Phylogeny and Avian Evolution

Phylogeny and Evolution of the Aves

I. Background

Scientists have speculated about evolution of birds ever since Darwin.

Difficult to find relatives using only modern animals

After publication of “Origin of Species” (~1860) some used birds as a counter-argument since there were no known transitional forms at the time!

- turtles have modified necks and toothless beaks
- bats fly and are warm blooded

With fossil discovery other potential relationships!

- Birds as distinct order of reptiles

Many non-reptilian characteristics (e.g. endothermy, feathers) but really reptilian in structure!

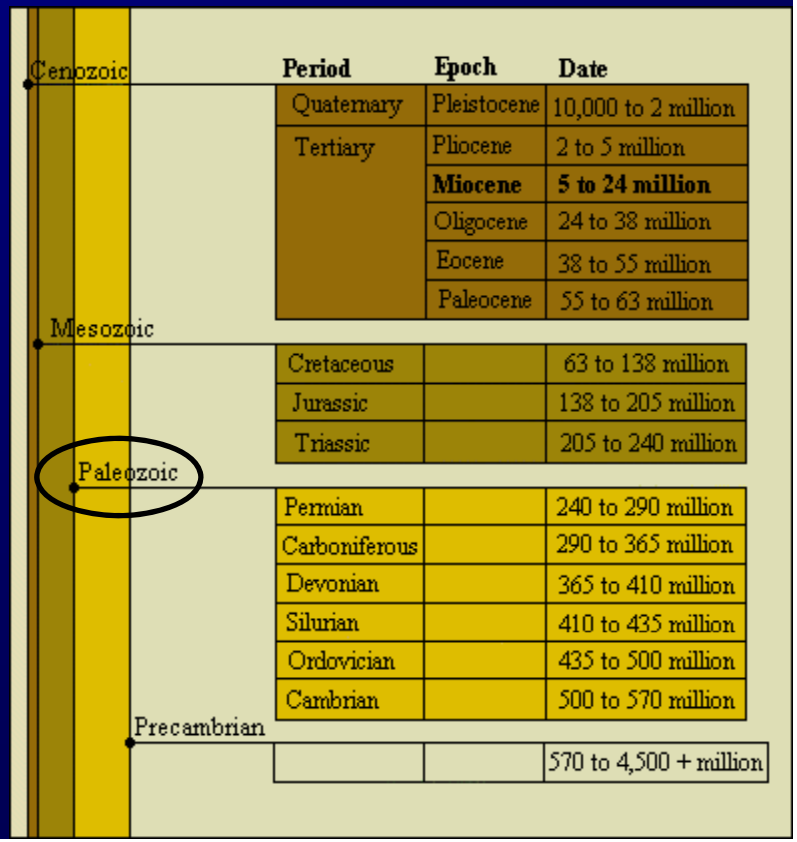
If birds only known from fossil record then simply be a distinct order of reptiles.

II. Reptile Evolutionary History

A. “Stem reptiles” - Cotylosauria

Must begin in the late Paleozoic

Cotylosauria – “stem reptiles”



	Period	Epoch	Date
Cenozoic	Quaternary	Pleistocene	10,000 to 2 million
	Tertiary	Pliocene	2 to 5 million
		Miocene	**5 to 24 million**
		Oligocene	24 to 38 million
		Eocene	38 to 55 million
		Paleocene	55 to 63 million
Mesozoic	Cretaceous		63 to 138 million
	Jurassic		138 to 205 million
	Triassic		205 to 240 million
Paleozoic	Permian		240 to 290 million
	Carboniferous		290 to 365 million
	Devonian		365 to 410 million
	Silurian		410 to 435 million
	Ordovician		435 to 500 million
	Cambrian		500 to 570 million
Precambrian			570 to 4,500 + million

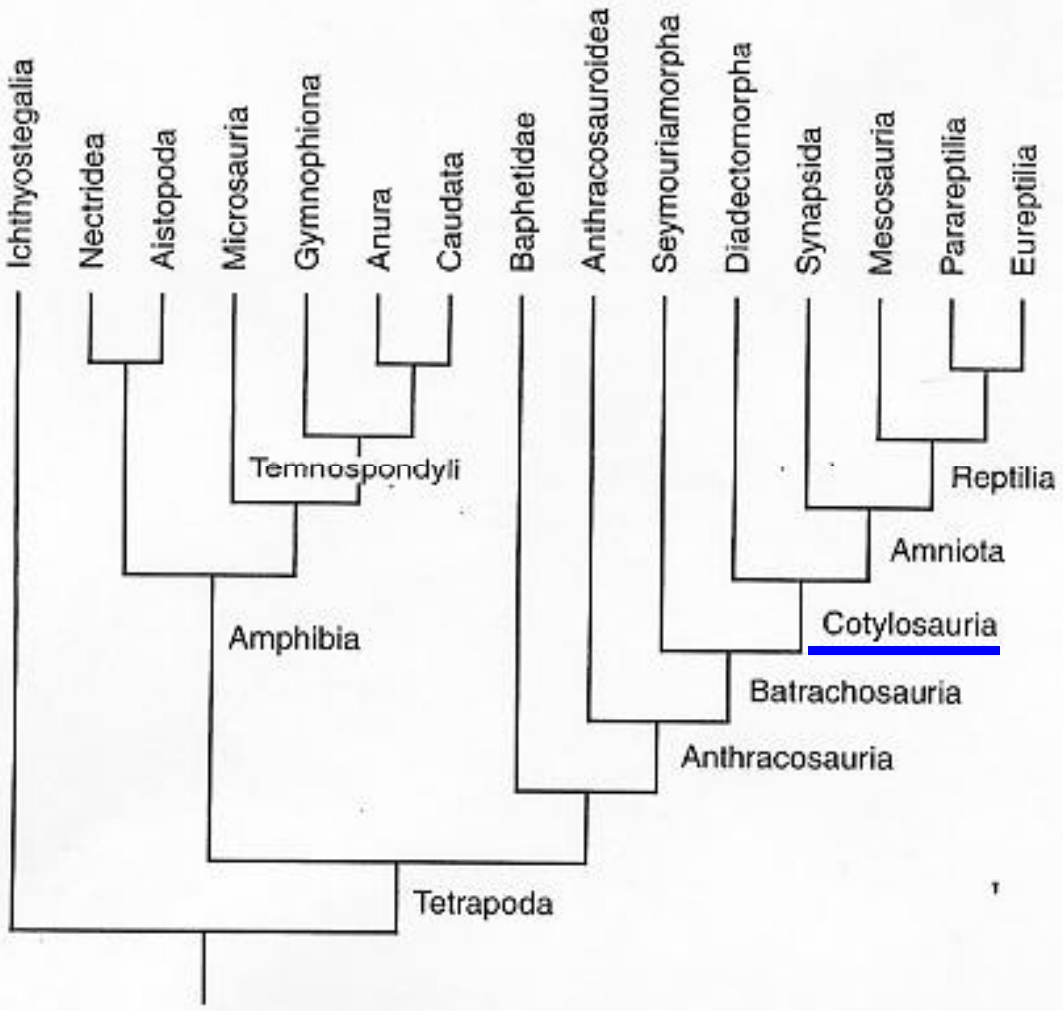


FIGURE 1.7 A branching diagram of the evolution within the Tetrapoda, based on sister-group relationships. The diagram has no time axis, and each name represents a formal clade-group name. After Clack (1998), Gauthier et al. (1988a,b, 1989), and Lombard and Sumida (1992); a strikingly different pattern is suggested by Laurin and Reisz (1997).

Radiation of reptiles from Cotylosauria can be organized on the basis of temporal fenestrae (openings in back of skull for muscle attachment).

Subsequent reptilian lineages developed more powerful jaws.

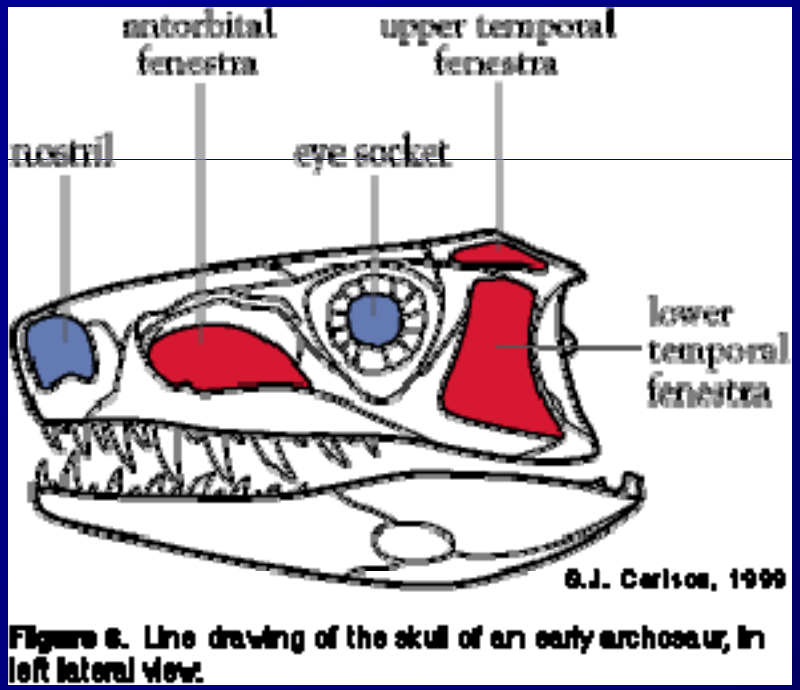
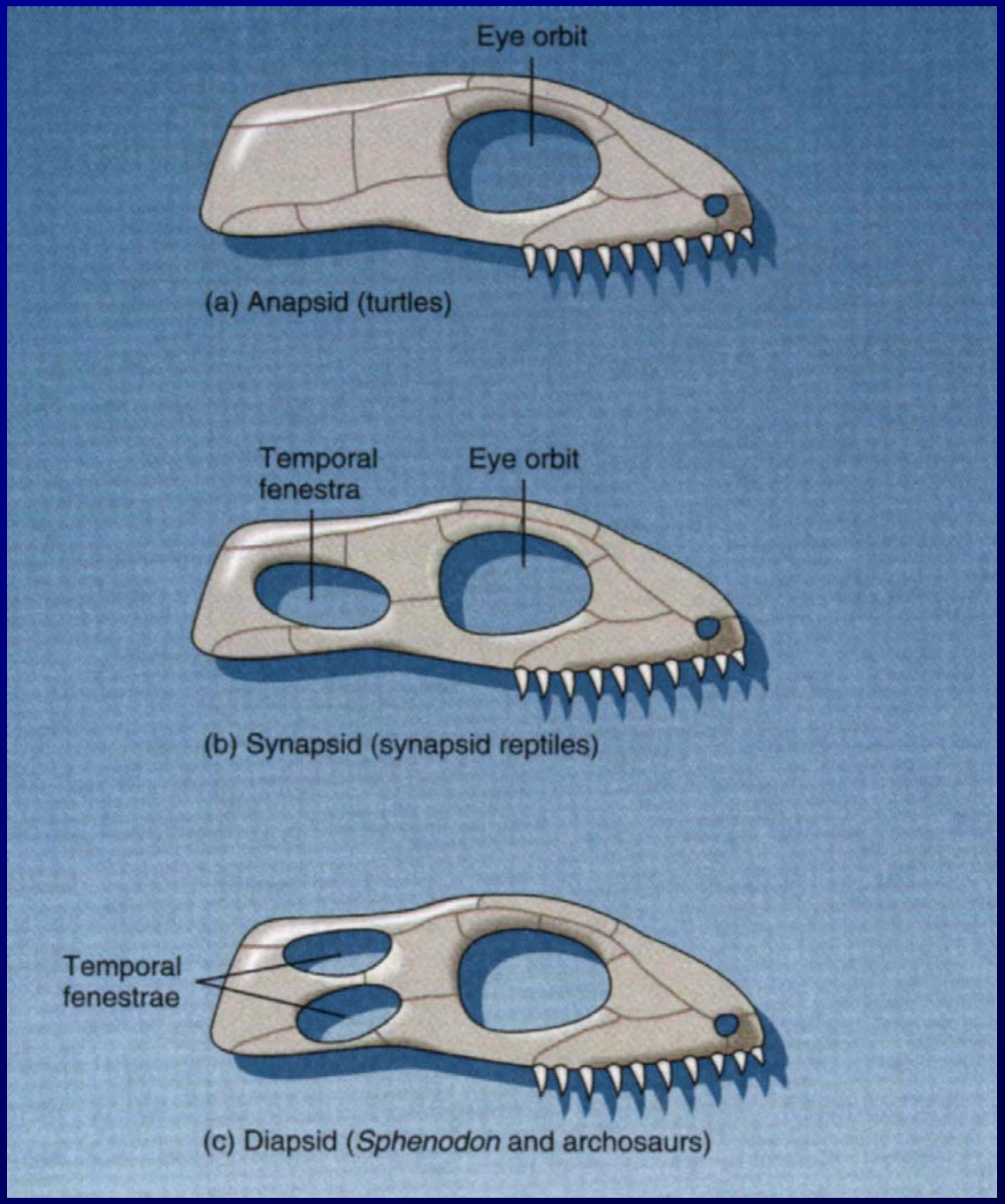
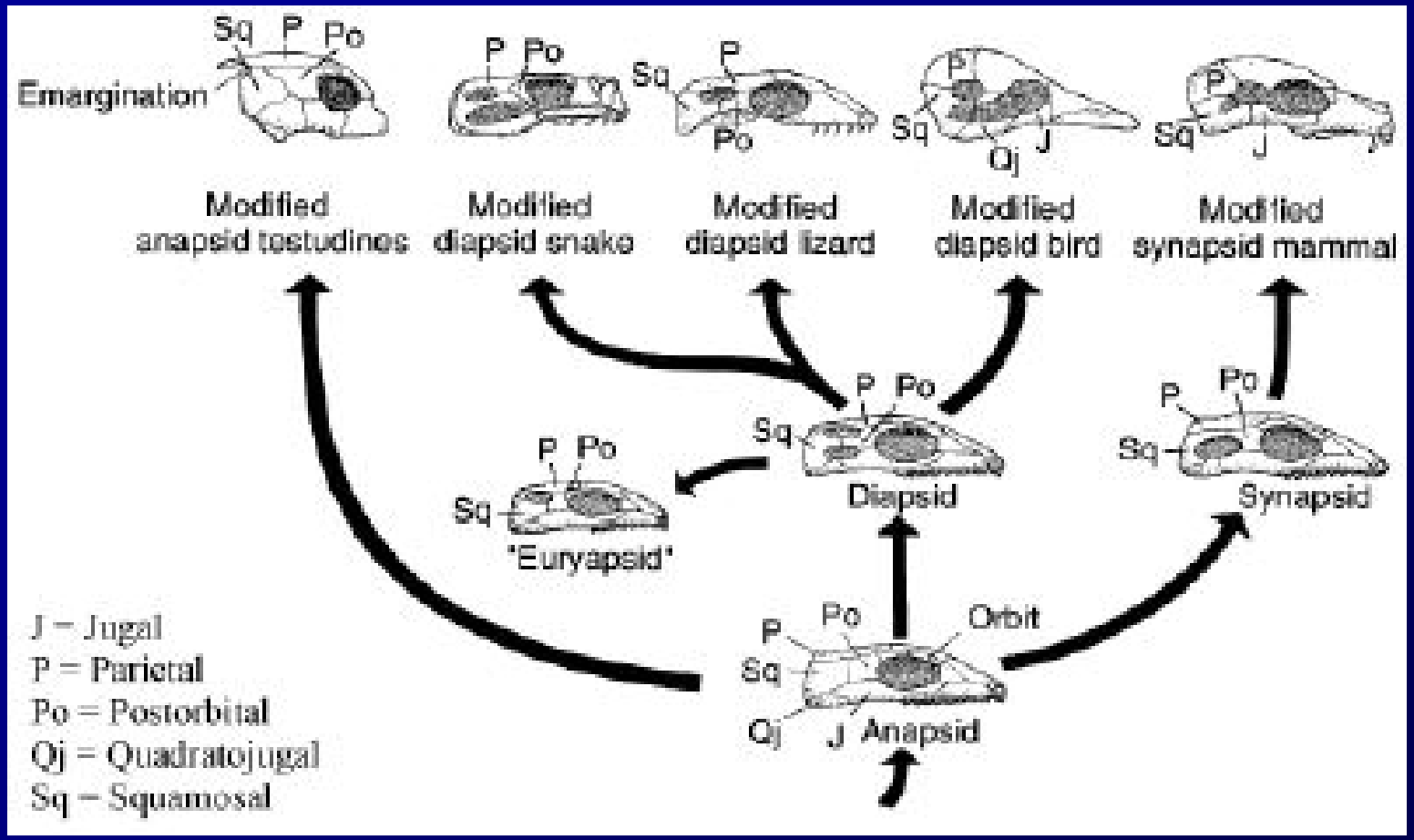


