

Extreme convergence in the body plans of an early suchian (Archosauria) and ornithomimid dinosaurs (Theropoda)

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Living archosaurs comprise birds (dinosaurs) and crocodylians (suchians). The morphological diversity of birds and stem group dinosaurs is tremendous and well-documented. Suchia, the archosaurian group including crocodylians, is generally considered more conservative. Here, we report a new Late Triassic suchian archosaur with unusual, highly specialized features that are convergent with ornithomimid dinosaurs. Several derived features of the skull and postcranial skeleton are identical to conditions in ornithomimids. Such cases of extreme convergence in multiple regions of the skeleton in two distantly related vertebrate taxa are rare. This suggests that these archosaurs show iterative patterns of morphological evolution. It also suggests that this group of suchians occupied the adaptive zone that was occupied by ornithomimosaur later in the Mesozoic.

Keywords: convergent evolution; *Effigia*; *Shuvosaurus*; suchian; Triassic; archosaur

1. INTRODUCTION

The specimens were discovered in unprepared blocks originally excavated in the 1940s by American Museum of Natural History field parties from the famous Ghost Ranch *Coelophysis* Quarry (also known as Whitaker Quarry). Until recently, this quarry was thought to represent a nearly monospecific death assemblage of the early theropod *Coelophysis* (Colbert 1989). However, many different kinds of reptiles have recently been reported (Long & Murry 1995; Clark *et al.* 2000; Harris & Downs 2002). Several specimens are referred to the new taxon. The skull has edentulous jaws, an enlarged orbit, a posteroventrally rotated squamosal and an anteroventrally angled quadrate. All of these features are identical to those of derived ornithomimid dinosaurs. Additional derived features of the pelvis, tail and vertebrae are convergent features that diagnose nested clades within Theropoda.

2. SYSTEMATIC PALEONTOLOGY

Archosauria (Cope 1869)

Suchia (Krebs 1974 *sensu* Benton & Clark 1988) *Effigia okeeffeae* gen. et sp. nov.

(a) Etymology

The generic name is derived from the Latin word *effigia* (ghost). The specific name is in honour of Georgia O'Keeffe for her numerous paintings of the badlands at Ghost Ranch and her interest in the *Coelophysis* Quarry when it was discovered.

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(b) Holotype

An articulated skeleton including a nearly complete skull, American Museum of Natural History Fossil Reptiles (AMNH FR) 30587.

(c) Referred specimens

AMNH FR 30588, articulated pelvis, femur and caudal vertebrae; AMNH FR 30589, a partial skull with associated cervical vertebrae and partial hindlimb; AMNH FR 30590, femur.

(d) Horizon and locality

Ghost Ranch, central New Mexico. From the *Coelophysis* Quarry in the 'siltstone member' (Norian–?Rhaetian) of the Chinle Formation (Stewart *et al.* 1972).

(e) Diagnosis

A suchian archosaur distinguishable from all other suchians except *Shuvosaurus* by the presence of an edentulous premaxilla, maxilla and dentary, a posteriorly long anterodorsal process of the premaxilla, a long preacetabular process of the ilium that connects to the posterior process by a large thin flange and a pubic boot that is 33% as long as the pubic shaft. Distinguished from *Shuvosaurus* by the presence of a dorsal and posterior process of the maxilla, small posterior process of the premaxilla, fossa on the posterior side of the lacrimal, absence of posterior process of the squamosal and a fossa on the posterior side of the squamosal.

(f) Description

AMNH FR 30587 (figure 1) includes a nearly complete skull missing only the quadratojugal and parts of the braincase. The premaxilla, maxilla and dentary are unusual in being edentulous, and are covered by an

