

Listening to the past: The extraordinary evolution of the mammalian middle ear

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Art by Zhao Chuang



2017 – 2021: MSci in Palaeontology and Evolution at University of Bristol



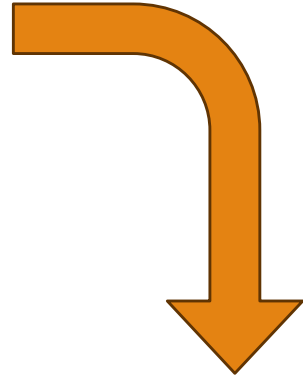
2021 – 2025: PhD at the University of Bristol titled “*The evolution, development and function of the mammalian jaw and middle ear*”



2025 – 2026: Research Associate at the University of Birmingham



Oct 2026: Research Fellow at King's College London





Produce milk



Hair or fur



Warm-blooded



Live young (mostly)

The mammalian jaw and middle ear



Other tetrapods:

- **Multiple** lower jaw bones
- **Quadrate-articular** jaw joint
- **One** middle ear ossicle



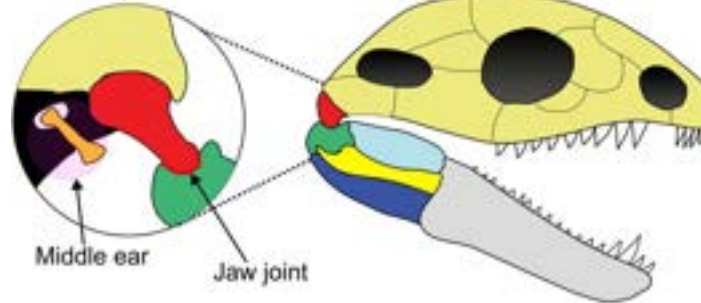
Mammals:

- Dentary **only**
- Jaw joint between **dentary** and **squamosal**.
- **Three** middle ear ossicles

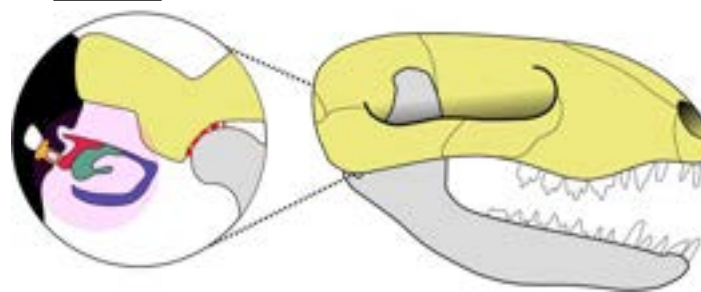


Postdentary bones lost or repurposed as ear bones, while the dentary develops a whole new joint

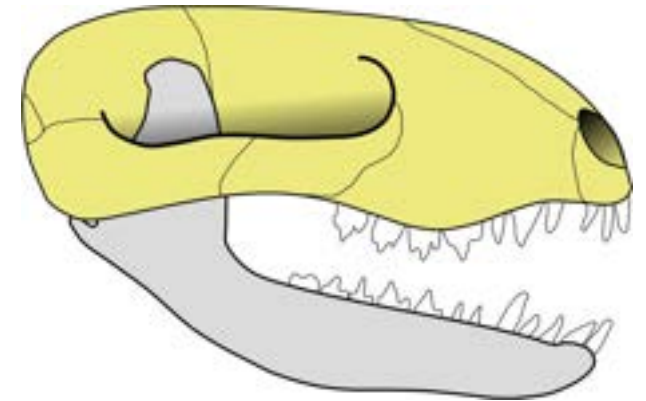
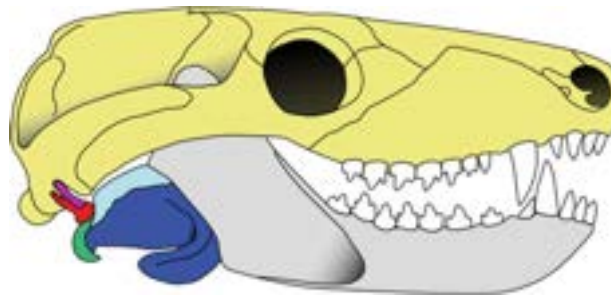
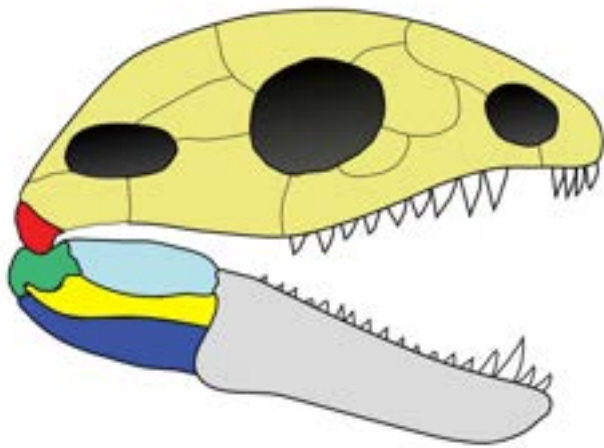
Basal synapsid



Mammal



- Dentary
- Skull
- Articular (malleus)
- Quadrate (incus)
- Angular (Tympanic)
- Stapes
- Prearticular
- Surangular
- Petrosal (part of skull)



How and why did the mammalian jaw and middle ear evolve?

The mammal family tree

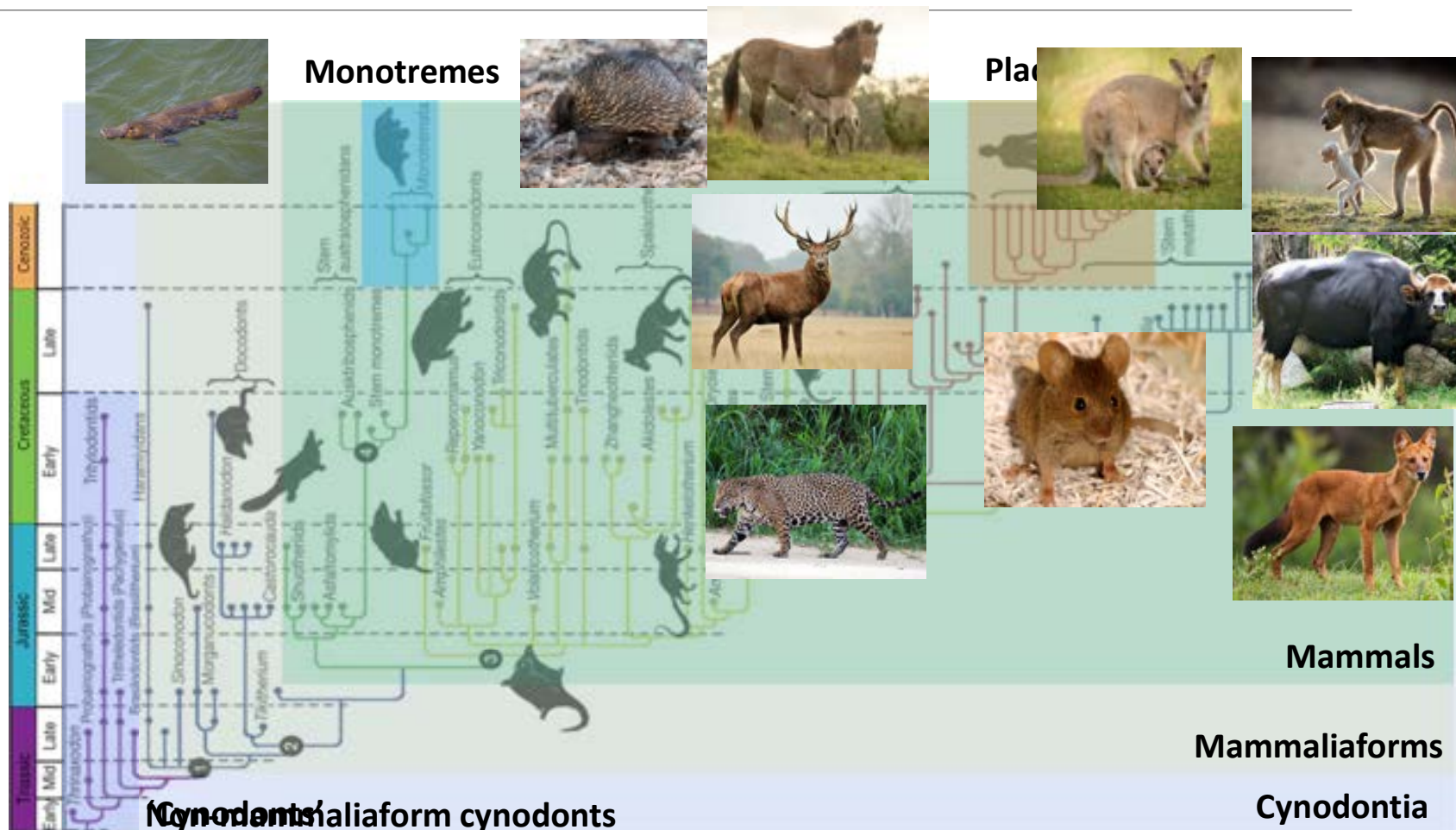


Figure from Luo et al., (2007)

Non-mammaliaform cynodonts – mammal precursors



Well over 100 described species from every continent



Late Permian – Early Cretaceous (~259 – 113 MYA)



Art by Mark Witton, WillemSvdMerwe, Gabriel Ugueto, Nix Illustration

The cynodont jaw and middle ear



Origin of many key mammalian features



"In no other saurian are incisors so divided from molars by a single canine, in none is the definition of three kinds of teeth so plain and unequivocal." **Richard Owen, 1845.**



