

## Evolution of Birds, step by step

### 1. Diapsida (Two Arches)

Before we start, let's address what the anatomical characteristics of our starting point is.

Ancestral/plesiomorphic condition of Amniotes and Sauropsids that is inherited by Basal diapsids:

Four limbs

Sprawling, Quadrupedal limb posture

Plantigrade

5 digits on hand and foot with claws

Legs slightly longer than arms

Several tarsal (ankle) bones, including 5 or more distal tarsals

Parietal foramin (pineal eye)

Single Occipital Condyle

Presence of the Cleithrum in shoulder girdle

Clavicles present, unfused

1-2 sacral vertebrae

Amniotic eggs, soft leathery shells

amphicoelous vertebrae (both ends of the vertebra are concave)

Palatal rows of teeth

Aglandular skin

Layer of keratin scales on skin

Nitrogenous waste expelled as uric acid

3 chambered heart

Ectothermic (cold blooded)

Bellows style lungs

Evolutionary changes to the Sauropsid condition that define diapsids:

Two openings in the skull behind eye socket: Infratemporal and supratemporal fenestrae

Suborbital opening in the palate appears as a broad suborbital fenestra

Limbs more long and slender

### 2. Sauria (Reptiles)

Abductor muscles of the jaw originate at the top of the skull

The cleithrum is lost.

The fifth distal tarsal is lost, so only 4 distal tarsals

The fifth metatarsal is hooked

Quadrate bone is curved/pushed in towards skull

extension of the back of the jaw that projects behind the jaw joint.

### 3. Archosauramorpha:

Longer necks

Long, overlapping cervical ribs

Rhombus shaped cervical vertebrae

Epiphyses (bony projections of the cervical vertebrae)

Scarf Joint between post orbital and jugal and between jugal and quadratojugal  
A lack of notochordal canals, and the loss of the entepicondylar foramen of the humerus

#### 4. Archosauriformes:

Antorbital fenestra (opening in skull in front of eye socket)  
Mandibular fenestra (opening in rear of lower jaw bone)  
Thecodont teeth (teeth set into sockets)  
Semi-erect stance  
Row of osteoderms (armor) is common  
Loss of pineal/parietal "eye"  
Laterosphenoid bone in the skull  
Hinge-like ankle joint  
Closing of the lower temporal bar

#### 5. Archosauria (Ruling Reptiles)

loss of palatal row of teeth  
Enlarged Fourth trochanter (protuberance on the shaft of the femur)  
Tall, narrow skulls  
Reduced 5th (pinky) toe  
4th and 5th fingers (ring finger and pinky) reduced in size  
3rd finger the longest  
Loss of tarsals, so only two distal tarsals (two ankle bones below the astragalus and calcaneum)  
Partially bipedal when running  
Gizzard-like section of the stomach  
Unidirectional air-flow respiration  
Egg nests in vegetation  
Eggs made of hard calcium shells instead of softer leathery shells like other reptiles  
Parental care for young  
Calcaneal Tuber  
Phalangeal formula of 2-3-4-5-3 on hand and foot is typical

#### 6. Avemetarsalia (bird ankle):

mesotarsal ankles: orientation operated on a single hinge which articulates between the astragalus+calcaneum and metatarsals.  
Loss of bony armor (osteoderms)  
Loss of heel on foot

#### 7. Ornithodira (bird neck)

"S" shaped neck, slender body  
advanced mesotarsal ankles: characterized by a large astragalus and a small calcaneum  
Erect (parasagittal) stance (legs straight under the body)  
Cervical vertebrae distinct from and different size than dorsal vertebrae  
Longer and more slender shin, ankle and foot bones  
"Fuzz" type of skin integument found in many members of this clade  
Calcaneal Tuber small/reduced

Possibly endothermic (warm blooded)

#### 8. Dinosauromorpha:

Process of the astragalus ascending onto the face of the tibia (small spike on ankle bone that invades onto the surface of the shin bone)

Digitigrade posture: standing on the toes or "balls of the feet" with the ankle held up, allowing for a longer stride

Mostly bipedal

elongate pubes and ischia

#### 9. Dinosauriformes:

Partially in-turned femoral head/medial femoral head orientation

Tibia longer than femur

Gap between the ilium and ischium along the edge of the pubis (partially open acetabulum)

Prominent deltopectoral crest: a forward directed bony flange on the upper part of the humerus which measures 30–40% of the length of the humerus.

