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The archosaurs: a phylogenetic study

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Students of archosaur phylogenetics are in much the same position today as were paleobiologists studying Tertiary mammals 100 years ago – too few specimens and too many gaps in the record. However, enough is known to make some firm conclusions about archosaur phylogeny. The chasmatosaurs are predatory rynchosaurs. Euparkeriids, garjainiids, erythrosuchids, vjushkoviids, prestosuchids, saurosuchids and poposaurids form a clade separate from the other archosaurs. Ornithosuchids form a clade with dinosaurs, and crocodilians and pterosaurs are sister groups of the dinosaurs. Dinosaurs are monophyletic, and archaeopterygids are early flying dromaeosaurid theropods. Character lists in the text are keyed to the cladogram (fig. 1).

Archosaurs have remarkably variable ankles, and a number of phylogenetic trees have been based on ankles alone (Cruickshank 1979). This is a misuse of the data. In particular, it is usually assumed that all the thecodonts and crocodilians that have the crocodilian type of ankle with a big calcaneum tuber belong to a monophyletic clade. However, the earliest known crocodilian, Trialestes, has a dinosaur-like, fully mesotarsal ankle (Reig 1963; Bonaparte pers. comm.). Since thecodonts did not evolve from crocodilians, it is clear that the crocodilian type of ankle evolved at least twice. This invalidates the main premise of most ankle phylogenies. Also, it is very unlikely that the crocodilian ankle and its big calcaneum tuber ever changed back into the simpler dinosaurian mesotarsal ankle because Hallopus, the most fully erect gaited crocodilian known, has a bigger calcaneum tuber than any other archosaur!

The earliest "archosaur" Chasmatosaurus (ch) shares with early rynchosaurs (ry), (R) unusual skull designs with sharply downturned premaxillas and peculiar ankles in which the tibia articulates with the medial centrale as well as the astragalus. In all other eosuchians and archosaurs there is no tibial-centrale contact. This suggests that rynchosaurs and chasmatosaurs form a clade of their own near the base of the archosaurs. Whether chasmatosaurs developed the antorbital fossa independently of archosaurs is not clear. Rynchosaurs and chasmatosaurs are apparently ectothermic.

Euparkeria (e) is usually considered to be a generalized

ancestoral type for most of the other archosaurs. However, it and Garjainia (g) form a clade because they share (E) a peculiar snout which is different from that of most other archosaurs. More importantly, they share with erythrosuchids and saurosuchids (G) derived palates with very small ectopterygoids and suborbital fenestras, very large ventral pterygoid wings and very large palatines that make the palate a very heavy parallelogram shaped box (fig. 1). Eosuchians and most other archosaurs have more open, lightly built palates.

Erythrosuchids (er), vjushkoviids (v), prestosuchids (ps), saurosuchids (sr) and poposaurids (pp) are also linked by another character, (TT) hipjoints in which the acetabulum's upper lip expands outwards over the femoral head, resulting in an erect hindlimb gait (fig. 1; Bonaparte 1984). This system is functionally analogous to – but morphologically very different from – the erect gait hip joints of ornithosuchids, dinosaurs and early crocodilians (see below).

These thecodonts are all similar in body plan – (G) big skulled, big toothed predators with large neck vertebra, plantigrade feet and long, low crocodile-like profiles. They tend to elongate the ilia, pubis and ischium and develop pubic boots, crocodile-like ankles, and big size. Big skulls and heavy necks indicate quadrupedality, a crocodile-like bounding gallop may have been the fastest gait. Large, grasping outer digits indicate that aboreality was good in the smaller forms. Bone histology and predator prey ratios suggest partial, tenrec-like endothermy. That euparkeriids, garjainiids, erythrosuchids, vjushkoviids, prestosuchids, saurosuchids and poposaurids share such distinctive heavy palates and, in the last five groups, unusual, overhanging acetabula suggests 1) they form a clade, and 2) their adaptations are so derived, unusual and different from dinosaurs that none of these thecodonts can be ancestral to any dinosaur group.

The maxilla and palate of phytosaurs (ph) are heavy and the former is similar to that of saurosuchids, so perhaps they belong to that clade. Gracilisuchids (gr) and aetosaurs (ae) share (GA) very aberrant temporal regions in which the the upper half of the lateral temporal fenestra is closed up and the superior temporal fenestra faces outwards. Perhaps gracilisuchids are basal aetosaurids, but this is not certain.

Proterochampsids (pc) are very basal archosaurs (A) that have euparkeriid style ankles. Yet they appear to be a little more dinosaur-like than most thecodonts in having (B) lightly built palates, slender scapular blades, and reduced outer pedal digits.

