

Fossil evidence of the avian vocal organ from the Mesozoic

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From complex songs to simple honks, birds produce sounds using a unique vocal organ called the syrinx^{1,2}. Located close to the heart at the tracheobronchial junction, vocal folds or membranes attached to modified mineralized rings vibrate to produce sound^{1–7}. Syringeal components were not thought to commonly enter the fossil record⁶, and the few reported fossilized parts of the syrinx are geologically young^{8–11} (from the Pleistocene and Holocene (approximately 2.5 million years ago to the present)). The only known older syrinx is an Eocene specimen that was not described or illustrated¹². Data on the relationship between soft tissue structures and syringeal three-dimensional geometry are also exceptionally limited⁵. Here we describe the first remains, to our knowledge, of a fossil syrinx from the Mesozoic Era, which are preserved in three dimensions in a specimen from the Late Cretaceous (approximately 66 to 69 million years ago) of Antarctica. With both cranial and postcranial remains, the new *Vegavis iaai* specimen is the most complete to be recovered from a part of the radiation of living birds (*Aves*). Enhanced-contrast X-ray computed tomography (CT) of syrinx structure in twelve extant non-passerine birds, as well as CT imaging of the *Vegavis* and Eocene syrinxes, informs both the reconstruction of ancestral states in birds and properties of the vocal organ in the extinct species. Fused rings in *Vegavis* form a well-mineralized pessulus, a derived neognath bird feature, proposed to anchor enlarged vocal folds or labia⁵. Left-right bronchial asymmetry, as seen in *Vegavis*, is only known in extant birds with two sets of vocal fold sound sources. The new data show the fossilization potential of the avian vocal organ and beg the question why these remains have not been found in other dinosaurs. The lack of other Mesozoic tracheobronchial remains, and the poorly mineralized condition in archosaurian taxa without a syrinx, may indicate that a complex syrinx was a late arising feature in the evolution of birds, well after the origin of flight and respiratory innovations.

In the mid-nineteenth century, T. H. Huxley named the unique vocal organ in birds as the syrinx¹. He also recognized that birds were most closely related to dinosaurs. However, neither he nor most subsequent authors that studied the syrinx^{2–4} addressed its origin, early evolution or probable ancestral states. More recently, it was noted that given the distribution of the syrinx in living birds, it was possibly ancestral to the crown clade *Aves*⁶. The few hypotheses about non-avian dinosaur vocal behaviour have focused on the possibility of a larynx-based sound source, the outgroup condition present in other tetrapods¹³, or speculated that most—those lacking an interclavicular air sac—might have been mute¹³. Others did not focus on the sound source (larynx or syrinx), but on possible resonating chambers in the skull of some ornithischian dinosaurs^{14,15}. Although there are also no fossils of the

laryngeal sound source in frogs, reptiles or mammals, data from the hyoid skeleton, skull and vertebral column have been proposed to inform evolutionary changes in its position in hominoids¹⁶ and in bats¹⁷. However, neither direct fossil evidence nor indirect inferential approaches have so far been used to inform our understanding of the origin of the syrinx.

A three-dimensionally preserved syrinx in a partial skeleton of a Late Cretaceous fossil bird from Vega Island, Antarctic Peninsula (MACN-PV 19.748 (MACN-Museo Argentino de Ciencias Naturales), Figs 1 and 2, Extended Data Figs 1, 2, 4–8, Supplementary Information, Supplementary Table 1 and Supplementary Fig. 1), is here referred to the species *Vegavis iaai*¹⁸ (Supplementary Information, Extended Data Figs 4 and 6). X-ray computed tomography (CT) was used to digitally extract syrinx remains from this fossil, as well as from the previously reported Eocene fossil anseriform specimen (*Presbyornis* sp¹²; USNM PAL 617185; (USNM-United States National Museum) Fig. 3, Extended Data Fig. 8, Supplementary Table 4 and Supplementary Fig. 2). Iodine-enhanced contrast CT (diceCT)¹⁹ data was acquired for 12 extant birds and one outgroup exemplar (Fig. 3, Extended Data Fig. 8, Supplementary Information, Supplementary Tables 1 and 4) to inform the placement of three displaced portions of the syrinx and inference of the location of sound-generating tissues (membranes or labia). These data provide insight into the three-dimensional geometry of the syrinx and the relationship between the structure of the mineralized rings and soft tissue²⁰.

Nine elements of the mineralized rings of the syrinx in MACN-PV 19.748 are preserved adjacent to the cranial-most thoracic vertebrae, close to their position in life (Fig. 2a, b, coloured elements I–IX). Three of these elements were preserved in articulation, whereas the remaining elements lay on either side of the thoracic vertebrae (Fig. 2b). Three are clearly bronchial elements (Fig. 2b elements V–VII, Extended Data Fig. 7 and Supplementary Table 3). They are half rings, two of which have slightly expanded ventral tips (Fig. 2c, Extended Data Fig. 7 and Supplementary Fig. 1). The reduction of the medial aspect of bronchial rings is the most consistent feature of an avian syrinx; in outgroup archosaurs and other saurians, these rings are typically complete. Bronchial half rings in all extant *Aves* support a membranous medial bronchial wall or medial tympaniform membrane that contributes to sound production²¹. In contrast to a rigid cartilaginous wall, a pliable medial bronchial non-muscular wall consisting of soft connective tissue and epithelium facilitates not only airflow-induced tissue vibration for sound production, but also tissue adduction through the development of a transmembraneous pressure differential.

