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## Original Article

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# Reexamination of the prepelvic vertebrae found in the holotype of *Annakacygna hajimei* (Aves, Anseriformes, Cygnini) revealed the adaptive morphology of vertebral column linked to the mode of life of the "ultimate bird"

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**Abstract:** *Annakacygna hajimei* is an extinct flightless bird described from the marine Miocene (11.5 Ma) of Annaka, Gunma, Japan. Totally 17 prepelvic vertebrae, 12 cervical and 5 free thoracic, included in the holotype of *A. hajimei* were reexamined here. As a result, the number of cervical vertebrae of *Annakacygna* in life totaled 23, and provides a strong reason to identify this genus as a member of Cygnini. The body length (bill-to-tail length) of *A. hajimei* was reconstructed to about 150 cm. The original description estimated that *A. hajimei* was about the same length as the black swan (120-130 cm), but this must be corrected. As a result of this simple calculation *A. yoshiiensis* was found to be a giant bird with a total body length of nearly 2 meters.

Morphological examination of the prepelvic vertebrae of *Annakacygna* revealed that the neck of this bird had a unique curve at its base, with a strong kyphosis at the cervical-thoracic boundary (CTB). Because of this kyphotic curve, the clavicular air sac at the base of the neck and the cervical air sac developed in and around the cervical vertebrae may be pushed ventrally below the water surface when the bird was on water. This "floating ring" found at the base of the bird's neck acts as the fulcrum on the body axis to give the buoyancy and stability to the bird's body when on the water surface. The thoracic vertebral column is regarded as a flexible "suspension bridge" that absorbed the weight of the chicks on the back. One of the diagnostic features of *Annakacygna*, "ribs with unfused uncinate processes", was interpreted as an adaptation that ensured flexibility of the entire ribcage. *Annakacygna* is a good example of "kin selection". We wholeheartedly agree with the recognition of *Annakacygna* as the "ultimate birds" to have ever existed.

**Key Words:** *Annakacygna*, Miocene, Annaka Group, flightless bird, Anatidae, Cygnini, prepelvic vertebra

## INTRODUCTION

*Annakacygna* described by Matsuoka and Hasegawa (2022) as a member of Cygnini (swans), are extinct flightless large birds found in the marine Miocene Haraichi Formation (11.5 Ma) of Annaka Group of the Annaka City, Gunma Prefecture, Japan. The genus *Annakacygna* includes two species: the type species *A. hajimei* and the larger second species *A. yoshiiensis*. The holotype of the type species (GMNH-PV-678, Gunma Museum of Natural History: **Fig. 1**) is a nearly complete associated skeleton (Matsuoka et al., 2001; 2002; 2004; 2022). A great advantage of this holotype under the scope of biological research is that the skeletal elements retain well their three-dimensional morphology and making it possible to see the musculoskeletal system of this bird in detail. In the original description (Matsuoka and Hasegawa, 2022), two unique features of this birds, one about the skull showing the food niche shift to filter-feeding and the other on the wings suggesting a specially adapted musculoskeletal system for the piggyback style, in which chicks must have been transported, and courtship behavior, were revealed. In the sense of biology, the authors think, the two most important roles of a living organism are to survive as individuals through daily feeding and to ensure the survival of the species by forming family bonds and ensuring future generations. In that sense, *Annakacygna* which had acquired remarkable evolutionary forms for these two biological imperatives, eating and reproduction, are the "ultimate birds" that ever existed (Matsuoka and Hasegawa, 2022; Asher, 2022).

As the evidence of vertebral elements, the holotype of *A. hajimei* includes 12 cervical vertebrae, 5 free thoracic vertebrae, synsacrum (pelvis), and 3 free caudal vertebrae (Matsuoka and Hasegawa, 2022). Of these, the pelvis and free caudal vertebrae were described and discussed relatively in detail, and 12 cervical vertebrae (CV) were identified as: the 3rd to 5th and 15th to 23rd (last) ones, and 5 thoracic vertebrae (TV) as the 1st, 2nd, and 5th to



**20 cm**

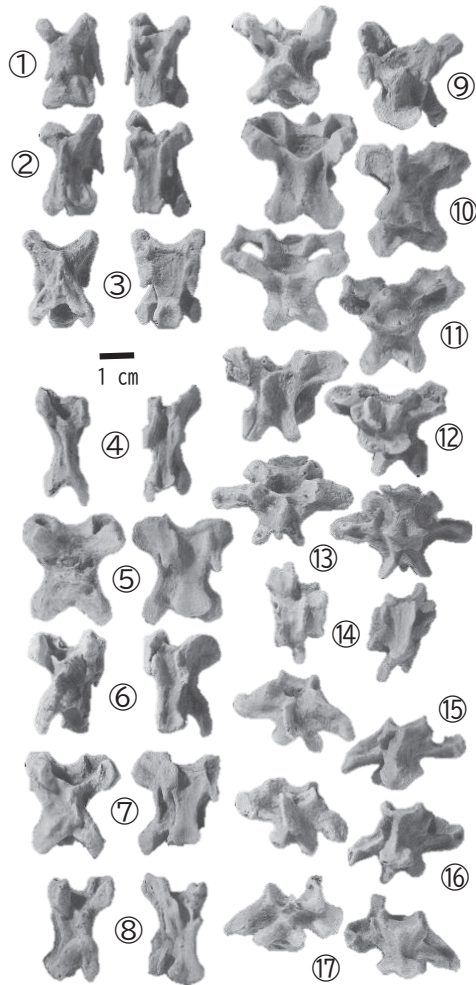Figure 1. The mode of fossil occurrences of the type specimen of *Annakacygna hajimei*.

Figure 2. The 17 prepelvic vertebral fossils belonging to the holotype of *Annakacygna hajimei*. The number (x) in circle mean the tNo.x of this study. Figure is reused from the **Fig. 4** of Matsuoka and Hasegawa (2022).

7th (last) ones in the original description. On the thoracic vertebrae, the authors assumed two missing thoracic vertebrae in between the 2nd and 5th ones because the ventral process of the 2nd thoracic vertebra is vast and requires (at least) two more thoracic vertebrae caudals to the 2nd TV to form a reasonable slope for the ventral process line. Based on the gradual change of morphology of totally eleven contiguous vertebrae, nine cervical and two thoracic vertebrae, and the size gap between the anterior three cervical vertebrae, Matsuoka and Hasegawa (2022) determined that the neck of *Annakacygna* was considerably long, and, based on this long neck and the morphology of pelvis, they placed *Annakacygna* as a member of Cygnini, the tribe of swans.

So, in both taxonomical and ecological viewpoints, the vertebral elements are important to understand the nature of *Annakacygna*. The description of the skeletal elements of *Annakacygna* by Matsuoka and Hasegawa (2022), however, was not detailed regarding the prepelvic vertebrae (cervical and free thoracic vertebrae). For the cervical and free thoracic vertebrae, only the identified position and short remarks on each vertebra in comparison with the corresponding position of *Cygnus atratus* were noted. The reason of such limited work was the heavily deformed condition of the vertebral fossils, that prevent detailed morphological study.

HM and YH are concerned that such scantiness of description of the prepelvic vertebrae may cast doubt on the phylogenetic position. In addition, the vertebral column is the literal principal axis in a vertebrate and so the morphology of vertebrae is

expected to be linked to the posture and lifestyle of the animal. Especially, in the case of *Annakacygna*, the neck and back, and body position supported by prepelvic vertebrae, are the parts by which the uniquely large head (the feeding organ) and trunk-hip (the chick carriage organ) are connected.

In birds, the prepelvic vertebrae are the skeletal elements significantly pneumatic and of lightweight structure. In the holotype of *Annakacygna hajimei* these are seriously deformed by the compaction of the host rock. In this study, we reexamine the prepelvic vertebrae of *Annakacygna hajimei* by decompacting them. After we show the result on the phylogeny of *Annakacygna* and the true position of each vertebral fossils, and we reconstruct the original form of the vertebral column and discuss the functional morphology of this unique bird. This study will contribute greatly to the elucidation of the whole-body movements of the "ultimate birds".

## SCOPE OF THIS STUDY

Through the description of each reconstructed vertebra and the articulated state, we aim to show the biological features and importance of the vertebral column in *Annakacygna* birds. The following two main themes will be discussed.

### 1- The vertebral column and phylogeny of *Annakacygna*:

The vertebral column of bird can, though the number of cervical and thoracic vertebrae vary from taxa to taxa (e.g., Samejima and Otsuka, 1984; Böhmer et al., 2019), commonly be divided into anterior, main, posterior, and basal cervical vertebrae and thoracic vertebrae based on the characteristics of each vertebra (**Fig. 4, 5**). This fact indicates a common functional constraint on the entire neck in birds (e.g., Leeuw et al., 2001; Kaiser, 2007). In fact, there is no known synapomorphy on vertebral morphology that can be attributed to a specific taxon in Anatidae (Woolfenden, 1961).

In the case of *Annakacygna hajimei*, a considerable number of prepelvic vertebrae continuous from the posterior neck to the thoracic vertebrae are included in the holotype. Then by using the cervical-thoracic vertebral boundary (CTB) point as a key, homologous morphological comparisons can be made. Because the number of cervical vertebrae is linked to the phylogeny (tribe) in Anatidae (Woolfenden, 1961), qualitative morphology and metric comparisons will be carried out to determine the missing part of vertebral column and the phylogeny of *Annakacygna* will be discussed.

### 2- Functional morphology of the prepelvic vertebral column in *Annakacygna*:

Based on the results, the vertebral column of *Annakacygna* is depicted and its functional characteristics will be discussed.
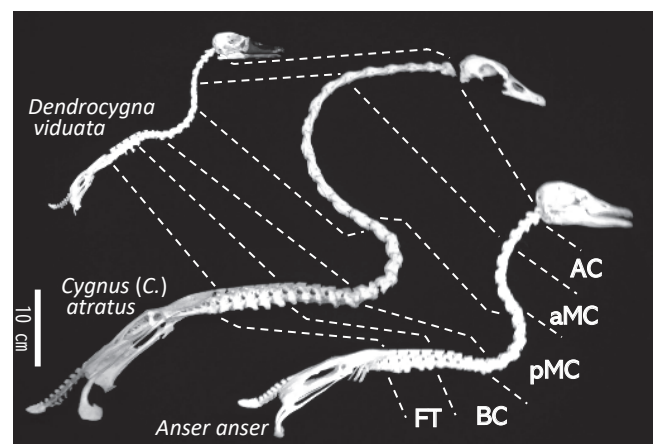


Figure 3. Subdivision of the prepelvic vertebrae in this study. From cranial to caudal: AC, anterior cervical vertebrae; aMC, anterior main cervical vertebrae; pMC, posterior cervical vertebrae; BC, basal cervical vertebrae; FT, free thoracic vertebrae.
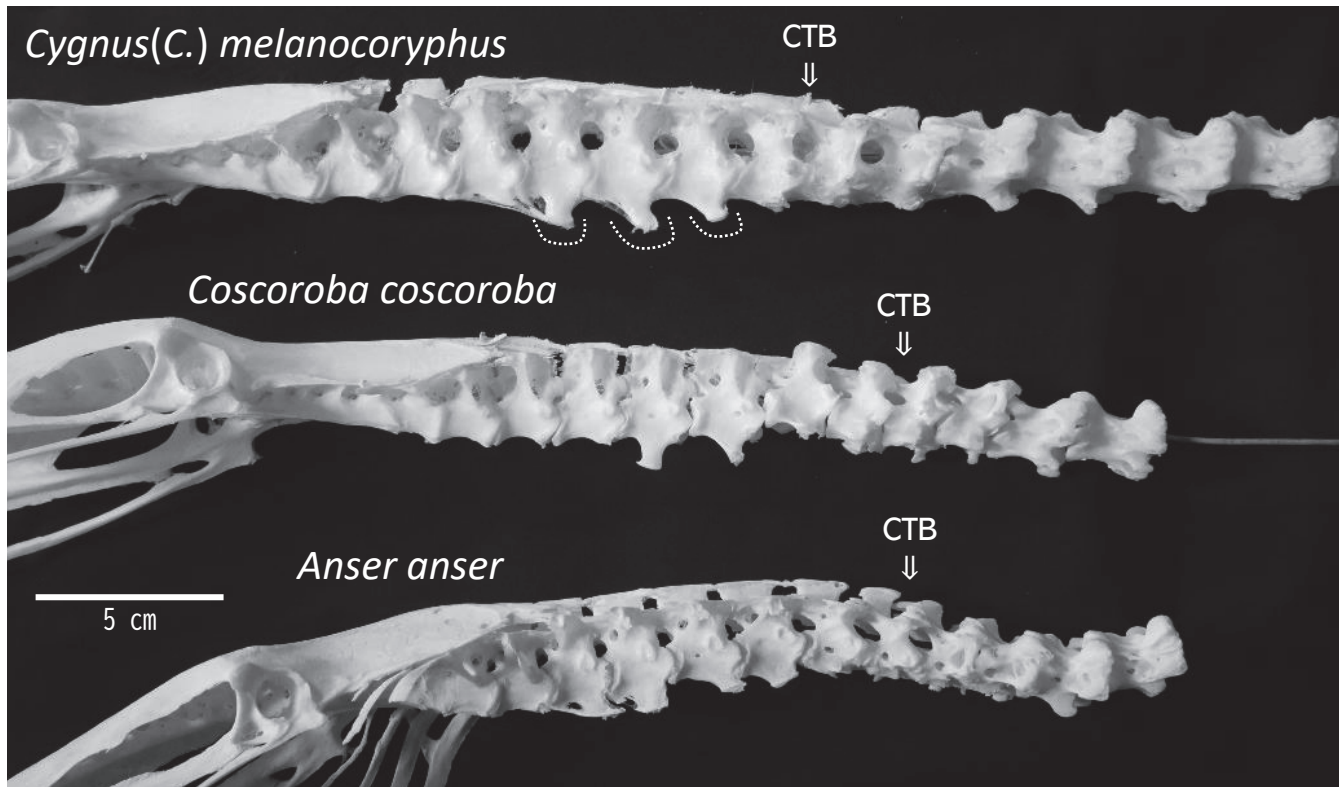
**Figure 4. Three examples of the prepelvic vertebral column of Anatidae, the basal portions.** Note the round outline of the ventral process on the thoracic vertebrae in *Cygnus*. CTB, cervical-thoracic boundary.

## MATERIALS AND METHODS

### Material (fossil):

The holotype of *Annakacygna hajimei* (GMNH-PV-678: Gunma Museum of Natural History, Tomioka City, Gunma Prefecture, Japan), comprises 17 prepelvic vertebral fossils, 12 cervical vertebrae and 5 free thoracic vertebrae. The holotype was excavated from the marine Miocene (11.5 Ma) Haraichi Formation, Annaka Group, exposed in the riverbed of the Usui River, Haraichi, Annaka City, Gunma Prefecture, Japan. The process of preparation, both during field excavation and laboratory cleaning on fossil bones, was done with great care and skill, and so the fossil bones have been prepared completely as they were preserved in the strata. No other prepelvic vertebrae were in/around the holotype, and so the lacking elements/parts are the ones not fossilized or lost by riverbed erosion before it was discovered.

The 17 prepelvic fossils in the holotype of *Annakacygna hajimei* all have deformities, but no damage by preparators. By the fused/unfused morphology of costal region, we are sure about the identification of cervical/thoracic vertebrae. In this study (and in the original description), cervical vertebrae are those that form a transverse foramen, and thoracic vertebrae are those in which fovea costalis exists in the lateral sides.

In this study, we are unconstrained by the result of Matsuoka and Hasegawa (2022) and reexamine all prepelvic fossils in the holotype of *Annakacygna hajimei*. By using the Fig. 4 of Matsuoka and Hasegawa (2022), arranged in the order of the original identification, temporal numbers tNo.1 – tNo. 17 are given to each fossil (**Fig. 2; Tab. 1**). Here, tNo. 1 to 12 are cervical vertebrae (abbreviation is C/CV), and tNo. 13 to 17 are free thoracic vertebrae (abbreviation, FT/TV).