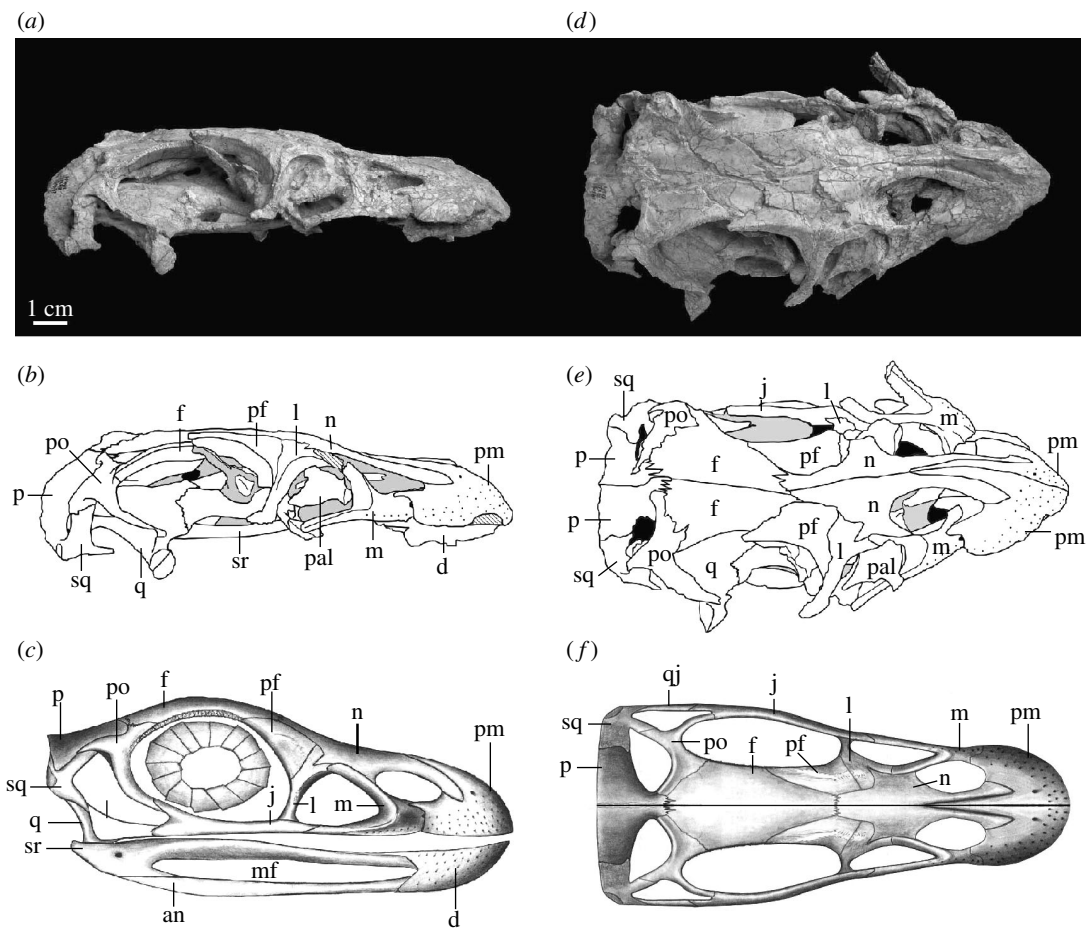


Figure 1. Skull reconstruction of *Effigia okeeffeae* (AMNH FR 30587). (a, b) Lateral view, (c) reconstruction, (d, e) dorsal view and (f) reconstruction. Abbreviations: an, angular; d, dentary; f, frontal; j, jugal; l, lacrimal; m, maxilla; mf, mandibular fenestra; n, nasal; p, parietal; pal, palatine; pf, prefrontal; pm, premaxilla; po, postorbital; q, quadrate; qj, quadratojugal; sq, squamosal; sr, surangular.

