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Evolution of axial regionalization in Aves during the Mesozoic and its impact on the survival of modern lineages to K/Pg mass extinction

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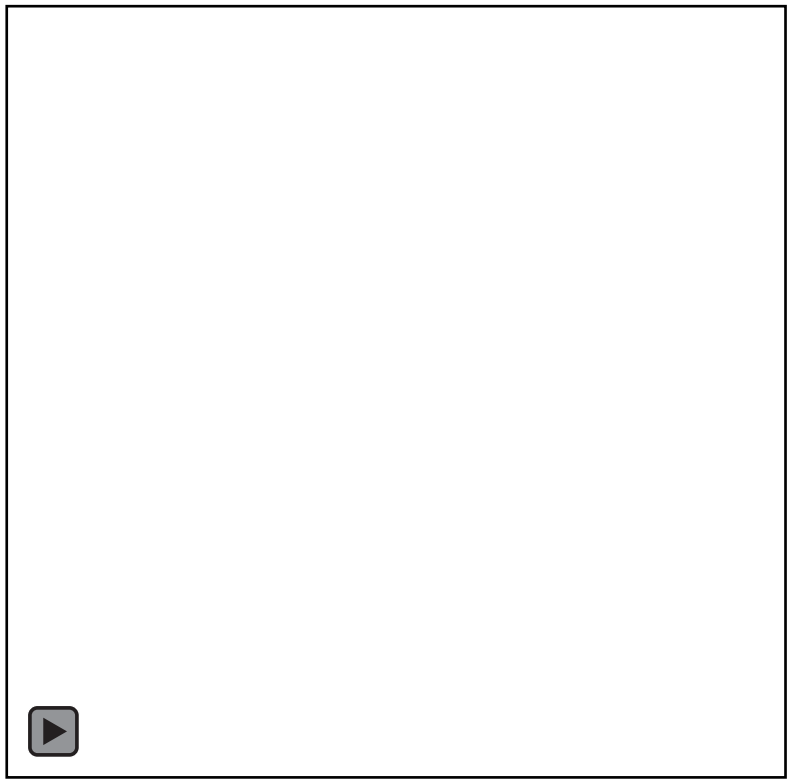
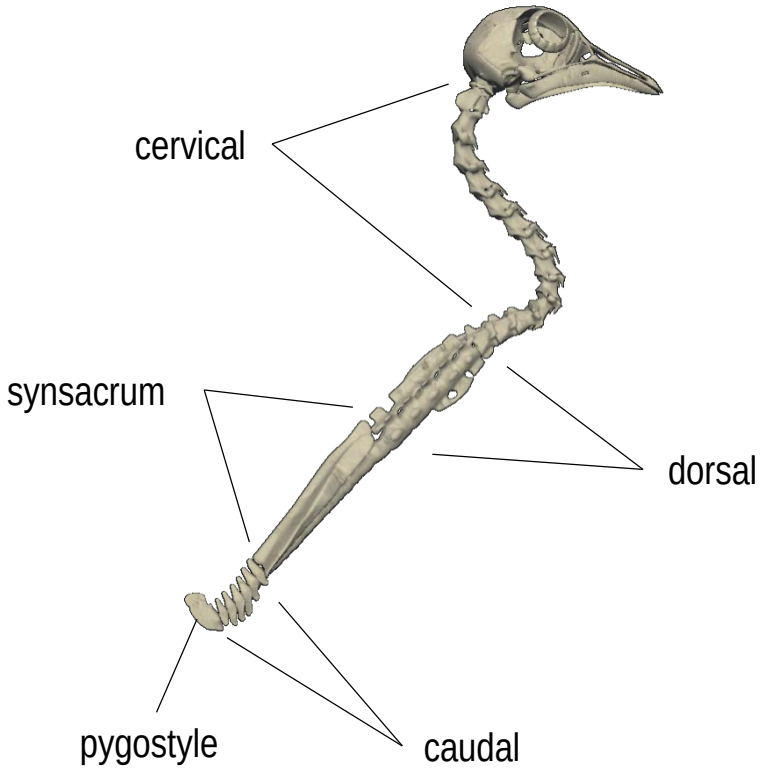
Birds' spine

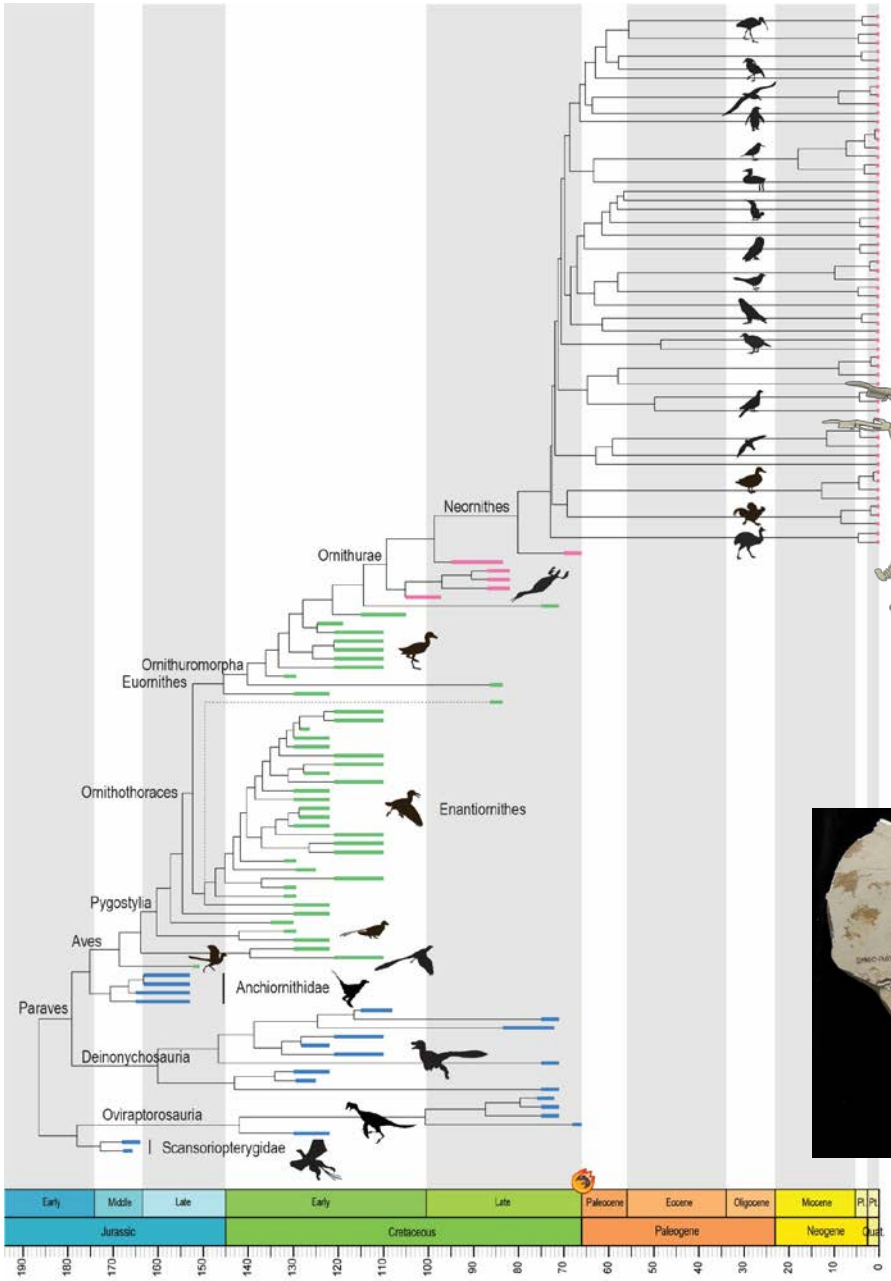
highly mobile neck for multiple function