### Comparative specimens:

The osteological specimens of the modern Anseriformes were observed and measured. They are: *Chauna torquata, Dendrocygna javanica, Dendrocygna viduata, Coscoroba coscoroba, Cygnus* (*Cygnus*) *melanocoryphus, Cygnus* (*Cygnus*) a*tratus, Cygnus* (*Cygnus*) *olor, Anser anser, Anser cygnoides, Cairina moschata,*

Table 1. The correlation table of the results of identification of 17 prepelvic vertebrae in three reports including this study.

| | ① | ② | ③ | ④ | ⑤ | ⑥ | ⑦ | ⑧ | ⑨ | ⑩ | ⑪ | ⑫ | ⑬ | ⑭ | ⑮ | ⑯ | ⑰ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Matsuoka et al. (2004) | C3 | C4 | C15 | C16 | C14 | C17 | C18 | C20 | T1 | C22 | C23 | C21 | T2 | T3 | T5 | T6 | T7 |
| Matsuoka and Hasegawa (2022) | C3 | C4 | C5 | C15 | C16 | C17 | C18 | C19 | C20 | C21 | C22 | C23 | T1 | T2 | T5 | T6 | T7 |
| **This study** | C3 | C4 | C5 | C15 | C17 | C18 | C16 | C19 | C20 | C21 | C22 | C23 | T1 | T2 | T5 | T6 | T7 |

**atlas**

Proc.artic. caudalis
後関節突起

Arcus atlantis
環椎弓

Incisula fossae
窩切痕

Fossa condyloidea
顆窩

Corpus atlantis
環椎体

**axis**

Proc. spinosus
棘突起

Proc. articularis caudalis
後関節突起

Dens
歯突起

Facies articularis
atlantica
環椎関節面

Corpus axis
軸椎体

Foraman transversarium
横突孔

Proc. artic. cranialis
- Facies articularis
前関節突起の関節面

Lamina
lateralis arcus
弓外側板

Proc. ventralis
corporis
体腹側突起

Fovea cranioventralis
前腹側窩

Arcus vertebrae
椎弓

Facies artic.
caudalis
後関節面

Corpus vertebrae
椎体

Facies articularis
cranialis
前関節面

**AC, anterior cervical vertebrae**

Proc. spinosus
棘突起

Proc. artic. caudalis
– Torus dorsalis
後関節突起の背側隆起

Foramen vertebrale
椎孔

Proc. artic. cranialis
前関節突起

Proc. caroticus
頸動脈突起

Sulcus caroticus
頸動脈溝

Foraman transversarium
横突孔

Lamina lateralis arcus
弓外側板

Concarvitas lateralis
外側凹面

Proc. costalis
肋骨突起

**aMC, anterior**

Proc. artic. caudalis
後関節突起

Crista
transversoobliqua
横斜稜

Proc. artic. cranialis
前関節突起

Proc. caroticus
頸動脈突起

Sulcus caroticus
頸動脈溝

Foraman transversarium
横突孔

Proc. costalis
肋骨突起

Lamina lateralis arcus
弓外側板

**pMC, posterior**

**main cervical vertebrae**

Proc.
transversus
vertebrae
椎骨横突起

Proc. artic. caudalis
– Facies articularis
後関節突起の関節面

Proc. ventralis
corporis
体腹側突起

Lamina
lateralis arcus
弓外側板

**BC,**
**basal cervical vertebrae**

Ossified tendon(s)
癒合した骨化腱

Proc. spinosus
棘突起

Proc.
transversus
vertebrae
椎骨横突起

Fovea costalis
肋骨窩

Eminentia
costolateralis
肋骨外側隆起

Proc. ventralis
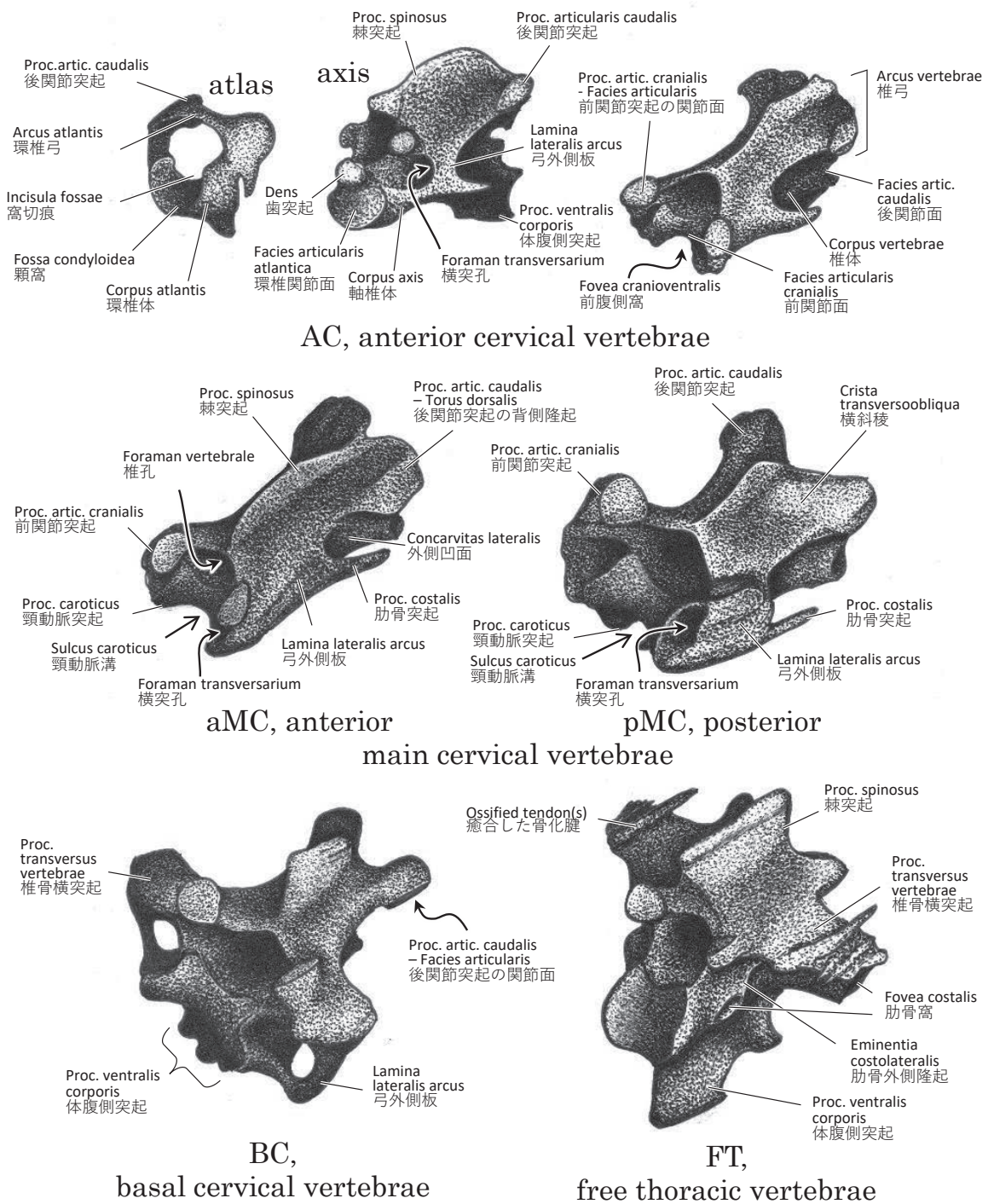corporis
体腹側突起

**FT,**
**free thoracic vertebrae**

Figure 5. General morphology of AC including atlas and axis, aMC, pMC, BC, and FT vertebrae of Anatidae.

*Aix galericulata, Aythya marila, Spatula clypeata, Anas* spp. including *A. falcata, A. penelope* etc. from the KUbb Collection, Department of Geology and Mineralogy, Graduate School of Science, Kyoto University, Kyoto, Japan, and *Cygnus* (*Olor*) *cygnus, Cygnus* (*Olor*) *bewickii* from the collection of the Gunma Museum of Natural History. Of them, a specimen of *Cygnus* (*Cygnus*) *melanocoryphus* in KUbb Collection is the one specially prepared to show the relationsip between osteology, myology and some feathers. This specimen was usefull to reconstruct the total body length including tail fethers.

Subgenus classification of the genus *Cygnus* is based on Stejiveger (1882) and Wetmore (1951). Osteological terminology follows Baumel and Witmer (1993).

### General morphology of anatid vertebral column and the terminology used in this study:

In this study, we consider that the general morphology of the regions of cervical and thoracic vertebrae of the Anatidae could be divided as shown in **Fig. 3**. Here, the neck is divided into four parts: AC, the anterior cervical vertebrae including atlas and axis; aMC, the anterior main cervical vertebrae; pMC, the posterior main cervical vertebrae; and BC, the basal cervical vertebrae. The subdividing of aMC and pMC is based on the difference whether they make dorsally arched kyphotic curve or ventrally arched lordotic curve. The free thoracic vertebrae, FT, can be clearly identified by the presence of a fovea costalis without rib fusion. The position of boundary between last cervical vertebra and the first thoracic vertebra is called CTB

(**Fig. 4**). The general morphologies of the four cervical vertebra types and the thoracic vertebrae are shown in **Fig. 5**.

To identify the position of each fossil vertebra (tNo.1-17) in the vertebral column, the qualitative osteological characteristics of each fossil vertebra were observed, and anteroposterior sequence was estimated. If any morphological gap were in the series of fossils, lacking part(s) may be supposed.

## Method of decompaction of fossil vertebra:

Deformation due to the strata compaction, especially for the pneumatic and lightweight structured bones in the fine and homogeneous matrix, occurs uniaxially to the direction of gravity (Briggs, 1990) (**Fig. 6**). Based on this principal physical rule, by using plural flattened specimens, three-dimensional morphology of soft bodied animals have been reconstructed (e.g., Doveton, 1979; Briggs and Williams, 1981). Motani (1997) extended this principle, in which the deformation could be described by a simple 2x2 square matrix, to the tectonic deformation of bedding planes. However, in the case of GMNH-PV-678 *Annakacygna* vertebrae, which are fossilized in three-dimensionally deformed and topically crushed states, it is not simple to find the original shape because the process requires topical restoration, complex 3D measurement, and 3x3 matrix calculation for them, that are not realistic.

Then, we developed a manual way to reconstruct the original form of bone from the deformed fossil. When we see a fossilized bone prepared out from the host rock, the projected outline of the fossil on the bedding plane the same as the projected image
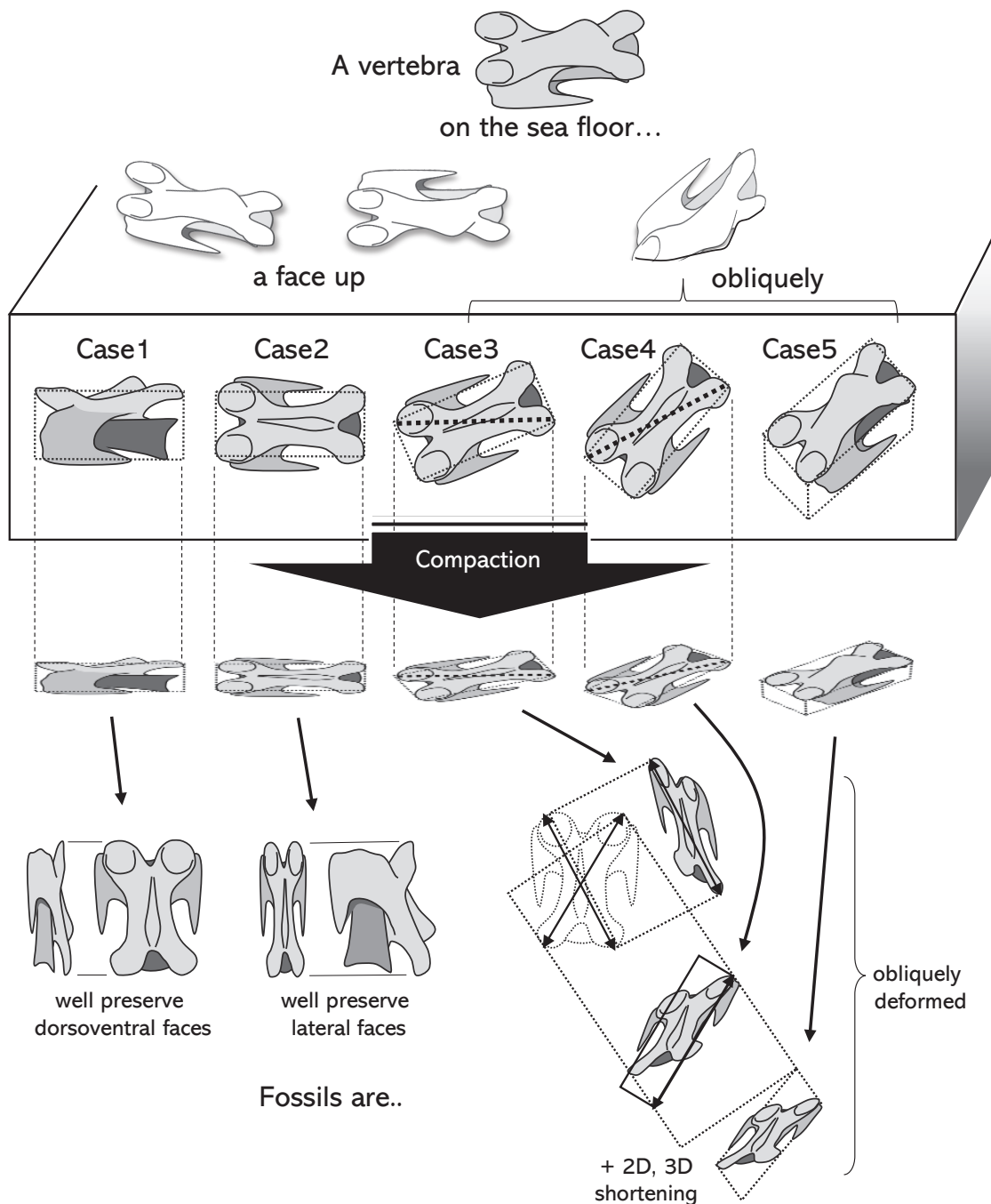


Figure 6. Relationship between the burial orientation of bones relative to the bedding plane and the fossil deformations. In cases 1 and 2, simple one-directional flattening occurs, but in cases 3-5, complex 2-D – 3-D shortening occur.

of the original bone, and, on the contrary, the fossil may shows shortening in the vertical direction. In such setting, if the original form is known, the compaction rate would be easily calculated from a single fossil. Even if the original form is not known, the morphologies of adjacent, similarly shaped, two vertebrae can be used to find the compaction rate. In the holotype of *Annakacygna hajimei*, fortunately, there is a set of two vertebrae that are morphologically similar, and one being laterally compacted and one being dorsoventrally so. By applying a single compaction rate, it is 2/3 in the case of GMNH-PV-678 as found in the following analysis chapter, we can decompact and reconstruct the original form of all vertebrae. As confirmation, by using some fossils settled obliquely in host rock and the original symmetric form being lost, we took the photographic image looking parallel to the bedding plane and then elongated the images with different values of "compaction rate" to explore the value that would reconstruct an image considered to be the most symmetrical and closest to the original form.

## Drawing of the original morphology of each vertebra and vertebral column:

There are always topical deformations and damages on actual fossils. For such incomplete parts, we manually restored individual details by considering symmetricity, articulation to the neighboring element, etc. And then we drew the reconstructed measured dorsal, ventral, cranial, and lateral images of each vertebra.

Once the reconstruction of the shape and size of all vertebrae is complete, with knowledge on the osteology of modern anatids, the total vertebral column was reconstructed. We reconstruct the vertebral column of *Annakacygna hajimei* in osteological neutral posture (ONP: the posture two vertebrae are articulated to fit in
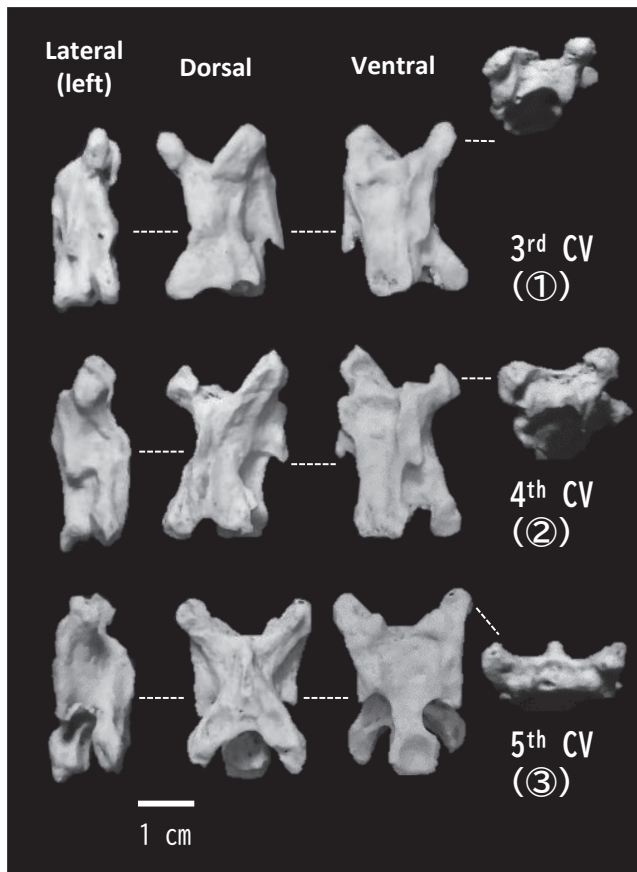


Figure 7. The fossils of prepelvic vertebrae of *Annakacygna hajimei* (1): tNo. 1, 2 and 3 that are identified to the 3rd, 4th and 5th cervical vertebra (CV) respectively.

the maximum articular surfaces at each joint: Stevens and Parrish, 1999; Cobley et al., 2003).

## RESULT

### Anatomical position of each vertebra

In the totally 17 prepelvic vertebrae belonging to the holotype of *Annakacygna hajimei* (**Fig. 2**: tNo. 1 to 17), there is no doubt that tNo. 1 to 12 are cervical vertebrae (CV) and tNo.13 to 17 are thoracic vertebrae (TV), due to the presence of fovea costalis, articular facets to ribs on the lateral surface of vertebra. Identification of these two types by Matsuoka and Hasegawa (2022) was correct. However, we found some cervical vertebra that must be changed regarding the order from the original description. The results are described below.

**tNo. 1 to 3 (Fig. 7):** These three vertebrae are clearly smaller than the others. The deformation is simple in all three fossils: tNo. 1 and tNo. 3 are compressed only in the dorsoventral direction, and tNo. 2 is slightly obliquely crushed and the right side of the fossil appears in the dorsal view. tNo. 1, 2and 3 ware identified respectively as 3rd, 4th and 5th CV by Matsuoka and Hasegawa (2022), on the contrary they were assigned to the 3rd, 4th and 15th CV by Matsuoka et al. (2004).

Reidentification. In common with tNo.1-3 vertebrae: zygapophysis cranialis is slender and projects anterolaterally; no proc. transversus; proc. spinosus is wide; lamina arcocostalis is as wide as to reach the middle of the vertebral length; sulcus caroticus are broad, with long and low proc. caroticus at the anterior sides; fovea cranioventralis is developed, but somewhat shallow in tNo. 5; slight proc. ventralis exists. Based on these features, tNo.1-3 vertebrae are identified to the anterior cervical vertebrae (AC).

