Shouldering the challenge of deciphering avian palate evolution

Juan Benito[1], Pei-Chen Kuo[2], Christopher R. Torres[3], Guillermo Navalón[1], Olivia Plateau[4,5], Alexander D. Clark[2], Elizabeth M. Steell[1], Daniel J. Field[1,5]

[1]Department of Earth Sciences, University of Cambridge, Cambridge CB2 3EQ, UK

[2]Negaunee Integrative Research Center, Field Museum of Natural History, Chicago, IL 60605, USA

[3]Department of Biological Sciences, University of the Pacific, Stockton, CA 95211, USA

[4]The Institute of Ecology and Evolution, University of Bern, Bern 63012, Switzerland

[5]Naturhistorisches Museum Bern, Bern 3005, Switzerland

[6]Museum of Zoology, University of Cambridge, Cambridge CB2 3EJ, UK

Abstract

Wilken et al. (1) investigate the evolution of avian palatal kinesis using comparative morphology and biomechanical modelling. While the study's topic and approach are timely, its conclusions are marred by inadequate taxon sampling and morphological misinterpretations.

Main text

Reinterpreting the *Janavis* pterygoid (2) as a juvenile bird coracoid (1) is contradicted by clear morphological and developmental evidence (Fig. 1). The concave, ossified 'sternal articulation' of the would-be coracoid (1) is unossified in juvenile bird coracoids, yet resembles the quadrate articulation of the pterygoid in several extant taxa (Fig. 1B). Similarly, *contra* (1), the basipterygoid articulation in *Janavis* closely resembles that of several extant neognathous birds in its form and position (Fig. 1C).

The authors identify a supposed glenoid and acrocoracoid on the purported coracoid (1), yet in developing bird coracoids these structures only arise after the scapular cotyle, which is absent in the fossil. Importantly, the positions of these structures do not shift relative to one-another throughout extant bird ontogeny, which would be necessary for the element to come to resemble a coracoid (Fig. 1B). Since ichthyornithine postcranial morphology and growth generally fall within the range of variation of extant birds (3), there is no reason to think these would be any different in *Janavis*. Crucially, the authors of (1) must have reduced the size of the *Janavis* scapula by ~50% to 'match' it with the putative coracoid (see their Supplementary Fig. 14A; our Fig. 1A), yet this is unmentioned.

The above issues notwithstanding, the ichthyornithine hemipterygoid alone—with an articular condyle like those of prokinetic neognaths —suggests a mobile intrapterygoid joint (Fig. 2A). Wilken et al. seemingly agree ("…*Ichthyornis...* possesses a segmented, potentially propulsive pterygoid..." (1)); yet, they interpret palatal kinesis as a neognath autapomorphy by asserting that stem bird musculature was incompatible with palate mobility. This rests upon misinterpretations of the functional correlates of quadrate morphology. First, elongate orbital processes in *Ichthyornis* and *Hesperornis* are declared to impose constraints on kinesis due to articulation with the neurocranium (1). However, many neognaths exhibit equivalently long (or longer) orbital processes closely approaching the neurocranium without precluding prokinesis (Fig. 2B; (5); https://doi.org/10.5281/zenodo.15619495). Second, *contra* (1), the bicondylar nature of the *Ichthyornis* quadrate would not have precluded coupled palatal kinesis, as evidenced by bicondylar Anseriformes (Fig. 2B) (6). Further morpho-functional misconceptions underpin problematic cranial linkage models in (1) (Fig. 2C), yet the authors' own ancestral reconstructions of cranial linkages and protractor force seemingly support palatal mobility as plesiomorphic for all crown birds (their Figs. 3A, 4), rather than being apomorphic for Neognathae as they argue.

Contemporary research in avian macroevolution seeks to evaluate associations between brain and skull transformations (7-9); however, this link is weakly substantiated by (1), as several taxa with

palatal kinesis (e.g., Anseriformes) share plesiomorphically low degrees of encephalization with akinetic palaeognaths and stem birds (10).

