei*.
All left side bones. For all cases: a, cranial; b, caudal views.

Plate 8. The reconstructed musculoskeletal system of head of *Annakacygna hajimei* (A) and *Cygnus cygnus* (B) in comparison.
The B (*Cygnus*) image is from Matsuoka et al. (2007).

Plate 9. The jaw muscular system of *Annakacygna hajimei* (A) and *Cygnus cygnus* (B) in comparison.
In both A and B images, the upper is the moment when the mouth closed, and the lower is when the mouth opened wide.
Legend: 1- the places where the mouth closer muscles attach (both origins and insertions); 2- the lower jaw adductors (m. adductor mandibulae externus superficialis, m. adductor mandibulae externus medialis, m. pseudotemporalis superficialis, and m. pseudotemporalis profundus); 3- mouth closers that act as both lower jaw adductor and upper jaw retractors (m. adductor mandibulae posterior and m. adductor mandibulae externus profundus); 4- the upper jaw retractors (mm. pterygoideus dorsalis lateralis et medialis, mm. pterygoideus ventralis medialis et lateralis); 5- the sequential actions of the posterior swing of "quadrate pendulum" and resultant upper jaw retraction; 6- the lower jaw adduction; 7- the origins and insertions of the mouth opener muscles (the upper jaw protractors, m. protractor pterygoideus and m. protractor quadratus + the lower jaw depressor, m. depressor mandibulae); 8- the lower jaw depressor (m. depressor mandibulae); 9- upper jaw protractors (mm. protractor pterygoideus et quadratus); 10- the sequential actions of the anterior swing of "quadrate pendulum" and resultant upper jaw protraction; 11- the lower jaw depression; 12- lig. prefrontomandibulare which limits the distance between lacrimal and the lower mandible at the position of jaw joint. Because of the strong lig. prefrontomandibulare, the bottom of the quadrate slides on the articular facet when it swings as "pendulum", and the articular facet forms a longitudinal structure.

Plate 10. Some unique wing and tail muscles (1–8) and motion (A-C) in *Annakacygna hajimei*.
Legend: 1- the origin (1o) and insertion (1i) of m. pectoralis (removed); 2- the m. supracoracoideus; 3- the m. coracobrachialis caudalis; 4- the m. subscapularis; 5- the m. scapulohumeralis caudalis; 6- the m. ulnimetacarpalis ventralis; 7- the mm. pubocaudalis externus et internus; 8- m. levator caudae pars vertebralis. A- the backward elevation of humerus (wing); B- the "hyperpronation" of palm; C- the depression of tail; D- the raising of tail.

Plate 11. An image of *Annakacygna hajimei* in life.