Among AC vertebrae, tNo. 1 has the remarkable feature that the right and left facies articularis are on a same plane facing anterodorsally, and then can be identified exactly as the 3rd CV. On tNo. 1, in addition, there is no lacuna interzygapophysialis caudalis and shows the characteristic general morphology of the post-axis aMC of anatids (**Fig. 5**).

The tNo. 2 is like tNo. 1, but has its own features such as: slightly larger than tNo. 1; facies articularis face slightly medially, and so the right and left ones are not in a same plane; lacuna interzygapophysialis caudalis slightly opens. We judged tNo. 2 as the one articulating caudal to tNo. 1, that is, the 4th CV.

The tNo. 3 fossil deforms in a very simple dorsoventral compaction, and then retains its original morphology in the dorsal and ventral views. The tNo. 3 has an enigmatic shape, and the shape led to the major change of identification results between the two reports: in 2004, identified as the 15th CV, but identified as the 3rd CV in 2022. An enigma is the protruding shape of zygapophysis caudalis, that is rather resembling the shape of a pMC vertebra and does not appear in typical AC of Anatidae. However, tNo. 3 could not be a pMC vertebra because it has a big size gap between the true pMC fossils (see below). Here, we regard the unique morphology of tNo. 3 as the adaptive shape unique to *Annakacygna* that might allow the lateral mobility in anterior neck as in pMC vertebrae, and consider tNo. 3 as on the line of gradual change from tNo. 1 to tNo. 2. That is, tNo. 3 is the 5th CV.

Our result, considering *Annakacygna* as animals that had lateral mobility in anterior neck, comes to a logical consequence to the view by Matsuoka and Hasegawa (2022) who concluded *Annakacygna* as filter feeders.

Concludingly, this study supports Matsuoka and Hasegawa (2022) and identifies tNo. 1, 2, 3 as 3rd, 4th, 5th cervical vertebra respectively.

**tNo. 4 to 9 (Fig. 8)**
**– tNo. 4 to 8:** The tNo. 4, 6 and 8 fossils are deformed mainly laterally, and tNo. 5 and 7 are deformed dorsoventrally. Therefore the appearances of these fossils are very different. However, these five vertebrae share morphological features such as: being relatively short anteroposteriorly; box-like overall
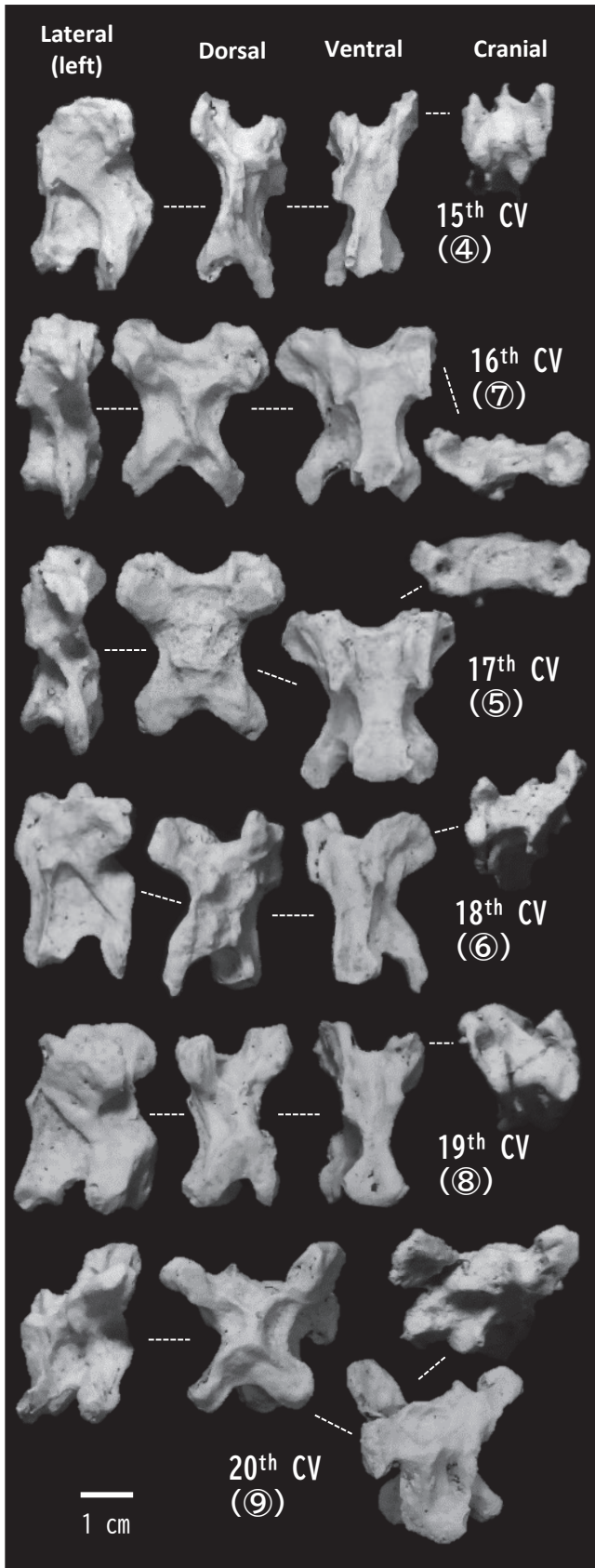
Figure 8. The fossils of prepelvic vertebrae of *Annakacygna hajimei* (2): tNo. 4, 7, 5, 6, 8, and 9 that are identified to the 15th, 16th, 17th, 18th, 19th, and 20th cervical vertebra (CV) respectively.

shape with nearly square transverse section; articular processes are highly independent and laterally developed, and so the dorsal view of the vertebra is X-shaped; dorsoventrally long lamina arcocostalis presents on the lateral portion of the anterior articular process; proc. spinousus is low but strong; proc. caroticus is developed; the length between the vertebral articular surfaces is longer than the length between the articular surfaces of anterior and posterior articular process, which forms ventral convexity in the articulated posture etc. So, these are identified as the posterior main cervical vertebrae (pMC).

While the appearance differs greatly due to deformity, close similarities between these six vertebrae led misidentification of the order of individual fossils. In this study, we found that the shapes of lamina arcocostalis and proc. caroticus are useful in determining the cranioposterior order of each vertebra. Based on our observations of modern birds, we have found: the lamina arcocostalis of anterior main cervical vertebrae (aMC) covers 50% or more of the length of the lateral surface of corpus vertebrae, while in the pMC the ratio decreases, i.e., the lamina becomes shorter posteriorly; the lateral surface of corpus vertebrae appears wider; and, on the proc. caroticus, it is bisected and each locate at the anterior sides of sulcus caroticus in the posterior portion of aMC, while proc. caroticus develop more as goes caudally in pMC and the left and right processes gradually becomes closer to form a single ventral process in the midline. The degree of such gradual transition can be the key to order identification.

With tNo. 4 to 8, when measured on the better-preserved side, the ratio of the length measured from the anterior end of the vertebral body to the anterior-most point of the posterior margin of lamina arcocostalis to the vertebral body length is: 0.42 (14 mm / 33 mm, same below) in tNo. 4, 0.30 (9.5/32) in tNo. 5, 0.29 (9/31.5) in tNo. 6, 0.35 (11/31.5) in tNo. 7, and 0.27 (9/33.5) in tNo. 8. The values are tNo. 4 < tNo. 7 < tNo. 5 < tNo. 6 < tNo. 8. The degree of development of the ventral process is consistent with this ordering. We concluded that the order should be changed from Matsuoka and Hasegawa (2022) to this result. The morphological changes between the vertebrae are gradual, and the five vertebrae should have been articulated continuously in life.

- **tNo. 9:** Although this was identified as the 1st thoracic vertebra by Matsuoka et al. (2004), it is clearly a pMC vertebra, because this has developed articular processes forming X-shaped dorsal view and has characteristically dorsoventrally long lamina arcocostalis.

The tNo. 8 and 9 show laterally wide proportion as a pMC vertebra and the feature indicates that they were at around the caudal termination of pMC. The characteristic feature is seen on the ventral process, which in tNo. 8 is bisected and extending from the lateral margins of the vertebral body, but in tNo. 9, two processes merge to form a sharp, posteriorly pointed arrowhead-shape process. The shape of tNo. 9 demonstrates the feature of the last pMC. In addition, although the arch of tNo. 9 retains its shape well, it is still shortened laterally by the lateral component of the overall oblique shortening. When it is decompressed, it fits the anterior articular process of tNo. 10, which is described next and considered to be the most anterior one of the basal cervical vertebrae (BV). As stated above, tNo. 9 is identified as the last pMC vertebra, which had been articulated caudal to tNo. 8 and anterior to tNo. 10.

**tNo. 10 to 12 (Fig. 9):** These three vertebrae are "basal cervical vertebrae" (BC), because: they are proportionally wide; foramen transversarium is transversely long oval in shape; the posterior articular processes are more strongly extended posteriorly than facies atrticularis caudalis of corpus vertebrae; and the ventral process is developed. The major difference between the three vertebrae is found in the ventral process. The ventral process of tNo. 10 is sharply hooked to point anteriorly. The tNo. 11 has a large granular process with small bulges on lateral sides. The tNo. 12 has typical ventral process seen on large anatids, that is low and consists of three anteroposteriorly

running ridges, long one in the middle and short ones in both sides.

Considered from the general characteristics of BC vertebrae of large anatids, we identify tNo. 10, 11 and 12 as the most caudal BC vertebrae in this order, caudal to tNo. 9 and in arrangement of tNo. 12 articulates to the first thoracic vertebra (tNo. 13).

On these three BC vertebrae, it is highly characteristic that they have strong posterior extension of posterior articular processes against facies atrticularis caudalis of corpus vertebrae, and results to form a strong kyphosis in this position of the vertebral column of *Annakacygna*. Also, because the transverse processes of these BC vertebrae are narrow anteroposteriorly, they indicate high lateral flexion mobility at the base of neck.

**tNo. 13 to 17 (Fig. 10):** These five fossils are of thoracic vertebra (TV), as they possess fovea costalis.

**- tNo. 13 :** The morphology of each part is perfectly preserved: facies articularis cranialis of corpus vertebrae is very



Figure 9. The fossils of prepelvic vertebrae of *Annakacygna hajimei* (3): tNo. 10, 11 and 12 that are identified to the 21st, 22nd and 23rd cervical vertebra (CV) respectively.

wide; ventral process is huge and club-shaped with three tubercles on the tip. Then this is reasonably identified as the 1st TV. As a thoracic vertebra, the transverse processes are narrow anteroposteriorly, and there is no fusion of ossified tendon.

**- tNo. 14:** Laterally compressed and so the arcus vertebrae are badly damaged, but the shape of the large and flat ventral process is well preserved. The combination of the club-shaped ventral process possessed in tNo. 13 (1st TV) and the large and flat and U-shaped ventral process like in tNo. 14 is characteristic of the anterior thoracic vertebrae of swans (**Fig. 4**). The tNo. 14, therefore, is identified as the 2nd TV.

It should be noted that the development of a flat ventral process on the thoracic vertebrae is not uncommon in birds, but the ventral process of these birds usually exhibit a boot-like or squared with angled anterior and posterior corners in lateral views. In contrast, a smooth U-shaped ventral process like tNo. 14 is a feature found only in swans, as far as the authors have experienced.

**- tNo. 15 to 17:** All are compressed in mainly a craniocaudal direction with slight oblique angle and look similar in appearance at a glance. In tNo. 15 and 16, the proc. spinosus are well preserved, but in tNo. 17 it is crushed. They have no ventral processes except the slightly keeled midline of the vertebral body of tNo. 15.

All fossils are well-preserved showing the articulations. The tNo. 15 and 16 had been articulated in this order. The facies articularis caudalis of tNo. 17 is square-shaped, and so we judged this to be the most caudal free thoracic vertebra anterior to the pelvis. In these three thoracic vertebrae, the transverse processes are characteristically short anteroposteriorly when we see their dorsal face. The relative width increases in the order tNo. 15 < 16 < 17. Then the three are identified as the last FT tNo. 17 and the two preceding (tNo. 16 and 15, to anterior).

The characteristically short transverse process of these three caudal vertebrae forming an "apex" in the lateral termination and produce big spaces in between them when articulated. Also, there is little tendon fusion on these transverse processes of free thoracic vertebrae. We assume that these characteristics are the adaptive morphology unique to *Annakacygna* and will be discussed in the following.

The morphological gap between the 2nd TV (tNo. 14) and the third-most caudal thoracic vertebra (tNo. 15) is too large when focusing on the ventral process. In the thoracic vertebral column of modern swans, a decrease in size of the ventral process from the largest one in anterior to the smaller ones in the continuous two or three posterior thoracic vertebrae is common (**Fig. 4**). We concluded that there were two more thoracic vertebrae in between tNo. 14 and tNo. 15. This means that the five remaining thoracic fossils in the holotype of *Annakacygna hajimei* are identified as the 1st, 2nd, 5th, 6th, and 7th CVs. The seven free thoracic vertebrae are consistent with the general number of thoracic vertebrae in many birds.

**Summary on the anatomical position of tNo. 1 to 17:** A summary is that the 17 prepelvic vertebrae of the holotype of *Annakacygna hajimei* can be divided into two groups: those with a specific order and those with a relative position. The former group consists of the 3rd to 5th cervical vertebrae and the 1st, 2nd, 5th, 6th, and 7th thoracic vertebrae. The latter group consists of a total of nine consecutive caudal cervical vertebrae. These are named here as the cervical vertebrae (CV) ctb-(cervical/thoracic boundary minus) 9th to ctb-1st, the relative number counted from the boundary between the last cervical vertebra and the most anterior thoracic vertebra (CTB). The estimation of how many cervical vertebrae are missing between the 5th CV and CVctb-9, in other words, how many cervical vertebrae were in the entire cervical vertebral column of *Annakacygna*, will be discussed later, because this problem is strongly linked to the phylogeny of this bird.
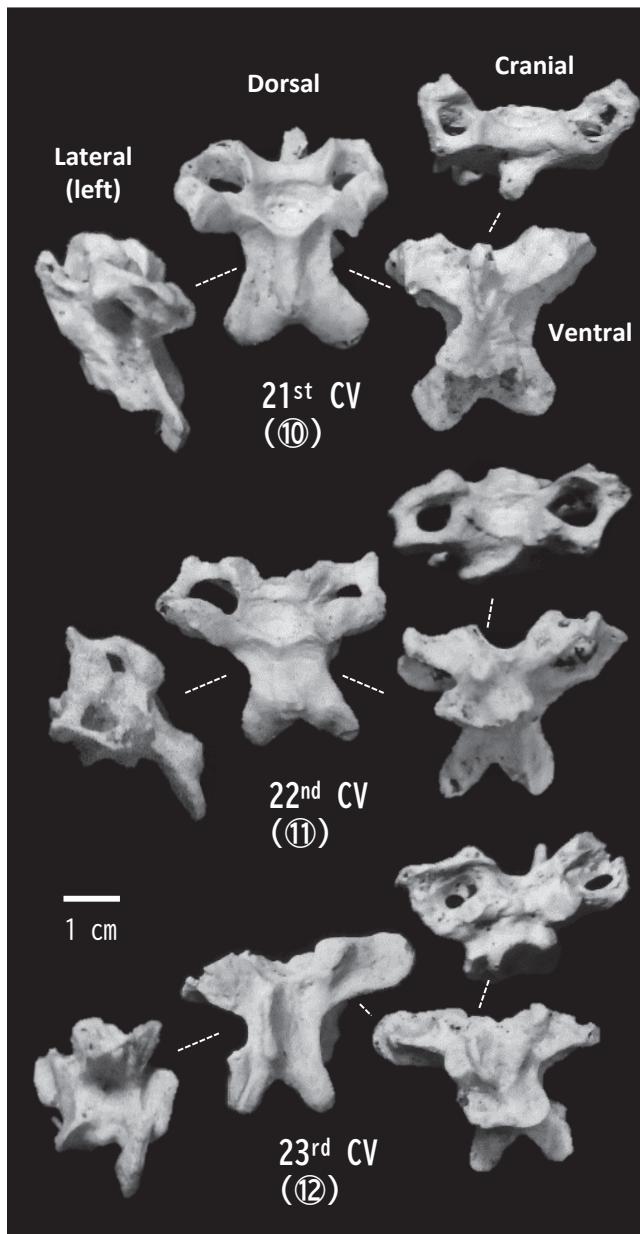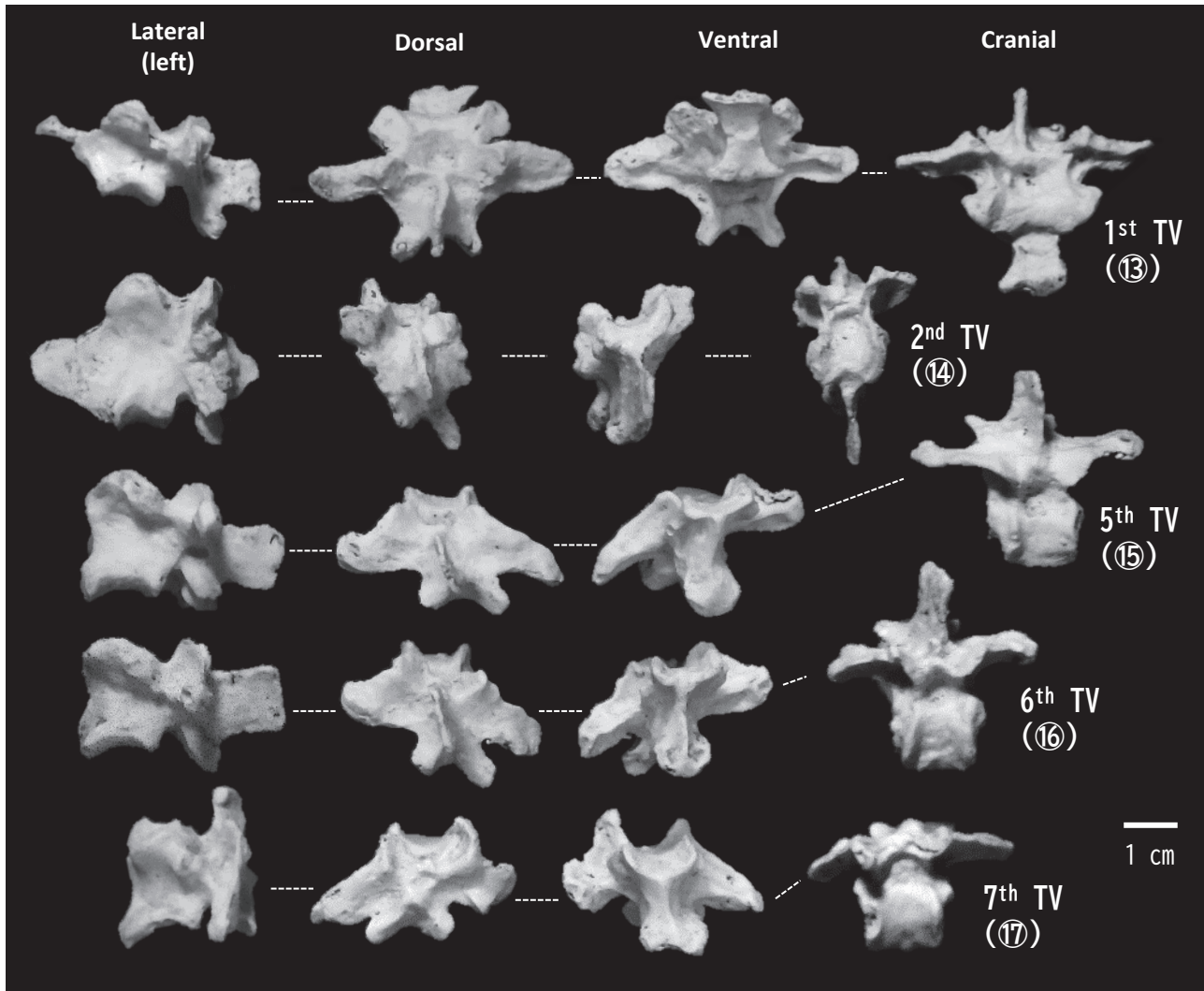
Figure 10. The fossils of prepelvic vertebrae of *Annakacygna hajimei* (4): tNo. 13, 14, 15, 16, and 17 that are identified to the 1st, 2nd, 5th, 6th, and 7th free thoracic vertebra (TV) respectively.