compact trunk acting as a rigid axis that provides stability during the flight





Birds' evolutionary history

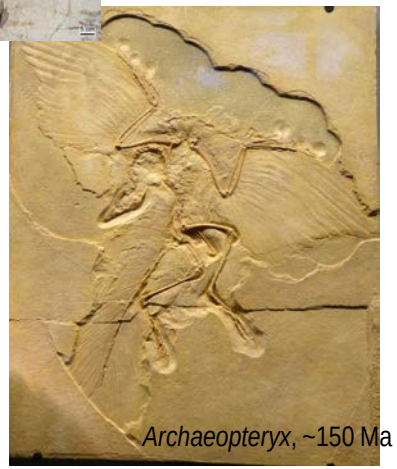


Columba

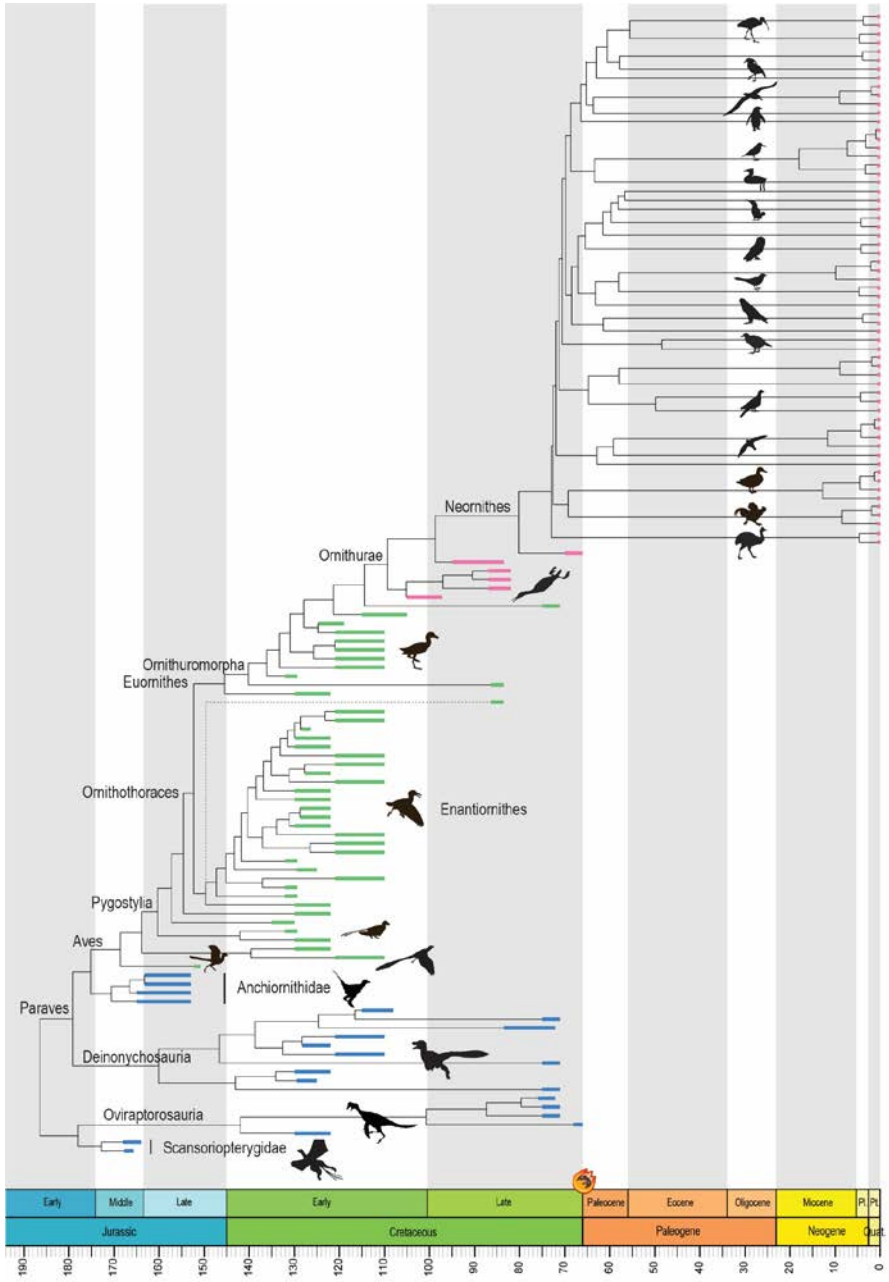
Confuciusornis, ~125 Ma

Parapengornis, ~125 Ma

Anchiornis, ~160



Archaeopteryx, ~150 Ma



QUESTIONS TO EXPLORE

1) how the spine regionalization evolved along the evolutionary history of birds?

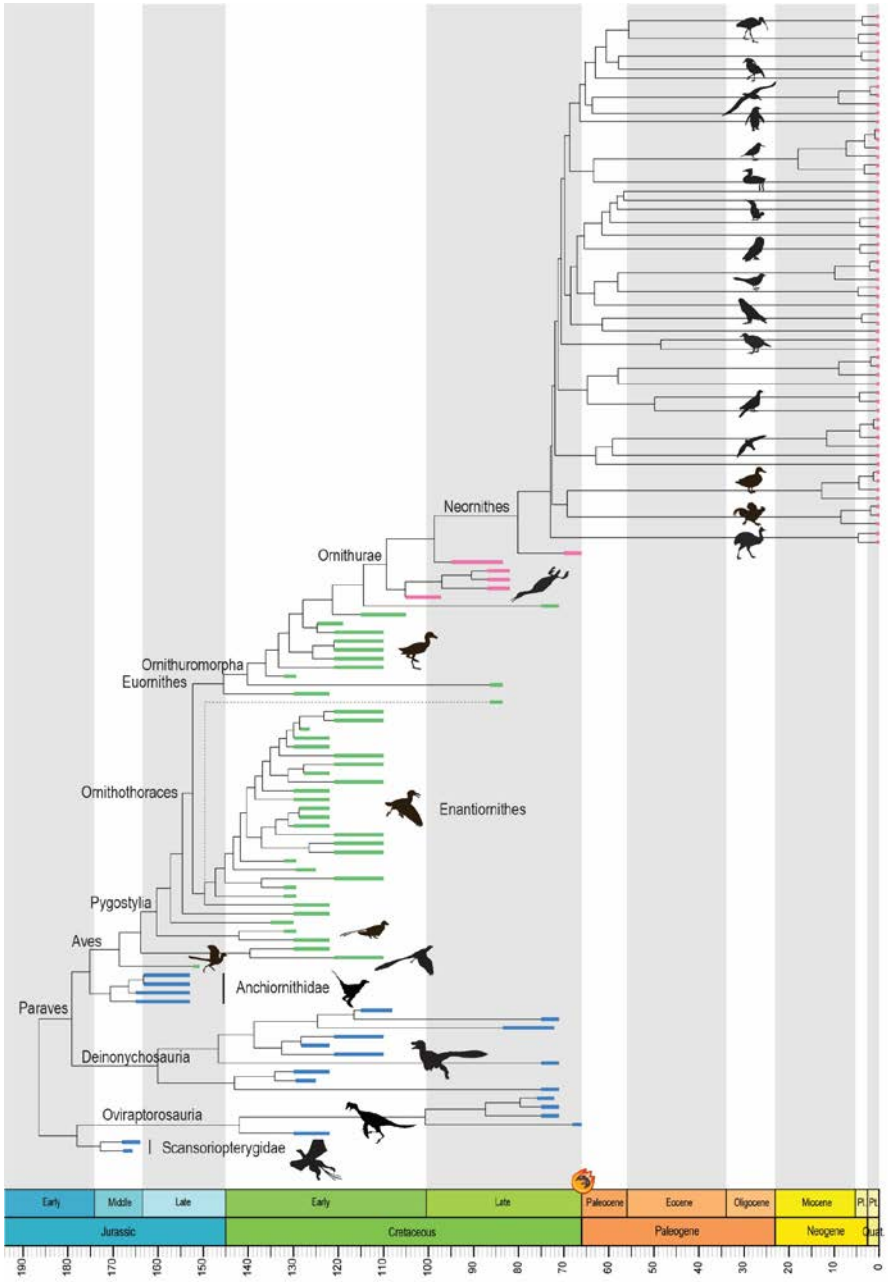
2) when and how the modern condition evolved?