Conclusions

The origin of palatal kinesis was a key milestone in avian evolutionary history—careful morphological interpretation will be crucial to clarify how this major transformation occurred and influenced avian evolutionary history.

Figures

Fig. 1. The pterygoid of *Janavis finalidens* is not a juvenile coracoid. A) The scapula of *Janavis* was downscaled to 50% of its real size by (1) (see their Fig. S14). When correctly scaled (Fig. 1a and Extended Data Fig 2b-d in (2)) the pterygoid and scapula do not match (nor does the pterygoid resemble a coracoid in the first place—see main text). **B)** If interpreted as an immature coracoid, the pterygoid of *Janavis* differs from all known avian coracoids in: 1) glenoid development ontogenetically preceding the scapular cotyle, procoracoid, and acrocoracoid; 2) exhibiting a 'dorsally' convex and 'laterally' flat shaft; 3) the authors' (1) 'sternal process' (presumably the sternolateral process) being medially, rather than laterally, oriented; 4) exhibiting fully ossified concave surfaces on both omal and sternal ends, which are instead open and hollow or formed by unfinished bone in immature bird coracoids (the sternal end of the coracoid is only concave in adult, highly derived Apodiformes); 5) being highly pneumatic with a simple trabecular structure, as pneumaticity only develops late in post-hatching development in extant birds. **C)** If correctly interpreted as a right pterygoid (*contra* (2), where it was considered a left pterygoid), all features of the element are found in fossil and extant neognathous bird pterygoids, including: 1) a large, medially-oriented basipterygoid process facet reaching the rostral end (present in Galliformes, *contra* (1)); 2) a laterally and often dorsally open, cup-shaped palatine contact (present across Galloanserae); 3) a tubular shaft that is medially flat and dorsally convex (present in Galliformes and Pelagornithidae); 4) a simple, concave quadrate articular surface (present in Anseriformes); 4) a marked orbito-pterygoid contact process (present in Galliformes and some Anseriformes); 5) a heavily pneumatised internal structure with simple trabeculae (present across Galloanserae). Bold letters indicate anatomical views: caudal (C), dorsal (D), lateral (L), medial (M), rostral (R). Cross-sectional (CS) planes are indicated with dotted lines over each element. All scale bars equal 5 mm.

Fig. 2. Morphology of the suspensorial system in Ichthyornithes suggests prokinetic capabilities. A) *Ichthyornis* exhibited a mobile intrapterygoid (hemipterygoid-pterygoid) articulation, like the condition in unsegmented immature (imm.) neognaths (hemipterygoid highlighted in teal shade). The condylar morphology of the pterygoid articular contact resembles that of prokinetic Galliformes and Neoaves, and contrasts with the long or wide overlapping contacts of palaeognaths. Long rostral processes of the palatine are obscured for clarity. **B)** The quadrates of *Ichthyornis* and *Hesperornis* (bicondylar, with long orbital processes interpreted as contacting the braincase (1)) would not preclude palatal kinesis. Both features are present across a wide range of prokinetic neognath taxa unsampled by (1). This includes taxa where the orbital process 1) wraps around and closely approaches the neurocranium; 2) terminates in an expansion whose lateral surface anchors the M. pseudotemporalis profundus; and 3) is presumably associated with depressions or 'cotylae' on the braincase (e.g., *Ardea*; see https://doi.org/10.5281/zenodo.15619495**)**. **C)** The ichthyornithine linkage model proposed by (1) enforces immobility at contacts between bones (e.g., the jugal and the lacrimal) which do not preclude prokinesis in extant birds. We present corrected linkage values following the scheme of (1), indicated in green, and illustrate the support for these from previous reconstructions of the skull of *Ichthyornis*. Bold letters indicate anatomical views: caudal (C), dorsal

(D), lateral (L), ventral (V). All scale bars equal 2.5 mm. Digitally segmented *Struthio camelus* palatine in A courtesy of Annabel K. Hunt.

References

1. A. T. Wilken *et al.*, Avian cranial kinesis is the result of increased encephalization during the origin of birds. *Proceedings of the National Academy of Sciences* **122**, e2411138122 (2025).