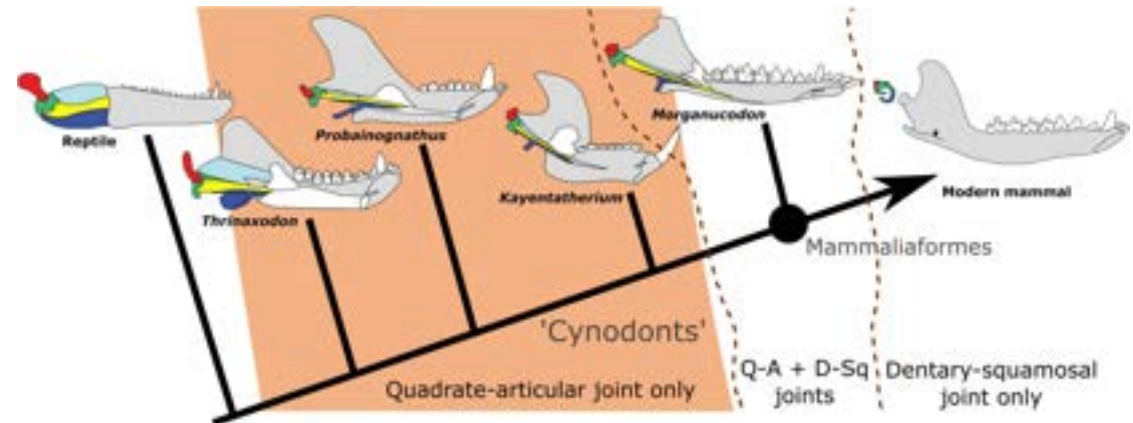
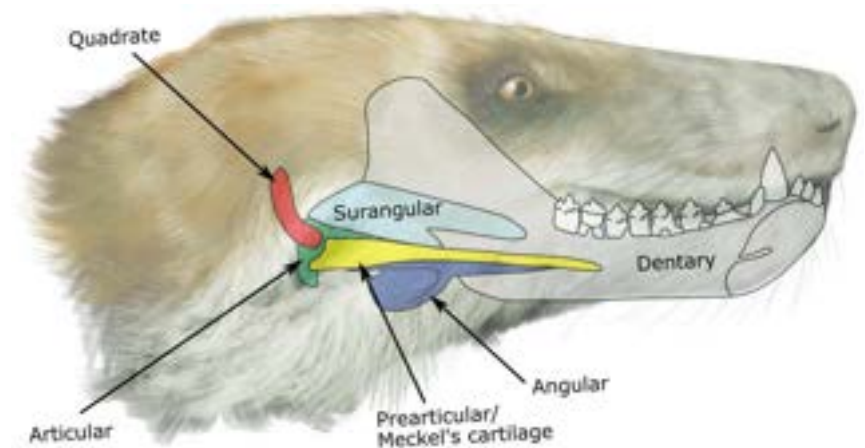
Loosely attached postdentary bones act as **both middle ear and jaw joint**

Postdentaries get **relatively smaller** across cynodont evolution

Dentary-squamosal jaw joint first appears in mammaliaforms



But.. **not many fossils** close to mammaliaforms



Jaw outlines modified from Luo & Manley (2020), Allin & Hopson (1992)

South American cynodonts



Santa Maria Supersequence, Rio Grande do Sul, Brazil has yielded exceptional Middle-Late Triassic fossils



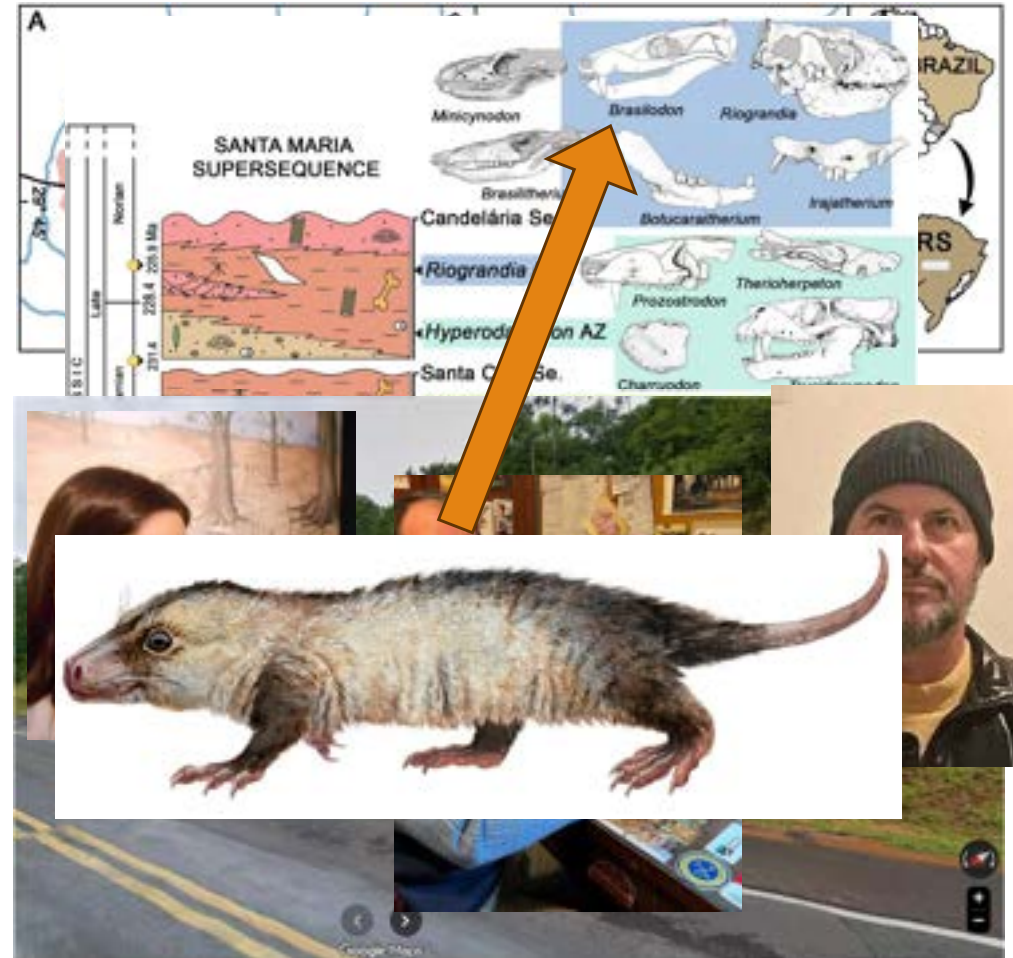
Fluvial and **alluvial** red sandstone, siltstone and mudstone with some conglomerates

U-Pb radiometric dating, **vertebrate assemblage zones** allow dating from other formations.



Why are these cynodonts important?

- **Closely related** to Mammaliaformes
- **Numerous** articulated skulls/jaws
- *Brasilodon* may possess a **D-Sq** jaw joint



Figures from Martinelli *et al.*, (2016). Illustration by Júlia d'Oliveira

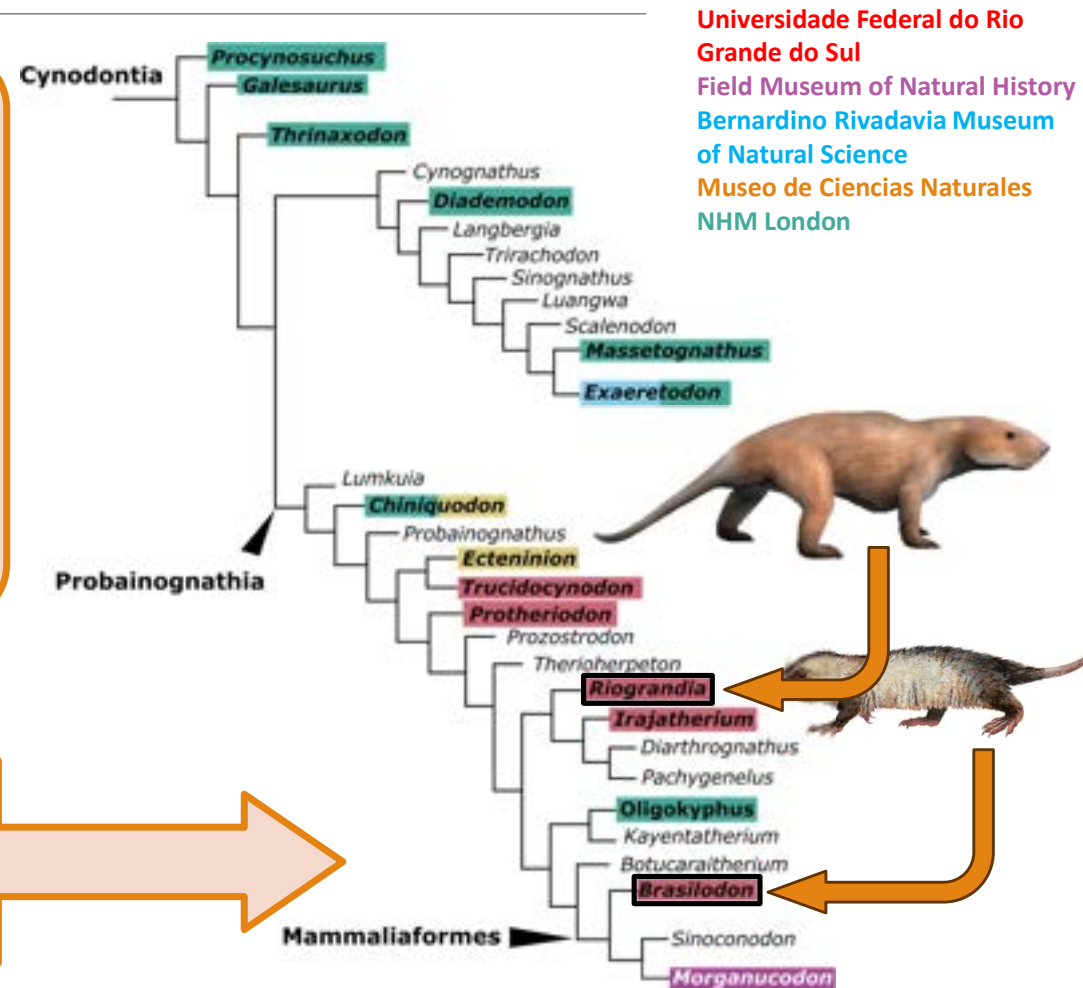
South American cynodonts

However...

Superficially described but jaw anatomy is **ambiguous**

A good foundation of postdentary anatomy across cynodont phylogeny is vital first step to understanding why the middle ear and jaw joint evolved

Micro-CT scanned **47** cynodont specimens from **17** species, including derived South American probainognathians like ***Brasilodon*** and ***Riograndia***



Tree adapted from Martinelli and Soares (2016). Illustration by Júlia d'Oliveira and Nobu Tamura