Plate 1

Plate 2

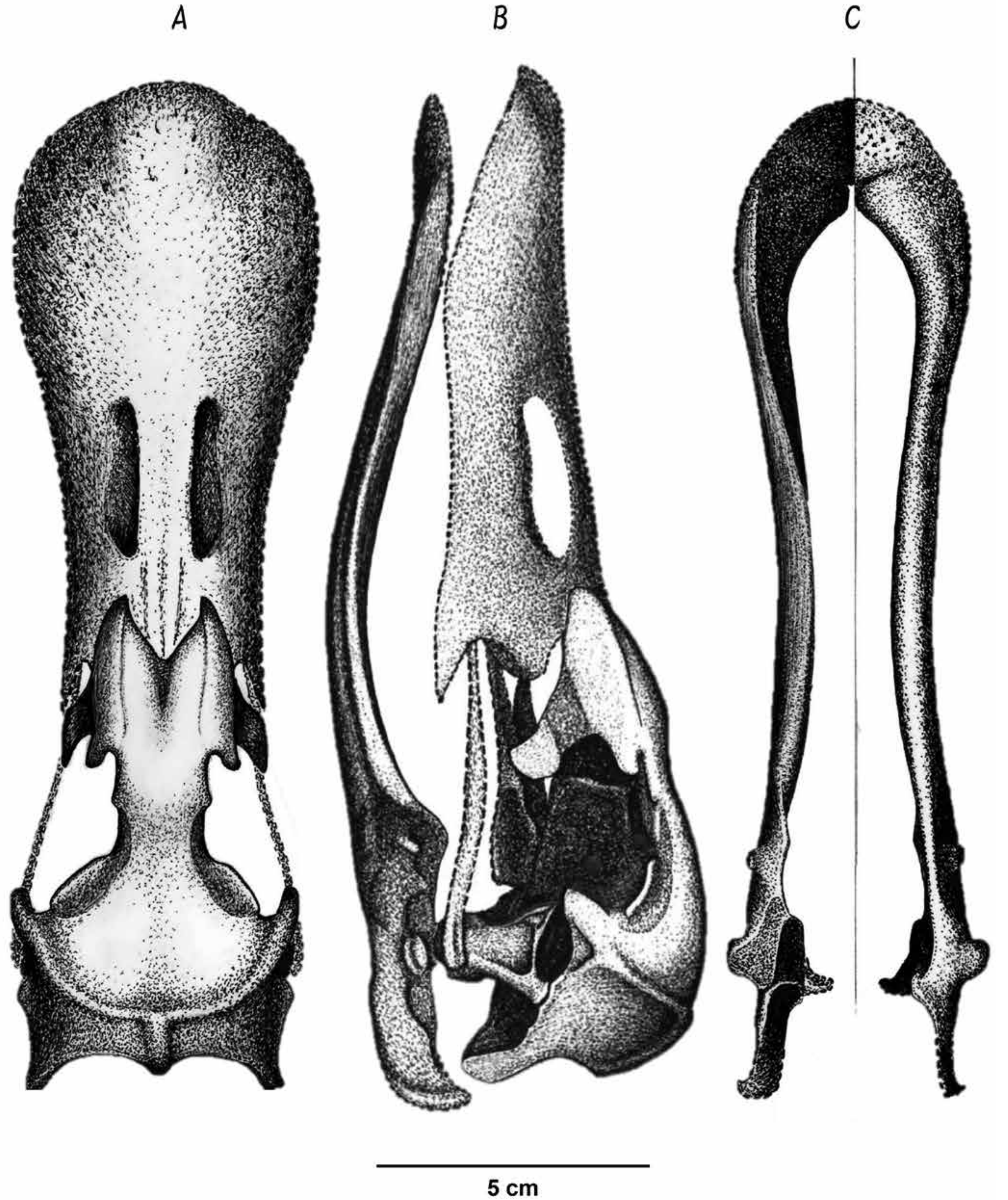


Plate 3