2. J. Benito, P.-C. Kuo, K. E. Widrig, J. W. M. Jagt, D. J. Field, Cretaceous ornithurine supports a neognathous crown bird ancestor. *Nature* **612**, 100-105 (2022).

3. J. Benito *et al.*, 40 new specimens of *Ichthyornis* provide unprecedented insight into the postcranial morphology of crownward stem group birds. *PeerJ* **10**, e13919 (2022).

4. C. R. Torres, M. A. Norell, J. A. Clarke, Bird neurocranial and body mass evolution across the end-Cretaceous mass extinction: The avian brain shape left other dinosaurs behind. *Science Advances* **7**, eabg7099 (2021).

5. P.-C. Kuo, G. Navalón, R. B. J. Benson, D. J. Field, Macroevolutionary drivers of morphological disparity in the avian quadrate. *Proceedings of the Royal Society B: Biological Sciences* **291**, 20232250 (2024).

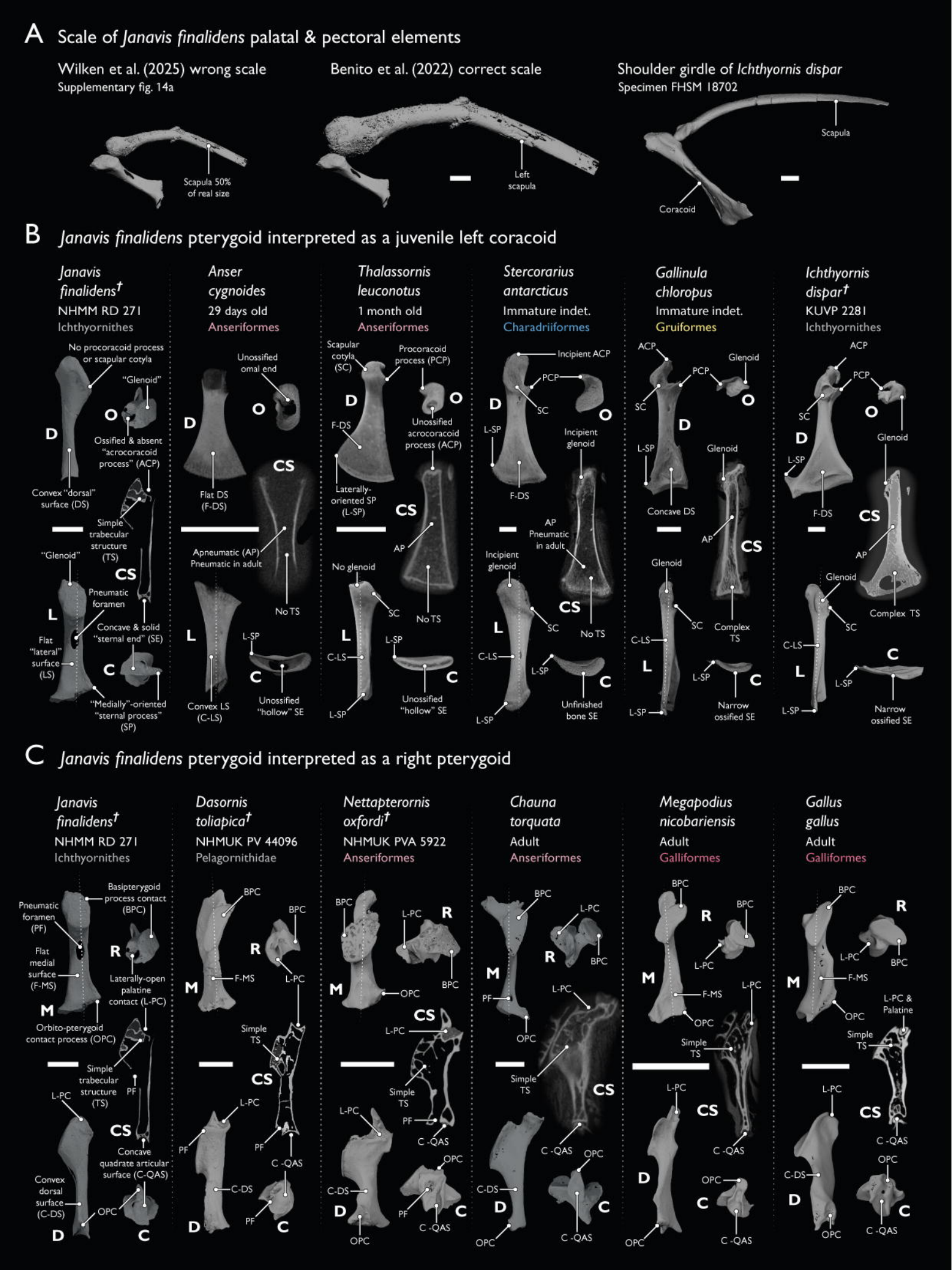
6. P.-C. Kuo, R. B. J. Benson, D. J. Field, The influence of fossils in macroevolutionary analyses of 3D geometric morphometric data: A case study of galloanseran quadrates. *Journal of Morphology* **284**, e21594 (2023).