3) how spine regionalization influenced on flight biomechanics?

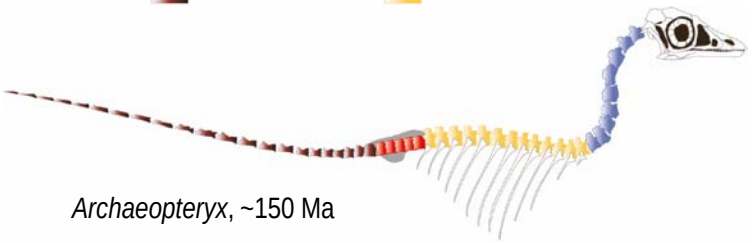
4) would provide this influence on flight performance different chances for surviving at the end-Cretaceous mass extinction?

MATERIAL AND METHODS

Dataset



synsacrum
cervical
caudal
dorsal



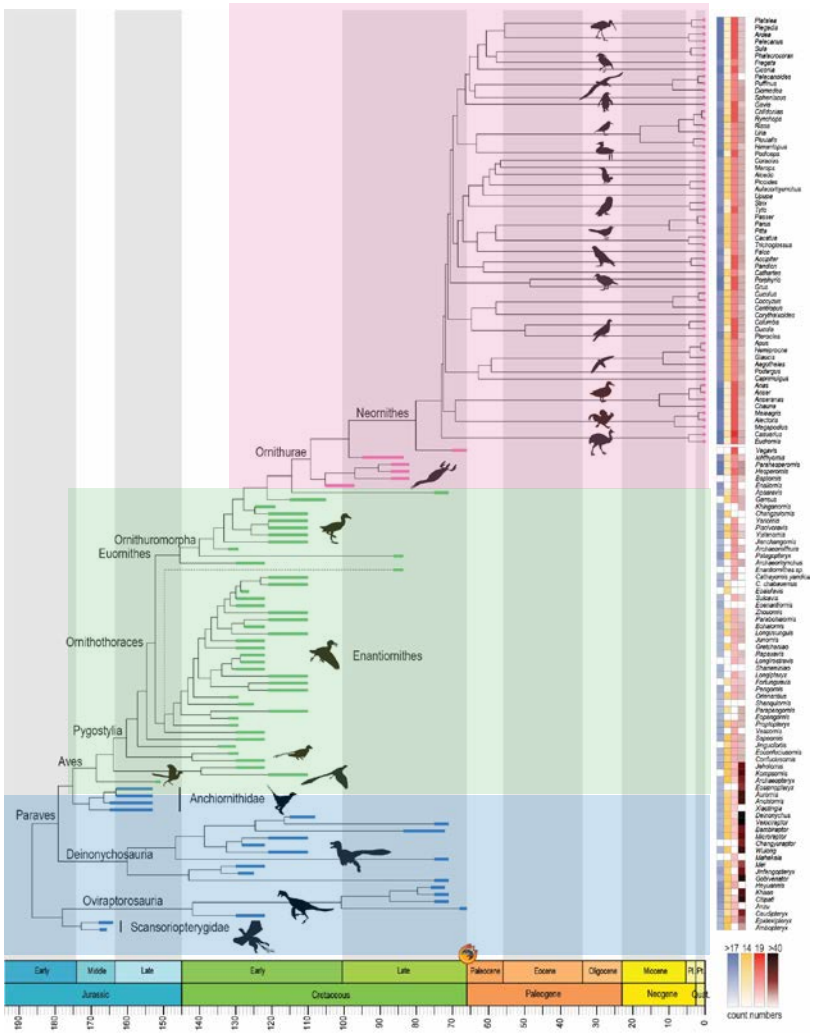
61 extant species (Neornithes)