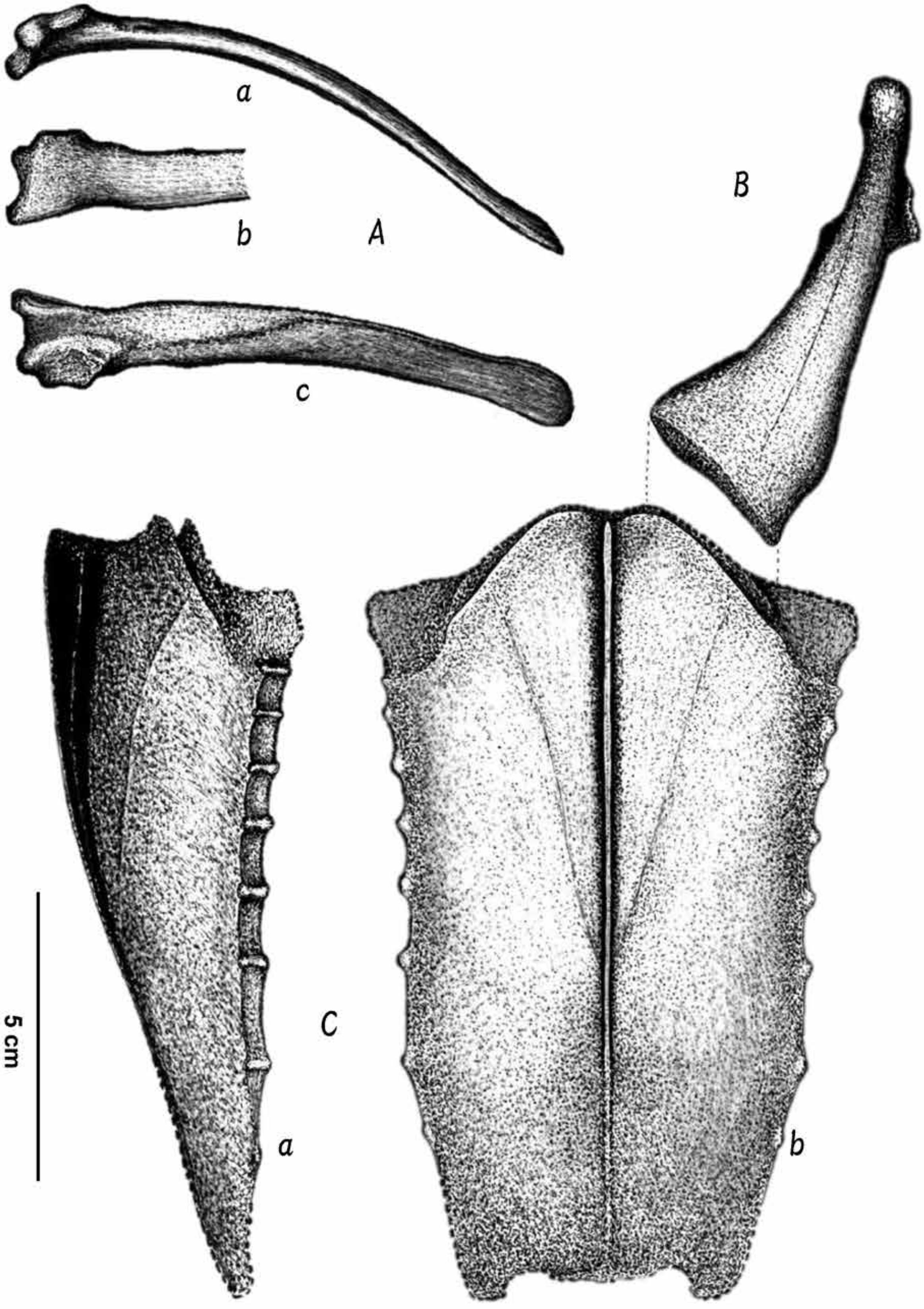
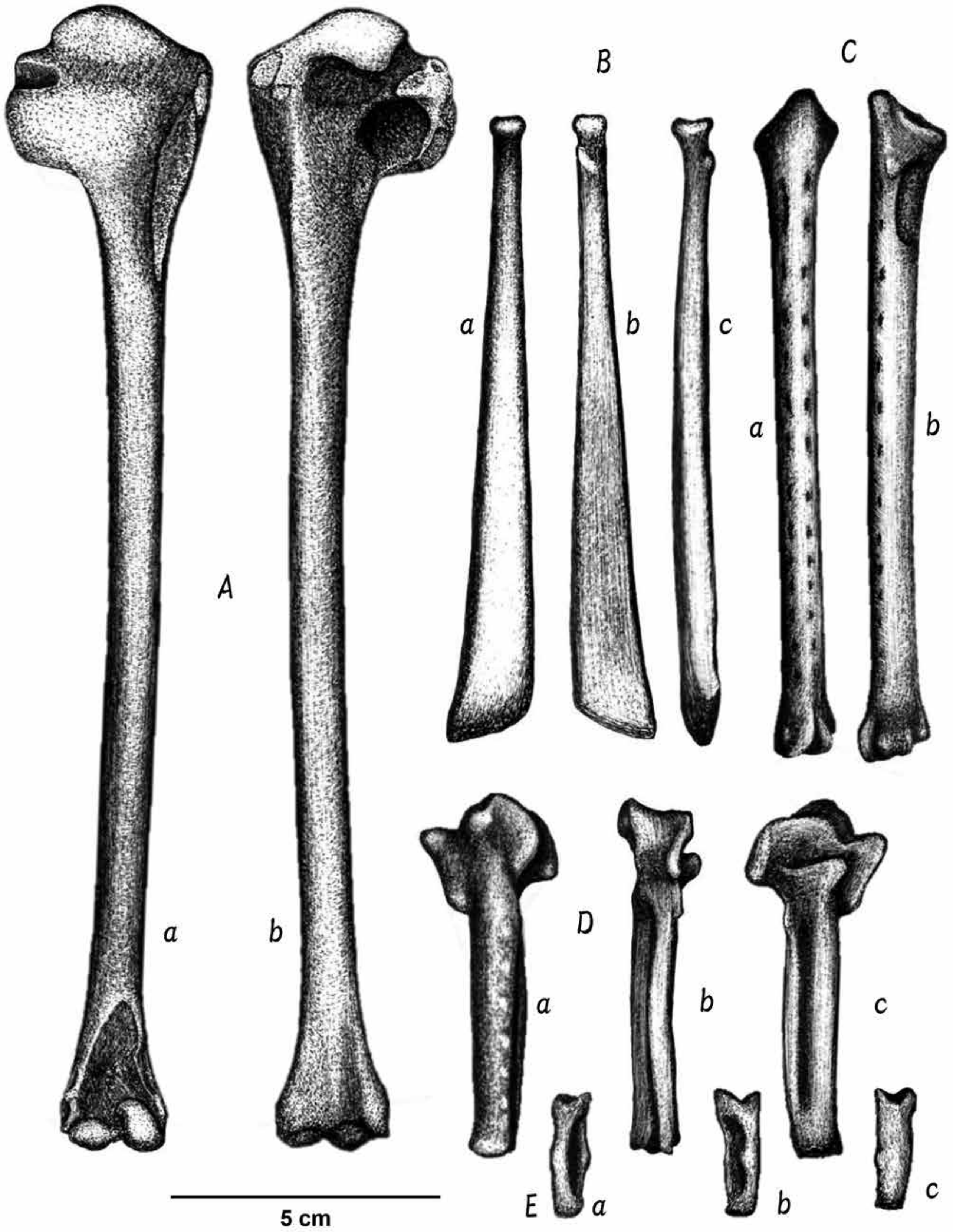