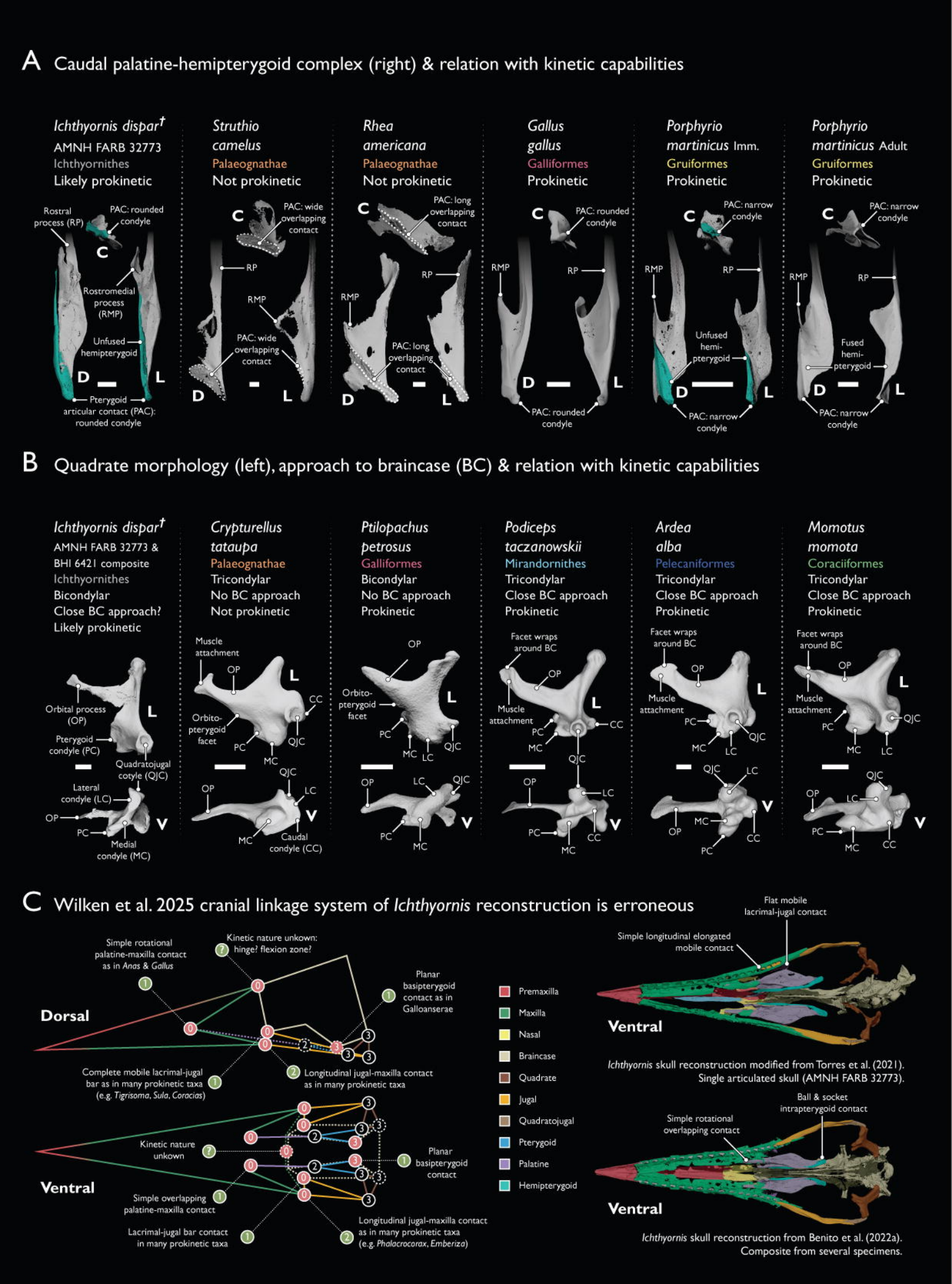
7. B.-A. S. Bhullar *et al.*, How to Make a Bird Skull: Major Transitions in the Evolution of the Avian Cranium, Paedomorphosis, and the Beak as a Surrogate Hand. *Integrative and Comparative Biology* 10.1093/icb/icw069 (2016).