#### 10. Dinosauria (great lizards/reptiles)

Ascending process of the astragalus (tall spike coming off the ankle which invades into the tibia (shin))

Fully in-turned femoral head

Perforated acetabulum (open hip socket) (semiperforate in the most primitive forms)

Fused sacrum, sacral vertebrae fused to sacrum

Enlarged, semi-opposable thumb

Reduced/shortened fingers 4, and 5. (Ring finger and pinky) (phalangeal formula of 2-3-4-3-2)

supratemporal fossa

Fibula reduced in size, thinner than tibia

More robust epiphyses

Forked posterior process of the jugal where it bifurcates around the quadratojugal

Bipedal (lost in derived Sauropods and Ornithomimids)

3 or more Sacral vertebrae

#### 11. Saurischia (lizard hips)

Longer neck

posterior cervicals are longer than anterior cervicals (neck vertebrae near trunk of body are larger than those near the skull)

pneumatic neck vertebrae

Pleurocoels in vertebrae

Metacarpal 1 (hand bone) reduced

Digit 2 is longer than other fingers

Enlarged claw on thumb

Pubic boot (large hook or bump on end of pubis)

Lacrima is tall and exposed on top of skull

Supraacetabular crest on pelvis

Sacral vertebrae fused to iliac crests

Antitrochanter of the pelvis

## 12. Theropoda (beast footed)

Fully Bipedal

Hollow/pneumatic limb bones

promaxillary fenestra (opening in upper jawbone in front of antorbital fenestrae)

Even more pneumatic vertebrae

Blade-like serrated teeth

Intramandibular joint

Enlarged hands with increased grasping ability

Pinky finger reduced to a vestige, phalangeal formula on hand 2-3-4-2-1

the second digit in hand is further enlarged

Big toe and pinky toe reduced in size, phalangeal formula on foot changed to 2-3-4-5-1

Big toe becomes a hallux toe, loses contact with ankle, but is on the side of the foot and not reversed like in birds

Evidence of endothermy (warm bloodedness)

## 13. Neotheropoda (new theropods)

Furcula (wishbone, formed by fusion of clavicles)

Pinky finger completely lost (4 fingers) 2-3-4-1-0 formula

Subnarial gap (Kink between Premaxilla and maxilla (upper jaw bones))

Loss of pinky toe, causing Tridactyl foot (three forward-facing toes) and a big toe which is now a hallux toe far up on side of the foot, phalangeal formula of the foot 2-3-4-5

Enlarged hip muscles, strong tail

5 or more sacral vertebrae typical

## 14. Averostra (bird snout)

Reduced number of maxillary teeth

Asymmetrical maxillary teeth

No teeth in the rear of the upper jaw, only in middle and tip of jaw

Reduced subnarial gap

Lacrimal fenestra (small hole on bone in front of eye)

Larger ilium

## 15. Tetanurae (stiff tails)

Maxillary fenestra (an extra opening between the antorbital and promaxillary fenestrae)

All Teeth restricted to front of jaws, never behind the eyes

Larger hands

Interlocking caudal vertebrae (stiff ends of the tail)

Proto-feathers found in many members of this clade

## 16. Neotetanurae/avetheropoda

Loss of ring finger (digit IV) (causing a hand with only 3 fingers)

Phalangeal formula of 2-3-4 on fingers

Strap-like scapula

Extremely complex air chambers/pneumatic bones, air sac lungs

Primitive Semilunate carpal block: a specialized half-moon shaped carpal bone structure which lets the hand fold up against the body)

Distal obturator process on the ischium

Reduced size of fibula

#### 17. Coelurosauria (hollow tail lizards):

a sacrum (series of vertebrae that attach to the hips) longer than in other dinosaurs

tail further stiffened towards the tip

Boat/kayak shaped chevrons on distal end of tail

Tail more slender

Longer, more slender hands and feet

Taller ascending process of the astragalus

bowed ulna (lower arm bone).

Smaller ischium

Feathers of various types as well as scales found in many fossils of this clade

Enlarged brain (larger than other dinosaurs but not as large as modern birds) least twice the size of those of other theropods of the same body size

Fewer than 45 caudal vertebrae (shortened tail)

#### 18. Maniraptora (hand grabbers/seizers)

Brain twice as large as other coelurosaurian dinosaurs (which have brains twice as large as other theropods)

Larger hands again

Downward or backwards facing pubis common (remained or reverted more forward in some lineages)

bony sternum common

Ossified sternal ribs

Ossified uncinat processes on ribs common (but still cartilaginous in some)

Feathers in all members of clade

Partial fusion of two carpals in the Semilunate carpal block

Note: the Glenoid fossa is still oriented caudoventrally (backwards) in basal members of this clade