The spacing, shape and position of the tracheal and bronchial half-rings provides a good proxy for the location of the sound-generating

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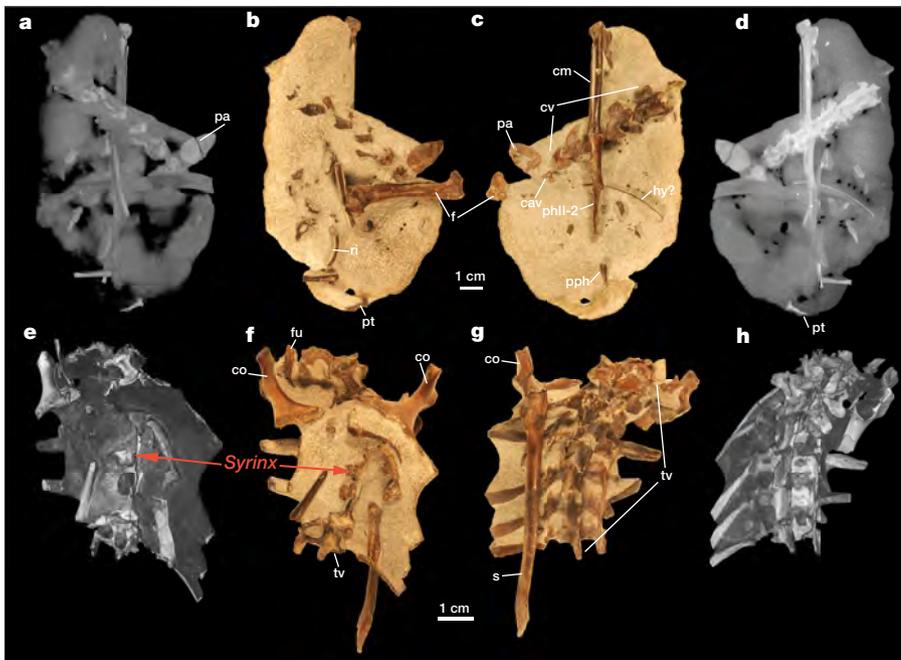


Figure 1 | The *Vegavis iaai* specimen showing the location of the syrinx. a–g, MACN-PV 19.748 (photographs (b, c, f, g) and X-ray computed tomography imaging (a, d, e, h)) comprises a pterygoid (pt), syrinx, the cervical (cv) and thoracic (tv) series and part of the caudal (cav) series, as well as the coracoid (co), scapula (s), furcula (fu), carpometacarpus (cm), manual phalanges II:1 and II:2 in articulation (phII-2), femur (f), patella (pa), pedal phalanges (pph), ribs (ri) and (hy?) a possible ceratobranchial element from the hyoid. Additional elements were prepared from the primary blocks (for example, caudal mandible, coracoid, humerus, ulna, radius, radiale, ulnare, femur, tibiotarsus and fibula; see Supplementary Methods and Extended Data Figs 1 and 2).

tissues (labia or membranes)⁵. In the *Vegavis* syrinx, the sound producing tissues are just caudal to the tracheobronchial juncture (between positions 0 and –1 or positions –1 and –2 in Fig. 2c, Supplementary Table 3). Given the irregular shape of the preserved half-rings and their articulations, a sound source located deeper in the bronchi is highly unlikely. In extant galloanserines and *Presbyornis*, these tissues are typically just below the tracheobronchial juncture (between position –1 and –2; Fig. 3, Extended Data Fig. 8, Supplementary Fig. 2 and Supplementary Table 4). By contrast, in Gaviidae and Procellariiformes, these tissues are located well below the juncture between positions –3 and –4 (Extended Data Fig. 8 and Supplementary Table 4). Whether this condition is more widespread in Neoaves, and possibly phylogenetically informative, awaits denser taxon sampling. There is also no marked shift in diameter across the tracheobronchial juncture in *Vegavis*, although one is seen in these sampled neoavian taxa (Fig. 3 and Extended Data Figs 7 and 8).

Vegavis has a distinct pessulus, a robust, ossified midline structure where the bronchial airways meet the trachea, thought by some to be key to anchoring larger vocal membranes or labia⁵ (Fig. 2 element III; Supplementary Table 3 and Supplementary Fig. 1). A well-mineralized pessulus is here identified as a derived feature of Neognathae (Fig. 3). A pessulus is absent in palaeognaths, with the exception of a diminutive and poorly mineralized structure in *Rhea*^{5,22}. Present in Galloanserines and most other neognath birds⁵, it is lost in columbiforms, and select derived taxa (for example, *Steatornis*, Cathartidae and some passeriforms). In *Vegavis*, this structure shows an angled ventral margin and a sharp cranial midline ridge. This ridge is also conspicuous in galloanserines (Fig. 3 and Extended Data Fig. 8). By contrast, in Gaviidae and some other Neoaves, this midline region is smooth (Extended Data Fig. 8 and Supplementary Table 4).