Figure 6. Line drawing of the skull of an early archosaur, in left lateral view.


Eye orbit
(a) Anapsid (turtles)
Temporal fenestra
Eye orbit
(b) Synapsid (synapsid reptiles)
Temporal fenestrae
(c) Diapsid (*Sphenodon* and archosaurs)


Emargination
Sq
P
Po
Qj
J
Modified anapsid testudines
Modified diapsid snake
Modified diapsid lizard
Modified diapsid bird
Modified synapsid mammal
"Euryapsid"
Diapsid
Synapsid
Anapsid
Orbit
J = Jugal
P = Parietal
Po = Postorbital
Qj = Quadratojugal
Sq = Squamosal

B. Anapsid

Cotylosauria and Chelonia have anapsid pattern

C. Synapsid – single fenestra

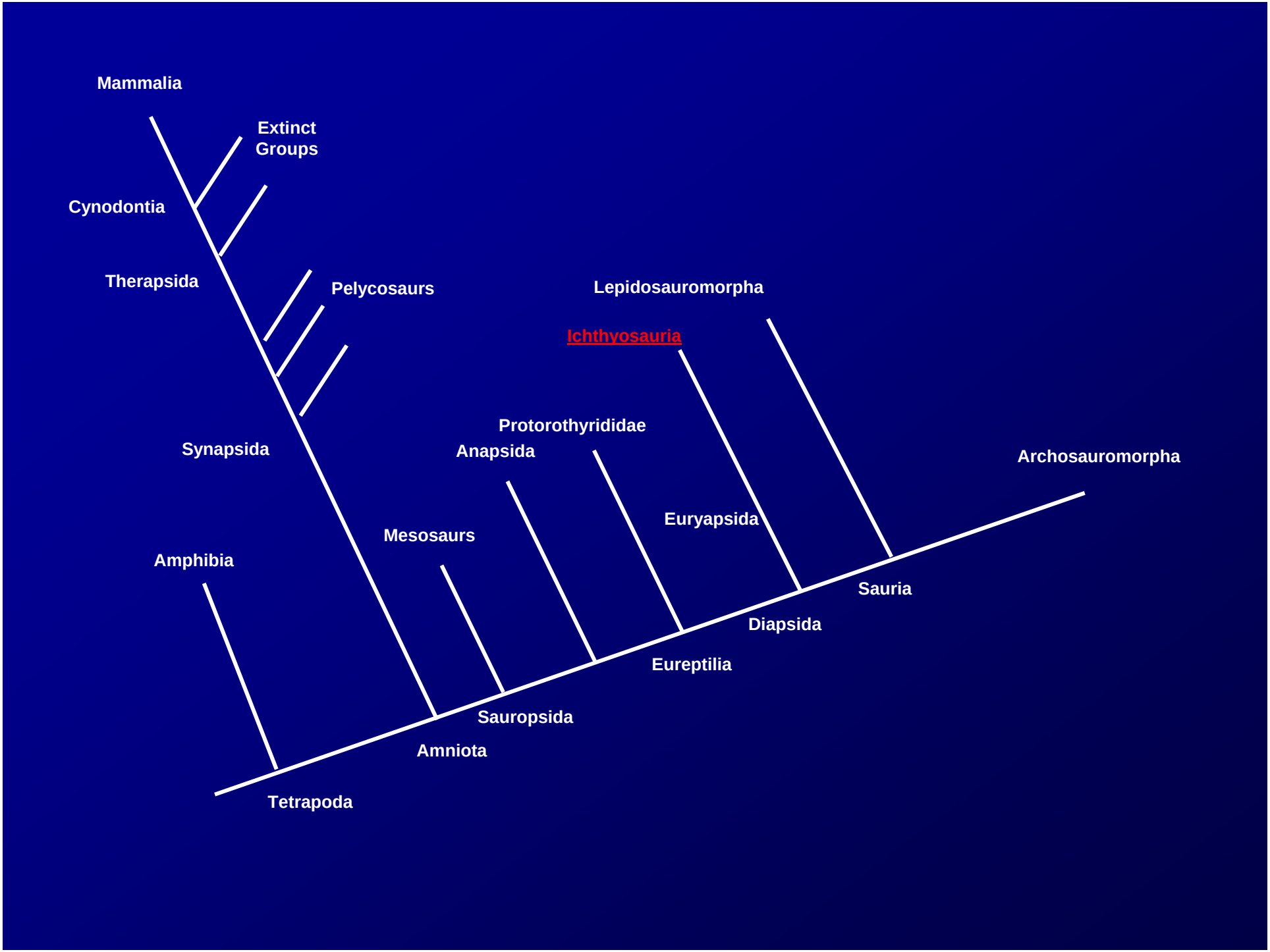
Includes order Therapsida which gave rise to mammalia

D. Diapsida – both supratemporal and infratemporal fenestrae

Pattern found in extinct archosaurs, surviving archosaurs and also in primitive lepidosaur – Sphenodon.

All remaining living reptiles and the lineage leading to Aves are classified as Diapsida

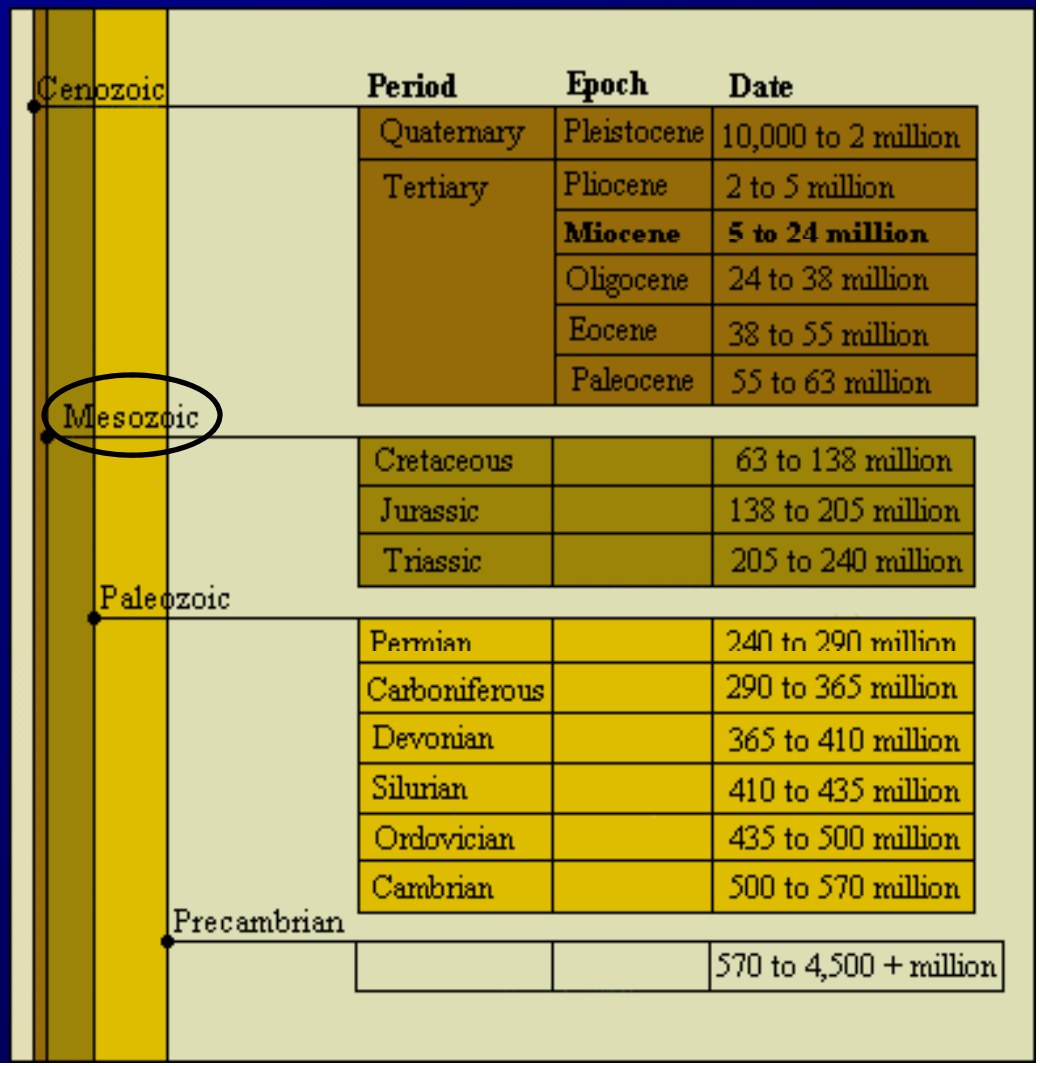
Handout


Mammalia
Extinct Groups
Cynodontia
Therapsida
Pelycosaurs
Synapsida
Lepidosauromorpha
Ichthyosauria
Protorothyrididae
Anapsida
Archosauromorpha
Euryapsida
Mesosaurs
Amphibia
Sauria
Diapsida
Eureptilia
Sauropsida
Amniota
Tetrapoda

III. Relationship to Reptiles

Most groups present during Mesozoic considered ancestors to birds.