Ornithosuchids (or) are intriguingly dinosaur-like in (O) lacking an clavicle-interclavicle brace (the removal of this brace greatly enhances scapular-coracoid mobility) and in having a slender scapula, a perforated acetabulum, and a reduced fifth pedal digit. However ornithosuchids are also derived in some very undinosaurian, aberrant ways in the snout, palate, occiput, and ankle. Hence, ornithosuchids are not early carnosaurs as Walker argues, but they are a sister group to dinosaurs.

Crocodilians (cr) and pterosaurs are also members of the dinosaur clade (Bakker pers. comm.). Protocrocodilians and early dinosaurs share (C) long, low, narrow skulls with rather short, vertical quadrates, loss of the clavicle-interclavicle brace, elongated

coracoids, large, distally placed deltopectoral crests, perforated acetabula, fully mesotarsal ankles, and laterally compressed digitigrade feet with splint metatarsal V's. Very striking is the similar body plan of lagosuchid protodinosaurs and protocrocodilians, very small, very slenderly built and very long-limbed. A bounding gallop and bipedal run were probably the fastest gaits. In a sense crocodilians are indeed a sister group to birds, but at the base of the dinosaur-avian clade. Crocodilians rapidly developed unique specializations including hyper elongated distal carpals and mobile pubes.

Pterosaurs (pt) share with protodinosaurs and protocrocodilians (C) a small, lightly built body form, loss of the clavicle-interclavicle brace, expanded deltopectoral crests, fully mesotarsal ankles and narrow digitigrade feet. Aboreality in these three small bodied archosaur groups is probably very good. Also, they and ornithosuchids all appear late in the Triassic. The size reduction in this clade is strikingly convergent and contemporary with the reduction of size in the therapsid-mammal transition. In both cases this probably marks the onset of higher level endothermy.

Dinosaurs are a monophyletic group that includes lagosuchids (l), staurikosaurs, herrerasaurs, theropods, birds, prosauropods, sauropods and ornithischians. The basal members of these groups share (D) antero-ventrally expanded antorbital fossa, tall lacrimals with short anterior prongs, 3-pronged jugals (antorbital prongs absent), very lightly built palates with long vomers and slender pterygoids, S curved necks that are slenderer than the dorsals, down and backwards facing shoulder joints, more hatchet shaped deltopectoral crests, medially divergent inner manul digits, deep, highly perforated hipjoints, large cnemial crests, tibias backing the ankle's ascending process, nonoverlapping, transversely compressed metatarsals, big manul and pedal claws, and a fully erect gait (Bakker & Galton 1974, Paul in press). I have confirmed the presence of a medially divergent thumb in the early ornithischian Heterodontosaurus, camptosaurid and iguanodontid ornithischians, the sauropods Tornieria and Apatosaurus, the protobird Archaeopteryx, birds, and theropods and prosauropods. The big, divergent, grasping inner digits of the hands and feet of dinosaurs and birds are completely different from those of thecodonts and crocodilians in which the outer digits are divergent and grasping. Many lines of evidence show high order endothermy. The dinosaur-bird clade is one of the strongest in the archosauria.

Above the lagosuchid grade two dinosaur clades are apparent, the theropod-bird clade and the herbivorous dinosaur clade.

Staurikosaurs (su) are more derived than lagosuchids with their longer, narrower, pubes and ischia. Staurikosaurus is believed to be predatory because of the great length of its jaws. However, Staurikosaurus shares with prosauropods and sauropods (S) a down curved dentary very different from the straight or upcurved dentaries of thecodonts, crocodilians and theropods. This tentatively suggests that staurikosaurs are early, predatory members of the herbivorous dinosaur clade.

Herrerasaurus (h) is another early, in this case aberrant, dinosaur. A complete juvenile pelvis shows that it does have a big footed, retroverted pubis unlike all other basal dinosaurs (Bakker pers. comm.). Herrerasaurus is certainly not a sauropod, otherwise its position is uncertain.

The herbivorous prosauropods (p), segnosaurs, early ornithischians and sauropods form a strong clade sharing (H) deeply recessed antorbital fossa, low occiputs, reduced parietals, depressed jaw joints, constricted waisted, spatulate crowned teeth, and big, crescent shaped sternals. Also, prosauropods and segnosaurs have (H) big inner toes and claws. Prosauropods have (H) a dentary shelf served by a single large foramina running beneath the posterior teeth, suggesting that cheeks were developing. Cheeks, beaks and diastemas (SO) are fully developed in segnosaurs (sg) and ornithischians (Paul in press). It is almost universally accepted that the ornithischians (o) and sauropods (s) each represent monophyletic groups. The long trunked prosauropods probably still galloped, stiff backed ornithischians probably trotted or ran, and sauropods ambled.

