Registro Fósil y Evolución de Vertebrados

Paleontología de Vertebrados

Theropoda

Sergio Soto Acuña
Paleontólogo de Vertebrados

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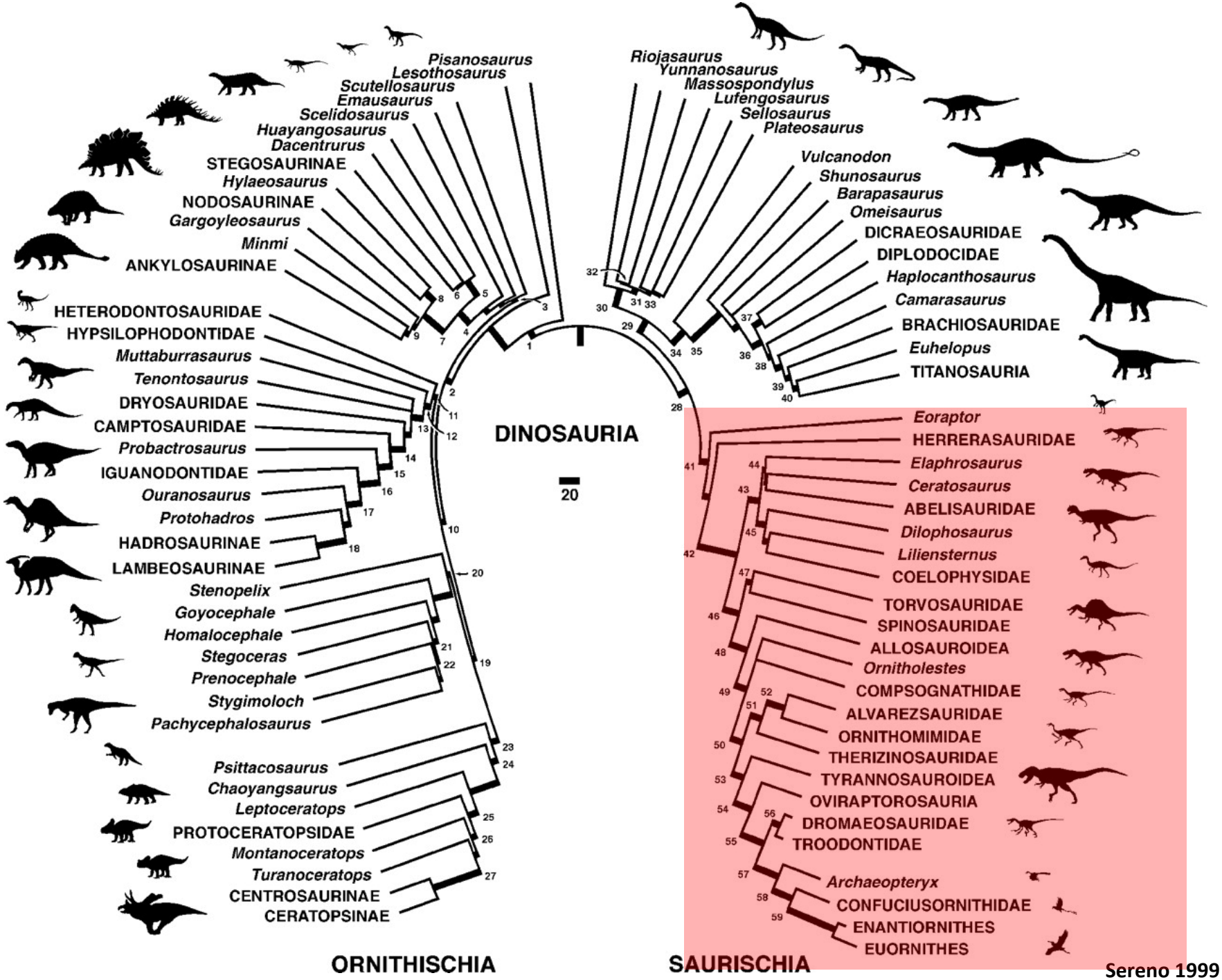
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Lesothosaurus
Scutellosaurus
Emausaurus
Scelidosaurus
Huayangosaurus
Dacentrurus
STEGOSAURINAE
Hylaeosaurus
NODOSAURINAE
Gargoyleosaurus
Minmi
ANKYLOSAURINAE
HETERODONTOSAURIDAE
HYPSILOPHODONTIDAE
Muttaburrasaurus
Tenontosaurus
DRYOSAURIDAE
CAMPTOSAURIDAE
Probactrosaurus
IGUANODONTIDAE
Ouranosaurus
Protohadros
HADROSAURINAE
LAMBEOSAURINAE
Stenopelix
Goyocephale
Homalocephale
Stegoceras
Prenocephale
Stygimoloch
Pachycephalosaurus
Psittacosaurus
Chaoyangsaurus
Leptoceratops
PROTOCERATOPSIDAE
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CENTROSAURINAE
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Riojasaurus
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Lufengosaurus
Sellosaurus
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Shunosaurus
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Omeisaurus
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DIPLODOCIDAE
Haplocanthosaurus
Camarasaurus
BRACHIOSAURIDAE
Euhelopus
TITANOSAURIA
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Ceratosaurus
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ALVAREZSAURIDAE
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THERIZINOSAURIDAE
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OVIRAPTOROSAURIA
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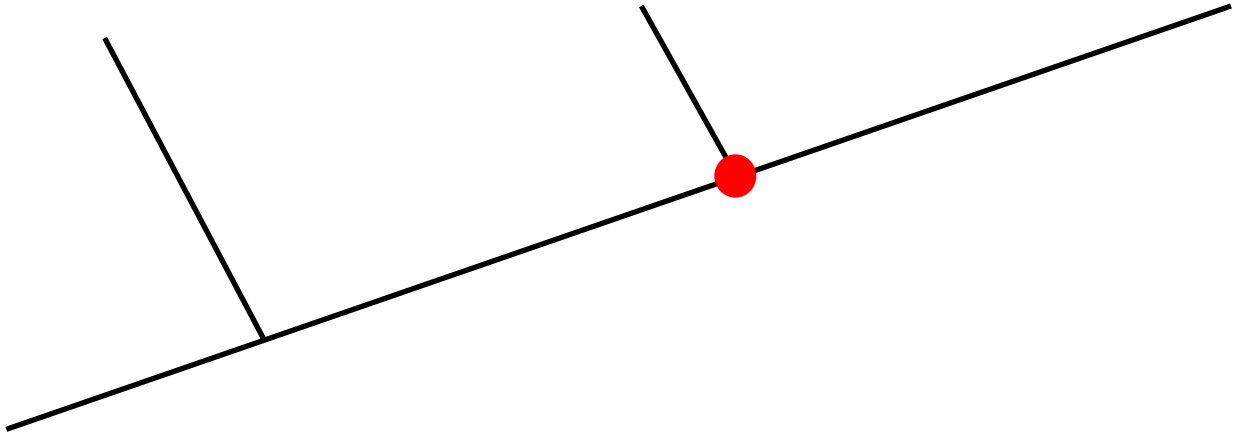
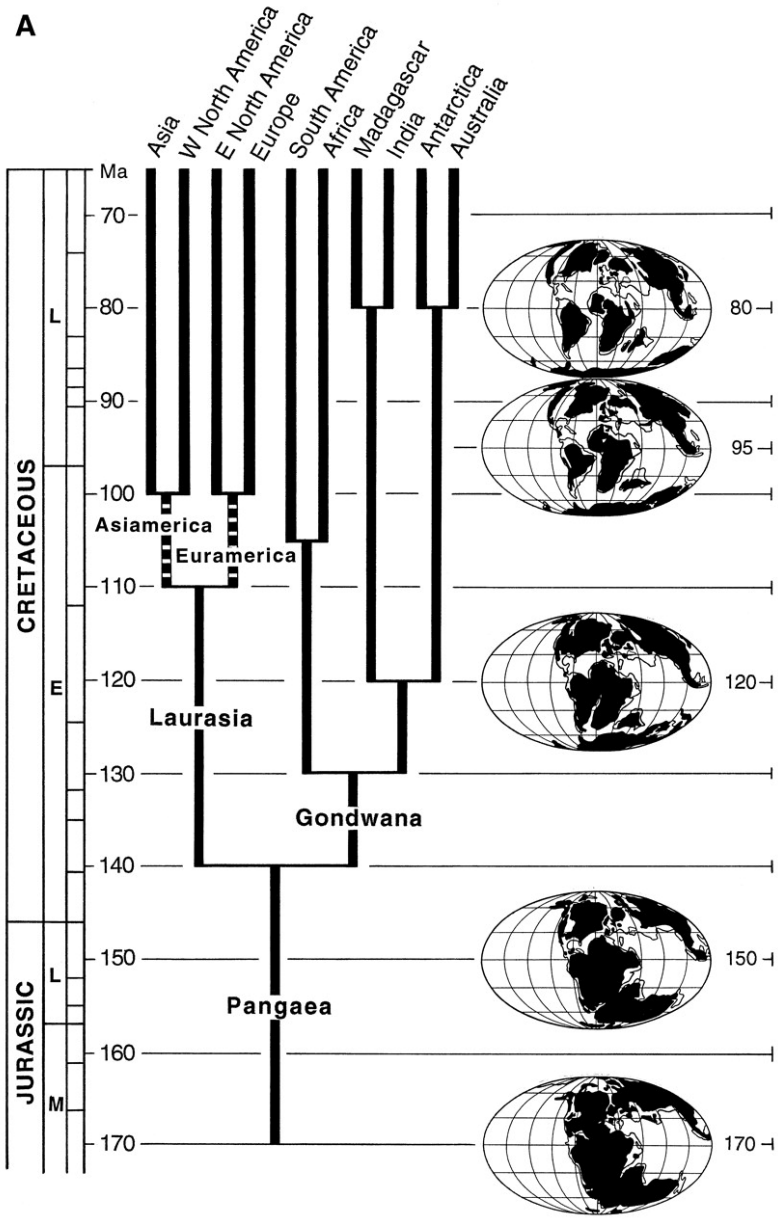
TROODONTIDAE
Archaeopteryx
CONFUCIUSORNITHIDAE
ENANTIORNITHES
EUORNITHES
SAURISCHIA

Sereno 1999

Theropoda Marsh, 1881

Definición de rama: Dinosaurios que comparten un ancestro común más reciente con la paloma *Columba livia* que con *Apatosaurus*

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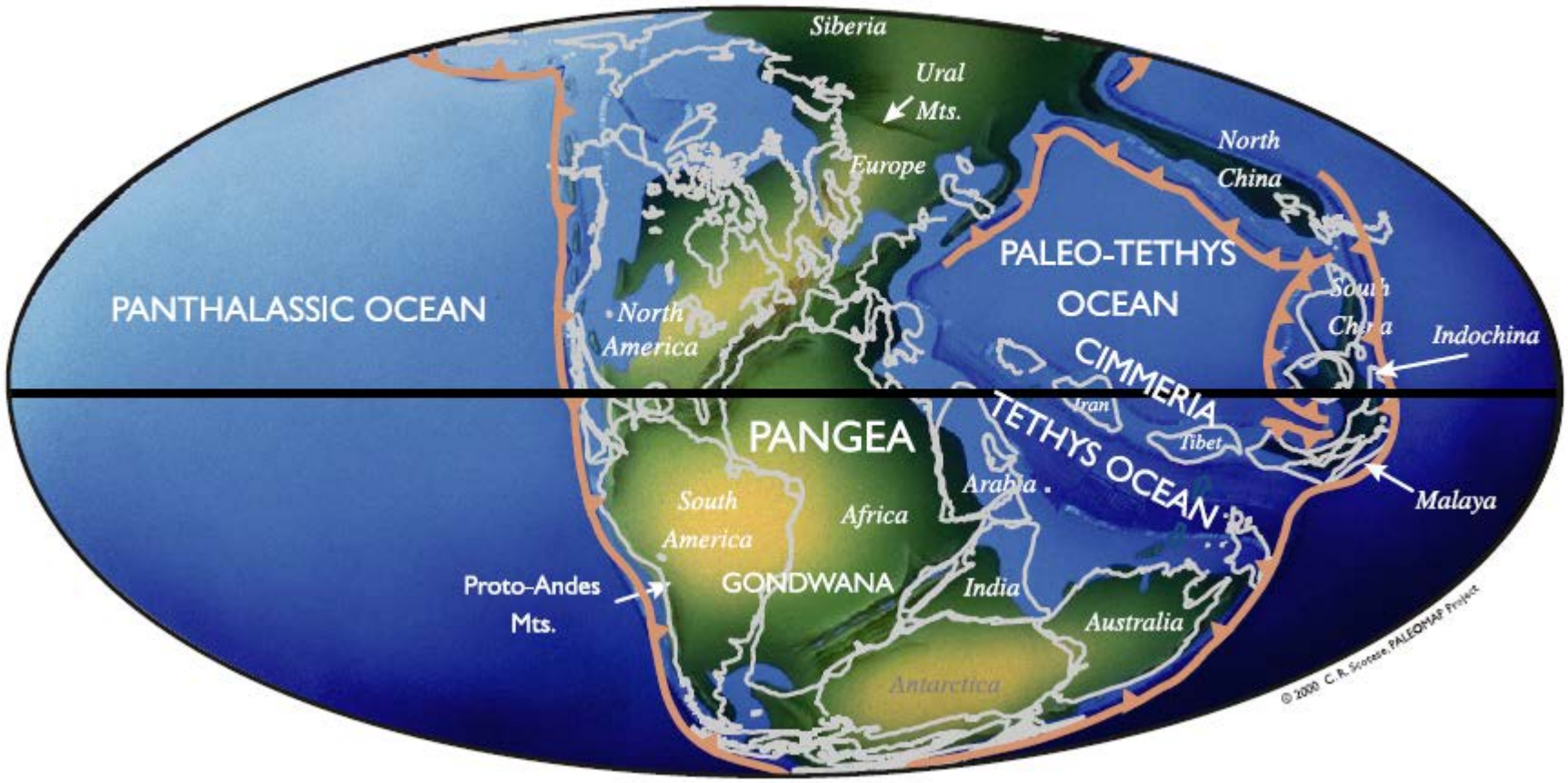
Sereno 1999

237 Ma Triassic

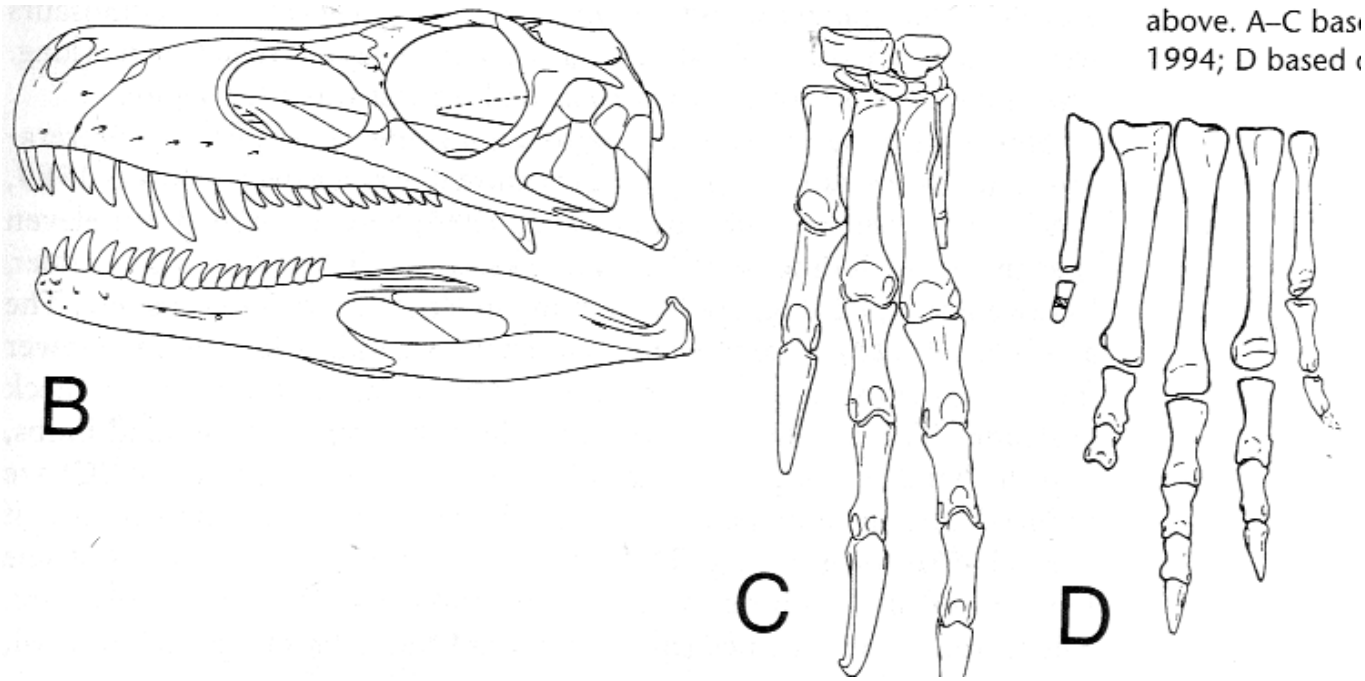


Gradstein 2012

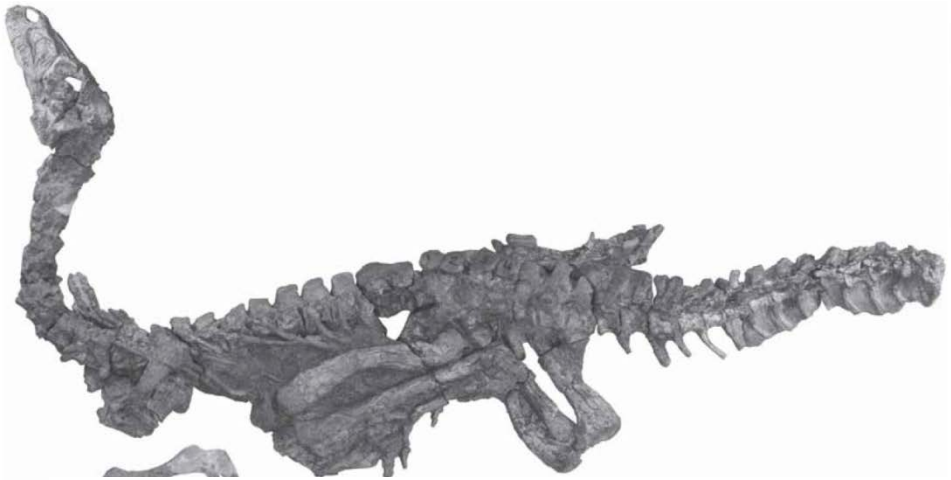
Theropoda

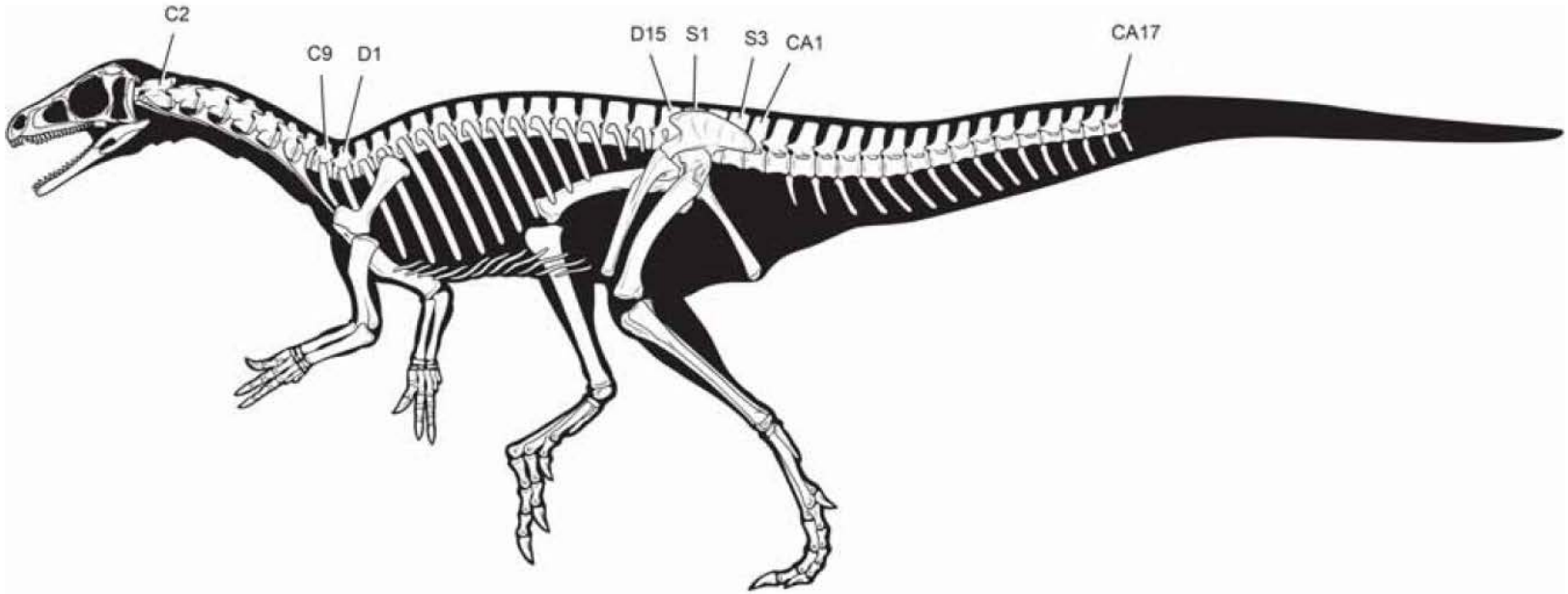
- Garras manuales recurvadas
- Alargamiento de las falanges penúltimas de las manos
- Fíbula muy próxima a la Tibia y unida a ella por medio de una cresta tibial
- Reducción del dígito V del pie, entre otros

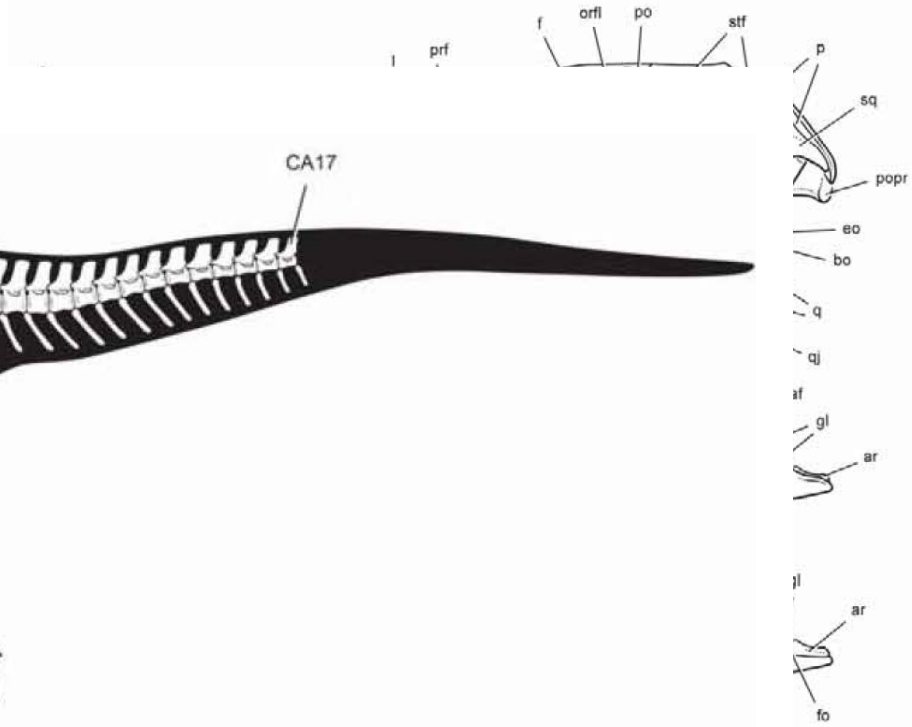
Cráneo y mano de *Herrerasaurus*



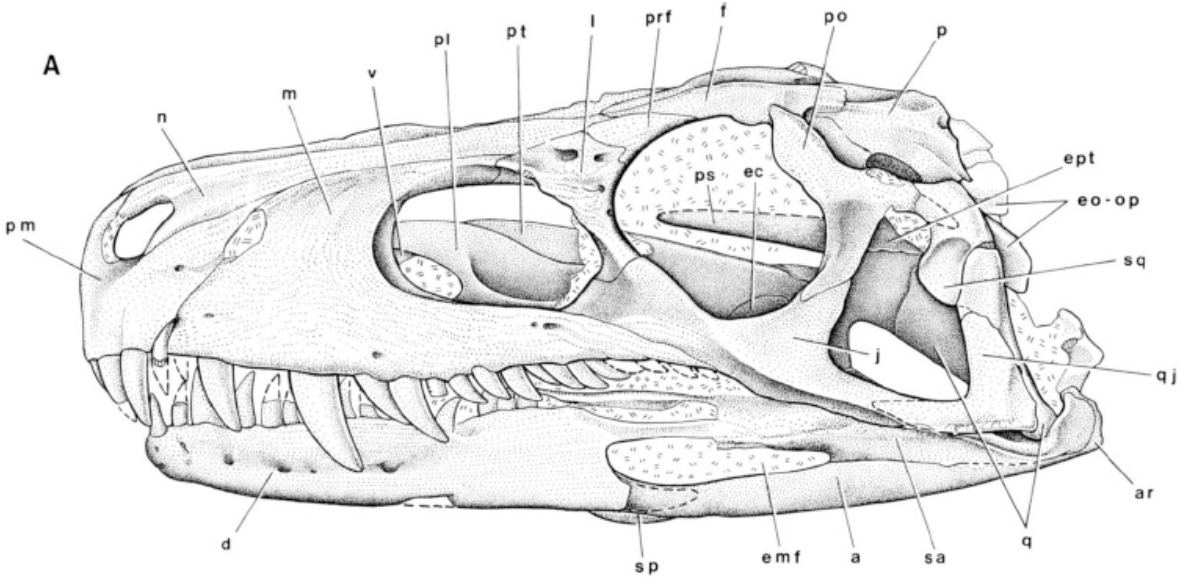
Eoraptor lunensis

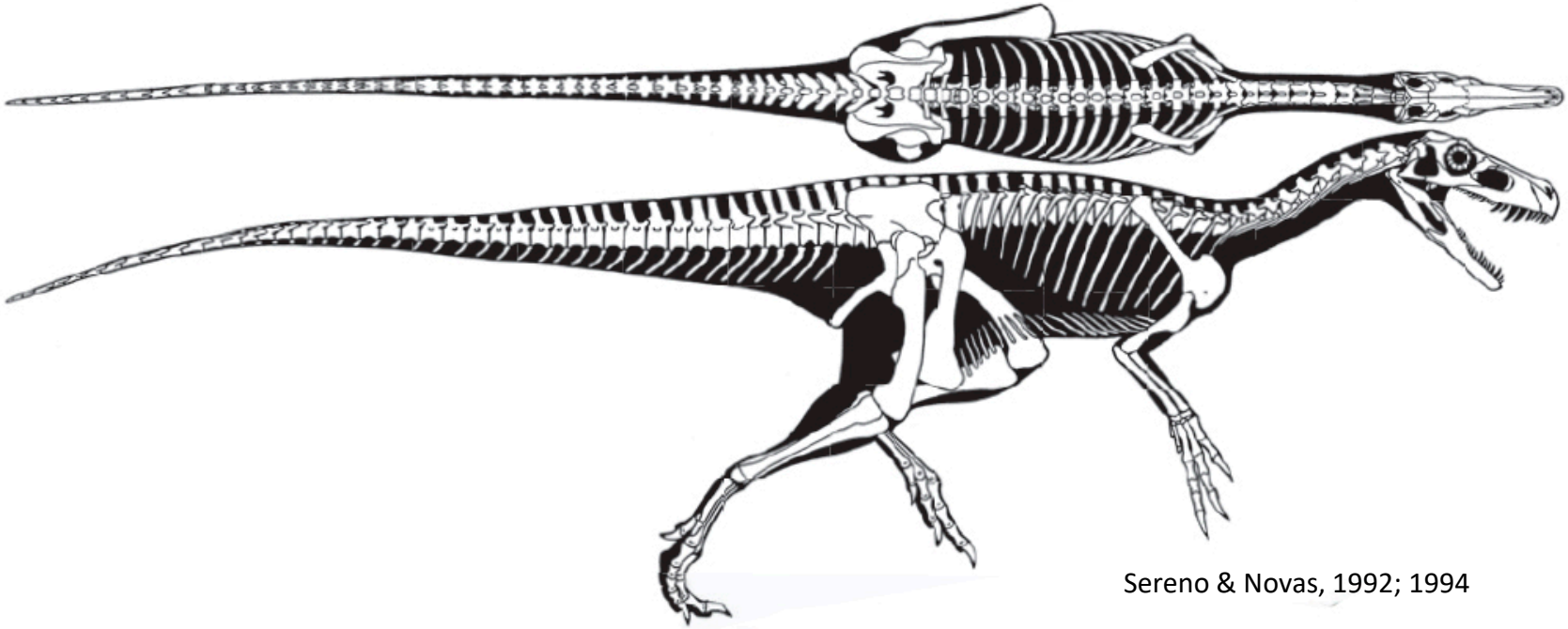




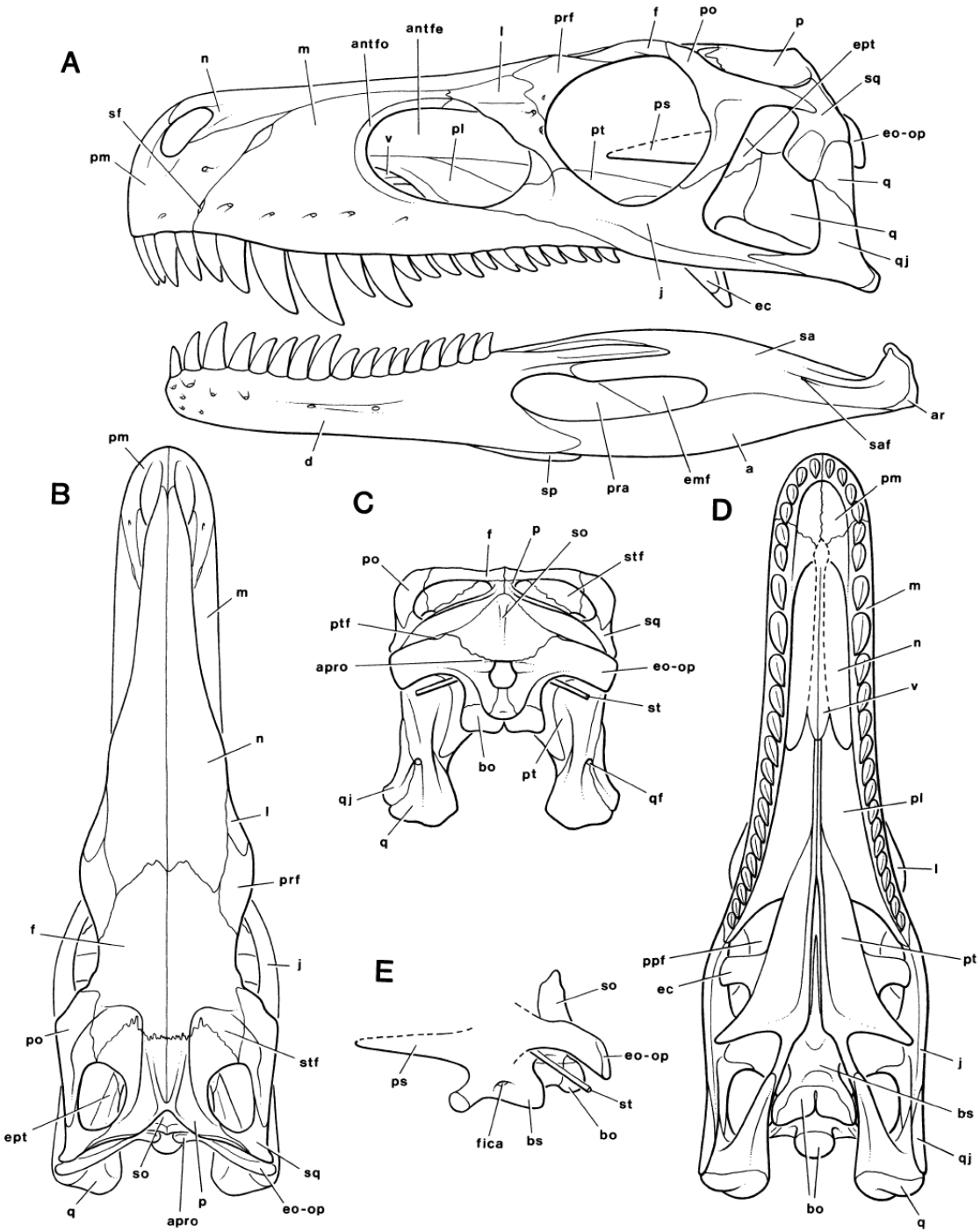


Herrerasaurus ischigualastensis

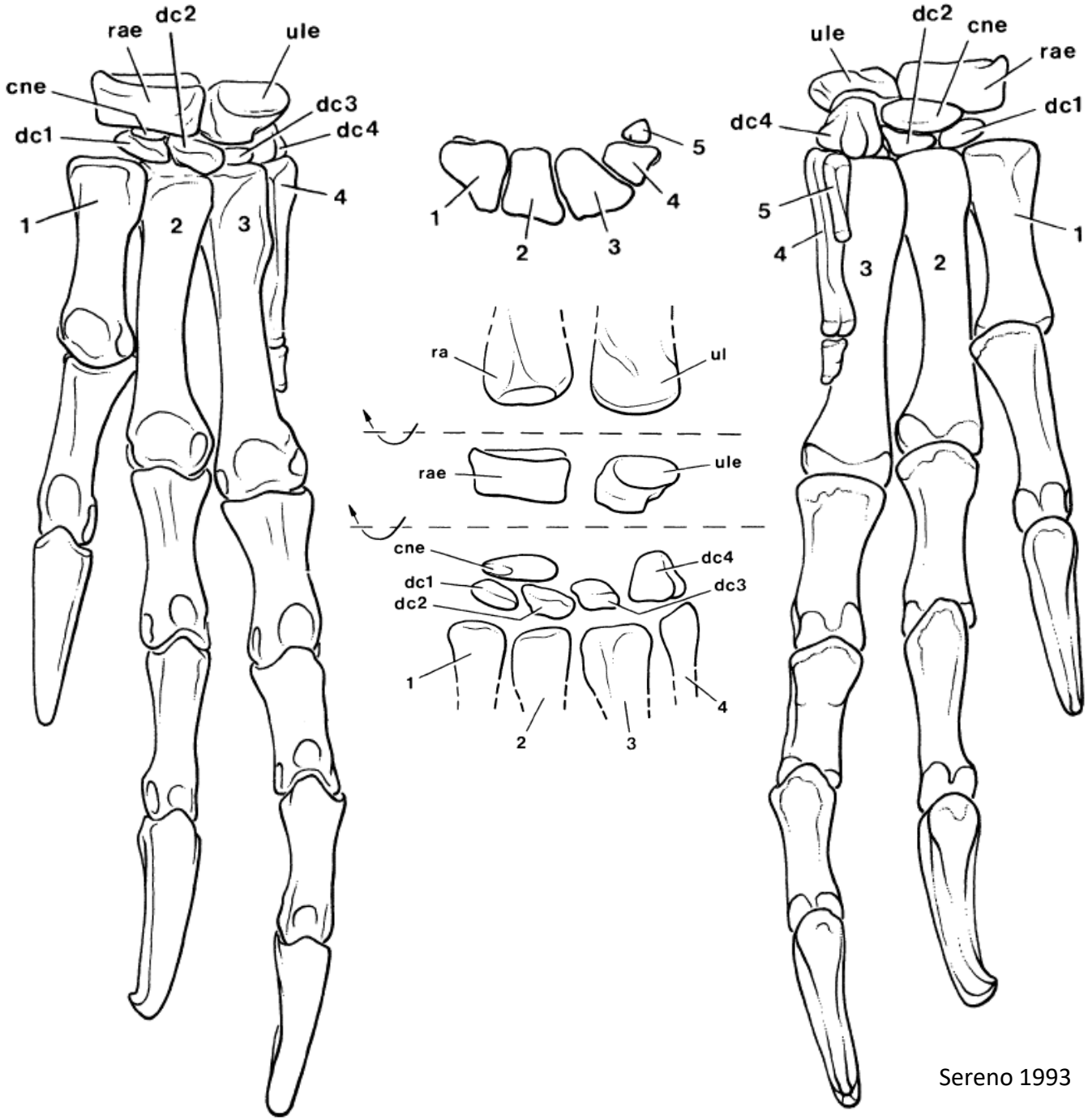




Sereno & Novas, 1992; 1994



Sereno & Novas, 1994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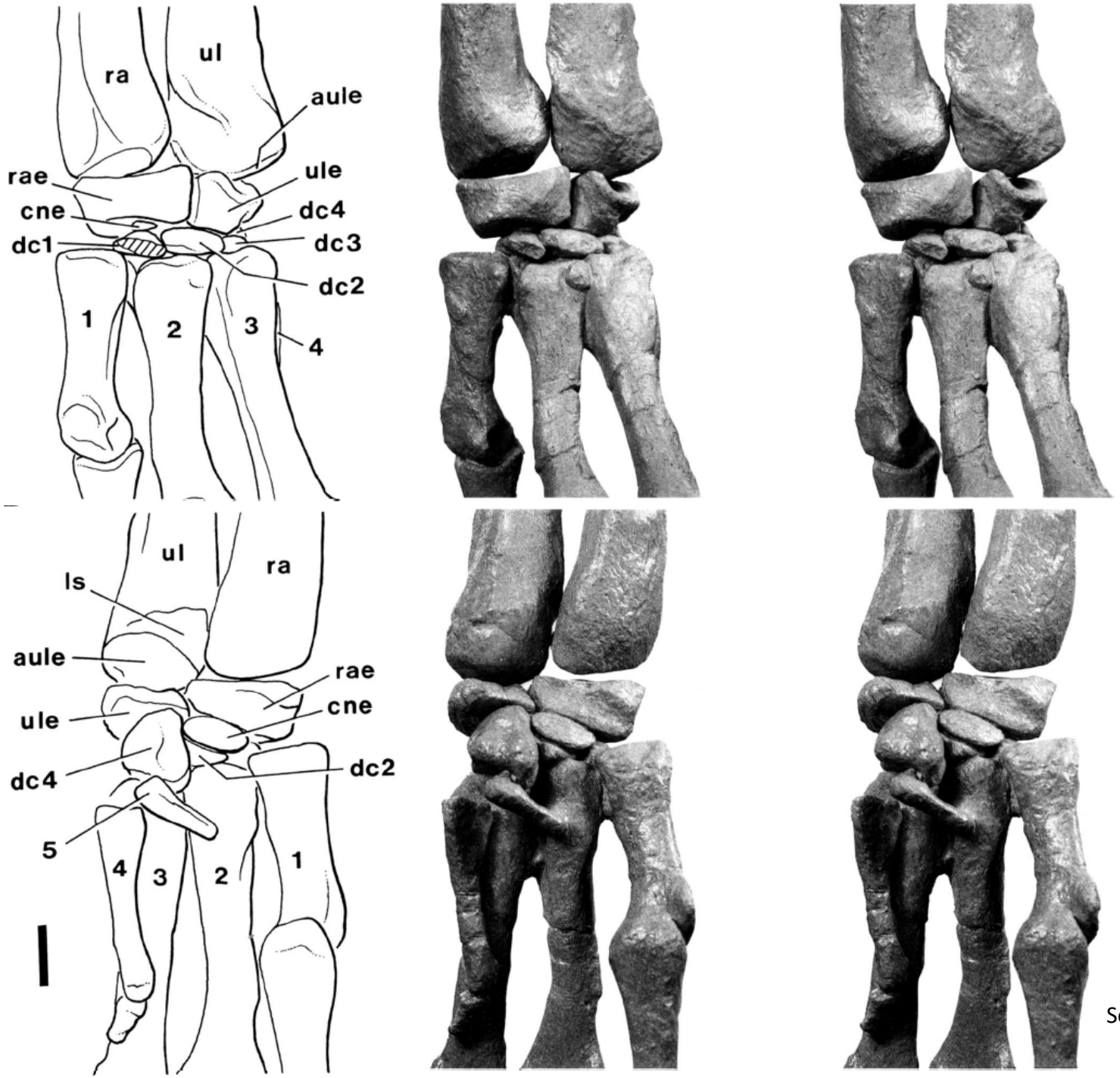
Sereno 1993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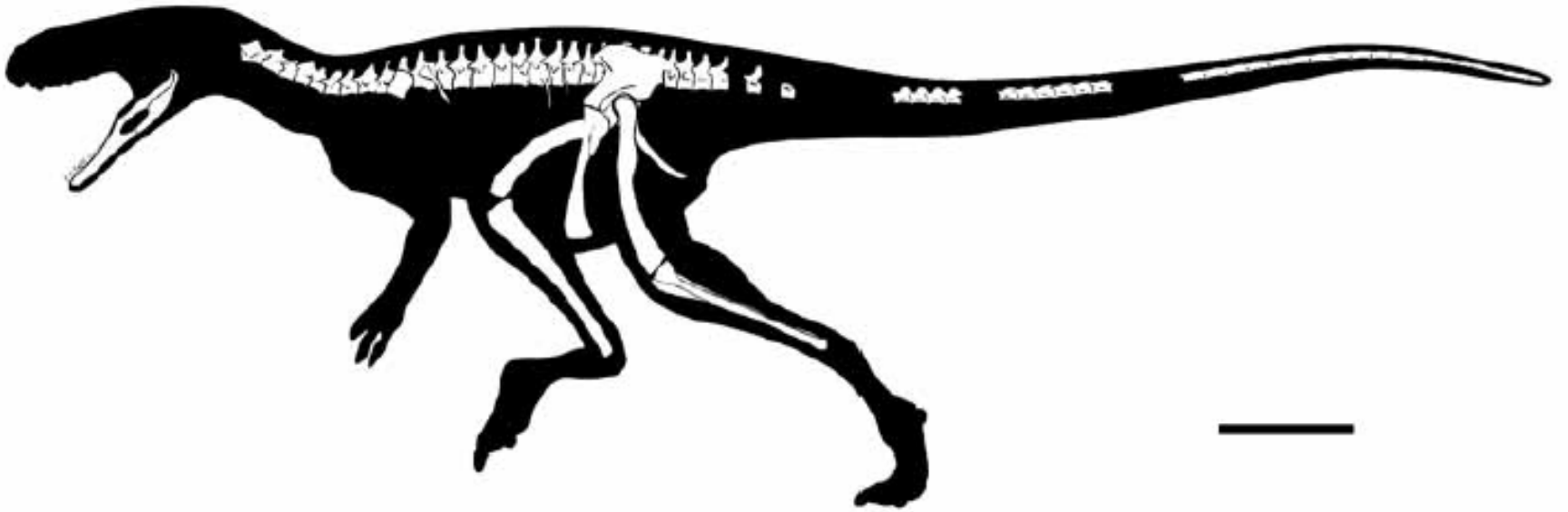
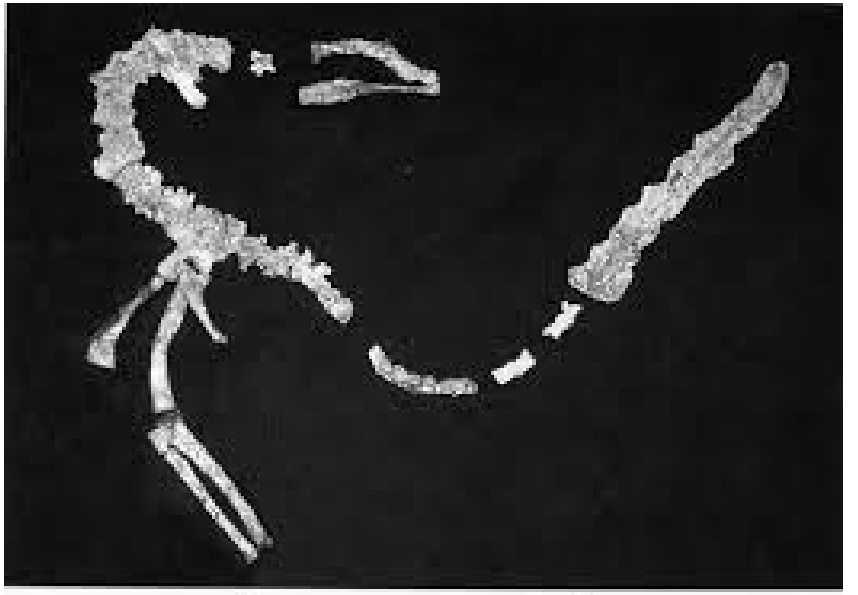
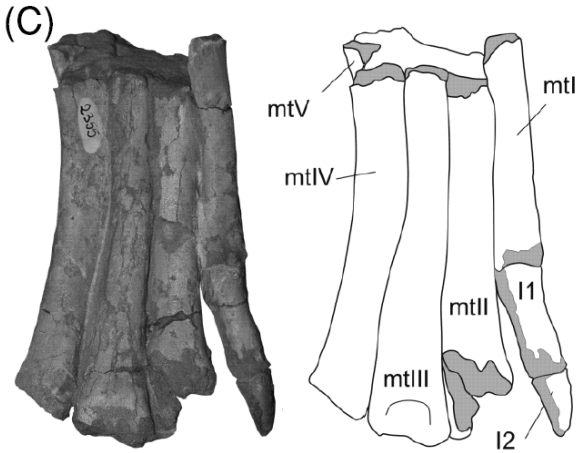
Sereno 1993

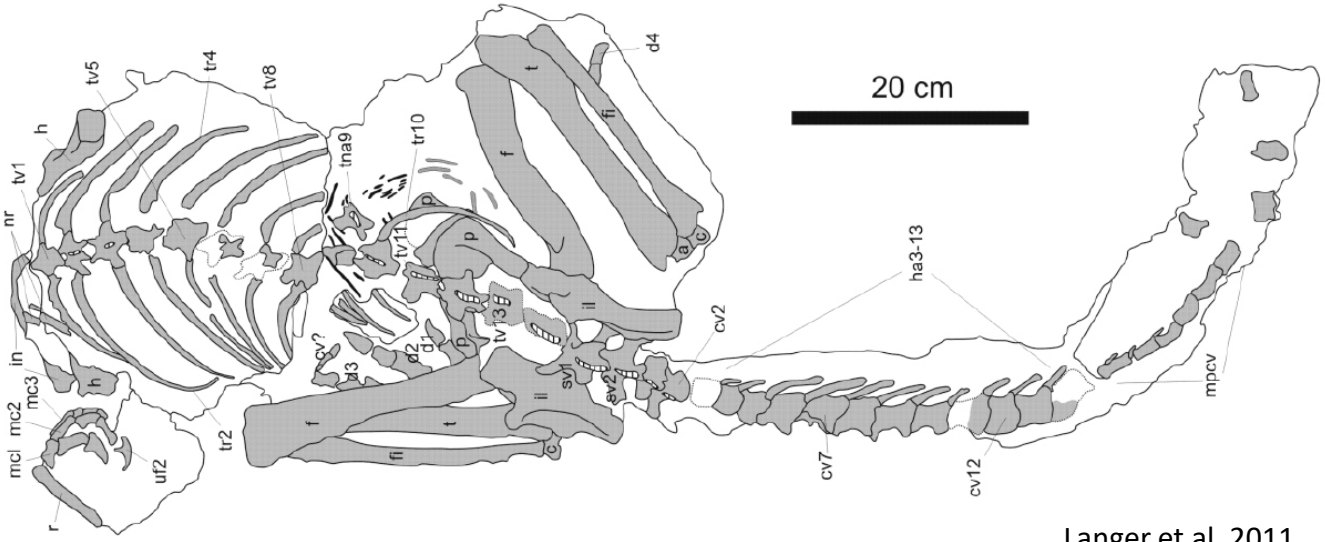
Staurikosaurus pricei

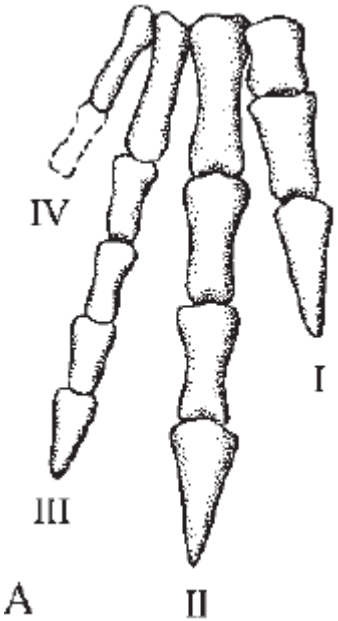




Guaibasaurus candelariensis







Langer et al, 2011

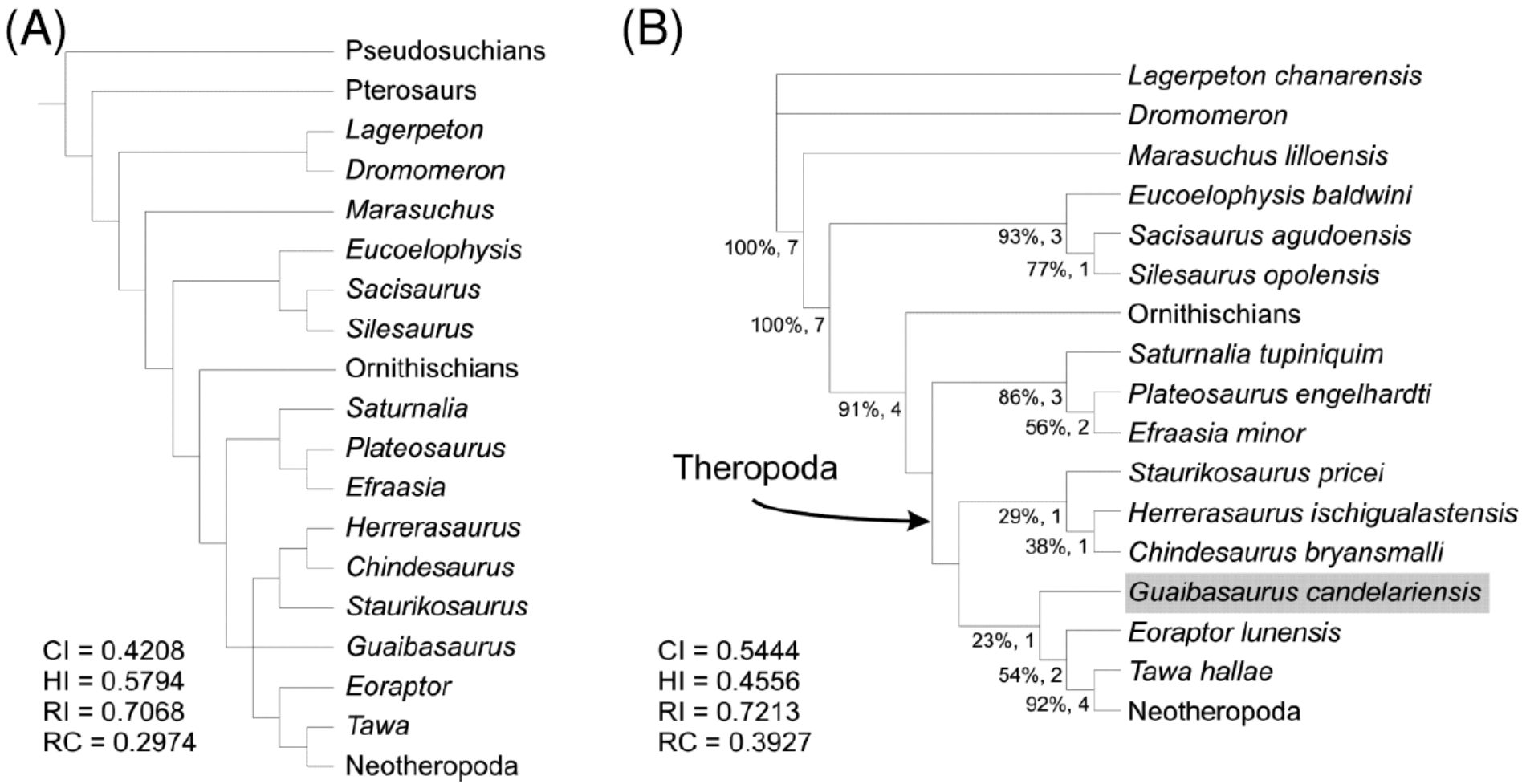


Figure 19 Strict consensus trees depicting the relationships of *Guaibasaurus candelariensis* within archosaurs: (A) simplified outcome of the inclusion of *G. candelariensis* in the data-set of Nesbitt *et al.* (2009b); (B) outcome of the analysis of the data-set modified from Nesbitt *et al.* (2009b); bootstrap (100 replicates) and 'bremer support' values are indicated for each clade. Abbreviations: CI=consistency index (excluding uninformative characters); HI=homoplasy index (excluding uninformative characters); RC=rescaled consistency index; RI=retention index.

Langer et al, 2011

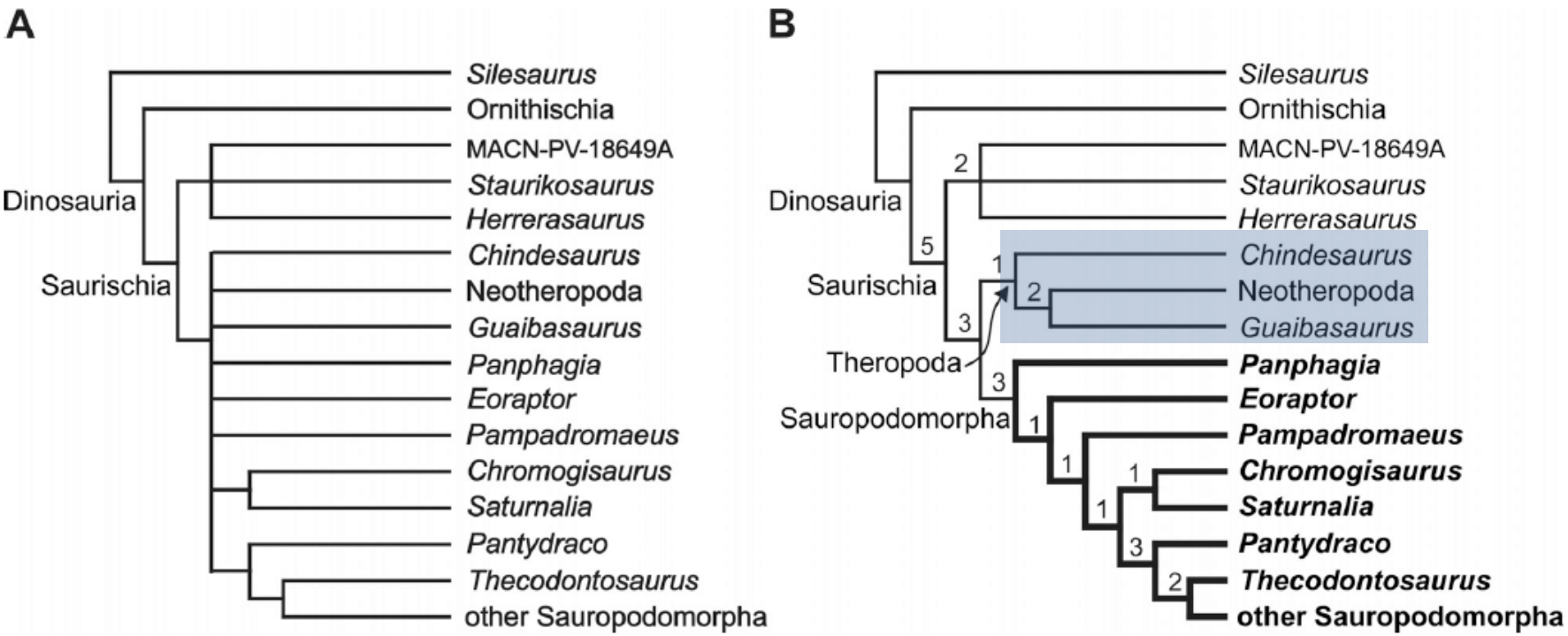
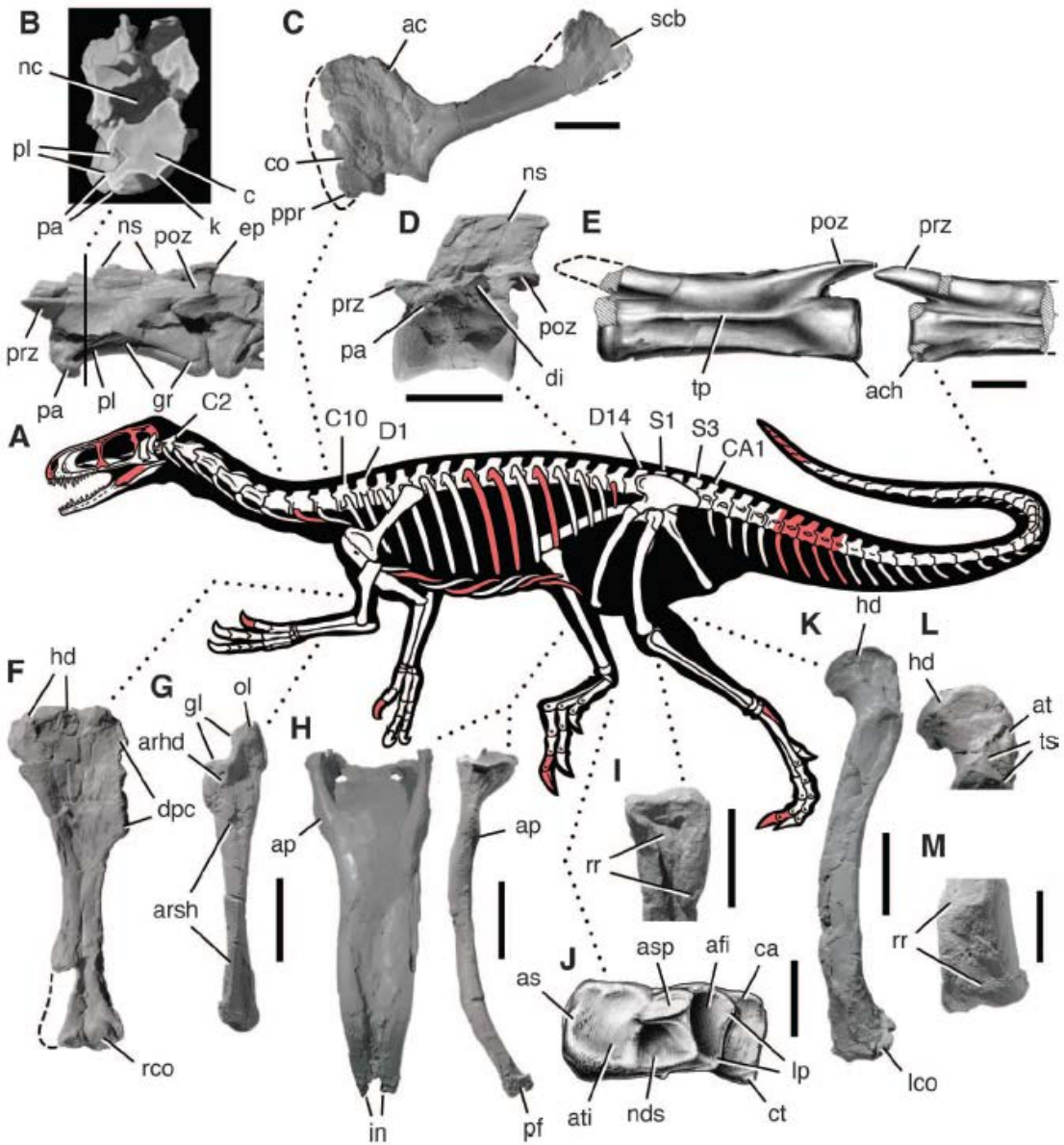


FIGURE 16. Simplified phylogenetic relationships of basal sauropodomorphs based on a data set of Ezcurra (2010). Strict consensus (**A**) and reduced consensus trees after the exclusion of *Agnosphytis* (**B**). Full black lines indicate Sauropodomorpha in **B**. Numbers within Sauropodomorpha indicate the decay indices.

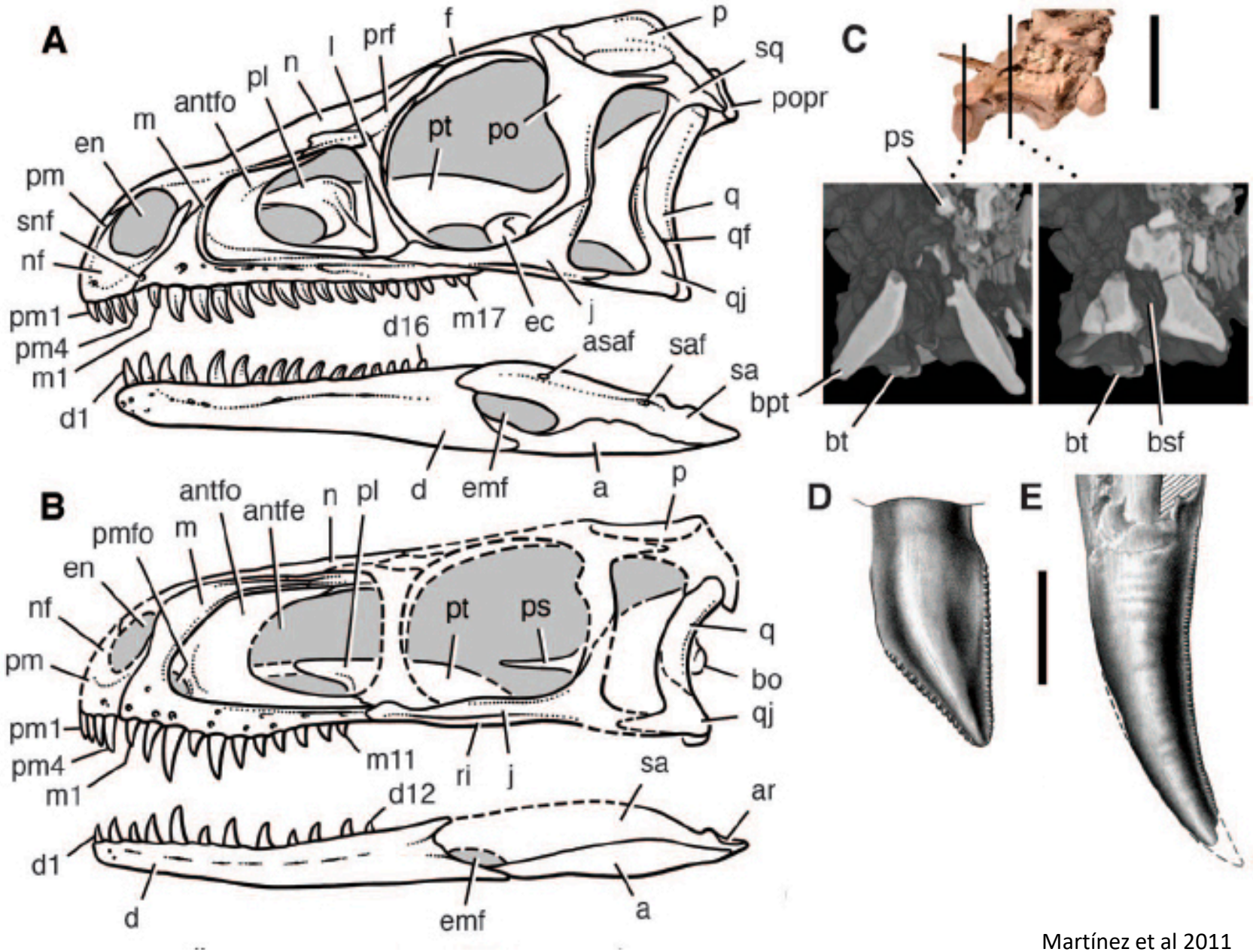
Martínez et al., 2013

Eodromaeus murphi



Martínez et al 2011

Eoraptor lunensis

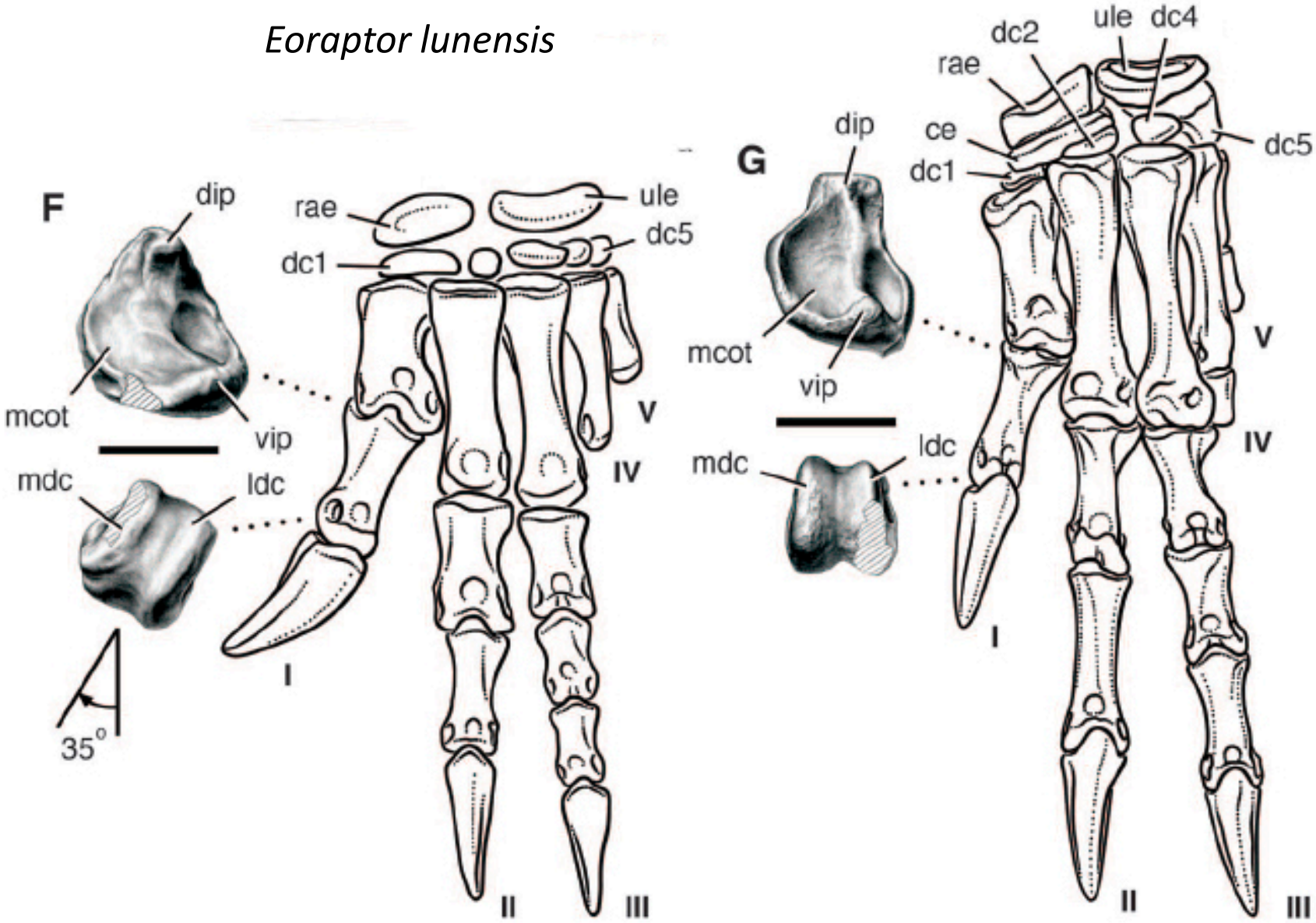


Martínez et al 2011

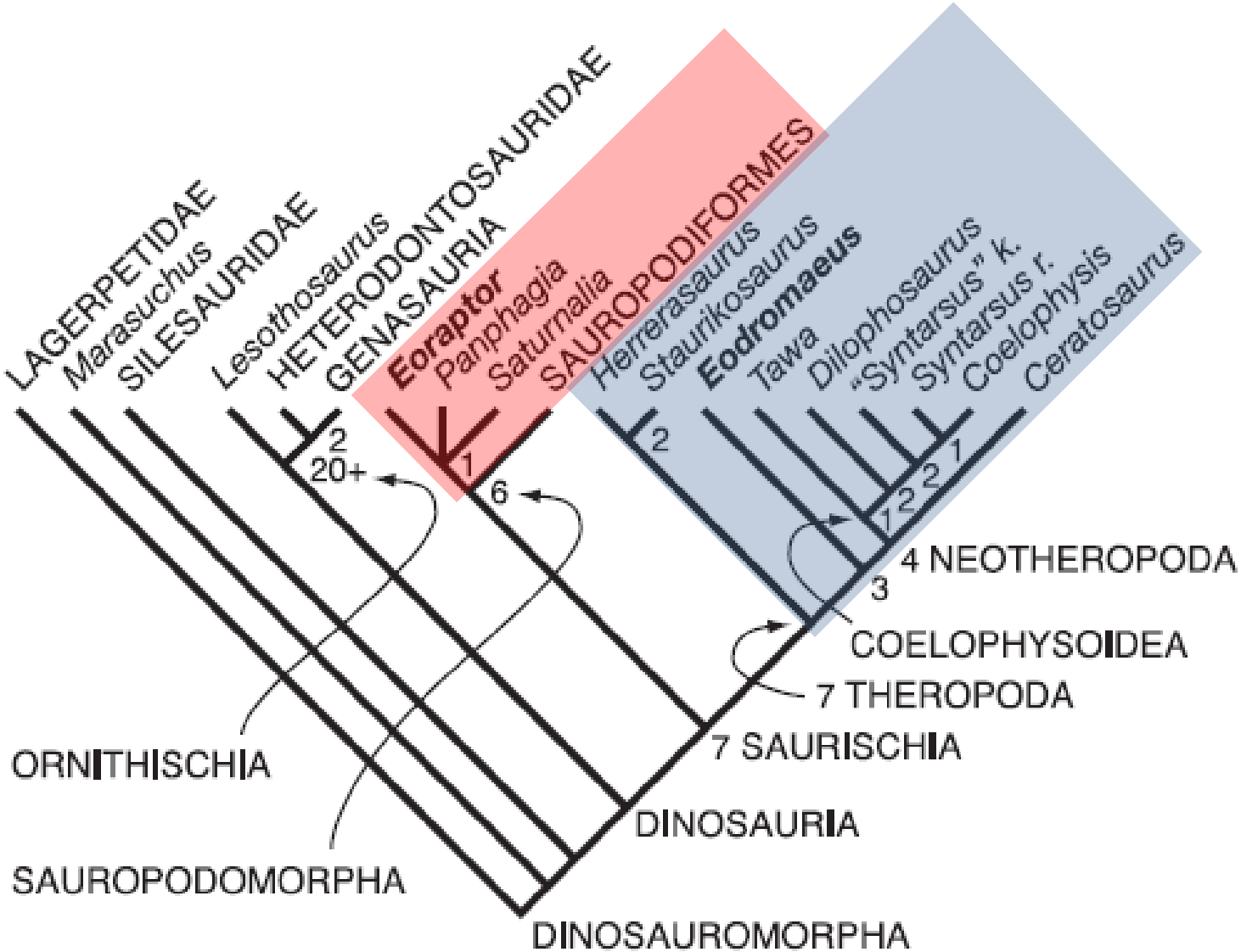
Eodromaeus murphi

Eodromaeus murphi

Eoraptor lunensis

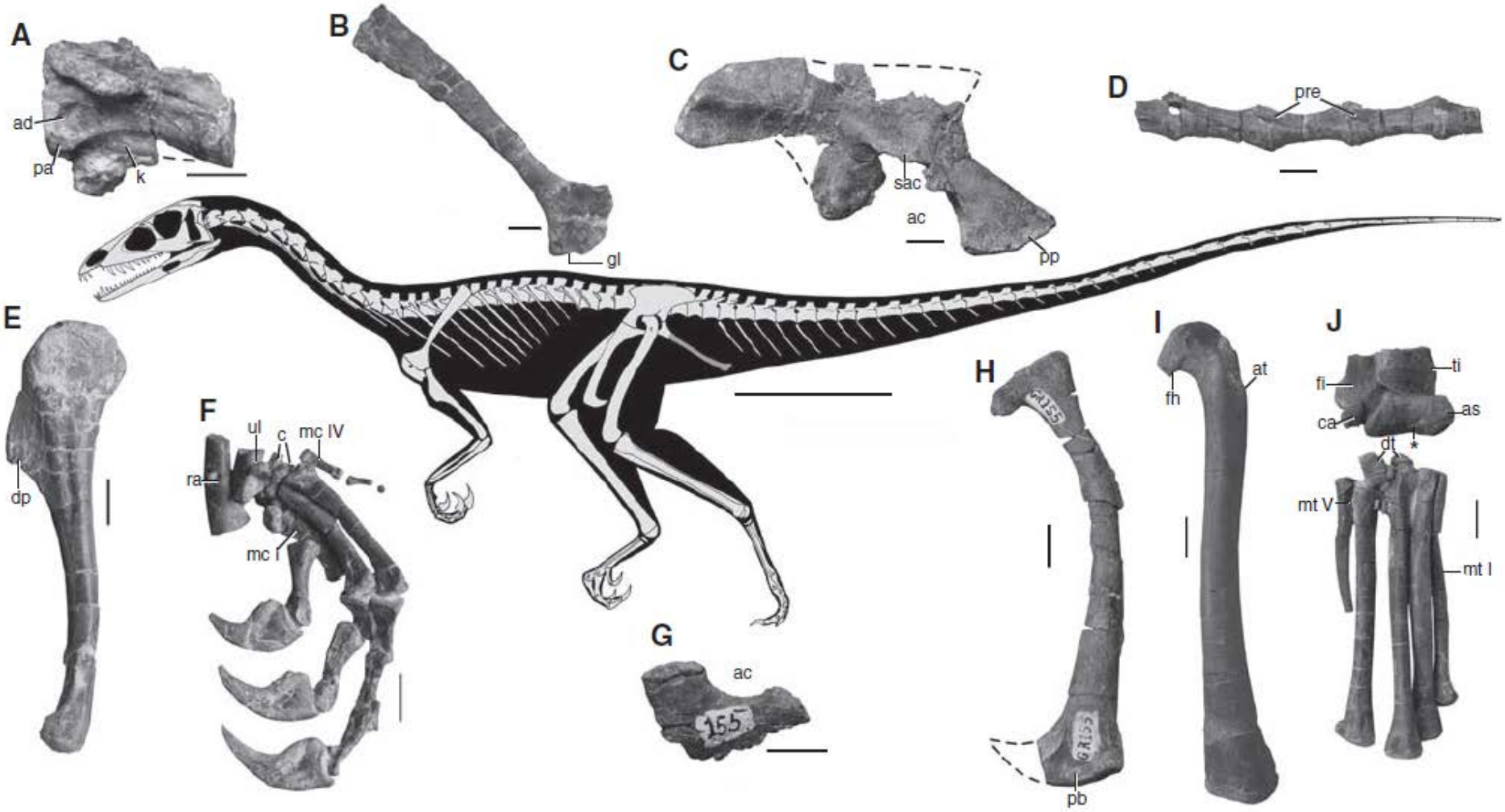


Martínez et al 2011



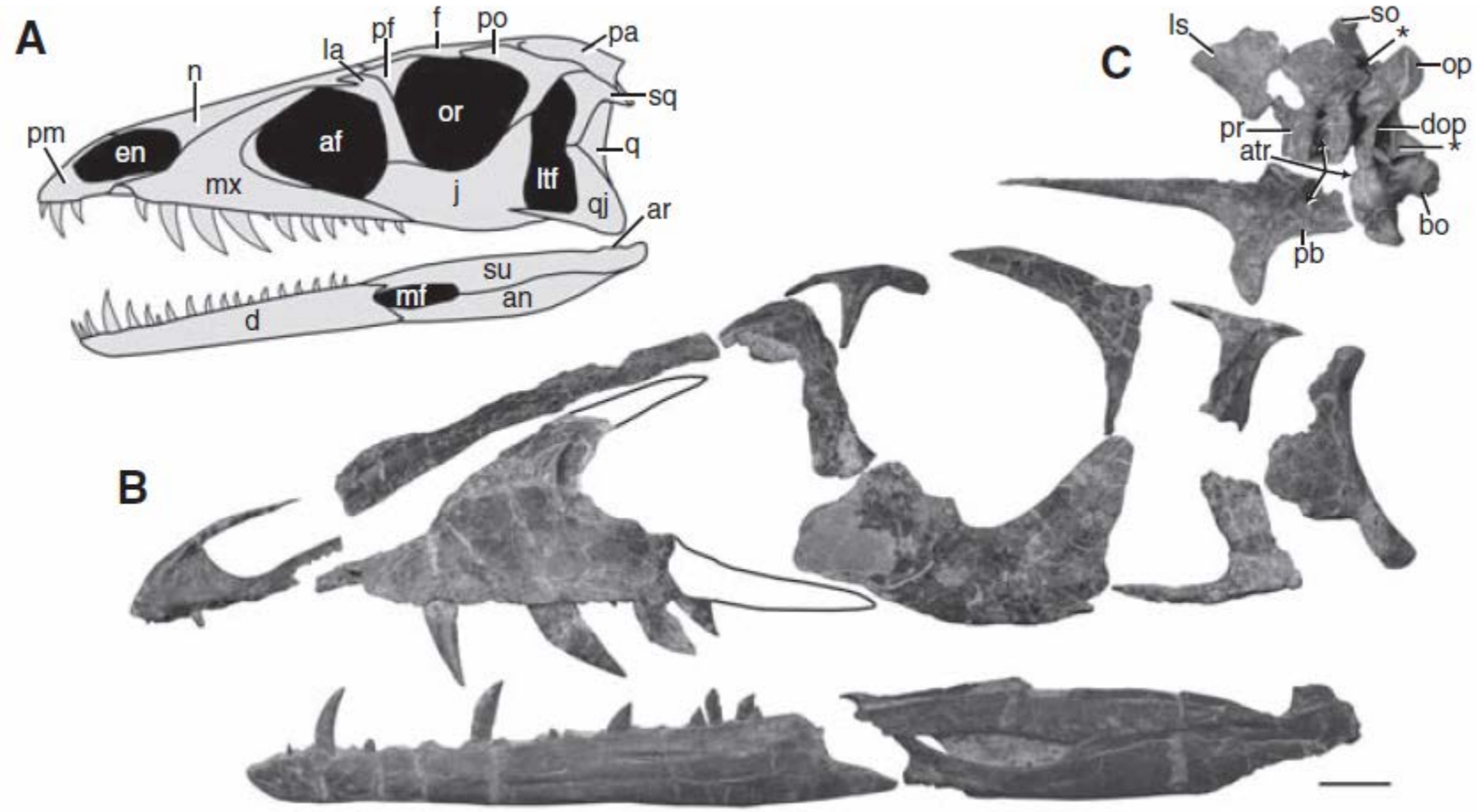
Martínez et al 2011

Tawa hallae



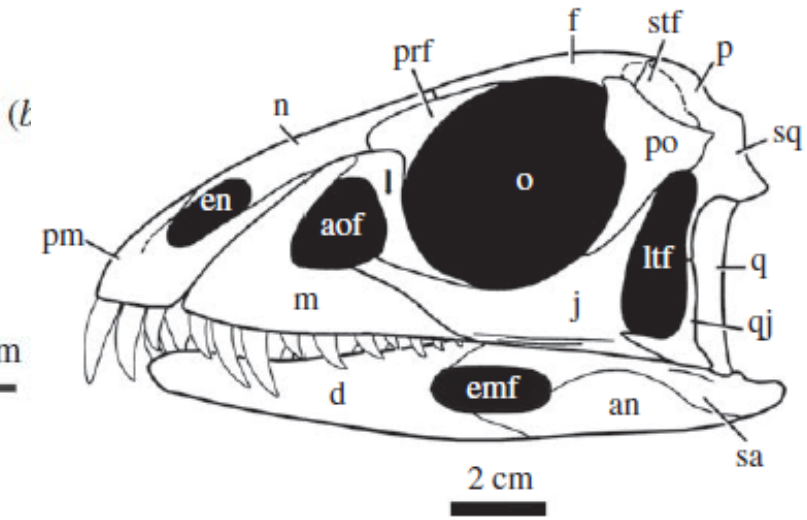
Nesbitt et al, 2009

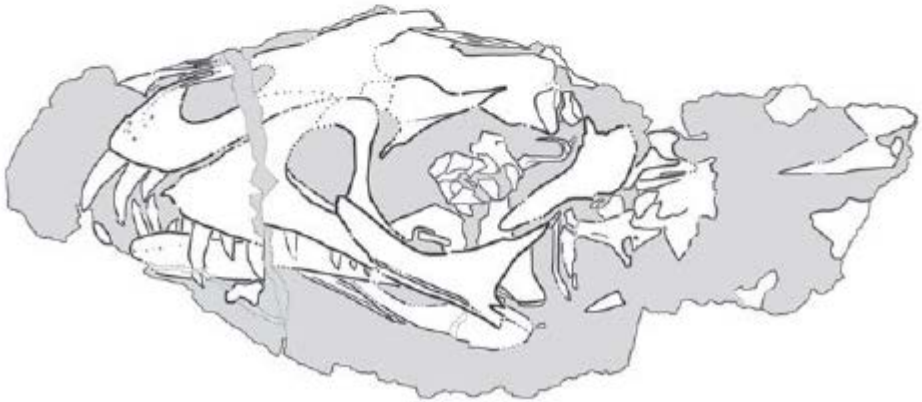
Tawa hallae



Nesbitt et al, 2009

Daimonosaurus chauliodus





Sues et al, 2011

Neotheropoda

-Articulación intramandibular
-Fúrcula
-Pérdida del dedo manual V
-5 o más vertebras sacrales
-Digitos pedales I & V reducidos

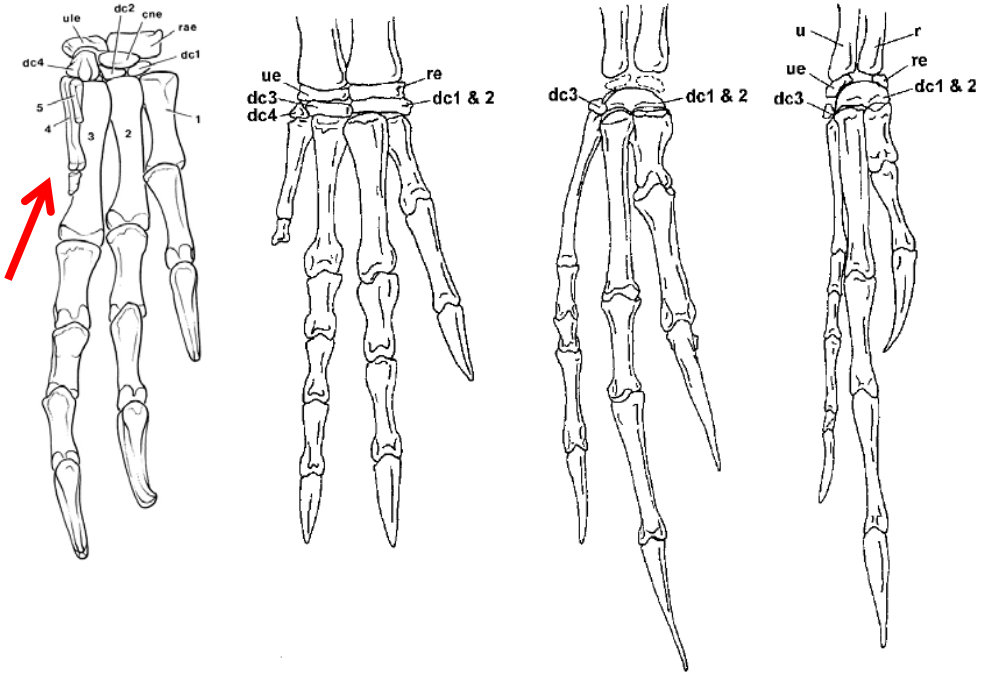


FIGURE 6 The wrists of *Coelophysis*, *Deinonychus*, and *Archaeopteryx* (modified from Colbert and Ostrom).

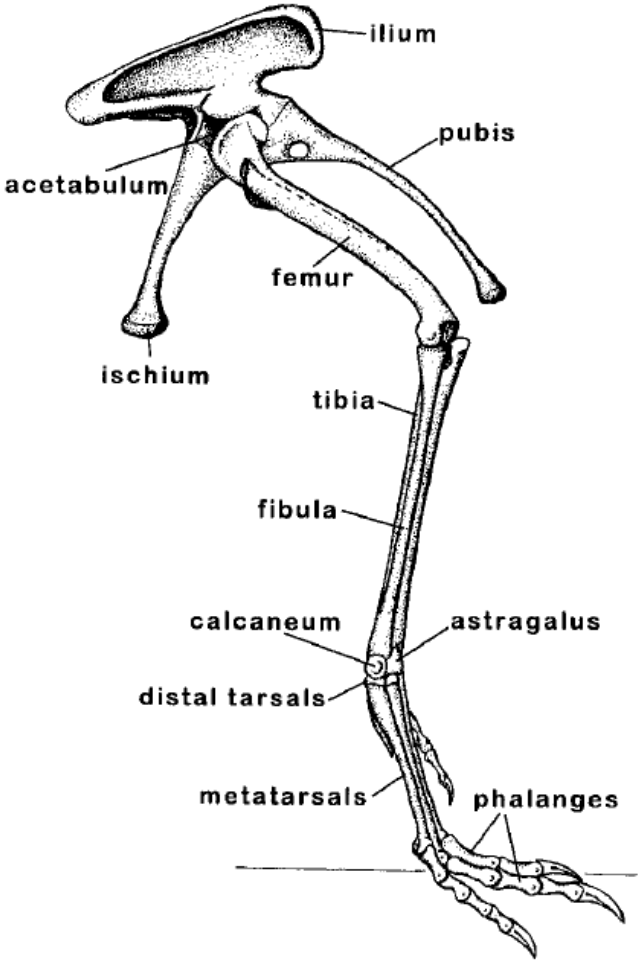
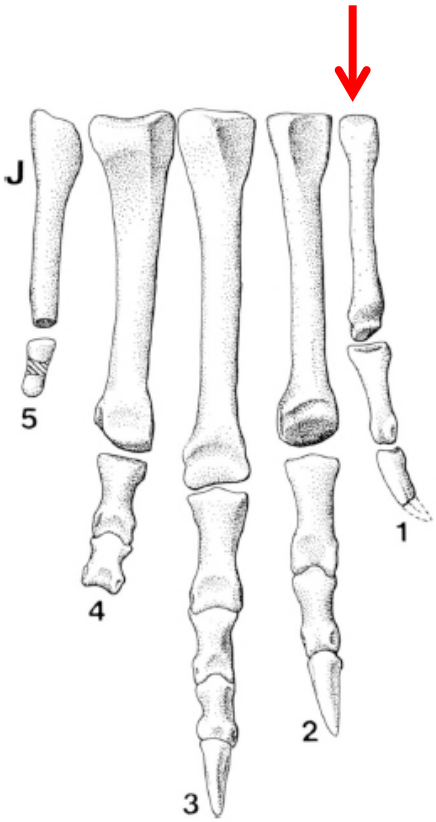
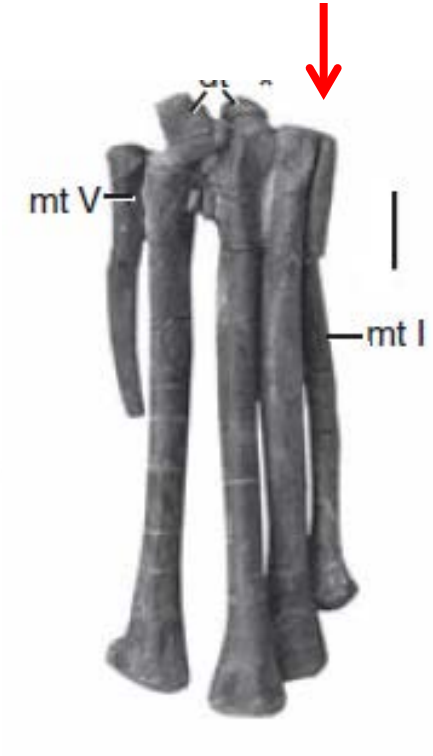


FIGURE 1 Hindlimb of a generalized theropod dinosaur (after *Coelophysis*).

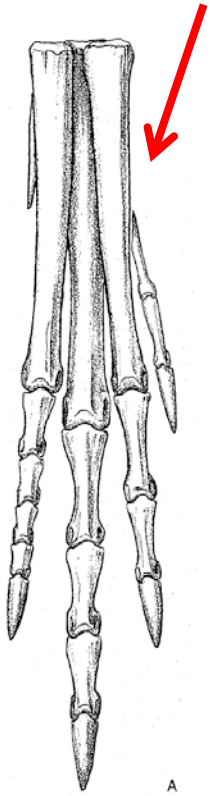
Pérdida del extremo proximal del metatarso I



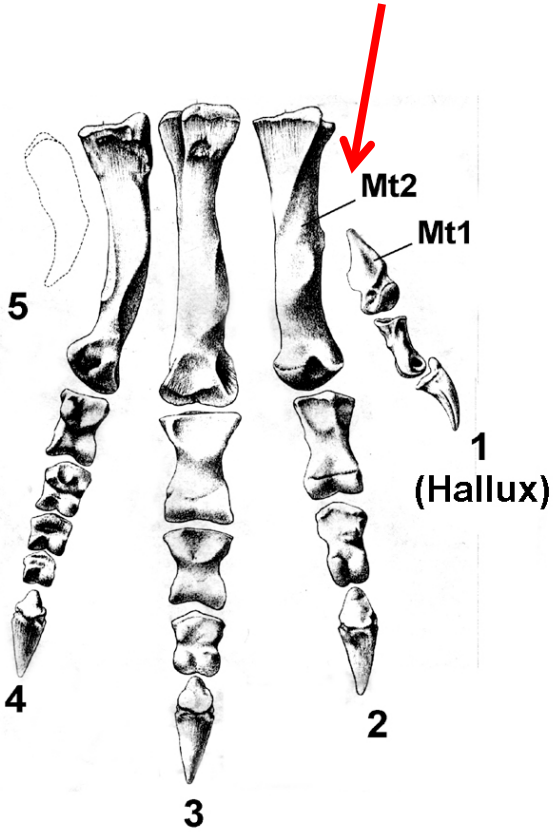
Herrerasaurus



Tawa

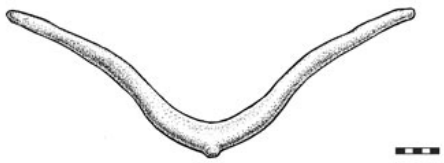


Coelophysis (Neotheropoda)

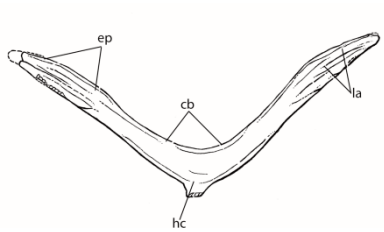


Allosaurus (Neotheropoda)

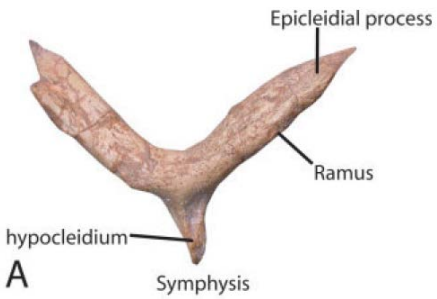
Clavículas medialmente fusionadas forman un nuevo elemento, la **fúrcula** (conservado en aves).
Herrerasaurus, *Eoraptor*, *Eodromaeus* y *Tawa* se desconoce la presencia de fúrcula/clavículas



Coelophysis



Suchomimus



Oviraptor

Bambiraptor

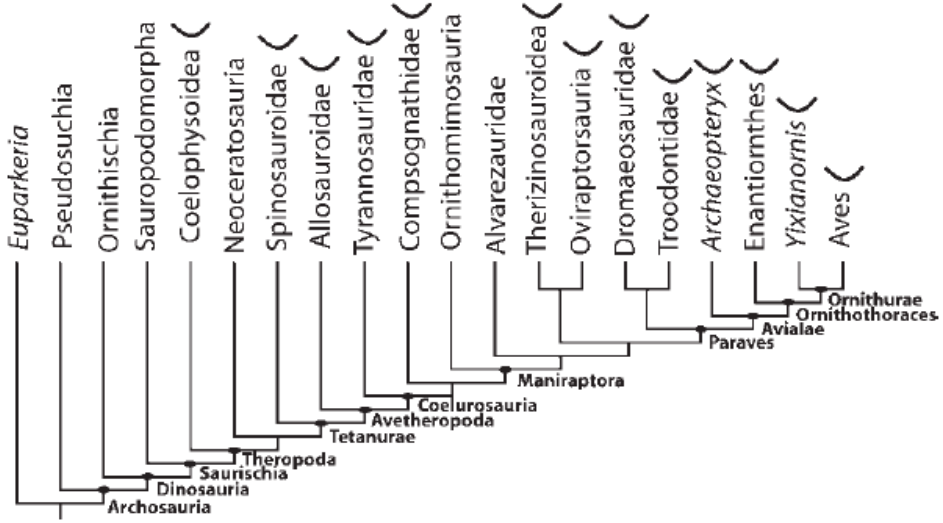
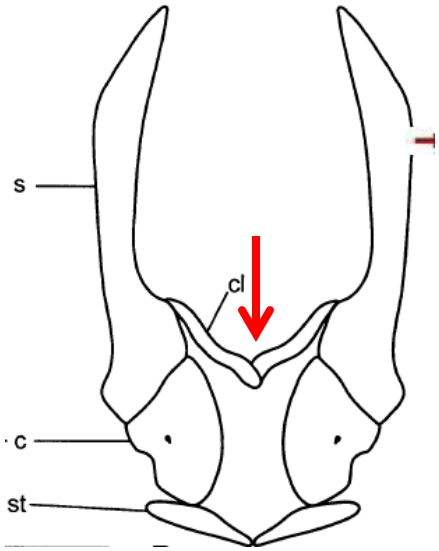


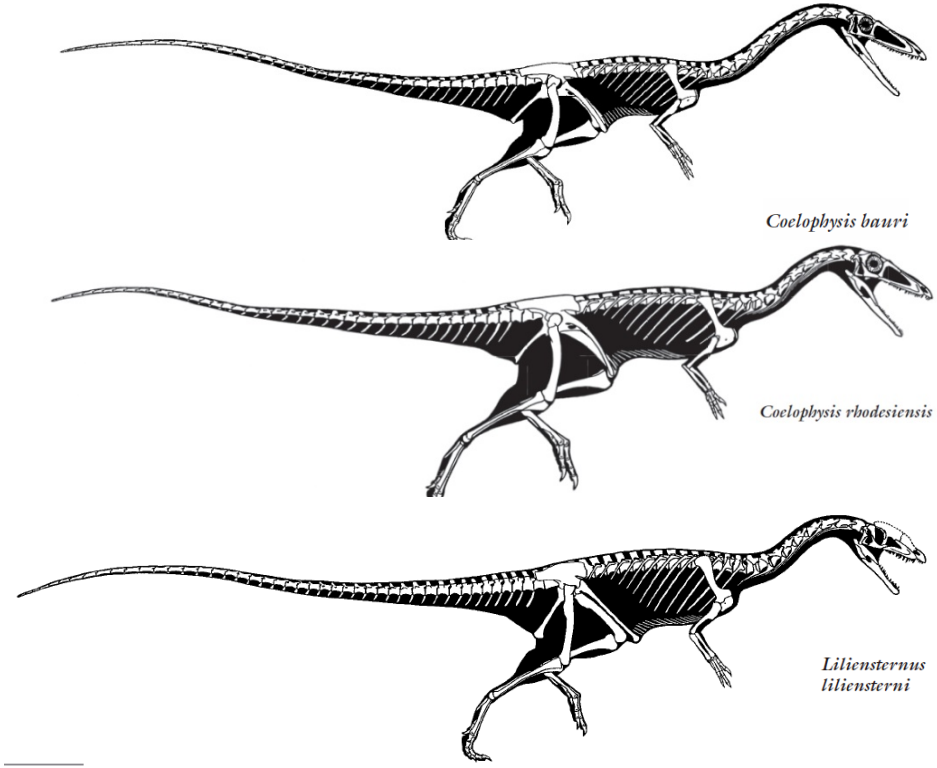
Fig. 1. Relationships among major clades of theropods. Relationships from Smith et al. (2007), the latest TWiG matrix in Turner et al. (2007a), and Clarke et al. (2006). The small furcula symbol indicates which clades have at least one member with an unambiguous furcula.