50 early birds (non-Neornithes) from Jurassic and Cretaceous

21 non-avian pennaraptorans from Jurassic and Cretaceous

RESULTS

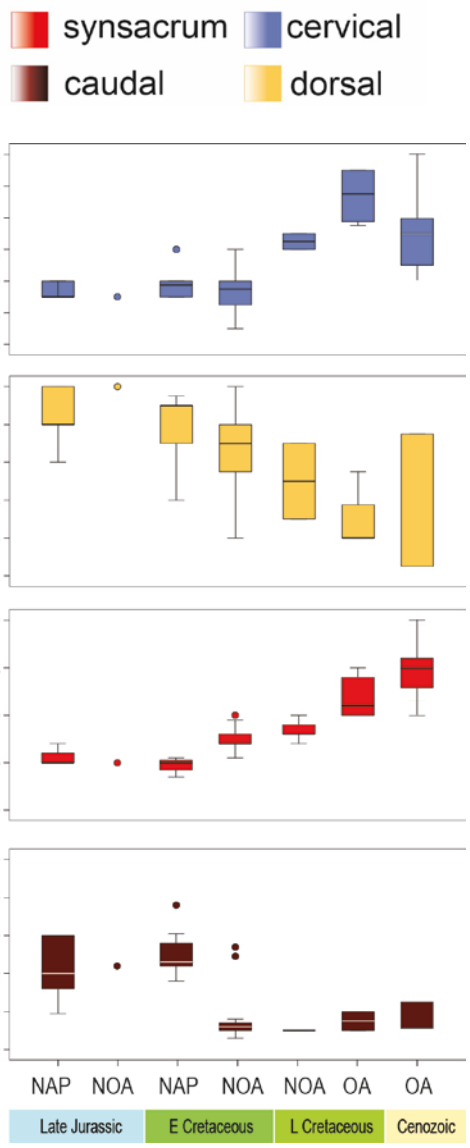
Vertebral count through time



Ornithurine avians, OA

Non-ornithurine avians, NOA

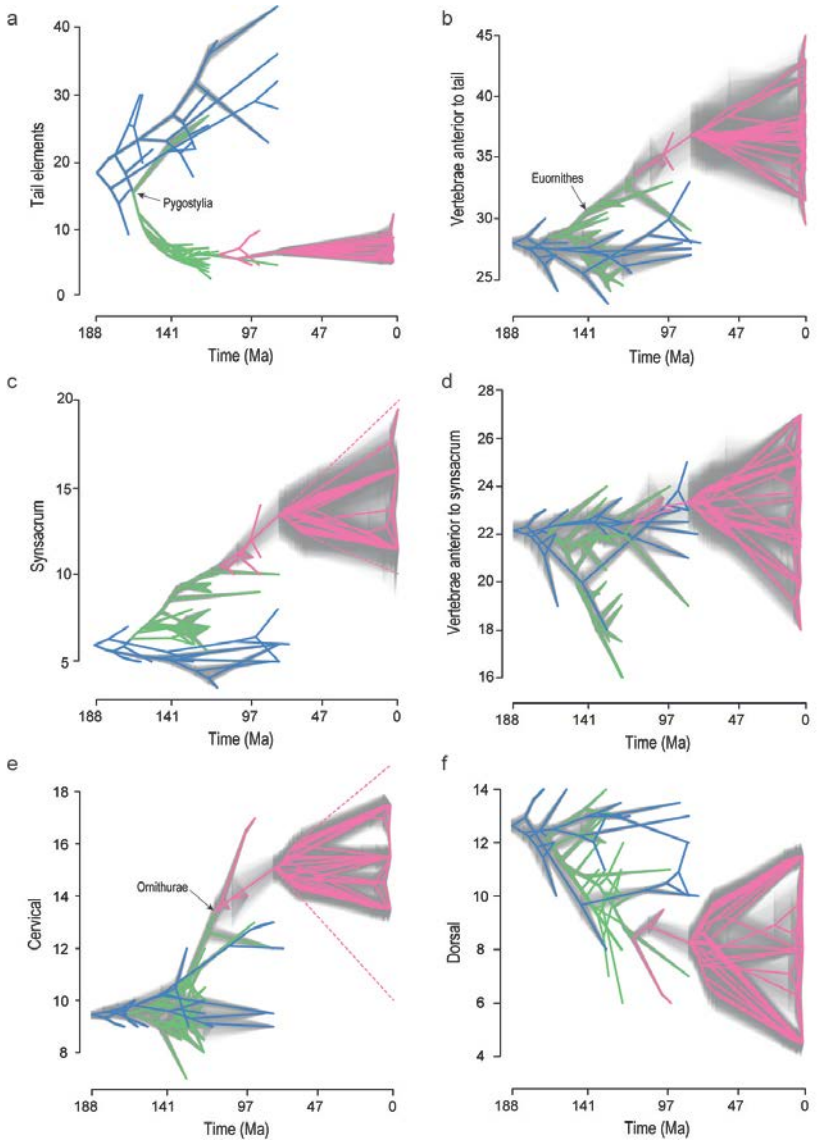
Non-avian pennaraptorans, NAP



Serrano et al. *under review*

RESULTS

Ancestral states reconstructions (ASR) and traitgrams



- NAP and earliest birds: Precaudal vertebrae kept roughly constant; caudal numbers increased

.

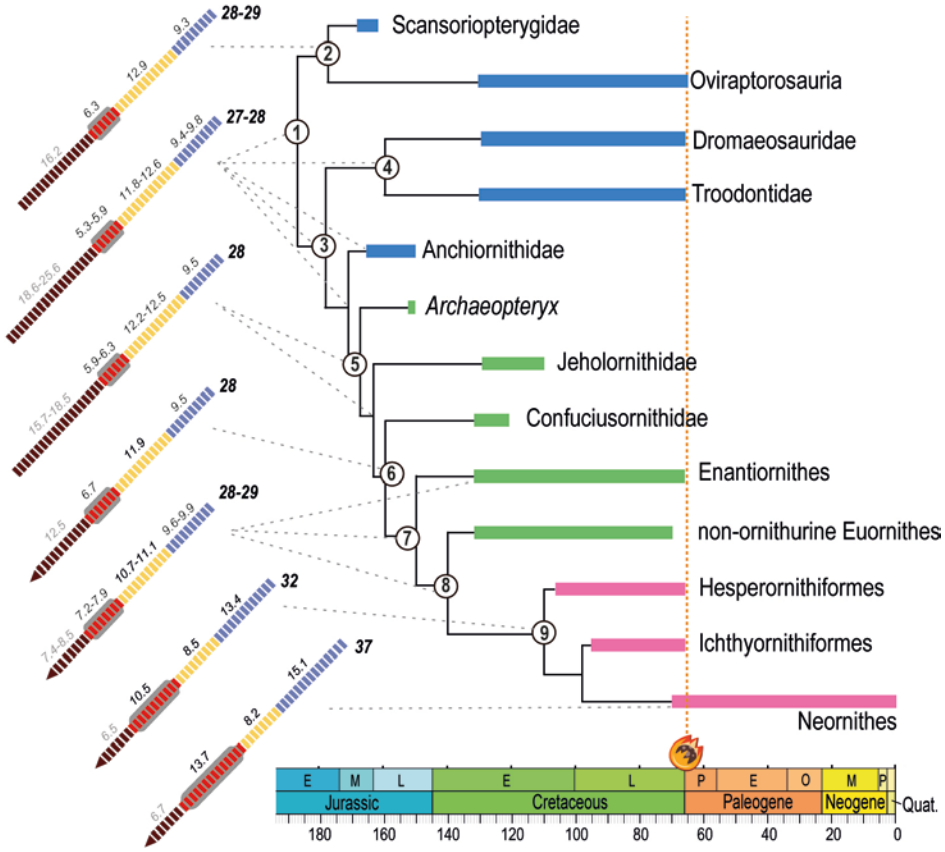
- No changes in precaudal numbers coupled with the abrupt tail reduction at Pygostylia

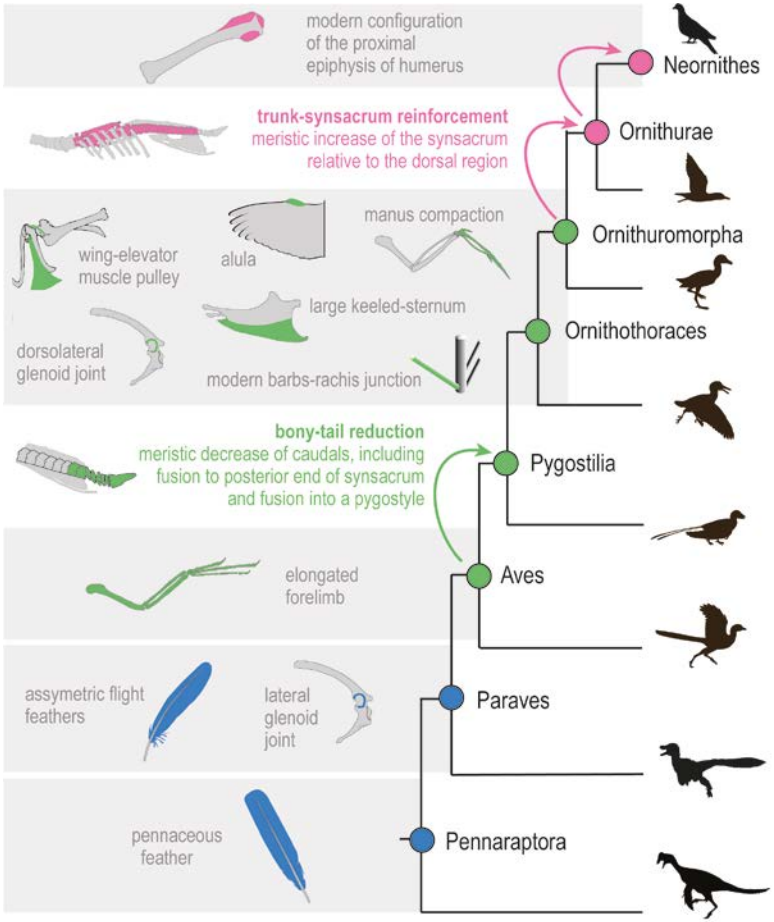
- Marked change to a modern-like precaudal regionalization in Ornithurae: increase of precaudal vertebrae, increasing cervicals and synsacrals, but losing dorsals

- Trend increasing cervical and synsacral vertebrae is kept in Neornithes, but dorsals remained roughly constant

Serrano et al. *under review*

DISCUSSION Spine changes and early evolution of flight





Changes in the precaudal spine, seem not to be important for improving the aerial competence of non-avian pennaraptorans and non-ornithurine avians