Element III, bearing the pessulus, (Fig. 2d structure marked ‘0’ and Extended Data Fig. 7) is asymmetric; the one preserved ring on the left is broader in craniocaudal width than either of the two fused on the right. Asymmetry in the fossil has functional implications. Specifically, it is correlated with the presence of a dual sound source and the presence of large soft tissue masses as vibrating structures, referred to as labia⁵. This interpretation is also supported by the relatively small lateral interbronchial spaces described by the positions of elements III–VI (Fig. 2, Supplementary Information and Supplementary Table 3). Larger lateral spaces between bronchial half-rings, such as those observed in galliform species⁵ (Fig. 3 and Extended Data Fig. 8) are located in the trachea and show laterally positioned membranes

involved in sound production. One end of the paired bronchial half-rings is expanded and slightly bulbous (elements V–VII); this expansion is also seen in many neognath taxa with paired labia^{4,5}

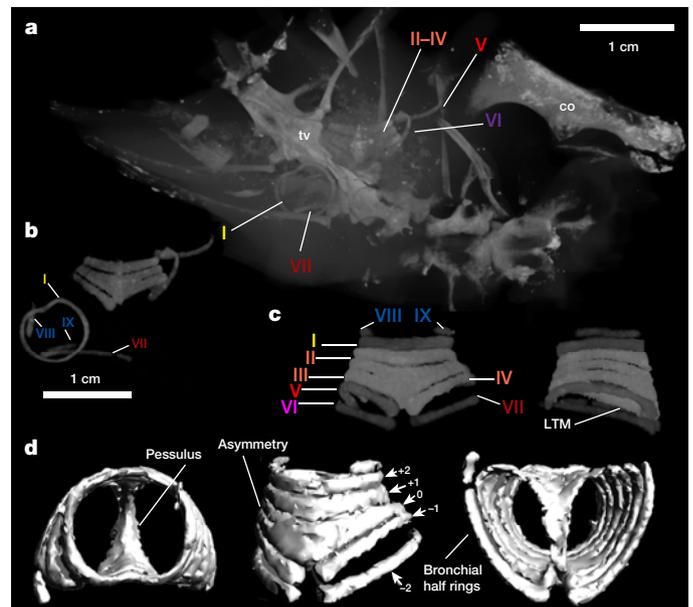


Figure 2 | Syrinx elements in *Vegavis iaai* (MACN-PV 19.748) from X-ray computed tomography data. a–d, Remains of the syrinx relative to other postcranial elements in the block shown in Fig. 1e–g (a), isolated from these elements (b), and reconstructed showing the inferred position of a lateral tympaniform membrane (LTM), between ring positions –1 and –2 (see main text, and Supplementary Information for more explanation) (c), extracted three dimensional volume of the syrinx, showing the preserved asymmetry, robust pessulus and morphology of the bronchial half rings (d). Element numbers I–IX (coloured) are shown in their original positions in the fossil and as reconstructed here (in c; see also Supplementary Table 3). We used the pessulus as reference for a functional differentiation of tracheal and bronchial elements (see also Supplementary Methods). Elements attached to the pessulus are referred to as 0 elements. Denotation +1, +2, +3 are used for element positions craniad from position 0, and –1, –2, –3, and so on are used for element positions caudad from 0. Co, coracoid; tv, thoracic vertebrae. See also Supplementary Information, Supplementary Fig. 1 and Extended Data Fig. 7.