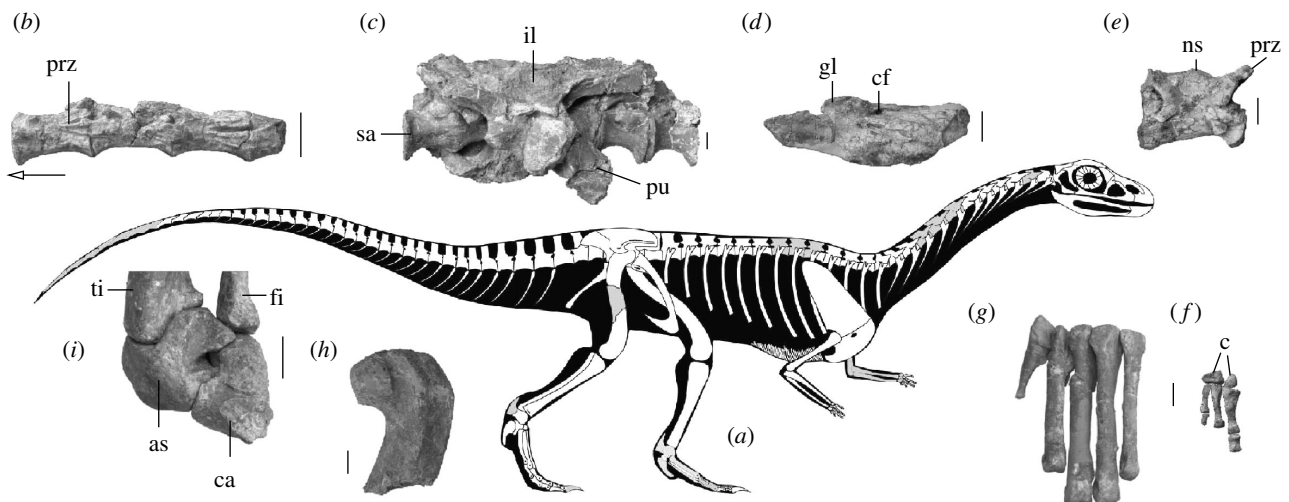


Figure 2. AMNH FR 30587. (a) Skeletal reconstruction of *Effigia okeeffeae*. The bones in grey are unknown. (b) Posterior caudal vertebrae (AMNH FR 30589) with overlapping prezygapophyses in lateral view. Arrow indicates anterior direction for the vertebrae only. (c) Articulated pelvis in lateral view. (d) Right coracoid in lateral view. (e) Anterior cervical vertebra in lateral view. (f) Incomplete right manus scaled to the right pes in dorsal view. (g) Right pes in dorsal view. (h) Right proximal part of the femur in medial view. (i) Articulation of the right ankle in posterior view. Abbreviations: as, astragalus; c, carpal; ca, calcaneum; cf, coracoid foramen; fi, fibula; gl, glenoid; il, ilium; ns, neural spine; prz, prezygapophysis; pu, pubis; sa, sacrum; ti, tibia. Scales = 1 cm.

extensive system of foramina that suggests the presence of a horny beak or rhamphotheca. The premaxilla bears a long posterior nasal process that meets the nasal dorsally and forms the internarial bar. The premaxillae are

separated from the nares dorsally by anterior narial processes of the nasals. Ventrally, the premaxillae meet to form a small secondary palate that contacts the anterior palatal shelves of the maxillae. The reduced maxilla has

both a dorsal process that separates the external naris from the antorbital fenestra and a tapered posterior process that contacts the jugal anterior to the antorbital bar. A pronounced, raised external rim forms the anterior and ventral margin of the antorbital fossa on the lateral surface of the maxilla. The ventral edge of the premaxilla and only the anterior half of the maxilla occlude with the dentary. The length of the posteriorly shortened and attenuated dentary corresponds to the beak-like premaxilla and anterior part of maxilla. The dentaries meet at the midline to form a posteriorly expanded symphysis that corresponds to the area created by the premaxillae. This area of the dentary is also covered with nutrient foramina, again suggesting a rhamphotheca. A huge mandibular fenestra is bounded dorsally and posteriorly by the surangular, ventrally by the angular and anteriorly (only slightly) by the dentary. A large surangular foramen is present on the posterolateral side just anterior to the quadrate shaft. The distal articular end of the anteroventrally projected quadrate articulates with the largely convex articular. A slightly dorsolaterally expanded area of the surangular also articulates with the quadrate (also an unambiguous synapomorphy of Ornithomimosauria; Makovicky *et al.* 2004).

Other specializations of the skull include an enlarged orbit and external naris. The crescentic postorbital forms both the posterior and part of the ventral and dorsal border of the orbit. A long ventral process of the postorbital and a large orbit are also found in derived ornithomimids (Makovicky *et al.* 2004). The elongate jugal creates most of the ventral border of the upper skull and forms part of the postorbital bar. It lacks an anterior dorsal process, so the lacrimal forms all of the antorbital bar. The dorsal surface of the skull is completely smooth and includes an enlarged frontal and prefrontal, but clearly lacks a postfrontal. The parietals form a sagittal crest and articulate with posteroventrally directed squamosals. As with *Shuvosaurus*, the parabasisphenoid is anteriorly elongated as in theropods (Rauhut 1997, 2003).