## The compaction rate and reconstruction of the original form

The vertebral fossils belonging to the holotype of *Annakacygna hajimei* were scattered on the host rock (**Fig. 1**), indicating that they were buried in a well decayed and disarticulated state. In this situation, each vertebra is individually encased in the host rock and has suffered compressive deformation. Through the observation on fossil bones, it is evident that all vertebral fossils are under even deformation and both centrum and arch parts are subjected to almost uniform compressive deformation. This may reflect the fact that the prepelvic vertebrae of *Annakacygna hajimei* are highly pneumatic.

Since the morphology of vertebrae usually changes in a gradual manner in avian vertebral columns, then in a bird of long neck, the shape and size of neighboring vertebrae are very similar. Based on this feature of avian vertebrae and the unique mode of fossil occurrences of the holotype of *Annakacygna hajimei*, we could find the compaction rate of fossil vertebrae.

An exemplary combination is the case of CVctb-9 and CVctb-7 (**Fig. 11**). (CVctb-8 is compressed nearly dorsoventrally but contains a slight lateral component and obliquely deformed overall, and so is not used.) CVctb-9 is compressed laterally, and anatomically near CVctb-7 which is compressed almost completely dorsoventrally. In this situation, as the original height (dorsoventral length) of two vertebrae do not change in between CVctb-9 and CVctb-7, by a simple image elongation of the

lateral view of CVctb-7 in the dorsoventral direction we can find a deformation rate to match the lateral view of CVctb-9 at the corresponding points (**Fig. 11 -4**). When the image of CVctb-7 was elongated dorsoventrally 1.5 times, we find a near match to the lateral view of CVctb-9. Then, the reciprocal 2/3 is the compaction rate.

We apply this compaction rate 2/3 to the obliquely compressed area. Since CVctb-9 contains a component of oblique compression as well as lateral compression, the dorsoventral view is deformed to make a parallelogram from a rectangle. From this deformed state, assuming the bedding plane (plane perpendicular to the compression axis) and by 1.5 times magnification of the image on the axis, left-right symmetry is restored. Through this process, the articular process of CVctb-9 becomes to fit to the articular process of the posterior vertebra (**Fig. 11 -4'**). Same processing results in a truly harmonic restoration, allowing reconstruction of the original forms in many cases (**Fig. 12**).

These values were also applied to the fossil vertebrae that are shortened in the nearly craniocaudal direction (**Fig. 13**). Applying the compaction rate 2/3, 1.5 times axial magnification, the approximate shape of fossils, which was a parallelogram, becomes a symmetrical rectangular form. This indicates that a single compaction rate, 2/3, is shared among all vertebral fossils belonging to the holotype of *Annakacygna hajimei*.

We tried an experiment to change the value and found that: an axial enlargement ratio 1.3x (less than 1.5) results in insufficient restoration to reach a rectangle, while the ratio of 2x (greater than 1.5) results in significant overextension (**Fig. 14**). So, for the prepelvic vertebrae of holotype of *Annakacygna hajimei*, the single compaction rate 2/3, and the reciprocal 1.5 for the axial enlargement to get the original form, was found to be common to all fossil vertebrae.

For all the fossil vertebrae, the approximate shapes were obtained by mechanical decompaction process from images with this value. Then, topical damages were restored manually based on anatomical symmetry and other factors. Then, the measured figures of dorsal, ventral, cranial, and the left lateral views of each vertebra were drawn (**Plates 1-4**). By measuring the figures, measurements of each vertebra were obtained (**Tab. 2**). For comparison, the measurements of the prepelvic vertebrae of several species of Anatidae were done (**Tab. 3**).

## DISCUSSION

### Determination of the number of prepelvic vertebrae, and phylogeny of *Annakacygna*

As resulted above, the 17 prepelvic vertebrae belonging to the holotype of *Annakacygna hajimei* were identified as the 3rd-5th cervical vertebrae (CV), CVctb-9 to CVctb-1 (final) cervical vertebrae, 1st, 2nd, and 5th-7th (final) thoracic vertebrae (TV). The question is what are the anatomical numbers for the CVctb-9 to CVctb-1, counting from atlas (1st CV) to posterior. The number of cervical vertebrae is an important feature as a synapomorphy of tribe level in Anatidae (Woolfenden, 1961). In other words, the determination of the number of cervical vertebrae has important implications for the tribe-level phylogeny of *Annakacygna*.

Here we estimate how many cervical vertebrae are missing between the 5th CV and CVctb-9 in the holotype of *Annakacygna hajimei*.
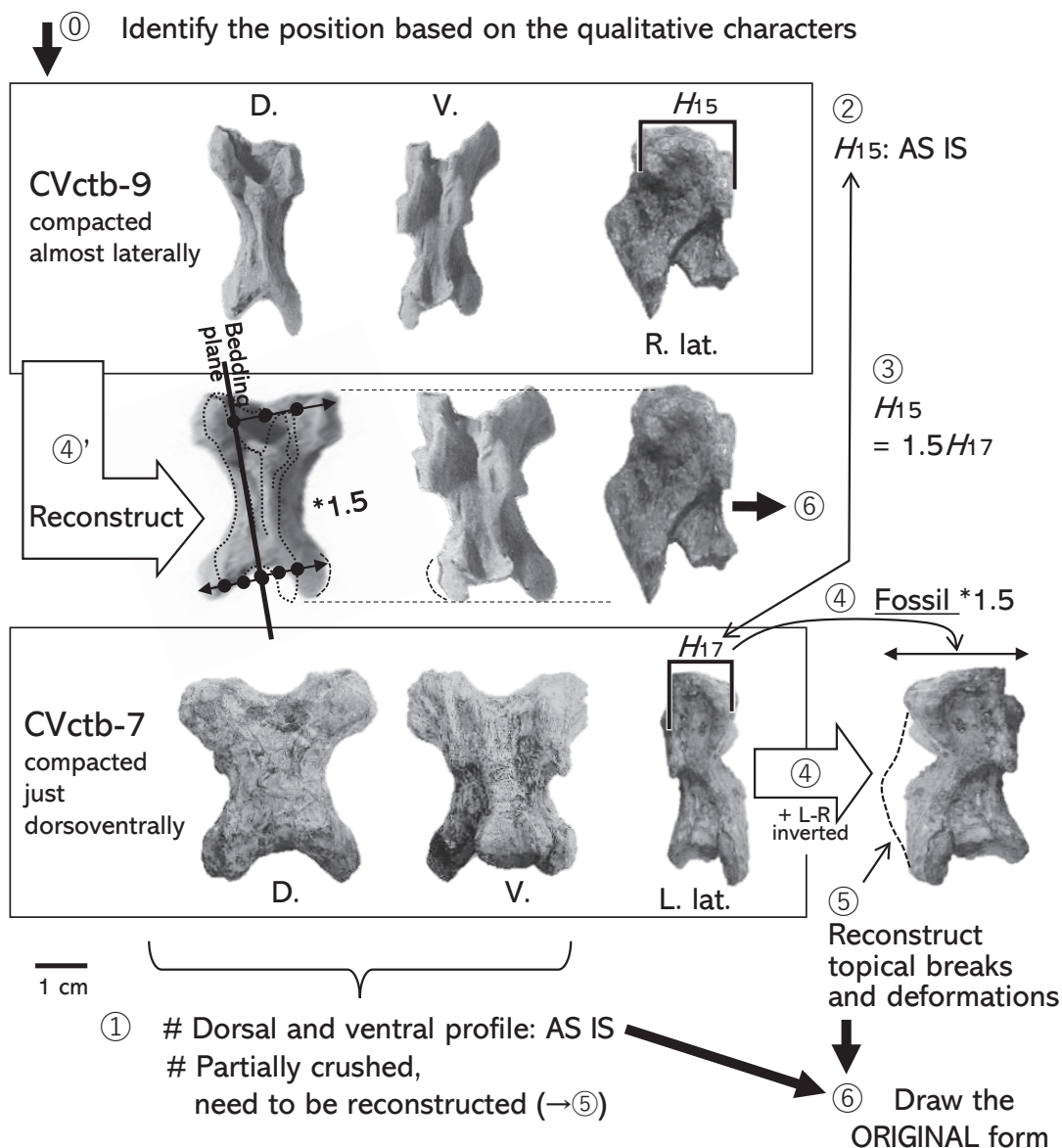


Figure 11. Process of finding "compaction rate" from the two vertebrae anatomically neighbored and fossilized in the positions of 90° rotated.
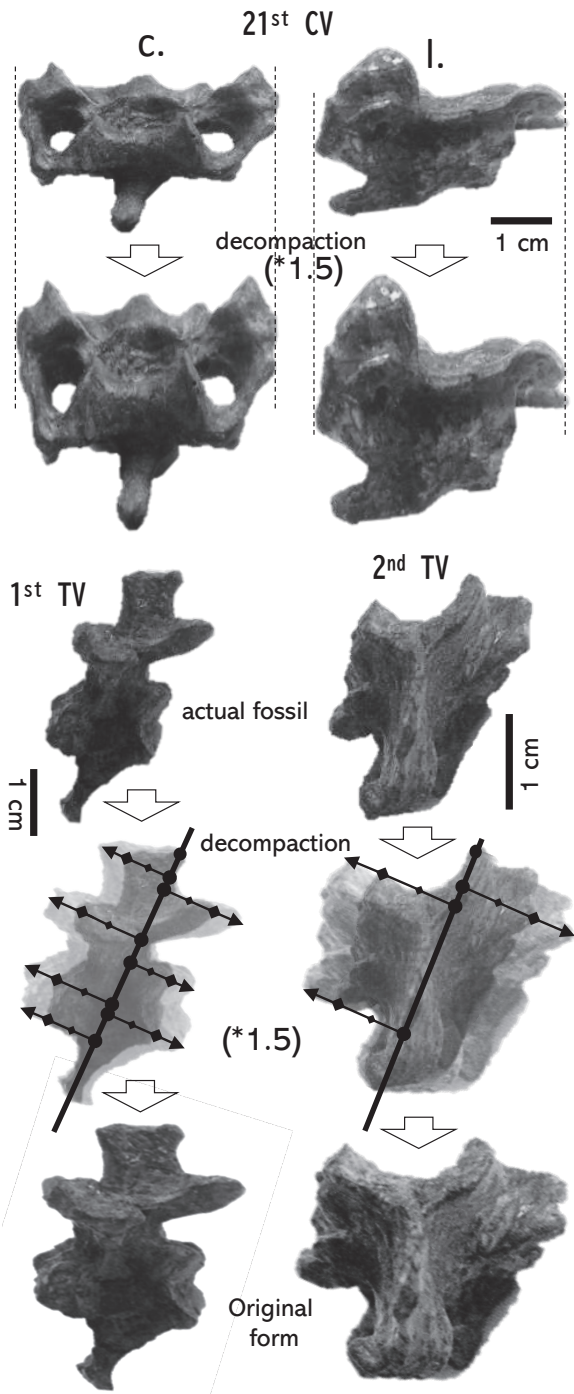
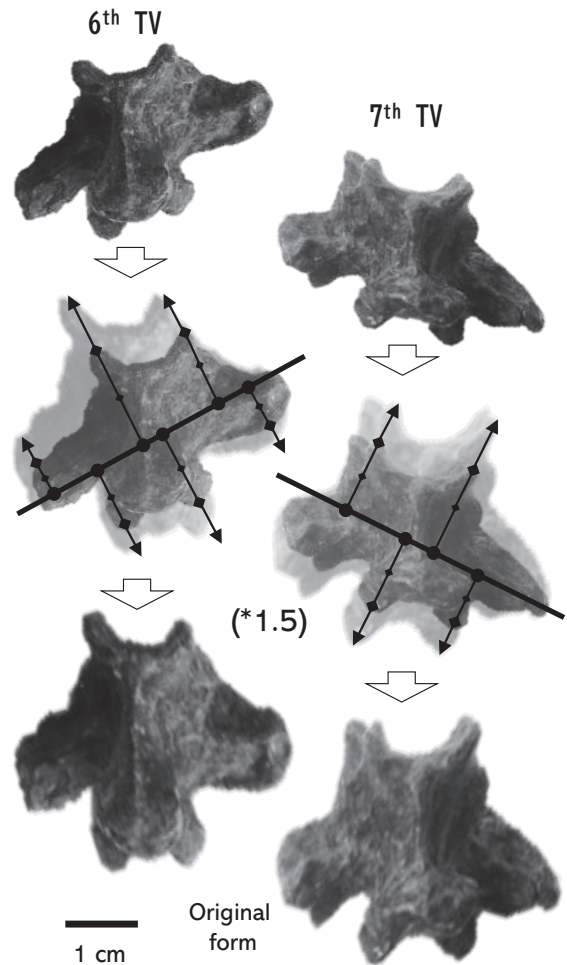Figure 12. Examples of decompaction process using compaction rate 2/3 (1).



Figure 13. Examples of decompaction process using compaction rate 2/3 (2). Note that the obliquely deformed fossil appearance is revised to a symmetric natural image after the decompaction.

portion") at the posterior part of the cervical vertebrae, especially in long-neckd species, after the monotonic increase at the anterior to middle neck ("monotonic increase portion"). The nine posterior cervical vertebrae remaining in the holotype of *Annakacygna hajimei* (especially the ones posterior to CVctb-6) may correspond to this "sharply increasing portion". The existence of such "sharply increasing portion" suggests that *Annakacygna* was a long-necked bird with a significant number of missing cervical vertebrae in between the CVctb-9 and 5th cervical vertebrae.

Fig. 15 also reveals that the anterior to middle portion of the neck has a constant and nearly uniform rate of increasing in size, "monotonic increase portion", regardless of taxonomic groups. For the seven species (**Fig. 15-b**), excluding *Cairina moschata* which is an outlier and *Dendrocygna viduata* that has the shortest neck and shows little size change in graph, the average rate of "monotonic increase portion" of the cervical vertebrae of these seven species was calculated to 0.44 mm/a vertebra (Standard deviation ($\sigma$) = 0.10).