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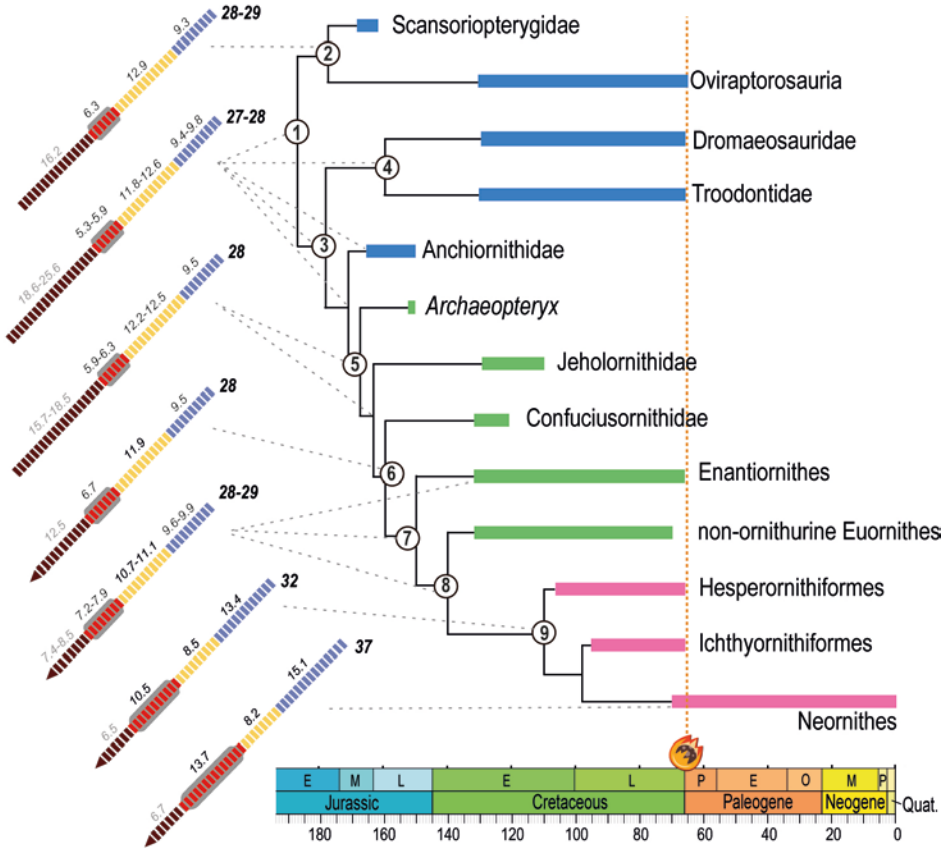
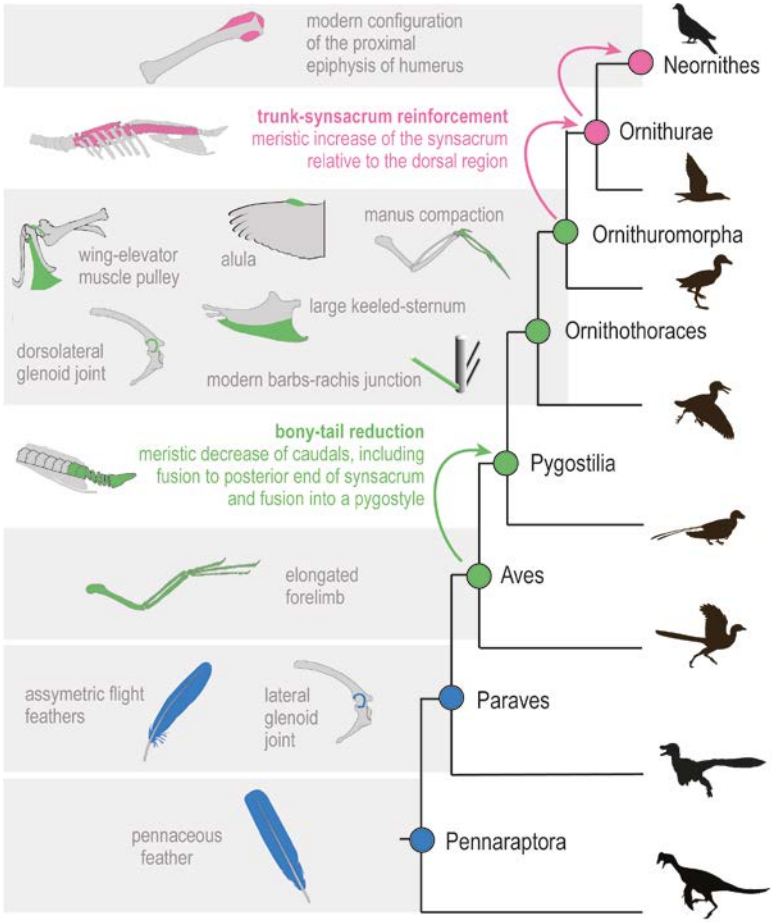
DISCUSSION Spine changes and early evolution of flight





Instead reconfiguration of dorsals and synsacrum in ornithurine avians could reinforce the compactness of the trunk, and hence the stability during the flight

Advantadge at the end of Cretaceous?

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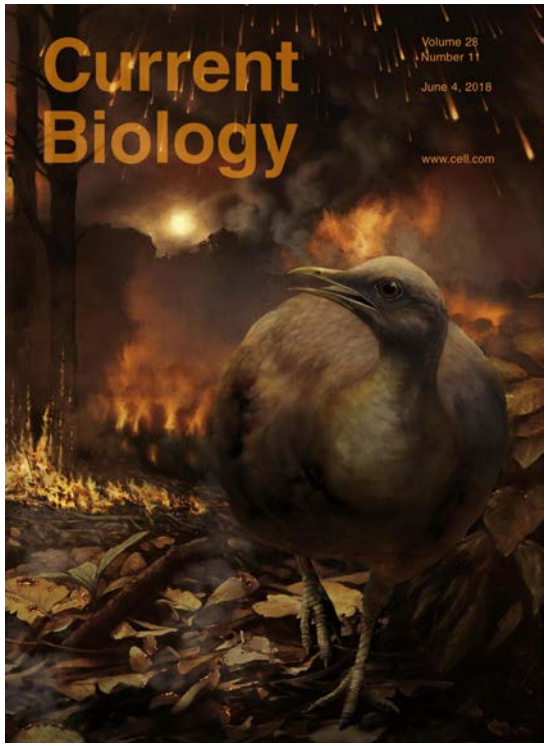
DISCUSSION | Spine changes and KPg mass extinction

> 70% species of the end-Cretaceous biota vanished

Spine changes and KPg mass extinction



HYPOTHESES FOR SURVIVORSHIP OF NEORNITHES

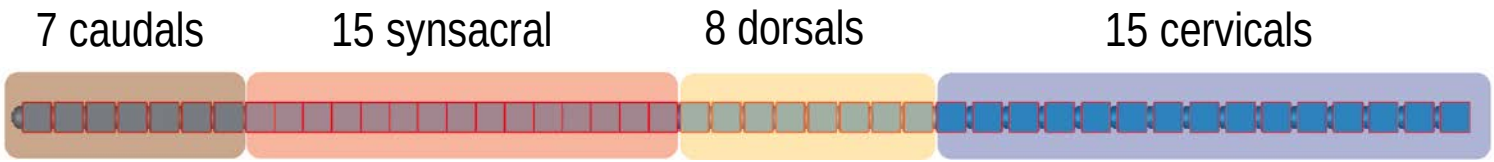
- ❑ Beaks for consuming hard seeds as the primary food available (Larsson et al 2016, *Current Biology*)
- ❑ Sediment-free nesting for more efficient incubation (Varricchio and Jackson 2016, *The Auk: Ornithological Advances*)
- ❑ Small body size for lower energetic requirements (Berv and Field 2018, *Systrematics Biology*)
- ❑ Non-arboreal habits that mitigated the impact of large-scale deforestation (Mayr 2017, Avian Evolution; Field et al 2018, *Current Biology*)