Theropods and birds form a very strong clade because they share (T) an obligatory bipedal stance in which the four or less fingered hand is useless for locomotion, and also rigid ribcages, expanded rectangular ilia, bigger cnemial crests, and highly distinctive tripodal bird-feet in which digit 1 is a semi-reversed or reversed hallux and metatarsal 1 does not reach the ankle. No other archosaur group has such a foot. Theropod members also share (T) a "carnosaurian pocket" in the ectopterygoid. There is no evidence that "coelurosaurs" and "carnosaurs" form clades.

Torvosaurus, Poekilopleuron and at least some of Buckland's original Megalosaurus (m) material may represent the same genus. These are the most archaic of theropods with prosauropod-like hands, short anterior iliac blades, short, broad pubes and ischia and small lesser femoral trochanters. Procompsagnathus (pr) is also archaic with its broad pubes. Coelophysis (cl), Syntarsus and ?Halticosaurus are con-generic, and with dilophosaurs (di) share (TA) more derived, narrow pubes and form their own clade sharing (CD), deep premaxillary-maxillary notches. Ceratosaurus (ce) is more derived in having (TC) a slenderer scapula blade, longer ilium, bigger lesser trochanter, and a taller astragular ascending process. Eustreptospondylus (eu) is further derived in (U) its slender scapular blade, bigger lesser trochanter, taller astragular ascending process and more compressed central metatarsal. Yangchuanosaurus (y) is very like Ceratosaurus in its skull, but it forms a clade with the more derived theropods in having (Y) cervical epipophysis, short anterior dorsal ribs, and a vertical, booted pubis.

The derived theropod-bird clade includes compsognathids (co), ornitholestids, allosaurs, tyrannosaurs, archaeopterygids, dromaeosaurs, saurornithoidids, birds, oviraptorids, chirostenotids, and struthiomimids. These share (TB) surangulars that do not overrun the dentary, avian type ribcages with short anterior ribs and long posterior ribs, very slender scapulas, very big deltopectoral crests, tridigit hands, proximal lesser trochanters, tall astragular ascending processes, proximally pinched metatarsal III's, and short pedal claws.

Ornitholestes (on) and Proceratosaurus (pr) both have nasal horns and form a clade with their (OP) conical, large rooted, poorly serrated teeth of which the premaxillary set are quite small. They form a clade with Allosaurus (al) sharing (AO) broad, down and forward sloping squamosal-quadratojugal contacts and L shaped metatarsal III's in proximal view.

Tyrannosaurids (ty) share with archaeopterygids and dromaeosaurs (TD) upcurved snouts, very narrow nasals, up bowed and kinked nasal-maxilary sutures, forward facing orbits and binocular vision, low arched parietal crests, short, deep opisthotic wings, short and vertical quadrates, exceptionally bird-like, short, deep ribcages, longer, less forwards pointing pubes, and more strongly laterally compressed metatarsals. On the other hand allosaurs share some derived characters with them too, so the position of tyrannosaurids is uncertain.

The archaeopterygid (a) and dromaeosaur (d) protobirds form a strong clade (Paul & Carpenter in prep.) sharing (PB) big premaxillas, depressed nasals, subtriangular frontals, low set upper temporal bars, inverted "T" shaped quadratojugals, expanded braincases, large, diamond shaped supraoccipitals, slender epipterygoids, dorsal ectopterygoid pits, short anterior caudal elements, hyper— elongated posterior caudal elements, very large, retroverted coracoids, bigger deltopectoral crests, lunate carpal blocks, parallelogram shaped ilia, retroverted pubic peduncles with scalloped pubic articulations, highly retroverted, triangular cross-sectioned pubes, short ischia and lateral cnemial crests. Many of these characters are also found in birds. Archaeopteryx has a normal theropod squamosal-quadrate articulation, postorbital bar, superior temporal bar, and palate, and it lacks any "enantiornithid" characters.

Velociraptor is congeneric with Deinonychus and Saurornitholestes. Surprizingly this genus forms a clade with birds above Archaeopteryx, sharing with birds (V) more rod-like quadratojugals, shorter, deeper opisthotic wings, less space between the supraoccipital and squamosal, shelves connecting the cervical diapophysis and postzygapophysis, hypopophysis beneath the cervo-dorsals, short, stout, nonoverlapping cervical ribs, shorter trunks, ossified uncinate processes, large ossified sternums, and lesser femoral trochanters that have merged with the femoral head and articulate with an avian antitrochanter. Dromaeosaurs are probably ground dwelling descendents of the flying archaeopterygids.