If the average value 0.44 mm/a vertebra fills the 4.5 mm difference between CVctb-9 Wa (29 mm) and the 5th CV Wa (24.5 mm) in the holotype of *Annakacygna hajimei*, we can conclude there were about nine (4.5/0.44 − 1) vertebrae in between. In this case, CVctb-9 was the 15th cervical vertebra, and the total number of cervical vertebrae in this bird would have been 23. (For − 1 $\sigma$ = 0.34, the number of missing cervical vertebrae was about 12 and the total number of cervical vertebrae was 26, which is too many and exceeds the maximum

The key is the size property through the cervical vertebrae. **Fig. 15** shows the maximum anterior vertebral width (Wa) in the vertebral column of nine anatid birds belonging to Dendrocygnini, Cygnini, Anserini, and Anatinae, in which the data of all species are adjusted at the cervical-thoracic boundary (CTB) because the numbers of vertebrae vary for species. The left end of all lines in Fig. 15-a (graph for each species) is the data of axis (2nd CV). From the graph of Fig 15-a, general trends on the anatid neck are seen. Firstly, Wa value increases sharply at between axis and 3rd CV. Because the holotype of *Annakacygna hajimei* lacks the axis, such sharp increase cannot be determined (**Fig. 15-b**). Another feature on the graph 15-a is that the Wa value increases sharply ("sharply increasing
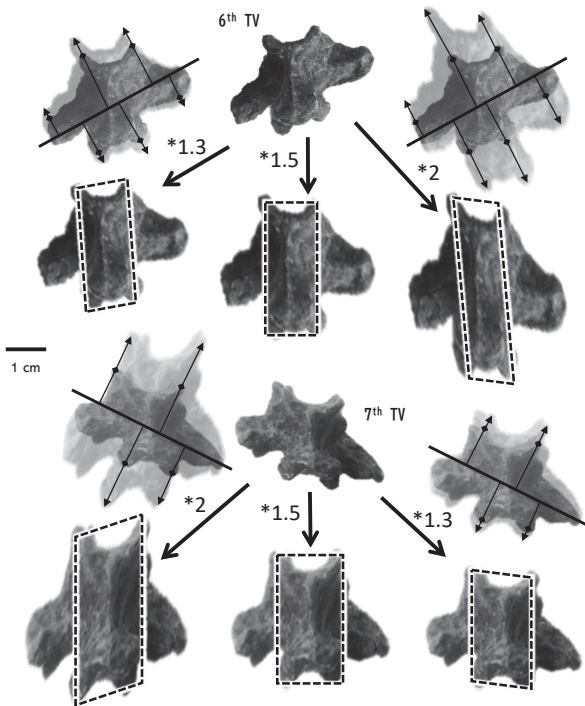
**Figure 14. Trials to find the best compaction rate.** Note that the "decompaction" is not enough to get a symmetric image in 1.3 times elongation and is too much in 2 times.

number of cervical vertebrae in birds (23-24). $1 \sigma = 0.54$ gives 7 missing cervical vertebrae and the total number of cervical vertebrae was 21.) Now we identify that CVctb-9 to ctb-1 are C15 to C23 (last) respectively.

The 23 is about the largest number counted on the cervical vertebrae among birds, and only the 22-24 of Cygnini (excluding *Coscoroba*) corresponds. There are probably no anatid with 21 cervical vertebrae, and the second largest number of cervical vertebrae is the 20 of *Coscoroba*. The phylogenetic position of *Coscoroba* has not yet been established. Recent molecular phylogeny (Sun et al., 2017) placed the clade of *Coscoroba* + *Cereopsis* as the sister group of the clade of Anserini + Cygnini. On the other hand, in many ornithological catalogs (e.g., Gill et al., 2023), *Coscoroba* is the sister group of the true swans (modern *Cygnus*).

Regardless of the taxonomic position of *Coscoroba*, *Annakacygna* having 23 cervical vertebrae can be placed as a member of Cygnini (excluding *Coscoroba*). Some supporting factors are the morphological characteristics of the posterior cervical to thoracic vertebrae. The posterior cervical and thoracic vertebrae of *Annakacygna hajimei* show a distinctive series of characteristic ventral processes. The ventral processes on the vertebrae of *A. hajimei* appear as the two processes ventrolateralis on the anterolateral margins of corpus vertebrae of the main cervical (MC) vertebrae (anterior to CVctb-5). Then posteriorly, two processes ventrolateralis merge into a knob-shape ventral processes (CVctb-6) and becomes a single large hook-like one (CVctb-7). CVctb-7 is the last posterior main cervical (pMC) vertebra. More posteriorly, the ventral process is low and massive with three-knobs on CVctb-2 and ctb-1, and then it becomes huge again in the anterior thoracic vertebrae (FT). The ventral processes is U-shaped and flat on FT2.

The same pattern can only be seen in true swans, and other large and relatively long-necked anatids (*Coscoroba* and geese) show a different pattern. *Coscoroba* and geese differ in the serial changing of the ventral processes, that are generally poorly developed in these birds, and the combination of both hook-like ones and knob-shape ones is never seen in these birds. In

addition, the ventral processes of the thoracic vertebrae are boot-shaped rather than U-shaped in *Coscoroba* and geese (Fig. 14). Only true swans are identical in the pattern of the series of ventral processes to *Annakacygna*.

Still, someone may say, because the ventral processes of the cervical and thoracic vertebrae develop functionally (Kuroda, 1962), it is theoretically possible that the vertebral morphology in *Annakacygna* is a purely functional convergence, independent of phylogeny. However, all features known on the skeleton of *Annakacygna* so far, the combination of the characteristics on the morphology of vertebrae, the serial vertebral column with the number of 23 cervical vertebrae found in this study, and the post-shoulder osteology adapted for the "piggybacking" parental care action described and discussed in Matsuoka and Hasegawa (2022), are linked to the morphology and habits exhibited only in true swans of modern genus *Cygnus*, especially those of the subgenus *Cygnus*. At present, there is no evidence to conclude that this is a convergence from a lineage other than Cygnini. Considering all factors, we conclude with confidence that *Annakacygna* are a member of Cignini, the tribe of swans.

## Body length estimation

As concluded above, through the reconstruction and drawing of the measured figures for the remaining 17 cervical and thoracic vertebrae (Plates 1-4), the number of cervical vertebrae in *Annakacygna* was 23. Here, we focus on the nine missing cervical vertebrae and reconstruct the total length of the vertebral column and body length (BL, length measured from the tip of bill to the tip of tail feather) of *Annakacygna*. For this purpose, we measured the length of vertebral centrum (CL) and the width of the caudal portion of centrum (CW) and analyzed the results (**Fig. 16**).

Fig. 16-a is the CL/CW bivariate plots of prepelvic vertebrae of several anatid species. For all species: the line which starts from the left bottom area of the graph steeply goes up; and then in the main cervical vertebrae CW increases but CL doesn't; then for the posterior cervical vertebrae, CW does not change much and CL decreases sharply. And, in the thoracic vertebrae, CL does not change much and CW decreases. On the whole, the graph shows a "$\rho$" (rho) shape generally. Typical examples of $\rho$-shape patterns are selected and shown in Fig16-b-above.

In addition to the $\rho$-curve, *Cygnus* swans show a characteristic "loop" on the top area of the graph (Fig. 16-b-bottom). In the graphs of swans, at around the $13^{th}$-$14^{th}$ CV, which are in MC, cervical vertebrae show the maximum CL. At around the CL maximum, in some vertebrae anterior to the peak, CL gradually increases while the CW does not increase so much, rather CW decreases near the peak. The decreasing of CW continues in some vertebrae posterior to the CL peak, and CL decreases to return to the top of "$\rho$". So, as a result, the entire graph for the main cervical vertebrae draws a loop on the top of $\rho$-curve. This loop on the graph is called "swan's loop" in this study.

The measured CL/CW plots (C5-7, C15-23, FT1-2, FT5-7) of *Annakacygna hajimei* in the Fig. 16-c graph can be considered to correspond to the parts of "$\rho$ + swan's loop" curve, except for the characteristic sizes of the posterior thoracic vertebrae. Then, the missing cervical vertebrae, C6 to C14, would be the warped part of the swan's loop as estimated by a wide line and white circles in the graph. On the assumption that the morphological transition in these missing vertebrae was constant, the estimated CL/CW of C6-14 are 30/12, 30.5/13.5, 32/14, 34/14.5, 35.5/14.5, 37.5/14.5, 39/14, 39.5/13, 38.5/11.5 (mm), respectively. Therefore, in total, about 30 cm by curve had been missing at this part of the neck. The CL/CW of the missing two thoracic vertebrae, FT3 and FT4, was estimated as 31.5/11.5 and 33.5/11.5 (mm) by proportional dividing calculated from the CL/CW of FT2 and FT5.

Now, finally, the total length of the prepelvic vertebral column including the missing parts can be determined. The atlas (C1) and axis (C2) are still unknown in the vertebral column, but since they are morphologically stable throughout the birds, they

Table 2. Measurements on the reconstructed prepelvic vertebrae of *Annakacygna hajimei*.

| | GL | Wa | Wp | CL | CW | H | CH | DVP |
|---|---|---|---|---|---|---|---|---|
| C3 | 30.0 | 21.5 | 20.0 | 26.0 | 9.5 | 17.0 | 8.0 | 1.5 |
| C4 | 32.5 | 24.0 | 22.0 | 28.0 | 10.5 | 18.0 | 8.5 | 1.0 |
| C5 | 30.5 | 24.5 | 22.5 | 29.0 | 11.0 | 18.0 | 9.0 | 0.0 |
| C15 | 38.0 | 29.0 | 26.5 | 36.5 | 11.5 | 22.0 | 10.0 | 3.0 |
| C16 | 34.0 | 30.0 | 27.5 | 32.5 | 12.0 | 22.0 | 10.5 | 3.0 |
| C17 | 34.5 | 32.5 | 29.5 | 32.5 | 13.5 | 22.0 | 10.5 | 4.0 |
| C18 | 31.5 | 34.0 | 33.0 | 33.5 | 15.0 | 22.5 | 11.0 | 4.5 |
| C19 | 32.0 | 40.0 | 32.5 | 33.5 | 17.5 | 23.0 | 12.0 | 4.5 |
| C20 | 34.5 | 44.0 | 32.0 | 31.5 | 17.5 | 26.0 | 14.0 | 6.0 |
| C21 | 38.0 | 43.5 | 28.5 | 28.0 | 20.0 | 27.0 | 14.5 | 10.0 |
| C22 | 36.0 | 47.5 | 26.5 | 26.5 | 21.0 | 29.0 | 14.5 | 6.0 |
| C23 | 33.0 | 50.0 | 27.0 | 25.0 | 19.5 | 30.0 | 15.0 | 8.0 |
| T1 | 31.5 | 53.0 | 21.0 | 26.0 | 19.0 | 31.0 | 14.0 | 13.0 |
| T2 | 30.0 | 52.5 | 20.0 | 30.0 | 13.0 | 33.0 | 15.0 | 14.5 |
| T5 | 33.0 | 49.5 | 23.0 | 34.0 | 12.5 | 40.0 | 16.0 | 1.0 |
| T6 | 32.0 | 48.0 | 22.0 | 33.0 | 15.0 | 39.0 | 16.0 | 1.0 |
| T7 | 34.5 | 46.5 | 22.0 | 32.0 | 16.5 | — | 16.0 | 0.0 |
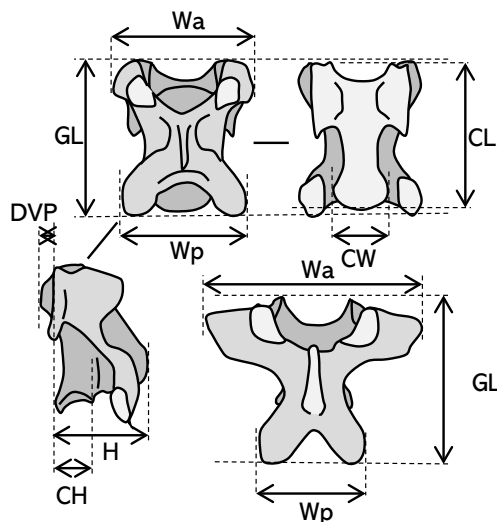
cause no problems in size reconstruction. The "osteological natural posture" (ONP) of *Annakacygna hajimei* was reconstructed and depicted in comparison with ONP of the mute swan (*Cygnus olor*) (**Plate 5**). Despite the relative differences in various parts, which will be discussed later, the two species have nearly the same curve length for the prepelvic vertebral column.

*Annakacygna hajimei* has a skull about 19 cm long, a neck length of about 70 cm, and free thoracic vertebral column of about 16 cm. The total of these three components is about 105 cm. Plus, the length of synsacrum, 15 cm, and as the total length of the free caudal vertebrae including pygostyle is estimated to be 15 cm, the total length of the axial skeleton, from the anterior tip of the bill to the posterior tip of the tail pygostyle is given to

about 135 cm by curve. For the estimation of the total length of the free caudal vertebrae including pygostyle, the skeletal specimen of *Cygnus melanocoryphus*, which has relatively well-developed free caudal vertebrae like *Annakacygna*, was referred.

We further estimated the ornithological "total length" (bill-to-tail body length, BL) of *Annakacygna hajimei*. Based on our observation on *Cygnus melanocoryphus*, in which the length from the tip of the pygostyle to the tip of the tail feathers is approximately equal to the total length of the free caudal vertebrae, the length of the part of tail feather-only in *Annakacygna hajimei* was estimated as 15 cm. As a result, the total length (BL) of *Annakacygna hajimei* is given as about 150 cm. This is same to that of mute swan *Cygnus olor*, a largest modern swan. Matsuoka and Hasegawa (2022) mentioned that *Annakacygna hajimei* was about the size of *Cygnus atratus*, whose BL is about 120 to 130 cm, but this must be corrected. The reexamination of vertebral fossils carried out in this study, that proposed longer vertebral column for this bird, requires re-drawing of the whole skeleton of *Annakacygna hajimei*. This is shown in **Plate 6**, and the comparison between the figure in the original description (Matsuoka and Hasegawa, 2022) and the result of this study is shown in **Fig. 17**.

In addition, Matsuoka and Hasegawa (2022) described a second species of *Annakacygna*, *A. yoshiiensis* which is "much larger than the type species, about 1.3 times larger". If we hypothesize that the "1.3 times" size difference can be applied to the proportion of birds, the BL of *A. yoshiiensis* would be calculated to 195 cm (**Fig. 18**). Together with *Cygnus falconeri* of the Maltese Pleistocene (Parker, 1865; Josep, 2000; Northcote, 2008; Watanabe, 2017), *Annakacygna yoshiiensis* is one of the largest swans to ever exist.

### Functional morphology of the vertebral column of *Annakacygna*

First, the unique, almost enigmatic, features in the prepelvic vertebrae of *Annakacygna* are listed below.

**1. Strong kyphosis at the base of neck:** In the lateral view of the osteological neutral posture, the prepelvic vertebral column of *Annakacygna* has a characteristic strong kyphosis (dorsally convex curve) at the portion of two-three posterior-most basal cervical vertebrae (BC) to CTB, and a strong lordosis (ventrally convex curve) at the portion of the anterior part of BC to the posterior part of pMC (**Fig. 19**, **Plates 5-7**). The strong kyphosis at around CTB is due to the characteristic morphology of the posterior-most cervical vertebrae C21-23, in which the posterior articular processes are significantly extended posteriorly than the level of posterior articular surface of corpus vertebrae while the anterior articular processes are at almost the same cranial level with the anterior articular surface of corpus vertebrae. Though a kyphosis at the base of neck is widely seen in birds, the degree in *Annakacygna*, which reaches nearly 50° against the line of thoracic vertebral column, and extremely exceeds the 20° state of *Cygnus cygnus*, is highly characteristic.

**2. Developed ventral process:** On the prepelvic vertebrae of *Annakacygna*, the ventral process develops in the posterior pMC, BC, and anterior FT vertebrae. The general pattern of morphological change of ventral process in vertebral column of *Annakacygna* is common with modern ("normal") swans, but the ventral processes in this genus are always huge in size relative to the size of each vertebra.

**3. Fat shape relative to the length:** The prepelvic vertebrae of *Annakacygna* do not differ in size of corpus vertebrae and in total length of vertebral column from those of modern large swans (see CL/CW graph of **Fig. 16**; **Plate 5**). On the other hand, as is evident in the graph of Wa values (**Fig. 15**), the width of each vertebra and size of the arch portion exceeds farther that of the modern largest *Cygnus olor*. Particularly it is significant in the posterior part of the cervical column.

**4. Wide concavitas lateralis, and short and thick proc. costalis in the cervical vertebrae:** In the cervical vertebrae of *Annakacygna*, the proc. costalis are very short and

Table 3. Measurements on the prepelvic vertebrae of modern Anatidae.