- pterosaurs
- crocodiles
- dinosaurs
- thecodonts



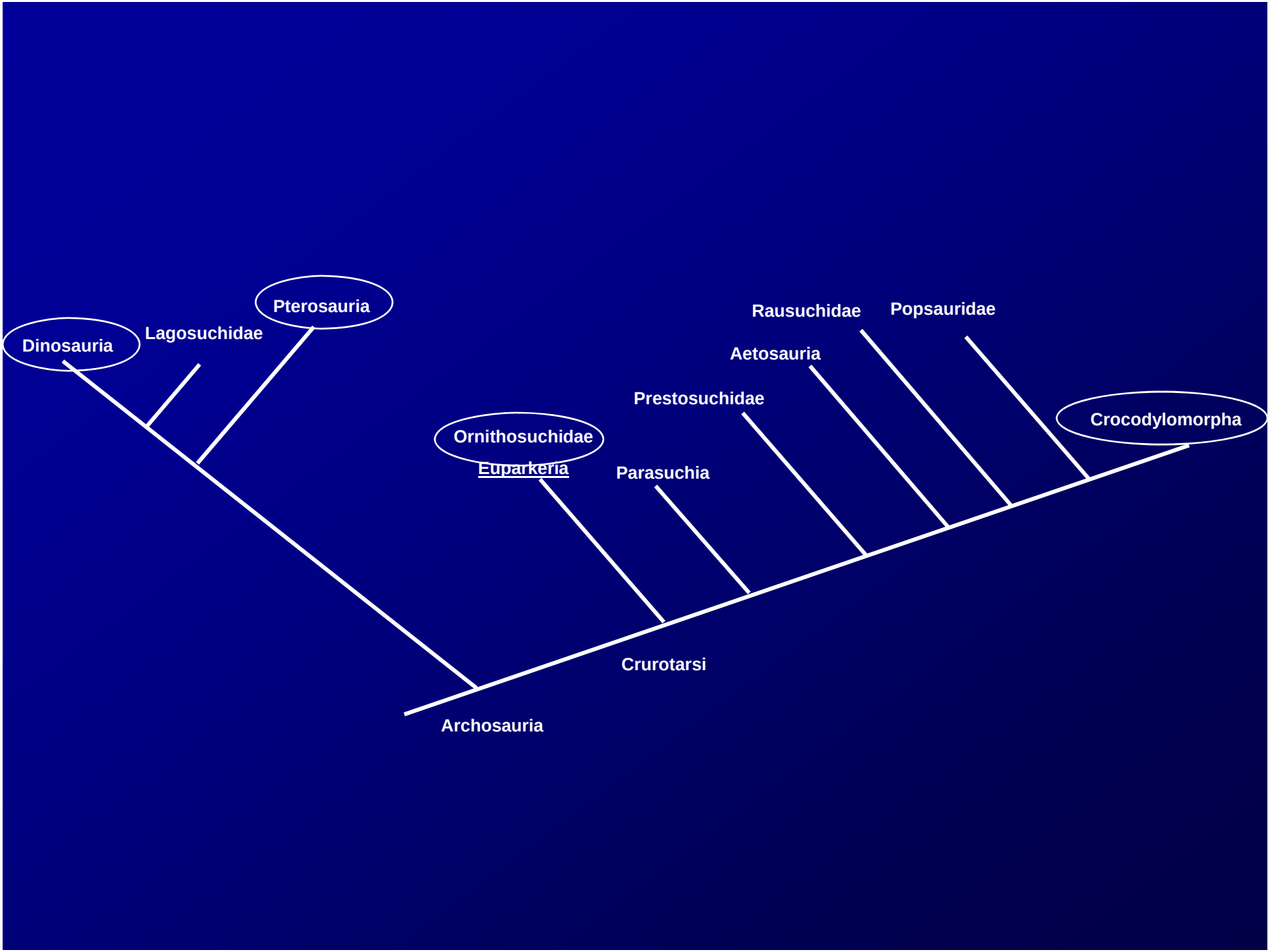
2 major hypotheses are accepted today

Differ with respect to lines of descent and the time when 1st bird appeared.

Aves derived from Diapsid ancestors, specifically through thecodonts (basal archosaurs)

Lineage ancestral to Birds ????

- Crocodilia
- Pterosauria
- Saurischia
- Ornithischia
- Pseudopsuchians


Pterosauria
Lagosuchidae
Dinosauria
Rausuchidae
Popsauridae
Aetosauria
Prestosuchidae
Crocodylomorpha
Ornithosuchidae
Euparkeria
Parasuchia
Crurotarsi
Archosauria

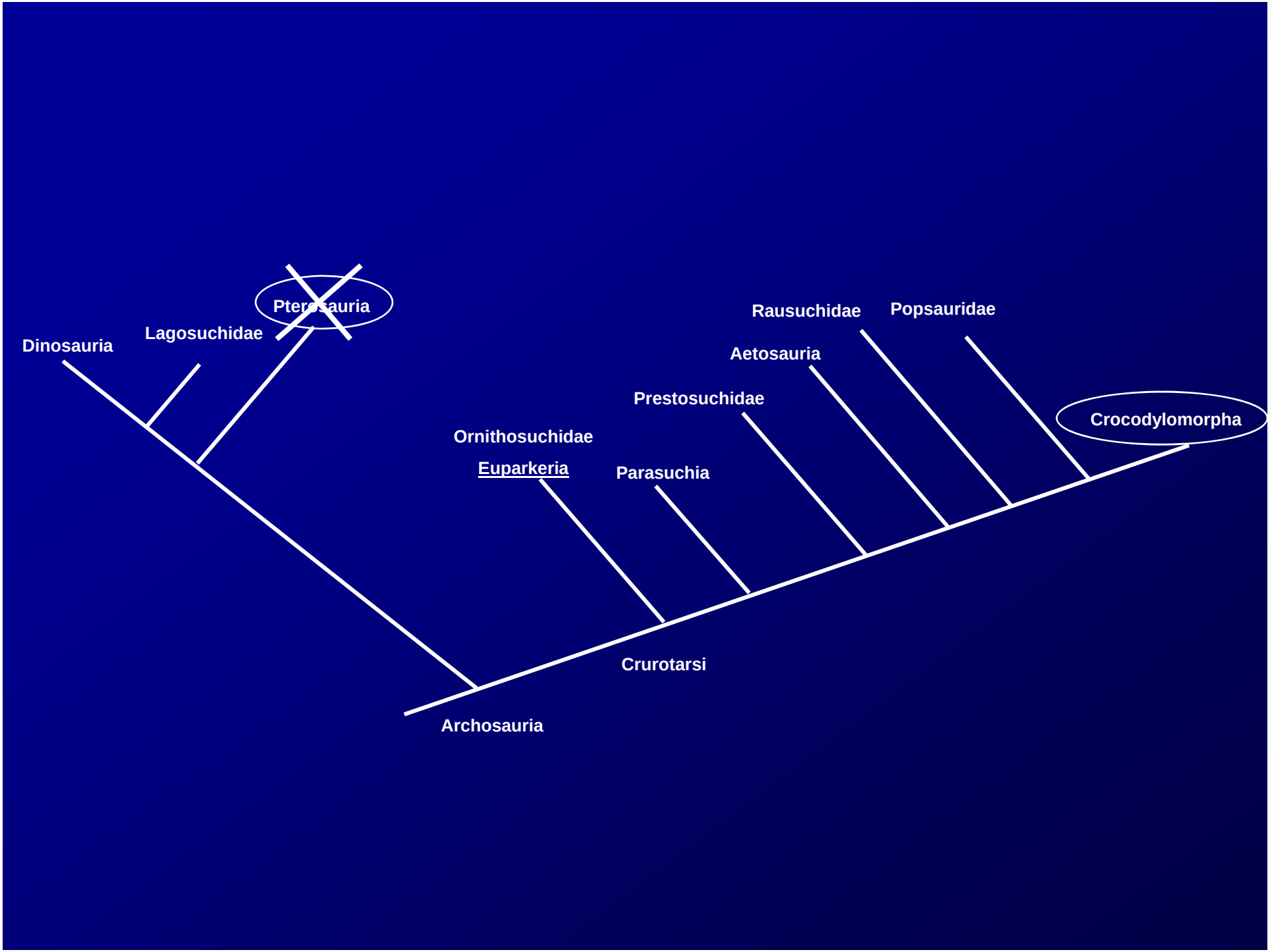
A. Hypotheses for immediate ancestry of birds

1. Pterosauria

Large membranous wings supported by single 4th digit

They are diapsids, large brains, and similar ankle joint but

- the wings are formed by completely different bones
- no clavicles
- scapula and coracoid are fused forming distinctive “L” shaped structure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Lagosuchidae
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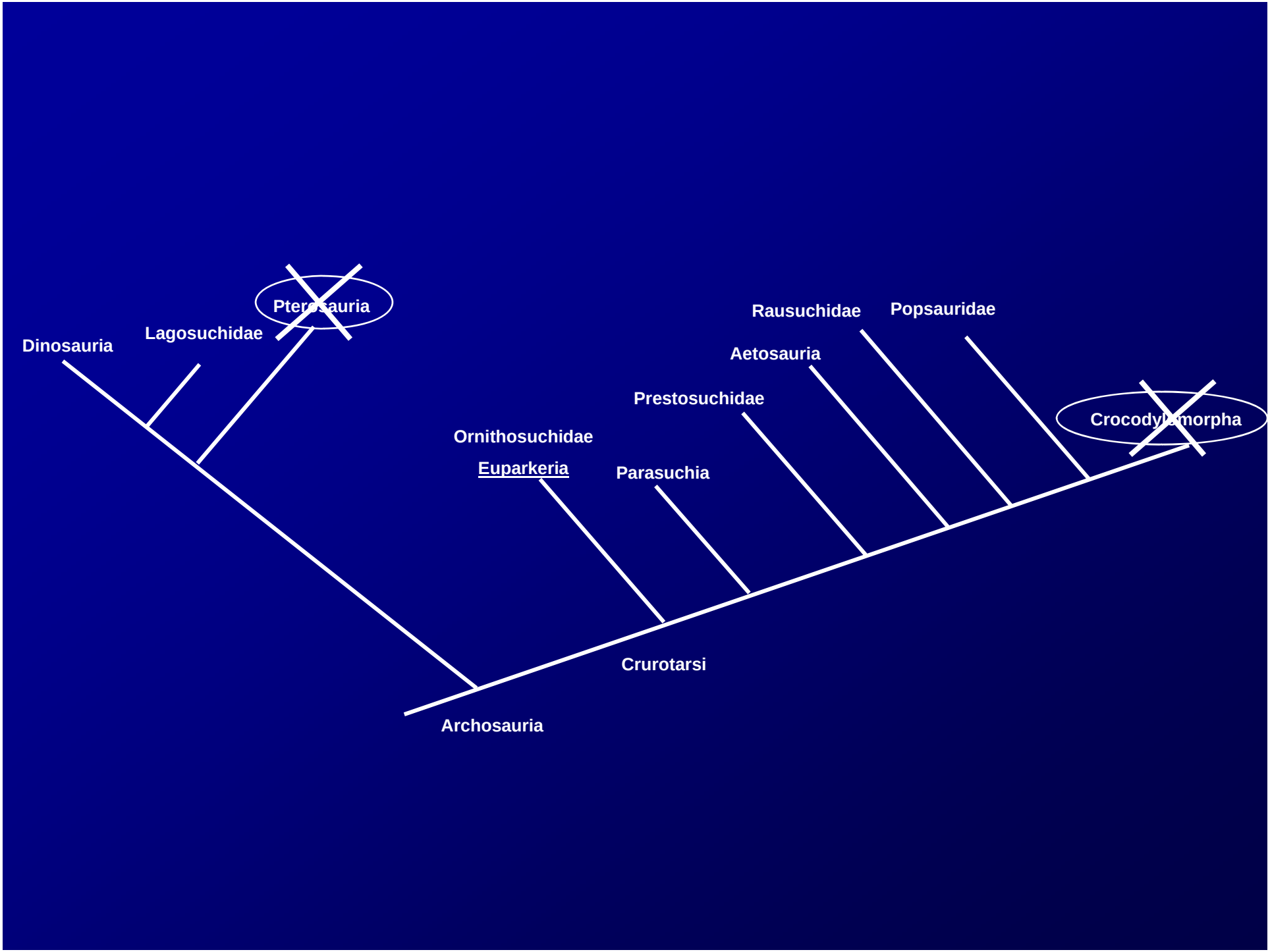
Aetosauria
Prestosuchidae
Crocodylomorpha
Ornithosuchidae
Euparkeria
Parasuchia
Crurotarsi
Archosauria