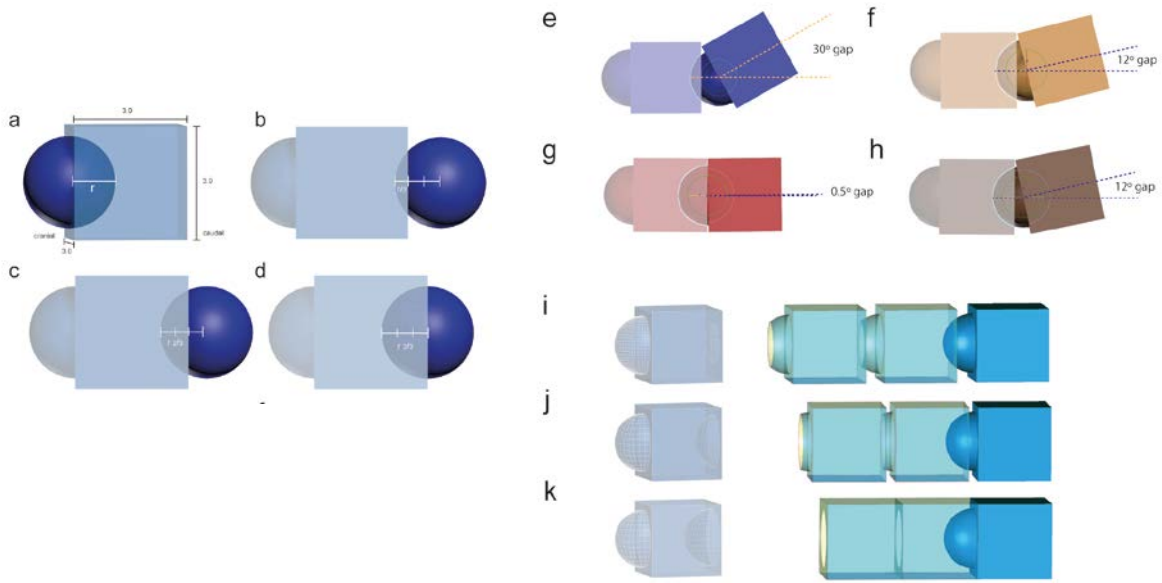
FLIGHT CAPACITY?

Spine changes and KPg mass extinction

Flight biomechanics tests on trunk-synsacrum configurations of birds present at the end of Cretaceous

Construction of 3D models





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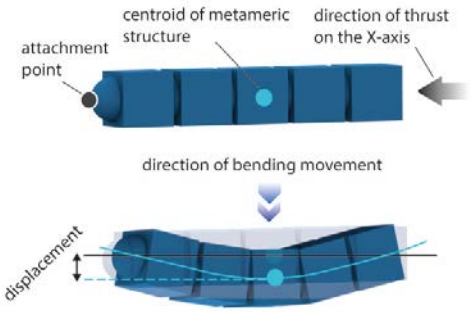
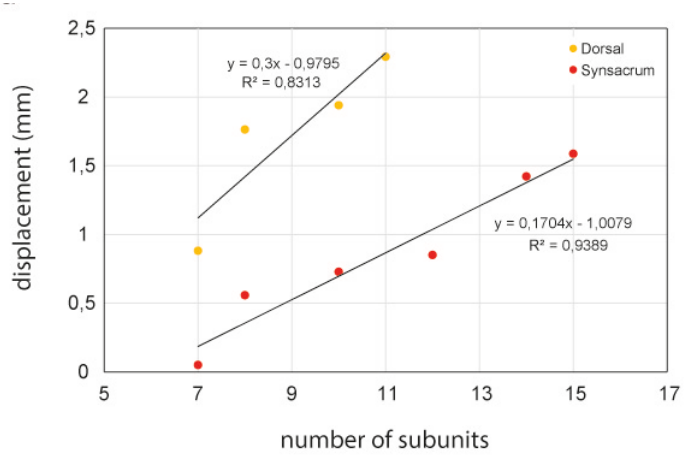
DISCUSSION

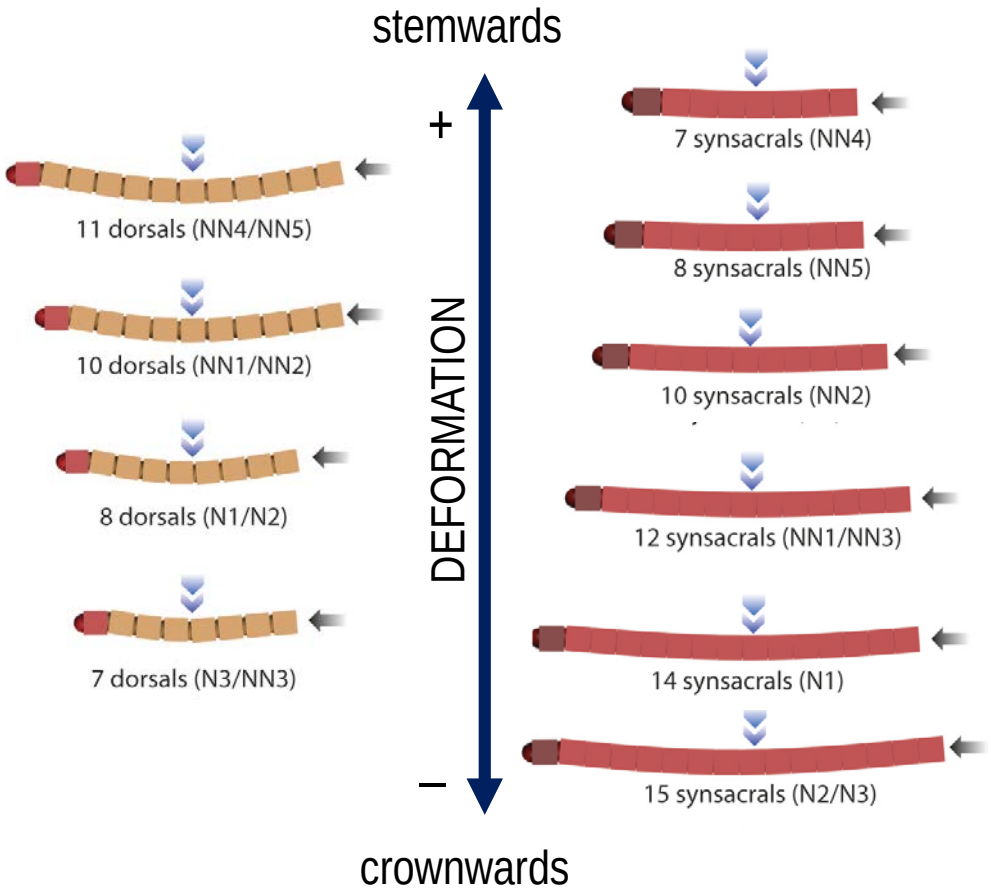
Spine changes and KPg mass extinction

Flight biomechanics tests on trunk-synsacrum configurations of birds present at the end of Cretaceous