Plate 4



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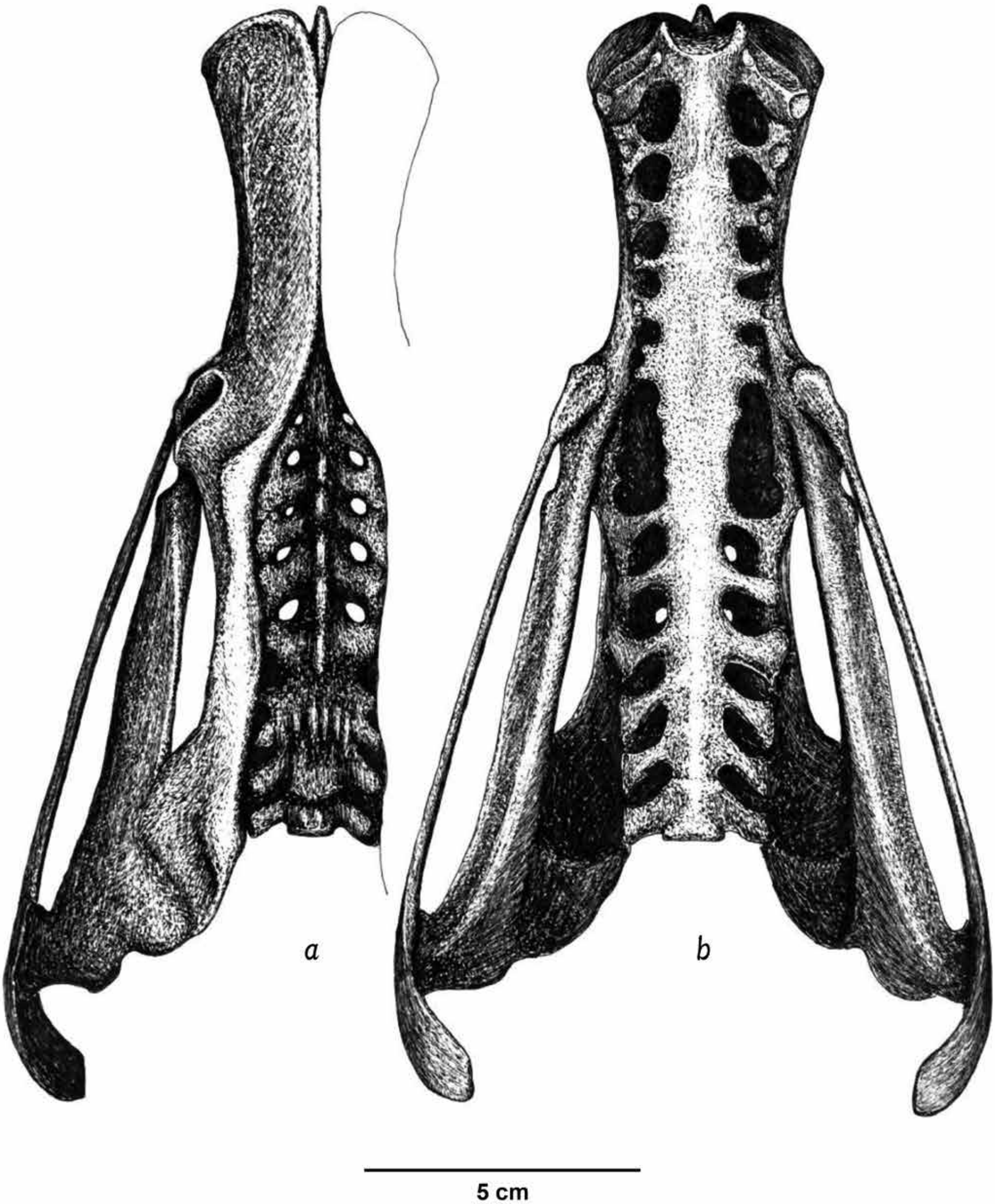