2. Crocodilia – evidence based on tooth and skull structure.

Largely unsupported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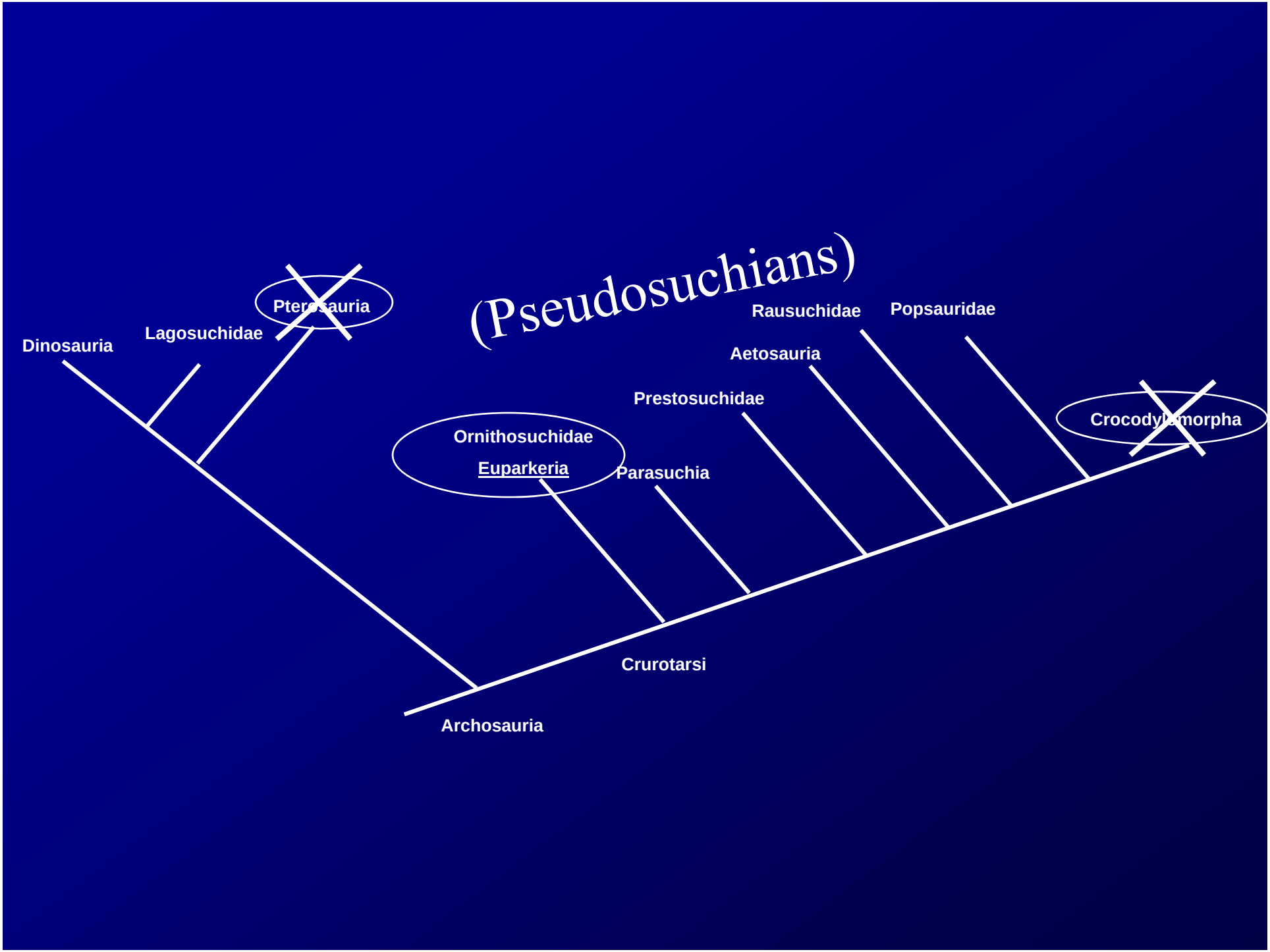
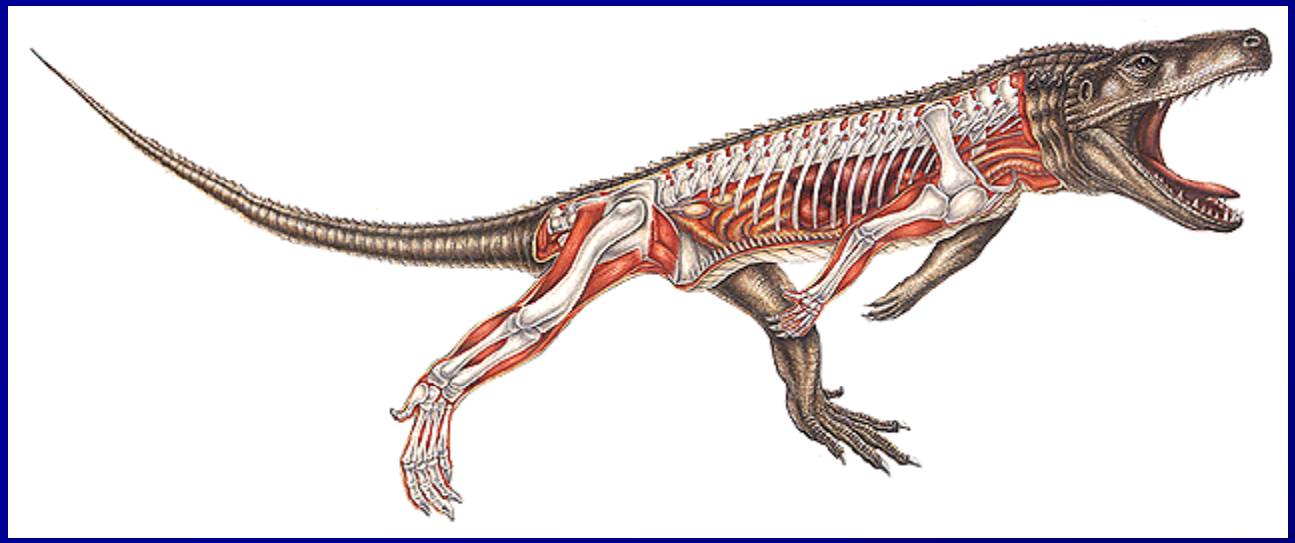
Crurotarsi
Archosauria

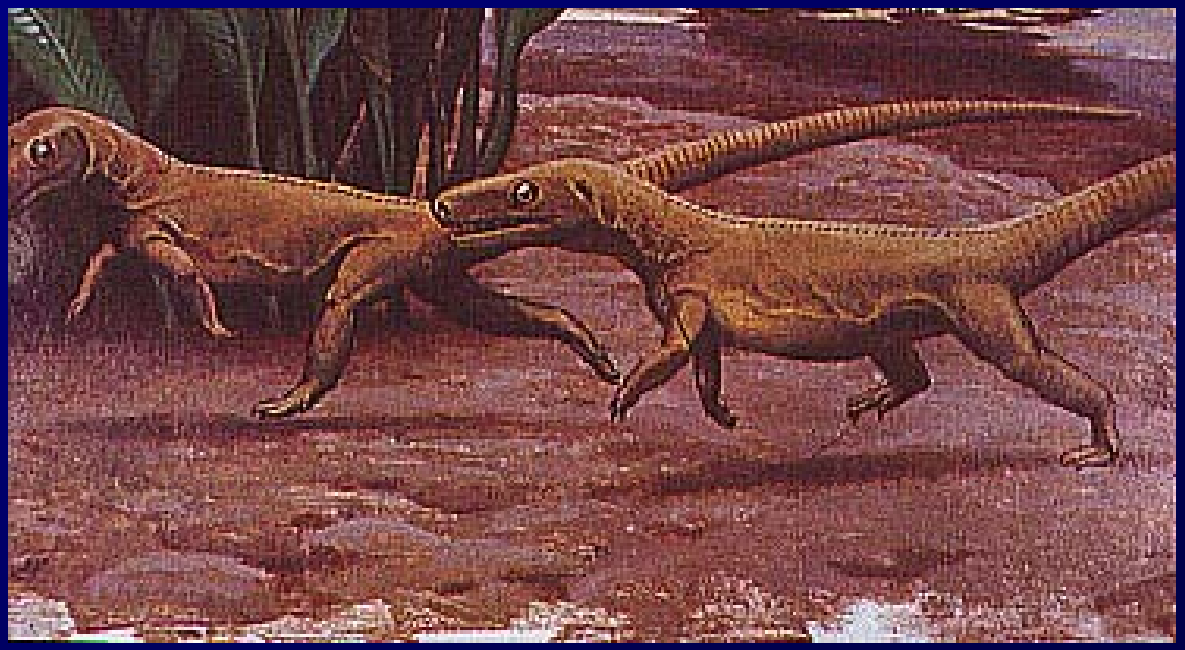

(Pseudosuchians)
Pterosauria
Lagosuchidae
Dinosauria
Rausuchidae
Popsauridae
Aetosauria
Prestosuchidae
Crocodylomorpha
Ornithosuchidae
Euparkeria
Parasuchia
Crurotarsi
Archosauria

3. Directly from the pseudosuchians – Euparkeria

Hypothesis put forth by Robert Broom 1910 – suggested Euparkeria as ancestral to birds



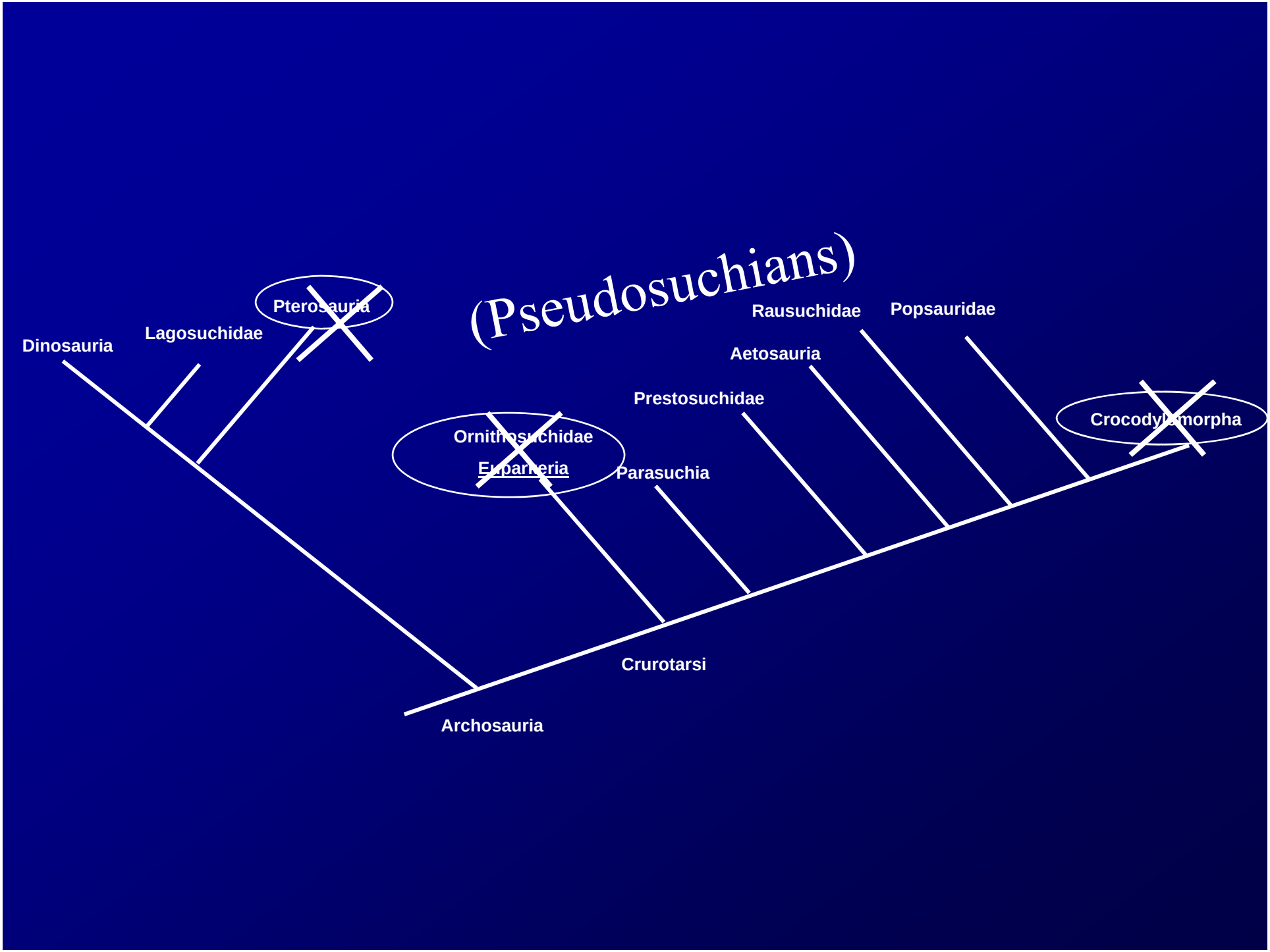
Early Archosaurs were quadrupeds but may have been able to run short distances on hindlimbs



Hypothesis mainly relies on presence of clavicle within pseudosuchians.