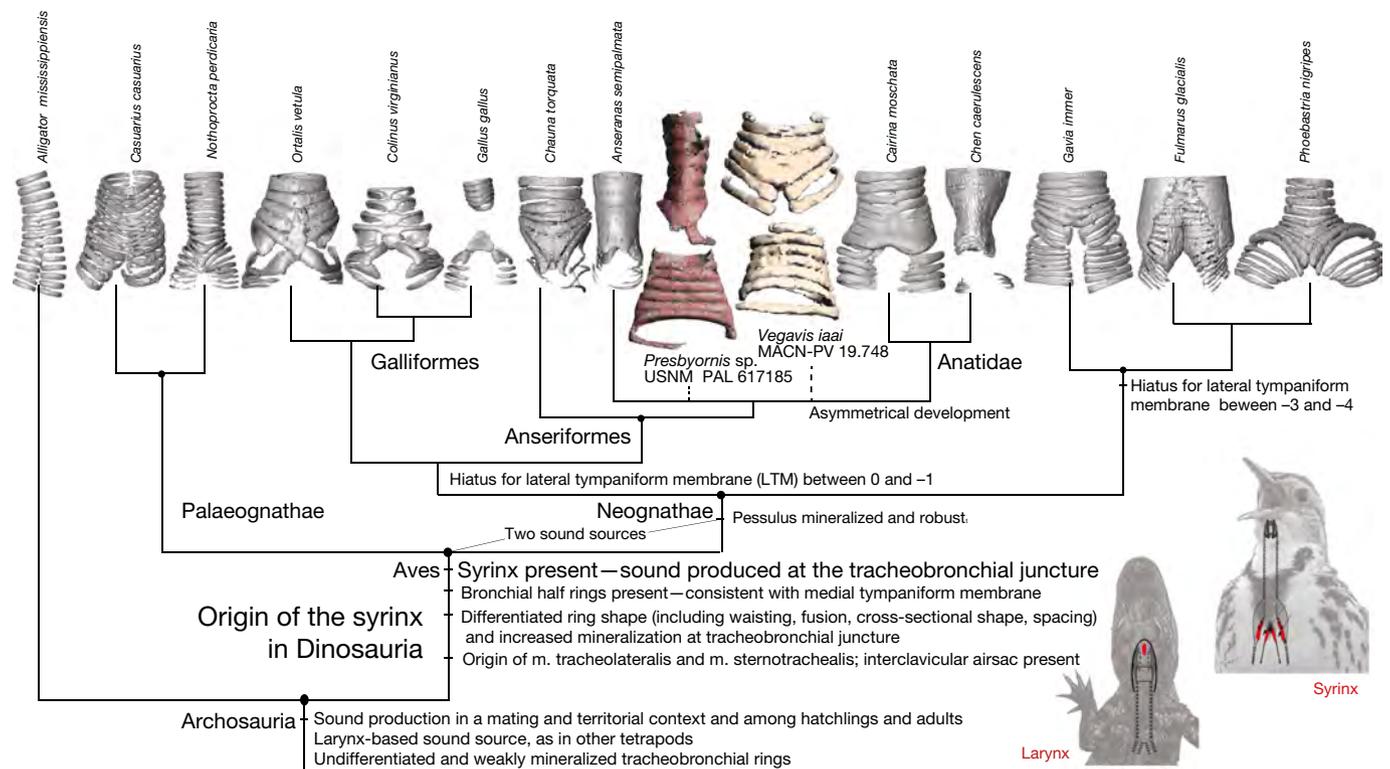


Figure 3 | Comparison of the Cretaceous *Vegavis* and Eocene *Presbyornis* syrinxes to extant avian exemplars showing the optimization of major traits present in the fossil and arising during the origin of living birds. The transition from the larynx-based sound source seen in outgroups to a syrinx, located at the tracheobronchial junction, (inset) occurred within Dinosauria, before or at the origin of Aves; unlike surveyed outgroup taxa, all extant birds (Aves) have some bronchial half-rings and a medial tympaniform membrane, the origin of which may represent a key first step in syrinx evolution. Many basally divergent Aves lack a pessulus, thought by some to be key to anchoring larger vocal membranes or labia³. A well mineralized pessulus, present in both fossils is here found to be ancestral to Neognathae with several subsequent losses of this trait (for example in Columbiformes and some Passeri).

(Fig. 3, Extended Data Fig. 8 and Supplementary Table 4). Two sound sources probably evolved multiple times in Neognathae, and they are variably developed in Palaeognathae^{5,22} as well. It is thus presently ambiguous whether they were ancestral to Aves (Fig. 3).

The asymmetry in *Vegavis* is limited and as such resembles the condition common in female ducks. This state may be consistent with limited, plesiomorphic development of this asymmetry shared with Anatidae or conceivably inform the sex of the individual represented. In Anatidae, the degree of asymmetry is especially pronounced in males where a large bulbous bulla is present on the left half of the tracheobronchial juncture. This asymmetry mediates specific resonance properties^{5,23,24}. *Vegavis* was previously recovered in a polytomy with *Presbyornis* and this clade. In the basal Anseriformes surveyed (in Anhimidae, *Anseranas*, *Presbyornis*) and outgroup Galliformes, no asymmetry is observed (Fig. 3 and Extended Data Fig. 8).

The presence of ventral and dorsal fusion, as well as the absence of more extensive lateral fusion of the lower tracheal rings (Fig. 2 element III, and Supplementary Table 3) is consistent with the absence of a fully fused tracheal tympanum. Formation of a tympanum has been associated with the evolution of intrinsic syringeal muscles⁵. However, although this is true in some groups such as songbirds (Passeriformes), many birds (for example, extant Anseriformes) show marked fusion without any novel muscles⁵. In light of a lack of identified proxies for muscle insertions on the syringeal skeleton, inferences about the presence or absence of intrinsic musculature cannot be made from fusion in element III, but given the estimated

phylogenetic position of the new fossil, they are considered unlikely to have been present. Both the preserved syringeal structures and phylogenetic position of *Vegavis* are consistent with the capability of producing duck-like or goose-like honks and other simple calls common in basal neognaths with two sound sources. By contrast, larynx-based sounds in adult extant archosaurs are limited to generally lower frequency booms, growls and hisses. Experimental data indicate sound production without an interclavicular air sac¹³ is possible even with a syrinx sound source³. Thus, the presence or absence of an interclavicular air sac or syringeal sound source inferred in different dinosaurs would not necessarily limit their potential for vocal behaviour or imply they were mute (in contrast to ref. 13). Many basal birds have expanded or elongated tracheas or phonate into an inflated oesophagus^{23,25}, and differentially closed-beak vocal behaviour is seen in larger-bodied species, reaching body sizes closer to those of some non-avian dinosaurs²⁵. More nuanced reconstructions of sound in *Vegavis* and other dinosaurs will require further data to inform the reconstruction of the vocal tract, muscles, and labia and membrane properties.

Despite extensive new discoveries of exceptionally preserved species on the avian stem lineage, the remains of tracheobronchial rings have not been recovered in Mesozoic archosaurs other than the new specimen. This is despite the preservation of such rings in birds from similar lacustrine and fluvial environments in the Cenozoic^{11,12,26,27}. A difference in preservation potential in non-avian archosaurs may be related to weak mineralization of tracheal and bronchial rings, a condition seen

in outgroups to Aves or Neognathae. Syrinxes not to scale. Three-dimensional PDFs of the fossils and detailed data on extant exemplars are provided as Supplementary Figs 1 and 2, as well as in Extended Data Fig. 8. For detailed images of referenced features of the extant and fossil specimens see <http://www.jsg.utexas.edu/syrinx-evolution/> and <http://dx.doi.org/10.5061/dryad.50n8j>.