Plate 6

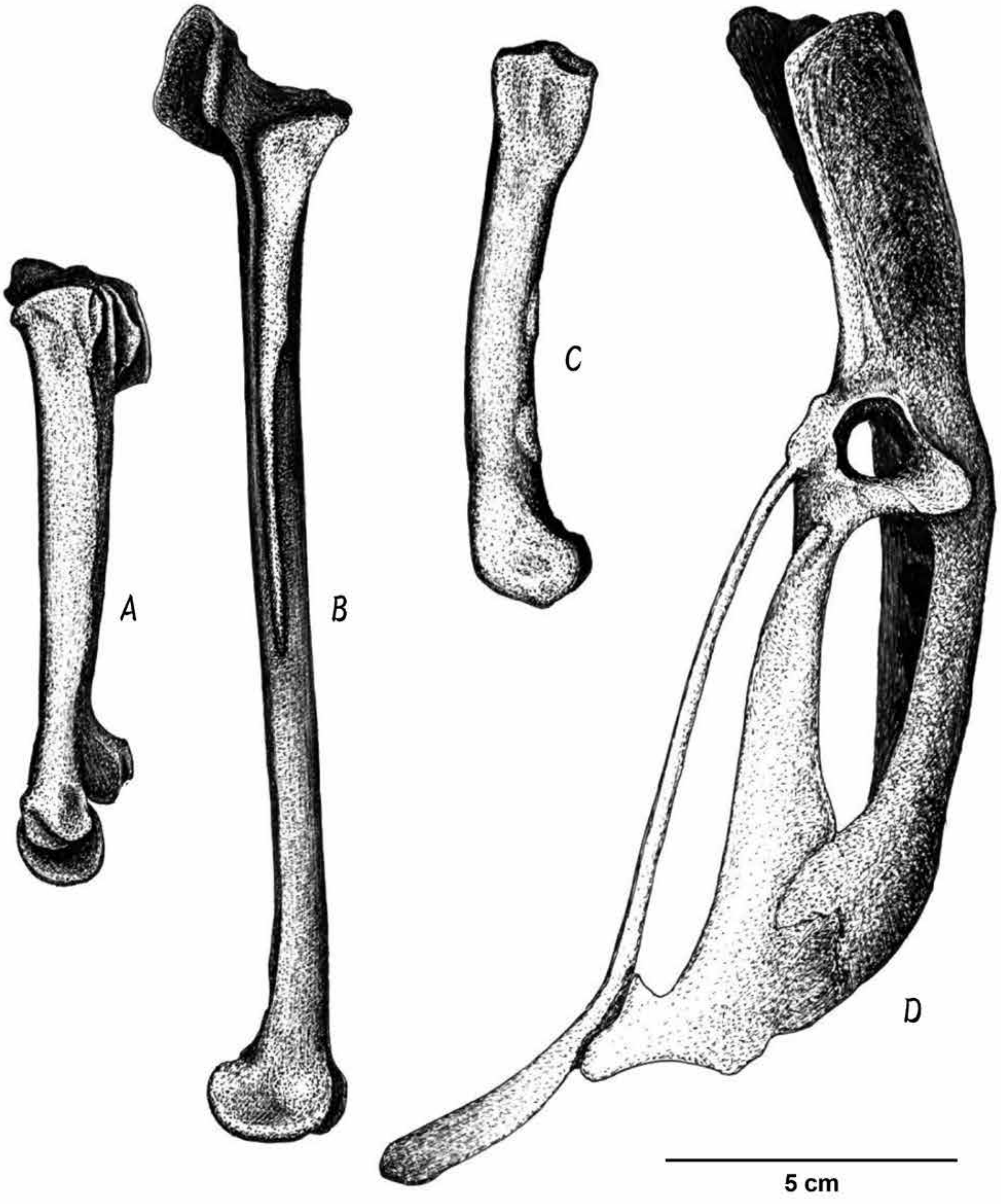

Plate 7