#### 19. Pennaraptora (fully feathered seizers)

Another increase in brain size

Laterally (sideways) directed shoulder joint (glenoid fossa) instead of backwards like other dinosaurs

Fully fused semilunate carpals (fusion of two carpal bones into a solid half-moon shaped wrist bone, allows for folding wrists up to the side of the body, like birds)

Pennaceous flight feathers

Brooding on nests of eggs (probably evolved earlier but direct evidence found in this clade)

Reduced 4th trochanter (absent in some lineages)

Possible propatagium (thin membrane of skin on arm between shoulder and wrist, part of wing)

M. supracoracoideus protracts humerus

## 20. Paraves/Eumaniraptora (true maniraptorans)

"T" shaped lacrimal bone due to fusion of the prefrontal bone to the lacrimal (sometimes remained unfused in some specimens)

Scapula + coracoid form an "L"-shape around the body (90° angle)

Coracoid longer and more slender

Smaller body size

Very long arms, arms longer or as long as legs (all other reptiles have legs longer than arms)

Large hands

Retractable sickle claw on foot

Tail very mobile near base, very stiff on the end

Hallux toe is lower and touches the ground and is more reversed than in previous theropods

Backwards facing pubis common except in derived troodonts

Reduced supraacetabular crest

Several species which exhibit possible flight, gliding, or are secondarily flightless..

## 21. Avialae (bird wing)

Tail reduced to 25 or fewer caudal vertebrae (except in Jeholornithidae which some species had 27)

Longer arms (humerus longer than scapula and ulna longer than femur)

Flight or gliding is likely for all members

Nasal opening posterior to premaxillary teeth

Larger brains than most maniraptorans

Fewer than 20 teeth

Mandibular fenestra lost in most lineages

Scapula+Coracoid form 90° angle when viewed from the side

The Separation of the scapulocoracoid into two separate bones called the scapula and coracoid is found in some specimens of some members of this clade but they are still fused in some others. (Fusion or separation of scapula and coracoid in Archaeopteryx is still being debated, both conditions are shown by different specimens, possibly fuses in adults)

Lengthening of the coracoid

Twisting of the orientation of the coracoid

More prominent acrocoracoid process, which redirects the tendon of the m. Supracoracoideus to be at or slightly above the glenoid, resulting in partial elevation of the humerus by the m. Supracoracoideus (however, at this stage flapping is facilitated mainly by the deltoid muscles)

Acrocoracoid process and Acromion process of the Scapula form the beginnings of the Triosseal Canal.

Hallux toe further reversed, possibly partially opposable but metatarsal 1 not fully twisted like in modern birds.

Larger eye socket

Quadratojugal becomes "L" shaped

## 22. Euavialae (true avialae)

Scapula+coracoid orientation forms an acute angle when viewed from the side

Supraacetabular crest reduced or lost

Forked lower Jugal process that articulates with the quadratojugal is reduced or lost

6 sacral vertebrae

## 23. Avebrevicauda (short bird tails)

Fewer than 10 caudal vertebrae (shorter tail)

fusion of the distal tarsals with the proximal end of metatarsals II-IV.(beginning formation of tarsometatarsus)

#### 24. Pygostylia (short tails)

Increase to 8 or more sacral vertebrae

Further reduction in the number of caudal vertebrae

A long rod-like pygostyle

Beginnings of a small keel on sternum

Fibula greatly reduced, shorter than tibia, doesn't contact the ankle

The tibiotarsus (fusion of the proximal tarsals to the tibia)

Change to knee based center of gravity due to lack of tail

Further formation of triosseal canal (canal formed by the articulation of the scapula, coracoid and furcula)

acrocoracoid process moves above glenoid fossa

Strut-like coracoid (Lengthening of coracoid)

Phalangeal formula on hand is still 2-3-4 on some members but there is a loss of some phalanges in the lineages which lead to the next clade

First evidence of keratinized beak in this clade

Pelvis Lengthened, more fused elements in pelvic girdle

Incipient Heterocoelous vertebrae in vertebrae that are in the middle portion of the neck

#### 25. Ornithothoraces ("bird chests")

9 or more sacra

Fully separated coracoids and scapulae

Carpometacarpus: complete fusion of the semilunate carpal block to the metacarpals, and all the metacarpals to each other (although basal bird groups include fusion between some of the metacarpals with the semilunate carpal, but not metacarpal I)

Reduction in the size of fingers and claws

alula: digit I supports feathers separate from the rest of the wing, for better control in flight