Digital Fossils



Digital Fossils

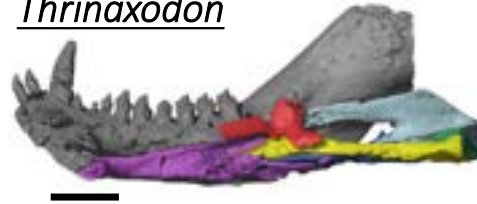
Procynosuchus



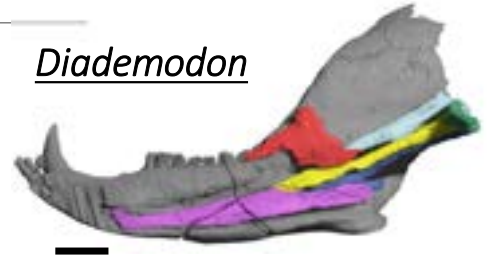
Galesaurus



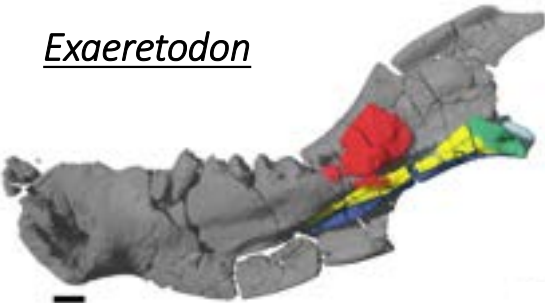
Thrinaxodon



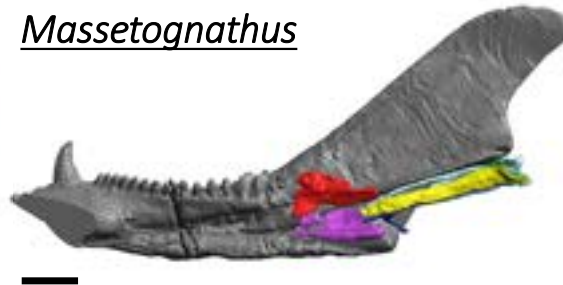
Diademodon



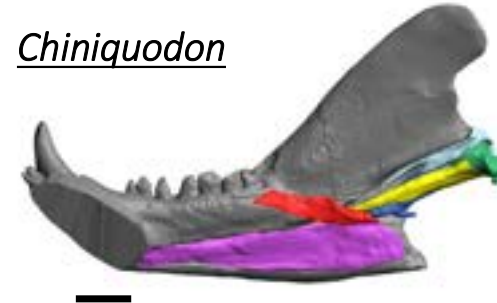
Exaeretodon



Massetognathus



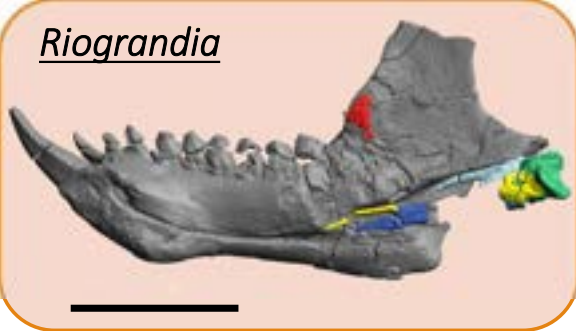
Chiniquodon



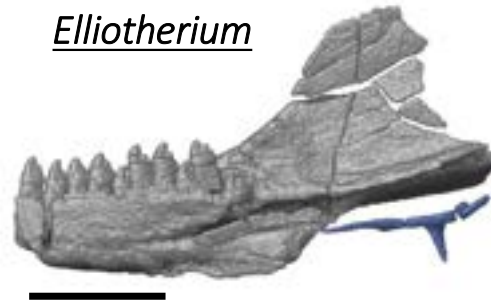
Ecteninion



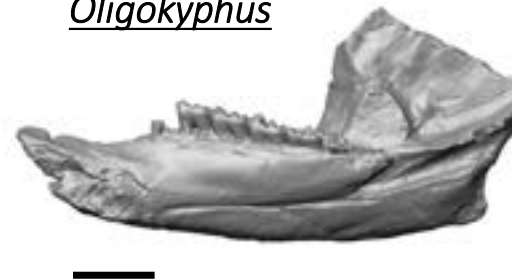
Riograndia



Elliotherium



Oligokyphus



Brasilodon



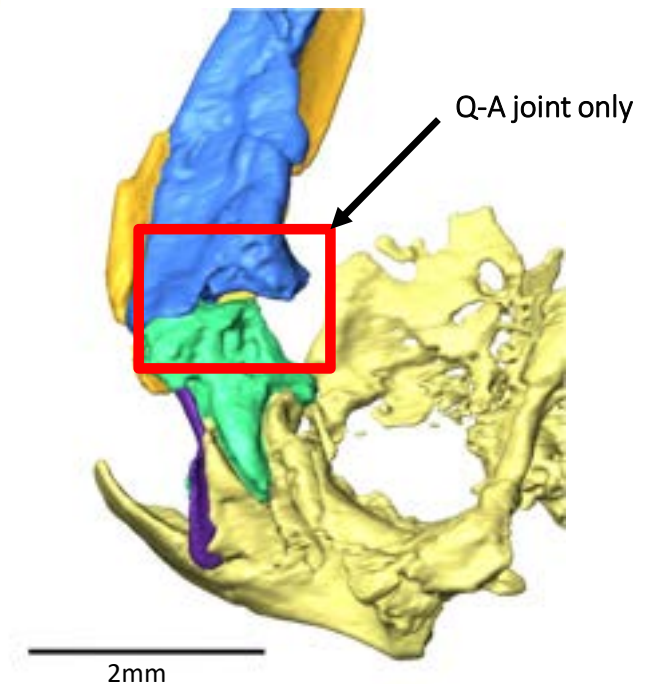
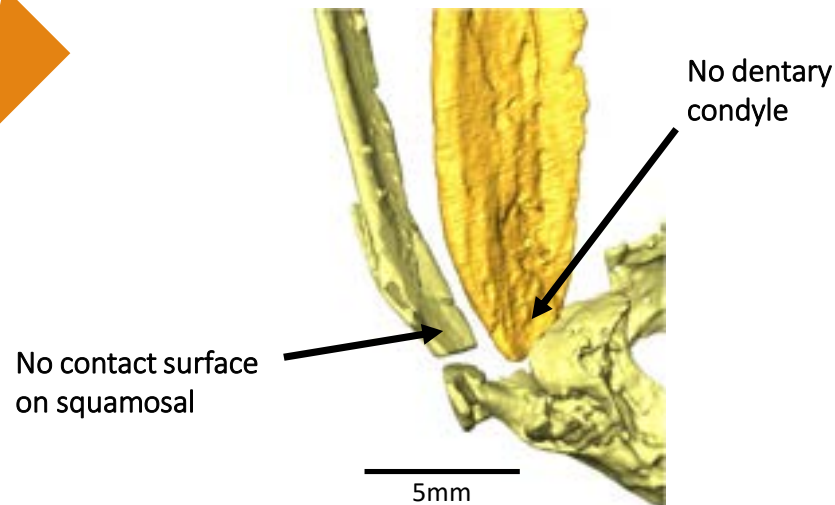
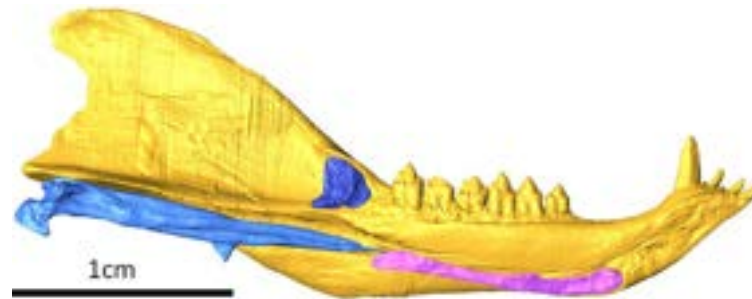
Scale bars 10mm

Brasilodon – the closest relative of mammaliaforms

3D data of *Brasilodon* shows PD's **larger** and more **primitive** than previously known.

Anatomy for dentary-squamosal jaw joint **absent**.

Brasilodon relied on primary **quadrate-articular joint only**.



Riograndia – an independent dentary-squamosal contact

Clear **dentary-squamosal** contact.

Joint morphology **distinct from mammaliaforms**

Riograndia evolved a contact between the dentary and squamosal **17 million years before** mammaliaforms