Birds also have clavicle but many of the more derived Archosaurs did not have a clavicle.

Hard to imagine structure lost and then reappearing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Lagosuchidae
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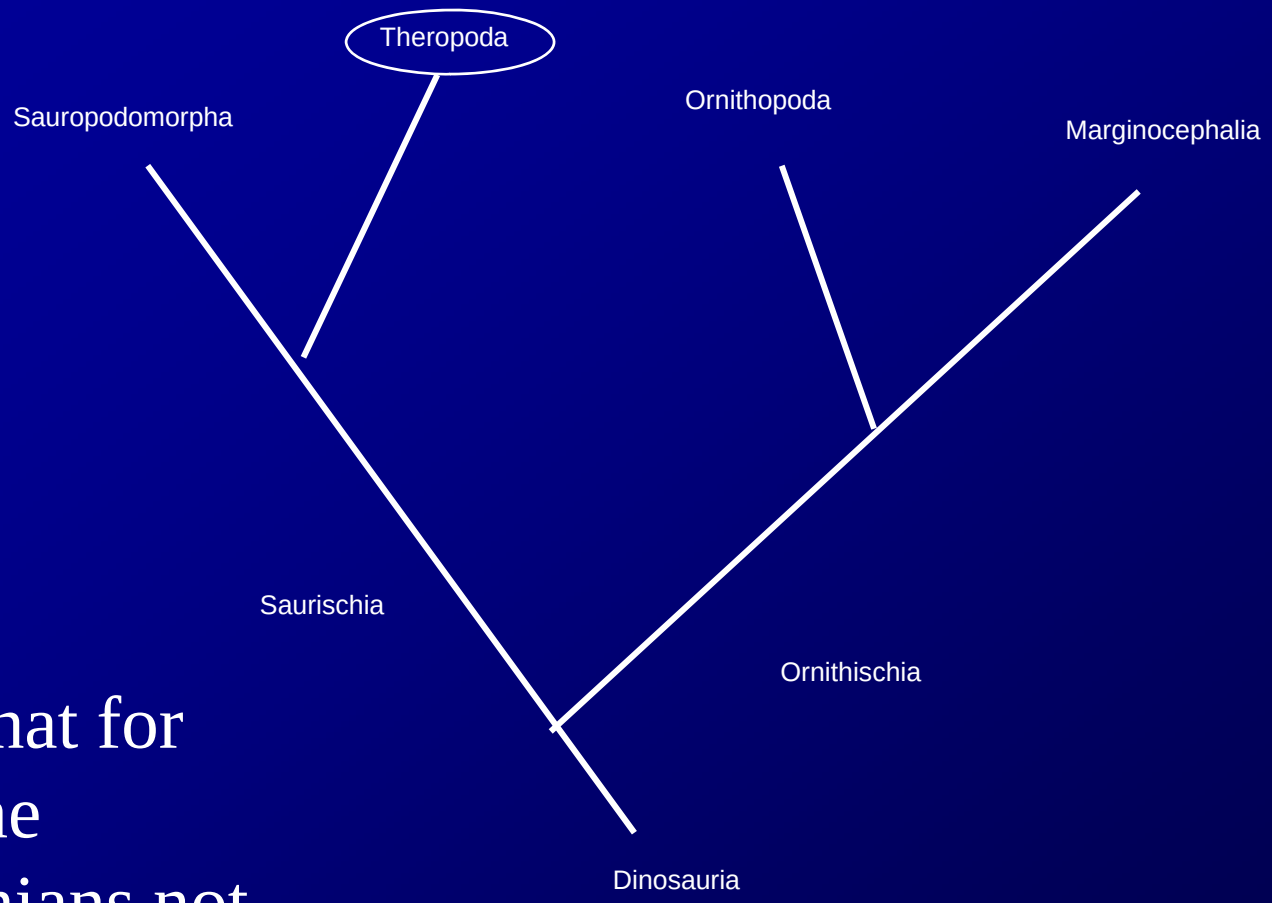
Ornithosuchidae
Euparkeria
Parasuchia
Crurotarsi
Archosauria

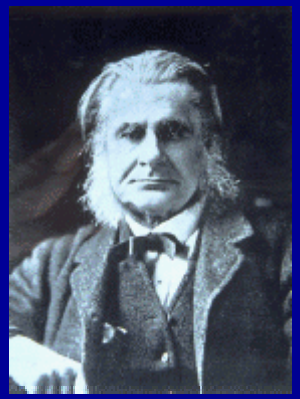


Recall that for long time Saurischians not known to have a clavicle

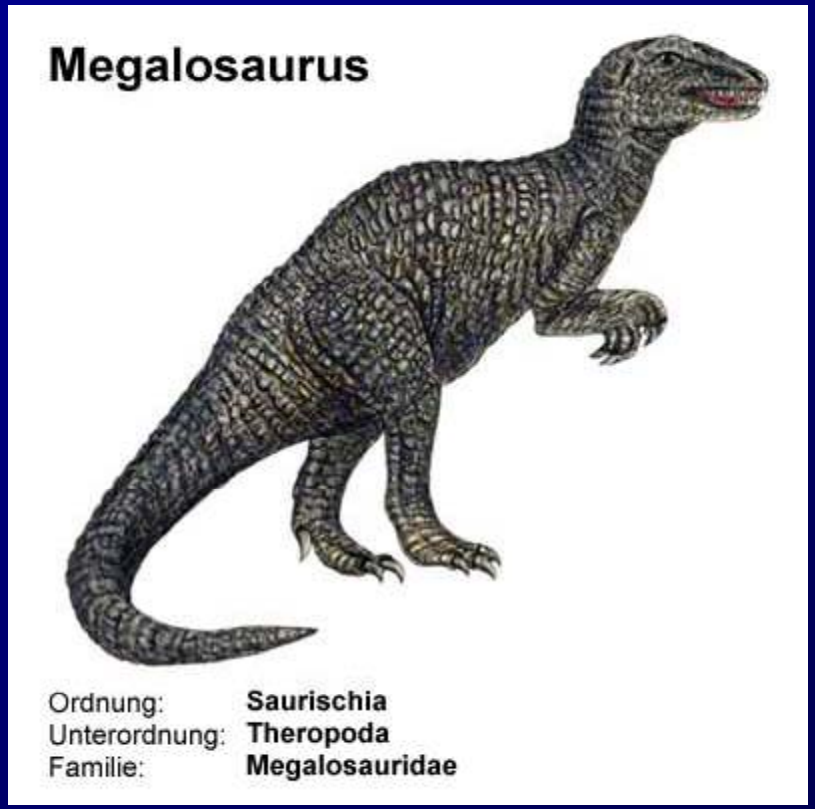
20 + years ago Polish Scientists working in Gobi desert found genus of Saurischian which did possess a clavicle!!!!

4. From Saurischian suborder Theropoda

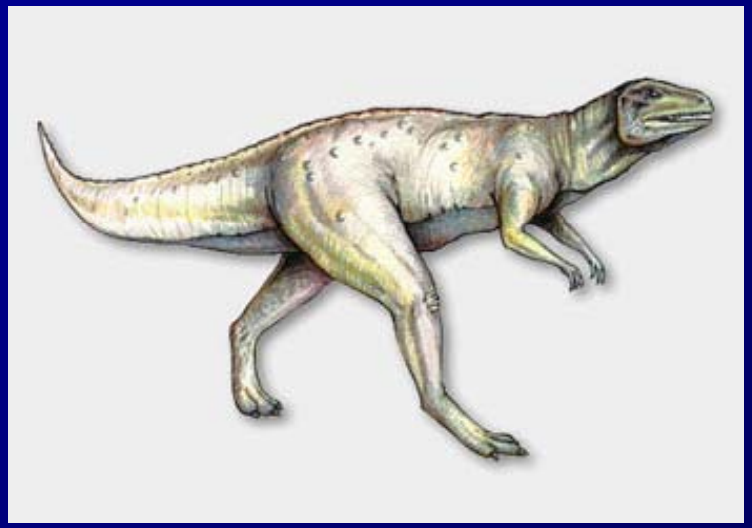
Brief history of this hypothesis



1871 - Thomas Henry Huxley compares hindlimb with ostrich 35 unique, shared characters!
Concluded – could be closely related.



Harry Seeley – disagreed and suggested similarity due to convergence



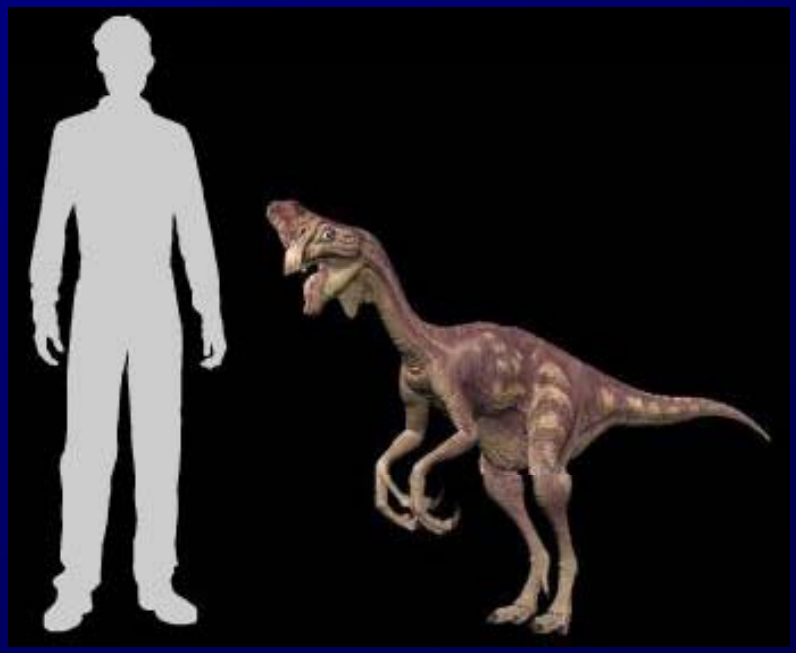
1916 – Gerhard Heilmann, rekindled interest in debate, “Origin of Birds”

Demonstrated that birds were anatomically more similar to theropods than any other group (major exception – known theropods at time lacked clavicle).