Plateosaurus

Lipkin et al, 2007; Nesbitt et al, 2009;
Yates and Vasconcelos, 2005

Coelophysoidea



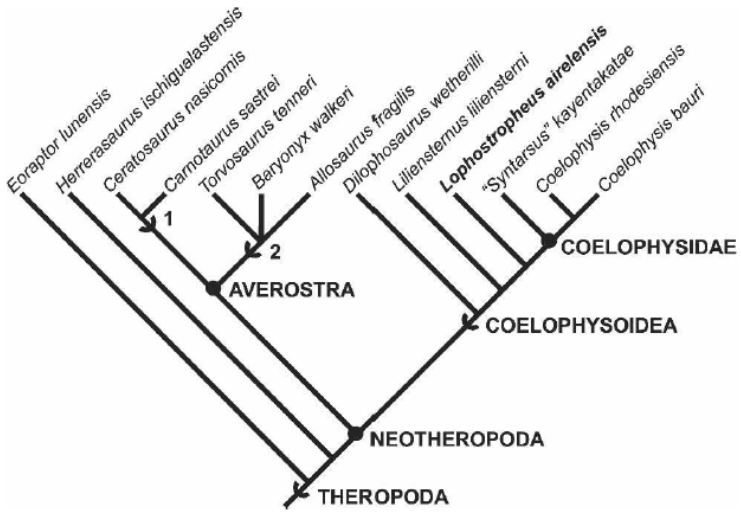
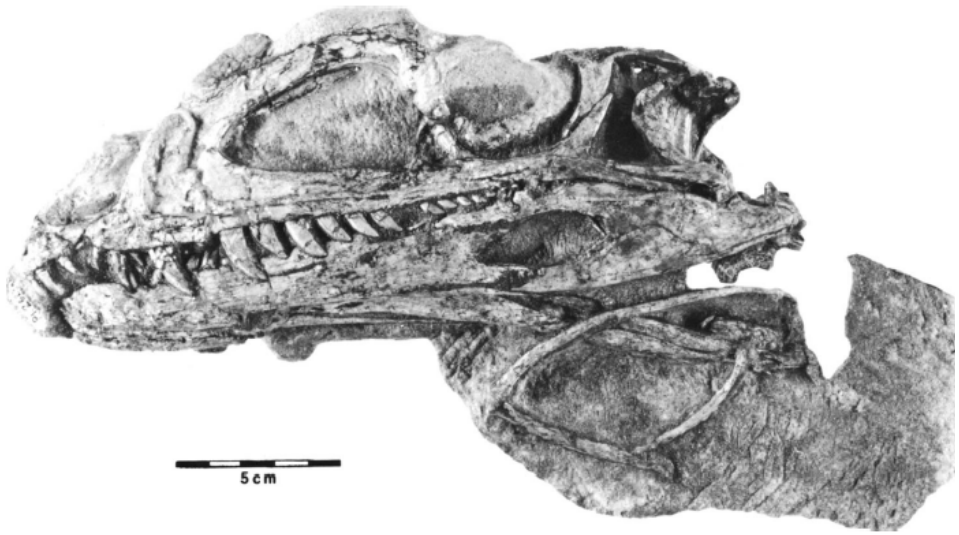
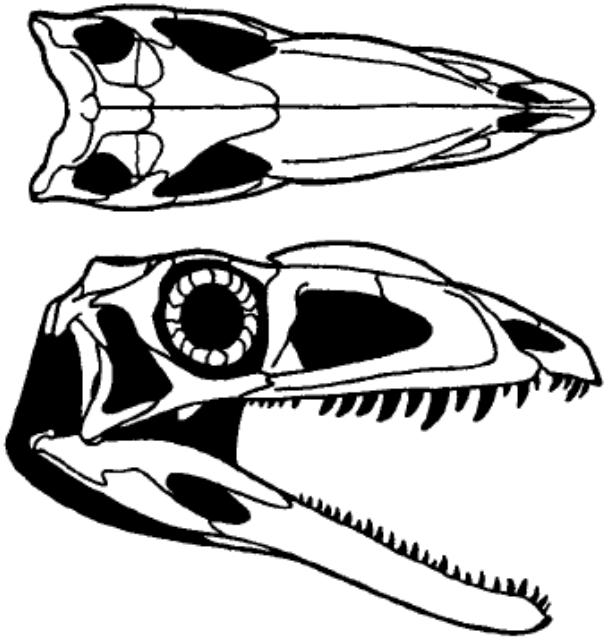


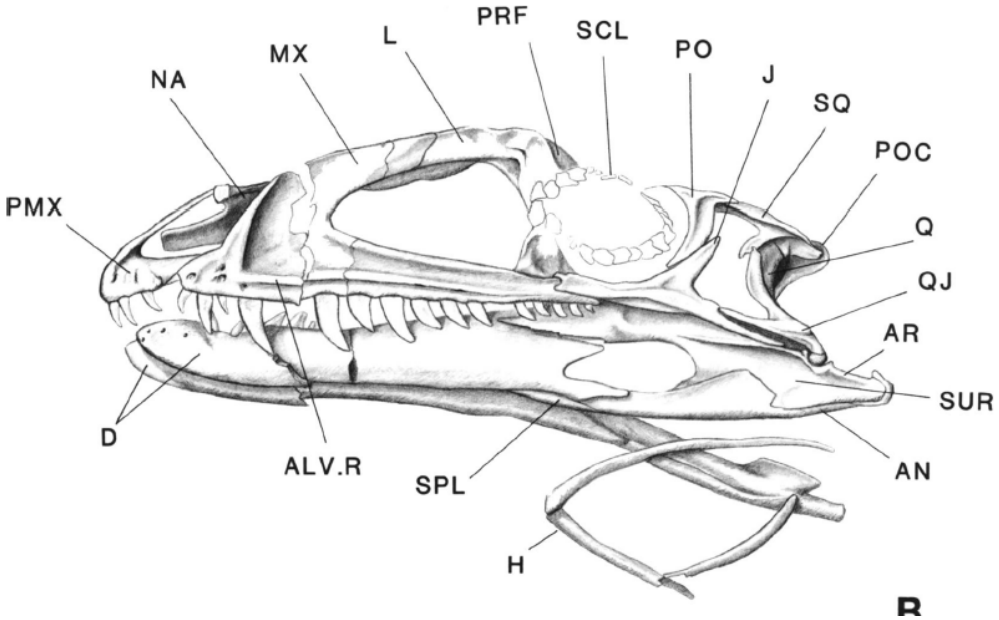
FIGURE 6. Cladogram showing the phylogenetic relationships of *Lophostropheus airelensis* among neotheropod dinosaurs. Strict consensus tree resulting from the analysis of the data matrix composed by cranial and post-cranial characters, length 295 steps, C.I. 0.61 and R.I. 0.74. Stem-based clades are indicated by arches and node-based clades are indicated by circles at the root of the node. **References**: **1**, Ceratosauria, and **2**, Tetanurae.

Los Coelophysoidea son más basales y antiguos y representan mejor el probable aspecto del ancestro de los Neotheropoda. Se caracterizan por un espacio o "muesca" entre los dientes del premaxilar y el maxilar. Destacan la agilidad, el cuello retráctil en forma de "s" y la cabeza liviana, especializado en la captura de presas más pequeñas, como ocurre en muchas aves actuales

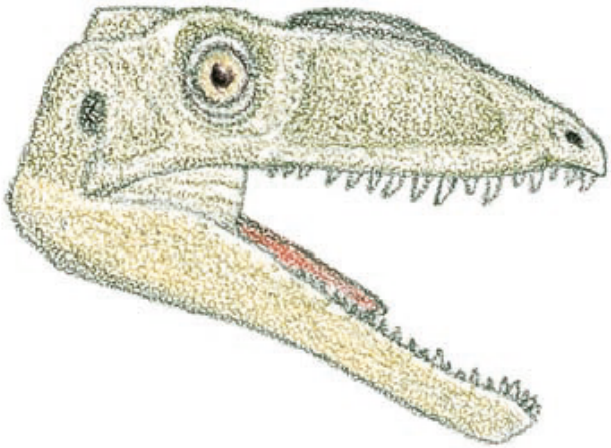
Megapnosaurus kayentakatae



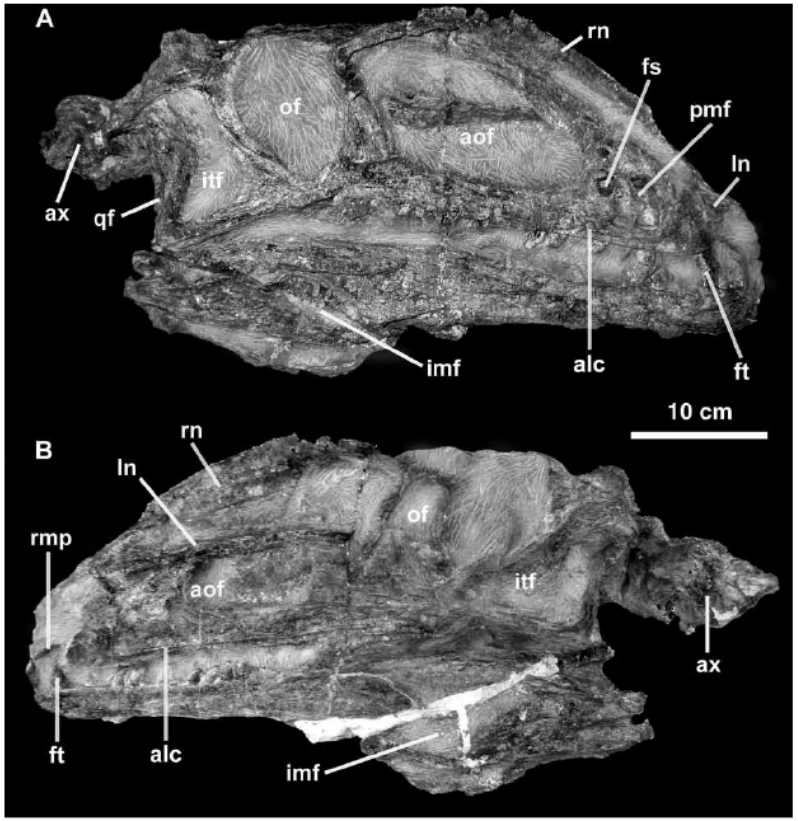


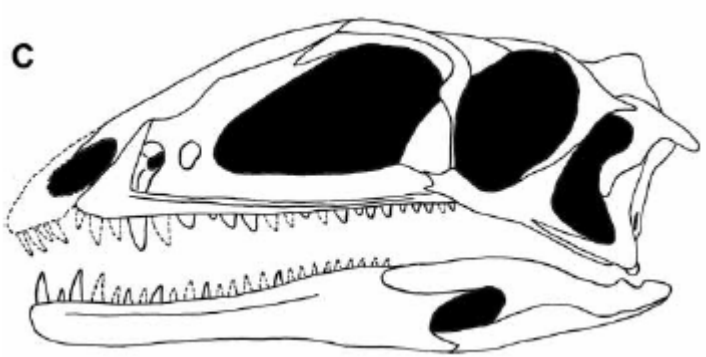


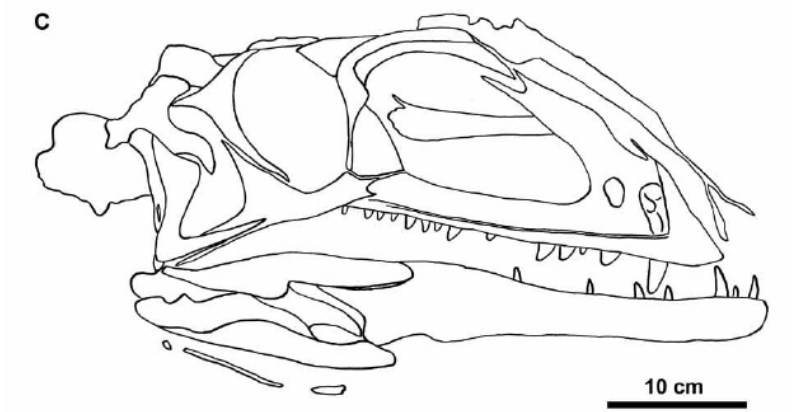
Coelophysis? kayentakatae skull and head

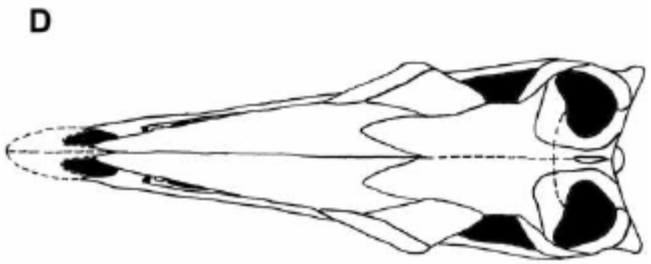


Zupaysaurus rougieri

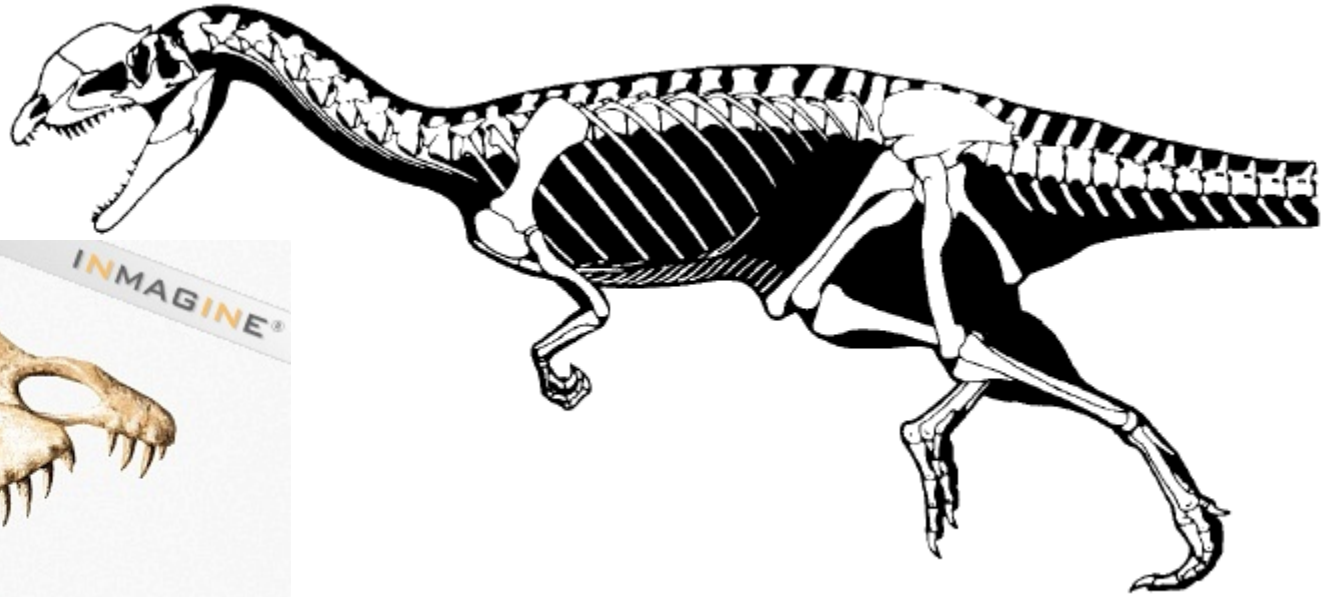


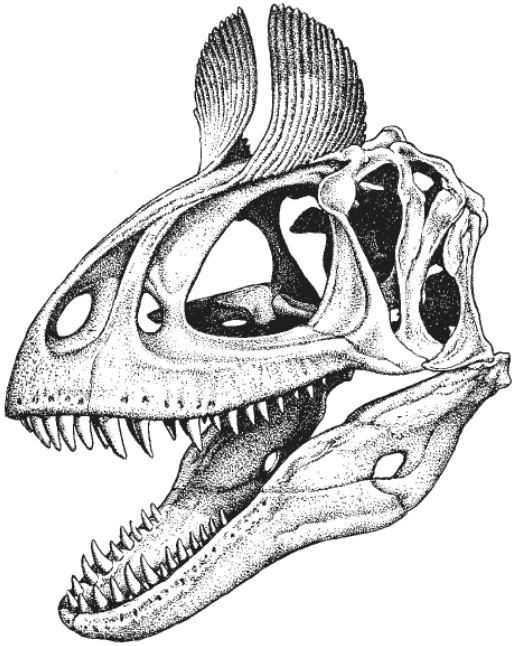






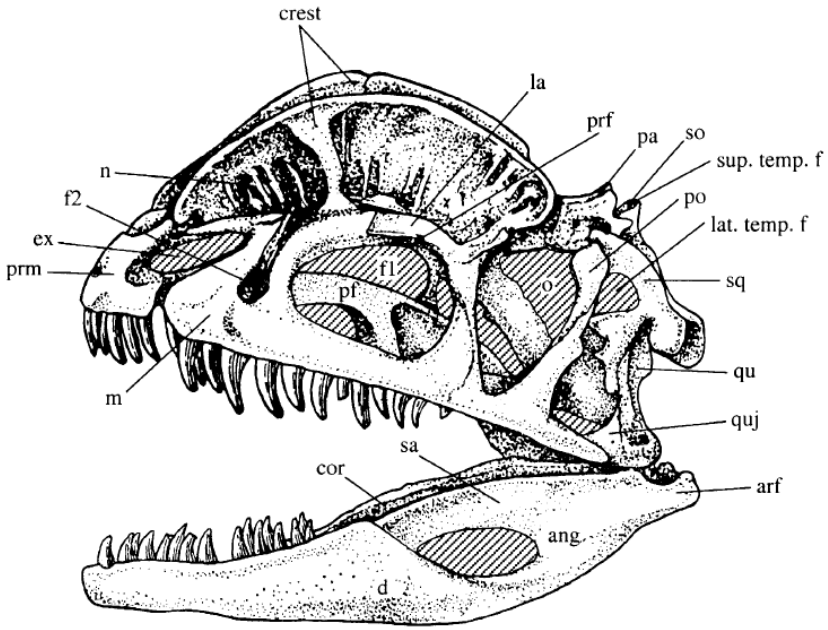
Dilophosaurus wetherilli

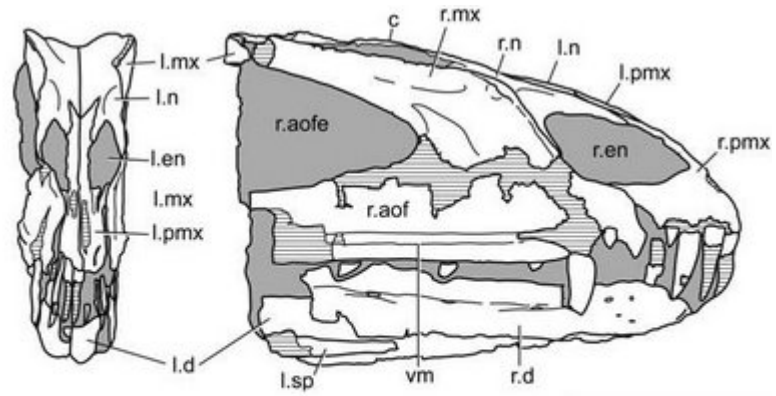




Cryolophosaurus ellioti

Figure 9.24. The skull of *Cryolophosaurus*, with its distinctive crest.

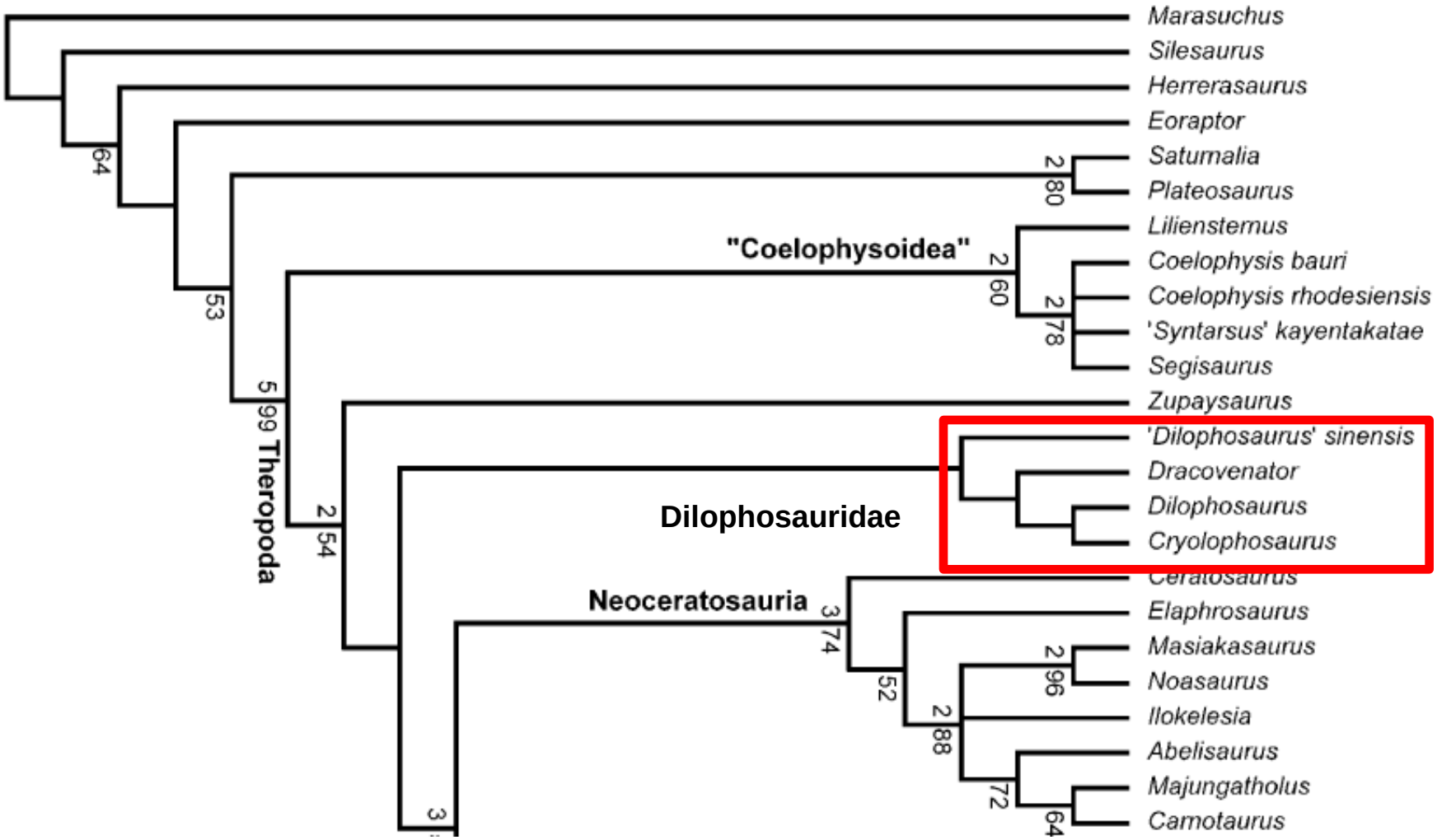




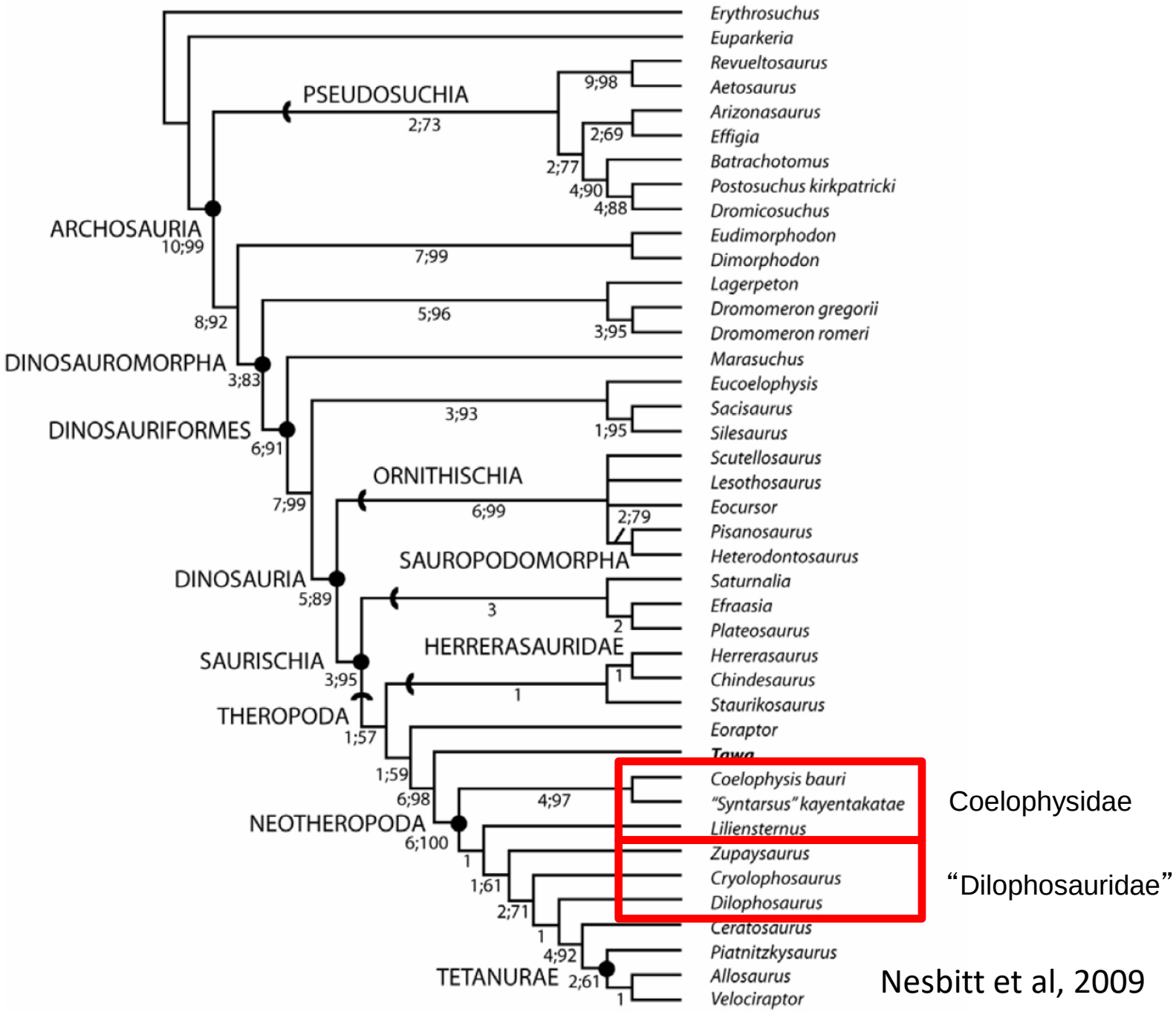
BP/1/5278 (juvenile Dracovenator regenti?)
From Yates, 2005

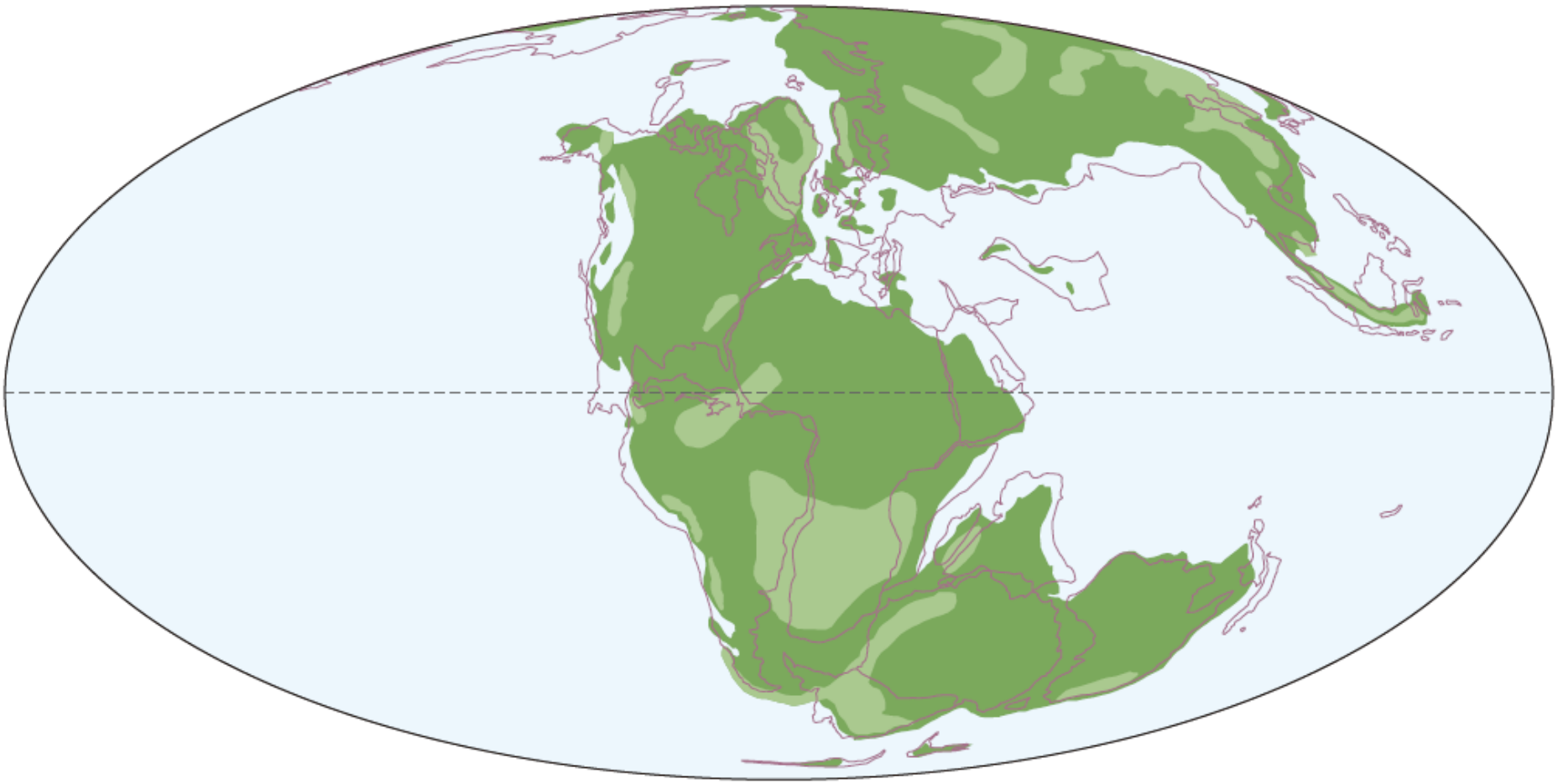
"Dilophosaurus"sinensis

Dracovenator regenti



Smith et al, 2007

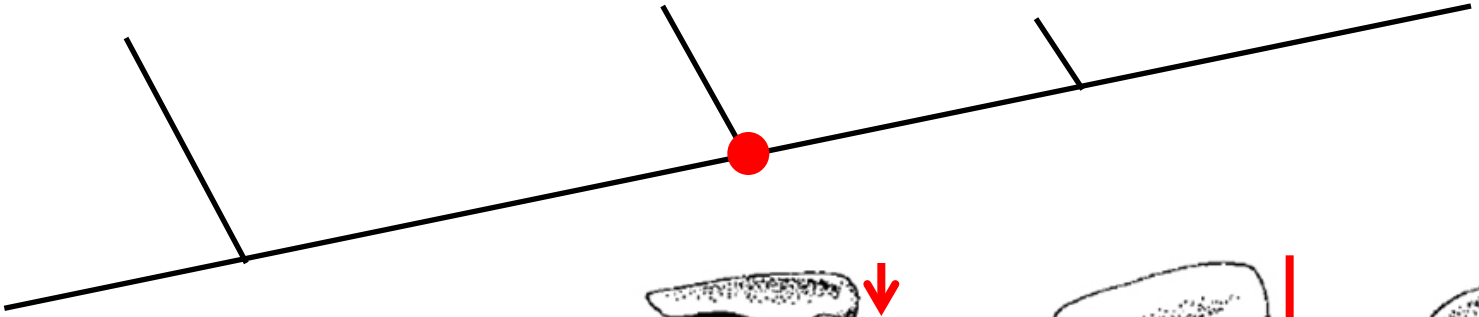

Erythrosuchus
Euparkeria
Revueltosaurus
Aetosaurus
Arizonasaurus
Effigia
Batrachotomus
Postosuchus kirkpatricki
Dromicosuchus
Eudimorphodon
Dimorphodon
Lagerpeton
Dromomeron gregorii
Dromomeron romeri
Marasuchus
Eucoelophysis
Sacisaurus
Silesaurus
Scutellosaurus
Lesothosaurus
Eocursor
Pisanosaurus
Heterodontosaurus
Saturnalia
Efraasia
Plateosaurus
Herrerasaurus
Chindesaurus
Staurikosaurus
Eoraptor
Tawa
Coelophysis bauri
"Syntarsus" kayentakatae
Liliensternus
Zupaysaurus
Cryolophosaurus
Dilophosaurus
Ceratosaurus
Piatnitzkysaurus
Allosaurus
Velociraptor
PSEUDOSUCHIA
2;73
9;98
2;69
2;77
4;90
4;88
ARCHOSAURIA
10;99
7;99
8;92
5;96
3;95
DINOSAUROMORPHA
3;83
3;93
1;95
DINOSAURIFORMES
6;91
ORNITHISCHIA
7;99
6;99
2;79
SAUROPODOMORPHA
DINOSAURIA
5;89
3
2
HERRERASAURIDAE
SAURISCHIA
3;95
1
1
THEROPODA
1;57
1;59
6;98
4;97
NEOTHEROPODA
6;100
1
1;61
2;71
1
4;92
TETANURAE
2;61
1
Coelophysidae
"Dilophosauridae"
Nesbitt et al, 2009

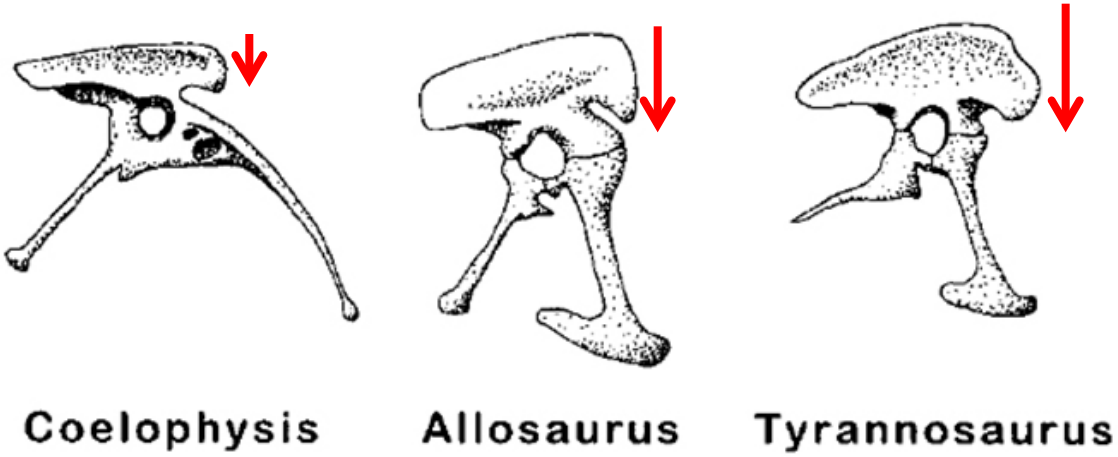


Early Jurassic (Sinemurian)

Averostra

Clado menos inclusivo que contiene a *Ceratosaurus nasicornis*, *Allosaurus fragilis*, ancestro común más reciente y todos sus descendientes (Ezcurra and cuny, 2007). Incluye los taxa Ceratosauria+Tetanurae.



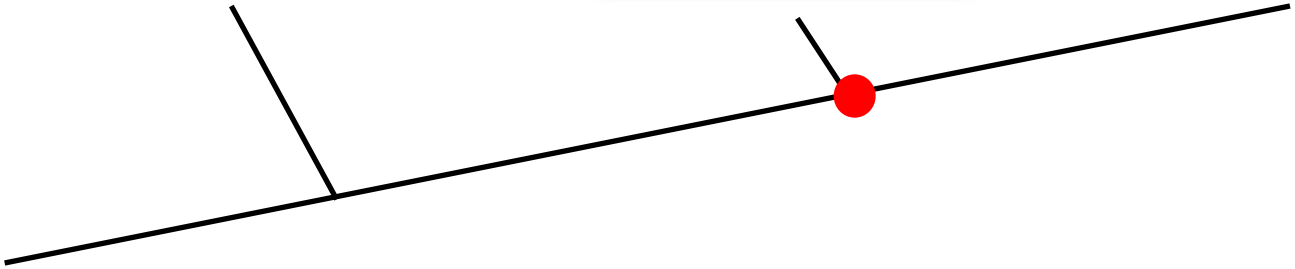


Synapomorfías de Averostra:

- Parte anterior de Ilium expandida

Ceratosauria

Clado más inclusivo que contiene a *Carnotaurus sastrei*, pero no a *Columba livia*



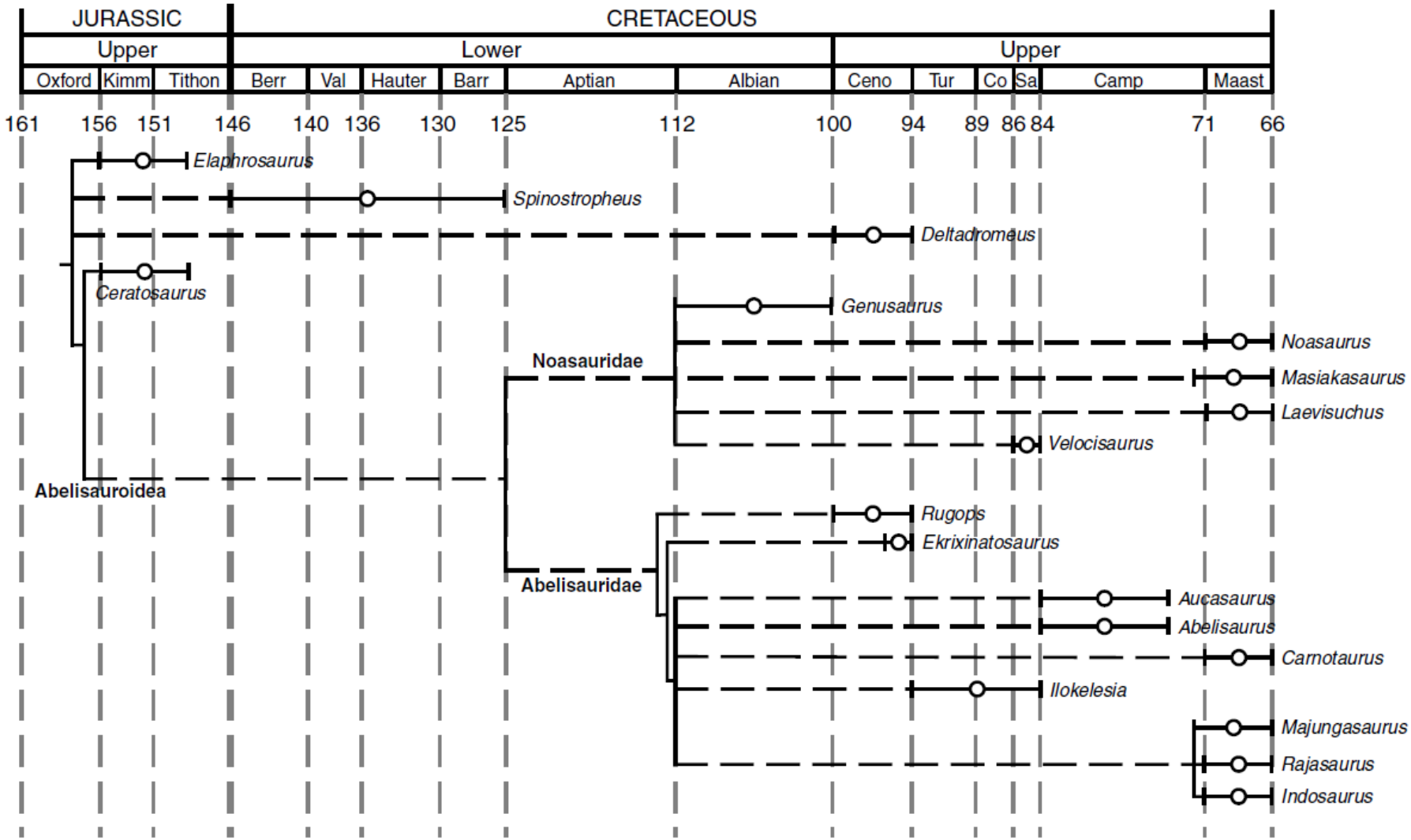


Figure 8 Stratigraphically calibrated phylogeny of Ceratosauria, based on present results (strict consensus). Minimum estimated divergence times are shown, based only on the taxa included in the phylogenetic analysis. Timescale from Gradstein *et al.* (2004). Abbreviations as listed in legend to Fig. 5.

Carrano and Sampson, 2008

Spinostropheus gautieri

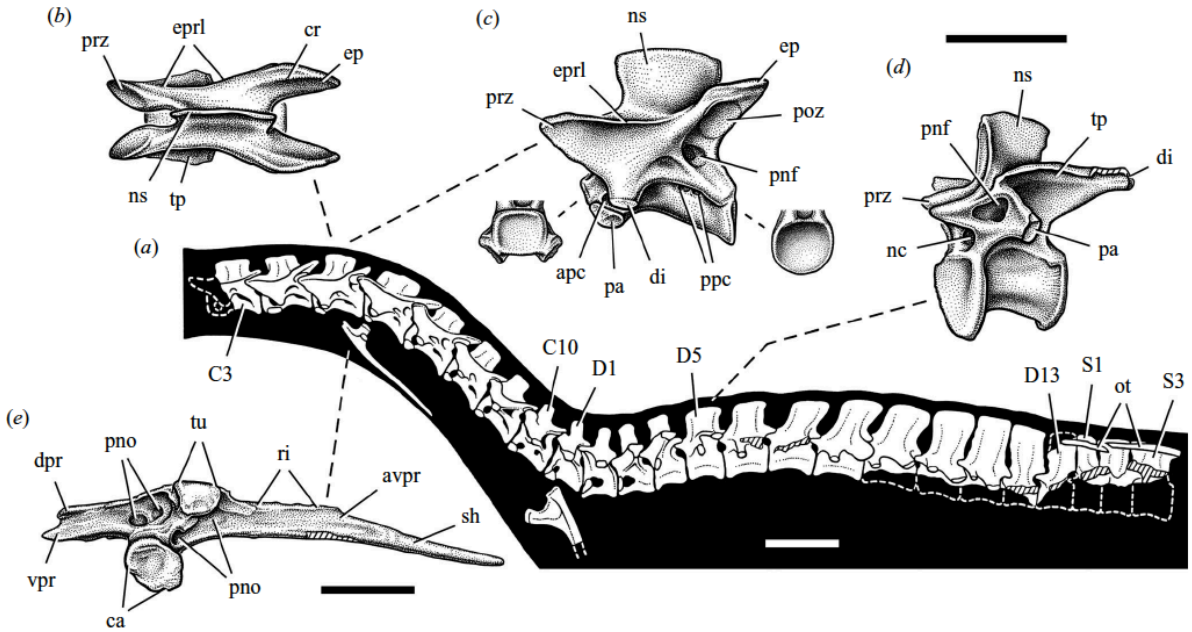
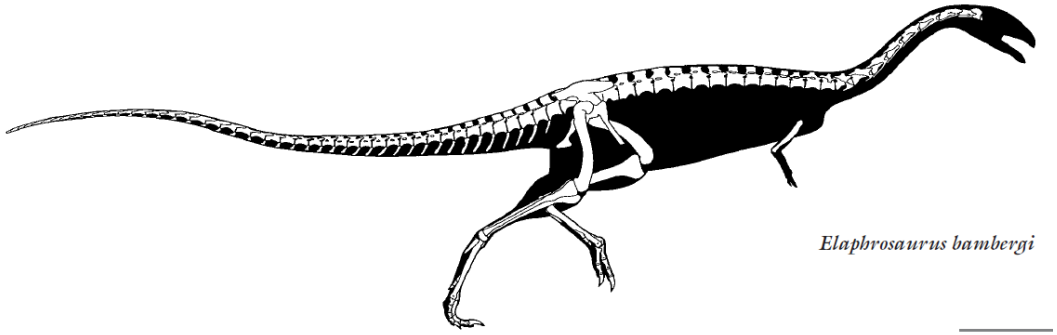
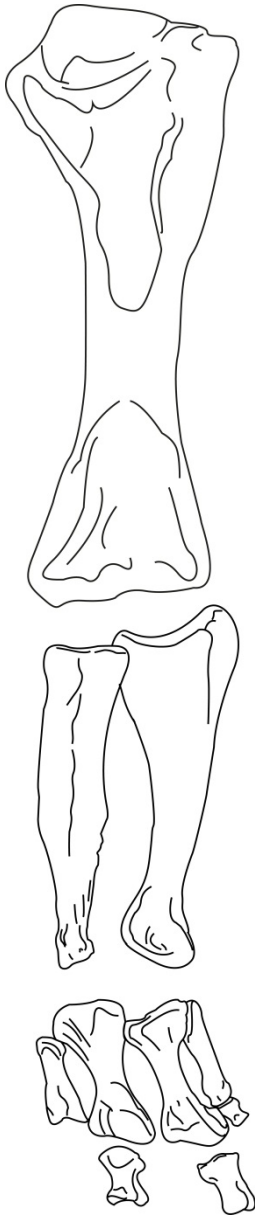
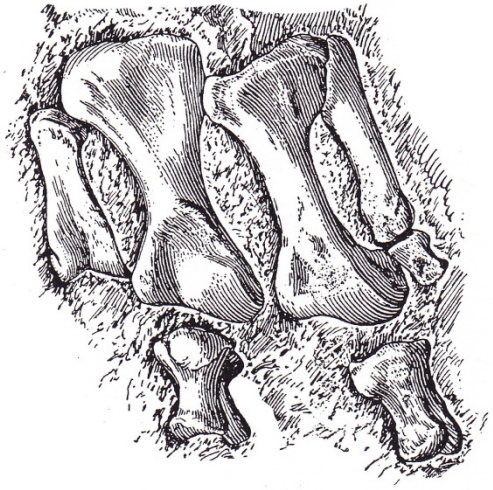


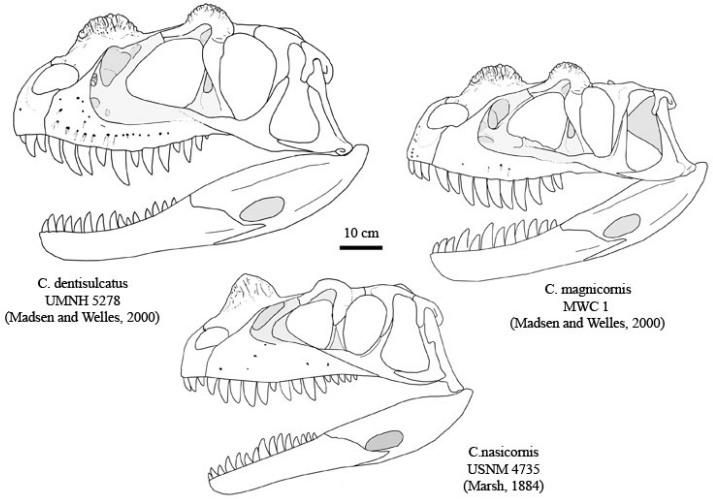
Figure 2. *Spinostropheus gautieri*, basal ceratosaurian (MNN TIG6). (*a*) Silhouette reconstruction in left lateral view based on an articulated presacral column. (*b*) Fifth cervical vertebra in dorsal view. (*c*) Fifth cervical vertebra in lateral view with anterior and posterior views of the articular faces of the centrum. (*d*) Fifth dorsal vertebra in anterolateral view. (*e*) Mid-cervical rib (reversed from left) in dorsomedial view. Cross-hatching indicates broken bone. Scale bars: (*a*) 10 cm; (*b*)–(*d*) 5 cm; (*e*) 2 cm. Abbreviations: 1–15, vertebral number; apc, anterior pleurocoel; avpr, articular surface for succeeding ventral process; C, cervical; ca, capitulum; cr, crest; D, dorsal; di, diapophysis; dpr, dorsal process; ep, epipophysis; eprl, epipophyseal-prezygapophyseal lamina; nc, neural canal; ns, neural spine; ot, ossified tendon; pa, parapophysis; ppc, posterior pleurocoel; pnf, pneumatic fossa; pno, pneumatic opening; poz, postzygapophysis; prz, prezygapophysis; ri, ridge; S, sacral; sh, shaft; tp, transverse process; tu, tuberculum; vpr, ventral process.

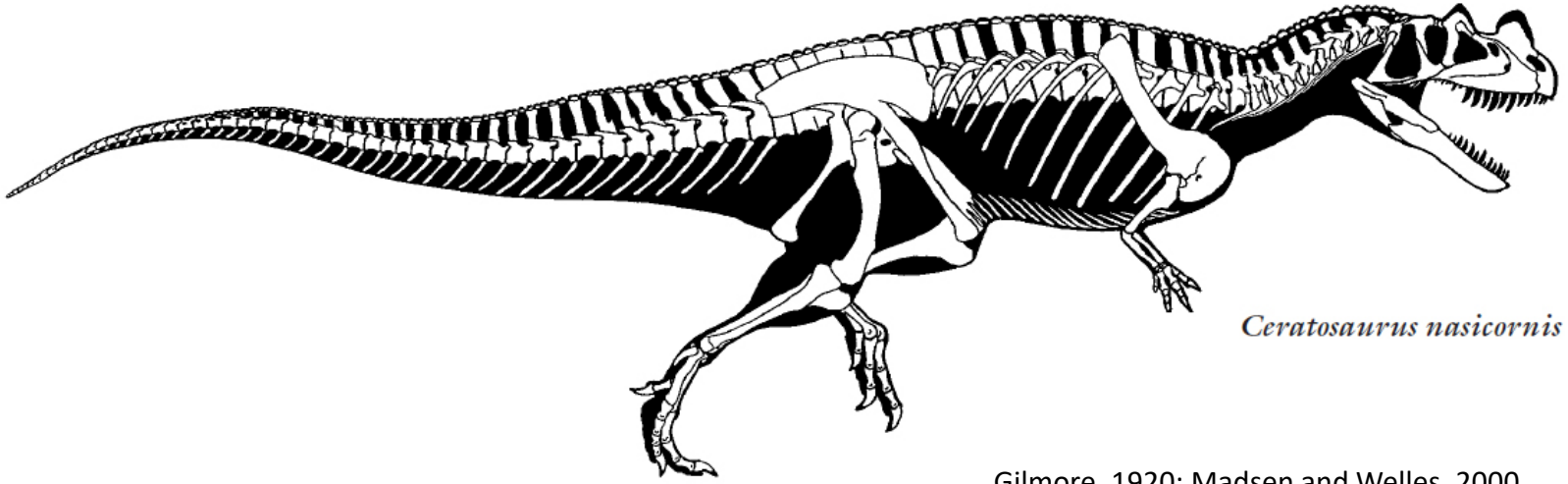


Ceratosaurus nasicornis



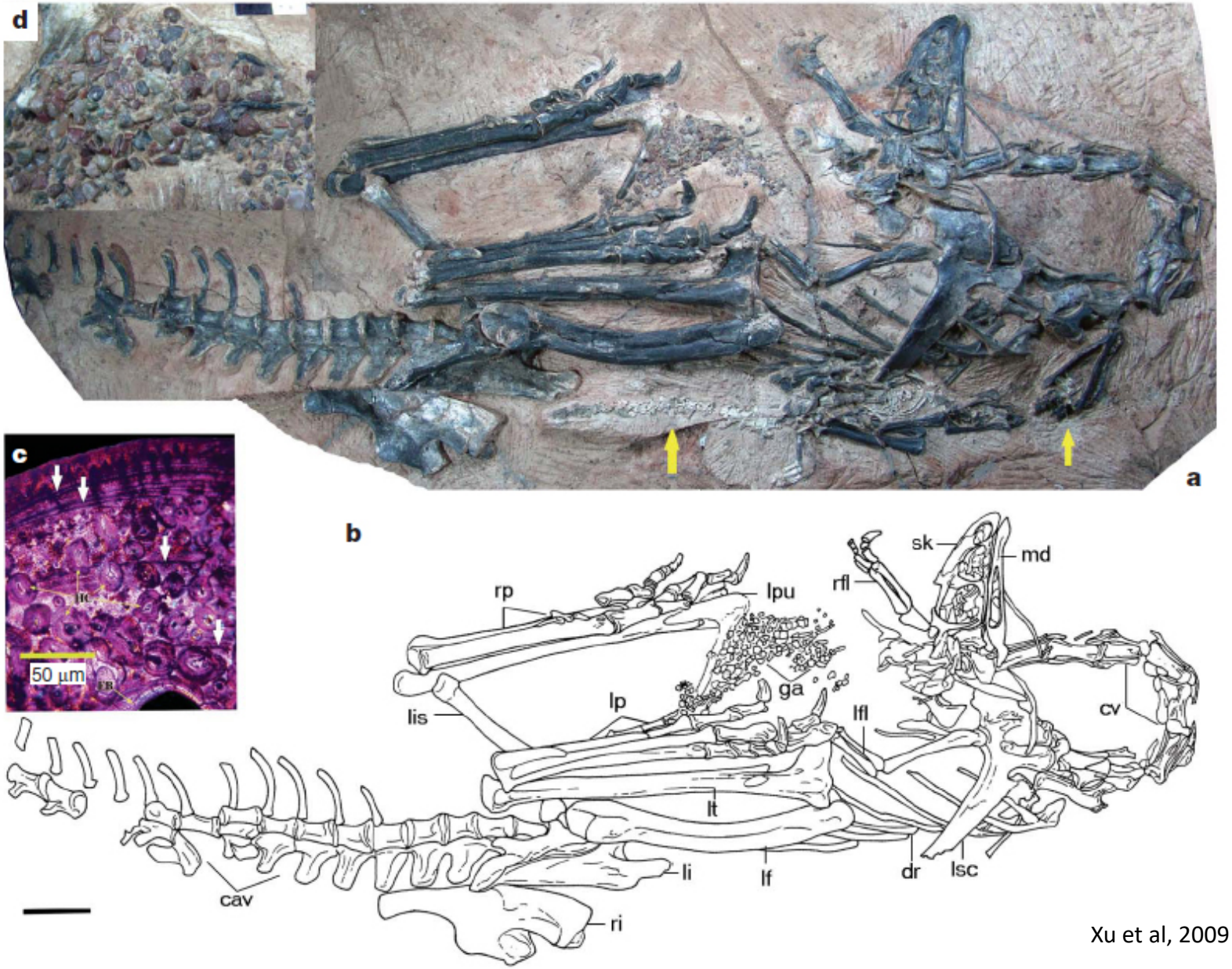






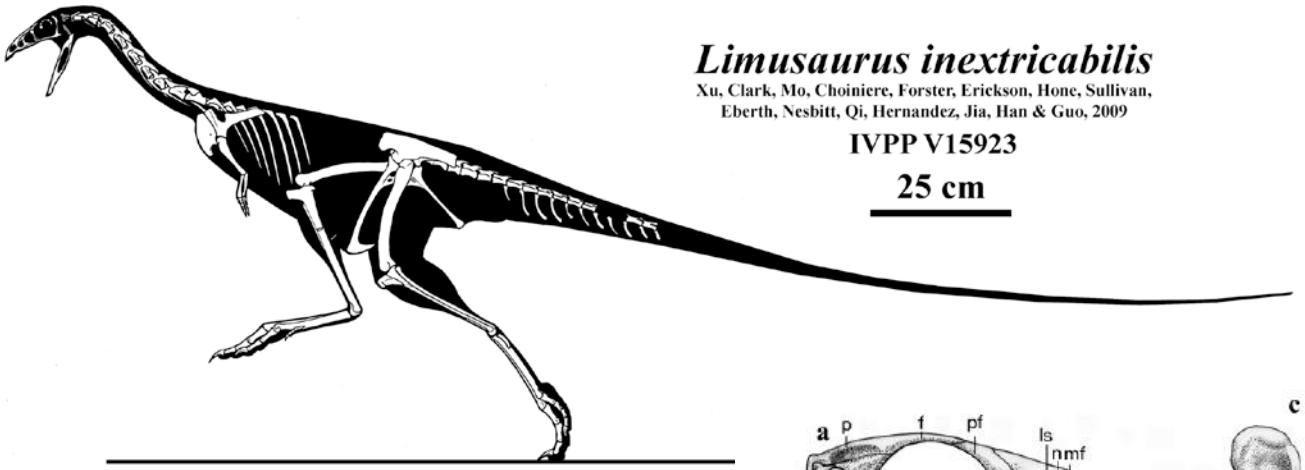
Gilmore, 1920; Madsen and Welles, 2000

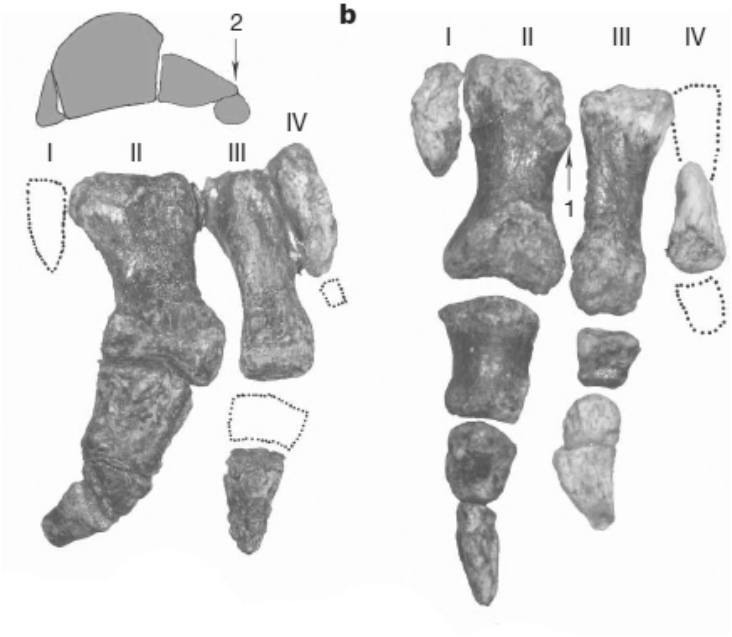
Limusaurus inextricabilis

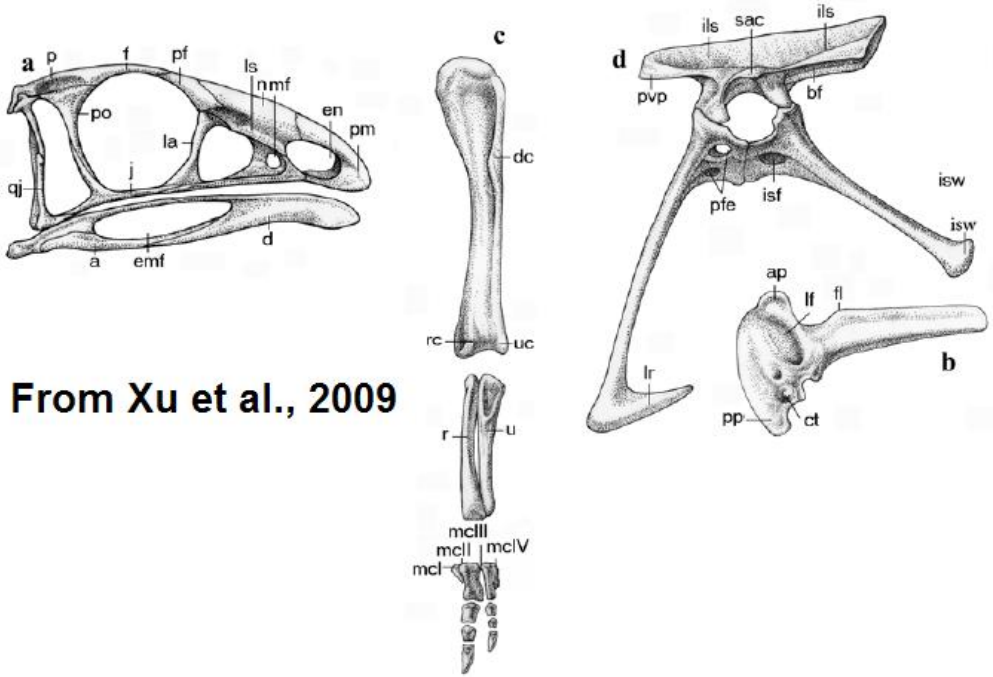


Xu et al, 2009

Xu et al, 2009







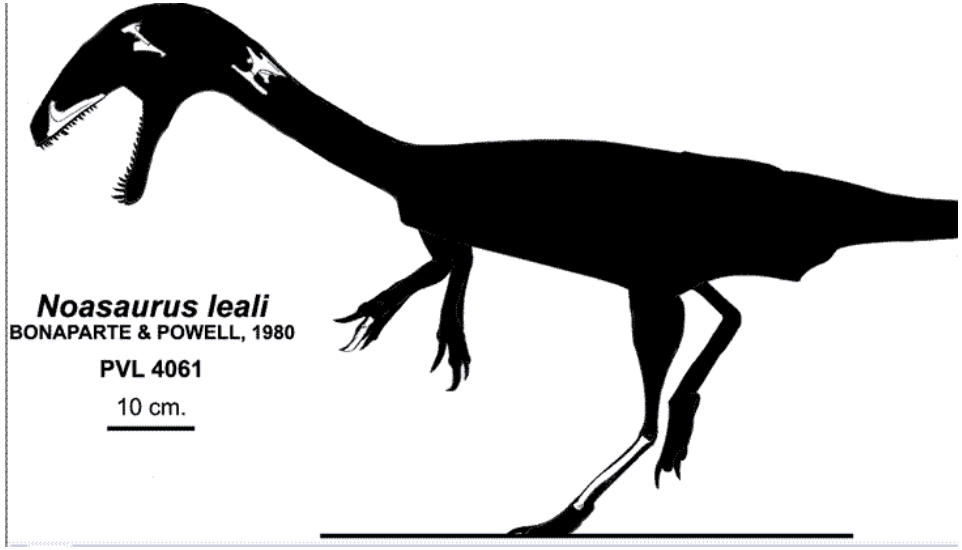
From Xu et al., 2009

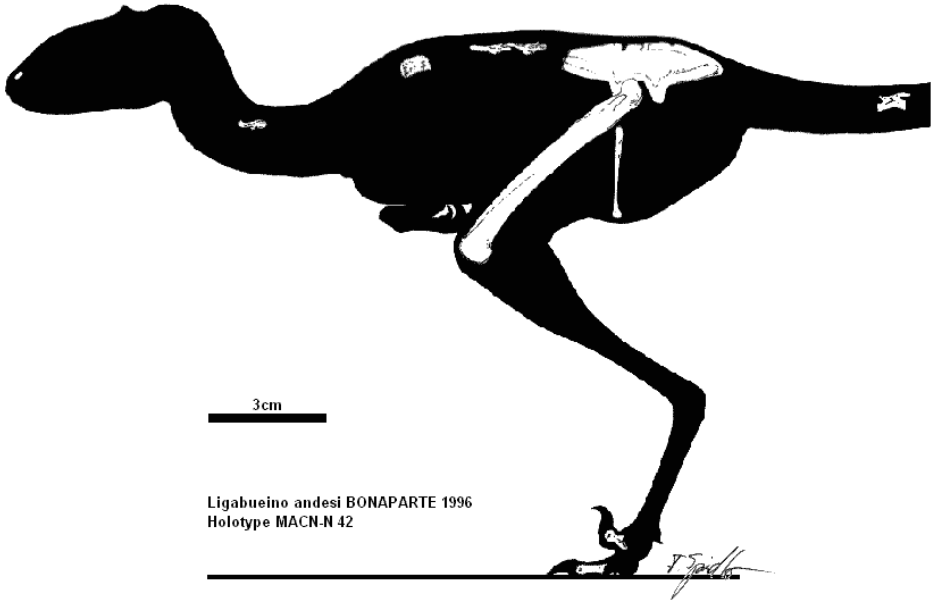
Figure S1. *Limusaurus inextricabilis* selected elements. **a**, Skull in lateral view; **b**, Left scapulocoracoid in lateral view; **c**, Left manus in dorsal view; **d**, Pelvis in lateral view. Abbreviations: a, angular; ap, acromion process; bf, brevis fossa; ct, coracoid tubercle; d, dentary; dc, deltopectoral crest; emf, external mandibular fenestra; en, external naris; f, frontal; fl, flange; lf, longitudinal furrow; ils, lateral shelf on ilium; ?isf, ischial foramen; lr, lateral ridge; ls, lateral shelf; mcI-IV, metacarpals I-IV; mf, maxillary fenestra; n, nasal; p, parietal; pf, prefrontal; pfe, pubic fenestra; pm, premaxilla; po, postorbital; pp, posterior process; qj, quadratojugal; r, radius; rc, radial condyle; sac, supraacetabular process; u, ulna; uc, ulnar condyle.

Noasauridae

Noasauridae es un supuesto grupo hermano de los Abelisauridae, conocidos solo por especies fragmentarias. Hay débil apoyo para la existencia de un grupo monofilético, pero poco conflicto de ragsos con esta hipótesis. Comparten con Abelisauridae la presencia una cresta en el femur y procesos especiales en las vértebras, por lo que se habla de un clado Abelisauroidea: Abelisauridae + Noasauridae

Húmero más esbelto que en Abelisauridae





Masiakasaurus

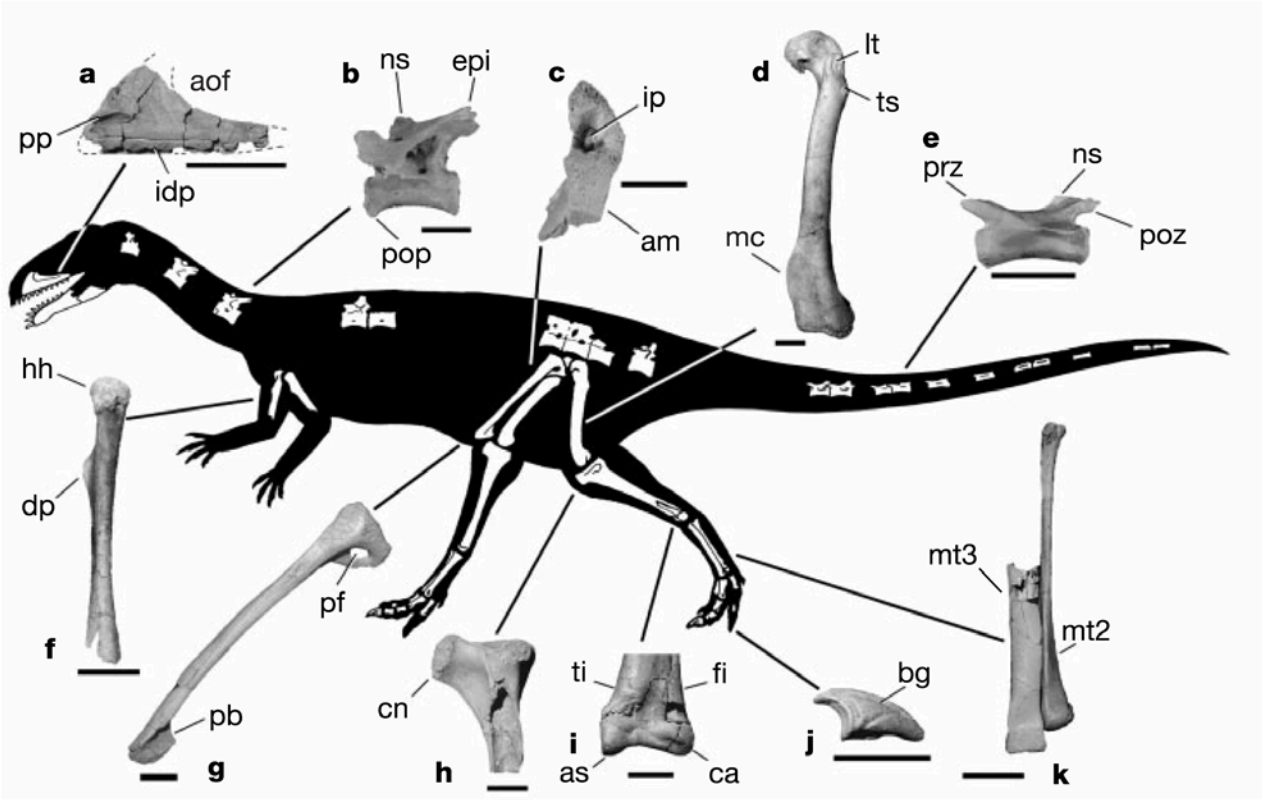


Figure 1 Skeletal anatomy of *Masiakasaurus knopfleri*, based on a composite of isolated specimens from locality MAD 93-18. **a**, Partial right maxilla (FMNH PR 2183) in medial view. Dashed lines indicate reconstructed outline of the element. **b**, Posterior cervical vertebra (FMNH PR 2139) in left lateral view. **c**, Left pubis (FMNH PR 2108) in dorsal view. **d**, Left femur (FMNH PR 2117) in cranial view. **e**, Medial caudal vertebra (FMNH PR 2126) in left lateral view. **f**, Partial right humerus (FMNH PR 2143) in medial view. **g**, Left pubis (FMNH PR 2108) in lateral view. **h**, Proximal left tibia (FMNH PR 2118) in lateral view. **i**, Left tibia/fibula/astragalocalcaneum (FMNH PR 2112) in cranial view. Dashed lines emphasize contacts between individual elements. **j**, Pedal ungual (FMNH PR 2155) in lateral view. **k**, Right metatarsals II (FMNH PR 2129) and III (FMNH PR 2151) in cranial view. Scale bars, 1 cm. am, acetabular margin; aof, antorbital fossa; as, astragalus; bg, blood groove; ca, calcaneum; cn, cnemial crest; dp, deltopectoral crest; epi, epipophysis; fi, fibula; hh, humeral head; idp, interdental plates; ip, pit for ilio-pubic articulation; lt, lesser trochanter; mc, mediodistal crest; mt2, metatarsal II; mt3, metatarsal III; ns, neural spine; pb, pubic boot; pf, pubic fenestra; poz, postzygapophysis; pop, parapophysis; pp, palatal process; prz, prezygapophysis; ti, tibia; ts, trochanteric shelf.

Masiakasaurus

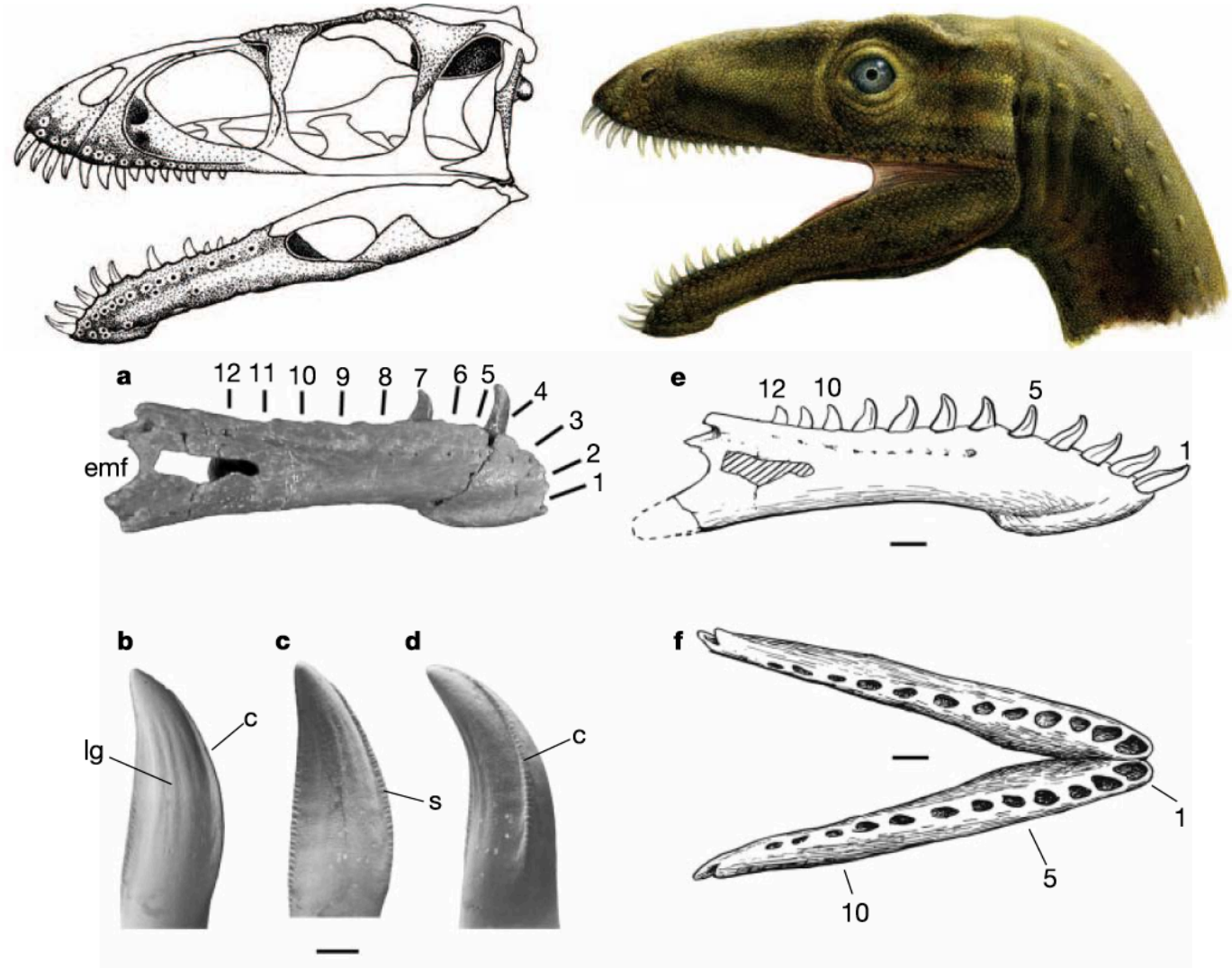


Figure 2 Dentary and lower dentition of *Masiakasaurus knopfleri*. **a**, Holotype dentary (UA 8680) in right lateral view. The tooth in position four has been displaced caudally post mortem. **b**–**d**, Scanning electron microscope photographs of isolated dentary teeth (FMNH uncatalogued). **b**, Anterior tooth, position 2–4 in lingual view. **c**, Anterior tooth, position 1–3, in lingual view. **d**, Anterior tooth, position 1–3, in lateral view. **e**, Reconstructed dentary with full complement of teeth in right lateral view. **f**, Reconstructed dentary in dorsal view, showing relative sizes and orientations of alveoli. c, carina; emf, external mandibular fenestra; lg, longitudinal groove; s, serration. Tooth positions are numbered sequentially from cranial to caudal positions. Scale bars, 10 mm (**a**, **e**–**f**); 5 mm (**b**–**d**).

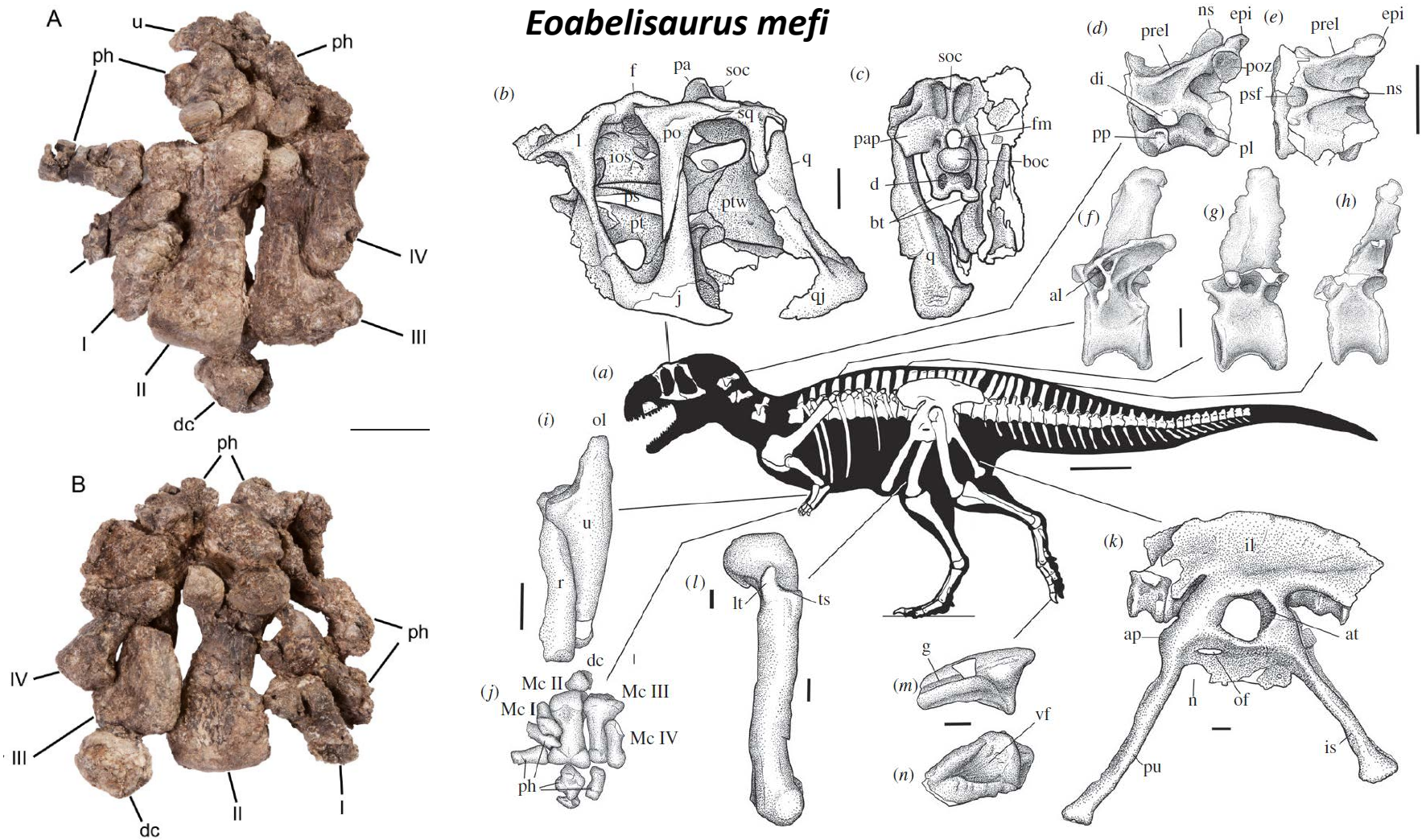


Figure 1. Middle Jurassic abelisaurid *Eoabelisaurus mefi*. (*a*) Skeletal reconstruction, showing preserved parts. Skull in left lateral (*b*) and posterior (*c*) views. Middle cervical vertebra in left lateral (*d*) and dorsal (*e*) views. (*f*) Anterior mid-dorsal vertebra in left lateral view. (*g*) Posterior dorsal vertebra in left lateral view. (*h*) Anterior caudal vertebra in left lateral view. (*i*) Right ulna and radius in medial view. (*j*) Right manus in plantar view. (*k*) Pelvic girdle in left lateral view. (*l*) Left femur in lateral view. Pedal ungual in lateral (*m*) and ventral (*n*) views. Abbreviations: al, additional lamina; ap, ambiens process; at, antitrochanter; boc, basioccipital condyle; bt, basal tubera; d, depression; dc, distal carpal; di, diapophysis; epi, epipophysis; f, frontal; fm, foramen magnum; g, groove; il, ilium; ios, interorbital septum; is, ischium; j, jugal; l, lacrimal; lt, lesser trochanter; Mc, metacarpal; n, notch; ns, neural spine; of, obturator foramen; ol, olecranon process; pa, parietal; pap, paroccipital process; ph, phalanges; pl, pleurocoel; po, postorbital; poz, postzygapophysis; pp, parapophysis; prel, prezygoepipophyseal lamina; ps, parasphenoid; psf, prespinal fossa; pt, pterygoid; ptw, pterygoid wing of the quadrate; pu, pubis; q, quadrate; qj, quadratojugal; r, radius; soc, supraoccipital crest; sq, squamosal; ts, trochanteric shelf; u, ulna; vf, ventral fossa. Scale bars: (*a*) 500 mm; (*b–l*) 50 mm; (*m*,*n*) 10 mm.

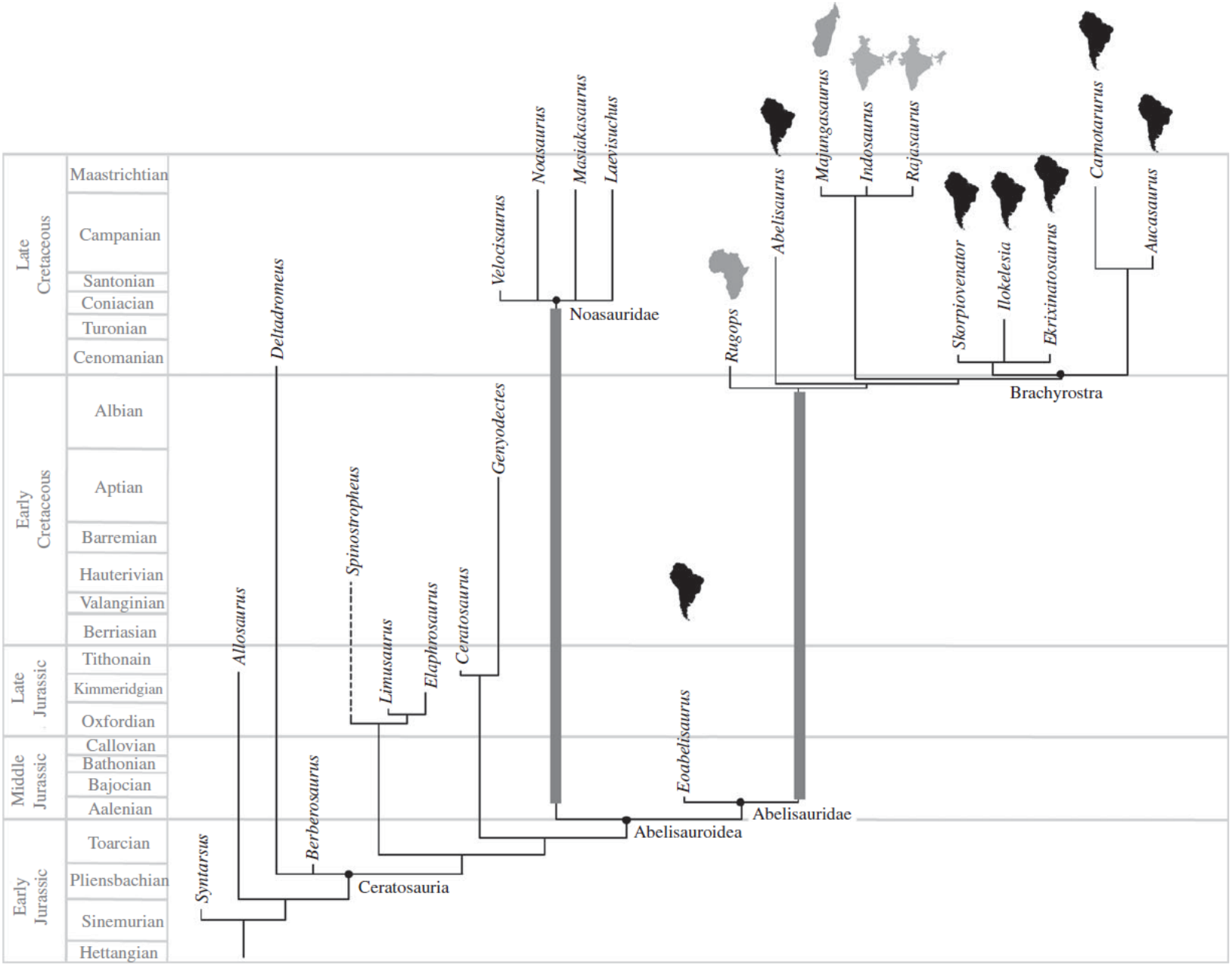
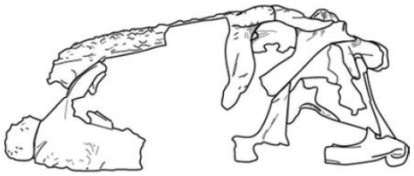


Figure 2. Calibrated phylogeny of ceratosaurian theropods. Thick grey lines indicate major ghost lineages in noasaurids and abelisaurids, resulting from the phylogenetic relationships of *Eoabelisaurus*. Dashed line in *Spinostropheus* indicates stratigraphic uncertainty for this taxon [16]. For abelisaurids, outlines of continents indicate geographical distribution.

Abelisauridae

Majungasaurus



Abelisaurus

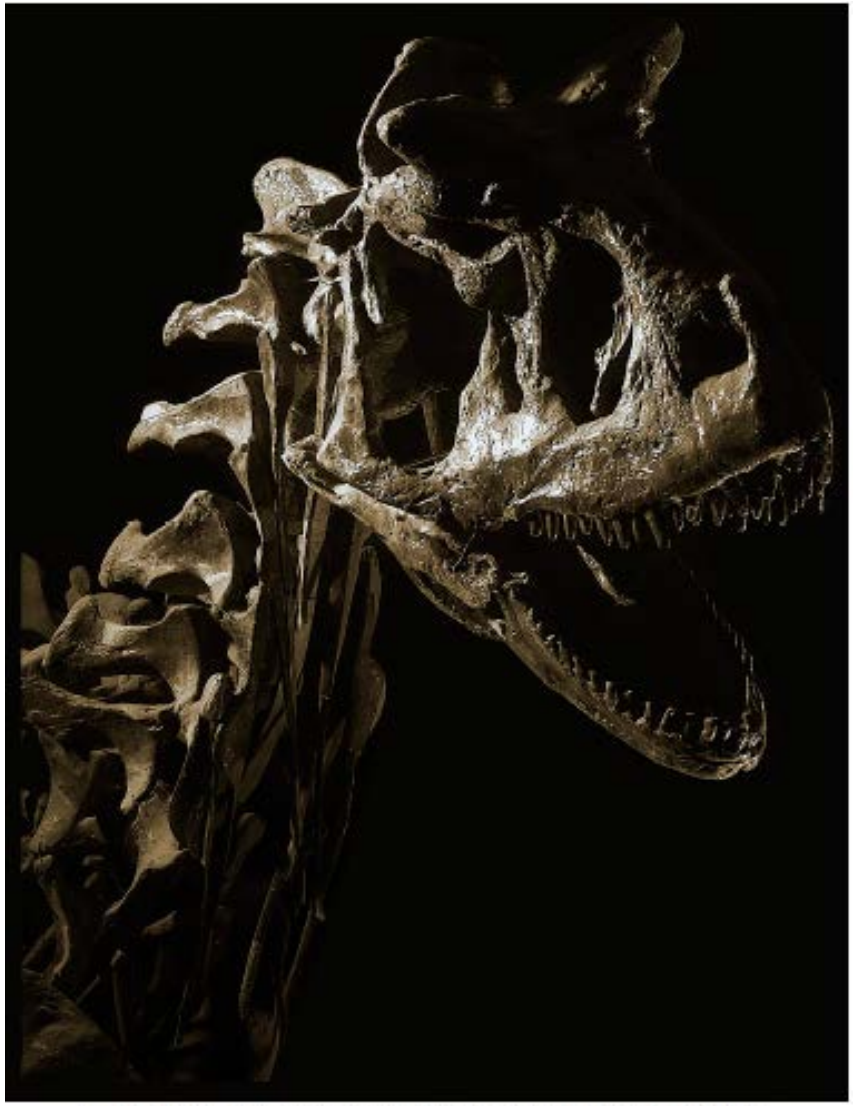
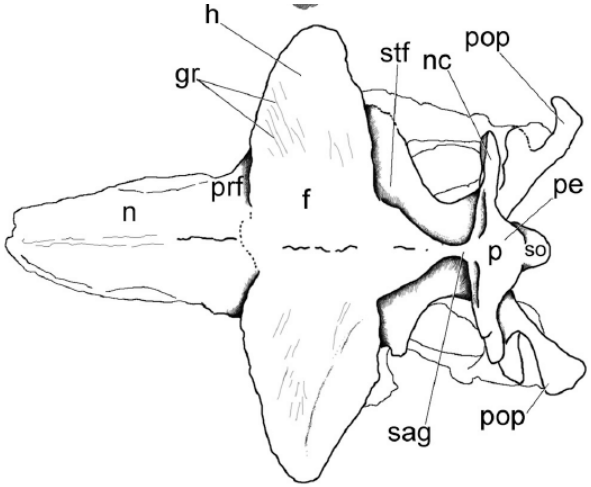
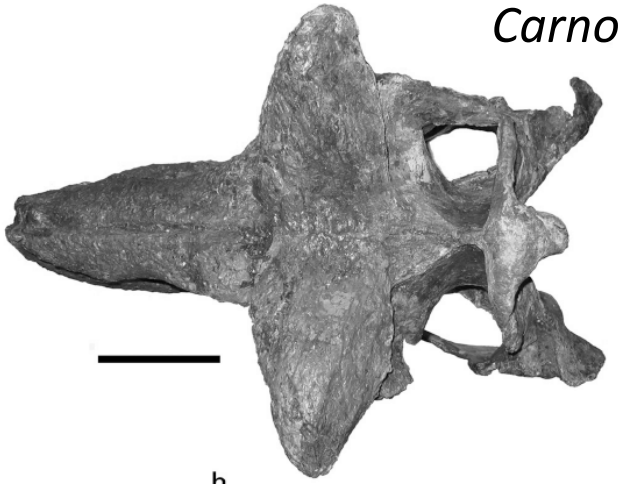


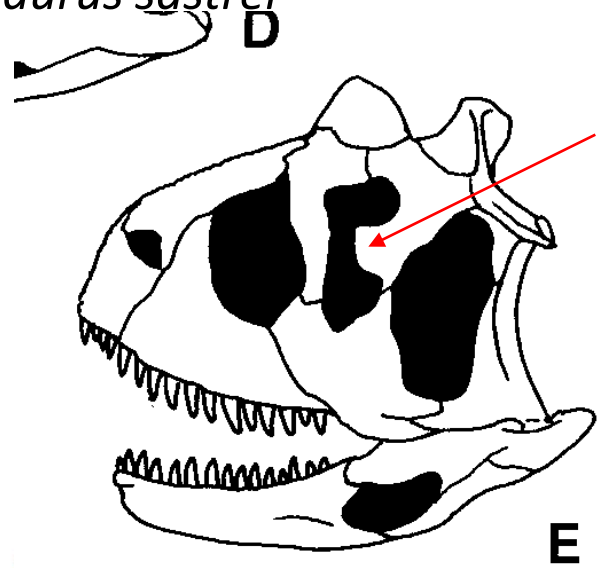
Fig. 2. Skull and neck of the aberrant abelisaurid Carnotaurus sastrei (MACN-Pv-CE 894, holotype). Note the well-developed frontal horns.