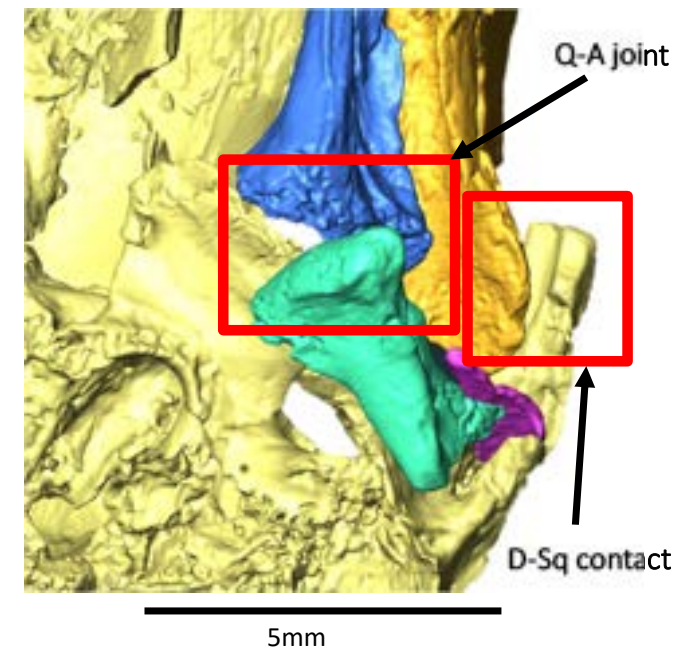
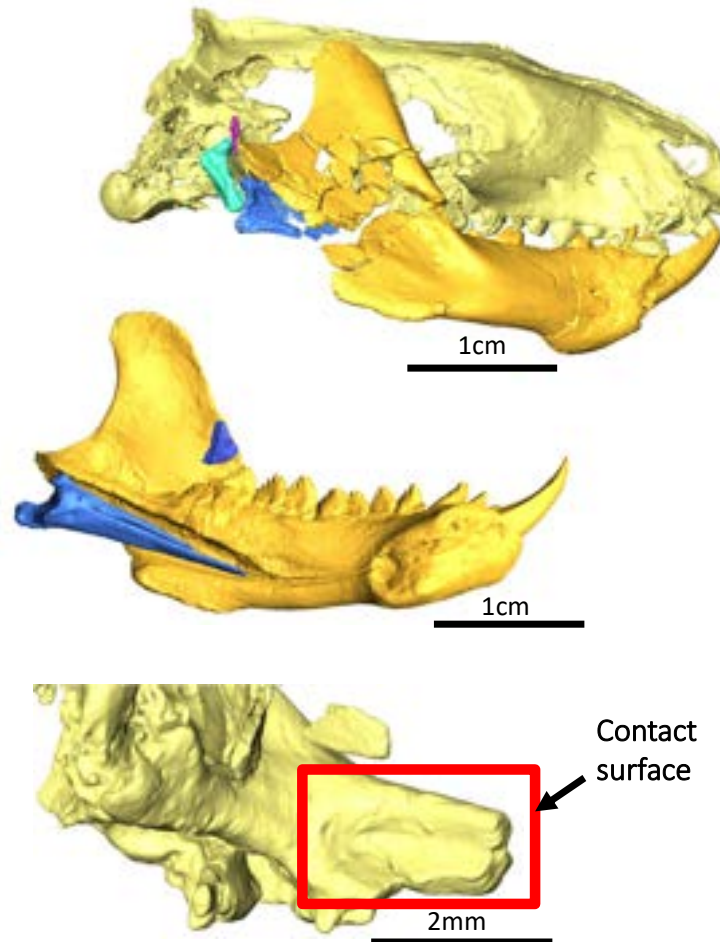
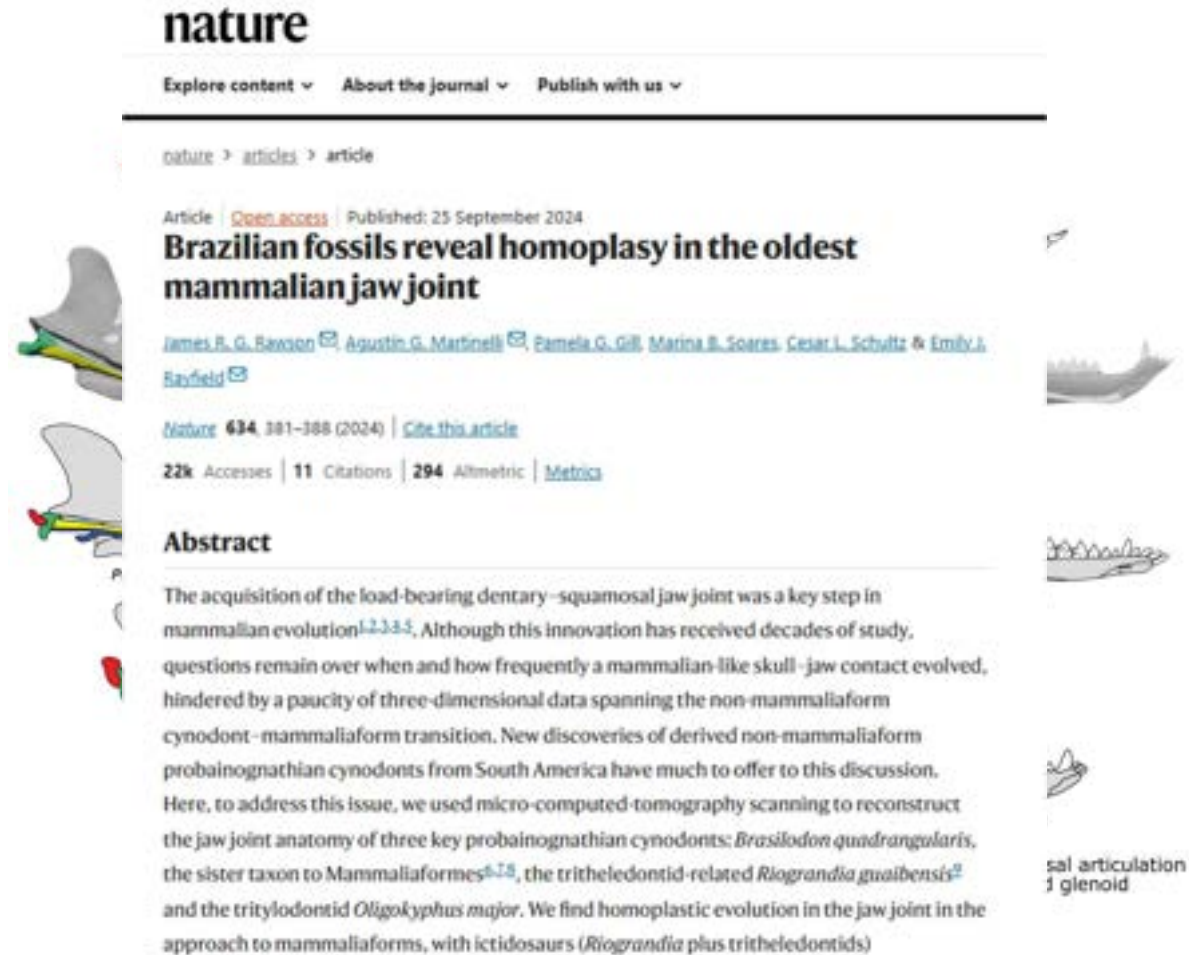
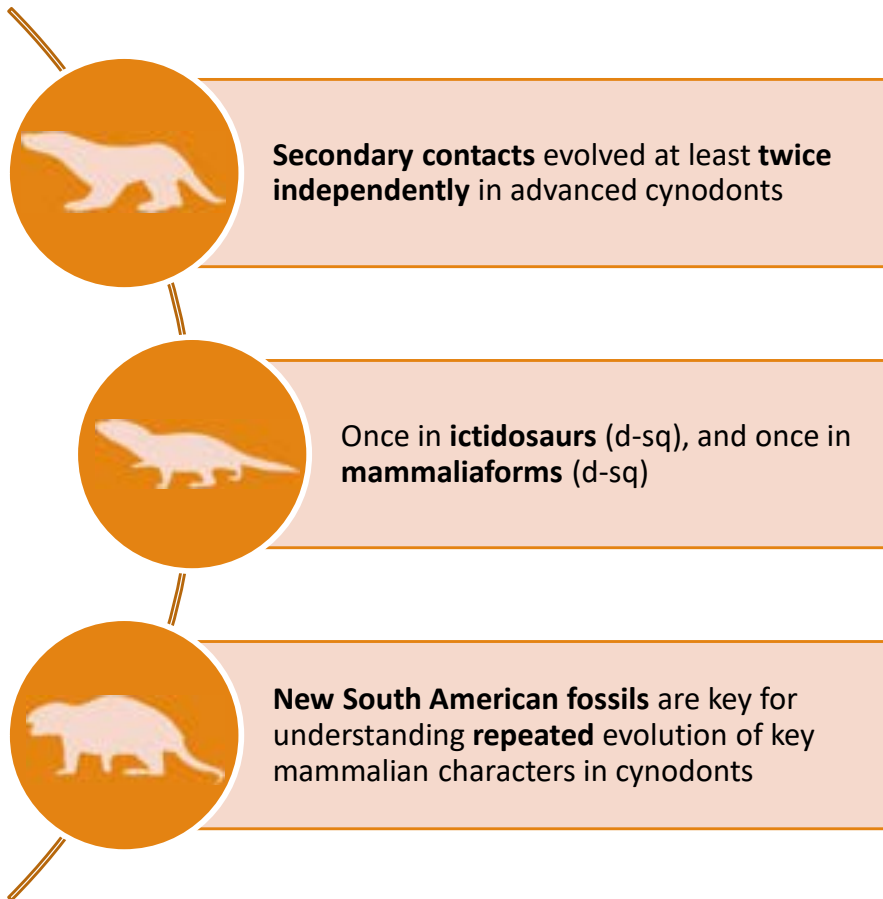
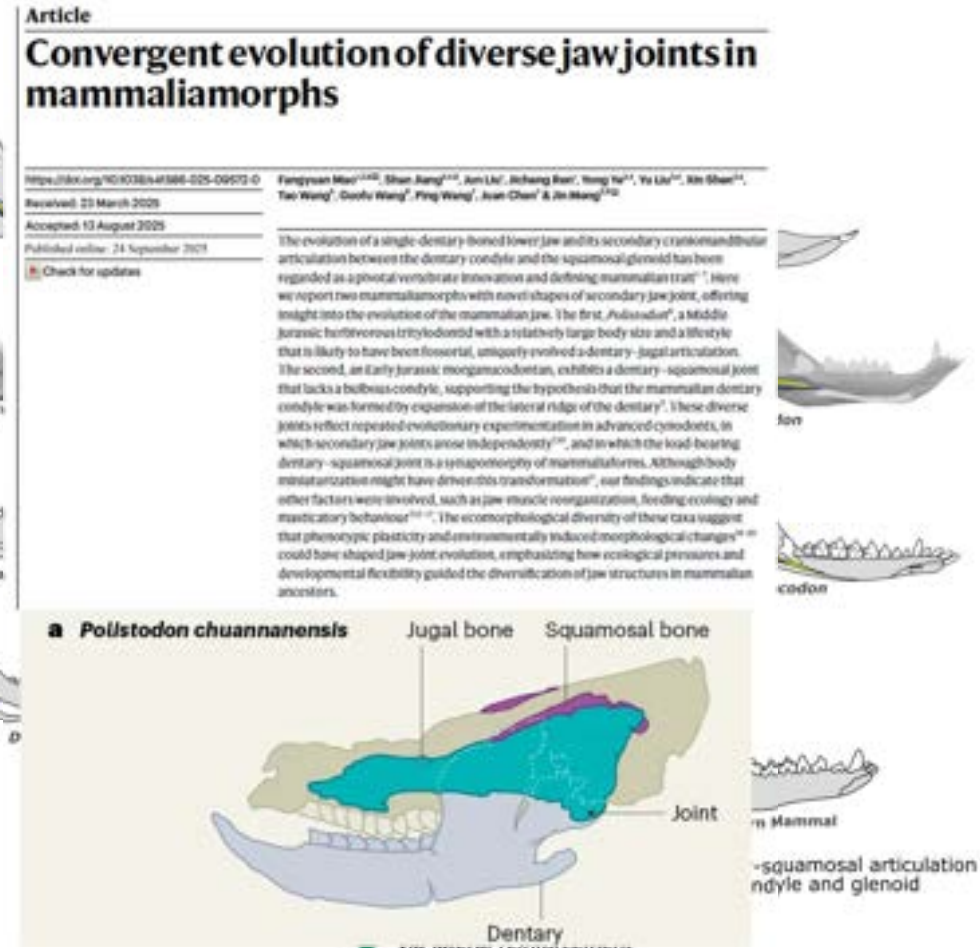
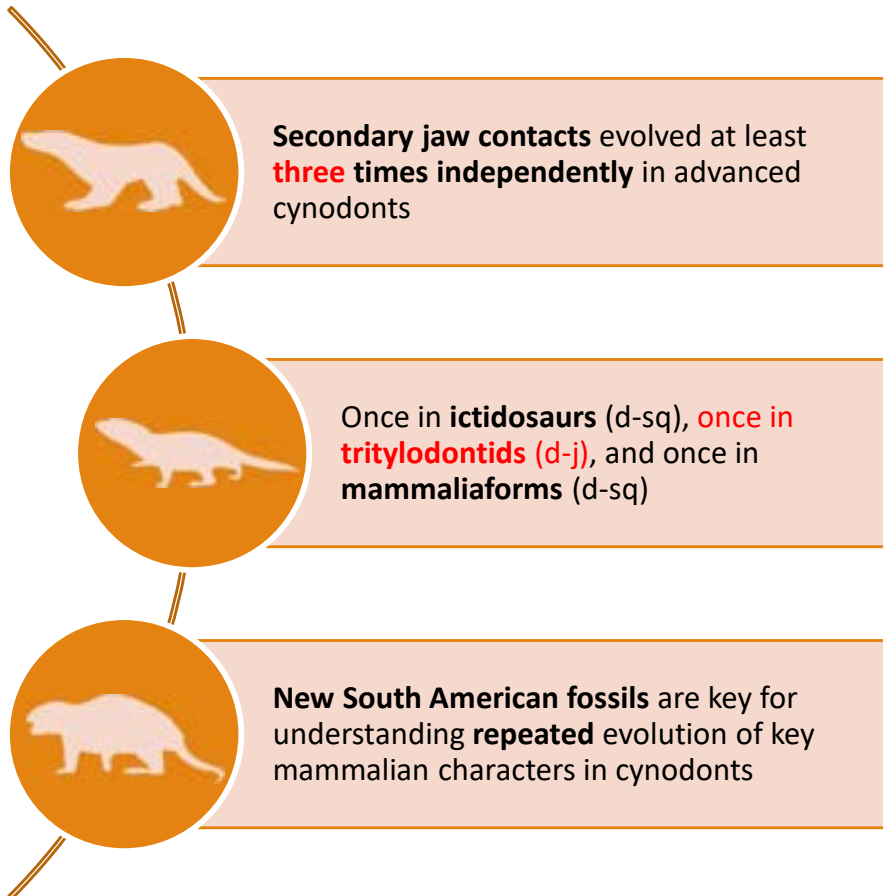


Illustration by Theropsida (<https://www.deviantart.com/theropsida>)

Jaw joint evolution revisited



Jaw joint evolution revisited



Mao et al., (2025), diagram from Panciroli, (2025)

Feeding or hearing: why not both?