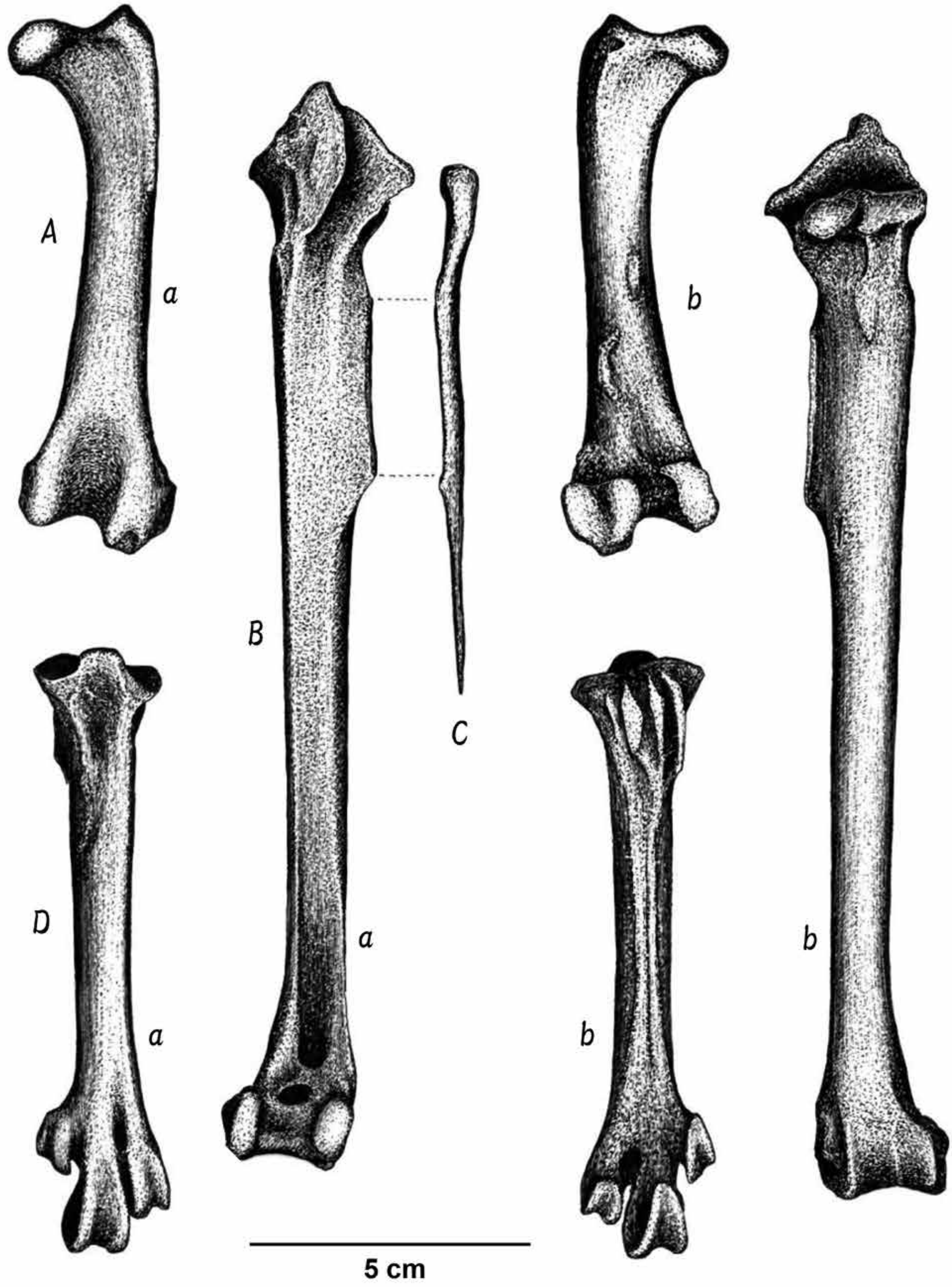

Plate 8

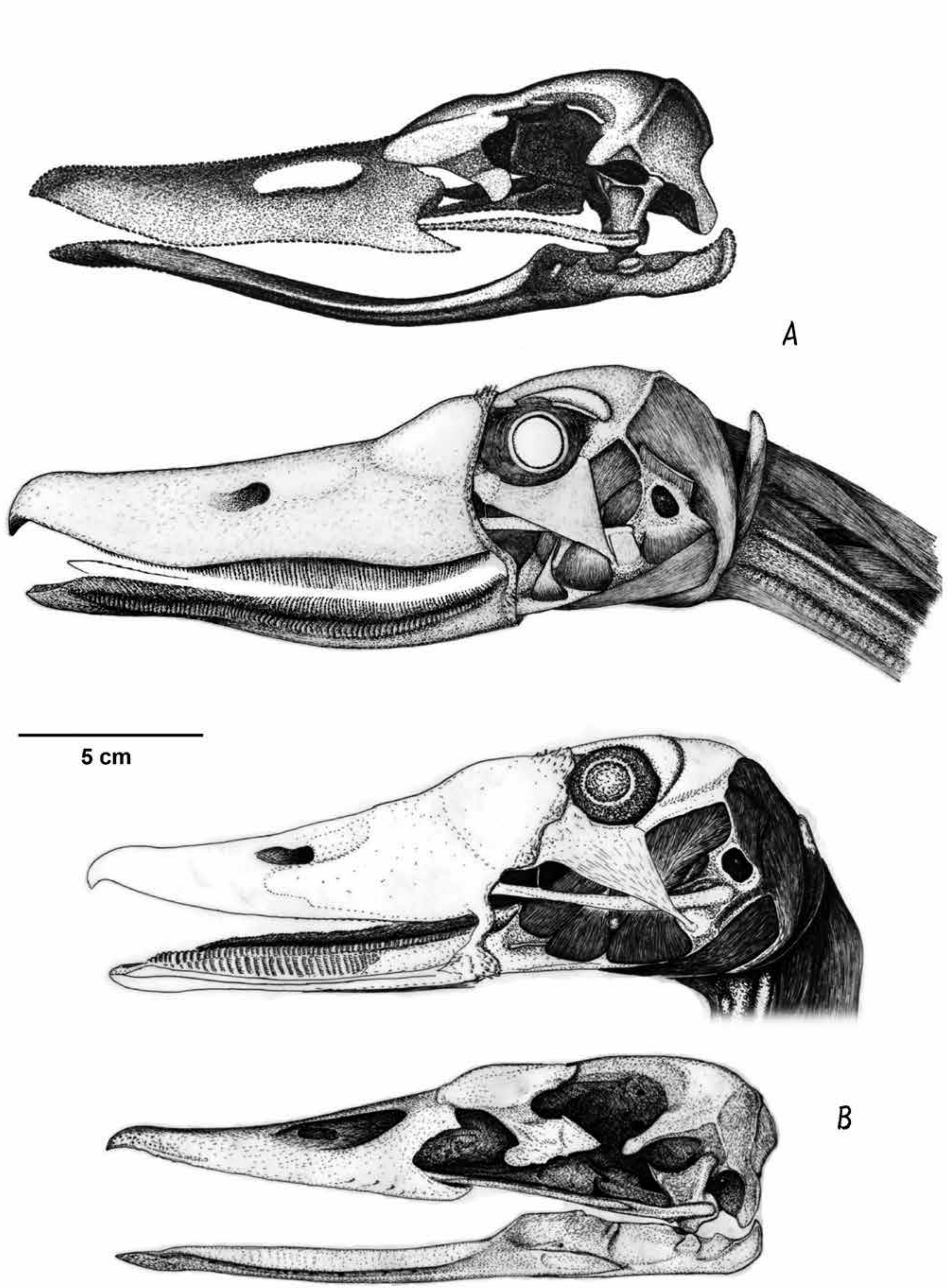