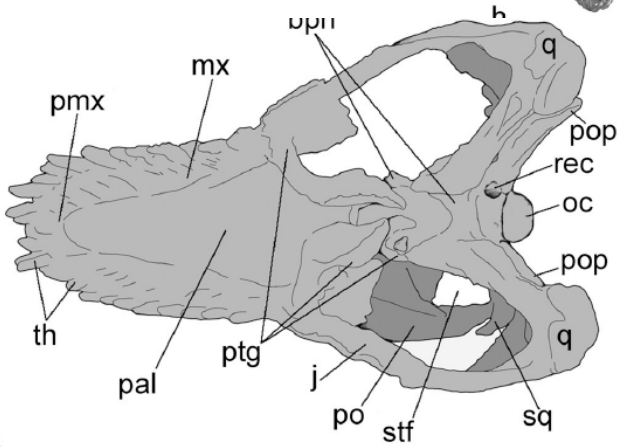
Carnotaurus sastrei

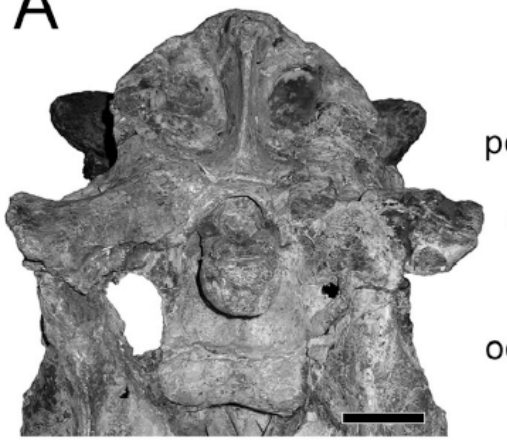
Carnotaurus sastrei

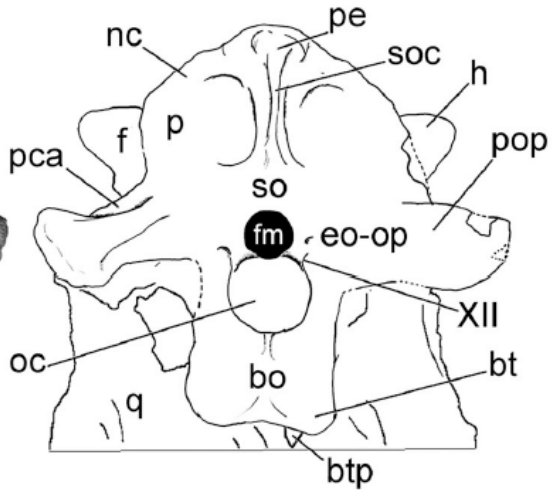












Anatomical Abbreviations—**apf**, fenestra rostral to the pituitary fossa; **bo**, basioccipital; **bphr**, basisphenoidal recess (filled with sediment); **bt**, basal tuber; **btp**, basipterygoid process; **bw**; basituberal web; **col**, columellar recess; **cul**, cultriform process; **eo-op**, exoccipital-opisthotic; **ept.lsph**, epipterygoid contact of laterosphenoid; **f**, frontal; **fm**, foramen magnum; **gr**, grooves on frontal; **h**, 'horn' on the frontal; **j**, jugal; **lsph**, laterosphenoid; **ltr**, lateral (anterior) tympanic recess; **mx**, maxilla; **mth**, mesethmoid; **n**, nasal; **nc**, nuchal crest; **oc**, occipital condyle; **osph**, orbitosphenoid; **p**, parietal; **pal**, palate (covered with sediment); **pe**, parietal eminence; **pmx**, premaxilla; **po.f**, postorbital contact of frontal; **po.lsph**, postorbital contact of laterosphenoid; **pop**, paroccipital process; **pp**, preotic pendant; **pca**, parietal caudolateral alae; **prf**, prefrontal; **pro**, prootic; **ptf**, postemporal fenestra; **ptg**, pterygoid; **q**, quadrate; **rec**, small recess lateral to the occipital condyle in which the metotic and CN XII foramina open; **sag**, sagittal crest; **scp**, supraoccipital caudomedial projection; **sep**, bony interorbital septum; **so**, supraoccipital; **soc**, supraoccipital crest; **sph**, sphenethmoid; **sq**, squamosal; **stf**, supratemporal fossa; **th**, teeth; **vasc**, vascular foramen of the olfactory tract; **I–XII**, cranial nerve foramina.

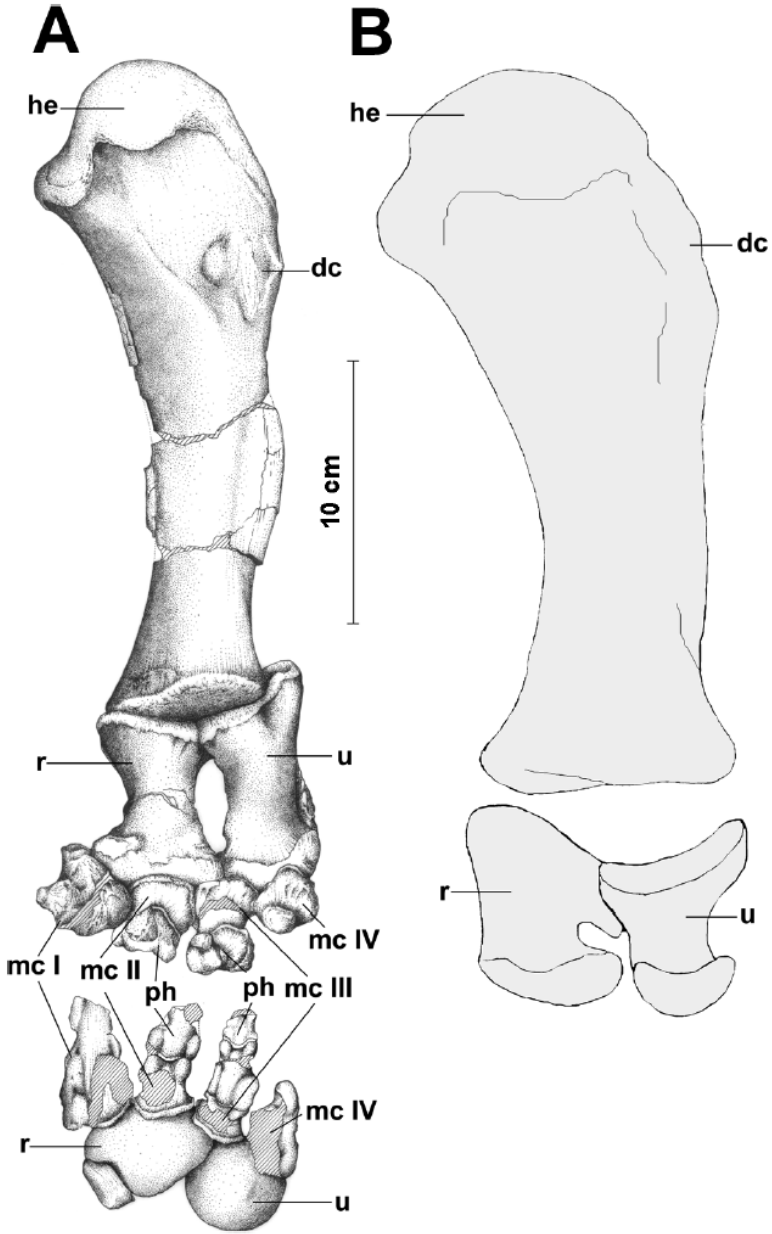


FIGURE 3. Forelimb of *Aucasaurus* in caudal and distal views (**A**) and caudal view of humerus, radius, and ulna of *Carnotaurus* (modified from Bonaparte et al., 1990) (**B**). Abbreviations: **dc**, deltopectoral crest; **h**, humerus; **he**, humeral head; **it**, internal tubercle; **mc I–IV**, metacarpals; **ph**, phalanges; **r**, radius; **u**, ulna.

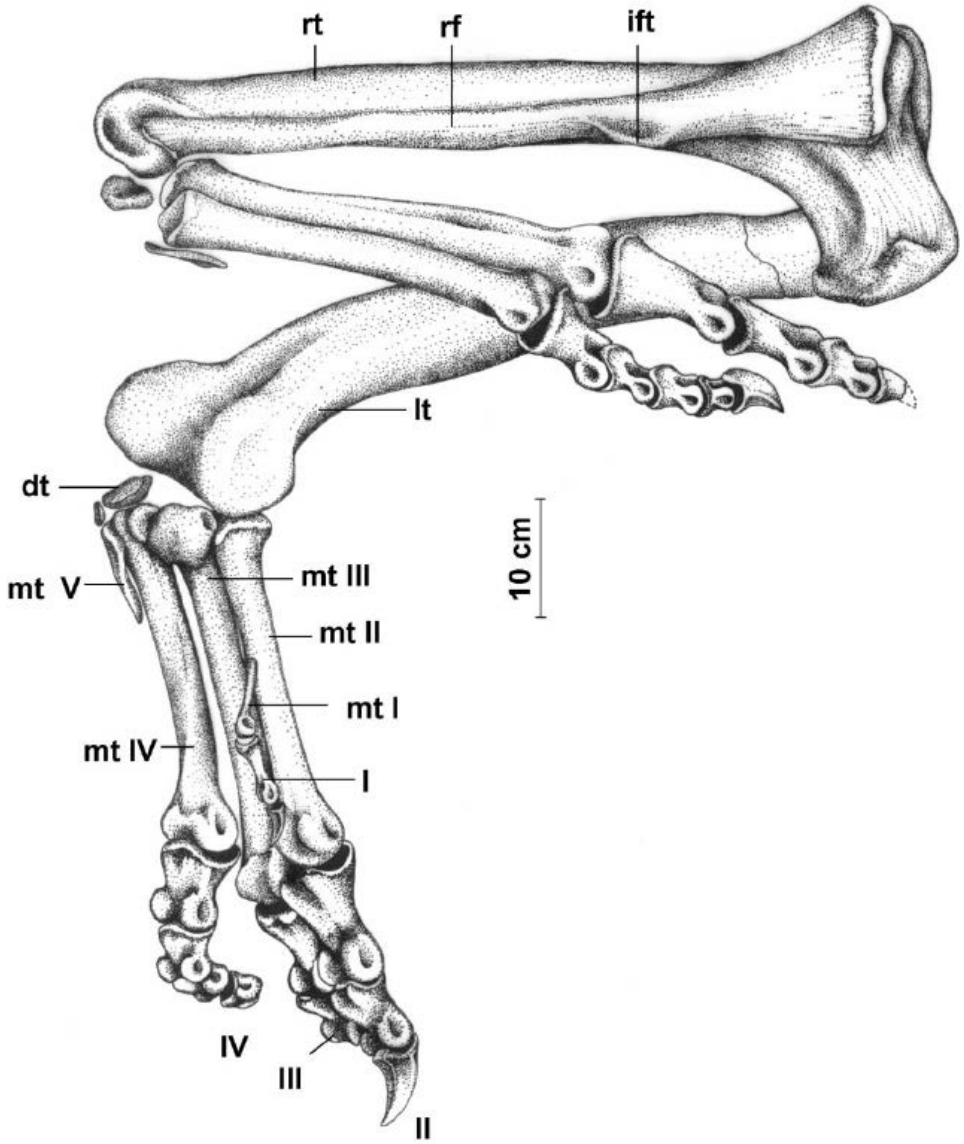


FIGURE 4. Articulated tibiae, metatarsi, and digits of *Aucasaurus* in lateral (**right**) and medial (**left**) views. **Abbreviations**: **dtg**, distal tarsal; **ift**, iliofibularis tubercle; **mt I–V**, metatarsals I–V; **rf**, right fibula; **rt**, right tibia; **I–IV**, digits I–IV.

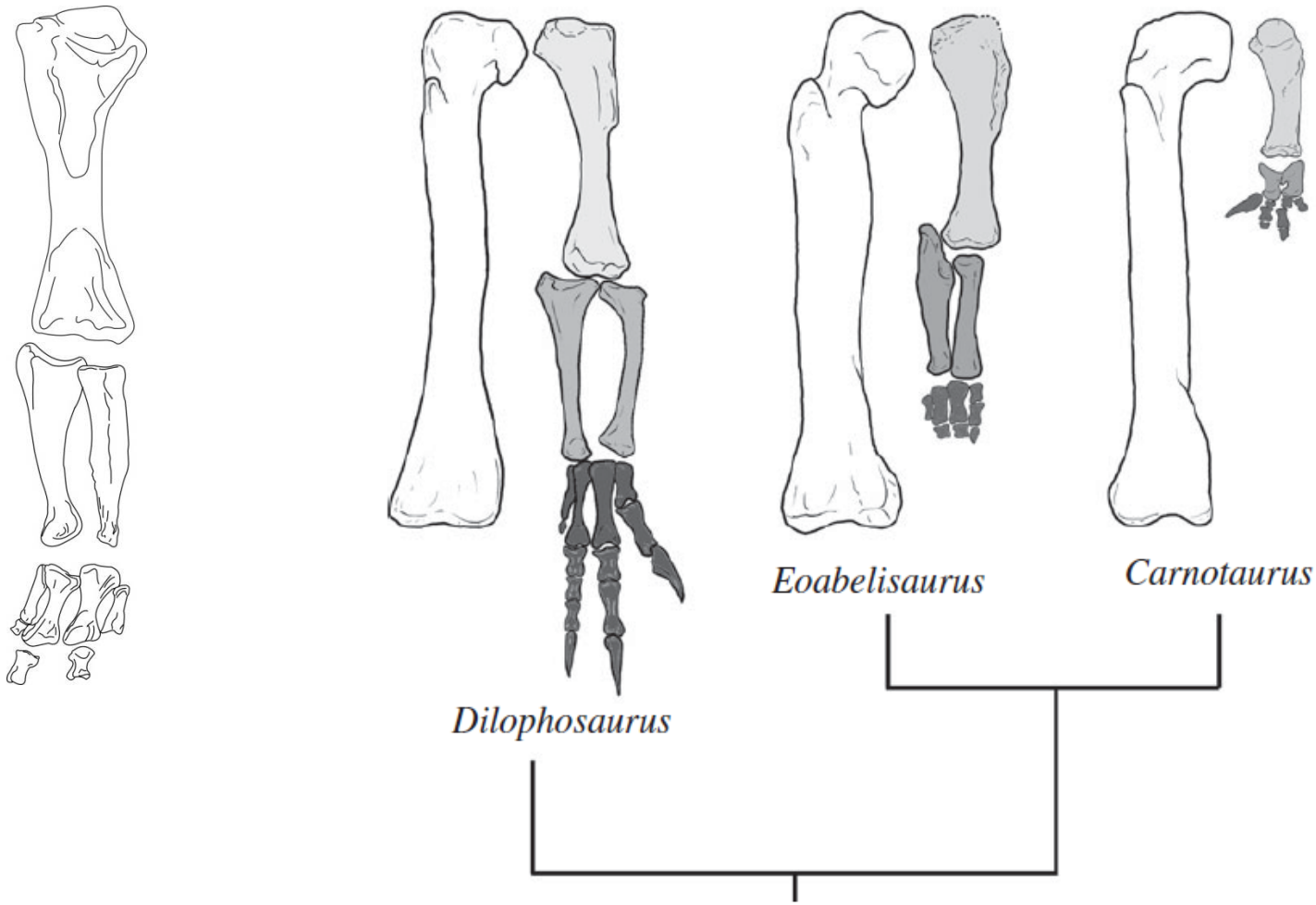
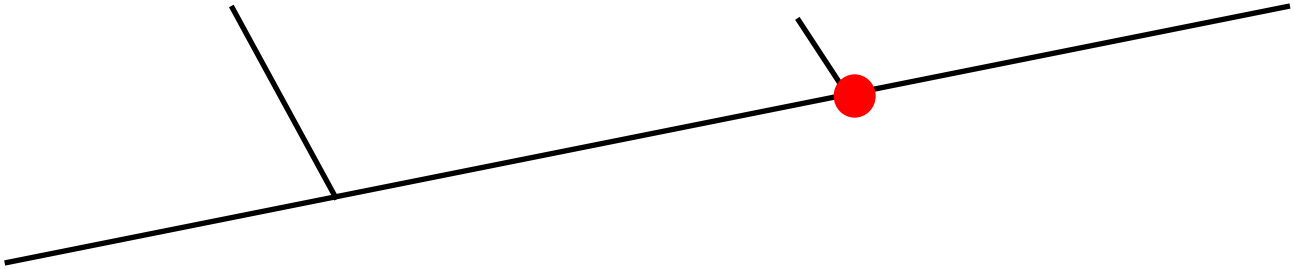
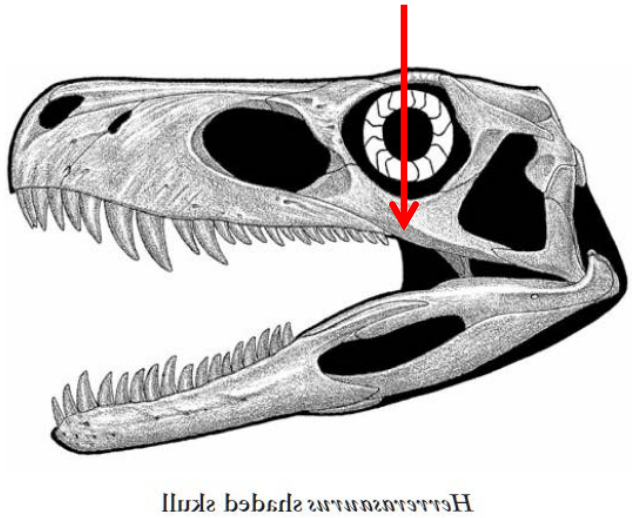


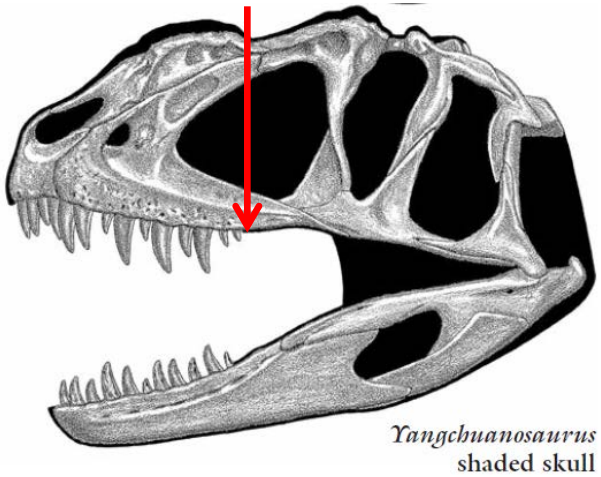
Figure 3. Limb proportions in several theropods, showing reduction of distal elements of the forelimb. Femur and forelimb of the basal theropod *Dilophosaurus* (left), basal abelisaurid *Eoabelisaurus* (middle) and the derived abelisaurid *Carnotaurus* (right). Drawn to same femoral length for comparison.

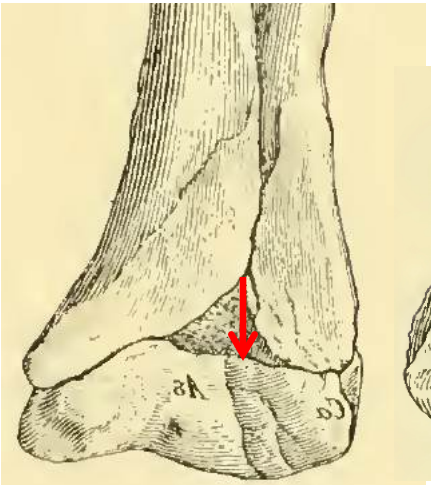
Tetanurae

Clado más inclusivo que contiene a la paloma (*Columba livia*) pero no a *Carnotaurus.*

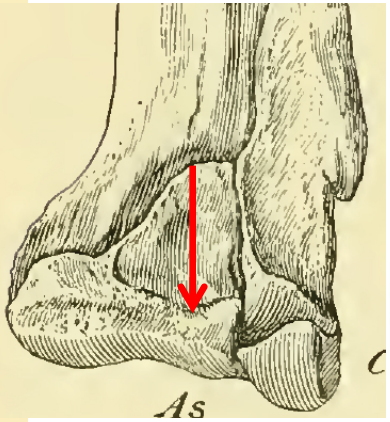




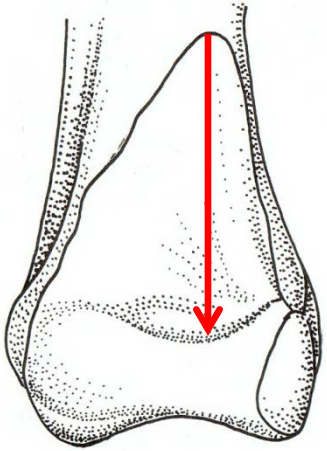




Ceratosaurus nasicornis



Allosaurus fragilis



Deinonychus anthirropus

Sinapomorfías:

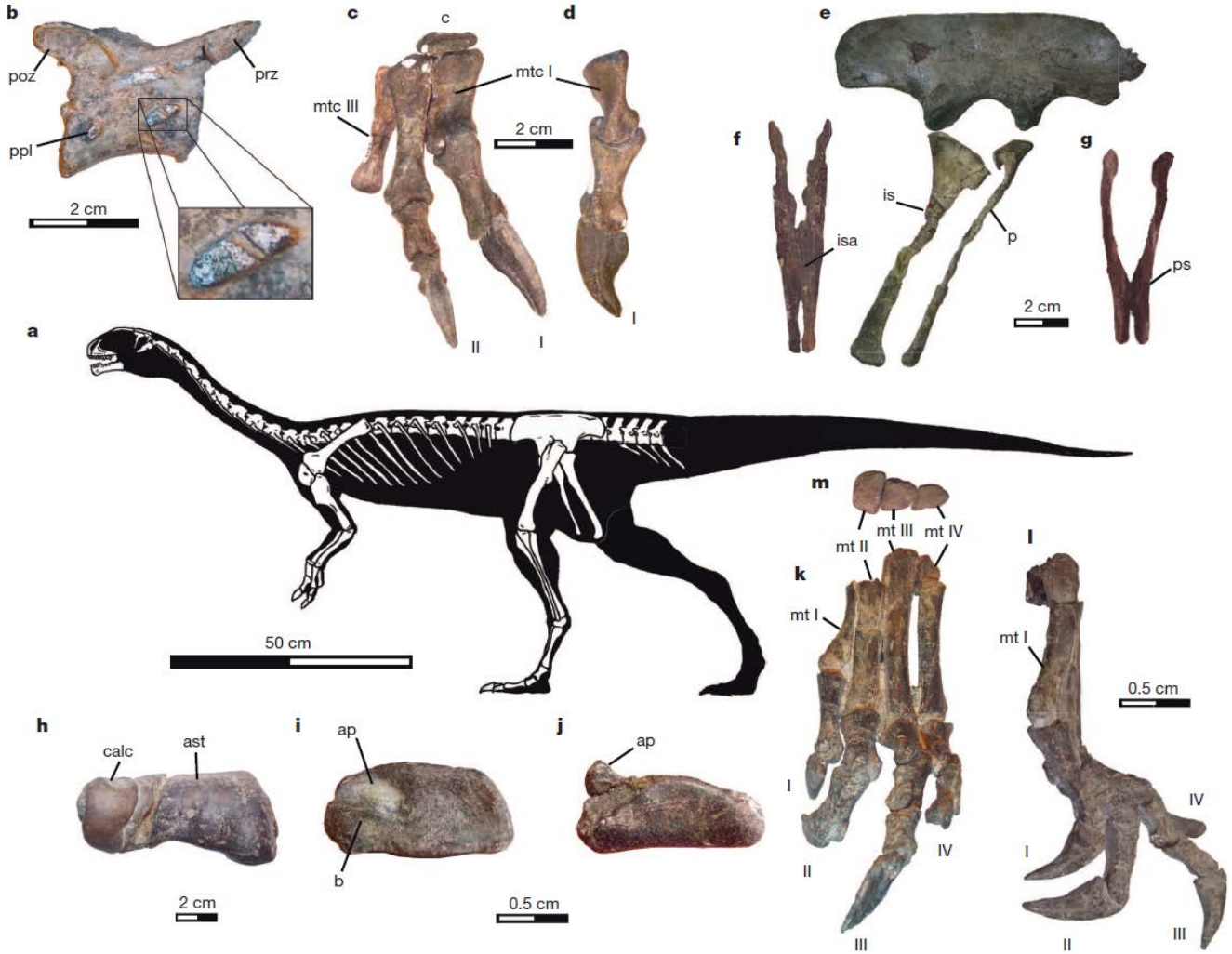
- Dientes maxilares restringidos a la parte anterior de la órbita
- Manos alargadas
- Zigapófisis caudales alargadas
- Proceso ascendente del astrágalo laminar y más alto que altura de la cara posterior del astrágalo
- El maxilar presenta una apertura (fenestra).
- El carpo presenta una forma semilunar

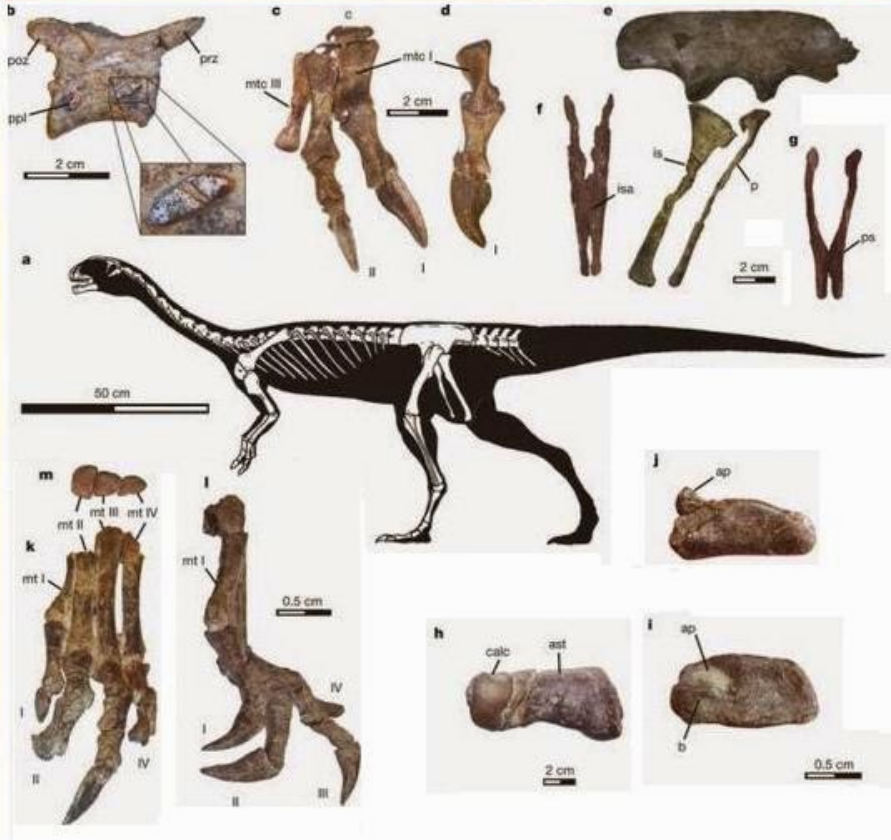
LETTER *Chilesaurus diegosuarezi*

doi:10.1038/nature14307

An enigmatic plant-eating theropod from the Late Jurassic period of Chile

Fernando E. Novas[1,2], Leonardo Salgado[1,3], Manuel Suárez[4], Federico L. Agnolín[2,5], Martín D. Ezcurra[6], Nicolás R. Chimento[2], Rita de la Cruz[7], Marcelo P. Isasi[1,2], Alexander O. Vargas[8] & David Rubilar-Rogers[8,9]

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Monolophosaurus

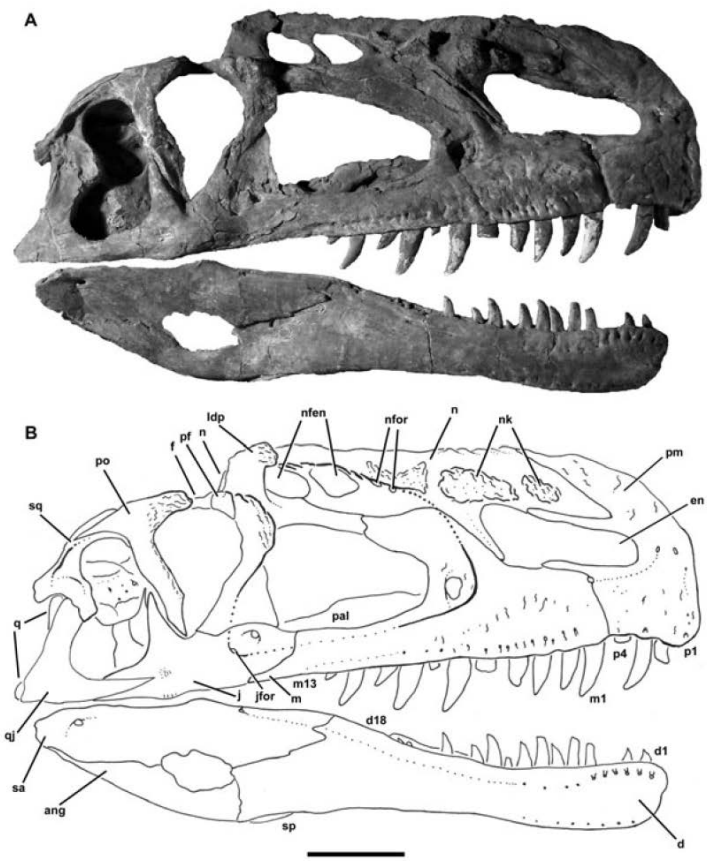


Figure 1. Skull of *Monolophosaurus jiangi* in right lateral view: A, photograph; B, line drawing. Abbreviations: ang, angular; d, dentary; en, external naris; f, frontal; j, jugal; jfor, jugal foramen; ldp, dorsal projection of the lacrimal; m, maxilla; n, nasal; nfen, nasal fenestrae; nfor, nasal foramina; nk, nasal knobs; pal, palatine; pf, prefrontal; pm, premaxilla; po, postorbital; q, quadrate; qj, quadratojugal; sa, surangular; sp, splenial; sq, squamosal. Numerals (e.g. p1) refer to premaxillary, maxillary and dentary tooth positions. Scale bar represents 100 mm.

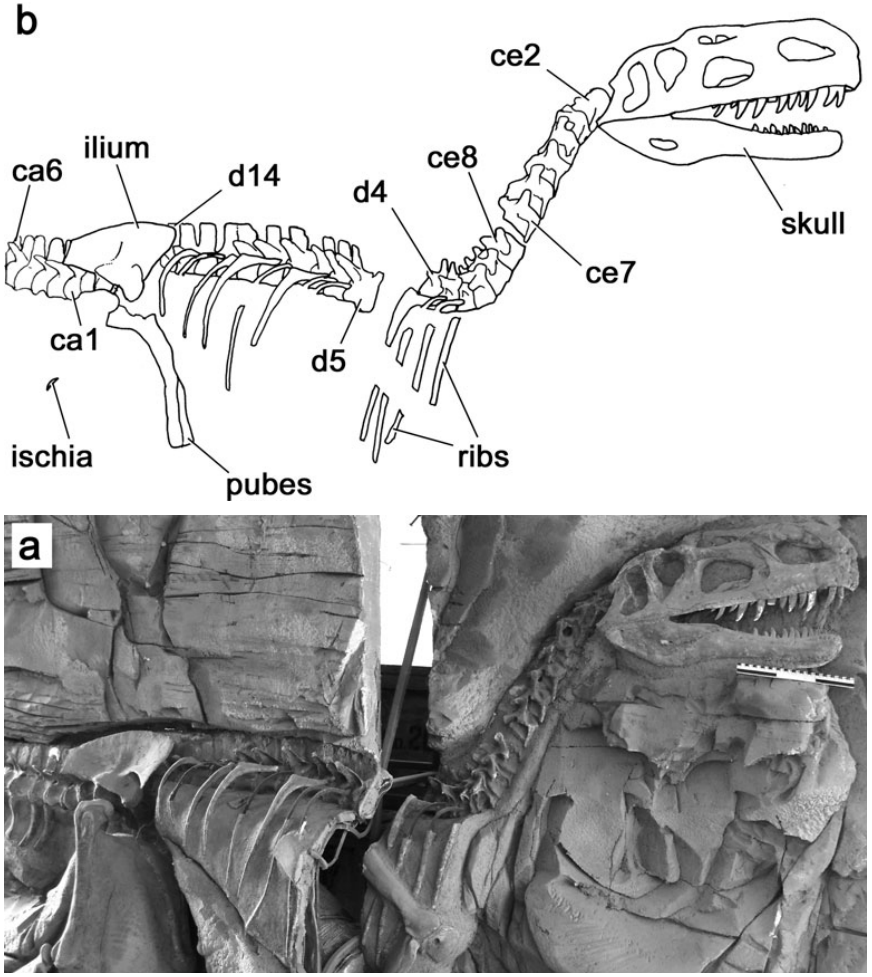


Figure 1. The mounted skeleton of *Monolophosaurus jiangi* (IVPP 84019) in right anterolateral view: (a) photograph; (b) line drawing indicating mounted bones. Abbreviations: ce2 – axis (second cervical vertebra); ce7 – seventh cervical vertebra; ce8 – eighth cervical vertebra; d4 – fourth dorsal vertebra; d5 – fifth dorsal vertebra; d14 – fourteenth dorsal vertebra; ca1 – first caudal vertebra; ca6 – sixth caudal vertebra. Scale bar (in a) = 300 mm (but image is attenuated to the left).

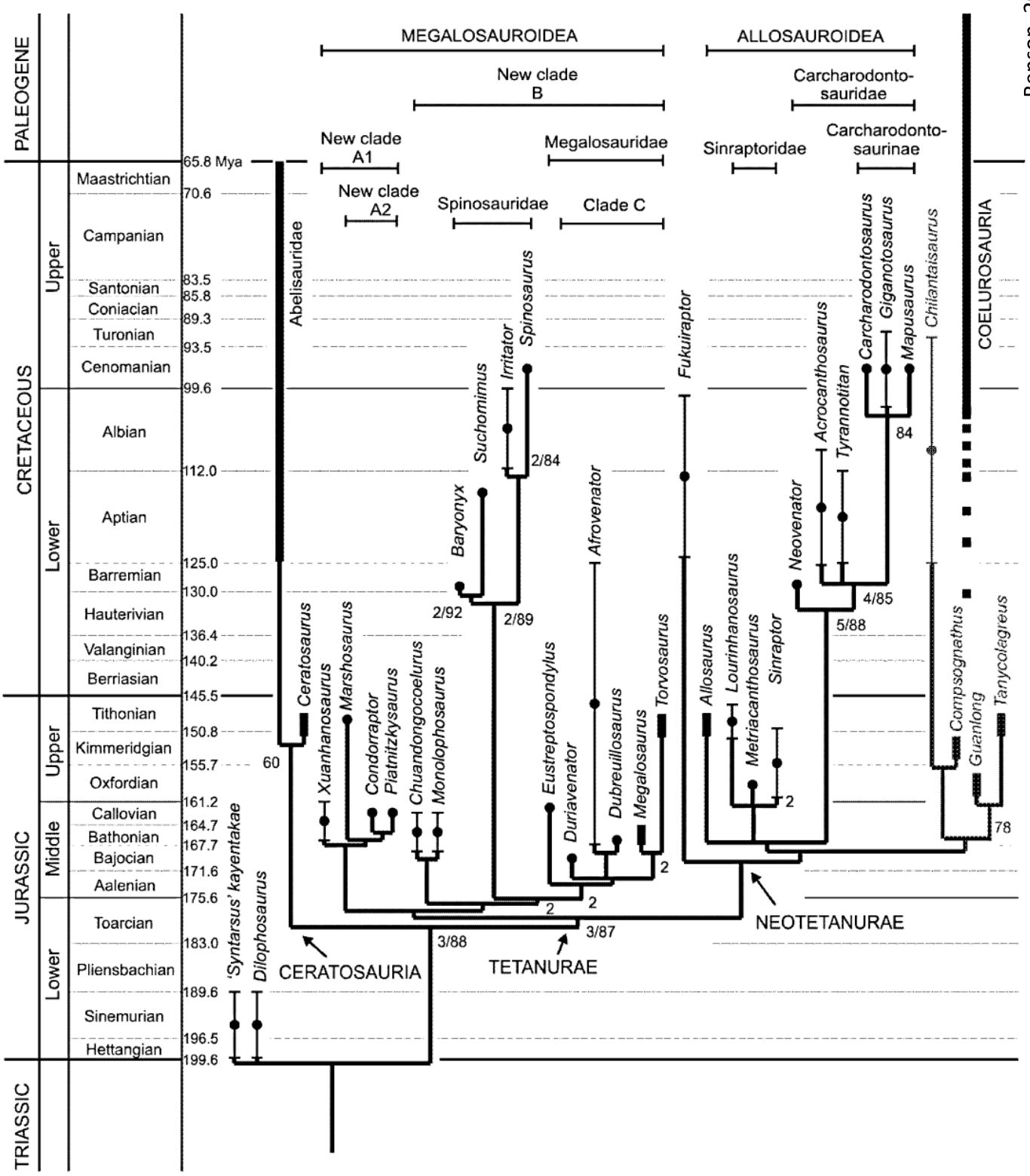
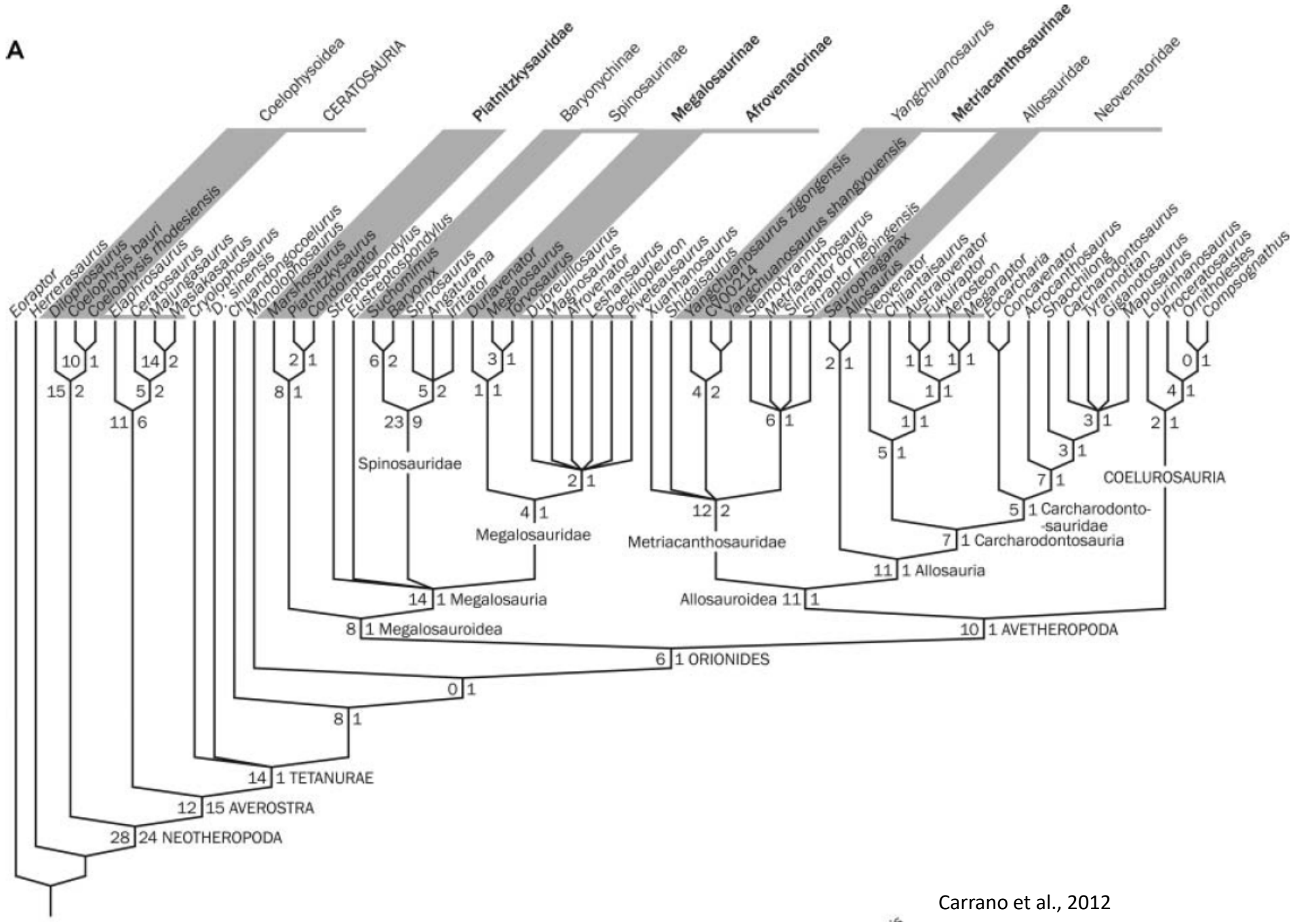


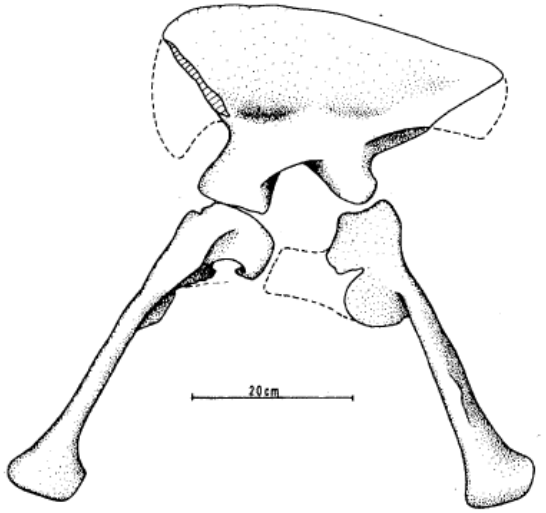
Figure 20. Time-calibrated strict reduced consensus of 24 unique tree topologies remaining after deletion of *Eocarcharia*, *Magnosaurus*, *Megaraptor*, *Piveteausaurus*, *Poekilopleuron* and *Streptospondylus* from 189 456 MPTs resulting from analysis of the total dataset (Appendix S3) of 41 taxa and 213 characters. Ensemble consistency index, 0.438; ensemble retention index, 0.604; ensemble rescaled consistency index, 0.264. Bremer support (single digit values) and bootstrap (multi-digit values) are recorded at the nodes.

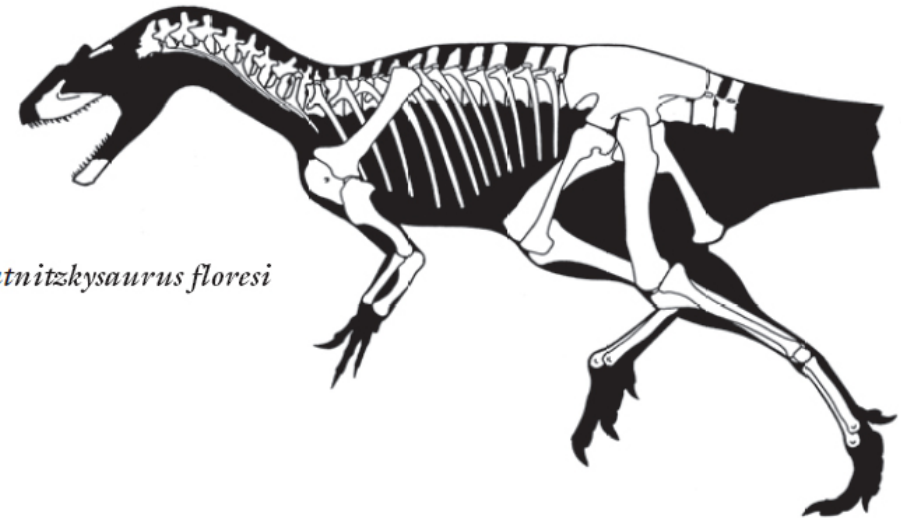


Carrano et al., 2012

Megalosauroidea (=Spinosauroidea)

Piatnitzkysauridae





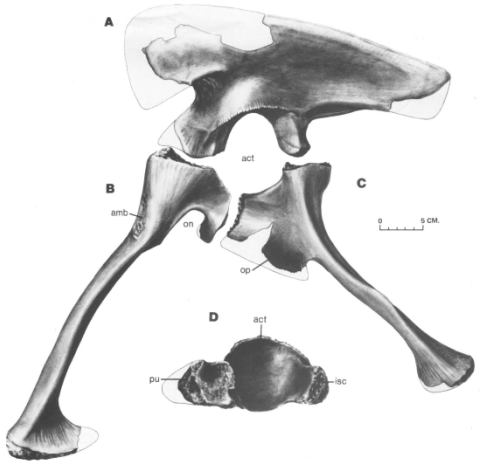
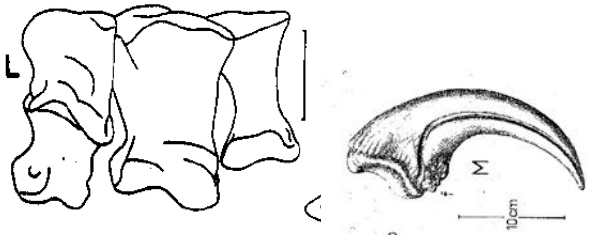


Figure 5. Left ilium (A), pubis (B), and ischium (C) of *Marshosaurus bicentesimus* in lateral view and acetabulum (D) in ventral view. Abbreviations: act–acetabulum, amb–probable origin of ambiens muscle, isc–ischiadic peduncle, on–obturator notch, op–obturator process, pu–pubic peduncle.

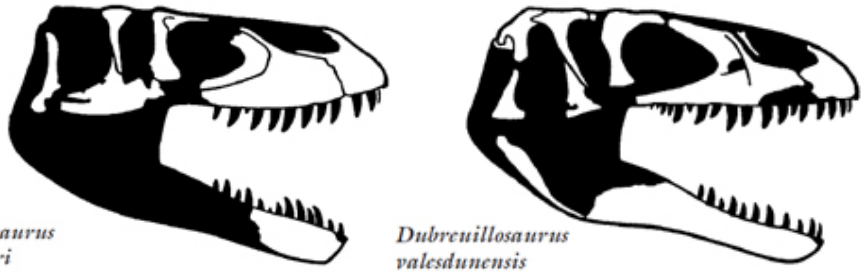
TEXT-FIG. 2. *Condorraptor currumili* gen. et sp. nov., Cañadón Asfalto Formation, Chubut, Argentina; outline drawing, showing preserved elements. Scale bar represents 50 cm.

Megalosauridae



Metacarpos y ungual de *Torvosaurus tanneri*

Torvosaurus tanneri



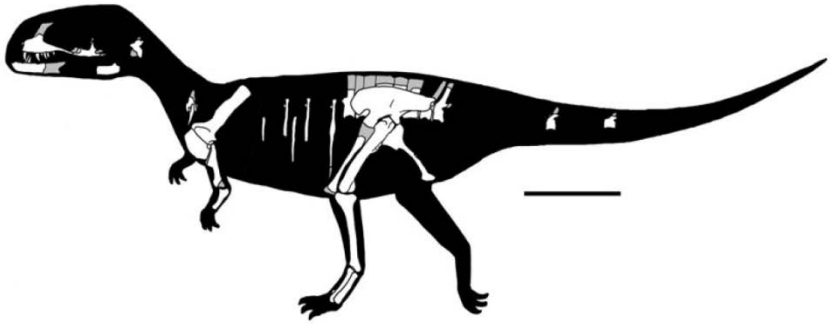


Figure 1. Silhouette of *Megalosaurus bucklandii* containing skeletal reconstruction. Known material is illustrated in white; grey tone indicates reconstructed areas. Scale bar, 1 m.

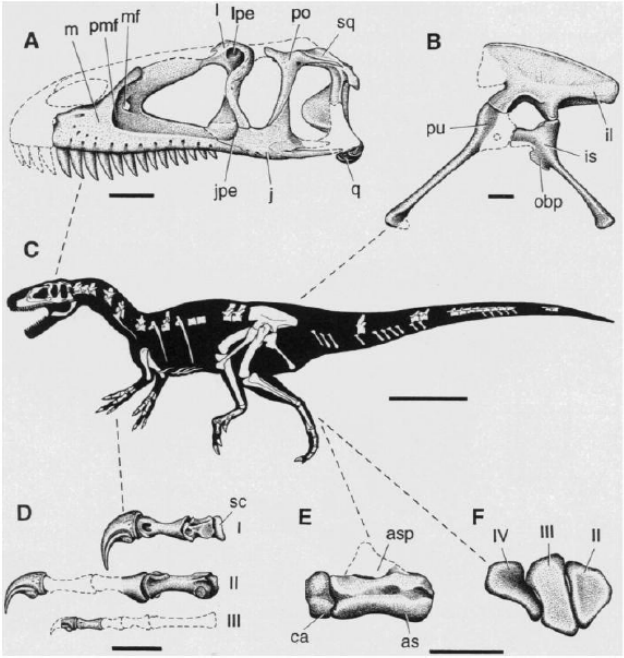
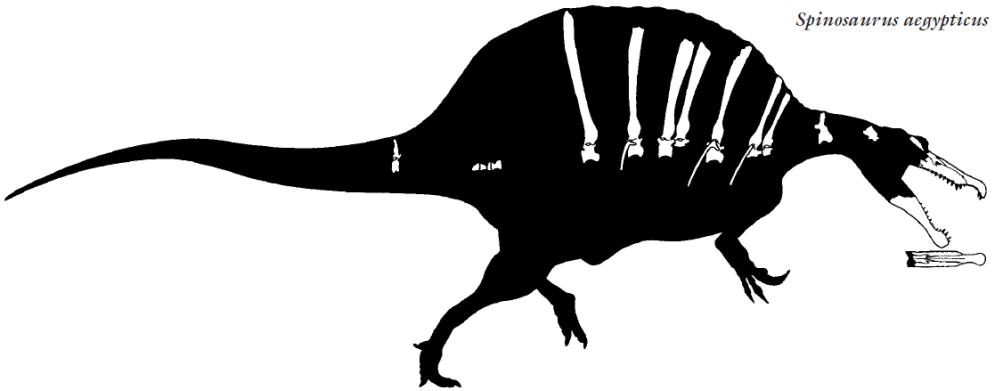


Fig. 2. Skeletal anatomy of *Afrovenator abakensis*. (**A**) Skull reconstruction in left lateral view; (**B**) pelvic reconstruction in left lateral view; (**C**) skeletal reconstruction (length is approximately 9 m); (**D**) partial left manus in lateral view; (**E**) right astragalus and calcaneum in anterior view (ascending process based on articular depression on distal tibia); (**F**) left metatarsus in proximal view (anterior toward top). Scale bar in (A), (B), and (D) to (F) is 10 cm. Scale bar in (C) is 1 m. I–IV, manual or pedal digits I–IV; as, astragalus; asp, ascending process; ca, calcaneum; il, ilium; is, ischium; j, jugal; jpe, jugal pneumatic excavation; l, lacrimal; lpe, lacrimal pneumatic excavation; m, maxilla; mf, maxillary fenestra; obp, obturator process; pmf, promaxillary fenestra; po, postorbital; pu, pubis; q, quadrate; sc, semilunate carpal; sq, squamosal.

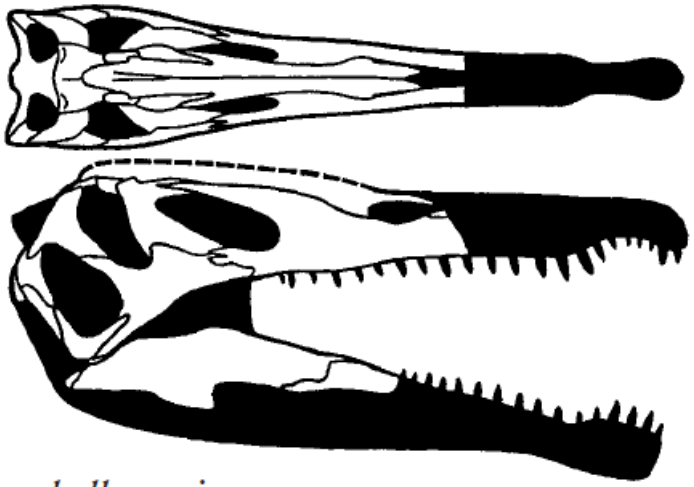
Spinosauridae

Baryonyx walkeri

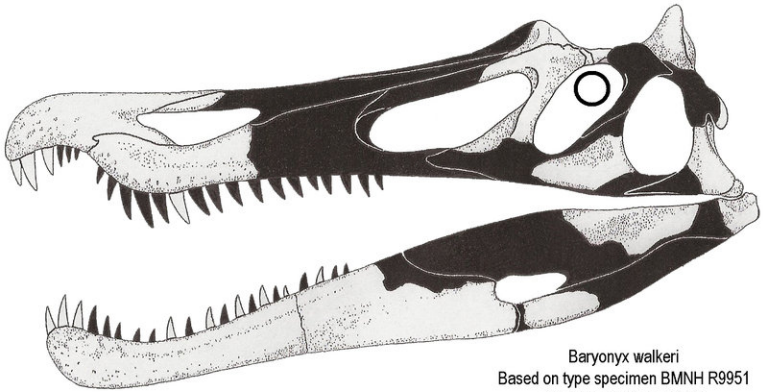
Baryonyx (=Suchomimus) tenerensis
(see illustration overleaf)



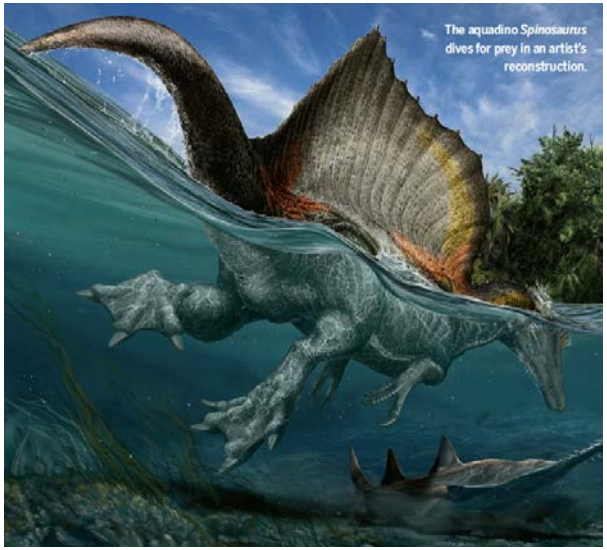
Spinosaurus aegypticus



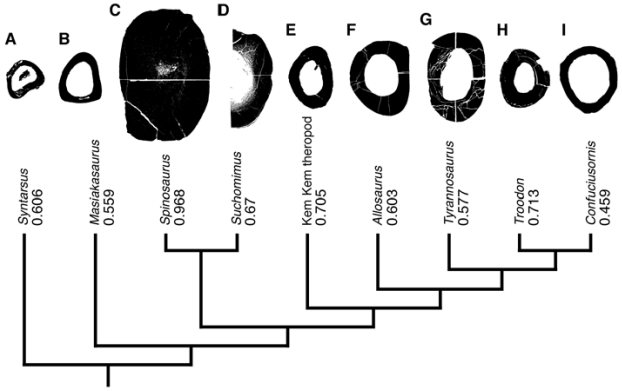
Irritator challengeri

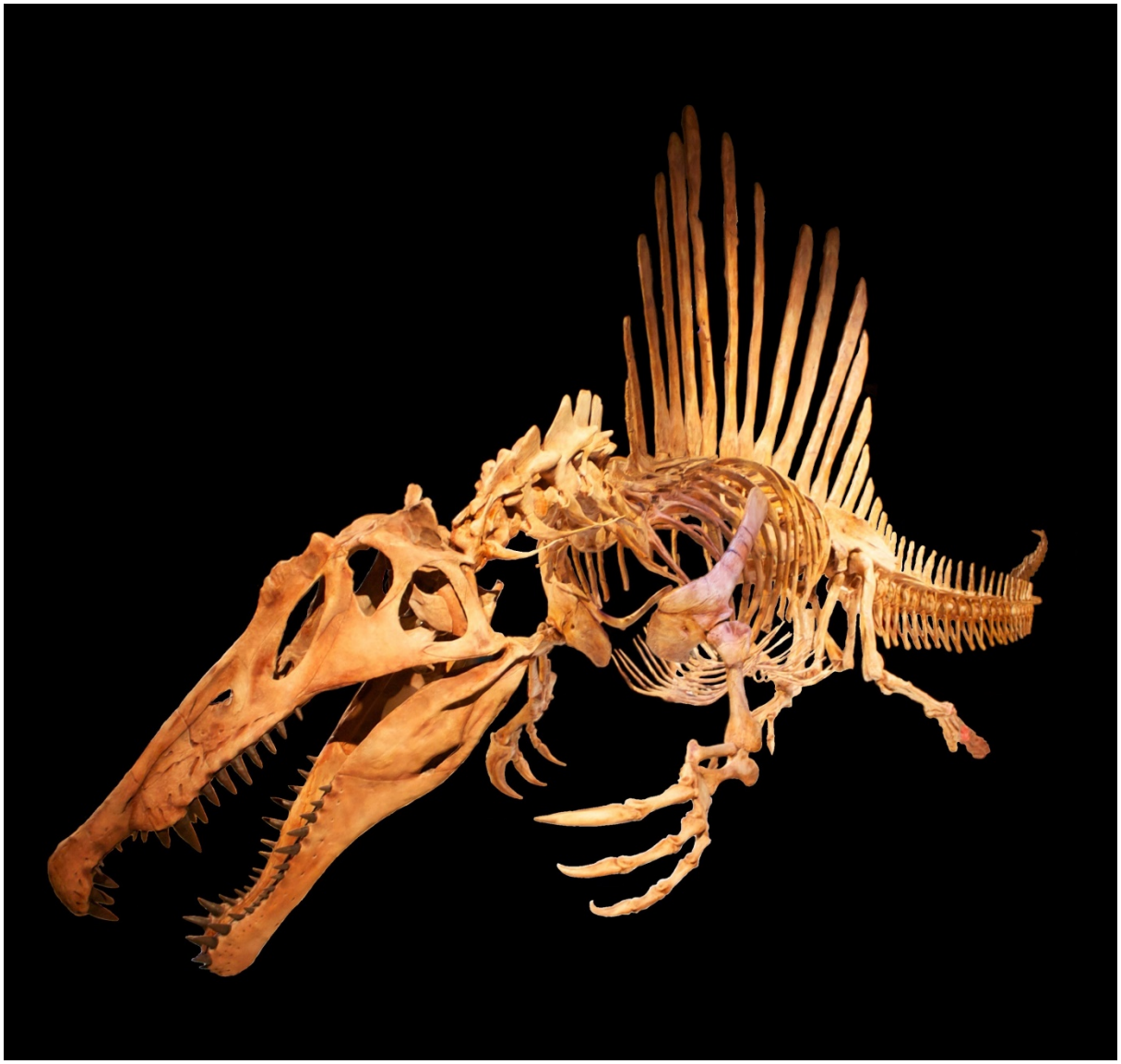


Baryonyx walkeri
Based on type specimen BMNH R9951
(Charig and Milner 1986)
Image COPYRIGHT © Miyess Mitri 2010



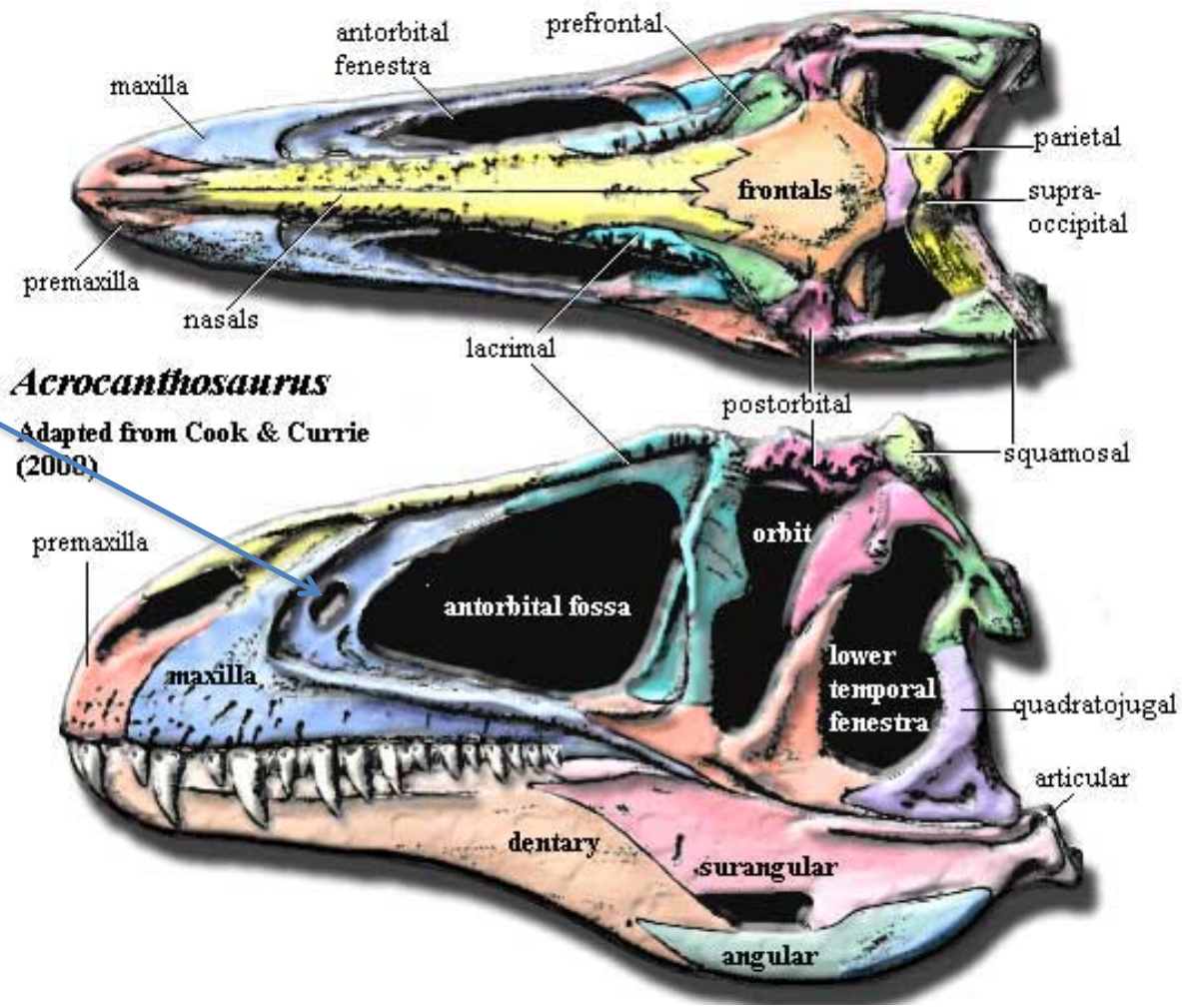
The aquadino *Spinosaurus* dives for prey in an artist's reconstruction.





Avetheropoda

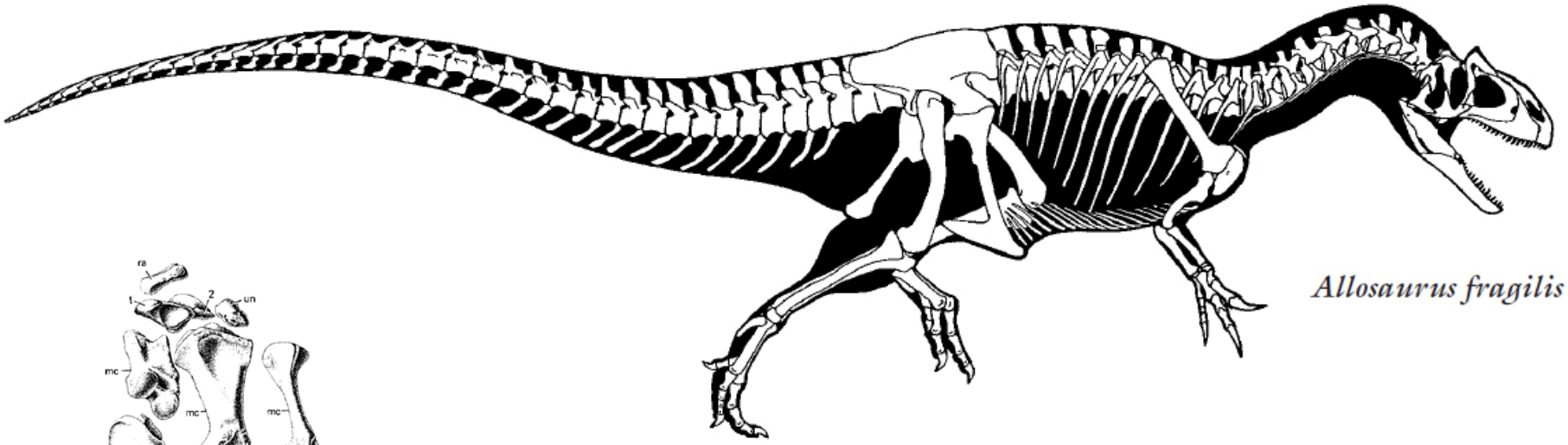
Fenestra maxilar

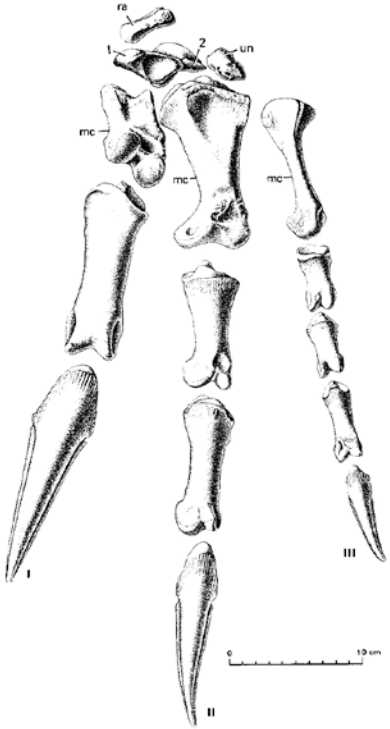


Sinapomorfías:

- El maxilar presenta una apertura (fenestra).
- Vértebras con complejo sistema de cámaras y pleurocelos
- Dígito IV ausente

Allosauroidea (=Carnosauria)





Metriacanthosauridae (=Sinraptoridae)

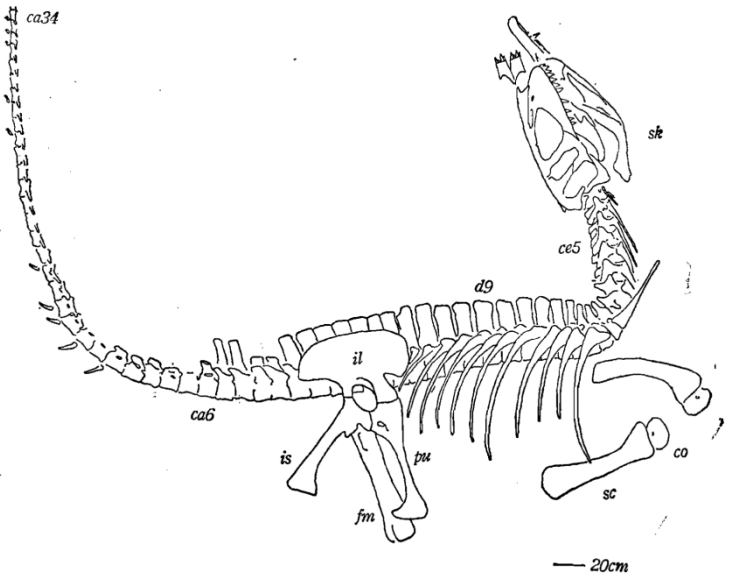
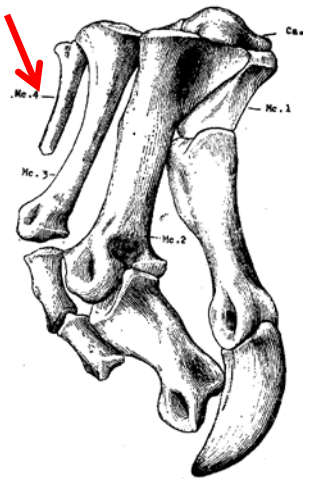


图 1 和平永川龙(新种)骨架埋藏图

Fig. 1 Burial skeleton of *Yangchuanosaurus hepingensis* sp. nov..

Yangchuanosaurus hepigengensis



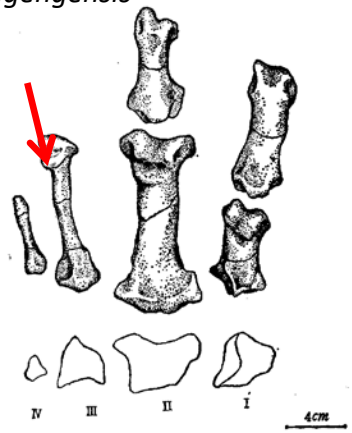


图 5 自贡四川龙(新种)的左掌骨和指骨顶视和后视 No. ZDM9011.

Fig. 5 Left metacarpus and phalanges of *Szechuanosaurus zigongensis* (sp. nov.), in superior and posterior views.No.ZDM9011.

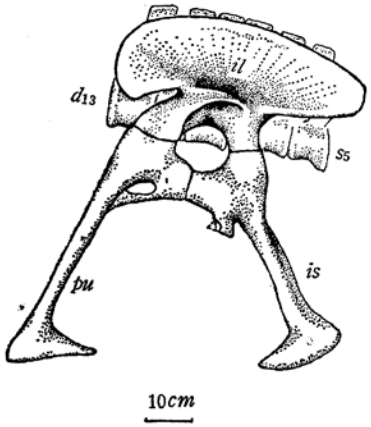


图 6 自贡四川龙(新种)的腰带和荐椎外侧视 No. ZDM9011.

Fig. 6 Left pelvis and sacrals of *Szechuanosaurus zigongensis* (sp. nov.), in lateral view. No. ZDM9011.

Xuanhanosaurus (Dong, 1984)

"Szechuanosaurus"zigongensis (Gao, 1993)

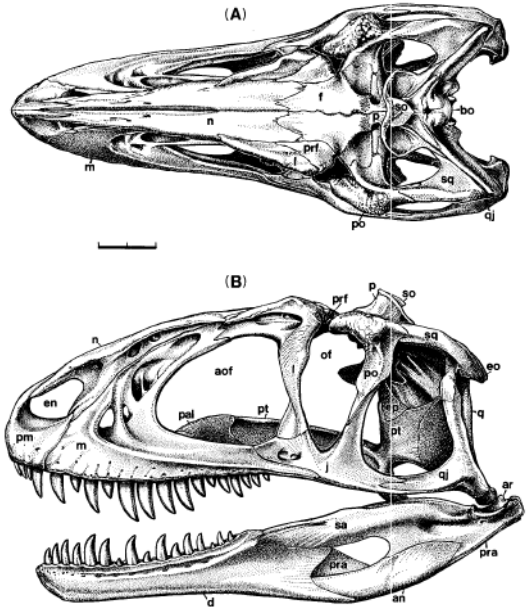
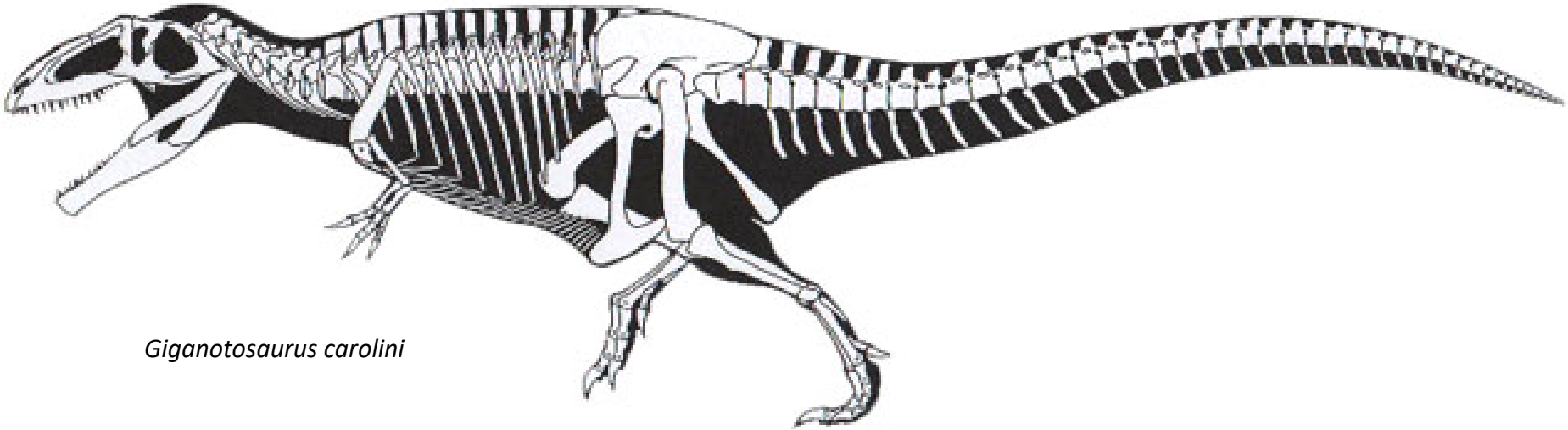


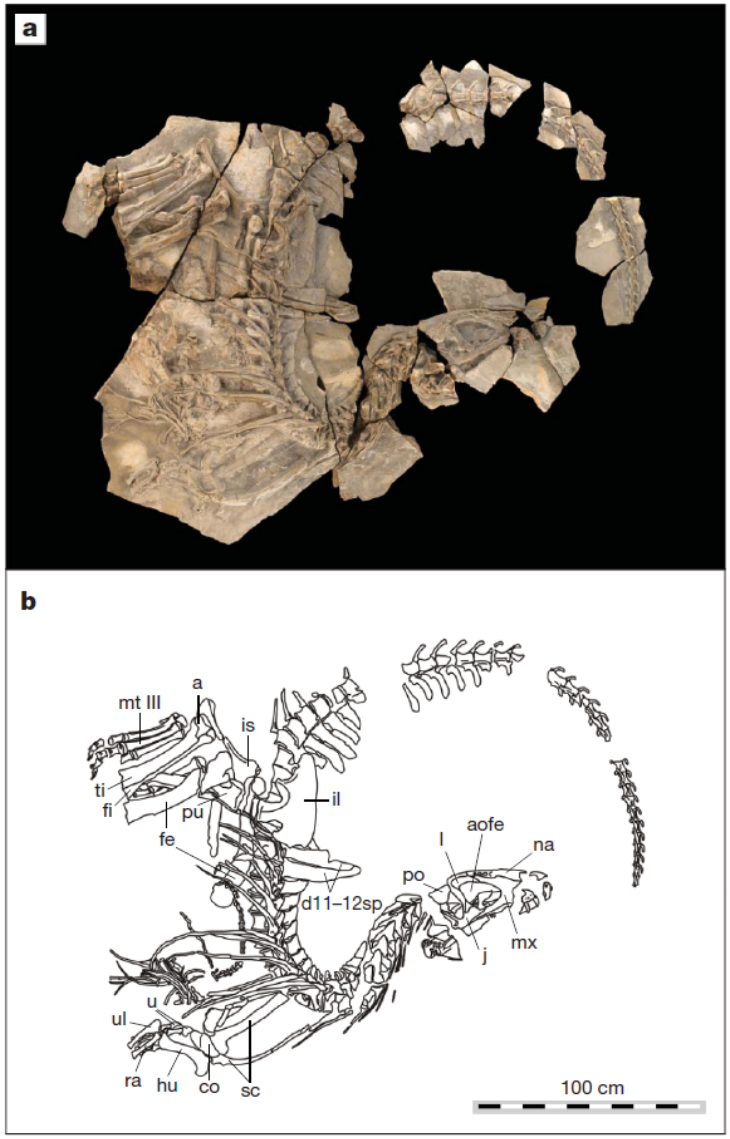
FIG. 3. Reconstruction of skull and mandible of *Sinraptor dongi* (IVPP 10600) in dorsal (A) and lateral (B) views. an, angular; aof, antorbital fenestra; ar, articular; bo, basioccipital; bs, basisphenoid–parasphenoid complex; d, dentary; ecpt, ectopterygoid; en, external naris; eo, exoccipital; ep, epipterygoid; f, frontal; j, jugal; l, lacrimal; m, maxilla; n, nasal; of, orbital fenestra; p, parietal; pal, palatine; pm, premaxilla; po, postorbital; prf, prefrontal; pra, prearticular; pt, pterygoid; qj, quadratojugal; q, quadrate; sa, surangular; so, supraoccipital; sq, squamosal; vo, vomer. Scale bar = 10 cm.

Formas basales de Tetanuros aún retienen un metacarpo IV bien desarrollado, pero carente de falanges

Carcharodontosauridae



Giganotosaurus carolini



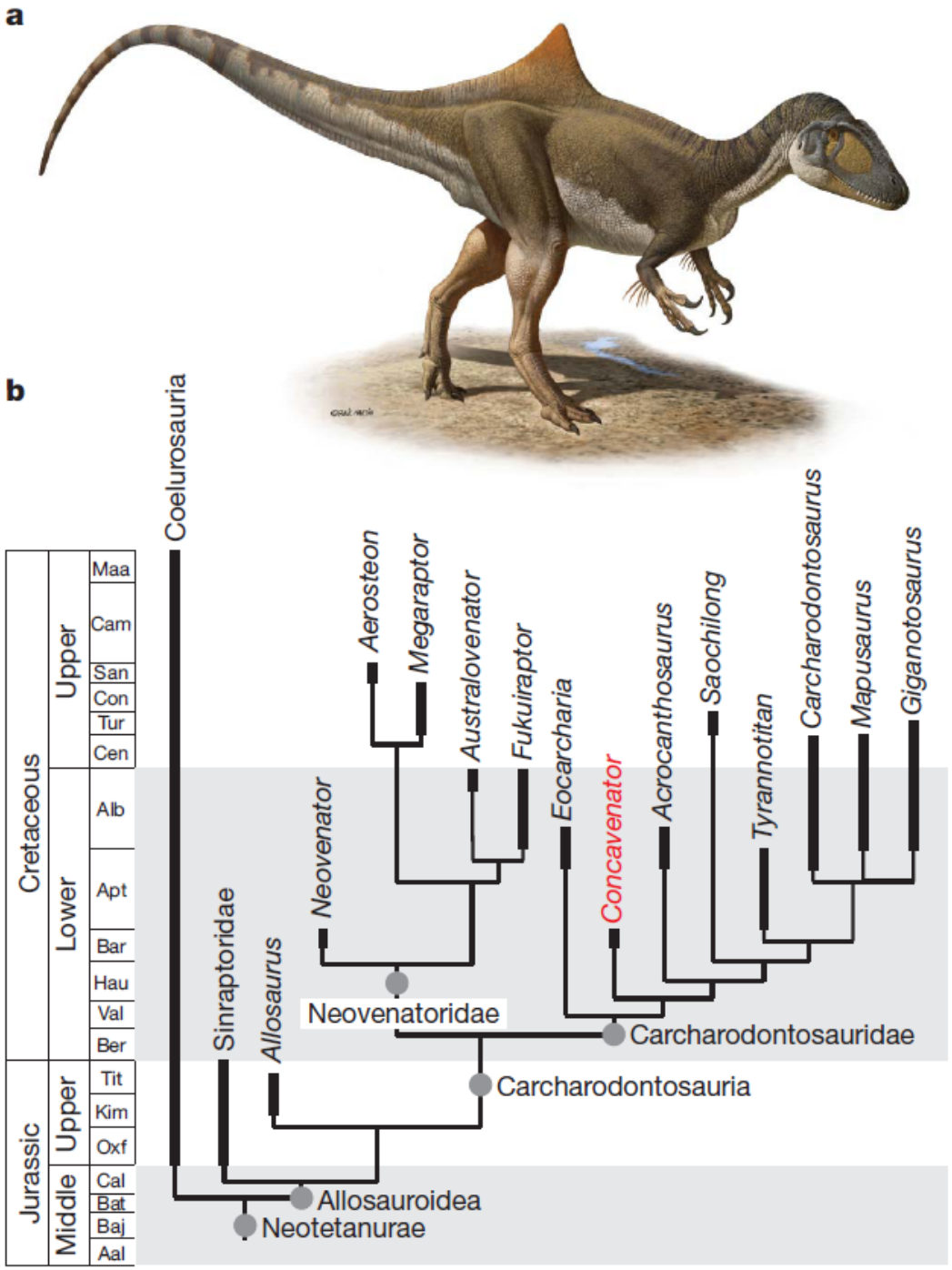
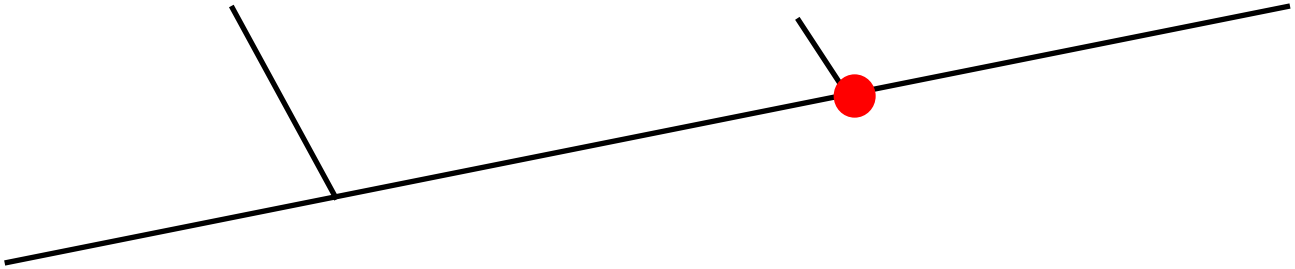


Figure 1 | Holotype of *Concavenator corcovatus*. Specimen MCCM-LH 6666 from the Lower Cretaceous series (Barremian stage) of Las Hoyas (Cuenca, Spain). **a**, Photograph under visible light. **b**, Schematic interpretation of the exposed right side of the skeleton. a, astragalus; aofe, antorbital fenestra; co, coracoid; d11–12sp, neural spines of the eleventh and twelfth dorsal vertebrae; fe, femur; fi, fibula; hu, humerus; il, ilium; is, ischium; j, jugal; l, lacrimal; mt III, third metatarsal; mx, maxilla; na, nasal; po, postorbital; pu, pubis; ra, radius; sc, scapula; ti, tibia; u, ungual phalanx; ul, ulna.

Coelurosauria

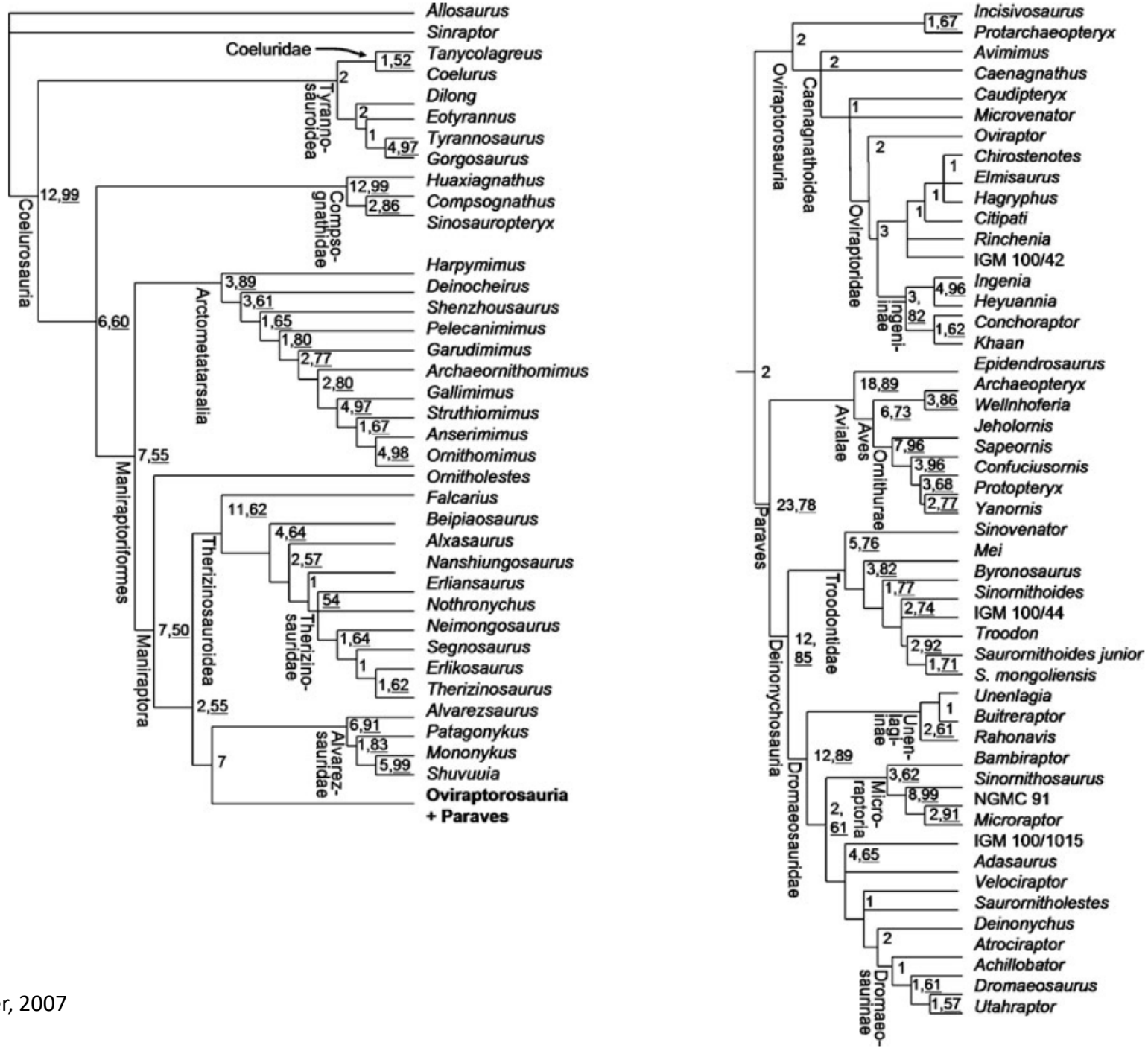
Clado más inclusivo que contiene a *Columba livia* pero no a *Allosaurus fragilis*



Coelurosauria is a diverse clade of tetanuran theropods that are phylogenetically defined as the most inclusive clade containing Passer domesticus but not Allosaurus fragilis, Sinraptor dongi and Carcharodontosaurus saharicus (Holtz, 1994; Sereno, 2005).

Sinpomorfías:

- Alargamiento de la tibia y los metatarsos
- Reducción del isquión
- Órbita circular y expandida
- 15 o menos vértebras caudales con procesos transversos


Allosaurus
Sinraptor
Coeluridae
Tanycolagreus
Coelurus
Dilong
Eotyrannus
Tyrannosaurus
Gorgosaurus
Tyranno-
sauroidea
Huaxiagnathus
Compsognathus
Sinosauropteryx
Compso-
gnathidae
Coelurosauria
Harpymimus
Deinocheirus
Shenzhousaurus
Pelecanimimus
Garudimimus
Archaeornithomimus
Gallimimus
Struthiomimus
Anserimimus
Ornithomimus
Arctometatarsalia
Ornitholestes
Falcarius
Beipiaosaurus
Alxasaurus
Nanshiungosaurus
Erliansaurus
Nothronychus
Neimongosaurus
Segnosaurus
Erlikosaurus
Therizinosaurus
Therizino-
sauridae
Therizinosauroidea
Maniraptoriformes
Maniraptora
Alvarezsaurus
Patagonykus
Mononykus
Shuvuuia
Alvarez-
sauridae
Oviraptorosauria
+ Paraves
Incisivosaurus
Protarchaeopteryx
Avimimus
Caenagnathus
Caudipteryx
Microvenator
Oviraptor
Chirostenotes
Elmisaurus
Hagryphus
Citipati
Rinchenia
IGM 100/42
Ingenia
Heyuannia
Conchoraptor
Khaan
Oviraptorosauria
Caenagnathoidea
Oviraptoridae
Ingenii-
nae
Epidendrosaurus
Archaeopteryx
Wellnhoferia
Jeholornis
Sapeornis
Confuciusornis
Protopteryx
Yanornis
Avialae
Aves
Ornithurae
Paraves
Sinovenator
Mei
Byronosaurus
Sinornithoides
IGM 100/44
Troodon
Sauromithoides junior
S. mongoliensis
Troodontidae
Deinonychosauria
Unenlagia
Buitreraptor
Rahonavis
Unen-
lagi-
nae
Bambiraptor
Sinornithosaurus
NGMC 91
Microraptor
Micro-
raptoria
IGM 100/1015
Adasaurus
Velociraptor
Sauromitholestes
Deinonychus
Atrociraptor
Achillobator
Dromaeosaurus
Utahraptor
Dromaeo-
saurinae
Dromaeosauridae

Senter, 2007

Coelurosauria basales

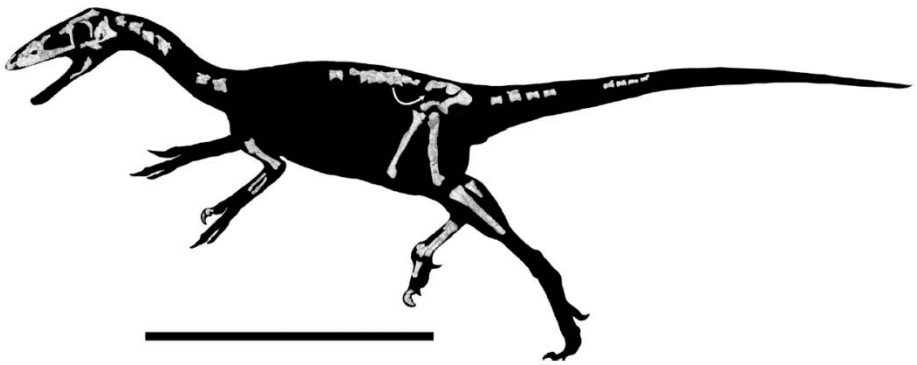


FIGURE 1. Skeletal map of *Zuolong salleei*. Scale bar equals 1 m.

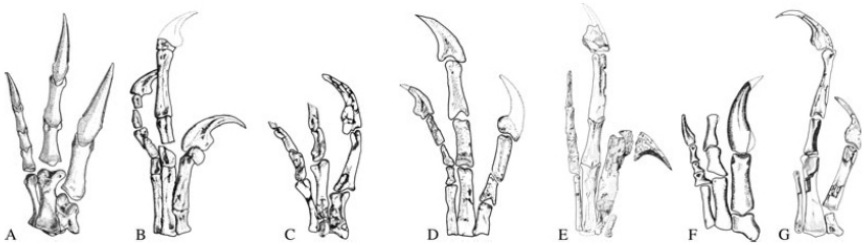
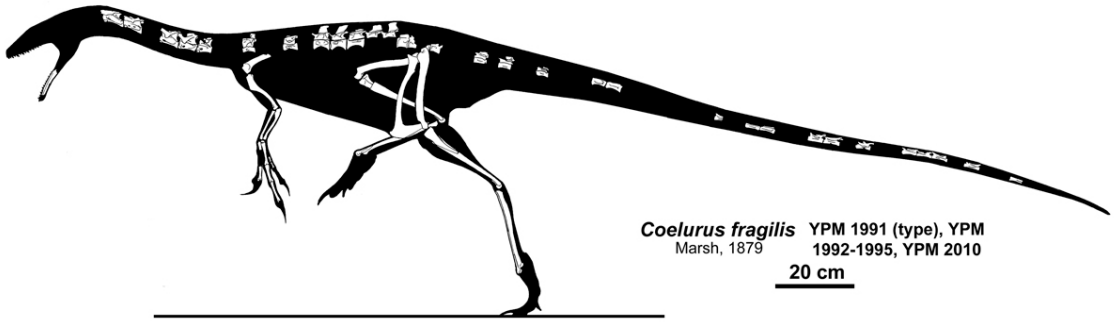


Figure 12. Comparison of hands of various coelurosaurs. A, *Allosaurus fragilis* (reconstructed from Madsen, 1976); B, *Scipionyx samnictus*; C, *Nqwebisaurus thwazi* (after DeKlerk *et al.*, 2000); D, *Huaxiagnathus orientalis* (after Hwang *et al.*, 2004); E, *Sinosauropteryx* sp. NGMC 21124; F, *Sinosauropteryx prima* (reconstructed from Currie & Chen, 2001); G, *Compsognathus longipes*.



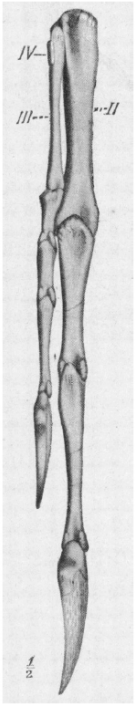


Fig. 2.—*Ornitholestes hermanni*. Amer. Mus. No. 587. Palmar view of left manus. × ½.

Tyrannosauroidea

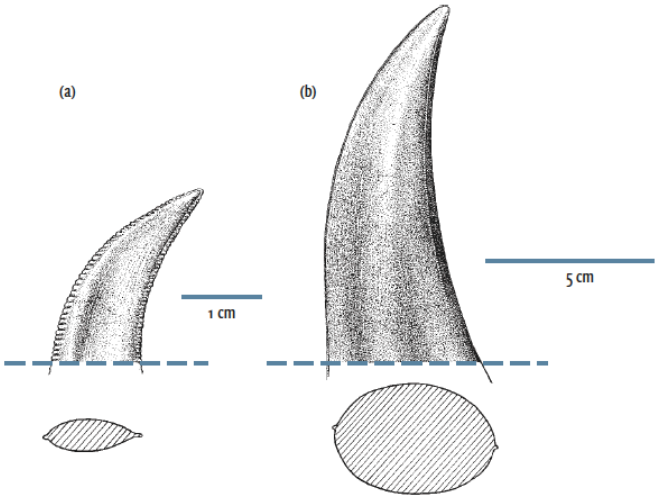


Figure 9.15. Extremes of theropod teeth compared. (a) Blade-like meat-slicing tooth of *Dromaeosaurus*; (b) bulbous bone-crunching (?) tooth of *Tyrannosaurus*.

Figure 9.17. The upper teeth of *Tarbosaurus* as seen from the right side of the skull. Scale in centimeters.