**Cygnus (Cygnus) olor**

| | C2 | C3 | C4 | C5 | C6 | C7 | C8 | C9 | C10 | C11 | C12 | C13 | C14 | C15 | C16 | C17 | C18 | C19 | C20 | C21 | C22 | C23 | C24 | T1 | T2 | T3 | T4 | T5 | T6 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CL | 11.1 | 19.6 | 32.4 | 33.4 | 35.8 | 35.3 | 35.4 | 37.2 | 37.4 | 39.3 | 38.9 | 38.1 | 39.9 | 39.6 | 38.0 | 36.7 | 35.2 | 33.4 | 33.3 | 32.3 | 29.9 | 25.8 | 23.5 | 23.1 | 26.3 | 27.1 | 26.2 | 26.3 | 25.5 |
| CW | 5.3 | 6.7 | 6.9 | 8.0 | 8.6 | 9.6 | 10.8 | 11.4 | 11.3 | 12.3 | 12.4 | 12.4 | 12.4 | 11.1 | 10.8 | 11.0 | 12.6 | 15.1 | 17.1 | 18.0 | 18.1 | 18.5 | 19.0 | 15.7 | 13.0 | 11.3 | 10.8 | 10.4 | 11.6 |
| Wa | 8.9 | 16.3 | 20.0 | 21.5 | 21.4 | 21.8 | 22.1 | 22.7 | 23.1 | 23.5 | 24.8 | 24.0 | 26.8 | 27.5 | 28.3 | 30.6 | 31.3 | 31.3 | 31.3 | 33.0 | 37.8 | 45.2 | 48.4 | 48.8 | 46.7 | 46.6 | 46.4 | 45.4 | 44.3 |

**Cygnus (Olor) cygnus**

| | C2 | C3 | C4 | C5 | C6 | C7 | C8 | C9 | C10 | C11 | C12 | C13 | C14 | C15 | C16 | C17 | C18 | C19 | C20 | C21 | C22 | C23 | T1 | T2 | T3 | T4 | T5 | T6 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CL | 20.9 | 25.9 | 28.4 | 30.8 | 31.5 | 31.1 | 31.4 | 32.0 | 32.4 | 32.7 | 32.4 | 33.2 | 35.3 | 35.9 | 35.0 | 34.5 | 33.4 | 33.2 | 32.9 | 31.1 | 27.2 | 24.0 | 22.3 | 23.6 | 26.1 | 26.6 | 26.0 | 25.7 |
| CW | 6.6 | 7.3 | 8.8 | 9.2 | 10.0 | 11.4 | 11.6 | 12.2 | 12.5 | 12.1 | 13.9 | 14.4 | 13.2 | 13.0 | 12.1 | 11.9 | 12.5 | 14.7 | 16.4 | 17.4 | 18.5 | 19.5 | 18.7 | 15.9 | 12.0 | 10.1 | 9.4 | 9.5 |
| Wa | 9.8 | 17.7 | 21.7 | 21.3 | 21.1 | 21.8 | 22.3 | 22.5 | 23.2 | 23.5 | 23.4 | 24.6 | 25.0 | 26.1 | 27.9 | 28.1 | 28.7 | 28.7 | 28.1 | 29.7 | 33.3 | 38.6 | 44.1 | 45.8 | 44.9 | 42.8 | 42.2 | 41.2 |

**C. (C.) melanocoryphus**

| | C2 | C3 | C4 | C5 | C6 | C7 | C8 | C9 | C10 | C11 | C12 | C13 | C14 | C15 | C16 | C17 | C18 | C19 | C20 | C21 | C22 | C23 | T1 | T2 | T3 | T4 | T5 | T6 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CL | 19.2 | 22.6 | 26.4 | 28.8 | 27.4 | 27.7 | 28.9 | 29.4 | 29.4 | 30.0 | 32.5 | 29.0 | 31.5 | 31.8 | 30.0 | 28.0 | 28.0 | 27.5 | 24.6 | 22.1 | 20.4 | 19.0 | 21.4 | 21.0 | 20.3 | 20.6 | 19.0 | 18.6 |
| CW | 4.6 | 5.6 | 6.0 | 7.1 | 7.0 | 7.9 | 8.2 | 8.5 | 9.3 | 8.5 | 8.9 | 10.5 | 8.3 | 8.0 | 10.2 | 9.8 | 10.4 | 12.9 | 14.7 | 15.3 | 16.3 | 13.8 | 9.3 | 8.9 | 7.0 | 7.4 | 8.0 | 7.4 |
| Wa | 5.7 | 13.8 | 15.8 | 16.5 | 16.4 | 16.8 | 16.1 | 16.1 | 16.0 | 16.4 | 16.4 | 17.4 | 19.4 | 20.9 | 22.2 | 22.4 | 23.5 | 25.2 | 25.2 | 28.2 | 31.4 | 29.3 | 31.2 | 31.6 | 31.2 | 31.2 | 30.7 | 29.3 |

**C. (C.) atratus**

| | C2 | C3 | C4 | C5 | C6 | C7 | C8 | C9 | C10 | C11 | C12 | C13 | C14 | C15 | C16 | C17 | C18 | C19 | C20 | C21 | C22 | C23 | T1 | T2 | T3 | T4 | T5 | T6 | T7 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CL | 21.0 | 25.3 | 28.4 | 30.1 | 31.0 | 31.9 | 32.7 | 32.2 | 32.6 | 33.1 | 33.4 | 33.4 | 34.2 | 34.0 | 33.5 | 32.4 | 31.0 | 29.5 | 29.4 | 27.3 | 24.0 | 21.0 | 19.8 | 19.7 | 19.9 | 20.2 | 21.0 | 20.9 | 20.5 |
| CW | 5.3 | 5.6 | 6.2 | 6.1 | 6.8 | 7.2 | 8.4 | 8.5 | 9.3 | 9.4 | 10.3 | 9.7 | 9.1 | 8.0 | 7.5 | 7.6 | 8.2 | 9.8 | 11.3 | 12.9 | 13.8 | 14.6 | 14.0 | 10.7 | 9.3 | 8.6 | 8.1 | 8.1 | 9.1 |
| Wa | 5.6 | 16.9 | 16.4 | 16.6 | 16.7 | 17.0 | 16.9 | 17.7 | 17.9 | 18.2 | 18.9 | 19.7 | 20.5 | 20.1 | 22.3 | 23.3 | 24.0 | 24.4 | 24.8 | 25.0 | 26.4 | 32.8 | 35.2 | 34.0 | 32.7 | 32.3 | 32.2 | 33.4 | 32.5 |

**Chauna torquata**

| | C2 | C3 | C4 | C5 | C6 | C7 | C8 | C9 | C10 | C11 | C12 | C13 | C14 | C15 | C16 | C17 | T1 | T2 | T3 | T4 | T5 | T6 | T7 | T8 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CL | 14.4 | 15.9 | 17.0 | 17.2 | 17.8 | 18.3 | 20.0 | 20.2 | 20.4 | 20.6 | 20.3 | 20.9 | 20.6 | 19.3 | 18.4 | 16.5 | 14.8 | 14.4 | 14.6 | 15.0 | 14.4 | 15.5 | 14.5 | 14.8 |
| CW | 3.6 | 3.7 | 4.4 | 4.7 | 5.4 | 6.1 | 6.4 | 6.4 | 6.4 | 6.4 | 6.4 | 6.9 | 6.7 | 7.1 | 6.9 | 6.7 | 7.4 | 7.6 | 8.0 | 8.1 | 7.6 | 7.8 | 8.4 | 9.6 |
| Wa | 5.4 | 12.5 | 12.5 | 12.7 | 12.6 | 13.1 | 15.1 | 15.6 | 16.6 | 16.5 | 16.5 | 17.7 | 17.6 | 18.0 | 18.1 | 19.7 | 22.5 | 24.5 | 26.2 | 27.8 | 28.4 | 30.3 | 30.0 | 31.7 |

**Cairina moschata**

| | C2 | C3 | C4 | C5 | C6 | C7 | C8 | C9 | C10 | C11 | C12 | C13 | C14 | C15 | T1 | T2 | T3 | T4 | T5 | T6 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CL | 18.0 | 20.0 | 20.5 | 21.6 | 22.7 | 24.9 | 25.4 | 25.3 | 24.6 | 24.6 | 24.2 | 24.7 | 21.1 | 18.0 | 15.9 | 17.2 | 19.8 | 19.4 | 19.4 | 18.0 |
| CW | 5.5 | 6.3 | 7.1 | 7.4 | 8.0 | 8.1 | 8.1 | 8.2 | 8.5 | 9.1 | 10.3 | 9.8 | 12.0 | 12.6 | 10.0 | 8.1 | 7.6 | 7.8 | 8.5 | |
| Wa | 6.1 | 15.9 | 17.4 | 18.8 | 18.6 | 18.5 | 24.6 | 22.3 | 24.6 | 24.4 | 24.1 | 24.2 | 24.0 | 30.7 | 29.4 | 27.0 | 26.9 | 25.8 | 27.8 | 29.9 |

**Dendrocygna viduata**

| | C2 | C3 | C4 | C5 | C6 | C7 | C8 | C9 | C10 | C11 | C12 | C13 | C14 | C15 | T1 | T2 | T3 | T4 | T5 | T6 | T7 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CL | 10.3 | 11.0 | 11.9 | 12.9 | 13.9 | 15.0 | 15.1 | 14.8 | 14.5 | 14.1 | 13.8 | 13.0 | 12.3 | 10.4 | 9.0 | 8.9 | 11.8 | 12.4 | 12.3 | 11.3 | 10.6 |
| CW | 2.2 | 2.8 | 3.1 | 3.5 | 3.7 | 4.0 | 4.2 | 4.1 | 4.1 | 4.2 | 4.5 | 4.3 | 5.5 | 5.6 | 5.4 | 5.2 | 4.2 | 3.7 | 3.6 | 4.2 | |
| Wa | 4.0 | 8.5 | 10.1 | 10.9 | 10.3 | 9.6 | 9.9 | 10.9 | 11.5 | 11.8 | 12.1 | 11.9 | 11.9 | 12.3 | 13.9 | 13.5 | 14.1 | 14.5 | 14.8 | 16.3 | 16.8 |

**Anser anser**

| | C2 | C3 | C4 | C5 | C6 | C7 | C8 | C9 | C10 | C11 | C12 | C13 | C14 | C15 | C16 | C17 | T1 | T2 | T3 | T4 | T5 | T6 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CL | 14.9 | 18.3 | 20.1 | 21.4 | 21.9 | 21.4 | 22.6 | 23.1 | 23.4 | 23.6 | 23.2 | 23.4 | 22.5 | 20.8 | 18.0 | 15.6 | 14.6 | 15.6 | 17.0 | 17.4 | 17.6 | 17.0 |
| CW | 4.5 | 5.5 | 6.0 | 6.0 | 6.0 | 7.1 | 7.3 | 7.3 | 6.6 | 6.9 | 7.6 | 8.2 | 9.3 | 10.0 | 10.9 | 11.4 | 11.4 | 10.0 | 7.7 | 6.1 | 6.8 | 6.0 |
| Wa | 5.1 | 14.2 | 15.0 | 15.8 | 16.1 | 15.9 | 15.7 | 15.8 | 20.1 | 17.8 | 19.8 | 21.0 | 20.2 | 19.2 | 20.5 | 25.0 | 28.0 | 26.4 | 24.1 | 27.4 | 28.6 | 27.1 |

**Cosoroba coscoroba**

| | C2 | C3 | C4 | C5 | C6 | C7 | C8 | C9 | C10 | C11 | C12 | C13 | C14 | C15 | C16 | C17 | C18 | C19 | C20 | T1 | T2 | T3 | T4 | T5 | T6 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CL | 15.8 | 19.8 | 22.5 | 23.0 | 23.6 | 24.0 | 24.7 | 25.0 | 26.0 | 26.5 | 26.0 | 25.1 | 24.2 | 24.4 | 23.6 | 23.9 | 20.7 | 17.3 | 16.1 | 16.7 | 18.4 | 18.9 | 18.5 | 18.0 | 16.7 |
| CW | 3.6 | 4.5 | 5.1 | 5.7 | 6.2 | 6.8 | 7.7 | 7.3 | 6.9 | 7.3 | 6.9 | 7.3 | 8.1 | 8.4 | 9.0 | 8.3 | 10.1 | 11.2 | 11.5 | 10.6 | 7.9 | 6.4 | 6.2 | 6.1 | 6.9 |
| Wa | 5.0 | 12.6 | 12.9 | 13.2 | 13.8 | 14.3 | 13.7 | 14.0 | 13.3 | 14.4 | 16.4 | 18.0 | 18.7 | 19.9 | 19.8 | 19.6 | 20.2 | 24.3 | 27.7 | 28.5 | 28.7 | 29.4 | 27.8 | 28.8 | 29.4 |

**Annakaygna hajimei**

| | C2 | C3 | C4 | C5 | C6 | C7 | C8 | C9 | C10 | C11 | C12 | C13 | C14 | C15 | C16 | C17 | C18 | C19 | C20 | C21 | C22 | C23 | T1 | T2 | T3 | T4 | T5 | T6 | T7 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CL | | 26 | 28 | 29 | | | | | | | | | | 36.5 | 32.5 | 32.5 | 33.5 | 33.5 | 31.5 | 28 | 26.5 | 2 | 26 | 30 | | | 34 | 33 | 32 |
| CW | | 9.5 | 10.5 | 11 | | | | | | | | | | 11.5 | 12 | 13.5 | 15 | 17.5 | 17.5 | 20 | 21 | 19.5 | 19 | 13 | | | 12.5 | 15 | 16.5 |
| Wa | | 21.5 | 24 | 24.5 | | | | | | | | | | 29 | 30 | 32.5 | 34 | 40 | 44 | 43.5 | 47.5 | 50 | 53 | 52.5 | | | 49.5 | 48 | 46.5 |

robust. Correlated with this feature, lamina arcocostalis never extends posteriorly beyond the anterior half of the vertebra, and in the lateral face of the posterior half of each vertebra, there is a wide concavitas lateralis. These features are seen in both the anterior cervical vertebrae (C3-5) and the posterior ones (C15-23) of *Annakacygna hajimei*, it must have been common in entire cervical vertebrae of this bird.

5. Long thoracic vertebrae: As shown in Fig. 16-c, the CL/CW plots for the cervical vertebrae of *Annakacygna hajimei* fit reasonably to the "$\rho$ + swan's loop" curve common in swans. However, the posterior three free thoracic vertebrae are much longer than expected and deviate from this general curve. FT5 is the longest among free thoracic vertebrae. FT5, FT6 and FT7 progressively decrease in length and increase in width.

6. Poor proc. transversus and proc. spinosus in thoracic vertebrae: Normally, birds, of course modern swans too, have anteroposteriorly broad and rectangular shaped proc. transversus in the free thoracic vertebrae. On thoracic vertebrae, there are also significant ossified tendons fused on the dorsal face of these processes, and they make the thoracic cage a basket-like rigid structure. Although not known in anatids, even a fused thoracic notarium is formed in many birds (Samejima and Otsuka, 1984). In the free thoracic vertebrae of *Annakacygna* (**Plate 3**), however, the proc. transversus is very thin relative to the long thoracic vertebra. The dorsal view of transverse processes of *Annakacygna* resembles airplane wings, and have big spaces between articulations. The fusion of ossified tendon is almost nonexistent, and only slight on the proc. transversus of FT7.

The same is for the proc. spinosus. Normally, birds have thick and anteroposteriorly long (wide in lateral view) developed proc. spinosus in thoracic vertebrae. However, in *Annakacygna*, the proc. spinosus is anteroposteriorly short, and there is a big space in between the neighboring vertebrae when articulated (**Plate 5**).

7. Low intercostal articulations in thoracic vertebrae: The thoracic vertebrae are characterized by the presence of two foveas costalis, one at the tip of the transverse process (fovea costalis to the tuberculum costae), and another on the lateral surface of corpus vertebrae (fovea costalis to the caput costae). The thoracic vertebrae of *Annakacygna* are characterized by a dorsoventrally low space in between both foveas in the lateral view (**Plate 4**). This is also evident when we look the ribs (**Fig. 20**). In a modern swan *Cygnus olor*, the collum costae is almost on the extension of the curvature of corpus costae, whereas in *Annakacygna* the collum costae is strongly turned cranially.

Now to elucidated enigmas, from the viewpoint of the functional morphology.

Some of the above listed features are relatively easy to understand, while others are highly enigmatic.

One matter that is easy to understand is the development of the ventral process (No. 2 of above enigmas). The ventral process is the origin of the muscle longus colli ventralis (Kuroda, 1962; Baumel, 1979; Berge, 1979; George and Berger, 1966) and it is likely to develop in *Annakacygna*, which was "head-heavy" (Matsuoka and Hasegawa, 2022) and had a long neck.

Another evident feature is the one related to the air sacs. Because the concarvitas lateralis of cervical vertebra is the space filled by the cervical air sac that wraps the carotid (e.g., Goodrich, 1930; Kent and Miller, 1997; König et al., 2009), the enigmas such as the development of the arch portion in cervical vertebrae (No. 3 of above enigmas), the anteroposteriorly short lamina arcocostalis and wide concavitas lateralis, and the short and robust proc. costails (ibid. No.4) are comprehensible as the indicator of well-developed cervical air sacs in and along the cervical vertebrae in this bird. And, the resultant swelling of the vertebral arch reflects the development of the attached dorsal

cervical muscles. Then the development of soft tissues, cervical air sac and muscles, can be the key to see the enigmatic osteology of prepelvic vertebrae of *Annakacygna*. *Annakacygna* must have been an animal of high neck mobility in life.

An assumption of developed air sac can also be the key to see the other osteological enigmas. At the ventral portion of the posterior neck, just anterior to CTB where it is over hanged by the vertebral column with strong kyphosis (as described in No. 1 of above enigma), large interclavicular and cervical air sacs should have been located and the large cervical vertebrae are highly pneumatic. Then, the strong kyphosis at the base of neck

would have pushed the set of these air-filled organs ventrally, to under the water surface in the floating bird.

For the waterfowls swimming on the surface of the water, the set of air-filled organs pushed under the water level would have served as a "float" (**Fig. 21**). Because of this simple dynamics, this "float" at the base of the neck provides buoyancy and stabilizes the body of swimming *Annakacygna*, in both situation when the bird raised her long and "head-heavy" neck and when her body was submerged with chicks on the back.