Plate 9

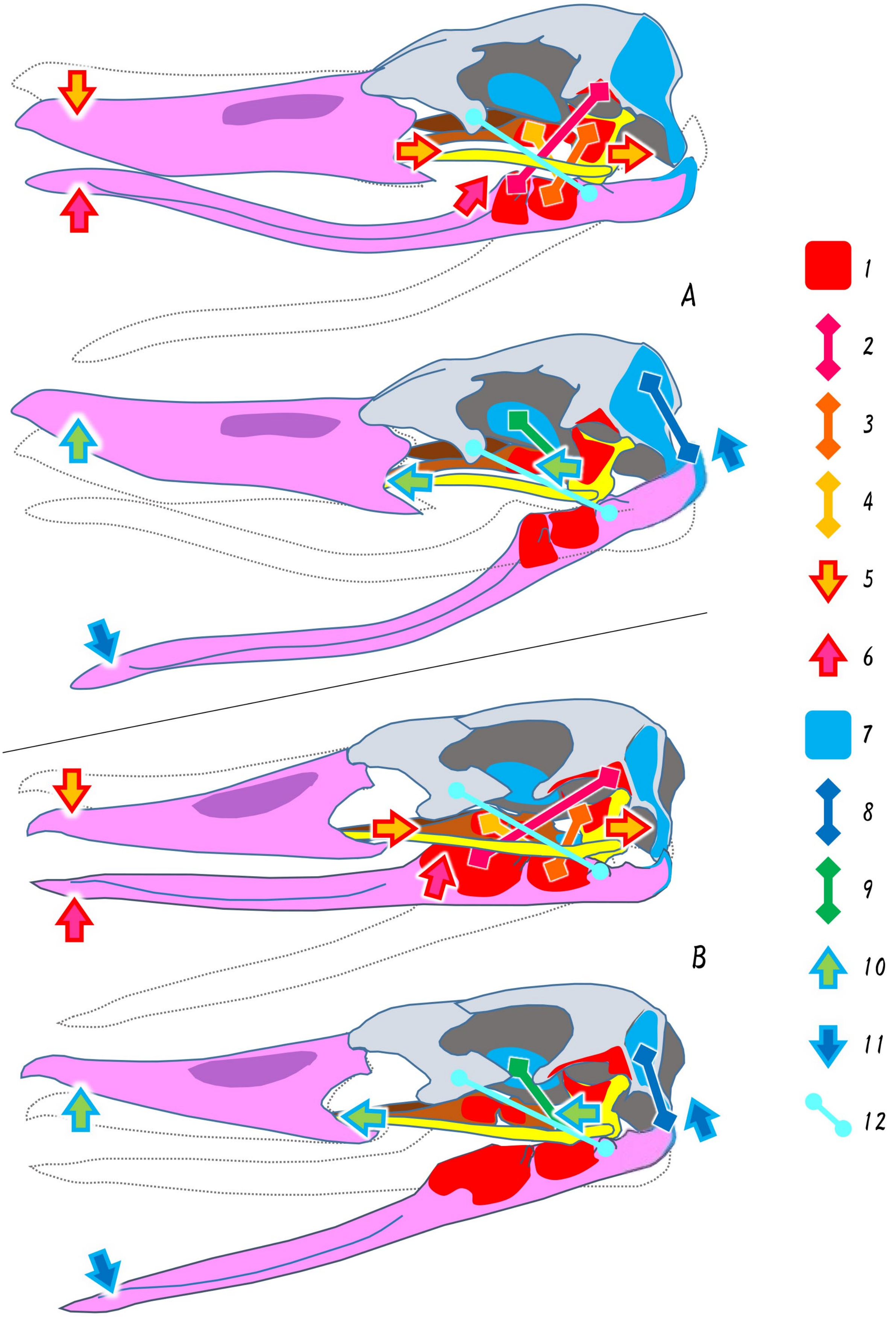