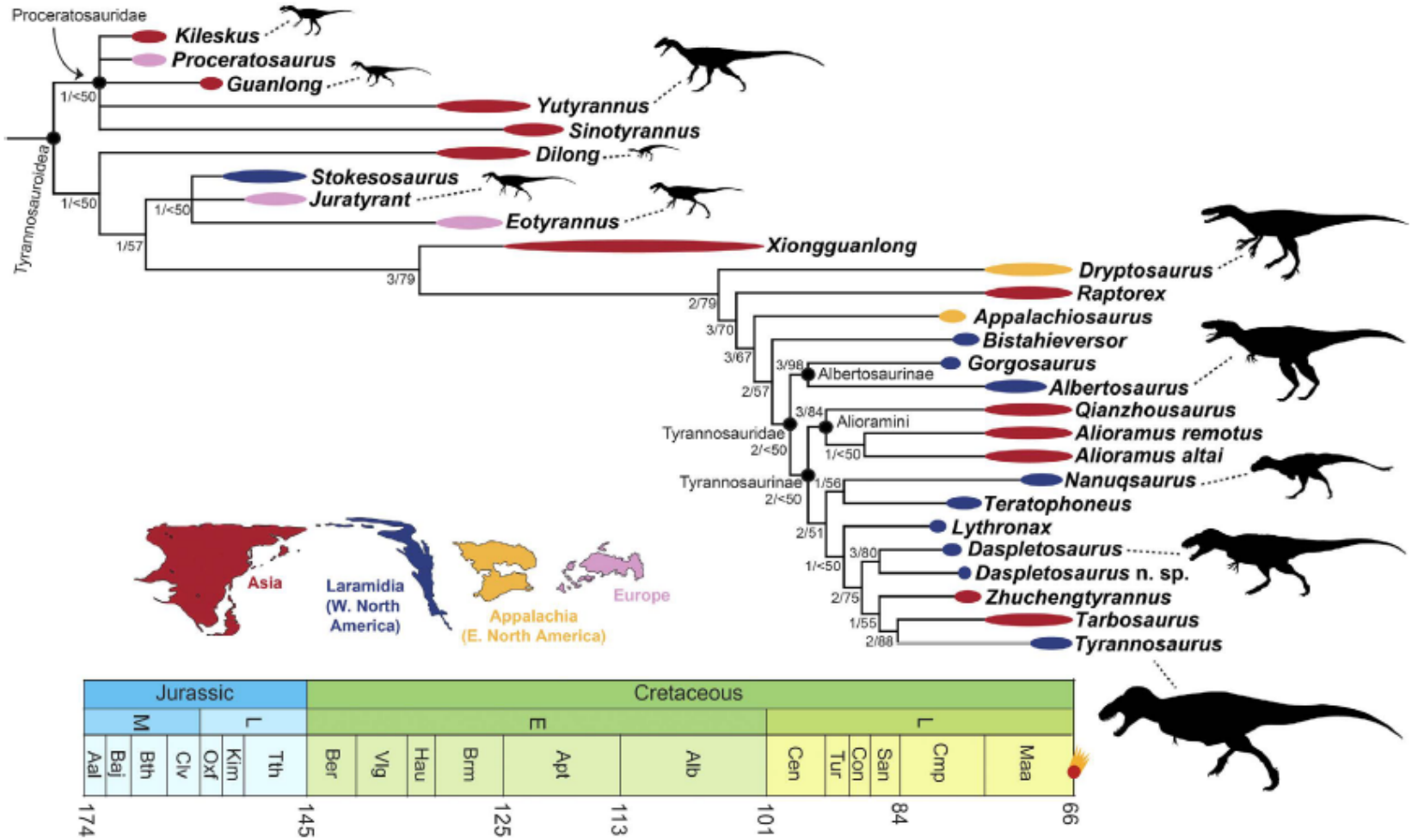


Figure 1. The phylogenetic relationships of Tyrannosauroidea, based on parsimony analysis. Strict consensus topology of five most parsimonious trees recovered from the cladistic analysis. Numbers by nodes indicate Bremer and jackknife support values. Thick lines next to each taxon depict temporal range, which in most cases is age uncertainty and not true range, and colors of lines denote geographic areas. Branches of the phylogeny are not scaled to time. Silhouettes are in relative proportion and scaled to total body length (*T. rex* = 13 meters). Geographic silhouettes from Loewen *et al.*[13] and taxon silhouettes from phylopic.org (*Kileskus*: T.M. Keesey; *Guanlong*: S. Hartman; *Yutyrannus*: S. Hartman; *Dilong*: FunkMonk; *Juratyrant*: S. Hartman, T.M. Keesey; *Eotyrannus*: S. Hartman; *Dryptosaurus* T.M. Keesey; *Albertosaurus* C. Dylke; *Nanuqsaurus* J. Headden; *Daspletosaurus* S. O'Connor, T.M. Keesey; *Tyrannosaurus* S. Hartman).

Proceratosauridae

Figure 1. *Proceratosaurus bradleyi*, type skull: NHM R 4860. A, left lateral view; B, right lateral view. Scale bars: 10 cm.

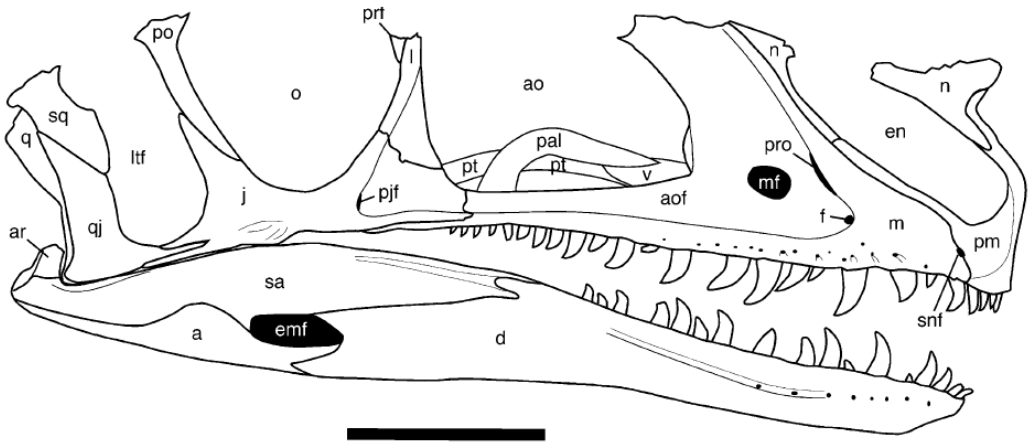
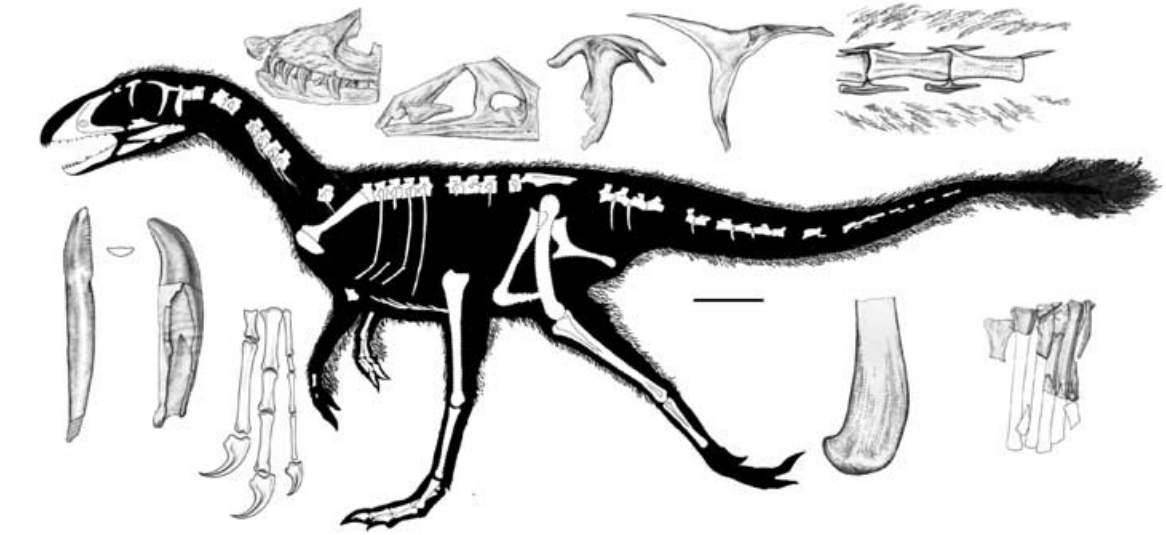
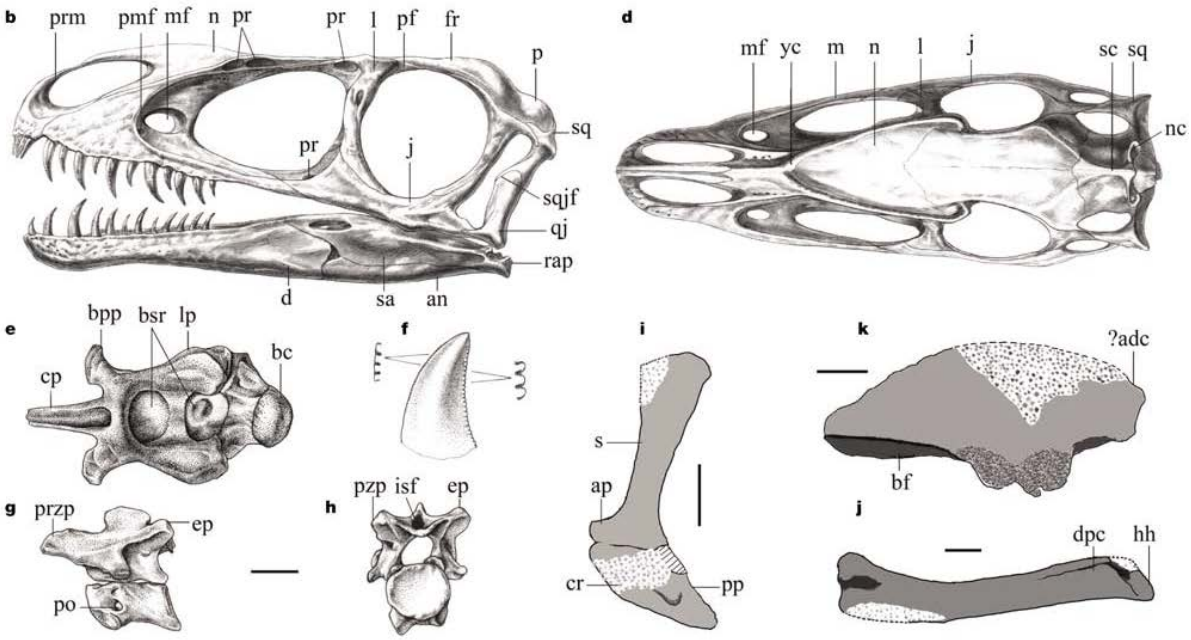
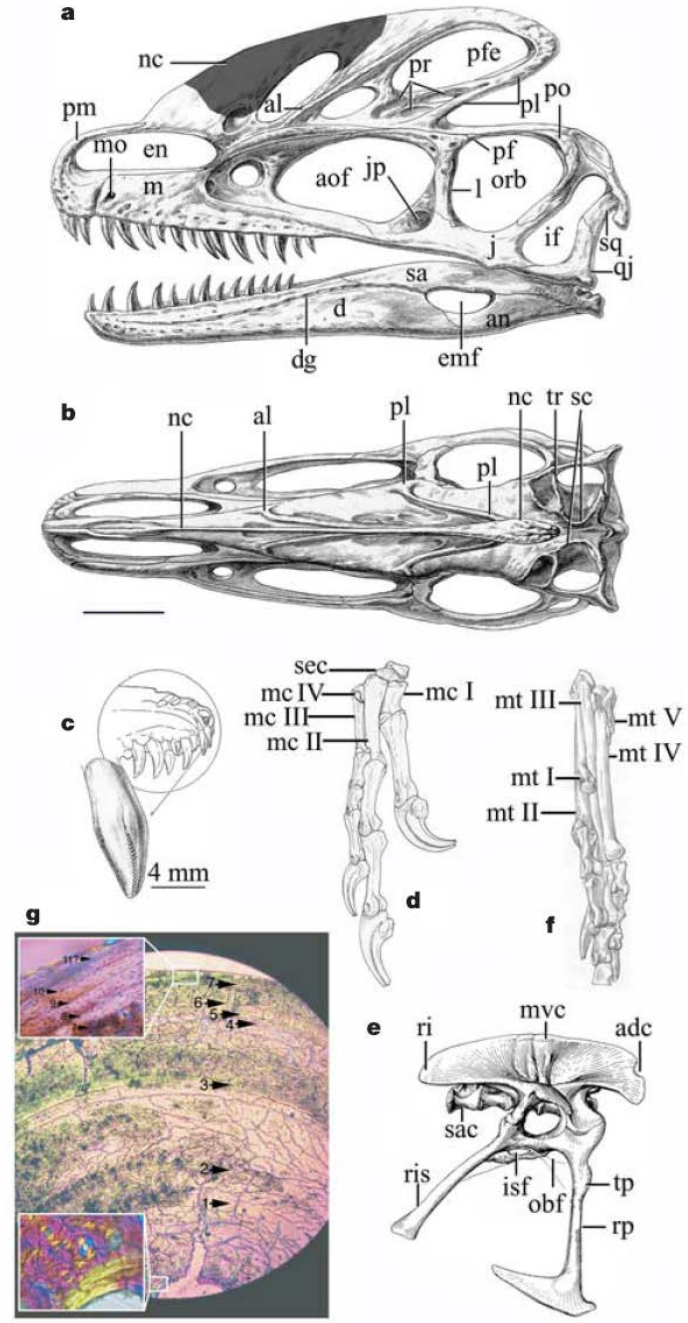


Figure 3. *Proceratosaurus bradleyi*. Reconstruction of the preserved parts of the skull in right lateral view. Abbreviations as in Figure 2, with the addition of: f, foramen; pjf, pneumatic jugal foramen. Scale bar: 50 mm.





Dilong paradoxus



Guanlong wucaii

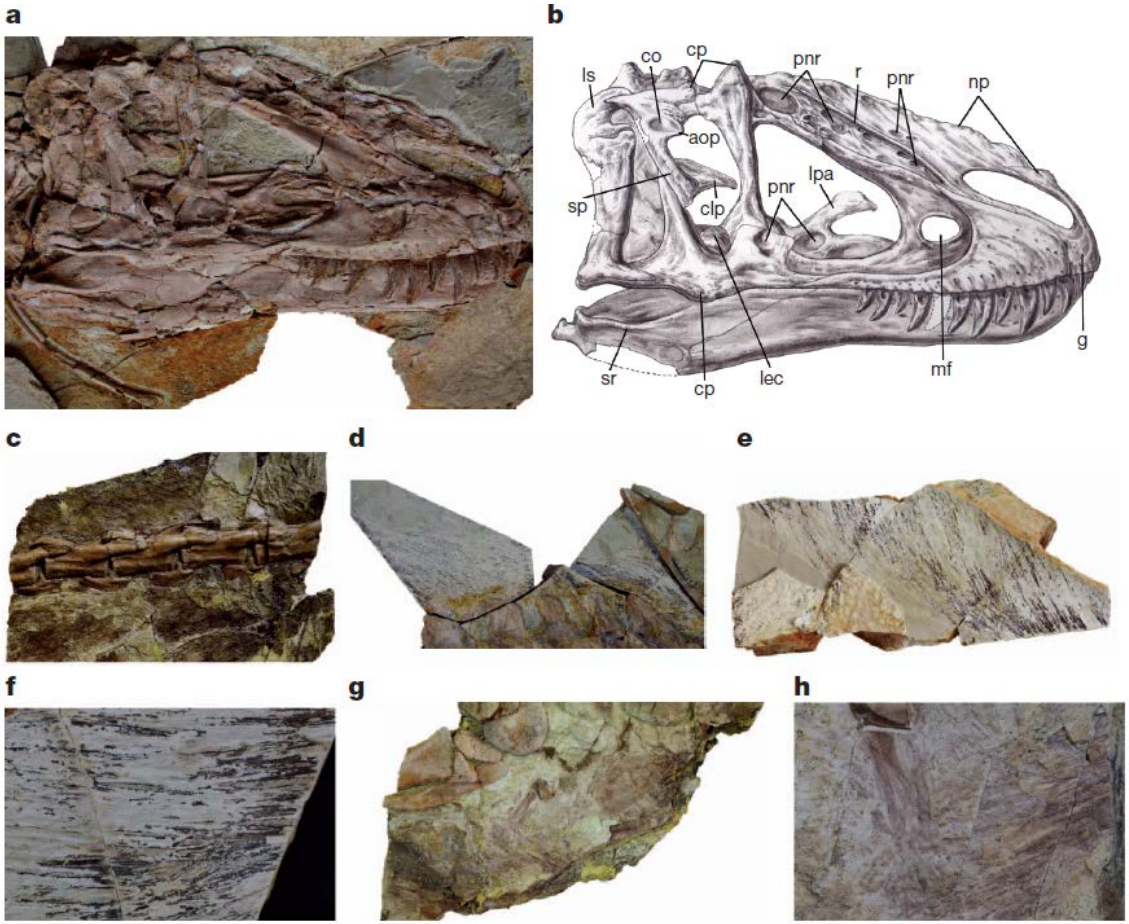


Figure 2 | Selected elements of *Y. huali* (ZCDM V5000, ZCDM V5001 and ELDM V1001). **a**, Photograph of the skull and mandible of ELDM V1001. **b**, Line drawing of the skull and mandible of ELDM V1001. **c–h**, filamentous integumentary structures preserved in the three specimens: **c**, along the posterior caudal vertebrae of ZCDM V5000; **d**, along the cervical vertebrae of ELDM V1001; **e**, **f**, along a limb bone of ELDM V1001; **g**, **h**, near the pes of ZCDM V5001 (**f** and **h** are close-up views). Abbreviations: aop, accessory orbital process; clp, cultriform process; co, concavity; cp, cornual process; g, groove; lec, left ectopterygoid; lpa, left palatine; ls, left squamosal; mf, maxillary fenestra; np, nasal prominences; pnr, pneumatic recesses; r, ridge; sp., suborbital process; sr, surangular ridge.

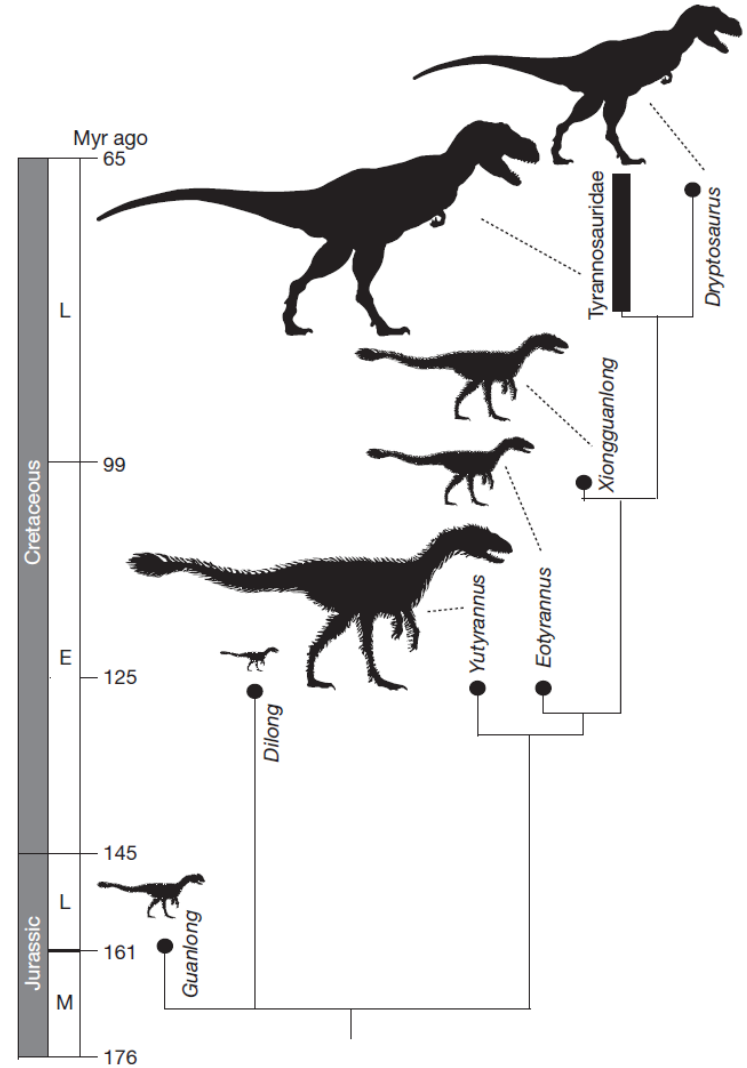
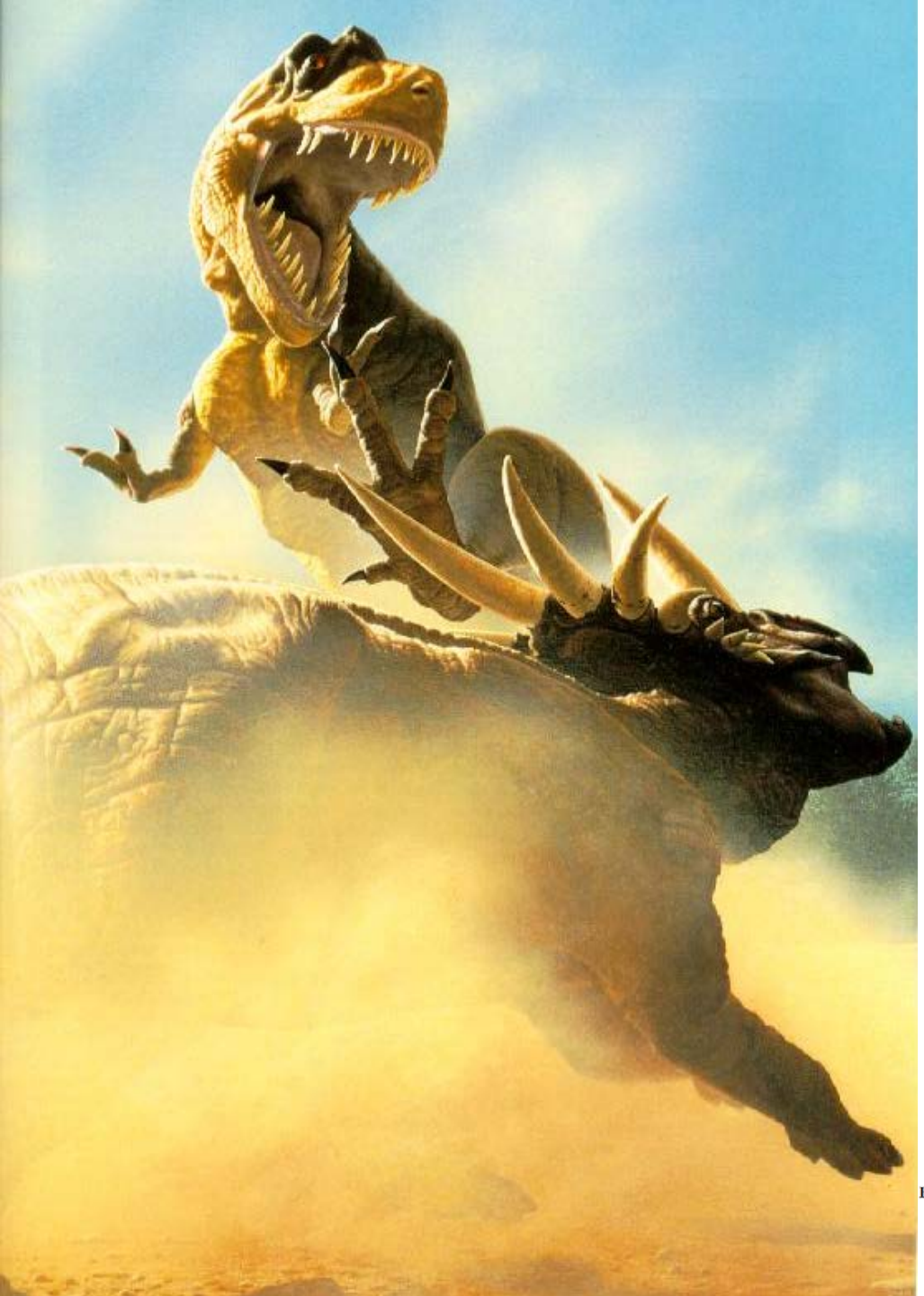


Figure 3 | A simplified cladogram showing the systematic position of *Y. huali* among the Tyrannosauroidea. Silhouettes indicate body size and possible extent of plumage. Different tyrannosauroids seem to have attained gigantic body size independently in the Early and Late Cretaceous, but only in the Early Cretaceous is there direct evidence of a gigantic form with an extensively feathered integument. This may reflect the relatively cold climate of the middle Early Cretaceous. See also Supplementary Information.



Tyrannosauridae

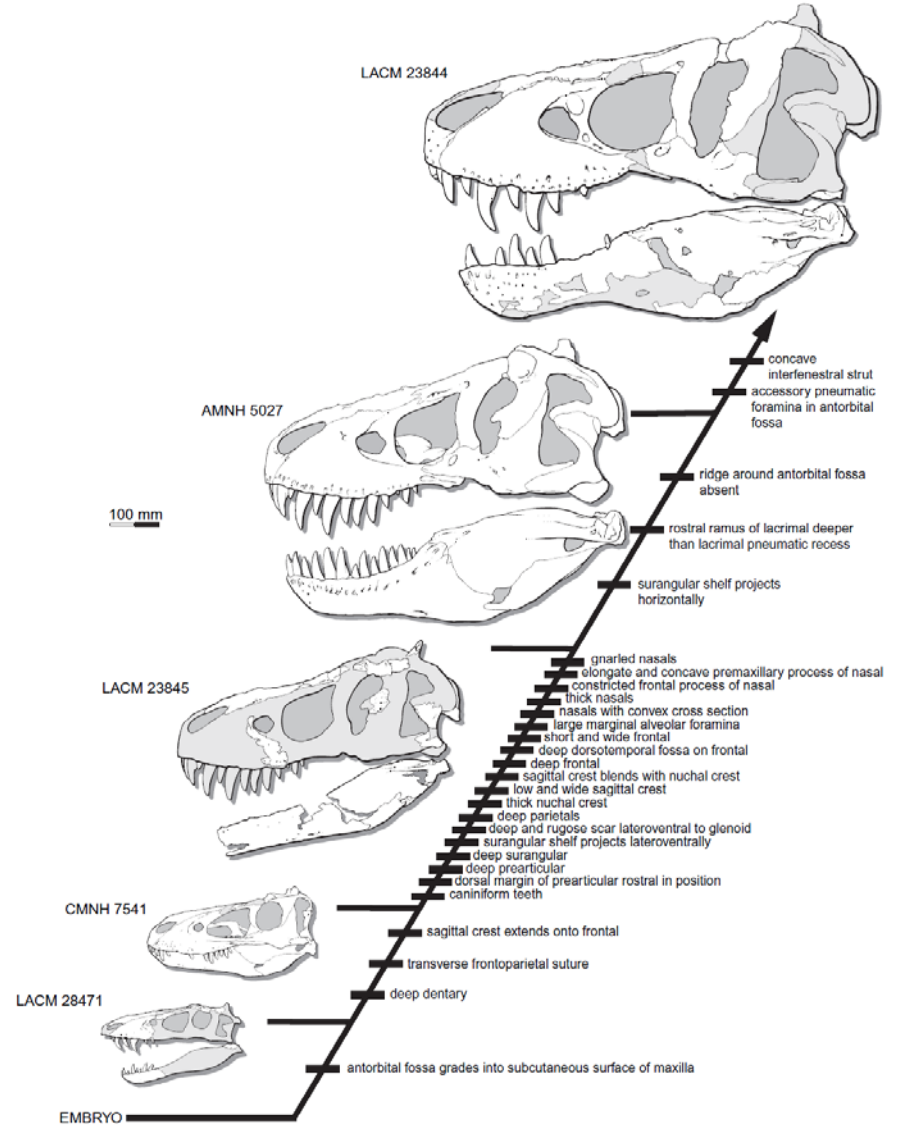
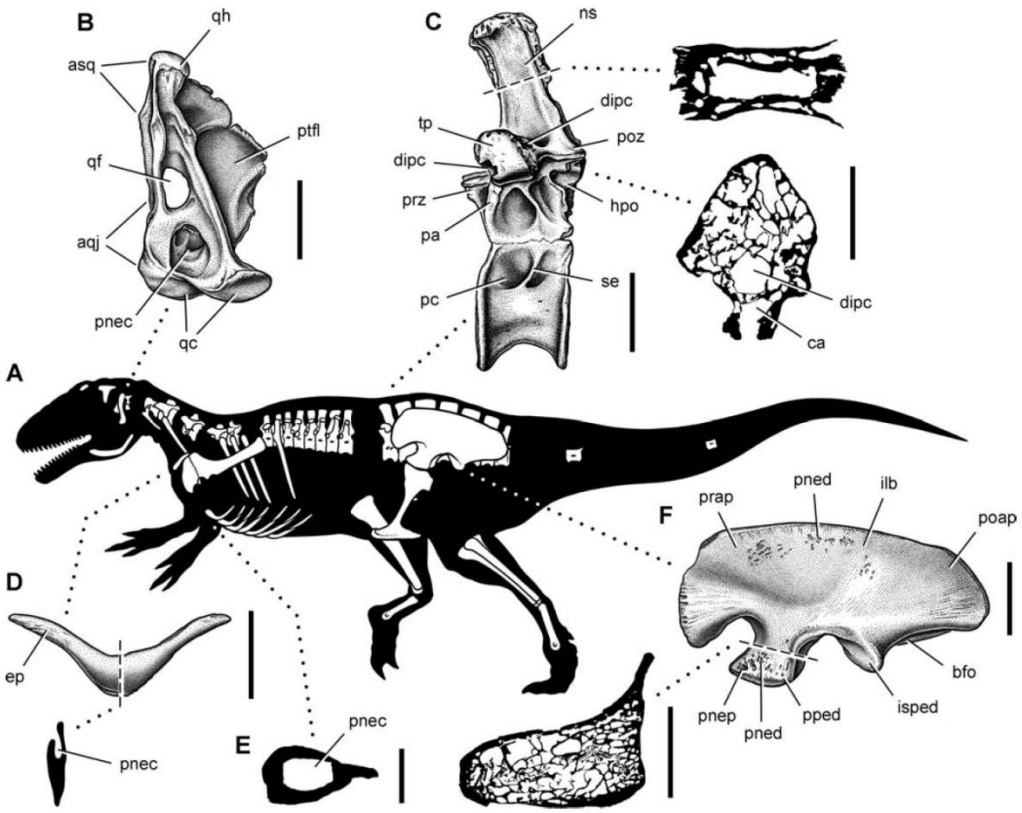
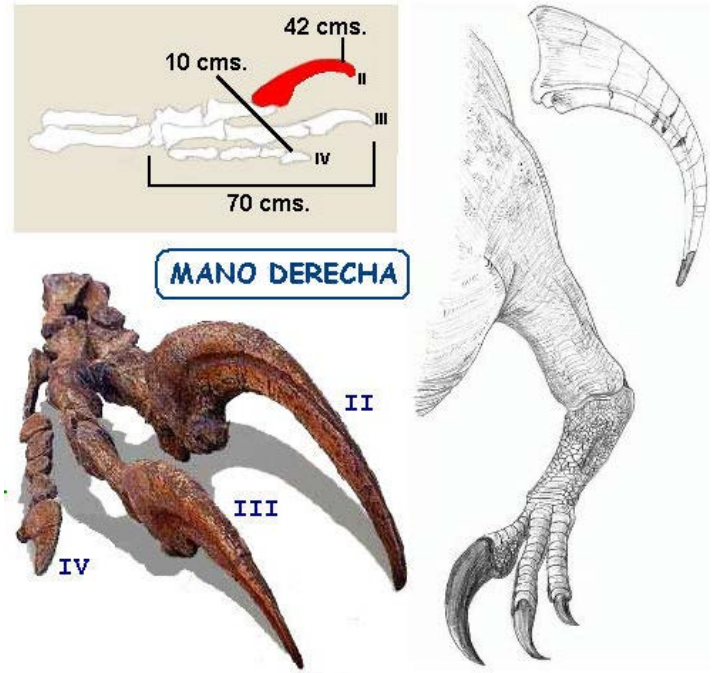


Figure 19. Diagram of the results of a quantitative reconstruction of a growth series of five *Tyrannosaurus rex* specimens

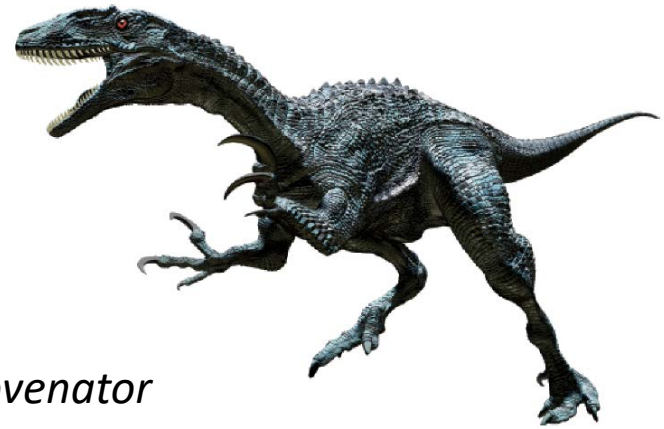
Megaraptoridae

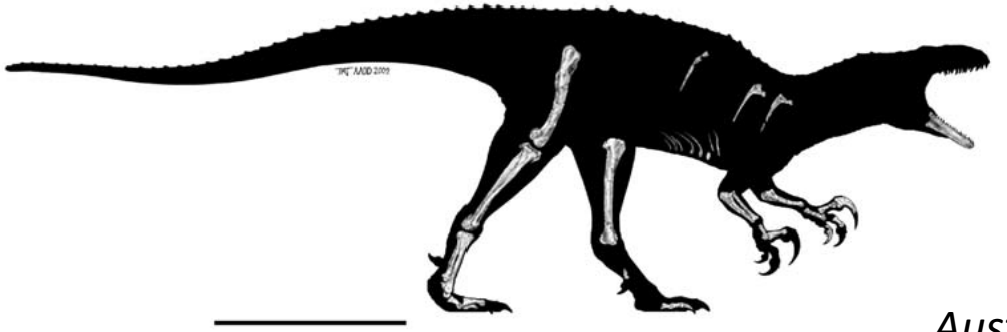
Aerosteon





Megaraptor





Australovenator

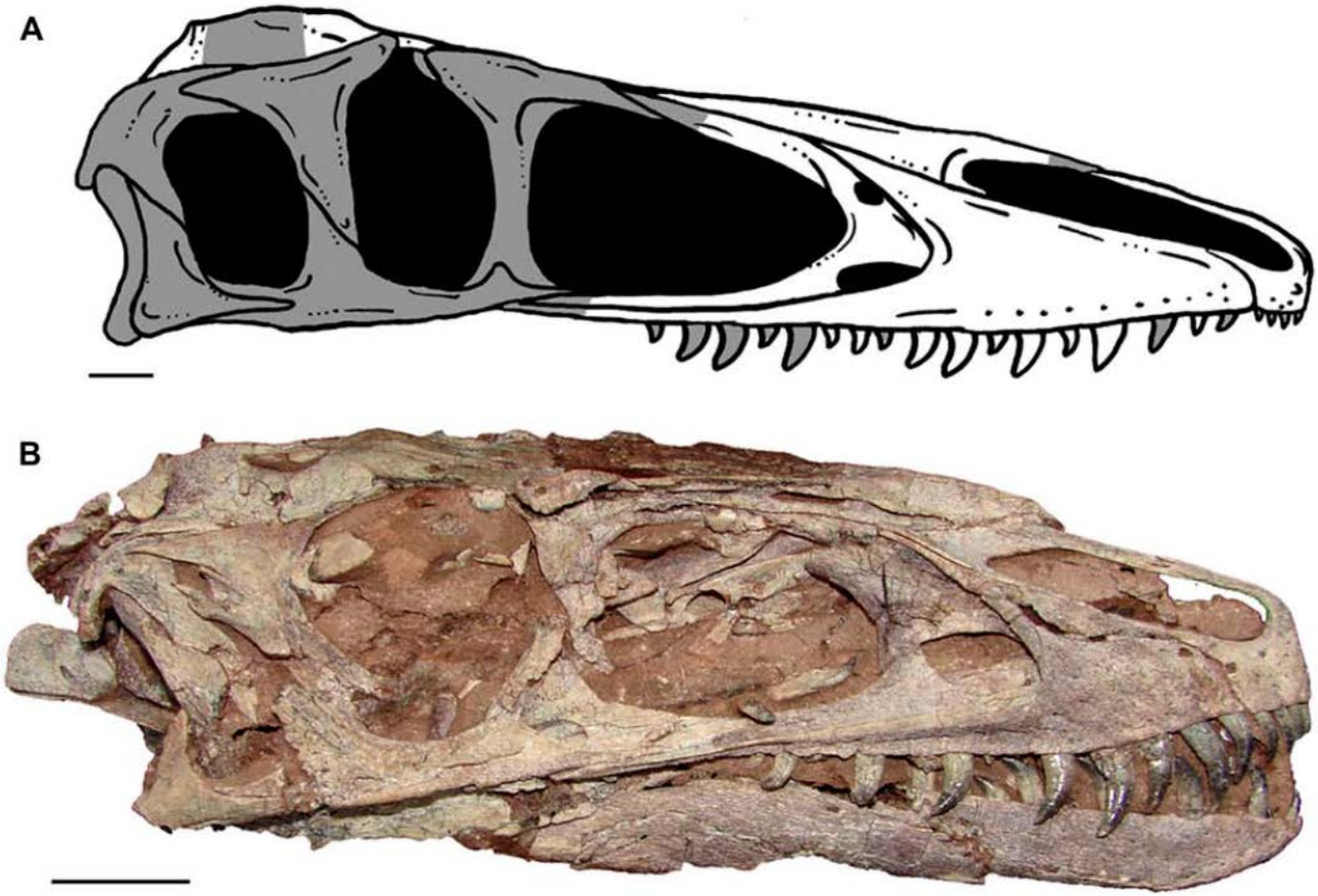
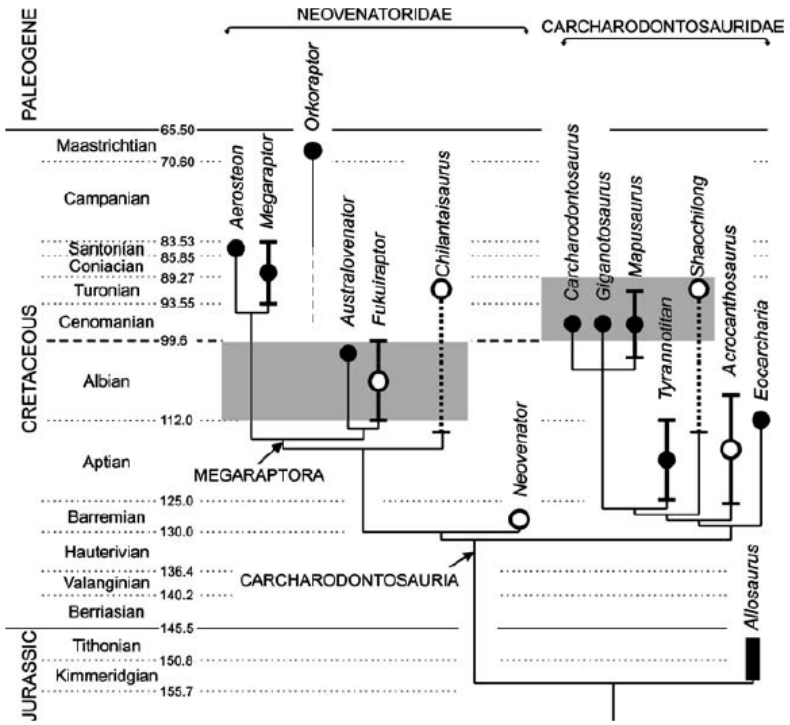


Fig. 14. (A) Cranial reconstruction of *Megaraptor namunhuaiquii* based on MUCPv 595 and (B) skull of *Dilong paradoxus* (IVPP V14243) in right lateral view. Grey tones indicate missing bones in MUCPv 595. Postorbital and quadratojugal partially based on *Orkoraptor burkei* (Novas et al., 2008). Scale bars equal 2 cm.

Porfiri et al 2014



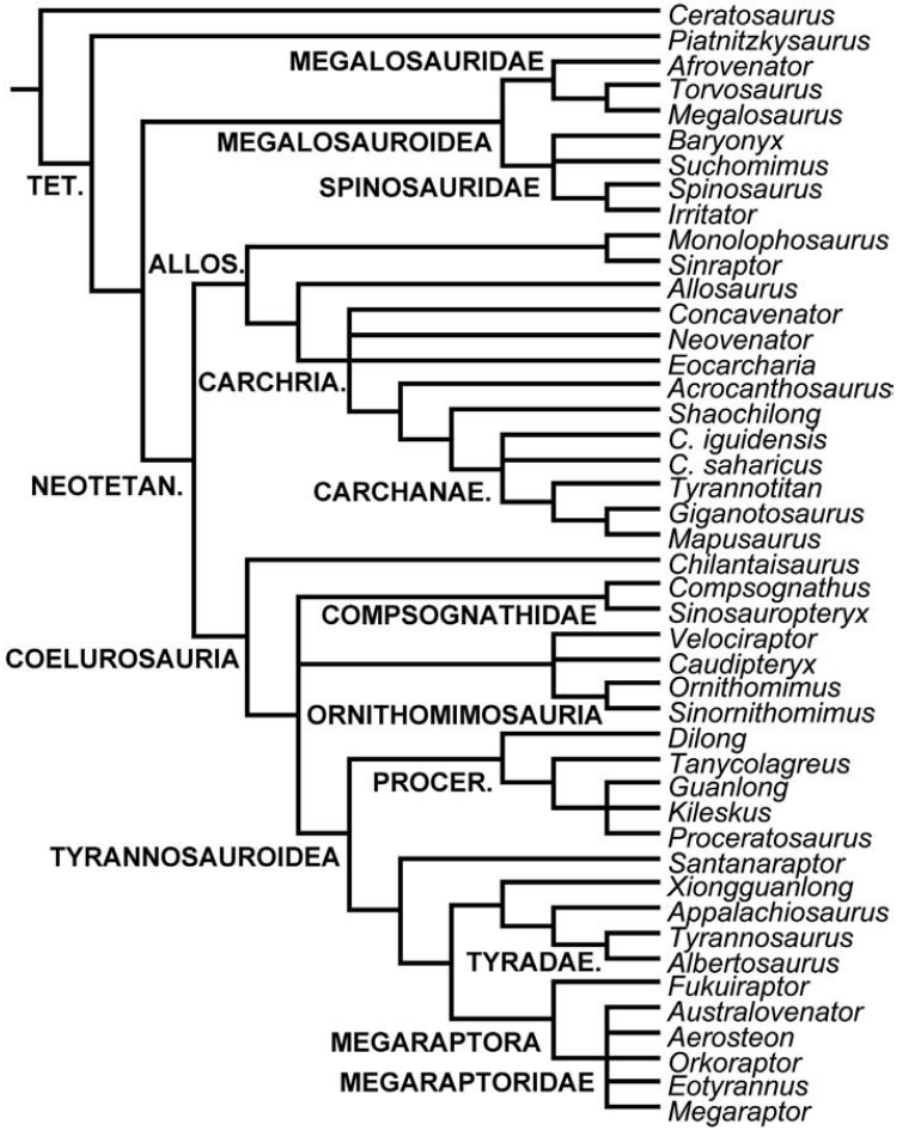
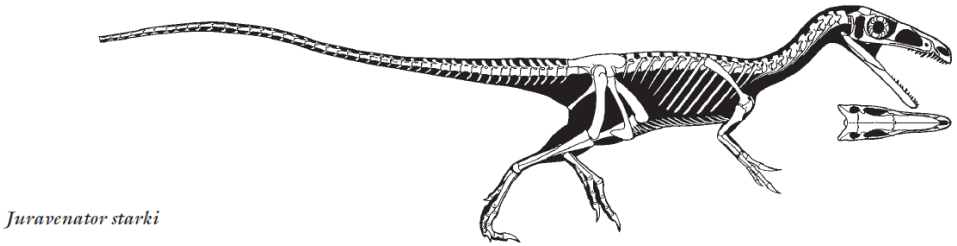
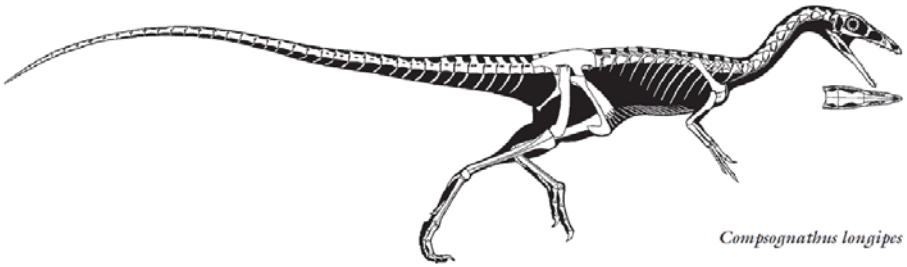


Fig. 12. Strict consensus tree of all the recovered MPTs of the present phylogenetic analysis. Abbreviations: ALLOS, Allosauroidea; CARCHANAE, Carcharodontosaurina Carcharodontosauria; NEOTETAN, Neotetanurae; PROCER, Proceratosauridae; TET, Tetanurae; TYRADAE, Tyrannosauridae.

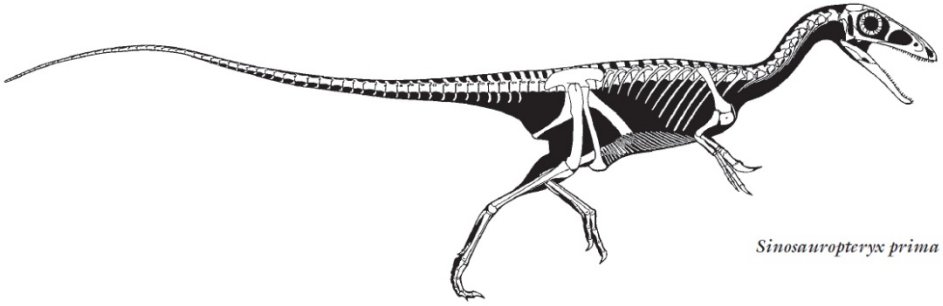
Compsognathidae



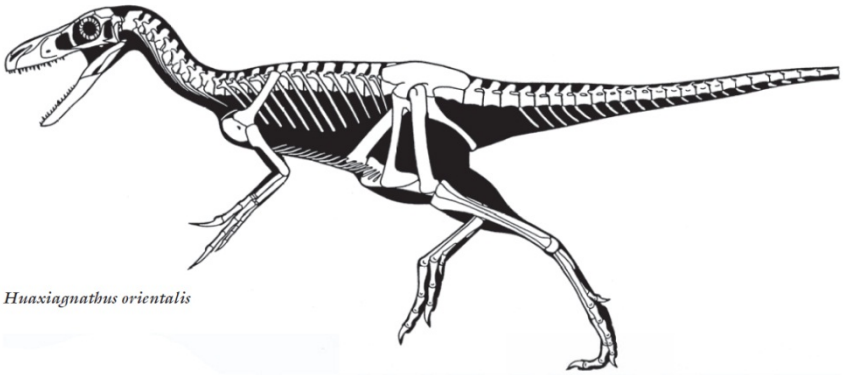
Juravenator starki



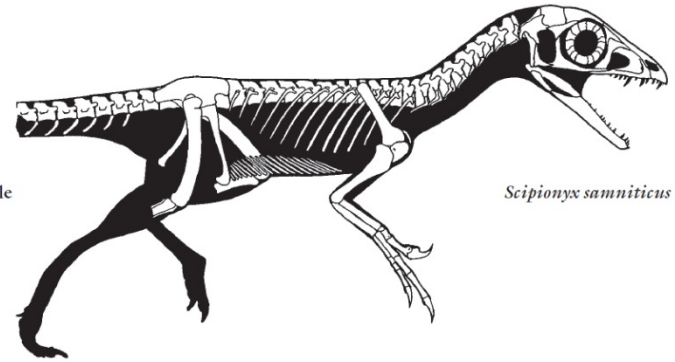
Compsognathus longipes



Sinosauropteryx prima

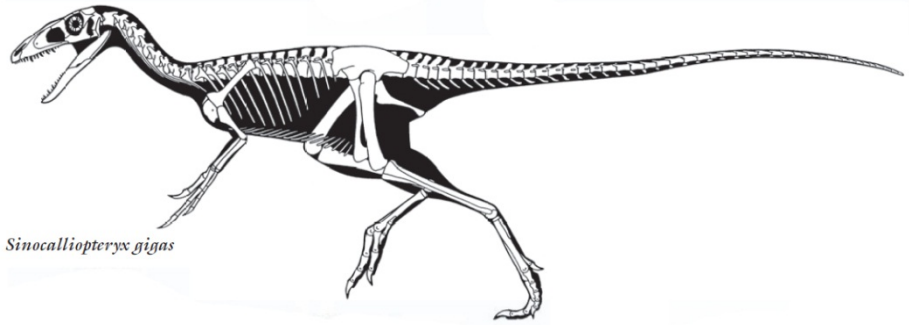


Huaxiagnathus orientalis



juvenile

Scipionyx samniticus



Sinocalliopteryx gigas


1586

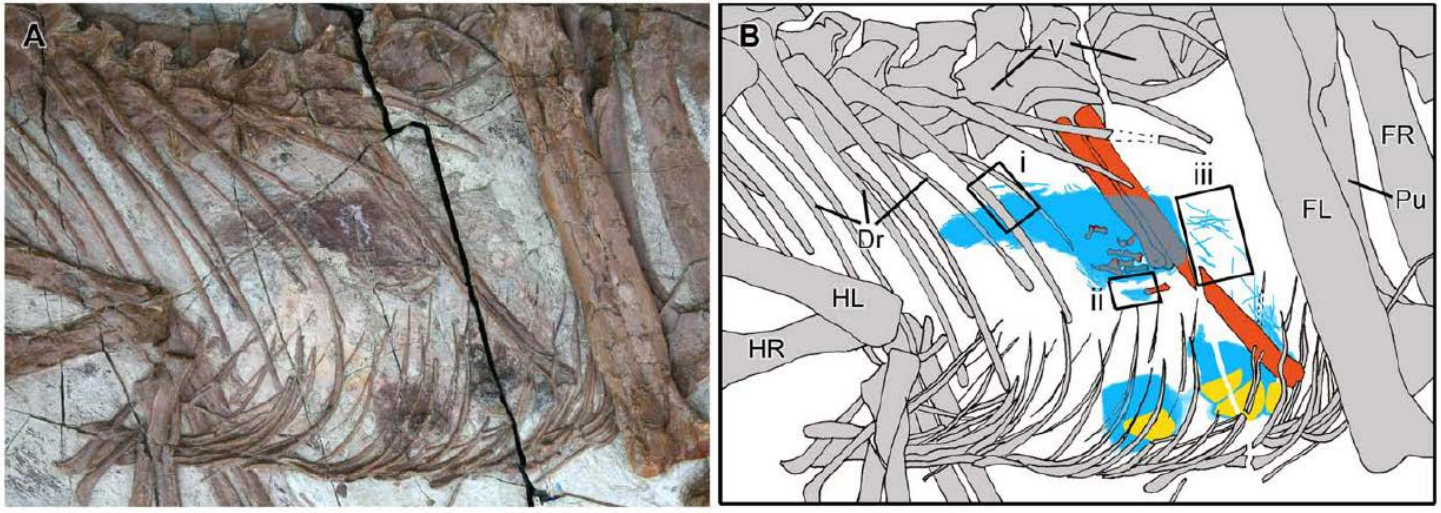


Figure 5. Abdominal contents of *Sinocalliopteryx gigas* (JMP-V-05-8-01). Blue, undigested feather-like structures; Red, dromaeosaurid hindlimb; Yellow, gastroliths. Greek numerals (i–iii) denote enlargements in Figure 5. Abbreviations: Dr, dorsal rib; F, femur; H, humerus; Pu, pubis.

Figure 8. *Sinocalliopteryx* as a stealth hunter feeding on the dromaeosaur *Sinornithosaurus* (left) and the primitive bird *Confuciusornis*

Maniraptoriformes

Clado menos inclusivo que contiene al ancestro de *Ornithomimus velox* y *Columba livia*, más todos sus descendientes. Incluye los taxa Ornithomimosauria y Maniraptora. (Holtz, 1994)

Sinapomorfías:
- Numerosos dientes en forma de hoja
- Aumento de volumen cerebral

"the cervical cranial zygapophyses are flexed; the caudal margin of the vertebral centra of cranial cervicals extends beyond the caudal margin of the neural arch; the caudal zygapophyses of the caudal cervicals are elongate; the internal tuberosity of the humerus is craniocaudally compressed and longitudinally elongate metacarpal III is subequal in length to metacarpal II; the pubic apron is limited
to the distal half of the pubic shaft; and the most proximal point
of the cranial trochanter of the femur extends above the proximal
margin of the femoral head" (Holtz, 2004)

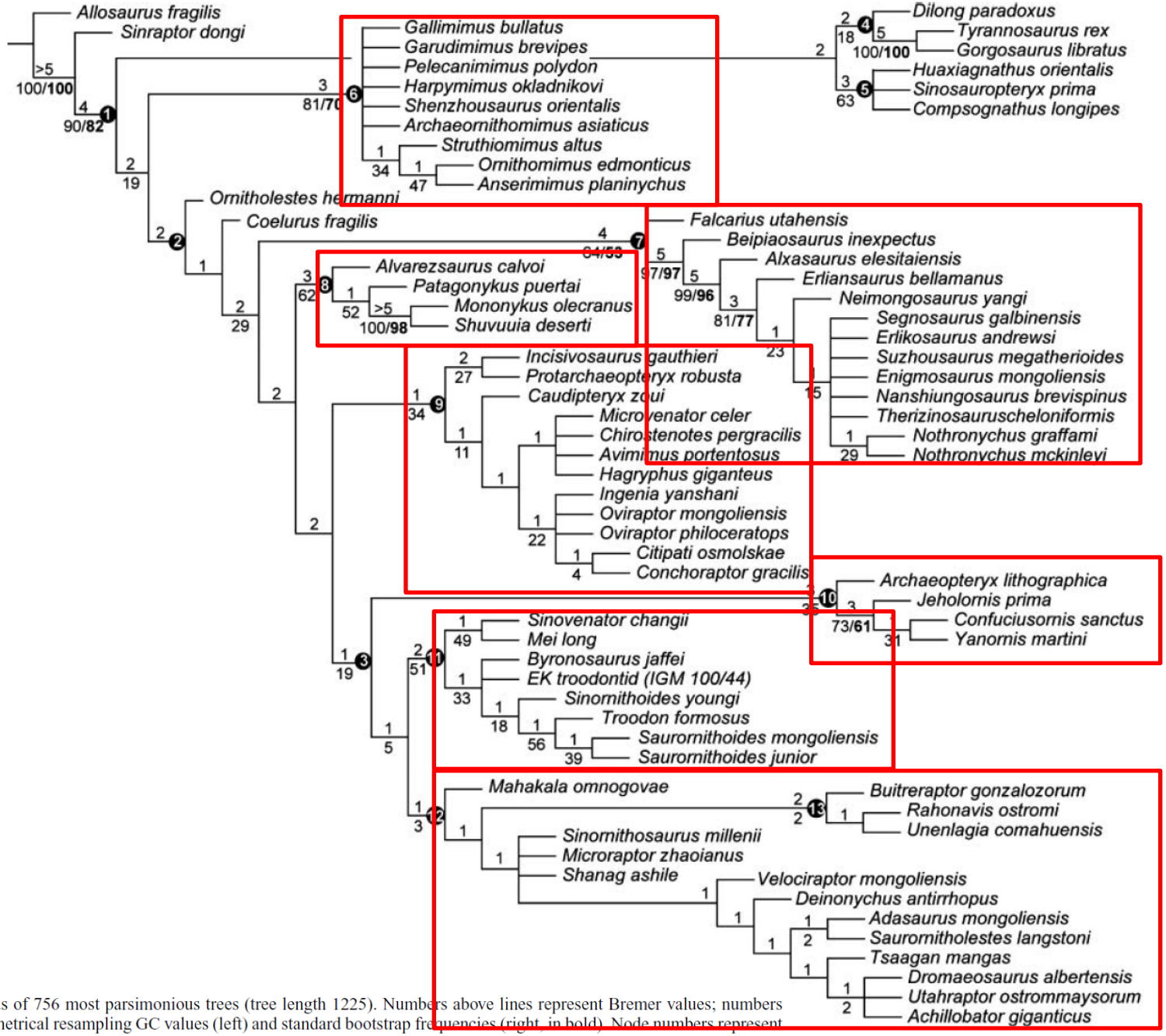
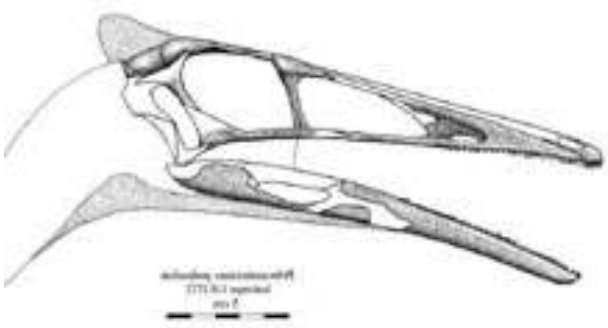


Figure 6. Strict consensus of 756 most parsimonious trees (tree length 1225). Numbers above lines represent Bremer values; numbers below line represent symmetrical resampling GC values (left) and standard bootstrap frequencies (right, in bold). Node numbers represent taxa as follows: (1) Coelurosauria; (2) Maniraptora; (3) Paraves; (4) Tyrannosauroidea; (5) Compsognathidae; (6) Ornithomimosauria; (7) Therizinosauria; (8) Alvarezsauridae; (9) Oviraptorosauria; (10) Aves; (11) Troodontidae; (12) Dromaeosauridae; (13) Unenlagiinae. Unambiguous synapomorphies shown in Appendix 3.

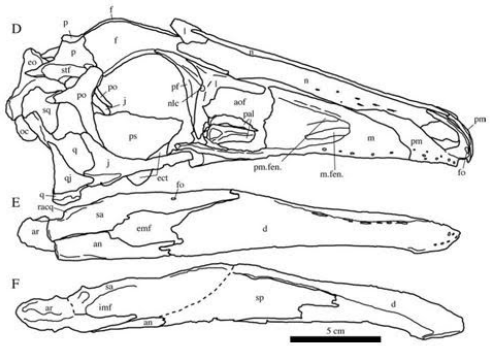
Zanno, 2010

Ornithomimosauria

Sinapomorfías:
- Cráneo pequeño
- Cuello alargado
- Metacarpales de igual longitud (de clado menos inclusivo, Ornithomimidae)
- Pérdida de dientes
- Arctometatarso

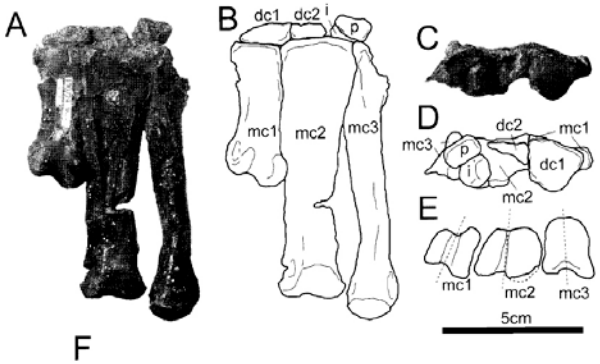


Pelecanimimus

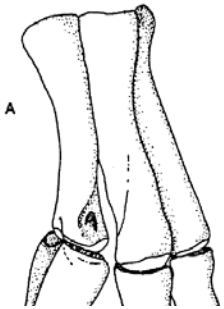


Garudimimus

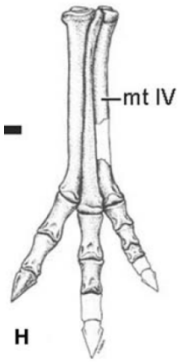
Ornithomimus



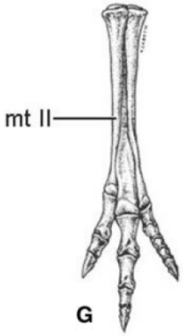
Harpymimus (Kobayashi et al 2005)



Struthiomimus
(Nicholls and Russell, 1985)



Harpymimus



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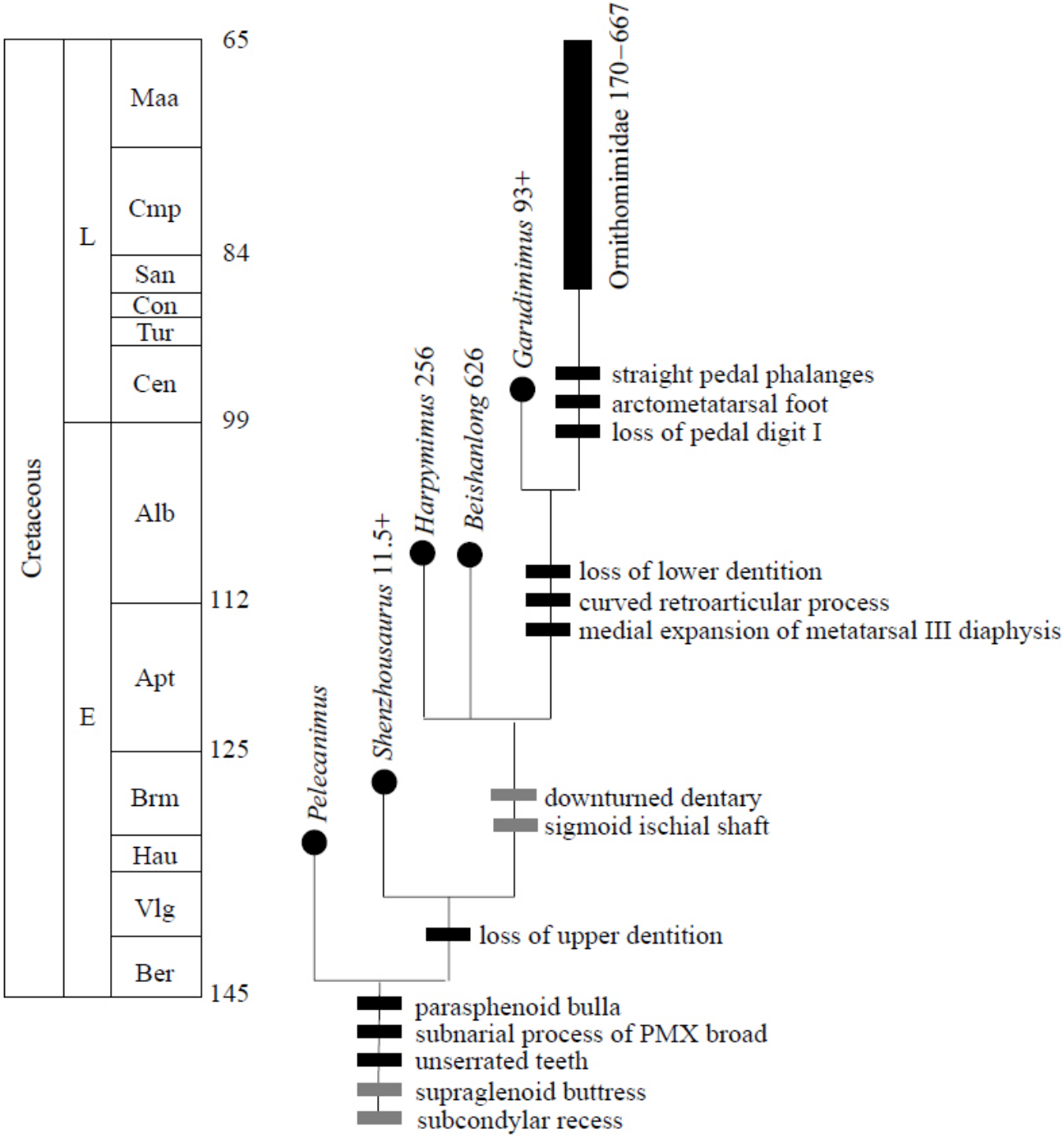
Cretaceous
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84
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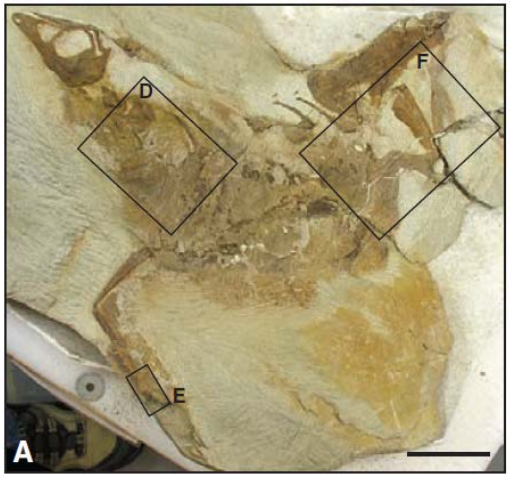
112
125
145
Ornithomimidae 170–667
Garudimimus 93+
Harpymimus 256
Beishanlong 626
Shenzhousaurus 11.5+
Pelecanimus
straight pedal phalanges
arctometatarsal foot
loss of pedal digit I
loss of lower dentition
curved retroarticular process
medial expansion of metatarsal III diaphysis
downturned dentary
sigmoid ischial shaft
loss of upper dentition
parasphenoid bulla
subnarial process of PMX broad
unserrated teeth
supraglenoid buttress
subcondylar recess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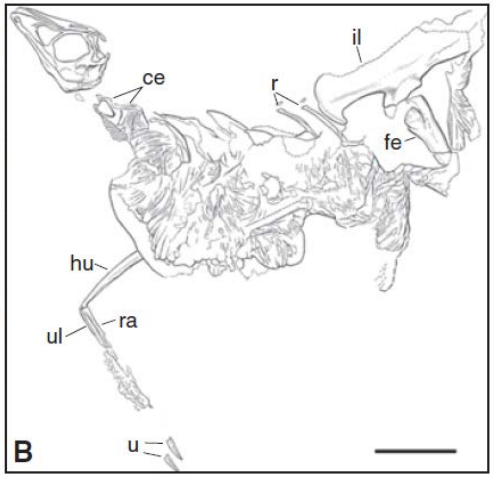
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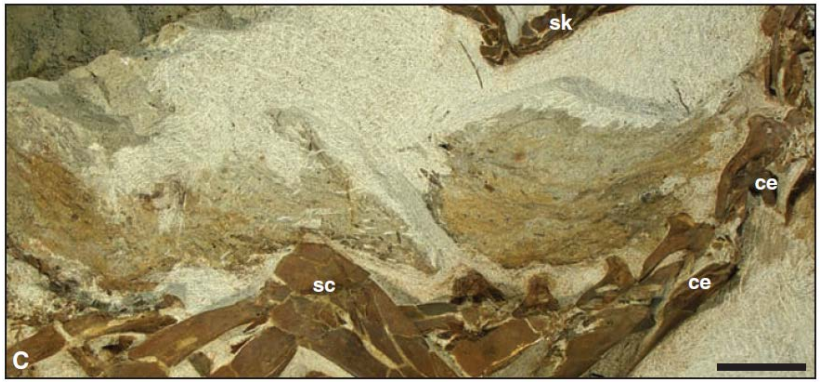
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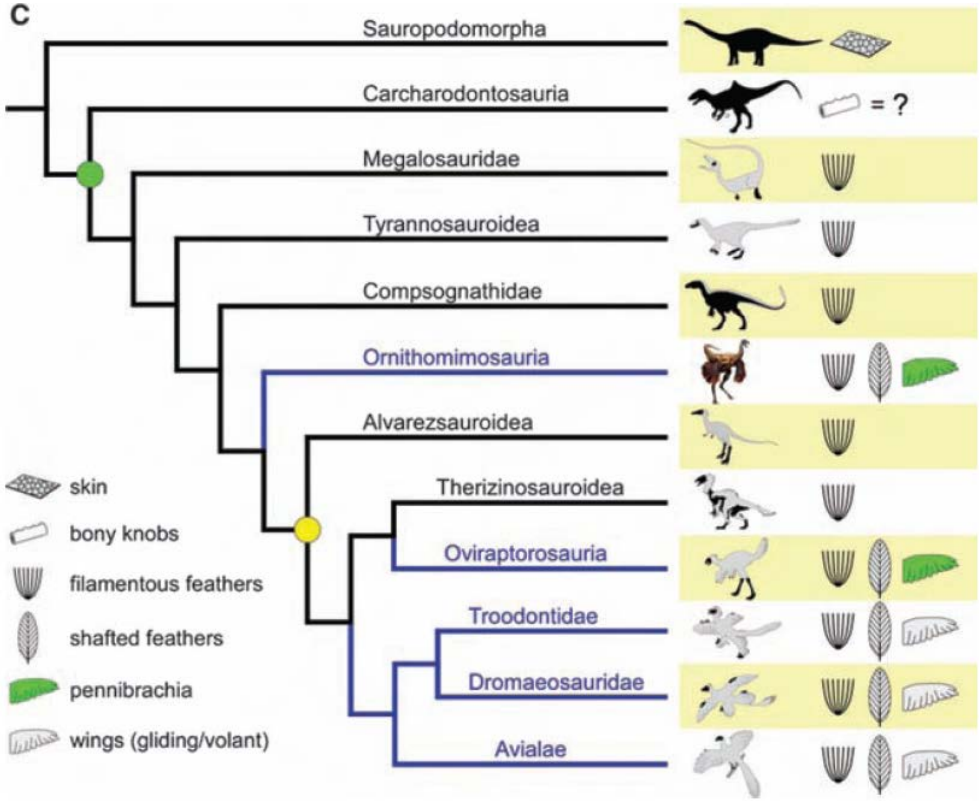
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Sauropodomorpha
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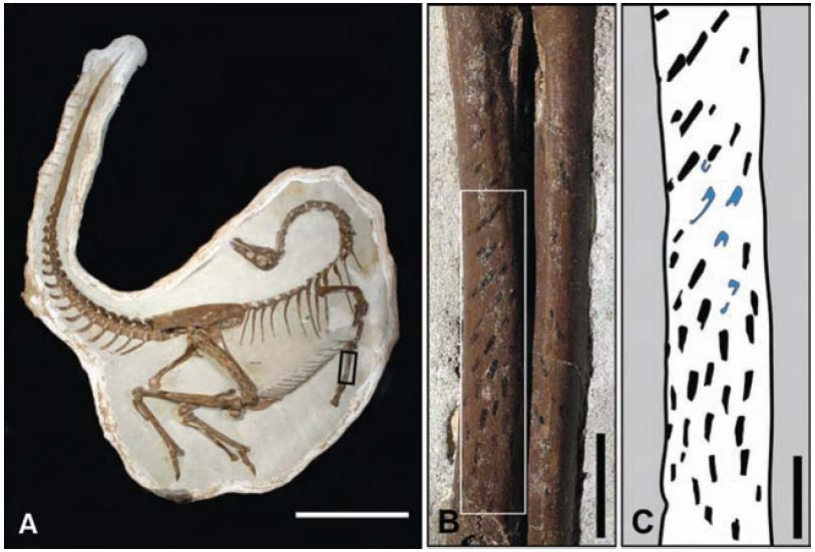
Megalosauridae
Tyrannosauroidea
Compsognathidae
Ornithomimosauria
Alvarezsauroidea
Therizinosauroidea
Oviraptorosauria
Troodontidae
Dromaeosauridae
Avialae
skin
bony knobs
filamentous feathers
shafted feathers
pennibrachia
wings (gliding/volant)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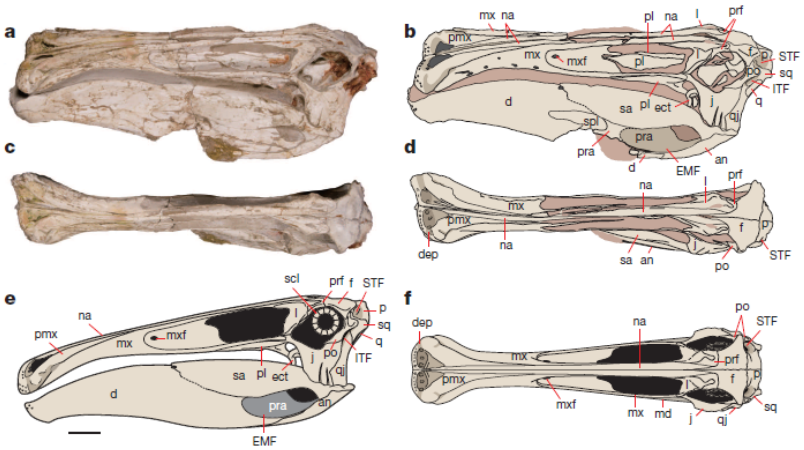


Figure 2 | Skull of *Deinocheirus mirificus* (MPC-D 100/127). **a**, **b**, Left lateral view. **c**, **d**, Dorsal view. **e**, Reconstruction in composite lateral view. **f**, Reconstruction in dorsal view. Scale bar, 10 cm. Abbreviations: an, angular; d, dentary; dep, depression; ect, ectopterygoid; EMF, external mandibular fenestra; f, frontal; ITF, infratemporal fenestra; j, jugal; l, lacrimal; md, mandible; mx, maxilla; mxf, maxillary fenestra; na, nasal; p, parietal; pl, palatine; pmx, premaxilla; po, postorbital; pra, prearticular; prf, prefrontal; q, quadrate; qj, quadratojugal; sa, surangular; scl, sclerotic ring; spl, splenial; sq, squamosal; STF, supratemporal fenestra.

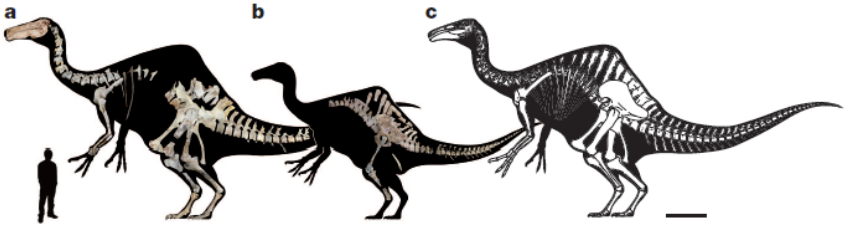
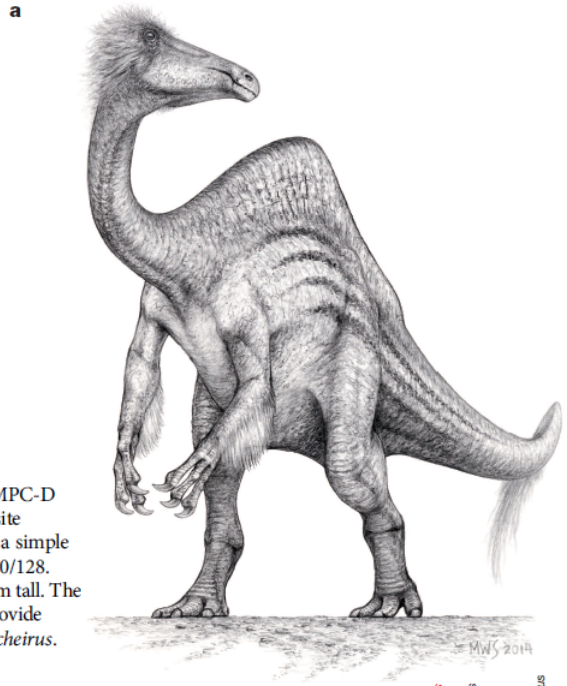


Figure 1 | *Deinocheirus mirificus*. **a**, MPC-D 100/127. **b**, MPC-D 100/128. **c**, Composite reconstruction of MPC-D 100/127 with a simple proportional enlargement of MPC-D 100/128. Scale bar, 1 m. The human outline is 1.7 m tall. The holotype and the two new specimens provide almost all skeletal information of *Deinocheirus*.



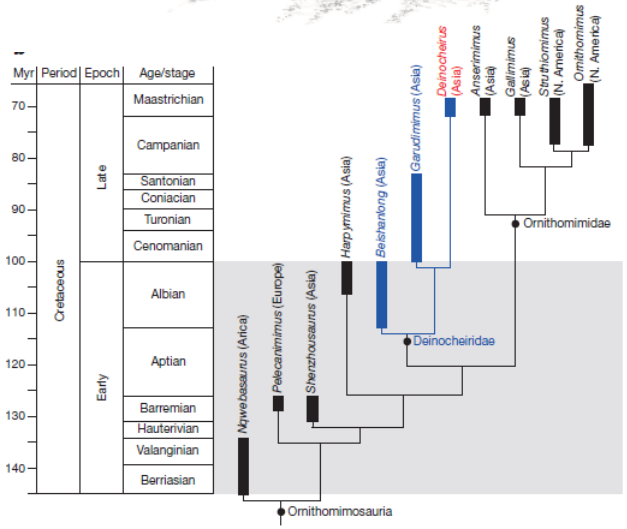
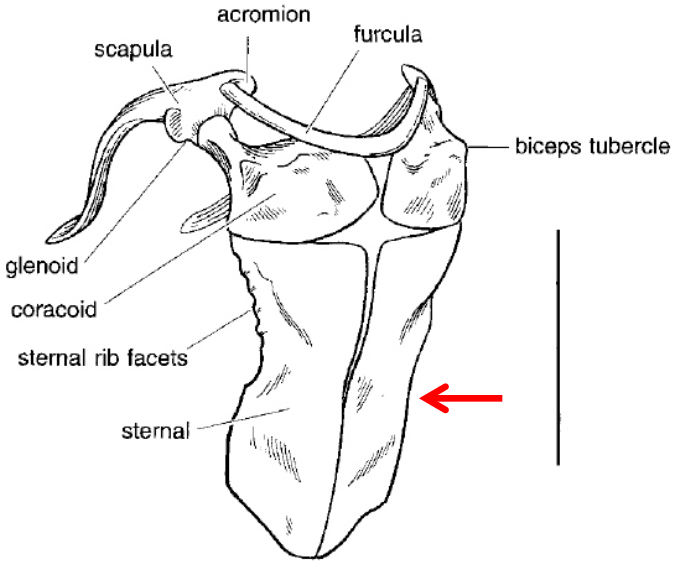


Figure 4 | Phylogenetic relationships of *Deinocheirus mirificus* within Ornithomimosauria. **a**, Hypothetical fleshed-out reconstruction of *Deinocheirus mirificus* (by Michael Skrepnick). **b**, Time-scaled strict consensus tree of the six most-parsimonious trees from our analysis (tree length = 2,927, consistency index = 0.22, retention index = 0.59; Supplementary Information). In this hypothesis *Deinocheirus* is a derived taxon of the Deinocheiridae, which is the sister-group of the Ornithomimidae.

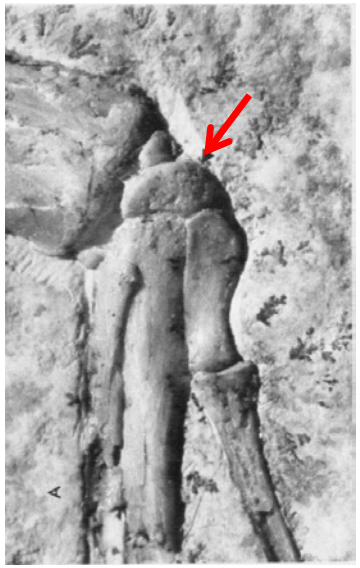
Maniraptora

Clado más inclusivo que contiene a *Columba livia*, pero no *Ornithomimus velox.*
Incluye los taxa Alvarezsauroidea, Therizinosauria, Oviraptorosauria y Paraves.

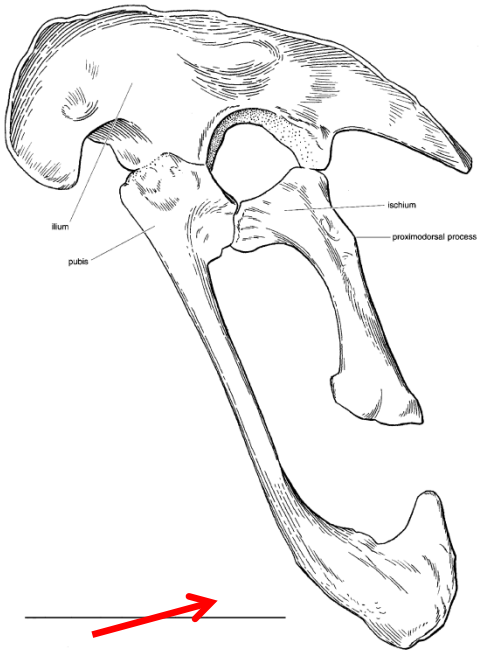
Sinapomorfías:
- Antebrazo alargado
- Esternón grande y osificado
- Carpal semilunar verdadero, formado por carpales distal 1 y 2 en igual proporción
- Pubis retrovertido



Bambiraptor



Deinonychus

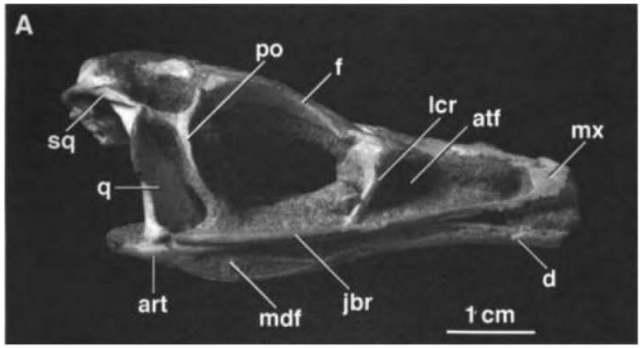


4. *Bambiraptor feinbergi* n. gen. and n. sp., holotype (FIP 001), pelvic girdle in lateral view. Scale bar: 5 cm (new).

Bambiraptor

Alvarezsauroidea

Clado más inclusivo que contiene a *Alvarezsaurus calvoi*, pero no a *Columba livia*.



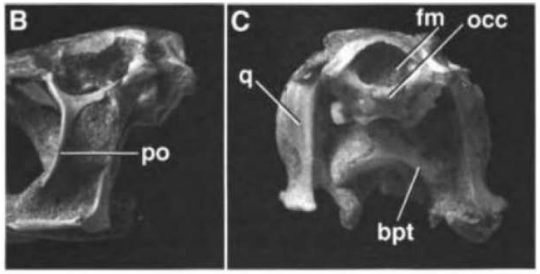
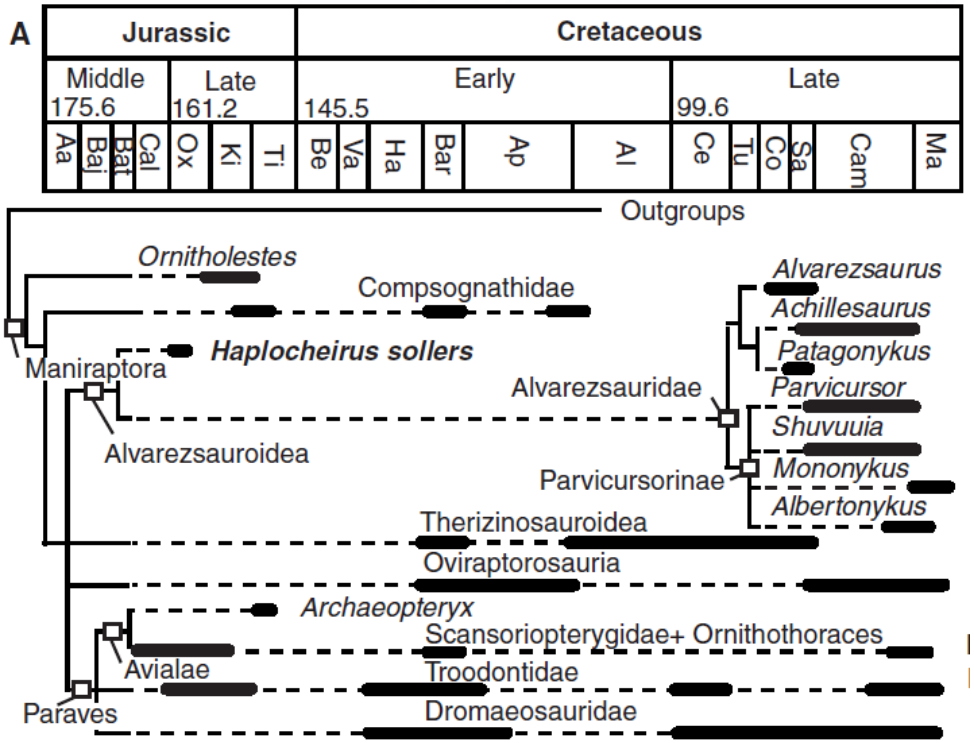


Figure 4.5. Skull of *S. deserti* (MGI 100/1001) in right lateral (A), left lateral (B; only postorbital region), and occipital (C) views. Abbreviations: bpt, basipterygoid process; fm, foramen magnum; others as in Figure 4.3.



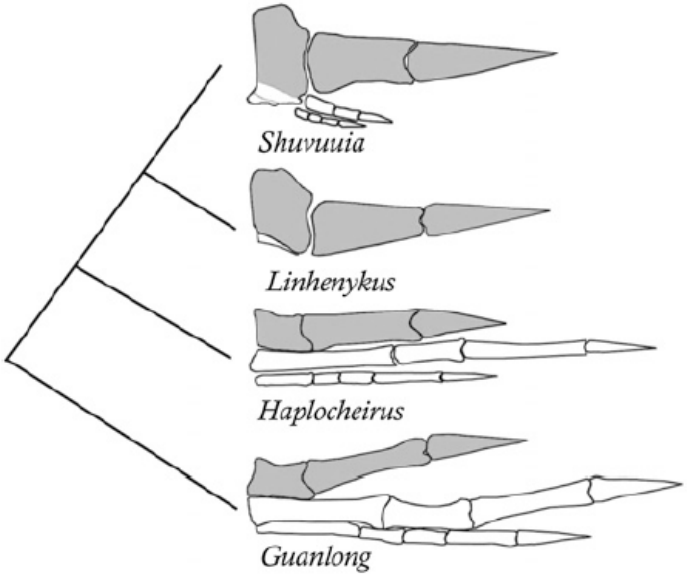


Fig. 4. Simplified alvarezsauroid phylogeny showing enlargement of manual digit II (in gray) and reduction of manual digits III and IV. *Linhenykus* has a less specialized digit II but much more reduced lateral digits compared with other derived alvarezsaurs. The basal tyrannosauroid *Guanlong* is used to illustrate the typical tetenuran manus. Mani are not to scale.

Xu et al, 2011

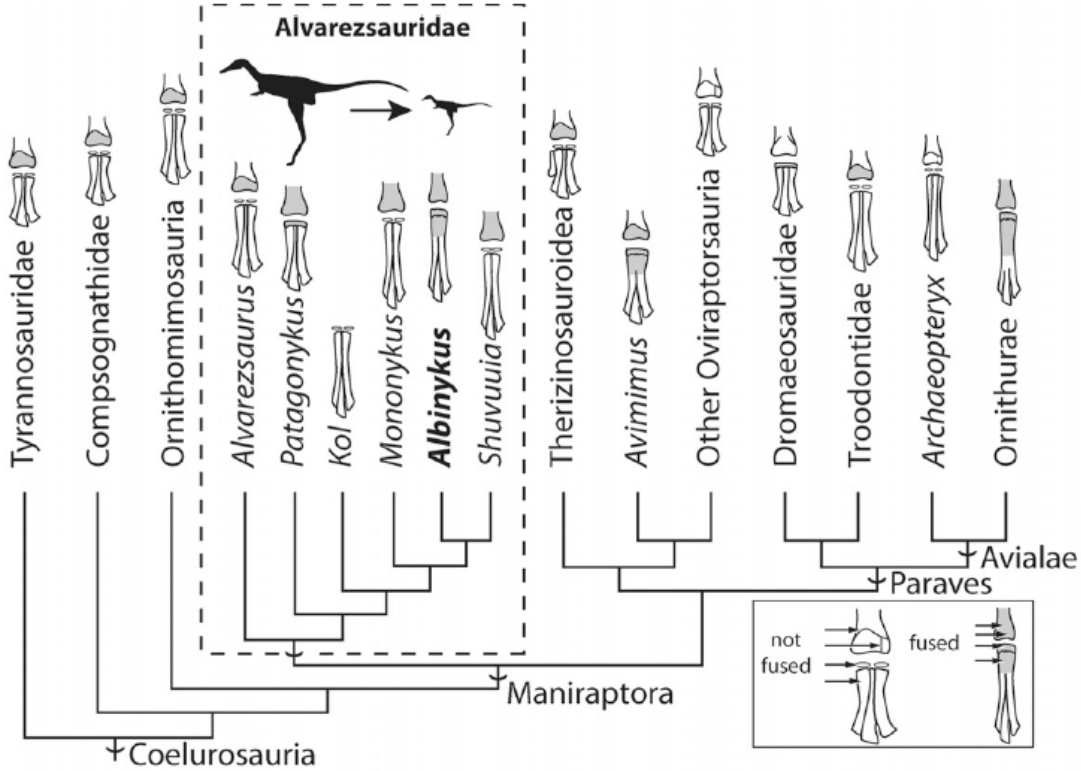
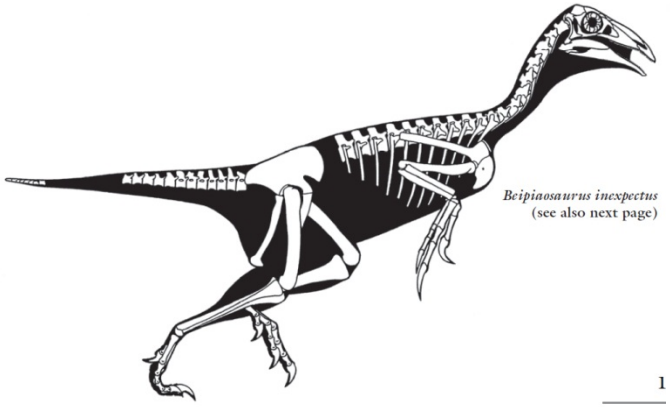


FIGURE 5. The phylogenetic position of *Albinykus baatar* and the mapping the distribution of coossified tarsal character states in Coelurosauria. Species-level taxa except in Alvarezsauridae were collapsed into larger clades for brevity, following Turner et al. (2007). The silhouettes indicate a decrease in body size from basal alvarezsaurids to more derived alvarezsaurids.

Nesbitt et al, 2011

Therizinosauria



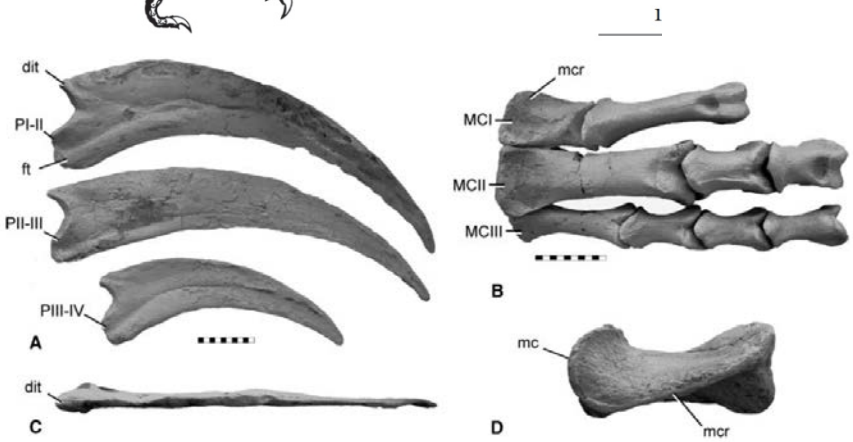
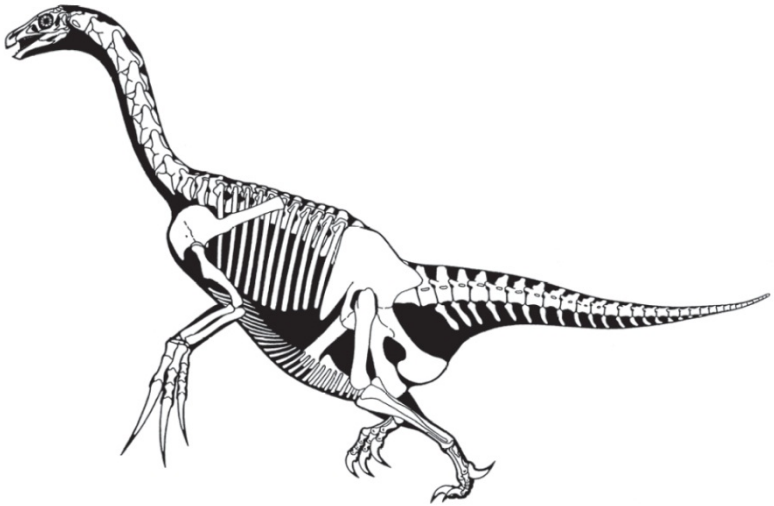


Figure 5. Diagnostic features of *Therizinosaurus cheloniformis*. Casts are a composite of referred materials IGM 100/15, 100/16, and/or 100/17. **A**, right lateral view of right manual unguals I-III, showing poor recurvature and hyperelongation; **B**, dorsal view of right manus, showing ratio of first to third metacarpals; **C**, dorsal view of right PI-II, showing extreme transverse compression; and **D**, lateral view of right MCI, showing enlarged medial crest. Abbreviations: dit, dorsal intercondylar tuberosity; ft, flexor tubercle; MCI-MCIII, metacarpals I-III; mc, medial condyle; mcr, medial crest; PI-II, first manual ungual; PII-III, second manual ungual; PIII-IV, third manual ungual. Scale bar 10 mm (A-B), C-D not to scale.