Although mineralized structures of the syrinx in *Vegavis* and many parts of extant Anatidae (for example, ducks) show asymmetry, *Presbyornis*, *Chauna* and Galliformes lack this asymmetry. Of the taxa surveyed here and in the literature, loons, penguins and other waterbirds show a caudal shift of the lateral tympaniform membrane (LTM) not seen in *Vegavis*. The origin of two sound sources is ambiguously optimized as ancestral to Aves or Neognathae. Syrinxes not to scale. Three-dimensional PDFs of the fossils and detailed data on extant exemplars are provided as Supplementary Figs 1 and 2, as well as in Extended Data Fig. 8. For detailed images of referenced features of the extant and fossil specimens see <http://www.jsg.utexas.edu/syrinx-evolution/> and <http://dx.doi.org/10.5061/dryad.50n8j>.

in living crocodylians, which lack a syrinx (Fig. 3). Thus, the absence of known tracheobronchial remains in all other Mesozoic dinosaurs may be indicative of a true shift towards avian vocalization and birdsong relatively late in their evolution. This hypothesized pattern would not only mean a very different aural landscape in Cretaceous forests, but may inform patterns in the acquisition of complex visual and vocal communication more generally.

Although the new fossil expands the temporal range of known syrinx remains, this distribution is limited to the extant avian radiation with an earliest fossil record of 66–68 million years ago from Antarctica. The syrinx and modern avian diversity in vocal production, if a relatively recent innovation, would be potentially preceded by both respiratory shifts, as well as by increases in metabolic rate^{28,29}, and an increased role for sexual selection evidenced by feather ornaments²⁸ (Fig. 3). A role for complexity in social structure and mating system has been extensively investigated with reference to increases in brain size in other vertebrates including humans³⁰; however, in the early evolution of birds these hypotheses have not been explored and the origin of aerial locomotion has been the sole hypothesis considered. The early evolution of first more complex visual signals, and then of vocal communication and song, may have played as important a role in the evolution of the avian brain.

Online Content Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

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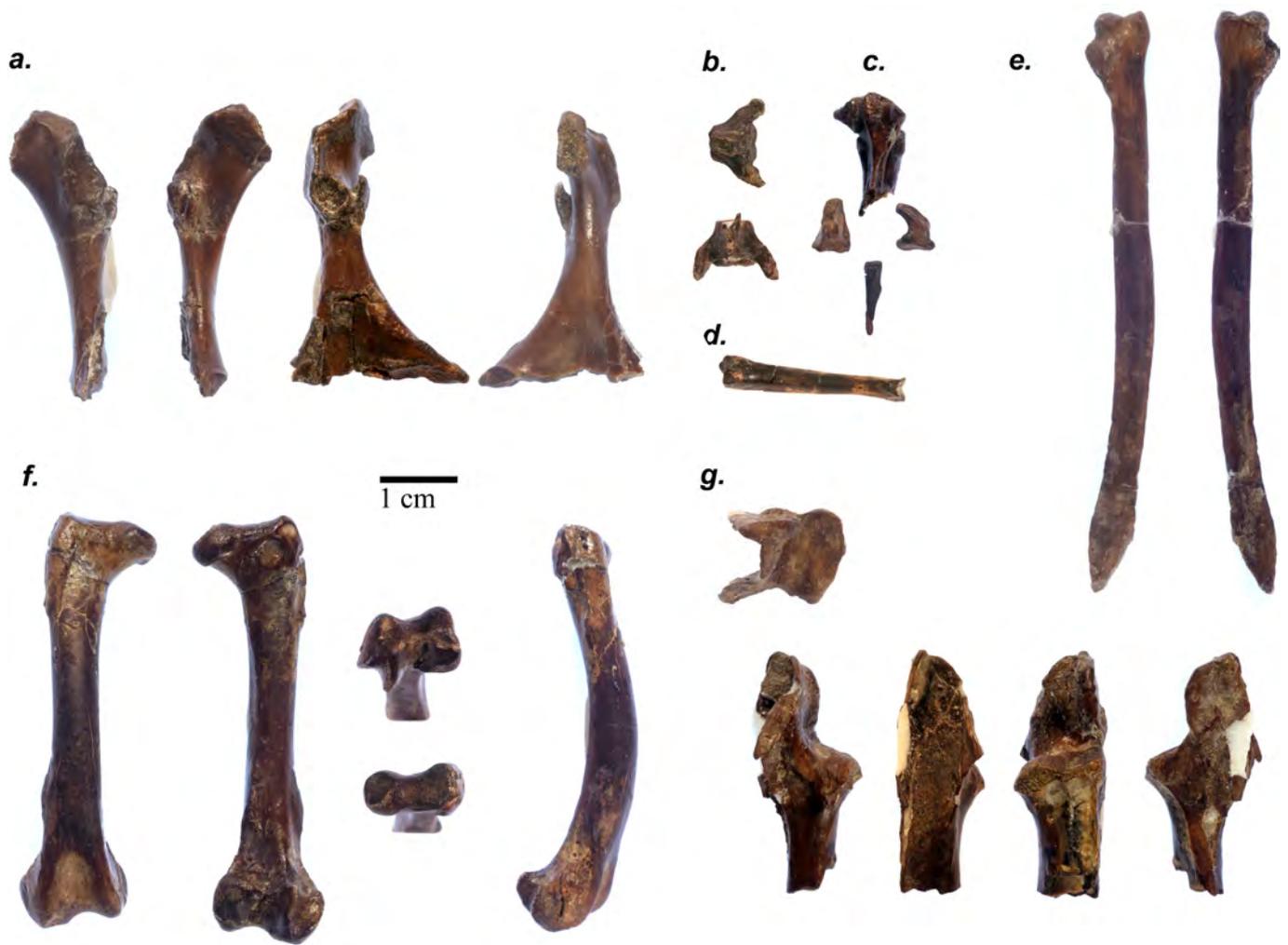
Supplementary Information is available in the online version of the paper.