8. A. M. Balanoff, G. S. Bever, T. B. Rowe, M. A. Norell, Evolutionary origins of the avian brain. *Nature* **501**, 93-96 (2013).

9. L. M. Chiappe, G. Navalon *et al.*, Cretaceous bird from Brazil informs the evolution of the avian skull and brain. *Nature* **635**, 376-381 (2024).

10. D. T. Ksepka *et al.*, Tempo and Pattern of Avian Brain Size Evolution. *Current Biology* **30**, 2026-2036.e2023 (2020).


A Scale of Janavis finalidens palatal & pectoral elements
Wilken et al. (2025) wrong scale
Supplementary fig. 14a
Scapula 50% of real size
Benito et al. (2022) correct scale
Left scapula
Shoulder girdle of Ichthyornis dispar
Specimen FHSM 18702
Scapula
Coracoid
B Janavis finalidens pterygoid interpreted as a juvenile left coracoid
Janavis finalidens†
NHMM RD 271
Ichthyornithes
No procoracoid process or scapular cotyla
"Glenoid"
Ossified & absent "acrocoracoid process" (ACP)
Convex "dorsal" surface (DS)
Simple trabecular structure (TS)
Pneumatic foramen
Concave & solid "sternal end" (SE)
Flat "lateral" surface (LS)
"Medially"-oriented "sternal process" (SP)
Anser cygnoides
29 days old
Anseriformes
Unossified omal end
Flat DS (F-DS)
Apneumatic (AP) Pneumatic in adult
No TS
Convex LS (C-LS)
Unossified "hollow" SE
Thalassornis leuconotus
1 month old
Anseriformes
Scapular cotyla (SC)
Procoracoid process (PCP)
F-DS
Unossified acrocoracoid process (ACP)
Laterally-oriented SP (L-SP)
AP
No glenoid
SC
No TS
C-LS
L-SP
Unossified "hollow" SE
Stercorarius antarcticus
Immature indet.
Charadriiformes
Incipient ACP
PCP
SC
L-SP
F-DS
Incipient glenoid
AP Pneumatic in adult
No TS
C-LS
Unfinished bone SE
Gallinula chloropus
Immature indet.
Gruiformes
ACP
PCP
Glenoid
SC
L-SP
Concave DS
AP
Complex TS
C-LS
Narrow ossified SE
Ichthyornis dispar†
KUVP 2281
Ichthyornithes
ACP
PCP
SC
L-SP
F-DS
Glenoid
AP
Complex TS
C-LS
Narrow ossified SE
C Janavis finalidens pterygoid interpreted as a right pterygoid
Janavis finalidens†
NHMM RD 271
Ichthyornithes
Basipterygoid process contact (BPC)
Pneumatic foramen (PF)
Flat medial surface (F-MS)
Laterally-open palatine contact (L-PC)
Orbito-pterygoid contact process (OPC)
Simple trabecular structure (TS)
Concave quadrate articular surface (C-QAS)
Convex dorsal surface (C-DS)
Dasornis toliapica†
NHMUK PV 44096
Pelagornithidae
BPC
F-MS
L-PC
Simple TS
PF
C-DS
C -QAS
Nettapterornis oxfordi†
NHMUK PVA 5922
Anseriformes
BPC
L-PC
OPC
Simple TS
PF
C -QAS
C-DS
Chauna torquata
Adult
Anseriformes
BPC
L-PC
PF
OPC
Simple TS
C -QAS
C-DS
Megapodius nicobariensis
Adult
Galliformes
BPC
L-PC
F-MS
OPC
Simple TS
C -QAS
Gallus gallus
Adult
Galliformes
BPC
L-PC
F-MS
OPC
L-PC & Palatine
Simple TS
C -QAS
C-DS