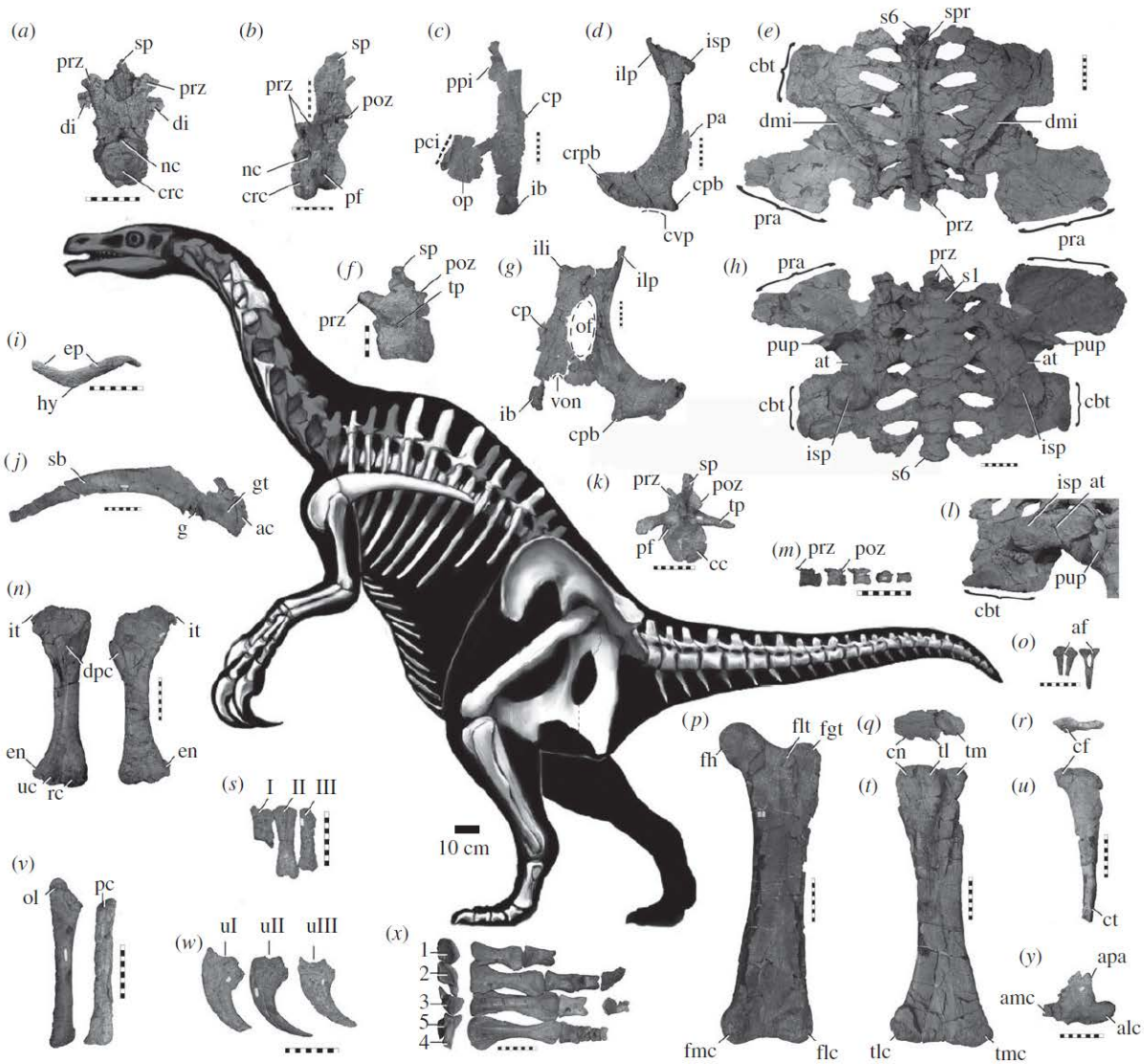


Figure 1. Skeletal reconstruction (preserved shown in white) and representative elements of *N. graffami* (UMNH VP 16420): (*a*) cranial dorsal vertebra, cranial view; (*b*) mid-dorsal vertebra, craniolateral view; (*c*) left ischium, lateral view; (*d*) left pubis, lateral view; (*e*) dorsoventrally crushed iliosacrum, dorsal view; (*f*) proximal caudal vertebra, left lateral view; (*g*) right ischium/pubis, lateral view; (*h*) iliosacrum, ventral view; (*i*) furcula, cranial view; (*j*) right scapulacoracoid, lateral view; (*k*) proximal caudal vertebra, caudal view; (*l*) right iliosacrum, oblique ventrolateral view, showing crushed peduncles, acetabulum, brevis fossa and cubic tuberosity of postacetabular process; (*m*) four distalmost caudal vertebrae, lateral view; (*n*) left and right humeri, cranial view; (*o*) chevrons, cranial view; (*p*) left femur, cranial view; left tibia (*q*) proximal and (*t*) caudal views; left fibula (*r*) proximal and (*u*) lateral views; (*s*) left metacarpus, dorsal view; (*v*) antebrachium; (*w*) manual unguals, lateral view; (*x*) proximal (left) and dorsal (right) views of pes (missing PI–II, PIII–II, PIII–IV and PIV–V); and (*y*) left astragalus, cranial view. For abbreviations, see electronic supplementary material. Scale bars: 10 cm (*a–e*, *g–y*); 5 cm (*f*). Skeletal drawing modified from Victor O. Leshyk, copyright 2007.

Zanno, 2010

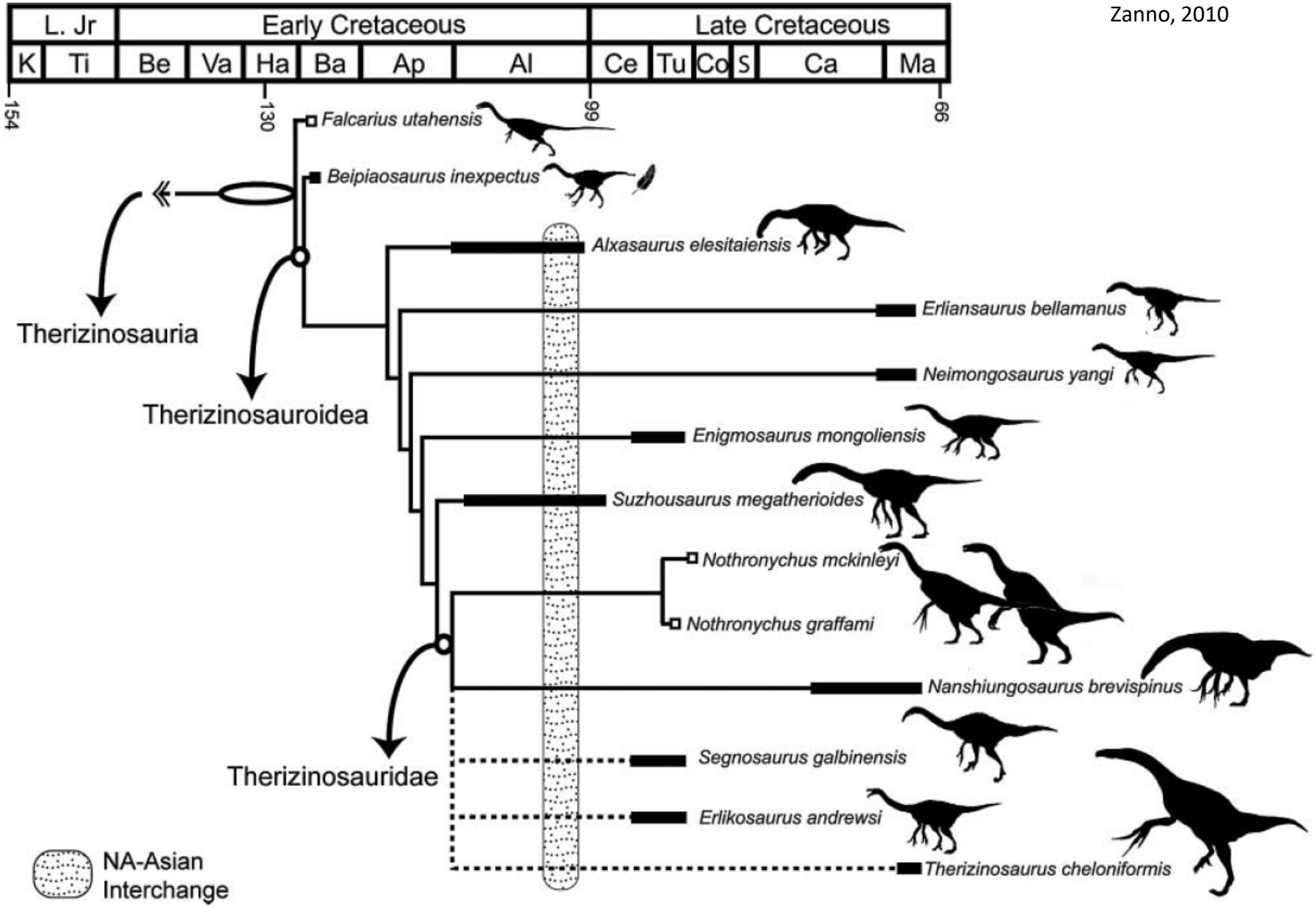


Figure 7. Time-calibrated phylogeny of Therizinosauria based on relationships recovered in the maximum agreement subtree of all MPTs. Shown temporal ranges represent uncertainties in chronostratigraphy, not actual species ranges. *Segnosaurus*, *Erlikosaurus* and *Therizinosaurus* are shown as unresolved therizinosaurids due to their lability in this study. Minimum temporal hypothesized faunal interchange events between North America and Asia in the Late Cretaceous shown.

Pennaraptora

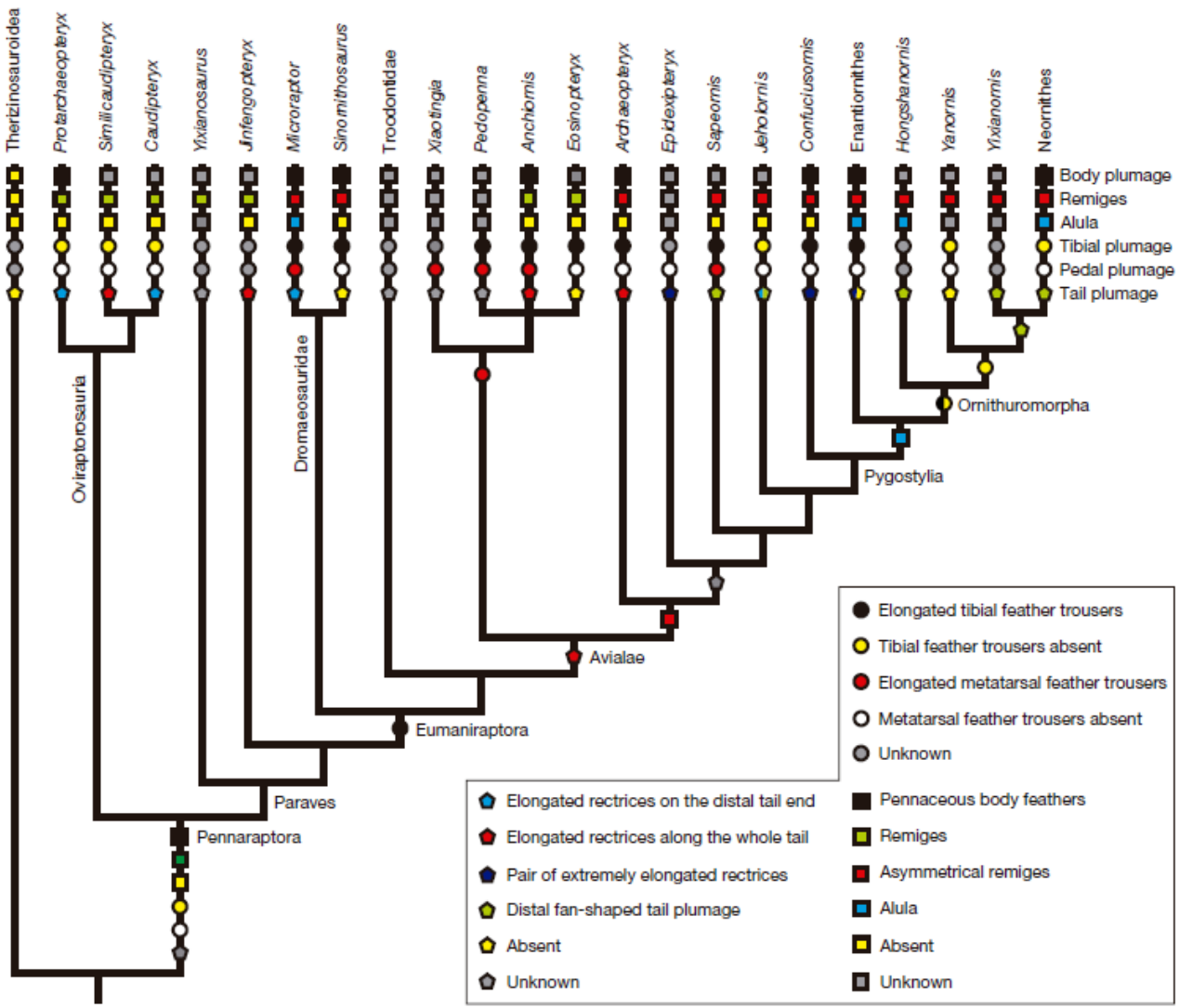
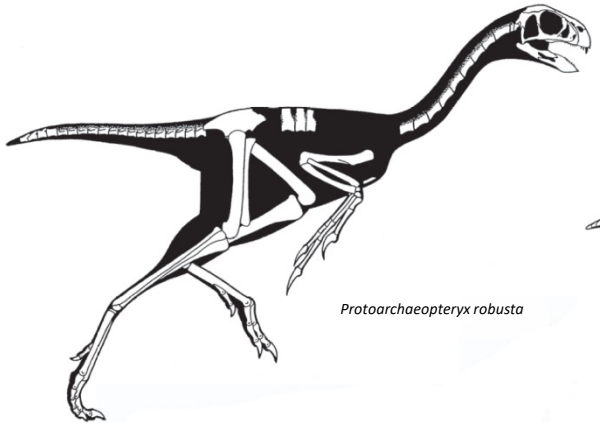
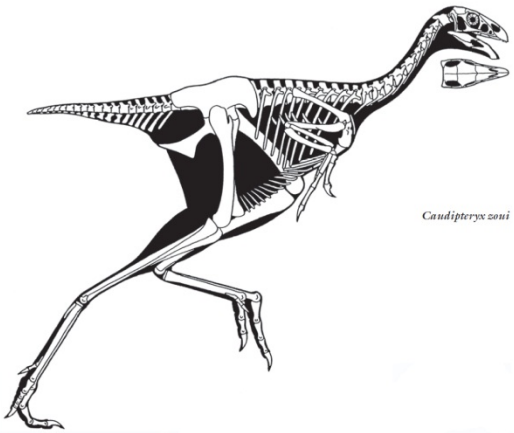


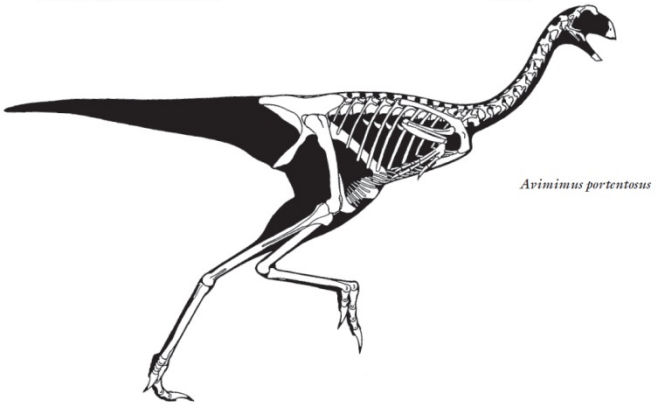
Figure 3 | Evolution of pennaceous feathers in maniraptoran theropods. Several character states referring to the presence/absence of pennaceous feathers on different parts of the body mapped onto a phylogenetic hypothesis of maniraptoran theropods. For details of phylogenetic analysis see Supplementary Information.

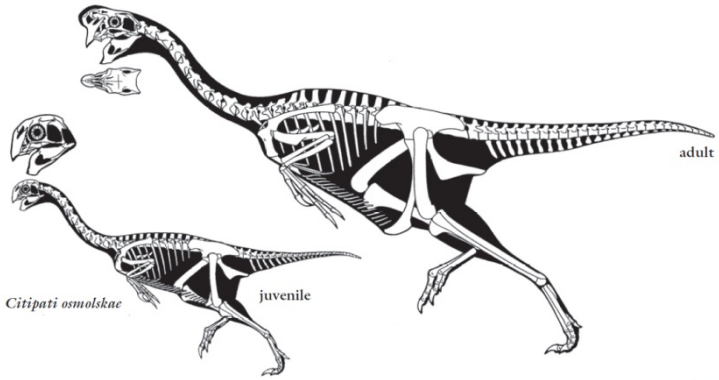
Oviraptorosauria

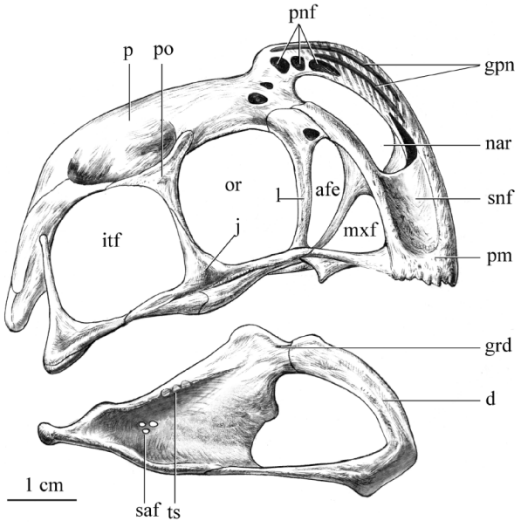
Sinapomorfías:
- Cráneos altos y cortos
- Pérdida de dientes (en formas derivadas)
- Arctometatarso (en formas derivadas)



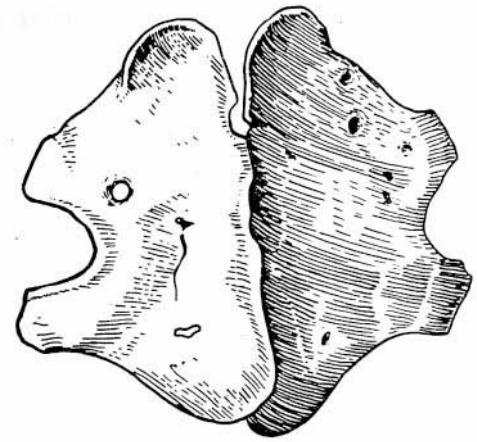




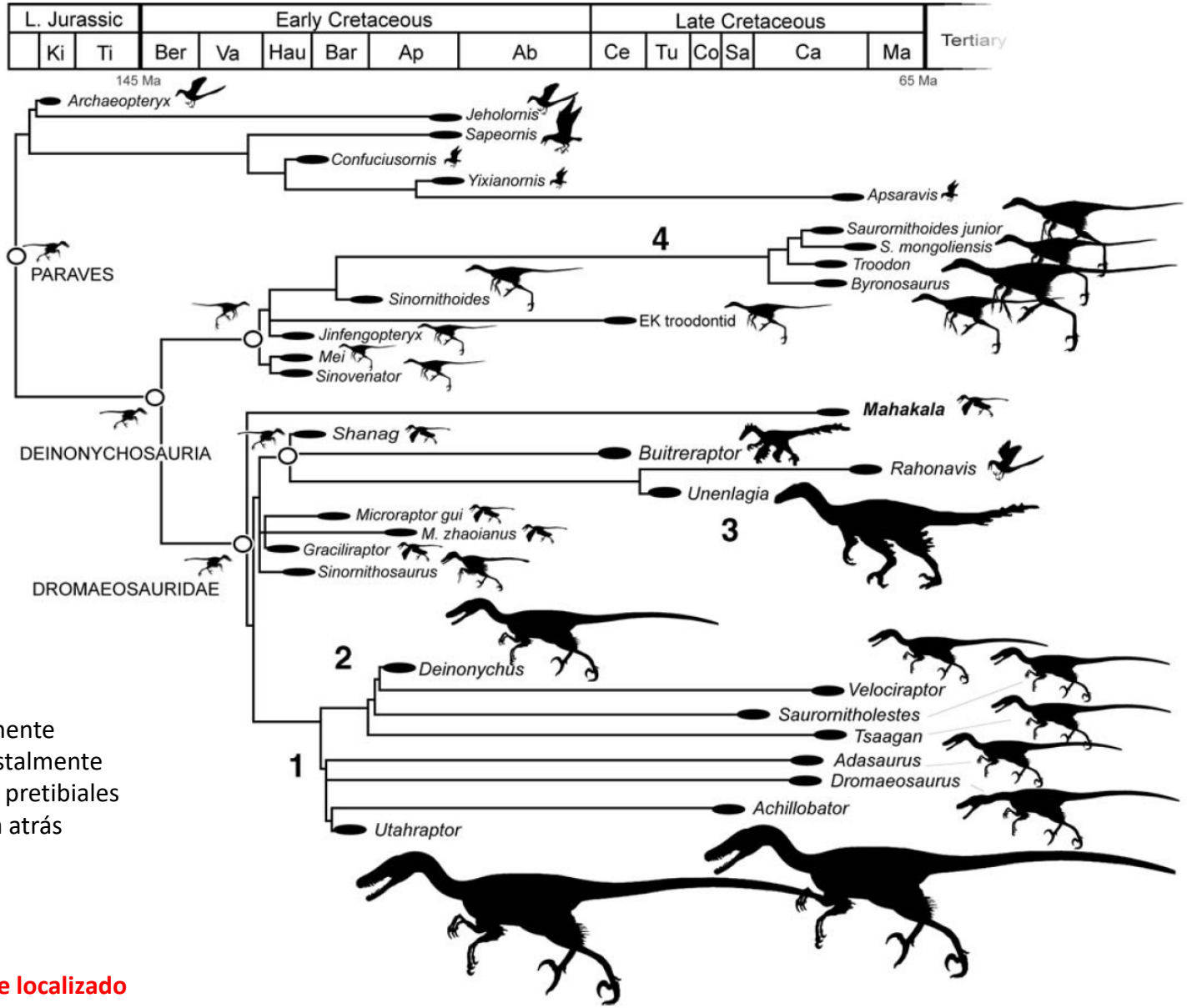




Banji long (Xu et al, 2010)



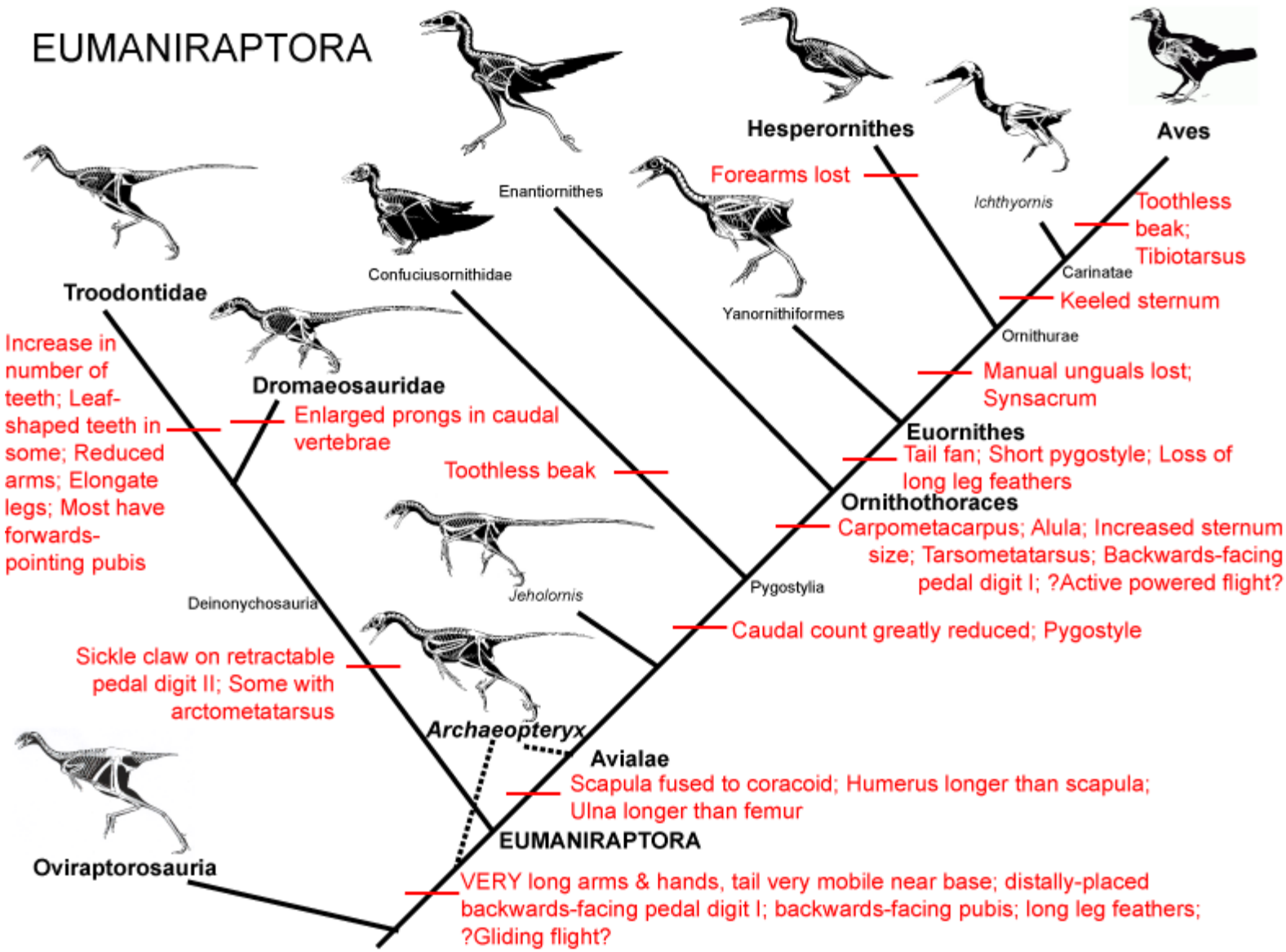
Paraves (=Eumaniraptora)

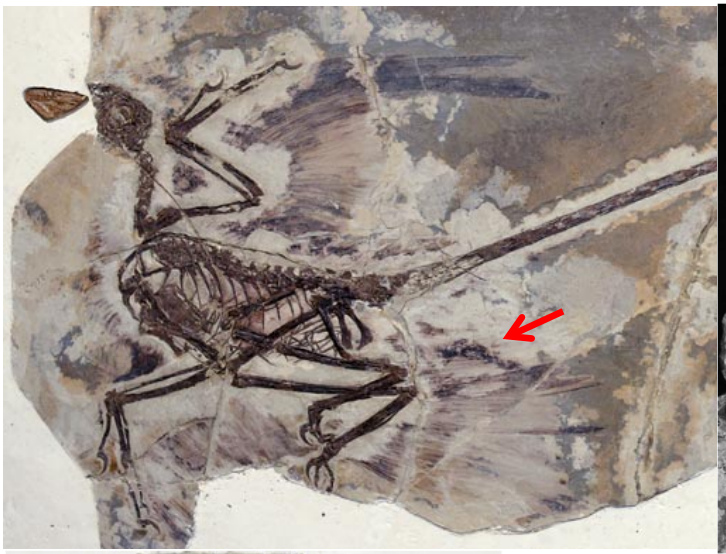


Sinapomorfías:

- Manos y brazos muy largos
- Metacarpo III curvado medialmente
- Cola movil en la base, rígida distalmente
- Plumas metatarsales, tibiales y pretibiales
- Pubis dirigido totalmente hacia atrás
- Lacrimal en forma de T

- **Dígito II hiperextensible**
- **Proceso posterior en isquion**
- **Proceso obturador distalmente localizado**


EUMANIRAPTORA
Hesperornithes
Aves
Forearms lost
Enantiornithes
Ichthyornis
Toothless beak; Tibiotarsus
Carinatae
Confuciusornithidae
Keeled sternum
Troodontidae
Yanornithiformes
Ornithurae
Manual unguals lost; Synsacrum
Increase in number of teeth; Leaf-shaped teeth in some; Reduced arms; Elongate legs; Most have forwards-pointing pubis
Dromaeosauridae
Enlarged prongs in caudal vertebrae
Euornithes
Tail fan; Short pygostyle; Loss of long leg feathers
Toothless beak
Ornithothoraces
Carpometacarpus; Alula; Increased sternum size; Tarsometatarsus; Backwards-facing pedal digit I; ?Active powered flight?
Jeholornis
Pygostylia
Deinonychosauria
Caudal count greatly reduced; Pygostyle
Sickle claw on retractable pedal digit II; Some with arctometatarsus
Archaeopteryx
Avialae
Scapula fused to coracoid; Humerus longer than scapula; Ulna longer than femur
EUMANIRAPTORA
Oviraptorosauria
VERY long arms & hands, tail very mobile near base; distally-placed backwards-facing pedal digit I; backwards-facing pubis; long leg feathers; ?Gliding flight?

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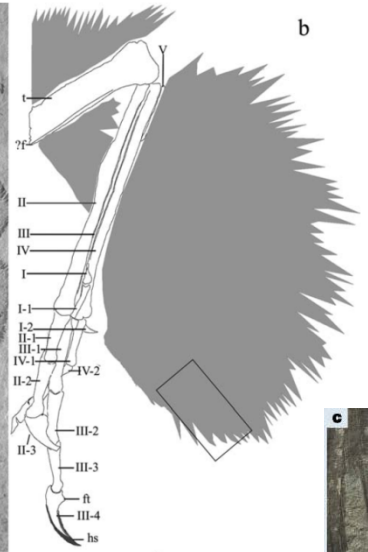
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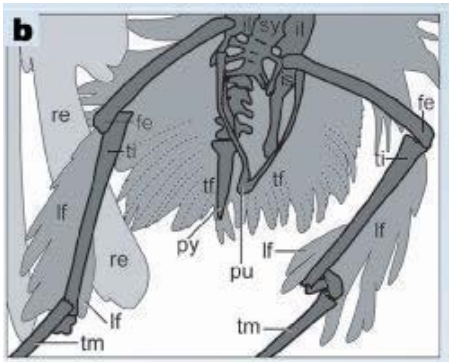
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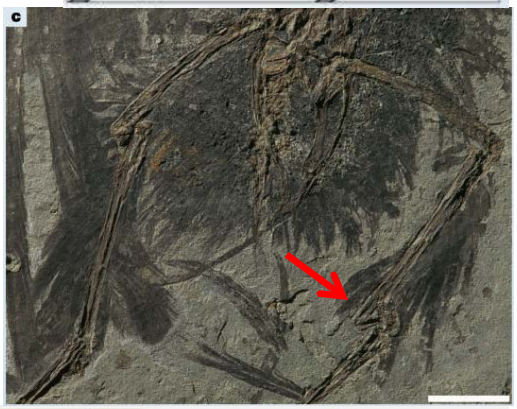
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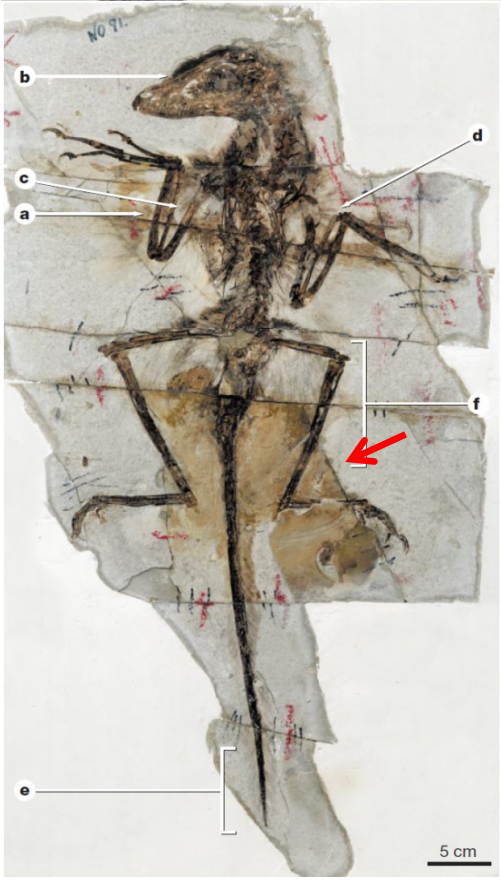
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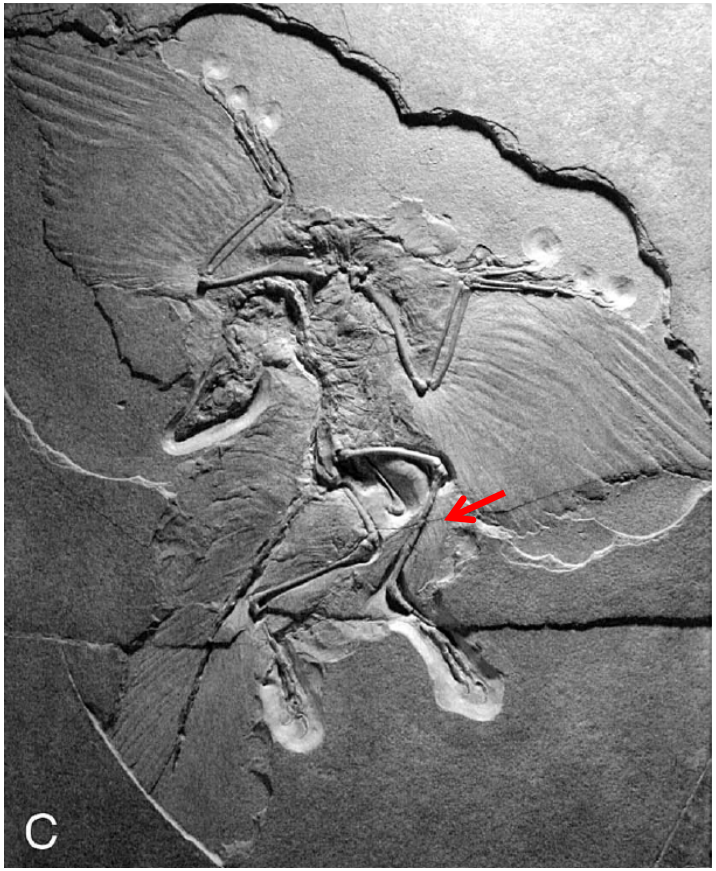
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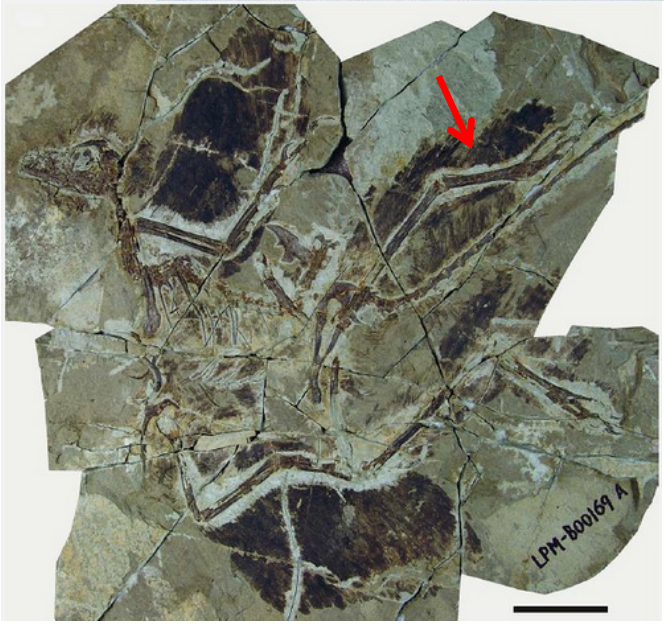
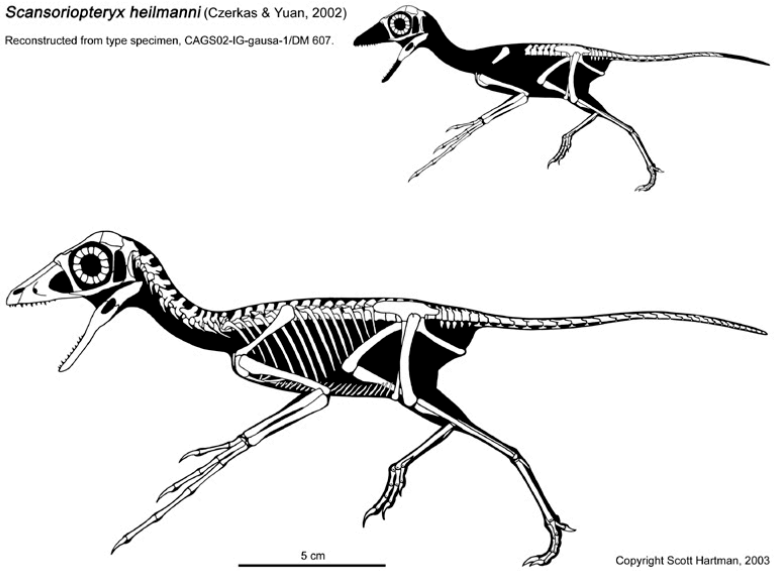
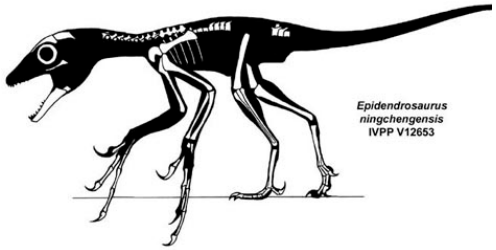

LPM-B00169 A

Scansoriopterygidae
(Czerkas & Yuan 2002)





Scansoriopteryx (Czerkas and Yuan 2002)

Epidendrosaurus ninchengensis (Zhang et al 2002)

Epidexipteryx hui
(Zhang et al 2008)

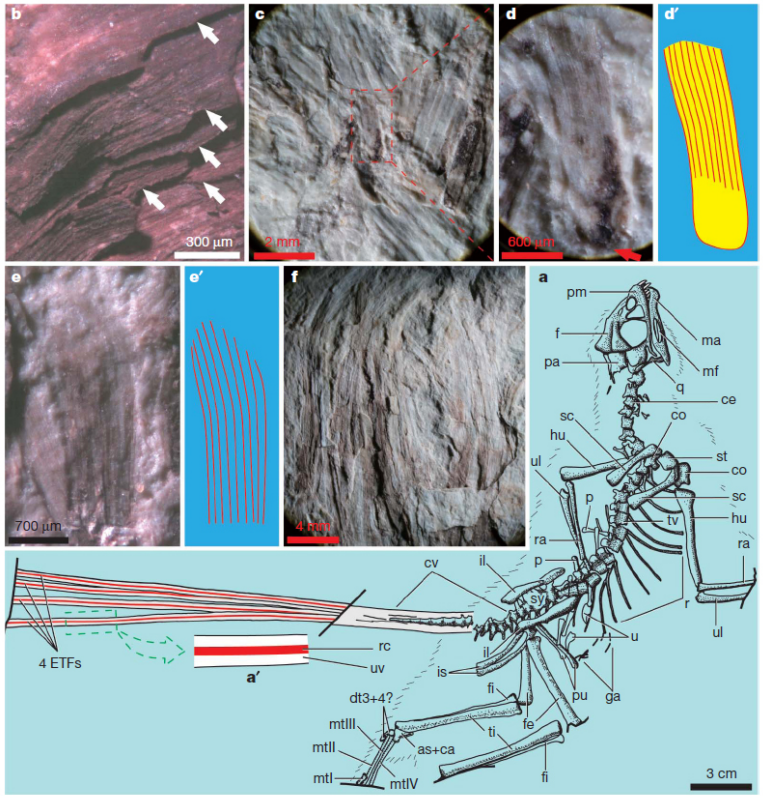
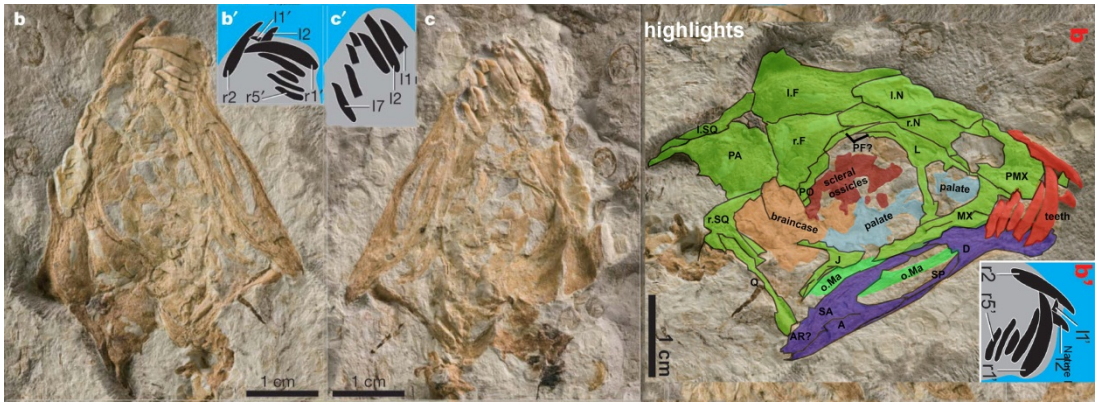
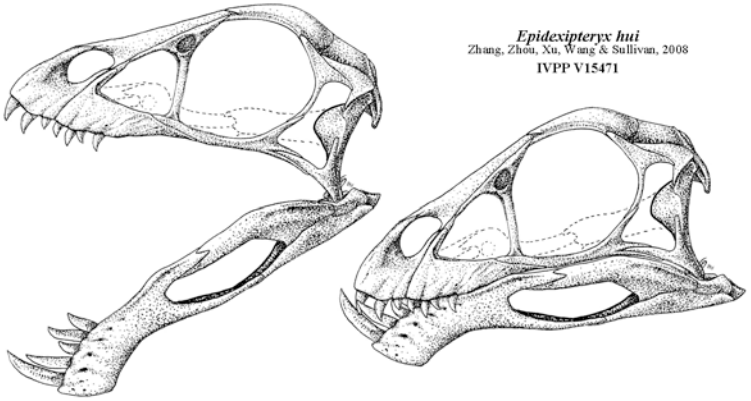
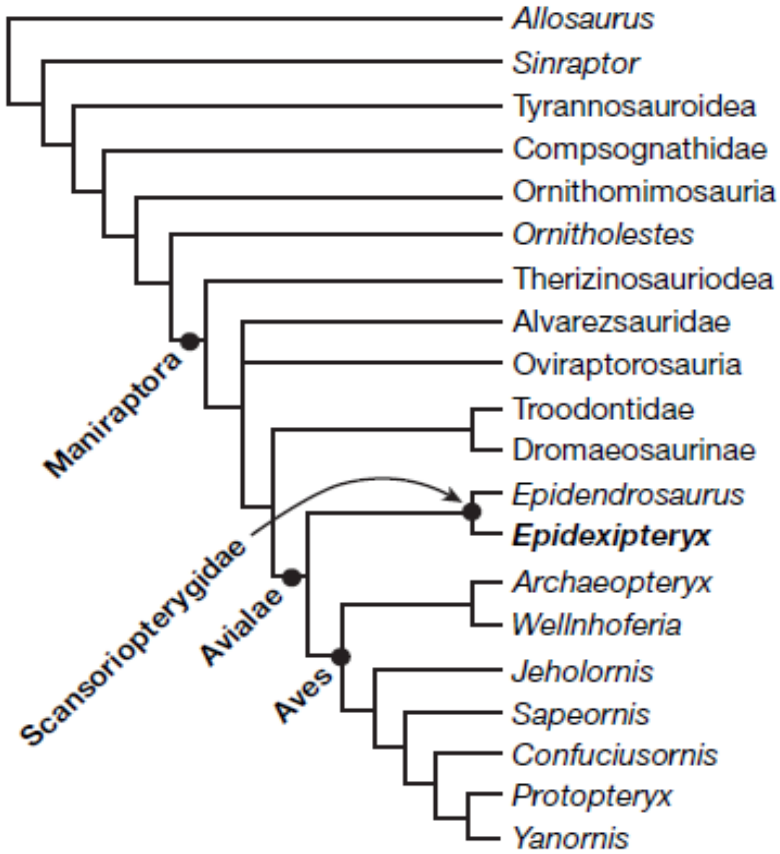
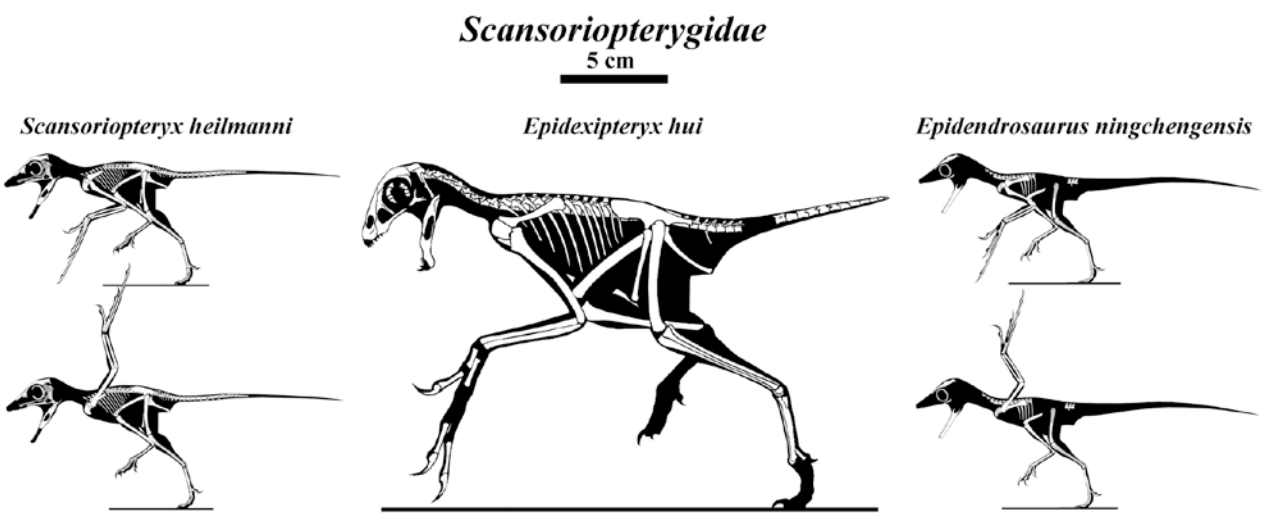


Figure 2 | Line drawings and close-up photographs of *Epidexipteryx hui* gen. et sp. nov. a, Skeleton and feather outline, based on both main slab and counterslab, showing that each shafted feather is formed by central rachis and two unbranched vanes (**a′**). **b**, **d**, **d′**, Proximal regions of non-shafted feathers; barbs are parallel and closely united as an unbranched membranous structure (**d**, **d′**), vanes are either layered, indicated by white arrows (**b**), or arranged irregularly (**c**). The red arrow indicates the proximal end of the feather (**d**). **e**, **e′**, **f**, Distal regions of non-shafted feathers, in which barbs appear loosely parallel. Abbreviations: as+ca, astragalus and calcaneum; ce, cervical vertebrae; co, coracoid; cv, caudal vertebrae; dt3+4, distal tarsals 3 and 4; f, frontal; fe, femur; fi, fibula; ga, gastralia; hu, humerus; il, ilium; is, ischium; ma, mandible; mtI–IV, metatarsals I–IV; p, phalanges or metacarpals; pa, parietal; pm, premaxilla; pu, pubis; q, quadrate; r, ribs; ra, radius; rc, rachis; sc, scapula; st, sternum; ti, tibia; tv, thoracic vertebrae; u, ungual phalanges; ul, ulna; uv, unbranched vane.

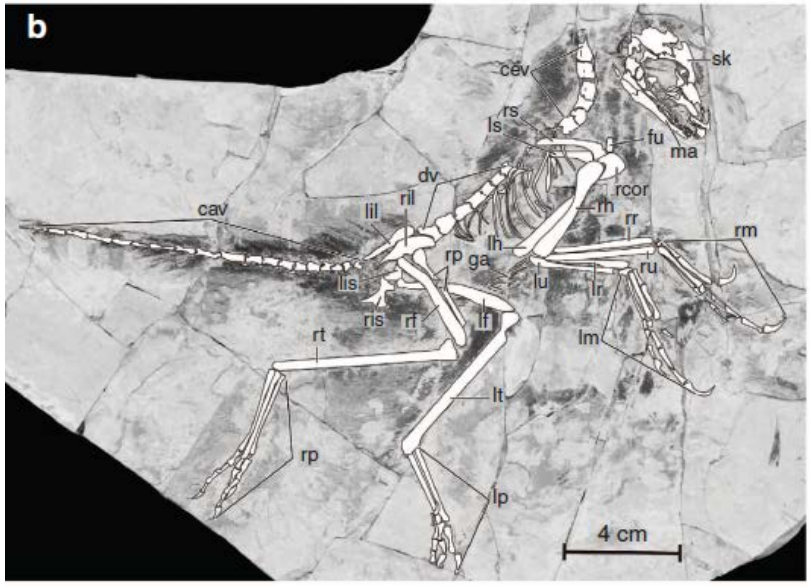


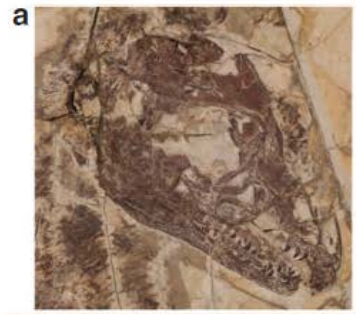


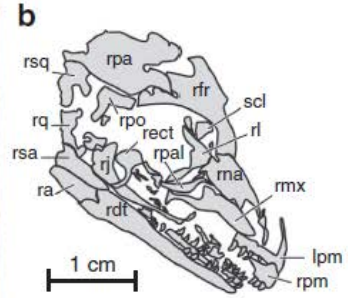

Allosaurus
Sinraptor
Tyrannosauroidea
Compsognathidae
Ornithomimosauria
Ornitholestes
Therizinosauriodea
Alvarezsauridae
Oviraptorosauria
Troodontidae
Dromaeosaurinae
Epidendrosaurus
Epidexipteryx
Archaeopteryx
Wellnhoferia
Jeholornis
Sapeornis
Confuciusornis
Protopteryx
Yanornis
Maniraptora
Scansoriopterygidae
Avialae
Aves

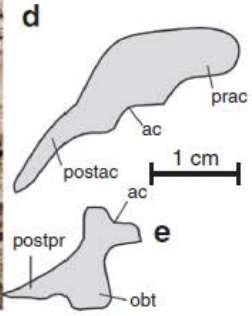

Scansoriopterygidae
5 cm
Scansoriopteryx heilmanni
Epidexipteryx hui
Epidendrosaurus ningchengensis

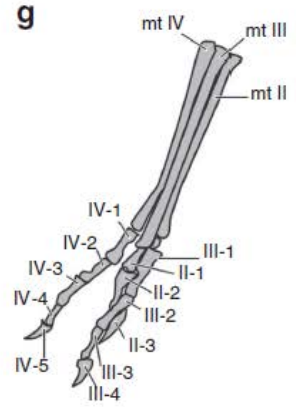
Eosinopteryx brevipenna



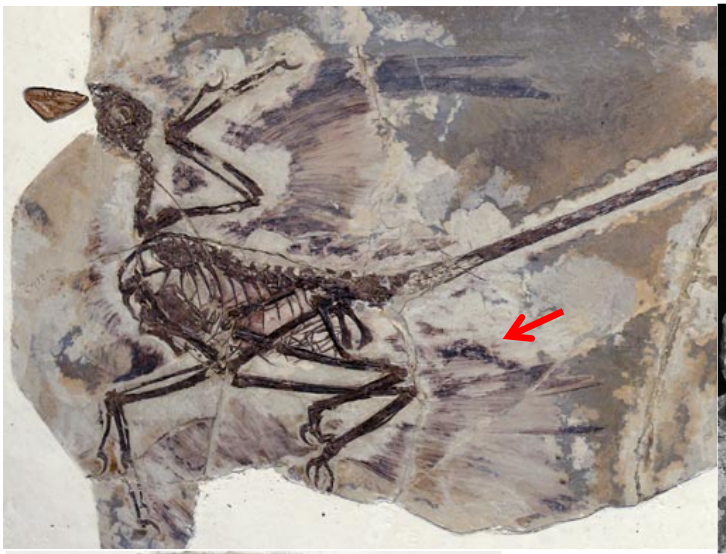








1 cm

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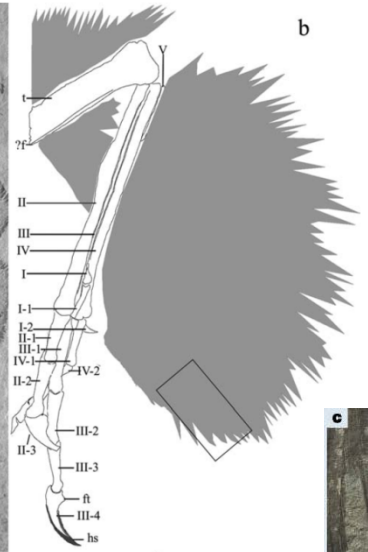
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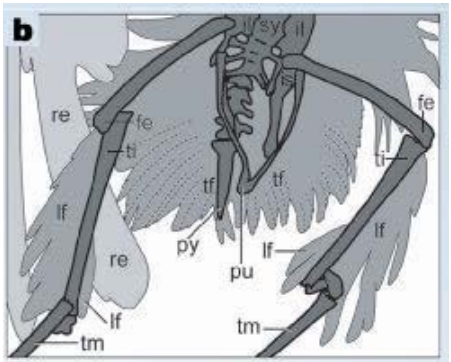
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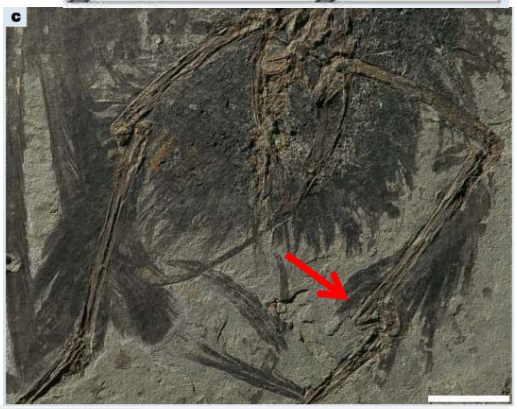
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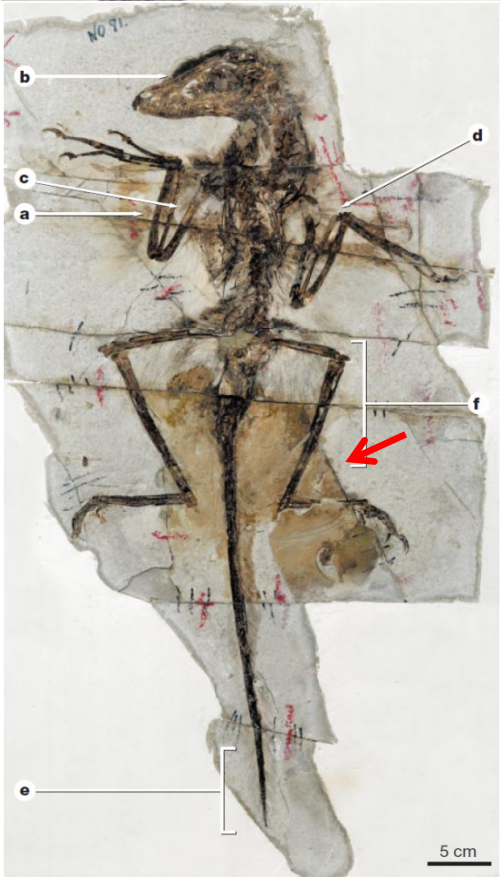
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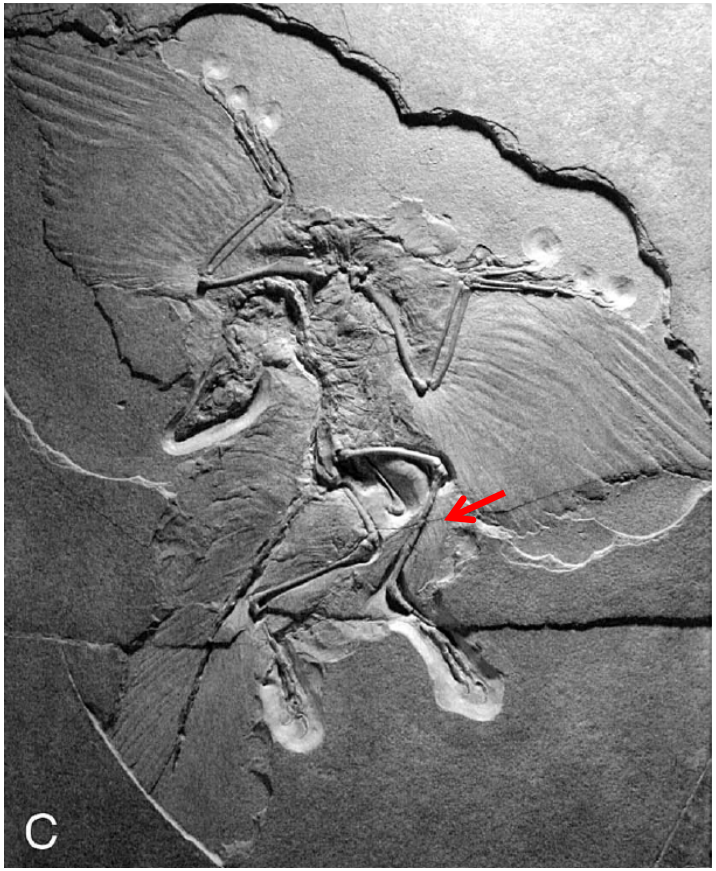
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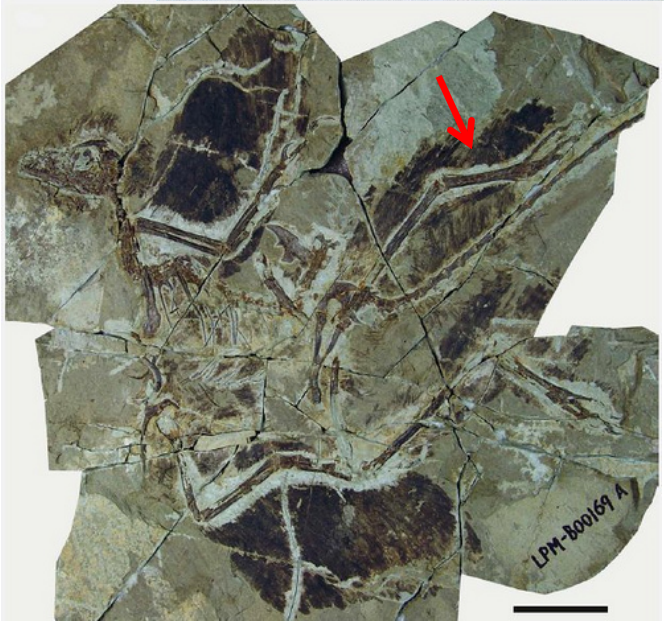
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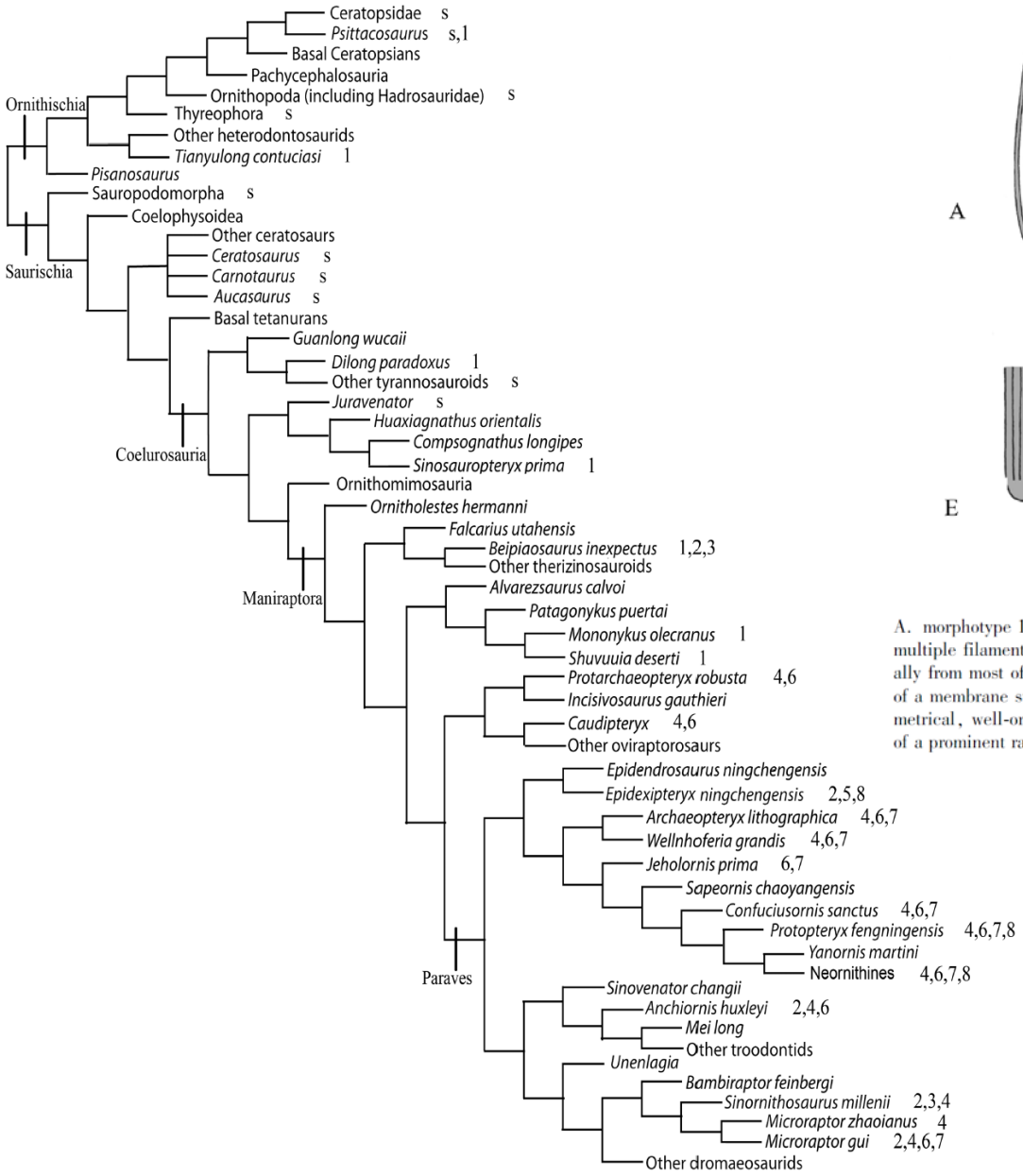


Fig. 5 Distribution of major feather morphotypes across a simplified dinosaurian phylogeny based on Sereno, 1999, Xu, 2002, and Butler et al., 2008
Numbers refer to the feather morphotypes identified in present paper and s refers to the presence of scaly integumentary structures

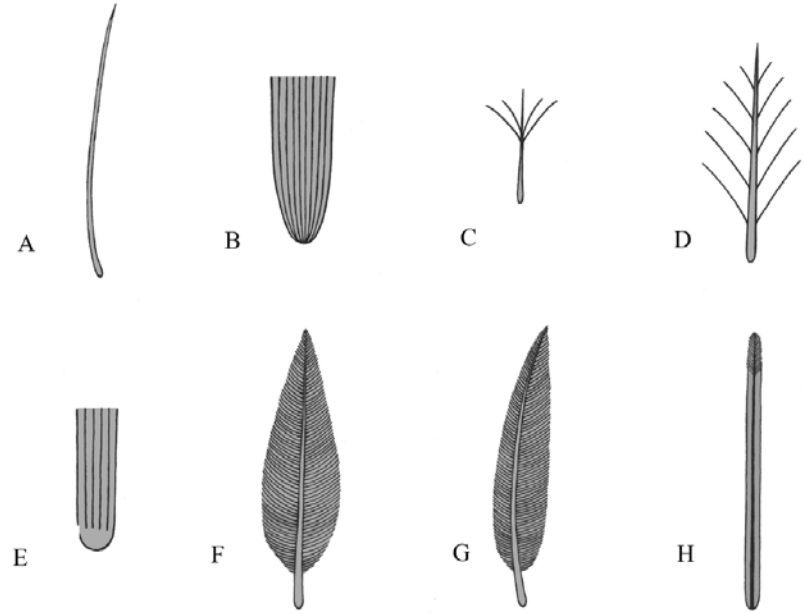
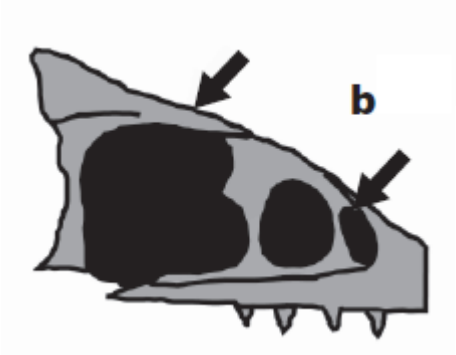


Fig. 4 Known feather morphotypes of non-avian dinosaurs
A. morphotype 1, single filament; B. morphotype 2, multiple filaments joined basally; C. morphotype 3, multiple filaments jointed basally on a central filament; D. morphotype 4, multiple filaments branching laterally from most of the length of a central filament; E. morphotype 5, multiple filaments arising from the edge of a membrane structure; F. morphotype 6, compound structure composed of a prominent rachis with symmetrical, well-organized and closed vanes on either sides; G. morphotype 7, compound structure composed of a prominent rachis with asymmetrical, well-organized and closed vanes on either side; H. morphotype 8, a prominent rachis with symmetrical, undifferentiated vanes on either side

Deinonychosauria

Clado más inlcusivo que incluye a *Deinonychus anthirrophus* pero no a *Columba livia*.
Incluye los taxa Troodontidae y Dromaeosauridae.

Sinapomorfías:
- Gran fenestra promaxilar (discutible, presente también en Archaeopteryx)
- Ungual dígito II hipertrofiada



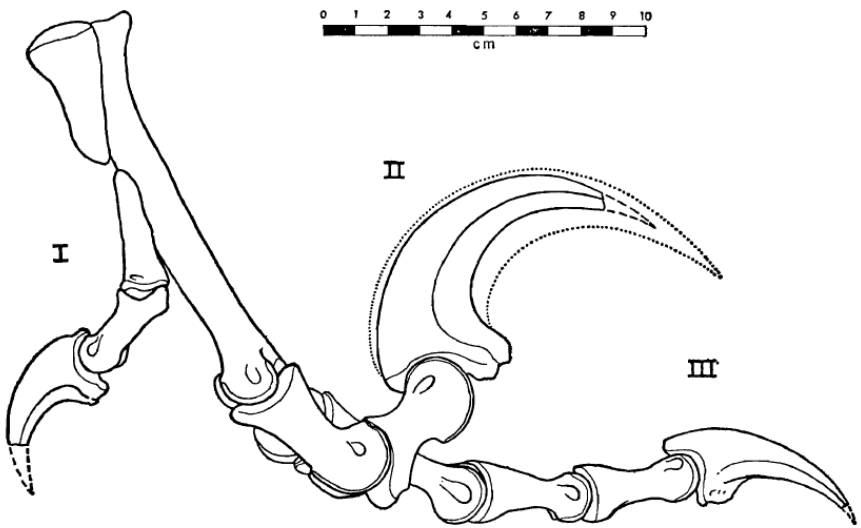
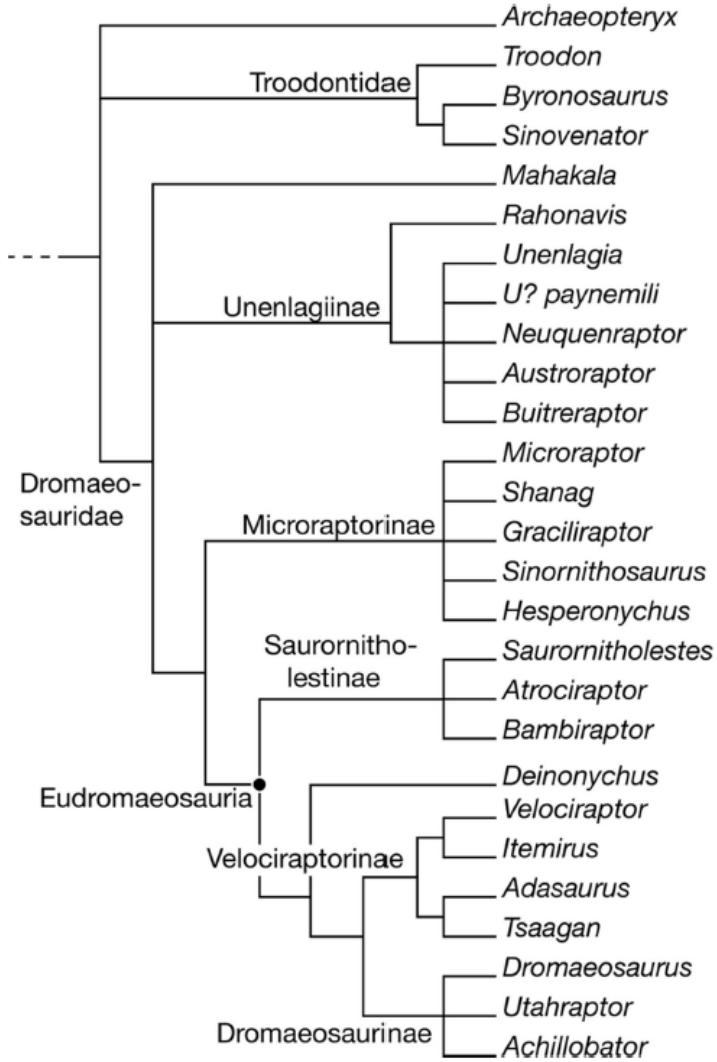


FIG. 74. Left pes of *Deinonychus antirrhopus* (YPM 5205) in internal aspect. Notice the extreme contrast in the form of the second and third unguals. The dotted line represents a conservative estimate of the size and shape of the horny claw carried by the ungual.

Dromaeosauridae



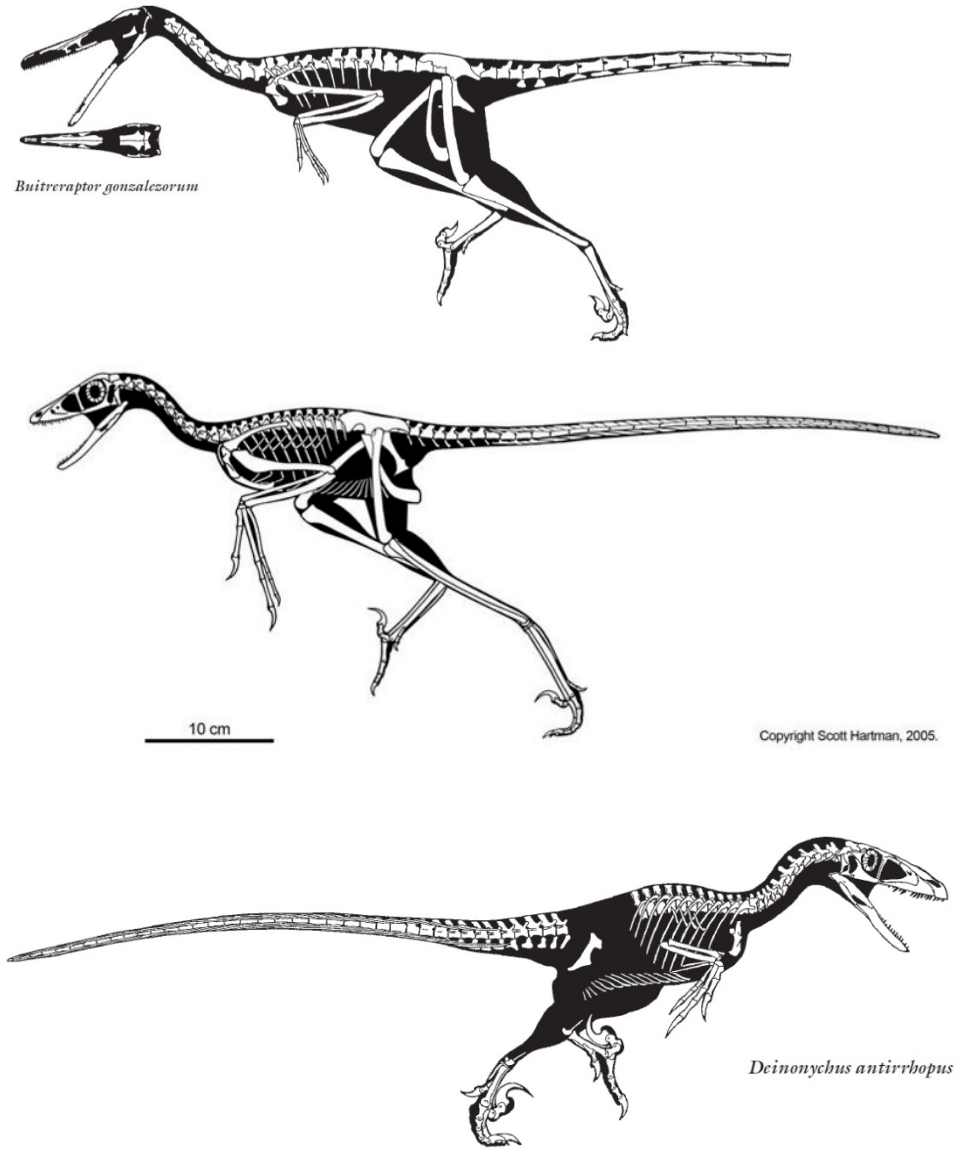


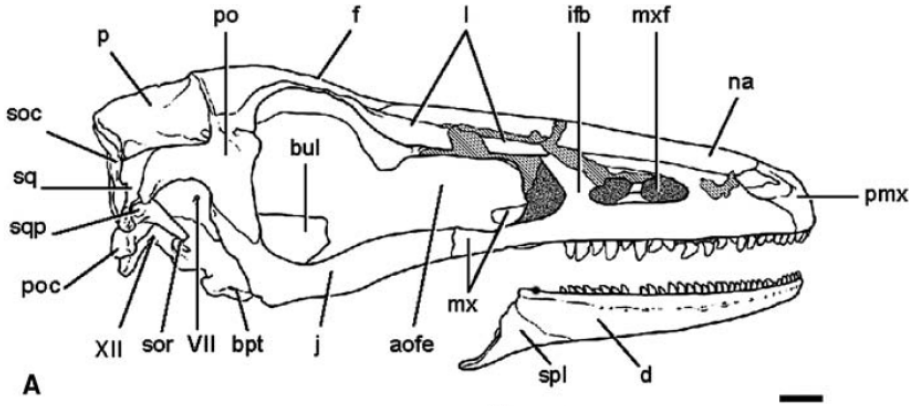
Fig. 3. Strict consensus of 5,292 most parsimonious trees resulting from phylogenetic analysis of 23 in-group taxa, 4 out-group taxa, and 114 characters. *H. elizabethae* was found to be part of the clade Microraptorinae. Tree length = 223, consistency index = 0.5430, retention index = 0.6930, rescaled consistency index = 0.3791.

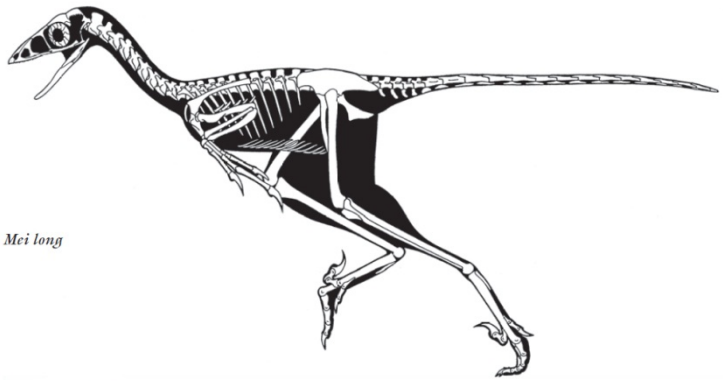
Troodontidae

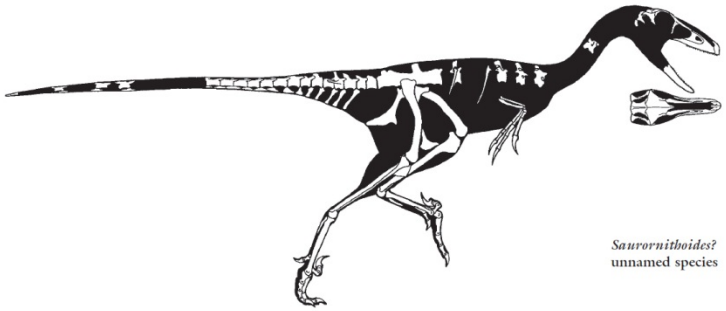
Clado más inclusivo que contiene a Troodn formosus, pero no a Velociraptor mongoliensis. Maniraptores gráciles, con dientes aserrados, manos raptoriales y garra hipertrofiada en el dígito II pedal. Grandes órbitas.

Sinapomorfías:

- Numerosos dientes maxilares empacados anteriromente, al igual que los dientes en el dentario
- Fenestra premaxilar desaparece en Troodontidos derivados
- Canal en cara labial del dentario con foraminas neurovasculares







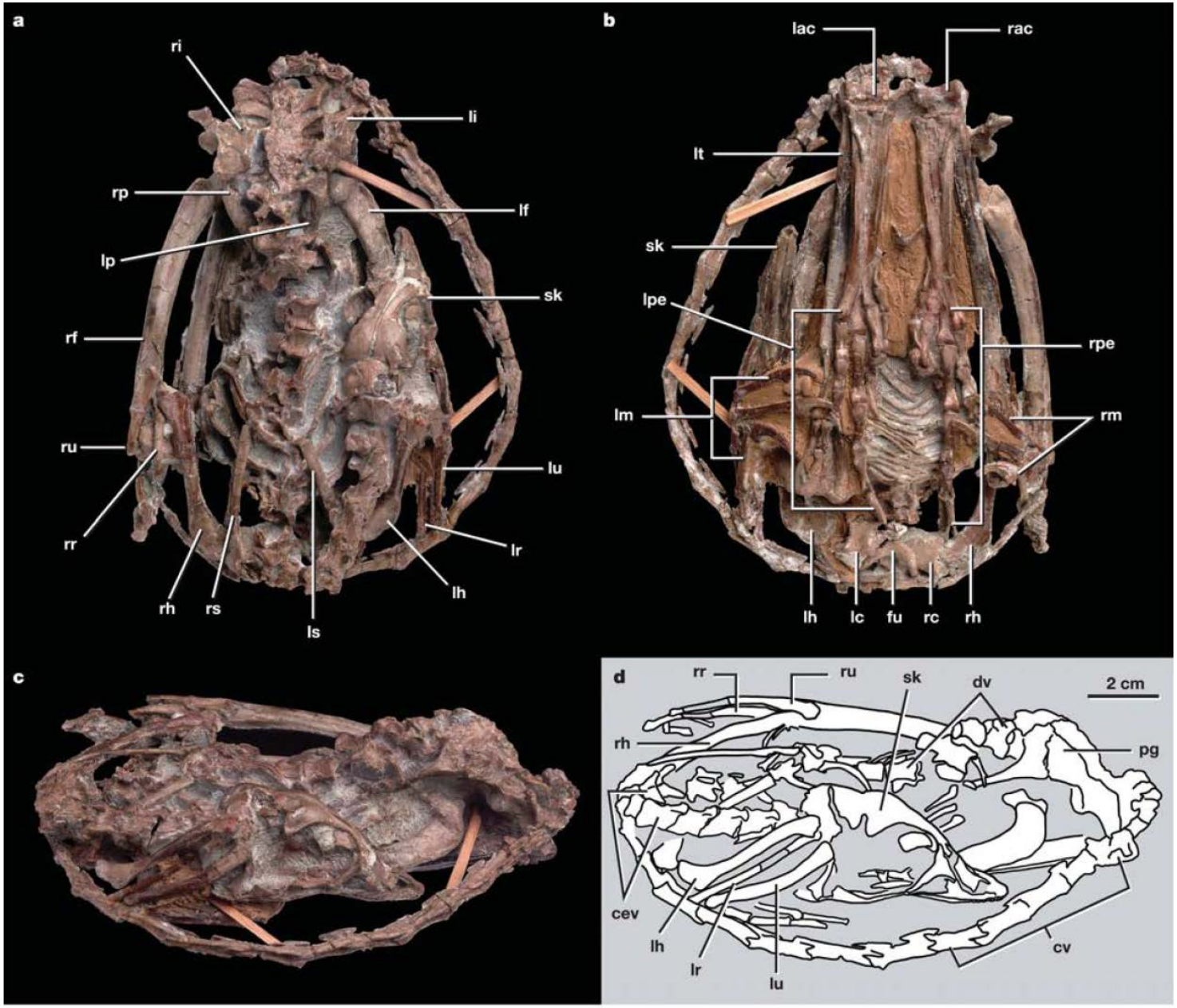


Figure 1 Holotype of *Mei long* (IVPP V12733). **a–c**, Photographs of the skeleton in dorsal (**a**), ventral (**b**) and dorsolateral (**c**) views. **d**, Line drawing of the skeleton in dorsolateral view. cev, cervical vertebrae; cv, caudal vertebrae; dv, dorsal vertebrae; fu, furcula; lac, left astragalus–calcaneum; lc, left coracoid; lf, left femur; lh, left humerus; li, left ilium; lm, left manus; lp, left pubis; lpe, left pes; lr, left radius; ls, left scapula; lt, left tibia; lu, left ulna; pg, pelvic girdle; rac, right astragalus–calcaneum; rc, right coracoid; rf, right femur; rh, right humerus; ri, right ilium; rm, right manus; rp, right pubis; rpe, right pes; rr, right radius; rs, right scapula; ru, right ulna; sk, skull. Scale bar, 2 cm.

Xu and Norrel, 2002

Anchiornis huxleyi

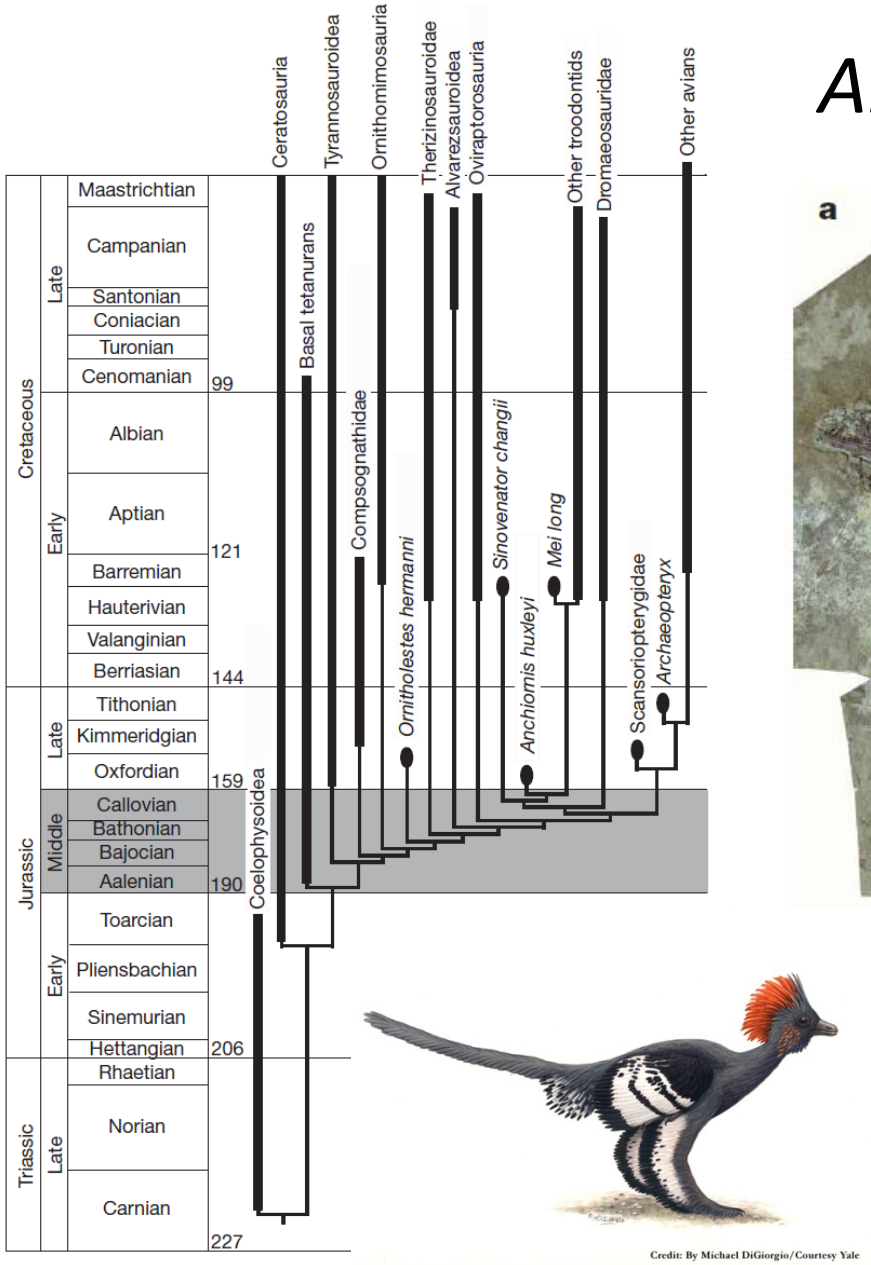
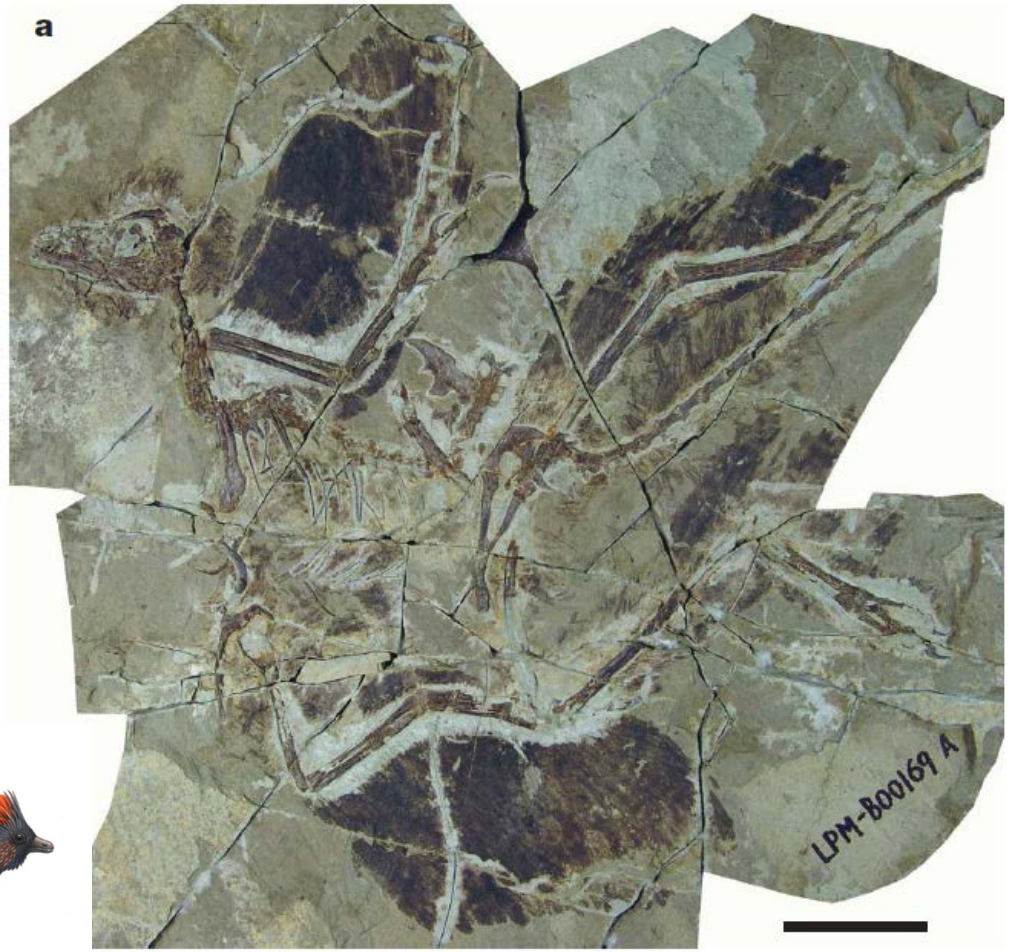
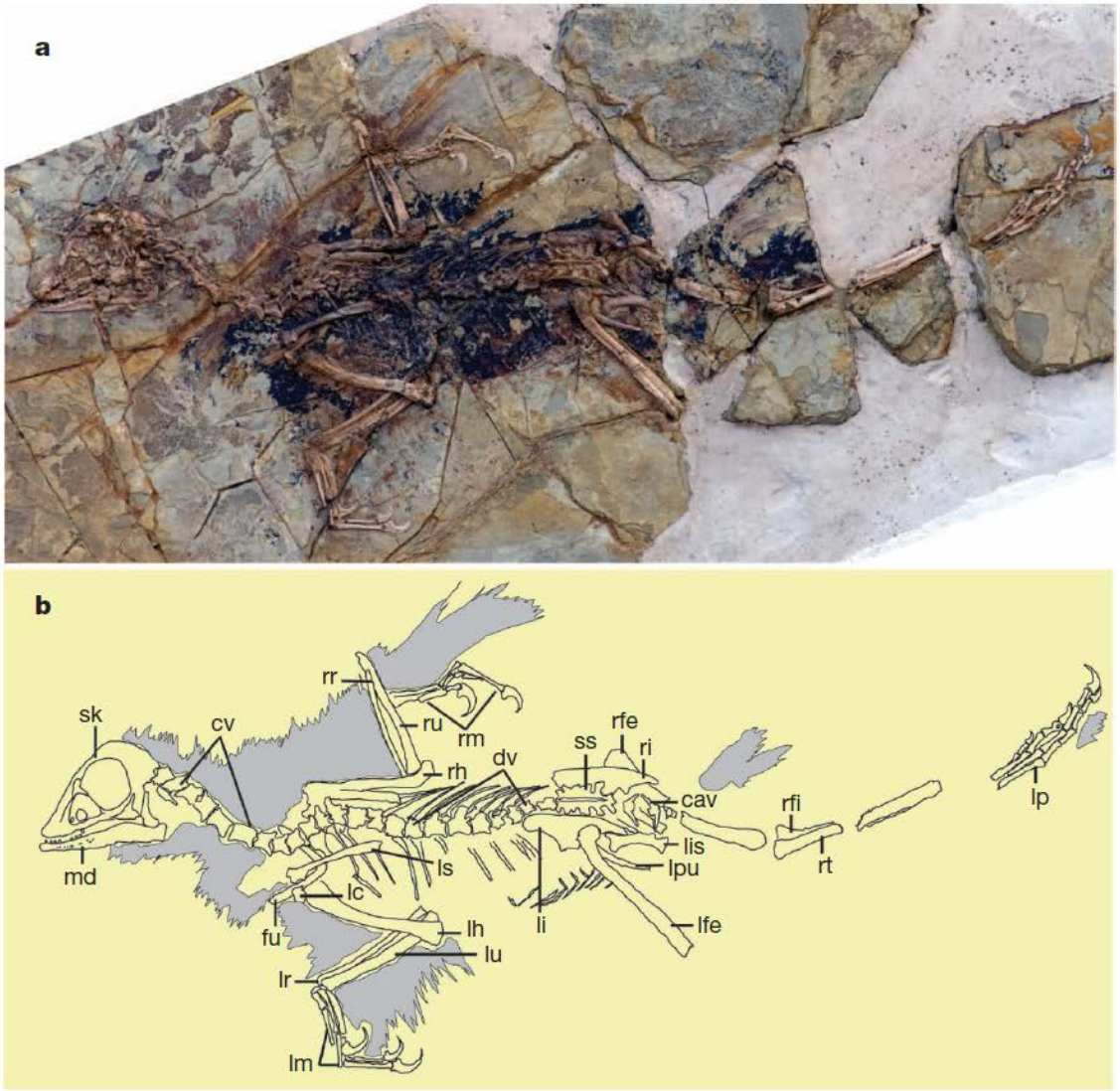


Figure 4 | Temporally calibrated phylogeny of the Theropoda. (See Supplementary Information for details.) The known temporal durations (solid bars) of the major theropod groups, based on well-corroborated fossil occurrences, indicate that the major tetanuran theropod groups diverged rapidly in the Middle Jurassic to earliest Late Jurassic.



Xu et al, 2009; Hu et al, 2009

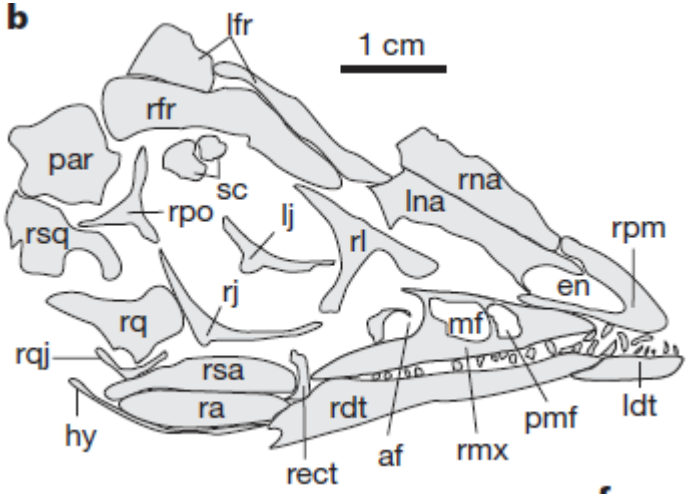
Xiatingia zhengi

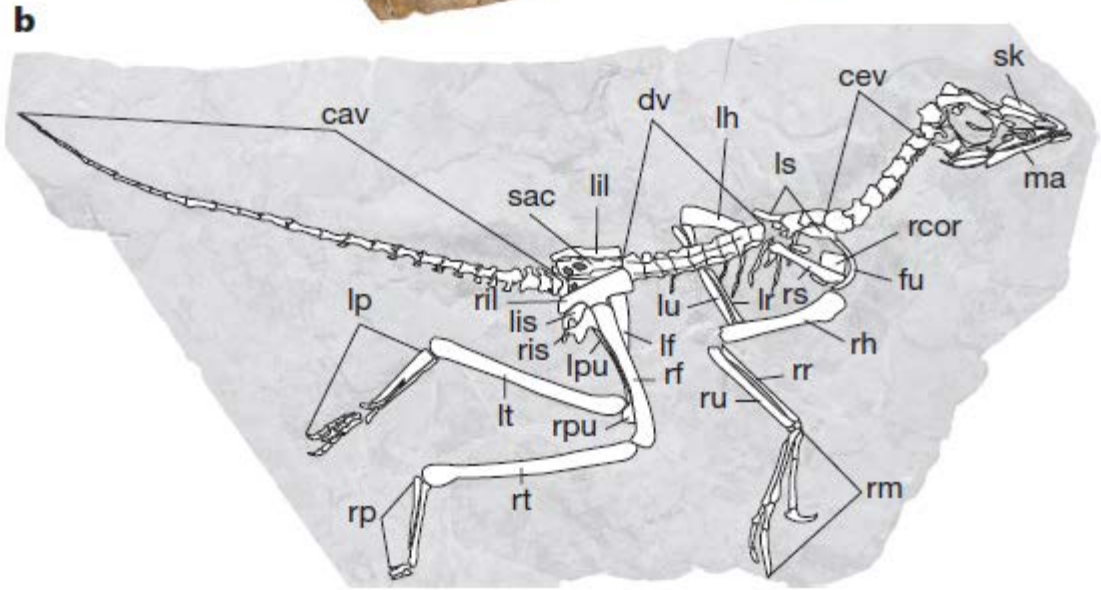


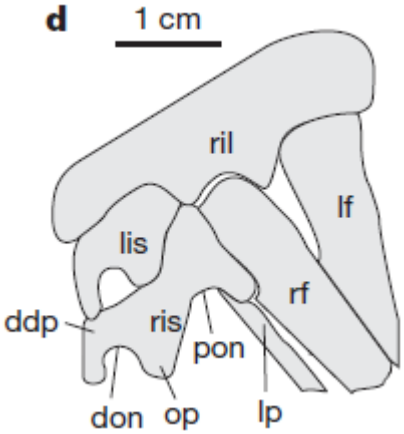
Xu et al., 2011

Figure 1 | ***Xiaotingia zhengi*** **holotype (STM 27-2).** **a**, **b**, Photograph (**a**) and line drawing (**b**). Integumentary structures in **b** are coloured grey. cav, caudal vertebra; cv, cervical vertebra; dv, dorsal vertebra; fu, furcula; lc, left coracoid; lfe, left femur; lh, left humerus; li, left ilium; lis, left ischium; lm, left manus; lp, left pes; lpu, left pubis; lr, left radius; ls, left scapula; lu, left ulna; md, mandible; rfe, right femur; rfi, right fibula; rh, right humerus; ri, right ilium; rm, right manus; rr, right radius; rt, right tibiotarsus; ru, right ulna; sk, skull; ss, synsacrum.