1. Range of motion (ROM)







Trunk-synsacrum of neornithines → less deformation

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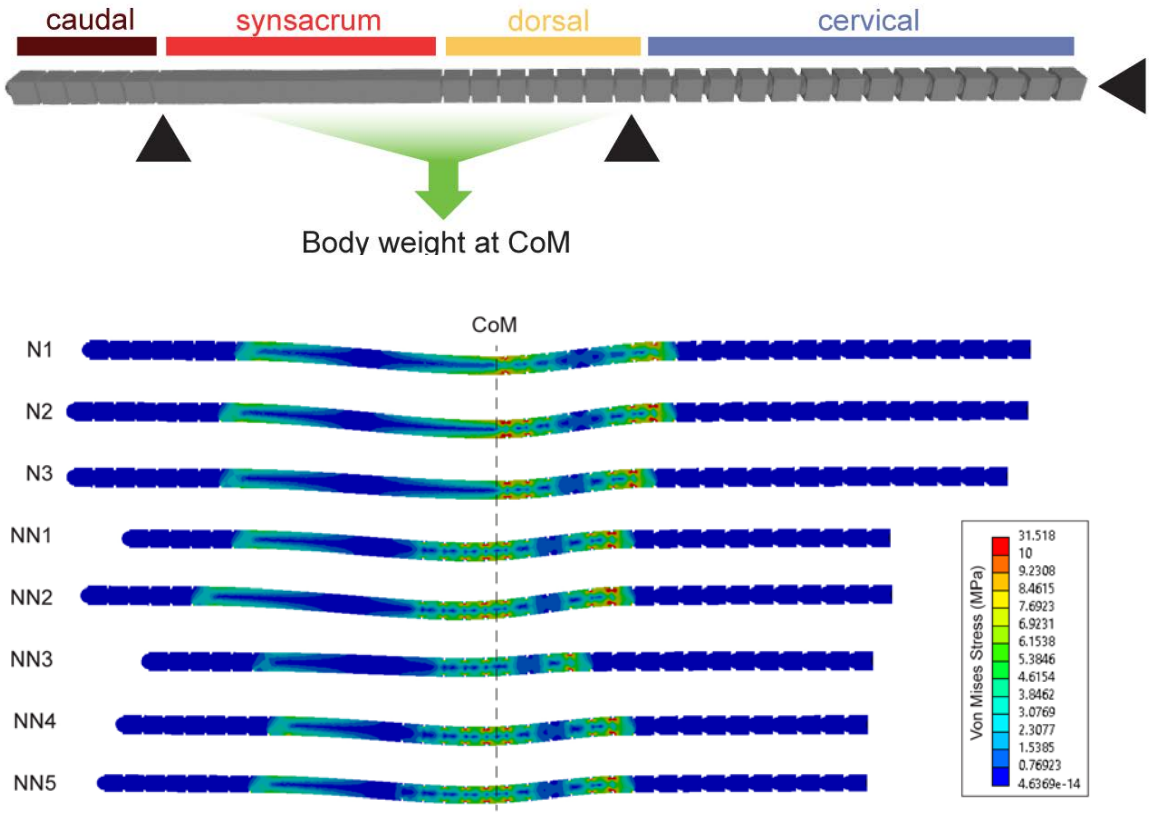
Spine changes and KPg mass extinction

Flight biomechanics tests on trunk-synsacrum configurations of birds present at the end of Cretaceous

2. Finite elements anlysis (FEA)



Neornithes models 1-3

Non-Neornithes models 1-5

Trunk-synsacrum of neornithines → dissipates better bending stress

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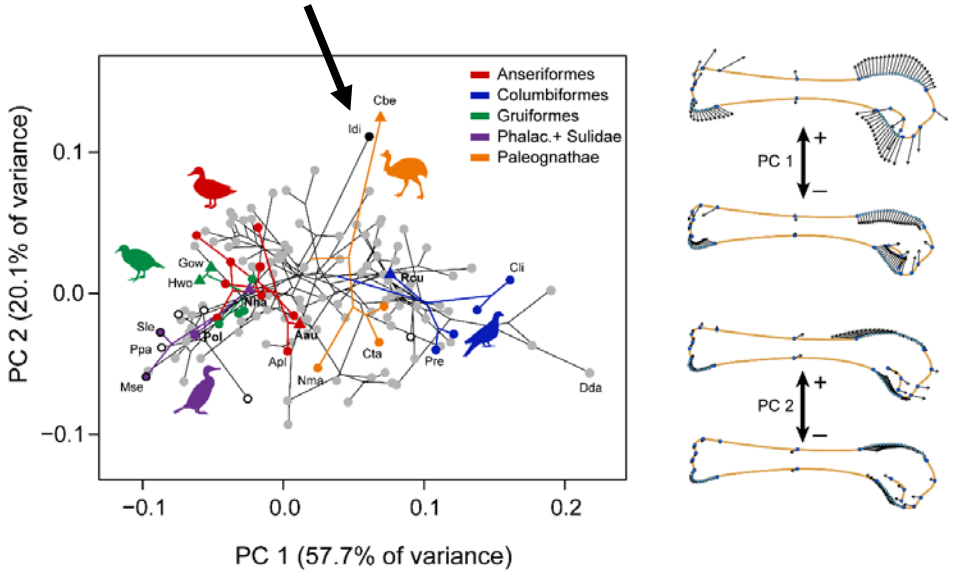
DISCUSSION

Spine changes and KPg mass extinction

Spine's results consistent with functional morphology of the humerus



Morphological transformation of the humerus → improved flapping mechanics

Serrano et al. 2020, *Diversity*

Spine changes and KPg mass extinction

More efficient biomechanics enhanced capacity for prolonged flights of Neornithes

- better escape from hostile areas (e.g. burning forests, acidified water bodies) in search for more benign regions (i.e. refugees)
- broader foraging areas
- to more quickly colonize recovered areas

CONCLUSIONS

- The entire spine remained almost unchanged in pennaraptorans until Pygostylia, and the precaudal spine until Ornithurae, while other anatomical innovations enabled the origin and initial refinement of flight. Hence, **the vertebral column played a minor role in the early evolution of flight** during the Jurassic and Early Cretaceous.

- The fully-modern spinal configuration was acquired only by Neornithes in the Late Cretaceous, by increasing the number of cervical and synsacral vertebrae at expense of the dorsals and free caudals. This configuration is **better optimized for flight derived stresses than other latest Cretaceous birds**