A Caudal palatine-hemipterygoid complex (right) & relation with kinetic capabilities
Ichthyornis dispar†
AMNH FARB 32773
Ichthyornithes
Likely prokinetic
Rostral process (RP)
PAC: rounded condyle
Rostromedial process (RMP)
Unfused hemipterygoid
Pterygoid articular contact (PAC): rounded condyle
Struthio camelus
Palaeognathae
Not prokinetic
PAC: wide overlapping contact
Rhea americana
Palaeognathae
Not prokinetic
PAC: long overlapping contact
Gallus gallus
Galliformes
Prokinetic
PAC: rounded condyle
Porphyrio martinicus Imm.
Gruiformes
Prokinetic
PAC: narrow condyle
Unfused hemi-pterygoid
Porphyrio martinicus Adult
Gruiformes
Prokinetic
PAC: narrow condyle
Fused hemi-pterygoid
B Quadrate morphology (left), approach to braincase (BC) & relation with kinetic capabilities
Ichthyornis dispar†
AMNH FARB 32773 & BHI 6421 composite
Ichthyornithes
Bicondylar
Close BC approach?
Likely prokinetic
Orbital process (OP)
Pterygoid condyle (PC)
Quadratojugal cotyle (QJC)
Lateral condyle (LC)
Medial condyle (MC)
Crypturellus tataupa
Palaeognathae
Tricondylar
No BC approach
Not prokinetic
Muscle attachment
Orbito-pterygoid facet
Caudal condyle (CC)
Ptilopachus petrosus
Galliformes
Bicondylar
No BC approach
Prokinetic
Podiceps taczanowskii
Mirandornithes
Tricondylar
Close BC approach
Prokinetic
Facet wraps around BC
Ardea alba
Pelecaniformes
Tricondylar
Close BC approach
Prokinetic
Momotus momota
Coraciiformes
Tricondylar
Close BC approach
Prokinetic
C Wilken et al. 2025 cranial linkage system of Ichthyornis reconstruction is erroneous
Dorsal
Simple rotational palatine-maxilla contact as in Anas & Gallus
Kinetic nature unkown: hinge? flexion zone?
Planar basipterygoid contact as in Galloanserae
Complete mobile lacrimal-jugal bar as in many prokinetic taxa (e.g. Tigrisoma, Sula, Coracias)
Longitudinal jugal-maxilla contact as in many prokinetic taxa
Ventral
Kinetic nature unkown
Planar basipterygoid contact
Simple overlapping palatine-maxilla contact
Lacrimal-jugal bar contact in many prokinetic taxa
Longitudinal jugal-maxilla contact as in many prokinetic taxa (e.g. Phalacrocorax, Emberiza)
Premaxilla
Maxilla
Nasal
Braincase
Quadrate
Jugal
Quadratojugal
Pterygoid
Palatine
Hemipterygoid
Flat mobile lacrimal-jugal contact
Simple longitudinal elongated mobile contact
Ventral
Ichthyornis skull reconstruction modified from Torres et al. (2021). Single articulated skull (AMNH FARB 32773).
Ball & socket intrapterygoid contact
Simple rotational overlapping contact
Ventral
Ichthyornis skull reconstruction from Benito et al. (2022a). Composite from several specimens.