Aurornis xui

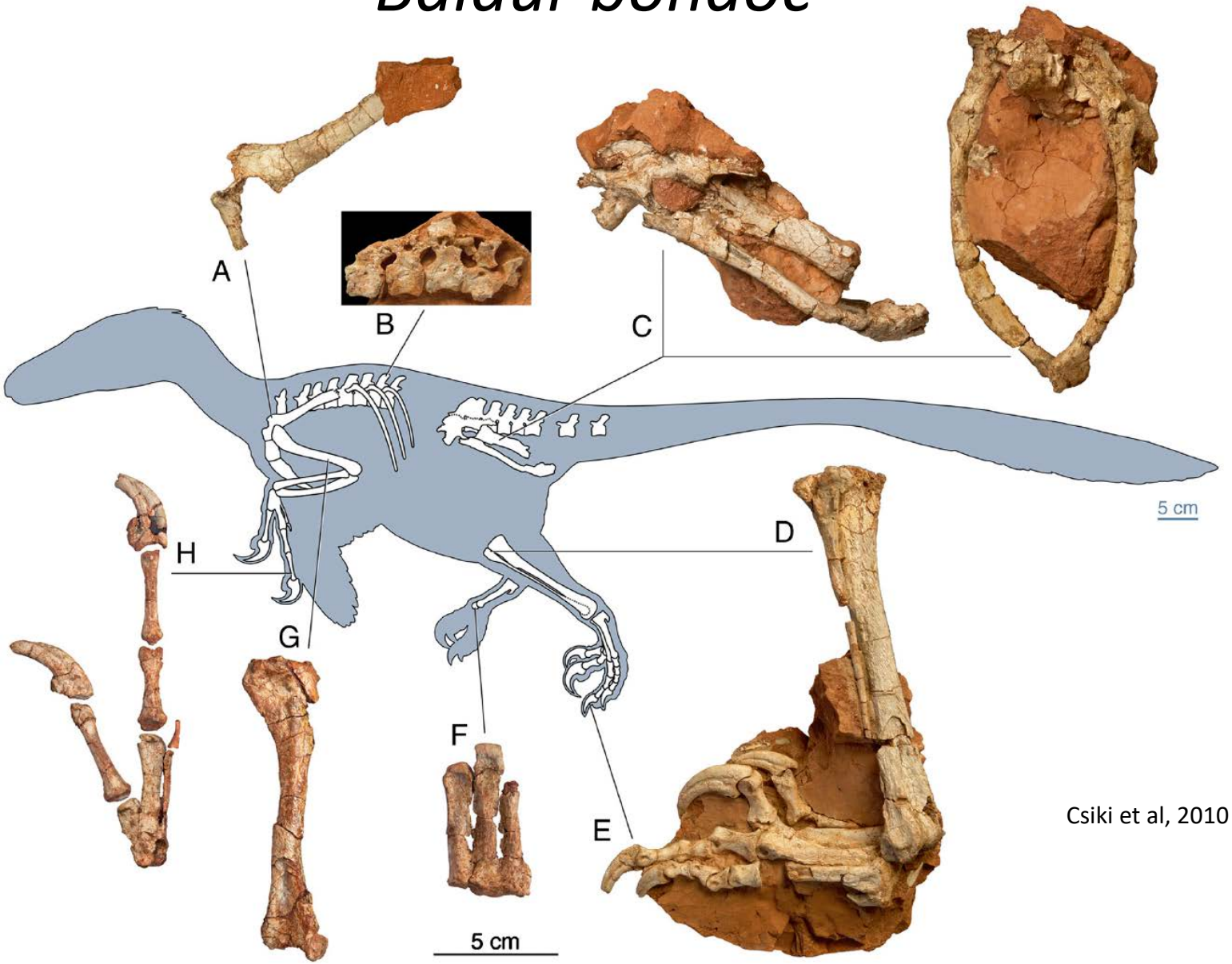






Godefroit et al., 2013

Balaur bondoc



Csiki et al, 2010

Fig. 1. Skeletal anatomy of *Balaur bondoc*. Reconstruction of the holotype with photos of individual bones. (*A*) Left scapulocoracoid (lateral view). (*B*) Middorsal vertebrae (lateral view). (*C*) Pelvis (left lateral and anterior views). (*D*, *E*) Left hindlimb and pes. (*F*) Right tarsometatarsus (extensor view). (*G*) right humerus (posterior view). (*H*) Right carpometacarpus and manual digits (extensor view). Scale bar at right refers to skeletal reconstruction and at bottom to all bones.

Unenlagiidae

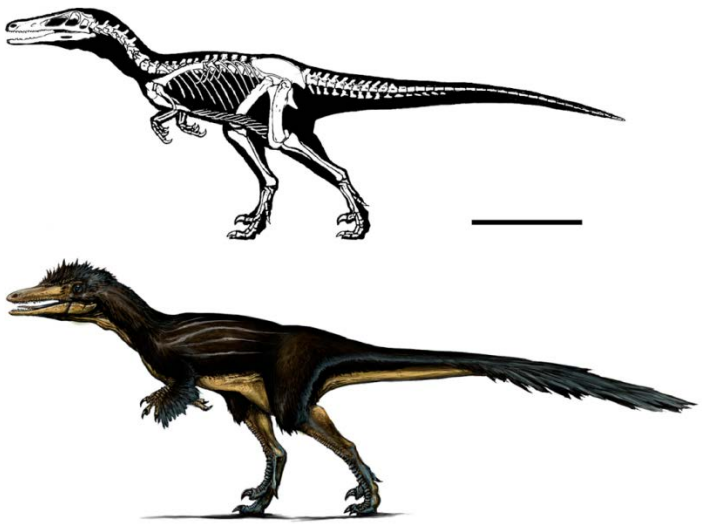


Fig. 21. Life reconstruction of *Austroraptor cabazai*. Scale bar equals 1 m (drawing by R. Vera).

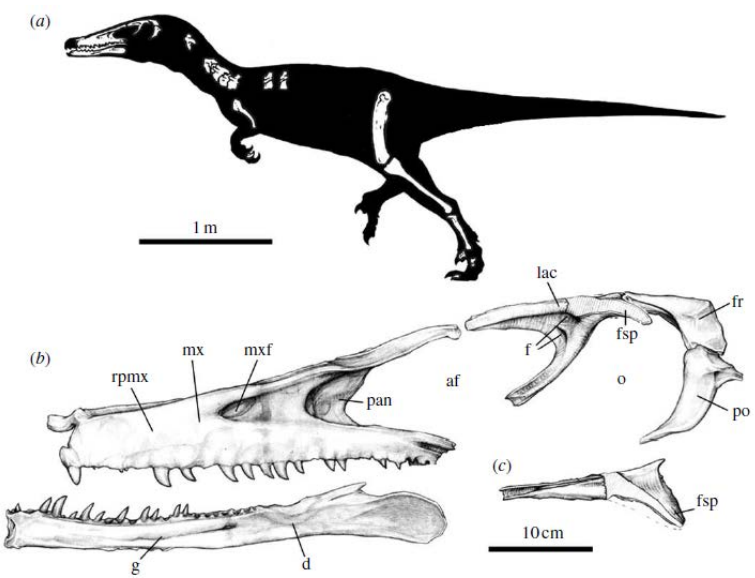


Figure 1. *Austroraptor cabazai* MML 195, holotype. (*a*) Skeletal reconstruction and body shape, indicating discovered bones. Body length was estimated following equations described by Turner *et al.* (2007). (*b*) Skull reconstruction in left lateral view. (*c*) Left lacrimal in dorsal aspect. (*d*) Cervical 3? in left lateral view. (*e,f*) Cervical 8? in (*e*) left lateral and (*f*) cranial views. (*g,h*) Dorsal 4? in (*g*) left lateral and (*h*) cranial views. (*i,k*) Pedal phalanx II-2 in (*i*) left lateral and (*k*) dorsal views. (*j,l*) Pedal phalanx IV-2 in (*j*) left lateral and (*l*) dorsal views. af, antorbital fenestra; cp, carotid process; d, dentary; dp, diapophysis; f, foramina; fr, frontal; fsp, fan-shaped process of lacrimal; g, groove; h, caudoventral heel; lac, lacrimal; mx, maxilla; mxf, maxillary fenestra; ns, neural spine; o, orbit; pan, postantral wall; po, postorbital; poz, postzygapophysis; pp, parapophysis; prz, prezygapophysis; rpmx, rostral process of maxilla; st, spine table.

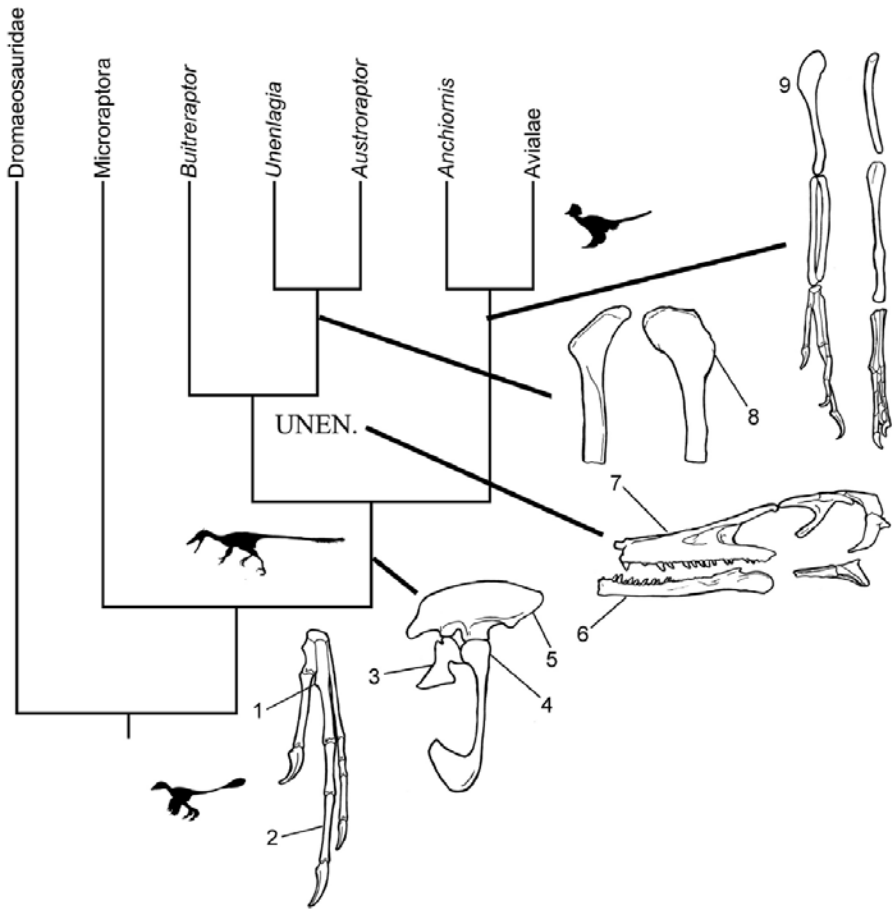
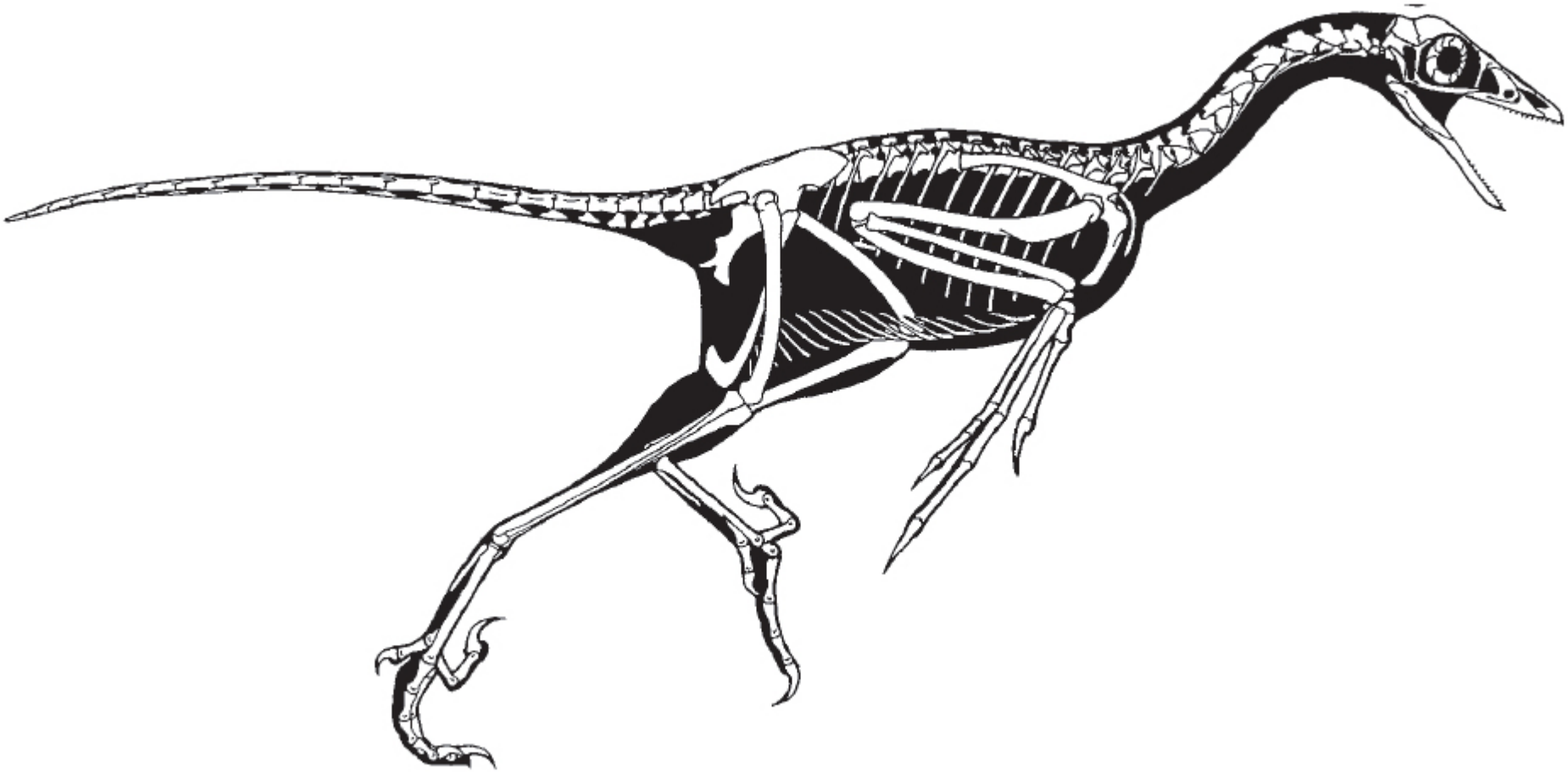


Fig. 22. Time calibrated phylogenetic tree depicting the relationships of the Unenlagiidae. Node 1: 1 – posterolateral flange on manual phalanx II-1, 2 – penultimate manual phlanax elongate and bowed. Node 2: 3 – short and stout ilium, 4 – proximal pubis rounded, 5 – preacetabular blade expanded. Node 3 (Unenlagiidae): 6 – low dentary carrying small unserrated teeth, 7 – elongate muzzle. Node 4 (*Unenlagia* + *Austroraptor*): 8 – reduced deltopectoral crest on humerus. Node 5 (*Anchiornis* + Avialae): 9 – elongate humerus and radius/ulna. Abbreviations: UNEN., Unenlagiidae.

Archaeopteryx lithographica



- Indiscutida ave estratigráficamente más antigua. Se conoce una especie *A. lithographica*, pero se ha propuesto la existencia de las especies *A. siemensii, A. bavarica* y el nuevo género *Welnhoferia grandis* (Elzanowski 2001; Elzanowski, 2002).


London Specimen


Berlin Specimen


Maxberg Specimen

Haarlem Specimen

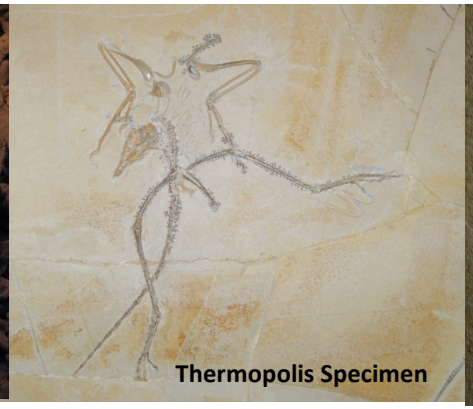

Eichstätt Specimen

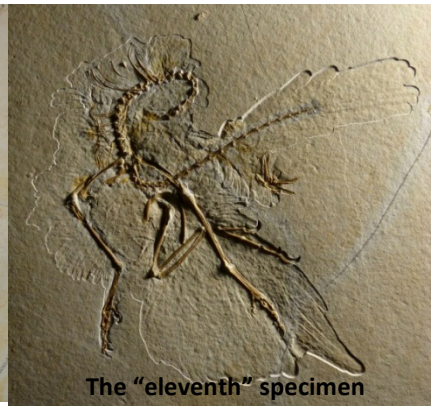

Solnhofen Specimen


Munich Specimen


Daiting Specimen


Bürgermeister-Müller Specimen


Thermopolis Specimen


The “eleventh” specimen

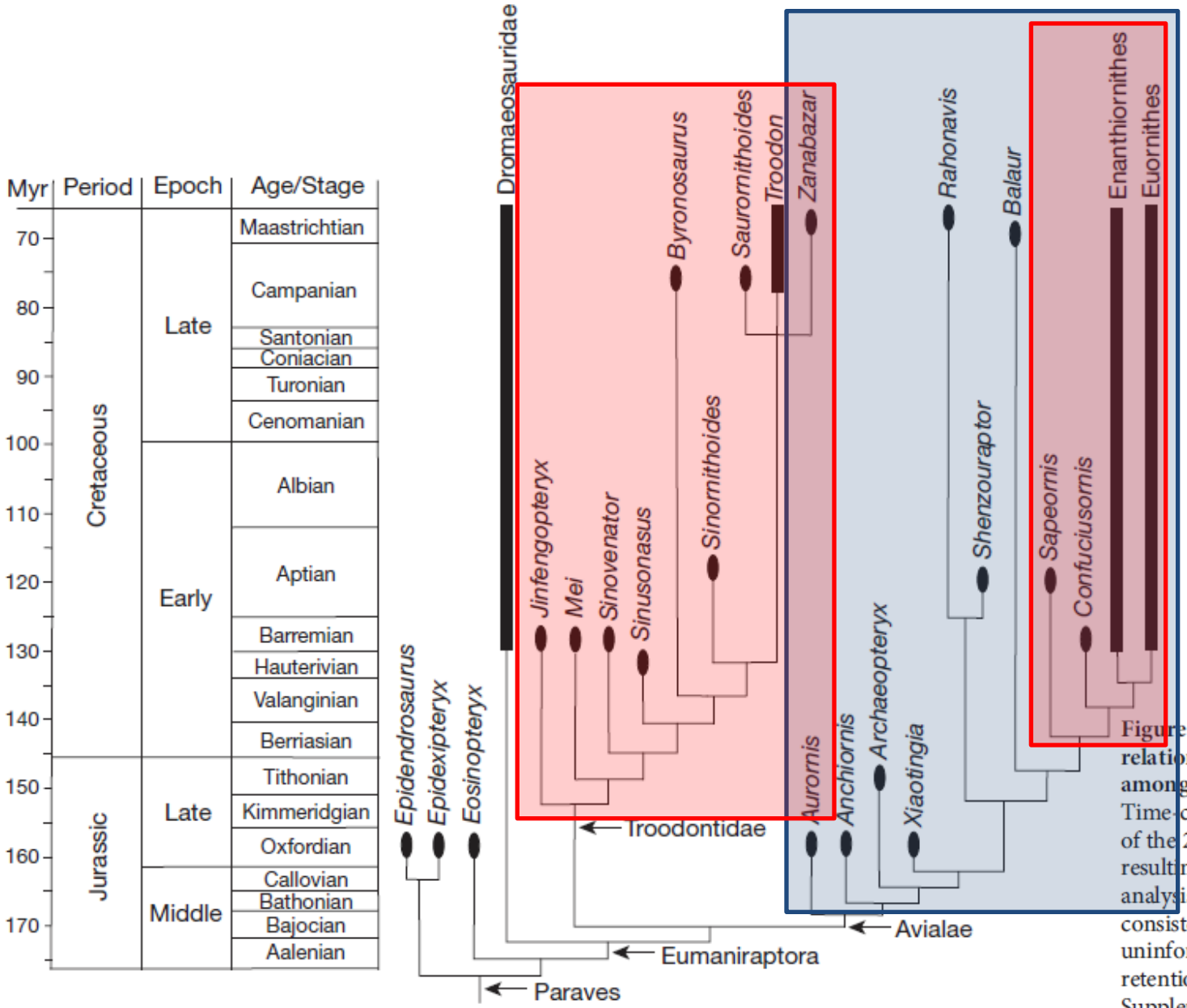
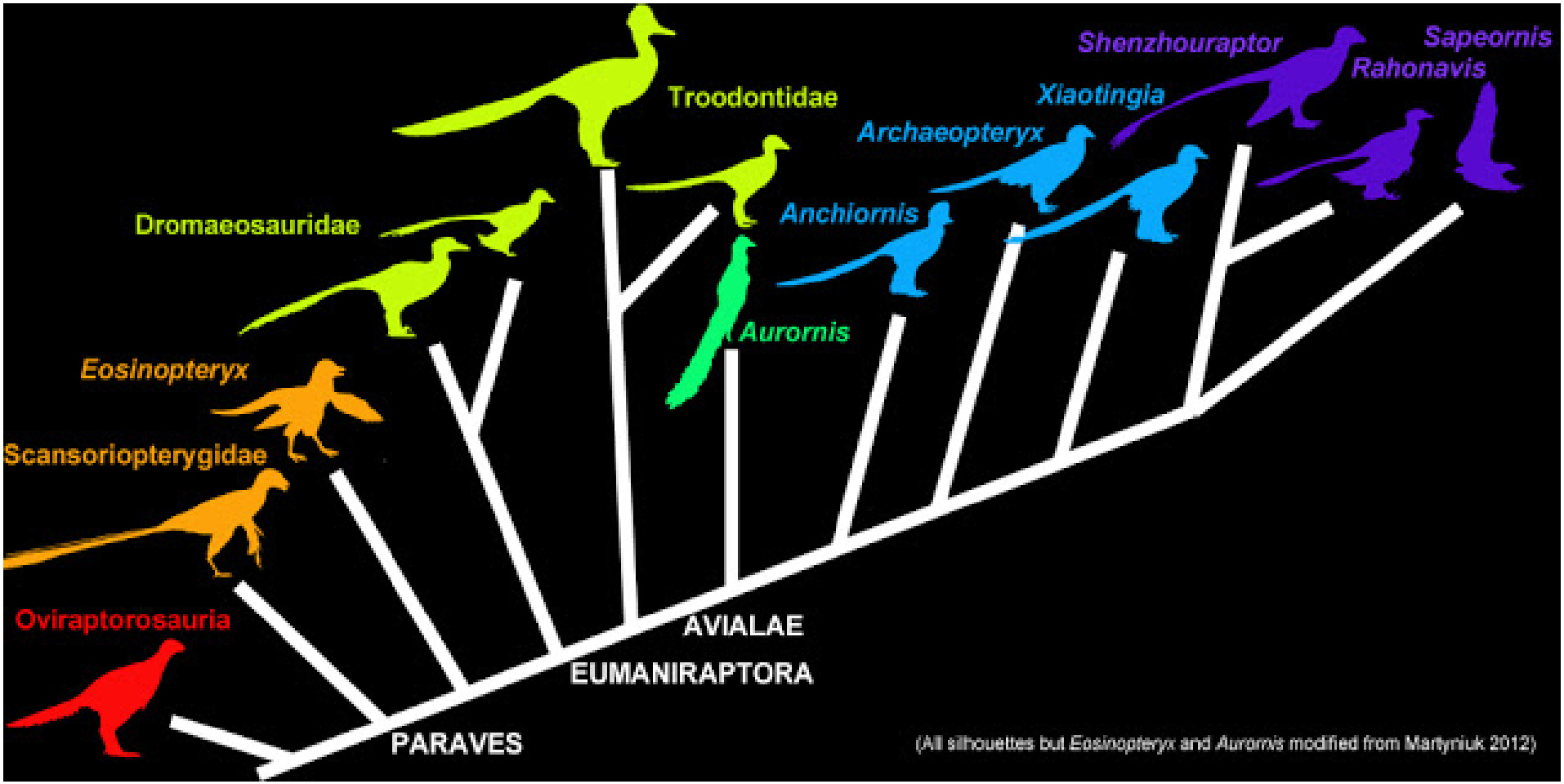
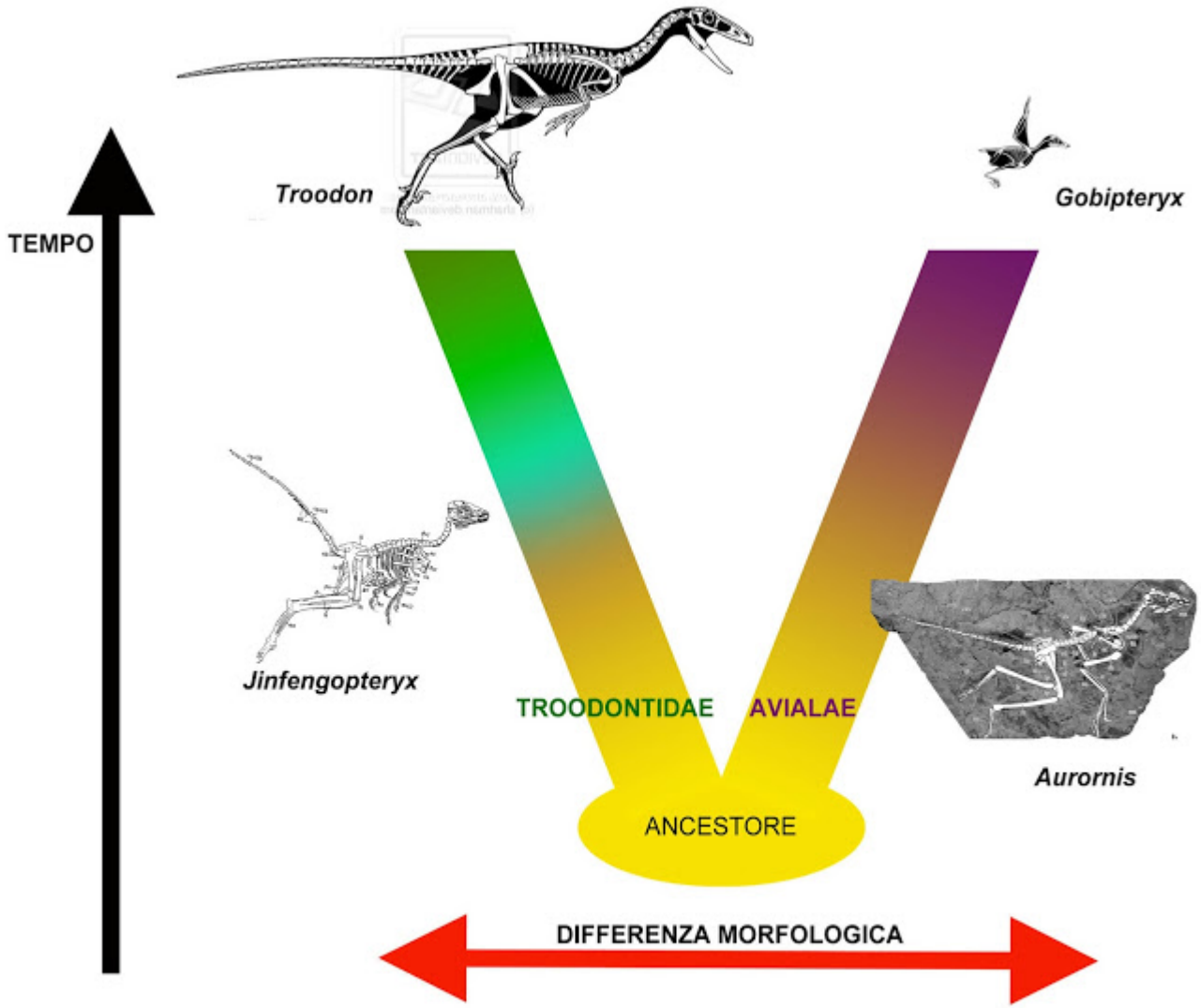
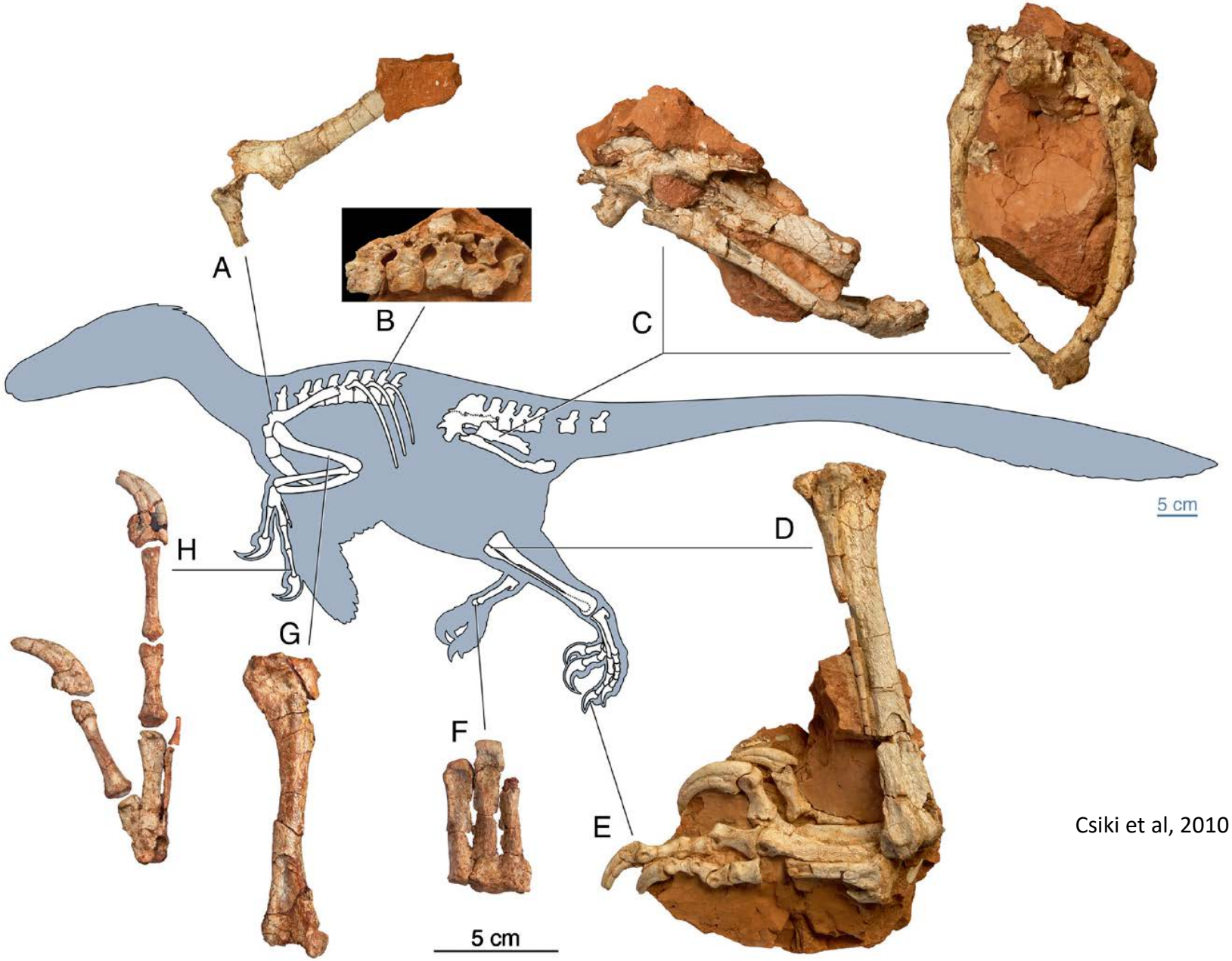


Figure 3 | Phylogenetic relationships of *Aurornis xui* among coelurosaurian theropods. Time-calibrated strict consensus tree of the 216 most-parsimonious trees resulting from our phylogenetic analysis (tree length = 4429; consistency index excluding uninformative characters = 0.27; retention index = 0.58; Supplementary Information). In this hypothesis *Aurornis* is an avialan more basal than *Archaeopteryx*, and Troodontidae is the sister-group of Avialae.


Shenzhouraptor
Sapeornis
Rahonavis
Xiaotingia
Troodontidae
Archaeopteryx
Anchiornis
Dromaeosauridae
Aurornis
Eosinopteryx
Scansoriopterygidae
Oviraptorosauria
AVIALAE
EUMANIRAPTORA
PARAVES
(All silhouettes but Eosinopteryx and Aurornis modified from Martyniuk 2012)



(*Troodon* modificato da opera di Hartman, *Gobipteryx* da opera di Auditore)



Csiki et al, 2010

Fig. 1. Skeletal anatomy of *Balaur bondoc*. Reconstruction of the holotype with photos of individual bones. (*A*) Left scapulocoracoid (lateral view). (*B*) Middorsal vertebrae (lateral view). (*C*) Pelvis (left lateral and anterior views). (*D*, *E*) Left hindlimb and pes. (*F*) Right tarsometatarsus (extensor view). (*G*) right humerus (posterior view). (*H*) Right carpometacarpus and manual digits (extensor view). Scale bar at right refers to skeletal reconstruction and at bottom to all bones.

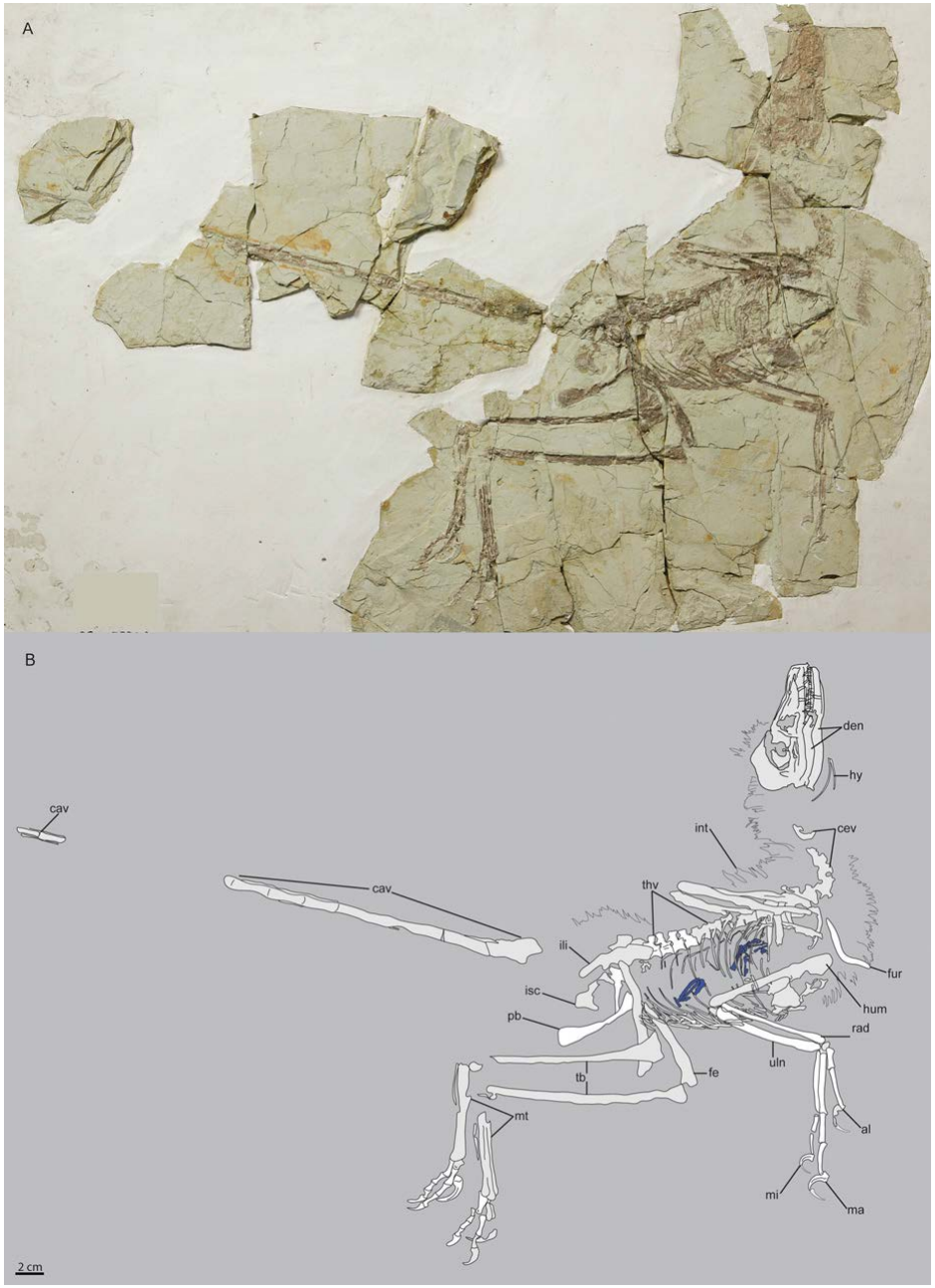


Fig. 1. Photograph (*A*) and line drawing (*B*) of IVPP V17972A. Anatomical abbreviations: ald, alular digit; cav, caudal vertebrae; cev, cervical vertebrae; den, dentary; fe, femur; fur, furcula; hum, humerus; hy, hyoid bones; ili, ilium; int, integument; isc, ischium; mad, major digit; mid, minor digit; mt, metatarsals; pb, pubis; rad, radius; tb, tibia; thv, thoracic vertebrae; ul, ulna.

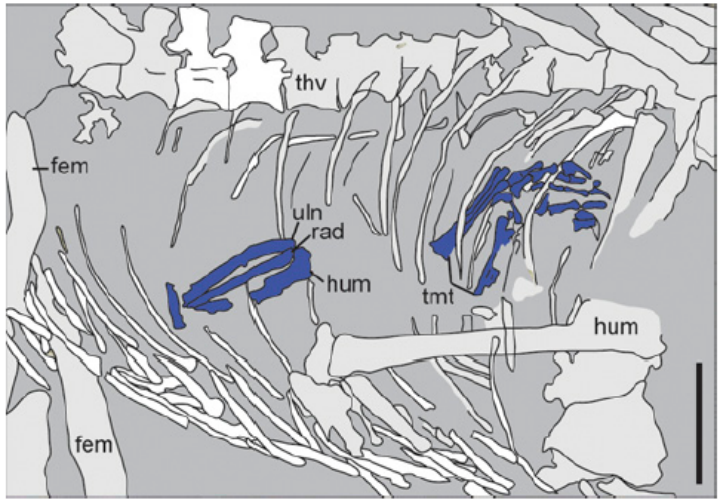


Fig. 2. Detail line drawing of stomach contents preserved in IVPP V17972A. Anatomical abbreviation not listed in Fig. 1: tmt, tarsometatarsus. (Scale bar, 10 mm.)

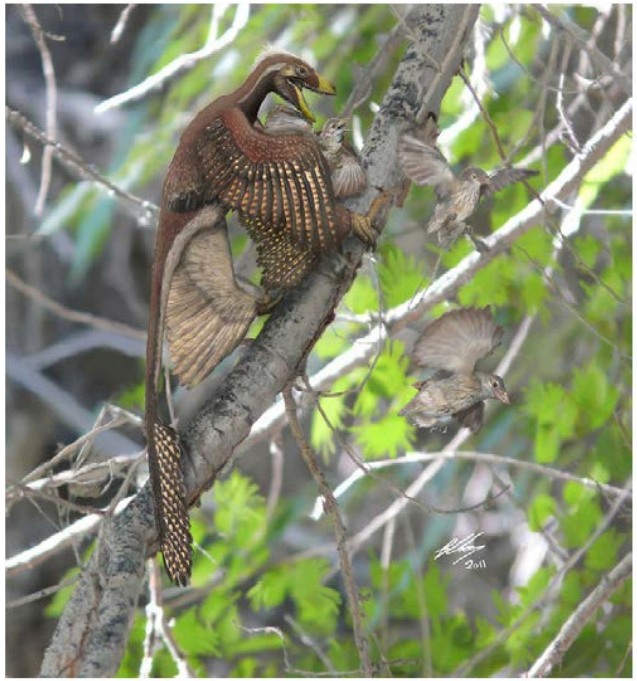
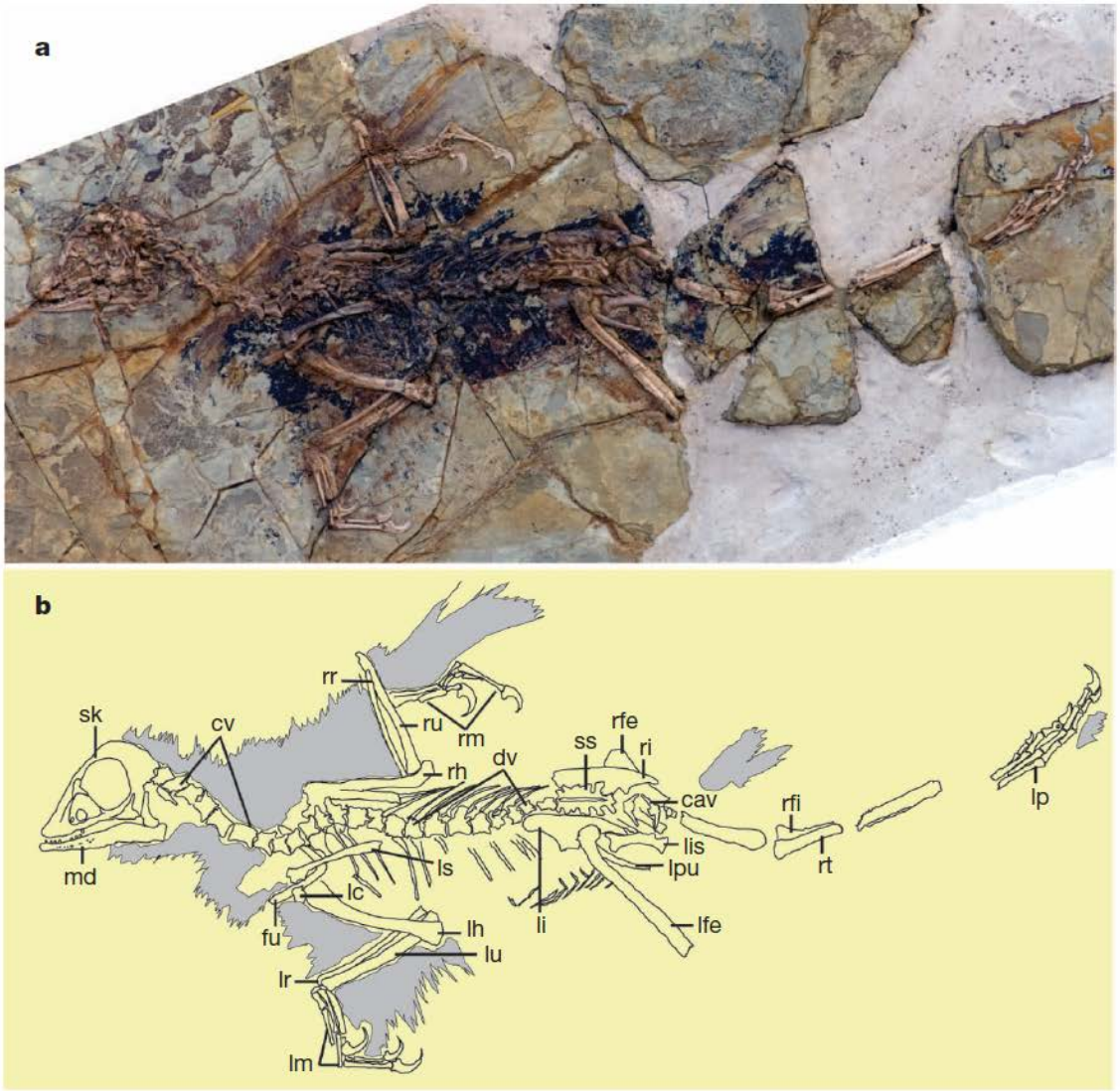


Fig. 3. Reconstruction of the life habits of *M. gui*.

Xiatingia zhengi



Xu et al, 2011

Figure 1 | ***Xiaotingia zhengi*** **holotype (STM 27-2).** **a**, **b**, Photograph (**a**) and line drawing (**b**). Integumentary structures in **b** are coloured grey. cav, caudal vertebra; cv, cervical vertebra; dv, dorsal vertebra; fu, furcula; lc, left coracoid; lfe, left femur; lh, left humerus; li, left ilium; lis, left ischium; lm, left manus; lp, left pes; lpu, left pubis; lr, left radius; ls, left scapula; lu, left ulna; md, mandible; rfe, right femur; rfi, right fibula; rh, right humerus; ri, right ilium; rm, right manus; rr, right radius; rt, right tibiotarsus; ru, right ulna; sk, skull; ss, synsacrum.

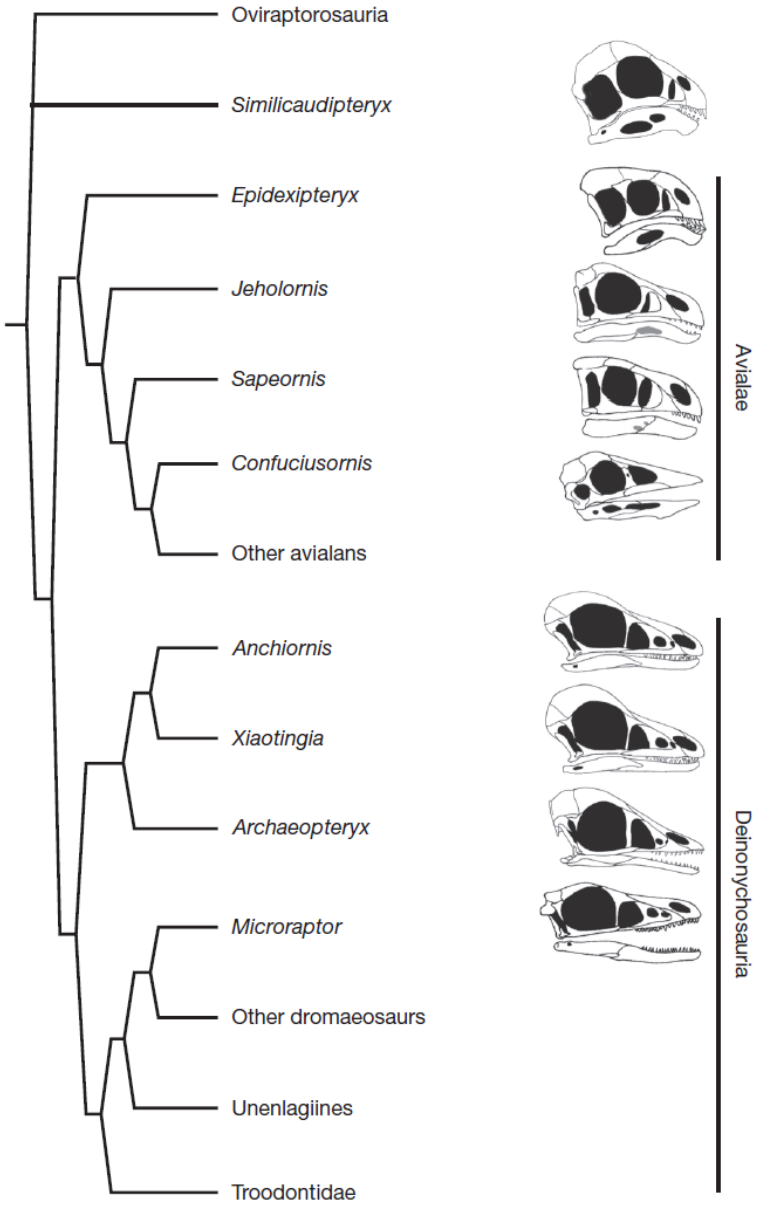


Figure 4 | A simplified cladogram showing the systematic position of *Xiaotingia* among the Coelurosauria (see Supplementary Information). Morphological features in grey areas need confirmation by better preserved specimens. Taxa recovered as basal avialans by our analysis are more similar in general morphology to the oviraptorosaurs than to the archaeopterygids and basal deinonychosaurs.

Xu et al, 2011

Origen y Evolución de Aves

Sergio Soto Acuña

Área de Paleontología, Museo Nacional de Historia Natural

Laboratorio de Ontogenia y Filogenia, Facultad de Ciencias Universidad de Chile

Avialae

Definición por apomorfía: Clado caracterizado por la presencia de miembros santeriores alargados transformados en alas (con capacidad voladora), incluye *Archaeopteryx* y Ornithurae (Gauthier, 1986)

Sinapomorfías:

- **Hipertrofia de miembro anterior en 120–140% o más relativo a miembro posterior**
- **Antebrazo 87% de la longitud total del húmero**
- **Cola reducida a 23 o menos caudales libres**

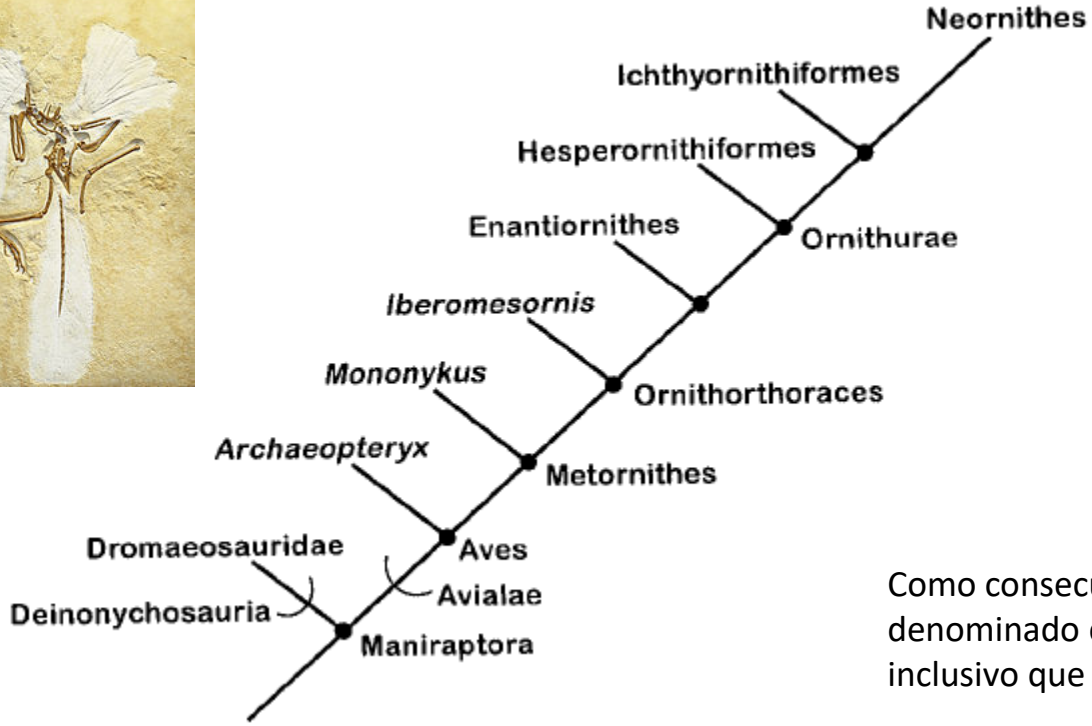
FIGURE 2–5 Skeletal features of (A) the reptilelike *Archaeopteryx* and (B) a modern bird, the domestic pigeon. In modern birds, (1) the braincase is expanded and the head bones are fused; (2) the separate hand bones of reptiles are fused into fewer rigid elements; (3) the separate pelvic bones of reptiles are fused into a single, sturdy structure; (4) the many tail vertebrae of *Archaeopteryx* are reduced in number and partly fused into a pygostyle; (5) the tiny cartilaginous sternum of *Archaeopteryx* has expanded to a large keeled bony structure for the attachment of flight muscles; and (6) the typical reptile rib cage is strengthened with horizontal uncinate processes. [*From Evolution of Vertebrates by E. H. Colbert. Copyright 1955 John Wiley & Sons, Inc.; reprinted by permission of John Wiley & Sons, Inc.*]

Avialae:

Definición de rama (Padian, 2001; Padian, 2004): Clado más inclusivo que contiene a *Columba livia* y todos los maniraptores más cercanos a Neornithes que a *Deinonychus*.

Aves:

Definición de nodo (Padian, 2001; Padian, 2004): Clado más inclusivo que contiene a *Archaeopteryx*, *Columba livia*, su ancestro común más reciente y todos sus descendientes.



Como consecuencia el clado denominado como Avialae es más inclusivo que Aves.

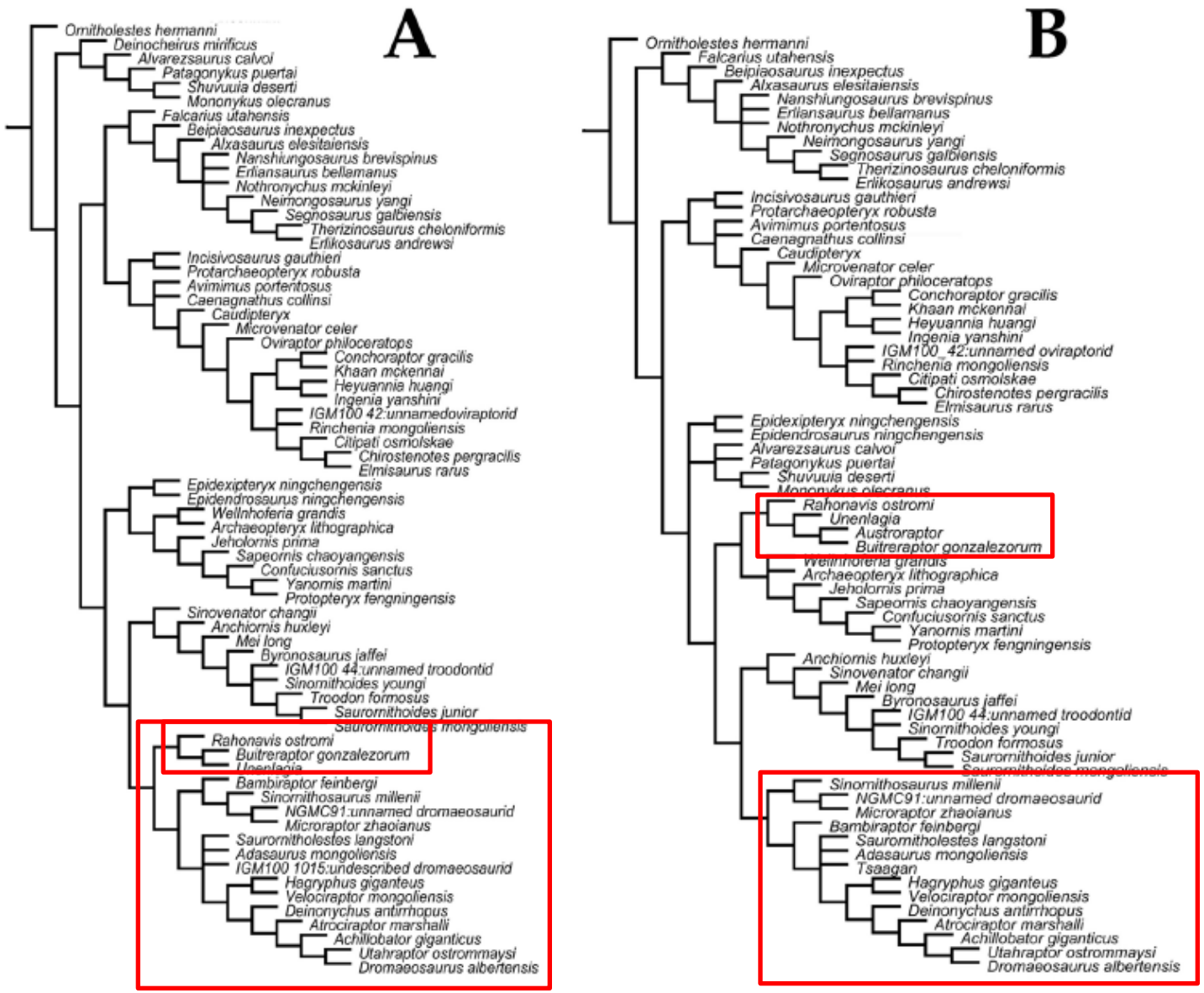


Fig. 1 – Alternative interpretations about the phylogenetic relationships of Unenlagiidae. **A**, phylogeny proposed by Hu et al. (2009), depicting unenlagiids as nested within Deinonychosauria and Dromaeosauridae; **B**, present analysis, depicting unenlagiids as the sister group of Aves.

Agnolin & Novas, 2011

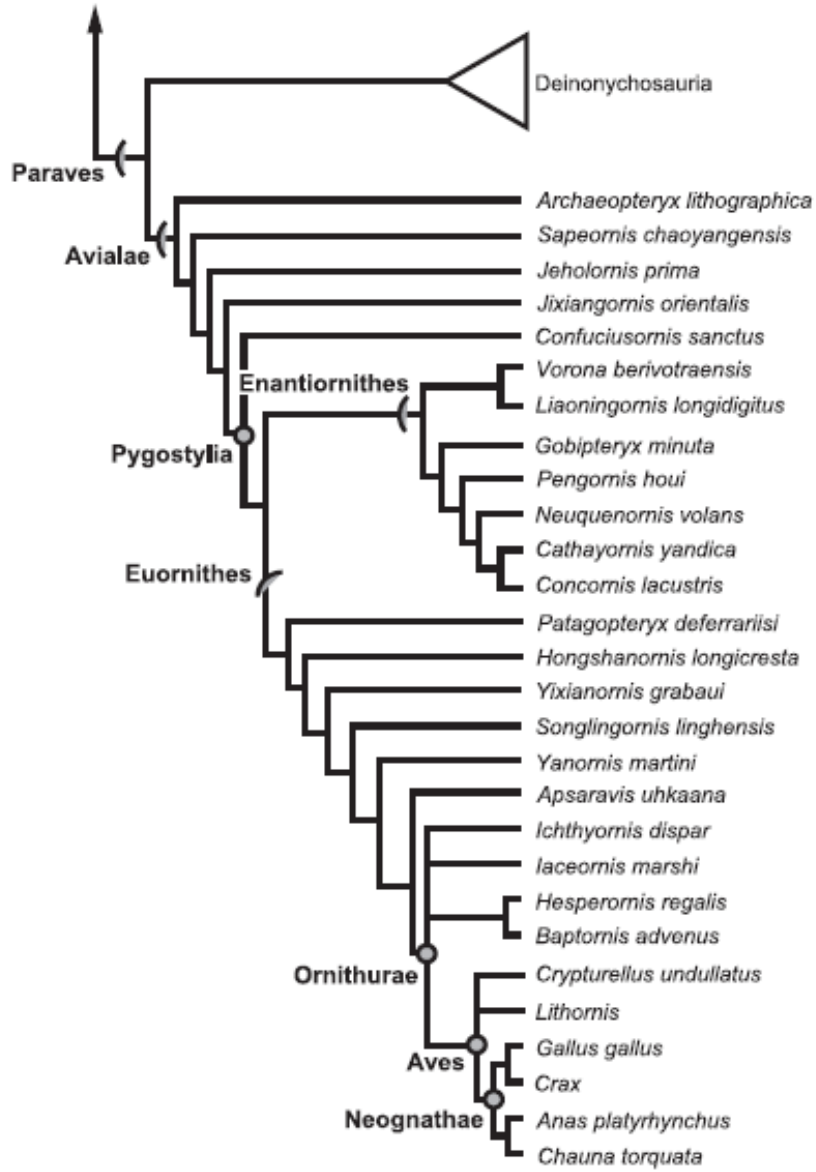
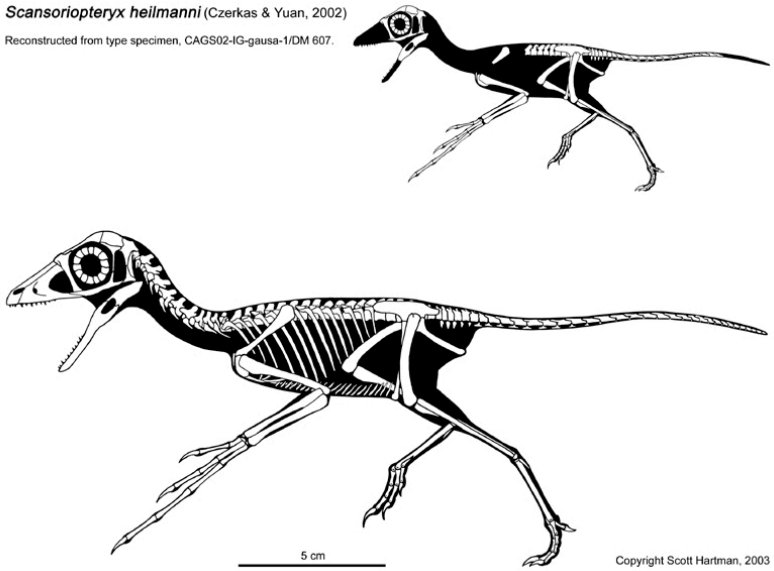


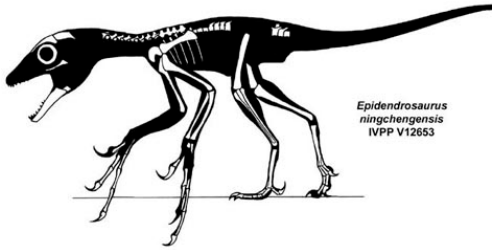
Fig. 65. Reduced strict consensus cladogram illustrating avialan relationships when the alternate positions of *Limenavis* are ignored. Deinonychosaurian taxa have been collapsed into a single terminal.

Turner et al, 2012

Scansoriopterygidae (Czerkas & Yuan 2002)

(stem group Aves)





Scansoriopteryx (Czerkas and Yuan 2002)

Epidendrosaurus ninchengensis (Zhang et al 2002)

Epidexipteryx hui
(Zhang et al 2008)

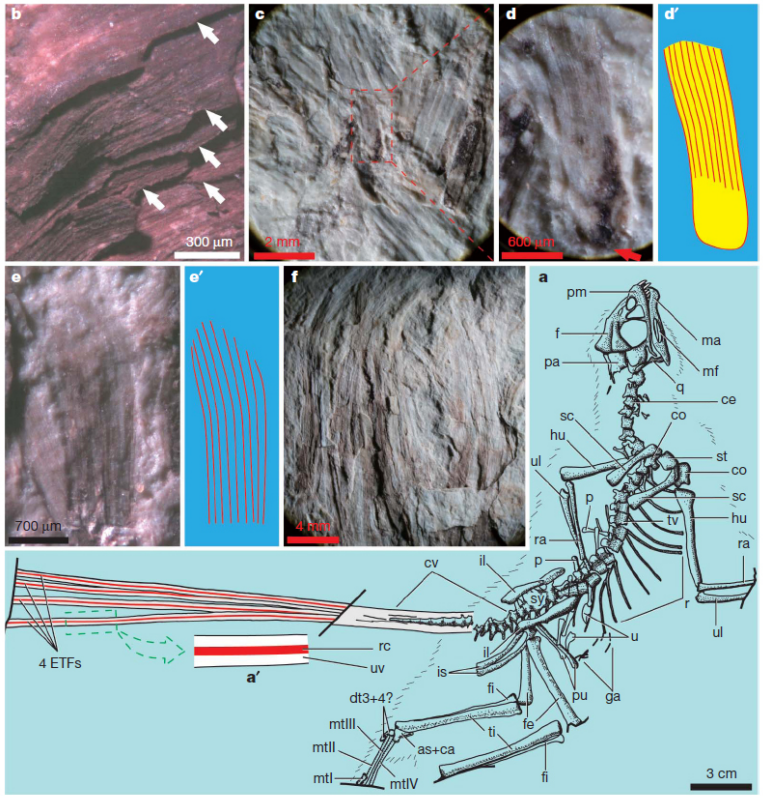
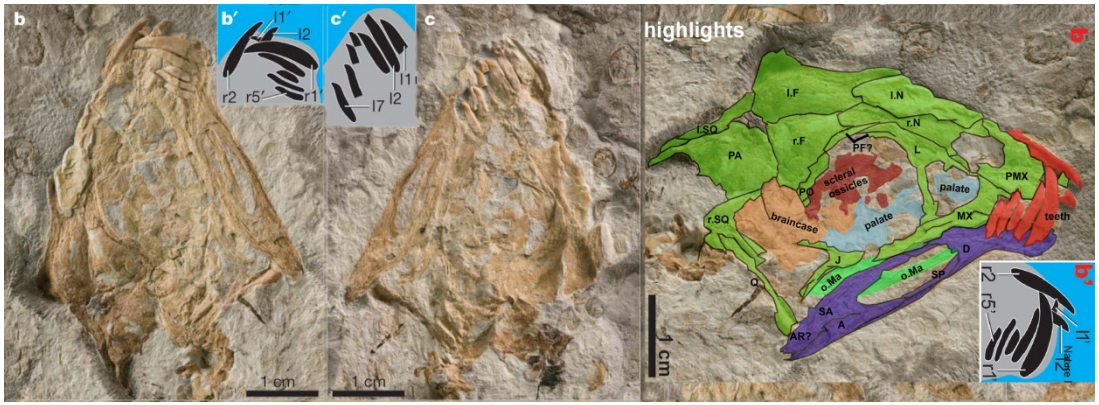
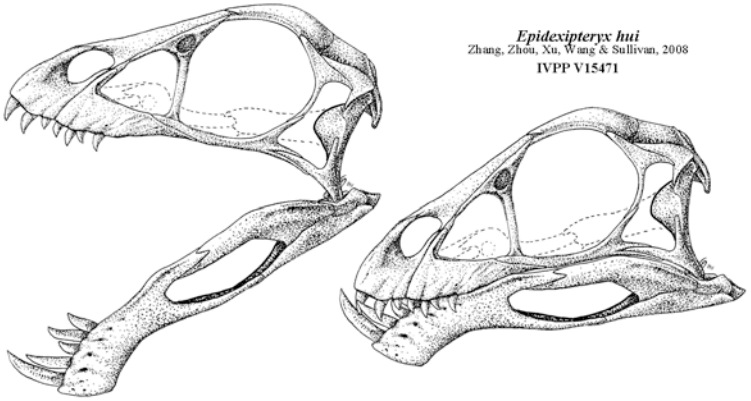
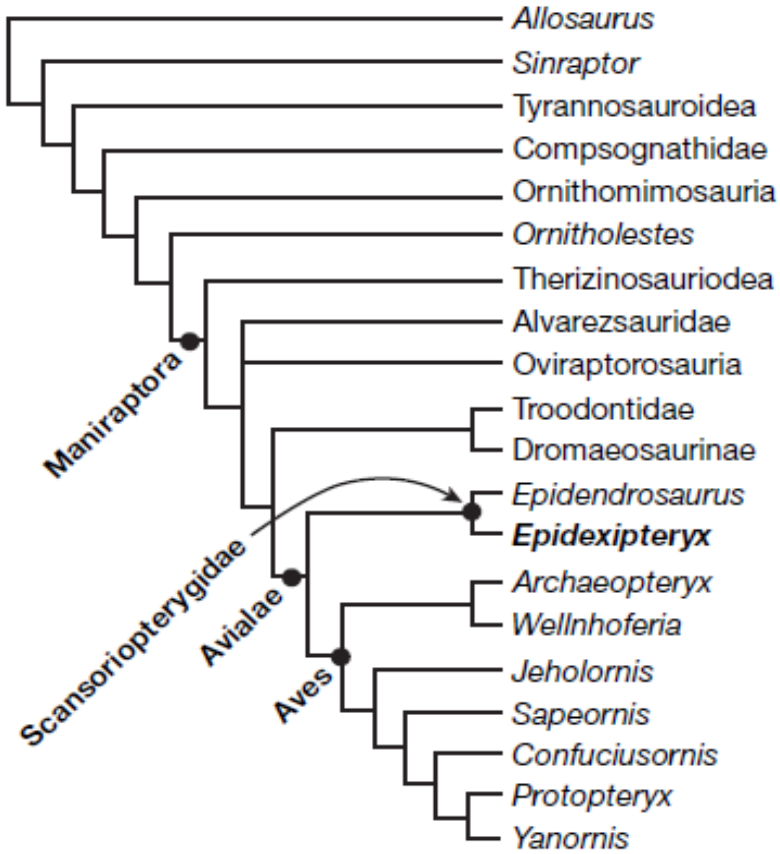
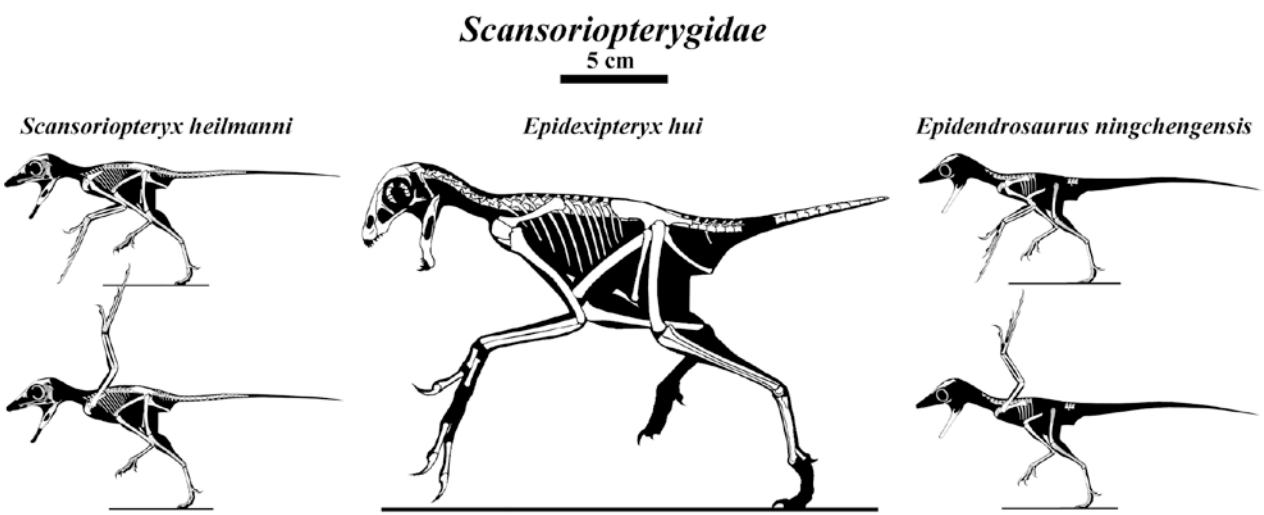


Figure 2 | Line drawings and close-up photographs of *Epidexipteryx hui* gen. et sp. nov. a, Skeleton and feather outline, based on both main slab and counterslab, showing that each shafted feather is formed by central rachis and two unbranched vanes (**a′**). **b**, **d**, **d′**, Proximal regions of non-shafted feathers; barbs are parallel and closely united as an unbranched membranous structure (**d**, **d′**), vanes are either layered, indicated by white arrows (**b**), or arranged irregularly (**c**). The red arrow indicates the proximal end of the feather (**d**). **e**, **e′**, **f**, Distal regions of non-shafted feathers, in which barbs appear loosely parallel. Abbreviations: as+ca, astragalus and calcaneum; ce, cervical vertebrae; co, coracoid; cv, caudal vertebrae; dt3+4, distal tarsals 3 and 4; f, frontal; fe, femur; fi, fibula; ga, gastralia; hu, humerus; il, ilium; is, ischium; ma, mandible; mtI–IV, metatarsals I–IV; p, phalanges or metacarpals; pa, parietal; pm, premaxilla; pu, pubis; q, quadrate; r, ribs; ra, radius; rc, rachis; sc, scapula; st, sternum; ti, tibia; tv, thoracic vertebrae; u, ungual phalanges; ul, ulna; uv, unbranched vane.

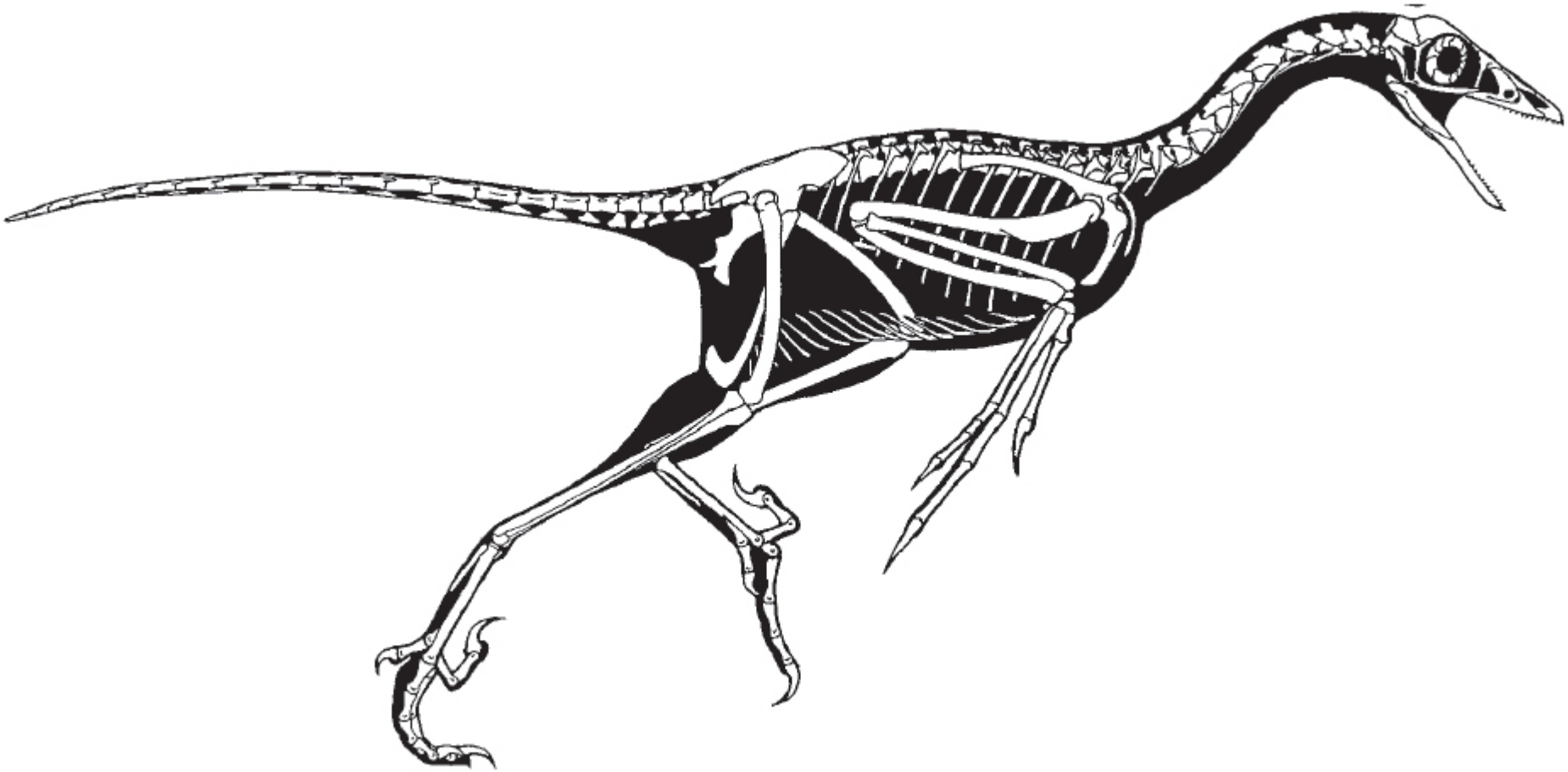





Allosaurus
Sinraptor
Tyrannosauroidea
Compsognathidae
Ornithomimosauria
Ornitholestes
Therizinosauriodea
Alvarezsauridae
Oviraptorosauria
Troodontidae
Dromaeosaurinae
Epidendrosaurus
Epidexipteryx
Archaeopteryx
Wellnhoferia
Jeholornis
Sapeornis
Confuciusornis
Protopteryx
Yanornis
Maniraptora
Scansoriopterygidae
Avialae
Aves


Scansoriopterygidae
5 cm
Scansoriopteryx heilmanni
Epidexipteryx hui
Epidendrosaurus ningchengensis

Archaeopteryx



- Indiscutida ave estratigráficamente más antigua. Se conoce una especie *A. lithographica*, pero se ha propuesto la existencia de las especies *A. siemensii, A. bavarica* y el nuevo género *Welnhoferia grandis* (Elzanowski 2001; Elzanowski, 2002).


London Specimen


Berlin Specimen


Maxberg Specimen

Haarlem Specimen

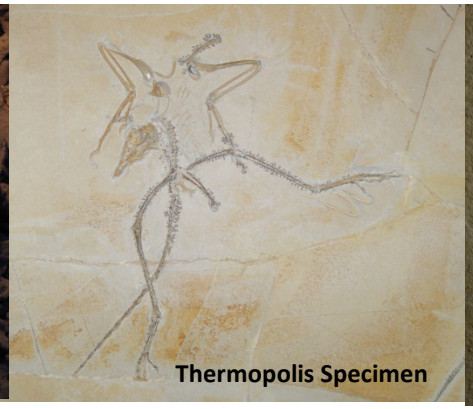

Eichstätt Specimen

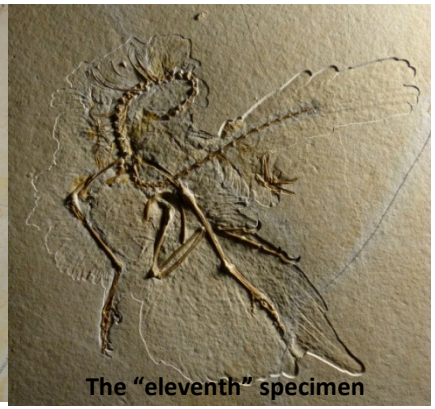

Solnhofen Specimen


Munich Specimen


Daiting Specimen


Bürgermeister-Müller Specimen


Thermopolis Specimen


The “eleventh” specimen

Long-Tailed Birds: *Jeholornis prima*

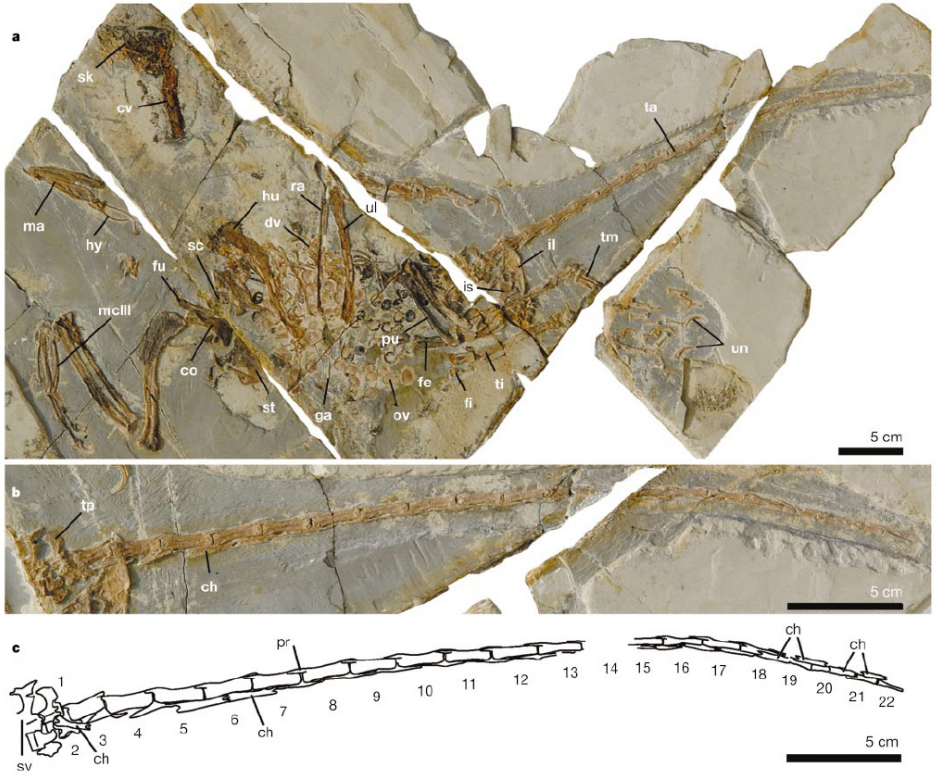
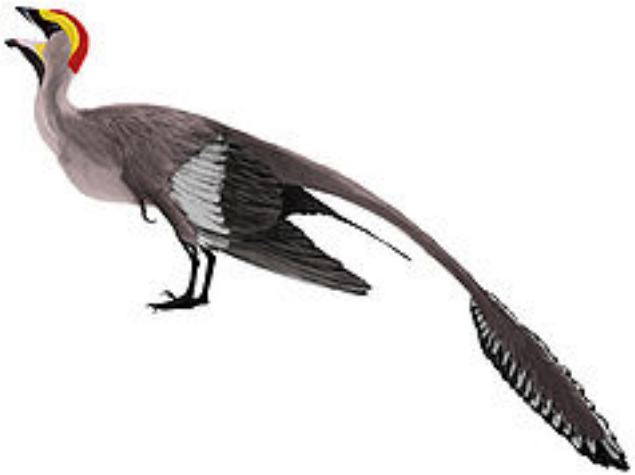
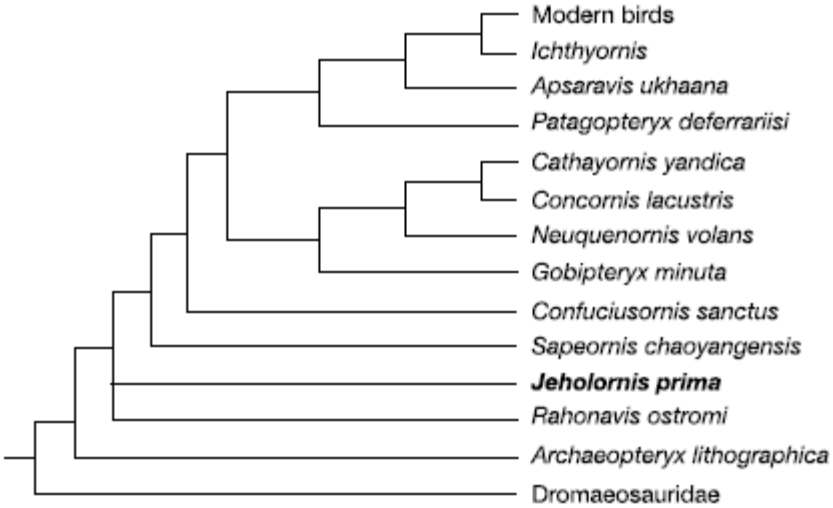


Figure 1 Complete holotype of *Jeholornis prima* gen. et sp. nov. (IVPP V13274). **a**, Skeleton. **b**, Caudal vertebrae. **c**, Line drawing of the caudal vertebrae. ch, chevron; co, coracoid; cv, cervical vertebra; dv, dorsal vertebra; fe, femur; fi, fibula; fu, furcula; ga, gastralia; hu, humerus; hy, hyoid bone; il, ilium; is, ischium; ma, mandible; mcIII, metacarpal III; ov, ovule; pr, prezygopophysis; pu, pubis; ra, radius; sc, scapula; sk, skull; st, sternum; sv, sacral vertebra; ta, tail; ti, tibia; tm, tarsometatarsus; tp, transverse process; ul, ulna; un, unguals; 1–22, caudal vertebrae 1–22.





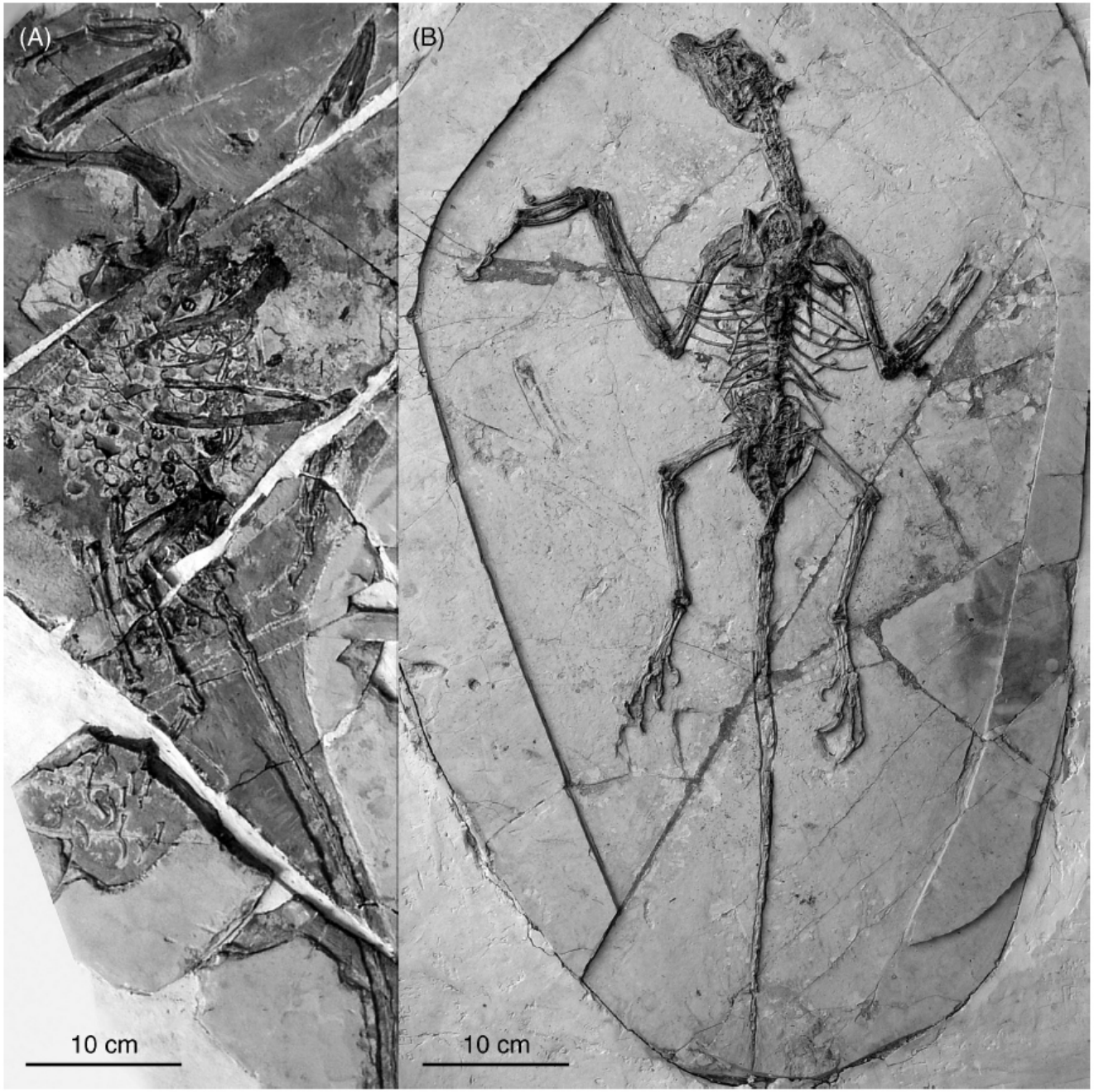
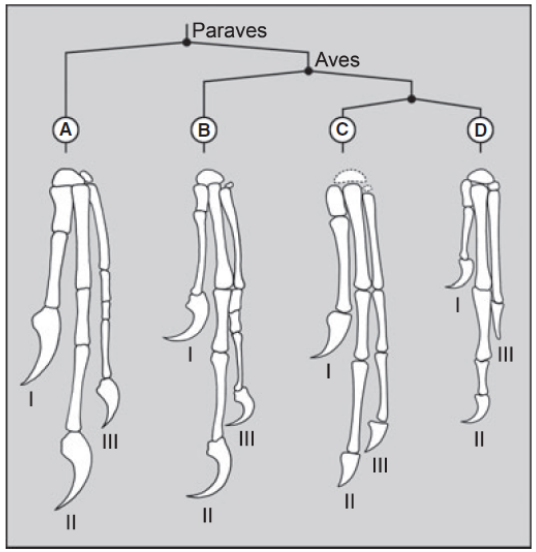


Fig. 3.7 Jiufotang Formation long-tailed birds: (A) holotype of *Jeholornis prima* IVPP V13274; (B) holotype of *Jixiangornis orientalis* CDPC-02-04-001. (Ji Shu-an, CAGS, with permission.)

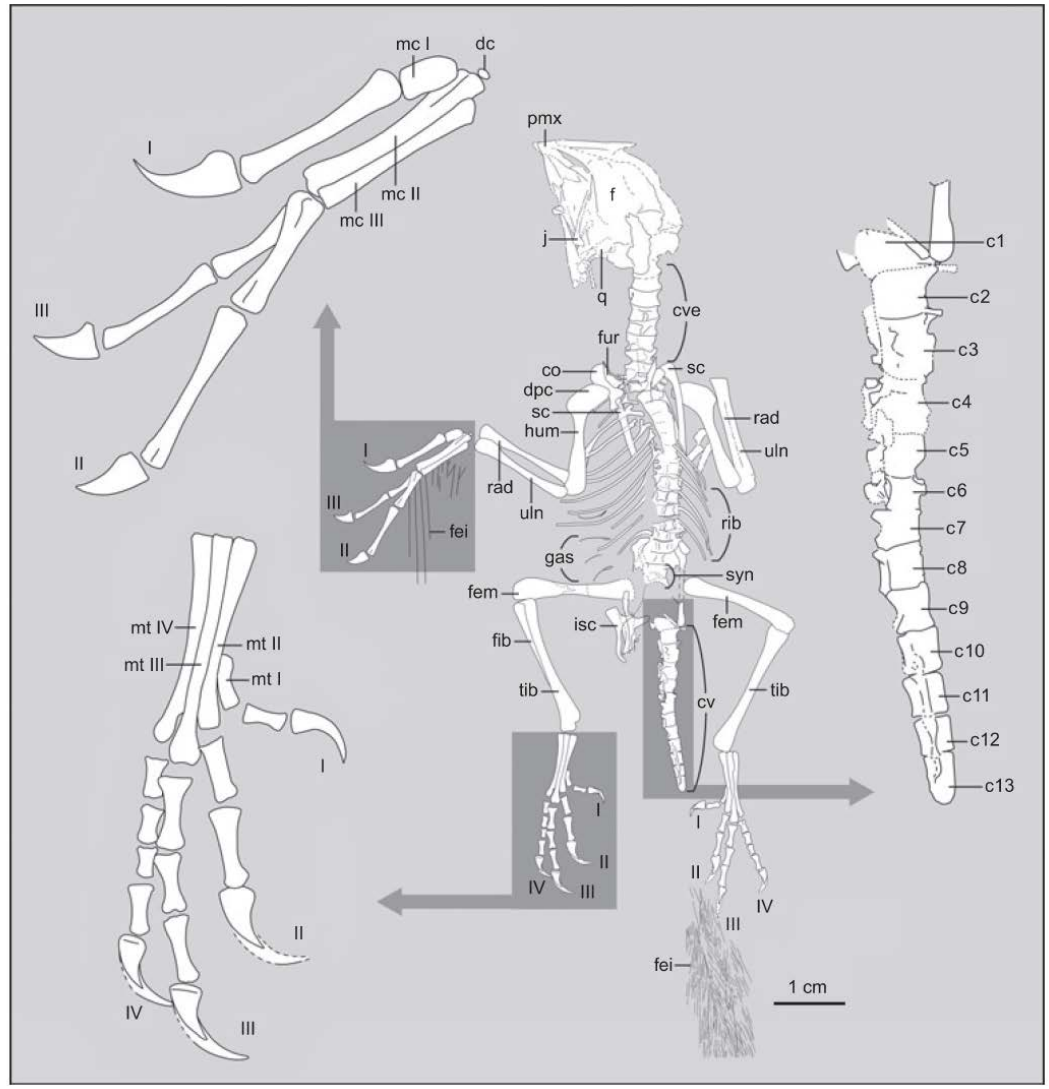
Dalianraptor cuhe Gao and Liu, 2005

Zhongornis haoae

Fig. 3.8 Holotype of the Yixian Formation nonpygostlian *Zhongornis haoae* with abbreviated tail: (A) DNHM D24
(B) DNHM D2456. (Photograph by Luis Chiappe.)