In the axial skeleton, the posterior cervical vertebrae bear posteriorly directed processes on each diapophysis (only in *Ornithomimus* and *Archaeornithomimus*; Makovicky *et al.* 2004). Cervical and dorsal vertebrae are anteroposteriorly elongated and have complicated transverse processes. The anterior cervical vertebrae have true pleurocoels on the posterior half of the centrum (Britt 1997). The posterior caudal vertebrae bear long prezygapophyses that overlap the adjacent vertebra.

The large scapula (figure 2) is long and triangular with a blunt posterior apex, and the coracoid is equally anteroposteriorly wide. The humerus, radius and ulna are about the same size and are unreduced; the distal ends of both the radius and ulna taper. Although the manus is incomplete, the preserved elements are extremely reduced (2 cm metacarpals), yet retain the relative proportions of a typical *Crocodylus* manus (Mook 1921).

The elongated, posteriorly concave pubis has a large boot that projects posteriorly. The appressed left and right ischium are laterally compressed. The ilium bears a thin dorsal flange that connects an elongated preacetabular process to a large postacetabular process. The ilium is oriented vertically and the acetabulum is closed medially. The supra-acetabular rim covers the head of the femur on both the dorsal and part of the lateral sides. The sacrum

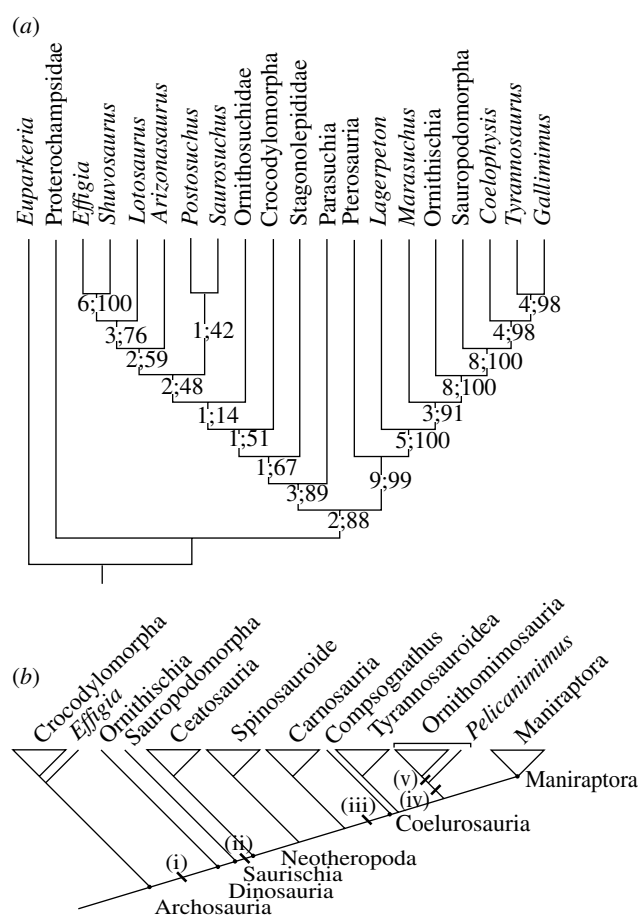


Figure 3. (a) Phylogenetic positions of *Effigia* and *Shuvosaurus* among basal archosaurs. Unique tree shown (81 characters, length=156, RI=0.8320, CI=0.5897). The placement of *Effigia* within Theropoda requires the addition of 27 steps and the placement sister to ornithomimids requires the addition of 30 steps. The first number is the decay value and the second number is the bootstrap value. (b) The convergences listed below are present in *Effigia* and are characters that describe the dinosaurian clade and nested theropod clade. (i) *Dinosauria*. Reduction of arm/leg ration, postfrontal absent, 'offset femoral head', elongated parabasisphenoid. (ii) *Neotheropoda*. Enlargement of the preacetabular process of the ilium, incorporation of additional sacral vertebrae, hollow limbs, 'antitrochanter', present on the ilium, fusion of sacral vertebrae into rigid rod, fusion of the sacral neural arches, left and right oppression of the ischium, cervical vertebra pleurocoels. (iii) *Coelurosauria*. Increased pubic boot size, elongated prezygapophyses in distal caudal vertebrae, preacetabular fossa. (iv) *Ornithomimosauria*. Enlargement of the orbit, posteroventral rotation of the squamosal, anteroventrally angled quadrate, lacrimal-frontal contact absent. (v) *Clade within Ornithomimosauria*. Posterior directed process on each diapophysis of the posterior cervical vertebrae, edentulous jaws.