Conclusion – similarities due to convergence

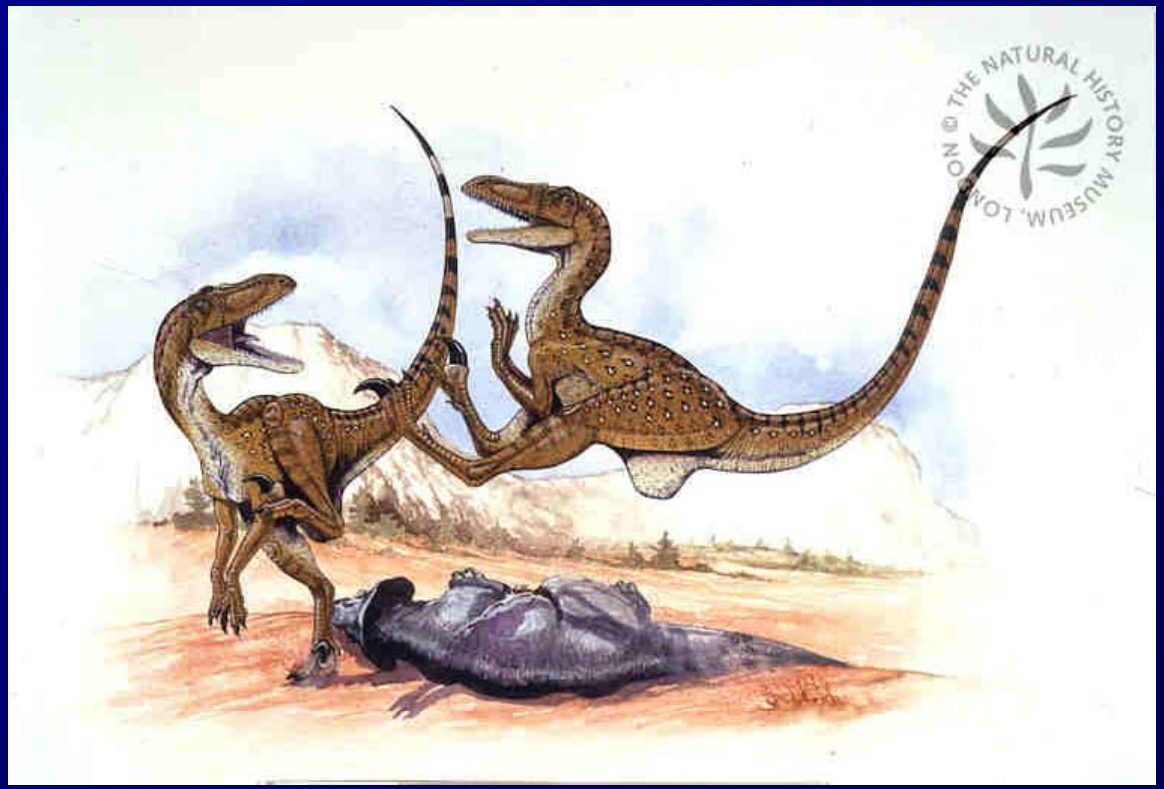
Heilmann influenced thinking for long time

1924 – published finding of Oviraptor

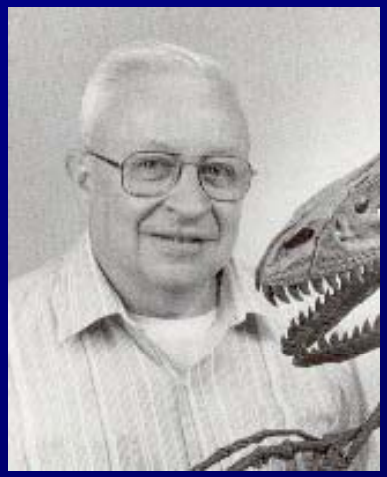


Skeleton has clavicle
but misidentified.

Recent studies have found clavicles in broad spectrum of theropods.



1960 – John Ostrum described skeletal anatomy of *Dienonychus* and found similarity with the first bird - *Archaeopteryx*.



Ostrum went so far as to say that if *Archaeopteryx* was discovered without feathers it would have been easily placed within the Theropods!

Prediction came true!

1970 – Specimen thought to be *Compsognathus* (since 1955) turned out to be *Archaeopteryx!!!*

Concluded – birds descended directly from small theropod dinosaurs.

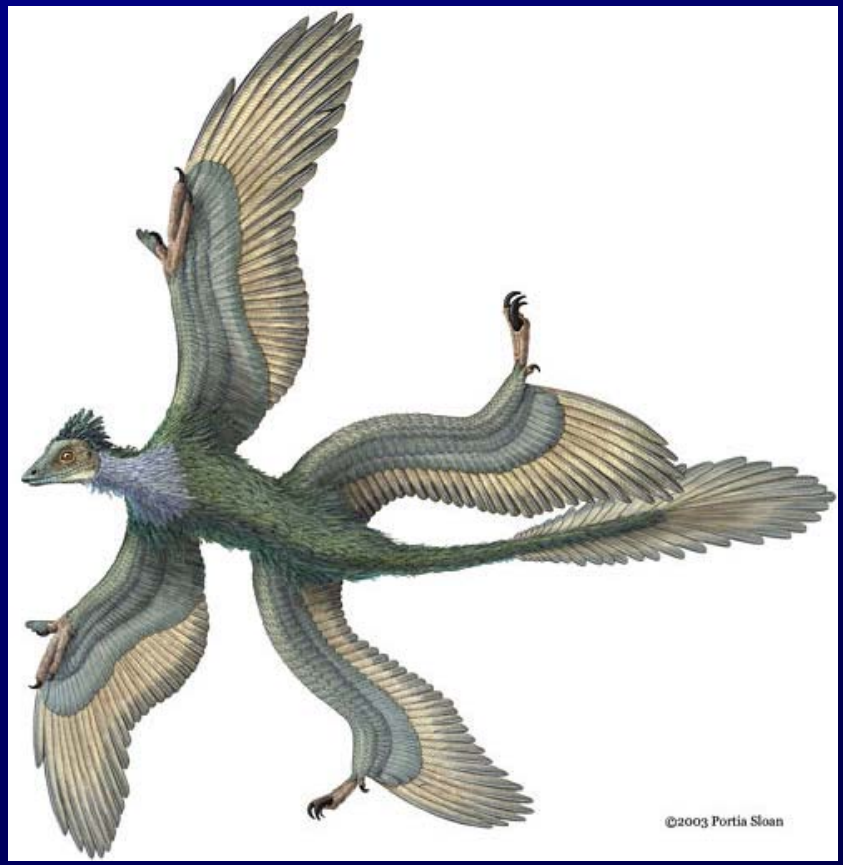
Recent use of phylogenetics indicates that not only are birds descendants of dinosaurs but they are in fact living dinosaurs.

B. Features birds share with theropods

- sclerotic ring
- fused clavicles
- flexible wrist with semilunate carpal
- straplike scapula
- hinge-like ankle joint
- elongation of digits

New feathered dinosaur!!