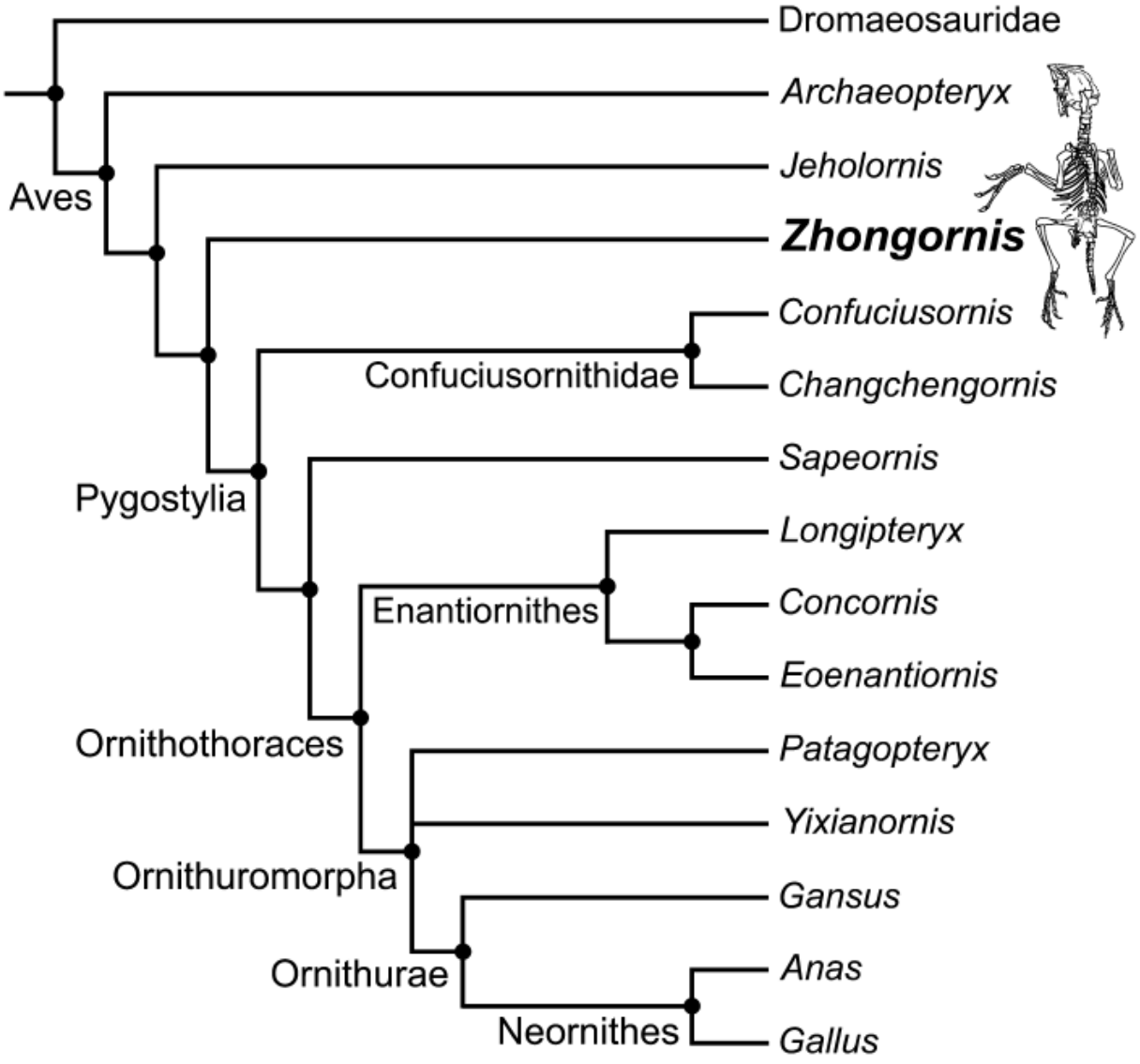


TEXT-FIG. 5. Comparative hands of the dromaeosaurid *Deinonychus* (A), *Archaeopteryx* (B), *Zhongornis* (C), and the enantiornithine bird *Longipteryx* (D). The hand of *Zhongornis* shows an intermediate phalangeal formula between 2-3-4-x-x (*Archaeopteryx* and most non-avian tetanuran theropods) and 2-3-1-x-x (typical of basal ornithothoracine birds: enantiornithines and primitive ornithuromorphs) (Chiappe 2007).

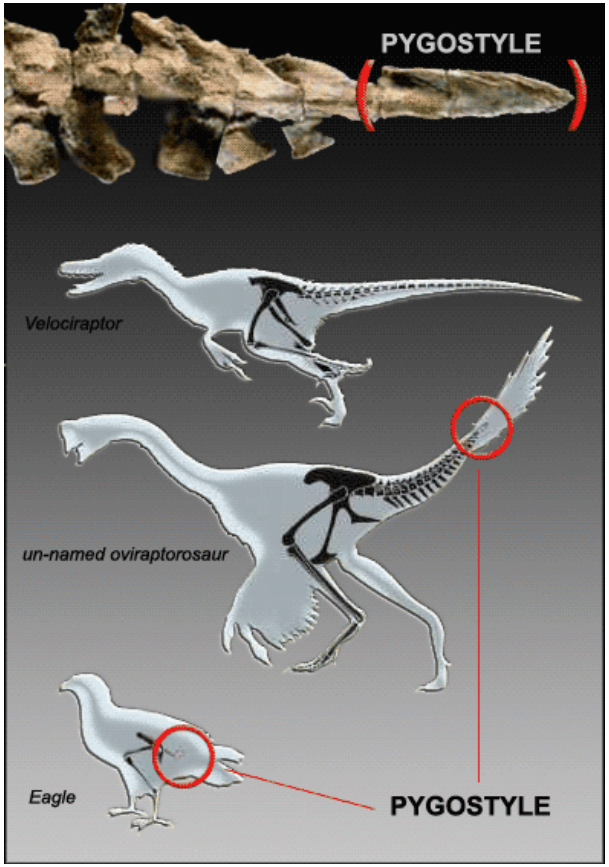


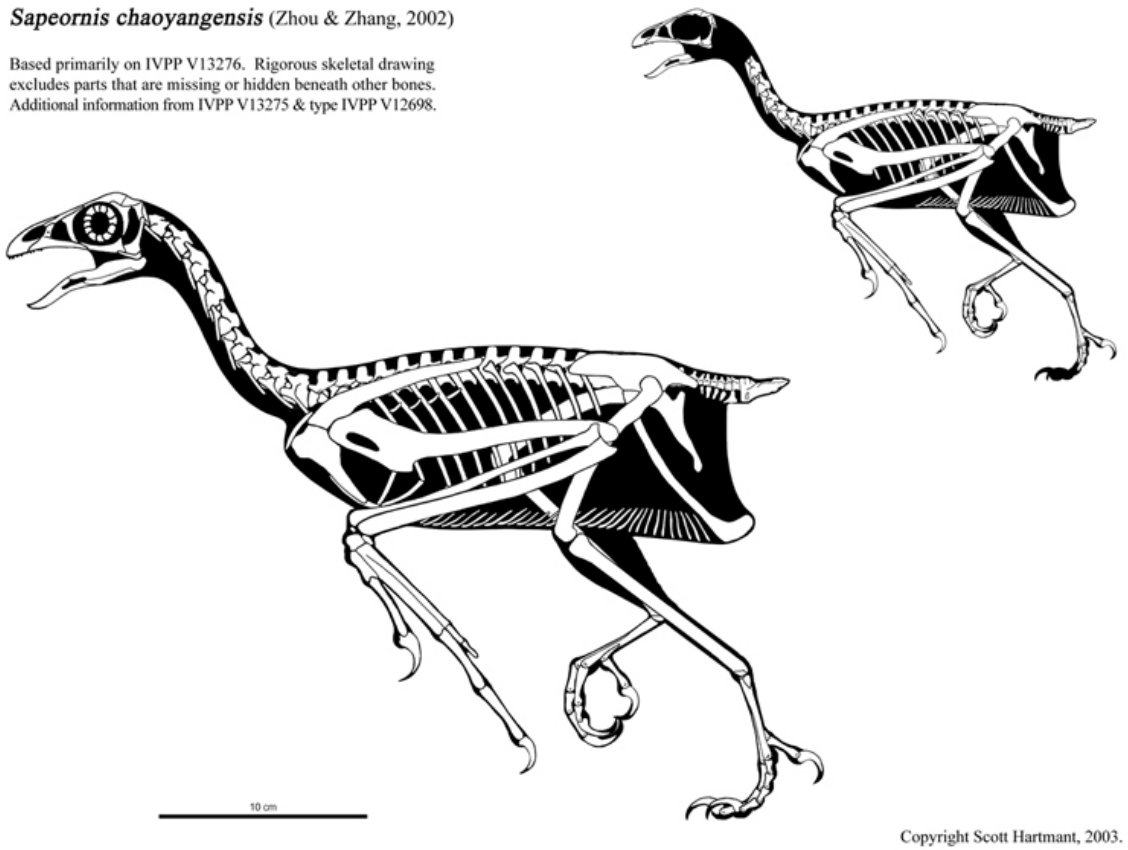
TEXT-FIG. 2. Interpretive drawing of slab (some portions added from information contained in counterslab) with close-ups of the manus, foot and caudal vertebrae. Abbreviations: co, coracoid; cv, caudal vertebrae (c1–c13); cve, cervical vertebrae; dc, distal carpal; dpc, deltopectoral crest; dv, dorsal vertebrae; gas, gastralia; f, frontal; fei, feather impressions; fem, femur; fib, fibula; fur, furcula; hum humerus; isc, ischium; j, jugal; mcI–III, metacarpals I–III; mtI–IV, metatarsals I–IV; pmx, premaxilla; q, quadrate; rad, radius; rib, thoracic ribs; sc, scapula; syn, synsacrum; tib, tibia; uln, ulna; I–IV, digits (manual or pedal) I–IV.

TEXT-FIG. 6. The single most parsimonious cladogram (length 363; consistency index 0.65; retention index 0.74) resulting from a cladistic analysis using 242 variables and 15 taxa (Dromaeosauridae plus 14 avians; the former used as outgroup) is shown. The cladistic analysis was conducted using 100 replications of random addition sequences of the taxa, each followed by tree bisection–reconnection (TBR) branch swapping, as implemented by NONA (Goloboff 1993) (see Appendix for character information, data matrix, and branch support). The results of the cladistic analysis place *Zhongornis* as the sister-taxon of Pygostylia, thus representing a critical stage in the evolution from basal, long-tailed birds to their short-tailed descendants.



Pygostylia

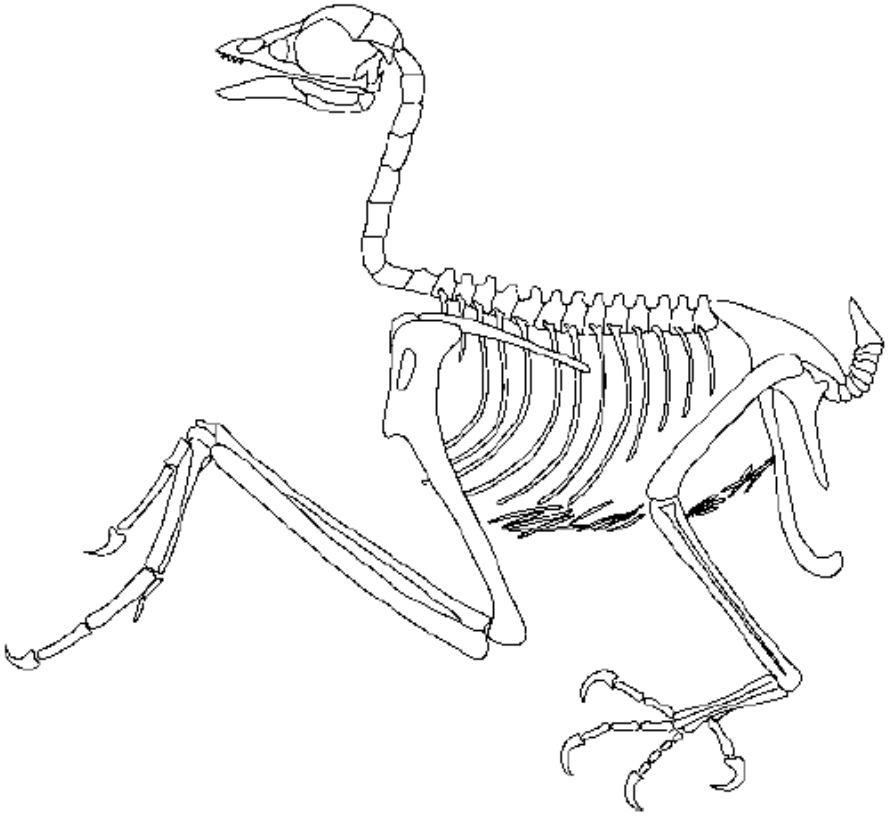

PYGOSTYLE
Velociraptor
un-named oviraptorosaur
Eagle
PYGOSTYLE


Sapeornis chaoyangensis (Zhou & Zhang, 2002)
Based primarily on IVPP V13276. Rigorous skeletal drawing excludes parts that are missing or hidden beneath other bones. Additional information from IVPP V13275 & type IVPP V12698.
10 cm
Copyright Scott Hartmant, 2003.

Sapeornitidae

Fig. 1 Photo of the holotype of *Sapeornis angustis* sp. nov. (V 13396) mainly in ventral view

Fig. 11. *Sapeornis chaoyangensis*. Reconstruction of the whole skeleton mainly based on IVPP V13275 and V13276.



Shensiornis primita

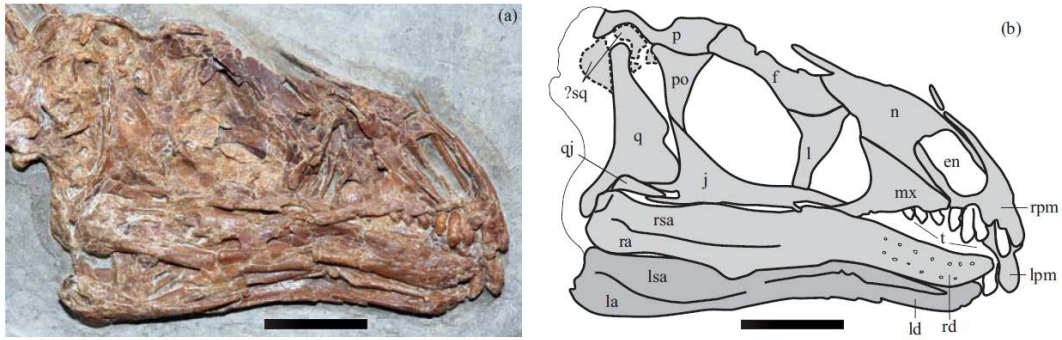


Fig. 3. Skull of *Shenshiornis primita* holotype (LPM-B00018) in right lateral view.
(a) close-up photograph and (b) line-drawing. Abbreviations: en, external nares; f, frontal; j, jugal; l, lacrimal; la, left angular; ld, left dentary; lsa, left surangular; mx, maxilla; n, nasal; p, parietal; po, postorbital; q, quadrate; qj, quadratojugal; ra, right angular; rd, right dentary; rpm, right premaxilla; rsa, right surangular; sq, squamosal; t, tooth. Scale bar = 10 mm.

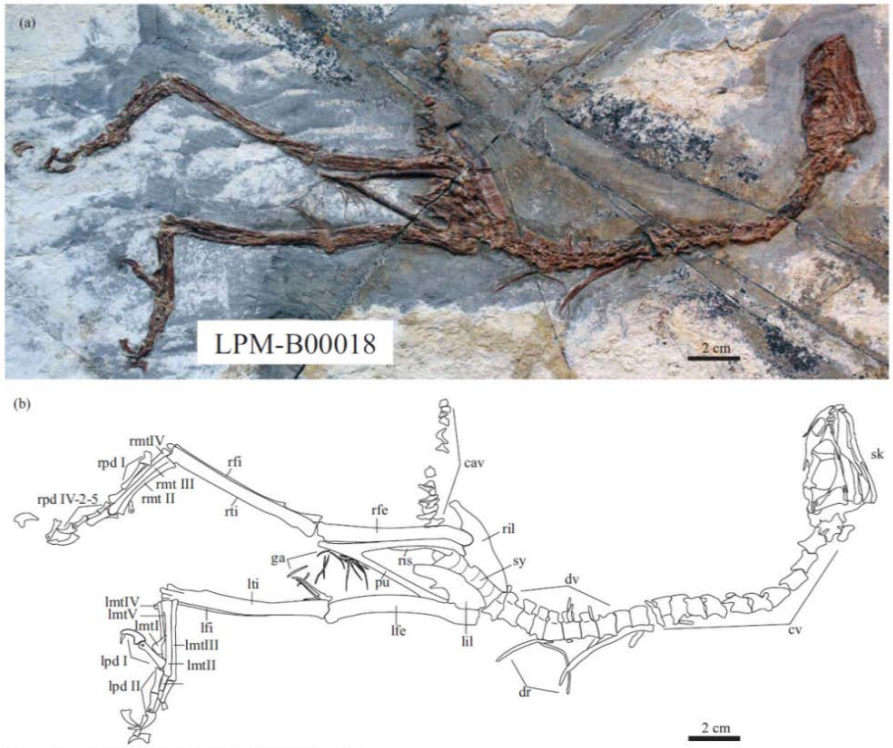


Fig. 2. *Shenshiornis primita* holotype (LPM-B00018).
(a) photograph and (b) line-drawing. Abbreviations: cav, caudal vertebra; cv, cervical vertebra; dr, dorsal rib; dv, dorsal vertebra; ga, gastralia; lfe, left femur; lfi, left fibula; lil, left ilium; lpdI-II, left pedal digit I-II; lti, left tibiotarsus; lmtI-V, left metatarsus I-V; pu, pubis; rfe, right femur; rfi, right fibula; ril, right ilium; ris, right ischium; rpdI, right pedal digit I; rpdIV2-5, second through firth phalanges of the right pedal digit IV; rmtII-IV, right metatarsus II-IV; rti, right tibiotarsus; sk, skull; sy, synsacrum. Scale bar = 20 mm.

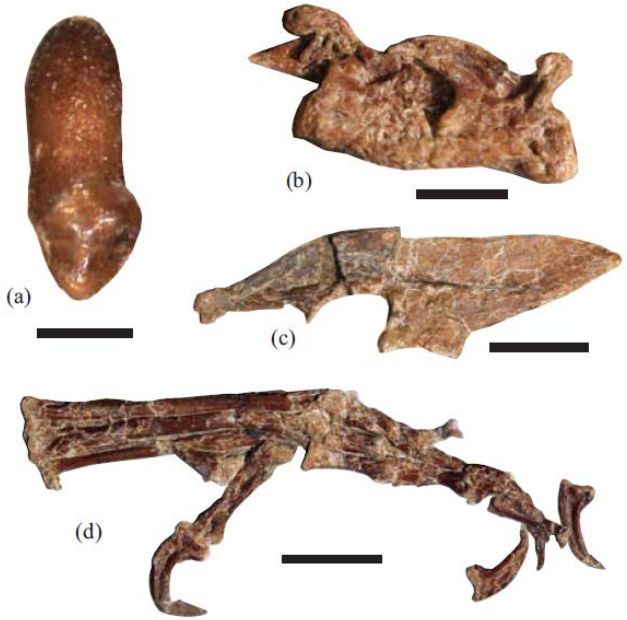


Fig. 4. *Shenshiornis primita* holotype: close-up photos of several skeletal elements of LPM-B00018.
(a) a premaxillary tooth in labial view; (b) two middle cervicals in right lateral view; (c) right ilium in lateral view; (d) left pes in mediocranial view. Scale bar = 1 mm for (a), 5 mm for (b), and 10 mm for (c) and (d).

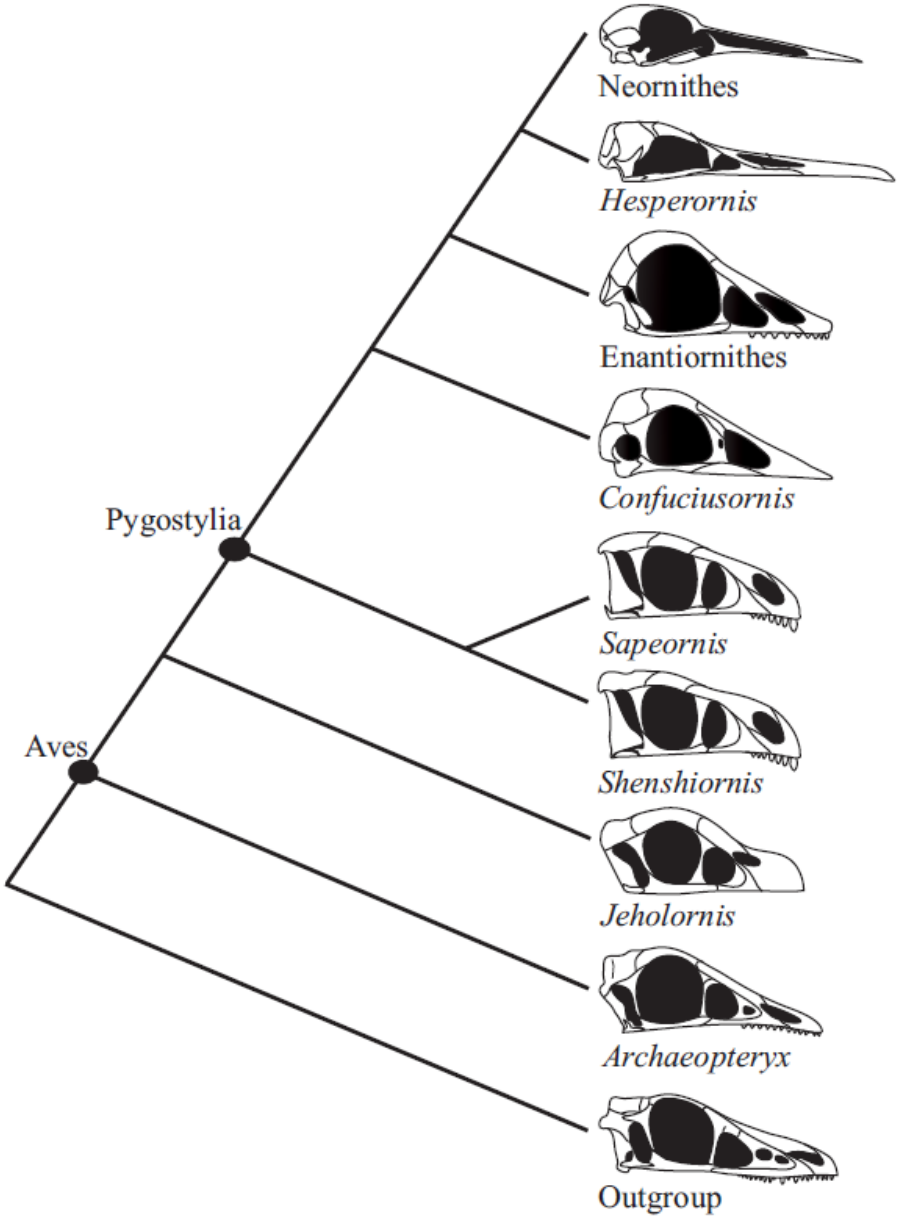


Fig. 5. A simplified tree from SI Fig. 1 showing the systematic position of *Shenshiornis primita* and the evolution of a streamlined and kinetic skull in the Aves.

Didactylornis jii

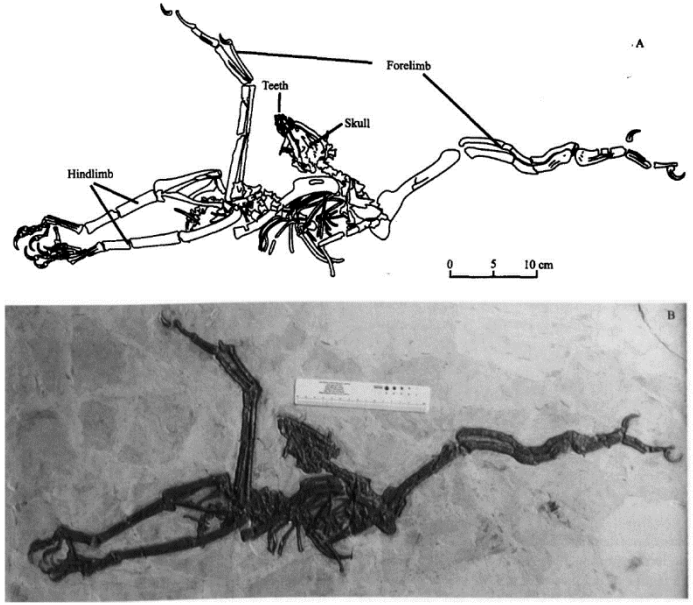


Fig. 1. Showing the osteological structures of the holotype of *Didactylornis jii* gen. et sp. nov.

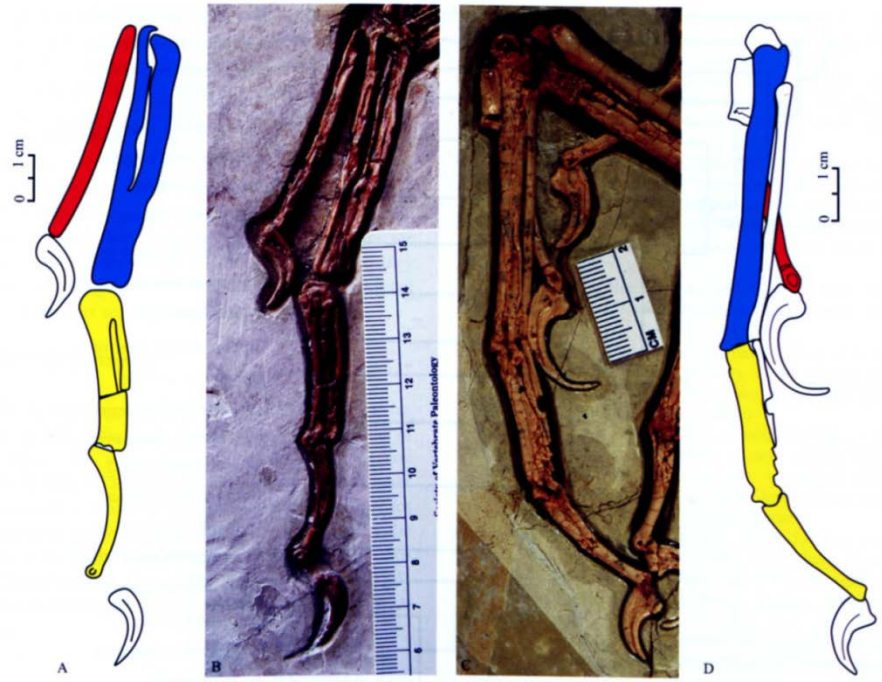


Fig. 3. Manual digits of *Didactylornis jii* gen. et sp. nov. and *Sapeornis chaoyangensis*.
(A) Sketch of manual digits of *Didactylornis jii* gen. et sp. nov. (B) Photo of manual digits of *Didactylornis jii* gen. et sp. nov. (C) Photo of manual digits of new material of *Sapeornis chaoyangensis* (CAGS-03-07-08) (D) Sketch of manual digits of new material of *Sapeornis chaoyangensis* (CAGS -03-07-08).

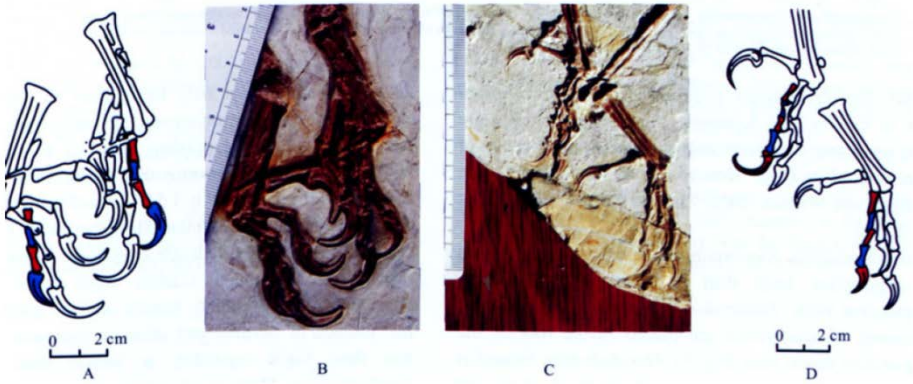


Fig. 4. Pedal digits of *Didactylornis jii* gen. et sp. nov. and *Sapeornis chaoyangensis*.
(A) Sketch of pedal digits of *Didactylornis jii* gen. et sp. nov. (B) Photo of pedal digits of *Didactylornis jii* gen. et sp. nov. (C) Photo of pedal digits of new material of *Sapeornis chaoyangensis* (JZPM-LSV-130) (D) Sketch of pedal digits of new material of *Sapeornis chaoyangensis* (JZPM-LSV-130).

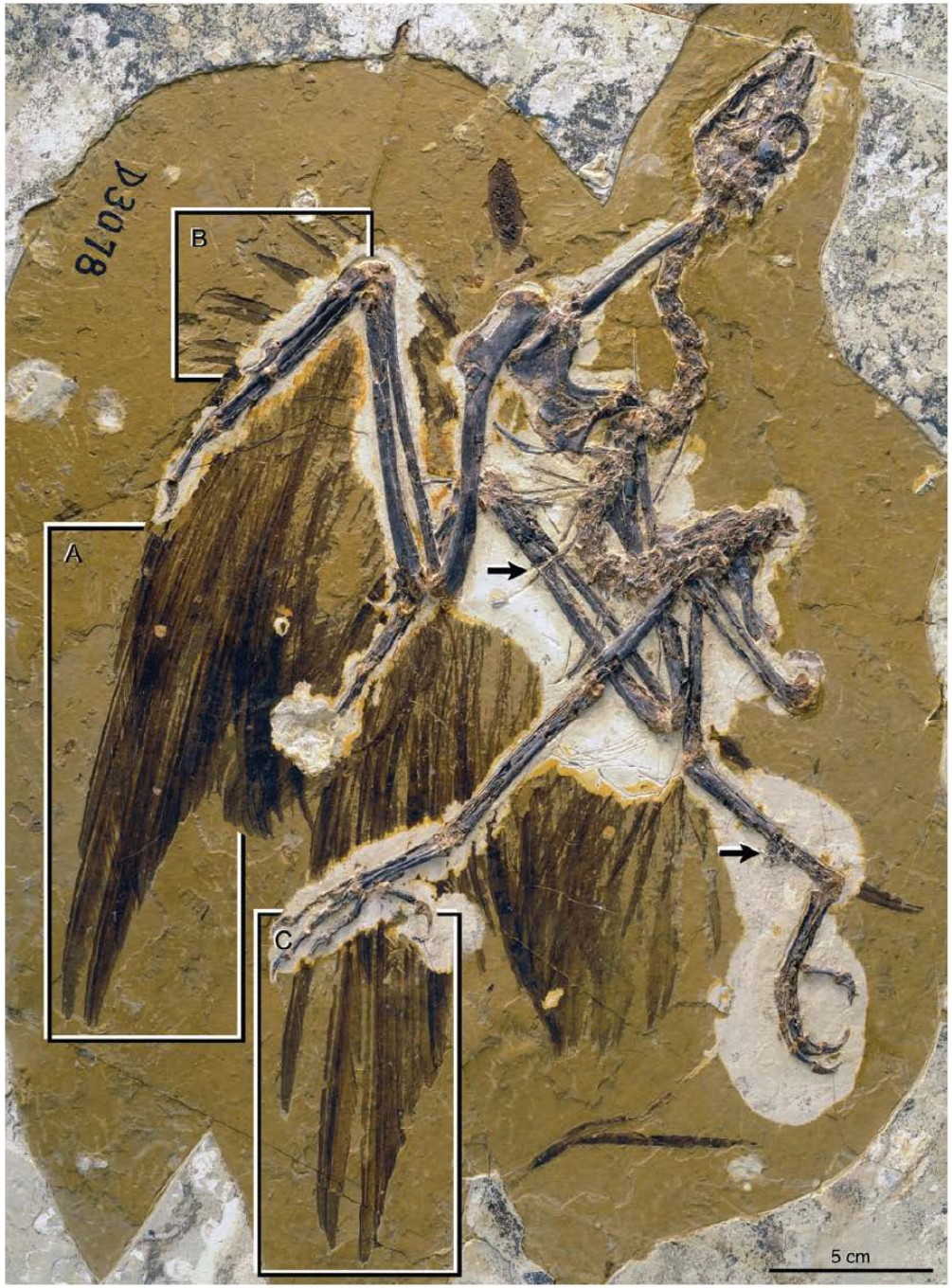


FIGURE 2. Photograph of DNHM-D3078. Boxes **A–C** refer to details of the plumage shown in Figure 8. Arrows denote locations of histological samples. Scale bar equals 5 cm.

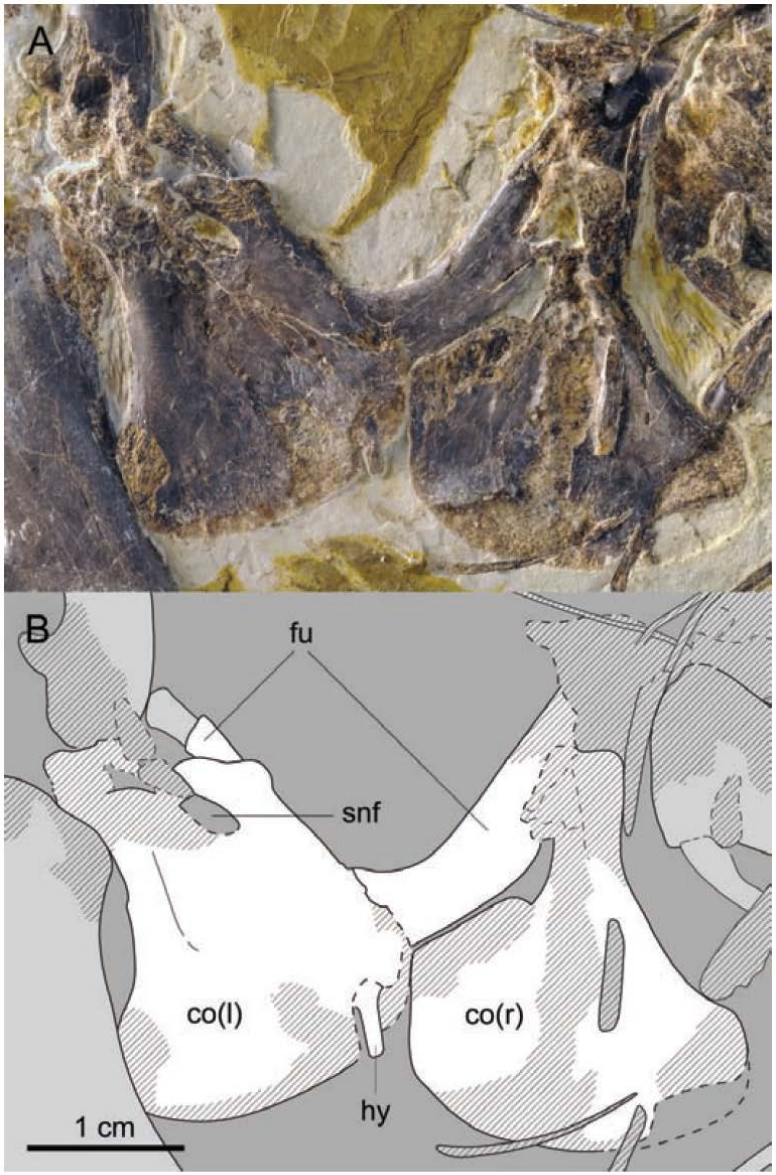


FIGURE 4. Furcula and right and left coracoids (highlighted in white) of DNHM-D3078 in dorsal view. **A**, photograph; **B**, interpretive drawing. Poorly preserved areas are indicated in hatched pattern. **Abbreviations**: **co**, coracoid; **fu**, furcula; **hy**, hypocleidium; **(l)**, left; **(r)**, right; **snf**, supracoracoid nerve foramen. Scale bar equals 1 cm. (Color figure available online).

Sapeornis

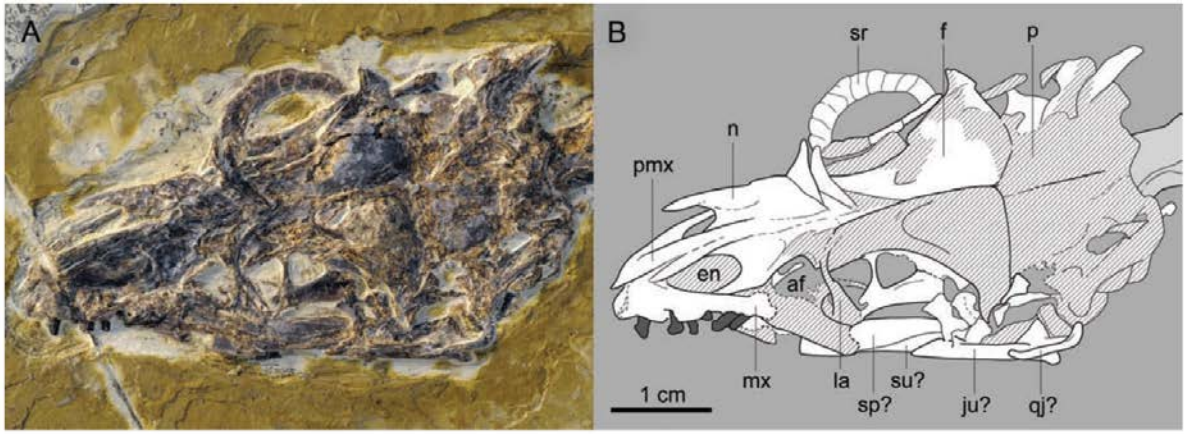


FIGURE 3. The skull (highlighted in white) of DNHM-D3078 in left laterodorsal view. **A**, photograph; **B**, interpretive drawing. Poorly preserved areas are indicated in hatched pattern. **Abbreviations**: **af**, antorbital fossa; **en**, external nares; **f**, frontal; **ju**, jugal; **la**, lacrimal; **mx**, maxilla; **n**, nasal; **p**, parietal; **pmx**, premaxilla; **qj**, quadratojugal; **sr**, sclerotic ring. Scale bar equals 1 cm. (Color figure available online).

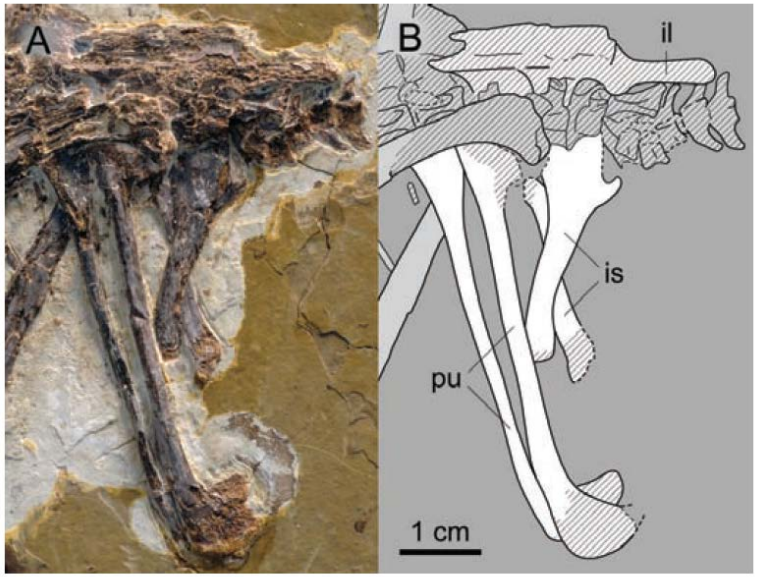


FIGURE 6. The pelvis (highlighted in white) of DNHM-D3078. **A**, photograph; **B**, interpretive drawing. Poorly preserved areas are indicated in hatched pattern. **Abbreviations**: **il**, ilium; **is**, ischium; **pu**, pubis. Scale bar equals 1 cm. (Color figure available online).

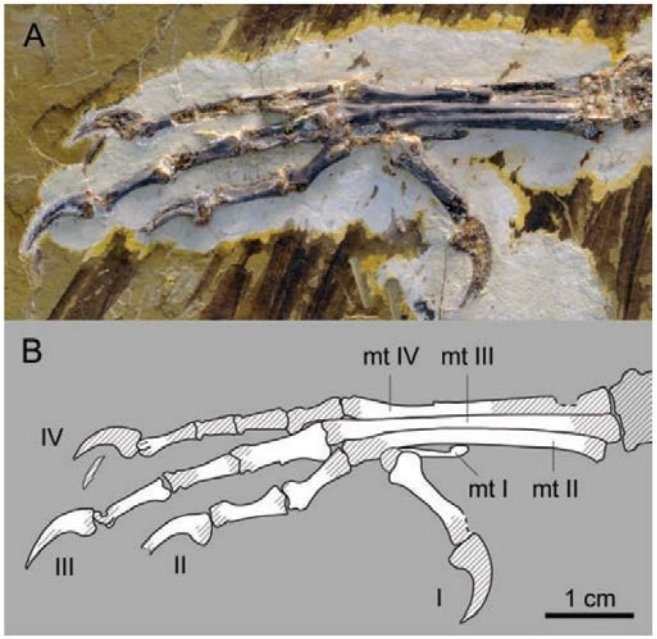


FIGURE 7. The left pes (highlighted in white) of DNHM-D3078. **A**, photograph; **B**, interpretive drawing. Poorly preserved areas are indicated in hatched pattern. **Abbreviations**: **mt I–IV**, metatarsals I–IV; **I–IV**, pedal digits I–IV. Scale bar equals 1 cm. (Color figure available online).

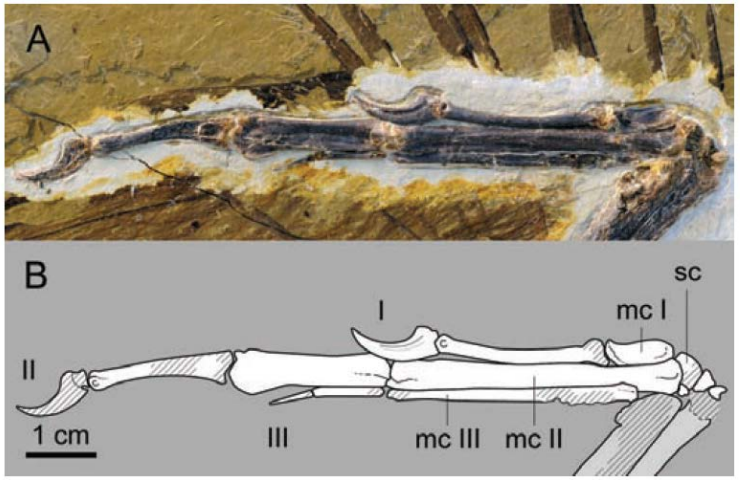
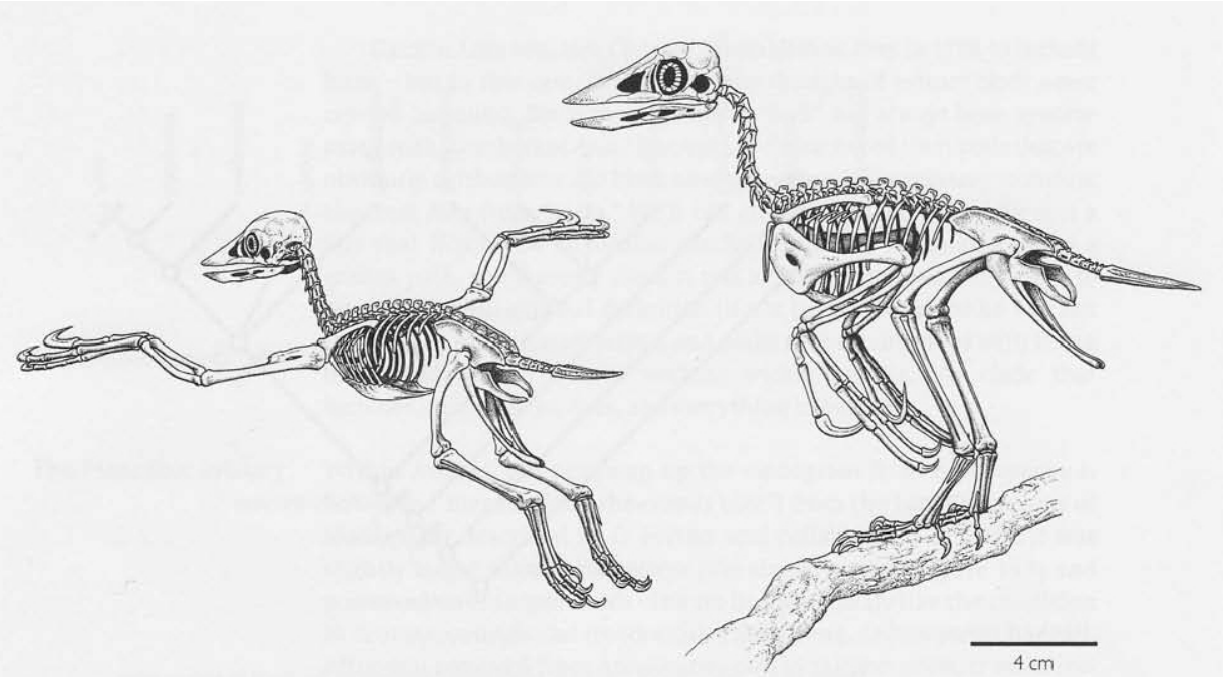
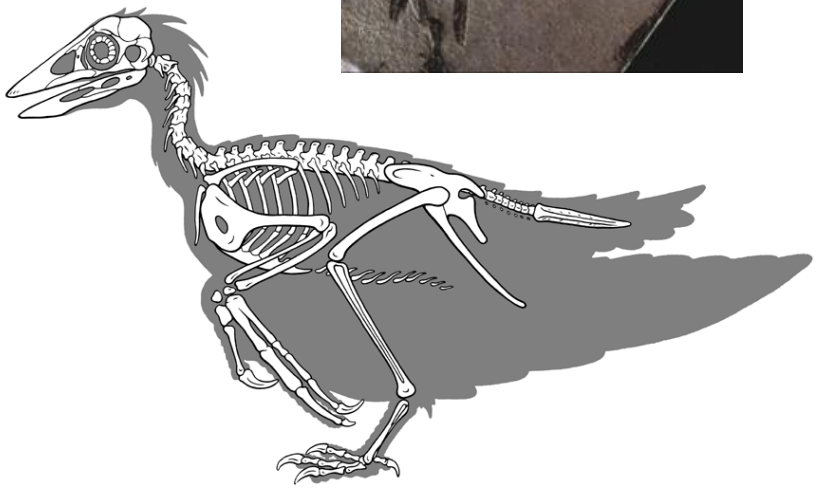


FIGURE 5. The left manus (highlighted in white) of DNHM-D3078 in dorsal view. **A**, photograph; **B**, interpretive drawing. Poorly preserved areas are indicated in hatched pattern. **Abbreviations**: **mc I–III**, metacarpals I–III; **sc**, semilunate carpal; **I–III**, manual digits I–III. Scale bar equals 1 cm. (Color figure available online).

Confuciusornithidae



Clado que contiene al ancestro común más reciente de *Confuciusornis sanctus y Changchengornis hengdaoziensis más todos sus descendientes*. (Chiappe et al, 1999)



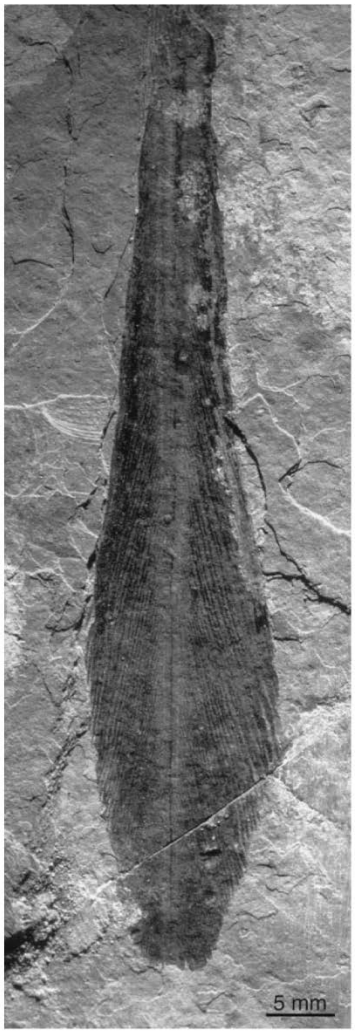


Fig. 49. Detail of distal end of the left elongate tail feathers of *Confuciusornis sanctus* (GMV-2150). Note the symmetrical rachis and barbed vanes.

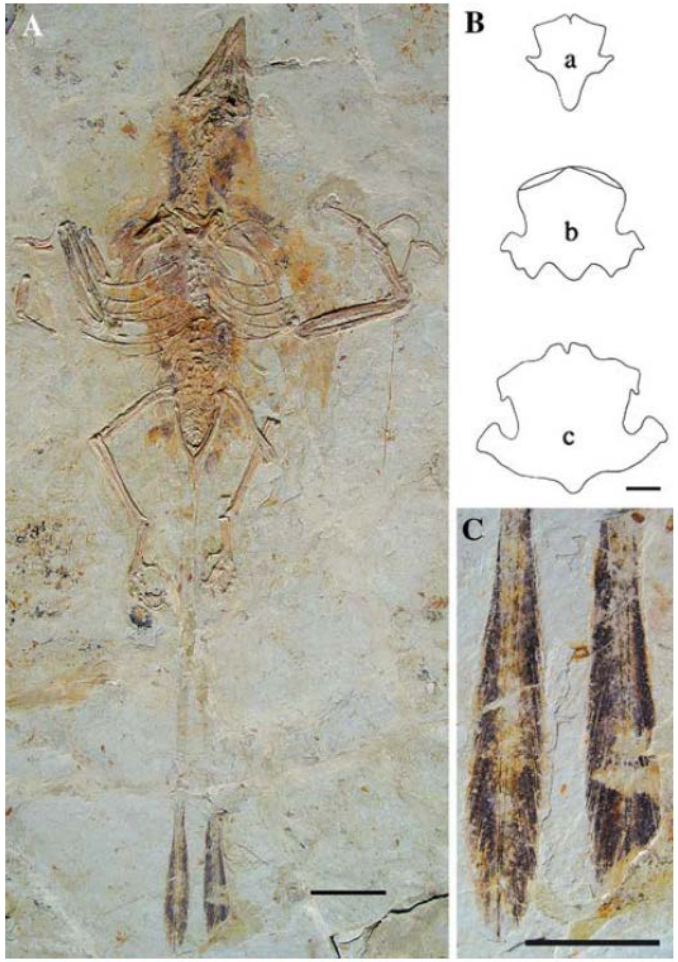


Fig. 1 **a** Holotype of *Confuciusornis feducciai* sp. nov., *scale bar* 5 cm; **b** comparison of sterna in *C. dui* (*a*) (Hou et al. 1999), *C. sanctus* (*b*) (Martin et al. 1998) and *C. feducciai* (*c*), *scale bar* 1 cm; **c** distal tail feathers of *C. feducciai*, *scale bar* 3 cm

Confuciusornis sanctus

Fig. 3.9 The most common pygostylian from the Early Cretaceous Yixian Formation, *Confuciusornis sanctus* IVPP 11372. (Photograph by Luis Chiappe.)

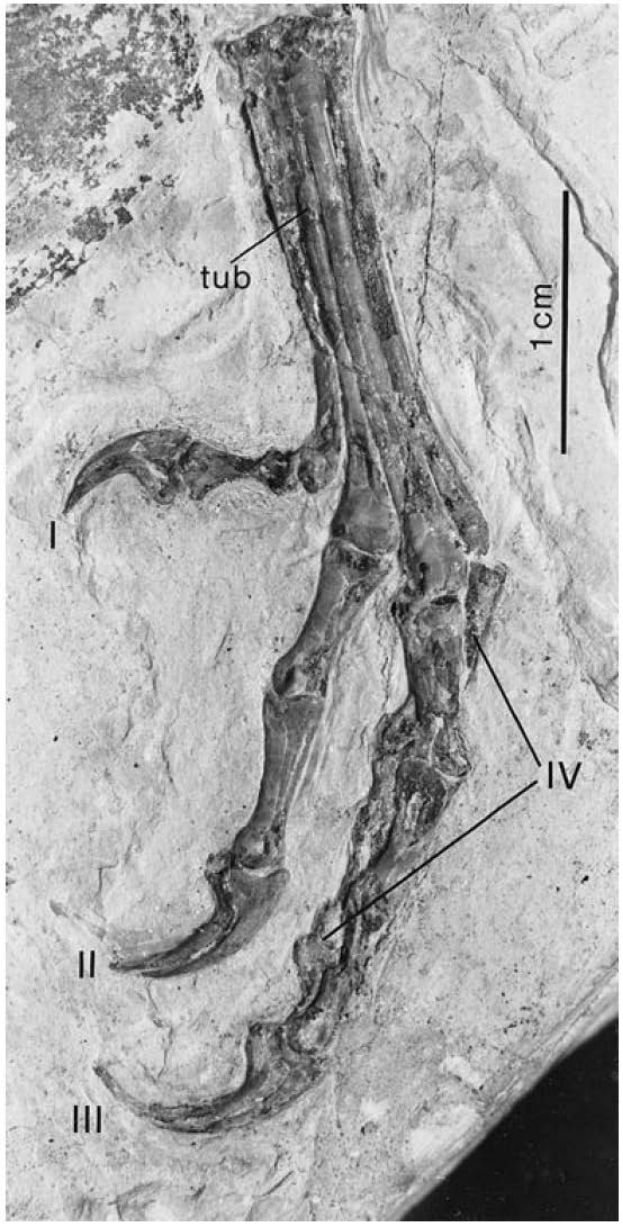


Fig. 44. Detail of left tarsometatarsus and foot of *Confuciusornis sanctus* (GMV-2130), dorsal view. See Anatomical Abbreviations for definition of labels.

Fig. 24. Detail of the synsacrum, free caudal vertebrae, pygostyle, and pelvis of *Confuciusornis sanctus* (GMV-2131), ventral view.

Fig. 33. Detail of gastralia and caudal end of the sternum of *Confuciusornis sanctus* (GMV-2152). See Anatomical Abbreviations for definition of label.

Confuciusornis sanctus

Ornithothoraces

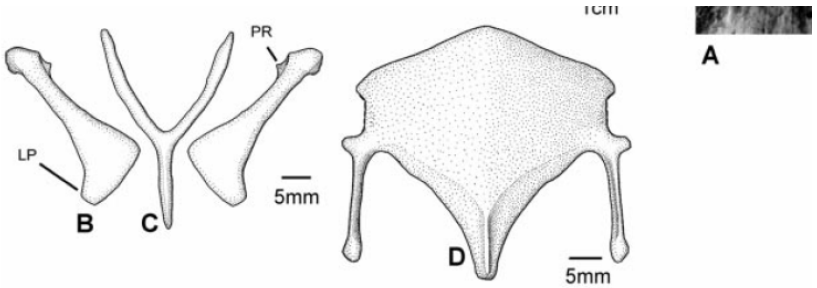
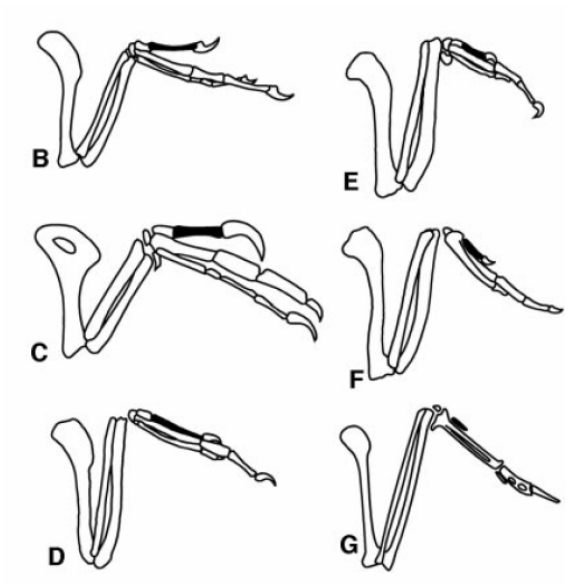


Fig. 3 (left). *Protopteryx fengningensis*, holotype V 11844. (**A**) The pectoral girdle and the sternum and the reconstruction of the coracoid (**B**), furcula (**C**), and sternum (**D**). Abbreviations: CA, carina; CO, coracoid; FU, furcula; LP, lateral process; and PR, procoracoid. **Fig. 4 (right).** The forelimb of *P. fengningensis*, holotype V 11665 (**A**) and comparisons of the forelimbs in *Archaeopteryx* (**B**) [after (*21*)], *Confuciusornis* (**C**), *Protopteryx* (**D**), *Eoenantiornis* (**E**) [after (*24*)], *Cathayornis* (**F**) [after (*3*)], and *Larus* (**G**) [after (*38*)]. Note the reduction of the first phalanx of the alular digit in the early evolution of the forelimbs. Abbreviations: AD, alular digit; AL, alula; HU, humerus; RA, radius; and UL, ulna.



Sinapomorfías:

- Presencia de álula
- Canal trióseo
- Esternón amplio
- Coracoides elongado

Enantiornithes: las aves opuestas

Figure 8.8. Silhouette reconstruction of *S. santensis* showing the preserved bones, based on BPV 538 and IVPP V9769.

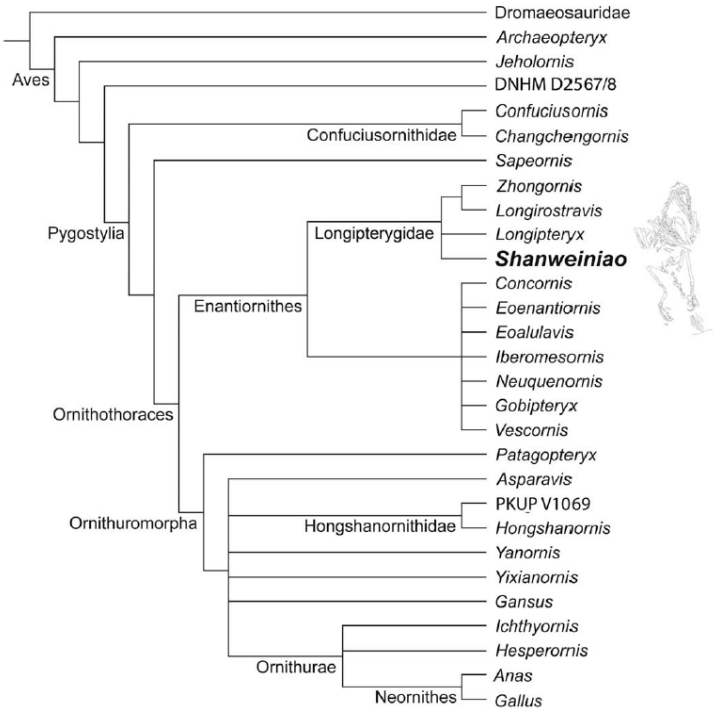
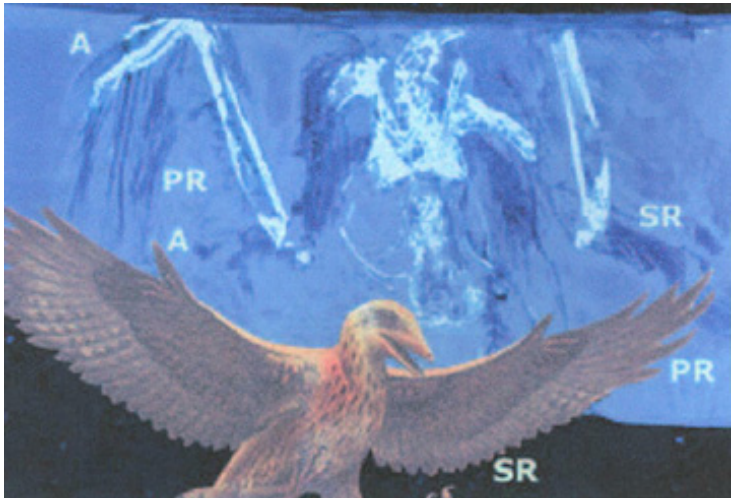


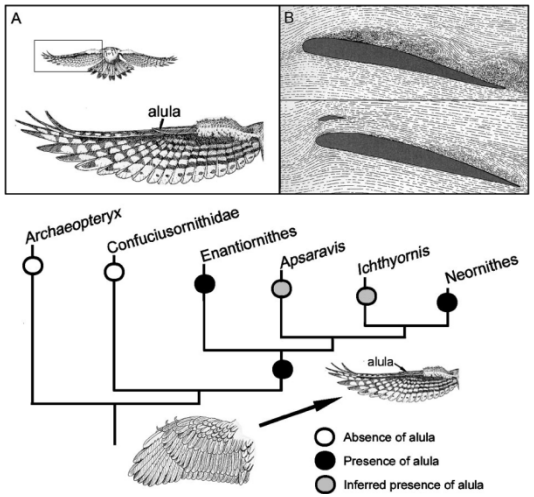
FIGURE 8. Strict consensus cladogram illustrating the phylogenetic position of *Shanweiniao cooperorum*. Tree length: 588 steps; consistency index = 48, retention index = 68.

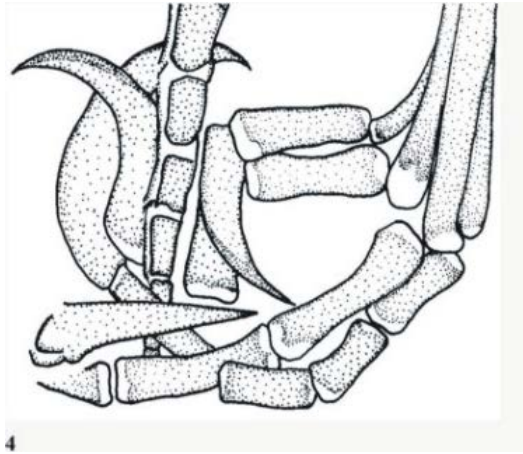
Sinapomorfías:

- Fúrcula en forma de Y
- Metacarpo III mayor que metacarpo II

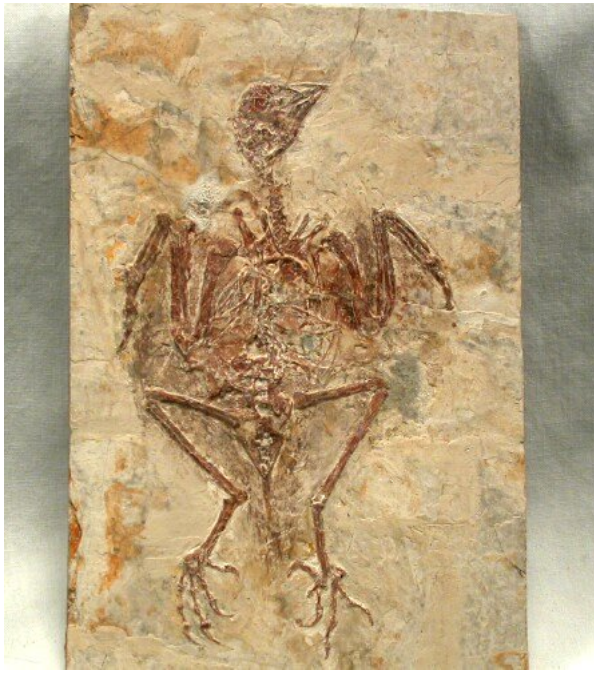


Eoalulavis





Dalingheornis



Protopteryx

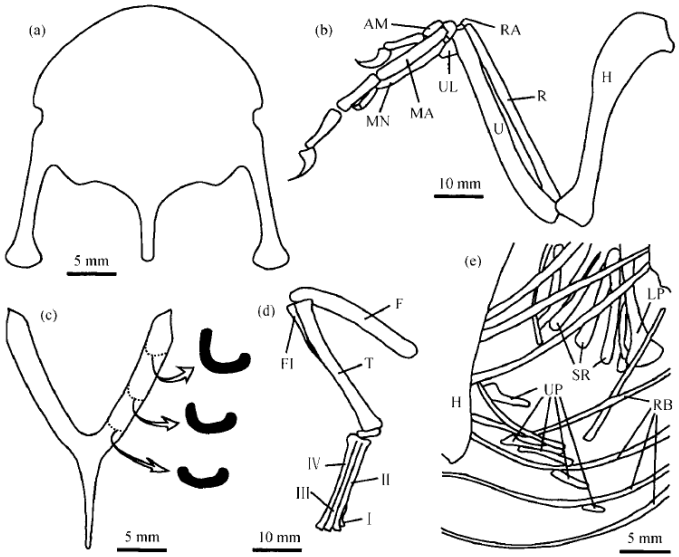


Fig. 2. *Longipteryx chaoyangensis* reconstructions. (a) Sternum; (b) wing, note that the second phalanx of the minor digit is small and triangle-shaped; (c) furcula; (d) femur, tibiotarsus, and tarsometatarsus, note that metatarsal Ⅳ is longer than Ⅱ and Ⅲ; (e) uncinate process and rib. AM, Alular metacarpal; F, femur; FI, fibula; H, humerus; Ⅰ-Ⅳ, metatarsals Ⅰ-Ⅳ; LP, lateral process of sternum; MA, major metacarpal; MN, minor metacarpal; R, radius; RA, radiale; RB, vertebral rib; SR, sternal rib; T, tibiotarsus; U, ulna; UL ulnare; UP, uncinate process

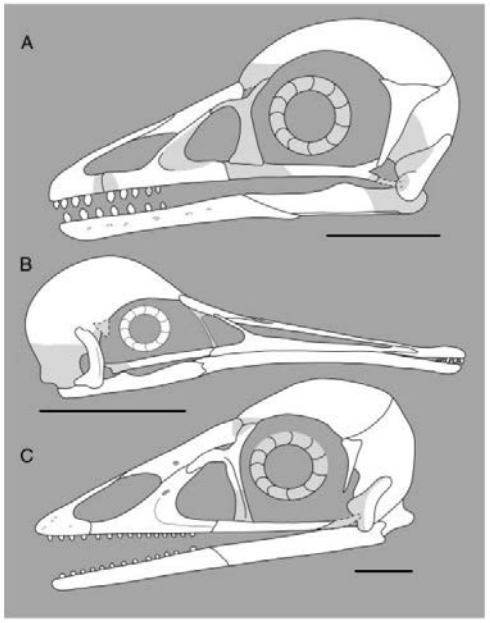


Figure 8. Reconstructions of the skulls of enantiornithines: **A,** *Shenqiornis mengi*; **B,** *Rapaxavis pani*; **C,** *Pengornis houi*. All scale bars = 1 cm.

Longipteryx

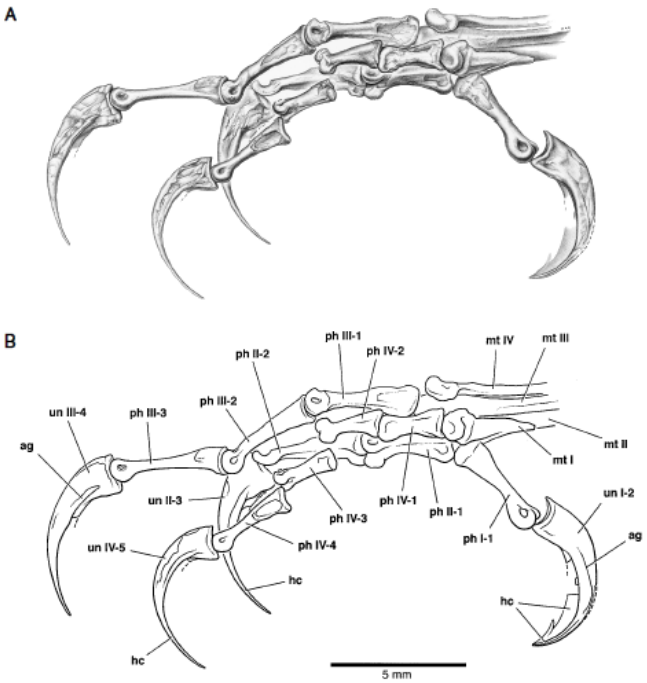


Figure 8.5. Left distal metatarsals (most in dorsal view) and pedal phalanges (most in medial view) of *S. santensis* (BPV 538a, epoxy cast) (A, B). Broken lines indicate the margins of bone or horny claw that are visible as impressions. Abbreviations: I–IV, metatarsals or digits I–IV; 1–5, phalangeal number; ag, attachment groove; hc, horny claw; mt, metatarsal; ph, phalanx; un, ungual.

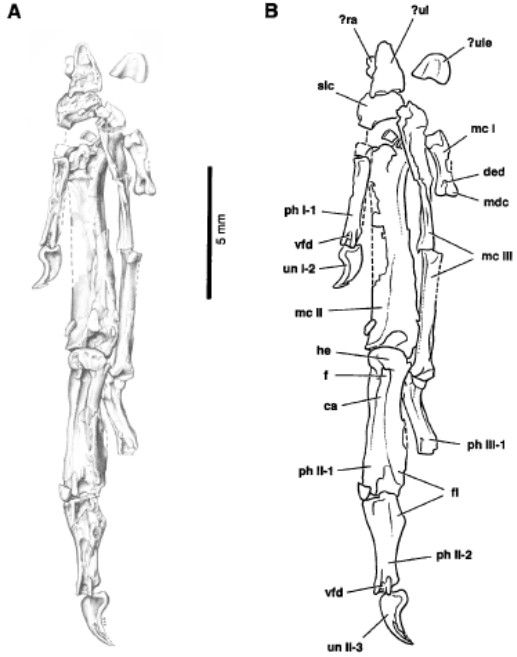


Figure 8.3. Right carpus and manus of *S. santensis* (BPV 538a, epoxy cast), mostly in ventral view (A, B). Metacarpal I is in dorsal view, digit I ungual is in medial view, and digit II ungual is in lateral view. Broken lines indicate bone margins visible as impressions. Abbreviations: I–III, metacarpals or digits I–III; 1–3, phalangeal number; ca, canal; ded, dorsal extensor depression; f, foramen; fl, flange; he, heel; mc, metacarpal; mdc, medial distal condyle; ph, phalanx; ra, radius; slc, semilunate carpal; ul, ulna; ule, ulnare; un, ungual; vfd, ventral flexor depression.

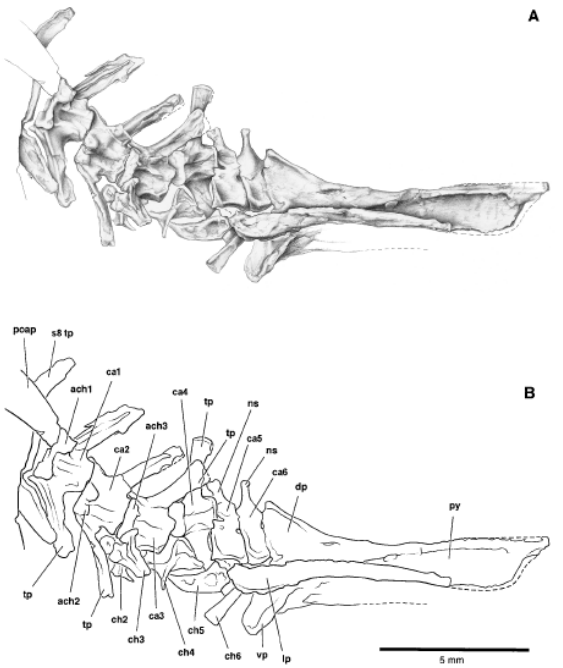


Figure 8.2. Caudal vertebrae and pygostyle of *S. santensis* (BPV 538a, epoxy cast) in left lateral view (A, B). Broken lines indicate bone margins visible as impressions. Abbreviations: ach1–3, articular surface for chevrons 1–3; ca1–6, caudal vertebrae 1–6; ch2–6, chevrons 2–6; dp, dorsal process; lp, lateral process; ns, neural spine; poap, postacetabular process; py, pygostyle; s8, eighth sacral vertebra; tp, transverse process; vp, ventral process.

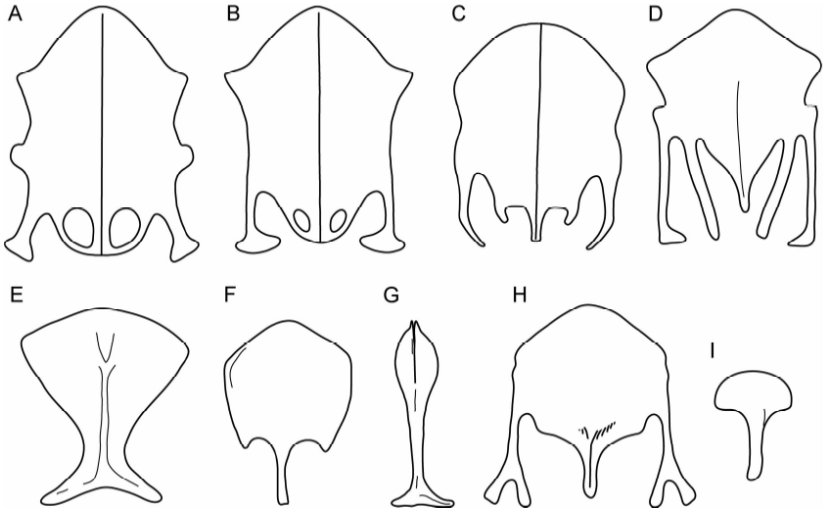


Fig. 4 Reconstructions of Early Cretaceous bird sterna

A. ornithurine *Yixianornis*; B. ornithurine *Yanornis*; C. ornithurine *Hongshanornis*; D. ornithuromorph FRDC-05-CM-021; E. *Liaoningornis*; F. enantiornithine *Eoenantiornis*; G. Spanish enantiornithine *Eoalulavis*; H. enantiornithine *Rapaxavis pani*; I. juvenile enantiornithine GMV 2159. Sterna not figured to scale

Figure 8.8. Silhouette reconstruction of *S. santensis* showing the preserved bones, based on BPV 538 and IVPP V9769.

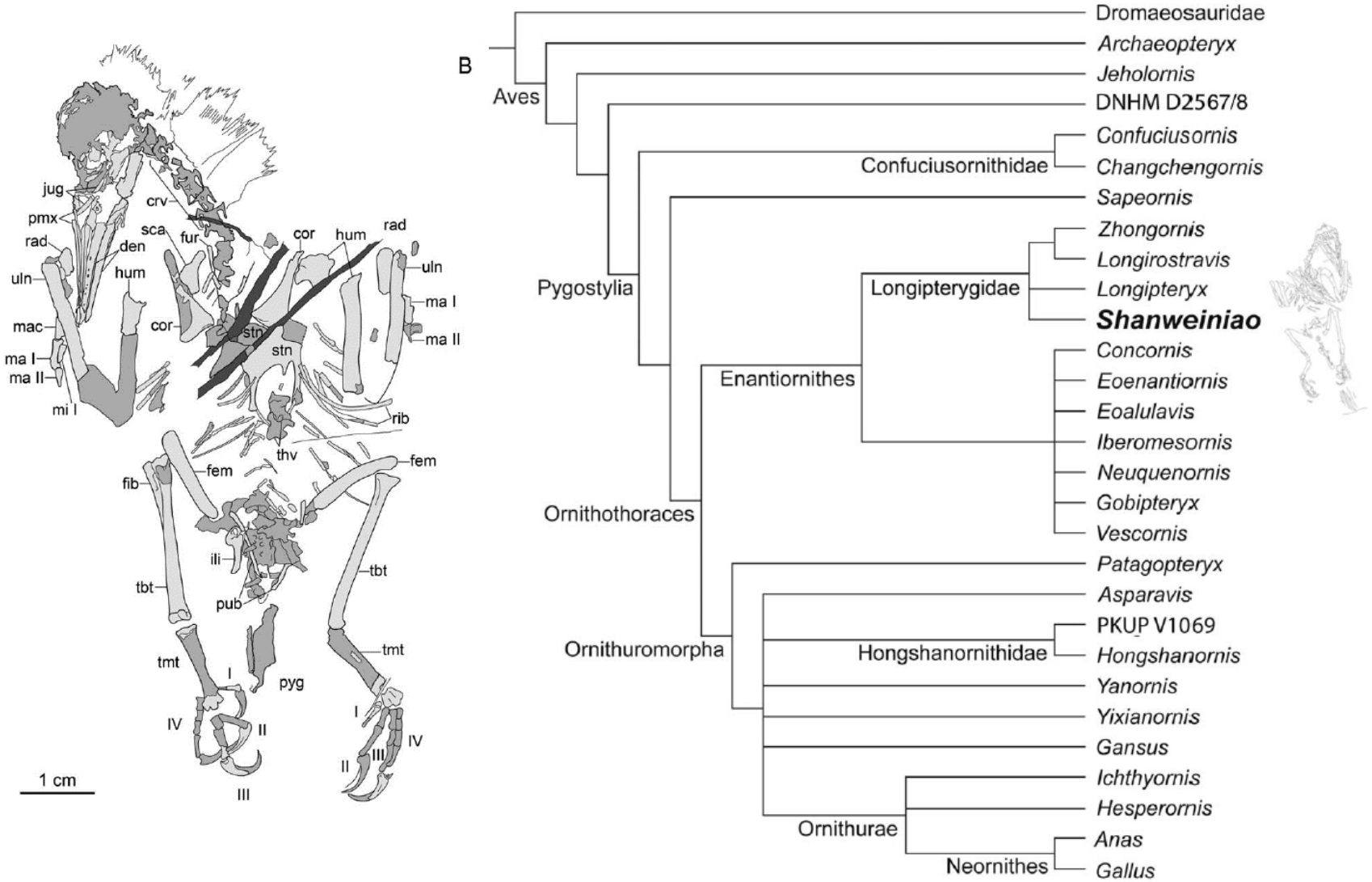
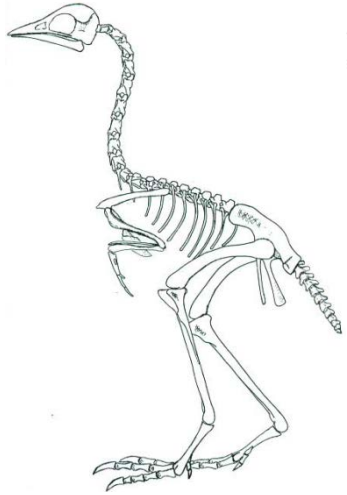
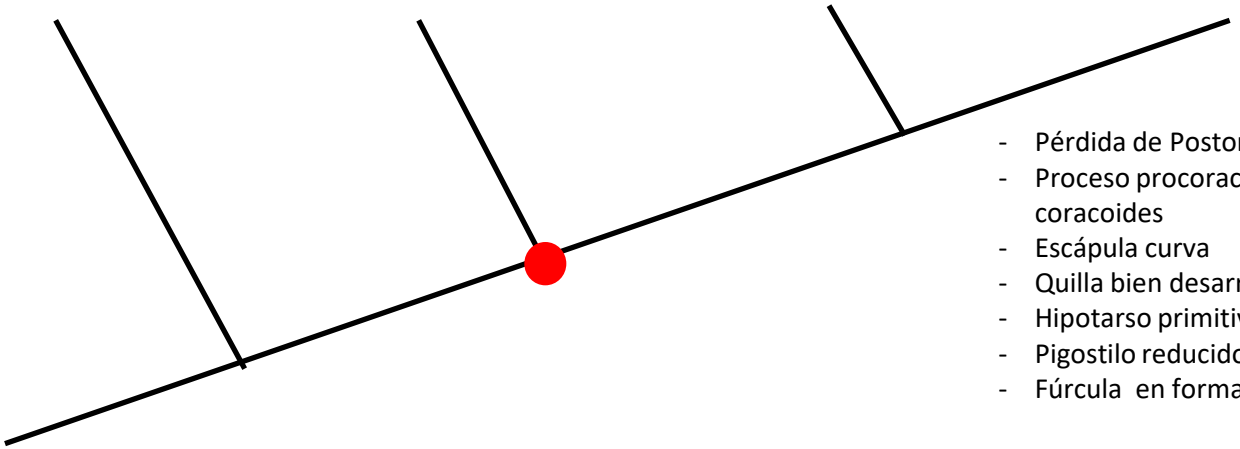


FIGURE 8. Strict consensus cladogram illustrating the phylogenetic position of *Shanweiniao cooperorum*. Tree length: 588 steps; consistency index = 48, retention index = 68.

Ornithuromorpha

- clado menos inclusivo que contiene a la Perdiz chilena (*Nothoprocta perdicaria*) y la paloma (*Columba livia*)





- Pérdida de Postorbital
- Proceso procoracoides y esternal en coracoides
- Escápula curva
- Quilla bien desarrollada
- Hipotarso primitivo
- Pigostilo reducido
- Fúrcula en forma de U

Patagopteryx deferrarisi

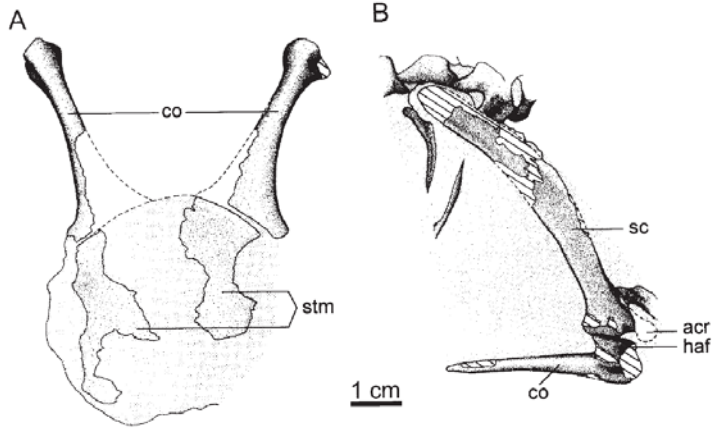


Figure 13.14. Thoracic girdle and sternum of *P. deferrariisi* (MACN-N-11). A, coracoids and sternum in ventral view; B, right scapula and coracoid in lateral view. Stipple pattern indicates matrix, and cross-hatch pattern indicates broken or poorly preserved bone. Abbreviations: acr, acromion; co, coracoid; haf, humeral articular facet; sc, scapula; stm, sternum.

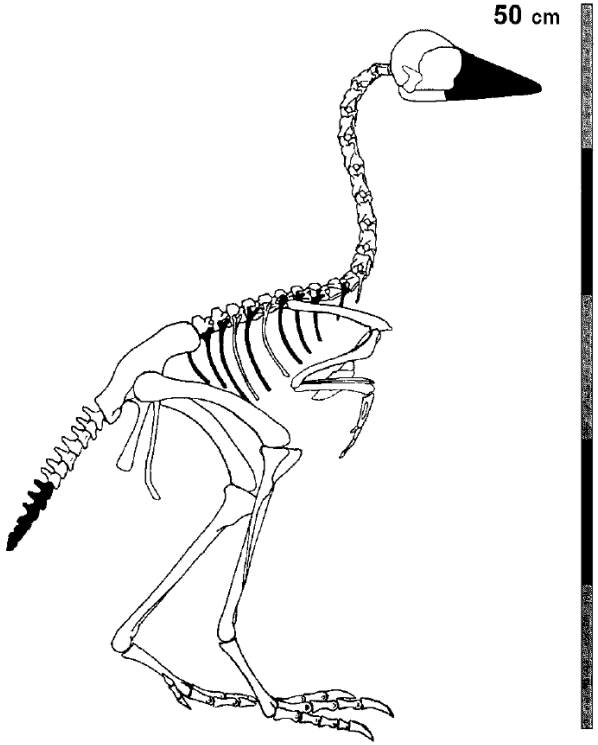
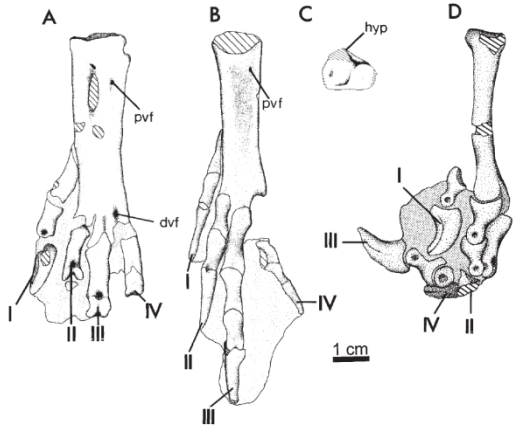


Figure 13.1. Skeletal reconstruction of *P. deferrariisi* (modified from Alvarenga and Bonaparte, 1992). Black areas are not preserved in any available specimen.



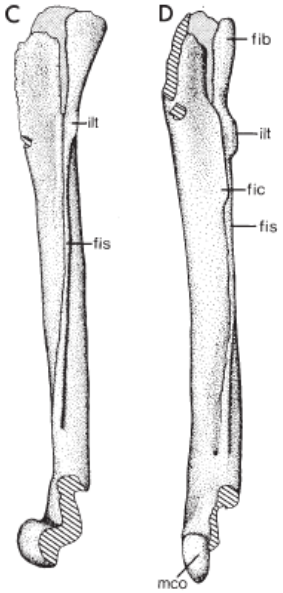


Figure 13.26. Tarsometatarsus and pes of *P. deferrariisi*. A, left tarsometatarsus and pes of MACN-N-03 in dorsal view; B, right tarsometatarsus and pes of MACN-N-11 in plantar view; C, proximal end of left tarsometatarsus of MACN-N-10 in proximal view; D, left tarsometatarsus and pes of MUCPv-48 in medial view. Abbreviations: dvf, distal vascular foramen; hyp, hypotarsus; pvf, proximal vascular foramen; I–IV, pedal digits I to IV.

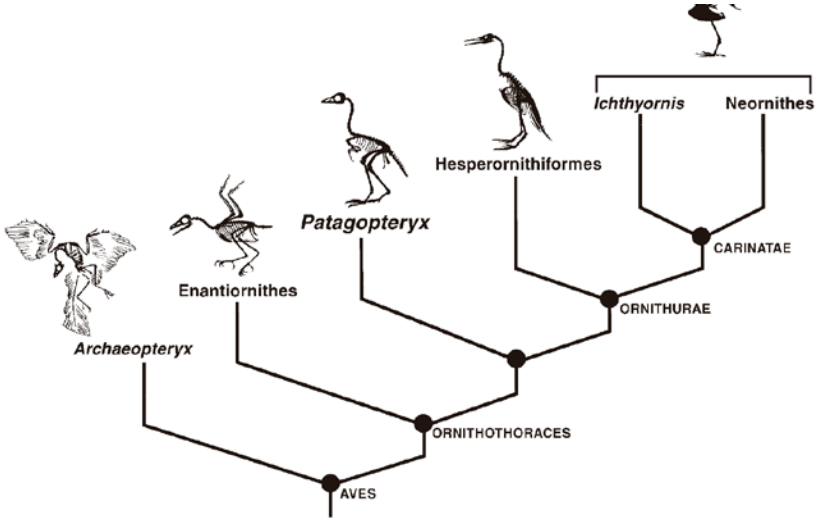


Figure 13.27. Cladogram depicting the relationship of *P. deferrariisi* to other basal birds (modified from Chiappe, 1996b).

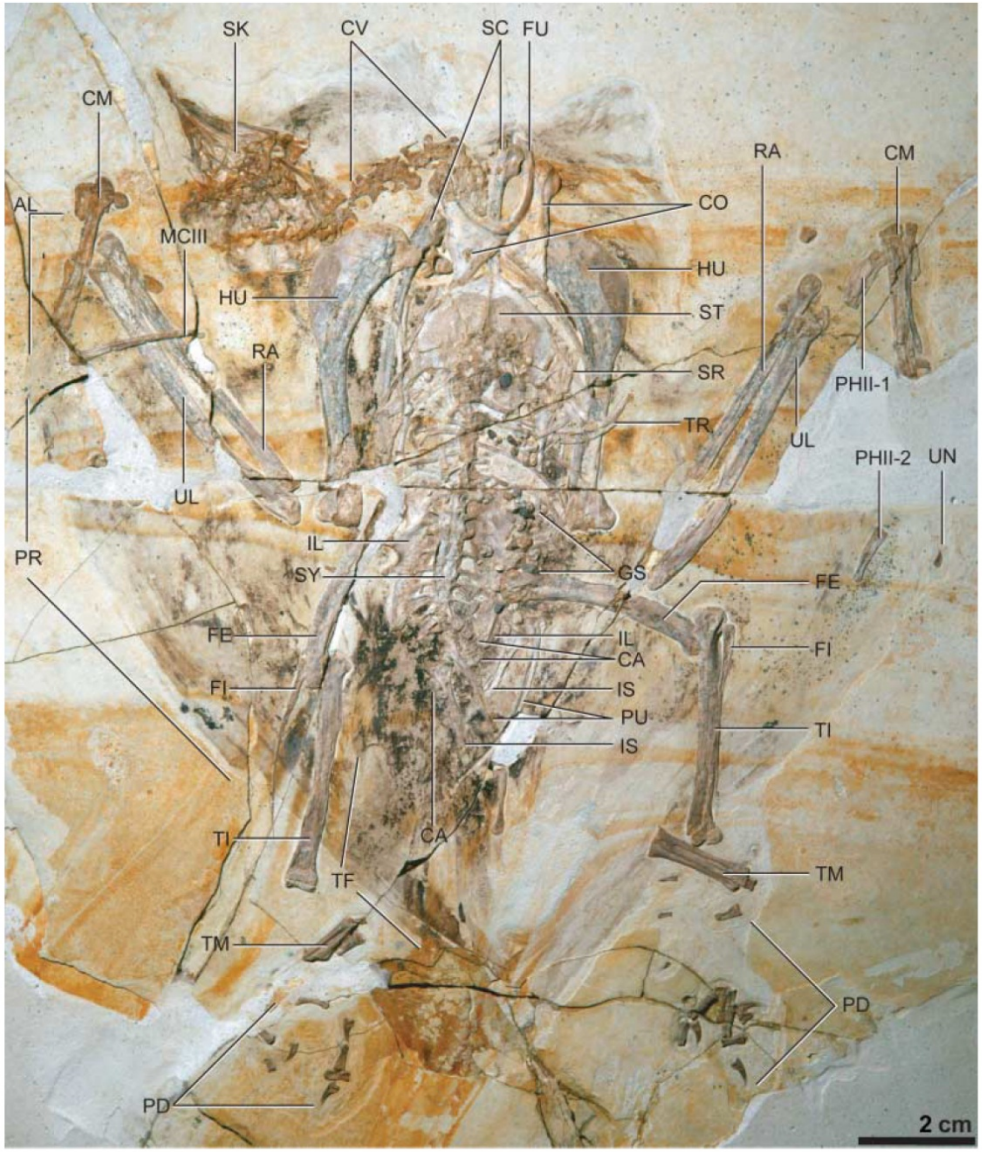


Fig. 1 A nearly complete skeleton of the holotype of *Archaeorhynchus spathula* gen. et sp. nov. (IVPP V14287). Abbreviations: AL, alula; CA, caudal vertebra; CM, carpometacarpus; CO, coracoid; CR, crest; CV, cervical vertebra; FE, femur; FI, fibula; FU, furcula; GA, gastralia; GS; gizzard stones; HU, humerus; IL, ilium; IS, ischium; MCIII, minor metacarpal; PD, pedal digits; PHII-1, first phalanx of major manual digit; PHII-2, second phalanx of major manual digit; PM, primaries; PU, pubis; RA, radius; SC, scapula; SK, skull; SR, sternal rib; ST, sternum; SY, synsacrum; TF, tail feathers; TI, tibia; TM, tarsometatarsus; TR, thoracic rib; UL, ulna; UN, ungual.

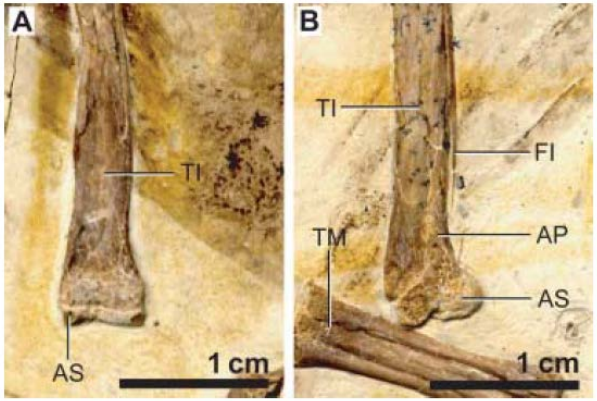
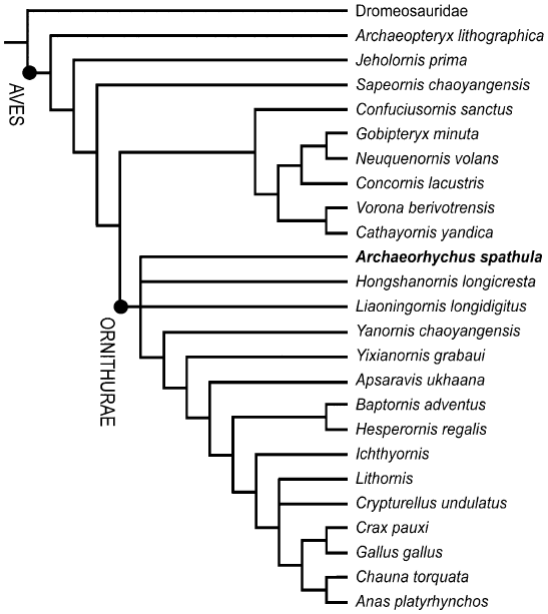


Fig. 4 A, B. Distal end of the tibiotarsus of *Archaeorhynchus spathula* gen. et sp. nov. (IVPP V14287). —A. right side in caudal view, showing the astragalus. —B. left side in cranial view, showing the broad ascending process of the astragalus. Abbreviations: AP, ascending process of the astragalus; AS, astragalus. See Fig. 1 for other abbreviations.



Archaeorhynchus spathula

Figure 12.3. Left femur of referred specimen FMNH PA 717 in (left to right) cranial, lateral, caudal, and medial views. Abbreviations: fcl, fossa for capital ligament; il, intermuscular line; t, tubercle on lateral supracondylar ridge.

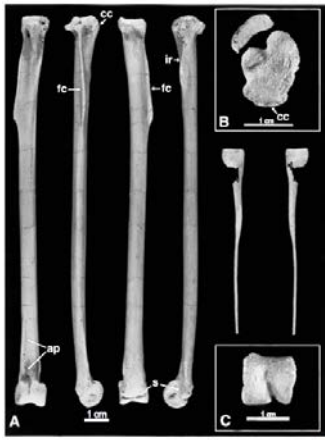


Figure 12.8. Referred specimen FMNH PA 717: A, right tibiotarsus in (left to right, on left) cranial, lateral, caudal and medial views and partial right fibula in (left to right, on right) lateral and medial views. B, articulated fibula and tibiotarsus in proximal view, cranial end facing down; C, tibiotarsus in distal view, caudal end facing up. Abbreviations: ap, ascending process of the astragalus; cc, cnemial crest; fc, fibular crest; ir, irregular ridge; s, suture between tibia and proximal tarsals.