The remaining enigmas (No. 6 and 7 of above list) on *Annakacygna* are both related to the thoracic vertebrae. The
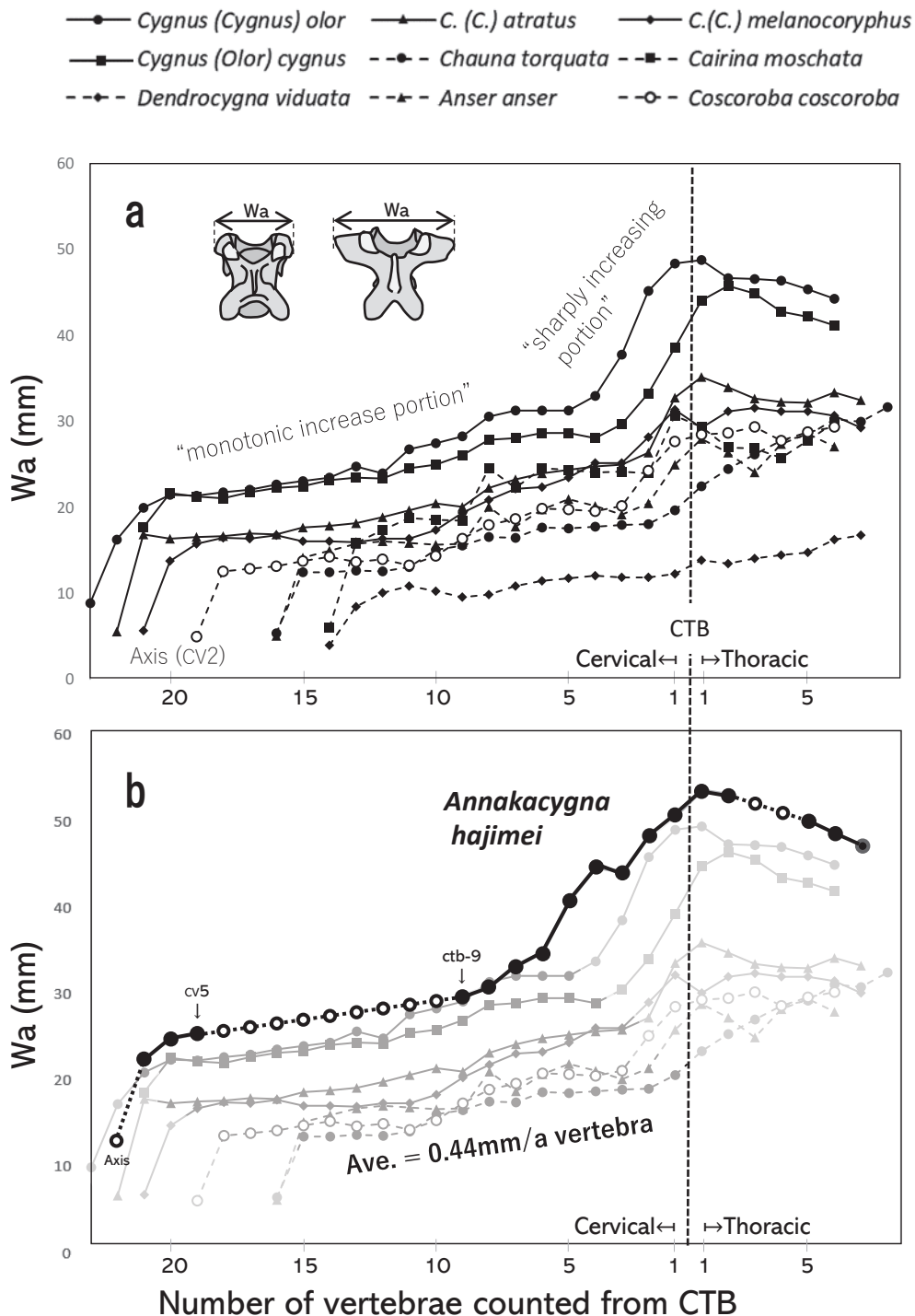


Figure 15. The line graph of Wa, width measured between the tips of transversal processes, arranged by the position in prepelvic vertebral column. **a**: modern Anatidae species, not only Cygnini. **b**: 7 modern species + *Annakacygna hajimei*. See text for the detail.
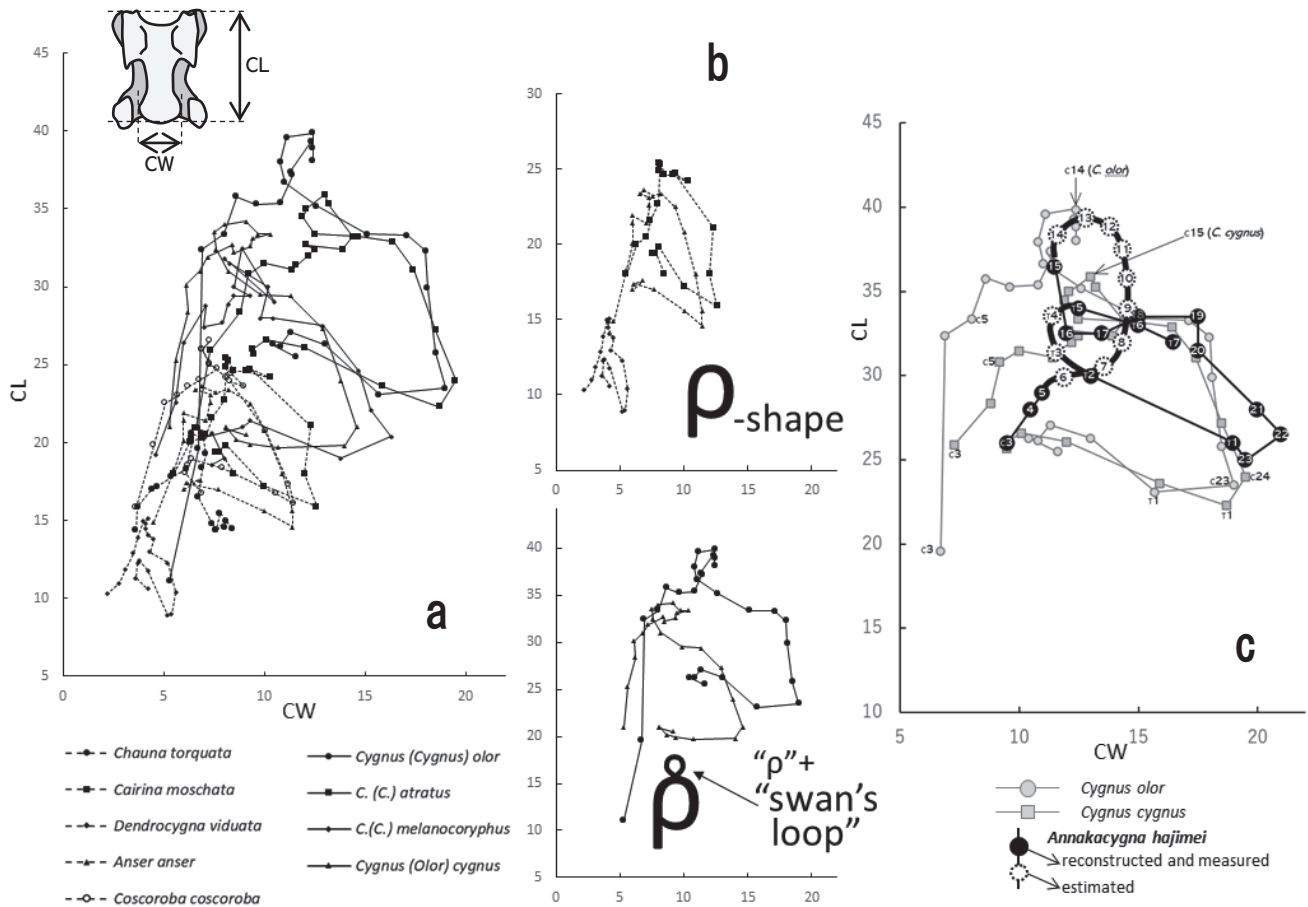
**Figure 16. The CL/CW graph.** CL/CW measurements were done for all prepelvic vertebrae except atlas, and neighboring vertebrae are linked by lines. **a**: graph of 9 measured modern anatid species. **b**: Two types of general curve of CL/CW graph line. Non-Cygnini anatids show " $\rho$ " (Greek Rho) shaped curve (b-top), while swans (Cygnini) have a loop (named "swan's loop" here) on top of the " $\rho$ " (b-bottom). **c**: The data plot of *Annakacygna hajimei*, with comparison to swans. The lacking portion in *Annakacygna hajimei* can be estimated in reference to the general trend in swans.

thoracic vertebral column is where the "piggybacked" chicks ride (Matsuoka and Hasegawa, 2022), and actually the enigmas on the thoracic cage can be explained from such view.

The first enigmatic matter is that the thoracic vertebrae of *Annakacygna* are anteroposteriorly quite long. The proc. spinosus and proc. transversus of all free thoracic vertebrae are, however, small and spaced in the articulated state. And there is no fusion of ossified tendons on free thoracic vertebrae of *Annakacygna*. To explain the combination of these features, we must assume that the thoracic vertebral column of *Annakacygna* was highly flexible.

Once a view of "flexible thoracic column" is assumed, it is then understandable that the thoracic vertebrae of *Annakacygna* had low intercostal articulations, as an adaptation to make the thoracic cage dorsoventrally flexible. The ribs of *Annakacygna* had the morphology that corresponds to the flexibility of the thoracic cage (**Fig. 20**), and this may have ensured their flexure in the dorsoventral direction. One of the diagnostic features of *Annakacygna*, "ribs without fused uncinate processes" (Matsuoka and Hasegawa, 2022) is revealed as an adaptation giving flexibility to the thoracic cage. Based on the anatomical knowledge on modern birds (e.g., Goodrich, 1930; Kent and Miller, 1997; Matsuoka and Seoka, 2021), *Annakacygna* would have had air sacs surrounding the ventral side of the thoracic vertebral column and proximal ribs in life. This air sac would have acted as the "cushioning material" to prevent the impact of the flexure of the thoracic vertebral column from being transmitted to the internal organs.

The development of this air sac may have contributed to the development of the ventral process in the anterior thoracic

vertebrae (FT1-2). The tip of the process was the origin of m. longus colli ventralis, but its base and sides would have been covered and filled by air sacs (Matsuoka and Seoka, 2021), so the ventral processes in *Annakacygna* must have been elongated to avoid being buried by the air sacs.

The free thoracic vertebral column is anchored to the coracoid-sternum system at the position of CTB as the anterior end, and to the pelvis as the caudal end. The long thoracic vertebral column, which was dorsoventrally flexible, was a structure like a "suspension bridge" between these two ends. This "suspension bridge" absorbed the weight of the chicks on the back. Moreover, the "floats" of the air sacs at the base of the neck kept the anterior "bridge pier" from being submerged. Even with many (heavy) chicks on board, the levelness of the entire back is relatively well maintained due to the ventral curvature (cushioning) of the thoracic vertebral column. It can be concluded that the long, flexible thoracic vertebral column in *Annakacygna* was indeed a well-designed structure for piggybacking.

Now a historically famous aphorism by Georges Cuvier who characterized a life as "l'ensemble des fonctions qui résistent à la mort" (in English, "ensemble of functions that resist death") (Cuvier, 1800-1805; Outram, 1986) recurs to the authors' minds.

The original description of *Annakacygna* (Matsuoka and Hasegawa, 2022) noted remarkable evolutionary structures of this birds and called *Annakacygna* the "ultimate birds" that ever existed. The "ensemble", however, was somewhat not harmonious in that paper, because two subjects, the head and the wings, were separated. Now, by this study, which revealed the
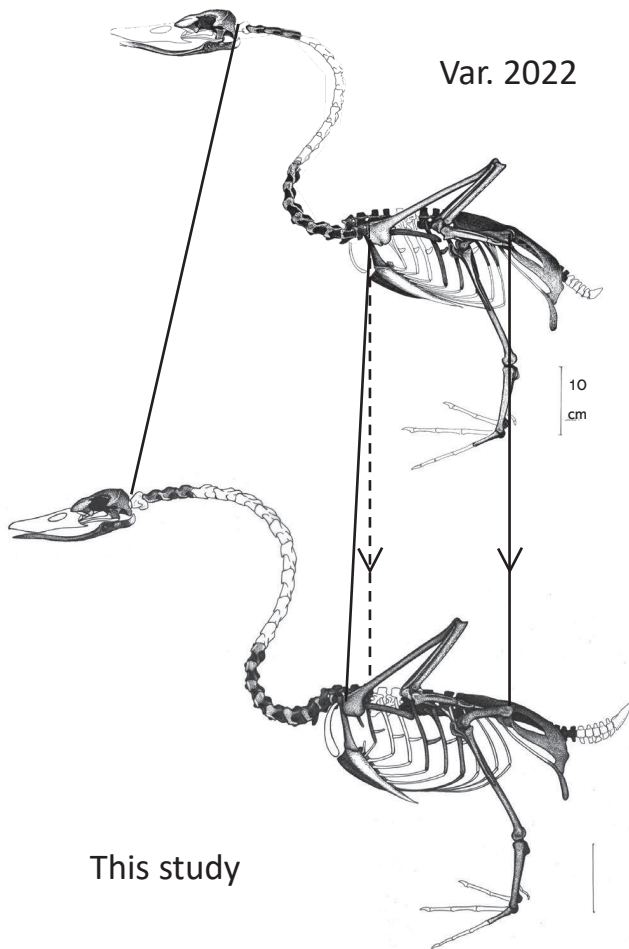
Figure 17. Comparison of drown whole skeletons between the one in the original description (top, from Matsuoka & Hasegawa, 2022) and the result (Plate 6) of this study (bottom). Note the longer neck and thoracic cage reconstructed in this study.

detailed morphology and the functions of the vertebral column and connected the head and pelvis, we think truly a harmonic "ensemble of function" has appeared here. The ensemble members are the "float" at the base of the neck, flexible free thoracic vertebral column and ribcage, the musculoskeletal system of wings which forms lateral walls in the back of parents, robust and flexible tail which form the caudal wall in the back of parents, and so on.

Curiously, it is the chicks who receive the benefit of "ensemble of function" and survive from "la mort", not the parents who carry the "ensemble". That means, except the specialization of head for food that is absolutely for the individual, the "ensemble" is the adaptive equipment for the next generation. So, the evolution of *Annakacygna* cannot be understood by classic "Darwinian Fitness" only, and should be discussed under the view of sociobiological "Inclusive Fitness" (Hamilton, 1964; Smith, 1998).

Then *Annakacygna* is a good example of "Kin Selection" (West et al., 2007). Among the kin, because the user of adaptive equipment is limited to the parents' own chicks, it is "chick selection" so to speak.

*Annakacygna* are truly exciting birds, which have been assembled through many evolutionary steps, such as food niche shift under the geohistorical and environmental background, flightlessness, reflection of ecology and sociality of family bonds on the osteology, and mechanical and functional harmony of all parts etc. Further investigation on the osteology of *Annakacygna*,

and exploration of ancestral new fossil material in older strata, may provide us many more new views and ideas on avian (animal) evolution.

## CONCLUSION

*Annakacygna* is an extinct flightless anatid bird belonging with Cygnini. The type species *A. hajimei* was found as the fossilized nearly complete associated skeleton from the marine Miocene Haraichi Formation (11.5 Ma) of the Annaka Group of Gunma Prefecture, Japan. The holotype of the type species (GMNH-PV-678, Gunma Museum of Natural History) has great advantage for the biological research as the skeletal elements retain their three-dimensional morphology.

This study reexamined the totally 17 prepelvic vertebral fossils of the holotype of *Annakacygna hajimei*, 12 cervical vertebrae and 5 free thoracic vertebrae, that were not well described in the original description (Matsuoka and Hasegawa, 2022) because the fossils are heavily deformed in the strata. As a result of this study, the 12 cervical fossils in the holotype are identified as the 3$^{rd}$ to 5$^{th}$ and the 15$^{th}$ to 23$^{rd}$ cervical vertebrae, and five thoracic fossils are the 1$^{st}$ and 2$^{nd}$ and 5$^{th}$ to 7$^{th}$ (last) free thoracic vertebrae. This is, as a result, the same as the original description, but the order of some fossils was changed. For each
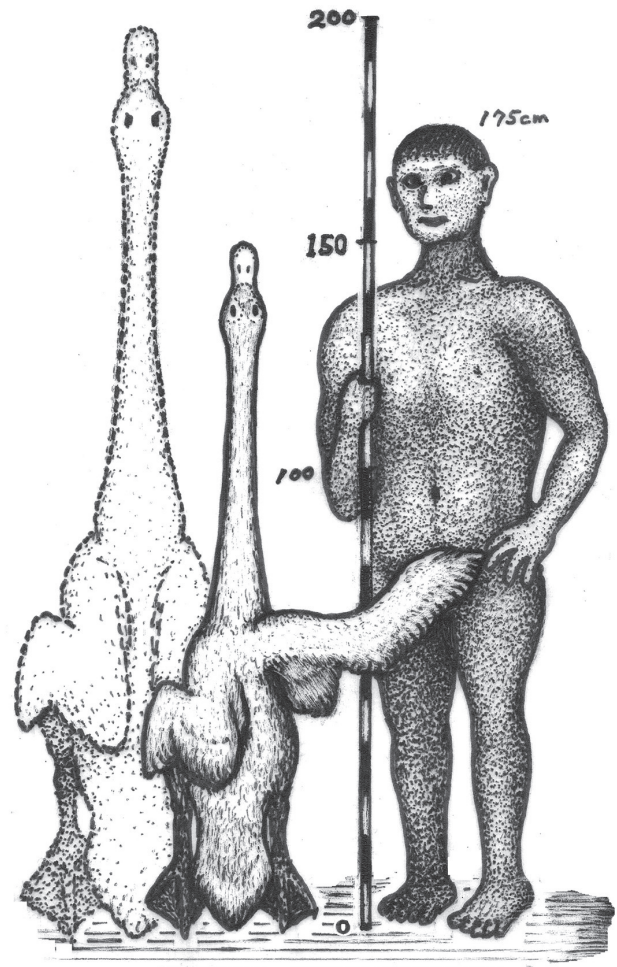