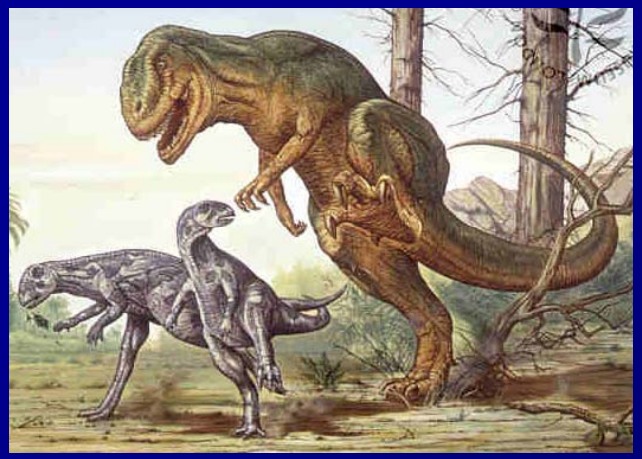
Microraptor gui

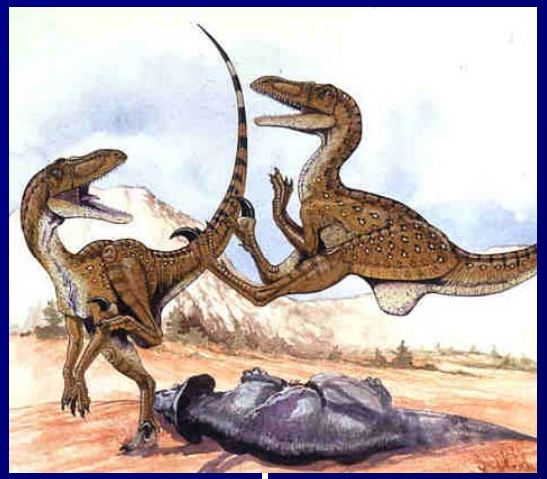


Velociraptor

Allosaurus

Coelophysis





Maniraptora

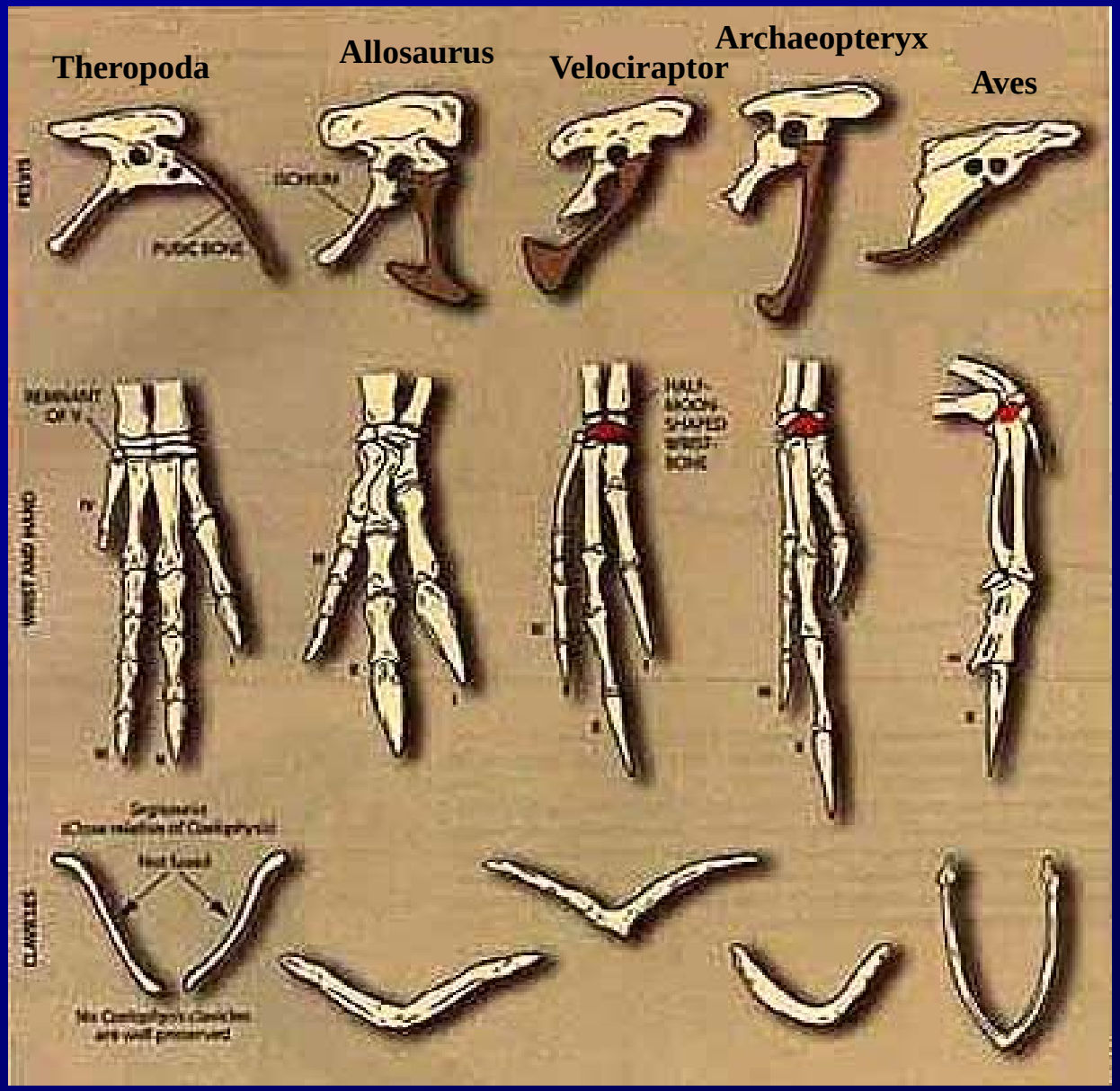
Tetanurae

Theropods

Archaeopteryx

Modern birds

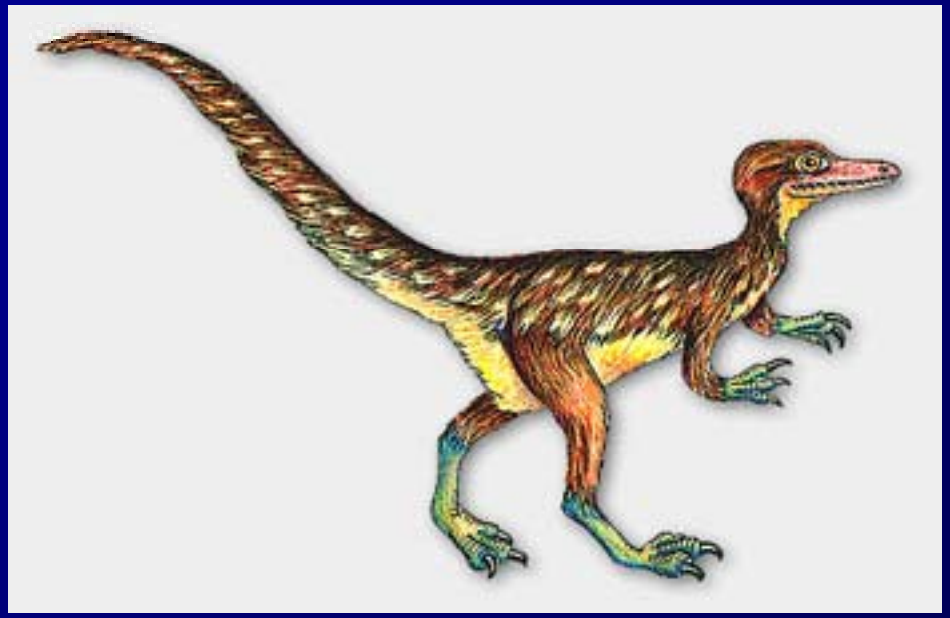
Aves

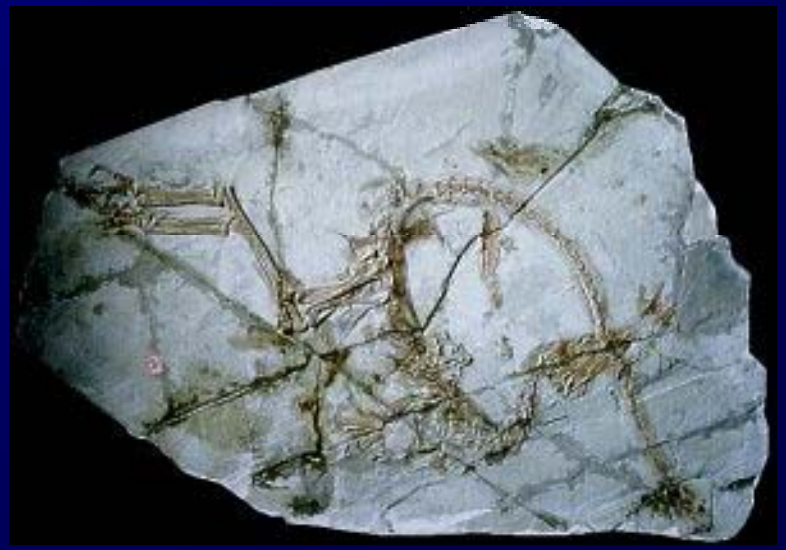

Theropoda
Allosaurus
Velociraptor
Archaeopteryx
Aves

New fossils strengthened case for a theropod origin of birds.

Sinosauropteryx – feathered theropod

Sinornis santensis – intermediate between *Archaeopteryx* and modern birds

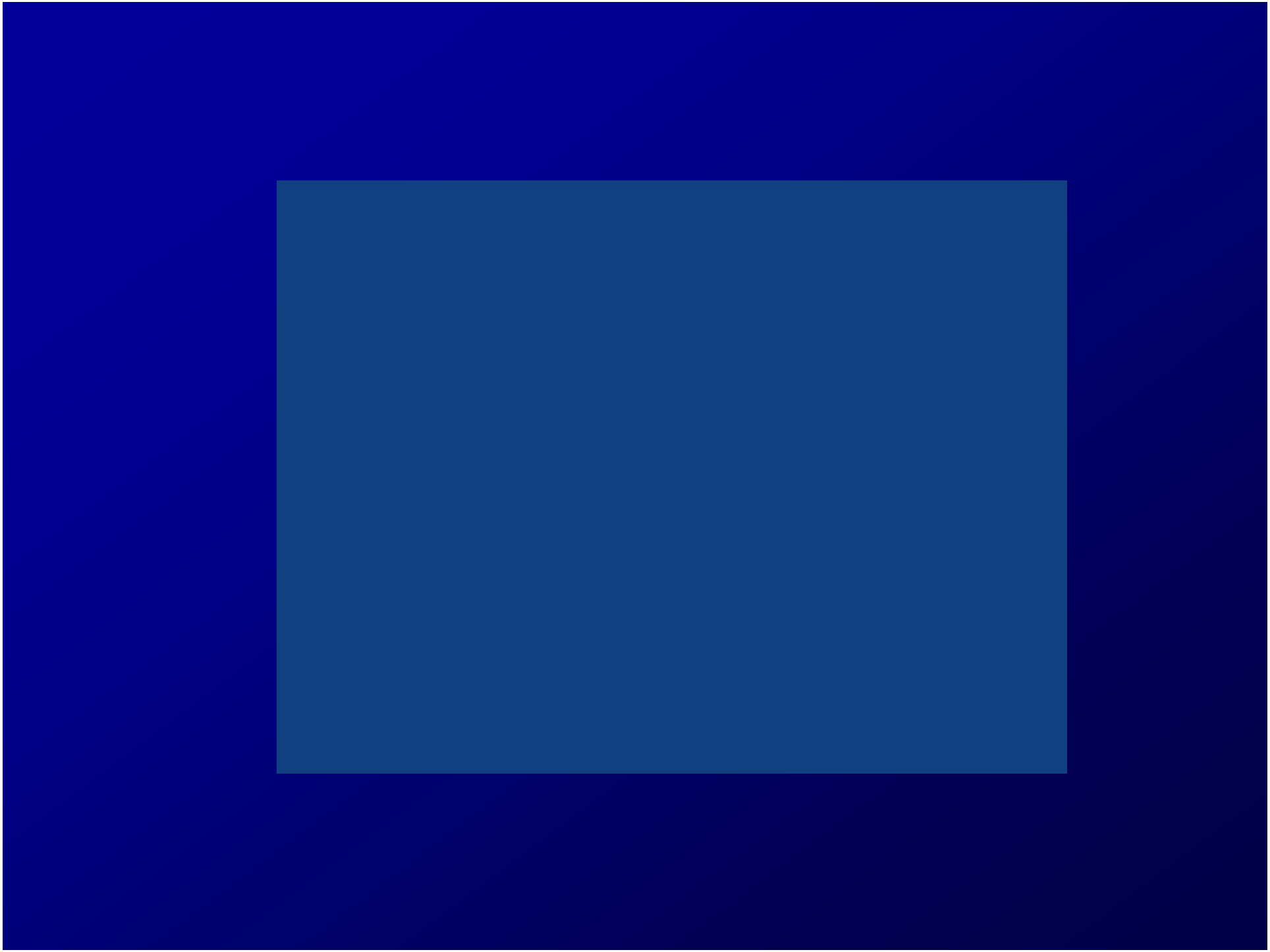




IV. Archaeopteryx

1st and best known fossil bird.

8 specimens provide linking form with reptilian and avian characters.



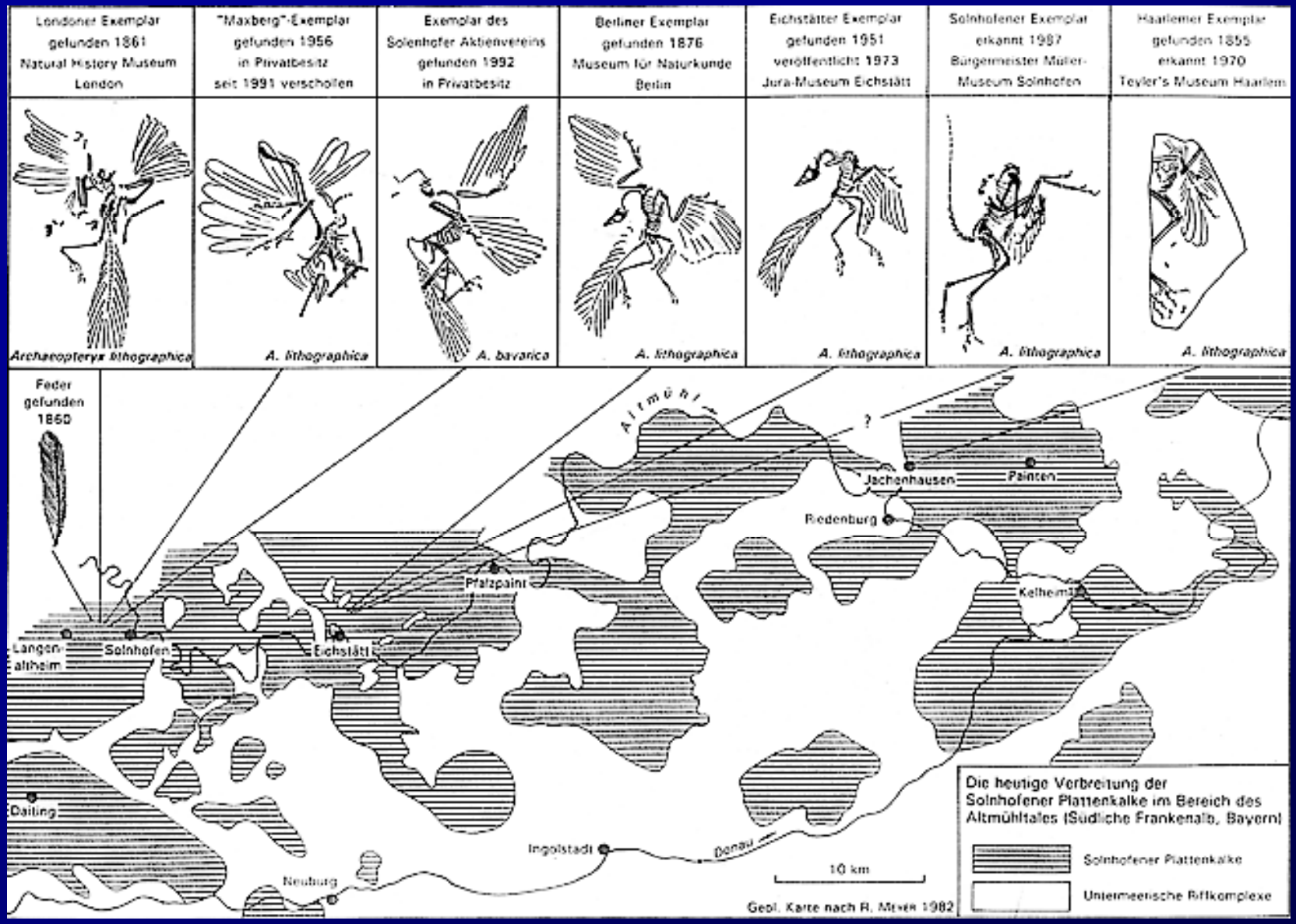
A. Skeletal Specimens

7 skeletal specimens

Lithographic slate quarry near Solnholfen, Bavaria, Germany


Germany


Nürnberg
BAYERN
Regensburg
Solnhofen
Danube
Passau
Isar
Augsburg
Munich
Inn
Lech
Salzburg
Garmisch-
Partenkirchen


Londoner Exemplar
gefunden 1861
Natural History Museum
London
"Maxberg"-Exemplar
gefunden 1956
in Privatbesitz
seit 1991 verschollen
Exemplar des
Solnhofer Aktienvereins
gefunden 1992
in Privatbesitz
Berliner Exemplar
gefunden 1876
Museum für Naturkunde
Berlin
Eichstätter Exemplar
gefunden 1951
veröffentlicht 1973
Jura-Museum Eichstätt
Solnhofener Exemplar
erkannt 1987
Bürgermeister Müller-
Museum Solnhofen
Haarlemer Exemplar
gefunden 1855
erkannt 1970
Teyler's Museum Haarlem
Archaeopteryx lithographica
A. lithographica
A. bavarica
A. lithographica
A. lithographica
A. lithographica
A. lithographica
Feder
gefunden
1860
Altmühl
?
Jachenhausen
Painten
Riedenburg
Pfalzpaint
Kelheim
Langen-
altheim
Solnhofen
Eichstätt
Dalling
Ingolstadt
Donau
Neuburg
10 km
Die heutige Verbreitung der
Solnhofener Plattenkalke im Bereich des
Altmühltales (Südliche Frankenalb, Bayern)
Solnhofener Plattenkalke
Untermeerische Riffkomplexe
Gepl. Karte nach R. Meyer 1982

1st – *London Bird* (1861)

Acquired by German Obstetrician

Sold to British Museum of Natural History.