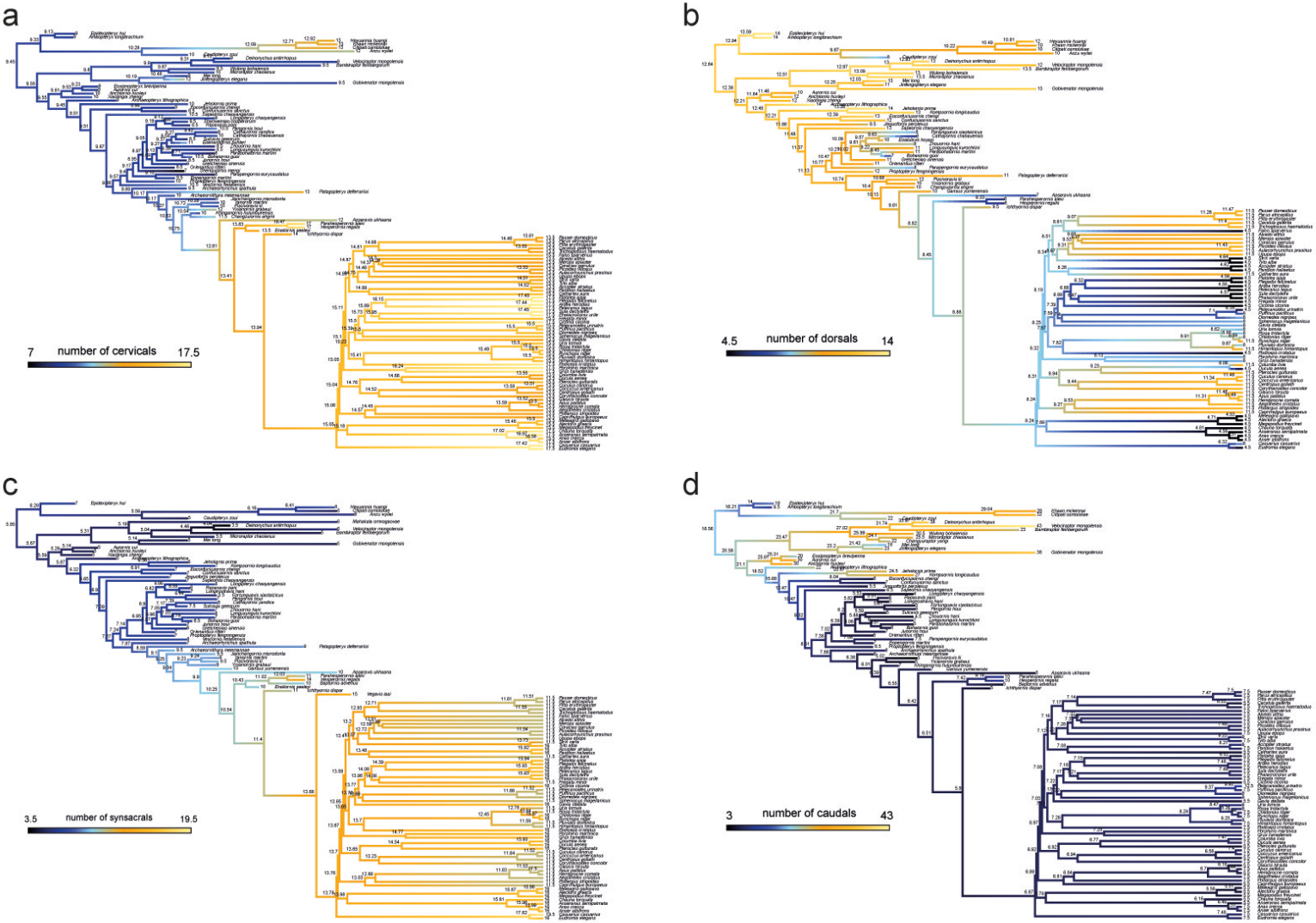
- We hypothesize that **higher flight performance**, underpinned by spinal reconfiguration and humeral morphology, **was key to the survival of neornithines during the end-Cretaceous mass-extinction**.

THANKS FOR YOUR ATTENTION

FUNDING PROJECTS:

CGL2015-68300-P
PID2019-111185GB-I00
P18-FR3193
PAIDI-DOC-00095
Project 'Aerodynamics of early birds'

RESULTS (III). Ancestral states reconstructions



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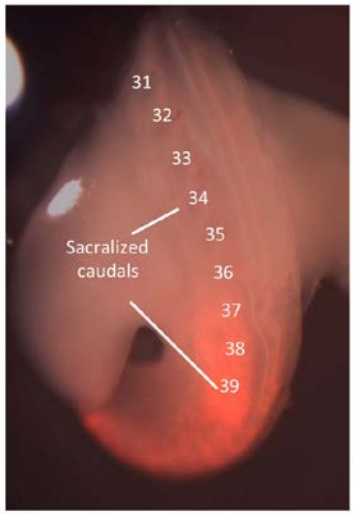
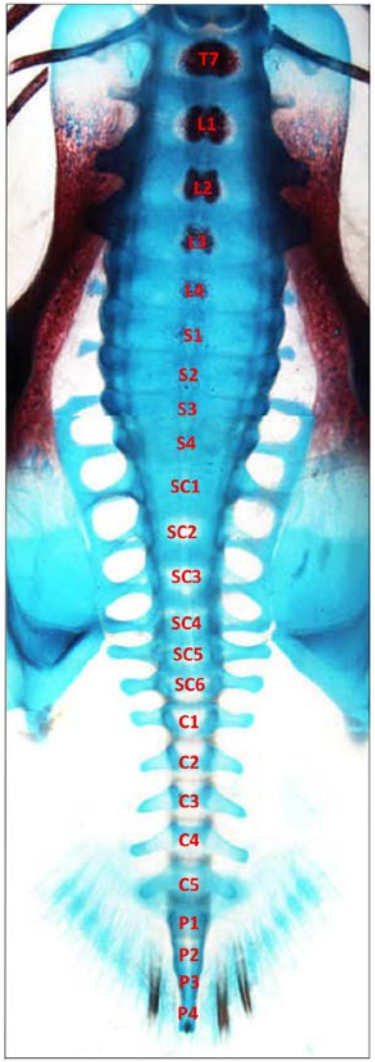
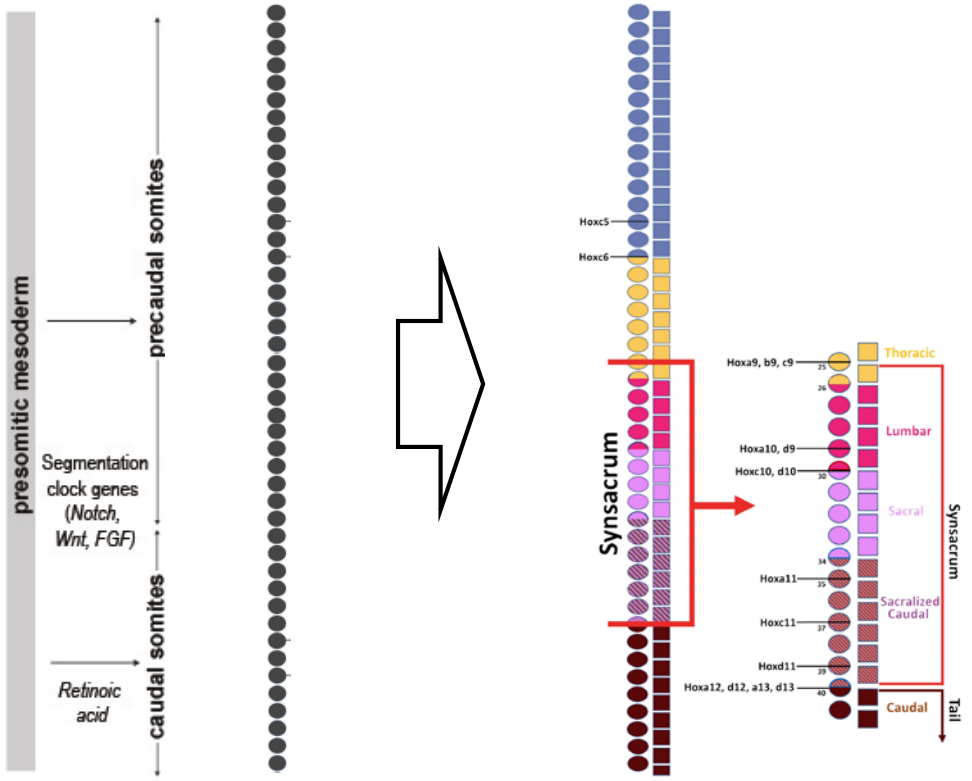

31
32
33
34
Sacralized
caudals
35
36
37
38
39


T7
L1
L2
L3
L4
S1
S2
S3
S4
SC1
SC2
SC3
SC4
SC5
SC6
C1
C2
C3
C4
C5
P1
P2
P3
P4

Vertebral formula

Vertebral number is a suitable proxy to investigate the evolution of spinal regionalization at large temporal scales



ACCELERATION/DECCELERATION OF SOMITOGENESIS → MERISTIC VARIATION

HOMEOTIC TRANSFORMATION → CHANGES IN REGIONALIZATION