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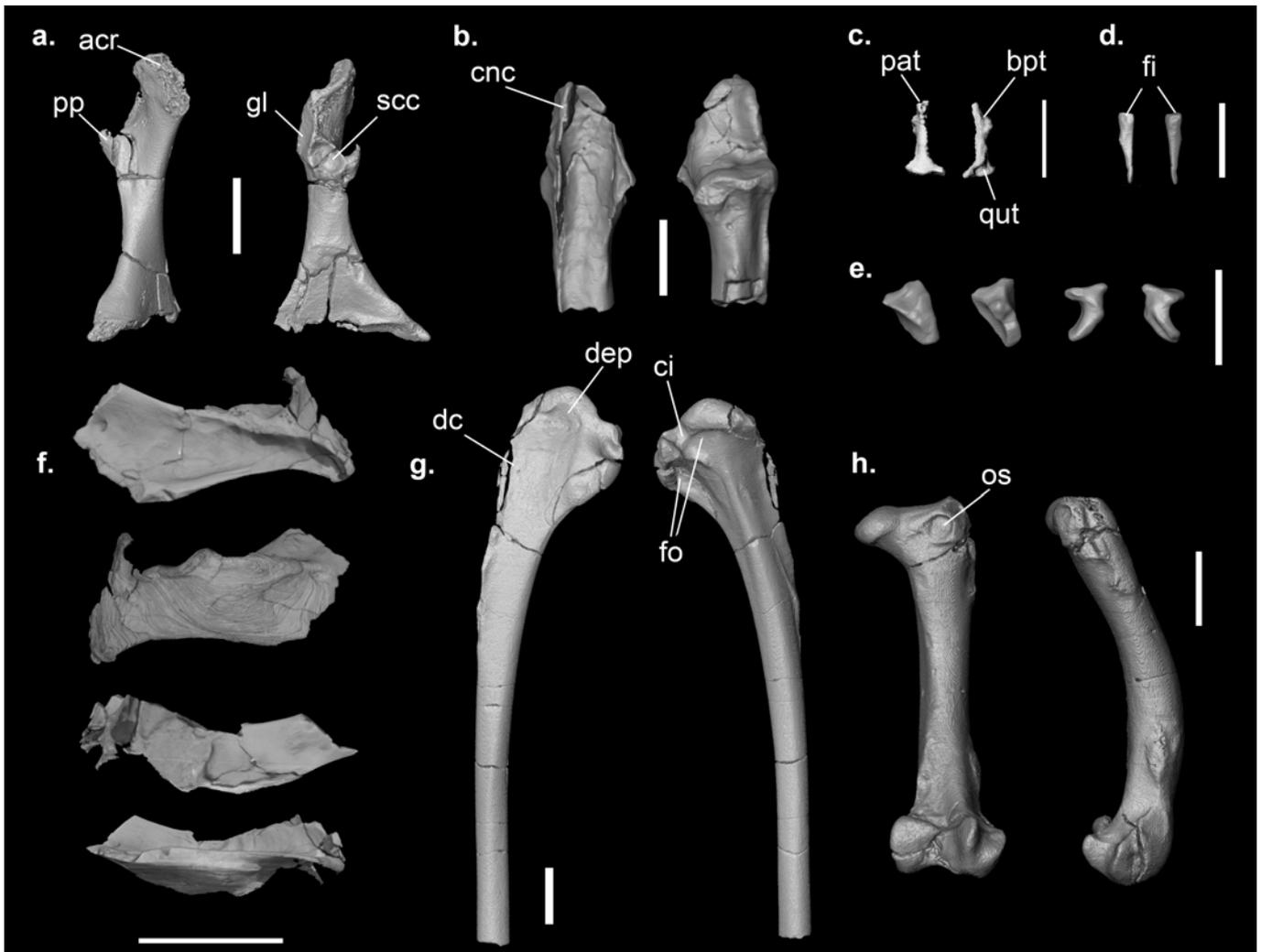
Author Contributions D.R.M. and F.J.M. collected the fossil specimen and contributed geological data. M.P.I. and S.C. contributed to the fossil specimen preparation and study. T.R., F.G., Z.L. and J.A.C. designed the study of the syrinx and collected primary data. Z.L. designed the enhanced contrast CT protocol and collected extant CT data. J.A.C. discovered the fossil syrinx remains and designed the project with F.E.N., S.C., T.R. and F.G. J.A.C., Z.L., F.A., F.E.N., T.R., F.G. and S.C. conducted morphological study of the specimen.

Author Information Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of the paper. Correspondence and requests for materials should be addressed to J.A.C. (Julia_Clarke@jsg.utexas.edu).

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Extended Data Figure 1 | Photographs of elements from the new *Vegavis iaii* specimen from Vega Island, Antarctica (MACN-PV 19.748) prepared from the primary block. **a–d.** Coracoid(**a**), caudal vertebra (**b**), (from top to bottom) distal radius, ulna with radiale in articulation, radiale and ulnare, and manual phalanx III:1 (**c**), pedal phalanx (**d**), scapula (**e**), femur (**f**), tibiotarsus (**g**). Scale bar, 1 cm.