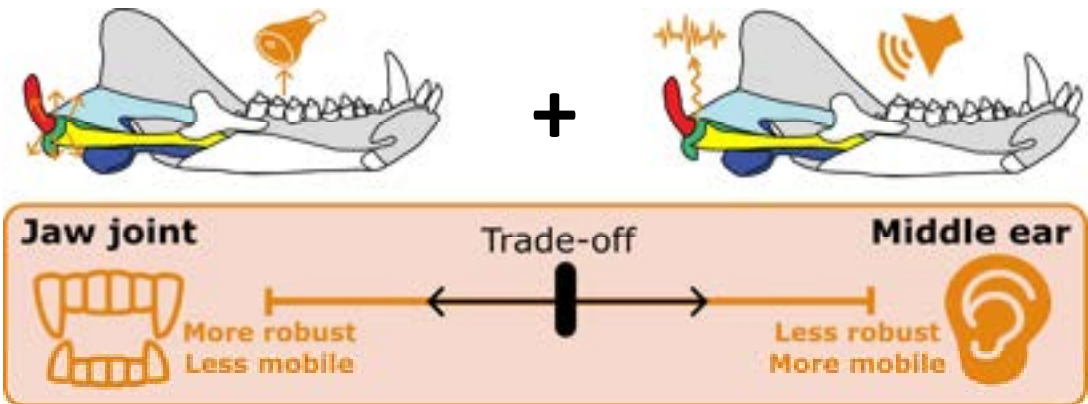
Repeated evolution of **secondary jaw contacts** in small Late Triassic cynodonts. **Why?**

A functional conundrum

- Postdentary bones must act as **both jaw joint** and **middle ear**.
- **Trade-off** between demands from **feeding** and **hearing**.
- To evolve a mammalian middle ear, loading on the postdentaries **MUST** be reduced **WHILE** maintaining a functioning jaw system

How?

- Extra jaw joint might **reduce** mechanical loading
- **Never actually tested**



Finite element analysis



An engineering technique adapted for **biomechanics**



Simulates the mechanical **response to loading** across a structure



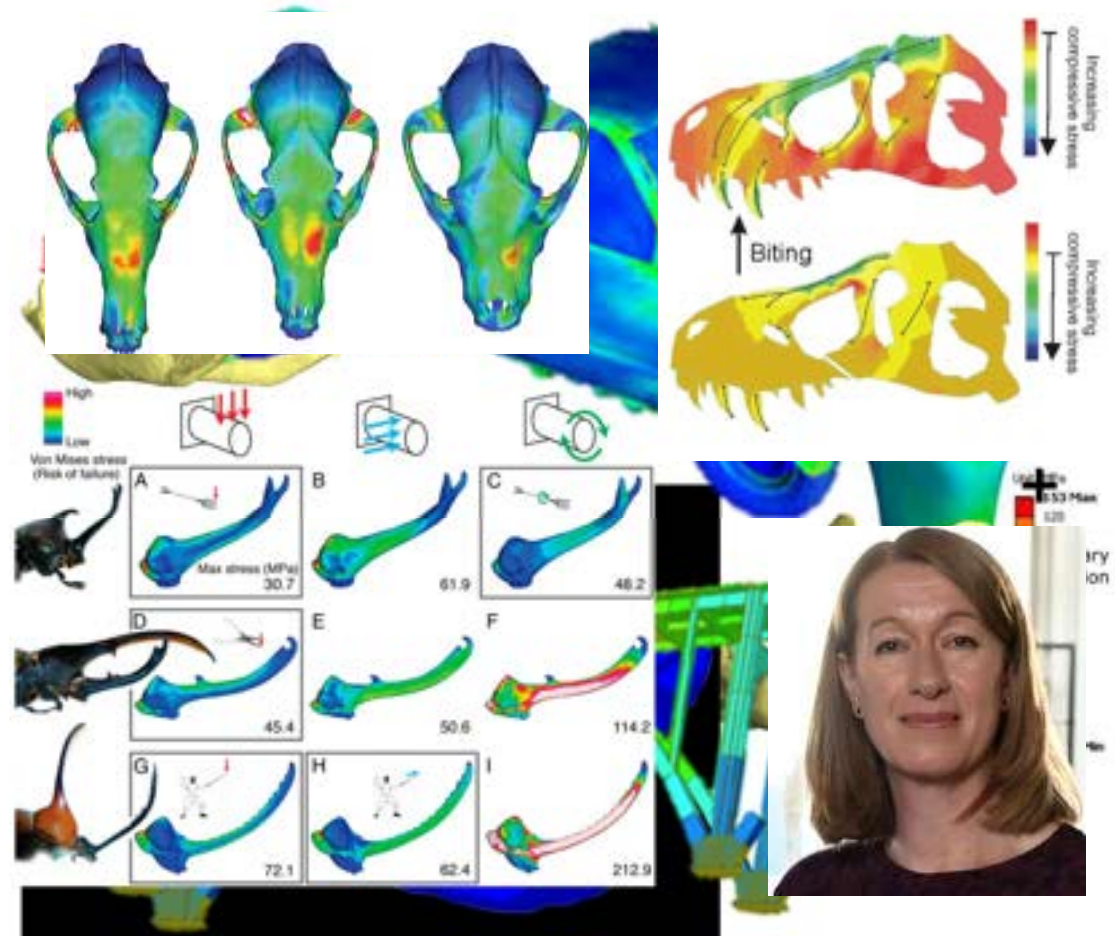
'Hotter' colours mark areas of highest **stress** and **strain** in a given scenario



Can compare results from different models to test links between **anatomy** and **function**



Hypothesis: Adding a **dentary squamosal contact** will **reduce stress** in the postdentaries





Secondary articulations were vital for middle ear evolution



Secondary points of contact **consistently reduce** stress in the postdentaries and shift it to the dentary.



First time this decades-old assumption has been tested



The origin of a dentary-squamosal joint was a **big functional shift** for the middle ear in mammal evolution

So far...



A dentary-squamosal jaw joint, a classic 'mammalian' feature, evolved multiple times within cynodonts.



This joint was a game-changing innovation that broke the functional trade-off between feeding and hearing in cynodonts, unlocking new functional possibilities



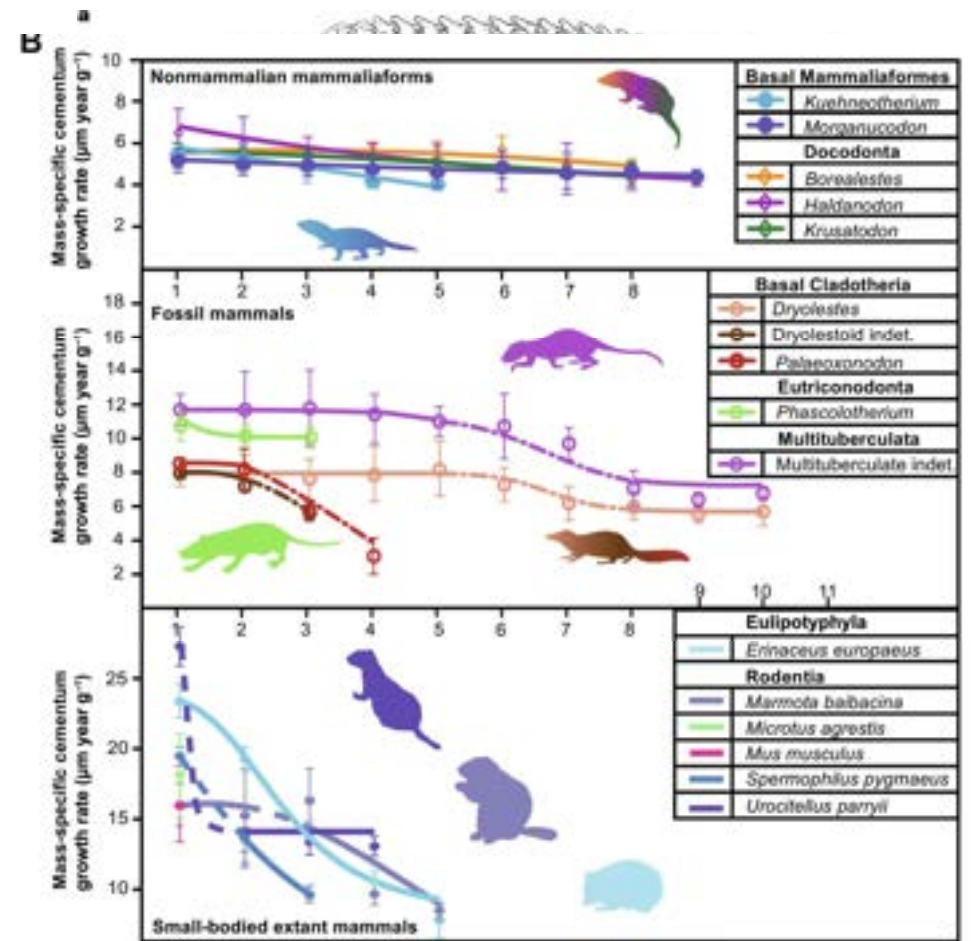
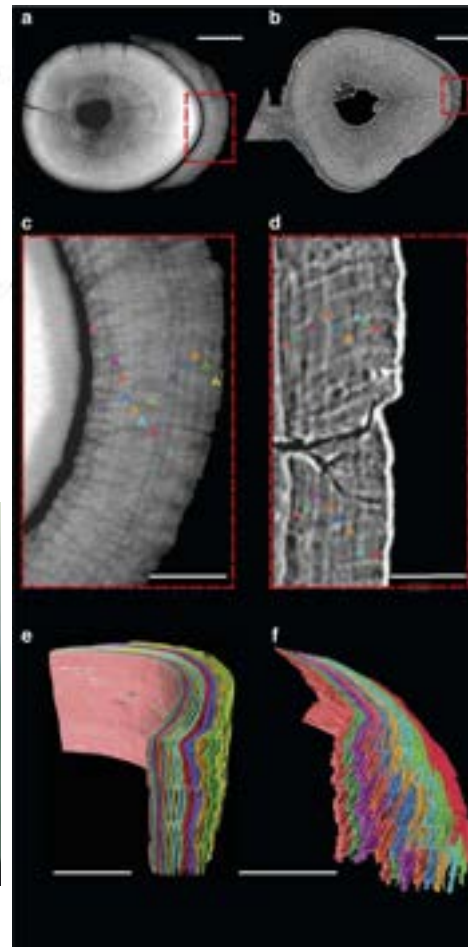
The process of separating the jaw from the middle ear had begun...