Increased sternum size

Glenoid Fossa directed dorsolaterally (up and to the side) as in modern birds

Fully Backwards facing hallux toe

M. supracoracoideus abducts/elevates the humerus

Furcula (wishbone) is "Y" or "U" shaped instead of boomerang shaped (hypsopleurion present)

Longer Coracoids

Heterocoelous cervical vertebrae (saddle shaped articular surfaces of vertebrae which allow greater neck flexibility)

(Note: The Epipophyses from Archosauriforms are still present on the birds in this clade, claws are still present on fingers, some members still display diapsid condition (two temporal fenestra) and have maxillary and premaxillary fenestra like Tetanuran Theropods, teeth are still prevalent, antorbital fenestra from Archosauria is still present in most, deltopectoral crest on humerus still prominent as in dinosaurs)

#### 26. Ornithomorpha/Euornithes (True birds)

Shorter, more compact pygostyle

The tail fan: many broad feathers coming out of a bulb surrounding a shortened pygostyle  
Fusion of the premaxillae (at least at the anterior end)  
A tiny prementary-like midline bone in front of the dentaries  
The complete tarsometatarsus: fusion of the distal tarsals to the metatarsals, and the metatarsals are all fused to each other  
Loss of long leg feathers  
Premaxilla larger, passes over the nasal and maxilla  
Nasal and maxilla reduced  
Loss of maxillary fenestra due to maxilla being reduced and compressed downward towards the palate which forms into a flat plate.  
Triosseal canal fully closed by bone due to presence of acrocoracoclavicular joint (joint between the furcular epicleideal process and the coracoid acrocoracoid process)  
Appearance of prementary bone (small tip of beak on lower jaw)  
Partial cranial kinesis  
Loss of contact between Jugal and Post-Orbital, post-orbital reduced in size and reduced length of jugal process, this results in:  
Reduction of the diapsid condition (loss of contact of the bony arches that frame the temporal openings: loss of one or both temporal fenestra)

#### 27. Carinatae (Keeled ones)

deeply keeled sternum to support the powerful wing muscles, as 10 or more sacral vertebrae greatly reduced (and sometimes loss of) claws on hand  
Synsacrum: fusion of the sacrum to the ilium, and fusion of all pelvic elements together  
loss of contact between the distal ends of the left and right pubes (loss of "pubic symphysis")  
More changes to shape of pelvis  
complete fusion of the premaxillae.  
Loss of postorbital bones due to fusion to the frontal bone  
Smaller and fewer gastralia

#### 28. Ornithurae (bird tails)

Greatly Enlarged premaxilla (beak)  
Further reduction of nasal and maxilla  
Probable loss of gastralia  
ectopterygoid reduced to a vestige  
Quadratojugal becomes a small peg that fuses to the end of the Jugal, jugal becomes Jugal Bar  
Post-Orbital greatly reduced, absent in many species  
Earliest fossil evidence of a Syrinx (Bird Vocalization organ)

#### 29. Aves/Neorniths (new birds)

Toothless beak  
15 or more sacral vertebrae common, always more than 10  
Premaxilla takes up almost the entire jaw, maxilla is further greatly reduced  
No gastralia  
No temporal fenestra (merged with eye socket or covered by enlarged cranium)  
Increased brain size in many lineages

Several joints in the palatal bones which allow for cranial kinesis (joint formed between quadrate and pterygoid)

Loss of predentary bone

Loss or fusion of ectopterygoid bone

Fibula is reduced to a tiny splint

Pneumatic coracoid

Several other bones of the cranium become fused:

Angular bone fused to other parts of jaw

Premaxilla and Maxilla: In many theropods, these bones were distinct, but in birds, they became more fused and integrated into the beak structure, contributing to the loss of teeth.

Nasal Bones: The nasal bones became fused in birds to form a more streamlined structure for respiration and feeding.

Postorbital and Squamosal Bones: These bones were fused in birds, unlike in theropods, where they were more distinct and separate.

Frontal and Parietal Bones: these bones became more fused, resulting in a more rigid skull structure, which is advantageous for flight and feeding.

Palatal Bones: The bones of the palate, such as the pterygoid, also became more fused in birds, contributing to the overall reduction and reorganization of the skull.

Note: phalangeal formula on foot is still 2-3-4-5

Note: most modern aves still have an antorbital fenestra although it is combined with the eye socket in some species

Note: 4th trochanter greatly reduced but still present in some modern birds, like Turkey Vultures.

Several bones that were lost, such as the post-orbital and frontal, appear as separate ossification centers during embryonic development,