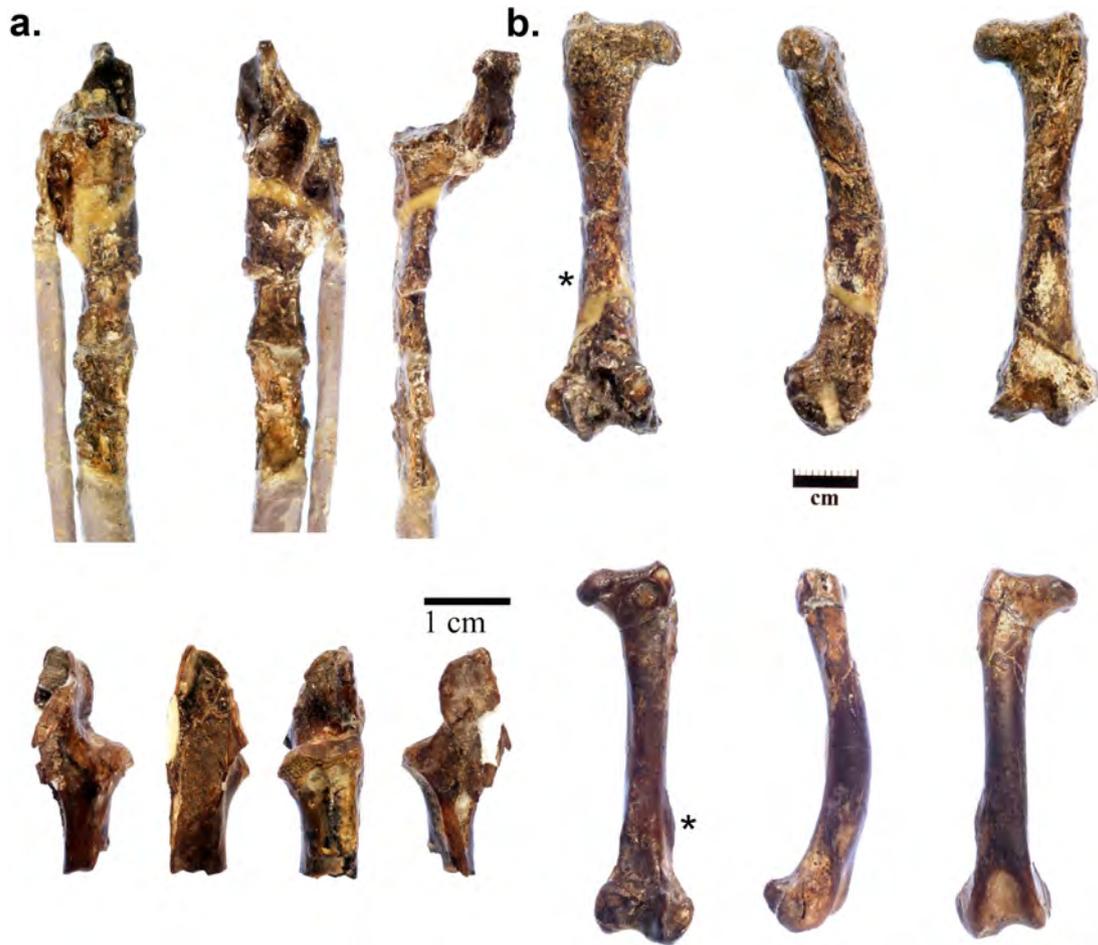


Extended Data Figure 2 | Images from X-ray computed tomography of selected elements of the new *Vegavis iai* specimen (MACN-PV 19.748). **a.** Coracoid (acr, acrocoracoid; gl, glenoid facet; pp, procoracoid process; scc, scapular cotyla). **b.** Proximal tibia (cnc, cranial cnemial crest). **c.** Pterygoid (bpt, basipterygoid articular facet; pat, palatine articular facet;

qut, quadrate articular facet). **d.** Fibula (fi). **e.** Radialae and ulnae. **f.** Caudal mandible. **g.** Proximal humerus (dep, depression; dc, deltopectoral crest; ci, capital incisure; fo, fossa). **h.** Femur (os, ovoid scar). Scale bar, 1 cm.



Extended Data Figure 3 | *Polarornis gregorii* holotype specimen from Seymour Island, Antarctic Peninsula. The specimen was damaged during original preparation and the existence of the previously described braincase and quadrate as well as morphologies from the skull and tibial shaft cannot be confirmed.



Extended Data Figure 4 | Comparison of elements in common between the *Polarornis gregorii* holotype specimen from Seymour Island (top) and the new specimen of *Vegavis iaai* (MACN-PV 19.748) (bottom). a, b, Tibiotarsus (a) and femur (b). The asterisk indicates the prominent

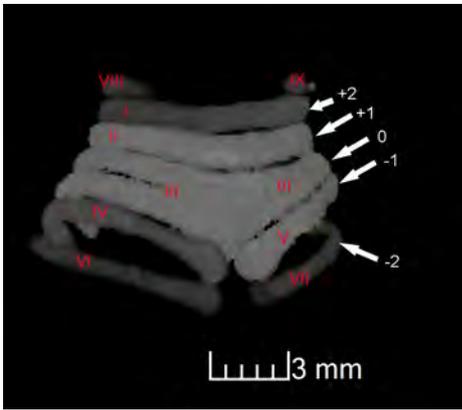
muscular ridge on the femur present in the *Vegavis iaai* holotype and the newly referred specimen (MACN-PV 19.748), but not seen in the *Polarornis* holotype. Scale bar, 1 cm.