Plate 10

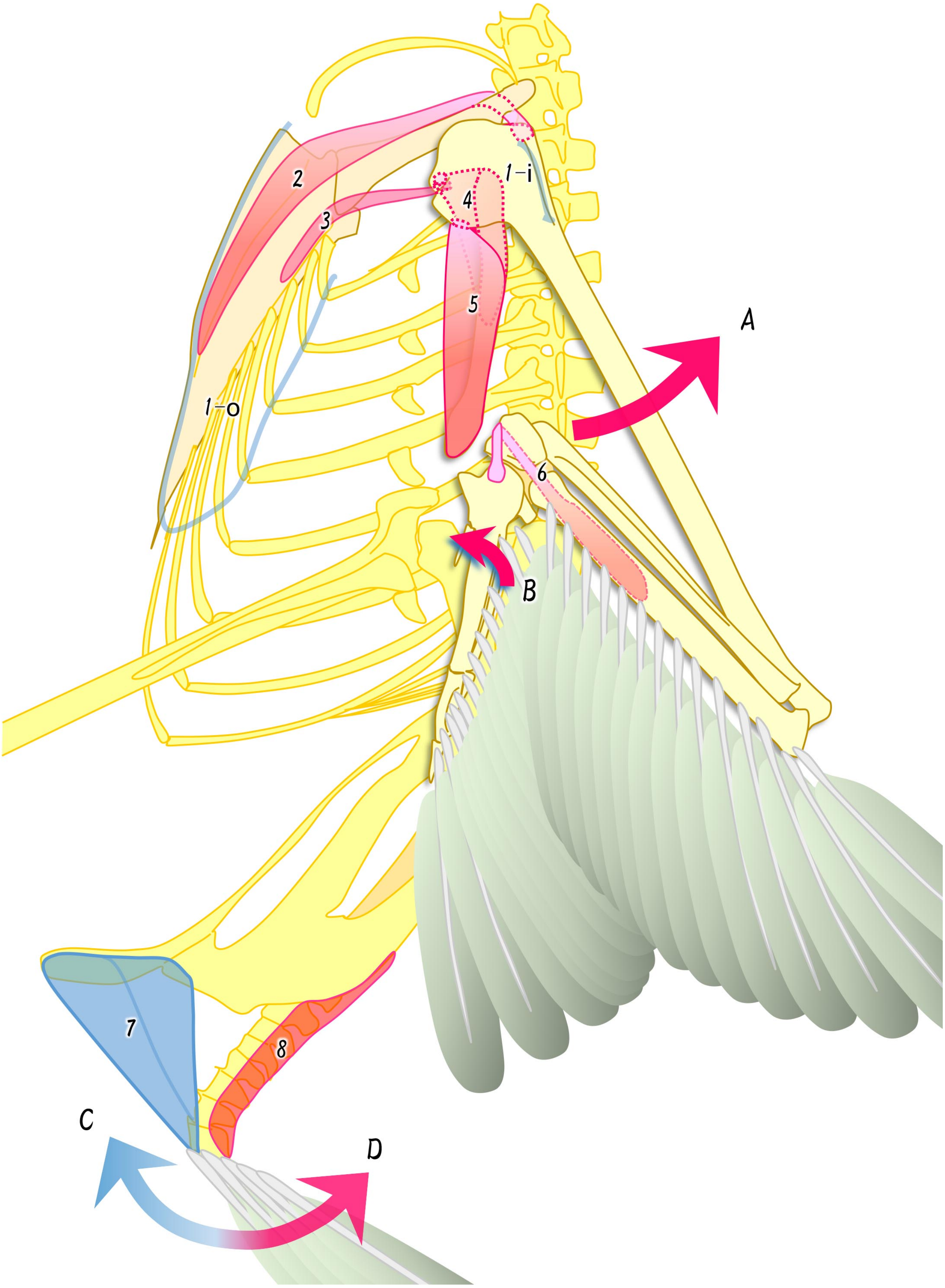

Plate 11