Figure 18. A cartoon to show the size of *Annakacygna* species. The smaller bird, next to the 175 cm tall human is *A. hajimei* (150 cm bill-to-tail length, BL), and the larger bird in the left of the figure is *A. yoshiiensis* (195 cm BL).
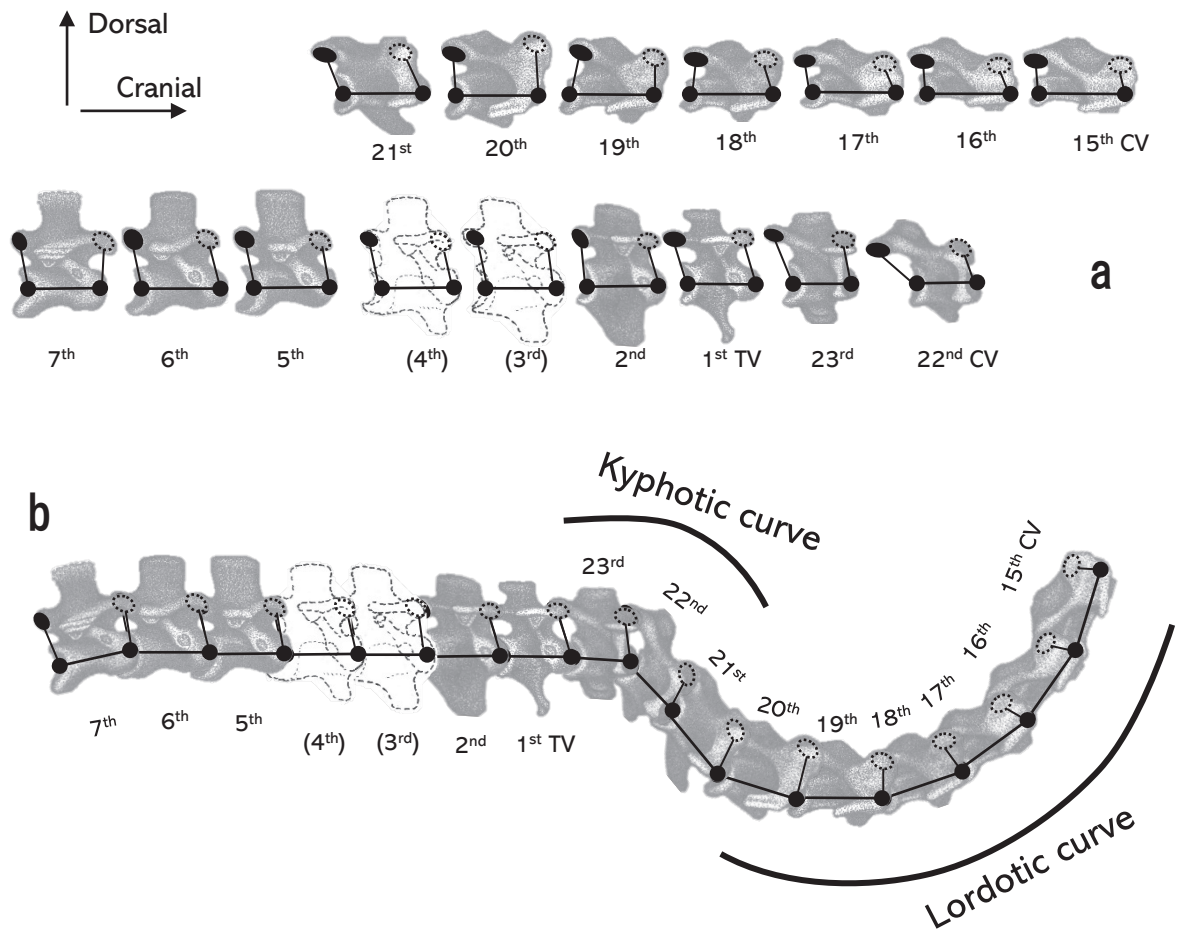
Figure 19. The lateral views of the prepelvic vertebrae of *Annakacygna hajimei*. The individual vertebrae (**a**) and the articulated column in ONP (**b**). On all vertebral views, the positions of (the central point of) the four articulation faces are indicated: the cranial top (broken oval) is the facies articularis of proc. artic. cranialis, the cranial bottom point is the center of facies articularis cranialis, the caudal top (solid oval) is the facies articularis of proc. artic. caudalis, and the caudal bottom point is the center of facies articularis caudalis. By laying over the anterior and posterior articulations of vertebrae, the ONP column was figured out.

fossil vertebra, the original shape was recreated by restoring the deformation due to compaction in strata.

The total length of the vertebral column of *Annakacygna hajimei* was reconstructed as 135 cm. Plus, as the length of the tail feather-only in *Annakacygna hajimei* was estimated as 15 cm, the total (bill-to-tail) length of *Annakacygna hajimei* is given as about 150 cm. This is the same as that of of the largest modern swan *Cygnus olor*. Matsuoka and Hasegawa (2022) mentioned that *Annakacygna hajimei* was about the size of *C. atratus*, which is about 120-130 cm in total, but this must be corrected. Calculating from the size of *A. hajimei*, the second and larger species of *Annakacygna*, *A. yoshiiensis* is reconstructed to a gigantic bird of 195 cm total length.

Through this study, we found that the prepelvic vertebrae of *Annakacygna* had many enigmatic morphological features. They are: 1) strong kyphosis at the base of neck; 2) developed ventral process; 3) expanded morphology relative to the length; 4) wide concavitas lateralis, and short and thick proc. costalis in the cervical vertebrae; 5) long thoracic vertebrae; 6) poor proc. transversus and proc. spinosus in thoracic vertebrae; and 7) low intercostal articulations in thoracic vertebrae. The ribs also have the peculiarity that the uncinate process is not fused to the rib body, as noted in the original description.

We considered all the enigmas to be interpretable in terms of the unique mode of life of *Annakacygna*. Many of the enigmas can be solved by assuming the developed air sac in life and the habit of "piggybacking", one of the important ecological features

described in the previous report as "the ultimate bird". The enigma relating the basal portion of the neck, No. 1-5 of above listing, can be explained by the development of air-filled organs at the base of the neck, which were used as a "float". The strong
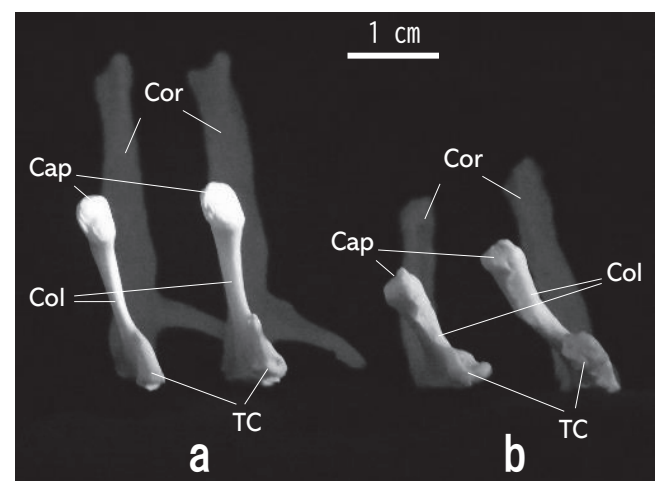


Figure 20. The proximal views of ribs of *Annakacygna hajimei* (right two), in comparison with them in mute swan (left two).
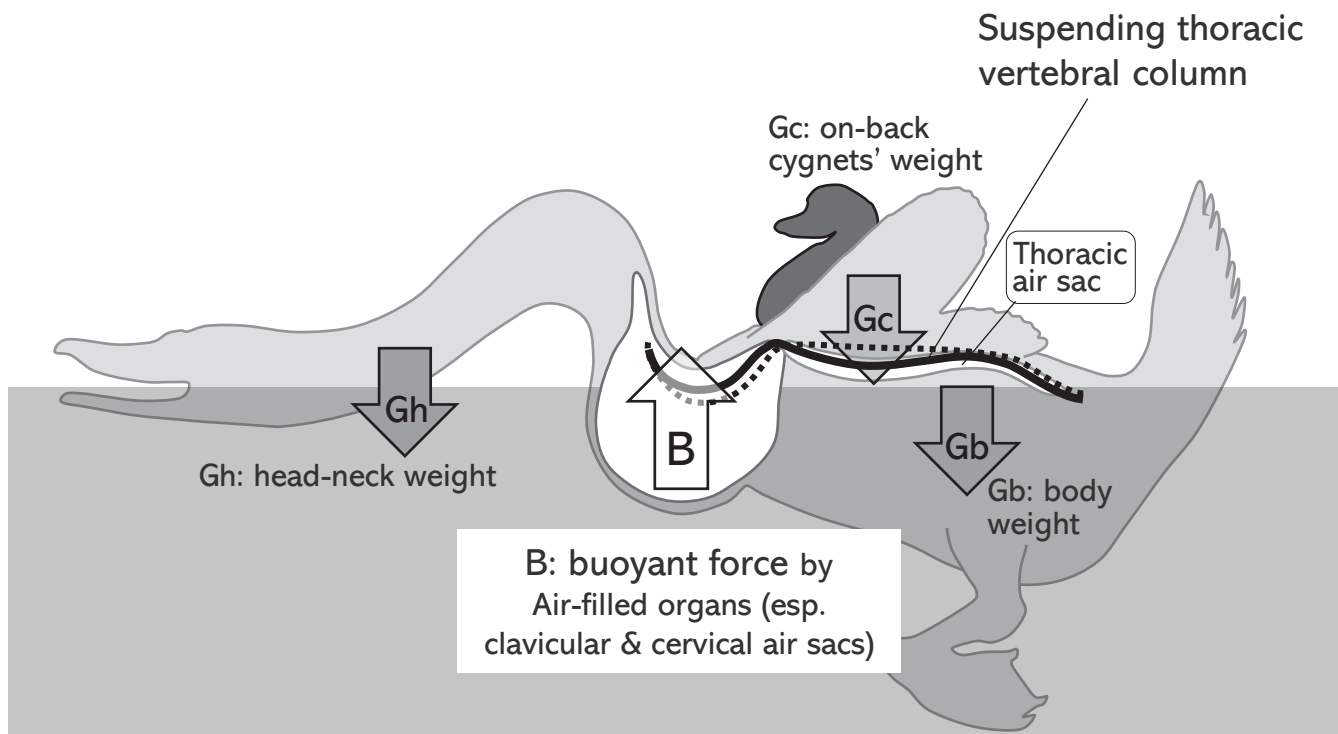
**Figure 21.** The reconstructed body plan and schematic dynamics of the prepelvic vertebral column in *Annakacygna hajimei*. By the "floating ring" air sac system at the base of parent's neck acts as the fulcrum on the body axis to give the buoyancy and stabilize the parent's body.

kyphosis at base of the neck would push this "float" strongly ventrally, and the "flotation ring" at the base of the neck provides buoyancy and stabilizes the body, whenever the bird raises its long neck or when the body is submerging with chicks on the back.

The enigmas about the thoracic vertebrae (No. 6 and 7 of above listing) and ribs are solved when considering the habit of "piggybacking". The back is the part of the body on which the piggybacked chicks ride. The thoracic vertebral column of *Annakacygna* was highly flexible due to the combination of long vertebrae, poor spinous and transverse processes on each vertebra, and the absence of ossified tendons. The articulation condition with the ribs suggests suppleness of the thoracic vertebral column in the dorsoventral direction. The thoracic air sacs are present in this area, encasing the vertebral part of the thoracic vertebral column, and are hypothesized to have provided a cushioning of the thoracic vertebral column to prevent the impact of its flexure from being transmitted to the internal organs. One of the diagnostic but enigmatic features of *Annakacygna*, "ribs without the fusion of uncinate process," is also understood to have been an adaptive form that ensured flexibility of the entire thoracic cage.

The prepelvic vertebral column is anchored to the coracoid at the position just posterior to the CTB and to the pelvis at the caudal end. The long thoracic vertebral column of *Annakacygna*, which is flexible dorsoventrally, is a "suspension bridge" structure between these two ends, which may have absorbed the weight of the chicks on the back. The cervical and thoracic sections together have mechanical properties that keep the anterior "pier" of this suspension bridge from submerging due to the "float" of the air sacs at the base of the neck. Then, even with many chicks on it, the levelness of the entire back is relatively maintained and sinking of the back did not occur due to the good flexibility of the thoracic vertebral column. In addition to the features noted by Matsuoka and Hasegawa (2022) on wings and tail, this study found that the back, where the chicks sit, was also "comfortable" to ride because shock was absorbed.

This result showed how well the body of *Annakacygna* had been structured for the "next generation". So, again, we absolutely think *Annakacygna* should be called the "ultimate birds". *Annakacygna* tell us the existence of an evolutionary process of one patten of kin selection, that should be called "chick selection".

Plate 8 is an authors' image of a family of *Annakacygna*.

## ACKNOWLEDGMENTS

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# *Annakacygna hajimei*（鳥綱ガンカモ目ハクチョウ族）の骨盤前方椎骨の再検討：
# 明らかになった"究極の鳥"としての本属の生態に関連した脊柱の適応形態

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**要旨**：*Annakacygna hajimei*は群馬県安中市の海成中新統安中層群原市層（11.5 Ma）から発見，記載された絶滅無飛翔鳥類である．本研究は*A. hajimei*のホロタイプ（群馬県立自然史博物館所蔵GMNH-PV-678）に含まれる頸椎12，自由胸椎5の，計17点の骨盤前方椎骨を再検討して，本種の系統と脊柱の機能形態を考察した．結果として，*Annakacygna*の生時の頸椎数は23と復元され，これに基づき本属はハクチョウ族の一員であると再確認された．

　各椎骨化石について圧密変形を戻して原形態を描出し，脊柱の正確な復元をした結果，*A. hajimei*は吻端から尾骨先端までの中軸骨格長が約135 cm，尾羽も含めた鳥の全長は150 cmと復元された．原記載ではコクチョウとほぼ同長（120 – 130 cm）と見積もったのであるが，それは修正しなければならないことになった．また，*Annakacygna*の第2の種*A. yoshiiensis*は全長2 m近い巨鳥と復元される．

　各椎骨の復元像の形態学的検討により，*Annakacygna*の頸は頸椎 – 胸椎境界（CTB）で強く背弯した特異なカーブをしていて，頸の付け根に発達した叉骨間気嚢と頸気嚢とからなる「浮き輪」を腹側（水中）に差し込むような構造になっていたと考えられる．これによって*Annakacygna*の親鳥は，長い頸をもたげ頭部が沈む状況にも背中にヒナが乗って胴が沈められる状況にも，頸の付け根の「浮き輪」が体軸上の支点となって，支点に浮力を与えて体を安定させる．胸椎柱は，各椎骨の長い椎体・貧弱な棘突起と横突起・骨化腱の不在などの特徴により，高い柔軟性を有していたと考えられる．関連して，*Annakacygna*の標徴的な特徴の一つ「カギ状突起が癒合しない肋骨」も，胸郭全体の柔軟性を確保させる適応形態であったと解された．背腹方向にしなる長い胸椎柱は，「つり橋」のような構造物で，背中に乗るヒナの重さを吸収したと考えられる．*Annakacygna*は血縁選択の好例である．*Annakacygna*の骨盤前方脊柱は実によくできた構造物であって，原記載で指摘された「究極の鳥」の適応形態が，ここにも現れていたことが明らかになった．

　**キーワード**：アンナカコバネハクチョウ，アンナカキグナ，中新世，安中層群，無飛翔性鳥類，カモ科，ハクチョウ族，骨盤前方椎骨

## Matsuoka, Seoka and Hasegawa: Plate captions

Plate 1. The reconstructed measured images of the 3$^{rd}$, 4$^{th}$, 5$^{th}$, 15$^{th}$, 16$^{th}$, and 17$^{th}$ cervical vertebra of *Annakacygna hajimei*.
The dorsal, ventral, and cranial images.

Plate 2. The reconstructed measured images of the 18$^{th}$, 19$^{th}$, 20$^{th}$, 21$^{st}$, 22$^{nd}$, and 23$^{rd}$ (last) cervical vertebra of *Annakacygna hajimei*.
The dorsal, ventral, and cranial images.

Plate 3. The reconstructed measured images of the 1$^{st}$, 2$^{nd}$, 5$^{th}$, 6$^{th}$, and 7$^{th}$ (last) thoracic vertebra of *Annakacygna hajimei*.
The dorsal, ventral, and cranial images basically, but no cranial image for 6$^{th}$ thoracic vertebra. The cranial image of the 5$^{th}$ thoracic vertebra is drowned with a rib.

Plate 4. The reconstructed measured right lateral images of 17 prepelvic vertebrae of *Annakacygna hajimei*, with possible outline of the missing 3$^{rd}$ and 4$^{th}$ thoracic vertebrae.

Plate 5. The reconstructed vertebral column of *Annakacygna hajimei* in "osteological neutral posture" (ONP), with comparison to that of modern mute swan *Cygnus olor*.

Plate 6. The newly reconstructed whole skeleton of *Annakacygna hajimei*.
In this figure, the left wing is folded and kept in the "piggy backing" posture, and the right wing is in the fully extended posture.

Plate 7. The skeleton of *Annakacygna hajimei* in possible mode of life, resulted in this study.

Plate 8. An authors' image of *Annakacygna* family.

Dorsal     Ventral     Cranial

3rd CV

4th CV

5 cm

5th CV

15th CV

16th CV

17th CV

Plate 2

Dorsal        Ventral        Cranial

18th CV

19th CV

5 cm

20th
CV

21st
CV

22nd
CV

23rd
CV

Plate 3



Dorsal

Ventral

Cranial

1st
TV

2nd
TV

5th
TV

6th
TV

7th
TV

5 cm

Plate 4

Plate 6



10 cm

Plate 7

Plate 8