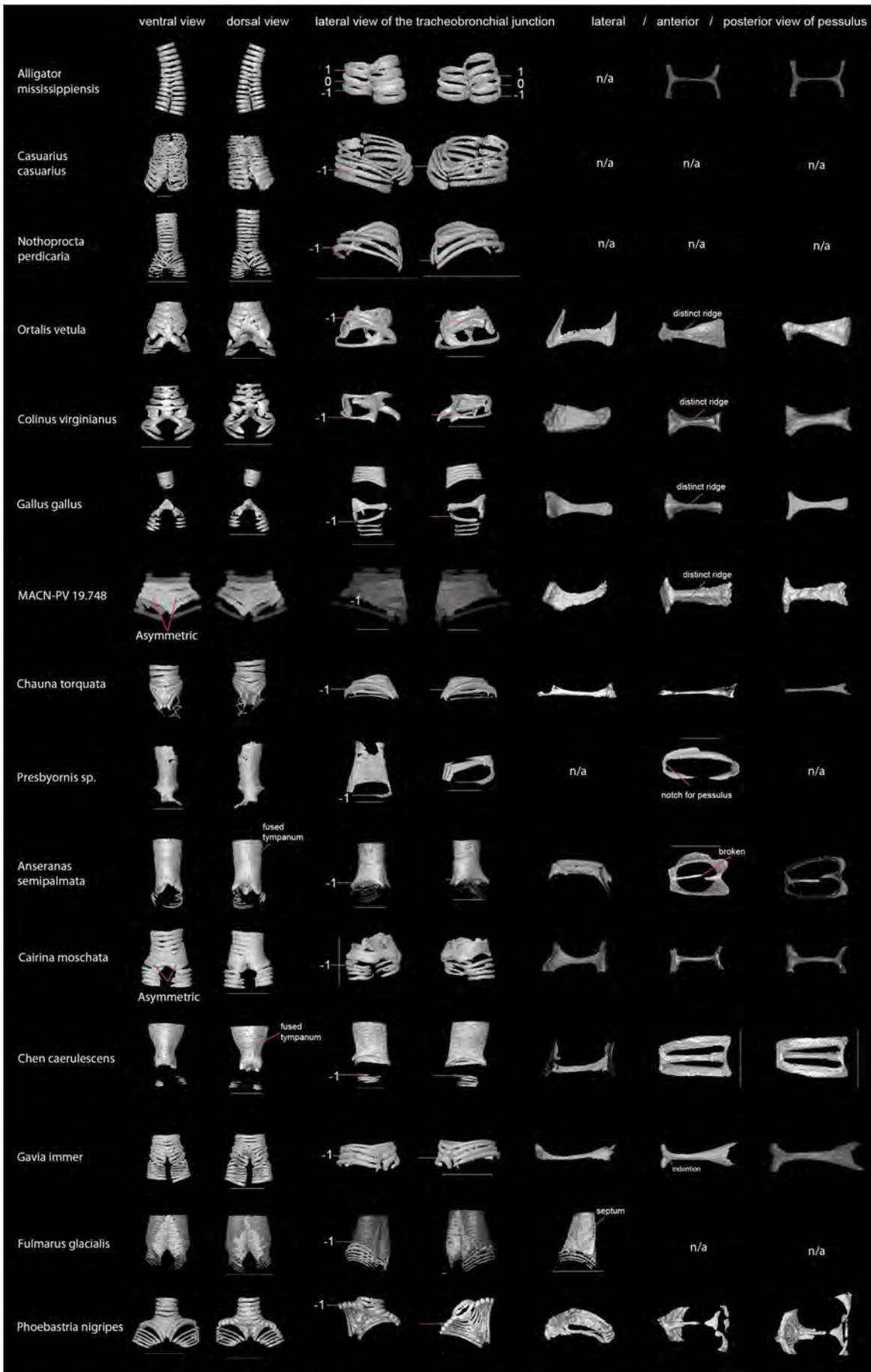
Extended Data Figure 5 | Comparison of select elements in common between the *Vegavis iaii* holotype and the new specimen (MACN-PV 19.748). Top, the circular depression on the proximal femur used in the diagnosis of *Vegavis* seen in the new specimen¹⁸. Bottom, the humeral crest (lateral to the capital ridge) also mentioned in that diagnosis of *Vegavis iaii* are shown. Although both of these characters show a complex distribution in Aves, and are not restricted to the species, their combination is unique.



Extended Data Figure 6 | The pterygoid in *Vegavis iaii* specimen MACN-PV 19.748 (right) compared to that of *Gavia immer* (left) highlighting the prominent basipterygoid facet in the *Vegavis iaii* referred specimen. See also Fig. 1, Extended Data Fig. 2 and Supplementary Information. Scale bar, 1 cm.



Extended Data Figure 7 | *Vegavis iaai* (MACN-PV 19.748) syrinx with position-based identities labelled. See also Fig. 2 and Supplementary Table 3.



Extended Data Figure 8 | See next page for caption.

Extended Data Figure 8 | Morphological comparison of the syrinx in the fossils and enhanced contrast CT images of avian and outgroup exemplars. Key features discussed in the text are illustrated. The numbers (−1, 0, 1) reference the position schema described in the main

text, Supplementary Information, Supplementary Tables 3 and 4, Extended Data Fig. 7. Enlarged images are available at <http://www.jsg.utexas.edu/syrinx-evolution/> and this image website is also available at Data Dryad as a zipped file at <http://dx.doi.org/10.5061/dryad.50n8j>.