Dated ~
147 mya

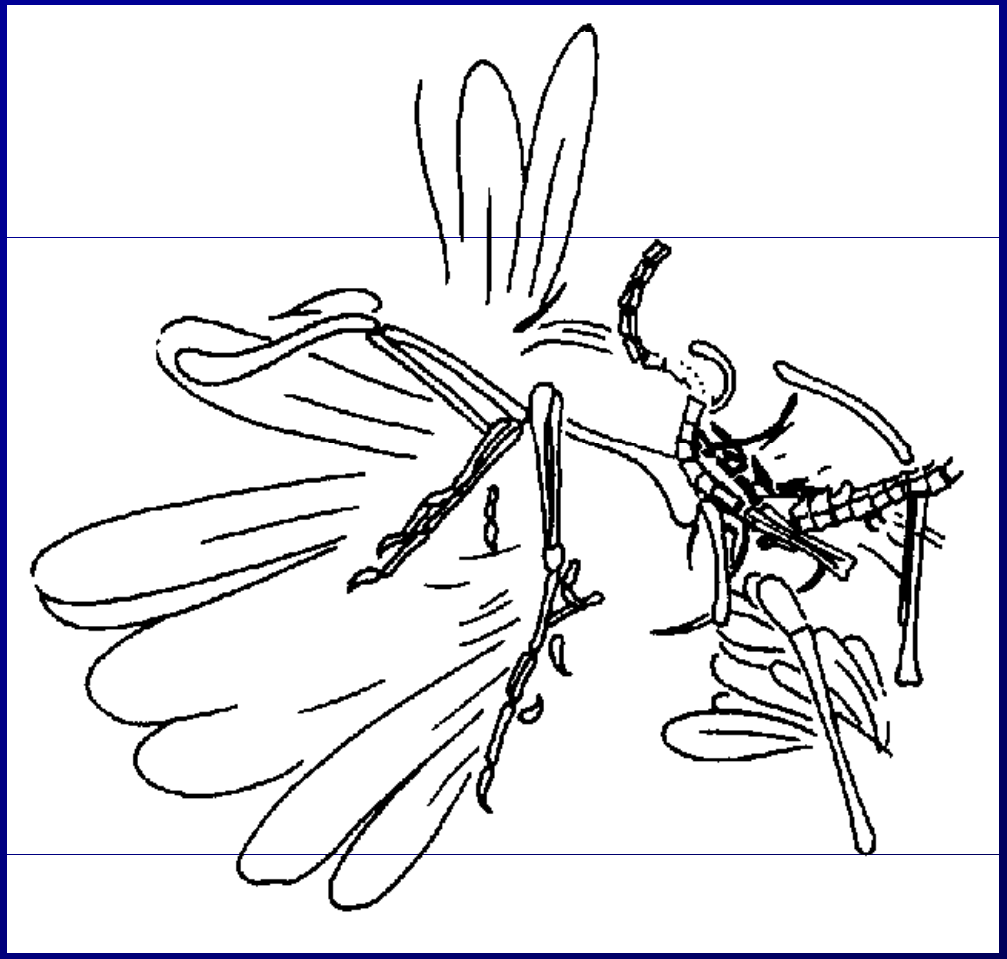
2nd – *Berlin Bird (1877)*

Acquired by Berlin

Museum

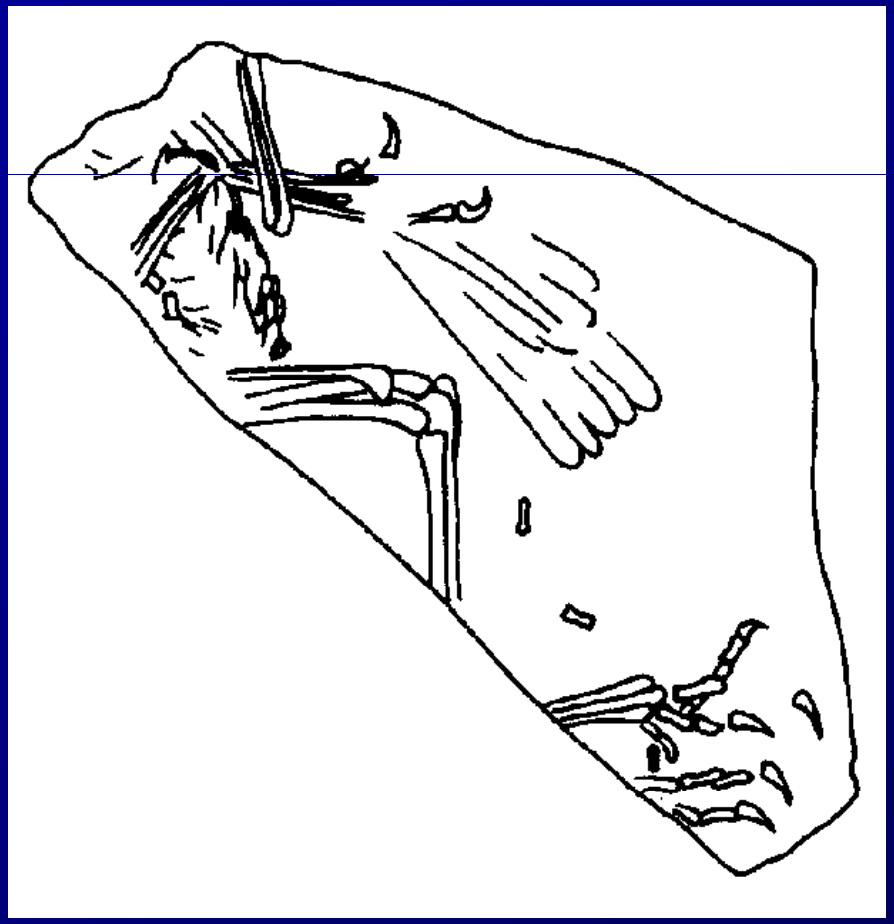
3rd – *Maxberg Bird (1955)* – Eduard Opitsch

Found in shed by quarry worker



4th – *Teyler Bird* (1855)

Found 5 yrs before feather but misidentified.



B. Avian and reptilian characters

Pubis loosely connected – fossilization displaced (different position in all specimens)

	Thecodontia	Pseudosuchians	Theropods	Archaeopteryx	Modern Birds
Quadrate immobile	X	X	X		
Cervical ribs	X	X	X		
Conical teeth	X	X	X		
Biconcave vertebrae	X	X	X	X	
Gastralia	X	X	X	X	
Broad, coracoid	X	X	X	X	
Long "bony tail	X	X	X	X	
Pubes perpendicular to ilium	X	X	X	?	
Pectoral girdle with clavicle	X	X	X[1]	X	X
Elongated scapula	X	X	X	X	X
Bipedal		X	X	X	X
Hind limbs longer than forelimbs		X	X	X	X

	Thecodontia	Pseudosuchians	Theropods	Archaeopteryx	Modern Birds
Tarsometatarsus + tibiotarsus			X	X	X
Elevated hallus			X	X	X
Clavicles fused to form furcula			X[2]	X	X
Quadrate and upper jaw movable			X[2]	X	X
Feathers				X	X
Ribs attached to sternum					X
Extended coracoid					X
Hind limbs NOT longer than forelimbs					X
Extensive reduction and fusion in manus					X

C. Did *Archaeopteryx* fly?

2 major hypotheses

1. Ground – up
2. Trees - down

1. Arboreal Hypothesis

Alan Feduccia

Intuitive – flight evolved from gliding stage from arboreal perch.

Also has claws on manus

Hoatzin

(*Opisthocomus hoazin*)

Used clawed digits to climb trees and glide down.

But –

No features of typical gliders

Claws typical of ground-dwelling birds and Theropods

No evidence of wear

Paleobotanical evidence – no large trees

2. Cursorial Hypothesis

Functional – ecological inferences

Strong agile biped

Originally suggested feathered wing used for food gathering

Now suggested for thermoregulation

Problems –

1) Dead end process – work against gravity
2) Need high speed to gain lift
3) Can selection favor improvements in both forelimbs and hindlimbs
4) Lacked trioseal canal!

3. Pouncing Proavis Hypothesis

Garner et al. 1999.

Predecessor to modern birds specialized in ambush attacks from elevated perches.

Lift generating surfaces evolved – distal portion of forelimb

Maximum control and power

4. Wing-assisted Incline Running

Dial 2003. Science 299:402-404 – see website for article

Forelimbs of proto-birds used to provide improved hindlimb traction


University of Montana
Flight Laboratory

Proponents of all hypotheses agree ultimate cause for evolution of feathers was heat conservation not flight.

Aerodynamic nature of feather derived secondarily and thus "exaptation"

Theropod with “downy” feathers!

D. Flight improvements after Arch.

Enantiornithines – Primitive Cretaceous birds

(Sinornis, Confuciusornis, Vorona)

Shortly after Arch. small Starling sized bird recovered with alula.

Early in history of birds wing mechanism evolved so that birds could fly at lower speeds.

Confuciusornis

- size of magpie
- feathered
- claws on forelimb
- tail reduced
- horny beak!!

Some have long quills projecting from tail

Many fossil birds dating to Cretaceous quickly gained characters found in modern birds.

E. Conclusions

1. Origins of birds likely Theropods in middle to late Jurassic
2. Archaeopteryx shows characteristics of both arboreal and cursorial bird
3. Clothes don’t necessarily make the man
4. After Archaeopteryx, bird evolution centered on improvements of flight apparatus

V. Post Jurassic Radiation

A. Lower Cretaceous

1. *Sinornis santensis* – toothed, sparrow-sized bird (discovered 1992)

Sinornis

the pectoral girdle and forelimb show many features related to advanced wing design

• wrist joint modified for hyperflexion of the manus against the forearm during the recovery phase of the flight stroke and for folding the wing against the body.

Shared many characteristics in common with Theropod dinosaurs and Archaeopteryx

Suggests occupied basal position in avian evolution

Reptilian characteristics

- toothed
- unfused carpals
- gastralia
- unfused metatarsals

Avian characteristics

- reduced # trunk vertebrae (11 compared to 14)
- pygostyle (reduction of tail to fan shape)
- wing folds
- manus shorter than antebrachium

B. Upper Cretaceous

Order Hesperornithiformes

1. Ichthyornis – described by Marsh 1873

Toothed, flying seabird, keeled sternum, ternlike.

Niobrara chalk beds of western Kansas


Dan Varner

2. Hesperornis – described in 1875 from the same formation.

Toothed but secondarily flightless

Resembled loon.

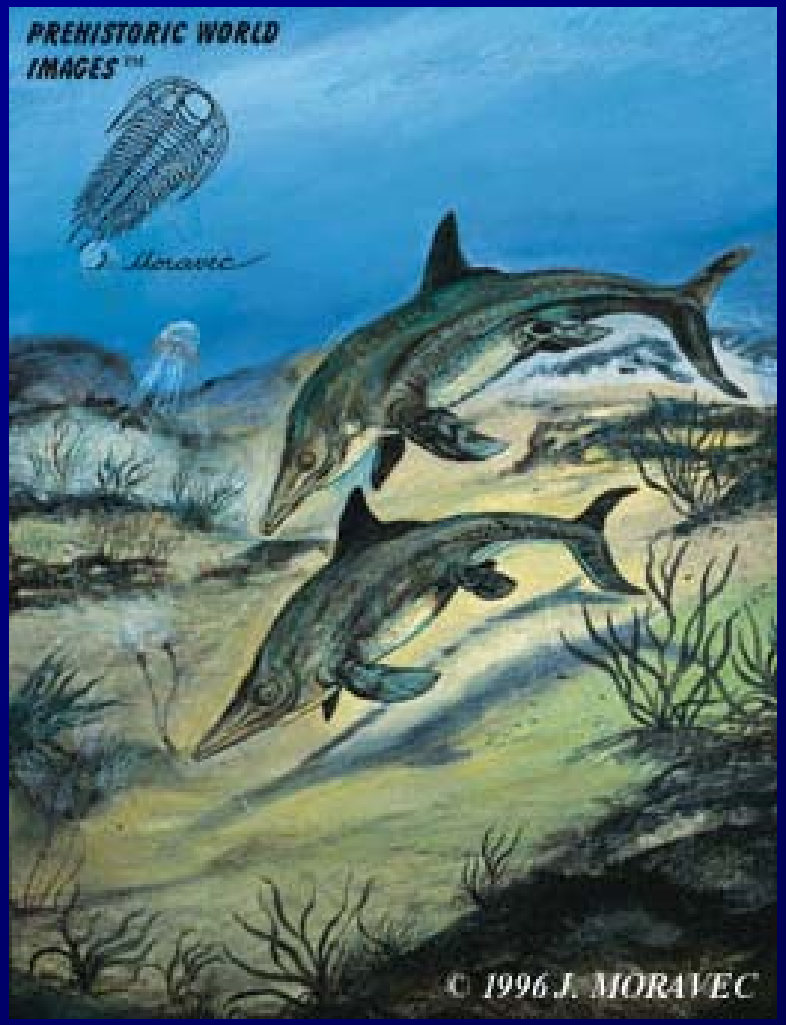
3. Survivors were the ancestors of the toothless modern birds

4. Following Cretaceous ~ 40 spp including representatives of modern orders

- Gruiformes
- Charadriiformes
- Pelecaniformes
- Ciconiiformes
- Gaviiformes
- Podicipediformes
- Strigiformes

C. Tertiary

1. Eocene – most if not all modern bird orders present
2. Oligocene – some modern genera present
3. Miocene – all non-passerine families and many passerine families present
4. Pliocene – all modern genera present, max diversity present
5. Pleistocene – all modern species found



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