Mesozoic mammals and their relatives



Figures from Luo et al., (2007). Art by Sergey Krasovskiy, Pedro Salas, M. Klingler, Nobu Tamura, Zhao Chuang, Andrey Atuchin

Mesozoic mammals: new discoveries!



Bi et al., (2026), Li et al., (2026), Newham et al., (2020, 2024)

Skye: An emerging site for mammal palaeontology



Middle Jurassic (~167 Mya)
Kilmaluag Formation on the Isle of Skye



Layered siltstone, mudstone and argillaceous limestones deposited in a low salinity lagoonal environment.

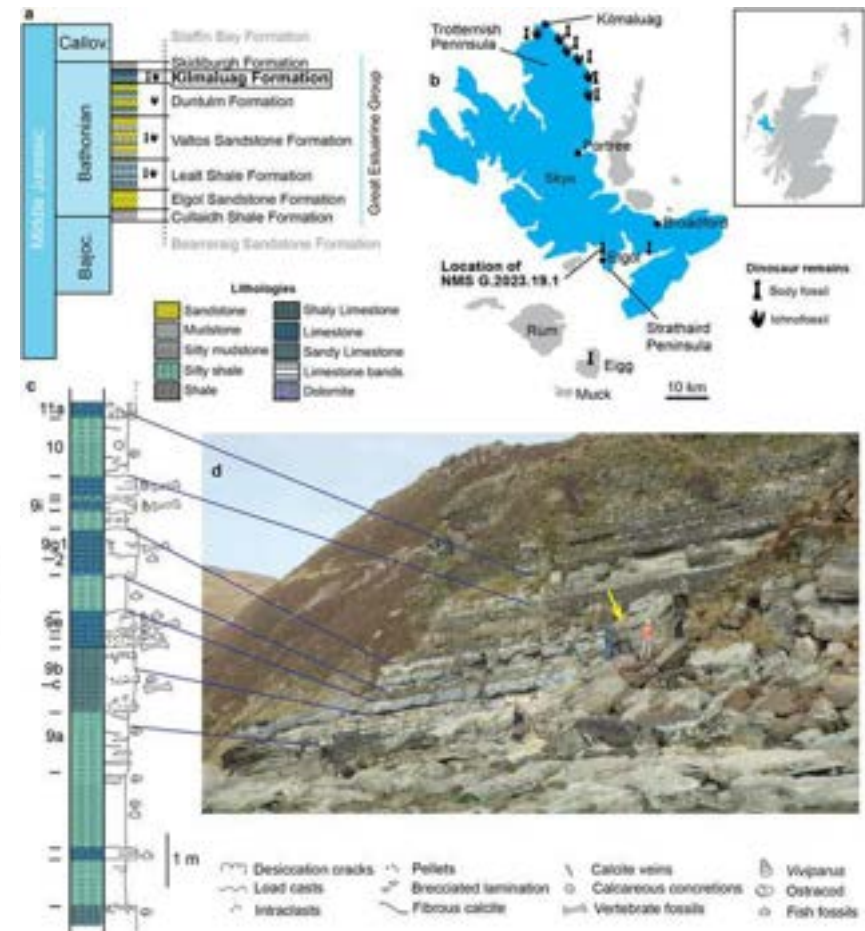


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Scotland

American Museum
of Natural History



Skye: An emerging site for mammal palaeontology



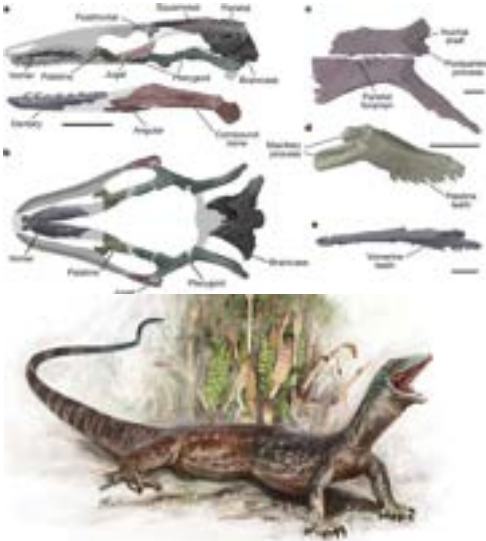
Figure from Panciroli et al., (2020)

Fossils of the Kilmaluag Formation

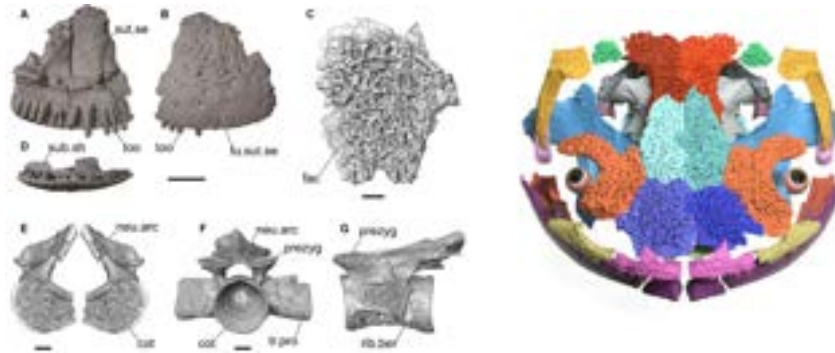
Turtles



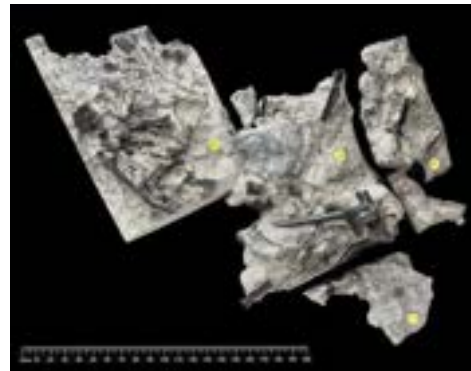
Lepidosaurs



Amphibians



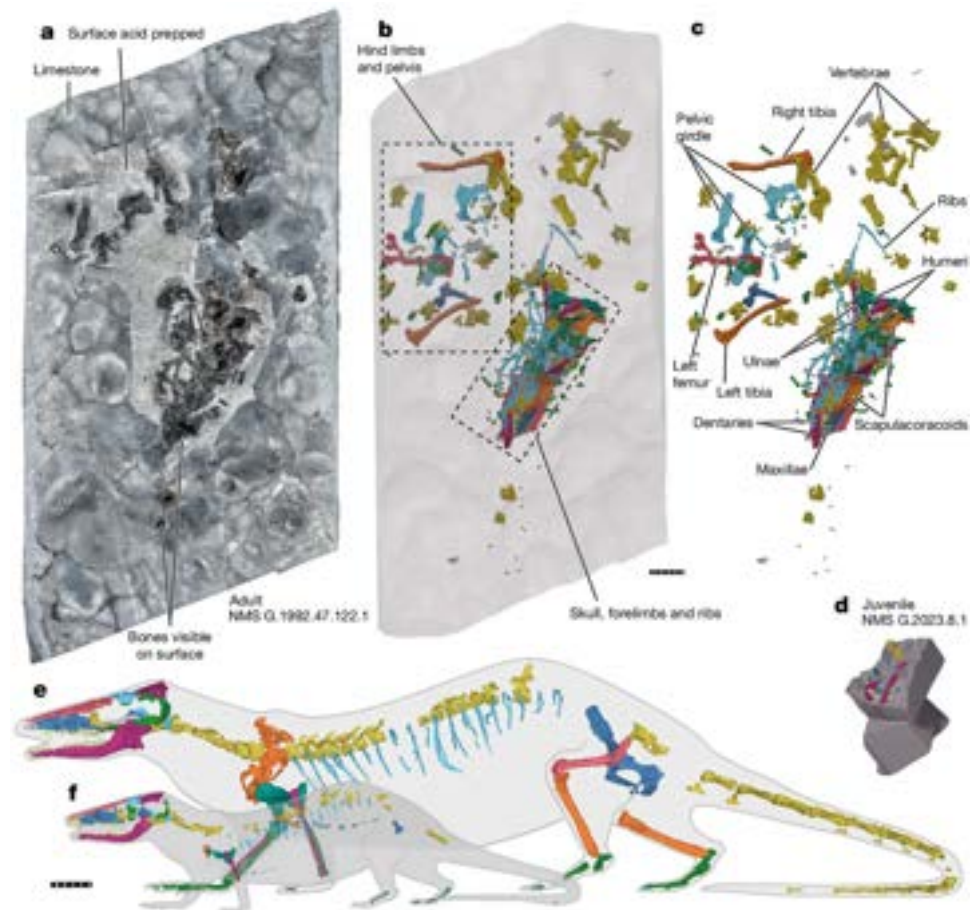
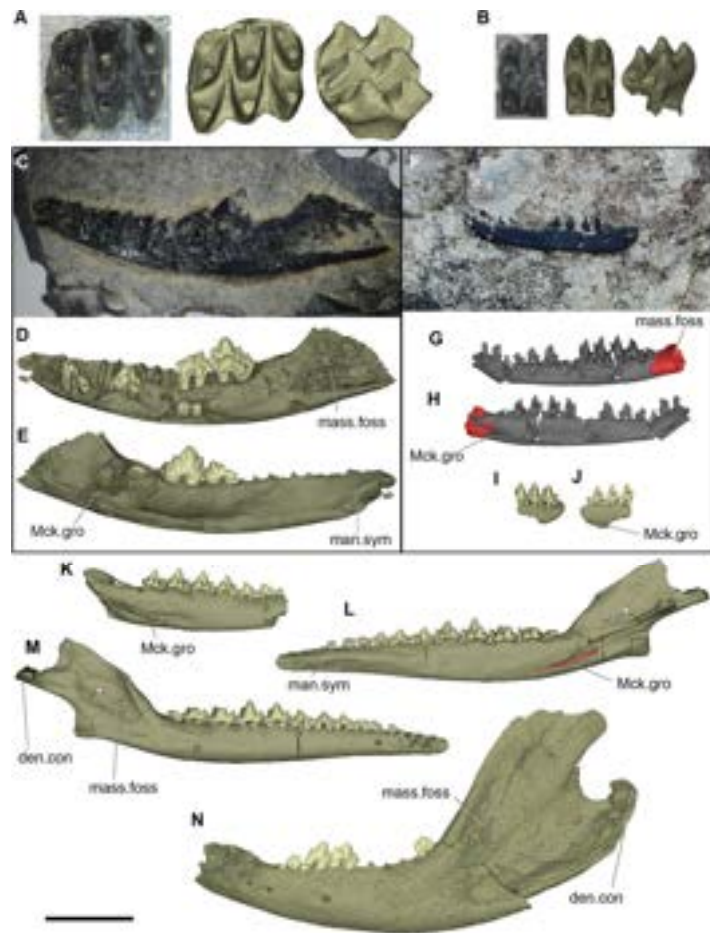
Pterosaurs