consists of four centra fused into a stiff rod. All of the sacral neural arches are fused.

The proximal portion of the femur bears two medial condyles; the anteromedial condyle is knob-like and hooks posteriorly, a condition reminiscent of the offset proximal head of a dinosaurian femur. However, the 'head' of the femur articulates anteriorly as in crocodylians and not medially as in dinosaurs. The shafts of the femur, tibia and fibula are thin-walled and hollow. The astragalus and calcaneum articulate in a crocodile-normal configuration and their morphology is similar to *Alligator*. The pes

consists of five metatarsals. The recurved ungual is dorsoventrally compressed.

3. DISCUSSION

Chatterjee (1993) named *Shuvosaurus* on the basis of a skull from the Miller (Post) Quarry; the specializations of its skull led him to attribute it to an ornithomimid dinosaur. Later, it was argued (Long & Murry 1995; Hunt *et al.* 1998) that the skull of *Shuvosaurus* belongs with the postcrania of *Chatterjeea*, a suchian archosaur found in the same quarry, although no overlapping elements had been found. The articulated cranial and skeletal material of *Effigia* strongly suggests that the skull of *Shuvosaurus* belongs to the postcrania of *Chatterjeea*. Therefore, *Chatterjeea* is very probably a junior subjective synonym of *Shuvosaurus*. The fully developed crocodile-normal ankle, crocodylomorph-like pes and articulation between the femur and ilium clearly place *Effigia* as more closely related to crocodiles than to birds. *Effigia* and *Shuvosaurus* were inserted into a modified version of Benton's (1999) basal archosaur phylogenetic analysis (see electronic supplementary material). The resultant analysis (figure 3a) produced a single tree that placed *Effigia* and *Shuvosaurus* within derived suchians. The characters that Chatterjee (1993) used to assign the skull of *Shuvosaurus* to the Ornithomimidae are now understood to be convergent, according to the phylogenetic analysis presented here. The postcrania of *Effigia* also contain characters that are convergent with those of theropods at more general taxonomic levels (figure 3b). This is particularly apparent in the pelvis, where *Effigia* shares the following characters with theropods: at least four sacral vertebrae are fused into a stiffened rod, the preacetabular process of the ilium is enlarged, a thin flange of bone connects the preacetabular process to the ischiadic wing of the ilium and the pubic boot is large and posteriorly expanded.

Characters shared between *Effigia* and *Shuvosaurus* are also present in the fragmentary taxon *Sillosuchus* (Alcober & Parrish 1997) including the presence of a thin supra-acetabular crest, thin dorsal flange of the ilium and similar ischial morphology. From the Late Carnian of Argentina, *Sillosuchus* indicates that *Effigia*-like taxa had a larger distribution than just North America and furthermore, *Effigia*-like taxa were present during most of the Late Triassic.

The Late Triassic is marked by a number of body plans convergent with later dinosaurs. The simple unspecialized bodies of Late Triassic theropods such as *Coelophysis* contrast strongly with the diversity of coeval crocodile-line archosaurs. An iterative pattern of morphological evolution suggests that some of the Late Triassic suchians may have occupied similar adaptive zones to subsequent clades of dinosaurs. The presence of ornithomimid-like suchians (as well as the carnosaur-like suchians such as *Postosuchus* (Chatterjee 1985) and ankylosaur-like suchians such as aetosaurs) suggest that only in the Jurassic after most clades of crocodile-line archosaurs became extinct, did dinosaurs begin to explore new adaptive opportunities.

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