Saurornithoides (= Stenonychosaurus) (sa) is even more bird-like. It shares with birds (b) (SB) middle ear depressions, downwardly directed posterior brainstems, big rectangular supraoccipitals that reach the squamosals, squamosals that sit atop very short, tall opisthotic wings, reduced basitubera, horizontal basipterygoids, bulbous parasphenoids, a straight posterior pterygoid, severely reduced ventral pterygoid wings, no ventral ectopterygoid processes, intense pneumatization of thin walled braincases, quadrates, pterygoids and limb bones, fibulae lost distally, and narrow, deep ankles.

Oviraptorids (ov) share with dromaeosaurs and saurornithoidids (V) big retroverted coracoids, big lunate carpals, parallelogram shaped ilia, and triangular ischial aprons, otherwise they are very aberrant. Struthiomimids (su), including garudimimids, are the most enigmatic of the theropods because they combine derived bird-like characters with some less derived theropod characters.

This study is a tentative outline of work in progress by R. T. Bakker and the author.

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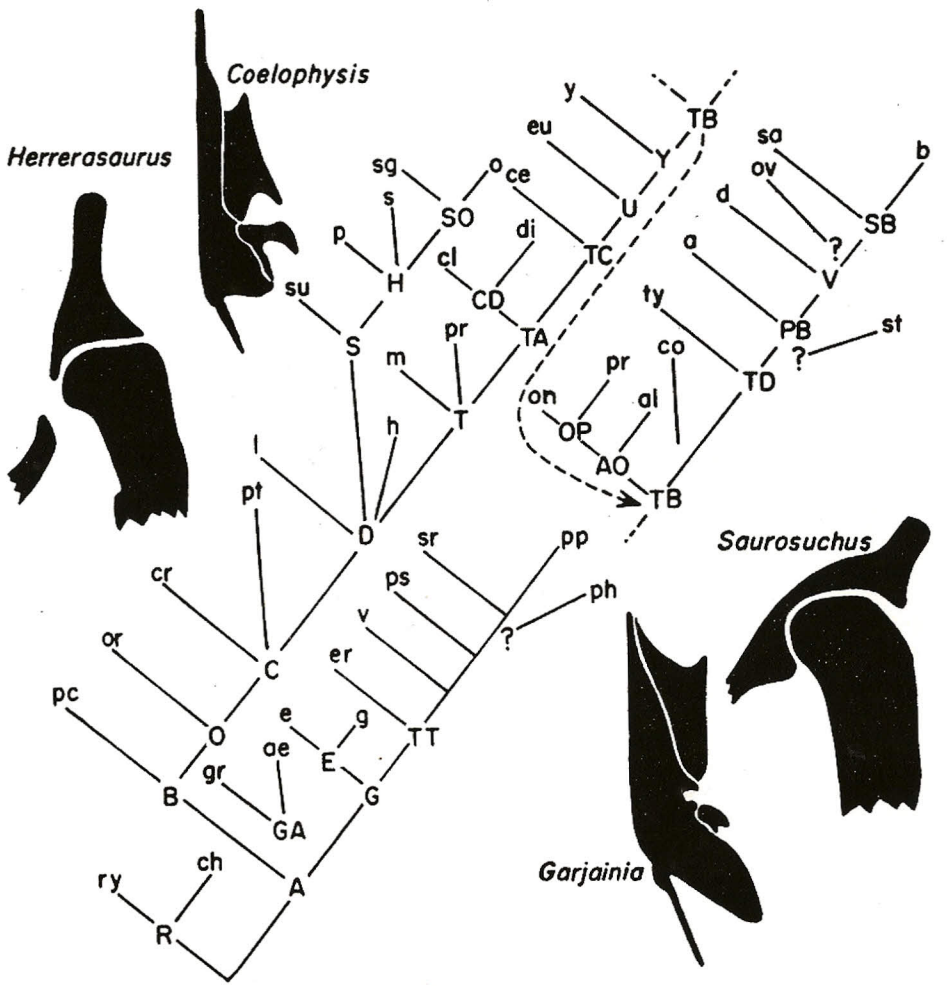

Fig. 1. Archosaur cladogram, character lists in text. Upper left, left palate in ventral view and hip joint in cross-section in dinosaur clade. Lower right, same in euparkeriid-poposaurid clade.