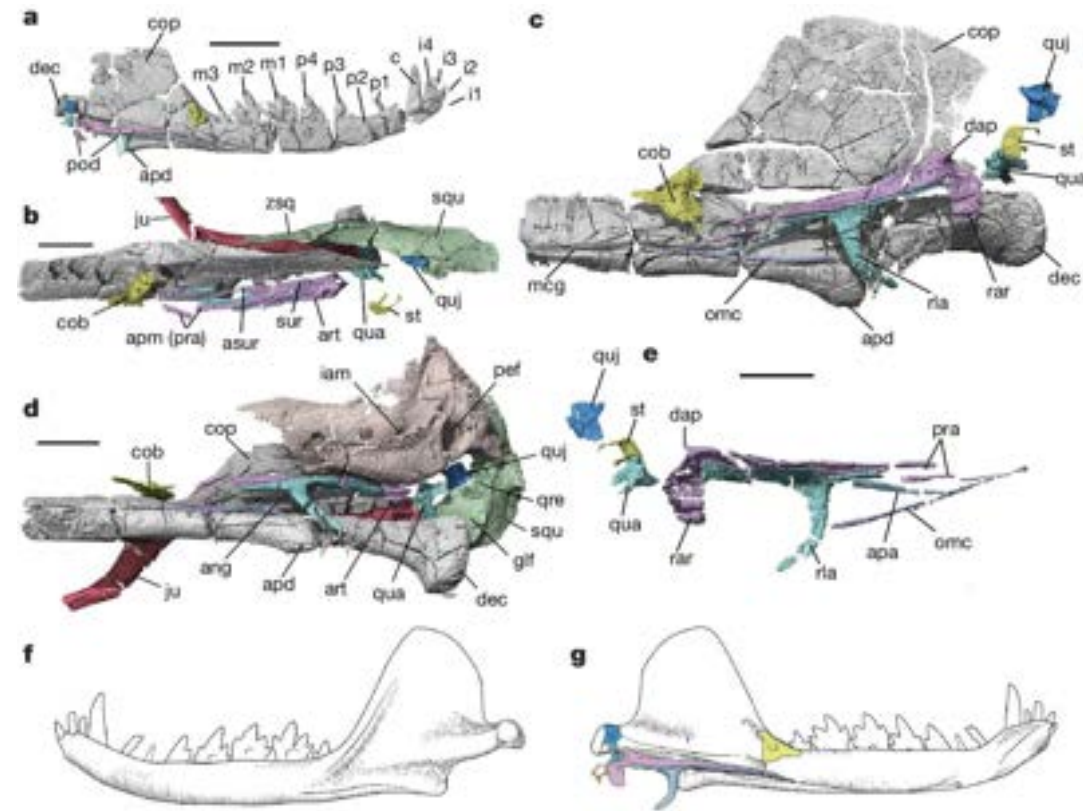
Dinosaurs



Fossils of the Kilmaluag Formation



The middle ear in early mammals



Figures from Wang et al., (2021), Mao et al., (2024)

The middle ear in early mammals



Dentary-squamosal jaw joint quickly **took over load bearing** in mammaliaforms



First true mammals known from the **Middle Jurassic** (170 – 160 Mya)

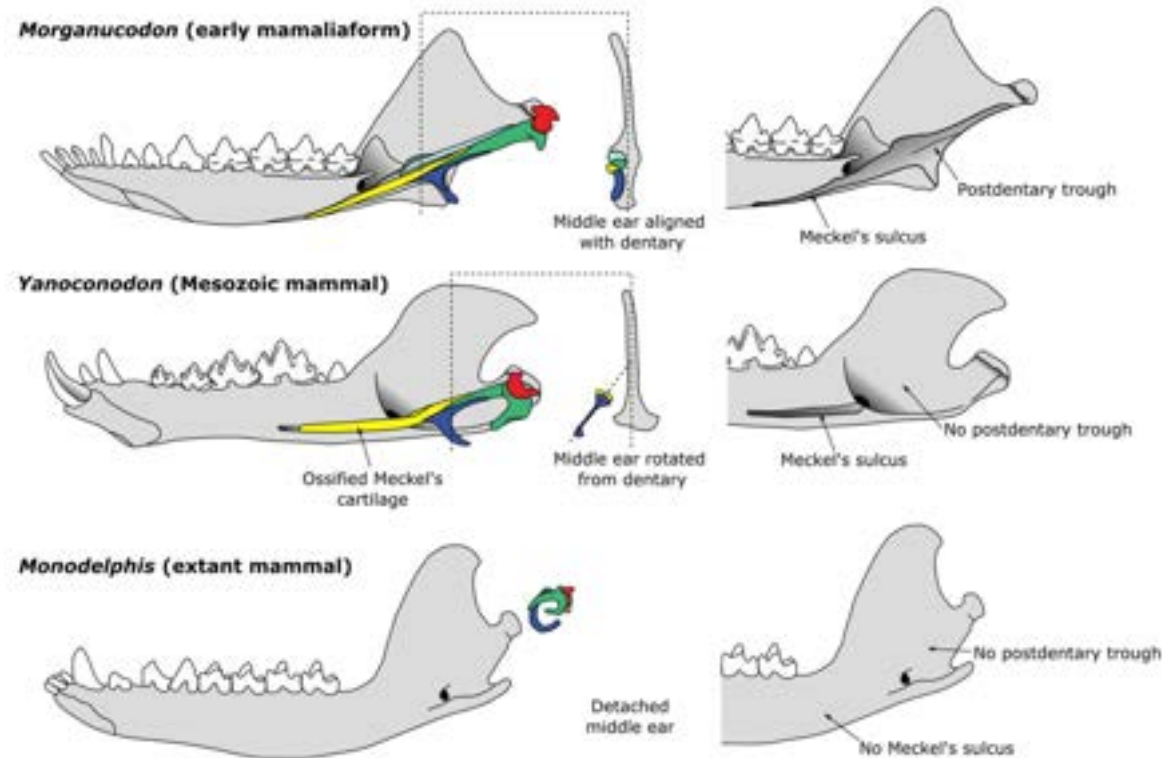


Jaw **still attached** to middle ear by an **ossified** (turned to bone) **Meckel's cartilage**

Middle ear now used **solely for hearing**.



Meckel's cartilage must be **broken down** to fully **separate** the middle ear from the jaw.



Detaching the middle ear



Fossils show when the mammal middle ear detached.



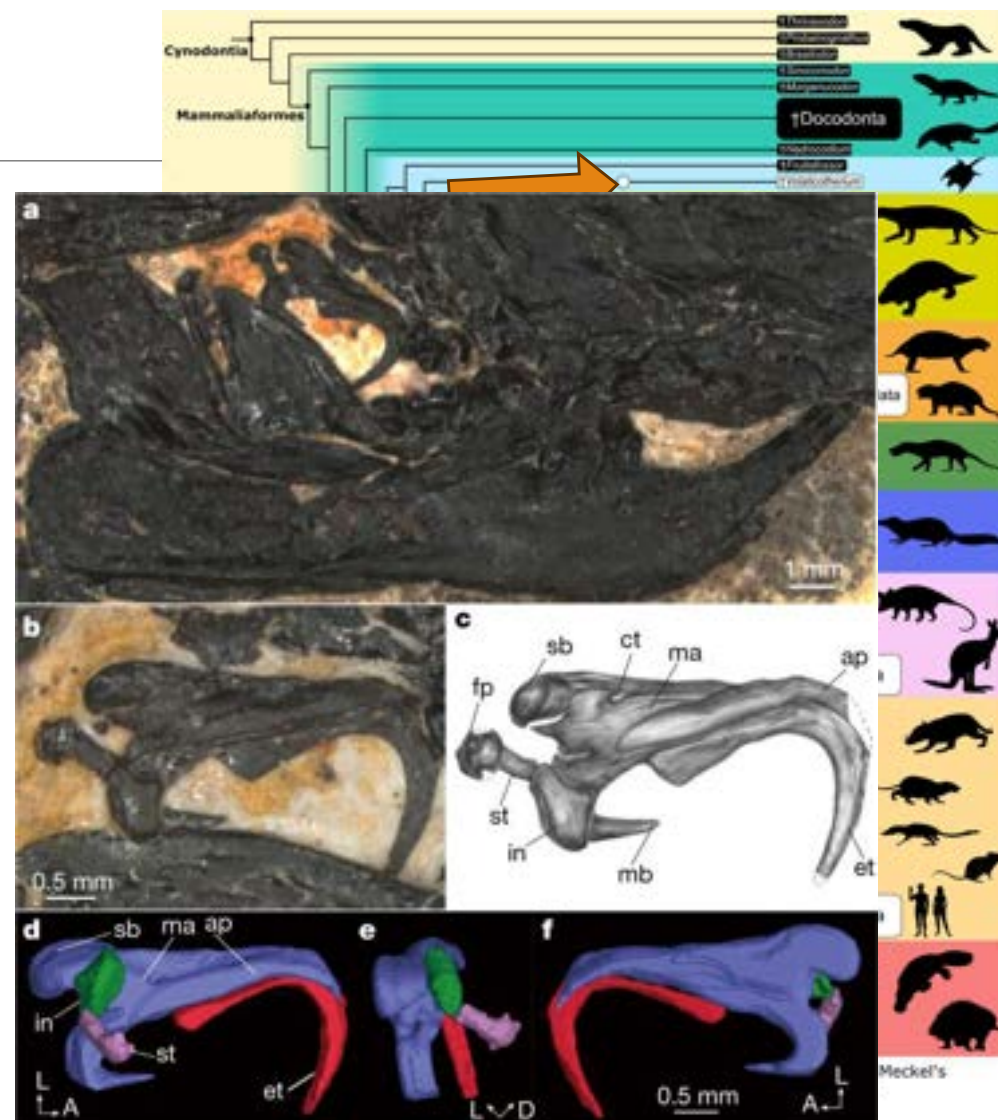
Meckel's cartilage breakdown occurred **independently** in ~8 mammal groups (incl. placentals, marsupials, monotremes)!



What mechanism was used to detach the middle ear?



Why so many times?