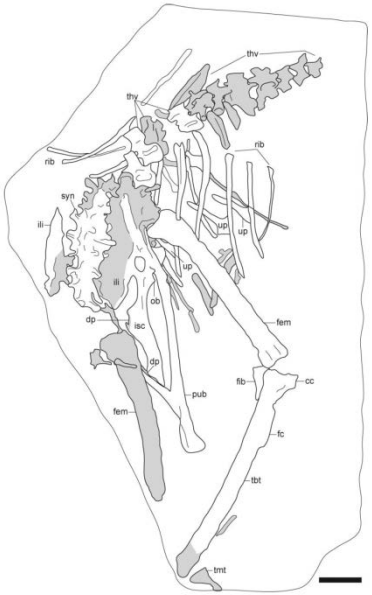


Figure 3. Camera lucida drawing of the main slab of the holotype specimen of *Chaoyangia beishanensis* (IVPP V9934). White indicates well-preserved bone and light grey represents poorly preserved bone. Anatomical abbreviations: cc, cnemial crest; dp, dorsal process; fc, fibular crest; fem, femur; fib, fibula; ili, ilium; isc, ischium; ob, obturator process; pub, pubis; rib, ribs; syn, synsacrum; tbt, tibiotarsus; thv, thoracic vertebrae; tmt, tarsometatarsus; up, uncinate process. Scale bar = 1 cm.

Chaoyangia beishanensis

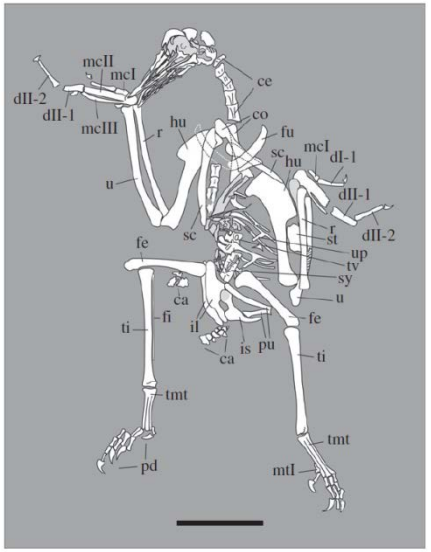


Figure 2. Line drawing of the holotype of *Zhongjianornis yangi* gen. et sp. nov. (IVPP V15900). Abbreviations: ca, caudal vertebra; ce, cervical vertebra; co, coracoid; dI-1, first phalanx of alular digit; dII-1, first phalanx of major digit; dII-2, second phalanx of major digit; fe, femur; fi, fibula; fu, furcula; hu, humerus; il, ilium; is, ischium; mcI, alular metacarpal, mcII, major metacarpal; mcIII, minor metacarpal; mtI, metatarsal I; pd, pedal digits; pu, pubis; r, radius; sc, scapula; st, sternum; sy, synsacrum; ti, tibia; tmt, tarsometatarsus; tv, thoracic vertebra; u, ulna; up, uncinate process of rib. Scale bar, 5 cm.

Zhongjianornis yangi

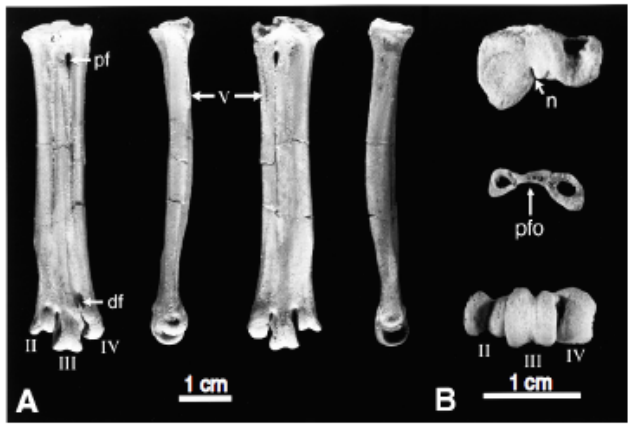
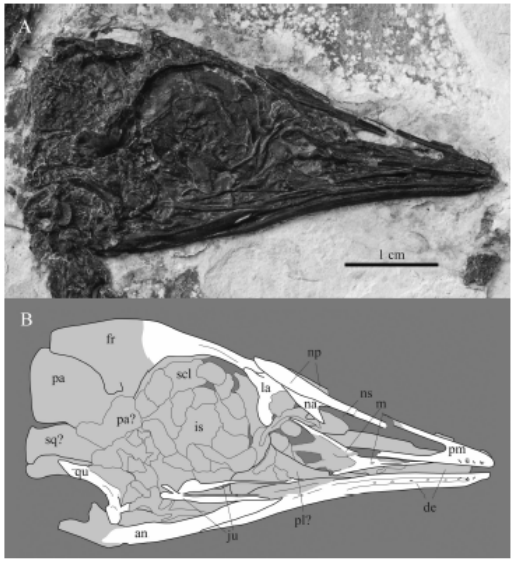
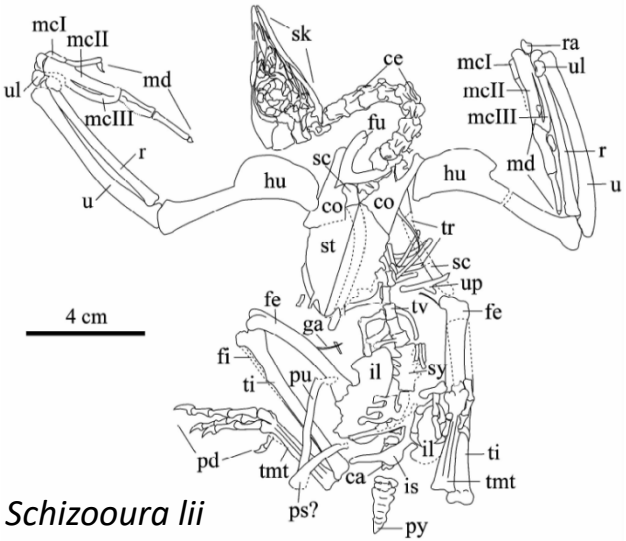


Figure 12.6. Left tarsometatarsus of holotype UA 8651: A, dorsal, lateral, plantar, and medial views (left to right); B, proximal view, plantar margin up (top); cross section at midshaft, dorsal margin up (middle); distal view, dorsal margin up. Abbreviations: df, distal foramen; n, notch between MTs III and IV; pf, proximolateral foramen; pfo, palmar fossa; Roman numerals refer to metatarsal number.

Vorona berivotrensis





Schizooura lii

Songlingornithidae

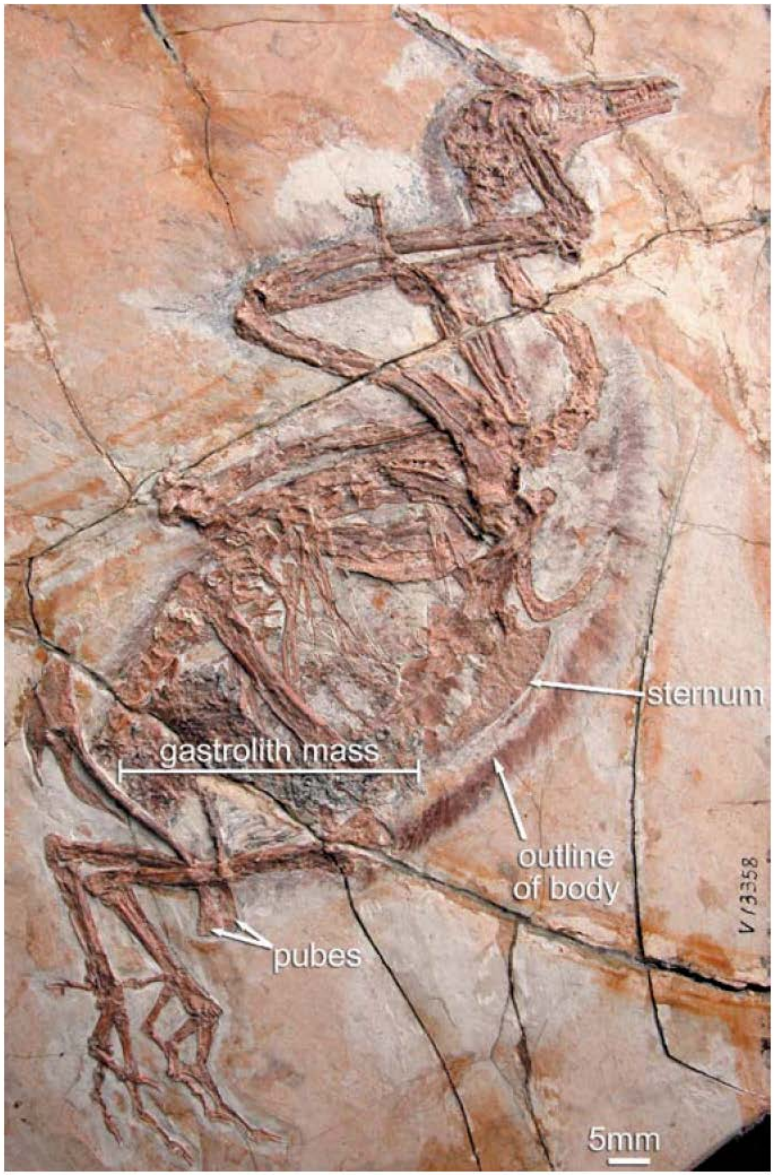


Fig. 2 A new specimen (IVPP V13358) of the fish-eating bird *Yanornis martini*, showing the grit mass in the abdominal region

Yanornis martini

Fig. 3.15 Holotype of the ornithuromorph *Yixianornis grabaui* IVPP V12631, from the Jiufotang Formation. (Photograph by Luis Chiappe.)

Yixianornis grabaui

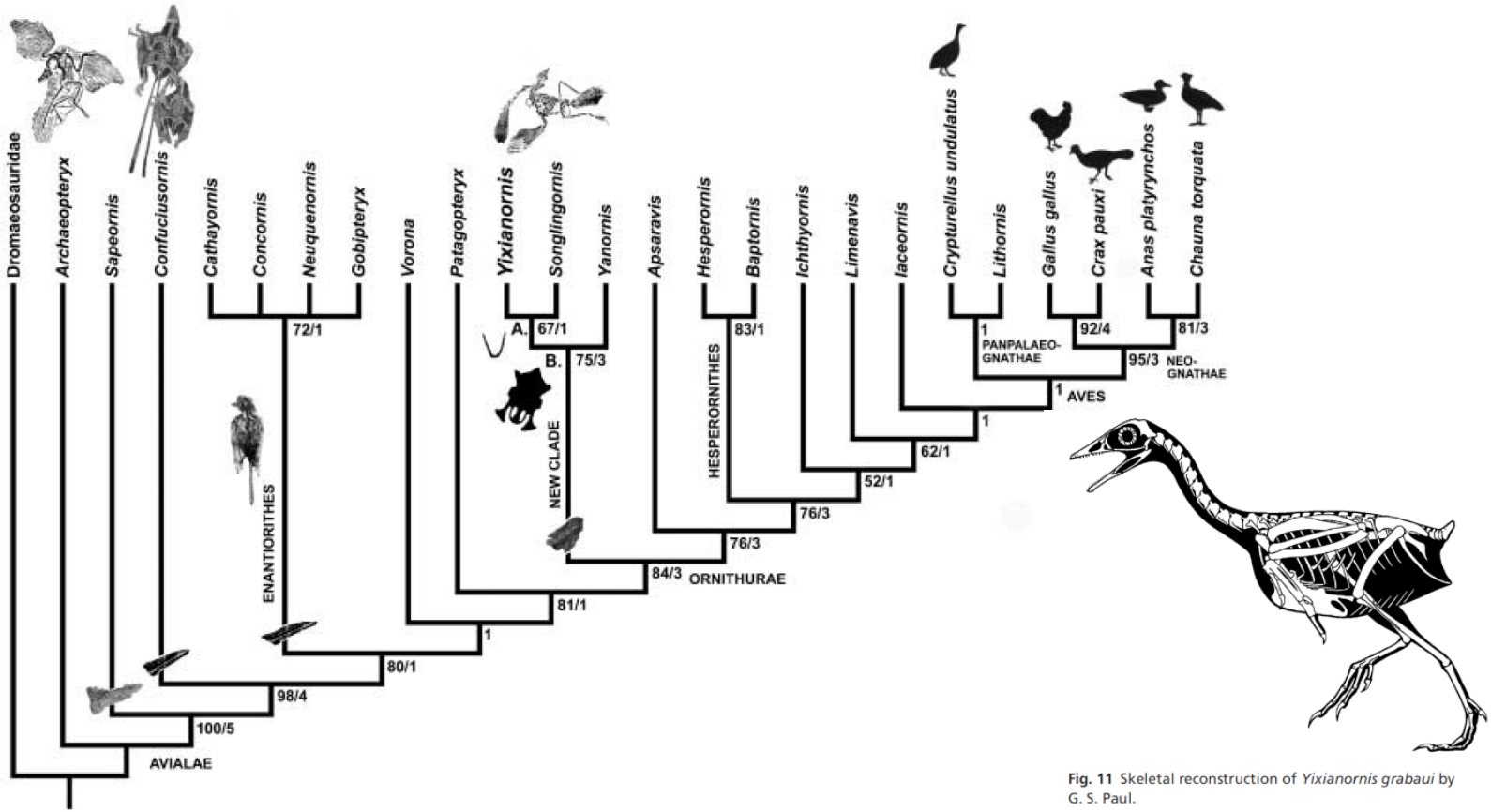


Fig. 11 Skeletal reconstruction of *Yixianornis grabaui* by G. S. Paul.

Fig. 10 Strict consensus cladogram of the two most parsimonious trees resulting from analysis of the characters and taxa in Appendices 2 and 3 [length: 422, CI: 0.63, RI 0.82, RC 0:51 (PIC only)]. Bootstrap support for those nodes recovered in greater than 50% of the 1000 replicates performed and Bremer (1988) support values are reported to the right of the node to which they apply (Format: Bootstrap/Bremer). Mesozoic avialans with tail feathering known are pictured, *Protopteryx* is shown for Enantiornithes as it is basally placed within that group. No Enantiornithes are known to possess more than two elongate rectrices, although some possess none at all (Zhang & Zhou, 2004). Pygostyle morphology is illustrated for *Sapeornis*, *Confuciusornis*, *Iberomesornis* and *Yixianornis* and shown in insets. One unambiguous synapomorphy supports the clade *Yixianornis* + *Songlingornis* (Node A). Monophyly of new clade of Chinese ornithurines (Node B) is supported by four unambiguously optimized synapomorphies (numbers refer to characters and states listed in Appendix 2): 53:0, cervical vertebrae not completely heterocoelous; 94:1, presence of a procoracoid process; 99:1, coracoid without groove at medial opening of n. supracoracoideus foramen; 79:2, medial posterior process of sternum joined to sternal midline to enclose sternal fenestra; 85:1, base of furcula with a truncate or squared base. Seven unambiguous synapomorphies support placement of the clade as more closely related to Aves than *Patagopteryx*: 55:2, ten or fewer thoracic vertebrae; 95:1, intermuscular line on ventral surface of the coracoid; 107:1, humeral head domed or globose; 143:1, metacarpal III narrow compared with diameter of metacarpal II; 152:1, phalanx II.1 strongly dorsoventrally compressed; 160:1, antitrochanter posterodorsally located with respect to acetabulum; 193:1, metatarsal III displaced posterior to II and IV proximally. *Apsaravis* is placed more closely to Aves than this new lineage by six unambiguous synapomorphies: 62:4, ten sacral vertebrae; 67:1, non contacting pre- and postzygopophyses in tail; 146:1, metacarpal I articulation developed as a shelf; 159:2, ischium and pubis subparallel and appressed; 169:1, pubis compressed mediolaterally; 188:2, posterior portion of distal articular surface of tibiotarsus for tibial cartilage with well-developed wings.

Hoshangornithidae

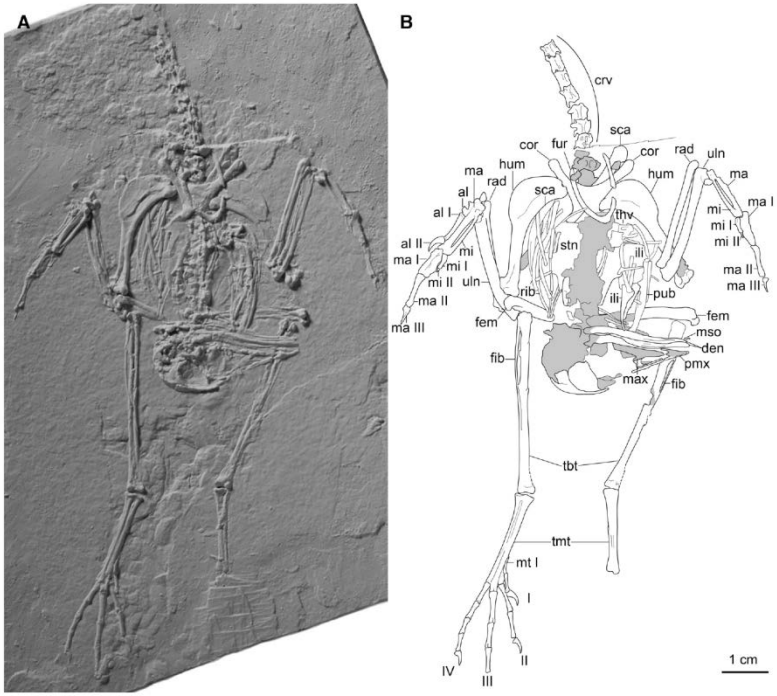
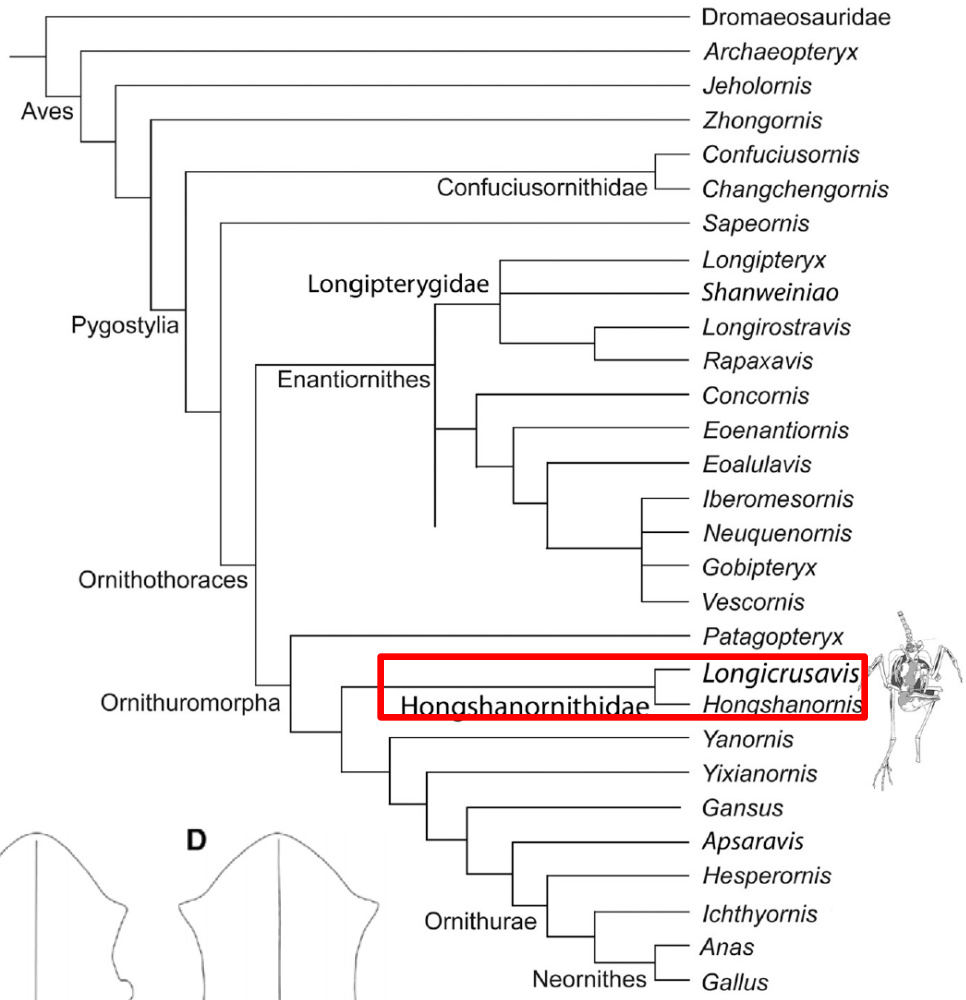


FIGURE 4. Cast of slab B of PKUP V1069, holotype of *Longicrusavis houi*, gen. et sp. nov. **A**, photograph and **B**, camera lucida drawing. The cast was dusted with magnesium to highlight the bones.



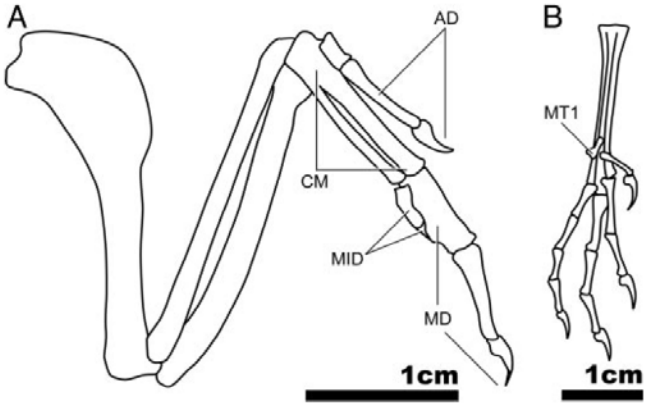


Fig. 5. Line drawing of the left wing (*A*) and left foot (*B*) of *Hongshanornis longicresta* gen. et sp. nov. (IVPP V14533). AD, alular digit; CM, carpometacarpus; MD, major digit; MID, minor digit; MT1, metatarsal I.

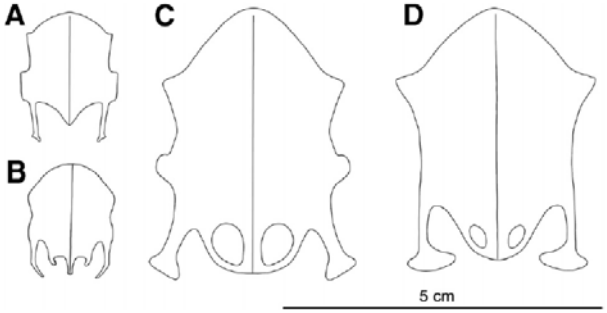


FIGURE 6. Comparative drawings of the sterna of Early Cretaceous ornithuromorphs from the Jehol Biota, China. **A**, PKUP V1069, holotype of *Longicrusavis houi*, gen. et sp. nov.; **B**, *Hongshanornis longicresta*; **C**, *Yixianornis grabaui*; **D**, *Yanornis martini*.

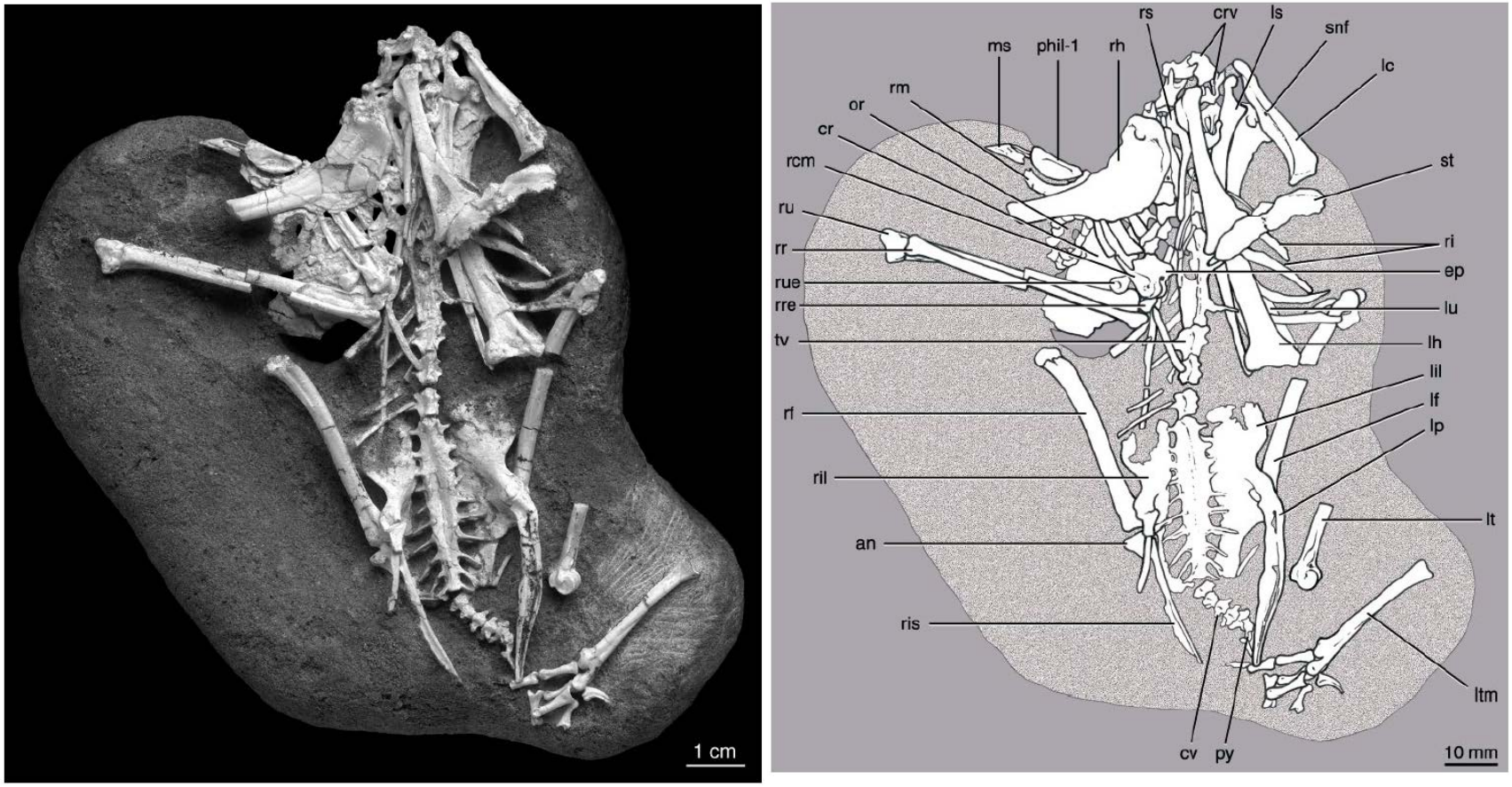
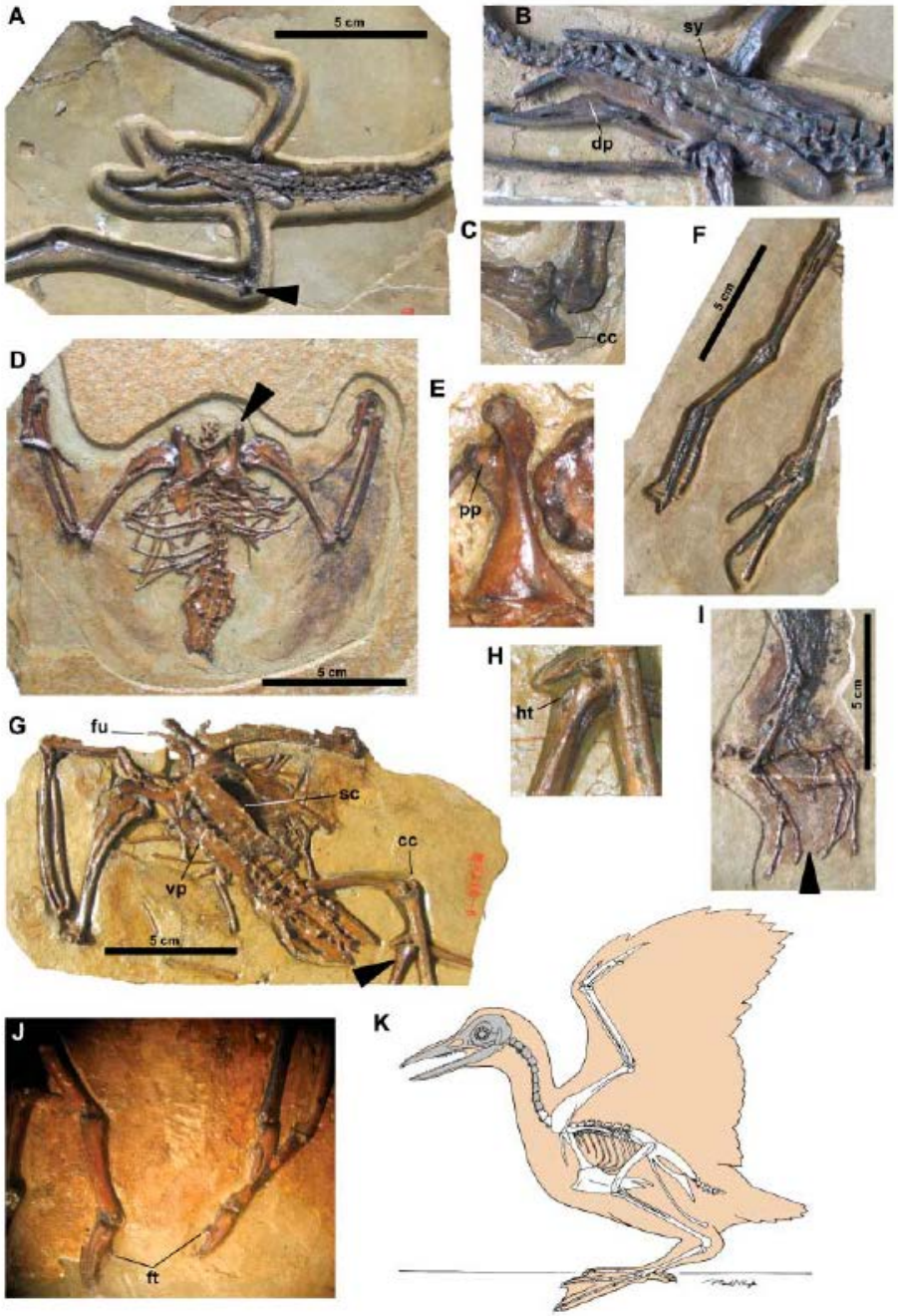


Fig. 3.18 Holotype of ornithuromorph *Apsaravis ukhaana* IGM 100/1017, from the Djadokhta Formation of Mongolia. (Mark Norell, AMNH, with permission.)

Apsaravis ukhaana



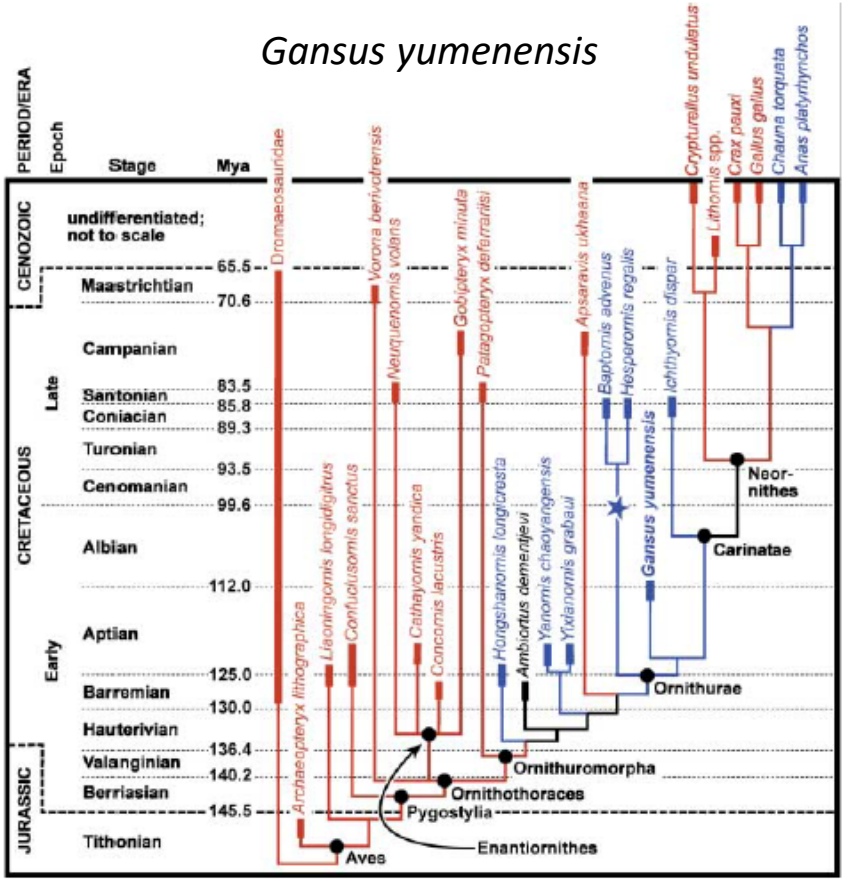
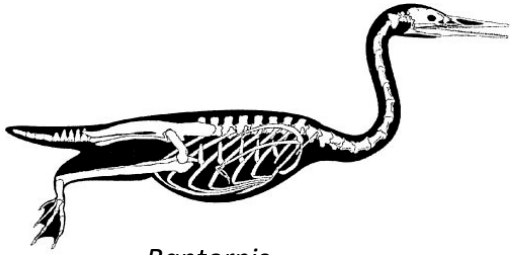


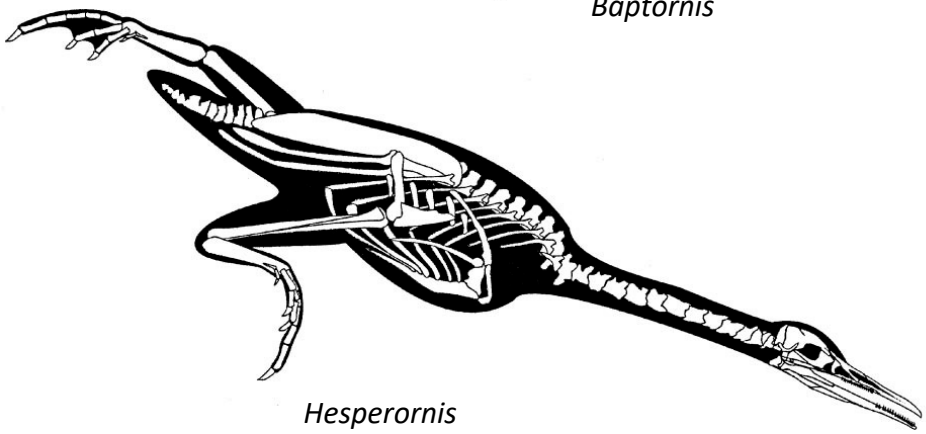
Fig. 3. Phylogenetic position of *G. yumenensis* (50% majority-rule consensus tree) based on holotype and new referred specimens; time scale is per (*28*). Thin line segments represent ghost lineages; thick line segments represent known ranges of terminal taxa. Clades are denoted by black circles (see supporting online material for clade definitions). The star represents the temporal position of *Enaliornis* spp. Colors indicate known or inferred ecologies as follows: brown, terrestrial/arboreal; blue, aquatic/amphibious; black, equivocal. Note the sequence of amphibious taxa basal to the Neornithes. Depicted divergence times are intended as approximations only, based on the oldest occurrence of an included species and subsequent divergences. Mya, million years ago.

Fig. 2. New specimens of *G. yumenensis* (Chinese Academy of Geological Sciences, Institute of Geology, prefix CAGS-IG-04-). (**A**) CM-002, articulated caudal cervical, thoracic, synsacral, and caudal vertebrae, pelvic girdle, and partial pelvic limbs in right dorsolateral view. (**B**) CM-002, pelvis and synsacrum. (**C**) CM-002, proximal right tibiotarsus [indicated by arrowhead in (A)]. (**D**) CM-004, nearly complete skeleton in ventral view with feathers (dark brown) on thoracic limbs, lacking cranium, cranial-midcervical vertebrae, and both pelvic limbs. (**E**) CM-004, left coracoid in ventral view [indicated by arrowhead in (D)]. (**F**) CM-001, partial right and left pelvic limbs. (**G**) CM-003, nearly complete skeleton in ventral view, lacking cranium, cervical vertebrae, distal left thoracic limb, and right and distal left pelvic limbs. (**H**) CM-003, proximal tarsometatarsus [indicated by arrowhead in (G)]. (**I**) CM-008, partial pelvic limbs with soft-tissue preservation. (**J**) CM-008, tubercular soft tissue preserved around toes [indicated by arrowhead in (I)]. (**K**) Reconstruction of *G. yumenensis* based on new specimens. Elements shaded gray remain unknown. Abbreviations in figure are as follows: cc, cnemial crests; ft, flexor tubercula; dp, dorsal process of ischium; fu, furcula; ht, hypotarsus; pp, procoracoid process; sc, sternal carina; sy, synsacrum; vp, ventral processes of cranial thoracic vertebrae.

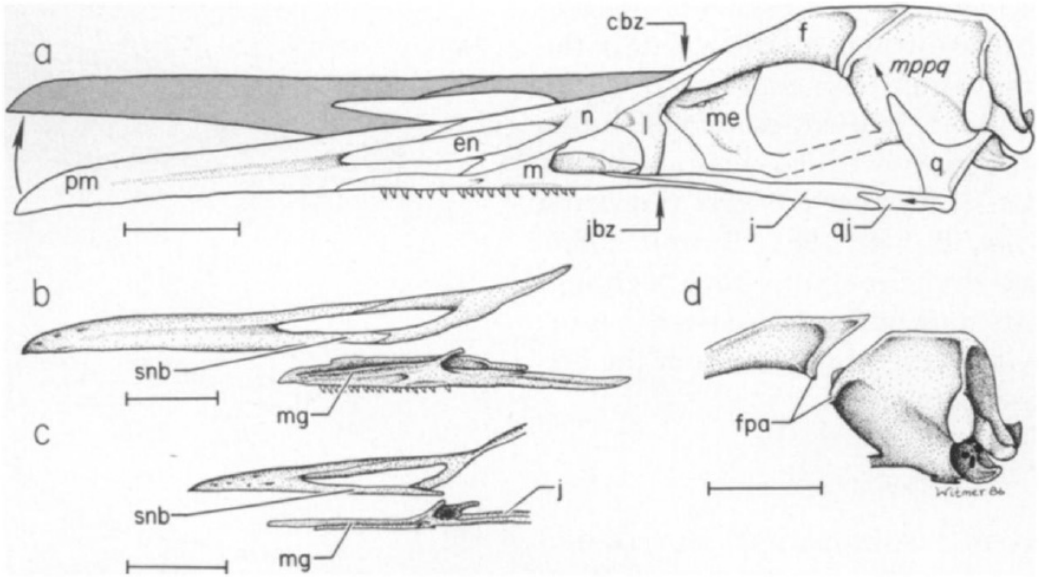
Hesperornithiformes

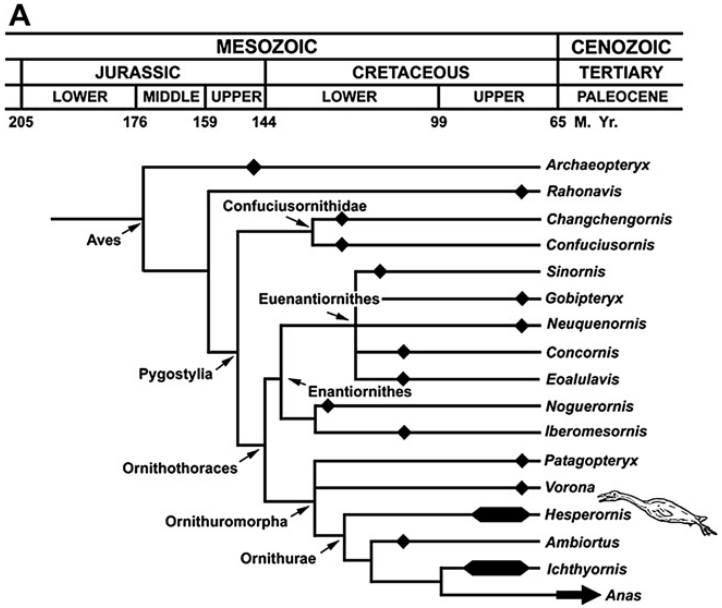


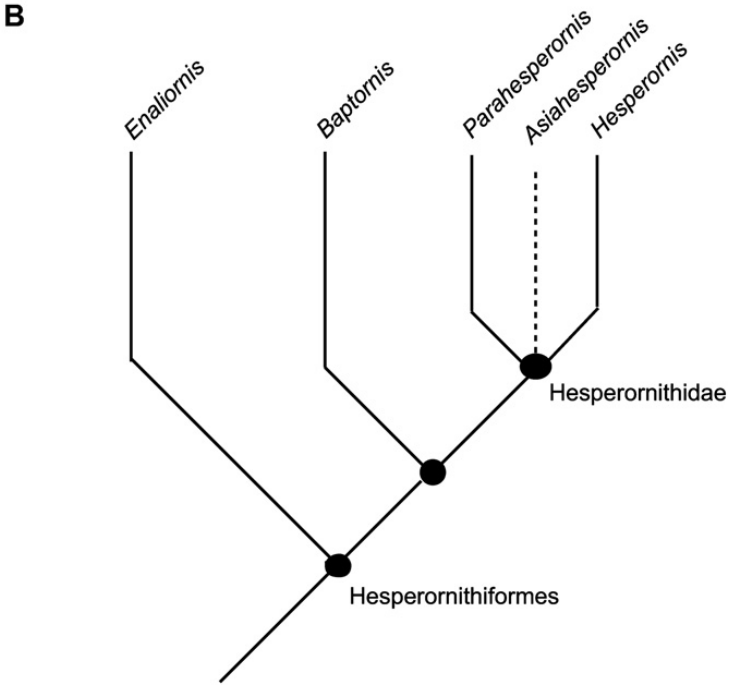
Baptornis



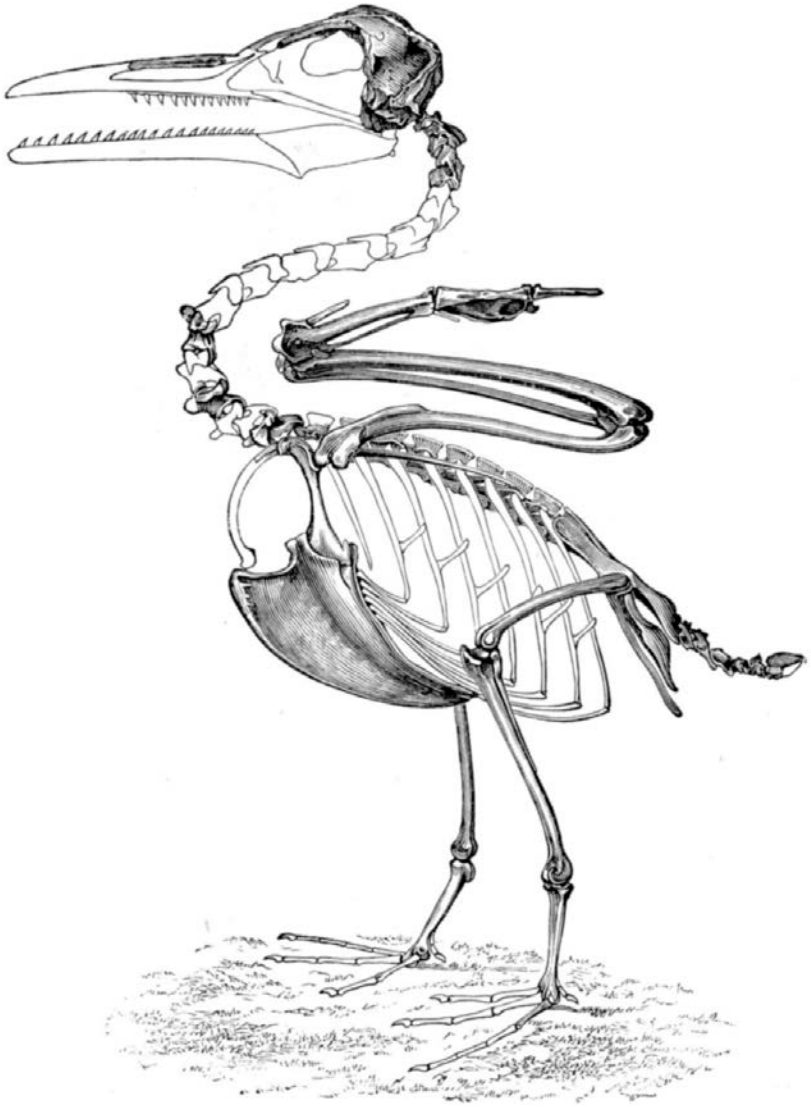
Hesperornis

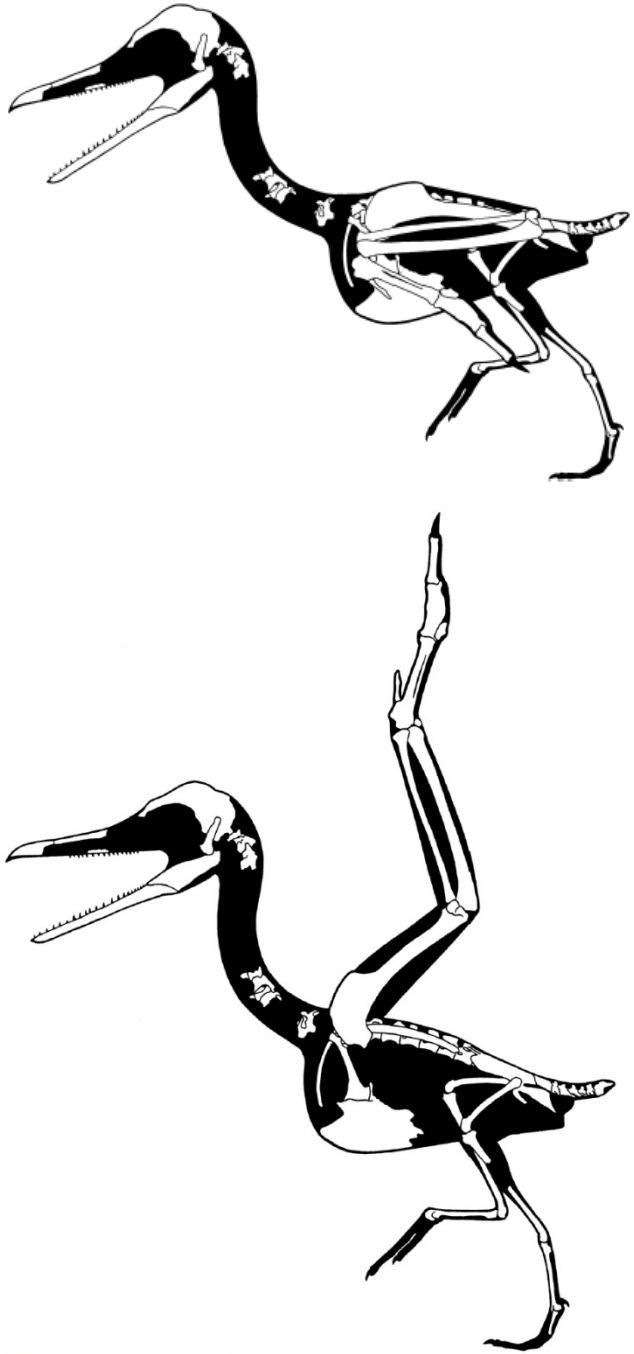






Carinatae:
Ichthyornis





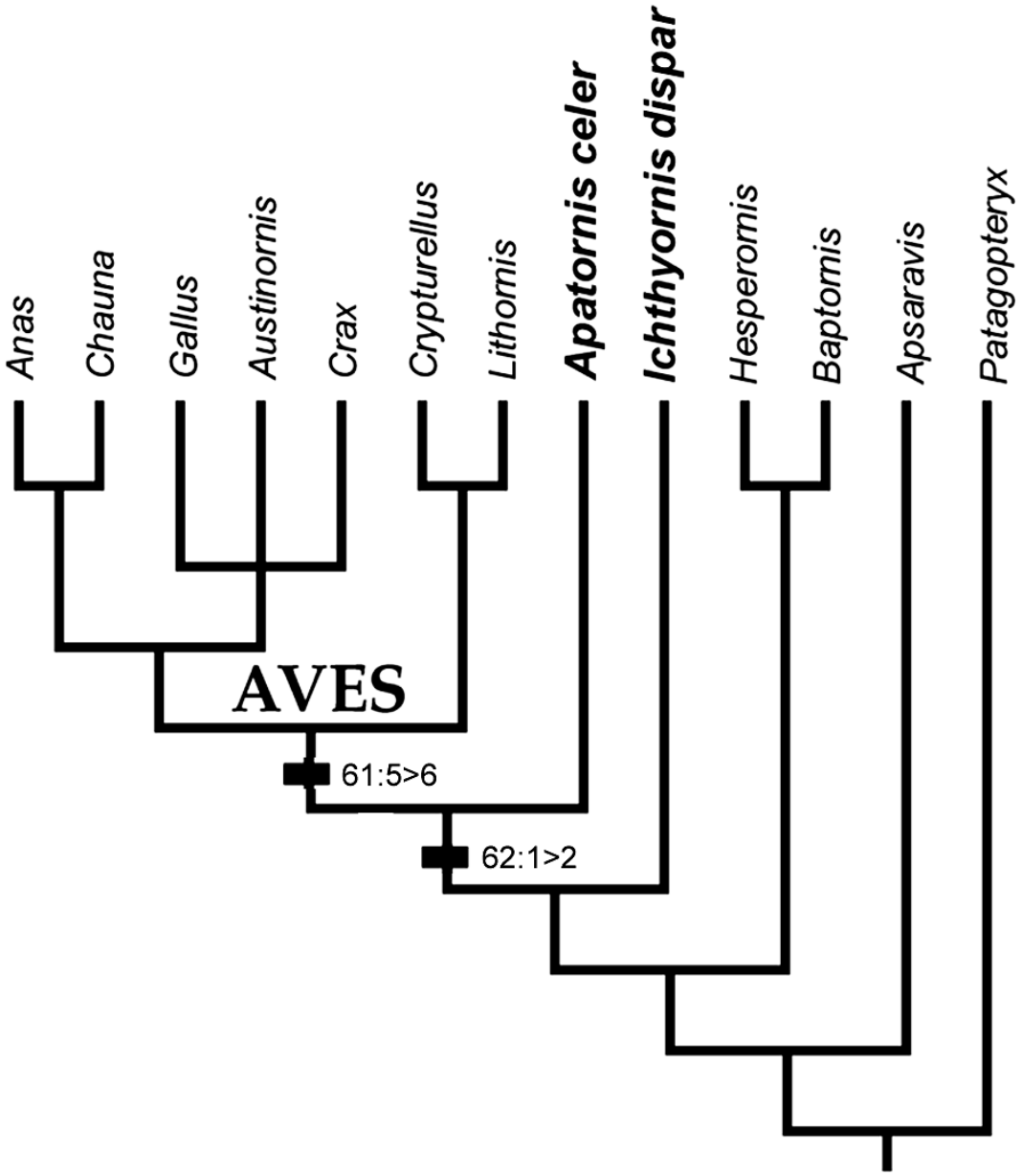
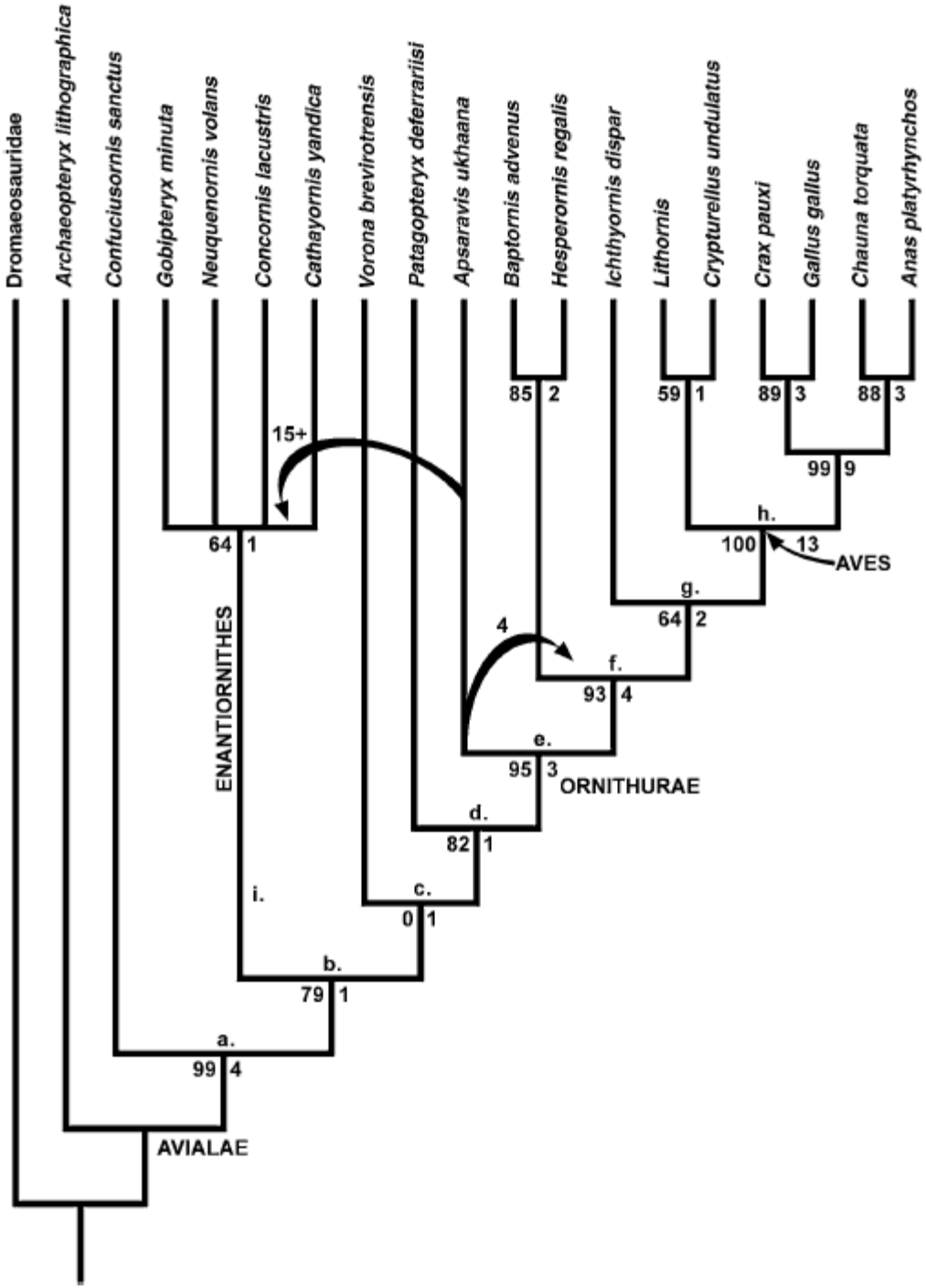


Fig. 66. Two silhouette reconstructions of *Ichthyornis dispar* by Gregory Paul showing the relative proportions of the elements discussed in the anatomical description. Elements known from *Ichthyornis* and discussed in the present monograph are in white.


Dromaeosauridae
Archaeopteryx lithographica
Confuciusornis sanctus
Gobipteryx minuta
Neuquenornis volans
Concornis lacustris
Cathayornis yandica
Vorona brevirotrensis
Patagopteryx deferrariisi
Apsaravis ukhaana
Baptornis advenus
Hesperornis regalis
Ichthyornis dispar
Lithornis
Crypturellus undulatus
Crax pauxi
Gallus gallus
Chauna torquata
Anas platyrhynchos
85 2
59 1
89 3
88 3
99 9
15+
64 1
h.
100 13
AVES
g.
64 2
4
f.
93 4
ENANTIORNITHES
e.
95 3
ORNITHURAE
d.
82 1
i.
c.
0 1
b.
79 1
a.
99 4
AVIALAE

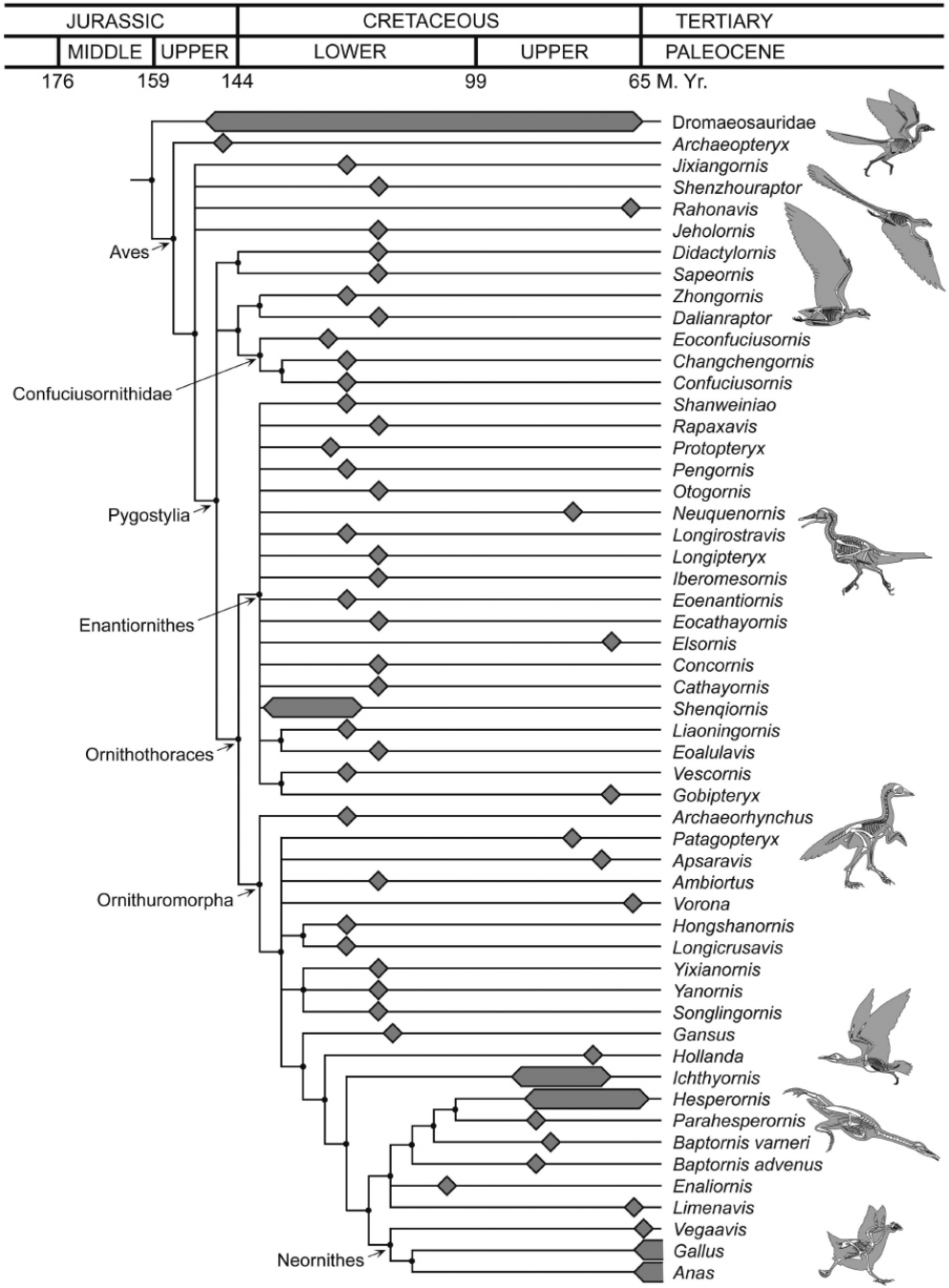


Fig. 3.20 Cladogram of Mesozoic bird relationships; the cladogram represents the strict consensus of the 1242 most parsimonious trees (length = 788 steps) derived from a cladistic analysis of 245 characters for 54 taxonomic units.

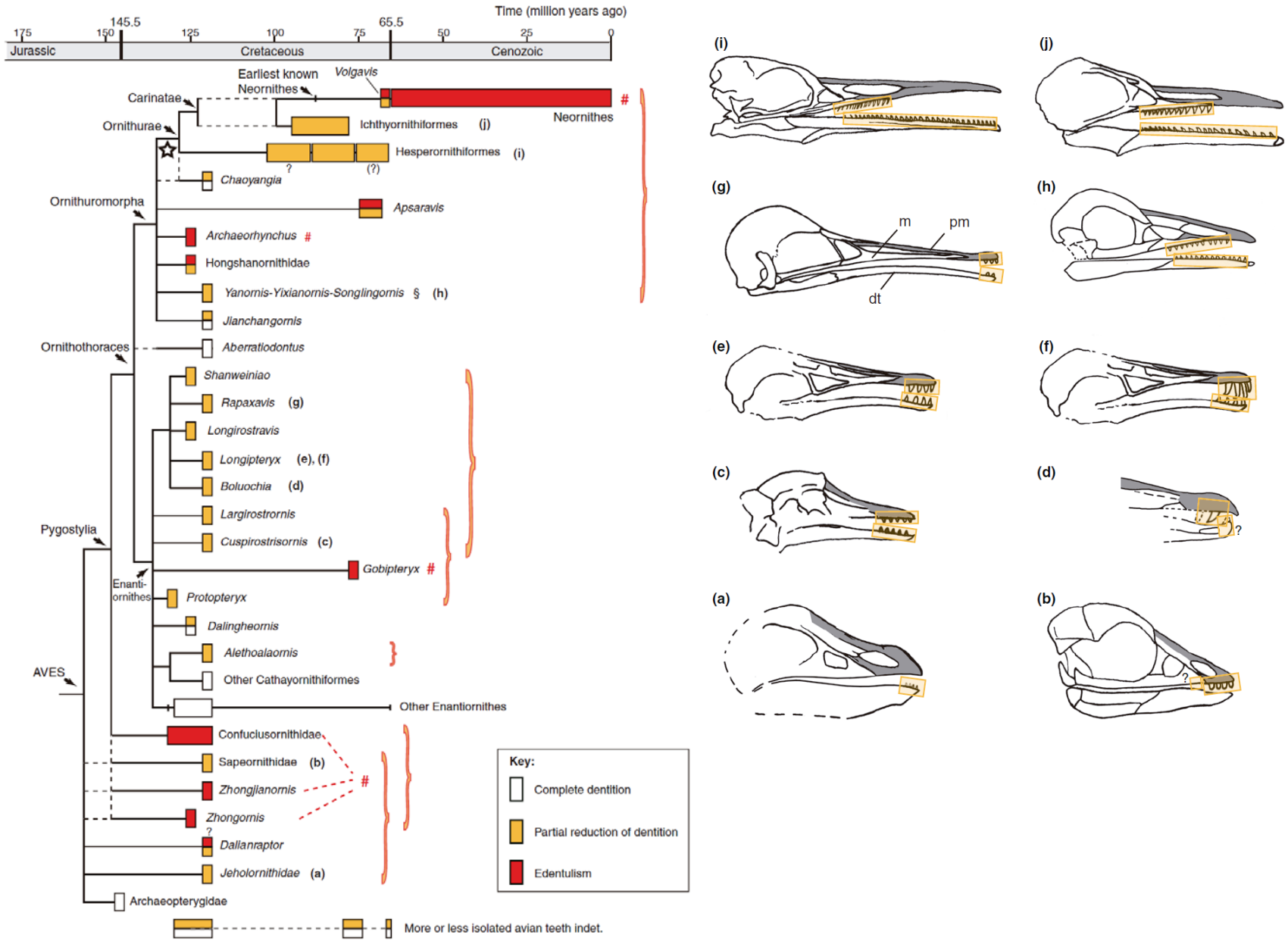


Figure 2. Examples of patterns of partial dentition reduction in birds, illustrated by different Cretaceous species (showing right side only). Toothed parts of jaws are highlighted in orange and the premaxillary in grey. Lettering refers to Figure 1. (a) *Jeholornis prima*, (b) *Sapeornis chaoyangensis*, (c) *Cuspirostrisornis houi*, (d) *Boluochia zhengi*, (e) *Longipteryx chaoyangensis*, (f) *Longipteryx* sp. [3], (g) *Rapaxavis pani*, (h) *Yanornis martini*, (i) *Hesperornis regalis*, (j) *Ichthyornis dispar*. Abbreviations: d, dentary; m, maxillary; pm, premaxillary. Other patterns are known (see the supplementary material online). Based on data and references in the supplementary material online.

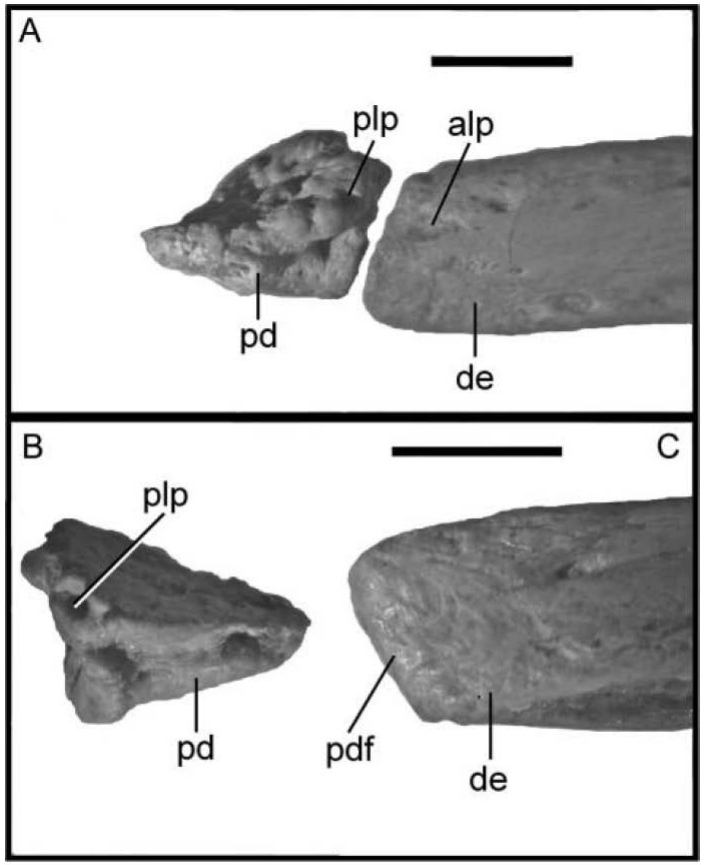


Figure 1. Photos of *Hesperornis regalis* (KUVP 71012). **A,** the predentary and tip of the left dentary in lateral view; **B,** the predentary in right view; **C,** the tip of the left dentary in medial view. Scale bar = 1 cm. Abbreviations: alp, anterior ligamental pit; de, dentary; pd, predentary; pdf, predentary facet; plp, posterior ligamental pit.

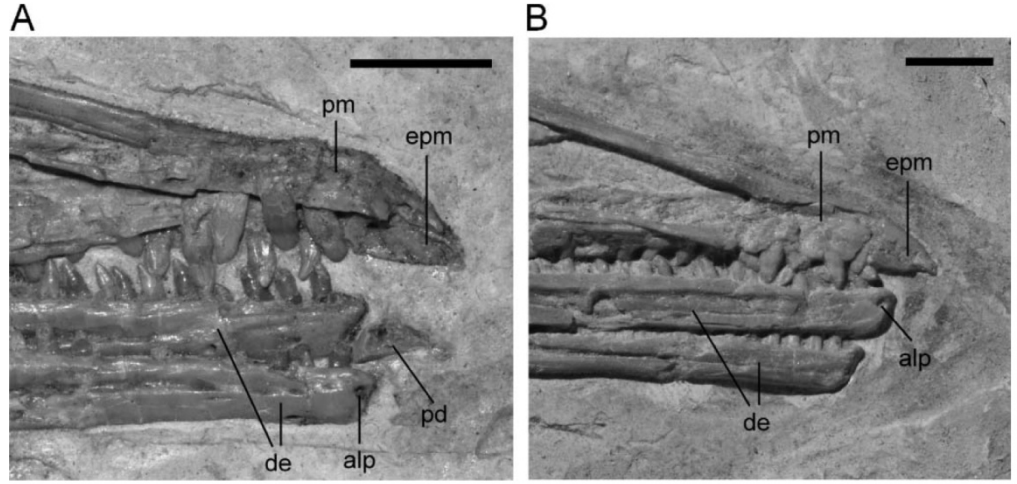


Figure 5. Photos of the anterior jaws of various specimens of *Yanornis*, showing the predentary and/or anterior dentaries. **A,** *Y. martini* (IVPP 13358) in right view; **B,** holotype of *Y. martini* (IVPP 12558) in right view. Scale bar = 5 mm. Abbreviations: epm, edentulous portion of the premaxilla. See Figs 1 and 4 for other abbreviations.

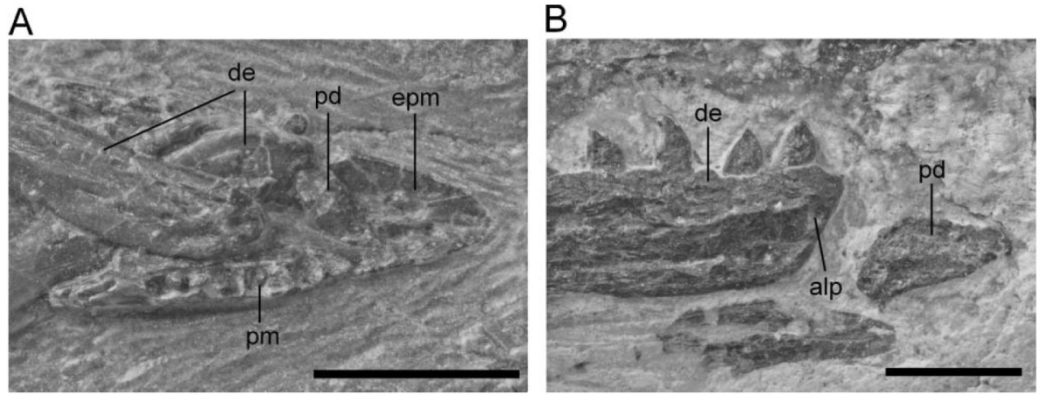


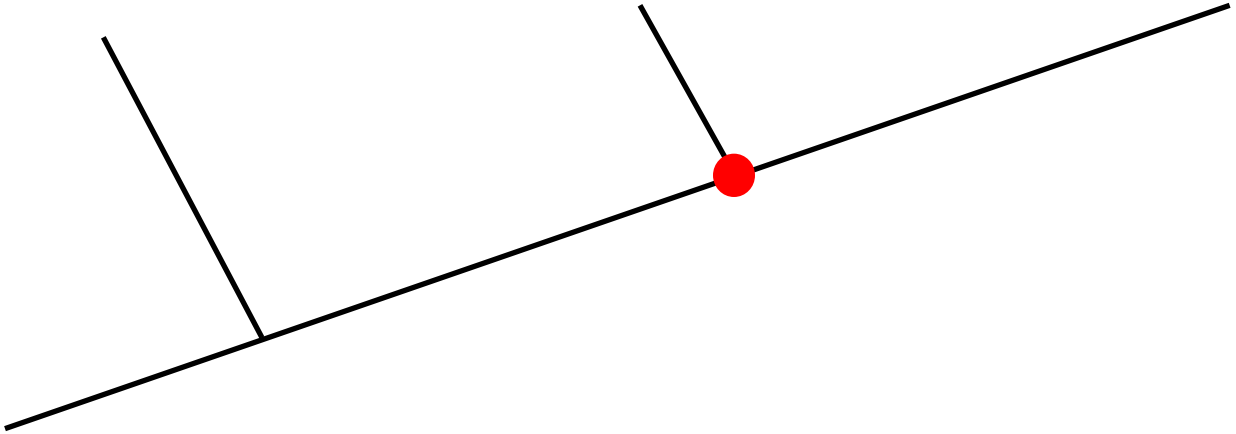
Figure 6. Photos of anterior portion of the skull of the holotypes of: **A,** *Yixianornis grabaui* (IVPP 12631) in ventral view; **B,** *Jianchangornis microdonta* (IVPP 15708) in right view, showing the predentary and anterior dentaries. Scale bar = 5 mm. Abbreviations as in Figs 1,5.

Neornithes

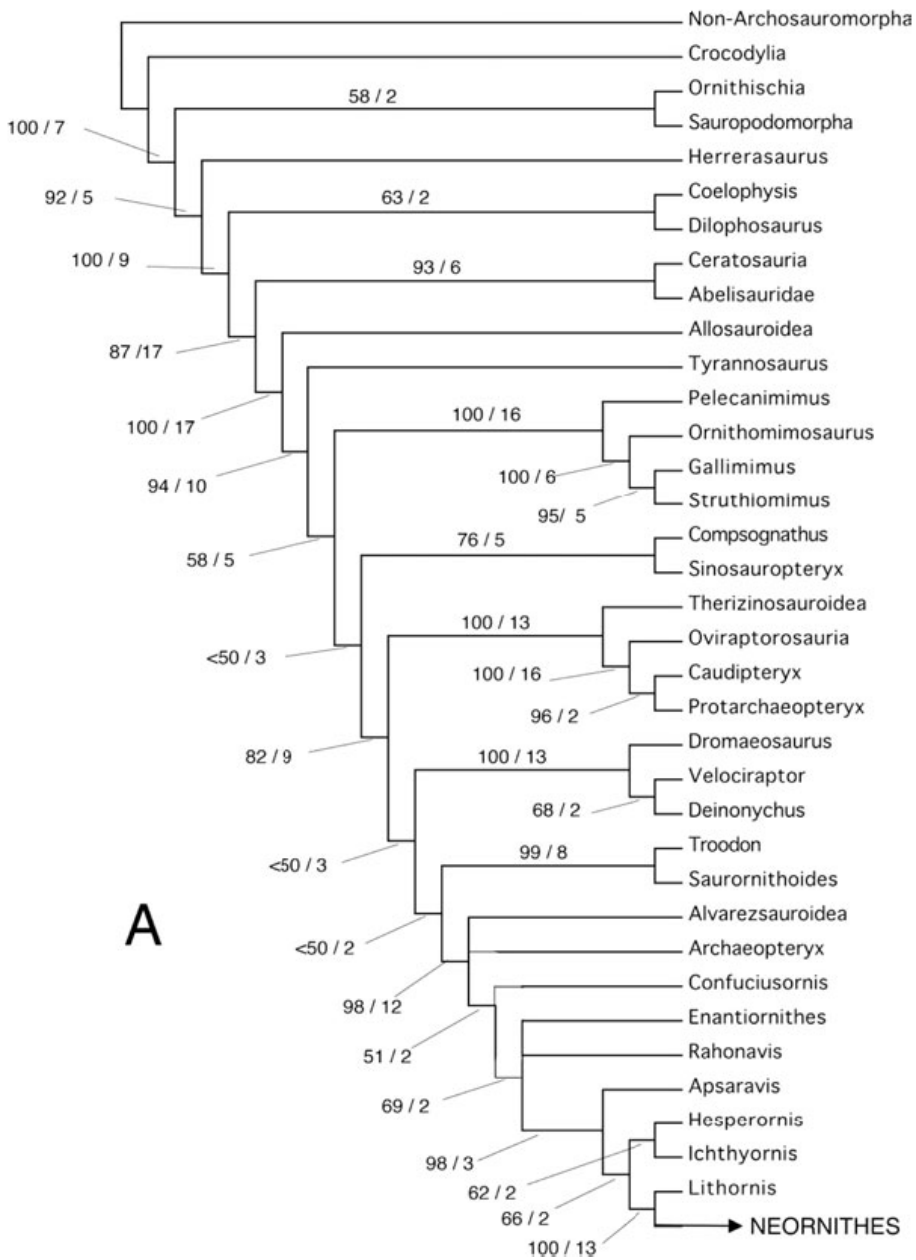
(crown group birds)

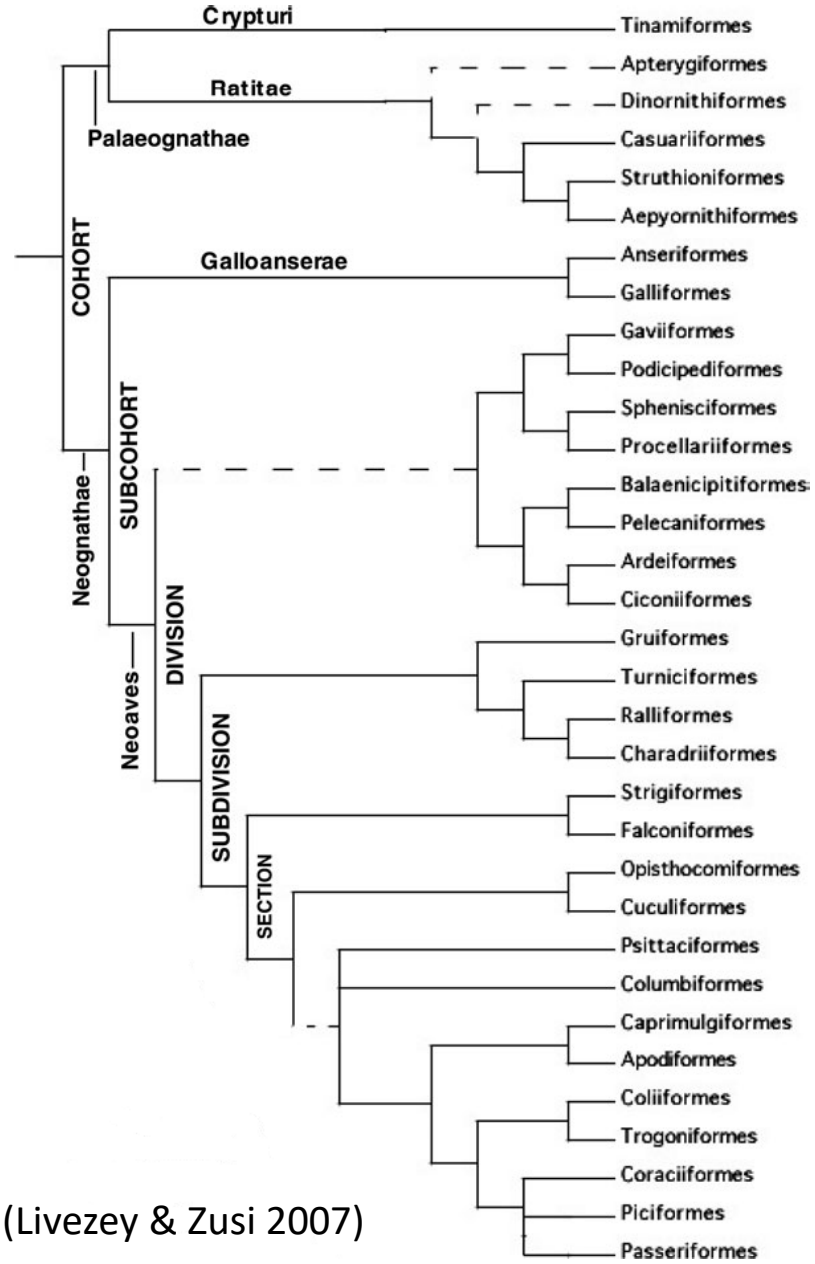
Neornithes

- Crown group birds: clado menos inclusivo que contiene a la perdiz chilena (*Nothoprocta perdicaria*) y la paloma (*Columba livia*)



Filogenia de Aves-Neornithes basada en caracteres morfológicos





(Livezey & Zusi 2007)

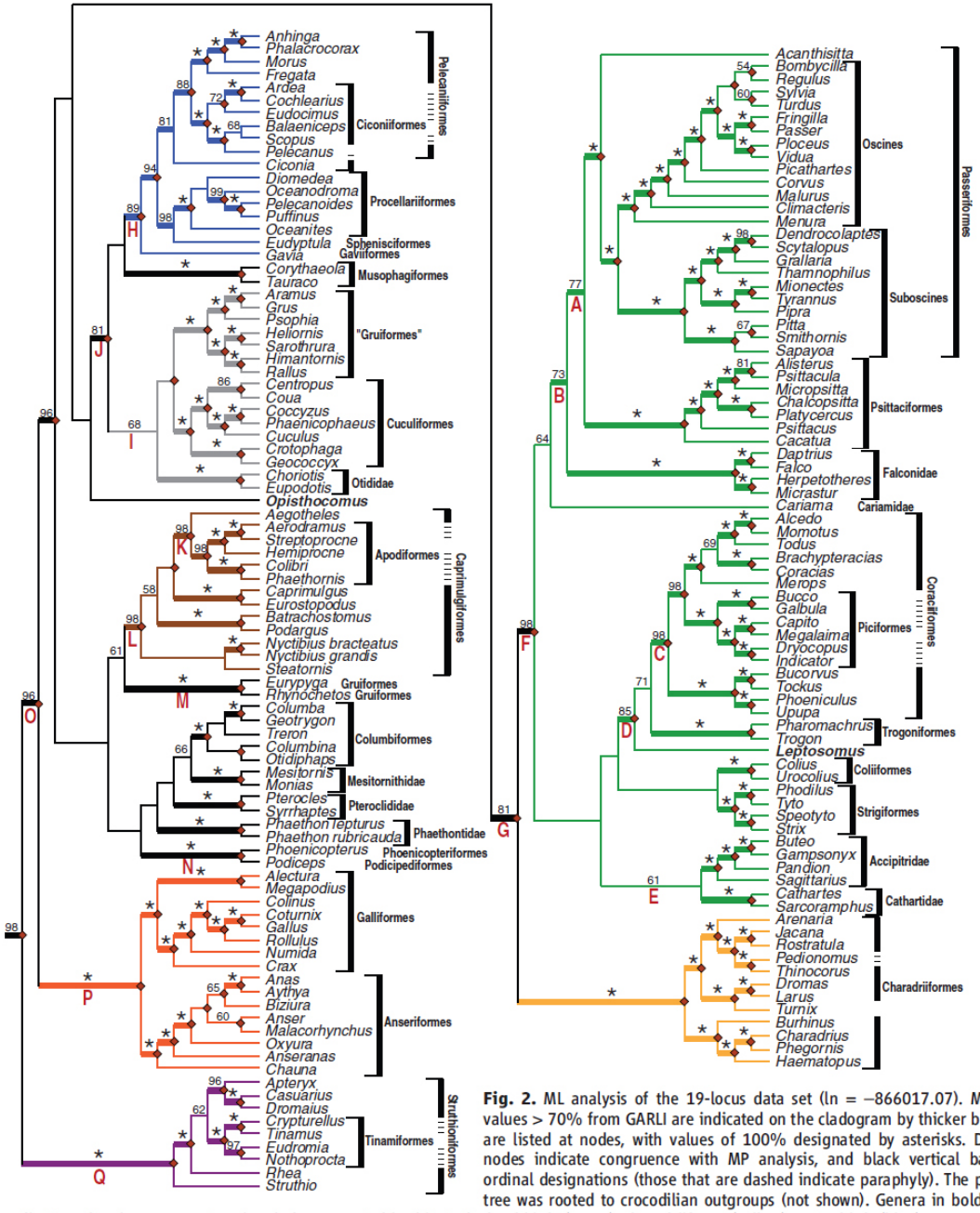


Fig. 2. ML analysis of the 19-locus data set (ln = −866017.07). ML bootstrap values > 70% from GARLI are indicated on the cladogram by thicker branches and are listed at nodes, with values of 100% designated by asterisks. Diamonds at nodes indicate congruence with MP analysis, and black vertical bars refer to ordinal designations (those that are dashed indicate paraphyly). The phylogenetic tree was rooted to crocodilian outgroups (not shown). Genera in bold are icertae sedis. Branch colors represent major clades supported in this study: land birds (green), charadriiforms (yellow), water birds (blue), core gruiforms and cuckoos (gray), apodiforms and caprimulgiforms (brown), galloanserae (orange), and paleognaths (purple). Large capital letters indicate groups discussed in the text and Fig. 1.

Filogenia de Neornithes basada en datos moleculares (secuencias de DNA nuclear)

(Hackett et al 2008)

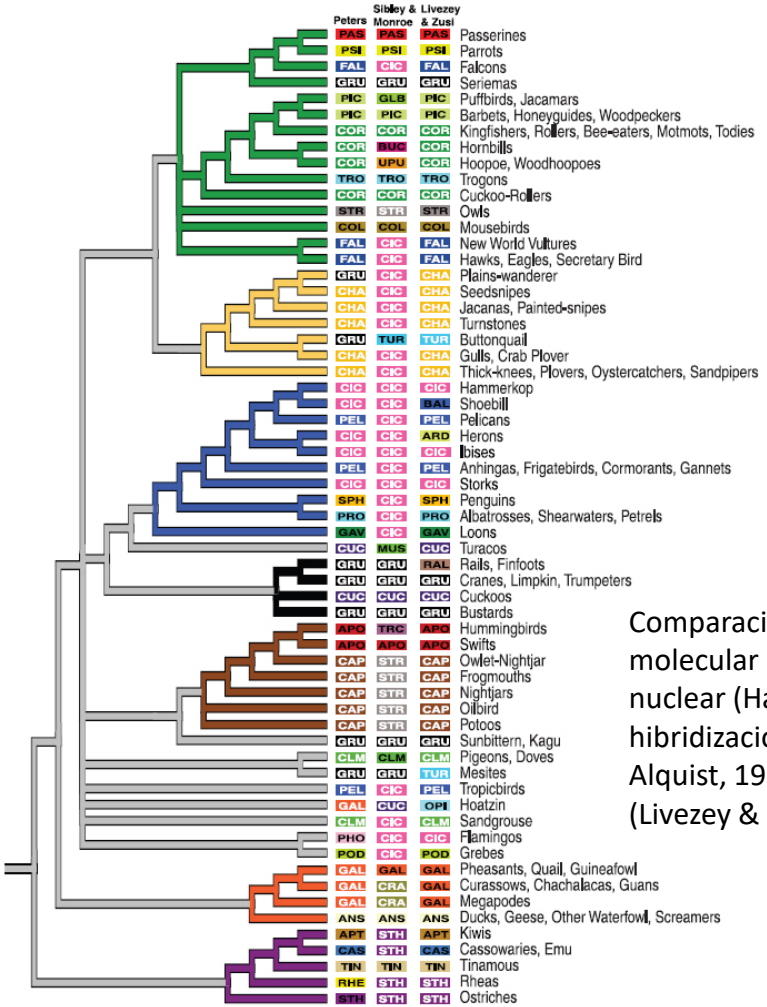


Fig. 4. Our phylogeny differs from and agrees with previous classifications. We merged well-supported (>70% bootstrap values) monophyletic clades at the tips with the same ordinal designation across all three classifications (e.g., 24 species called Passerines). Only higher relationships supported by bootstrap values >50% are shown. Colors are as in Fig. 2. Color bars to the right of the tree show membership in three different classifications: Peters' (*25*) (left), Sibley and Monroe's (*30*) (middle), and Livezey and Zusi's (*13*) (right). Black text within the bars indicates monophyletic orders in our phylogeny, whereas white text within the bars indicates nonmonophyletic orders. Ordinal name codes: ANS (Anseriformes), APO (Apodiformes), APT (Apterygiformes), ARD (Ardeiformes), BAL (Balaenicipitiformes), BUC (Bucerotiformes), CAP (Caprimulgiformes), CAS (Casuariiformes), CHA (Charadriiformes), CIC (Ciconiiformes), CLM (Columbiformes), COL (Coliiformes), COR (Coraciiformes), CRA (Craciformes), CUC (Cuculiformes), FAL (Falconiformes), GAL (Galliformes), GAV (Gaviiformes), GLB (Galbuliformes), GRU (Gruiformes), MUS (Musophagiformes), OPI (Opisthocomiformes), PAS (Passeriformes), PEL (Pelecaniformes), PIC (Piciformes), POD (Podicipediformes), PRO (Procellariiformes), PSI (Psittaciformes), RAL (Ralliformes), RHE (Rheiformes), SPH (Sphenisciformes), STH (Struthioniformes), STR (Strigiformes), TIN (Tinamiformes), TRC (Trochiliformes), TRO (Trogoniformes), TUR (Turniciformes), and UPU (Upupiformes).

Hipótesis filogenética de consenso entre 2 filogenias moleculares (Ericson et al., 2006; Mayr 2008)

Comparación entre filogenia molecular basada en DNA nuclear (Hackett et al 2008), hibridización DNA-DNA (Sibley & Alquist, 1990) y morfológica (Livezey & Zusi, 2007)

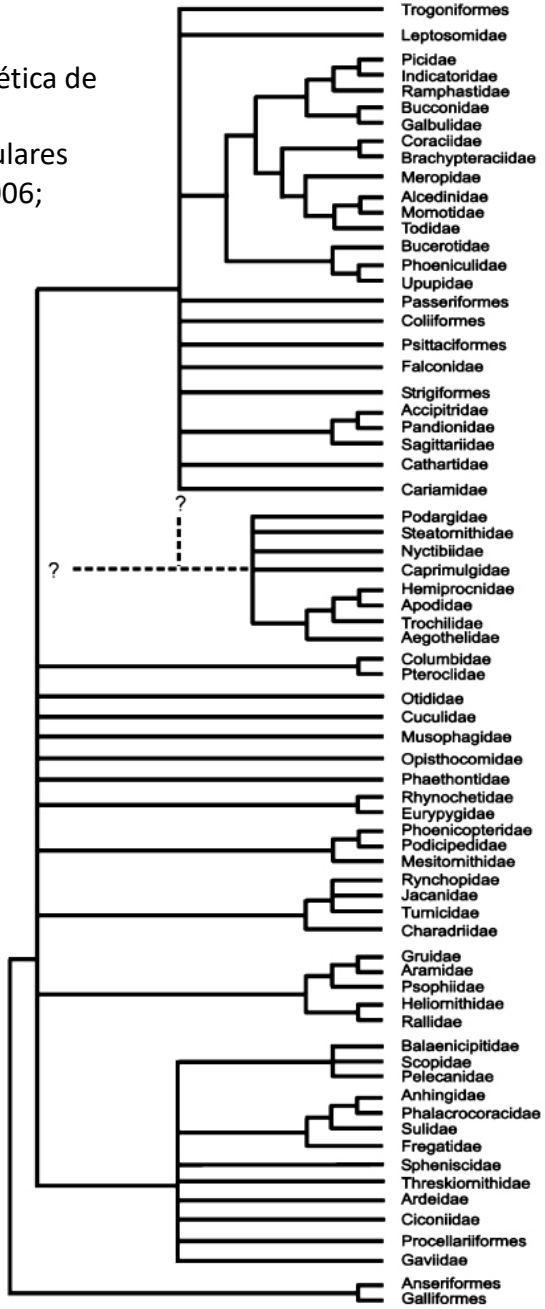


Fig. 3. Summary tree for neognathous birds with the well-supported clades discussed in the present study and those which are recovered in both gene trees in Fig. 2a and b

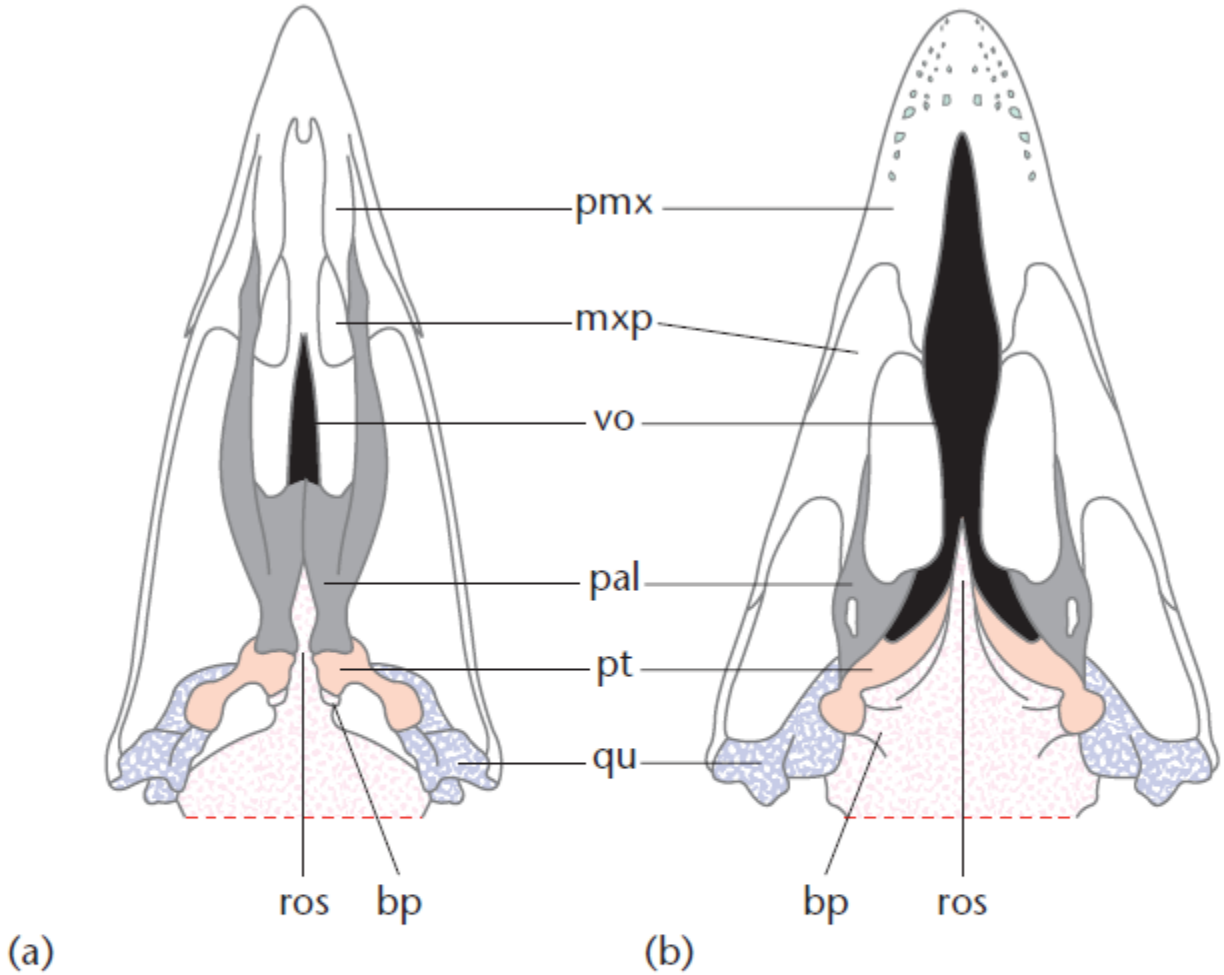


Figure 1 Palate bones, in ventral view, of (a) domestic fowl (*Gallus gallus*, Neognathae); (b) emu (*Dromaius novaehollandiae*, Palaeognathae). After Pycraft 1901b. Key: bp, basipterygoid process; mxp, maxillopalatine; pal, palatine; pmx, premaxilla; pt, pterygoid; qu, quadrate; ros, parasphenoid rostrum; vo, vomer. Note the reduced vomers (black) and juxtaposed palatines (dark grey) in Neognathae. In Palaeognathae, the palatines are separated by relatively large vomers.