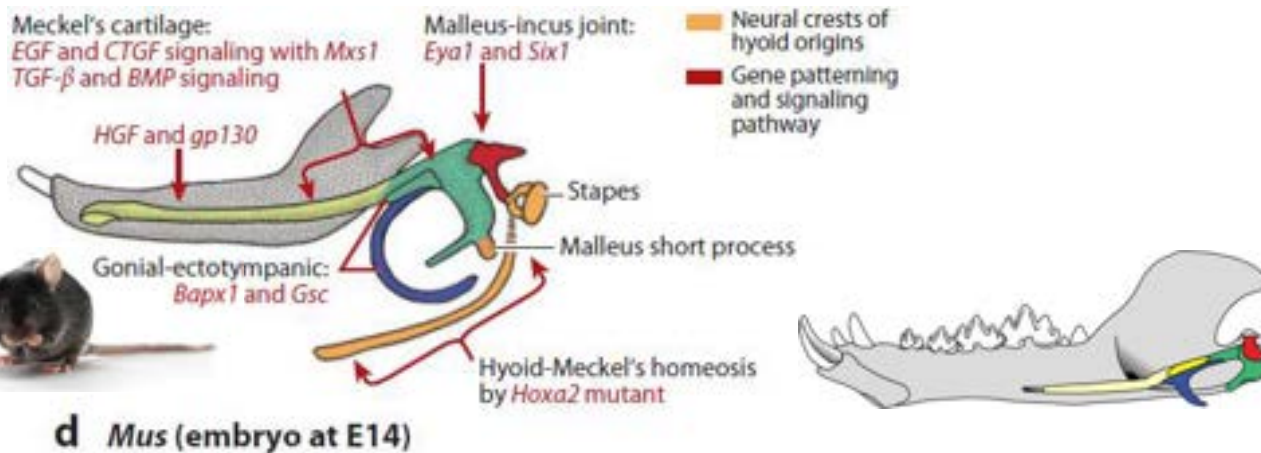
Growing a mammalian middle ear



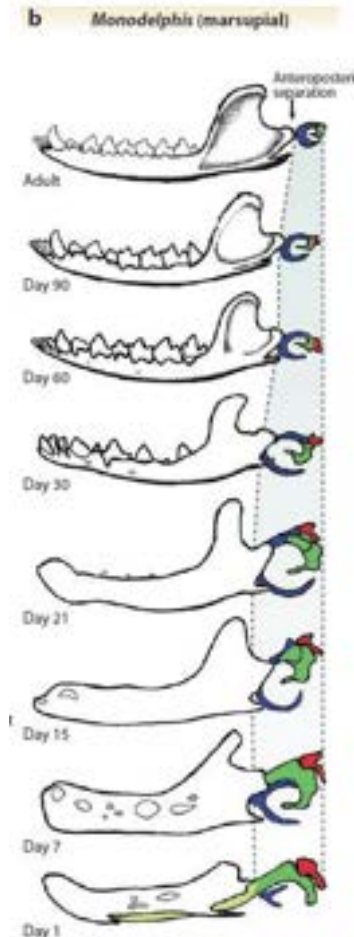
Placentals: Meckel's cartilage breaks down before birth



Marsupials: Meckel's cartilage breaks down just after birth



Age



Adult



Growing a mammalian middle ear



Mutant cFos mice retain attached Meckel's cartilage (like Mesozoic mammals).

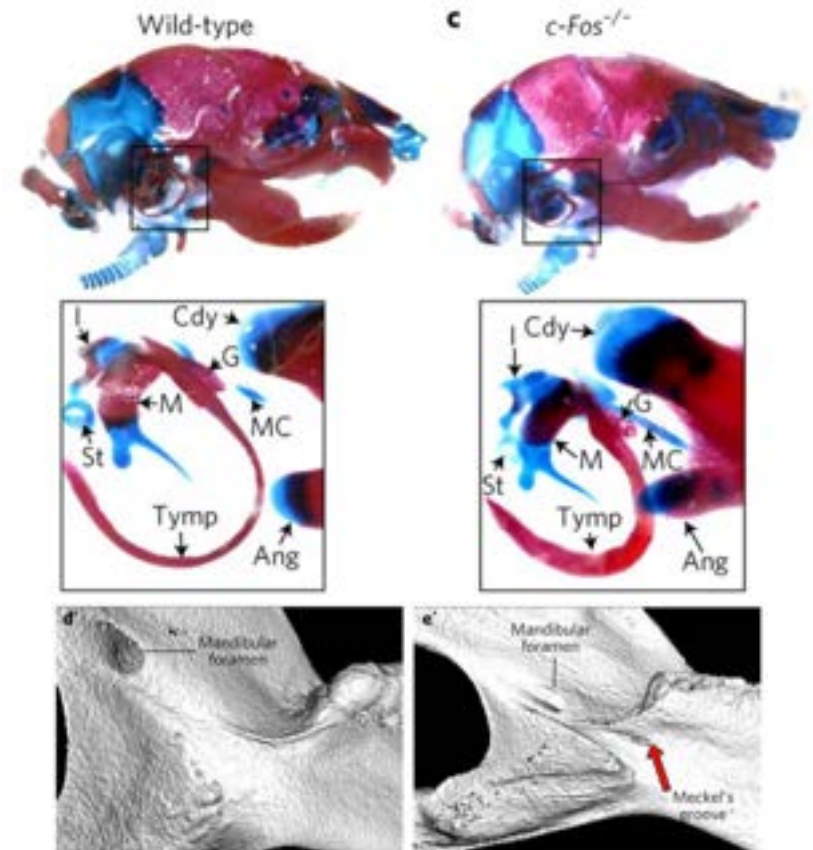


Disrupting special cells **chondroclast** cells prevents Meckel's cartilage breakdown in mice and opossums.

Recruit chondroclasts early in development to **separate** the middle ear in placentals and marsupials



What about the fossil mammals?





Monotremes



Monotreme middle ear does not separate until later in life. **How late?**



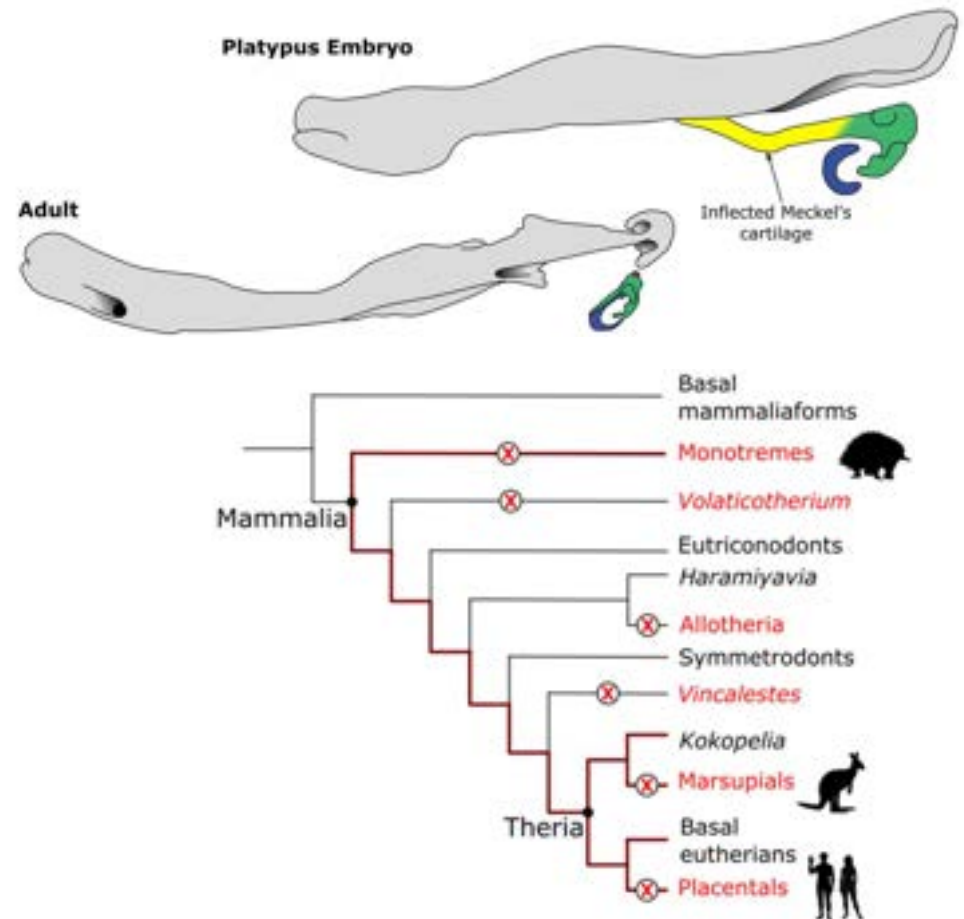
Monotremes and marsupials/placentals “**bracket**” all other mammals on the family tree.



Features **shared** by monotremes and marsupial/placentals likely shared by **extinct** mammal groups too.



What mechanism controls Meckel's cartilage breakdown in monotremes?



Data and methods



6 specimens of *Tachyglossus* from day 0 to a sub-adult



Micro-CT scans:

- Soft tissue (stained with 1% phosphotungstic acid solution or iodine)



Histological slicing:

- Sectioned at 80 μ m thick.
- Sections stained with trichrome, TRAP, H&E.



Meckel's cartilage retained for >50 days



Meckel's cartilage is the **dominant** structure of the lower jaw **at birth**.



Meckel's became medially inflected from the dentary at day 20, **similar to adult Mesozoic mammal**.



Dentary-squamosal joint fully formed by **day 50**. Middle ear separates after.

Chondroclasts break down Meckel's cartilage in monotremes



Histology lets us see
Meckel's breakdown at a
cellular level!



Chondroclasts can be seen
breaking down the cartilage,
same as mouse/opossum



Chondroclasts **recruited
early** to separate middle ear
in all living mammals

Mechanisms for middle ear separation likely ancestral to all mammals!

Conclusions



Developmental data is really useful for understanding middle ear evolution

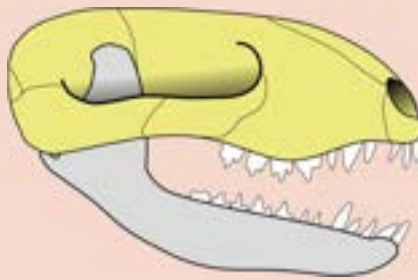
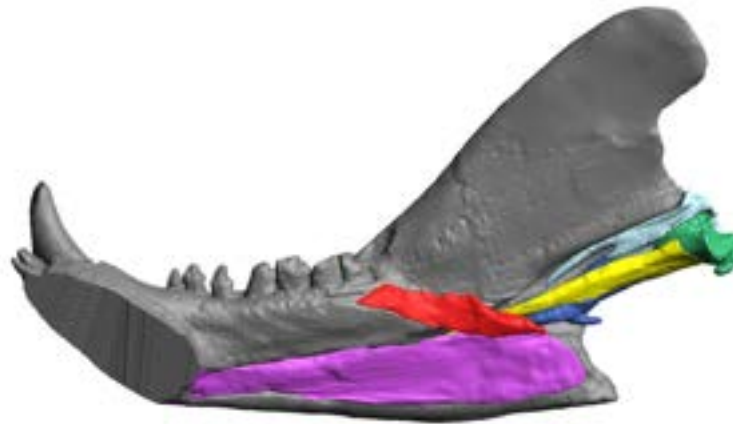


Fossil mammals likely used chondroclasts as the mechanism for breaking down Meckel's cartilage across their evolution.



This is how mammals evolved a separated middle ear multiple times

Conclusion



The mammal middle ear is an extraordinary evolutionary story

Lots more research to do!

Acknowledgements



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Art by Mark Witton, Nix Illustration